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RHOMBOGNATHINAE (ACARI: HALACARIDAE) FROM THE GREAT BARRIER REEF, AUSTRALIA

I. BARTSCH

Bartsch, I. 2000 06 30: Rhombognathinae (Acari: Halacaridae) from the Great Barrier Reef, Australia. *Memoirs of the Queensland Museum* 45(2): 165-203. Brisbane, ISSN 0079-8835.

Samples from tidal and subtidal zones from the Great Barrier Reef area off eastern Australia contained one species of *Isobactrus* and 11 of *Rhombognathus*. Three of these 12 rhombognathine species, *Isobactrus ponapensis* Abé, *Rhombognathus papuensis* Bartsch, and *R. scutulatus* Bartsch, have been recorded previously from areas outside eastern Australia. The nine species *R. cyrtanotus* sp. nov., *R. delicatulus* sp. nov., *R. lathridius* sp. nov., *R. levigatus* sp. nov., *R. longipes* sp. nov., *R. reticulifer* sp. nov., *R. seminotatus* sp. nov., *R. tericulus* sp. nov. and *R. validipes* sp. nov. are described. A key is given to the eastern Australian rhombognathines. □ *Eastern Australia, Great Barrier Reef, Halacaridae, rhombognathines, new records, new species, descriptions, key.*

Ilse Bartsch, Forschungsinstitut Senckenberg, Notkestr. 31, 22607 Hamburg, Germany; (e-mail Bartsch@meeresforschung.de); 29 September 1999.

Rhombognathine mites inhabit intertidal and shallow subtidal substrata and marine and brackish waters. Rhombognathines are algivorous, accordingly they are found either on algal fronds or on substrata with epiphytes. Two rhombognathine genera, *Rhombognathus* and *Isobactrus*, are widely spread in the Pacific. To date, 34 species of *Rhombognathus* and nine of *Isobactrus* are recorded from the western Pacific (Abé, 1998; Bartsch, 1999). Still the fauna of large areas is unknown, especially that of the Great Barrier Reef. To fill this gap of knowledge, J.C. Otto took numerous samples in the Great Barrier Reef Marine Park which later proved to contain 12 rhombognathine species, representing two genera (*Isobactrus* – 1 species and *Rhombognathus* – 11 species). Three of these species had been recorded previously, the others are new to science.

MATERIAL AND METHODS

The rhombognathine mites from the Great Barrier Reef Marine Park area were collected and sorted by J.C. Otto, Australian Institute of Marine Science, Townsville.

The mites were cleared in lactic acid and mounted in glycerine jelly. Holotypes are deposited in the Museum of Tropical Queensland, Townsville (MTQ), paratypes and voucher specimens in the MTQ, the Queensland Museum, Brisbane (QM), the Western Australian Museum, Perth (WAM), the Zoological Institute and Zoological Museum, Hamburg (ZMH), and the author's halacarid collection (IB).

Abbreviations used: AD = anterior dorsal plate; AE = anterior epimeral plate; AP = anal

plate; ds-1 to ds-5 = first to fifth pair of dorsal setae; E = epimera, numbered I to IV; GA = genitoanal plate; GO = genital opening; GP = genital plate; OC = ocular plate(s); P = palp, P-2 to P-4 = second to fourth palpal segment; pas = parambulacral setae; PD = posterior dorsal plate; PE = posterior epimeral plate(s); pgs = perigenital setae, numbered 1 to 5 from anterior to posterior; sgs = subgenital setae. Legs numbered I to IV, leg segments 1 to 6 are trochanter, basifemur, telofemur, genu, tibia and tarsus.

Drawings were prepared with a camera lucida. Unless stated otherwise, adjunct and adanal setae are shown either in dorsal or in ventral aspect.

Length of the idiosoma is that from the anterior margin of the AD to the end of the anal valves. The length of the PD includes the pair of posteriorly projecting cones. The position of a seta is given in a decimal system, with reference to the length of a plate from the anterior to posterior margin; the position of the legs with reference to the length of the idiosoma. The length of a leg segment is that along the dorsal margin. In the setation formula of the legs, the number of pas, solenidia and famuli is excluded. Unless stated otherwise, the setation formula of the telofemora presents the number of dorsal/ventral setae. Measurements in micrometres unless otherwise stated.

In *Rhombognathus*, the number of adjunct setae on the AE and PE, the number of perigenital setae and the setation on the legs is known to vary. Each description is supplemented with notes on, generally unilateral, variants; the number of cases are in parentheses.

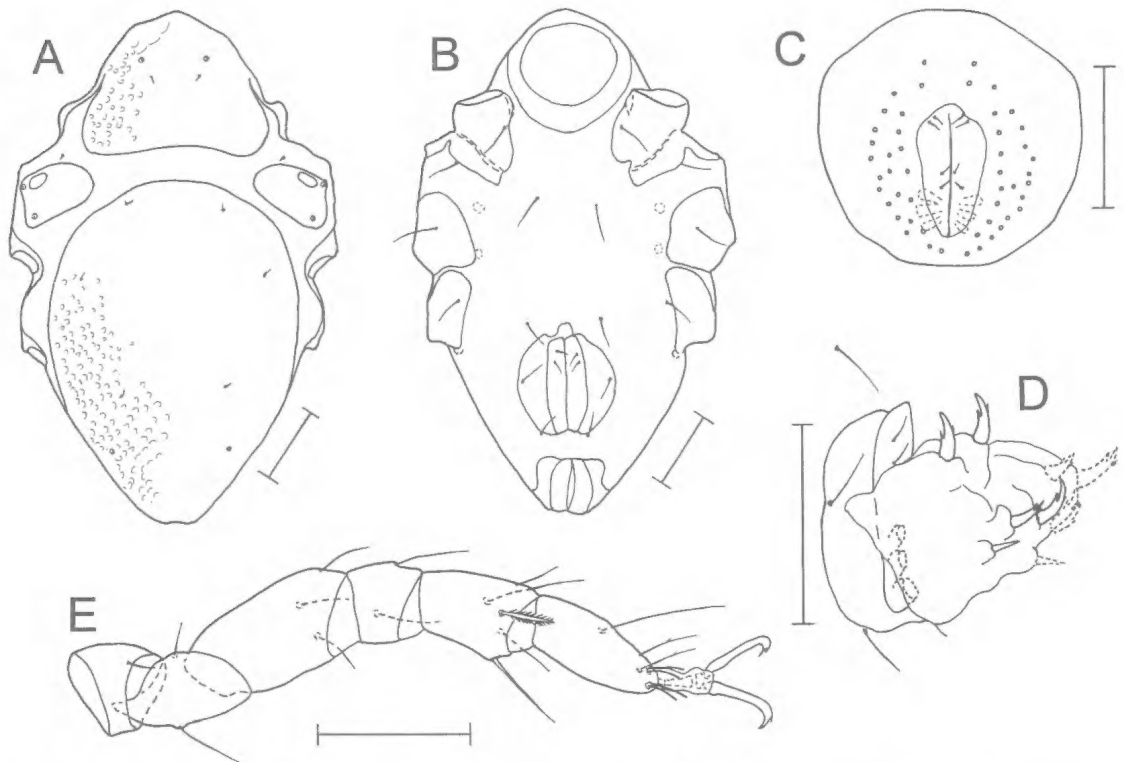


FIG. 1. *Isobactrus ponapensis* Abé, 1996; A, idiosoma, dorsal, male; B, idiosoma, ventral, female; C, genitoanal plate, male; D, ovipositor, female (genital spines of left half dashed); E, leg I, ventromedial, female. Scale bar = 50 μ m.

SYSTEMATICS

RHOMBOGNATHINAE Viets, 1927

Isobactrus Newell, 1947

TYPE SPECIES (by original designation). *Isobactrus setosus* (Lohmann, 1889) = *Aletes setosus* Lohmann, 1889.

DIAGNOSIS. Dorsal plates AD, OC and PD present, sometimes fused. AD with pair of setae. OC with 0 (rarely 1) setae, 2 gland pores and 0-1 corneae. PD (or area representing PD) with 1-3 pairs of setae. Adanal setae absent. Ventral plates reduced, epimera I and II rarely fused in the median; epimera III with 1-2 setae, epimera IV with 1 seta which may insert within the striated integument. Genital plate not fused with anal plate. Females with 3(-4) pairs of pgs; males with 32-98 pgs. Gnathosoma short, generally concealed in dorsal aspect. Both pairs of maxillary setae on rostrum. Palps 4-segmented. P-2 with 1 seta; P-3 without seta; P-4 with 3 (rarely 4) basal setae. Legs shorter than idiosoma. Tibiae I and II each with a pair of ventral setae; generally 1 seta bipectinate and 1 seta smooth.

Tarsi I, II and IV with 3 dorsal setae each (one species with 4 setae), tarsus III generally with 4 setae, rarely with 3 or 5. Tarsi lack ventral setae. Solenidion on both tarsus I and II dorsolateral in position. Tarsi I-IV each with carpite (rod-like sclerite) between end of tarsus and central sclerite. Central sclerite lacks tine-like process. The 2 claws smooth or with tines.

Isobactrus ponapensis Abé, 1996 (Fig. 1)

Isobactrus ponapensis Abé, 1996: 17-24, figs 1-4.

MATERIAL. ♀, ♂, 1 tritonymph (MTQ), Great Barrier Reef, Long Island, Whitsundays, sand at 0.5m, 28 February 1997; coll. J.C. Otto. ♀, 1 tritonymph (QM S50961), collection data as above. ♀ (IB), collection data as above.

DESCRIPTION. Idiosoma of female 322-335 long, of male 332. Gland pore on AD immediately anterior to ds-1 (Fig. 1A). OC wider than long. PD large, marginally foveate, reaching beyond OC. Setae ds-2 within striated integument. Setae ds-3 to ds-5 on PD, ds-3 and ds-4 anterior and level with insertion of leg III, ds-5

posterior to the level of leg IV. Epimera I and II with a seta each. Epimera III and IV separated by striated integument (Fig. 1B); EIII with ventral seta; succeeding seta within margin of EIV. Female GO surrounded by plate; anterior pair of pgs within striated integument, succeeding 2 pairs of pgs on and in margin of genital plate, respectively. Genital sclerites with 2 pairs of sgs. Ovipositor with 10 well-sclerotised genital spines (Fig. 1D); 2 pairs each anteroapically and posteroapically, the latter followed by pair of spiniform genital spines. Two pairs of anteroapical genital spines large, equal in size, each with median process flanked by 2 small tines. Posteroapical genital spines in shape similar to but slightly smaller than anteroapical pairs of genital spines. Male GP with 49 pgs; genital sclerites with 4 pairs of sgs (Fig. 1C). Gnathosoma slightly wider than long. Legs shorter than idiosoma. Leg chaetotaxy from trochanter to tarsus: legs I and II, 1, 2, 3, 2, 5, 3; leg III, 1, 1, 2, 2, 4, 4; leg IV, 0, 1, 2, 1, 4, 3. Ventromedial seta on tibia I (Fig. 1E) and II bipectinate. Apical pair of fossary setae delicately furcate. Carpite between tip of tarsus and central sclerite solid. Accessory process on claws with single tooth.

Idiosoma of tritonymph 272-278. Setae ds-2 and ds-3 within striated integument. Arrangement of gland pores as in adults. Small genital plate with pair of subgenital setae and pair of perigenital setae, another pair of pgs within striated integument. Shape and setation of legs same as in adults.

REMARKS. *Isobactrus ponapensis* was described originally on the basis of females, males and juveniles from Ponape, Micronesia (Abé, 1996). The individuals from the Great Barrier Reef are larger than the adults from Micronesia which have an idiosomal length of 255-280, and there are small differences in the insertion of the three pairs of setae on the PD — in the adults from the Great Barrier Reef the interval between ds-3 and ds-4 is shorter than between ds-4 and ds-5, in those from Micronesia the distance ds-3 to ds-4 and ds-4 to ds-5 is almost the same.

The ovipositor of *Isobactrus ponapensis* bears 10 genital spines whereas the Northern Atlantic species *I. setosus* (Lohmann, 1889) and *I. uniscutatus* (Viets, 1939) have 11 genital spines (Bartsch, 1975a).

DISTRIBUTION. Micronesia, Ponape Island, from intertidal coarse coral sand (Abé, 1996),

and Australia, Great Barrier Reef, from shallow water sandy deposits.

Rhombognathus Trouessart, 1888

TYPE SPECIES (by original designation). *Rhombognathus notops* (Gosse, 1855) = *Pachygnathus notops* Gosse, 1855.

DIAGNOSIS. Dorsal plates AD, OC and PD present, sometimes fused. AD with pair of setae. OC with 2 setae, 2 gland pores, and 0-2 corneae. PD with 1-2 pairs of setae. Adanal setae on anal plate. Ventral plates often fused. AE with 3 pairs of ventral setae plus 0-6 adjunct setae; PE with 1 dorsal, 3 ventral and 0-3 adjunct setae. Females with 1-45 pairs of pgs; males with 7-25 pairs of, generally plumose, pgs. Both pairs of maxillary setae on rostrum. Palps 4-segmented. P-2 with 1 dorsal seta in distal half; P-4 with 3 basal setae; apically an often spur-like seta. Legs shorter than idiosoma. Tibiae with 2 ventral setae, one or both bipectinate. Tarsi I-IV with 3, 3, 3-4, 3 dorsal setae, respectively, and 0 ventral setae. Solenidion on both tarsus I and II dorsolateral in position. Tarsi with 2 claws. Central sclerite between claws lacks tine-like process. Carpite (rod-like sclerite) present between end of tarsus and central sclerite.

Rhombognathus cyrtonotus sp. nov. (Figs 2, 3)

ETYMOLOGY. For the curved (kyrtos, Greek) back (notos, Greek), in contrast to the rather flattened idiosoma of the majority of *Rhombognathus*.

MATERIAL. HOLOTYPE. ♂ (MTQ), Great Barrier Reef, 19°20.12'S, 149°02.85'E, Elizabeth Reef, medium coarse sand at 10m, 24 December 1997; coll. J.C. Otto. PARATYPES. 2 ♀, 1 tritonymph (MTQ), collection data as above. 2 ♀ (QM S50962), collection data as above. 2 ♀ (ZMH A96/99), collection data as above. 4 ♀ (IB), collection data as above. OTHER MATERIAL. ♂ (WAM 99/1439), Great Barrier Reef, Lizard Island, Site 'Washing Machine', coarse sand and rubble at 7m depth, 14 October 1998; coll. J.C. Otto.

DESCRIPTION. *Male*. Idiosoma 202-211 long; holotype 211 long, 140 wide. Dorsum raised. AD, OC and PD separated (Fig. 2A). Plates uniformly covered with faint reticulum, each mesh subdivided. AD 57 long, 75 wide; anterior margin broadly arched, posterior margin rounded; gland pores in lateral margin; posterior line of internal muscle scars at 0.67. OC 65 long, 48 wide; with 2 corneae, 2 gland pores and a pore canaliculus; posterior gland pore by 2-3 times its diameter removed from lateral margin of OC.

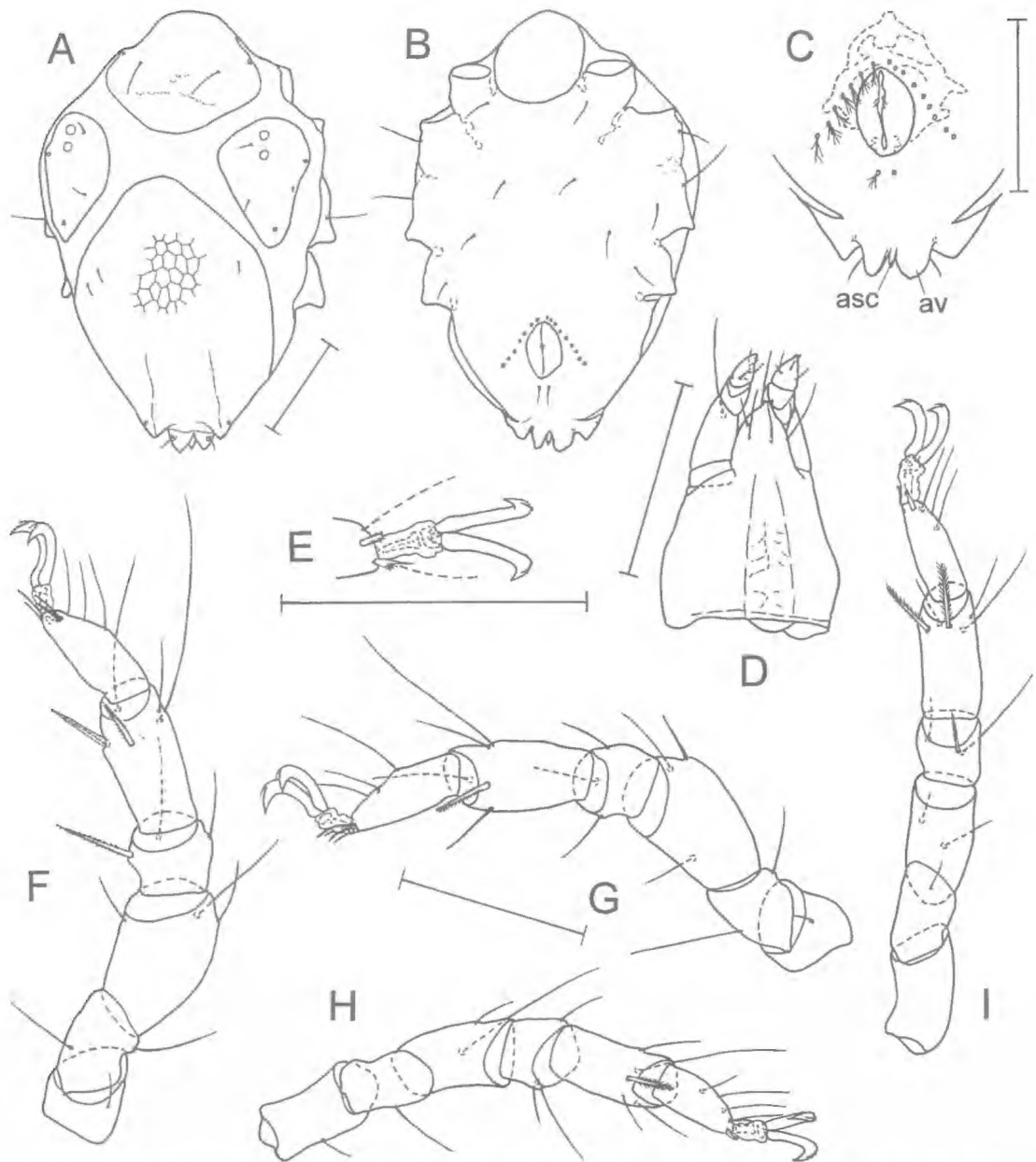


FIG. 2. *Rhombognathus cyrtonotus* sp. nov.; A, idiosoma, dorsal, male; B, idiosoma, ventral, male; C, posterior portion of idiosoma, ventral, male; D, gnathosoma, ventral, male; E, tip of tarsus IV, ventral (dorsal setae dashed), female; F, leg I, medial, female; G, leg II, medial, female; H, leg III, ventromedial, female; I, leg IV, ventral, female. asc = anal sclerite; av = anal valve. Scale bar = 50 μ m.

PD 127 long, 97 wide. Plate evenly and delicately reticulated; posteriorly with pair of narrow ridges but no wide costae. Posterior cones extending beyond median margin of PD. Pair of gland pores near posterior margin of PD. Anal sclerites small, squeezed between lamellar anal valves. Setae

ds-1 17 long; succeeding setae 7-8 long. Posterior seta on OC at 0.60. PD in holotype unilaterally with 2 setae, else with pair of single setae. Adanal setae on anal valves.

Ventral plates AE, PE, GP and AP fused to a ventral shield (Fig. 2B), this shield 169 long.

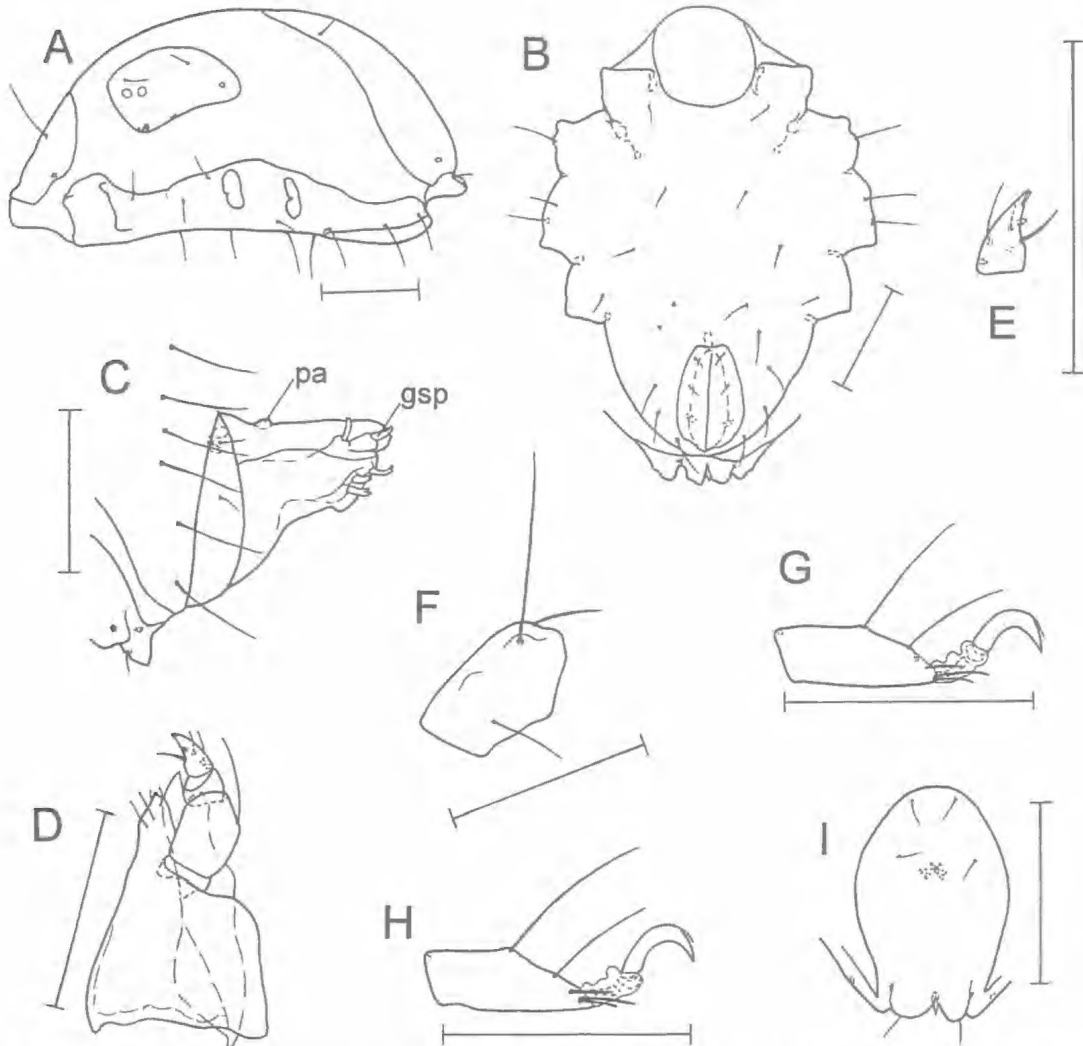


FIG. 3. *Rhombognathus cyrtonotus* sp. nov.: A, idiosoma, lateral, female; B, idiosoma, ventral, female; C, ovipositor, female (perigenital setae and genital spines of left side omitted); D, gnathosoma, lateral, female; E, fourth palpal segment, lateral; F, telofemur II, lateral, female; G, tarsus I, lateral, female (medial setae and claw omitted); H, tarsus II, lateral, female (medial setae and claw omitted); I, posterior portion of idiosoma, tritonymph. gsp = genital spines; pa = papilla. Scale bar = 50 μ m.

Areas corresponding to AE and PE lack adjunct setae. On PE ventral setae shorter than dorsal seta. GO 27 long, 17 wide; not reaching the level of insertion of leg IV. Perigenital setae plumose, arranged trapezoidally; holotype with 7 and 9 setae lateral to GO and 1 pair of basilar setae, close together, posterior to GO (Fig. 2C). Spermatopositor 42 long, 45 wide; extending beyond anterior perigenital setae.

Gnathosoma 56 long, 48 wide; 1.2 times longer than wide (Fig. 2D). Rostrum 19 long, anteriorly narrowed; 2 pairs of maxillary setae inserted

adjacent; rostral tip with one slender and 1 very reduced pair of rostral setae. Tectum slightly convex.

Legs I and IV equal in length; approximately 0.7 of idiosomal length. Insertion of leg III at 0.51, that of leg IV at 0.65. Legs as in female (Fig. 2F-I). Chaetotaxy of trochanter to tarsus: leg I, 1, 2, 3, 3, 5, 3; leg II, 1, 2, 3, 3, 5, 3; leg III, 1, 1, 2, 3, 5, 4; leg IV, 0, 1, 2, 3, 5, 3. Tarsus IV with 2 short, pectinate spiniform pas (Fig. 2E). Tarsus III with setiform medial pas and short, spiniform lateral pas.

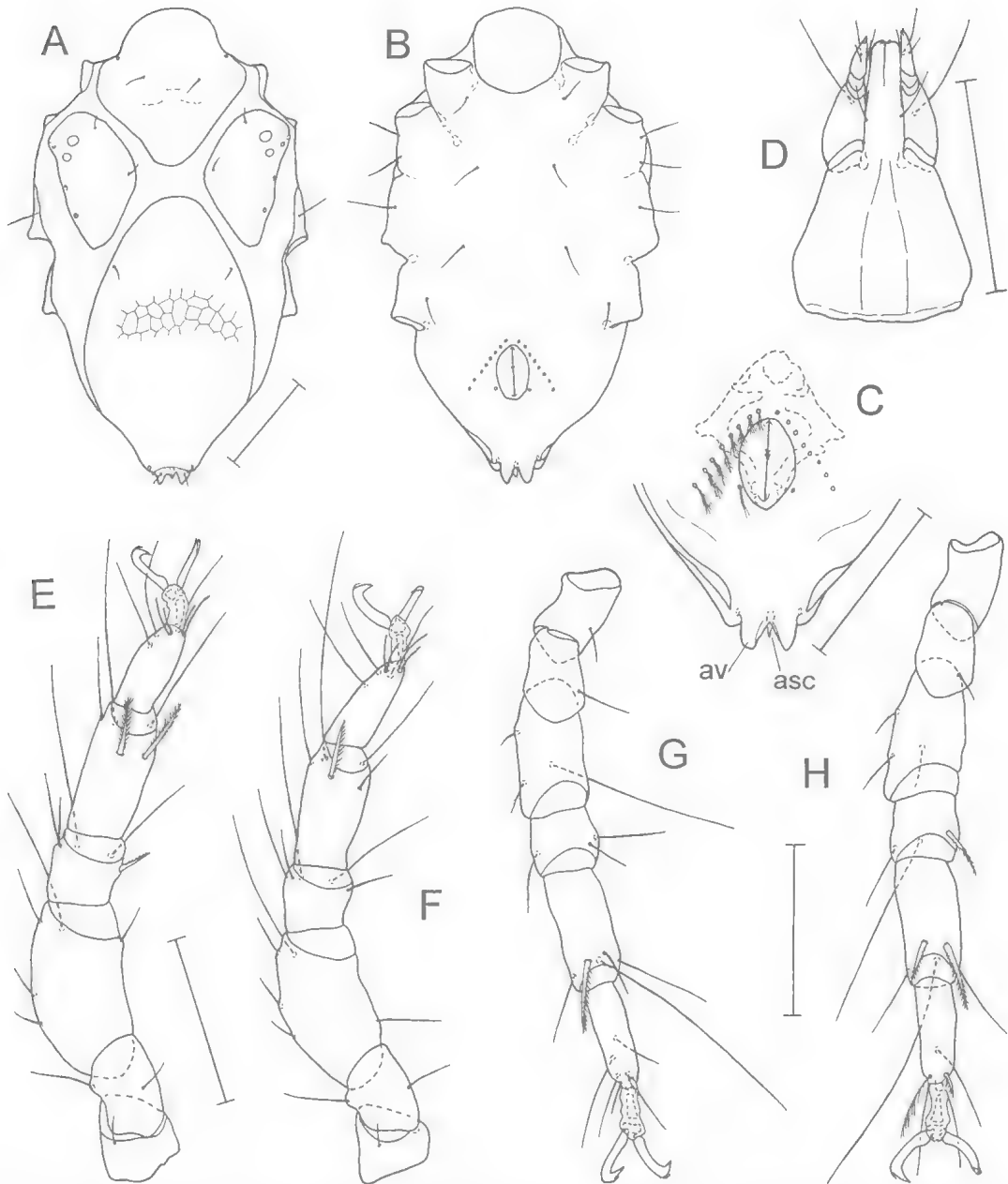


FIG. 4. *Rhombognathus delicatulus* sp. nov., male; A, idiosoma, dorsal; B, idiosoma, ventral; C, posterior portion of idiosoma, ventral; D, gnathosoma, ventral; E, leg I, ventromedial; F, leg II, ventromedial; G, leg III, ventral; H, leg IV, ventral. asc = anal sclerite; av = anal valve. Scale bar = 50 μ m.

Carpites of tarsi I and II 5 long, those of tarsi III and IV 6 long. Each claw with accessory process but no further tines.

Female. Idiosoma 223-247 long. Areas with striated integument wider than in males; dorsum distinctly raised (Fig. 3A). PD somewhat shorter

than in male. Ventral plates AE, PE and GP fused to a ventral shield; AP separated by wedge of striated integument (Fig. 3B). AE and PE lack adjunct setae. GO not reaching the level of insertion of leg IV. GO surrounded by 5 (rarely 6) pairs of pgs; anterior pairs of pgs positioned

somewhat anterior to the level of insertion of leg IV. Genital sclerites each with 2 sgs. Genital acetabula obscured. Extended ovipositor approximately 55 long; with pair of small, cone-like papillae basally and 5 pairs of sclerotised genital spines apically (Fig. 3C); each spine 6-7 long and ending with 5 tines.

Palps of gnathosoma extending beyond tip of rostrum (Fig. 3D). P-4 with one wide and 2 slender setae and a spur-like process (Fig. 3E). Chelicera 62 long; claw with serrate dorsal edge.

Length:width ratio of telofemora: 1.7, 1.8, 1.6, 1.6. Tibiae I and II slightly shorter than telofemora I and II. Tarsi I and II slightly shorter than tibiae; tarsi III and IV as long as tibiae III and IV, respectively. Telofemora I and II (Fig. 3F) each with 2/1 dorsal/ventral setae, telofemora III and IV with 2/0 setae. Ventrolateral seta on genu I long, stout and bipectinate (Fig. 2F); these setae on genua II and III short, seta-like; ventrolateral seta on genu IV slightly pectinate and larger than seta on genu III. Tibiae I-IV with 2, 1, 1, 2 bipectinate setae. Tarsus I with papilliform famulus, setiform solenidion and pair of doubled pas (Fig. 3G); tarsus II (Fig. 3H) without famulus, else similar to tarsus I. Tarsi III and IV resembling those of male.

Tritonymph. Idiosoma 185 long. PD smaller but with pair of ridges and reticulation as in adults. AE and PE separated. GP and AP fused; this GA with 2 pairs of pgs and 1 pair of minute sgs (Fig. 3I). Number of setae of legs same as in adults; telofemora I-IV with 2/1, 2/1, 2/0, 2/0 setae.

Variations. Varieties in characters of adults: length of idiosoma, ♀: 223-247 (10); length of idiosoma, ♂: 202-211 (2); number of adjunct setae on either side of AE: 0 (19), 1 (1); number of adjunct setae, PE: 0 (19), 1 (1); number of pgs on either side of GO, ♀: 5 (16), 6 (4); number of pgs plus basilar setae in either half, ♂: 7+1 (3), 9+1 (1); number of setae of leg segments 2 to 5:

segment	leg I	leg II	leg III	leg IV
2	2(24)	2(24)	1(24)	1(24)
3	2/1(24)	2/1(24)	2/0(24)	2/0(24)
4	3(24)	3(24)	2(1), 3(23)	3(24)
5	5(24)	5(24)	5(24)	5(24)

REMARKS. *Rhombognathus cyrtonotus* is characterised by the combination of: idiosoma wide; PD with 1 pair of setae; AE, PE and GP fused in both males and females; AE and PE generally lack adjunct setae; female with 5 pairs of pgs; in males pair of basilar setae posterior to GO; gnathosoma 1.2 times longer than wide; telofemora I-IV with 2/1, 2/1, 2/0, 2/0 setae, and

tarsal claw with accessory process but without additional tines.

R. cyrtonotus resembles *R. cebuus* Bartsch, 1983, a species recorded from the Philippines (Bartsch, 1983). Females of *R. cyrtonotus* are distinguished from *R. cebuus* by the number of perigenital setae — 5 pairs in *R. cyrtonotus*, 11 pairs of setae in *R. cebuus*. Male *R. cyrtonotus* have the pair of basilar setae posterior to the GO; in *R. cebuus* these setae are level with the posterior edge of the GO.

At low magnification, *Rhombognathus cyrtonotus* is separated from eastern Australian congeners by the combination of: idiosoma wide; anal sclerites narrow; gnathosoma short; telofemora I and II each with 2/1 dorsal/ventral setae; claws with single tooth. In contrast to the majority of *Rhombognathus* species, the posterior gland pore on the OC of both adult and juvenile *R. cyrtonotus* is not close to the lateral margin but removed by 2-3 times the diameter of that pore. Males can be separated from congeners on the basis of the position of the basilar setae.

In contrast to the majority of *Rhombognathus* species, tritonymphs of *R. cyrtonotus* have the genital plate fused with the anal plate.

Rhombognathus delicatulus sp. nov. (Figs 4-6)

ETYMOLOGY. For the delicate (*delicatulus*, Latin) ornamentation of the dorsal plates.

MATERIAL. HOLOTYPE. ♂ (MTQ), Great Barrier Reef, 19°22.36'S, 149°01.05'E, Club 21 Reef, coarse sand and rubble at 15m, 26 December 1997; coll. J.C. Otto. **PARATYPES.** ♀, ♂, 1 tritonymph (MTQ), collection data same as above. ♀ and ♂ (QM S50963), collection data same as above. ♀ (WAM 99/1440), ♂ (WAM 99/1441), collection data same as above. ♀, ♂ (ZMH A97/99), collection data same as above. 3 ♀, 2 ♂, 2 tritonymphs (IB), collection data same as above. **OTHER MATERIAL.** ♀, ♂ (MTQ), Great Barrier Reef, 19°20.12'S, 149°02.85'E, Elizabeth Reef, coral rubble at 16-26m, 24 December 1997; coll. J.C. Otto. ♂ (IB), Great Barrier Reef, 19°20.12'S, 149°02.85'E, Elizabeth Reef, coarse sand and rubble at 10m, 25 December 1997; coll. J.C. Otto. 2 ♀, 2 ♂ (IB), Great Barrier Reef, 18°26.36'S, 146°42.24'E, Bramble Reef, coarse sand at 5m, 9 April 1998; coll. J.C. Otto.

DESCRIPTION. Male. Idiosoma 223-260 long; holotype 235 long, 137 wide. Dorsal plates delicately reticulated (Fig. 4A); each mesh subdivided. AD 78 long, 75 wide; anterior margin rounded; posterior portion of AD triangular; posterior scars of muscle strings in an almost straight line at 0.60 relative to length of

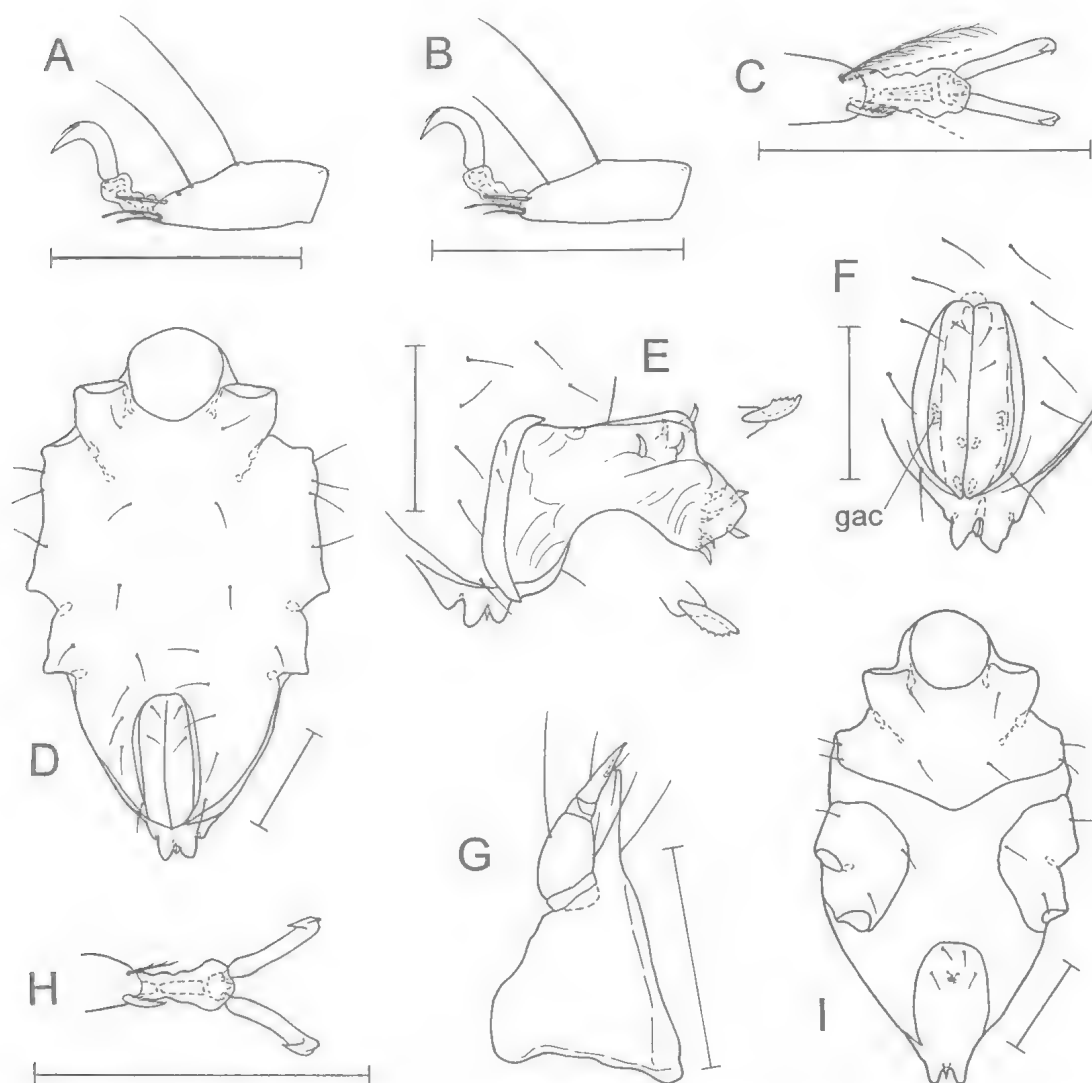


FIG. 5. *Rhombognathus delicatulus* sp. nov.; A, tarsus I, lateral, male (medial claw and setae omitted); B, tarsus II, lateral, male (medial claw and setae omitted); C, tip of tarsus IV, ventral, male (dorsal setae dashed); D, idiosoma, ventral, female; E, ovipositor and two of the genital spines (enlarged), female; F, posterior portion of idiosoma, ventral, female; G, gnathosoma, lateral, female; H, tip of tarsus IV, ventral, female (dorsal setae omitted); I, idiosoma, ventral, tritonymph. gac = genital acetabula. Scale bar = 50µm.

AD. Pair of gland pores in lateral margins at the level of insertion of leg I. OC 67 long, 37 wide; with 2 corneae and 2 glands pores in lateral margin; pore canaliculus almost halfway between gland pores. PD 137 long, 85 wide; evenly reticulated; each mesh with 12-18 minute pits. Anterior portion of PD rounded; posterior cones hardly extending beyond median margin of PD. Anal valves prolonged, extending beyond narrow anal sclerites. Dorsal idiosomatic setae small; ds-1 10 long and hardly longer than setae on OC

and PD. Posterior seta on OC at 0.44 relative to length of OC, that equals level of median edge. Single pair of setae on PD at 0.26. Adanal setae on anal valves.

AE, PE, GP, and AP fused to a ventral shield (Fig. 4B); this shield 195 long. Integument of ventral plates delicately punctate. Portion representing AE with 1 pair of adjunct setae. No adjunct setae on PE. GO 27 long, 17 wide. Anterior margin of GO almost level with insertion of leg IV; interval between posterior

edge of GO and end of idiosoma 1.4 times length of GO. Perigenital setae plumose; arranged trapezoidally; on either side a line of 8 setae; basilar setae adjacent to GO and at 0.80 relative to length of GO. Spermatopositor 40 long, 45 wide; extending beyond GO and anterior perigenital setae (Fig. 4C).

Gnathosoma 67 long, 42 wide; 1.6 times longer than wide (Fig. 4D). Rostrum slender, 30 long, 11 wide. Basal pair of maxillary setae almost 18 long; succeeding adjacent pair of setae distinctly shorter. Tectum truncate.

Leg I inserted at 0.11, leg IV at 0.64. Legs shorter than idiosoma. Leg I and IV subequal in length, about 0.8 times of length of idiosoma. Form of telofemora as in female. Tibiae cylindrical; each tibia slightly shorter than telofemur of that leg. Leg chaetotaxy, from trochanter to tarsus: leg I, 1, 2, 5, 5, 5, 3; leg II, 1, 2, 5, 5, 5, 3; leg III, 1, 1, 3, 3, 5, 4; leg IV, 0, 1, 3, 3, 5, 3. Telofemora I-IV with 4/1, 4/1, 3/0, 3/0 setae. Ventrolateral seta on both genu I and IV bipectinate (Fig. 4E, H); these setae on genua II and III slender (Fig. 4F, G). Tibia I with pair of stout, bipectinate setae; tibiae II and III each with slender, smooth ventrolateral and stout, bipectinate ventromedial seta. Tibia IV with large ventrolateral and shorter ventromedial seta; both bipectinate. Dorsal setae on tarsi at low magnification plain, under oil immersion delicate plumosity recognizable. Solenidion on tarsus I 10 long; funulus papilliform, 1 long, positioned halfway between solenidion and dorsal fossary seta (Fig. 5A). Solenidion on tarsus II 10 long (Fig. 5B). Tarsi I and II each with pair of doubled pas. Tarsus III with setiform, eupathid medial pas and spiniform, pectinate lateral pas. Medial pas on tarsus IV long and plumose; lateral pas spiniform and intensely pectinate (Fig. 5C).

Carpites on tarsi I and II 6 long, on tarsi III and IV 7-8 long. Accessory process of claws with single tooth.

Female. Idiosoma 192-269 long. Dorsal aspect same as in male. Setae ds-1 slightly longer than following setae. Ventral plates AE, PE and GP fused; this ventral shield contiguous with anal plate. GO surrounded by 10 perigenital setae. Anterior pair of pgs level with ventral setae on epimera IV. Second pair of pgs almost level with anterior edge of GO (Fig. 5D). Interval between pgs-4 and pgs-5 slightly larger than between the other pgs. Genital sclerites 63 long, each sclerite with 2 sgs. Ovipositor with 5 pairs of claw-like

genital spines; each genital spine with one large medial tooth and 4-5 lateral teeth (Fig. 5E). Genital acetabula very small, positioned immediately posterior to the level of pgs-4 (Fig. 5F).

Gnathosoma 1.5-1.6 times longer than wide. Palps straight; extending beyond end of rostrum (Fig. 5G). Basal pair of rostral setae almost as long as apical pair of maxillary setae. Chelicera 70 long. Cheliceral claw short.

Telofemora I-IV 1.9, 2.0, 2.0, 1.9 times longer than high. Medial pas on tarsus IV setiform, delicately plumose; lateral pas spiniform, pectinate (Fig. 5H).

Tritonymph. Idiosoma 182-212 long. PD smaller than in adults; median and lateral portions foveate, not reticulate. Ventral plates AE, PE and GA separate. AE with pair of adjunct setae. No adjunct setae on PE. GP and AP fused (Fig. 5I); GA with 2 pairs of pgs and 1 pair of sgs; 3 pairs of minute genital acetabula. Leg chaetotaxy from trochanter to tarsus: legs I and II, 1, 2, 4, 5, 5, 3; leg III, 1, 1, 3, 3, 5, 4; leg IV, 0, 1, 2-3, 3, 5, 3. Telofemora I to IV with 3/1, 3/1, 3/0 and 2-3/0 setae.

Variations. Amongst the material examined, several individuals, e.g. from Elizabeth Reef (MTQ), differ from those from the type locality in the following characters: gnathosomal base and rostrum short, gnathosoma 1.3-1.4 times longer than wide (Fig. 6A, B); reticulation of PD rather prominent; ds-1 about twice the length of the succeeding setae; ds-3 slightly posterior to medial corner of OC; bipectinate ventral seta on genu I as long as ventral setae of tibia I (Fig. 6C); ventral seta on genu IV slender, not pectinate (Fig. 6D); ventromedial seta on tibia IV slender, its pectination very faint or lacking; telofemora hardly longer than tibiae. Most marked is the short gnathosoma. Within the rhombognathines, such a difference in the length of the gnathosoma is unusual. Nonetheless, the specimens outlined are presently not regarded as belonging to a separate species.

Varieties of characters in adults: length of idiosoma, ♀: 192-269 (10); length of idiosoma, ♂: 223-260 (10); number of adjunct setae on either side of AE: 0 (2), 1 (33), 2 (5); number of adjunct setae on PE: 0 (40); number of pgs on either side of GO, ♀: 5 (20); number of pgs plus basilar setae

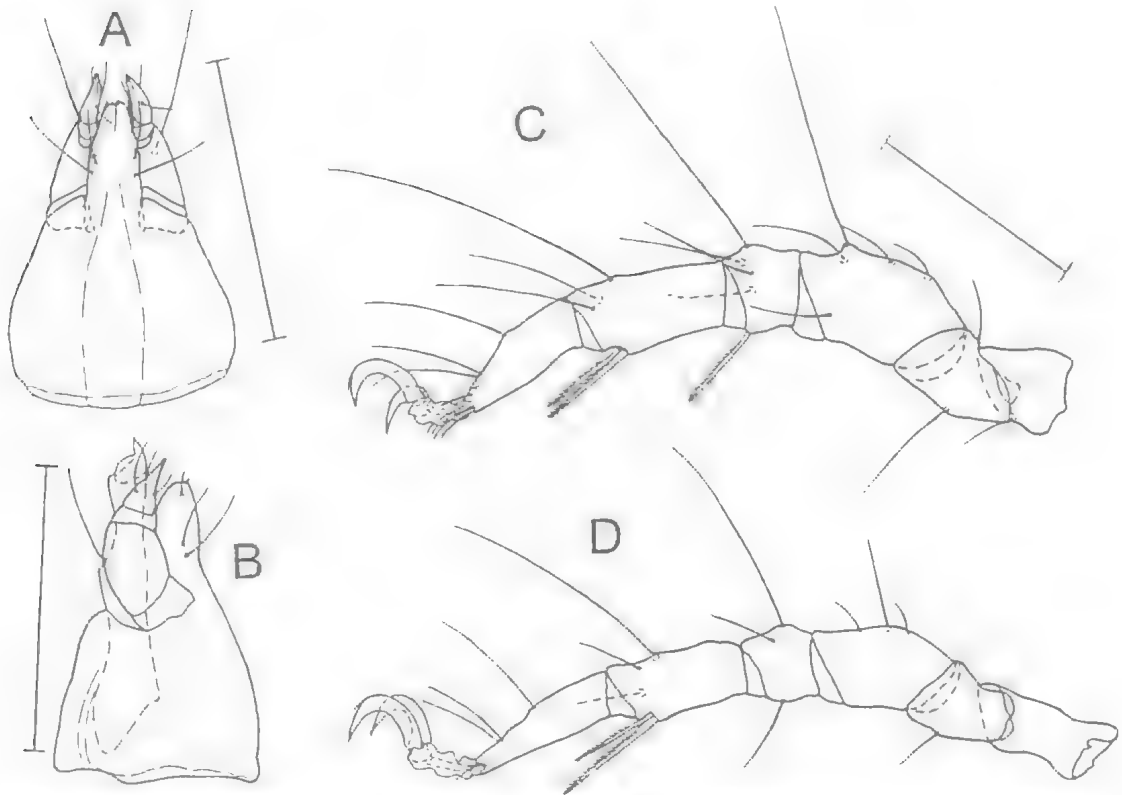


FIG. 6. *Rhombognathus delicatulus* sp. nov. from Elizabeth Reef: A, gnathosoma, ventral, male; B, gnathosoma, lateral, female; C, leg I, lateral, female; D, leg IV, medial, female. Scale bar = 50 μ m.

in either half, δ : 7+1 (3), 8+1 (10), 9+1 (7); number of setae of leg segments 2 to 5:

segment	leg I	leg II	leg III	leg IV
2	2(40)	2(40)	1(40)	1(40)
3	3/1(1), 4(0(1), 4/1(38)	4/1(40)	3-0(39), 4/0(1)	3/0(40)
4	5(40)	5(40)	3(40)	3(40)
5	5(40)	5(40)	5(40)	5(40)

REMARKS. The most obvious characters of *Rhombognathus delicatulus* are: the uniformly reticulated PD with a single pair of setae; the ventral shield; the narrow anal sclerites surpassed by the anal valves, the low number of adjunct setae; the slender gnathosoma; the combination 4/1, 4/1, 3/0, 3/0 setae on the telofemora I-IV; and the claws with a single tine. At a superficial glance, *R. delicatulus* resembles the western Pacific *R. neptunellus* Bartsch, 1992. *R. oblongus* Bartsch, 1989a, *R. teurimus* Abé, 1996, and the western Australian *R. psammophilus* Bartsch, 1993.

R. neptunellus and *R. teurimus* differ from *R. delicatulus* in the outline of the AD, the insertion of ds-3 on the OC, and the shape of the

gnathosoma. The PD of *R. oblongus* is more slender than that of *R. delicatulus*. *R. psammophilus* lacks the reticulation on the dorsal plates, the series of muscle scars is closer to the posterior margin of the AD, and the ds-4 are closer to the anterior margin of the PD than in *R. delicatulus*.

***Rhombognathus lathridius* sp. nov.**
(Figs 7, 8)

ETYMOLOGY. Because of the shape of the body and legs, this species is believed to live hidden (*lathridios*, Greek) in sandy deposits.

MATERIAL. HOLOTYPE. δ (MTQ), Great Barrier Reef, 18°48.92'S, 146°25.76'E, Pandora Reef, St. 1, coarse sand, 1m, 22 January 1998; coll. J.C. Otto. PARATYPES. 2 δ , 1 tritonymph (MTQ), collection data as above. \varnothing , δ (QM S50964), collection data as above. 2 \varnothing (WAM 99/1442, 1443), collection data as above. \varnothing , δ (ZMH A98/99), collection data as above. 4 \varnothing , 3 δ , 2 tritonymphs (IB), collection data as above.

DESCRIPTION. *Male*. Idiosoma 229-254 long, holotype 248 long, 145 wide. Dorsal plates very faintly and minutely reticulated. AD, OC and PD

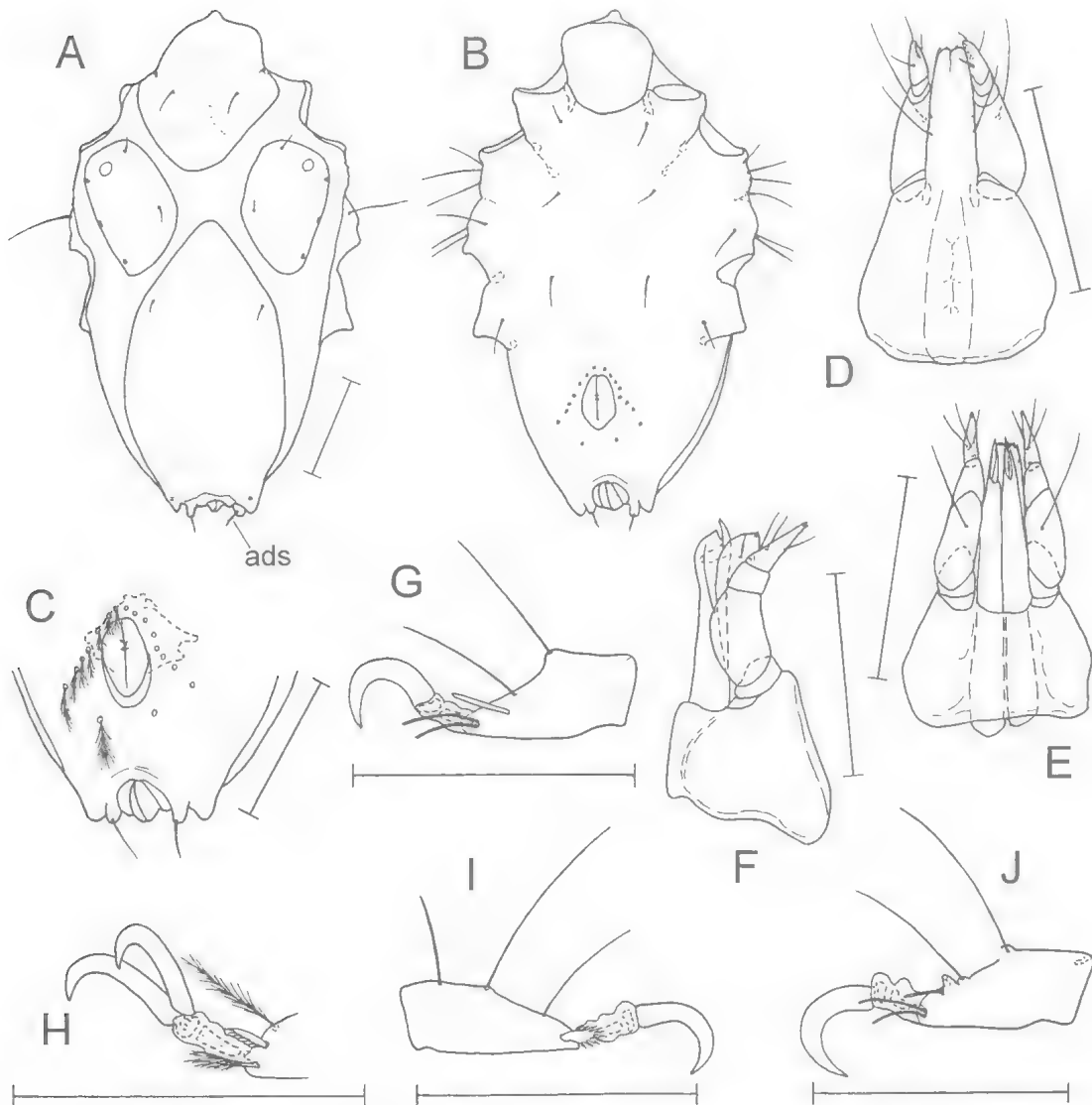


FIG. 7. *Rhombognathus lathridius* sp. nov.; A, idiosoma, dorsal, male; B, idiosoma, ventral, male (adanal setae illustrated both in A and B); C, posterior portion of idiosoma, ventral, male; D, gnathosoma, ventral, male; E, gnathosoma, dorsal, male; F, gnathosoma, lateral, male; G, tarsus II, lateral, male (medial claw and setae omitted); H, tip of tarsus IV, ventral, male (dorsomedial seta omitted); I, tarsus III, lateral, male (dorsomedial seta, medial pas and claw omitted); J, tarsus I, lateral, female (medial claw and setae omitted). ads = adanal seta. Scale bar = 50 μ m.

separated (Fig. 7A). AD 82 long, 72 wide; anterior margin with small, rounded process; posterior margin ovate. Pair of gland pores in lateral margins at the level of insertion of leg I. OC 67 long, 42 wide; each plate with single cornea; two gland pores in lateral margin; pore canaliculus between pores. PD 145 long, 80 wide. Anterior portion of PD triangular. Pair of gland pores at base of posterior cones. Dorsal

setae small; ds-1 approximately 10 long, not markedly longer than posterior pairs of setae. Setae ds-1 on AD posterior to the level of gland pores and at 0.52-0.54. Setae ds-3 at 0.52 relative to length of OC. Single pair of setae on PD at 0.27. Adanal setae 7 long, on tube-like pedestals.

Ventral plates AE, PE, GP, and AP fused to a ventral shield (Fig. 7B). Surface of plate delicately punctate. AE with 2-3 pairs of adjunct

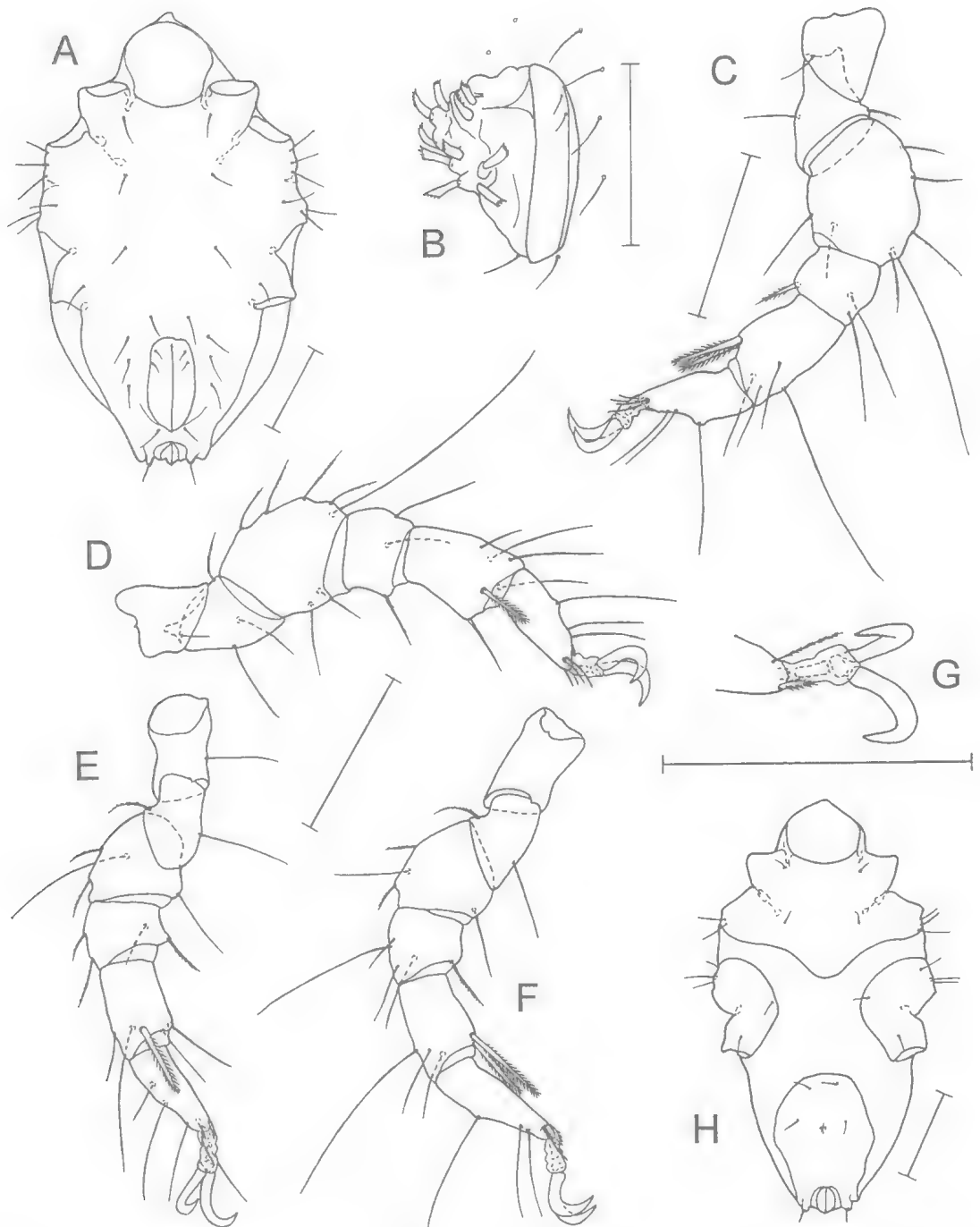


FIG. 8. *Rhombognathus lathridius* sp. nov.; A, idiosoma, ventral, female; B, ovipositor, ventrolateral, female; C, leg I, medial, female; D, leg II, medial, female; E, leg III, medial, female; F, leg IV, medial, female; G, tip of tarsus IV, ventral, female (dorsal setae omitted); H, idiosoma, ventral, tritonymph. Scale bar = 50µm.

setae. PE with 1 dorsal, 3 ventral and 2 marginal adjunct setae. GO 25 long, 15 wide. Perigenital

setae plumose; 7-8 setae arranged trapezoidally around GO; pair of basilar setae posterior to GO

(Fig. 7C). Spermatopositor 37 long, 40 wide, extending somewhat beyond anterior perigenital setae.

Gnathosoma slender, 75 long, 46 wide, 1.6 times longer than wide (Fig. 7D). Rostrum 32 long, 15 wide, almost parallel-sided. Tectum truncate (Fig. 7E). Basal pair of maxillary setae in basal half of rostrum. Palps slightly flattened, extending beyond tip of rostrum. P-2 with long dorsal seta. Chelicera 71 long. Cheliceral claw narrow (Fig. 7F), 10 long, its dorsal margin smooth.

Legs short, without claws and carpite about half as long as the idiosoma. Insertion of legs III and IV at 0.47 and 0.64, respectively. Number and arrangement of setae on trochanters to tibiae as in female. Tarsi I-IV with 3, 3, 4, 3 dorsal setae. Tarsi I and II each with pair of doubled pas; as in female, famulus on tarsus I 2 long (Fig. 7J), solenidion 6 long. Solenidion on tarsus II 10 long, conspicuously wide (Fig. 7G). Lateral pas on tarsus III flattened, bipectinate (Fig. 7I); medial pas setiform. On tarsus IV dorsolateral fossary seta plumose; lateral pas flattened, bipectinate; medial pas plumose (Fig. 7H).

Carpite short, on tarsi I and II 4 long; on tarsi III and IV 5 and 6 long. Claws short and smooth, they lack accessory processes and tines.

Female. Idiosoma 235-254. In dorsal aspect similar to male, though areas of striated integument larger. Pair of setae on PD at 0.25-0.28. Ventral plates AE, PE, GP, and AP fused to a ventral shield (Fig. 8A). GO surrounded by 10 perigenital setae. Anterior portion of GO not extending to the level of insertion of leg IV. Four anterior pairs of setae positioned almost equidistant. Anterior pairs of pgs 15 anterior to GO but not extending beyond the level of insertion of leg IV. Genital sclerites with 2 pairs of sgs. Ovipositor with 5 pairs of claw-like genital spines (Fig. 8B); spines 5 long, 3 wide; each with 5-6 tines.

Legs I and II flattened. Telfemora I-IV 1.3, 1.3, 1.2, and 1.3 times longer than high, respectively. Tibiae I-IV slightly shorter than telfemora. Leg chaetotaxy: leg I (Fig. 8C), 1, 2, 7, 3, 6, 3; leg II (Fig. 8D), 1, 3, 7, 3, 6, 3; leg III (Fig. 8E), 1, 2, 4, 4, 5, 4; leg IV (Fig. 8F), 0, 2, 4, 5, 5, 3. Basifemora, genua and tibiae dorsally with short slightly plumose setae which are less than length of each segment, and 0-1 long smooth setae which are much longer than length of the segment. Ventral seta on genua delicately pectinate. Tibiae I-IV with 2, 1, 1, 2 bipectinate setae. Ventral setae on tibia I equal in length; on

tibia IV ventrolateral seta slightly smaller than ventromedial one. Slender ventrolateral seta of tibiae II and III as long as coarsely bipectinate ventromedial seta. Dorsal setae on tarsus IV smooth; lateral pas short, flattened, pectinate; medial pas slender, lightly plumose (Fig. 8G).

Tritonymph. Idiosoma 232 long. Shape of AD and OC similar to that of adults. PD shorter; ds-4 inserted at 0.22. Plates AE, PE and GA separated (Fig. 8H). AE with 1-2 pairs of adjunct setae; PE with 1 pair of adjunct setae; GA with 2 pairs of pgs. Leg chaetotaxy, from trochanter to tarsus: leg I, 1, 2, 6, 3, 6, 3; leg II, 1, 3, 6, 3, 6, 3; leg III, 1, 2, 3, 3, 5, 4; leg IV, 0, 2, 2-3, 4, 5, 3. Arrangement of pectinate setae on tibiae same as in adults. Tarsi III and IV each with flattened bipectinate lateral pas, and slender, setiform medial pas.

Variations. Varieties of characters in adults: length of idiosoma, ♀: 235-254 (9); length of idiosoma, ♂: 229-254 (6); number of adjunct setae on either side of AE: 1 (9), 2 (21), 3 (2); number of adjunct setae, PE: 1 (10), 2 (22); number of pgs on either side of GO, ♀: 4 (1), 5 (18), 6 (1); number of pgs plus basilar setae in either half, ♂: 7+1 (11), 8+1 (1); number of setae of leg segments 2 to 5:

segment	leg I	leg II	leg III	leg IV
2	2 (28)	3(28)	2(27)	2(27)
3	5/2(28)	5/2(27), 6/2(1)	3/1(26), 4/0(1)	3/1(26), 4/1(1)
4	3(28)	3(27), 2(1)	4(26), 3(1)	5(27)
5	6(28)	6(28)	5(27)	5(27)

REMARKS. In the shape of the body, gnathosoma and legs, *Rhombognathus lathridius* is similar to *R. caudiculus* Bartsch, 1983, *R. conjunctus* Bartsch, 1986, *R. intermedius* Schulz, 1933, *R. latens* Bartsch, 1993 and *R. latibulus* Bartsch, 1993.

R. latens, a species known from Western Australia (Bartsch, 1993), can be separated from the others on the basis of the two pairs of setae on the PD and the enlarged number of perigenital setae around the female GO. *R. conjunctus*, an inhabitant of the Mediterranean (Bartsch, 1986), has the dorsal plates AD, OC and PD fused to a dorsal shield. *R. intermedius*, widely spread in sandy deposits in the shores of the Baltic, North Sea and northeastern Atlantic (Bartsch & Schmidt, 1979), has a short gnathosoma, slender telfemora and the adanal setae do not stand on small pedestals. *R. caudiculus* and *R. latibulus*, recorded from the Philippines and Western Australia (Bartsch, 1983, 1993), respectively, are most similar to *R. lathridius*, but the former species bears a single pair of adjunct setae on both

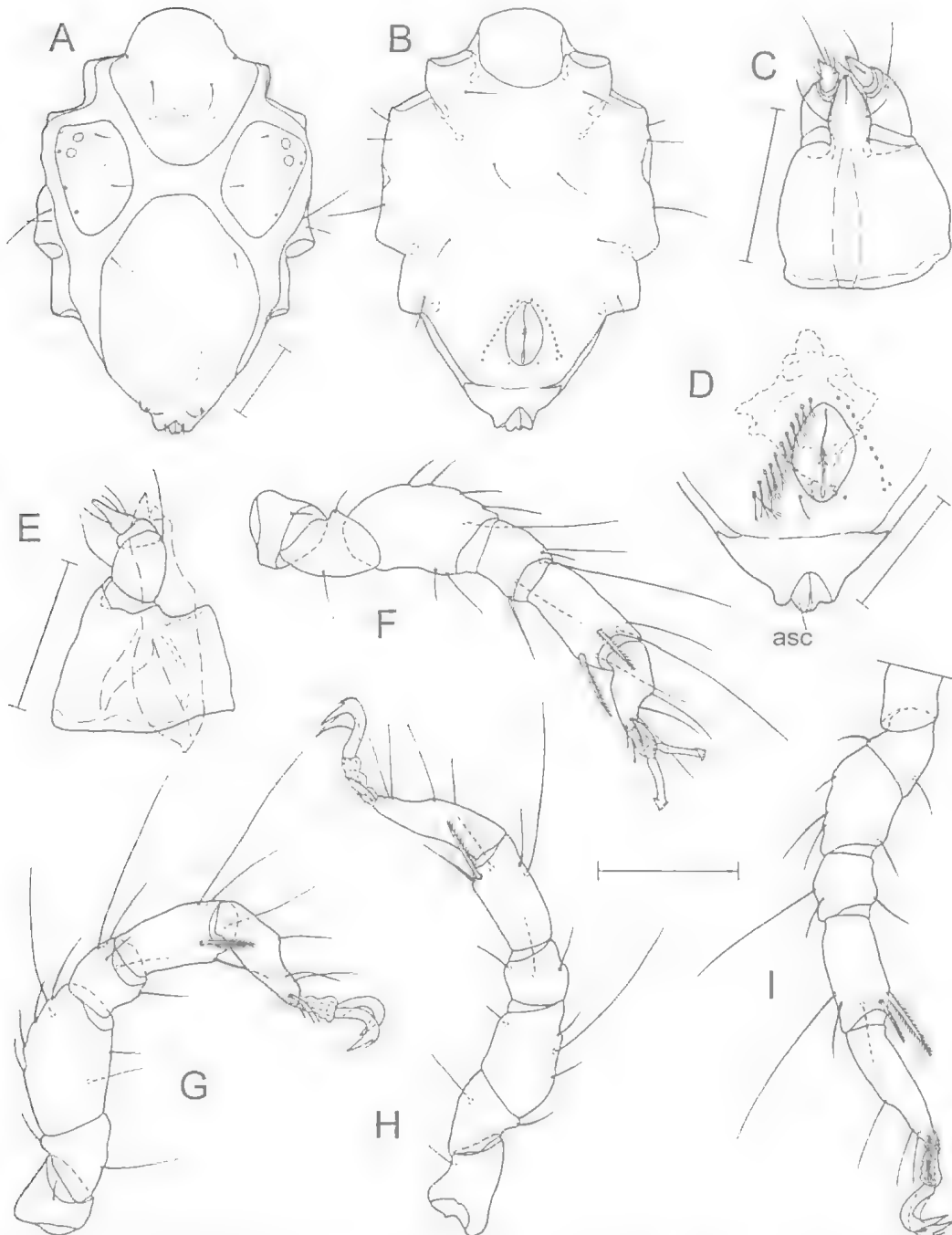


FIG. 9. *Rhombognathus levigatus* sp. nov., male; A, idiosoma, dorsal; B, idiosoma, ventral; C, gnathosoma, ventral; D, posterior portion of idiosoma, ventral; E, gnathosoma, lateral (chelicera dashed); F, leg I, ventromedial; G, leg II, medial; H, leg III, medial; I, leg IV, medial. asc = anal sclerite. Scale bar = 50 μ m.

AE and PE, and the anterior portion of the PD is broadly rounded, whereas *R. lathridius* has 3-4 pairs of adjunct setae on the AE, 2 pairs of adjunct

setae on the PE, and the anterior portion of the PD is triangular. Further distinguishing characters are: in the male of *R. caudiculus* the pair of basilar

setae is level with the posterior margin of the GO; and the telofemora I-IV of *R. latibulus* bear 4/2, 4/2, 2/1, 2/1 setae.

All specimens of *R. lathridius* have an elongate gnathosoma with a slender rostrum; there is no tendency of reduction of the gnathosomal length.

Tritonymphs of *R. lathridius* have the GP and AP fused, a character shared with *R. cyrtonotus* and *R. delicatulus*.

Rhombognathus levigatus sp. nov.
(Figs 9, 10)

ETYMOLOGY. From *levigare* (Latin), to smooth, for the almost smooth surface of the dorsal plates.

MATERIAL. HOLOTYPE, ♂ (MTQ), Great Barrier Reef, 18°48.92'S, 146°25.76'E, Pandora Reef, St. 1, coral rubble, 0.3m, 22 January 1998; coll. J.C. Otto. PARATYPES. 2♀, 1 tritonymph (MTQ), collection data as above. ♂ (QM S50965), collection data as above. ♀ (WAM 99/1444), collection data as above. ♀ (ZMH A99/99), collection data as above. ♀, ♂ (IB), collection data as above.

DESCRIPTION. *Male*. Idiosoma 267-276 long; holotype 267 long, 173 wide. Surface of plates almost smooth; integument of lateral portions of AD and PD and medial portions of OC pierced by minute pores (Fig. 9A). AD 98 long, 93 wide. Anterior margin arched; posterior margin broadly rounded. Posterior transverse line of muscle scars at 0.69. OC 75 long and 48 wide. Lateral margin with 2 gland pores and, halfway between, a pore canaliculus. PD 140 long, 110 wide; wider than AD, and its anterior margin in the median truncate. Very slightly raised pair of oblong areolae with minute pores; posterior portion of PD faintly reticulated in the median and laterally. Anal sclerites not surpassed by anal valves. Setae ds-1 approximately 12 long; inserted at 0.44. Setae ds-2 and ds-3 on OC; ds-3 at 0.57. Single pair of setae on PD at 0.28. Adanal setae on anal valves.

Ventral plates AE, PE and GP fused; GP and AP contiguous (Fig. 9B). Ventral shield from camerostome to tip of anal cone 219 long. AE and PE each with 1 pair of adjunct setae. GO 40 long, 23 wide. Perigenital setae plumose, arranged trapezoidally, with 11 setae in a line and 1 pair of basilar setae level with posterior edge of GO (Fig. 9D). Anterior edge of GO slightly surpassing the level of insertion of leg IV. Distance between posterior edge of GO and end of anal cone equalling length of GO. Genital sclerites with 2 pairs of sgs. Spermatopositor 60 long, 57 wide; extending beyond anterior pgs.

Gnathosoma short, 70 long, 58 wide, length:width ratio 1.2. Rostrum 25 long, 13 wide, triangular, shorter than gnathosomal base (Fig. 9C). Palps tightly appressed to rostrum. Chelicera 75 long (Fig. 9E). Cheliceral claw serrate.

Length of legs (claws included) 0.7 times that of idiosoma. Relative to length of idiosoma, insertion of legs III and IV at 0.55 and 0.72, respectively. Telofemora I-IV each about 1.7 times longer than high. Tibiae I and II somewhat shorter than telofemora (Fig. 9F, G); tibiae III and IV as long as telofemora (Fig. 9H, I). Tarsi I and II as long as these legs, tibiae; tarsi III and IV longer than tibiae III and IV, respectively. Leg chaetotaxy: leg I, 1, 2, 7, 5, 5, 3; leg II, 1, 2, 7, 5, 5, 3; leg III, 1, 2, 4, 3, 5, 4; leg IV, 0, 2, 4, 3-4, 5, 3. Telofemora I-IV with 5/2, 5/2, 3/1, 3/1 setae. On both genu I and II ventrolateral seta longer than ventromedial one; both setae almost plain. Tibiae I-IV with 2, 1, 1, 2 bipectinate spiniform setae. On tibia IV ventromedial spine shorter than ventrolateral one. Tarsus III with 4 dorsal setae; distance between 2 basal ones equalling half height of tarsus. Tarsus I with 1- long papilliform famulus and 8- long setiform solenidion (Fig. 10A). As in female, solenidion on tarsus II 10-11 long (Fig. 10D). Both tarsus I and II with pair of doubled pas. Medial pas on tarsus III setiform; lateral pas spiniform, delicately pectinate. Medial pas on tarsus IV long and plumose, lateral pas short and bipectinate (Fig. 10B).

Carpites on tarsi I and II 8-9 long; carpites on tarsi III and IV 10 long. Accessory process on claws widened, about 4-5 wide, bearing 5-6 small tines. No tines on claw shaft.

Female. Idiosoma 285-305 long. Outline of dorsal plates as in male though ornamentation lightly reticulate. Median portion of AD between ds-1 reticulate. Anterior margin of PD truncate; setae ds-4 at 0.21-0.24. AE, PE and GP fused; this ventral shield separated from anal plate by narrow lateral wedges of striated integument. GO extending anteriorly almost to level of insertion of leg IV. Area of genital plate with 5 pairs of pgs; two anterior pairs inserted distinctly anterior to GO (Fig. 10C). Genital sclerites with 2 pairs of sgs. Three pairs of tube-like genital acetabula. Genital spines claw-like. Tarsus III with spiniform lateral pas and 1-2 eupathid setiform medial pas (Fig. 10E). Lateral pas of tarsus IV similar to that of tarsus III; medial pas of tarsus IV slightly smaller than lateral pas.

Tritonymph. Idiosoma 248 long. Ventral plates separate; AE and PE each with a pair of adjunct

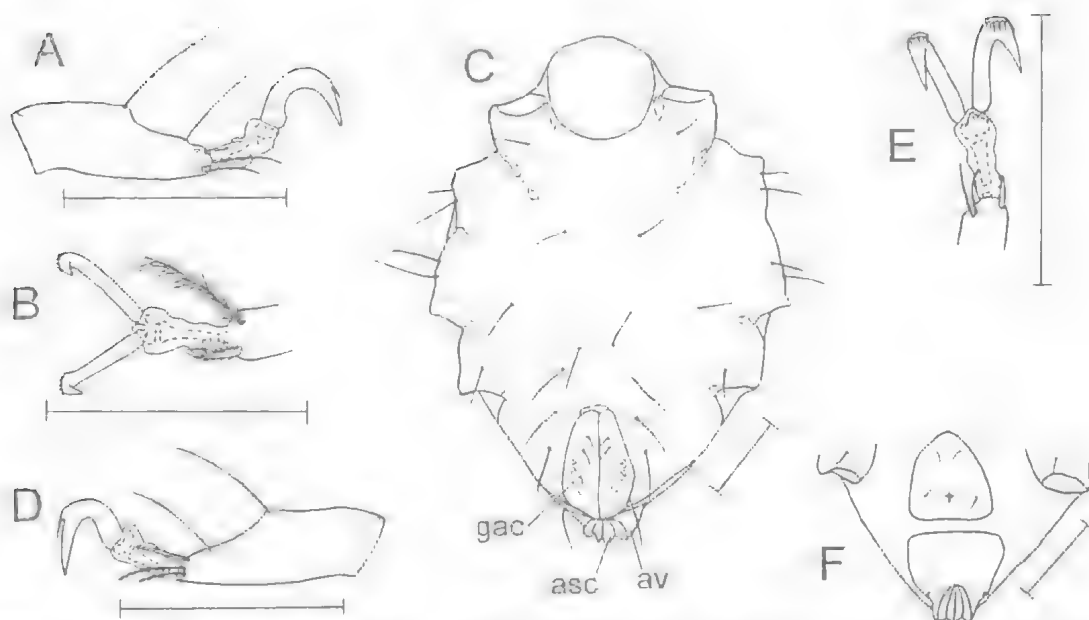


FIG. 10. *Rhombognathus levigatus* sp. nov., A, tarsus I, lateral, male (medial claw and setae omitted); B, tip of tarsus IV, ventral, male (dorsal setae omitted); C, idiosoma, ventral, female; D, tarsus II, lateral, female (medial claw and setae omitted); E, tip of tarsus III, ventral, female (dorsal setae omitted); F, posterior portion of idiosoma, ventral, tritonymph asc = anal sclerite; av = anal valve; gac = genital acetabula. Scale bar = 50µm.

setae. GP and AP separate (Fig. 10F). GP with 2 pairs of pgs and 1 pair of sgs. Telfemora I-IV with 4/2, 4/2, 3/1, 2-3/1 dorsal/ventral setae. Setation of the other segments same as in adults.

Variations. Varieties of characters in adults: length of idiosoma, female: 285-305 (5); length of idiosoma, male: 267-276 (3); number of adjunct setae on either side of AE: 1 (12), 2 (4); number of adjunct setae, PE: 1 (15), 2 (1); number of pgs on either side of GO, female: 5 (10); number of pgs plus basilar setae in either half, male: 9+1 (2), 10+1 (2), 11+1 (2); number of setae of leg segments 2 to 5:

segment	leg I	leg II	leg III	leg IV
2	2(16)	2(16)	2(16)	2(16)
3	4/2(2), 5/2(14)	4/2(2), 5/1(1), 5/2(13)	3/1(14), 4/1(1), 5/1(1)	2/1(4), 3/1(12)
4	5(16)	5(16)	3(16)	3(15), 4(1)
5	5(16)	5(16)	3(16)	5(16)

Anomaly. In one of the females the left OC is lacking and replaced by striated integument.

REMARKS. *Rhombognathus levigatus* is characterised by: smooth PD with single pair of setae; AE, PE and GP fused; area of AE and PE each with 1 pair of adjunct setae; female with 5 pairs of pgs; male with 10-12 pairs of plumose pgs; short gnathosoma 1.2 times longer than wide;

telfemora I-IV with 5/2, 5/2, 3/1, 3/1 dorsal/ventral setae. Slightly widened accessory process with 5-6 tines.

In the samples from the Great Barrier Reef, three species, *Rhombognathus levigatus*, *R. reticulifer* sp. nov. and *R. tericulus* sp. nov., have claws with the slightly widened accessory process bearing a few tines. In contrast to *R. levigatus*, the dorsal plates of *R. reticulifer* and *R. tericulus* have a distinct reticulate ornamentation and long ds-1. The three species also differ in the number of dorsal/ventral setae on the telfemora I to IV.

Compared to *Rhombognathus* species from other parts of the world, *R. levigatus* is similar to *R. notopsoides* Bartsch, 1979, *R. semireticulatus* Bartsch, 1977, *R. sinensis* Bartsch, 1990, and *R. ventralis* Newell, 1984. *R. notopsoides* is a brackish water species from eastern North America (Bartsch, 1979b), *R. sinensis* is recorded from southern China and Japan (Bartsch, 1990; Abé 1996), and *R. semireticulatus* and *R. ventralis* from the Eastern Pacific (Bartsch, 1977; Newell, 1984). The dorsal plates of *R. notopsoides* are distinctly ornamented. In *R. semireticulatus*, too, each of the dorsal plates bears a distinct ornamentation, and, in contrast to *R. levigatus*, each of the telfemora I and II has 5 dorsal setae but only 1 ventral seta. In *R. sinensis*,

the arrangement of the setae on the telofemora I to IV is the same as in *R. levigatus* but the outline and the ornamentation of the PD is different, and the number of tines on the accessory processes is somewhat larger than in the latter species. The telofemora I to IV of *R. ventralis* bear 6, 6, 4, 4 setae, the ds-1 are rather long, whereas in *R. levigatus* the ds-1 are short and the telofemora bear 7, 7, 4, 4 setae.

Rhombognathus longipes sp. nov.
(Figs 11-13)

ETYMOLOGY. From (Latin) *longus*, long, and *pes*, foot, leg, for the long legs.

MATERIAL. HOLOTYPE. ♂ (MTQ), Great Barrier Reef, 18°25.93'S, 147°21.11'E, Faraday Reef, coarse sand and rubble, 10m, 13 April 1998; J.C. Otto. PARATYPES. 3♀, 2♂, 1 protonymph (MTQ), collection data as above. ♀, ♂ (QM S50966), collection data as above. 2♀ (WAM 99/1445, 1446), collection data as above. One ♀, ♂ (ZMH A100/99), collection data as above. 6♀, 2♂, 1 tritonymph, 2 deutonymphs (IB), collection data as above. OTHER MATERIAL. ♂ (MTQ), Great Barrier Reef, 18°25.93'S, 147°21.11'E, Faraday Reef, coarse sand and rubble, 2m, 13 April 1998; J.C. Otto.

DESCRIPTION. *Male*. Idiosoma slender, 317-328 long; holotype 335 long, 185 wide. Dorsal plates with delicate reticulation. AD 112 long, 100 wide; anterior margin broadly rounded; posterior margin ovate. Line of internal scars at about 0.75 (Fig. 11A). OC 100 long, 55 wide; anterior cornea slightly larger than posterior one. Distance between gland pores 50; pore canaliculus almost halfway between gland pores. PD 167 long, 97 wide, 1.7 times longer than wide. Pair of posterior cones of PD almost extending to end of anal cone; each cone with gland pore. Setae ds-1 10-15 long, positioned in posterior half of AD at 0.64, i.e. somewhat anterior to transverse line of scars. Second pair of setae on OC almost at 0.43. PD with single pair of setae at 0.16. Adanal setae distally on anal plate. Anal sclerites well developed.

AE, PE, GP, and AP fused (Fig. 11B). Area of AE with pair of adjunct setae, that of PE with 0 and 1 adjunct seta. GO 35 long, 25 wide; anterior margin level with insertion of leg IV. With 9 and 10 pgs on either side of GO; pair of basilar setae incorporated in line of pgs (Fig. 11C). Spermatopositor 52 long, 46 wide, slightly extending beyond GO.

Gnathosoma 90 long, 67 wide, 1.3 times longer than wide. Rostrum slender, apically pointed (Fig. 11D); almost as long as gnathosomal base. Narrow tectum truncate. Basal pair of maxillary

setae in middle of rostrum; apical pair almost as long as basal pair. Slender palps appressed to rostrum.

Legs slender; the four pairs similar in length and approximately 0.9 of length of idiosoma. Legs III and IV at 0.53 and 0.69, respectively. Telofemora I-IV 2.7, 2.9, 2.7, 2.5 times longer than high. Leg chaetotaxy: leg I, 1, 2, 5, 5, 5, 3; leg II, 1, 2, 5, 5, 5, 3; leg III, 1, 1, 3, 3, 5, 4; leg IV, 0, 1, 3, 3, 5, 3. Telofemora I-IV with 4/1, 4/1, 3/0, 3/0 setae. Two basidorsal setae on telofemora I and II short, spiniform (Figs 11E, F). Bipectinate setae on tibiae I-IV numbering 2, 1, 1, 2; these setae on tibiae I, II and III conspicuously long; on tibia IV ventrolateral bipectinate seta distinctly longer than ventromedial one. Tarsi slender. Basal setae of tarsi III and IV inserted in apical half of these segments (Figs 12A, B). Two basal setae on tarsus III adjacent. Tarsus I slender, with elongate papilliform famulus and solenidion 14- long. Tarsi I and II with doubled pas; on tarsus III medial pas setiform, lateral pas short, spiniform (Fig. 12D); on tarsus IV medial pas long, plumose; lateral pas flattened, pectinate (Fig. 12E).

Carpites on tarsi I and II 10 long, those on tarsi III and IV 11-12 long. Claws short; rounded apex with small accessory process.

Female. Idiosoma 335-365 long. Dorsal aspect similar to that of male. AE, PE and GP fused. AE with 1, rarely 2 adjunct setae on either side; PE with 1, rarely 0, adjunct seta. GO 85 long; genital sclerites each with 2 sgs. With 5 pairs of pgs (Fig. 12F). Two anterior pairs of pgs anterior to level of anterior edge of GO; anteriormost pair of setae slightly anterior to level of insertion of leg IV; its distance to edge of GO equalling 0.3 times length of GO. Posterior pair of pgs distinctly removed from the other setae. Ovipositor in rest reaching beyond GO (Fig. 12F). Extended ovipositor long; with basal pair of conical papillae and 5 pairs of apical genital spines (Fig. 12G). Genital spines 8-9 long, each with 4 lateral tines. Gnathosoma with slender palps (Fig. 12H). P-4 with setae in basal whorl as illustrated (Fig. 12I); tip with 2 spurs and 1 setula. On tarsus IV medial pas shorter and less plumose than in male; lateral pas flattened and pectinate (Fig. 12J).

Tritonymph. Idiosoma 340 long, 185 wide. Posterior margin of AD truncate (Fig. 13A). OC short, only slightly extending beyond posterior gland pore; ds-2 within or just anterior to margin. PD much shorter than in adults. Ventral plates AE, PE, GP, and AP separated. Posterior portion of AE with projecting triangular or obtuse

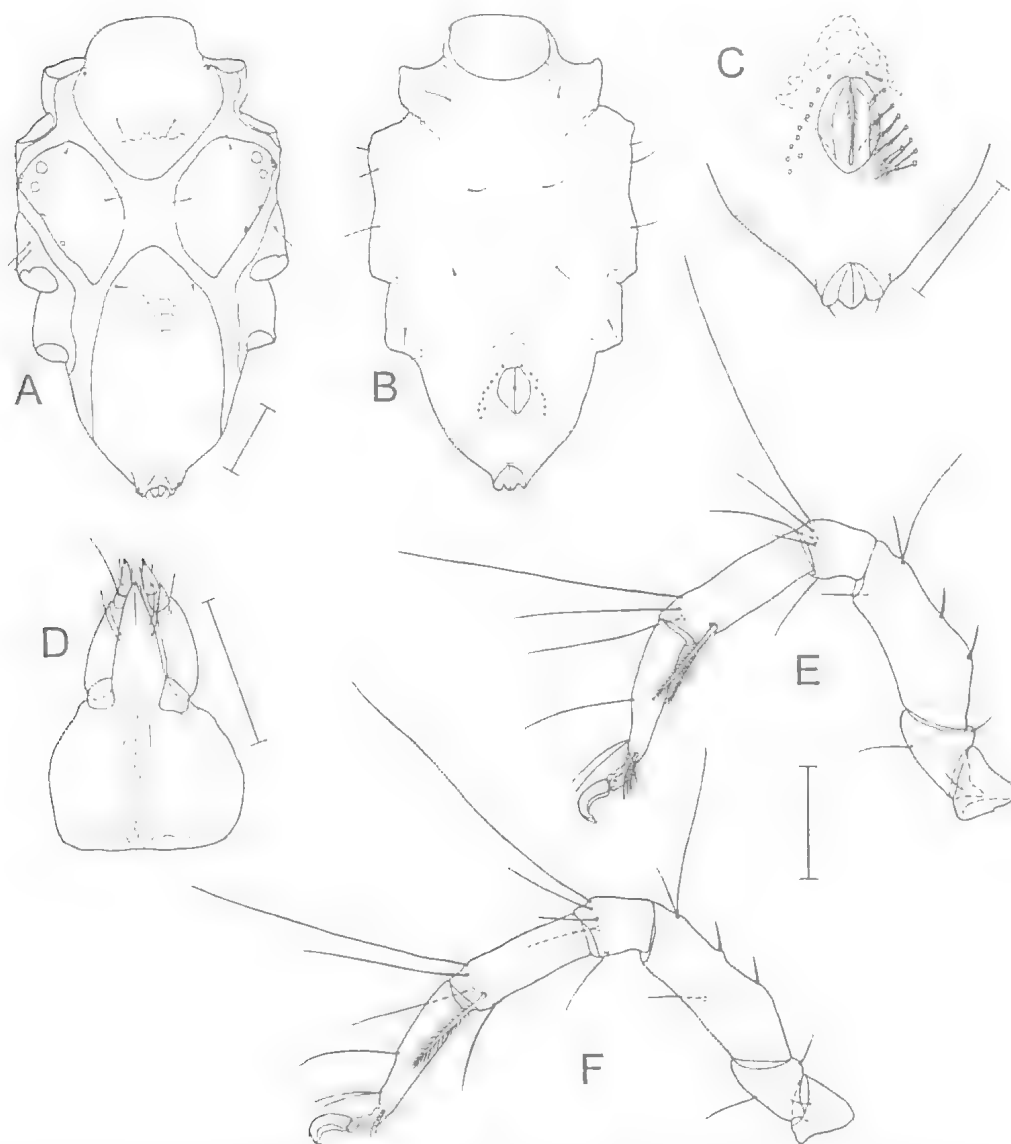


FIG. 11. *Rhombognathus longipes* sp. nov., male; A, idiosoma, dorsal; B, idiosoma, ventral; C, posterior portion of idiosoma, ventral; D, gnathosoma, ventral; E, leg I, medial; F, leg II, medial. Scale bar = 50 μ m.

portion, similar as figured in protonymph (Fig. 13E). AE and PE each with 1 pair of adjunct setae. GP with 2 pairs of pgs and 1 pair of sgs; 3 minute pairs of internal genital acetabula (Fig. 13B). Telo femora I-IV with 4/1, 4/1, 2/0, 2/0 setae. Setation of the other leg segments same as in adults.

Deutonymph. Idiosoma 236-263 long. In dorsal aspect similar to tritonymph. GP and AP fused (Fig. 13C); plate with 2 pairs of minute internal genital acetabula.

Protonymph. Idiosoma 178 long, 105 wide. AD posteriorly truncate; PD short, ovate (Fig. 13D). AE with 3 pairs of setae (Fig. 13E); PE with 1 dorsal and 1 ventral seta. Genua I-IV with 4, 4, 3, 3 setae; telofemora I-III with 2/1, 2/1, 2/0 setae, femur IV with 2/0 setae.

Variations. Varieties of characters in adults: length of idiosoma, ♀: 335-365 (10); length of idiosoma, ♂: 317-328 (8); number of adjunct setae on either side of AE: 1 (28), 2 (11); 3 (1); number of adjunct setae, PE: 0 (5), 1 (35);

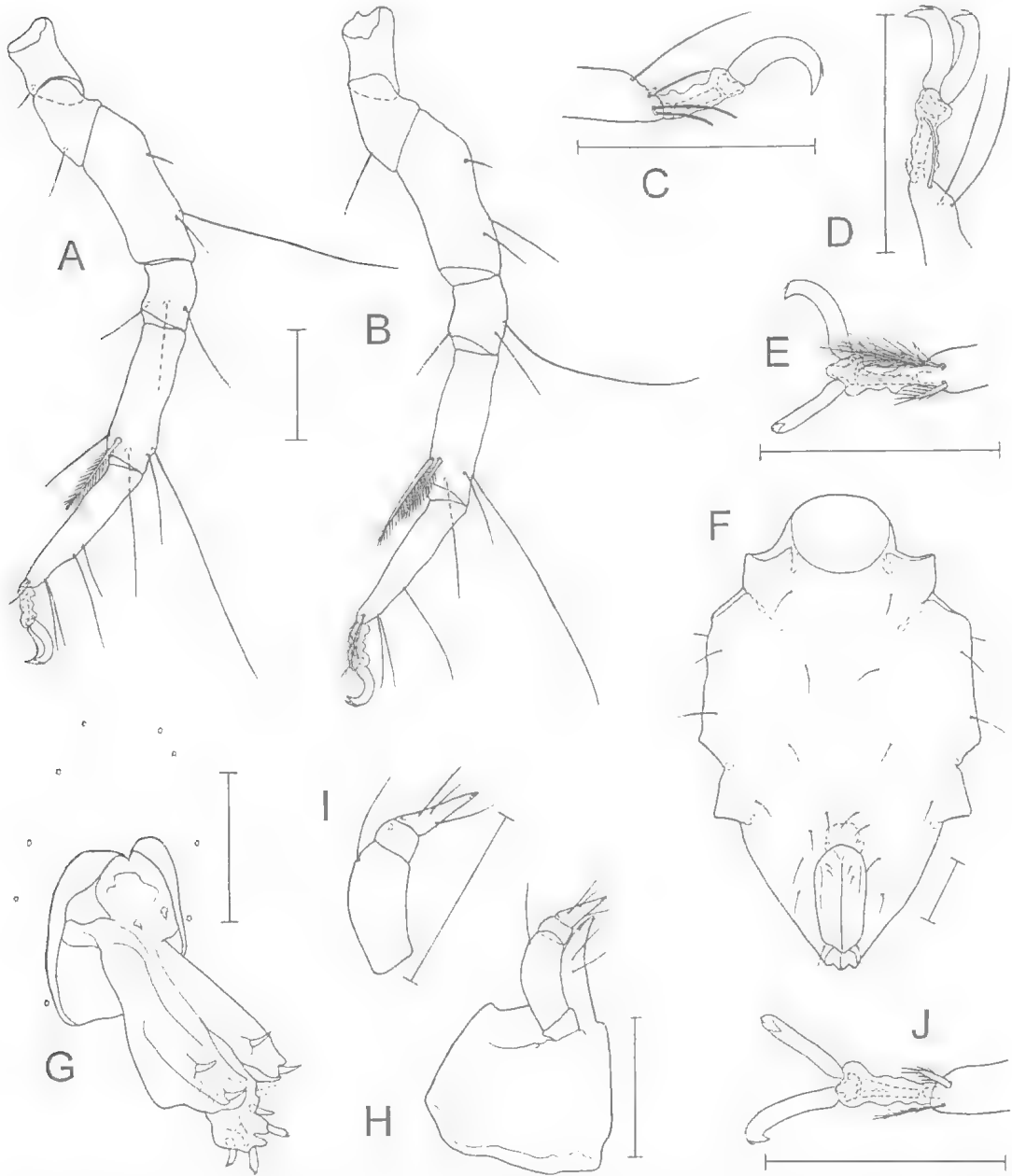


FIG. 12. *Rhombognathus longipes* sp. nov.; A, leg III, medial, male; B, leg IV, medial, male; C, tip of tarsus I, lateral, male (medial claw and setae omitted); D, tip of tarsus III, lateral, male; E, tip of tarsus IV, ventral, male (dorsal setae omitted); F, idiosoma, ventral, female; G, ovipositor, ventrolateral, female (spine in dotted line broken); H, gnathosoma, lateral, female; I, P-2 to P-4, lateral, female; J, tip of tarsus IV, ventral, female (dorsal setae omitted). Scale bar = 50µm.

number of pgs on either side, ♀: 5 (20); number of pgs on either side, ♂: 8 (8), 9 (7), 10 (1); number of setae of leg segments 2 to 5:

segment	leg I	leg II	leg III	leg IV
2	2(40)	2(40)	1(40)	1(40)
3	4/1(40)	2/1(1), 4/1(36), 5/1(3)	2/0(2), 3/0(38)	2/0(1), 3/0(39)
4	5(40)	5(40)	3(40)	3(40)
5	5(40)	5(40)	5(40)	5(40)

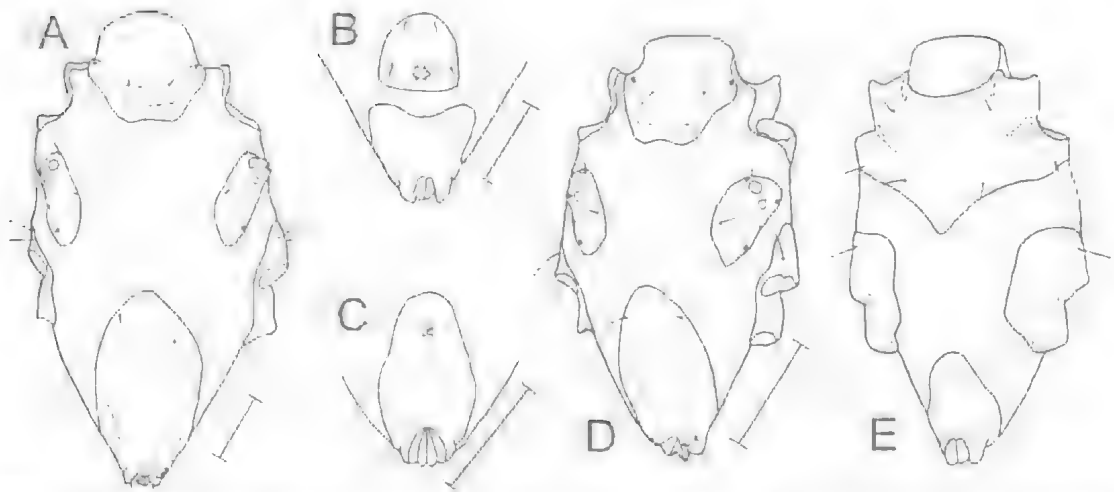


FIG. 13. *Rhombognathus longipes* sp. nov.: A, idiosoma, dorsal, tritonymph; B, posterior portion of idiosoma, ventral, tritonymph; C, posterior portion of idiosoma, ventral, deutonymph; D, idiosoma, dorsal, protonymph; E, idiosoma, ventral, protonymph. Scale bar = 50 μ m.

REMARKS. *Rhombognathus longipes* can be separated from congeneric Australian species on the basis of the slender idiosoma with long, slender legs, leg I being almost as long as the idiosoma. *R. longipes* is most similar to *R. longisetus* Bartsch, 1999, a species known from New Caledonia. The most marked difference is the length of the ds-1 — in *R. longipes* short, less than 1/4 of the length of the AD, in *R. longisetus* as long as the AD. Apart from few exceptions, e.g. the ds-5 in the Mediterranean *Copidognathus gibbus* (Trouessart, 1889) and *C. majusculus* (Trouessart, 1894), the length of a seta is generally a stable character within a species. Further distinguishing characters are: The position of the ds-1 (in *R. longipes* inserted at 0.64, in *R. longisetus* at 0.57), the length of the ovipositor (in *R. longipes* distinctly extending beyond the GO, in *R. longisetus* only slightly surpassing the GO), the arrangement of the pgs around the female GO (in *R. longisetus* almost equidistant whereas in *R. longipes* the posterior pair of the setae is distanced from the preceding pair). The male GA of *R. longisetus* has a post-genital papilla which is lacking in *R. longipes*.

***Rhombognathus papuensis* Bartsch, 1989**
(Figs 14, 15)

Rhombognathus papuensis Bartsch, 1989a: 236, figs 50-55
not *Rhombognathus papuensis* - Chatterjee, 1995, 282-284,
figs 1-14.

MATERIAL. ♀, ♂ (MTQ), Great Barrier Reef, Magnetic Island, Alma Bay, rocky littoral, algae at 0.5m, 16 March 1998; coll. J.C. Otto. ♀, ♂ (QM S50967), collection data

as above. ♀, ♂ (MTQ), Great Barrier Reef, 18°41.29'S, 147°05.83'E, Loadstone Reef, *Halimeda* at 3-6m, 11 April 1998; coll. J.C. Otto. ♀, ♂ (QM S50968), collection data as before. 4♀, 1 tritonymph (1B), collection data as before. ♂, 1 tritonymph (1B). Great Barrier Reef, 19°20.12'S, 149°02.85'E, Elizabeth Reef, *Halimeda* sp. (Chlorophyta) at 10m, 25 December 1997; coll. J.C. Otto.

DESCRIPTION (based on specimens from shallow water habitats from Magnetic Island). Idiosomal length of female 310, of male 277-285. Dorsal plates with foveate sculpturing. Posterior AD broadly rounded; foveate areolae distinct in area anterior to short ds-1, OC large, with 2 corneae and 2 short setae; 2 gland pores and one pore canaliculus in lateral margin. PD with pair of wide costae; foveate areolae lateral and medial to costae (Fig. 14A). PD with single pair of setae, in females inserted at 0.24, in males at 0.31. Ventral plates AE, PE and GA fused. On either side of AE and PE (0-)1 adjunct setae. Female with pair of lateral wedges between GP and AP; 5 pairs of pgs inserted almost equidistant (Fig. 15F). Male with 9-13 plumose pgs arranged in a line on either side of GO, and pair of basilar setae adjacent to posterior part of GO (Fig. 14B). Spermatopositor 75 long, 66 wide, extending far beyond GO (Fig. 14C).

Gnathosoma short; length:width ratio 1.1 (Fig. 15A). Rostrum conical, short, hardly more than 1/3 of length of gnathosoma. Basal pair of maxillary setae longer than apical pair. Palps short.

Legs I and II slightly shorter than legs III and IV. Telofemora I to IV approximately 2.4 times longer than high. Telofemora I and II longer than

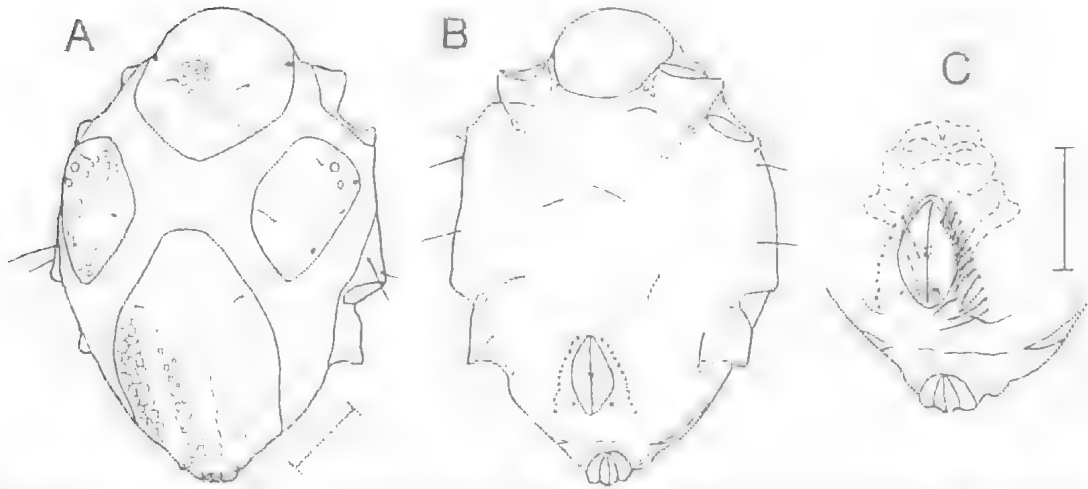


FIG. 14. *Rhombognathus papuensis* Bartsch, male: A, idiosoma, dorsal; B, idiosoma, ventral; C, posterior portion of idiosoma, ventral. Scale bar = 50 μ m.

telofemora III and IV (Figs 15B-E). Tibiae I-IV almost equal in length. Tarsi I and II about as long as these legs' tibiae; tarsi III and IV distinctly longer than tibiae. Leg chaetotaxy (rare variants in parentheses): leg I, 1, 2, (4-)6, (4-)5, 5, 3; leg II, 1, 2, (5-)6, 5, 5, 3; leg III, 1, 2, 3, 3, 5, 4; leg IV, 0, 2, 3(-4), 3, 5, 3. Telfemora I-IV with (3/1, 3/2) 4/2, (3/2) 4/2, 3/0, 3/0 dorsal/ventral setae. Ventral seta on genu I slender. Tibiae I-IV with 2, 1, 1, 2 bipectinate setae. Two basal setae on tarsus III inserted adjacent. Two distal fossary setae on all tarsi equal in size and barbate. Tarsus I with papilliform famulus and slender, setiform solenidion (Fig. 15G).

Claws widened; truncate edge of this portion 17 wide and provided with 18-20 tines. Apical end of claw separated from truncate and widened portion (Fig. 15H).

Variations. Varieties of characters in adults: length of idiosoma, ♀: 310 (2); length of idiosoma, ♂: 277-285 (2); number of adjunct setae on either side of AE: 0 (1), 1 (7); number of adjunct setae, PE: 0 (1), 1 (6); number of pgs on either side of GO, ♀: 5 (4); number of pgs plus basilar setae in either half, ♂: 9+1 (1), 12+1 (2), 13+1 (1); number of setae of leg segments 2 to 5:

segment	leg I	leg II	leg III	leg IV
2	2(8)	2(8)	2(8)	2(8)
3	3/1(2), 3/2(1), 4/2(4)	3/2(3), 4/2(4)	3/0(8)	3/0(8)
4	4(1), 5(7)	5(8)	3(8)	3(8)
5	5(8)	5(8)	5(8)	5(8)

REMARKS. The specimens from the Elizabeth Reef and Loadstone Reef, from 10m and 3-6m

depth, respectively, differ slightly from the above outlined characters. Females are 204-275 long and males 223-241 long. The dorsal plates are more distinctly reticulated. The PD is slightly more slender; its costae are distinctly separated from the reticulate remainder. The number of pgs on the male GP is slightly smaller. The widened truncate edge of the claws are 12 wide.

Variation in the number of setae in specimens from the Elizabeth Reef and Loadstone Reef is as follows: number of adjunct setae on either side of AE: 1 (17); number of adjunct setae on PE: 1 (17), 0 (1); number of pgs on either side of GO, female: 5 (6); number of pgs on either side plus basilar setae, male: 9+1 (5), 10+1 (1); number of setae of leg segments 2 to 5:

segment	leg I	leg II	leg III	leg IV
2	2(17)	2(18)	2(18)	1(2), 2(16)
3	3/2(1), 4/2(16)	4/2(18)	2/0(6), 3/0(12)	2/0(1), 3/0(17)
4	5(17)	5(18)	3(17)	3(18)
5	5(17)	5(18)	5(17)	5(18)

The tritonymphs from Elizabeth Reef and Loadstone Reef are characterised by: Idiosoma 205-229 long. Ventral plates separated. GP separate from AP. AE with 1 pair of adjunct setae; PE with 0-1 adjunct setae. GP with 2 pairs of pgs, 1 pair of sgs. Leg chaetotaxy from trochanter to tarsus (rare variants in parentheses): leg I, 1, 2, (4-)5, 5, 5, 3; leg II, 1, 2, (4-)5, 5, 5, 3; leg III, 1, 2, 2, 3, 5, 4; leg IV, 0, 2, 2, 3, 5, 3. Telfemora I-IV with (2/2) 3/2, (3/1) 3/2, 2/0, 2/0 dorsal/ventral setae. Two basal setae on tarsus III adjacent. Edge of claws 8 wide, with approximately 15 tines.

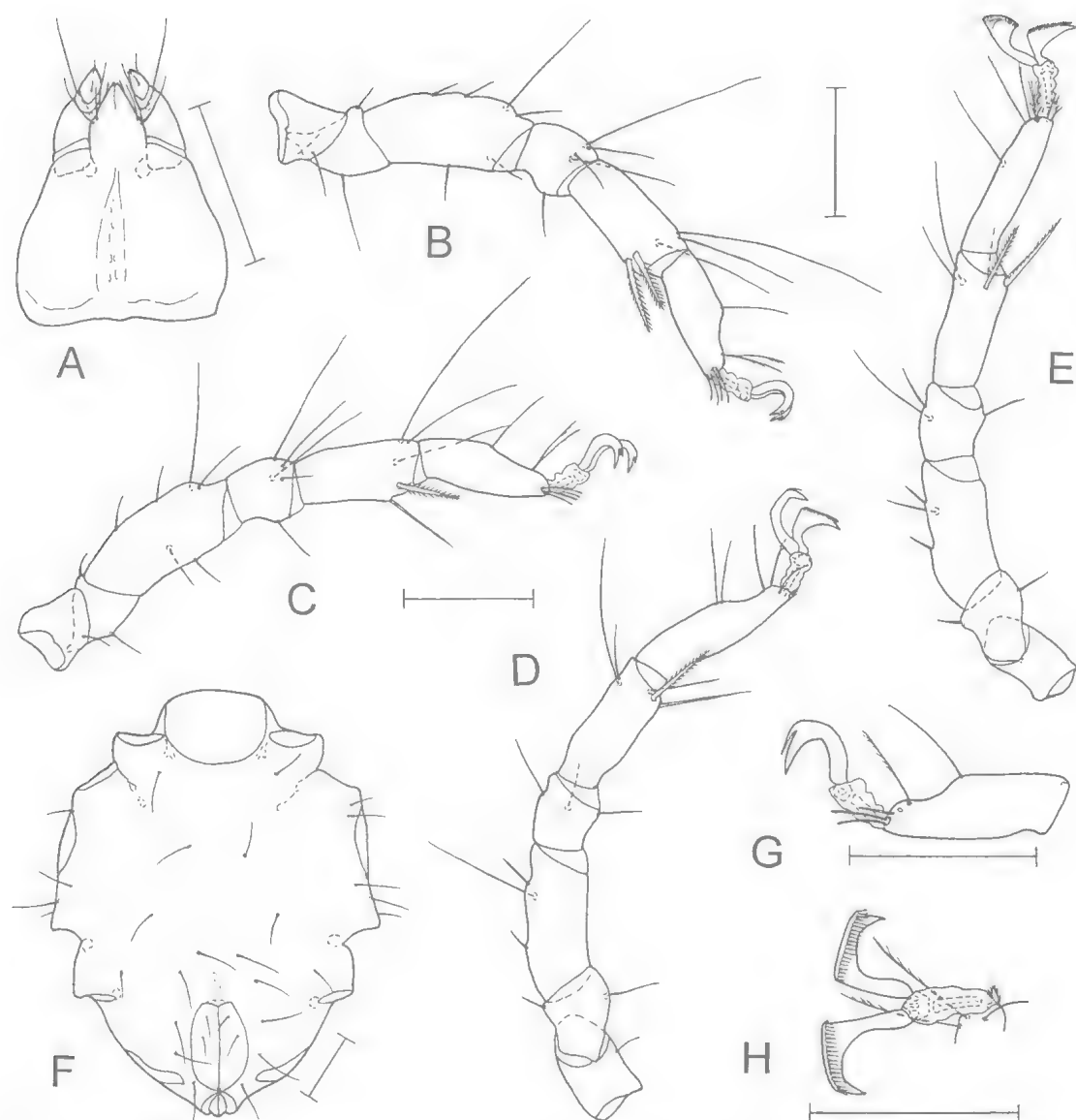


FIG. 15. *Rhombognathus papuensis* Bartsch; A, gnathosoma, ventral, male; B, leg I, medial, male; C, leg II, medial, male; D, leg III, medial, male; E, leg IV, ventromedial, male; F, idiosoma, ventral, female; G, tarsus I, lateral, female (medial claw and setae omitted); H, tip of tarsus III, medial, female. Scale bar = 50µm.

The specimens from the Great Barrier Reef differ slightly from those from Papua New Guinea (Bartsch, 1989a). In the specimens from Papua, the setae on the PD insert further posterior, and the wedges between GP and AP seem to be larger than in adults from the Great Barrier Reef. Unless more material will prove the opposite, the individuals from Magnetic Island, Elizabeth Reef and Loadstone Reef are considered as conspecific with *R. papuensis*.

The individuals recorded from the Indian Ocean (Chatterjee, 1995) are not conspecific with *Rhombognathus papuensis*. According to the description of that species, the OC are much wider than in *R. papuensis* and the PD bears 2 pairs of setae (Chatterjee, 1995: Fig. 1).

DISTRIBUTION. New Guinea, 10°S, 148°E, shallow water (Bartsch, 1989a) and Great Barrier Reef, from shallow water to 10m depth.

Rhombognathus reticulifer sp. nov.
(Figs 16, 17)

ETYMOLOGY. For the dorsal plates which bear (*ferre*, Latin) a *reticulum* (Latin).

MATERIAL. HOLOTYPE. ♂ (MTQ), Great Barrier Reef, 19°20.12'S, 149°02.85'E, Elizabeth Reef, large chunks of coral rubble at 10m, 24 December 1997; coll. J.C. Otto. PARATYPES. 2♀ (MTQ), collection data as above. ♀, ♂ (QM S50969), collection data as above. ♀, 1♂ (ZMH A101/99), collection data as above. ♂ (IB), collection data as above. OTHER MATERIAL. 7♀, 2♂, 2 tritonymphs (IB), Great Barrier Reef, 19°20.12'S, 149°02.85'E, Elizabeth Reef, *Halimeda* (Chlorophyta) at 15m, 24 December 1997; coll. J.C. Otto.

DESCRIPTION. *Male*. Idiosoma slender, 186-205 long; holotype 203 long, 132 wide. Dorsal plates coarsely reticulated (Fig. 16A); meshes 8-10 long and faintly subdivided. Plates with delicate pores. AD 62 long, 65 wide. Anterior margin arched, posterior margin broadly rounded. Transverse series of muscle scars level with 0.80. OC 54 long, 30 wide. Each plate with 2 small corneae, 2 gland pores in lateral margin and pore canaliculus halfway between gland pores. PD 105 long, 62 wide; not as wide as AD. Plate evenly reticulated; meshes 8-11 long. Posterolateral portions of PD hardly projecting beyond median portion of plate. Pair of gland pores in posterolateral margin of PD. Anal sclerites extending beyond anal valves. Setae ds-1 40 long, inserted on AD. Setae ds-2 and ds-3 on OC; ds-3 at 0.51. PD with single pair of setae, inserted at 0.25 and 0.29.

Ventral plates AE, PE, GP and AP fused to a ventral shield (Fig. 16B). Shield delicately punctate. Area of AE with 1-2 adjunct setae; PE with 1 pair of adjunct setae. GO 28 long, 16 wide. GO extending to the level of insertion of leg IV. Perigenital setae arranged trapezoidally; holotype with 7 pairs of setae in a line and 1 pair of basilar setae near posterior edge of GO. Pgs plumose. Spermatopositor 37 long, 40 wide; extending beyond anterior pair of pgs (Fig. 16C).

Gnathosoma short; 57 long, 46 wide; 1.2 times longer than wide (Fig. 16D). Rostrum short, 22 long, triangular.

Legs I and IV almost equal in length, about 0.7 of length of idiosoma. Insertion of legs III and IV level with 0.56 and 0.71, respectively. Length: height ratio of telofemora I-IV 1.7, 1.7, 1.5, 1.6 (Figs 16E-H). Telofemora and tibiae of each leg almost equal in length. Tarsi III and IV only slightly longer than these legs' tibiae. Leg chaetotaxy, from trochanter to tarsus: leg I, 1, 2, 6, 5, 5, 3; leg II, 1, 2, 6, 5, 5, 3; leg III, 1, 1, 3, 3, 5, 4; leg IV, 0, 1, 3, 3, 5, 3. Lateral seta on each

basifemur II and III long, about twice height of these segments. Telofemora I-IV with 4/2, 4/2, 3/0, 3/0 setae. Dorsolateral seta on telofemur III hardly longer than the 2 dorsomedial setae. Ventral seta on genu I delicately pectinate. Tibiae I-IV with 2, 1, 1, 2 bipectinate ventral setae. Ventrolateral seta on both tibia II and III almost as long as ventromedial seta. Two basal setae on tarsus III inserted close together. On each of the tarsi 2 distalmost dorsal setae slightly plumose. Tarsus I with short papilliform famulus, 1 long; solenidion 7 long (Fig. 17A); ambulacrum flanked by pair of doubled pas (Fig. 17B). Apart from absence of famulus, tarsus II similar to tarsus I; solenidion 8 long (Fig. 17C). Medial pas on tarsus III setiform, lateral pas short, pectinate (Fig. 17D); pas on tarsus IV (Fig. 17E) more plumose than on tarsus III.

Carpites on tarsi I and II 5-6 long; carpites on tarsi III and IV 6-7 long. Accessory processes of claws widened; 4 wide, with 7-8 small tines (Figs 17D, E).

Female. Idiosoma 217-241 long. Areas with striated integument between plates larger than in males. Female PD somewhat shorter, ds-4 at 0.20-0.23 relative to length of PD. Ventral shield including AE, PE and GP; AP separated from ventral shield by wedges of striated integument (Fig. 17F). Anterior margin of GO not reaching the level of insertion of leg IV. Genital acetabula small, often obscured. Five pairs of pgs arranged in a wide ring around GO; 2 anterior pairs of pgs anterior to the level of insertion of leg IV. Genital spines claw-like, with median tooth and 4-5 smaller teeth along lateral margin. Genital sclerites with 2 pairs of sgs. Palps extending slightly beyond rostrum. Chelicera 70 long, 16 wide; dorsal margin of its claw dentate. Pas on tarsus III similar to male tarsus; pas on tarsus IV (Fig. 17H) less plumose than on male tarsus IV.

Tritonymph. Idiosoma 151-195 long. OC more narrow and PD shorter than in adults (Fig. 17I). Reticulate pattern same as in adults. Setae ds-1 long; setae ds-4 near anterior margin of PD. Ventral plates AE, PE, GP, and AP separated (Fig. 17J). Posteromedian margin of AE convex. AE and PE each with 1 pair of adjunct setae. Genital plate small; with 2 pairs of pgs and 1 pair of sgs. Gnathosoma short; 1.1 times longer than wide. Legs I and II with 1, 2, 4, 5, 5, 3 setae, from trochanter to tarsus; leg III with 1, 1, 2, 3, 5, 4 setae, and leg IV with 0, 1, 2, 3, 5, 3 setae. Telofemora I-IV with 3/1, 3/1, 2/0, and 2/0 setae.

Variations. Varieties of characters in adults: length of idiosoma, ♀: 217-241 (11); length of idiosoma, ♂: 186-205 (6); number of adjunct

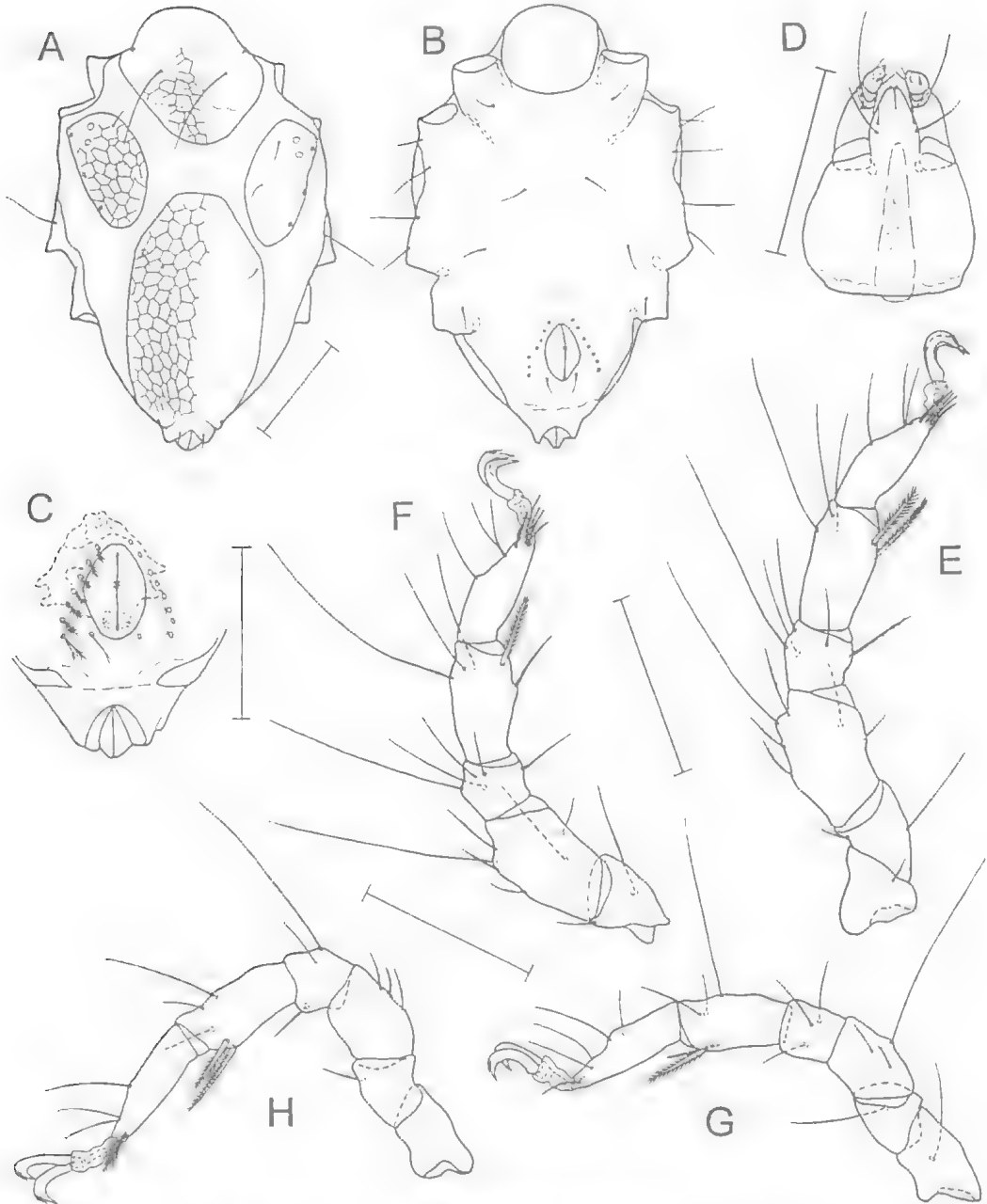


FIG. 16. *Rhombognathus reticulifer* sp. nov., male: A, idiosoma, dorsal; B, idiosoma, ventral; C, posterior portion of idiosoma, ventral; D, gnathosoma, ventral; E, leg I, medial; F, basifemur to tarsus II, medial; G, leg III, medial; H, leg IV, medial. Scale bar = 50µm.

setae on either side of AE: 1 (29), 2 (5); number of adjunct setae on PE: 0 (3), 1 (30), 2 (1); number of pgs on either side of GO, ♀: 5 (20), 6 (2); number of pgs plus basilar setae in either half, ♂: 7+1 (11), 8+1 (1); number of setae of leg segments 2 to 5:

segment	leg I	leg II	leg III	leg IV
2	2(34)	2(34)	1(34)	1(34)
3	3/2(4), 4+1(1), 4/2(29)	1/2(4), 4+2(30)	2/0(7), 2+1(1), 3/0(26)	2/0(9), 2+1(1), 3/0(24)
4	5(34)	5(34)	3(34)	3(34)
5	5(34)	5(34)	5(34)	5(34)

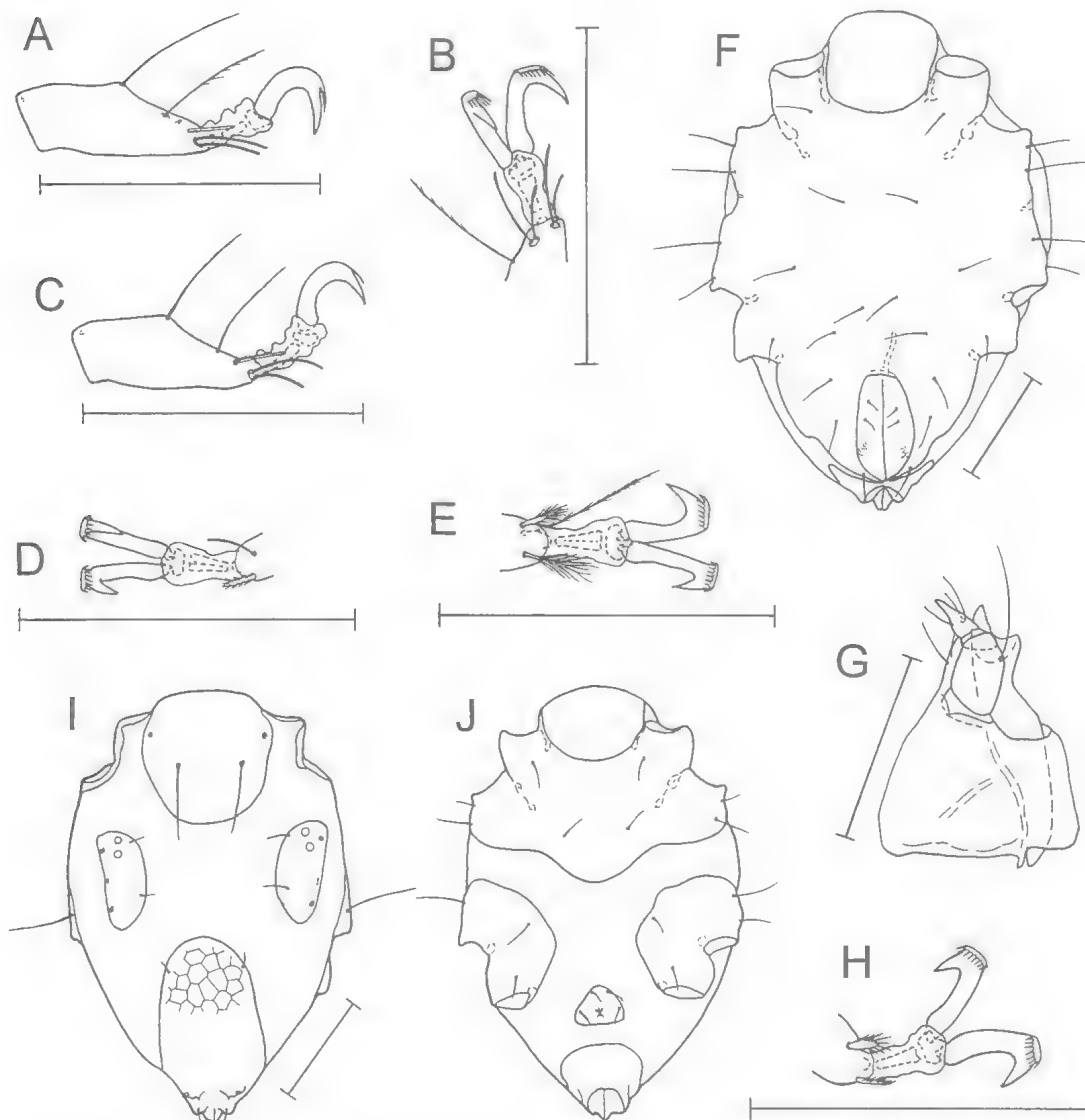


FIG. 17. *Rhombognathus reticulifer* sp. nov., A, tarsus I, lateral, male (medial claw and setae omitted); B, tip of tarsus I, ventromedial, male (dorsolateral fossary seta omitted); C, tarsus II, lateral, male (medial claw and setae omitted); D, tip of tarsus III, ventral, male (dorsal setae omitted); E, tip of tarsus IV, ventral, male (dorsomedial fossary seta omitted); F, idiosoma, ventral, female; G, gnathosoma, lateral, female; H, tip of tarsus IV, ventral, female (dorsal setae omitted); I, idiosoma, dorsal, tritonymph; J, idiosoma, ventral, tritonymph. Scale bar = 50 μ m.

REMARKS. *Rhombognathus reticulifer* is characterised by the combination: dorsal plates distinctly reticulated; ds-1 much longer than the succeeding setae; PD with single pair of setae; in males all ventral plates fused; females with wedges of striated integument between ventral shield and AP; area representing AE and PE generally with 1 adjunct seta on either side; males with 8 pairs of pgs, females with 5 pairs of pgs; gnathosoma short, 1.2 times longer than wide;

telofemora I-IV with 4/2, 4/2, 3/0, 3/0 setae; accessory process on claws slightly widened, with 7-8 tines.

Amongst the rhombognathines from the Great Barrier Reef, the species *R. levigatus* and *R. tericulus* sp. nov. (description below) are most similar to *R. reticulifer*. The smooth PD of *R. levigatus* is wider than in *R. reticulifer*, and the telofemora I to IV of *R. levigatus* bear 5/2, 5/2, 3/1, and 3/1 setae. Discriminating characters

between *R. reticulifer* and *R. tericulus* are outlined after the description of the latter species.

R. ventralis Newell, 1984 and *R. lateralis* Newell, 1984, both known from the South American Pacific coast (Newell, 1984), resemble *R. reticulifer* in general aspect. These two species have, in contrast to *R. reticulifer*, 4 setae on telofemur IV.

Rhombognathus scutulatus Bartsch, 1983

Rhombognathus scutulatus Bartsch, 1983: 413-415, figs 46-57. *Rhombognathus scutulatus* Bartsch, 1993: 20, 21, fig. 1A-C; Chatterjee, 1995: 284, figs 15-19.

MATERIAL. ♂ (MTQ), Great Barrier Reef, Cape Ferguson, AIMS beach, algae at low tide mark, 2 March 1997; coll. J.C. Otto. ♀, ♂ (QM S50970), collection data as before. ♂ (IB); collection data as before. ♀, ♂ (MTQ), Great Barrier Reef, Magnetic Island, Alma Bay, rocky littoral, algae at 0.5m, 16 March 1998; coll. J.C. Otto. 2♀, ♂ (IB); collection data as before.

DIAGNOSIS. Female idiosoma 300-335, male 285-310 long. Dorsal plates AD, OC and PD fused. Dorsal shield with foveate ornamentation. Dorsal idiosomatic setae subequal in size. Area representing PD with single pair of setae. Ventral plates AE, PE and GP fused in females and males; GP partly fused with AP. Areas of AE and PE each with 1 pair of adjunct setae. Female with 5 pairs of pgs and 2 pairs of sgs. Males with 9-13 pairs of trapezoidally arranged plumose pgs, 1 pair of basilar setae and 2 pairs of sgs. Gnathosoma 1.16 times longer than wide. None of the setae on genua I-IV pectinate. Telofemora I to IV with 4/2, 4/2, 3/0, 3/0 setae. Tarsi I-IV with 3, 3, 4, 3 dorsal setae. Apical fossary setae with their distal portion flattened, pilose. Accessory process of claws widened; claw with 22-24 tines.

Variations. Varieties of characters in adults: length of idiosoma, ♀: 300-335 (4); length of idiosoma, ♂: 285-310 (5); number of adjunct setae on either side of AE: 0 (1), 1 (17); number of adjunct setae on PE: 1 (17), 2 (1); number of pgs on either side of GO, ♀: 5 (8); number of pgs on either side plus basilar setae, ♂: 9+1 (2), 10+1 (3), 11+1 (2), 12+1 (1), 13+1 (2); number of setae of leg segments 2 to 5:

segment	leg I	leg II	leg III	leg IV
2	2(18)	2(18)	2(18)	2(18)
3	4/2(18)	4/2(17), 4/3(1)	2/0(1), 3/0(17)	2/0(1), 3/0(17)
4	5(18)	5(18)	3(17), 4(1)	3(18)
5	5(18)	5(18)	5(18)	5(18)

REMARKS. In the samples from the Great Barrier Reef area, *Rhombognathus scutulatus* is the only species with a dorsal shield.

DISTRIBUTION. Philippines; eastern and western coast of India; Western Australia (Bartsch, 1983, 1993; Chatterjee, 1995). Found in a variety of tidal and shallow subtidal algal substrata.

Rhombognathus seminotatus sp. nov. (Figs 18, 19)

ETYMOLOGY. For the sculpturing of the PD with half (*semi*, Latin) of the plate being ornamented (*notatus*, Latin).

MATERIAL. HOLOTYPE. ♂ (MTQ), Great Barrier Reef, Cape Ferguson, AIMS beach, algae at low tide mark, 2 March 1997; coll. J.C. Otto. OTHER MATERIAL. ♀, ♂ (MTQ), Great Barrier Reef, Magnetic Island, Alma Bay, rocky littoral, algae at 0.5m, 16 March 1998; coll. J.C. Otto. ♀, ♂ (QM S50971), collection data as above. ♀ (ZMH A102/99), collection data as above. 2♀, 2♂ (IB), collection data as above.

DESCRIPTION. *Male.* Idiosoma slender 278-313 long; holotype 278 long, 161 wide. AD 100 long, 82 wide. Anterior and posterior margin broadly rounded. Median portion with reticulate ornamentation; anterior, lateral and posterior portions smooth (Fig. 18A); lateral areas pierced by minute pores. Transverse line of muscle scars at 0.78. OC 75 long, 48 wide; with 2 corneae; gland pores in lateral margin. PD 130 long, 85 wide. Posterolateral cones of PD hardly extending beyond posteromedian margin of the plate; each cone with a gland pore. Median and posterolateral portions of PD reticulate; costae slightly raised, smooth apart from minute pores. Anterior portion of PD in holotype almost smooth; in other specimens that portion covered by delicate epicuticular reticulum (Fig. 18C). Anal valves not extending beyond anal sclerites. Setae ds-1 30 long, inserted on AD at 0.50. Succeeding setae 15 long; posterior seta on OC in posterior half of the plate. PD with single pair of setae at 0.28. Adanal setae on anal valves.

Ventral plates AE, PE, GP, and AP fused to a ventral shield (Fig. 18B); shield 218 long. Areas representing AE and PE each with a pair of adjunct setae. GO extending anteriorly far beyond the level of insertion of leg IV. GO 45 long, 21 wide. Distance to end of anal cone equalling length of GO. Perigenital setae arranged trapezoidally, 12 and 14 plumose setae in line and 1 pair of basilar setae at the level of 0.8 relative to length of GO (Fig. 18D). Genital sclerites with 2 pairs of sgs. Spermatopositor 62 long, 62 wide; extending beyond anterior pair of pgs.

Gnathosoma short, 71 long, 57 wide; length: width ratio 1.24 (Fig. 18E). Tectum slightly arched

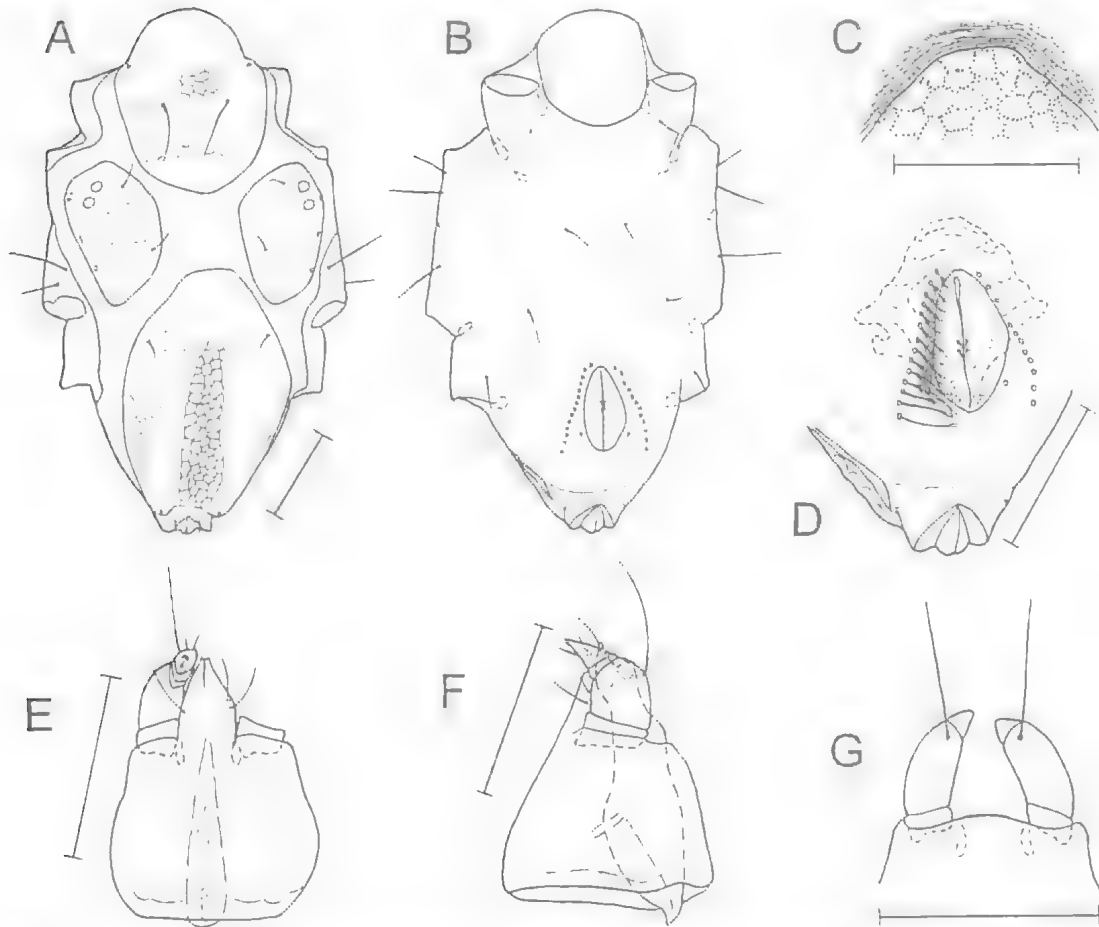


FIG. 18. *Rhombognathus seminotatus* sp. nov., male; A, idiosoma, dorsal; B, idiosoma, ventral; C, anterior portion of PD; D, posterior portion of idiosoma, ventral; E, gnathosoma, ventral; F, gnathosoma, lateral; G, tectum and P-1 to P-3, dorsal. Scale bar = 50 μ m.

(Fig. 18G). Rostrum 25 long; apex pointed. Palps short, appressed to the rostrum. P-4 directed ventrad (Fig. 18F), generally obscured in dorsal aspect (Fig. 18G).

Legs approximately 0.8 times of length of idiosoma. Insertion of leg I at 0.12, that of leg IV at 0.72 relative to length of idiosoma. Telfemora I-IV 2.5, 2.4, 2.3, and 2.3 times longer than high. Telfemora I and II markedly longer than tibiae I and II, respectively (Fig. 19A, B), telfemora III and IV somewhat longer than these legs, tibiae (Figs 19C, D). Tarsi I and II approximately as long as tibiae I and II; tarsi III and IV longer than tibiae. Leg chaetotaxy: leg I, 1, 2-3, 5-6, 5, 5, 3; leg II, 1, 2, 6, 4-5, 5, 3; leg III, 1, 2, 3-4, 2-3, 5, 4; leg IV, 0, 2, 3, 3, 5, 3. None of ventrolateral setae on genua bipectinate. Tibiae I-IV with 2, 1, 1, 2 bipectinate setae. On tibia IV ventromedial seta

smaller than ventrolateral one. Paired dorsal setae of tarsi slightly plumose. Tarsus III with 4 dorsal setae; the 2 basal ones inserted adjacent. Solenidia on tarsi I and II 9 and 11 long, respectively. Famulus on tarsus I papilliform, 2 long (Fig. 19F). Tarsi I (Fig. 19E) and II each with pair of doubled pas. Medial pas on tarsus III setiform, lateral pas spiniform, bipectinate. Medial pas on tarsus IV long, plumose (Fig. 19H).

Tarsi I and II each with 9-10 long carpite; tarsi III and IV with 12 long carpite. Claws distally widened, with 12-13 tines. End of claw clearly set off from line with tines.

Female. Idiosoma 310-322. Striated integument between dorsal plates wider than in males. AE, PE and GP fused to a ventral shield. Narrow striated integument separates anal plate from ventral shield. GO 67 long, 45 wide; extending to

the level of insertion of leg IV. Seven to nine pairs of pgs arranged in a wide ring around GO (Fig. 19I); anterior pair of pgs level with insertion of leg IV. Genital sclerites with 2 pairs of sgs.

Variations. Several individuals from Magnetic Island have the dorsal plates covered by an epicuticular reticulum, the reticulum formed by delicate droplets (Fig. 18C).

Varieties of characters in adults: length of idiosoma, ♀: 310-322 (4); length of idiosoma, ♂: 278-313 (5); number of adjunct setae on either side of AE: 1 (20); number of adjunct setae on PE: 0 (3), 1 (17); number of pgs on either side of GO, female: 7 (3), 8 (4), 9 (3); number of pgs plus basilar setae in either half, male: 10+1 (1), 11+1 (5), 12+1 (2), 13+1 (1), 14+1 (1); number of setae of leg segments 2 to 5:

segment	leg I	leg II	leg III	leg IV
2	2(17), 3(1)	2(18)	2(18)	2(18)
3	2/1(1), 4/1(1), 4/2(15)	4/2(18)	2,0(3), 3/0(14), 3/1(1)	2/0(1), 3/0(17)
4	5(18)	4(1), 5(17)	2(1), 3(17)	3(17), 4(1)
5	5(18)	5(18)	5(18)	5(18)

REMARKS. *Rhombognathus seminotatus* is characterised by the distally widened claws bearing 12-13 tines. Other characters are: AE and PE each with pair of adjunct setae; females with 7-9 pairs of pgs, males with 11-15 pgs; telofemora I-IV with 4/2, 4/2, 3/0, 3/0 setae. In the majority of species the 2 basal setae on tarsus III insert immediately adjacent.

The majority of congeners of the Great Barrier Reef area have claws which are smooth or have an accessory process with 0-8 tines, other species have distally widened claws with more than 15 tines (*R. papuensis*, *R. scutulatus*), whereas *R. seminotatus* has 12-13 tines. Widened claws are present also in the eastern Pacific species *R. atuy* Abé, 1990, *R. guamensis* Bartsch, 1989, and *R. sinensoideus* Bartsch, 1992, recorded from Hokkaido, Guam, New Guinea, and southern China, respectively (Abé, 1990; Bartsch, 1989a, 1992). In contrast to *R. seminotatus*, the PD of both *R. atuy* and *R. sinensoideus* has 2 pairs of setae. The claws of *R. guamensis* have unusually wide tines, evidently wider than in *R. seminotatus*. *R. insularis* Bartsch, 1989, a species from islands of the Hawaii Archipelago (Bartsch, 1989a) and *R. lateralis* Newell, 1984, recorded from South America (Newell, 1984), also have claws similar to those of *R. seminotatus*. The three species can be distinguished on the basis of the setation of the telofemora I to IV; in *R. insularis* there are 5/2, 5/2, 3/1, 3/1 dorsal/ventral

setae, in *R. seminotatus* 4/2, 4/2, 3/0, 3/0 setae, and, according to Newell (1984), the setal formula of the telofemora I-IV in *R. lateralis* is 6, 6, 3-4, 4.

Females of *R. seminotatus* can be rapidly discriminated from congeners on the basis of the combination of: GA with 7-9 pairs of pgs; AE, PE and GP fused to a ventral shield; and claws with approximately 12 tines. The other rhombognathine species from the Great Barrier Reef area have 5 pairs of perigenital setae. A high number of perigenital setae, similar to that in *R. seminotatus*, is present in the Subantarctic species *R. auster* Bartsch, 1989b and *R. darwini* Newell, 1984, the eastern Pacific *R. ellipticus* Bartsch, 1977, and the northeastern Atlantic *R. procerus* Bartsch, 1975b, but none of these species have claws with a widened accessory process bearing more than 10 tines.

Rhombognathus tericulus sp. nov. (Figs 20, 21)

ETYMOLOGY. *Tericulus*, an anagram of *reticulum* which refers to the reticulate ornamentation of the dorsal plates.

MATERIAL. HOLOTYPE. ♂ (MTQ), Great Barrier Reef, 18°25.25' S, 146°40.65' E, Bramble Reef, chunks of coral rubble, 3-6m, 10 April 1998; coll. J.C. Otto. **PARATYPES.** ♀, ♂ (QM S50972), collection data as above. 2♂ (MTQ), collection data as above. **OTHER MATERIAL.** ♀ (MTQ), Great Barrier Reef, 19°20.12' S, 149°02.85' E, Elizabeth Reef, coarse sand and rubble, 3m, 25 December 1997; coll. J.C. Otto. ♂ (QM S50973), same collection data as before. ♂ (WAM 99/1447), same collection data as before. ♀, ♂ (IB), same collection data as before. 2♀, ♂, 1 tritonymph (IB), Great Barrier Reef, 18°41.91' S, 147°06.49' E, Loadstone Reef, coarse sand and rubble at 2m, 12 April 1998; coll. J.C. Otto. ♀ (IB), Great Barrier Reef, 18°42.05' S, 147°05.98' E, Loadstone Reef, coarse sand and rubble, 8m, 12 April 1998; coll. J.C. Otto. 2♀ (MTQ), Great Barrier Reef, 14°36' S, 145°38' E, Yonge Reef, coarse sand and rubble, 9m, 10 October 1998; coll. J.C. Otto. ♀, ♂ (ZMH A103/99), collection data as before. 2♀, ♂ (IB), collection data as before.

DESCRIPTION. Male. Idiosoma 205-223 long; holotype 220 long, 143 wide. Dorsal plates conspicuously reticulated (Fig. 20A). AD 75 long, 75 wide; reticulation of anterior portion of plate indistinct; posterior line with muscle scars inserted at 0.72. OC 68 long, 42 wide; distinctly projecting beyond posterior gland pore. PD 127 long, 82 wide; prominent reticulation uniformly covering the plate. Posterior margin of PD not extending beyond anal cone. Setae ds-1 very long, approximately 40; inserted in anterior half of AD and close to the level of gland pores.

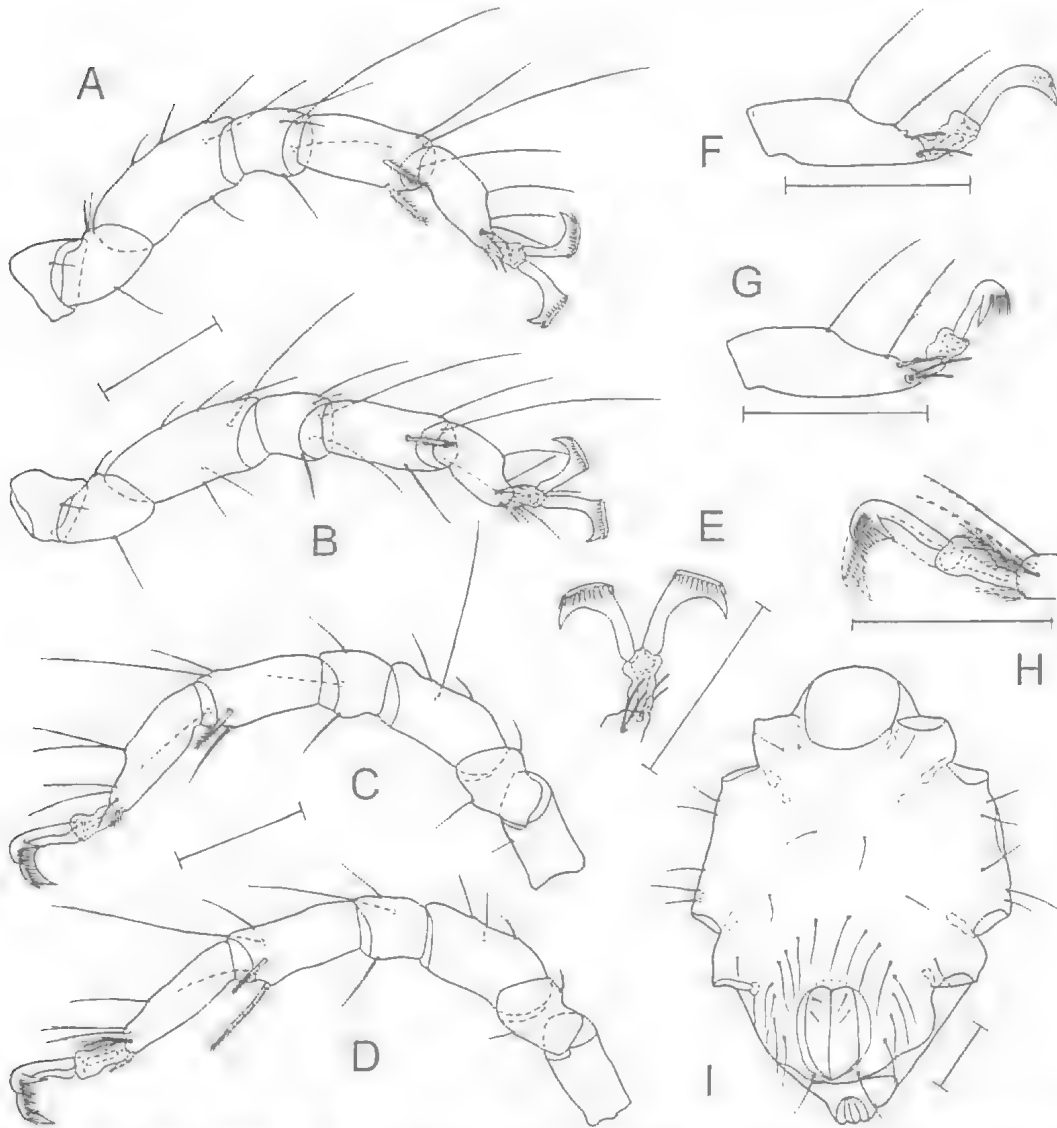


FIG. 19. *Rhombognathus seminotatus* sp. nov.: A, leg I, ventromedial, male; B, leg II, ventromedial, male; C, leg III, medial, male; D, leg IV, medial, male; E, tip of tarsus I, ventral (dorsal setae omitted); F, tarsus I, lateral, male (medial claw and setae omitted); G, tarsus II, lateral, male (medial claw and setae omitted); H, tip of tarsus IV, medial, male (lateral setae and claw dashed); I, idiosoma, ventral, female. Scale bar = 50 μ m.

Following setae 10-12 long. Setae ds-4 on PD at 0.37. Adanal setae on anal plate.

Ventral plates AE, PE and GA fused (Fig. 20B). Area of AE and PE each with one pair of adjunct setae. Marginal setae long. GO 30 long, 19 wide; distance to apex of anal cone more than length of GO. On either side of GO line with 8 plumose pgs and 1 basilar seta; the latter inserted anterior to posterior end of GO (Fig. 20E). Spermatopositor 32 long, 39 wide.

Gnathosoma short, 65 long, 52 wide. Rostrum 27 long. Tectum truncate (Fig. 20C). Chelicera 70 long; its claw wide, cutting edge serrate (Fig. 20D). Palps short.

Four pairs of legs subequal in length and approximately 0.7 of length of idiosoma. Legs III and IV inserted at 0.56 and 0.71, respectively. Telofemora I-IV 1.3-1.4 times longer than high. Telofemora I and II slightly longer than tibiae of these legs; telofemora III and IV slightly shorter

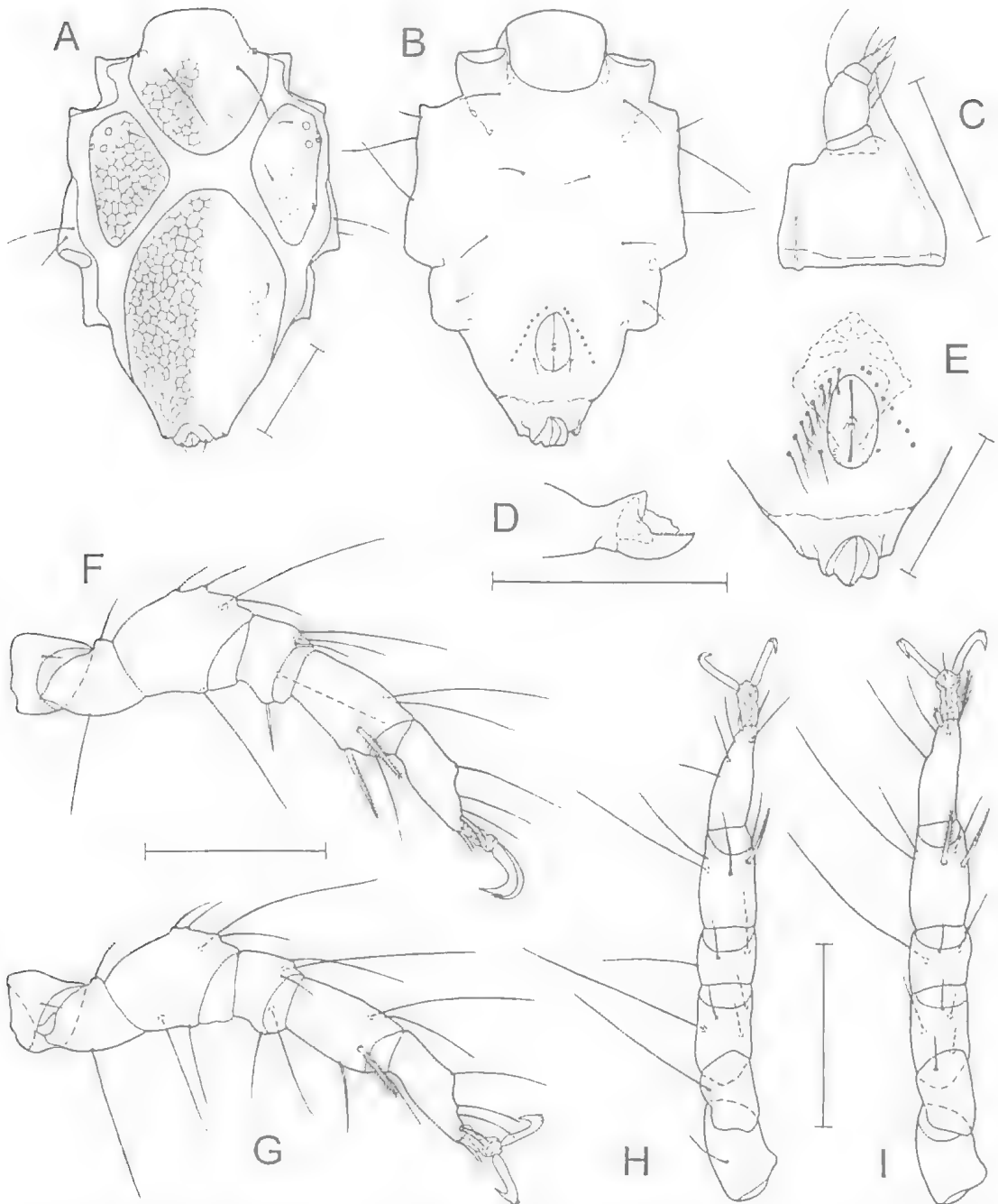


FIG. 20. *Rhombognathus tericulus* sp. nov., male; A, idiosoma, dorsal; B, idiosoma, ventral; C, gnathosoma, lateral; D, tip of chelicera; E, posterior portion of idiosoma, ventral; F, leg I, ventromedial; G, leg II, ventromedial; H, leg III, ventral; I, leg IV, ventral. Scale bar = 50 μ m.

than tibiae. Leg chaetotaxy, from trochanter to tibia: leg I, 1, 2, 5, 5, 5, 3; leg II, 1, 2, 6, 5, 5, 3; leg III, 1, 1, 4, 3, 5, 4; leg IV, 0, 1, 4, 3, 5, 3. Telofemora I-IV with 4/1, 4/2, 3/1, 3/1 setae (Fig.

20F-I). Tibiae I-IV with 2, 1, 1, 2 bipectinate ventral setae. Distal pair of fossary setae delicately plumose. As in female, solenidion on tarsus I setiform, 7 long; famulus 1 long (Fig.

21E). Tarsi I and II each with pair of doubled pas. Lateral pas on tarsi III and IV flattened, pectinate; medial pas on tarsus III setiform, on tarsus IV plumose (Fig. 21A).

Carpites on tarsi I and II 5 long, on tarsi III and IV 6 long. Accessory process on each of claws widened and with 3-4 minute tines (Fig. 21A).

Female. Idiosoma 205-260 long. In dorsal aspect similar to male. Ventral plates AE, PE and GP fused; GP and AP laterally separated by wedges of striated integument (Fig. 21B). With 5 pairs of pgs; 2 anterior pairs positioned anterior to GO. GO 52 long. Genital sclerites with 2 pairs of sgs. Ovipositor with 5 pairs of genital spines, 7-11 long and ending with 5-6 tines (Fig. 21C). Length:width ratio of gnathosoma 1.23. Rostrum shorter than gnathosomal base (Fig. 21D). On tarsus IV, lateral pas flattened and pectinate, medial pas setiform (Fig. 21F).

Tritonymph. Idiosoma 204 long. Ornamentation of dorsal plates foveate rather than reticulate (Fig. 21G). Posterior margin of AD truncate, ending immediately posterior to line of muscle scars. OC and PD smaller than in adults. Ventral plates separated; GP and AP not fused (Fig. 21H). Posterior margin of AE convex. AE and PE each with pair of adjunct setae. GP with 2 pairs of pgs and 1 pair of sgs. Number of setae of trochanter to tibia of legs I and II: 1, 2, 4, 5, 5; of legs III and IV 1, 1, 4, 3, 5, and 0, 1, 2, 3, 5. Telofemora I-IV with 3/1, 3/1, 3/1, and 2/0 setae, respectively.

Variations. Varieties of characters in adults: length of idiosoma, ♀: 205-260 (10); length of idiosoma, ♂: 205-223 (8); number of adjunct setae on either side of AE: 0 (1), 1 (36), 2 (2); number of adjunct setae on PE: 1 (38), 2 (2); number of pgs on either side, of GO ♀: 5(20); number of pgs plus basilar setae in either half, ♂: 6+1 (1), 7+1 (7), 8+1 (11), 9+1 (1); number of setae of leg segments 2 to 5:

segment	leg I	leg II	leg III	leg IV
2	2(40)	2(40)	1(40)	1(39), 2(1)
3	3/1(6), 4/1(34)	3/2(3), 4/1(8), 4/2(27)	3/0(2), 3/1(35)	2/1(2), 3/1(37), 4/1(1)
4	5(40)	5(40)	2(1), 3(39)	3(40)
5	5(40)	5(40)	5(40)	5(40)

REMARKS. *Rhombognathus tertentulus* closely resembles *R. reticulifer*. In both species the PD is reticulate, the ds-1 are very long, AE and PE each have 1 pair of adjunct setae, the anal cone is of normal size, the gnathosoma is short, the leg chaetotaxy is rather similar, the distally widened apex of the claws bears few small tines. Differences are: *R. tertentulus* has a more prominent

reticulation, its PD is wider, the telofemora are shorter, the telofemora III and IV each have 3/1 dorsal/ventral setae, and there are only 3-4 tines on the apex of the claws. Tritonymphs of *R. tertentulus* have a foveate PD, whereas the PD of *R. reticulifer* is reticulated; the GP of *R. tertentulus* is larger than in *R. reticulifer*.

Both species are easily separated from similar-sized Indo-West Pacific species on the basis of the enlarged ds-1.

Rhombognathus validipes sp. nov. (Figs 22, 23)

ETYMOLOGY. For its strong (*validus*, Latin) legs (*pes*, Latin).

MATERIAL. HOLOTYPE. ♀ (MTQ), Great Barrier Reef, 18°16.46'S, 147°22.88'E, Myimidon Reef, dead coral overgrown with algae at 3-15m, 13 April 1998; J.C. Otto. PARATYPES. ♀ (QMI S50974), collection data as above. ♂, 1 tritonymph (ZMH A104/99), collection data as above. OTHER MATERIAL. 1 tritonymph (MTQ), Great Barrier Reef, Undine Reef, off Cape Tribulation, growth on corals at 6m, 16 November 1997; coll. J.C. Otto. ♀ (IB), collection data as above.

DESCRIPTION. *Female*. Idiosoma 315-353 long, holotype 327 long, 217 wide. Dorsal plates separated from each other by wide areas of striated integument (Fig. 22A). AD 97 long, 105 wide; anterior margin broadly rounded, posterior margin ovate. Pair of gland pores in lateral margin. Line with muscle scars at approximately 0.7. OC slender, 75 and 85 long, 28 wide; lateral margin with 2 corneae and pore canaliculus; the latter closer to posterior than to anterior gland pore. OC with 2 corneae, the posterior one subdivided. PD 122 long. Integument within pair of slightly raised costae with delicate pores; median portion of plate with faint reticulate ornamentation. Pair of gland pores in posterolateral corners, the latter slightly extending beyond median margin of PD. Anal sclerites of normal size, not extended by anal valves. Setae ds-1 18 long; slightly wider and twice the length of the posterior setae; ds-1 inserted at 0.50 relative to length of AD. Setae ds-2 and ds-3 on OC, the posterior one at 0.64-0.68. Setae ds-4 and ds-5 on PD; anterior pair at 0.05, posterior seta at 0.47. Adanal setae on anal plate.

Ventral plates AE, PE and GP fused to a ventral shield; median portion of AP contiguous to ventral shield, else separated by pair of wide lateral wedges of striated integument (Fig. 22B). AE with 2-3 pairs of adjunct setae; PE with 2 adjunct setae. Distance from camerostome to GO

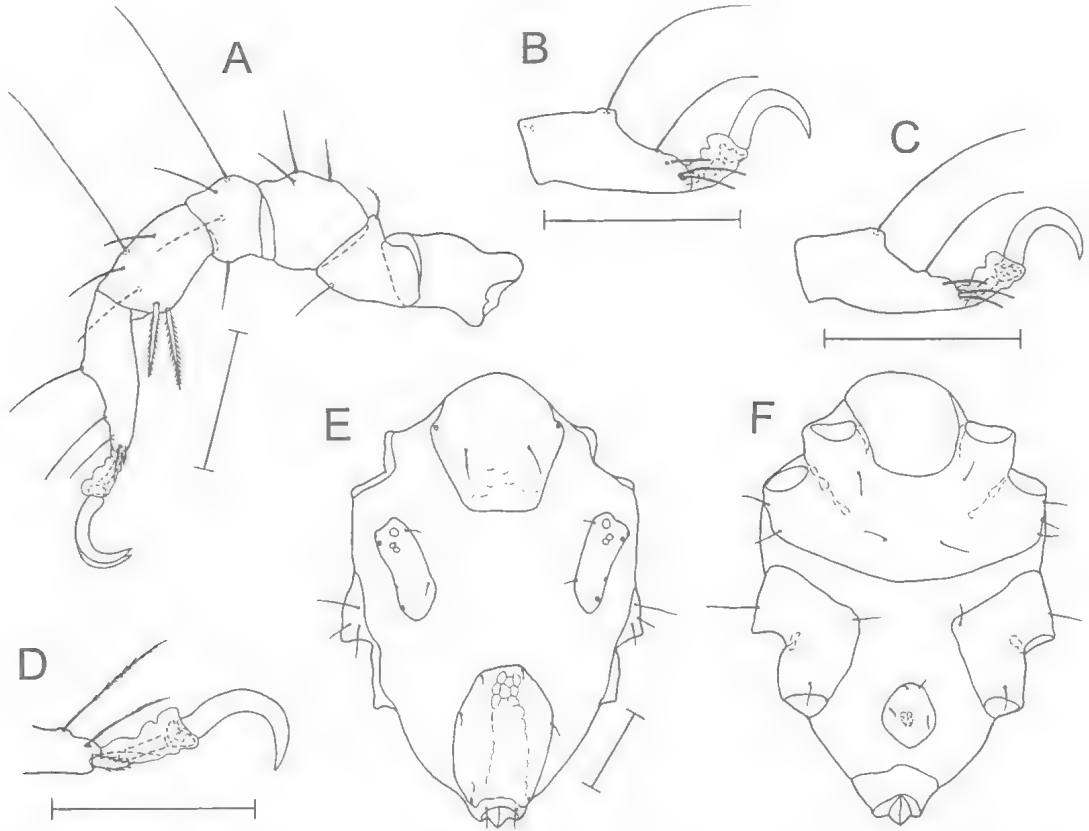


FIG. 21. *Rhombognathus tericulus* sp. nov.; A, tip of tarsus IV, ventrolateral, male (dorsomedial fossary seta omitted); B, idiosoma, ventral, female; C, ovipositor, lateral, and 3 genital spines (enlarged), female (spines of opposite side dotted); D, gnathosoma, ventral, female; E, tarsus I, lateral, female (medial claw and setae omitted); F, tip of tarsus IV, ventral, female (dorsal setae omitted); G, idiosoma, dorsal, tritonymph; H, idiosoma, ventral, tritonymph. Scale bar = 50µm.

165; GO 67 long. With 5 pairs of pgs, anterior pair of pgs at the level of insertion of leg IV. Genital sclerites with 2 pairs of sgs. Ovipositor with 10 pairs of genital spines (Fig. 22C); each spine trifold with equal-sized tines.

Gnathosoma 105 long, 77 wide, 1.36 times longer than wide. Gnathosomal base large (Fig. 22D). Rostrum 27 long, 20 wide, triangular in outline (Fig. 22E), much shorter than gnathosomal base. Rostrum with 2 pairs of maxillary setae and pair of long lateral rostral setae. Palps appressed to and slightly surpassing rostrum.

Legs stout; their length approximately 0.7 of that of idiosoma. Legs III and IV inserted at 0.54 and 0.68 relative to length of idiosoma. Telfemora I and II shorter than these legs' tibiae, telfemora III and IV slightly shorter than tibiae. Telfemora I and II 1.5 times longer than high (Fig. 22F, G); telfemora III and IV 1.1-1.2 times

longer than high (Figs 22H, 23A). Leg chaetotaxy: leg I, 1, 2, 7, 6-7, 7, 3; leg II, 1, 3, 7, 7, 3; leg III, 1, 2, 4, 3, 6, 4; leg IV, 0, 2, 3, 4, 6, 3. Telfemora I and II each with 5/2 dorsal/ventral setae, telfemora III and IV with 3/1 and 3/0 dorsal/lateral setae, respectively. Ventral seta on each of genua I-IV bristle-like, slightly serrate. Both ventral setae on each of tibiae I-IV stout and serrate or bipectinate. Tarsus III with 4 dorsal setae; the 2 basal setae distinctly separated. Basal fossary setae at basis of claw fossa; 2 apical fossary setae inserted within fossa area. On tarsi III and IV apicalmost (dorsolateral) fossary seta near tip of tarsi and resembling medial pas. Tarsi I and II each with dorsolateral solenidion, 10 and 12 long, respectively (Fig. 23B, C); apex with pair of doubled pas. Famulus on tarsus I papilliform. Tarsi III and IV each with setiform medial pas and scaliform pectinate lateral pas.

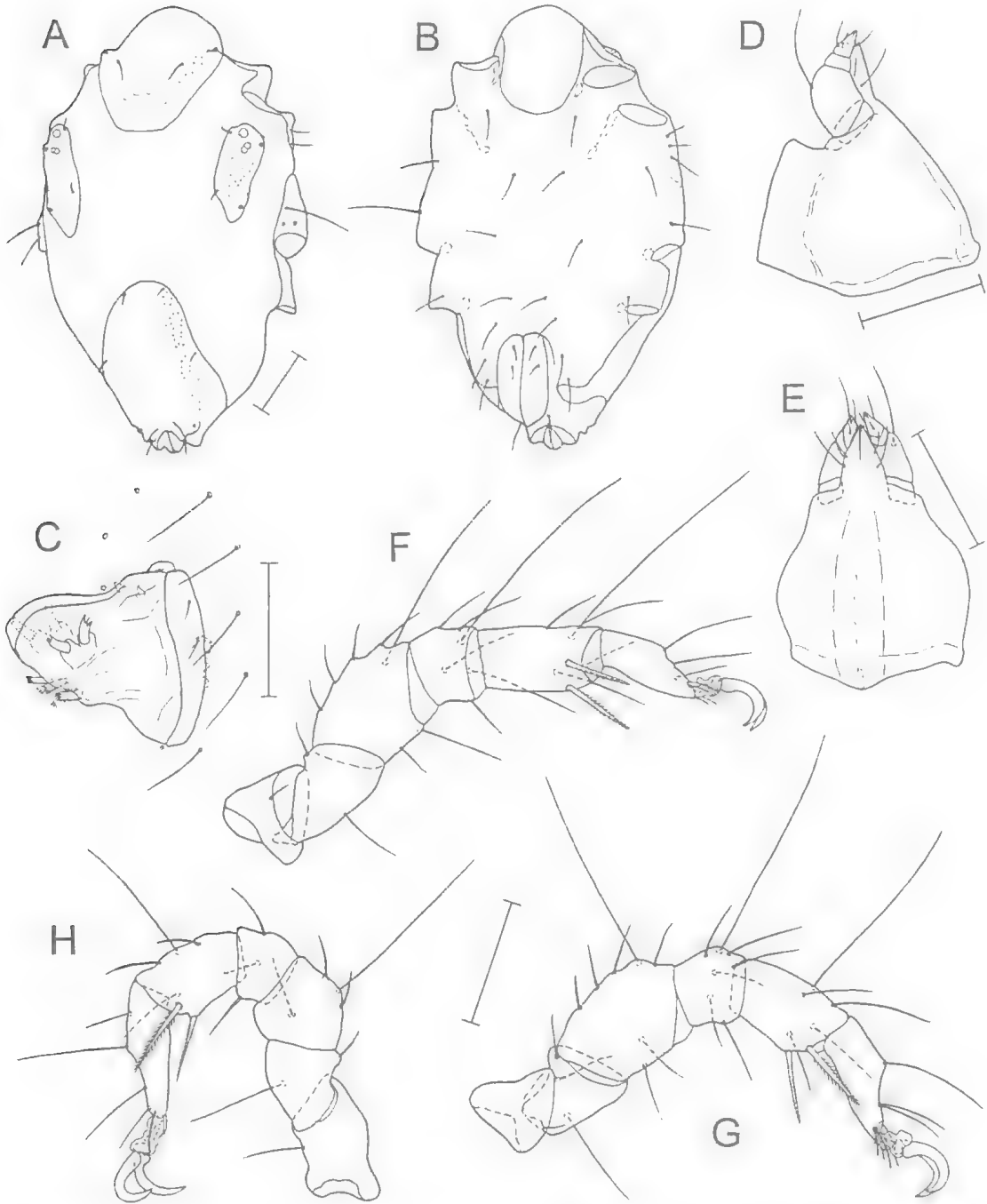


FIG. 22. *Rhombognathus validipes* sp. nov., female; A, idiosoma, dorsal; B, idiosoma, ventral; C, ovipositor, lateral (spines of opposite side dotted); D, gnathosoma, lateral; E, gnathosoma, ventral; F, leg I, ventromedial; G, leg II, medial; H, leg III, medial. Scale bar = 50µm.

Carpites of tarsi I-IV 6, 7, 10, 10 long. Claws smooth.

Tritonymph. Idiosoma 267-291 long, 173 wide. Posterior margin of AD more truncate than in female. OC slender as in female; posterior cornea

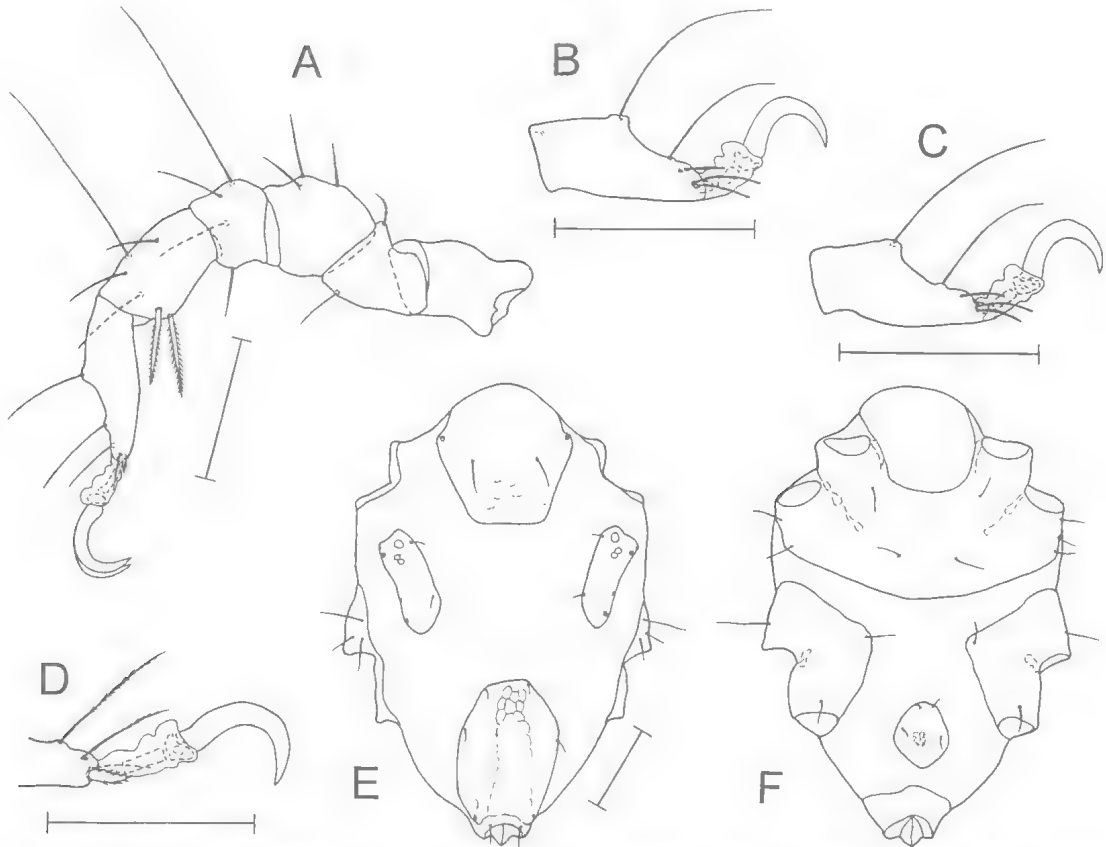


FIG. 23. *Rhombognathus validipes* sp. nov., female; A, leg IV, medial, female; B, tarsus I, lateral, female (medial claw and setae omitted); C, tarsus II, lateral, female (medial claw and setae omitted); D, tip of tarsus IV, lateral, female; E, idiosoma, dorsal, tritonymph; F, idiosoma, ventral, tritonymph. Scale bar = 50 μ m.

subdivided (Fig. 23E). Ventral plates AE, PE, GP, and AP separated. AE with 1-2 pairs of adjunct setae; PE each with 2 adjunct setae. GP ovoid (Fig. 23F); with 2 pairs of pgs and 1 pair of sgs. Three pairs of genital acetabula adjacent to primordial genital slit. Gnathosoma as in male. Leg chaetotaxy: leg I, 1, 2, 6, 7, 7, 3; leg II, 1, 3, 6, 7, 7, 3; leg III, 1, 2, 4, 3, 6, 4; leg IV, 0, 2, 3, 4, 6, 3. Telfemora I and II each with 4/2 dorsal/ventral setae, telfemora III and IV with 3/1 and 3/0 dorsal/lateral setae, respectively. Tibiae I-IV each with 2 stout ventral setae.

Variations. Varieties of characters in adults: length of idiosoma, female: 315-353 (4); number of adjunct setae on either side of AE: 2 (6), 3 (2); number of adjunct setae on PE: 1 (1), 2 (7); number of pgs on either side of GO, female: 5 (8); number of setae of leg segments 2, 4 and 5, and number of dorsal/ventral setae of telfemora I and II and dorsal/lateral setae of telfemora III and IV:

segment	leg I	leg II	leg III	leg IV
2	2(8)	3(8)	2(8)	2(8)
3	5/2(8)	5/2(8)	3/1(7)	3/0(8)
4	6(1), 7(7)	7(8)	3(7)	4(8)
5	7(8)	7(8)	6(7)	6(8)

REMARKS. Adults and juveniles of *Rhombognathus validipes* are characterised by the two pairs of setae on the PD, whereas the other species from the Great Barrier Reef have a single pair of setae.

In the rhombognathine fauna presently known from northeastern Australia, the two species *Rhombognathus lathridius* and *R. validipes* have smooth claws. *R. validipes* is larger than the psammobiont *R. lathridius*; its gnathosoma is wider and the adanal setae do not arise from small pedestals as in *R. lathridius*.

In dorsal and ventral aspect of the idiosoma and the outline of the gnathosoma and the claws, *R. validipes* resembles *R. leurodactylus* Krantz, 1976 and *R. robustus* Bartsch, 1977, both are

recorded from the eastern Pacific coast (Krantz, 1976; Bartsch, 1977). In contrast to the two latter species, the OC of *R. validipes* are more slender. Other characters which separate *R. validipes* from *R. leurodactylus* are: the number of setae of the telofemora I-IV - 5/2, 5/2, 3/1, 3/0 in *R. validipes*, but 3/2, 3/2, 2/1, 2/1 in *R. leurodactylus*; the number of perigenital setae in females, 5 pairs in *R. validipes*, no more than 3 pairs in *R. leurodactylus*. Tibiae I-IV of *R. robustus* bear 6, 6, 5, 5 setae, those of *R. validipes* 7, 7, 6, 6 setae.

KEY TO ADULT RHOMBOGNATHINES OF THE GREAT BARRIER REEF

- 1. Gnathosoma completely hidden beneath AD. OC wider than long; without seta. PD with 3 pairs of setae. Venter with small plates and large areas of striated integument (Fig. 1B) *Isobactrus ponapensis*
 Gnathosoma extending beyond anterior margin of idiosoma. OC longer than wide; with 2 setae. PD with 1-2 pairs of setae. Ventral AE and PE fused to ventral shield *Rhombognathus*

KEY TO ADULT RHOMBOGNATHUS

- 1. Plates AD, OC and PD separate 2
 All dorsal plates fused. Claws with more than 20 tines *scutulatus*
- 2. Anterior margin of AD evenly rounded (Fig. 2A). Anal plate without pedestals 3
 AD with minute frontal process. Adanal setae on small pedestals (Fig. 7A); gnathosoma 1.5 times longer than wide; telofemora I-IV with 5/2, 5/2, 3/1, 3/1 dorsal/ventral setae. Claws smooth *lathridius*
- 3. Telofemora I-IV with 4-5/1-2, 4-5/1-2, 3/0-1, 3/0-1 dorsal/ventral setae 4
 Telofemora I-IV with 2/1, 2/1, 2/0, 2/0 dorsal/ventral setae *cyrtonotus*
- 4. Claws widened and provided with more than 10 tines (Figs 15H, 19E) 5
 Claws smooth or with accessory process, the latter with 1-8 tines (Figs 5H, 17E) 6
- 5. Claws with 12-13 tines. Setae ds-1 longer than following setae (Fig. 18A); female with 7-9 pairs of pgs (Fig. 19I); male with 11-15 pairs of pgs. *seminotatus*
 Claws with 18-20 tines. Setae ds-1 hardly longer than following setae (Fig. 14A); female with 5 pairs of pgs (Fig. 15F); male with 10-14 pairs of pgs *papuensis*
- 6. Length of ds-1 not exceeding twice length of following setae (Figs 4A, 9A) 7
 Setae ds-1 3-4 times longer than following setae (Figs 16A, 20A); anal valves not extending beyond anal sclerites; dorsal plates reticulate 10
- 7. Telofemora I and II each with 4/1 dorsal/ventral setae. 8
 Telofemora I and II each with 5/2 dorsal/ventral setae 9
- 8. Length:height ratio of telofemora 1.9-2.0; anal valves extending beyond small anal sclerites (Fig. 4C) *delicatulus*
 Telofemora slender, length:height ratio 2.5-2.9; anal cone of normal shape with anal valves and anal sclerites similar in size (Fig. 11C) *longipes*

- 9. OC 1.6 times longer than wide; two corneae equal in shape; PD with single pair of setae (Fig. 9A); claws with accessory process (Fig. 10A) *levigatus*
 OC slender, more than 2.5 times longer than wide; posterior cornea subdivided; PD with 2 pairs of setae (Fig. 22A); claws smooth (Fig. 23B) *validipes*
- 10. PD with large-sized, faint reticulum, its meshes 8-10µm long (Fig. 16A); telofemora I-IV with 4/2, 4/2, 3/0, 3/0 dorsal/ventral setae; claws with 7-8 minute tines (Figs 17B, E) *reticulifer*
 PD with conspicuous and dense reticulation (Fig. 20A); telofemora I-IV with 4/1, 4/2, 3/1, 3/1 dorsal/ventral setae; claws with 3-4 minute tines (Fig. 21A, F) *tericulus*

DISCUSSION

In the Great Barrier Reef area, 11 species of *Rhombognathus* and 1 of *Isobactrus* were found. Future collections will certainly result in records of more species. The number of *Rhombognathus* species is similar to that known from southwestern Australia, viz. 10 species (Bartsch, 1993), and from the boreal and warm temperate northwestern Pacific, 11 species from Hokkaido (Abé, 1996) and 8 species from the Hong Kong area (Bartsch, 1992). The number of species of *Isobactrus* recorded from the north- and southwestern Pacific area is small. *Isobactrus ponapensis* is the first representative of this genus from the shores of Australia. The low number of records of *Isobactrus* may partly be due to the lack of collections from adequate habitats.

Species of *Rhombognathus* recorded from various regions of the Pacific and the tropical Indian Ocean are summarised in Table 1. The knowledge of the rhombognathine fauna in the Pacific and Indo-West Pacific region still is poor, and several of the published records are based on sporadic and short-time sampling activities with halacarids being just one of the accessory taxa. Accordingly, the data summarised in Table 1 far from completely mirror the number and distribution of the genus *Rhombognathus* in these geographic regions. The status of *Rhombognathus denticulatus* Sokolov, 1952 is not clear; the absence of a bipectinate seta on tibia III may be an evidence of close relationship to the genus *Isobactrus*.

Noteworthy is the low number of wide-spread species. *R. leurodactylus* obviously is an amph-Pacific boreal species. The species was taken on the shores of Oregon/US (Krantz, 1976) and all around Hokkaido/Japan, here both on the coastlines influenced by subarctic water currents (Okhotsk Sea and Western North Pacific) and by the warm (subtropical) Kuroshio current (Japan Sea) (Abé, 1996). *R. sinensis* inhabits a wide

TABLE 1. (cont.)

Species	Geographical Area												References
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	
<i>novaezelandicus</i> Bartsch, 1985									x				Bartsch, 1985
<i>oblongus</i> Bartsch, 1989							x						Bartsch, 1989a
<i>pacificus</i> Newell, 1984				x									Newell, 1984
<i>papuensis</i> Bartsch, 1989							x	x					Bartsch, 1989a, present paper
<i>placidus</i> Bartsch, 1993												x	Bartsch, 1993
<i>plumifer</i> Trouessart, 1889				x									Newell, 1984
<i>psammophilus</i> Bartsch, 1993												x	Bartsch, 1993
<i>reticulatus</i> Krantz, 1976	x												Krantz, 1976
<i>reticulifer</i> sp. nov.								x					present paper
<i>robustus</i> Bartsch, 1977			x										Bartsch, 1977
<i>scutulatus</i> Bartsch, 1983							x	x				x	Bartsch, 1983, 1993; Chatterjee, 1995; present paper
<i>semiarmatus</i> Bartsch, 1983							x						Bartsch, 1983
<i>seminotatus</i> sp. nov.								x					present paper
<i>semireticulatus</i> Bartsch, 1977			x										Bartsch, 1977
<i>setellus</i> Bartsch, 1992						x							Bartsch, 1992
<i>setifer</i> Bartsch, 1983							x						Bartsch, 1983
<i>similis</i> Bartsch, 1977			x									x?	Bartsch, 1977; Chatterjee, 1995
<i>sinensis</i> Bartsch, 1990					x	x							Bartsch, 1990
<i>sinensoideus</i> Bartsch, 1992						x							Bartsch, 1992
<i>tenuiformis</i> Abé, 1996					x								Abé, 1996
<i>tericulus</i> sp. nov.								x					present paper
<i>terminalis</i> Sokolov, 1952					x								Sokolov, 1952
<i>teurinus</i> Abé, 1996					x								Abé, 1996
<i>thalassinus</i> Bartsch, 1993												x	Bartsch, 1993
<i>validipes</i> sp. nov.								x					present paper
<i>ventralis</i> Newell, 1984				x									Newell, 1984
<i>verrucosus</i> Bartsch, 1992						x							Bartsch, 1992

range along the coast of Asia, from Hokkaido to Hong Kong (Abé, 1996; Bartsch, 1992). *R. scutulatus* is an Indo-West Pacific species; records are from the Philippines, eastern and western coast of India, Western Australia (Bartsch, 1983, 1993; Chatterjee, 1995) and, now, from eastern Australia. From the Indian Ocean, Chatterjee (1995) published a record of *R. similis* Bartsch, 1977, a species also known from the Galapagos Islands (Bartsch, 1977); because of differences in the arrangement of the perigenital setae in females, the eastern Pacific and Indian Ocean specimens may belong to different species. *R. papuensis* is known from Papua New Guinea (Bartsch, 1989a) and eastern Australia. Though often not identical species, there are close similarities between the rhombognathines of

northeastern Australia and the Philippines, e.g. *R. lathridius*/*R. caudiculus* and *R. cyrtotus*/*R. cebuus*.

On the basis of data on the geography and ecology of rhombognathines, Bartsch (1982) concluded that within *Isobactrus* many of the species have a high tendency to tolerate environmental changes but a low speciation rate. In contrast, within *Rhombognathus* there seems to be a high evolutionary potential. Rather than tolerate a wide range in the environmental parameters, species genetically diversify, and when being brought into a new habitat, exposed to changing hydrographic or climatic challenges or biological interactions, new species evolve in the local scene. The large numbers of *Rhombognathus* may be the result of adaptations to the numerous niches in the Great Barrier Reef area.

In the material from the Great Barrier Reef Marine Park area at hand, a few individuals could not be identified, they demonstrated characters of two species, namely *R. delicatulus* and *R. tericulus*. Are these specimens extreme variants, separate species, or hybrids? Nothing is reported on genetic barriers, or hybridisation, between halacarid species sharing a habitat. In the course of the author's studies in the northern Atlantic, thousands of rhombognathines have been examined microscopically. The variation of characters is low, apart from a few anomalies, namely deformations, intersexes which showed characters of both males and females, or adults with unilaterally a leg form and setation equalling that of juveniles. Hybrid-like forms, with characters of two species, were not found. The rhombognathine fauna of the northern Atlantic includes the genera *Isobactrus*, *Metarhombognathus*, *Rhombognathides* and *Rhombognathus*. From the Pacific and Indian Ocean only *Isobactrus* and *Rhombognathus* are known. The genus *Rhombognathus* is characterised by a large number of different forms; there are species with a slender, elongate idiosoma, others are short and flattened; some species are small and cryptic, others very large; species have short legs with wide segments or the telofemora and tibiae are elongate and the legs almost as long as the idiosoma; the numbers of setae of the legs vary considerably. Beside the wide range of interspecific differences, the genus is characterised by a high intraspecific variability. In contrast to *Rhombognathus*, *Isobactrus* demonstrates a considerable uniformity. The shape of the idiosoma and legs is rather similar in all species and even interspecific difference in the setation is small within the faunas of the northern and southern oceans, respectively.

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NEW RECORDS OF TRAPEZIID CRABS (CRUSTACEA: BRACHYURA: TRAPEZIIDAE) FROM THE CORAL SEA AND NORTHERN TASMAN SEA. *Memoirs of the Queensland Museum* 45(2): 204, 2000:- Trapeziid crabs belonging to *Tetralia* and *Trapezia* are obligate symbionts of reef-building corals, while species of *Quadrella* inhabit antipatharians, alcyonaceans, gorgonians and azooxanthellate corals. The trapeziids inhabiting the Coral Sea region were studied by Castro (1997). Examination of collections deposited in the Australian Museum, Sydney (AM), Queensland Museum, Brisbane (QM) and the Muséum National d'Histoire Naturelle, Paris (MNHN) has revealed the presence of additional species for the region. Two species are recorded for the first time from eastern Australia and two from New Caledonia. Five species of *Tetralia*, twelve of *Trapezia* and three of *Quadrella* are now known from the Coral Sea and northern Tasman Sea. Only one wide-ranging Indo-West Pacific species, *Trapezia tigrina* Eydoux & Souleyet, 1848, remains unknown from the region.

***Quadrella coronata* Dana, 1852**

For synonymy see Castro, 1999a: 95.

AMP17448, ♂, ♀, New Caledonia, Ilot Amadée, 30-35m, 12 Sept. 1929, B. Conseil & G. Bangibout. New record for New Caledonia. The only previous Coral Sea record was from southwestern Vanuatu (Castro, 1997). The species is known from across the Indian Ocean and the western Pacific (Castro, 1999a). To additional species, *Q. maculosa* Alcock, 1898 and *Q. serenei* Galil, 1986 (the Vanuatu specimen referred to as *Q. maculosa* by Castro, 1997; see Castro, 1999a: 96), is also known from the Coral Sea.

***Tetralia vanninii* Galil & Clark, 1988**

For synonymy see Castro, 1999a: 103.

AMP17232, 2♂, Queensland, North East Cay, Herald Group, 17°20'S, 148°28'E, 6 Nov. 1964, D.F. Mc Michael & J.C. Yaldwyn; QMW25176, ♂, ♀, Wreck Reef, Porpoise Cay, 22°17'S, 155°25'E, outer reef slope, 12 m, 10 May 1988, J. Short & S. Mullers; AMP39689, ♂, ♀, Sugarloaf Island, Lord Howe Island, 31°30.2'S, 159°04.3'E, 17m, 27 Dec. 1979, N. Coleman. First record for the Coral Sea region. The species is found through most of the Indo-West Pacific region.

***Trapezia formosa* Smith, 1869**

For synonymy see Castro, 1998: 178.

AMP38228, ♂, ♀, Elizabeth Reef, reef flat near 'Yoshin Maru Iwaki' wreck, 29°55.8'S, 159°01.3'E, small coral head, J.K. Lowry & R.T. Springthorpe. First record from eastern Australian waters. The only previous Coral Sea record was from the Chesterfield Islands (Castro, 1997). The species is widely distributed across the Indo-West Pacific and eastern Pacific regions (Castro, 1998).

***Trapezia lutea* Castro, 1997**

Trapezia lutea Castro, 1997: 84-87, figs 2C, D, 3A-C, pls 2C, 5A.

QMW25186, 2♂, ♀, Queensland, Flinder's Reef, off Cape Moreton, 26°59'S, 153°29'E, P.J.F. Davie & J. Short. First record from eastern Australian waters. Previous Coral Sea records were from New Caledonia and the Loyalty and Chesterfield Islands (Castro, 1997). The species is widely distributed through most of the Indo-West Pacific region; first recorded from Indonesia by Castro (1999b: 52).

***Trapezia punctipes* Castro, 1997**

Trapezia punctipes Castro, 1997: 87-89, figs 4A-C, pl. 2D.

MNHN-B26249, ♀, New Caledonia, Baie St. Vincent, 22E25'S, 166E50'E, Aug. 1961, Y. Plessis. The species was described from material collected at Lizard Island, northern Queensland. This is the first record from New Caledonia. It is generally uncommon; known from the Andaman Sea coast of Thailand to the Mariana Islands and Fiji (Castro, 1999b).

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P. Castro, *Biological Sciences Department, California State Polytechnic University, Pomona, CA 91768, U.S.A.; 12 May 2000.*

SPECIES OF *DISCOCELIS* (PLATYHELMINTHES: POLYCLADIDA) FROM QUEENSLAND, WITH DESCRIPTION OF A NEW SPECIES

I. BEVERIDGE

Beveridge I. 2000 06 30: Species of *Discocelis* (Platyhelminthes: Polycladida) from Queensland, with description of a new species. *Memoirs of the Queensland Museum* 45(2): 205-213. Brisbane. ISSN 0079-8835.

Two species of *Discocelis* are described from intertidal waters from northern Queensland. The first species is characterised by the marginal eyes extending to the posterior region of the body, the presence of a seminal vesicle, cerebral eyes distributed more or less in anterior and posterior groups and a male antrum with complex lobes in dorso-ventral views. This species differs clearly from all congeners and is named *D. parvimaiculata* sp. nov. The second has marginal eyes extending to the level of the cerebral organ, cerebral eyes arranged more or less in two groups, lacks a seminal vesicle and has prostatoids in the wall of the male antrum as well as in the penis papilla itself. The species is closely related to *D. pusilla* Kato, 1938. It is probably distinct but is not named owing to the poor description of *D. pusilla*. The records presented suggest that several species of *Discocelis* are present in Australian coastal waters and that the distribution of prostatoids seen in dorso-ventral views of the male antrum provides useful characters for distinguishing species within the genus. □ *Polycladida*. *Discocelis*, new species, taxonomy.

I. Beveridge, Department of Veterinary Science, University of Melbourne, Parkville 3052, Melbourne, Australia; 24 April 1999.

The polyclad family Discocelidae Laidlaw, 1903 is a cosmopolitan family of essentially intertidal polyclads characterised by the presence of marginal eyes and small secretory organs, termed prostatoids, associated with the male reproductive system (Faubel, 1983). The family is currently represented by a single Australian species, *Discocelis australis* Hyman, 1959, found under rocks in the intertidal region close to Sydney (Hyman, 1959) and from West I., South Australia (Prudhoe, 1982). Faubel (1983) transferred *D. australis* to the related genus *Thalamoplana* Laidlaw, 1904, distinguished from *Discocelis* Ehrenberg, 1836 by possessing separate male and female gonopores. By contrast, Prudhoe (1985) considered that *Thalamoplana* warranted only sub-generic rank.

The presence of only a single Australian representative of the family is probably the result of lack of collecting rather than the family being poorly represented in Australian intertidal waters. This paper reports the presence of two additional species of *Discocelis* from Townsville, Queensland, one of which is clearly a new species.

METHODS

Polyclads were collected at low-tide from under rocks on exposed mud-flats. Fixation followed the technique of Newman & Cannon (1995) in which polyclads were placed on filter paper in a dish of sea-water and when fully

extended, the filter paper was rapidly placed on a block of frozen fixative, either 4% formaldehyde in sea-water or formaldehyde-calcium acetate-propylene glycol-propylene phenoxetol. Following fixation, worms were dehydrated in a graded series of ethanols, cleared in Canada balsam and mounted in Canada balsam. The median posterior sections of individual polyclads were removed using a scalpel blade, embedded in paraffin and serial longitudinal sections, cut at a thickness of 7µm, were stained with Gill's haematoxylin and eosin. Drawings were made using a drawing tube attached to an Olympus BH microscope. Measurements are presented in millimetres as the range followed by the mean in parentheses.

All specimens collected have been deposited in the Queensland Museum (QM).

Type specimens of *D. australis* from New South Wales (Australian Museum W3685) were compared with the new material.

POLYCLADIDA Lang, 1884
ACOTYLEA Lang, 1884
DISCOCELIDAE Laidlaw, 1903

Discocelis parvimaiculata sp. nov.
(Figs 1-6)

MATERIAL HOLOTYPE: Rowe's Bay, Townsville, Qld (19°16'S, 146°49'E), 17.vi.1997, coll. I. Beveridge, whole mount, unstained (QM G217321); 2 colour slides.

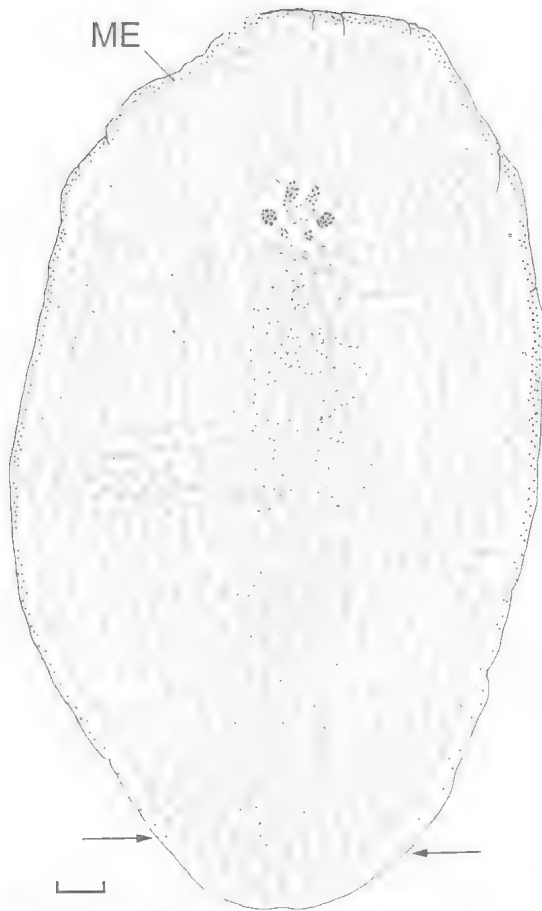


FIG. 1. *Discocelis parvimaclata* sp. nov., entire polyclad, dorsal view, showing pattern of pigmented maculae and extent of marginal eyes (ME arrows). Scale bar = 1mm.

PARATYPES: 5 entire specimens and fragments of 1 specimen, whole mounts; 1 set of sections stained with haematoxylin and eosin, Rowe's Bay, Townsville, Qld, coll. I. Beveridge, 1.vii.1994, 29.vi.1995 (QM G217322-7, serial sections G217328).

DESCRIPTION. Large, oval polyclads; holotype non-gravid specimen 13 long, 10 wide; gravid specimens, 18-21(19) long, 7-12(10) wide; dorsal surface fawn, darker in centre, covered with numerous small brown circular areas of pigment, larger brown patches in central regions, becoming smaller towards periphery (Fig.1); ventral surface pale grey; nuchal tentacles absent; cerebral organ 0.41×0.55 in holotype, $0.39-0.48$ (0.43) $\times 0.46-0.56$ (0.51) in paratypes, 2.58 from anterior extremity in holotype, $2.94-4.60$ (3.77) in paratypes; marginal eyes 3-4 deep, extend to posterior quarter of body, number of rows of

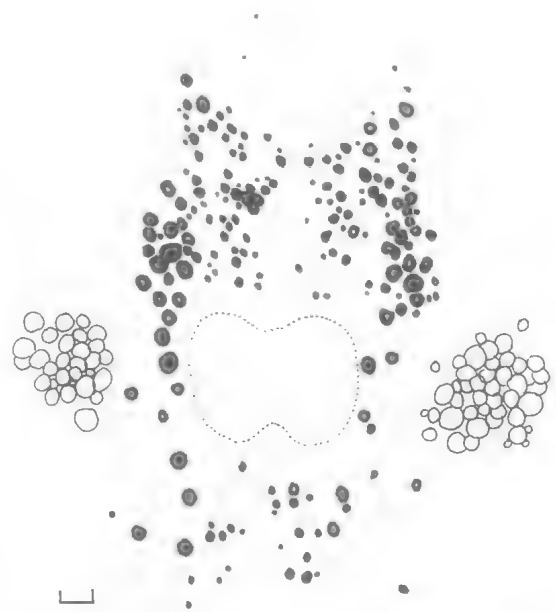


FIG. 2. *Discocelis parvimaclata* sp. nov., cerebral organ, tentacular and cerebral eyes showing variation between individual specimens (see Fig. 3). Scale bar = 0.1mm.

ocelli diminishes posteriorly; in most specimens, including holotype, eyes reach level of gonopore; in some specimens, eyes encircle body; cerebral eyes arranged in elongate groups, on either side of mid-line, 41-65 ocelli anterior to cerebral organ, 5-20 posterior to cerebral organ, anterior and posterior groups usually but not invariably separated (Figs 2,3); tentacular eyes with 25-40 ocelli per cluster; ruffled pharynx in mid-body, with 10-12 lateral folds, 11 in holotype; mouth at posterior end of pharynx, 4.9 from posterior end in holotype, 7.0-8.1(7.6) in paratypes; single gonopore 3.13 from posterior end in holotype, 5.5-6.8(6.0) in paratypes; antrum masculinum voluminous, folded in both dorso-ventral views and sagittal sections; in ventral views (Figs 4,5), antrum with prominent anterior lobe containing penis papilla and two lateral lobes each partially subdivided; in sagittal section (Fig. 6), several muscular lobes descend from dorsal surface of antrum; antrum with numerous pyriform prostatics opening into lumen; in ventral view, prostatics arranged in subcircular cluster on penis papilla and on posterolateral margins; in sagittal sections, prostatics present on all pendant processes; no prostatics present in wall of antrum; prostatics of two histological types; most with faintly eosinophilic content; prostatics

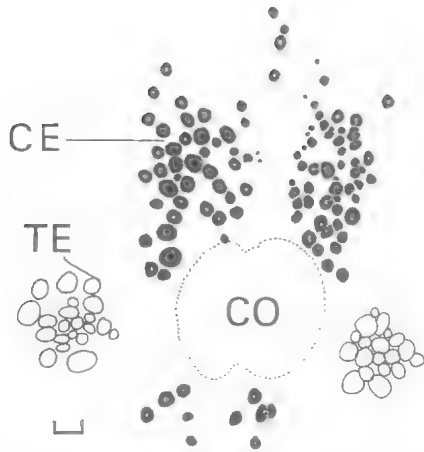


FIG. 3. *Discocelis parvimaculata* sp. nov., cerebral organ, tentacular and cerebral eyes showing variation between individual specimens. CE = cerebral eyes; CO = cerebral organ; TE = tentacular eyes. Scale bar = 0.1mm.

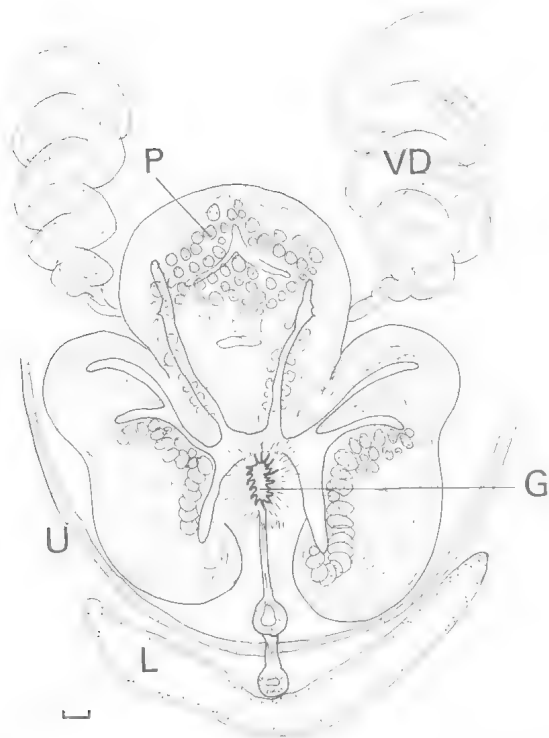


FIG. 4. *Discocelis parvimaculata* sp. nov., gonopore and genital complex, ventral view. G = gonopore; L = Lang's vesicle; P = prostatoids; U = uterine duct; VD = vas deferens. Scale bar = 0.1mm.

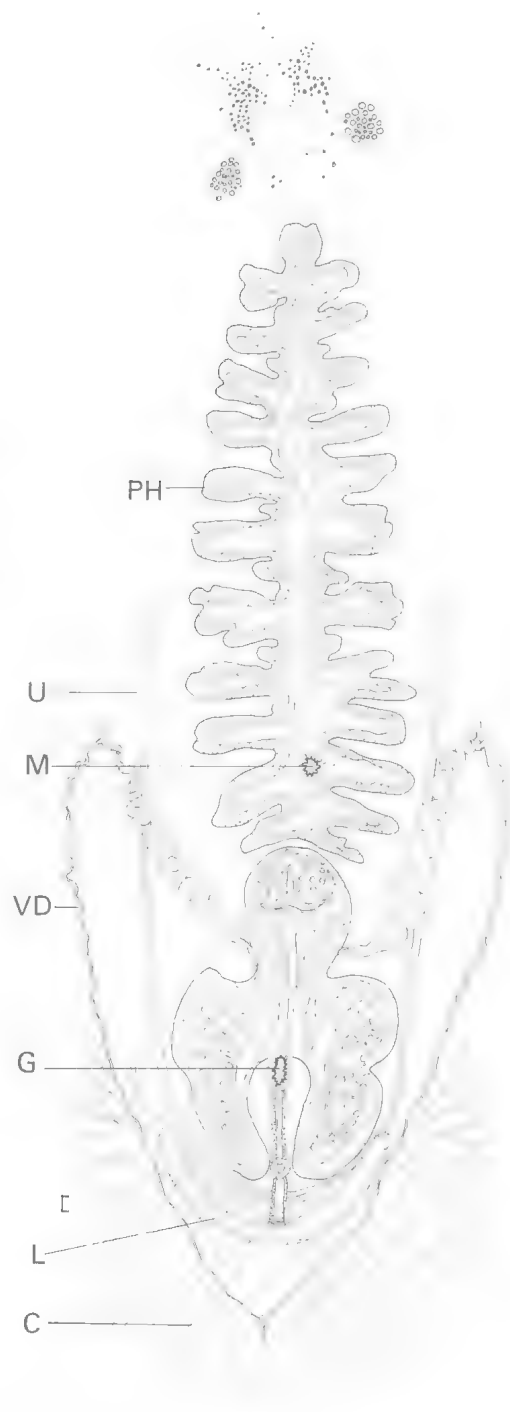


FIG. 5. *Discocelis parvimaculata* sp. nov., ventral aspect showing cerebral organ, eyes, pharynx and genital complex. C = cement glands; G = gonopore; L = Lang's vesicle; M = mouth; PH = pharynx; U = uterine duct; VD = vas deferens. Scale bar = 0.1mm.

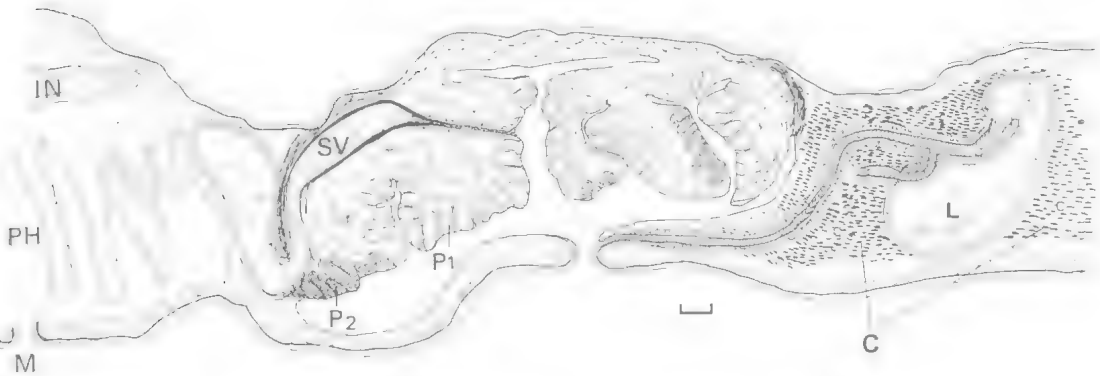


FIG. 6. *Discocelis parvimaculata* sp. nov., median sagittal section showing mouth, gonopore and histological details of genital ducts. C = cement glands; IN = intestine; L = Lang's vesicle; M = mouth; P1 = eosinophilic prostatoids, P2 = basophilic prostatoids; PH = pharynx; SV = seminal vesicle. Scale bar = 0.1mm.

at anterior extremity of antrum and on ventral or anterior surfaces of pendant processes of penis papilla with basophilic content; penis papilla fleshy, prominent, in anterior part of antrum; ejaculatory duct simple, straight; prostate absent; ejaculatory duct leads to pyriform seminal vesicle with thin but highly eosinophilic wall, passes ventrally, divides; walls of spermiducal bulbs highly muscular; vasa deferentia thin-walled, pass anterolaterally from male complex, to level of mouth, then divide; posterior branches coil posteromedially, uniting posterior to Lang's vesicle. No separate female gonopore; vagina opens into male antrum immediately posterior to common gonopore; vagina with thick muscular walls, ciliated lining, curves anteriorly to short, horizontal region; uterine canals empty into vagina immediately anterior to termination of vagina into prominently Y-shaped Lang's vesicle; uterine canals extend anteriorly on either side of pharynx; cement glands prominent in horizontal region of vagina, extend posteriorly and laterally into parenchyma, branched distally.

***Discocelis* sp.**
(Figs 7-12)

MATERIAL. Two specimens, Rowe's Bay, Townsville, Qld, 1.vii. 1994, coll. I. Beveridge, whole mount and serial sections stained with haematoxylin and eosin (QM G217329-30, serial sections G217331).

DESCRIPTION. Oval polyclads; gravid specimens 12-16 long, 5-8 wide; dorsal surface fawn, darker in centre, covered with numerous brown circular areas of pigment, larger patches in central regions, becoming smaller towards periphery (Fig. 7); ventral surface pale grey; nuchal tentacles absent; cerebral organ 0.33-0.45 ×

0.42-0.44, 2.5-4.6 from anterior extremity; marginal eyes in rows 3-4 deep, extend around anterior quarter of body, reach level of cerebral organ; cerebral eyes arranged in elongate groups, either side of mid-line, 31-42 ocelli anterior to cerebral organ, more or less separate from 4-7 posterior to cerebral organ (Figs 8,9); tentacular eyes with 18-30 ocelli per cluster; ruffled pharynx in mid-body, with 10 lateral folds; mouth at posterior end of pharynx, 5.2 from posterior end; single gonopore 3.4 from posterior end; antrum masculinum voluminous; prominent anterior penis papilla, circular in ventral view (Figs 10,11), with numerous prostatoids; wall of antrum encircling penis papilla bearing single row of prostatoids; antrum with 2 laterally directed branches on each side, immediately anterior to gonopore; anterior pair of lateral branches with row of prostatoids along posterior margin; in sagittal section (Fig. 12), large muscular penis papilla descends from dorsal surface of antrum, with numerous pyriform prostatoids; prostatoids present in wall of antrum, restricted to anterior ventral region; prostatoids with faintly eosinophilic content; ejaculatory duct simple, straight; prostate absent; seminal vesicle absent; ejaculatory duct divides into vasa deferentia which pass anterolaterally from male complex, to level of pharynx, then re-divide; posterior branches coil posteromedially, uniting posterior to Lang's vesicle. No separate female gonopore; vagina opens into male antrum immediately posterior to common gonopore; antrum anterior to vaginal opening, prominent, muscular with thicker epithelium; vagina with thick muscular walls, ciliated lining, curves anteriorly; uterine canals empty into vagina anterior to prominent dorsal loop; vagina passes ventrally to enter

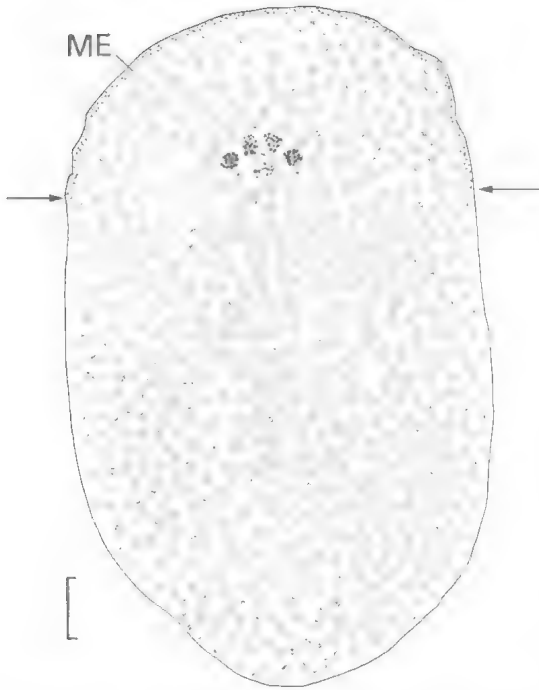


FIG. 7. *Discocelis* sp., entire polyclad, dorsal view, showing pattern of pigmented maculae and extent of marginal eyes (ME arrows). Scale bar = 1mm.

Y-shaped Lang's vesicle; uterine canals extend anteriorly on either side of pharynx; cement glands prominent, extend posteriorly and laterally into parenchyma.

DISCUSSION

Both species described above belong to the family Discocelidae since they possess marginal eyes and prostatoids opening into the male antrum (Faubel, 1983; Prudhoe, 1985). Generic distinctions within the family are not well defined, and although both Faubel (1983) and Prudhoe (1985) accept the validity of *Discocelis*, *Adenoplana* Stummer-Traunfels, 1933 and *Coronadena* Hyman, 1940, their definitions of these genera differ. In addition, *Thalamoplana* Laidlaw, 1904, accepted by Marcus & Marcus (1966), de Beauchamp (1961) and Faubel (1983), was not accepted as a valid genus by Prudhoe (1985). Both species described here differ from *Coronadena* in lacking the 7-11 large prostatic organs arranged radially around the male antrum in addition to the more numerous small prostatoids. *Adenoplana* was characterised by Stummer-Traunfels (1933) as having an interpolated prostatic organ. Faubel (1983) by contrast interpreted the prostatic organ of

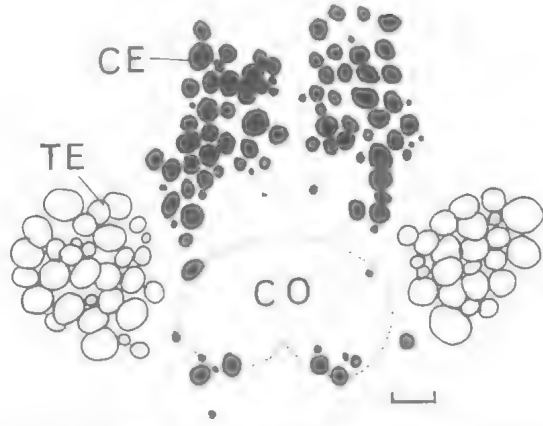


FIG. 8. *Discocelis* sp., cerebral organ, tentacular and cerebral eyes showing variation between individual specimens (see Fig. 9). CE = cerebral eyes; CO = cerebral organ; TE = tentacular eyes. Scale bar = 0.1mm.

Adenoplana as an ejaculatory duct lined with a glandular epithelium. Whatever the precise definition of the structures involved may be, *Adenoplana* differs from the species described here in possessing distinctly separate gonopores.

The remaining genera, *Discocelis* and *Thalamoplana*, are distinguishable on the basis of gonopores, with the former possessing a single gonopore and two gonopores in the latter. However, *D. australis*, which Faubel (1983) assigned to *Thalamoplana*, possesses a single gonopore, a feature which was confirmed by examination of the type specimens, while *D. insularis* Hyman, 1955 has the male and female systems opening at essentially the same point, which as Prudhoe (1985) has observed, is intermediate between the condition present in the type species of the two genera. For the present, Faubel's (1983) separation of *Discocelis* from *Thalamoplana* is accepted but *australis* is considered, following Prudhoe (1985), to be a

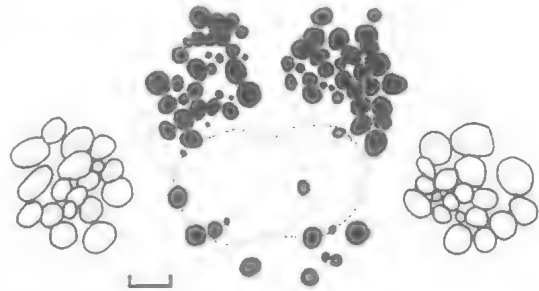


FIG. 9. *Discocelis* sp., cerebral organ, tentacular and cerebral eyes showing variation between individual specimens. Scale bar = 0.1mm.

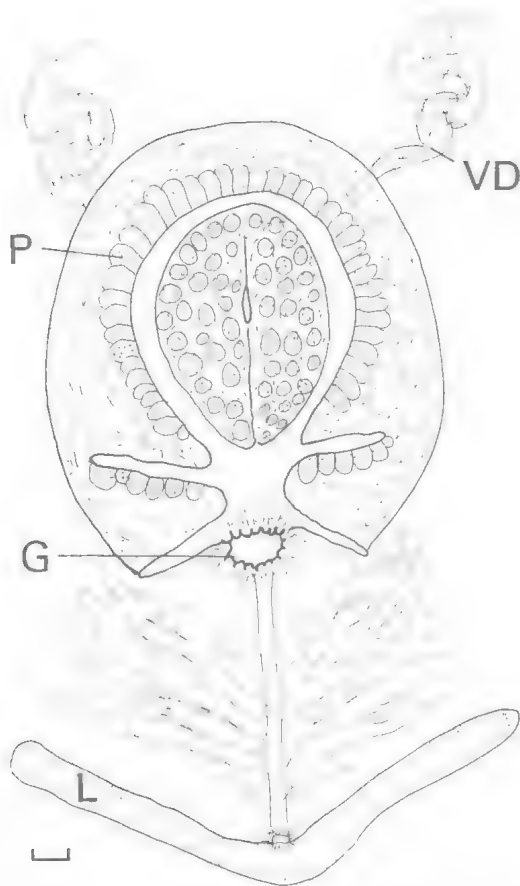


FIG. 10. *Discocelis* sp. gonopore and genital complex, ventral view. G = gonopore; L = Lang's vesicle; P = prostatoids; VD = vas deferens. Scale bar = 0.1 mm.

member of *Discocelis*. Both species described above are therefore assigned to *Discocelis* which consists of *D. australis*, *D. tigrina* (Blanchard, 1847), *D. fulva* Kato, 1944, *D. japonica* Yeri & Kaburaki, 1918 and *D. pusilla* Kato, 1938. The type species, *D. lichenoides* (Mertens, 1832), is considered unrecognisable (Hyman, 1959; Faubel, 1983; Prudhoe, 1985) and was treated as a species inquirenda by Faubel (1983).

Within *Discocelis*, the first species described above is immediately distinguishable from all congeners on the basis of the extent of the eyes, which in other species extend only as far as the region of the cerebral organ but in this species extend to, or almost to, the posterior end of the body. The marginal eyes also extend to the posterior part of the body in *Adenoplana* and *Coronadena*. The species described here differs from all congeners except *D. australis* in

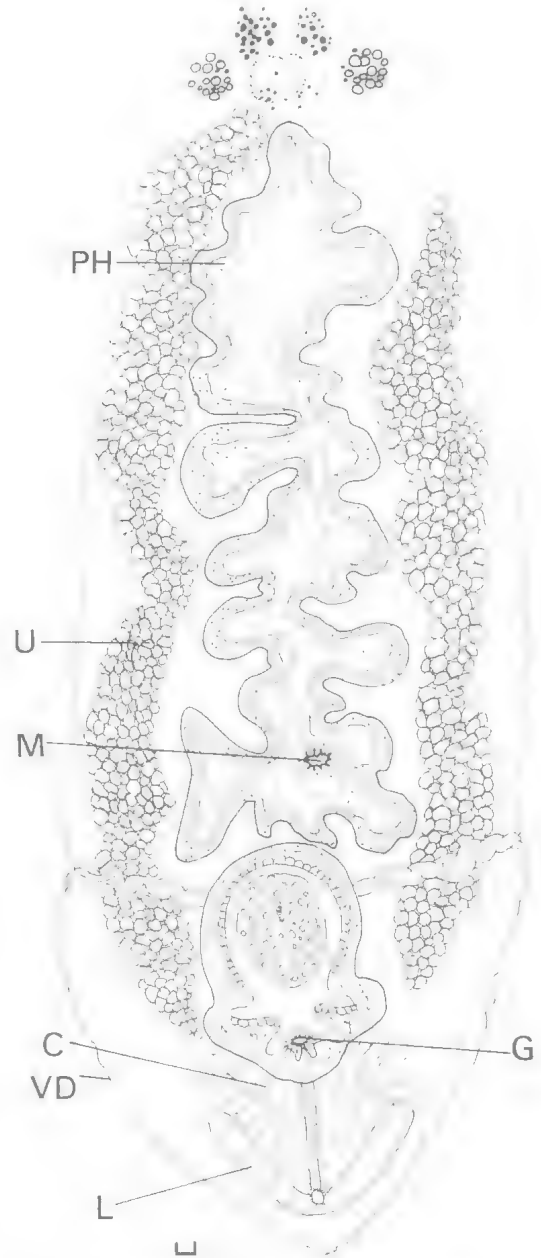


FIG. 11. *Discocelis* sp., ventral aspect showing cerebral organ, eyes, pharynx and genital complex. C = cement glands; G = gonopore; L = Lang's vesicle; M = mouth; PH = pharynx; U = uterine duct; VD = vas deferens. Scale bar = 0.1 mm.

possessing a seminal vesicle, though this was described as a muscular organ in *D. australis* by Hyman (1959) but has a thin, highly eosinophilic wall in the specimens described above. The specimens described here differ from *D. tigrina*



FIG. 12. *Discocelis* sp., median sagittal section showing mouth, gonopore and histological details of genital ducts. C = cement glands; IN = intestine; L = Lang's vesicle; P = prostatoids; VD = vas deferens. Scale bar = 0.1mm.

and *D. australis* in having a male antrum which forms five distinct lobes in dorsoventral views. In both of the other species the antrum is rounded, based on plate 13, fig. 1 of Lang (1884) for *D. tigrina* and observations of the type specimens in the case of *D. australis*. The morphology of the male antrum in dorsoventral view has not been described for the remaining species. The separation of the cerebral eyes into two clusters separates the species described here from *D. tigrina*, *D. australis* and *D. fulva* and the colour pattern of the dorsal surface, with numerous brown circular areas separates the species from *D. fulva* which lacks a distinctive pattern (Kato, 1944). The two types of prostatoids, one with eosinophilic content and the other with basophilic content may also distinguish this species from all congeners, although Kato (1944, fig. 2) illustrated two types of prostatoids in *D. fulva*, but did not describe the differences shown in the illustration. The morphological differences noted therefore indicate that the described specimens represent a new species for which the name *D. parvimaclata* is proposed based on the small size of the dorsal maculae compared with other

species in which the patterns on the dorsal surface have been adequately described.

The second species described above is distinguishable from *D. australis* and *D. parvimaclata* in lacking a seminal vesicle and from the latter species in having the marginal eyes restricted to the anterior region of the body. It differs from *D. tigrina* in having the mouth at the posterior end of the pharynx rather than in the middle and in having the cerebral eyes divided into anterior and posterior groups. In addition, the arrangement of the prostatoids in ventral view (Fig. 10) differs from that found in *D. tigrina* in which they are arranged in a U-shaped cluster around the anterior half of the penis papilla, with two lateral rows extending posteriorly (Lang, 1884, pl. 13, fig. 1).

The species is therefore most closely related to *D. fulva*, *D. japonica* and *D. pusilla*, all from Japan. The specimens are distinguishable from *D. fulva* since this species has no dorsal colour pattern, has numerous cerebral eyes arranged in a

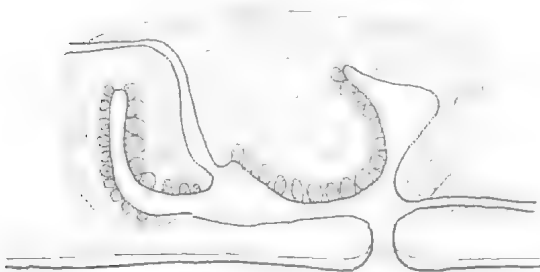


FIG. 13. Schematic representation of genital atrium of *Discocelis tigrina*, redrawn from Lang (1884).



FIG. 14. Schematic representation of genital atrium of *Discocelis pusilla*, redrawn from Kato (1938).

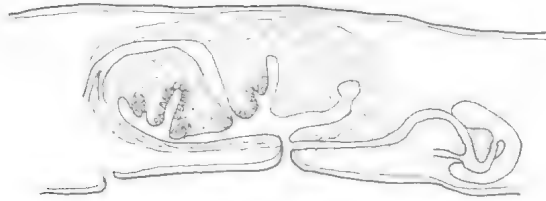


FIG. 15. Schematic representation of genital atrium of *Discocelis fulva*, redrawn from Kato (1944).

single elongate group and, according to the illustrations of the species, has prostatoids of two distinct sizes (Kato, 1944, fig. 2) (Fig. 15).

D. japonica differs in having 15-16 eyes in each posterior cerebral cluster rather than the 4-7 in the present specimens, and differs in the anatomy of the antrum masculinum and distribution of prostatoids (Fig. 16). In *D. japonica*, there are a number of projections into the antrum apart from the penis papilla, while in the current specimens only the penis papilla projects into the antrum. In addition, in *D. japonica*, a particularly elongate projection, lying dorsal to the vagina bears numerous prostatoids on both surfaces (Kato, 1937, fig. 2), while in the present specimens, the region of the antrum anterior to the vaginal opening is devoid of projections and prostatoids. Unfortunately, no ventral views of the antrum of *D. japonica* have been published. Finally, there are prostatoids in the ventral wall of the antrum in the current species and these are lacking in *D. japonica*.

The species described here is most similar to *D. pusilla* in colour pattern, having eyes restricted to the anterior part of the body, mouth at the posterior end of the pharynx and cerebral eyes divided into anterior and posterior clusters with only one or two ocelli in the posterior clusters (Kato, 1938). The genital atrium is also similar in that there is, according to the illustration of the species (Kato, 1938, fig. 3) a large penis papilla projecting into the antrum masculinum (Fig. 14), although Kato (1938) stated in the description that there were many muscular villus-like projections, as in *D. japonica*. Furthermore, there are no prostatoids in the posterior region of the antrum. The most obvious differences between the present specimens and *D. pusilla* are that there appear to be very few prostatoids in the antrum of *D. pusilla* and that prostatoids do not occur in the ventral wall of its antrum.

However, Kato's (1938) specimens of *D. pusilla*, were evidently immature as he describes the prostatoids as rudimentary and Lang's vesicle as being represented merely by a mass of nuclei. As a consequence, the number and distribution of prostatoids may not have been reliably determined in *D. pusilla*. The current specimens may therefore be *D. pusilla* or may represent a new species. However, since only two specimens are available and since *D. pusilla* has been inadequately described, no new name is proposed for them.

The descriptions presented here indicate that *Discocelis* is represented in Australia by several species rather than the single species, *D. australis*, currently known (Hyman, 1959). While one of the two additional species found can unequivocally be identified as new, limitations in the descriptions of existing species prevent a definitive name being applied to the second species.

The descriptions presented above suggest that in addition to the distribution of marginal eyes, the occurrence of cerebral eyes in a single band or two groups, and the presence of a seminal vesicle, the distribution of prostatoids within the antrum masculinum as seen in ventral views of cleared specimens provide useful taxonomic characters. In *D. tigrina*, the prostatoids are arranged in an arc anterior to the gonopore (Lang, 1884), in *D. parvimaculata*, the prostatoids are arranged in a cluster in the anterior lobe of the antrum and along the postero-lateral margins while in the un-named species the prostatoids occur throughout the penis papilla and are present along the posterior margin of one pair of lateral diverticula within the male antrum. The type specimens of *D. australis* were examined but they are now very dark and the distribution of prostatoids cannot be determined. In the remaining species, this character has not been investigated, but current observations suggest that it might provide additional features for the separation of species within the genus *Discocelis*.

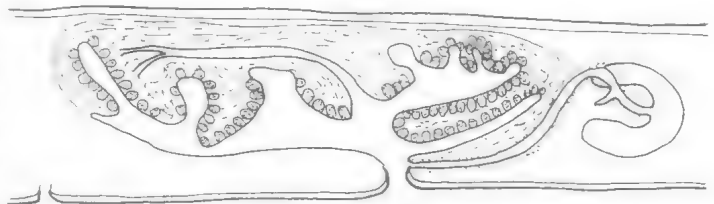


FIG. 16. Schematic representation of genital atrium of *Discocelis japonica*, redrawn from Kato (1944).

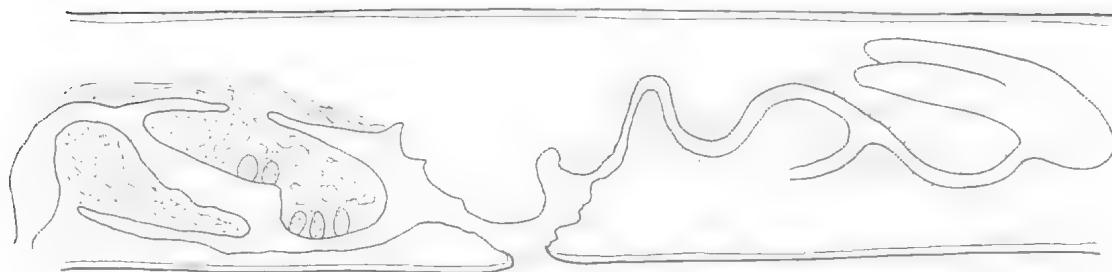


FIG. 17. Schematic representation of genital atrium of *Discocelis australis*, redrawn from Hyman (1959).

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Dr L.R.G. Cannon of the Queensland Museum is thanked for comments on a draft of this manuscript.

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NOTOPLANA DUBIA (SCHMARDA) (PLATYHELMINTHES: POLYCLADIDA) FROM QUEENSLAND

I. BEVERIDGE AND T.H. CRIBB

Beveridge, I. & Cribb, T.H. 2000 06 30. *Notoplana dubia* (Schmarda) (Platyhelminthes: Polycladida) from Queensland. *Memoirs of the Queensland Museum* 45(2): 215-220. Brisbane. ISSN 0079-8835.

The intertidal polyclad *Notoplana dubia* (Schmarda) (Platyhelminthes) is reported for the first time from Australian coastal waters in Queensland. The significance of morphological differences observed between the Queensland specimens and the original descriptions are discussed as well as relationships with congeners in Australia and southeast Asia. □ *Polycladida*, *Acotylea*, *Notoplana dubia*, new record.

I. Beveridge, Department of Veterinary Science, University of Melbourne, Parkville 3052, Melbourne, Australia; T.H. Cribb, Department of Microbiology & Parasitology, University of Queensland, St Lucia 4072, Australia; 28 April 1999.

Species of the polyclad genus *Notoplana* Laidlaw, 1903 occur commonly in the intertidal zone in southern Australia (Prudhoe, 1981, 1982). The commonest species, *N. australis* (Schmarda, 1859), has a wide distribution, ranging from South Australia to Sydney (Prudhoe, 1981, 1982) and occurs also in New Zealand. Of the remaining known species, *N. longiducta* Hyman, 1959 and *N. longisaccata* Hyman, 1959 have been described from the Sydney region, while *N. distincta* Prudhoe, 1982 and *N. longicrumena* Prudhoe, 1982 occur in South Australia (Hyman, 1959; Prudhoe, 1981, 1982). No species have been reported from northern Australian waters although several members of the genus occur in New Britain and southeast Asia (Prudhoe, 1985).

Faubel (1983) subdivided *Notoplana* based on the presence or absence of a penis stylet and transferred *N. longiducta* and *N. longisaccata* to a new genus, *Notocomplana* Faubel, 1983, leaving *N. australis*, *N. distincta* and *N. longicrumena* in *Notoplana*. Prudhoe (1985) adopted a less formal approach, subdividing the genus into four groups to facilitate identification, the subdivision being based on the presence or absence of a penis stylet, penis papilla and penis sheath. Prudhoe's (1985) groups A and B correspond with Faubel's (1983) definition of *Notoplana*. Therefore, based on Faubel's (1983) definition, there are currently three species of *Notoplana* in southern Australia, all occurring south of the latitude of Sydney.

This paper reports the finding of a species of *Notoplana* from northeastern and southeastern Queensland and its identification as *N. dubia* (Schmarda, 1859), the type species of the genus.

METHODS

Polyclads were collected at low-tide from under rocks on exposed mud-flats. Mangroves (*Avicennia* spp.) were the dominant trees on the shorelines. Fixation followed the technique of Newman & Cannon (1995) in which polyclads were placed on filter paper in a dish of sea-water and when fully extended, the filter paper was rapidly placed on a block of frozen fixative, either 4% formaldehyde in sea-water or formaldehyde-calcium acetate-propylene glycol-propylene phenoxetol. Following fixation, worms were dehydrated in a graded series of ethanols, cleared in methyl salicylate and mounted in Canada balsam. One polyclad was stained in Mayer's haematoxylin prior to dehydrating and clearing. The median posterior sections of two polyclads were removed using a scalpel blade, embedded in paraffin and serial longitudinal sections, cut at a thickness of 7µm, were stained with Gill's haematoxylin and eosin. Drawings were made with a drawing tube attached to an Olympus BH microscope. All measurements are in millimetres and are presented as the range for 10 specimens.

All specimens collected have been deposited in the Queensland Museum (QM).

Specimens from Queensland were compared with the type specimens of *Centrostromum dubium* from the Naturhistorisches Museum, Vienna (NMV) and of *Notoplana evansi* Laidlaw, 1903, now a junior synonym, from the British Museum (Natural History) (BMNH). In addition other specimens in BMNH and the Swedish Museum of Natural History, Stockholm (SMNH) were examined and compared with those from Queensland.

POLYCLADIDA Lang, 1884
 ACOTYLEA Lang, 1884
 LEPTOPLANIDAE Stimpson, 1857

Notoplana dubia (Schmarda, 1859)
 (Figs 1-6)

Centrostromum dubium Schmarda, 1859
Imogene truncata Schmarda, 1859
Leptoplana dubia Lang, 1884
Notoplana evansi Laidlaw, 1903

MATERIAL. Four specimens, Port Denison, 5km S of Bowen, Qld, (20°2'S, 148°12'E) coll. I. Beveridge, 3.vii.1994 (QM G217332-5, serial sections G217343); 2 specimens, Scarborough, Moreton Bay, Qld, (27°12'S, 153°7'E) coll. T.H. Cribb, 15.v.1994 (G217336-7); 4 specimens, Wellington Point, Moreton Bay, Qld, (27°27'S, 153°14'E) coll. T.H. Cribb, 11.v.1994, 8.iii.1995, 1.ix.1997 (G217338-41, serial sections G217342).

DESCRIPTION. Large, oval polyclads; mature specimens 22-30 long, 13-16 wide; immature specimens 18-20 long, 9-11 wide; dorsal surface brown, darker in centre, ventral surface pale grey; nuchal tentacles diminutive, 3.9-5.6 from anterior margin; cerebral organ 0.54-0.57 × 0.52-0.61; eyes arranged in two elongate groups, on either side of mid-line, 45-55 anterior to cerebral organ, 15-18 posterior to cerebral organ; mouth 6.8-8.0 posterior to cerebral organ; ruffled pharynx in mid-body, with 10-16 lateral folds; male genital pore 2.8-3.9 posterior to mouth; antrum masculinum elongate, with folds; penis papilla elongate, prominent, with distinctive penis sheath; penis stylet prominent, 0.57-0.65 long, sclerotised, brown in colour; ejaculatory duct convoluted, leads to spherical prostate with epithelial tubes lying parallel to ejaculatory duct; seminal vesicle large, muscular, convoluted, passes dorsally then ventrally, terminating blindly; vasa deferentia enter seminal vesicle anterior to its extremity, coil posterolaterally then turn anteriorly to testes. Female genital opening 2.0-2.8 from male antrum, 4.6-6.5 from posterior end; vagina externa prominent with thick walls, leading to elongate, horizontal vagina media surrounded by masses of cement glands; vagina media passes anteriorly almost to level of male genital opening, terminating in blind diverticulum; diverticulum clearly visible in sections, not distinguishable in whole mounts; posterior to diverticulum, vagina interna passes dorsally either as sinuous tube, or, in less mature specimens in a coil, then leads posteriorly; uterine canals empty into vagina interna immediately anterior to termination of vagina in inconspicuous Lang's vesicle; no histological differentiation noted between vagina interna and Lang's vesicle;

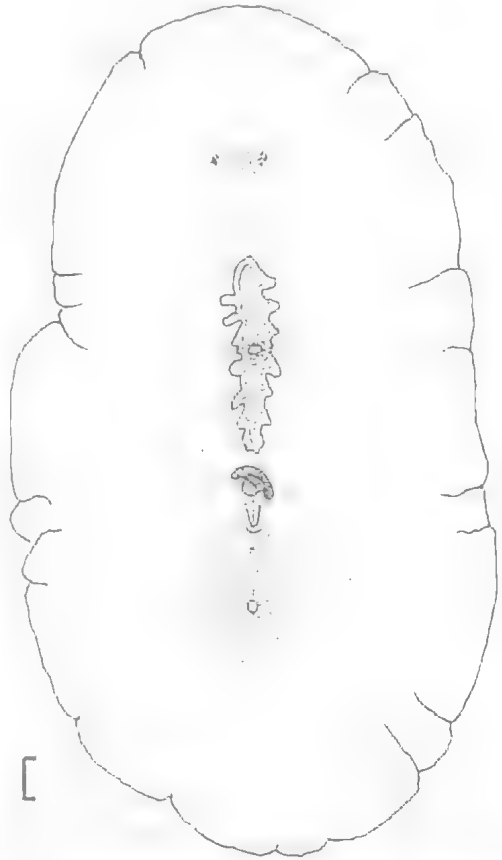


FIG. 1. *Notoplana dubia*, whole polyclad. Scale bar = 1mm.

uterine canals extend anteriorly on either side of pharynx.

DISCUSSION

The polyclad described above belongs to *Notoplana*, as defined by Faubel (1983), since it lacks a sucker, possesses cerebral and tentacular but not marginal eyes, an interpolated prostate subdivided into longitudinal chambers and a prominent penis stylet. The species belongs to Prudhoe's (1985) group A since it possesses both a penis stylet and a penis sheath. It most closely resembles the type species, *N. dubia*, in possessing a large, muscular, convoluted seminal vesicle, an elongate vagina media surrounded by cement glands and an extremely diminutive Lang's vesicle.

N. dubia has been described on a number of occasions. The original description by Schmarda (1859) is very brief but Stummer-Traunfels (1933) provided a comprehensive redescription

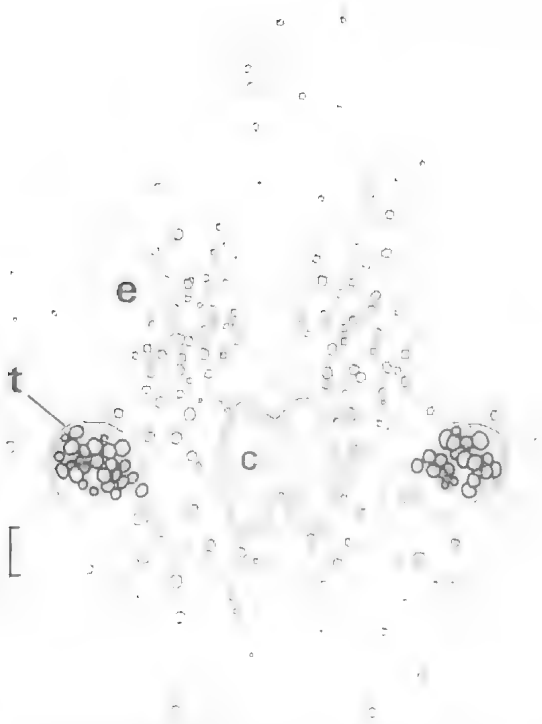


FIG. 2. *Notoplana dubia*, tentacles and cerebral organ. c = cerebral organ; e = eye; t = tentacle. Scale bar = 0.2mm.

based on the original specimens. The original description of Laidlaw's (1903) species, *N. evansi*, was poor, but the species was redescribed in some detail by Bock (1913), prior to the name being made a synonym of *N. dubia* by Stummer-Traunfels (1933). Hence, there is ample published data on the anatomy of *N. dubia*. The specimens described above from coastal Queensland agree in virtually all respects with published descriptions of the anatomy of *N. dubia*, with the exception of the diverticulum of the vagina media present in the Queensland specimens, which is not mentioned in any of the published descriptions. The type specimen in NMV was examined (NMV 13345) but consisted only of the anterior half of the specimen preserved in alcohol; the serial sections of the posterior region of the body were missing. The type of *N. evansi* (BMNH 1949.13.19.7) consists of the anterior part of the body mounted in balsam and nine slides of transverse serial sections. Because of the transverse orientation of the sections, the features of the vagina interna were not easy to distinguish, but there was no obvious indication of a diverticulum or of a coiled or sinuous ascending vagina. In the specimens of *N.*

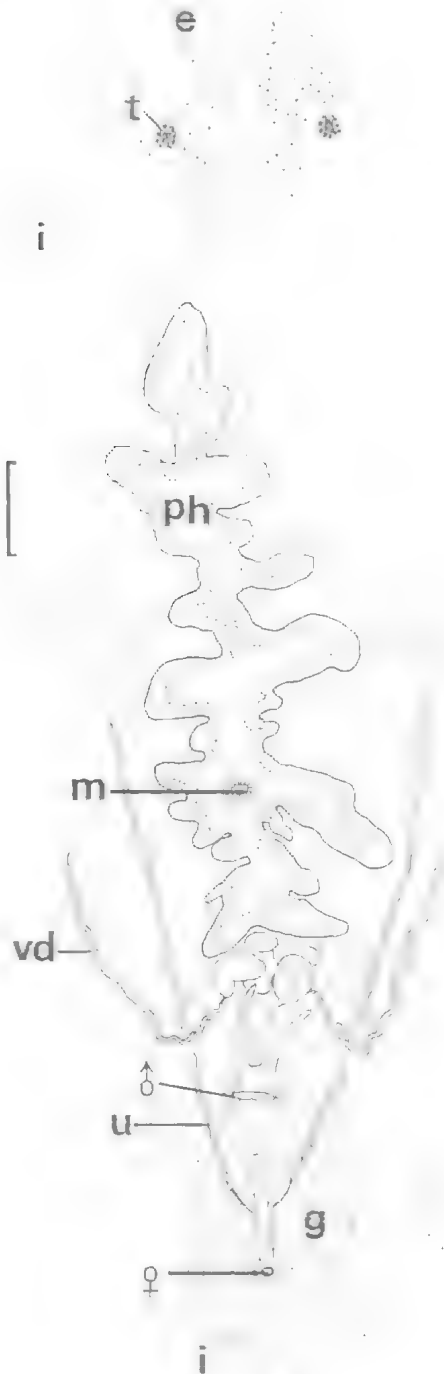


FIG. 3. *Notoplana dubia*, mouth and pharynx, showing positions of male and female genital openings. e = eye; g = cement glands; i = intestine; m = mouth; ph = pharynx; t = tentacle; u = uterine duct; vd = vas deferens. Scale bar = 0.5mm.

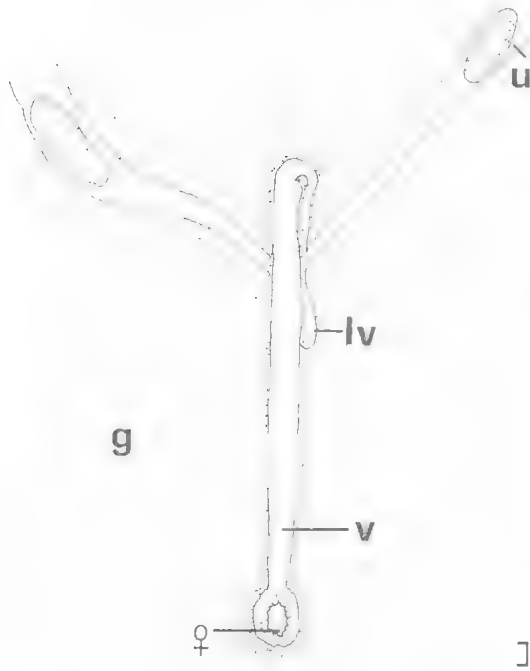


FIG. 4. *Notoplana dubia*, female genital system, ventral view. g = cement glands; lv = Lang's vesicle; u = uterine duct; v = vagina. Scale bar = 0.1mm.

dubia described by Prudhoe (1950) from Burma (BMNH 1950.10.24.8) however, the diverticulum of the vagina media, while not particularly elongate, was evident and the ascending part of the vagina interna was straight. Bock's (1913) material consists of one whole mount and 20 slides of serial sections. The vagina media was clearly visible only in one specimen and a diverticulum was detected. In this specimen, the vagina media was widely dilated with sperm while the diverticulum contained no sperm and had only a small lumen. The lack of prominence of the diverticulum may be the reason it was apparently overlooked by Bock (1913). Assuming that Bock's (1913) and Prudhoe's (1950) specimens are correctly identified, it appears that the vagina media of *N. dubia* has a prominent, anteriorly directed diverticulum. The specimens described above are identical with those of *N. dubia* identified by Bock (1913) and Prudhoe (1950). The form of the ascending region of the vagina interna appears to be variable and may be

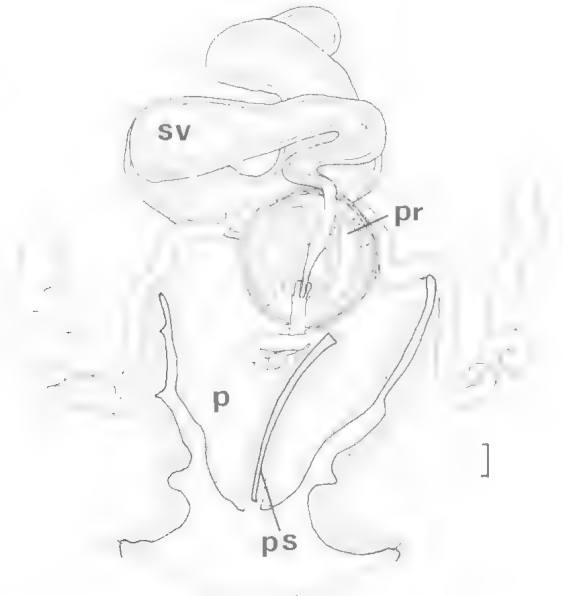


FIG. 5. *Notoplana dubia*, male genital system, ventral view. p = penis; pr = prostate; ps = penis stylet; sv = seminal vesicle. Scale bar = 0.1mm.

coiled in immature specimens with the coils extending into a sinuous or straight duct as the animal matures. The necessity of caution in interpreting coiled or folded structures in polyclads which may be subject to maturation and method of fixation has been emphasised by Prudhoe (1985) and Cannon & Grygier (1991).

In spite of these limitations, the current specimens have been identified as *N. dubia*. However, the possibility cannot be excluded that the current descriptions of *N. dubia* include two species, one with and one without an anterior diverticulum to the vagina media.

Other species of *Notoplana* recorded by Prudhoe (1985) from the Indo-West Pacific region were *N. willeyi* Jacobova, 1906 from New Britain, *N. mortenseni* Bock, 1913 and *N. parvula* Palombi, 1924 from Borneo and *N. tavoyensis* Prudhoe, 1950 from Burma. *N. mortenseni* was transferred to *Pleioiplana* by Faubel (1983) and *N. tavoyensis* to *Notocomplana*.

N. willeyi was described from Blanche Bay, New Britain and is similar to *N. dubia* in many anatomical features, differing in being relatively narrower and in possessing a more obvious Lang's vesicle (Jacobova, 1906). Jacobova (1906) also distinguished *N. willeyi* from *N. dubia* (= *evansi*) based on colour, though there is no difference in colour between the two species

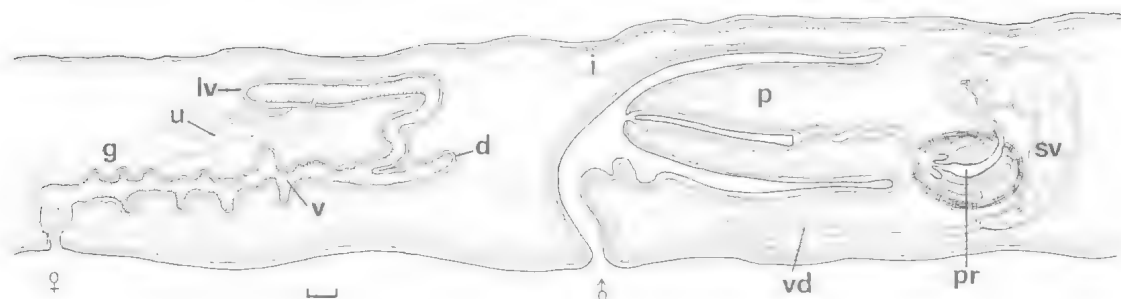


FIG. 6. *Notoplana dubia*, transverse section through genital openings. d = diverticulum; g = cement glands; lv = Lang's vesicle; p = penis; pr = prostate; sv = seminal vesicle; t = tentacle; u = uterine duct; v = vagina; vd = vas deferens. Scale bar = 0.1mm.

based on Willey's (1897) notes and those described above. She also distinguished the two species based on the position of the female genitalia, but the precise difference utilised were not specified (Jacobowa, 1906). Thus the differentiation of *N. willeyi* from *N. dubia* remains to be verified. Of particular interest in the description of *N. willeyi* is the illustration by Jacobowa (1906) (pl. 8, fig.8) of a small anterior diverticulum to the vagina media. Her sections were apparently slightly oblique making the significance of the diverticulum difficult to evaluate, but the structures illustrated warrant further investigation.

N. parvula is readily distinguishable from *N. dubia* since it possesses only a short vagina media and has far fewer cerebral eyes (Palombi, 1924, pl. 2, fig.15).

N. dubia is a widespread species occurring off the coasts of Burma, Malaysia and Sri Lanka (Bock, 1913; Stummer-Traunfels, 1933; Prudhoe, 1950). The present report extends this distribution to the east coast of Australia.

ACKNOWLEDGEMENTS

Thanks are due to Dr L.R.G. Cannon for comments on a draft of the manuscript, Dr Cannon and Dr R.A. Bray for help with obtaining relevant literature and to Drs D. Gibson, U. Jondelius and H. Stattmann for access to specimens in their collections.

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CIRRIPEDES AS PALAEOECOLOGICAL INDICATORS IN THE TE AUTE LITHOFACIES LIMESTONE, NORTH ISLAND, NEW ZEALAND

JOHN BUCKERIDGE

Buckeridge, J. 2000 06 30: Cirripedes as palaeoecological indicators in the Te Aute Lithofacies Limestone, North Island, New Zealand. *Memoirs of the Queensland Museum* 45(2): 221-225. Brisbane. ISSN 0079-8835.

The Te Aute lithofacies limestone complex lies on the east coast of New Zealand's North Island. It is comprised of a series of uniform to poorly bedded calcarenites and coquinas of late Neogene age. This limestone complex was deposited off-shore, to the east of the current land mass, and during the late Tertiary-Quaternary period was structurally accreted to the mainland as a series of longitudinal prisms. This paper reviews the current interpretation of the depositional environment, which implies a facies change in the limestone from shallow water in the west, to deeper water in the east. Primarily utilising barnacle palaeobathymetry, it is shown that one of the oldest and most westerly limestones (the mid-Pliocene Titiokura Limestone) was deposited in moderately deep water.

Living barnacles have clearly defined bathymetric ranges and temperature tolerances. When barnacles are abundant in fossil remains, especially of late Cainozoic age, they are often useful palaeoenvironmental indicators. The barnacle fauna of the Titiokura Limestone is characterised by the presence of the deep water balanomorph *Pachylasma*. Species of *Pachylasma* are widely distributed in the living shelf fauna, being found in middle to outer shelf environments, although on very rare occasions specimens may be found living in waters as shallow as 55m. Therefore, on the basis of the abundant and comparatively well preserved plates of *Pachylasma*, it may be inferred that the Titiokura Limestone accumulated in moderately deep, off-shore conditions.

This interpretation is confounded however, by the presence, in the same horizons, of a species of an exclusively intertidal balanomorph, *Epopella*. Whilst it is apparent that the bathymetric ranges of some taxa change through time, all known species of *Epopella* are demonstrably intertidal to uppermost subtidal. They are also characteristic of temperate waters.

Sedimentological observations suggest that the Titiokura limestone is a mixed thanatocoenosis that accumulated in the middle to outer shelf environment. Shallow water elements were introduced as components within submarine avalanches and slurry deposits. Intertidal temperature regimes were probably similar to those currently existing along the New Zealand coastline. □ *Te Aute lithofacies limestone, balanomorph cirripedes, Quaternary, palaeobathymetry, palaeotemperatures, submarine avalanches.*

John Buckeridge, Auckland University of Technology, P.O. Box 92006, Auckland, New Zealand; 7 July 1998.

Cirripedes (barnacles) are very much a Cainozoic phenomenon. Charles Darwin was so taken with their post-Cretaceous abundance that he described Tertiary seas as abounding 'with species of *Balanus* to an extent now quite unparalleled in any quarter of the world' (Darwin, 1854). The Sessilia, or 'acorn' barnacles, are also the ocean's great opportunists, their choice of substrate, both animate and inanimate, being unparalleled amongst the invertebrates. Many sessile barnacles have become sufficiently specialised to be host specific (Buckeridge, 1998). Cirripede palaeoecology is a relatively recent pursuit (Foster & Buckeridge, 1987), with barnacles traditionally interpreted by non-cirripede specialists as shallow water taxa. However improved sampling techniques, in conjunction with deep

ocean surveys and recent advances in cirripede phylogeny and biogeography, show a distribution extending well beyond shelf and slope, with taxa recorded from depths in excess of 4000m (Buckeridge, 1997; 1999).

What is of great interest however, is the palaeoecological inferences that we can make regarding balanomorph barnacles through time. The earliest confirmed balanomorphs are known from the Palaeocene of the Chatham Islands (Buckeridge, 1983; 1993; 1996). These include taxa within the genera *Bathylasma* and *Pachylasma* in what, from sedimentological and associated faunal associations, are clearly shallow water sediments (Buckeridge, 1993). No deep water sessilians are known from the early Palaeogene.

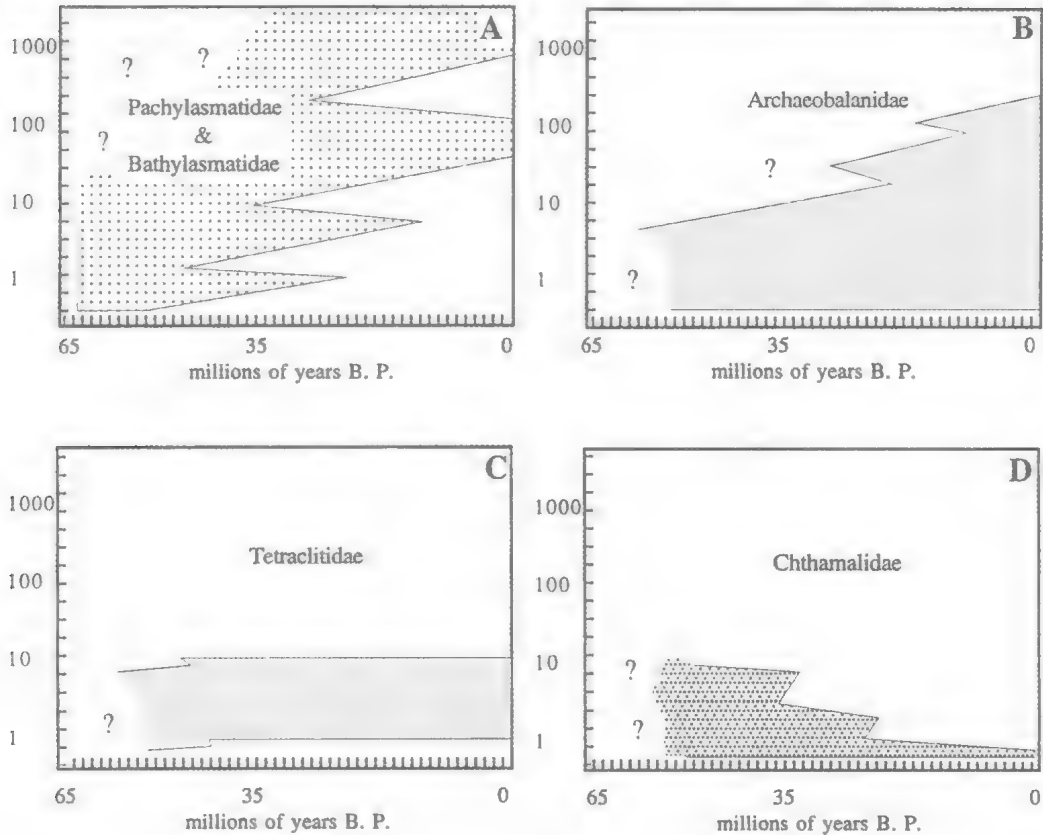


FIG. 1. Schematic representation of preferred environments for 'primitive' balanomorph families in time. Vertical scale: estimated water depth (in metres). A, Pachylasmatidae and Bathylasmatidae; B, Archaeobalanidae; C, Tetracitidae; D, Chthamalidae. All taxa are interpreted as arising in shallow water environments, with the absence of pachylasmatids and bathylasmatids from shallow water, and chthamalids from all except the uppermost intertidal, being a result of competition, particularly from selected archaeobalanids and the balanids. The balanids become abundant in the Miocene, with many species being characterised by active feeding, high metabolism and early onset of sexual maturity.

The first deeper water balanomorphs are recorded from the earliest Miocene, Cape Rodney Formation in Auckland's Hauraki Gulf (Buckeridge, 1983). There, large numbers of disarticulated plates of *Bathylasma aucklandicum* (Hector, 1888), are found in beds surrounding fossil sea mounts. The inferred depth of deposition for these beds is in excess of 100m. In the Neogene, species of *Bathylasma* and *Pachylasma* are not found in shallow water facies anywhere, with only one living species, *Pachylasma japonica* Hiro, 1933, being found occasionally at depths of less than 80m. The deepest water balanomorph known is the bathylasmatid *Tetrachaelasma tasmanicum* Buckeridge, 1999, which is extremely abundant, both living and as 'sub-fossil', adjacent to deep sea mounts of the

South Tasman Rise in depths of 2200-3600m. Preliminary investigations of the balanomorph fauna at, and adjacent to, these sea mounts show distinct zonation of the Sessilia, with the balanomorph species *Bathylasma alearum* (Foster, 1978), and the verrucosomorph *Altiverruca gibbosa* (Hoek, 1883) restricted to a shallower zone of 800-2300m. An important characteristic of the deep sea barnacle accumulations is that they have a very low biodiversity. This is certainly the case with the *Tetrachaelasma* beds on the South Tasman Rise; further, the lowest horizons of the Cape Rodney Formation contain abundant *Bathylasma aucklandicum*, but rarely any associated macro-fauna except another deep water barnacle, *Metaverruca recta* (Aurivillius, 1898). Interestingly, stratigraphically higher

fossiliferous horizons in the Cape Rodney Formation are supplemented by an influx of shallow water elements, introduced as 'turbid slurries'.

Modern shallow water and intertidal environments in New Zealand and Australia are dominated by chthamalids, tetracitids and balanids (Fig. 1). The first two groups are known only from shallow water; chthamalids, in particular, are confined to the upper littoral zone, whilst tetracitids extend to the middle littoral. Providing no evidence of transportation can be demonstrated, this restriction makes both of these families very useful in defining shallow water marine facies.

THE TE AUTE LIMESTONE COMPLEX

The Te Aute lithofacies limestone is a dominant part of the physiography of the central to southern east coast of New Zealand's North Island (Fig. 2). It is comprised of a series of uniform to poorly bedded calcarenites and coquinas of late Neogene age. This limestone complex was deposited off-shore, to the east of the current land mass, and during the late Pliocene-Quaternary was structurally accreted to the mainland as a series of longitudinal prisms.

The term 'Te Aute Limestone' was first used in 1887 by James Hector in his summary of Alexander McKay's geological report for the region (Hector, 1887; MacKay, 1887). At that time, Te Aute was the name of an area characterised by extensive limestone outcrops, south of Hastings in central Hawke's Bay. The term 'Te Aute lithofacies limestone' was coined by Beu (1995) and reflects a greater complexity in the limestones of the region than was perhaps perceived by earlier authors, such as Kingma (1971) and Beu et al. (1980). Beu (1995) established that the Te Aute lithofacies limestone was deposited from Tongaporutuan to early Nukumaruan age (late Miocene to earliest Pleistocene).

Of particular note is the type and nature of the biota comprising the Te Aute lithofacies limestone. Unlike tropical limestones, which are characterised by high levels of lime mud (Campbell et al., 1988), the temperate conditions under which the Te Aute lithofacies limestone was deposited has resulted in a much higher proportion of skeletal material. Of particular interest here is the remarkable dominance of barnacle remains in many horizons. Kamp et al. (1988) recognise the barnacle content to be approximately 13-22% of total rock volume, with the highest percentage characteristic of the Scinde Island Formation (outcropping near Napier). The

most impressive 'cirripede dominated lithologies', however, occur in horizons of the Castlepoint Formation, also of Nukumaruan age, which outcrop to the southeast of the Te Aute limestones. In a coarse coquina outcropping at Castlepoint, I have estimated balanomorph content (primarily *Fosterella tubulatus* (Withers, 1924)), to be close to 50%.

PALAEOENVIRONMENT OF THE TE AUTE LITHOFACIES LIMESTONE

Although barnacle limestones are not common, sediment dominated by shells of the barnacles *Notobalanus vestitus* (Darwin, 1854) and *Austrorhynchobalanus decorus decorus* (Darwin, 1854), is currently accumulating at depths of 30m in the Hauraki Gulf, Auckland. Inner to middle shelf deposits, dominated by species of the balanomorph *Fosterella*, were a feature of cooler southern seas in the Pleistocene (Buckeridge, 1983). However, with the extinction of *Fosterella* in the early Holocene, no barnacle species has moved to dominate the shelf environment to the same degree.

Better sampling and recording of the living fauna in recent years has shown that balanomorph barnacles can be significant contributors to sediments forming at depths of 2000m or more (e.g. extensive beds of *Tetrachaelasma* spp. are known from the Southern Ocean off Madagascar, Chile, Cape Horn and Tasmania). In some of these locations, the barnacle shells are found to comprise more than 90% of the calcitic remains (Newman & Ross, 1971; Buckeridge, 1999).

The balanomorph shells preserved in the Te Aute lithofacies limestone are comprised of calcite rather than aragonite (as for many bivalve molluscs). The greater chemical stability of calcite has contributed to the dominance of balanomorphs in many limestone horizons, although this is not the prime factor for their abundance. The environment suited barnacles, especially the now extinct *Fosterella tubulatus* that is so common in Nukumaruan lithologies. Apart from molluscs, the other relatively abundant groups preserved are bryozoans, which possess both aragonitic and calcitic skeletons. According to Kamp et al. (1988), bryozoans never reach the abundance of the barnacles in the Te Aute lithofacies limestones.

PALAEOTEMPERATURES. Barnacles are generally of value in interpreting palaeotemperatures through association, e.g. species of the reef coral symbionts *Hexacreusia* and *Creusia* are characteristic of tropical seas. The

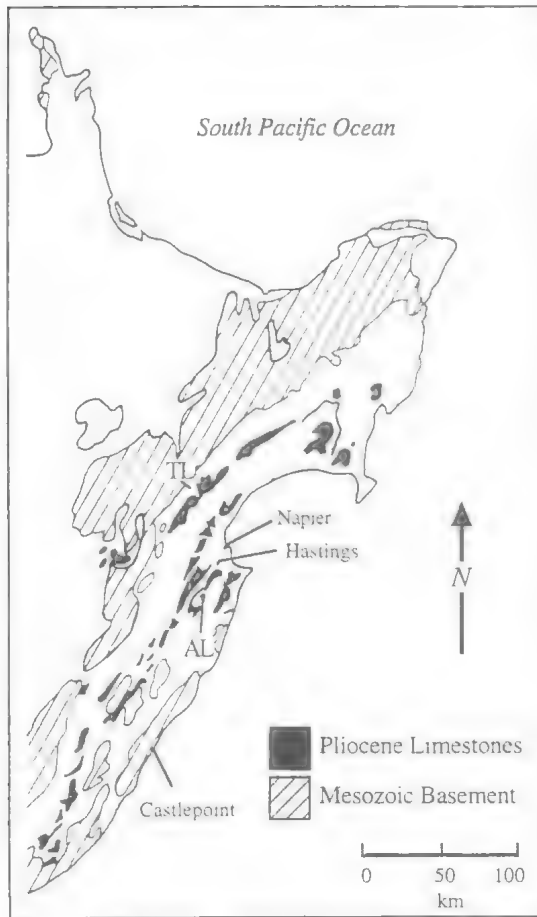


FIG. 2. East coast of New Zealand's North Island, showing localities mentioned in text and distribution of Pliocene 'Te Aute lithofacies limestones' and Mesozoic Basement. TL = summit outcrop of the Titiokura Limestone, AL = Kahuranaki outcrop of the Awapapa Limestone. (Modified from Kamp et al., 1988).

tetraclitid, *Austrobalanus imperator* (Darwin, 1854), is currently known from shallow tropical and subtropical seas off central and northeast Australia. It has also been recorded from the Oligocene of the South Island, a period when sea temperatures were at least as warm as the present. Not surprisingly, it is not found in present New Zealand waters. Species of *Epopella*, another tetraclitid, are found throughout New Zealand and Southern Australia. *Epopella* sp. is also present in the Awapapa Limestone, outcropping on the slopes of Mount Kahuranaki (Fig. 2). Chthamalids are useful indicators of temperature, with the endemic New Zealand species *Chamaesipho brunnea* (Moore, 1944) restricted

to warm, temperate intertidal environments. Beu (1995) and Milliman (1974) suggest that the Te Aute lithofacies limestone was deposited in 'shallow subtidal waters'. If this is accepted, the absence of intertidal species (with thick, solid shells like *C. brunnea*), indicates that temperatures were likely to have been cool temperate. This is consistent with the molluscan evidence of Beu (1995).

PALAEOBATHYMETRY. Current interpretation of the depositional environment (Kamp et al., 1988; Beu, 1995), implies a facies change in the limestone deposits, from shallow water in the west, to gradual deepening conditions in an easterly direction. Further to the east again, shallower conditions developed, with the uplift of the East Coast Highlands. It is perceived that a broad NE-SW trending, open seaway, with strong tidal currents (the 'Ruataniwha Strait') characterised the waters between the two land masses.

In Kamp et al. (1988) and Beu (1995) it is proposed that 'large carbonate sand dune-forms' colonised by a barnacle-bivalve-bryozoan assemblage, formed at the margins of the Ruataniwha Strait, and in a moderately high energy 'tidal' environment, migrated to deeper water (i.e. mid-channel). However, Beu (loc. cit.) also refers to Milliman (1974) who states that the porous nature, low resistance to abrasion and fragility of barnacle plates ensures that they 'do not survive transportation from living sites of more than a few tens of metres'. Strong cross bedding, with tangential foreset beds in tabular sets is recognised by Beu (loc. cit.) as confirming that the depositional environment was shallow, and dominated by strong tidal currents.

There are some unusual anomalies here, particularly in light of the barnacles present in some mid-Waipipian limestones in the west and central regions. The Titiokura Limestone, outcropping to the northwest, is characterised by a mixed assemblage of barnacles, including *Pachylasma* sp., *Austromegabalanus miodecorus* Buckeridge, 1983, and *Epopella* sp. c.f. *E. plicata* (Gray, 1843). The Awapapa Limestone, which outcrops in the central region south of Hastings, also possesses a mixed barnacle assemblage, including *A. miodecorus*, *Notobalanus vestitus*, *Fosterella tubulatus* and *Epopella* sp., but lacking *Pachylasma*. As discussed earlier, *Pachylasma* comprises exclusively deep water taxa; further, like *Epopella* the shell is non-porous. If the shell is moderately thick, as is the case with large specimens of *Epopella*, it is

likely that transportation, albeit with some abrasion, is possible for distances of many hundreds of metres. What is even more important is that *Epopella* is found in the same horizons as *Pachylasma*.

ANALYSIS

A revised sedimentary regime for the New Zealand mid-Pliocene is proposed here. Utilising barnacles as indicators of palaeobathymetry, it is suggested that the western deposits, such as the Titiokura Limestone, represent a depositional environment in water depths of 100m (or more). Shallow water sediments, building up on the margins of the Ruataniwha Strait, were triggered by local overloading, and perhaps micro-seisms, to carry intertidal elements, including *Epopella*, as slurries into the deeper water. The process, although not unlike traditional turbidites, differs primarily in scale, with the distances sediment being transported, and the energy involved in that process, being at least an order of magnitude less than anticipated in 'flysch' deposition. Nonetheless, the mixed thanatocoenosis that the Titiokura Limestone represents is consistent with deposition from a submarine avalanche, which, during the process of its journey, incorporated intertidal (*Epopella*), subtidal (*Austromegabalanus*) and deep water elements (*Pachylasma*).

It is also proposed that the Awapapa Limestone, with a barnacle fauna comprising elements from intertidal (*Epopella*), subtidal (*Austromegabalanus* and *Notobalanus*) and upper-mid shelf (*Fosterella*) environments, formed in a similar manner, but was deposited at depths of only 30-40m. Although there are some similarities, the Awapapa Limestone almost certainly formed in slightly shallower conditions than the extraordinary '*Fosterella coquinas*' of the Castlepoint Formation, outcropping further to the south.

ACKNOWLEDGEMENTS

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EASTERN RANGE EXTENSION FOR *MORETHIA RUFICAUDA* COURTESY OF A CAT STOMACH.

Memoirs of the Queensland Museum 45(2): 226. 2000.- Identification of mammalian remains from predator pellets and seats has provided valuable information on the distributions of many species. Smith (1977) identified 14 species of native mammals that had not been previously recorded in the Flinders Ranges of South Australia from owl pellet deposits found in caves. More recently, analysis of carnivore seats led to a number of significant range extensions of species that are rare and/or difficult to detect using conventional fauna censusing techniques (for example Meek & Triggs, 1997 and references within).

Such techniques have not been as successful for reptiles, which usually lack the hard body parts required for identification following passage through the gut of a predator. Stomach contents of predators, however, offer a better chance of identifying reptile remains to species level. Probably the best known result from this type of sampling was the rediscovery of the Adelaide pygmy blue-tongue (*Tiliqua adelaidensis*) from the stomach of an eastern brown snake (*Pseudonaja textilis*) in 1992 (Armstrong & Reid, 1992). This note reports a considerable range extension for *Morethia ruficauda* following the identification of this species from the stomach of a feral cat from Diamantina Lakes National Park in far-western Queensland.

The skink remains (hindbody, pelvic region and tail base) were found in the stomach of a male cat shot by the Park Ranger during the day at the Diamantina Gates (23°42'S, 141°08'E) on the 14th June 1994. The remains were identified on the combination of size and colouration, particularly the width, intensity and position of the pale dorsolateral stripes, and the reddish tail base (QM J63647). The seasonally dry shrublands and stony hills of the Hamilton Range that the Diamantina River cuts at the Diamantina Gate is very similar to the preferred habitat of *M. ruficauda* described by Cogger (1992).

Cogger (1992) lists the distribution of *M. ruficauda* as the northwestern section of the continent, from west of the Northern Territory/Queensland border, extending to the Western Australian coast and north to the Northern Territory coast. More recently, *M. ruficauda* was recorded in the spinifex dunefields of the northern Simpson Desert (23°46'S, 138°28'E) in western Queensland (Downey & Dickman, 1993), and from Lawn Hill National Park in far northwestern Queensland (18°35'S, 138°35'E) (McKay & Clarke, 1999). No voucher specimens were collected from these sites. A number of *M. ruficauda* were also previously observed on the limestone ridges at the Riversleigh fossil site (75km southeast of Lawn Hill National Park) in May 1987 (P. Couper, pers. comm.). A voucher specimen of this species from Riversleigh (20km northwest of the homestead) was collected in May 1989, but has only recently been lodged with the Queensland museum (QM J71441).

McFarland (1992) failed to uncover any further records of this species in an extensive review of historical information on the fauna of the Channel Country bioregion of southwestern Queensland. Our record extends the known range of this species by approximately 270km in an easterly direction from the Simpson Desert record and over 600km to the southeast from the Lawn Hill National Park observation.

A review of cat diets by Dickman (1996) found that reptiles were relatively common dietary items during summer especially in drier areas. Cats tend to prey mostly on nocturnal species and dragons, which reflects their nocturnal hunting habits. However, under the dry conditions experienced in the Diamantina region during 1994, cats were commonly seen hunting on mild winter days. This type of behaviour was not observed in the subsequent years of the study when conditions improved and staple prey species were more abundant (R. Palmer, pers. obs). Thus, it is not surprising that cat stomachs collected during 1994 contained a large number of diurnal reptiles.

Acknowledgments

This work was part of a larger study on feral cats funded by Environment Australia. Thanks goes to 'Chook' Robertson for providing this and other cat stomachs.

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R.A. Palmer, Department of Zoology and Entomology, University of Queensland, St Lucia, 4072; G.M. Shea, Department of Veterinary Anatomy and Pathology, University of Sydney, Sydney 2006, Australia; 5 September 1999.

STEM CASTS OF *LEPTOPHLOEUM AUSTRALE* (MCCOY) WALTON AND THE RESPONSE OF THEIR LEAF-CUSHION BASES TO COMPRESSION

H. TREVOR CLIFFORD AND MICHAEL R. PEMBERTON

Clifford, H.T. & Pemberton, M.R. 2000 06 30: Stem casts of *Leptophloeum australe* (McCoy) Walton and the response of their leaf-cushion bases to compression. *Memoirs of the Queensland Museum* 45(2): 227-233. Brisbane. ISSN 0079-8835.

The distribution patterns of the widths of leaf-cushion bases on the surfaces of *Leptophloeum australe* casts may be used to determine whether they were elliptical or circular in section prior to their compression. Given the outline shape of a cast and its maximum width and length in section the diameter of the original stem can be calculated. □ *Leptophloeum*, cast, leaf-cushion, compression.

H. Trevor Clifford, Queensland Museum, PO Box 3300, South Brisbane 4101; Michael R. Pemberton, University of Queensland, St Lucia 4072, Australia; 10 July 1998.

Casts and moulds of *Leptophloeum australe* (McCoy) Walton have been reported from Upper Devonian and Lower Carboniferous fresh-water deposits throughout Laurasia (Anderson & Anderson, 1985; Cai & Wang, 1995; Dawson 1862, McCoy, 1874) and Gondwana except for South America and Antarctica (Edwards & Berry, 1991). The absence of the species from these two continents may merely reflect inadequate collecting because in those times they were closely connected with the remainder of Gondwana (Scotese & McKerrow, 1990).

The casts derive mainly from the infilling of hollow stems whose central tissues decayed leaving only a thin sheath of outer cortex and leaf-cushion bases. The evidence for the stems of *Leptophloeum* being herbaceous is compelling. None of the casts studied taper and none bear the scars of shed branches as do those of *Lepidodendron* (*Ulodendron*); the outlines of the leaf-cushion bases, irrespective of the cast diameter, are all of the same shape and meet along their margins; in contrast the leaf-cushion bases on larger *Lepidodendron* casts are often laterally distended and are more or less separated thereby confirming that they grew out from stems which had experienced secondary growth. Assuming the stems of *Leptophloeum* were herbaceous they may be compared with those of present-day *Agave* spp. which shortly after flowering rapidly decay except for a sheath of encircling leaf-bases. Though *Agave* stems are initially erect and circular in section (Fig. 1) the dying or dead flowering stems soon topple to the ground where, under the influence of gravity, they become elliptical in outline. As a result of the slow decay of the sheathing leaf-bases, with

the passage of time, the minor axis of the ellipse becomes shorter and its major axis longer.

Infilling and burial of the hollow stems of *Leptophloeum australe* results in the formation of internal casts on whose surfaces are imprinted the outlines of the leaf-cushion bases as seen from the centre of the stem (Fig. 2A). Their outlines are rhomboidal and they have concave surfaces (Fig. 2C). Therefore the leaf-cushion impressions on moulds derived from these casts are rhomboidal in outline with convex surfaces. Casts of whole stem segments with details of the stem surfaces preserved thereon are rare and readily distinguished from internal casts. Depending upon the amount of decay experienced by the stem surface, prior to the formation of the cast, the outlines of the leaf-cushion bases are more or less distinct but their surfaces are always convex (Fig. 2B,D). Consequently the surfaces of the leaf-cushion bases on moulds derived from such casts are concave.

By far the majority of casts derive from decaying stems which are aligned parallel to the bedding planes of the host sediments. In section these casts are elliptical in outline with their major axes disposed parallel to the bedding planes and so are presumed to have formed from axes that had toppled over at the site of growth or had been transported to a swamp before infilling. Only two casts with cylindrical sections have been noted. One had eroded from its investing matrix and was collected from a surficial deposit (Queensland Mines Department L1526); the other was erect and preserved in situ (Morris, 1977).



FIG. 1. Erect decaying stem of *Agave vivipara*.

MATERIAL AND METHODS

An internal cast of *Leptophloeum australe* which is elliptical in section and has the pattern of leaf-cushion bases preserved over its whole surface was the starting point for these studies (Clifford, 1996). Assuming, that before burial and compression, the cast was circular in section, the length of its perimeter, was ascertained by multiplying the number of leaves per whorl by the width of the least distorted leaf-cushion base on its surface. Using this length the diameter of the uncompressed stem was calculated. The result revealed that the length of the major axis of the elliptical cast and that of the diameter of the uncompressed circular cast were similar thereby confirming that during compression the width of the cast had not expanded in the plane at right angles to the direction of the applied pressure. Therefore, it can be assumed that when compressed, buried casts suffer little or no lateral expansion. Because the shape and width of leaf-cushion bases in each whorl are similar, their distribution around a circular stem may be expressed as equal arcs on the perimeter of the circle which results from sectioning the stem at right angles to its length. Likewise, the distribution of leaf-cushion bases around the perimeter of the ellipse derived by compression of a circle may also be represented by a series of

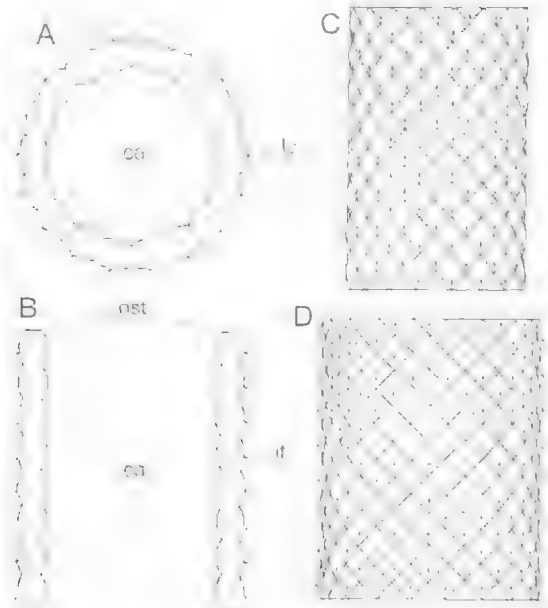


FIG. 2. Diagrammatic view of a decaying stem of *Leptophloeum australe* and two casts derived therefrom; A, transverse section of stem; B, longitudinal section of stem; C, internal cast; D, stem cast. ca, cavity; lc, leaf-cushion; lt, leaf-trace; ost, outer stem tissue.

equal-length arcs. The procedure for determining the co-ordinates which define the margins of the individual leaf-cushion bases around the perimeter of an ellipse is complex. However, with the advent of symbolic manipulators such as Maple, mathematical problems like those encountered in this paper are easily solved. Maple V Release 4 was chosen to furnish these results as described in Appendix 1. Whereas during the compression of a circle into an ellipse the length of its perimeter is conserved, the length of the major axis of the ellipse always exceeds the diameter of the parent circle (Fig. 3).

To explore the responses of leaf-cushion base widths to compression, a circular cast of unit diameter (for practical purposes the unit employed was 100mm) with 32 leaves per whorl was taken as a model. This number of leaves was chosen both because it is close to that observed on the cast previously studied (Clifford, 1966) and is exactly divisible by four thereby giving a whole number per quadrant. The theoretical responses of leaf-cushion bases to compression were investigated for the four uncompressed elliptical and one circular cast whose sections are illustrated in Fig. 3. The perimeters of all sections

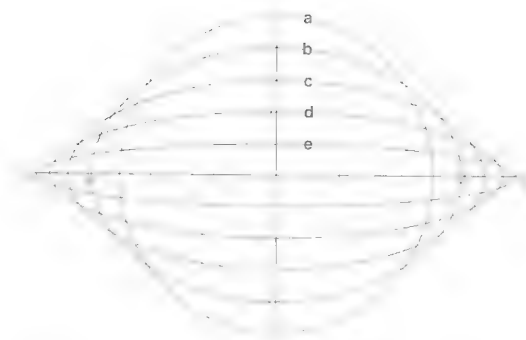


FIG. 3. Circle (a) and four of the ellipses (b-e) which result from its compression.

are of the same length and each bears the same number of evenly distributed equal-sized leaf-cushions. The circular cast was subjected to four levels of compression (Fig. 4) and the elliptical to 3, 2 and 1 level respectively (Fig. 5). The dispositions of the leaf-cushion bases around the perimeters of the sections of the theoretical casts may be calculated as arc lengths but because of the irregularities which occur on cast surfaces it is customary to measure the widths of their leaf-cushion bases in terms of the chord lengths joining their margins. Therefore to permit direct comparisons of the amount of change in the widths of leaf-cushion bases which occurs during compression, chord rather than arc lengths were investigated throughout this study. With theoretical models chord lengths are calculated from the co-ordinates which define the boundaries of the leaf-cushion bases, but on casts the chord lengths are measured directly with a pair of dividers.

RESULTS

The relationships between arc and chord lengths for two leaf-cushion bases from the same whorl about the perimeter of two casts, one of which is circular and the other elliptical in section, are shown in Table 1.

The manner in which the widths of leaf-cushion bases, expressed as chords, vary on the surfaces of theoretical casts of *Leptophloeum* that have been subjected to several levels of compression are given in Table 2 for an initially circular, and in Table 3 for initially elliptical, casts. In both Tables the width of the leaf-cushion bases is expressed as a fraction of that prior to their compression.

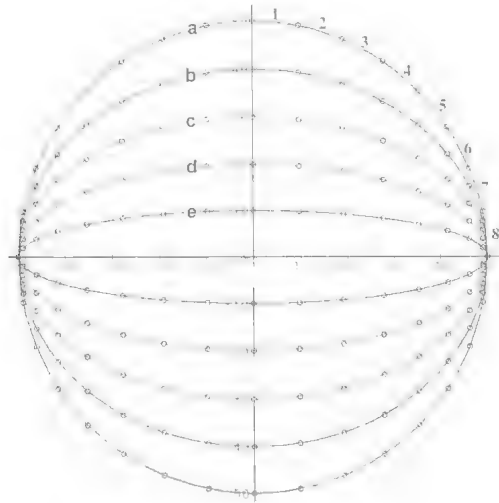


FIG. 4. Circle (a) and four of the ellipses (b-e) which result from its compression subject to the condition that the major axes of the ellipses and the diameter of the circle have of the same length.

DISCUSSION

Whereas for a circle the relationship between chord and arc lengths is constant for leaf-cushion bases arranged around its perimeter, with an ellipse this relationship depends on the position of the leaf-cushion base on its perimeter (Table 1). On surfaces of little curvature arc and chord lengths are similar, but when the curvature is considerable arc lengths are conspicuously longer than chord lengths. Nonetheless, except where the curvature is extreme, the difference between the length of the chord and its associated arc is insufficient for the former not to stand as a surrogate for the latter. Indeed, the greater the compression the more closely the chord length approximates to the arc length on surfaces of minimum compression (Table 1). It is clear from

TABLE 1. Chord lengths expressed as a fraction of their associated arc lengths for two nodes on the perimeters of a circle and those of four ellipses derived therefrom by compression. a-e and 1-8 as in Fig. 4.

Perimeter	Chord length	
	Node 1	Node 8
a	0.99839	0.99839
b	0.99947	0.99486
c	0.99981	0.98393
d	0.99994	0.96106
e	0.99999	0.95799

TABLE 2. Relative widths of leaf-cushion bases expressed as a fraction of their original widths for eight nodes around a quadrant of the perimeters of four elliptical casts derived by compression without lateral expansion of one initially circular in section. b-e and 1-8 as in Fig. 4.

Node no.	Length of minor axis of ellipse as a percentage of the diameter of the parent circle			
	80 (b)	60 (c)	30 (e)	20 (d)
1	1.00	1.00	1.00	1.00
2	0.99	0.97	0.96	0.96
3	0.96	0.92	0.90	0.89
4	0.92	0.86	0.81	0.78
5	0.89	0.79	0.71	0.66
6	0.85	0.71	0.59	0.50
7	0.82	0.64	0.48	0.35
8	0.80	0.61	0.41	0.22

Tables 2 & 3 that irrespective of whether the cast was originally circular or elliptical in section, the widths of leaf-cushion bases, respond in a similar, though not identical, manner to compression.

Furthermore, the amount by which successive leaf-cushion bases differ in width around the perimeter of the cast reflects both its original shape and the amount of compression it has experienced. If the original cast was circular in section a reduction in width by 10% or less is experienced only by those leaf-cushion bases immediately adjacent to the position of minimum curvature on its surface. That is, in proceeding from the position of minimum to that of maximum curvature on the cast surface there is a relatively rapid decrease in leaf-cushion base widths but the amount of decrease between successive nodes is not constant. Close to the positions of greatest and least curvature on the cast surface the difference in the widths of adjacent leaf-cushion bases is less than for pairs of leaves midway between the two (Fig. 6A).

In contrast, if prior to its compression the cast was elliptical in section, a reduction of 10% or less in width is experienced by several, rather than a few of the leaf-cushion bases close to the position of minimum curvature. Furthermore, in progressing from the position of least to greatest curvature on the surface of the cast the differences in the widths of successive leaf-cushion bases increases consistently (Fig. 6B). Therefore, provided they are sufficiently represented, the relative widths of successive leaf-cushion bases in the same whorl offer a reliable guide to the

TABLE 3. Relative chord widths of leaf-cushion bases expressed as a fraction of their original widths for eight leaves disposed around the perimeters of three families of ellipses each resulting from the compression of an ellipse. n-p,r-s and u as in Fig. 5; numbers 1-8 also as labelled in Fig. 5.

Node no.	Minor axis of initial cast/minor axis of compressed cast					
	40/30 (n)	40/20 (o)	40/10 (p)	30/20 (r)	30/10 (s)	20/10 (u)
1	1.00	1.00	1.00	1.00	1.00	1.00
2	0.99	0.99	0.99	1.00	1.00	1.00
3	0.98	0.97	0.96	0.99	0.99	1.00
4	0.96	0.93	0.91	0.98	0.97	0.97
5	0.93	0.87	0.84	0.96	0.94	0.98
6	0.88	0.78	0.71	0.93	0.88	0.96
7	0.81	0.65	0.53	0.85	0.75	0.92
8	0.76	0.52	0.30	0.70	0.45	0.68

cross-sectional shape of the cast before its compression.

GENERAL DISCUSSION

The shape of a cast prior to its compression though of interest, is often of less importance than a knowledge of the length of the diameter of the stem from which it derived. If the leaf-cushion pattern on an elliptical cast indicates it was originally circular in section, then the lengths of its major axis and that of the stem diameter are the same. However, if the pattern of leaf-cushion bases indicates that prior to its compression the cast was elliptical in section, estimation of the diameter of the original axis is more complicated. The complexity arises because two processes are involved. The first of these is the collapse, under the influence of gravity, of the original circular hollow stem into one elliptical in outline before becoming infilled to form a cast; the second is the response of that cast to compression. Because the girdle of leaf-cushion bases encircling the decaying circular stem forms only a narrow band of tissue its collapse under the influence of gravity results in the stem assuming one of an infinite number of elliptical outlines. The length of the major axis of this ellipse is fixed prior to its being infilled to form a cast (Fig. 1). With one exception, the lengths of the major axes do not provide a direct estimate of the size of the original cast. The exception is when the transectional area of the cast approaches zero in which circumstance the length of the perimeter of the ellipse approaches twice that of its major axis. Such ribbon-like casts are abundant and derive from hollow stems which have collapsed completely

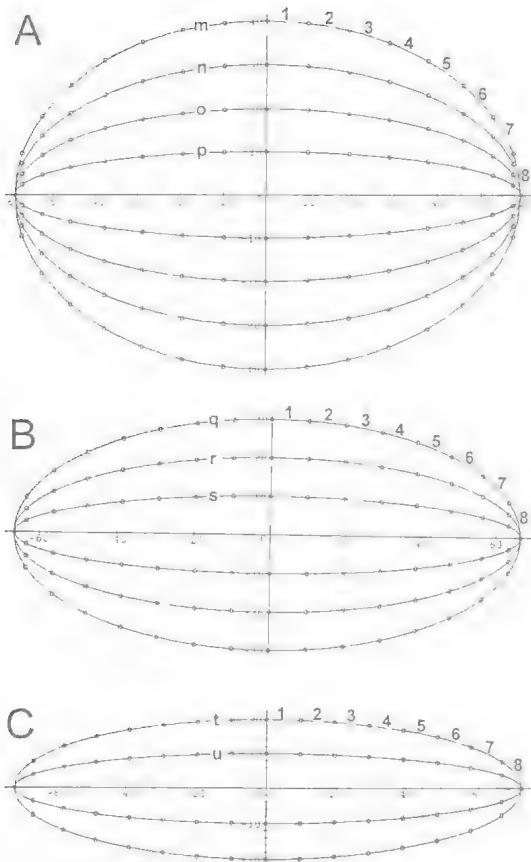


FIG. 5. Ellipses resulting from the compression of three ellipses (b-d of Fig. 4), each subject to the constraint that the length of its major axis is not affected by the compression.

or almost so, before being infilled to form a cast. The surface of such ribbon-like casts corresponds with that of the parent stems and so their leaf-cushion bases have convex surfaces (Fig. 2D).

When the minor axis of the elliptical section is much shorter than its major axis, the perimeter of the original circular stem can still be estimated provided the amount of compression is known. One estimate of this amount is provided by the cast previously reported upon (Clifford, 1996). During compression its cross-sectional area was reduced to 50% of the original. As this cast is typical of all others encountered it has been assumed that they too will have experienced a similar amount of compression. Therefore the lengths of minor axes of casts known to have been elliptical in section before compression will have been reduced by a half although their major axes will not have changed in length. The minor

axis of the uncompressed cast must be twice that of the observed cast, a statement that is confirmed by the following relationship between the area of an ellipse and that of its axes:

$$A = \pi ab$$

where A is the area of the ellipse, a is the length of its semi-major axis, b is the length of the semi-minor axis.

Given the lengths of the semi-major and semi-minor axes of an ellipse the length of its perimeter may be calculated. For high accuracy it would be necessary to use elliptical integrals to resolve the problem but for the present purposes the following approximation is sufficiently accurate:

$$P = \frac{\pi}{3}(a + b + \sqrt{8(a^2 + b^2)})$$

where P is the perimeter, a and b are defined as above.

It should be noted that to determine the perimeter of a cast prior to its compression the value of b to be employed is twice that observed on the compressed cast. The above discussion has assumed that the shape of the cast previous to its compression was determined from a study of the dimensions of the leaf-cushion bases on its surface. However, even if the leaf-cushion pattern is incomplete or absent an estimate of the diameter of the original cast is still possible assuming that during compression about half its volume has been lost. Accepting such loss the shape of a cast which is elliptical in section prior to compression may be determined by comparing the length of twice its minor axis with that of its major axis. If the two lengths are similar the original cast will have been circular in outline; if double the length of the minor axis is less than that of the major axis the original cast will have been elliptical in outline. These results stem from the simple relationship between the area of an ellipse (of which the circle is a special example) and the length of its two axes. Should twice the length of the minor axis exceed the length of the major axis it would follow that the cast had lost less than 50% of its original volume, a situation as yet not encountered. The procedure for determining the diameter of a stem whose cast was elliptical before its compression will now be demonstrated using data from a specimen in the collection of the Australian Museum (F6449). The outline of the cast as seen in transection is shown in Fig. 7 together with some points on the perimeter of the ellipse calculated from its maximum and minimum width. The close

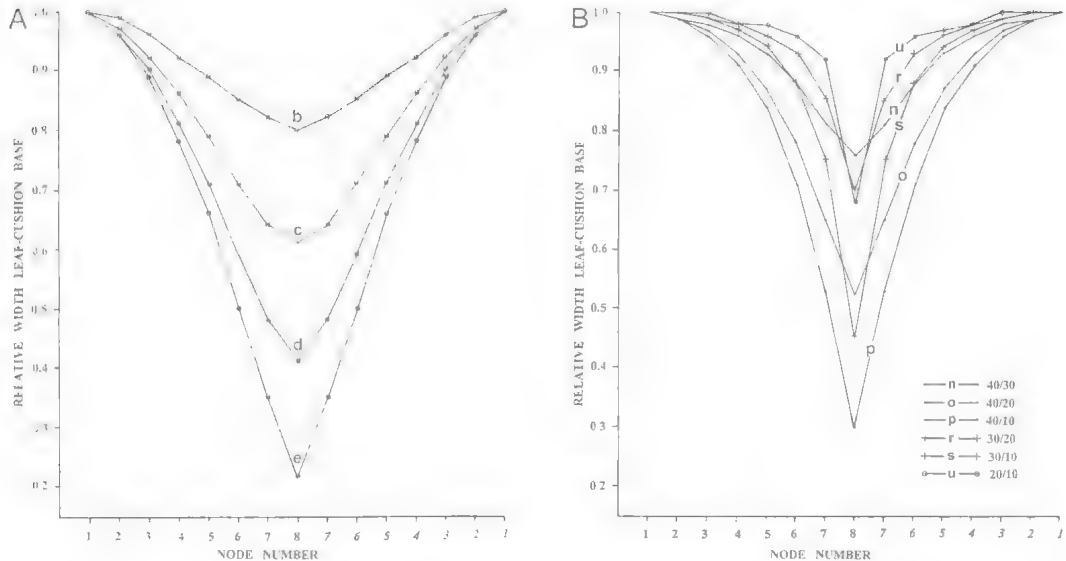


FIG. 6. A, The lengths of the leaf-cushion base widths, expressed as a fraction of their uncompressed value, for 16 leaves arranged around the semi-perimeters of the four ellipses (b-e) illustrated in Fig. 4; B, The lengths of leaf-cushion base widths expressed as a fraction of their uncompressed value for 16 leaves arranged around the semi-perimeters of the ellipses n-p,r,s and u illustrated in Fig. 5; node numbers 1-8 and their mirror images (*italics*) as in Figs 4 and 5.

agreement between the outline of the cast (Fig. 7, a) and the superimposed points supports the view that the cast arose by deformation of one which was circular in section.

Doubling the length of the minor axis of the ellipse (Fig. 7, a), without altering the length of its major axis results in a new ellipse (Fig. 7, b) which may be taken to represent the transectional outline of the cast prior to its compression. However, as it is postulated that the uncompressed cast arose by the infilling of a circular but hollow stem which had collapsed into an ellipse under the influence of gravity, the length of the perimeter of the uncompressed cast and that of the stem will be the same. The width of the persistent outer stem tissues within which the uncompressed cast is formed may be neglected for it is small compared with the diameter of the cast. The perimeter of the uncompressed cast may be calculated from the formula cited above, and using the result, the diameter determined of a circle with the same length perimeter. This circle (Fig. 7, c) may be taken to represent the outline of the original stem. It should be noted that whereas the transectional area of the compressed cast is only 40% that of the stem it is 50% that of the uncompressed cast. The difference between these two numbers arises because during the deformation of a circle into an ellipse the length of the perimeter is unchanged

but the enclosed area is reduced. Had cast F6449 resulted from the direct compression of a specimen which was circular in section it would have lost c. 80% of its volume. In this circumstance the length of the diameter of the uncompressed cast and that of the major axis of the compressed elliptical cast would have been the same. If such a large loss of volume is acceptable, the width of the uncompressed cast would be intermediate between the length of the major axis of the cast and that of the diameter of a circle derived on the assumption that the hollow stem had collapsed into an ellipse before infilling and then losing 50% of its volume. At present only one cast is known whose surface pattern is sufficiently well preserved to allow its precompression, transectional area to be estimated with confidence. Therefore until further data are available it is necessary to accept that 50% compression of *Leptophloeum* axes is the norm, at least in eastern Australia, and to use this value together with the maximum and minimum widths of casts to calculate their precompression diameters.

ACKNOWLEDGEMENTS

It is a pleasure to thank the Director of the Australian Museum and Dr Sue Palfrey of the Queensland Mines Department for providing hospitality and access to the collections in their

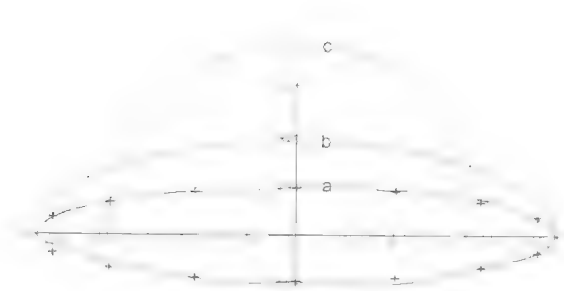


FIG. 7. Outline of an internal cast of *Leptophloeum australe* (Australian Museum F6449) as seen at right angles to its length (a). Points on the perimeter of an ellipse whose major and minor axes are the same lengths as the maximum and minimum widths of the cast (+). Ellipse whose major axis is the same length as that of the cast but twice its area in section (b). Circle with same perimeter as that of ellipse b (c).

charge; Dr Alex Cook for his critical appraisal and support of the project; Natalie Camilleri for her conversion of my rough drawings and diagrams into such fine Figures.

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APPENDIX 1

Method of calculation using symbolic manipulator; Maple V Release 4. Maple V Release 3, 4 or 5 can be used for the determination of the various calculations required in this paper and these problems are now discussed in general. Given the circumference of a circle, so that its diameter can be calculated, it is required to find the major and minor axes of ellipses which result from keeping their perimeters fixed as that of the original circle, but whose minor axes are reduced to some fraction of its radius. To find the perimeter of an ellipse it is necessary to calculate an elliptical integral which must be evaluated numerically. In fact, the perimeter is given by:

$$P = 4 \int_0^{\frac{\pi}{2}} \sqrt{a^2 \cos^2 u + b^2 \sin^2 u} du$$

where a and b are the semi-major and semi-minor axes of the ellipse. Maple allows the setting up of this integral in terms of a and b and, once the circumference of the original circle is ascertained, it is possible to calculate the semi-major axes of the ellipses whose semi-minor axes are reduced in a given ratio of their original value (Fig. 3). To do this a numerical method must be set up which starts with an initial approximation to the solution and then uses a steepest descent method to generate closer and closer approximations to the required solution. The degree of accuracy can be chosen as desired. Once the new ellipses have been found the positions of the margins of the leaf-cushion bases must be calculated. Again this must be done numerically. If it is assumed that the leaves are equally spaced around the perimeters of the ellipses then, since the perimeters have been calculated, the arc lengths corresponding to the widths of the leaf-cushion bases are known — it was assumed there were eight leaves per quadrant (see Fig. 4). A similar steepest descent method is now used to step round the perimeter of the ellipse, successively finding the co-ordinates which define the margins of each leaf. This method was also used to produce Tables 2 and 3. Once the co-ordinates of these leaf-margins have been found, those on the contracted ellipses with the same major axes but smaller minor axes are found by merely holding their X co-ordinates constant and decreasing their Y co-ordinates in the appropriate ratios of the required contraction (see Fig. 4). Information on the Maple program can be obtained from M.R. Pemberton at e-mail mrp@maths.uq.edu.au

FOSSIL *TYPHA* IN AUSTRALIA. *Memoirs of the Queensland Museum* 45(2): 234. 2000;- Recent investigation of oil shales recovered from a bore put down in the Casuarina Basin, about 25km SE of Rockhampton, Queensland has revealed seeds and fruits in the sediments. These were encountered in the course of a palynological study and would have otherwise been overlooked on account of their small size. In a forthcoming paper the seeds have been assigned to Typhaceae and the fruits to Restionaceae (Dettmann & Clifford, in press). Because seeds of Typhaceae are operculate it is important they not be confused with moss capsules. The two are usually readily distinguished: unlike a seed the moss capsule is usually attached to a seta and has a peristome which is revealed when the operculum separates from the theca. However, if the moss capsule has become detached from its seta and lacks a peristome it will resemble a *Typha* seed whose chalazal region has been damaged. These considerations led us to reconsider the identity of *Muscites yallournensis* Clifford & Cookson which was described on the basis of a single specimen isolated from a sample of brown coal (Clifford & Cookson, 1953) of Miocene age from Yallourn (Blackburn & Sluiter, 1994).

A comparison of the cell structure of the operculum of *M. yallournensis* with that of the extant *Typha domingensis* Pers. revealed no significant differences (Fig. 1). Further support for the view that the specimen of *M. yallournensis* is a seed of *Typha* rather than a moss capsule is provided by the collar of cells from within which the operculum is shed and the ragged skirt of cells around the base of the supposed 'capsule'. Both of these are features of *Typha* seeds and are clearly visible on the photograph of the holotype of *M. yallournensis*. Accordingly, the species is here formally transferred to that genus.

Systematic Palaeobotany

TYPHACEAE

Typha yallournensis (Clifford & Cookson) comb. nov.
(Fig. 1A-C)

Muscites yallournensis Clifford & Cookson, 1953: 54-55.

MATERIAL. HOLOTYPE: NMV P15724; Latrobe Valley Coal Measures, Yallourn Seam; Miocene.

REMARKS. There are no previous reports of *Typha* (type species *T. latifolia* L.) from the Australian fossil flora though MacPhail et al. (1994) and Blackburn & Sluiter (1994) report the presence of macro- and/or microfossils with affinities to Typhaceae and Sparganiaceae but make no positive identifications to either. Therefore *Typha yallournensis* (Clifford & Cookson) comb. nov. becomes the first definite fossil record of the genus from Australia.

Elsewhere fossil *Typha* seeds have been described from Maastrichtian and younger sediments of Europe (Chandler, 1963; Collinson, 1983; Herendeen & Crane, 1995). Seeds of *T. latissima* A. Braun closely resemble those of *T. yallournensis* but until the anatomy of the latter is known the two species cannot be regarded as conspecific.

Acknowledgements

We thank the Director of the Museum of Victoria and Dr S. McLoughlin, University of Melbourne for arranging access to the negative of the holotype of *Typha yallournensis*.

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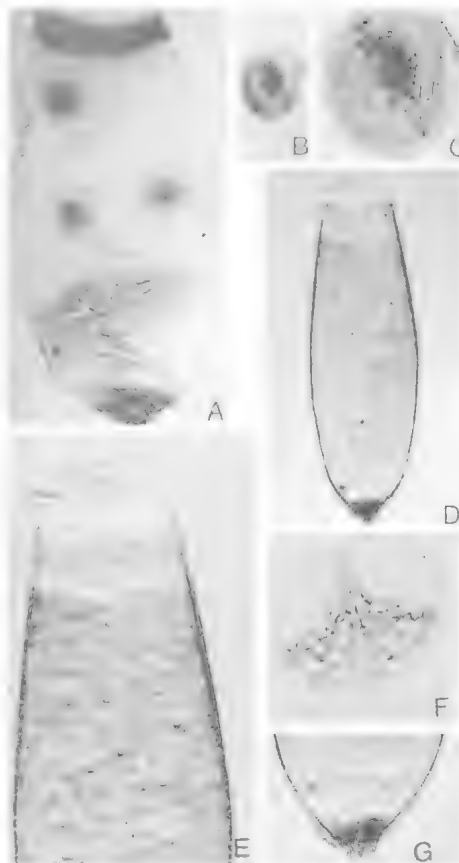


FIG. 1. *Typha yallournensis* (Clifford & Cookson) comb. nov. and *T. domingensis* Pers. A-C, *T. yallournensis*, holotype (NMV P15724). A, seed body showing chalazal region at base ($\times 60$). B-C, detached operculum ($\times 60$ and $\times 120$). D-G, *T. domingensis*. D, E, G, QM F50036 seed showing partially detached operculum and chalazal region at base (D, $\times 33$, E, $\times 133$, G, $\times 50$). F, specimen QM F50037, detached operculum in lateral view ($\times 133$).

fossil moss capsule from Yallourn, Victoria. The Bryologist 56: 53-55.

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H. Trevor Clifford, Queensland Museum, PO Box 3300, South Brisbane 4101, Australia. Mary E. Dettmann, The University of Queensland, St Lucia, 4072, Australia. 11 January 2000.

TRACE FOSSILS FROM THE UPPER CARBONIFEROUS JERICHO FORMATION, CENTRAL QUEENSLAND

ALEX G. COOK AND KERRIE BANN

Cook, A.G. & Bann, K. 2000 06 30: Trace fossils from the Upper Carboniferous Jericho Formation, central Queensland. *Memoirs of the Queensland Museum* 45(2): 235-251. Brisbane. ISSN 0079-8835.

A new trace fossil assemblage from lacustrine deposits of the Upper Carboniferous Jericho Formation, Joe Joe Group, Galilee Basin, Queensland, is described; it is similar to the *Umfolozia* ichnocoenosis found in other parts of Gondwanaland during the Late Carboniferous to Early Permian. The assemblage comprises exclusively of bedding-parallel tracks interpreted as arthropod locomotory traces, mainly *Tasmanudia glaussneri* ichnosp. nov., and *Alphaichnus alphaensis* ichnogen. et ichnosp. nov. Other new taxa are *Isopodichnus queenslandensis* ichnosp. nov., *Rusophycus devisi* ichnosp. nov. and *Wadeichnus maryue* ichnogen. et ichnosp. nov. □ *Trace fossils, Carboniferous, arthropod trails, Queensland.*

Alex G. Cook & Kerrie Bann, Queensland Museum, PO Box 3300, South Brisbane 4101, Australia; 10 September 1998.

Delicate and diverse trace fossil assemblages are known from Late Carboniferous to Early Permian of Gondwanaland, most notably the Dwyka Series, South Africa (Savage, 1971; Anderson, 1975, 1976, 1981), South America (Rocha-Campos, 1967; Aceñolaza & Buatois, 1991, 1993; Buatois & Mangano, 1993, 1994, 1995) and Australia (Chapman, 1929; Glaessner, 1957). Uniformity in these Gondwanan ichnofaunas allows recognition of inter alia *Umfolozia*, *Isopodichnus* and *Mermia* ichnocoenoses (Aceñolaza & Buatois, 1993) which are useful biogeographic and broad biostratigraphic indicators, as well as reflecting widespread glacial conditions or their onset. This paper is concerned with well-preserved trace fossils from shallow quarries of the Jericho Formation along the Sedgwick-Alpha Rd, SSE of Alpha, central Queensland (Queensland Museum Locality QML993).

The Jericho Formation is a dominantly fine-grained, siliciclastic unit forming part of the Joe Joe Group of the Galilee Basin. The unit was formally defined by Gray & Swarbrick (1975) who noted arthropod trails and suggested a lacustrine depositional environment in association with periglacial conditions. Biostratigraphic control on the Joe Joe Group was reviewed by Jones & Truswell (1992) who placed the Jericho Formation in the latest Carboniferous (Stephanian), postdating the onset of glaciation. In order to elucidate the depositional context for these trace fossils we examined recovered core from the same sequence.

DEPOSITIONAL SETTING

Examination of interval 770-740m in GSQ Jericho No. 1 (see Swarbrick, 1974: fig. 2) revealed a fining upward sequence, interpreted as a deepening alluvial to lacustrine environment (Fig. 1). At the base of the unit, unbioturbated, medium- to coarse-grained pebbly sandstone represents alluvial deposition. Above, the sequence grades to fine-grained sandstone with a *Macaronichnus* ichnofabric and possible escape traces, which we interpret as a deltaic environment. The sequence grades progressively into a bioturbated, interbedded sandstone and siltstone unit with sinuosity cracks, contorted bedding and flame structures, possibly reflecting influx of sediment due to storms or seasonal input in a lacustrine environment. The upper portion of this unit is composed of pinstriped siltstone and very fine-grained sandstone with *Tasmanudia*. This part of the sequence we interpret to represent seasonal varves. The trace fossil assemblage is interpreted as a *Rusophycus* ichnofacies. The top 7.5m of the section contains bioturbated, interbedded very fine-grained sandstone and siltstone and reflects deposition in a distal, quiet lacustrine environment. The sequence is overlain by a series of prograding deltaic deposits.

RUSOPHYCUS ICHNOFACIES. In this study the eponymous ichnogenera are not italicised (following Bromley, 1996), because it is a facies and not an ichnotaxon that is under discussion (this is in line with the usage of taxa in biostratigraphical zones, e.g. Bifrons zone).

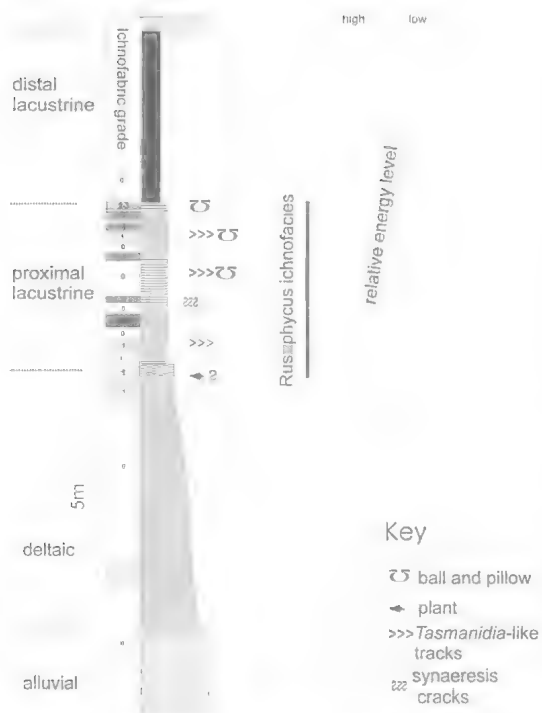


FIG. 1. Graphic log of GSQ Jericho No. 1 interval 770-740m, showing relative depositional energy, interpreted depositional environments and ichnofabrics adapted from Taylor & Goldring (1993).

This assemblage falls into the *Rusophycus* ichnofacies that was suggested tentatively by Bromley (1996: 249) to represent a freshwater (fluvial and shallow lacustrine) ichnofacies dominated by *Repichnia* and *Cubichnia*.

In the Jericho Formation the *Rusophycus* ichnofacies is characterised by *Repichnia*, *Cubichnia* and *Praedichnia* (Table 1).

Aceñolaza & Buatois (1993) reviewed late Palaeozoic trace fossil assemblages of Argentina and identified four ichnocoenoses pertaining to differing lacustrine and fluvial sedimentary facies. They regarded the *Umfolozia* ichnocoenosis as representing arthropod activity within a shallow lake, and the *Isopodichnus* ichnocoenosis as representing activity within ephemeral, shallow pools, and channel and floodplain deposits. The Queensland material belongs within an *Umfolozia* ichnocoenosis, with arthropod crawling traces dominant. Keighley & Pickerill (1996) reviewed the interwoven taxonomic status of *Isopodichnus*, *Rusophycus* and *Cruziana*, and provided a convincing argument against retaining *Isopodichnus*, placing ribbon like members of that taxon in

Cruziana, and bilobate coffee-bean shaped members within *Rusophycus*. However Trewin (1976), Pollard (1985) and Aceñolaza & Buatois (1993) pointed out that *Isopodichnus* is generally smaller, with flaring ends. Furthermore the genus has a significant ecological and stratigraphic utility, and is here retained.

FUNCTIONAL INTERPRETATION. The absence of body fossils associated with the assemblage makes identification of the track-maker(s) difficult. The biserial nature of many of the traces indicates that they were made by arthropods. In *Wadeichnus*, interpreted antennae marks strengthens the arthropod identification. Groove markings on *Isopodichnus queenslandensis*, interpreted to have been made by telson drag, and the presence of paired scratch marks suggestive of at least 5 pairs of appendages on the related *Rusophycus devisi*, throws some light on the organisms responsible. The bifurcate distal appendage marks in *Alphaichnus* indicate that appendages were in the equally biramial (primitive) state, possibly representing activity of syncarid crustacea.

Terminology follows Osgood (1970) for 'trail', 'track', 'pair' and 'imprint'. 'Distal' and 'proximal' refer to the distance from the axis of the trace fossil, 'medial' pertains to features within the axial zones of tracks and 'lateral' to those in the marginal zones. Most material is preserved in hyporelief and all descriptions should be read as such. No attempt is made to establish higher order systematics.

SYSTEMATIC PALAEOICHOLOGY

Isopodichnus Bornemann, 1889

TYPE SPECIES. *Isopodichnus problematicus* Bornemann 1889, from the Triassic of Germany.

REMARKS. *Isopodichnus* is a problematic ichnogenus, and has been variably placed in *Rusophycus* and *Cruziana*, with considerable taxonomic confusion, further obfuscated by well known intergradation between the three ichnogenera (also see below). Full accounts and differing opinions on its resolution are given by Osgood (1970), Hantzschel (1975) Keighley & Pickerill (1996) and Bromley (1996). The problems are intertwined and we do not propose to resolve this significant controversy. Bromley (1996: 184) provided the most accurate summary of this nomenclatural debate: 'I cannot see how *Isopodichnus* can be considered available other than a muddled junior synonym of both *Cruziana*

TABLE 1. Ethological classification of ichnotaxa described from the Jericho Fmn near Alpha.

Ethological classification	Ichnotaxon	Figure numbers
Repichnia	<i>Isopodichmus queenslandicus</i>	Figs 2A,B, 13B
Cubichnia	<i>Rusophycus devisi</i>	Fig. 3
Repichnia	<i>Tasmanadia glaessneri</i>	Figs 6, 7
Repichnia with Praedichnia	<i>Wadeichmus maryae</i>	Fig. 4
Repichnia with Praedichnia	<i>Alphaidichmus alphaensis</i>	Figs 8, 9, 10A, 12, ?10B,C
?Fugichnia	Indet. sweep and scurry marks	Fig. 13D
?Praedichnia	Indet. paired appendage marks	Fig. 12

and *Rusophycus*'. The taxonomic stand of Keighley & Pickerill (1996) would have *Isopodichmus queenslandensis* within *Cruziana*. We retain *Isopodichmus* here as a genus-of-convenience awaiting resolution of the tripartite nomenclatural confusion. We note the considerable difference in the classic Early Palaeozoic *Cruziana* morphology and this material. The dichotomy between type specimens of *Cruziana* and those of *Isopodichmus* must be further investigated.

***Isopodichmus queenslandensis* ichnosp. nov.**
(Figs 2A,B, 11 (part), 12B)

ETYMOLOGY. From Queensland.

MATERIAL. HOLOTYPE: QMF32233. PARATYPES: QMF34026, 39062 all from QML993.

DIAGNOSIS. Exclusively elongate and continuous *Isopodichmus*.

DESCRIPTION. Straight, gently curved or weakly sinuous ribbon-like trail, up to 7mm wide consisting of (in hyporelief) 2 parallel marginal longitudinal furrows and a central (axial) channel containing up to 6 subparallel longitudinal striae. Axial channel occupying slightly over 1/2 track width, with numerous fine longitudinal threads and a weak central ridge deviating from the mid-line along the length of the trail. Outermost longitudinal ridge in the axis with sporadic but numerous oblique, short striae. Marginal ridges with fine obliquely transverse striae, extending sub-perpendicularly beyond the edge of the trail. In some specimens these striae bifurcate, particularly as the trail shallows. There are numerous tiny (1-2mm wide) examples of the track (Fig. 9, large arrow) preserved in epirelief,

the marginal parts of the track are slightly more pronounced than in larger specimens.

REMARKS. The central threads represent the drag marks of a telson with furcae, with the sporadic striae representing setae on the furcae. Short imprints on the edge of the track represent appendage marks. The relative depth of the track reflects the softness of the muddy substrate. The elongate nature of the trace and the internal striae separate this ichnospecies from material figured as *Isopodichmus osbornei* Glaessner, 1957: pl. 10, fig. 2a,b (partim); fig. 3, pl. 11 figs 1-3) from the Carboniferous near Seaham, NSW. The holotype of *Isopodichmus queenslandensis* is associated with *Rusophycus*. Smaller representatives of this taxon are interpreted as representing juveniles.

***Rusophycus* Hall, 1852**

TYPE SPECIES. Significant problems with the nominate type ichnospecies are still to be resolved (Keighley & Pickerill, 1996).

REMARKS. Osgood (1970) restricted *Isopodichmus* Bornemann to small *Rusophycus*-like imprints of non-trilobite origin as well as to those of trilobite origin. Hantzschel (1975) suggested that *Rusophycus* be restricted to identifiable trilobite resting traces based on a genetic and stratigraphic methodology rather than an ethological/morphological approach. Use of *Isopodichmus* for small short traces was discussed by Glaessner (1957), Osgood (1970), Birkenmajer & Bruton (1971) and Hantzschel (1975). Keighley & Pickerill (1996) argued against *Isopodichmus* and placed bilobate coffee-bean shaped members in *Rusophycus*. Buatois & Mangano (1993) followed this using *Rusophycus* for non-marine, late Palaeozoic traces with this short bilobate morphology.

In the Alpha material *Isopodichmus queenslandensis* and *Rusophycus devisi* are associated and intergrade (Fig. 3C).

***Rusophycus devisi* ichnosp. nov.**
(Figs 3, 7A (part))

ETYMOLOGY. For C.W. De Vis, who described the first trace fossils from Queensland (De Vis, 1911).

MATERIAL. HOLOTYPE: QMF32232. PARATYPES: QMF34026 (several specimens), 34090, 34069 (several specimens), all from QML993.

DIAGNOSIS. Small, elongate longitudinally subsymmetrical to irregular bilobate trace, showing at least 5 curved paired ridges in hyporelief within each lobe.

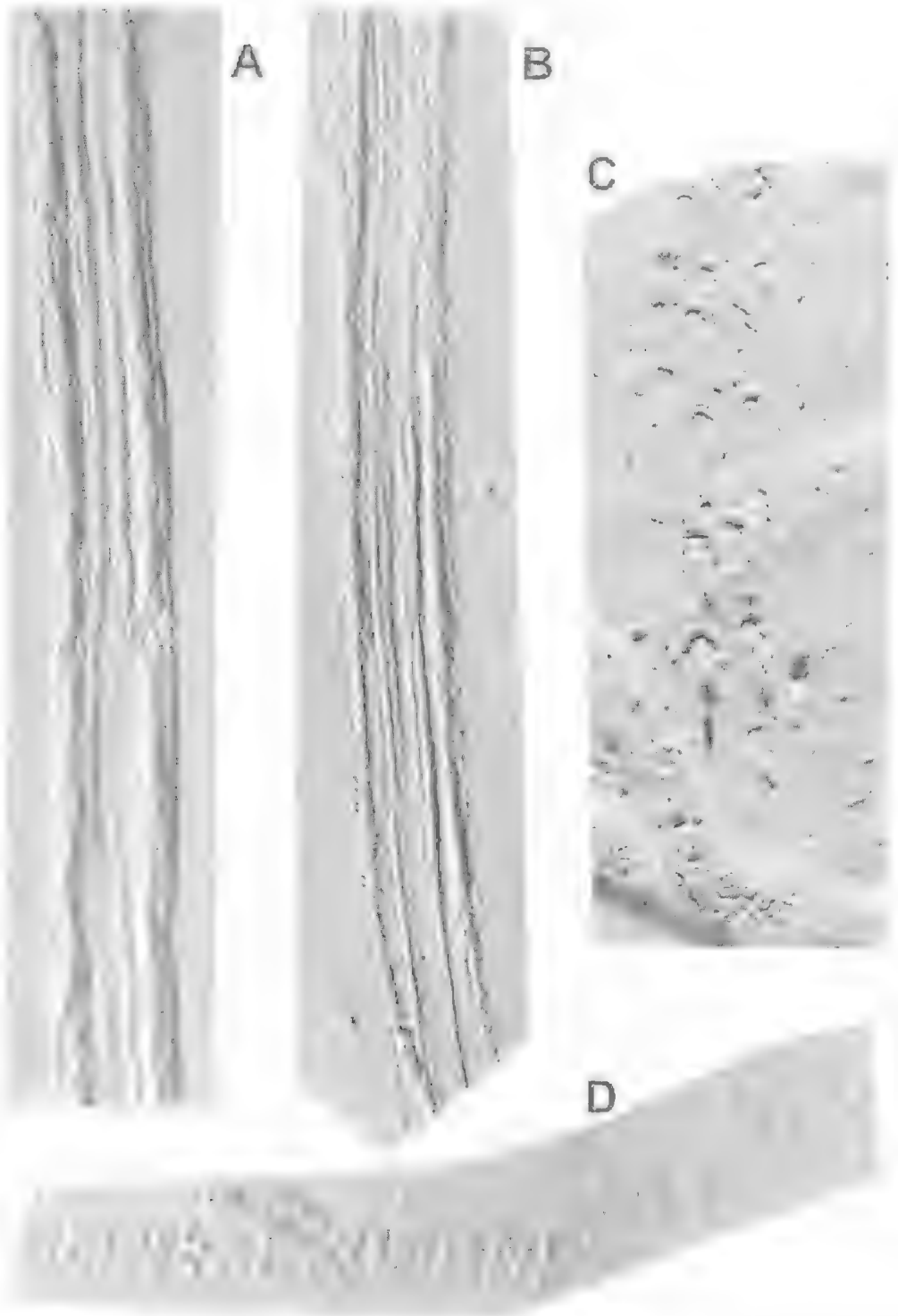


FIG. 2. A,B, *Isopodichnus queenslandensis* ichnosp. nov.; A, QMF34026 $\times 2$; B, F32233 holotype $\times 2$. C,D, *Wadeichnus maryae* ichnogen. et ichnosp. nov.; C, F34065 $\times 1$; D, F39061 $\times 1$.

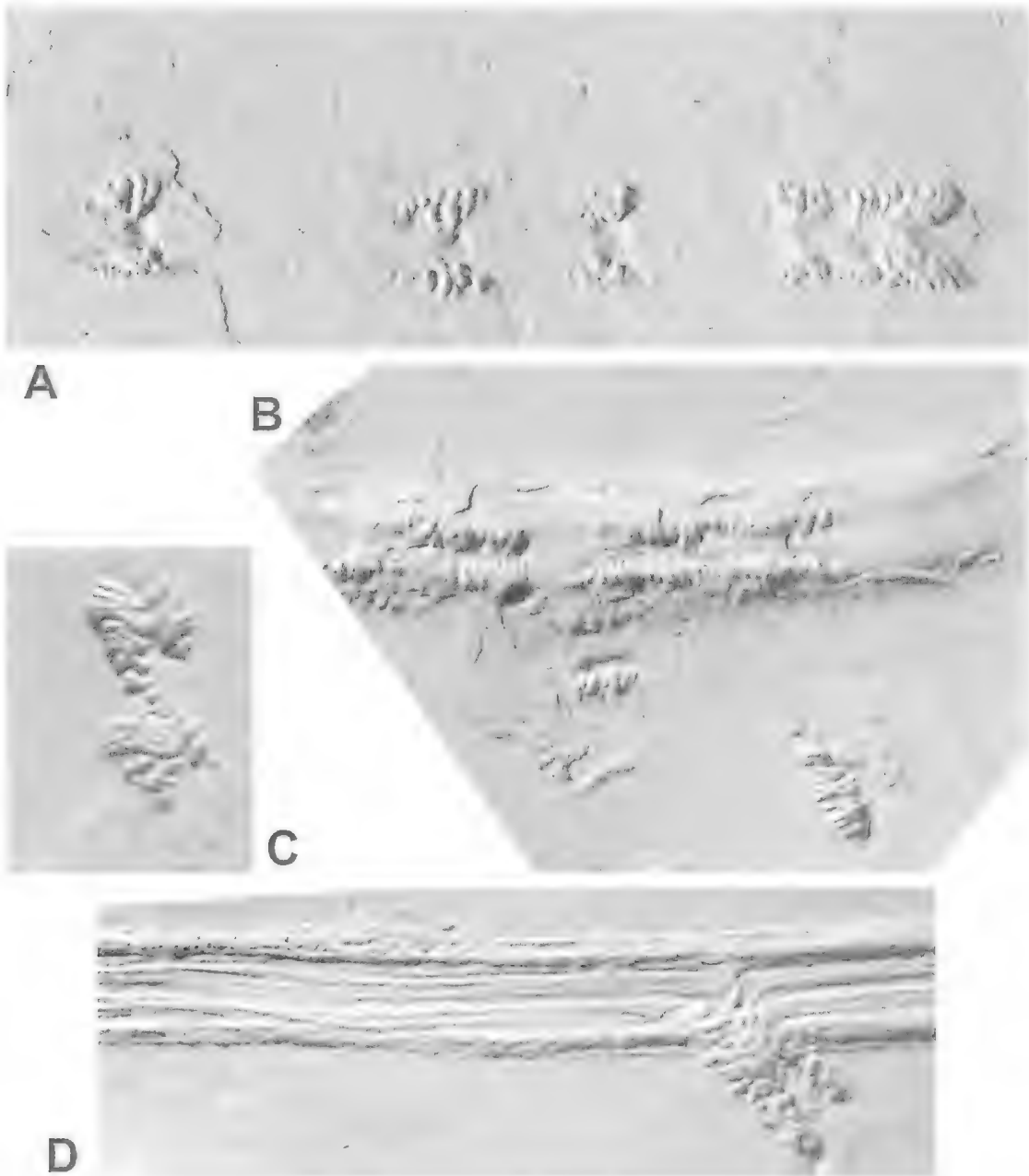


FIG. 3. *Rusophycus devisi* ichnogen. et ichnosp. nov.; A, QMF32232 holotype $\times 1$; B, F34026 $\times 1$; C, F34026, another track on of same slab; D, F32233, *Rusophycus devisi* ichnogen. et ichnosp. nov. in association with *Isopodichnus queenslandensis* ichnosp. nov. $\times 1$.

DESCRIPTION. Small trace up to 11mm wide and 13mm long, 2 lobes subsymmetrical about a midline or irregular. Each lobe with at least 5 arcuate transverse ridges of which some are slightly divergent. Midzone of trace with an arcuate depression in hyporelief.

REMARKS. QMF32232 has 5 parts to this trace, 2 of which are coalesced (Fig. 3A) representing saltation-style locomotion between short resting traces. QMF34026 has 2 small asymmetrical specimens and an undertracked specimen of a transitional trace between *Rusophycus* and

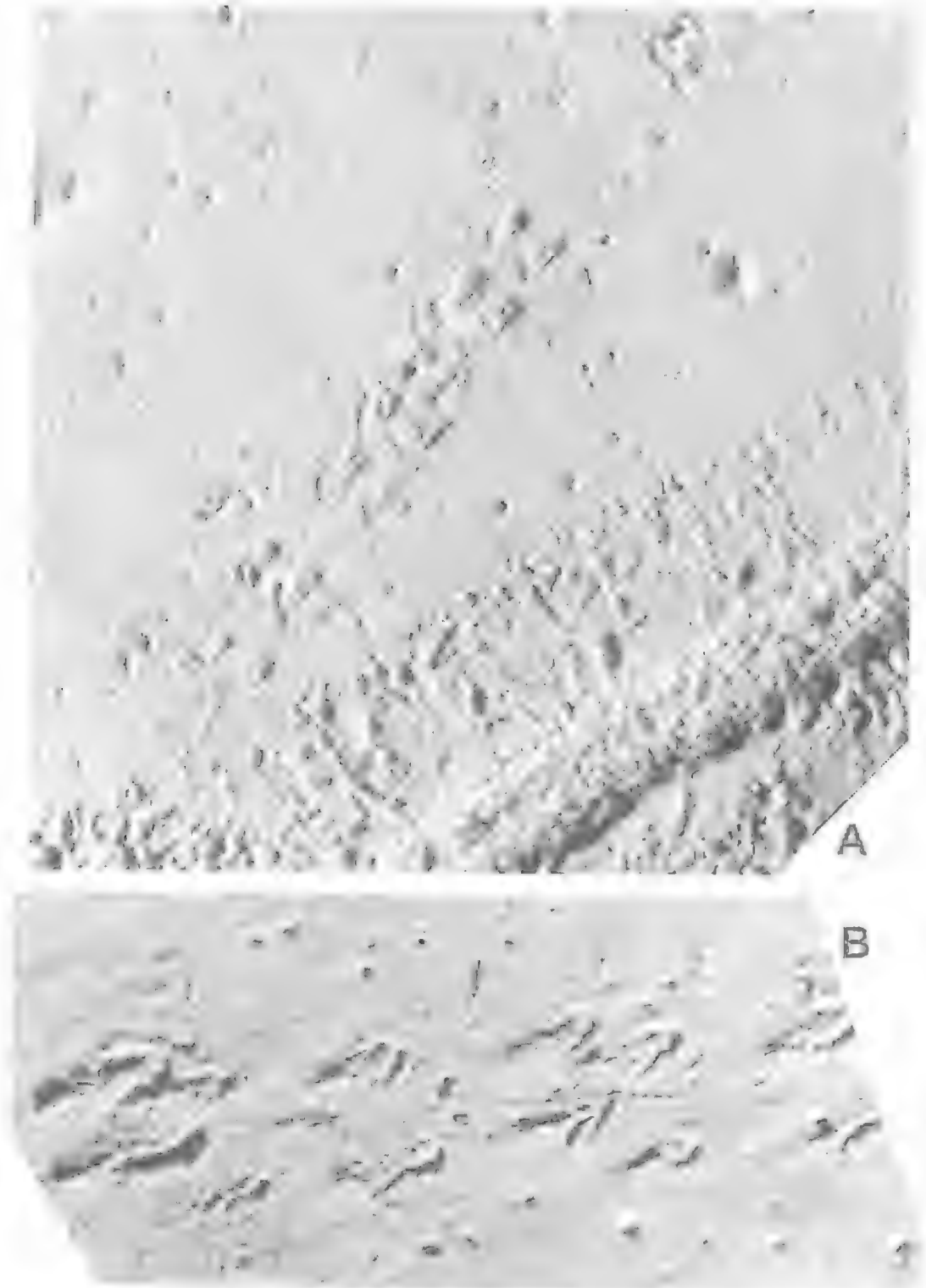


FIG. 4. *Wadeichmus maryae* ichnogen. et ichnosp. nov. A, holotype QMF39063, $\times 1$; B, F39065, $\times 2$.

Isopodichnus (Fig. 3B). QMF32233 shows *Rusophycus* in association with *Isopodichnus* (Fig. 3D) where the track may have been utilised twice by the same type of trace-producing organism. Other specimens are associated with *Tasmanadia*.

Tasmanadia Chapman, 1929

TYPE SPECIES. *Tasmanadia twelvetreeensis* Chapman, 1929 from the Upper Carboniferous Wynyard Tillite, Tasmania.

REMARKS. Chapman (1929) erected *Tasmanadia* for purported Cambrian annelid body fossils, reinterpreted to be Carboniferous arthropod tracks by Glaessner (1957) and Gulline (1967). Bromley & Asgaard (1979) regarded *Tasmanadia* as a junior synonym of *Diplichnites* but contrarily indicated significant differences in the fine morphology of the tracks; their extreme 'lumping' view where many arthropod track genera were synonymised is not here adopted.

Tasmanadia glaessneri ichnosp. nov. (Figs 6, 7A (part))

ETYMOLOGY. For the late M. F. Glaessner.

MATERIAL. HOLOTYPE: QMF39069. PARATYPES: QMF32229, 34054, 34060, 34065, 34081, 34083, 34088, 34090, all from QML993.

DIAGNOSIS. Biserial track 8-11mm wide, of 2 near-symmetrical rows of fine ridges, nearly perpendicular to the track axis, in close, slightly divergent pairs.

DESCRIPTION. Track biserial, elongate, gently curved, of near symmetrical rows of fine ridges in hyporelief, 8-11mm in total width, with 3-4mm between inner ends of rows of ridges. Fine ridges in closely spaced pairs diverging slightly or subparallel, individually very weakly arcuate, perpendicular to the track axis. Sporadically finer, more strongly divergent appendage marks marginal to the track pairs. Rare lengthwise, but short marks along the track axis. Some specimens over 500mm long.

REMARKS. The paired track marks indicate *Tasmanadia*. This material is differentiated from the type species by the greater divergence of the distal ends of the ridges forming the track pairs. *Permichnium* Guthörl, 1934 has slightly more divergent paired ridges, but they emerge from subcircular foot impressions, lacking in this material. *Maculichna* Anderson, 1975 possesses rows of paired spots, and lacks the paired divergent elongate marks of this material.



FIG. 5. Interpreted schema for *Wadeichnus maryae* ichnogen. et ichnosp. nov. based on holotype specimen, $\times 2$.

Umfolozia Savage 1971 also possesses a series of paired and complexly arranged dots in contrast to the simplicity of this material. Specimens of this ichnotaxa grade into *Rusophycus* and *Alphaichnus*, the latter evidenced by the rare occurrence of fine marks adjacent to the paired ridges. Shallow undertracking suggests greater substrate firmness than for *Alphaichnus* and *Isopodichnus*.

Alphaichnus ichnogen. nov.

TYPE SPECIES. *Alphaichnus alphaensis* ichnogen. et sp. nov.

DIAGNOSIS. Biserial, gently curved, to straight trace consisting of subsymmetrical rows of up to three sets of paired ridges which are distally



FIG. 6. *Tasmantidia glaessneri* n. sp. nov., specimens from slab QMI 34090. A, overprinted hyporelief specimens and indeterminate sweep traces (small arrows). $\times 1$; B, further detail same specimen $\times 1$.

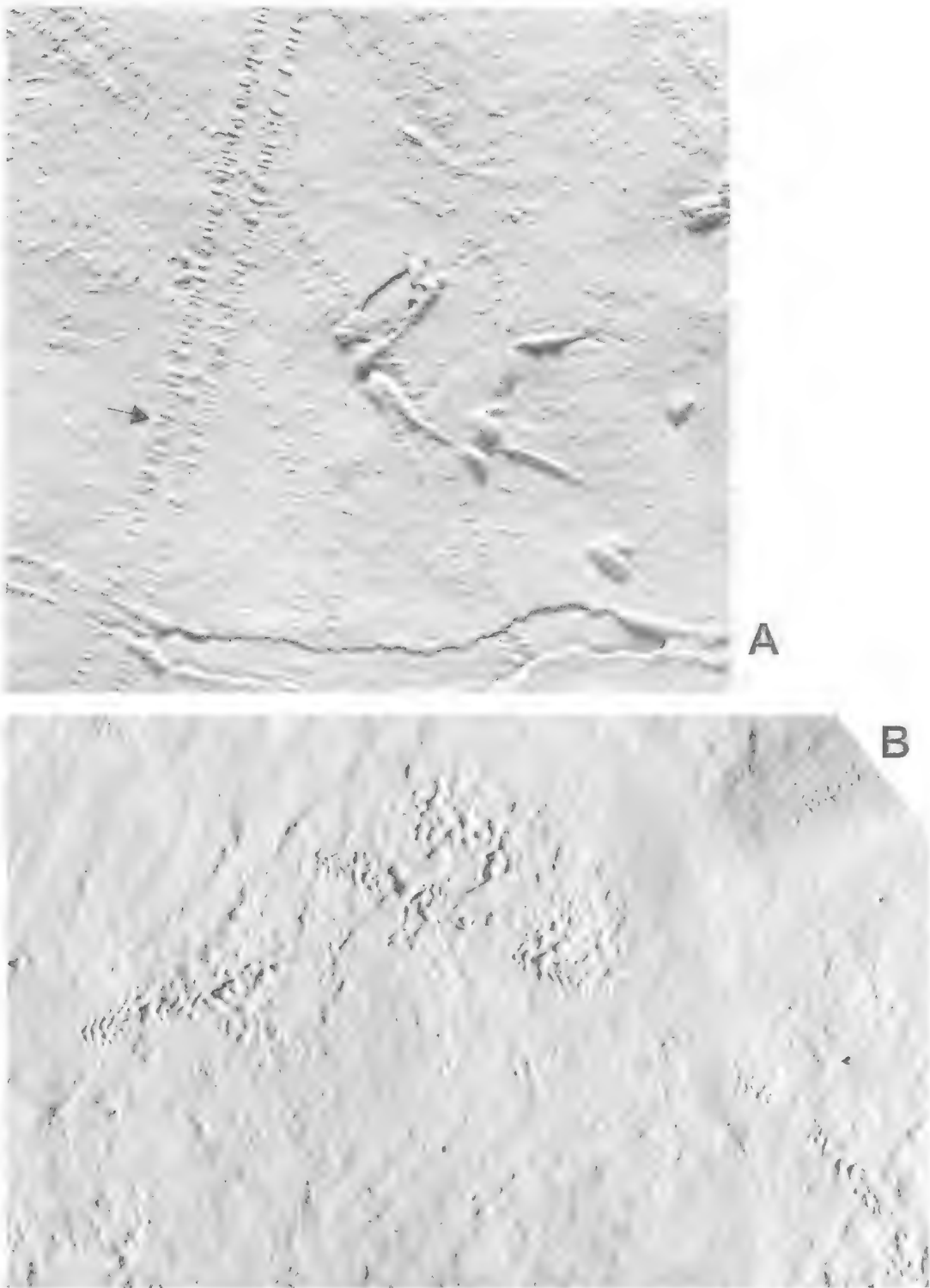


FIG. 7. A, *Tasmanadia glaessneri* ichnosp. nov., QMF39069 holotype, (arrow) with associated *Rusophycus devisi* ichnosp. nov. and indeterminate traces $\times 1$. B, indet. appendage marks, QMF34067 $\times 2$.

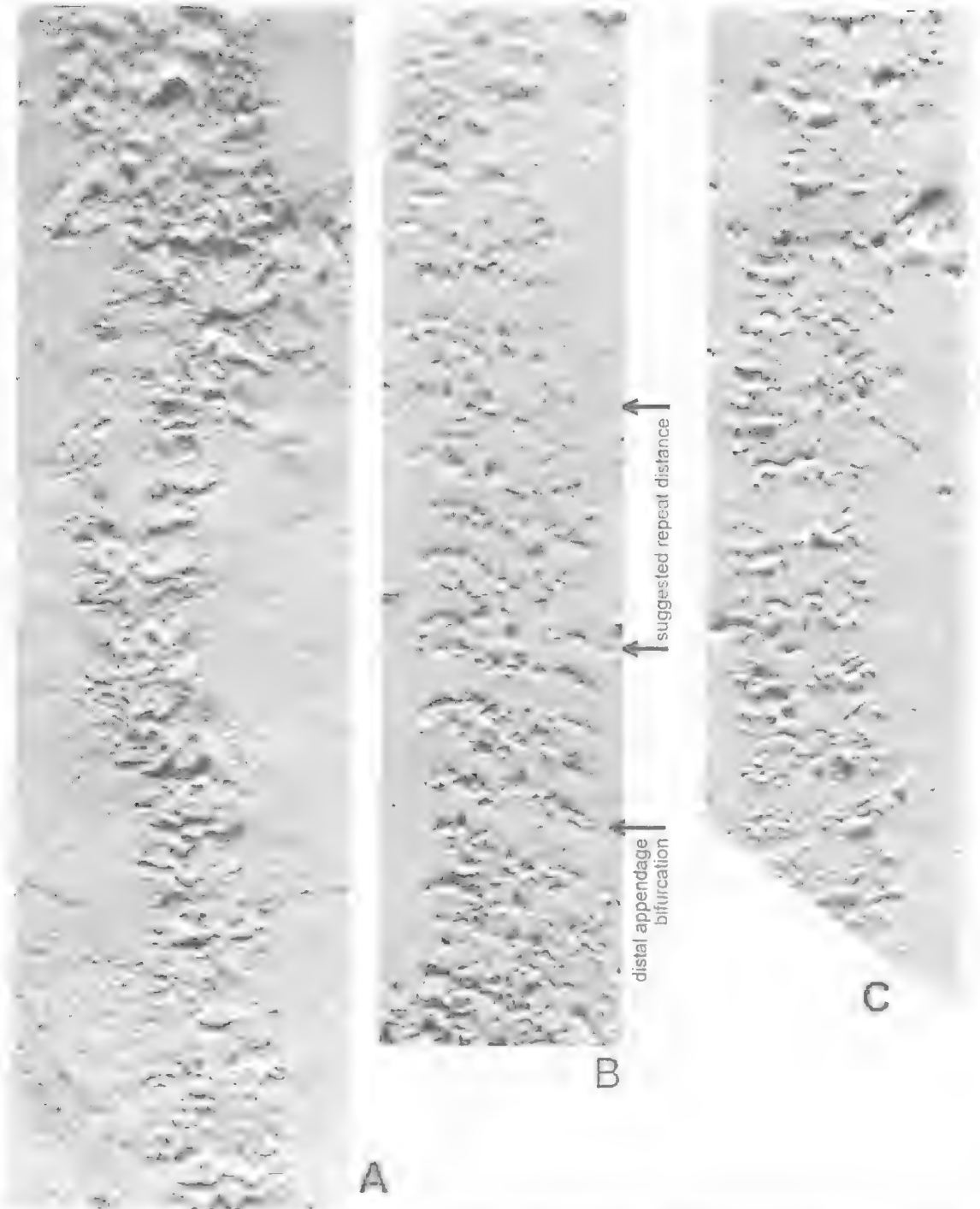


FIG. 8. *Alphacelmis alphacensis* ichnogen. et ichnosp. nov. QMF 34068 $\times 2$. B, holotype F34084 $\times 2$; C, F34084, track on different part of same slab $\times 2$.

branched and have short fine striae. Axis with or without arcuate ridges or transverse oblique ridges.

Alphaichnus alphaensis ichnogen. et sp. nov.
(Figs 8-11)

ETYMOLOGY. From the town of Alpha.

MATERIAL. HOLOTYPE: QMF34084. PARATYPES: QMF32231, 34033, 34039, 34043, 34057, 34059, 34066-34068, 34072.

DIAGNOSIS. As for genus.

DESCRIPTION. Long, straight to gently curved, irregular biserial trace, without closing loops, up to 18mm outer width, 8mm inner width. Internal organisation complex of subparallel track sets of up to 3 pairs of variable length transverse ridges, each of which may be distally bifurcate or trifurcate, with short, very fine longitudinal striae perpendicular to their length. Length of individual ridges in each set increasing towards the margin of the track. Central zone of the track with up to 3 distinct or 2 axially connected, curved transverse ridges, or a series of up to 4 irregularly disposed oblique short ridges. On some specimens additional asymmetrical curved transverse ridges at the margins of the track. Individual pairs highly variable, but approach symmetry when the trace is nearly straight. Longitudinal striae, oblique and arcuate ridges sporadic along length of track, within the axial zone. In some specimens medial arcuate, symmetrical ridges, with tiny longitudinal striae with a series of adaxially disposed divergent ridges at their margins, and a number of lateral short marks fanning around the individual paired ridges.

REMARKS. There are a large number of biserial arthropod tracks superficially similar to this material, but most lack the internal variability and complexity of this ichnotaxon, particularly within the track axis. *Diplichnites govenderi* Savage, 1971, lacks the flaring and branching of individual tracks, lacks medial ridges and is, in general, a simpler trace. The considerable variation in this genus reflects similar morphological variation encountered by Anderson (1975) in *Umfolozia* Savage, 1971, but *Umfolozia* bears appendage marks and sinuously arranged oval marks in the medial zone and lacks the complexity of medial arcs and branching ridges present in *Alphaichnus*.

Walter (1983) discussed many late Palaeozoic ichnotaxa attributed to arthropods. *Heterotripodichnus divaricatus* Walter and *H. longitarsalis* Walter approach the present material in

complexity, but in both, the appendage marks are more longitudinally arranged within the trace.

Irregular morphology makes the identification of repeat distances difficult. Repetition of medial ridges is interspaced by 5 track pairs, which suggests minimum track repetition. Track pairs are interpreted as appendage marks with their distal bifurcations and other branchings representing the 2 roughly equally-sized rami. Medial oval and arcuate marks are interpreted as pleopod imprints and withdrawal marks. Longitudinal striae on the appendage marks setae. Distal fine arcuate marks are interpreted as traces of antennae.

The differing depth of track penetration displayed by the many slabs examined with undertracks suggests that substrate firmness was variable, but was high in the case of generation of this track compared to the occurrences of *Iso-podichnus queenslandensis*.

Wadeichnus ichnogen. Nov.

TYPE SPECIES. *Wadeichnus maryae* ichnogen et ichnosp. nov.

ETYMOLOGY. For Mary Wade.

DIAGNOSIS. Biserial track of elongate, lobate, longitudinally disposed marks, consisting of up to 5 elongate striae, terminating in a horseshoe-shaped depression within which the striae fan slightly; with or without marginal arcuate ridges perpendicular to track axis, and with or without a bounding pair of longitudinal fine ridges.

Wadeichnus maryae ichnogen. et ichnosp. nov.
(Figs 2C,D, 4, 5, 12C)

MATERIAL. HOLOTYPE: QMF39063. PARATYPES: QMF39065, 39061.

ETYMOLOGY. For Mary Wade.

DIAGNOSIS. As for genus.

DESCRIPTION. Biserial, somewhat discontinuous track, up to 14mm wide, of symmetrical or subsymmetrical lobate marks, up to 8mm long, of 3-5 longitudinal striae which diverge slightly within a horseshoe-shaped depression, accompanied by marginal fine ridges, papillate, which are perpendicular to the trace axis and a pair of longitudinal fine threads at the margin of the trace. Some specimens show a central thread running lengthwise along the trace. In two specimens the orientation of the appendage marks (striae sets) are oblique to the trace axis.

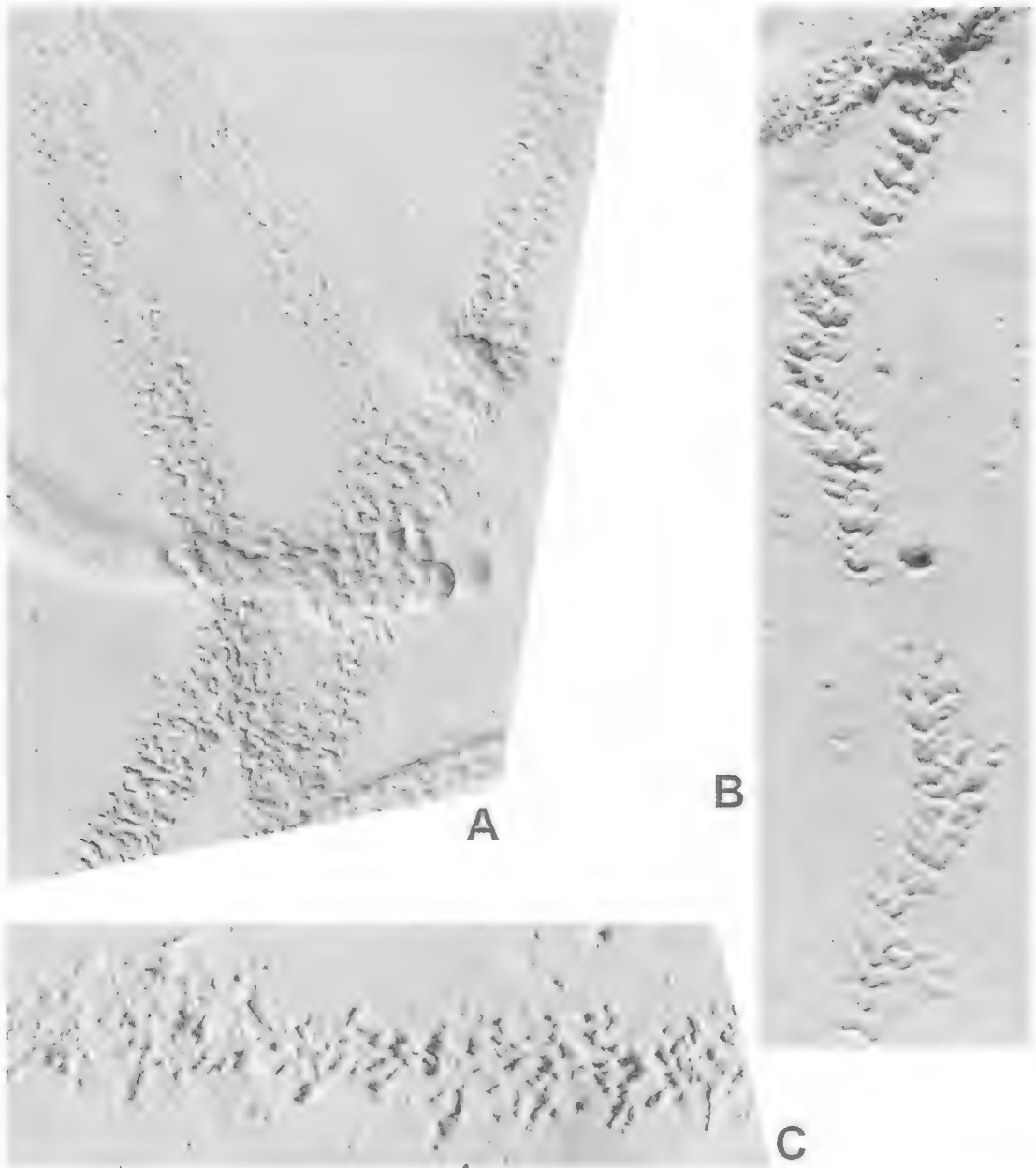


FIG. 9. A, *Alphaichnus alphaensis* ichnogen. et ichnosp. nov. QMF32231 \times 1. B, C, cf. *Alphaichnus*. QMF34036 and F39064 respectively.

REMARKS. The arcuate ridges perpendicular to the axis are interpreted as antennae marks elongate striation pairs as pleopod marks and horseshoe depressions (in hyporelief) interpreted as withdrawal markings (sensu Osgood, 1970). The sporadically present central thread may be a telson drag mark. It is likely that the specimen assigned to cf. *Alphaichnus* (Fig. 9B,C) is

transitional between *Alphaichnus* and this ichnotaxon. *Wadeichnus* probably was formed on a semifirm substrate with only minimal contact of the arthropod body and the surface sediment.

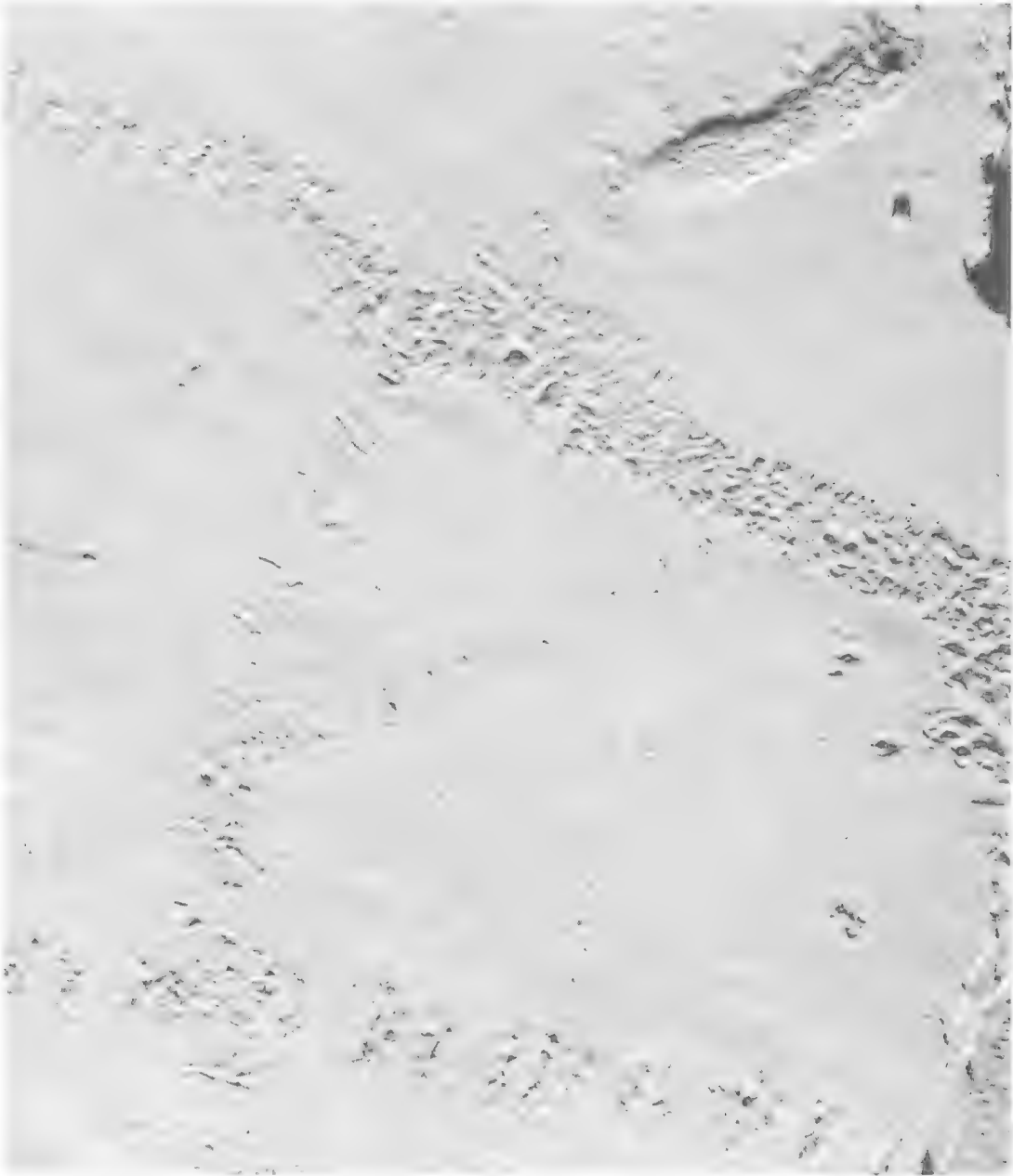


FIG. 10. *Alphaichnus alphaensis* ichnogen. et ichnosp. nov. QMF39068 $\times 1$.

indet. appendage marks
(Fig. 7B)

an individual series, with discontinuous sets in close association.

MATERIAL. QMF34067.

DESCRIPTION. Small elongate series, 11mm long and 5mm wide of arcuate or lunulate to v-shaped wrinkle marks in hyporelief, up to 6 in

REMARKS. These marks probably represent asymmetrical appendage falls upon the substrate with subsequent, but penecontemporaneous plastic deformation, probably on a low slope. The lack of material available and the unusual



FIG. 11. *Alphaichnus alphaensis* ichnogen. et ichnosp. nov. QMF34084, holotype (small arrow) part of composite slab, $\times 1$. *Isopodichnus queenslandensis*, juvenile specimens (large arrow). Note the numerous indeterminate appendage marks (open triangles).

morphology prevents any accurate assignment. Anderson (1975) described bedding surface slump structures similar to those found in the Alpha material.

indet. paired appendage marks
(Fig. 11 (part))

MATERIAL. Part of slab with QMF34084.

DESCRIPTION. Almost all slabs containing *Wadeichnus* and *Alphaichnus* have isolated, shallow small paired or more rarely single holes (in epirelief). They are commonly triangular with one apex deeper, or they are subquadrate with no directional shallowing. Pairs are separated by 2-3mm. No continuity in sets of pairs can be identified.

REMARKS. We interpret these holes as appendage pluck-out or withdrawal marks

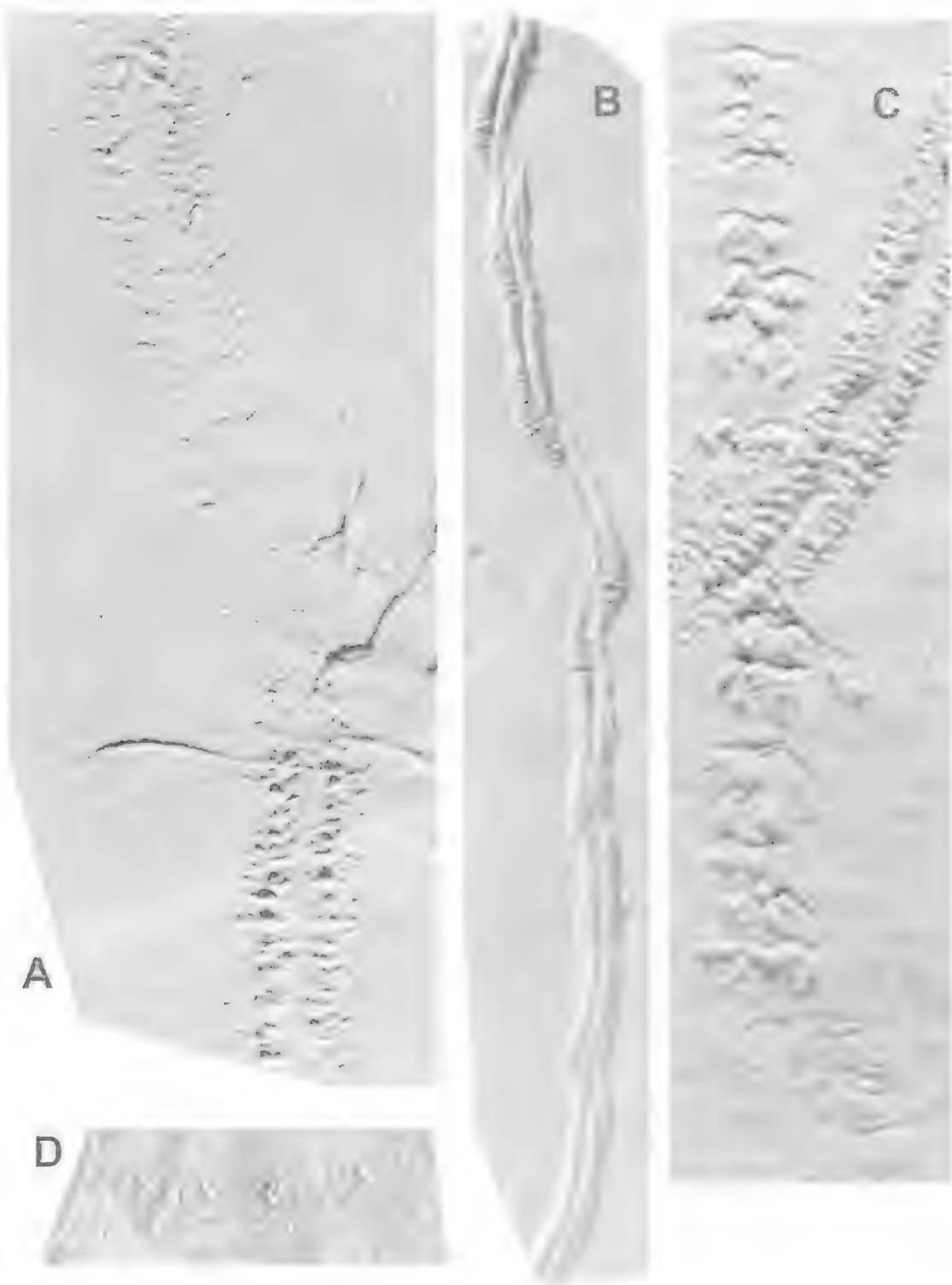


FIG. 12. A, *Alphaichnus alphaensis* ichnogen. et ichnosp. nov., and indeterminate 'sweep' mark, QMF34066 $\times 2$. B, *Isopodichnus queenslandensis* ichnosp. nov. QMF39062, showing sinuosity, $\times 1$. C, *Wadeichnus maryae* ichnogen. et ichnosp. nov. QMF39061 $\times 2$. D, indeterminate scurry marks QMF39067 $\times 1$.

associated with isolated substrate interactions. The association of these holes with the more complex traces shows differing behaviour between the maker of *Alphaichmus* and the originator of these marks, but we cannot determine whether it would be a similar animal.

indeterminate 'sweep' marks
(Fig. 6 (part))

MATERIAL. QMF34090

REMARKS. On a number of specimens are elongate curved and recurved ridges which lack repetitive association or are in groups of 1 or 2. These ridges are up to 25mm long, and <1mm thick, gently curved with a stepped weak bilateral symmetry, if at all. These structures are interpreted as sweep marks from some organism; they are much too small and non-persistent to be *Undichnia* (sensu Anderson, 1976; Buatois & Mangano, 1994) and are indeterminate. The material resembles *Stialia pillosa* Smith of Walker (1985), but lacks the abundant scratch marks.

indeterminate scurry marks
(Fig. 12D)

MATERIAL. QMF 39067.

REMARKS. Small, disordered set of weakly to strongly divergent ridges with an impersistent, marginal sinuous set of bordering threads. Imprints (ridges in hyporelief) are in groups of 3 or more and are short, sporadically divided and bear fine transverse striae. The specimen is interpreted as a set of arthropod pleopod marks where the pleopods bear setae and are probably biramal. The trace architecture is inferred as resulting from an arthropod scurrying across the firm substrate. The sinuous threads are interpreted as antennae marks.

ACKNOWLEDGEMENTS

We thank Mary Wade and Peter Jell for their assistance and encouragement; Luis Buatois & Gabriela Mangano, Geological Survey of Kansas, Ron Pickerill, University of New Brunswick for providing important literature; Tony Wright for topotype material of *Isopodichmus osbornei* from Seaham; Natalia Camilleri, Paul Tierney, Chris & Dawn Schnur, Terry Smith and Colin McHenry are thanked for assistance in the field; Jeff Wright is thanked for his patience with photographs. Amy Robinson

for her assistance with preparation, Barry Webby for helpful criticism on the manuscript.

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AUSTRALONEMA FROM THE SILURIAN OF THE YASS BASIN, NEW SOUTH WALES. *Memoirs of the Queensland Museum* 45(2): 252. 2000:- The gyronematine gastropod *Australonema* Tassell has hitherto not been recorded from the Silurian of Australia despite its abundance in Australian Early Devonian gastropod faunas (Tassell, 1980) and its presence in the Silurian elsewhere (Gubanov & Yochelson, 1994). *Australonema* recovered from the Barrandella Shales of the Yass Basin NSW extends the range of the genus within Australia. It confirms that Silurian *Australonema* belong to base stock of Gyronematinae, whose plesiomorphic state is characterised by one order of cords, lacking nodes. The specimen here described was recovered from the Barrandella Shales, Hattons Corner near Yass NSW. Recent work, summarised by Strusz (1989: 17), assigned a Ludlovian (Gorstian) age to the Barrandella Shale. This occurrence establishes the presence of basal stock of this subfamily in Australia prior to a significant Devonian diversification of gyronematines.

Systematic Palaeontology
 ARCHAEOGASTROPODA
 TROCHIINA Cox & Knight, 1960
 PLATYCERATOIDEA Hall, 1859
 HOLOPEIDAE Wenz, 1938
 GYRONEMATINAE Knight, 1956

***Australonema* sp.**
 (Fig.1)

Material. QMF40825. Collected A.J. Wright., Barrandella Shales, Hattons Corner, Yass, NSW.

Description. Large turbiniform shell 41mm high, 33mm wide, anomphalous, sutures impressed. Shell profile well rounded, meeting suture at an angle of approximately 15° from horizontal. Mid-whorl at periphery. Upper whorl face bears 4 strong cords which lack nodes. Lower whorl face with at least 1 cord, but imperfectly preserved lower face ornament otherwise. Growth lines are fine and numerous, orthocline to very slightly opisthocline. Protoconch unknown.

Remarks. The specimen is noteworthy but I am reluctant to erect a new species based on a single occurrence. *Australonema australis* (Etheridge Jr, 1890) from the Lilydale Limestone has more numerous spiral cords. The specimen is closest to *Australonema* sp. A of Tassell (1980) from the Silurian of Dudley, UK, but it also has a greater number of cords on the whorl face.

Acknowledgements

I thank Tony Wright for forwarding the specimen and Natalie Camilleri for photography.

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Alex G. Cook., Queensland Museum, PO Box 3300, South Brisbane 4101, Australia; 10 September 1999.

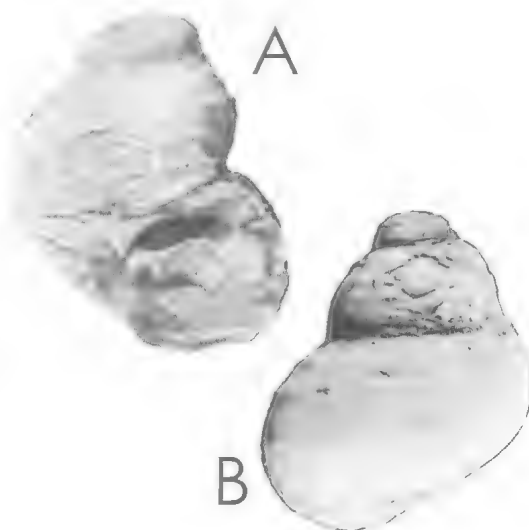


FIG. 1. *Australonema* sp. QMF40825. ×1; A, apertural view; B, side view.

AUSTRALIAN LEAF-TAILED GECKOS: PHYLOGENY, A NEW GENUS, TWO NEW SPECIES AND OTHER NEW DATA

P.J. COUPER, C.J. SCHNEIDER, C.J. HOSKIN AND J.A. COVACEVICH

Couper, P.J., Schneider, C.J., Hoskin, C.J. & Covacevich, J.A. 2000 06 30: Australian leaf-tailed geckos: phylogeny, a new genus, two new species and other new data. *Memoirs of the Queensland Museum* 45(2): 253-265. Brisbane. ISSN 0079-8835.

Phylogenetic analyses of the leaf-tailed geckos, based on DNA sequences from the mitochondrial cytochrome b gene, show that *Saltuarius*, as currently constituted, is paraphyletic. *Saltuarius cornutus*, *S. salebrosus*, *S. wyberba* and *S. swaini* form a well-supported monophyletic group which is the sister group to the apparently monophyletic *Phyllurus*. '*Saltuarius*' *occultus* is the sister group to the clade containing *Phyllurus* and all other *Saltuarius* spp. Thus, '*Saltuarius*' *occultus* represents a long, independent, evolutionary lineage within the leaf-tailed geckos and is recognised from both morphological and molecular data as distinct at the generic level (*Orraya* gen. nov.). *Orraya* gen. nov. can be distinguished from all other Australian padless carphodactylines by a combination of four apomorphies, the most obvious being greatly elongated cervical vertebrae. The phylogenetic analyses also revealed genetically distinct populations from Chaelundi State Forest, New South Wales and Oakview State Forest, southeast Queensland. These specimens are assigned to *S. wyberba* and *P. caudiannulatus* respectively, pending examination of more material. Description of *Phyllurus amnicola* sp. nov. and *P. championae* sp. nov. brings to 12 the number of leaf-tailed geckos from eastern Australia. The former, known only from Mt Elliot, NEQ, is separated from its congeners by a combination of characters (large size; very small, spinose body tubercles; a leaf-shaped tail with the anterior-most band broken, but spanning full tail width; and a partially-divided rostral with 5-6 scales along its dorsal margin). *Phyllurus championae* sp. nov. from only two localities (Cameron Ck and Blue Mtn, MEQ), is the only *Phyllurus* species with a leaf-shaped tail and a fully divided rostral scale. Large genetic distances between *P. amnicola* sp. nov., *P. championae* sp. nov. and previously recognised *Phyllurus* spp. further support the recognition of these species. They join a long list of rainforest reptile taxa known from only single localities or very narrow ranges. The distribution of 'leaf-tails' reflects the preservation of ancient taxa in relictual rainforest and elevated heath fragments in eastern Australia. Despite these narrow ranges, and because all collection localities for leaf-tails are in reserves, for conservation purposes under IUCN definitions, they should be classed 'Data Deficient'. □ *Reptilia, Gekkonidae, Phyllurus* spp., *Saltuarius* spp., *Orraya* gen. nov.; phylogeny; eastern Australia.

Patrick Couper & Jeanette Covacevich, Queensland Museum, PO Box 3300, South Brisbane 4101, Australia; Christopher J. Schneider, Department of Biology, Boston University, Boston MA 02215, USA; Conrad Hoskin, Department of Zoology & Entomology, University of Queensland, St Lucia 4072, Australia; 7 February 2000.

Australia's rainforests and adjoining moist sclerophyll forests and heaths are well known for their high diversity and for many species confined to either single localities, or very narrow ranges. Leaf-tailed geckos from such forests well illustrate these characteristics. For nearly 200 years of discovery and description of Australia's reptiles, only two species of 'leaf-tails', *Phyllurus platurus* (Shaw, 1790) and *P. cornutus* (Ogilby, 1892) = *Saltuarius cornutus* (Ogilby, 1892), were known. Morphological studies since 1975 have resulted in the recognition of many new species and the genus *Saltuarius* Couper, Covacevich & Moritz, 1993 — *P. caudiannulatus* Covacevich, 1975; *P. isis*

Couper, Covacevich & Moritz, 1993; *P. nephys* Couper, Covacevich & Moritz, 1993; *P. ossa* Couper, Covacevich & Moritz, 1993; *S. salebrosus* (Covacevich, 1975); *Saltuarius occultus* Couper, Covacevich & Moritz, 1993 and *S. swaini* (Wells & Wellington, 1985). Eight of the 12 presently known species have narrow distributions with four confined to single localities. Molecular analyses, which have both confirmed and refined previous morphologically-based taxonomic work on these padless Australian carphodactylines geckos, commenced in the mid-1990s. For the first time, a combination of both methods was used in the description of *S. wyberba* Couper, Schneider &

Covacevich, 1997. From joint morphological/molecular comparisons and field work in previously unexplored rainforests, we can now present a phylogeny (based on DNA sequences from the mitochondrial cytochrome *b* gene), erect a new genus to accommodate '*Saltuarius*' *occultus* and provide substantial new data (including descriptions of two new species) on *Phyllurus* spp.

METHODS

GENETICS. A 399 base pair fragment of the mitochondrial cytochrome *b* gene, corresponding to codons 1-133, was amplified and sequenced from at least two individuals from each species of leaf-tailed gecko (Appendix 1). Protocols for amplification and sequencing follow those outlined in Couper et al. (1997). Sequences were aligned by eye using the translated amino acid sequences. For phylogenetic analyses, each nucleotide position was treated as a single character with up to four unordered states. The most parsimonious tree was found using equal-weights parsimony (all characters equally weighted and unordered), as well as a variety of weighting schemes. Additionally, maximum likelihood analyses, with a variety of models of nucleotide substitution were performed. In all analyses, sequences from *Carphodactylus laevis* Günther, 1897 were used as an outgroup to root the tree. Bootstrap resampling and parsimony criteria were used to assess support for the recovered phylogeny. PAUP* 4.0b2 (Swofford, 1999) was used for all phylogenetic analyses.

MORPHOMETRICS. All specimens examined are held in the Queensland Museum. Measurements were taken using Mitutoyo electronic callipers. Supralabials, infralabials and subdigital lamellae were counted on both sides of specimens examined. External morphological characters follow Covacevich (1975) and Couper et al. (1993). Skeletal definitions follow Bauer (1990). Abbreviations: SVL, snout to vent length; T, tail length, from posterior margin of cloaca to tip of tail; TT, attenuated tip of original tail; HL, head

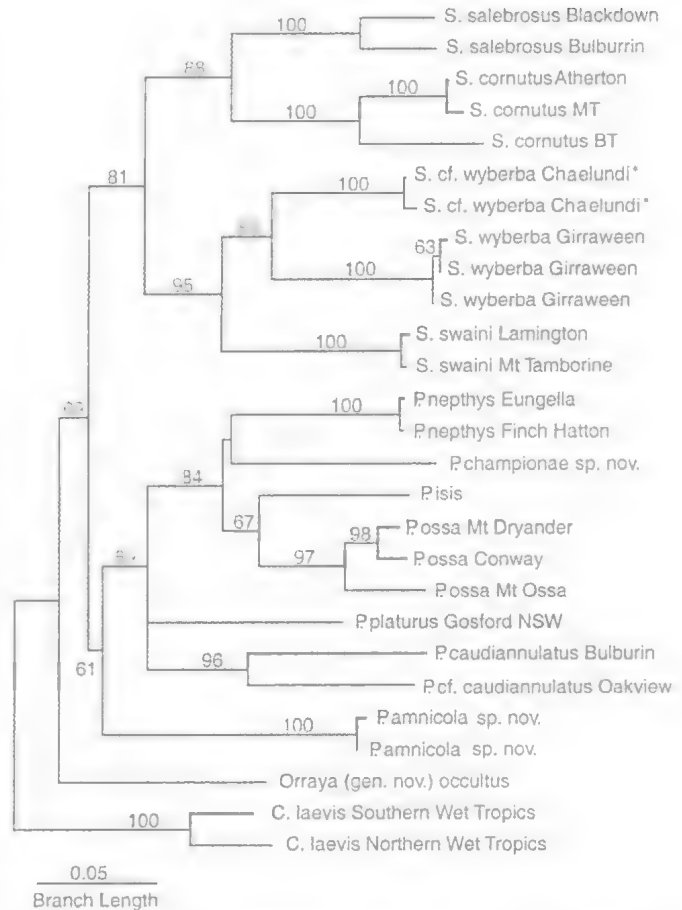


FIG. 1. Phylogeny of leaf-tailed geckos based on a 399 base pair fragment of MtDNA cytochrome *b* gene. Sequences from *Carphodactylus laevis* were used as an outgroup to root the tree and bootstraps >50% are presented (see Appendix 1 for specimen details). * Possible new species; here referred to *Saltuarius* cf. *wyberba*, pending collection of more specimens.

length; HW, head width; S, snout length; L1, length of front leg, axilla to tip of longest digit; L2, length of hind leg, groin to tip of longest digit; NL, neck length, axilla to posterior margin of ear.

PHYLOGENY. The mitochondrial cytochrome *b* DNA sequence data contained 183 parsimony-informative characters which provided good resolution of the phylogenetic relationships among species of leaf-tailed geckos. One hundred heuristic searches with random taxon addition and all characters unordered and equally weighted resulted in three equally parsimonious trees of 620 steps (C.I = 0.463). The strict consensus of these trees, which differed only in the placement of *P. platyrus*, is shown in Fig. 1. Bootstrap support for the clade containing all

Saltuarius, except '*Saltuarius*' *occultus* (here recognised as generically distinct) is relatively high, while support for the monophyly of *Phyllurus* is somewhat weaker. Phylogenetic analyses and bootstrap resampling with various weighting schemes to account for differences among codon positions in rates of substitution and transition/transversion ratios resulted in the identical topology with similar bootstrap support to the equal weights bootstrap tree. Similarly, maximum likelihood analyses under a wide range of nucleotide substitution models (Jukes-Cantor, HKY85G, General time reversible) resulted in trees that did not differ from the equal weights parsimony tree. Species in the genus *Phyllurus*, exclusive of *P. amnicola*, are characterised by a derived karyotype as well as a number of morphological synapomorphies (see *Phyllurus* spp. nov.). The karyotype of *P. amnicola* is unknown but morphological synapomorphies are consistent with the DNA sequence data in supporting the inclusion of *P. amnicola* in the genus *Phyllurus*.

Authorships for three sections of this paper (*Orraya* gen. nov., *Phyllurus amnicola* sp. nov. and *Phyllurus championae* sp. nov.) do not follow that of the paper as a whole.

Orraya gen. nov.

Couper, Covacevich, Schneider & Hoskin
(Fig. 2)

Saltuarius occultus Couper, Covacevich & Moritz, 1993.

A parsimony analysis of morphological and karyotypic characters performed by Couper et al. (1993) resulted in the recognition of two monophyletic subgroups within the leaf-tailed geckos — *Phyllurus* Goldfuss, 1820 (*P. caudiannulatus*, *P. isis*, *P. nepthys*, *P. ossa* and *P. platurus*) and *Saltuarius* Couper, Covacevich & Moritz, 1993 (*S. cornutus*, *S. occultus*, *S. salebrosus* and *S. swaini*). These clades were strongly supported in a bootstrap analysis present in 98% of pseudoreplicates. However, Couper et al. (1993) also observed '... evidence for grouping of *S. swaini*, *S. cornutus* and *S. salebrosus* to the exclusion of *S. occultus* ...' and that *Saltuarius occultus* has skeletal characters (elongation of the cervical vertebrae and 3 lumbar vertebrae) that are unique amongst its congeners. Derived characters, including elongate cervical vertebrae, along with DNA sequences from the mitochondrial cytochrome b gene (Fig. 1, Table 1), support the recognition of a new genus to accommodate '*Saltuarius*' *occultus*. In our phylogenetic analyses, this taxon is the sister

group to the clade containing *Phyllurus* spp and *Saltuarius* spp.

TYPE SPECIES. *Orraya occultus* (Couper, Covacevich & Moritz, 1993).

ETYMOLOGY. 'Orraya' is the Morrobalama language word for 'older brother' (Gunnawarra, N. & Kullakulla, M., 1994) referring to the phylogenetic relationship between *occultus* and its *Phyllurus* and *Saltuarius* 'siblings'. Peach Ck, the type locality of *Orraya occultus* drains the Mellwraith Ra. the traditional land of the Morrobalama.

DIAGNOSIS. *Orraya* gen. nov. can be separated easily from all other Australian padless carphodactyline genera by the following combined apomorphies: cervical vertebrae greatly elongated; three lumbar vertebrae (defined as non-rib-bearing vertebrae, immediately anterior to sacrum); male preanal organs greatly enlarged; regrown tail with broad, spinose tubercles on margins. A detailed description of *Orraya occultus* (as *Saltuarius occultus*) was provided by Couper et al., 1993: 104-106. For details of original tail, see Lethbridge et al., 1994.

Phyllurus spp.

NEW SPECIES. The new species (from Mt Elliot, NEQ and Cameron Ck/Blue Mtn, MEQ) are assigned to *Phyllurus* by the following synapomorphies: anterior-most autotomy septum in fifth caudal vertebra; no enlarged postmental scales; tail finely-attenuated and terminating in a small knob; rostral scale partially, or totally divided; males without preanal pores (polarity determined by Bauer, 1990). This assignment is supported further by the following character states (after Couper et al., 1993): nostril not in contact with rostral scale; anterior margin of interclavicle with a distinct process; axilla invaginated; epipubic cartilage small to moderate and original tail simply flared.

Phyllurus amnicola sp. nov.

Hoskin, Couper, Schneider & Covacevich
(Fig. 3)

ETYMOLOGY. From the Latin 'dwelling by a river', a reference to the type locality.

MATERIAL. HOLOTYPE: QMJ64408 ♀, Alligator Ck, Mt Elliot, Bowling Green Bay NP (19°28'S, 146°59'E) NEQ, C. Hoskin & J. Gratten, 1 Feb 1998. PARATYPES: QMJ64406-07, J67852 as for holotype.

DIAGNOSIS. *P. amnicola* can be separated from its congeners by the following combined characters: large size (maximum SVL >110 mm);

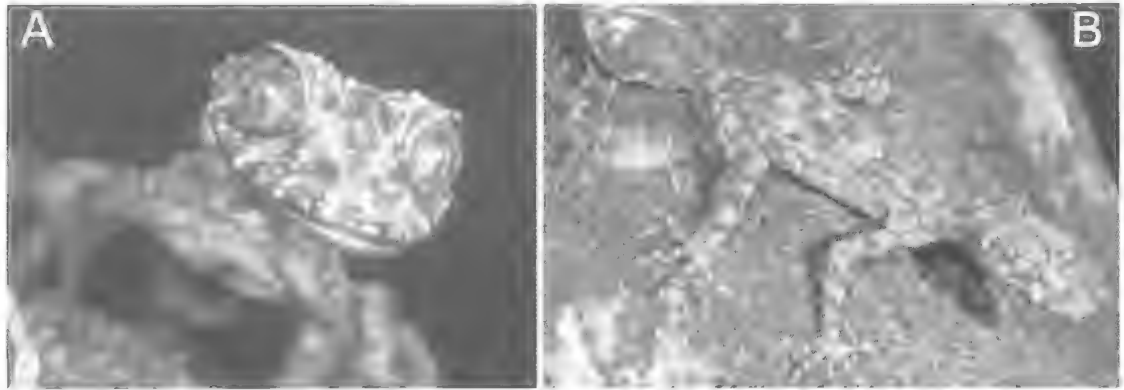


FIG. 2. *Orraya occultus* (QMJ62596), Peach Ck, McIlwraith Ra., Cape York Peninsula (13°45'S, 143°19'E) NEQ. (Jeff Wright)

spinose body tubercles very small; leaf-shaped tail with anterior-most band broken but spanning full tail width; rostral partially divided with 5-6 scales along its dorsal margin. (Note: SVL includes three specimens measured by one of us (CJH) in the field (2♂ 104mm, ♀ 113mm). These measurements have been included in the diagnosis but not in the morphometrics for the species description.)

DESCRIPTION. SVL (mm): 90.3-103 (n = 4, mean = 96.5). Proportions as % SVL: L1 43.9-45.1 (n = 4, mean = 44.6); L2 53.8-58.9 (n = 4, mean = 56.2); T 86.1 (n = 1); TT 36.9 (n = 1); HL 27.7-29.1 (n = 4, mean = 28.2); HW 20.7-21.4 (n = 4, mean = 21.1); S 12.4-13.2 (n = 4, mean = 12.7); NL 20.7-23.3 (n = 4, mean = 21.6).

Head large, depressed, triangular, distinct from neck; covered in small granules which are intermixed with larger conical tubercles; skin of head not co-ossified with skull; deep, vertical groove partially dividing rostral scale (n = 4); rostral excluded from nostril; 5-6 scales along the dorsal margin of rostral shield (n = 3); ear opening elliptical, vertical, much less than half as large as eye; supralabials 15-16 (n = 8, mean = 15.5); infralabials 13-15 (n = 8, mean = 13.9). Neck broad. Body depressed, covered in small granules; dorsal granules intermixed with larger conical tubercles; tubercles very small on back, flanks and sides of neck; basal scales surrounding flank tubercles not enlarged; no enlarged tubercles or granules on ventral surface of body. Preanal pores absent. Axilla moderately to deeply invaginated. Limbs long, covered in small pointed tubercles dorsally; lacking enlarged tubercles on ventral surface, except on upper forelimb; digits strong, strongly compressed

distally; subdigital lamellae (fourth toe) 22-25 (n = 8, mean = 20.3). Original tail (n = 1) depressed, flared, contracted at base and attenuated at tip, terminating with a minute rounded knob; dorsal surface of flared portion with prominent enlarged spinose tubercles on basal 1/3rd and along margins; 6 rows of minute spines across basal portion of attenuated tail-tip; attenuated tip accounts for 42.9% of total tail length; ventral surface smooth with a slight depression along midline (excluding attenuated tip). Regenerated tail (n = 3) depressed, broad and strongly flared, contracted at base and attenuated at tip; covered with uniform granules, except on basal margin which has small spinose tubercles; ventral surface without groove along midline.

Pattern. In spirit, dorsal base colour beige with irregular dark brown blotches on head, body and limbs; blotches on body tend to be aligned transversely. Limbs banded; digits strongly banded; inner anterior digit with reduced pigment. Body and limbs ventrally off-white to cream (immaculate); labials off-white, mottled with brown. Original tail dorsally tan/grey, marked with irregular dark brown blotches; six cream bands on tail, only those on attenuated portion (4) extending to ventral surface; ventrally cream, peppered with brown specks. Regenerated tail lacking cream bands; dorsally tan/grey, mottled with dark brown blotches; ventral surface similar, but with reduced pigmentation.

Skeletal Features. Material examined: (radiographs) QMJ64406-08; (alizarin stained) QMJ67852. Supraocular portion of frontal grooved; anterior process of interclavicle pronounced; epipubic cartilage moderately expanded; presacral vertebrae 26; sacral vertebrae 2; lumbar vertebrae 2; first autotomy



FIG. 3. *Phyllurus amnicola* sp. nov. (holotype, QMJ64408; QM photographic collection, image ref. NW982), Mt Elliot, NEQ. (Jeff wright)

septum on postsacral vertebra 5; abdominal vertebrae bearing reduced ribs 4; rib-free cervicals 3; sternal ribs 3; mesosternal ribs 2.

Holotype Data. QMJ64408, ♀; SVL 90.3mm; L1 40.6mm; L2 53.2mm; T 77.8mm; TT 33.4mm; HL 25.1mm; HW 18.8mm; S 11.3mm; NL 19.0mm; supralabials 15/16; infralabials 15/14; subdigital lamellae 22/22.

COMPARISON. *Phyllurus amnicola* can be confused with only its congeners. *P. amnicola* is distinguished from *P. caudiannulatus* by tail shape (flared vs cylindrical); from *P. platurus* by pattern of original tail (flared portion with distinct white bands vs without white bands); from *P. isis* by pattern of original tail (anterior-most band spanning full width of tail vs anterior band reduced, with two narrowly-spaced midline blotches); from *P. nephys* by colour/pattern of ventral surface (immaculate vs peppered with brown specks); from *P. championae* by spinosity of original tail (enlarged spinose tubercles restricted to anterior third of tail and tail margins vs tail covered with spinose tubercles) and from *P. ossa* by the rostral groove/s (one groove partially dividing rostral vs 1-3 grooves, usually 3, only rarely 1 or 2, partially dividing rostral). *P. amnicola* is further distinguished from *P. isis* and *P. ossa* by the

number of scales along dorsal margin of rostral shield (5-6 vs 9-11 and 8-11, respectively).

GENETICS. *Phyllurus amnicola* shows a 21-27% sequence divergence from all other *Phyllurus* spp. for the cytochrome *b* portion of mtDNA (Table 1, Fig. 1). The phylogenetic position of *P. amnicola* as the sister group to the remaining *Phyllurus* is not strongly supported by the cytochrome *b* data (Fig. 1), but morphological characters support its placement in a monophyletic *Phyllurus*.

HABITAT & DISTRIBUTION. Mt Elliot, Bowling Green Bay NP, 30kms SE of Townsville (19°28'S, 146°59'E) NEQ (Fig. 4). Found amongst boulders at 450m, in a moist 'tongue' of forest along a creek running from the rainforested upper slopes of Mt Elliot (Fig. 5). Dense rainforest is the dominant vegetation above 750m. A recent survey (CJH and J. Gratten, Oct., 1999) showed *P. amnicola* to be relatively common between 400-1000m along a major drainage line. Surveys on the summit of Mt Elliot have failed to locate this species.

HABITS. Most specimens were found head down, on granite boulders close to permanent water. Several were foraging on rocks directly above flowing water and one was observed



FIG. 4. Occurrence of *Phyllurus* spp. in eastern Australia; 1 = *P. amnicola*, 2 = *P. ossa*, 3 = *P. nephys*, 4 = *P. isis*, 5 = *P. championae*, 6 = *P. caudiannulatus*, 7 = *P. platurus*.

foraging in a thin film of water in the splash zone of a cascade. All specimens, but one, have been found on rocks. The exception was on a thin tree trunk amongst boulders. Activity began soon after dark, even during persistent rain. Of 27 specimens (14♂'s, 11♀'s and 2 juveniles) encountered during two nights (Oct., 1999), 70% had regenerated tails. This proportion was similar in both sexes.

REPRODUCTION. One gravid female, captured and released (4 Feb., 1998), contained a single, shelled egg. A male (QMJ67852) that died in captivity (Dec., 1998) was sexually mature, with



FIG. 5. Alligator Ck, Mt Elliot, NEQ, the type locality for *P. amnicola* sp. nov. (Conrad Hoskin)

sperm present in its epididymis (inferred by opacity). Fourteen mature females were encountered on the first two nights of Oct., 1999. Eight of these carried well-developed, shelled eggs (3 with 1 egg, 4 with 2 eggs, 1 with 3 eggs).

CONSERVATION. *P. amnicola* is one of the most narrowly restricted reptile species in Queensland. However, it is well protected. The only known locality for this species is in Bowling Green Bay NP which is not subject to any known threatening processes. The potential effect of fire on pockets of riparian rainforest at and near the type locality is not known.

***Phyllurus championae* sp. nov.**
Schneider, Couper, Hoskin & Covacevich
(Fig. 6)

ETYMOLOGY. Named for Irene Champion, a Resource Ranger with Queensland Parks and Wildlife Service, Mackay, MEQ, who focussed the attention of one of us (CJS) on Cameron Ck/Black Mtn, as a phytogeographically interesting area, possibly pointing to the presence of unusual fauna.



FIG. 6. *Phyllurus championae* sp. nov. (QM photographic collection, image ref. NX758) Cameron Ck, MEQ. (Jeff Wright)

MATERIAL. HOLOTYPE: QMJ64847 ♂, Cameron Ck, 6.5km WNW Koumala (21°34'24"S, 149°11'06"E) MEQ, P. Couper & C. Hoskin, 18 April 1998. PARATYPES: QMJ62757-58, J62766, J63907, J64845-46, J64848, locality as for holotype; J64854-64 Blue Mtn (21°36'S, 148°58'E) MEQ.

DIAGNOSIS. *P. championae* almost invariably (18/19) has a fully divided rostral scale. This feature, combined with a leaf-shaped tail, distinguish it from all other *Phyllurus* spp. A specimen of *P. championae* with an only partially divided rostral could be confused with some specimens of *P. ossa* which have a rostral partially divided by a single groove. (This is a rare state in *P. ossa* which usually has 2 or 3 partial grooves). From such specimens of *P. ossa*, 'partial single groove' specimens of *P. championae* can be distinguished readily by a straight groove vs a Y-shaped groove.

DESCRIPTION. SVL(mm): 33.3-80.6 (n = 19, mean = 61.5). Proportions as % SVL: L1 41.2-48.0 (n = 19, mean = 44.0); L2 52.5-60.5 (n = 19, mean = 56.50); T 64.2-81.7 (n = 8, mean = 75.7); TT 28.9-40.7 (n = 8, mean = 35.7); HL 28.9-31.8 (n = 19, mean = 30.1); HW 23.1-26.4 (n = 19, mean = 24.40); S 12.4-14.6 (n = 19, mean = 13.1); NL 18.8-23.6 (n = 19, mean = 20.6).

Head large, depressed, triangular, distinct from neck; covered in small granules which are intermixed with larger, conical tubercles, extremely prominent on snout; skin of head co-ossified with skull; deep, vertical groove totally dividing rostral scale (n=18) or (rarely) partially dividing rostral scale (n=1); rostral excluded from nostril; 5-8 scales along dorsal margin of rostral shield (n = 10); ear opening elliptical, vertical, much less than half as large as eye; supralabials 12-14 (n=38, mean=13.3, mode=14); infralabials 11-15 (n=38, mean=12.7, mode=13). Neck broad. Body depressed, covered in small granules; dorsal granules intermixed with larger, conical tubercles; tubercles small on back, pronounced on flanks, most prominent on sides of neck; basal scales surrounding flank tubercles only slightly enlarged; no enlarged tubercles or granules on ventral surface of body. Preanal pores absent. Axilla deeply invaginated. Limbs long, covered in large pointed tubercles dorsally; without enlarged tubercles on ventral surface, except on upper forelimb; digits strong, compressed distally; subdigital lamellae (fourth toe) 16-20 (n = 38, mean = 17.9, mode = 17). Original tail (n = 8) depressed, flared to carrot-shaped, contracted at base and attenuated at tip, terminating with a

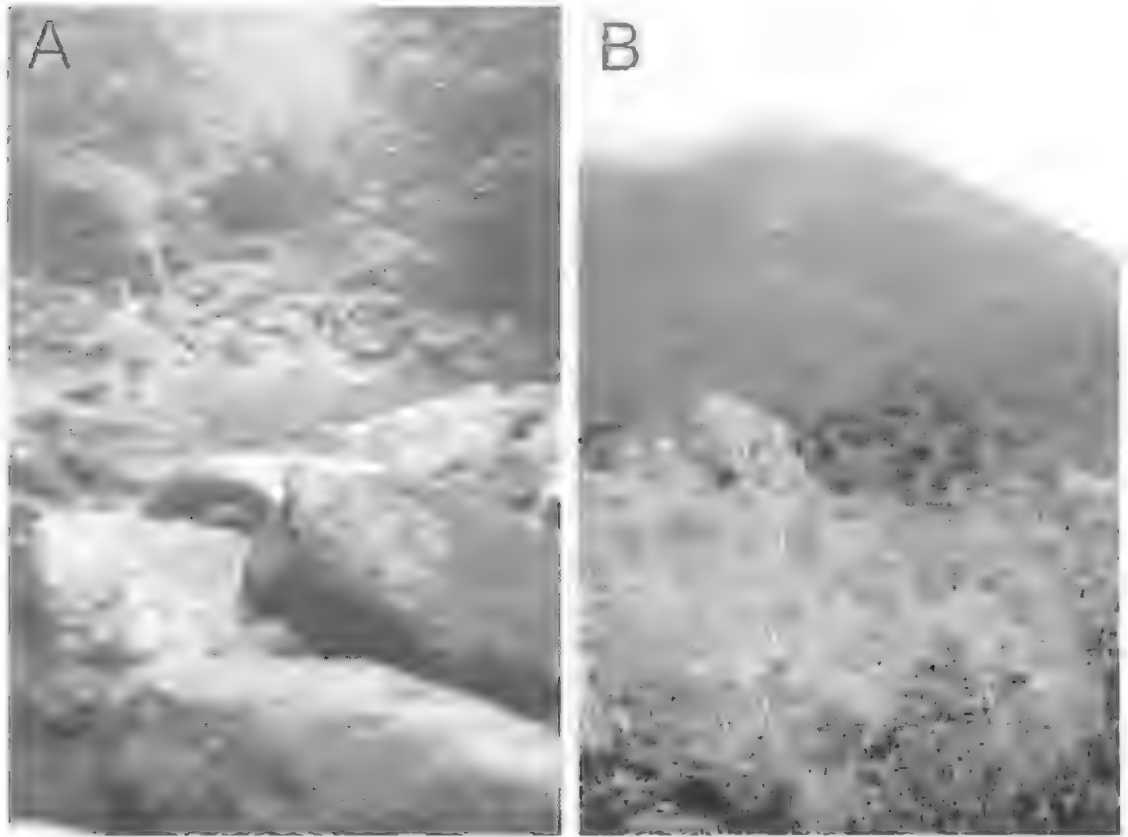


FIG. 7. A, Cameron Ck, MEQ, the type locality for *P. championae* sp. nov. B, dry rainforest below the summit of Blue Mtn, MEQ, the second known locality for *P. championae* sp. nov. (Conrad Hoskin)

minute rounded knob; covered dorsally with numerous moderate-sized, spinose tubercles which become smaller along the vertebral line; tubercles terminate approximately half-way along the attenuated tip which is long; 8 rows of enlarged spines across the basal portion of attenuated tail-tip; attenuated tip accounts for 38-52% of total tail length; ventral surface smooth, or with slight depression along midline. Regenerated tail: (n = 10) depressed, broad and strongly flared, contracted at base and attenuated at tip; with small, spinose tubercles which are most prominent around the edges; ventral surface without groove along midline. The Cameron Ck specimens are significantly smaller than those from Blue Mtn (max SVL = 69mm, n = 7, small juveniles excluded, mean = 61.9mm vs max SVL = 81mm, n = 9, small juveniles excluded, mean = 69.6mm; Student's T-Test, $t_{1,14} = 2.14$, $0.05 > P > 0.025$).

Pattern. In spirit, dorsal base colour mid brown with irregular, black blotches on head, body and

limbs. Digits obscurely banded; inner anterior digit not significantly lighter than others. Body and limbs ventrally off-white to cream; labials off-white, mottled with brown. Original tail dorsally tan, heavily mottled with black (almost entirely black in hatchlings); five white bands on tail, only those (2-3) on attenuated portion extending to ventral surface; ventrally cream with grey mottling. Regenerated tail lacking cream bands; dorsally, tan/grey with black blotches; ventral surface similar, but with reduced pigmentation.

Skeletal Features. Material examined: (radiographs) QMJ63907, J64845-48, J64854-55, J64858-59, J64864; (alizarin stained) QMJ64863. Supraocular portion of frontal flat; anterior process of interclavicle pronounced; epipubic cartilage not expanded; presacral vertebrae 26; sacral vertebrae 2; lumbar vertebrae 2; first autotomy septum on postsacral vertebra 5; abdominal vertebrae bearing reduced ribs 4; rib-free cervicals 3; sternal ribs 2; mesosternal ribs 3.

TABLE 1. Kimura 2-parameter distance estimates (Kimura, 1980) between species and populations within species for 399bp cytochrome *b* sequence data. Species are numbered in the same order across the top of the data matrix. See Appendix 1 for specimen details.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1 <i>S. salebrosus</i> Blackdown	-													
2 <i>S. salebrosus</i> Bulburrin	0.0625	-												
3 <i>S. cornutus</i> Atherton	0.1833	0.1760	-											
4 <i>S. cornutus</i> MalbonThompso	0.1872	0.1722	0.0076	-										
5 <i>S. cornutus</i> BigTableland	0.2039	0.1785	0.0894	0.0960	-									
6 <i>S. cf. wyberba</i> Chaelundi	0.1987	0.2119	0.2677	0.2726	0.2733	-								
7 <i>S. cf. wyberba</i> Chaelundi	0.1987	0.2119	0.2677	0.2726	0.2733	0.0054	-							
8 <i>S. wyberba</i> Girraween	0.2280	0.2376	0.2640	0.2687	0.2921	0.1321	0.1321	-						
9 <i>S. wyberba</i> Girraween	0.2244	0.2384	0.2602	0.2648	0.2878	0.1288	0.1288	0.0025	-					
10 <i>S. wyberba</i> Girraween	0.2208	0.2347	0.2563	0.2610	0.2835	0.1255	0.1255	0.0050	0.0025	-				
11 <i>S. swaini</i> Lamington	0.2251	0.2087	0.2296	0.2383	0.2627	0.1520	0.1600	0.1733	0.1700	0.1668	-			
12 <i>S. swaini</i> MtTamborine	0.2244	0.2081	0.2260	0.2346	0.2585	0.1514	0.1594	0.1727	0.1694	0.1661	0.0050	-		
13 <i>P. nephys</i> Eungella	0.2980	0.3093	0.2862	0.2862	0.2756	0.2514	0.2610	0.2889	0.2849	0.2810	0.2602	0.2594	-	
14 <i>P. nephys</i> Finch Hatton	0.2929	0.3041	0.2813	0.2813	0.2806	0.2561	0.2658	0.2840	0.2800	0.2761	0.2555	0.2548	0.0025	-
15 <i>P. isis</i>	0.3051	0.2911	0.2966	0.3065	0.2973	0.2591	0.2688	0.2797	0.2757	0.2718	0.2642	0.2591	0.1544	0.1581
16 <i>P. ossa</i> MtDryander	0.2765	0.2679	0.2909	0.3007	0.2774	0.2453	0.2546	0.2869	0.2876	0.2836	0.2591	0.2585	0.1512	0.1549
17 <i>P. ossa</i> Conway	0.2757	0.2765	0.2966	0.3065	0.2884	0.2457	0.2551	0.2925	0.2933	0.2893	0.2642	0.2636	0.1516	0.1553
18 <i>P. ossa</i> MtOssa	0.3020	0.2831	0.3033	0.3134	0.2748	0.2719	0.2719	0.3042	0.3051	0.3010	0.2992	0.2983	0.1416	0.1452
19 <i>P. championae</i> sp. nov.	0.3001	0.3010	0.3218	0.3271	0.3136	0.2685	0.2786	0.2942	0.2951	0.2911	0.2893	0.2885	0.1563	0.1600
20 <i>P. platurus</i>	0.2510	0.2752	0.2496	0.2586	0.2702	0.2499	0.2596	0.2414	0.2376	0.2339	0.2518	0.2510	0.1936	0.1975
21 <i>P. caudiannulatus</i>	0.2610	0.2853	0.2829	0.2925	0.3130	0.2650	0.2749	0.2789	0.2797	0.2757	0.2983	0.3024	0.2405	0.2450
22 <i>P. cf. caudiannulatus</i> Oakvie	0.2742	0.3010	0.2558	0.2649	0.3094	0.2699	0.2799	0.2781	0.2742	0.2702	0.2642	0.2681	0.2056	0.2097
23 <i>P. amnicola</i> sp. nov.	0.2579	0.2496	0.2688	0.2734	0.2859	0.2563	0.2470	0.2514	0.2476	0.2438	0.2558	0.2508	0.2420	0.2376
24 <i>P. amnicola</i> sp. nov.	0.2534	0.2451	0.2688	0.2734	0.2861	0.2516	0.2424	0.2470	0.2432	0.2395	0.2514	0.2508	0.2376	0.2333
25 <i>Orraya</i> (gen. nov.) <i>occutus</i>	0.2632	0.2640	0.2309	0.2351	0.2575	0.2336	0.2336	0.2565	0.2572	0.2534	0.2489	0.2482	0.2427	0.2383
26 <i>C. laevis</i> BigTableland	0.3033	0.2893	0.2448	0.2491	0.2759	0.2702	0.2801	0.2880	0.2840	0.2880	0.2656	0.2649	0.2521	0.2568
27 <i>C. laevis</i> Atherton	0.3074	0.3033	0.2530	0.2574	0.2803	0.2845	0.2948	0.3020	0.2980	0.3020	0.2558	0.2642	0.2559	0.2606

	15	16	17	18	19	20	21	22	23	24	25	26	27
15 <i>P. isis</i>	-												
16 <i>P. ossa</i> MtDryander	0.1230	-											
17 <i>P. ossa</i> Conway	0.1235	0.0206	-										
18 <i>P. ossa</i> MtOssa	0.1306	0.0595	0.0568	-									
19 <i>P. championae</i> sp. nov.	0.1682	0.1727	0.1694	0.1787	-								
20 <i>P. platurus</i>	0.2000	0.1857	0.1853	0.1941	0.1970	-							
21 <i>P. caudiannulatus</i>	0.2383	0.2145	0.2194	0.2280	0.2223	0.1887	-						
22 <i>P. cf. caudiannulatus</i> Oakvie	0.2333	0.2211	0.2217	0.2145	0.2390	0.1853	0.1452	-					
23 <i>P. amnicola</i> sp. nov.	0.2097	0.2450	0.2488	0.2442	0.2310	0.2123	0.2451	0.2687	-				
24 <i>P. amnicola</i> sp. nov.	0.2139	0.2405	0.2442	0.2398	0.2266	0.2081	0.2407	0.2640	0.0025	-			
25 <i>Orraya</i> (gen. nov.) <i>occutus</i>	0.2290	0.2046	0.1931	0.1970	0.2555	0.2122	0.2563	0.2451	0.2314	0.2272	-		
26 <i>C. laevis</i> BigTableland	0.2555	0.2656	0.2713	0.2829	0.2450	0.2390	0.2831	0.2951	0.2625	0.2579	0.2092	-	
27 <i>C. laevis</i> Atherton	0.2782	0.2791	0.2849	0.2970	0.2580	0.2383	0.2870	0.2749	0.2773	0.2726	0.2127	0.0599	-

Holotype Data. QMJ64847, ♂; SVL 59.28mm; L1 25.57mm; L2 32.80mm; T 48.13mm; TT 24.13mm; HL 17.81mm; HW 14.20mm; S 7.77mm; NL 11.34mm; supralabials 13/14; infralabials 13/13; subdigital lamellae 18/17.

COMPARISON. *P. championae* can be confused with only its congeners. *P. championae* is distinguished from *P. caudiannulatus* by tail shape (leaf-like vs cylindrical); from *P. platurus* by colour pattern of anterior portion of original tail (with white bands vs without white bands); from *P. amnicola* by spinosity of original tail (tail covered with spinose tubercles vs enlarged spinose tubercles restricted to anterior 1/3rd of tail and tail margins); from *P. isis* by spinose flank tubercles (pronounced vs very small); from *P. nephys* by colour/pattern of ventral surface (plain vs peppered with brown specks)

and from *P. ossa* by rostral groove/s (usually one groove dividing rostral, or a straight vertical groove partially dividing rostral vs 1-3 grooves, usually 3, only rarely 1 or 2, partially dividing rostral).

GENETICS. *P. championae* shows 16-24% sequence divergence from all other *Phyllurus* spp. for the cytochrome *b* portion of mtDNA (Table 1). The Cameron Ck and Blue Mtn populations showed no within, or between, population polymorphism. Phylogenetic analyses firmly place *P. championae* within the monophyletic MEQ species group of *Phyllurus* (*P. isis*, *P. nephys* and *P. ossa*, Fig. 1), though its precise relationship to these taxa is not well resolved.

HABITAT & DISTRIBUTION. *P. championae* is known from only two localities, Cameron Ck (21°34'24"S, 149°11'06"E) and (21km to the west) Blue Mtn (21°36'S, 148°58'E) MEQ, (Fig. 4). The type specimens were collected at altitudes between 200m (Cameron Ck) and 700m (Blue Mtn) in notophyll rainforest/microphyll rainforest.

HABITS. All specimens have been on rocks or on the trunks of trees near rocks. The Cameron Ck (21°34'24"S, 149°11'06"E) specimens were collected on the edges of a permanent creek on the eastern side of Black Mtn (Fig. 7a). Blue Mtn (21°36'S, 148°58'E) specimens were active on a scree slope, in dry rainforest, just below the summit (Fig. 7b). Activity began soon after dark.

REPRODUCTION. Gravid females were present in the Cameron Ck population during Dec., 1996/Jan., 1997. A female measuring 68.7mm SVL and weighing 6.2g (QMJ62757) laid two oval-shaped eggs on 6 Jan., 1997. These measured 18.35 × 9.01mm and 17.72 × 8.90mm and weighed 1.0g and 0.9g, respectively. The relative clutch mass (RCM (1) after Greer, 1989) equalled 30.6%. This corresponds closely with that of *P. platurus* (29%, Greer, 1989).

A male (QMJ64863, SVL 72.3mm) from Blue Mtn, collected on 19 Apr., 1998, was in peak reproductive condition with sperm present in its epididymis (inferred by opacity) and a turgid testis. From this we infer that mating may occur in autumn and that females store sperm through winter. A similar reproductive strategy has been suggested for *P. platurus* (Greer, 1989).

CONSERVATION. *P. championae* appears to be common at both localities from which it is known. Suitable similar habitat in adjacent areas may support this species. Blue Mtn is freehold and thus, potentially, could be cleared. However, given that the known leaf-tail site is on an elevated scree slope, the chance that this area would be further disturbed by stock or humans seems remote. Cameron Ck, the type locality, is in State Forest and may be subject to timber harvesting.

Phyllurus caudiannulatus

The discovery of specimens treated tentatively as *P. caudiannulatus* (QMJ62817, J63849-53, J63857) at Oakview SF (26°07'23"S, 152°19'01"E), SEQ extends the range of this species 195km south of the only other known population (Bulburin SF, 24°31'S, 151°29'E), SEQ.

Morphological differences between the Oakview and Bulburin populations cannot be fully assessed presently, due to small sample size. Surveys in the intervening areas should help assess the significance of these differences. For conservation purposes, the Oakview population of '*P. caudiannulatus*' must be recognised as a genetically distinct unit (Fig. 1), given its geographic and genetic isolation and its uncertain taxonomic status.

KEY TO AUSTRALIAN LEAF-TAILED GECKOS

1. Nostril in contact with rostral scale 2
Nostril not in contact with rostral scale 6
2. Neck extremely elongate and slender *O. occultus*
Neck broad 3
3. Throat strongly tuberculate *S. salebrosus*
Throat smooth 4
4. Lower flank tubercles hooked and surrounded by spinose basal scutes. *S. cornutus*
Lower flank tubercles not as above 5
5. Original tail bluntly tipped with large tubercles *S. swaini*
Original tail finely tipped with only minute tubercles *S. wyberba*
6. Tail cylindrical *P. caudiannulatus*
Not as above (leaf-shaped) 7
7. Anterior portion of original tail without white crossbands or blotches *P. platurus*
Not as above (with white crossbands) 8
8. Venter distinctly 'peppered' with brown *P. nephys*
Not as above (plain) 9
9. Rostral scale completely divided *P. championae*
Not as above (partially divided) 10
10. Rostral scale partially divided by 2 or 3 grooves, occasionally by a single Y-shaped groove *P. ossa*
Not as above (partially divided by a straight groove) 11
11. Anterior flared portion of original tail uniformly covered with enlarged spinose tubercles *P. championae*
Not as above 12
12. Tail predominantly black, with distinct white blotches present on either side of the vertebral line *P. isis*
Not as above (tail predominantly tan/grey, with anterior-most bands broken, but spanning tail width) *P. amnicola*

DISCUSSION

Twelve species of leaf-tailed geckos in three genera occur in eastern Australia (13°45'S - 33°53'S). Nine are obligatory rainforest/adjacent wet sclerophyll forest species: Mcllwraith Ra., NEQ, *Orraya occultus* (Couper, Covacevich & Moritz, 1993); Wet Tropics (Big Tableland - Paluma), NEQ, *S. cornutus* (Ogilby, 1892); Mt Elliot, NEQ, *Phyllurus amnicola* Hoskin, Couper, Schneider & Covacevich, 2000; Mt

Dryander - Mt Ossa, MEQ, *P. ossa* Couper, Covacevich & Moritz, 1993; Mt Blackwood and Mt Jukes, MEQ, *P. isis* Couper, Covacevich & Moritz 1993; Clarke Ra. (Mt David - Crediton), MEQ, *P. nephys* Couper, Covacevich & Moritz, 1993; Black Mountain and Blue Mountain, MEQ, *P. championae* Schneider, Couper, Hoskin & Covacevich, 2000; Many Peaks Ra. and Oakview State Forest, SEQ, *P. caudimaculatus* Covacevich, 1975; Great Dividing Range and foothills and Border Ranges (Mt Tamborine - Buladelah), SEQ-MENSW, *S. swaini* Wells & Wellington, 1985. Two species are confined to heaths associated with either sandstone or granites: Girraween National Park, SEQ, *S. wyberba* Couper, Schneider & Covacevich, 1997; and Hawkesbury R. region, MENSW, *P. platurus* (Shaw, 1790). One species, *S. salebrosus*, occurs amongst sandstone in open forests: Blackdown Tableland - Cracow, MEQ. It is also found in rainforest in the Many Peaks Range (24°31'S, 151°29'E), where it is sympatric with *P. caudimaculatus*. This is the only known area to support more than one species of leaf-tail.

The genetic analyses (Fig. 1, Table 1) show that the depth of divergence amongst leaf-tails is high and that more-than-trivial differences between some taxa/populations remain to be clarified. Relative rates tests show that substitution rates among lineages do not differ significantly suggesting that a molecular clock may apply. By using the break-up of Gondwanaland to estimate substitution rates in this portion of cytochrome *b* among carphodactylid geckos from Australia, New Zealand and New Caledonia (Schneider, unpublished) it is estimated that the Kimura two-parameter distance between two lineages accrues at a rate of ca. 0.0042 ± 0.0002 per million years (0.0021 per lineage per million years). Using this calibration, the split between *Saltuarius* sensu stricto and *Phyllurus* is ca. 58-74mya. The divergence among species in MEQ is ca. 31-38mya, and this is nearly identical to the estimated time of divergence between the Oakview and Bulburin populations of *P. caudimaculatus*. Estimating genetic distances among taxa using only transversions (which are more likely to accrue linearly with time) does not substantially change these time estimates. '*Saltuarius wyberba*' populations from Chaelundi SF, NSW (30°01'07"S, 152°30'02"E) and Girraween, SEQ (28°50'S, 151°56.04E, the type locality) differ to the same degree as *P. isis* (from Mt Blackwood, 21°02'S, 148°56'E) and *P. ossa* (Mt Ossa, 20°56'S, 148°49'E, only 14km to the

north). However, more specimens must be examined before the status of the Chaelundi *Saltuarius* specimens can be determined.

Recognition of *Orraya occultus* as distinct from the other large leaf-tails (*Saltuarius* spp.) is significant given the general paucity of endemism in the reptiles of the McIlwraith Ra. rainforest isolate. (Couper et al., 1993 observed this in relation to the Wet Tropics rainforests where 2/3 of the rainforest reptile species are endemic to the area). *Orraya* is the sole terrestrial vertebrate genus not represented in rainforest isolates further south.

The discovery of *P. amnicola* on Mt Elliot, NEQ is noteworthy for two reasons. First, recognition of this species brings to two the number of vertebrate species endemic to Mt Elliot (the other species is the microhylid frog, *Cophixalus mcdonaldi* Zweifel, 1985), highlighting the evolutionary uniqueness of this rainforest isolate. Second, it extends the range of *Phyllurus* some 200km NW of its previously-known, northern limit of occurrence (Mt Dryander, 20°15'S, 148°33'E, MEQ), across what has been termed the 'Burdekin Gap' (Joseph et al., 1993). This expanse of dry woodland between Mt Elliot (19°30'S, 146°58'E), NEQ and Bowen (20°01'S, 148°15'E), MEQ has separated the faunas of two major zoogeographic regions, the Wet Tropics and Central Mackay Coast, for an 'evolutionarily long period' (Joseph et al., 1993). There is a deep divergence between *P. amnicola* and its congeners immediately south of the Burdekin Gap (ca. 50-60 mya). The mtDNA sequence divergence between *P. amnicola* on the one hand, and *P. championae*, *P. isis*, *P. nephys*, *P. ossa*, on the other, is thus nearly as great as that between these species and those of *Saltuarius* spp. With the recognition of *P. amnicola*, there is now an overlap in the max SVL between the largest member of *Phyllurus* (*P. amnicola*, max SVL = 113mm) and the smallest species of *Saltuarius* (*S. wyberba*, max SVL = 109mm).

Description of *P. championae* brings to four the number of *Phyllurus* species known to be confined to rainforests of the Central Mackay Coast Biogeographic Region, MEQ. Couper et al. (1993) commented on aspects of the zoogeography of the other species confined to this area, all within 100km of each other (*P. isis*, *P. nephys* and *P. ossa*). It is now clear that the species of leaf-tailed geckos in rainforests of MEQ represent the relictual distribution of an ancient group. It has been thought that

Pleistocene ice age contraction of rainforest resulted in speciation among rainforest endemics, but the deep genetic divergence among leaf-tailed geckos precludes any role for Pleistocene speciation.

Whether *P. caudiannulatus* (sensu stricto) occurs between Bulburin and Oakview State Forests, SEQ or is confined to the northernmost locality, remains to be ascertained. If the latter is the case, the Oakview '*P. caudiannulatus*' may represent another new species, pointing to a replication of patterns of relictual isolation already observed in MEQ.

Most leaf-tails (*Phyllurus* spp., *Saltuarius* spp. and *Orraya occultus*) are very narrowly distributed. Several (*Orraya occultus*, *P. amnicola*, *P. isis* and *P. nephtys*) are known from only single localities. Four other species (*S. cornutus*, *S. swaini*, *S. wyberba* and *P. caudiannulatus*) are narrowly distributed, being confined to small rainforest or rainforest and heath blocks. Under IUCN (1994) criteria, notwithstanding narrow distributions, all species should be categorised 'Data Deficient'. Higher IUCN categories, which reflect concerns based on such single locality/narrow ranges are all tied to knowledge of declines in populations and/or potential threatening processes. Virtually all known leaf-tail localities are in state conservation or timber reserves where, generally speaking, threats are presently low. Impacts of possible future timber harvest in some areas are not known. However, most of the known, still healthy leaf-tail localities have, in the past, already been selectively logged, some extensively.

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APPENDIX 1

SPECIMENS EXAMINED. The following have been examined in addition to other material cited in Couper et al., 1993.

Morphology:

- P. caudiannulatus* - QMJ15619 (holotype), J33684-86, J33706, J33709, J62817, J63849-53, J63857
- P. isis* - QMJ53511 (holotype), J53485-86, J53518, J53480, J53591, J53602-3
- P. nephtys* - QMJ34058 (holotype), J34057, J35114, J57031, J65511, J65575, J65578, J65580, J65582, J65584, J65674
- P. ossa* - QMJ53444 (holotype), J53389, J53392, J53426, J53428, J53443, J53445, J53447, J56311, J56773, J56791
- P. platurus* - QMJ160, J31978, J56880-81, J56895

Orraya occultus - QMJ37040 (holotype), J37037, J37038-9
J60717, J62596
C. laevis - QMJ31004, J65410-11, J65419

Genetics:

Phyllurus amnicola - liver samples from QMJ64406-7 (Mt Elliot - 19°28'S, 146°59'E).
P. caudiammulatus - (Bulburin SF - 24°31'S, 151°29'E) liver sample from QMJ51103.
P. caudiammulatus (Oakview - 26°07'23"S, 152°19'01"E) - liver sample from QMJ62817.
P. championae - liver samples from QMJ62757-58, J62766, J63907 (Cameron Ck - 21°34'24"S, 149°11'06"E) and 4 liver samples from the following series:- J64854, J64857, J64859, J64861-62 (Blue Mtn - 21°36'S, 148°58'E).
P. isis - tail tips from Mt Blackwood (21°02'S, 148°56'E).
P. nepthys - liver samples from QMJ51101 & J51098 (Finch Hatton NP - 21°06'S, 148°38'E).
P. ossa - tail tips from Mt Ossa (20°56'S, 148°49'E), Brandy Ck (20°21'S, 148°41'E) and Mt Dryander (20°15'S, 148°33'E).

P. platurus - liver samples from QMJ56880-1 (via Gosford - 33°24'S, 151°21'E).
Saltarius cornutus - liver samples from QMJ51632 (Malbon Thompson Ra. - 17°07'S, 145°54'E) and tail tips from Atherton (17°16'S, 145°29'E) and Big Tableland (15°43'S, 145°17'E).
S. salebrosus - liver samples from QMJ51091 (Blackdown Tableland - 23°46'S, 149°06'E) and J51090 (Bulburin SF - 24°31'S, 151°29'E).
S. swaini - liver samples from QMJ51640 (Lamington NP - 28°14'S, 153°08'E) and J51095 (Mt Tamborine - 27°58'S, 153°11'E).
S. wyberba - liver sample from QMJ51633 and tail tips (Girraween NP - 28°50'S, 151°55'E).
S. cf. wyberba - (Chaclundi SF population - 30°01'07"S, 152°30'02"E & 30°03'04"S, 152°21'36"E) tissues from AMR141964-5.
Orraya occultus - tissues from QMJ60717, J62596 (Mellwraith Ra. - 13°45'S, 143°19'E).
Carphodactylus laevis - tails from Big Tableland (15°43'S, 145°17'E) and Mt Bartle Frere (17°24'S, 145°49'E).

THE SCINCID LIZARD *EGERNIA MCPHEEI* WELLS & WELLINGTON, 1984 IN QUEENSLAND. *Memoirs of the Queensland Museum* 45(2): 266. 2000.- Saxicoline members of the *Egernia striolata* complex in eastern Australia have had a complex taxonomic history. Cogger (1960) demonstrated ecological and morphological separation of sympatric saxicoline and arboreal species of this complex in the Warrumbungle Ranges, NSW, identifying the arboreal species as *E. striolata* and describing the saxicoline species as *E. saxatilis saxatilis*. Other saxicoline populations from SE Australia were described as *E. saxatilis intermedia*, the subspecies name referring to the intermediate morphology of these populations, which were allopatric to *E. striolata*. Subsequently, some workers have assumed that all saxicoline members of the complex in SE Australia, including the New England Tableland, are *E. saxatilis* (see Horton, 1972; Cogger, 1988). Wells & Wellington (1984) named an additional species, *E. mcphoei*, from 3 specimens from the Coffs Harbour area, NSW, but did not differentiate it from either subspecies of *E. saxatilis*, or resolve the limits of the distribution of either species. The description of *E. saxatilis intermedia* refers to two atypical northern NSW specimens subsequently reidentified as *E. mcphoei* (see Shea & Sadlier, 1999 for the reidentification and type status).

A single Queensland Museum record of *E. saxatilis* was reported from SE Qld, close to the NSW border, by Covacevich & Couper (1991). The specimen on which this record was based was exchanged with the United States National Museum (USNM) in 1976, and was not re-examined prior to publication of the record.

We here report re-examination of this specimen (formerly QM J28654, now USNM 203953), another specimen from nearby, and an unambiguous photographic record from a third Queensland locality, and identify all three as *Egernia mcphoei*. Thus, this species is added to, and *E. saxatilis* removed from, the list of Queensland reptiles (Covacevich & Couper, 1991).

USNM 203953, preserved 1 Aug. 1973, is one of a litter of more than three born to a wild-caught female from near Girraween, SE Qld, collected 2 Dec. 1972. It is brown dorsally, with 28 midbody scales, 23 lamellae below the fourth toe, and dorsal scales smooth. The snout-vent length is 61.6mm, and tail length 79mm (TL/SVL 128.2%).

On 27 Jan. 1999, two large adult individuals were closely observed on a large rock outcrop at the summit of the McPherson Range at Moss Garden (28°17'S 152°26'E) on the NSW/Qld border by GS and RS. One (Australian Museum R153859) was on the NSW side of the border fence, while the other, not collected, was observed one metre distant on the Qld side of the fence. The rock outcrop created an exposed sunny area in what was otherwise wet sclerophyll/ rainforest. The collected specimen has 30 midbody scales, 23/22 lamellae below the fourth toe, dorsal scales bluntly keeled, snout-vent length 124mm, and tail length 157mm (TL/SVL 126.6%).

At least three individuals were observed, and one photographed, by RJ on 6 April 1997, on the southern peak of Mt Mitchell, SEQld (28°04'S 152°23'E), inhabiting closed rocky grassland with shrubs and grasses, above a mosaic of wet sclerophyll/rainforest. The photographed individual displayed dark brown dorsum, bright orange body venter, and bluntly keeled dorsal scales.

Based on unpublished studies by the senior author, *E. mcphoei* is distributed along the coast and E side of the Great Dividing Range of NE NSW, from the Barrington Tops area to the records reported herein. These records are the most inland localities known for the species, and probably represent a migration along the Clarence River valley from more coastal populations. The species is differentiated from the

e geographically proximate *E. striolata* in its larger size (SVL up to 143mm vs 119mm), more chocolate-brown dorsal coloration (vs grey), more brightly coloured venter (bright orange to orange-yellow vs dull orange-yellow to yellow); longer tail (tail length = 0.907(snout-vent length)^{1.077} vs tail length = 1.352(snout-vent length)^{0.951}; tail length as % of SVL 111.6-143.0%, mean = 127.1% vs 95.7%-123.3%, mean = 109.6%) and greater number of lamellae below the fourth toe (21-28, mean = 24.7 vs 16-26, mean = 20.2). It may be differentiated from *E. saxatilis* by having dorsal scales bluntly keeled in adults and smooth in juveniles (as in *E. striolata*; vs sharply keeled in adults, more weakly keeled in juveniles), fewer midbody scale rows (27-32 vs 35-41, mean = 37.0 for *E. s. saxatilis*, 30-42, mean = 34.5 for *E. s. intermedia*) and a reduced dark upper lateral zone (vs strong). The nearest populations of *E. saxatilis* are in the Warrumbungle Mtns (*E. s. saxatilis*) and in the Wornes Plateau W of Sydney (*E. s. intermedia*), *Egernia mcphoei* and *E. striolata*, which are allopatrically distributed, both inhabit crevices in trees and rocks when in isolation from other members of the complex, so that the ecological separation observed by Cogger (1960) between *E. striolata* and *E. saxatilis* in sympatry is not applicable in this instance.

Comparative Material

E. mcphoei: AM 4873, R8108, R11859, R12740, R16990, R16992, R16994-95, R41174, R41815, R41826, R54308, R54456, R54797-99, R54807, R59315, R60487, R62338, R66154-57, R68239, R68474-75, R71400, R76514, R90602, R93468, R96830, R96834, R96894, R97704, R108766, R111944-46, R112279, R120490; Northern Territory Museum R4808-10.

E. striolata: AM R1050, R1054-55, R1499, R1825, R2005, R2896-98, R4171, R9315, R9403-05, R11055, R11596ab, R11597ab, R13899, R14961-67, R15250, R15254-60, R15284-86, R15288, R15290, R15376, R15538-48, R15550-59, R16778-79, R17095-96, R17664-66, R17869-70, R18773, R18909-18, R18924, R20281, R20315-17, R20671, R20731-35, R21448, R27980-81, R28027-30, R30328, R31597-98, R31770-72, R41803-09, R41811-14, R41818-24, R41827-29, R41831, R41840-41, R43439-57, R43462-67, R44663, R44762, R47338-39, R52717, R52947-50, R52951, R57769-70, R57873, R58259, R60481, R60483-86, R60494, R60496, R66144-45, R66148-49, R67921-22, R68311, R69589-90, R69599, R92464, R92465-66, R92468, R92470-74, R92475-76, R94727-28, R94783, R96550, R96628, R110746, R110755-56, R112852, R112953, R113327, R121037-42; Australian National Wildlife Collection R3201, R36067, R408258, R4544-56; Museum of Victoria D9273-75, D9276-77, D9278-79, D14037, D54283; QM J51, J263, J412-13, J415-22, J10487, J13354, J13356-57, J13358-59, J14246, J28526-27, J30095-96, J30717, J30664, J31862, J34125, J34797, J35413; South Australian Museum R15418

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BOUNTIANA, A NEW GENUS FOR *ERIPHIA NORFOLCENSIS* GRANT & MCCULLOCH, 1907 (CRUSTACEA: BRACHYURA: ERIPHIIDAE)

PETER J.F. DAVIE AND PETER K.L. NG

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Eriphia norfolcensis is separated from *Eriphia* sensu stricto and placed into a new genus *Bountiana*. The two genera differ in many features including carapace shape, eye size and shape; differentiation of efferent branchial openings; length of second antennular segment; length and disposition of basal antennal segment; conformation of gonopod 2; and distinctness of suture between male thoracic sternites 2 and 3. A lectotype is designated for *E. norfolcensis* Grant & McCulloch, 1907. □ *Brachyura, Eriphiidae, Eriphia, Norfolk Island, Lord Howe Island, Australia, new genus.*

P.J.F Davie, Queensland Museum, PO Box 3300, South Brisbane 4101, Australia; P.K.L. Ng, Department of Biological Sciences, National University of Singapore, 10 Kent Ridge Crescent, Singapore 119260, Republic of Singapore; 21 March 2000.

Eriphia Latreille, 1817 (type species *Cancer spinifrons* Herbst, 1785, a junior synonym of *Cancer verrucosus* Forskål, 1775) (Eriphiidae sensu Ng, 1998) currently contains seven species, viz. *E. verrucosa* (Forskål, 1775), *E. gonagra* (Fabricius, 1781), *E. sebana* (Shaw & Nodder, 1803), *E. smithii* MacLeay, 1838, *E. scabricula* Dana, 1852, *E. squamata* Stimpson, 1860, *E. granulosa* A. Milne Edwards, 1880, and *E. norfolcensis* Grant & McCulloch, 1907. *Eriphia verrucosa* is found in the Mediterranean, *E. gonagra* is known from the western Atlantic, and *E. squamata* is known only from the Pacific coast of tropical America. Three species, *Eriphia sebana*, *E. smithii* and *E. scabricula* all have wide Indo-West Pacific distributions. The remaining species, *Eriphia norfolcensis* is only known from Norfolk Island, Lord Howe Island and the coast of New South Wales. Examination of a series of specimens of *E. norfolcensis* shows that this species is aberrant within *Eriphia*, and more closely allied to *Globopilumnus* Balss, 1933. A new genus is here established for *E. norfolcensis*.

Measurements provided are of the carapace width and length respectively (including spines). G1 and G2 are abbreviations for male first and second gonopods respectively. Specimens are deposited in the Australian Museum (AM), Sydney, and Queensland Museum (QM), Brisbane.

ERIPHIIDAE Alcock, 1898

***Bountiana* gen. nov.**

TYPE SPECIES. *Eriphia norfolcensis* Grant & McCulloch, 1907, by monotypy.

ETYMOLOGY. Named after H.M.S. *Bounty*, in remembrance of the group of mutineers who lived undiscovered in the South Seas for so long. The ancestors of the mutineers were, many years later, moved from Pitcairn Island to Norfolk Island where their descendents live to this day.

DIAGNOSIS. Carapace transversely oval, strongly vaulted anteriorly; regions poorly defined. Front obliquely deflexed, with transverse ridge either side of notch. Anterolateral margin with three small, blunt, well separated, spines. Eyes relatively small with small corneas (see Fig. 3A). Efferent branchial openings not distinct, almost completely covered by third maxillipeds, endostomial ridges weak, not forming circular opening with epistome; antero-external margin of third maxillipeds rounded; third maxillipeds gaping. Second antennular segment very short, less than half length of basal segment. Basal antennal segment with outer distal lobule just touching front, and placed close to inner angle of orbit (Fig. 3A); orbit closed. Chelipeds asymmetrical. Fingers of chelipeds gaping. Ambulatory legs short, stout; dactyli very short. Gonopod 2 flagellum subequal in length to basal portion. Suture between male thoracic sternites 2 and 3 distinct.

REMARKS. The ovate, longitudinally strongly convex and bulging carapace of *Eriphia norfolcensis* immediately separates it from typical *Eriphia* species, which are hexagonal or transversely hexagonal, and only moderately convex. This alone is sufficient to necessitate the establishment of a new genus, *Bountiana*, for *Eriphia norfolcensis*. There are also, however,



FIG. 1. *Bountiana norfolcensis* (Grant & McCulloch, 1907), lectotype male, 12.2 × 18.1mm, Norfolk Island; A, dorsal view; B, ventral view.

many other characters of generic significance and these are summarised in Table 1. All species of *Eriphia*, including the type species, *E. verrucosa* (Forskål, 1775), have been examined and taken into account when constructing Table 1; this material forms part of a separate revision of *Eriphia* by S.K. Koh & P.K.L. Ng (unpubl. data).

Bountiana norfolcensis is closer in general appearance to species of *Globopilumnus*, the only other genus within the Eriphiidae. It can be effectively separated from this genus because in *Globopilumnus* the supra- and infra-orbital angles do not meet, such that the antenna enters the orbit through an orbital hiatus.

A

B

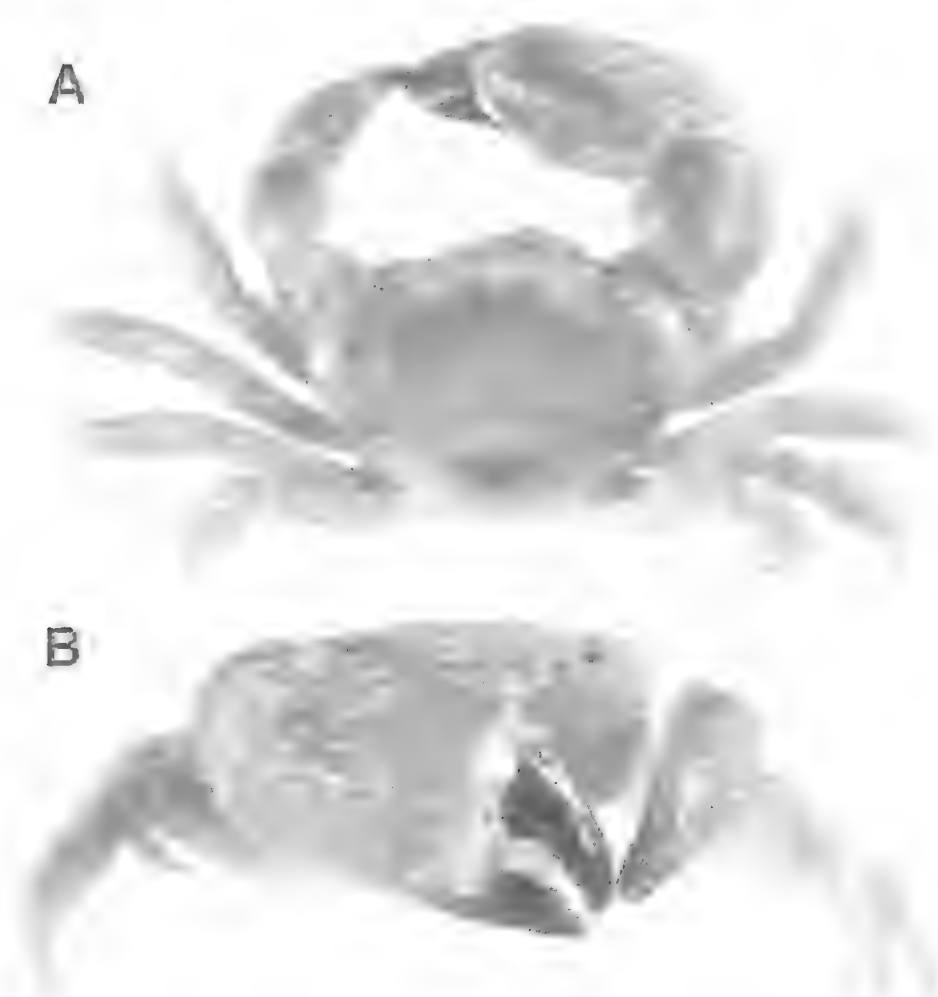


FIG. 2. *Bountiana norfolcensis* (Grant & McCulloch, 1907), female, 16.5 × 11.8mm, QMW24902, Norfolk Island; A, dorsal view; B, frontal view showing claws.

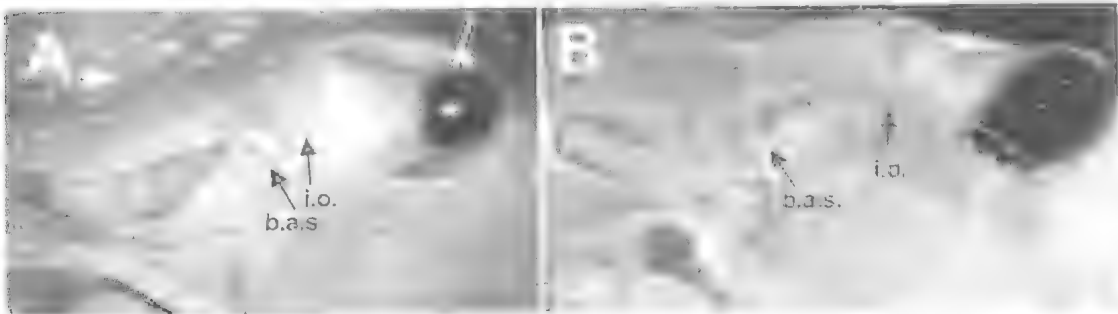


FIG. 3. Orbit and frontal regions: A, *Bountiana norfolcensis* (Grant & McCulloch, 1907), male, 16.3 × 11.2mm, QMW24902; B, *Eriphia scabricula* Dana, 1852, male, 19.3 × 13.3mm, QMW12117 Lady Elliot Island, St Qld. (b.a.s. = basal antennal segment; i.o. = inner orbital angle).

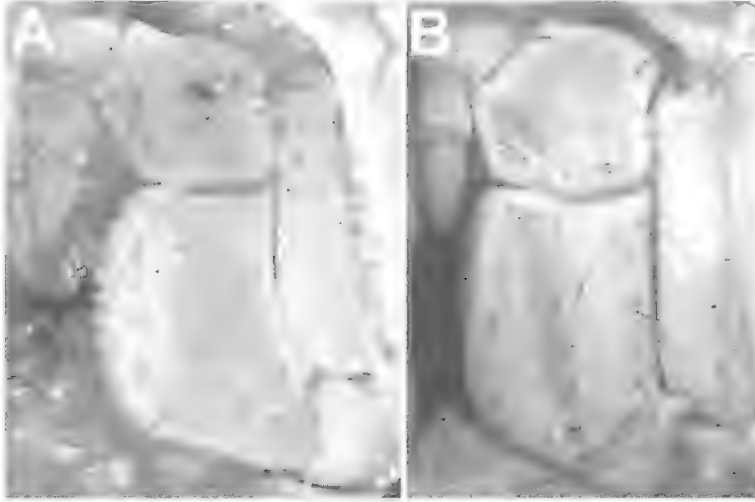


FIG. 4. Third maxillipeds; A, *Bountiana norfolcensis* (Grant & McCulloch, 1907), female, 16.5 × 11.8mm, QMW24902; B, *Eriphia scabricula* Dana, 1852, male, 19.3 × 13.3mm, QMW12117, Lady Elliot Island, SE Qld.

Bountiana norfolcensis
(Grant & McCulloch, 1907)
(Figs 1, 2, 3A, 4A, 5)

Eriphia norfolcensis Grant & McCulloch, 1907: 151, pl. 1; McNeil & Ward, 1930: 381; Holthuis, 1968: 218.
Pseudozius sp. Bennett, 1964: 67-68, figs 62-68, 132; Dell, 1968: 17-18; Guinot, 1968: 330-331.

MATERIAL. LECTOTYPE: AMG5827, ♂ (12.2 × 18.1mm), Norfolk I., Tasman Sea, 29°02.5'S 167°57'E, F.E. Grant. PARALECTOTYPES: AMG5827, ♀ (10.8 × 15.7mm), 1 juvenile (7.5 × 10.0mm), Norfolk I., Tasman Sea, 29°02.5'S 167°57'E, F.E. Grant. OTHER MATERIAL: AMP446, ♀, AMP448, ♀, AMP449, ♂, Lord Howe I., no other data. AMP4032, ♂ (7.6 × 11.0mm), ♀ (9.8 × 14.4mm), AMP5254, ♂ (10.0 × 14.6mm), 2♀ (10.7 × 15.6, 8.7 × 12.6mm), Lord Howe I., 31°33'S 159°05'E, E.A. Briggs. AMP5255, ♂,

2♀, AMP5256, 5♂, ♀, Lord Howe I., A.R. McCulloch. AMP10328, ♂, ♀, Lord Howe I., reef, April, 1932, A.A. Livingstone. AMP6285, ♂, AMP6842, ovig. ♀, AMP7889, ♀, Shell Harbour, NSW, 34°35' S, 150°53'E, 1923, G. McAndrew. AMP11285, ♂, Harbord, NSW, 33°47' S, 151°17'E, 24.11.1947, E. Pope. AMP17289, 2♀ (18.9 × 13.0; 10.9 × 7.8mm), 3♂ (9.3 × 6.7; 11.5 × 8.3; 18.2 × 12.4mm), Slaughter Bay, Norfolk I., under coral rubble and weed, outer reef crest, low tide, 21.03.1969, D.J. Griffin. QMW24902, 2♀ (16.5 × 11.8; 18.5 × 12.8mm), 2♂ (16.3 × 11.2; 18.3 × 12.6mm), same data as AMP17289.

DESCRIPTION. Carapace transversely ovate, strongly vaulted anteriorly; dorsal surface smooth except for

scattering of low tubercles anterolaterally; regions poorly defined, gastric region weakly separated by grooves. Front with transverse ridge, deflexed downwards, slightly denticulated. Eyes relatively small with small corneas. Infraorbital margin with about eight denticles. Anterolateral margin armed with four widely separated, low tubercles. Second antennular segment very short, less than half length of basal segment. Antennae very short, not reaching orbital margin; basal antennal segment with outer distal lobule just touching front, and placed very close to inner angle of orbit. Third maxillipeds gaping medially; outer surfaces relatively smooth, pubescent with long stiff setae; merus irregularly pentagonal, slightly

TABLE 1. Differences between *Bountiana* gen. nov. and *Eriphia* Latreille, 1817.

	<i>Bountiana</i>	<i>Eriphia</i>
Carapace	strongly vaulted anteriorly	moderately convex to almost flat anteriorly
Eyes	relatively small with small corneas (see Fig. 3A)	large, corneas bulbous (see Fig. 3B)
Carapace shape	transversely oval	sub-hexagonal
Efferent branchial openings	not distinct, almost completely covered by third maxillipeds (Fig. 3A), endostomial ridges weak, not forming circular opening with epistome	very distinct, not covered by third maxillipeds (Fig. 3B), endostomial ridges strong, forming circular opening with epistome
Third maxillipeds	antero-external margin rounded (Fig. 4A)	antero-external margin sub-auriciform (Fig. 4B)
Antennules	second segment very short, less than half length of basal segment (Fig. 3A)	second segment long, three-quarters or more length of basal segment (Fig. 3B)
Antennal position	basal antennal segment with outer distal lobule just touching front, and placed very close to inner angle of orbit (Fig. 3A)	basal antennal segment with outer distal lobule not touching front, and widely separated from inner angle of orbit (Fig. 3B)
Ambulatory dactylus	short and stout	long and slender
Gonopod 2	flagellum subequal in length to basal portion	flagellum distinctly shorter than basal portion
Male thoracic sternites	suture between sternites 2 & 3 distinct	suture between sternites 2 & 3 not discernible

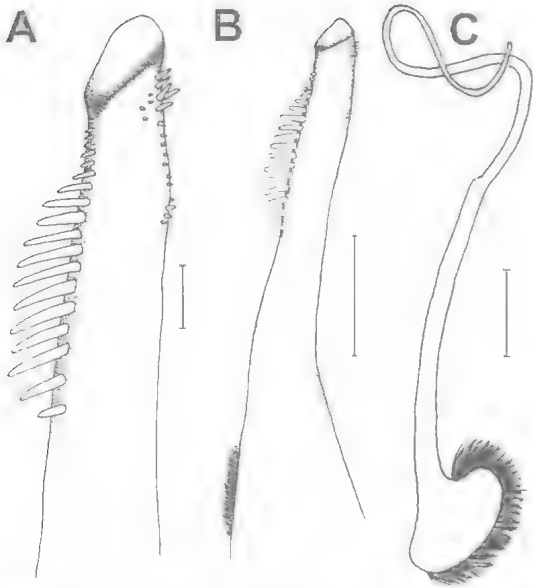


FIG. 5. *Bountiana norfolcensis* (Grant & McCulloch, 1907), lectotype male, 12.2 × 18.1mm, AMG5827, Norfolk Island; A, enlargement of apex of gonopod 1; B, gonopod 1; C, gonopod 2.

notched at distal outer margin, antero-external margin rounded, not sub-auriculiform; with a few long, stiff setae. Efferent branchial openings not distinct, almost completely covered by third maxillipeds, endostomial ridges weak, not forming circular opening with epistome. Pterygostomial region smooth. Suborbital region relatively smooth.

Chelipeds markedly dimorphic; inner margins of all segments pubescent; distal end of merus pubescent, surfaces smooth. Distal blunt spine present at ventral surface of basis-ischium. Carpus with acute spine on median-inner margin, smaller one present ventrally; surfaces tuberculated anteriorly. Chelae relatively short, stout, with longitudinal rows of tubercles. Pubescence present on entire dorsal surface of palm, less dense on ventral surface. Small basal non-molariform tooth present on dactylus. Fingers of major chela strongly curved, closing with a prominent gape. Cutting edges of fingers of minor chela minutely denticulated. Female claws similar to male.

Ambulatory legs short, stout, smooth, both anterior and posterior margins with prominent long and short setae; merus with minute tubercles anteriorly.

Anterior male thoracic sternites smooth. Abdominal surfaces smooth. G1 short, stout,

broad at base tapering distally, terminating in broad tip; long stout spinules present on distal half of inner edge, longest medially; minute spinules on outer surfaces over distal third. G2 relatively long, slender; distal half forming curled flagellum.

REMARKS. Since Grant & McCulloch (1907) described the species from Norfolk Islands, there have been only two subsequent reports by McNeil & Ward (1930) and Holthuis (1968). McNeil & Ward (1930) added Lord Howe Island and New South Wales as localities for this species.

The *Pseudozius* sp. of Bennett (1964) from Campbell Island, south of New Zealand, is without doubt synonymous with *Bountiana norfolcensis*. This was first noted by Guinot (1968: 330) whilst reviewing *Pseudozius* and we concur with her conclusion. Furthermore, Dell (1968: 17) provided strong evidence that this species could not have come from Campbell Island, and must have been collected from an unknown locality elsewhere in the Pacific. This is based on the fact that it has not been recorded since, despite subsequent extensive collecting expeditions to the island. Also it was apparently collected during a trip by the government vessel *Hinemoa* whose captain, Mr J.A. Bollons, was notoriously inaccurate in recording where specimens were found.

Grant & McCulloch's (1907) original specimens (AMG5827) were examined and a lectotype male (12.2 × 18.1mm) is here designated.

DISTRIBUTION. Norfolk Island, Lord Howe Island, and New South Wales, Australia.

ACKNOWLEDGEMENTS

We thank Penny Berents and Roger Springthorpe of the Australian Museum, Sydney, for assistance during our respective visits, and loan of specimens. Also we express our gratitude to S.K. Koh and S.H. Tan for help with photographs and drawings.

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MALARINA, A NEW SPIDER GENUS (ARANEAE: AMAUROBIOIDEA: KABABININAE) FROM THE WET TROPICS OF QUEENSLAND, AUSTRALIA

VALERIE TODD DAVIES AND CHRISTINE L. LAMBKIN

Davies, V.T. & Lambkin, C.L. 2000 06 30: *Malarina*, a new spider genus (Araneae: Amaurobioidea: Kababininae) from the Wet Tropics of Queensland, Australia. *Memoirs of the Queensland Museum* 45(2): 273-283. Brisbane. ISSN 0079-8835.

Four species of *Malarina* gen. nov. are described indicating the local endemism of species in North Queensland. These are *M. monteithi*, *M. masseyensis*, *M. collina* and *M. carthwell*. A cladistic analysis suggests that the Kababininae form a well supported monophyletic group though its placement in a family remains problematical, □ *Malarina*, Araneae. Kababininae. spider, Queensland.

Valerie Todd Davies, Queensland Museum, PO Box 3300, South Brisbane 4101; Christine L. Lambkin, Department of Zoology & Entomology, University of Queensland, St Lucia 4072, Australia; 17 March, 1999.

Malarina is the third genus to be described in the Kababininae, the others being *Kababina* Davies, 1995 and *Carbinea* Davies, 1999. For nomenclatural purposes Davies is designated the author of this new genus and its species' names.

METHODS

All the spiders are from rainforests in the Wet Tropics region of North Queensland between latitudes 17°16' and 18°36'S. Collection methods include litter-sieving followed by heat extraction in funnels, pit-fall collection, pyrethrum spraying of tree-trunks and fallen logs, hand collecting from under logs in daylight and night collecting. Co-ordinates are given in square brackets when these are not given in the original data. Measurements are in millimetres. Notation of spines follows Platnick & Shadab (1975). The illustrations were drawn with the aid of a camera lucida; the left male palp is illustrated. All material is lodged in the Queensland Museum (QM).

Table 1 lists anatomical abbreviations used in the text and in Table 3; abbreviations on illustrations are explained in the legends to figures. Collectors: DC, D. Cook; DY, D. Yeates; GBM, G.B. Monteith; GT, G. Thompson; HJ, H. Janetzki; RR, R. Raven; SH, S. Hamlet; VED, V.E. Davies.

SYSTEMATICS

KABABININAE

DIAGNOSIS. Epigynum with medial atrium (previously referred to as 'fossa'), which is wider than long; spermathecae posterior or lateral to atrium. Male palp with rounded tegulum with prolateral groove; the course of sperm duct

showing clearly. Membraneous conductor; median apophysis absent. Tibial apophysis with ventral and dorso-retrolateral branches. Posterior spinnerets long with slender terminal segment (Fig. 1F).

DESCRIPTION. Three clawed. Carapace highest in foveal region (Fig. 1B); posterior eye row straight or slightly recurved; AME reduced (Fig. 1C). Chelicera with two retromarginal and two promarginal teeth (Fig. 1E); prolateral filamentous seta at base of fang longer than other setae. Labium about as wide as long; sternum pointed posteriorly (Fig. 1D). Legs 1423; feathery hairs, ridged cuticle. Tarsal trichobothria in a single line increasing in length distally; bothrium collariform. Tarsal organ slit-like broadening distally. Male palpal embolus with or without proximal embolic apophysis. Cribellum (two fields) present or absent in females, absent in males; proximal calamistrum with one row of setae; large broad colulus present when cribellum is absent. Two major ampullate gland spigots of unequal size on female ALS, one and a nubbin in male.

Malarina gen. nov.

ETYMOLOGY. Derived from the Aboriginal word, *malar*, meaning spider's web in the Dyirbal language of North Queensland.

TYPE SPECIES. *M. monteithi*.

DIAGNOSIS. Cribellate spider (cf. *Carbinea*) with paracribellar spigots on female PMS. Epigynum having a posterior knob and narrow postero-lateral insemination ducts (cf. *Kababina* which lacks the well-marked epigynal knob and has wide anterior insemination ducts). Embolus

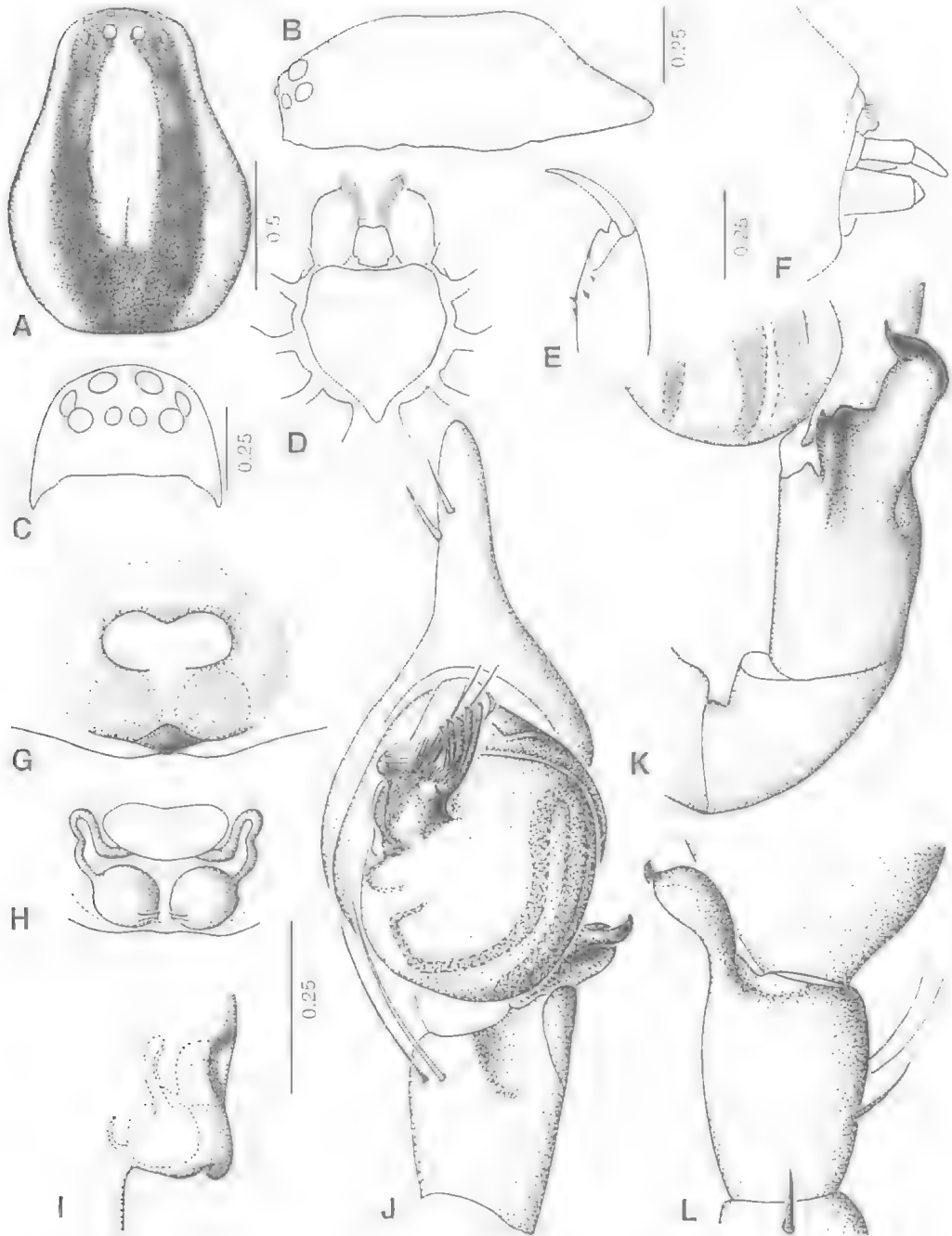


FIG. 1. A-L, *Malarina monteithi* sp. nov. A-I, ♀; A-C, carapace (dorsal, lateral, frontal); D, endites and sternum; E, chelicera; F, spinnerets (lateral); G-I, epigynum (ventral, dorsal, lateral). J-L, ♂; J, palp (ventral); K, L, tibial apophysis (retrolateral, dorsal).

and conductor arising antero-ventrally on tegulum (Fig. 5A); the embolus having an elaborate embolic apophysis like *Carbinea* but here it is unbranched. Male palpal tibia with 2-4

long ventral setae reaching about half way up cymbium (Fig. 1J) and a small sub-central prolatero-dorsal spine (Fig. 1L); the tibial apophysis is dorso-retrolateral.

TABLE 1. List of anatomical abbreviations.

AL	abdomen length
ALE	anterior lateral eyes
ALS	anterior lateral spinnerets
AME	anterior median eyes
APOPH	apophysis
AW	abdomen width
CAL	calamistrum
CB	cymbium
CH	cheliceral
CL	carapace length
CR	cribellum
CW	carapace width
E	embolic
EPIG	epigynal
ID	insemination duct
MAP	major ampullate spigots
MT	metatarsal
PCR	paracribellar spigots
PLD	prolaterodorsal
PLE	posterior lateral eyes
PLS	posterior lateral spinnerets
PME	posterior median eyes
PMS	posterior median spinnerets
RTA	retrolateral tibial apophysis
T	tarsal
TRICH	trichobothria

***Malarina monteithi* sp. nov.**
(Figs 1A-L, 2A,B, 6; Table 2)

ETYMOLOGY. For Dr GB. Monteith, entomologist, who has collected widely in the tropics of N Queensland.

MATERIAL. HOLOTYPE: ♀, Malanda Falls, 17°21'S, 145°35'E, N Qld, 750m, pyrethrum spray logs and trees, 31 Dec. 1989, GBM (QM S35253). PARATYPES: N Qld, 2 ♂, same data as holotype (S35254); ♀, 2 ♂, Millaa Millaa Falls, 17°28'S, 145°36'E, 800m, sieved litter, 17 May 1995, GBM (S35255); ♀, The Crater Nat. Park, 17°26'S, 145°29'E, 950m, pyrethrum logs, 28 Dec. 1989, GBM (S 35256); ♂, 3 ♀, Maalan State Forest (17°35'S, 145°35'E) in and under logs, 20-24 April 1978, VED, RR (S35257); ♀, Majors Mtn (17°38'S, 145°32'E) same data (S35258); ♀, Mt Father Clancy, Maalan, litter, 21 April 1978, RR (S35259); ♀, Ravenshoe, 17°39'S, 145°30'E, 920m, pitfall, 1 Dec. 1997-5 Feb. 1998, GBM, DC (S39202); ♂, Red Rd turnoff, 17°49'S, 145°33'E, Tully Falls Rd, pitfall, 8 Dec. 1989-5 Jan. 1990, GBM, GT, HJ (S35263).

DIAGNOSIS. Small (2.8-3.6) cribellate spiders; proximal calamistrum. The insemination ducts are simple. The embolic apophysis has two long setae extending beyond the rest (Fig. 2B).

DESCRIPTION. *Female*. CL 1.4, CW 1.1, AL 1.7, AW 1.2. Carapace with two dark longitudinal bands (Fig. 1A); highest at fovea. Viewed from top, eye rows straight. Ratio of AME:ALE: PME:PLE is 6:10:10:10. Legs 1423 (Table 2),

TABLE 2. Palp and leg measurements (mm) of ♀ (♂) *Malarina monteithi* sp. nov.

	Femur	Patella/ Tibia	Metatarsus	Tarsus	Total
Palp	0.6 (0.8)	0.6 (0.9)	-	0.5 (0.9)	1.7 (2.6)
Leg I	1.5 (1.8)	2.0 (2.3)	1.4 (1.9)	0.9 (1.2)	5.8 (7.2)
II	1.3 (1.5)	1.6 (1.8)	1.1 (1.4)	0.7 (0.9)	4.7 (5.6)
III	1.1 (1.4)	1.4 (1.5)	1.1 (1.3)	0.7 (0.7)	4.3 (4.9)
IV	1.5 (1.8)	1.9 (2.2)	1.5 (1.9)	0.8 (1.0)	5.7 (6.9)

banded. Notation of spines: Femora, I, D010, P010; II, D110, P001; III, D100, P001; IV, D110, P001, R001. Patellae, I, D001; II, D100; III, D001; IV, 001. Tibiae: I, V020; II, V010; III, D100, P001, R011; IV, D100, P011, V110, R011. Metatarsi, all spined with a distal whorl of 4-5. Epigynum (Figs 1G-L) short insemination ducts with anterior loop to spermathecae. These are large, together exceeding the width of the atrium. Cribellum with two fields; ALS with two major ampullate spigots and about 20 piriform spigots and some tartipores; PMS with an anterior minor ampullate spigot, and about 12 other spigots – two cylindrical spigots (mesal and posterior), four smaller paracribellar spigots with strobilate shafts and about six aciniform spigots. PLS with spigots of two sizes. Females varied in length from 2.8-3.6.

Male. CL 1.5, CL 1.2, AL 1.7, AW 1.1. Coloration and eyes like female. Legs 1423 (Table 2). Notation of spines: Femora, I, D110, P010; II, D110, P001, R001; III, D110, P001, R011; IV, D100, P001, R001. Patellae, I, D001; III, D001; IV, D001. Tibiae, I, D100, P010, V020, R001; II, D001, P011, V020, R001; III, D101, P011, V111, R011; IV, D101, P011, V111, R011. Metatarsi spined, with distal whorl 4-5. Male palp (Fig. 1J-L), sperm duct looping over retrolateral tegulum and forward again to base of embolus. Embolic apophysis fringed with a prolater cluster of hair-like setae and five plate-like setae terminally (Fig. 2A,B). Under (strictly dorsal to) these there is also a row of straight setae, two of which are longer than the rest and protrude beyond them.

DISTRIBUTION. Collected from sites on the Atherton Tableland (Fig. 6).

***Malarina masseyensis* sp. nov.**
(Figs 2C,D, 3A-F, 6)

ETYMOLOGY. From the type locality, Massey Range.

MATERIAL. HOLOTYPE: ♀, Massey Range, 17°16'S, 145°49'E, 1250m, sieved litter, 10 Oct. 1991, GBM, HJ (QMS35260). PARATYPES: ♂, ♀, same data as holotype

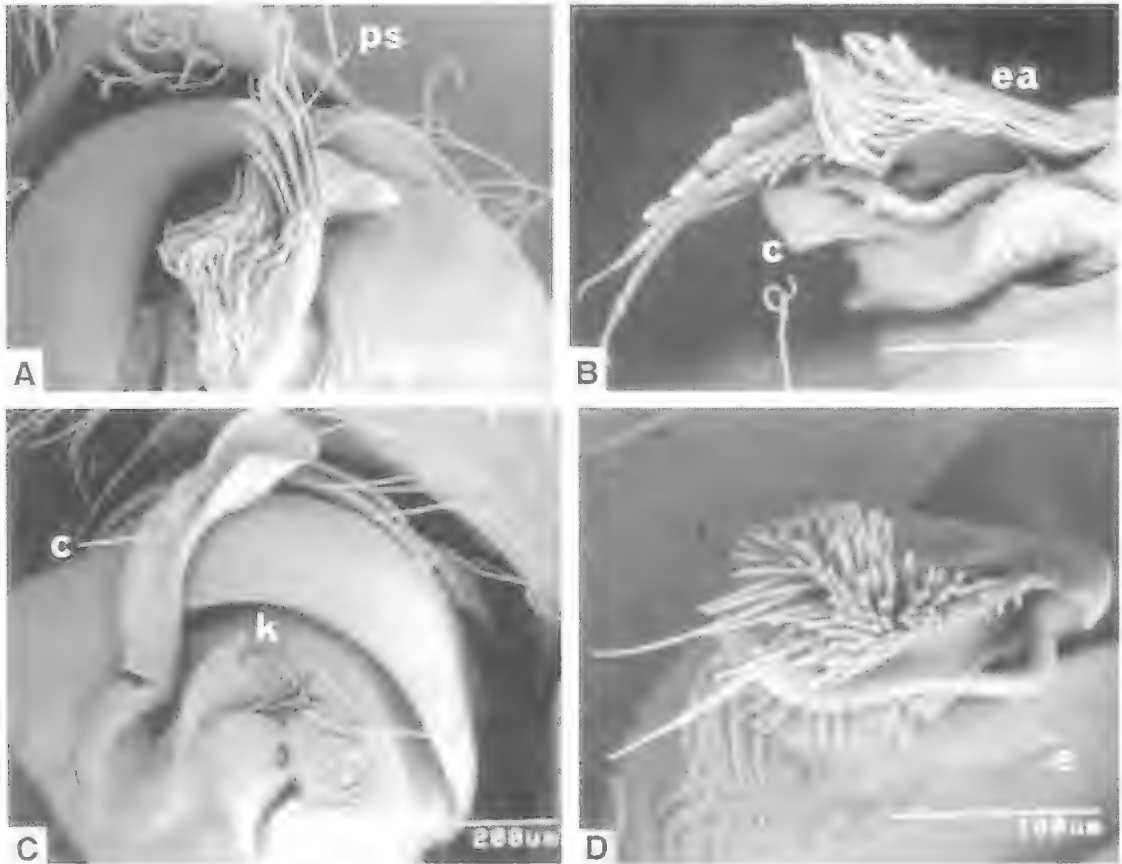


FIG. 2. A-D, ♂ *Malarina* spp.nov. embolic region of ♂ palp. A, B, *M. monteithi* (ventral, prolateral); C, D, *M. masseyensis* sp.nov. (ventral, prolateral). c = conductor, e = embolus, ea = embolic apophysis, k = keel, ps = plate-like setae.

(S39185); ♀, Massey Range, 4km W of Centre, Bellenden Ker, 1250m, 9-11 Oct. 1991, GBM, HJ, DC (S35261); ♀, Bellenden Ker Range Summit, 17°16'S, 145°51'E, 1560m, in litter, 28 Oct. 1983, GBM, DY, GT (S35294); ♀, Bellenden Ker, Cable Tower 3, 1054m, under logs, 17-24 Oct. 1981, Earthwatch/QM, (S35295); ♂, Bellenden Ker Range, pitfall trap, 500m, 17-24 Oct. 1981, Earthwatch/QM (S 39186).

DIAGNOSIS. Larger spider (♀'s 3.9-4.7) than *M. monteithi*. Epigynum with simple insemination ducts; spermathecae together not exceeding the width of atrium (cf. *M. monteithi*). Palpal tibia with two large distal prolaterodorsal spines (cf. *M. monteithi*) as well as the sub-central spine.

DESCRIPTION. *Female.* CL 2.1, CW 1.5, AL 2.3, AW 1.3. Carapace without dark longitudinal bands. Eyes similar to *M. monteithi*. Legs 1423: I, 8.6; II, 6.7; III, 6.3; IV, 8.1, not markedly banded. Epigynum (Fig. 3A-C) with simple insemination

ducts with a transverse loop before entering spermathecae. Length 3.9-4.7.

Male. CL 1.9, CW 1.2, AL 2.0, AW 1.3. Legs: I, 9.1; II, 7.0; III, 6.3; IV, 8.6. Palp (Fig. 3D-F): large conductor; embolic apophysis curves strongly with marked keel; plate-like setae absent (Fig. 2C,D). Palpal tibia with two stout prolaterodorsal spines distally (Fig. 3F). Length 3.2-3.9.

DISTRIBUTION. Collected from sites on the Bellenden Ker/Massey Range (Fig. 6).

***Malarina collina* sp.nov.**
(Figs 4A-D, 5A,B, 6)

ETYMOLOGY. Latin *collis*, a hill, referring to the location.

MATERIAL. HOLOTYPE: ♀, Palmerston Nat. Park (17°34'S, 145°41'E) under logs, July 1992, J. Wunderlich (QM S35262). PARATYPES: 2♂, 2♀, same data as holotype (S39187); ♂, Upper Boulder Ck, 8km N. Tully, 17°50'S, 145°54'E, 250m, pitfalls, 4-7 Dec. 1989, GBM,

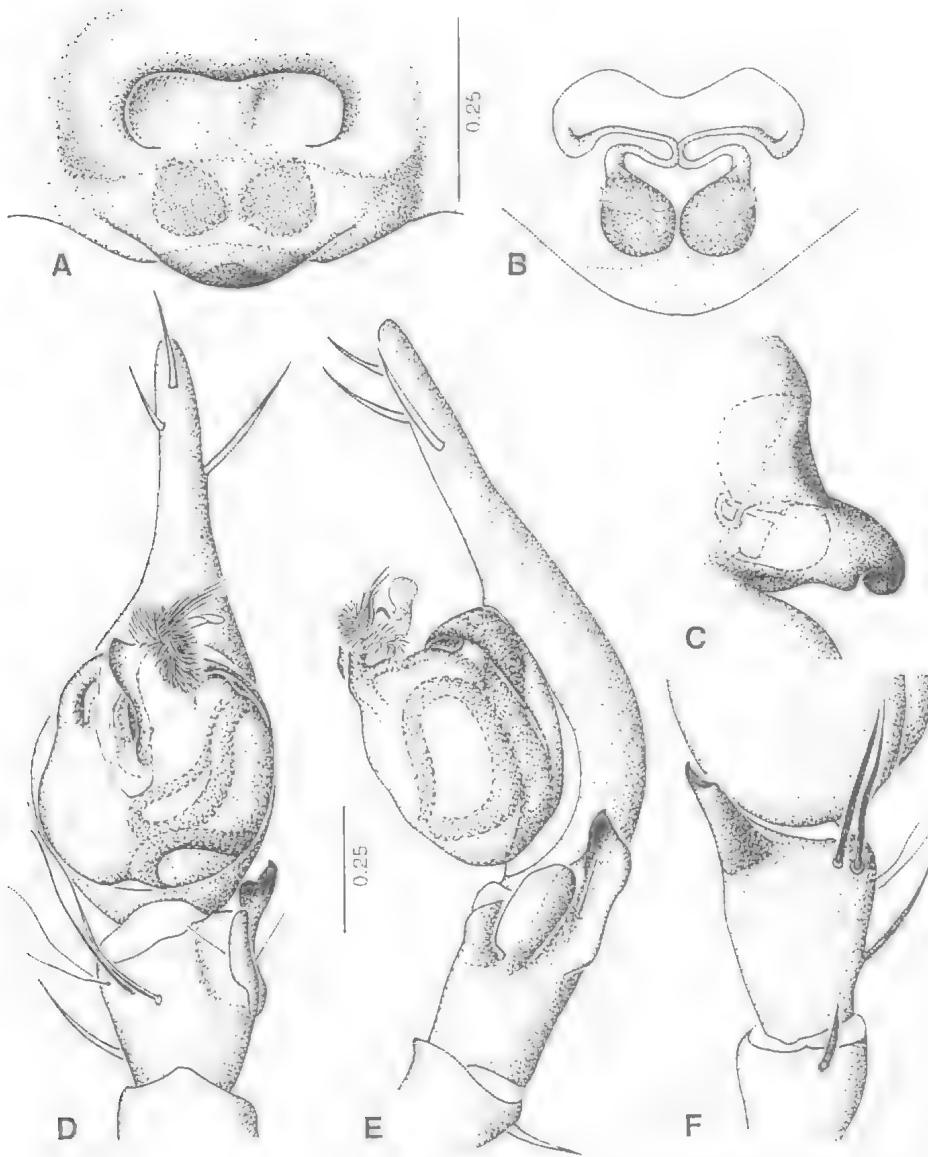


FIG. 3. A-F, *Malarina masseyensis*. A-C, ♀ epigynum (ventral, dorsal, lateral); D-F, ♂ palp; D, E (ventral, retrolateral); F, tibial apophysis (dorsal).

GT, HI (S35264); ♂, Boulder Ck via Tully, 17°50'S, 145°54'E, 650m, sieved litter, 27 Oct. 1983, GBM, DY, GT (S35265); ♀, same data (S39188).

DIAGNOSIS. Small spiders (♀'s 2.4-3.6). Insemination ducts coiled (cf. *M. monteithi*, *M. masseyensis*). Tibial apophysis shorter and broader than *M. monteithi* (Fig. 4D). All setae on embolic apophysis about same length (cf. *M.*

monteithi). Without two long prolaterodorsal spines on palpal tibia (cf. *M. masseyensis*).

DESCRIPTION. *Female.* CL 1.5, CW 1.1, AL 1.8, AW 1.1. Legs, I, 6.7; II, 5.3; III, 4.7; IV, 6.4. Epigynum (Fig. 4A-C) with coiled insemination ducts. Length 2.4-3.6

Male. CL 1.5, CW 1.1, AL 1.4, AW 1.0. Legs, I, 6.5; II, 5.1; III, 4.5; IV, 6.4. Palp (Figs 4D, 5A,B),

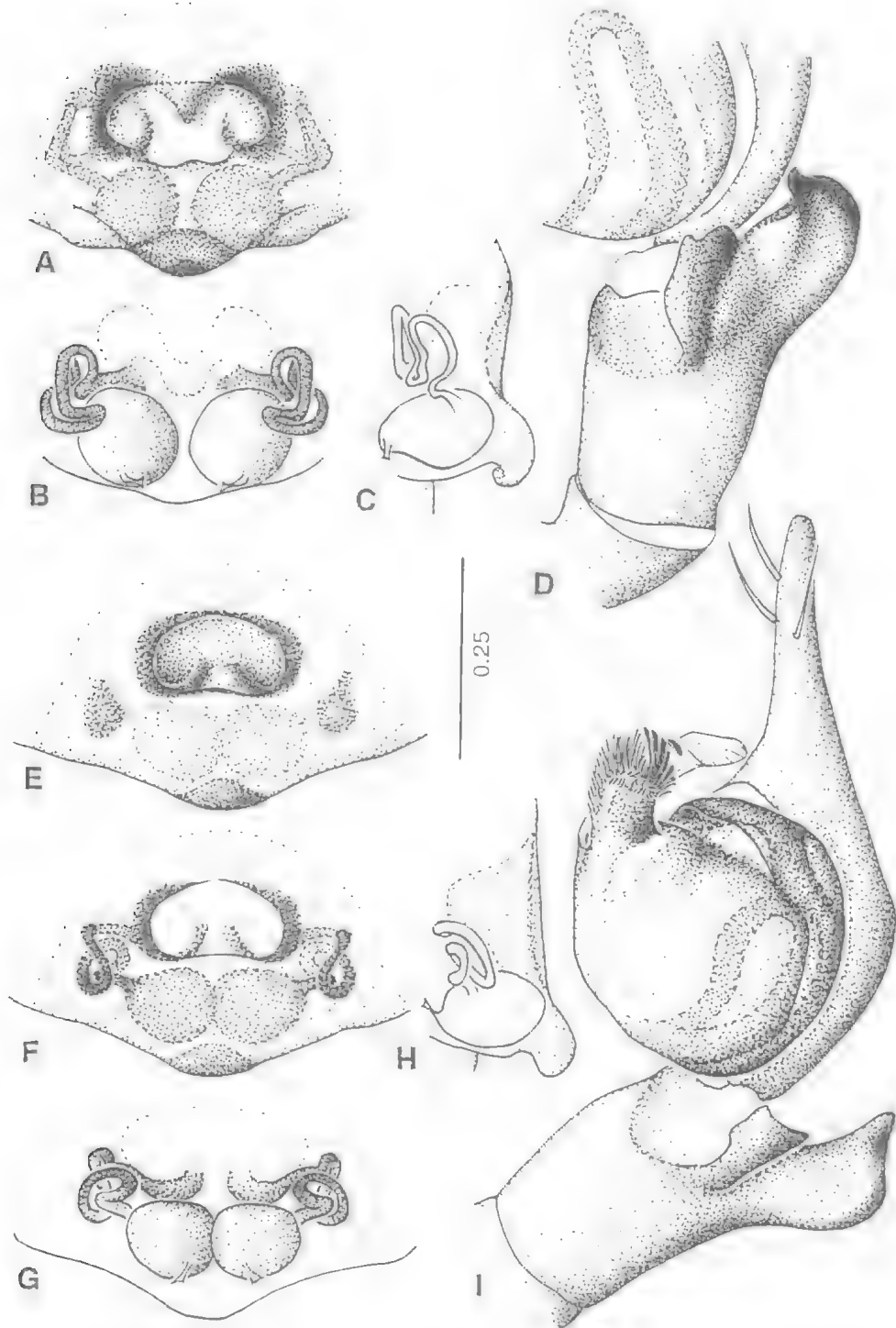


FIG. 4. A-I, *Malarina* spp. nov. A-D, *M. collina* sp. nov.; A-C, ♀, epigynum (ventral, dorsal, lateral); D, ♂ tibial apophysis. E-I, *M. cardwell* sp. nov.; E-H, epigynum (ventral, ventral cleared, dorsal, lateral); I, ♂ palp (ventral).

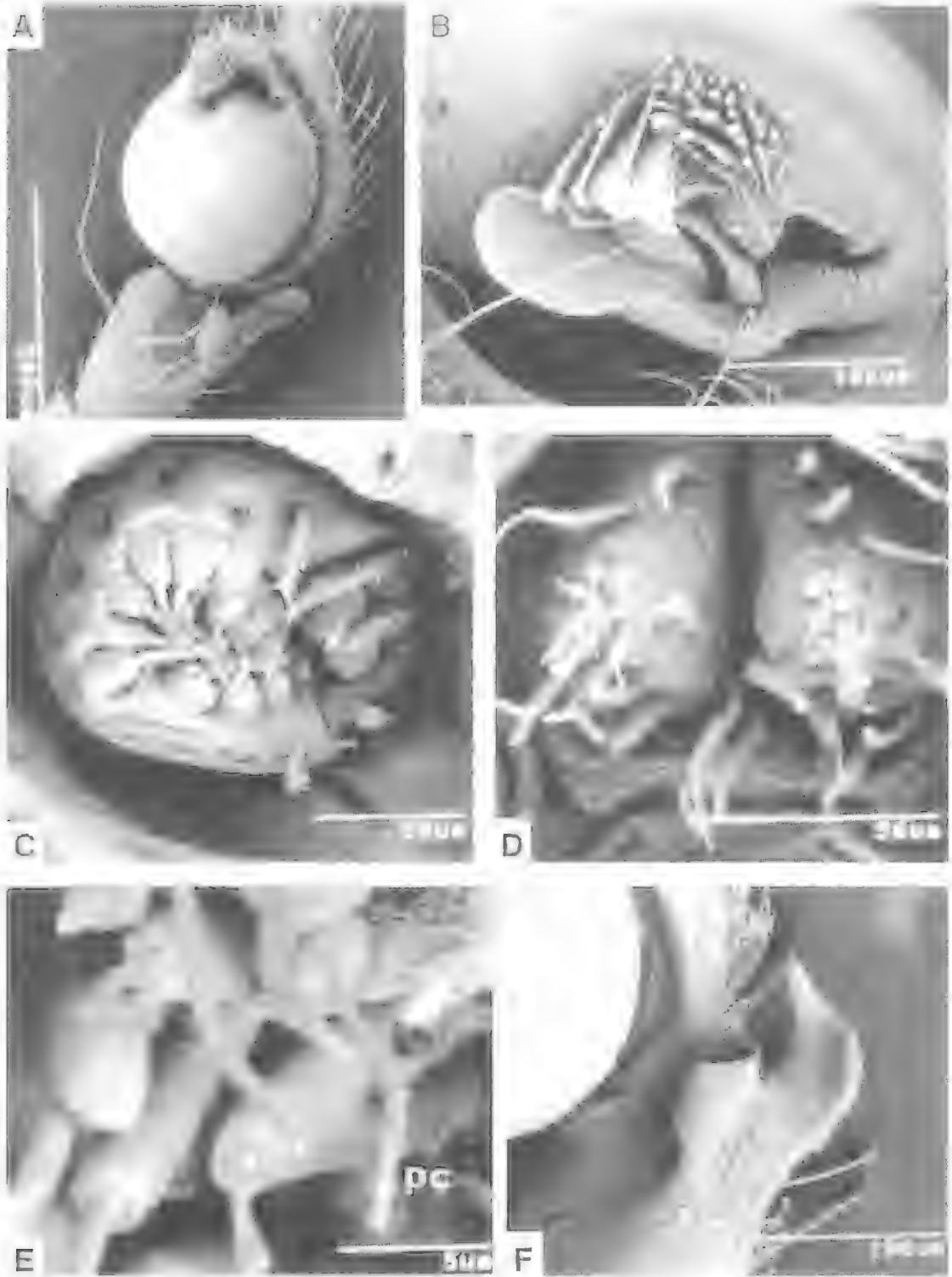


FIG. 5. A-F, *Malarina* spp. A, B, *M. collina* ♂; A, ♂ palp; B, embolic region (prolateral). C-F, *M. cardwell*; C-E, ♀ spigots; C, ALS (right); D, PMS; E, paracribellar spigots (pc) on PMS. F, ♂ palp, tibial apophysis.

TABLE 3. Characters and character states. * Multi-state character treated as unordered.

1. AME: as large or larger than ALE (0); smaller (1)
2. Retromarginal CH teeth: 2+ (0); 2 (1); 1 (2); 0 (3)
3. Promarginal CH teeth: 3+ (0); 3 (1); 2 (2); 0 (3)
4. Long prolateral seta at base of fang: absent (0); present (1)
5. Large frontal CH seta: absent (0); present (1)
6. CH lamina: absent (0); present (1)
7. Foveal area highest: absent (0); present (1)
8. ♀ leg I: shorter than leg IV (0); equal to or longer than leg IV (1)
9. Stridulatory ridges on ♂ coxa I: absent (0); present (1)
10. Enlarged ventral spines on tibia and MT I, II: absent (0); present (1)
11. Featherly hairs: absent (0); present (1)
12. MT preening comb: absent (0); present (1)
13. MT TRICH: 2+ (0); 1 (1)
14. T TRICH: 0 (0); 2+ (1); double row (2)
15. T rod: absent (0); present (1)
16. CR spinning fields: 2 (0); 1 (1); absent (2)
- 17.* CR spigots: absent (0); longitudinally ribbed (1); annulate (2)
- 18.* CAL: absent (0); proximal (1); medial (2)
19. MAP ♀ ALS: 2 (0); 1 and nubbin (1); 1 (2)
20. MAP ♀ ALS: mesal (0); anterior (1)
21. PCR ♀ PMS: one shaft per base (0); more than one shaft (1); absent (2)
22. EPIG gonopores: absent (0); present (1)
23. Medial EPIG atrium: absent (0); present (1)
24. ID: absent (0); simple (1); loosely coiled (2); tightly coiled (3)
- 25.* Posterior EPIG scape: absent (0); short (1); medium (2); long (3); small knob (4)
26. EPIG acellular lateral projections: absent (0); present (1)
27. E direction: straight (0); clockwise (1); anti-clockwise (2)
28. Proximal E APOPH: absent (0); unbranched (1); branched (2)
29. E APOPH 2-3 long setae: absent (0); present (1)
- 30.* E APOPH plate-like setae: absent (0); small (1); large (2)
31. PLD setae E APOPH: absent (0); present (1)
32. ParE process: present (0); absent (1)
- 33.* Conductor: absent (0); rounded (1); large T-shaped (2); s-shaped - falciform (3)
34. 2⁰ conductor: absent (0); present (1)
35. Median APOPH: absent (0); present (1)
36. Orientation of CB to bulb: dorsal (0); mesal (1)
37. Paracymbium: absent (0); present (1)
38. RTA to CB length: absent (0); quarter or less (1); third (2); half (3); more than half (4)
39. RTA dorsal branch: absent (0); present (1)
40. RTA lateral edge: straight (0); intorned (1)
41. Palpal tibia with 2 stout dorsal spines: absent (0); present (1)
42. Palpal patella APOPH: absent (0); present (1)

all setae on embolic apophysis about same length. Broad colulus. ALS with one major ampullate spigot and nubbin, about 17 piriform spigots and some tartipores. PMS with large anterior spigot (minor ampullate) and 16 spigots of uneven size. Length 2.6-3.1

DISTRIBUTION. Collected at lower altitudes at Palmerson Nat. Park and the Walter Hill Range (Fig. 6).

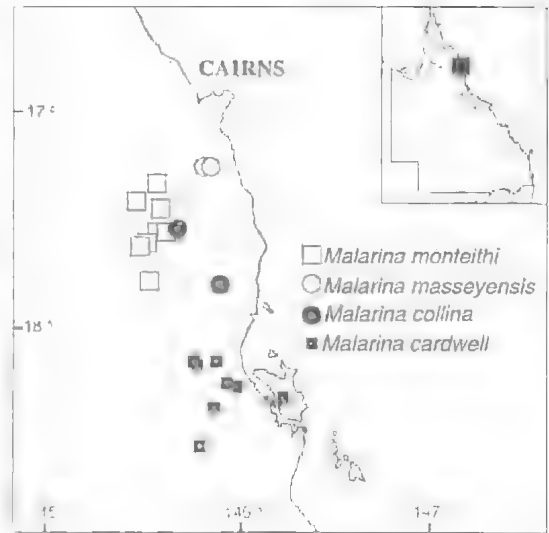


FIG. 6. Map of North Queensland showing the distribution of *Malarina* spp.

***Malarina cardwell* sp.nov.**
(Figs 4E-I, 5C-F, 6)

ETYMOLOGY. For the locality, Cardwell Range.

MATERIAL. HOLOTYPE: ♀, Mt Macalister, 18°18'S, 145°56'E, Cardwell Ra., 800-900m, 13-16 Jan. 1987, SH (QM S35266). **PARATYPES:** ♂, Mt Macalister, Cardwell Ra., 1000m, sieved litter, 20 Dec. 1986, GBM, GT (S35267); ♀, ♂, Mt Macalister, Cardwell Ra. 850m, pitfall traps 18-20 Dec. 1986, GBM, GT, SH (S39189); 3♂, 900m, pitfall trap, 18 Dec., 1986-14 Jan. 1987, (S39190); ♂, pitfall, 18 Dec. 1986-14 Jan. 1987 (S39191); 4♂, ♀, Upper Broadwater Ck, 18°19'S, 145°59'E, Cardwell Ra., 750m, pitfalls, 18 Dec. 1986-14 Jan. 1987, GBM, GT, SH (S35268); 2♀, Mt Graham, 18°25'S, 145°52'E, 8km N Abergowrie, 600-700m, pitfall, 26 Dec. 1986-17 Jan. 1987, SH (S14157); ♂, ♀, Kirrama Ra., Main Rd., W side, 18°13'S, 145°47'E, 700m, pitfall traps, 10 Dec. 1986-11 Jan. 1987, GBM, GT, SH (S39192); ♀, Kirrama Ra., Mt Smoko turnoff, 18°12'S, 145°46'E, 600m (S39193); ♂, Broadwater Park, 35km NW Ingham, 18°12'S, 145°53'E, 500m, pitfall, 22 Dec. 1986-3 Jan. 1987, SH (S35271). ♂, Wallaman Falls, 18°36'S, 145°48'E, 620m, pitfalls in open forest, 5-12 Feb. 1996, GBM (S35269); ♂, Hinchinbrook I., 18°22'S, 146°13'E, 10m, sieved litter, 9 Nov. 1984, VED, GT, J. Gallon (S35270); ♂, Hinchinbrook I., Gayndah Ck, 10m, pitfalls, 8-17 Nov. 1984, VED, J. Gallon (S39194); ♀, 2♂, same data (S39195); ♂, ♀, 8-18 Nov. 1984, GBM, GT, DC (S39196).

DIAGNOSIS. Small spiders (♀'s 2.9-3.1). Insemination ducts tightly coiled presenting dark lateral spots on ventral surface (cf. all other spp.)

TABLE 4. Data matrix. Unknown characters are represented by '?', inapplicable characters by '-'.

Taxa	Character Number				
	1	10	20	30	40
<i>Wandella barbarella</i> Gray	033001010	0000000212	000-0-0000	000000000-	-00
<i>Dictynidae</i> sp.	120000010	0001001112	1010300100	0012001010	000
<i>Badumna longinqua</i> (Koch)	010000010	0000100110	0111100100	0013010010	000
<i>Paramatchia decorata</i> Dalmás	010000010	0000101120	0010100100	0013000010	001
<i>Desis</i> sp.	110000010	0000202002	1-10300100	0013010010	000
<i>Quemusia aquilonia</i> Davies	111000010	0000100110	0210100200	0013100010	000
<i>Jalkaraburra alta</i> Davies	111000010	0000102000	0-10100200	0013100010	000
<i>Amphinecta milina</i> Forster & Wilton	110000000	001010200?	0-10200100	0011010010	000
<i>Amaurobius fenestralis</i> (Stroem)	000000010	0010100110	0010100100	0011010011	000
<i>Storenosoma terranea</i> Davies	112000001	0010102001	0-10100100	0011010011	000
<i>Otira</i> sp.	112000001	0010112001	0-10100100	0011010011	000
<i>Tamarubrius milvinus</i> (Simon)	112000000	0010102000	0-10101100	0011010111	000
<i>Procambridgea</i> sp.	100100010	0000100110	0110100100	0011000010	000
<i>Stiphidion facetum</i> Simon	011100010	0100100120	0110100100	0012000010	000
<i>Stiphidion adornatum</i> Davies	011100010	0100100120	0110300100	0012000010	000
<i>Midgee binnaburra</i> Davies	102110000	1000102001	0-10100100	0011000010	000
<i>Midgee thompsoni</i> Davies	102110000	1000102001	0-10200100	0011000010	000
<i>Dardurus spinipes</i> Davies	100100010	1000101110	0211100100	0011000010	001
<i>Manjala plana</i> Davies	110110010	1000100111	0?11100100	0013010010	000
<i>Malala lubinae</i> Davies	100010010	1000102001	0-10100100	0013000010	000
<i>Kababina alta</i> Davies	112100110	0100100110	0011100100	0011000040	000
<i>Carbinea longiscapa</i> Davies	112100110	0100102000	0-11130120	0011000040	000
<i>Carbinea breviscapa</i> Davies	112100110	0100102000	0-11110120	0011000010	000
<i>Carbinea wunderlichi</i> Davies	112100110	0100102000	0-11120120	0011000020	000
<i>Carbinea robertsi</i> Davies	112100110	0100102000	0-11120120	0011000030	000
<i>Malarina monteithi</i> sp. nov.	112100110	0100100110	0011140111	2111000010	000
<i>Malarina masseyensis</i> sp. nov.	112100110	0100100110	0011140111	0111000010	010
<i>Malarina collina</i> sp. nov.	112100110	0100100110	0011240110	2111000010	000
<i>Malarina cardwell</i> sp. nov.	112100110	0100100110	0011340110	1111000010	100

Tibial apophysis short with inturned lateral margin. (cf. other spp.)

DESCRIPTION. *Female*. CL 1.6, CW 1.2, AL 1.8, AW 1.3. Legs, I, 6.9; II, 5.5; III, 5.0; IV, 6.8. Epigynum (Fig. 4E-H) with tightly coiled insemination ducts. Spinnerets (Fig. 5C-E), ALS with two major ampullate spigots and about 17 piriform spigots. PMS with a large anterior spigot (minor ampullate) and about 12 other spigots including 2 (mesal and posterior) with larger shafts (cylindrical) and 3-4 with strobilate shafts (paracribellar). PLS with spigots of two sizes. Length 2.6-3.4.

Male. CL 1.4, CW 1.1, AL 1.5, AW 1.1. Legs, I, 6.4; II, 5.5; III, 4.8; IV, 6.4. Palp (Fig. 4I), embolic apophysis with all setae about same length; plate-like setae reduced in length. Tibial apophysis short with inturned edge (Fig. 5F). Length 2.9-3.1.

DISTRIBUTION. Collected from Kirrama/Cardwell Ra., Seaview Ra. and Hinchinbrook I. (Fig. 6).

RELATIONSHIPS OF *MALARINA*

A cladistic analysis examined 42 characters (Table 3) for relationships of the 4 *Malarina* spp and 25 other taxa. Outgroup comparison was with the Australian filistatid spider *Wandella barbarella* Gray and an undescribed Australian dictynid. A data matrix for the 29 taxa, names and authors given (Table 4), was assembled in McClade 3.01 (Maddison & Maddison, 1992).

The data was analysed in PAUP version 3.1.1. (Swofford, 1993) and replicated in Hennig 86 Version 1.5 (Farris, 1988). A heuristic search of the data with 10 random-addition sequences and TBR branch swapping generated two most parsimonious trees differing only in placement of *M. masseyensis* — either with *M. monteithi* or basal to a clade containing *M. monteithi*, *M. collina* and *M. cardwell*. The preferred tree (Fig. 7) has length 123, CI = 0.53, CI excluding uninformative characters = 0.49, RI = 0.73, RC = 0.39. Characters were mapped in CLADOS version 1.2 (Nixon, 1992) with DELTRAN optimisation.

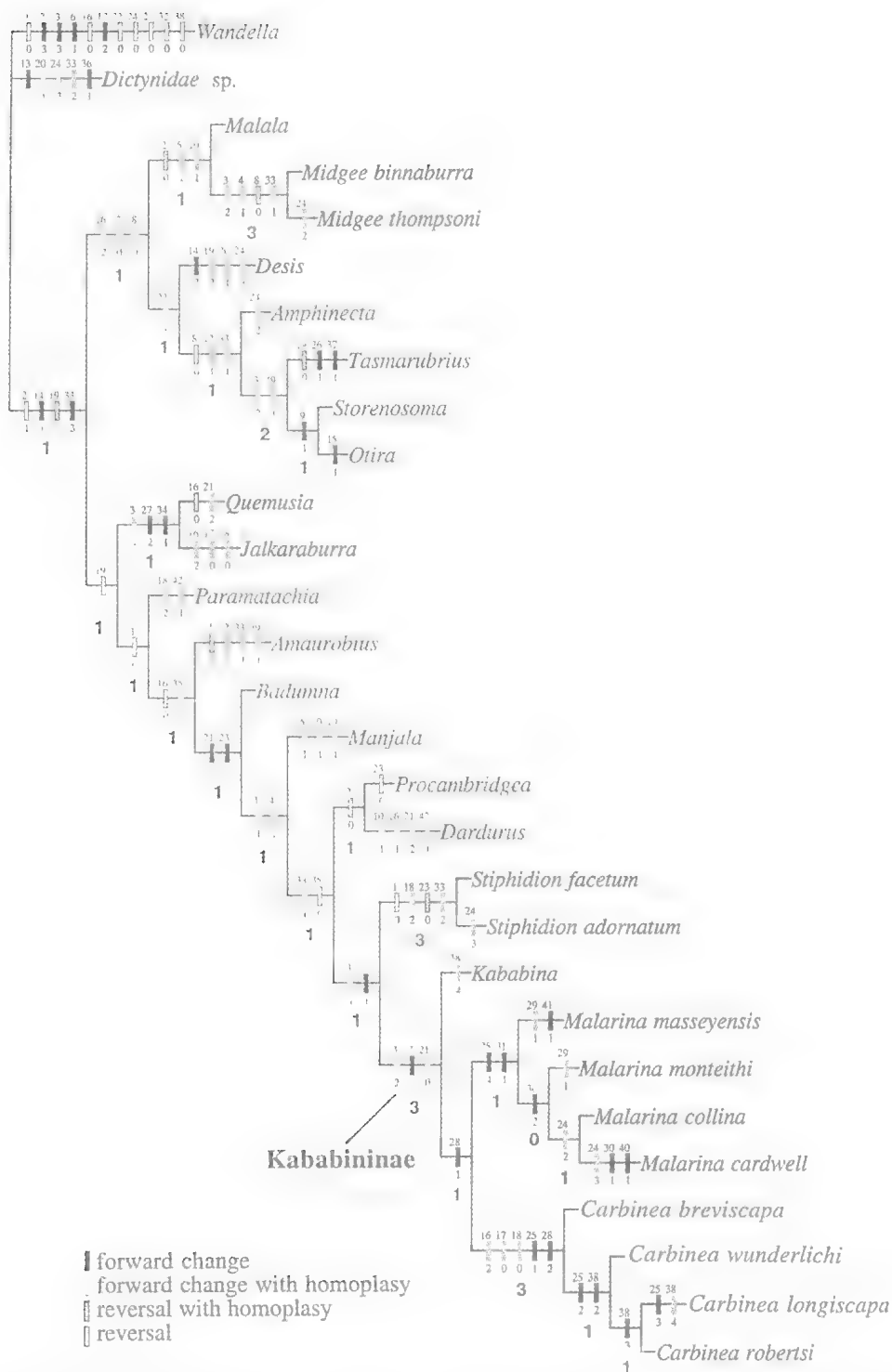


FIG. 7. Preferred most parsimonious tree showing the cladistic relationships of some Amaurobioidea (branch support for nodes in bold type).

Branch support (Bremer, 1994) for the nodes on the preferred most parsimonious tree was calculated using Autodecay (Eriksson & Wikstrom, 1996) and is given in bold type beneath each node in Fig. 7.

CONCLUSIONS

Wandella and Dictynidae sp. appear as distinct from the ingroup which is regarded as the superfamily Amaurobioidea. Again this is composed of two clades, one including *Desis* (Desidae) and *Amphinecta* (Amphinectidae), the other including *Amaurobius* (Amaurobiidae), *Stiphidion* (Stiphidiidae) and the metallines *Quemusia* and *Jalkaraburra*. The Kababininae, with the addition of *Malarina* spp. continues to form a well supported monophyletic group (Davies, 1999).

The families at the base of the clade are paraphyletic therefore the placing of Kababininae within any of the existing families remains problematic. The group appears to be closest to the Stiphidiidae but this is based on a single character (feathery hairs) which is also found in other genera not represented here.

While the Kababininae is well supported as is the Stiphidiidae, the other families are either paraphyletic (eg. Desidae as presently constituted) or poorly supported. Support for placing the Kababininae within the Stiphidiidae is low. Further descriptions and cladistic analyses of the Amaurobioidea are necessary to determine family relationships and placement of genera.

ACKNOWLEDGEMENTS

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also supports Kylie Stumkat, SEM technician. We thank the Council of the Australian Biological Resources Study for funding rainforest surveys during which some of this material was collected and for the financial support of illustrator and co-author, Christine Lambkin, who also set up the phylogenetic analysis resulting in the cladogram. We are grateful for the support of other members of the Queensland Museum, particularly Jennifer Cannon and Katie Laws for their help in preparation of this paper.

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NEW LOCALITY FOR THE ENDANGERED SHEATHTAIL BAT, *TAPHOZOUS TROUGHTONI* TATE, 1952. *Memoirs of the Queensland Museum* 45(2): 284. 2000:- *Taphozous troughtoni* was first described by Tate (1952). Subsequently, the taxon was considered a subspecies (McKean & Price, 1967) but was re-established as a full species by Chimimba & Kitchener (1991). It is known from only six specimens, four of which are lodged in the Australian National Wildlife Collections in Canberra (Chimimba & Kitchener, 1991). The three known localities are all in the vicinity of Mount Isa in NW Queensland. The species has not been recorded for 34 years.

We have identified a specimen of *T. troughtoni* among specimens in the Queensland Museum collection. This specimen, registration number QMJ17608, was originally registered as *Tadarida australis*, but was later re-identified as *Taphozous australis*. We examined QMJ17608 while verifying identifications of *Taphozous australis* specimens outside of the species' known distribution (Churchill, 1998).

QMJ17608 is an adult female. It is in spirit (70% alcohol) and in fair condition, although the back of its head has been badly damaged. We identified it as an emballonurid by its tail protruding from the upper surface of the uropatagium, and in the genus *Taphozous* by its wing pouches and lack of throat pouch. We determined QMJ17608 to be *T. troughtoni* on the basis of lengths of its forearm, metacarpal III, and skull dimensions. Its forearm was slightly longer than the four *T. troughtoni* (76.2 vs 72.7-75.6mm) specimens of Chimimba & Kitchener (1991), and did not overlap with any other *Taphozous* (Table 1).

It can be difficult to distinguish between *Taphozous georgianus* and *T. troughtoni* from external characters. Examination of morphometric data in Chimimba & Kitchener (1991: 211, table 1b) indicate that the external character with the least overlap between these species is the size of the digit III metacarpal. The length of this character in the specimen we examined was 68.0mm, 0.1mm below the range of *T. troughtoni* (68.1-70.2mm, n=4), and 2.1mm above that of *Taphozous georgianus* (52.7-65.9mm, n=302) (Chimimba & Kitchener, 1991).

The locality recorded for QMJ17608 is 'two miles S.E. Cloncurry' (20°43'S, 140°32'E). It was collected on 15 September 1969, although the identity of the collector was not recorded. The 1971 edition of the Cloncurry 1:100,000 map (PCC 7056) indicates the probable locality is south of the North Western Highway, close to Mount Avarice, with quarries and numerous mines within five kilometres. This record is around 60-65km to the east of existing locality records for *T. troughtoni*, and so extends its known range. The three other locality records for this species are close to each other (50km) around Mt Isa.

An additional specimen and collection locality for this species is noteworthy as only six specimens of this species have been collected from three localities (Tate 1952; Chimimba & Kitchener 1991). This species has not been seen since 1967 (Duncan et al., 1999). The national conservation status of *T. troughtoni* determined by the Action Plan for Australian Bats (Duncan et al., 1999) is 'endangered', while its conservation status in Queensland is 'endangered' (*Nature Conservation Act 1994 (and amendments)*). A management recommendation determined by Duncan et al. (1999) is to examine museum specimens of *Taphozous georgianus* from

TABLE 1. Dimensions of morphological characters of QMJ17608, *T. georgianus* and *T. troughtoni* (from Chimimba & Kitchener, 1991). All measurements in mm.

Character	QMJ17608	<i>T. georgianus</i>	<i>T. troughtoni</i>
Body length	77.1	61.6-80.0	79.4-86.3
Tail length	33.8	22.9-39.4	31.5-36.9
Ear length	24.7	16.5-24.1	22.4-27.1
Ear width	12.1	11.8-25.6	16.2-19.9
Tragus length	7.0	4.9-8.9	7.7-9.4
Forearm length	76.2	61.1-73.4	72.7-75.6
Tibia length	32.3	24.2-30.8	30.6-31.8
Pes length	15.7	9.8-14.7	13.8-15.5
Digit II metacarpal length	65.1		
Digit III metacarpal length	68.0	52.7-65.9	68.1-70.2
Digit III phalanx I	23.3	17.7-23.7	22.2-24.6
Digit III phalanx II	26.1	19.8-29.1	25.4-28.4
Digit IV metacarpal length	54.8		
Digit IV phalanx I	15.9		
Digit IV phalanx II	11.6		
Digit V metacarpal length	47.3		
Digit V phalanx I	15.9		
Digit V phalanx II	71.8		
Inter upper canine distance	4.5	3.4-4.5	4.5-4.8
Inter lower canine distance	3.2	2.6-3.3	3.2-3.4
Zygomatic width	14.7	12.1-14.4	14.7-14.9

northwest Queensland for additional records of *T. troughtoni*. Our findings indicate that examination of presumed *Taphozous australis* specimens may also result in further records of *T. troughtoni*.

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M.P. Rhodes, *Queensland Parks and Wildlife Service, PO Box 155, Albert Street, Brisbane 4001; A.P. Amey, Queensland Museum, PO Box 3300, South Brisbane 4101; Australia; 10 April 2000.*

GEMMAE OF THE MARCHANTIALES FROM THE WINTON FORMATION (MID-CRETACEOUS), EROMANGA BASIN, QUEENSLAND

MARY E. DETTMANN AND H. TREVOR CLIFFORD

Dettmann, M.E. & Clifford, H.T. 2000 06 30: Gemmae of the Marchantiales from the Winton Formation (mid-Cretaceous), Eromanga Basin, Queensland. *Memoirs of the Queensland Museum* **45**(2): 285-292. Brisbane. ISSN 0079-8835.

Hepatophyte gemmae are described from latest Albian sediments of the Winton Formation, Eromanga Basin, Queensland. The discoid gemmae are borne on a single-celled stalk and midway along each lateral margin there is a shallow notch in which is situated a growing point. The gemmae are comparable to those of extant Marchantiales and are referred to *Marchantites marguerita* sp. nov. □ *Marchantiales, gemmae, Late Albian, Eromanga Basin, Queensland.*

Mary E. Dettmann, Department of Botany, University of Queensland, St Lucia 4072;
H. Trevor Clifford, Queensland Museum, PO Box 3300, South Brisbane 4101, Australia;
28 March 2000.

Hepatophytes are believed to have formed an important component of the mid-Cretaceous vegetation of Australia as indicated by the widespread, sometimes abundant occurrence of diverse hepatic-like spores in Albian and Cenomanian sediments (Dettmann, 1994). However, apart from the likely affinity of *Triporoletes Mtchedlishvili* to the Marchantiales, ordinal or family alliance of the spore dispersae remains speculative. Further support for the presence of the Marchantiales in the Albian flora of southeastern Australia is provided by the thalli taxa, *Hepaticites discoides* Douglas and *H. profusus* Douglas, both of which are accepted as representatives of a possibly extinct, marchantialean group (Krassilov & Schuster, 1984). Spores associated with fertile *H. discoides* conform with the spore genus *Triporoletes* and its junior synonym *Rouseisporites* Pocock (Douglas, 1973).

In contrast to the common occurrence of hepatophyte megafossils, particularly *H. profusus*, at some Albian localities in the Otway Basin (Douglas, 1973), there are no records of hepatophyte thalli in Albian-Cenomanian megafloras described from elsewhere in Australia. These include the Burrum and Styx compression floras (Walkom, 1919); the Winton flora, known from impressions and permineralised cones and foliage taken from outcrops (McLoughlin et al., 1995; and references cited therein); and recently described compressions and cuticles recovered from core material of subsurface strata (Pole, 1999; 2000, Pole & Douglas, 1999). During palynological processing of a core from the Winton Formation in GSQ Thargomindah No. 3,

numerous mesofossils including megaspores, fern sporangia, and discoid hepatophyte gemmae were recovered. This account details the gemmae and illustrates associated fern sporangia.

MATERIAL AND METHODS

The gemmae were isolated from a siltstone intersected at 163.5m in GSQ Thargomindah No. 3, a continuously cored stratigraphic borehole drilled by the Geological Survey of Queensland at 27°16'S, 142°55'E, 120km NW of Thargomindah within the Eromanga Basin, SW Queensland (Figs 1, 2). A routine check of organic matter extracted from the sediment after treatment with 50% hydrofluoric acid followed by thorough washing in distilled water revealed the presence of numerous small discoid plant fossils up to 440µm in diameter. These were picked from the residue and transferred to small petri dishes prior to mounting in glycerine jelly on glass microscope slides. No further chemical treatment was required, and indeed mild oxidation in dilute nitric acid resulted in destruction of the disc-shaped fossils. After recognising that the discs represented hepatophyte gemmae, a thorough search was undertaken for any associated hepatophyte tissues; none was found, except for occasional hepatophyte-like dispersed spores (*Triporoletes reticulatus* (Pocock) Playford, *T. simplex* (Cookson & Dettmann) Playford, and *T. radiatus* (Dettmann) Playford). Other plant meso/microfossils represented in the residue included fern sporangia, woody tissues and palynomorphs. Fern sporangia were picked from unoxidised portions of the residue and mounted either in glycerine jelly for light



FIG. 1. Map of Australia showing location of GSQ Thargomindah No. 3 and Eromanga Basin.

microscope examination or on stubs and sputter coated with gold for scanning electron microscope analysis. Palynomorphs were extracted after treatment with nitric acid for 2 minutes, followed by thorough washing in distilled water, brief immersion in 1% ammonium hydroxide and further washing in distilled water prior to mounting for light microscope analyses.

The palynoflora contained in the sediment indicates assignment to the upper part of the *Phimopollenites pannosus* spore-pollen Zone (of Helby et al., 1987) and thus a latest Albian age.

Gemmae of living *Marchantia berteroa* Lehm. et Lindenb., *Lunularia cruciata* (L.) Dum. and *Neohodgsonia mirabilis* (Perss.) Perss. were examined after clearing in a mixture of glacial acetic acid and hydrogen peroxide in proportions 7:1 to remove chlorophyll and cell contents. The gemmae were then washed in distilled water and mounted in glycerine jelly on microscope slides.

Type and other figured specimens are lodged in the Queensland Museum, Brisbane. Registered numbers of that institution are designated in Table 1.

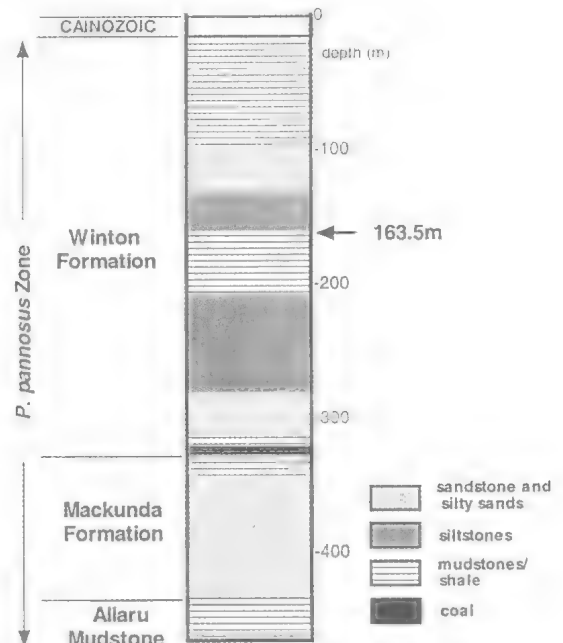


FIG. 2. Stratigraphic sequence in GSQ Thargomindah No. 3, and sampling horizon.

SYSTEMATIC PALAEOLOGY

HEPATOPHYTA MARCHANTIALES

Marchantites Brongn., 1849 emend. Walton, 1925

TYPE SPECIES. *Marchantites sezannensis* Brongn., 1849.

Marchantites marguerita sp. nov. (Fig. 3A-K)

ETYMOLOGY. For the late Margaret Derham, beloved sister and friend of MED.

MATERIAL. HOLOTYPE: QMF50093. Fig. 3A-C. Gemma discoid, 430 μ m long, 350 μ m greatest width, with a stalk scar at one end, and a notch on opposite sides on the periphery situated lateral to the stalk. Cells polygonal, 30-40 μ m in diameter, with anticlinal walls up to 6 μ m high.

DIAGNOSIS. Gemmae discoid, 1-2 cells thick and sometimes with a short, one-celled stalk up to 60 μ m long and 60 μ m wide. In outline each gemmae is bilaterally symmetrical about the vertical axis. A pair of shallow notches occurs opposite to each other on the perimeter of each gemmae midway between the apex and stalk. Cells adjacent to stalk elongate (up to 80 μ m long, 30-40 μ m wide), elsewhere isodiametric, pentagonal to hexagonal, 25-40 μ m in diameter

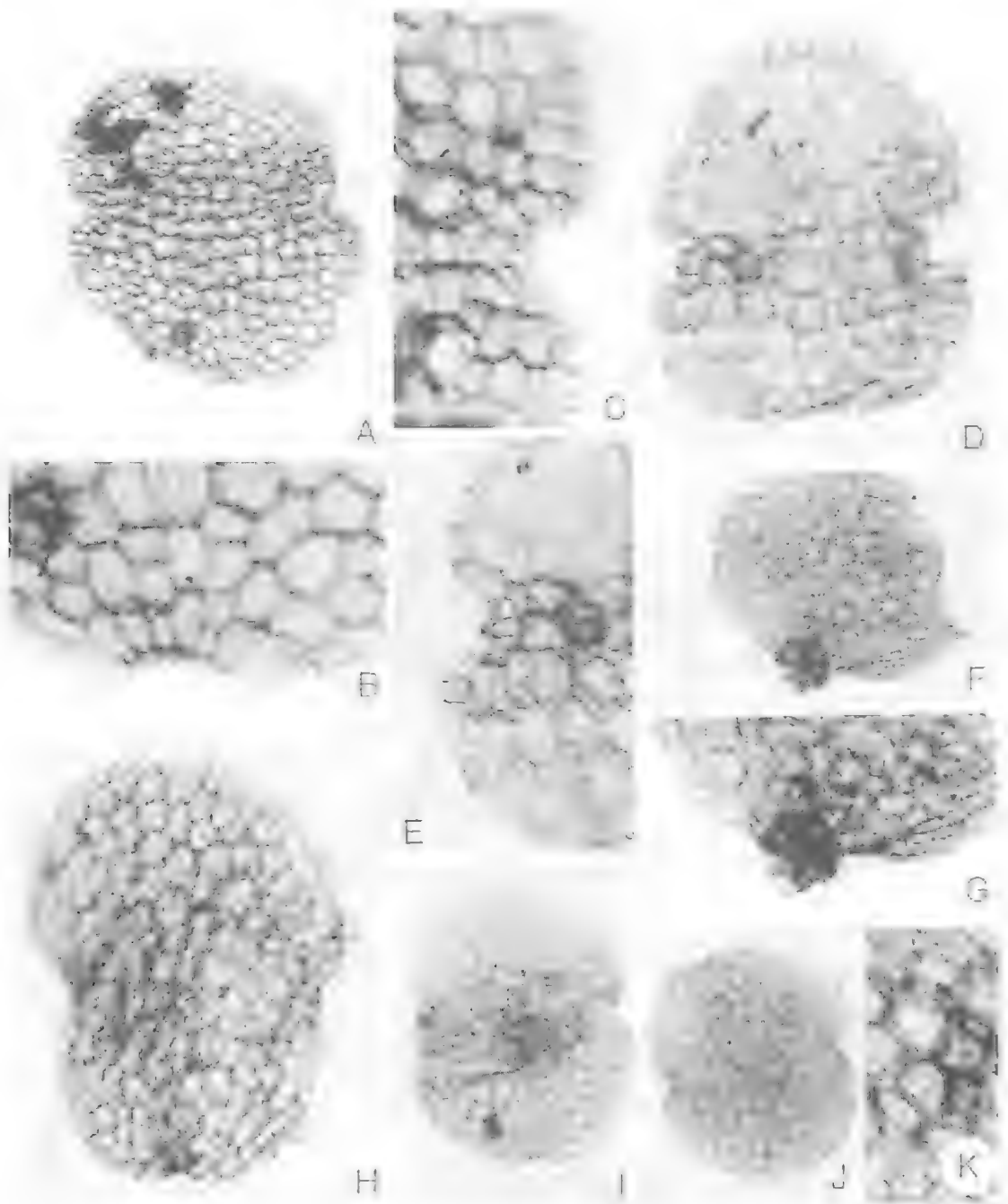


FIG. 3. Micrographs of *Marchantites marguerita* sp. nov.: A-C, holotype. A, $\times 100$; B, basal cells at site of stalk attachment $\times 300$; C, cells in region of notch, $\times 300$; D,E, whole specimen, $\times 200$, and detail of notch cells, $\times 300$; F,G, specimen with stalk attached, $\times 100$, and detail of stalk cell, $\times 150$; H, I, specimen $\times 150$ and $\times 100$; J, K, specimen, $\times 100$, and detail of cells, $\times 300$.

and with anticlinal walls 2-6 μ m high, but grading to 20 μ m in diameter at the growing points centred in each lateral notch.

DIMENSIONS. (longitudinal \times lateral dimensions) 200-(320)-440 μ m \times 160-(270)-400 μ m (20 specimens).

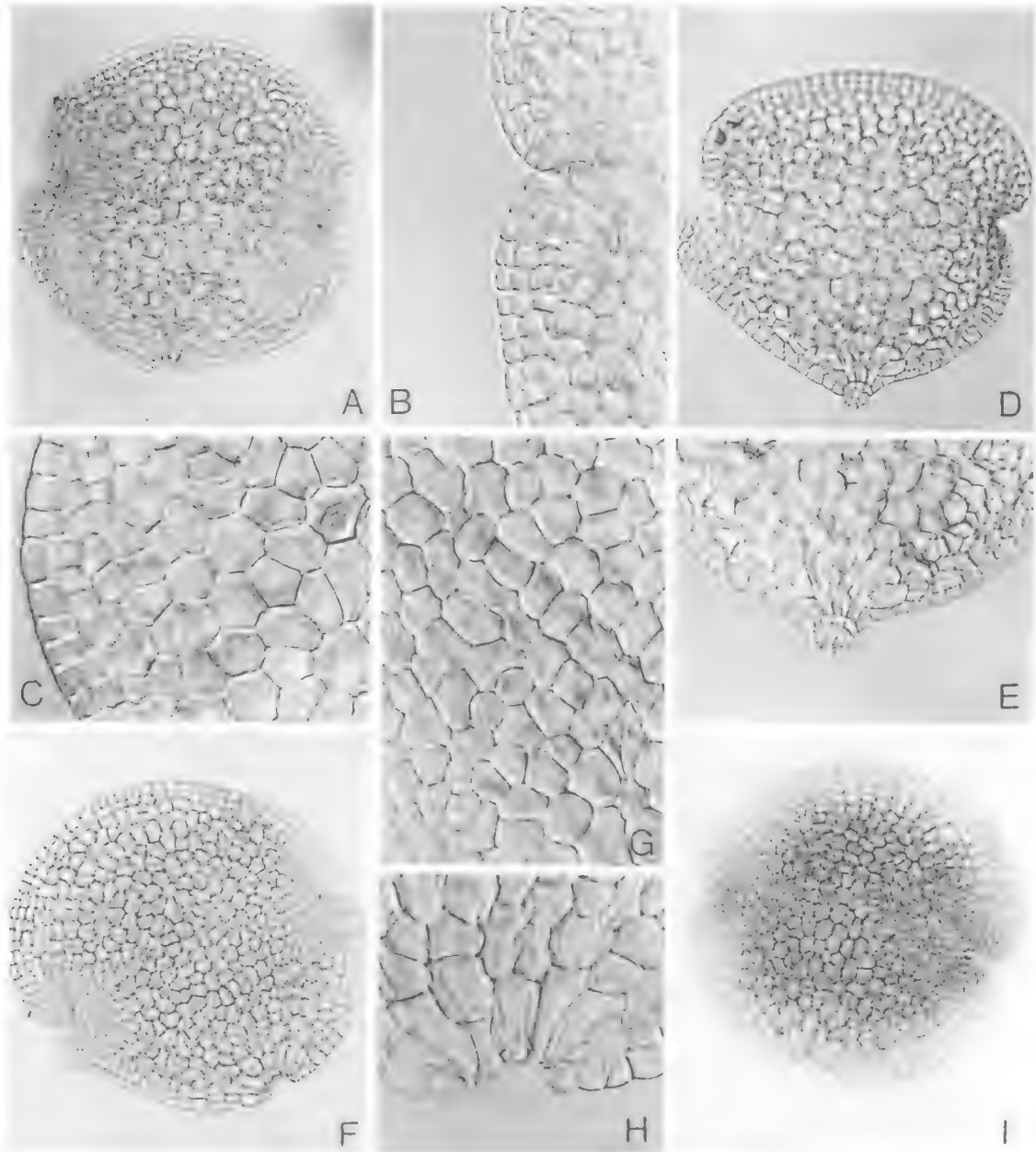


FIG. 4. A-F. Gemmae of *Marchantia berteriana* Lehm. et Lindenb; A, $\times 100$; B, C, detail of notch and peripheral cells, $\times 300$; D, E, specimen with stalk cell, $\times 100$ and detail of stalk, $\times 150$. F-I. Gemmae of *Lunularia cruciata* (L.) Dum; F-H, specimen, $\times 100$, and detail of cells in central and basal regions, $\times 300$; I, specimen, $\times 100$.

TYPE LOCALITY. GSQ Thargomindah 3, 163.5m; upper *P. pannosus* Zone, latest Albian.

REMARKS AND COMPARISON. In possessing a single-celled stalk and peripheral lateral notches in each of which is centred a small growing point, the discoid fossils are

morphologically consonant with gemmae of *Marchantia* L. (Marchantiaceae) and *Lunularia* Adanson (Lunulariaceae). Cells of *Marchantites marguerita* are more similar in size (25-40 μ m in diameter) to those of gemmae of *Marchantia berteriana* (cells 25-40 μ m in diameter; Fig.

4A-E) than those of *Marchantia polymorpha* L. (Smith, 1955: fig. 30; 15-30µm in diameter) and *Lunularia cruciata* (cells 15-30µm; Fig. 4F-I). The monospecific *Neohodgsonia* (*N. mirabilis*) H. Persson, (Marchantiaceae) also has disc-shaped gemmae, but they differ from those examined of *Marchantia* and *Lunularia* in possessing only one growing point associated with a lateral or subapical notch. Plate-like gemmae occur in several extant taxa of the Metzgeriales, but in these there is only one growing point, which is situated at the margin opposite to the stalk (Watson 1964).

The likely Marchantiales origin of the fossil gemmae may argue for assignment to *Marchantiolites* Lunblad, also demonstrated to be consistent with the Marchantiales. However, *Marchantiolites* is based on thalli with rhizoids on the undersurface and air pores on the upper surface, and is thus inappropriate for the gemmae described here. Pending recovery of the gemmae in organic association with hepatophyte thalli, the fossils are included in the broader category *Marchantites*.

DISCUSSION. Because of their firm thalli and preference for growing on mineral soil adjacent to stream banks, members of the Marchantiales are likely candidates for burial and subsequent fossilisation. Indeed from the Triassic onwards marchantioid-type thalli are well known (Krassilov & Schuster, 1984). It is therefore surprising that *Marchantia*-like gemmae have not been previously recognised.

The similarity of *Marchantites marguerita* to gemmae of extant *Marchantia* and *Lunularia* suggests that growth habitats of the Winton hepatophytes were within the range of those occupied by the extant genera, both of which are restricted to temperate climates. The Thargomindah region of the Eromanga Basin was situated at ~55°S during the latest Albian. Palaeotemperature data are lacking but those deduced from belemnites and bivalves from the underlying marine sequence indicate sea water temperatures of 12-16°C (Dettmann et al., 1992). Temperatures adduced from Global Grossplots are near 15°C (Frakes, 1997) and from other sources approximate 10°C (Frakes, 1997, Fig. 4). Today, the 15°C MAT isotherm passes through

southern New South Wales/northern Victoria at latitudes close to 35°S and the 10°C MAT isotherm to the south of Tasmania (Anon, 1988).

Associated with the fossil gemmae are numerous fern sporangia, one type possibly osmundaceous (Fig. 5A-D; apical annulus and containing in situ *Osmundacidites* cf. *wellmanii* Couper), and another with a vertical annulus and containing *Cyathidites minor* Couper (Fig. 5E-I). Also represented are lycophytic and hydropteridean megaspores and a restricted spore-pollen flora dominated by filicean spores referable to *Ruffordiaspora* Dettmann & Clifford (Schizaeaceae), *Baculatisporites* Thomson & Pilug and *Osmundacidites* Couper (Osmundaceae), and *Cyathidites* Couper. Hepatic spores (*Triporoletes reticulatus*, *T. simplex* and *T. radiatus*), gymnosperm (*Araucariacites* Cookson ex Couper, *Podocarpidites* Cookson ex Couper, *Microcachrydites* Cookson ex Couper) and dicotyledonous angiosperm pollen (*Phimopollenites* Dettmann) occur in low frequencies.

ACKNOWLEDGEMENTS

Grateful acknowledgment is extended to the Queensland Department of Mines and Energy for enabling sampling of core material; Dr Mike Pole, Department of Botany, University of Queensland for assistance with sample collection; Dr David Bedford, Royal Tasmanian Botanical Gardens for provision of material of *Marchantia berteriana*; and Dr Patrick Brownsey, Museum of New Zealand - Te Papa, Tongarewa, New Zealand for provision of material of *Neohodgsonia mirabilis*. We acknowledge helpful reviewers comments of Dr D. Cantrill and Dr J. Douglas. MED extends sincere thanks to Dr P. Jell Acting Director, Queensland Museum for providing facilities. The research was supported by Australian Research Council Grant A19531899 to MED and Professor George Stewart.

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FIG. 5. A, B, Osmundaceous sporangia, ×150. C, D, *Osmundacidites wellmanii* Couper, ×750; C, spore associated with sporangium, D, dispersed spore. E, *Baculatisporites comaumensis* (Cookson) Potonié, dispersed spore ×750. F-I, Fern sporangia with vertical annulus; F, ×400, G, with in situ spores, ×200, H, I, ×250. J, *Cyathidites minor* Couper, spore from sporangium, ×750. K, *Triporoletes simplex* (Cookson & Dettmann) Playford, dispersed spore, ×750.

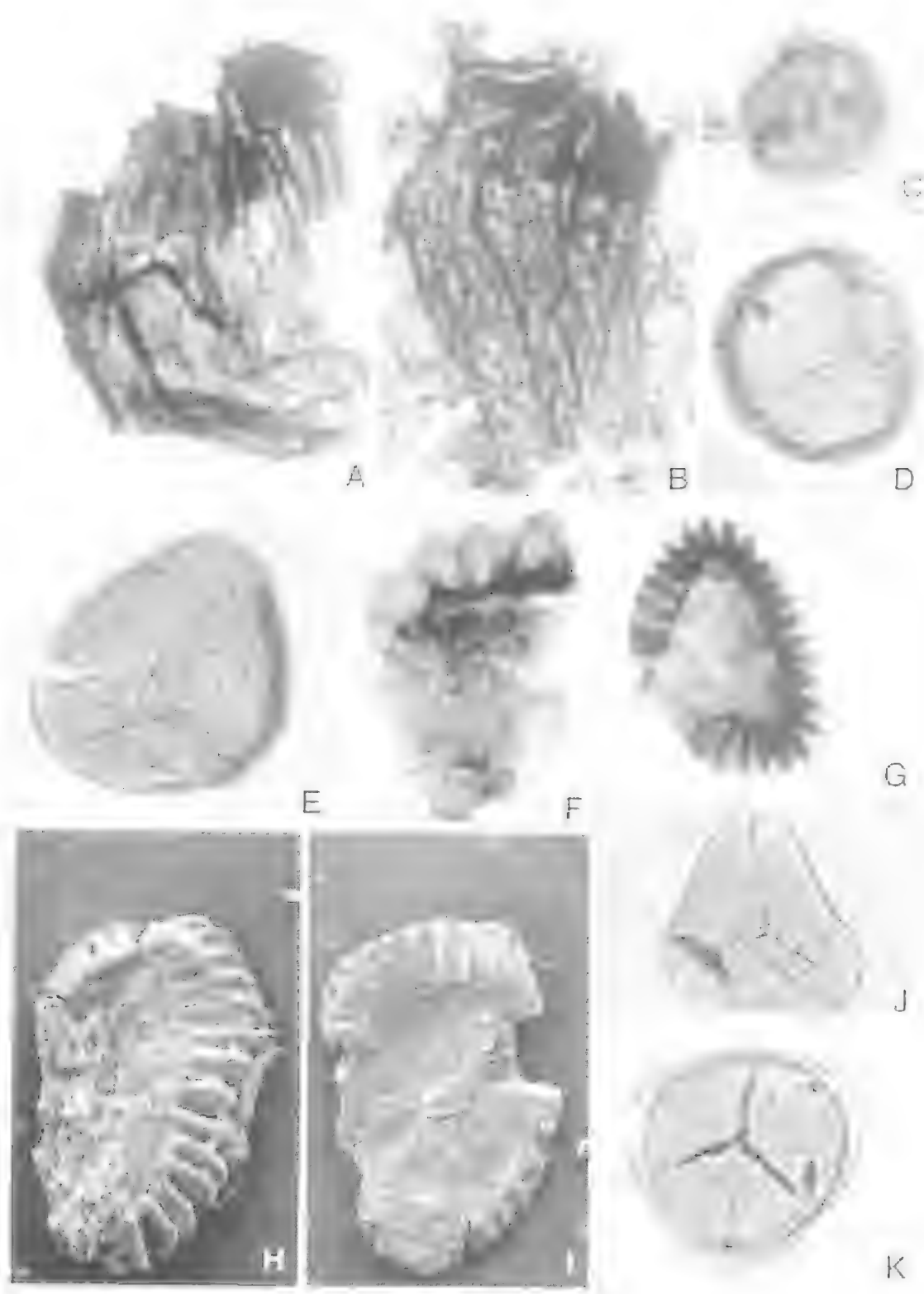


TABLE 1. Register of figured specimens. * denotes holotype.

Taxon/Fig. No.	Slide	Co-ordinates (England Finder)	Registered No.
Gemmae			
<i>Lunularia cruciata</i>			
Fig. 4F-H	LUN/2	K28/1	QMF50110
Fig. 4I	LUN/1	L34/2	QMF50111
<i>Marchantia berteriana</i>			
Fig. 4A-C	MAR/1	Q41	QMF50112
Fig. 4D,E	MAR/1	K26/3-4	QMF50113
<i>Marchantites marguerita</i>			
Fig. 3A-C *	THA 163.5/A2	M27	QMF50093
Fig. 3D,E	THA 163.5/A5	E37/1	QMF50094
Fig. 3F,G	THA 163.5/A11	O52/4	QMF50095
Fig. 3H	THA 163.5/A8	G29	QMF50096
Fig. 3I	THA 163.5/A2	C16/4	QMF50097
Fig. 3J,K	THA 163.5/A1	K41/1	QMF50098
Sporangia			
Osmundaceous sporangia			
Fig. 5A	THA 163.5/A7	P38	QMF50099
Fig. 5B	THA 163.5/K	F29/4	QMF50100
Sporangia with vertical annulus			
Fig. 5F	THA 163.3/A6	J33/3	QMF50101
Fig. 5G	THA 163.5/A3	H27	QMF50102
Fig. 5H	THA 163.5/A16	L38/1	QMF50103
Fig. 5I	THA 163.5/A16	M37	QMF50104
Spores			
<i>Baculatisporites comaumensis</i>			
Fig. 5E	THA 163.5/2	F31	QMF50105
<i>Cyathidites minor</i>			
Fig. 5J	THA 163.5/2	K50/2	QMF50106
<i>Osmundacidites wellmanii</i>			
Fig. 5C	THA 163.5/2	J45/3	QMF50107
Fig. 5D	THA 163.5/2	Q46/4	QMF50108
<i>Triporoletes simplex</i>			
Fig. 5K	THA 163.5/2	J43	QMF50109

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BOWER SYSTEM AND STRUCTURES OF THE GOLDEN BOWERBIRD,
PRIONODURA NEWTONIANA (PTILONORHYNCHIDAE)

CLIFFORD B. FRITH AND DAWN W. FRITH

Frith, C.B. & Frith, D.W. 2000 06 30: Bower system and structures of the Golden Bowerbird, *Prionodura newtoniana* (Ptilonorhynchidae). *Memoirs of the Queensland Museum* 45(2): 293-316. Brisbane. ISSN 0079-8835.

We examined 60 Golden Bowerbird, *Prionodura newtoniana*, bower sites, involving a total of 98 main (decorated) bower structures during 1978-1997. Only one main bower structure was decorated actively at any bower site during any one season. Bower sites were traditional ($n = 49$) or rudimentary ($n = 11$). Traditional sites were dispersed spatially throughout suitable topography at an average of one per 4.2ha, and at a mean nearest neighbour distance of $151 \pm 44\text{m}$ ($n = 12$). Eighty-four per cent of 25 traditional sites were regularly attended consecutively for 20 seasons. Rudimentary sites were located $78 \pm 36\text{m}$ from traditional sites and were rarely active for more than two seasons. Traditional bowers consisted of a single (36%) or two (64%) towers when first found; 14 of the single tower bowers later became two tower structures. Each bower had a bower perch of woody vine, near-horizontal living sapling, fallen dead branch or tree root averaging $4.6 \pm 6.5\text{cm}$ diameter. Where they abutted the bower perch, tower sticks were aligned tightly into a platform(s), upon which decorations, typically greyish-green lichen *Usnea* sp. and creamy-white seed pods of *Melicope broadbentiana*, were placed. Mean minimum age of a traditional bower was 9.6 ± 6.3 years ($n = 48$), at a mean of two per site over time. Six such bowers were attended for 20 seasons. Mean distance of a new traditional bower structure from the replaced one was $14.3 \pm 12.7\text{m}$. New main bower structures started as small single arboreal conical or maypole-shaped structures. It took two to three seasons for them to reach full size. Fourteen arboreal towers of main bowers subsequently became terrestrial, because sticks accumulated beneath them. Small arboreal and terrestrial subsidiary bower structures, built at a mean distance of $5.4 \pm 4.2\text{m}$ from main bower structures, sometimes formed the bases for a new main one; suggesting a function of subsidiary structures. We conclude that while bower size and shape are not conservative in this bowerbird, the platform area(s) upon which decorations were placed, are conservative in being specifically located, better constructed and in being decorated. The significance of bower form and adult male plumage in the Golden Bowerbird are discussed. □ *Golden Bowerbird, Prionodura newtoniana, Ptilonorhynchidae, bower sites, structures, building, dispersion.*

Clifford B. Frith and Dawn W. Frith, Honorary Research Fellows of the Queensland Museum, 'Prionodura', PO Box 581, Malanda 4885, Australia; 17 September 1999.

The Golden Bowerbird, *Prionodura newtoniana*, represents a distinctive monotypic genus endemic to the Atherton Region of the Australian Wet Tropics, tropical northeast Queensland, above 680 m asl (Blakers et al., 1984; Nix & Switzer, 1991). This species, the smallest bowerbird (25 cm in length and averaging 75g), is strikingly sexually dimorphic. Adult-plumaged males are predominantly brilliant yellow on their underparts, brownish olive above with a small bright yellow crest on the central crown, and a larger yellow nape patch. Females and immature males are pale grey below and brownish olive above.

The Golden Bowerbird is one of 16, of the total 19, bowerbird species (Ptilonorhynchidae) that has a polygynous mating system, in which males are promiscuous and females build and attend nests alone. Males build a large stick bower (Fig.

1) of the 'maypole' type, as do the four gardener bowerbirds of the New Guinea genus *Amblyornis*. This is quite unlike the cleared 'court' of *Scenopoeetes*, the 'mat' of accumulated fern fronds of *Archboldia*, or the stick or grass 'avenue' type bowers of *Ptilonorhynchus*, *Chlamydera* and *Sericulus* spp. (Marshall, 1954; Gilliard, 1969; Cooper & Forshaw, 1977; Borgia, 1986; Frith, 1989; Frith et al., 1994, 1996a,b; Frith & Frith, 1989, 1993, 1994, 1995; Donaghey, 1981, 1996). Bowders of most bowerbird species require rebuilding or major refurbishment within and between each display season, but maypole bowders of Golden Bowerbirds, and of some of the closely related gardener bowerbirds, persist year to year (Pruett-Jones & Pruett-Jones, 1982, 1983).

The Golden was the last bowerbird to be discovered in Australia. For its early history see



FIG. 1. A traditional twin tower bower and its adult male Golden Bowerbird owner. Note where tower sticks meet the bower perch (black in this picture) they are more skillfully placed and aligned, into a discrete 'platform', than are sticks of the rest of the structure. Decorations are placed on and adjacent to these 'platforms' and those seen here are beard lichen *Usnea* sp., seed pods of *Melicope broadbentiana* and the creamy white flowers of *Darlingia darlingiana* (one in bird's bill).

Chisholm & Chaffer (1956). Bowers were first described by Broadbent (in Campbell, 1900), Day (in North, 1904); Broadbent, 1902; North, 1909; Sharp (in North, 1914) and De Vis (in Mathews, 1926). Photographs of a bower appeared in Jackson (1909), but it was not until much later that more bowers were described (Bourke & Austin, 1947; Warham, 1962; Chisholm & Chaffer, 1956; Chaffer, 1958, Chisholm, 1957, 1963; Gilliard, 1969; Marshall, 1954). Bowers typically consist of two stick towers, which may or may not be of equal height, or a bulky and irregularly-shaped single mass of sticks with a bower perch protruding from one side. Structures vary considerably (Frith, 1989). Each tower is built upon and around a supporting central sapling(s) or tree. Twin tower bowers are up to 1 m apart and are interconnected by a living or dead, arboreal or terrestrial, horizontal or

near-horizontal, perch. Bower decorations are placed on the more neatly-aligned tower sticks adjacent to and on the bower perch. These include: greyish-green lichen *Usnea* sp., creamy-white seed pods of *Melicope broadbentiana*, and whitish flowers of several plant species (Chisholm & Chaffer, 1956; Chaffer, 1958; 1984; Warham, 1962, Frith & Frith, 2000a). Several other, smaller, stick subsidiary bower structures ('gunyahs' of Broadbent, in Campbell, 1900), are built close to the main (decorated) bower structure. Bower building/maintenance/decoration reaches a peak during the display season, from late August–December on the Paluma Range. Such activity declines during the heavier wet season rains of January and/or February, and when birds are moulting. Renewed, post-moult, activity commences in mid-March and April (Frith & Frith, 2000a,b).



FIG. 2. Dispersion of 41 traditional bower sites of male Golden Bowerbirds: 12 in study area 1, 10 in study area 2, and 19 in adjacent extralimital areas. Each 50ha study area measured 1×0.5 km. Those numbered are the 25 traditional sites examined seasonally (S78-S97; see Table 4). Note: single lines show creek systems, double parallel lines represent the dirt road from Paluma Township (entering at bottom) to Paluma Dam (to north) with a side track through SA1; the dotted line shows a snig-track through SA2 forest.

Bowerbird studies are numerous, but few deal systematically with variation in bower/court structures/sizes (as opposed to bower decorations) or provide comparative measurements of them. Exceptions are those of Borgia (1985) for the Satin, Diamond (1987) for Vogelkop, *Amblyornis inornatus*, Lenz (1993) for Regent, *Sericulus chrysocephalus*, Frith & Frith (1994) for the Tooth-billed, *Scenopoeetes dentirostris*, Frith et al. (1996a) for Archbold's, *Archboldia papuensis*, and Frith et al. (1996b) for Great Bowerbirds, *Chlamydera nuchalis*. The present study, carried out during 1978-1997, provides the first detailed information on variation in the structure and size of bowers of Golden Bowerbirds. It includes information on bower site location and dispersion, bower site constancy, bower age and bower building. Data on male seasonal activities at bowers, including attendance levels, bower maintenance, vocalisations, displays, decoration theft, and home ranges are presented elsewhere (Frith & Frith, 2000a,b), as

will be data on bower ownership, male survival and home ranges (Frith & Frith, unpubl. data).

METHODS

STUDY AREA. This study was performed in upland tropical rainforest, classified as simple notophyll vine forest (Tracey, 1982), at about 850m asl, 7km from Paluma Township on the Paluma Range, NE Queensland. The main 50ha study area (SA1, at $19^{\circ}00'S$, $146^{\circ}10'E$) measured 1×0.5 km and was permanently gridded with metal stakes (see also Frith & Frith 1994, 1995). A narrow dirt road bisected the length of the broad main ridge line of SA1 (Figs 2, 3). To the north of this road was a broad flattish ridge 30-50m wide and 600m long; with a discrete hill from which a slope, dissected by gullies, fell steeply down to a perennial creek. To the south the ridge was flatter and wider (240m); interspersed with patches of *Calamus*-dominated undergrowth and a system of creeks, except at the western end where it rose to a ridge and another

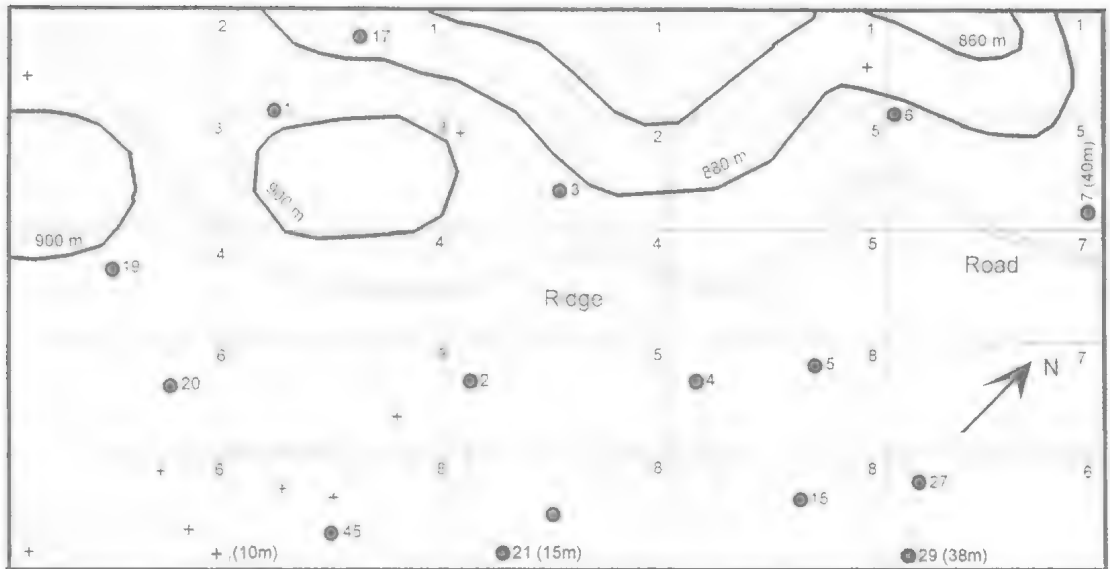


FIG. 3. Dispersion of 15 traditional (●) and 10 rudimentary (+) bower sites of male Golden Bowerbirds in study area 1 and outside (distance indicated in figure) its perimeter. Note: one rectangular quadrat = 2ha; number in top right hand corner of each = topographic type predominant (>75%) in that quadrat. Faint lines indicate location of seasonal gullies.

hill. Beyond this area the terrain dropped away steeply. A second hill-side study area (SA2) of the same size was not gridded. It was contiguous with SA1 and extended northwestwards up a hill to 950m asl. An old forestry snig-track bisecting a narrow ridge provided access up this hill (Fig. 2). Both study areas were searched systematically for bowers by CBF during August 1978-February 1981 for a total of 975h, besides innumerable unrecorded hours of random searching during the course of this and other bowerbird studies (Frith & Frith, 1994, 1995, 1998). Extralimital areas along tracks and ridges for a distance of up to 2km beyond SA1 and SA2 were also casually searched, as were other areas around Birthday Creek Falls and Paluma Dam.

DEFINITIONS. 'Site' describes the location of any active bower found, and any replacement bower(s) built subsequently during the course of the study. A traditional bower site was one attended for at least two seasons (Frith & Frith, 1994). A traditional bower was a large and well-established (single or twin tower) structure that was regularly attended, maintained, and decorated, throughout subsequent seasons by its traditional adult male owner. In a few instances, after the disappearance of a long-term traditional adult male owner, a traditional bower site was irregularly attended by immature (female-

plumaged) males, who either maintained the existing traditional bower or built a new rudimentary structure at that site (Frith & Frith, 2000b). Such a rudimentary bower subsequently became larger, and a traditional one, once an adult male again attended the site regularly.

A rudimentary bower site was one established near a traditional site by the construction of a rudimentary bower. Such bowers were poorly constructed, maintained, decorated and irregularly attended for only a few days/weeks each season, by immature males. We use regularly attended to imply full-time seasonal attendance by traditional owners at traditional bowers, and 'irregularly attended' to imply part-time seasonal attendance by immature males at traditional or rudimentary bowers. We refer to a display season by the year in which it started (S78, S79 etc).

BOWER SITES, THEIR LOCATION AND DISPERSION. We located 60 bower sites and 98 main bower structures (Table 1). Each bower site was plotted and each bower numbered (site number followed by suffix a, b, etc., for every bower built at a site) and tagged with a scored aluminium label on a tree supporting a bower tower.

The possible influence of differing topography upon bower structure and dispersion of 12 traditional bower sites in SA1 was examined.

TABLE 1. Number of bower sites, bower types (traditional or rudimentary) and bower structure of male Golden Bowerbirds and the type of bower structure (single or twin tower) when first found on the Paluma Range, north Queensland. * = at least 14 became twin tower bowers during the study.

	Total number		Number of old bowers (before 1978)			Number of new bowers (1978-1997)		
	Sites	Bowers	Single tower	Twin towers	Total	Single tower *	Twin towers	Total
Traditional	49	86	1	11	12	30	44	74
Rudimentary	11	12	3	0	3	8	1	9
	60	98	4	11	15	38	45	83

Various quadrat grid sizes were uniformly applied to a topographic map of the study area to find the most suitable grid size that resulted in each quadrat containing >75% of a given topographic type (see Frith & Frith, 1995). This proved to be a grid of 25 quadrats each of 2ha, or 200 × 100m. Each quadrat was assigned to the topographic type predominating (Fig. 3) as follows: 1) very steep slopes of >40° dissected by gullies (8ha); 2) steep hill slopes of 20-40° (4ha); 3) hill tops with 10-20° slopes (4ha); 4) gentle hill slopes of 5-10° (6ha); 5) ridge-side with <10° slopes (8ha); 6) open flat or <5° sloping areas (6ha); 7) disturbed flat areas with dense understorey dominated by *Calamus* (4ha); 8) flattish to <5° sloping areas dominated by creek systems and dense understorey (10ha). To test whether dispersion of bower sites was random, the numbers of sites per quadrat was compared to expected Poisson distributions. Coefficients of dispersion (C.D: variance to mean ratio) were calculated as a quantitative description of dispersion. This method is based on the variance being equal to the mean in the Poisson distribution. Variance to mean values of 1.0 imply random, >1 implies clumped, and <1 implies a regular or spatially uniform distribution (Sokal and Rohlf, 1969). The significance level of an observed deviation of the C.D. from 1.0 was determined by a t-test (n-1, one-tailed), the t-value being calculated by dividing the difference between the C.D. and 1.0 by the standard error of the deviation.

Mean distances between traditional bowers at 12 traditional sites in SA1 and at three other sites just outside its perimeter (Fig. 3) were estimated in two ways. First, nearest neighbour distances (NND) between sites were analysed using the method of Clark & Evans (1954). In this method: when two sites are closer together than they are to any other ones then the same distance is included twice. Secondly, although bower sites were not arranged linearly in this area, we estimated the mean inter-bower distance. This involved taking

the measurement from one bower to the next closest and so on throughout the whole 50ha. This allowed us to compare linear inter-bower distances with those presented in other bowerbird studies.

BOWER CHARACTERISTICS. Seventy-seven traditional bowers were measured and photographed. The following measurements were taken: height and base circumference of each tower and, in twin tower bowers, the distances between tower bases and apices; the type, axis direction, height and diameter of the bower perch and, in twin tower bowers, the length of perch exposed between the platforms of the towers; the number and girth at breast height (gabh) of saplings and trees incorporated into each tower. Number and size of associated arboreal and terrestrial subsidiary structures were measured and their distances relative to the main bower perch plotted. Means are given ± one standard deviation.

To give an indication of relative bower size we estimated bower volume by multiplying tower height with base circumference. Spearman rank correlation (one-tailed test corrected for ties) was applied to test whether there was a correlation between bower size (= volume) and situation (= degree of slope) at 42 traditional sites. When we measured two bowers at a site (n = 6) we took the mean value of each measurement.

BOWER SITE CONSTANCY, BOWER AGE, BOWER BUILDING AND STRUCTURAL CHANGES. To provide data on site constancy we examined 25 traditional bower sites from S78-S97 but excluding S91, S94 and S96 (Fig. 1). Our absences during these latter seasons did not affect our results as all sites save one (site 27) remained actively attended by birds during the subsequent season(s). We omitted season 91 because it was excessively dry, bowers were seldom attended and were poorly decorated. Rainfall typically averaged 259mm (S78-S90) for September-November; but in S91 only 94mm of rain fell, mostly after 12 November.



FIG. 4. Shapes and sizes of single tower bowers. (scales = a one metre stick marked every 10cm or CBF (180cm tall) or DWF (162cm tall) in picture). A, bower 37a: a compact single tower with a curved vine bower perch (right) with small terrestrial subsidiary (left in background). April 1979. B, bower 23a: a bulky single irregular-shaped massif with a sloping living sapling bower perch (right). April 79. The few irregularly-placed sticks to the right end of the bower perch never became a second tower and the bower changed little in shape or size over six seasons. C, bower 22a: an amorphous three-peaked massif with a rotten bower perch on the ground (left of photograph). April 1979. The owner had replaced this bower with a new one by September 1979 (see Fig. 11C). D, bower 19a: an arboreal tower with a bower perch 161cm above ground. April 1979. The few irregularly-placed sticks to the right end of the bower perch subsequently became a second tower. E, bower 2a: a tall massif supported by a vine that also formed the bower perch 116cm above ground. April 79. It later became a twin tower structure.

The 25 traditional bower sites involved a total of 51 bowers. These bowers were described, photographed and or measured during April 1979, August 1984 and February 1990; and in

other seasons if their structure changed notably. Photographs were taken from the same location and height each time, so that temporal changes in bower shape and structure could be assessed

accurately. These data provided us with information on age of bowers, changes to bower structure and bower building.

RESULTS

BOWER SITES, THEIR LOCATION AND DISPERSION. *Traditional Bower Sites.* We located 49 traditional bower sites (Table 1): 12 in SA1, 10 in SA2, 19 in adjacent extralimital areas (see Fig. 2), two near Birthday Creek Falls and six around Paluma Dam. Bower sites had medium to large forest trees, many saplings, and the odd tree ferns above and around them. Woody lianas and climbing pandans were common, but large stands of *Calamus* were not close to bowers. Canopy foliage cover was estimated above 37 sites: 12 having a coverage of >90%, 7 of 80-90%, 11 of 70-80%, five of 60-70% and 2 of 50-60%. Thus, 51% of sites had a cover of >80%, and 81% of >70%.

The direction of ground slope down and away from the bower was recorded for 45 bower sites: 20 were on a N to E bearing of 0-90°, 11 on E to S bearing of 100-175°, 2 on a S to W bearing of 210-240°, 8 on a W to N bearing of 280-360° and 4 were on flattish ground with no slope. The degree of slope on which bowers were placed at 45 sites were as follows: 17 on flat to 10° gentle slopes, 9 on 11-20° slopes, 6 on 21-30° slopes, 7 on 31-40° slopes and 6 on 41-45° slopes. Thus, bowers were built on slopes that averaged $21 \pm 15^\circ$, with 71% being on slopes of <31°. On 0-10° slopes bower size (= volume; see Methods) averaged $740 \pm 214\text{cm}^3$, on 11-20° slopes $589 \pm 208\text{cm}^3$, 21-30° slopes $625 \pm 223\text{cm}^3$, 31-40° slopes $620 \pm 240\text{cm}^3$, and 41-45° slopes $684 \pm 393\text{cm}^3$. There was no significant correlation between bower size and degree of slope built upon ($r_s = 0.22$, $P > 0.05$).

Bower sites were on flatter terrain and along ridge slopes either side of tracks or road, on gentle slopes and ridges immediately around the hill crest, and below steeper slopes where terrain levelled (Fig. 2). The 12 traditional sites in SA1 averaged one per 4.2ha, and were spatially dispersed throughout suitable topographic types (CD = 1.45, $t = 1.54$, $P > 0.1$). Eight of the 12 were located on flat to gently sloping (<10°) ground (mean = one per 3.8ha) of topographical types 4, 5, 6 and 8 (Fig. 3). The remaining four sites (1, 3, 6 and 17) were located in topographical types 1 and 2 (one per 3.0ha), on steeper ground. No bower sites were found in topographic types 3 and 7.

In S78, the mean inter-bower linear distance from one site to the next closest one in SA1 ($n = 12$), and three additional sites (7, 21 and 29) just outside its perimeter (see Fig. 3), was $165 \pm 41\text{m}$ (range 110-222m). Mean NND distance was $151 \pm 44\text{m}$ (range 110-222m). During seasons S78-S90, the mean NND of bowers at these 15 sites varied from 138 ± 52 to $151 \pm 47\text{m}$ (mean of mean = 147m). Differences were due to temporary disuse of bower site 20 during S87 and S88, and the establishment of replacement bowers at different locations within a site.

Rudimentary Bower Sites. We found 11 rudimentary bower sites (Table 1): ten in SA1 (including one just outside it; see Fig. 3) and another 140m outside SA1. Eight were on flat to gentle (<11°) slopes and the others on 21-30° slopes. Canopy cover was 70-85% ($n = 3$). Rudimentary sites in SA1 averaged $78 \pm 36\text{m}$ ($n = 8$) from a traditional bower site. Of 11 rudimentary sites, three were attended for one season, one for two, and four non-consecutively for two, three ($n = 2$) and four seasons. Three others were abandoned when found (pre-S78).

BOWER CHARACTERISTICS. *Structure and Size of Traditional Bowlers.* Traditional bowers were single or twin tower structures of sticks of varying lengths, texture and diameter (Fig. 1). Only one (the main) bower structure at any bower site was attended consistently, maintained and decorated during a season. We examined a total of 86 traditional bowers at 49 traditional sites: 12 were disused old bowers (11 being twin towered) that had been active before S78, but the other 74 were attended during some part of the study (Table 1). Of the 86 bowers, 36% had a single tower and 64% two towers when found. At least 14 single tower bowers subsequently became twin tower bowers (see Table 4), thus increasing the percentage of twin tower bowers to 80.

Single tower bowers varied greatly in shape and size from: a single compact conical structure with a curved vine bower perch (Fig. 4A); a single bulky, irregular-shaped large massif with a sloping living sapling bower perch (Fig. 4B); a huge amorphous multi-peaked massif with a base circumference 615cm and a rotten ground bower perch (Fig. 4C); an entirely arboreal structure with bower perch 161cm above ground (Fig. 4D); to a 205cm tall single massif with a 'liane' bower perch 116cm above ground (Fig. 4E). Single tower bowers had only one platform, even though a handful of sticks was placed at the opposite end of the bower perch in a few cases (see Fig. 4B,D).



FIG 5. Shapes and sizes of twin tower bowers. A, bower 29b: a bower with one tower terrestrial and the other arboreal. August 1984. Note: the sticks on the two bower perch platforms are conspicuously more neatly and tightly aligned. B, bower 4a: a bower with one terrestrial tower much larger than the other. April 1979. This bower changed little during the entire study. C, bower 20a: a 'classic' compact U-shaped terrestrial structure with two well-formed platforms. April 1979. Note: the sticks of the platforms meet on the bower perch and those of the towers have met and are fused beneath it. D, bower 17a: a bower with two widely-spaced but compact tall towers of similar height built on a large woody vine that also partly supported the tower on the right. April 1979. E, bower 10a: a bower with two widely-spaced amorphous towers. The vine bower perch also partly supports the tower on the right. April 1979. This bower changed little during the entire study (see Table 4). Note: it is easy to see how a bower like this may have originated from two low arboreal subsidiaries such as the ones in Fig. 8B. F, bower 16a: a skeletal bower with a rotten bower perch that, despite its appearance, was regularly attended from 578-585 before being replaced by a new one. April 1979. The terrestrial subsidiary in the centre background rotted away.

at which site the second tower could be built to develop a twin tower structure.

A few either arboreal (Fig. 5A) or terrestrial (Fig. 5B) twin bowers had markedly

TABLE 2. Size (cm) and volume (cm³) of single and twin tower traditional bowers of male Golden Bowerbirds on the Paluma Range, north Queensland. * = sample sizes vary because not all parameters of each bower were measured of each bower; ** = height (base to top apex) × base circumference.

	Single tower bowers			Twin tower bowers						Both towers		
	Height	Base circumference	Volume **	Larger tower			Smaller tower			Both towers volume ** combined	Distance between tower apices	Shortest distance between tower bases
				Height	Base circumference	Volume **	Height	Base circumference	Volume **			
Sample number*	15	13	13	60	39	39	60	39	39	39	34	38
Mean	148.6	439.0	646.6	130.3	347.1	456.6	82.8	209.5	197.0	654.0	98.4	24.6
s.d.	32.3	102.2	215	27.92	98.4	178.0	44.3	91.6	157.6	262.1	20.9	17.7
Range	100-205	274-615	320-1010	70-190	200-534	186-982	13-193	65-390	104-579	309-1449	70-150	0-80

asymmetrical towers. Eleven bowers had one larger terrestrial tower and a smaller arboreal one when first found. At least six arboreal towers subsequently became terrestrial due to an accumulation of dropped sticks beneath the structure. Typically, however, twin bowers had two well-formed towers with one tower taller and/or more massive than the other and their towers extending down to the ground. They varied greatly in shape and size: from a compact U-shaped structure (Fig. 5C) to widely-spaced neat (Fig. 5D), more amorphous (Fig. 5E), or skeletal (Fig. 5F) structures. The towers of the largest terrestrial bower were 174 and 198cm tall, with base circumferences of 5m and 3m respectively (Fig. 6A). In two bowers both towers were arboreal, with their bower perches 2m above ground (Fig. 6B).

Mean bower measurements for 15 single, and 60 twin, tower bowers are given in Table 2, where ranges exhibit the cumulative variation of bower structure outlined above. Single tower bowers averaged 13% taller, 21% larger around the base, and 29% bulkier (volume), than the larger tower of a twin bower. Moreover, their mean volume was similar to that of the mean combined volume of both towers of twin structures (= 654cm³). In 55 twin bowers, the larger tower was both bulkier and taller than the smaller one, but in five bowers the bulkier tower was the same height (n = 3) or slightly shorter (n = 2; by 19 and 34cm). Distances between tower apices averaged 98 ± 21cm (n = 34), and between their bases 25 ± 18cm (n = 38). The bases of eight twin tower bowers were connected beneath the bower perch by the amalgamation of sticks of each tower (see Figs 5C, 10F).

Towers were built around, and supported by, saplings and vines (<25cm gabh) and/or trees (>25cm gabh). Larger single towers, and those of twin bowers, encompassed more such supports than did the smaller tower of a twin (Table 3). The gabh of saplings within bowers averaged 7.9 ± 5.7cm, and of trees 62.8 ± 23.6cm. Of 272 examined tower supports, 83% were saplings, 12% trees and 5% vines (12 woody vines and a *Calamus* vine). Four of the vines and two of the saplings also formed the bower perch.

The bower perch protruded from a single tower bower, or connected the two towers of a twin (see Figs 4-6). The axis of the bower perch was at right angles to the axis of the inter-tower bower 'avenue'. Bower perch compass alignment was recorded at 49 traditional bowers: 20 were aligned between 0-45°, 8 between 45-90°, 9 between 90-135° and 12 between 135-180°. The bower perch in 61 bowers consisted of: a woody vine (43%), living saplings leaning toward the horizontal (24%), a rotting dead branch or vine (24%) or a narrow tree root (3%; see Figs 4 & 5). Bower perches averaged 4.6 ± 6.5cm in diameter (Table 3). The top of bower perches averaged 42 ± 40cm (n = 59) above ground; but if the 4 atypically arboreal towers, with resultant unusually high perches, are excluded (see above) the average becomes 33 ± 19cm.

Where tower sticks met the bower perch they were conspicuously more neatly and tightly aligned into what we term a platform(s); see Fig. 1. Whereas single tower bowers had only one platform, twin structures had a platform at either end of the exposed bower perch. The mean length of exposed bower perch of twin tower bowers was 18 ± 8cm (n = 49), but the platforms of 4 such bowers actually met atop the bower perch

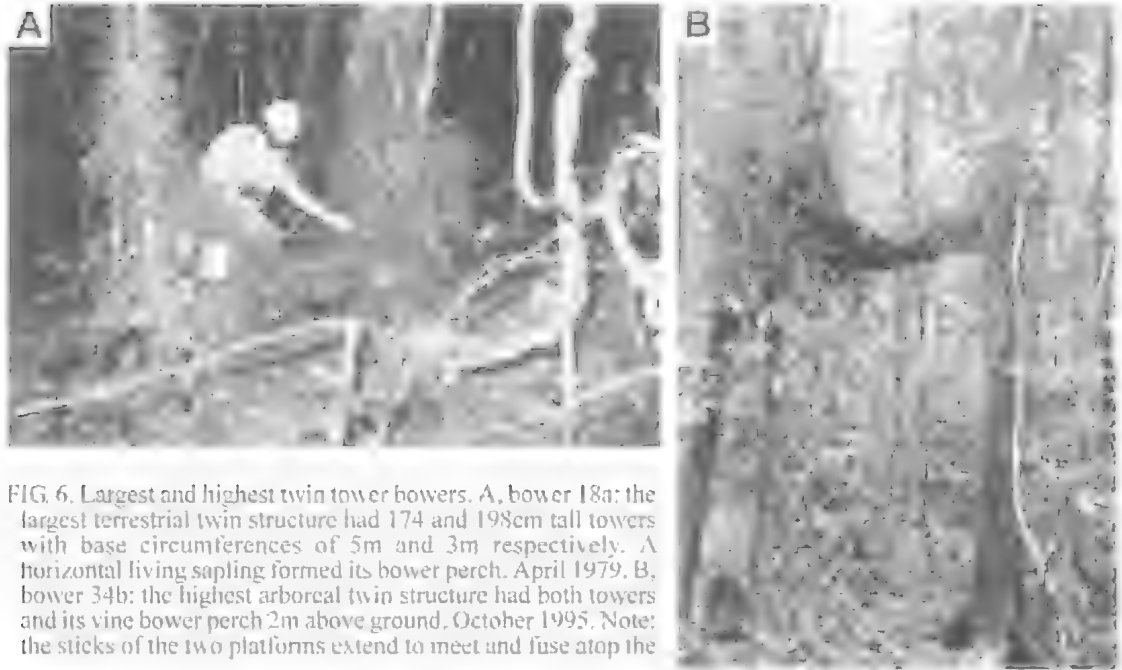


FIG. 6. Largest and highest twin tower bowers. A, bower 18a: the largest terrestrial twin structure had 174 and 198cm tall towers with base circumferences of 5m and 3m respectively. A horizontal living sapling formed its bower perch. April 1979. B, bower 34b: the highest arboreal twin structure had both towers and its vine bower perch 2m above ground. October 1995. Note: the sticks of the two platforms extend to meet and fuse atop the

(see Figs 5C & 6B). Bower decorations were placed only on platform sticks and those just beside/above them (Fig. 1). The relative quantities of each decoration type and their placement (i.e. on one or both platforms) varied from bower to bower and season to season. During peak display season, decorations consisted of a carpet (30-40 pieces) of greyish-green lichen *Usnea* sp. and 5-20 sprigs of creamy-white dehiscent ripe fruit with attached black seed (seed pods hereafter) of melicope, *Melicope broadbentiana* (see Fig. 1). Other, less frequently used, decorations included creamy-white flowers of jasmine (*Jasminum kajewskii*), Brown Silky Oak (*Darlingia darlingiana*) and *Dendrobium* spp. orchids.

Structure and Size of Rudimentary Bowers. We examined 12 rudimentary bowers at 11 rudimentary sites (one site had two bowers built/attended during different seasons; see Table 1). These were poorly constructed, maintained, decorated and attended irregularly for only a few days/weeks each season, by immature males. They consisted of a conical-shaped loose mass of sticks lacking a platform, or with only an ill-defined one, and often lacking a bower perch or decorations (Fig. 7A). Height of their towers averaged $84 \pm 12\text{cm}$ ($n = 9$; 3 being too old to measure), and mean volume $304 \pm 188\text{cm}^3$ ($n = 3$). Only one rudimentary bower had a second tower, a mere 50cm tall pile of sticks placed on the ground.

Following the disappearance of their long-term traditional adult male owners, a few traditional sites were irregularly attended by immature male(s) who built new rudimentary bower structures there. Rudimentary bowers at traditional sites were better formed, with a bower perch and more obvious platform (see Fig. 7B), than those built at rudimentary sites. They were all conical single towers (mean height = $95 \pm 25\text{cm}$, $n = 5$; mean volume $312 \pm 102\text{cm}^3$, $n = 2$). Some became a larger, and a traditional, bower once an adult male again regularly attended the site.

Structure and Size of Subsidiary Bower Structures. The frequent use, by males, of one or more favoured horizontal perches around bower sites resulted in birds placing, or leaving, sticks on them at the point they diverged from the trunk. Such sticks accumulated, became fused by fungi, and thus developed, over time, into subsidiary structures. Some subsidiaries were in the immediate vicinity of the main bower(s); (see Figs 4A, 5F), while others were up to 20m distant.

We recorded 36 terrestrial and 115 arboreal subsidiary structures at 46 traditional bowers: located at an average of $5.3 \pm 4.2\text{m}$ from the main bower perch, and averaging 3.3 (range 1-16) in number per site (Table 3). All but four of the 46 bowers had several arboreal subsidiary structures (mean = 2.7, range = 1-13), but only 18

TABLE 3. Number and measurements (cm) of bower perches, tower supports and associated subsidiary bower structures at traditional bower sites of male Golden Bowerbirds on the Paluma Range, north Queensland. Sample sizes vary because not all parameters of each bower were measured. ** = mean of means.

Sample number *	Tower supports						Bower perches			
	Saplings/vines			Tree			Exposed length	Highest point (all bowers)	Highest point (excluding arboreal bowers)	Diameter
	Single tower bowers & larger tower of twin bowers	Smaller tower of twin bowers	Girth at breast height	Single tower bowers & larger tower of twin bowers	Smaller tower of twin bowers	Girth at breast height				
Mean	3.8	1.4	7.9 **	0.54	0.1	62.8 **	17.7	41.7	32.6	4.6
s.d.	2.6	1.3	5.7	0.7	0.4	23.6	8.1	39.3	18.8	6.3
Range	1-12	0-5	1-23	0-3	0-1	28.5-133	0-38	3-200	3-80	1.4-45

had terrestrial ones (mean = 2, range = 1-5). The height of arboreal subsidiaries, from their base to apex, averaged 168cm (range = 36-388cm) and that of the terrestrial ones 69cm (range = 15-106cm) from ground to apex.

Terrestrial subsidiary structures were built mostly around saplings, but a few incorporated a tree (Fig. 8A). Two subsidiaries were often built close together (<1m apart) on the same horizontal plane and resembled a miniature twin tower bower (Fig. 8B). A few subsidiary structures, particularly such pairs of them, subsequently became the basis for new main bowers. Arboreal subsidiaries were built where a branch forked horizontally from a sapling/tree trunk (Fig. 8C), or where a leaning sapling or vine crossed a sapling/tree trunk (Fig. 8D). Most ($n = 90$) were too high (>1.5m above ground at base) to measure. Those nearer the ground (<1.5m) were usually larger and conical, and averaged 61cm (range 20-120cm, $n = 25$) tall (Fig. 8D). As dropped sticks accumulated beneath them ($n = 3$), such arboreal structures became terrestrial ones. We recorded only one terrestrial and three arboreal subsidiaries at rudimentary bower sites.

Bower Site Constancy and Bower Age. Of the 25 traditional bower sites monitored seasonally (S78-S97), 84% were attended every season for 20 years (Fig. 2; Table 4). Of the 4 remaining sites: site 20 was attended for 18 (unattended S87-S88), site 27 also for 18 (unknown in S96, and derelict in S97), site 16 for 11, and site 21 for 5 (S78-S82) consecutive seasons.

Twin tower bowers were established and attended for the first 8 and 14 seasons at bower sites 20 and 27 respectively, but when their long-term adult male owners disappeared

Subsidiary bower structures					
Terrestrial		Arboreal		Total number per bower site	Distance from bower perch
Number	Height	Number	Height above ground		
18	18	42	42	46	46
2	68.6 **	27	168 **	13	532
1	26	26	94.9	3.3	415
1-5	15-106	1-13	36-388	1-16	0-2000

immature males took over and built and attended rudimentary bowers (2 at site 20 and 1 at 27, Table 4). Site 16 had 2 single tower traditional bowers attended consecutively by 2 adult males over 11 seasons (until S88) and was then abandoned (Table 4). There was only a rudimentary bower at site 21 in S78, but 14m away was a disused large twin tower flattened by a tree fall; it had obviously been attended during previous seasons. Its rudimentary bower did not change (S78-S82), was not replaced, and was only irregularly attended by one to several immature males before being abandoned.

The 25 traditional sites had a total of 51 bowers at them during the study (Table 4). Seven of these 25 sites had one main bower, 12 two bowers, 4 three and 2 four bowers; at a mean of 2 per bower site over time. Two bowers (15a and 20d) remained rudimentary for many seasons before becoming larger and traditional ones (see below), whereas three other rudimentary bowers (20c, 21a, 27b) did not progress and were abandoned (Table 4). Thus, of the 51 bowers, 48 were/became traditional and 3 remained rudimentary. The mean minimum 'life' of a traditional bower was 9.6 ± 6.3 ($n = 48$) years. Six traditional

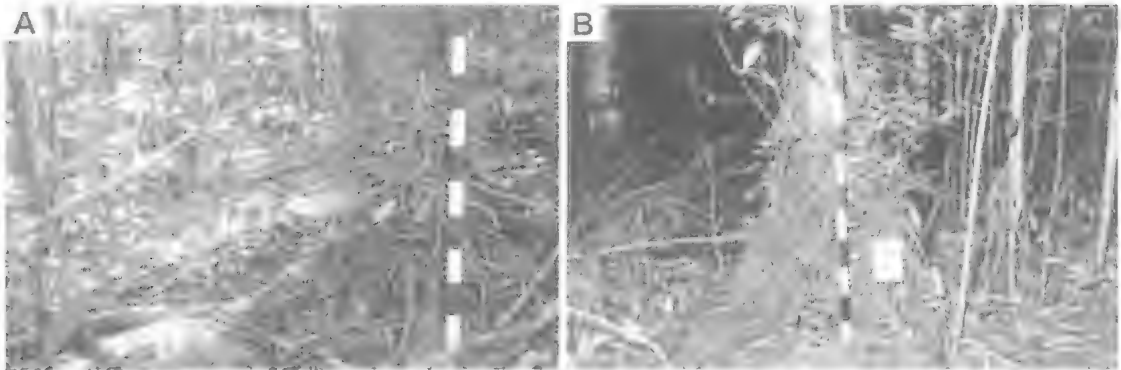


FIG. 7. Shapes and sizes of rudimentary bowers. A, this newly-built rudimentary bower (30) was first found at a new rudimentary site in August 1979. B, this rudimentary bower (21a) was built at a traditional site after a tree had destroyed the previous twin tower structure. It never increased in size and the site was eventually abandoned.

bowers were attended for a minimum of 20 seasons (Table 4).

BOWER BUILDING AND STRUCTURAL CHANGES. We observed construction of 10 traditional bowers. Four (1a, 17b, 45b, 45c) started as completely new arboreal structures, 4 (3b, 6b, 20b, 47b) developed from an existing subsidiary bower structure, and 2 (15a, 20d) were built from existing rudimentary bowers, as follows:

In S78 we found only a derelict (pre-S78) bower at site 1. In March 1979 a handful of sticks had been newly-placed on a fallen horizontal sapling where it met a vertical tree, 20m distant from the derelict structure. This new bower (1a) resembled a sparse arboreal subsidiary, but it was decorated with two sprigs of melicope seed pods and one piece of lichen placed on *Freycinetia* sp. vine above the bower perch (Fig. 9A). By April 1980 the structure was a small conical arboreal subsidiary. By June 1980 it was an untidy tower of unfused sticks, lacking a platform and resembling a terrestrial rudimentary bower decorated with 10-12 lichen pieces (Fig. 9B, compare with Fig. 8A). By S80 it was a small terrestrial single tower, and by S81 a larger massif with a well-formed platform. Its bower perch subsequently slipped to the ground and a small handful of sticks placed on it 14cm from the large tower. By S82 this bower was a terrestrial twin, its second tower much the smaller (Table 4). It took 3.5 years to reach this stage.

Bower 17a was flattened by a tree fall in S85. In November 1986 we found a small conical arboreal bower (17b), of loosely-placed unfused sticks, where a leaning sapling crossed a vertical one, about 45m from the flattened bower and 63cm above ground. By October 1987 this was a

terrestrial single tower, and a pile of sticks had been placed further along (20cm) the sapling where it crossed a large tree. By February 1990 the latter pile of sticks was a small second arboreal tower, and by November 1991 this was larger and terrestrial. It thus took four years for this bower to become a large twin tower structure (Table 4).

In December 1979 we found a newly-constructed small single conical arboreal tower of unfused sticks, piled between the vertical trunks of three saplings, 50cm above ground. This new bower (45b) was 20m from a derelict one of the previous season (Table 4). In S80 bower 45b was still small, but by S81 was a substantial terrestrial single tower bower that remained so until S88, but by which time it had deteriorated. In October 1989 replacement bower 45c, about 20m from 45b, was a single tall arboreal tower 60cm above ground. By September 1990 it was a twin tower bower with its second tower an arboreal one. By November 1991 both towers had become terrestrial (Table 4).

Four traditional bowers developed from an existing arboreal (6b and 47b) or terrestrial (3b and 20b) subsidiary bower (Fig. 9C,D). These took two to four years to become large single (47b) or twin (3b, 6b, 20b) tower structures (see Table 4). Traditional bower site 15 was attended only by immatures males from S78-S87, and its bower was small and rudimentary. When an adult male took over the site in S88 the rudimentary structure, unchanged for many years, became a larger single tower bower. By S90 it was a twin structure (see Table 4). Similarly, in S89 bower 20d was a new loosely-constructed rudimentary terrestrial tower attended by immature males. It

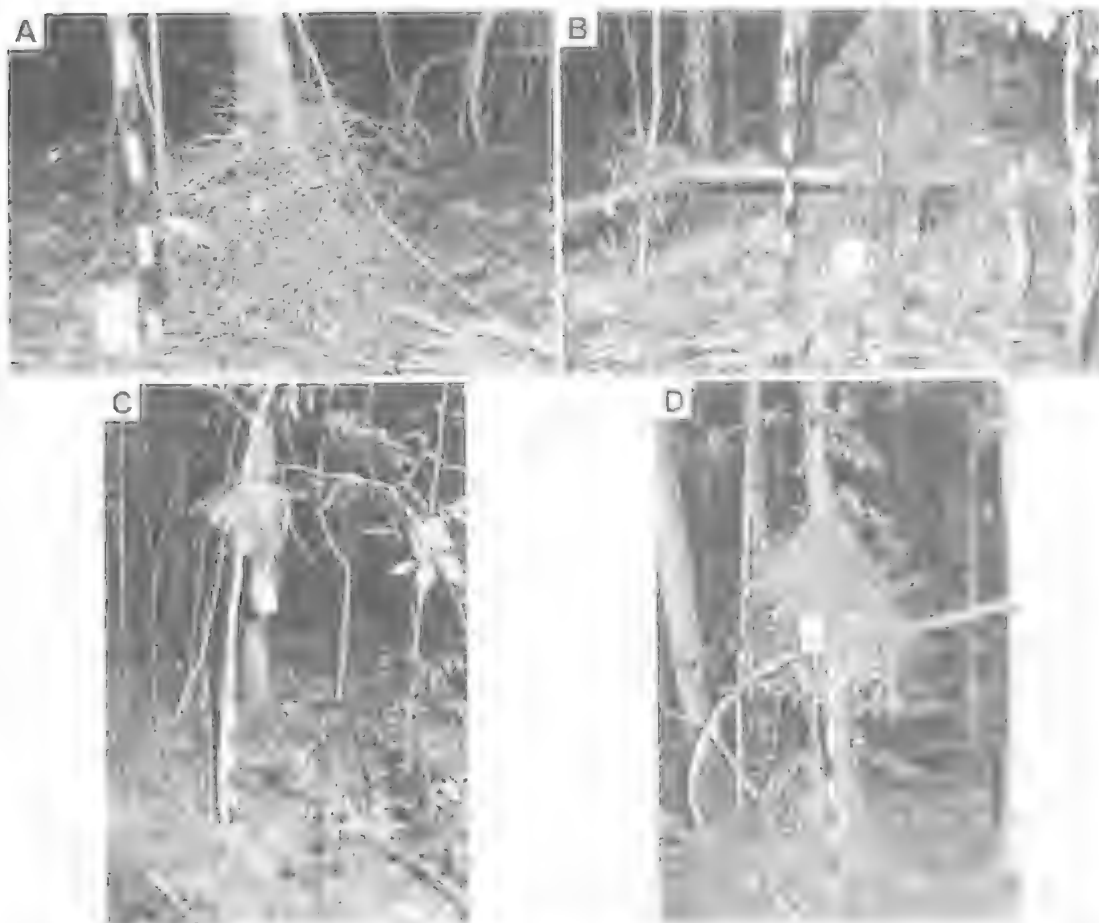


FIG 8. Shapes and sizes of subsidiary bower structures. A, this terrestrial subsidiary was 4m from the main bower structure (20a) in April 1979. When bower 20a (see Fig. 5C) was damaged by a tree fall in January 1981, this terrestrial structure formed the basis of the new bower (20b). By S82 it was a twin tower bower. B, often two arboreal subsidiaries were built close together (<1 m apart) on the same horizontal support so that they resembled a miniature twin tower bower. April 1979. C, arboreal subsidiaries were usually built where a branch forked horizontally from the trunk of a sapling/tree. April 1979. D, this arboreal subsidiary was built where a vine crossed the trunk of a small tree. April 1979. Note: This subsidiary deteriorated but could have become an arboreal bower such as the one shown in Fig. 4D.

remained so until at least S93, but by S97 it was a substantial single tower bower (its ownership unconfirmed).

Numerous bowers progressed through stages of structural development similar to the above. Of the 48 traditional bowers examined at 25 traditional sites, 20 were initially single towers, but 14 of them were changed subsequently into twin structures (Table 4 and Fig. 10A-D). The original tower of these bowers remained the larger of the two. Moreover, the main towers of 8 arboreal (2 single and 6 twin) bowers subsequently became terrestrial ones, as did the

smaller towers of 6 twin tower bowers (Table 4 and Fig. 10E,F).

Most second towers started as arboreal structures, because the bower perch was above ground. For example, bower 19a was an arboreal (128cm tall) single tower in S78, with but a handful of sticks at the far end of its bower perch (see Fig. 4D). Heavy rains in January 1981 caused the entire bower structure to slip toward the ground (bower perch from 161cm down to 60cm). In S82 it was an arboreal twin bower, the handful of sticks having been developed into the second tower, but both towers soon became



FIG. 9. Bower construction at traditional sites. A, B, bower 1a: this was little more than a handful of newly-placed sticks on a fallen horizontal sapling where it met a vertical tree in March 1979 (A) but by June 1980 (B) this had become a terrestrial tower of unfused sticks that lacked a platform. By September 1982 it was a twin tower structure. C, bower 6b: this originated in March 1980 from an arboreal subsidiary. The subsidiary formed the main tower and a second smaller tower was subsequently built at the opposite end of the bower perch about a small tree (right). This photograph was taken in August 1984, three and half years since building was commenced. D, bower 3b: this originated from a terrestrial bulky maypole-shaped subsidiary. May 1982. The subsidiary became the main tower and the handful of sticks on the right hand end of the bower perch later became the second tower/platform.

terrestrial, as dropped sticks accumulated beneath them. Similarly, bower 2a obviously started as an arboreal single tower, but sticks steadily accumulated beneath it until they reached its base and thus formed a huge single terrestrial massif (see Fig. 4E). It became even larger during subsequent seasons, but it was not until S90 that we noted the beginnings of a second tower at the opposite end of its bower perch (see Table 4).

The height of some single, and the larger of some twin, towers changed surprisingly little from season to season (Fig. 11A,B), whereas others increased in bulk as sticks were added (Figs 11C,D). Some reached the same or greater height (but not the bulk) of the larger tower (Table 4). After several seasons, some bowers deteriorated and became smaller as their towers

decomposed or collapsed (Table 4). For example, in S78 bower 27a was a 'classic' twin tower structure with well-formed platforms (Fig. 11E). By February 1990 it had deteriorated, and its bower perch collapsed (Fig. 11F). It was replaced in S92, as were bowers 19a and 22b, after the extremely dry S91. Replacement was due to general bower deterioration, including the collapse of a main tower support and/or bower perch ($n = 13$), tree fall ($n = 6$) or mammal damage ($n = 2$). The mean distance of a replacement bower from the replaced one was $14.3 \pm 12.7\text{m}$.

We did not seasonally monitor subsidiary bower structures, but in August 1984 we did note that most of those recorded in S79 were deteriorating, or had disappeared, and new ones had replaced them at other locations about the main bower on the bower site.

DISCUSSION

We discuss our results in the light of previous Golden Bowerbird bower studies, and compare them mostly with data for the closely related rainforest-dwelling bowerbirds *Scenopoeetes*, *Archboldia* and *Amblyornis* spp. (see Kusmierski et al., 1993).

BOWER SITES, THEIR LOCATION AND DISPERSION. Traditional bower sites of Golden Bowerbirds were found on flattish to gently sloping ground along ridge flanks above steeper slopes, and mostly with >70% canopy cover above. None occurred on hill or ridge crests, or in disturbed forest dominated by *Calamus* palms and creek lines and their adjacent, typically steeper, slopes were avoided. Bowers have been described as occurring in similar sites on the Atherton Tableland (Day in North, 1904; Bourke & Austin, 1947; Chisholm & Chaffer, 1956; Chaffer, 1958; Warham, 1962; Gilliard, 1969; Crome & Moore, 1989; Frith & Frith, unpubl. data).

Bowers of the closely related gardener bowerbirds in New Guinea occur mostly on ridge crests or slopes below them (Simson, 1907; Rand in Mayr & Rand, 1937; Gilliard, 1969; Schodde & McKean, 1973; Diamond, 1972, 1987, 1982a). Pruett-Jones & Pruett-Jones (1982) examined 46 active bowers of Macgregor's Bowerbird, *Amblyornis macgregoriae*, on Mt Missim, Kuper Range and found 87% on ridge crests and the remainder 3-30m below crests on relatively level areas of the slope. They concluded that the habitat variables influenced the choice of bower site by Macgregor's Bowerbird rather than the selection of the ridge itself. They found such things as degree of canopy closure (>80%), slope and width of the ridge important factors for site selection. They found 42 bowers of Macgregor's Bowerbird spaced linearly and regularly along ridge crests at an inter-bower distance of 169 ± 64 m. This figure is comparable with our Golden Bowerbird linear inter-bower measurement of 169 ± 40 m, rather than our NND of 151 ± 44 m (see RESULTS). Diamond (1987) estimated that distances between five Vogelkop Bowerbird, *Amblyornis inornatus*, bowers were several 100m. He pointed out that this was similar to the inter-bower spacing in Macgregor's Bowerbird and the 0.5km separation for eight bowers of the Golden-fronted Bowerbird, *A. flavifrons* (Diamond, 1982a).

Dispersion in Macgregor's Bowerbirds appears to be largely the result of socially interacting

males utilizing available favoured topography. Its mating system has been characterized as being intermediate between lek behaviour and territoriality, with birds maintaining even dispersion in part by 'buffering their display space against intruder pressure' (Pruett-Jones & Pruett-Jones, 1982; pers. obs.). Traditional bower sites of the Golden Bowerbird averaged one per 4.2ha and were spatially dispersed, not clumped (contra Gilliard 1969: 321), throughout suitable topography. Male Golden Bowerbirds disperse their bower sites over suitable topography and habitat in an even way, similar to Macgregor's Bowerbird and apparently as a result of a similar social system. Dispersion of the bowers of Archbold's Bowerbird is also relatively even throughout suitable habitat (Frith et al., 1996a) and not clumped into leks (contra Diamond, 1982b).

Leks have been defined as requiring the following characteristics: clumped distribution of males; the ability of females to freely choose mates; no parental care by males; and no resources of value to females available at male display sites other than sperm (Bradbury, 1981). True lek behaviour has not been demonstrated in any bowerbird species (Donaghey, 1981; Pruett-Jones & Pruett-Jones, 1982; Diamond, 1986a; Borgia, 1986; Oakes, 1992; Lenz, 1993; Frith & Frith, 1995; Frith et al., 1996a,b, this study), as this requires that males at their bowers be in visual contact (Frith & Beehler, 1998). Rainforest-dwelling Tooth-billed Bowerbirds may be the only exception, as courts on the Paluma Range showed a dispersion intermediate between an even spread and true (i.e. exclusive) clumping (true lek) over suitable habitat (Frith & Frith, 1995). It remains to be demonstrated conclusively, that 'clumping' of male Tooth-bill courts does form a lek, albeit an exploded one. It is possible the dispersion of courts was the result of males utilising the only appropriate topography available, as appears to be the case in Golden and gardener bowerbirds.

Rudimentary bower sites and structures were short-lived, built and used sporadically by one or more immature males during one, several consecutive, or non-consecutive seasons. Similar rudimentary structures have been described for Macgregor's (Pruett-Jones & Pruett-Jones, 1982), Regent (Chaffer, 1984; Lenz, 1993), Satin (Vellenga, 1970; Donaghey, 1981; Borgia, 1986), Archbold's (Frith et al., 1996a), Great and Spotted (Frith & Frith, unpubl. data) Bowerbirds. Rudimentary bowers of *Amblyornis* spp., probably built by younger males, are often found at lower

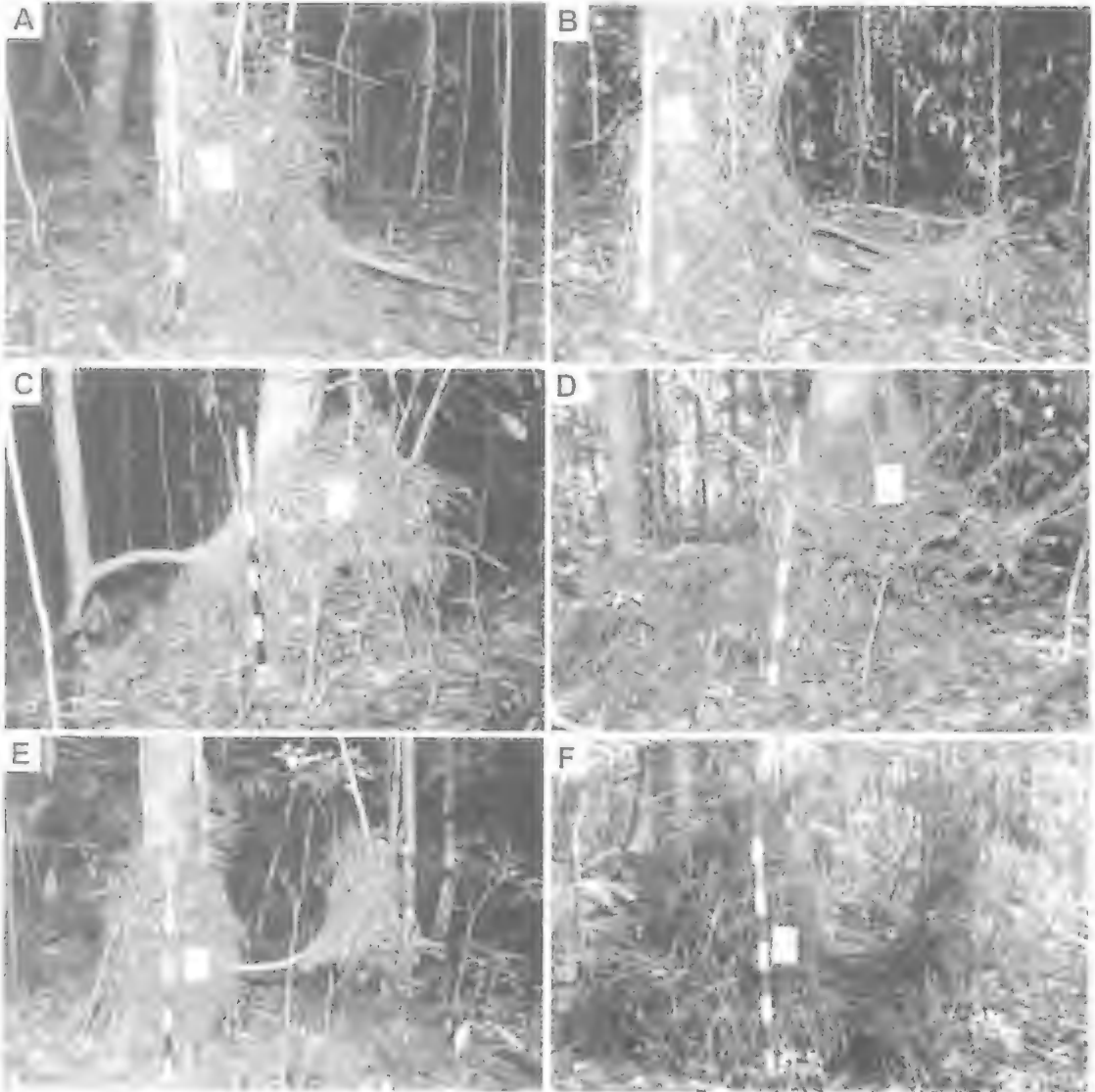


FIG. 10. Seasonal changes to the towers of traditional bowers. A, B, bower 34a: this was a single tower bower in April 1979 (A) but by August 1984 (B) was a twin tower structure with its main tower then 180cm tall. C, D, bower 8a: this was a single tower bower in April 1979 (C) but by February 1990 (D) was a massive twin tower structure. E, F, bower 33a: this had one of its towers small and arboreal in April 1979 (E) but by August 1984 (F) both towers were terrestrial. Note: sticks of both towers were fused beneath the bower perch.

altitudes than the traditional bower structures presumably built/owned by older males (Diamond, 1986b, 1987 and references therein).

BOWER CHARACTERISTICS. Previously the bower of the Golden Bowerbird was thought to consist only, or typically, of two towers, and with one tower usually taller than the other (De Vis in Meston, 1889; Campbell, 1900; Meston in Mathews, 1926; Cooper & Forshaw, 1977;

Johnsgard, 1994; Schodde & Tideman, 1988; Donaghey, 1996). Our findings clearly show that bowers may be of one or two towers, and that their size and shape varies greatly (Table 4). In the case of traditional bowers, the structure of a single tower averaged some 20% larger than the average size of the larger tower of a twin structure. Moreover, its mean volume was similar to that of the mean combined volume of both towers of a twin

structure. Thus, single tower bower structures may demonstrate to conspecifics that the owning male has expended similar effort in building as have males constructing a twin tower bower.

Golden Bowerbird bower perches or their 'avenues' did not exhibit a pattern of compass orientation, as is the case in several true avenue bower builders in which the avenue is aligned on or about the north-south axis (see Frith et al., 1996b). This orientation apparently enhances illumination of bower decorations and the displaying males (Marshall, 1954; Frith et al., 1996b). We did find that almost twice as many bower perches of Golden Bowerbirds were orientated to within 45° of the north-south axis, or the north-south half of the compass, than were to within 45° of east-west, or the east-west half of the compass rose. Thus, given bower perches were at right angles to the avenue between twin tower bowers, the orientation of the 'avenue' was predominantly within the east-west half of the compass. We can offer no explanation for these observations at present.

Sticks of Golden Bowerbird bowers, other than recently placed ones, become firmly fused together by the action of a fungus (Mathews, 1926; Chisholm & Chaffer 1956; Warham, 1962; Frith 1989, this study) ubiquitous to the lower forest sub-canopy (Jackson in Chisholm, 1957). Certainly, birds do not glue sticks together with saliva, or anything else, as suggested by some authors (e.g. Schodde, 1976; Diamond, 1987; Schodde & Tidemann, 1988).

Our long-term observations of rudimentary and traditional bowers indicated that most bower sticks are placed in a somewhat dishevelled fashion, resulting in great variation in bower shape and bulk. Their untidy construction suggests gross bower features are of less significance to females than is the discrete part of them modified into a 'platform(s)' for the exclusive placement of decorations. While traditional single or twin towered bowers varied greatly, they all had a conspicuous platform of more carefully and better aligned finer sticks to one end, or both ends, of the display perch. In view of bower structure quality in other bowerbirds (Borgia 1985, 1995; Borgia et al., 1985), it is possible that the quantity and quality of sticks/construction incorporated into the bower platform(s) is of significance to mate selection by females. Older and more dominant male Satin Bowerbirds that retain more bower decorations mate more often (Borgia 1985, 1995; Borgia et al., 1985). This suggests that bower platform(s)

and their decoration represent characters of significance in female Golden Bowerbird mate selection. For a discussion and review of the significance of bower decoration, see Frith & Frith (2000a).

Broadbent (in Mathews, 1926) noted that larger main bowers of Golden Bowerbirds were surrounded by several 'gunyahs', dwarf-like hut structures, that we term subsidiary structures. Bulmer (in Gilliard, 1969: 305-6) reported similar subsidiary structures in Macgregor's Bowerbird. Of 151 subsidiary bower structures we recorded, 76% were arboreal and the remainder may have been originally arboreal. Often two such subsidiary structures, placed at an interval along the same length of horizontal branch, resembled a diminutive bower (Fig. 8B). Four such subsidiary structures had sticks added to them to subsequently replace, and become, the main bower.

It is possible that some subsidiary structures, around the main bower, at a traditional site are 'the casual products of social activity in non-breeding periods' (Chisholm & Chaffer, 1956: 13). Sharp (in Chisholm, 1929) claimed that only (adult) male Golden Bowerbirds attended large bowers and that subsidiary structures are built by females, but this is erroneous and may be a result of misidentification of female-plumaged, immature, males at such structures. It is our experience that these are initiated by the traditional bower owner, as a result of a bird leaving sticks at a favoured singing/perching perch(es). Adult males actively decorated only their single main bower structure, but would occasionally temporarily leave the odd decoration on a subsidiary one.

BOWER SITE CONSTANCY, BOWER AGE, BOWER BUILDING AND STRUCTURAL CHANGES. Most (84%) Golden Bowerbird bower sites were attended over 20 consecutive courtship seasons, predominantly by adult males (Table 4 and Frith & Frith, unpubl. data). Bower sites of Satins have persisted for up to 30 years (Vellenga, 1980), Spotted for 13 years (Frith & Frith, unpubl. data), Greats for 13 years (Frith et al., 1996b), Tooth-bills for 20 years (Frith & Frith, 1995; unpubl. data) and Archbold's Bowerbird for 11 years (Frith et al., 1996a).

The mean minimum active 'life' of a Golden Bowerbird traditional bower structure was 9.6 ± 6.3 ($n = 48$) years. The main causes of structure replacement were deterioration due to age, the collapse of a tower(s) resulting from loss of supporting plants, or a falling tree directly



FIG. 11. Seasonal changes to the shape of traditional twin tower bowers. A,B, bower 3a: this changed little in size and shape between April 1979 (A) and February 1990 (B) despite the collapse of the dead trunk that was supporting the main tower. C,D, bower 22b: this changed little in overall shape from between September 1979 (C) and February 1990 (D), save becoming more massive. E,F, bower 27a: this changed dramatically in size and shape between April 1979 (E) and February 1990 (F), becoming smaller as its towers decomposed and collapsed.

damaging the bower and/or opening the canopy above the bower site. The larger traditional stick maypole bowers of *Amblyornis* spp. also persist year to year (Pruett-Jones & Pruett-Jones, 1982, 1983; pers. obs.). Conversely, bowers of the avenue-building *Chlamydera*, *Sericulus* and *Ptilonorhynchus* bowerbirds are refurbished and reused, or are replaced annually at the traditional

bower site, but not always at the same location (Vellenga, 1980; Donaghey, 1981; Lenz, 1993, and references therein). Male Tooth-billed Bowerbirds annually re-create their court, more often than not in exactly the same place (Frith & Frith, 1994, 1995). Archbold's Bowerbirds typically renovate bowers at the beginning of each season (Frith et al., 1996a).

Earlier descriptions of Golden Bowerbird bower building were simplistic. For example, Day (in North, 1904) and Marshall (1954) noted that when a bower is first built it consists of sticks and twigs placed around two small trees growing about a metre apart. Each season sticks are added to the structures around two saplings until they are joined to form a U-shaped structure. In the centre, near the bottom of the U, a horizontal vine, stick or root is left bare (i.e. the bower perch). Our findings clearly demonstrate, however, that males in fact started each bower structure at a point above ground, where a leaning or horizontal branch (sapling, vine, fallen branch) crosses a vertical sapling or small tree trunk. New main bower structures started as small, single, arboreal, conical or maypole-shaped structures. They typically became fully terrestrial later, when dropped/fallen sticks accumulating on the forest floor reached their bases. Some bowers remained single tower bowers while others continued to grow into twin towers taking two to three seasons for them to reach full size.

Towers of some traditional bowers changed in shape and size from one season to the next, and often incorporated more saplings as they increased in size, whereas towers of others changed little from one season to the next. Dropped sticks may accumulate beneath the bower perch to there fuse to form a solid wall or 'a sort of hedge' (cf. Chisholm & Chaffer, 1956: 11); thus reinforcing the false impression of the structure originating on the ground. That most, if not all, Golden Bowerbird bowers originated above ground is a significant finding, given that all bowerbird species were thought to begin bower construction on the ground until Borgia & Sejkora (in Kusmierski et al., 1997: 310) stated that the Vogelkop Bowerbird builds its bower 'from the top down'. Thus the 'foundation' of the Golden (and Vogelkop?) Bowerbird's bower is not the clearing/cleaning of an area of ground (contra Stresemann 1953).

Diczbalis (1968) noted that male Macgregor's Bowerbirds start to clear a space around a young sapling, plucking off its leaves, bringing moss to form a basal ring around the sapling and 'trimming the space between base of sapling and the outside ring till it is clean and level. At the same time, the bird was bringing in its beak dry sticks and arranged these with its beak into spoke like shape around the sapling' to form a tower. He noted the structure was completed within a month, but would be improved and strengthened throughout the display season. Considering the

arboreal beginnings of Golden Bowerbird bowers, clarification of bower development of the closely related *Amblyornis* species would be valuable. Were the original bowers of *Amblyornis* and *Archboldia* spp. arboreal, or has *Prionodura* 'raised' its point of initial bower construction from the terrestrial form of its ancestors?

SIGNIFICANCE OF BOWER FORM AND ADULT MALE PLUMAGE IN THE GOLDEN BOWERBIRD. The bowers, their decoration, the levels of attendance at them by males, and the plumage morphology and courtship displays of the Golden Bowerbird are of particular interest within the bowerbirds with regard to the 'transferral effect' postulated by Gilliard (1956, 1969). This theoretical effect suggests that, within several bowerbird genera, the degree of ornate/colourful plumage in adult males is inversely proportional to the complexity of their bowers. Thus, males of species developing more complex bowers, as external symbols of their dominance/fitness, have been able to replace their personal, and possibly costly (in making them conspicuous to predators), plumage ostentation with a bower structure and its decoration. The more impressive examples of this relationship occur within *Amblyornis* and the *Sericulus-Ptilonorhynchus-Chlamydera* clade. While the Golden Bowerbird is clearly most closely related to, and originated from ancestral, gardener bowerbird stock (Schodde, 1976; Sibley & Monroe, 1990; Kusmierski et al., 1993, 1997) it does not conform to the transferral effect discernible within these maypole builders. The maypole bower of the Golden has certainly lost some of the intricacies of *Amblyornis* bowers, in that it lacks a terrestrial moss base 'dish' (as in Macgregor's and Golden-fronted Bowerbirds) and its sticks do not form a 'hut' roof over a moss 'lawn' or 'court' (as in Streaked *A. subalaris* and Vogelkop Bowerbirds). Nevertheless it is a massive stick structure, with a discretely located platform(s), the construction of which is commenced above the ground. To what extent the arboreal point of initial bower construction is related to the significantly divergent adult male plumage in Golden Bowerbirds merits investigation.

Given its bower and, for present purposes, considering the Golden Bowerbird a member of *Amblyornis*, the transferral effect would lead one to predict a drab adult male plumage; at least no more colourfully ornamented than are the yellow- and orange-crested (but otherwise dully

plumaged) simple maypole-building Golden-fronted and Macgregor's Bowerbirds. How then is the, apparently contradictory, massive maypole-bower building yet brilliantly-plumaged adult male Golden Bowerbird to be interpreted? Its colourful plumage is not dorsally confined to a crest, as in gardener and Archbold's Bowerbirds, but is also extensive on the nape and tail feathers. Moreover, the entire ventral surface of the bird is brilliantly colourful. This extensive colourful pigmentation of both dorsal and ventral plumage is, among bowerbirds, more reminiscent of adult male regent bowerbirds (*Sericulus* spp.). Adult male Regent Bowerbirds perch on exposed forest canopy branches, to advertise their bower location, and subsequently descend to the bower. During this initial advertisement, and descent, their bright plumage is doubtless conspicuous to females. Thus, we concur with Schodde's (1976) suggestion that, while bower-based courtship has apparently ornamented/coloured the dorsal plumage of more terrestrially-displaying adult male bowerbirds, the morphology of adult male Golden Bowerbirds, with bright underparts, reflects its elevated bower perch. It also reflects an extensive courtship flight display (Frith & Frith, 2000a). We view the bright central crown patch and the nape patch of the adult male Golden Bowerbird as homologous to the extensive crest of the gardener (especially *Amblyornis flavifrons* and *A. macgregoriae*) and Archbold's Bowerbirds. These characters, together with the brilliant yellow long forked tail, entire underparts, and pale iris lead us to concur with Kusmierski et al. (1993) in considering the Golden a highly ornamented bowerbird (contra Møller & Cuervo, 1998).

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TABLE 4. Continuity of 51 bower structures at 25 traditional bower sites of male Golden Bowerbirds on the Paluma Range, north Queensland and structural changes over 20 consecutive seasons, from 1978-1997. * = AS = arboreal subsidiary; TS = terrestrial subsidiary; A = arboreal; T = terrestrial; NM = not measured; NC = no change; STB = single tower bower; TTB = twin tower bower; RB = rudimentary bower; ** = bowers found when under early construction.

Bower site and number	Number of seasons (=S) bower site attended	When examined	Main tower		Second tower		Status history *	Figure number
			Height (cm)	A or T *	Height (cm)	A or T *		
1a **	10 (S78-S87)	Mar 79	25	A			STB	9A
		Apr 80	NM	A			STB	
		June 80	75	T			STB	9B
		Sept 80	NM	T			STB	
		Sept 82	NM	T			TTB	
		Aug 84	110	T	48	T	TTB	
1b	10 (S88-S97)	Oct 88	NM	T			STB	
		Feb 90	141	T	13	T	TTB	
2a	20 (S78-S97)	Apr 79	205	T			STB	4E
		Aug 84	200	T			STB	
		Feb 90	198	T	10	A	STB	
		Oct 97	NM	T	15	A	TTB	
3a	14 (S78-S81, S84-S93)	Apr 79	148	T	47	T	TTB	11A
		Aug 84	NC	T	NC	T	TTB	
		Feb 90	170	T	57	T	TTB	
3b **	2 (S82-S83)	Apr 79	65	T			TS	
		May 82	133	T		A	STB	9D
		Sept 83	NM	T		A	TTB	
3c	4 (S94-S97)	Oct 95	NM	T		T	TTB	
4a	20 (S78-S97)	Apr 79	125	T	35	T	TTB	5B
		Aug 84	NC	T	NC	T	TTB	
		Feb 90	125	T	15	T	TTB	
		Oct 97	NM	T	45	T	TTB	
5a	20 (S78-S97)	Apr 79	184	T	30	T	TTB	
		Aug 84	NC	T	NC	T	TTB	
		Feb 90	140	T	20	T	TTB	

TABLE 4. *cont.*

Bower site and number	Number of seasons (=S) bower site attended	When examined	Main tower		Second tower		Status history *	Figure number
			Height (cm)	A or T *	Height (cm)	A or T *		
6a	2 (S78-S79)	Mar-79	93	T	75	T	TTB	
6b **	19 (S80-S97)	Mar-80	30	A			AS	
		Oct 80	NM	T	NM		STB	
		Sept 81	NM	T	NM	A	TTB	
		Aug 84	110	T	65	T	TTB	9C
		Feb 90	145	T	87	T	TTB	
7a	18 or 19 (S78-S95 or S96)	Apr 79	104	T	81	T	TTB	
		Aug 84	120	T	100	T	TTB	
		Feb 90	111	T	111	T	TTB	
7b	1 or 2 (S96 or S97)	Oct 97	NM	T	NM		STB	
8a	8 (S78-S85)	Apr 79	118	T			STB	10c
		Aug 84	NC	T			STB	
8b	3 (S86-S88)	Nov 86	NM	T			STB	
8a	9 (S89-S97)	Aug 89	NM	T		A	TTB	
		Feb 90	1070	T	55	T	TTB	10D
10a	20 (S78-S97)	Apr 79	122	T	83	T	TTB	5E
		Oct 85	NC	T	NC	T	TTB	
		Feb 90	114	T	88	T	TTB	
15a **	15 (S78-S92)	Apr 79	109	A			RB	
		Sept 84	NM	T			RB	
		Sept 88	NM	T	NM		STB	
		Feb 90	169	T	610	T	TTB	
15b	5(S93-S97)	Dec 93	30	T			STB	
		Oct 97	NM	T	20	T	TTB	
16a	8 (S78-S85)	Apr 79	150	T			STB	5F
		Aug 84	NC	T			STB	
16b	3 (S86-S88)	Nov 86	BM	T			STB	
17a	8 (S78-S85)	Apr 79	107	T	98	T	TTB	5D
		Aug 74	NC	T	NC	T	TTB	
17b **	12 (S86-S97)	Nov 86	NM	A			STB	
		Oct 87	NM	T			STB	
		Feb 90	168	T	121	A	TTB	
		Oct 97	NM	T	NM	T	TTB	
19a	14 (S78-S91)	Apr 79	128	A			STB	4D
		Oct 82	NM	A	NM	A	TTB	
		Aug 84	110	A	30	A	TTB	
		Nov 86	NM	T	NM	T	TTB	
		Feb 90	120	T	51	T	TTB	
19b	4 (S92-S97)	Nov 82	60	T	35	T	TTB	
		Oct 97	100	T	100	T	TTB	
20a	2 (S78-S79)	Feb 79	151	T	120	T	TTB	5C
20b **	6 (S80-S85)	Apr 79	66	T			TS	8A
		Jan 81	66	T	66		STB	
		Sept 82	NM	T	NM	T	TTB	
		Aug 84	110	T	110	T	TTB	
20c	1 (S87)	Oct 86	NM	T			RB	

TABLE 4. *cont.*

Bower site and number	Number of seasons (=S) bower site attended	When examined	Main tower		Second tower		Status history *	Figure number
			Height (cm)	A or T *	Height (cm)	A or T *		
20d	9 (S89-S97)	Jan 90	980	T			RB	
		Oct 97	125	T			STB	
21a	5 (S78-S82)	Apr 79	124	T			RB	7B
22a	1 (S78)	Apr 79	143	T			STB	4C
22b	13 (S79-S91)	Sept 79	110	T	95	T	TTB	11C
		Aug 84	170	T	130	T	TTB	
		Feb 90	174	T	95	T	TTB	11D
22c	6 (S92-S97)	Nov 92	NM	T	NM	T	TTB	
23a	9 (S78-S86)	Apr 79	128	T			STB	4B
		Aug 84	NC	T			STB	
23b	11 (S87-S97)	Oct 87	NM	T			STB	
		Oct 97	NM	T	15	A	TTB	
24a	5 (S78-S82)	Mar 79	112	T	111	T	TTB	
24b	6 (S83-S88)	Aug 84	125	T			STB	
24c	9 (S89-S97)	Feb 90	106	T	69	T	TTB	
26a	20 (S78-S97)	Sept 79	95	T	45	T	TTB	
		Aug 84	125	T	80	T	TTB	
		Feb 90	102	T	61	T	TTB	
27a	14 (S78-S91)	Apr 79	173	T	136	T	TTB	11E
		Aug 84	120	T	145	T	TTB	
		Feb 90	70	T	156	T	TTB	
27b	4 or 5 (S92-S95 or S96)	Nov 92	60	T			RB	
29a	5 (S78-S82)	Aug 79	120	T	30	T	TTB	
29b	15 (S83-S97)	Aug 84	140	T	35	A	TTB	5A
		Feb 90	140	T	101	A	TTB	
33a	20 (S78-S97)	Apr 79	130	T	128	A	TTB	10E
		Aug 84	160	T	140	T	TTB	10F
		Feb 90	141	T	155	T	TTB	
34a	16 (S78-S93)	Apr 79	100	T			STB	10A
		Aug 84	180	T	145	T	TTB	10B
		Feb 90	190	T	55	T	TTB	
34b	4 (S94-S97)	Oct 95	100	A	45	A	TTB	6B
45a	1 (S78)	Dec 79	NM	T		T	TTB	
45b **	10 (S79-S88)	Dec 79	50	A			AS	
		Nov 80	NM	A			STB	
		Oct 81	NM	T			STB	
45c **	7 or 8 (S89-S95 or S96)	Aug 84	120	T			STB	
		Oct 89	125	A			STB	
		Sept 90	160	T	80	A	TTB	
		Nov 92	NM	T	NM	T	TTB	
		Oct 97	NM	T	NM	T	TTB	
47a	6 (S78-S83)	June 80	100	T	95	T	TTB	
47b **	2 (S84-S85)	June 80	38	A			AS	
		Nov 84	165	T			STB	
47c	12 (S86-S97)	Nov 86	NM	T			STB	

ATTENDANCE LEVELS AND BEHAVIOUR AT BOWERS BY MALE GOLDEN
BOWERBIRDS, *PRIONODURA NEWTONIANA* (PTILONORHYNCHIDAE)

CLIFFORD B. FRITH AND DAWN W. FRITH

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Attendance levels, bower maintenance, and behaviour of male Golden Bowerbirds *Prionodura newtoniana* at their bower sites were studied over the display seasons of 1982 and 1983 in 50ha of upland rainforest. The display season typically started in late August/early September and terminated in December/January when wet season rains commenced, but its length varied year to year apparently in response to climate and/or food availability. During season 1982 males spent an average of 36% of daylight at their bowers; at a mean of 2.7 visits per hour, and each visit averaging 8mins. During season 1983, males spent longer at bowers (mean = 63%); at a mean of 3.4 visits per hour, and each visit averaging 11mins. Lower attendance in 1982 involved all males during each month and different times of the day, and was attributed to excessively dry conditions, bower activity ceased by early December. Males spent on average 6% of their time at bower sites giving advertisement song, 8% other calls, 4% maintaining bowers, 2% displacement chasing and displaying, and the remaining 80% perched silently above their bower. Vocalisations were given from habitually-used, mostly horizontal (99%), perches averaging 9.3m from the bower perch and 5.6m above ground. Advertisement song consisted of a prolonged, pulsating *rattle* repeated an average of nine times, with each series averaging 33secs. Other calls included *squeals*, *screeches*, *wolf-whistles*, *scolds*, frog- and cicada-like notes, given as single notes or as a medley with fine vocal avian mimicry of at least 22 model species. Most (95%) bower decorations were collected away from the bower site; having been harvested, or stolen from a neighbouring rival's bower. Others were retrieved from a 'store' near the bower, where they had been left previously. Intruding rival bower-owners managed to steal a decoration on 83% of their visits, obviously being most successful (100%) in the owner's absence. Of 144 displacement chases of birds from a bower/bower site, 76% were directed at conspecifics and 24% at other birds (at least seven spp.). Males instantly displaced and chased off conspecific visitors (79%), mostly from the bower perch. Males were seen to display to a female-plumaged individual 26 times, 20 times being before/after displacement chases. Three display elements were performed by males at bower sites: *Bow*, *Head nod and Shake*, and *Flight/hover*. A total of 146 displays consisted of one (n = 78), or a combination of (n = 68), these elements, and an element was often repeated more than once during a display; there being no apparent sequence of elements. Copulation was not witnessed. □ *Golden Bowerbird, Prionodura newtoniana, Ptilonorhynchidae, bower attendance, time budgets, behaviour, vocalisations.*

Clifford B. Frith and Dawn W. Frith, Honorary Research Fellows of the Queensland Museum, 'Prionodura', P.O. Box 581, Malanda 4885, Australia; 17 September 1999.

Until recently the Golden Bowerbird *Prionodura newtoniana* remained one of the least studied of bowerbirds. The first quantitative studies of its nesting biology, dispersion and constancy of bower sites, variation and seasonal changes in bower structures, home ranges and associated sociobiology and ecology have only recently appeared (Frith & Frith, 1998, 2000a, 2000b). Male attendance levels at bowers have been examined in other bowerbird species (Veselovsky, 1978; Donaghey, 1981; Pruett-Jones & Pruett-Jones, 1982, 1985; Frith & Frith, 1994; Lenz, 1993), but until this study no such data were available for Golden Bowerbirds. Previous

contributions provide qualitative casual observations of male bower attendance and behaviour, but no quantitative data (Bourke & Austin, 1947; Marshall, 1954; Chisholm & Chaffer, 1956; Warham, 1962; Chaffer, 1984).

The display season and male attendance of the Golden Bowerbird starts in late August/early September with bower-owners giving loud, prolonged, rattle-like advertisement song above traditional bowers, adding fresh sticks, and placing decorations upon them (Frith, 1989; Frith & Frith, 2000a,b). Other bower calls include squeals, screeches, croaks, rasps and churrings (Schodde & Tideman, 1988; Frith, 1989;

Donaghey, 1996). Males also produce fine vocal avian mimicry, as do other bowerbird species (Loffredo & Borgia, 1986; Frith & Frith, 1990a,b; 1993; 1994; Frith & McGuire, 1996; Frith et al., 1996). All individually known bowerbirds regularly attending and vocalising at bowers have proved to be male (Marshall, 1954; Vellenga, 1980; Gilliard, 1969; Cooper & Forshaw, 1977; Frith & Frith, 1993).

Male Golden Bowerbirds spend most time at their bower site perched silently above and around their bowers, the remaining time being spent in calling, displaying, and maintaining and/or decorating the bower (Frith, 1989). The bower consists typically of one or two roughly conical towers of accumulated sticks constructed around one or several supporting saplings and/or small trees, a perch protruding from single towers or connecting twin tower bowers (Frith & Frith, 2000a). Where tower sticks meet the bower perch they are more skilfully placed and aligned to form a discrete 'platform' where bower decorations are exclusively placed. Frith & Frith (2000a) considered the platform(s) the most significant part of the bower structure. For further introduction, and details of structures and dispersion, see Frith & Frith (2000a).

Males display on their bower perch by bowing and nodding, with drooped wings, sometimes with a bower decoration held in the bill. They also display by flying and hovering around the immediate bower area (bower site), thus dramatically emphasising their brilliant yellow plumage (Chisholm & Chaffer, 1956; Chaffer, 1958, 1984; Schodde & Tidemann, 1988). Copulation has not been observed, and may occur on or close to the bower. Males leave their bower site to forage, bathe, collect new bower sticks and harvest, or steal, decorations. That male bowerbirds steal decorations from the bowers of rivals, with a preference for particular colours and items, has long been known (Marshall, 1954 and references therein), but has been only briefly alluded to with respect to Golden Bowerbirds (Frith, 1989). It has been described for several bowerbird species (Borgia, 1985b,c, 1986; Borgia & Gore, 1986; Pruett-Jones & Pruett-Jones, 1994; Frith & Frith 1993, 1994, 1995; Hunter & Dwyer, 1997).

In this contribution, we initially define and describe seasonality of bower attendance over the first three display seasons of our study (1978-80) in relation to rainfall, temperature and fruit and insect food availability. However, most data

presented here deal with bower site attendance levels of males over two display seasons (1982-83), diurnal, monthly and seasonal variations in these, and behaviour and vocalisations at the bower. We discuss these results in the context of knowledge of this and other bowerbirds.

METHODS

STUDY AREA AND CLIMATE. The main study area comprised 50ha of upland tropical rainforest, at about 875m asl, on the Paluma Range (19°00'S, 146°10'E), northeastern Queensland, 7km from Paluma Township and 80km north of Townsville. This area, measuring 1 × 0.5km, was permanently gridded with metal stakes (see Frith & Frith, 2000a; fig. 2). The rainforest has been classified as simple notophyll vine forest (Tracey, 1982).

Annual rainfall and temperature show marked seasonality on the Paluma Range (Frith, 1984; Frith & Frith, 1985, 1994; D. Frith & C. Frith, 1990). The dry season extends from April-November, with June-August the driest and coldest months. Rainfall and temperatures increase during September-October and decrease during April-May. The hotter wet season is from December-March, with most rain falling during January-March.

DEFINITIONS. Bower site describes the location of a traditional bower; regularly attended, maintained and decorated throughout each season by the traditional adult male owner (Frith & Frith, 2000a). A traditional bower owner was an individually-marked (colour-banded), bower-attending, bird known to have attend a particular bower during at least one previous season(s). Male attendance refers to known individual males perching, calling, displaying at or maintaining their own bower. Thus a male visiting the bower of another to steal a decoration was not attending it. As we could see only the male bower-owner during most displays we refer to them as 'displays', as distinct from 'courtship displays' (i.e. display directed at a conspecific). We use 'regularly attended' to imply full-time seasonal attendance by traditional owners at traditional bower sites, and write about males unless stated otherwise. To 'harvest' a bower decoration was to obtain it from a plant or the forest floor, as distinct from stealing it from the bower of a rival male. We refer to a display season by the year in which it started (S78, S79 etc).

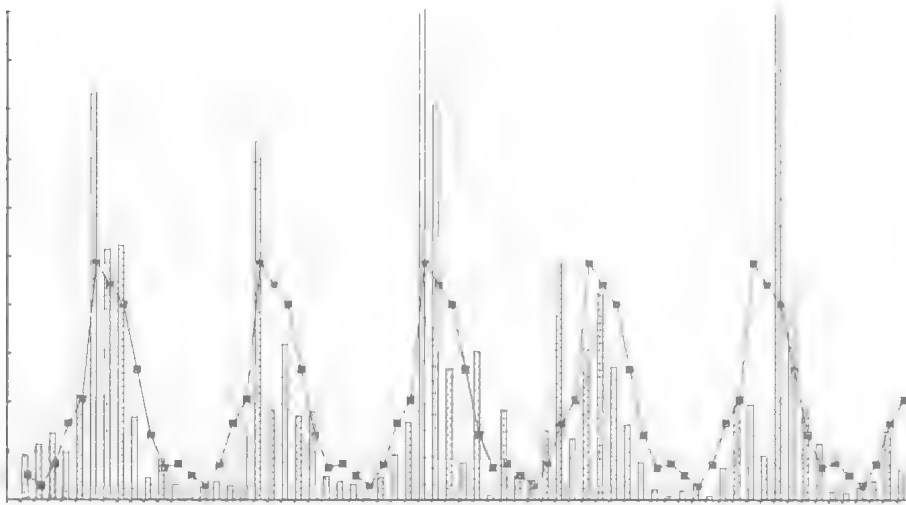


FIG. 1. Monthly rainfall (= columns) from August 1978-December 1983, incorporating five display seasons (S78-S83), and monthly averages for 1978-1990 (= ■) on the Paluma Range, north Queensland.

ANNUAL SEASONALITY OF BOWER ATTENDANCE BY MALES. Seasonality of bower attendance was assessed during S78-S81 by (a) estimating numbers of bower decorations on bowers at our visits (see Frith & Frith, 2000a,b) and subjectively categorising them as being poorly (<10 decorations), moderately (10-20) or well (>20) decorated; (b) noting how many times we heard advertisement songs at traditional bower sites during 280h of transect foraging walks from August 1979 to February 1981; and (c) collecting defaecated seeds on black mesh catchment traps suspended beneath favoured perches above or adjacent to, up to ten, bowers at regular intervals during December 1978-May 1979 and September 1979-February 1981.

Seasonality of bower attendance during S78-S81 was examined in relation to rainfall (Fig. 1), temperature, relative fruit crop and insect numbers (Fig. 2). We collected tree fruiting phenology data from 602 trees during September 1978-April 1979, and thereafter about 500 of these trees were examined at six- (July 1979-August 1980) or eight- (November 1980-February 1981) weekly intervals (Frith & Frith 1985, 1994). Diurnal insect populations were monitored each month from August 1978-April 1979, and July 1979-February 1981, using Malaise traps (Frith & Frith, 1985). We present here the mean diurnal number of all insects trapped per month, and for Coleoptera separately because 80% of any animals remains

found in faecal samples during August 1978-February 1981 were coleopteran (Frith & Frith, unpubl. data).

MALE BOWER ATTENDANCE LEVELS. Male bower attendance levels were monitored during the peak display period of 7 September-15 November 1982. Season 82 was exceptionally dry and bower attendance decreased considerably by early November. We therefore repeated observations the following season, during 3 November-5 December, when rainfall was only just below average, and bowers were regularly attended. Observations over two seasons provided comparative data on seasonal, monthly and diurnal variations.

Six adjacent bowers were monitored during both seasons (bowers 1, 2, 3, 4, 19 and 20; see Frith & Frith, 2000a: fig. 2). We established cryptic canvas hides six metres from each bower two weeks before starting observations. Each observation lasted six uninterrupted hours, during 0600-1200 or 1200-1800h, over peak seasonal activity. Each cycle of observations consisted of two (at 0600-1200h and at 1200-1800h) periods at each of the six bowers (thus 12×6 h observations). When a cycle was completed we repeated it. Observation periods at three sets of two adjacent bowers (bowers 1 and 3 at 260m apart; 2 and 4 at 210m apart; 19 and 20 at 130m apart) were made simultaneously by us, DWF in one hide and CBF in another. During S82 we made 150, 147 and 72h of direct observation

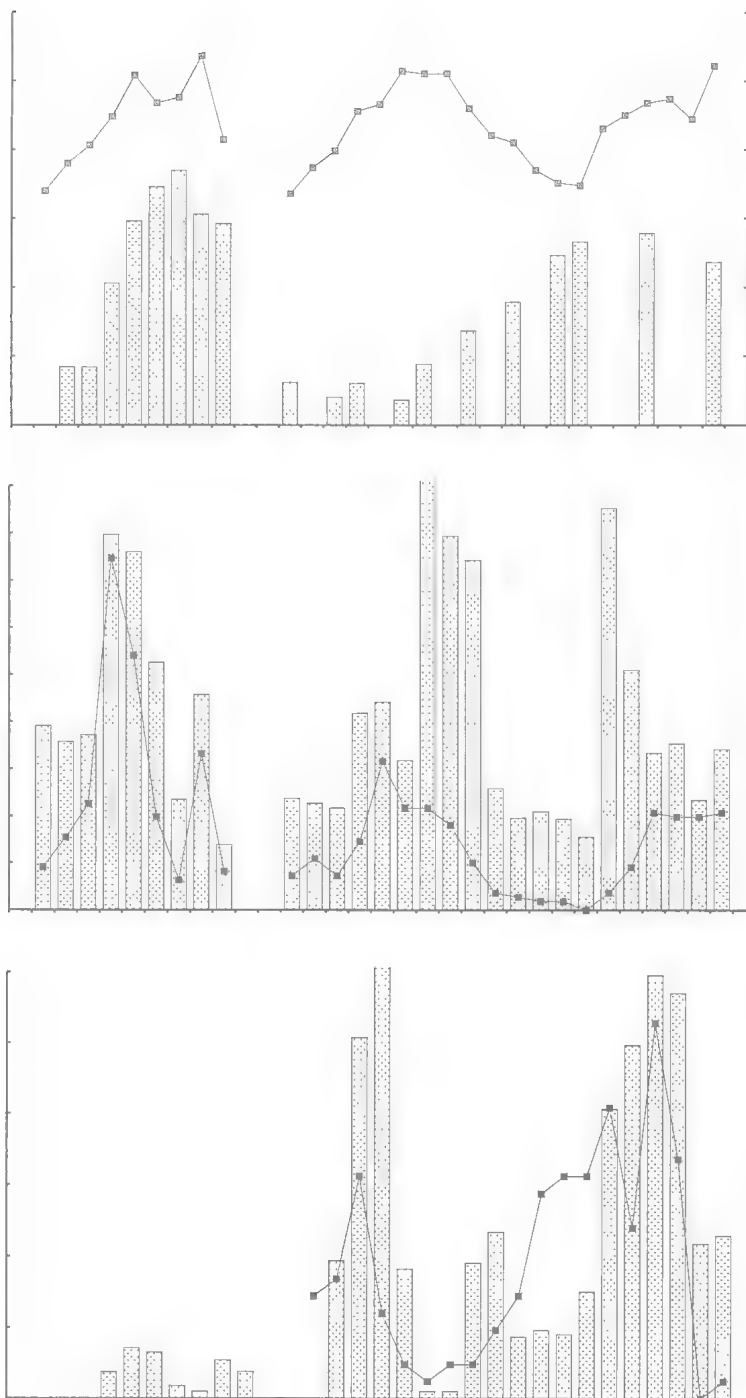


FIG. 2. A, mean monthly temperatures (= ■) and percentages of trees (= columns) sampled monthly that were in fruit. B, mean monthly numbers of all diurnal insects (= columns) and of only Coleoptera (= ■) sampled by Malaise traps. C, mean monthly numbers of defaecated seeds (= columns) collected beneath Golden Bowerbird singing perches and the number of advertisement songs (= ■) heard during track transect walks (see Methods), from August 1978-February 1981 and incorporating three display seasons (S78-S80), on the Paluma Range, N Queensland.

TABLE 1. Bower site attendance levels by individual male Golden Bowerbirds during the display seasons of 1982 (September, October and November) and 1983 (November). * = minimum number for males at bowers 2, 4, 19 and 20 who may have been at that site pre-S78; ** = immature plumage in season 82, adult plumage in season 83; *** = a different adult male regularly attended this bower site during the first two September watches; **** = a different adult male each season; see Methods.

Season	Bower site number	Number of seasons owned *	Hours and (numbers) of observations	Absence		Presence	
				Mean mins per absence	% of total time absent	Mean mins per presence	% of total time present
1982	1	5	46 (8)	12.1	67.9	5.9	32.1
	2	5	60 (10)	13.8	67.1	6.9	32.9
	3**	1	60 (10)	16.2	66.4	8.6	33.6
	4***	5	60 (10)	11.6	53.0	10.4	47.0
	19****	5	66 (12)	13.0	63.5	7.6	36.5
	20	5	63 (11)	17.3	66.9	9.1	33.1
Total/Mean/%			357 (61)	13.9	64.0	8.0	36.0
1983	1	6	12 (2)	7.8	47.5	8.2	52.5
	2	6	24 (4)	5.5	38.8	8.8	61.2
	3**	2	12 (2)	7.8	32.6	16.7	67.4
	4	6	18 (3)	5.2	35.0	9.6	65.0
	19***	1	18 (4)	9.6	38.8	14.2	61.2
	20	6	18 (4)	6.3	31.4	13.5	68.6
Total/Mean/%			102 (19)	6.6	37.0	11.0	63.0

during September, October and November, respectively. Fieldwork terminated in November due to extremely dry conditions resulting in males irregularly attending bowers. During S83 we made 90h of direct observation during November, until heavy rains hampered fieldwork. The last 12h observation cycle in November had to be postponed until 5 December, but December data are combined with November results herein. Fieldwork then ceased because continuing torrential rains resulted in males irregularly attending bowers.

To analyse diurnal variation we subdivided the totals for male attendance levels into four periods (0600-0900, 0900-1200, 1200-1500, 1500-1800h). This made data directly comparable with a similar study of Tooth-billed Bowerbirds *Scenopoetes dentirostris* (see Frith & Frith, 1994). We used the same periods to analyse vocalisation frequencies (see below).

Determining actual time a bower-owning male spent at his bower site was often difficult. Most times we saw an absent male return by flying to one of his favoured perches, or onto his bower perch. However, sometimes the first indication of his renewed presence was when he called. If he remained out of sight but continued to call we assumed he was present, especially if later he flew to another perch, to the bower, or away from his bower site. If we did not re-sight or hear him

we considered his time present to be ended at his last recorded call, even though he may have subsequently remained above the bower for some (limited, in our experience) time. We usually saw the male fly off, but sometimes he would fly unseen higher into the canopy and we were unsure if he had left, unless he gave progressively distant vocalisations as departing. Thus, times presented in Tables 1-3 for males spent at their bower sites are minimums. Having said that, the times we recorded each of the six males at their bower sites were similar each season. This suggests that any discrepancy between the time we recorded present and the actual time involved may be minimal. Single call notes (see below), occasionally heard some distance (>30-40m) from bower sites during a male's apparent absence, were discounted as indicative of his presence, as we could not confirm they were in fact given by the bower owner.

BOWER OWNERSHIP. Males were mist-netted at or near bowers and marked with a metal Australian Bird and Bat Banding Scheme band and a unique two colour band combination (= marked), and released at the capture location. Banded males included not only the owners of the six bowers under intensive observation, but also males intruding from adjacent bowers.

Males attending four of the six bowers in S82 had regularly attended their respective bowers as

TABLE 2. Monthly bower attendance by male Golden Bowerbirds during September, October and November of the display season of 1982.

Months	Bower site number	Hours and (numbers) of observations	Absence		Presence	
			Mean mins per absence	% of total time absent	Mean mins per presence	% of total time present
September	1	12 (2)	13.6	75.3	4.6	24.7
	2	24 (4)	18.6	72.5	7.2	27.5
	3	24 (4)	18.3	67.2	9.6	32.8
	4	24 (4)	15.6	48.8	16.4	51.2
	19	27 (5)	14.7	60.0	9.5	40.0
	20	27 (5)	16.9	57.2	13.6	42.8
Total/Mean/%		138 (24)	16.4	62.0	10.3	38.0
October	1	24 (4)	11.2	62.0	7.0	38.0
	2	24 (4)	11.4	62.6	6.8	37.4
	3	24 (4)	13.4	61.5	8.5	38.5
	4	24 (4)	10.0	54.6	8.5	45.4
	19	27 (5)	10.4	63.1	6.4	36.9
	20	24 (4)	16.1	70.2	7.0	29.8
Total/Mean/%		147 (25)	11.8	62.0	7.3	37.6
November	1	12 (2)	12.7	72.2	5.0	27.8
	2	12 (2)	11.8	65.3	6.4	34.7
	3	12 (2)	18.5	74.4	6.8	25.6
	4	12 (2)	10.5	58.1	7.4	41.9
	19	12 (2)	17.9	72.1	7.2	27.9
	20	12 (2)	21.1	82.2	4.9	17.8
Total/Mean/%		72 (12)	14.8	71.0	6.3	29.0

adult-plumaged individuals since at least S78. In S83 three of them (at bowers 2, 4 and 20) remained in attendance, but the male at bower 19 had been replaced by another male we first caught (at bower 19) in adult plumage in May 1982. The male attending bower 1 in S82 was first caught as an immature in March 1979, when he had just taken the site over and was building a new bower there. He acquired adult-plumaged in S80. The male attending bower 3 was still immature (female-plumaged) during the first season (S82) of this study. We first banded him in March 1979, at a point 140m from bower site 3. He attained adult-plumage during the second season (S83) of this study.

MALE BEHAVIOUR AT BOWERS. Male behaviour at bowers was categorised as: periods of advertisement song, or other calls (including single notes and medleys); bower maintenance; displacement chases; displays; and silence. Advertisement song and other calls were given from favoured perches above or within 15m of the bower, and were timed and totalled separately as they involved no other behaviour. Single calls were too brief (mostly <2secs) to time

meaningfully, and so we estimated their totals by allowing 2secs for each. Calls given during bower maintenance, displacement chases and display periods were, however, included in time periods totalled for those activities. The number, behaviour and vocalisations of female-plumaged and adult male visitors/intruders to bowers were monitored and their presences timed. Numbers of decoration thefts by rival bower-owners were recorded. Numbers, distances from bowers, and heights of habitually-used perches were noted. The length of time favoured perches were used at bower sites 2, 4 and 19 during S82 was recorded.

Bower maintenance periods included time a male was on the bower perch and adding a decoration or a stick to it, or adjusting and/or tidying. Most visits to the bower perch were solely for maintenance, but some were exclusively to display. Sometimes a male displayed on the bower perch before starting maintenance. In the latter case each behaviour was timed separately. Similarly, when a display was instantly followed by a displacement chase both periods of behaviour were treated separately even when directed at the same visitor/intruder.

TABLE 3. Variation in diurnal bower attendance levels of male Golden Bowerbirds during the display seasons of 1982 and 1983.

Season/time	Month	Hours and (number) of observations	Absence		Presence	
			Mean mins per absence	% of total time absent	Mean mins per presence	% of total time present
1982 0600-0900	September	33 (11)	9.8	57.3	7.4	42.7
	October	36 (12)	7.4	51.6	7.0	48.4
	November	18 (6)	9.0	62.3	5.6	37.7
	Total/Mean/%	87 (29)	8.6	56.0	6.8	44.0
0900-1200	September	39 (13)	11.5	49.5	11.7	50.5
	October	39 (13)	12.3	59.3	8.7	40.7
	November	18 (6)	13.8	65.0	7.9	35.0
	Total/Mean/%	96 (32)	12.3	56.4	9.7	43.6
1200-1500	September	33 (11)	24.9	69.2	12.4	30.8
	October	36 (12)	15.5	71.8	6.4	28.2
	November	18 (6)	21.7	82.4	5.1	17.6
	Total/Mean/%	87 (29)	19.4	73.0	7.8	27.0
1500-1800	September	33 (11)	29.1	74.9	10.6	25.1
	October	36 (12)	12.4	67.1	6.4	32.9
	November	18 (6)	16.1	73.1	6.2	26.9
	Total/Mean/%	87 (29)	17.2	71.3	7.3	28.7
1983 0600-0900	November	30 (10)	5.5	34.2	10.4	65.8
0900-1200	November	30 (10)	6.2	37.2	10.2	62.8
1200-1500	November	25 (9)	8.4	44.3	10.6	55.7
1500-1800	November	17 (6)	6.1	31.7	12.5	68.3

Each period of display included one to several display elements. A display element consisted of any one of the three distinct displays performed by male Golden Bowerbirds.

Chi-squared tests and Student's two-tailed *t*-tests were used for statistical comparisons. Percentage data were normalised by applying arcsin transformation. Means are given as \pm one standard deviation. In some instances we also present standard error, to facilitate comparisons with data presented by other bowerbird studies.

RESULTS

ANNUAL SEASONALITY OF BOWER ATTENDANCE BY MALES. Regular seasonal attendance of traditional sites and bowers, by their traditional owners, typically started on the Paluma Range in late August/early September. The commencement, length, and termination, of a display season varied from year to year, primarily in response to climate and/or fruit phenology, as illustrated by results of the first three seasons of our study (August 1978 to February 1981).

We recorded the seasonally first bower advertisement songs during 14-17 August at the start of S78, and by 21 August some bowers had a few decorations on them. By early September most bowers were moderately decorated, with new sticks added to them. From the second week of September until the end of December bower sites were regularly attended by their traditional owners. Rainfall was slightly above average for the time of year (Fig. 1). Temperatures increased during these months, from an average of 19°C in September to 25°C in December, and fruits and insects were plentiful (Fig. 2A, B). Bowes remained moderately decorated and attended until the end of December, but then activities decreased as rainfall increased. During the last week of January, 594mm of rain fell and bower attendance ceased. Rain continued throughout February, to 15 March, as bower decorations deteriorated. No advertisement song was heard, but limited faeces beneath favoured perches indicated some males had briefly visited bower sites (Fig. 2C). During brief dry spells, one or two fresh decorations were sometimes placed on bowers. There was then a brief period of renewed activity during late March to the first week of

May, but bowers were poorly decorated and few advertisement songs given (Fig. 2C).

Bowers were undecorated/unattended during June/July 1979, and not until 19 August did we hear the first advertisement song, marking the commencement of S79. During September 1979, rainfall was average for the month and temperatures rose, but the fruit crop was sparse and remained so throughout the display season (Figs 1, 2A). Insects, including Coleoptera, were less abundant than the previous season (Fig. 2B). October and November were exceptionally dry and hot with rainfall (64mm) well below the seasonal average (230mm). During November, fewer advertisement songs were heard and, while bowers were poorly/moderately decorated, faecal samples indicated males were attending bowers if not maintaining them (Fig. 2C). It remained dry until 25 December; by which time bower attendance had declined, few calls were given, and bower decorations dried and were not replenished. It rained heavily from the last week of December until 12 March, with little or no bower attendance. As in the previous year, there was renewed activity during March, as rains eased, that lasted until about the second week of May.

There was a notable increase in available fruit crop during winter months of 1980 (Fig. 2A). Some bower owners placed a few decorations on traditional bowers by mid-June-July, started advertisement song, and accumulating faeces indicated males were now spending time at bowers (Fig. 2). This winter attendance continued through to August, possibly because of a larger fruit crop. By August 1980 all bowers were regularly attended, despite lack of rain (Fig. 1). Temperatures increased notably in September, insects were abundant, and fruit plentiful; and bowers were well attended as indicated by faeces at them (Fig. 2). Rainfall during September-December was near seasonal average, but from 1 January was excessive, falling every day until 26th (2201mm; see Fig. 1). Bower decorations deteriorated during January and, while no advertisement song was heard, faeces indicated males occasionally visited bower sites (Fig. 2C).

We did not monitor bower activities as closely over the next three years, but seasonal trends showed a similar pattern with regard to relative rainfall. In S81 bower activities commenced during mid-August and lasted until mid-November when, due to heavy rain (468mm), they slowed and then ceased in December (Fig. 1). During

October and November of S82 it was exceptionally dry (71mm), and bower activity levels were similar to those described for S79 (see above). The display season commenced earlier the following season, much as for S80. In S83 rainfall was near the seasonal average, and bower activities persisted until the commencement of the January rains. Bower attendance levels, and behaviours and vocalisations at traditional bowers during S82 and S83, are discussed in detail below.

RELATIVE LEVELS OF BOWER ATTENDANCE BY MALES. Seasonal variation. During S82 males spent an average of 36% of total time at their bowers (Table 1), proportional differences between individuals not being significant ($\chi^2 = 4.46$, $P > 0.30$). During S83 males spent an average of 63% of total time at their bowers (Table 1), proportional differences between individuals likewise not being significant ($\chi^2 = 2.72$, $P > 0.70$). Males spent an average of 8 (SE = 0.8) and 11 (SE = 1.3) mins at bowers per presence, and absences averaged 13.9 (SE = 1.7) and 6.6 (SE = 0.7) mins during S82 and S83 respectively. Mean number of visits per hour was 2.7 (range 2.2-3.3) and 3.4 (range 2.6-4.2) during S82 and S83 respectively. Thus, all males attended their bowers for far less (27%) time, less frequently, and for less time per visit, during S82 than during S83 (Table 1).

Monthly variation. During S82 there was a significant difference between the proportion of total time individual males spent at bowers during September ($\chi^2 = 13.74$, $P < 0.02$), because not all started attending bowers at the same time and/or with the same intensity (Table 2). At bower 1, the owner was not sighted on 13 September (the first S82 observation), but two immature males were briefly (<5% of observation) seen adjusting its decorations and sticks. These young males gave occasional *screech* and *scold* notes near the bower, but no advertisement song. No birds were here on 14 September but at our next observation, on the 27th, the traditional owner was regularly attending; but at a mean duration per presence lower than other males (Table 2).

At bower 4, male attendance was notably high in September 1982 (Table 2); apparently because a male new to it, in his first year of adult plumage, was regularly attending (51% of total time) on 9 and 10 September (the first two S82 observations). We assumed he was the new owner, but during our next two observations, of 21 and 22

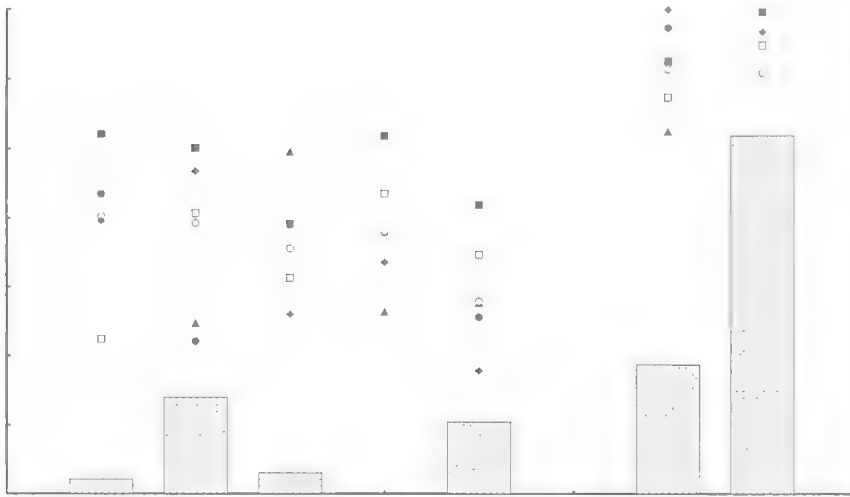


FIG. 3. The percentage of total time that each of six adult male Golden Bowerbirds spent attending their traditional bower site, during bi-weekly periods of the display seasons of 1982 (1 Sept.-15 Nov. 1982) and 1983 (Nov. 1- Dec. 15), relative to the amount of rain (column) that fell during each period. Symbols indicate the bower sites: † = 1, □ = 2, ● = 3, ■ = 4, ○ = 19, u = 20 (see Tables 1 & 2).

September, the traditional owner was in regularly attendance (50% of total time); presumably having displaced the challenger. Mean duration per presence of the challenger (28.9 mins) during the first two September observations was far greater than that of the owner (11.4 mins) during the latter two observations, and was greater than that of other individuals during September or any other month (Table 2). Male attendance at bower 4 remained relatively high throughout S82.

September S82 rainfall was average, but October was exceptionally dry and hot (only 6mm of rain, on the 4th; Fig. 1). Male bower attendance levels increased little during October over those of September, actually decreasing slightly in the middle of the month, with mean duration per presence lower (Table 2, Fig. 3). There was no significant difference between the proportion of total time individual males spent at bowers ($\chi^2 = 3.54$, $P > 0.50$). November rainfall (68mm) was well below the average (157mm), the first two weeks being particularly dry (21mm). By mid-November bowers were poorly maintained and decorated, few advertisement songs were given, and attendance levels decreased considerably (Table 2, Fig. 3). There was a significant difference between time individual males spent at bowers during November ($\chi^2 = 11.55$, $P < 0.05$), because they stopped attending bowers at different times (Table 2). Despite much more

rain in December, attendance levels did not recover, males were rarely sighted at bowers.

In S83 rainfall was near average (Fig 1). Although we made observations only during November 1983, bower attendance by all individuals was much higher (63%) than in September (38%), October (38%) or November (27%) of S82 (Tables 1, 2; Fig. 3). There was no significant difference between the proportion of total time individual males spent at bowers ($\chi^2 = 2.72$, $P > 0.70$) in November of S83.

Diurnal variation. During 0600-0900, 0900-1200, 1200-1500 and 1500-1800h of S82 males spent 44, 44, 27 and 29% of total time attending bowers respectively, differences between these proportions being significant ($\chi^2 = 7.15$, $P < 0.10$). Thus males spent much more S82 time attending bowers in mornings than afternoons, a trend apparent during September, October and November (Table 3).

During the same four diurnal periods of S83 males spent 66, 63, 56 and 68% of total time attending bowers respectively, differences between these not being significant ($\chi^2 = 1.41$, $P > 0.70$). Thus, male attendance levels at bowers were much higher in S83 than in S82, both in mornings (by 21%) and afternoons (by 34%). Mean duration per bower attendance was higher throughout the day in S83 than in S82 (Table 3).

MALE BEHAVIOUR AT BOWERS. *Habitual perches.* Males had several favoured perches

TABLE 4. Time-budgeted activities performed by individual male Golden Bowerbirds at bower sites during the display seasons of 1982 (September, October and November) and 1983 (November). * = immature male during season 82; ** = data for bower 3 excluded; see Results.

Season	Bower site number	Advertisement song			Other calls		Maintenance		
		Mean secs per song	Mean no. rattles per song	% of time present	Single	Medley	Mean secs per period	% of time present	
					% of time present	Mean secs per call			% of time present
1982	1	38	8	9.1	1.1	105	3.6	61	7.8
	2	39	7	7.1	1.5	121	3.9	70	7.1
	3 *	36	10	5.1	2.0	279	34.5	63	5.8
	4	32	9	5.4	1.0	125	4.3	48	4.9
	19	37	6	6.2	1.0	119	2.9	56	5.3
	20	35	7	6.5	1.0	107	4.8	62	4.7
	Total/Mean/%		36	8	6.4	1.2	177 (111**)	8.7 (5.4**)	59
1983	1	31	9	7.8	0.4	72	2.9	62	3.0
	2	31	9	4.4	0.2	101	4.6	45	3.5
	3 *	33	9	6.8	0.4	110	6.1	20	0.6
	4	34	10	4.9	0.3	63	2.7	43	3.6
	19	28	8	4.6	0.7	143	15.4	37	5.4
	20	27	7	4.2	0.4	106	3.6	22	0.5
	Total/Mean/%		30	9	5.1	0.4	110	5.9	40

Season	Bower site number	Displacement chases		Display		Silence	Total time present (mins)
		Mean secs per chase	% of time present	Mean secs per display	% of time present	% of time present	
1982	1	34	0.9	59	1.6	75.9	925
	2	11	0.2	44	1.5	78.7	1185
	3 *	20	0.4	60	0.9	51.3	1210
	4	50	1.0	66	1.0	82.4	1693
	19	20	0.2	64	0.8	83.6	1444
	20	34	1.1	48	1.0	80.8	1250
	Total/Mean/%		31	0.6	58	1.1	76.2
1983	1	36	1.1	76	1.3	83.5	378
	2	39	0.4	35	1.2	85.7	881
	3 *	43	1.3	60	1.0	83.8	485
	4	47	1.5	51	1.8	85.2	702
	19	31	0.6	36	0.8	72.5	665
	20	21	0.3	35	0.6	90.4	741
	Total/Mean/%		38	0.8	43	1.1	83.9

above and around their bower, on which they gave advertisement vocalisations, perched silently, or preened. Of a total 947 occasions (S82 and S83 combined) that males were recorded perched above/around the bower, 99.6% involved horizontal branches, mostly of saplings or small trees, and the remainder horizontal to gently sloping vines. Where some of these horizontal branches abutted the plant's vertical trunk (5% of perches used), males sometimes

placed sticks to form small arboreal subsidiary bower structures. During S82 males used an average of 11.7 ± 3.9 perches per observation period ($n = 61$), at a mean of 4.9 ± 2.5 m above ground, and 9.5 ± 2.6 m distant from the bower perch. During S83 these figures were 13.1 ± 4.1 m, 6.3 ± 1.9 m and 9.0 ± 2.6 m ($n = 19$) respectively. During S82 males at bowers 2, 4 and 19 spent 15% of their time perched above their bowers on perches known to be favoured ones.

Advertisement song. This consisted of a prolonged pulsating *rattle* note, typically lasting one or two seconds, that was usually repeated a number of times. It was difficult to precisely locate a bird giving this call, and others. Occasionally males gave only one *rattle*, or a series of one to three, when first arriving back at the bower and before commencing a much longer song (up to 27 *rattles* being recorded). Number of *rattles* per song averaged eight in S82 and nine in S83, each song averaging 36 and 30 secs respectively (Table 4). During some visits males only maintained bowers, and did not give advertisement song, whereas during others they gave several sets of *rattle* song (10 songs being the most during a single visit). Males gave advertisement song on 48% of 1706 bower visits in S82, and on 61% of 645 visits in S83.

Males spent 6.4 and 5.1% of time present at bowers giving advertisement song during S82 and S83 respectively (Table 4). There was no significant difference between the proportion of time individual males spent giving advertisement song at their bowers each season (82: $\chi^2 = 1.57$, $P > 0.90$; 83: $\chi^2 = 2.02$, $P > 0.80$), nor were differences between them for the two seasons significant (arcsin transformation $t_{10} = 1.39$, $P > 0.20$). Mean duration of each song period was similar during each month of S82 (Tables 5 & 6).

During September of S82, as males re-established themselves, individuals spent more time at bowers giving advertisement song (7.5%) than in October (5.9%) and November (5.0%). Mean duration of each song was also longer (Table 5). The male at bower 1 did not start bower attendance until late September, but was particularly vociferous (Table 5). The lower S82 October and November figures may have reflected extremely dry conditions; but in S83, when climate was more favourable, males still spent only 5.1% of their presence giving advertisement song (Table 4; Figs 1,2).

Males spent more of their presence at bowers giving advertisement song during mornings than afternoons during S82 and S83 (Table 6); proportional differences between diurnal periods (data for both seasons combined) being significant (arcsin transformation, $t_4 = 5.33$, $P < 0.01$). Mean duration of songs was similar at different times of day (Table 6). In S82 males performed 37, 43, 11 and 9% of songs ($n = 819$) during 0600-0900, 0900-1200, 1200-1500 and 1500-1800h respectively. In S83 they performed 46, 27, 14 and 13% of songs ($n = 391$) during the same periods respectively.

Other calls. These consisted of single calls or a continuous medley of them. Single ones were a *squeal*, *screech*, *scold-rasp*, or *wolf whistle* as follows: *squeal* was a high-pitched thin and variable note; *screech* a variable, harsher and lower, but louder and more assertive, note sometimes delivered with a rather braying-like quality; *scold-rasp* a loud and urgent note(s); and *wolf-whistle* a powerful, two note, harsh and dry, *squeal/screech* notes with the same cadence and timing as a human 'wolf-whistle'.

Single calls, such as *screech* and *wolf-whistle*, were mostly given as males approached or left their bower site, or when conspecifics were close. They were also heard some distance away from bowers, while owners were absent and presumably foraging. The *scold-rasp* was sometimes given when an inter-specific bird, larger than the bower-owner, such as a Spotted Catbird, *Ailuroedus melanotis*, or Satin Bowerbird, *Ptilonorhynchus violaceus*, came close to or onto the bower. Once when an Australian Brush-turkey, *Alectura lathami*, walked over a bower the male owner scolded it for 60secs, until it left.

During S82 and S83 males gave single calls for 1.2% and 0.4% of time present at bowers, respectively (Table 4). The proportion of single calls given was broadly similar each month of S82 (Table 5), and for different times of the day (Table 6), during both seasons.

A medley included a continuous series of single calls interspersed with frog- and cicada-like notes, a single *rattle* with a *squeal(s)* and/or vocal avian mimicry. At least 22 bird species were identified as models for mimicry performed: White-headed Pigeon, *Columba leucomela*; Red-tailed Black Cockatoo, *Calyptorhynchus banksii*; Sulphur-crested Cockatoo, *Cacatua galerita*; Australian King-Parrot, *Alisterus scapularis*; Crimson Rosella, *Platycercus elegans*; a cuckoo; Noisy Pitta, *Pitta versicolor*; Yellow-throated Scrub Wren, *Sericornis citreogularis*; Large-billed Scrubwren, *S. magnirostris*; Brown Gerygone, *Gerygone mouki*; Mountain Thornbill, *Acanthiza pusilla*; Bridled Honeyeater, *Lichenostomus frenatus*; Grey-headed Robin, *Heteromyias albispectus*; Chowchilla, *Orthonyx spaldingii*; Eastern Whipbird, *Psophodes olivaceus*; Bower's Shrike Thrush, *Colluricincla boweri*; Barred Cuckoo-shrike, *Coracina lineata*; Pied Currawong, *Strepera graculina*; Victoria's Riflebird, *Ptiloris victoriae*; Spotted Catbird; Tooth-billed Bowerbird; Satin Bowerbird and many small passerine notes we did not identify.

TABLE 5. Monthly time-budgeted activities performed by individual male Golden Bowerbirds at bower sites during September, October and November of the display season of 1982. * = immature male during season 82; ** = % of time present with data for bower 3 excluded; see Results.

Months	Bower site number	Advertisement song		Other calls			Maintenance	
		Mean secs per song	% of time present	Single	Medley		Mean secs per period	% of time present
				% of time present	Mean secs per call	% of time present		
September	1	40	16.2	0.7	58	2.2	47	10
	2	54	8.7	1.7	150	7.0	71	7.8
	3*	37	4.6	1.4	439	38.8	46	2.6
	4	31	5.9	1.1	197	6.2	50	2.5
	19	40	8.1	0.8	195	3.5	47	3.2
	20	34	7.5	0.8	80	3.1	63	3.3
Total/mean/%		38	7.5	1.1	237 (140**)	9.7 (5.8**)	54	4
October	1	38	8.4	1.2	69	3.4	66	7.7
	2	33	6.7	1.8	77	2.1	71	7.3
	3*	39	5.4	2.9	227	30.0	74	8.5
	4	35	4.7	1.2	77	2.9	50	7.3
	19	33	5.4	1.0	66	1.9	67	7.9
	20	36	4.6	1.4	138	8.0	52	5.1
Total/mean/%		36	5.9	1.6	144 (87**)	7.9 (5.0**)	28	7.4
November	1	34	4.8	1.1	139	5.8	80	6.0
	2	31	5.6	0.5	142	2.8	64	5.6
	3*	28	5.2	1.1	195	37.1	51	6.0
	4	30	5.5	0.4	79	2.6	43	5.6
	19	31	2.5	1.5	121	4.0	37	4.0
	20	36	7.0	0.3	94	3.7	87	11.3
Total/mean/%		31	5.0	0.8	154 (112**)	8.5 (5.4**)	56	6.1

Months	Bower site number	Displacement chases		Display		Silence	Total time present
		Mean secs per chase	% of time present	Mean secs per display	% of time present	% of time present	
September	1	30	0.3	23	0.4	70.2	178
	2	0	0	36	0.6	74.2	396
	3*	22	0.3	33	0.1	52.2	472
	4	66	0.9	56	0.3	83.5	737
	19	23	0.2	62	0.5	76.7	646
	20	31	0.8	49	0.8	83.8	693
Total/mean/%		37	0.5	48	0.5	76.8	3122
October	1	36	1.1	59	1.3	76.9	547
	2	9	0.2	53	1.3	80.6	539
	3*	19	0.6	75	1.4	51.2	554
	4	47	1.4	61	0.9	81.6	656
	19	38	0.2	58	1	82.6	597
	20	32	0.7	48	1.5	78.7	429
Total/mean/%		30	0.7	58	1.2	75.3	3320
November	1	29	0.7	71	3.6	78	200
	2	18	0.4	63	3.4	81.7	250
	3*	0	0.0	44	1.6	49	184
	4	31	0.5	74	2.9	82.5	302
	19	10	0.3	84	1.4	86.3	201
	20	39	4.0	0	0	73.7	128
Total/mean/%		28	0.8	67	2.4	76.4	1265

Golden Bowerbirds mimicked more than one call of a given bird species. For example, both the whistle call and alarm flock note of Crimson Rosellas, the whistled single note and the 'cheep-cheep' greeting calls of Grey-headed Robins, the whip-crack song and the 'chip-chop' calls of Eastern Whipbirds, the single 'tick' note, 'e-i-or' and 'any-higher' calls of Spotted Catbirds, and both 'chuck' and coarse rattling flight alarm calls of Tooth-billed Bowerbirds. We once witnessed mimicry of the flight wing-noise of adult male Victoria's Riflebirds.

Mimicry was sometimes opportunistic; that is to say in immediate response to the call or sighting of a model bird species. For example, a male Golden Bowerbird returned to his bower to find a Spotted Catbird perched three meters from it and then immediately mimicked a catbird call, even though the visitor was silent. Neighbouring Golden Bowerbirds often instantaneously respond to each others vocalisations, as between males at bowers 19 and 20 located 130m apart. When one male gave a song of *rattles* the neighbour would immediately do likewise.

During S82 and S83 males gave medleys for 8.7 and 5.9% of their time present at bowers, these vocalisations averaging 177 and 106secs, respectively (Table 4). The higher percentage of medleys in S82 was primarily due to the vocal efforts of the immature male at bower 3, in his first season of regular attendance. During S82 he spent 35% of his bower presence giving medleys, averaging 278secs in duration (Table 4). This percentage was high every month of S82 (Table 5). This immature gave some medleys from the bower perch, unlike adult males, (for a total of 8mins). Adult males gave medleys for an average of only 5.4% of time, at an average of 111sec duration, from favoured perches. By excluding bower 3 data, results for S82 were similar to those of S83 (see Tables 4-6). The male at bower 3 was in adult plumage in S83 and during this, his second year of regular bower attendance, gave fewer medley calls (Table 4). The new (but adult-plumaged) male at bower 19 in S83 gave a greater proportion of medleys, and for longer periods, than other males during that season (see Table 4).

During S82 males gave more afternoon medleys than morning ones, a trend reflected not just by the male at bower 3 (see above) but by other individuals (Table 6). During S83 such diurnal variation was not apparent, and males spent more of their time giving medleys during both

0600-1200 and 1200-1800h than during these periods in S82.

Of 228 and 125 medley calling periods in S82 and S83, we confirmed a conspecific (usually female-plumaged) was near/at the bower on 14% and 29% of occasions, respectively. Medley calls were sometimes given before/after displacement chases or displays (see Table 7).

Bower maintenance. Bower maintenance involved a male placing a newly collected decoration/stick on the bower, flying down to the ground below the bower perch to retrieve a fallen decoration, or flying up onto a tower to adjust/move a stick. It also included brief visits to the bower to inspect and/or to remove a leaf from the structure. Sometimes the owner flew to a nearby vertical sapling (<1m from the bower) specifically to be able to inspect his newly adjusted bower decorations/sticks; before returning to continue bower maintenance, flying off to a favoured perch, or flying directly out of the bower site.

Males flying to their bower to maintain it were usually silent (77% of 615 such visits in S82 and S83), but during 140 other visits males called briefly as they landed on their bower perch. Such calls included: a single *rattle* with one or two *squeal(s)* (n = 101), a single *rattle* with *squeals* followed by brief mimicry or *screeches* (n = 10), a single *rattle* with a *cicada* or *screech* call (n = 9), or just one *rattle*, *squeal*, mimicry or *screech* (n = 20). Most such calls (94%) occurred when males were not carrying anything. Males remained silent once decorating/maintaining bowers.

Males returning to their bower site with a decoration or stick usually went directly to the bower, to add it to the structure. Most decorations (95%) were collected by males during their absence from the bower, having harvested them or stolen them from a neighbouring bower. A few times (5%) males did not leave the bower area to collect a decoration, but merely flew to a tree (often out of our sight) to return within <30secs with a decoration. On four such occasions we confirmed the male had gone to a 'store' to retrieve a decoration. We also twice saw a male fly from his bower with a decoration to 'store' it in a tree crevice. Three times we saw a male take a decoration from his bower to place it on a favoured perch, only to subsequently collect it and return it to his bower. Unlike bower decorations, most sticks (77%) were collected near (10-20m distant) the bower. Sticks (to 30cm long) were usually collected one at a time, but a couple

TABLE 6. Variation in diurnal time-budgeted activities performed by individual male Golden Bowerbirds at bower sites during the display seasons of 1982 and 1983. * = data for bower 3 excluded; see Results.

Season/time	Month	Advertisement song		Other calls			Maintenance	
		Mean secs per song	% of time present	Single % of time present	Medley Mean secs per call	% of time present	Mean secs per period	% of time present
1982 0600-1200	September	40	10.2	0.9	129	4.9 (3.3*)	57	5.4
	October	38	7.5	1.4	106	5.0 (1.5*)	69	8.8
	November	32	6.9	0.5	171	6.2 (2.1*)	56	5.8
Total/mean/%		38	8.5	1.1	124	5.2 (2.4*)	62	6.8
1200-1800	September	30	2.5	1.4	398	18.6 (5.0*)	42	1.3
	October	30	3.4	1.8	185	12.1 (4.8*)	51	5.2
	November	28	2	1.3	142	12.3 (4.8*)	57	6.5
Total/mean/%		30	2.8	1.6	236	14.6 (4.9*)	51	4.0
1983 0600-1200	November	30	6.2	0.3	114	6.1	41	2.6
	1200-1800	November	30	3.4	0.5	104	5.7	37

Season/time	Month	Displacement chases		Display		Silence	Total time present (mins)
		Mean secs per chase	% of time present	Mean secs per display	% of time present	% of time present	
1982 0600-1200	September	39	0.7	48	0.6	77.3	2016
	October	32	0.8	61	1.3	75.2	1999
	November	37	0.6	62	2.1	77.9	785
Total/mean/%		35	0.7	58	1.1	76.6	4800
1200-1800	September	13	0.1	31	0.3	75.8	1106
	October	26	0.7	53	1.1	75.7	1321
	November	24	1	73	2.8	74.1	480
Total/mean/%		25	0.5	56	1.1	75.4	2907
1983 0600-1200	November	40	1.0	45	1.2	82.6	2316
	1200-1800	November	32	0.5	41	1.0	85.6

of times two or three sticks fused together were carried in. Most sticks were taken from the ground, but three times a male broke a dead stick off a sapling.

During S82 males visited bowers 451 times to maintain them, adding a new decoration on 222 (49%) occasions, and a stick on 47; remaining visits involving only maintenance. Of 222 decorations, 56% were beard lichen (*Usnea* sp.), 32% the creamy-white persistent flowers, or seed pods of *Melicope* (*Melicope broadbentiana*), 3% jasmine (*Jasminium kajewskii*) or orchid (*Dendrobium* sp.) flowers, and 9% unidentified. During S83 males visited their bowers 168 times to maintain them; adding a new decoration on 64 (38%), and a stick on five, occasions. Remaining visits involved only maintenance. Of 64 decorations, 36% were beard lichen, 20% *Melicope*, 22% jasmine or Brown Silky Oak (*Darlingia*

darlingiana) flowers, and 22% unseen or unidentified.

Males spent more time in bower maintenance during S82 (5.8%) than during S83 (2.8%), and for longer durations per period (Table 4). There was no significant difference between the proportion of time various individual males spent maintaining their bowers each season (82: $\chi^2 = 1.33$, $P > 0.90$; 83: $\chi^2 = 6.5$, $P > 0.20$), but differences between them for the two seasons were significant (arcsin transformation $t_{10} = 6.92$, $P < 0.001$). In September S82 most individuals spent less time maintaining bowers, particularly in the afternoon, than during October and November (Tables 5, 6).

In S82 males performed 48, 22, 13 and 17% of total maintenance visits ($n = 451$) during 0600-0900, 0900-1200, 1200-1500 and 1500-1800h, respectively. Most decorations (70% of

222) and sticks (72% of 47) were collected during the morning (0600-1200h). In S83 males performed 24, 29, 30 and 17% of total maintenance visits ($n = 164$) during the same periods, respectively. Most decorations (67% of 64) were added in the morning (0600-1200h). Of the five S83 stick collections (see above), two were in the morning and three the afternoon.

Displacement chases. When a conspecific or other bird landed on the bower perch, or one near it, bower-owners usually responded by flying at, and displacing, the visitor to chase it out of the bower site. While chasing, the bower-owner often fanned his tail and, when landing on the bower perch to displace the visitor, gave a single *rattle* with *squeal*(s). During the ensuing chase, calls also included a single *rattle* followed by *ecada* and/or other brief mimicry.

Of 95 displacement chases observed during S82, 80 were directed at conspecifics, 11 at other birds, and recipients of four were unseen. Of 49 displacement chases seen during S83, 29 were directed at conspecifics, nine at other birds, and recipients of 11 were unseen. Thus, of 144 displacement chases, 76% were directed at conspecifics and 24% at other birds. Other species included: White-throated Tree-creeper, *Cormobates leucophaeus* ($n = 1$); Bridled Honeyeater ($n = 1$); Yellow-throated Scrub-wren ($n = 2$); Grey-headed Robin ($n = 10$); Eastern Whipbird ($n = 2$); Bower's Shrike-thrush ($n = 1$); and small unidentified passerines ($n = 3$). Ten of these chases involved displacement from the bower perch and the others (e.g. Yellow-throated Scrub-wren, Eastern Whipbird, Grey-headed Robin) from within 5m of it. An Australian Brush-turkey ($n = 1$), Spotted Catbird ($n = 2$) and Satin Bowerbird ($n = 4$) perching close to and/or on the bower were not chased, but were scolded.

During S82 and S83 conspecifics were seen visiting bowers on 136 and 46 occasions, respectively. Of these 182 visitations: 103 were by female-plumaged (unmarked/sex unknown) individuals; 25 by non-bower-owning immature (female-plumaged) males (identified by bands and/or behaviour); and 54 by neighbouring (marked) bower-owners (Table 7). We usually saw only one visitor at a time, on or near a bower perch, but four times we confirmed a second visitor simultaneously in the bower area.

Female-plumaged individuals (gender unknown) were furtive as they approached a bower, usually via several perches. When they reached the bower perch they adopted a 'sleeked'

and/or 'frozen' posture and peered about, without calling or touching decorations. During 99 of 103 visits by female-plumaged visitors, the bower-owner was present at the bower site (Table 7). On 80 of these 99 visits the owner typically instantly displaced and chased off the visitor, mostly (81%) from the bower perch. After being chased away, some individuals ($n = 8$) immediately circled back to the bower perch, only to be chased off again by the owner. Consecutive displacement of the same visiting individual from a bower perch involved 2 ($n = 6$), 3 ($n = 1$) or 4 ($n = 1$) chases. Owners briefly displayed to some (18%) female-plumaged birds when they first arrived, but once the visitor reached the bower perch it was displaced and chased away. After some chases (8%) owners returned to their bower, sometimes accompanied by the same visitor, to then display (Table 7). On 19 of the 99 visits by female-plumaged birds they were not chased away; the owner displaying to ($n = 6$), or ignoring them as they perched above ($n = 8$) or on ($n = 5$) the bower perch. These visitors may have been female.

Non bower-owning immature males were seen to visit bower sites five times in the owner's absence and 20 times in the owner's presence, these visits averaging 38secs (Table 7). During an owner's absence young males spent more time (mean visit duration = 104secs) on the bower, adjusting decorations and/or sticks, than when an owner was present (mean visit duration = 24 secs). On 18 visits in the owner's presence young males were typically instantly displaced and chased off by the owner, and always so from the bower perch, sometimes giving one or two *squeal/screech* calls as they were chased. Some individuals ($n = 4$) immediately circled back to the bower perch after the chase, only to be chased again. Consecutive chases directed at the same individual involved 2 ($n = 2$), 4 ($n = 1$) and 6 ($n = 1$) chases. Twice an owner displayed and/or gave medley calls when a young male first arrived near his bower, but when the visitor reached the bower perch it was displaced and chased. After two such chases the owner returned to the bower to display briefly (Table 7). On two visits in one owner's presence, young males were not chased away, but this was because the male-owner of bower 3 was immature. He tolerated another young male on his bower for 100 and 159secs (see also below).

Male bower owners visited adjacent males' bowers 54 times, 35 being in an owner's absence and 19 in an owner's presence. On 11 of the latter visits the intruder was chased off the bower perch

TABLE 7. Conspecific visits to six Golden Bowerbird bower sites (data for S82 and S83 combined) and the bower owners reaction to them when in attendance.

		Visiting conspecifics	Female-plumaged: sex unknown	Non-bower-owning young males	Bower-owning males	Total/Mean/%
Visits to bower sites		No. to bower perch	76	22	50	148
		No. to other perches (<5m distant)	27	4	5	35
		Total number of visits	103	25	54	182
		Mean time per visit (secs)	52	38	17	36
		Bower-owner absent (No.)	4	5	35	44
		Bower-owner present (No.)	99	20	19	138
Reaction of bower owners to visitors	Displacement chases	No. from bower perch	64	18	10	92
		No. from other perches (<5m distant)	15	0	1	16
		Total number	80	18	11	109
		% of times owner present	81	90	58	79
	Displays	No. before a chase	14	2	1	17
		No. after a chase	6	2	0	8
		No. without a chase	6	0	0	6
		Total number	26	4	1	31
	Medley calls	No. before a chase	6	1	0	7
		No. after a chase	19	1	1	21
		No. before a display	6	0	0	6
		No. after a display	21	0	0	21
		No. with no chase or display	10	2	1	13

by the owner, but 4 times successfully stealing a decoration. Displacement chases twice involved body contact between adult males. One owner rapidly displaced a rival from his bower perch to grapple with him, the two tumbling toward the ground before separating. The marauder then flew off, pursued by the owner. On 8 of the 19 intrusions there was no chasing; twice the intruder flying off at the owner's return before it could steal. On 6 occasions a thief stole unmolested in the presence of the immature male owner of bower 3.

Thieves managed to steal a decoration during 83% of their visits to bowers of rival males, obviously being most successful (100%) in the owner's absence. Time spent at a rival's bower was brief (mean = 17secs). Decoration theft between adjacent bower-owners was rife. Having apparently noted a neighbouring rival male's absence, by lack of his calls, bower-owners often flew immediately in the direction of the presumably unattended bower to then immediately return with a decoration. For example, when the male at bower 19 was absent (DWF observing there), his immediate neighbour at bower 20 (CBF simultaneously observing there) would fly

to bower 19 and immediately return to his own bower with a stolen decoration.

During our second (14 September) S82 observation, the immature owner of bower 3 was challenged for the site by a male in his first year of adult plumage. Both birds were present at the site for 211 of the 360min observation. Some of this time they perched close to each other, the immature owner continuously giving medley calls with mimicry, frog-like notes and scolds (for 139mins); and the adult-plumaged challenger frog-like notes, scolds and sometimes mimicry. At other times they chased each other in prolonged tail-fanning flights about the bower, or in short flights from perch to perch while fluttering/flicking wings in agitated manner. The adult was mostly chased by the immature, but sometimes this was reversed, the immature twice displacing the adult from a perch but four times the reverse. The adult once performed *Bow* and *Head nod and shake* displays. The immature retained his site, however, and attained adult plumage the following season.

Males spent little (<1%) time present at bower sites in performing displacement chases (Tables 4-6). Displacement chases averaged 34 secs, but varied much between individuals.

Displays. Males performed three basic display elements (*Bow*, *Head nod and shake*, and *Flight/hover*) at bower sites. In the *Bow* the male lowered his bill and head rigidly downwards and erected his crown and nape feathering, thus emphasising his brilliant yellow 'crest', while his wings were slightly to fully drooped (depending on display intensity) and occasionally flicked. The tail was pulled forward beneath the lowered head, and sometimes held to one side.

The *Head nod and shake* involved the male nodding his rigidly downward-pointing bill and head up and down with erect head plumage and, when displaying intensely, also shaking his head from side to side. As he nodded he peered intently at, and sometimes pecked, his perch (usually a vertical sapling trunk). This display also emphasised the yellow central crown and nape 'crest'. The wings were slightly to fully drooped and occasionally fluttered. *Bow* and *Head nod and shake*, or vice versa, may be performed consecutively on the same perch when displaying is intense.

In *Flight/hover* display a male flew with slow and deliberate 'butterfly-like' beats of extensively-opened wings around his bower at 0.5-4m (usually 1-2m) above ground, occasionally with a decoration in his bill. During this display flight the tail may be fully fanned during brief mid-flight hovers; thus exposing the yellow outer rectrices. Also in this display, males typically stopped to hover in front of a vertical sapling trunk or its leaves, with bill tip touching the stem/leaves, while repeatedly and alternately fully fanning and closing the tail. The bird then flew 'butterfly-like' to another sapling to perform the hover/tail fanning display again. During *Flight/hover* the male may briefly perch on a vertical sapling stem where he may also perform a *Head nod and shake* display.

Each display consisted of one, two, or all the above three elements. An element was often repeated during a display. During S82 and S83 we recorded a total of 146 displays, involving 238 separate elements: 62 *Bows*, 104 *Head nod and shakes* and 72 *Flight/hovers* (Table 8). Of the 62 *Bow* elements: 48% were performed on bower perches, 44% on vertical sapling trunks and 8% on horizontal perches. The *Bow* was performed alone (24%) or, during other displays, was performed before (23%) or after (29%) *Head nod and shake*, or before (11%) or after (13%) a *Flight/hover* (see Table 8).

Of a total of 104 *Head nod and shakes*: 13% were performed on bower perches; 75% on

vertical sapling trunks; and 12% on horizontal perches (Table 8). Most (90%) times a male performed the *Head nod and shake* on one perch only, but a few times flew to one ($n = 5$) or two ($n = 5$) additional perches in continuous display. The *Head nod and shake* was performed alone (38%) or, during other displays, was performed before (17%) or after (14%) *Bow*, or before (14%) or after (17%) *Flight/hover* (see Table 8).

Of a total of 72 *Flight/hover* displays: 96% were performed at vertical sapling trunks or leaves and the remainder at decorated bower platforms, prior to landing on the bower perch. The number of hovers given during a *Flight/hover* display varied. Most times ($n = 52$) a male performed only one hover; but at other times performed 2 ($n = 9$), 3 ($n = 5$), 4 ($n = 1$) or 5 ($n = 1$). Four flight displays lacked a hover. *Flight/hover* was performed alone (33%) or, during other displays, was performed before (11%) or after (10%) *Bow*, or before (25%) or after (21%) *Head nod and shake* (see Table 8). We could discern no clear sequence in which the three display elements might typically be performed, possibly because no complete successful courtship, to copulation, was observed.

When males landed on their bower perch to display (*Bow* or *Head nod and shake*) they sometimes gave one *rattle* and *squeal*, but on other perches gave only a *squeal(s)*. During *Flight/Hover* displays males often gave a *squeal(s)* and/or brief mimicry, as flying from one perch to another (Table 8). During *Bow* and *Head nod and shake* displays given on bower and other perches, males occasionally (9%) held a decoration in the bill, but only twice when a female-plumaged individual was known to be in the area. Points of saplings used during displays averaged 2.1 ± 1.3 m above ground, and were 3.2 ± 1.8 m ($n = 36$) from bowers.

Total numbers of elements performed during each display (including repetition of any elements; see above) are summarised in Table 9. Most displays involved one (63%), two (23%) or three (16%) elements; but five displays consisted of four, six ($n = 3$) and nine. Of the 238 elements observed: 18 (1.4 per display) were performed exclusively on bower perches, 137 (1.4 per display) on/at vertical perches, 13 (1.1 per display) on horizontal perches and 70 (3.0 per display) on a combination of perch types (Table 9). There was no apparent sequence to display elements. Of total displaying time only 12% was on the bower perch.

TABLE 8. Number and sequence of display elements (n = 238) performed by male Golden Bowerbirds at their bower sites during 146 displays, and the number of times males called and carried a decoration in their bill during display (data for display seasons of 1982 and 1983 combined). * = hovers performed in front of vertical trunk or its leaves; ** = hovers directed at the bower tower before landing on the bower perch; see Results.

Display elements		Bow	Head nod and shake	Flight/hover	Total number of display elements	% of total number	
Display elements	Number given on/directed at *	bower perch	30	13	3 **	46	19.3
		vertical support	27	79	69	175	73.6
		horizontal perch	5	12	0	17	7.1
		Total number	62	104	72	238	
	Number of single elements only		15	39	24	78	32.8
	Number given with other elements	before a bow	-	18	8	26	10.9
		before a nod& shake	14	-	18	32	13.5
		before a flight/ hover	7	15	-	22	9.2
		after a bow	-	14	7	21	8.8
		after a nod& shake	18	-	15	33	13.9
		after a flight/ hover	7	15	-	26	10.9
		Total number	62	104	72	238	
	Calls	No. given on bower perch	12	8	0	20	8.4
		No. given on other perches	4	13	14	31	13.0
Decoration held in bill	No. held on bower perch	10	4	0	13	5.5	
	No. held on other perches	3	6	0	9	3.8	

Numbers of elements during a display did not increase as S82 progressed, possibly because it was extremely dry. During September, October and November 56, 46 and 61% of displays involved one element, 33, 29 and 26% two, and 11, 11 and 18% three elements respectively. Two six-element displays occurred in late October, and one four-, one six- and one nine-element display in November of S82. During November of S83, display involved one (79%), two (19%) or three (2%) elements.

Of the total 146 displays by bower-owning males we saw a female-plumaged individual simultaneously at the bower site 26 times (22 on the bower perch and 4 perched close by; see Table 7). On these 26 occasions males displayed before/after a displacement chase (n = 20) or displayed only (n = 6); performing one display element (n = 17: five *Bows*, five *Head nods and shakes*, and seven *Flight/hovers*), or two (n = 5), three (n = 3) or nine (n = 1) elements.

The longest display observed (17mins) involved performing display elements nine and three times, each group of them interspersed with much medley calling. A female-plumaged individual was perched on a vertical sapling initially, but then moved to the lower side of a bower tower to perch motionless, with sleeked plumage, and stare at the male. Once, when the visitor landed on the bower perch, it was

immediately displaced and chased by the owner. As in all other display/calling sequences with a female-plumaged individual present, this did not terminate in copulation.

Males spent little (1.1%) time displaying during S82 or S83 (Table 4). During S82 fewer and briefer displays were recorded in September, during both mornings and afternoons, than in November despite decreasing bower attendance during the latter (Tables 5, 6). Mean display duration was 67 secs (Tables 4-6).

Silence and other behaviour. Males spend much time silently on perches above their bower, when they preen, bill-wipe, sun, change perches, turn 180° to face the opposite direction to sing or to better listen to neighbours' calls, or forage locally. When males returned from an absence, having obviously bathed, they flicked their wings, shook and fluffed their damp feathers and continuously preened. Once during a brief rain shower a male shook his wings and fluffed his plumage, before bathing by flying into sapling foliage and briefly fluttering/hovering amongst the wet leaves. On two occasions (at 0942 and 1245) different males perched in direct sunlight above the bower and sunned themselves; with erected breast, rump, head and nape feathers, down-pressed tail and drooped wings. We witnessed males fly from a favoured perch (n = 28) to snatch an insect from nearby foliage or

trunk, or to hawk ($n = 2$) an insect from the air. Males were twice seen to fly to take a vine fruit, twice to feed on a fruit on the ground and twice to retrieve fruit from a food store near the bower (a crevice in a vertical trunk).

The proportion of time at a bower that males spent silently (other than during bower maintenance periods, displays or chases) averaged 76% during S82 and 84% during S83 (Table 4). The lower S82 figure was in part due to the continuous medley calls given by the male establishing himself at bower 3. Periods of silence were similar for each individual for each month (Table 5), and during different times of the day during S82 (Table 6).

DISCUSSION

ANNUAL SEASONALITY AND RELATIVE LEVELS OF BOWER ATTENDANCE BY MALES. Paluma Range male Golden Bowerbirds typically started attending traditional bowers in late August/early September, as temperatures initially rise from mid winter ones, approximately 6 to 8 weeks before females commenced egg-laying (Frith & Frith, 1998). On the Atherton Tableland, especially at slightly lower and thus warmer altitudes, the display season starts a few weeks earlier (Marshall, 1954; Frith & Frith, unpubl. data). Bower attendance declined in December; particularly when pre-wet season rains commenced (Warham, 1962; Frith & Frith, 2000b and this study). During the wet season proper, few advertisement songs were heard, decorations deteriorated, and few males briefly visited bowers to add decoration during dry spells. Males moult at this time (Frith & Frith, unpubl. data). A brief period of activity occurred in late March-early May, when bowers were poorly decorated and few songs given, as noted by Warham (1962) on the Atherton Tableland. This post-courtship activity is in part reflected by infrequent attendance of traditional bowers by immature males, a situation also found in Tooth-billed Bowerbirds at the same location (Frith & Frith, 1994; 2000b).

Seasonal variation in time invested at/on bowers by male Golden Bowerbirds may vary year to year subject to prevailing weather conditions, particularly excessive wet season rains and drought, and thus food resource availability (see Lenz, 1993; Frith & Frith, 1994; and this study). During abnormally dry seasonal conditions (as in S79 and S82 of this study), when rainforest fruit crop was poor and invertebrate numbers and biomass low, not only was the

display season shorter and male attendance at bowers reduced, but fewer females attempted to nest or did so successfully (Frith & Frith, 1998). A similar situation was recorded for Paluma Range Tooth-billed Bowerbirds during the dry S79 (Frith & Frith, 1994; 2000b). During seasonally typical conditions, male Golden Bowerbirds attended their bowers at consistent levels throughout the day, as did Macgregor's Bowerbirds *Amblyornis macgregoriae* (see Pruett-Jones & Pruett-Jones, 1982), but in adversely dry conditions they did so almost twice as much during the mornings than during afternoons. Drought conditions had similar impacts upon both sexes of a polygynous, lekking, neotropical hummingbird (Stiles 1992).

Adult male Golden Bowerbirds ($n = 7$) spent an average of 50% (range 32-69%) of daylight within 15-20m of their bowers, at a mean of 2.9 (range 2.2-4.2) bower visits per hour and each averaging 9.5mins in duration. The former figures are similar to those found for male Macgregor's Bowerbirds ($n = 5$) that spent an average of 54% (range 20-75%) of daylight within 15-20m of their bowers, but did so at a mean of 1.4 bower visits per hour (range 0.6-2.0) and each averaging 4.6mins in duration (Pruett-Jones & Pruett-Jones, 1982). Both species are predominantly frugivorous (Pruett-Jones & Pruett-Jones, 1985; Frith & Frith, unpubl. data). Male Tooth-billed Bowerbirds, almost exclusively frugivorous during their peak courtship and mating season, spent an average of 64% of daytime at or near (<10 m) their courts, at a mean of 2.9 court visits per hour and each visit averaging 23mins in duration (Frith & Frith, 1994). Male rainforest Satin Bowerbirds, with a 67% fruit component of annual diet, spent an average of 73% of daytime within 50m of bowers (Donaghey, 1981). A male Great Bowerbird, *Chlamydera nuchalis*, a species considered predominantly frugivorous (Diamond, 1986a; Schodde & Tidemann, 1988), but probably less so than the above species, spent 47% of daylight hours at or near his bower at peak mating season (Veselovsky, 1978).

Regent Bowerbird, *Sericulus chrysocephalus*, annual diet includes 81% fruit, and yet males spent a mere 3% of daytime at or near their bowers at an average of 0.43 bower visits per hour, and each visit averaging 6.7mins in duration (Lenz, 1994). Similarly, a Flame Bowerbird, *S. aureus*, spent 6% of daytime at/near its bower (Dwyer & Minnegal in Coates, 1990) and a Fire-maned Bowerbird, *S. bakeri*,

TABLE 9. The number of display elements ($n = 238$) performed by male Golden Bowerbirds during 146 displays on the bower perch and elsewhere in the bower site (data for the display seasons of 1982 and 1983 combined). * these include bower perches, horizontal perches and vertical sapling trunks that Bow and Head nod and shake display elements were performed on, and vertical tree trunks or its leaves that the Flight/hover display were directed at; ** = during a display any element may be performed more than once; see Results.

Location *	Number of display elements per display **						Total no. of displays (% of total)	Total no. of display elements (% of total)
	one	two	three	four	six	nine		
Bower	12	0	0	0	1	0	13 (8.9)	18 (7.6)
Vertical	68	21	9	0	0	0	99 (67.8)	138 (58.0)
Horizontal	10	1	0	0	0	0	11 (7.5)	12 (5.0)
Bower to vertical	0	7	1	0	0	0	8 (5.5)	17 (7.1)
Bower to vertical to bower	0	1	1	0	1	0	3 (2.1)	11 (4.6)
Vertical to bower	0	2	1	0	0	0	3 (2.1)	7 (3.0)
Vertical to bower to vertical	0	0	2	1	1	0	4 (2.7)	16 (6.7)
Vertical to horizontal	0	2	2	0	0	1	5 (3.4)	19 (8.0)
Total number (% of total)	91 (63.1)	34 (23.2)	16 (10.2)	1 (0.7)	3 (2.1)	1 (0.7)	146	238

<1% of daytime at its bower (Mackay, 1989 and in Lenz, 1993). An explanation postulated for this exception is that regent bowerbirds, *Sericulus* spp., represent an early stage in the evolution of bower-building, in which bowers have not yet replaced elaborate male nuptial plumage. Male Regent Bowerbirds initiate courtship in the forest canopy, before accompanying the female to the bower where a prolonged courtship display primarily presents colourful nuptial plumage (and less so bower/decorations) to the female (Lenz, 1994). Thus the bower plays a less significant role in courtship.

It has been observed that a disproportionately large percentage of tropical rainforest-dwelling passerines, with a polygynous mating system based upon court/bower/arena displaying promiscuous males, are predominantly frugivorous. The seasonal abundance of rainforest fruits, economically undefendable because of their spatial/temporal distribution, both promotes the emancipation of males from nest duties and enables females to raise offspring unaided by conspecifics (Snow, 1976, 1982; Frith & Beehler, 1998). This said, Donaghey (1981) found that both adults and nestlings of the monogamous Green Catbird, *Ailuroedus crassirostris*, are more frugivorous than the polygynously breeding Satin Bowerbird, and noted that frugivory is but one of many factors involved in the evolution of avian promiscuity. Male Golden Bowerbirds also store, or cache, fruit foods around their bower site (Frith, 1989 & pers. obs.), as do male Macgregor's Bowerbirds (Pruett-Jones &

Pruett-Jones, 1985). Such storing of fruits around bowers would enable males to spend more time in bower attendance.

MALE BEHAVIOUR AT BOWERS. *Habitual perches, vocalisations and silence.* Bower-attending male bowerbirds studied to date advertise their bower location with specific calls given (Tooth-billed Bowerbird excepted) relatively infrequently from favoured perches (Gilliard, 1969; Veselovsky, 1978; Donaghey, 1981; Frith & Frith, unpubl. data). Male Golden Bowerbirds gave the distinctive bower advertisement *rattle*, single notes (*squeal*, *screech*, *scold-rasp* and *wolf-whistle*) and a medley of calls that included much mimicry of frog- and cicada-like notes, and fine vocal avian mimicry, from habitual perches. The Tooth-billed, Archbold's (*Archboldia papuensis*), gardener (*Amblyornis* spp.), Regent, Satin, Spotted (*Chlamydera maculata*), Western (*C. guttata*), Great, and Fawn-breasted (*C. cerviniventris*) Bowerbirds include avian mimicry in their bower advertisement and/or other non courtship vocalisations (Marshall, 1950; Gilliard, 1969; Bradley, 1987; Loffredo & Borgia, 1986; Frith, 1989; Lenz, 1993; Frith & McGuire, 1996; Frith et al., 1996, & pers. obs.). Male bowerbirds usually use a distinctly different, quieter and more complex, subsong in courtship display that, in the case of all of the above except the *Chlamydera* species, includes avian mimicry. During this study we did not hear Golden Bowerbirds giving subsong mimicry while displaying, but have done so subsequently. We

observed that long medleys of calls including much mimicry were given before/after display posturing, and particularly if a female-plumaged bird was present (see Table 7). We think it likely that this is more informative to females than advertisement song, as it has been demonstrated that female Satin Bowerbirds use the quality of more intimate male mimicry to assess the relative merits of prospective mates (Loffredo & Borgia, 1986).

Immature males lacking a bower gave medley calls with mimicry when visiting bowers, as did younger adult males in their first year of bower ownership (Frith & Frith, 2000b and this study). Adult males gave fewer medleys with mimicry, but it is possible that the quality of their avian vocal mimicry is higher than that of younger birds. Among competing male Satin Bowerbirds, older males produce longer bouts of higher-quality avian vocal mimicry than do younger males and also gain higher mating success (Loffredo & Borgia, 1986). Thorpe (1985) stated that there is some evidence that variety in male bird song is attractive to females, and suggested that mimicry may simply be a way of increasing repertoire size. Robinson & Curtis (1996) demonstrated that most mimicry content of lyrebird (*Menura* spp.) calls is learned, is culturally transmitted, and its quality and sequence (of model spp) could therefore provide conspecifics, particularly females assessing male quality, with a clear indication of potential mate experience/survival.

Male Golden Bowerbirds spent 80% of their time present at bower sites in perching silently above the bower, this being 9% more than in Macgregor's Bowerbird (Pruett-Jones & Pruett-Jones, 1982). While adult male Regent Bowerbirds spent only 17% of time present at the bower site in perching silently this figure merely reflects the small proportion (3%) of total daylight they spent at bowers (see above; Lenz, 1994). It would appear that male Satin Bowerbirds spent 87% of time present at the bower site in silence (Donaghey, 1981: 181-182). In marked contrast, male Tooth-billed Bowerbirds spend <2% of time perched at the court in silence, most of their time there (96%) being spent singing loudly. Court advertisement vocalisations of Tooth-bills are thus much more frequent, males having no epigamic adult plumage but a most elaborate vocal display (Frith & Frith, 1994).

Bower maintenance. Male Golden Bowerbirds spent an overall average of 4% of time at the bower site in maintaining the bower structure/

decorations. In more typical climatic conditions males spent an average of 3% of time at the bower site in bower maintenance, but during adversely dry conditions spent almost twice this time doing so. The limited time birds spent on the bower presumably reflects (a) the low maintenance required once it is largely built (given its fungus-fused and 'traditional' nature) and decorated; and (b) the fact that adult male nuptial plumage remains a predominant part of courtship in this species. Limited compatible figures for bower maintenance by: Macgregor's (12%; Pruett-Jones & Pruett-Jones, 1982), Tooth-bills (1.2%; Frith & Frith, 1994), Regent (61%; Lenz, 1994), Satin Bowerbirds (8% of all daylight; Donaghey, 1981) are variable. The figure for Tooth-bills is so low because males spend so much of daylight above the court (but at its site); whereas the high figure for the Regent, which builds a most rudimentary and sparsely-decorated bower, is because males spend little time at the bower site (Lenz, 1994).

In restricting its decorations to beard lichen, melicope seed pods and whitish flowers, the Golden Bowerbird is far less catholic in bower decorations than all other polygynous bowerbirds with the exception of the Tooth-bill which uses only leaves of various plants (Frith & Frith, 1993, 1994) and the Fawn-breasted Bowerbird which uses only green fruits, leaves and the occasional flower (Peckover, 1970; Pruett-Jones & Pruett-Jones, 1994). Bower decorations of greater significance to some bowerbird species are items rare in the birds' environment (Frith & Frith, 1990c; Frith et al., 1996), and an abundance of such decorations on bowers enhances the mating success of the bower owner (Borgia, 1985b, 1986; Borgia & Gore, 1986). Thus, rare decorations might indicate something significant to females, and rival males, about the owner's fitness/dominance levels. But are bower decorations used by Golden Bowerbirds rare in their habitat? The answer needs to be framed in the context of extensive undisturbed upland rainforest, lacking the roads, tracks and clearings of today. In this context, we suggest that melicope seed pods would have been relatively hard to find, as *M. broadbentiana* is a pioneer shrub (Hyland & Whiffin, 1993) that is today found on track/clearing edges. Before the latter were available the plant would have been largely confined to areas of small-scale natural forest damage, such as larger tree falls and cyclones.

While beard lichen is far more widespread in upland forest than the melicope it is sun-loving

and would, in extensive primary upland forest, have been predominantly confined to woody twigs and branches of upper canopy and emergent trees — an exposed part of the forest not typically frequented by Golden Bowerbirds (pers. obs.). Fresh orchid flowers are never spatio-temporally abundant in Australian upland rainforest and in any event, like the whitish flowers of other plants, provide inferior bower decorations because they wilt and need replacement. Golden Bowerbirds can thus be seen to fit the broad pattern of male bowerbirds using some items that are relatively rare as bower decorations.

Adult males briefly visited the bower of rival males, usually in their absence, in order to steal bower decorations. Such decoration theft has been documented for several other bowerbirds; including the Tooth-billed (Frith & Frith, 1993, 1994), Vogelkop (Diamond, 1986a,b, 1987, 1988), Regent (Lenz, 1994), Satin (Borgia 1985b; Borgia & Gore 1986; Hunter & Dwyer, 1997), Fawn-breasted (Coates, 1990) and Yellow-breasted (*C. lauterbachii*) Bowerbirds (Pruett-Jones & Pruett-Jones, 1994).

Bower marauding is known in Macgregor's, Vogelkop, Regent, Satin, Spotted, Fawn-breasted and Yellow-breasted Bowerbirds (Pruett-Jones & Pruett-Jones, 1994). While male Golden Bowerbirds may (but not observed) steal the odd, unfused (i.e. recently placed), stick from the bower apex of a rival male, we did not see any attempt to damage ('maraud' of Pruett-Jones & Pruett-Jones 1994: 609) a bower of a rival. Bower-owning male Macgregor's Bowerbirds attempt to damage bowers of rivals as well as steal their decorations, including the moss of the tower base (Bulmer in Gilliard, 1969: 305; Pruett-Jones and Pruett-Jones, 1982; pers. obs.). Stealing of the latter is noteworthy, suggesting it may function as decoration (analogous to beard lichen on Golden Bowerbird bowers) and not a structural element.

It has been demonstrated that a strategy of bower decoration theft by males is an evolutionarily stable one, as opposed to the contrary strategy of guarding bowers and not stealing (Pruett-Jones & Pruett-Jones, 1994). Male Satin Bowerbirds with more decorations on bowers tend to steal more often than they are stolen from (Borgia & Gore, 1986). This is because relative levels of bower decoration enable females to assess an individual male's quality (fitness), based upon his success in conflict with rival males. The greater numbers of more favoured

decorations on a bower positively influenced relative male mating success (Borgia, 1985a,b, 1986; Borgia et al., 1985; Pruett-Jones & Pruett-Jones, 1994). Bower quality has also been found to correlate well with relative male mating success in both Satin and Regent Bowerbirds; and males of both species mostly maraud and damage bowers of their nearest neighbours, their most likely sexual competitors (Borgia, 1986; Lenz, 1993). The reason for theft by rival males is thought to be sexual selection resulting from females choosing to mate only with males 'honestly advertising' their fitness with such 'rare' bower decorations (cf. Zahavi & Zahavi, 1997).

Displacement chases and displays. As 81% of all female-plumaged conspecifics perching on the bower were immediately displaced and aggressively pursued out of the bower site by the bower-owning male Golden Bowerbirds it is likely, in view of what is known of other bowerbirds, that such behaviour typically greets females as well as adult and immature males. Of the 19% of visiting female-plumaged birds not immediately chased off, half were displayed to and half ignored. Adult males displaced and chased immature and adult males from their bower/site but we only twice saw physical combat, as did Chisholm & Chaffer (1956).

Display by a male concealing himself from a visiting female, by crouching behind a court tree or central maypole bower base to give subsong with mimicry, is typical initial Tooth-billed, Macgregor's and Streaked (*Amblyornis subalaris*) Bowerbird courtship (Diczbalis, 1968; Gilliard, 1969; Frith & Frith, 1993 & pers. obs.). We saw no male Golden Bowerbird attempting to hide from a visiting female to give subsong with mimicry during this study, but have subsequently done so. In hindsight, we understand this was due to limited field of view from hides, a point of great importance to students of bowerbird behaviour (Frith & Frith, unpubl. data).

It is probable that the three basic display elements we observed are performed during successful courtship, perhaps in a typical progressive sequence, but as we witnessed few displays to (unsexed) female-plumaged birds ($n = 26$), and no copulations, we could not confirm this. The *Head nod and shake* display is only broadly similar to postures and movements known to be performed by courting male Gardener and Archbold's bowerbirds (Gilliard, 1969; Frith et al., 1996; pers. obs.). The *Bow* display, which enhances the contrastingly

brilliant yellow mid-crown patch and nape 'crest', appears unrecorded in other bowerbirds.

The *Flight/hover* display is unique to the Golden Bowerbird. This is not surprising, as this display clearly functions to visually present both the (uniquely within Ptilonorhynchidae) brilliantly coloured dorsal and ventral contour and flight plumage of adult males. The deliberate slow flight display punctuated with hover(s) with conspicuously repeated tail-fanning, to expose the pure yellow outer rectrices, is visually spectacular. This might be performed with a bower decoration held in the bill (Chaffer in Chisholm & Chaffer, 1956; and this study). The closest any other bowerbird comes to a courtship flight display is the vigorously repeated to-and-fro 'extra-bower' fluttering flight/leaps, between vertical sapling stems, by closely related Macgregor's Bowerbird (Stevens in Greenway, 1935; Mackay & Cheeseman, 1990; pers. obs.). It has been noted that bowers of Macgregor's Bowerbird are often built adjacent to numbers of vertical sapling trunks (Gilliard, 1969: 302; Pruett-Jones and Pruett-Jones, 1982), and they might be a prerequisite bower site feature to accommodate the 'flight' display. In the light of this, and in view of the elements of its *Flight/hover* display, it is possible saplings appropriate for hovering at/perching on might influence bower site selection by Golden Bowerbirds.

Male Golden Bowerbird behaviour at bower sites is mostly cryptic, given they are displacement chasing and/or displaying for <2% of their total time present there. Males apparently depends largely upon bower/decorations and, subsequently, their colourful plumage to impress females, rather than a complex bower. Thus, it has been observed that in this bowerbird, unlike most, untidy bower construction and variation in their shape/bulk suggests gross bower features are of less significance to females than is the discrete and relative small part of them modified into a 'platform(s)' for the exclusive placement of decorations (Frith & Frith, 2000a). Maintenance and decoration of the platform(s) requires but a small proportion of bower attendance time, once the basic bower is accumulated. The platform(s) does, however, provide a quickly and easily located 'marker' (cf. Borgia, 1985a; Borgia et al., 1985) for females seeking older, more experienced, males to assess as potential mates.

No data were obtained on relative reproductive success rates within male Golden Bowerbird populations. The possibility that older males are

more successful than younger rivals has been found, or indicated, to be the case in other non-lekking bowerbirds (Borgia, 1985a) and in unrelated lekking passerines in which promiscuous males court females at traditional sites (Lill, 1974a,b; McDonald, 1989a,b, Andersson, 1991). Clearly, promiscuous adult males establishing themselves within a lek, exploded lek or more dispersed population, enjoy a high survivorship (Frith & Frith, unpubl. data). Evidence from sexually dimorphic polygynous bowerbirds, and other species, suggests that the strong mating skew in favour of older individuals has forced males into a long-term mating strategy involving much-delayed morphological and physiological development (Beehler & Foster, 1988; Collis & Borgia, 1992; Frith & Beehler, 1998).

Bower site ownership by Golden Bowerbirds is highly stable over years, with few successful attempts by newcomer (predominantly younger) males to establish themselves within bower-owning male society. Given this scenario, and that experience/age has been found to play a highly significant role in relative male bowerbird mating success (Loffredo & Borgia, 1986; Collis & Borgia, 1992; Borgia, 1995), there is a high expectancy of the latter within local male Golden Bowerbird populations. This remains to be tested.

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HOME RANGE AND ASSOCIATED SOCIOBIOLOGY AND ECOLOGY OF MALE GOLDEN BOWERBIRDS *PRIONODURA NEWTONIANA* (PTILONORHYNCHIDAE)

CLIFFORD B. FRITH AND DAWN W. FRITH

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Home range and social interactions of male Golden Bowerbirds, *Prionodura newtoniana*, during display seasons and other months of the year, prior to and during bower ownership, were studied for six years (1978-1984) in upland rainforest. Display season was late August to December, the wet season rains terminating activity at bowers. A brief period of post-moult activity occurred in late March to early May. A traditional bower owner never occupied more than one traditional bower site simultaneously or consecutively. Traditional bower sites were usually attended by traditional (>2 seasons) bower owners. In a few instances (n = 3) the disappearance of a long-term traditional site owner resulted in it being temporarily visited for a season(s) by immature males, until one became established as its new owner. Similarly, a rudimentary bower site (n = 4) was established near (50-150m) a traditional site if the latter lost its long-term owner. The rudimentary site was then irregularly attended by immature males, until one became the new owner of the adjacent traditional site. Young bowerless males actively attended bower sites during peak display season (38% of sightings of them) and during the post-peak display season of March to early May (45% of sightings). From five to two years before attaining traditional bower ownership, immature males visited many bower sites, at an average distance of 391m from the one they eventually came to occupy. The year before attaining full bower site occupancy this distance diminished, to an average 186m, as older immature-plumaged birds focused their activities nearer the site they would eventually occupy. Most males were adult-plumaged by the time they came to actively occupy a traditional site full time, but a few were in immature/sub-adult plumage.

Traditional owners left bowers to forage, bathe, drink, and collect sticks and decorations. They foraged relatively close (mean = 110m) to their bowers, overlapping foraging ranges of neighbouring rival males on occasion. They visited other bowers (mean distance = 191m), mostly (82%) during the display season, to steal decorations. The mean distance travelled from bower sites for all purposes averaged 143m, with a median of 121m (n = 152). Estimated mean home range size of eight adult males was 7ha (range 3-10ha). □ *Golden Bowerbird, Prionodura newtoniana, Ptilonorhynchidae, home ranges, bower acquisition, social interactions.*

Clifford B. Frith and Dawn W. Frith, Honorary Research Fellows of the Queensland Museum, 'Prionodura', PO Box 581, Malanda 4885, Australia; 17 September 1999.

Interest in bowerbirds (Ptilonorhynchidae) has seen a recent revival, due to their significance to studies of the evolution of social systems and sexual selection theory (Donaghey, 1981; Pruett-Jones & Pruett-Jones, 1982, 1983; Borgia, 1986; Frith & Frith 1993, 1995; Lenz 1993). Bower structures and building behaviour of male bowerbirds provide opportunities to examine the evolution of symbolic, externalised, secondary sexual characters (Frith & Frith, 1993, 1999a; Borgia, 1995), the evolution of culturally transmitted traits (Diamond, 1986a) and origins of aesthetic sense in animals (Diamond, 1982, 1986b). In view of almost no knowledge of its biology and the potential significance to theoretical considerations of animal social

organisations and mating systems in general, and to the evolution of same in bowerbirds particularly, we began studying Golden Bowerbirds *Prionodura newtoniana*, in 1978.

We examined 60 traditional bower sites, involving a total of 98 main (decorated) bower structures, during 1978-1997 on the Paluma Range, and presented a comparative and quantified review of them (Frith & Frith, 2000a). A traditional bower was a large, well-established, structure built at a traditional site that was regularly attended, maintained and decorated throughout subsequent seasons by its traditional adult male owner. We also described short-term, rudimentary, bowers built by immature males at bower sites established near to traditional ones

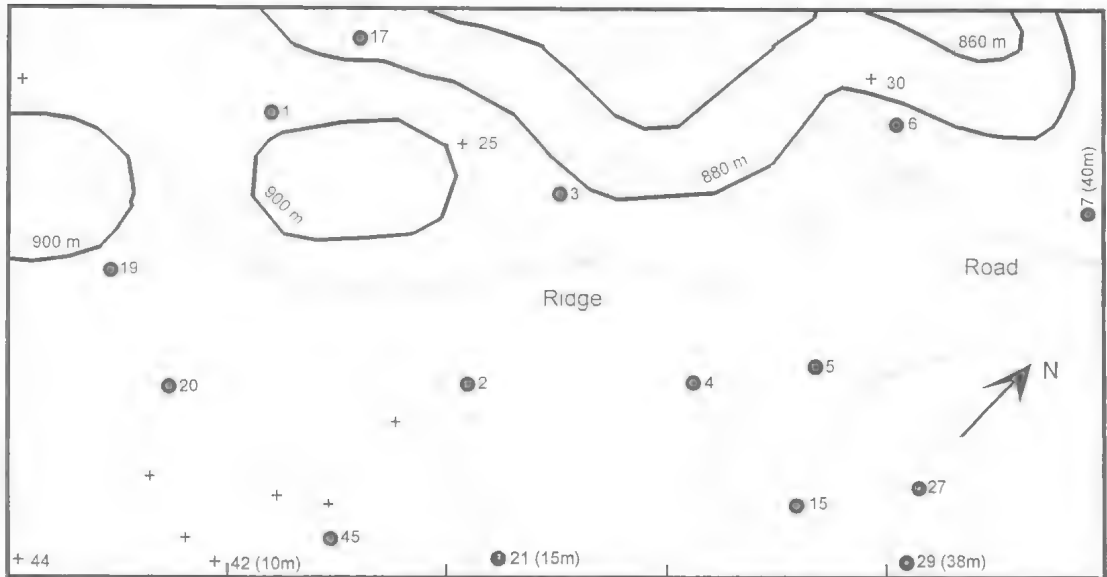


FIG. 1. Dispersion of 15 (including 3 just outside) traditional (●) and 10 (including one on the perimeter) rudimentary (+) male Golden Bowerbird bower sites within 50ha (1 × 0.5km) study area 1 (SA1). Only rudimentary sites at which marked individual birds were sighted are numbered. Faint lines indicate seasonal drainage gullies. Grid marks are indicated at each 200m within the 1km southern boundary on the figure. Bower sites just on/outside the perimeter of SA1 are plotted within the boundary line and their actual distances outside it indicated.

(Frith & Frith, 2000a), a scenario observed in other bowerbirds (Vellenga, 1970, 1980; Donaghey, 1981; Pruett-Jones & Pruett-Jones, 1982; Chaffer, 1984; Borgia, 1986; Lenz, 1993; Frith & Frith, 1994, 1995, 1999a; Frith et al., 1996).

During the display season (late August–December), bower-owning males perch above their bowers and give loud advertisement song and other vocalisations including fine vocal avian mimicry, maintain and decorate their bowers, evict rival males and display to potential mates (Frith & Frith, 2000b). Advertisement song consists of a prolonged, pulsating *rattle*. Other calls include *squeals*, *screeches*, *wolf-whistles*, *scolds*, frog- and cicada-like notes, given as single notes, or as a medley together with fine vocal avian mimicry of >22 model species. Males leave their bower site to harvest sticks and decorations, and steal decorations from rival males for their bower, and to bathe and forage (Frith & Frith, 2000b). They are predominantly frugivorous but also eat beetles, cicadas, and spiders (Frith, 1989; Donaghey, 1996; Frith & Frith, unpubl. data). Availability of fruits, in both time and space, may affect profoundly the home ranges of bowerbirds, but data detailing home ranges of fixed-point courting promiscuous male

frugivorous bowerbirds are available only for the Satin, *Ptilonorhynchus violaceus* (Donaghey, 1981), Macgregor's (Pruett-Jones & Pruett-Jones, 1983) and Tooth-billed, *Scenopoeetes dentirostris* (Frith et al., 1994) bowerbirds.

The present study provides the first information on distances travelled by traditional bower-owning male Golden Bowerbirds away from their bower sites. It also describes for the first time activities of immature males prior to becoming the owners of traditional bowers. Seasonal activities at, and away from, bowers during different times of the year are discussed. Data on male attendance levels and their time-budgeted activities at bowers are presented elsewhere (Frith & Frith, 2000b). Results of long-term studies of male survival, histories of bower ownership by individual males, and acquisition of adult plumage will appear elsewhere.

METHODS

STUDY AREA. This study was carried out in upland rainforest, at about 850m asl, on the Paluma Range, 7km from Paluma Township and 80km north of Townsville, northeastern Queensland. The study area (19°00'S, 146°10'E) was a 50h plot, 1 × 0.5km, permanently gridded

with metal stakes (Fig. 1). For a detailed description of this area, see Frith & Frith (2000a). The present study deals mostly with the ownership and movements of male Golden Bowerbirds based at 15 traditional and 4 rudimentary bower sites within, or just outside the perimeter of our study area (Fig. 1). In a few instances, however, birds marked as immature males and resighted within our study area eventually took up ownership of traditional bower sites ($n = 6$) beyond it. For the location of these bower sites (numbers 16, 22, 23, 24, 33 & 34) see Frith & Frith (2000a: fig. 2).

DEFINITIONS. Definitions of bower sites and structures appear in Frith & Frith (2000a), and of the display season and vocalisations in Frith & Frith (2000b). We refer to a display season by the year in which it started (S78, S79 etc). An immature male was one in female-plumage and a sub-adult male one with some to almost complete adult male plumage intruding into female plumage. We use 'regularly attended' to imply full-time seasonal attendance by traditional owners at traditional bowers, and 'irregularly attended' to imply part-time seasonal attendance by immature males at traditional or rudimentary bowers. All statements refer to males unless stated otherwise.

HOME RANGES. Movements of individually marked males were examined over six display seasons (S78-S84) and additional months of the year. Intensive fieldwork was from 1 August 1978 to 28 February 1981, save 1 May to 18 July 1979 when we were absent (but relative bird activity at bowers was then assessed by André Griffin). In studying Golden and other bowerbird species during this period, 1547 hours were spent carrying out systematic work: 788h during four hour random walks, 572h during fixed transect walks, and 187h of random searching for nests (see Frith, 1984; Frith & Frith 1994, 1995, 1998). Of the total 1547h, 893h were during display season months August-December; 282h during January-February when it was excessively wet and/or males were moulting (Frith & Frith, unpubl. data); 268h during March-May when there was some post-moult activity at bowers; and 104h during winter months June-July. We also spent 343h mist-netting at bowers, as well as marking/retrapping individuals elsewhere during a standardised avifaunal netting programme (Frith & Frith, unpubl. data).

Fieldwork continued through the display season months of S81-S84, and non-display season months of June 1981, February, May and

August 1982, June 1983 and March 1984. During S82 and S83 we made observations at six bower sites in September-November 1982 for 369h, and November-December 1983 for 102h. Sightings of marked birds at bowers are presented here, but levels of attendance at bowers and time-budgeted activities at them appear elsewhere (Frith & Frith, 2000b). We continued netting at bower sites and for a general avifaunal netting programme during S81-S84.

Each captured bird was metal banded and with a unique two colour band combination (= marked). Biometrical, morphological and moult data will appear elsewhere (Frith & Frith, unpubl. data). Band colours on bower-owning birds were confirmed each season by direct observation at bowers, to avoid disturbance by retrapping, although many birds were retrapped opportunistically away from bowers. Band colours were also noted during bird sightings at and away from bowers during other fieldwork. The present study deals with 26 confirmed males, first marked during S78-S81 in adult ($n = 11$) or immature ($n = 15$) plumage. Numbers of sightings of marked individuals at bower sites were totalled for the months of August-December, January-February, April-May and May-July (S78-S84), in view of the above.

RESULTS

BOWER SITES AND EXISTING OCCUPANCY.

Traditional Bower Sites with Traditional Owners. Fifteen traditional bower sites were monitored during S78-S84: 12 within the study area and 3 (7, 21 and 29) just beyond it (Fig. 1). All save site 21, which was abandoned after 5 seasons, remained active throughout this study. Twelve of the 15 traditional bower sites were regularly attended over different seasons by a total of 20 individual traditional bower owners. An adult never occupied more than one traditional bower site, simultaneously or consecutively.

Traditional Bower Sites Lacking Traditional Owners. Three of the 15 traditional bower sites (5, 15 and 21) lacked traditional owners throughout the study (Fig. 1). The bower at site 5 was a large and traditional one but those at sites 15 and 21 were rudimentary structures. These three bower sites were irregularly attended by immatures, as follows:

During S78-S84 we made 114 sightings of female-plumaged individuals (43 sightings of 19 marked males, and 71 of unmarked birds whose behaviour indicated they were male) at sites 5, 15 and 21. Most (62%) of the 114 sightings were at

traditional bower site 5, with fewer sightings at the rudimentary bowers of traditional sites 15 (14%) and 21 (24%). These data are biased, however, because we visited site 5 most often, because more consistent activity was to be observed there. During these sightings we observed immature birds giving single call notes (25 times), continuous medley calls with mimicry (33 times), and advertisement song typical of traditional bower-owners, only 9 times. The latter song was only heard during the display season, but other calls, although mostly (57%) heard during August-December, were also given during January-February (19%), March-April (19%) and May-July (5%).

At these traditional sites, young males rearranged bower sticks and/or decorations, or brought in new ones obtained elsewhere. Bowers had few (<10) decorations, in part because neighbouring adult traditional bower-owners stole them (confirmed by five observations of such thefts). Up to four young males often visited such sites together, where they called, displacement-chased each other whilst flicking/fluttering their wings, and sometimes performed brief display postures.

Rudimentary Bower Sites Lacking Traditional Owners. Four rudimentary bower sites were established near to (mean = 104, range 30-150m) traditional bower sites during S78-S84 and were active for one (site 42), two (site 25) or three non-consecutive (sites 30 and 44) seasons. Another rudimentary site (28) was 150m from traditional site 31 (both sites being outside SA1 beyond traditional site 6 — see Figs 4D & 6A). These rudimentary sites were irregularly attended by immatures, but adults visited them occasionally, presumably to steal decorations.

Rudimentary bower sites were usually first established near a traditional site after the disappearance of the latter's owner. For example, the adult owner of traditional site 31 had been badly injured (base of his rear skull bald, torn and bleeding) prior to being seen at his bower on 29 November 1978. The next day we netted and marked him at nearby rudimentary site 28, where we had sighted a sub-adult and two immatures on several previous occasions. We saw this adult male again in April 1979, his head now healed, being chased about his own traditional site by an unmarked immature. We did not see the healed adult again, and in S79 an unmarked adult occupied traditional site 31 and the adjacent rudimentary site was abandoned.

In October 1979 we marked an apparently diseased adult at rudimentary site 42, who may have been the present/previous owner of nearby traditional site 45 (Fig. 1). This bird's plumage was in poor condition and he had a swollen (21.5mm long × 14.6mm diameter) hard fatty 'bag', possibly an infected preen gland, above his central tail feather bases. He was not seen again, and an immature (black/red) took over traditional site 45 during the latter part of S79.

Rudimentary bowers were usually established during the non-display months of March-July, by immatures which had previously limited their activities to the area surrounding the adjacent traditional site. Sometimes two or three immatures temporarily attended such a rudimentary bower site. By the beginning of the following display season (August/September) the immature(s) would challenge the owner of the adjacent traditional site for occupancy, and by late October/early November the victor exclusively occupied it. The rudimentary site was then abandoned.

During S78-S84 we made 30 sightings of female-plumaged individuals (15 subsequently confirmed males and 15 unmarked birds that were probably male) at four rudimentary bowers (sites 25, 30, 42 and 44; see Fig. 1). During these sightings we heard medley calls with mimicry 14 times, and advertisement song only 3 times. We saw adult males at rudimentary sites 5 times, but did not confirm if they visited them to steal decoration.

ACQUISITION OF A TRADITIONAL BOWER SITE. Fifteen males were marked as immatures: 13 were first captured at an average of 317 ± 243 m (range 110-900m) from, and two at, the traditional bower site they subsequently came to occupy. Of these 15 individuals, 14 were first captured within the study area: 8 at/near site 5; 2 at site 21; 1 at rudimentary site 44 (sites lacking traditional owners); and 3 at sites 1, 3 and 6 (sites with traditional owners). The initial capture sites of each of these 14 individuals are indicated in Fig. 2. The 15th bird (pink/red) was first captured at a traditional site outside the study area, but subsequently visited bowers within it (see Fig. 3D).

Males in Adult Plumage. Nine of the 15 marked immatures had acquired adult-plumage before first occupying a traditional bower site. The year in which two of these nine became adult was unknown (orange/orange and green/white; see Fig. 2). Six of them were in their first year of adult plumage when acquiring a traditional bower site,

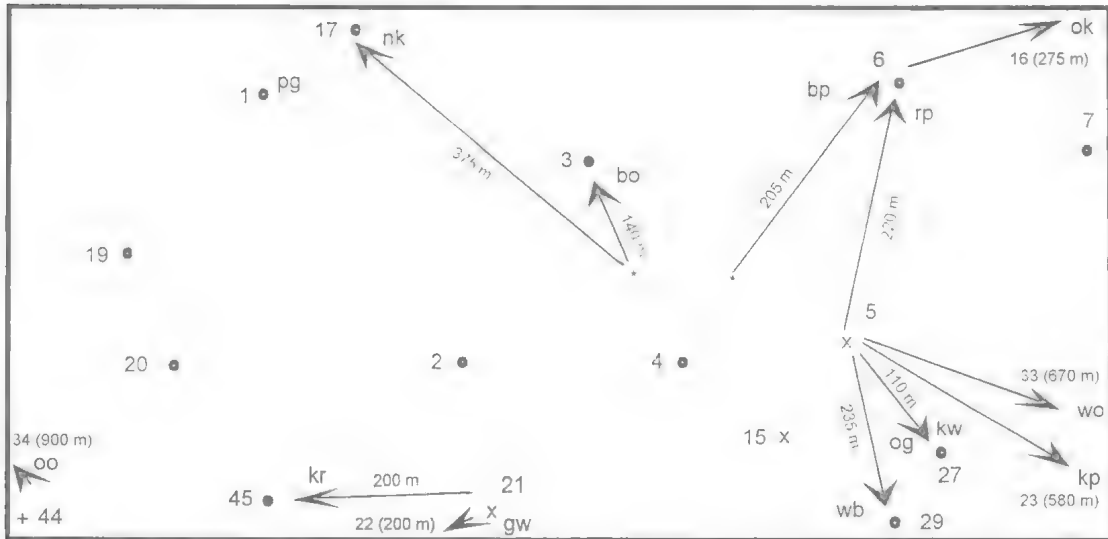


FIG. 2. Schematic plan to scale of localities at which 14 immature male Golden Bowerbirds were captured and marked within study area SA1. The traditional site they subsequently came to occupy and the distance to it from the point of their first capture are indicated. Note: b = blue; g = green; k = black; n = pink; o = orange; p = purple; r = red; w = white; * = capture sites not at bower sites; ● = traditional bower sites with traditional owners; x = traditional bower sites lacking traditional owners; + = rudimentary bower site. Bower sites actually located immediately beyond the SA1 perimeter are here plotted within the boundary line (see Fig. 1 for their distance beyond it).

and another had been adult plumaged for one year, as follows:

Black/white was marked at site 5 in March 1980 as an immature. During March-July 1980 he visited traditional sites with traditional owners, including site 27 (which he later came to own), as well as sites 5 and 15 lacking traditional owners (Fig. 3A). During S80 he was seen at/near site 5 and also at site 6, and its nearby rudimentary bower site 30, while a challenge was underway for ownership of traditional site 6 (see below). Over the next three years (1981-83) we saw him four times, the last being at rudimentary site 30 when he was possibly again challenging for site 6. In August 1984 he was the new owner of traditional site 27, 110m from site 5 where marked 4.5 years previously (Fig. 3A).

White/blue was marked at site 5 in April 79 as an immature. During April 1979-July 80 he visited sites with traditional owners, including site 29 (which he later came to own), as well as sites 5, 15 and 21 lacking traditional owners (Fig. 3B). From August 1980-December 81 he was mostly seen at/near site 5. Early in September 1982, in his first year of adult plumage, he regularly attended site 4 and we assumed he was its new owner, but later that month he was displaced by the owner of the previous season. By

September 1983 white/blue was the new owner of traditional site 29, 235m from site 5 where marked 4.5 years previously (Fig. 3B).

White/orange and black/purple were marked at site 5 in March 1980, as immatures. They subsequently took ownership of traditional sites 23 and 33, being 580 and 670m distant from site 5, respectively (Fig. 2). From March 1980 to November 1982 white/orange visited various bowers in the study area but in S84, 4.5 years after marking, he became the new adult-plumaged owner of site 33 (Fig. 3C). Black/purple was re-sighted twice after marking, once in March 1980 at site 27, and again there in January 1981 when in sub-adult plumage and in company of immature white/orange (Fig. 3C). In S82, 2.5 years after marking, black/purple was the adult-plumaged owner of site 23. Another immature, pink/red, was marked in December 1978 at traditional site 24, beyond SA1 but near sites 23 (220m distant) and 33 (165m distant). We saw him six times in SA1 during November 1979 to May 1982, including once with immature white/orange at sites 15 and 27 (Fig. 3D). In S83 he was the new adult owner of site 24, almost five years after being marked there. Thus, the above three males, often sighted together, as immatures, occupied adjacent traditional sites when adults.

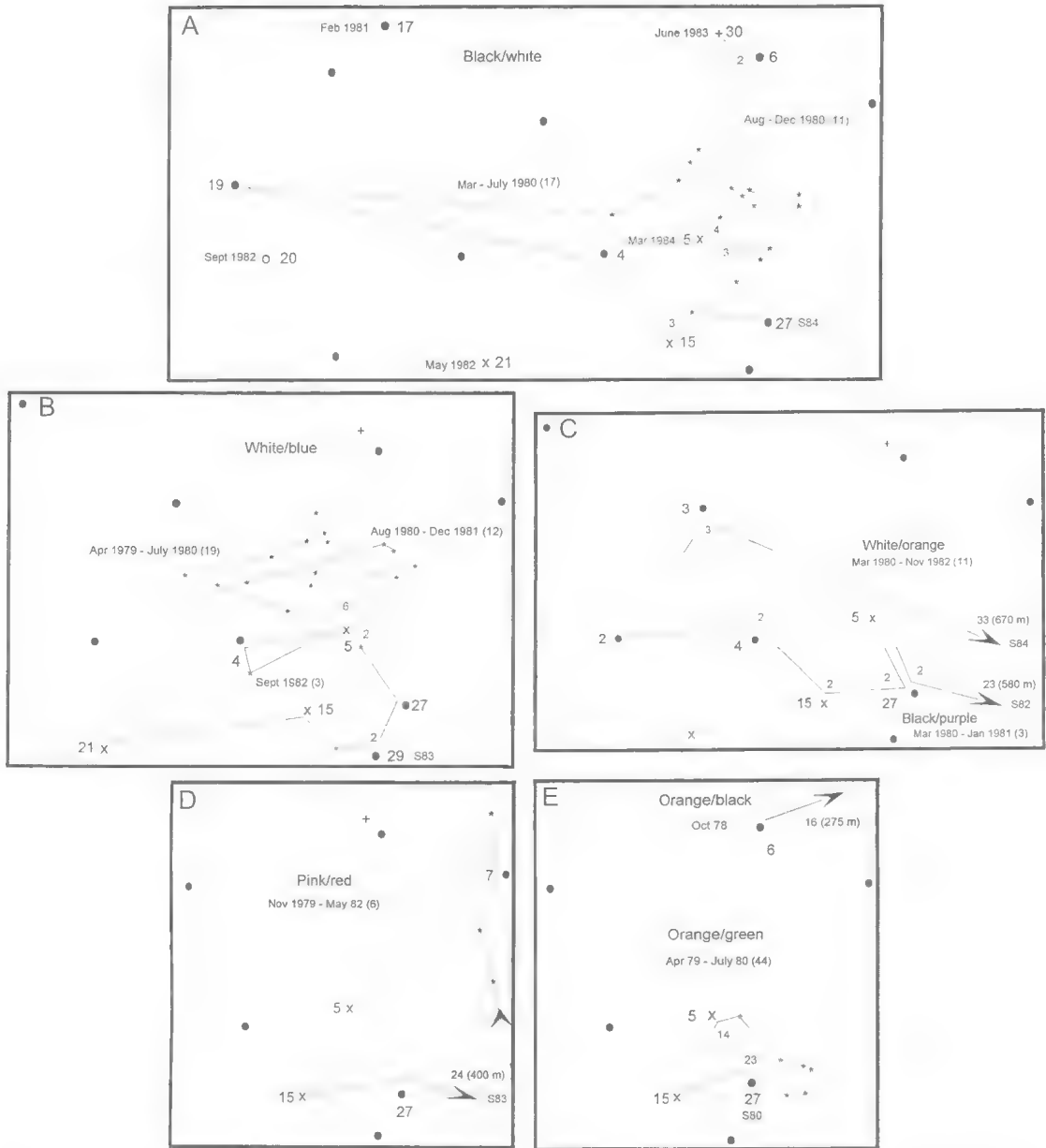


FIG. 3. Schematic plans to scale showing movements of seven immature male Golden Bowerbirds prior to them attaining adult plumage and then acquiring a traditional bower site, during S78-S84 within parts of study area SA1. Number of sightings, months they were made and the season (S) an individual male acquired a traditional bower site are noted within Fig. 3A-E. Bower sites actually located immediately beyond the perimeter are here plotted within the boundary line (see Fig. 1 for their distance beyond it). Distances travelled to bower sites beyond the SA1 boundary are indicated. ● = traditional bower sites with traditional owner; x = traditional bower site lacking traditional owner; and + = rudimentary bower site; * = sightings made other than at bowers.

Two young males took over traditional sites the year after we marked them: orange/black was marked in sub-adult plumage in October 1978 at

traditional site 6 and was next seen in S79, as the newly adult-plumaged owner of traditional site 16, 275m from site 6 (see Fig. 3E). Orange/green

was marked at site 5 in April 1979, as an immature. During March-July 1980, having just moulted into adult plumage, he challenged the traditional owner at site 27, being seen there 23 times; including 9 in the traditional owner's presence (Fig. 3E). During August-October of S80 both adults apparently attended site 27. Twice in late October we saw the challenger chasing the owner from the immediate bower area, and in early November he had become the new owner.

Males in Immature Plumage. Six of the 15 marked immatures remained in immature plumage when first occupying a traditional bower site, as follows:

Blue/orange was first marked 230m from bower site 5 in March 1979. From then until July 1980 we sighted him 17 times (see Fig. 4A). During S80 and S81 blue/orange remained closer to bower site 3, which he subsequently came to occupy. By May 1982 blue/orange had built a new bower based upon a pre-existing terrestrial subsidiary structure at site 3, 20m from the old one. He attained adult-plumage in 1983.

Pink/purple, first marked in December 1981 140m from site 3, was seen visiting site 3 and nearby traditionally-owned bowers several times (Fig. 4B). In early September 1982 he regularly attended bower site 1 before being displaced later that month by the owner of the previous season. In S84, still in immature plumage, he was the new owner of site 17. He acquired adult plumage the following year.

During early S78 the bower at traditional site 6 was attended by an adult male, that we marked there on 11 October, but was unseen again after 17 November. Another male, blue/purple, originally marked as an immature 205m from site 6 in January 1979, was seen four times at site 6 during February-March, and once at site 5 in April (Fig. 4C). During the winter months of 1979 a new rudimentary site (site 30) was established, 35m from site 6 (Figs 1 & 4C), and an immature male(s) was attending it but we could not confirm if he was banded. By October immature male blue/purple was the new occupant of site 6, and no more activity was seen at rudimentary site 30 that season. Our last sighting of blue/purple was in May 1979.

Red/purple, first marked in April 1979, started attending rudimentary site 30 together with immature black/white in July 1980, when a challenge was again underway for ownership of traditional site 6 (see above). By late November of S80 red/purple was the established new

occupant of site 6 (Fig. 4D). Red/purple may have acquired traditional site 6 early, due to the disappearance of immature-plumaged blue/purple (see above), because he did not become adult-plumaged until 1984, four years after becoming the traditional owner of that site. The bower at rudimentary site 30 was not attended until June 1983, when we saw red/purple (still the owner of site 6) there with black/white. Both birds were now in sub-adult plumage and black/white was possibly again challenging for site 6, but red/purple remained its traditional owner. Rudimentary site 30 was not used again.

Two other immatures had just acquired traditional sites (1 & 45) when first marked. Each site had a derelict bower, which had been abandoned for at least one season. Attendance by these two young males during their first nine months of occupancy was sporadic; as follows:

In March 1979 we found a handful of sticks, 20m from the old bower at site 1 and we marked its immature builder purple/green. In S79, he added little to the new structure, but was seen at rudimentary site 25 (first located by us in S78) and at sites 7, 15 and 27, some 580, 625 and 770m from site 1, respectively (Fig. 5). By S80 he was in adult-plumage and the new traditional owner of site 1. Rudimentary site 25 was abandoned.

In December 1979 we found a small new bower under construction at site 45, 30m from the derelict one. Its builder was immature black/red, who we marked at traditional site 21 (lacking a traditional owner) in October 1979 (Fig. 5). In March 1980 black/red was calling at newly established rudimentary bower site 42, 100m from site 45. By S80 he was the new traditional owner at site 45. Rudimentary site 42 was abandoned. Black/red was sub-adult in S81 and adult plumaged in S82.

HOME RANGES. Of Non-traditional Bower Owners. Of 15 immatures, 13 did not own a traditional site when marked and two (purple/green, black/red) were just acquiring one. Three of the 13 bowerless immatures (orange/black, green/blue and green/white) were not sighted after initial capture until adult bower-owners (see Fig. 2). During S78-S84 we made 182 sightings of the remaining 10 individuals: 113 at bower sites and 69 elsewhere (usually foraging; Table 1). Of the 113 sightings at bower sites: 38% were during August-December (courtship season), 5% January-February (wet season), 45% March-May (post-moult activity) and 12% June-July (Table 1).

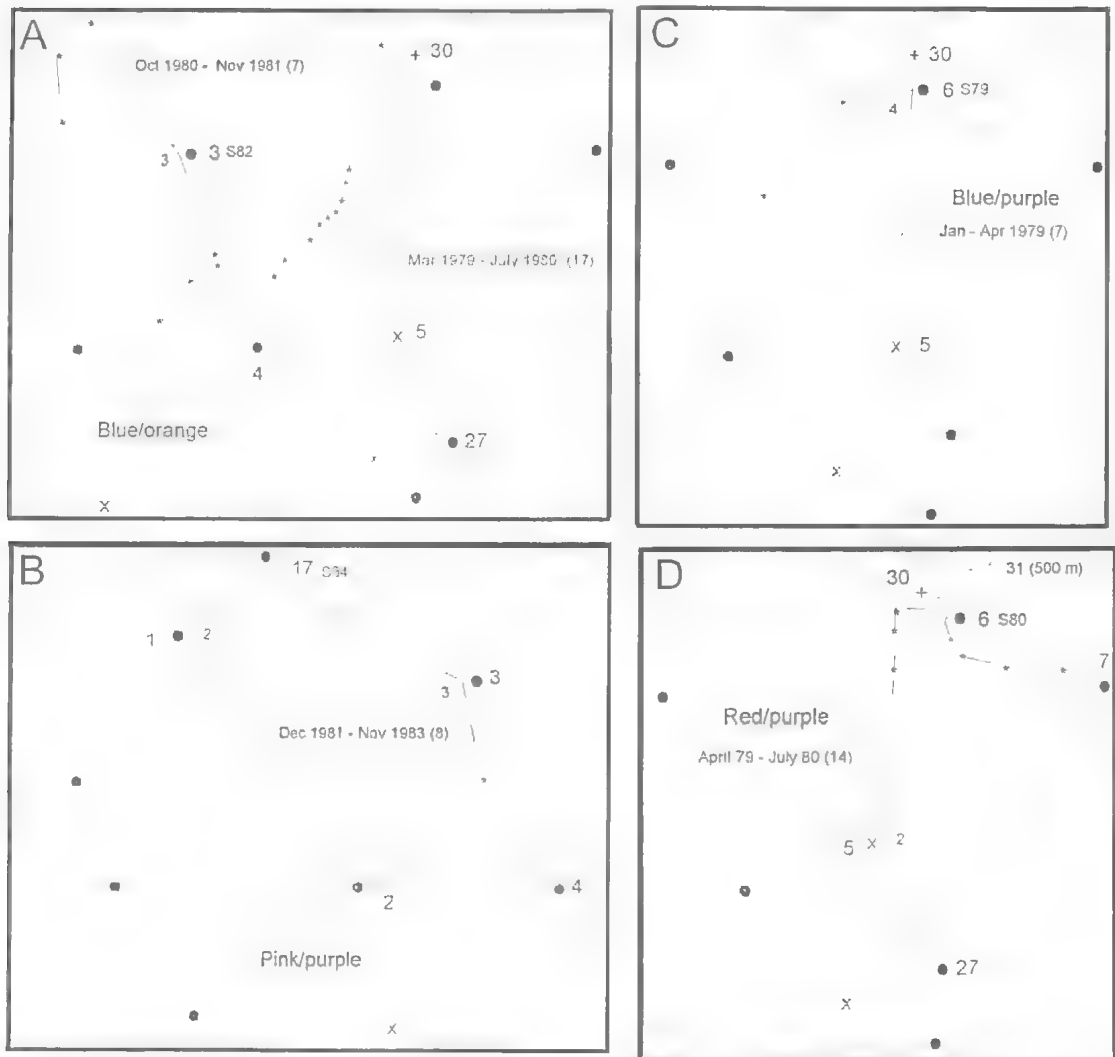


FIG. 4. A-D, Schematic plans to scale showing movements of four immature male Golden Bowerbirds prior to them occupying a traditional bower site while still wearing immature plumage, during S78-S84 within parts of study area SA1. Number of sightings, months they were made, and the season (S) an individual male acquired a traditional bower site are noted. Bower sites actually located immediately beyond the perimeter are here plotted within the boundary line (see Fig. 1 for their distance beyond it). Distances travelled to other bower sites beyond the SA1 boundary are indicated. ● = traditional site with traditional owner; x = traditional bower site lacking traditional owner; and + = rudimentary bower site; * = sightings made other than at bowers.

Of 113 sightings at bower sites: 58% were at traditional sites owned by traditional owners; 39% at sites 5, 15 and 21, lacking traditional owners; and 3% at rudimentary bower sites. These relative proportions varied, however, with individual bird age. Five to two years before the young males owned a traditional site these proportions were 51, 45 and 4%, but one year before such ownership they were 67, 31 and 2%, respectively (see Table 1). These differences

reflect the fact that in the year before occupying a traditional site, birds visited it more often, and particularly during March-July (24 of 25 sightings). Between five to two years before establishing bower tenure, immatures visited traditional bower sites more distant (mean = 391m) from their site of future occupancy than they did during the year immediately prior to occupying it (mean = 186m). But sightings of birds away from bowers involved distances

TABLE 1. Histories of sightings of 10 male Golden Bowerbirds marked as immatures (female-plumage) during different periods of months from August 1978-December 1984 at various bower site types and elsewhere. * = only 4 individuals were marked 5 seasons before coming to own a traditional bower site; the other 6 individuals were marked 3 (n = 3), 2 (n = 2) and 1 (n = 1) season before bower occupancy; ** = numbers in parenthesis are sightings of the young males at the bower site of their future occupancy; *** = number of sightings at traditional bower sites 5, 15 and 21 without a traditional owner; **** = 1 sighting represented up to 4 conspecifics visiting a bower simultaneously; see Results.

No. of seasons individuals were marked prior to occupying a traditional bower (no. of individuals *)	Sightings at bower sites						Sightings elsewhere		
	At traditional bower sites		At rudimentary bower sites	At all bower sites	In company of of a conspecific (s) ****	Mean distance (m) from bower site of future occupancy	In total	In company of a conspecific(s) ****	Mean distance (m) from bower site of future occupancy
	with atraditional owner **	lacking a traditional owner ***							
August-December									
5 (n = 4)	2 (1)	0	0	2	1	165	0	0	0
4 (n = 4)	4 (2)	5	1	10	3	408	7	1	88
3 (n = 7)	0	4	0	4	0	230	5	5	315
2 (n = 9)	10 (1)	1	0	11	2	516	1	0	264
1 (n = 10)	5	11	0	16	2	211	10	2	185
Total/mean	21 (4)	21	1	43	8	332	23	8	201
January-February									
5 (n = 4)	0	0	0	0	0	0	0	0	0
4 (n = 4)	2	0	0	2	2	625	0	0	0
3 (n = 7)	1	0	0	1	0	925	0	0	0
2 (n = 9)	1	0	0	1	0	400	0	0	0
1 (n = 10)	2 (2)	0	0	2	0	0	1	0	205
Total/mean	6 (2)	0	0	6	2	650	1	0	205
March-May									
5 (n = 4)	4 (1)	7	0	11	4	356	6	1	150
4 (n = 4)	3	3	0	5	3	444	7	2	325
3 (n = 7)	2	3	0	6	1	358	8	0	166
2 (n = 9)	2	6	1	9	7	250	5	0	202
1 (n = 10)	16 (15)	4	0	20	4	197	4	0	54
Total/mean	27 (16)	23	1	51	19	316	30	3	144
June-July									
5 (n = 4)	0	0	0	0	0	0	4	1	124
4 (n = 4)	1	0	0	1	1	220	5	1	312
3 (n = 7)	0	0	0	0	0	0	0	0	0
2 (n = 9)	1	0	1	2	0	255	0	0	0
1 (n = 10)	9 (9)	0	1	11	0	40	6	2	39
Total/mean	11 (9)	0	2	13	1	193	15	4	165
August-September									
5 (n = 4)	6 (2)	7	0	13	5	344	10	2	142
4 (n = 4)	10 (2)	8	1	19	9	430	19	4	225
3 (n = 7)	3	7	1	10	1	430	13	5	265
2 (n = 9)	14 (1)	7	2	23	9	415	5	2	207
1 (n = 10)	32 (26)	15	1	48	6	186	19	4	123
Total/mean	65 (31)	44	4	113	30	345	69	15	177

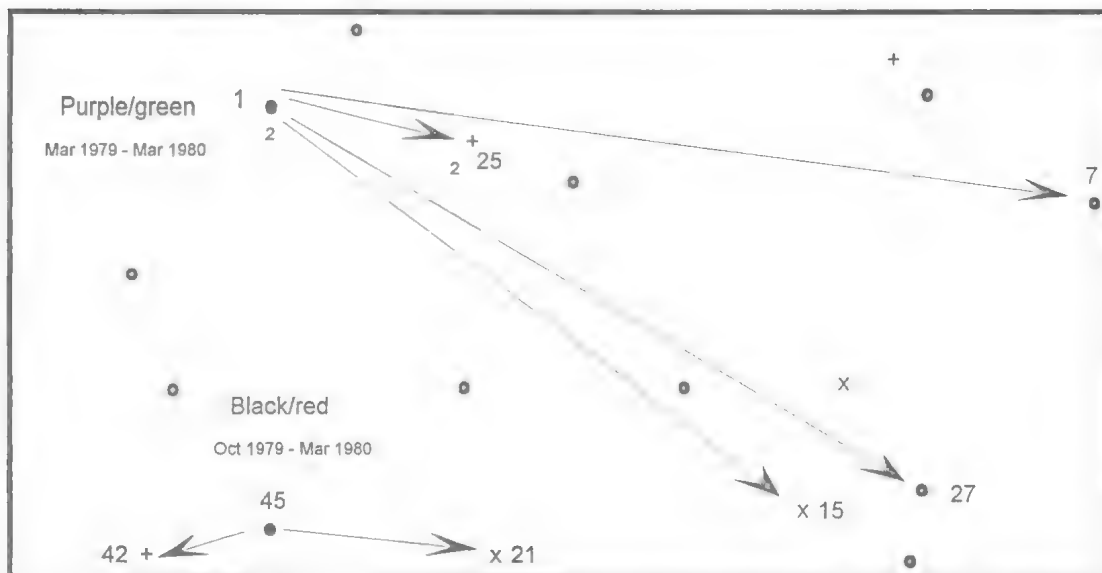


FIG. 5. Schematic plan to scale of the movements of two immature male Golden Bowerbirds that had just occupied a traditional bower site while still wearing immature plumage, during S78-S84 within parts of study area SA1. Number of sightings are indicated. Bower sites actually located immediately beyond the perimeter are here plotted within the boundary line (see Fig. 1 for their distance beyond it). ● = traditional site with traditional owner; x = traditional bower site lacking traditional owner; and + = rudimentary bower site.

closer to the site of their future occupancy, particularly during the season prior to bower ownership (see Table 1).

Of a total of 182 sightings, at bower sites and elsewhere, a marked immature was seen with 1 ($n = 29$), 2 ($n = 8$), 3 ($n = 7$) or 4 ($n = 1$), marked or unmarked, female-plumaged conspecifics (see Table 1). Twice we saw an immature together with an adult, other than the bower owner, at a bower site. Most sightings (67%) of marked immatures at bower sites 5, 15 and 21 involved two or more individuals, particularly during March-May (63% of sightings).

Of Traditional Bower Owners. During S78-S84 we made 152 sightings of 18 of the total 20 individually marked traditional bower-owners of 12 traditional bower sites in SA1. Sixty-eight were of birds at bower sites neighbouring their own, and 84 elsewhere (Table 2). Of the former 68 sightings: 71% were at traditional sites occupied by a traditional owner; 20% at traditional sites (5, 15 and 21) irregularly attended by immatures; and 9% at rudimentary bower sites attended by young males (Table 2). It is noteworthy that all visits to rudimentary sites were by immatures in their first year of traditional bower-ownership (see *Males in immature plumage*).

Most visitations (82% of 68 sightings) to other bower sites, particularly traditional ones with traditional owners (92%), occurred during display months of late August-December (Table 2). We confirmed that >57% of such visits were to steal decorations (Table 2). Nearly all thefts were from adjacent sites, although a few males travelled further afield to steal (Fig. 6A). Thefts only occurred during the display season.

Distances travelled to other bower sites and elsewhere varied little during different months of the year (summarised in Table 2). Visits by males to bower sites other than their own involved an average distance of 191m ($n = 68$, range 40-488m) with a median of 195m, and to elsewhere (usually to forage) averaged 110m ($n = 84$, range 13-300m) with a median of 88m (Table 2). Thus, males remained closer to their traditional sites when foraging (or harvesting a decoration) than in visiting other bowers. Foraging home ranges rarely overlapped those of neighbouring male bower owners (Fig. 6B). Mean distance travelled from bower sites to all localities averaged 144m ($n = 152$) with a median of 121m. By plotting all sightings of marked owners at eight traditional bower sites (i.e. Fig. 6A and B combined), and drawing polygons based upon the outermost for each (Fig. 6C), we estimated

TABLE 2. Histories of sightings of 18 traditional bower-owning male Golden Bowerbirds at 12 traditional sites during different periods of months from August 1978-December 1984 at bower sites other than their own and elsewhere. * = number of sightings at traditional bower sites 5, 15 and 21 lacking a traditional owner; ** = decoration theft confirmed, but some other sightings probably also involved theft; *** = one sighting was with one conspecific; see Results.

Months	Sightings at bower sites						Sightings elsewhere			
	At traditional bower sites		At rudimentary bower sites	At all bower sites	For decoration theft **	In company of a conspecific ***	Mean distance (m) travelled to other bower sites	Away from their bower site	In company of a conspecific ***	Mean distance (m) travelled to other bower sites
	with a traditional owner	lacking a traditional owner *								
August-December	45	9	2	56	39	1	205	35	4	125
January-February	2	0	0	2	0	0	168	9	0	106
March-May	1	3	3	7	0	1	156	28	1	110
June-July	0	2	1	3	0	2	175	12	0	102
Total/mean	48	14	6	68	39	4	191	84	5	110

mean overall home range to be 7ha (range 3-10ha).

On nine occasions we saw an adult in the company of an immature, four whilst an adult visited another traditional site, and five times while foraging in the same fruiting tree (Table 2). While bower owning males vigorously displaced, and then chased, rival males out of their bower site, we recorded only one instance of apparent territoriality beyond bower sites. Adult males, from two adjacent bower sites, were aggressively challenging each other along a 200m length of narrow trail in rainforest equidistant between their bower sites. The birds gave scold and other calls, and flicked their wings in agitated fashion, while flying back and forth along their respective sides of, but not across, the trail. On another occasion two adult males foraged in the same fruiting tree without aggression.

DISCUSSION

Most traditional Golden Bowerbird bower sites are occupied by successive generations of adult males (Frith & Frith, 2000a; unpubl. data). Takeovers of traditional sites usually involved an intruding male being in his first year of adult plumage. In a few instances, a traditional bower-owner was not replaced immediately by another adult male and, then, one of three things happened. a) A short-term rudimentary bower site was established close to the vacated traditional site, by immature males building a rudimentary structure there. This was abandoned once one male began regular attendance at the

traditional site. b) A vacated traditional bower site was temporarily and irregularly attended by immature males who maintained the existing traditional bower, or built a rudimentary one. Such a new rudimentary bower might subsequently become a larger traditional one, as a new owner regularly attended the site (Frith & Frith, 2000a, unpubl. data). c) But rarely, a traditional site was simply abandoned. Abandoned traditional sites may, however, be re-established during subsequent seasons.

An immature male Golden Bowerbird wanders among the male population for at least five to six years before attaining first signs of adult plumage (Frith & Frith, unpubl. data). This wandering period possibly permits the novice to experience the social/sexual environment, while his female appearance avoids stimulating aggressive responses from adult males. This provides a gradual 'apprenticeship' into the intensely competitive male mating hierarchy, as has also been postulated for males of the sexually dimorphic polygynous manakin (Pipridae) and bird of paradise (Paradisaeidae) species (Lill, 1974a,b; Snow, 1976; Frith & Beehler, 1998). It has been suggested that the long retention of female plumage by males of such species might be part of a mating strategy, involving sexually active males thus concealing their reproductive status (Rohwer et al. 1980, Laska et al., 1992). Immature male Goldens moved extensively about the habitat visiting bower sites, mostly during display months of late August-December, and during the brief period of renewed activity that occurred in late March-

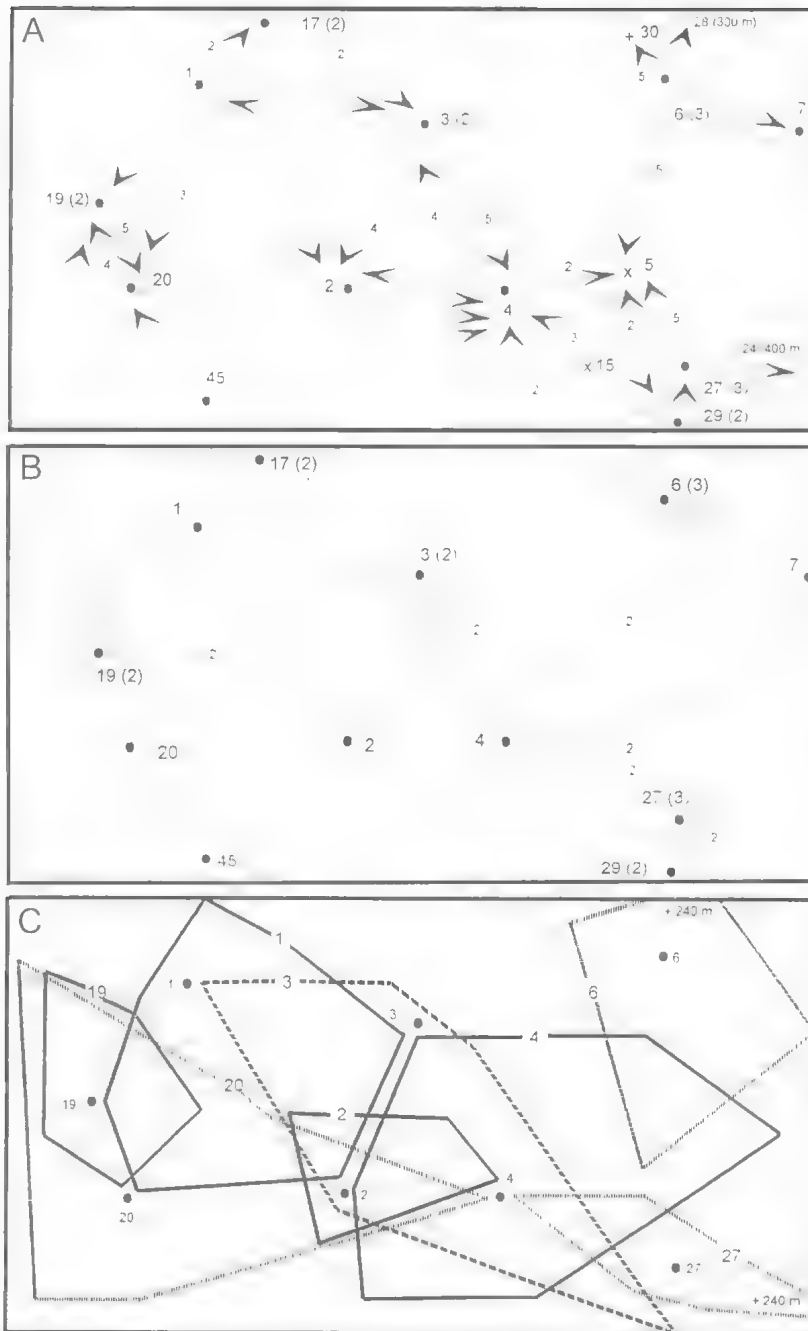


FIG. 6. Schematic plans to scale of the movements of 18 traditional male owners of 12 traditional Golden Bowerbird bowers: A, to neighbouring bower sites; or B, to elsewhere; usually when foraging within part of study area SA1, during S78-S84. C, Approximated home ranges, produced by encompassing all bower visits and sightings elsewhere into polygons. Note: a number in parenthesis after a bower site number indicates the number of consecutive individual traditional owners during this study. Smaller typeface numbers on arrow lines indicate the number of movements/visits. Bower sites actually located immediately beyond the perimeter are here plotted within the boundary line (see Fig. 1 for their distance beyond it). Distances travelled to other bower sites beyond SA1 are indicated. ● = traditional site with traditional owner; x = traditional bower site lacking traditional owner; and + = rudimentary bower site.

early May. Having completed their moult, young males were also notably active at traditional sites during March-early May, when traditional owners were less often in attendance and completing their moult (Frith & Frith, unpubl. data). One year before becoming full-time bower owners themselves, immatures spent more time at traditional sites occupied by traditional owners, especially at the site they were challenging for and subsequently occupied. Such visits increased notably during March-July of the season of subsequent tenure, the challenger having usually just attained adult plumage.

Bower attendance by traditional owners at their own sites was mainly during display and breeding months (Frith & Frith, 1998, 2000b). During this time of year they frequently visited bowers of rival males to steal decorations (Table 2). In recent years bower decoration theft has been studied intensively in other species, and it has been demonstrated that males steal predominantly from immediate neighbours (Borgia, 1985; Pruett-Jones & Pruett-Jones, 1994; Frith & Frith, 1993, 1994, 1995, 2000b). Our observations show Golden Bowerbirds do likewise, as demonstrated in Figure 6. For a discussion on bower decorations and their theft see Frith & Frith (2000b).

Distances traditional bower-owning Golden Bowerbirds travelled from their own bower to other bower sites to steal decorations averaged 191m (median 195m). Distances covered to forage and harvest decorations, were shorter (mean = 110m, median = 88m). The overall median distance males travelled from their bower sites was 121m. This latter figure for male bower-owning Macgregor's Bowerbird was 88m (Pruett-Jones & Pruett-Jones, 1983) and for court-owning Tooth-billed Bowerbirds was 59m (Frith et al., 1994), despite the latter species travelling longer distances to bathe/drink at creeks (not observed in Golden Bowerbirds by us). Similarly, the median distance of 88m travelled by Goldens to forage is more than double that (32m) observed in Tooth-bills (Frith et al., 1994). These differences may reflect the sparsely and evenly dispersed males/bowers of Macgregor's and Goldens, in contrast with the densely clumped, dispersion of 'Tooth-bills' courts. It could also indicate the relative abundance of foods of the latter species.

Male Satin Bowerbirds were found to mostly (82%) forage within 50m of their bowers during the breeding season of October-December

(Donaghey, 1981). These are far more insects during this period than at other times (40-50% of their November-December diet). During winter, however, 81% of foraging males were up to 200m from their bowers, and the furthest 350m. Male Satins do not form leks, but disperse bowers linearly along forest edges at a mean inter-bower distance of 312m (Donaghey, 1981) to 500m (Marchant, 1992). The latter author wrote of males thus having 'a territory of about 20 ha'. Vellenga (1980) wrote of each adult male Satin holding a territory that included the rudimentary bowers of (dominated) younger males. Although territoriality beyond the bower site would be less surprising in this more insectivorous bowerbird than in highly frugivorous ones (Beehler & Pruett-Jones, 1983; see below) this requires study and clarification.

We estimated the mean year-round home range of (one or several consecutive) Golden Bowerbird male owners of eight traditional bower sites to be 7ha. Mean home range of four radio-tracked adult male Tooth-billed Bowerbirds was determined to be 9.5ha, although males foraged over a smaller area (Frith et al., 1994). Data available for fixed-point-displaying polygynous and frugivorous species of other passerine groups so studied include the neotropical Manakins, and Cotingas (Cotingidae), (Snow, 1970; Snow, 1962a,b, 1992; Lill, 1974a,b, 1976; McDonald, 1989; Thery, 1990; Prum et al., 1996). These studies found that adult males defend a focal display site, or territory, while foraging over a far more extensive undefended area, or home range. Beehler and Pruett-Jones (1983) reviewed spatial dispersion of adult males in nine polygynous bird of paradise species, in which males are known or presumed to be promiscuous and to court at fixed point display sites (Frith & Beehler, 1998). They related dispersion to diets, and found that males of species with a predominantly arthropod diet were territorial whilst those of predominantly frugivorous ones were not. Obligate insectivores defended exclusive territories, highly frugivorous species formed leks, and species with intermediate diets showed intermediate patterns of dispersion. Thus while males of all species defend their display sites, only those of the more insectivorous species defend a foraging territory while males of more frugivorous ones forage over an undefended home range.

Adult male Golden Bowerbirds vigorously defended their bower site against rivals, but we saw too little of adult males together away from bowers to assess the nature of interactions there.

While male Macgregor's Bowerbirds aggressively defend bower sites, few aggressive interactions occurred away from them (Pruett-Jones & Pruett-Jones, 1982). Our findings suggest the observation that 'Although males do not defend territories in the usual sense, they do occupy areas over which they exert dominance. We do not mean that males exclude rivals from the area (beyond the bower site) or prevent them from foraging there, but that they do prevent rivals from establishing courtship sites' (Beehler & Foster, 1988) is applicable to male Golden Bowerbirds. Further field work is required to clarify the question of (undefended) foraging home range versus the extent of (defended) territory in this species.

Fruit in tropical rainforest is largely economically undefendable by passerine birds, as a result of its spatial and temporal unpredictability (Snow, 1976; Lill, 1976; Beehler, 1983; Beehler & Pruett-Jones, 1983; Frith & Beehler, 1998). Thus the loss of extensive territoriality in predominantly frugivorous species, such as the Golden Bowerbird. Fruit availability in time and space may therefore have profound effects upon home ranges of bowerbirds (Beehler & Pruett-Jones, 1983; Frith et al., 1994). Male bowerbirds must remain close to their bowers if they are to successfully defend their structures and decorations from rivals, and attract and mate females (Frith & Frith, 1993). They attempt to maximise time spent at their bowers, as do Tooth-billed Bowerbirds at their courts (Moore, 1991; Frith & Frith, 1994). This is predictable behaviour for a population of promiscuous males that must compete for opportunities to fertilise numerous females at a fixed focal site during a relatively brief mating season (Frith & Frith, 1993, 1995).

Snow (1976) considered a predominantly frugivorous diet the main pre-condition to a polygynous mating system, in which rainforest dwelling male passerines spend most of their time in advertising/attending/defending a traditional focal courtship area and performing elaborate courtship. Seasonal abundance of fruit in the habitat is theoretically so great as to enable males to be emancipated from nesting duties, and females to nest alone and unaided. In tropical rainforest-dwelling and predominantly frugivorous Golden Bowerbirds, and in many other ecologically similar passerines, the fruit diet would appear to have greatly influenced the evolution of a polygynous mating system, associated morphology, male survival and longevity, dispersion, focal courtship sites with

territoriality limited to them, and undefended home ranges (Snow, 1976; Frith & Beehler, 1998).

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SOME NEW GIVETIAN (LATE MIDDLE DEVONIAN) GASTROPODS FROM THE
PAFFRATH AREA (BERGISCHES LAND, GERMANY)

JIRI FRÝDA

Frýda, J. 2000 06 30: Some new Givetian (late Middle Devonian) gastropods from the Paffrath area (Bergisches Land, Germany). *Memoirs of the Queensland Museum* 45(2): 359-374. Brisbane. ISSN 0079-8835.

Revision of Givetian (Middle Devonian) gastropods from the Paffrath area (Bergisches Land, Germany) has identified a large number of new taxa described herein. These are *Retispira tasselli* sp. nov., *Stenoloron (Paffratholoron) goldfussi* subgen. et sp. nov., *Quadricarina (Blodgettina) reticulata* subgen. et sp. nov., *Kirchneriella* gen. nov., *Eiserhardtia inepta* gen. et sp. nov., *Cerithioides whidbornei* sp. nov., *Plagiothyra multispiralis* sp. nov., *Naticopsis (Paffrathopsis)* subgen. nov., *Paffrathia lotzi* gen. et sp. nov., *Cookiloxa pulchra* gen. et sp. nov., *Palaeozygopleura (Rhenozyga)* subgen. nov. and *Heteroloxonema* gen. nov. □ *Gastropods, Devonian, Givetian, Germany.*

Jiri Frýda, Czech Geological Survey, Klárov 3, 118 21 Praha 1, Czech Republic, (fryda@cgu.cz); 14 January 2000.

During the last fifteen years the number of studies on Devonian gastropods has increased rapidly (e.g., Blodgett & Rohr, 1989; Blodgett, 1992, 1993; Blodgett & Johnson, 1992; Kase & Nishida, 1986, 1988; Horný, 1992, 1994; Horný & Jordan, 1993; Frýda, 1992, 1998c,d, 1999b; Frýda & Manda, 1997; Frýda & Bandel, 1997; Gubanov et al., 1995; Cook, 1993, 1997; Cook & Camilleri, 1997; Bandel & Frýda, 1998). Impetus for increased interest in this relatively neglected group of Devonian fossils were the seminal studies of Blodgett et al. (1988, 1990) who identified the great potential utility of Palaeozoic gastropods as paleobiogeographic indicators. In addition, research focused on the higher taxonomy of the Devonian gastropods, based on protoconch morphology, has shown that during Devonian time a large change-over occurred from a fauna of typical Early Palaeozoic cast, to one of a more modern aspect (see Frýda, 1999a and references therein). Revision of the Givetian (Middle Devonian) gastropods from Germany (Frýda, 1998a) have identified a large number of new taxa and revised material untouched for up to 150 years (Goldfuss, 1844). The results of this revision have only partially been published (Bandel & Frýda, 1998, 1999; Frýda, 1998b, 1999a) and the majority of them have been prepared for monographic publication. Because new taxonomic names established in an unpublished study (Frýda, 1998a) are prepared to be used in non-taxonomic studies by other authors, there is a problem with their priority as well as the fact that some of them would be *nomina nuda*. For this reason, some new Givetian (Middle Devonian) gastropods

from the Paffrath area (Bergisches Land, Germany) are established herein. Monographic treatment with detailed descriptions of all species belonging to newly established taxa as well as the evaluation of their palaeogeographical and stratigraphical distributions is in preparation (Frýda & Bandel, in prep.). All described gastropods come from the collection of Dr Volker Ebbighausen and are deposited in the Senckenberg Museum in Frankfurt au Main (Germany).

SYSTEMATIC PALAEOONTOLOGY

AMPHIGASTROPODA Simroth, 1906
BELLEROPHONTOIDEA M'Coy, 1851
BELLEROPHONTIDAE M'Coy, 1851
KNIGHTITINAE Knight, 1956

Retispira Knight, 1945

TYPE SPECIES. *Retispira bellireticulata* Knight, 1945.

REMARKS. *Retispira* (Knight, 1945) is a complex genus within Knightitinae later regarded as a subgenus of *Knightites* Moore, 1941 (Knight et al., 1960). Batten (1972) suggested that *Retispira* represents a separate genus and this was followed by Gordon & Yochelson (1987). *Retispira* ranges from the Devonian to the Permian.

Retispira tasselli sp. nov.

(Fig. 1F-J)

ETYMOLOGY. For the Australian paleontologist Chris Tassell.

MATERIAL. 6 specimens from Herrenstrunden, locality 9, Bergisches Land, Germany (coll. Ebbighausen). Holotype: figured herein as Fig. 1F,G

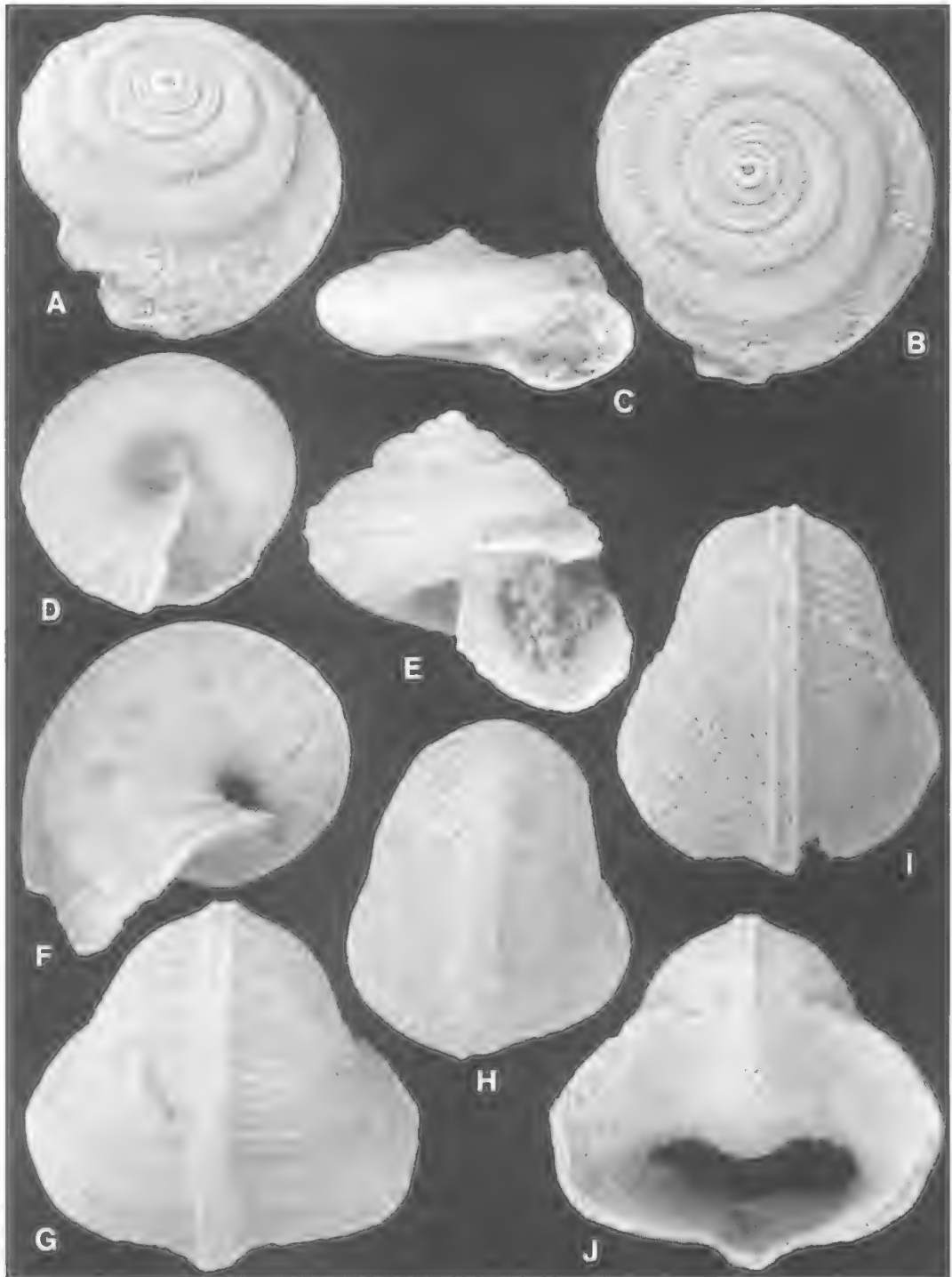


FIG. 1. A-C, *Stenoloron (Paffratholoron) goldfussi* sp. nov. A, Holotype, oblique view $\times 3.5$; B, Holotype, apical view $\times 3.6$; C, Paratype, apertural view $\times 3.8$. D, E, *Quadricarina (Blodgettina) reticulata* sp. nov. D, Holotype, basal view showing a reticular pattern $\times 4$; E, Holotype, apertural view $\times 5$. F-J, *Retispira tasselli* sp. nov. F, Holotype, lateral view showing a shell ornamentation $\times 4.8$; G, Holotype, dorsal view $\times 4.8$; H, Paratype A, dorsal view $\times 7$; I, Paratype B, dorsal view $\times 4.5$; J, Paratype C, apertural view $\times 5$.

TYPE LOCALITY. Bücheler Schichten, Middle Devonian (Givetian), Herenstrunden, Bergisches Land, Germany.

DIAGNOSIS. Species of *Retispira* with small shell having a broad, flat selenizone raised above the shell dorsum; shell narrowly and deeply phaneromphalous; lateral portions of whorl profile rounded into narrow umbilici without any angulation; apertural lip of mature whorl is slightly expanded on its lateral and umbilical portions; shell ornament consisting of spiral and collabral lirae forming a reticulate pattern of longitudinally elongated rectangles.

DESCRIPTION. Small bellerophontid shell bearing a broad, flat selenizone raised above shell dorsum. Shell narrowly and deeply phaneromphalous. Whorl profile slightly concave on each side of selenizone and gently convex in dorsolateral portions. Lateral portions of whorl profile curve into narrow umbilici without any angulation. Shallow and wide sinus in anterior margin of the outer lip culminates in a slit generating a raised selenizone. Selenizone bounded by two distinct spiral threads; width of the selenizone about 15% of width of shell dorsum. Apertural lip of the mature whorl slightly expanded on its lateral and umbilical portions. Shell ornament consists of spiral and collabral lirae; collabral lirae widely spaced and more expressed than closely spaced spiral lirae; spiral lirae crossing the collabral lirae form a reticulate pattern of longitudinally elongate rectangles. Distances of both spiral and collabral lirae vary considerably during the ontogeny.

REMARKS. *Retispira tasselli* resembles *Retispira leda* (Hall, 1861) from the Middle Devonian of North America in its similar whorl expansion in the adult whorl. However, *R. tasselli* sp. nov. differs by having a narrower shell, raised selenizone and by the absence of ornamentation of its selenizone. *Bellerophon elegans* de Ferussac & Orbigny, 1840 noted by Archiac & Verneuil (1842: 354, pl. 29, fig. 2) from the Paffrath region is similar to *Retispira tasselli* and most probably also belongs in *Retispira*. It is distinguished from the latter by the absence of a raised selenizone. *Retispira tasselli* is also similar to *Retispira* sp. of Blodgett (1992) from the Eifelian of Alaska, but may be distinguished by its more raised selenizone.

Rollins et al. (1971) discussed similarities of *Retispira* and *Bucanopsis* which have similar shell shapes. *Merriamites* Blodgett & Johnson, 1995 (= *Merriamella* Blodgett & Johnson, 1992,

previously occupied homonym), based on the Middle Devonian species *Merriamites eurekae* from Nevada, is also similar to *Retispira* in having a reticulate ornamentation. *Merriamites* differs from *Bucanopsis*, the latter having an ornament of spiral threads, in having a much broader longitudinal keel on the inner floor of the whorl, a prominent reticulate pattern and a prominent, rounded parietal tooth. The presence of a keel on the inner floor of the whorl is a character by which *Bucanopsis* and *Merriamites* (both are placed in Carinaropsinae) differ from *Retispira*. Similarities in these genera with some Knightitinae were also noted by Blodgett & Johnson (1992).

ARCHAEOGASTROPODA Thiele, 1925
GOSSELETINIDAE Wenz, 1938

Stenoloron Oehlert & Oehlert, 1888
Stenoloron (*Paffratholoron*) subgen. nov.

TYPE SPECIES. *Stenoloron* (*Paffratholoron*) *goldfussi* sp. nov.

ETYMOLOGY. *Paffratholoron*, for the type locality.

DIAGNOSIS. Subgenus of *Stenoloron* Oehlert & Oehlert, 1888 having low spired, phaneromphalous shell with slowly expanding whorls.

REMARKS. *Stenoloron* (*Paffratholoron*) subgen. nov. has slowly expanding whorls. The distance of the upper suture from the shell periphery (measured in the apical view) is about 15% of its total shell width. This value is double (i.e. 30%) in the generic type species, *Stenoloron viennayi* (Oehlert & Oehlert, 1888). In addition, Devonian species of *Stenoloron* Oehlert & Oehlert, 1888, such as *Stenoloron subaequitera* (Chapman, 1916) from the Early Devonian of Australia, *Stenoloron minor* Blodgett & Johnson, 1992, from the Middle Devonian of North America, and *Stenoloron pollens* Pernier, 1903 from the Early Devonian of Europe have similar values of whorl expansion as the type species (i.e. about 30%). For this reason the species described below is placed in a new subgenus.

Stenoloron (*Paffratholoron*) *goldfussi* sp. nov.
(Fig. 1A-C)

ETYMOLOGY. For the German paleontologist August Goldfuss, who studied Devonian gastropods of the Paffrath area.

MATERIAL. 3 specimens from Unterthal, Paffrath area, Bergisches Land, Germany (coll. Ebbighausen). Holotype: figured herein as Fig. 1A,B.

TYPE LOCALITY. Unterer Plattenkalk, Middle Devonian (Givetian), Unterthal, locality 63, Bergisches Land, Germany.

DIAGNOSIS. As for subgenus.

DESCRIPTION. Small, turbiniform shell with a wide umbilicus, width about one quarter of total shell width. Width of shell having about 7 whorls measures about 15mm. Sides of shell slightly convex (i.e. cyrtocoenoid) due to decrease of the pleural angle in the last two whorls. Narrow, slightly convex selenizone situated high on the whorl bounded by a single shallow groove on the each side. Whorl profile above the selenizone rounded and nearly subhorizontal at the upper suture; sutures are shallow. Suture just below its selenizone in younger whorls; in the mature whorl, the distance of the lower groove bounding the selenizone and the lower suture is about one half of selenizone width. Shell surface smooth.

The initial portion of the shell is lost in the holotype but it is preserved in another specimen from the same locality figured herein as Fig. 1C. The high spired early whorls distinctly protrude above the upper, convex shell surface. During the further shell growth, the pleural angle continually increases, but in the last two whorls it again slightly decreases. For this reason the sides of the early shell are concave and slightly convex in the mature shell.

REMARKS. *Stenoloron (Paffratholoron) goldfussi* sp. nov. is the only species assigned to the subgenus. It is distinguished from the species of *Stenoloron (Stenoloron)* by shape of its many-whorled shell and characteristic slow expansion. The selenizone in *Stenoloron (Paffratholoron) goldfussi* sp. nov. is wider than in the generic type species *Stenoloron (Stenoloron) viennayi* and *Stenoloron (Stenoloron) subaequitera* (Chapman, 1916), but is similar in width to *Stenoloron (Stenoloron) minor* Blodgett & Johnson, 1992. *Stenoloron (Paffratholoron) goldfussi* represents the youngest occurrence of the genus, previously reported from the Early Devonian and Silurian. The only other Middle Devonian species known is *Stenoloron (Stenoloron) minor* Blodgett & Johnson, 1992 from the Eifelian of central Nevada.

EOTOMARIIDAE Wenz, 1938

Quadricarina Blodgett & Johnson, 1992 *Quadricarina (Blodgettina)* subgen. nov.

TYPE SPECIES. *Quadricarina (Blodgettina) reticulata* sp. nov.

ETYMOLOGY. For the American paleontologist Robert B. Blodgett.

DIAGNOSIS. Similar to *Quadricarina (Quadricarina)*, with low spired shell having distinctly raised selenizone above the whorl surface; shell ornament consisting of reticulate pattern.

REMARKS. *Quadricarina* Blodgett & Johnson, 1992 is represented by four Middle Devonian species. Three species, including its type species *Quadricarina glabrobasis* Blodgett & Johnson, 1992, come from the Eifelian of Nevada. Blodgett & Johnson (1992) also include *Pleurotomaria lenticularis* Goldfuss, 1844 from the Givetian of Germany. The turbiniform, phaneromphalous shells of *Quadricarina* species are characterised by a selenizone bordered by two pairs of revolving cords. A gently concave selenizone is situated at mid-whorl height. Shell ornament consists of fine collabral ribs. *Quadricarina (Blodgettina)* subgen. nov., is similar to hitherto known species of *Quadricarina (Quadricarina)* in general shell shape and the position of the selenizone, but differs in having a distinctly raised selenizone above the whorl surface and reticulate shell ornament.

Quadricarina (Blodgettina) reticulata sp. nov. (Fig. 1D,E)

ETYMOLOGY. In reference to the presence of reticulate ornamentation.

TYPE LOCALITY. U. Plattenkalk limestones, Middle Devonian (Givetian), Unterthal, locality 63, Bergisches Land, Germany.

MATERIAL. 10 specimens from Unterthal, locality 63, Bergisches Land, Germany (coll. Ebbighausen). Holotype: figured herein as Fig. 1D,E.

DIAGNOSIS. As for subgenus.

DESCRIPTION. Small, turbiniform shell with a selenizone situated at shell periphery. Mature spire consisting of about six whorls, width approximately 13mm. Outer lip of aperture forms a shallow sinus culminating in a peripheral carina that gives rise to a flat selenizone; selenizone distinctly protruding above whorl surface. Selenizone bordered by two pairs of revolving cords; outer pair forming its margin and inner pair spaced between outer cords. Inner cords always slightly thinner than the outer cords. Very narrow groove between the inner cords. Upper and lower whorl surfaces convex; sutures deep and impressed. Whorl profile below selenizone forms a rounded shell base with a deep, funnel-

like umbilicus. Width of umbilicus about one quarter of total shell width. Whorls embrace below the selenizone. Distance between lower margin of selenizone and lower suture greater than width of the flat, protruding selenizone. Shell ornament above and below spiral and collabral threads forming a reticulate pattern. About 25 spiral threads below the selenizone form small tubercles where they are crossed by collabral threads.

REMARKS. *Quadricarina* (*Blodgettina*) *reticulata* subgen. et sp. nov. may be distinguished from all species of *Quadricarina* (*Quadricarina*) by the presence of peripheral carina bearing a selenizone and by its reticulate ornamentation. However, it resembles *Quadricarina* sp. nov. B of Blodgett & Johnson (1992) in its low-spined shell, wide umbilicus and slightly raised, carinate periphery but differs by having the selenizone distinctly situated above the suture, and having reticulate ornament. Whorls embrace slightly above the selenizone in *Quadricarina* sp. nov. B. The carinate periphery suggests that the poorly known *Quadricarina* sp. nov. B may belong to *Quadricarina* (*Blodgettina*).

RAPHISTOMATIDAE Koken, 1896
OMOSPIRINAE Wenz, 1938

Kirchneriella gen. nov.

TYPE SPECIES. *Turbo striatus* Hisinger in Goldfuss, 1844.

ETYMOLOGY. For the German paleontologist Heinrich Sylvester Kirchner, who in 1915 published 'Mittel-devonische Gastropoden von Soetenich in der Eifel'.

DIAGNOSIS. Turbiniform, relatively low-spined shell with a very indistinct selenizone situated high on the whorls; lateral side of whorls rounded; shell ornament consisting only of spiral cords; spiral cords on the phaneromphalous shell base generally regularly spaced; more closely spaced than those on the upper whorl surface; a spiral cord is also present on the selenizone surface.

REMARKS. *Kirchneriella* gen. nov. closely resembles the Permian *Callistadia* Knight, 1945 in general shell shape, position of the indistinct selenizone and shell ornament. Carboniferous and Permian species of *Callistadia* may be distinguished from *Kirchneriella* gen. nov. by the shape of the lateral whorl profile which is rounded in *Kirchneriella*, but nearly vertical and straight or gently concave in *Callistadia* (see

Knight, 1945; Hoare & Sturgeon, 1978). *Kirchneriella* also shows some similarities with the type species of *Gyroma* Oehlert, 1888, *Pleurotomaria baconnierensis* (Oehlert, 1888), from the Lower Devonian of France, however this species has collabral and spiral ornaments, in contrast to *Kirchneriella*. Nevertheless, some Devonian species assigned to *Gyroma*, like the Frasnian *Gyroma altaica* (Verneuil, 1845) and *Gyroma subcapillaria* Vostokova, 1966, lack collabral ornament and probably belong to *Kirchneriella*. Blodgett (1992) noted the first occurrence of pre-Carboniferous *Callistadia* in Middle Devonian rocks (Eifelian of Alaska). Unfortunately, only two, poorly preserved specimens are known, preventing determination of whether they belong to *Callistadia* or to *Kirchneriella*. The Middle Devonian '*Turbo*' *multistriatus* Kirchner, 1915 and '*Turbo*' *aequistriatus* Kirchner, 1915 may belong to *Kirchneriella*, but need to be restudied in detail. *Kirchneriella striata* (Hisinger in Goldfuss, 1844) is the only known species of this genus.

Family UNCERTAIN

Eiserhardtia gen. nov.

TYPE SPECIES. *Eiserhardtia inepta* sp. nov. by monotypy.

ETYMOLOGY. For the German paleontologist Klaus Eiserhardt for his kind help with SEM photos.

DIAGNOSIS. Discoidal shell having a very wide and flat selenizone which forms the whorl periphery; shell base phaneromphalous; width of umbilicus about one quarter of the shell width; selenizone of younger whorls is situated in distinct, U-shaped groove close to upper suture; upper suture forms abapical margin of the selenizone; shell ornamentation consisting of spiral and collabral elements forming a reticular pattern.

REMARKS. *Eiserhardtia inepta* sp. nov. is distinguished by its U-shape groove opening of the selenizone on the preceding whorl (Fig. 2G). In addition, the very wide and flat selenizone forming the whorl periphery is not common among Palaeozoic gastropods. *Eiserhardtia* resembles some Palaeozoic genera like the Ordovician *Latitaenia* Koken, 1925, *Chepultapecia* Ulrich in Weller & Clair, 1928, and *Liospira* Ulrich & Scofield, 1897 and the Devonian *Umbotropis* Perner, 1903 in general shell shape. However, the unusual subsutural groove easily differentiates it from all these genera.



FIG. 2. A-C, *Kirchneriella striata* (Hisinger in Goldfuss, 1844); A, apertural view $\times 4.5$; B, basal view showing a spiral ornamentation, same shell as A, $\times 3.6$; C, apical view $\times 5$. D, *Cerithioides whidbornei* sp. nov., lateral view $\times 3.8$. E-G, *Eiserhardtia inepta* sp. nov., Holotype; E, apical view showing shell ornamentation $\times 11$; F, apertural view $\times 13$; G, oblique view showing a subsutural groove $\times 13$.

Eiserhardtia inepta sp. nov.
(Fig. 2E-G)

ETYMOLOGY. Latin, *ineptus*, inept, unable.

MATERIAL. Only one complete shell, Unterthal, locality 63, Bergisches Land, Germany (coll. Ebbighausen). Holotype: figured herein as Fig. 2E-G

TYPE LOCALITY. U. Plattenkalk limestones, Middle Devonian (Givetian), Unterthal, locality 63, Bergisches Land, Germany.

DIAGNOSIS. As for genus.

DESCRIPTION. Medium-sized, dextrally coiled, discoidal shell with a wide and flat selenizone situated at the shell periphery. Mature spire with about four whorls; width more than double its height. Outer lip of aperture forms a shallow sinus culminating at a peripheral selenizone. Selenizone parallel with shell axis and ornamented by irregularly spaced lunulae. Width of flat selenizone about one quarter of the whorl height. Outline of aperture elliptical with longer axis roughly perpendicular to shell axis. Whorl profile above selenizone slightly convex, except close to the upper suture where it forms a U-shaped groove. Selenizone of younger whorls situated in this U-shaped groove (Fig. 2G); upper suture just below selenizone. Width of umbilicus about a quarter of the total shell width. Shell ornament consists of spiral and collabral threads forming a reticulate pattern. About 15 regularly spaced, spiral threads on the shell above the selenizone are crossed by backward curving collabral threads.

MURCHISONIIDAE Koken, 1896

Cerithioides Haughton, 1859

TYPE SPECIES. *Cerithioides telescopium* Haughton, 1859.

REMARKS. *Cerithioides telescopium*, was described from the Carboniferous of Ireland. Donald (1892) placed in its synonymy two additional Carboniferous species, *Murchisonia maxima* and *Glyptobasis conica*, both earlier described by de Koninck (1883). Batten (1966), who revised the type species of *Cerithioides*, expressed the opinion that *Cerithioides conicus* (de Koninck) is an independent species having *Cerithioides maximus* (de Koninck) as a junior synonym. He also agreed with Donald's placement of *Murchisonia* (*Cerithioides?*) *oweni* Donald, 1895 into *Cerithioides* and additionally placed *Cerithioides?* *gleanensis* Longstaff, 1926 into synonymy with this species. Batten (1966)

placed *Murchisonia eversolensis* Stauffer, 1909 from the Middle Devonian of Ohio into *Cerithioides* and considered it to be the earliest representative of the genus. Small shells of *Cerithioides incomptum* Linsley, 1968 from the Middle Devonian of the North America probably do not belong to *Cerithioides*. *Cerithioides whidbornei* sp. nov. has a similar whorl profile to *C. eversolensis* (Stauffer, 1909) and also lacks the spiral costae on shell base. Both species may belong to a new subgenus within *Cerithioides* using the latter characters differing them from the Carboniferous *Cerithioides* species.

Cerithioides whidbornei sp. nov.
(Fig. 2D)

ETYMOLOGY. For the British paleontologist G.F. Whidborne who contributed much to our knowledge of the Devonian gastropods.

MATERIAL. 10 specimens from the type locality (coll. Ebbighausen). Holotype: figured herein as Fig. 2D.

TYPE LOCALITY. Middle Devonian (Givetian) limestones, Bergisch Gladbach, locality 65, Bergisches Land, Germany.

DIAGNOSIS. Species of *Cerithioides* lacking spiral costae on the shell base; wide selenizone situated in the middle of whorl.

DESCRIPTION. High-spined, dextrally coiled shell with almost straight sides. Whorl profile distinctly convex close to both upper and lower sutures and nearly flat or slightly concave at the mid-whorl. Suture moderately deep. Shell base rounded and anomphalous. Wide selenizone situated at mid-whorl with width about 20% of the distance between the lower and upper sutures. Outer apertural lip bears a wide sinus culminating in a wide slit. Margins of apertural sinus form an angle of about 90°. Inner lip covered by thin inductura. Ornamentation consists only of growth lines. Selenizone limited by a fine, spiral groove on each side and ornamented by irregularly spaced lunulae.

REMARKS. *Cerithioides whidbornei* sp. nov. may be distinguished from *Cerithioides eversolensis* by the position of the selenizone. In *C. whidbornei*, the wide selenizone is situated mid-whorl, however, in *C. eversolensis* (Stauffer, 1909) it is distinctly below mid-whorl. Its upper margin runs closely to mid-whorl and the distance between its lower margin and the lower suture is smaller than the width of the selenizone (see Stauffer, 1909, pl. 16, fig. 13). *Cerithioides*

whidbornei sp. nov. may be also distinguished from the type species *C. telescopium* Haughton, 1859, by the absence of spiral costae on its shell base. *Cerithioides oweni* Donald, 1895, differs from both Devonian species and the type species by its whorl profile which has a distinct angulation below the selenizone (see Donald, 1895: pl. 10, figs 1, 1a).

NERITIMORPHA Golikov & Starobogatov,
1975

NERITOIDEA Rafinesque, 1815

PLAGIOTHYRIDAE Knight, 1956

Plagiothyra Whidborne, 1892

TYPE SPECIES. *Monodonta purpurea* Archiac & Verneuil, 1842.

REMARKS. Whidborne (1892) established *Plagiothyra* for species *Monodonta purpurea* Archiac & Verneuil, 1842 and his new species *Plagiothyra archon* Whidborne, 1892. The latter was described from the Middle Devonian of southwest England. Vostokova (1966) suggested a placement of the species *Palaeotrochus praecursor* Clarke, 1885 into *Plagiothyra*, but earlier Vostokova (1961) had established *Pseudoplagiothyra* for that species. Two new undescribed species of *Plagiothyra* occur in the Devonian of the North America (R.B. Blodgett, pers. comm.); one in the Eifelian age Cheenectnuk Limestone of the west-central Alaska and a second species in the Emsian age Disappointment Bay Formation, Canadian Arctic Islands. The last species is the first Early Devonian occurrence, and thus the oldest representative of *Plagiothyra*.

Plagiothyra multispiralis sp. nov.
(Fig. 3E-H)

ETYMOLOGY. *multispiralis*, referring to the shell ornamentation formed by many spiral threads.

MATERIAL. More than 30 specimens from the Unterthal, locality 63, Bergisches Land, Germany (coll. Ebbighausen). Holotype: figured herein as Fig. 3G,H.

TYPE LOCALITY. U. Plattenkalk limestones, Middle Devonian (Givetian), Unterthal, locality 63, Bergisches Land, Germany.

DIAGNOSIS. Species of *Plagiothyra* ornamented by many spiral threads; plate-like ridge bearing a triangular tooth within aperture smaller than in type species.

DESCRIPTION. Dextrally coiled, turbiniform shell with a rapidly expanding whorls, shell height about 15mm. Shell base anomphalous,

sutures shallow and adpressed. Whorl profile shows distinctly stronger convexity near upper suture where it forms a small ramp. Whorls join the preceding whorl below its periphery. The margin of the outer apertural lip passes downward from the upper suture with strong backward obliquity, but without any curvature. Columellar lip covered by a thick inductura. Prominent, triangular tooth occurs on a very low platelike ridge in the middle of the parietal wall. Shell ornamentation consists of many spiral threads that may be crossed by fine growth lines. Number of spiral threads between the sutures is about 20. Threads more distinct on adapical part of outer whorl surface.

REMARKS. *Plagiothyra multispiralis* sp. nov. differs from the type species, *Plagiothyra purpurea* Archiac & Verneuil, 1842, by having a lower-spined shell that is ornamented by many spiral threads. Shell ornamentation on *Plagiothyra purpurea* consists of several distinct rows of tubercles. The number of spiral elements between the sutures is about 20 in *Plagiothyra multispiralis* sp. nov., but only 8 in *Plagiothyra purpurea*. Shell ornament on *P. multispiralis* resembles that of the other two genera in the family Plagiothyridae, *Dirachis* Whidborne, 1891, and *Littorinides* Knight, 1937. However, shells of the Middle Devonian *Dirachis*, being ornamented by a lower number of more distinct spiral elements, bear two teeth in the aperture. The Carboniferous *Littorinides* has one low tooth on the columellar lip in contrast *Plagiothyra multispiralis* sp. nov. The similar shape of the apertural tooth and its position within the aperture, as well as the similar shell shape of *P. purpurea* and *P. multispiralis*, necessitate placement of the new species in the *Plagiothyra*.

NERITOPSIDAE Gray, 1847

NATICOPSINAE Miller, 1889

Naticopsis M'Coy, 1844

Naticopsis (Paffrathopsis) subgen. nov.

TYPE SPECIES. *Natica subcostata* Archiac & Verneuil, 1842.

ETYMOLOGY. For the type area, Paffrath, Germany.

DIAGNOSIS. *Naticopsis* having moderately low spined shells with strong collabral cords extending across entire whorl surface.

REMARKS. Yochelson (1953) placed *Natica subcostata* Archiac & Verneuil, 1842 into *Naticopsis (Jedria)* based on the Carboniferous

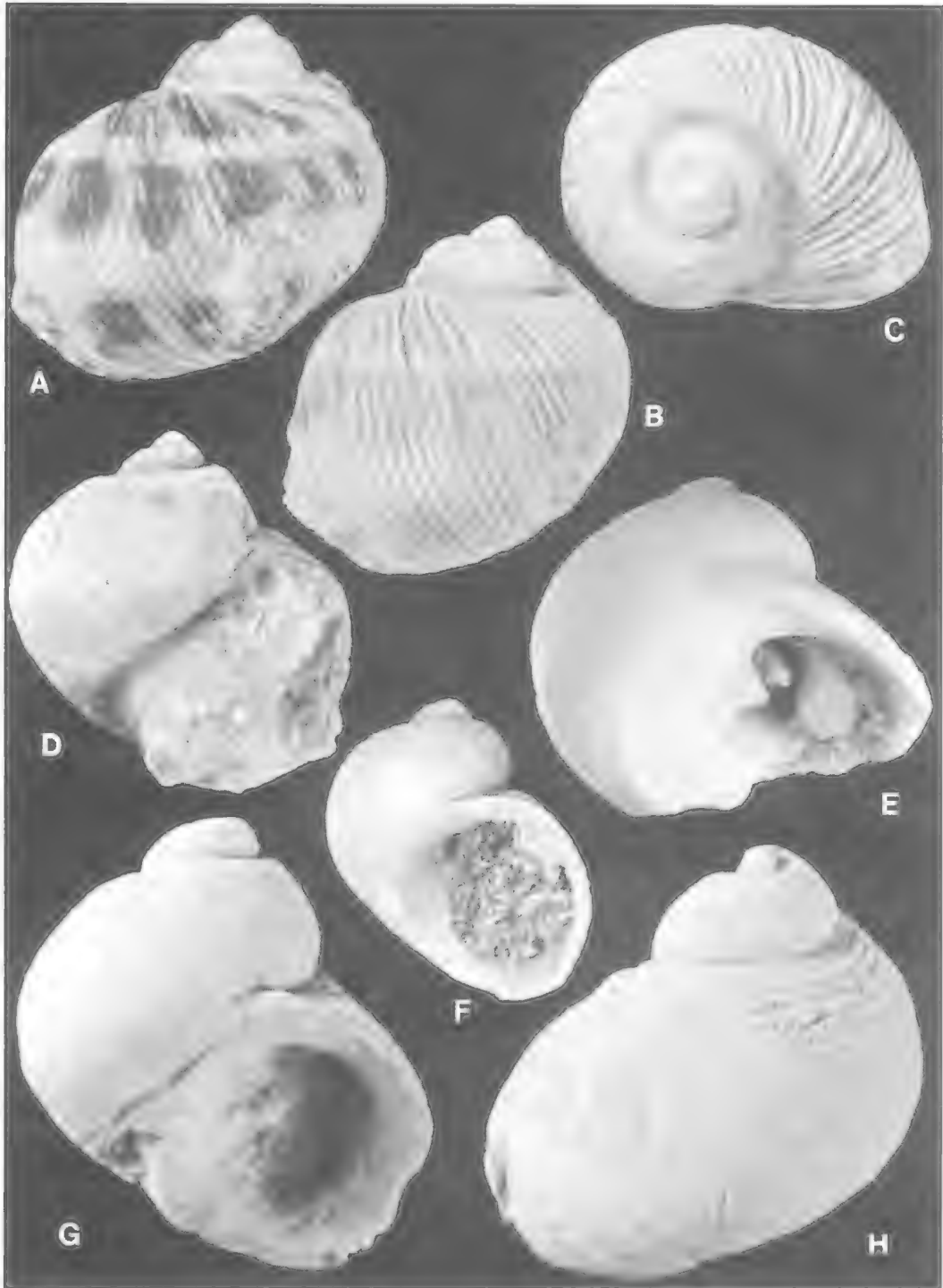


FIG. 3. A-D, *Naticopsis (Paffrathopsis) subcostata* (Archiac & Verneuil, 1842); A, abapertural view of shell with well preserved colour pattern $\times 3.3$; B, same shell covered with ammonium chloride $\times 3.3$; C, apical view $\times 3$; D, apertural view $\times 3$. E-H, *Plagiothyra multispiralis* sp. nov.; E, Paratype A, apertural view showing a triangular tooth on low platelike ridge of the parietal wall $\times 7$; F, Paratype B, apertural view $\times 3.5$. G, Holotype, apertural view $\times 5$; H, Holotype, abapertural view $\times 5$.

Naticopsis meeki Knight, 1933, *Naticopsis (Jedria) subcostata* was the only Devonian species placed into *Naticopsis (Jedria)*. Blodgett (1992) described *Naticopsis (Jedria) deckeri* from the Eifelian (Middle Devonian) of Alaska which is the oldest representative of this subgenus. Gordon & Yochelson (1987) noted that the body whorl extended downward rather than outward, and that the swelling on the outer whorl face above the periphery indicates the subgenus *Jedria*. All these shell characters may be seen in the Carboniferous species of *Naticopsis (Jedria)* as well as in *Naticopsis (Jedria) deckeri*, but not in *Natica subcostata* Archiac & Verneuil, 1842. *N. subcostata* has a moderately low spired shell with strong collabral cords extending across the entire whorl surface. These shell characters distinguish this species from all species included in *Naticopsis (Jedria)* as well as from other subgenera of *Naticopsis*. *Naticopsis (Paffrathopsis) subcostata* is the only species currently known.

Naticopsis (Paffrathopsis) subcostata
(Archiac & Verneuil, 1842)
(Fig. 3A-D)

non *Buccinites subcostatus*, Schlotheim 1820: 130; Schlotheim 1822: 63, pl. 12, fig. 3.
Natica subcostata, 1842: 366, pl. 34, figs 5, 5a, 6; Goldfuss 1844: 116, pl. 198, fig. 22.
Turbonitella subcostata (Archiac & Verneuil) Lotz 1900: 212; Kirchner 1915 (partim): 238; Paeckelmann 1922: 41.

MATERIAL. Five complete shells and several fragments from the Unterthal, locality 63, and one complete shell from Bergisch Gladbach, locality 76, Bergisches Land, Germany (coll. Ebbighausen).

REMARKS. Goldfuss (1844) synonymised the species *Buccinites subcostatus* Schlotheim, 1820 and *Natica subcostata* Archiac & Verneuil, 1842. However, Schlotheim's figure (see Schlotheim, 1822, pl. 12, fig. 3) of *Buccinites subcostatus* differs from that of *Natica subcostata* (compare with Archiac & Verneuil, 1842, pl. 34, figs 5, 6). Material from Paffrath evidently belongs to the species *Natica subcostata* Archiac & Verneuil, 1842, which is the first unquestionable illustration of this species. For this reason, Archiac & Verneuil's name is considered to be a valid species name.

Colour Pattern. Traces of original colour pattern in *Naticopsis (Paffrathopsis) subcostata* (Archiac & Verneuil, 1842) were observed in specimens from Unterthal, locality 63, and Bergische Gladbach, locality 76. The geometry of the colour pattern in specimens from the both localities is the same. The colour pattern consists

of three spiral bands of black irregular spots (Fig. 3A). The distance between the spots in each band is about equal to their diameter. The whorl surface close to the upper suture is without any colour. Archiac & Verneuil (1842: pl. 34, figs 5, 6) and Roemer (1876: pl. 32, fig. 8) figured the same colour pattern as described herein in their figures of *Natica subcostata* (= *Naticopsis (Paffrathopsis) subcostata*).

***Paffrathia* gen. nov.**

TYPE SPECIES. *Paffrathia lotzi* sp. nov.

ETYMOLOGY. For the type area, Paffrath, Germany.

DIAGNOSIS. Small, low spired turbiniform shell ornamented by strong, sharp collabral ribs extending across the entire whorl surface; shell wall very thick; whorl profile suboval.

REMARKS. Characteristic shell ornament consisting of the distinct collabral ribs (Fig. 4A, B) distinguishes *Paffrathia* from all Palaeozoic members of the family Neritopsidae. Absence of spiral elements and the presence of distinct collabral elements of the shell ornamentation have complicated the subfamily-level position of *Paffrathia* gen. nov. as well as *Naticopsis (Paffrathopsis) subcostata* (Archiac & Verneuil, 1842) within the Neritopsidae. According to Knight et al. (1960) the Naticopsinae unites shells without ornament (except for subsutural collabral threads or cords in some species). On the other hand, Palaeozoic members of the Neritopsinae are ornamented with pustules. Only the type species *Paffrathia lotzi* sp. nov. is known.

***Paffrathia lotzi* sp. nov.**
(Fig. 4A,B)

Turbonitella sp.?, Lotz, 1900: 213, pl. 3, fig. 8.

ETYMOLOGY. For H. Lotz who originally figured this species.

MATERIAL. One complete shell from the Unterthal, locality 63, Bergisches Land, Germany (coll. Ebbighausen). Holotype: figured herein as Fig. 4A,B.

TYPE LOCALITY. U. Plattenkalk limestones, Middle Devonian (Givetian), Unterthal, locality 63, Bergisches Land, Germany.

DIAGNOSIS. As for genus.

DESCRIPTION. Small, low spired turbiniform shells with at least four whorls. Whorl profile convexly arched. Height of the adult shell approximately equals width. Whorls embrace near base. Inner whorl profile suboval, sutures

very deep. Whorl profile runs from the upper suture laterally for short distance to rounded spiral angulation, far from this angulation it curves downward forming convex lateral part of the whorl, and then continues across the rounded whorl base into deep umbilicus. Outer apertural lip is prosocline. Shell wall in adult whorl is relatively thick; about 20% of inner apertural diameter. Shell ornament consists of strong, sharp collabral ribs extending across the entire whorl surface. Ribs regularly spaced and their distance roughly equals half of the diameter of the aperture. Fine growth lines may be observed on the surface between collabral ribs.

REMARKS. *Paffrathia lotzi* is a rare element of gastropod fauna of the Givetian (Middle Devonian) U. Plattenkalk limestones of Germany, with the illustrated specimen (Fig. 4A,B) the only shell available for study. The specimen figured by Lotz (1900: pl. 3, fig. 8) seems to belong to this species. However, a larger collection of this species is needed for the study of shell variability.

? LOXONEMATOIDEA
Koken, 1889

Cookiloxa gen. nov.

ETYMOLOGY. For the Australian paleontologist Alex Cook.

TYPE SPECIES. *Cookiloxa pulchra* sp. nov.

DIAGNOSIS. Slender, regular, high-spined and multiwhorled shell with straight sides having a gently convex whorl profile; sutures deep, whorls more arched close to both upper and lower sutures; external surface of whorls ornamented by collabral costae which are asymmetrically bent and crossed in the mid-whorl by one spiral costa.

REMARKS. *Cookiloxa* resembles *Australoxa* Cook & Camilleri, 1997 in its shell ornamentation. The latter genus is based on *Australoxa tasselli* Cook & Camilleri, 1997 from the Middle Devonian of Australia. The angular whorls of *A. tasselli* are ornamented by prominent opisthocline ribs and a low, sharp sinus is developed on the angular whorl periphery (see Cook & Camilleri, 1997: fig. 9E-L). One spiral cord occurs just above the lower suture. *Cookiloxa* gen. nov. differs from *Australoxa* in having a rounded whorl profile, a much smaller shell and by the absence of a peripheral sinus and lower spiral cord. *Cookiloxa* also resembles the Permian genera *Loxosonia* Batten, 1985 and *Cibecuia*

Winters, 1963 in shell ornament. Batten (1985) interpreted the spiral groove-like element of their shell ornamentation as a selenizone. *Cookiloxa* differs from *Cibecuia* by a different whorl profile, being distinctly convex in contrast to the latter genus which has a flat whorl profile. *Cookiloxa* has a similar whorl profile as both known species of *Loxosonia*, i.e. *Loxosonia horrmotoma* Batten, 1985 and *Loxosonia zygo-leuroides* Batten, 1985. *Cookiloxa* may be distinguished from both species of *Loxosonia* by the position of its spiral element of shell ornamentation. In *Cookiloxa* costa-like spiral element is situated in the middle of the whorl, but in *Loxosonia* the groove-like spiral element (?=selenizone) occurs close to the upper suture. *Cookiloxa* also resembles the Ordovician genera *Spiroecus* Longstaff, 1924 and *Donaldiella* Cossmann, 1903. *Spiroecus* Longstaff, 1924, differs from *Cookiloxa* in having a more prominent spiral ornamental element being situated above the mid-whorl and forming a distinct angulation (see holotype in Knight, 1941: pl. 48, fig. 10). In addition *S. girvanensis* differs from *Cookiloxa pulchra* by the absence of collabral costae (but see specimen figured by Wenz, 1938: fig. 929b). *Cookiloxa* may be distinguished from the genus *Donaldiella* by its differing shape of the whorl profile and outer apertural lip. The Middle Devonian *Cookiloxa pulchra* sp. nov. from Germany is the only known species.

Cookiloxa pulchra sp. nov.
(Fig. 4C,D)

ETYMOLOGY. Latin, *pulcher*, beautiful.

MATERIAL. About 30 specimens from the Herrenstrunden, locality 9, Bergisches Land, Germany (coll. Ebbighausen). Holotype: figured herein as Fig. 4D.

TYPE LOCALITY. Bücheler Schichten, Middle Devonian (Givetian), Herrenstrunden, locality 9, Bergisches Land, Germany.

DIAGNOSIS. As for genus.

DESCRIPTION. Small high-spined, dextrally coiled shell, up to 13 whorls present. Sides of shell nearly straight, whorl profile distinctly convex; maximum convexity close to both upper and lower sutures. Whorl profile nearly flat at mid-whorl. Sutures moderately deep. Lateral part of the whorl curves uniformly to base part, forming a smooth curvature without any angulation. Shell base rounded and anomphalous. Shell ornamentation consists of asymmetrically bent collabral costae being crossed in the mid-whorl

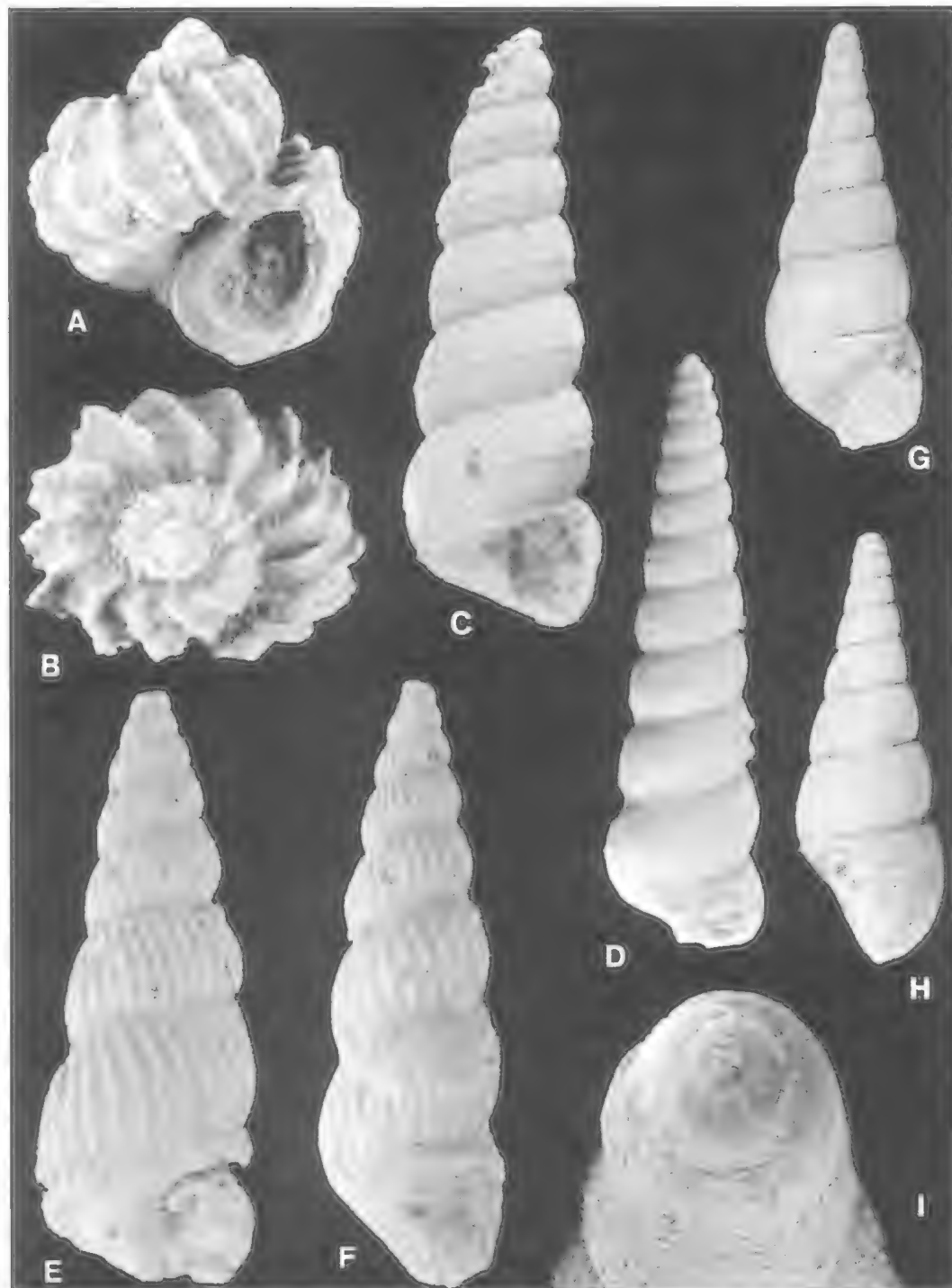


FIG. 4. A, B, *Paffrathia lotzi* sp. nov., Holotype; A, apertural view $\times 4.5$; B, apical view $\times 4.5$. C, D, *Cookiloxa pulchra* sp. nov.; C, Paratype A, lateral view $\times 14$; D, Holotype, lateral view $\times 9$. E, F, *Palaeozygopleura* (*Rheinozyga*) *retrostriatum* (Kirchner, 1915) comb. nov.; E, lateral view showing the regularly spaced orthocline costae $\times 15$; F, lateral view of larger shell $\times 9$. G-I, *Heteroloxonema moniliforme* (Goldfuss, 1842) comb. nov.; G, apertural view $\times 3.4$; H, lateral view $\times 3.4$; I, oblique view showing an early whorl $\times 125$.

by one spiral costa. Beginning at the upper suture, the collabral costae run in prosocline direction, gradually curve in an orthocline direction, and then in opisthocline direction near the mid-whorl forming a wide, asymmetrical arched sinus

REMARKS. Shape of the collabral costae in *Cookiloxa pulchra* sp. nov. resemble those of some species of *Palaeozygopleura* Horný, 1955 (i.e. the Early Devonian *P. chlapaci* Frýda, 1993, *P. devonicans* (Perner, 1907) and the Middle Devonian, *P. hamiltonae* (Hall, 1861)). Spiral costa in *Cookiloxa pulchra* is most probably just elements of the shell ornamentation and not a narrow selenizone. Without knowledge of the initial part of the shell *Cookiloxa* gen. nov. its higher taxonomic position remains questionable.

PALAEOZYGOPLURIDAE

Horný, 1955

Palaeozygopleura Horný, 1955

Palaeozygopleura (*Rhenozyga*) subgen. nov.

TYPE SPECIES. *Loxonema retrostriatum* Kirchner, 1915 (herein Fig. 4E,F).

ETYMOLOGY. *Rhenozyga* referring to Latin *Rhenus*, for the river Rhine.

DIAGNOSIS. *Palaeozygopleura* with orthocline or slightly opisthocyrt collabral costae; whorl between sutures strongly arched; shell cyrtocoid or with straight sides.

REMARKS. *Palaeozygopleura* (*Rhenozyga*) subgen. nov. differs from all other subgenera of *Palaeozygopleura* by the shape of its collabral costae which are orthocline or slightly opisthocyrt. *Palaeozygopleura* (*Rhenozyga*) may be distinguished by its strongly arched whorls which are also higher than in all other subgenera of *Palaeozygopleura*. The orthocline or slightly opisthocyrt shape of costae resemble that of *Devonozyga* Horný, 1955. The whorls in *Devonozyga* Horný, 1955 are distinctly shouldered and in the median region flattened, in contrast to that in the *Palaeozygopleura* (*Rhenozyga*) subgen. nov. which has strongly arched whorl sides, Blodgett (1992) described a new genus *Alaskozygopleura* based on the Eifelian *Alaskozygopleura crassicosata* Blodgett, 1992 which he tentatively placed in the family Pseudozygopleuridae Knight, 1930. *Palaeozygopleura* (*Rhenozyga*) subgen. nov. resembles *Alaskozygopleura* in its shell ornamentation, but the former taxon may be distinguished from the latter its much narrower shell and circular

aperture. Blodgett (1992) noted broad variability of his *Alaskozygopleura crassicosata*, but all of the figured shells of his species have ovoid, apically narrower apertures, considerably wider shells and higher whorls than *Palaeozygopleura* (*Rhenozyga*) *retrostriatum* (Kirchner, 1915).

Unfortunately there are no data about the early shell in the Givetian species of *Palaeozygopleura* (*Rhenozyga*) subgen. nov. All other subgenera of *Palaeozygopleura* have protoconchs of the archaegastropod type (Frýda & Bandel, 1997). The placement of *Rhenozyga* in the genus *Palaeozygopleura* should be proved by type of its protoconch. Besides the type species, *Palaeozygopleura* (*Rhenozyga*) *retrostriatum* (Kirchner, 1915), several other 'Loxonema' species from the Middle Devonian of Germany like *Loxonema spiraglobosum* Kirchner, 1915 may belong to the new *Palaeozygopleura* (*Rhenozyga*), *Palaeozygopleura mawhemyi* Cook, 1997 from the Middle Devonian of Australia also is transferred to the new *Palaeozygopleura* (*Rhenozyga*). A detailed study of all Middle Devonian species resembling the genus *Palaeozygopleura* as well as comparison with the Eifelian *Alaskozygopleura crassicosata* Blodgett, 1992 is in preparation.

? *Heterostrophia* Fischer, 1885

Heteroloxonema gen. nov.

TYPE SPECIES. *Turritella moniliformis* Goldfuss, 1844.

ETYMOLOGY. A combination of the generic name *Loxonema* and the prefix *hetero-* because of the presumed heterostrophic coiling of its early shell.

DIAGNOSIS. Slender, high-spired and multi-whorled shell; first whorl planispirally or slightly sinistrally coiled; shell apex blunt and dome-like; teleconch sides slightly convex; whorl profile gently convex between shallow, but with distinct sutures; teleconch surface smooth.

REMARKS. The smooth teleconch of *Heteroloxonema* gen. nov. resembles that of many loxonematids including *Loxonema*, but may be distinguished by its dome-like shell apex formed by planispirally or slightly sinistrally coiled early whorl. All known Devonian loxonematoidean gastropods such as *Katoptychia* Perner, 1907, *Stylonema* Perner, 1907, *Palaeozygopleura* (*Palaeozygopleura*) Horný, 1955, *Palaeozygopleura* (*Palaeozyga*) Horný, 1955, and *Palaeozygopleura* (*Bohemozyga*) Frýda & Bandel, 1997 have an acute shell apex which is formed by the archaegastropod-type protoconch. *Heteroloxonema* gen. nov. having a planispirally

or slightly sinistrally coiling of its early whorl may be distinguished by this character from all known loxonematoideans. This character distinguishes *Heteroloxonema* gen. nov. also from the genus *Donaldina* Knight, 1933, based on the Carboniferous *Aclisina grantonensis* Donald, 1898. According to Knight (1941), the latter species has 'earliest two whorls free from the spire, the first whorl planispirally coiled and tilted', in contrast to the blunt and dome-like shell apex of *Heteroloxonema*. In addition, the shells of the type species are ornamented by numerous spiral lirae (see Knight 1941: pl. 48, fig. 3a-e). *Heteroloxonema moniliforme* (Goldfuss, 1844) from the Middle Devonian of Germany is the only known species.

Heteroloxonema moniliforme
(Goldfuss, 1844)
(Fig. 4G-I)

Turritella moniliformis, Goldfuss 1844, p. 103, pl. 196, fig. 1.
Loxonema moniliforma (Goldfuss), Bandel 1994, pl. 4, figs. 9-10.

Donaldina moniliforma (Goldfuss), Nützel, 1997: 209, pl. 34 S-1.

MATERIAL. 13 complete shells from the Unterthal, locality 63, Paffrath area, Germany (coll. Ebbighausen).

DIAGNOSIS. As for genus.

DESCRIPTION. Medium sized, high-spined, dextrally coiled shells having at least 9 whorls. Shell sides slightly convex; sutural slope approximately 10°. The first whorl planispirally or slightly sinistrally coiled. Shell apex blunt and dome-like. Whorl profile gently convex and slightly flattened in median region; width of whorl almost twice of its height. Sutures are shallow but distinct. Shell base anomphalous, teleoconch surface smooth.

REMARKS. Bandel (1994) figured the early whorl in *Heteroloxonema moniliforme* (Goldfuss, 1844) which is, according to his observation, sinistrally coiled. For this reason he considered it to be a member of the Heterostropha. If his interpretation is correct, then *Heteroloxonema moniliforme* represents the oldest known member of this subclass (Bandel, 1994) and also the only heterostrophid gastropod older than the Frasnian/Famennian mass extinction. Nevertheless, no protoconch/teleoconch boundary was hitherto observed in this species.

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RELATIONSHIP BETWEEN MASS AND LENGTH IN AUSTRALIAN ELAPID SNAKES

A.E. GREER AND R. SHINE

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Least squares regression analysis of log mass on both log snout-vent and log total length for individuals of each sex of 14 populations of ten species of Australian elapid snakes indicates that in the 37 most robust data sets isometry occurs in 21 cases, negative allometry in ten cases and positive allometry in six. Isometry seems to be the most common kind of allometry in 'colubroid'-shaped snakes. There are no cases of different kinds of allometry between the sexes in any one species. However, in *Austrelaps ramsayi* both measures of length indicate that mass is relatively greater in males than in females over the middle and large end of the size range. The population of regression lines for log mass on log length for large diurnal, surface-active elapids are bounded by *Austrelaps ramsayi* on the heavy side and by *Pseudonaja textilis* on the light side. These extreme morphological differences may be related to the species' extreme ecological differences. The former species is a frog eating, live-bearing inhabitant of a cool environment with a short growing season, whereas the latter is a lizard, bird and mammal eating, egg-laying inhabitant of a warm environment with a longer growing season. □ *Allometry, elapids, mass, sexual dimorphism.*

A.E. Greer, Australian Museum, 6 College Street, Sydney 2010; R. Shine, Biological Sciences A08, University of Sydney 2006, Australia; 26 November 1999.

Mass is probably the single most important co-variate of an organism's other biological variables (McMahon & Bonner, 1983; Schmidt-Nielsen, 1984; Calder, 1996). Although there is a vast amount of raw data on mass for Australian vertebrates in the literature, unpublished theses and researchers' notes, little of this information has been collated and summarised. In this paper we analyse published and unpublished data on mass and length in ten species of Australian elapid snakes in order to determine the nature of the allometric relationships and whether sexual dimorphism exists.

MATERIALS AND METHODS

Data on mass (gm) and snout-vent and total length (mm) were gathered from the literature and our own notes (for origin of R. Shine's data and up-dated identifications, see Shine 1977 and 1989, respectively). All data were transformed to base 10 logs prior to analysis.

The relationship between mass and length was analysed initially for each sex using least squares regression. The comparison between mass and each measure of length between the sexes was examined using analysis of covariance with length as the covariant and sex as the factor. Homogeneity of residual mean squares of the regressions was verified prior to the ANCOVA. All analysis was done using SYSTAT 9.0 software. The 0.05, 0.01, and 0.001 levels of

significance are indicated by *, ** and ***, respectively.

Mass data were rejected if the specimen was known to be gravid, and total length data were rejected if the specimen had part of the tail missing.

RESULTS

We found unanalysed data suitable for regression analyses of log mass on log length for 14 populations of ten species of Australian elapid snakes. Data sufficient for a comparison of the regressions between the sexes of the same species were available for nine species (all except *Suta suta* which was only represented sufficiently by males). The results of these analyses are given in Table 1. We also include for the sake of completeness, but do not discuss, some basic regression statistics for *Acanthophis antarcticus* which are the only previously published results with possible relevance for allometry in Australian elapids.

The data are of variable quality for the purposes of our analysis. For example, we discount data for any sex based on fewer than ten specimens. We also discount the data for the female *Notechis ater* as they almost certainly include gravid individuals. The specimens were collected in period of 19 October to 15 February, and although no note was made of whether females

appeared gravid or not (Mirtschin & Bailey, 1990), the collection period coincides with the reproductive season (Shine, 1987b). We also discount the data for *Austrelaps superbis* from King Island due to the apparent rounding off of both lengths and weights, the latter in some cases apparently to the nearest 50g (Fearn, 1994). We also suspect that the relatively low r^2 values for female *Notechis scutatus* from Melbourne may be indicative of an atypical variable (Watharow, 1997, 1999). Finally, we note that the lack of small females in *Hemiaspis signata*, may distort both the allometry and the comparison with males (data R. Shine). In the following discussion we put to one side these qualified data (indicated by italics in Table 1) and focus on the remainder.

DISCUSSION

Methodologically, mass correlates with both snout-vent length and total length about equally well. In those cases where the r^2 values differ, snout-vent length has a higher value in three cases, and total length has a higher value in five cases. However, in no case does the difference exceed 0.01. Furthermore, both length measures gave the same indication of allometry in all cases except for *Pseudechis porphyriacus* from New England. For each sex in this species, the data for the total length indicated a relatively larger increase in mass with length than did snout-vent length. This could be due to a relatively larger increase in mass of the tail with length in this species.

The relationship between mass and length in Australian elapids can be in positive allometry, isometry, or negative allometry, depending on species. However, isometry is the most common form of allometry, occurring in 21 of 37 cases ('total samples' and 'combined' sexes excluded); negative allometry occurs in ten cases, and positive allometry occurs in six cases. In terms of the kind of allometry, there is no difference between the sexes of any species. Therefore we assume that for species represented adequately by only one sex, the allometry of that sex is indicative for the species.

In terms of the kind of allometry shown, the only comparable data set we are aware of is that for 12 species of North American colubrids, a group which is similar in shape and ecology to Australian elapids. The data for these species were based on combined sexes, but they indicated that the mass on length relationship was in isometry in 11 species and in negative allometry in only one, *Heterodon platyrhinos* (Kaufman &

Gibbons, 1975). Hence it may be that isometry is widespread in 'colubroid'-shaped snakes.

Assuming that isometry is the null condition, the cases of negative and positive allometry in Australian snakes are of interest. Negative allometry occurs in *Hemiaspis signata*, *Notechis scutatus* from the New England area, and *Parasuta dwyeri*. Positive allometry occurs in *Notechis scutatus* from Melbourne, *Pseudechis porphyriacus* from Macquarie Marshes and, in terms of total length only, in *P. porphyriacus* from New England. We have no explanation for these differences, but take note of the practical as well as the biological implications of the difference between two populations of the one species, *Notechis scutatus*.

Differences between the sexes in the elevations in the slopes occur in three species: with both measures of length in *Austrelaps ramsayi* and in *Notechis scutatus* from the New England area, and in total length in *Hemiaspis daemeli*. However, in the latter two species, the difference in elevations is so slight that we are reluctant to interpret it. In the case of *Austrelaps ramsayi*, it is clear on both measures of length that mass is relatively greater in males than in females over the middle and large end of the size range (Fig. 1). This may be due to more, or denser, muscle mass as has recently been demonstrated in two colubrids and one viperid in Europe (Bonnet et al., 1998).

The only species in which the residual mean squares of the regressions for each sex were significantly different was *Pseudechis porphyriacus* from the New England area; the unexplained variance in mass was significantly higher in males than in females in both length measures (Table 1). Again we are unable to offer a biological explanation, but we note the statistical implications for other studies of sexual dimorphism in mass on length relationships.

The mass on length regressions examined here form a distribution of roughly similar regression lines. Looking more closely at males only from the largest data sets (basically the Shine data) and restricting the analysis to snout-vent length for simplicity's sake, the boundaries of this distribution of regression lines are set by *Austrelaps ramsayi* on the relatively heavy side and *Pseudonaja textilis* (total sample) on the relatively light side (Fig. 2). The regression lines of the males of *Hemiaspis daemeli*, *H. signata*, *Notechis scutatus*, *Parasuta dwyeri* and *Pseudechis porphyriacus* (not figured to avoid crowding) fall

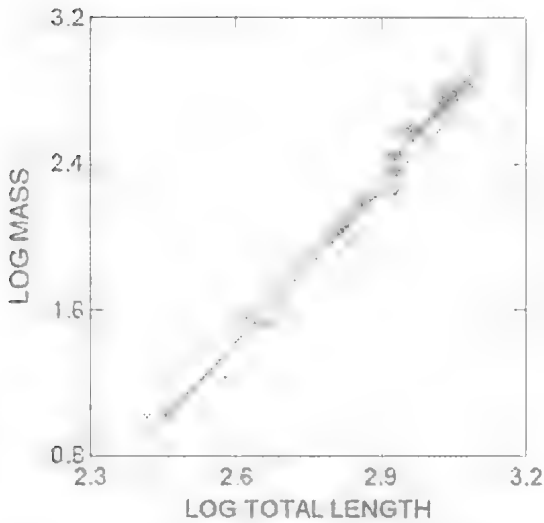


FIG. 1. Plot of log mass on log total length for both sexes of *Austrelaps ramsayi* from the New England area of New South Wales. \circ = males, \times = females.

between the regression lines for *Austrelaps ramsayi* and *Pseudonaja textilis*. In many ways these latter two taxa represent the near extreme ends of the range of diversity of active-searching, surface dwelling Australian elapids. For example, the former occurs at relatively high altitudes with shorter, cooler growing seasons, feeds largely on frogs and is live bearing (Shine, 1987a) whereas the latter occurs at lower altitudes with a longer, warmer growing season, feeds largely on reptiles, birds and mammals and is egg laying (Shine, 1989). We do not know what tissue differences may be contributing to the overall differences in mass in these two species. However, if it is fat, the heavier body in the species occupying the cooler climate with the shorter growing season makes adaptive sense. If it is muscle, the heavier body in the species hunting the generally less active prey and carrying the reproductive load for longer periods is also expected (the mass on length differences in the females of the two species are almost, but not quite, as well separated as in the males). We suspect that *Demansia psammophis* and perhaps *Oxyuranus scutellatus* would be even lighter for their length than is *Pseudonaja textilis*, but we lack the data to test this.

This review of mass and length data for Australian elapids suggests to us several ways to improve the quality of these kinds of data. First, the two measures of length used, snout-vent length and total length, are about equally robust

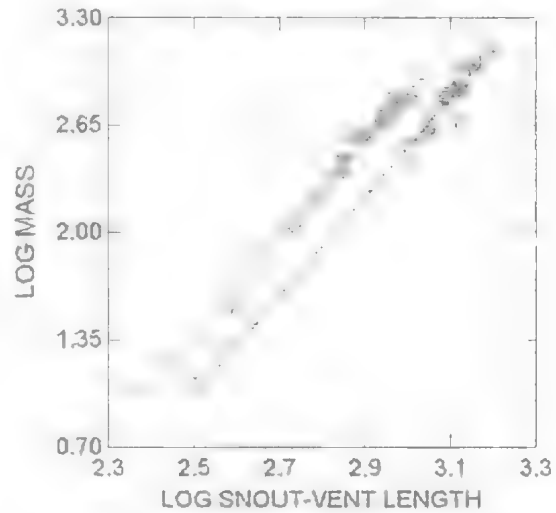


FIG. 2. Plot of log mass on log snout-vent length for males of *Austrelaps ramsayi* (\circ) and *Pseudonaja textilis* (\times).

in their relationship with mass. Hence although both measures are usually taken, either will do by itself. Second, data on mass and length are most useful if specimens with potential confounding features are noted. Specifically, specimens with missing tails, in obvious poor health, recently fed, or gravid should have their condition indicated. Sexes should also be determined. Furthermore, the larger the sample size, the smaller the sampling area, and the more constrained the collecting period, the tighter the mass on length relationship is likely to be. Finally, it would be very useful to have additional data for the smaller species of elapids, as the current data set is primarily for large species.

ACKNOWLEDGEMENTS

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TABLE 1. Parameters for least squares regression analysis of log₁₀ weight (g) on log₁₀ length (mm) for ten species of Australian elapid snakes. ci = 95 percent confidence interval of the slope. A slope of 3.00 indicates isometry. All regressions are significant at the 0.001 level.

Species	Regression Parameter					Comparison of Regressions (F values)				
	inter	slope	ci	r ²	n	allometry	homogen	slopes	elevations	Reference
Snout-vent Length										
<i>Austrelaps ramsayi</i> New England										
males	-5.92	2.92	±0.21	0.93	57	0	1.32 ^{ns}	0.96 ^{ns}	5.01*	R. Shine data
females	-5.48	2.74	±0.28	0.97	13	0				
<i>A. superbis</i> Melbourne										
males	-3.16	1.94	0.66	0.90	6	-	2.22 ^{ns}	4.95*	-	Watharow, 1997, 1999
females	-5.80	2.86	0.54	0.93	10	0				
<i>A. superbis</i> King Island										
males	-2.98	1.95	0.40	0.85	20	-	2.96 ^{ns}	13.34**	-	Fearn, 1994; Fearn & Munday, 1995
females	-8.60	3.82	1.24	0.84	9	0				
<i>Hemiaspis daemeli</i> Macquarie Marshes										
males	-6.20	2.95	±0.25	0.96	26	0	2.38 ^{ns}	0.02 ^{ns}	0.81 ^{ns}	R. Shine data
females	-6.10	2.92	±0.40	0.94	15	0				
combined	-6.15	2.93	±0.22	0.95	41	0				
<i>H. signata</i> New England area										
males	-4.79	2.39	±0.26	0.94	24	-	1.08 ^{ns}	0.12 ^{ns}	1.32 ^{ns}	R. Shine data
females	-5.02	2.49	±0.57	0.85	17	0				
<i>Notechis ater</i> Flinders Ranges										
males	-10.81	2.43	±0.57	0.94	9	0	1.07 ^{ns}	3.38 ^{ns}	6.89***	Data in Mirtschin & Bailey, 1990
females	-13.89	2.92	±0.44	0.95	39	0				Data in Mirtschin & Bailey, 1990

TABLE 1. (cont.)

Species	Regression Parameter						Comparison of Regressions (F values)				Reference
	inter	slope	ci	r ²	n	allometry	homogen	slopes	elevations		
<i>Notechis scutatus</i> Melbourne area											
males	-7.39	3.38	±0.36	0.94	26	+	1.34 ^{ns}	4.52*	-	Data in Watharow, 1997	
females	-5.29	2.63	±0.67	0.79	20	0					
<i>N. scutatus</i> New England area											
males	-5.35	2.66	±0.15	0.95	73	-	1.13 ^{ns}	1.45 ^{ns}	4.42*	R. Shine data	
females	-5.66	2.79	±0.15	0.97	51	-					
<i>Parasuta dwyeri</i> New England area											
males	-5.31	2.63	±0.23	0.93	39	-	1.37 ^{ns}	0.057 ^{ns}	1.28 ^{ns}	R.Shine data	
females	-5.17	2.58	±0.31	0.91	31	-					
combined	-5.17	2.58	±0.18	0.93	70	-					
<i>Pseudechis porphyriacus</i> Macquarie Marshes											
males	-7.04	3.25	0.17	0.98	37	+	1.47 ^{ns}	12.08**	-	R. Shine data	
females	-3.35	2.02	0.58	0.91	7	-					
<i>P. porphyriacus</i> New England area											
males	-6.68	3.12	0.20	0.89	128	0	3.37***	-	-	R. Shine data	
females	-6.67	3.11	0.19	0.96	49	0					
<i>Pseudonaja textilis</i> Macquarie Marshes											
males	-6.15	2.89	±0.52	0.83	27	0	1.05 ^{ns}	1.20 ^{ns}	0.004 ^{ns}	R. Shine data	
females	-7.78	3.42	±0.80	0.91	9	0					
combined	-6.17	2.90	±0.18	0.97	37	0					
<i>P. textilis</i> New England area											
males	-6.54	3.02	±0.14	0.99	18	0	1.36 ^{ns}	0.05 ^{ns}	0.83 ^{ns}	R. Shine data	
females	-6.49	3.00	±0.18	0.99	11	0					
combined	-6.56	3.03	±0.10	0.99	29	0					
<i>P. textilis</i> Total Sample											
males	-6.46	2.99	±0.14	0.98	45	0	1.09 ^{ns}	0.05 ^{ns}	0.32 ^{ns}	R. Shine data	
females	-6.54	3.01	±0.15	0.99	20	0					
combined	-6.52	3.01	±0.10	0.99	65	0					
<i>Suta suta</i> New South Wales											
males	-5.90	2.83	±0.24	0.98	14	0	-	-	-	A. Greer data and Shine, 1988	
Total Length											
<i>Acanthophis antarcticus</i> Eyre Peninsula											
combined	-6.76	3.09	?	0.97	206	?	?	?	?	Johnston, 1987	
<i>Austrelaps ramsayi</i> New England area											
males	-6.42	3.02	±0.19	0.95	54	0	1.01 ^{ns}	2.23 ^{ns}	5.09*	R. Shine data	
females	-5.76	2.76	±0.29	0.97	13	0					
<i>Austrelaps superbis</i> Melbourne area											
males	-3.24	1.93	0.68	0.89	6	-	1.31 ^{ns}	2.59 ^{ns}	1.00 ^{ns}	Watharow, 1997, 1999	
females	-5.80	2.86	0.54	0.93	10	0					
<i>A. superbis</i> King Island											
males	-3.72	2.14	0.44	0.84	20	-	3.08 ^{ns}	11.22**	-	Fearn, 1994; Fearn & Munday, 1995	
females	-9.44	3.99	1.34	0.83	9	0					
<i>Hemiaspis daemeli</i> Macquarie Marshes											
males	-6.54	2.99	±0.25	0.96	26	0	2.00 ^{ns}	0.01 ^{ns}	6.25*	R. Shine data	
females	-6.41	2.97	±0.36	0.95	15	0					

TABLE 1. (cont.)

Species	Regression Parameter						Comparison of Regressions (F values)				Reference
	inter	slope	ci	r ²	n	allometry	homogen	slopes	elevations		
<i>Hemiaspis signata</i> New England area											
males	-5.20	2.46	±0.25	0.95	23	-	1.12 ^{ns}	0.09 ^{ns}	4.26*	R. Shine data	
females	-5.39	2.55	±0.54	0.86	17	0					
<i>Notechis ater</i> Flinders Ranges											
males	-11.62	2.49	±0.59	0.93	9	0	1.10 ^{ns}	2.54 ^{ns}	7.26*	Data in Mirtschin & Bailey, 1990	
females	-14.49	2.95	±0.24	0.94	38	0					
<i>Notechis scutatus</i> Melbourne area											
males	-7.80	3.43	±0.29	0.93	46	+	1.97 ^{ns}	6.47*	-	Data in Watharow, 1997	
females	-5.58	2.67	±0.72	0.76	19	0					
<i>Notechis scutatus</i> New England Area											
males	-5.77	2.74	±0.14	0.96	70	-	1.25 ^{ns}	0.06 ^{ns}	5.71*	R. Shine data	
females	-5.80	2.76	±0.15	0.97	48	-					
<i>Parasuta dwyeri</i> New England area											
males	-5.51	2.65	±0.23	0.93	39	-	2.07*			R. Shine data	
females	-5.30	2.58	±0.31	0.91	31	-					
combined	-5.25	2.56	±0.18	0.93	70	-					
<i>Pseudechis porphyriacus</i> Macquarie Marshes											
males	-7.52	3.33	±0.17	0.98	36	+	1.33 ^{ns}	11.66**	-	R. Shine data	
females	-3.75	2.10	±0.62	0.92	6	-					
<i>P. porphyriacus</i> New England											
males	-7.20	3.23	±0.20	0.89	117	+	3.51***	-	-	R. Shine data	
females	-7.20	3.22	±0.20	0.96	44	+					
<i>Pseudonaja textilis</i> Macquarie Marshes											
males	-7.05	3.10	±0.65	0.80	25	0	1.15 ^{ns}	0.43 ^{ns}	0.06 ^{ns}	R. Shine data	
females	-8.21	3.47	±0.86	0.90	9	0					
combined	-6.49	2.92	±0.20	0.96	35	0					
<i>P. textilis</i> New England											
males	-6.66	2.98	±0.10	0.99	16	0	3.11 ^{ns}	0.019 ^{ns}	0.52 ^{ns}	R. Shine data	
females	-6.72	3.00	±0.21	0.99	10	0					
combined	-6.71	3.00	±0.10	0.99	26	0					
<i>P. textilis</i> Total sample											
males	-6.64	2.97	±0.13	0.98	41	0	1.37 ^{ns}	0.05 ^{ns}	0.59 ^{ns}	R. Shine data	
females	-6.72	2.99	±0.16	0.99	19	0					
combined	-6.70	2.99	±0.10	0.98	60	0					
<i>Suta suta</i> New South Wales											
males	-5.98	2.79	±0.24	0.98	14	0	-	-	-	A. Greer data	

FRESHWATER DALYELLIID FLATWORM, *GIEYSZTORIA SUPERBA* SP. NOV.
(DALYELLIIDAE: RHABDOCOELA) FROM SOUTHEAST QUEENSLAND,
AUSTRALIA

V. HARTENSTEIN AND K.A. DWINE

Hartenstein, V. & Dwine, K.A. 2000 06 30: Freshwater dalyelliid flatworm, *Gieysztoria superba* sp. nov. (Dalyelliidae: Rhabdocoela) from southeast Queensland, Australia. *Memoirs of the Queensland Museum* 45(2): 381-383. Brisbane. ISSN 0079-8835.

A new dalyelliid flatworm, *Gieysztoria superba* sp. nov. is described from a freshwater creek in southeast Queensland, Australia. With characters of the genus, it appears to be closely related to the cosmopolitan species *G. rubra*, but differs significantly in the number of spines (approx. 40) in the sclerotic armature of the male copulatory organ. □ *Freshwater, Dalyelliidae, taxonomy, Australia.*

V. Hartenstein, Department of Molecular, Cell and Developmental Biology, UC Los Angeles, PO Box 951 606, Los Angeles CA 90095-1606, USA; K.A. Dwine, Queensland Museum, PO Box 3300, South Brisbane 4101, Australia; 26 November 1999.

The Dalyelliidae contains many, mostly free-living, freshwater species of flatworms that are known from around the world (Luther, 1955), and in Australia ultrastructural studies have been conducted on an unidentified species of the cosmopolitan genus *Gieysztoria* by Rohde, Cannon & Watson (1988) and Watson & Rohde (1995). No taxonomic study of the family or its members, however, has been conducted here.

METHODS

Freshwater plants and sediments were collected from Gold Creek, Brookfield (27°27'58"S; 152°53'03"E), returned to the laboratory, and the worms extracted by careful examination using a stereo microscope. Worms were examined alive with bright field and Nomarski interference contrast microscopy. Whole mounts in Canada balsam were made after specimens were fixed in 5% buffered formalin and dehydrated through a graded alcohol series. Specimens were not stained. Sclerotic armature preparations were made by squash preparation and mounting in Epon or by immersing live worms in de Faure's fluid (Evans et al., 1961). Sections (2µm) were obtained serially from worms fixed in 4% glutaraldehyde in phosphate buffered saline and embedded in Epon. Sections were stained with toluidine blue.

Drawings of the anatomy were made using a camera lucida and digitised using Adobe *Illustrator*®. Measurements are in micrometres (µm) unless otherwise stated.

This material is lodged at the Queensland Museum (QM) as a wholemount (WM), serial sections (TS) and squash preparations (S).

DALYELLIIDAE Graff, 1908

Gieysztoria superba sp. nov.
(Figs 1-2)

MATERIAL. HOLOTYPE: Gold Ck, Brookfield SEQ (27°27'58"S, 152°53'03"E). Feb. to Apr. 1998, V. Hartenstein, WM, QMG217989. PARATYPES: same data, TS (Epon: toluidine blue), QMG217990. OTHER MATERIAL: same data, Sclerotic armature preparation (squash preparation, Epon) QMG217991.

ETYMOLOGY. Named *superba* for the large number of spines in the male copulatory armature.

DESCRIPTION. HOLOTYPE: 550 long × 200 wide (Fig. 1), clear, filled with brown algal? bodies and posteriorly red pigment bands. Swims swiftly over substrate; frequently rotates around length axis while swimming. Anatomically (from live material and sections) consistent with the genus and having finger-like vitellaria. Arising from the distal portion of the muscular bulb surrounding the ejaculatory duct and prostate secretions there is a fenestrated girdle (20 wide) with irregular holes (Fig. 2). Suspended distally from the girdle are about 40 fine spines of about equal length, evenly arranged around the whole duct. Each spine is fluted with a fine tip and approx. 43 long.

DIAGNOSIS. With characters of the genus and a male copulatory organ with a moderately narrow, fenestrated girdle and about 40 spines of equal length.

HABITAT AND DISTRIBUTION. Found in the sediments and plants of freshwater creek at

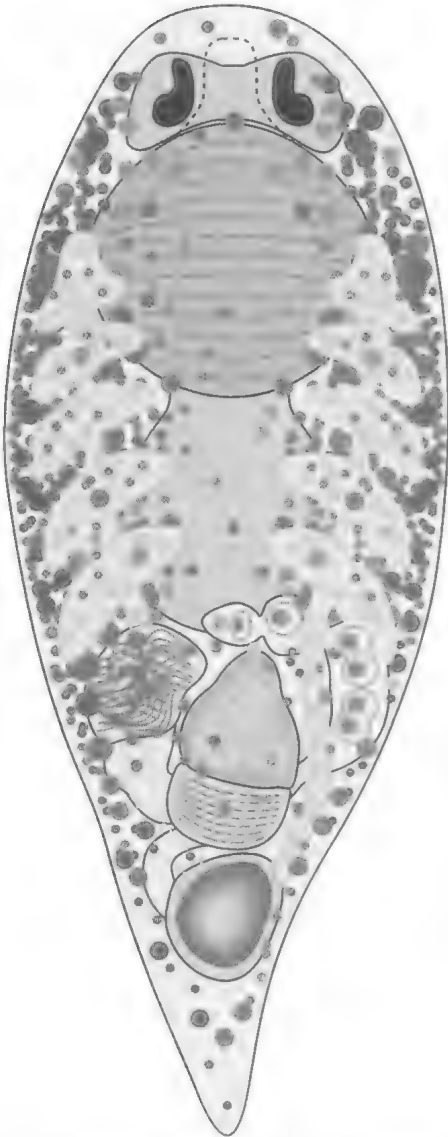


FIG. 1. *Gieysztoria superba* sp. nov. Habitus. Scale = 200 μ m.

Brookfield, SE Queensland. Numbers appear to decline in the colder months (May-September).

REMARKS. Luther (1955) divided the 46 species of *Gieysztoria* then described into two groups: 'aequales' with a sclerotic armature displaying a wreath of homogeneous spines (about 25 species) and 'inaequales' for the rest. *G. superba* belongs to the first group: it has a sclerotic armature with a girdle and possesses papillose vitellaria. In the numerous spines *G. superba* resembles *G. knipovici* Beklemishev

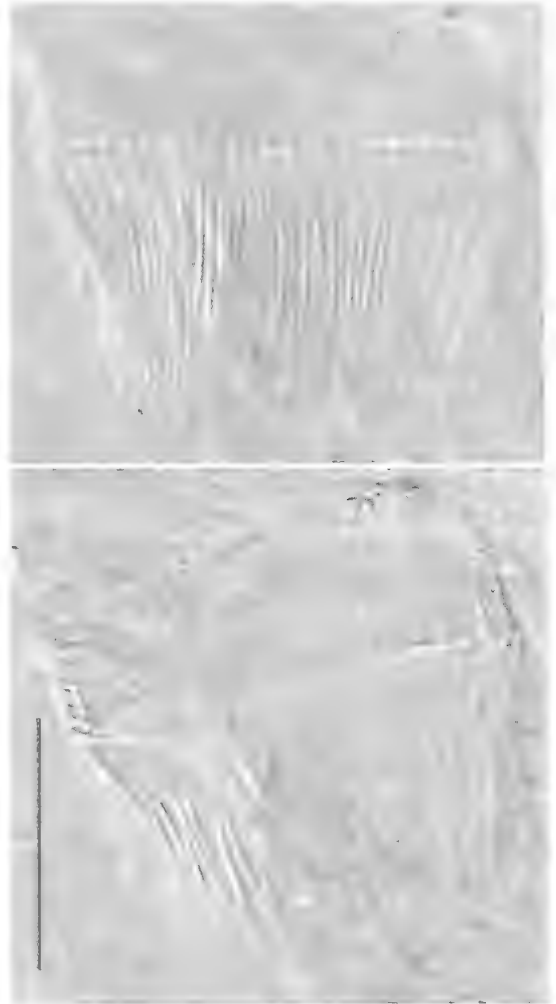


FIG. 2. *Gieysztoria superba* sp. nov.; two focal planes of the sclerotic armature in a squash preparation (QM G217991). Scale = 50 μ m.

1953 which has at least 30 spines in its armature, but *G. superba* differs in having vitellaria with long, digitate extensions (not short papillae). *G. superba* has similar vitellaria to *G. bellis* Marcus 1946 and *G. rubra* Fuhrmann 1894. *G. superba* can be distinguished because its spines lack the cone-shaped tip found in *G. bellis*, and although the armature of *G. superba* looks very similar to that of *G. rubra*, it has a wider girdle and shorter spines. Most characteristic of *G. superba* is the number of spines in its armature. While *G. bellis* and *G. rubra* have approx. 19 spines, *G. superba* has approx. 40.

DISCUSSION. The inter-specific variation in spine number between *G. superba* and *G. rubra* is

far greater than the intra-specific variation within *G. rubra* that is associated with geographic location. (Marcus, 1946; Luther, 1955; Young, 1977). We, therefore, have no hesitation in considering this a new species, the first taxonomic account of any member of the Dalyelliidae from Australia.

ACKNOWLEDGEMENTS

We thank Amelia Hartenstein for her help in the field and laboratory and Lester Cannon for comments on the MS. Without the support of the NIH grant NS 29367 for VH this work would not have been initiated. The study was part of a broader study by KD supported on a grant to Dr L.R.G. Cannon from ABRIS.

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NEMATODES FROM FISH FROM THE KEPPEL ISLANDS, KEPPEL BAY, QUEENSLAND. *Memoirs of the Queensland Museum* 45(2): 384. 2000:- Seventy six fishes comprising 24 species collected (by members of the Capricorn Scuba Club) from three sites; the waters off Ross Reef (23°03'S, 150°22'E), Barron Island (23°08'S, 151°03'E) and North Keppel Island (23°04'S, 150°53'E) in Keppel Bay on the central Queensland coast, were examined for nematodes. Thirteen species of nematode, all new locality records, were found (Table 1). No nematodes were found in *Choerodon venustus* De Vis or *Acanthurus dussumeri* Valenciennes and only unidentifiable larvae in *Siganus lineatus* (Valenciennes). Names of the fish hosts follow Randell, et. al. (1990). Ascaridoid larvae were identified following Cannon (1977) but citing *Thymascaris* as a synonym of *Hysterothylacium* (Deardorff & Overstreet, 1981). Comparisons between the fish examined in this study and from Heron Island (Lester & Sewell, 1989) showed differences in the nematode communities. Of five nematode species recorded from Heron Island two, *Philometra* sp. and *Metabronema magna*, were not present in Keppel Bay.

Cucullanus sp. and *Hysterothylacium* sp. larvae were found in *C. venustus* at Heron Island but not Keppel Bay, while *Terranova* sp. larvae was found only in *Epinephalus ongus* at Heron Island.

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L.R. Smales, School of Biological and Environmental Sciences, Central Queensland University, Rockhampton 4702, Australia; 14 February 2000.

TABLE 1. Nematode parasites found in 24 species of fish collected in Keppel Bay, September 1989 to July 1990. b = body wall, in = intestine, li = liver, me = mesentery, st = stomach.

Parasite Taxon	Site	Host Species	Parasite Taxon	Site	Host Species	
Trichuridae			cont.		<i>Kyphosus</i> sp.	
<i>Capillaria</i> sp.	st.	<i>Caranx ignobilis</i> (Forsskål)			<i>P. batavianus</i>	
	in.	<i>Diagramma pictum</i> (Thunberg)			<i>P. teira</i>	
		<i>Epinephalus ongus</i> (Bloch)			<i>Pl. schotaf</i>	
		<i>E. tauvina</i> (Forsskål)			<i>Plectrapomus leopardus</i> (Lacépède)	
		<i>Kyphosus</i> sp.	<i>Terranova</i> sp.	in.	<i>C. ignobilis</i>	
		<i>Plectrohinchus flavomaculatus</i> (Cuvier)	larva type 11	me.	<i>Choerodon schoenleinni</i> (Valenciennes)	
		<i>Pl. gibbosus</i> (Lacépède)			<i>Cr. altivelis</i>	
				<i>D. pictum</i>		
				<i>E. cyanopodus</i>		
Cucullanidae					<i>E. ongus</i>	
<i>Cucullanus australiensis</i> Baylis 1927	in.	<i>C. ignobilis</i>			<i>E. tauvina</i>	
		<i>D. pictum</i>			<i>Kyphosus</i> sp.	
		<i>Pl. schotaf</i>			<i>Lutjanus carponotatus</i> (Richardson)	
<i>Dichelyne</i> (<i>Dichelyne</i>) sp.	in.	<i>Pl. gibbosus</i>			<i>L. russelli</i> (Bleeker)	
Anisakidae					<i>Naso hexacanthus</i> (Bleeker)	
<i>Anisakis</i> sp. larva type 1	li.	<i>Pl. schotaf</i>			<i>N. unicornis</i> (Forsskål)	
		<i>D. pictum</i>			<i>P. teira</i>	
<i>Contracaecum</i> sp. larva type 11	in.	<i>C. ignobilis</i>			<i>P. batavianus</i>	
<i>Hysterothylacium</i> sp. larva type 11		<i>E. cyanopodus</i> Richardson			<i>Pl. flavomaculatus</i>	
		<i>Pl. flavomaculatus</i>			<i>Pl. gibbosus</i>	
<i>Hysterothylacium</i> sp. larva type 111	me.	<i>Cromileptes altivelis</i> (Valenciennes)			<i>Pl. schotaf</i>	
	in.	<i>E. cyanopodus</i>			<i>S. sordidus</i> (Forsskål)	
		<i>E. tauvina</i>				
		<i>Hemigymnus melapterus</i> (Block)	Camallanidae			
		<i>Kyphosus</i> sp.	<i>Procamlanus lonis</i> Cribb, 1989			<i>P. batavianus</i>
		<i>Pl. flavomaculatus</i>	<i>Camallanus</i> sp.	st.		<i>Pl. flavomaculatus</i>
		<i>Pl. gibbosus</i>				
<i>Pl. schotaf</i>	Cysticolidae					
	<i>Ascarophis</i> sp.	st.		<i>D. pictum</i>		
				<i>E. cyanopodus</i>		
				<i>E. tauvina</i>		
				<i>N. unicornis</i>		
				<i>Pl. gibbosus</i>		
<i>Hysterothylacium</i> sp. larva type IV	me.	<i>C. ignobilis</i>			<i>Pl. schotaf</i>	
	in.	<i>D. pictum</i>			<i>N. unicornis</i>	
	st.	<i>H. melapterus</i>	<i>Cristitectus</i> sp. larvae	in.	<i>Pl. schotaf</i>	
					<i>N. unicornis</i>	

A NEW SPECIES OF *STREPTOCEPHALUS* (*PARASTREPTOCEPHALUS*)
(CRUSTACEA: ANOSTRACA: STREPTOCEPHALIDAE) FROM NORTH
QUEENSLAND, AUSTRALIA

B. HERBERT AND B.V. TIMMS

Herbert, B. & Timms, B.V. 2000 06 30: A new species of *Streptocephalus* (*Parastreptocephalus*) (Crustacea: Anostraca: Streptocephalidae) from North Queensland, Australia. *Memoirs of the Queensland Museum* 45(2): 385-390. Brisbane. ISSN 0079-8835.

Streptocephalus (*Parastreptocephalus*) *queenslandicus* sp. nov. is described from temporary ponds near Atherton, north Queensland. It is related to four species of the recently erected subgenus *Parastreptocephalus* from Africa mainly because of male antennal morphology and the production of tetrahedral eggs, a unique feature within the family Streptocephalidae. This confirms the presence of *Streptocephalus* in Australia in a continent whose fairy shrimp fauna is dominated by *Branchinella* and *Parartemia*. □ *Parastreptocephalus*, new species, *Streptocephalus archeri*, control in fish ponds, biogeography, fairy-shrimp.

B. Herbert, Department of Primary Industries, Kennedy Highway, Walkamin, 4872; B.V. Timms, Department of Geography and Environmental Science, University of Newcastle, Callaghan, 2308, Australia; 24 May 1999.

Despite the early description by Sars (1896) of *Streptocephalus archeri* from the Rockhampton area of central Queensland, and a further collection of six females from the same area (Linder, 1941), no other specimens of the Streptocephalidae have been found in Australia. Adding to the enigma, the description was based entirely on females, so that it is difficult to determine the relationships of *S. archeri* within the genus. It is not surprising then that subsequent studies on *Streptocephalus* have reported little on *S. archeri* (see Brendonck et al., 1992; Belk & Brtek, 1995) and reviews of aquatic invertebrates in Australia have discounted the presence of *Streptocephalus* in Australia (Geddes, 1981, 1983; Williams, 1980, 1981).

Over the last few years fairy shrimps have been encountered by one of us (BH) each time aquaculture ponds were filled at the Freshwater Fisheries and Aquaculture Centre, Walkamin, on the Atherton Tablelands in north Queensland. Specimens collected in February 1997 were identified by BVT as a species of *Streptocephalus*. Further collections in October 1997 confirmed their presence and provided data on development times. The males are different to any known species of *Streptocephalus* and the females appear different from those of *S. archeri*, so they are described here as a new species.

CRUSTACEA
ANOSTRACA
STREPTOCEPHALIDAE Daday, 1910
Streptocephalus Baird, 1852
Parastreptocephalus Brendonck, Hamer &
Thiery, 1992

***Streptocephalus* (*Parastreptocephalus*)
queenslandicus sp. nov.**
(Figs 1-3)

ETYMOLOGY. From Queensland, where the specimens were found. This complements names based on localities in Africa for many other species of the *Parastreptocephalus* (Brendonck et al, 1992).

MATERIAL. HOLOTYPE: ♂, QMW24520. PARATYPES: 9 ♂s, QMW24521; 10 ♀s, QMW24522. Queensland Museum. Lengths: ♂ holotype and paratypes 12.1 ± 1.2mm; ♀ paratypes 12.1 ± 0.9mm. OTHER MATERIAL: 46 adults collected from rearing ponds at the Walkamin Research Station, Walkamin, via Atherton, N Qld, Feb. 1997, B. Herbert, QMW24579 Queensland Museum. 100+ immature specimens from a subsequent filling of the same ponds collected by B. Herbert on 16 Oct. 1997, QMW24580, Queensland Museum.

TYPE LOCALITY. Fish rearing ponds, Walkamin Research Station, Walkamin, via Atherton, N Qld, 17°8'S, 145°26'E, altitude 590m a.s.l. Collector B. Herbert, Feb. 1997 2-3 weeks after flooding of ponds.

DESCRIPTION. *Male*. Antennules simple and long, almost reaching end of antennal base, tapering slowly towards a blunt tip which bears three setae (Fig. 1E). Lateral processes of antennae smooth, slightly curved backward and

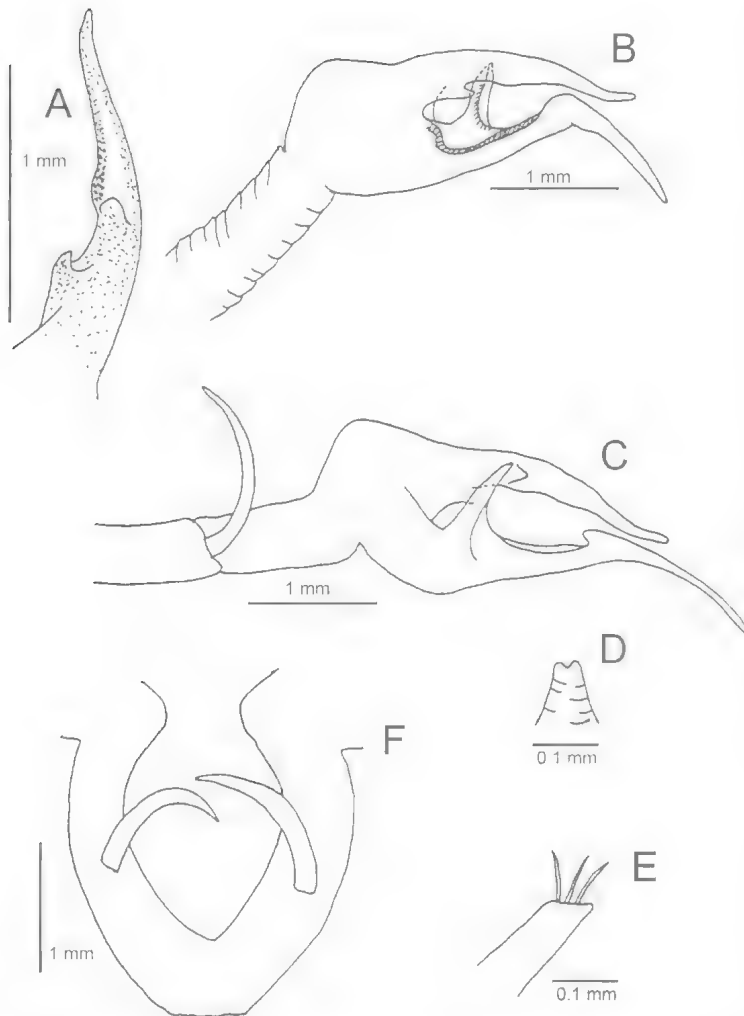


FIG. 1. *Streptocephalus* (*Parastreptocephalus*) *queenslandicu* sp. nov., ♂; A, dorsal view of finger of antenna; B, inner or medial view of right hand of antenna; C, lateral view of right hand of antenna; D, dorsal view of frontal organ; E, tip of antennule; F, base of antenna.

inserted at posteriobackward margin of distal end of basal segment (Fig. 1C,F). Median process of antenna continuing at same thickness of basal segment consisting of a short, slightly bent middle part and a terminal hand (Fig 1B,C). Basal part of hand about twice as wide as middle and whole hand about twice the length of the middle part. Much of the outside of the hand with a warty surface, as opposed to a smooth surface on the middle part and inner surface of the thumb and finger. Basal part of thumb grooved, with chitinised wavy edges (Fig 1B,C). The outer base carrying a curved pointed spur having one margin continuous with the chitinised wavy edge of the

basal groove of the thumb (Fig. 1B,C). Distal half (anterior) of thumb attached at an obtuse angle ($140-160^\circ$) and with a basal protuberance marking the end of the groove (Fig. 1B,C). Distal end of the thumb tapering to a slightly recurved point reaching well beyond the tip of the finger. Finger with two teeth, one on the inner margin and the other on the upper surface, so that the spur of the thumb extends near both (Fig. 1A-C). The upper marginal tooth recurved and with a blunt point, while the tooth on the inner surface is rounded (Fig. 1A). Distal to the rounded tooth is a smooth groove flanked on the inner margin with a warty protuberance near the tooth and a warty surface elsewhere (Fig. 1A). Apical part of tooth curved backward. Frontal appendage small with a double blunt point (Fig. 1D).

Thoracopods with five endites, decreasing markedly in size distally. Many long posterior setae, but with a restricted number of anterior setae, as itemised in Table 1 and shown in Fig. 2A-F. Endopodite broadly truncated with an apical shallow notch medially. External margin of endopodite with hook-like setae, but medially, especially towards the medial-distal

corner setae longer, straighter and plumose (Fig. 2G,H). Base of endopodite setae with 2-8, usually 3-4, very small spines. Exopodite ladle-shaped and with numerous long plumose setae, but with a few small stout tooth-like setae at the base of the external margin (Fig. 2A,I,J). The long setae also attended at their base with very small spines, 2-6 in number but usually 3-4. Epipodite rather similar in shape to the exopodite, but smaller and without marginal setae. Preepipodite lamelliform and with irregular small hooks on the external margin (Fig. 2A,K).

First ten pairs of thoracopods similar except for two extra anterior setae on endite 5 of limb 1.

Occasionally there may be reductions in the number of long anterior setae of endites 3-5 of limbs 2-10. Eleventh pair of thoracopods reduced, mostly at the inner proximal corner, so that endites 1 and 2 much reduced, but other components only a little smaller and less setose than for thoracopods 1-10. Anterior setae on the endites of limb 11 much reduced and the number of posterior setae reduced, but still >10, on endites 1 and 2.

Basal and nonretractable parts of penes each bearing near its base a posteriorly curved median sausage-like outgrowth with 3-4 teeth on the proximal surface (Fig. 3A,B).

Cercopods (Fig. 3C) lanceolate and separately attached to posteriorlateral margin of a short telson. Each bears plumose setae on its inner and outer margins and the tip.

Female. Antennules filamentous, slightly longer than antennae or of equal length. Tip with three setae as in male. Antennae foliaceous and oval with broadly rounded margins and no apex (Fig. 3E). Slight notch sometimes on the mid-distal margin. Margins edged with small weak setae, with very few near the basal portion. Brood pouch cylindrical, elongate, extending to the end of the sixth abdominal segment in mature specimens, i.e. pouch is four segments long (Fig. 3D).

Immature eggs spherical, but mature shelled eggs tetrahedral (Fig. 3F). Corners somewhat rounded and hyaline; edges also hyaline and slightly thickened. Planar surfaces slightly convex and with a small raised area in the middle. Within the hyaline thickening on the edges and corners the embryo is round.

Thoracic appendages and cercopods as in male.

DIAGNOSIS. The present specimens easily lie within *Streptocephalus* because the antennae in the male have a medial outgrowth from the basal joint which terminates in a cheliform structure (Brendonck, 1990). Because of the tetrahedral eggs of the female and the well developed spur of the thumb and the lack of teeth between this spur and the anterior (main) part of the thumb, they lie within the subgenus *Parastreptocephalus* as presently defined (Brendonck et al., 1992).

Though the general structure of the antennae, thoracopods, cercopods and the nonretractable part of the penes of the male are very similar to those of the four species of *Streptocephalus* so far assigned to *Parastreptocephalus* (Brendonck et al., 1992), none have the same antennae structure

TABLE 1. Idealised arrangement of setae on the 5 endites of male thoracopods of *S. queenslandicus*. First figure indicates number of anterior setae, second the number of posterior setae. m = many (> 10).

Thoracopod	Endite				
	1	2	3	4	5
1st pair	3 + m	2 + m	2 + 3	2 + 2	3 + 2
1st - 10th pair	3 + m	2 + m	2 + 3	2 + 2	1 + 2
11th pair	1 + m	1 + 3	2 + 2	2 + 1	1 + 1

or setation of the endites of the thoracopods as in *S. (P.) queenslandicus*. The teeth of the antennal finger are more rounded, spaced further apart and in different planes than in the other three species of *Parastreptocephalus* with teeth on the finger. The endite setae are very similar to those of *S. (P.) sudanicus* and *S. (P.) zuluensis*, the two species of *Parastreptocephalus* that have been studied in detail (Brendonck et al., 1992). The only consistent difference is the presence of three instead of four anterior setae on the first endite in *S. (P.) queenslandicus*.

Although *S. archeri* was incompletely described by Sars, there are a number of differences between it and *S. queenslandicus*. The medial distal part of the antenna has no short pointed projection in *S. queenslandicus* as it has in *S. archeri*. The brood pouch is four segments long in *S. queenslandicus* whereas it is only two in *S. archeri*. Part of this difference may be explained by the greater overall length of *S. queenslandicus* (12mm as against 9mm for *S. archeri*). The tetrahedral eggs of *S. archeri* 'exhibit plane or very slightly concave faces connected by obtuse, prominent ribs' (Sars, 1896), though the diagrams show them with markedly concave planar surfaces. By contrast the eggs of *S. queenslandicus* have slightly convex surfaces and the ribs (i.e. the edges of each tetrahedral surface) are not obtuse or particularly prominent. *S. archeri* eggs, while tetrahedral, are more like those of *S. sudanicus*, while those of *S. queenslandicus* are more like those of *S. zuluensis* particularly in the rib structure, though the planar surfaces are slightly convex in *S. queenslandicus* and slightly concave in *S. zuluensis* (see Brendonck et al., 1992). These apparent differences in egg structure may be artefacts of preparation and so of limited diagnostic value (L. Brendonck, pers. comm.).

The type localities are quite different for the two species. *S. archeri* apparently inhabits water-holes near sea level that become saline at very

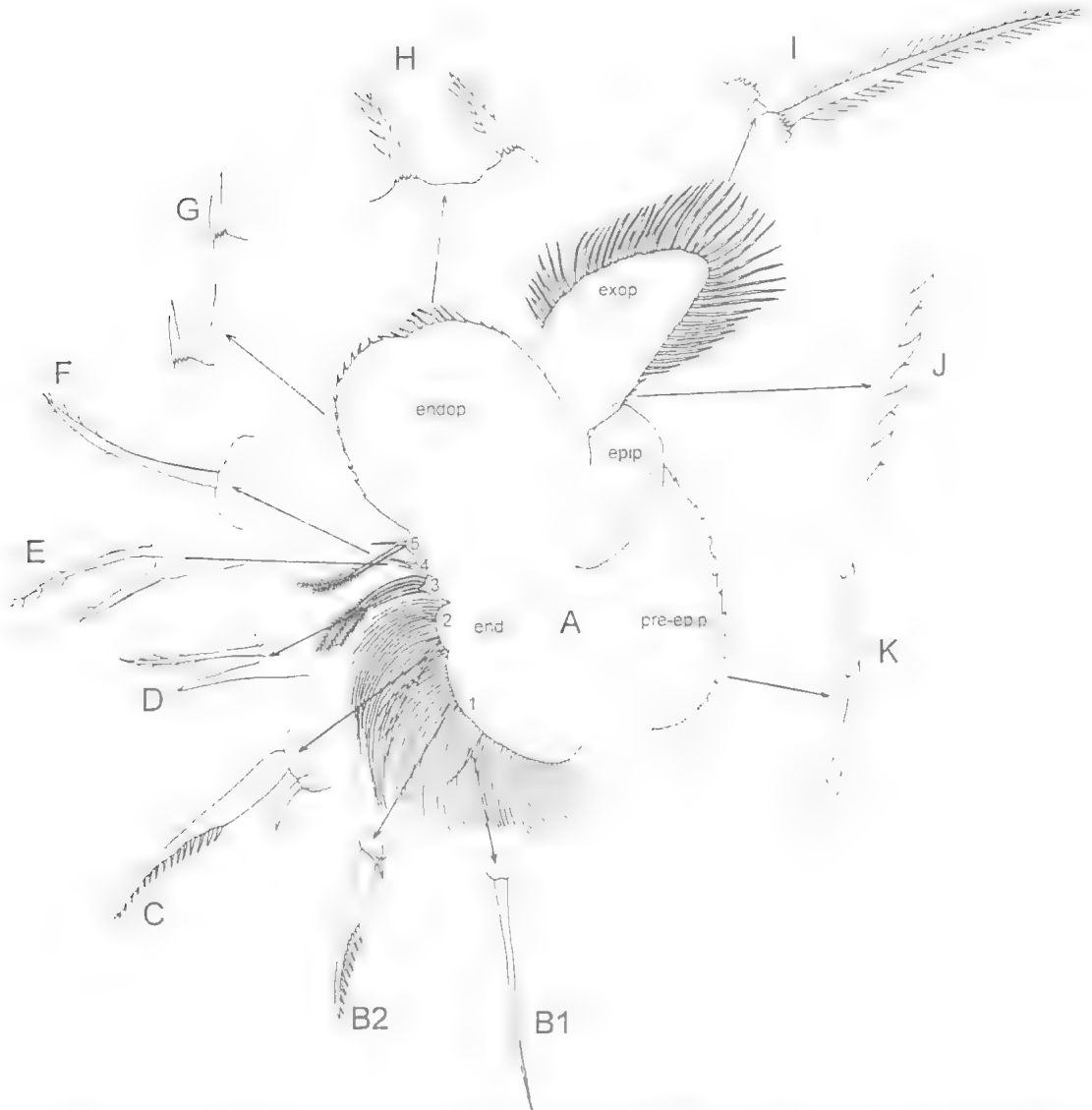


FIG. 2. *Streptocephalus* (*Parastreptocephalus*) *queenslandicus* sp. nov. ♂; A, 3rd right thoracic appendage; B1, detail of 1st anterior setae of first endite; B2, details of 2nd and 3rd anterior setae of 1st endite; C, details of anterior setae of 2nd endite; D, details of anterior setae of 3rd endite; E, details of the anterior setae of 4th endite; F, details of anterior setae of 5th endite; G, detail of hook-like setae on median margin of endopodite; H, detail of small plumose setae on distal margin of endopodite; I, detail of setae of exopodite; J, detail of hook-like setae on external margin of exopodite; K, detail of edge of preepipodite. Abbreviations: end. = endite; endop. = endopodite; exop. = exopodite; pre-epip. = preepipodite.

high tides (though there is no suggestion that it lives in saline waters), while *S. queenslandicus* lives in fish hatchery ponds at 590m a.s.l. on the Atherton Tableland 860km NW of Rockhampton.

While the differences between the females of *S. archeri* and *S. queenslandicus* are small and of unknown reliability, the balance of probabilities

suggest they are separate species. Only the re-discovery of *S. archeri* at or near its type locality and the recovery of males will provide the basis for a more convincing differential diagnosis.

ECOLOGY. Like most anostracans, *S. queenslandicus* has been observed to hatch soon (24

hours) after the filling of a pond and take 2-3 weeks to reach maturity. Hatching can occur in any season, with growth hardly affected by temperature which varies annually from 17-28°C. They generally persist in the ponds for about a month, with males dying much earlier than females. Only after the ponds are drained, dried and refilled do they reappear. It is possible that dispersal is only by resting eggs in mud, as so far newly constructed ponds using water from ponds infested with *S. queenslandicus* have not developed populations.

Shrimps feed on algae and do best when phytoplankton is abundant soon after hatching. They seem incapable of using either *Volvox* or *Anabaena* which often predominate in the hatchery ponds. Sometimes they die out before reaching maturity — this happened in the October 1997 hatching and seems to have been due to a large reduction in the algae in the pond caused either by their own feeding or by a large population of the cladoceran *Moina micrura*. In hatchery ponds *S. queenslandicus* is a serious competitor for the more desirable *M. micrura* and copepods. It is controlled by the use of hydrated lime at 40-50ppm applied 3-6 days after filling of the ponds.

BIOGEOGRAPHY

The confirmed presence of *Streptocephalus* in Australia raises interesting biogeographical questions. This genus is represented in tropical and warm temperate areas of the Neartic, Palaearctic and especially the African biogeographic realms by about 50 species (Banarescu, 1990; Belk & Brtek, 1995), and now the Australian region has at least two species. Significantly both species occur in the tropics. However, while

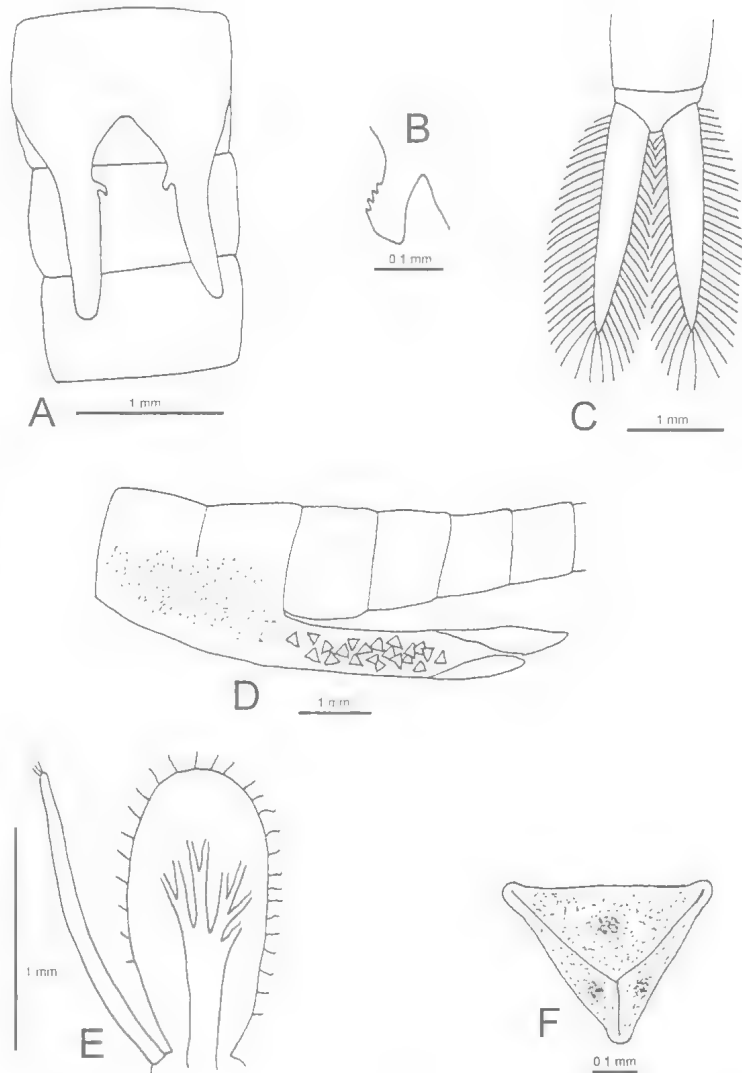


FIG. 3. *Streptocephalus* (*Parastreptocephalus*) *queenslandicus* sp. nov.; A, ventral view of ♂ genital region; B, detail of median process on basal part of penis; C, male telson; D, lateral view of ♀ abdomen with brood pouch; E, ♀ antenna; F, ♀, tetrahedral egg.

Streptocephalus is the dominant anostracan in Africa and *Branchinella* uncommon (Banarescu, 1990), in Australia the position is reversed. Geddes (1981, 1983) in his studies of Australian anostracans had numerous collections of *Branchinella* but none of *Streptocephalus*. There is no apparent reason for this difference, but perhaps *Streptocephalus* arrived later in Australia than *Branchinella* and is unable to successfully compete with a relatively large endemic fauna. In this context Banarescu (1990) believes that

Branchinella spread from a Gondwana base before *Streptocephalus*. Adding further evidence for the later arrival of the Streptocephalidae in Australia is the fact that all forms so far found belong to the subgenus *Parastreptocephalus* which seems to be a derived form of *Streptocephalus*. Or could it be that the tetrahedral eggs of this subgenus give it some advantage in competition against other species (Brendonck et al., 1992), so that only these forms, rather than *Streptocephalus* sensu strictus, have some chance in the competition against incumbent dominant *Branchinella*?

ACKNOWLEDGEMENTS

We thank Dr Luc Brendonck for his comments on the manuscript and Dr M Geddes for access to literature.

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NEW DISTRIBUTION AND HABITAT DATA FOR THE VULNERABLE PYGOPODID,
DELMA TORQUATA (KLUGE, 1974)

BARNEY M. HINES, DAVID HANNAH, MELANIE VENZ AND TERESA EYRE

Hines, B.M., Hannah, D., Venz, M. & Eyre, T. 2000 06 30: New distribution and habitat data for the vulnerable pygopodid, *Delma torquata* (Kluge, 1974). *Memoirs of the Queensland Museum* 45(2): 391-393, Brisbane, ISSN 0079-8835.

The vulnerable pygopodid, *Delma torquata* (Kluge, 1974), has been regarded as confined to scattered localities in southeastern Queensland. Here we report on the first two instances for this species occurring in the southern section of Queensland's Brigalow Belt Bioregion. In addition, the habitat at two new localities, Bunya Mountains and Western Creek are different from others in which *D. torquata* has been recorded. □ *Delma torquata*, pygopodid, distribution, habitat, Brigalow Belt Bioregion

Barney M. Hines, P O, Box 7, Point Lookout 4183; David Hannah, Queensland Parks and Wildlife Service, PO Box 906, Emerald 4720; Melanie Venz, 49 Ellerslie Cr, Taringa 4068; Teresa Eyre, FERA, Dept of Natural Resources, 80 Meters Rd, Indooroopilly 4075, Australia; 14 September 1999

Delma torquata has been regarded as confined to scattered localities in southeastern Queensland (e.g. Kluge, 1974; Davidson, 1993; McFarland, 1999; Queensland Museum records), in the area between Ulam (23°35'S, 150°36'E) near Rockhampton, the Bunya Mountains (26°52'S, 151°14'E) and Brisbane's western suburbs (27°31'S, 152°58'E). Recent systematic vertebrate fauna surveys on public lands in southern Queensland (e.g. Eyre et al., 1999) have extended the known range of this species northwest to Blackdown Tableland and inland to Western Creek. These are the first two records for this species in the southern section of Queensland's Brigalow Belt Bioregion (BBB), an area seriously assailed by land-clearing (Young et al., 1999).

Blackdown Tableland National Park (23°48'58"S, 149°10'56"E) is an isolated sandstone plateau some 200km west of Gladstone (23°51'S, 151°14'E). Here, a specimen of *D. torquata* was captured in a pitfall trap by T. Eyre, M. Schulz, G. Ford and M. Mathieson on 29 November, 1997. It was photographed and released (QM slide # NW438 QM). At Western Creek State Forest (28°04'37"S, 150°53'57"E), an area of rolling sandstone hills near Millmerran, an adult *D. torquata* was hand captured by M. Venz on 3 October 1998. This specimen was lodged with the Queensland Museum (J66808).

Five additional specimens of *D. torquata* were found during these surveys. On the 19 June, 1997, two *D. torquata* were hand-captured by B. Hines and A. Fletcher at Grongah State Forest (25°58'02"S, 152°05'17"E), via Kilkivan. One was lodged with the Queensland Museum

(J63361), the other released after tissues were taken for genetic studies (University of Queensland, Molecular Zoology Laboratory, vial number QRFA043). On 19 September 1997, a single specimen of *D. torquata* was similarly captured by D. Hannah in Yarraman State Forest (26°52'51"S, 151°50'12"E). The identification of this species was confirmed by Queensland Museum staff. It was photographed (QM transparency NV 739-761) and released at the capture site. A fourth *D. torquata* specimen, hand captured by B. Hines and I. Gynther at Bunya Mountains State Forest (26°49'35"S, 151°35'46"E) on 30 April 1998, was released following tissue sampling (University of Queensland, vial number QRFA256). Lastly, a specimen of *D. torquata* was collected by Queensland National Parks and Wildlife staff during a fauna survey of Bullyard Conservation Park (24°57'59"S, 152°03'06"E), near Gin Gin, on 26 February 1997. This specimen was also lodged with the Queensland Museum (J67859).

The identification of animals at four of the six localities was confirmed with voucher specimens registered at the Queensland Museum. Identification at the other two localities, (Blackdown Tableland and Bunya Mountains), was confirmed by multiple observers at each site, with two observers in each case having prior, first-hand experience in identifying this species (i.e. MM and MS; BH and IG). In each example, the pattern and scalation of the individuals were consistent with that described in Cogger (1996).

The Western Creek and Blackdown localities are significant as they are outside the Southeast

Queensland Bioregion (SEQB), in the southern section of the BBB. The only other record for this species from outside the SEQB is of a hatchling, collected in 1943 at Ulam (Kluge, 1974), in the northern section of the BBB.

HABITAT

Habitat features of the localities described in this paper vary to that documented elsewhere. For example, Wilson & Knowles (1988) report *D. torquata* as an inhabitant of eucalypt/acacia woodland usually associated with rocky outcrops on ridges. This description is comparable to the Blackdown Tableland, Grongah and Yarraman localities, which support narrow-leaved ironbark (*Eucalyptus crebra*) open forest with grassy understoreys on ridges. It is also similar to the site where Porter (1998) conducted the only detailed investigations into the ecology of *D. torquata*. In contrast, the Bunya Mountains and Western Creek sites are different from others in which *D. torquata* occurs. The former supports forest red gum (*E. tereticornis*) woodland, while the latter is an area of brigalow (*Acacia harpophylla*) and belah (*Casuarina cristata*) forest with a wilga (*Geijera parviflora*) dominated midstorey. Both sites are in low lying areas.

Differences were also noted in soil type. At Porter's (1998) *D. torquata* study site soils are shallow, stony lithosols on ridges and texture contrast soils on slopes. In contrast, those at Western Creek are fine-grained, grey, cracking clay sediments, while those at the remaining sites are dark-brown to black cracking clays of various depths. In addition, most of the specimens captured by Porter (1998) were sheltering under stones. However, his results indicated that rock may not be a necessary component of *D. torquata* habitat, as some individuals were captured in pitfall traps set away from rock cover. Neither the Western Creek nor the Yarraman sites contained significant rock components.

CONSERVATION STATUS

A review of known localities for *D. torquata* indicates that its current status is justified. *D. torquata* is listed as vulnerable in both The Action Plan for Australian Reptiles (Cogger et al., 1993) and under the Queensland Nature Conservation (Wildlife) Regulation 1994. The discovery of this species at additional sites indicates that it is more widespread than has been surmised. However, many of the localities in the western suburbs of Brisbane are threatened by urban development (Czechura & Covacevich,

1985; McDonald et al., 1991). In addition, of the six new localities discussed here, three are in communities considered either 'vulnerable' or 'endangered' (Table 1) (Young, 1999; Young et al., 1999). These findings highlight the need for further research into the biology and conservation requirements of this species.

ACKNOWLEDGEMENTS

We thank the field and office staff involved in the fauna component of the Comprehensive Regional Assessment program in southern Queensland; Jeanette Covacevich and Patrick Couper of the Queensland Museum for assistance with the preparation of this paper; the Queensland Dept of Environment and Heritage, the Queensland Dept of Natural Resources and Environment Australia which funded the surveys on which these specimens were recorded. In addition, we thank Queensland National Parks and Wildlife Service staff Paul Horton, Adrian Kampf and Steve Clark for the Bullyard CP specimen and John Hodgson for information regarding this record.

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TABLE 1. Conservation status and description of Regional Ecosystems at *D. torquata* locations. Regional Ecosystem numbers and edited descriptions are derived from Young (1999) and Young et al. (1999).

Site	Regional Ecosystem	Extent reserved	Extent remaining	Conservation status
Blackdown Tableland NP	not described			
Bullyard Conservation Park	<i>Corymbia citriodora</i> ± <i>Eucalyptus acmenoides</i> ± <i>C. intermedia</i> , <i>E. fibrosa</i> subsp. <i>fibrosa</i> , <i>C. trachyphloia</i> , <i>E. moluccana</i> (lower slopes), <i>E. crebra</i> , <i>E. exserta</i> tall woodland on complex of remnant Tertiary surfaces and Tertiary sedimentary rocks	Low	71%	
Grongah SF	<i>Eucalyptus crebra</i> grassy woodland on Mesozoic to Proterozoic igneous rocks (12.12.7).	Low	26%	Vulnerable
Bunya Mts SF	<i>Eucalyptus tereticornis</i> open forest to woodland on Cainozoic alluvial plains including older floodplain complexes. (12.3.3)	Low	10%	Vulnerable
Yarraman SF	not described			
Western Creek SF	<i>Acacia harpophylla</i> A <i>Casuarina cristata</i> shrubby open forest on Cainozoic to Proterozoic consolidated, fine grained sediment. Lowlands. Deep texture contrast soils and cracking clays, often gilgaid. (11.9.5).	Low	~11%	Endangered

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YOUNG, P.A.R., WILSON, B.A., McCOSKER, J.C., FENSHAM, R.J., MORGAN, G. & TAYLOR, P.M. 1999. Chapter 11. Brigalow Belt. In Sattler, P.S. & Williams, R.D. (eds) The conservation status of Queensland's bioregional ecosystems. Conservation Technical Report. (Queensland Department of Environment and Heritage: Brisbane).

ADDITION TO THE HERPETOFAUNA OF QUEENSLAND'S BRIGALOW BIOGEOGRAPHIC REGION. *Memoirs of the Queensland Museum* 45(2): 394. 2000.- The herpetofauna of the Brigalow Biogeographic Region has been assessed and documented in some detail (Covacevich et al. 1996). Their work comprised a review and synthesis of material held in several museums, collation of sight records from numerous authorities within the region and reports of extensive fieldwork. One hundred and forty five species of reptiles were recorded as occurring within the Brigalow Biogeographic Region (Covacevich et al. 1996).

In December 1997, I located a previously unrecorded species, *Varanus storri*, in the northern portion of the region. A single specimen was found on the Nebo to Collinsville road, c.10km north of the Newlands turnoff and 50km S of the junction with the Mt Coolon - Collinsville road at 21°09'S, 148°13'E. The road passes through Homevale and Emu Plains. The specimen was located beneath a large rock on the road verge (Fig. 1). A transparency of the specimen has been lodged with the Queensland Museum images collection (Reg. no. OG37).

The low rolling hill area where the specimen was found is a mixed eucalypt open woodland of Mountain Coolibah (*Eucalyptus argadophila*) and Poplar Box (*E. populnea*) interspersed with open grassland patches of Bluegrass

(*Bothriochloa decipiens*, *Dichanthium scriceum*) and Kangaroo Grass (*Themeda australis*). Soils in this area are clay loams derived from shales. Some outcropping of these shales occurs on the peaks of the low hills. At the point where the specimen was located surface rocks were well embedded.

Varanus storri is found usually where rocks provide cover for their shallow burrows (pers. obs.). Abundant surface outcropping occurs within 10km to the north of the site where the specimen was located, though this area was not searched. It seems likely that rocks on roadside verges may provide corridors of suitable habitat. *V. storri* is common in similar habitat approximately 150km west of this site, in the Desert Uplands Biogeographic Region (pers. obs.).

Acknowledgements

Juliana McCosker of the Department of Environment, Emerald, identified botanical samples from the site.

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Steve McAlpin, 14 Mills Street, Alice Springs 0870, Australia; 17 May 2000.



FIG. 1. *Varanus storri* on the Nebo to Collinsville road.

DEVONIAN AND EARLY CARBONIFEROUS POLYPLACOPHORA FROM WESTERN AUSTRALIA

RICHARD D. HOARE AND ALEX G. COOK

Hoare, R.D. & Cook, A.G. 2000 06 30: Devonian and Early Carboniferous Polyplacophora from Western Australia. *Memoirs of the Queensland Museum* 45(2): 395-403. Brisbane. ISSN 0079-8835.

Three new taxa of polyplacophorans are described from the Carboniferous (Tournaisian) Septimus Limestone and Viséan Utting Calcarenite of the Bonaparte Gulf Basin, Western Australia. New taxa are *Gryphochiton collectus* sp. nov., *Compsochiton formosus* gen. et sp. nov. and *Harpidochiton auctus* gen. et sp. nov. A single plate representing *Archochiton* Hoare & Sturgeon, 1976 is described from the Devonian Frasnian Sadler Limestone, Canning Basin, Western Australia. □ *Polyplacophora, Devonian, Carboniferous, Bonaparte Gulf Basin, Canning Basin, Western Australia.*

Richard D. Hoare, Department of Geology, Bowling Green State University, Bowling Green, Ohio 43403 USA; Alex G. Cook, Queensland Museum, PO Box 3300, South Brisbane 4101, Australia; 21 March 2000

Plates of Palaeozoic polyplacophorans have not been commonly reported from Australia. The first recorded occurrence was *Chelodes calceoloides* by Etheridge (1897), from the Upper Silurian of New South Wales (NSW). Iredale & Hull (1926) described a Permian taxon from NSW, *Permochiton australianus* and Farrell (1992) described *Chelodes intermedius* Bergenhayn, 1960 and *Helminthochiton* sp. nov. from the Early Devonian of NSW. The Devonian and Carboniferous specimens described herein from Western Australia (WA) add substantially to our knowledge of Palaeozoic Polyplacophora in the continent.

GEOLOGY AND AGE

The onshore Bonaparte Gulf Basin, WA, includes a number of Lower Carboniferous units which have yielded a rich and diverse fossil fauna. Those faunas studied include brachiopods, (Roberts, 1971; Thomas, 1971), conodonts (Druce, 1969) and ostracodes (Jones, 1989). Studies of molluscan elements of the Carboniferous faunas are now underway. The present work is concerned with polyplacophoran plates recovered from silicified faunas in the Utting Calcarenite on the northwestern shelf, and the Septimus Limestone on the eastern shelf of the onshore Bonaparte Gulf Basin. For a recent summary of the stratigraphy and regional geology see Mory & Beere (1990). A detailed biostratigraphic summary was provided by Roberts (1985).

The Septimus Limestone crops-out in the SE of the Bonaparte Basin and has been assigned a Tournaisian (latest Tn₂ to Tn₃) age, *Schellweinella*

australis Zone to lower *Spirifer spiritus* Zone, primarily based on brachiopod faunas (Roberts, 1971). Chitons described from the Septimus Limestone are from the upper part of the unit and are hence regarded as Tn₃ in age. The Utting Calcarenite is a laterally restricted unit which crops out in the NW of the onshore basin and has been assigned a Viséan (V_{3b-c}) age. *Punctospirifer pauciplicatus* Zone.

In addition to the Carboniferous taxa, a new Late Devonian occurrence is described. The single plate was recovered from the Late Devonian (Frasnian) Pillara Limestone, in the Hull Range, Canning Basin, WA. All material is held in the Queensland Museum Palaeontology collections (QMF).

List of Localities. QML1095 Utting Calcarenite, Utting Gap, Ningbing Station, Bonaparte Gulf Basin, WA, 14°58.17'S, 128°35.82'E. Coll. A. Cook, P. Jell, May 1996; A. Cook, T. Smith, July 1998. QML1096 Septimus Limestone, low spur on NW side of Mt Septimus, Ivanhoe Station, Bonaparte Gulf Basin, WA, 15°42.5'S, 128°59.22'E. Coll. A. Cook, P. Jell, May 1996; A. Cook, T. Smith, July 1998. QML1160. Sadler Limestone, SW side of Paddy's Valley, SSE Wade Knoll, Canning Basin, WA, 18°40'07" S, 125°59'31"E. Coll. A. Cook, T. Smith. This is near Stop 2/Day 1 of Playford (1981).

RECONSTRUCTIONS

The reconstructions (Fig. 1) illustrate plate relationships in the three Carboniferous taxa described herein. Head plates are unknown for *Gryphochiton collectus* sp. nov. and *Harpidochiton*

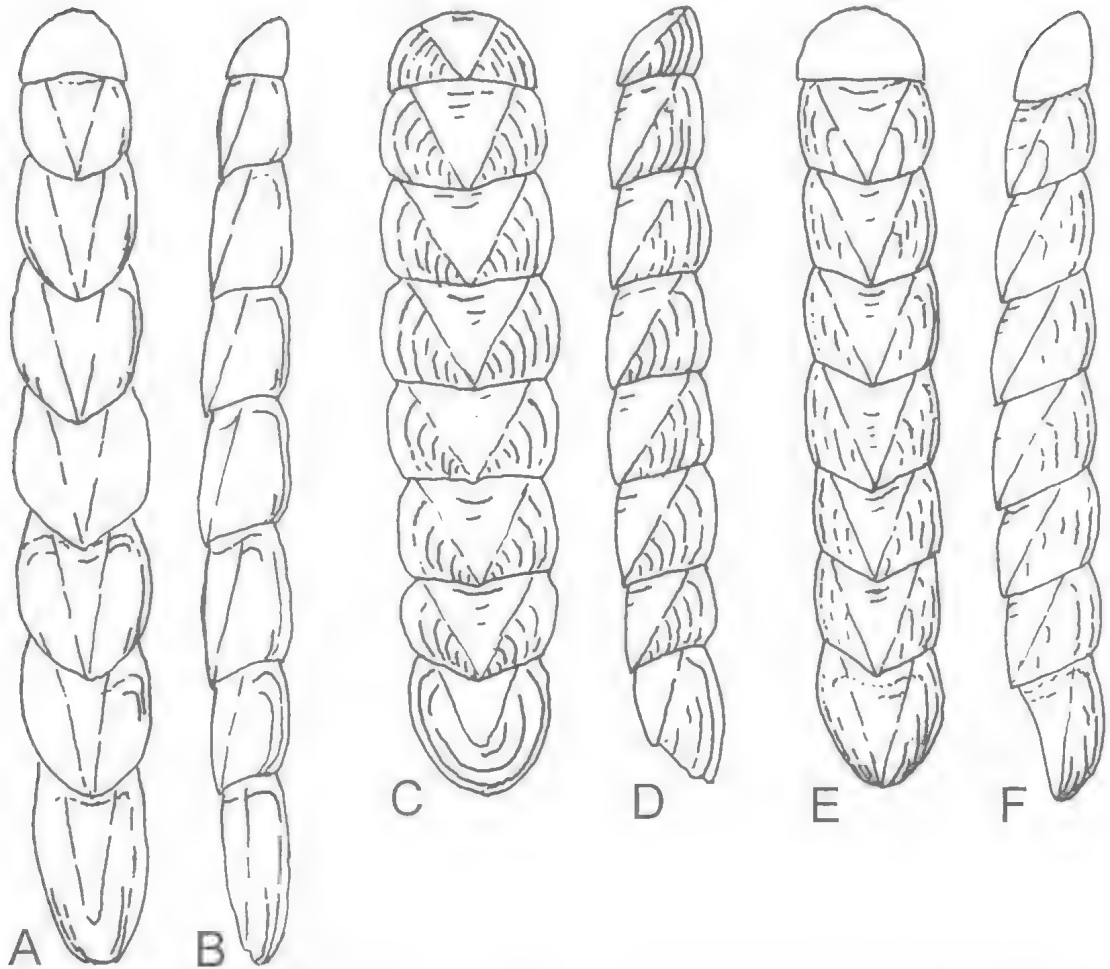


FIG. 1. Reconstructions. A, B, *Gryphochiton collectus* sp. nov., dorsal and right lateral views, approx. $\times 1.0$. C, D, *Compsochiton formosus* gen. et sp. nov., dorsal and right lateral views, approx. $\times 1.0$. E, F, *Harpidochiton auctus*, gen. et sp. nov., dorsal and right lateral views, approx. $\times 1.0$.

auctus gen. et sp. nov., but the number of other plates present for each taxon allows some basis in forming arrangements as presented. No information as to size of girdle or presence of girdle spines or plates is present.

SYSTEMATIC PALAEOLOGY

POLYPLACOPHORA de Blainville, 1816
LEPIDOPLEURIDAE Thiele, 1910
GRYPHOCHITONIDAE Pilsbry, 1900
Gryphochiton Gray, 1847

***Gryphochiton collectus* sp. nov.**
(Figs 1A, B, 2)

ETYMOLOGY. Latin, *collectus*, narrowed, contracted.

MATERIAL. HOLOTYPE: QMF51013, from QML1096, Septimus Limestone, Tournaisian, Bonaparte Gulf Basin. PARATYPES: QMF51014-51022 from QML1096.

DIAGNOSIS. Tail plate narrowly elongate; intermediate plate elongate, wider posteriorly than anteriorly, strongly arched.

DESCRIPTION. Plates of moderate size (Table 1). Tail plate elongate, narrow, strongly arched. Jugal area prominently set off from lateropleural areas, mucro small, just anterior to posterior margin. Posterior margin slightly arched; anterior margin straight. Sutural laminae relatively wide, long. Surface smooth with prominent comarginal growth ridges posteriorly and laterally. Angle of jugal area 20° .

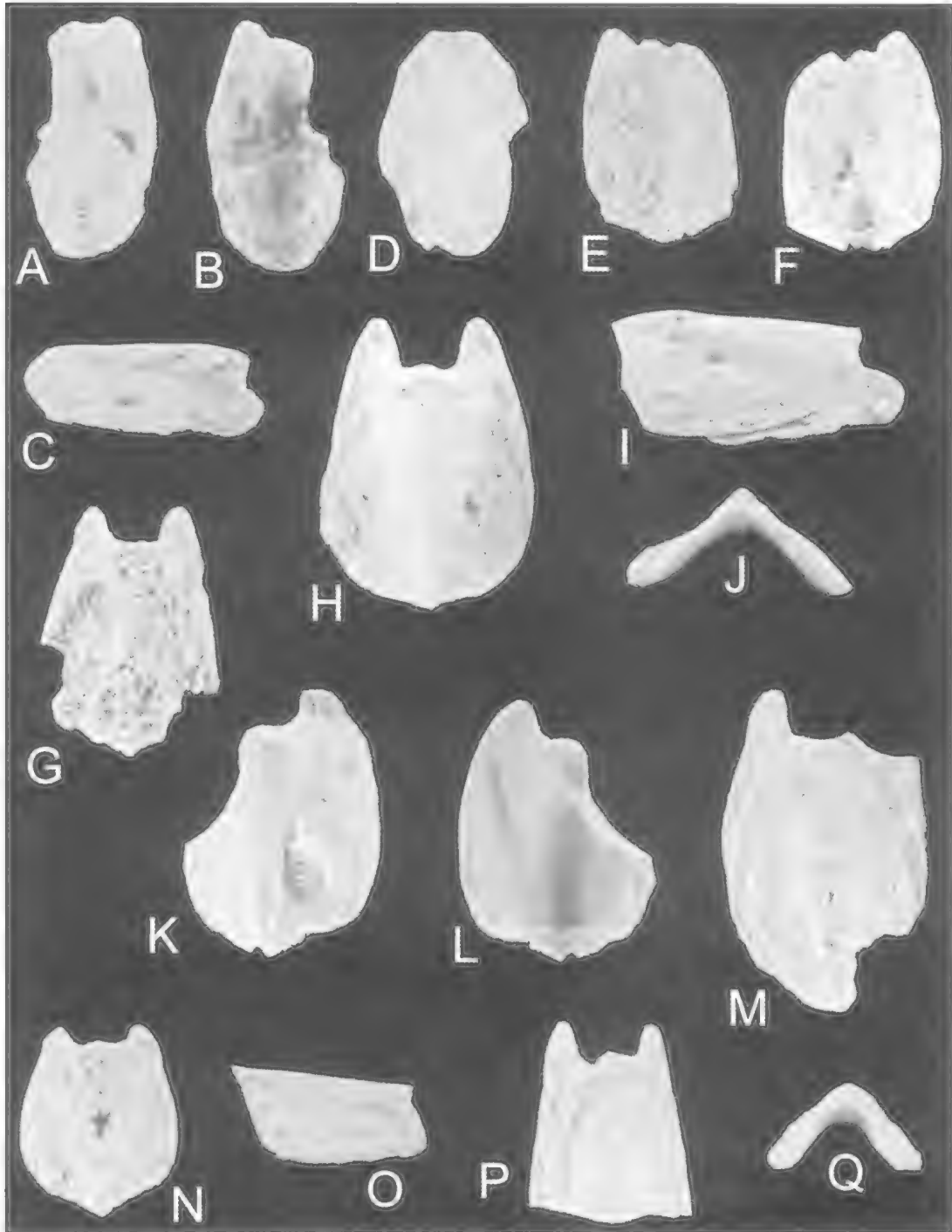


FIG. 2. *Gryphochiton collectus* sp. nov. A-C, Holotype QMF51013, tail plate, dorsal, ventral and right lateral views; D, Paratype QMF51020, tail plate, dorsal view; E, F, Paratype QMF51015, intermediate plate, dorsal and ventral views; G, Paratype QMF51018, intermediate plate, dorsal view; H-J, Paratype QMF51014, intermediate plate, dorsal, right lateral and posterior views; K, L, Paratype, QMF51016, intermediate plate, dorsal and ventral views; M, Paratype QMF51018, intermediate plate, dorsal and right lateral views; P, Q, Paratype QMF51019, intermediate plate, dorsal and anterior views. All $\times 2.5$

TABLE 1. Measurements for *Gryphochiton collectus* sp. nov.

Specimen	Length (mm)	Width (mm)	Height (mm)	Plate
QMF51013*	13.5	7.8	2.4	T
QMF51014	16.0	12.5	5.9	I
QMF51015	12.9	9.2	3.9	I
QMF51016	14.9	11.6	5.4	I
QMF51017	18.5	11.8	5.5	I
QMF51018	13.7	10.2	4.7	I
QMF51019	10.6	9.2	4.3	I

Intermediate plates longer than wide, tapering anteriorly, strongly arched. Lateral margins gently convex, anterior margin straight to slightly convex, posterior margin slightly mucronate. Jugal area distinct from lateropleural areas. Apical area large, extending as broad band along posterior margin. Surface smooth with prominent comarginal growth ridges on lateropleural areas. Apical angle 94° to 112°, angle of jugal area 18° to 23°. Headplate unknown.

REMARKS. *Gryphochiton collectus* sp. nov., although smaller, is most similar to *G. nervicanus* (de Ryckholt, 1845), the type species of *Gryphochiton* Gray, 1847b. Comparisons were made with three tail plates and one intermediate plate of *G. nervicanus* in the collections of the Museum of Comparative Zoology, Harvard University. The major difference lies in the much larger sutural laminae, larger apical areas, and less strongly arched posterior margin of the tail plate in *G. collectus*.

Compsochiton gen. nov.

TYPE SPECIES. *Compsochiton formosus* sp. nov.

ETYMOLOGY. Greek, *kompsos*, elegant, pretty; *chiton*, tunic.

DIAGNOSIS. Tail plate with broadly angular jugum, posterior margin flatly convex and curved dorsally; intermediate plate mucronate; sutural laminae large.

DISTRIBUTION. Carboniferous (Tournaisian), Septimus Limestone, Bonaparte Gulf Basin, WA.

REMARKS. *Compsochiton* differs from *Gryphochiton* Gray, 1847a by having differentiation of jugal and lateropleural areas on the head plate, a small falsebeak on the tail plate, and lack of the subquadrangular to subrectangular shaped intermediate plates of the latter genus. *Euleptochiton* Hoare and Mapes, 1985, has a much wider than long tail plate with a narrower jugal area, and mucro located anterior to midlength.

Compsochiton formosus sp. nov. (Figs 1C,D, 3)

ETYMOLOGY. Latin, *formosus*, beautifully formed.

MATERIAL. HOLOTYPE: QMF50123, from QML1096, Septimus Limestone, Tournaisian, Bonaparte Gulf Basin. PARATYPES: QMF50124-50136, from QML1096.

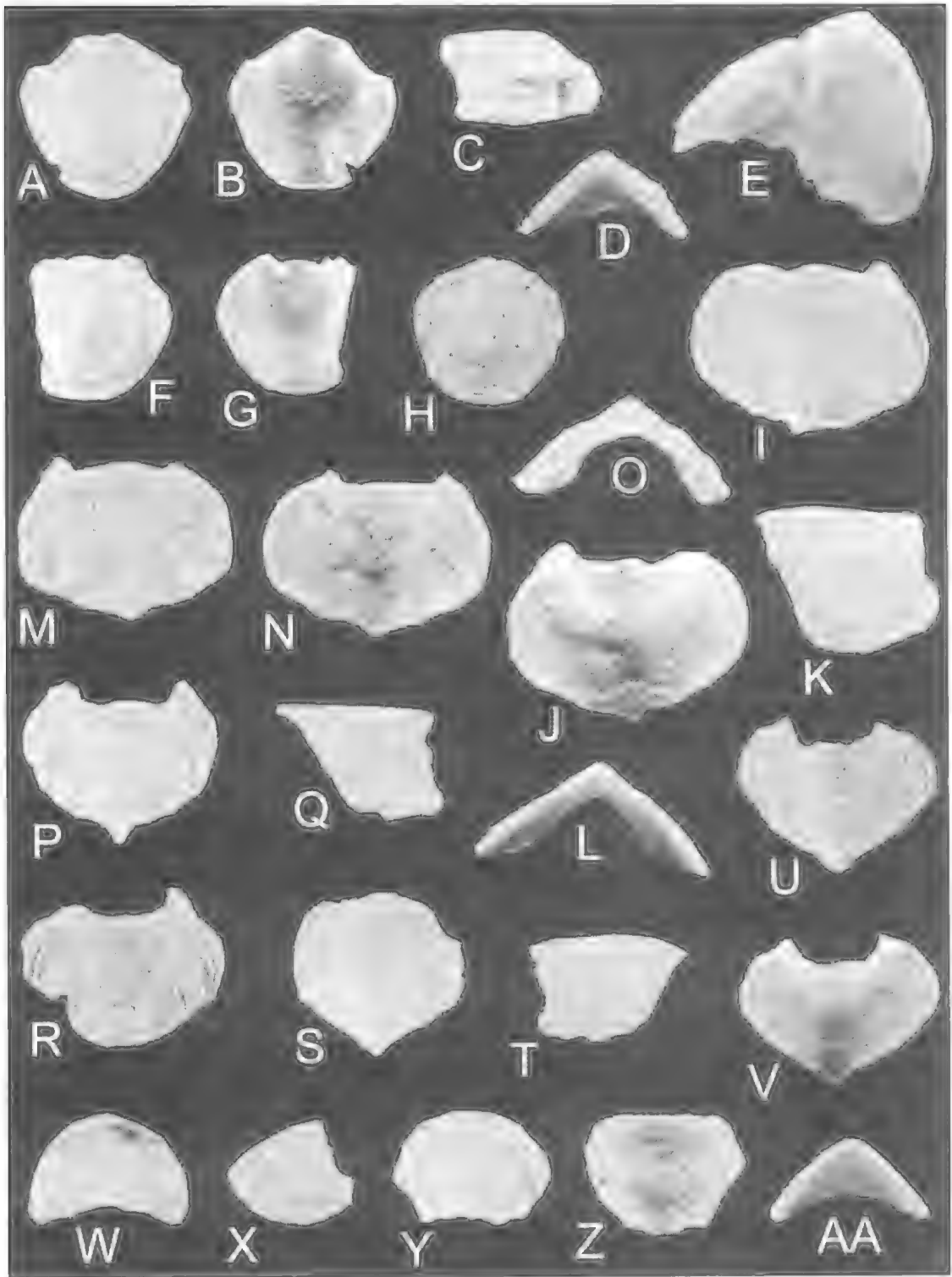
DIAGNOSIS. As for the genus.

DESCRIPTION. Plates of moderate size (Table 2). Tail plate strongly arched with broadly angular jugal area, mucro low and posterior to midlength. Posterior margin flatly convex, lateral margins diverging anteriorly, anterior margin with small false beak. Jugal area slightly set off from lateropleural areas, the latter marked by distinct comarginal growth ridges. Sutural laminae wide, long, extending to anterolateral corners. Surface ornamented with fine, closely spaced pustules. Angle of jugal area 70°.

Intermediate plates wider than long, strongly arched, with broadly angular jugal area, slightly to distinctly set off from lateropleural areas. Posterior margin mucronate, lateral margins convex, anterior margin ranging from slightly convex to slightly concave. Apical area large medially, extending as narrowing band to posterolateral corners. Surface with fine, closely spaced pustules and distinct comarginal growth ridges on lateropleural areas. Apical angle 93° to 106°, angle of jugal area 48° to 60°.

Head plate strongly arched with broadly angular jugal area distinct from lateropleural areas.

FIG. 3. *Compsochiton formosus* gen. et sp. nov. A-E, Holotype QMF51023, tail plate, dorsal, ventral, left lateral, anterior and oblique ventral views; F,G, Paratype QMF51024, tail plate, dorsal and ventral views; H, Paratype QMF51026, tail plate, dorsal view; I-L, Paratype QMF51028, intermediate plate, dorsal, ventral, right lateral and posterior views; M-O, Paratype QMF51027, intermediate plate, dorsal, ventral and anterior views; P,Q, Paratype QMF51029, intermediate plate, dorsal and right lateral views; R, Paratype QMF51030, intermediate plate, dorsal view; S,T, Paratype QMF51031, intermediate plate, dorsal and left lateral views; U,V, Paratype QMF51033, intermediate plate, dorsal and ventral views; W,X, Paratype QMF51034, head plate, dorsal and left lateral views; Y-AA, Paratype QMF51035, head plate, dorsal, ventral and posterior views. All $\times 2.5$ except E $\times 4$.



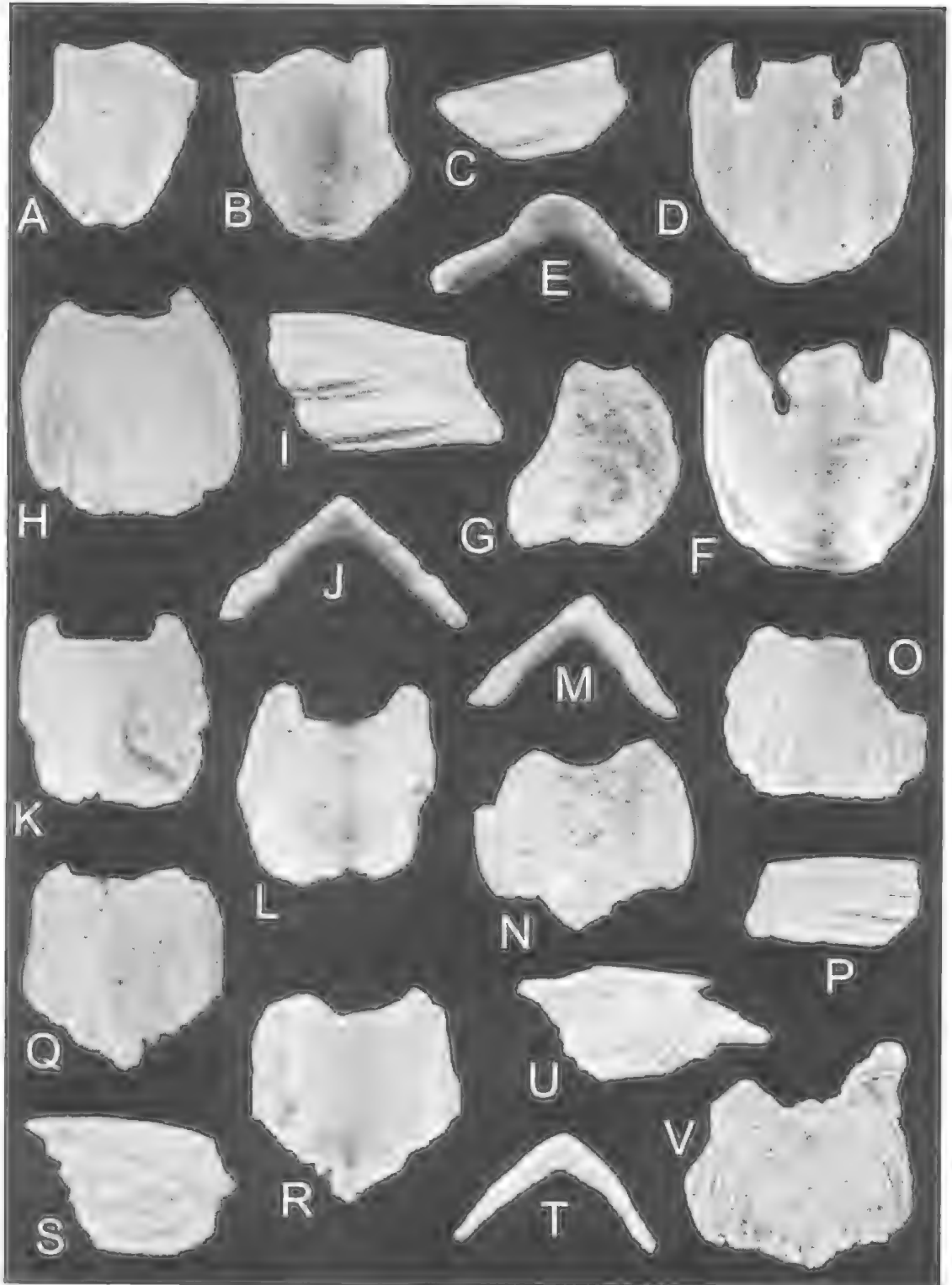


TABLE 2. Measurements for *Compsochiton formosus* gen. et sp. nov.

Specimen	Length (mm)	Width (mm)	Height (mm)	Plate
QMF50123*	9.3	9.7	5.2	T
QMF50124	9.4	9.4	3.8	T
QMF50125	8.7	9.0	4.2	T
QMF50126	8.4	8.7	4.7	T
QMF50127	9.8	12.6	5.5	I
QMF50128	10.3	14.0	6.7	I
QMF50129	9.5	11.1	5.1	I
QMF50130	9.4	11.4	5.6	I
QMF50131	10.0	9.9	5.2	I
QMF50132	9.5	12.0	5.8	I
QMF50133	8.8	11.2	5.3	I
QMF50134	6.3	9.2	5.1	H

Anterior and lateral margins broadly curved, posterior margin nearly straight. Apical area large, extending along posterior margin to posterolateral corners. Surface with fine pustules and distinct comarginal growth ridges in lateropleural areas. Apical angle 106°, angle of jugal area 60°.

REMARKS. At first appearance *C. formosus* looks similar to *Gryphochiton parvus* (Stevens, 1858), although the plates are three times the size of the latter species. Other than size, the distinct, broadly angular, jugal area, large sutural laminae, false beak on the tail plate, and the finely pustulose ornamentation on *C. formosus* clearly differentiate the two taxa.

INJURY. The holotype of *Compsochiton formosus* gen. et sp. nov., a tail plate, has an injury in the posterolateral margin (Fig. 3B, C, E). A notch, approximately 0.75mm wide and 1.5mm high, extends through the shell material. It is evident that the chiton was alive at the time of the injury by the presence of new shell material deposited on the ventral surface to block off the opening. No indication is present as to the cause of the injury although the bulging inward shape of the repair made by the individual would indicate that either the mantle at the site had been injured or that the predator was present within the notch in

the original shell layers. This is the first example of plate injury and repair of a fossil polyplacophoran that we are aware of.

LEPIDOPLEURIDAE? Pilsbry, 1892

Harpidochiton gen. nov.

TYPE SPECIES. *Harpidochiton auctus* sp. nov.

ETYMOLOGY. Greek, *harpidos*, shoe or sandal; *chiton*, tunic.

DIAGNOSIS. Tail plate subtriangular, longitudinally concave, mucro terminal; intermediate plates subquadrangular, strongly arched, apical area large.

DISTRIBUTION. Carboniferous (Tournaisian), Septimus Limestone, Bonaparte Gulf Basin, Western Australia; (Viséan) Utting Calcarenite, Bonaparte Gulf Station, WA.

REMARKS. *Harpidochiton* differs from genera of the family Acutichitonidae Hoare, Mapes & Atwater, 1983, also with subtriangularly shaped tail plates, by lacking a hypotyche on the ventral surface. *Systemochiton* Hoare (in press), from the Mississippian (Osagean) of Iowa lacks the longitudinal concavity in the subtriangular tail plates, has a subcentral mucro, and has much smaller sutural laminae than is present in *Harpidochiton*.

The characters of *Harpidochiton* do not conform well with those of the other lepidopleurids, nor with other described families. It is assigned here temporarily pending additional material on which to base a new family.

Harpidochiton auctus sp. nov.

(Figs 1E, F, 4)

MATERIAL. HOLOTYPE: QMF50137, from QML1096, Septimus Limestone, Tournaisian, Bonaparte Gulf Basin. PARATYPES: QMF50138-50144, from QML1096, QMF40826-40829, from QML1095, Utting Calcarenite, Viséan, Bonaparte Gulf Basin.

DIAGNOSIS. As for the genus.

DESCRIPTION. Plates of moderate size (Table 3). Tail plate subtriangular. Lateral margins convex, anterior margin straight to weakly convex.

FIG. 4. *Harpidochiton auctus* gen. et sp. nov. A-C, Holotype QMF51037, tail plate, dorsal, ventral and left lateral views; D-F, Paratype QMF51038, tail plate, dorsal, anterior and ventral views; G, Paratype QMF51039, tail plate, dorsal view; H-J, Paratype QMF51040, intermediate plate, dorsal, right lateral and posterior views; K-M, Paratype QMF51041, intermediate plate, dorsal, ventral and anterior views; N, Paratype QMF51043, intermediate plate, dorsal view; O, P, Paratype QMF51042, intermediate plate, dorsal and left lateral views; Q-T, Paratype QMF40826, intermediate plate, dorsal, ventral, right lateral and posterior views; U, V, Paratype QMF48027, intermediate plate, right lateral and dorsal views. All $\times 2.5$.

TABLE 3. Measurements for *Harpidochiton auctus* gen. et sp. nov.

Specimen	Length (mm)	Width (mm)	Height (mm)	Plate
QMF50137*	10.9	11.0	5.9	T
QMF50138	13.8	13.2	7.9	T
QMF50139	10.8	12.1	7.0	T
QMF50140	13.7	13.1	7.0	I
QMF50141	11.6	11.2	6.0	I
QMF50142	10.7	12.3	5.6	I
QMF50143	11.1	12.9	6.5	I

Jugal area set off from lateropleural areas by pronounced grooves; mucro terminal. Lateral profile longitudinally concave. Sutural laminae large. Surface smooth with strongly developed comarginal growth ridges on lateropleural areas. Angle of jugal area 33° .

Intermediate plates subquadrangular, strongly arched, sharply curved transversely in jugal area. Lateral margins gently convex, anterior margin with wide, shallow jugal sinus, posterior margin straight to slightly mucronate. Jugal area prominent, set off by grooves. Sutural laminae large, extending to anterolateral corners. Apical area large, extending to posterolateral corners, often marked by comarginal growth ridges. Surface smooth with prominent growth ridges on lateropleural areas. Apical angle 93° to 103° , angle of jugal area 35° to 39° . Head plate unknown.

REMARKS. The concavity of the tail plate, the smooth surface, and the coarse, comarginal growth ridges restricted to the lateropleural areas are diagnostic of *H. auctus*.

ACUTICHITONIDAE Hoare, Mapes
& Atwater, 1983

Arcochiton Hoare & Sturgeon, 1976

Arcochiton sp.
(Fig. 5)

MATERIAL. One tailplate QMF39839 from QML1160.

DESCRIPTION. Small (3.2mm long, 3.3mm wide, 2.4mm high) tail plate, subtriangular in dorsal and lateral views. Jugal area narrow, slightly set off from steep lateral slopes, mucro terminal posteriorly. Anterior margin with deep jugal sinus, large, well-developed hypotyche on ventral surface. Surface granulate, augmented by silica replacement, especially near lateral margins. Evidence of narrow sutural laminae on ventral surface paralleling margins of jugum, their projections not preserved.

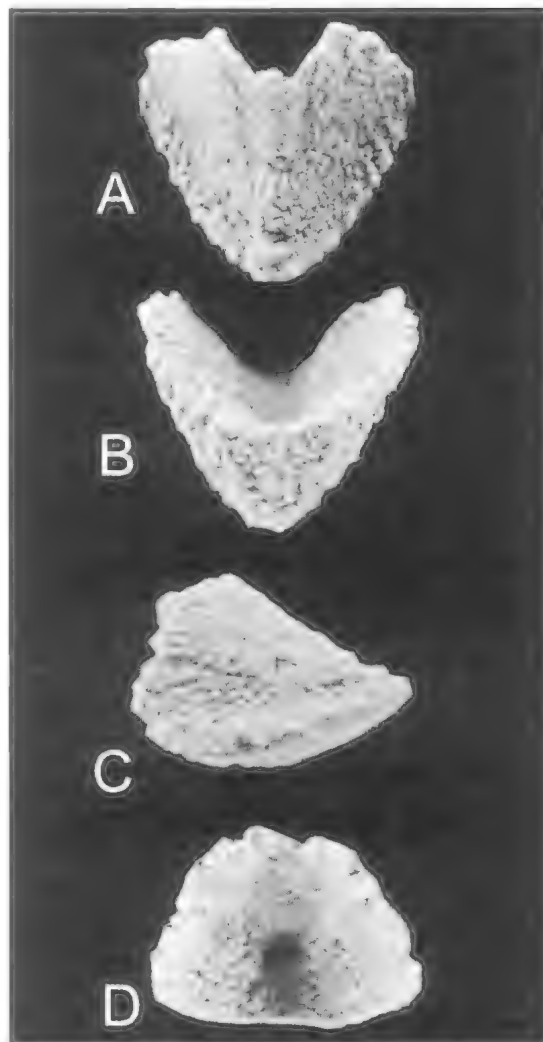


FIG. 5. *Arcochiton* sp. A-D, Hypotype QMF39839, tail plate, dorsal, ventral, left lateral and anterior views. All $\times 10$.

REMARKS. The presence of this Australian specimen extends the known range of the family Acutichitonidae from the Pennsylvanian to the Upper Devonian and specimens from Oregon further extend that range into the Permian (Hanger et al., 2000). The coarse preservation partially masks the characters of the plate. The shapes and curvature of the plate and hypotyche are distinctive of *Arcochiton*. More and better preserved material would allow the establishment of a new species.

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MESOZOIC FRESHWATER AND ESTUARINE BIVALVES FROM AUSTRALIA

SCOTT A HOCKNULL

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Australian freshwater and estuarine bivalves are described from the Hyriidae, Glauconomidae and Sphaeriidae. The following taxa are now known from the Mesozoic of Australia: from the Triassic, Hyriidae, comprising *Prohyria cyrensis*, *Megalovirgus* gen. nov., *Megalovirgus clellandi*, *Megalovirgus jaenschii* and *Mesohyridella ipsvicensis*, Glauconomidae, *Unionella wianamattensis*, *Protovirgus dunstani* and *Protovirgus brookvalensis* sp. nov.; from the Jurassic, Hyriidae, *Hyridella* (*Protohyridella*) sp. *Prohyria skeptici* sp. nov., ?Sphaeriidae, *Protosphaerium talbragarensis* gen. et sp. nov. and *Protosphaerium gainae* sp. nov.; and, from the Cretaceous, Hyriidae, *Megalovirgus wintonensis*, *Hyridella macmichaeli*, *Hyridella* (*Protohyridella*) *goundiwitindiensis*, *Hyridella whitecliffsensis*, *Alytharia jaqueti*, *Alytharia coatsi* and *Palucohyridella godthelpi* gen. et sp. nov. It is apparent that over the course of freshwater bivalve evolution in Australia there has been a distinct faunal dichotomy between large and small taxa. The large forms are exclusively hyriids and dominate lacustrine, riverine and lagoonal environments and the small forms, either glauconomids, sphaeriids and/or corbiculids dominate brackish and estuarine environments. This dichotomy is also present in the modern estuarine and freshwater taxa. The presence of glauconomids during the Triassic is the first and earliest record, providing good evidence for estuarine depositional environment of the Wianamatta Shales, Sydney Basin. This is also the earliest record of sphaeriids in Australia. Little is known of the evolutionary relationships within these groups due to their conservative morphology. □ *Megalovirgus* gen. nov. *Palucohyridella godthelpi* gen. et sp. nov. *Prohyria skeptici* sp. nov., *Protosphaerium talbragarensis* gen. et sp. nov. *Protosphaerium gainae* sp. nov. *Protovirgus brookvalensis* sp. nov. Hyriidae, Sphaeriidae, Glauconomidae.

Hocknull, S.A. (email: scotth@qm.qld.gov.au), *Invertebrate Palaeontology*, Queensland Museum, P.O. Box 3300 South Brisbane 4101, Australia; 29 October 1999.

Australian fossil freshwater and estuarine molluscs are poorly known, with few publications on the higher taxonomy of present day and extinct taxa. A review is offered here for the Mesozoic freshwater bivalves comprising the families Hyriidae, Glauconomidae and Sphaeriidae, with redescription of previously described species and description of new forms. Detailed illustrations and measurements are provided so that further collection does not confuse issues of variation and taxonomic position.

Etheridge Jr (1888, 1892) described several forms from Australia assigning most to *Unio*, apart from the smaller forms to which he assigned *Unionella*. Newton (1915) described new Cretaceous unionoids from Lightning Ridge and White Cliffs, also allocating these to *Unio*. At this point the Unionoida comprised the Unionidae, Margretifidae and Mutelidae.

Later, McMichael (1956) revised Etheridge Jr's and Newton's material, presenting detailed descriptions of fossil nonmarine taxa from Australasia in an effort to alleviate some of the taxonomic confusion within these morphologically

conservative groups. McMichael proposed that these fossil unionoids were from a Mutelidae lineage, and included the modern fauna within this family in a regional revision (McMichael & Hiscock, 1958). Most of McMichael's fossil descriptions were paraphrased from Etheridge Jr's and Newton's earlier work and little new material was incorporated into his study.

McMichael (1956) did, however, erect three mostly Mesozoic genera of mutelids: *Prohyria*, *Mesohyridella* and *Protovirgus*, neatly accommodating large and medium-sized bivalve taxa. Ludbrook (1961) described new taxa from the Triassic Leigh Creek Formation, South Australia, proposing that the genus *Unio* was valid for some Australian unionoids and that this confirmed the presence of Unionoida in Australia. I provide evidence to the contrary. Ludbrook also assigned one species to McMichael's *Protovirgus*, which is now placed within *Alathyria*.

Parodiz & Bonnetto (1963) provided evidence for a separate endemic Gondwanan lineage on the presence and morphology of the glochidial larval stage. They proposed that the Australian

radiation was distinct enough to allow familial unicity and several taxa in South America were also assignable to this new group, Hyriidae, instead of the dominant Mutelidae. These conclusions suggest that the unionoids from Australia are mostly Gondwanan in origin with recent, presumably Pleistocene – Holocene, invasions from southeast Asia. This view is supported by the present study.

Since McMichaels' review, more material has come to light that has shed new and interesting information on the taxonomic validity and position of the fossil taxa. Shell characteristics that McMichael & Hiscock (1958) put forward for the subfamilies within the Hyriidae have also assisted herein in allocating the fossil taxa to these subfamilies.

Smaller Triassic bivalves (*Unionella*) described by Etheridge Jr (1888) and reviewed by McMichael (1956) from the Sydney Basin and Bowral posed problems for McMichael with his only suggestion that they were Triassic holdovers of the Permo-Carboniferous family Anthracosiidae. This family has a conspicuous presence in North America (Rogers, 1965), United Kingdom (Weir, 1960) and the former Soviet Union (Haas, 1969) during the Carboniferous and Permian. I place these small bivalves with the modern family Glauconomidae, but do not rule out distant phylogenetic links to the anthracosiids. There is a strong possibility that convergence has been acting on both these groups, indeed all freshwater and estuarine bivalves reported here. However, enough characteristics have been found that ally these small Triassic bivalves to the Glauconomidae.

Most recently, Hocknull (1994) described a new taxon from the Late Triassic of southeast Queensland allocating it to *Protovirgus*, here revised to *Megalovirgus* gen. nov. Hocknull (1997) described new taxa from the Cretaceous of Queensland placing all taxa within previously recognised genera. The understanding that there is considerable confusion over the taxonomy of the unionoids and the presence of unrecorded families of small freshwater faunas prompted the present review.

New material from the Talbragar Fossil Fish Beds, New South Wales, indicate the possible presence of Sphaeriidae in Australia. Hampered by the lack of well-preserved specimens the allocation of the small bivalves to Sphaeriidae is tentative.

As there is an apparent dichotomy between bivalve faunas, depositional environment, their sizes and phylogenetic history, it remains to be seen whether the assignment of different sized faunas should lie at the family level. Such possibilities are discussed later. Fossils are given the prefix SAMF (South Australian Museum), QMF (Queensland Museum), UQF (University of Queensland) and AMF (Australian Museum) and are deposited in their respective institutions.

AGE AND STRATIGRAPHY

Ten major sites, containing nonmarine bivalves, are recognised from Queensland (Qld), New South Wales (NSW) and South Australia (SA) (Fig. 1). The hyriids are restricted in the Triassic to the Ipswich Coal Measures, Qld and the Leigh Creek and Springfield Basins, SA. During the Jurassic they occur sporadically in the Waloon Coal Measures, Warwick, SE Qld and the Koonwarra Fossil Bed, South Gippsland, Victoria. In the Cretaceous the family is abundant throughout the entire Eromanga Basin, especially the Coreena, Griman Creek and Winton Formations of northern NSW and Qld.

Small freshwater and estuarine bivalve fossil faunas (glauconomids and sphaeriids) are restricted in the Triassic to the Wianamatta Shales, Sydney Basin, and in the Jurassic to the outlying Talbragar Fossil Fish Bed derived from the Pur-lawaugh Formation. No small nonmarine bivalves are as yet known from the Australian Cretaceous.

There are three major stratigraphic units, in which Triassic freshwater bivalves are preserved. In SE Qld, the units containing hyriids are the Blackstone and Tingalpa Formations, both considered Late Triassic (Carnian) in age by de Jersey (1975) and de Jersey & Hamilton (1965), respectively. Both formations consist of fine grained to coarse-grained sandstones and siltstones/shales, with most of the bivalves being derived from the finer carbonaceous siltstones and shales. Preservation is good, with most individuals having both valves intact and fine ornamentation preserved. The valves are generally external moulds with little internal morphology preserved. The cavities have been replaced with ferrous sediment. The preservation of both valves suggests an in situ taphonomy.

Playford & Dettman (1965) ascribe the Leigh Creek Formation, SA, a Late Triassic age on the basis of similar palynological floras to those in Ipswich. Whilst other authors ascribe ages between Late Triassic (Rhaetic) to Early Jurassic

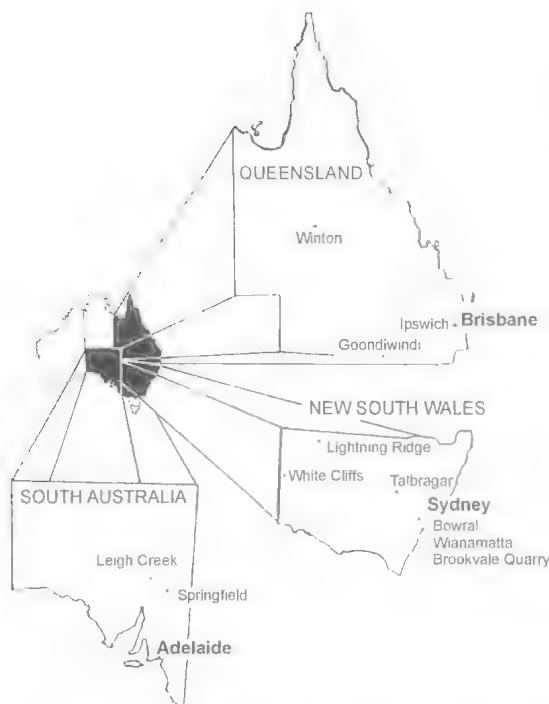


FIG. 1. Map illustrating Australian localities for Mesozoic freshwater and estuarine bivalve fossils.

(Liassic) on the basis of fish faunas (Wade, 1953), plant floras (Chapman & Cookson, 1926) and unionoids such as *Prohyria eyrensis* (Ludbrook, 1961). The Springfield Coal Basin, SA, is also attributable to the Late Triassic from diagnosis of equivalent sediments to the Leigh Creek Formation (Johnson, 1960) and, again, the presence of the distinctive *Dicroidium* and *Thinnfeldia* floras with the presence of the hyriid; *Prohyria eyrensis* (= *Unio springfieldensis* Ludbrook, 1961).

Like the Blackstone Formation, the bivalves are preserved as moulds with both valves intact. The deposit is interpreted as in situ.

The Brookvale Quarry and Bowral Quarry expose sections through the Wianamatta Shales, Sydney Basin, NSW. Small valved glauconomids occur at all sites and are attributable to the Late Triassic, being derived from the Hawkesbury Sandstone and Wianamatta Group (Lovering & Elroy, 1969). The shells are preserved as whole specimens or as singular valves. Mass accumulations suggest fast burial and aggregation of these taxa in the bottom sediment. Little is known of the aggregation behaviour/taphonomy of modern glauconomids, therefore,

no interpretation of the depositional environment is given here.

There is one occurrence of small freshwater bivalves in the Jurassic of eastern Australia from the Talbragar Fossil Fish Beds, derived from the Purlawaugh Formation. The beds are an outlier group so an exact age is uncertain (Dulhunty & Eadie, 1969). They consist of 'chert containing Jurassic plant and fish fossils ... in soil derived by weathering from Jurassic Purlawaugh sediments ...' (Dulhunty & Eadie, 1969). The small bivalve fauna shows a mixture of depositional environments, preserving both isolated, singular valves and whole animals in aggregations. Modern sphaeriids and corbiculinids exhibit such mass aggregations after flooding (pers. obs.).

Fossil hyriids identified herein occurring in the Jurassic have an unknown position within the Waloon Coal Measures due to inaccuracies in locality data. They are badly preserved and are isolated throughout the measures. Both valves are usually found intact.

Three major units containing unionoids are derived from the Eromanga Basin; Winton, Griman Creek and Coreena Formations. The Griman Creek and Coreena Formation, derived from the Rolling Downs Group is considered Early Cretaceous (early-middle Albian) in age by Exon & Senior (1976) and Burger (1986, 1995) and consists of a brackish water unit with outcrops within the Surat Basin (Exon & Senior, 1976). This unit is comprised generally of lithic glauconitic sandstones, siltstones and mudstones. The younger Winton Formation, in central and southwestern Eromanga Basin, is of latest Albian to Cenomanian age (Senior et al., 1978), consisting for the most part of lacustrine and fluvial siliciclastic sediments that produced labile sandstones, siltstones and mudstones.

All three units contain mass aggregations of bivalves with whole animals preserved in situ. Mass aggregations of hyriids occurring today tend to be observed after flooding, hence the Griman Creek, Winton and Coreena Formations may be considered to be more fluvial than brackish-marine. The presence of marine molluscs in two of the formations (Griman Creek & Coreena) may then be attributed to marine incursions onto the fluvial systems. As there is very poor, if any, recorded stratigraphy the occurrence of the taxa in sympatry cannot be analysed. The relative abundance, however, may give clues to the placement of former drainage systems and in what direction they

flowed. For example, the Winton Formation has no record of marine taxa, whereas the Griman Creek and Coreena formations have. The Griman Creek formation specimens seem to be dominated by hyriids and the Coreena formation dominated by marine taxa. Examination of all the available species and their analogous environments need to be assessed in greater detail before such conclusions can be evaluated.

PALAEOECOLOGY

The families of freshwater bivalves present in the Mesozoic (Hyriidae, Glauconomidae and ?Sphaeriidae) illustrate analogous faunal assemblages to those occurring in modern Australia freshwater and estuarine systems. Regardless of climate dynamics, one large and several small bivalve groups have continually dominated the freshwater and estuarine bivalve faunas since the Triassic. The large bivalve fauna is comprised entirely of the hyriids, and the small bivalve faunas of either; glauconomids, sphaeriids or corbiculids. During the Mesozoic, there is an apparent faunal change occurring at the end of the Triassic, early Jurassic, and within the Jurassic toward the Cretaceous.

At the end of the Triassic there were two major faunal groups, the large *Prohyria* and *Megalovirgus* hyriids and the small *Unionella* and *Protovirgus* glauconomids. Both these faunas have been preserved separately in the fossil record and reveal no sign of overlap into either faunal system. It is, therefore, probable that the small glauconomids inhabited environments not suited for the larger unionoids and visa versa. Indeed, today glauconomids are only known from estuarine environments, and are therefore, quite distinct from the freshwater hyriids. This provides good evidence that the Wianamatta Shales were derived from such a system of deposition.

An analogous system is found today in the brackish to estuarine dwelling sphaeriids and corbiculids with the modern intercontinental riverine hyriid radiation. One can then speculate at the life habits of the Mesozoic taxa. The heavy shelled, large hyriids were presumably living in more lacustrine, fluvial regions of Australia's Mesozoic, whereas the smaller valved glauconomids and ?sphaeriids would have been respectively confined to the brackish, estuarine and riverine regions of coastal Mesozoic Australia.

SYSTEMATIC PALAEONTOLOGY

HYRIIDAE Ortmann, 1911
VELESUNIONAE Iredale, 1934

Prohyria McMichael 1956

TYPE SPECIES. *Prohyria johnstoni* (Etheridge Jr, 1892); from the Oligocene, West Tamar River.

DIAGNOSIS. (After McMichael, 1956) 'Medium sized to large freshwater mussels of the subfamily Velesunionae, the anterior end moderately to markedly swollen, the posterior end drawn out into a bluntly rounded rostration, which is of maximum length at a position in the middle of the height of the shell; hinge well developed, with large cardinal teeth.' Rostration of the posterior end is distinct in all growth forms. Escutcheon broad, extending almost the entire length of the valves. Anterior adductor muscle scars deep, elongate, orientated antero-ventrally and relatively small. Umbones consistently eroded. Prominent hinge with one elongate lateral tooth and large cardinals.

REMARKS. The genus is placed within Velesunionae due to the absence of beak sculpturing. McMichael (1956) erected this genus for the placement of two species, *P. johnstoni*, from the Oligocene of Launceston Basin and *P. eryensis*, from the Late Triassic of Leigh Creek, SA and Ipswich Coal Measures, SE Qld, within the velesunionines. Ludbrook (1961) assigned another large unioid from the Late Triassic, *Unio springfieldensis*, considered as *Prohyria springfieldensis* here, from the Springfield Basin, SA. Recently, an additional form, *P. macmichaeli*, was described by Hocknull (1997) from the Cretaceous of Qld, however, new specimens attributable to this taxon from Lightning Ridge, NSW, suggests alliance with the hydrellines. All three taxa are distinct from any other velesunionine genus by their large size, thick ornamented shell, rostrate posterior profile and distinctly inflated umbones.

Prohyria eyensis (Etheridge Jr, 1892) (Fig. 2K)

Unio eyensis Etheridge Jr 1892: 389, pl. 28(1); 1941: 11, pl. 3(1-3).

Prohyria eyensis (Etheridge Jr) McMichael 1957: 228, pl. 13(8, 11) (non 9, 10).

Unio springfieldensis Ludbrook, 1961: 145, pl. 2(1,2).

MATERIAL. AMF51624, 51651, 51642, 51647, 51644, 51648, 51649, 51625, 51626, 51638, 51640. SAM15473, 15474.

AGE AND DISTRIBUTION. Late Triassic from the Black Stone, Tingalpa, Bundamba formations, SE Qld. Leigh Creek Formation and Springfield Coal Basin, SA.

DIAGNOSIS. Large, elongate-oval, equivalved unioid with distinct rostration in the posterior end. Anterior end inflated and rounded. Hinge distinct with strong escutcheon produced along most of the dorsal margin. Lunule large and excavated. Beaks high and unsculptured, usually eroded. Commarginal ornamentation with coarse growth lines. Shell thick. From Ludbrook (1961); 'hinge with two triangular pseudo-cardinal and one long posterior lateral in the right valve, one triangular pseudo-cardinal and two long posterior laterals in left valve'. Anterior adductor muscles deep, elongate-oval and orientated antero-ventrally.

DESCRIPTION. Shell equivalved, inequilateral, umbones inflated and anteriorly placed 1/3 from anterior end. Beaks unsculptured but usually eroded. Shell thick with coarse growth lines producing ridged ornamentation. From Etheridge Jr (1892); 'Hinge line straight, ventral margin rounded, passing rather sharply upwards into the anterior and posterior margins. Anterior end small, somewhat acutely curved, posterior end narrow, obtusely pointed'. Anterior adductor muscle scars deeply set, behind beaks, elongate-ovoid and postero-ventrally orientated. Large cardinal teeth, with long bifurcating lateral tooth. Morphometrics given in Table 1.

REMARKS. *P. eyrensis* is one of the most common taxa found in the Ipswich and Leigh Creek deposits. It is a cosmopolitan taxon and is the largest in the Mesozoic. Attaining sizes over 12cm long it is comparable to modern species of *Velesunio* and *Alathyria*. These modern genera have been restricted to coastal river systems and lakes and may provide good analogues to the depositional environment of the Triassic coal deposits of SE Qld and SA.

P. eyrensis was reviewed by McMichael (1956) and placed within *Prohyria* when he erected the genus to fit one other taxon, *P. johnstoni*. Its placement within *Prohyria* is due to the large size, wedge-shaped profile, inflated beaks

positioned anteriorly and the prominent hinge. *Prohyria eyrensis* differs from *Prohyria johnstoni* in its size, size proportions and amount of tapering. *Prohyria johnstoni* tapers more sharply to the posterior than *Prohyria eyrensis*. *Prohyria springfieldensis* is markedly similar to *Prohyria eyrensis* and is synonymised here; however, it differs having: finer comarginal ornamentation; more rostrate appearance in oclusal view; straighter, more prominent hinge line. *P. eyrensis* differs from *Hyridella macmichaeli* formally placed within *Prohyria* by Hocknull (1997) by being much larger, with a more rostrate posterior profile. The beak sulcus is relatively less produced in *P. eyrensis*. Juvenile forms of *P. eyrensis* do not possess the characteristic V-shaped beak sculpture, as seen in *Hyridella macmichaeli*.

On inspection of the holotype and comparison to a series of specimens referable to *P. eyrensis*, including the holotype, from the Leigh Creek Basin and Ipswich Coal Measures, there is little evidence for the separation of these specimens from what is obviously a cosmopolitan taxon, *P. eyrensis*.

***Prohyria skepticsi* sp. nov.**
(Fig. 3)

TYPE SPECIES. *Prohyria johnstoni* (Etheridge, 1892).

ETYMOLOGY. For the Australian Skeptics.

MATERIAL. HOLOTYPE: UQF52158. PARATYPES: UQF52160, UQF29708A/B.

AGE AND DISTRIBUTION. Jurassic, Waloon Coal Measures, Warwick District, SE Qld.

DIAGNOSIS. Medium-sized, equivalved velesunionine hyriid. Elongate-ovoid, thick shell with rugose comarginal ornamentation. Shell tapering to the posterior to produce a triangulate wedge-shaped posterior margin. Umbones placed anteriorly and orientated antero-laterally to the shells' anterior-posterior axis. Anterior adductor muscle scar small, rounded and placed high, underneath the beaks. Beaks not sculptured. Lateral teeth simple, comprising a single tooth and socket in at least the left valve. Hinge line long and robust.

TABLE 1. Morphometrics (in mm) for *Prohyria eyrensis* (Etheridge Jr).

	Length	Height	Width	Beak Length	Beak Height	Beak Width	Ligament Length
Mean	85.75	46.57	34.09	15.85	41.04	16.65	46.78
s.d.	18.11	10.41	7.53	4.02	9.28	3.69	7.75
Number	12	12	12	12	12	12	12

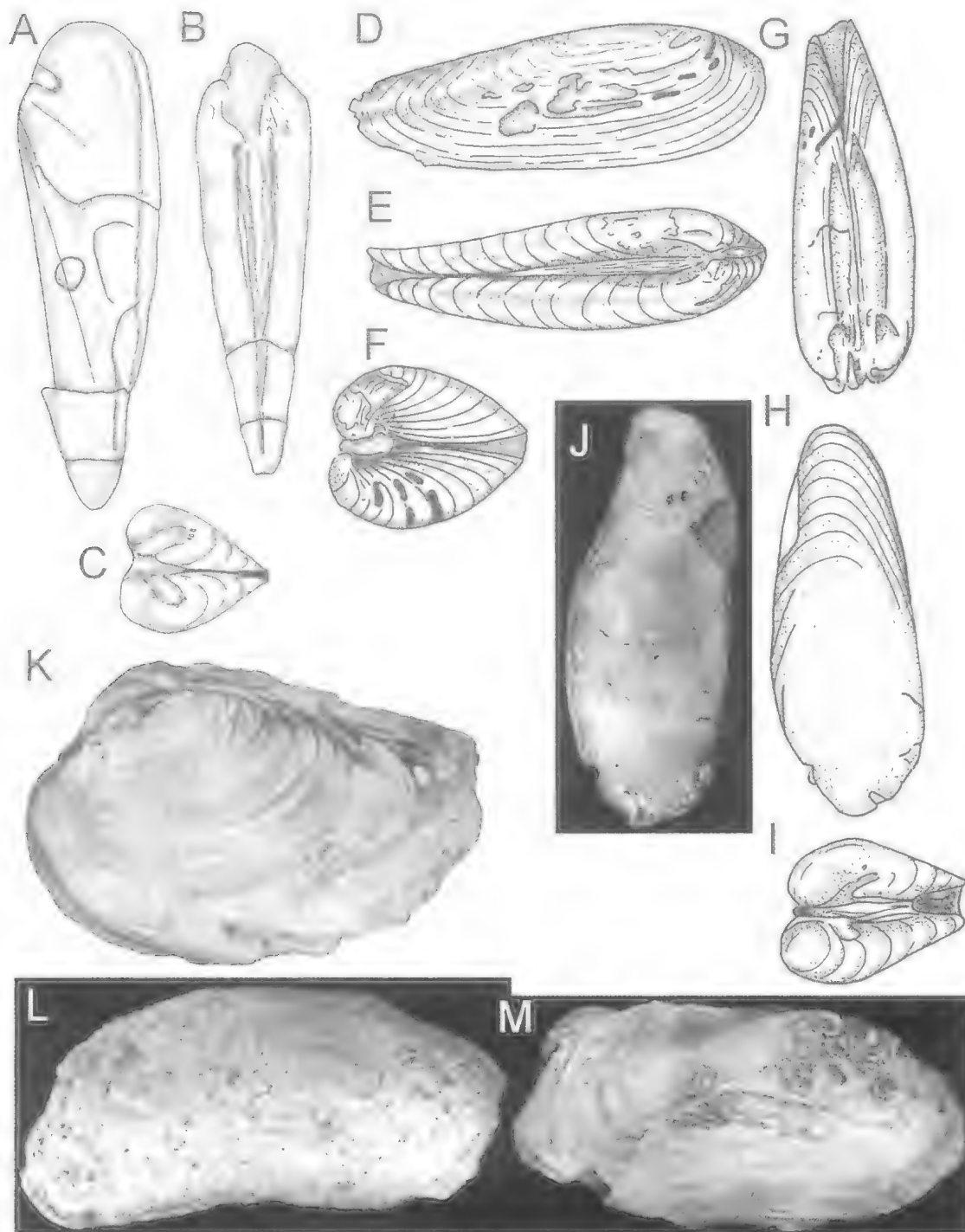


FIG. 2. A-C, *Megalovirgus clellandi* Holotype QMF29473; A, right valve $\times 0.5$; B, dorsal view $\times 0.44$; C, anterior view $\times 0.5$. D-F, *Megalovirgus wintonensis* Holotype QMF34635; D, right valve $\times 0.7$; E, dorsal view $\times 0.7$; F, anterior view $\times 0.8$. G-I, *Megalovirgus jaenschi* Holotype SAMF1547a; G, dorsal view $\times 0.46$; H, right valve $\times 0.46$; I, anterior view $\times 0.44$; J, right valve $\times 0.56$. K, *Prohyria eyrensis* Holotype SAMF15473, right valve $\times 0.7$. L, *Alathyria coatsi* Holotype SAMF15477, right valve $\times 0.8$. M, *Alathyria jaqueti*, QMF103903 right valve $\times 1.0$.

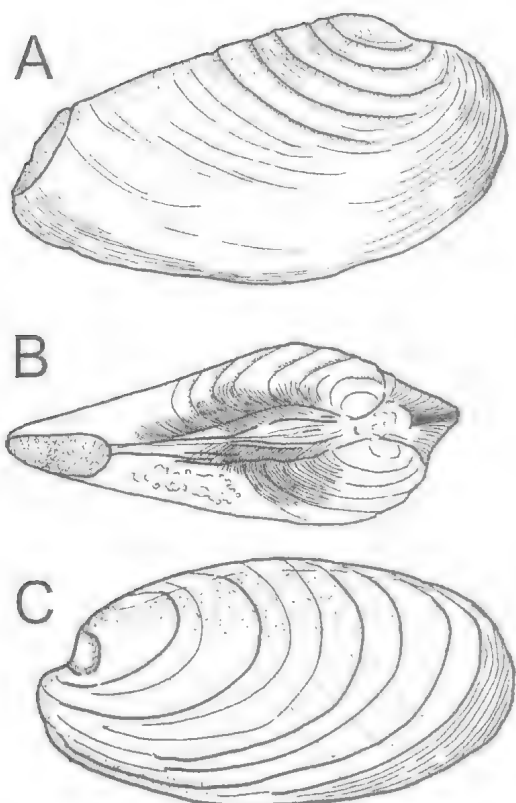


FIG. 3. *Prohyria skepticsi* sp. nov.; A, UQF52158 right valve $\times 1.2$; B, UQF52158 dorsal view $\times 1.0$; C, UQF29708 left valve $\times 1.5$.

DESCRIPTION. Medium-sized, elongate-ovoid hyriid with rugose comarginal ornamentation. Shell thick with long thick ligament. Hinge broad near umbones and tapers gradually to posterior margin. Umbones placed anterior at about 1/5 of total length. Posterior margin rounded. Anterior margin rounded and begins slightly below beak. Beaks not sculptured but possess fine lines conspicuous around margin. Escutcheon inconspicuous. Anterior adductor muscles placed antero-ventrally to anterior edge of beak. Muscle scar small and ovoid. Dentition simple comprising single lateral tooth in the left valve and possibly two cardinal teeth. Rugose ornamentation interspersed by fine growth lines. Umbones orientated anteriorly to lateral axis of valves. The shell immediately posterior to umbones is inflated and produces a slight ridge that runs the length of the shell to the posterior margin. The ventral is straight and rounded to both ends.

REMARKS. The absence of sculpture and the elongate-ovoid shape places this hyriid within the velesunionines. Its placement within *Prohyria* is warranted due to the rugose and thick shell interspersed with fine growth lines, triangulate-ovoid outline of the posterior margin, small ovoid highset anterior adductor scar and anteriorly placed umbones with laterally orientated beaks. *Prohyria skepticsi* differs from *Prohyria eyrensis* and *Prohyria johnstoni*, by its smaller size, more elongate outline, relatively smaller adductor muscle, and relatively broader hinge line. Morphometrics given in Table 2.

Alathyria Iredale, 1934

Alathyria jaqueti (Newton, 1916)
(Fig. 2M)

Unio jaqueti Newton, 1916: 230, pl. 6(2-6).
Velesunio jaqueti (Newton) McMichael, 1957.

MATERIAL. QMF10887, 15812, 103859, 103862, 103868, 103879, 103880, 103892, 103894, 103898, 103899, 103903.

AGE AND DISTRIBUTION. Uppermost Albian – Cenomanian Formations, Winton, Griman Creek and Coreena. Localities: QML229, QML379, QML570, Lightning Ridge and White Cliffs.

DIAGNOSIS. Large velesunionine hyriid, elongate-ovoid with distinct winged dorsal posterior rim. Ventral margin of valves in lateral aspect show distinct concave form. Beaks posterior, relatively inflated. Anterior margin tapers sharply from umbonal region. Umbonal region always eroded in large individuals. Long indistinct lateral tooth with small indistinct cardinals of unknown number.

DESCRIPTION. Shell large, elongate, medium sized, equivalved. Shell width narrow in young individuals, inflating as the shell becomes larger. Anterior margin tapers away sharply from beak, to a rounded profile. Dorsal edge subparallel with ventral margin with a truncated posterior producing a 'winged' profile. Beaks relatively anterior placed 1/3 from the anterior end. Pronounced inflation just postero-ventral of umbones carrying down to the postero-ventral edge. Umbones characteristically eroded with some being broken off post-deposition. Beaks unsculptured. Anterior adductor muscle scars inconspicuous, being small and just anterior to the cardinal teeth. Hinge relatively strong and short. Ventral margin concave toward the mid region. The concavity is more pronounced in larger individuals. Posterior adductor muscle

TABLE 2. Morphometrics (in mm) for *Prohyria skepticsi* sp. nov.

UQF No.	Length	Height	Width	Beak Length	Beak Height	Beak Width	Hinge Length
UQF52158	52.41	30.14	23.84	13.35	28.67	10.35	32.32
UQF52160	43.65	25.64	?	6.04	18.23	?	?
UQF29708A	48.59	29.75	15.90	11.13	26.72	10.09	27.64

scars indistinct. Cardinal teeth typically unionid. Lateral teeth obscured. Escutcheon narrow and encompasses most of the hinge area. Ligament is prominent within this area. Morphometrics given in Table 3. Shell allometry is illustrated in Figure 8. Note that the specimens allied to this taxon are distinct from *Megalovirgus wintonensis* on the basis of height to length ratios.

REMARKS. Newton (1915) placed this taxon within *Unio*, as with most other unionoids at that time. McMichael's reinterpretation of the material lead him to place the taxon within Velesunionae, as *Velesunio jaqueti*. The present review agrees with McMichael's placement within the velesunionines, based on the absence of any distinct umbonal sculpturing in small individuals. The shells are also less quadrate than those seen most prevalently in the hyridellines. The large size, winged posterior and tapering anterior margin show close similarities to *Alathyria*. The current study has examined many more specimens and the overall size shows that the taxon shares more similarities to *Alathyria* than *Velesunio*. *A. jaqueti* differs from its sympatric taxa by possessing a unique height to length ratio (only similar to *H. macmichaeli*). It differs from *H. macmichaeli* because it is winged posteriorly and does not possess juvenile beak sculpture.

***Alathyria coatsi* (Ludbrook, 1961)**
(Fig. 2L)

Protovirgus coatsi Ludbrook 1961: 146, pl. 2(6).

MATERIAL. SAM15477.

AGE AND DISTRIBUTION. Early Cretaceous (Neocomian), Blythesdale Group. Localities: as in Ludbrook (1961).

DIAGNOSIS. Medium-sized, equivalved, inequilateral hyriid with fine comarginal ornamentation. Umbones relatively deflated. Dorsal margin convex, with ventral margin highly concave in lateral profile.

DESCRIPTION. From Ludbrook (1961); 'Shell of medium size, compressed, elongate ... dorsal and ventral margins slopes approximately

parallel; dorsal margin gently convex and elevated posterior to beaks then curving more sharply downwards to the posterior margin ... Posterior ridge fairly well marked and gently arcuate. Beaks flattened, apparently unsculptured, not prominent; ligament moderately prominent, no lunule visible'.

REMARKS. Ludbrook placed this taxon within *Protovirgus* with no direct characteristic defining its position within the genus. Inspection of the holotype allowed the present study to place *P. coatsi* within the extant genus *Alathyria*. This placement is on the basis of the following characters present in *P. coatsi* and *Alathyria*: convex dorsal and concave ventral margins; flattened beaks in most members of the group; and marked postero-dorsal wing. The specimen differs from other species of *Alathyria* by its smaller size, more pronounced convexo-concavo lateral profile and less prominent winged postero-dorsal face.

HYRIDELLINAE Iredale, 1934

***Megalovirgus* gen. nov.**

TYPE SPECIES. *Megalovirgus jaenschii* (Ludbrook), from the Upper Triassic, Leigh Creek Formation, SA.

ETYMOLOGY. *Megalos*, Greek, pertaining to the taxons large size; *-virgus* for the genus *Virgus* which it resembles closely.

DIAGNOSIS. Shells medium to large, elongate, knife-like, with umbones inflated and positioned extremely anterior. Anterior adductor muscle scar set on platform, oblong, ventro-laterally orientated. Shell thin with little or no ornamentation. V-shaped sculpturing in the umbones with sculpture proceeding down a postero-dorsal ridge in smaller individuals. Ornamentation lost in most adult valves. Posterior musculature unknown. Escutcheon long and broad with distinct ligament.

DESCRIPTION. Shells that are distinctly hyridelline in juvenile morphology, losing this in the larger individuals. Medium to large shells, equivalved, inequilateral, elongate with beaks placed extremely anterior. Posterior margin tapering moderately to sharply, all knife-like.

TABLE 3. Morphometrics (in mm) for *Alathyria jaqueti* (Newton).

	Length	Height	Width	Beak Length	Beak Height	Beak Width	Ligament Length
Mean	61.82	34.2	23.57	17.09	34.28	11.12	27.44
s.d.	12.49	7.73	5.67	4.96	7.73	3.40	6.72
Number	12	12	12	9	12	7	3

Anterior margin truncated and rounded, with indistinct lunule, producing weak beak sulcus. Fine comarginal growth lines, with smooth ornamentation. Anterior adductor muscle elongate and placed high in the shell, in front of beaks; orientated postero-ventrally or just ventrally. Raised on small platform. Dorsal and ventral margins run subparallel producing elongate tear-shaped outline to valves. Escutcheon broad, housing distinct hinge with prominent ligament. Teeth comprise of one large lateral tooth, weakly preserved and two weak cardinal teeth. Typical unionid teeth. Valves produced laterally to provide distinct height.

REMARKS. This genus is erected to house species that have been confused with another family (the glauconomids) of freshwater bivalves inhabiting other areas at similar times. The Glauconomidae, presented later, has an unusual presence within Australia and has evolved to fill an ecology not used by unionoids. The species formally placed within *Protovirgus* by McMichael (1956) are now placed within *Megalovirgus* except for the type species, *P. dunstani*. This is because all of the other taxa are believed to be hyriids, whereas, *P. dunstani*, is thought to be a glauconomid. The reasons for this will be presented under *P. dunstani*.

Megalovirgus differs from all other hyriid genera on the basis of the following differences: elongate profile with indistinct beak sculpture (cf. Cucumerunionae); indistinct lunule and weak sulcus; fine growth lines with no ornamentation; and distinct anterior adductor muscle, raised on platform, just in front of beaks. The new genus is now used for *M. jaenschi*, *M. femingi*, *M. clellandi* and *M. wintonensis*. *Protovirgus coatsi* Ludbrook, 1961, is redescribed above as, *Alathyria coatsi*.

Megalovirgus jaenschi (Ludbrook, 1961)
(Fig. 2G-J)

Protovirgus jaenschi Ludbrook, 1961: 145 pl. 2(3-4).

MATERIAL. HOLOTYPE: SAM1547a and PARATYPE 1547b. AMF51627, 51639, 51645, 51650, 51635, 51664.

AGE AND DISTRIBUTION. Late Triassic, formations: Leigh Creek, Springfield Coal Basin. Localities: Leigh

Creek Coal Fields, Leigh Creek Golf Course, Springfield Coal Fields, SA.

DIAGNOSIS. Large elongate, inflated hyrideline with fine comarginal ornamentation. Shell thin and valves deep. Posterior edge tapering to a relatively pointed end. Anterior rim rounded and short. Beaks placed at 1/10 the length from the anterior end.

DESCRIPTION. See Ludbrook (1961), Morphometrics given in Table 4.

REMARKS. *M. jaenschi* is distinct from the other species within this genus due to the placement of the beaks, narrow form, overall size and orientation of the anterior adductor muscle scars. *M. jaenschi* is longer than *M. wintonensis* with beaks placed more anteriorly. The anterior adductor muscle scar is set more ventrally in *M. jaenschi* than in *M. wintonensis*. The valves are relatively narrower than in *M. wintonensis*. When compared to *M. clellandi*, *M. jaenschi* is shorter, wider with less height. The anterior adductor muscles are placed higher in *M. clellandi*. *M. femingi* is smaller, narrower with thicker ornamentation. Beaks are placed more posteriorly than in *M. jaenschi*.

Megalovirgus clellandi (Hocknull, 1994)
(Fig. 2A-C)

Protovirgus clellandi Hocknull, 1994: 146 (fig. 1A-D).

MATERIAL. HOLOTYPE: QMF29473; 29475.

AGE AND DISTRIBUTION. Late Trassic, formations: Black Stone, Tingalpa, SE Qld. Localities: Ebbw Vale and Tingalpa, SE Qld.

DIAGNOSIS. Large, equivalved, elongate hyriid with inflated umbonal area and fine comarginal ornamentation. Hinge straight and long with escutcheon broad and distinct. Tapering posterior to a very pointed posterior margin. Anterior adductor muscle scars raised on platform just anterior to beaks and lunule.

DESCRIPTION. See Hocknull (1994).

REMARKS. *M. clellandi* differs from *M. jaenschi* in it's larger size, higher placed adductor scars, more tapering posterior and more anterior

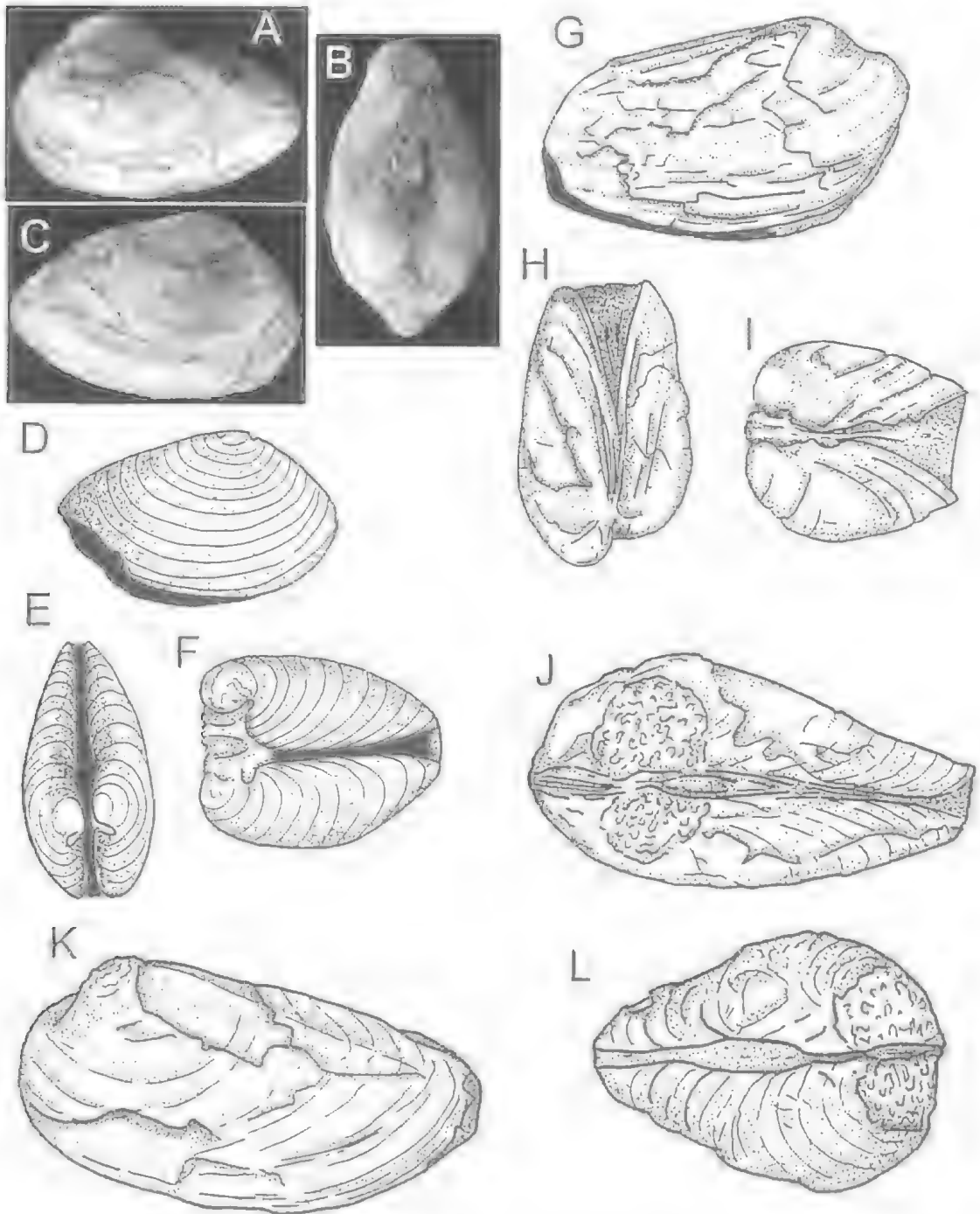


FIG. 4. A-F, *Hyridella (Protohyridella) goondlwindiensis*; A-C, AMF103849, A, left valve $\times 1.3$, B, dorsal view $\times 1.4$, C, right valve $\times 1.3$; D-F, Holotype QMF5684, D, left valve $\times 1.4$, E, anterior view $\times 2.0$, F, dorsal view $\times 1.4$. G-I, *Hyridella (Hyridella) macmichaeli* Paratype QMF34637, G, right valve $\times 1.3$, H, dorsal view $\times 0.9$, I, anterior view $\times 1.5$, Holotype QMF34636, J, dorsal view $\times 1.5$, K, left valve $\times 1.5$, L, anterior view $\times 1.75$.

TABLE 4. Morphometrics (in mm) for *Megalovirgus jaenschi* (Ludbrook).

	Length	Height	Width	Beak Height	Beak Length	Beak Width	Ligament Length
Mean	85.93	30.51	34.89	27.21	9.53	13.9	44.49
s.d.	9.51	7.91	1.75	5.78	2.61	2.04	8.03
Number	10	10	10	10	10	10	10

umbonal-beak region. *P. jaenschi* also has a greater height to length ratio. *M. clellandi* is longer, narrower, tapers more sharply, has a more anteriorly placed beak and has a larger height to length ratio than *M. wintonensis*. *M. flemingi* is much smaller and the umbones are placed more posteriorly than in *M. clellandi*.

Megalovirgus wintonensis (Hocknull, 1997)
(Fig. 2D-F)

Protovirgus wintonensis Hocknull, 1997: 223 (fig. 1A-E).

MATERIAL. HOLOTYPE: QMF34635. PARATYPES: QMF5681-5682, 34645, 34646, 34634, 34644, 34647, 34648. AMF15815, 47175, 68358, 103838, 103841, 103843, 103844, 103847, 104848, 103850, 103852, 103857, 103867, 103873, 103893, 103897, 103901, 103911.

AGE AND DISTRIBUTION. Latest Albian – Cenomanian, formations: Winton, Griman Creek, Coreena Formation. Localities: QML229, L379, L570, Lightning Ridge, White Cliffs, NSW.

DIAGNOSIS. Medium-sized hyriid, equivalved, inequilateral, slightly inflated umbones and fine comarginal ornamentation. Hinge straight; anterior adductor muscle raised on platform. Tapering strongly to the posterior with short well rounded anterior end. Umbones 1/15 length of shell from anterior end.

DESCRIPTION. Medium to large hyriid with produced posterior end. Elongate with umbones inflated. Umbones 1/15 length from the anterior end. Anterior margin rounded. Hinge straight, ligament long and thick. Dorsal margin long and straight tapering to a knife-like posterior profile. Ventral margin gracile, tapering sharply to meet posterior edge of dorsal margin. Fine growth lines producing fine comarginal ornamentation. Hinge teeth long and thin, cardinals short and indistinct, distinctly unionid. Beaks usually eroded or small, closely set. Escutcheon long and

narrow. Lunule short and broad. Anterior muscle scars elongate and orientated antero-ventrally. Posterior muscle scar unknown, presumably small and indistinct. Juveniles possess V-shaped rugae on their beaks, being eroded later in life. Rugae also occur along the margins of the escutcheon. Shell relatively thin. Juveniles start out being triangular in profile and becoming more elongate produced shell. Morphometrics given in Table 5. Allometry given in Figure 8.

REMARKS. *M. wintonensis* differs from *M. clellandi* in having a smaller profile, wider and thicker shell, less anterior umbones, narrower escutcheon and less tapering at the posterior end. *M. jaenschi* is larger, has a less developed anterior adductor muscle scar which is placed lower in the valve than in *M. wintonensis*. *M. flemingi* is smaller, with the umbones less anterior than in *M. wintonensis*.

Hyridella (Hyridella) Swainson, 1840

Hyridella (Hyridella) macmichaeli
(Hocknull, 1997)
(Fig. 4G-L)

Prohyria macmichaeli Hocknull, 1997: 224 (fig. 2A-C), (non fig. 1F-H).

MATERIAL. HOLOTYPE: QMF34636. PARATYPES: 5677, 34637, 34638. Additional Material. AMF68346, 103864, 103866, 103869, 103870, 103871, 103874, 103878, 103882, 103884, 103886, 103889, 103890, 103910.

AGE AND DISTRIBUTION. Cenomanian, formations: Winton Formation (type) and Griman Creek. Localities: QML379, QML570, QML229 and Lightning Ridge.

DIAGNOSIS. 'Medium-sized, equivalved unionid, ovate, rugose ornamentation, umbones anterior and inflated, beak slightly sculptured, shell thick' Hocknull (1997). Juveniles with V-shaped ornamentation. Anterior muscle scar

TABLE 5. Morphometrics (in mm) for *Megalovirgus wintonensis* (Hocknull).

	Length	Height	Width	Beak Length	Beak Height	Beak Width	Ligament Length
Mean	51.83	22.7	16.42	11.63	20.76	7.10	20.34
s.d.	20.98	9.71	9.19	5.7	9.10	3.72	8.5
Number	20	20	20	18	19	17	14

set below beak and raised slightly on platform. Simple unionid teeth, with two peg-like cardinals and one long lateral tooth.

DESCRIPTION. Medium-sized, elongate-ovoid unionid. Equivalved with slightly inflated umbones. Hinge line distinct and convex, tapering to the posterior to produce a pointed posterior profile. Beaks 1/5 from the anterior end, usually eroded. Fine growth lines produce ridged commarginal ornamentation. Thick shell. Escutcheon broad and ligament short and distinct. Juveniles have V-shaped rugae on the beaks, absent in the adults as the beak is eroded. Anterior adductor muscle scars small and set below the beaks, raised on platforms. Unionid teeth with a long lateral tooth and small indistinct cardinals. Morphometrics given in Table 6. Allometry shown in Figure 8.

REMARKS. The presence of V-shaped rugae as beak sculpturing in smaller individuals places this taxon within the hyridellines and more specifically *Hyridella*. The anteriorly placed, inflated and thick shelled umbones coupled with tapering elongate-ovoid profile ally *P. macmichaeli* to *Prohyria*. The taxon is smaller than the other members of this small but cosmopolitan genus. The type species, *P. johnstoni* (Etheridge Jr, 1892) of McMichael (1956) is longer, wider and the dorsal margin produces a sharper, tapering edge. *P. eyrensis* is also longer, wider with the umbones placed further anterior. *Unio springfieldensis* has similar attributes as *P. eyrensis*, being longer, wider with anteriorly placed umbones. This taxon also tapers more, as in *P. johnstoni*. It seems that *Hyridella* shares many similarities with *Prohyria*; however, this is apparently due to convergence and not homology.

Hyridella (Protohyridella) Cotton & Gabriel, 1932

Hyridella (Protohyridella) goondiwindiensis (Hocknull, 1997)
(Fig. 4A-F)

Velesunio goondiwindiensis Hocknull, 1997: 225 (fig. 2D-J)

MATERIAL. HOLOTYPE: QMF5684, 5683. PARATYPES: 5685, 5686, 34639-36341 AMF68342, 103849,

103853, 103858, 103865, 103881, 103883, 103895, 103896, 103900, 103902, 103904, 103906, 103907.

AGE AND DISTRIBUTION. Latest Albian - Cenomanian, formations: Griman Creek Formation (type) and Coreena Formation. Localities: Goondiwindi (type), Lightning Ridge and White Cliffs.

DIAGNOSIS. Small, unionid with fine comarginal ornamentation. Quadrate-angulate with strong posterior ridge. Umbones relatively inflated and positioned anteriorly. Beaks sculpturing, V-shaped in juveniles, eroded in adult forms. Teeth simple and unionoid. Anterior adductor muscle small placed just in front of beaks. Shell expanded posteriorly, forming a slight winged appearance in adult forms.

DESCRIPTION. Small, equivalved quadrate-angulate hyriid. Fine growth lines form ridges producing distinct commarginal ornamentation. Beaks distinct and usually eroded laterally. Umbones anterior, situated 1/3 from the anterior margin. Ligament short and distinct producing a strong hinge. Hinge line tapers smoothly to a rounded posterior margin. Antero-ventral margin distinctly convex. Shell relatively thick. Juveniles with distinct V-shaped rugae on the beak, lost in the adult. Juveniles are more ovoid without the pronounced posterior ventral margin of adults. Lunule small and indistinct. Escutcheon broad with the borders smooth and tapering to the posterior. Anterior adductor muscle scars small, oval and just beneath the beak. Teeth simple unionid. Morphometrics given in Table 7. Valve growth pattern is illustrated in Figure 8.

REMARKS. Initially, Hocknull (1997) placed *H. goodiwindiensis* within *Velesunio* due to its overall similarities in morphology. However, *Hyridella (Protohyridella) goodiwindiensis* is distinctly hyridelline because of the presence of distinct V-shaped beak sculpture in the juvenile forms (McMichael & Hiscock, 1958), now known from additional specimens. Placement in *Hyridella* is somewhat tentative, due to the marked difference in maximum sizes and relative sizes, when compared to modern taxa of the same genus. However, the overall variation within

TABLE 6. Morphometrics (in mm) for *Hyridella (Hyridella) macmichaeli* (Hocknull).

	Length	Height	Width	Beak Length	Beak Height	Beak Width	Ligament Length
Mean	43.15	26.04	19.52	11.79	23.64	8.21	14.80
s.d.	15.74	9.80	7.28	4.94	8.75	3.34	6.74
Number	14	14	13	14	14	12	11

TABLE 7. Morphometrics (in mm) for *Hyridella (Protohyridella) goondiwindiensis* (Hocknull).

	Length	Height	Width	Beak Length	Beak Height	Beak Width	Ligament Length
Mean	28.6	18.68	14.36	8.55	18.61	6.55	10.39
s.d.	4.48	3.87	2.23	1.79	3.82	1.46	3.31
Number	14	14	14	14	14	14	14

Hyridella supports a conservative approach to higher taxonomy in this group (McMichael & Hiscock, 1958) and therefore placement within *Hyridella* is warranted. When compared to modern *Hyridella* species it is evident that this taxon is much smaller with finer growth and thinner shell and is, therefore, distinct from them. It does, however, bear striking similarities to the type species of the monotypic subgenus *Protohyridella*. The small size, quadrate-angulate form with posterior ridge prominent is characteristic of *Hyridella (Protohyridella) glenelgensis* (Dennant). Extinct *Hyridella* species are also a lot larger than this taxon, with the exception of *Palaeohyridella godthelpi* gen. et sp. nov., suggesting that this species is a dwarf representative of the hyridellines leading towards *Protohyridella*. Whether this provides evidence for separation of *Protohyridella* as a distinct genus is controversial when dealing with unioid species concepts (McMichael & Hiscock, 1958). When comparing the allometry seen in *H. (P.) goondiwindiensis* with that of *Palaeohyridella godthelpi* gen. et sp. nov. it can be shown that, even though they develop similarly sized adults, the growth pattern to this end is quite different, being positive allometry in *H. (P.) goondiwindiensis* and negative allometry in *Palaeohyridella godthelpi* gen. et sp. nov.

Hyridella whitecliffensis (Newton, 1916)

Unio whitecliffensis Newton, 1916: 231 pl. 6 (7-8).
Hyridella whitecliffensis (Newton), McMichael, 1957: 240.

AGE AND DISTRIBUTION. Early Cretaceous, formations: Coreena. Localities: White Cliffs NSW.

DIAGNOSIS. Shell small, equivalve, ovoid hyriid of hyridelline affinity. Moderately inflated valves with V-shaped beak sculpturing. 'Periodic growth divisions, and numerous, close-set, microscopical concentric striations ... posterior ridge become angulate' (Newton, 1916).

DESCRIPTION. See Newton (1916).

REMARKS. The holotype of this taxon was unavailable for study during this review, however, it is possible to diagnose this taxon from other members of *Hyridella*. The most apparent

distinguishing features being the angulate posterior margin and concentric growth striae. It differs from *H. (Protohyridella) goondiwindiensis* by its smaller size and more angulated posterior profile. It differs from *Palaeohyridella godthelpi* gen. et sp. nov. by its smaller size, less pronounced posterior ridge, closer growth ornamentation, more ovoid profile and narrower shell.

Hyridella (Protohyridella) sp. (Fig. 5A-C, D-E)

MATERIAL. UQF52157, UQF52159, UQF52161, UQF44278, UQF44276, UQF44277.

AGE AND DISTRIBUTION. Jurassic, Waloon Coal Measures, Warwick District and Rathdowney area, SE Qld.

DESCRIPTION. Medium-sized, equivalved, ovoid hyriid with the comarginal ornamentation. Beaks eroded. Posterior margin tapers abruptly at the posterior 2/5 of valve, producing a tri-angulate-ovoid posterior margin. Small anterior adductor muscle scar placed antero-laterally to umbone. The escutcheon is shallow. The anterior margin begins 2/3 of the beak height and produces a small rounded margin about 8.19mm to the anterior. The dorsal margin is inflated distal to the anterior and is inflated past the umbones, tapering to the posterior. This produces a wedge-shaped hinge jutting out of the general line of the shell. The umbones are placed anteriorly to the general line of the valves. The ventral margin is rounded to both ends. Ligament short. UQF52157 & 52161 are both medium-sized inequivalved, ovoid inflated hyriids. The inflation and inequilateral morphology is interpreted as an abnormal growth form for the shells. The general morphology follows that described above. Morphometrics given in Table 8.

REMARKS. The material is placed within *Hyridella (Protohyridella)* based on the following characteristics: 1, beak sculptured and eroded; 2, inflation posterior to beak and producing a flanged ventral margin; 3, shell thin with fine comarginal ornamentation. Due to the paucity of specimens and closeness in morphology to

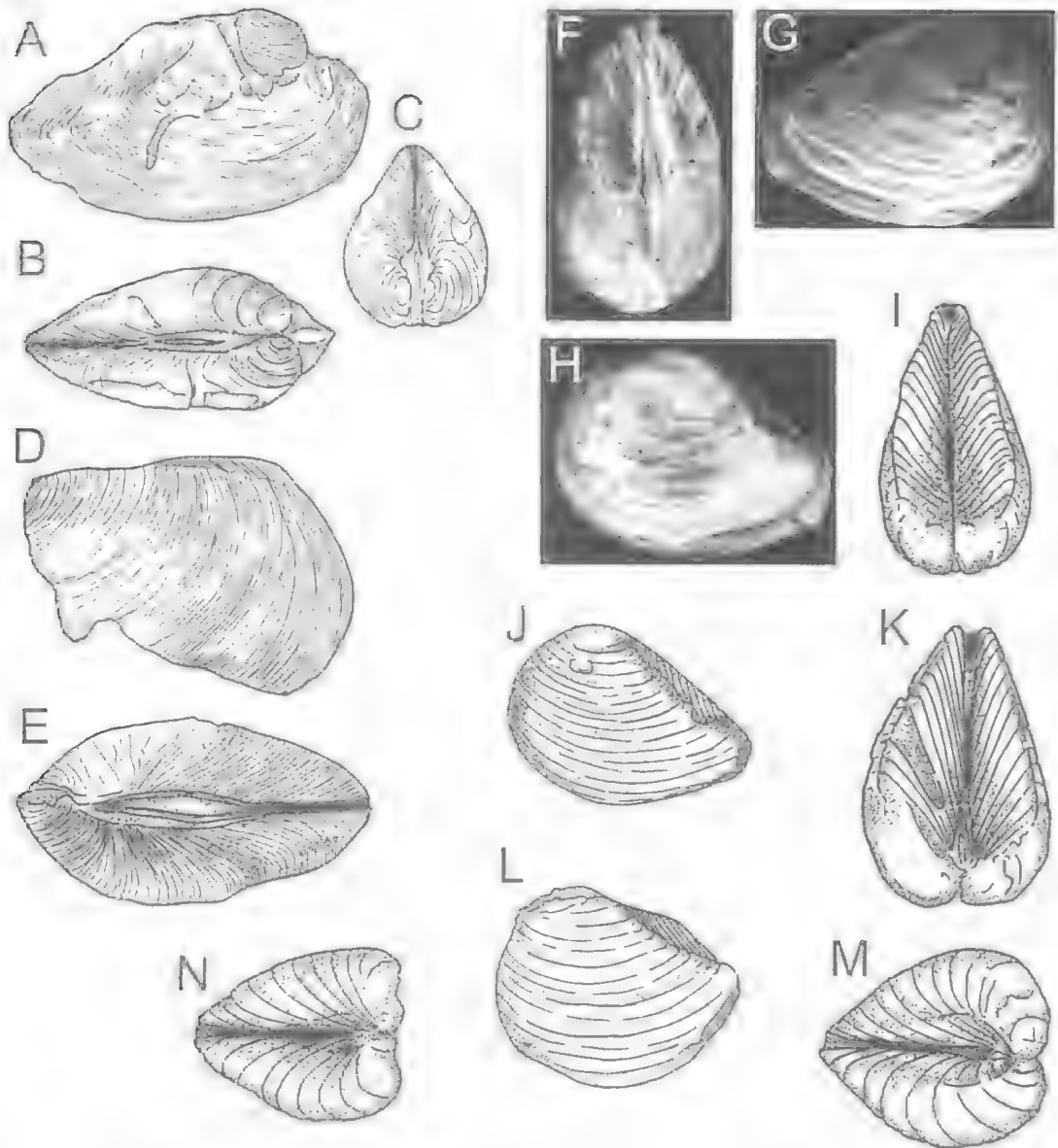


FIG. 5. A-C, *Hyridella (Protohyridella)* sp. UQF52159; A, right valve $\times 0.8$; B, dorsal view $\times 1.0$; C, anterior view $\times 0.7$. D-E, deformed individual of *Hyridella (Protohyridella)* sp. UQF52161; D, left valve $\times 0.8$; E, dorsal view $\times 0.3$. F-I, *Palaeohyridella goondiwindli* gen. et sp. nov., F-I, M, Holotype AMF103912; F, dorsal view $\times 2.0$; G, right valve $\times 2.0$; H, left valve $\times 1.4$; I, dorsal view $\times 1.4$; J, left valve $\times 1.4$; L, anterior view $\times 1.6$. K-L, N, Paratype AMF103913; K, left valve $\times 1.4$; L, dorsal view $\times 1.4$; N, anterior view $\times 1.6$.

Hyridella (Protohyridella) goondiwindliensis specific assignment is not warranted until more specimens are available.

Mesohyridella McMichael, 1956

TYPE SPECIES. *M. ipswichensis* (Etheridge Jr, 1892) from the Upper Triassic, Ipswich Coal Measures.

DIAGNOSIS. Small hyridelline unioid with elongate-oval, equivalved, inequilateral valves. Beaks anteriorly placed with small anterior adductor muscle scar, ovoid and set anteriorly to beaks. Both posterior and anterior margins produced, widely concave. Moderately inflated.

TABLE 8. Morphometrics (in mm) for *Hyridella* (*Protohyridella*) sp.

UQF No.	Length	Height	Width	Beak Length	Beak Height	Beak Width	Hinge Length
UQF52157	37.76	28.95	?	?	27.54	?	?
UQF52159	45.46	31.24	23.65	8.17	28.79	10.83	27.36
UQF52161	50.73	35.26	?	?	31.90	15.03	28.34

REMARKS. McMichael (1956) erected this genus to place one species of small ?hyridelline, *M. ipsviciensis*. It's affinities with modern subfamilies is thought to be hyridelline, however, this is superficial. Unfortunately, no more material has shed any light on its relations within the hyriids.

Mesohyridella ipsviciensis (Etheridge Jr, 1892)

Unio ipsviciensis Etheridge Jr, 1892: 388 pl. 42(2-3).
Mesohyridella ipsviciensis (Etheridge Jr) McMichael, 1957: 238 pl. 8(5).

AGE AND DISTRIBUTION. Late Triassic, formations: Black Stone, Tingalpa, Bundamba, SE Qld; Springfield Coal Basin. Localities: Ebbw Vale, Bundamba, Tingalpa, Bundamba, SE Qld, Springfield Coal Fields.

DIAGNOSIS. Shell small, elongate-oval with little winged posterior. Shell thick with strong ornamentation.

DESCRIPTION. From McMichael (1956); 'Small freshwater mussels of uncertain affinity, but possibly belonging to the subfamily Hyridellinae. Shells elongate-oval, not winged, moderately swollen. Dorsal margin behind the beaks more or less straight, then curving rather sharply downwards, and descending obliquely to form a rather blunt posterior end with the ventral margin. Beaks not elevated or swollen, heavy corroded, sculptural characters unknown. Shell surface marked with fairly strong growth lines. Hinge characters and muscle scars unknown'.

REMARKS. Etheridge Jr (1892) described *M. ipsviciensis* within *Unio*. McMichael (1956) proposed a genus for the species, in the absence of the holotype, and called it *Mesohyridella*. The present study has not located the holotype either, however, on inspection of many more unionoids recovered from the Ipswich Coal Measures (the type locality is within this formation) other specimens are allocated for this species. The hyriids that resemble the descriptions of Etheridge Jr and McMichael have strong ornamentation, relatively uninflated umbones and beaks placed more central than *P. eyrensis*, the other large ovoid hyriid present in the fauna. This morphologically

distinct group of bivalves are present in the Blackstone formation, Tingalpa formation of the Ipswich Coal Measures, SE Qld and the Springfield Basin, SA.

Palaeohyridella gen. nov.

TYPE SPECIES. *Palaeohyridella godthelpi* gen. et sp. nov. from uppermost Albian – Cenomanian Griman Creek Formation, Lightning Ridge.

ETYMOLOGY. *Palaeos*, Greek, representing the ancient aspects of the taxon and *-hyridella* for the affinity to the freshwater bivalve genus *Hyridella*.

DIAGNOSIS. Small hyriid unioid of the hyridelline subfamily. Umbones inflated and placed extremely anterior, 1/13 of total length from anterior end. Posterior margin quadrate-angular with prominent umbones to posterior ridge. Ridge preserving prominent ridging, developing into V-shaped sculpturing toward the beaks. Escutcheon broad, relative to length. Ornamentation coarse with fine comarginal growth lines. Anterior profile truncated and rounded, producing weak beak characteristics.

DESCRIPTION. Small, equivalved, inequilateral, hyriid with inflated umbones. Umbones greatly anterior being less than 1/13 the length from the anterior. Anterior profile truncated and rounded. Posterior end produced, producing a tear drop valve shape. Shell thick, growth lines fine, producing ridged comarginal ornamentation. Ventral margin gracile and convex. Hinge line straight with short thick ligament. Escutcheon broad and distinct with ornamentation producing a postero-dorsal ridge extending down both valves to the posterior end. V-shaped rugae on beaks and along postero-dorsal ridge on juveniles and adults. The rugae being present on the ridges in adults only. Beaks distinct and close-set. Lunule very short but relatively broad. Muscle scars unknown.

REMARKS. This genus is erected due to the presence of a taxon unlike any hyriid described previously. The V-shaped beak sculpturing in the juvenile and adult allies the new genus to the hyridelline lineage (McMichael & Hiscock 1958). When compared to *Hyridella* (*Hyridella*)

spp. and *Hyridella* (*Protohyridella*) spp. there are marked differences; these are 1, umbones more anteriorly situated; 2, broad, distinct escutcheon; 3, posteriorly rostrate profile; and 4, truncated, convex anterior margin.

***Palaeohyridella godthelpi* gen. et sp. nov.**
(Fig. 5F-N)

ETYMOLOGY. For Henk Godthelp, a good friend who brought some of the specimens to my attention.

MATERIAL. HOLOTYPE: AMF103912; 26 Paratypes.

AGE AND DISTRIBUTION. Uppermost Albian–Cenomanian, formations: Griman Creek Formation. Locality: Lightning Ridge.

DIAGNOSIS. As for genus.

DESCRIPTION. As for genus. Morphometrics given in Table 9. Allometry given in Figure 8.

GLAUCONOMIDAE Gray, 1853

Glauconomids are a group of estuarine to brackish water bivalves from the east coast of Australia, inhabiting mangrove systems, mudflats and sands. There are four extant species recognised from Lamprell & Healy (1998); *Glaucome plankta*, *G. virens*, *G. rugosa* and *G. cerea*.

***Unionella* Etheridge, 1879**

TYPE SPECIES. *Unionella wianamattensis* Etheridge Jr, 1888 from Late Triassic, Gibraltar Tunnel.

DIAGNOSIS. Small, elongate-oval glaucomid. Beaks anterior and close-set. Umbonal region slightly inflated devoid of sculpturing. Posterior margin slightly winged in larger individuals. A series of characteristically elongate beak muscle scars is present just below the beak commissure. Hinge short and indistinct. Anterior adductor muscle scars deep, elongate and usually placed anteriorly to umbones. Muscle scar triangular in lateral profile. Two to three cardinal teeth present, median and posterior most distinct.

REMARKS. The small size, ovoid shape, deep adductor muscle scar and winged posterior along with the ‘clumping’ nature of the taxa suggest that this genus has evolutionary affinities to the

modern Glauconomidae, and certain morphological features similar in Anthracosiidae. Anthracosiids have a well known presence in the Carboniferous and Permian of Eurasia. McMichael (1956) in his review of these forms suggested such an affinity of *Unionella* with the anthracosiids. When comparing these shells to the modern *Glaucome* spp. there are marked similarities: valves are closely set with the beak not well produced; a series of small beak muscle scars occur under the lip of each beak; shell is produced anteriorly, directly in front of the beaks, compared to on the midline as seen in the anthracosiids; two to three small cardinal teeth, increasing in size from the anterior end. The median and posterior cardinals are largest and are close-set.

This genus was described for three apparently distinct forms, *Unionella bowralensis*, *U. wianamattensis* and *U. carnei*. Comparing the overall morphological diversity in species from anthracosiids and glauconomids it is apparent that Etheridge Jr (1882) did not take into account the possible phenotypic plasticity. I have clumped the three forms into one species, as I believe there is not enough consistent variation to propose different species. The taxon available for this is *U. wianamattensis*.

***Unionella wianamattensis* Etheridge Jr 1888**
(Fig. 6K)

Unionella bowralensis Etheridge Jr, 1888: 13, pl. 1 & 2, figs 8-14; McMichael, 1956: 236, pl. 13, fig 6.
Unionella carnei Etheridge 1888: 14, p. 2, figs 5-7; McMichael, 1956: 237, pl. 13, fig. 7.

MATERIAL. LECTOTYPE: AMF35775; 20183, 21085, 35769, 35771, 3987, 20184, 35766, 35764, 35778, 35773A, 3577B.

AGE AND DISTRIBUTION. Late Triassic, Formations: ‘transition beds between the Hawesbury Sandstone and the Wianamatta Group’ (McMichael, 1956). Localities: Gibraltar Tunnel, Bowral, Smith’s Brick Quarry at Crown Street, Waterloo and Surrey Hills, NSW.

DIAGNOSIS. Shell small, equivalved, elongate-ovate, with fine comarginal ornamentation. Valves inflated mid-laterally, however, umbones relatively flattened. Shell slightly winged posteriorly. Anterior adductor muscle scar deep,

TABLE 9. Morphometrics (in mm) for *Palaeohyridella godthelpi* gen. et sp. nov.

	Length	Height	Width	Beak Length	Beak Height	Beak Width	Ligament Length
Mean	21.88	15.5	12.47	3.65	14.39	4.12	9.21
s.d.	2.59	1.99	2.56	0.62	2.5	0.79	1.42
Number	15	15	15	15	15	15	15

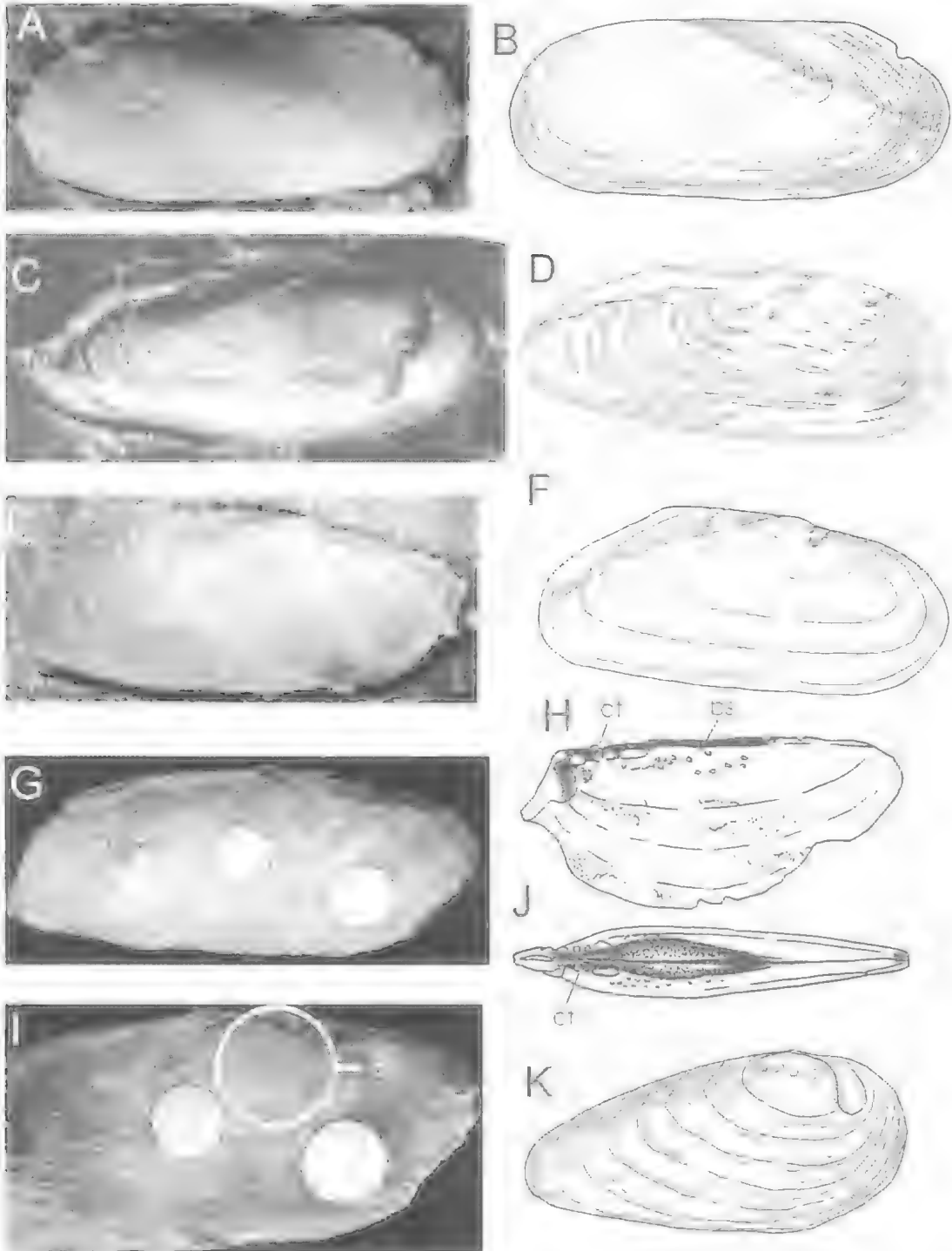


FIG. 6. A-F, *Protovirgus brookvalensis* sp. nov.: A-B, Paratype AMF41440, right valve $\times 3.0$, C-D, Paratype AMF41442, left valve $\times 3.0$, E-F, Holotype AMF19773, left valve $\times 3.0$. G-J, *Protovirgus dunstani*; G, AMF35693, right valve $\times 2.0$, H, AMF35776, left valve showing beak sculpture (bs) and cardinal teeth (ct) $\times 1.6$, I, AMF35693, right valve showing beak sculpture $\times 2.25$, J, AMF35776, dorsal view showing cardinal teeth $\times 1.7$. K, *Unionella wianamattensis* AMF35775, right valve $\times 3.0$.

elongate and postero-ventrally orientated. A series of beak muscle scars extend just postero-dorsally of the anterior adductor scar.

DESCRIPTION. From Etheridge (1888): 'Shell ovate-obliquely oblong, laterally compressed, thin. Dorsal margin or hinge line straight posteriorly, angulated at the anterior end, but in its entire length not as long as the shell; ligament small, and projecting but little above the dorsal margin. Ventral margin nearly straight, with a slight sinus at the middle. Anterior end small, very much compressed, and with the margin rounded; posterior end compressed, the diagonal ridge well marked. Although not strong; the flanks of the valves decrease rapidly in convexity from this ridge to the ventral margin, but an almost imperceptible sinus traverses them upwards from the ventral marginal inflections'. Forms initially described as *Unionella bowralensis* and *Unionella carnei* the shell shows more inflation in the valves. When height to length was measured for the specimens described by Etheridge Jr (1888) a consistent allometry is illustrated.

Morphometrics are presented for *Unionella bowralensis*, *Unionella carnei* and *Unionella wianamattensis* in Table 10.

REMARKS. The three species initially described within *Unionella* are here synonymised as one species on the basis of the following similar but variable characteristics: elongate-ovoid shells that have similar growth allometries; slight winged postero-dorsal margin; and sympatric occurrence in the same horizon. As alluded to in McMichael (1956)'s review of *Unionella*, the overall shell variation in anthracosiid taxonomy is well documented and provides evidence that these three taxa are one. Glauconomids are also highly variable.

Protovirgus McMichael, 1956

TYPE SPECIES. *Protovirgus dunstani* (Etheridge Jr) from the Upper Triassic Wianamatta Shale, Sydney Basin.

DIAGNOSIS. Small, elongate, equivalved, inequilateral glauconomid with long tapering posterior profile. Umbones flattened and placed extremely anterior. Deep, long, posteroventrally orientated anterior adductor muscle scars. A series of beak muscle scars placed just below the beak commissure. Three cardinal teeth, median and posterior cardinal largest and closely spaced. Reduced or no lateral tooth.

TABLE 10. Morphometrics (in mm) for *Unionella wianamattensis* (= *Unionella bowralensis*) (Etheridge Jr), *Unionella wianamattensis* (= *Unionella carnei*) (Etheridge Jr), *Unionella wianamattensis* (Etheridge Jr).

AMF No.	Length	Height	Width	Beak Length
<i>Unionella wianamattensis</i> (= <i>Unionella bowralensis</i>)				
20183	21.7	8.75	5.15	6.8
20185	12.4	7.7	5.6	3.05
35769	12.15	6.7	5.4	3.15
35771	9.2	5.7	4.15	2.15
Mean	13.86	7.212	5.075	3.78
<i>Unionella wianamattensis</i> (= <i>Unionella carnei</i>)				
3987	12.45	6.7	4.05	3.75
20184	12.55	7.7	5.9	3.1
35764	18.35	9.6	7.5	5.9
35766	18	8.6	7.7	5.1
35778	16.7	8.55	6.05	4.7
Mean	15.01	8.23	6.24	4.51
<i>Unionella wianamattensis</i>				
35773a	15.4	8.7	5.65	4.9
35773b	12.15	8.75	5.4	3.55
35775	14.8	8.8	4.5	3.85
Mean	14.11	8.75	5.183	4.1

REMARKS. This genus is related to *Unionella* in the possession of beak muscle pits, deep, elongate anterior adductor muscle pits and slightly wider postero-dorsal margin and three small cardinal teeth. The genus was described by McMichael (1956) to accommodate two species, *P. dunstani* and *P. flemingi*, from the Late Triassic of Sydney and Cretaceous of New Zealand, respectively. Unfortunately, *P. flemingi* was not examined during this study and will not be considered here.

Protovirgus dunstani (Etheridge Jr, 1888) (Fig. 6G-J)

Unionella dunstani Etheridge Jr 1888: 11 pl. 1(11-19).
Protovirgus dunstani (Etheridge Jr) McMichael, 1957: 232 pl. 14(8).

MATERIAL. LECTOTYPE: AMF35693; 35776, 35777, 35870.

AGE AND DISTRIBUTION. Late Triassic, formations: 'transition beds between the Hawesbury Sandstone and the Wianamatta Group' (McMichael, 1956). Localities: Gibraltar Tunnel, Bowral, Smith's Brick Quarry at Crown St, Waterloo, and Surrey Hills, NSW.

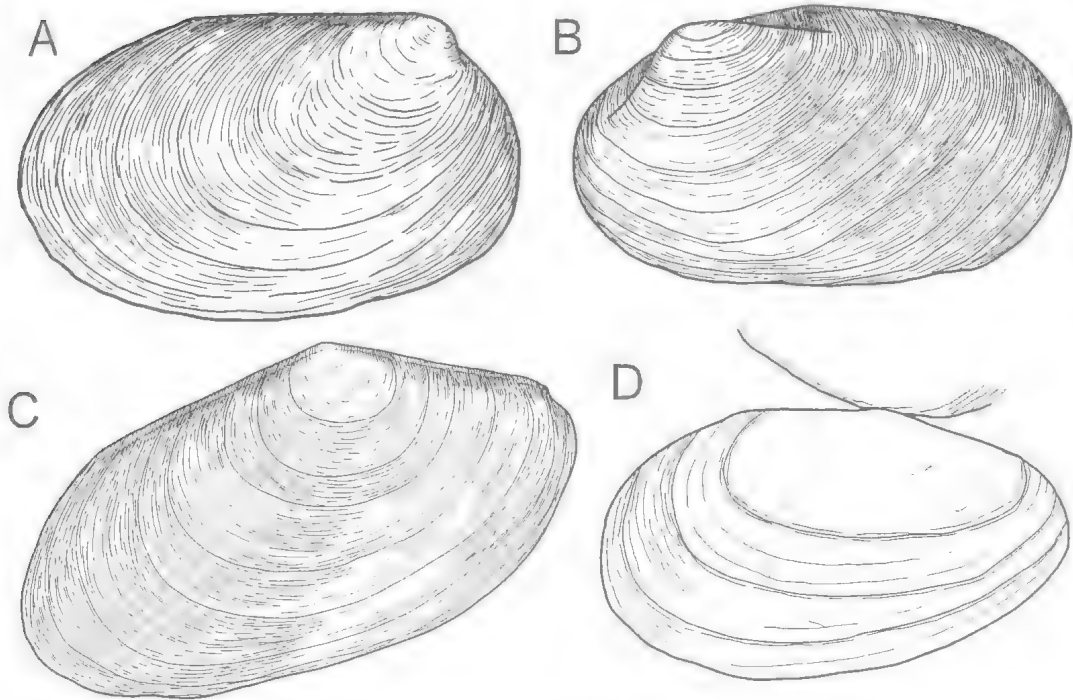


FIG. 7. A-B, *Protosphaerium gianae* sp. nov.; A, AMF38165 Holotype, right valve $\times 4.0$, B, AMF103934b Paratype, left valve $\times 5.0$. C-D, *Protosphaerium talbragarensis* gen. et sp. nov.; C, AMF103934a Holotype, right valve $\times 4.0$, D, AMF103929 Paratype right valve $\times 5.4$.

DIAGNOSIS. Small, equivalved, glauconomid. Elongate shell, tapering to posterior end. Beaks anterior, with flattened umbonal region. Beaks insignificant and closely set. Postero-dorsal margin slightly winged. Three cardinal teeth; large median and posterior cardinal and small anterior cardinal, no lateral tooth.

DESCRIPTION. From Etheridge (1879), 'Shell narrow, very transversely elongate, thin and compressed throughout its length ... cardinal margin very long and slightly arched ... anterior end very much compressed, the margin rounded, posterior end thin, attenuate ... umbones placed close to the anterior end, small, and laterally flattened ... anterior adductor impression fan-shaped, situated very high up under the anterior cardinal margin; umbonal scars very strongly marked, two immediately behind adductor scars in a line ...'.

Morphometrics given in Table 11.

REMARKS. *P. dunstani* is unique within its fauna, differing from other members of *Unionella* by the extremely elongate nature of the valves. The presence of beak scars illustrates genetic relation to *Unionella*, however, it differs

so markedly from them that separation at the generic level is relevant. *P. dunstani* differs from *P. flemingi* by its smaller size and less tapering profile. The only other species of this genus is *Protovirgus brookvalensis* sp. nov. which differs in being smaller and more rounded posteriorly. The anterior adductor muscle in *P. brookvalensis* sp. nov. is much longer and situated higher than *P. dunstani*. The umbones are more flattened in *P. dunstani* than in *P. brookvalensis* sp. nov.

***Protovirgus brookvalensis* sp. nov.**
(Fig. 6A-F)

ETYMOLOGY. For the type locality, Brookvale quarry.

AGE AND DISTRIBUTION. Late Triassic, formations: Wianamatta Shale. Localities: Brookvale Quarry, NSW.

MATERIAL. HOLOTYPE: AMF19773. **PARATYPES:** 19805, 43401, 41438, 41442, 41440, 41439, 49805.

DIAGNOSIS. Small, equivalved glauconomid with umbones anteriorly placed. Elongate valve shape with tapering posterior edge. Winged dorsal margin produced by ridge emanating from the umbonal area and terminating toward the

TABLE 11. Morphometrics (in mm) for *Protovirgus dunstani* (Etheridge Jr).

AMF No.	Length	Height	Width	Beak Length
35693	34.7	11.9	?	8.85
35776	37.2	12.2	6.05	8.65
35777	25.8	11.8	4.8	5
35870	40	16.6	8.75	9.05
Mean	34.42	13.12	6.53	7.88

posterior end. Umbonal region anterior with beaks closely set.

DESCRIPTION. Holotype F19773, is a small equivalved, inequilateral, elongate-ovoid anthracosiid. Umbones anteriorly placed at 1/5 from the anterior end. Beaks weak with no sculpturing. Hinge line straight and long producing a straight dorsal profile. Rounded posteriorly. Anterior end rounded. Muscle scar unknown. Teeth unknown. Subumbonal ridge runs postero-ventrally away from the umbo. Fine comarginal growth lines with weak ornamentation.

Morphometrics presented in Table 12.

REMARKS. The elongate nature of the valves, anteriorly placed umbones and tapered posterior end place this taxon firmly within *Protovirgus*. Morphological features that differentiate *P. brookvalensis* from *P. dunstani*, the only other member of this genus, are it's smaller size, weakly defined umbones, more rounded posterior end, weaker anterior muscle scars.

?SPHAERIIDAE Jefferys, 1862

Protosphaerium gen. nov.

TYPE SPECIES. *Protosphaerium talbragarensis* gen. et sp. nov. Jurassic, Talbragar Fossil Fish Beds.

ETYMOLOGY. *Proto*, pertaining to this being the first of it's kind. *-sphaerium*, for the genus *Sphaerium*.

DIAGNOSIS. Small, equivalved, ovoid bivalve with beaks subcentral. Fine comarginal growth lines with rugose comarginal ornamentation. Hinge short and convex in lateral profile. Ventral margin rounded to form distinct 'pea shell' like shape.

DESCRIPTION. Small, equivalved, equilateral with fine growth lines. Little or no ornamentation. Shell very thin with umbones just slightly inflated. Ovoid with beak 1/3 length from anterior end. Posterior profile rounded continuous with convex hinge outline. Anterior profile also rounded with a small insignificant lunule. Escutcheon narrow and also insignificant. Hinge short with hinge ligament relatively thick.

TABLE 12. Morphometrics (in mm) for *Protovirgus brookvalensis* sp. nov.

AMF No.	Length	Height	Width	Beak Length
43401	22.5	9.85	?	9.85
41438	23.15	9.95	?	10.7
19773	25	10.5	?	12.1
41442	23.8	8.75	?	11.6
41440	22.4	8.7	?	4.45
41439	21.5	9.2	?	10.55
19805	20.7	9.1	?	8.6
Mean	22.72	9.43		9.69

Muscle scars unknown, presumed weak. Teeth unknown or insignificant.

REMARKS. The pea-shell shaped valves, subcentral beaks, small size and clumping deposition post death, are all characteristics of members of the Sphaeriidae (Kuiper, 1983) and Corbiculidae. As this genus is smaller than those normally found within the corbiculids it is conceivable that this taxon belong within the sphaeriid lineage. As the tooth morphology of the type species is unknown it is with some degree of uncertainty that this placement within the Sphaeriidae is given.

Protosphaerium talbragarensis gen. et sp. nov.
(Fig. 7C-D)

ETYMOLOGY. For the type locality of Talbragar.

MATERIAL. HOLOTYPE: AMF103934A. PARATYPES: AMF103929, 103935(b), 59823.

AGE AND DISTRIBUTION. Jurassic, formations: Talbragar Fossil Fish Beds. Localities: Talbragar.

DIAGNOSIS. As for genus.

DESCRIPTION. As for genus. Morphometrics given in Table 13.

REMARKS. This taxon bears marked affinities to the small freshwater bivalves from the family Sphaeriidae. Uncertainty surrounds the decision to place *Protosphaerium talbragarensis* within the Sphaeriidae, however, it seems plausible that this group has a Jurassic presence in Australia and has remained here since then. Since it fits in no other family and the erection of a new family seems unwarranted, it is here placed within the sphaeriids.

Protosphaerium gianae sp. nov.
(Fig. 7A-B)

ETYMOLOGY. For Gian Holmes.

TABLE 13. Morphometrics (in mm) for *Protosphaerium talbragarensis* gen. et sp. nov.

AMF No.	Length	Height	Width	Beak Length
103929	6.9	4.3	?	2.9
103934	11.5	6.8	?	4.25
103935b	10.75	6.25	?	4.2
59823	10.45	6.15	?	4.15
Mean	9.9	5.87	0	4.93

MATERIAL. HOLOTYPE: AMF38165. PARATYPES: AMF103931, 103932, 103934B.

AGE AND DISTRIBUTION. Jurassic, formations: Talbragar Fossil Fish Beds. Localities: Talbragar.

DIAGNOSIS. Small, equivalved, inequilateral freshwater bivalve of possible corbiculid affinity. Fine con marginal growth lines and weak ornamentation placed periodically along the valves. Characteristically winged toward the posterior, producing a quadrate lateral profile to the valves. Beaks closely set and anteriorly placed. Hinge long with one thin, indistinct lateral tooth. Cardinals and anterior laterals unknown.

DESCRIPTION. Small, equivalved, inequilateral with fine growth lines. Subtriangular. Some periodic ornamentation produced by thickenings in the shell. Winged posterior produced from ridge originating from the umbonal region. Posterior end produced and somewhat rostrate. Anterior profile rounded. Beaks weak, closely set and placed anteriorly. Hinge weak with one thin

TABLE 14. Morphometrics (in mm) for *Protosphaerium giana* sp. nov.

AMF No.	Length	Height	Width	Beak Length
38165	9	6.25	?	3.7
103931	5.7	4.1	?	2.5
103934B	6.55	4	?	3.1
103932	7.65	4.5	?	3.1
Mean	7.22	4.71	0	3.1

indistinct lateral tooth. Cardinals and anterior laterals unknown. Muscle scars unknown, presumed weak. Morphometrics given in Table 14.

REMARKS. Placed tentatively within *Protosphaerium*, this species shares some characters with *Protosphaerium talbragarensis*. Until more material presents itself, this genus provides an adequate position. In some respects, *Protosphaerium talbragarensis* sp. nov. is similar to *Batissa (Batissa) violacea* (Lamarck) within the corbiculids. While similar in morphology this is not considered as having close genetic affinity. *Proto. giana* is much smaller and with reduced hinge length.

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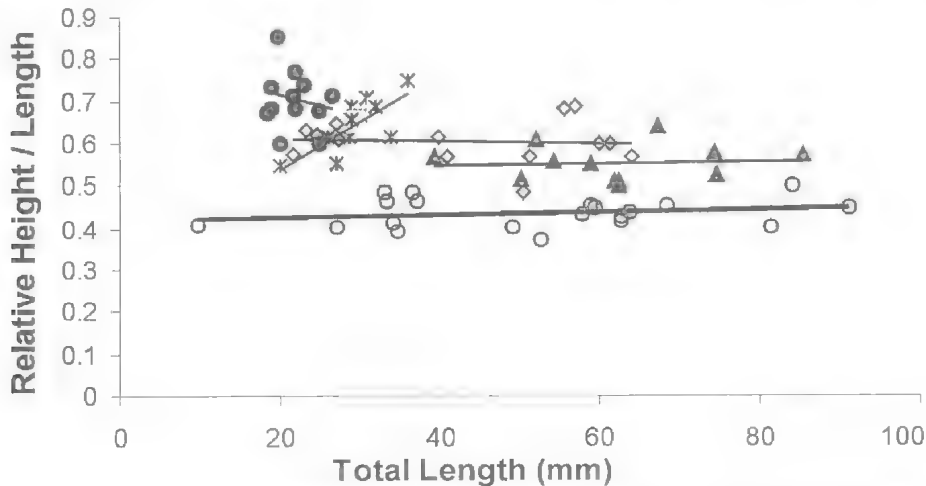


FIG. 8. Bivariate plot of relative height/length, plotted against length for hyriids from the Cretaceous. ● = *Palaeohyridella godthelpi* gen. et sp. nov., ◇ = *Hyridella (Hyridella) macmichaeli*, * = *Hyridella (Protohyridella) goondiwindiensis*, ○ = *Protovirgus wintonensis*, ▲ = *Alaytharia jaqueti*.

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A NEW *CLATHRIA* (PORIFERA: DEMOSPONGIAE: MICROCIONIDAE) FROM THE WESTERN INDIAN OCEAN

JOHN N.A. HOOPER, MICHELLE KELLY AND JOHN A. KENNEDY

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A new species of microcionid marine sponge *Clathria (Microcina) richmundi* sp. nov. is described from Zanzibar, Tanzania, and is highly unusual in having extremely large accolada toxas that form dragmata and skeletal tracts within the choanosomal and ectosomal skeletons, rudimentary spination on echinating acanthostyles, a live blue colouration and a prominent sub-surface aquiferous system with radiate arrangement around oscules. The new species is compared with the other 64 species of *Clathria* described from the Western Indian Ocean, Southeast Africa and Arabian Gulf-Red Sea provinces, and other species known to have toxodragmata. □ *Porifera, Demospongiae, Paeciloseclerida, Microcionidae, new species, taxonomy, Zanzibar, Western Indian Ocean.*

John N.A. Hooper (email, JohnH@qm.qld.gov.au) and John A. Kennedy, Queensland Museum, PO Box 3300, South Brisbane 4101, Australia; Michelle Kelly, Marine Ecology and Aquaculture, National Institute of Water and Atmospheric Research (NIWA), Private Bag 109-695, Newmarket, Auckland, New Zealand; 14 December 1999.

The extensive literature on sponges of the Western Indian Ocean is evidence of a rich and diverse fauna (Table 1). Even though this inventory already contains 'several hundred' species (Kelly, 1997), it is undoubtedly far from complete. For example, Van Soest (1994b) collected 240 species from the Seychelles and Amirante islands whereas only 167 species were known previously from the region.

Within the Western Indian Ocean (i.e. extending along the continental shelf from Natal to Somalia and including the islands from Madagascar to the Seychelles; Richmond, 1997), Southeast African regions (Natal to the Cape) and Arabian Gulf-Red Sea provinces 74 species of Microcionidae have been reported (Hooper, 1996a), of which 64 belong to *Clathria*, 10 still unnamed (Table 2). Of these, 44 (or 69%) have not yet been found outside the region. This number of 'apparent endemics' may decrease over time as the region's biodiversity becomes better known, but it still represents an extraordinarily high level of endemism compared to other sponge genera and other phyla. For example, Van Soest (1994b) found about 24% of all sponges collected from the Seychelles and Amirante islands were endemic to the W Indian Ocean fauna, and Richmond (1997) suggested that only about 15% of all the regional marine biota may be endemic to the W Indian Ocean region.

Biogeographic affinities of the sponge fauna are thought to be essentially Tethyan (Van Soest,

1994a), with southern incursions of species of Gondwanan origin (Hooper & Lévi, 1994; Hooper, 1996a). This fauna is thought to be most similar to the central Indian Ocean and Indo-Malaya regions (Van Soest & Hajdu, 1997), and in this regard follows the general pattern seen in other marine invertebrate phyla (e.g. scleractinarian corals; Veron, 1986; Veron, 1993). Richmond (1997) suggested that about 35% of the West Indian Ocean marine biota was widely distributed, extending into the Red Sea and perhaps as far as the Indo-Malay region, 35% ranged across the whole Indo-Pacific region, and 15% extended into the warm temperate regions of the Atlantic Ocean. To date only one microcionid, *Clathria (Thalysias) vulpina* (Lamarck), appears to be truly Indo-Pacific 'cosmopolitan', with a confirmed distribution extending from Tonga to the Red Sea (i.e. with conspecificity confirmed through morphological comparisons between recent collections of living populations; Hooper, 1996a). However, even this finding has yet to be confirmed through genetic analysis to determine whether slight morphological differences between regional populations represent intraspecific variability or indicate the existence of a series of possible allopatric sibling species.

Van Soest (1994b) also noted a high level of regional heterogeneity between sponge faunas of the Seychelles and Amirante Island groups, with only 17% of species common to both regional faunas. This supports a similar finding from

TABLE 1. Literature on the sponges of the Western Indian Ocean, Southeast Africa and Arabian Gulf-Red Sea provinces.

Province	Locality	Sponge literature
Coastal East Africa	Zanzibar	Lendenfeld, 1897; Baer, 1905; Jenkin, 1908; Burton, 1959; Thomas, 1976a, 1979b; Pulitzer-Finali, 1993; Kelly, 1997; Magnino & Gaino, 1998
	Tanzania	Jenkin, 1908; Thomas, 1976a; Pulitzer-Finali, 1993; Magnino & Gaino, 1998
	Mozambique	Lévi, 1964; Thomas, 1979a, 1979c, 1980a, 1980b; Laghi et al., 1984; Schmidt et al., 1997
	Kenya	Marsden, 1975; Bruce, 1976; Thomas, 1981a; Vacelet et al., 1991; Pulitzer-Finali, 1993
	Somalia	McCabe et al., 1982; Finamore et al., 1983; Hooper, 1996a
	South Africa	Ehlers, 1870; Carter, 1871; Gray, 1873; Vosmaer, 1880; Kirkpatrick, 1900, 1901, 1902a, 1902b, 1903, 1904, 1908, 1913; Sollas, 1908; Stephens, 1915; Burton, 1926, 1929, 1931, 1933a, 1933b, 1936, 1958; Lévi, 1963, 1967; Borojevic, 1967; Day, 1981; Schleyer, 1991; Pettit et al., 1993b; Rudi et al., 1993, 1994a, 1994b, 1995; Barkai et al., 1996; Hooper et al., 1996; Samaai, 1997; Beukes et al., 1998; Koren Goldshlager et al., 1998; McPhail et al., 1998
Offshore East Africa	Madagascar	Bosraug, 1913; Decary, 1946; Lévi, 1956; Vacelet & Vasseur, 1965, 1966, 1971, 1977; Vacelet, 1967a, 1967b, 1977; Vacelet et al., 1976; Ivanova et al., 1993; Hooper, 1996b
	Aldabra	Lévi, 1961
	Comoros	Sarà et al., 1993b; Pettit et al., 1993a, 1994a, 1994b
	Réunion	Lévi, 1986; Akinin et al., 1996
	Mauritius	Thomson, 1868; Duncan, 1880; Topsent, 1890; Dendy, 1922; Van Soest, 1993
	Saya de Malha	Dendy, 1922; Kolbasov, 1992
	Seychelles	Wright, 1881; Ridley & Dendy, 1887; Topsent, 1893a; Dendy, 1922; Lévi, 1961; Thomas, 1973, 1979c, 1981b; Hooper & Krasochin, 1989; Ngoc Ho, 1990; James et al., 1991; Venkateswarlu et al., 1991; Van Soest, 1994b; Van Soest et al., 1994; Trimurtulu & Faulkner, 1994; Hooper, 1996a; Pettit et al., 1997
	Amirante	Carter, 1880; Ridley, 1884; Ridley & Dendy, 1887; Dendy, 1922; Van Soest et al., 1994; Braekman et al., 1998
Northwest Indian Ocean	Red Sea	Keller, 1889, 1891; Topsent, 1892; Row, 1911; Lévi, 1958, 1965; Burton, 1959; Delseth et al., 1979; Sarà et al., 1979; Kashman et al., 1982, 1989; Mergner, 1982; Sokoloff et al., 1982; Mebs, 1985; Carmely & Kashman, 1986; Vine, 1986; Gebreyesus et al., 1988; Ilan & Loya, 1988, 1990; Carmely et al., 1990; Kolbasov, 1990; Isaacs & Kashman, 1992; Rinkevich et al., 1993; Rudi & Kashman, 1993; Kelly-Borges & Vacelet, 1995; Guo et al., 1996, 1997a, 1997b; Ramadan, 1997; Beer & Ilan, 1998; Wörheide, 1998
	Ethiopia	Isaacs et al., 1991
	Eritrea	Hooper, 1996a
	Arabian Sea	Carter, 1869; Topsent, 1893b; Dendy, 1913, 1915, 1916a, 1916b, 1916c, 1922; Kumar, 1924a, 1924b, 1924c, 1925; Burton & Rao, 1932; Burton, 1959; Thomas, 1975, 1976b, 1979b, 1988, 1989; Rahim, 1979; Kamat et al., 1981; Patel et al., 1985; Kondracki & Guyot, 1987; James et al., 1989; Parameswaran et al., 1989, 1992a, 1992b, 1994, 1997; Kobayashi et al., 1992a, 1992b; Pettibone, 1993; Sarà & Bavestrello, 1995; Bavestrello et al., 1996; Thomas et al., 1997
	Oman	Sarà & Bavestrello, 1995; Bavestrello et al., 1996

sponge surveys of NW and NE Australian reefs (Hooper, 1994; Hooper et al., 1999), with the implication that taxonomic inventories of regional sponge faunas are largely incomplete, with possibly many new taxa remaining to be discovered within these highly heterogeneous and 'apparent endemic' regional populations. The present study describes one such species discovered during routine surveys of Zanzibar undertaken by MK as part of a project to produce an inventory of the marine fauna and flora and popular field guide to the region (Richmond, 1997).

Methods for preparation and examination of material are described by Hooper (1996a). Spicule measurements refer to (minimum-(mean)-maximum) dimensions of lengths and widths taken from 25 random samples of each spicule category

and are given in micrometres unless otherwise stated. Abbreviations: BMNH, The Natural History Museum, London; QM, Queensland Museum, Brisbane. MK is grateful to Dr Matthew Richmond for facilitating her participation in the East Africa marine surveys.

SYSTEMATICS

PORIFERA Grant
DEMOSPONGIAE Sollas
POECILOSLERIDA Topsent
MICROCIONINA Hajdu, Van Soest & Hooper
MICROCIONIDAE Carter

Clathria Schmidt, 1862

Clathria (*Microcionia*) Bowerbank, 1862
Refer to synonymy in Hooper (1996a)

Clathria (Microciona) richmondi sp. nov.
(Figs 1-4)

ETYMOLOGY. For Dr Matthew D. Richmond, Institute of Marine Sciences, Zanzibar, in recognition of his substantial contribution towards documenting the marine flora and fauna of the E. African coastline (Richmond, 1997).

MATERIAL. HOLOTYPE. QMC1306785 (fragment BMNH 1995.6.29.96). E. side of Pange Sandbank Reef, Zanzibar Town, Unguja I., Tanzania, 6°10.0'S, 39°9.3'E, 10m depth, 7.viii.1995. coll. M. Kelly, SCTJBA.

DISTRIBUTION. Known only from the fringing reefs off Zanzibar Town, Unguja Island, encrusting dead coral substrate on a shallow fringing reef.

DESCRIPTION. *Shape.* Very thinly encrusting (0.2-0.7mm thick) in small patches (10-20cm diameter) or completely enveloping coral rubble.

Colour. Royal blue with a violet tinge alive, brownish-orange in ethanol.

Oscules. Large (up to 5mm diameter), raised on membranous lip (approximately 4mm high), scattered over entire surface and with prominent, vein-like, radial subsurface drainage canals radiating towards each oscule; oscules and drainage canals collapsed upon preservation.

Texture and Surface Characteristics. Slimy, very smooth, fleshy surface.

Ectosome. No special category of ectosomal spicules present, although choanosomal principal styles arising from the underlying skeleton, standing perpendicular to the substrate, may protrude a long way through the surface. Bundles of toxodragmata occasionally lie on the surface, although most of these appear to be confined below the peripheral skeleton.

Subectosome. Below the surface are plumose bundles of auxiliary subtylostyles, mostly running perpendicular and paratangential to, or occasionally protruding through, the surface. These subectosomal skeletal bundles form stellate brushes associated with (or parallel to) the larger protruding choanosomal principal styles. Toxodragmata form thick bundles below the peripheral skeleton, resembling megasclere spicule tracts, lying tangential to the surface and scattered between the erect choanosomal principal styles.

Choanosome. Microcionid skeletal structure, with thin hymedesmioid basal layer of spongin fibre, approximately 50 thick, highly collagenous, granular, dark brown pigmented, with

calceitic detritus embedded beneath; basal spongin with sparsely dispersed echinating acanthostyles embedded and standing perpendicular to substrate, and bulbous spongin fibre nodes up to 150 thick found only in thicker sections of the encrustation; each bulbous fibre node discrete, erect, without any anastomoses between adjacent nodes, and each with 1-5 choanosomal principal styles embedded and perpendicular to substrate, with spicules diverging slightly, becoming plumose towards surface and protruding up to 350 through ectosome; smaller echinating acanthostyles confined mostly to hymedesmioid basal spongin fibre, rarely seen on bulbous fibre nodes; conversely, principal styles only seen on bulbous fibre nodes and not on hymedesmioid basal fibres. Dense horizontal bands of accolada toxodragmata (up to 70 thick) occur about midway through the choanosomal skeleton cross-section, and also in the ectosomal region, lying on or below the surface; few single toxas observed in the mesohyl mostly comprising wing-shaped forms, whereas most toxas forming dragmata. Palmate isochelae moderately abundant within mesohyl; collagen within mesohyl dense, relatively smooth, moderately heavily pigmented orange-brown; choanocyte chambers elongate-oval, up to 40 × 12.

Megascleres. Choanosomal principal styles and subtylostyles very long, slender, slightly curved near basal end, long tapering fusiform points, base either slightly constricted or non-tylote, smooth or very occasionally with anisoxeote terminations. Length 178-(403.7)-622, width 6-(10.2)-12.

Subectosomal auxiliary subtylostyles very long, very slender, straight, fusiform points, with well developed, entirely smooth subtylote bases. Length 198-(351.5)-428, width 2-(3.8)-5.

Echinating acanthostyles relatively uncommon, short, slender, straight or very slightly curved at centre, fusiform-pointed, with moderately well-developed basal constriction; shaft and base with vestigial granular spines confined mainly to basal half of spicule. Length 58-(89.6)-134, width 3-(5.4)-8.

Microscleres. Palmate isochelae moderately common, well-silicified, with thick, well-developed alae comprising over 70% of spicule length. Length 14-(15.2)-17.

Toxas in two forms: Accolada toxas extremely abundant, exceptionally long and very slender, with slight central curvature and straight

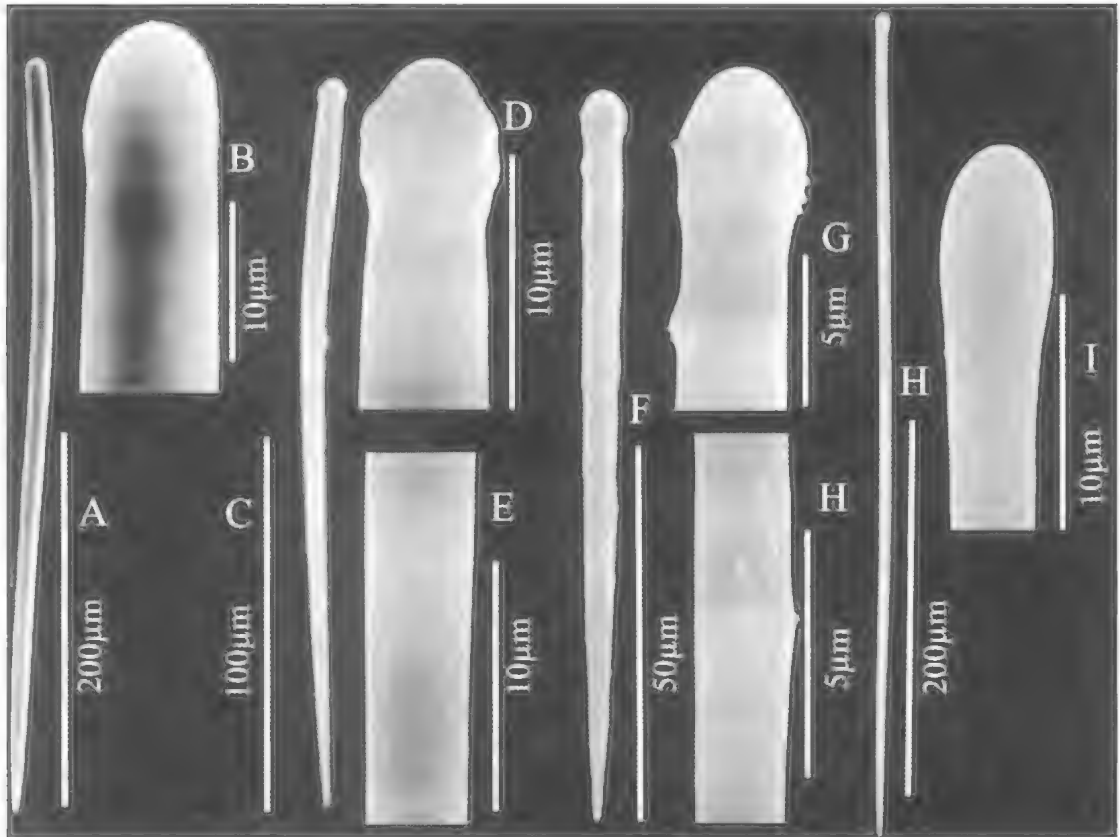


FIG. 1. Megascleres from *Clathria (Microcionia) richmondi* sp. nov. (holotype QMG306785). A-B, Choanosomal principal style and subtylote base. C-E, Larger echinating acanthostyle, base and shaft, illustrating mostly smooth, tuberculate ornamentation. F-H, Smaller echinating acanthostyle, base and shaft with rudimentary small spines. I-J, Subectosomal auxiliary subtylostyle and smooth base.

(non-reflexed) arms, invariably forming toxodragmata. Length 262-(501.3)-975, width 1.5-(1.9)-2.0. Shorter toxas present but uncommon, intermediate between wing-shaped and accolada in morphology, with slight to moderate central curvature, slightly reflexed arms; found in toxodragmata together with accolada toxas and also occasionally singly within the mesohyl. Length 84-(114.8)-154, width 0.8-(1.04)-1.5.

REMARKS. *Clathria (Microcionia) richmondi* sp. nov. is unusual in having 1) huge accolada toxas in dragmata, forming dense bands both within the mesohyl and lying tangential to the surface; 2) a second, less common and much smaller form of toxas, intermediate between wing-shaped and accolada morphology, scattered singly within the mesohyl; 3) a skeleton composed of hymedesmioid basal spongin fibres in thinner sections and microcionid bulbous spongin fibre nodes in thicker parts of the

skeleton, each node with one or few choanosomal principal styles perpendicular to the surface; 4) relatively uncommon echinating acanthostyles, with rudimentary spination, apparently confined to the hymedesmioid basal skeleton; and 5) distinctive field characteristics including a royal blue colour, large oscules with a prominent raised 'lip' and prominent subsurface drainage canals radiating towards each oscule. Although individually these distinctive characters are not unique amongst known species of *Clathria*, in combination they clearly differentiate the Zanzibar species from others.

1) Microsclere morphology, including toxas, appears to be a relatively consistent and useful character to differentiate between similar species (Hooper, 1996a). Six species of *Clathria* have been recorded with accolada toxas forming toxodragmata (*C. (Thalysias) cactiformis* (Lamarck), *C. (Microcionia) densa* (Burton),

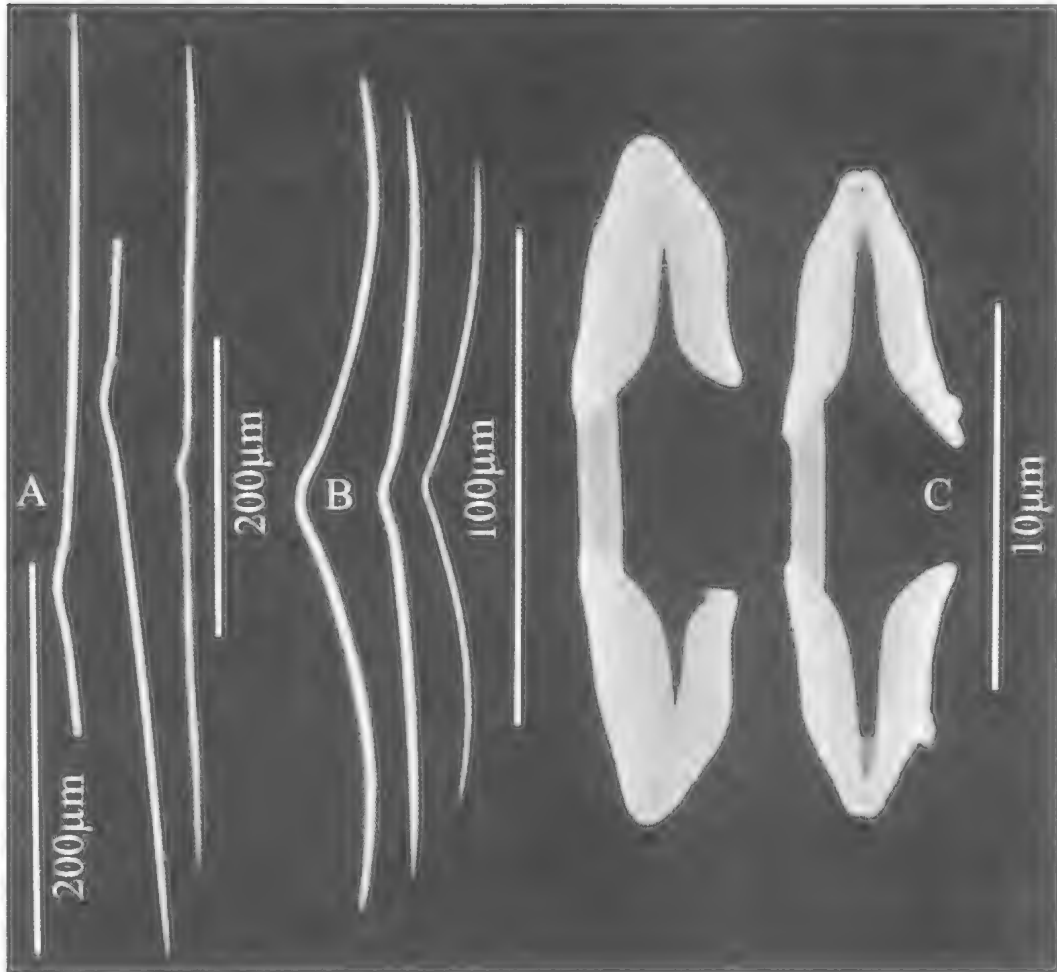


FIG. 2. Microscleres from *Clathria (Microcionia) richmondi* sp. nov. (holotype QMG306785). A, Longer accolada toxas. B, Smaller toxas, intermediate between wing-shaped and accolada forms. C, Palmate isochelae.

C. (T.) lendenfeldi Ridley & Dendy, *C. (T.) oxitoxa* Lévi, *C. (Axociella) thetidis* (Hallmann) and *C. (T.) vulpina* (Lamarck) (Hooper, 1996a)); refer to Table 2 for known distributions. In *C. richmondi* the accolada toxas are exceptionally large compared to most species of *Clathria* (262-975 long), and also form very prominent bands within the skeleton. By comparison, those of *C. (T.) cactiformis* are 8-355 long, *C. (M.) densa* (205-305), *C. (T.) lendenfeldi* (7-361) and *C. (T.) vulpina* (8-200), and are scattered throughout the skeleton in loose bundles not forming skeletal tracts. In contrast, accolada toxas of *C. (A.) thetidis* and *C. (T.) oxitoxa* are much larger than those of *C. (M.) richmondi* (175-1280 and 170-3000 long, respectively), and moreover those of *C. (T.) oxitoxa* also form skeletal tracts

within the skeleton (Lévi, 1963). In this regard *C. oxitoxa* is most similar to *C. richmondi*, although all three taxa differ in virtually every other respect (see redescription of *C. oxitoxa* below and *C. thetidis* in Hooper (1996a)).

2) Many species of *Clathria* have two toxa morphologies, and this feature is probably of little diagnostic importance above the species level. Of the species mentioned above only *C. densa* and *C. vulpina* lack both morphologies of toxas.

3) Hymedesmioid – microcionid skeletal structure has been used in the past as a primary diagnostic character for several nominal microcionid genera (e.g. *Axocielita* de Laubenfels, *Hymantho* Burton, *Leptoclathria* Topsent), although this view is no longer widely held (Van

Soest, 1984; Hooper, 1996a). Within *Clathria* these species are now placed in either the subgenera *Microcionia* or *Thalysias*, depending on whether ectosomal specialisation is absent or present, respectively. Worldwide there are hundreds of encrusting microcionid species with hymedesmioid and/or microcionid spongin fibre skeletons and a mineral skeleton composed of perpendicular and/or plumose spicule tracts, of which 22 occur in this region (Table 2; species annotated (2)).

4) The presence or absence of echinating spicules, the degree to which they are smooth or spined, and the morphology of spines have been used as generic characters within Microcionidae at one time or another (e.g. *Anaata* de Laubenfels, *Axociella* Hallmann, *Folitispa* de Laubenfels, *Isociella* Hallmann, *Ophlitaspongia* Bowerbank, *Paratenaciella* Vacelet & Vasseur, *Tenaciella* Hallmann). The absence of echinating megascleres remains a valid diagnostic character (at the subgeneric level) for some taxa (e.g. *Isociella*, *Axociella*, *Ophlitaspongia*), by virtue of the consistent combination of this feature and the possession of unusual skeletal structures characterising each of the taxa (Hooper, 1996a; Howson & Chambers, 1999). Within *Clathria* s.s. there are also several species that have lost echinating spicules (e.g. *C. (C.) paucispicula* (Burton), *C. (T.) craspedia* Hooper). By comparison, the absence (loss), rudimentary development and shape of spines on echinating spicules vary widely amongst the many hundreds of species of *Clathria*, although these features appear to be consistent at the species level (e.g. *C. (M.) aceratoobtusa* (Carter) with virtually

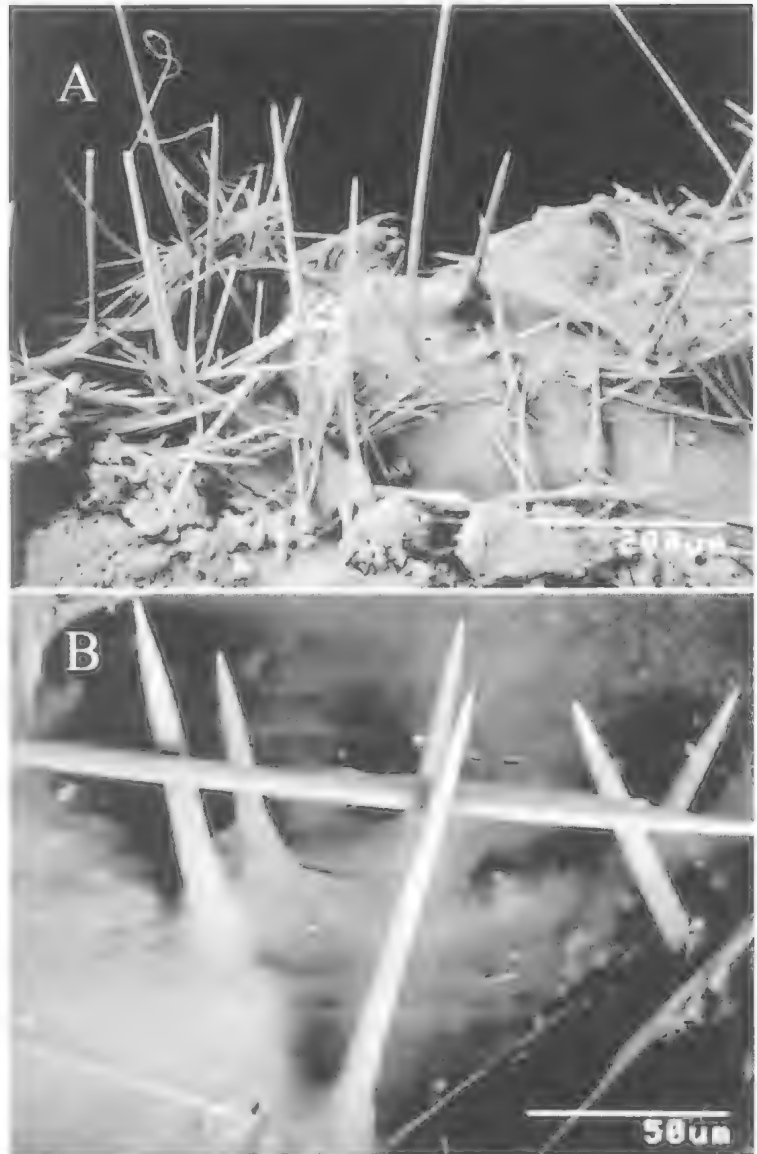


FIG. 3. Skeletal structure of *Clathria (Microcionia) richmondi* sp. nov. (holotype QMG306785). A, Hymedesmioid-microcionid basal skeleton with tracts of auxiliary subtylostyles lying in multispicular bands within the choanosome. B, Erect echinating acanthostyles (mostly smooth) perpendicular to the hymedesmioid basal skeleton.

smooth spicules, *C. (C.) kylista* Hooper & Lévi with rudimentary spination, *C. (T.) dubia* (Kirkpatrick) with large, heavy spines). Within this continuum *C. richmondi* is most similar to the *C. kylista* condition.

5) As far as can be ascertained from the literature and from personal experience with the Microcionidae of the Indo-Pacific no other species

has a deep royal blue colour in life, but the importance of this character is limited by the lack of good knowledge of their living characters, most taxa known only from preserved specimens. Prominent raised oscules and a subsurface water canal system (radiating towards the oscules and producing a stellate surface pattern) are features common to many encrusting sponges (in which the aquiferous system is marginalised onto the external surface by virtue of the reduced choanosomal thickness), whereas in many microcionids this drainage system often has a different pigmentation from the adjacent ectosome.

Of the 64 species of *Clathria* recorded from the Western Indian Ocean, Southeast Africa and Arabian Gulf-Red Sea provinces 19 have accolada toxas (Table 2; species annotated (1)). Most of these species differ substantially from *C. richmondi* in major features such as growth form, skeletal structure, spicule geometries, spicule sizes, possession of specialised ectosomal skeleton (i.e. *Thalysias* condition) etc., whereas in 5 species these differences are more subtle.

Clathria (T.) oxitoxa Lévi (1963) is erect, bushy, flattened lamellate branches, yellow alive; skeleton plumo-reticulate with fibres irregularly cored by very large principal styles and bundles (dragmata) of large oxete toxas scattered throughout the sponge skeleton; ectosomal skeleton with plumose brushes of both ectosomal and subectosomal styles; principal styles regularly curved, with smooth non-tylote bases (450-800 × 35-40); subectosomal auxiliary subtylostyles with microspined bases (350-500 × 9); ectosomal auxiliary subtylostyles similar (100-150 × 4); echinating acanthostyles entirely spined with large spines (75-90 × 10); palmate isochelae in 2 size classes (6 and 13-14); accolada toxas nearly oxete, ranging from hair-like and faintly curved arms (170-250 × 0.5-1), thickly oxete with straight arms (750-1300 × 4-7) and extremely long oxetes with straight arms and only slight central curvature (2400-3000 × 10-11); smaller wing-shaped toxas with large central curvature (35-40 × 0.5). This species is most similar to *C. (M.) richmondi* in having exceptionally large accolada toxas in dragmata forming skeletal bands, but differs significantly in its live colouration, growth form, skeletal structure and the geometry and size of all spicules (in particular the huge upper size range of accolada toxas).

Clathria (M.) densa (Burton, 1959) is massive, dense choanosomal skeleton with semi-plumose

ascending spongin fibres cored by principal styles, interconnected by few transverse fibres and spicule tracts; dense ectosomal skeleton of auxiliary subtylostyles; principal styles with subtylote spined bases (175-298 × 18-35); subectosomal auxiliary subtylostyles with thick spined bases (130-275 × 4-8), echinating acanthostyles thick, slightly curved, heavily spined with aspinose neck (118-156 × 9-16); palmate isochelae (9-13); hair-like accolada toxas, distinctly sinuous and raphidiform forming dragmata (205-305 × 0.5-1.5). This species is a borderline case between the subgenera *Microcionia* and *Clathria* given that its choanosomal skeleton is a well-developed microcionid architecture that is verging on reticulate given the existence of vestigial interconnecting fibres and spicule tracts. It also differs from *C. (M.) richmondi* in spicule geometry, spicule sizes, and absence of smaller wing-shaped toxas: in fact the two species are only similar in possessing accolada toxas forming dragmata.

Clathria (C.) inhaensis Thomas (1979b) is thinly encrusting, surface conulose; ectosome reduced; choanosomal skeleton reticulate, with well developed ascending primary fibres cored by plumose tracts of principal styles, interconnected by thinner transverse fibres in which few spicules are found and fully embedded within fibres, and both echinated by acanthostyles; subtylostyles interstitial and in brushes arising from tips of main fibres; principal styles with smooth bases (121-172 × 4-5); subectosomal subtylostyles with smooth bases (124-181 × 2-4); echinating acanthostyles with variably spined shaft and spined bases (41-58 × 3-5); palmate isochelae (8-10); accolada toxas hair-like (110-145 × 0.5-1.5). This species clearly sits within subgenus *Clathria* given its possession of a reticulate skeletal architecture. It also differs significantly from *C. (M.) richmondi* in spicule geometry, spicule size and absence of toxodragmata.

Clathria (T.) longitoxa (Hentschel, 1912) ranges from thinly encrusting to massive growth form; hymedesmioid to closely reticulate skeleton of stout fibres, with larger and smaller principal styles coring fibres in plumose arrangement, echinated by acanthostyles; subectosomal auxiliary subtylostyles scattered; principal styles curved with smooth non-tylote bases (592-840 × 22-26); smaller principal styles with subtylote granular bases (120-408 × 8-20); subectosomal auxiliary subtylostyles with faintly microspined bases (430-584 × 4-9); ectosomal auxiliary subtylostyles similar (190-320 × 3-5); echinating

acanthostyles evenly spined with spined points ($64-80 \times 6-7$); palmate isochelae ($12-20$); accolada toxas with central U-bend and straight arms ($400-820 \times 1-2$). This species differs from *C. (M.) richmondi* in most respects, showing similarities only in growth form, skeletal structure and possession of accolada toxas.

Clathria (C.) oculata Burton (1933a) has an erect branching anastomosing growth form, drab colouration with tinges of occasional purple; skeletal architecture composed of a subsodictyal reticulation of spongin fibres fully cored by principal styles and evenly echinated by acanthostyles; principal styles with smooth non-tylote bases ($140-7$); subectosomal auxiliary subtylostyles with smooth bases (160×3); echinating acanthostyles evenly spined with small spines (65×4); accolada toxas slightly curved (160 long); palmate isochelae very small (6 long). This species is only similar to *C. (M.) richmondi* in possessing accolada toxas, differing in most other features.

In addition to these species there are three unnamed species described from Madagascar by Vacelet & Vasseur (1971) showing similarities to *C. richmondi* in the morphology of their accolada toxas, skeletal structure and growth form, although differing in most all other characters.

Clathria (T.) sp. 4 (Vacelet & Vasseur, 1971; see Table 2) is thinly encrusting, yellow alive; choanosomal skeleton microcionid with columns of fibres cored by principal styles and acanthostyles; ectosomal specialisation with some surface brushes but these are not thick; principal styles very slightly subtylote, smooth bases

($130-440 \times 6-12$); subectosomal auxiliary subtylostyles with smooth bases ($150-320 \times 4$); ectosomal auxiliary subtylostyles with microspined bases ($110-200 \times 3$); echinating acanthostyles slightly subtylote, poorly developed spines ($55-60 \times 5$); palmate isochelae in 2 size classes, the smaller contort (5 and 12.5 long); accolada toxas nearly



FIG. 4. Ectosomal skeleton of *Clathria (Microcionia) richmondi* sp. nov. (holotype QMG306785). A, Bundles of subectosomal auxiliary subtylostyles paratangential to and protruding through the surface, loosely associated with erect principal styles. B, Toxodragmata (bundles of accolada toxas) lying on or close to the surface.

TABLE 2. List of *Clathria* species recorded from the Western Indian Ocean, Southeast Africa and Arabian Gulf-Red Sea provinces. Refer to Hooper (1996a) for full synonymy and taxonomic references. Annotation: 1 = species with accollada toxas; 2 = encrusting species with hymedesmioid-microcionid skeletal structure; 3 = identification has yet to be confirmed from examination of voucher specimen; 4 = identification unconfirmed, specimen voucher material missing; 5 = new combination; 6 = currently unrecognisable.

Current taxonomic assignment	Published name	Author	Western Indian Ocean records	Other known distribution
<i>C. (Thalysias) abietina</i> (Lamarck)	<i>C. aculeata</i> Ridley	Burton (1959), Vacelet et al. (1976, 1977)	Red Sea, S Arabian coast, Madagascar	Tropical Australia, central NW Pacific, Philippines
<i>C. (Microcionia) affinis</i> (Carter) ²	<i>M. affinis</i> Carter	Burton (1959)	S Arabian coast, Zanzibar	Gulf of Manaar
<i>C. (Thalysias) amirantiensis</i> Hooper ¹	<i>Colloclathria ramosa</i> Dendy (preocc.)	Dendy (1922), Hooper (1996)	Amirante, Coëtivy, Seychelles	-
<i>C. (Thalysias) anomala</i> (Burton) ¹	<i>R. anomala</i> Burton	Burton (1933)	S South Africa	-
<i>C. (Thalysias) anonyma</i> (Burton) ^{2,5}	<i>M. anonyma</i> Burton	Burton (1959)	Zanzibar	-
<i>C. (Clathria) arbuscula</i> (Row)	<i>Ophlitaspongia arbuscula</i> Row, <i>O. horrida</i> Row	Row (1911)	Red Sea	-
<i>C. (Microcionia) atrasanguinea</i> (Bowerbank) ²	<i>M. atrasanguinea</i> Bowerbank	Carter (1880), Dendy (1922), Burton & Rao (1932), Lévi (1965), Van Soest (1993)	Seychelles, Red Sea, Arabian Sea, Mauritius	Caribbean, NE Atlantic, Mediterranean, coast of India, Gulf of Manaar, Bay of Bengal, Andaman Sea
<i>C. (Clathria) axociona</i> Lévi	<i>C. axociona</i> Lévi	Lévi (1963)	S South Africa	Namibia
<i>C. (Thalysias) cactiformis</i> (Lamarck) ¹	<i>Rhaphidophlus typicus</i> (Carter), <i>C. (T.) cactiformis</i> (Lamarck), <i>Rhaphidophlus</i> sp. 2; Vacelet & Vasseur	Vacelet et al. (1971, 1976, 1977), Hooper (1996)	Madagascar, Somalia, E Africa, Seychelles, Red Sea	S, W & E coasts of Australia
? <i>C. (Clathria) caespes</i> (Ehlers) ⁶	<i>Scopalina caespes</i> (Ehlers)	Hooper (1996)	S South Africa	-
<i>C. (Wilsonella) cercidochela</i> Vacelet & Vasseur	<i>Clathriopsamma cercidochela</i> Vacelet & Vasseur	Vacelet et al. (1971, 1977)	Madagascar	-
<i>C. (Clathria) conica</i> Lévi	<i>C. conica</i> Lévi	Lévi (1963)	S South Africa	-
<i>C. (Thalysias) cullingworthi</i> Burton	<i>C. cullingworthi</i> Burton	Burton (1931)	Natal	-
<i>C. (Clathria) dayi</i> Lévi	<i>C. dayi</i> Lévi	Lévi (1963)	S South Africa	(? Korea ³)
<i>C. (Thalysias) delaubenfelsi</i> (Lévi)	<i>Rhaphidophlus delaubenfelsi</i> Lévi	Lévi (1963)	S South Africa	-
<i>C. (Microcionia) densa</i> (Burton) ^{1,2}	<i>M. densa</i> Burton	Burton (1959)	S Arabian coast	-
<i>C. (Clathria) elastica</i> Lévi	<i>C. elastica</i> Lévi	Lévi (1963)	S South Africa	-
<i>C. (Axociella) fauroti</i> (Topsent)	<i>Axosuberites fauroti</i> Topsent	Topsent (1893)	Gulf of Aden	-
<i>C. (Thalysias) flabellata</i> (Burton)	<i>Rhaphidophlus flabellata</i> Burton	Burton (1936)	S South Africa	-
<i>C. (Clathria) foliascens</i> Vacelet & Vasseur	<i>C. foliascens</i> Vacelet & Vasseur	Vacelet et al. (1971, 1976, 1977)	Madagascar	-
<i>C. (Thalysias) fusterna</i> Hooper	<i>C. fusterna</i> Hooper	Hooper (1996)	Eritrea	N & NE Australia
<i>C. (Clathria) hexagonopora</i> Lévi ¹	<i>C. hexagonopora</i> Lévi	Lévi (1963)	S South Africa	-
<i>C. (Clathria) indica</i> Dendy	<i>C. indica</i> Dendy	Burton (1931), Thomas (1979)	Natal, Mozambique	SE India, Gulf of Manaar
<i>C. (Clathria) inhaensis</i> Thomas ¹	<i>C. inhaensis</i> Thomas	Thomas (1979)	Mozambique	-
<i>C. (Clathria) irregularis</i> (Burton)	<i>Marleyia irregularis</i> Burton	Burton (1931)	Natal	-

TABLE 2. (cont.)

Current taxonomic assignment	Published name	Author	Western Indian Ocean records	Other known distribution
<i>C. (Clathria) juncea</i> Burton	<i>C. juncea</i> Burton	Burton (1931)	Natal	-
<i>C. (Microcionia) laevisissima</i> (Dendy) ²	<i>H. laevisissima</i> Dendy	Dendy (1922)	Mauritius	-
<i>C. (Thalysias) lambda</i> (Lévi)	<i>Leptoclathria lambda</i> Lévi	Lévi (1958)	Red Sea	-
<i>C. (Thalysias) lendenfeldi</i> Ridley & Dendy ¹	<i>C. spicata</i> Hallmann, <i>C. whiteleggii</i> Dendy	Dendy (1922), Burton (1931, 1959), Hooper (1996)	Red Sea, Gulf of Aden, S Arabian coast, Cargados Carajos, Saya de Malha, Somalia, Natal	SE, NE, N. & NW Australia, E Indonesia, Andaman Sea, Gulf of Manaar
<i>C. (Thalysias) lissoclada</i> (Burton)	<i>Rhaphidophlus lissocladus</i> Burton	Lévi (1963)	S South Africa	Falkland Is
<i>C. (Clathria) lobata</i> Vosmaer	<i>C. lobata</i> Vosmaer	Vosmaer (1880), Ridley & Dendy (1887), Stephens (1915), Lévi (1963)	S South Africa	-
<i>C. (Thalysias) longistyla</i> (Burton) ^{2,5}	<i>M. longistyla</i> Burton	Burton (1959)	S Arabian coast	(? Korea ³)
<i>C. (Thalysias) longitoxa</i> (Hentschel) ¹²	<i>M. longitoxa</i> (Hentschel)	Burton (1959)	Gulf of Aden	E Indonesia, Madras
<i>C. (Microcionia) microxea</i> (Vacelet & Vasseur) ²	<i>Paratenaciella microxea</i> Vacelet & Vasseur	Vacelet & Vasseur (1971)	Madagascar	-
<i>C. (Wilsonella) mixta</i> Hentschel	<i>C. mixta</i> Hentschel	Burton (1959)	S Arabian coast	E Indonesia ³
<i>C. (Thalysias) nervosa</i> (Lévi)	<i>Axociella nervosa</i> Lévi	Lévi (1963)	S South Africa	-
<i>C. (Clathria) oculata</i> Burton ¹	<i>C. oculata</i> Burton	Burton (1933, 1959)	Natal	-
<i>C. (Thalysias) oxitoxa</i> Lévi ¹	<i>C. oxitoxa</i> Lévi	Lévi (1963)	S South Africa	-
<i>C. (Clathria) pachystyla</i> Lévi	<i>C. pachystyla</i> Lévi	Lévi (1963)	S South Africa	-
<i>C. (Axociella) parva</i> Lévi	<i>C. parva</i> Lévi	Lévi (1963)	S South Africa	Namibia
<i>C. (Thalysias) procera</i> (Ridley)	<i>Rhaphidophlus procera</i> Ridley, <i>Echinonema gracilis</i> Ridley	Ridley (1884), Ridley & Dendy (1887), Dendy (1922), Burton & Rao (1932), Burton (1931, 1959), Lévi (1963), Thomas (1973)	Cargados Carajos, Seychelles, Amirante, Red Sea, Arabian coast, Natal	NE, N & NW Australia, E Indonesia, Gulf of Manaar, (? Hawaii ³)
<i>C. (Clathria) rhaphidotoxa</i> Stephens ¹	<i>C. rhaphidotoxa</i> Stephens	Stephens (1915), Lévi (1963)	S South Africa	-
<i>C. (Microcionia) rhopalophora</i> (Hentschel) ²	<i>M. rhopalophora</i> (Hentschel)	Burton (1959)	Maldives	E. Indonesia, Cocos-Keeling, Gulf of Manaar
<i>C. (Thalysias) robusta</i> (Dendy) ^{1,2}	<i>M. robusta</i> Dendy	Dendy (1922)	Amirante	Singapore
<i>C. (Microcionia) seriata</i> (Grant) ^{2,4}	<i>Ophlitaspongia seriata</i> (Grant)	Lévi (1963)	S South Africa	NE. Atlantic, Mediterranean, New Zealand
<i>C. (Clathria) spongodes</i> Dendy	<i>C. spongodes</i> Dendy, <i>C. spongiosa</i> Burton, <i>C. madrepora</i> Dendy	Dendy (1922), Burton (1959), Vacelet et al. (1976)	Red Sea, Gulf of Aden, Amirante, Madagascar, Seychelles	(? Korea ³)
<i>C. (Microcionia) stephensae</i> Hooper	<i>M. similis</i> Stephens (preocc.)	Stephens (1915)	S South Africa	-
<i>C. (Microcionia) tenuis</i> (Stephens) ²	<i>M. tenuis</i> Stephens	Stephens (1915)	S South Africa	-
<i>C. (Clathria) transiens</i> Hallmann ⁴	<i>C. transiens</i> Hallmann	Burton (1959)	Red Sea	S Australian provinces

TABLE 2. (cont.)

Current taxonomic assignment	Published name	Author	Western Indian Ocean records	Other known distribution
<i>C. (Clathria) typica</i> Kirkpatrick (virtually unrecognisable)	<i>C. typica</i> Kirkpatrick	Kirkpatrick (1904)	Natal	-
<i>C. (Microciona) vacelettia</i> Hooper ²	<i>M. curvichela</i> Vacelet & Vasseur (preocc.)	Vacelet & Vasseur (1965), Hooper (1996)	Madagascar	-
<i>C. (Thalysias) vulpina</i> (Lamarck) ¹	<i>C. frondifera</i> (Bowerbank), <i>C. dichela</i> (Hentschel)	Ridley (1884), Ridley & Dendy (1887), Topsent (1892), Row (1911), Burton (1959), Lévi (1961), Thomas (1973, 1979), Vacelet et al. (1971, 1976, 1977), Pulitzer-Finali (1993), Hooper (1996), Kelly (1997)	Madagascar, Amirante, Seychelles, Red Sea, Mozambique, Aldabra, Zanzibar	Tropical Australia, W & E coasts of India, Gulf of Manaar, Mergui Archipelago, Andaman Sea, Malaysia, E & W Indonesia, N Papua New Guinea, Vietnam, Philippines, Micronesia, S Japan, New Caledonia
<i>C. (Clathria) zoanthifera</i> Lévi	<i>C. zoanthifera</i> Lévi	Lévi (1963)	S South Africa	-
<i>Clathria (Thalysias)</i> sp.; Vacelet & Vasseur ¹	<i>Rhaphidophlus</i> sp. 1; Vacelet & Vasseur	Vacelet & Vasseur (1971)	Madagascar	-
<i>Clathria (Thalysias)</i> sp.; Vacelet & Vasseur	<i>Rhaphidophlus</i> sp. 3; Vacelet & Vasseur	Vacelet & Vasseur (1971)	Madagascar	-
<i>Clathria (Thalysias)</i> sp.; Vacelet & Vasseur ^{1,2}	<i>Rhaphidophlus</i> sp. 4; Vacelet & Vasseur	Vacelet & Vasseur (1971)	Madagascar	-
<i>Clathria (Thalysias)</i> sp.; Vacelet & Vasseur ^{1,2}	<i>Rhaphidophlus</i> sp. 5; Vacelet & Vasseur	Vacelet & Vasseur (1971)	Madagascar	-
<i>Clathria (Thalysias)</i> sp.; Vacelet & Vasseur ^{1,2}	<i>Rhaphidophlus</i> sp. 6; Vacelet & Vasseur	Vacelet & Vasseur (1971)	Madagascar	-
<i>Clathria (Thalysias)</i> sp.; Vacelet & Vasseur	<i>Rhaphidophlus</i> sp. 7; Vacelet & Vasseur	Vacelet et al. (1971, 1977)	Madagascar	-
<i>Clathria (Microciona)</i> sp.; Vacelet & Vasseur ²	<i>Microciona</i> sp. 1; Vacelet & Vasseur	Vacelet & Vasseur (1971)	Madagascar	-
<i>Clathria (Microciona)</i> sp.; Vacelet & Vasseur ^{1,2}	<i>Microciona</i> sp. 2; Vacelet & Vasseur	Vacelet & Vasseur (1971)	Madagascar	-
<i>Clathria (Microciona)</i> sp.; Vacelet & Vasseur ²	<i>Microciona</i> sp. 3; Vacelet & Vasseur	Vacelet et al. (1971, 1976)	Madagascar	-
<i>Clathria (Microciona)</i> sp.; Vacelet, Vasseur & Lévi ^{1,2}	<i>Microciona</i> sp. 4; Vacelet, Vasseur & Lévi	Vacelet et al. (1976)	Madagascar	-

oxeote, with slight to virtually no central curvature (85-820 × 0.5-2.5); U-shaped to wing-shaped toxas very small (5-7.5).

Clathria (T.) sp. 5 (Vacelet & Vasseur, 1971) is encrusting, orange alive; hymedesmioid skeleton of principal subtylostyles and acanthostyles erect on basal spongin fibres; subectosomal and ectosomal auxiliary subtylostyles differ only in size and both contribute to both subectosomal and ectosomal surface brushes; principal subtylostyles slender, moderately subtylote microspined bases (140-280 × 5-8); subectosomal auxiliary subtylostyles slightly subtylote, smooth bases (up to 360 × 3); ectosomal auxiliary subtylostyles similar (from 90 × 2); echinating acanthostyles slender, evenly spined (50-60 × 2-3); palmate isochelae in two size classes (4-5 and 12-12.5 long); accolada toxas nearly oxeote,

with straight or only very slightly curved arms and slight angular central flexion (35-250 long).

Clathria (M.) sp. 2 (Vacelet & Vasseur, 1971) is encrusting, pinkish to red alive, with white subectosomal drainage canals clearly visible on the otherwise smooth surface; skeleton microcionid; principal subtylostyles with smooth or microspined bases (330-550 × 13-15); subectosomal auxiliary subtylostyles with smooth bases (120-550 × 2.5-5); echinating acanthostyles slender, entirely spined (100-120 × 5-7.5); palmate isochelae (7.5-20); accolada toxas with only slight curvature of arms and central flexion (130-320); small oxhorn toxas (7.5-20).

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NEW SPECIES OF TOXIC *TEDANIA* FROM NORTHERN VANUATU (PORIFERA:
DEMOSPONGIAE: POECILOSCLERIDA: TEDANIIDAE)

JOHN A. KENNEDY AND JOHN N.A. HOOPER

Kennedy, J.A. & Hooper, J.N.A. 2000 06 30: New species of toxic *Tedania* from Northern Vanuatu (Porifera: Demospongiae: Poecilosclerida: Tedaniidae). *Memoirs of the Queensland Museum* 45(2): 445-451. Brisbane. ISSN 0079-8835.

Tedania (Tedania) strongylostyla sp. nov. is described, compared with *T. ignis*, another toxic species from the Caribbean, and other *Tedania* species from tropical and subtropical Pacific waters. □ Porifera, Demospongiae, Poecilosclerida, Tedaniidae. *Tedania*, new species. Vanuatu. West Pacific, taxonomy, dermatitis, toxic sponge.

John A. Kennedy & John N.A. Hooper, Marine Biology Laboratory, Queensland Museum, South Brisbane 4101, Australia; 13 August, 1999.

Toxic reactions from handling marine sponges are well documented for species of *Neofibularia*, *Biemna*, *Lissodendoryx*, *Tedania*, and also recorded from some species of *Microclona* and *Haliclona* (see Wilkinson, 1978; Hooper, Capon & Hodder, 1991; Hooper, 1996; Rifkin, 1996). Of these toxic species, the most notorious is *Tedania ignis* (Duchassaing & Michelotti, 1864) from the Caribbean, earning it the name of 'fire sponges' (de Laubenfels, 1949). De Laubenfels (1949; 1954) reported that *T. ignis* was abundant in shallow-waters throughout the West Indies and compared its dermatitis effects to those of poison-ivy (*Rhus toxicodendron*), producing a 'somewhat painful, itching, burning feeling lasting for several days' (1949: 17).

Tedania ignis was described subsequently from Hawaii and Palau by de Laubenfels (1950, 1954), with some hesitation. Their identification of these Pacific specimens was influenced by its similarity of dermatitis reaction to that of *T. ignis*. Identification was provisional, and after considering their geographic isolation, de Laubenfels suggested that they should be recognised as *T. ignis* subspecies *pacificu*.

With the possible exception of a casual observation by Bergquist (reported in Southcott & Coulter, 1971), such dermatitis reactions have not been reported from any other species of *Tedania*. Bergquist informed Southcott & Coulter (1971) that she had received skin irritations from handling *Tedania* in New Zealand waters, but her observation was not accompanied by identification or description of the offending species.

Recent collection of a red sponge from Vanuatu produced a skin irritation similar to that described for *T. ignis*. Subsequent taxonomic identification confirmed it was a *Tedania*,

differing from its congeners in spiculation and skeletal structure. This paper describes the material as a new species, detailing differences between it and similar species from tropical and subtropical waters.

MATERIALS AND METHODS

Specimens were collected from the intertidal zone, preserved initially in 95% ethanol for four days, then transferred to 70% ethanol for permanent storage. Histological techniques for light and scanning electron microscopy (SEM) follow Hooper (1996). Spicule morphometric analysis was conducted using a light microscope and camera-lucida, with reference to a template drawn from a stage micrometer. Spicule measurements are based on 25 spicules of each spicule category for each individual, and pertain to maximum dimension, denoted as range (and mean) of length and width. Spicule measurements are in micrometres.

Abbreviations: ORSTOM, Institut Français de Recherche Scientifique pour le Développement en Coopération, Centre de Noumea; QM, Queensland Museum, Brisbane; ZMA, Zoölogische Museum, Universiteit van Amsterdam, Amsterdam.

SYSTEMATICS

PORIFERA Grant

DEMOSPONGIAE Sollas

POECILOSCLERIDA Topsent, 1928

TEDANIIDAE Ridley & Dendy, 1886

DEFINITION. Encrusting, massive or digitate sponges; choanosomal skeleton predominantly plumoreticulate or even plumose, composed of tracts of smooth or spined styles, or smooth axes, enclosed within light or moderate spongin fibres, or with no visible fibres and spicules

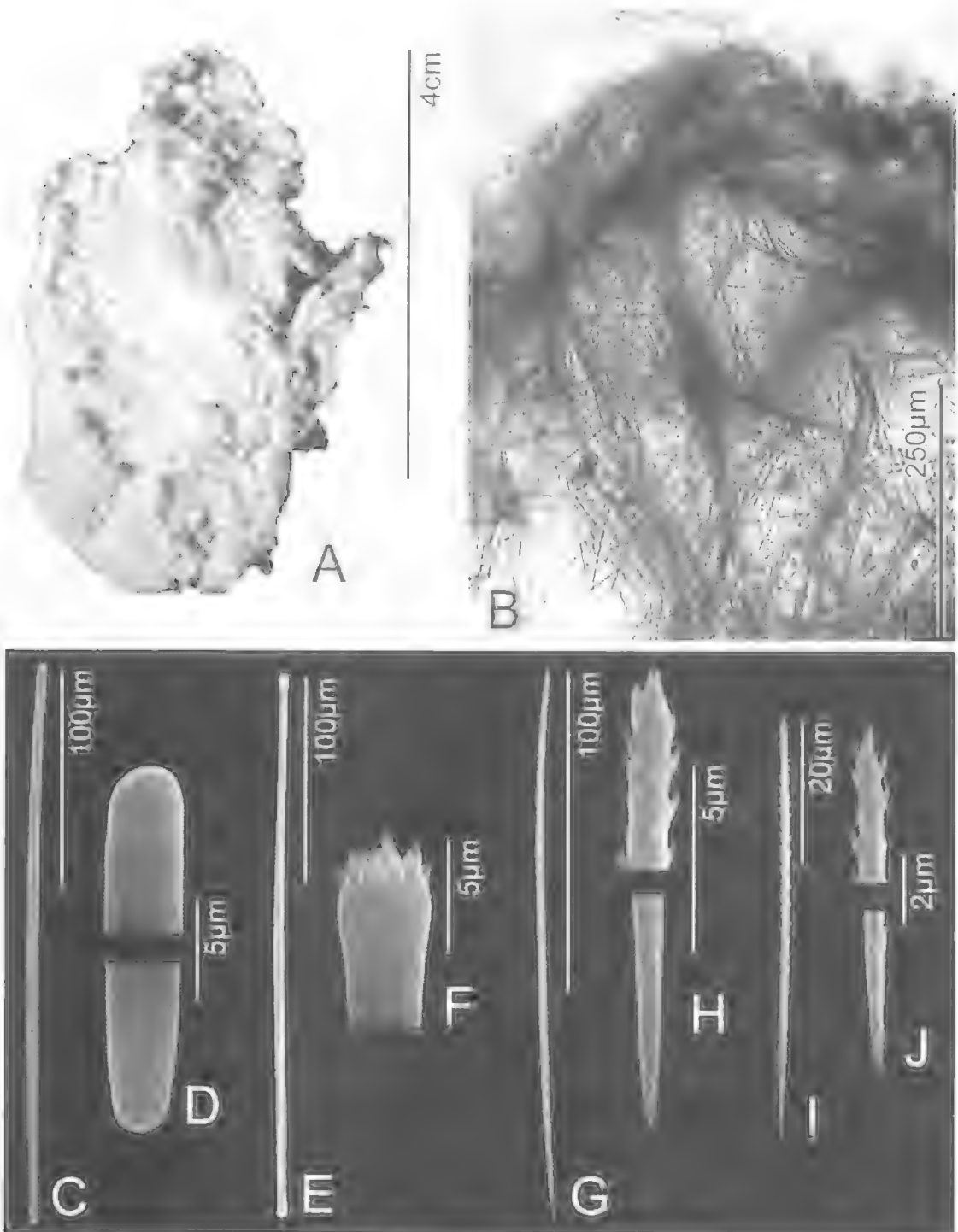


FIG. 1. *Tedania (Tedania) strongylostyla* sp. nov. (holotype QM G315594). A, Holotype. B, section through peripheral skeleton. C, strongylote style and D, terminations. E, tylote and F microspined base. G, larger onychaete and H, asymmetrical terminations. I, smaller onychaete and J, asymmetrical terminations.

merely cemented together with collagen at their nodes; ectosomal spicules are tylotes or tornotes, usually with basal spination, lying tangentially, paratangentially or erect on the surface, although usually not in bundles; microscleres are onychaetes; chelae absent (from Hooper & Wiedenmayer, 1994).

REMARKS. Discussions surrounding the family are well summarised in Hooper & Wiedenmayer (1994).

Tedania Gray, 1967

Tedania Gray, 1867: 520.

Trachytedania Ridley, 1881: 122 (type species *Trachytedania spinata* Ridley, 1881, by original designation).

Tedaniopsis Dendy, 1924: 366 (type species *Tedaniopsis turbinata* Dendy, 1924, by original designation).

Parantedania Burton, 1929: 441 (type species *Oceanapia tantula* Kirkpatrick, 1907, by original designation).

Oxytedania Sarà, 1978: 61 (type species *Oxytedania bifaria* Sarà, 1978, by original designation).

TYPE SPECIES. *Reniera digitata* Schmidt, 1862, by subsequent designation (see Koltun, 1959: 154).

DEFINITION. Massive; ectosomal skeleton composed of tylotes or tornotes with microspined bases forming tangential or paratangential surface tracts; choanosomal skeleton composed of styles with smooth or microspined bases, producing reticulate, plumo-reticulate, plumose or even dendritic architecture; microscleres are onychaetes (from Hooper, 1998).

REMARKS. The synonymy of *Tedania* follows Burton (1932), with the addition of *Oxytedania* Sarà, 1978 proposed by Desqueyroux-Faúndez & van Soest (1996) on the basis that the genus was unrecognisable, conditionally qualifying it as a junior synonym. Desqueyroux-Faúndez & van Soest (1996) further propose retaining *Tedania*, *Tedaniopsis* and *Trachytedania* as subgenera.

Subgenus **Tedania** Gray, 1867

DEFINITION. *Tedania* possessing smooth, relatively small, occasionally strongylote styles as structural megascleres, and microspined tylotes as ectosomal megascleres (from Desqueyroux-Faúndez & van Soest, 1996).

REMARKS. *Tedania* differs primarily from *Tedaniopsis* and *Trachytedania* in having tylote (rather than tornote) ectosomal megascleres.

Tedania (Tedania) strongylostyla sp. nov. (Fig. 1, Table 1)

ETYMOLOGY. *Strongylostyla*, for the strongylote-like ends of the styles which differentiate this species from its congeners.

MATERIAL. HOLOTYPE: QM G315594: inlet leading to Yeu Métenia Bay (Picot Bay), Hiu (North Island), Torres Islands, Vanuatu, 13°05.340'S, 166°33.061'E, inlet with rocky coralline substrate and moderately turbid water (about 20cm visibility), 0.3m depth, 22.vii.1999, coll. J.A. Kennedy.

COMPARATIVE MATERIAL. PARALECTOTYPE: ZMA POR.2373 *Thalysias ignis* Duchassaing & Michelotti, 1864 from St Thomas, Caribbean..

HABITAT DISTRIBUTION. Marine, less than 1m depth, on rocky coralline substrate and partially buried in surrounding sand, occurring in moderately turbid water; Torres Islands, Vanuatu.

DESCRIPTION. *Shape*. Thickly encrusting, amorphous mats, up to 16cm in greatest horizontal width and 2cm thick; loosely adhering to rocky coralline substrate and partially buried in sand, with surface barely protruding through substrate.

Colour. Bright orange-red externally (Munsell 10R 6/12), drab greenish-grey in the peripheral Choanosome (2.5GY 6/2), becoming lighter brownish-grey in deeper regions (2.5Y 7/2) when alive; ethanol preserved material has drab milky-orange exterior, grading toward beige deeper in the choanosome.

Oscules. Small, approximately 1mm diameter when alive, scattered indiscriminately over the surface, commonly apical on short conulose projections up to 4mm high and 8mm diameter, but also flush with surface; less obvious in preserved state.

Texture. Soft, spongy, compressible, easily torn.

Surface characteristics. Opaque, with approximately two-thirds of surface covered by sandy silt and fine algal filaments which extend into choanosome; lightly rugose, covered with small irregular ribs, lightly membranous over irregularly scattered, minute, subdermal depressions commonly about 1mm but up to 2mm wide.

Ectosome. Difficult to detach from choanosome; about 60-100µm thick; consisting of a tangential to paratangential layer of loose paucispicular — multispicular tracts of tylotes in wispy, dendritic-plumose arrangement, with abundant single tylotes and scattered onychaetes between

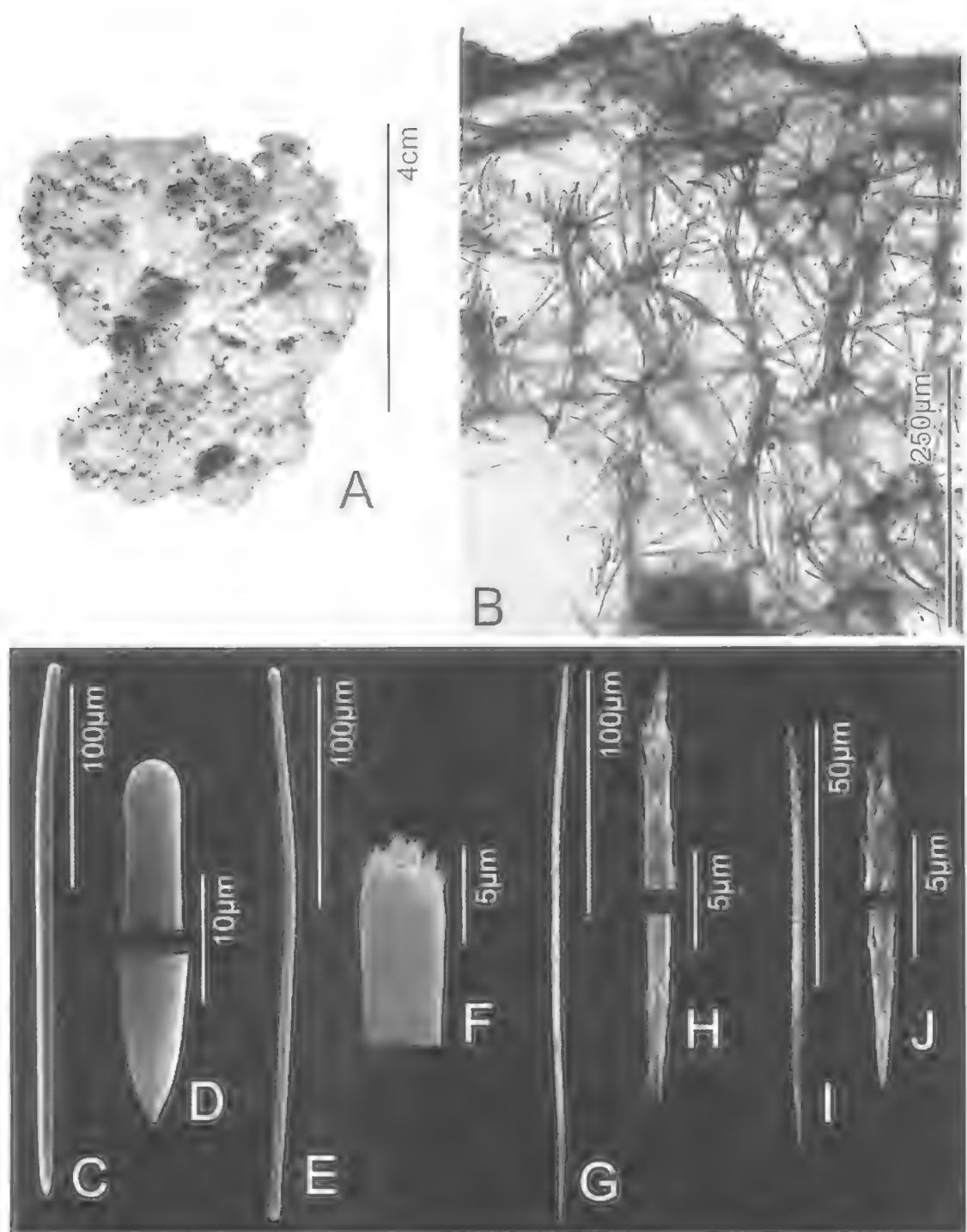


FIG. 2. *Tedania (Tedania) ignis* (Duchassaing & Michelotti, 1864). (paralectotype ZMA POR.2373). A, Paralectotype. B, section through peripheral skeleton. C, strongylote style and D, terminations. E, tylote and F, microspined base. G, larger onychaete and H, asymmetrical terminations. I, smaller onychaete and J, asymmetrical terminations.

tracts; ectosomal membrane appears very granular and contains fine detritus fragments.

Choanosome. Skeleton consists primarily of a vaguely ascending plumo-reticulate arrangement of paucispicular tracts composed mainly of strongylote styles and fewer tornotes, with abundant megascleres and microscleres scattered individually between tracts; mesohyl is granular, containing both fine and larger detritus fragments scattered throughout; fibres absent; bright orange-red larvae, about 500µm diameter, common in deeper choanosome.

Megascleres. Strongylote styles, thin, smooth, straight or very faintly curved, not tapering along entire length; with strongylote terminations that are lightly telescoped (210-(235)-304 × 2.5-(3.5)-5). Tylotes, smooth, straight, with oval, microspined apices (213-(228)-240 × 2-(3.5)-5).

Microscleres. Onychaetes, in two size classes, with abundant spination. Both larger (118-(185)-220 × 1-(1.2)-1.5) and smaller onychaetes (43-(55)-103 × 0.5-(0.7)-1) are asymmetrical/styloid due to microspination located one end.

REMARKS. *Tedania strongylostyla* sp. nov. is superficially similar to the Caribbean *T. ignis* (Duchassaing & Michelotti, 1864) in growth form, spicule dimensions (Table 1) and in producing a dermatitis reaction upon contact with skin. This similarity in their spicule dimensions is not surprising, since Lehnert & van Soest (1996: 69) state, '*Tedania* (*Tedania*) from tropical localities all over the world display similar spiculation, so that may not be a good species criterion'. Irrespective of these similarities, *T. strongylostyla* sp. nov. differs from *T. ignis* in having distinctly different style terminations and skeletal architecture.

Tedania ignis was redescribed comprehensively by van Soest (1984). It has an irregular renieroid choanosomal skeletal reticulation, whereas *Tedania strongylostyla* sp. nov. has a loose, vaguely ascending, plumo-reticulate choanosomal skeletal arrangement. Similarly, *T. strongylostyla* sp. nov. has distinctly strongylote styles compared with the unmodified styles of *T. ignis* (SEM examination of the paralectotype's spiculation is presented in Fig. 2 for comparison). Apart from the single record of strongylote modifications of styles observed in a single Jamaican deep-water specimen tentatively assigned to *T. (T.) cf. ignis* by Lehnert & van Soest (1996), differences in skeletal arrangement, spicule morphology and disjunct biogeographical

distributions support the recognition of *T. strongylostyla* sp. nov. as distinct from *T. ignis*.

Other species of *Tedania* from the tropical Pacific with two size classes of onychaetes include *T. dirhaphis* Hentschel, 1912, *T. galapagensis* Desqueyroux-Faúndez & van Soest, 1996 and *T. strongyla* Jinhe, 1986. The first two species differ significantly from *T. strongylostyla* sp. nov. in having styles of typical morphology and mesh-type choanosomal skeletal structure. *Tedania strongyla* Jinhe, 1986, described from Chinese waters (Jinhe, 1986) is similar to *T. strongylostyla* sp. nov. in its skeletal arrangement and in possessing choanosomal strongyles, but as observed for *T. ignis* these spicules clearly represent malformed styles and do not constitute the principal choanosomal spicule type. *Tedania brasiliensis* Mothes et al., 2000 from Brazil also has two size classes of onychaetes but differs from *T. strongylostyla* sp. nov. in having a subsodietyal choanosomal skeletal arrangement similar to that of *T. ignis*.

It is possible that other species of *Tedania* may also have two size classes of onychaetes, even though they were originally recorded as having only one. For example, a second category of onychaete was discovered by van Soest (1984) in *T. ignis*, and in several *Tedania* (*Trachytedania*) spp. by Desqueyroux-Faúndez & van Soest (1996).

The dermatitis reaction experienced by the primary author through contact with *T. strongylostyla* sp. nov. commenced as a mild itching sensation lasting for about five minutes, intensifying to severe itching, mild swelling and reddening of the skin lasting for three days, with subsequent skin loss experienced after one week. The extent of the reaction varied between collectors, ranging from only mild itching to more severe reactions as described above. Experimental application of an alcohol preserved specimen failed to produce any irritation.

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TABLE 1. Comparison between spicule dimensions of *Tedania* (*T.*) *strongylostyla*, *T. (T.) strongyla*, *T. (T.) ignis*, *T. (T.) brasiliensis*, *T. dirhaphis* and *T. (T.) galapagensis*. Measurements given in μm , denoted as range (and mean), L=length; W=width.

Species	Locality	Styles	Tylotes	Large onychaetes	Small onychaetes
<i>T. strongylostyla</i> sp. nov.	Northern Vanuatu, W. Pacific Ocean	Strongylote styles L. 210-(235)-304; W. 2.5-(3.5)-5	L. 213-(228)-240; W. 2-(3.5)-5	L. 118-(185)-220; W. 1-(1.2)-1.5	L. 43-(55)-103; W. 0.5-(0.7)-1
<i>T. strongyla</i> Jinhe, 1986	Gulf of Tonkin, South China Sea	Typical styles L. 190-310; W. 6-8. Strongylote styles L. 212-224; W. 6-8.	L. 201-218; W. 3-4	L. 126-182; W. 2-3	L. 50-62; W. 1
<i>T. ignis</i> (Duch. & Mich., 1864) (Paralectotype; van Soest, 1984)	Jamaica, Caribbean Sea	L. 220-240; W. 4-8	L. 210-225; W. 3	L. 180	L. 50
<i>T. ignis</i> (Duch. & Mich., 1864) (van Soest, 1984)	Caribbean Sea	L. 202-(248.8)-281; W. 4-(6.31)-9	L. 180-(217.1)-248; W. 2.5-(3.38)-4.5	L. 154-(211.1)-247; W. 0.5-(1.61)-2.5	L. 30-(64.0)-95; W. 0.5
<i>T. cf. ignis</i> (Duch. & Mich., 1864) (Lehnert & van Soest, 1996)	Jamaica, Caribbean Sea	L. 250-300; W. 9-11	L. 215-240; W. 3-4	L. 215-240; W. 3-5	L. 35-70; W. 1
<i>T. ignis pacifica</i> (Duch. & Mich., 1864) (de Laubenfels, 1954)	Hawaii, Central Pacific Ocean	L. 160-210; W. 6-8	L. 180-210; W. 3-4	L. up to at least 200; W. 1-2	
<i>T. ignis pacifica</i> (Duch. & Mich., 1864) (de Laubenfels, 1954)	Palau, W. Pacific Ocean	L. 225; W. 3.5	L. 245-260; W. 5-6	L. <215; W. <1	
<i>T. brasiliensis</i> Mothes et al., 2000	Chilean Coast, E. Pacific Ocean	Strongyles L. 151-228	L. 151-257	L. 95-200	L. 40-78
<i>T. dirhaphis</i> Hentschel, 1912	Arafura Sea	L. 218-312	L. 224-248	L. 200-312	L. 40-112
<i>T. galapagensis</i> Desqueyroux-Faúndez & van Soest, 1996	Galapagos, E. Pacific Ocean	L. 192-246; W. 6-7	L. 179-234; W. 3-4	L. 173-205; W. 2	L. 61-93; W. 0.5-1

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RESOLVING THE 'JASPIS STELLIFERA' COMPLEX

JOHN A. KENNEDY

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Five species included in synonymy with *Jaspis stellifera* (Carter, 1879) (Coppatiidae) by authors were re-evaluated from type material for the first time since originally described. Original descriptions were found to be mostly incomplete, with subsequent synonymies excessive. Only two (*Stellettinopsis coriacea* Carter, 1886 and *Stellettinopsis purpurea* Carter, 1886) are retained in synonymy with *J. stellifera*. *Stellettinopsis carteri* Ridley, 1884 is synonymised with *Rhabdastrella globostellata* (Carter, 1883) (Ancorinidae). *Stellettinopsis lutea* Carter, 1886 is retained in *Jaspis* and *S. tuberculata* Carter, 1886 is referred to *Stelletta*, both reinstated as valid species. Two new species (*Asteropus radiocrusta*, *Jaspis cristacorrugatus*) were described from one misidentified syntype of *S. tuberculata* Carter, 1886 and other new material superficially resembling '*J. stellifera*' of authors. Tropical and subtropical specimens of '*J. stellifera*', comprising much of the material described in the marine natural products literature, were found to have been misidentified specimens of *R. globostellata*, apparently lacking triaenes. With the exception of *R. globostellata*, which has a distribution throughout much of tropical and subtropical Indo-Pacific, species were found to have restricted distributions in Victorian and Tasmanian waters. □ *Porifera*, *Demospongiae*, *Coppatiidae*, *Ancorinidae*, *Jaspis stellifera*, taxonomy, new species, revision, Australia.

John A. Kennedy, Queensland Museum, South Brisbane 4101, Australia (e-mail: JohnK@qm.qld.gov.au); 20 October, 1999.

The name '*Jaspis stellifera*' (Carter, 1879) is widely cited in the marine natural products chemistry and other biological literature (e.g. Ravi et al., 1981; Ravi & Wells, 1982; McCaffrey & Endean, 1985; Fuerst et al., 1999; Wilkinson et al., 1999). This species has an alleged distribution throughout the tropical West Pacific region, also reportedly occurring along Australia's NE and S coasts, extending into Victoria and Tasmania (Hooper & Wiedenmayer, 1994). Chemical investigations of various populations of '*Jaspis stellifera*' discovered two molecule types: cyclic peptides and malabaricane-type triterpenes (van Soest & Braekman, 1999). However, van Soest & Braekman (1999) concur with Fusetani & Matsunaga (1993) that cyclic peptides are most probably products of various microsymbionts, since similar compounds have been isolated from many orders of Demospongiae, cyanobacteria and ascidians. Conversely, malabaricane-type triterpenes have been reported from specimens of '*J. stellifera*' from Fiji and the Great Barrier Reef (Ravi et al., 1981; Ravi & Wells, 1982), and are suggested as good markers for *Stelletta* s.l. (including closely related *Rhabdastrella*) (van Soest & Braekman, 1999). Consequently, van Soest & Braekman (1999) proposed that specimens of '*J. stellifera*'

containing malabaricane triterpenes belong to *Stelletta*, lacking triaenes, and not to *Jaspis*.

Jaspis stellifera was erected by Carter (1879), as *Amorphina stellifera*, for material from Tasmania. Within the following decade, several morphologically similar species were described from Australia, including *Stellettinopsis lutea* Carter, 1886b, *S. tuberculata* Carter, 1886a, *S. coriacea* Carter, 1886a and *S. purpurea* Carter, 1886b, from Victoria, and *S. carteri* Ridley, 1884, from Torres Strait, N Queensland. Shaw (1927), under the direct supervision of Maurice Burton of the BMNH, synonymised all these species into *Jaspis stellifera*. Subsequently, '*J. stellifera*' was described from the Low Isles (Burton, 1934) and Heron Island (Bergquist, 1969) on the Great Barrier Reef, apparently filling the gap in distribution between Victoria in the south and Torres Strait in the north. In Bergquist's (1969) remarks, however, she disputed Shaw's (1927) inclusion of *S. coriacea* and *S. purpurea* in the synonymy of *Jaspis stellifera*, based on two inconsistencies in the published data, both of which are demonstrated here to be invalid or unsupported (see remarks for *J. stellifera*, below). Nevertheless, Bergquist's (1969) revised synonymy for *J. stellifera* was subsequently adopted by Wiedenmayer (1989), who examined whole type specimens only superficially, and this



FIG. 1. Known distributions of species described in this paper. 1 = *Jaspis stellifera*; 2 = *Jaspis lutea*; 3 = *Jaspis cristacorrugatus*; 4 = *Asteropus radiocrusta*; 5 = *Stelletta tuberculata*; 6 = *Rhabdastrella globostellata*.

decision was perpetuated in the Porifera volume of the Zoological Catalogue of Australia (Hooper & Wiedenmayer, 1994).

In light of the probable widespread misidentifications of tropical West Pacific specimens of '*J. stellifera*', it is appropriate to re-evaluate this species complex, to produce a better informed synonymy and a revised distribution of species within this complex. Thus it was necessary to redescribe comprehensively all type material, given that most original descriptions of nominal species were incomplete, illustrated poorly and, as discovered here, often incorrect. This paper re-evaluates all *Jaspis* species described previously from Australia, since they are all contained in the '*J. stellifera*' complex, re-examining key voucher material and relevant type specimens, and providing a revision of species and their corresponding distributions.

MATERIALS AND METHODS

Histological techniques for light microscopy and scanning electron microscopy (SEM) follow Hooper (1996).

Morphometric analysis of spicules was conducted using a light microscope and camera-lucida, with reference to a template drawn from a stage micrometer. At least 25 spicules of each spicule category were measured in all specimens (except where noted). Measurements refer to length and width of monactinal spicules, rhabd length and clad length of tetractinal spicules, and diameter of astrose microscleres. Measurements refer to maximum dimensions of each spicule,

denoted as size-range (and mean in parentheses) for each spicule type. All measurements are given in micrometres unless stated otherwise. Centrum percentages for each aster type were also noted.

Conventional morphological terms follow Boury-Esnault & Rützler (1997).

Abbreviations. AIMS, Australian Institute of Marine Science, Townsville; BMNH, The Natural History Museum, London; LMJG, Abteilung für Zoologie am Landes-museum Joanneum (Landes Museum Jubileum Graz), Graz; NTM, Northern Territory Museum of Arts and Sciences, Darwin; GBR, Great Barrier Reef, Queensland; NCI OCDN-, United States National Cancer Institute, Coral Reef Research Foundation shallow water collection contract, Chuuk State & Republic of Palau, (1992-present); NCI Q66C-, United States National Cancer Institute, Australian Institute of Science shallow water collection contract (1984-91); ORSTOM, Institut Français de Recherche Scientifique pour le Développement en Coopération, Centre de Noumea; QM, Queensland Museum, Brisbane.

RESULTS

Changes to the synonymy of *Jaspis stellifera*, extending from the work of Shaw (1927) to Bergquist (1969) and the present study, are presented in Table 1. These data propose major changes to species groupings within the '*J. stellifera*' complex. Figure 1 summarises the revised known distributions for species included in this complex.

TABLE 1. Changing taxonomic status of the '*Jaspis stellifera*' complex. Bold type = species considered valid; species in parentheses are considered synonyms of the valid species preceding; ¹ = originally syntype, for *Stellettinopsis tuberculata* (Carter); ² = identified by Bergquist (1969) as *Jaspis stellifera* from Heron Island, Great Barrier Reef; ³ = included to avoid possible confusion with *Jaspis lutea*.

1879-1886 (6 species): <i>Amorphina stellifera</i> Carter, 1879; <i>Stellettinopsis coriacea</i> Carter, 1886a; <i>Stellettinopsis purpurea</i> Carter, 1886b; <i>Stellettinopsis lutea</i> Carter, 1886b; <i>Stellettinopsis carteri</i> Ridley, 1884; <i>Stellettinopsis tuberculata</i> Carter, 1886a
Shaw (1927) (1 species): <i>Jaspis stellifera</i> (syn. <i>Jaspis coriacea</i> , <i>Jaspis purpurea</i> , <i>Jaspis lutea</i> , <i>Jaspis carteri</i> , <i>Jaspis tuberculata</i>)
Bergquist (1969) (3 species): <i>Jaspis stellifera</i> (syn. <i>Jaspis lutea</i> , <i>Jaspis carteri</i> , <i>Jaspis tuberculata</i>); <i>Jaspis coriacea</i> ; <i>Jaspis purpurea</i>
Current assignment (7 species): <i>Jaspis stellifera</i> (syn. <i>Jaspis coriacea</i> , <i>Jaspis purpurea</i>); <i>Jaspis lutea</i> ; <i>Stelletta tuberculata</i> ; <i>Asteropus radiocrusta</i> sp. nov. ² ; <i>Crella</i> sp. ² ; <i>Rhudadrella globostellata</i> ¹ (syn. <i>Jaspis carteri</i>); <i>Jaspis cristacorrugatus</i> sp. nov. ³

SYSTEMATICS

PORIFERA Grant

DEMOSPONGIAE Sollas

TETRACTINOMORPHA Lévi

ASTROPHORIDA Lévi, 1973

COPPATIIDAE Topsent, 1898

DEFINITION. Encrusting to massive growth forms; megascleres only oxeas forming a confused, vaguely radial choanosomal skeleton; megascleres also form a tangential layer in ectosome; triaenes absent; microscleres euasters (never sterrasters), sometimes sanidasters (modified from Hooper & Wiedenmayer, 1994).

REMARKS. A summary of synonymies and discussion of the family are provided by Hooper & Wiedenmayer (1994). Hajdu & van Soest (1992) suggested that the absence of triaenes is a suspect diagnostic character for the family and proposed that the concept of Coppatiidae be retained provisionally, pending more detailed re-evaluation of its probable polyphyletic nature.

Jaspis Gray, 1867

Coppatias Sollas, 1888: 206 (Type species: *Stellettinopsis coriacea* Carter, 1886, by original designation).

Astropeplus Sollas, 1888: 416, 422 (Type species: *Astropeplus pulcher* Sollas, 1888, by monotypy)

TYPE SPECIES. *Voa johnstonii* Schmidt, 1862: 78, by monotypy.

DEFINITION. Coppatiidae with euasters as microscleres.

REMARKS. Lendenfeld (1896) demonstrated that *Astropeplus pulcher* Sollas, 1888 (type species of *Astropeplus*) was synonymous with *Voa johnstonii* Schmidt, 1862 (type species of *Jaspis*), but mistakenly placed it in *Xenospongia* Gray, 1858 (family Tethyidae). In recognising this, Topsent (1898) relegated *V. johnstonii* to

Coppatias Sollas, 1888, rejected Gray's generic name *Jaspis* on the basis that it was of no scientific value, and then later reinstating *Jaspis* as a valid genus (Topsent, 1904). In ratifying this later decision, Dendy (1916) again synonymised *Coppatias* with *Jaspis*, the senior name.

Hajdu & van Soest (1992) questioned whether or not *Jaspis* constituted a monophyletic assemblage, since two species groups were recognisable based on the presence or absence of 'microxeas'. However, this is not accepted here as these 'microxeas' are considered to be a smaller category of oxeote megascleres. The existence of graded oxeote size-distributions with intermediate size categories often presents difficulties in differentiating between smaller ('microxeas') and larger oxeotes. Hence, the present concept of *Jaspis* retains both assemblages, although it is acknowledged that further work is required to reconcile the taxonomic significance of smaller oxeotes.

Jaspis stellifera (Carter, 1879)

(Figs 1, 2, Table 2)

Amorphina stellifera Carter, 1879: 344

Stellettinopsis stellifera; Ridley, 1884: 477.

Coppatias stellifera; Sollas, 1888: 208.

Jaspis stellifera; Shaw, 1927: 422.

not *Jaspis stellifera*; Burton, 1934: 522.

Stellettinopsis coriacea Carter, 1886a: 126.

Coppatias coriaceus; Sollas, 1888: 207.

Jaspis coriacea; Hooper & Wiedenmayer, 1994: 143.

Stellettinopsis purpurea Carter, 1886b: 459.

Coppatias purpureus; Sollas, 1888: 207.

Jaspis purpurea; Hooper & Wiedenmayer, 1994: 143.

MATERIAL. HOLOTYPE: BMNH1869.1.22.25 (dry): Tasmania (also marked with Carter no 315.E.J.19). Holotype of *Stellettinopsis coriacea* Carter, 1886a BMNH1886.12.15.441 (dry): Port Phillip Heads, Victoria. Holotype of *Stellettinopsis purpurea* Carter, 1886b BMNH1886.12.15.51 (wet): Westport Bay, Victoria. **OTHER MATERIAL:** BMNH unregistered (second specimen in same container as holotype and also marked

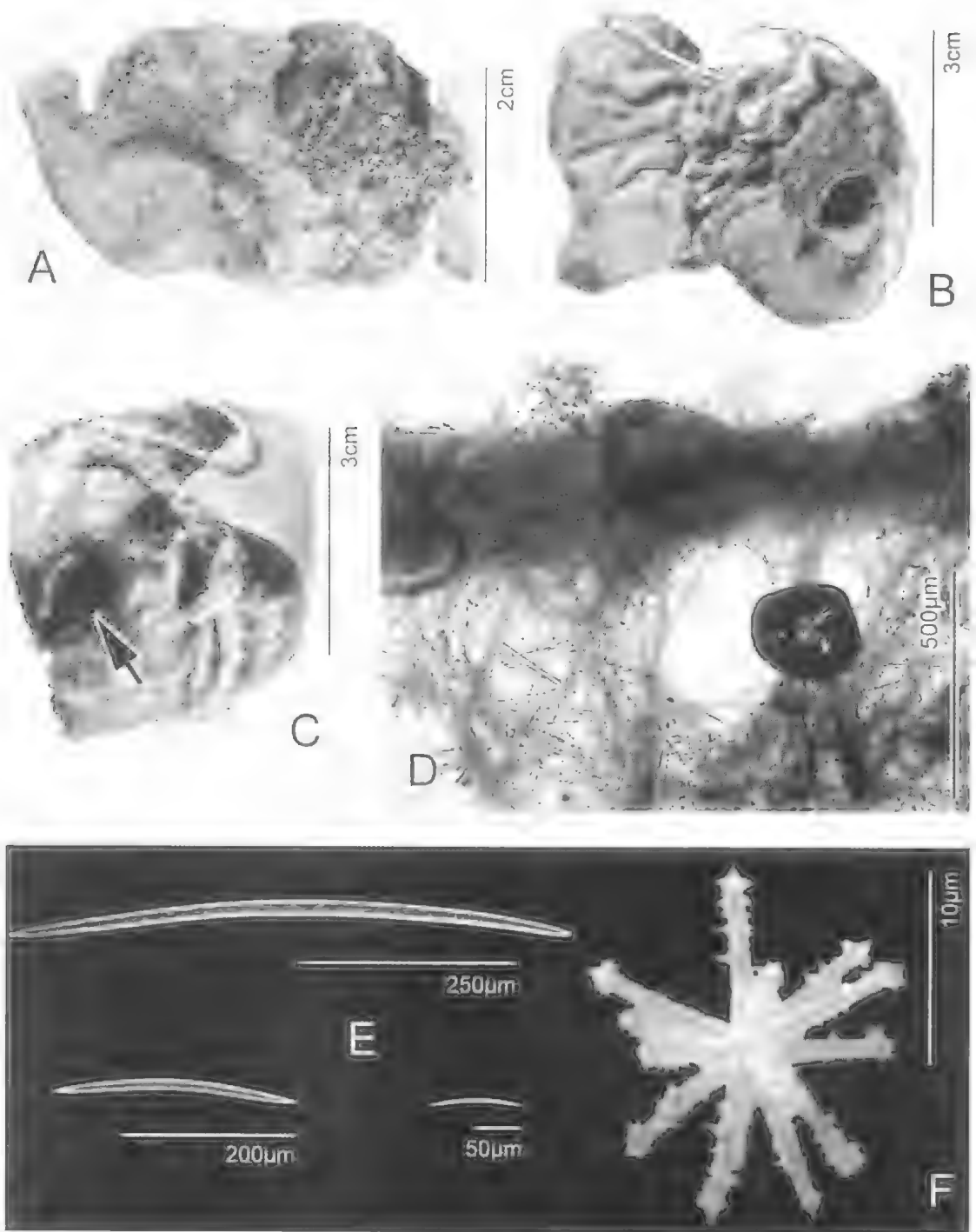


FIG. 2. *Jaspis stellifera* (Carter, 1879) (holotype BMNH1869.1.22.25). A, holotype; B, holotype of *S. coriacea* BMNH1886.12.15.44; C, holotype of *S. purpurea* BMNH1886.12.15.51 (arrow indicates position of oscule); D, section through peripheral skeleton; E, oxeas; F, oxyaster.

TABLE 2. Comparison between present and published descriptions of *Jaspis stellifera*. Measurements in μm , denoted as range (and mean) (N=25). L = length; W = width; D = diameter.

	Oxeas	Oxyasters
Holotype BMNH1869.1.22.25	L 113-(388)-726 W 3-(12)-16	D 11-(15)-22
Holotype (Original description Carter, 1879)	L 725; W 17	D 17
BMNH unregistered Bowerbank collection Carter no. 315,E,h,19	L 120-(354)-730 W 3-(10)-16	D 7-(12)-16
BMNH1886.12.15.441 holotype of <i>J. coriacea</i>	L 62-(265)-898 W 2-(8)-21	D 7-(11)-13
BMNH1886.12.15.51 holotype of <i>J. purpurea</i>	L 53-(347)-781 W 3-(10)-18	D 7-(10)-12
NMV F5193 (Wiedenmayer, 1989)	L 89-(364.8)-682.8 W 2-(9)-18	D 8-(12)-15

with Carter no. 315.E.h.19) (dry): South Australia, 1859, J.S. Bowerbank collection. COMPARATIVE MATERIAL: Holotype of *Vioa johnstonii* Schmidt, 1862 LMJG 15648/0 Sebenico, Adriatic Sea. Syntype of *V. johnstonii* var. Schmidt, 1868 LMJG 15256/0: Sebenico, Adriatic Sea.

HABITAT DISTRIBUTION. Subtidal to 37m depth, amidst dense algal growth; Westernport Bay and Port Phillip Heads, Victoria; Erith Island, Bass Strait; Tasmania.

DIAGNOSIS. Irregularly lobate-massive; dull pinkish purple-brown alive; surface optically smooth, even, unornamented; ectosomal skeleton consisting of a densely packed tangential arrangement of oxeas largely obscuring microscleres; choanosomal skeleton of singular and loose bundles of oxeas in confused arrangement, with scattered oxyasters; oxeas in wide size-range (length 53-(339)-898, width 2-(11)-21), microspined oxyasters (diameter 7-(12)-22).

DESCRIPTION. *Shape.* Holotype massive, amorphous, irregularly lobate, may envelop other materials such as algae, shells or detritus. Height 4.7cm, width 2.6 \times 2.5cm. Other specimens up to 5.5 \times 4.5 \times 3.5cm.

Colour. Fresh specimens described as dull-purple to brownish-drab (5RP 5/6-8) (Wiedenmayer, 1989); dry holotype creamy-white (Munsell 2.5Y 8/3) with dark-pink (2.5R 5/4) diffuse patches scattered over surface, with greyish-beige (7.5YR 8/2) choanosome; ethanol preserved specimen dark greyish-purple (5RP 3/2) throughout.

Oscules. Not visible in dry holotype but Carter (1879) describes 'vents in pit-like depressions'; one incomplete specimen (BMNH1886.12.15.51) has a single apical depression approximately 4mm

deep and 11mm in greatest width, containing several oscules up to 3mm diameter.

Texture. Firm, compressible, leathery.

Surface characteristics. Opaque, optically smooth, even, unornamented.

Ectosome. Thin, approximately 400-700 thick; skeleton composed of oxeas in confused arrangement, with oxyasters scattered throughout but largely obscured, and with clumped pinkish-purple pigment cells scattered over surface.

Choanosome. Permeated by canals approximately 0.15-1.10mm diameter, with smallest canals near periphery; skeleton comprised of loose, multispicular bundles of oxeas in confused arrangement, with abundant scattered oxeas and oxyasters; mesohyl contains clumps of scattered, dark-pinkish pigment bodies approximately 2-8 diameter, and spherical translucent and transparent bodies.

Megascleres. (Refer to Table 2 for spicule dimensions) Oxeas in one wide size-range, typically curved over their entire length; variations rare but include straight, lightly flexuous, singly and doubly bent, and styloid forms.

Microscleres. (Refer to Table 2 for spicule dimensions) Oxyasters with approximately 10-20 fine, lightly tapering rays with recurved microspines on distal two-thirds of rays, centrum approximately 13% of spicule diameter; variations rare, but include vestigial spination over full ray length, to exaggerated clumping of microspines on distal portion of ray, thus vaguely resembling tylote terminations.

REMARKS. The BMNH specimen box containing the holotype includes two specimens. Only one specimen is pierced by a tag bearing the registration number BMNH69.1.22.25, along with the locality 'Van Diemen's Land' (Tasmania). The other specimen is from the J.S. Bowerbank collection and comes from 'Southern Australia'. Carter gave both specimens his number '315, E, h, 19'. While both specimens are confirmed here to belong to *J. stellifera*, only the specimen bearing the BMNH tag is taken here to be the holotype.

Little information is added here to the original description except for some detail regarding spiculation. As previously noted by Wiedenmayer (1989), the oxeas have a wide size-range, with little concordance between length and width. While smaller oxeas are relatively abundant, the presence of many intermediate sizes precludes recognising more than one variable size-class of

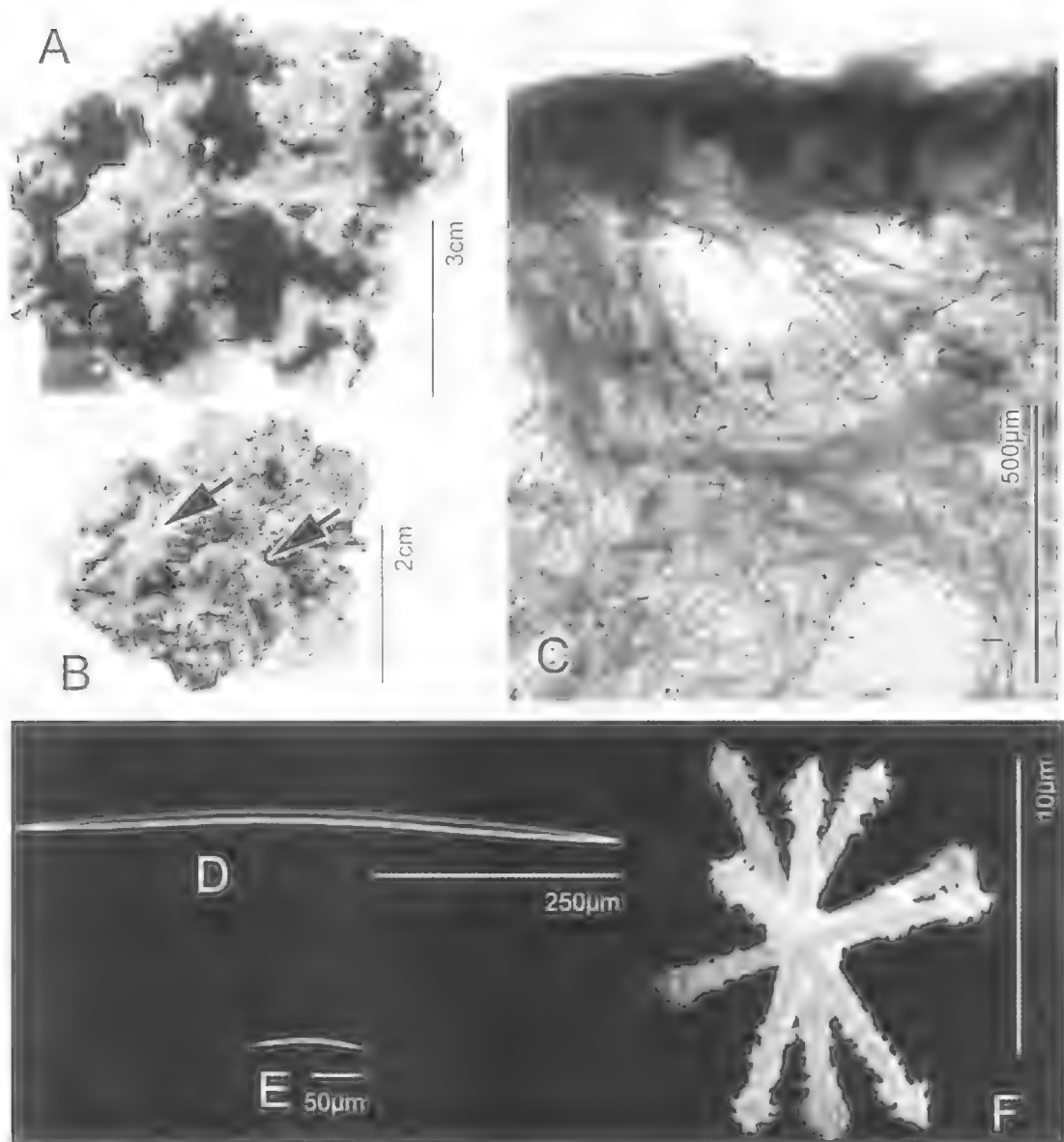


FIG. 3. *Jaspis lutea* (Carter, 1886) (lectotype BMNH1886.12.15.356). A, lectotype; B, paralectotype BMNH1886.12.15.93 (arrows indicate position of specimen on substrate); C, section through peripheral skeleton; D, large oxea; E, small oxea; F, oxyaster.

oxeas. SEM examination revealed that microspination of the oxyaster rays is commonly recurved toward the centrum. Spicule measurements undertaken here confirmed Wiedenmayer's (1989) suspicion that Carter provided only the measurements for the largest spicules, ignoring the range of spicule sizes actually present.

Stellettinopsis coriacea Carter, 1886a and *S. purpurea* Carter, 1886b are retained here in

synonymy with *J. stellifera* (Carter, 1879), based on re-examination of all type specimens, revealing that they are morphologically identical in virtually all respects. This partially ratifies Shaw's (1927) synonymy for *J. stellifera*, and contrasts to Bergquist's (1969) revised synonymy. While Shaw's synonymy was excessive, Bergquist's difficulty in accepting the inclusion of *S. coriacea* and *S. purpurea* was based on two

supposed inconsistencies in the published data, both of which are invalid. Firstly, Bergquist noted that Shaw's specimen reportedly did not have asters; secondly, she stated that '*Jaspis coriacea* and *J. purpurea* have two distinct categories of asters, a feature never noted in *J. stellifera*'. In this debate, it is unimportant whether or not Shaw's specimen had asters because it was not the type. Carter's (1879) original description of the holotype clearly described only one category of aster, confirmed here from re-examination of type material. Bergquist's (1969) second point of dispute is also unsupported since original descriptions of *S. coriacea* and *S. purpurea* also include only one category of aster, rather than two, also confirmed from re-examination of type material.

Original descriptions of *S. coriacea* and *S. purpurea* report the presence of 'microxeas', whereas re-examination of type material revealed that, as described above, these microxeas represent only smaller examples of a wide size-range of oxeas, with many intermediate sizes.

Comparison between *J. stellifera* and the type species of *Jaspis* (*Vioa johnstonii* Schmidt, 1862), including both type material and published descriptions (Dendy, 1916; Burton & Rao, 1932) confirms that *J. stellifera* is a true *Jaspis*. Both *J. johnstonii* and *J. stellifera* have a tangential ectosome composed of oxeote spicules and a choanosome containing oxeotes in confused and vaguely radial arrangement. Euasters are oxyasters, some with rays that are minutely microspined (a feature not described previously for the type species). *Jaspis johnstonii* differs in having a bimodal size distribution of oxeas (with the larger size-class primarily restricted to the choanosome), whereas *J. stellifera* has a wide, unimodal size-distribution. Irrespective, both clearly belong to the present concept of *Jaspis*, with the issue of unimodal versus bimodal oxeote size distributions remaining unresolved.

Examination of a slide of Burton's (1934) specimen (BMNH1930.8.13.86) identified as '*Jaspis stellifera*' from the Low Isles, GBR, revealed that it too had been misidentified (Hooper et al., 1999; present study). Burton's specimen clearly differs from *J. stellifera* in lacking a distinct ectosome and in having two categories of asters, one being slightly bipolar and resembling diplastets or short spirasters. Gross morphological differences cannot be commented on here since only a slide was available for examination, and Burton did not publish any

descriptive detail regarding the specimen. It may well represent a new species, since it does not correspond to any *Jaspis* species described previously from Australian waters.

Wiedenmayer's (1989) description of a specimen of *J. stellifera* from southern Australia included only superficial comparison of his material with various type specimens (*Amorphitua stellifera*, *Stellettinopsis tuberculata* and *S. lutea*). Because of circumstances preventing him from examining slides of these types, he was unable to reveal the distinctive nature of each of these species. This is discussed further below.

Jaspis lutea (Carter, 1886) (Figs 1, 3, Table 3)

Stellettinopsis lutea Carter, 1886b: 459
Coppattus luteus; Sollas, 1888: 207.

MATERIAL. LECTOTYPE: BMNH1886.12.15.356 (wet); Westernport Bay, Victoria, coll. J.B. Wilson, PARALLECTOTYPE: BMNH1886.12.15.93 (dry); Westernport Bay, Victoria, coll. J.B. Wilson, OTHER MATERIAL: BMNH1954.2.12.256 (slide of type prepared by A. Dendy).

HABITAT DISTRIBUTION. Subtidal to 13m depth; Westernport Bay, Victoria.

DIAGNOSIS. Lobate-massive, agglomerating substrate fragments; surface lobate, tuberculate; ectosome distinct, comprising a fine layer of small oxeas overlaying tangentially-arranged larger oxeas; choanosomal skeleton primarily a confused arrangement of oxeas; oxeas in two size classes (larger oxeas length 180-(516)-712, width 6-(12)-19; smaller oxeas length 52-(81)-110, width 1-(3)-5), microspined oxyasters (diameter 8-(13)-18).

DESCRIPTION. *Shape*. Irregularly lobate, agglomerating calcareous substrates, sand and shell fragments. Types incomplete, with largest portion 8cm high, 12 × 8cm wide.

Colour. Live colouration unknown; wet lectotype has tan-brown surface (Munsell 2.5Y 5-7/6) with golden-brown choanosome (2.5Y 7/8); dry paralectotype has dull-creamy yellow surface (2.5Y 6-7/4) with dull golden-yellow choanosome (2.5Y 7/8).

Oxentes. Numerous, approximately 0.5-8.2mm diameter, flush with, and regularly distributed over surface.

Texture. Firm, slightly friable, leathery.

Surface characteristics. Opaque, membranous, optically smooth, uneven, with clusters of lobate tubercles irregularly distributed over surface.

TABLE 3. Comparison between syntypes and published descriptions of *Jaspis lutea*. Measurements in μm , denoted as range (and mean) ($N=25$). L = length; W = width; D = diameter; * Spicule dimensions not included in Carter's (1886b) original description, but included by Sollus (1888).

	Large oxea	Small oxea	Oxyasters
Ecotype BMNH 1886.12.15.356-360	L 228-(535)-670 W 3-(11)-27	L 52-(83)-110 W 3-(5)-5	D 8-(13)-16
Present type BMNH 1886.12.15.93-97	L 180-(496)-712 W 5-(11)-16	60-(70)-110 W 2-(3)-5	D 6-(13)-18
Reinst. description (Sollus, 1888)	60-110, W 3-5	Not described	D 8

Ectosome. Distinct from choanosome, approximately 400-600 thick; skeleton highly spiculose, densely packed, comprised of two layers; outer layer largely indistinct, very fine, approximately 50 thick, with small oxeas in confused arrangement; inner layer comprised of a tangential arrangement of both large and small oxeas; aquiferous canals, approximately 200 diameter, regularly traverse ectosome; oxyasters present but largely obscured by megascleres.

Choanosome. Permeated by large canals up to 11mm diameter; skeleton composed of a confused arrangement of single small and large oxeas, as well as large oxeas in loose paucispicular to multispicular bundles; oxyasters scattered throughout the choanosomal skeleton but slightly more abundant in canal linings.

Megascleres. (Refer to Table 3 for spicule dimensions) Oxeas, in distinctly bimodal size-distribution. Larger oxeas slightly curved over entire length, with very faintly telescoped points and occasionally with a few terminal microspines; variations rare but include styloid modifications.

Smaller oxeas, angular, with 1-2 bends and hastate terminations.

Microscleres. (Refer to Table 3 for spicule dimensions) Oxyasters, with 6-12 lightly tapering rays that have conical to recurved microspines on distal two-thirds; centrum approximately 15% of spicule diameter.

REMARKS. *Jaspis lutea* is reinstated as a valid species of *Jaspis*, distinct from *J. stellifera* in several important respects. There are important differences in spiculation, with *J. lutea* having two size classes of oxeas in a distinctly bimodal size-distribution (cf. *J. stellifera* having a unimodal, wide size-range of oxeate spicules). Skeletal differences include *J. lutea* having a more localised distribution of smaller oxeas, primarily in a distinct ectosome (cf. no such localisation of oxeate spicule types, and with a far

less prominent ectosome). There are also differences in colour and external morphology, with *J. lutea* being golden yellow-brown and having a lobate-tuberculate growth form (cf. dull pinkish-purple-brown with an unornamented, irregularly lobate-massive shape).

Important information provided here, adding to Carter's (1886b) original description, includes the description of a second size-class of oxea (perhaps previously dismissed as merely smaller examples of a presumed unimodal size-distribution of oxeate spicules), the provision of spicule dimensions, and details of microspination on oxyaster rays.

***Jaspis cristacorrugatus* sp. nov.**
(Figs 1, 4, 8A,B, Table 4)

ETYMOLOGY. Latin *crista*, ridge; Latin *corrugatus*, wrinkled; for the corrugated oscular ridge.

MATERIAL, HOLOTYPE: QMG312071 (NCI Q66C5149-N): W side of channel, in middle of Breaksea Island, Port Davey, Tasmania, Australia, 43°19.70'S, 145°57.60'E, exposed rock slope, boulders, walls, gullies, kelp, 10m depth, 17.ii.1991, coll. AIMS/NCI. **PARATYPE:** QMG312073 (NCI Q66C-5151-P): S end of Breaksea Island, Port Davey, Tasmania, Australia, 43°20.20'S, 147°57.80'E, rocky slope to flat rocky bottom with many crevices and caves, 15m depth, 17.ii.1991, coll. AIMS/NCI.

HABITAT DISTRIBUTION. 10-15m depth, on rocky substrate with walls, gullies and outcrops; Port Davey, Tasmania.

DIAGNOSIS. Massive, subspherical to slightly lobate; leathery, firm; slate-grey alive; dark-brown to golden out of water; tan-brown in ethanol; slightly rugose surface; many small oscules in furrows between corrugations on wide oscular ridge; distinct ectosome, primarily of densely packed smaller oxeas; choanosome riddled with canals, and skeleton of single and paucispicular bundles of large oxeas in confused to loosely plumose reticulation vaguely ascending toward surface, with scattered smaller oxeas and oxyasters between tracts; oxeas in two size classes (larger oxeas length 290-(453)-629, width 2-(9)-15); smaller oxeas length 80-(133)-267, width 3-(5)-12); microspined oxyasters (diameter 6-(13)-21).

DESCRIPTION. *Shape.* Preserved specimen incomplete but when living was massive, subspherical, slightly lobate, with a thick,

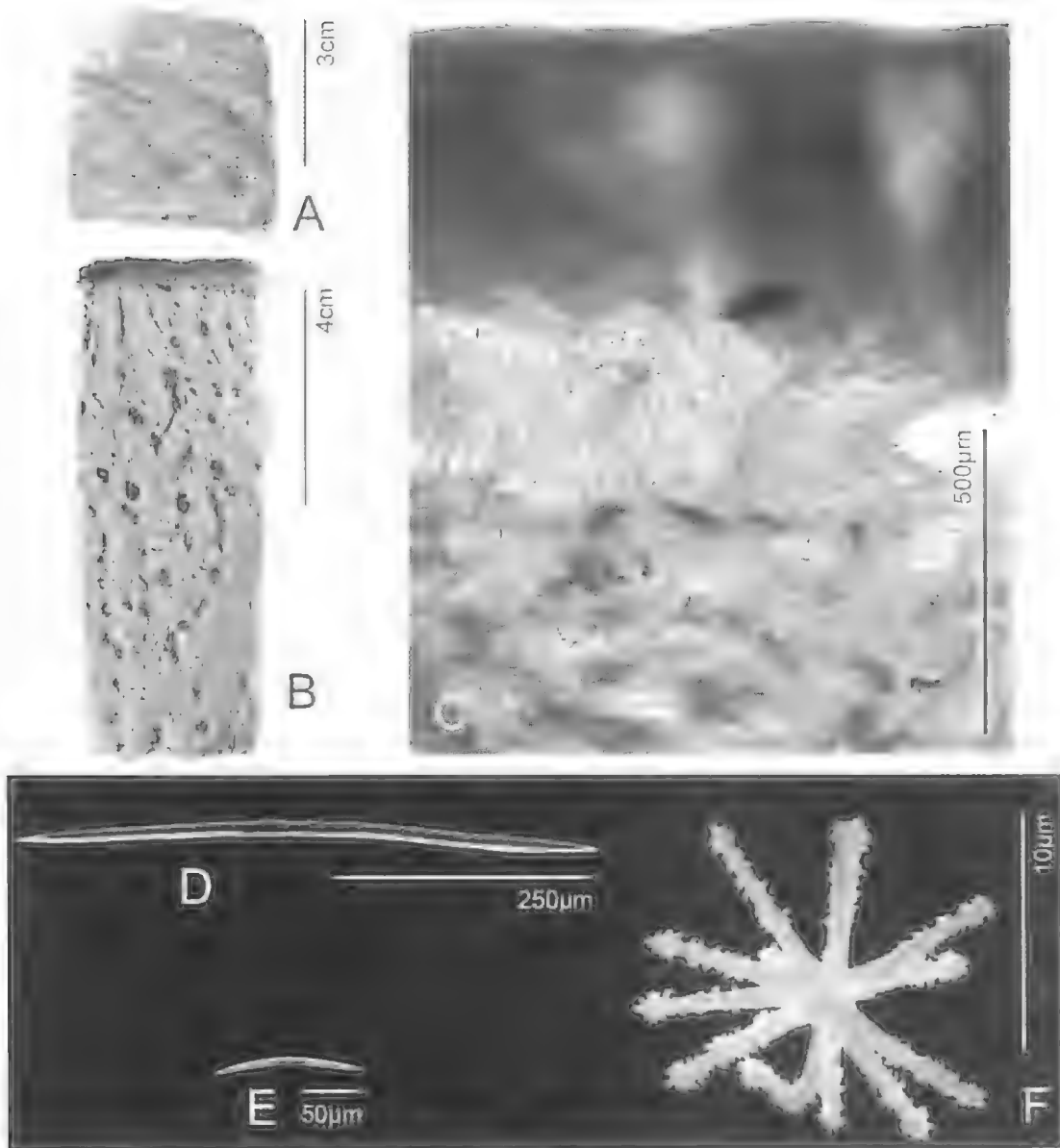


FIG. 4. *Jaspis cristacorrugatus* sp. nov. (holotype QMG312071). A, oscular ridge surface; B, perpendicular section; C, section through peripheral skeleton; D, large oxea; E, small oxea; F, oxyaster.

corrugated, oscular ridge along the apex (from photographic record, Fig. 8A-B). Height 15cm, width 20 × 20cm when alive and complete.

Colour: Slate-grey ectosome (Munsell 2.5Y 6/1) with lemon-yellow (2.5Y 8/5) in membrane surrounding oscules when alive; golden-yellow (7.5Y 7/8) to dark-brown (5YR 2.5/2) ectosome, with golden-yellow choanosome (7.5YR 7/8) when fresh; chocolate-brown (7.5YR 4/2)

ectosome with tan-brown (7.5YR 5/6) membrane surrounding oscules, with tan-brown (7.5YR 5/6) choanosome in ethanol.

Oscules. Many, small oscules, approximately 0.5mm diameter, clustered in linear arrangement, 1-2 oscules wide in furrows between corrugations of oscular ridge.

Texture. Very firm, rubbery, with leathery surface.

Surface characteristics. Opaque, optically smooth, uneven, with regularly distributed low rounded surface swellings tending toward slightly rugose.

Ectosome. Distinct from choanosome, 400-1400 thick, regularly traversed by aquiferous canals approximately 200 diameter; skeleton highly spiculose, with a densely packed layer of smaller oxeas in confused arrangement that largely obscures a scattering of oxyasters.

Choanosome. Riddled with aquiferous system canals up to 11mm diameter; skeleton of single oxeas and loose paucispicular bundles of oxeas in confused to vaguely plumo-reticulate arrangement; oxyasters present and slightly more abundant in aquiferous system linings.

Megascleres. (Refer to Table 4 for spicule dimensions) Oxeas, in distinctly bimodal size-distribution. Larger oxeas lightly curved over entire length, occasionally fusiform, with acerate to slightly telescoped points.

Smaller oxeas centrally curved, with hastate to slightly telescoped points.

Microscleres. (Refer to Table 4 for spicule dimensions) Oxyasters, with 9-15 lightly tapering rays that have recurved microspines primarily on distal two-thirds; centrum approximately 10-15% of spicule diameter. Variations rare but include vestigial spination, to clumping of spines near terminations, thus resembling tylotes when viewed under light microscopy.

REMARKS. Even though this material is described as a new species, and has not been previously synonymised with *J. stellifera*, it is included here because it may be easily confused with the newly reinstated *J. lutea* (if the subtle differences described here were not elucidated). Although *J. cristacorrugatus* is similar to *J. lutea* in spiculation and choanosomal skeletal structure, the two are clearly differentiated by several important characteristics. The external morphology is the most obvious difference between the two, with *J. cristacorrugatus* being massive in growth form (cf. *J. lutea* being irregular-lobate), and does not agglomerate foreign materials. Further, oscules are grouped into furrows across a thick oscular ridge (cf. regularly distributed over the surface). Significant differences in texture also differentiate the two species, with *J. cristacorrugatus* being very firm and rubbery (cf. crumbly and friable). The main differences in skeletal structure is that *J. cristacorrugatus* has an ectosome composed of smaller oxeas, lacking the underlying tangential layer of oxeas found in *J. lutea*.

ANCORINIDAE Schmidt, 1870

DEFINITION. Growth forms encrusting or massive, or more specialised with spherical body and long inhalant and exhalant tubes at opposite ends (the latter with a stellate, spicular, funnel-shaped end); megascleres long-shafted triaenes (with shaft directed inwards and clads on the surface) and oxeas; microscleres euasters and microrhabds; without sterrasters or amphiasters; triaenes may be absent or reduced (modified from Hooper & Wiedenmayer, 1994).

REMARKS. Ancorinidae Schmidt, 1870 is best known under its junior synonym Stellettidae Carter, 1875 (Hooper & Wiedenmayer, 1994). Hajdu & van Soest (1992) provide an informative discussion on the relationship between Ancorinidae and Coppatiidae.

Asteropus Sollas, 1888

TYPE SPECIES. *Stellettinopsis simplex* Carter, 1879: 349, by original designation.

DEFINITION. Ancorinidae with oxeas, oxyasters and sanidasters to which trichodragmata may be added.

REMARKS. Bergquist (1965, 1968) and Hajdu & van Soest (1992) proposed that two species groups exist within *Asteropus* based on microscle type. They argued that species with true sanidasters may be placed in the 'simplex'-like complex, whereas those with spiny microrhabds should be placed in the 'sarasinorum'-like group, the latter ascribing the name *Meloplhus* Thiele, 1899 and possibly valid at the subgeneric level.

Asteropus radiocrusta sp. nov. (Figs 1, 5, Table 5)

Stellettinopsis tuberculata (in part) Carter, 1886a: 126.

ETYMOLOGY. *Radius*, Latin, ray; *crusta*, Latin, hard outer surface of a body; for the radial arrangement of megascleres in the cortical ectosome.

MATERIAL. HOLOTYPE: BMNH1886.12.15.146: Port Phillip Heads, Victoria, coll. J.B. Wilson (originally one of three syntypes of *Stellettinopsis tuberculata* Carter, 1886a).

HABITAT DISTRIBUTION. 3-6m depth; on granite boulders with algae; Port Phillip Heads, Victoria.

DIAGNOSIS. Massive, subspherical; ectosome forming a highly distinct cortex 2.4-3.1mm thick, of densely packed oxeas in radial arrangement, with sanidasters and few oxyasters scattered throughout; choanosome with oxeas in confused

arrangement, with oxyasters and few sanidasters scattered throughout; oxeas (length 530-(1063)-1730, width 5-(24)-44), microspined oxyasters (diameter 18-(25)-33), microspined sanidasters (length 9-(13)-18).

DESCRIPTION. *Shape.* Massive, subspherical, with slightly irregular surface. (Attached to the holotype is a second species of sponge that is subspherical and has a highly conulose, membranous surface).

Colour. Live colouration unknown; beige-grey (Munsell 7.5YR 6/2) cortical ectosome with light beige choanosome (7.5YR 7/4) in ethanol.

Oscules. None visible.

Texture. Harsh, firm, barely compressible.

Surface characteristics. Opaque, optically smooth, even, microscopically hispid and densely spiculose.

Ectosome. Approximately 2.4-3.1mm thick, forming a cortex that is highly distinct from choanosome; skeleton comprised primarily of oxeas arranged radially in loose multispicular bundles forming an almost continuous palisade, with oxea terminations commonly penetrating the surface; sanidasters are scattered throughout the ectosomal skeleton but are slightly more common at the surface, while oxyasters are rare; containing abundant subspherical pigment bodies approximately 25 diameter.

Choanosome. Skeleton consists of a confused arrangement of both single and very loose paucispicular bundles of oxeas, with an abundance of interstitial oxyasters, but few sanidasters.

Megascleres. (Refer to Table 5 for spicule dimensions) Oxeas in a single, wide size-range, typically curved over entire length, with lightly telescoped terminations; variations rare but include styloid forms.

Microscleres. (Refer to Table 5 for spicule dimensions) Oxyasters, with 7-14 tapering rays that have abundant, recurved microspines occurring along the entire ray length; centrum approximately 12% of spicule diameter.

Sanidasters, with conical microspines and approximately 10-16 rays in 2-4 whirls.

REMARKS. The holotype of this species was originally part of the syntype series of *Stellettinopsis tuberculata* Carter, 1886a. However, it is clearly different from the other syntype (now lectotype, BMNH1886.12.15.434) of *S. tuberculata*, with the most significant differences involving spiculation, skeletal structure and

TABLE 5. Spicule dimensions of *Asteropus radiocrusta*. Measurements in μm , denoted as range (and mean) (N=25). L = length; W = width; D = diameter.

	Oxeas	Oxyasters	Sanidasters
Holotype BMNH1886. 12.15.146	L 530-(1063)-1730 W 5-(24)-44	D 18-(25)-33	L 9-(13)-18

external morphology. *Asteropus radiocrusta* has a single size category of oxeas, as well as oxyaster and sanidaster microscleres (cf. *S. tuberculata* which has two sizes of slightly flexuous oxeas and triaenes as megascleres and only oxyasters as microscleres). These substantial differences in spiculation are alone sufficient to clearly separate these two taxa at the generic level. However, they also differ significantly in the skeletal structure of the ectosome, with *A. radiocrusta* having a highly distinct, thick cortical ectosome of oxeas in erect to plumose bundles, forming an almost completely radial palisade (cf. an arenaceous cortical ectosome with sand-grains largely obscuring scattered oxyasters). In addition, their respective growth forms are greatly different, with *A. radiocrusta* being small, subspherical and lacking surface ornamentation (cf. massive-lobate and covered with prominent, irregular tubercles and ridges).

The presence of sanidasters places the present species within the 'simplex'-like group, as described above (see Remarks for the genus). *Asteropus simplex* (Carter, 1879) is the only other species of *Asteropus* described so far from Australia. *Asteropus radiocrusta* sp. nov. is similar to *A. simplex*, based on its original description, apparently falling within the published geographical distribution of *A. simplex* (Hooper & Wiedenmayer, 1994), which includes most of S Australia as well as New Zealand and the Indo-Malay region of the Indian Ocean. However, this purportedly extensive distribution of *A. simplex* is dubious since re-examination of a type slide of *A. simplex* from Carter's collection by Hajdu & van Soest (1992) revealed that the original description was incomplete, failing to recognise a second size category of oxyaster as well as the presence of trichodragmata. Consequently, *A. simplex* may also prove to contain a sibling species-complex, with its junior synonym, *A. haekeli* Dendy, 1905 (taxonomic decision by Dendy, 1924), certainly warranting its re-evaluation. Nonetheless, *A. radiocrusta* is clearly distinct from *A. simplex* by the absence of both the second size class of oxyaster and trichodragmata.

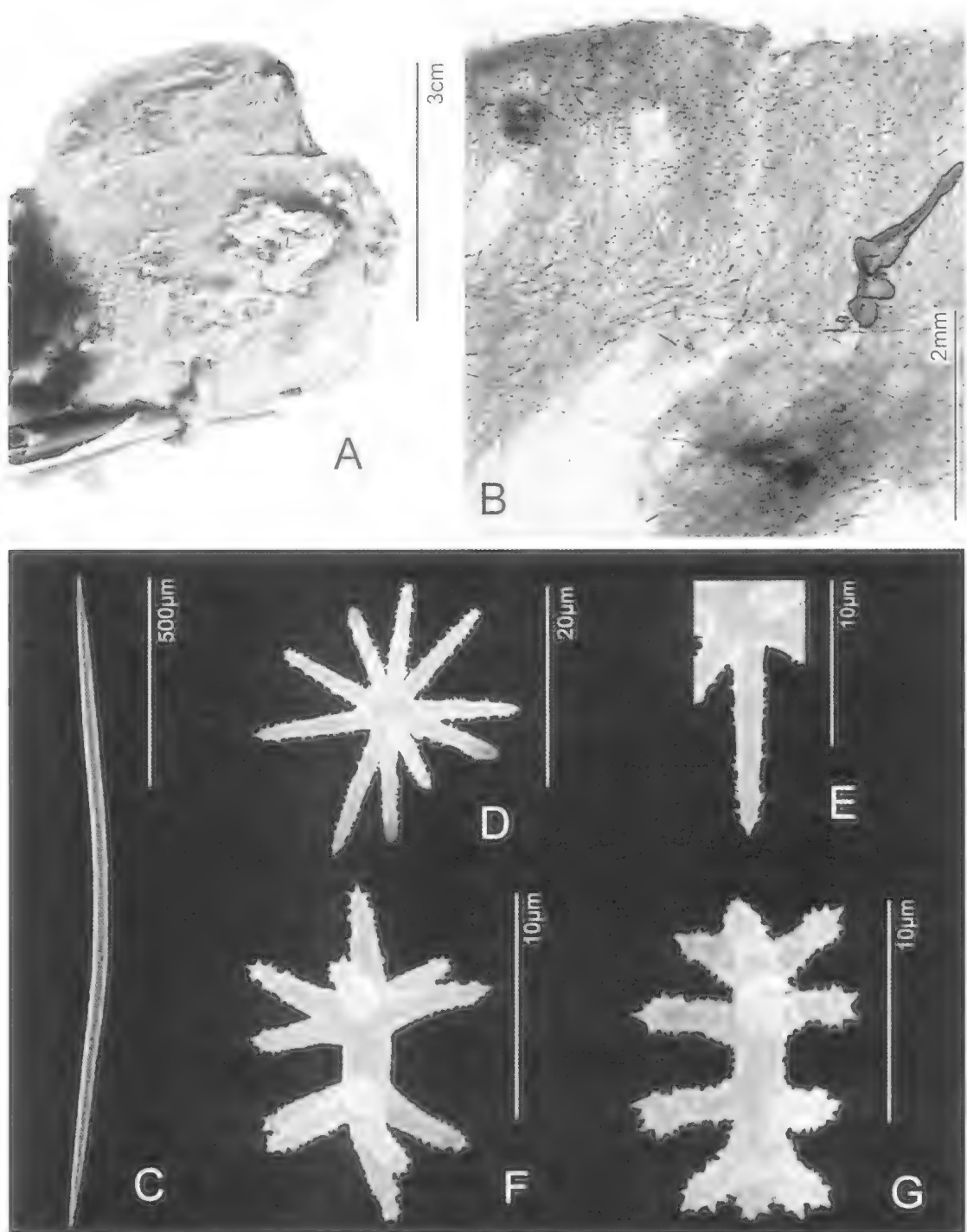


FIG. 5. *Asteropus radiocrusta* sp. nov. (holotype BMNH1886.12.15.146). A. holotype; B, section through peripheral skeleton; C, oxea; D, oxyaster; E, oxyaster ray; F, sanidaster with two whirls of rays; G, sanidaster with four whirls of rays.

In a revision of *Asteropus* from the Atlantic, Hajdu & van Soest (1992) described three species (*A. brasiliensis*, *A. vasiformis* and *A. niger*). *Asteropus radiocrusta* differs from each of these in spiculation, at least by the absence of trichodragmata or the second size-class of oxyaster. This, in conjunction with other morphological and wide biogeographic differences, indicates significant variation at the species level.

Stelletta Schmidt, 1862

Myriastr Sollas, 1886: 187 (Type species: *Myriastr subtilis* Sollas, 1886, by subsequent designation, see Sollas, 1888).

Pilochrota Sollas, 1886: 189 (Type species: *Pilochrota haekeli* Sollas, 1886, by subsequent designation, see de Laubenfels, 1936).

Anthastr Sollas, 1886: 191 (Type species: *Anthastr pulchra* Sollas, 1886, by subsequent designation, see Sollas, 1888).

Dorypleres Sollas, 1888: 426 (Type species: *Dorypleres dendyi* Sollas, 1888, by monotypy.).

Incertae sedis: *Astrolakina* Dendy & Burton, 1926: 230 (Type species: *Astrolakina stelligera* Dendy & Burton, 1926, by monotypy).

Incertae sedis: *Zaplathea* de Laubenfels, 1950 (Type species: *Zaplathea digonoxea* de Laubenfels, 1950, by original designation).

TYPE SPECIES. *Stelletta grubii* Schmidt, 1862, by subsequent designation (see Burton & Rao, 1932: 310).

DEFINITION. Ancorinidae with fine-centrum euasters (oxyasters, strongylasters or tylasters) only as microscleres.

REMARKS. Lendenfeld (1903) synonymised *Myriastr*, *Pilochrota* and *Anthastr* with *Stelletta*, disregarding the presence of a second category of aster in the latter. However, Dendy (1916) found it convenient to retain *Myriastr*, but agreed with merging *Pilochrota* into it, since both had only one category of aster. Similarly, de Laubenfels (1936) maintained *Myriastr* as separate from *Stelletta*, but Bergquist (1968) again ratified the synonymy of *Myriastr* with *Stelletta* after assessing that three specimens in her collection were *S. crater* Dendy, 1924 which possessed two mutually exclusive categories of asters.

Dorypleres has classically been considered to be closely related to *Jaspis*, and hence has been commonly placed in the Coppatiidae (or one of its junior synonyms), as either a distinct genus or a junior synonym of *Jaspis*. The genus was erected originally by Sollas (1888), without a generic diagnosis, but with a designated type species (*Dorypleres dendyi* Sollas, 1888), described as having two categories of aster. It was referred to *Jaspis* by Topsent (1904), although

Burton & Rao (1932) noted that it did not conform to the typical structure of *Jaspis* 'having large oxeads only irregularly arranged, and asters of two kinds'. Indeed, Burton & Rao (1932) remarked how similar *J. dendyi* was to certain species of *Stelletta*, and were it not for the absence of triaenes, they claimed that they would have had little reservation in assigning the species to *Stelletta*. De Laubenfels (1954: 228) reversed Topsent's (1904) decision, restoring *Dorypleres* to generic status, defining the genus to include 'those species which have two or more distinct categories of asters, where *Jaspis* has just one category of aster'. This decision was subsequently reversed by Bergquist (1968: 33), noting that 'two categories of asters are not recognisable in sponges assigned to *Jaspis dendyi*', a point corroborated by the present author after examining a slide of type material (holotype BMNH1889. 1.1.100). Consequently, in agreement with Bergquist's (1968) remarks, *Dorypleres* cannot be reinstated, as de Laubenfels (1954: 228) suggested, for 'those species (of Coppatiidae) which have two or more distinct categories of aster', and in which he placed *Dorypleres splendens* de Laubenfels, 1954.

Hajdu & van Soest (1992) briefly discuss *Dorypleres*, highlighting the differences between it and *Jaspis* and remarking on its *Stelletta*-like nature (despite its lack of triaenes). They proposed that if the lack of triaenes was found to be a synapomorphic character, then *Dorypleres* may be reinstated as a *Jaspis*-like Stellettid lacking triaenes.

Recent morphological and chemical studies on jasplakinolide-containing sponges by Sanders et al. (1999) concluded in ratifying the synonymy between *Dorypleres* and *Jaspis*. They undertook morphological studies at the supraspecific level on several nominal *Jaspis* species (including *Dorypleres splendens* de Laubenfels, 1954), concluding that only one genus (*Jaspis*) was valid. This conclusion was based largely on similarities in skeletal composition and arrangement, the authors claiming that 'all species possess oxeads, a confused choanosomal arrangement and paratantential arrangement of small spicules at the surface' (Sanders et al., 1999: 526). Although strictly correct, they did not distinguish between the nature of the 'small spicules' comprising the ectosome of each species. *Dorypleres splendens* has an ectosome containing a thin crust of oxyasters, whereas *Jaspis*, including the type species, *J. johnstonii* (Schmidt, 1862), has a

tangential ectosome composed of oxoate spicules. In contrast to their supraspecific conclusions based on morphological comparisons, their conclusions based on chemical analyses pertain only to the species level of classification, and hence are unable to provide any reliable generic characteristic. Sanders et al. (1999) concluded that 'all of the jasplakinolide-containing sponges studied were found to be conspecific' and that '*Jaspis splendans* (de Laubenfels, 1954) is the senior-most available name for these specimens'. A consequence of this logic is that the present chemical name 'jasplakinolide' is misleading, since it pertains only to a single species ('*Dorypleres splendans*'), and not to a genus diagnostic marker, and perhaps should be renamed using some derivation of the species name '*splendans*' (perhaps 'splendenolide') (although nomenclaturally this is probably not a feasible proposition).

Since *Dorypleres* does not have a tangential ectosome of oxoate spicules, it falls outside the diagnosis of Coppatiidae, and is considered here to be a *Stelletta* lacking triaenes.

Sanders et al. (1999) also synonymised the monotypic genus *Zaplethea* de Laubenfels, 1950 with *Jaspis*, based on ectosomal skeletal arrangement of the type species (*Z. dogonaxea* de Laubenfels, 1950), again without elucidating the component spicule types. Their illustration of a cross section of the type specimen ectosome does not show the diagnostic tangential layer of oxoates that is typical of Coppatiidae, and the original description (de Laubenfels, 1950) states that there is 'no sharply defined cortical region'. The twice-bent 'microxoas', described by de Laubenfels as being diagnostic for the genus, were interpreted by Sanders et al. (1999) as being a diagnostic feature at the species level only. It is speculated that *Zaplethea* is also a *Stelletta* lacking triaenes, like *Dorypleres* above, although further research is needed to confirm this.

Astroplakina Dendy & Burton, 1926, is a monotypic genus containing only *A. stelligera* Dendy & Burton, 1926. The type species is described as having a range of spicule types, ranging from diacts to octacts. It is apparent from the original figures that the diacts are oxoates and the 'triaets to octacts' are oxyasters. Indeed, Dendy & Burton (1926) noted the similarities of these spicules to the oxy- or strongylasters of the Stellettidae (= Ancorinidae), particularly where the rays are microspined. Unfortunately, the skeletal structure was not described because the

specimen was dry and unable to be sectioned adequately. As for *Zaplethea* and *Dorypleres*, *Astroplakina* is speculated to be a *Stelletta* lacking triaenes, although further confirmation is necessary, particularly relating to the ectosomal skeletal arrangement.

***Stelletta tuberculata* (Carter, 1886)
(Figs 1, 6, Table 6)**

Stellettinopsis tuberculata Carter, 1886a: 126.

Coppatia tuberculatus Sollas, 1888: 207

Stelletta arentecta Wiedenmayer, 1989: 20.

MATERIAL. LECTOTYPE: BMNH1886.12.15.474 (dry); Port Phillip Heads, Victoria. **OTHER MATERIAL:** BMNH1954.2.12.253; marked 'slide of type' (prepared by A. Dendy).

HABITAT DISTRIBUTION. 3-6m depth; on granite boulders with algae; Victoria, Bass Strait.

DIAGNOSIS. Massive, with irregular tubercles, ridges and lobes; dull-purple to red-brown alive; numerous minute oscules in depressions between tubercles; distinctly arenaceous surface; cortical ectosome of sand-grains largely obscuring minute oxyasters; choanosomal skeleton primarily composed of oxoas in confused arrangement largely obscuring scattered oxyasters; megascleres flexuous; oxoas in two size classes differentiated mainly by their thickness (thicker oxoas length 630-(788)-863, width 11-(16)-19; thinner oxoas length 313-(521)-684, width 2-(5)-8), rare ortho/plagiotriaenes in two size classes (thicker triaenes rhabd length 670-(771)-821, clad length 10-(16)-20; thinner triaenes rhabd length 535-(611)-668, clad length 7-(7.5)-8), microspined oxyasters (6-(10)-12µm).

DESCRIPTION. *Shape.* Massive, covered with twisted, irregular nodulose ridges, lobes and tubercles on the top and sides, with furrows and depressions between; tubercles 3-12mm thick and 5-18mm deep. Height 7.2cm, width 5.5 × 12cm.

Colour. Dull purple-brown (Carter, 1886a) to reddish-brown (Wiedenmayer, 1989) when fresh; dry lectotype with greyish beige-brown cortical ectosome (Munsell 2.5Y 7/4-5/2) and light beige choanosome (2.5Y 8/3).

Oscules. Numerous, almost indistinct oscules, approximately 0.5mm diameter, appear as slightly darker spots in the furrows and sulci between tuberculate lobes.

Texture. Dry lectotype is hard, stony, coarse; wet material is reported as firm, barely compressible, easily torn (Wiedenmayer, 1989).

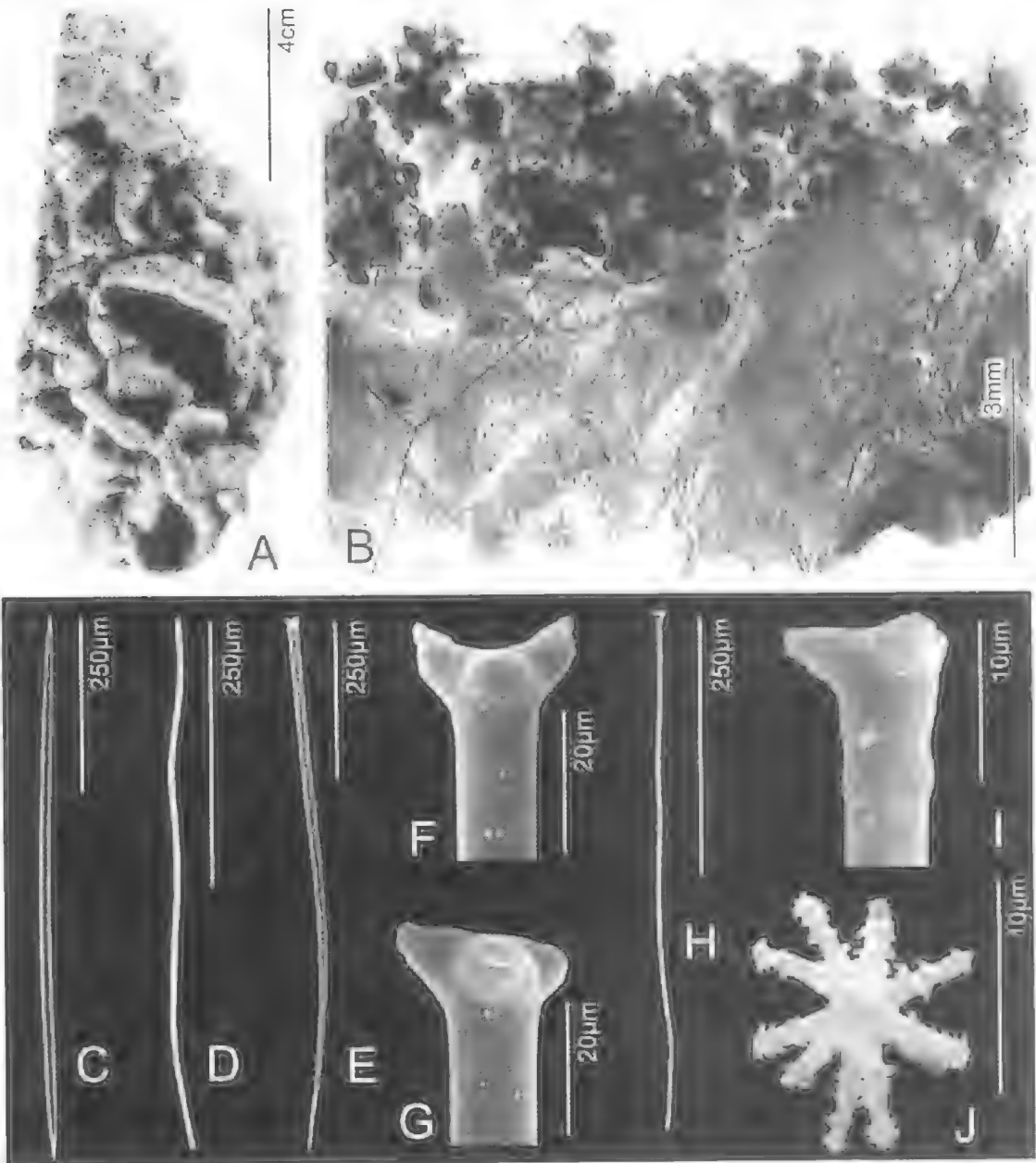


FIG. 6. *Stelletta tuberculata* (Carter, 1886) (lectotype BMNH1886.12.15.434). A, lectotype; B, section through peripheral skeleton (BMNH1954.2.12.253); C, thick oxea; D, thin oxea; E, thick ortho plagiotriaene; F, G, cladomes of thick ortho plagiotriaenes; H, thin ortho plagiotriaene; I, thin ortho plagiotriaene cladome; J, oxyaster.

Surface characteristics. Highly tuberculate and conspicuously arenaceous.

Ectosome. Approximately 1-2mm thick, forming a cortex that is distinct from choanosome due to the presence of abundant large sand-grains;

minute oxyasters are scattered throughout but are largely obscured by the sand.

Choanosome. Skeleton comprised of a confusion of single and very loose paucispicular bundles of oxeas that largely obscure the abundant oxyasters

TABLE 6. Comparison between present and published descriptions of *Stelletta tuberculata*. Measurements in μm , denoted as range (and mean) (N=25 in present study except where noted). L = length; W = width; RL = rhabd length; CL = clad length; D = diameter.

	Oxeas (Thick)	Oxeas (Thin)	Triaenes (Thick)	Triaenes (Thin)	Oxyasters
Lectotype BMNH1886.12.15.434 Present study	L 630-(788)-863 W 11-(16)-19	L 313-(521)-684 W 2-(5)-8	RL 670-(771)-821 CL 10-(16)-20; (N=7)	RL 535-(611)-668 CL 7-(7.5)-8; (N=4)	D 6-(10)-12
Syntype, original description (Carter, 1886a)	L 762 W 13	Not described	Not described	Not described	D 8.5

in the dense matrix; ortho/plagiotriaenes present, with clads just below the cortical ectosome and rhabds directed vaguely inward.

Megascleres. (Refer to Table 6 for spicule dimensions) Oxeas in two size categories differentiated primarily by their thickness and extent of flexion; thicker oxeas lightly flexuous, infrequently fusiform, with acerate to finely telescoped ends.

Thinner oxeas similar in geometry but much more flexuous.

Ortho/plagiotriaenes in two size classes also differentiated by their thickness; rhabd terminations slightly telescoped; clads stumpy.

Microscleres. (Refer to Table 6 for spicule dimensions) Oxyasters with 10-17 lightly tapering rays that have 10-20 recurved spines on distal half, thus giving a slightly tylote appearance particularly when examined using light microscopy; centrum approximately 25% of spicule diameter.

REMARKS. The original description by Carter (1886a) was obviously based on specimen BMNH1886.12.15.434, nominated here as the lectotype, since the other two syntypes are clearly different species. One syntype (BMNH1886.12.15.113) is a *Crella* of uncertain specific identity, and at first was thought to have been a mislabelled holotype of Carter's (1885) *Echinonema (Crella) incrustans* (BMNH1886.12.15.123) (i.e. considering the similar registration numbers). However, this is not the case because this latter specimen was also examined by the author and is different again. The remaining syntype (BMNH1886.12.15.146) is clearly yet another species (described above as *A. radiocrusta* sp. nov.).

Stelletta tuberculata is reinstated here as a valid species, distinct from *J. stellifera* in several important respects. *Stelletta tuberculata* has both oxeas and triaenes as megascleres (cf. *J. stellifera* which only has oxeas). Further, *S. tuberculata* has a highly arenaceous cortical ectosome of sand-grains, largely obscuring scattered minute oxyasters (cf. a tangential layer of oxeas in confused

arrangement). The vestigial nature of the triaene clads makes it difficult to properly resolve their form as orthotriaene or plagiotriaene.

As Wiedenmayer (1989) remarked, there are very few *Stelletta* species that contain foreign detritus and relatively rare, reduced triaenes. He addressed the differences between these species in his remarks for *S. arenitecta*, which is synonymised here with *S. tuberculata*.

Rhabdastrella Thiele, 1903

Aurora Sollas, 1888: cxxxix, 187 (preoccupied, junior homonym of *Aurora* Ragonot, 1887 (Lepidoptera)) (Type species: *Stelletta globostellata* Carter, 1883, by original designation).

Rhabdastrella Thiele, 1903: 934; Bergquist, 1968: 54.

Diastra Row, 1911: 300; Bergquist, 1968: 54 (Type species: *Diastra sterrastraea* Row, 1911, by monotypy).

Aurorella De Laubenfels, 1957: 245 (nomen novum for *Aurora* Sollas, 1888); Wiedenmayer, 1989: 21.

TYPE SPECIES. *Coppatias distinctus* Thiele, 1900, by original designation.

DEFINITION. Ancorinidae with thick centred euasters (oxyspherasters or spherasters) in a cortical ectosome.

REMARKS. *Aurora* was originally proposed for Carter's *Stelletta globostellata* and *S. reticulata* because they possessed large oxyspherasters. Lendenfeld (1903) merged the genus with *Stelletta*, followed by Hentschel (1909). Dendy (1916) argued that it was desirable to retain Sollas's genus, since the large (oxy)spherasters form such a characteristic and well-defined feature, and are known from many species. He also proposed the addition of *Diastra sterrastraea* Row, 1911, *A. cribroporosa* Dendy, 1916 and *Coppatias (Rhabdastrella) distinctus* Thiele, 1900. Thus, he proposed the synonymy of *Rhabdastrella* and *Aurora*. He also suggested that the type species of *Aurora*, *A. globostellata*, did not have trichodragmata, as Sollas 1888 suggested (corroborated in the present study). Dendy also asserted that the loss of triaene megascleres has taken place several times within *Aurora*,

giving several examples of similar species differing in the presence of triaenes.

De Laubenfels (1957) proposed the name *Aurorella* to replace the preoccupied *Aurora*, but still maintained it as distinct from *Rhabdastrella* (which he merged into *Dorypleres*). He restored *Diastra* to full and valid generic status based on the possession of sterrasters.

Bergquist (1968) synonymised *Aurora* and *Diastra* into *Rhabdastrella* on the basis of Dendy's (1916) argument. She used *Rhabdastrella* to receive all *Aurora* species because the latter name was pre-occupied, also drawing attention to Dendy's observation that three pairs of species within *Rhabdastrella* (s.s), *Diastra* and *Aurora* were only distinguishable by the presence or absence of triaenes. It appears that these observations have led to the modification of the definition of *Rhabdastrella* (e.g. Wiedenmayer, 1989: 21) to include the character 'with reduced triaenes or without triaenes ...'.

Hechtel (1983) used *Aurorella* as a subgenus of *Rhabdastrella* on the basis that it lacked triaenes. As has been suggested (Hajdu & van Soest, 1992) for the Ancorinidae (and Coppatiidae), the lack of triaenes is a suspect diagnostic character. Evidence is given here to support this, whereby *R. globostellata* is shown to have a gradation of triaene development, ranging from well-developed, through to vestigial or absent.

***Rhabdastrella globostellata* (Carter, 1883)**
(Figs 1, 7, 8C-F, Table 7)

Stelletta globostellata Carter, 1883: 353-354.

Aurora globostellata Sollas, 1888: 187-188.

Stellettinopsis carteri Ridley, 1884: 476.

Coppatias carteri Sollas, 1888: 208-209.

Jaspis stellifera Bergquist, 1969: 69.

MATERIAL. HOLOTYPE: BMNH1883.5.3.1 (dry): Galle, Sri Lanka (Ceylon), coll. Dr. Ondaatji. **HOLOTYPE** of *Stellettinopsis carteri* Ridley, 1884 BMNH1882.2.23.276 (wet): Prince of Wales Channel, Torres Strait, coll. R.W. Coppinger. **OTHER MATERIAL:** Australia – Western Australia, NTMZ3352, QMG301116, QMG301142; Northern Territory, NTMZ96, Z582, Z588, Z599, Z1325, Z2182, Z3248, QMG303634, G313548; Queensland, NTMZ4011, QMG300041, G301179, G303170, G303487, G303509, G304341, G304450, G304606, G304481, G304884, G305457, G305779, G306240, G313432, G313472, G313508, G313589, G314452, G314563, G314624, G315114, G315227, G315249, G315503. New South Wales, QMG301398. Fiji – QMG312735 (NCIOCDN-4165-M), QMG312803. Malaysia – QMG301224, G301227, G301228, G304613. Palau – QMG305951. Philippines – QMG312576. Tonga – QMG313264. Vanuatu – QMG306826, G306893 (ORSTOM R1624).

HABITAT DISTRIBUTION. Intertidal-53m depth; on coral reef, rocky outcrops, broken reefs, reef flats, drop-offs and overhangs; tropical and subtropical Indian and Pacific Oceans; Sri Lanka, Singapore, Zanzibar, Indonesia, Malaysia, Palau, Philippines, Vanuatu, Fiji, Tonga, Australia; N Western Australia, Northern Territory, Queensland, Great Barrier Reef, N New South Wales coast.

DIAGNOSIS. Massive, globular, subspherical; brown to yellowish-tan cortex, with yellow choanosome alive; apical depressions with numerous small oscules in clumps; ectosome of oxyspherasters; peripheral choanosomal skeleton variable, with plumose brushes of oxeads and orthotriaenes (sometimes absent) that have rhabds directed inward; deeper choanosome contains oxeads in confused arrangement, with oxyasters in variable abundance between specimens; oxeads (length 220-(814)-1521, width 0.5-(13)-38), orthotriaenes (rhabd length 70-(600)-1309, clad length 7-(104)-239), oxyspherasters (diameter 5-(36)-91), oxyasters (diameter 3-(28)-96).

DESCRIPTION. *Shape.* Dry holotype is incomplete, amorphous, and has an irregularly folded surface which Carter (1883: 353) described as 'corrugated'. Living and wet-preserved specimens are typically globular, subspherical, sometimes raised on a short, thick base that is attached at several points, commonly with one to several shallow, concave depressions (up to 5mm depth) on apical surface. Incomplete holotype 5.5cm long, 3.5 × 2.5cm wide; larger specimens up to 30cm high, 45 × 45cm wide.

Colour. Dry holotype has dull greyish beige-brown (Munsell 7.5YR 7/2-6/4) ectosome, with beige-tan choanosome (7.5YR 6/4). Living specimens have variable ectosomal colouration between specimens, ranging from from yellowish-tan (2.5Y 7/4) to deep chocolate brown (7.5YR 4/4), and occasionally dusty purple (10R7/2), however the choanosome is always vivid yellow (2.5Y 8/10).

Oscules. Not visible in incomplete, dry holotype, but Carter (1883: 353) originally describes 'vents congregated in one part of the surface'. Recently collected material typically has numerous (about 20-40) small oscules (1-4mm diameter) clustered in one to three, large concave depressions (up to 5cm deep) on apical surface, with larger oscules in more central regions of clusters.

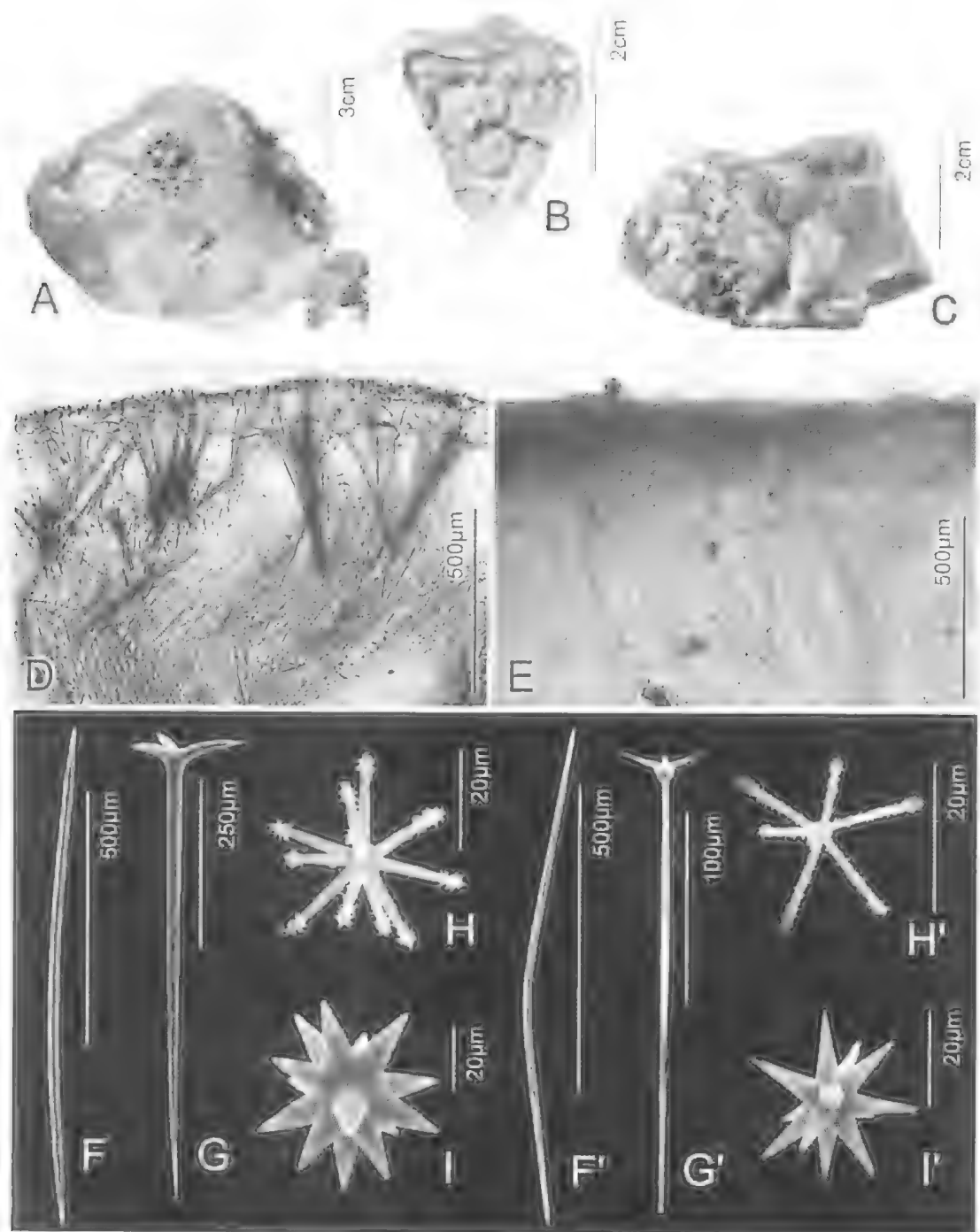


FIG. 7. *Rhabdastrella globostellata* (Carter, 1883). A, whole wet specimen from Vanuatu (QMG306893); B, holotype of *Stellattinopsis carteri* Ridley, 1884 (BMNH1882.2.23.276 wet; Torres Strait, Australia); C, holotype (BMNH1883.5.5.1 dry; Sri Lanka); D, E, sections through peripheral skeletons showing differences in structure between low latitude (D, specimen QMG306893; Vanuatu) and higher latitude (E, QMG313432; Heron Island, GBR, Australia) material; F, F' - I, I', examples of spiculation differences between specimens (F-I, holotype of *S. carteri* Ridley, 1884 BMNH1882.2.23.276; Torres Strait, Australia; F'-I', QMG306893; Vanuatu) (F, F', oxeas; G, G', orthotriaenes; H, H', oxyasters; I, I', oxyspherasters).

TABLE 7. Comparison between holotype and other material of *Rhabdastrella globostellata* by region. Measurements in μm , denoted as range (and mean). L = length; W = width; RL = rhabd length; CL = clad length; D = diameter.

Region/material	Oxeas	Orthotriaenes	Oxyspheraster euasters	Oxyaster euasters
Holotype, Sri Lanka, BMNH1883.5.3.1	L 628-(831)-1030 W 5-(14)-23	RL 223-(650)-857 CL 65-(126)-172	D 8-(25)-55	D 11-(25)-72
Holotype of <i>Stellimopsis carteri</i> , Torres Strait, Qld, BMNH1882.2.23.276	L 730-(889)-1020 W 13-(18)-25	RL 569-(647)-810 CL 70-(93)-110 (rare)	D 6-(7)-64	D 23-(36)-46
Sabah State, Malaysia, 4 specimens	L 611-(1072)-1521 W 4-(21)-33	RL 254-(835)-1309 CL 21-(127)-239	D 15-(43)-61	D 8-(26)-56
Philippines, 1 specimen	L 790-(970)-1150 W 6-(18)-26	RL 326-(657)-946 CL 37-(102)-138	D 20-(46)-63	D 33-(48)-63
Palau, 1 specimen	L 566-(756)-963 W 2-(7)-15	RL 320-(559)-753 CL 50-(104)-166	D 8-(34)-50	D 6-(15)-21
Vanuatu, 2 specimens	L 310-(641)-875 W 2-(5)-9	RL 220-(431)-638 CL 7-(38)-85. (rare)	D 9-(27)-43	D 7-(22)-39
Fiji, 1 specimen	L 570-(736)-940 W 3-(10)-16	RL 330-(356)-382 CL 43-(52)-65. (rare)	D 15-(36)-54	D 15-(18)-23
Tonga, 1 specimen	L 599-(976)-1165 W 10-(20)-37	RL 654-(726)-848 CL 94-(148)-185	D 11-(40)-66	D 9-(15)-23
N Western Australia, 3 specimens	L 472-(863)-1425 W 4-(12)-19	RL 219-(806)-1107 CL 53-(128)-215	D 11-(37)-72	D 10-(43)-71
Northern Territory, Australia,	L 687-(998)-1456 W 4-(19)-38	RL 367-(818)-1240 CL 53-(122)-215	D 6-(42)-91	D 11-(47)-96
Queensland, Australia, 13 specimens	L 220-(541)-936 W 0.5-(6)-15	RL 70-(121)-247 CL 55 (Very rare: 2 specimens)	D 5-(29)-55	D 3-(22)-45
N New South Wales, Australia, 1 specimen	L 265-(527)-718 W 2-(7)-13	None	D 15-(36)-53	D 14-(24)-31

Texture. Dry holotype is hard; fresh and wet-preserved material is firm, compressible, and leathery.

Surface characteristics. Opaque, optically smooth, uneven, with low, rounded tubercles, corrugations, bumps and ridges forming a tuberculate surface becoming smoother toward the base; extent of tuberculation varies between specimens, ranging from prominently tuberculate to nearly completely smooth.

Ectosome. About 150-500 thick; skeleton composed exclusively of oxyspherasters. Variable degrees of packing of oxyspherasters occurs, ranging from very densely packed in tropical material, to relatively sparsely packed in subtropical specimens. Canals, approximately 70 diameter, regularly traverse the ectosome. Subectosomal region is relatively clear of microscleres.

Choanosome. Deeper choanosomal skeleton consists of a confusion of loosely scattered single oxeas and paucispicular bundles of oxeas. These bundles become more ordered in the peripheral choanosome, where they may also include orthotriaenes, forming variably distinct paucispicular plumose brushes, with the rhabds of the triaenes directed inward and clads supporting the ectosome. There is substantial variability in absolute

abundance of microscleres and relative abundance of microsclere categories between specimens, without any obvious correlation between geographic regions or latitudinal gradients.

Megascleres. (Refer to Table 7 for spicule dimensions) Oxeas, slightly bent, with finely telescoped ends; variations very rare but include styloid forms and oxeas with terminations that are split or sharply bent (similar to promonaenes).

Orthotriaenes, with variable clad development, with rhabds tapering toward fusiform, hastate or faintly blunt terminations; each cladome contains three identical clads with shapes ranging from typical geometries, to lightly telescoped, sharply angled near tips, or stunted forms. Orthotriaenes more commonly observed and robust in tropical rather than subtropical specimens where they may be highly vestigial or apparently absent.

Microscleres. (Refer to Table 7 for spicule dimensions) Oxyspheraster euasters, with 9-18 conical rays; centrum approximately 29% of spicule diameter; rays may be entirely smooth or have up to 15 microspines on distal end.

Oxyaster euasters, with about 9-17 lightly tapering to isodiametric rays, with approximately 11-25 recurved microspines on the distal half.

thus giving a slightly tylote appearance under light microscopy; centrum approximately 10% of spicule diameter; variations very rare, with only one spicule displaying forward projecting microspination over entire ray length.

REMARKS. This is undoubtedly the same species referred to by Bergquist (1969) as '*J. stellifera*' from Heron Island, GBR, with the qualification that her specimens are representative of subtropical material found typically to have reduced spiculation. In agreement with her published remarks, and corroborated by more recent surveys of this region, it is one of the most common and more prominent species of sponges on the reef flat, easily recognisable for its massive, subspherical shape, brown exterior and distinctive (mango-like) bright-yellow interior. Spicule diversity and size are similar between Bergquist's (1969) and recent collections, with the qualification that the tylasters described by Bergquist are actually oxyasters with micropines clumped near the terminations and only seen properly under SEM. This species, however, is clearly different from *J. stellifera* in many significant respects.

While both species are essentially subspherical, they differ greatly in size and colouration, but most significantly in ectosomal skeletal structure and spicule compliment. *Jaspis stellifera* is about 4.7cm in largest dimension and pinkish-white to purple, whereas *R. globostellata* is at least up to 45cm in diameter and has a brown exterior and bright yellow interior. Both species have choanosomal skeletons that are essentially confused arrangements of oxeas, with oxyasters scattered in the interstices. However, the ectosome of *R. globostellata* has a distinct layer of oxyspherasters, in contrast to that of *J. stellifera*, which is comprised of a tangential layer of oxeas. Further, *J. stellifera* has only oxeas and oxyasters as spicules, whereas *R. globostellata* also has orthotriaenes and oxyspherasters.

The synonymy of *Stellettinopsis carteri* Ridley, 1884 with *R. globostellata* is based on the presence of orthotriaenes and oxyspherasters in the holotype of *S. carteri* in addition to the oxeas and oxyasters as originally described. Further, spicule sizes (refer Table 7) lie within the range described for *R. globostellata*. Unfortunately, the type specimen is no longer complete, as originally described by Ridley (1884), now consisting only of a small fragment (height 8mm, width 21 × 25mm), with only a small portion of surface intact. However, the original description of the

gross-morphology of *S. carteri* is consistent with characteristics of *R. globostellata* (e.g. having a 'short cylindrical stalk passing gradually into a massive, somewhat flattened upper portion'; colouration being tan with a yellow interior; and with an undulate, dimpled, corrugated surface). Unfortunately, the ectosome is barely intact in the holotype of *S. carteri*, and consequently it is difficult to ascertain its true nature. It is vaguely distinct from the choanosome (although not explicit in Ridley's (1884) original description), being smooth and probably composed of oxyspherasters. This synonymy is further supported by the type locality of *S. carteri* being well within the distribution of *R. globostellata*.

In *R. globostellata*, orthotriaenes were more abundant in specimens from more northerly tropical localities, where spiculation was generally more highly silicified. By comparison, specimens from more southern regions (central GBR to N NSW), typically lacked triaenes and spicules were more poorly silicified and less robust. This is similar to the latitudinal trend observed by Hooper & Bergquist (1992) for *Cymbastella* (Axinellidae), and Hooper (1996) for *Clathria* (*Thalysias*) *vulpina*. Failure to recognise the absence of triaenes in specimens may perpetuate misidentifications of this species in the future, and so the distinctive shape and colouration of this species will undoubtedly remain an important, albeit superficial, distinguishing features.

The reassignment of tropical sponges, previously misidentified as '*J. stellifera*', to *Rhabdastrella globostellata* is based primarily on morphological evidence and is supported by chemical evidence in the possession of malabaricane-type triterpenes (e.g. Ravi et al., 1981; Ravi & Wells, 1982), determined by van Soest & Braekman (1999) to be a good chemotaxonomic marker for Stellettids. It is possible that '*J. stellifera*' from Japanese waters are also misidentified specimens of *S. globostellata* since they too have been reported to contain malabaricane-type triterpenes (Tsuda et al., 1991; Kobayashi et al., 1996).

DISCUSSION

Examination of all type material previously assigned to, or associated with, '*Jaspis stellifera*' revealed that many important details were omitted from original descriptions. Failure to recognise these details has certainly contributed to an oversimplified synonymy for this species. For example, re-examination of type material showed clearly that the syntype series of

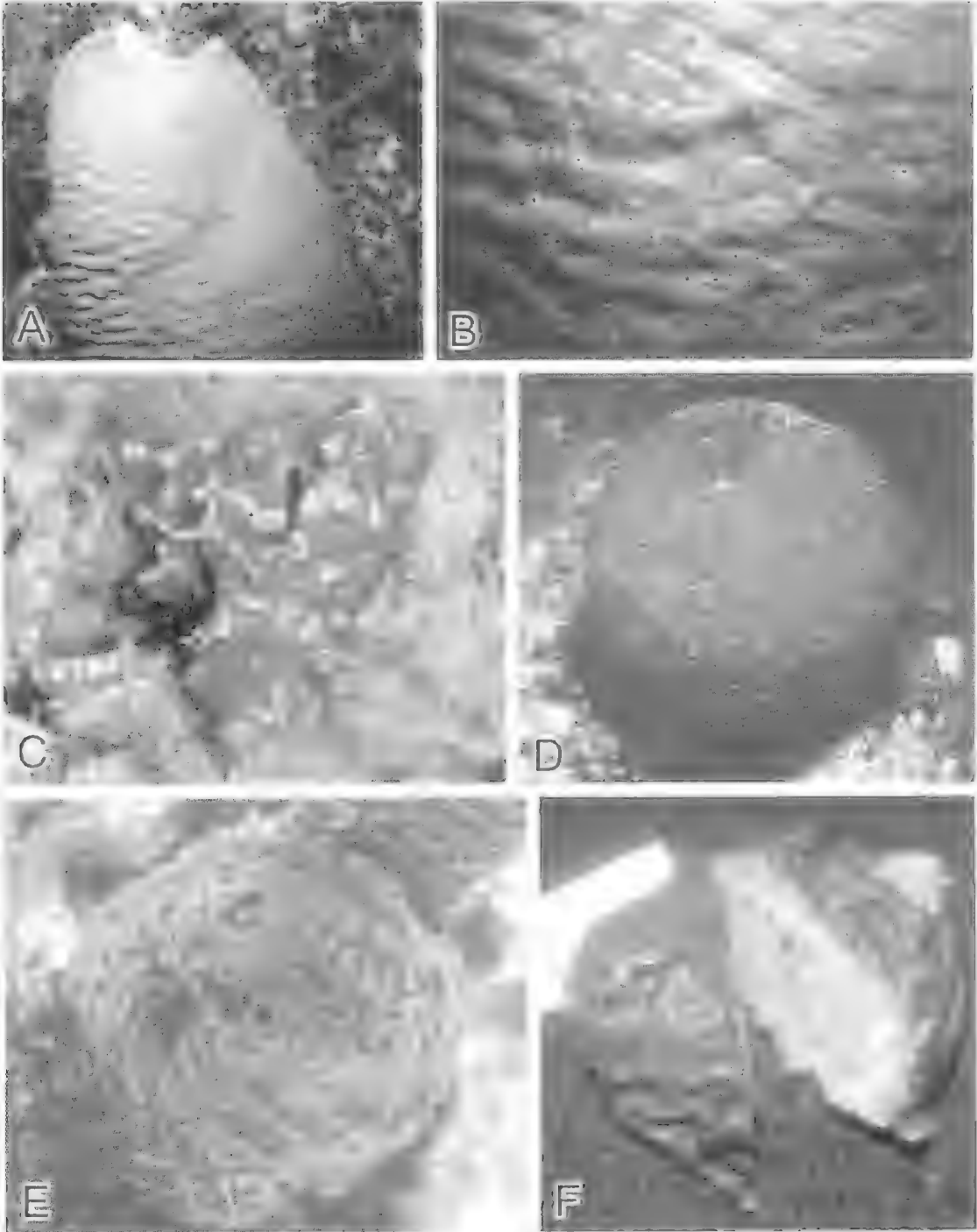


FIG. 8. A-B, *Jaspis cristacorrugatus* sp. nov. (QMG312071, Port Davey, Tasmania, 10m, photo NCI); A, specimen in situ; B, close-up view of oscular ridge surface. C-F, *Rhabdastrella globostellata* (Carter, 1883); C, NTMZ2182, Darwin, NT, intertidal, photo J. Hooper; D, QMG306893, Emae, Vanuatu, 20m, photo ORSTOM; E, QMG313432, Heron Island, Qld, intertidal, photo author; F, QMG304884, Mudjimba Island, Qld, 12m, photo J. Hooper.

f *Stellettinopsis tuberculata* was composite, containing specimens from different orders. This example is perplexing because the original synonymy was proposed by Shaw (1927), under the direct supervision of Maurice Burton at the BMNH, who had complete access to the vast type collections housed there. It is probable, therefore, that this synonymy was based on superficial comparison of type material rather than re-examination of histological preparations.

In recognising the oversimplification of Shaw's (1927) synonymy, Bergquist (1969) reinstated *J. coriacea* and *J. purpurea* as valid species, based on two supposed inconsistencies in the published literature, both of which were demonstrated here to be invalid. In contrast, the proposed synonymy of *J. stellifera*, based on redescribed type material, incorporates only *J. coriacea* and *J. purpurea*. Consequently, *J. stellifera* is not as widely distributed as reported by Hooper & Wiedenmayer (1994). Its corroborated distribution appears to be restricted to waters between Victoria and Tasmania. Most of the remaining species previously placed in the '*J. stellifera*' complex also appear to have very limited distributions, with the exception of *R. globostellata* which has an apparent widespread tropical/subtropical Indo-Pacific distribution.

The clue to misidentified tropical and subtropical populations of *R. globostellata* as '*J. stellifera*' is largely based on the presence of triaenes within specimens, even though these range from present to vestigial or sometimes absent in individual specimens. It was only through thorough examination of many specimens that this anomaly concerning presence/absence of triaenes was recognised. Triaenes were more common in tropical specimens, where spicules were generally more robust than in southern populations. The apparent lack of triaenes in some material, or failure to recognise their vestigial occurrence in other specimens, may lead easily to the misidentification of this species as *Jaspis* (which by definition lacks triaenes). The graded development of triaenes across tropical to subtropical waters has implications regarding the debate surrounding the relationship between Coppatiidae and Ancorinidae. According to present diagnoses, the presence of triaenes confirms that this species belongs to Ancorinidae, whereas specimens lacking triaenes could be justifiably included in Coppatiidae. The rare, vestigial, or complete loss of triaenes in *R. globostellata* provides evidence supporting the proposition of Hajdu & van Soest (1992) that the

absence of triaenes is a dubious synapomorphic character used to separate Coppatiidae and Ancorinidae.

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PERCA LINEATA AND P. VITTATA ESTABLISHED AS VALID SPECIES OF
PLECTORHINCHUS (PERCIFORMES: HAEMULIDAE)

JOHN E. RANDALL AND JEFFREY W. JOHNSON

Randall, J.E. & Johnson, J.W. 2000 06 30: *Perca lineata* and *P. vittata* established as valid species of *Plectorhinchus* (Perciformes: Haemulidae). *Memoirs of the Queensland Museum* 45(2): 477-482. Brisbane. ISSN 0079-8835.

The Linnaean fishes *Perca lineata* and *P. vittata* are established as valid species of the haemulid genus *Plectorhinchus*. *Plectorhinchus goldmanni* (Bleeker) is a junior synonym of *P. lineatus*, and *P. orientalis* (Bloch) is a junior synonym of *P. vittatus*. Meristic data are tabulated to provide an additional basis for separating four other striped species of *Plectorhinchus* that at some stage resemble either *P. lineatus* or *P. vittatus*. □ *Linnaeus, fishes, haemulidae, Plectorhinchus, goldmanni, lineatus, orientalis, vittatus.*

J.E. Randall, Bishop Museum, 1525 Bernice Street, Honolulu, Hawaii 96817-2704, USA;
J.W. Johnson, Queensland Museum, PO Box 3300, South Brisbane 4101, Australia; 21 April 2000.

Many fishes of the haemulid genus *Plectorhinchus* undergo remarkable changes in colouration with growth. There has been considerable confusion, particularly in the identification of some striped species. In the literature, juveniles have often been mismatched with adults, and various life stages have been incorrectly described as valid species, often with the adult or juvenile form unknown. In the latest review of the family, Smith (1962) failed to correctly associate many of the species with their synonyms, and he described *G. gaterinoides* (a junior synonym of *P. lineatus*). He also presented a figure depicting seven colour phases of *P. orientalis* from 135 to 550mm in length. The second to fourth specimens in the figure (fig. 15 B, C and D) range from 175 to 233mm and clearly illustrate blotched individuals, however our studies indicate that specimens of this size are often, if not usually, striped as in larger specimens. The purpose of this paper is to validate two Linnaean species, both of which have a juvenile phase with horizontal stripes, and to compare meristic values of other similarly striped species of *Plectorhinchus*.

Perca lineata and *P. vittata* are among the 29 species classified in *Perca* by Linnaeus (1758). Both were described with reference to volumes of Museum Adolphi Friderici as having five longitudinal white bands, but no locality details were provided. Cuvier in Cuvier and Valenciennes (1830: 309) was the first to correctly relate *lineata* with haemulid fishes when he placed it in the genus *Diagramma*. He gave the dorsal-ray count for the species as XII, 20, thus resolving the count of XVII, 16 dorsal rays of Linnaeus by noting the small size and poor

condition of the specimen and implying a miscount. Smith (1962: 495) suggested that the difference in dorsal-ray count might be a misprint.

Fernholm & Wheeler (1983: 245) reported on the type specimen, NRM LP 8, 41mm SL, in the Swedish Museum of Natural History, Stockholm. They stated that the labels with the fish represent a continuous record of its history and confirm it as having been part of King Adolf Fredrik's collection. They agreed with Cuvier that Linnaeus probably miscounted the dorsal rays on the small specimen; their corrected count is XIII, 19. They wrote that Linnaeus failed to make reference to the illustration of this fish on plate 31 of volume I of Museum Adolphi Friderici, adding, 'Had he done so, much of the uncertainty surrounding the application of the name in later years might have been avoided'.

Fernholm & Wheeler (1983: 246) also found the holotype of *Perca vittata*, NRM LP 11, 162mm SL, and were the first to report it as a species of Pomadasyidae (= Haemulidae), identifying it as *Plectorhinchus* sp. Linnaeus gave the dorsal-ray count as XII, 18 and the anal-ray count as I, 6; these counts were corrected by Fernholm & Wheeler to XII, 20 and III, 7, respectively. They noted that 'Habitat in America' was added to the species account in Linnaeus' 12th edition of Systema Naturae, an error which could well explain the long delay in correctly placing this fish to genus. The genus *Plectorhinchus* is confined to the Indo-Pacific region.

Most of the species of *Plectorhinchus* show dramatic changes in colour pattern with growth, and apparently depending on the environmental

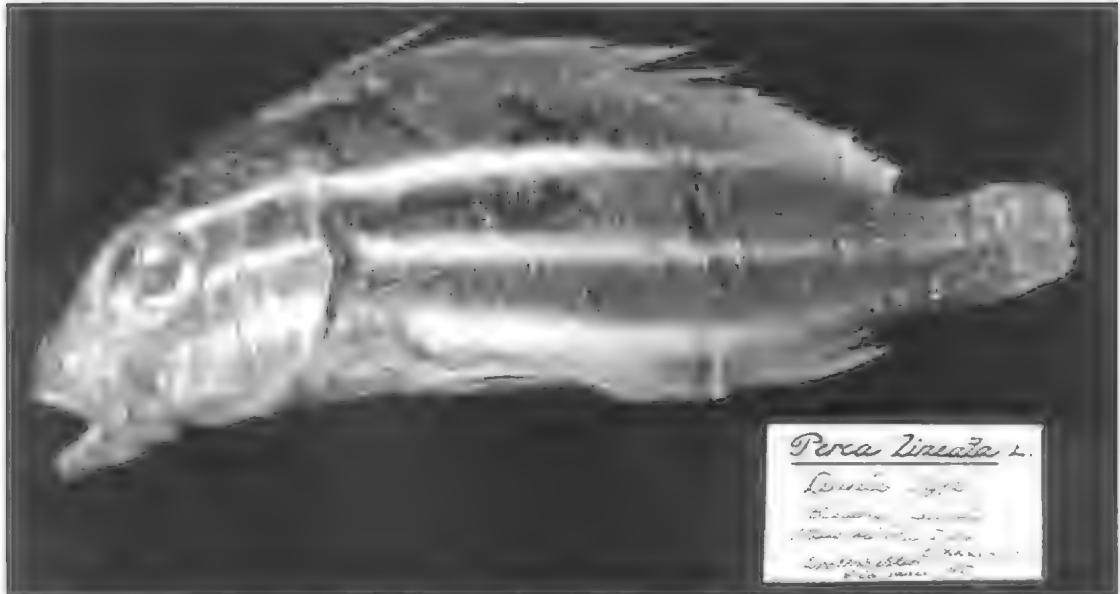


FIG. 1. *Perca lineata* Linnaeus, 1758. Holotype, NRM LP 8 (SL 41mm, TL 46mm).

conditions, the changes can take place at different lengths by fish of the same species from different localities.

We are aware of six species of *Plectorhinchus* that can be striped at the lengths of the two holotypes. To provide unambiguous evidence of the association between the two Linnaean names and these species, we requested photographs of the type specimens, as well as meristic data and observations on colour pattern from the Swedish Natural History Museum. Sven O. Kullander kindly provided the photographs (reproduced here as Figs 1 and 2). He also obtained a radiograph of the type of *Perca vittata*, which enabled us to correct the number of dorsal rays to XII, 18. He counted the outer first-arch gill rakers of *P. lineata* as 9 + 21, and those of *P. vittata* as 10 + 21. He determined that the stripes on the head of *P. vittata* pass straight across the forehead and snout and do not incline downward or break into spots.

We have obtained counts of the dorsal spines and rays, pectoral rays, and gill rakers of available specimens of six striped species of *Plectorhinchus* in the Australian Museum, Sydney (AMS), Bernice P. Bishop Museum, Honolulu (BPBM), California Academy of Sciences, San Francisco (CAS), CSIRO Marine Laboratories, Hobart (CSIRO), Hokkaido University, Hakodate (HUMZ), Miyazaki University, Miyazaki (MUFS), Natural History

Museum, London (BMNH), Northern Territory Museum, Darwin (NTM), Queensland Museum, Brisbane (QM) and Western Australian Museum, Perth (WAM). From these data (Table 1) and examination of type descriptions and figures and documentation of colour pattern change (Fig. 3), we can confirm the synonymy of Senou & Shimada (1991) that *Plectorhinchus lineatus* is the senior synonym of *Diagramma goldmanni* Bleeker (the large adult with oblique stripes on the back), *D. radju* Bleeker (a large juvenile), *D. haematochir* Bleeker (subadult), and *Gaterin gaterinoides* Smith (large juvenile). Senou & Shimada (figs 7-12) illustrated individuals from 22.5 to about 200mm SL in colour, but not the large adult 'goldmanni' form.

We can confirm that *Plectorhinchus vittatus* is the senior synonym of *P. orientalis* (Bloch), the name used by most recent authors for this species, and as recognised by R.J. McKay as early as 1992 (pers. comm.). We recommend acceptance of *vittatus* over *orientalis* as conditions relating to the current International Code of Zoological Nomenclature (1999), pertaining to the validity of names and principal of priority (Article 23.9: Reversal of precedence) are not met in this instance. R.J. McKay had previously recognised that *P. lineatus* and *P. vittatus* were senior subjective synonyms of *Plectorhinchus goldmanni* (Bleeker) and *P. orientalis* respectively, following an



FIG. 2. *Perca vittata* Linnaeus, 1758. Holotype, NRM LP 11 (SL 162mm, TL 195mm).

investigation of the type specimens (R.J. McKay, pers. comm., 1992). Indeed, following his recommendation, the name *P. vittatus* has been used by authors after 1899 (e.g. Randall & Anderson, 1993; Winterbottom & Anderson, 1997; Randall et al., 1997).

Although the number of dorsal-spines and pectoral-rays of the holotype of *P. vittatus* are not modal for counts of museum specimens presented in Table 1, they are within the range for the species, and the soft dorsal count is modal. More convincing is the total outer first-arch gill-raker count of 31 for the holotype of *P. vittatus* (see Table 1); not only is it modal, but it is also outside the range of the other five striped species. In addition, the pattern of the stripes as shown in Figure 2 and augmented by Kullander provide further confirmation. Note on the horizontally striped phases of the two species in Figures 3 and 4 that a dark stripe passes through the centre of the eye in *P. lineatus* but not *P. vittatus*. The remarkable changes in colour pattern of this species with growth have been illustrated by Smith (1962: fig. 15) and Senou (1991: figs 13-18), as *P. orientalis*. Other synonyms include *Bodian cuvier* Bennett (*Bodian* is an incorrect spelling of *Bodianus*), and *Diagramma sebae* Bleeker.

Plectorhinchus lineatus occurs in the western Pacific from the Ryukyu Islands south to the Great Barrier Reef and east to the Caroline

Islands and New Caledonia. The more wide-ranging *P. vittatus* is known from Samoa to the east coast of Africa (but not the Great Barrier Reef or inshore waters of western and northern Australia or the seas of the Arabian Peninsula).

MATERIAL. (lengths in mm are standard lengths)

Plectorhinchus albovittatus. AMSIA9433, 93.5mm, Fiji; AMSI19346-006, 87mm, Philippines; BPBM5166, 125mm, Viti Levu, Fiji; BPBM26766, 87mm, Jenepono, Sulawesi, Indonesia; BPBM29349, 125mm, Bali, Indonesia; CAS-SU20264, 3: 52-57mm, Aparri, northern Luzon, Philippines; CAS uncat., 78mm, Koror, Palau; CAS uncat., 3: 59-95mm, Babelthuap, Palau; CAS-SU27372, 88mm, Palau; QMI7746, 431mm, Magnetic I., Qld; QMI11319, 583mm, off Cairns, Qld; QM I20290, 97mm, fish market, S of Denpasar, Bali.

Plectorhinchus gaterinus. BPBM17589, 4: 41-144mm, Mafia I., Tanzania; BPBM18150, 228mm, Dahab, Gulf of Aqaba, Egypt; BPBM18178, 49mm, Gulf of Aqaba; BPBM28035, 2: 79-81mm, Lamu, Kenya; BPBM29464, 6: 94-227mm, Bahrain (Persian Gulf); BPBM33259, 64mm, Tanura, Saudi Arabia (Persian Gulf).

Plectorhinchus lessonii. AMSI17491-030, 139mm, Savo I., Solomon Islands; AMSIB150, 105.5mm, Bali; AMSI1324, 175mm, Iran Jaya; AMSI23694-001, 265mm, Queensland, Australia; AMSI17142-018, 234mm, Santo, New Hebrides (Vanuatu); AMSI20774-141, 273mm, off Cape Melville, Qld, Australia; BPBM8886, 87mm, Philippines (aquarium trade); BPBM9473, 3: 205-239mm, Malakal Harbour, Palau; BPBM18666, 174mm, Hou-Pi-Hoo, southern Taiwan; BPBM19175, 285mm, Okinawa, Ryukyu Islands; BPBM20889, 64mm and

TABLE 1. Meristic data for striped *Plectorhinchus* species. Symbols signify counts for holotypes, * = *P. lineatus*, ** = *P. vittatus*.

	Dorsal Spines			Dorsal Rays						Pectoral Rays		
	XII	XIII	XIV	17	18	19	20	21	22	16	17	18
<i>P. albovittatus</i>	1	15	-	-	14	2	-	-	-	-	14	2
<i>P. gaterinus</i>	-	14	1	-	7	6	2	-	-	14	1	-
<i>P. lessonii</i>	28	8	-	-	1	12	18	5	-	-	30	4
<i>P. lineatus</i>	1	37*	-	-	4	24*	10	-	-	5	25*	1
<i>P. polytaenia</i>	16	8	-	-	-	-	3	10	11	2	20	1
<i>P. vittatus</i>	2**	19	1	3	11**	8	-	-	-	-	4**	18

	Upper Gill Rakers							Lower Gill Rakers										
	5	6	7	8	9	10	11	14	15	16	17	18	19	20	21	22	23	24
<i>P. albovittatus</i>	-	-	-	5	11	-	-	-	-	-	-	-	1	5	10	-	-	-
<i>P. gaterinus</i>	-	-	-	10	5	-	-	-	-	-	-	7	7	1	-	-	-	-
<i>P. lessonii</i>	3	27	5	-	-	-	-	8	23	3	1	-	-	-	-	-	-	
<i>P. lineatus</i>	-	-	2	22	14*	-	-	-	-	-	-	1	9	23	5*	-	-	
<i>P. polytaenia</i>	-	-	4	9	10	1	-	-	-	-	-	2	10	10	2	-	-	
<i>P. vittatus</i>	-	-	-	-	9	9**	4	-	-	-	-	-	4	3	6**	6	1	2

	Total Gill Rakers																
	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35
<i>P. albovittatus</i>	-	-	-	-	-	-	-	-	-	4	4	8	-	-	-	-	-
<i>P. gaterinus</i>	-	-	-	-	-	-	-	5	7	2	1	-	-	-	-	-	
<i>P. lessonii</i>	2	7	18	6	2	-	-	-	-	-	-	-	-	-	-	-	
<i>P. lineatus</i>	-	-	-	-	-	-	1	-	8	14	13	2*	-	-	-	-	
<i>P. polytaenia</i>	-	-	-	-	-	-	-	3	8	5	6	2	-	-	-	-	
<i>P. vittatus</i>	-	-	-	-	-	-	-	-	-	1	5	3	7**	2	2	1	1

BPBM29350, 132mm, Bali, Indonesia; BPBM26672, 48mm, Manado, Sulawesi, Indonesia; BPBM29999, 140mm and BPBM30098, 69mm, Lombok, Indonesia; BPBM38708, 141mm, Ishigaki, Ryukyu Islands; CAS49579, 199mm, Siluag I., Sulu Archipelago, Philippines; CAS51980, 4: 24-64.5mm, Dumaguete, Negros, Philippines; CAS88540, 86mm, Bolinao, Luzon; CAS-SU39054, 130mm, Manila Bay, Luzon; NTMS10663-001, 105mm, Barang-Lompo, Ujung Pandang, Sulawesi, Indonesia; QM uncat, 2: 160-228mm, Qld; QMI11322, 325mm, off Bundaberg, Qld; QMI12006, 294mm, off Cairns, Qld; QMI13205, 307mm, Big Broadhurst Reef, off Cape Bowling Green, Qld; QMI15377, 236mm and QMI15378, 251mm, Flinders Reef, off Cape Moreton, Qld; QMI19093, 300mm, off Cairns, Qld; QMI19147, 346mm, Swain Reefs, Qld; QMI20053, 327mm SL, Keeper Reef, Qld; QMI29832, 323mm, Boulton Reef, Bunker Group, Qld.

Plectorhinchus lineatus. AMSIB149, 130mm, Bali; AMSI8309, 90mm, Malaysia; AMSI9138, 96mm, Hood Bay, Papua New Guinea; AMSI9201, 73mm, same data; AMSI13412, 294mm, same data; AMSI10512, 90.5mm, Mindanao, Zamboanga, Philippines; AMSI13411, 177mm, Port Moresby, Papua New Guinea; AMSI1072, 218mm, same data; AMSI13840, 186mm, Admiralty

Islands; AMSI15360-078, 333mm, Bita-Ama Reef, N. side, Solomon Islands; BPBM7264, 170mm, Ishigaki, Ryukyu Islands; BPBM22203, 2: 40-64mm, Negros, Philippines; BPBM26653, 108mm, Bunaken, Sulawesi, Indonesia; BPBM30099, 2: 65-77mm and BPBM38709, 43mm, Lombok, Indonesia; CAS7070, 73mm, Mindanao, Philippines; CAS51930, 39mm and CAS53446, 170mm, Siluag I., Sulu Archipelago, Philippines; CAS-SU26961, 179mm, Culion, Philippines; CAS-SU26962, 5: 32-80mm, Dumaguete, Negros, Philippines; CAS-SU62720, 142mm, Zamboanga, Mindanao, Philippines; QMI6749, 495mm, Cape Cleveland, Qld; QMI12909, 177mm, QMI19094, 441mm, QMI19095, 458mm, QMI19096, 417mm and QMI19097, 334mm, off Cairns, Qld.

Plectorhinchus polytaenia. BMNH1859.4.21.226, 120mm and BMNH1859.4.21.222, 167mm, Amboina; BMNH1870.8.31.41, 161mm, Mosil I.; BMNH1880.4.21.47-48, 2: 129-138, no data; BPBM17436, 2: 304-315mm, Kendrew I., Western Australia; BPBM22176, 215mm, Sumilon I., Philippines; BPBM32370, 124mm, Komodo, Indonesia; CAS-SU26968, 2: 137-155mm, Jolo, Philippines; NTMS10590-004, 285mm, New Year I., Arafura Sea; NTMS11289-002, 321mm, White I., Cape Arnhem, NT;

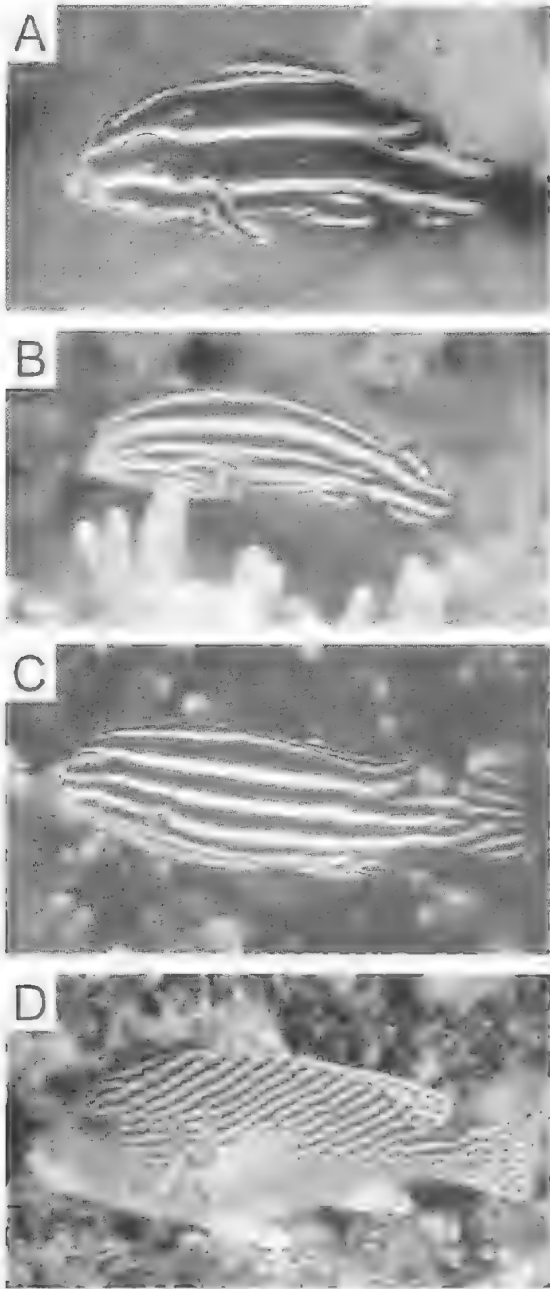


FIG. 3. *Plectorhinchus lineatus*; A, Sanur, Bali, TL 90mm (photo, Takamasa Tonozuka); B, Palau, TL 110mm; C, Tulamben, Bali, TL 180mm (photo, Rudie Kuiter); D, Yonge Reef, Australia, TL 450mm. Total length (TL) given for fishes photographed underwater is an estimate.

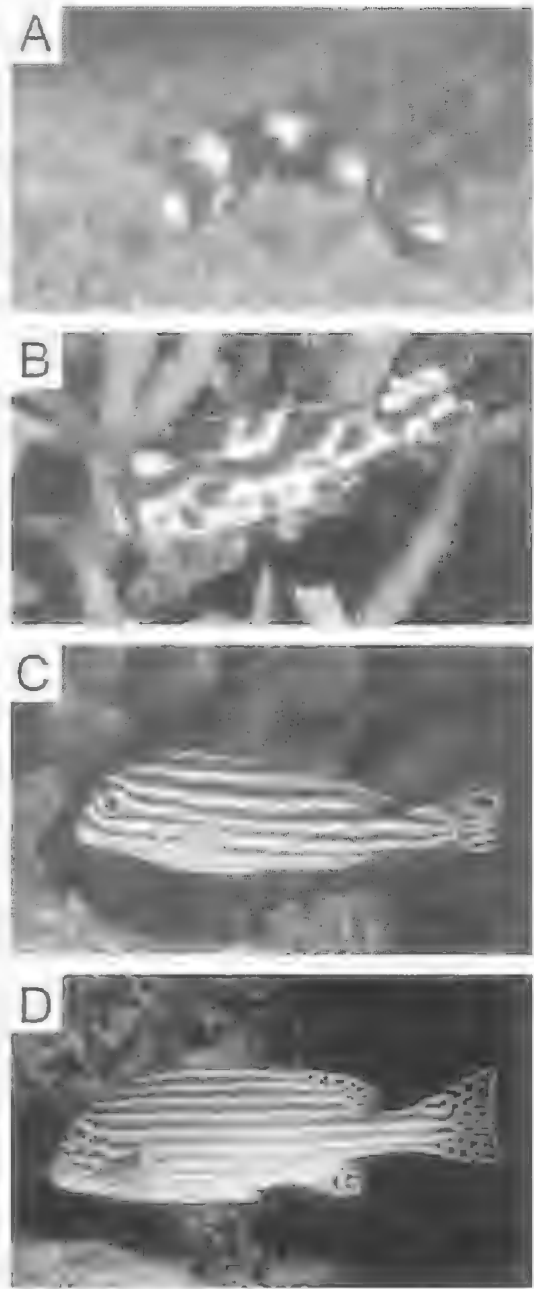


FIG. 4. *Plectorhinchus vittatus*; A, Mahe, Seychelles, TL 50mm; B, Maldives, TL 165mm; C, Sri Lanka, TL 180mm; D, Maldives, TL 300mm. Total length (TL) given for fishes photographed underwater is an estimate.

NTMS10451-011, 270mm, off Table Head, Port Essington, NT; QMI10210, 345mm, Exmouth Gulf, WA.

Plectorhinchus vittatus. AMS 115360-077, 161mm, Malaita, Solomon Islands; AMS 1220, 106mm, Admiralty Islands, Papua New Guinea; AMS 19748, 241mm, Hood Bay, Papua New Guinea; BPBM 4020, 335mm, Guam, Mariana Islands; BPBM 9015, 2: 83-92mm, BPBM 18790, 214mm, and BPBM 27171, 65mm, Sri Lanka; BPBM 11650, 294mm, Fiji; BPBM 13636, 85mm, Madang, Papua New Guinea; BPBM 16061, 153mm, Guadalcanal, Solomon Islands; BPBM 16191, 129mm, Alite Reef, Solomon Islands; BPBM 17624, 166mm, Mafia I., Tanzania; BPBM 21577, 44mm and BPBM 35510, 25mm, La Digue, Seychelles; BPBM 29336, 179mm, Bali, Indonesia; CAS 7462, 97mm, Viti Levu, Fiji; CAS 65609, 96mm, Bagabag I., Madang, Papua New Guinea; CAS 120475, 108mm, Cakayan I., Cagayan Prov., Philippines; NTM S13162-004, 220mm, Telama fish landing, Negombo, Sri Lanka; NTM S13435-022, 83mm, Ilibernia Reef, Timor Sea; WAM P20925-001, 356mm, unspecified offshore atolls, WA.

OTHER MATERIAL. (examined by colleagues)

Plectorhinchus lessonii. HUMZ41407, 157mm, Ishigaki, Ryukyu; HUMZ48226, 207mm, Marshall Islands.

Plectorhinchus lineatus. HUMZ69941, 185mm, Naha, Okinawa, Ryukyu Islands; MUF6353, 228mm, MUF6359, 193mm, MUF6360, 240mm, MUF6373, 196mm, MUF6374, 262mm and MUF6375, 347mm, Okinawa, Ryukyu Islands.

Plectorhinchus polytaenia. CSIROCA450, 288mm, N of Eighty Mile Beach, WA; CSIROH4017-01, 250mm, N of Cape Preston, WA; CSIROCA1648, 267mm, NW of Bathurst I., NT; WAMP7377-001, 380mm, Black Ledge, Onslow, WA; WAMP20213-001, 295mm, Dampier Archipelago; WAMP20243-001, 300mm, Delambre I., WA; WAMP22859-001, 240mm, Kendrew I., off Museum Bay; WAMP24556-001, 330mm, Western Australia; WAMP25354-007, 230mm, Monte Bello I., WA.

ACKNOWLEDGEMENTS

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of the Northern Territory Museum and Anthony C. Gill of the Natural History Museum for providing loans of specimens under their care and Sue Morrison of the Western Australian Museum, Alastair Graham of CSIRO Marine Laboratories, Hiroyuki Motomura of the Miyazaki University and Kouichi Hoshino of Hokkaido University for sending meristic and collection data of specimens in their collections. Rudie H. Kuiter kindly allowed us to reproduce photographs of juvenile *P. lineatus*.

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REVISION OF AN EARLY CRETACEOUS MACROFLORA FROM THE MARYBOROUGH FORMATION, MARYBOROUGH BASIN, QUEENSLAND, AUSTRALIA

STEPHEN McLOUGHLIN, ANNE-MARIE P. TOSOLINI AND ANDREW N. DRINNAN

McLoughlin, S. Tosolini, A.P. & Drinnan, A.N. 2000 06 30: Revision of an Early Cretaceous macroflora from the Maryborough Formation, Maryborough Basin, Queensland, Australia. *Memoirs of the Queensland Museum* 45(2): 483-503. Brisbane. ISSN 0079-8835.

An Early Cretaceous (Aptian or earliest Albian) impression flora is described from the upper part of the Maryborough Formation in the Maryborough Basin, southern Queensland. The flora is preserved in marine sediments hosting an abundant invertebrate fauna dominated by bivalve molluscs. The flora incorporates single species attributable to the Polypodiophyta, Pentoxylales and Bennettitales. Two cuneate leaves have affinities either with the Ginkgoales or seed-ferns. Four species of conifer foliage are represented together with araucariacean ovulate cones. Fossils considered by previous workers to be plant roots are reinterpreted as invertebrate burrows, and forms attributed to equisetalean nodal diaphragms may alternatively represent gastropod opercula. An Aptian or earliest Albian age based on past studies of the fossil fauna is supported by the presence of the stratigraphic index fossil *Phyllopteroides serrata* Cantrill & Webb. □ Aptian. *Phyllopteroides*, *Araucariaceae*, *Pentoxylales*, *Bennettitales*, *Cretaceous palaeoenvironments*.

Stephen McLoughlin, Anne-Marie P. Tosolini, and Andrew N. Drinnan, School of Botany, University of Melbourne, Parkville, Victoria 3012, Australia; 4 October 1999

In 1918, A.B. Walkom described a small assemblage of plant fossils from the Maryborough Formation, Maryborough Basin, SE Queensland. Most of the plant fossils had been collected by Mr Daniel Jemmett and his son during quarrying operations at the Corporation Quarry, Maryborough (Dunstan, in Walkom, 1918). The plant remains were illustrated with a series of simple line-drawings, which in some cases did not express the full suite of morphological characters available in the fossils. Since that date, improved understanding of the systematics, phylogenetic affinities, and stratigraphic ranges of some plant groups has necessitated revision of some of Walkom's identifications. Several plant fossils from the Maryborough Formation, including counterparts of some of Walkom's studied specimens, were subsequently sent to the Natural History Museum, London, by B. Dunstan, then Queensland Chief Government Geologist. This paper presents revised systematic descriptions of the Maryborough Formation macroflora. The study is part of a broader project to describe and revise a series of fossil floras from eastern Australia in order to better resolve the stratigraphic and palaeobiogeographic ranges of Mesozoic plant taxa.

GEOLOGICAL SETTING

The Maryborough Basin (Fig. 1) covers an area of around 24,600km² and incorporates a terrestrial, paralic and marine succession at least

4000m thick. Subsidence in the Maryborough Basin initiated during latest Triassic times was roughly contemporaneous with development of the contiguous Nambour, Clarence-Moreton, Surat, Eromanga, Carpentaria, and Laura basins elsewhere in Queensland. Initial deposits in the basin are represented by the uppermost Triassic to Lower Jurassic, Myrtle Creek Sandstone (Fig. 2) deposited predominantly in high-energy fluvial settings (Cranfield, 1993). Subsequently, the Tiara Coal Measures (Lower to ?Middle Jurassic) were deposited in a range of fluvial settings dominated by high-sinuosity rivers and incorporating extensive floodbasin mire deposits. The Tiara Coal Measures also incorporate a distinctive 30m thick interval containing prominent beds of pisolitic and oolitic ironstone that are useful marker horizons for correlation with sequences in neighbouring basins (Cranfield, 1993). The Grahams Creek Formation (?Upper Jurassic to ?Neocomian) unconformably overlies the Tiara Coal Measures, but the hiatus in sedimentation is not well resolved due to poor palynological age constraints on the upper Tiara Coal Measures and entire Grahams Creek Formation (Cranfield, 1993). The Grahams Creek Formation is dominated by intercalated intermediate to felsic volcanics and volcanigenic sediments. The unit was deposited in continental settings and some sediments have

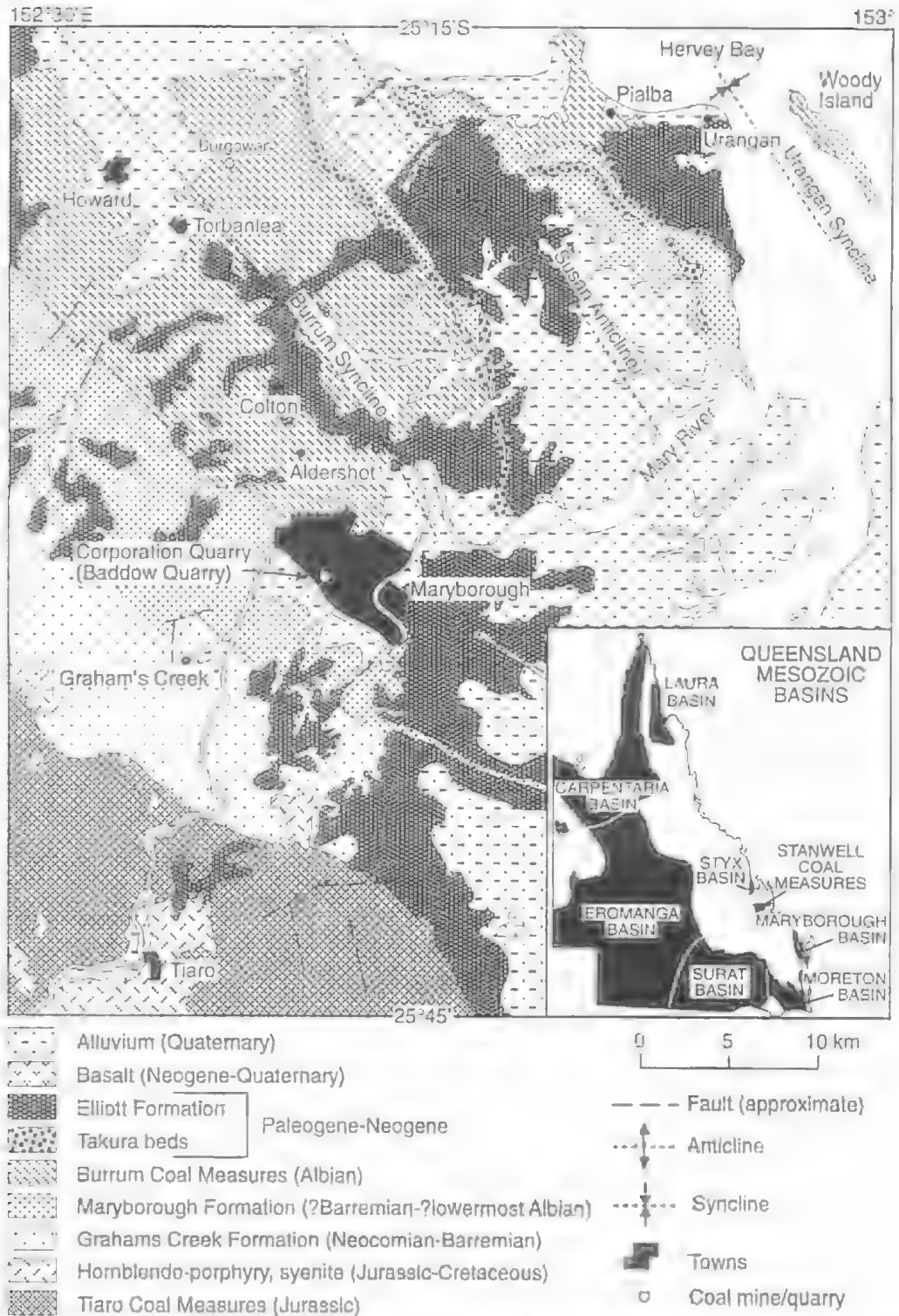


FIG. 1. Geological map of the Maryborough district showing the location of Corporation Quarry, the main site yielding plant fossils.

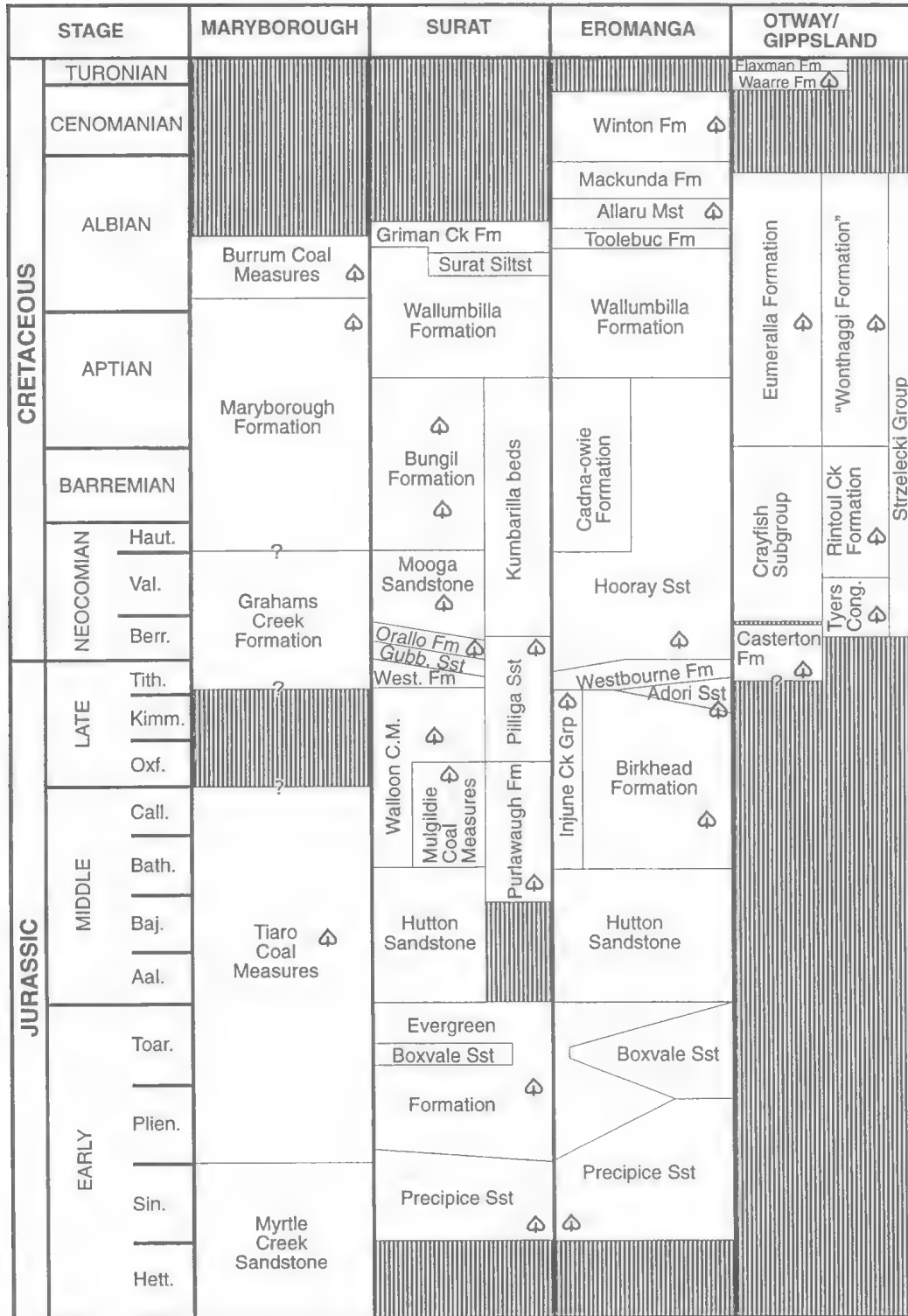


FIG. 2. Stratigraphic chart showing correlation of the Maryborough Basin succession with sequences in the Surat, Eromanga, and southern Victorian basins. Leaf symbol indicates plant-bearing unit.

been interpreted as the deposits of alluvial fans (Cranfield, 1993).

The disconformably overlying Maryborough Formation (?Neocomian to ?lowermost Albian) was deposited in a range of sedimentary environments. The formation ranges in thickness from 600 to 2500m (Day et al., 1983). The basal conglomeratic beds were probably deposited in continental settings (Draper, 1971) but a subsequent (late Neocomian) marine transgression saw the remainder of the formation deposited in a mosaic of paralic to shallow marine settings. Sandstones within the unit have been identified as potential hydrocarbon reservoir targets (Siller, 1961; Ellis, 1966). The assemblage of plant remains studied here is derived from the upper part of the formation where invertebrate macrofossils are also abundant. The conformably overlying Burrum Coal Measures (?lower to middle Albian) were deposited within fluvial settings hosting extensive peat-forming mires in floodbasin environments. Sedimentation ceased after deposition of the Burrum Coal Measures (Fig. 2) and the basin was subjected to faulting and moderate folding before deposition of fluvio-lacustrine Elliot and Takura formations in the mid-Cenozoic.

Gentle post-Albian deformation was probably associated with the breakup of Australia and Tasmantis (comprising New Zealand, the Lord Howe Rise, and associated submarine plateaux) and asymmetrical opening of the Tasman Sea (Coleman, 1980; Bryan et al., 1997). As a result of this deformation, the Maryborough Formation is now exposed along the flanks of a series of NW-SE trending anticlines/synclines (Fig. 1).

MATERIAL AND METHODS

Material from the Maryborough Formation held in the collections of both the Geological Survey of Queensland, Brisbane (prefixed QSQF), and the Natural History Museum, London (prefixed NHMV) was investigated. All studied specimens are derived from Corporation Quarry, also known as Baddow Quarry (Fleming, 1966b) in the western part of Maryborough city near the junction of the main Aldershot railway with the Brisbane-Maryborough railway (Fig. 1). Specimens cited by Walkom (1918) as being from 'Argyle Creek, three miles northwest of Aldershot' are probably derived from the overlying Burrum Coal Measures. All of the plant fossils are from the upper part of the Maryborough Formation and are preserved as impressions (lacking cuticular details) in pale

grey, commonly silicified, siltstone. All specimens were illustrated under strong unilateral, low-angle light using Kodak Techpan film. Line-drawings were composed from photo-enlargements.

SYSTEMATIC PALAEOBOTANY

POLYPODIOPHYTA OSMUNDALES OSMUNDACEAE

Phyllopteroides (Medwell) emend. Cantrill & Webb 1987

TYPE SPECIES. *Phyllopteroides dentata* (Medwell) Cantrill & Webb 1987; upper Eumeralla Formation (Albian); Killara Bluff, Otway Basin, Victoria.

Phyllopteroides serrata Cantrill & Webb 1987 (Fig. 3A-C)

Sphenopteris sp. Walkom, 1918: p. 6; pl. 1, figs 4,5.

MATERIAL. HOLOTYPE: NMVP167486; Koonwarra fish beds, upper Strzelecki Group (Aptian); Koonwarra, Gippsland Basin, Victoria (Cantrill & Webb, 1987). OTHER MATERIAL: GSQF959a,b, NHMV24605.

DIAGNOSIS. See Cantrill & Webb (1987, p. 66).

DESCRIPTION. This species is represented by isolated lanceolate to ?oblanceolate pinnules 38-53mm long and 10-12mm wide. The base of each pinnule is not preserved; apices are acute and finely toothed. Pinnule margins are undulate or weakly crenate with typically four denticles developed on each lobe (Fig. 3B). Denticles are less than 0.5mm long and broad and each one corresponds to a vein terminus. The midrib is robust (1mm wide) in the proximal portion of the pinnule but tapers and becomes indistinct in the distal part (Fig. 3A). Lateral veins are alternate, depart acutely from the midrib, arch slightly across the lamina and intersect the margin at 25-40°. Vein density is 4-6 per 5mm along the margin. One specimen (GSQF959a, Fig. 3C) is obovate, has more densely spaced venation and the margins are not clearly denticulate.

REMARKS. Specimen GSQF959a is atypical and may represent a separate taxon but it is an incompletely preserved pinnule. *Phyllopteroides lanceolata* (Walkom) Medwell, 1954 from the Albian Burrum and Styx coal measures in the Maryborough and Styx basins of Queensland is morphologically closest to *P. serrata* but is distinguished by its greater vein density (9-16 per 5mm) and more obtuse secondary veins (marginal angles of 50-70°). *Phyllopteroides dentata* Medwell, 1954, known only from Albian strata

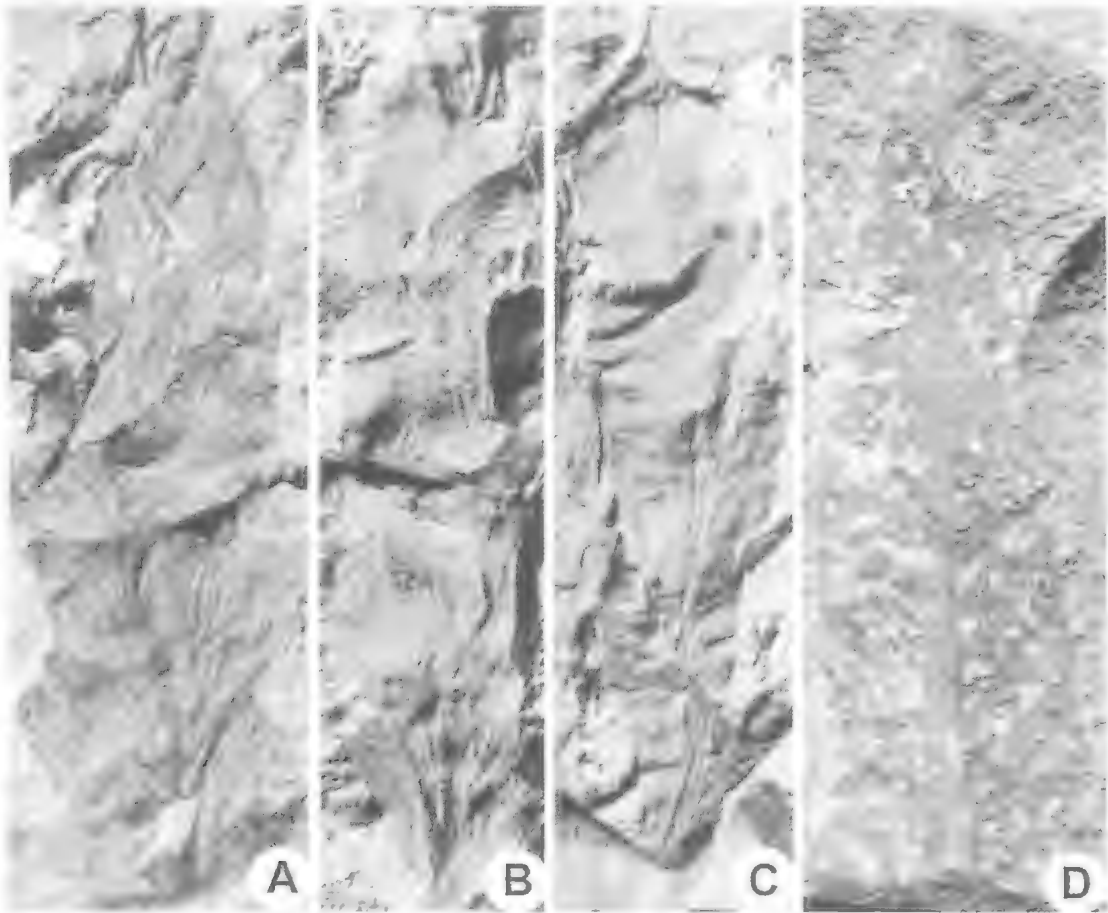


FIG. 3. A-C, *Phyllopteroides serrata* Cantrill & Webb 1987. A, Pinnule with undulate and denticulate margins, NHMV24605 $\times 3$; B, pinnule with denticulate margins, GSQF959b $\times 3$; C, atypical obovate pinnule, GSQF959a $\times 2$. D, *Taeniopteris daintreei* McCoy 1874, apex of leaf, GSQF836 $\times 5$.

of the Otway Basin is a much larger leaf with deeply dentate margins. *Phyllopteroides laevis* Cantrill & Webb, 1987 and *P. westralensis* McLoughlin, 1996 from the Victorian, Queensland and Western Australian Neocomian-Barremian strata are distinguished from *P. serrata* by their finely denticulate or entire margins. In most cases, *P. laevis* also differs in shape having elliptical pinnules. *Phyllopteroides macclymontae* from the Cenomanian Winton Formation, Eromanga Basin, generally has more obtuse venation and a more finely denticulate margin than *P. serrata*.

DISTRIBUTION. Aptian to basal Albian strata of the Gippsland and Otway basins, Victoria (Cantrill & Webb, 1987); and Maryborough Formation (Aptian or lowermost Albian) of the Maryborough Basin, Queensland.

GYMNOSPERMS

?BENNETTITOPSIDA PENTOXYLALES

Taeniopteris Brongniart 1832

TYPE SPECIES. *Taeniopteris vittata* Brongniart 1832; Jurassic; Whitby, England.

Taeniopteris daintreei McCoy 1874 (Figs 3D, 4A,C)

Taeniopteris elongata Walkom, 1918: p. 6; pl.1, figs 1-3.
Taeniopteris Tenison-Woodsii (Etheridge Jr) Walkom, 1918: p. 8.
Taeniopteris sp. Walkom, 1918: p. 8.

LECTOTYPE. NMVP12270; upper Strzelecki Group (Aptian); Cape Paterson, Gippsland Basin, Victoria, Australia (selected by Drinnan & Chambers, 1985).

MATERIAL. GSQF836, GSQF843, GSQF845, GSQF846, GSQF958, GSQF961, GSQF962; NHMV24613.

DIAGNOSIS. See McCoy (1875: 15), Seward (1904: 168) and Drinnan & Chambers (1985: 90) for diagnostic characters.

DESCRIPTION. No complete leaves have been preserved. Leaves are elongate spatulate, with entire to slightly undulate margins tapering gently to form a narrow, cuneate, acute base (Fig. 4A). Leaves reach >120mm long and 13-21mm wide. One leaf tip bears a pointed acute apex (Fig. 3D). The prominent midrib is stout, usually 1.5-2mm wide, and narrows towards the apex. Secondary veins are subparallel at 70°-90° to the midrib becoming more acute (50°-60°) towards the apex (Figs 3D, 4C). They dichotomize at or very near the midrib producing a tuning fork shape; few divide further away. Vein density is approximately 18 per 5mm at the margin.

REMARKS. Walkom assigned the *Taeniopteris* specimens from the Maryborough Formation (Walkom, 1918) and Burrum Coal Measures (Walkom, 1919) to several species, however, there is insufficient morphological evidence to establish that these leaves represent distinct taxa. Australian Jurassic-Cretaceous *Taeniopteris* leaves show few consistent morphological distinctions between established species. Taxa have been differentiated on the basis of secondary venation angles, margin form and average size (McLoughlin & Drinnan, 1995). However, Drinnan & Chambers (1985) showed that *Taeniopteris daintreei* leaves may incorporate a considerable range of forms at a single locality. Most Jurassic to Cenomanian specimens from all parts of Australia (e.g. forms illustrated by Seward, 1904; Walkom, 1921; White, 1981; Glaessner & Rao, 1955; Gould, 1980; Douglas, 1969, 1973; Drinnan & Chambers, 1985, 1986; McLoughlin et al., 1995; McLoughlin, 1996) are now assigned to, or closely compared with, *Taeniopteris daintreei* in its broader sense (Drinnan & Chambers, 1985). *Taeniopteris howardensis* described by Walkom (1919) from the Burrum Coal Measures is a small obovate leaf that probably represents an end member of the morphological spectrum encompassed by *T. daintreei*. Australian species are also morphologically comparable to the Early Cretaceous *T. spatulata* from India (Bose & Banerji, 1981) and *T. stipulata* from New Zealand (McQueen, 1956). Clear demarcation between these species on gross morphological features is not possible but cuticular differences may be present (Douglas, 1969; Drinnan & Chambers, 1985). Additionally, Drinnan & Chambers (1985) noted

that *Taeniopteris* leaves were associated with different microsporangia (*Sahnia*) and fruits (*Carnoconites*) in India, Australia and New Zealand and on this basis we consider it preferable to retain the Australian leaves in *T. daintreei*.

DISTRIBUTION. Widely distributed in Australian basins in Middle Jurassic (Walkom, 1921) to Aptian (Douglas, 1969) strata. *Taeniopteris* leaves from Albian and Cenomanian strata of the Maryborough and Eromanga Basins (Walkom, 1919; McLoughlin et al., 1995) are closely comparable to *T. daintreei*.

BENNETTITALES

Otozamites Braun in Münster, 1843

TYPE SPECIES. *Otozamites (Zamites) brevifolius* Braun in Münster, 1843. (See Watson & Sincock, 1989 for discussion of typification).

DISCUSSION. Bennettite foliage genera are typically discriminated on the basis of cuticle data and the shape of pinna bases (Watson & Sincock, 1992). *Ptilophyllum* species are defined by having a decurrent, basiscopic, pinnule base whereas *Otozamites* species have an auricle on the acroscopic side of the base. Bose & Kasat (1972) and Bose (1974) reassigned many Indian species of *Otozamites* to *Ptilophyllum*, leaving only five species within *Otozamites*. However, Bose & Kasat (1972) noted that many of the Indian *Ptilophyllum* species have characteristics that are gradational between the two genera, with regard to the definitions used by Watson & Sincock (1992). Harris (1969) and Watson & Sincock (1992) also discussed gradational characteristics between these bennettite genera. *Otozamites* and *Ptilophyllum* may be useful as descriptive form genera but their separation may not have phylogenetic significance.

Otozamites sp. (Fig. 4B)

Ptilophyllum (Williamsonia) pecten (Phillips) Walkom, 1918: p. 10; pl. 1, fig. 7.

MATERIAL. GSQF957.

DESCRIPTION. The single available incomplete frond is pinnate but its gross shape is indeterminate. The frond is 7mm wide and has a length >45mm (total estimated length about 150mm). The rachis is 0.5mm wide. The pinnule bases are not preserved completely so their insertion on the rachis is not clear. The bases appear to expand on the acroscopic side and may form an auricle. On the basiscopic side, the bases appear to contract.

Adjacent pinnules are slightly imbricate, falcate, with pointed, acute and distally inclined apices (Fig. 4B). The pinnules arise at 50°-70° from the rachis and reach 4.5mm long and 1.75mm wide (average = 4 × 1mm). Veins emerge from the centre of pinnule bases and are divergent, dichotomous and lack anastomoses. Around 3-4 veins are evident across the centre of the pinnules.

REMARKS. Based on the slightly expanded acroscopic bases of some pinnules we assign this frond to *Otozamites*. However, the incomplete specimen lacks key frond features and cuticle details to enable assignment to an established species. Walkom (1918) assigned this specimen to *Ptilophyllum pecten* based on comparisons with fronds from the Stanwell Coal Measures, Queensland (Neocomian), and the Yorkshire Jurassic. Both the Stanwell specimens (Walkom, 1917), and the Maryborough Formation frond are transferable to *Otozamites*. The Maryborough form has similarities to bennettite impressions described previously from India as *Otozamites bengalensis* (Oldham & Morris, 1863), *Ptilophyllum cutchense* (Bose & Kasat, 1972) and with the smaller, basal pinnae of *Ptilophyllum acutifolium* fronds (Bose & Kasat, 1972). *Otozamites bengalensis* has been reassigned both to *Ptilophyllum acutifolium* (Bose, 1974) and *Ptilophyllum cutchense* (Bose & Kasat, 1972). It is possible that the morphology of fronds from a single plant may have varied sufficiently to account for the differences between these form species but without cuticular evidence this cannot be verified. Within Australia, the Maryborough Formation specimen most closely resembles leaves from: the Neocomian Algebuckina Sandstone in South Australia (*Otozamites bengalensis* in Glaessner & Rao, 1955); the Neocomian-Barremian Broome Sandstone and Leederville and Bullsbrook Formations, Western Australia (described as *Ptilophyllum cutchense* by McLoughlin, 1996); the Neocomian Stanwell Coal Measures, Queensland (assigned to *P. pecten* by Walkom, 1917); and the Albian Burrum Coal Measures (assigned to *P. pecten* by Walkom, 1919).

DISTRIBUTION. Maryborough Formation, Maryborough Basin, Queensland. Comparable forms are discussed above.

PINALES ARAUCARIACEAE

Araucariacean ovulate cones (Figs 4E, 5B)

Araucarites polycarpa Tenison-Woods. Walkom, 1918: p. 10.
Araucarites sp. Walkom, 1918: pl. 2, fig. 10.

MATERIAL. GSQF842, GSQF853.

DESCRIPTION. Two cones are available; one (GSQF853) is preserved as a slightly off-centred axial impression (Figs 4E, 5B), the other (GSQF842) is an incomplete lateral impression (Fig. 5B). The cones are circular in transverse section and elliptical or oblong in longitudinal section. The cones are 25-28mm in diameter and >55mm long (apex and base absent). The cones are composed of tightly packed, helically arranged scales with transversely elongate apical ends. Scale apices are 4-7mm wide and 2-3mm deep. The apices are truncate to gently rounded, or in some cases may have a short, blunt point, but prominent spines are absent. Although the cone compressed in an apical orientation has undergone slight distortion, an 8:13 phyllotaxy is evident (Fig. 5B).

REMARKS. We refrain from placing these cones in an established taxon or under new nomenclature owing to the dearth of available cone-scale characters. The absence of prominent apical spines on the cone scales favours an affinity with *Agathis* rather than *Araucaria* or *Wollemia* amongst extant Araucariaceae. Walkom (1918) assigned these specimens to two species of *Araucarites* but there are insufficient morphological differences to warrant specific differentiation. Numerous detached araucariacean cone scales have been described from the Australian Mesozoic (e.g., Walkom, 1921; Drinnan & Chambers, 1986; McLoughlin et al., 1995). However, the absence of any detached cone scales in the Maryborough assemblage prevents assessment of whether the seeds were shed independently of the scale (as in modern *Agathis* and *Wollemia*) or whether the scales retained their seeds (as in *Araucaria*) after detachment from the cone. Similar cone fragments with tight, spirally arranged scales occur in the Stanwell Coal Measures near Rockhampton (Walkom, 1917), although the scale apices of the Maryborough species are about twice as broad. Substantially smaller and narrower araucariacean cones were recorded from the Victorian upper Strzelecki Group (Drinnan & Chambers, 1986: fig. 30A,B) but it is

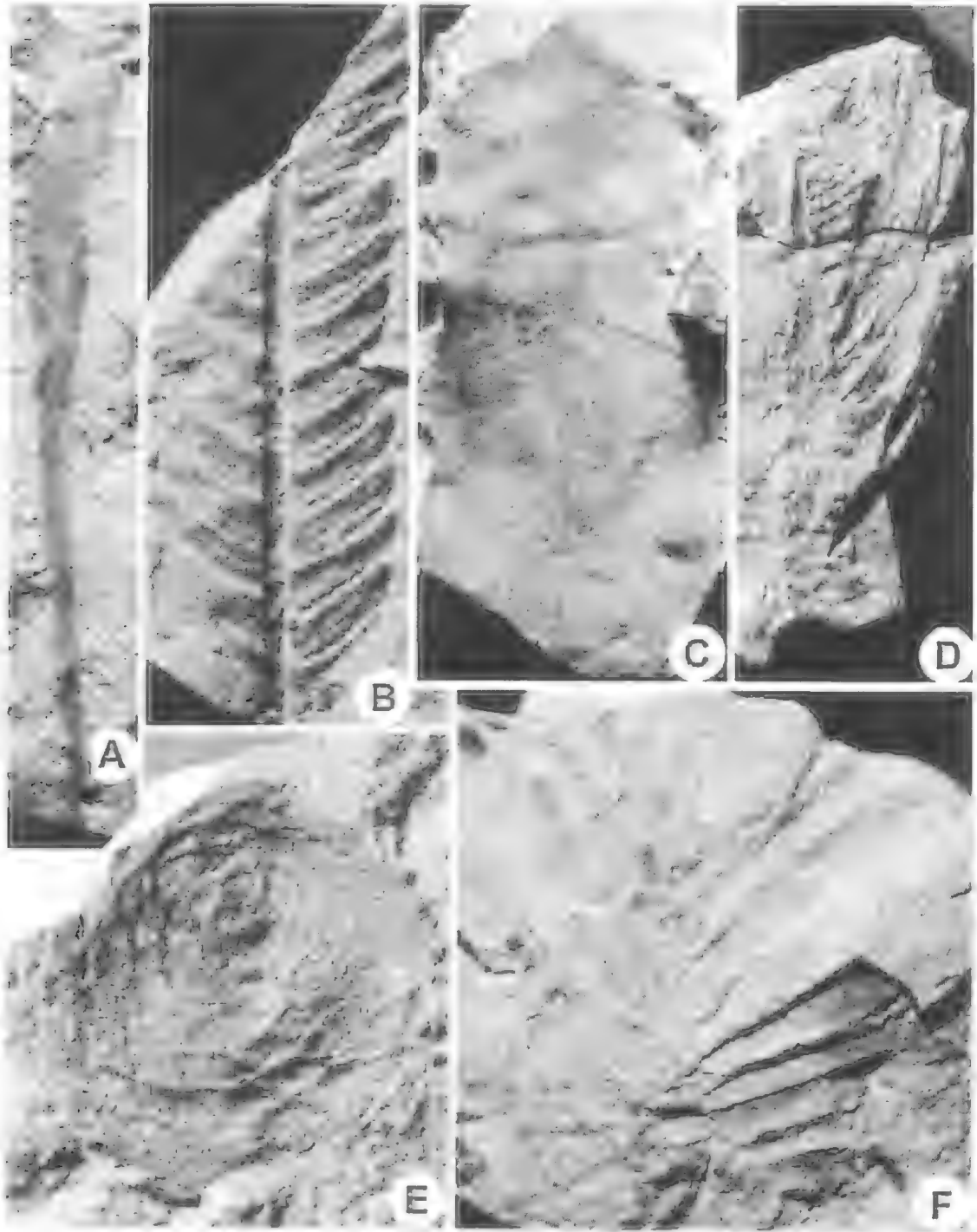


FIG. 4. A, C, *Tacniopteris dauntreei* McCoy 1874; A, elongate leaf showing gently tapering base, GSQF845 \times 1; C, broad leaf with undulate margins showing venation details, GSQF961 \times 2. B, *Otozamites* sp., fragment of pinnate frond, GSQF957 \times 5. D, F, *Podozamites mesozoica* Walkom comb. nov.; D, axis with rhythmic growth increments, GSQF954 \times 1; F, terminal portion of axis with helically arranged leaves, NHMV24611 \times 2. E, near-axial impression of an araucariacean ovulate cone, GSQF853 \times 2.

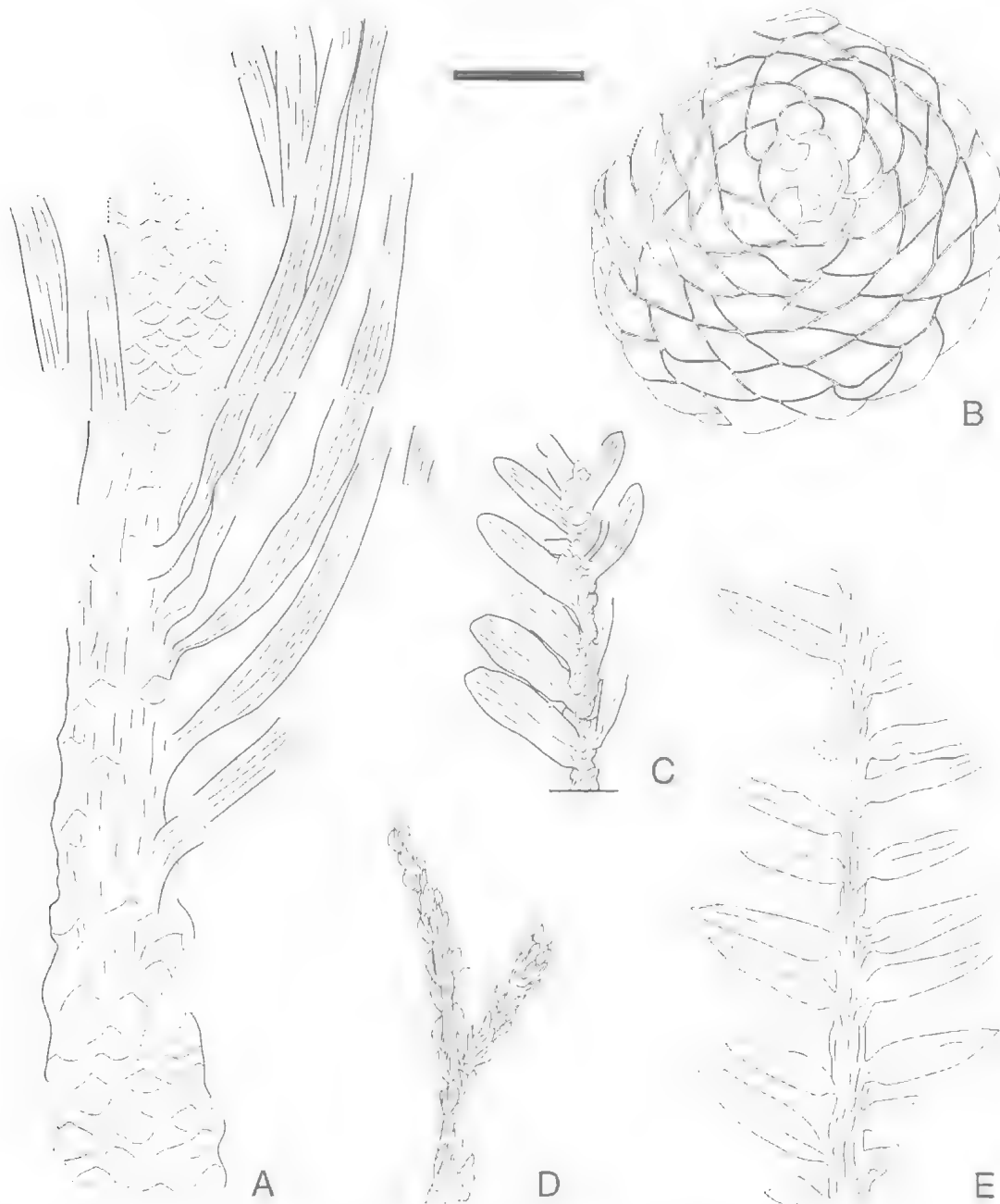


FIG. 5. Line-drawings of conifer remains from the Maryborough Formation. A, *Podozamites mesozoica* Walkom comb. nov., GSQF954; B, Araucariacean ovulate cone, GSQF853; C, *Pagiophyllum jemmetti* Walkom 1918, GSQF1133; D, *Pagiophyllum* sp., NHMV24614; E, *Elatocladus baddowensis* sp. nov., GSQF853. Scale bar 10mm.

unclear whether the Victorian specimens represent complete cones, cone axes, or even whether these cones were ovulate or microsporangiate.

DISTRIBUTION. Maryborough Formation (Aptian or earliest Albian), Maryborough Basin; possibly Stanwell Coal Measures (Neocomian), Yarrol Block, Queensland.

INCERTAE FAMILIAE

Podozamites (Brongniart) Braun 1843

TYPE SPECIES. *Podozamites distans* (Presl) Braun, in Münster 1843; Lower Liassic, Bayreuth, Bavaria.

Podozamites mesozoica Walkom comb. nov.
(Figs 4D,F, 5A, 6A,E)

Araucarites mesozoica Walkom, 1918: p. 11; pl. 2, figs 1-3.

MATERIAL. LECTOTYPE: GSQF954 (Figs 4D, 5A, 6E); Baddow Quarry, Maryborough Formation (Aptian or earliest Albian), Maryborough, Queensland (here designated). OTHER MATERIAL. NHMV24610, NHMV24611.

DIAGNOSIS. Stout axes with rhombic leaf scars showing rhythmic growth increments or bearing linear leaves with around 4 parallel veins. Leaves slightly tapered but connected to axis by a broad base, apices rounded.

DESCRIPTION. Axes reaching >66mm long and up to 9mm thick bearing spirally arranged, linear, multiveined leaves (Figs 4D,F, 5A, 6E). Leaf scars on the axis are broadly rhombic, mostly 3mm wide, and 1.5-3mm high. The distal adaxial margin of each leaf scar is typically more deeply impressed into the sediment matrix than the proximal (abaxial) margin. Variable leaf scar spacing along the axis represents rhythmic growth increments (Figs 4D, 5A, 6A). Scar spacing varies from 2-3mm (separated by featureless areas of the axis) to closely abutting. The leaves are linear, 20->40mm long, 2.5-3mm wide. The entire margins gently taper towards the base but the leaves retain a broad basal attachment; leaf apices are blunt to rounded. The leaves are arrayed at 20-70° from the axis and may be straight, or gently inflexed or reflexed. At least four parallel veins are present in each leaf; dichotomies and anastomoses are not evident.

REMARKS. The lectotype selected here is the only specimen of this species figured by Walkom (1918). The cone-like feature reported by Walkom (1918) at the distal end of this specimen (Fig. 4D, 5A) is here interpreted to be a region of closely abutting rhomboid leaf scars. The species is transferred to *Podozamites* (Presl) Braun, a genus used for coniferous remains of uncertain familial affinity having strap-shaped leaves with several longitudinal veins. *Araucarites* by contrast is typically applied to isolated cone-scales of araucariacean affinity (Taylor & Taylor, 1993). Some *Podozamites* species may be allied to the Araucariaceae but a lack of cuticle characters or

attached fruits for *P. mesozoica* prevents definite assignment to an established conifer family. Several *Podozamites* species were described from the overlying Burrum Coal Measures (Albian) in the Maryborough Basin by Walkom (1919) but these all have substantially smaller leaf length:width ratios than *P. mesozoica*. Cantrill (1991) described three *Podozamites* species with preserved cuticle from the Albian part of the Otway Group of Victoria. Of these taxa *P. taenioides* and *P. notabilis* can be distinguished by their distinctly decurrent leaf bases. *Podozamites pinnatus* is similar to *P. mesozoica* in its more abbreviated, rhombic leaf base and the presence of around four prominent veins/striations in the lamina but the leaves of the former are typically twice as wide. Some forms of the conifer complex assigned to *Araucaria* sp. cf. *A. mesozoica* from the Winton Formation (Cenomanian) of Queensland by McLoughlin et al. (1995) are similar to the Maryborough species. However, the Winton Formation forms mostly have broader leaves with more numerous veins. Nevertheless, the Winton forms do show rhythmic leaf development on the axes (Dettmann et al., 1992) suggesting a similar seasonal growth habit. *Podozamites mesozoica* is also comparable in terms of gross morphology to the foliage of other fossil genera such as *Lindleycladus* Harris (1979) but these are generally differentiated on the basis of cuticular features that are unavailable in the Maryborough specimens.

DISTRIBUTION. Maryborough Formation (Aptian or earliest Albian), Queensland.

INCERTAE FAMILIAE

Pagiophyllum Heer 1881 emend. Harris 1979

TYPE SPECIES. *Pagiophyllum circinicum* (Saporta) Heer 1881; Upper Jurassic, Sierra de San Luiz, Portugal.

Pagiophyllum jemmetti Walkom 1918
(Figs 5C, 6C,D, 7A, C)

Pagiophyllum Jemmetti Walkom, 1918: p. 13; pl. 2, figs 7,8.

MATERIAL. LECTOTYPE: Here selected as GSQF1133 (Figs 5C, 6D); illustrated by Walkom (1918; pl. 2, fig. 7). GSQF851, GSQF952, GSQF953, GSQF956, NHMV24608.

DIAGNOSIS. Straight ultimate shoots bearing densely packed, helically arranged, oblong, ovate, to awl-shaped leaves lacking cuticle, inserted at 45-90° to the axis. Leaf length:width ratio 2:1-4:1.

DESCRIPTION. Axes reaching >76mm long and 6mm wide, bearing spirally arranged leaves. The

leaves are oblong, ovate or awl-shaped, closely spaced but spreading, and inserted at 45-90° to the axis (Figs 5C, 6D, 7A,C). The leaves are thick at the base but otherwise dorsiventrally flattened, straight or slightly inflexed (Fig. 6C,D). The leaves are 5-13mm long, 1.5-5.5mm wide, with rounded or obtusely pointed apices and broadly attached or slightly decurrent bases. Where the leaves are broken or detached a 2.5mm wide, 1-2 mm high rhombic scar is retained on the axis. The leaf margins are entire. The leaves generally possess >2 parallel longitudinal striations per leaf but the venation is generally indistinct.

REMARKS. A specific diagnosis is provided here as Walkom (1918) gave only a general description of this taxon. Axes with similar crowded, short, lanceolate leaves from the Broome Sandstone (Neocomian) assigned to *Araucaria* sp. C by McLoughlin (1996) are distinguished by their acutely pointed leaf apices. A number of Laurasian *Pagiophyllum* species have grossly similar morphology to *P. jemmetti* (see for example: Harris, 1979) but these are mostly differentiated on cuticular characters unavailable in the Maryborough specimens. *Pagiophyllum jemmetti* can, nevertheless, be distinguished from most species by its densely crowded, spreading foliage, relatively low leaf length:width ratio and blunt leaf apices. *Pagiophyllum*- or *Geinitzia*-type remains from the Early Cretaceous of southern Australia are generally typified by smaller, narrower, acutely inserted leaves (Cantrill & Douglas, 1988).

DISTRIBUTION. Maryborough Formation (Aptian or earliest Albian), Maryborough Basin, Queensland.

***Pagiophyllum* sp. A**
(Figs 5D, 8C)

MATERIAL. NHMV24614.

DESCRIPTION. This branched twig bears spirally arranged, awl-shaped leaves (Figs 5D, 8C). The axes are >26mm long (apex not preserved), <1mm wide and branch at 15-20°. The leaves are 2mm long, 0.75mm wide and 0.5mm thick. They are univeined and most are closely appressed to the axis, slightly overlapping the bases of leaves in the succeeding spiral. In a few cases the leaves are slightly divergent from the axis. Deep imprints in the sediment left by some leaves suggest that they were trifacial (i.e., they possessed a prominent abaxial keel). The leaves are broadly based and

perhaps slightly decurrent. The apices are blunt and incurved, and the margins are entire.

REMARKS. Walkom (1918) either overlooked this species or the specimen was not available in his studied collections. The only available specimen is currently held in the collections of the Natural History Museum, London. The generic boundaries between *Pagiophyllum*, *Brachyphyllum* and *Geinitzia* are arbitrary and differentiation of these form genera has little phylogenetic meaning at present. *Brachyphyllum* has leaves that are shorter than broad, *Geinitzia* has leaves that are as thick as they are broad, and *Pagiophyllum* typically has leaves that are longer than broad and broader than thick. The Maryborough specimen is therefore assigned to *Pagiophyllum* but the poor preservation of the single available specimen prohibits confident assignment to an established species or warrants erection of a new species. It is similar in leaf size, shape and arrangement to some specimens assigned to cf. *Austrosequoia wintonensis* Peters & Christophel 1978 from the Winton Formation, Queensland, and to *Araucaria* sp. A of McLoughlin (1996) described from the Broome Sandstone (Neocomian), Western Australia.

DISTRIBUTION. Maryborough Formation (Aptian or earliest Albian). Several other fossils from northern Australia of Neocomian-Cenomanian age are closely comparable.

INCERTAE FAMILIAE

***Elatocladus* Halle emend. Harris 1979**

TYPE SPECIES. *Elatocladus heterophylla* Halle 1913; Jurassic, Hope Bay, Graham Land, Antarctica.

***Elatocladus baddowensis* sp. nov.**
(Figs 5E, 7B,D, 8A,B)

?*Pterophyllum* sp. Walkom, 1918: pl. 1, fig. 6.
?*Taxites* sp. Walkom, 1918: p. 13; pl. 1, fig. 9.

MATERIAL. HOLOTYPE: GSQF853 (Fig. 5E, 7B), counterpart = NHMV24609 (Fig. 7D); Baddow Quarry (Corporation Quarry), Maryborough Formation (Aptian or earliest Albian), Maryborough, Queensland. OTHER MATERIAL: GSQF838, GSQF7267, NMHV24606, NHMV24609.

DIAGNOSIS. Slender axes with spirally inserted but basally twisted leaves forming a distichous, opposite to sub-opposite arrangement. Leaf bases slightly contracted and decurrent for 1-2mm along axis. Leaves oblong to lanceolate

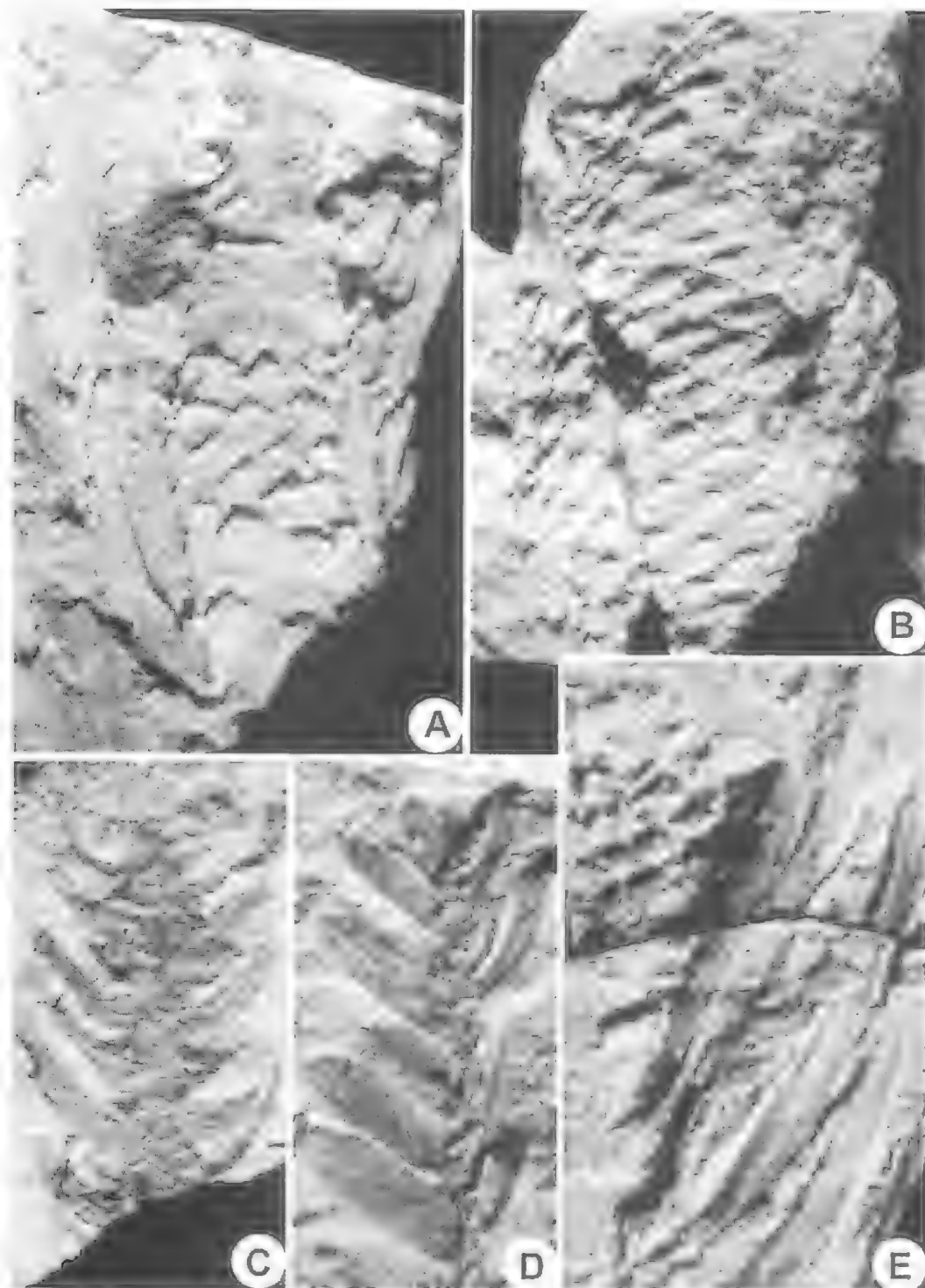


FIG. 6. A, E, *Podozamites mesozoica* Walkom comb. nov.; A, stout axis with rhombic leaf scars and linear leaves, NHMV24610 $\times 3$; E, details of venation and leaf attachments, GSQF954 $\times 3$. B, lateral impression of an araucariacean ovulate cone, GSQF842 $\times 2$. C, D, *Pagiophyllum jenmetti* Walkom 1918; C, lateral imprint showing awl-shaped leaves, GSQF952 $\times 3$; D, terminal portion of branch with oblong leaves, GSQF1133 $\times 3$.

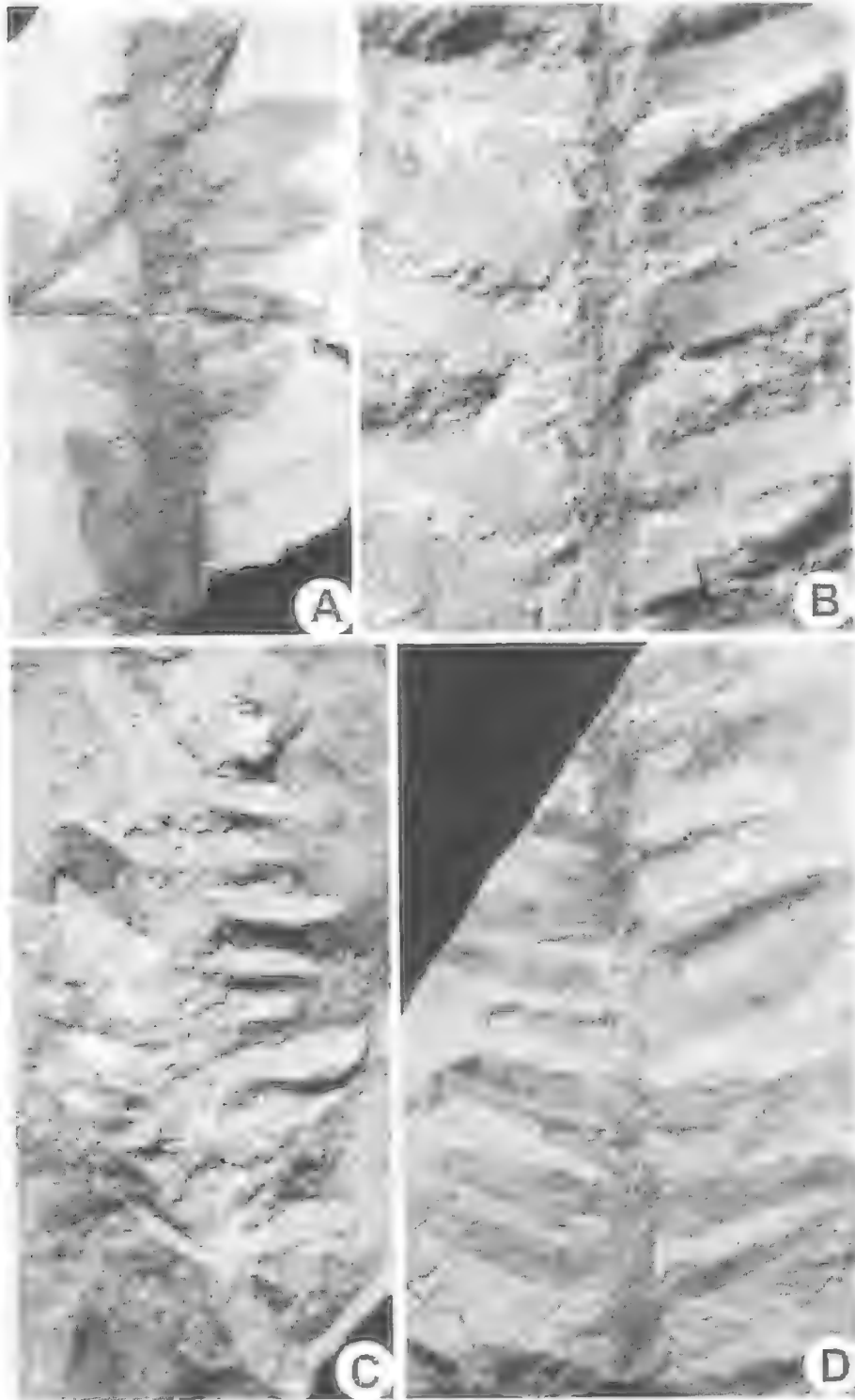


FIG. 7. A, C, *Pagiophyllum jemmetti* Walkom 1918; A, stout axis with ovate leaves, NHMV24608 $\times 2$; C, axis with helically arranged leaves, GSQF956 $\times 3$. B, D, *Elatocladus baldowensis* sp. nov.; B, details of leaf insertion on the axis, GSQF853 $\times 4$; D, twig bearing univeined, distichous leaves, NHMV24609 $\times 3$.

with a length:width ratio of 4.5:1 to 5.5:1. Venation ill-defined and cuticle unknown.

DESCRIPTION. Slender (1.5-3mm wide) axes reaching >41 mm long, bearing spirally inserted but basally twisted leaves in a distichous arrangement (Figs 7B,D, 8A,B). The leaves are opposite to sub-opposite, and leaf pairs are typically 1.5-2mm apart. Leaves are 6-17mm long and 1.5-2.5mm wide. They are typically straight or slightly inflexed and arranged at 45-80° to the axis. Leaves are dorsiventrally flattened and slightly contracted towards the base (Fig. 7B). The leaves are oblong to lanceolate with rounded apices and entire margins. The base may be decurrent for 1-2mm along the axis. The venation is generally indistinct. A single median vein is evident on a few leaves and several parallel striations are evident on others.

REMARKS. *Elatocladus* has been used for conifer remains of widely varying morphology since its erection by Halle (1913). Some, like specimens assigned to *Elatocladus planus* (Feistmantel) Seward from the Jurassic Talbragar fish beds of New South Wales (Walkom, 1921), have atypical features such as transverse striae on the lamina and probably warrant generic segregation. Some species have a spiral arrangement of leaves whereas others show a distinctly distichous arrangement. Harris (1979) provided the history of generic emendations for *Elatocladus*. It is employed here in its broadest sense (Harris, 1979) to include 'fossil conifer shoots bearing elongated, dorsiventrally flattened leaves with a single vein. Leaves divergent from the stem'. Basal twisting of the spirally inserted leaves to a distichous arrangement is common amongst *Elatocladus* species but the majority of forms assigned to this genus have a more contracted, commonly petiolate, leaf base. Most *Elatocladus* species, and forms assigned to the morphologically similar genera *Rissikia* Townrow 1967 and *Mataia* Townrow 1967, have a more prominent midrib in the leaves than *E. baddowensis*. The leaves of this species may have developed ill-defined longitudinal creases during desiccation giving the false impression of multiple veins in the lamina. Longitudinal creasing and basal twisting of the leaves is similar to that illustrated by Florin (1931) for extant *Podocarpus rospigliosii*. A podocarpacean alliance is possible for *E. baddowensis* given the podocarpacean affinities of morphologically similar foliage from the Australian Mesozoic (Townrow, 1967, 1969). However, if the sparse

longitudinal creases represent multiple parallel veins in the lamina then a close comparison can be drawn with the smaller (distichous) foliar twigs assigned to *Araucaria* sp. cf. *A. mesozoica* from the Winton Formation of the Eromanga Basin (McLoughlin et al., 1995). Walkom's (1918, pl. 1, fig. 6) ?*Pterophyllum* sp. appears to be a poorly preserved example of *E. baddowensis*.

DISTRIBUTION. Maryborough Formation (Aptian or earliest Albian), Maryborough Basin, Queensland.

ORDER UNCERTAIN

Ginkgophyllum Saporta 1875

TYPE SPECIES. *Ginkgophyllum grassertii* Saporta 1875; Permian, Lodève, France.

Ginkgophyllum sp. (Fig. 8E)

Ginkgo digitata (Brongniart) Walkom, 1918: p. 9; pl. 2, figs 4,5.

MATERIAL. GSQF850.

DESCRIPTION. This spatulate leaf is >23mm long (base not preserved), 19.5mm wide; the widest point occurring 9mm from the apex. Proximal to the widest point the leaf's margins are entire and taper acutely towards the base. The apical margin is deeply dissected into five or six narrowly rectangular to slightly spatulate lobes 2.5-4.5mm wide (Fig. 8E). Notches between these lobes are narrowly acute and 2-10mm deep. The apices of the lamina lobes are poorly defined but range from broadly rounded to gently undulate or slightly toothed. The venation is mostly indistinct. It consists of sub-parallel, sparsely dichotomous veins that gently arch in the distal part of the lamina and terminate along the distal margin of the apical lobes. Vein density is around 28 per 10mm across the distal part of the lamina.

REMARKS. Although the base is not preserved, the gently tapering margins of the available specimen suggest that the leaf was not strictly petiolate, a feature more reminiscent of the leaf bases of early Mesozoic seed-ferns such as *Sphenobaeira* and *Kannaskoppifolia* (Anderson & Anderson, 1989; in press) rather than the Ginkgoaceae. Apart from *Ginkgophytopsis truncata* sp. nov. (described below) other fan-shaped leaves with dichotomous venation from the Australian Lower Cretaceous (see Walkom, 1919; Douglas, 1965; Drinnan & Chambers, 1986; McLoughlin et al., 1995) consistently have

petiolate bases and can be more confidently attributed to the Ginkgoaceae. *Ginkgophytopsis truncata* differs from *Ginkgophyllum* sp. by its non-dissected, truncate apex. The former also has sparse cross-connections between the veins although this feature may not be discernable in *Ginkgophyllum* sp. owing to the poor preservation of venation details.

DISTRIBUTION. Known only from the type formation.

***Ginkgophytopsis* (Høeg)
emend. Retallack 1980**

TYPE SPECIES. *Ginkgophytopsis flabellata* (Lindley & Hutton) Høeg 1967; Newcastle Coal Measures (upper Carboniferous), England.

***Ginkgophytopsis truncata* sp. nov.
(Fig. 8D)**

Ginkgo sp. Walkom, 1918: p. 9; pl. 2, fig. 6.

ETYMOLOGY. For the truncate apex of the leaf.

MATERIAL. HOLOTYPE: GSQF964; Maryborough Formation (Aptian or earliest Albian); Baddow Quarry (Corporation Quarry), Maryborough, Queensland, Australia.

DIAGNOSIS. Cuneate leaf with truncate apex, subparallel venation with most dichotomies developed on the marginal vein, rarely amongst veins of the central lamina. Leaf length:width ratio >2:1. Vein anastomoses rare.

DESCRIPTION. Leaf is cuneate, >65mm long (base not preserved; estimated total length = 82mm), and reaches a maximum width of 29mm at the apex. The margins are entire and taper gently towards the base. The apex is sharply truncate. Veins are mostly parallel to subparallel. Marginal veins (located 0.5mm inside the lamina margin) regularly dichotomize to produce inner lamina veins which in most cases run the length of the leaf and terminate at the apical margin without further dichotomies (Fig. 8D). In a few cases these inner lamina veins undergo a further dichotomy or more rarely they recombine with adjacent veins. Vein density ranges from 20 per 10mm near the leaf base to around 14 per 10mm at the apex.

REMARKS. This form is one of the largest foliar fragments in the fossil assemblage. It is unclear whether the apex of the illustrated specimen is complete or whether the leaf has been broken transversely below the apex. A sharply truncate apex is consistent with several other *Ginkgo*-like

leaves recorded from the Gondwanan Early Mesozoic (Retallack, 1980; Anderson & Anderson, in press). However, if the apex has been detached then this leaf form may be conspecific with *Ginkgophyllum* sp. with which it shares a number of additional characters. Both leaves are atypical of the Ginkgoaceae sensu stricto in lacking a petiole. The specimen with sparsely reticulate venation is here assigned to the form-genus *Ginkgophytopsis* following the usage of Retallack (1980) without inferring a natural affinity with the Ginkgoaceae. Retallack (1980) recognized six species in this genus. *Ginkgophytopsis truncata* sp. nov. differs from the other species by its truncate apex and predominance of vein dichotomies adjacent to the leaf margins. It is possible that these leaves are late-surviving representatives of fan-leaved seed-fern groups that included *Kannaskoppifolia* and *Sphenobaiera*, which were more abundant and diverse in the early Mesozoic.

DISTRIBUTION. Known only from the type formation.

INCERTAE SEDIS

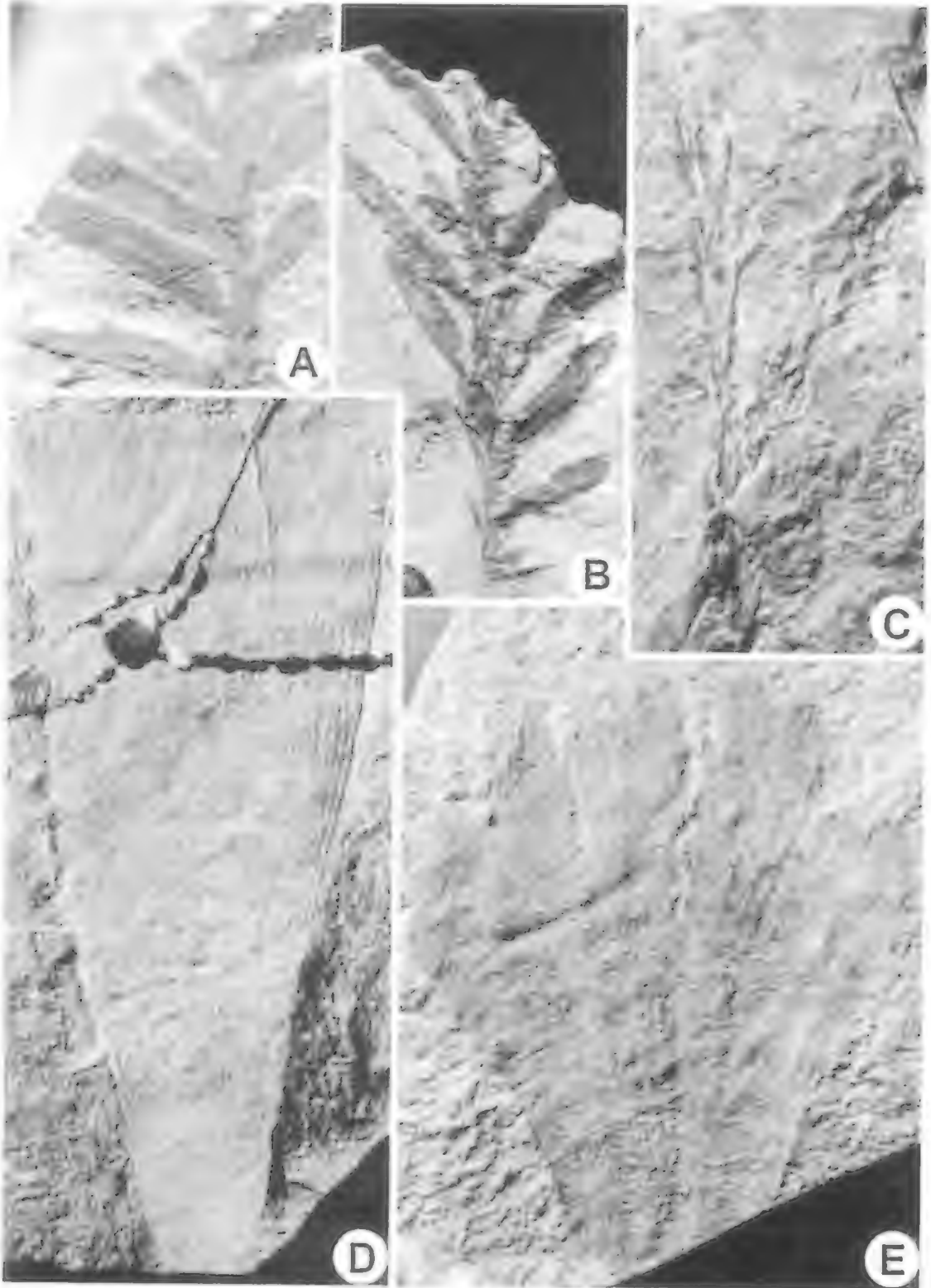
***Equisetalean diaphragms or
gastropod opercula*
(Fig. 9A,B)**

Equisetites sp. cf. *E. rajmahalensis* Oldham & Morris
Walkom, 1918: p. 5; pl. 1, fig. 8.

MATERIAL. GSQF852, NHMV24604.

DESCRIPTION. Circular organs 15mm in diameter consisting of an inner disc and an outer ribbed rim. The inner disc is either featureless or has a low, indistinct spiral ridge (Fig. 9B). The rim is marked by a 1.5mm wide zone of radially arranged ridges and grooves, each around 0.5-1mm wide (Figs 9A,B).

REMARKS. Walkom (1918) assigned these fossils to *Equisetites* sp. cf. *E. rajmahalensis* Oldham & Morris. Tenison-Woods (1884) illustrated similar equisetalean axis diaphragms from the Walloon Coal Measures (Jurassic) of the Moreton Basin and Walkom (1915) also figured comparable impressions from the Stanwell Coal Measures (Neocomian) near Rockhampton. Although no foliage is preserved with either the Maryborough or Stanwell fossils their similarity to equisetalean remains illustrated elsewhere probably led him to interpret the fossils as nodal diaphragms. The marginal ribs may correspond to either the positions of vascular bundles or indentations in the diaphragm adjacent to radially



disposed leaves. However, equisetalean nodal diaphragms typically have more prominent radiating grooves/ridges corresponding to vascular bundles that extend from a small, central vascular ring to the diaphragm margin (Gould, 1968). Both the Maryborough and Stanwell fossils are associated with marine fossils and could be alternatively interpreted as gastropod opercula with marginal teeth and sockets. The indistinct spiral ridge in the centre of one specimen (GSQF852: Fig. 9B) supports this interpretation but a lack of preserved carbonaceous matter or shell material precludes confirmation of either interpretation.

DISTRIBUTION. Maryborough Formation (Aptian or earliest Albian), Maryborough Basin; conspecific or closely related forms occur in the Stanwell Coal Measures (Neocomian), Yarrol Block.

INVERTEBRATE BURROWS

Chondrites (Brongniart) Sternberg 1833

TYPE SPECIES. *Chondrites targionii* (Brongniart) Sternberg 1833; by subsequent designation of Andrews (1955); age uncertain, England.

Chondrites sp. (Fig. 9C)

? Roots. Walkom, 1918: p. 14; pl. 2, fig. 9.

MATERIAL. GSQF841, GSQF846, NHMV24612.

DESCRIPTION. Burrows, circular in cross-section, 1-1.5mm wide, and reaching in excess of 32mm long. The burrows are variably orientated with respect to bedding and show sparse branching and cross-cutting relationships (Fig. 9C). The burrows are generally filled with white to grey mud or fine silt, and are typically paler than the siltstone to very fine sandstone host sediments. The burrows lack obvious linings.

REMARKS. Walkom (1918) tentatively regarded these fossils as the remains of plant roots but he also considered the possibility that they represented 'worm-casts'. His preferred interpretation as roots was based on his observation that the fossils had a whorled arrangement of appendages. Re-examination of Walkom's (1918) illustrated specimen, its counterpart in the

Natural History Museum, London, and associated specimens in the Geological Survey of Queensland collections failed to support a whorled interpretation of the fossils. We argue that their irregular branching and sediment-filled structure favours interpretation as invertebrate burrows and this is supported by a marine depositional environment for the host rocks based on the associated rich invertebrate fossil assemblage (Fleming, 1970). The fossils probably represent feeding structures (Fodinichnia) of infaunal invertebrates (Simpson, 1975).

AGE OF THE ASSEMBLAGE

Plant remains preserved in the Maryborough Formation are co-fossilised with an abundant but relatively low-diversity, marine, invertebrate fauna dominated by bivalves. Invertebrate assemblages from the upper part of the formation in the eastern part of the basin (from the same beds hosting the plant remains) have been regarded as indicative of an Aptian age (Etheridge, 1872; Whitehouse, 1926a,b; Day, 1963; Fleming, 1966a,b,c; 1970; 1976; Barnbaum, 1976). Exposures in the Gundiah area in the southwestern part of the basin have yielded assemblages considered to be of Neocomian-?Barremian age (Fleming, 1966a,b,c, 1970, 1976; Day, 1969). However, palynological studies of bore-core samples from the same area have indicated a wholly Aptian age for the Maryborough Formation (McKellar, 1980). Helby & Partridge (1977) assigned a late Neocomian to early Aptian age for palynomorph assemblages from the basal Maryborough Formation in the eastern part of the basin. Cranfield (1993) indicated an early Aptian to ?early Albian age for the unit in the central part of the basin based on preliminary studies of foraminifera and radiolarians. Walkom (1918) assigned a broad, Early Cretaceous age to the plant fossil assemblages from the Maryborough Formation. Most of the plant taxa recognized in the Maryborough Formation (Table 1) have distributions either restricted to the host unit or they are wide-ranging throughout the Early Cretaceous of Australia. However, the presence of *Phyllopteroides serrata*, a stratigraphic index taxon in southeastern Australian basins (Cantrill & Webb, 1987) favours an Aptian or earliest Albian age for the upper part of the formation.

FIG. 8. A, B, *Elatocladus baddowensis* sp. nov.; A, details of leaf insertion on the axis, GSQF838 \times 4; B, twig with oblong to lorate leaves, GSQF7267 \times 2. C, *Pagiophyllum* sp., branched axis with tightly appressed, awl-shaped leaves, NHMV24614 \times 4. D, *Ginkgophytopsis truncata* sp. nov., cuneate leaf with sparsely anastomosing veins, GSQF964 \times 2. E, *Ginkgophyllum* sp., apical fragment of leaf showing terminal notches, GSQF850 \times 4.

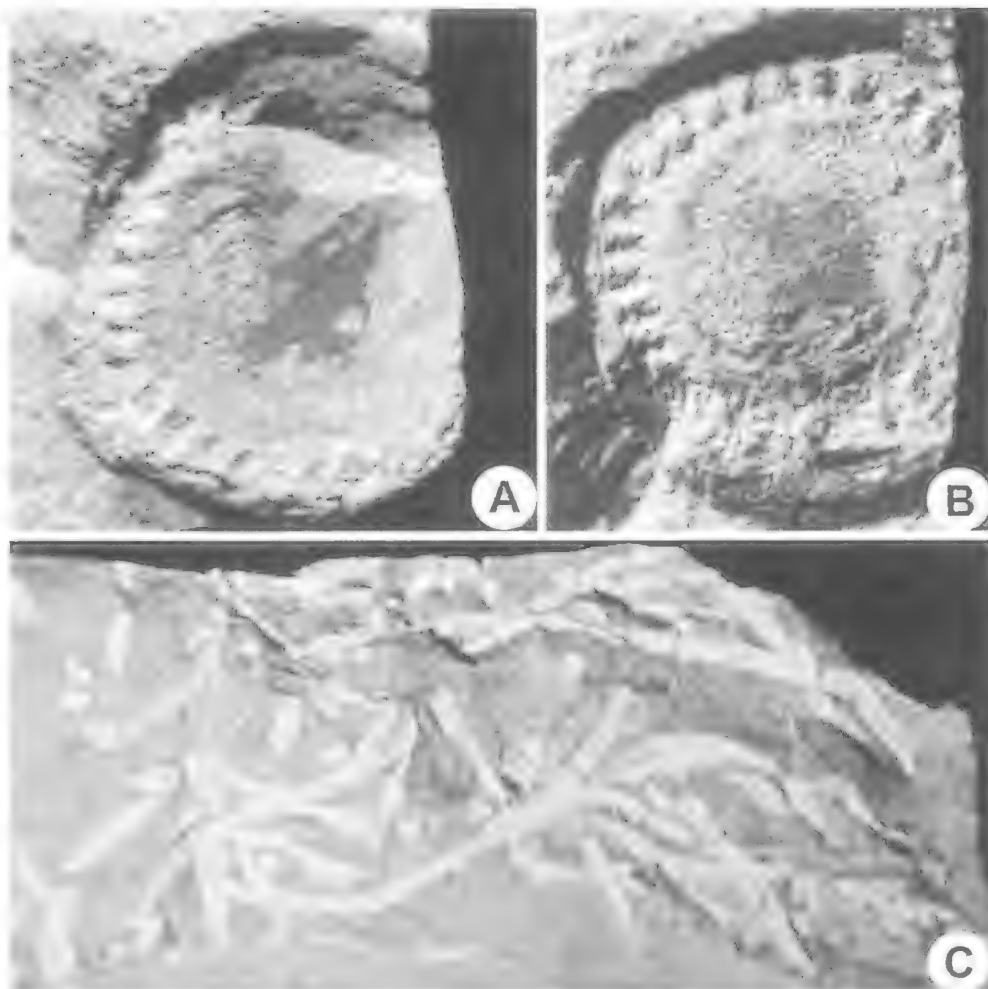


FIG. 9. A, B, circular fossils representing equisetalean nodal diaphragms or molluscan remains with a rim of regular ridges and sockets; A, NHMV24604 $\times 4$; B, GSQF852 $\times 4$ (counterpart of Fig. 9A illustrated in reverse orientation). C, *Chondrites* sp., irregular, mud-filled burrows showing sporadic branching and cross-cutting relationships, NHMV24612 $\times 2.5$.

PALAEOENVIRONMENT

The basal, conglomeratic part of the Maryborough Formation was deposited in fluvial depositional environments (Draper, 1971). The middle part of the formation includes a mixture of black mudstones, green glauconitic sandstones, dark grey shales with invertebrate fossils, and conglomeratic units with scoured bases. These features have been interpreted to reflect deposition within a beach-barrier to shallow marine complex (Cranfield, 1980, 1993). The abundance of invertebrate shells and trace fossils in the upper part of the Maryborough Formation suggests the prevalence of marine conditions.

However, the occurrence of relatively well-preserved plant foliage and fruiting structures suggests that deposition of some beds occurred close to terrestrial environments in relatively low-energy settings. The complex anastomosing burrow-forms within the predominantly fine-grained, lenticular, wavy laminated to symmetrically (wave) rippled sediments are also indicative of quiet-water conditions with only minor reworking by waves. Thin beds containing disarticulated, abraided, and regularly orientated bivalve shells near the top of the formation indicate periodic episodes of higher energy conditions involving wave or current reworking of the sediment (Barnbaum, 1976). Fleming

TABLE 1. Comparison of taxonomic identifications of Maryborough Formation fossil plants by Walkom (1918), and in this study.

Walkom (1918)	This study
<i>Sphenopteris</i> sp.	<i>Phyllopteroides serrata</i> Cantrill & Webb
<i>Taeniopteris elongata</i> sp. nov.	<i>Taeniopteris daintreei</i> McCoy
<i>Taeniopteris tenison-woodsii</i> (Etheridge Jr)	<i>Taeniopteris daintreei</i> McCoy
<i>Taeniopteris</i> sp.	<i>Taeniopteris daintreei</i> McCoy
<i>Ptilophyllum</i> (<i>Williamsonia</i>) <i>pecten</i> (Phillips)	<i>Otozamites</i> sp.
? <i>Pterophyllum</i>	<i>Elatocladus baddowensis</i> sp. nov.
<i>Araucarites polycarpa</i> Tenison-Woods	Araucariacean ovulate cones
<i>Araucarites mesozoica</i> sp. nov.	<i>Podozamites mesozoica</i> (Walkom) comb. nov.
<i>Araucarites</i> sp.	Araucariacean ovulate cones
<i>Pagiophyllum jemmetti</i> sp. nov.	<i>Pagiophyllum jemmetti</i> Walkom
not mentioned	<i>Pagiophyllum</i> sp. A
? <i>Taxites</i>	<i>Elatocladus baddowensis</i> sp. nov.
<i>Ginkgo digitata</i> (Brongniart)	<i>Ginkgophyllum</i> sp.
<i>Ginkgo</i> sp.	<i>Ginkgophytopsis truncata</i> sp. nov.
<i>Equisetites</i> sp. cf. <i>E. rajmahalensis</i> Oldham & Morris	Equisetalean nodal diaphragms or gastropod opercula
?Roots	<i>Chondrites</i> sp. (invertebrate burrows)

(1970) suggested that the invertebrate fauna's low-diversity may be indicative of cold-water conditions in the Early Cretaceous, however, the limited faunal diversity may alternatively reflect environments under the influence of restricted water circulation, low oxygen levels, or high salinity. The collective palaeontological and sedimentological characteristics of the upper Maryborough Formation suggest that it was deposited in a range of shallow marine settings where plant-rich units were deposited in low-energy coastal lagoons or marine embayments.

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SIMOGNATHINAE (ACARINA: HALACARIDAE) FROM THE GREAT BARRIER REEF AND CORAL SEA. DESCRIPTION OF THIRTEEN NEW SPECIES

JÜRGEN C. OTTO

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The simognathine fauna of the Great Barrier Reef and reefs of the Coral Sea has been investigated and one new species of *Acaromantis* and twelve new species of *Simognathus* were found: *Acaromantis diazpuhidoi*, *Simognathus abnormalus*, *S. actius*, *S. aspidiotus*, *S. clypeatus*, *S. corneatus*, *S. exoticus*, *S. platyaspis*, *S. pygmaeus*, *S. specialis*, *S. trachys*, *S. versicolor* and *S. xandarus*. A key to Australian species of Simognathinae is provided, *Acaromantis* is redefined, and the definition of *Simognathus* is commented on. □ *Simognathus*, *Acaromantis*, *Simognathinae*, *Great Barrier Reef*, *Coral Sea*, *Australia*, *Halacaridae*, *marine mites*, *Acarti*.

Jürgen C. Otto, (email: j.otto@aims.gov.au), Australian Institute of Marine Science, PMB 3, Townsville 4810, Australia; 10 September 1999.

Mites of the family Halacaridae are benthic inhabitants of marine and freshwater habitats and are assumed to have diverged from semiaquatic prostigmatid ancestors more than 200 million years ago (Bartsch, 1996). Of the 14 subfamilies of Halacaridae which are currently recognised (Abé, 1998; Otto, 1999c), the Simognathinae is among the most conspicuous. Species of this entirely marine subfamily are spindle-shaped and heavily armoured by large dorsal plates which are covered with broad shallow pits (foveae). Their gnathosoma is relatively short and the palps which are inserted close to each other dorsally on the gnathosomal base have no more than three segments. The most remarkable feature is their front legs which possess a large ventral or medial spine on the tibia and a hook-like unpaired claw at the end of the tarsus. The unpaired claw and the tarsus itself are movable and oppose the spine on the tibia, an arrangement which appears suited to catching and holding prey, although, feeding has not been observed.

Simognathine mites are common in intertidal habitats and shallow waters around the globe but are yet to be recorded from the deep sea. The 34 described species are subdivided into two genera, *Acaromantis* Trouessart & Neumann, 1893 and *Simognathus* Trouessart, 1889. So far 25 species of *Simognathus* have been described, seven of these from Australia (Bartsch, 1993b, 1994). *Acaromantis* appears less diverse. Only nine species have been described and none from Australia.

During the present study, which forms part of a broader survey of the halacarid fauna of the Great Barrier Reef and Coral Sea (Otto, 1999a,b,c;

Otto, 2000a,b,c; Otto & Bartsch, 2000; Bartsch, 2000), one species of *Acaromantis* and 12 species of *Simognathus* were found. These represent the first records of Simognathinae from the eastern half of Australia.

METHODS

Sand, coral rubble and pieces of dead coral were collected either intertidally or subtidally using SCUBA equipment. Mites were extracted by washing the substrates in a bowl of water and decanting the supernatant through a 100µm sieve. All material was collected by the author except where stated otherwise. Mites were cleared in lactic acid and mounted in PVA (Boudreaux & Dosse, 1963). Drawings were made with the aid of a camera lucida.

In the accounts of each species only one sex is described in detail, while for the opposite sex only characters that differ are described. Measurements are in micrometres.

Terminology follows Bartsch (1993a, 1994). To make a clear distinction between parambulacral setae (pas) and ventral setae, only those ventral, ventromedial or ventrolateral setae which are inserted distal to the most distal of the dorsal setae (= fossary setae) are here referred to as pas. In some cases the number of parambulacral setae and ventral setae may therefore differ from those Bartsch (1994) described for similar species. In *Acaromantis* and at least one species of *Simognathus* the tibia and tarsus of leg I is twisted by 90° compared with other halacarid genera. The tarsal claw is therefore pointing inwards instead of downwards in uncompressed

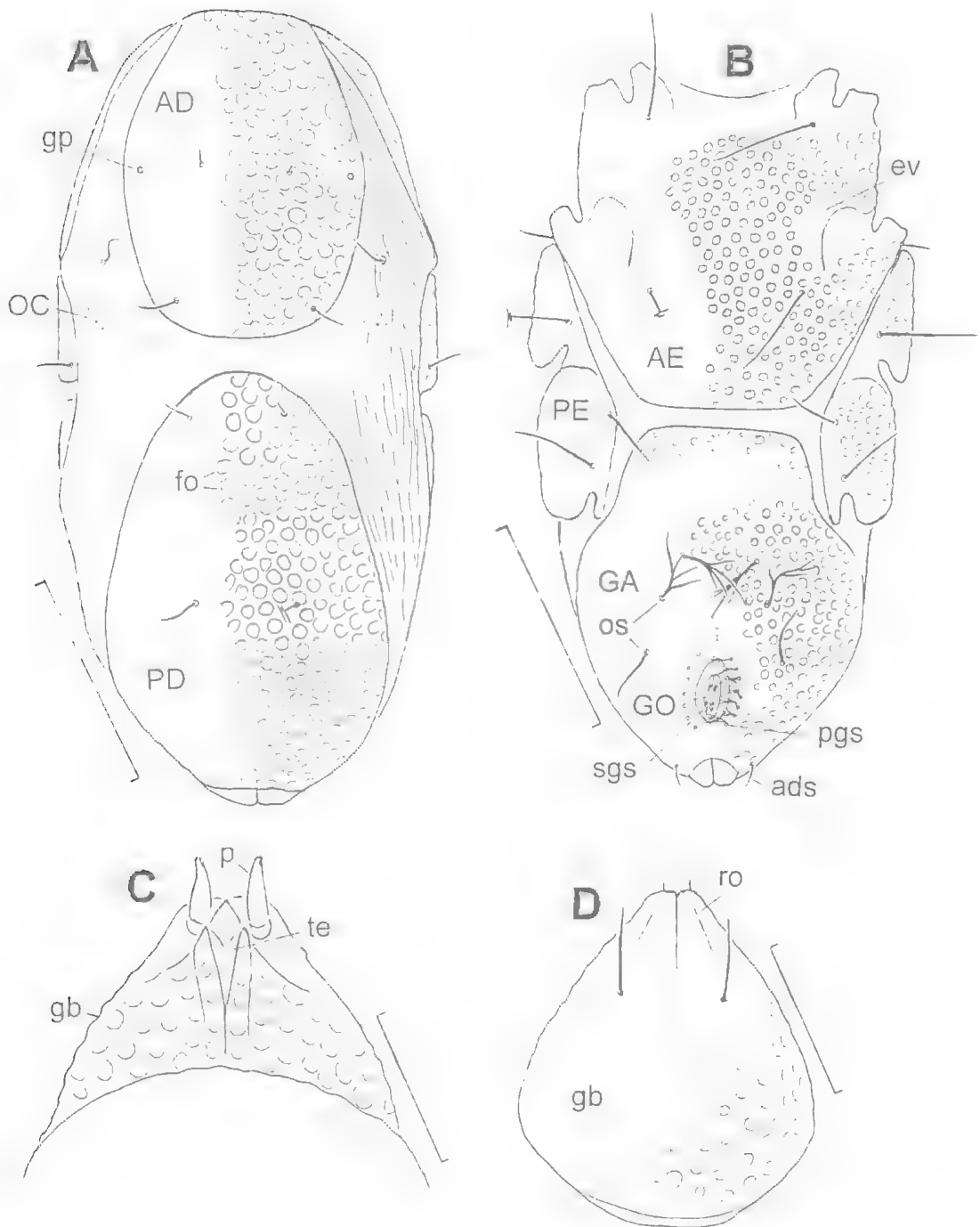


FIG. 1. *Acaromantis diazulpidoi* sp. nov., ♂: A, idiosoma, dorsal view (AD, anterior dorsal plate; fo, foveae; gp, gland pore; OC, ocular plate; PD, posterior dorsal plate); B, idiosoma, ventral view (ads, adanal seta; AE, anterior epimeral plate; ev, epimeral vesicle; GA, genitoanal plate; GO, genital opening; os, outlying setae; PE, posterior epimeral plate; pgs, perigenital setae; sgs, subgenital setae); C, gnathosoma, dorsal view (gb, gnathosomal base; p, palp; te, tectum); D, gnathosoma, ventral view (ro, rostrum). Scale bars: A,B = 100µm; C,D = 50µm.

specimens. To be consistent with descriptions of other genera the terms medial, lateral, dorsal and ventral for tibia and tarsus I are applied as if these segments were oriented in the usual way with the tarsal claw pointing downwards. Accounts of chaetotaxy are from trochanter to tibia only.

Abbreviations: Descriptive - AD, anterior dorsal plate; AE, anterior epimeral plate; GA, genitoanal plate; GO, genital opening; OC, ocular plate; PD, posterior dorsal plate; PE, posterior epimeral plate; P-2, P-3, second and third palp segments, respectively, counted from base of palp; I-IV, leg I to leg IV; pas, parambulacral seta(e); pgs, perigenital seta(e); sgs, subgenital seta(e). Additional abbreviations in the illustrations are explained in the captions. GBR, Great Barrier Reef Marine Park; I, Island; Rf, Reef. Other abbreviations: ANIC, Australian National Insect Collection, Canberra (Australia), MTQ, Queensland Museum branch of the Museum of Tropical Queensland, Townsville (Australia); ZMH, Zoologisches Museum Hamburg (Germany). All specimens with the accession number prefix QMS are deposited in the MTQ.

SYSTEMATICS

Acaromantis Trouessart & Neumann

Acaromantis Trouessart & Neumann 1893: 207; André, 1946: 138; Viets, 1956: 696; Morselli, 1970: 109; Bartsch, 1974: 280; 1976: 664; 1977: 92(530); 1980: 401; 1983: 194; Bartsch & Schmidt, 1978: 22 (644).

TYPE SPECIES. *Acaromantis squilla* Trouessart & Neumann, 1893, by monotypy and original designation.

DIAGNOSIS. Body spindle-shaped. Dorsal plates covered by foveae. Palps separated by less than their width, inserted dorsally on gnathosoma and two-segmented. Tibia of front leg at least as long as three times its height, apically narrowing and equipped with a heavy spine. Tarsus of same leg shorter than 1/3 the length of tibia, with a heavy apical claw but no paired claws. Genu of leg I with a spinose seta. Telson I with a single seta.

Acaromantis diazpulidoi sp. nov. (Figs 1, 2)

ETYMOLOGY. For Guillermo Diaz-Pulido who collected the holotype.

MATERIAL. HOLOTYPE: QMS105316, ♂, Coral Sea (Queensland Plateau), Chilcott I., 16°56.51'S 150°0.4'E, 14 Sep. 1998, G. A. Diaz-Pulido coll., coarse sand at 10-15m.

DESCRIPTION. *Male*. Idiosoma 354 long. AD longer than wide; foveate throughout (Fig. 1A); two pairs of setae and pair of barely visible gland pores as illustrated; scattered canaliculi around pores. OC reduced to more or less oval subcuticular platelet carrying few canaliculi. Anterior to OC with seta on a small subcuticular platelet. PD clearly longer than wide; anterior margin rounded; with two pairs of setae. GA foveate except for an anterior transverse smooth area (Fig. 1B); two pairs of branched outlying setae anterior to GO and one pair of unbranched setae level with anterior margin of GO; 14 branched pgs surrounding GO; three pairs of short sgs. Adanal setae ventrally on anal cone.

Tectum with an upper split part and a lower pointed part (Fig. 1C). Ventral gnathosomal base with foveae posterolaterally and posteriorly, medially smooth (Fig. 1D). Palp two-segmented (Fig. 2A); P-2 with heavy ventral seta, one slender dorsal seta and two apical setae.

Outline of legs as shown in Fig. 2B-E. Chaetotaxy: I 1-2-1-4-5 (Fig. 2B), II 1-2-2-4-5 (Fig. 2C), III 1-1-2-3-5 (Fig. 2D), IV 1-1-2-3-5 (Fig. 2E). Genu I with a strongly spinose ventral seta. One small branched seta dorsally on tibiae III and IV, two such setae on genua III and IV, one on telofemur III and two on telofemur IV (oil immersion). Tibial spine and tarsal claw of leg I prior to compression of slide medially directed. Tibiae II-IV with pair of ventral coarsely bipectinate setae. Paired fossary setae of tarsi II-IV slightly serrated. Tarsi II-IV without median claw. Tarsus III with ventral seta and pair of pas. Tarsus IV with two ventral setae and pair of pas. Paired claws of tarsi II-IV with accessory process and pecten.

Female. Unknown.

REMARKS. *Acaromantis diazpulidoi* sp. nov. is the first species of *Acaromantis* known from Australia. With its two palp segments, single seta on telofemur I, presence of a spinose seta on genu I, short tarsus I, slender and in the proximal half conspicuously widened tibia I and lack of paired claws on tarsus I, *A. diazpulidoi* is a typical representative of *Acaromantis*. It differs from all its congeners by the shape of its tectum, which is characteristically split in contrast to being entire and scale-like. Males can also be identified by the presence of three pairs of outlying setae, of which the two anteriormost pairs are branched. Such an arrangement of setae is unknown for any other species of *Acaromantis*.

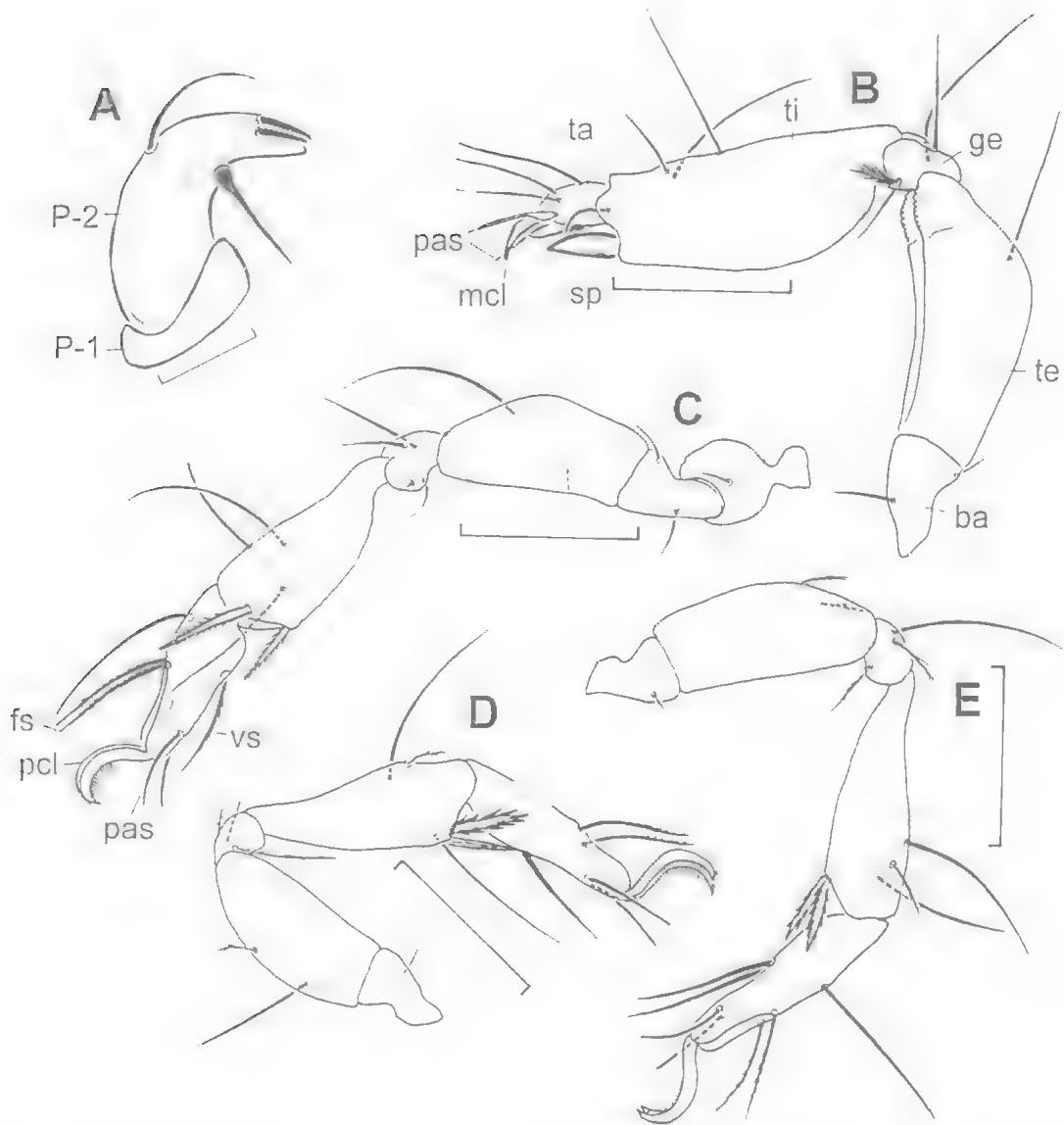


FIG. 2. *Acaromantis diazpulidoi* sp. nov., ♂: A, palp, medial view (P-1, P-2, palp segments); B, leg I, medial view (ba, basifemur; ge, genu; mcl, median claw; pas, parambulacral setae; sp, spine; ta, tarsus; te, telofemur; ti, tibia); C, leg II, medial view (fs, fossary setae; pas, parambulacral setae; pcl, paired claw; vs, ventral seta); D, leg III, medial view); E, leg IV, medial view. Scale bars: A = 10µm; B-E = 50µm.

Simognathus Trouessart

Simognathus Trouessart, 1889: 1180; Viets, 1927: 151; 1936: 421; 1940: 94; 1956: 694. André, 1946: 135; Fountain, 1953: 357; Monniot, 1961: 585; 1962: 288; Bartsch, 1974: 275; 1977: 87 (525); 1978: 19; 1983: 193; 1985: 554; 1993b: 95; 1994: 135; Newell, 1947: 23; 1971: 36; 1984: 264.

Ischyrogathus Trouessart, 1901; Newell, 1947: 23, 37; Viets, 1956: 694; Synonymy by Bartsch, 1974.

TYPE SPECIES. *Pachygnathus sculptus* Brady, 1875 (= *Pachygnathus minutus* Hodge, 1863; synonymy by Fountain (1953)); by original designation.

DIAGNOSIS. Body spindle-shaped. Dorsal plates covered by foveae. Palps separated by less than their width, inserted dorsally on gnathosoma and three-segmented. Tibia of front legs usually shorter than three times its height (exception: *S.*

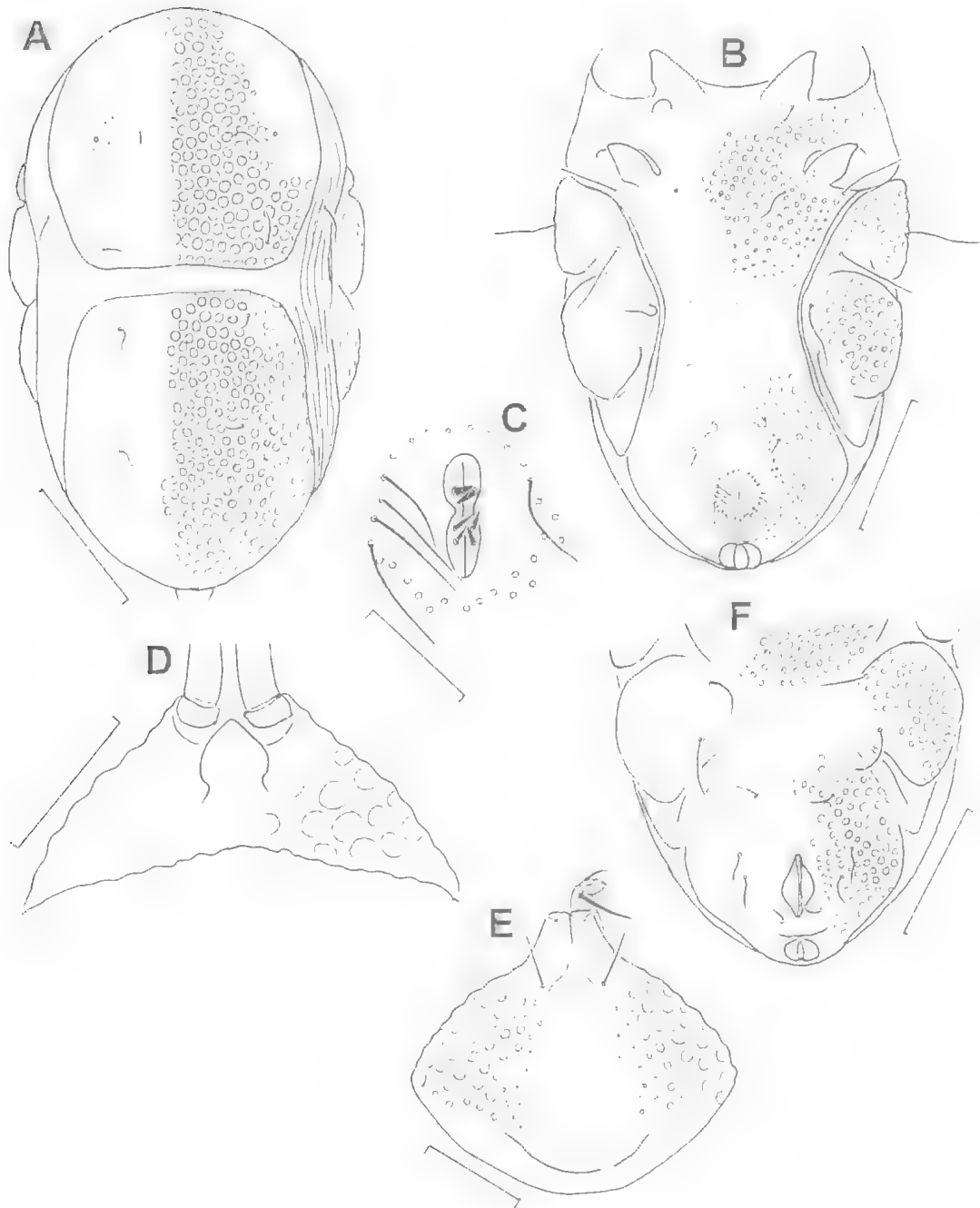


FIG. 3. *Simognathus abnormalus* sp. nov., adult: A, idiosoma, dorsal view; B, ♂ idiosoma, ventral view; C, ♂ genital opening; D, gnathosoma, dorsal view; E, gnathosoma, ventral view; F, posterior half of ♀ idiosoma, ventral view. Scale bars: A,B = 100µm; C = 25µm; D,E = 50µm; F = 100µm.

abnormalus, *S. scutatus*), equipped with a heavy spine and tarsus of same legs with a heavy apical claw and slender seta-like paired claws. Tarsus I

usually longer than 1/3 the length of tibia (exception: *S. abnormalus*, *S. scutatus*), with heavy median claw and slender, sometimes seta-

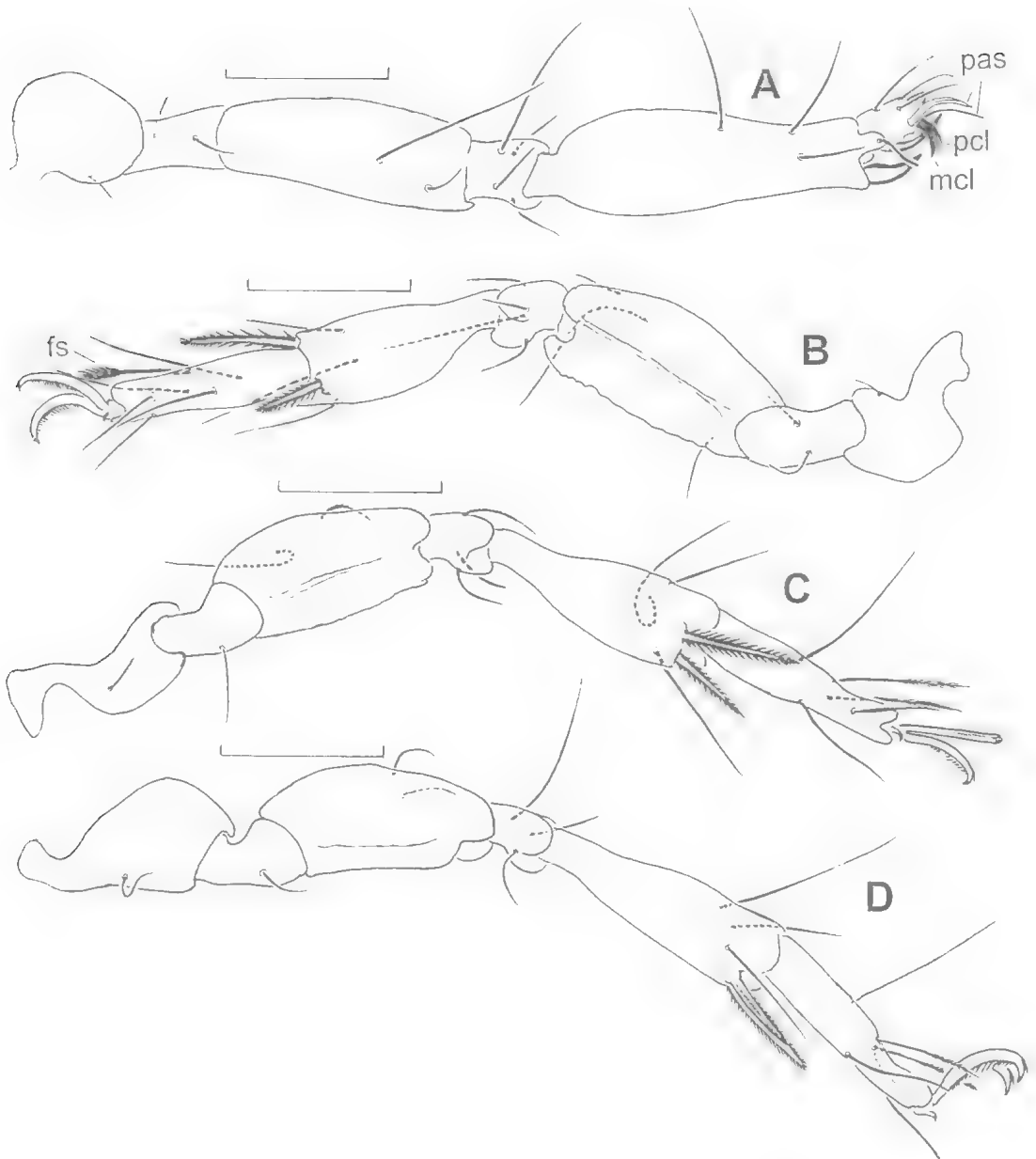


FIG. 4. *Simognathus abnormalus* sp. nov., adult: A, leg I, dorsal view (mcl, median claw; pcl, paired claws; pas, parambulacral setae); B, leg II, ventral view (fs, fossary seta); C, leg III, ventral view; D, leg IV, lateral view. Scale bars: A-D = 50 μ m.

like paired claws. All setae of genu of leg I glabrous. Telfemur I usually with two setae (exception: *S. pygmaeus* sp. nov).

***Simognathus abnormalus* sp. nov.**
(Figs 3, 4)

ETYMOLOGY. Referring to the front legs' short tarsus and slender tibia, and the peculiar orientation of these leg segments.

MATERIAL. HOLOTYPE: QMS105317, ♂, GBR, 18°41.91'S 147°06.49'E, Loadstone Rf, 12 Apr. 1998, sand & rubble at 2m. PARATYPES: QMS105318, ♀, data as for holotype; QMS105319, ♀, ANIC, ♀, GBR, 18°16.69'S 147°23.21'E, Mymidon Rf, 14 Apr. 1998, coarse sand at 12m; ZMH A32/99, ♀, GBR, 19°20.12'S 149°02.85'E, Elizabeth Rf, 25 Dec. 1997, coarse sand & rubble at 3m; QMS105320, ♀, QMS105321, ♂, GBR, Rosser Rf, ca. 15°37'S 145°33'E, 8 Oct. 1998, sand at 2m; QMS105322, ♂, QMS105323, ♀, Coral Sea (Queensland Plateau), Chilcott I., 16°56.51'S 150°0.4'E, 14 Sep. 1998, G.A. Diaz-Pulido, coarse sand at 10-15m; QMS105324/105325, 2 ♀s, Coral Sea (Queensland Plateau), South Willis I., ca. 16°18'S 149°58'E, 15 Sep. 1998, G.A. Diaz-Pulido, coral rubble (fine) at 0-10m.

DESCRIPTION. *Male.* Idiosoma 412-424 long (holotype 424). AD of subequal length and width; with a non-foveate area anterolaterally (Fig. 3A). OC reduced to oblong subcuticular platelet which carries a seta anteriorly. PD slightly longer than wide; anterior margin truncated; with three pairs of setae (including adanal setae). AE broadly fused to GA (Fig. 3B), in some specimens AE and GA also fused to PE (as shown for ♀ in Fig. 3F). AE and PE foveate throughout (Fig. 3B). GA foveate except for area along median axis (Fig. 3B); two pairs of outlying setae anterior to GO; 28-30 pgs surrounding GO in a circle (Fig. 3B,C); GO with three pairs of short sgs (Fig. 3C).

Gnathosomal base wider than long (Fig. 3D,E); tectum wide, narrowing anteriorly (Fig. 3D); ventrally foveate except for a relatively wide area along the median axis (Fig. 3E). Palp three-segmented; P-2 with heavy ventral seta; P-3 with three short setae and one longer seta.

Outline of legs as in Fig. 4. Chaetotaxy: I 1-2-2-4-5 (Fig. 4A), II 1-2-3-4-5 (Fig. 4B), III 1-1-2-3-5 (Fig. 4C), IV 1-1-2-3-5 (Fig. 4D). Tibia I long and slender, narrowing apically. All setae of genu I slender and glabrous. In uncompressed specimens tibial spine and tarsal claw of leg I medially directed. Tarsus II with the medial fossary seta apically widened and serrated. Tarsi III and IV with single ventral seta and one unpaired pas. Distal pair of fossary setae of tarsi III and IV apically serrated. Tarsi II-IV with small median claw; paired claws bearing pecten along most of the shaft, most conspicuous on tarsus IV.

Female. Idiosoma 417-420 long. GA with four pairs of pgs and no sgs (Fig. 3F). OC in some specimens shorter and more rounded than illustrated for male.

REMARKS. *Simognathus abnormalus* is most similar to *S. scutatus* Bartsch, 1993b. Both

species possess fused ventral plates, oblong OC and a relatively slender tibia and short tarsus on leg I, a combination of characters that is unknown for other species in the genus. *Simognathus abnormalus* can be distinguished from *S. scutatus* by having wider dorsal plates, a larger body, and a wide non-foveate area medially on the ventral gnathosomal base.

***Simognathus actus* sp. nov.**
(Figs 5, 6)

ETYMOLOGY. Latin, *acta* = coast, referring to this species' occurrence on beaches.

MATERIAL. HOLOTYPE: QMS105326, ♀, GBR, 19°16.09'S 147°03.05'E, Cape Ferguson, 8 Nov. 1997, intertidal sand on beach, sediment depth 40cm. PARATYPES: QMS105327, ♀, ANIC, ♀, ZMH A33/99, ♀, QMS105328, ♂, data as for holotype; QMS105329, ♂, GBR, Wonga Beach, 16°21'S 148°26'E, 31 July 1998, sand below high tide mark, sediment depth 40cm; QMS105330-105334, 5 ♀s, GBR, Lizard I., Mermaid Cove, 14 Oct. 1998, coarse sand at high tide level, sediment depth 10-20cm.

Female. Idiosoma 244-272 long (holotype 267). All dorsal setae short (Fig. 5A). AD uniformly pale, either of similar width in anterior and posterior half or posterior half slightly wider; posterior margin rounded; laterally with scattered pits. OC reduced to minute plate with a setae. PD pear-shaped; with three pairs of setae including adanal setae. AE with foveae only laterally and along posterior margin (Fig. 5B); remainder of plate punctate; epimeral vesicle large. GA with foveae in posterior 2/3 and along anterior margin; remainder of plate punctate; 3-4 pairs of pgs.

Dorsal gnathosomal base with large irregularly shaped foveae (Fig. 5D). Tectum pointed. Ventral gnathosomal base foveate except medially (Fig. 5E). P-2 with a ventral seta and a poorly developed ventral protuberance proximal to seta. P-3 longer than half the length of P-2.

Outline of legs as in Fig. 6. Telofemora with few foveae, on leg I more numerous and more conspicuous than on other legs (Fig. 6A). Chaetotaxy: I 1-2-2-4-5 (Fig. 6A), II 1-2-2-4-5 (Fig. 6B), III 1-1-2-3-5 (Fig. 6C), IV 1-1-1-3-5 (Fig. 6D). Heavy ventral spine of tibia I without proximal swelling; seta adjacent to spine branched (Fig. 6A, arrowed). Tarsus II with pair of pas but without ventral seta, tarsi III and IV with single ventral seta but without pas. Paired claws of tarsi II-IV with apical cluster of pecten.

Male. Idiosoma 241-250 long, GA with 16-17 pgs (Fig. 5C). Sgs not seen.

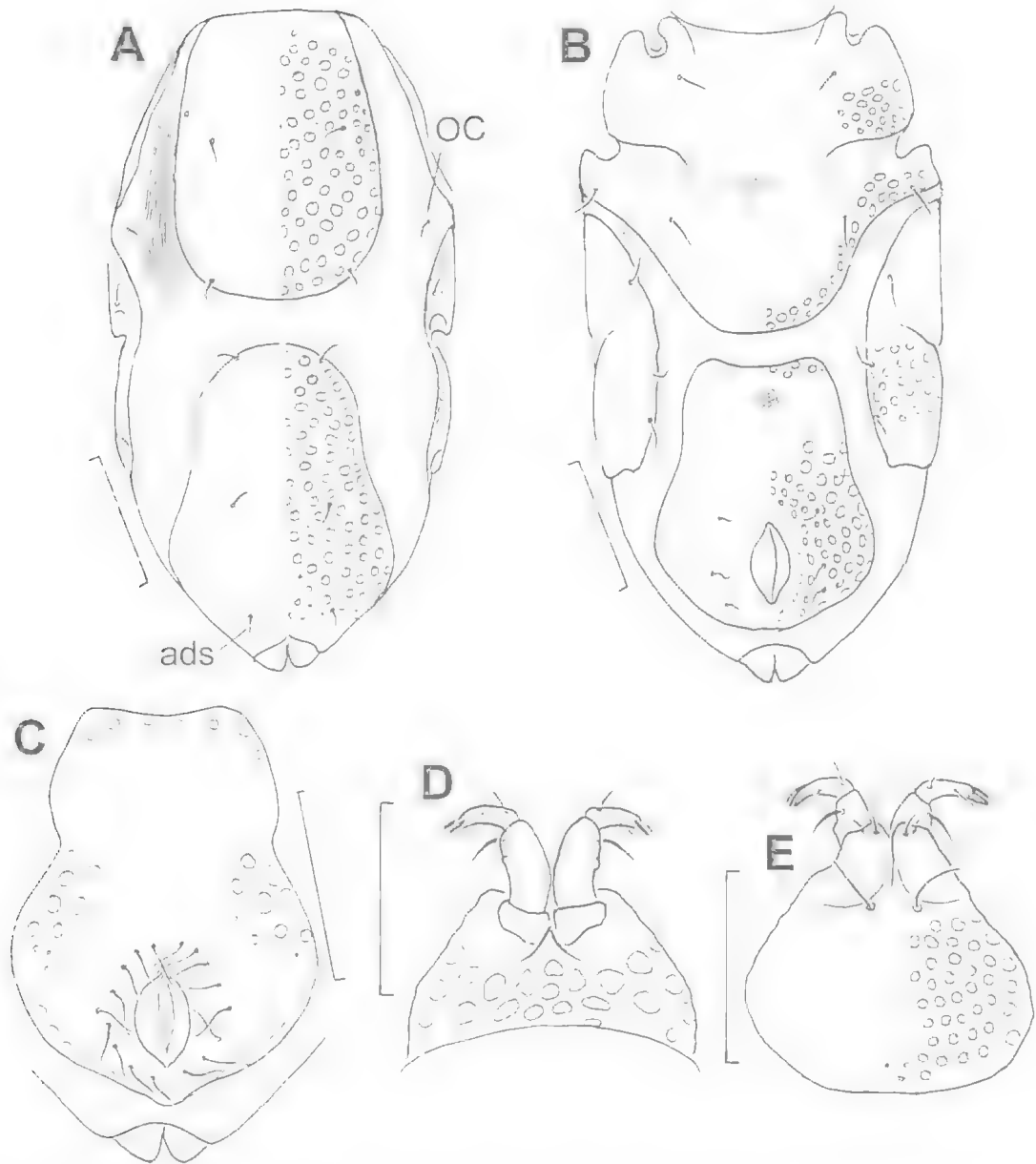


FIG. 5. *Simognathus actius* sp. nov., adult: A, idiosoma, dorsal view (OC, ocular plate; ads, adanal seta); B, ♀ idiosoma, ventral view; C, ♂ genitoanal plate; D, gnathosoma, dorsal view; E, gnathosoma, ventral view. Scale bars: A-E = 50µm.

REMARKS. *Simognathus actius* sp. nov. differs from its congeners by having a branched seta on tibia I adjacent to the ventral spine and a narrow band of foveae along the posterior margin of the AE.

Although all examined specimens are identical in the characters described above they differ

slightly in the striation of the membranous cuticle. In the specimens from Cape Ferguson the striation is conspicuously finer (Fig. 5A) than in all remaining specimens. This character is here not regarded as sufficient evidence for separating these specimens into different species although it

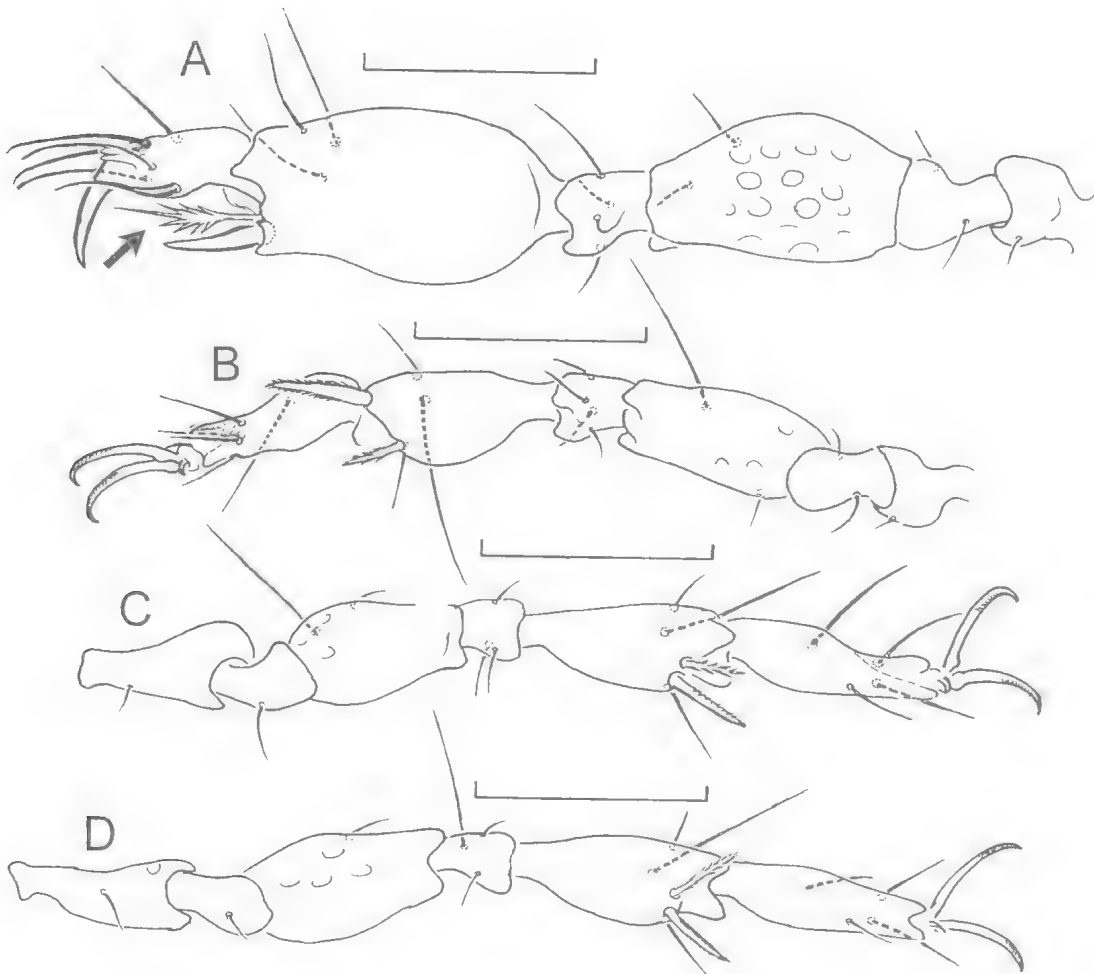


FIG. 6. *Simognathus actius* sp. nov., adult: A, leg I, lateral view; B, leg II, ventromedial view; C, leg III, ventromedial view; D, leg IV, ventromedial view. Scale bars: A-D = 50 μ m.

may indicate a certain amount of genetic isolation between them.

***Simognathus aspidiotus* sp. nov.**
(Figs 7, 8)

ETYMOLOGY. Greek, *aspidiotes* = shield bearer, referring to the species' fused ventral plates.

MATERIAL. HOLOTYPE: QMS105335, ♀, GBR, Myrmidon Rf, 18°16.69'S 147°23.21'E, 14 Apr. 1998, coarse sand & rubble at 15m. PARATYPES: QMS105336, ♀, ANIC, ♀, ZMH A34/993, ♀, GBR, 19°20.12'S 149°02.85'E, Elizabeth Rf, 25 Dec. 1997, coarse sand & rubble at 3m; QMS1053371, ♀, GBR, 18°42.03'S 147°06.54'E, Loadstone Rf, 12 Apr. 1998, coarse sand & rubble at 12-15m; QMS105338/105339, 2 ♀s, GBR, 18°38.25'S 147°04.42'E, John Brewer Rf, 11 Apr. 1998, coarse sand at 15m; QMS105340/S105341, 2 ♀s, GBR,

Rosser Rf, ca. 15°37'S 145°33'E, 8 Oct. 1998, sand at 2m; QMS105342, ♂, GBR, Boulder Rf, ca. 15.24'S 145.27'E, 8 Oct. 1998, coarse intertidal sand; QMS1053431, ♀, GBR, Boulder Rf, ca. 15°24'S 145°27'E, 8 Oct. 1998, A. Thompson, coarse sand at 2m; QMS105344, ♀, Coral Sea (Queensland Plateau), Lihou Rf, ca. 17°25'S 151°40'E, 22 July 1998, D. Fenner, sand at 7m; QMS105345, ♀, Coral Sea (Queensland Plateau), Flinders Rf, ca. 17°35'S 148°27'E, July 1998, D. Fenner, sand; QMS105346/S105347, 2 ♂s, QMS105348, ♀, Coral Sea (Queensland Plateau), Herald Cays, 16°57.171'S 149°12.036'E, 16 Sep. 1998, G.A. Diaz-Pulido, coarse sand at 5-15m; QMS105349, ♀, Coral Sea (Queensland Plateau), South Willis I., ca. 16°18'S 149°58'E, 15 Sep. 1998, G.A. Diaz-Pulido, coral rubble (fine) at 0-10m; QMS105350, ♀, Coral Sea (Queensland Plateau), Chilcott I., 16°56.51'S 150°0.4E', 14 Sep. 1998, G.A. Diaz-Pulido, coarse sand at 10-15m.

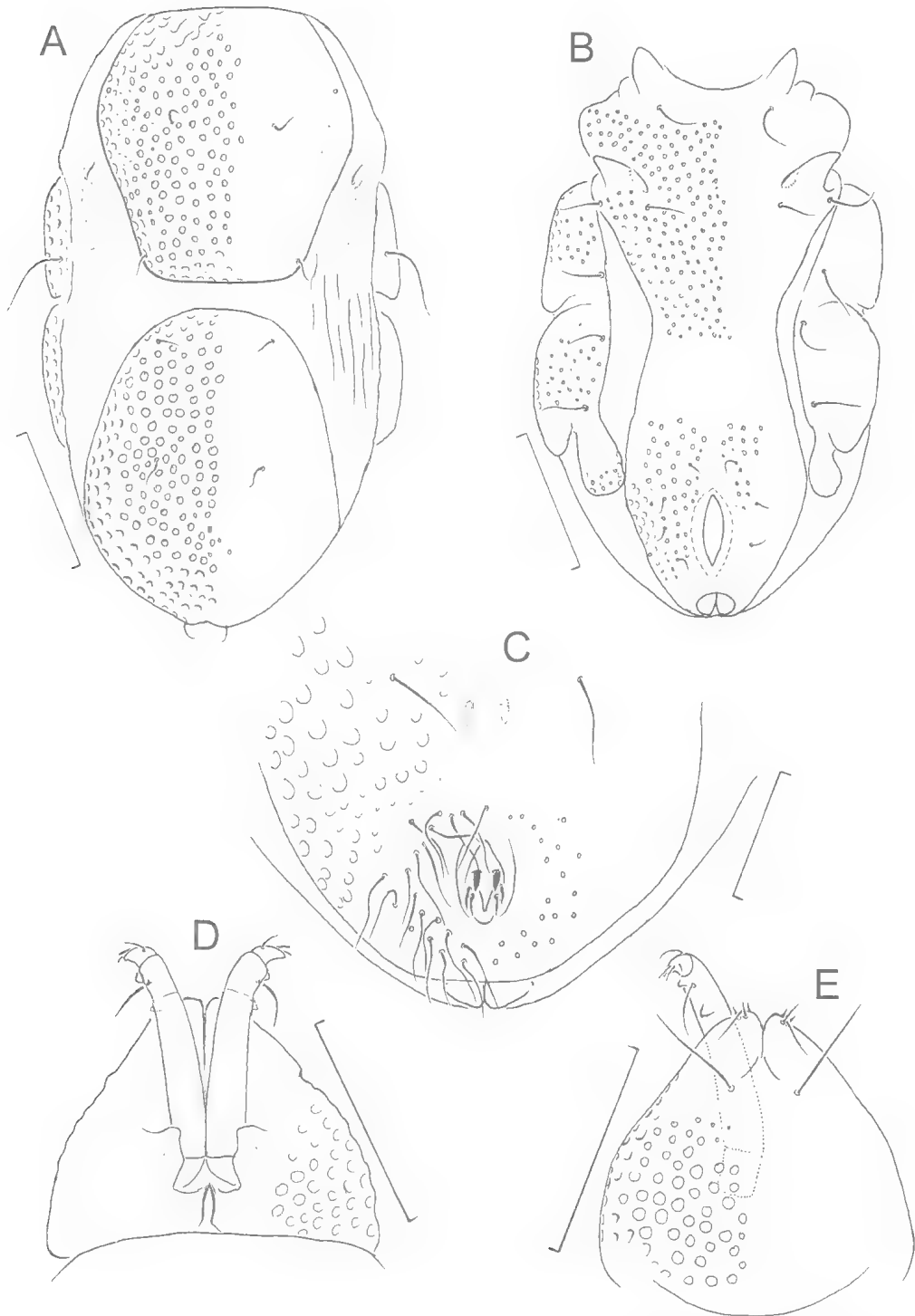


FIG. 7. *Simognathus aspidiotus* sp. nov., adult: A, idiosoma, dorsal view; B, ♀ idiosoma, ventral view; C, posterior part of ♂ genitoanal plate; D, gnathosoma, dorsal view; E, gnathosoma, ventral view. Scale bars: A,B,D,E = 100µm; C = 25µm.

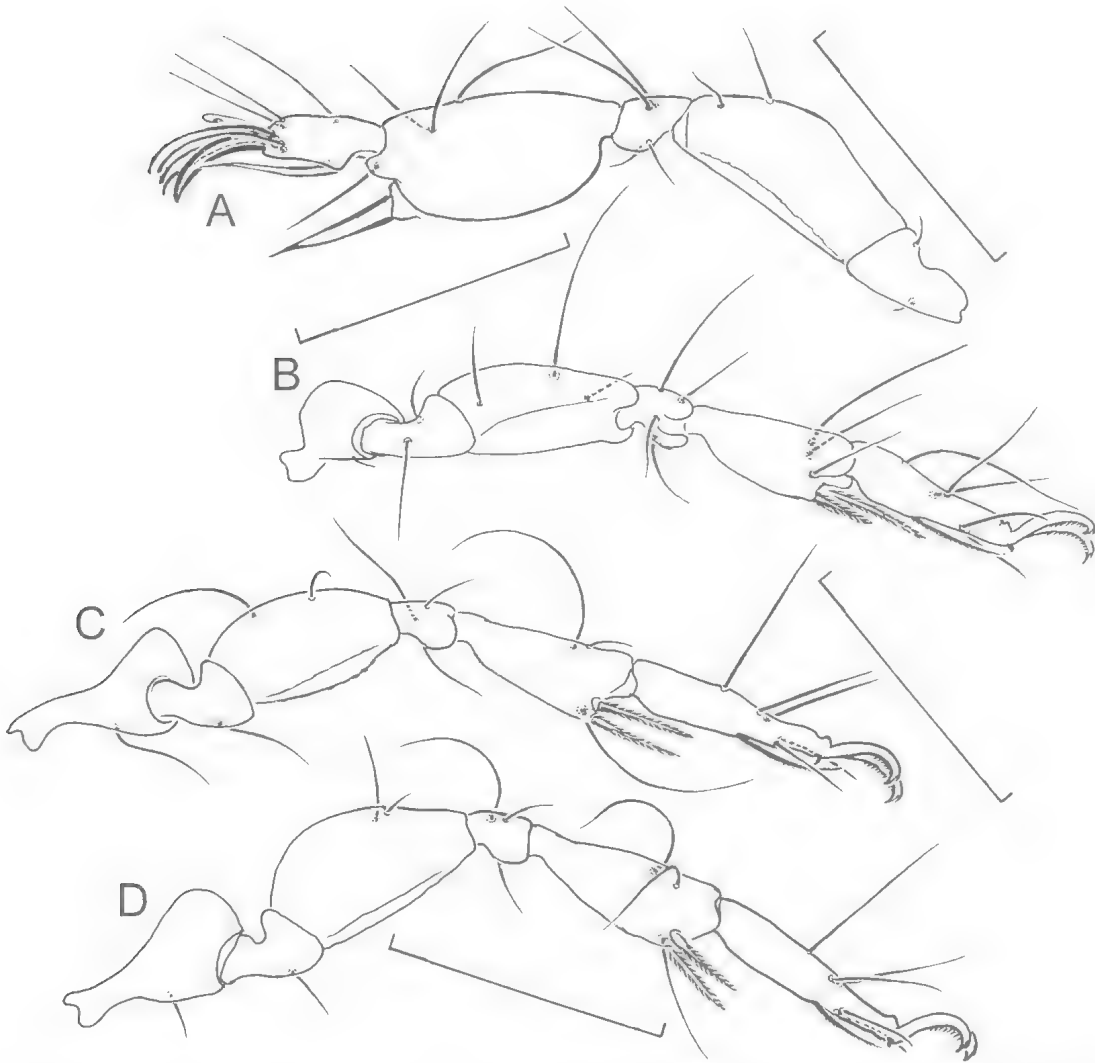


FIG. 8. *Simognathus aspidiotus* sp. nov., adult: A, leg I, medial view, trochanter excluded; B, leg II, lateral view; C, leg III, medial view; D, leg IV, medial view. Scale bars: A-D = 100 μ m.

DESCRIPTION. *Female.* Idiosoma 376-476 long (holotype 404). AD uniformly pale; anteriorly widened, posterior margin truncated (Fig. 7A). OC reduced to small oblong subcuticular platelet which carries a seta anteriorly. PD with three pairs of setae (including adanal setae). AE broadly fused to GA (Fig. 7B). AE foveate throughout; epimeral vesicles inconspicuous; four pairs of pgs, in some specimens with four setae on one side and three on the other (Fig. 7B).

Tectum narrow (Fig. 7D). Ventral gnathosomal base foveate throughout. Palps inserted on posterior half of dorsally visible part of gnathosomal base (Fig. 7D). Segment P-2 with one

ventral seta inserted between two protuberances (Fig. 7E); P-3 shorter than 1/4 of P-2.

Outline of legs as in Fig. 8. All segments without foveae. Telfemora slender. Chaetotaxy: I 1-2-2-4-5 (Fig. 8A), II 1-2-3-4-5 (Fig. 8B), III 1-1-2-3-5 (Fig. 8C), IV 1-1-2-3-5 (Fig. 8D). Ventral spine of tibia I without proximal swelling. Tarsi II-IV with ventral slightly serrated seta and pair of pas. Paired claws of tarsi II-IV with coarse pecten along most of shaft.

Male. Idiosoma 368-420 long. GA with pair of outlying setae anterior to GO and 38-41 pgs surrounding GO (Fig. 7C); three pairs of sgs, anteriormost pair thickened, other two pairs slender.

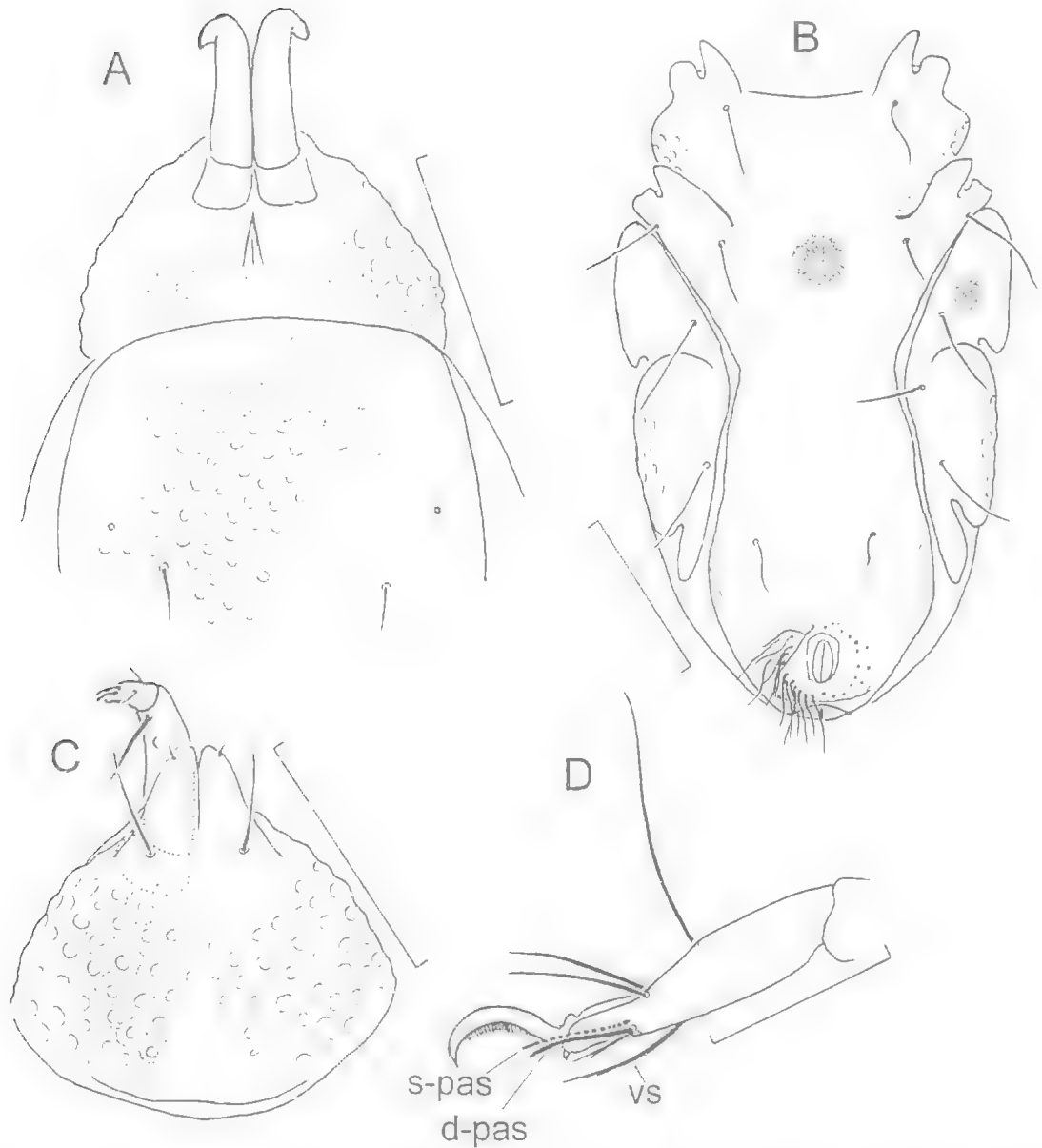


FIG. 9. *Simognathus clypeatus* sp. nov., adult: A, gnathosoma and anterior part of idiosoma, dorsal view; B, ♂ idiosoma, ventral view; C, gnathosoma, ventral view; D, tarsus IV, medial view (s-pas, single pas; d-pas, doubled pas). Scale bars: A-C = 100µm; D = 50µm.

REMARKS. The only other species of *Simognathus* in which the ventral plates are fused, the OC are reduced to oblong subcuticular platelets and the seta on P-2 is inserted between two cuticular projections is *S. uniscutatus* Bartsch, 1994. *Simognathus aspidiotus* sp. nov. differs from it in having two pas (instead of one) on each of tarsi III

and IV and two instead of three setae on basifemur I. The overall similarity between both species suggests a close relationship.

***Simognathus clypeatus* sp. nov.**
(Fig. 9)

ETYMOLOGY. Latin, *clypeatus* = provided with a shield, referring to this species' fused ventral plates.

MATERIAL. HOLOTYPE: QMS105351, ♂, Coral Sea (Queensland Plateau), Herald Cays, 16° 57.171'S 149° 12.036'E, 16 Sep. 1998, G.A. Diaz-Pulido, coarse sand at 5-15m. PARATYPES: QMS105352, ♀, data as for holotype.

DESCRIPTION. *Male*. Idiosoma 408 long. AD, OC, and PD as described for *Simognathus aspidiotus* sp. nov. except anterior AD without foveae and instead with canaliculi arranged in lines that form a loosely reticulated pattern (Fig. 9A). AE and GA fused, both without foveae, except for an area posterior to insertions of leg I and, less conspicuously, lateral on GA (Fig. 9B); non-foveate remainder of plate finely punctate. GA with 32 pgs around GO and one pair of outlying setae. Sgs not seen. PE finely punctate, posterior to insertions of leg III foveate.

Tectum narrow and pointed (Fig. 9A). Dorsal gnathosomal base in deeper cuticular layers with series of canaliculi arranged as shown in Fig. 9A; similar arrangement of canaliculi also on ventral gnathosoma (Fig. 9C). Palps inserted well anterior on gnathosomal base; P-2 with poorly developed protrusion proximal to ventral seta (Fig. 9C).

Morphology and setation of legs as described for *S. aspidiotus* except tarsus IV with a doubled medial pas, of which the ventral branch is much thinner than the dorsal one (Fig. 9D).

Female. Idiosoma 432 long. GA with foveae lateral and anterolateral to GO and with four pairs of pgs (as illustrated for *S. aspidiotus*, Fig. 7B).

REMARKS. *Simognathus clypeatus* has the AE and GA fused and the OC reduced to subcuticular oblong platelets, a combination of characters otherwise only known for *S. abnormalus* sp. nov., *S. aspidiotus* sp. nov., *S. scutatus* Bartsch, 1993b and *S. uniscutatus* Bartsch, 1994. *Simognathus clypeatus* differs from these species in having most of the AE finely punctate instead of foveate.

***Simognathus corneatus* sp. nov.**
(Figs 10,11)

ETYMOLOGY. Referring to the large cornea of this species.

MATERIAL. HOLOTYPE: QMS105353, ♂, GBR, Elizabeth Rf, 19°20.12'S 149°02.85'E, 25 Dec. 1997, coarse sand & rubble at 3m. PARATYPES: QMS105354,

♀, ANIC, ♀, GBR, John Brewer Rf, 18°38.25'S 147°04.42'E, 11 Apr. 1998, coarse sand at 15m.

DESCRIPTION. *Male*. Idiosoma 388 long. AD uniformly pale; anteriorly narrowing, with rounded dome-like protuberance; truncated posteriorly (Fig. 10A). OC well developed, not longer than twice its width; with seta anteriorly. Cornea covering most of OC, with 2-3 depressions posteriorly. PD ca. 1.15 times as long as AD, with two pairs of setae and fewer than 200 foveae; truncate anteriorly. AE distinctly foveate only posterolateral to insertions of leg I but with further one or two inconspicuous depressions posterior to insertions of legs II. AE superficially smooth but in deeper layers finely punctate in median area (Fig. 10B). GA foveate lateral and posterior to GO. GO flanked by a pair of outlying setae and surrounded by 37 pgs; three pairs of short sgs. Adanal setae ventrally on anal cone.

Tectum wide and rounded (Fig. 10E). Ventral gnathosomal base foveate except for a wide area along median axis (Fig. 10F). Segment P-2 with ventral blunt protuberance and a seta inserted distal to protuberance.

Outline of legs as in Fig. 11. Telofemora ventrally smooth or with few shallow foveae. Chaetotaxy: I 1-2-2-4-5 (Fig. 11A), II 1-2-3-4-5 (Fig. 11B), III 1-1-2-3-5 (Fig. 11C), IV 1-1-2-3-5 (Fig. 11D). Claw-like seta of tibia I with proximal swelling. Paired claws of tarsi II-IV with accessory process but without pecten. Tarsus II with one ventral seta and pair of pas, tarsus III with one ventral seta and one pas, tarsus IV with two ventral setae but no pas.

Female. Idiosoma 380-390 long. AE in one female with few foveae posterior to insertions of leg II (Fig. 10C), in the other female without foveae at that position. GA with four pairs of pgs (Fig. 10D) or with four setae on one side and three setae on the other.

REMARKS. The only other species of *Simognathus* in which the cornea covers most of the OC is *S. exoticus* sp. nov. In *S. corneatus* sp. nov. the cornea is relatively shorter than in *S. exoticus* and the dome-like swelling of the AD is more developed. Also, the PD in *S. corneatus* is only about 1.15 times the length of the AD and carries less than 200 foveae whereas in *S. exoticus* it is 1.3 times the length of the AD and bears more than 250 foveae. Both species are otherwise similar and are undoubtedly closely related.

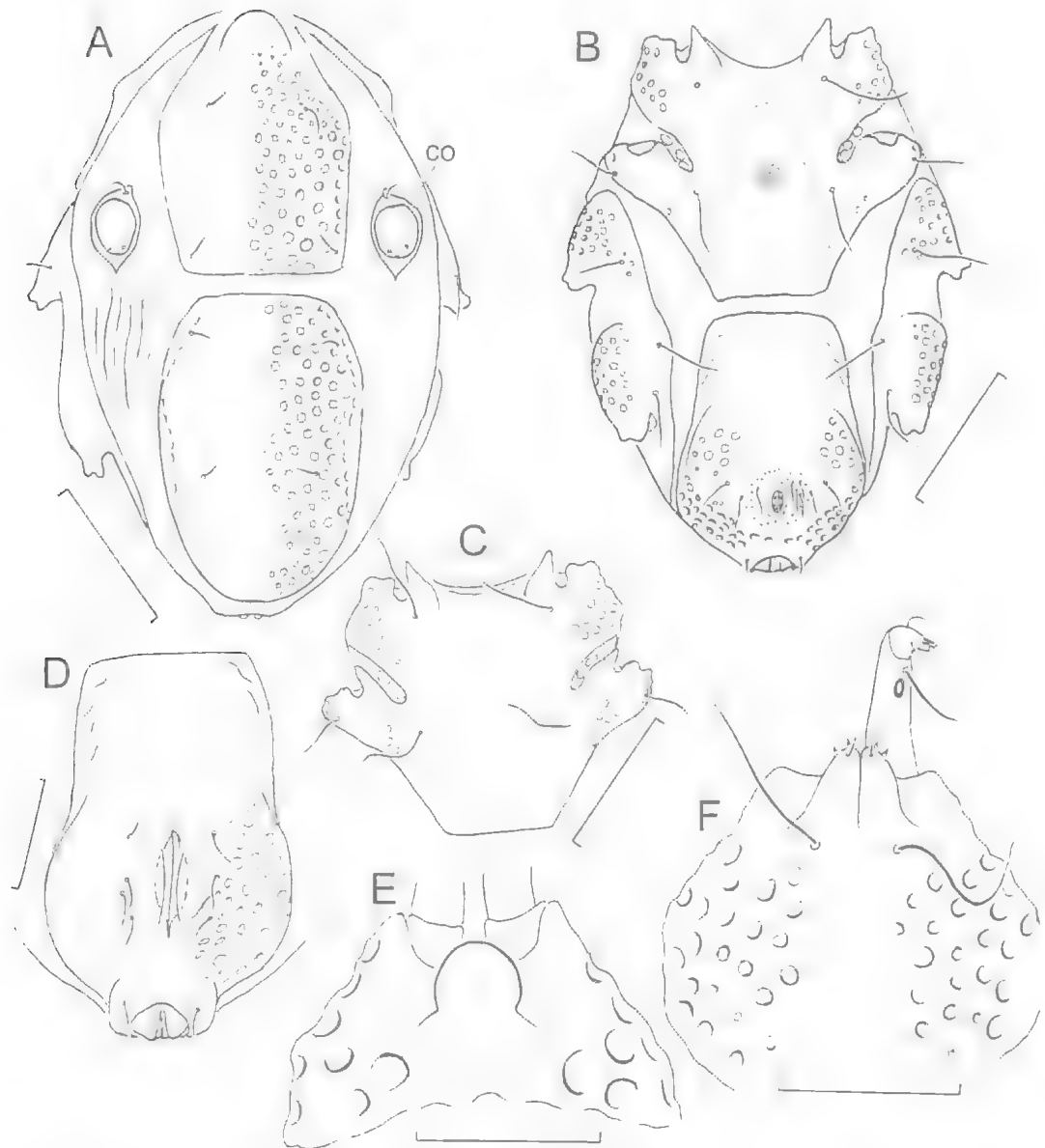


FIG. 10. *Simognathus corneatus* sp. nov., adult: A, idiosoma, dorsal view (co, cornea); B, ♂ idiosoma, ventral view; C, anterior epimeral plate of one leg; D, ♀ genitoanal plate; E, gnathosoma, dorsal view; F, gnathosoma, ventral view. Scale bars: A-C = 100µm; D-F = 50µm.

***Simognathus exoticus* sp. nov.**
(Figs 12, 13)

Etymology. Greek, *exotikos* = alien, referring to this species' occurrence on the remote reefs of the Queensland Plateau.

MATERIAL. HOLOTYPE: QMS105355, ♂, Coral Sea (Queensland Plateau), Lihou Rf, ca. 17°25'S 151°40'E, 22 July 1998, D. Fenner, sand at 7m. **PARATYPES:**

QMS105356, ♀, data as for holotype; ANIC, ♀, ZMH A35/99, ♀, data as for holotype except for: 20 July 1998, sand at 5m; QMS105357, ♀, Coral Sea (Queensland Plateau), Flinders Rf, ca. 17°35'S 148°27'E, July 1998, D. Fenner, sand.

DESCRIPTION. Male. Idiosoma 356 long. AD uniformly pale; anteriorly with slight swelling (Fig. 12A). OC at least twice as long as wide;

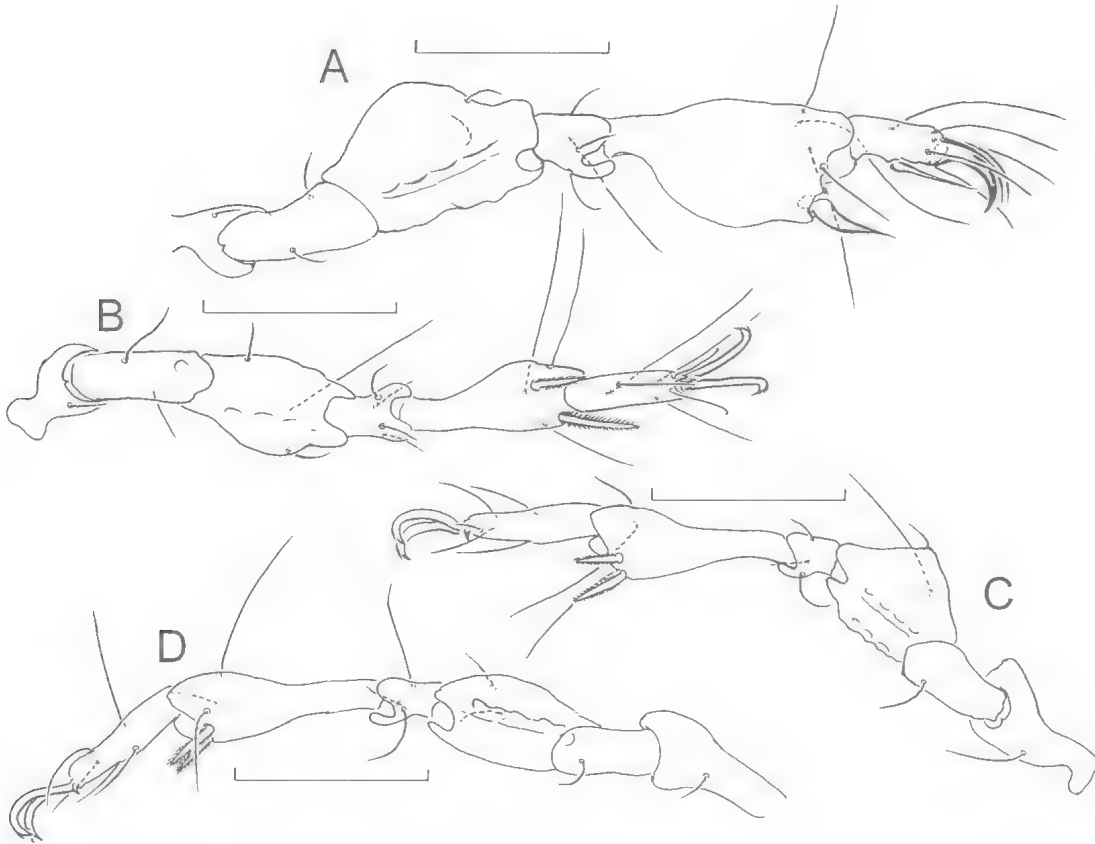


FIG. 11. *Simognathus corneatus* sp. nov., adult: A, leg I, medial view; B, leg II, ventral view; C, leg III, ventromedial view; D, leg IV, ventromedial view. Scale bars: A-D = 50 μ m.

anteriorly with seta on an extension of plate; cornea covering most of plate, posteriorly with few pore-like depressions. PD ca. 1.3 times longer than AD, with two pairs of setae and at least 250 foveae. AE with groups of foveae posterior to insertions of legs I and II (Fig. 12B). GA foveate laterally; with one pair of outlying setae, ca. 47 pgs and three pairs of short sgs. Pair of adanal setae positioned ventrally on anal cone.

Tectum wide and rounded (Fig. 9C). Ventral gnathosomal base laterally foveate, medially smooth (Fig. 9E). Segment P-2 with blunt ventral protuberance and seta.

Outline of legs as in Fig. 13. All segments without foveae. Chaetotaxy: I 1-2-2-4-5 (Fig. 13A), II 1-2-3-4-5 (Fig. 13B), III 1-1-2-3-5 (Fig. 13C), IV 1-1-2-3-5 (Fig. 13D). Claw-like ventral seta of tibia I with proximal swelling (Fig. 13A). Paired claws of tarsi II-IV with accessory process but without pecten. Tarsus II with ventral seta and

pair of pas, tarsus III with two ventral setae but no pas.

Female. Idiosoma 380-400 long. GA with 3-4 pgs (Fig. 12D); foveate area on either side of GO surpassing GO anteriorly.

REMARKS. The only other species of *Simognathus* in which the cornea covers most of the OC is *S. corneatus* sp.nov. For differences between these two species see the 'Remarks' to the latter.

***Simognathus platyaspis* sp. nov.**
(Figs 14, 15)

ETYMOLOGY. Greek, *platys* = wide, *aspis*, Greek = shield, referring to the species' wide anterior dorsal plate.

MATERIAL. HOLOTYPE: QMS105358, ♀, GBR, Bramble Rf, 28°26.36'S 146°42.24'E, 9 Apr. 1998, coarse sand & rubble at 6m. PARATYPES: ANIC, ♀, GBR, 18°25.25'S 146°40.65'E, Bramble Rf, 10 Apr. 1998, chunks of coral rubble at 3-6m; QMS105359, ♀, GBR, 18°40.60'S 146°34.29'E, Great Palm I., channel, 8 Apr. 1998, sand & rubble at 6m; QMS105360, ♀, GBR,

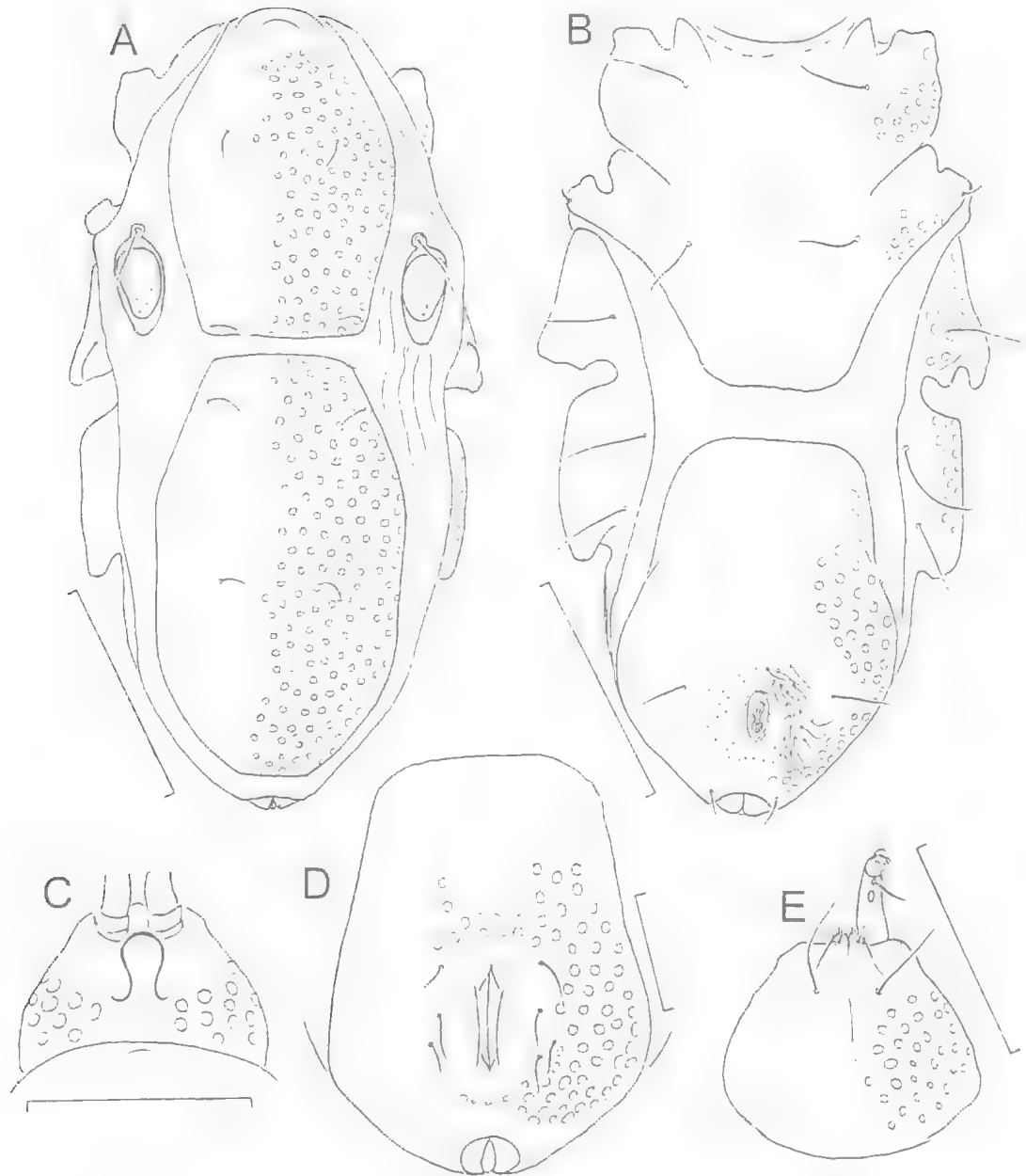


FIG. 12. *Simognathus exoticus* sp. nov., adult: A, idiosoma, dorsal view; B, ♂ idiosoma, ventral view; C, gnathosoma, dorsal view; D, ♀ genitoanal plate; E, gnathosoma, ventral view. Scale bars: A-C, E – 100 μ m; D – 50 μ m.

18°58.49'S 146°36.94'E, Phillips Rf, 16 Apr. 1998, chunks of rubble at 3-6m; QMS105361, ♀, GBR, 18°48.92'S 146°25.76'E, Pandora Rf, 22 Jan. 1998, coarse sand at 1 m; QMS105362, ♀, GBR, Boulder Rf, ca. 15°24'S 145°27'E, 8 Oct. 1998, A. Thompson, coarse sand at 2m; ZMH, ♀, GBR, Rosser Rf, ca. 15°37'S 145°33'E, 8 Oct. 1998, sand at 2m.

DESCRIPTION. *Female.* Idiosoma 306-364 long (holotype 329). AD slightly longer than PD; length/width ratio of AD 1.48-1.53 (Fig. 14A); anteriorly with swelling; posterior 2/3 of plate with conspicuous brown pigmentation. OC well developed; with several depressions in inner half;

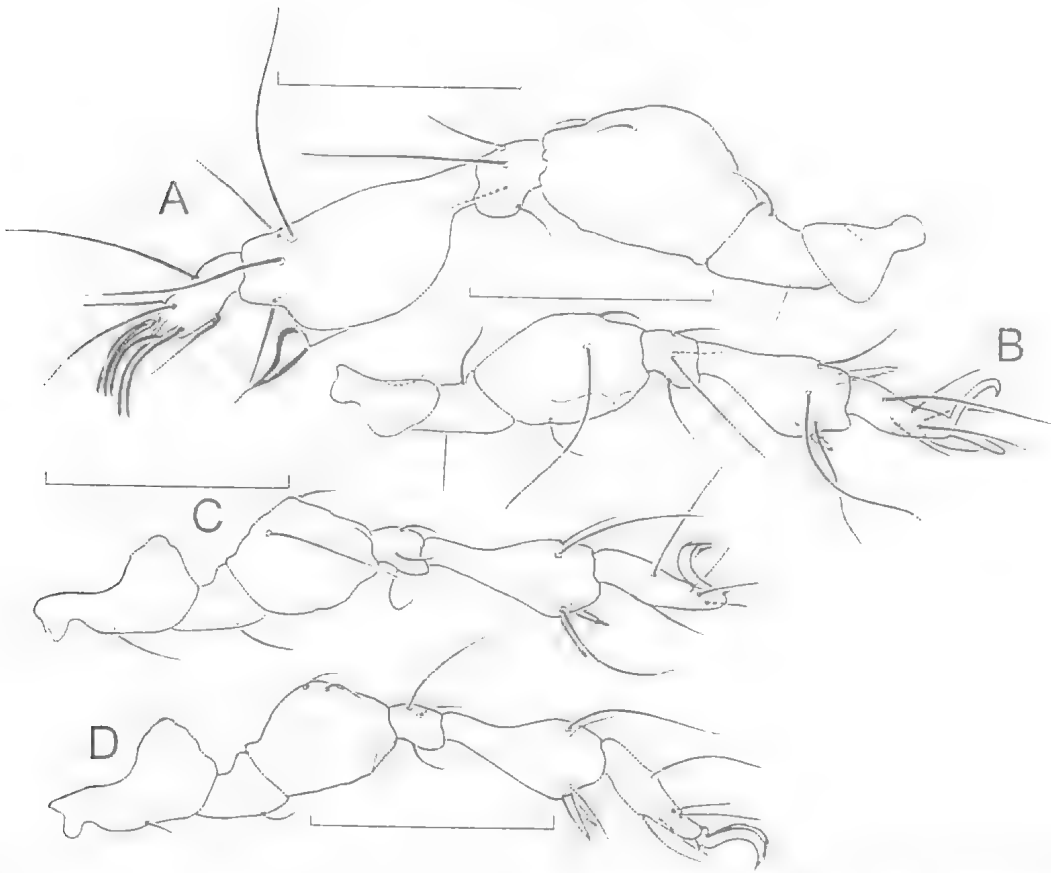


FIG. 13. *Simognathus exoticus* sp. nov., adult: A, leg I, lateral view; B, leg II, dorsal view; C, leg III, lateral view; D, leg IV, lateral view. Scale bars: A-D = 100 μ m.

seta either situated on OC or slightly separated from OC on a minute platelet. PD with two pairs of setae. AE foveate throughout except for an area between epimeres I and II. PE foveate. Underneath membranous cuticle posterior to AE with four conspicuous apodemes (Fig. 14B). Adanal setae positioned ventrally on anal cone.

Tectum shaped as in Fig. 14C. Ventral gnathosomal base foveate throughout. Segment P-2 with blunt protuberance proximal to ventral seta (Fig. 14D).

Outline of legs as in Fig. 15. Chaetotaxy: I 1-2-2-4-5 (Fig. 15A), II 1-2-3-4-5 (Fig. 15B), III 1-1-2-3-5 (Fig. 15C), IV 1-1-2-3-5 (Fig. 15D). Claw-like seta of tibia I with proximal swelling. Tarsi II-IV with paired claws bearing accessory process but no pecten. Tarsus II with ventral seta and pair of pas, tarsus III with ventral seta and single pas, and tarsus IV with two ventral setae but no pas.

Male. Unknown.

REMARKS. *Simognathus platyaspis* sp. nov. possesses brown pigmentation on the AD and foveae on the median part of the AE but lacks setae in the membranous dorsal cuticle. This combination of characters is otherwise known only for *S. fuscus* Viets, 1936, from the Caribbean and Bermuda. *Simognathus platyaspis* differs from *S. fuscus* by the length/width ratio of the anterior dorsal shield being less than 1.55 in contrast to 1.72 in *S. fuscus*.

***Simognathus pygmaeus* sp. nov.**
Figs 16, 17

ETYMOLOGY. Greek, *pygmaios* = dwarf, referring to the small size of this species.

MATERIAL. HOLOTYPE: QMS105364, ♀, GBR, Wonga Beach, 16°21'S 145°26'E, 31 July 1998, sand

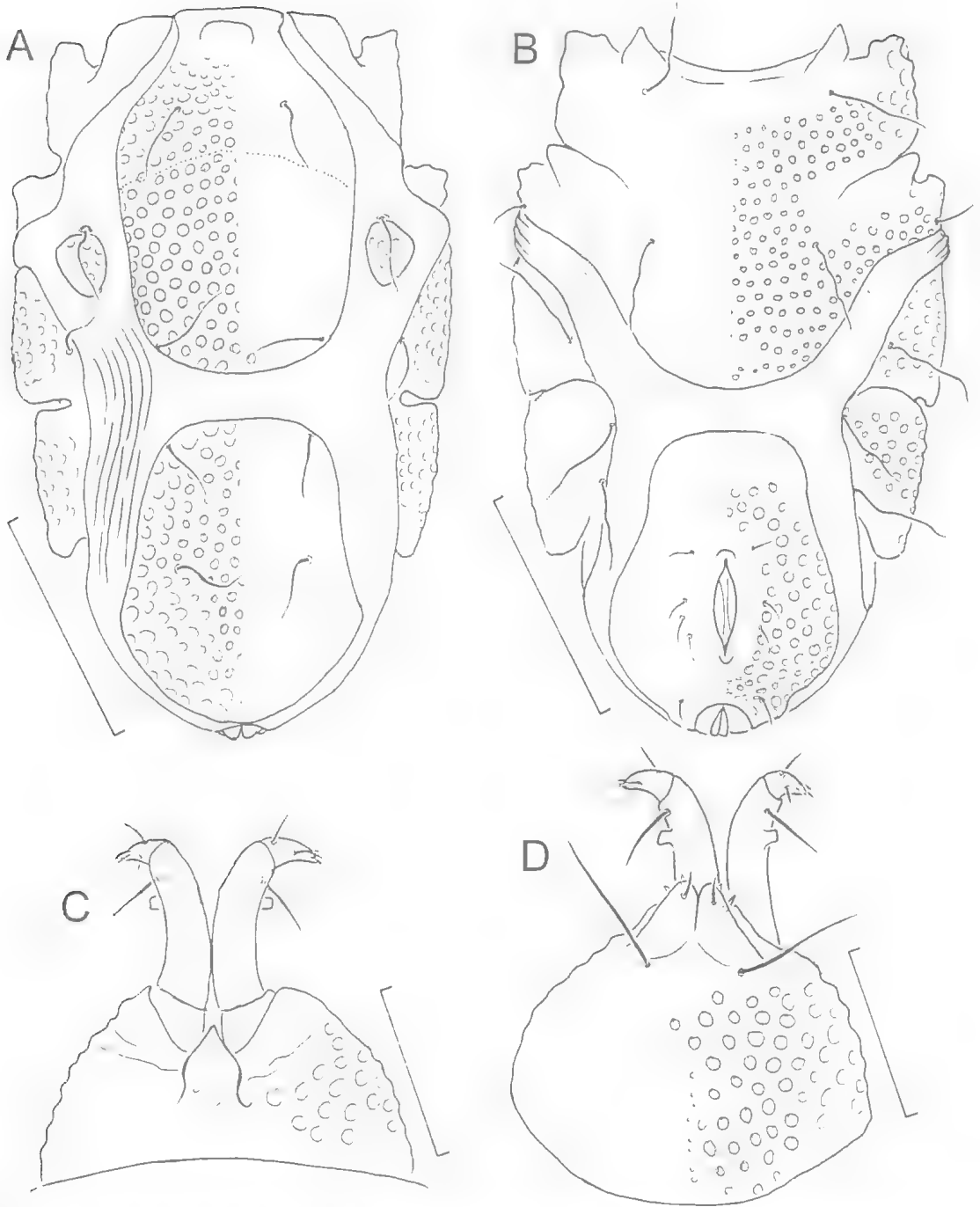


FIG. 14. *Simognathus platyaspis* sp. nov., adult: A, idiosoma, dorsal view (dotted line indicates anterior margin of brown part of plate); B, ♀ idiosoma, ventral view; C, gnathosoma, dorsal view; D, gnathosoma, ventral view. Scale bars: A,B = 100µm; C,D = 50µm.

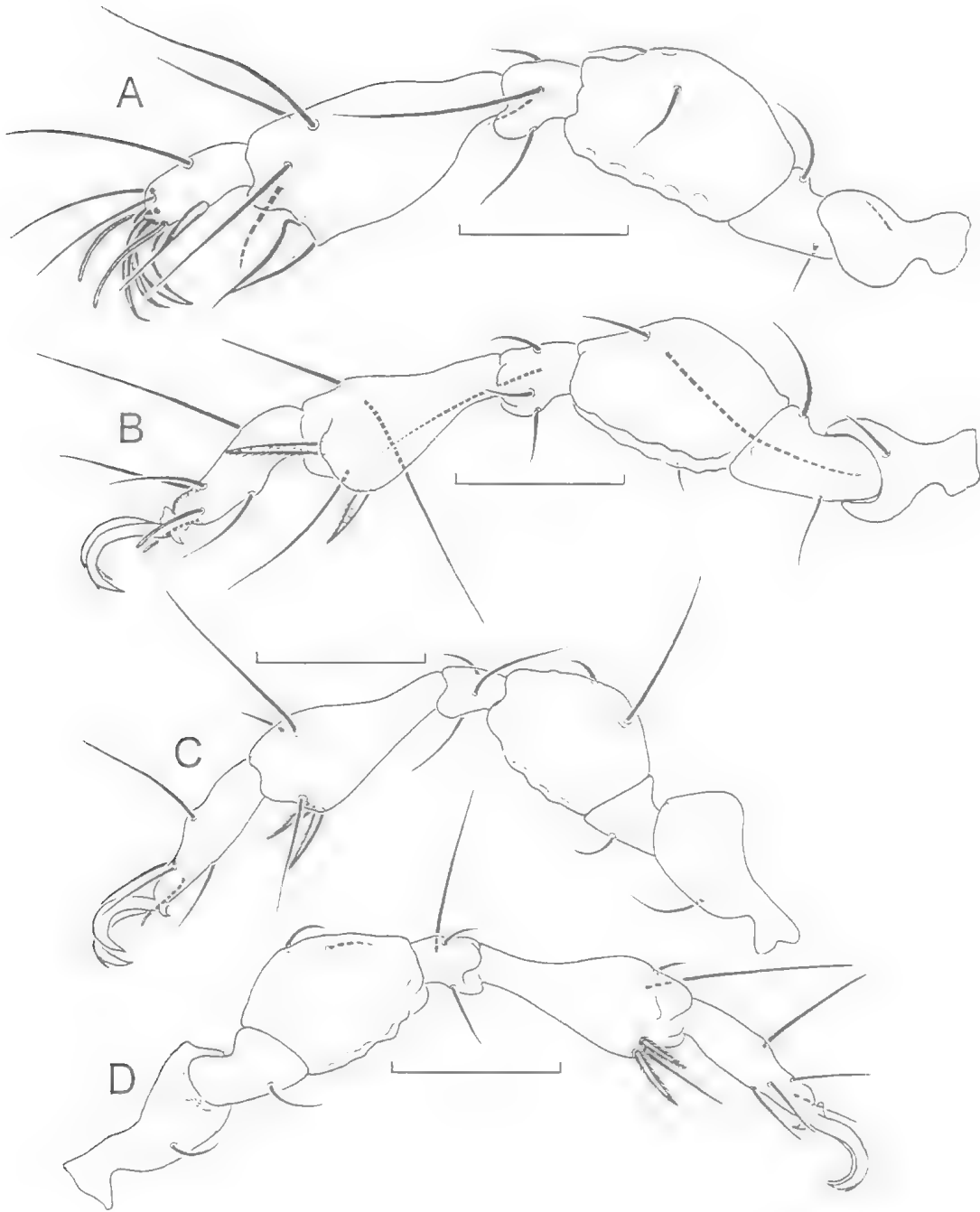


FIG. 15. *Simognathus platyaspis* sp. nov., adult: A, leg I, lateral view; B, leg II, medial view; C, leg III, lateral view; D, leg IV, medial view. Scale bars: A-D = 50 μ m.

below high tide mark, ca. 40cm below surface.
PARATYPE: QMS105365, ♀, data as for holotype.

DESCRIPTION. *Female*. Idiosoma 240-250 long (holotype 250). AD slender (Fig. 16A);

posterior margin rounded. OC reduced to narrow subcuticular platelets with pair of setae at anterior margin. Membranous cuticle anterior to PD with pair of setae. PD with two pairs of setae including

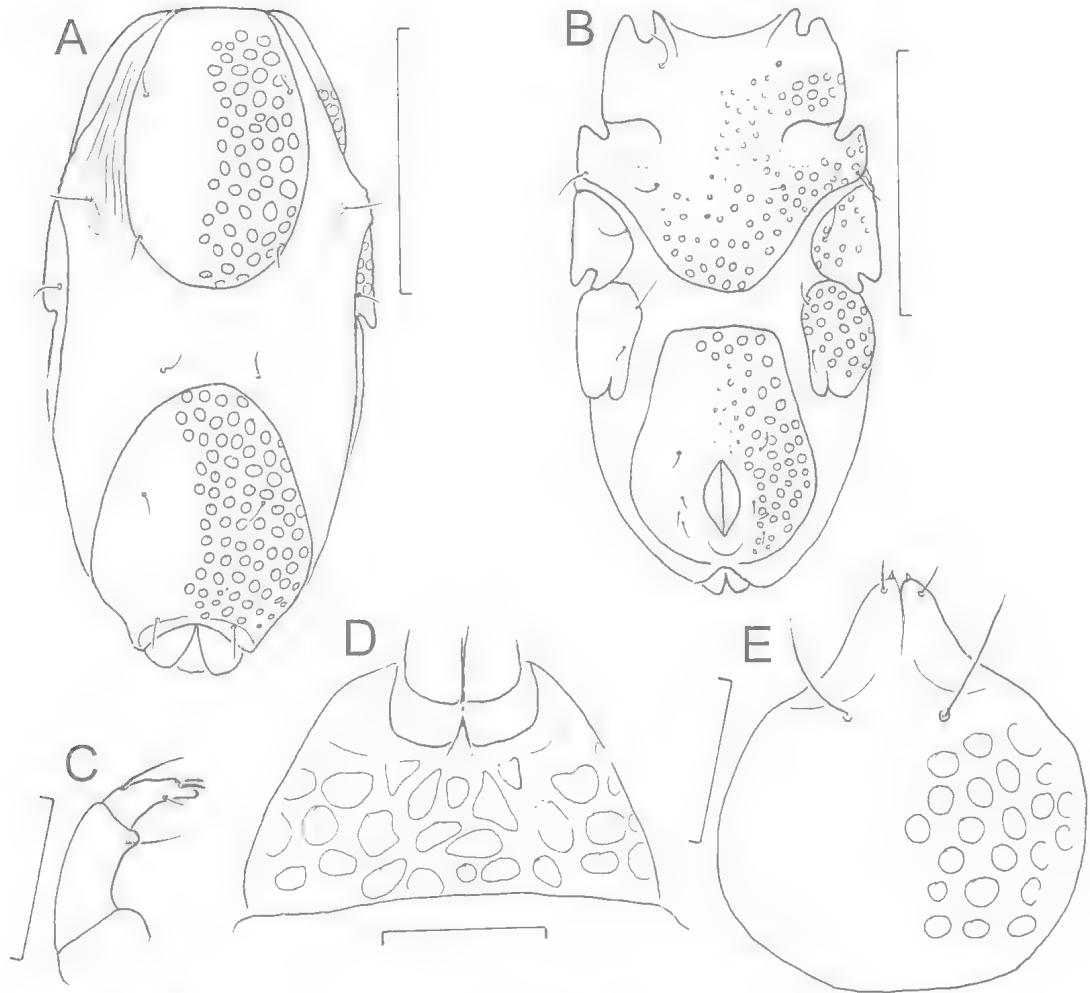


FIG. 16. *Simognathus pygmaeus* sp. nov., adult: A, idiosoma, dorsal view; B, ♀ idiosoma, ventral view; C, palp, medial view; D, gnathosomal base, dorsal view; E, gnathosoma, ventral view. Scale bars: A,B = 100 μ m; C-E = 25 μ m.

pair of adanal setae. AE with foveae throughout (Fig. 16B), marginal foveae more conspicuous than medial foveae; three pairs of setae as illustrated; epimeral vesicles large. GA foveate throughout.

Dorsal gnathosomal base with large irregular shaped foveae; tectum minute, pointed (Fig. 16D). Ventral gnathosomal base with relatively few large foveae (Fig. 16E). Segment P-2 with an apical swelling associated with a ventral seta (Fig. 16C); P-3 at least as long as half of P-2.

Outline of legs as in Fig. 17. Telofemur and tibia I with cuticular bars forming a reticulated pattern, inside each polygon with shallow pits (Fig. 17A). Chaetotaxy: I 1-2-1-4-5 (Fig. 17A), II

1-2-2-4-5 (Fig. 17B), III 1-1-2-3-5 (Fig. 17C), IV 1-1-1-3-4 (Fig. 17D). Ventral claw-like seta of tibia I relatively small compared with median claw of tarsus and without proximal swelling. Tibia II and III each with two ventral slightly denticulate spines; tibia IV with only one ventral spine (Fig. 17D). Tarsi II-IV with pair of pas and single ventral seta. Paired claws of tarsi II-IV with cluster of tines apically.

Male. Unknown.

REMARKS. With its posteriorly rounded AD, the minute OC, the relatively long palp tarsus in comparison to the palp tibia, the small body size, the irregular shaped foveae on the dorsal

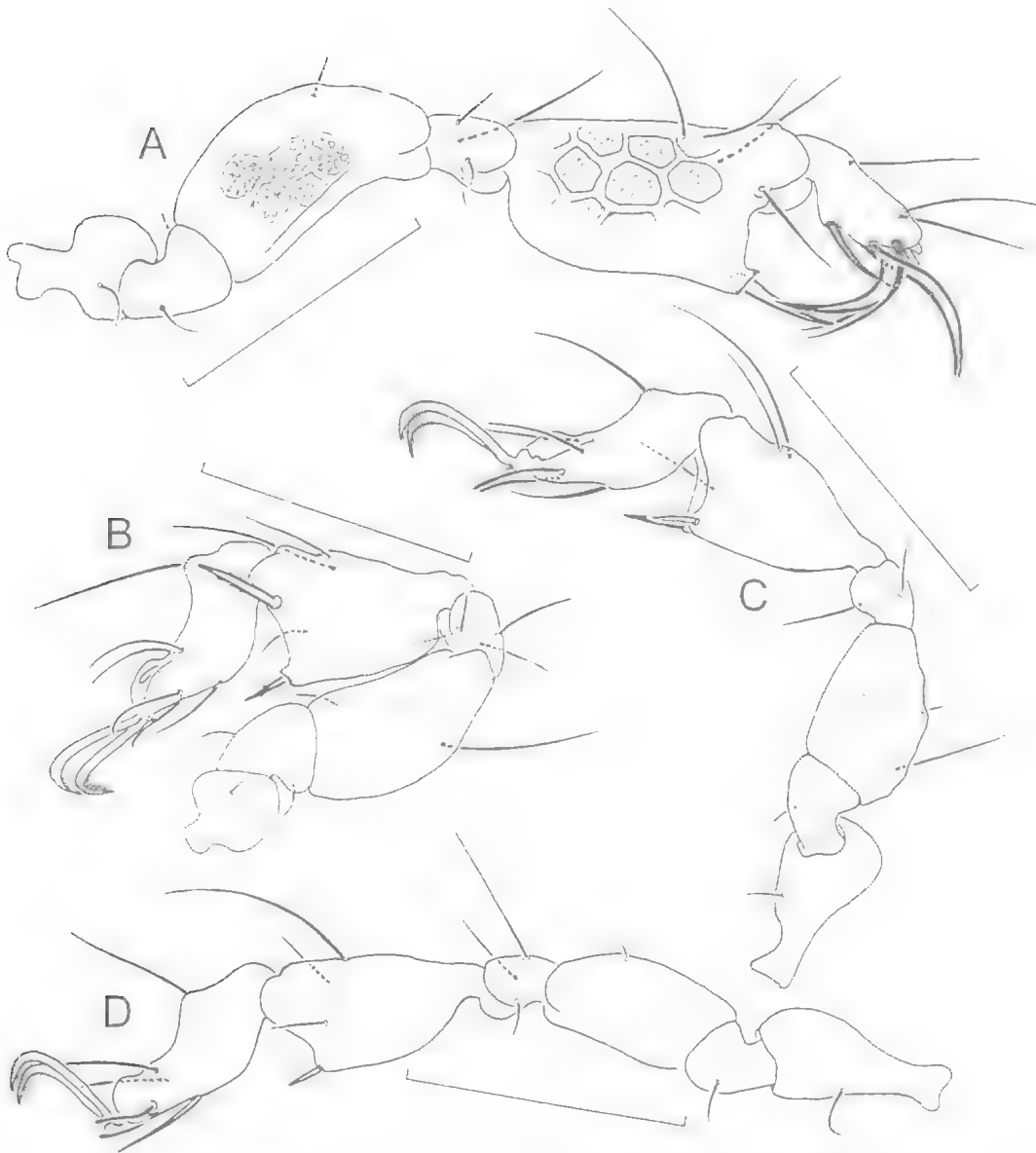


FIG. 17. *Simognathus pygmaeus* sp. nov., adult: A, leg I, medial view; B, leg II, medial view; C, leg III, medial view; D, leg IV, lateral view. Scale bars: A-D = 50 μ m.

gnathosomal base, and the apical cluster of pecten on the paired claws of legs II-IV, *Simognathus pygmaeus* sp. nov. appears most similar to *S. actius* sp. nov. and is likely to be the latter species' closest known relative. *Simognathus pygmaeus* differs from *S. actius* most conspicuously by the reticulated pattern on telofemur I. Other distinguishing characters are the presence of a pair of setae in the dorsal

membranous cuticle, foveae medially on the AE and having only one spine on tibia IV.

***Simognathus specialis* sp. nov.**
(Figs 18, 19)

ETYMOLOGY. Latin, *specialis*, = individual, particular, referring to the unusual shape of the foveae.

MATERIAL. HOLOTYPE: QMS105366, ♀, GBR, Myrmidon Rf, 18°16.46'S 147°22.88'E, 13 Apr. 1998,

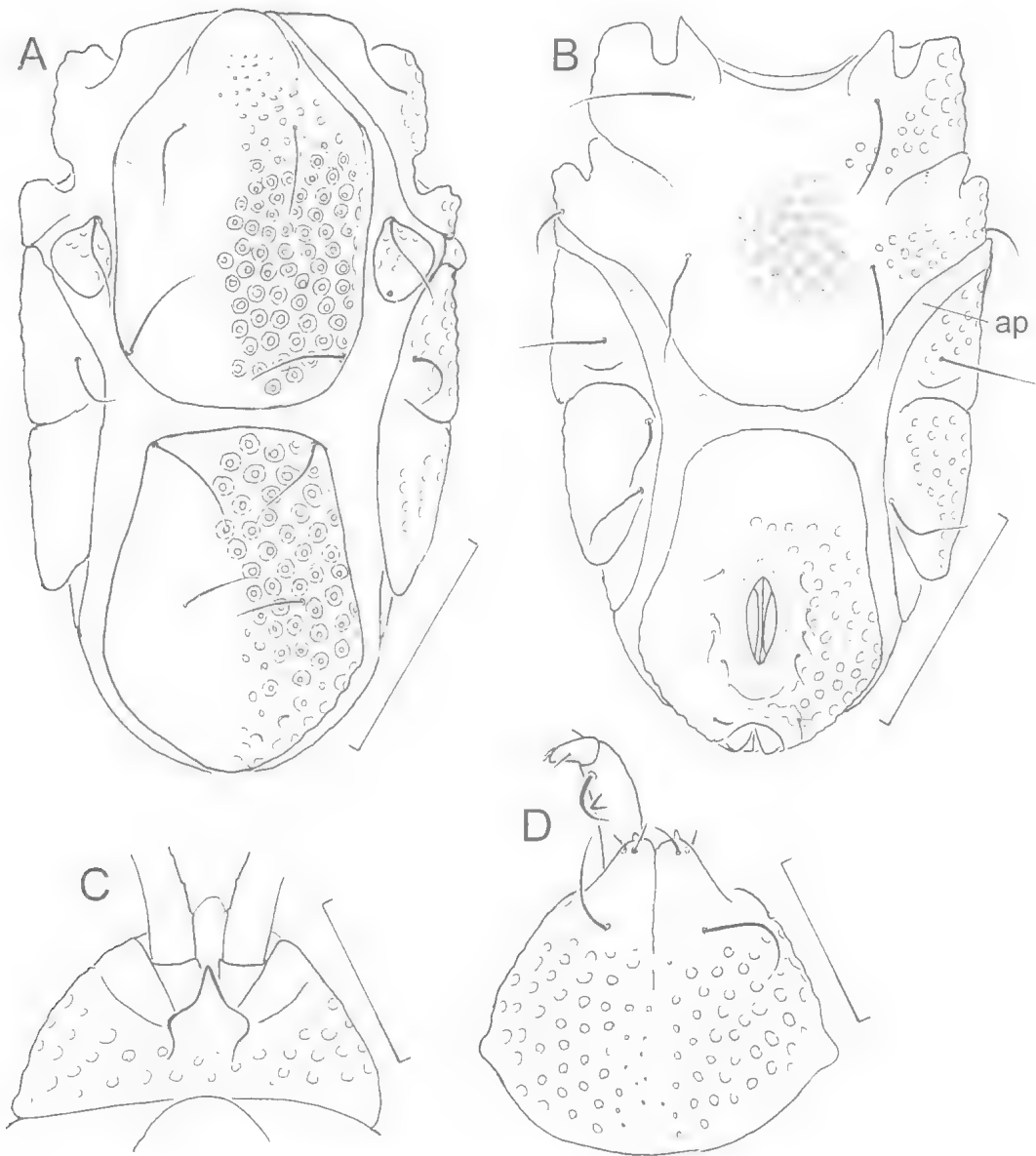


FIG. 18. *Simognathus specialis* sp. nov., adult: A, idiosoma, dorsal view (dotted line indicates anterior margin of brown part of plate); B, ♀ idiosoma, ventral view (ap, apodeme); C, gnathosomal base, dorsal view; D, gnathosoma and palp, ventral view. Scale bars: A,B = 100µm; C,D = 50µm.

coral rubble at 15m. PARATYPES: QMS105367, ♀, ANIC, ♀, ZMH A36/99, ♀, GBR, Myrmidon Rf, 18°16.46'S 147°22.88'E, 13 Apr. 1998, dead coral overgrown with algae, at 3-15m; QMS105368, ♀, GBR, Myrmidon Rf, 18°16.69'S 147°23.21'E, 14 Apr. 1998, coarse sand & rubble at 15m; QMS105369, ♀, GBR, Yonge Rf, ca. 14°36'S 145°38'E, 10 Oct. 1998, coarse sand & rubble at 9m; QMS105370, ♀, Coral Sea (Queensland Plateau), Chilcott I., 16°56.61'S 150°0.177'E, 14 Sep. 1998, G.A. Diaz-Pulido, coarse sand at 0.5m.

DESCRIPTION. *Female*. Idiosoma 276-320 long (holotype 320). AD slightly longer than PD, anteriorly narrowing and with dome-like swelling (Fig. 18A); posterior 2/3 of plate with brown pigmentation; setae long; foveae consisting of an inner depression and an outer less depressed rim. OC well developed; with several depressions in inner half, a seta anteriorly and a pore posteriorly. PD with foveate

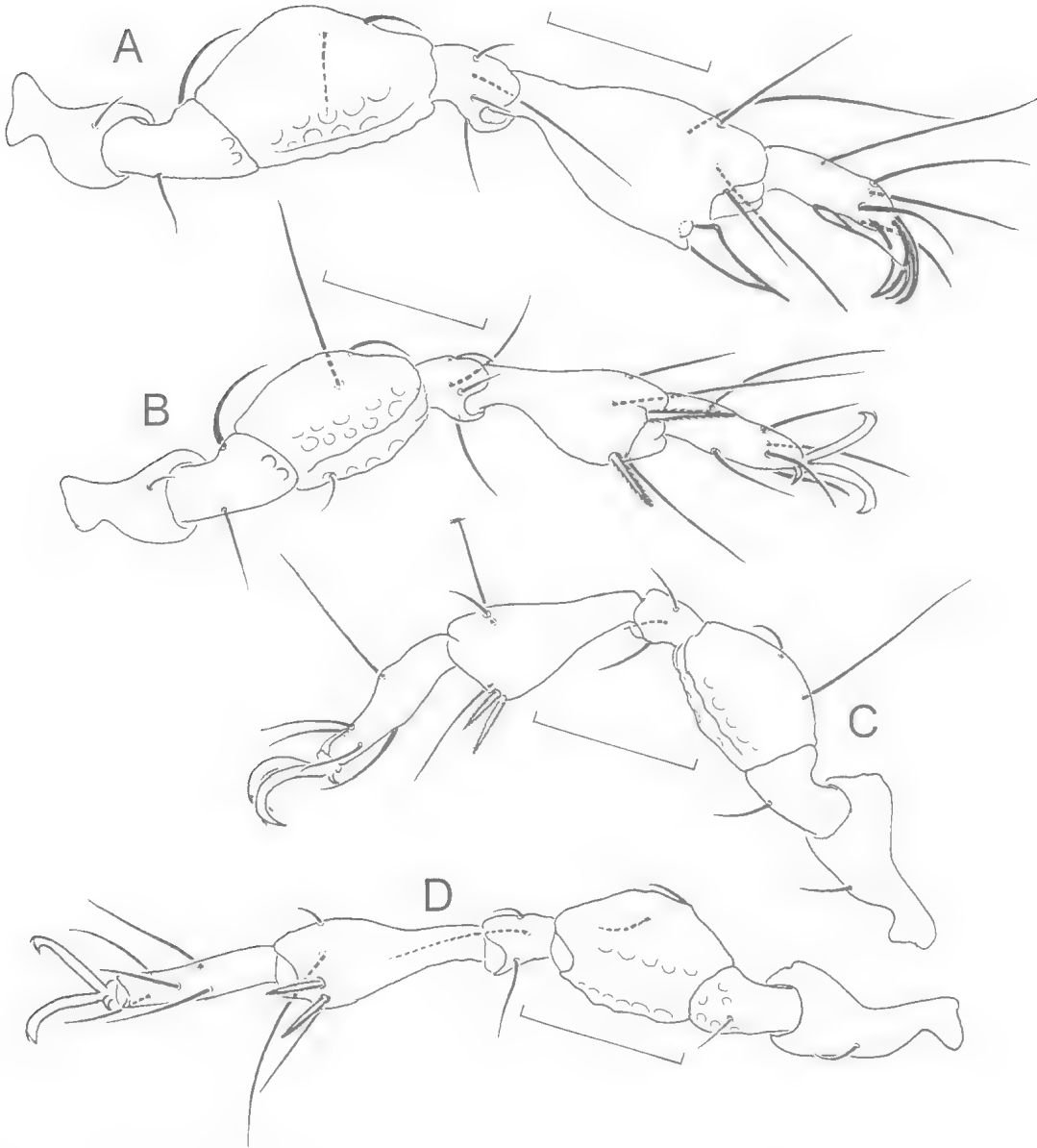


FIG. 19. *Simognathus specialis* sp. nov., adult: A, leg I, medial view; B, leg II, medial view; C, leg III, medial view; D, leg IV, medial view. Scale bars: A-D = 50 μ m.

ornamentation similar to that on AD; with two pairs of long setae. AE with foveae posterior to insertions of legs I and II; remainder of plate punctate with punctations forming groups (Fig. 18B). Underneath membranous cuticle between AE and GA with four conspicuous apodemes. GA foveate except for anterior third of plate. Adanal setae positioned ventrally on anal cone.

Shape of tectum as in Fig. 18C. Ventral gnathosomal base foveate throughout. P-2 with a pointed protuberance proximal to ventral seta.

Outline of legs as in Fig. 19. Telfemora with distinct foveae ventrally. Claw-like ventral seta of tibia I with proximal swelling (Fig. 19A). Chaetotaxy: I 1-2-2-4-5 (Fig. 19A), II 1-2-3-4-5 (Fig. 19B), III 1-1-2-3-5 (Fig. 19C), IV 1-1-2-3-5 (Fig. 19D). Paired claws of tarsi II-IV with

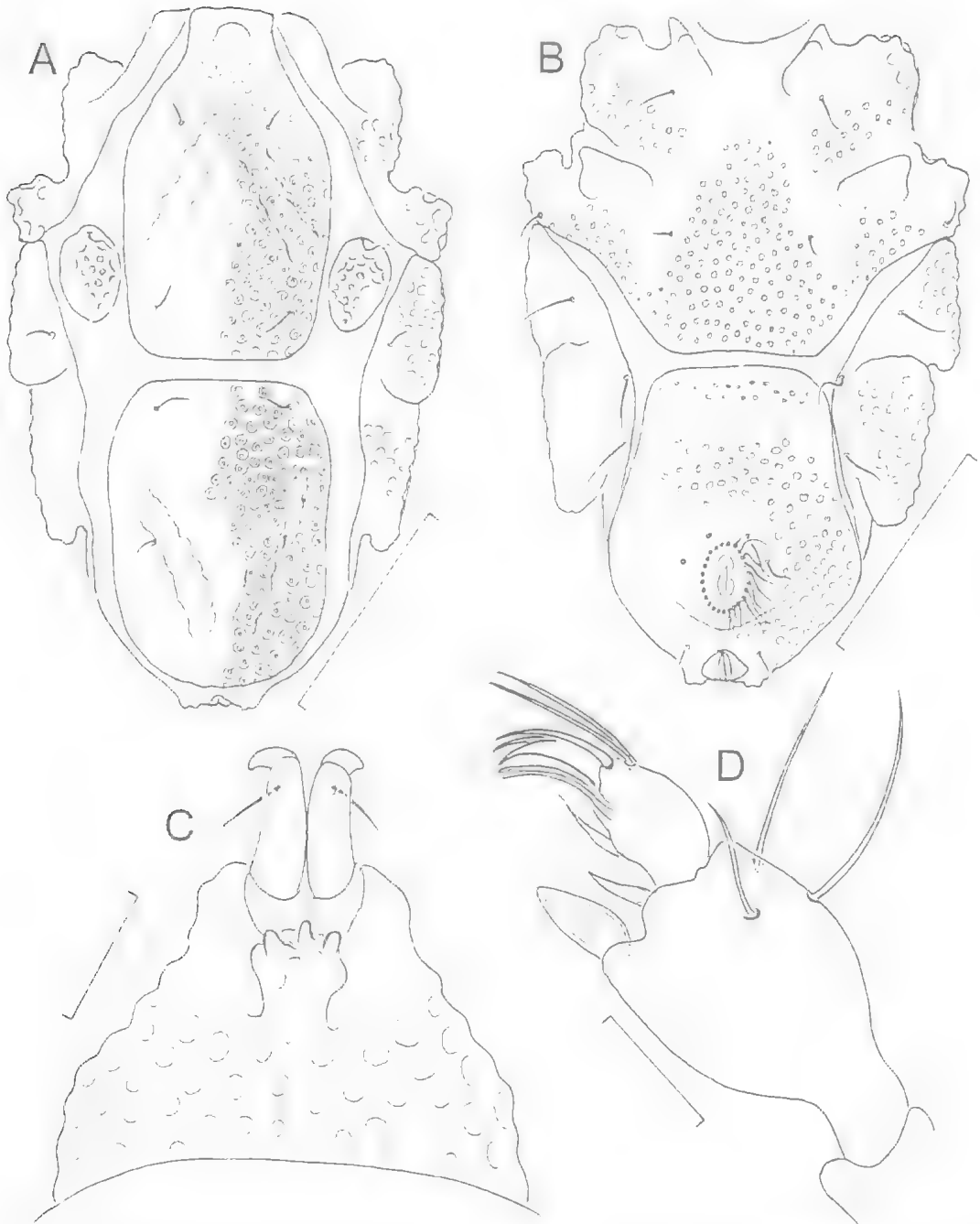


FIG. 20. *Simognathus trachys* sp. nov., adult. A, idiosoma, dorsal view; B, ♂ idiosoma, ventral view; C, gnathosoma, dorsal view; D, tibia and tarsus of leg I, medial view. Scale bars: A,B = 100µm; C,D = 25µm.

accessory process but without pecten. Tarsus II with one ventral seta and pair of pas, tarsus III with one pas and one ventral seta, tarsus IV with two ventral setae but no pas.

Male. Unknown.

REMARKS. In *Simognathus specialis* sp. nov. the dorsal idiosomal foveae consist of a deep

inner pit and a flat rim. Such foveae are otherwise known only for *S. trachys* sp. nov. from which *S. specialis* differs in a number of aspects: punctations on the AE arranged in groups, shape of the tectum and morphology of the claw of tibia I.

***Simognathus trachys* sp. nov.**
(Fig. 20)

ETYMOLOGY. Greek, *trachys* = rough, referring to the rough appearance of the tectum.

MATERIAL. HOLOTYPE: QMS105371, ♂, GBR, Elizabeth Rf, 19°20.12'S 149°02.85'E, 24-25 Dec. 1997, coral rubble at 10m. PARATYPES: QMS105372, ♀, ANIC, ♀, ZMH A37/99, ♀; QMS105373, ♂, data as for holotype; QMS105374/105375, 2 ♀s, data as for holotype, except from medium coarse sand at 10m.

DESCRIPTION. *Male*. Idiosoma 284-299 long (holotype 299). AD slightly longer than PD, uniformly pale, posteriorly truncated; covered with foveae which consist of deep depression and a shallower rim (Fig. 20A); anteriorly narrowing and with a swelling; two pairs of setae inserted as illustrated; with pair of slightly elevated ridges that converge anteriorly; no canaliculi seen in deeper cuticular layers on either AD or PD. OC well developed; covered with foveae except for posterolateral smooth area (cornea); anteriorly with a seta. PD truncated anteriorly; anteriorly and posteriorly of similar width; with two pairs of setae as illustrated; pair of slightly elevated ridges, converging posteriorly. AE covered by foveae except for a smooth gable-like area (Fig. 20B). GA separated from AE; with foveae except for a transverse area anteriorly. GO surrounded by a circle of ca. 25 pgs; one or two pairs of outlying setae anterolateral to GO. Adanal setae inserted ventrally on anal cone.

Gnathosomal base dorsally and ventrally foveate. Tectum of variable shape but always with several protuberances (Fig. 20C). Palps inserted well anteriorly, segment P-2 with a ventral seta but no protuberance.

Leg chaetotaxy: I 1-2-2-4-5, II 1-2-3-4-5, III 1-1-2-3-5, IV 1-1-2-3-5. Tibia I with a blunt ventral spine and adjacent to it with a thickened seta (Fig. 20D). Paired claws of tarsi II-IV with accessory process but without pecten. Tarsus II with one ventral seta and pair of pas, tarsus III with one pas and one ventral seta, tarsus IV with two ventral setae but no pas.

Female. Idiosoma 309-329 long. GA with distribution of foveae as in male but with 3-4 pairs of pgs on either side of GO.

REMARKS. With its short and blunt ventral spine and thickened seta on tibia I *Simognathus trachys* sp. nov. closely resembles *S. gibberosus* Bartsch, 1994, from Rottneest I. Both species are also similar in most other respects, for example the distribution of the foveae on the AE and the shape of the tectum, which indicates their close relationship. However, the AD in *S. gibberosus* carries canaliculi in deeper cuticular layers which are absent in *S. trachys*. Further, the PD in *S. gibberosus* narrows posteriorly, whereas in *S. trachys* it is of similar width anteriorly and posteriorly, and the foveae in *S. trachys* possess a wide rim which is unknown for *S. gibberosus*. Finally, in the males of *S. gibberosus* the AE and GA are fused according to Bartsch (1994), while such fusion has not been observed in *S. trachys*. However, I examined a male paratype of *S. gibberosus* (WAM 93/440) in which the AE was not fused to the GA, and thus it appears this character may not be reliable.

***Simognathus versicolor* sp. nov.**
(Fig. 21)

ETYMOLOGY. Latin, *versicolor* = variegated, of various colours, referring to the pigmented AD.

MATERIAL. HOLOTYPE: QMS105376, ♀, GBR, Elizabeth Rf, 19°20.12'S 149°02.85'E, 24 Dec. 1997, large chunks of coral rubble at 10m.

DESCRIPTION. *Female*. Idiosoma 311 long. AD and PD subequal in length (Fig. 21A); posterior 2/3 rd of plate with brown pigmentation. OC well developed; on inner half with several depressions; anteriorly with a seta. AE foveate posterior to insertions of legs I and II, remainder of plate uniformly punctate (Fig. 21B). Underneath membranous cuticle between AE and GA with four conspicuous apodemes. Morphology of GA as described and illustrated for *S. specialis*. Adanal setae inserted ventrally on anal cone.

Tectum shaped as in Fig. 21C. Ventral gnathosomal base foveate except for a narrow strip along median axis. Segment P-2 with a blunt ventral protuberance.

Legs as described and illustrated for *S. specialis*.

REMARKS. *Simognathus versicolor* sp. nov. lacks foveae on the median part of the AE and has brown pigmentation on the posterior part of the AD. This combination of characters is otherwise

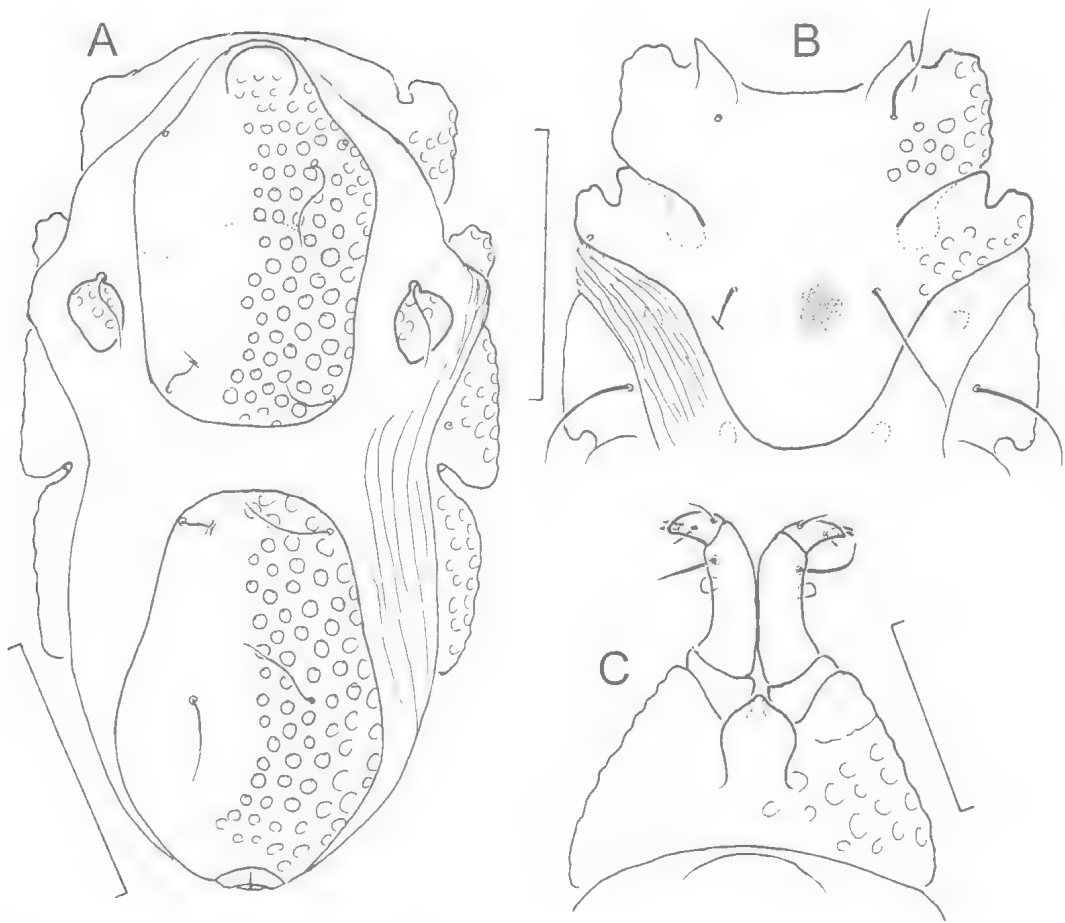


FIG. 21. *Simognathus versicolor* sp. nov., ♀: A, idiosoma, dorsal view (dotted line indicates anterior margin of brown part of plate); B, anterior half of idiosoma, ventral view; C, gnathosoma, dorsal view. Scale bars: A,B = 100µm; C = 50µm.

known only for *S. maculatus* Bartsch, 1994, from Rottneest I., and *S. specialis* sp. nov. from the Great Barrier Reef. *Simognathus versicolor* differs from *S. specialis* by lacking a rim around the dorsal foveae and from *S. maculatus* by its smaller size, relatively larger foveae on the dorsal plates, and by the posteriorly widened PD.

***Simognathus xandaros* sp. nov.**
(Fig. 22)

ETYMOLOGY. Greek, *xandaros*, = a fabulous sea-monster.

MATERIAL. HOLOTYPE: QMS105377, ♀, GBR, Turner Cay, NE, ca. 21°43'S 152°33'E, reef flat, 8 Dec. 1998, G. Coleman, medium coarse sand at 3m. PARATYPE. QMS105378, ♀, GBR, John Brewer Rf, 18°38.25'S 147°04.42'E, 11 Apr. 1998, coarse sand at 15m.

DESCRIPTION. *Female*. Idiosoma 333-339 long (holotype 333). AD as long as PD (Fig. 22A), ca. 1.3 times longer than wide; posterior 2/3 of plate with brown pigmentation, in deeper cuticular layers with numerous fine canaliculi. OC well developed; anteriorly with several depressions and a seta. AE laterally foveate, remainder of plate uniformly punctate (as for *S. versicolor* in Fig. 21B). Underneath membranous cuticle between AE and GA with four conspicuous apodemes. Morphology of GA as described and illustrated for *S. specialis*. Adanal setae inserted ventrally on anal cone.

Tectum pointed (Fig. 22B). Ventral gnathosomal base foveate throughout. Segment P-2 with a blunt ventral protuberance proximal to seta. Rostrum not extending to level of ventral protuberance.

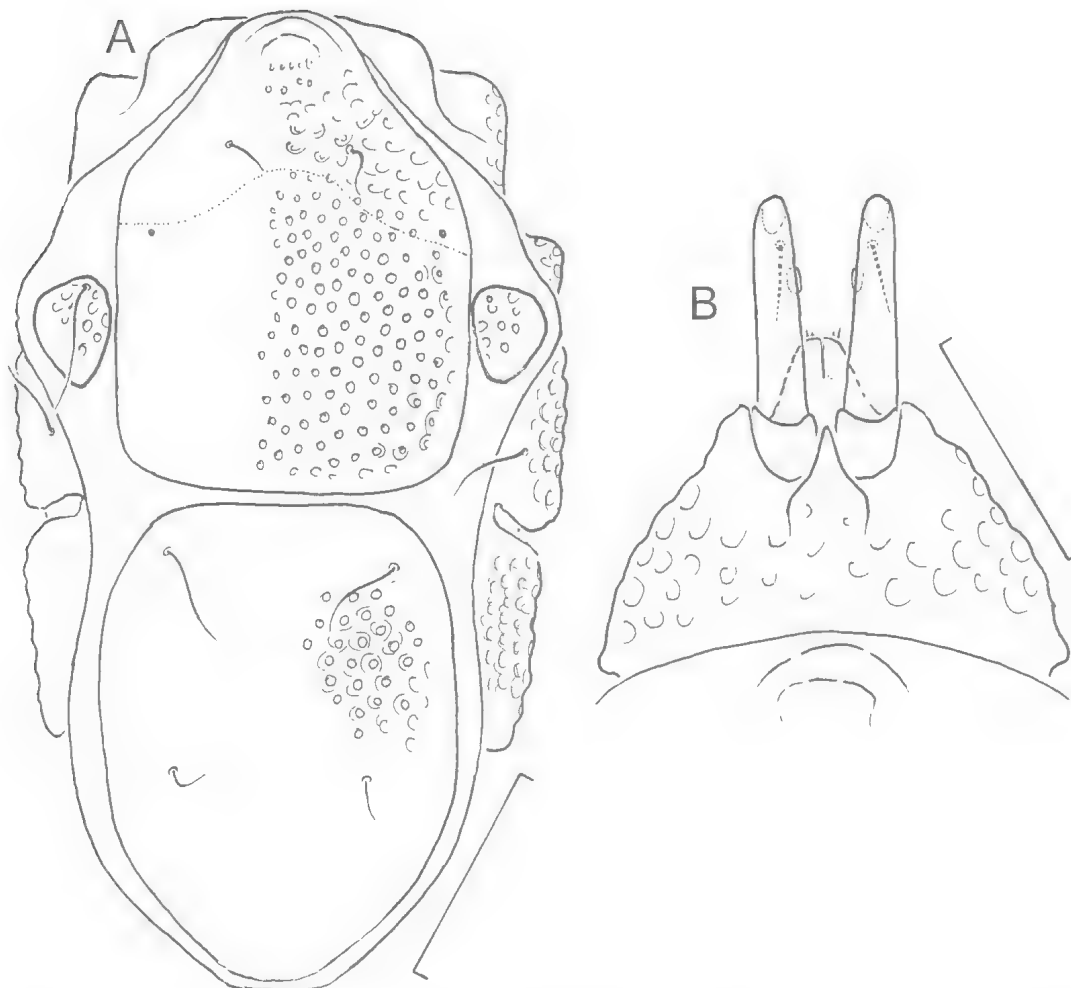


FIG. 22. *Simognathus xandarus* sp. nov., ♀: A, idiosoma, dorsal view; B, gnathosoma, dorsal view. Scale bars: A, B = 50µm.

Legs as described and illustrated for *S. specialis*.

REMARKS. The only other species with dark brown pigmentation in the posterior 2/3 of the AD and foveae on the AE restricted to the margins of the plate are *S. maculatus* Bartsch, 1996, *S. specialis* sp. nov. and *S. versicolor* sp. nov. *Simognathus xandarus* sp. nov. differs from all these species by a relatively wider AD. In addition, *S. xandarus* may be distinguished from *S. maculatus* by the rostrum not reaching the level of the ventral protuberance on P-2, from *S. specialis* by lacking a distinct rim around the foveae on the AD and not having the punctations on the AE arranged in groups, and from *S. versicolor* by having a larger number of foveae on the AD and a distinctly pointed tectum.

KEY TO AUSTRALIAN SPECIES OF SIMOGNATHINAE

1. Palp two-segmented (Fig. 2a); genu I with a spinose seta (Fig. 2B) *Acaromantis diazpulidoi* sp. nov.
 Palp three-segmented (Fig. 5d), genu I without a spinose seta (Fig. 4A). 2, *Simognathus*
2. Posterior 2/3 of AD with dark brown pigmentation (Fig. 14A) 3
 AD uniformly pale 7
3. AE with foveae throughout (Fig. 14B) *S. platyaspis* sp. nov.
 AE with foveae only marginally (Figs 18B, 21B) 4
4. Foveae of AD consisting of an inner deep depression and a flat rim (Fig. 18A); AE with punctations that form distinct groups (Fig. 18B) *S. specialis* sp. nov.
 Foveae of AD consisting of only a simple depression without a rim (Fig. 21A); AE in non-foveate areas evenly punctate (Fig. 21B). 5

5. PD pear-shaped, distinctly wider posteriorly than anteriorly, anterior margin rounded (Fig. 21A) *S. versicolor* sp. nov.
 PD posteriorly not distinctly widened, anterior margin truncate (Fig. 22A) 6
6. Length of AD ca. 1.3 times its width (Fig. 22A); rostrum not reaching level of ventral protuberance on P-2 (Fig. 22B) *S. xandarus* sp. nov.
 Length of AD ca. 1.5 times its width; rostrum reaching beyond level of ventral protuberance on P-2 *S. maculatus* Bartsch, 1994
7. OC well developed, not obscured by membranous cuticle (Fig. 10A) 8
 OC plates strongly reduced or absent, if present then hidden underneath membranous cuticle (Figs 3A, 5A, 7A) 11
8. Cornea (= non-foveate part of plate) covering most of OC (Figs 10A, 12A), AE foveate only marginally (Figs 10B, 12B) 9
 Cornea smaller (Figs 14A, 18A, 20A); AE foveate marginally and medially (Fig. 14B) 10
9. Cornea as in Fig. 12A; PD ca. 1.15 times the length of AD (Fig. 12A) *S. exoticus* sp. nov.
 Cornea as in Fig. 10A; PD ca. 1.3 times the length of AD (Fig. 10A) *S. corneatus* sp. nov.
10. PD narrowing posteriorly; foveae of AD and PD without a rim; AD and PD with canaliculi in deeper cuticular layers; idiosoma of ♀ 357-408µm long, of ♂ 325-376µm *S. gibberosus* Bartsch, 1994
 PD anteriorly and posteriorly of similar width (Fig. 20A); foveae of AD and PD with a rim (Fig. 20A); AD and PD without canaliculi in deeper cuticular layers; idiosoma of ♀ 309-329µm long, of ♂ 284-299µm *S. trachys* sp. nov.
11. AE and GA fused (Figs 3B, 7B, 9B) 12
 AE and GA separated (Fig. 5B) 16
12. AE foveate (Figs 3B, 7B) 13
 AE finely punctate (Fig. 9B) *S. clypeatus* sp. nov.
13. Tarsi of leg I (excluding claws and setae) about ¼ of tibia length, length of tibia I ca. 3 times its height (Fig. 4A) 14
 Tarsi of leg I (excluding claws and setae) longer than 1/3 of tibia, length of tibia I ca. twice its height (Fig. 8A) 15
14. AD of subequal length and width (Fig. 3A); ventral gnathosomal base with a wide non-foveate area medially (Fig. 3E) *S. abnormalus* sp. nov.
 AD clearly longer than wide; ventral gnathosomal base lacking a wide non-foveate area *S. scutatus* Bartsch, 1993b
15. Tarsi III and IV with two pas (Fig. 8C,D) *S. aspidiotus* sp. nov.
 Tarsi III and IV with one pas *S. uniscutatus* Bartsch, 1994
16. AE foveate throughout (Fig. 16B) 17
 AE foveate only posterior to insertion of leg I *S. delicatulus* Bartsch, 1994
 AE foveate posterior to insertion of leg I and II, and along posterior margin (Fig. 5B) *S. actius* sp. nov.
17. Telofemur I with one seta (Fig. 17A), tibia IV with one spine (Fig. 17D) *S. pygmaeus* sp. nov.
 Telofemur I with two setae (Fig. 8A), tibia IV with two spines (Fig. 8D) 18

18. Tarsus IV with two pas and two ventral setae *S. variolosus* Bartsch, 1994
 Tarsus IV with one pas and one ventral seta *S. gracilis* Bartsch, 1994

DISCUSSION

Simognathus and *Acaromantis* are very similar in many characters which makes their separation difficult. According to Bartsch (1983, 1993b) *Acaromantis* possesses two palp segments while *Simognathus* has three segments, P-2 in *Simognathus* has a cuticular protuberance which is lacking in *Acaromantis*, the tarsus of leg I is shorter in *Acaromantis* than in *Simognathus* and paired claws are absent in *Acaromantis* while present in *Simognathus*. However, several species do not fit this diagnosis: *Simognathus gibberosus* Bartsch, 1994, and *S. gracilis* Bartsch, 1994, seem to lack a ventral protuberance on P-2 and *S. scutatus* Bartsch, 1993b, has a front leg tarsus which is as short as that of *Acaromantis* species. *Acaromantis* is therefore here redefined as all those simognathine species that have two palp segments, a spinose seta on genu I and no paired claws on tarsus I, and *Simognathus* as those that have three palp segments, slender seta-like paired claws on tarsus I and lack a spinose seta on genu I.

While *Acaromantis* defined as above is most likely a monophylum this is uncertain for *Simognathus*. Paired claws on tarsus I and lack of a coarsely spinose seta on genu I are a common character of halacarids and are therefore plesiomorphic in *Simognathus*. The possession of three palp segments may be synapomorphic for *Simognathus* but is more likely an intermediate step between the four segments typical for most other halacarid genera and the two segments of *Acaromantis* in which case it would not constitute a synapomorphy.

Support for the hypothesis that *Simognathus* may be paraphyletic comes from the observation that the closely related species *S. scutatus* and *S. abnormalus* both have a slender tibia and very short tarsus of leg I, which is typical of *Acaromantis* but not present in other *Simognathus* species. Further, in *S. abnormalus* these segments are oriented so that the spine of the tibia and the median claw of the tarsus are medially directed, and in all alcohol-preserved material leg I is held distinctly raised above the body, characters which are both typical of *Acaromantis* (Bartsch, 1977; pers. comm.). The peculiar orientation of tibia and tarsus of leg I can also vaguely be seen in the holotype and a paratype of

S. scutatus which I examined, although due to the compression of the specimens and the fact that some of the legs are detached it is difficult to detect. Thus both species, *S. abnormalus* and *S. scutatus*, may in fact be more closely related to species of *Acaromantis* than to their congeners. A further character which may indicate a possible paraphyly of *Simognathus* is the reduced OC, common to all species of *Acaromantis* and several species of *Simognathus*. While it is possible that the reduction of OC has occurred several times, there is no evidence for it and it is therefore more parsimonious to assume that reduction has occurred once and therefore that species of *Simognathus* with reduced plates are more closely related to *Acaromantis* than to their congeners with well developed plates. However, at present the current classification is here retained.

Simognathus now contains 37 species. Together with the seven species described from Rottneest I., 19 species are known from Australia, which has the highest recorded number of *Simognathus* species of any continent. Two species are currently known from North America and the Caribbean, nine from South America (including the Galapagos), one from Africa, four from Europe, two from Asia and four from New Zealand and subantarctic islands. Since the halacarid fauna of the northern hemisphere has been studied much more thoroughly than that of the southern hemisphere it appears almost certain that this genus is more diverse in the southern hemisphere.

Acaromantis now contains ten species: *A. arenarius* Bartsch, 1980, from the east coast of North America, *A. armatus*, *A. grandiculus*, *A. fastigatus*, *A. punctulatus* and *A. subasper* from the Galapagos I. (Bartsch 1977), *A. minutus* Bartsch, 1976, and *A. squilla* Trouessart and Neumann, 1893, from the French Atlantic coast, *A. monnioti* Morselli, 1970, from the Mediterranean, and *A. diazpulidoi* sp. nov. from the Coral Sea.

ACKNOWLEDGEMENTS

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Bartsch for comments on the manuscript and supply of much of the needed literature. The comments of two anonymous referees are much appreciated. Furthermore I wish to thank Katharina Fabricius and Paula Tomkins for giving me the opportunity to participate in their field trips, and Peter Doherty, Doug Fenner and Guillermo Diaz-Pulido for providing me with specimens from the Coral Sea reefs. This publication is contribution no. 940 of the Australian Institute of Marine Science.

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HALACARIDAE FROM THE GREAT BARRIER REEF AND CORAL SEA: THE
GENERA *LOHMANNELLA*, *SCAPTOGNATHIDES* AND *SCAPTOGNATHUS*
(ACARINA: HALACARIDAE: LOHMANNELLINEAE)

JÜRGEN C. OTTO

Otto, J.C. 2000 06 30: Halacaridae from the Great Barrier Reef and Coral Sea: the genera *Lohmannella*, *Scaptognathides* and *Scaptognathus* (Acarina: Halacaridae: Lohmannellinae). *Memoirs of the Queensland Museum* 45(2): 535-555. Brisbane. ISSN 0079-8835.

Nine new species of the lohmannelline genera *Scaptognathus* and *Scaptognathides* were found among sand and coral rubble, collected intertidally or from shallow water in the Great Barrier Reef Marine Park and on reefs of the Coral Sea: *Scaptognathides heraldensis* sp. nov., *S. tomkinsae* sp. nov., *S. undulatus* sp. nov., *Scaptognathus gracilipalpus* sp. nov., *S. exquisitus* sp. nov., *S. insularis* sp. nov., *S. kolybus* sp. nov., *S. monstrosus* sp. nov., and *S. oceanus* sp. nov. *Lohmannella dictyota* Bartsch, *Scaptognathus ornatus* Bartsch and *Scaptognathus kunzi* Bartsch are newly recorded from Australia and a key to Australian species of *Lohmannella*, *Scaptognathides* and *Scaptognathus* is presented. □ *Halacaridae*, *Lohmannellinae*, *Lohmannella*, *Scaptognathides*, *Scaptognathus*, *Great Barrier Reef*, *Coral Sea*.

Jürgen C. Otto (email j.otto@aims.gov.au), Australian Institute of Marine Science, PMB 3, Townsville 4810, Australia; 16 August 1999.

This paper is one of a series of publications reporting on halacarid mites found during a survey of the Great Barrier Reef, adjacent coast and reefs of the Coral Sea. The subject of previous publications in this series were the genera *Agauopsis* and *Halacaropsis* (Otto, 1999a), *Australacarus* (Otto, 2000a), *Rhombognathus* and *Isobactrus* (Bartsch, 2000), *Simognathus* and *Acaromantis* (Otto, 2000b), *Agaue* (Otto, 1999b), *Tropihalacarus* (Otto & Bartsch, 2000) and *Corallihalacarus* (Otto, 1999c), while the present paper deals with the lohmannelline genera *Lohmannella*, *Scaptognathides* and *Scaptognathus*.

Bartsch (1993a) was the first to record Lohmannellinae from Australia, describing *Lohmannella arenaria*, *Scaptognathides australis*, *Scaptognathus australis*, and *S. peregrinus* from Rottneest Island, Western Australia. Abé & Green (1994) added *Scaptognathus bassianus* from Tasmania, and Otto (1994) described *Lohmannella pinggi* from southeastern Australia. Two further species from Rottneest I., one of *Scaptognathus* and one of *Lohmannella*, have been reported by Bartsch (1993a) but are as yet undescribed. Thus, no Lohmannellinae have previously been reported from the northern half of Australia.

METHODS

Sand and coral rubble were collected by hand. Mites were extracted by washing the substrates in

a bowl of water and decanting the supernatant through a 100µm sieve. All material was collected by the author except where stated otherwise. Mites were cleared in lactic acid and mounted in PVA or glycerine jelly. Drawings were made with the aid of a *camera lucida*.

In the accounts of each species only one sex is described in detail, while for the opposite sex only characters that differ are stated. Measurements are in micrometres (µm). Terminology follows Bartsch's (1993b) glossary. 'Areola' is an area on a plate or a leg segment where the cuticular structure differs from that on the remainder of the plate or segment. In the accounts of leg chaetotaxy, numbers of setae present on both sides of a specimen but variable within a species are separated by a slash. Abbreviations: AD, anterior dorsal plate; AE, anterior epimeral plate; OC, ocular plate; GA, genitoanal plate; GO, genital opening; PD, posterior dorsal plate; PE, posterior epimeral plate; P-2, second palp segment counted from base of palp; I-IV, leg I to leg IV; pas, parambulacral seta(e); pgs, perigenital seta(e); sgs, subgenital seta(e). Further abbreviations used in the illustrations are explained in the captions. Great Barrier Reef Marine Park is abbreviated 'GBR'.

All material with the registration number prefix QMS is deposited in the Queensland Museum's branch, Museum of Tropical Queensland in Townsville. Abbreviations for other depositories are: ANIC, Australian National Insect Collection,

Canberra; SMF, Zoologisches Institut und Naturmuseum Senckenberg, Frankfurt; ZMH, Zoologisches Institut und Zoologisches Museum, Universität Hamburg.

SYSTEMATICS

Lohmannella Trouessart, 1901

Leptognathus Hodge, 1863: 302. Trouessart, 1894: 175. Lohmann, 1893: 87; 1907: 354. Fountain, 1953: 363. Nec Swainson, 1839 (Pisces).
Trouessartella Lohmann, 1901. Nec Cossmann, 1899 (Mammalia).
Lohmannella Trouessart, 1901: 250. Viets, 1927: 148; 1940: 91; 1956: 691. André, 1946: 125. Newell, 1947: 23; 1967: 92; 1971: 34; 1984: 248. Imamura, 1968: 472. Bartsch, 1977b: 141; 1983: 194; 1986: 231; 1992: 457; 1993a: 91; 1993b: 145. Otto, 1994: 32.

TYPE SPECIES. *Leptognathus falcatus* Hodge, 1863, by monotypy.

DIAGNOSIS. Idiosoma wide, flattened. Dorsal plates AD, OC and PD well developed, with four pairs of gland pores, one on AD, one on OC and two on PD. AE usually with four, rarely three, pairs of setae. Both pairs of maxillary setae on rostrum. Palps inserted dorsally on gnathosomal base, separated from each other by an interval less than the width of their most proximal segment, usually longer than gnathosomal base, four-segmented; P-2 much longer than other segments, with two setae; P-3 with cuticular spine; P-4 with one slender basal seta and one spiniform seta. Tibia I with 4-8 bipectinate setae. Tarsus I in addition to parambulacral setae with at least two other ventral setae.

Lohmannella dictyota Bartsch, 1992

Lohmannella dictyota Bartsch, 1992: 458.

MATERIAL. QMS105379-105382, 4♀, GBR, Elizabeth Reef, 19°20.12'S 149°02.85'E, 25 Dec. 1997, coarse sand & rubble at 3m; QMS105383-105385, 3♀, GBR, Myrmidon Reef, 18°16.69'S 147°23.21'E, 14 Apr. 1998, coarse sand & rubble at 12-17m; QMS105386-105388, 3♀, GBR, Loadstone Reef, 18°42.03'S 147°06.54'E, 12 Apr. 1998, coarse sand & rubble at 12-15m; A63/99 (ZMH), ♀, GBR, Loadstone Reef, 18°41.91'S 147°06.49'E, 12 Apr. 1998, sand & rubble at 2m; ANIC ♀, GBR, Club 21 Reef, 19°22.36'S 149°01.05'E, 26 Dec. 1997, coarse sand & rubble at 15m; QMS105389, ♀, GBR, Great Palm I., Cannon Bay, 18°40.98'S 146°35.19'E, 8 Apr. 1998, sand & gravel at 3m; QMS105390, ♀, GBR, Boulder Reef, ca. 15°24'S 145°27'E, 8 Oct. 1998, A. Thompson, coarse sand at 2m; QMS105391, ♀, GBR, No Name Reef, ca. 14°39'S 145°40'E, 9 Oct. 1998, medium coarse sand at 6m; QMS105392, ♀, Coral Sea (Queensland Plateau), Lihou Reef, ca. 17°25'S 151°04'E, 20 July 1998, D. Fenner, sand at 5m.

REMARKS. I have compared the above material from Australia with the holotype from Bora Bora (SMF) and did not find significant differences. The specimens listed above are the first records of this species from Australia. The species was previously known only from its type locality. Other species of *Lohmannella* known from Australia are *L. arenaria* Bartsch, 1993a, and *L. pinggi* Otto, 1994. All Australian *Lohmannella* species can be distinguished from each other by the number of protuberances on the palp (two in *L. arenaria*, one in *L. dictyota* and none in *L. pinggi*).

Scaptognathides Monniot, 1972

Scaptognathides Monniot, 1972: 361. Bartsch, 1977a: 85; 1983: 196; 1988: 221; 1993a: 93; 1996: 146. Bartsch & Schmidt, 1978: 18.

DIAGNOSIS. Dorsal plates AD, OC, and PD well developed. GA of female and male undivided. Rostrum slender, apically not widened. One pair of maxillary setae on rostrum, the other on gnathosomal base. Palps two-segmented; apical segment with one seta basally, and three fine setae and four spines distally. Leg I larger than succeeding legs. Telofemur I ca. twice as long as tibia I; paired claws of tarsus I with an umbrella-like arrangement of pecten. Tibia I with no more than two thickened or bipectinate setae. Tibiae II-IV and genu I without thickened or bipectinate setae.

Scaptognathides heraldensis sp. nov.

(Fig. 1)

ETYMOLOGY. Referring to the species' type locality.

MATERIAL. HOLOTYPE: QMS105393, ♀, Coral Sea (Queensland Plateau), Herald Cays, 16°57.171'S 149°12.036'E, 16 Sep. 1998, GA. Diaz-Pulido, coarse sand at 5-15m. PARATYPES: QMS105394, ♂, A55/99 (ZMH), ♀, ANIC ♂, data as for holotype.

DESCRIPTION. *Female*. Idiosoma 188-190 long (holotype 188). All dorsal setae inserted on plates, none in membranous integument (Fig. 1A). All plates ornamented with numerous minute depressions. AD with three pairs of setae as illustrated. OC ca. twice as long as wide; single gland pore in anterolateral corner. PD with two pairs of setae on anterior 1/2 of plate; two pairs of gland pores, the anterior level with posterior pair of setae, the other at posterior margin of plate and associated with cuticular projections; directly posterior to anterior pair of gland pore lateral margin of plate distinctly convex (Fig. 1A). AE finely punctate (Fig. 1B). GA much longer than

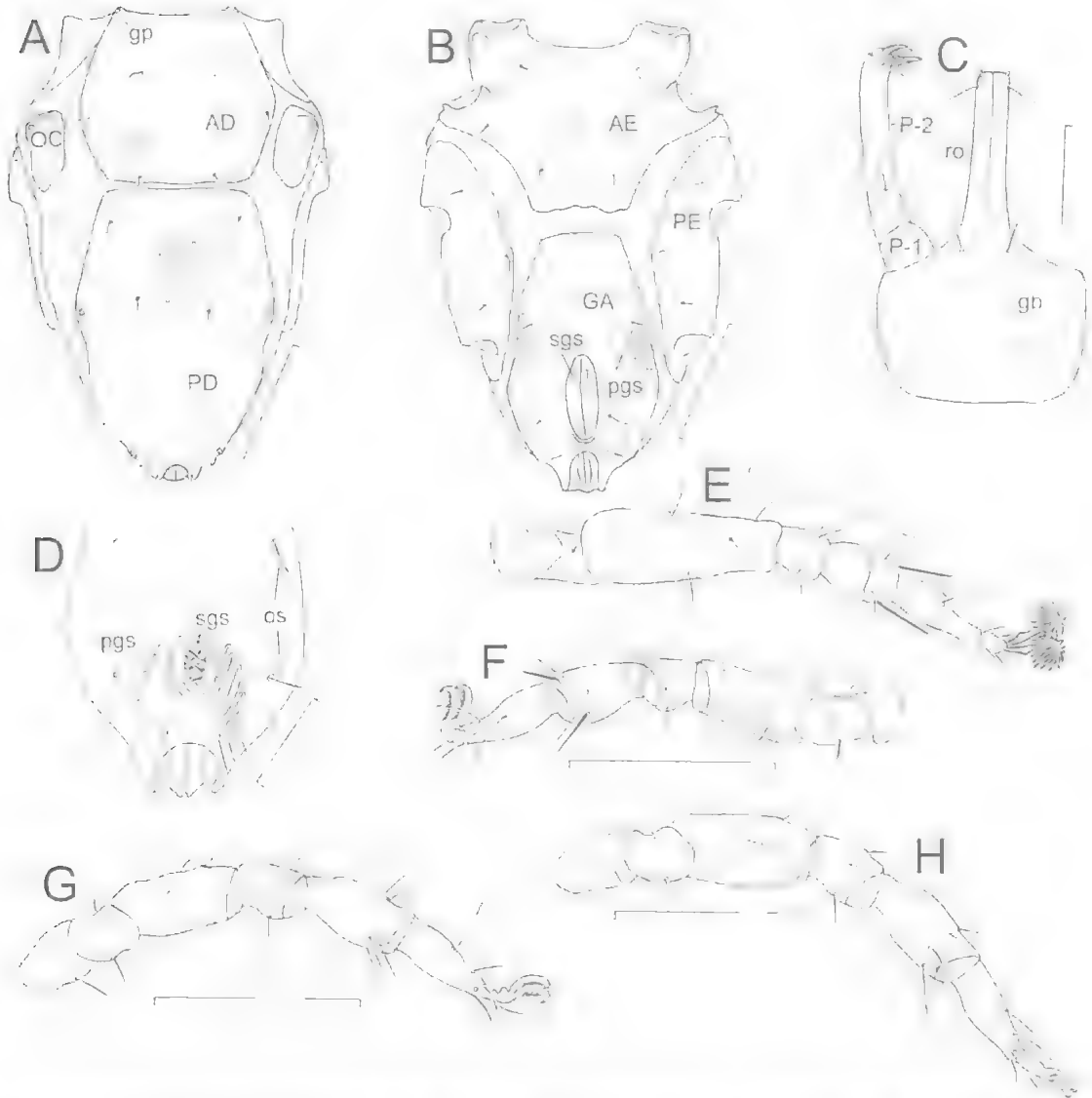


FIG. 1 *Scaptognathides heraldensis* sp. nov., adult. A, idiosoma, dorsum (AD = anterior dorsal plate; gp = gland pore; OC = ocular plate; PD = posterior dorsal plate); B, ♀ idiosoma, venter (AE = anterior epimeral plate; GA = genitoanal plate; PE = posterior epimeral plate; pgs = perigenital seta; sgs = subgenital seta); C, gnathosoma, venter (gb = gnathosomal base; P-1, P-2 = palp segments; ro = rostrum); D, genitoanal plate of ♂ (os = outlying setae); E, leg I, dorsal view; F, leg II, ventromedial view; G, leg III, ventromedial view; H, leg IV, ventromedial view. Scales: A, B, E, F, G, H = 50µm; C = 25µm.

wide; anterior margin truncate; laterally slightly papillate, remainder of plate nearly smooth, lacking punctations; two pairs of pgs as illustrated (Fig. 1B). GO with one pair of sgs.

Gnathosoma (Fig. 1C) 0.43-0.45 times the length of idiosoma.

Telosemora of legs ventrally papillate (Fig. 1F,G). Chaetotaxy (trochanter – tibia): I

1-2-4-4-5 (Fig. 1E), II 1-2-4-4-5 (Fig. 1F), III 1-2-2-3-5 (Fig. 1G), IV 1-2-2-3-5 (Fig. 1H). Tarsus III with three dorsal setae, lacking conspicuously thickened and blunt seta.

Male. Idiosoma 182-198 long. GA with ca. 17 pgs flanking GO laterally and posterolaterally (Fig. 1D); two pairs of outlying setae, one pair anteriorly, the other pair at level of GO.

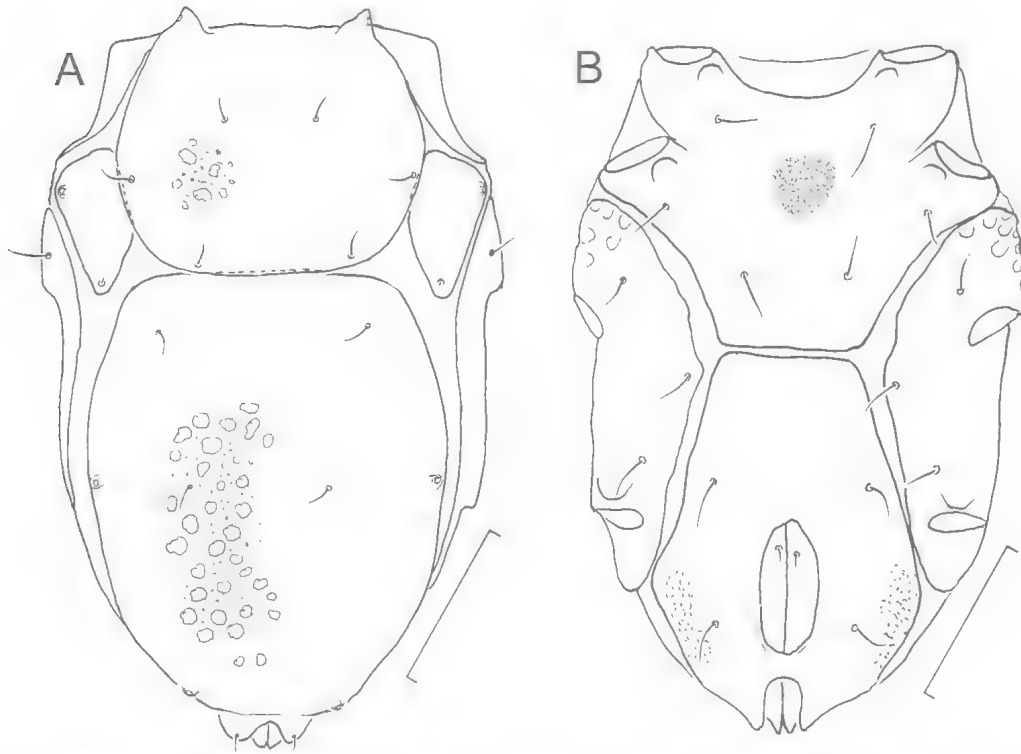


FIG. 2. *Scaptognathides tomkinsae* sp. nov., adult. A, idiosoma, dorsum; B, idiosoma of ♀, venter. Scale: A, B = 50µm.

REMARKS. The only other species of *Scaptognathides* with one gland pore on the OC are *S. hawaiiensis* Bartsch, 1988, *S. australis* Bartsch, 1993a, and *S. tomkinsae* sp. nov. All other congeners have two gland pores on the OC. *Scaptognathus heraldensis* differs from *S. australis* most markedly by the OC being about twice as long as wide instead of four times as long as wide, and from *S. hawaiiensis* by having two pairs instead of one pair of gland pores on the PD. For differences between *S. heraldensis* and *S. tomkinsae* see below.

***Scaptognathides tomkinsae* sp. nov.**
(Fig. 2)

ETYMOLOGY. For Paula Tomkins who collected the sample from which the specimens were extracted.

MATERIAL. HOLOTYPE: QMS105395, ♀, GBR, Sand Bank No. 1, 14°18'S 145°12'E, 21 Oct. 1998, P. Tomkins, coarse sand at 3-4m. **PARATYPES:** QMS105396, ♂, A56/99 (ZMH), ♀, data as for holotype.

DESCRIPTION. Female. Idiosoma 206-222 long (holotype 206). Dorsal plates foveate and finely punctate, less conspicuously on OC. All

dorsal setae inserted on plates (Fig. 2A). AD with three pairs of setae inserted as illustrated. OC ca. twice as long as wide; single gland pore in anterolateral corner; posteriorly with a minute seta. PD with two pairs of setae in anterior 1/2; two pairs of gland pores, the anterior level with posterior pair of setae, the other at posterior margin of plate; lateral margin posterior to anterior pair of gland pore almost straight, not distinctly convex. Adanal setae inserted dorsally on anal cone. AE and GA finely punctate; anterior margin of GA truncate (Fig. 2B); two pairs pgs; one pair sgs. PE anterolaterally with few foveae.

Gnathosoma 0.45 times the length of idiosoma; outline and setation as illustrated for *S. heraldensis* (Fig. 1C).

Outline of leg segments and chaetotaxy as illustrated for *S. heraldensis*. Chaetotaxy (trochanter - tibia): I 1-2-4-4-5, II 1-2-4-4-5, III 1-2-2-3-5, IV 1-2-2-3-5. Tarsus III with three dorsal setae, lacking conspicuously thickened and blunt seta. Telofemur IV without thickened seta.

Male. Idiosoma 206 long. GA with 17 pgs flanking GO laterally and posterolaterally; two pairs of outlying setae, one pair anteriorly, the other pair at level of GO (as for *S. heraldensis* in Fig. 1D).

REMARKS. Foveate dorsal plates are also known for *S. australis* Bartsch, 1993a, and *S. bicornis* Bartsch, 1977a (see Bartsch, 1996). *Scaptognathides tomkinsae* may be distinguished from *S. bicornis* by having all dorsal setae inserted on the plates instead of three pairs in the membranous cuticle, and from *S. australis* by the OC being about twice as long as wide instead of four times longer than wide.

***Scaptognathides undulatus* sp. nov.**
(Fig. 3)

ETYMOLOGY. Latin, *undulatus* = wavy; referring to the undulated ventral ridge of the telofemora.

MATERIAL. HOLOTYPE: QMS105397, ♀, Coral Sea (Queensland Plateau), Herald Cays, 16°57.171'S 149°12.036'E, 16 Sep. 1998, G.A. Diaz-Pulido, coarse sand at 5–15m.

DESCRIPTION. *Female*. Idiosoma 182 long. All dorsal setae inserted on dorsal plates, which are ornamented with shallow pits within polygons (Fig. 3A). AD with three pairs of setae as illustrated (Fig. 3A). OC ca. twice as long as wide; two gland pores, one anteriorly, the other posteriorly. PD with two pairs of setae on anterior 1/2 (only insertion sockets visible in the only available specimen, setae most likely broken off); two pairs of gland pores. AE and GA ornamented by scattered pits (Fig. 3B); two pairs of pgs and one pair sgs.

Outline and setation of gnathosoma as illustrated for *S. heraldensis*; 0.45 times the length of idiosoma.

Telofemora ventrally with undulated sharp ridge (Fig. 3C–F). Chaetotaxy (trochanter-tibia): I 1-2-4-4-5 (Fig. 3C), II 1-2-5-4-5 (Fig. 3D), III 1-2-2-3-5 (Fig. 3E), IV 1-2-2-3-5 (Fig. 3F). Telofemur I, tarsus III and telofemur IV with a thickened blunt seta. Tarsus III with four dorsal setae.

Male. Unknown.

REMARKS. Other species of *Scaptognathides* with a polygonal pattern on the dorsal plates are *S. ornatus* Bartsch, 1984, *S. planus* Monnot, 1972, and *S. reticulatus* Bartsch, 1996. *Scaptognathides undulatus* differs from them by the presence of an undulated ventral ridge on the telofemora. In addition it may be distinguished

from *S. reticulatus* by the OC being shorter than three times its width, from *S. ornatus* by having a thickened seta proximally on tarsus III and from *S. planus* by having a pair of setae inserted on the AD close to its posterior margin.

***Scaptognathus* Trouessart, 1889**

Scaptognathus Trouessart, 1889: 248; 1894: 176. Monnier 1964: 491. Newell, 1971: 35. Bartsch, 1983: 196; 1993a: 95. Abé, 1988: 47, 1990a: 349, 1990b: 251, 1991: 436. Abé and Green, 1994: 169.

TYPE SPECIES: *Scaptognathus tridens* Trouessart, 1889, by monotypy.

DIAGNOSIS. Dorsal plates AD and PD well but OC poorly developed. GA of female usually bipartite or tripartite (only in *S. monstrosus* sp. nov. undivided). All maxillary setae on rostrum, none on gnathosomal base; paired claws smooth or with a minute process, never with umbrella-like arrangement of pecten; rostrum either slender posteriorly and conspicuously broadened anteriorly or broad throughout. Palp two-segmented. Palp segment P-2 with one seta proximally, another seta 1/2 way along segment or on distal 1/2, and several slender setae plus two, rarely three (latter only in *S. monstrosus*), large claws apically. Telofemur I shorter than twice the length of tibia I. Genu I with at least one bipectinate seta, tibia I with at least three and tibiae II–IV each with at least two such setae.

***Scaptognathus exquisitus* sp. nov.**
(Fig. 4)

ETYMOLOGY. Latin, *exquisitus* = excellent, fine

MATERIAL. HOLOTYPE: QMS105402, ♀, GBR, Yonge Reef, ca. 14°36'S 145°38'E, 10 Oct. 1998, A. Thompson, fine-medium coarse sand at 5m. PARATYPES: QMS105403–105405, 3♀, 2 ANIC ♀, A57/99 (ZMH), 2♀, GBR, Yonge Reef, ca. 14°36'S 145°38'E, 20 Sep. 1998, G. Diaz-Pulido, medium coarse sand at 7m; QMS105406–105407, 2♀, GBR, Elizabeth Reef, 19°20.12'S 149°02.85'E, 24 Dec. 1997, medium coarse sand at 10m; QMS105408, ♀, GBR, Elizabeth Reef, 19°20.12'S 149°02.85'E, 25 Dec. 1997, coarse sand at 3m; QMS105409, ♀, GBR, 18°16.46'S 147°22.88'E, Myrmidon Reef, 13 Apr. 1998, coarse sand & rubble at 7m; QMS105411–105413, 3♀, GBR, Carter Reef, ca. 14°32'S 145°35'E, 11 Oct. 1998, coarse sand at 0.5m; QMS105414, ♀, GBR, Lizard I., Coconut Beach, 13 Oct. 1998, medium coarse sand at 0.5m; QMS105415, ♀, GBR, Myrmidon Reef, Back, 17°46.03'S 146°26.38'E, 6 Mar. 1998, L. Levantier, medium coarse sand at 7m; QMS105416–105417, 2♀, A57/99 (ZMH), ♀, GBR, No Name Reef, reef flat, ca. 14°39'S 145°40'E, 9 Oct. 1998, A. Thompson, coarse sand at ca. 5m; QMS105410, ♀, Coral Sea (Queensland Plateau), Diamond Islet, ca.

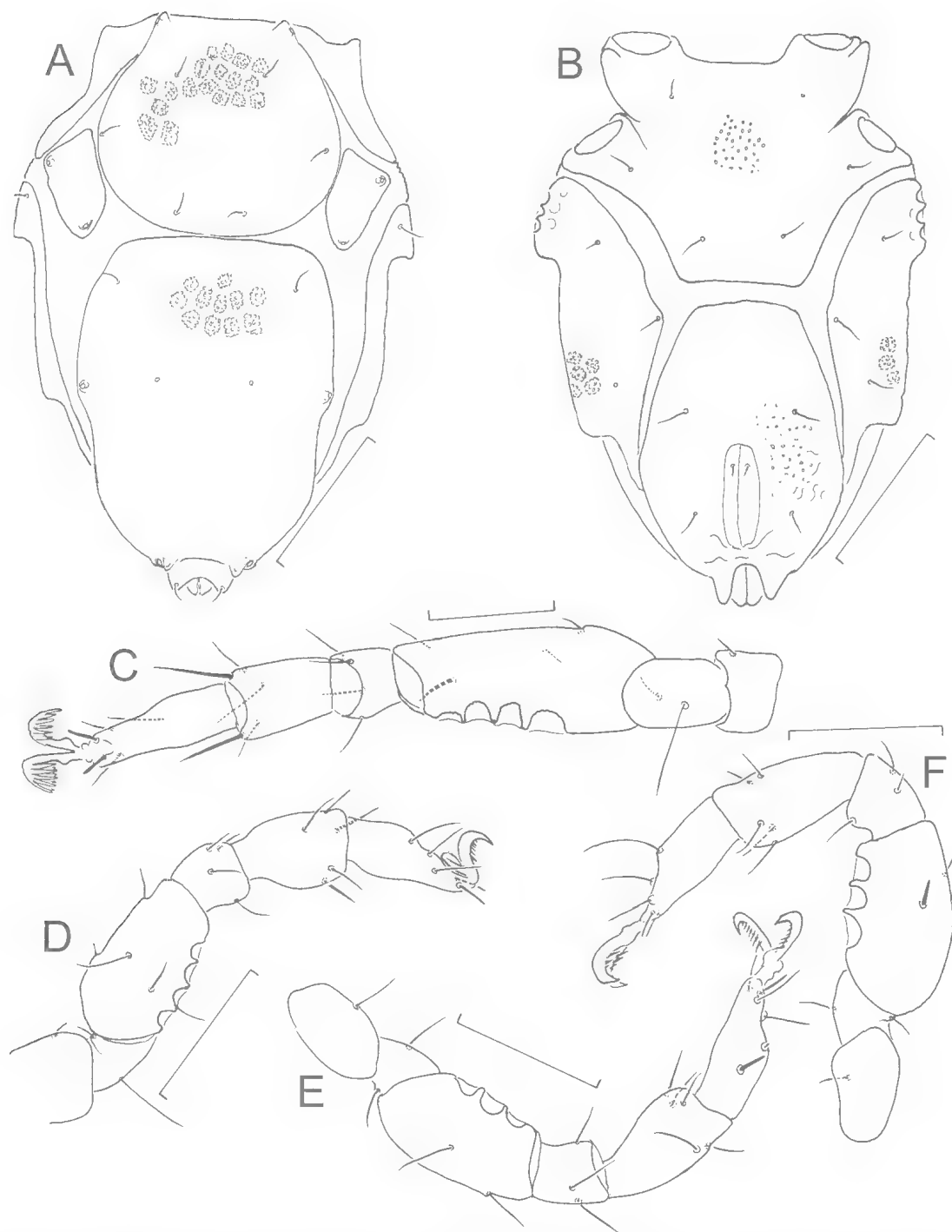


FIG. 3. *Scaptognathides undulatus* sp. nov, adult. A, idiosoma, dorsum; B, idiosoma of ♀, venter; C, leg I, ventromedial view; D, leg II, dorsolateral view; E, leg III, dorsolateral view; F, leg IV, medial view. Scales: A, B, D, E, F = 50µm; C = 25µm.

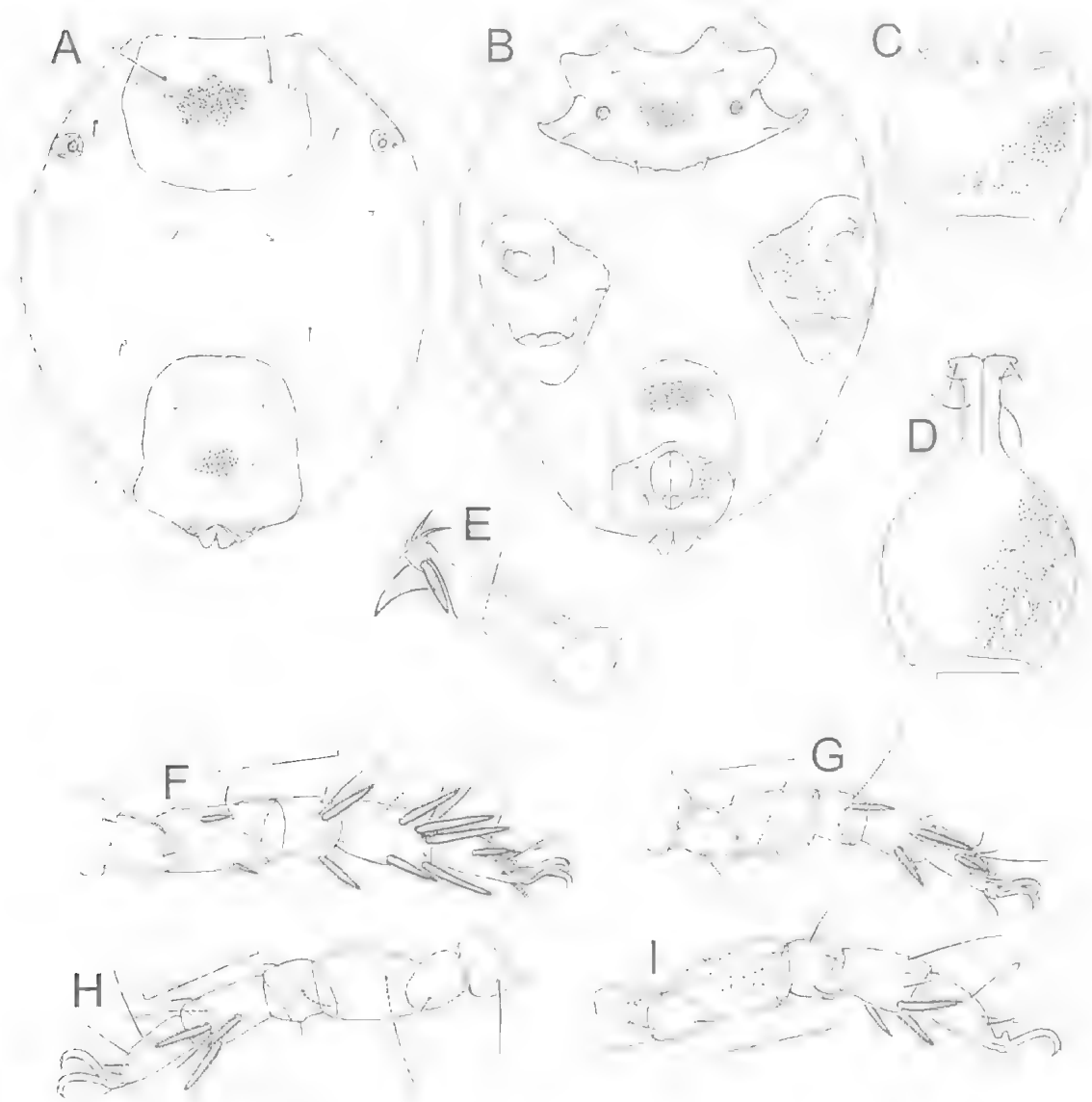


FIG. 4. *Scaptognathus exquisitus* sp. nov., adult. A, idiosoma, dorsum; B, ♀ idiosoma, venter; C, gnathosomal base, dorsal view; D, gnathosomal base and rostrum, ventral view; E, palp, ventral view; F, leg I, ventromedial view; G, leg II, ventromedial view; H, leg III, ventromedial view; I, leg IV, lateral view. Scales: A, B 100µm; C, D, F, G, H, I = 50µm; E, 25µm.

17°26'S 151°04'E, 20 July 1998, D. Fenner, subtidal sand; QMS105418-105426, 9♀, GBR, Sand Bank No.1, ca. 14°18'S 145°12'E, 21 Oct. 1998, P. Tomkins, coarse sand at 3-4m.

DESCRIPTION. *Female.* Idiosoma 232-307 long (holotype 273). Four pairs of setae in membranous cuticle (Fig. 4A). AD wider than long, with numerous shallow irregularly shaped pits arranged inconspicuously within polygons; numerous delicate canaliculi in deeper cuticular

layers; pair of setae which are much longer than other idiosomal setae inserted at level of gland pores in smooth area of plate. OC wider than long; with large central pore and few minute pits. PD furnished with numerous pits as on AD, but polygonal pattern less conspicuous than on AD or absent; two pairs of setae. AE (Fig. 4B) with ornamentation similar to that on AD; two pairs of large epimeral pores; several relatively wide but shallow panels near centre of plate and along

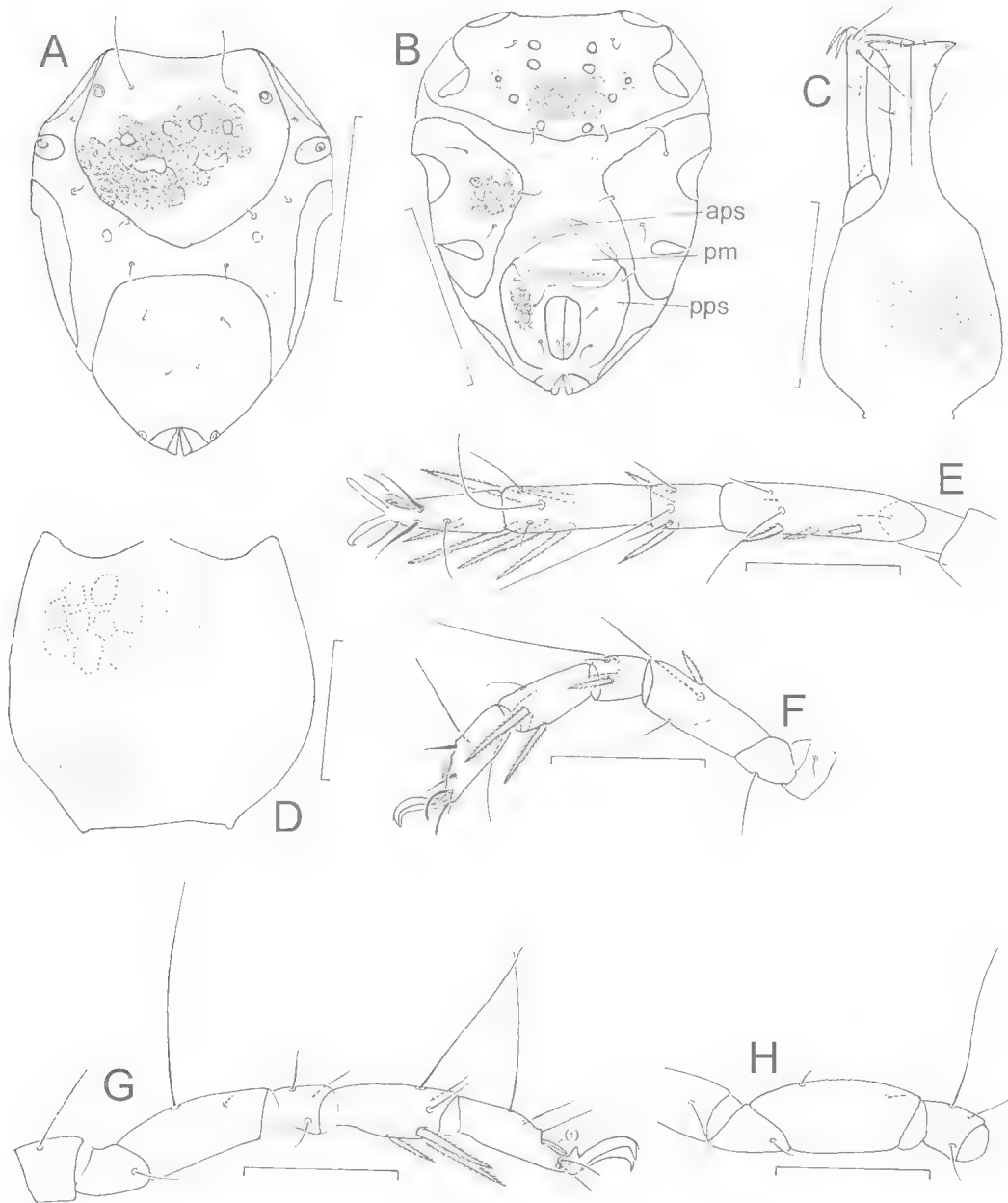


FIG. 5. *Scaptognathus gracilipalpus* sp. nov., ♀. A, idiosoma, dorsum; B, idiosoma, venter; C, gnathosoma, ventral view; D, gnathosomal base, dorsal view; E, right leg I, dorsal view; F, leg II, ventromedial view; G, leg III, ventrolateral view (ω = solenidium); H, trochanter to genu of leg IV, ventrolateral view. Scales: A, B, C = 100 μ m; D, E, F, G, H = 50 μ m.

posterior margin. GA bipartite; anterior margin of *pars sclerosum* distinctly convex; two pairs pgs; one pair sgs anteriorly.

Ventral and dorsal gnathosomal base with numerous minute pits (Fig. 4C,D), similar to those on idiosomal plates; in deeper cuticular

layers with larger scars (dotted in Fig. 4C,D), those in posterior 1/2 of ventral gnathosomal base surrounded by series of smaller surface pits (Fig. 4D). Rostrum with setae arranged as in Fig. 4D. Palp as in Fig. 4E.

Trochanters and telofemora of all legs with numerous pits laterally (illustrated for leg IV in Fig. 4I). Chaetotaxy (trochanter - tibia): I 1-1-6-5-9 (Fig. 4F), II 1-1-5-4-5 (Fig. 4G) (1-1-5-5-5 in single specimen), III 1-1-2-3-6 (Fig. 4H), IV 1-1-2-3-6 (Fig. 4I). Bipectinate setae (I-II-III-IV): telofemur 2-0-0-0; genu 2-1-0-0 (2-2-0-0 in single specimen), tibia 5-2-3-3, tarsus 1-1-0-0. Tarsus I with two ventral setae and pair of doubled pas, ventral member of medial doubled pas barely visible. Tarsus II with pair of doubled pas, one member in each duplet minute. Tarsi III and IV with pair of pas singlets.

Male. Unknown.

REMARKS. The only other species of *Scaptognathus* with 5-2-3-3 bipectinate setae on the tibiae (I-II-III-IV respectively) are *S. punctatus* Bartsch, 1981, *S. ornatus* Bartsch, 1984, and *S. gracilipalpus* sp. nov. *Scaptognathus exquisitus* differs from them by lacking bipectinate setae on telofemur II.

***Scaptognathus gracilipalpus* sp. nov.**
(Fig. 5)

ETYMOLOGY. Latin, *gracilis* = slender; referring to the species' slender palps.

MATERIAL. HOLOTYPE, QMS105436, ♀, GBR, Bylund Cay, ca. 21°47'S 152°24'E, 17 Apr. 1999, coarse sand just above low tide mark, sediment depth 10-20cm. PARATYPES: QMS105437, ♀, A58/99 (ZMH), 2♀, ANIC ♀, data as for holotype.

DESCRIPTION. *Female.* Idiosoma 212-220 long. Four pairs of setae in membranous cuticle (Fig. 5A); Dorsal and ventral plates ornamented with pitted polygons, best developed on AD, PD and AE, less conspicuous on PE and GA; reticulation disappearing towards anterior margin of AD. AD in addition with few smooth panels; along anterior margin polygonal pattern replaced by roughened cuticle; posterior margin convex. OC wider than long, with few pits and large central pore. Membranous cuticle posterior to AD with pair of small platelets. PD with two pairs of setae. AE among pitted polygons with four pairs of round to ovoid smooth panels; epimeral pores conspicuous; two pairs of setae. PE with three pairs of ventral setae but no dorsal seta seen. GA tripartite; anterior *pars sclerosum* poorly developed; anterior margin of posterior *pars sclerosum* distinctly concave; three pairs of pgs, the two anterior pairs not closely associated; one pair sgs seen.

Gnathosoma 0.92-0.94 times the length of idiosoma. Surface of ventral gnathosomal base almost smooth, only few scattered pits overlying ovoid scars (Fig. 5C). Dorsal gnathosomal base on anterior 1/2 with small pits arranged in a polygonal pattern; series of scars in deeper cuticular layers (Fig. 5D). Palps conspicuously slender.

Cuticle of all leg segments slightly roughened but without pits. Chaetotaxy (trochanter - tibia): I 1-1-6-5-8 (Fig. 5E), II, 1-1-4-4-5 (Fig. 5F), III 1-1-2-3-6 (Fig. 5G), IV 1-1-2-3-6 (Fig. 5H). Bipectinate setae (I-II-III-IV): telofemur 3-1-0-0, genu 2-1-0-0, tibia 5-2-3-3, tarsus 1-0-0-0. Tarsi I and II with pair of doubled pas, one seta of each duplet much smaller than the other; tarsus III medially with doubled pas (one seta of each duplet much smaller than the other), laterally with pas singlet; all tarsi with solenidion. Leg IV similar to leg III except for both setae on telofemur of subequal length, one seta on genu longer than the other, and the tarsus possessing a pair of pas singlets.

Male. Unknown.

REMARKS. The only other *Scaptognathus* species with the combination of five and two bipectinate setae on tibiae I and II respectively, and three bipectinate setae on telofemur I, are *S. ornatus* Bartsch, 1984 (see below), *S. punctatus* Bartsch, 1981, and *S. insularis* sp. nov. *S. gracilipalpus* differs from them by having two instead of three pairs of setae on the AE, three instead of four setae on the PE, much more slender palps, and the anterior margin of the posterior *pars sclerosum* in the female distinctly concave. A further peculiarity by which *S. gracilipalpus* may also differ from all other congeners is in the presence of solenidia on tarsi III and IV. These have not been reported for any other species of *Scaptognathus* but due to their small size could have been overlooked.

***Scaptognathus insularis* sp. nov.**
(Fig. 6)

ETYMOLOGY. Latin, *insularis* = of islands, referring to the species having been collected on a coral cay.

MATERIAL. HOLOTYPE: QMS105438, ♀, GBR, Bylund Cay, ca. 21°47'S 152°24'E, 17 Apr. 1998, coarse sand just above low tide mark, sediment depth 10-20cm. PARATYPES: QMS105439, ♀, A59/99 (ZMH), ♀, ANIC ♀, data as for holotype.

DESCRIPTION. *Female.* Idiosoma 375-415 long (holotype 415). Four pairs of setae in membranous cuticle (Fig. 6A). AD wider than long,

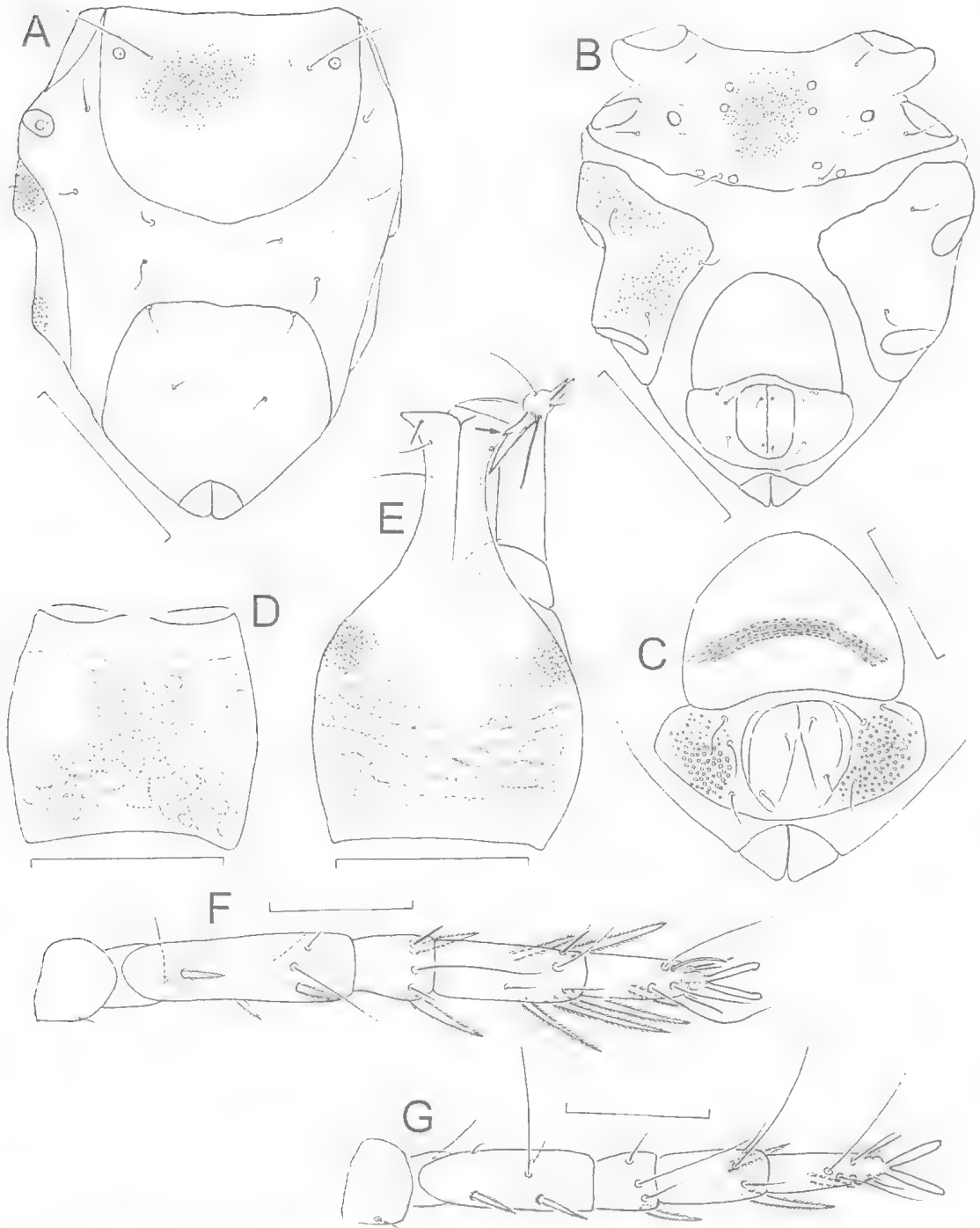


FIG. 6. *Scaptognathus insularis* sp. nov., ♂. A, idiosoma, dorsum; B, idiosoma, venter; C, genitoanal plate; D, gnathosomal base, dorsum; E, gnathosoma, venter; F, left leg I, dorsal view; G, left leg II, dorsal view. Scale: A, B, D, E = 100µm; C, F, G = 50µm.

posterior margin distinctly convex; numerous irregularly shaped pits within polygons; no canaliculi in deeper cuticular layers; pair of setae much longer than other idiosomal setae and inserted at level of gland pores in smooth area of plate. OC wider than long; with large central pore. PD furnished with numerous pits as on AD; usually two pairs of setae on PD, of which the anterior pair is situated at the extreme anterior margin of plate; in two specimens one seta of the anterior pair inserts in membranous cuticle anterior to plate. AE with ornamentation similar to that on AD; two pairs of large epimeral pores; several relatively wide but shallow panels near centre of plate and along posterior margin (Fig. 6B). GA bipartite, anterior margin of *pars membranosum* and *pars sclerosum* (Fig. 6C) convex; three pairs of pgs of which the two anterior pairs are closely associated; two pairs of sgs.

Dorsal gnathosomal base evenly pitted throughout anterior 2/3 (Fig. 6D). Ventral gnathosomal base with fewer pits, these forming transverse bands; anterolaterally with an areola consisting of relatively deep pits. Dorsal and ventral gnathosomal base in deeper layers with rounded scars (dotted in Fig. 6D,E). The smaller of the two palp claws with protuberance (Fig. 6E, arrowed).

Trochanters and telofemora of all legs with numerous pits laterally. Chaetotaxy (trochanter-tibia): I 1-1-6-5-9 (Fig. 6F), II 1-1-5-4-5 (Fig. 6G), III 1-1-2-3-5/6, IV 1-1-2-3-5/6. Bipectinate setae (I-II-III-IV): telofemur 3-2-0-0; genu 2-1-0-0, tibia 5-2-2/3-2/3, tarsus 1-1-0-0. Tarsus I with two ventral setae and pair of doubled pas. Tarsus II with pair of doubled pas, one seta in each duplet minute. Tarsi III and IV with pair of pas singlets.

REMARKS. The only other species of *Scaptognathus* with 3-2-0-0 bipectinate setae on the telofemora (I-IV respectively) are *S. punctatus* Bartsch, 1981, and *S. ornatus* Bartsch, 1984. *S. insularis* can be distinguished from *S. ornatus* by lacking ornamentation on the palps and lacking well defined areolae on the legs, and from *S. punctatus* by the female idiosoma being 375-415 µm instead of 229-257 µm long. A further difference between both species is in the number of pgs in the female, *S. insularis* possesses three pairs, while *S. punctatus* has two pairs (Bartsch, 1982).

***Scaptognathus kolymbus* sp. nov.**
(Fig. 7)

ETYMOLOGY. Greek, *kolymbos* - diver, swimmer

MATERIAL. HOLOTYPE: QMS105427, ♀, Coral Sea (Queensland Plateau), Lihou Reef, ca. 17°25'S 151°40'E, 20 July 1998, D. Fenner, sand at 5m. PARATYPES: QMS105428, ♀, GBR, Boulder Reef, 8 Oct. 1998, A. Thompson, coarse sand at 2m; ♀, A60/99 (ZMH), GBR, Yonge Reef, ca. 14°36'S 145°38'E, 20 Sep. 1998, medium coarse sand at 7m

DESCRIPTION. *Female.* Idiosoma 248-277 long (holotype 248). Four pairs of setae inserted in membranous cuticle (Fig. 7A). AD of subequal length and width; pair of setae longer than other dorsal setae; covered with numerous minute pits, except for a small area surrounding each seta; numerous canaliculi and faint reticulation pattern visible when focusing deeper. OC of subequal length and width; with large central pore. PD almost rectangular; ornamentation similar to that of AD; two pairs of setae as illustrated (Fig. 7A). AE posteriorly drawn out into a broad nose; pitted except for anterior parts of epimeral fields I and II (Fig. 7B); GA bipartite; pitted *pars sclerosum* with three pairs of pgs, the two anterior ones closely associated; two pairs sgs.

Gnathosomal base dorsally with small pits over the entire anterior 2/3 (Fig. 7C); ventrally with pits only laterally (Fig. 7D); in deeper cuticular layers dorsally as well as ventrally with larger scars (dotted in Fig. 7C,D). Widened anterior part of rostrum with three pairs of setae, narrow posterior part with one pair.

Cuticle of all leg segments relatively smooth, not covered by pits as deep as those on dorsal plates. Chaetotaxy (trochanter - tibia): I 1-2-5-4-9 (Fig. 7E), II 1-2-4-5-6 (Fig. 7F), III 1-1-2-3-7 (Fig. 7G), IV 1-1-2-3-7 (Fig. 7H). Bipectinate setae (I-II-III-IV): telofemur 2-0-0-0, genu 2-1-0-0, tibia 6-3-4-4, tarsus 1-1-0-0.

Male. Unknown.

REMARKS. *S. kolymbus* is most similar to *S. pauciporus* Bartsch, 1977a, from the Galapagos, but can be distinguished from it by the posterior margin of the AE being strongly convex and medially drawn out into a broad nose. A second distinguishing character is the number of setae on telofemur II, three in *S. pauciporus* and four in *S. kolymbus*. The number of setae on telofemur I (four illustrated for *S. pauciporus*, five in *S. kolymbus*) does not reliably distinguish between both species, as some specimens of *S. pauciporus*

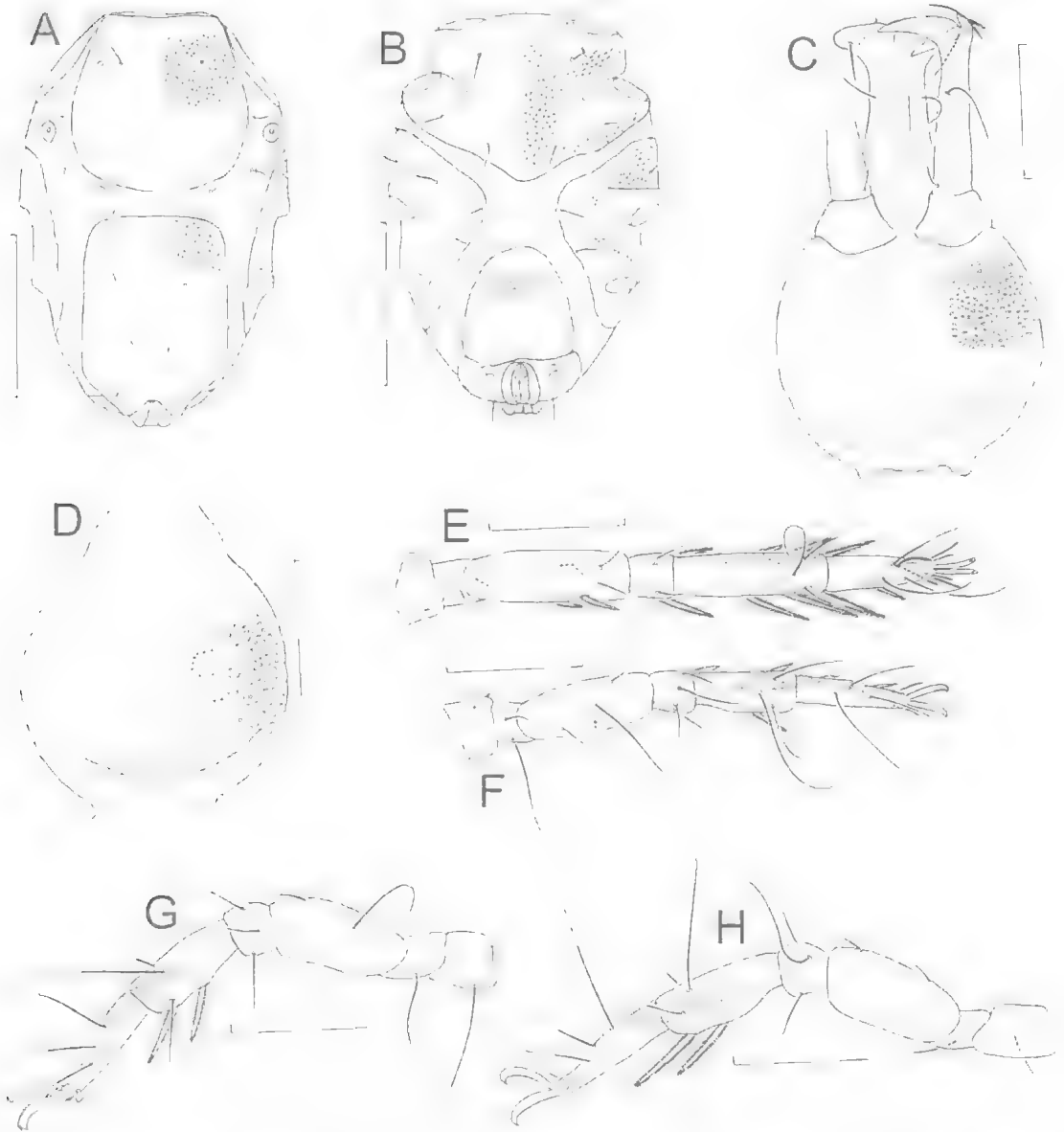


FIG. 7. *Scaptognathus kolymbus* sp. nov., adult. A, idiosoma, dorsum; B, idiosoma of ♀, ventral view; C, gnathosoma, dorsal view; D, gnathosomal base, ventral view; E, leg I, dorsal view; F, leg II, dorsal view; G, leg III, dorsolateral view; H, leg IV, dorsolateral view. Scales: A, B = 100µm; C, D, E, F, G, H = 50µm.

have also five setae on that segment (Bartsch, pers. comm.).

***Scaptognathus kunzi* Bartsch, 1988**
(Fig. 8A-C, E-K)

Scaptognathus kunzi Bartsch, 1988: 219. Abé, 1990a: 361.

MATERIAL. QMS105430, ♀, GBR, Elizabeth Reef, 19°20.12'S 149°02.85'E, 25 Dec. 1997, coral rubble at 10m; QMS105431, ♀, GBR, Pandora Reef, 18°48.84'S

146°26.16'E, 22 Jan. 1998, sand & rubble at 0.2 m; ANIC ♀, GBR, Great Palm I., channel, 18°40.60'S 146°34.29'E, 8 Apr. 1998, sand & rubble at 6m; A61/99 (ZMH), ♀, GBR, Great Palm I., Cannon Bay, 18°40.98'S 146°35.19'E, 8 Apr. 1998, sand - gravel at 3m; QMS105432, ♀, GBR, Yonge Reef, ca. 14°36'S 145°38'E, 10 Oct. 1998, coarse sand & rubble at 9m.

DESCRIPTION. *Female*. Idiosoma in uncompressed specimen 202 long, in compressed

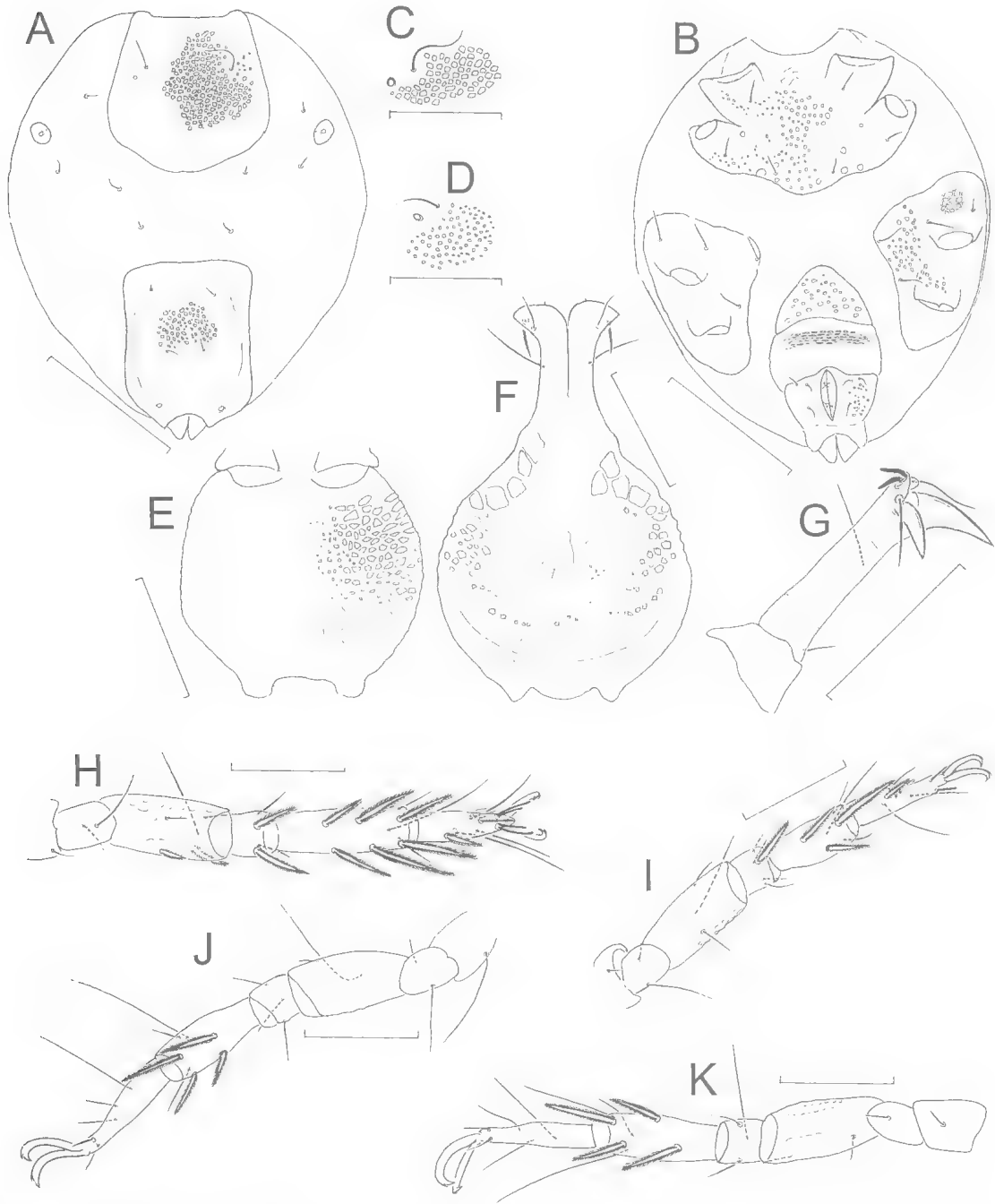


FIG. 8. A-C, E-K, *Scaptognathus kunzi* Bartsch, adult; A, idiosoma, dorsum; B, idiosoma of ♀, venter; C, detail of ornamentation of anterior dorsal shield (AD) near left seta and pore; E, gnathosomal base, dorsal view; F, gnathosomal base and rostrum, ventral view; G, palp, dorsal view; H, leg I, ventral view; I, leg II, ventromedial view; J, leg III, ventromedial view; K, leg IV, ventral view. D, *Scaptognathus oceanus* sp. nov., ♀; detail of ornamentation of anterior dorsal shield (AD) near left seta and pore. Scales: A, B = 100µm; C, D = 50µm; H-K = 50µm; E, F, G = 50µm.

specimens 252-275 long; four pairs of setae in membranous cuticle (Fig. 8A) on minute subcuticular platelets. AD rounded posteriorly; ornamented with pits, which on average are wider than the cuticular bars between them (Fig. 8C); delicate canaliculi in deeper cuticular layers; pair of setae inserted anteromedial to pair of pores. OC with large central pore. PD almost rectangular; ornamentation similar to that of AD; posteriorly with pair of gland pores; two pairs of setae as illustrated (Fig. 8A). AE ornamented with shallow pits (Fig. 8B) which are spaced further apart and are more rounded than those on AD and PD; posteriorly with few wider pits. PE anterior to insertions of leg III ornamented as on AD, on remainder of plate as on AE. GA tripartite; anterior *pars sclerosum* with shallow pits, posterior *pars sclerosum* with slightly deeper pits, three pairs of pgs and two pairs sgs.

Gnathosomal base dorsally in anterior 2/3 with irregularly shaped angular panels (Fig. 8E) and in posterior 1/3 with larger but less conspicuous panels; ventrally with several small panels and few larger panels along anterolateral margin; in deeper cuticular layers with several large round or oval scars (dotted in Fig. 8F). Rostrum apically widened, with one of the dorsal setae distinctly heavier than the other. Palp as in Fig. 8G.

Chaetotaxy (trochanter – tibia): I 1-2-5-4-9 (Fig. 8H), II 1-2-4-5-6 (Fig. 8I), III 1-2-2-3-7 (Fig. 8J), IV 1-1-2-3-7 (Fig. 8K). Bipectinate setae (I-II-III-IV): telofemur 2-0-0-0, genu 2-1-0-0, tibia 6-3-4-4, tarsus 1-1-0-0. Tarsus I with pair of doubled pas. Tarsi II-IV with pair of pas singlets.

Male. Unknown.

REMARKS. *Scaptognathus kunzi* was previously only known from the Hawaiian holotype. Comparison between it and the Australian material revealed slight differences in the position of the setae on the PD. In the Australian material the distance between the setae of the anterior pair is 1.33 – 1.92 times greater than that between the setae of the posterior pair in contrast to 1.1 times in the holotype. Further, in most Australian specimens the anterior pair of setae on the PD is inserted somewhat closer to the anterior margin of the plate and the pore on the AD is positioned slightly more posterior in relation to the seta on the AD. It may be that these differences indicate a separation between the Hawaiian and Australian populations. However, this remains uncertain until the variability of these characters in Hawaii can be assessed.

Meanwhile Australian and Hawaiian specimens are regarded as conspecific.

***Scaptognathus monstrosus* sp. nov.**
(Fig. 9)

ETYMOLOGY. Latin, *monstrum* = an abnormal wonder.

MATERIAL. HOLOTYPE: QMS105429, ♀, GBR, Elizabeth Reef, 19°20.12'S 149°02.85'E, 25 Dec. 1997, coarse sand & rubble at 3m. PARATYPE: QMS 105440, ♀, GBR, Reef 21-149, 21°06'S 151°43'E, reef flat, 22 Apr. 1999, coarse sand at 0.5m.

DESCRIPTION. *Female.* Idiosoma 394-396 (396 in holotype) long. Four pairs of setae in membranous cuticle (Fig. 9A). AD and PD with conspicuous reticulation formed by densely packed rows of papillae; floor of each polygon with numerous scattered papillae and in deeper cuticular layers delicate canaliculi. PD reticulated only on anterior 1/2; posterior 1/2 papillate. Anterior margin of AD with protruding edges of gnatho-idiosomal articulation and slightly posterior a pair of pore-like marks; pair of setae inserted distinctly posterior to pair of gland pores. OC wider than long (Fig. 9B); large pore near inner margin. PD with two pairs of setae, gland pores not seen. AE with a deeply excavated anterior part which is distinctly reticulated throughout but lacks the minute papillae and delicate canaliculi present on remainder of plate (Fig. 9B); epimeral processes large and pair of epimeral pores conspicuous; posterior margin of plate convex. PE with ornamentation similar to that of AE. GA undivided, with ornamentation similar to that of AE but reticulation less developed and posteriorly breaking up into isolated cuticular papillae; three pairs of pgs and three pairs of sgs.

Gnathosomal base joined to idiosoma by a sclerite which attaches on the dorsal flank of the gnathosomal base (Fig. 9C, arrowed). Rostrum broad throughout (Fig. 9D). Ventral gnathosomal base with reticulate ornamentation, in deeper integumental layers with rounded scars (dotted in Fig. 9D), anteriorly finely punctate. Dorsal gnathosomal base with scale-like pattern posterolaterally (Fig. 9C), in deeper integumental layers with row of 5-6 scars on either side. Palps obscured by broad rostrum (Fig. 9D); three large claws apically.

Tibia of leg I slender, almost twice as long as tarsus (excluding claws) (Fig. 9E). Chaetotaxy (trochanter – tibia): I 1-1-4-4-9 (Fig. 9E), II 1-1-4-4-5 (Fig. 9F), III 1-1-3-3-5 (Fig. 9G), IV 1-1-3-3-5 (Fig. 9H). Bipectinate setae (I-II-III-IV):

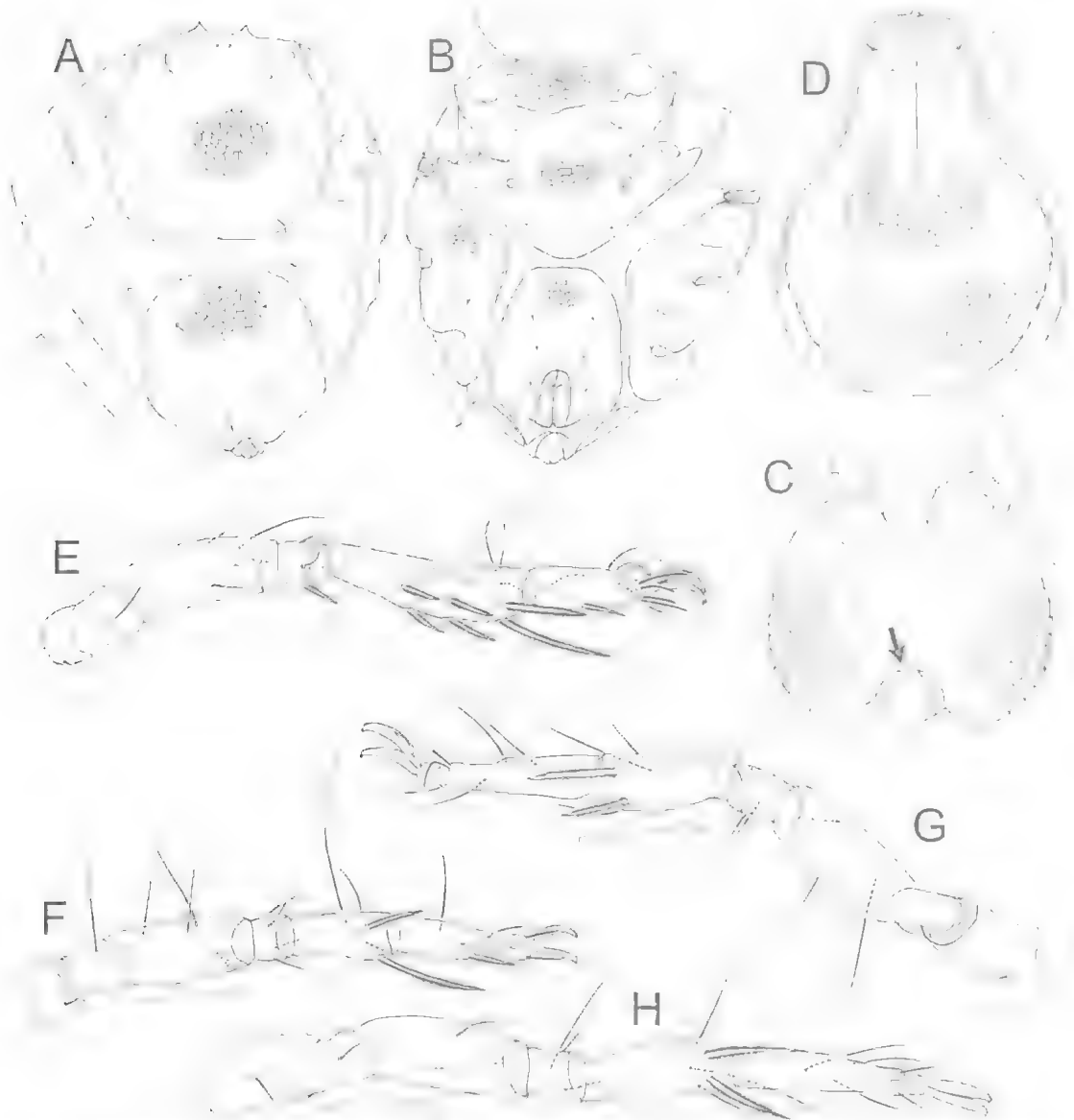


FIG. 9. *Scaptognathus monstrosus* sp. nov.: A, idiosoma, dorsum; B, idiosoma, venter; C, gnathosomal base, dorsal view; D, gnathosoma, ventral view; E, leg I, ventromedial view; F, leg II, ventral view; G, leg III, ventromedial view; H, leg IV, ventral view. Scales: A, B, C, D = 100 μ m; E, F, G, H = 50 μ m.

telofemur 1-1-0-0, genu 1-0-0-0, tibia 6-2-2-2, tarsus 1-1-0-0. Tarsus I with pair of doubled pas. Tarsus II with pair of pas singlets. Tarsus III with pas singlet and doubled pas. Tarsus IV with pair of ventral pas singlets. Claws of tarsi I and II more delicate than those of III and IV. Tibiae and telofemora I and II posteriorly with a very wide mesh of delicate cuticular bars (as shown for tibia I in Fig. 9E).

REMARKS. *Scaptognathus monstrosus* is most similar to *S. peregrinus* Bartsch, 1993a, from Rottneest Island. Both species share the wide rostrum and the peculiar sclerite which connects gnathosoma and idiosoma, both of which are unknown for other species of *Scaptognathus*. However, *S. monstrosus* is significantly larger than *S. peregrinus* (idiosoma length of *S. peregrinus* 297 μ m) and possesses a bipectinate seta

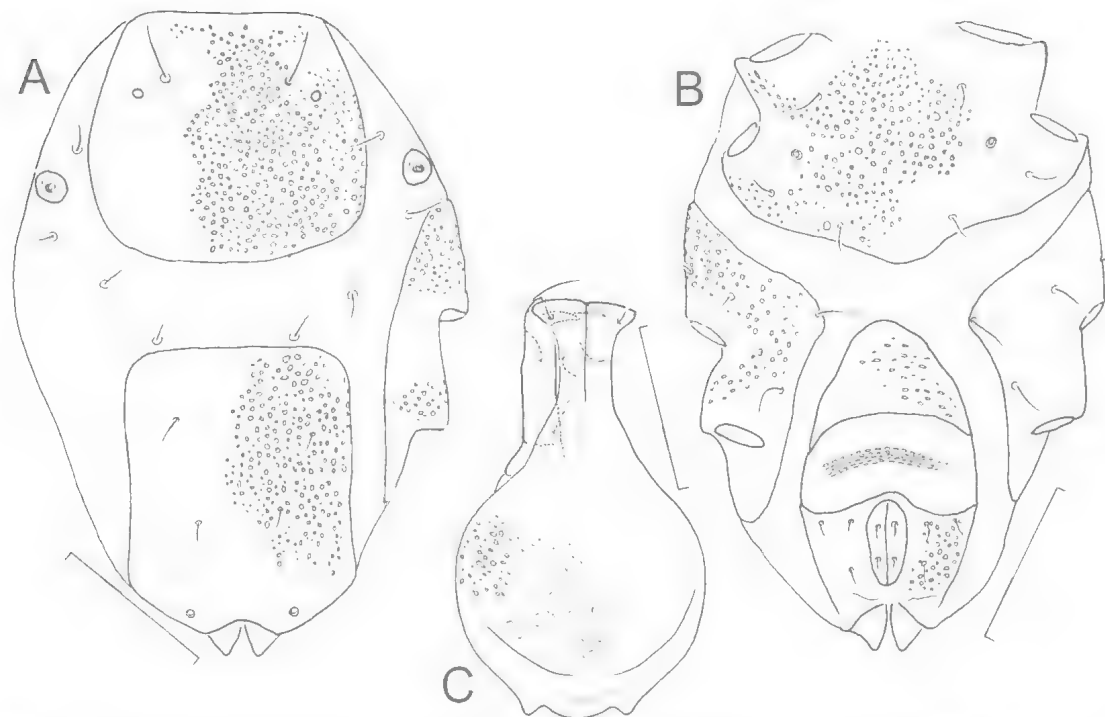


FIG. 10. *Scaptognathus oceanus* sp. nov., ♀. A, idiosoma, dorsum; B, idiosoma, venter; C, gnathosoma, venter. Scales: A, B, C = 50µm.

on genu I, which is absent in *S. peregrinus*. *S. monstrosus* also differs from *S. peregrinus* by having two instead of one bipectinate setae on tibia II, five instead of six setae on tibia III and three instead of two claws on the apical palp segment. Based on the similarities between both species it may be argued that *S. monstrosus* is simply the undescribed female of *S. peregrinus*. However, this is unlikely as the number of palp claws and the number of leg setae are unknown to differ between sexes in *Scaptognathus*.

S. monstrosus is the only species of *Scaptognathus* for which the female is known to have an undivided GA. However, the female of *S. peregrinus* is unknown as yet and may share this character with *S. monstrosus*.

***Scaptognathus oceanus* sp. nov.**
(Figs 8D, 10)

ETYMOLOGY. Latin, *oceanus* = the sea.

MATERIAL. HOLOTYPE: QMS105433, ♀, Coral Sea (Queensland Plateau), Herald Cays, 16°57.171'S 149°12.036'E, 16 Sep. 1998, G.A. Diaz-Pulido, coarse sand at 5-15m. PARATYPES: QMS105434, ♀, A62/99 (ZMH), ♀, ANIC ♀, data as for holotype.

DESCRIPTION. *Female*. Idiosoma 190-202 long (holotype 202). AD slightly widened in posterior 1/2; ornamented with pits, which on average are not wider than the space between them (Figs 8D, 10A); pair of setae inserted anteromedial to pair of pores. OC with large central pore. PD almost rectangular; ornamentation similar to that of AD; posteriorly with pair of gland pores; two pairs of setae as illustrated (Fig. 10A). AE ornamented with shallow pits which are spaced further apart than those on AD and PD (Fig. 10B). Dorsal part of PE anteriorly and posteriorly pitted, remainder of dorsal PE smooth. GA tripartite; anterior *pars sclerosum* with shallower pits than posterior *pars sclerosum*; three pairs of pgs, the two anterior pairs at same level; two pairs sgs.

Gnathosoma (Fig. 10C) distinctly shorter than idiosoma. Dorsal gnathosomal base with irregularly shaped pits throughout anterior 2/3 (as for *S. kunzi*, Fig. 8E); ventral gnathosomal base with pits laterally; in deeper cuticular layers with several large round or oval scars (dotted in Fig. 10C). Rostrum apically widened.

Morphology and setation of legs as illustrated for *S. kunzi*. Chaetotaxy (trochanter - tibia): I 1-2-5-4-9, II 1-2-4-5-6, III 1-2-2-3-7, IV

1-1-2-3-7. Bipectinate setae (I-II-III-IV): telofemur 2-0-0, genu 2-1-0-0, tibia 6-3-4-4, tarsus 1-1-0-0. Tarsus I with pair of doubled pas. Tarsi II-IV with pas singlets.

Male. Unknown.

REMARKS. *Scaptognathus oceanus* closely resembles *S. kunzi* Bartsch, 1988, *S. sabularius* André, 1961, and *S. tereninus* Bartsch, 1986, in the number of bipectinate setae of the legs and the tripartite GA. It differs from *S. kunzi* in the pits on AD and PD being on average not wider than the spaces between them and from *S. sabularius* and *S. tereninus* by having only one pair of setae inserted on the AD instead of two pairs.

Among the material I examined from the type locality is a female (QMS105435) whose GA is bipartite but agrees with the above description. It is unknown whether this specimen represents an unusual specimen of *S. oceanus* or belongs to a different species. If it belongs to *S. oceanus* then the partition of the GA may not always be a reliable character to separate between species.

Scaptognathus ornatus Bartsch, 1984
(Fig. 11)

Scaptognathus ornatus Bartsch, 1984: 192. Abé, 1990a: 361.

MATERIAL. QMS105398/105399, 2♀, A63/99 (ZMH). ♀, ANIC ♀, Coral Sea (Queensland Plateau), Herald Cays, 16°57.171'S 149°12.036'E, 16 Sep. 1998, G.A. Diaz-Pulido, coarse sand at 5-15m; QMS105400-105401, 2♀, GBR, Carter Reef, ca. 14°32'S 145°35'E, 11 Nov. 1998, coarse sand at 0.5m.

DESCRIPTION. *Female.* Idiosoma in Australian specimens 291-343 long. Four pairs of setae in membranous cuticle (Fig. 11A). AD wider than long; ornamented with a network of pitted polygons; area just posterior to level of setae with pits shallower and less densely packed than on remainder; area surrounding pair of pores and pair of setae smooth; setae much longer than setae in membranous cuticle. OC slightly wider than long, with several small pits and a large central pore. Membranous cuticle posterior to AD with three pairs of small platelets. Dorsal part of PE pitted anteriorly and posteriorly, ventral part over most of its surface. PD with ornamentation similar to that of AD, but reticulation less conspicuous or absent on median part of plate; two pairs of setae as illustrated (Fig. 11A). AE much shorter than wide; pitted and with reticulate ornamentation similar to dorsum, but pits shallower. GA bipartite (Fig. 11B), *pars sclerosum* with three pairs of pgs of which the two anterior

pairs are closely associated. GO with two pairs sgs.

Dorsal gnathosomal base with polygonal pattern over most of its surface (Fig. 11C), most polygons with numerous minute pits, but those closer to posterior margin with pits only along the inside of each polygon. Ventral gnathosomal base with deeply pitted polygons anterolaterally (Fig. 11D), remainder furnished with pits forming a loose network under which in deeper cuticular layers lay larger ovoid scars (Fig. 11D). Proximal 1/2 of P-2 with dorsal ornamentation as illustrated (Fig. 11C).

All leg segments except genu I with pitted areolae (Fig. 11E-H). Chaetotaxy (trochanter - tibia): I 1-1-6-5-9 (Fig. 11E), II, 1-1-5-4-5 (Fig. 11F), III 1-1-2-3-6 (Fig. 11G), IV 1-1-2-3-6 (Fig. 11H). Bipectinate setae (I-II-III-IV): telofemur 3-1-0-0, genu 2-1-0-0, tibia 5-2-3-3, tarsus 1-1-0-0. Tarsi I and II with pair of doubled pas; tarsus III medially with doubled pas, laterally with pas singlet; tarsus IV with pair of pas singlets. Paired claws of all legs with minute accessory process but no pecten.

Male. Unknown.

REMARKS. The above material constitutes the first specimens of this species recorded from Australia. Other records are from Venezuela and Puerto Rico (Bartsch, 1984).

The posteriormost seta on telofemur II in the Australian specimens appears to be slightly more delicate than in the type material, and the bipectination of this seta, described by Bartsch (1984), could not be seen under oil immersion. However these differences are not regarded here as sufficient to separate Australian and South American/Puerto Rican specimens.

S. ornatus is most similar to *S. punctatus* Bartsch, 1981 (see also Bartsch, 1982), from the Moçambique channel. Both species can be distinguished by the extent of the pitted areolae on the legs. In *S. ornatus* such areolae are present on almost all leg segments, while in *S. punctatus* only the telofemora possess them (Bartsch, 1984).

KEYS TO DESCRIBED AUSTRALIAN
LOHMANNELLINAE

LOHMANNELLA

- Second most proximal palp segment (P-2) with two cuticular protuberances *L. arenaria* (see Bartsch, 1993a)
- P-2 with one cuticular protuberance *L. dictyota* (see Bartsch, 1992; present paper)
- P-2 without a protuberance *L. pinggi* (see Otto, 1994)

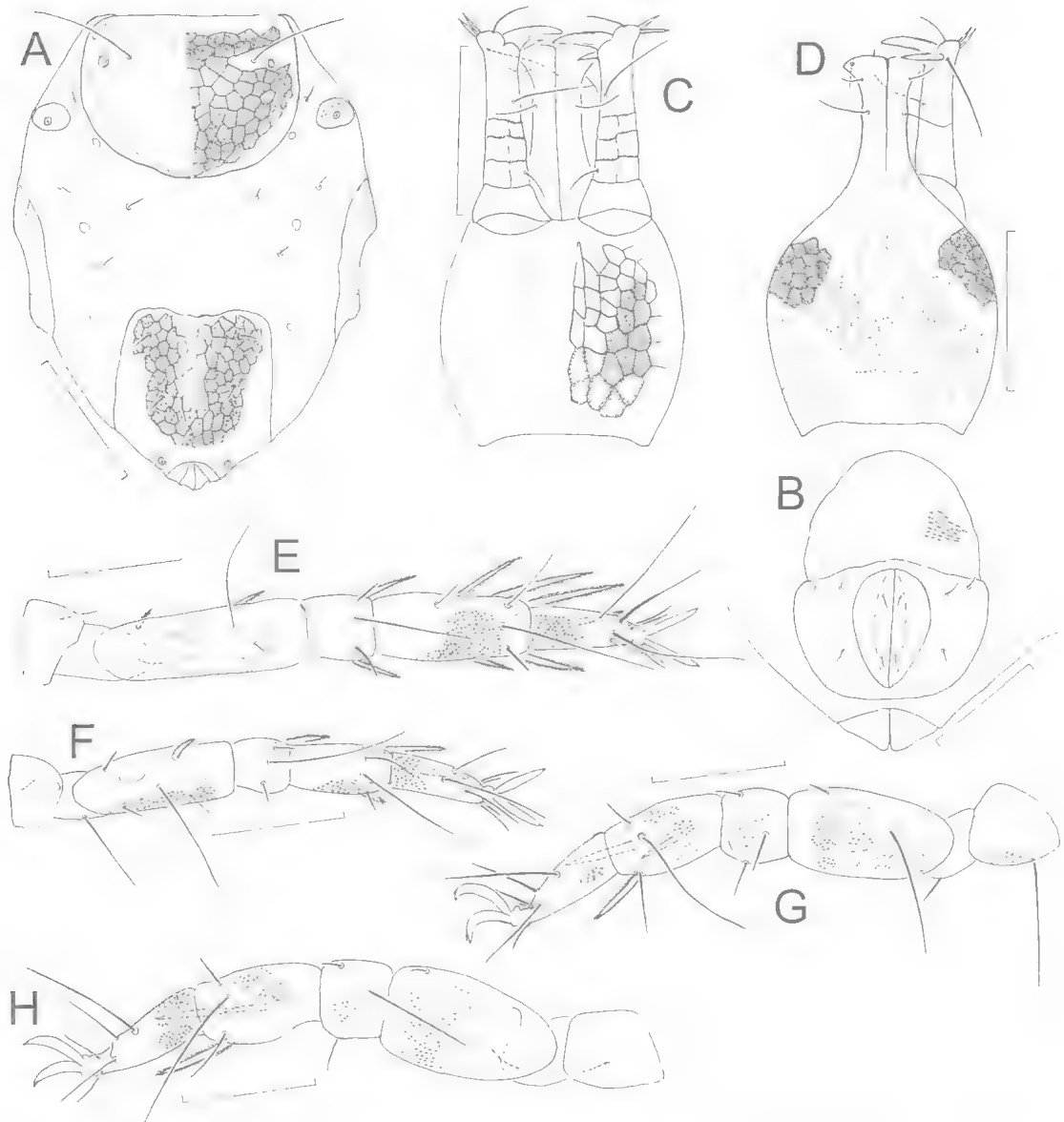


FIG. 11. *Scaptognathus ornatus* Bartsch, adult. A, idiosoma, dorsum; B, genitoanal shield of ♀; C, gnathosoma, dorsal view; D, gnathosoma, ventral view; E, leg I, dorsal view; F, leg II, dorsal view; G, leg III, dorsolateral view; H, leg IV, dorsolateral view. Scales: A, C, D = 100µm; B, E, F, G, H = 50µm.

SCAPTOGNATHIDES

- 1. Ocular plates (OC) ca. four times longer than wide
 *S. australis* (see Bartsch, 1993a)
 OC ca. twice as long as wide (Fig. 1A) 2
- 2. Anterior dorsal plate (AD) and posterior dorsal plate (PD) with polygonal pattern (Fig. 3A); telofemora with undulated ventral ridge (Fig. 3C-F); tarsus III with thickened proximal seta (Fig. 3E)
 *S. undulatus* sp. nov.
- 3. AD and PD finely punctate and finely or coarsely pitted but no polygonal pattern (Fig. 1A, 2A); telofemora without an undulated ridge (Fig. 1E-H); tarsus III without thickened proximal seta (Fig. 1G) 3
- 3. Dorsal plates with wide pits (foveae) (Fig. 2A); OC posteriorly with a minute seta (Fig. 2A)
 *S. tomkinsae* sp. nov.
- Dorsal plates with smaller pits (Fig. 1A); OC without minute posterior seta *S. heraldensis* sp. nov.

SCAPTOGNATHUS

1. Rostrum broad throughout (Fig. 9D) 2
 Rostrum posteriorly slender and apically widened
 (Fig. 4D) 3
2. Genu I with one bipectinate seta (Fig. 9E); tibia II with two
 bipectinate setae (Fig. 9F); tibia III with five setae (Fig.
 9G) *S. monstruosus* sp. nov.
 Genu I without bipectinate seta; tibia II with one bipec-
 tinate seta; tibia III with six setae *S. peregrinus*
 (see Bartsch, 1993a)
3. Tibiae I-IV with 6-3-4-4 bipectinate setae
 (Fig. 7E-II) 4
 Tibia I-IV with 5-2-2/3-2/3 bipectinate setae
 (Fig. 4F-I) 6
 Tibia I-IV with 6-4-4-4 bipectinate setae. *S. bayssianus*
 (see Abé & Green, 1994)
4. Female GA bipartite; basifemur III with one seta.
S. kolymbus sp. nov.
 Female GA tripartite; basifemur III with two setae. 5
5. Pits on AD and PD on average distinctly wider than the
 spaces between them (Fig. 8A,C) *S. kunzi* (see Bartsch, 1988; present paper)
 Pits on AD and PD on average not wider than the spaces
 between them (Fig. 8D; 10A) *S. oceanus* sp. nov.
6. Telofemur I with two bipectinate setae 7
 Telofemur I with three bipectinate setae 8
7. Farsi I and II with pitted areolae; three pairs of setae in
 dorsal membranous cuticle; female with three pairs pgs;
 telofemur II with one bipectinate seta. *S. australis*
 Bartsch (see Bartsch, 1993a)
 Farsi I and II without pitted areolae (Fig. 4F-I); four pairs
 of setae in dorsal membranous cuticle (Fig. 4A); female
 with two pairs pgs (Fig. 4B); telofemur II without
 bipectinate seta (Fig. 4G) *S. exquisitus* sp. nov.
8. Most leg segments with well defined deeply pitted areolae
 (Fig. 11E-H), palp with dorsal ornamentation as shown
 in Fig. 11C *S. ornatus* Bartsch (see Bartsch, 1984)
 All leg segments without such well defined deeply pitted
 areolae; palp without dorsal ornamentation. 9
9. Telofemur II with one bipectinate seta (Fig. 5F)
 *S. gracilipalpus* sp. nov.
 Telofemur II with two bipectinate setae (Fig. 6G)
S. insularis sp. nov.

COMMENTS

Including the species described here, 28 species of *Lohmannella*, 10 of *Scaptognathides* and 27 of *Scaptognathus* are now described world-wide. The presence of eight *Scaptognathus* and three *Scaptognathides* species in the Coral Sea comes as no surprise as both genera are well represented in warm water regions (Abé & Green, 1994; Bartsch, 1996). The poor representation of *Lohmannella* was also to be expected as this genus appears to have reached its highest diversity in colder areas, for example Antarctica (Bartsch, 1993b; Newell, 1984).

Perhaps the most interesting aspect of the Lohmannellinae described in the present paper is

the finding of *Scaptognathus monstruosus* sp. nov. This is the only species of its genus where the female is known to have an undivided genitoanal plate and three palp claws. Present in all other halacarid genera, the undivided genitoanal plate is probably a plesiomorphic character and if so may indicate that *S. monstruosus* is perhaps an early derivative species in *Scaptognathus*. Alternatively, the undivided GA could be due to reversal, but this appears less parsimonious.

Different opinions exist in regard to the taxonomic rank of Lohmannellinae (subfamily versus family rank) and the number of genera it contains. Abé (1998) following the traditional view of Newell (1947), Viets (1956) and Bartsch (1983, 1996) lists four lohmannelline genera, *Scaptognathus*, *Scaptognathides*, *Lohmannella* and *Parolohmannella*. By contrast, Newell (1984) decided to elevate Lohmannellinae to family and to include in it all those genera which have the palps inserted dorsally on the gnathosoma, *Lohmannella*, *Scaptognathus*, *Simognathus*, *Parolohmannella*, *Soldanellonyx*, *Parasoldanellonyx*, and further genera by implication. While the position of the palp dorsally on the gnathosoma may indeed be a synapomorphy for Lohmannellidae it is unsatisfactory in my view to alter the classification on the basis of this single character. Since the palps are also inserted dorsally in the Pezidae Harvey, 1990, which Harvey (1990) considers to be the sister group of the remaining halacaroids, dorsal palp insertions may be a plesiomorphy for Lohmannellidae. I am therefore inclined to concur with Abé (1998) to maintain Lohmannellinae as a subfamily of four genera, although in my view the monophyly of this subfamily is also little supported.

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A SOUTHERN RIGHT WHALE *EUBALAENA AUSTRALIS* (DESMOULINS, 1822) IN SOUTHERN QUEENSLAND WATERS. *Memoirs of the Queensland Museum* 45(2): 556. 2000:- The southern right whale is distributed around the Southern Hemisphere generally between latitudes 30° and 60°S. Like many species of baleen whales, it undertakes an annual migration from high latitude summer feeding grounds to lower latitude winter breeding areas (Best et al., 1993; Bannister et al., 1997).

In Australia right whales are found along the southern coastline between May and October. During this time calving females display strong site fidelity to certain areas (Burnell & Bryden, 1997) with approximately 90% of calvings occurring between Cape Leeuwin, WA, and Ceduna, SA (S. Burnell, unpubl. data). Whales without calves display less site fidelity and may move some distance along the coast (Burnell & Bryden, 1997). They frequently occur off the S coast of New South Wales, with reports from as far north as Coff's Harbour (30°20'S) and Cape Byron (28°38'S) (P. Hodda, pers. comm.).

This report is the first published sighting of a southern right whale in Queensland waters. At 7:45am, July 24 1998, the author observed a whale 'spy hopping' approximately 100m off Point Lookout, North Stradbroke Island (27°26'S, 153°32'E). The whale swam slowly past the point in the company of several bottlenose dolphins (*Tursiops* spp.). It lifted its head partially out of the water on several occasions displaying large white 'callosities' and a highly arched mouth (Fig. 1). The back was broad and lacked a dorsal fin. Short square pectoral fins were also evident when the whale rolled onto its back and when it breached (Fig. 2). All these features are characteristic of a right whale (Cummings, 1985). It appeared to be smaller than a mature humpback whale (many of which are observed in the area in July) suggesting it was immature (Cummings, 1985; Tormosov et al., 1998).

At approximately 8:15am the whale turned north and disappeared from view. Despite posting experienced observers on the headlands for the remainder of the day, it was not seen again.

The author is aware of only one previous sighting of a southern right whale in Queensland waters. In the mid-1950s the crew of 'Kos I', a Tangalooma whale chaser, saw a right whale near Flinders Reef at the north end of Moreton Island (26°58'S, 153°29'E) (L. Nash, pers. comm.). It was approached, identified, and left unmolested due to its protected status.

The southern right whale population is currently recovering from heavy over-exploitation from the late 18th century until as recently as the early 1970s (Tormosov et al.,

1998). As the population recovers, visits to Queensland waters by this species may occur with increasing frequency.

After this sighting, more were reported from the area. On 8 August a whale with a rounded back, no dorsal fin, 'crusts' on its head and 'stubbie flippers' was seen again off Point Lookout by an experienced humpback whale observer. It remained in the area for at least six hours. The next day the same observer again saw a similar whale that remained for at least one-and-a-half hours. On 10 August a right whale and calf were engaged by a commercial whale-watching vessel near Flinders Reef. This encounter lasted some time and was videotaped. Species identification was unambiguous. The calf was lively and dark in colour.

Acknowledgements

Fiona Macknight, Tim Page and Paula den Hartog provided sighting information and helped mount the watch for the return of the whale. Robert Paterson encouraged the production of this note and passed on additional sighting information from Jenny Truman and Kerrie McTaggart. Les Nash told the story of the whalers' right whale. Stephen Burnell and Michael Bryden provided useful information and comments regarding the manuscript. The Australian Marine Mammal Research Centre kindly provided the funding that enabled us to be in the right place at the right time.

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M.J. Noad, *Department of Veterinary Anatomy and Pathology, University of Sydney 2006, Australia; 2 March 1999.*



FIG. 1. Dorsum of the southern right whale seen at Point Lookout on 24 July. Callosities are visible on the rostrum. There is no dorsal fin.



FIG. 2. A breach demonstrating a short broad pectoral fin characteristic of the southern right whale.

AN ADULT DWARF MINKE WHALE *BALAENOPTERA ACUTOROSTRATA*
LACÉPÈDE, 1804 FROM FRASER ISLAND, QUEENSLAND

R.A. PATERSON, D.H. CATO, H.A. JANETZKI AND S.C. WILLIAMS

Paterson, R.A., Cato, D.H., Janetzki, H.A. & Williams, S.C. 2000 06 30: An adult dwarf minke whale *Balaenoptera acutorostrata* Lacépède, 1804 from Fraser Island, Queensland. *Memoirs of the Queensland Museum* 45(2): 557-568. Brisbane. ISSN 0079-8835.

A 7.0m long male dwarf minke whale *Balaenoptera acutorostrata* Lacépède, 1804, stranded at Fraser Island, is the second recorded stranding of an adult from Queensland. The complete skeleton, baleen and larynx were collected and are described. In addition to the previously noted osteological features of the dwarf form of this species another characteristic differentiating it from the dark shoulder form is described, viz. a ratio > 1.50 of breadth to height in the centrum of the fifth cervical vertebra. □ *Dwarf minke whale, Balaenoptera acutorostrata, stranding, osteology, Queensland.*

R.A. Paterson, H.A. Janetzki & S.C. Williams, Queensland Museum, PO Box 3300, South Brisbane 4101; D.H. Cato, Defence Science and Technology Organisation, PO Box 44, Pyrmont 2009, Australia; 8 July 1999.

Based on the external and baleen appearances of captured and stranded minke whales in South Africa, Best (1985) described a diminutive or Type 3 form. In addition, he described Type 1 and 2 forms which he also referred to as 'bonaerensis'-type because of their baleen similarity to an Argentinian specimen described as *Balaenoptera bonaerensis* (Burmeister, 1867). Rice (1998) has recently assigned Type 1 and 2 forms as *Balaenoptera bonaerensis*. Arnold et al. (1987) described the osteology of the Type 3 form, which they termed the dwarf minke whale, primarily from a 7.1m long sexually mature female which died after 'entrapment' in Hook Reef lagoon (19°52'S, 149°13'E) in the Great Barrier Reef.

Immature minke whales of all forms predominate in museum collections derived from strandings rather than captures (Horwood, 1990; Paterson, 1994; Paterson et al., 1997; Watson & Fordyce, 1993; Zerbini et al., 1996). The following description of another adult dwarf minke whale from Queensland complements the initial osteological study of Arnold et al. (1987). A 7.0m long male was found dead at Dundubara (25°10'S, 153°17'E) on the eastern (oceanic) shore of Fraser Island on 1 July 1997. The border between the area of white pigmentation and darker colouration in the shoulder region (at least on the right) was 'serrated' (Fig. 1) and differed from other records in the Queensland Museum (Paterson, 1994). The skull and mandible as well as the baleen and larynx were collected the following day and the post-cranial skeleton six

weeks later. The specimen is registered as QM JM11761.

DESCRIPTION

BALEEN. The baleen is illustrated from the buccal aspect in Fig. 2. A count of the small anterior hairs was not attempted. There are 252 plates on the right and 243 on the left. Most plates are all-white (more precisely creamy-white) but those with a predominant dark outer border number 19 (7.5%) on the right and 21 (8.6%) on the left and most are posterior. The largest plates do not exceed 20cm in length. These features are typical of the dwarf form (Best, 1985; Arnold et al., 1987).

LARYNX. In the past fifteen years baleen and toothed whale larynges have been collected whenever possible by Queensland Museum staff for comparative study (Paterson, 1994; Paterson et al., 1993; Quayle, 1991). The present specimen is illustrated and annotated (Fig. 3) in conformity with the dissection by Quayle (1991) of a humpback whale *Megaptera novaeangliae* calf. It measures 41cm from the antero-inferior aspect of the epiglottic cartilage to the distal aspect of the ventral diverticulum. The latter structure is unique to baleen whales (Hosokawa, 1950; Slijper, 1962). Apart from size differences, the larynx of QM JM11761 is similar to the above-mentioned calf with the exception of thicker muscle between the dorsal aspect of the diverticulum and the ventral aspect of the trachea.



FIG. 1. Right shoulder colour pattern of QMJM11761.

SKULL, MANDIBLE AND HYOID. These are illustrated in Figs 4-8 and measurements based on Omura (1975), Arnold et al. (1987) and Paterson et al. (1997) are contained in Table 1. Paterson et al. (1997), when describing the osteology of '*bonaerensis*' specimens from southern Queensland (which they termed 'dark shoulder' following Arnold et al., 1987), discussed problems arising from immaturity and the paucity of specimens. Immaturity is not at issue in the present specimen but as it is only the second adult stranding record from Queensland some of the cranial differences relative to the Hook Reef specimen may merely reflect individual and/or gender variation.

Parietal incorporation into the vertex with an angulato-ovate interparietal (Fig. 5, left), elongation of the hamular processes of the pterygoids and posterior palatine angularity (Fig. 5, right) considered to be characteristic of the dwarf form (Arnold et al., 1987), are confirmed. However, the anterior aspects of the nasals are almost straight or minimally concave (Figs 4 & 5)

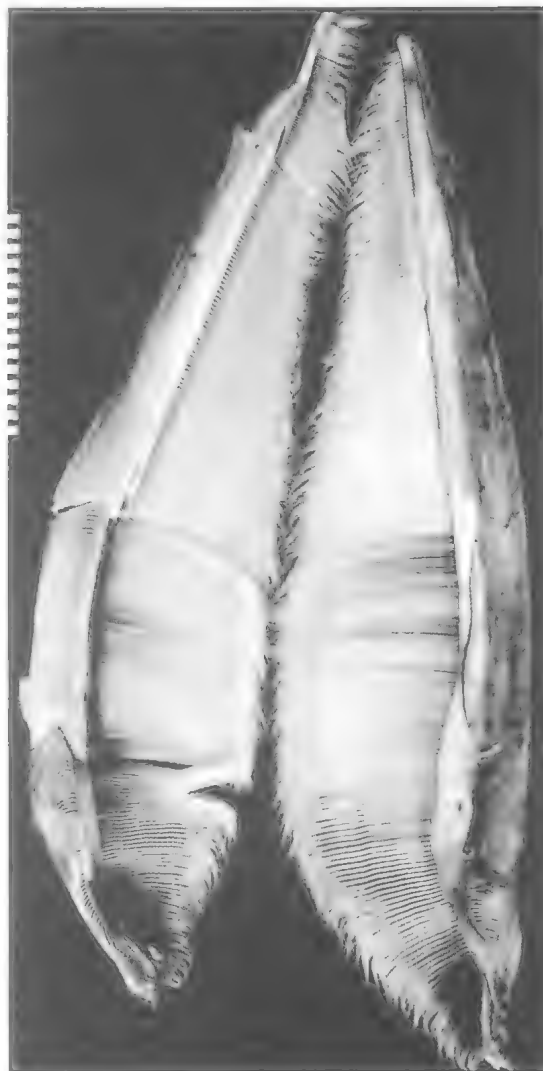


FIG. 2. Baleen of QMJM11761 from buccal aspect. Right baleen row is on the left of the figure. (Scale in cm).

compared with the Hook Reef specimen. Zerbini et al. (1996) noted that the anterior border of the nasals was less convex in mature specimens. The posterior extent of the premaxillae is 'limited' by lateral prominences of the junction of the middle and posterior thirds of the nasals (Fig. 5, left). These appearances and positions are different from the posterior premaxillary extent and smooth lateral nasal surfaces in the Hook Reef specimen (fig. 5c in Arnold et al., 1987). The malars and hyoid components (Figs 6, 7) are of finer proportion than the Hook Reef specimen but this may result from individual or gender

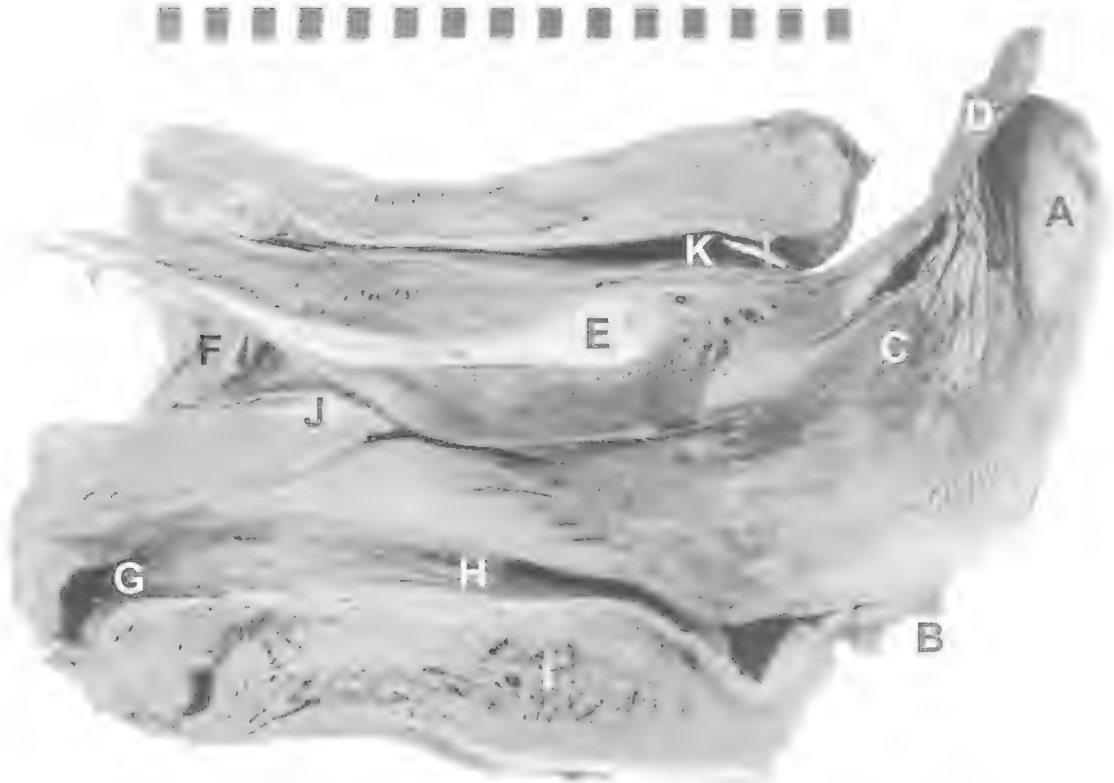


FIG. 3. Longitudinal section of the larynx of QMJM 11761 in medial aspect with thyroid cartilage removed. A, epiglottic cartilage; B, fibrous attachment to thyroid cartilage; C, arytenoid cartilage-carpus; D, arytenoid cartilage-rostral end; E, cricoid cartilage; F, tracheal lumen; G, fundus of ventral diverticulum; H, neck of ventral diverticulum; I, thyroarytenoid muscle; J, interarytenoid fibro elastic connection; K, oesophageal lumen. (Scale in cm).

variation. The mandibular appearances (Fig. 8) are unremarkable.

VERTEBRAE AND CHEVRONS. Measurements, including mean vertebral length (Omura, 1971; Paterson et al., 1997), are contained in Table 2. The vertebral formula (C7, T10, L13, Ca18 = 48) differs slightly from that (C7, T11, L12, Ca18 = 48) in a dark shoulder form (QM JM10961) described by Paterson et al. (1997). The formula of the Hook Reef specimen was not stated by Arnold et al. (1987) but they noted that the epiphyses (in that 7.1m long female) were fused to the centra only in the first two cervicals and the distal caudals. In contrast the central epiphyses were fused in all vertebrae (Fig. 9) in QM JM11761 (a 7.0m long male), indicating physical maturity.

A tuberculate parapophysis on C7 (Fig. 10) is present. This is characteristic of the dwarf form (Arnold et al., 1987) in contrast to its lack or almost complete absence in QM JM10961 and other dark shoulder forms described by Omura

(1975). When comparing that feature in QM JM11761 and QM JM10961 apparent differences in the shape of the centra from C5 to at least T1 were noted. Those of the dwarf form were more ovoid than the dark shoulder form (Fig. 10). The limitation in ascribing significance to osteological differences from a small series is appreciated. Accordingly, the ratios of central breadth to height in the C5-T1 vertebra from other specimens of known form were calculated. The provenance of the specimens and the measurements (including ratios) are contained in Table 3. In both dwarf and dark shoulder forms the ratio of breadth to height shows little variation between individuals for a particular vertebra, even though there is wide variation in maturity and in the dimensions of breadth and height. The ratio is generally larger in the dwarf form. For C5 and the mean of C5, C6, C7 and T1, all values for all individuals of the dwarf form are larger than all those of the dark shoulder form. The mean

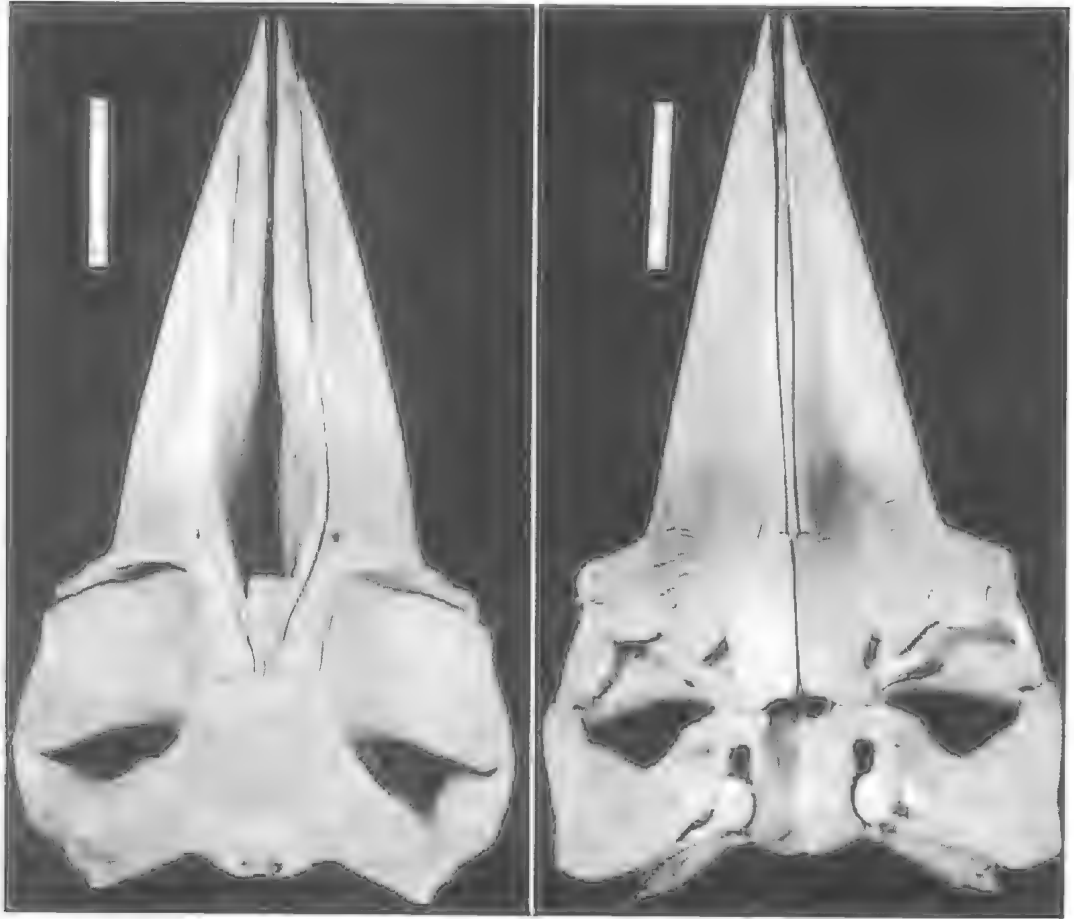


FIG. 4. Skull of QM JM11761 from dorsal aspect (left) and ventral aspect (right). (Scale in cm).

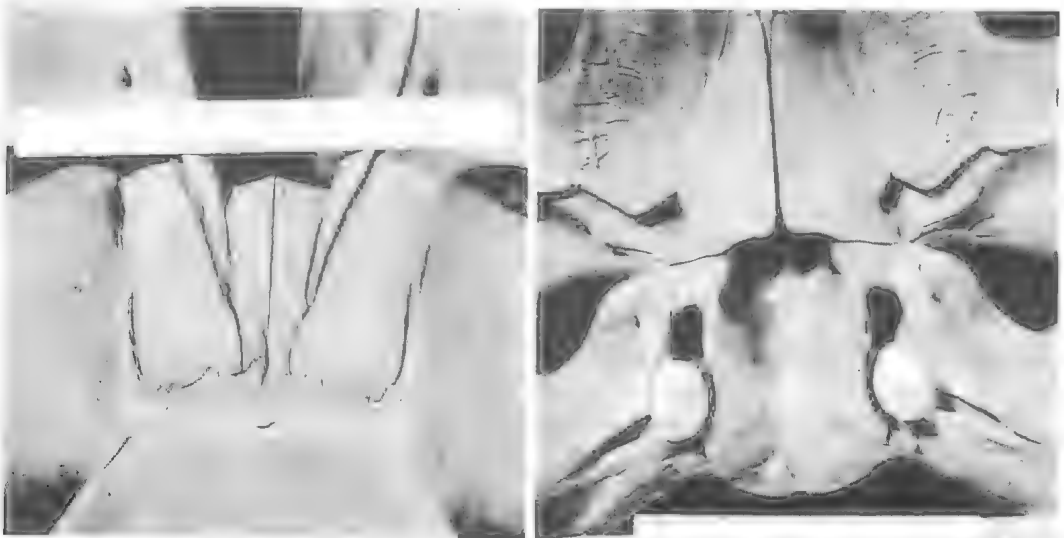


FIG. 5. Skull of QM JM11761 with close-up views of nasals (left) and hamular processes (right). (Scale in cm).



FIG. 6. Malars of QM JM11761. (Scale in cm).



FIG. 7. Basihyoid (below) and stylohyals (above) of QM JM11761. (Scale in cm).



FIG. 8. Mandible from dorsal aspect of QM JM11761. (Scale in cm).

values are 1.32, 1.23, 1.24, 1.26, 1.37 and 1.33 (dark shoulder) and 1.53, 1.58 and 1.44 (dwarf).

Because the sample size is small a non-parametric test, the randomisation test for two independent samples (Siegel, 1956), is used to determine the significance of the difference in ratios. This test is independent of the probability distribution of the variables sampled. Under the null hypothesis, the number of ways that six values (representing the dark shoulder samples) can be drawn from the nine (both samples pooled) for a particular vertebra, without regard for the order in which they are drawn, is 84. Since the result for C5 is the extreme case where all values for a particular vertebra of one form are less than all of the other form, the probability of this result is $1/84 = 0.012$. The same result is obtained if the means of the values of the four vertebrae are used. For C6, C7 and T1, the smallest ratio for the dwarf samples equals the largest of the dark shoulder samples, so that there are 2 ways out of 84 of obtaining the above result, a probability of 0.024. Thus the differences in the value of this ratio between the dwarf and dark shoulder forms are significant statistically at the levels shown.

Figure 11 shows the breadth and height of C5, together with the ratios (of breadth to height), as functions of total length for all individuals (Table 3). For each form the breadths and heights show an almost linear dependence on length. On the

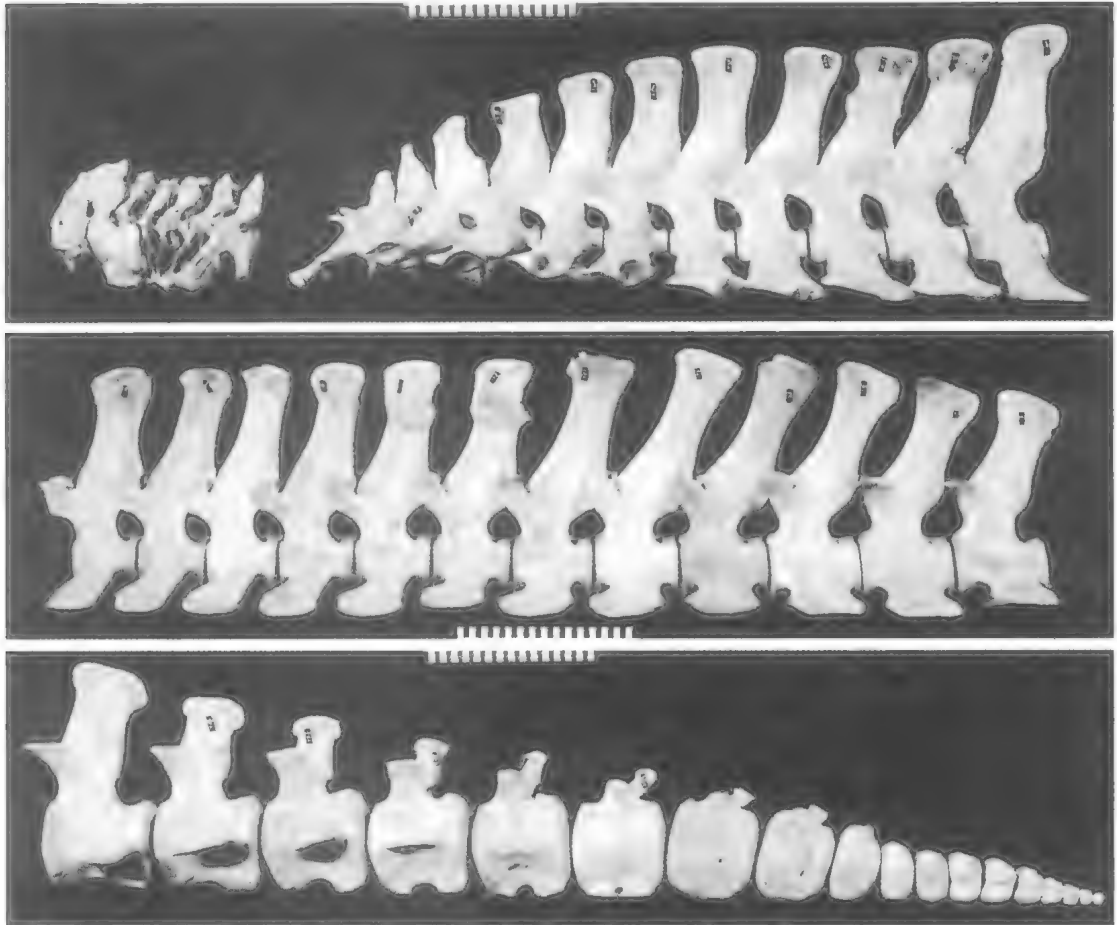
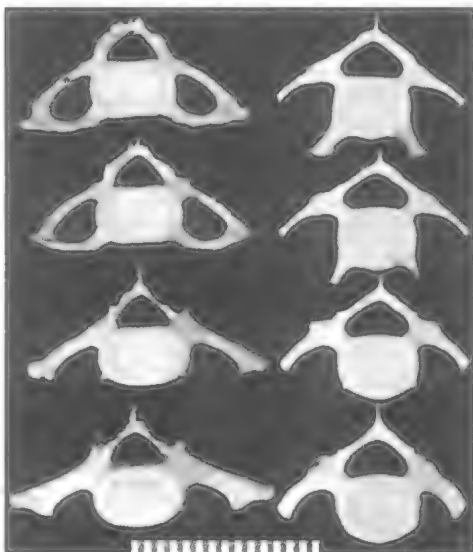


FIG. 9. Vertebral column from lateral aspect of QM JM11761. Top, cervical and thoracic vertebrae; centre, lumbar vertebrae (L1 was inadvertently included with the thoracics); bottom, caudal vertebrae. (Scale in cm).



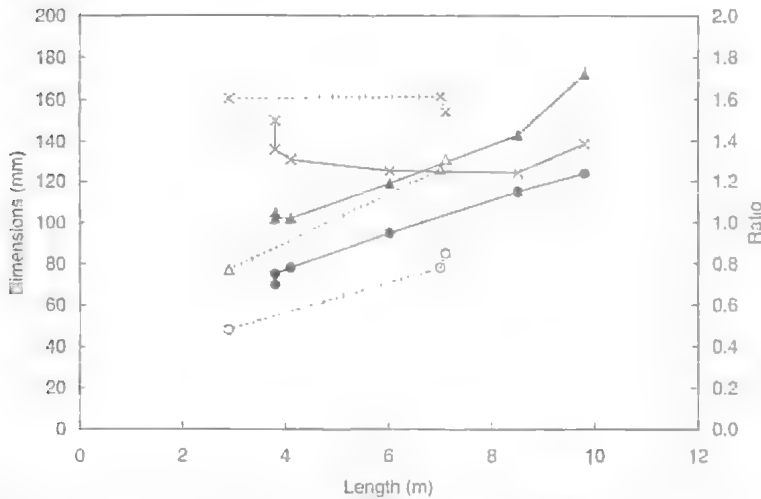


FIG. 11. Comparison of C5 dimensions for 6 dark shoulder and 3 dwarf minke whales (Table 3). Solid curves and filled data points show the values for the dark shoulder minke whale samples while the dotted curves and open data points show the values for the dwarf minke whale samples. The triangular data points show breadths, the round data points show heights and the crosses show the ratios of breadth to height.

considerable difference in the dwarf and dark shoulder specimens shown in Fig. 10. However, the dark shoulder specimen (QM JM10961) is less mature than the dwarf specimen. Adult dark shoulder specimens (Table 3) described by Omura (1975) have similar lateral elements in the relevant vertebrae compared with QM JM11761. Individual variation in these elements was noted in New Zealand minke whales of unspecified form (Watson & Fordyce, 1993). The left C4 diapophysis was completely absent in one of the two described specimens.

There are nine chevrons (Fig. 12) and the first has unfused laminae. Paterson et al. (1997) described twelve in a dark shoulder form and Watson & Fordyce (1993) noted ten and thirteen in their specimens.

RIBS AND STERNUM. There are ten pairs of ribs and they are illustrated with the sternum in Fig. 13. Their measurements are contained in Table 4.

SCAPULAE AND FORELIMB BONES. The scapulae, humeri, radii and ulnae are illustrated in Fig. 14 and their measurements are contained in Table 5. The phalangeal formula (including the metacarpals) derived from X-rays is I₄ II₇ III₆₋₇ IV₃₋₄.

DISCUSSION

Watson & Fordyce (1993) discussed the importance of anatomical studies as well as biochemical techniques, in discriminating between cetacean populations and species. Those authors suggested a comprehensive review of skull structures for New Zealand minke whales and emphasised the importance of the post-cranial skeleton with regard to functional studies. Paterson et al. (1997) when describing cranial and post-cranial osteology of a dark shoulder form also recommended detailed examination of available minke whale material (particularly adult specimens) in Australasian museum collections.

The present osteological description, of the second adult dwarf form recovered in Queensland, complements the initial study of Arnold et al. (1987) and adds a further distinction (the ratio of breadth to height in the body of C5) between dwarf and dark shoulder forms. A more comprehensive study using material collected from all available southern hemisphere sites is awaited to confirm or exclude this additional osteological character of the dwarf minke whale as well as further establishing the characters previously determined by Arnold et al. (1987).

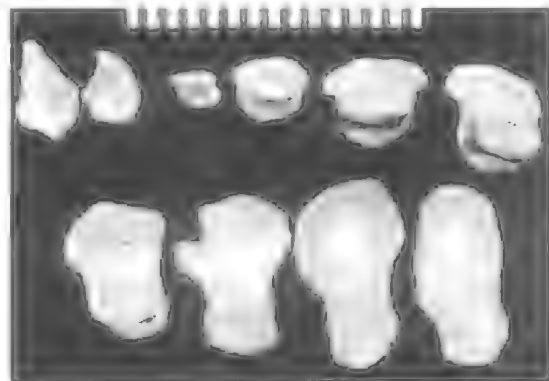


FIG. 12. Chevrons of QM JM11761. (Scale in cm).

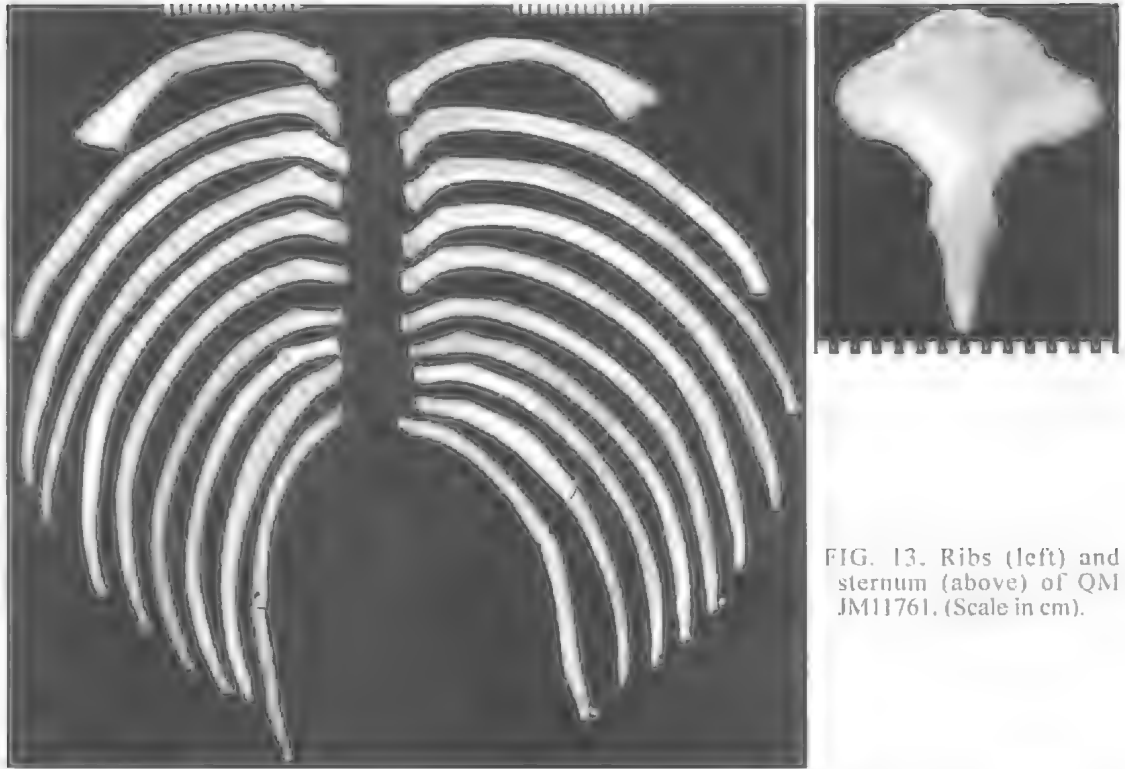


FIG. 13. Ribs (left) and sternum (above) of QM JM11761. (Scale in cm).

ACKNOWLEDGMENTS

John Ford of the Queensland Parks and Wildlife Service secured the specimen following its stranding. Stephen Van Dyck assisted with flensing and retrieval and Jeff Wright took the laryngeal and skeletal photographs. Peter Arnold kindly provided the vertebral measurements of QM JM3861.

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TABLE 1. Skull, mandibular and hyoid measurements (in mm) of QM JM11761.

Condyllo-premaxillary length	1535
Length of premaxillary, right (sl. broken at tip)	1136
Length of premaxillary, left (sl. broken at tip)	1128
Length of maxillary, superior, right	1099
Length of maxillary, superior, left	1091
Tip of premaxillary to vertex	1179
Tip of premaxillary to nasals	1032
Length of nasals, median	178
Breadth of nasals, anterior (between premaxillaries at ant. end of nasals)	92
Length of rostrum	1038
Breadth of rostrum at middle	349
Breadth of rostrum at base	520
Breadth across maxillaries at vertex	157
Breadth of frontal across nasals	241
Breadth between maxillaries at nares	235
Breadth of skull, squamosal	864
Breadth of skull, frontal	830
Breadth of skull, maxillaries	751
Length of orbit, frontal, right	168
Length of orbit, frontal, left	171
Breadth of occipital bone	592
Breadth across occipital condyles (to base of spongy bone)	165
Height of occipital condyle, right	88
Height of occipital condyle, left	82
Breadth of foramen magnum aperture	67
Height of foramen magnum aperture	52
Length from foramen magnum to vertex (measurement at post. parietals)	360
Lachrymal breadth, right	65
Lachrymal breadth, left	missing

Tip of premaxillary to ant. vomer, median	236
Tip of premaxillary to ant. palatine, median	1010
Tip of premaxillary to post. palatine, median	1275
Tip of premaxillary to post pterygoid	1383
Breadth across hamular process of pterygoid	116
Length of mandible, straight, right	1482
Length of mandible, straight, left	1477
Length of mandible, curved, right (outside curve) (inside curve)	1589 1534
Length of mandible, curved left (outside curve) (inside curve)	1583 1524
Height of mandible at coronoid, right	179
Height of mandible at coronoid, left	173
Height of mandible at condyle, right	160
Height of mandible at condyle, left	162
Tympanic bulla, length, right	79
Tympanic bulla, length, left	76
Tympanic bulla, greatest breadth, right	63
Tympanic bulla, greatest breadth, left	64
Tympanic bulla, thickness at middle, right	46
Tympanic bulla, thickness at middle, left	46
Malar, length, right	174
Malar, length, left	176
Malar breadth, right	67
Malar breadth, left	68
Lachrymal length, right	120
Lachrymal length, left	missing

	Hyoids	Breadth (mm)	Length (mm)
Basihyoid		362	116
Stylohyal, right		47	253
Stylohyal, left		49	247



FIG. 14. Scapulae (above); humeri, radii and ulnae (right) of QM JM11761. (Scale in cm).

TABLE 2. Vertebral and chevron measurements (in mm) of QM JM11761.

Vertebral No.	Greatest Breadth	Greatest Height	Centrum Breadth (a)	Centrum Height (b)	Centrum Length (c)	Mean Vertebral Length $(a \times b \times c)^{1/3}$
C 1	290	164	167	90	42	86
2	436	164	164	95	34	81
3	364	132	137	75	21	60
4	321	140	130	74	25	62
5	331	145	126	78	27	64
6	334	158	125	80	32	68
7	366	169	128	82	35	72
T 1	401	173	131	83	45	79
2	385	214	130	83	62	87
3	387	253	131	84	75	94
4	441	287	128	86	83	97
5	510	323	127	88	85	98
6	565	349	127	86	93	101
7	593	364	125	85	96	102
8	620	356	125	85	100	102
9	635	355	128	86	102	104
10	580 *	376	130	88	108	108
L 1	602	403	131	90	110	109
2	607	412	131	90	118	112
3	615	414	134	101	121	118
4	612	414	133	101	124	119
5	622	421	133	108	133	124
6	600	433	134	108	132	124
7	574	437	132	111	137	126
8	534	447	138	113	139	129
9	485	457	141	115	140	131
10	448	450	146	116	150	136
11	440	445	145	121	157	140
12	394	427	147	122	157	141
13	358	385	147	127	154	142
Ca 1	338	354	150	128	150	142
2	301	310	152	135	140	142
3	250	281	158	140	135	144
4	202	242	153	139	124	138
5	175	218	153	136	124	137
6	140	194	140	134	121	131
7	125	176	125	135	110	123
8	119	155	119	128	93	112
9	112	120	94	92	58	85
10	94	90	64	62	45	57
11	78	88	63	58	42	56
12	75	80	62	60	44	55
13	66	70	51	51	40	47
14	54	61	44	42	35	40
15	39	50	33	32	28	31
16	29	39	27	24	25	25
17	20	27	16	16	21	18
18	16	19	14	13	17	15

TABLE 2. *continued.* * = damaged.

Chevron	Length	Height
1	(a) 84 (b) 69	(a) 59 (b) 60
2	86	177
3	107	179
4	113	155
5	103	131
6	91 *	106
7	73	82
8	76 *	59
9	43	37

TABLE 3. Comparison of vertebral body (C5-T1) breadth/height ratios between dwarf and dark shoulder minke whales. (Measurements other than specimen length are in millimetres)

Specimen (Registration, Length, Sex, Reference)	Vertebra	Breadth	Height	Ratio
Dark Shoulder Forms				
71 J2883, 9.8m, ♀, Omura (1975)	C5	172	124	1.39
	C6	170	132	1.29
	C7	171	132	1.30
	T1	174	132	1.32
71 J2793, 8.5m, ♂, Omura (1975)	C5	143	115	1.24
	C6	141	118	1.19
	C7	142	118	1.20
	T1	149	118	1.26
QM JM10961, 6.02m, ♀, Paterson et al. (1997)	C5	119	95	1.25
	C6	119	97	1.23
	C7	121	99	1.22
	T1	123	98	1.26
QM JM8513, 4.1m, ♀, Paterson (1994)	C5	102	78	1.31
	C6	100	80	1.25
	C7	106	88	1.20
	T1	108	85	1.27
QM JM5434, 3.8m, ♀, Paterson (1994)	C5	102	75	1.36
	C6	103	76	1.36
	C7	106	78	1.36
	T1	110	78	1.41
QM J21708, 3.8m, ♀, Paterson (1986)	C5	105	70	1.50
	C6	95	75	1.27
	C7	95	72	1.32
	T1	94	76	1.24
Dwarf Forms				
QM JM3861, 7.1 m, ♀, Arnold et al. (1987)	C5	131	85	1.54
	C6	130	86	1.51
	C7	131	88	1.49
	T1	134	86	1.56
QM JM11761, 7.0m, ♂, Present Study	C5	126	78	1.62
	C6	125	80	1.56
	C7	128	82	1.56
	T1	131	83	1.58
QM JM7301, 2.9m, ♀, Paterson (1994)	C5	77	48	1.60
	C6	75	55	1.36
	C7	75	55	1.36
	T1	79	56	1.41

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TABLE 4. Rib and sternal measurements (in mm) of QM JM11761. * = broken.

Rib	Straight Length	
	Right	Left
1	575	584
2	846	850
3	945	962
4	992	995
5	969	963
6	913	924
7	860	874
8	824	829
9	775	784 *
10	815 *	815 *
Sternum	Breadth 238	Length 293

TABLE 5. Scapular and forelimb measurements (in mm) of QM JM11761. * = possibly missing.

	Scapula		Humerus, Radius, Ulna					
	Right	Left		Breadth		Length		
				Right	Left	Right	Left	
Greatest breadth	570	572						
Greatest height	349	349	Humerus	126	130	251	254	
Ratio of breadth to height	1.6	1.6	Radius	76	75	385	390	
Length of acromion-inferior	124	119	Ulna	49	49	347	352	
Breadth of acromion, distal end	46	40						
Length of coracoid, inferior	77	73						
Breadth of coracoid, distal end	28	30						
Length of glenoid fossa	135	132						
Breadth of glenoid fossa	90	90						
Length of Phalanges								
Phalanx	Right				Left			
	I	II	III	IV	I	II	III	IV
1	57	71	57	46	57	71	57	46
2	59	72	61	43	59	74	61	43
3	49	54	50	35	48	55	50	35
4	27	36	36	6	29	37	36	
5		25	24			24	23	
6		15	14			15	15	
7		7	*			7	5	
8		*				*		

TAXONOMICA ARANEAE I: BARYCHELIDAE, THERAPHOSIDAE, NEMESIIDAE
AND DIPLURIDAE (ARANEAE)

ROBERT J. RAVEN

Raven, R.J. 2000 06 30: Taxonomica Araneae I: Barychelidae, Theraphosidae, Nemesiidae and Dipluridae (Araneae). *Memoirs of the Queensland Museum* 45(2): 569-575. Brisbane. ISSN 0079-8835.

In the Barychelidae, *Idioctis sierramadrensis* Barrion & Litsinger, 1995 is placed in the synonymy of *Rhianodes atratus* (Thorell, 1890) and *Aganippe bancrofti* Rainbow & Pulleine, 1918 is transferred to the barychelid genus *Trittame*. In the Theraphosidae, *Phlogiellus* Pocock, 1897 is the senior synonym of *Baccallbrapo* Barrion & Litsinger, 1995; *Chilocosmia* Schmidt & von Wirth, 1992 and *Selenopelma* Schmidt & Krause, 1995 are newly placed in the synonymy of *Selenocosmia* along with *Phlogius* Simon, 1887 which is replaced into synonymy. In the Nemesiidae, *Chenistonina* is removed from the synonymy of *Aname* and includes only species of the *Aname maculata* group of Raven, 1984. The contentious question of the identity of *Aname diversicolor* Hogg, 1902 is revisited. The invalidly designated neotype is used as the type of *Aname mainae*, sp. nov. In the Dipluridae, the Dominican amber fossil genus, *Microsteria* Wunderlich, 1988, is placed in the synonymy of *Masteria* L. Koch, 1873. □ *Taxonomy, Mygalomorphae, spiders, Australia, amber, fossil.*

Robert J. Raven, Queensland Museum, PO Box 3300, South Brisbane 4101, Australia; 20 April 2000.

A number of new taxa and nomenclatural changes have occurred in mygalomorph spiders in southeast Asia, Australia and fossils from the Dominican amber since Main (1985) and Raven (1985b). Some have been a result of taxonomic revisions. Some have been isolated descriptions. Some have been forced as a result of wider changes. Most changes do not require full revisions but only a brief note. That is the purpose of this series.

Institutional and morphological abbreviations follow those of Raven (1985a).

BARYCHELIDAE

Rhianodes atratus (Thorell, 1890)

Rhianodes atratus Thorell, 1890: 277; Roewer, 1942: 224.
Rhianodes atratus: Raven, 1994: 697; Platnick, 1998: 143.
Idioctis sierramadrensis Barrion & Litsinger, 1995: 25;
Platnick, 1998: 137. (New synonymy)

MATERIAL. HOLOTYPE: ♂, Philippines, Quezon Prov., Real, Llavac Vill., R. Apostol, 16 Jan 1985; in International Rice Research Institute, Philippines.

REMARKS. Barrion & Litsinger (1995) described a new *Idioctis* based on a male and juvenile female from slash and burn upland rice fields in the Philippines on Luzon Island. However, *Idioctis* is an intertidal spider (Raven, 1988, Churchill & Raven, 1992, Raven, 1994) known rarely far from the littoral zone. The diagnosis of *Idioctis* given by Barrion & Litsinger (1995) is a slightly changed version of that given by Raven

(1988: 2) and its descriptive statement is also essentially that of Raven (1988). The figures of *Idioctis sierramadrensis* are of sufficient detail to clarify its true identity. The species is clearly not referable to *Idioctis*. The eye group is too deep, the sternum is 'as long as wide' not about 1.5 times wider than long, the shape of the carapace is ovoid, not elongate, and the abdomen is dark with patterning. All of these are the characters of the monotypic *Rhianodes* into which genus the species is here transferred.

The long spines overhanging the chelicerae are mentioned by Raven (1994) in *R. atratus*, and the palp and diagnostic first leg of the male of *Idioctis sierramadrensis* do not show differences from that of *R. atratus*. Hence, I am transferring the species into the synonymy of *R. atratus*.

DISTRIBUTION. Singapore, Malaysia, Philippines. Raven (1994) incorrectly listed Maxwell's Hill in Singapore; it is in Malaysia. This is the first report of the species from the Philippines.

Trittame bancrofti (Rainbow & Pulleine, 1918), comb. nov.
(Fig. 1)

Aganippe bancrofti Rainbow & Pulleine, 1918: 95; Main, 1985: 14.

MATERIAL. LECTOTYPE: (designated Main, 1985: 14), AMKS 6151, Eidsvold, SE Qld; ♀, paralectotype, same data; KS6152, ♀ paralectotype, *Aname distincta* (Rainbow, 1914, det. RJR).

DIAGNOSIS. Females share with those of *T. gracilis* the presence of thorn spines (3-4 strong) on patellae III and well developed posterior median spinnerets but differ in that the chelicerae lack a rastellum, the ALE are clearly more than their diameter apart and the PME are large.

REMARKS. This transfer also removes the secondary homonymy with *Aganippe bancrofti* identified by Main, 1985. Raven (1990, 1994) failed to deal with this species listed by Main (1985) as incertae sedis in the Barychelidae. The lectotype has dense claw tufts, numerous maxillary cuspules, no labial cuspules and short PLS and is clearly *Trittame*. Rainbow & Pulleine's type series also includes a female *Aname distincta* which, by default, also is a paralectotype.

This increases the already high beta diversity of *Trittame* in southeast Queensland. Although some in the area are known only from one sex, there is no doubt that the species is distinct from others in the region. The thorn spines on the patella were found by Raven (1990) to be present in both males and females of *T. gracilis*. Hence, *T. bancrofti* females are not conspecific from the geographically close but allopatric *T. mccoilli* Raven, 1995 or *T. stonieri* Raven 1995.

THERAPHOSIDAE

Phlogiellus Pocock, 1897.

Phlogiellus Pocock, 1897: 595; Raven, 1985b: 118.
Baccallbrapo Barrion & Litsinger, 1995: 21; Platnick, 1998: 153. Type species, *Baccallbrapo bundokalbo* Barrion & Litsinger, 1995.

MATERIAL. HOLOTYPE: *Baccallbrapo bundokalbo*, ♂, Philippines, Laguna Prov, Siniloan, Magsaysay Vill., 16 Jan 1985, A, Barrion, M. Perez. **PARATYPES:** Subadult ♀'s, Philippines, Quezon Prov., Real, Llavac Vill., R. Apostol, 16 Jan 1985. All in International Rice Research Institute, Philippines. (New synonymy)

HABITAT DISTRIBUTION. Rainforests in Southeast Asia, islands of the northwest Pacific, and in northern Australia.

REMARKS. None of the characters (marginal differences on scopula density on tarsi) used by Barrion & Litsinger (1995) to distinguish

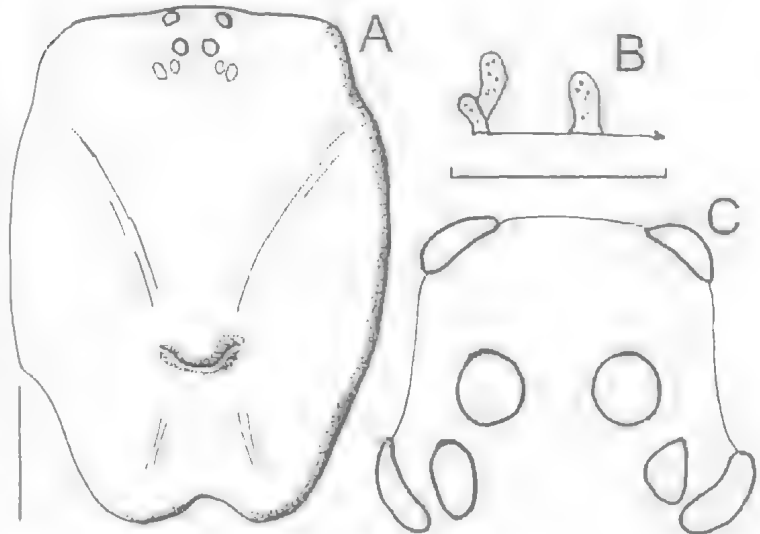


FIG. 1. *Trittame bancrofti* (Rainbow & Pulleine, 1918), lectotype female, AMKS6152. A, carapace; B, spermathecae; C, eyes. Scale bars = 1mm.

Baccallbrapo alone are adequate to support the recognition of a new genus and the variability falls adequately within the known generic variation. The types have a third claw and cracked tarsus IV, both characters of *Phlogiellus* (see Raven, 1985b), *P. bundokalbo* is unusual in having tarsi III and IV cracked.

Many references to *Selenocosmia* in the rainforests of north Queensland should mostly likely be referred to *Phlogiellus*. Queensland Museum records (determined by RJR) include many *Phlogiellus* from that region.

Selenocosmia Ausserer, 1871

Selenocosmia Ausserer, 1871: 204. Type species by monotypy *Ahygale javanensis* Walckenaer, 1837. Type presumed lost.
Phricetus Koch, 1874: 488. type species by monotypy, *Phricetus crassipes* Koch, 1874. Type in ZMH, examined.
Phlogius Simon, 1887: excv. replacement name for *Phricetus* Koch, 1874 preoccupied by *Phricetus* Spinola, 1839 in the Hemiptera; Schmidt, 1995: 10. Replaced into synonymy.
Psophopveus Thorell, 1897: 175. type species by subsequent designation of Bonnet (1958: 3825), *Phricetus validus* Thorell, 1881. First synonymised by Simon, 1903: 995.
Chilocosmia Schmidt & von Wirth, 1992: 9. Type species by original designation *Chilocosmia dichromata* Schmidt & von Wirth, 1992. (New synonymy)
Selenopelma Schmidt & Krause, 1995: 22. Type species *Selenopelma kovariki* Schmidt & Krause, 1995. (New synonymy)

REMARKS. Schmidt (1995) removed the Australian *Selenocosmia crassipes* (Koch, 1873) and *Selenocosmia stirlingi* Hogg, 1901 and transferred them to the restored genus name *Phlogius* Simon, 1887. The removal from

Selenocosmia was based upon differences from a putative paratype of *Selenocosmia javanensis* (Walckenaer, 1837), the type species of *Selenocosmia* Ausserer, 1871. Indeed, the type species needs to be studied, the species variability documented, the types found, and other species may then be understood and their relationship with the type species and differences from it understood. None of that has been done in the above three papers written or coauthored by Schmidt.

The type material of *Selenocosmia javanensis* (Walckenaer, 1837) has not been examined or even located. Schmidt claims to have examined a 'paratype' of *Selenocosmia javanensis* in the Museum of Wiesbaden but Jäger (1998) found no such material. Type material of other species of Walckenaer has been found in the Musée National d'Histoire Naturelle, Paris but Heurtault (1980) lists only BMNH with Walckenaer types. In any case, since Walckenaer did not designate a holotype, paratypes do not exist either. Hence, Schmidt was in error and did not see a paratype of *Selenocosmia javanensis* (Walckenaer, 1837).

I have examined the specimen considered the paratype of *Selenocosmia javanensis* (Walckenaer, 1837). It has two labels; one is a Museum Wiesbaden label with faded ink inscription, the other is a more legible pencil label. The information on both is the same:

Museum no. 637
'*Selenocosmia javanensis* Walck.
Java Krakau
G: Prof. Kulczynski 1900'

Type material of Walckenaer should be labelled with the original name, '*Mygale javanensis*'. The name *Selenocosmia* was first used by Ausserer (1871). Hence, the label reflects nothing but the locality and a subsequent identification. Walckenaer (1837) gave no further data than 'Java'. Hence, the specimen was not labelled by Walckenaer, cannot be considered a type of any kind and has no nomenclatural status.

Other material studied included an exuvium from a zoo specimen, a specimen (former pet?) identified by Weichmann (outside of a published revision).

The type specimen of *Phlogius crassipes* Koch, 1874 was examined as were other material (former illegally exported pets) identified by Charpentier (also informally and outside of a revision).

No type material of *Selenocosmia stirlingi* Hogg, 1901 was examined by Schmidt but material so labelled in the South Australian Museum was, as well as some other *Selenocosmia* species.

Schmidt (1995) lists a number of differences in the material mentioned. No variational study supports the species significance of those differences. More importantly, Schmidt does not explain how other species of *Selenocosmia* belong to a different monophyletic group from those he places in *Phlogius*.

Differences in characters previously used, e.g. relative leg length and diameter, are not thoroughly examined. Indeed, in that character alone, *Selenocosmia crassipes* is more similar to *Selenocosmia javanensis* than with *Selenocosmia stirlingi*.

Also, Schmidt (1995) lists the distribution of *Selenocosmia crassipes* as Australia and New Guinea and so perpetuates an error from Roewer (1945), repeated without critical review by Smith (1992; Smith, in litt.). The type locality is Rockhampton, central coastal Queensland and the species is centred on that area (Queensland Museum Records, Raven, unpublished data).

No support is given in Schmidt (1995) for the restoration of *Phlogius* or in Schmidt & von Wirth (1992) and Schmidt & Krause (1995) for the new genera *Chilocosmia* and *Selenopelma*, respectively.

Because the somatic and sexual morphology of mygalomorphs are so conservative it is very difficult to establish sound specific and sometimes even generic boundaries. Theraphosid systematic studies in the past 20 years, in reflecting this difficulty, have mostly been characterised by the descriptions of new species and genera, outside of revisions. The result has been that many new species and some genera have been described in isolation without sound reference to other species in the genus. Raven (1985b) synonymised genera in which no differences of generic significance existed among the type species. However, the elevation of new genera, or resurrection of synonymised genera, has occurred for a similar but reciprocal reason: that a species differs (extent and status unspecified) from the type species. Schmidt (1995) and other works of Schmidt (Schmidt & von Wirth, 1992; Schmidt & Krause, 1995) fail on such grounds.

NEMESIIDAE

Chenistonia Hogg, 1901

Chenistonia Hogg, 1901: 262. Type species by original designation. *Chenistoma maculata* Hogg, 1901.

DIAGNOSIS. *Chenistonia* differs from *Aname* by males having a medial spur and megaspine on tibia I, a long slender palpal tarsus, a pear-shaped palpal bulb with the embolus very short or absent, and by both sexes having small marginal sternal sigilla. *Chenistonia* shares with *Namea* and *Teyl* the elongate palpal tarsus in males but differs from *Namea* in lacking the reflexed embolus and further from *Aname* in that in males the basal process on metatarsus I opposite the tibial spur is either very small or absent. *C. trevallynia* breaches that concept in having the plesiomorphically short male palpal tarsus.

REMARKS. Raven (1985b) maintained *Chenistonia* in the synonymy of *Aname*, following Raven (1981). However, Main (1986, without explanation) has maintained their respective validity. Phylogenetically, *Chenistonia* is here confined only to the *Aname maculata* group of Raven (1984).

Main (1982a, 1986) continued to place *Aname tepperi* in *Chenistonia*. However, it has a long embolus. Hence, the inclusion of *A. tepperi* in *Chenistonia* makes the group concept polythetic. The only illustration of the male of *A. tepperi* is in Main (1964) and since then there has been no phylogenetic analysis of the species nominally included by Main (1985) in *Chenistonia* save for Raven (1984, 1985a, b).

The following species are explicitly included in *Chenistonia* and *Aname*, respectively.

Species included in *Chenistonia*:

- Aname caeruleomontana* Raven, 1984, NSW
- Aname hickmani* Raven, 1984, NSW
- Chenistonia maculata* Hogg, 1901, VIC
- Aname montana* Raven, 1984, NSW
- Chenistonia trevallynia* Hickman, 1926, Tas.

Species included in *Aname*:

- A. armigera* Rainbow & Pulleine, 1918, WA
- A. ara* (Strand, 1913), SA, NT
- A. amei* Rainbow & Pulleine, 1918, NSW
- A. barrera* Raven, 1985, Qld, NSW
- A. blackdownensis* Raven, 1985, Qld
- A. coenosa* Rainbow & Pulleine, 1918, SA
- A. cantara* Raven, 1985, Qld
- A. carlina* Raven, 1985, Qld
- A. collinsorum* Raven, 1985, Qld
- A. cuspidata* (Main, 1954), WA
- A. distincta* (Rainbow, 1918), Qld
- A. diversicolor* (Hogg, 1902), Qld, SA

- A. fuscocincta* Rainbow & Pulleine, 1918, WA
- A. grandis* Rainbow & Pulleine, 1918, SA
- A. humptydoo* Raven, 1985, NT
- A. inimica* Raven, 1985, NSW, Qld
- A. kirrama* Raven, 1984, Qld
- A. longithecra* Raven, 1985, Qld
- A. maculata* (Rainbow & Pulleine, 1918), WA
- A. pallida* Koch, 1873, Qld
- A. robertsorum* Raven, 1985, Qld
- A. robusta* Rainbow & Pulleine, 1918, SA
- A. tasmanica* Hogg, 1902, Tas
- A. tepperi* (Hogg, 1902), WA, SA
- A. tigrina* Raven, 1985, Qld
- A. tropica* Raven, 1984, Qld
- A. narrigera* Main, 1994, SA, WA
- A. villosa* (Rainbow & Pulleine, 1918), WA
- A. wariakda* Raven, 1985, NSW, Qld

Aname diversicolor (Hogg, 1902)

(for full synonymy see Raven, 1985a)

DISTRIBUTION. Deka Station, near Blackall, western Queensland.

REMARKS. Raven (1985a) gave ample reasons that the neotype designation of *Dekana diversicolor* Hogg, 1902 by Main (1982b) was invalid. Apart from anything else, in Main (1982b) making such a designation outside of and before a revision, it was not possible to assert that the identity of species could not be established from Hogg's (1902) figures. Indeed, in his revision, Raven (1985a) found Hogg's figures were perfectly adequate to recognise the species. Also, comparison of the morphology of other species described by Hogg with his own figures indicates that his figures were accurate. Main (1982b) also placed *Aname atra* (Strand, 1913) into the synonymy of *A. diversicolor* but Raven (1985a) found that the two species were readily distinguishable. To accept Main's (1982b) neotype designation requires that Hogg's figures showed significant differences in relative sizes and shapes from the original. Main (1982b:29) stated that the [neotype designation] was 'in the interests of nomenclatural stability for a common and widespread species which frequently attracts human attention and to which references have already been made in medical literature.' However, Southcott (1976, 1978) writing from South Australia did not mention it and at that time I can find only Main (1976) making comments about bites of *Dekana diversicolor*.

Subsequently, Harvey & Main (1996) found that indeed Deka Station, Queensland was the correct interpretation of the type locality of *Dekana diversicolor*. The neotype designated by

Main (1982b) is hence here considered the holotype of a new species, *Aname mainae*.

***Aname mainae* sp. nov.**

Aname diversicolor, Main, 1982b: 29.

MATERIAL. HOLOTYPE (= 'neotype'): SAM N1980196, ♂, 26km NW of Elliston, SA, 20 Dec 1952, B.Y. Main; SAM N1980195, ♀, same data, examined.

DIAGNOSIS. Males differ from those of *Aname diversicolor* (Hogg, 1902) in having a centrally placed, not clearly distal, tibial spur and the embolic shaft being straight not bent (see Raven, 1985a: 396, 397).

DISTRIBUTION. South Australia.

DIPLURIDAE

***Masteria* L. Koch, 1873**

- Masteria* L. Koch, 1873: 458. Type species by monotypy, *Masteria hirsuta* L. Koch, 1873.
Accola Simon, 1889: 191. Type species by subsequent designation of Simon (1892), *Accola lucifuga* Simon, 1889. First synonymised by Raven, 1979.
Antrochares Rainbow, 1898: 332. Type species by monotypy, *Antrochares macgregori* Rainbow, 1898. First synonymised by Raven, 1979.
Microsteria Wunderlich, 1988: 46. Type species by monotypy, *Microsteria sexoculata* Wunderlich, 1988. (New synonymy)

***Masteria sexoculata* (Wunderlich), comb. nov.**

Microsteria sexoculata Wunderlich, 1988: 47: holotype male examined.

REMARKS. Wunderlich (1988) raised *Microsteria* on the grounds that the teeth on the third claw are sessile and not tuberculate or not on a common process as in other other masteriine genera (*Masteria* Koch, 1873, *Striamea* Raven, 1981). Raven (1981) showed that in existing masteriine, the teeth basally fuse before reaching the claw. I examined the holotype of *Microsteria sexoculata* (sent to me for identification prior to Wunderlich's paper). Two teeth are present on the third claw. The anterior tooth is shorter and the division between the two teeth deep. It was not possible to determine the very subtle difference between a low anterior tooth on the claw and a common tubercle. I concluded it was *Masteria* and still do, so the genus is placed in synonymy.

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SOUTHERN RIGHT WHALES *EUBALAENA AUSTRALIS* (DESMOULINS, 1822) IN MORETON BAY, QUEENSLAND. *Memoirs of the Queensland Museum* 45(2): 576. 2000:- Southern right whales, *Eubalaena australis*, occur primarily between latitudes 30°S and 60°S, with annual winter migrations from higher latitude summer feeding grounds to lower latitude breeding areas (Best et al. 1993). In Australian waters, the Great Australian Bight is a major calving area (Burnell & Bryden 1997). However, sightings occur further north along the east and west coasts (Bannister 1986). The most northerly was at Flinders Reef (26°59'S, 153°29'E) in August 1998. This and other sightings in 1998 were the first published record of *E. australis* in Queensland waters (Noad 2000).

This note records 1999 sightings of *E. australis* in Moreton Bay. At 15:10 on 2 August 1999, two *E. australis* were seen at 27°17'S, 153°18'E, between Mud Island and Shark Spit on Moreton Island (Fig. 1A). Observations were made from a vessel conducting dolphin research. The pair was observed for 45 minutes, while travelling slowly south. The larger and darker whale breached 5-6 times (Fig. 1B,C). The other was smaller and distinctly brown with dark mottles (Fig. 1D). It did not breach.

Other sightings of *E. australis* in Moreton Bay preceded this record. On 22 July two were observed breaching and travelling north out of Moreton Bay from Tangalooma jetty and on 30 July two were sighted travelling south into the Bay (27°10'S, 153°20'E) (S.J. Allen pers. comm.). On 27 July a whale-watch vessel encountered a single *E. australis* near Bribie I. (27°03'S, 153°14'E; K. McTaggart pers. comm.).

E. australis populations are currently increasing after near extirpation over the past 200 years (Bannister 1986, Tormosov et al. 1998). The full extent of their pre-whaling range is unknown. Best (1993) suggested that when mysticete populations are reduced, their ranges contract and conversely, as they recover, their ranges may expand. Peripheral areas such as southern Queensland waters, which may have been frequented previously, appear to be re-inhabited seasonally. Noad

(2000) suggested that visits to Queensland waters may become more common as recovery occurs. These records and the 1998 sightings, demonstrating the occurrence of *E. australis* in SE Queensland waters in consecutive years, supports Noad's prediction.

Acknowledgments

Thanks to Grant Sherwin, the skipper of the research vessel 'Resolute' for sighting information, and Robert Paterson for encouraging production of this note. Thanks also to Micheal Noad, Simon Allen and Kerry McTaggart for additional information and Peter Corkeron for useful comments on the manuscript. Funding from the Earthwatch Institute led to this opportunity.

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B.L. Chilvers, School of Tropical Environmental Studies and Geography, James Cook University, Townsville 4811, Australia; 29 October 1999.

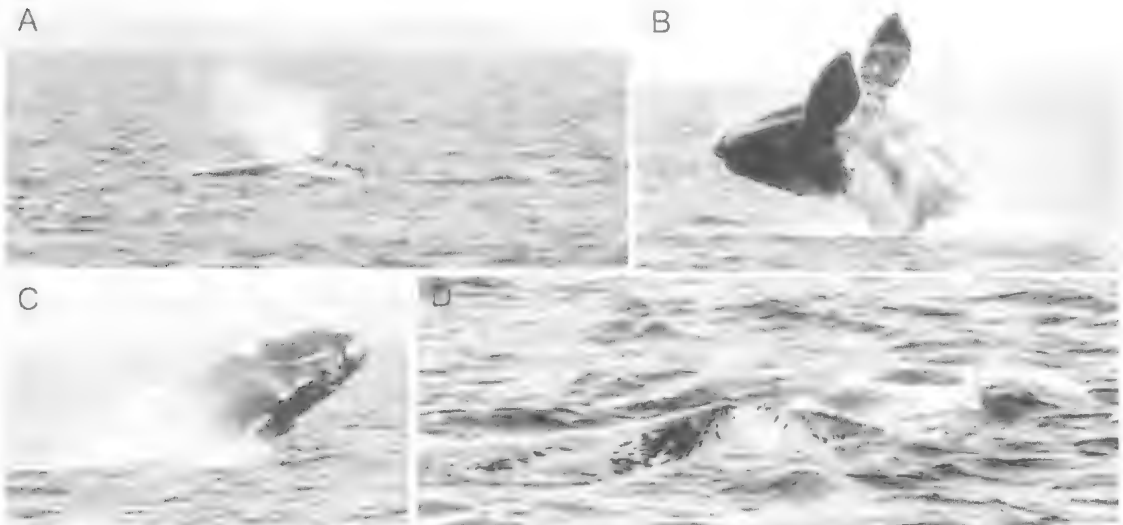


FIG. 1. A, two *Eubalaena australis* in Moreton Bay (2 August 1999); B, C, breaching demonstrates characteristic pectoral fins and rostral callosities; D, dorsum of lighter, brown animal with mottled pattern.

REVISED STATUS OF THE GENUS *HETAERICA* RAINBOW (ARANEAE:
ZODARIIDAE)

ROBERT J. RAVEN AND BARBARA C. BAEHR

Raven, R.J. & Baehr, B.C. 2000 06 30: Revised status of the genus *Hetaerica* Rainbow (Araneae: Zodariidae). *Memoirs of the Queensland Museum* 45(2): 577-583. Brisbane. ISSN 0079-8835.

Adult male and female material of *Hetaerica aresca* Rainbow, 1916 from the type locality, Pentlands, NE Queensland, is described and found to be conspecific with the type species of *Australorena* Jocqué, 1995, previously described as *Habronestes scenicus* Koch, 1872. The new combination, *Hetaerica scenica* (Koch, 1872), is established and the male palp and female epigyne are redescribed. A new species *H. harveyi* is described from Western Australia. □ *Taxonomy, Zodariidae, Hetaerica, envenomation, Australia.*

Robert John Raven & Barbara C. Baehr, *Queensland Museum, PO Box 3300, South Brisbane 4101, Australia; 21 July 1999.*

Rainbow (1916) described a new zodariid genus, *Hetaerica*, from Pentlands, north Queensland. The type material of the type species, *Hetaerica aresca* Rainbow, 1916, was juvenile, hence Jocqué (1991, 1995) was unable to resolve its affinities. No further collections had since been made from the type locality. However, Jocqué (1995) did note, in his description of the new genus *Australorena*, that 'The type species of this new genus has several somatic features in common with *Hetaerica aresca*, the only species of *Hetaerica*, known only from a juvenile specimen'. On three occasions, one author (RJR) attempted to collect adult material from Pentlands and was only successful on the final attempt. That material is here described and is unequivocally conspecific with that of *Australorena scenica* (Koch, 1872), revised by Jocqué (1995).

SYSTEMATICS

***Hetaerica* Rainbow, 1916**

Hetaerica Rainbow, 1916: 48. Type species by monotypy, *Hetaerica aresca* Rainbow, 1916.

Australorena Jocqué, 1995: 126. Type species by original designation *Habronestes scenicus* Koch, 1872. (New synonymy)

DIAGNOSIS. As for *Australorena* Jocqué, 1995 plus the apical conductor is a folded, sclerotised cone.

DESCRIPTION (supplementary to Jocqué, 1995). 10-11 teeth on paired claws; teeth long and set on inner edge distally (Fig. 5C). Unpaired claw long, straight. Tarsal organ set centrodorsally on distal edge of tarsus cuticle. Tarsal cuticle smooth save for light irregularly placed fine grooves. Tarsus predistally intact. Bothrial

cup collariform; trichae long and smooth for basal half becoming finely fimbriate distally; trichobothria present on mesal setose process of tibial apophysis. Tibial apophysis tripartite with distal bifurcate lobe, mesal hirsute extension of tibia and asetose basal prong. Female epigyne with unsclerotised zones laterally.

SPECIES INCLUDED. *Hetaerica scenica* (Koch, 1872); *Hetaerica harveyi* sp. nov.

REMARKS. We note that the palp of *Hetaerica* and an undescribed species of *Chilumena* are similar in the male, but that the latter has a distinct sclerotised, hooked tegular apophysis (?median apophysis) and lacks the prolateral cymbial groove and associated flange. *Hetaerica* has a rough carapace cuticle but in *Chilumena* the surface is deeply rugose or corrugated and this remains the most distinct feature of the genus (Jocqué, 1995). Because of these similarities we regard the two as sister genera and await the description of further species of both to determine whether the cuticular difference is sound.

The tibial apophysis of *Hetaerica* presents an unusual character not before noted. The mesal lobe has at least two trichobothria apically on it (Fig. 2B) and is strictly speaking only an extension of the tibia; tibial apophyses do not usually have trichobothria in spiders. This raises a question about homologising the lobes of the retrolateral tibial apophysis (RTA).

***Hetaerica scenica* (Koch, 1872), comb. nov.**
(Figs 1-4)

Habronestes scenicus Koch, 1872: 301, 316.

Storena scenica Simon, 1893: 427; Rainbow, 1911: 151; Davies, 1985: 121.

Hetaerica aresca Rainbow, 1916: 48, figs 21-23; Jocqué, 1991: 59, figs. 113-116. (New synonymy)

MATERIAL. *Hetaerica aresca*: Holotype: AMKS6744, juv., Pentlands, NE Qld, A Girault; QMS42917, ♂, ♀, Pentlands, 20°26'S 145°32'E, NE Qld, 9 Mar 1999, B. Baehr, R. Raven; QMS4354, ♂, ♀, Bluff Downs, 60m NW Charters Towers, 19°40'S 145°32'E, NE Qld, 19 Apr 1974, M. Archer, A. Elliot; QMS22751, ♂, 2♀, Cape Cleveland Rd, 19°20'S 147°00'E, ME Qld, pitfall, 25 Oct 1991-27 Jul 1992, R. Raven, P. Lawless, M. Shaw; QMS22752, ♂, same data; QMS22915, ♂, 3 juv., Eight Mile Ck, 18°40'S 144°42'E, NE Qld, dry eucalypt forest, pitfall, 1 Dec 1992-14 Apr 1993, R., J. & S. Raven, P. & E. Lawless; QMS4487, 7♂, 3♀, 5 juv., Forty Mile Scrub, 18°04'S 144°50'E, NE Qld, vine thicket, 10-14 Apr 1978, V. Davies, R. Raven; QMS25711, 3♂, 4 juv., same locality, 1 Dec 1992-15 Apr 1993, P. Lawless, M. Shaw, R., J. & S. Raven; QMS41772, ♂, 1 juv., Fraser I, Orchid Beach (F04), 24°57'S 153°18'E, SE Qld, heathland, pitfall, 20 Aug 1997-17 Dec 1997, R. Raven, P. Lawless; QMS3681, 3♂, 1 juv., Homevale, 21°23'S 148°33'E, ME Qld, sclerophyll by creek, 6 Apr 1975, R. Kohout; QMS19703, ♂, Karalee, 27°34'S 152°49'E, SE Qld, spider bite, 10 Mar 1993, A.J. Tuskes; QMS37730, ♀, Keysland, 26°12'S 151°44'E, SE Qld, open forest, pitfall, 29 Sep 1994-15 Dec 1994, G. Monteith; QMS27987, ♂, Kinuna NP, 21 Apr 1992, M. Shaw; QMS15727, ♀, Lake Broadwater, Site 3, 27°20'S 151°05'E, SE Qld, pitfall, 3 Jan-25 Feb 1986, Qld Museum party & M. Bennie; QMS15735, 5♂, 5♀, Lake Broadwater, Site 8, 27°20'S 151°05'E, SE Qld, pitfall, 25 Feb-22 Apr 1986, Qld Museum party & M. Bennie; QMS26162, ♂, Magnetic I, 19°07'S 146°50'E, NE Qld, spider bite, 9 Mar 1995, per Sr. Deborah Larter; QMS30720: ♂, Mulgowie, Laidley Valley, 27°44'S 152°22'E, SE Qld, eucalypt woodland, pitfall, 21 Jan-1 Feb 1981, M. Grant; QMS30722, ♂, Rochedale SF, 27°37'S 153°08'E, SE Qld, pitfall, 20 Dec 1979-17 Jan 1980, V. Davies, R. Raven; QMS30721, 2♂, same locality, 24 Apr-12 Jun 1980, V. Davies, R. Raven; QMS21911, ♂, S. Rifle Range Rd, N. Ellis Beach (N Qld 14), 16°40'S 145°34'E, NE Qld, pitfall, 1 Nov 1991-22 Jul 1992, P. Lawless, R. Raven, M. Shaw; QMS41920, ♂, p♂, Saunders Beach, 19°10'S 146°36'E, NE Qld, open forest, pitfall, 04-12 Feb 1998, G. Monteith, D. Cook; QMS27500, 2♀, South Percy I, NW Bay, 21°45'S 150°17'E, ME Qld, intercept flight trap, 26 Nov 1992-mid Apr 93, G. Monteith, G. Thompson, D. Cook, H. Janetzki; QMS24503, ♂, Tooloombah Ck, (NQ 41), 22°42'S 149°33'E, ME Qld, eucalypt woodland, pitfall, 29 Jul 1992-24 Nov 1992, R. Raven, P. & E. Lawless, M. Shaw; QMS24081, ♂, same locality, pitfall, 10 Nov 1991-29 Jul 1992, R. Raven, P. Lawless, M. Shaw.

DIAGNOSIS. This species is recognised by the divided chilum, the long fang of the chelicerae, the promargin with one small tooth, the abdominal pattern with elongate dorsal scutum, two elongate pale patches on anterior half and one in front of the spinnerets, the palpal structure. Only one tegular apophysis (DTA) = suprategular apophysis (Jocqué 1991), is the conductor of the embolus, directed in embolus direction. The palp



FIG. 1. *Hetaerica scenica* (Koch), male, habitus, dorsal view.

of *H. scenica* differs from that of *H. harveyi* sp. nov. in the acute tegular process.

DESCRIPTION. *Male.* NT (QMS42917): Measurements (mm). Total length 6.1. Cephalothorax 3.3 long, 2.26 wide. Abdomen 2.8 long, 1.8 wide. Sternum 1.46 long, 1.13 wide. Legs I 7.8, II 6.93, III 6.8, IV 9.3. Eye sizes and distances between them: AME 0.1, ALE 0.16, PME 0.16, PLE 0.18, AME-AME 0.03, AME-ALE 0.05, PME-PME 0.06, PME-PLE 0.13, ALE-PLE 0.01; median ocular quadrangle 0.38 long, 0.23 wide at front, 0.36 wide at back. Clypeus 0.43 high. Chilum 2×0.41 long. Chelicera fang 0.91 long.

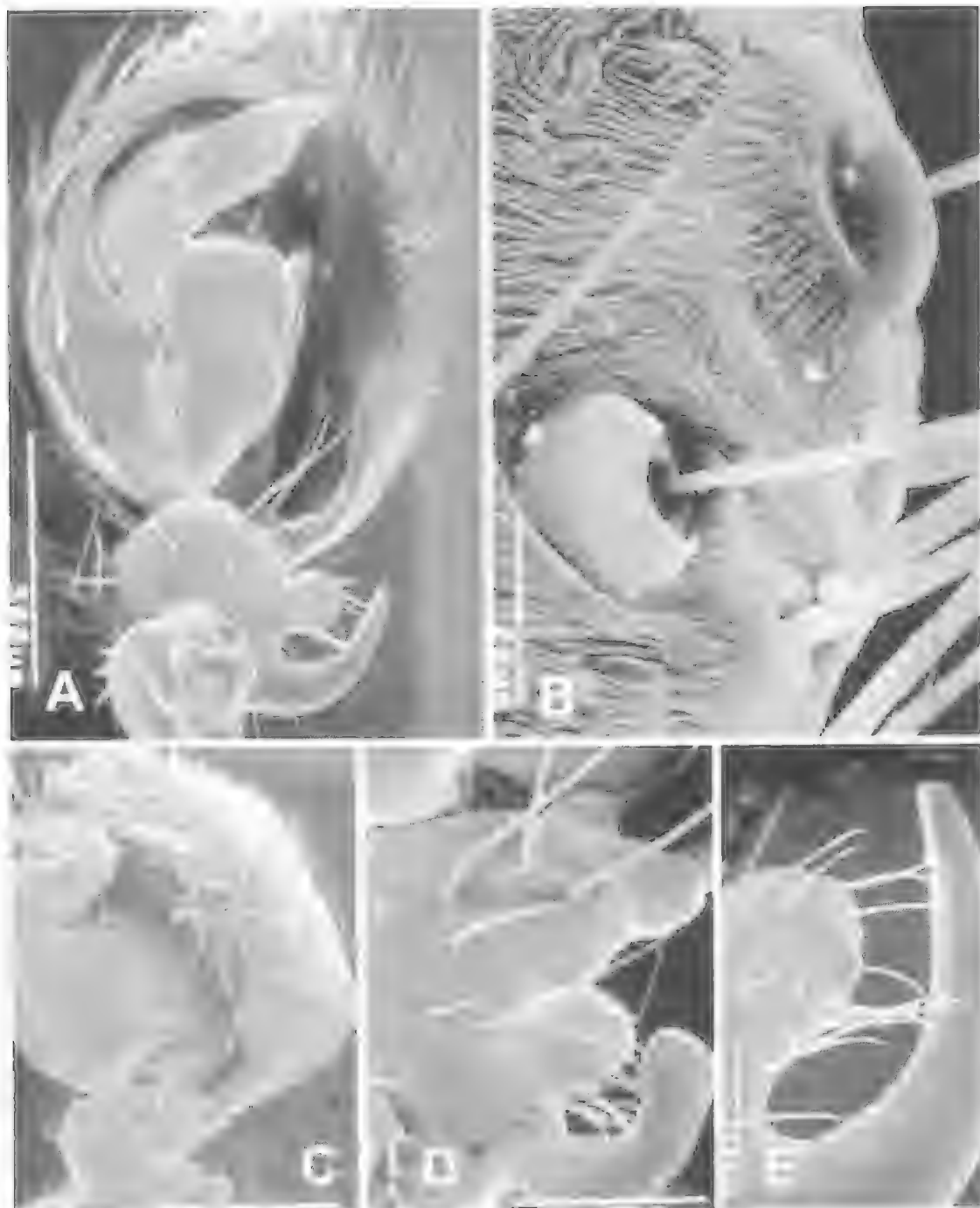


FIG. 2. *Hetaerica scenica* (Koch), male pedipalp, tibia, cymbium and bulb, dorsal left, scanning electron micrograph. A, ventral view; B, trichobothria on tibial apophysis; C, lateral view showing paracymbial flange and tibial apophysis; D, tibial apophysis, retroventral, and E, ventral view.

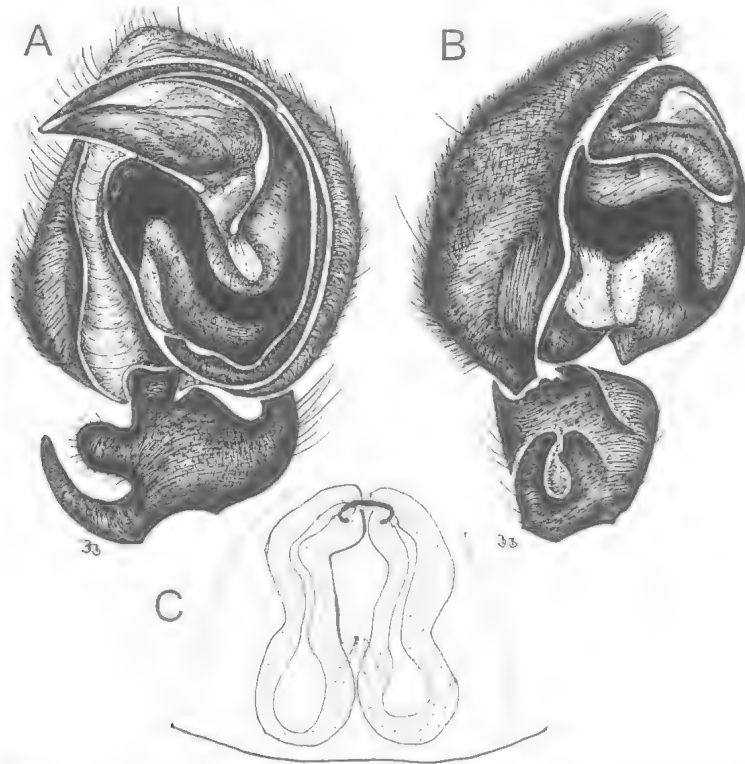


FIG. 3. *Hetaerica scenica* (Koch). A, B, male pedipalp, tibia, cymbium and bulb, dorsal right, A, ventral view, B, retrolateral view. C, female, external epigyne, cleared showing spermathecae.

Colour and Structure. Cephalothorax, granulated, dark brown, with rebordered margins. Chelicerae short, dark brown, promargin with single small tooth. Maxillae brown, anteromesally pale, strongly tapering, curved inward, with small anteromesal scopula. Sternum reddish brown, basically triangular, with rounded sides; provided with triangular 8 extensions, each side, corresponding with coxal concavities, pointed behind. Abdomen dark brown with 2 elongate pale spots on anterior half, reddish brown scutum in between, one pale spot in front of the spinnerets. Spinnerets dark brown; venter dark brown with 3 elongate pale spots, booklung covers and epigastric area with weak reddish brown scutum. Legs: all legs dark brown, tarsi slightly paler. Palp: tibia with one elongate ventral rounded dorsal apophysis and two apophyses in front. Cymbium as wide as long, retrolaterally widened, with short flange and shallow concavity. Bulb with one retrolateral directed enrolled distal tegular apophysis, functioning as conductor in same direction as the embolus and one tiny lateral tegular spine.

DESCRIPTION. *Female.* Carapace brown, legs green brown; abdomen dorsally dark brown with pair of irregular clear zones showing white gut, zones anteriorly narrow reniform narrowing posteriorly and widening to two large spots centrally; a pallid spot above spinnerets, ventrally brown with three short longitudinal bands. Sternum redbrown.

Carapace. With uniformly distributed pallid setal bases bearing short, fine black setae; cuticle lightly coriaceous. Fovea very short, deep.

Eyes. PLE on low mounds.

Chelicerae. Small, coniform with short triangular fang about twice as long as width of base; lobe anterior to fang with ca. 8 long curved black setae.

Maxillae. Roughly coniform, tapering ectally from base to tip which has dense bush of black hair; covered basally and ectally with many short thorn-like and several long bristles; maxillae almost touch in front of labium; shallow crescentic depression entally.

Labium. Longer than wide, almost flat, converging from basal notches to narrow rounded tip.

Sternum. Widely cordate, with slight intercoxal point, distally rounded; margins slope quickly to flat broad central plateau. Uniform cover of fine and thick black bristles, all posteriorly directed.

Legs. For measurements see Table 1. Coxal bases with slightly produced extensions on III, IV. Trochanters convex and without notches. Coxae I

TABLE 1. Leg measurements of *Hetaerica harveyi*, holotype male.

	Leg 1	Leg 2	Leg 3	Leg 4	Palp
Femur	1.38	1.38	1.19	1.69	0.73
Patella	0.69	0.69	0.65	0.81	0.38
Tibia	1.08	0.92	0.73	1.23	0.31
Metatarsus	1.08	0.92	1.12	1.85	
Tarsus	0.85	0.85	1.23	1.23	0.81
Total	5.08	4.76	4.27	6.81	2.23



FIG. 4. Distribution map of *Hetaerica scenica* (Koch).

with uniform retroface. Leg cuticle smooth, shiny, without hair, only bristles and spines. Distoventral metatarsi III, IV with denser cluster of black bristles and preening combs of 4-6 bristles retrolaterally. Long erect bristles on tibia (2-3) and metatarsi (1), I, II.

Spines. I: fe p1d1, pa0, ti v.1.2.2w, me v.2.1.2.2.3, ta pv4rv6. II: fe p1d1, pa0, ti v.1.1.1w, me v2.2.2, ta pv5, rv4. III: fe p2d3r1, pa plr1, ti p2d1r2v2.2.2; me pl.1.2d2r1.1.2v2.2.2, ta pv6rv6. IV: fe p1d2r1, pa plr1, ti p2d2r2v2.2.2, me pl.1.2d2r1.1.2v1.1.1.3, ta pl pv7rv7. Palp: fe d2, pa pl, ti plv2w, ta p3v9.

Claws. Palpal claw directed diagonally across longitudinal plane, centrally dentate. Tarsus tapers to tip; c. 6-8 long teeth in slightly curved line down claw; paired claws long, curved with ca. 10 teeth in narrowly sinuous row; third claw distinct, edentate.

Trichobothria. Several short and 2-3 long trichae in two basal rows on tibiae; 2-3 long distally in irregular line on metatarsi; 5 on tarsi in straight line and lengthening distally.

Spinnerets. ALS long, cylindrical with domed apical segment; PMS short, wide; PLS more slender than PMS but slightly longer with apical dome.

Abdomen. Spiracle ridge short, roughly triangular hirsute patch = vestigial colulus.

Epigyne. Sclerotised zone along each side.

HABITAT & DISTRIBUTION. *H. scenica* occurs in open sclerophyll forest, heath and vine thickets in litter for much of eastern Queensland.

TOXICITY. Two bites from this species are reported from material listed: one produced only mild pain; the other happened under a tree (dropped) and a 2cm white area surrounded by 5cm red cellulitic area developed.

REMARKS. Jocqué (1995) noted the presence of an undescribed species from Lake Broadwater (no registration number given) which Jocqué (pers. comm.) notes subsequently is not congeneric with *Hetaerica* and is not conspecific with males and females he listed from that locality in the material of *Australorena scenica* (QM S15735).

Other material of *H. scenica* differs from that from Pentlands only in that the anterior lateral white bars on the dorsal abdomen are broken in the posterior third; the palps are indifferntiable.

Also, we report here, in males from Pentlands and elsewhere, the presence of a weak dorsal and epigastric scutum and that the conductor is apically rolled; neither were noted by Jocqué (1995).

***Hetaerica harveyi* sp. nov.**
(Fig. 5)

ETYMOLOGY. In honour of Dr Mark Harvey, friend and colleague.

MATERIAL. HOLOTYPE: ♂, WA; O'Neill Rd State Forest, site NR02, wet pitfalls 1-5; 35°02'27"S 117°10'17"E, 13 Oct 1997-14 May 1998, Paul van Heurck, CALM-WAM survey, WAM98/1675. PARATYPE: ♂, same data, WAM98/1676.

DIAGNOSIS. Differs from *H. scenica* in the triangular fold rather than spine-like process on the tegulum.

DESCRIPTION. Holotype male WAM98/1675: Carapace 2.57 long, 1.84 wide. Abdomen 2.23 long, 1.42 wide.

Colour. Carapace, chelicerae, sternum and maxillae as for *H. scenica*. Abdomen dark brown dorsally with two pairs of large ovoid white spots anteriorly, subcircular smaller pair centrally and semicircle posteriorly over spinnerets, ventrally with two white biconvex len-shaped spots around small white central spot. Dorsal scute narrow,

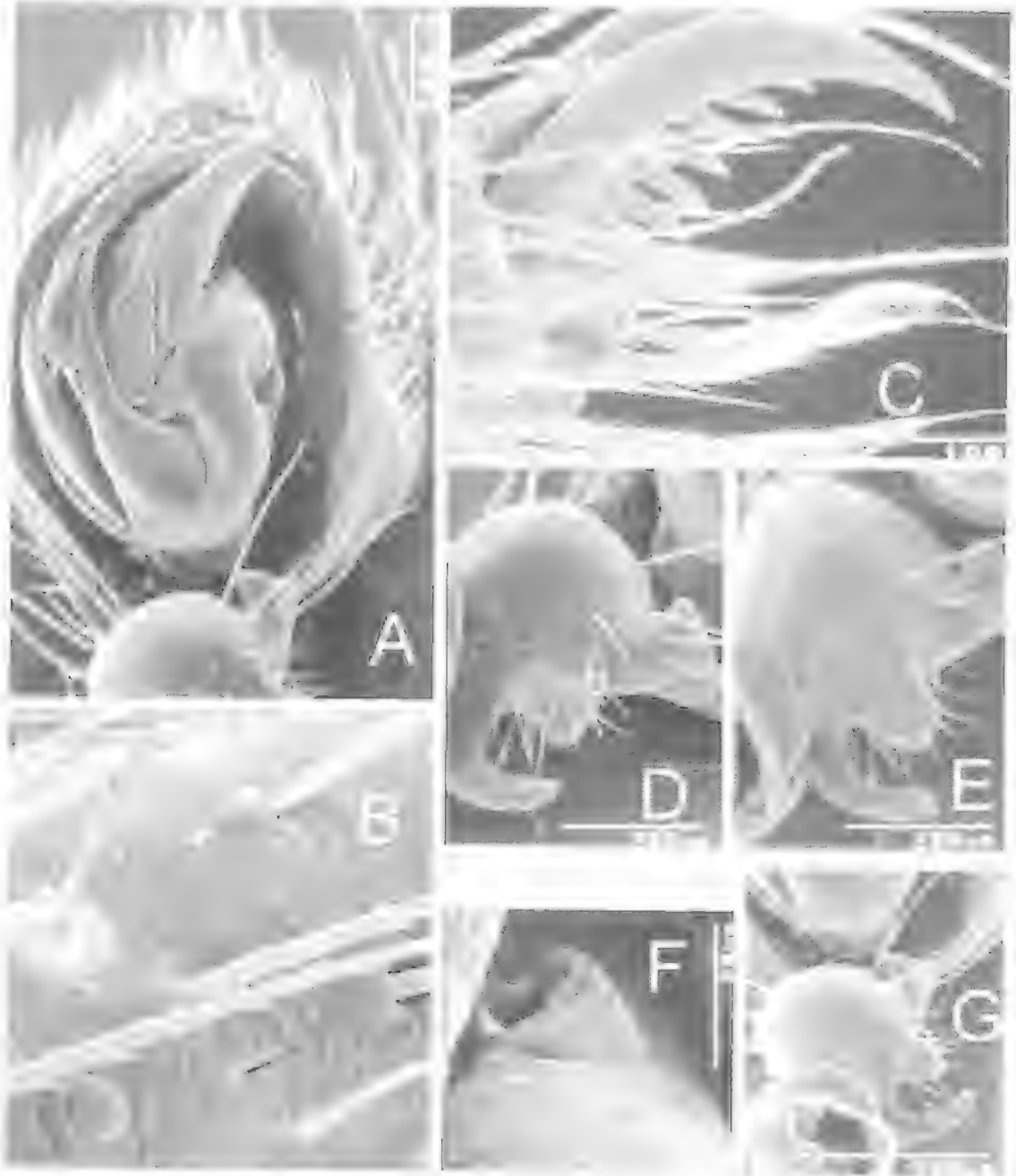


FIG. 5. *Hetaerica harveyi* sp. nov., holotype male. Pedipalp, tibia, cymbium & bulb, ventral right A, D-G. Scanning electron micrographs. A, ventral view. B, tarsal dorsal view showing trichobothria and other sensory structures. C, claws, lateral view. D, tibial apophysis, retroventral view. E, tibial apophysis, ventral view. F, tegular process, ventral view. G, tibial apophysis, ventral view.

thin but distinct for half length. Abdominal cuticle with iridescent sheen. Separate genital scute distinct. Legs dark brown with sheen, coxae and metatarsi and tarsi lighter. Spinnerets brown.

Eyes. AME:ALE:PME:PLE, 4:7:6:6.

Spines. I, II: fe-ti, 0; me I, v1.2.2.3, some are short blunt thorns but not consistent on left and right leg. II: tibiae with midventral line of 3 long curved spines; me v1.2.3. Tarsi I, II with no more than thick bristles. III: fe p1d3r1; pa plr1; ti p1d1r1v1.2.3; me p3d1r3v2.1.3; ta v2.2.2.2.2. IV: fe d2r1; pa plr1; ti p2d1r2v2.2.0; me p3d2r3v1.1.1.1.2.3; ta v2.2.2.2.2.

Palp. As for *H. scenica* but with spine-like process adjacent to the embolus tip.

Spinnerets. PLS are short (ca. 0.5 of ALS length) cylinders with noticeable gap to smaller PMS. PLS & PMS almost in line; colulus only a hirsute area of cuticle. Tracheal spiracle indistinct.

Female unknown.

DISTRIBUTION. Known only from southwestern Western Australia.

ACKNOWLEDGEMENTS

We are grateful to Mrs Helen Stark for Fig. 1. Travel funds from grants from DFG and

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A NEW CORAL-EATING BARNACLE: THE FIRST RECORD FROM THE GREAT BARRIER REEF, AUSTRALIA

ARNOLD ROSS AND WILLIAM A. NEWMAN

Ross, A. & Newman, W.A. 2000 06 30: A new coral-eating barnacle: the first record from the Great Barrier Reef, Australia. *Memoirs of the Queensland Museum* 45(2): 585-591. Brisbane. ISSN 0079-8835.

The Hoekiini Ross & Newman, 1995 includes four genera of coral-eating, pyrgomatid barnacles. They parasitise only the zooxanthellate, scleractinian coral *Hydnophora* Fischer, 1807, which occurs throughout most of the Indo-West Pacific. All of the known species have an irregularly shaped shell found nestled cryptically beneath the tissues between the hydroids of the coral. These barnacles are readily distinguished from the setose-feeding pyrgomatids not only by subsisting on the soft tissues of the host that cover the minute orifice, but also in apparently being absorptive parasites. Until now *Hydnophora* of the Great Barrier Reef was not known to be infested by these parasites. The few samples available not only harbour a far greater concentration of individuals than noted previously, but also display a distinctive morphology. These represent a new genus and species for which we propose *Australhoekia cardenae*. □ *Cirripedia*, *Pyrgomatidae*, *Hoekiini*, parasite. *Australhoekia cardenae* gen. nov., sp. nov., *Hydnophora* sp.

Arnold Ross & William A. Newman, Scripps Institution of Oceanography, La Jolla, California 92093-0202 USA: 30 July, 1999.

The term 'coral-eating barnacle' was proposed by Ross & Newman (1969) for a coral-inhabiting pyrgomatid first described by J.E. Gray in 1831 and presently known as *Hoekia monticulariae*. What contributed to the uniqueness of this and similar species in the Hoekiini Ross & Newman, 1995, which occur exclusively on the faviid *Hydnophora* Fischer, 1807, is the aberrant or vestigial cirri, highly modified mouth appendages, and a wall having no fixed outline that is best described as protean. In addition, the wall has a characteristic hypertrophied lateral margin which comes in broad and intimate contact with the soft tissues of the host coral. It is through the tissue covering this finely divided (deliquescent) margin that we believe the barnacle mediates its nutritional as well as physical relationship with the host. In some respects these bizarre barnacles tend to resemble or mimic the host corals upon which they live and feed (Ross & Newman, 1995).

We report herein that at least one species of coral found on the Great Barrier Reef (GBR) of Australia is subject to infestation by an unusual new genus of coral-eating barnacle, and also call attention to the likelihood there are other species of this or related genera to be discovered on corals of the GBR. Related genera and species are known to occur on other coral reefs, such as those of New Caledonia, Japan, Singapore, Indonesia, Mauritius, the Red Sea and elsewhere (Ross & Newman, 1973, 1995; Ross, in prep.).

What is surprising about the present species is not only its relatively large size coupled with an exceptionally minute orifice, but also in one sample, its high population density on relatively slender, round branches of *H. rigida* (Dana, 1846). In general, we have not had the opportunity to examine as many dried specimens as those before us. Because of their unique wall and opercular morphology we propose a new genus and species for them.

SYSTEMATICS

PYRGOMATIDAE Gray, 1825
PYRGOMATINAE Gray, 1825
HOEKIINI Ross & Newman, 1995

REMARKS. Ross & Newman (1995) proposed this tribe to include *Hoekia* Ross & Newman, 1973 (3 species), *Eohoekia* Ross & Newman, 1995 (2 species), *Parahoekia* Ross & Newman, 1995 (1 species) and *Ahoekia* Ross & Newman, 1995 (2 species) all of which have a wall that is irregular and protean in outline. The definitions of these genera and the new genus are based on the presence or absence of internal lacunae and the mode by which the barnacle's circulatory system accesses the circumferential channel and marginal fringe of the wall.

All measurements herein are in millimetres unless otherwise stated.

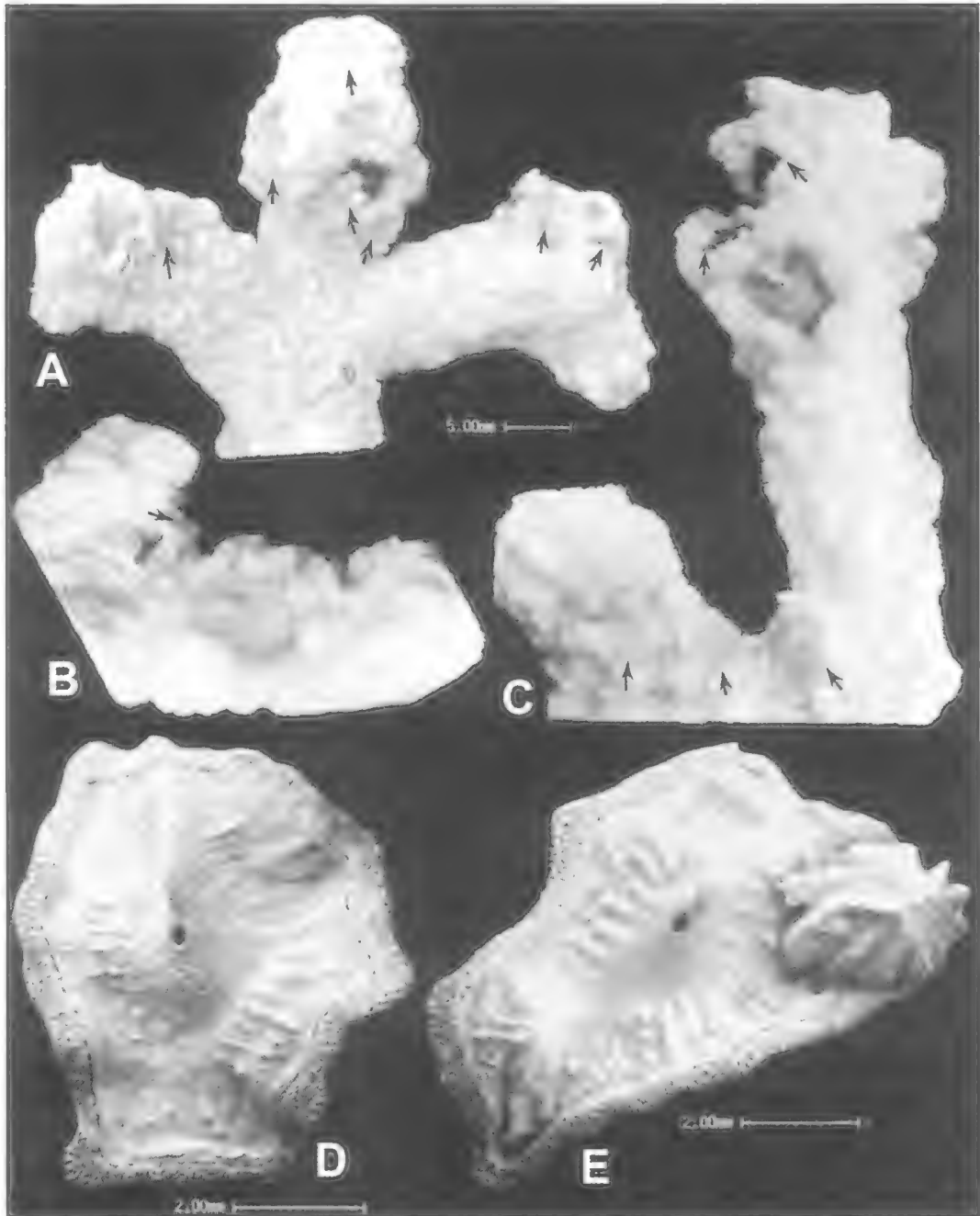


FIG. 1. *Australhoekia cardenae* gen. nov., sp. nov.; on *H. rigida*; Bowden Reef, GBR; QM coral G6734. A, view of coral with several barnacles in situ. Note proximity of individuals and orientation relative to one another, suggesting ability to cross-fertilise (paratypes, QM W24862). B, large individual on different branch of same coral. Note the minute size of the orifice relative to the major axis of the wall (paratype, QM W24862). C, dark coloured wall of holotype (QM W24861) in situ at top. The hydrons of the coral form a palisade surrounding the barnacle. D, SEM, apical view of holotype, carinal end at top. Note the uniformly narrow marginal fringe. E, SEM, oblique view of paratype (QM W24863) with large hydnon on outer lamina of wall (from this perspective it appears the hydnon is actually growing on the marginal fringe); carinal end toward upper right. Arrows indicate presence of other individuals on coral.

KEY TO THE GENERA OF HOEKIINI

1. Wall alacunate (lacking lumena connecting to circumferential channel); marginal fringe filigreed, simple . . . 2
 Wall lacunate (with lumena connecting to circumferential channel); marginal fringe not filigreed, complex . . . 3
2. Outer lamina lobate, not reflexed; marginal fringe narrow, not reflexed; carinal and rostral ridges prominent . . .
 *Parahoekia*
 Outer lamina ovate, reflexed; marginal fringe wide, reflexed; carinal ridge obscure, rostral ridge lacking
 *Eohoekia*
3. Distal margin of outer and inner lamina strongly ascendant, higher than orifice *Ahoekia*
 Distal margin of outer and inner lamina slightly ascendant, lower than orifice 4
4. Orifice relatively large (r-c >0.37mm); carinal ridge obscure; pronounced gap between laminae; width of marginal fringe variable, deliquescence diffuse *Hoekia*
 Orifice relatively small (r-c <0.37mm); carinal ridge prominent; minute gap between laminae; width of marginal fringe uniform, deliquescence compact
 *Australhoekia* gen. nov.

***Australhoekia* gen. nov.**

TYPE SPECIES. *Australhoekia cardenae* sp. nov.; Recent, Great Barrier Reef, Australia (details below).

ETYMOLOGY. Latin, *Austral-*, or southern, and *-Hoekia*, in reference to its occurrence in Australia and its affinities with *Hoekia* and related taxa.

DEFINITION. Wall moderately thin, somewhat delicate in appearance; lacunate; peritreme prominent; carinal ridge slender, long, exceedingly prominent; orifice minute, subapical on rostral slope; distal portion of outer (upper) lamina essentially flat; marginal fringe of inner (lower) lamina relatively uniform in width, slightly ascendent, lower than orifice, compact; lacunae on inner wall separate, irregular in outline, dispersed to concentrated laterally, connecting via lumena directly to circumferential channel.

REMARKS. The presence of lacunae (pits opening to active or abandoned lumena) on the internal surface of the wall indicates a derived grade of organisation previously known only in *Hoekia* and *Ahoekia*. *Hoekia* differs by having a generally larger orifice (>0.37), a more diffuse marginal fringe which is exceedingly variable in width and especially wide at the extremities, a thin wall, a pronounced gap between the margin of the outer and inner laminae and a relatively inconspicuous carinal crest. The two species of *Ahoekia* have a relatively larger orifice (0.4-0.5) standing below or at nearly the same elevation as the strongly ascendent marginal fringe, but it has a thick and more massive wall, a pronounced gap

between the margin of the outer and inner laminae, a compact or dense marginal fringe varying considerably in width and especially wide at the extremities, and a relatively inconspicuous carinal ridge.

In contrast *Australhoekia* has a relatively small orifice (<0.37) situated well above the slightly ascendent marginal fringe, a decidedly thick but somewhat delicate wall, a minute gap between the laminae, a relatively narrow and compact marginal fringe that is essentially uniform in width, and an exceedingly prominent carinal ridge. It is noteworthy that in *Hoekia* the inner lamina develops at a greater rate and extends significantly farther than the outer lamina, whereas in *Australhoekia* both laminae develop at essentially the same rate and therefore extend to much the same degree.

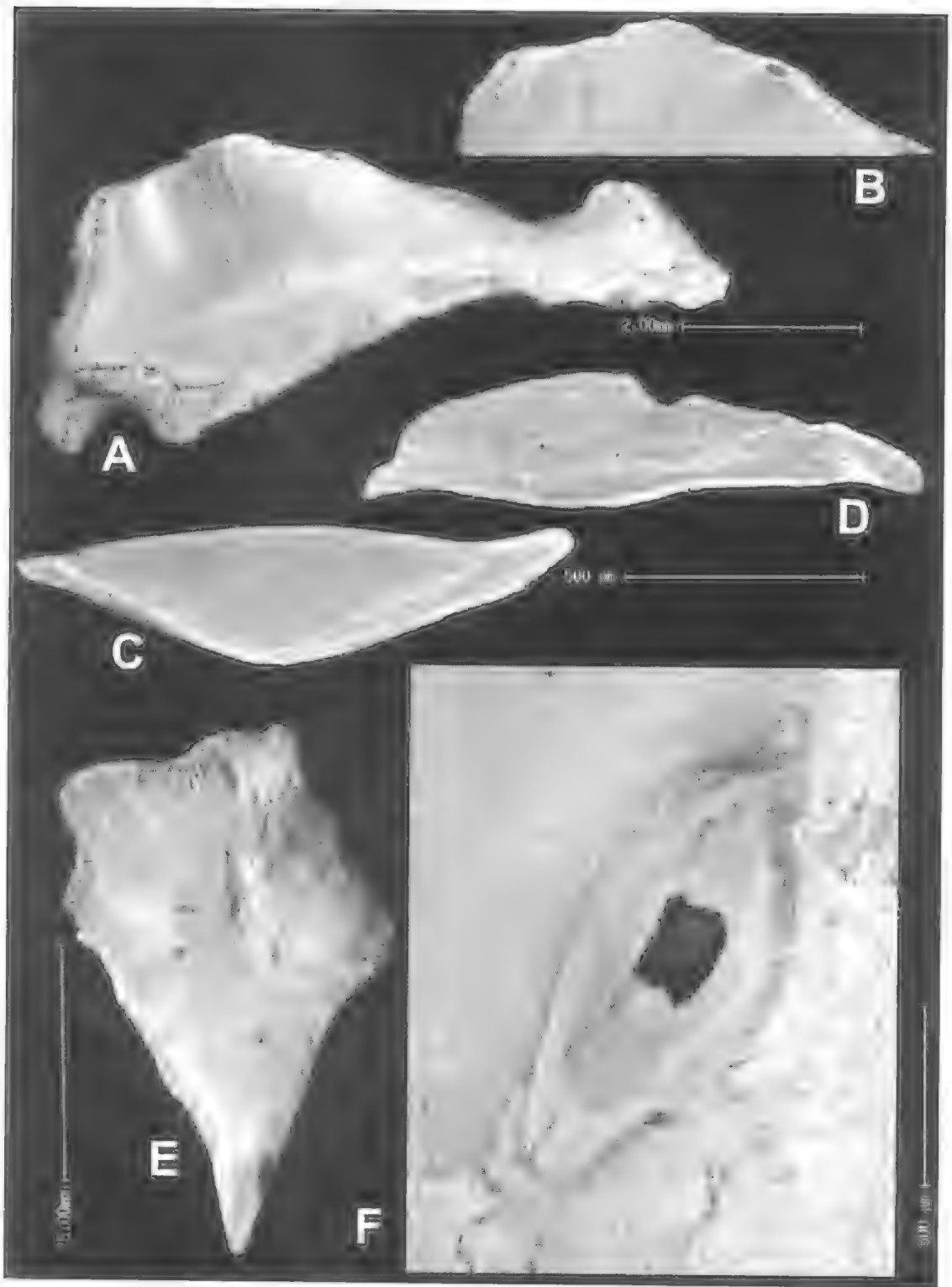
***Australhoekia cardenae* sp. nov.**
(Figs 1-2)

ETYMOLOGY. In honor of Carden C. Wallace, Museum of Tropical Queensland, Townsville, Australia, who collected the corals and for her keen interest in all that relates to them.

MATERIAL. Queensland Museum (QM): all specimens dried; 19 complete specimens on 21cm branch, 13 complete specimens on 16cm branch of *H. rigida*; QM coral G6734; on side of small opening in south end of Bowden Reef, GBR, NE Queensland (Qld), Australia; Carden C. Wallace coll., 25-VII-1972; 0.6-3.1m; coral tissue pale pink-brown; associated with a calcareous alga, vermetids and 4 specimens of *Galkinia* sp. cf. *G. indica* (Annandale, 1924). HOLOTYPE: QM W24861. PARATYPES: (28 walls with bases, 19 bases only) QM W24862, W24863 (Fig. 1E), W24864 (Fig. 2E-F); 1 specimen (wall and opercular plates only), Scripps Institution of Oceanography, Benthic Invert. Coll., C-9980. OTHER MATERIAL. Museum of Tropical Queensland (MTQ). 2 specimens on *H. rigida*, first barrier reef NE of Murray I., Qld, 09°55'S, 144°05'E, 0-5m, MTQ coral G40321 (AIMS site 87). 1 specimen on *H. exesa* Pallas, 1776, Falcon I., Palm Is, Qld, 18°46'S, 146°32'E, 1.5-10m, MTQ coral G38995 (AIMS site 9). 2 specimens on *H. rigida*, Eclipse I., Palm Is, Qld, 18°46'S, 146°33'E, 3-15m, MTQ coral G38964 (AIMS site 126).

DIAGNOSIS. As for the genus.

DESCRIPTION. Wall white to slightly yellow, opaque (translucent when immersed in water), large (Fig. 1A-C), commonly covered with sclerites (Fig. 1D) and/or hydrons (Fig. 1E); concentric growth ridges slightly beaded; rostro-carinal (r-c) diameter of adults ranging from 4.8 to 14.8 (holotype 6.8); lateral diameter seldom exceeding r-c diameter; peritreme



protuberant, tall, elongate-oval (major axis significantly greater than minor axis, Fig. 1C); carinal ridge tall, narrow, prominent, generally higher than orifice, extending to periphery (Fig. 2A); orifice in small specimens with slightly raised rim (Fig. 2B), r-c diameter 0.27-0.37 (holotype 0.27); distal edge of outer lamina flat to slightly ascendent; marginal fringe of inner lamina finely divided (deliquescent), compact, same as or slightly higher than outer lamina, relatively uniform in width (Fig. 1D), elevated on both sides of carinal ridge; outer lamina and marginal fringe of inner lamina separated by an indistinct or slight gap (Fig. 1E); ratio of r-c diameter of wall to orifice ranging from approximately 26:1 to 43:1; inner surface of wall smooth to chalky, roughened, irregular, secondary layers often flaky, apparently teratologically disorganised in all specimens (Fig. 2F); sheath short, about 1/5 to 1/3 height of peritreme; lacunae of different sizes, discrete to confluent, uniform to irregular in outline, irregularly spaced, arrayed somewhat concentrically to concentrated laterally (Fig. 2E), major carinal lumen leading to carinal sinus; under transmitted light (immersed in water) lumina can be seen to radiate from area immediately distal to sheath to circumferential channel; ancillary channels commonly extending distally to extremities of marginal fringe.

Opercular plates compound (Fig. 2C-D), thin, translucent, bilaterally symmetrical (Fig. 2F), arcuate lengthwise and in cross-section; limbus occludens (occludent ledge) large, slightly inflated; length of plates essentially equal (Fig. 2F); height about 1/4 length.

Basis irregular in outline; lower portion thinly calcareous, irregular or hummocky, not smooth; upper portion not preserved; greatest depth 11.4 (holotype 4.9).

Appendages and body unknown.

REMARKS. Several specimens in the type lot are represented solely by the basis cavity, 11 on

the large branch and 8 on the small, all of which have a characteristic amoeboid outline. Although we have not seen the soft parts of this species, in spite of the minute orifice we have no reason to believe they will not resemble those of other *Hoekiini* (see Ross & Newman, 1995). While there is no disparity in length of the opercular plates, which is readily apparent in other species, the plane in which the distal end of the scutum and tergum lie is not as reflexed as it is in others and the plates are proportionately smaller as are the fenestrae they form (see Ross & Newman, 1995: 150).

Secondary deposition of calcareous material either in parietal tubes or on the inner surface of the wall is not uncommon in sessile barnacles. What is of interest here is that in one specimen (MTQ 38964), once the wall was removed from the basis, large flakes of calcareous material remained attached to the tissue adhering to the basis, and on several other specimens the inner surface of the wall was lined with loosely attached flakes (Fig. 2F). Normally, secondarily deposited calcite becomes an integral part of the wall, but in these cases the flakes are separate and more or less randomly arranged, and their functional significance is obscure. Indeed, these flakes appear teratological but they are unknown in other *Hoekiini* and other balanomorphs in general.

In the smaller specimens the orifice has a narrow raised rim that apparently developed early in its ontogeny (Fig. 2B). In larger individuals this rim is either worn away and/or obscured by a thin layer of coral skeleton on the outer lamina of the wall. However, there is no obvious difference between size of the orifice in the smallest, compared with largest individuals.

DISCUSSION

HOST SELECTION. The faviinid *Hydnophora* is unusual because the corallite centres are arranged around protuberant collines or hydrons, which result from circummural budding. The

FIG. 2. Scanning electron micrographs of *Australhoekia cardenae* gen. nov., sp. nov., from *H. rigida*. A, lateral view of wall showing relationship of orifice to carinal ridge; NE Murray Is (ex MTQ coral G40321). B, lateral view of same showing the pronounced lip surrounding the orifice. C, external view of left opercular plate, scutal portion on right, slightly inflated limbus occludens at top (holotype, QM W24861). D, Internal view of right opercular plate, scutal portion on right, limbus occludens at top (holotype, QM W24861). E, internal view of wall with opercular plates in situ; the lacunae are irregular in outline and occur at different distances from the sheath (paratype, QM W24864). F, enlarged view of same, opercular plates in situ. Note the plates are similar in shape and length, but because the plates are agape and photographed at a different angle from the disassociated plates (above) it appears the fenestrae are absent, whereas there is a small fenestra at the scutal end but virtually none at the tergal end of the plate. Also, note the presence of exfoliating flakes still held in place on wall (paratype, QM W24864).

base of each hydron is surrounded by short tentacles, with a single tentacle between each pair of sclerites (Veron, 1993: 428). Unlike most corals, wherein each polyp occupies a corallite, *Hydnophora* lacks distinct corallites. Consequently, while the mouth may occur where there are several contiguous tentacle-encircled hydrons, there may be no mouth in a similar array of hydrons. In preserved specimens the wall of the barnacle, which is encircled by one or two rows of tentacles and covered with a cloak of coral tissue consisting of two layers separated by radial mesenteries, clearly resembles or mimics the associated tissues surrounding and covering the hydrons of the coral (Ross & Newman, 1995: 157).

Why species of *Hydnophora* are the only corals infected by coral-eating barnacles is unknown, and then of the some 22 species (Veron, 1993) only four have been identified as hosts (Ross & Newman, 1995). The presence of these barnacles solely on *Hydnophora* can likely be ascribed to their unusual topography, and to the thick, soft coral tissue in the 'valleys' between the hydrons, together providing a large fleshy area through which significant metabolic exchange and chemical mediation can occur. In the present specimens there is a broad gap between the marginal fringe and the coral hydrons and a halo of thick, dark, dried tissue surrounding the barnacle.

Based on earlier studies (Ross & Newman, 1969, 1995) these parasites also have a veil of soft coral tissue covering the wall, extending from the marginal fringe and covering the orifice where it is fed upon by the barnacle, as evidenced by nematocysts among the stomach contents.

The type specimens from Bowden Reef occur on *H. rigida*, and only the second species documented from this coral; the first being *Ahoekia chuangi* Ross & Newman, 1995 from the Bay of Batavia, Java.

Ogawa & Matsuzaki (1992) and Ogawa et al. (1998) reported the facultative occurrence of the coral barnacle *Galkinia indica* (Annandale, 1924) on several species of *Hydnophora*, but surprisingly Ogawa et al. (1998) did not find any Hoekiini on this coral in Mauritius where it is known to occur (Ross & Newman, 1969, 1995). Thus the distribution of these barnacles appears to be very patchy. The Bowden Reef sample also contains several barnacles perched on the hydrons that are tentatively identified as *G. indica*, but we place no great significance on this association

other than to note the surface topography in some species of *Merulina* Ehrenberg, 1834 is similar to that of *Hydnophora*, and *G. indica* is known to settle on these corals.

None of the present corals show evidence of recently settled individuals, nor is there any indication there had been juveniles present. Throughout our studies of the Hoekiini we have been perplexed by the apparent lack of recent recruitment, and thus the reproductive success of these parasites. Although apparently producing small eggs, the reproductive effort generally does not appear to be high (Ross & Newman, 1995: 166). The different sizes of the otherwise mature individuals in the present material may be related to the constraints imposed by settling at sites where wall growth is limited by the hydrons as well as to some recruitment, and therefore all of the individuals may have become established over a relatively short period of time. The proximity to adjoining individuals in most instances is adequate to insure cross fertilisation, but in others it appears to be an impossibility. The reproductive period(s) in coral barnacles in general, as well as the majority of Hoekiini, remains unknown.

MODE OF GROWTH. Balanoid barnacles in general develop a conical wall with a flat-lying basis, where vertical and lateral growth proceed essentially simultaneously. Generalised 4-plated pyrgomatids follow the same basic pattern, whereas in derived forms the wall and basis exhibit rapid lateral growth to maximum diameter, developing a discoidal wall, followed thereafter by deepening of the basis in concert with growth of the host (Ross & Newman, 1973; Anderson, 1992).

Wall development in the coral-eating barnacles represents a significant departure from the general pyrgomatine theme. The initial form of the wall is somewhat conical which is expressed by the shape of the peritreme of the adult. Growth thereafter is by lateral expansion to maximum size before a definitive hypertrophied inner lamina develops. Although presumably capable of developing a wall with a circular or ovate outline, the barnacle is constrained by having settled between hydrons and therefore it can only extend into the space available between them, the spatial arrangement of which dictates the barnacle's protean outline. In certain cases growth of the coral exceeds the rate of basal elongation by the barnacle and the hydrons form a tall palisade surrounding it, but there is no

indication of successful coalescence with and burial of, the barnacle.

CORAL OVERGROWTHS. The ideal condition in *Hoekiini* is apparently a full cloak of soft tissue, upon which it feeds, extending to and covering the orifice, without the production of sclerites on the outer lamina of the wall. In all of the species we have studied, most do not have a recognisable pattern of sclerites on the outer lamina of the wall. This contrasts with the present species from Bowden Reef in which the majority of the walls have clearly defined skeletal elements of the coral and a few even have small hydrons (Fig. 1E).

The growth of sclerites and hydrons on the wall in some of the present specimens suggests they are either diseased and/or becoming senescent and no longer capable of inhibiting overgrowth. Alternatively, they may allow the growth of this covering, which would further conceal their presence on the host. Although we favor the first inference, the second may represent a means of forestalling predation, as is evident in many other pyrgomatids.

BIOGEOGRAPHY. According to Ogawa & Matsuzaki (1992) the relatively generalised *Galinkia indica* (Annandale, 1924) and *Cantellius eupinulosa* (Broch, 1931) occur on *Hydnophora*. It is important to note that while these species occur on numerous other coral genera, the *Hoekiini* only occur on *Hydnophora*. This is in accord with the hypothesis that relatively generalised species exploit a greater variety of hosts than do more specialised species, and that they also have a broader geographical distribution (Newman et al., 1976). Even though the highly specialised *Hoekiini* ranges throughout most of the Indo-West Pacific region, it is noted that both genera and species of this tribe have relatively narrow latitudinal and longitudinal ranges, perhaps more so than is documented for any other pyrgomatid genus. But why the genera as well as the species are so regional when the host species are apparently wide-ranging is not intuitively obvious. It likely has something to do

with modest larval dispersal capabilities, but the type of larva produced by the *Hoekiini* is yet unknown.

ACKNOWLEDGEMENTS

We thank Stephen D. Cook, Queensland Museum, Brisbane for permission to study the specimens comprising the type material. We also thank Carden C. Wallace, Museum of Tropical Queensland, Townsville, for forwarding reference specimens and SEM photographs of them. We are indebted to the many student volunteers at the Museum of Tropical Queensland, especially Michelle Lee, for taking the time to search the collections for these and other coral barnacles. The SEM photographs used herein were taken by Charles Graham, Scripps Institution of Oceanography Analytical Facility, A Contribution of the Scripps Institution of Oceanography, new series.

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REVISION OF THE FOSSIL CHELID TURTLES (PLEURODIRA) DESCRIBED BY
C.W. DE VIS, 1897

S.A. THOMSON

Thomson, S.A. 2000 06 30: A revision of the fossil chelid turtles (Pleurodira) described by C.W. de Vis, 1897. *Memoirs of the Queensland Museum* 45(2): 593-598. Brisbane. ISSN 0079-8835.

With increasing knowledge of the morphology of Australian chelid turtles and major changes in taxonomy it has become necessary to assign, where possible, the fossil species described last century by C.W. de Vis. It was found that four of these, *Chelymys uberima*, *C. arata*, *C. antiqua* and *Pelecomastes ampla*, were synonymous, with *C. uberima* being the senior synonym. *Chelymys uberima* was determined to be a member of the *Elseya* whose affinities lie with the *Elseya lavarackorum* group of species. The paralectotypes of *Chelymys antiqua* were found to be a new species of the genus *Rheodytes* and sister to *R. leukops*. These specimens are described as a new species. *Chelodina insculpta* was found to be a valid taxon whose affinities probably lie with *C. expansa*, □ Testudines, side-necked turtle, Chelidae, Miocene, Pleistocene.

S.A. Thomson. Applied Ecology Research Group and CRC for Freshwater Ecology, University of Canberra, Canberra 2601, Australia. (e-mail: thomson@acrq.canberra.edu.au); 29 October 1999.

The identification of fossil forms is an important addition to the understanding of the evolution and zoogeography of any species group. This is made difficult when the taxonomy of the extant forms is not well defined, as is the case for the Australian chelid turtles (Cogger et al., 1983; Thomson et al., 1997). With some recent advances on the skeletal morphology of chelids (Thomson & Georges, 1996; Thomson et al., 1997) it is now possible, and appropriate, to examine the fossil forms that have been described formally. For example, the recent description of a fossil turtle from Riversleigh, *Elseya lavarackorum* (White & Archer, 1994), and the subsequent discovery of a living population of this species (Thomson et al., 1997).

Fossil turtles in Australia have for many years been ignored due to the lack of detailed description of extant species. Rarely have skeletal diagnoses accompanied descriptions of the Australian chelid turtles, even those more recent. This makes the identification and placement of fossils difficult or impossible.

Apart from *Elseya lavarackorum* and *E. nadibajagu* Thomson & Mackness, 1999, only five other species of fossil chelid turtles have been described from Australia (Gaffney, 1981), all by C.W. de Vis (1897). Gaffney (1981) found that the available material was indeterminate below family or genus level was the last to revise the de Vis specimens. Three of the species, *Chelymys uberima*, *C. antiqua* and *C. arata*, were

identified as *Emydura* sp. (= *Emydura* + *Elseya* of Gaffney, 1977); another, *Chelodina insculpta*, was identified as *Chelodina* sp.; and the last, *Pelecomastes ampla*, could not be identified to family (Gaffney, 1981). These species were all described from fragmentary material from the Darling Downs with no holotypes identified (de Vis, 1897) hence Gaffney (1981) set lectotypes from each set of fragments and placed the rest of the specimens as syntypes. The specimens were originally diagnosed using differences in sulci (de Vis, 1897) but it seems that they were actually arranged according to scute ornamentation (Gaffney, 1981). This is a highly variable character and I agree with Gaffney (1981) that it is of little phylogenetic significance.

In this paper the fossil turtles described by de Vis (1897) are reanalysed and, where appropriate, resurrected or placed in synonymy. They are placed in their correct genera using previously published diagnostic characters and their affinities and phylogenetic implications discussed. The purpose of this paper is to solve the nomenclatural problems associated with having described specimens of unknown affinity. It is not the purpose of this paper to present a review of the living genera with respect to the fossils.

METHODS

Turtles representing all extant Australasian species have been borrowed from museums, collected or otherwise obtained, and skeletonised

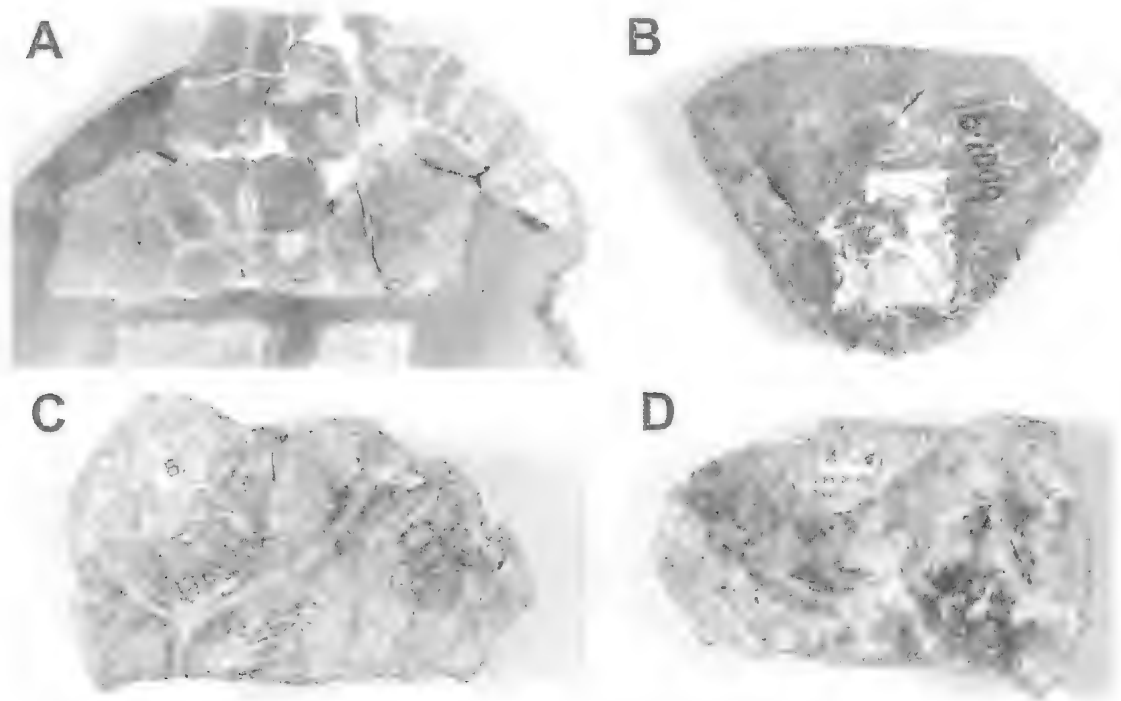


FIG. 1. A, Lectotype of *Elseya uberima*, QMF9040, showing the enlarged first vertebral. B, Lectotype of *Elseya arata*, QMF16-1099B, now synonymised with *Elseya uberima*. C-D, dorsal and ventral views of the Lectotype of *Pelecomastes ampla*, QMF1102D, now synonymised with *Elseya uberima*; ventral view shows the large deviation of the anterior bridge strut from the rib/gomphosis.

as per methods outlined in Thomson et al. (1997). This turtle collection of some 350 specimens is housed at the University of Canberra. Characters described in Thomson et al. (1997) were used for diagnosis and the fossils were then assigned to genus and their affinities demonstrated. A complete list of specimens examined can be found in Thomson et al. (1997). Further specimens with locality data will be presented in a future major analysis of the *Elseya* genus.

SYSTEMATICS

Elseya uberima (de Vis, 1897)

Chelymys uberima de Vis, 1897: 3.

Chelymys antiqua de Vis 1897: 4.

Chelymys arata de Vis 1897: 5.

Pelecomastes ampla de Vis 1897: 6-7.

MATERIAL. HOLOTYPE: none set (de Vis, 1897). **LECTOTYPE:** QMF9040 by subsequent designation (Gaffney, 1981) (Fig. 1A). **PARALECTOTYPES:** QMF1104, 1105 by subsequent designation (Gaffney, 1981). **LECTOTYPE** of *Chelymys arata* QMF16-1099B by subsequent designation (Gaffney, 1981) (Fig. 1B). **LECTOTYPE** of *Pelecomastes ampla* QMF1102D by subsequent designation (Gaffney, 1981) (Fig. 1C-D).

LECTOTYPE of *Chelymys antiqua* QMF16-1106E by subsequent designation (Gaffney, 1981).

HORIZON. Pliocene or Pleistocene.

LOCALITY. Darling Downs, Queensland, Australia.

DISCUSSION. Material consists of: QMF9040, nuchal, right peripherals 1-3, left and right pleural 1, articulated; QMF1104, numerous unarticulated carapace fragments including peripherals and pleurals; QMF1105, numerous unarticulated plastral fragments.

The lectotype assigned by Gaffney (1981) is suitably diagnostic and can be recognised as an *Elseya* without difficulty. The first vertebral scute is significantly wider than the second (Fig. 1A), a character found only in the *Elseya* and *Chelodina* (see Thomson et al., 1997). The *Chelodina* have either an anterior bridge strut restricted to the peripheral bones and not continuing on to the pleural bones, e.g. *C. longicollis* group except *C. novaeguineae* (see Thomson, in press; Thomson et al., in press), or the strut continues on to the pleurals but not contributed to

by the rib gomphosis, although it crosses it in some species, is wide throughout its length with a significant enlargement at the medial end, e.g. *C. expansa* group and *C. novaeguineae* (see Thomson, in press; Thomson et al., in press). The structure of the anterior bridge struts in *Chelymys uberima* is consistent with neither of the *Chelodina* conditions and is similar in structure to that described for the *Elseya lavarackorum* group (Thomson et al., 1997) (Fig. 2.). The structure of the first pleural and the indentation at the nuchal region places this species in the *Elseya lavarackorum* group of species. The fact that this species has a cervical scute is not unusual among fossil *Elseya*, particularly those from western flowing drainages. Specimens in the South Australian Museum from Lake Palankarina and Lake Ngapakaldi all exhibit this feature and may represent an entire extinct radiation of *Elseya* turtles.

The four species synonymised above are, in this paper, recognised as a single diagnosable taxon, with *C. uberima* being the senior-most available name (page priority). The genus *Chelymys* has been synonymised in recent years with *Emydura* (Cogger et al., 1983), the genus *Pelecomastes* is considered here a junior synonym of the genus *Elseya*, Gray 1867.

These species were differentiated largely by shell ornamentation (Gaffney, 1981), an unsatisfactory method since this character can vary significantly even within a single population of turtles. The lectotype of *Chelymys antiqua* is not easily diagnosable. Based on the morphology of the pygal bone of extant species it would be attributed to almost any short-necked taxon in that the posterior suture of the ilium is in close proximity to the vertebral column. The *Elseya latisternum* group and *Pseudemydura* have a triangular suture on the pygal (unpublished data) ruling out these taxa. This pygal is either *Elseya* or *Emydura* but without the eighth pleural it is impossible to identify further (Thomson & Mackness, 1999). As there are no other diagnostic features between these specimens, all are considered as a single diagnosable taxon and assigned to *Elseya*.

Rheodytes devisi sp. nov.

ETYMOLOGY. This species is named for C.W. de Vis who described most of the material presented in this paper as well as many other taxa within Australia.

MATERIAL. HOLOTYPE: QMF16-1106B (Fig. 3A-B).
PARATYPES: QMF16-1106A, C-D.



FIG. 2. Comparative diagrams of representative short-necked genera. A, *Elseya latisternum*; B, *Elseya dentata*; C, *Rheodytes leukops*; showing the angle between the rib/gomphosis (R) and the anterior bridge strut suture (BCS) on the first pleural (P1). (From Thomson et al., 1997).

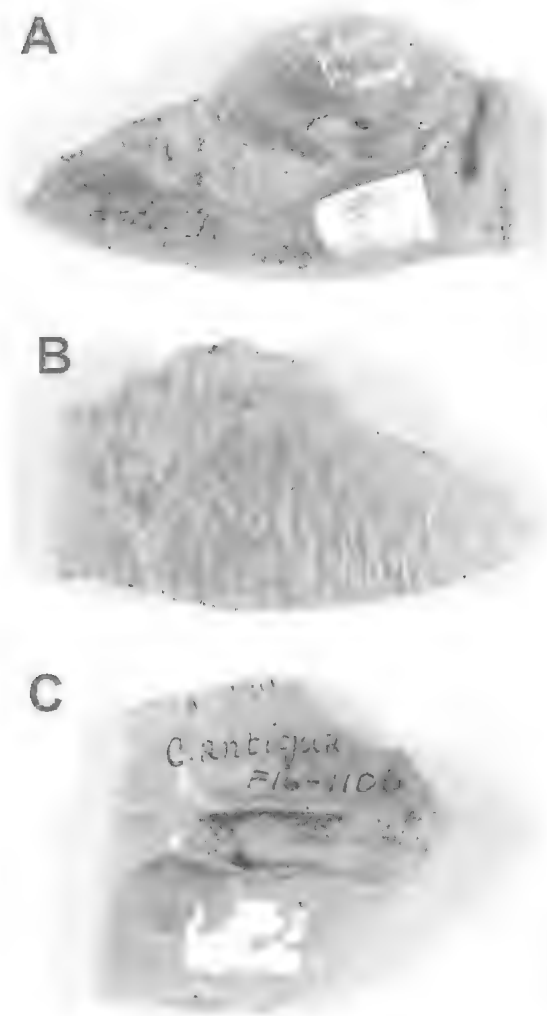


FIG. 3. Ventral and dorsal views of *Rheodytes devisi*, the ventral views showing parallel sutural edges and low angle of the anterior bridge strut. A-B, Holotype, QMF16-1106B; C, Paratype QMF16-1106C.

HORIZON. Pliocene or Pleistocene.

LOCALITY. Darling Downs, Queensland, Australia.

DIAGNOSIS. The genus *Rheodytes* can be diagnosed by the presence of a 10-15° angle between the anterior bridge strut and the rib/gomphosis of pleural one, and by the parallel sutural edges of the bridge strut with intervening deep socket like sutural surface (Thomson et al., 1997) (Fig. 2C). This combination of characters is unique to this genus and is present in both specimens of first pleurals in the type series (Fig.

3B-C). The species *Rheodytes devisi* is diagnosed by its thicker, better formed, carapacial bones. Deeper insertion of the anterior bridge strut suture and the failure of the anterior bridge strut to either break through, or come close to breaking through, the pleural surface.

DISCUSSION. Material consists of: QMF16-1106B, right first pleural, almost complete (Fig. 3A-B); QMF16-1106C, distal section of a right first pleural (Fig. 3C); QMF16-1106D, left partial pleural of indeterminate position but likely from the seventh pleural.

Rheodytes leukops is an inhabitant of the Fitzroy River in eastern Queensland, whereas *R. devisi* is found in the western flowing drainages of the Darling Downs. Among the extant taxa *Rheodytes leukops* can be identified by its extremely thin shell, to the point that the ilium and bridge strut often break through the carapace, all other genera have thicker shells ranging from the *Elseya latisternum* group through to the *Emydura* and *Elseya* groups. *R. devisi* has a thick shell much like other short-necked species and hence it can be diagnosed from its congener *R. leukops*. The species are allochronic and allopatric and appear to have inhabited different environments.

***Chelodina insculpta* de Vis, 1897**

Chelodina insculpta de Vis, 1897.

MATERIAL. HOLOTYPE: none set (de Vis, 1897). LECTOTYPE: QMF1109A by subsequent designation (Gaffney, 1981) (Fig. 4). PARALECTOTYPES: QMF16-1107, F1109B-G by subsequent designation (Gaffney, 1981).

HORIZON. Pliocene or Pleistocene.

LOCALITY. Darling Downs, Queensland, Australia, restricted (this study).

DISCUSSION. Material consists of: QMF16-1107 (fig. V in de Vis, 1897), numerous carapace fragments including parts of pleurals and peripherals. Most of these are not particularly diagnostic. There is a partial articulated 6th and 7th pleural from the left side that has characters diagnostic of *Chelodina*. The fragment listed as D in de Vis' figure V is actually a 7th pleural not a 6th. QMF1109a-g (fig. VI in de Vis, 1897), various plastral units which can clearly be diagnosed as *Chelodina* using the lectotype, QMF1109A (Gaffney, 1981). This would appear, however, to represent at least two animals as sutural surfaces are preserved yet there is no match between the anterior and posterior halves of the plastron.



FIG. 4. Ventral view of Lectotype of *Chelodina insculpta*, QMF1109A, showing large area of the intergular scute on this unit.

The material available is diagnosable to genus using the scute sulci arrangements of the lectotype, an entoplastron in which there is clearly a large intergular which is separated from the margin anteriorly by the gulars a unique feature of the *Chelodina* (Gaffney, 1981) (Fig. 5). There is further evidence of generic assignment from the relative widths of the anterior and posterior parts of the posterior lobe of the plastron and from the positioning of the pelvic suture on pleural seven of the carapace.

Chelodina insculpta possessed a large, robust bridge strut, a character unique to the *C. expansa* group of species (Thomson, in press; Thomson et al., in press.). Further, this specimen had a large carapace excluding many species from the *C. expansa* group, such as *C. rugosa*, which have a reduced margin. However, the margin is not as flared at the posterior or as wide as *C. expansa*. Therefore, *C. insculpta* is recognised as a valid taxon.

The locality data for this species was originally given as a combination of the Darling Downs, Queensland; Warburton River, South Australia; and Eight Mile Plains near Brisbane, Queensland (de Vis, 1897). In the original description de Vis states that the Warburton material was not figured and consisted of seven carapace fragments. As the name bearing lectotype is an entoplastron this

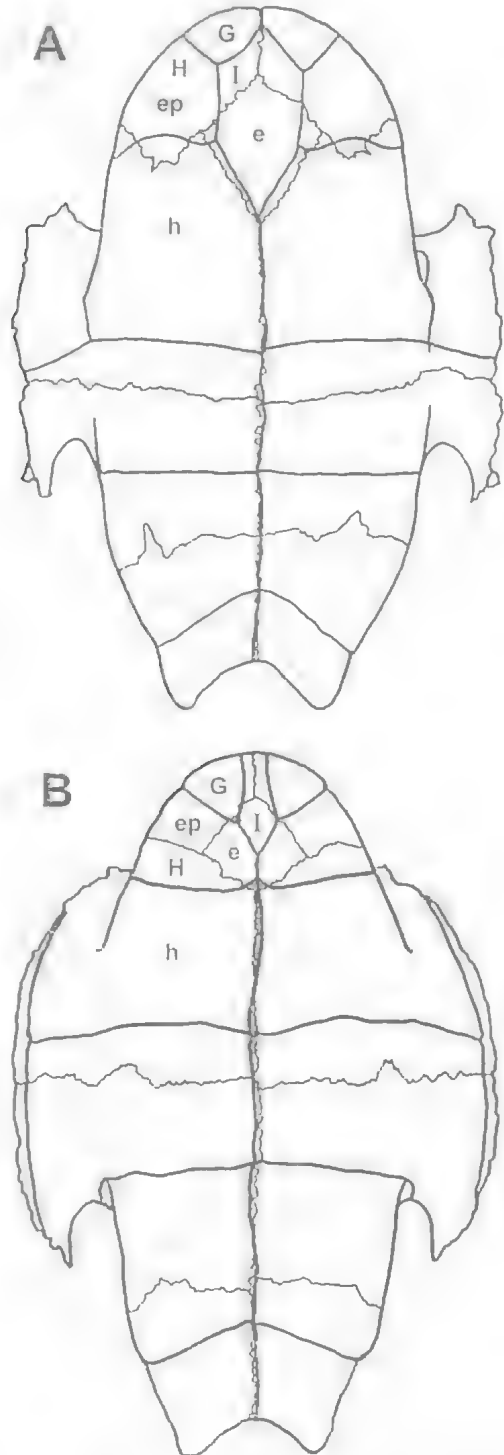


FIG. 5. Comparison of the intergular region of A, *Chelodina rugosa* and B, *Elseya dentata*; showing difference between the *Chelodina* and Short-necked Chelid conditions.

rules out the Warburton River as a type locality. There is no mention of Eight Mile Plains until the locality section of the paper and de Vis clearly states that 'in addition to the fragments of carapace figured, sixteen others from the Darling Downs ...'. It seems clear that despite other material examined only Darling Downs material was figured. As the lectotype (QMF1109a) is clearly identifiable in figure VI of de Vis (1897) I am restricting the type locality to the Darling Downs of Queensland.

DISCUSSION

The five species and one genus described by de Vis (1897) are reduced to three species and *Chelymys* and *Pelecomastes* are synonymised with *Elseya*. *Elseya uberima* is an extinct form of snapping turtle belonging to a large group that possibly contains the New Guinea forms as their sole surviving relatives. They would appear to be the sister group of the *Elseya lavarackorum* group (sensu Thomson et al., 1997). *Rheodytes devisi* is the first fossil record of this highly restricted genus of turtles. Clearly sister taxa, they were found on opposing sides of the Great Dividing Range. *Chelodina insculpta* is a large long neck turtle from an area where *C. expansa* may still be found. This species would appear to be part way between the body forms associated with *C. expansa* and *C. rugosa*, and likely to be the sister species of *C. expansa*.

ACKNOWLEDGEMENTS

I thank the Queensland Museum for loan of the type material of de Vis (1897). I thank those who have supplied specimens for the skeletal collection at the University of Canberra and Arthur Georges for his continuing support of my research on turtle morphology.

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BREEDING, FEEDING AND ARBOREALITY IN *PARADELMA ORIENTALIS*: A
POORLY KNOWN, VULNERABLE PYGOPODID FROM QUEENSLAND,
AUSTRALIA

PETER R. TREMUL

Tremul, P.R. 2000 06 30: Breeding, feeding and arboreality in *Paradelma orientalis*: a poorly known, vulnerable pygopodid from Queensland, Australia. *Memoirs of the Queensland Museum* 45(2): 599-609. Brisbane. ISSN 0079-8835.

On Boyne Island, in central Queensland, *Paradelma orientalis* (Gunther, 1876) is nocturnal and (at least) partly arboreal. Specimens are found frequently on the trunks of *Acacia falciformis*. They feed, but not exclusively, on the sap of *A. falciformis* while scats analysis has also revealed remains of arthropods. *P. orientalis* is active in warm months and inactive when the night maximum temperature falls below 19°C. One female specimen encountered during this study laid two elongate eggs (34 × 12mm, 37 × 11mm) which hatched 81 ± 1 and 82 ± 1 days later. At emergence, neonates measured 69.0 and 72.0mm, respectively. □ *Pygopodidae*, *Paradelma orientalis*, sap-feeding, arboreality, reproduction, Brigalow Belt.

P.R. Tremul, 5 Kilman Court, Boyne Island 4680, Australia: 20 July 1999.

Paradelma orientalis (Gunther, 1876) is one of four pygopodids confined to Queensland. Its distribution has been reviewed recently by Schulz & Eyre (1997). *P. orientalis* occurs in a wide variety of open forest habitats on several soil types between the Carnarvon Ranges (25°19'S 148°20'E) and Eena State Forest, (28°19'S 150°50'E), via Inglewood; and between the Chesteron Ra. (26°09'S 147°14'E), via Charleville, and Boyne Island (23°56'S 151°20'E), via Gladstone. Although Wilson & Knowles (1988) reported *P. orientalis* to be '... moderately abundant, particularly on sandstone ridges ...', it has been regarded as 'restricted to specific habitats, vulnerable' (McDonald et al., 1991) and 'vulnerable' (Cogger et al., 1993; Nature Conservation Wildlife Regulation, 1994).

Most recently, under (IUCN definitions) it has been treated as 'vulnerable' with 'population reduction ... decline in area of extent of occurrence and ... quality of habitat ...' (Covacevich et al., 1998).

The bulk of this species' range lies in Queensland's Brigalow Belt, a region in which habitats are known to be seriously assailed by extensive clearing (e.g. Johnson, 1996).

Greer (1989) observed that two species of pygopodids (*Pygopus nigriceps* and *P. orientalis*) are 'largely, if not exclusively nocturnal'. Of the latter, he noted, '... active at night' (in captivity) but '... inactive by day'. Data on the biology of this species are scant. Save for one recent, brief account of sap-feeding by *P. orientalis* (Tremul, 1997), nothing has been added to knowledge of the habits of the species since the summary by

Greer (1989) 'Little is known of the biology ... found in woodland under cover ... reproduction in late spring and early summer ...'.

An apparently substantial and healthy population of *P. orientalis* was discovered on Boyne I., near the Lilly Hills Boyne Island Conservation Park in 1989. Observations made on specimens encountered there over ten years provide new data on arboreality, feeding and breeding behaviour and daily and seasonal activity cycles of *P. orientalis*. Hopefully this data will assist the conservation of a vulnerable species and highlight the significance of the *Acacia falciformis* woodlands on Boyne I.

STUDY SITE

Lilly Hills is in the SE portion of Boyne I. (23°56'54"S 151°20'53"E). Some 43.9ha of the hills are reserved under the Lilly Hills Boyne Island Conservation Park. A triangular section (defined by two almost perpendicular ridges) in the NE region (adjacent to the park) was selected as a study site, an area of approximately 13,000m² (Fig. 1). The vegetation in this area is a *Corymbia citriodora*/*Eucalyptus exserta*/*E. clarksoniana*/*E. crebra* tall woodland with a sparse upper-mid-stratum of *Acacia falciformis*, a sparse mid-stratum dominated by *Pogonolobus reticulatus*/*Jacksonia scoparia*/*Acacia conferta* and a sparse ground stratum dominated by *Xanthorrhoea latifolia* and clumps of *Entolasia stricta*, *Themeda triandra* and other tussock grasses. The substrate is covered by a dense layer of dry *Eucalyptus*/*Acacia* leaf litter. Soils are shallow and contain quartz, greywacke,

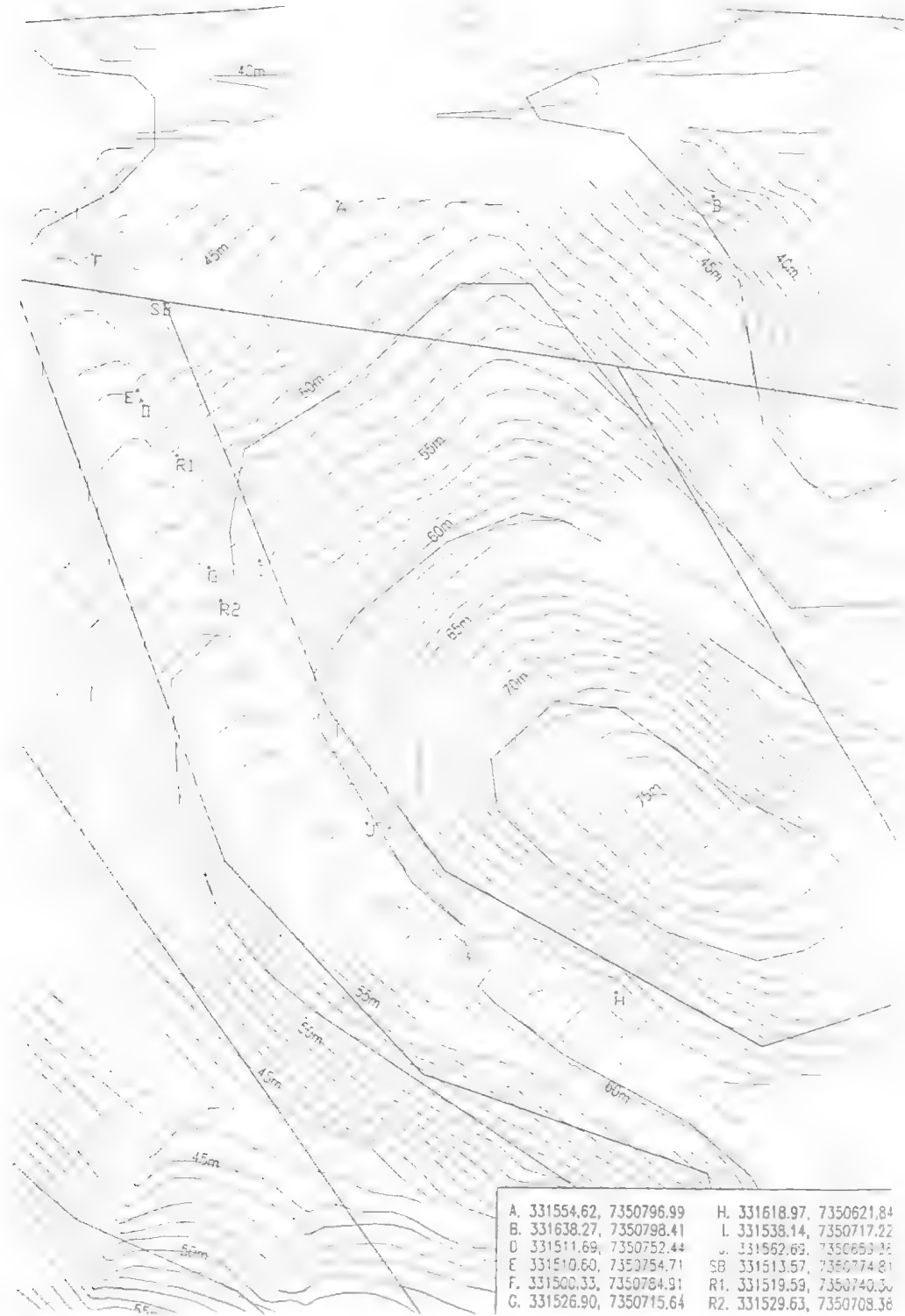


FIG. 1. Study area showing the coordinates of *P. orientalis* feeding trees A-J and SB. R1 = sugar glider feeding tree; R2 = *Gehyra dubia* feeding tree. Scale: distance between tree F and site SB = 17.7m.

mudstone and rare chert rock fragments. Very few large rocks occur in the area.

METHODS

Early observations indicated that *P. orientalis* was easily found at night, but difficult to locate by day; so all searches were made after sundown. Between 1989 and 1996 random searches were conducted throughout the northern region of Lilly Hills and alongside roads adjacent to the area. Observations of any activity were recorded. The data collected suggested that *P. orientalis* was reasonably common and active throughout the warmer months of the year. Some of the feeding trees during this period were measured and labeled as sites (Site A-H). Unfortunately many of these early sites on private land became inaccessible and were damaged by fire. As a result, in 1997 a smaller area, more suitable for comprehensive study, was selected (Fig. 1). On the 5/8/97 a maximum/minimum thermometer was placed in the shade of a grass-tree near the top of the SE ridge. Previous observations had suggested early August to be a dormant period and a suitable time to record the gradual temperature increases during late winter and monitor the commencement of activity of *P. orientalis*. The following night the SE ridge was searched on foot by torchlight. Maximum, minimum and current ground temperature were recorded, and a roughly diagonal path was taken to the top of the E ridge then back to the base corner (tree F, Fig. 1). A search of approximately one hour was conducted within an hour after dusk. This sequence of events was repeated for 48 consecutive nights. All observations were recorded and when any arboreal activity was seen the position of the specimen was estimated and the tree measured and labeled (tree A-G). Spacing between trees were later measured and exact positions were plotted by use of a compass and GPS (refer Fig. 1). Random searches were conducted again until late February 1998, when it was decided to measure as many individuals as possible during 12 consecutive nights. Four of these individuals were marked with white 'correction fluid' to enable them to be identified for a short period of time. This would hopefully give some indication of population size and establish whether or not individuals frequently visited the same tree. Random searches continued once again until May 1999. Searches during the following three months were increased to observe the beginning of the dormant period. The study concluded towards the

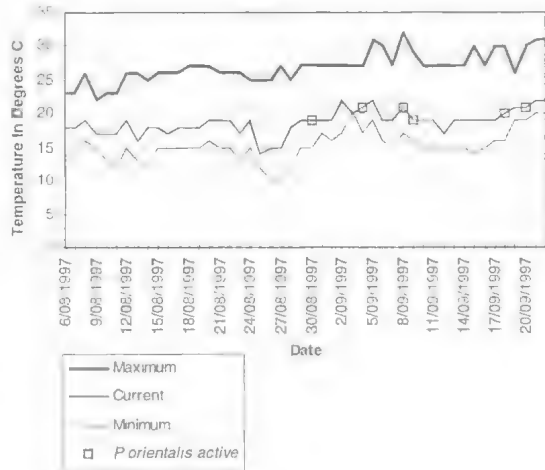


FIG. 2. Temperatures and activity recorded at *P. orientalis* site during August-September 1997.

end of July 1999. Seats were collected to ascertain if the species was an exclusive sap feeder.

RESULTS AND DISCUSSION

POPULATION SIZE. During the ten years of studying *P. orientalis* in the field, only 36% of specimens were handled and measured to minimise observer effect on behaviour. Between the 25/2/98 and the 8/3/98 (12 nights) 19 specimen measurements were recorded. Of these, 16 could be distinguished easily by dimensions and autotomy (Table 2). From these data, it seems reasonable to surmise that on Boyne I. at least, *P. orientalis* is fairly common. However, with land clearing of areas neighbouring the Lilly Hills, human population increase on the island and the introduction of roadside lighting, pressures are undoubtedly mounting. Lilly Hills Reserve and other areas supporting *Acacia falciiformis* woodlands do provide a viable habitat and food source for *P. orientalis*.

DAILY ACTIVITY. Weather conditions on nights when *P. orientalis* were observed were generally warm, clear and still (Table 1). Hand-searches in the study area (1989) resulted in the collection of only one inactive specimen under a rock. Sporadic visual-searches (not listed in tables) over the following 10 years revealed no obvious diurnal activity, although disturbance to the areas was minimal. By contrast, using a battery-operated light for *P. orientalis* from early evening (within the first hour post sundown) till

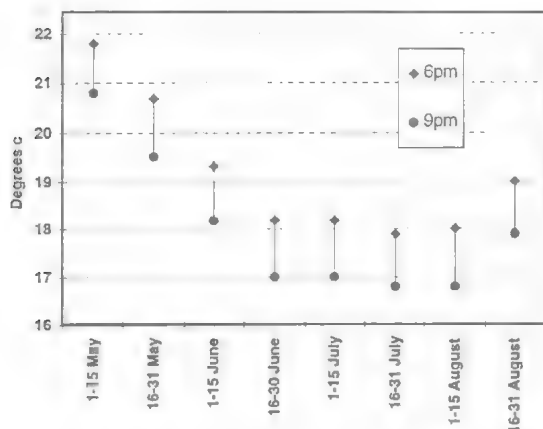


FIG. 3. Average ten-yearly temperatures (1989-1998). Temperatures recorded at Gladstone (Bureau of Meteorology).

0120 hours was successful. This study confirms that *P. orientalis* is nocturnal.

SEASONAL ACTIVITY. On Boyne Island *P. orientalis* is active between late August and early June (i.e. late Winter-Autumn). Data relating to late winter temperature ranges and associated behavioural observations of *P. orientalis* are summarised in Fig. 2 for August-September, 1997. No activity has been observed when the maximum night temperature was below 19°C. Observations throughout late autumn and winter (obs. #121-140 and obs. #42-65) and the ten yearly average temperatures for the Gladstone region (Fig. 3) suggest a dormant period between mid June and late August.

ARBOREALITY. Many pygopodids are known to climb into thick vegetation or on shrubs and trees. Greer (1989) summarises reports of such behaviour in *Pygopus lepidopodus*, *Lialis burtonis*, some *Delma* spp. and *Pletholax gracilis* noting that members of only two genera of pygopodids (*Ophidiocephalus*, *Aprasia*) do not climb. However, he records no evidence of arboreality in *P. orientalis*. Table 1 summarises observations of close to 10 years' encounters with *P. orientalis* specimens in trees or above ground. *P. orientalis* is rather conspicuous when perched on a feeding tree, the lead-grey colour often deeply contrasting. Specimens are able to climb the trunk by obtaining purchase on the rough, flaky bark (Fig. 4), and have been observed at heights in excess of 2m. Only the trunk and main branches are scaled. Feeding trees have been at varying growth stages (refer Table 3) and have only included *A. falciformis*. Specimens found



FIG. 4. *P. orientalis* scaling an *Acacia falciformis* trunk.

in/on these acacias represent 75% of all specimens encountered during the study. From the recorded data, only 25 of a total of 101 specimens/observations were encountered on the ground, of these, 10 were observed on roads (7 active and 3 roadkills). Of the 4 individuals that were marked, one specimen was observed active on Tree I during 3 consecutive nights (obs. #101-103). It appears likely that trees which provide an accessible supply of sap are visited frequently until the sap source dries up. Tree I was investigated closely and no bark or crevices were suitable for daily refuge of an animal of such size. However, Tree I was a small *A. falciformis* (refer Table 3) and other much larger trees may provide shelter as well as sap. The possibility of a 'home,' feeding tree could not be investigated properly without severe damage to the trees. Shea (1987) records finding a specimen of *P. orientalis* inactive in a fold in a sheet of stringybark lying alongside a large fallen eucalypt in the Moura district (CQ).

FEEDING. Pygopodids are known to include both generalist arthropod feeders (e.g. *Pygopus* spp.) and specialist ant and skink feeders (*Aprasia* spp. and *Lialis burtonis*, respectively), (Greer, 1989). However, until a preliminary observation from this study (Tremul, 1997), sap feeding was unknown amongst pygopodids and

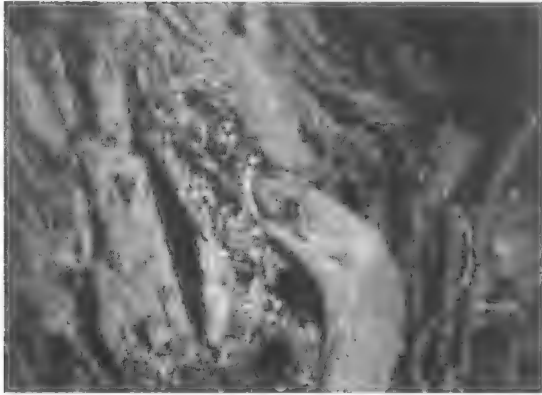


FIG. 5. *P. orientalis* feeding on sap.

nothing was known about the feeding habits of *P. orientalis* (see Greer, 1989).

Table 1 details observations of sap-feeding on *Acacia falciformis* specimens by juvenile and adult specimens of *P. orientalis*. Sap constitutes a significant portion of the diet of *P. orientalis*. Newly hatched individuals have a natural instinct to climb in search of this food. A specimen measuring 69mm snout-vent-length (SVL) and 76mm tail length (TL) and weighing 1.5g (body measurements and weight consistent with those taken of the hatched neonates) was observed on the trunk of *A. falciformis*, 30cm from the ground (obs. #93). Sap feeding continues through to adulthood with observations being recorded during all seasonal activity (Fig. 5). Of the 76 specimens/observations on trees, 20% were feeding and a further 9 were in very close proximity to sap. Adult specimens have remained perched at feeding sites for up to 46 minutes. However, the species is not an exclusive sap feeder. Scats collected from an individual from the study site (obs. #111) have also contained spider and some cricket-like, orthopteroid remains and many unidentified insect fragments. Three other scats collected (25/1/99) outside of Boyne I. (20km, N of Dingo, CQ) have consisted of tightly compressed membranous material (mostly plant) and the remains of a large spider and cricket. Other animals also feed on the sap of *A. falciformis*. The Sugar Glider (*Petaurus breviceps*) and *Gehyra dubia*, a common gecko, both do so in the study area (obs. #88, #103, #107). The former is well known as a sap feeder and noted for its ability to make incisions into the bark of trees to assist sap flow. These gliders have been observed feeding on sap at a height and position well within reach of *P. orientalis*. The latter was reported recently to include sap in its

diet with feeding trees known to include *Acacia leiocalyx*, *A. conferta* and *A. decora* (Couper et al., 1995).

BREEDING. There is little data on breeding in all pygopodid lizards, no direct observation on any aspects of breeding in *P. orientalis* have been reported. It was believed to be an egg layer with a clutch size of two (e.g. Wilson & Knowles, 1988; Greer, 1989). During this study one gravid female *P. orientalis* was collected (27 October, 1994, obs. #30) and held captive in a closed container, consisting of leaf litter and moist, friable soil.

Between 6-8 November, 1994 this specimen deposited two pale, elongate eggs (34 × 12mm; 37 × 11mm). The latter weighed 3.9g (to maximise hatching chances, the former was not handled). Eggs hatched (81 and 82 ± 1 days later, during an estimated temperature range of 18-36°C) on 27 and 28 January, 1995. The hatching process took from 7.5-53 hours. First indication that the smaller egg was hatching occurred at 9.00am, 25 January, when transparent fluid exuded from a small slit in the shell. This continued for 12 hours, when a small, serrated object (possibly an egg tooth) protruded from the slit. Twenty-two and a half hours after the process had begun, the serrated object had been shed; at 28 hours the neonate began to emerge; final detachment from the egg/yolk was complete at 53 hours (on 27 January, 1995); refer Fig. 6. The second egg (diameter 12mm) began to hatch at 7.00am on 28 January. The process was similar but was completed in considerably less time (7.5 hours). At emergence, the neonates had the following dimensions and weights: SVL 69mm, 72mm; TL 71mm, 78mm; weight 1.5g, 1.7g. Both were released with their mother at the point of capture.

AUTOTOMY/AGGRESSION. Of the 16 individuals measured, 75% had varying stages of obvious autotomy (Table 2). No evidence of intraspecific aggression has been observed. Large adults feeding off the same clump of sap, and two sub-adults and a juvenile within very close proximity have not displayed any agonistic behaviour (obs. #41, #75). Predation on *P. orientalis* was not seen during this study. Vocalisation was only heard from one specimen handled (obs. #115) with the call consisting of a soft squeak. Specimens pursued in the open have occasionally flung themselves into the air (obs. #8, #32, #93), a habit shared by some species of *Delma* (see Greer, 1989).

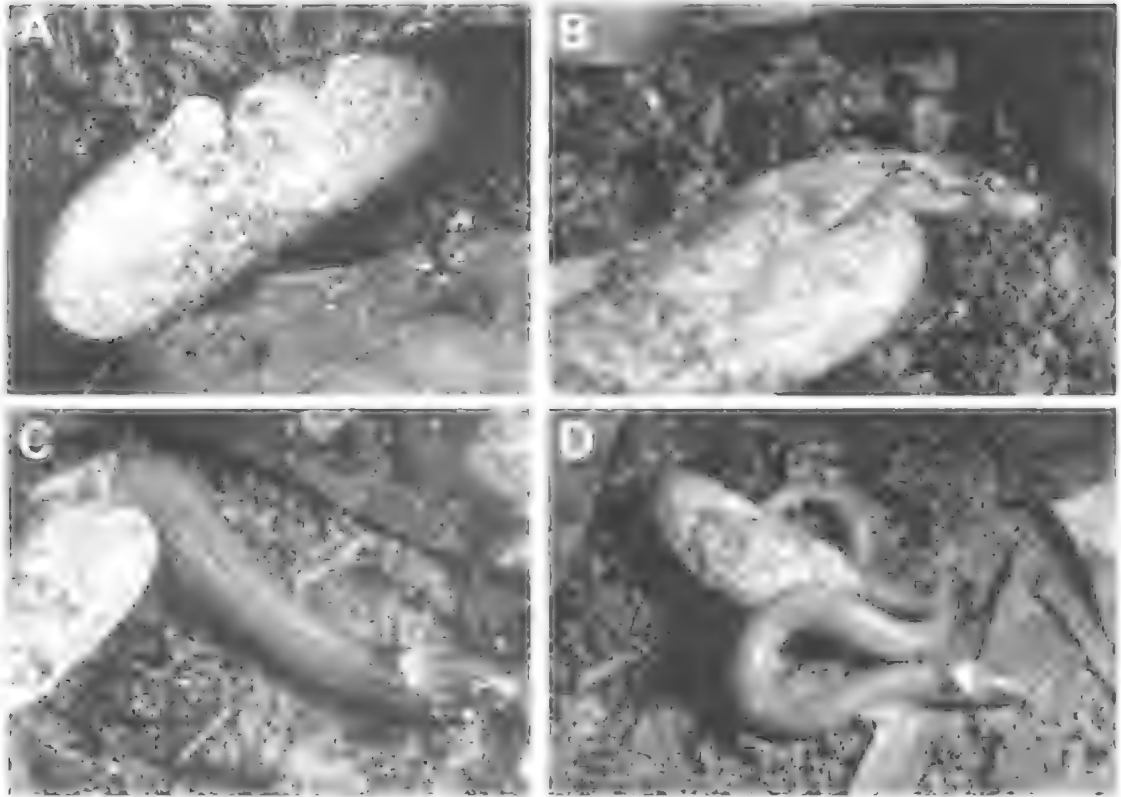


FIG. 6. *P. orientalis* hatching: A, fluid exuding from egg; B,C, neonate emerging from egg; D, neonate detaching from egg.

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TABLE 1. Observations of *P. orientalis*. # = observation number; Cu = current temp., m = minimum temp., M = maximum temp.; P = *P. orientalis*, J = juvenile, A = adult, S = sub-adult; rd = road, rk = road kill, T = tree, G = ground; u = up, d = down, hz = horizontal; y = yes, n = no, l = likely; nr = not recorded. Temperatures in bold measured at Lilly Hills, temperatures in italics measured at Gladstone (Bureau of Meteorology).

#	Date	Time	Temp. °C			Active/ loc.	Tree/ Grd.	Height/ Facing	Feed- ing	Weather / comments
			Cu	m	M					
1	18/4/89	7-9pm	<i>nr</i>	<i>20</i>	<i>29</i>	S/ site b	T	0.4m/d	n	nr
2	22/4/89	7-9pm	<i>nr</i>	<i>21</i>	<i>27</i>	S/ site a	T	0.15m	n	nr
3	28/4/89	7.40pm	<i>nr</i>	<i>19</i>	<i>29</i>	J/ site c	T	0.2m/d	n	cloudless, no wind
4	10/12/89	7.20pm	<i>nr</i>	<i>21</i>	<i>30</i>	P/ n r	T	nr	n	nr
5	11/12/89	7.30pm	<i>nr</i>	<i>21</i>	<i>32</i>	P,P/n r	T,T	nr	n	nr
6	14/12/89	8.05pm	<i>nr</i>	<i>23</i>	<i>32</i>	P/ n r	T	nr	n	nr
7	17/12/90	8.50pm	<i>nr</i>	<i>23</i>	<i>31</i>	S/ site c	T	nr/d	l	nr/ sap present near head
8	17/12/90	9.00- 10.00pm	<i>nr</i>	<i>23</i>	<i>31</i>	A/ rd	G	-	-	nr/ specimen flung itself up into the air when pursued
9	18/12/90	10.20pm	<i>nr</i>	<i>22</i>	<i>31</i>	J/ nr	G	-	l	nr/ specimen had its head in a groove of a trunk which contained sap
10	19/12/90	n/r	<i>nr</i>	<i>23</i>	<i>32</i>	A/ n r	G	-	-	nr/ active in dense leaf litter, opposite study site
11	20/12/90	11.28pm	<i>nr</i>	<i>23</i>	<i>32</i>	J/ site d	T	nr/ u	n	nr/ specimen retreated down burrow when disturbed
12	20/12/90	nr	<i>nr</i>	<i>23</i>	<i>32</i>	S/ site c	G	nr	-	nr
13	21/12/90	8.08 - 8.54p.m	<i>nr</i>	<i>24</i>	<i>32</i>	A/site e	T	nr/ u	y	nr/ specimen feeding for 46 minutes
14	4/1/91- 5/1/91	11.15pm- 12.01am	<i>nr</i>	<i>21</i>	<i>25</i>	none	-	-	-	100% overcast; strong to moderate wind heavy rain fell during the day; ground and trunks of Acacias damp.
15	5/1/91- 6/1/91	11pm- 12.01am	<i>nr</i>	<i>23</i>	<i>29</i>	none	-	-	-	100% overcast, high humidity; calm, heavy rain fell during the day; ground and trunks of Acacias damp.
16	6/1/91- 7/1/91	11.15pm- 12.15am	<i>nr</i>	<i>25</i>	<i>30</i>	none	-	-	-	75% overcast; calm; light drizzle occasionally; ground and trunks of Acacias saturated.
17	8/1/91	9.15pm- 10.10pm	<i>nr</i>	<i>23</i>	<i>29</i>	none	-	-	-	cloudless; moderate to strong SE wind; trunks of Acacias dry; ground damp.
18	9/1/91	8.30pm- 9.30pm	<i>nr</i>	<i>21</i>	<i>28</i>	none	-	-	-	moderate to strong SW wind, light rain during the day; ground and Acacia trunks dry.
19	10/1/91	8.20pm- 9.15pm	<i>nr</i>	<i>21</i>	<i>28</i>	none	-	-	-	strong SW wind; 75% overcast; ground and trunks of Acacias dry.
20	11/1/91	8.20pm- 9.15pm	<i>nr</i>	<i>21</i>	<i>30</i>	S,A,S/ site d,d, nr	T,G,T	nr	n	nr/ 3 specimens active; large <i>Lialis burtonis</i> active on ground at site c
21	15/1/91	9.15pm- 10.05pm	<i>nr</i>	<i>22</i>	<i>31</i>	P,P/ nr	T,T	nr	n	10% cloud cover; no wind
22	29/8/91	8.10pm	<i>21</i>	<i>18</i>	<i>29</i>	P/nr	T	0.2m/u	y	10% cloud cover
23	30/8/91	8.30pm	<i>22</i>	<i>19</i>	<i>28</i>	A/nr	T	0.05m/d	n	no cloud cover
24	30/10/91	8.45pm	<i>nr</i>	<i>19</i>	<i>27</i>	P/rk	G	-	-	nr/ found on Handley Drive
25	13/9/93	nr	<i>nr</i>	<i>17</i>	<i>25</i>	P,P/nr, rd	T,G	0.03m /nr	-	nr/ second specimen found on Centenary Drive
26	20/9/93	nr	<i>nr</i>	<i>19</i>	<i>31</i>	P/rd	G	-	-	specimen active on Handley Drive
27	3/4/94	nr	<i>nr</i>	<i>21</i>	<i>31</i>	S/rk	G	-	-	found on Centenary Drive, opposite study site.

TABLE 1. (cont.)

#	Date	Time	Temp. °C			Active/ loc.	Tree/ Grd.	Height/ Facing	Feed- ing	Weather / comments
			Cu	m	M					
28	11/10/94	8.00pm	nr	18	28	P,P/nr	T,T	-	l	<10% cloud cover/ both specimens had their heads between loose bark and a clump of sap
29	21/10/94	nr	nr	20	30	P/rd	G	-	-	nr/ active on Handley Drive
30	27/10/94	nr	nr	18	28	P/rd	G	-	-	nr/ active on Handley Drive; gravid.
31	11/1/95	nr	nr	22	32	A/rd	G	-	-	nr/ active on Handley Drive.
32	21/3/95	7.45pm	nr	23	nr	S/rd	G	-	-	<10% cloud cover. warm/active on Handley Dr specimen flung itself into the air in a similar manner to <i>Delma</i> .
33	27/3/95	7.30-8.00pm	nr	26	nr	P,P,P/ nr	T,T,T	nr,nr, 1n/nr	-	<10% cloud cover/ there is an abundance of sap.
34	25/9/95	nr	nr	20	30	P,P,P/ nr	T,T,T	0.67, 1.2, 1.3/u,u,u	l,y,n	humid, cloudless night/ sp. 1 had sap present near head; sp.2 was feeding; sp.3 had sap 0.76m above it.
35	8/2/96	nr	nr	25	34	P,P,P/ nr	T,T,G	nr	n	a warm, humid and cloudless night.
36	18/8/96	7.00pm	21	18	26	none	-	-	-	nr/ <i>Heteronotia bynoei</i> and <i>Morelia spilota</i> active.
37	17/11/96	8.00pm	nr	24	32	A/nr	T	0.2m/d	n	cloudless night/ sap 0.1m below head
38	18/11/96	nr	nr	24	36	A/nr	T	0.3m/up	n	cloudless, high humidity / specimen slowly moved up tree towards sap exudates.
39	22/1/97	nr	nr	20	28	A,A,A, A,A/ tree f, nr	T,T,T, T,T	nr	y,n,n, n,n.	nr/ three specimens clumsily fell to the ground when disturbed.
40	24/1/97	7.45-8.45pm	nr	22	nr	A/tree f	T	nr	y	nr/ specimen was photographed feeding on sap.
41	28/1/97	7.45-8.45pm	nr	26	32	A,A,P, P,P,P/ nr	T,T,T, T,G	2m,2.5m, nr/up,n, nr	y,y	warm, high humidity / one specimen climbing to a clump of sap (2m); another specimen from higher above (2.5m) climbed down to the same sap; both specimens fed off sap simultaneously, the presence of another individual tolerated.
42	6/8/97	7.35pm	18	13	23	none	-	-	-	40% cloud cover, no wind.
43	7/8/97	7.50pm	18	15	23	none	-	-	-	no cloud cover or wind.
44	8/8/97	8.00pm	19	16	26	none	-	-	-	50% cloud cover, no wind/ <i>Oedura rhombifer</i> active on tree
45	9/8/97	8.10pm	17	15	22	none	-	-	-	30% cloud cover, no wind/ heavy rain fell at 3am.
46	10/8/97	8.00pm	17	13	23	none	-	-	-	no cloud cover or wind/ a windy day; <i>Gehyra dubia</i> active.
47	11/8/97	8.10pm	17	12	23	none	-	-	-	no cloud cover or wind.
48	12/8/97	8.15pm	19	15	26	none	-	-	-	20% cloud cover, no wind/ <i>Gehyra dubia</i> active on ground.
49	13/8/97	7.45pm	16	13	26	none	-	-	-	no cloud cover, slight breeze/ strong moonlight.
50	14/8/97	8.10pm	18	12	25	none	-	-	-	no cloud cover, slight breeze/ waxing gibbous, strong moonlight.
51	15/8/97	7.35pm	18	15	26	none	-	-	-	no cloud cover, slight breeze/ strong moonlight.
52	16/8/97	7.55pm	17	15	26	none	-	-	-	no cloud cover, slight breeze/ strong moonlight.
53	17/8/97	8.05pm	18	15	27	none	-	-	-	no cloud cover or wind/ strong moonlight.
54	18/8/97	8.15pm	18	15	27	none	-	-	-	no cloud cover or wind/ full moon.
55	19/8/97	8.05pm	18	15	27	none	-	-	-	no cloud cover or wind.
56	20/8/97	7.55pm	19	16	27	none	-	-	-	no cloud cover or wind/ no moonlight; <i>Heteronotia bynoei</i> active.
57	21/8/97	7.40pm	19	15	26	none	-	-	-	10% cloud cover, slight breeze/ no moonlight.
58	22/8/97	7.35pm	19	15	26	none	-	-	-	10% cloud cover, slight breeze/ no moonlight.
59	23/8/97	7.55pm	17	13	26	none	-	-	-	no cloud cover or wind/ no moonlight.
60	24/8/97	7.40pm	19	15	25	none	-	-	-	no cloud cover, slight breeze/ no moonlight.
61	25/8/97	7.35pm	14	12	25	none	-	-	-	no cloud cover or wind/ no moonlight
62	26/8/97	8.00pm	15	10	25	none	-	-	-	no cloud cover, slight breeze/ no moonlight; sugar glider seen.
63	27/8/97	7.45pm	15	10	27	none	-	-	-	no cloud cover or wind/ no moonlight, calm and cold.
64	28/8/97	7.50pm	18	12	25	none	-	-	-	no cloud cover, slight breeze/ no moonlight.
65	29/8/97	7.40pm	19	15	27	none	-	-	-	40% cloud cover, slight breeze/ no moonlight.
66	30/8/97	8.00pm	19	15	27	S/ tree a	T	nr	n	40% cloud cover, moderate wind/ no moonlight, humid.
67	31/8/97	7.50pm	19	17	27	none	-	-	-	no cloud cover, slight breeze/ rat active in <i>A. falciformis</i>
68	1/9/97	7.55pm	19	16	27	none	-	-	-	no cloud cover slight breeze/ no moonlight.
69	2/9/97	7.52pm	22	17	27	none	-	-	-	60% cloud cover, moderate wind/ no moonlight.
70	3/9/97	8.15pm	20	20	27	none	-	-	-	30% cloud cover, slight breeze/ leaf litter damp, heavy rain fell during the day; no moonlight.
71	4/9/97	8.10pm	21	17	27	S/ tree b	G	-	-	40% cloud cover, no wind/ no moonlight.
72	5/9/97	8.15pm	22	19	31	none	-	-	-	no cloud cover, slight breeze/ <i>Oedura rhombifer</i> active on <i>A. falciformis</i> ; no moonlight.
73	6/9/97	8.17pm	19	16	30	none	-	-	-	no cloud cover, slight breeze/ waxing crescent.
74	7/9/97	8.35pm	19	15	27	none	-	-	-	no cloud cover or wind/ sugar glider seen; partial moonlight.

TABLE 1. (cont.)

#	Date	Time	Temp. °C			Active/ loc.	Tree/ Grd.	Height/ Facing	Feed- ing	Weather / comments
			Cu	m	M					
75	8/9/97	8.20pm	21	17	32	S,S,I, S,S/ tree c, d, d, d, a	T,G, G,G, T	nr	y,y	no cloud cover or wind, humid, poor moonlight/ five specimens active, two up trees; the other three on the ground at the base of tree d and in very close proximity to each other.
76	9/9/97	8.10pm	19	16	29	P/ tree e	T	nr	n	no cloud cover, slight breeze/ poor moonlight. (first qu.)
77	10/9/97	8.13pm	19	15	27	none	-	-	-	no cloud cover or wind/ moderate moonlight; nippy.
78	11/9/97	8.15pm	19	15	27	none	-	-	-	70% cloud cover, cool breeze, light rain/ <i>Gehyra dubia</i> active on ground; filtered moonlight.
79	12/9/97	8.05pm	17	15	27	none	-	-	-	no cloud cover, moderate to strong wind/ ground and leaf litter damp; sugar glider seen at clump of sap; heavy rain fell during the day.
80	13/9/97	8.10pm	19	15	27	none	-	-	-	no cloud cover, cool breeze/ bright moonlight. (waxing gibbous.)
81	14/9/97	8.05pm	19	15	27	none	-	-	-	no cloud cover or wind/ very bright moonlight; nippy.
82	15/9/97	8.25pm	19	14	30	none	-	-	-	no cloud cover or wind/ very bright moonlight (full moon).
83	16/9/97	8.12pm	19	15	27	none	-	-	-	no cloud cover or wind/ very bright moonlight
84	17/9/97	8.30pm	19	16	30	none	-	-	-	no cloud cover or wind/ bright moonlight.
85	18/9/97	8.20pm	20	16	30	A/ tree f	T	nr	n	10% cloud cover, slight breeze/ full moon, rising.
86	19/9/97	8.40pm	21	19	26	none	-	-	-	80% cloud cover, slight breeze/ no moonlight, an overcast day with light rain.
87	20/9/97	8.30pm	21	19	30	A/ tree g	T	1m/nr	n	10% cloud cover, cool breeze/ no moonlight.
88	21/9/97	8.30pm	22	20	31	none	-	-	-	40% cloud cover, no wind/ two sugar gliders observed, one feeding on sap of <i>A. falciformis</i> , tree r1; heavy rain fell at 7.45pm.
89	22/9/97	8.30pm	22	20	31	none	-	-	-	20% cloud cover, no wind/ no moonlight; <i>Gehyra dubia</i> active on <i>A. falciformis</i> 4m up, next to clump of sap; <i>Pogona barbata</i> 2m's up an <i>A. falciformis</i> , motionless; vernal equinox
90	4/11/97	7.15pm	nr	20	31	A/ tree f	T	0.3m/nr	n	nr/ sugar glider active on <i>A. falciformis</i> .
91	14/11/97	8.00pm	nr	24	31	A/ tree d	T	nr	y	nr/ adult, gravid female feeding on sap
92	9/2/98	8.15pm	nr	25	33	A/ tree h	T	1.5m/nr	n	nr
93	25/2/98	8-9.00pm	nr	23	31	S,I/ nr	T,T	nr, 0.3m/nr, up	l	nr/ sap present near head of sub-adult; juvenile has weight (1.5 grams) and dimensions (s.v. 69, t.l. 76mm) similar to newly hatched individuals; when continually disturbed specimen flung itself up into the air (similar to <i>Delma</i>), no vocalisation was heard.
94	26/2/98	1.10- 1.20am	25	24	31	A,A/ nr, tree a	G,G	-	-	no cloud cover, slight breeze/ first specimen was active at base of unmarked <i>A. falciformis</i> , the other specimen was 3m from tree a.
95	26/2/98	9.30pm	27	24	31	I/ nr	T	0.3m/ nr	y	<10% cloud cover.
96	26/2/98	11.00pm	25	24	31	A/ tree t	T	2m/dn	n	light rain/ a large adult
97	27/2/98	8.15- 8.45pm	26	23	32	I/ nr	T	0.25m/ nr	n	10% cloud cover.
98	27/2/98	9.45- 11.00pm	nr	23	32	none	-	-	-	nr/ sugar glider observed at clump of sap on <i>A. falciformis</i> .
99	28/2/98	7.50- 8.30pm	27	23	32	A,A/ tree h, tree e	T,T	0.3, 0.9m/ nr, up	y, n	nr/ two large individuals; sap present near head of second specimen.; both specimens marked with whiteout, sp. A- one mark, 1cm back from dark neck band; sp. B- two marks, 2 cm back from dark neck band.
100	1/3/98	7.45- 8.45pm	24	23	30	none	-	-	-	no cloud cover/ leaf litter damp; heavy rain fell mid-afternoon.
101	2/3/98	7.30- 8.30pm	25	23	32	S,S/ tree l, nr	T, G	0.6m/ up	n	30% cloud cover/ both specimens marked with whiteout, sp. C- three marks, 3cm back from dark neck band; sp. D- one mark on mid-body.
102	3/3/98	7.30- 8.15pm	25	22	32	S,A,S/ tree l, f, nr	T,T,T	nr, 0.8, 0.2m/ nr, up, up	n,n,n	no cloud cover/ first specimen is sp. C, second consecutive night at tree l; specimen fell to ground when disturbed.
103	4/3/98	7.30- 8.15pm	26	23	30	S,A,S/ nr, nr, tree l	T,T,T	0.9m, nr, nr/ up, nr	n,n,n	40% cloud cover, humid/ the first two specimens were active on the same tree, third specimen is sp. C, third consecutive night at tree l; <i>Gehyra dubia</i> photographed feeding on sap of <i>A. falciformis</i> , (tree r2).
104	5/3/98	7.30- 8.30pm	26	23	32	none	-	-	-	no cloud cover, moderate moonlight (first quarter).
105	6/3/98	7.30- 8.30pm	26	23	34	none	-	-	-	no cloud cover; moderate moonlight.

TABLE 1. (cont.)

#	Date	Time	Temp. °C			Active/ loc.	Tree/ Grd.	Height/ Facing	Feed- ing	Weather / comments
			Cu	m	M					
106	7/3/98	8-8.45pm	27	23	36	S,A,S,P/ tree j, d, f, f	T,G,T, T	0.8, 2, 0.9m/ up, dn, dn	l,n,n,n	no cloud cover, moderate moonlight (waxing gibbous)/ sap present near head of first specimen; second specimen resting head on base of tree d; both other specimens active on tree f.
107	8/3/98	8.45- 9.40pm	24	24	33	S,S/ tree l, nr	G,T	<0.1m/ nr	n,l	40% cloud cover, light rain/ first specimen was at base of tree l; second specimen had sap near head; <i>Gehyra dubia</i> observed feeding on sap of <i>A. falciformis</i> , tree r2.
108	12/4/98	8.05pm	nr	23	31	S/ nr	T	0.8m/ up	l	80% cloud cover, humid/ sap present near head.
109	31/12/98	8-9pm	27	23	31	A,J/ nr	T,T	<0.1, 1.5 m/ up,hz	n,l	30% cloud cover/ sap present near head of juvenile.
110	11/1/99	9-10pm	26	22	32	J,S/ tree d, rk	T,G	0.1m/ dn	n	no cloud cover, slight breeze/ faecal sample collected from first specimen.
111	9/3/99	7-9pm	nr	23	30	P, nr	T	nr	n	nr/ faecal samples collected for analysis.
112	2/5/99	7-8.00pm	nr	14	26	none	-	-	nr	nr
113	7/5/99	7-8.00pm	18	18	26	none	-	-	-	nr/ <i>Diplodactylus vittatus</i> active on ground.
114	8/5/99	7-8.00pm	19	18	25	none	-	-	-	nr/ <i>Diplodactylus vittatus</i> active in leaf litter.
115	15/5/99	8-8.45pm	19	17	28	S/ nr	T	0.5m/ dn	n	no cloud cover/ specimen emitted a soft squeak when handled roughly.
116	22/5/99	6.15-7pm	20	18	nr	none	-	-	-	nr/ <i>Gehyra dubia</i> and <i>Heteronotia bynoei</i> active.
117	28/5/99	6.15-7pm	21	18	26	none	-	-	-	no cloud cover or wind/ <i>Gehyra dubia</i> active on ground.
118	29/5/99	6.30- 7.15pm	20	18	26	none	-	-	-	no cloud cover; full moon.
119	31/5/99	7-7.45pm	20	18	28	none	-	-	-	no cloud cover; full moon.
120	1/6/99	7-8pm	20	19	27	J,J,J/ nr	T,T,T	<0.1, <0.1, 1.1 m/up,up, up	y,y,y	slight breeze; waning gibbous, rising/ <i>Heteronotia bynoei</i> active on ground.
121	2/6/99	6.30- 7.15pm	19	16	26	none	-	-	-	slight breeze, cool.
122	3/6/99	6.30- 7.15pm	20	17	25	none	-	-	-	overcast, slight breeze/ <i>Gehyra dubia</i> active on ground.
123	4/6/99	6.30- 7.15pm	19	16	nr	none	-	-	-	no cloud cover or wind
124	5/6/99	6.30- 7.15pm	19	17	nr	none	-	-	-	100% overcast, no wind, drizzle.
125	6/6/99	6.30- 7.15pm	18	17	24	none	-	-	-	30% cloud cover, no wind; light rain fell during the day, ground damp, tree trunks dry.
126	12/6/99	6.15- 6.45pm	14	10	21	none	-	-	-	no cloud cover or wind.
127	13/6/99	6.10- 6.45pm	19	12	23	none	-	-	-	no cloud cover, moderate wind/ juvenile <i>Gehyra dubia</i> active on <i>A. falciformis</i> trunk.
128	20/6/99	6-6.30pm	16	13	23	none	-	-	-	no cloud cover or wind/ moderate moonlight.
129	30/6/99	7.30- 8.15pm	18	15	22	none	-	-	-	overcast, slight breeze/ rain during the day, trunks of trees and leaf litter still damp.
130	5/7/99	6.45- 7.15pm	18	15	22	none	-	-	-	no cloud cover or wind/ <i>Gehyra dubia</i> active on <i>A. falciformis</i> trunk; <i>Pogona barbata</i> perched on limb of <i>A. falciformis</i> .
131	7/7/99	7.15-8pm	17	16	23	none	-	-	-	no cloud cover or wind.
132	8/7/99	7.45- 8.15pm	17	15	23	none	-	-	-	no cloud cover or wind; nippy.
133	11/7/99	7.15-9pm	18	16	23	none	-	-	-	no cloud cover or wind; warm.
134	12/7/99	6.30- 7.20pm	19	17	24	none	-	-	-	10% cloud cover; slight breeze/ <i>Oedura rhombifer</i> active on <i>A. falciformis</i> ; <i>H. bynoei</i> active on ground.
135	17/7/99	6.30-7pm	16	13	23	none	-	-	-	no cloud cover or wind.
136	19/7/99	6.30-7pm	18	13	25	none	-	-	-	no cloud cover or wind; moderate moonlight.
137	20/7/99	6.30- 7.15pm	16	13	25	none	-	-	-	no cloud cover or wind.
138	23/7/99	6.15- 6.45pm	17	11	20	none	-	-	-	misty; no wind.
139	24/7/99	6.30- 7.00pm	13	13	17	none	-	-	-	30% cloud cover; no wind/ consistent light rain throughout the day.
140	25/7/99	6.20- 7.00pm	17	12	20	none	-	-	-	100% cloud cover; strong wind; mild.

TABLE 2. Body measurements of *P. orientalis*. SVL = snout-vent length, TL = tail length.

Date	SVL (mm)	TL (mm)	Total length (mm)	No. of distinguishable individuals 25/2/98-8/3/98
18/12/90	122	157, regrown	279	N/A
3/4/94	155	regrown	?	N/A
11/1/95	170	192, regrown	362	N/A
26/1/95	69	71, original	140	N/A
28/1/95	72	78, original	150	N/A
21/3/95	152	215, regrown	367	N/A
30/8/97	137	98, regrown	235	N/A
4/9/97	153	232, original	385	N/A
8/9/97	147	201, original	348	N/A
8/9/97	150	189, original	339	N/A
8/9/97	111	111, regrown	222	N/A
8/9/97	151	75, regrown	226	N/A
25/2/98	69	76, original	145	1
26/2/98	182	73, regrown	255	2
26/2/98	174	215, regrown	389	3
26/2/98	70	76, original	146	1?
26/2/98	182	227, regrown	409	4
27/2/98	79	85, original	164	5
28/2/98	182	110, regrown	292	6
28/2/98	190	257, end regrown	447	7
2/3/98	156	188, regrown	344	8
2/3/98	128	156, regrown	284	9
3/3/98	188	165, regrown	353	10
3/3/98	166	249, original	415	11
4/3/98	152	148, regrown recently	300	12
4/3/98	178	240, regrown	418	13
7/3/98	152	202, original	354	14
7/3/98	188	261, end regrown	449	7?
7/3/98	154	151, regrown	305	15
8/3/98	152	207	359	14?
8/3/98	132	183, end regrown	315	16
12/4/98	148	195, original	343	N/A
31/12/98	172	225	397	N/A
31/12/98	97	114	211	N/A
11/1/99	108	132, end regrown	240	N/A
11/1/99	160	broken (roadkill)		N/A
15/5/99	145	212, end regrown	357	N/A
1/6/99	77	90, original	167	N/A
1/6/99	104	118, end regrown	222	N/A

TABLE 3. Measurements of feeding trees of *P. orientalis*.

Tree	SA	SB	SC	SD	SE	SF	SG	SH	A	B	C	D	E	F	G	H	I	J
Dia. 1m up (mm)	55	150	105	110	55	35	55	55	125	150	60	85	75	230	50	130	100	140
Est. height (m)	4	6	5	6	4	4	4	4	5	6	4	5	4	10	5	7	5	5



REASSESSMENT OF NORTHERN REPRESENTATIVES OF THE *ANTECHINUS STUARTII* COMPLEX (MARSUPIALIA: DASYURIDAE): *A. SUBTROPICUS* SP. NOV. AND *A. ADUSTUS* NEW STATUS

S. VAN DYCK AND M.S. CROWTHER

Van Dyck, S. & Crowther, M.S. 2000 06 30: Reassessment of northern representatives of the *Antechinus stuartii* complex (Marsupialia: Dasyuridae): *A. subtropicus* sp. nov. and *A. adustus* new status. *Memoirs of the Queensland Museum* 45(2): 611-635. Brisbane. ISSN 0079-8835.

Antechinus subtropicus sp. nov. is described from the subtropical rainforests of southeastern Queensland and northeastern New South Wales, and *A. adustus* from tropical rainforests in northeastern Queensland is elevated to full specific status from *A. stuartii adustus*. *Antechinus subtropicus* differs from other members of the *A. stuartii* complex (which includes *A. stuartii*, *A. agilis* and *A. adustus*) by its larger size (weight, body length and cranial length), relatively longer and narrower rostrum, extremely large palatal vacuities and large entoconid on M₃. *Antechinus adustus* differs from other members of the *A. stuartii* complex by its darker pelage, short, broad rostrum, very large crowned upper incisors, small alisphenoid tympanic wings and fixed differences at 15% of isozymes screened. These species and current research show that much work is still needed to resolve the taxonomy of the *A. stuartii*-*A. flavipes* species complex, and that a combined morphological and biochemical approach is likely to be most productive. □ *Antechinus subtropicus*, *Antechinus adustus*, *Antechinus stuartii*, rainforests, Queensland, northern New South Wales, morphometrics, dasyurid.

S. Van Dyck, Queensland Museum, PO Box 3300, South Brisbane 4101; M.S. Crowther, School of Biological Sciences and Institute of Wildlife Research, University of Sydney 2006, Australia; 29 October 1999.

Continuing uncertainty surrounds the taxonomic status of populations currently allocated to *Antechinus stuartii* and *A. flavipes* (Marsupialia: Dasyuridae) in eastern Australia, with substantial morphological variation existing within and between both taxa (Dickman et al., 1998). A lack of reliable diagnostic characters separating these two taxa has persisted for some three decades following the resurrection of *A. stuartii* from synonymy with *A. flavipes* by Wakefield & Warneke (1967).

Macleay (1841) erected the genus *Antechinus* and described *stuartii* on the basis of the collector's notes of a lost specimen from Sydney, although he later examined a skeleton from the same locality (Macleay, 1842). Wakefield & Warneke (1967) selected a neotype from Waterfall, Royal National Park, near Sydney. Prior to Wakefield & Warneke's revision, *A. stuartii* had been synonymised with *A. flavipes* by most authors from Iredale & Troughton (1934).

Dickman et al. (1988, 1998) discovered that *A. stuartii* as recognised by Wakefield & Warneke (1967) actually consisted of more than one electrophoretically and morphologically distinct species. These species appear to be reproductively isolated in sympatry by synchronisation of

ovulation and mating at different rates of change of photoperiod (McAllan & Dickman, 1986; Dickman et al., 1988). *Antechinus stuartii sensu stricto* was found to occur from Kioloa (35°32'S, 150°23'E) in the south to Barrington Tops (32°03'S, 151°27'E) in the north with the new species, *A. agilis*, occurring in southern New South Wales (NSW) and Victoria (Vic.). No electrophoretic sampling of *Antechinus* had been done in northern NSW until Sumner & Dickman (1998), who suggested further that *A. stuartii* extends into southern Queensland (Qld).

Van Dyck (1982a) found that *A. stuartii* from the subtropical rainforest in southeastern Qld differed greatly in morphology from the type of *A. stuartii* and populations in NSW and Vic. Van Dyck (1997) raised the southeastern Qld populations to subspecies level (*A. stuartii subtropicus*) but even at that time suspected that *subtropicus* likely warranted full specific rank. *Antechinus stuartii subtropicus* and *A. stuartii* showed substantial overlap in their distributions, which alerted us to their possible full species status (Van Dyck, 1997).

The distinct nature of *Antechinus adustus* was first realised by Thomas (1923). Initially, he assigned it to *Phascogale flavipes adusta*, but a

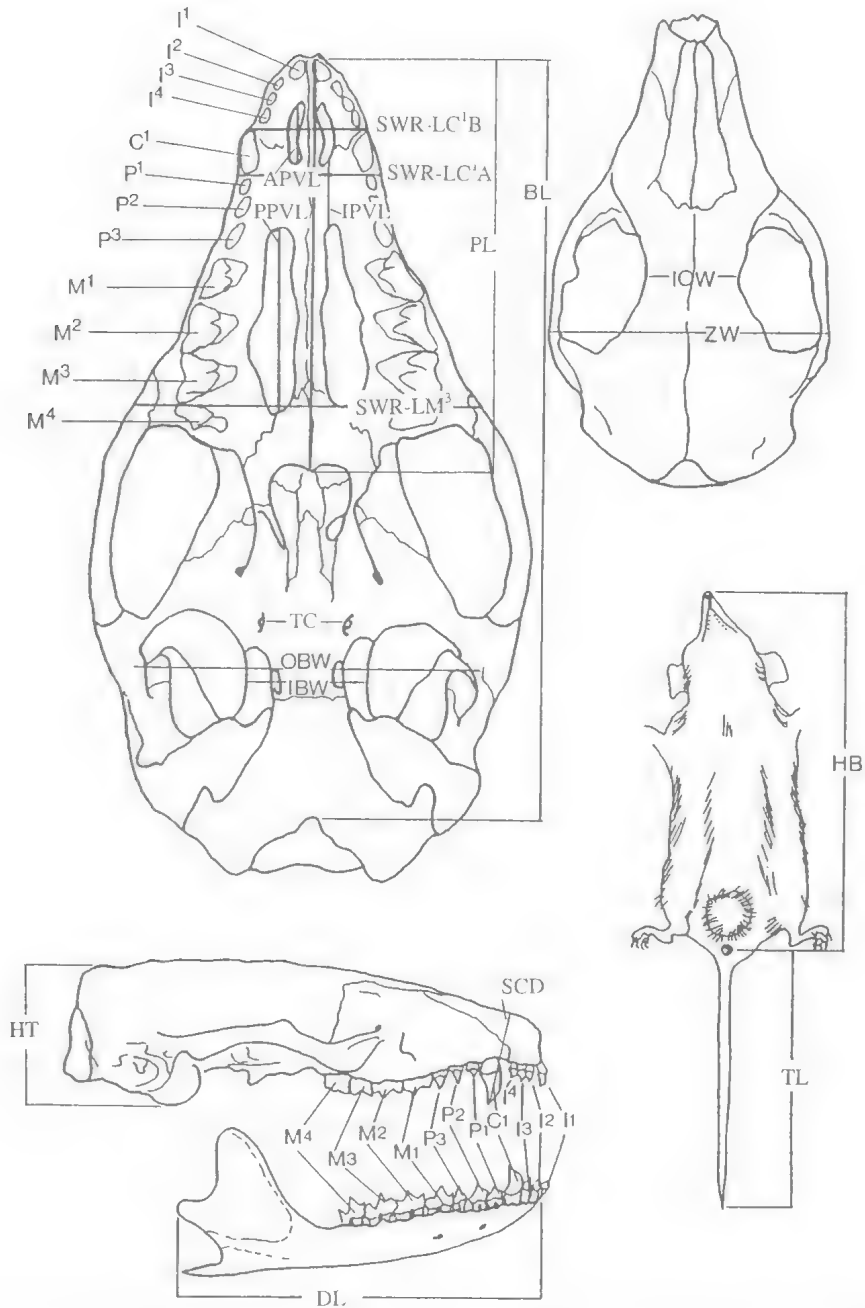


FIG. 1. Measurements taken of skull, dental and external characters of *Antechinus*. Basicranial skull length (BL); length of palate (PL); crown length P¹ to P³ (P¹⁻³), crown length P¹ to P² (P¹⁻²); skull width across anterior of C¹-C¹ (SWR-LC¹B); skull width across posterior of C¹-C¹ (SWR-LC¹A); crown length C¹ to M⁴ (C¹M⁴); inter-palatal vacuity distance (IPVL); skull width level with junction M³-M⁴ (SWR-LM³); minimum separation between transverse canals (TC); interbulla width (IBW); maximum width across bullae (OBW); interorbital constriction (IOW); zygomatic width (ZW); snout-C¹ depth, at right angle to dorsal surface of rostrum (SCD); anterior palatal vacuity length (APVL); posterior palatal vacuity length (PPVL); dentary length, excluding incisors (DL); crown length from M¹ to M³ (M¹⁻³); crown length from M¹ to M⁴ (M¹⁻⁴); skull height (HT); snout-vent length (HB); Tail length, from vent (TV); ear length from the notch to pinna tip (EAR); pes length taken from the heel to distal tip of toe (PES); body weight (WT).

year later, recognising a great similarity between the syntypes of *Phascogale unicolor* and *P. adusta*, assigned his *P. adusta* to Gould's *P. unicolor* (= *A. stuartii stuartii*) (see Thomas, 1924). However, it was another 44 years before *P. adusta* was formally disentangled, along with *A. stuartii*, from synonymy with *A. flavipes* (Wakefield & Warneke, 1967). Since its description until 1967, it was referred to in the literature as a subspecies of *A. flavipes* (e.g., Troughton, 1941 (as *Antechinus*); Tate, 1947; Tate, 1952; Brass 1953; Homer & Taylor, 1959; Marlow, 1961; Walker, 1964). However, Jenkins & Knutson (1983) still considered the *P. adusta* holotype (BMNH 1922.12.8.54) referable to *A. flavipes*. Wakefield & Warneke (1967) concluded that there were insufficient specimens and distribution data to assess the status of the tropical population but noted that 'The population of northeast Qld probably warrants separate subspecific status' (p. 73). Van Dyck (1982a) presented a range of morphological and distributional data supporting the subspecific nature (at the least) of *A. adustus*, but added 'while the subspecific status of *adustus* is justified on the basis of pelage, cranial and dental uniqueness, these factors combined with its geographical isolation should accord it with full specific rank. Its status, however may be revealed more reliably through such channels as reproductive biology and biochemical comparison (Van Dyck 1982a: 749). Results of isozyme electrophoresis have since showed *A. adustus* from Ravenshoe to differ from *A. stuartii* and *A. agilis* from south coastal NSW at 15% of 32 loci scored (Baverstock et al., 1982; Dickman et al., 1998).

In this paper we define a new species, *Antechinus subtropicus*, and raise *A. stuartii adustus* to full species.

METHODS

Listed in Figure 1 are the 21 skull and dental, and 5 external measurements taken, their abbreviations, and the manner in which the measurements were made. Skull and dental dimensions were taken with digital calipers. Age variation was minimised for statistical analysis by using only those skulls which possessed fully erupted permanent P³, and no measurements were taken from sub-adult animals captured in the four months prior to April in any year.

Tooth number follows Luckett (1993), tooth nomenclature follows Archer (1974) and basicranial nomenclature follows Archer (1976).

Colour nomenclature follows Ridgway (1912) and is designated with a capital letter in the text.

Univariate summary statistics and tests, and multivariate statistical analyses were undertaken with Systat 7 (SPSS 1997). Samples were tested for normality with the Kolmogorov-Smirnov Lilliefors test and homogeneity of sample variances was tested with Levene's test. Canonical variates analysis, discriminant function analysis and one-way ANOVA with Tukey's Post Hoc test were used to compare species. Tests were considered significant at the experiment-wide error rate $\alpha < 0.05$ after application of the sequential Bonferroni test (Rice, 1989).

The *A. stuartii* and *A. agilis* used in the analyses were specimens used in Dickman et al. (1998); some were electrophoretically typed, others were from localities mentioned in Dickman et al. (1988). This was to allow for variation within these species as well as minimising the use of undescribed or misidentified taxa. Exact locations are given in Dickman et al. (1998) and are lodged with the Australian Museum.

Institution abbreviations. In the course of this study, many specimens were examined from the Queensland Museum, Brisbane (QM); Australian Museum, Sydney (AM); Museum of Victoria, Melbourne; Australian National Wildlife Collection, Canberra (CSIRO); British Natural History Museum, London (BMNH); and American Museum of Natural History.

SYSTEMATICS

Antechinus subtropicus sp. nov. (Figs 2, 3; Table 1)

ETYMOLOGY. The species name is a reference to the subtropical distribution and habitat of the species.

MATERIAL HOLOTYPE: QM J17407, adult male skull, dentaries and puppet skin; 2 July 1969, T.H. Kirkpatrick. **OTHER MATERIAL:** Anstead, Moggill 27°33'S 152°52'E (QM JM9737); Ballandean 28°48'S 151°50'E (J6080); Bellthorpe 26°51'S 152°43' (QM JM9803); Binna Burra 28°12'S 153°11'E (QM J11442); Blackfellow Creek, Gatton 27°45'S 152°13'E (QM JM10269); Border Ranges National Park 28°15'S 153°05'E (QM JM7943-7948, 7965); Ferny Grove 27°24'S 152°56'E (QM JM7813); Jolly's Lookout 27°24'S 152°48'E (QM JM5500); Conondale Range 26°51'S 152°43'E (QM JM2258-2261, 2263-2266) Cunninghams Gap 28°03'S 152°24'E (QM JM256); Eastern Border Ranges National Park 28°27'S 152°50'E (QM JM7941, 7942, 7959-7962); Emu Vale 28°14'S 152°15'E (QM J15888, 9996, 9997); Farm Creek, Mt Colliery 28°17'S 152°09'E (QM J21315); Joyners Ridge 27°16'S 152°52'E (QM JM5504);

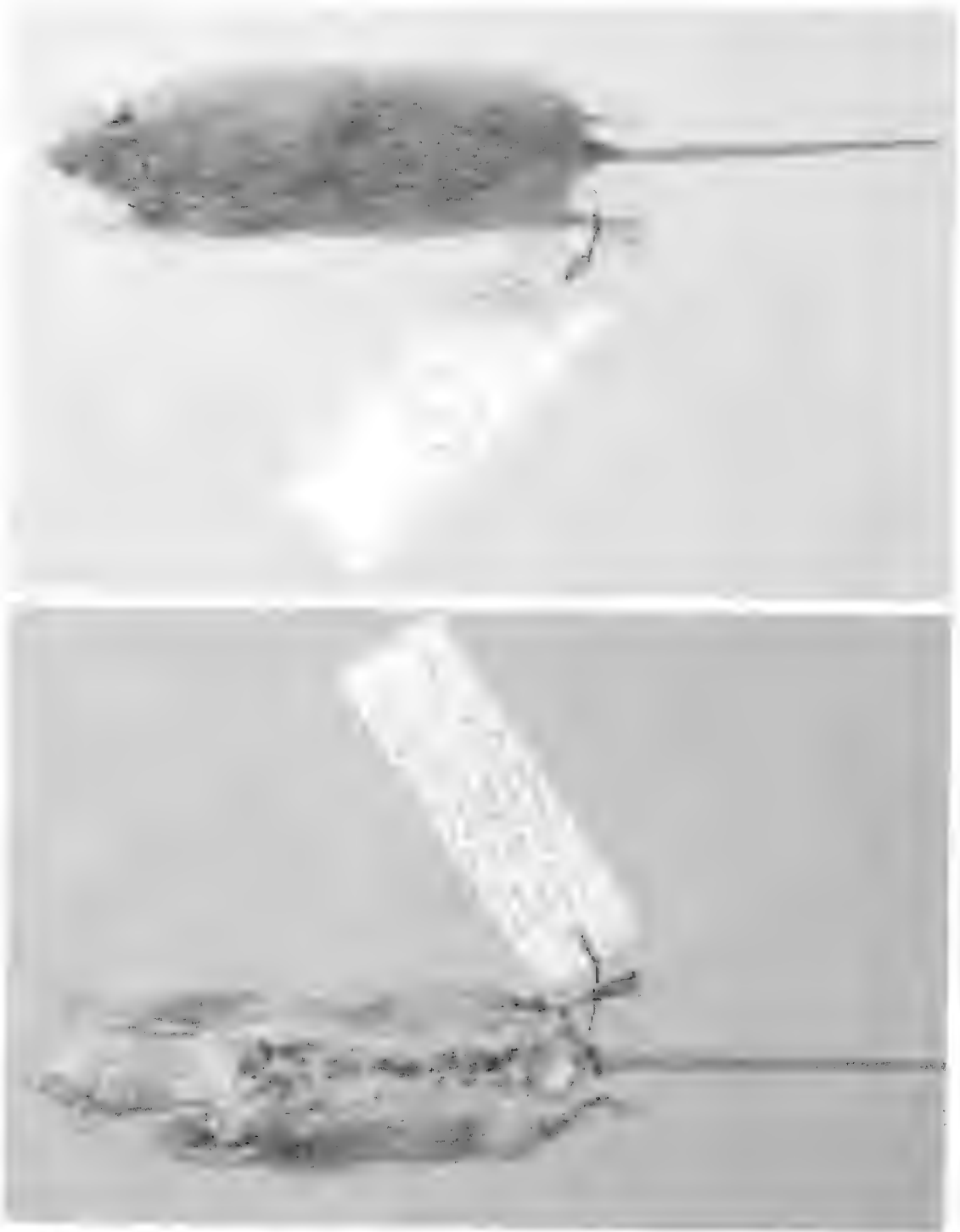


FIG. 2. Study skin of the holotype of *Antechinus subtropticus* (QM J17407). Dorsal view (above) and ventral view (below).

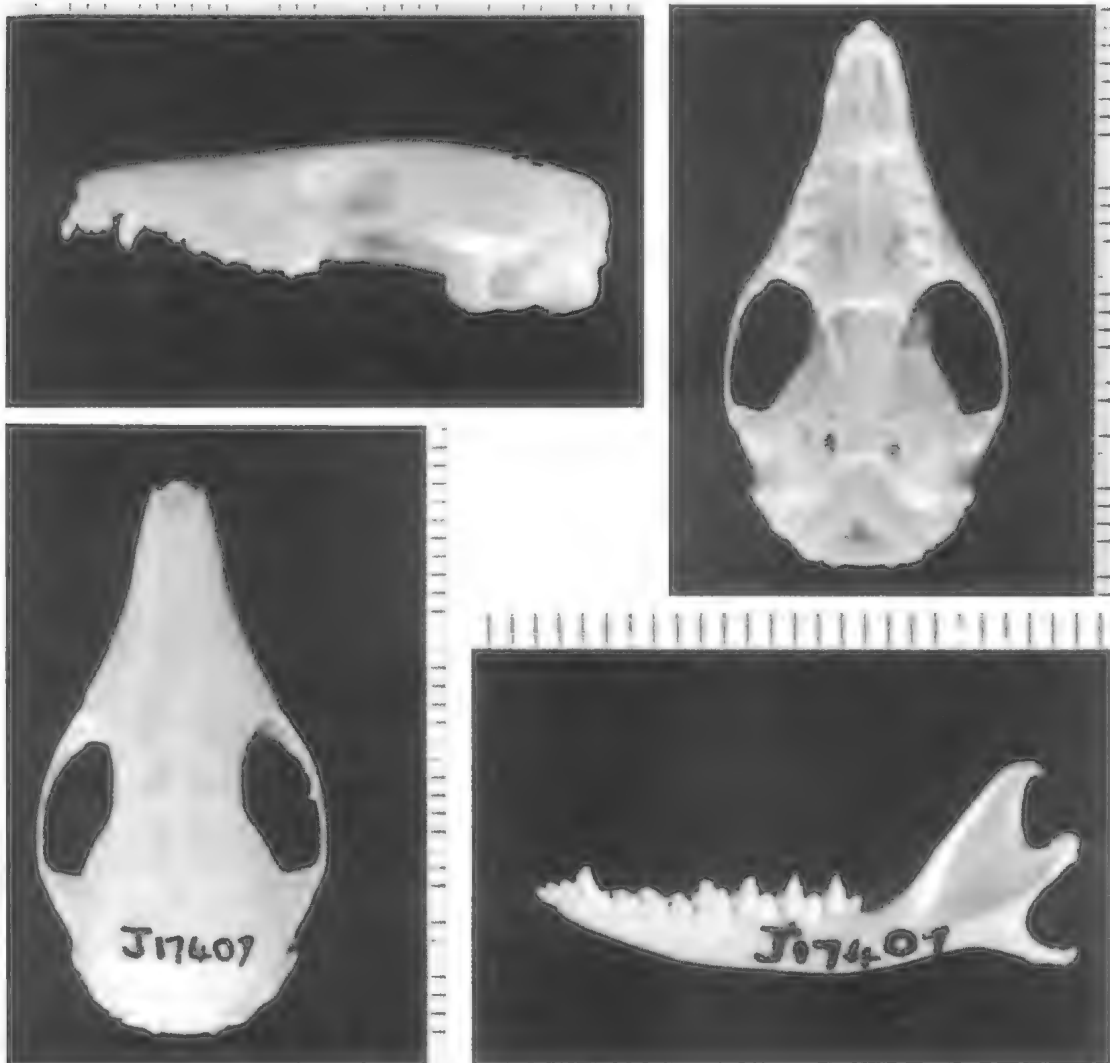


FIG. 3. Skull and left dentary of the holotype of *Antechinus subtropicus*. (QM J17407). Scales in millimetres.

Kondalilla National Park 26°40'S 152°52'E (QM JM1597-1599); Lamington Plateau 28°16'S 153°09'E (QM JM3570); Mapleton 26°38'S 152°52'E (QM JM9944); Mebbin State Forest 28°28'S 153°10'E (CSIRO CM2988, 2991, 3713); Montville 26°41'S 152°54'E (QM JM2770); Morans Falls 28°14'S 153°08'E (QM JM9941); Mt Gannon 28°12'S 153°19'E (QM JM5654, 5655, 6932, 6933); Mt Glorious 27°20'S 152°46'E (QM JM7, 9-15, 19, 22-27, 30, 47, 51, 134, 136-170, 183, 185-188, 205, 206, 569, 570, 1221, 1229, 1421, 1912, 1913, 1920-1936, 2204, 2205, 2290-2292, 2773-2775, 2841, 2850, 2878, 2879, 5653, 5656, 6181-6183, J10471, J10773, J10882, J11098, J11443, J11486, J12669, J13234, J13235, J13244, J13383, J16158, J16458, J16535, J16543, J17410, J17429-J17432, J19864); Mt Nebo 27°24'S 152°47'E (QM JM6184, 5501); Mt Nullum 28°50'S 153°26'E (AM M24904, 24905); Mt Roberts 28°13'S 152°27'E (QM J11618, 11619); Mt

Tamborine 27°56'S 153°12'E (QM J3716); Numinbah Arch, Nerang Valley 28°13'S 153°14'E (QM JM1420); O'Reillys 28°14'S 153°08'E (QM JM7107, 7108); Rozens Lookout, Beechmont 28°08'S 153°12'E (QM JM1418); Rummery Park, Whian Whian State Forest 28°38'S 153°19'E (AM M29961); Sheepstation Creek, Border Ranges National Park 28°24'S 153°01'E (AM M22782-22785, 22789); Sunday Creek 26°44'S 152°30'E (QM JM1601); Uki 28°28'S 153°14'E (QM JM4432); Upper Tallebudgera Creek 28°06'S 153°27'E (QM J20265); Warrie National Park 28°13'S 153°17'E (QM JM1600, 1596); Warwick district 28°13'S 152°02'E (QM J17400-17403, 17406, 17407); Whian Whian State Forest, via Dunoon 28°38'S 153°19'E (QM JM1919, 1419); Woondum State Forest, near Gympie 26°15'S 152°44'E (QM J15870).

TABLE 1. Selected measurements of type specimens (all male) of *Antechinus subtropicus*, *A. adustus*, *A. stuartii*, *A. agilis*, *A. unicolor*, *A. flavipes burrelli* and *A. flavipes* based on measurements taken by Van Dyck, Crowther and Dickman. Abbreviations as in Fig. 1.

Measurement (mm)	<i>A. subtropicus</i> QM J17407	<i>A. adustus</i> BMNH 22.12.18.54	<i>A. stuartii</i> AM M5294	<i>A. agilis</i> AM M33319	<i>A. unicolor</i> BMNH 54.11.19.2	<i>A. flavipes burrelli</i> AM M2593	<i>A. flavipes</i> BMNH 55.12.24.75
BL	27.93	26.2	26.76	25.16		24.4	
PL	15.76	14.8	15.13	13.45		c. 12.2	18.0
P ¹⁻³	3.89	3.29	3.88	3.29	3.46	2.3	3.16
P ¹⁻²	2.82		2.57	2.37		3.3	
SWR-LC ¹ A	4.68	5.45	5.15	4.28	5.51	4.9	5.29
C ¹ M ⁴	11.44		11.00	10.36			
IPVL	2.09		4.44	5.21			
SWR-LM ³	12.04	13.09	12.85	11.28	14.27	12.3	14.1
IBW	4.36	4.68	4.00	4.04	4.34	3.7	
OBW	10.95	10.72	10.87	10.33	11.69		
IOW	7.08	6.65	7.19	6.47	7.21	6.0	6.95
ZW	15.98	16.09	16.73	14.71	17.67	c. 14.3	
SCD	5.26	5.0	5.75	4.46			
APVL	4.16	2.96	2.85	2.30	c. 3.0	2.7	2.99
PPVL	6.82	4.7	5.16	4.15	c. 5.9	5.2	
DL	22.29		21.45	19.80	22.5		
HB	111	107	101	94	127	90	114
TV	91	94	94	79	92	80	85
EAR	16	18	17	15			18
PES	20	21	18	16.5	20		20
WT (g)	36.7			27			

TYPE LOCALITY. Emu Creek 28°13'03"S 152°24'54"E (38km E of Warwick), SE Qld.

DIAGNOSIS. *Antechinus subtropicus* differs from *A. stuartii* in having more highly developed entoconids on M₃; longer posterior and anterior palatal vacuities, and shorter inter-palatal vacuity distance (Fig. 7); relatively narrower rostrum and less expanded lachrymals and jugals (Fig. 9).

Antechinus subtropicus differs from *A. agilis* in larger body size (Fig. 7); dorsal fur brown rather than grey-brown; longer posterior and anterior palatal vacuities with a shorter inter-palatal vacuity distance, both in relative and absolute terms (Fig. 7, Tables 2,4); relatively longer pre-molar row; significantly more developed entoconids on M₃ and the first interdigital pad is not usually fused with the first inner metatarsal pad.

Antechinus subtropicus differs from *A. adustus* in lighter colour fur; relatively longer, narrower rostrum (Fig. 9); larger alisphenoid tympanic bullae (Fig. 8); relatively longer pre-molar row; significantly more developed entoconids on M₃;

less pronounced enlargement of I¹⁻⁴; and females have eight nipples instead of six.

Antechinus subtropicus differs from *A. flavipes* in absence of prominent buff fur surrounding the eyes; absence of tannish patch of post-auricular fur, uniform dorsal fur colour compared with a prominent change in antero-posterior fur colour from grizzled greyish shoulders to tannish rump; tail tip generally a uniform colour; relatively narrower rostrum; less expanded lachrymals and jugals; longer pre-molar row; less massive canines; and significantly more developed entoconids on M₃ (Van Dyck, 1982a).

Antechinus subtropicus differs from *A. bellus* by its darker, more uniform colour; much narrower rostral width; less expanded lachrymals and jugals; a well-developed entoconid and a non-thickened supratragus (Van Dyck, 1997).

Antechinus subtropicus differs from *A. godmani* in having relatively smaller inter-palatal vacuities and a correspondingly greater inter-palatal vacuity distance; a smaller body size; and a non-thickened supratragus (Van Dyck, 1982b).

Antechinus subtropicus differs from *A. leo* by its narrower rostral width at the level of the upper canine; a smaller body size; and having a non-thickened supratragus (Van Dyck, 1980).

Antechinus subtropicus differs from *A. swainsonii* in lighter colouring; having shorter claws; relatively larger ears and eyes; relatively shorter premolars; relatively shorter inter-palatal vacuity distance; a diastema between I¹ and I²; more developed styler cusp B on M¹; having posterior cingula on the upper molars; M₃ talonid wider than the trigonid; and more procumbent upper incisors.

Antechinus subtropicus differs from *A. minimus* in having a relatively longer tail; shorter claws; relatively shorter premolars; having posterior cingula on the upper molars; an upright I¹; a diastema between I¹ and I²; the M₃ talonid wider than the trigonid; and no posterior accessory cusp on I³.

DESCRIPTION OF HOLOTYPE. *Pelage* (Fig. 2). The fur of the mid-back is up to 12mm long with basal 9mm Slate colour, median 2mm Isabella colour and apical 1mm black. The overall dorsal impression is one of speckled Buffy Brown (a mid biscuit-brown), however, mid-way along the dorsum fur colour warms to become a slightly darker Saccardo's Umber to the base of the tail. Guard hairs, interspersed thinly through the fur, are 13mm on the rump, and reduce to 5mm where they terminate at the crown of the head. Fur on and below the shoulders, thighs, flanks and chin lacks black tips and these areas, and the belly, appear as Chamois (a light fawn).

There is no head-stripe and no impression of a dark head 'patch', nor are there any eye-rings (although animals in the field appear to have a head-stripe). The soft ventral fur (8mm long on the belly) is Mouse Gray on the basal half and Cartridge Buff on the apical half, and is interspersed with colourless medially thickened guard hairs 11mm long. The belly is thus an overall Chamois. Forefeet and hindfeet are thinly covered with Cartridge Buff hairs. The tail is moderately thickly covered with hair and is very weakly bicoloured dorso-ventrally. Hairs average 2.0mm along the tail length but increase to 6.5mm at the tip. Dorsally, the tail hairs are uniform Buffy Brown with Fuscous Black tips, but the distal third is covered with Olive Brown hairs dorsally and Deep Olive Buff ventrally which form a ventral 'crest'. Ventrally, the black

tips are lost completely and the hairs become almost colourless toward the tip.

Vibrissae. There are approximately 22 mystacial vibrissae on each side which are up to 31mm long. The more dorsal mystacial vibrissae are Fuscous Black while those lower are colourless; supra-orbital vibrissae number 2 (left), 1 (right); genals (Fuscous Black and colourless) number 5 (left) and 6 (right); ulna-carpals (colourless) number 4 (left) and 5 (right); submentals (colourless) number 3.

Tail. The tail is shorter than the nose-vent length. It is thin, tapers toward the tip and has a weak ventral crest.

Hindfoot. The interdigital pads are separate and are elongate and striate. Enlarged, unfused, hallucal, post-hallucal and metatarsal pads are present on both feet.

Ears. The ears are rounded with a ventral lobe defined by a shallow notch in the posterior margin. The supratragus is simple and leaf-like with no pronounced thickened posterior-margin or distal-end reflex.

Dentition. (Fig. 3). Upper Incisors. I¹ roots are narrow, crowns are short and high, relatively broad and weakly cingulated buccally. They are procumbent but the crowns are uncurved posteriorly. The roots of LI¹ and RI¹ are separated by a diastema but they contact at the crown tips. For I²⁻⁴ crown height, I²>I³>I⁴. All upper incisors have very weak buccal cingula. The root and crown are clearly differentiated. I⁴ carries no anterior cusp and the root of I⁴ is narrow.

Upper Canines: C¹ is narrow and caniniform with a distinct boundary between the root and the crown. A weak buccal cingulum and a very weak lingual cingulum are present. There is no anterior cusp, but a minute posterior cingular cusp is present.

Upper Premolars: A very slight diastema occurs between C¹ and P¹, P¹ and P² and P² and P³. All upper premolars carry strong buccal and lingual cingula. P¹ crown (broken off in RP¹) is shorter than P², which is shorter than P³. Small but clearly definable anterior and posterior cusps are present on P¹, P² and P³. P¹ and P² possess very weak postero-lingual lobes.

Upper Molars: The posterior tip of P³ is positioned in the parastylar corner of M¹ but lingual to and explanar with styler cusp A. The anterior cingulum below styler cusp B is very broad and complete. Styler cusp B and the paracone are relatively unworn, and a minute protoconule is present at the base of the paracone

apex. The protoconule is accompanied by a small bulge of enamel directly below it on the face of the anterior protocrista. The paracone on M^1 is approximately half the height of the metacone. Styler cusps C and E are not visible. M^1 has a very weak posterior cingulum. Styler cusp D is greatly enlarged and makes a great contribution to endoloph bulk.

In M^2 the broad anterior cingulum, which contacts the metastylar corner of M^1 , tapers quickly as it progresses down and along the base of the paracrista, however it is complete and does not degenerate totally at the base of the paracone apex. A minute protoconule is visible. M^2 lacks styler cusps A and E. Styler cusp D is slightly reduced, broad and there is a very weak posterior cingulum. Styler cusp C is just visible on LM^2 , however it is absent on RM^2 .

In M^3 the anterior cingulum is as in M^2 , and is narrow but complete. Styler cusp D is reduced to a small, sharp peak. Styler cusps C and E are absent. There is a very weak posterior cingulum.

In M^4 the metastylar corner is very poorly developed. The narrow anterior cingulum reduces quickly away from the anterior corner of M^3 and runs to the trigon basin. A posterior cingulum is weakly present. The protocone is reduced but relatively broad. In occlusal view, the angle made between the post-paracrista and the post-protocrista is close to 110° .

Lower Incisors: The crown height of I_1 is taller than I_2 . I_1 and I_2 are oval in antero-lateral view and gouge-like in occlusal view. The crown height of I_2 is larger than in I_3 . I_3 is incisiform in lateral view with an insignificant posterior cusp at the base of the crest, which descends posteriorly from the apex of the primary cusp. The lower canine rests lingually to the posterior cusp. In occlusal view, a small notch separates the posterior cusp from the prominent postero-lingual lobe, and crown enamel of the primary and posterior cusps folds noticeably lingually such that the crest of the two cusps bisects the tooth longitudinally.

Lower Canines: C_1 is caniniform and characterised by upward projection and moderate curvature from root to crown tip. It has weak buccal and lingual cingulation and a weak posterior cusp. Some thegotic wear is evident just anterior to the posterior cusp.

Lower Premolars: There are no diastemata between the premolars, however only P_1 and P_2 contact. Between C_1 - P_1 , and P_2 - P_3 , there is a minute gap between the crowns. All are weakly

cingulated buccally and lingually. In crown height, P_2 is taller than P_1 , which is taller than P_3 . P_1 and P_2 are broad and long. P_3 is narrower and short. All possess posterior cusps. P_1 has weak postero-lingual lobing.

Lower Molars: The M_1 talonid is wider than the trigonid and a very weak anterior cingulum is present. There is no buccal cingulum. The narrow paraconid appears, in occlusal view, as a small inclined spur, the lingual edge of which makes a slight swelling on the endoloph of M_1 . The paracristid is almost horizontal from the paraconid to the paracristid fissure and vertical from the paracristid fissure to the protoconid. The metacristid and hypocristid are roughly oblique to the long axis of the dentary. The short cristid obliqua extends from the hypoconid to the posterior wall of the trigonid intersecting the trigonid at a point just buccal to that point directly below the tip of the protoconid. The hypocristid extends from the hypoconid to the hypoconulid. The entoconid is long but low. From the metaconid posteriorly, the talonid endoloph follows a line more lingual to the axis of the dentary until the base of the hypoconulid.

In M_2 , the trigonid is slightly narrower than the talonid. The anterior cingulum is moderately well-developed originating lingually in a weak parastyloid notch into which the hypoconulid of M_1 is tucked. There is a very weak buccal cingulum. A very narrow, weak posterior cingulum extends from the hypoconulid to the posterior base of the hypoconid. The paraconid is well developed and is the smallest trigonid cusp. A very large entoconid, as tall as the protoconid, is present. The cristid obliqua extends from the hypoconulid to the posterior wall of the trigonid intersecting the trigonid at a point directly below the tip of the protoconid but well buccal to the metacristid fissure. The hypocristid (worn in LM_2) extends from the hypoconulid to the tip of the hypoconid. From the base of the metaconid posteriorly, the endoloph follows a line of orientation more lingual than the line of the dentary axis.

In M_3 , the width of the trigonid is equal to that of the talonid. A weak parastyloid wraps around the hypoconulid of M_2 and there is a moderately well developed anterior cingulum on M_3 . Buccal and posterior cingula are as in M_2 . The reduced cristid obliqua intersects the trigonid at a point well lingual to the longitudinal vertical mid-line drawn through the tip of the protoconid, but slightly buccal to the metacristid fissure. The

entoconid on M_3 is very well developed and just shorter than the well-developed paraconid. The endoloph on the talonid of M_3 takes a more buccal orientation than that seen in M_2 . The rest of M_3 morphology is as in M_2 .

In M_4 , the trigonid is much wider than the talonid. The anterior cingulum is as in M_2 . The posterior cingulum is absent. Of the three main trigonid cusps, the metaconid is slightly taller than the paraconid but both are dwarfed by the protoconid. The hypoconid of M_4 is small but distinct. Between the hypoconid and the base of the metacristid, the cristid obliqua forms a low crest, which contacts the anterior base of the well-developed entoconid directly below the metacristid fissure. The hypoconulid is reduced to a low crest.

Skull. (Fig. 3). The rostrum is slightly concave due to a depression between the lacrymals at the nasal-frontal sutures. The left and right (damaged) alisphenoid tympanic bullae are widely separated and poorly developed. The foramen pseudovalve is large and is not bisected by a bridge of the alisphenoid. The eustachian canal opening is very large. The internal jugular canal foramina are large, the canals are raised and prominent. The posterior lacerate foramina are large and exposed, as are the entocarotid foramina. The large premaxillary vacuity extends from the level of the I^1 root back to the level of the P^1/P^2 diastema. The very large maxillary vacuities extend from the level of the anterior root of P^3 and extend back to the level of the M^3/M^4 interface. Palatine vacuities are not present. There is minimal anterior flaring of the jugals, and the lacrymals are unexpanded, giving the skull a long and narrow appearance when viewed dorsally.

HABITAT AND DISTRIBUTION (Fig. 6). In SE Qld *A. subtropicus* is essentially restricted to subtropical vine-forests, and occurs from sea level (Tallebudgera Creek 28°08'S 153°26'E) to altitudes of 1000m (Lamington Plateau 28°16'S 153°05'E). It is abundant in major tracts of vine-forest on or east of the Great Dividing Range south of Gympie 26°11'S 152°40'E to NE New South Wales. Structural features of typical complex notophyll vine-forests inhabited by *A. subtropicus* include the abundance of notophylls and microphylls, lianas, vascular epiphytes, plant buttresses, compound entire leaves and trunk-obscuring aroids such as *Pothos* (Webb 1959). The uneven canopy of mixed evergreens and occasional deciduous emergents range in height

from 21-45m. *Antechinus subtropicus* is found rarely in sclerophyll associations, where its presence is limited to humid, dense areas such as fern gullies and vine entanglements along watercourses. It is particularly abundant in the perimeter vegetation of vine forests and favours dense tangled stands of invasive pioneer shrubs such as *Lantana camara*, wild raspberry *Rubus* spp., bleeding heart *Omolanthus* spp., and bracken *Pteridium esculentum*. Braithwaite (1973) studied a population at Mt Glorious (27°20'S 152°47'E) and found that *A. subtropicus* avoids both mature forest with sparse ground cover and disturbed areas with cunjevoi (*Alocasia machorhiza*) and young palm growth. He found a greater preference for areas of tangled and fallen lianas, and rotten logs. All areas where *A. subtropicus* occurs experience relatively high average annual rainfall of up to 2000mm (Van Dyck, 1982a).

REPRODUCTION. At Mount Glorious, SE Qld, mating occurs only in the last two weeks of September each year and is followed immediately by the death of all males (Wood, 1970; Braithwaite, 1973). Females of *A. subtropicus* gestate for 25-26 days and all births at Mt Glorious occur in the last two weeks of October. The young remain in the pouch for approximately 5 weeks and are weaned after three months (Wood, 1970). Litter size at Mt Glorious averages 7.5 young (Wood, 1970). In more northerly districts mating occurs slightly earlier than at Mt Glorious (SVD pers. obs.). At the Conondale Range (26°52'S, 152°40'E), female *A. subtropicus* captured from 21 to 25 October had pouches containing seven or eight 1-1.5cm young. Their ages were therefore approximately 12-20 days (cf. Marlow, 1961); their births having taken place early in October. In New South Wales (near Sydney) *A. stuartii* reproduces nearly six weeks earlier than *A. subtropicus* from SE Qld (Dickman, 1982).

Nipple Number. Nipple numbers appear to be regular in SE Qld. Of 32 female specimens, representing localities over the entire range of *A. subtropicus* in SE Qld, all had pouch areas containing eight nipples. A.B. Rose (pers. comm.) also reported this for animals from the Border Ranges National Park in NE New South Wales. Eight nipples were also found by Cockburn et al. (1983) for SE Qld females.

DECIDUOUS PREMOLAR MORPHOLOGY. The dP^3 may be double- or triple-rooted. When double-rooted the tooth is less molariform, with a

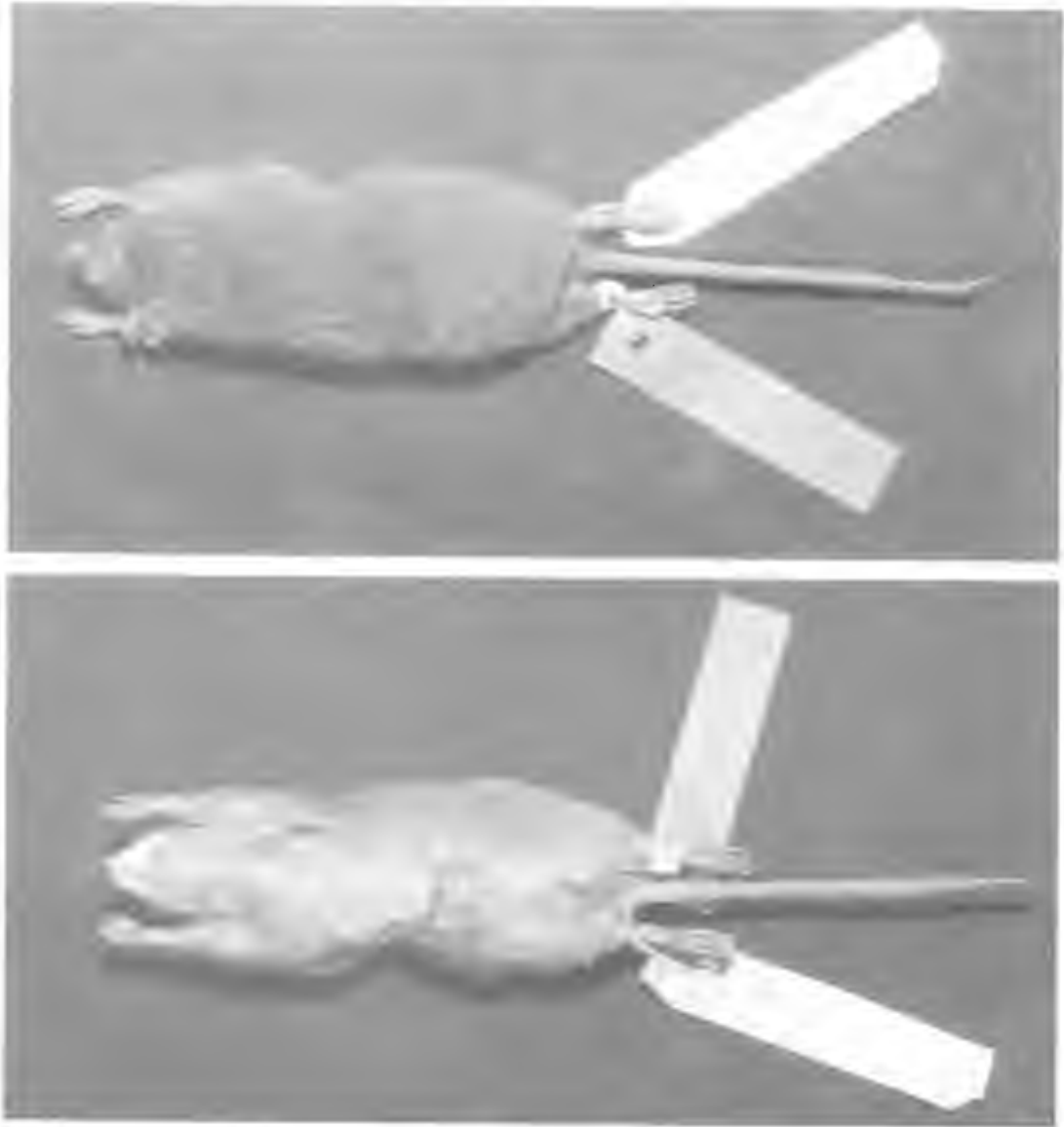


FIG. 4. Study skin of the holotype of *Phascogale flavipes adusta* Thomas, 1923 (now *Antechinus adustus*) (BMNH 1922.12.18.54). Dorsal view (above) and ventral view (below).

poorly developed protocone, well-developed paracone, and a small metacone. When triple-rooted this tooth is more molariform with a well-developed protocone, but with the paracone and metacone coalescing into a single cusp. Buccal cingulation is strong.

The dP_3 may be single or double-rooted. When single-rooted, it is premolariform, exhibiting a single anterior cusp. When double-rooted it is rounded and more molariform with a large

protoconid and possible traces of a metaconid and hypoconid.

***Antechinus adustus* (Thomas, 1923)**
(Figs 4, 5; Table 1)

Phascogale flavipes adusta Thomas, 1923.

Phascogale unicolor adusta Thomas, 1924.

Antechinus stuartii adustus Wakefield & Warneke, 1967.

MATERIAL. HOLOTYPE: BMNH1922.12.18.54, adult male, skull, dentaries and puppet skin, 1 Jun 1922, T.V. Sherrin. OTHER MATERIAL: Bellenden Ker 17°16'S

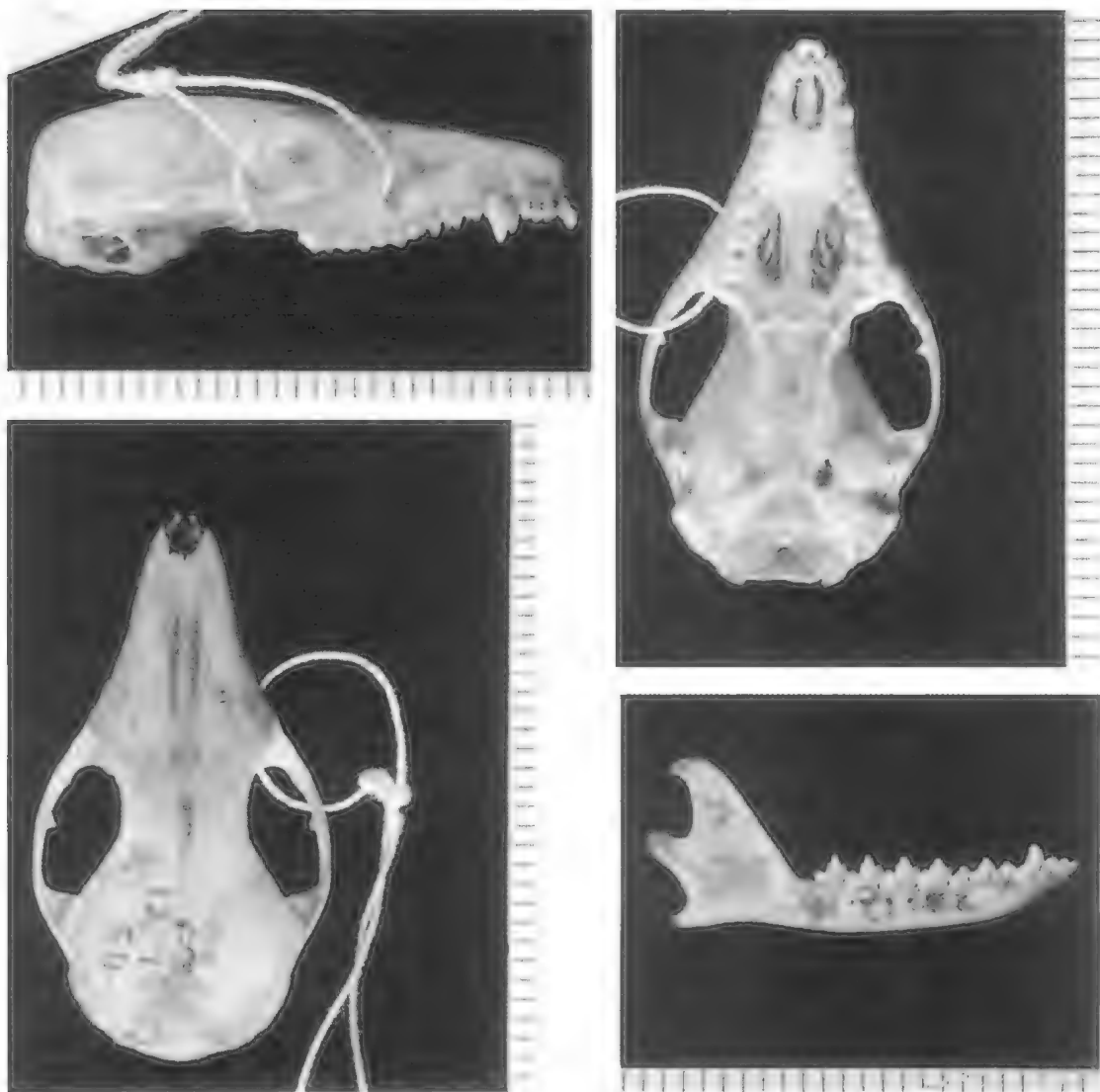


FIG. 5. Skull and right dentary of the holotype of *Phascogale flavipes adusta* Thomas, 1923. (BMNH 1922.12.18.54). Scales in millimetres.

145°55'E (QM J19669); 'Bluewater', 17km S of Rollingsstone 19°10'S 146°23'E (QM JM3755, 3756); Charappa Creek, near Ravenshoe 17°38'S 145°35'E (AM M8302, 8317); Ebony Road, Forestry track 20km SE of Ravenshoe 17°44'S 145°33'E (QM JM6715); Ebony Road, 850m 17°44'S 145°32'E (QM JM1785, 1897-1901, 1903-1906, 1910, 1911, 1915, 2751, 3919, 5543); Ebony Road, 780m 17°44'S 145°33'E (QM JM5540-5542); Forestry track 15km SE of Ravenshoe, 840m 17°43'S 145°31'E (QM JM1902); George Creek area 17°49'S 145°32'E (QM JM6898); Koombooloomba Creek 17°51'S 145°35'E (QM JM6889); Macalister Mountains, W of Cardwell, 650m 18°19'S 145°57'E (QM JM6560); Mt Lewis 16°35'S 145°16'E (QM JM3758, 3619); Mt

Lewis 16°36'S 145°15'E (QM JM3757); Mt Lewis Forestry hut, 0.5km S 16°35'S 145°16'E (QM JM6906); Mt Lewis Forestry hut, 1km NW 16°35'S 145°16'E (QM JM6905); Mt Spec, NW of Townsville 18°58'S 146°09'E (QM J10108); Mt Spurgeon 16°26'S 145°12'E (QM JM809, J7143, J7144); Niblet Creek, Kooroomool Saddle Road, 5km ENE of Koombooloomba 17°49'S 145°38'E (QM JM6716, 6717); North Koombooloomba Dam 17°48'S 145°37'E (QM JM6896); Palmerston Range, Forestry road to Maalan, 710m 17°36'S 145°39'E (QM JM1907-1909); Paluma 19°00'S 146°12'E (QM JM2788) Paluma Dam, Forestry track approach, 780m 18°58'S 146°09'E (QM JM1847, 1893-1896 JM1914); Paluma township 19°00'S 146°12'E (QM JM2789); Severin State

Forest 17°11'S 145°40'E (CSIRO CM10561-10563); Windsor Tableland 16°15'S 145°02'E (QM JM2822).

TYPE LOCALITY. Dinner Creek (now Charmillan Creek), Ravenshoe, Qld, 17°42'S 145°31'E, altitude 885m.

DIAGNOSIS. *Antechinus adustus* differs from *A. stuartii* in having a longer, darker pelage; relatively smaller and more widely spaced bullae (Fig. 8) and females have six nipples compared with eight to ten nipples.

Antechinus adustus differs from *A. agilis* in having a longer, darker pelage; a relatively broader rostrum (Fig. 9); relatively smaller bullae (Fig. 8); the first interdigital pad not usually fused with the first inner metatarsal pad; and females having only six nipples.

Antechinus adustus differs from *A. subtropicus* in having a smaller body size (Fig. 7, Tables 2, 3); relatively shorter, broader rostrum (Fig. 9); relatively smaller palatal vacuities with a corresponding larger inter palatal vacuity distance (Fig. 7); longer, darker pelage; less developed entoconids on M_3 and females with only six nipples.

Antechinus adustus differs from *A. flavipes* in having a smaller body size; a longer, darker pelage; absence of prominent buff fur surrounding the eyes; absence of tannish patch of post-auricular fur; uniform dorsal fur colour compared with a prominent change in antero-posterior fur colour from grizzled greyish shoulders to tannish rump; tail tip generally a uniform colour, more developed entoconids on M_3 ; and females with only six nipples.

Antechinus adustus differs from *A. bellus* by its much darker and more uniform colour; smaller body size; well-developed entoconids; much narrower rostral width from the level of the upper canine; through to the level of the upper third molar; and a non-thickened supratragus.

Antechinus adustus differs from *A. godmani* in having a much smaller body size; darker colouration; shorter skull length; relatively shorter, broader rostrum; shorter premolar row; and a non-thickened supratragus (Van Dyck, 1982b).

Antechinus adustus differs from *A. leo* by its narrower rostral width at the level of the upper canine; well-developed entoconids; a smaller body size; darker colour; and non-thickened supratragus (Van Dyck, 1980).

Antechinus adustus differs from *A. swainsonii* in having a narrower inter-orbital width; shorter anterior palatal vacuities; shorter premolar row; a

relatively broader rostrum; smaller body size; shorter claws; more massive I^1 ; more massive I^{2-4} ; prominent postero-lingual lobes on P^{1-3} ; having posterior cingula on the upper molars; an upright I^1 ; and no posterior accessory cusp on I^3 .

Antechinus adustus differs from *A. minimus* in having a relatively longer tail; a relatively broader rostrum; a smaller body size; shorter claws; more massive I^1 ; more massive I^{2-4} ; prominent postero-lingual lobes on P^{1-3} ; having posterior cingula on the upper molars; an upright I^1 and no posterior accessory cusp on I^3 .

DESCRIPTION OF HOLOTYPE. *Pelage* (Fig. 4). Fur of the mid-back (8mm long) with basal 6mm Slate Colour, median 1mm Tawny Olive and apical 1mm Fuscous Black. The back appears overall to be Sepia. Medially thickened guard hairs, interspersed thinly through the fur, are 11mm long on the rump, and reduce to 3mm where they terminate at the crown of the head. Fur on and below the shoulders, thighs, flanks and chin lacks black tips or coarse guard hairs and these areas and belly appear Cinnamon Buff.

The soft ventral fur (7mm long on the belly) is Mouse Gray on the basal 1.5mm and Cinnamon Buff on the apical 5.5mm and is interspersed by Cinnamon Buff guard hairs (8mm long). The belly is thus an overall Cinnamon Buff. Fore and hindfeet are covered with hairs which are coloured Saccardo's Umber. The tail appears weakly bicoloured, this being an illusion due to the denser coverage of hairs ventrally, which are 3.6mm long midway along the tail, and 6.4mm long at the ventral tip. Dorsally, the hairs are 2.7mm long midway down the tail and 2.7mm long at the dorsal tip. All tail hairs are Fuscous Black.

Vibrissae. Approximately 24 mystacial vibrissae occur on each side and are up to 27mm long. The more dorsal vibrissae are coloured Fuscous Black while those lower are colourless; supra-occipital vibrissae (Fuscous Black) number 2 left and 2 right; genals (Fuscous Black and colourless) number 9 left and 9 right; ulna-carpals (colourless) number 4 right and 6 left; submentals (colourless) number 4.

Tail. The tail is shorter than the nose-vent length. It is thin and tapers toward the tip.

Hindfoot. Interdigital pads are separate. The apical pad is enlarged, elongate and striate. Hallucal and post-hallucal pads are separate on both feet. Metatarsal pads or granules are not present in the holotype although a minute calcaneal granule is visible. An auxiliary apical

granule is visible outside left and right third digit apical granules.

Ears. It was not possible to closely examine supratragus morphology in the holotype dry skin. (In other specimens, the supratragus is simple).

Dentition (Fig. 5). Upper incisors: I^1 is massive, broad, very procumbent, strongly curved and taller-crowned than all other upper incisors. It is caniniform with a greatly developed crown. Left and right I^1 touch. I^1 and I^2 are so highly developed that they almost contact, and the diastema traditionally separating I^1 from I^2 in *Antechinus* (other than *A. minimus* and *A. swainsonii*) is minute. In other incisors, $I^3 > I^2 > I^1$ and all have strong buccal cingula. Roots of I^{2-3} are narrow while the crowns are very broad. I^4 carries no anterior cusp but a minute posterior cusp is present.

Upper canines: C^1 is short, stout and caniniform with a distinct boundary between root and crown. It carries a weak buccal and weak lingual cingulum. A minute anterior cingular cusp is present along with a slightly larger posterior cusp.

Upper premolars: There are no diastemata between premolars. All right upper premolars contact. Left P^1 and P^2 crowns are slightly separate. P^1 and P^2 carry strong buccal and lingual cingula. In crown size $P^3 > P^2 > P^1$. There is a small posterior cusp on P^2 and a large posterior cusp on P^3 . P^1 and P^2 bear heavy postero-lingual lobes and in occlusal view appear almost square.

Upper Molars: The posterior tip of P^3 lies in the parastylar corner of M^1 but lingual to and coplanar with stylar cusp A (right dentary) and just below stylar cusp A in the left dentary. The anterior cingulum below stylar cusp B is short, broad and just complete. Stylar cusp B is tall and the paracone is slightly worn. A minute protoconule is present at the base of the paracone apex. The minute protoconule is accompanied by a small bulge of enamel directly below it on the face of the anterior protocrista. The paracone on M^1 is approximately half the height of the metacone. Stylar cusp C is not visible on either LM^1 or RM^1 , and stylar cusp E is not visible. M^1 has a poorly developed posterior cingulum. Stylar cusp D is very large and broad.

In M^2 a broad anterior cingulum which contacts the metastylar corner of M^1 tapers slowly as it progresses down and along the base of paracrista and finally unites with the trigon basin. A small protoconule is visible. M^2 lacks

stylar cusps A, C and E. Stylar cusp D is slightly reduced, but broad, and there is a weak posterior cingulum.

In M^3 the anterior cingulum is as broad as in M^2 , but becomes more indistinct after covering $2/3$ distance between stylar cusp B and the base of the paracone. It does, however, unite with the trigon basin. Stylar cusp D is reduced to a very small, broad peak. Stylar cusp E is absent, as is stylar cusp C.

In M^4 the metastylar corner is poorly developed. The broad, complete anterior cingulum narrows quickly away from the metastylar corner of M^3 , and a posterior cingulum is absent. The protocone is much reduced and narrow. In occlusal view, the angle made between the post-protocrista and the post-paracrista is close to 90° .

Lower Incisors: The gross development of the upper incisors is not reflected in the lowers. The first lower incisor is almost $1\frac{1}{2}$ times the crown height of I_2 . I_1 and I_2 are oval in antero-lateral view and gouge-like in occlusal view. I_2 is subequal in crown height to I_3 . I_3 is incisiform in lateral view but with a conspicuous posterior cusp at the base of the crest, which descends posteriorly from the apex of the primary cusp. The lower canine rests against this posterior cusp. In occlusal view, a small notch separates the posterior cusp from the prominent postero-lingual lobe, and crown enamel of the primary and the posterior cusps fold noticeably lingually, such that the crest of the two cusps bisects the tooth longitudinally.

Lower Canines: C_1 is caniniform, broad and erect, and is characterised by maximum curvature from root to crown tip. It has strong buccal and lingual cingulation and a strong posterior cusp.

Lower Premolars: P_{1-3} are large, rectangularly shaped and all in contact. They are strongly cingulated buccally and lingually. In crown height, P_2 is taller than P_1 , which is taller than P_3 . All possess small posterior cusps; P_1 possesses a very weak anterior cusp. P_1 and P_2 do not have postero-lingual lobes.

Lower Molars: All molars are broad. The M_1 talonid is much wider than the trigonid and the anterior cingulum is present but poorly developed. It terminates at the posterior base of the protoconid. There is no buccal cingulum. The narrow paraconid appears in occlusal view as a small steeply sided spur, the lingual edge of which makes no appreciable swelling on the endoloph of M_1 . The paracristid is almost 45° to

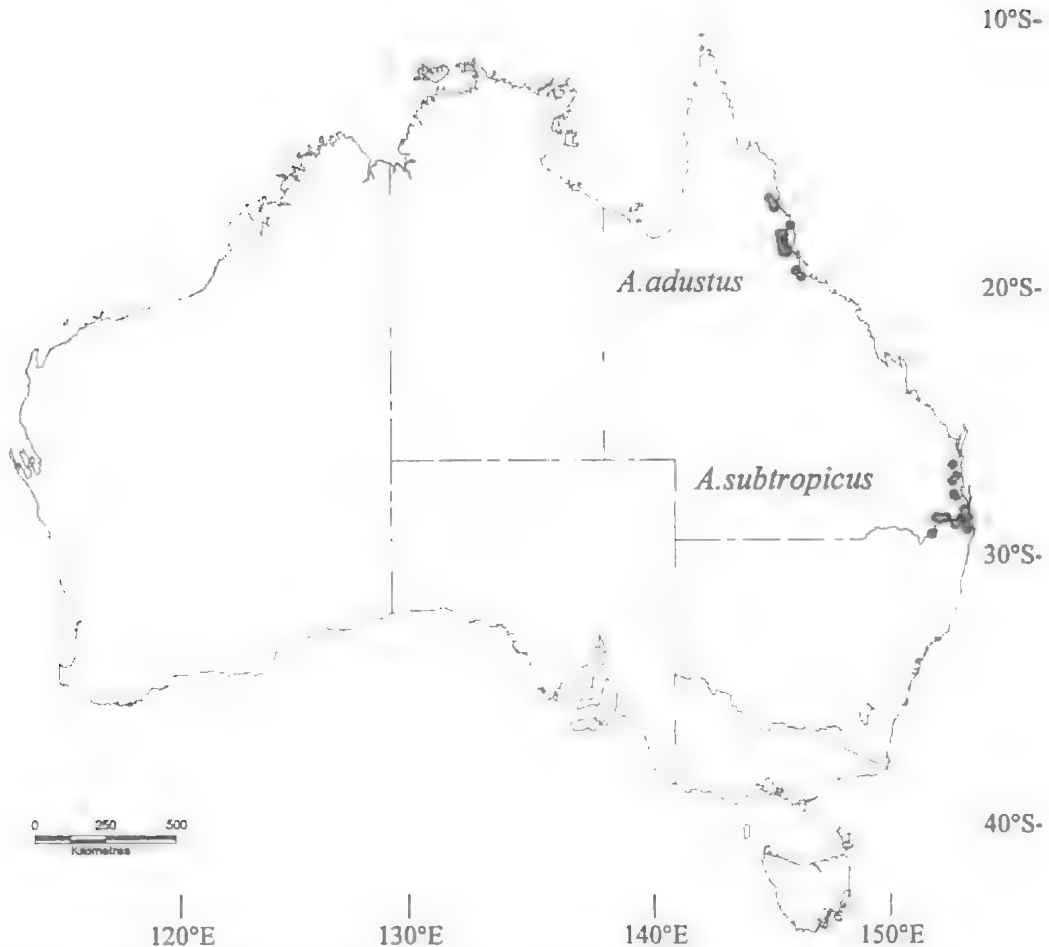


FIG. 6. Distribution of *Antechinus subtropicus* and *A. adustus*.

the horizontal from the paraconid to the paracristid fissure and 45° from the paracristid fissure to the protoconid. The metacristid is roughly oblique to the long axis of the dentary while the hypocristid is oblique. The cristid obliqua is long and extends from the hypoconid to the posterior wall of the trigonid, intersecting the trigonid at a point slightly lingual to that point directly below the tip of the protoconid. The hypocristid terminates midway between the hypoconid and the metastylid. The entoconid is very low. From the base of the metaconid posteriorly, the talonid endoloph follows the line of the dentary until the base of the hypoconulid.

In M_2 , the trigonid is slightly narrower than the talonid. The anterior cingulum is poorly developed, originating lingually in a weak parastylid notch into which the hypoconulid of M_1 is tucked. There is no buccal cingulum. A

strong, broad, posterior cingulum extends from the hypoconulid to the posterior base of the trigonid. The paraconid is well developed and is the smallest trigonid cusp. A well developed, but narrow entoconid is present. The cristid obliqua extends from the hypoconulid to the posterior wall of the trigonid intersecting the trigonid at a point directly below the tip of the protoconid but well buccal to the metacristid fissure. The hypocristid extends from the hypoconulid to the tip of the hypoconid. From the base of the metaconid posteriorly, the endoloph follows the line of the dentary axis.

In M_3 , the trigonid is as wide as the talonid. A prominent parastylid wraps around the hypoconulid of M_2 and there is a strong anterior cingulum on M_3 . The posterior cingulum is as in M_2 but more poorly developed. The reduced cristid obliqua intersects the trigonid at a point

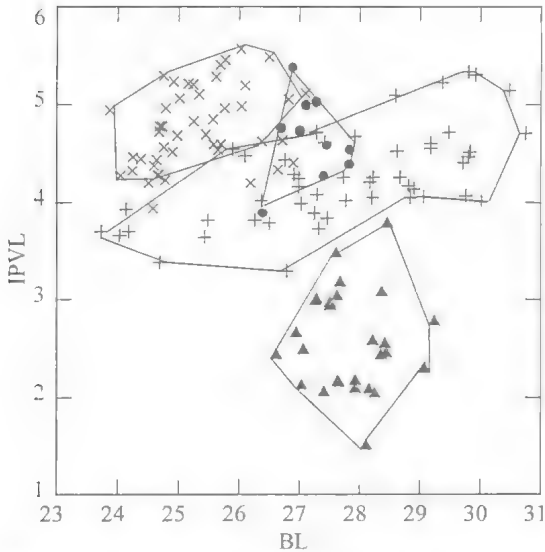


FIG. 7. Bivariate plot of inter-palatal vacuity distance (IPVL) (mm) against basicranial skull length (BL) (mm) for male *Antechinus subtropicus* (▲), *A. adustus* (●), *A. stuartii* (+) and *A. agilis* (×).

well lingual to the longitudinal vertical mid-line drawn through the tip of the protoconid, but slightly buccal to the metacristid fissure. The entoconid on M_3 is small. The endoloph on the talonid of M_3 follows the line of the dentary axis. The rest of M_3 morphology is as in M_2 .

In M_4 , the trigonid is wider than the talonid. The anterior cingulum is as in M_2 but more poorly developed. The posterior cingulum is absent. Of the three main trigonid cusps, the metaconid is slightly taller than the paraconid but both are dwarfed by the protoconid. The hypoconid of the M_4 talonid is the only cusp. Between the hypoconid and the base of metacristid, the cristid obliqua forms a low, weak crest, which contacts the trigonid wall just lingual to the metacristid fissure. A significant feature of the M_4 morphology is the reduction of talonid crown enamel below the cristid obliqua, which results in the talonid appearing (in occlusal view) as a narrow oblique spur jutting off the trigonid wall.

Skull. (Fig. 5). The rostrum is slightly grooved longitudinally by a depression running along the nasal sutures. There is no concavity at the nasal-frontal sutures. The left and right alisphenoid tympanic bullae are moderately widely separated and only moderately enlarged. The foramen pseudovale is large and not bisected by a bridge of the alisphenoid. The eustachian canal opening is moderately large. The internal jugular canal

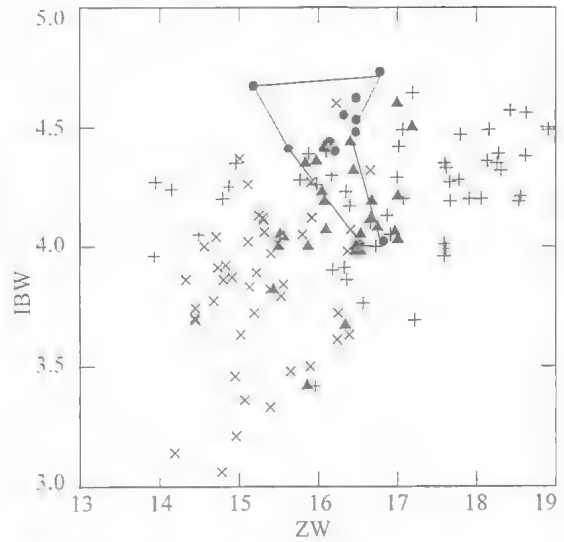


FIG. 8. Bivariate plot of interbulba width (IBW) (mm) against zygomatic width (ZW) (mm) for male *Antechinus subtropicus* (▲), *A. adustus* (●), *A. stuartii* (+) and *A. agilis* (×).

foramina are large, the canals are raised and prominent. The posterior lacerate foramina are large and exposed, as are the entocarotid foramina. The premaxillary vacuity extends from the level of the I^2 root back to the level of the posterior edge of the C^1 root. The small maxillary vacuities extend from the level of the posterior root of P^3 back to the level of the metacone root of M^3 . There are no palatine vacuities.

HABITAT AND DISTRIBUTION (Fig. 6). This small species is restricted to dense tropical vine-forests (mostly complex mesophyll on basalt) from Paluma $19^{\circ}00'S$, $146^{\circ}12'E$ (60km north of Townsville) to Mount Spurgeon $16^{\circ}26'S$, $145^{\circ}12'E$ (near Mossman), a geographically isolated distribution with a north-south range of approximately 300km. It does not inhabit lowland vine-forest and is found only in very wet and cloudy uplands, at altitudes above approximately 800m, in areas that receive highly seasonal rainfall of up to 1500mm annually. This species appears to have similar habitat preferences to *A. subtropicus* and has been trapped most frequently along perimeter vegetation in entanglements of ferns and wild raspberry and around recently fallen and decaying logs. Around Ravenshoe it occurs sympatrically with *A. godmani* and *A. f. rubeculus* (see Van Dyck, 1982a).

TABLE 2. Univariate summary statistics for cranial, dental and external characters of *Antechinus subtropicus*. Abbreviations as in Fig. 1.

Variable	n	Mean	s.d.	Min.	Max.	CV
<i>A. subtropicus</i> males						
BL	28	27.87	0.63	26.62	29.24	2.27
ZW	27	16.31	0.51	15.43	17.19	3.15
IOW	28	7.15	0.20	6.86	5.27	2.84
SWR-LC ¹ B	28	4.74	0.23	4.19	5.83	4.87
SWR-LC ¹ A	28	5.23	0.22	4.89	13.26	4.16
SWR-LM ³	28	12.39	0.51	11.09	13.26	4.15
DL	28	21.88	0.64	20.66	22.97	2.93
C ¹ M ⁴	28	11.13	0.32	10.42	11.74	2.90
APVL	28	3.66	0.64	2.6	4.78	17.40
PPVL	28	6.09	0.44	5.41	7.13	7.23
IPVL	27	2.57	0.51	1.5	3.78	19.90
IBW	28	4.13	0.25	3.42	4.6	6.06
OBW	27	10.88	0.44	9.83	11.78	4.00
PL	28	15.03	0.39	14.22	15.76	2.63
P ¹⁻³	28	3.57	0.24	3.14	4.02	6.60
P ¹⁻²	27	2.46	0.15	2.23	2.82	6.00
M ¹⁻³	27	5.98	0.26	5.43	6.5	4.39
M ₁₋₄	19	7.30	0.29	6.74	7.83	3.97
SCD	28	5.86	0.56	5.01	6.9	9.63
HT	27	9.82	0.46	8.87	10.92	4.65
HB	115	116.59	0.63	102	136	5.80
TV	114	96.54	0.54	84	106	6.00
WT	11	60	5.30	52	67	
<i>A. subtropicus</i> females						
BL	16	26.37	1.19	23.85	24.31	4.52
ZW	16	15.50	0.71	13.66	14.43	4.58
IOW	16	7.12	0.25	6.74	6.74	3.53
SWR-LC ¹ B	16	4.49	0.30	3.86	3.86	6.67
SWR-LC ¹ A	16	5.03	0.33	4.33	4.33	6.60
SWR-LM ³	16	11.78	0.48	10.66	10.66	4.10
DL	16	20.79	0.87	18.9	19.44	4.18
C ¹ M ⁴	16	10.76	0.26	10.11	10.11	2.42
APVL	16	3.39	0.64	2.26	2.26	19.03
PPVL	16	5.68	0.46	5.05	5.05	8.19
IPVL	16	2.64	0.40	1.89	1.89	15.00
IBW	16	4.11	0.37	3.37	3.37	8.90
OBW	16	10.39	0.54	9.2	9.2	5.22
PL	16	13.49	2.59	4.32	4.32	19.17
P ¹⁻³	16	3.33	0.24	2.75	2.75	7.12
P ¹⁻²	16	2.33	0.17	2.03	2.03	7.49
M ¹⁻³	16	5.80	0.26	5.3	5.3	4.56
M ₁₋₄	8	7.21	0.24	6.78	6.84	3.27
SCD	16	5.45	0.54	4.44	4.44	9.90
HT	15	9.30	0.57	8.43	8.6	6.16
HB	32	102.19	1.02	94	112	5.60
TV	32	88.47	0.91	64	100	5.80
WT	6	28	2.44	24	32	

TABLE 3. Univariate summary statistics for cranial, dental and external characters of *Antechinus adustus*. Abbreviations as in Fig. 1.

Variable	n	Mean	s.d.	Min.	Max.	CV
<i>A. adustus</i> males						
BL	10	27.20	0.47	26.4	27.84	1.71
ZW	11	16.28	0.49	15.19	16.83	3.00
IOW	11	7.09	0.22	6.76	7.58	3.15
SWR-LC ¹ B	10	4.87	0.17	4.55	5.08	3.51
SWR-LC ¹ A	11	5.39	0.22	5.02	5.75	4.03
SWR-LM ³	11	12.67	0.48	11.99	13.54	3.79
DL	11	21.06	0.42	20.08	21.7	2.00
C ¹ M ⁴	11	10.65	0.21	10.38	11.06	1.99
APVL	10	2.67	0.19	2.42	2.99	7.02
PPVL	11	4.74	0.56	3.25	5.27	11.91
IPVL	10	4.66	0.42	3.89	5.37	9.04
IBW	11	4.44	0.24	4.01	4.73	5.30
OBW	11	10.94	0.43	10.34	11.67	3.91
PL	10	14.69	0.27	14.13	15	1.86
P ¹⁻³	11	3.34	0.14	3.12	3.58	4.20
P ¹⁻²	11	2.26	0.12	2.06	2.42	5.44
M ¹⁻³	11	5.82	0.07	5.72	5.95	1.27
M ₁₋₄	11	7.11	0.19	6.74	7.34	2.60
SCD	10	5.43	0.30	4.91	5.92	5.54
HT	10	9.39	0.41	8.65	9.93	4.42
HB	9	101.67	8.72	94.00	119.00	7.90
TV	9	98.33	3.77	91.00	103.00	3.80
WT	15	33.4	3.31	30	42	10
<i>A. adustus</i> females						
BL	11	25.84	0.59	25.24	26.94	2.30
ZW	10	15.23	0.44	14.64	16.12	2.91
IOW	11	6.89	0.10	6.74	7.05	1.47
SWR-LC ¹ B	11	4.51	0.26	4.06	4.9	5.84
SWR-LC ¹ A	11	5.12	0.24	4.66	5.43	4.71
SWR-LM ³	11	11.53	0.49	10.68	12.16	4.25
DL	11	19.98	0.48	19.34	20.84	2.38
C ¹ M ⁴	11	10.43	0.24	10.1	10.83	2.31
APVL	11	2.52	0.28	2.17	3.13	11.24
PPVL	10	4.73	0.46	4.14	5.45	9.80
IPVL	11	4.62	0.43	3.93	5.08	9.35
IBW	11	4.41	0.33	3.83	4.95	7.38
OBW	11	10.61	0.42	10.15	11.32	4.00
PL	10	14.19	0.26	13.74	14.61	1.85
P ¹⁻³	11	3.36	0.20	2.95	3.68	6.07
P ¹⁻²	11	2.32	0.15	2.08	2.61	6.66
M ¹⁻³	11	5.72	0.17	5.31	5.96	2.90
M ₁₋₄	11	7.02	0.22	6.66	7.41	3.08
SCD	11	5.13	0.37	4.67	5.74	7.16
HT	11	9.24	0.48	8.33	9.96	5.18
HB	10	93.00	3.05	89.00	100.00	3.30
TV	10	90.10	1.07	89.00	93.00	1.50
WT	15	24.07	3.86	21.00	34.00	16.11

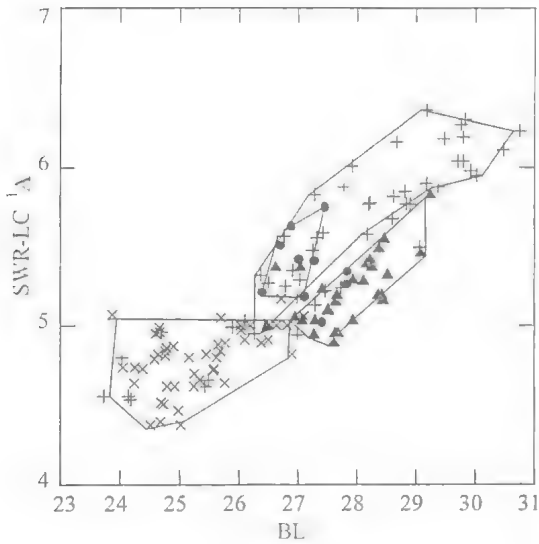


FIG. 9. Bivariate plot of skull width across C¹-C¹ (SWR-LC¹A) (mm) against basicranial skull length (BL) (mm) for male *Antechinus subtropicus* (▲), *A. adustus* (●), *A. stuartii* (+) and *A. agilis* (×).

REPRODUCTION. Van Dyck (1982a) reported that several specimens (e.g., QM JM1907, 1908, 1911) collected near Maalan (17°37'S 145°40'E) on 2 August 1976 had well-developed pouch areas. One of these females (QM JM1908) gave birth to six young on 4 August 1976. From this information, Van Dyck (1982a) suggested that this species probably mates early in July and gives birth early in August. Of thirteen males collected live between 30 June 1976 and 18 July 1976, none survived captivity beyond 29 July 1976 (SVD pers. obs.). Preliminary post-mortem examinations revealed gastric and duodenal haemorrhages, hepatic necrosis, degeneration in proximal tubules of kidneys, and anaemia. Van Dyck (1982a) concluded that male *A. adustus* experience a yearly die-off similar to that described for *A. stuartii* but which probably takes place at the end of July each year. Watt (1997) concluded that mating in *A. adustus* took place from late June to late July. Pouch young were first observed in early August, were carried in the pouch for four to five weeks and suckled until the end of November. All males in the population had died by the first week of August. If *A. adustus* breeds at specific rates of change of photoperiod like those observed in *A. stuartii* and *A. agilis* (McAllan & Dickman, 1986; Dickman et al., 1988), then it is responding to a rate of change as little as 20s day⁻¹.

TABLE 4. F-test values after One-way ANOVA for the four species. See text for results of comparisons after Tukey's *Post Hoc* test. Abbreviations as in Fig. 1.

Variable	Male			Female		
	F	d.f.	P	F	d.f.	P
BL	38.68	3/131	<0.001	22.35	3/95	<0.001
ZW	24.189	3/132	<0.001	10.213	3/93	<0.001
IOW	44.003	3/134	<0.001	19.065	3/96	<0.001
SWR-LC ¹ B	28.547	3/133	<0.001	11.207	3/97	<0.001
SWR-LC ¹ A	31.263	3/133	<0.001	12.964	3/95	<0.001
SWR-LM ³	7.966	3/134	<0.001	4.816	3/94	0.004
DL	33.993	3/133	<0.001	19.278	3/95	<0.001
C ¹ M ⁴	36.404	3/134	<0.001	19.718	3/97	<0.001
APV	51.135	3/131	<0.001	21.696	3/95	<0.001
PPV	95.15	3/133	<0.001	45.906	3/94	<0.001
IPVL	139.056	3/131	<0.001	62.736	3/95	<0.001
IBW	22.048	3/132	<0.001	8.895	3/93	<0.001
OBW	28.352	3/131	<0.001	40.292	3/93	<0.001
PL	27.716	3/132	<0.001	5.472	3/93	0.002
P ¹⁻³	19.411	3/133	<0.001	9.183	3/94	<0.001
P ¹⁻²	16.232	3/132	<0.001	12.832	3/94	<0.001
M ¹⁻³	26.108	3/124	<0.001	19.255	3/92	<0.001
M ¹⁻⁴	12.467	3/115	<0.001	14.798	3/81	<0.001
SCD	15.87	3/131	<0.001	6.655	3/93	<0.001
HT	19.531	3/130	<0.001	12.448	3/92	<0.001

Nipple Number. Of 10 specimens examined from three collecting localities, all pouches contained six teats. This is consistent with the findings of Cockburn et al. (1983) and Watt (1997).

REMARKS. Several authors (Wakefield & Warneke, 1967; Van Dyck, 1997) synonymised two previously described taxa *Phascogale unicolor* Gould (1854) and *A. flavipes burrelli* (Le Souef & Burrell, 1926) with *A. stuartii*. Thomas (1924) noted the similarity between *A. unicolor* and *A. adustus* and assigned them to the same species. We concur that neither *unicolor* or *flavipes burrelli* are *A. subtropicus* or *A. adustus*. From comparisons of zygomatic breadths, *A. unicolor* appears too large to be *A. adustus* and too broad to be *A. subtropicus* (ZW = 15.67mm). The colour of *A. flavipes burrelli* and *A. unicolor* appears to be too light to be *A. adustus*. No location was given for *A. unicolor* (Gould 1854 said only 'by way of Sydney') but the location for *A. burrelli* is the Guy Fawkes region of New South Wales. No animals showing the characteristics of *A. subtropicus* or *A. adustus* are known at that location.

COMPARISONS WITH OTHER TAXA

A plot of scores for individuals on the three canonical-variate axes based on cranial measurements shows a broad separation of each species for each sex (Fig. 10). The first three canonical-variate axes accounted for all the variation. The classification function generated from linear discriminant-function analysis of the same data enabled allocation of most individuals to correct species for both sexes. One male *A. adustus* was misclassified as *A. stuartii* and one female *A. stuartii* and one female *A. agilis* were misclassified as each other (Table 6).

Antechinus subtropicus separated from all the other taxa on the first canonical-variate axis. Standardised coefficients on the first canonical-variate axis (Table 5) suggests that the characters contributing to species separation are a contrast between BL, C¹M⁴ with ZW, IPVL and SWR-LM³.

Antechinus adustus separated from the other taxa on the third canonical-variate axis. Standardised coefficients on the third canonical-variate axis suggests that the characters contributing to species separation are a contrast between BL, IBW, SWR- LC¹A and SWR-LM³ with ZW, DL and PPVL (Table 5).

COMPARISON BETWEEN *A. SUBTROPICUS* AND *A. ADUSTUS*.

External Characters. Males of *Antechinus subtropicus* are the largest of the *A. stuartii* complex yet described. Braithwaite (1973) recorded the mean weight of *A. subtropicus* caught in September from 1963-1966 as 60g for males (n = 11, range = 52-67) and 28g for females (n = 6, range = 24-32). One male individual collected from Tallebudgera Creek, West Burleigh (J20265) weighed 72g. Collections made by A.B. Rose (pers. comm.) from Border Ranges National Park (NE NSW) in July 1977 had a mean for males of 57g (n = 12, range = 48-68) and a mean for females of 32g (n = 5, range = 22-54).

Antechinus adustus is much smaller than *A. subtropicus*. Males have a mean weight of 33g (n = 15, range = 30-42) and females a mean of 24g (n = 15, range = 21-34). Watt (1997) recorded the average weight of male *A. adustus* from three locations (Mt Spec, Koolmoon Creek and Mt Father Clancy) as 33g (n = 51, range = 23-41) and female *A. adustus* as 28g (n = 63, range = 19-38).

Antechinus subtropicus is much longer than *A. adustus*. The mean male head-body length of *A. subtropicus* from southeastern Qld is 117mm (n =

115, range = 102-136) whereas the mean for *A. adustus* is 98mm (n = 9, range = 91-103) (Van Dyck, 1982a). Braithwaite (1973) recorded an average head-body length of males in September from Mt Glorious as 127mm (n = 8, range = 120-131) and A. B. Rose recorded an average head-body length for males from Border Ranges National Park as 120mm (n = 12, range = 113-130). The mean female head-body length for female *A. subtropicus* from southeastern Qld is 102mm (n = 32, range = 64-100) as opposed to female *A. adustus* which is 90mm (n = 10, range = 89-93) (Van Dyck, 1982a). Braithwaite recorded an average head-body length for first-year females from Mt Glorious as 94mm (n = 6, range = 91-112) and for second-year females as 109mm (n = 5, range = 102-117); and A.B. Rose (pers. comm.) for Border Ranges National Park females as 102mm (n = 5, range = 92-120).

The tails of *A. adustus* are relatively longer than those of *A. subtropicus*. The tails of male *A. adustus* average around 0.89 of the head-body length while the tails of females average around 0.96 of the head-body length (Van Dyck, 1982a). The tails of male *A. subtropicus* average around 0.78 of the head-body length while the tails of females average around 0.87 of the head-body length (Van Dyck, 1982a).

Based on study skins and extensive field observations, fur of *A. adustus* is a much darker brown than that of *A. subtropicus*.

Cranial and Dental Characters. *Antechinus adustus* tends to be much smaller than *A. subtropicus* as reflected by the smaller BL and ZW (Tables 2-4, Figs 7, 8). *Antechinus adustus* has both relatively and absolutely smaller anterior and posterior palatal vacuities and a correspondingly larger inter-palatal vacuity distance (Fig. 7, Tables 2, 4; P < 0.001) than *A. subtropicus*. The larger IBW of *A. adustus* reflects its relatively smaller alisphenoid tympanic wings (Fig. 8, Tables 2, 3, 4; P = 0.003 for males). The rostrum of *A. adustus* also tends to be relatively wider as indicated by the relatively greater SWR-LC¹A (Fig. 9). Entoconids are well developed on M₃ in both *A. adustus* and *A. subtropicus* but they are much more enlarged in *A. subtropicus* (see Van Dyck 1982a, fig. 21).

The incisors of *A. adustus* are much more specialised than the incisors of *A. subtropicus*. I¹ in particular of *A. adustus* is much more massively crowned and procumbent than I¹ in *A. subtropicus*. I²⁻⁴ are also more massive in *A.*

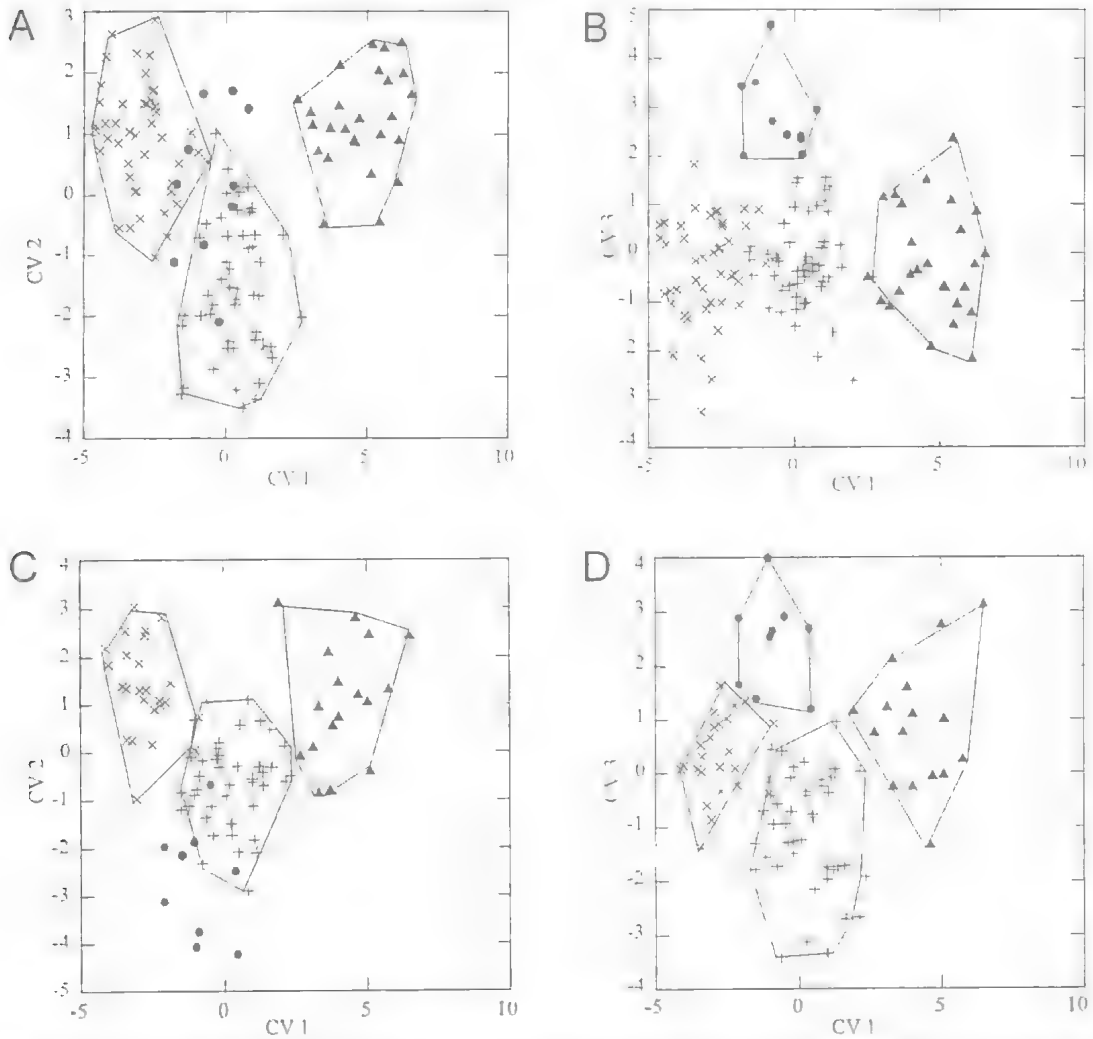


FIG. 10. Plot of canonical-variate (CV) scores for first three CV axes based on 18 cranial and dental measurements for: (A), (B) male *Antechinus* and (C), (D) female *Antechinus*. *Antechinus subtropicus* (▲), *A. adustus* (●), *A. stuartii* (+) and *A. agilis* (×).

adustus than the spatulate incisors of *A. subtropicus*. I² and I³ are also higher crowned in *A. adustus*.

The prominent postero-lingual lobes on P¹⁻³ of *A. adustus*, which cause the premolars to appear more rounded, are accentuated in comparison with *A. subtropicus*.

COMPARISONS OF *A. ADUSTUS* AND *A. SUBTROPICUS* WITH *A. STUARTII*.

MATERIAL of *A. stuartii*. Barrington Tops (AM M32936-32949); Jervis Bay (AM M32831-32887); Kioloa (AM M32889, 32891, 32905); Kangaroo Valley (AM M22623); Myall Lakes (AM M3173-3176, 3178,

3179, 3181-3184, 3186, 12591-12593, 12595, 12596); Waterfall (AM M5294).

External Characters. *Antechinus stuartii* is generally smaller than *A. subtropicus*, although the southern-most populations approach *A. subtropicus* in weight. The mean weights of various *A. stuartii* populations are Jervis Bay males 51g (n = 33, range = 32-70), Jervis Bay females 26g (n = 25, range = 20-33); Ku-ring-gai Chase National Park males 47g (n = 14, range = 38-59), Ku-ring-gai Chase National Park females 27g (n = 14, range = 22-37); Myall Lakes males 27g (n = 10, range = 18-43) and Barrington Tops males 29g (n = 34, range = 20-38), Barrington

TABLE 5. Standardised canonical coefficients for each character for canonical-variate analysis of skull and dental measures of *Antechinus*. Abbreviations as in Fig. 1.

Variable	Male			Female		
	1	2	3	1	2	3
BL	0.601	1.637	1.602	0.379	0.072	2.283
ZW	-0.271	-0.330	-0.968	-0.655	1.259	-0.566
IOW	0.356	-0.346	0.206	0.408	-0.21	0.281
SWR-LC ¹ A	0.110	-1.032	0.581	-0.013	-0.738	-0.083
SWR-LM ³	-0.371	0.124	0.147	-0.093	-0.014	0.179
DL	-0.041	-0.629	-1.39	0.209	0.081	-0.897
C ¹ M ⁴	0.405	0.363	0.088	0.574	0.398	-0.669
APVL	0.132	0.023	-0.174	0.188	0.018	-0.139
PPVL	0.058	-0.704	-0.266	-0.09	-0.313	-1.027
IPVL	-0.942	-0.414	0.090	-0.865	-0.605	-0.339
IBW	0.074	-0.250	0.334	0.032	-0.223	0.509
OBW	0.332	0.239	0.643	0.419	-0.873	0.216
P ¹⁻³	-0.287	-0.046	-0.102	-0.422	-0.162	0.023
P ¹⁻²	-0.075	-0.178	-0.536	0.187	-0.289	-0.057
Eigenvalue	7.956	1.549	0.701	5.358	1.714	1.310
Variance (%)	77.95	15.17	6.87	63.92	20.45	15.63

Tops females 21g (n = 30, range = 15-28). There appears to be clinal variation within *A. stuartii*, with larger animals in the south and smaller in the north (MSC, pers. obs.).

Antechinus stuartii tends to be smaller in head-body-length than *A. subtropicus*. The mean head-body lengths of various *A. stuartii* populations are Jervis Bay males 117mm (n = 33, range = 99-126); Jervis Bay females 98mm (n = 25, range = 93-105); Ku-ring-gai Chase National Park males 120mm (n = 13, range = 108-140), Ku-ring-gai Chase National Park females 94mm (n = 15, range = 85-105); Myall Lakes males 100mm (n = 8, range = 85-118), and Barrington Tops males 101mm (n = 32, range = 84-120), Barrington Tops females 92mm (n = 30, range = 75-108).

The tails of *A. stuartii* appear to be relatively longer than the tails of *A. subtropicus*. The tails of males from Jervis Bay average 0.97, Ku-ring-gai Chase National Park 0.80, Myall Lakes 0.83 and Barrington Tops 0.89 of head-body length. The tails of females from Jervis Bay average 1.00, Ku-ring-gai Chase National Park 0.93 and Barrington Tops 0.87 of head-body length.

Cranial and Dental Characters. The skull length of *A. stuartii* tends to be shorter than in *A. subtropicus* as reflected by the smaller BL. The skull also tends to be more brachycephalic with a

TABLE 6. Classification results from discriminant-function analysis based on 16 cranial and dental measurements for individual *Antechinus*, showing percentage and number (in parentheses) of individuals allocated to groups by species males and females.

Males					
	n	<i>A. subtropicus</i>	<i>A. adustus</i>	<i>A. stuartii</i>	<i>A. agilis</i>
<i>A. subtropicus</i>	26	100 (27)	0	0	0
<i>A. adustus</i>	10	0	100 (10)	0	0
<i>A. stuartii</i>	48	0	2 (1)	98 (48)	0
<i>A. agilis</i>	45	0	0	2 (1)	98 (44)
Females					
	n	<i>A. subtropicus</i>	<i>A. adustus</i>	<i>A. stuartii</i>	<i>A. agilis</i>
<i>A. subtropicus</i>	16	100 (16)	0	0	0
<i>A. adustus</i>	9	0	100 (9)	0	0
<i>A. stuartii</i>	43	0	0	98 (42)	2 (1)
<i>A. agilis</i>	25	0	0	4 (1)	96 (24)

broader rostrum in *A. stuartii* as reflected by the absolutely and relatively greater ZW (Fig. 8, Tables 2, 4; P = 0.021 for males) and SWR-LC¹A (Fig. 9, Tables 2, 4; P = 0.005 for males). The palatal vacuities in *A. stuartii* also tend to be relatively shorter as reflected by the relatively shorter APVL (Table 2; P < 0.001) and PPVL (Table 2, P = 0.043 for males) and the corresponding longer IPVL (Tables 2, 4, Fig. 7; P < 0.001).

The incisors of *A. adustus* are much more specialised than the incisors of *A. stuartii*. I¹ of *A. adustus* is much more massively crowned and procumbent than I¹ in *A. stuartii*. I²⁻⁴ are also more massive in *A. adustus* than the spatulate incisors of *A. stuartii*. I² and I³ are also higher crowned in *A. adustus*. The prominent postero-lingual lobes on P¹⁻³ of *A. adustus*, which cause the premolars to appear more rounded, are accentuated in comparison with *A. stuartii*. The alisphenoid tympanic bullae tend to be larger in *A. stuartii* compared to *A. adustus* as reflected by the smaller IBW (Tables 3, 4, Fig. 8; P = 0.037 for females).

COMPARISONS OF *A. ADUSTUS* AND *A. SUBTROPICUS* WITH *A. AGILIS*.

MATERIAL of *A. agilis*. Bega (AM M33046, 33048, 33050-33068, 33073-33078); Bodalla (AM M32912); Brindabella Ranges (AM M32913-32916, 32918-32920, 32888, 33011, 33015-33017, 33029-33033, 33036-33038, 33157-33159, 33319, 33342, 33343); Gundaroo (AM M33160, 33161); Kioloa (AM M32890, 32892-32911); Mt Canobolas (AM M33344).

External Characters. *Antechinus agilis* is much smaller and lighter than *A. subtropicus*. The mean weights of various *A. agilis* populations are Loch Valley males 30g (n = 29, range = 16-41), Loch Valley females 21g (n = 5, range = 17-26); Mitta Mitta males 26g (n = 21, range = 16-36), Mitta Mitta females 19g (n = 31, range = 14-26) and Brindabella Range males 26g (n = 24, range = 17-35), Brindabella Range females 18g (n = 14, range = 14-26).

Antechinus agilis has a much smaller head-body length than *A. subtropicus*. The mean head-body lengths of various *A. agilis* populations are Loch Valley males 95mm (n = 58, range = 77-107), Loch Valley females 85mm (n = 13, range = 76-93) (Wakefield & Warneke 1967); Mitta Mitta males 104mm (n = 21, range = 85-124), Mitta Mitta females 98mm (n = 29, range = 85-115); Bega males 96mm (n = 13, range = 89-102), Bega females 87mm (n = 15, range = 82-95) and Brindabella Range males 100mm (n = 26, range = 89-110), Brindabella Range females 89mm (n = 13, range = 70-100).

Antechinus agilis generally has a relatively longer tail than *A. subtropicus* but the proportion is similar to that found in *A. adustus*. The tails of males from Loch Valley average 1.03 (Wakefield & Warneke, 1967), Mitta Mitta 0.77, Bega 0.99 and Brindabella Range 0.9 of head-body length. The tails of females from Loch Valley average 1.03 (Wakefield & Warneke, 1967), Mitta Mitta 0.79, Bega 1.00 and Brindabella Range 0.9 of head-body length.

The fur colour of *A. agilis* tends to be a more greyish brown rather than the much darker brown of *A. adustus*. However, Wakefield & Warneke (1967) claim that dark specimens of *A. agilis* from high altitude areas of Victoria (e.g. Mt Macedon, Mt Arnold and Loch Valley) were hard to distinguish on pelage from *A. adustus*.

Cranial and Dental Characters. *Antechinus agilis* tends to be much smaller than *A. subtropicus* as reflected by the absolutely smaller BL (Fig. 7, Tables 2, 4; $P < 0.001$). The skull of *A. agilis* appears to be more brachycephalic than that of *A. subtropicus* as reflected by the relatively greater ZW (Fig. 8). *Antechinus agilis* has both relatively and absolutely smaller anterior and posterior palatal vacuities and a correspondingly larger IPVL (Fig. 7, Tables 2, 4; $P < 0.001$).

The incisors of *A. adustus* are much more specialised than the incisors of *A. agilis*. I¹ in particular of *A. adustus* is much more massively

crowned and procumbent than I¹ in *A. agilis*. I²⁻⁴ are also more massive in *A. adustus* than the spatulate incisors of *A. agilis*. I² and I³ are also higher crowned in *A. adustus*. *Antechinus agilis* is smaller than *A. adustus* as reflected by the smaller basicranial length (Tables 3, 4; $P < 0.001$). *Antechinus agilis* has a relatively and absolutely narrower rostrum as reflected by the larger SWR-LC¹Λ (Fig. 9, Tables 3, 4; $P < 0.001$). The alisphenoid tympanic wings of *A. agilis* are relatively larger as reflected by the relatively and absolutely smaller IBW (Tables 3, 4, Fig. 8; $P < 0.001$).

COMPARISONS OF *A. ADUSTUS* AND *A. SUBTROPICUS* WITH *A. FLAVIPES*.

External Characters. *Antechinus flavipes* is much larger and heavier than *A. adustus* (Van Dyck, 1982a; Tables 3, 4).

Antechinus flavipes differs from both *A. subtropicus* and *A. adustus* in the colouration of its pelage. *Antechinus flavipes* is lighter in colour, possesses prominent buff fur surrounding the eyes and tannish patches of post-auricular fur, has dorsal fur with a prominent change in antero-posterior fur colour from grizzled greyish shoulders to a tannish rump and a black tail tip.

Cranial and Dental Characters. Most of the cranial and dental comparisons between *A. subtropicus* and *A. flavipes* are given in Van Dyck (1982a). In summary, *A. flavipes* has: a relatively and absolutely greater zygomatic width (Van Dyck, 1982a fig. 17, table 2); relatively and absolutely shorter anterior and posterior palatal vacuities with corresponding longer inter-palatal vacuity distance (Van Dyck, 1982a, figs 13, 14, 15, table 2); a wider rostrum (Van Dyck, 1982a, fig. 16, table 2); a narrower inter-orbital width (Van Dyck, 1982a, fig. 17, table 2); greater snout-canine depth (Van Dyck, 1982a, fig. 20, table 2); relatively shorter and wider premolars with corresponding shorter premolar row (Van Dyck, 1982a, figs 18, 25, table 2); narrower separation of transverse canal foramina (Van Dyck, 1982a, fig. 19, table 2); and absent to tiny entoconids (as opposed to large entoconids) and narrower talonids on M₃ (Van Dyck, 1982a, fig. 21).

Antechinus flavipes differs from *A. adustus* in larger basicranial length, relatively larger alisphenoid tympanic wings, more massive canines and much smaller entoconids on M₃.

DISCUSSION

This study, and that by Dickman et al. (1998), shows that a reappraisal of interpopulation variation and taxonomic status of eastern Australian populations currently attributed to *A. stuartii* and *A. flavipes* is required.

Since *A. adustus* is geographically isolated from the rest of the *A. stuartii* complex, it would be difficult to grant it species status on isozymes or morphology alone. It differs from both *A. stuartii* and *A. agilis* at 15% of loci (Baverstock et al., 1982; Dickman et al., 1998), which is higher than the isozyme differentiation of *A. stuartii* and *A. agilis* (see Dickman et al., 1988) and almost as high as the isozyme differentiation of *A. stuartii* from *A. flavipes* (see Baverstock et al., 1982). This work and Van Dyck (1982a) demonstrate the marked morphological distinctiveness between *A. adustus* and the other members of the *A. stuartii* complex, confirming its species status. It is surprising that *A. adustus* is morphologically closer to *A. stuartii* and *A. agilis* than it is to the geographically closest member of the complex, *A. subtropicus*. Watt (1997) found that *A. adustus* is much more similar in ecology to *A. stuartii* and *A. agilis* than it is to *A. subtropicus*, which could explain the morphological similarity.

Sumner & Dickman (1998) found some electrophoretic differences between *A. subtropicus* populations from Mt Glorious and NSW *A. stuartii*. The lack of fixed differences could be caused by examination of an insufficient number of isozymes (*A. stuartii* and *A. agilis* only differ slightly electrophoretically) or the northern NSW sample of *A. stuartii* they examined actually consisted of both *A. stuartii* and *A. subtropicus* which would mask the differences between taxa. Reanalysis of the allozyme work of Sumner & Dickman (1998) is in progress and there are differences in allele frequencies between the species (Crowther & Sumner unpublished). Current work (Crowther, Elphinstone & Baverstock unpubl.) using the control region of mitochondrial DNA also is showing some genetic difference between *A. stuartii* and *A. subtropicus*. Morphological work in progress will indicate whether the species described in this paper correspond with the genetic forms (Crowther unpubl.).

The larger size of *A. subtropicus*, together with its relatively longer, narrower rostrum could be attributed to character release because of a lack of competition from *A. swainsonii* compared to that in *A. agilis* and *A. stuartii*. This has been

suggested by Crowther (1996). Competition has previously been demonstrated between *A. agilis* and *A. swainsonii* (see Dickman, 1986). The large and long rostrumed *A. swainsonii* is absent or very uncommon within the range of *A. subtropicus* (see Van Dyck & Ogilvie, 1977). This could imply that *A. subtropicus* consumes relatively more larger, softer, terrestrial prey than *A. stuartii* or *A. agilis*. The relatively longer tail of *A. agilis* may assist it in climbing trees (Dickman, 1983).

The small size, rounded premolars with shortened premolar row and broad rostrum of *A. adustus* could be the response to competition with the ecological equivalent of *A. swainsonii* in NE Qld, *A. godmani*. *Antechinus adustus* may have to consume more smaller, abrasive and arboreal prey than *A. godmani*. The large, procumbent incisors of *A. adustus* resemble those of the arboreal *Phascogale* and could imply convergence in feeding niche.

In *A. subtropicus*, the premaxillary vacuities extend posteriorly to a position midway between P¹ and P². Although Archer (1981) found that a direct correlation existed between the degree of aridity of habitat and length of palatal vacuities in *Sminthopsis* such that those species occupying arid climates have larger vacuities and vice versa; the opposite is true for species of *Antechinus*. In fact, *A. subtropicus* from the vine-forests of SE Qld and NE NSW has a greater proportion of palatal fenestration than most other dasyurids. The size of the palatal vacuities is of great use in diagnosing species of dasyurids, particularly *Antechinus* species (Van Dyck, 1982a; Dickman et al., 1998), and the extremely large palatal vacuities of *A. subtropicus* distinguish it from any other *Antechinus*.

Entoconid size on M₃ was claimed by Van Dyck (1982a) to be a good diagnostic feature separating *A. stuartii* from *A. flavipes*. Dickman et al. (1998) found that this was not the case and that it was often difficult to tell apart *A. stuartii*, *A. agilis* and *A. flavipes* using entoconids alone. The very large entoconids on the M₃ of *A. subtropicus* make it an extremely useful diagnostic character. Archer (1981) could suggest no reason for the difference in entoconid size between *Sminthopsis* species, except that more inland forms tended to have smaller entoconids than coastal forms. He found no clear relationship between the food consumed and the presence or absence of entoconids in dasyurids.

The small alisphenoid tympanic bullae found in *A. adustus* are possibly an adaptation to its dense vine forest habitat. Webster (1961, 1962) and Lay (1972) have produced evidence in rodents and Archer (1981) in *Sminthopsis*, that there is a direct correlation between bulla size and increasing aridity. Webster & Webster (1975) concluded that larger bullae in rodents enhance sensitivity to low frequency sounds such as produced by the attack flight of owls and the strike of snakes. *Antechinus adustus* does not need to forage far from cover and so may not require large bullae. *Antechinus flavipes* inhabits drier, more open country and may thus require larger alisphenoid tympanic bullae.

Extensive examination of specimens from the Queensland Museum shows that *A. subtropicus* is not the only member of the *A. stuartii* complex in southern Qld. Specimens from near Wallangarra 28°55'S 151°55'E (e.g. J7727-7729) and Pyramid Creek, Wyberba 28°50'S 151°57'E (e.g. J8088, J8089) can be currently allocated to *A. stuartii*. The habitat is dry sclerophyll woodland with abundant granite outcrops and bracken gullies as opposed to the subtropical rainforest habitat preferred by *A. subtropicus*. The specimens from these areas have reduced entoconids, smaller palatal vacuities and flaring of the jugals with expansion of the lachrymals which is more typical of *A. stuartii*. The pelage colour and patterning more resemble that of *A. flavipes* than *A. subtropicus*. Further biochemical and morphological work needs to be done on specimens from this area as well as in northern NSW. A complete study of variation within *A. stuartii* and *A. flavipes* has to be completed before any confidence can be placed on the identifications of these specimens. It is even possible that some specimens represent *A. unicolor*, despite synonymisation of this taxon with *A. stuartii* by Wakefield & Warneke (1967).

As stated in Dickman et al. (1998), resolution of species limits among Australian mammals has been neglected during the past four decades, and it is evident from this study, those of Dickman et al. (1988, 1998) and unpublished morphological and molecular by MSC, that *A. stuartii* and possibly *A. flavipes* consist of species-complexes. The results of these studies emphasise the critical importance of a sound taxonomic framework both to mammalian research generally and to conservation management in particular (Parnaby, 1991). An example of the former is geographical differences in nipple number (Cockburn et al., 1983), attributed previously to plasticity within

A. stuartii that now appear to be due in part to interspecific variation. Although '*A. stuartii*' is one of the most intensively studied small mammals in eastern Australia, much of the research in the past two decades will require reassessment in the light of taxonomic revision. At present, '*A. stuartii*' is considered one of the commonest and most widespread species of small mammals in eastern Australia and is not believed to be of conservation significance. This belief will require urgent reassessment and further taxonomic clarification of the group, as it appears that taxa currently included under '*A. stuartii*' comprise several species each with a concomitantly reduced geographic range. We recommend that relevant land-management and conservation agencies acknowledge the importance of studies of combined morphological and biochemical systematics to conservation management.

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NEW SYNONYMY BETWEEN *OXYOPES GRACILIPES* (WHITE) AND *OXYOPES MUNDULUS* L. KOCH (OXYOPIDAE: ARANEAE)

COR J. VINK AND PHIL J. SIRVID

Vink, C.J. & Sirvid, P.J. 2000 06 30: New synonymy between *Oxyopes gracilipes* (White) and *Oxyopes mundulus* L. Koch (Oxyopidae: Araneae). *Memoirs of the Queensland Museum* 45(2): 637-640. Brisbane. ISSN 0079-8835.

A new synonymy is proposed between *Oxyopes gracilipes* (White, 1849) and *Oxyopes mundulus* L. Koch, 1878. It is based on the examination and comparison of the type of *O. mundulus* and authenticated samples of *O. gracilipes*. A neotype is designated for *O. gracilipes*. The distribution of *O. gracilipes* in Australia is shown. It is proposed that *O. gracilipes* is Australian in origin. □ *Oxyopidae, Oxyopes, synonymy, Australia, New Zealand, neotype.*

Cor J. Vink, Ecology & Entomology Group, PO Box 84, Lincoln University, New Zealand (email: vinkc@lincoln.ac.nz); Phil J. Sirvid, Museum of New Zealand Te Papa Tongarewa, PO Box 467, Wellington, New Zealand (email: phils@tepapa.govt.nz); 13 April 2000.

The Oxyopidae (lynx spiders) of New Zealand were revised and found to comprise only one species *Oxyopes gracilipes*, also present in Tasmania (Vink & Sirvid, 1998). Shortly after the publication of that paper one of the authors (CJV) had the opportunity to examine specimens of Oxyopidae in the Western Australian Museum, Perth and the Australian Museum, Sydney. Specimens identified by Judy Grimshaw as *Oxyopes mundulus* in both collections appeared identical to *O. gracilipes*.

To clarify the situation, we borrowed the holotype *O. mundulus* and compared it to specimens of *O. gracilipes* and other specimens identified as *O. mundulus*.

Roewer (1954) listed 16 Australian species in the family Oxyopidae, of which 14 were in the genus *Oxyopes*. The only published taxonomic work on Australian oxyopids since then was the description of two new species in the genus *Hamataliwa* by Grimshaw (1989). This was part of an unpublished revision of the Oxyopidae of Australia (Grimshaw, 1991).

Abbreviations. AM = Australian Museum, Sydney; LUNZ = Entomology Research Museum, Lincoln University; MONZ = Museum of New Zealand Te Papa Tongarewa, Wellington; WAM = Western Australian Museum, Perth.

COMPARISON OF THE TWO SPECIES

Koch's (1878) description and illustrations of *Oxyopes mundulus* were not accurate enough for a conclusive comparison with *O. gracilipes*. The female holotype of *O. mundulus* was borrowed from the Zoological Museum, Hamburg, examined and compared to specimens of *O.*

gracilipes. Overall appearance, size, colour pattern, spination and genitalic structure of the type of *O. mundulus* were identical to those of specimens of *O. gracilipes*. No significant qualitative differences were found among specimens of *O. gracilipes* and *O. mundulus*, including comparisons of male palpal structure and internal female genitalia.

We have also examined the types of *Oxyopes rubicundus* L. Koch, 1878, *Oxyopes elegans* L. Koch, 1878 and specimens of an undescribed Australian *Oxyopes*. It appears that *O. gracilipes* is part of a group of closely related Australian species, which includes *O. rubicundus*, *O. elegans* and an undescribed *Oxyopes* sp.

SYNONYMY

Oxyopes gracilipes (White, 1849)

Sphasus gracilipes White, 1849: 5.

Oxyopes mundulus L. Koch, 1878: 1025, pl. xc, fig 3. (New synonymy)

Sphasus gregarius Urquhart, 1885: 51, pl. xi, figs 20a-e.

Oxyopes gracilipes (White); Vink & Sirvid, 1998: 1-9.

TYPE MATERIAL. *Sphasus gracilipes* White 1849:5. This species was described from an unspecified number of unsexed specimens collected from New Zealand. Type/s not located by CJV after a thorough search in the Natural History Museum, London (BMNH), where type specimens of other species described by White were deposited.

O. mundulus L. Koch 1878:1025. This species is described from a female collected from Sydney, Australia. The type is part of the Godeffroy Museum collection housed in the Zoological

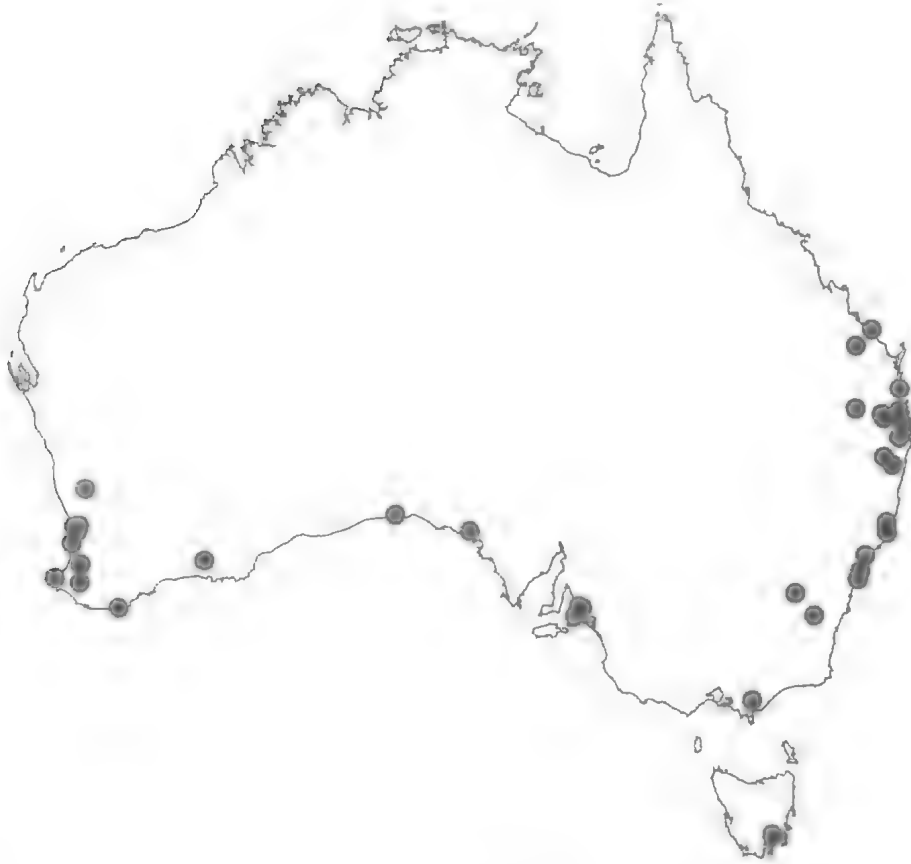


FIG. 1. Distribution of *Oxyopes gracilipes* (White) in Australia.

Museum, Hamburg (ZMH) (Godeffroy Collection Nr. 16501 (Rack, 1961)).

COMMENTS. Our examination of a large range of material leads us to conclude that the type and other Australian specimens identified as *O. mundulus* are the same species as *O. gracilipes*. We therefore consider *Oxyopes mundulus* L. Koch, 1878 to be a junior synonym of *Sphasus gracilipes* White, 1849.

NEOTYPE DESIGNATION

White's (1849) description of *Sphasus gracilipes*, while limited, is sufficient to identify New Zealand's single oxyopid species. His placement of this species in the genus *Sphasus* and his description of the abdomen as 'attenuated at the end' clearly indicate a species of Oxyopidae. White, a British entomologist, would almost certainly have been familiar with oxyopids because of the presence of *Oxyopes heterophthalmus* Latreille, 1804 in England.

White's type material was reported to be in the BMNH (Forster, 1967), but could not be located after thorough searching and is now presumed lost.

With only one species of oxyopid recognised for New Zealand, designation of a neotype was not considered necessary. However, the subsequent discovery of this species in Australia, and the recognition of the synonymy with *O. mundulus* means it is now advisable to designate a neotype to fix the concept of *Sphasus gracilipes* White, 1849 as interpreted and redescribed in Vink & Sirvid (1998).

NEOTYPE. Here designated, male, in 70% ethanol, from New Zealand, AK, near Clevedon, Thorps Bush, sweeping streamside vegetation, 27.xi.1982, P. Maddison, deposited in New Zealand Arthropod Collection, Auckland, New Zealand. The neotype locality within New Zealand is arbitrary as White simply recorded it

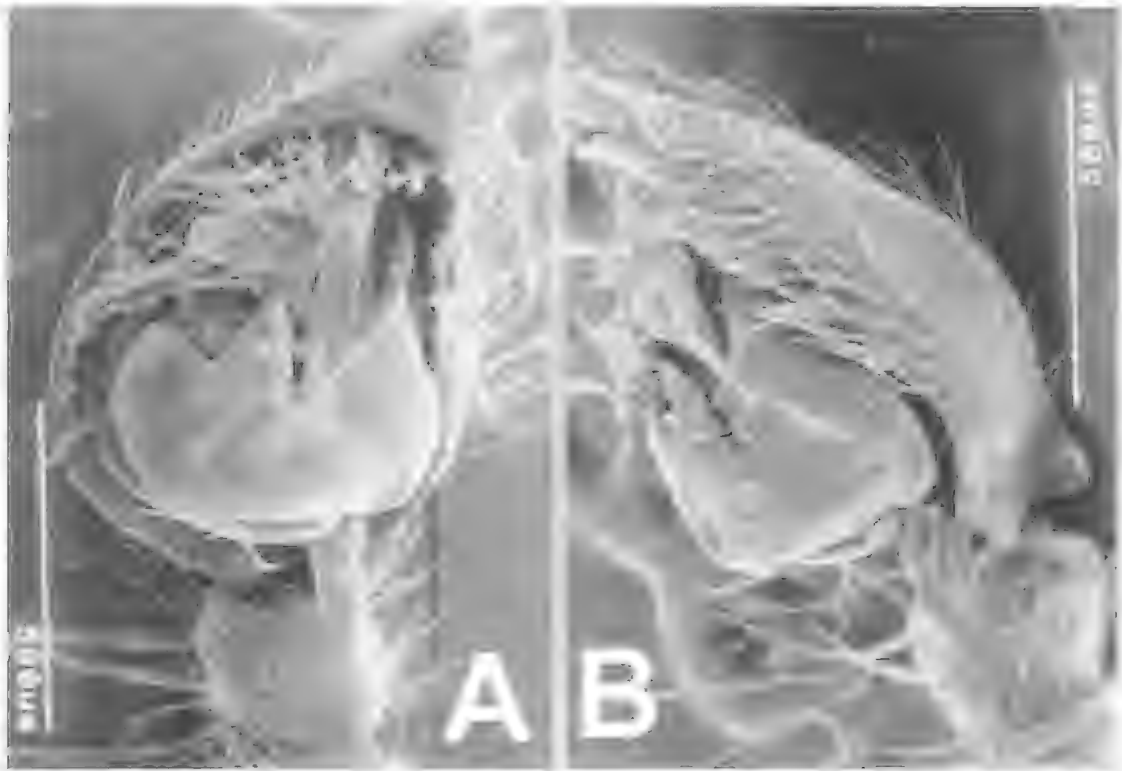


FIG. 2. *Oxyopes gracilipes* (White), male palp, tibia, bulb and cymbium, dorsal left; A, ventral view; B, retrolateral view.

as '*Hab. New Zealand*'. This specimen is described and illustrated in Vink & Sirvid (1998).

OTHER MATERIAL. QUEENSLAND: ♀, Eurimbula, SE of Gladstone, 24°11'S, 151°50'E, iii.1975, C. Horseman (AMKS12784); QMS49010: ♀, Lake Broadwater, Lakeview, 27°20'S 151°05'E, SE Qld, lake edge, 26 Jan 1984, M. Bennie; QMS49011: ♂, Brisbane, Acacia Ridge, 27°28'S 153°02'E, SE Qld, malaise trap, Jan 1979, E.C. Dahms; QMS49012: ♀, Lake Broadwater via Dalby, 27°20'S 151°05'E, SE Qld, on grass, 20 May 1984, M. Bennie; QMS49013: ♂, ♀, Mt Tamborine, 27°55'S 153°11'E, SE Qld, sweeping/beatng, 10 Jul 1974, C. L. Wilton; QMS49014: ♀, Junction View, S Gatton, 27°34'S 152°16'E, SE Qld, 30 Dec 1984, A. Rozefelds; QMS49015: ♀, 1 juv., Laidley Ck, Laidley, 27°44'S 152°22'E, SE Qld, 27 Dec 1980, M. Grant; QMS49016: 2♀, Lake Broadwater, 27°20'S 151°05'E, SE Qld, 12 Feb 1984, M. Bennie; QMS49017: ♀, Monto, 3.2k N, 24°50'S 151°07'E, SE Qld, 19 Apr 1971, R. Monroe; QMS49018: 3♂, 3♀, Lake Broadwater, NE shore, 27°20'S 151°05'E, SE Qld, sweeping, 26 Nov 1984, M. Bennie; QMS47944: ♀, Mt Coolum, W slopes, 26°34'S 153°05'E, SE Qld, open forest, Jan 1984, B.R. Jahnke.

WESTERN AUSTRALIA: ♂, Miling, 30°29'S, 116°22'E, 22.xi.1974, A. Page (WAM 87/1739); ♂, Darlington, 31°54'S, 116°04'E, v.1975, G.H. Lowe (WAM

87/1551); ♂, Darlington, 31°54'S, 116°04'E, iii.1976, G.H. Lowe (WAM 87/1553); ♂, Mt Lawley, 31°56'S, 115°53'E, 19.x.1986, J.M. Waldock (WAM 87/1763); ♂, Forrestfield, Whistlepipe Gully, 31°59'S, 115°58'E, 4.ix.1986, J.M. Waldock (WAM 87/1558); ♀, Kelmscott High School, 32°07'S, 116°01'E, A. Page (WAM 87/1722); ♂, Furnissdale, 32°34'S, 115°46'E, 22.x.1984, F.H. Uther-Baker (WAM 87/1560); ♂, Grass Patch, Fitz., 33°14'S, 121°43'E, 16.xi.1978, A.F. Longbottom (WAM 87/1567); ♂, Grass Patch, Fitz., 33°14'S, 121°43'E, A.F. Longbottom (WAM 87/1569); ♀, Glenbourne, near Margaret River, 33°53'S, 115°00'E, 2.i.1978, P.G. Kendrick (WAM 87/1732); ♂, 15km SW of Bridgetown, 34°04'S, 116°06'E, 8.xii.1985, J.M. Waldock (WAM 87/1533); ♀, 15km SW of Bridgetown, 34°04'S, 116°06'E, 29.xi.1986, D.Terry (WAM 87/1535); ♀, 15km SW of Bridgetown, 34°04'S, 116°06'E, 29.xi.1986, D. Terry (WAM 87/1536); ♂, 15km SW of Bridgetown, 34°04'S, 116°06'E, 29.xi.1986, D. Terry (WAM 87/1537); ♂, 15km SW of Bridgetown, 34°06'S, 116°06'E, 29.xi.1986, D. Terry (WAM 87/1539).

NEW SOUTH WALES: ♂, Green Pidgeon near Kyogle, 28°30'S, 153°04'E, 21.xi.1984, E.D. Scambler (AM KS16310); ♀, Washpool SF, Moogem Rd, 29°16'S, 152°22'E, 9.ii.1982, C. Horseman (AMKS9077); ♀, 18km N of Taree, 31°48'S, 152°29'E, 10.xii.1981, M. Gray & C. Horseman (AM KS10188); ♂, 7km N of Taree, 31°53'S,

152°29E, 6.xii.1981, M. Gray et al. (AMKS9384); ♂, 6km S of Forster, 32°12S, 152°31E, 10.xii.1981, M. Gray & C. Horseman (AM KS10206); ♀, 6km S of Forster, 32°12S, 152°31E, 10.xii.1981, M. Gray & C. Horseman (AM KS10210); ♀, Pittwater, Sydney, 33°38S, 151°18E, 1.i.1967, J. Child (AM KS17305); ♂, Mascot, 33°56S, 151°12E, 21.x.1969, R.E. Mascord (AMKS17308); ♂, ♀, Botany, 33°57S, 151°12E, 3.x.1965, R.E. Mascord (AM KS17284).

AUSTRALIAN CAPITAL TERRITORY: ♀, Canberra, 35°17S, 149°13E, 7.iii.1970, H. Evans (AM KS17285).

TASMANIA: ♀, Queens Domain, Hobart, 42°52S, 147°19E, 2.xii.1963, V.V. Hickman (AM KS30787); ♀, Queens Domain, Hobart, 42°52S, 147°19E, 13.xii.1963, V.V. Hickman (AM KS30788); ♀, Queens Domain, Hobart, 42°52S, 147°19E, 1.xii.1966, V.V. Hickman (AM KS30790); Queens Domain, Hobart, 42°52S, 147°19E, ii.1977, V.V. Hickman (AM KS30789); 2♀, Queen's Domain, Hobart, 42°52S, 147°19E, 20.xi.1997, L.J. Boutin, (MONZ); ♂, New Town, 42°53S, 147°19E, x.1967, V.V. Hickman (AM KS30785).

NEW ZEALAND: 2♀, Cuvier I., 36°26S, 175°46E, vii.1943, R.R. Forster, (MONZ); 4♂, 2♀, Korapuki I., 36°40S, 175°51E, 29.xi.1997, B.M. Fitzgerald, (MONZ); ♂, Stump Bay Swamp, near Lake Taupo, 38°57E, 175°49S, 9.xi.1994, C.J. Vink & A.D. Blest (LUNZ); ♂, ♀, Cape Palliser, 41°37S, 175°15E, 26.xi.1974, (MONZ); ♀, Travis Swamp, Christchurch, 43°30S, 172°42E, 1.xii.1995, R.P. MacFarlane (LUNZ); ♂, Hinewai Reserve, malaise trap, 43°50S, 173°04E, 10.xi.1997, J.B. Ward (LUNZ); 3♀, Cardrona Valley, 44°47S, 169°05E, 9.i.1999, C.J. Vink, (LUNZ).

DISTRIBUTION. *Oxyopes gracilipes* is found in Australia south of 24°11'S. The Australian geographic distribution (based on museum collection records) of *O. gracilipes* is shown in Fig. 1.

REMARKS. A full description of *Oxyopes gracilipes* and notes on its biology are given in Vink & Sirvid (1998).

DISCUSSION

O. gracilipes is the only species of oxyopid found in New Zealand (Vink & Sirvid, 1998) and has been collected from sub-tropical and temperate regions of Australia. A comparison of the palps and epigyna of *O. gracilipes* and those of *O. rubicundus*, *O. elegans* and another undescribed Australian *Oxyopes* sp. reveals that these four species are closely related.

The presence of at least four similar species of *Oxyopes* in Australia and the presence of only one of these species, *O. gracilipes*, in New Zealand leads us to believe that *O. gracilipes* has established in New Zealand from Australia relatively recently. *Oxyopes* species are known to disperse by ballooning (Brady, 1964) and it is

possible that *O. gracilipes* arrived in New Zealand from Australia by this method. Its widespread distribution throughout Australia and New Zealand and lack of divergence in New Zealand indicates that this species is highly mobile.

ACKNOWLEDGEMENTS

We thank the following individuals and institutions for the loan of material under their care: Hieronymus Dastych (Zoological Museum, Hamburg), Mike Gray and Graham Milledge (Australian Museum), Mark Harvey and Julianne Waldock (Western Australian Museum). Thanks to Rob Raven (Queensland Museum) for providing the SEM of the male palp, for extremely valuable comments and for providing us with Queensland locality records. Thanks to David Hirst (South Australian Museum) for providing us with South Australia locality data. We thank Rowan Emberson (Lincoln University) and Ricardo Palma (Museum of New Zealand) for taxonomic advice and for critically reviewing the manuscript. Thanks to Adrian Paterson for critically reviewing the manuscript.

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ADDITIONAL MATERIAL OF *DASYURUS DUNMALLI* FROM THE PLIOCENE
CHINCHILLA LOCAL FAUNA OF QUEENSLAND AND ITS PHYLOGENETIC
IMPLICATIONS

STEPHEN WROE AND BRIAN S. MACKNESS

Wroe, S. & Mackness, B.S. 2000 06 30: Additional material of *Dasyurus dunmalli* from the Pliocene Chinchilla Local Fauna of Queensland and its phylogenetic implications. *Memoirs of the Queensland Museum* **45**(2): 641-645. Brisbane. ISSN 0079-8835.

New material of *Dasyurus dunmalli* from the Pliocene Chinchilla Local Fauna provides previously unknown data relevant to determining its phylogenetic position. The presence of a V-shaped lower incisor arcade in *D. dunmalli* detracts from the case for a special relationship between this fossil taxon and *Dasyurus maculatus*, suggested by a previous investigation. Parsimony-based analysis also supports a special relationship between *Sarcophilus harrisi* and *Dasyurus maculatus*. □ *Dasyuridae*, *Dasyurinae*, *Dasyurus dunmalli*, *Chinchilla Local Fauna*, *Pliocene*, *Queensland*.

Stephen Wroe, Institute of Wildlife Research, School of Biological Sciences, A08, University of Sydney, Sydney 2006; Centre for Research into Australia's Total Ecosystems, Mammal Section, Australian Museum, 6-8 College Street, Sydney 2000; School of Biological Sciences, University of New South Wales, Kensington 2052 (e-mail: s.wroe@student.unsw.edu.au). Brian Mackness, Institute of Wildlife Research, School of Biological Sciences, A08, University of Sydney, Sydney 2006; Current address: PO Box 560 Beerwah 4519, Australia (e-mail: megalania@compuserve.com); 12 July 1999.

Determining the relationship of *D. dunmalli* to other *Dasyurus* has proven problematic with significant levels of homoplasy indicated regardless of phylogenetic interpretation (Bartholomai, 1971; Archer, 1982; Van Dyck, 1987; Wroe & Mackness, 1998). Hypotheses put forward to date include *D. dunmalli* as a sister taxon to: *D. viverrinus* (Bartholomai, 1971; Archer 1982); all extant *Dasyurus* (Archer, 1982); all extant *Dasyurus* except *D. hallucatus* (Archer, 1982); *D. spartacus* + *D. albopunctatus* (Van Dyck, 1987) and *D. maculatus* (Wroe & Mackness, 1998). Alternatively, Archer (1982) suggested that *D. dunmalli* may have shared no special relationship with any living species of *Dasyurus*.

A paucity of material has clearly constrained elucidation of the position of *D. dunmalli* relative to other *Dasyurus*. With the inclusion of newly discovered material from the Chinchilla Local Fauna we re-analyse the data and method presented by Wroe & Mackness (1998) in their parsimony-based investigation of relationships among species of *Dasyurus*.

Dental nomenclature follows Flower (1867) and Luckett (1993) regarding the molar-premolar boundary, where the adult (unreduced) postcanine cheektooth formula of marsupials is P1-3 and M1-4. Dental terminology follows Wroe (1999). Systematic terminology incorporates amendments to Archer's (1982)

classification as suggested by Krajewski et al. (1994) and Wroe (1996, 1997, 1999). QMF = Queensland Museum fossil collection.

SYSTEMATICS

DASYUROMORPHIA (Gill, 1872) Wroe 1996
DASYURIDAE Goldfuss, 1820
DASYURINAE (Goldfuss, 1820)
Krajewski et al., 1994

***Dasyurus dunmalli* Bartholomai, 1971**
(Fig. 1)

REFERRED MATERIAL. QM F3357, partial right dentary, preserving roots of I₁₋₃, C₁, P₁, and complete P₂₋₃, M₁₋₂.

LOCALITY AND AGE. North bank of the Condamine River, Chinchilla Rifle Range (26°48'S, 150°41'E). The Chinchilla Sand was named by Woods (1960) for a sequence of weakly consolidated grey to yellowish and light brown sands, ferruginised heterogeneous conglomerates, grits, sandy clay and clays. These outcrops range from shallow beds to sections several metres deep. The specimens described come from a fossil-bearing unit within the Wilkinson's Quarry that lies unconformably on an indurated layer of fine sand. The sediments are primarily fluvial in nature and represent a number of depositional events. Most fossils in these units occur as isolated pieces. On the basis

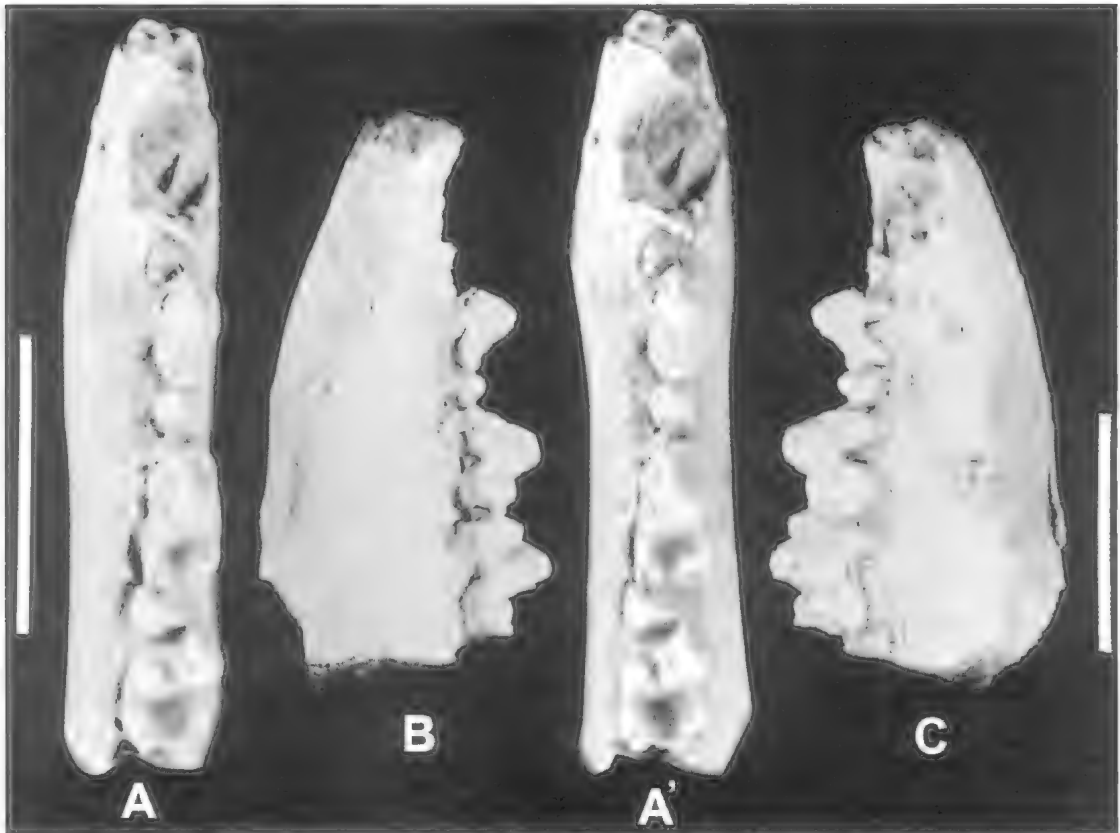


FIG. 1. *Dasyurus dunmalli*. QM F3357, partial right dentary, preserving roots of I_{1-3} , C_1 , P_1 , and complete P_{2-3} , M_{1-2} in A-A', stereo pair occlusal view; B, lingual view; C, buccal view. Scale bar = 1cm.

of biocorrelation with the Kanuka Local Fauna of the Tirari Desert in South Australia, Tedford et al. (1992) suggest an age of around 3.4 million years for the Chinchilla Local Fauna.

DESCRIPTION. The crowns of I_{1-3} are broken away. In anterior view, the root of I_1 is positioned ventral to that of I_2 and lingual to that of I_3 . This gives a V-shaped lower incisor row. The anterior tip of the dentary is compressed on the lingual-buccal axis. Observable morphology of C_1 , P_{1-3} , and M_{1-2} is consistent with that of other *D. dunmalli* from the Chinchilla Local Fauna, as described by Bartholomai (1971), Archer (1982) and Wroe & Mackness (1998).

PHYLOGENETIC ANALYSIS

The arrangement of the lower incisors and anterior of the dentary have not been previously described for *D. dunmalli*. This region differs between dasyurid taxa and is consequently of significance in phylogenetic reconstruction. In

most dasyurids, the lower incisors form roughly a V-shaped profile in occlusal view. *Sarcophilus harrisii* and *Dasyurus maculatus*, with linear profiles, represent the only exceptions. Wroe & Mackness (1998) posited a special relationship between *D. maculatus* and *D. dunmalli* based on the results of a computer-generated parsimony analysis. We have re-run this analysis incorporating this additional character. In the process we detected some errors in both our own (Wroe & Mackness, 1998) character analysis, as well as that of Van Dyck (1987). Corrections and additions are listed below and have been added to Tables 1-2. Results are presented in Fig. 2. Dental measurements are given in Table 3. Method otherwise follows Wroe & Mackness (1998).

a) Wroe & Mackness (1998) and Van Dyck (1987) consider only two character states regarding the shape of the upper incisor row (V-shaped and U-shaped). As observed by Archer (1976), a third state is evident in *D. maculatus* and *Sarcophilus harrisii*, i.e. 'straight'.

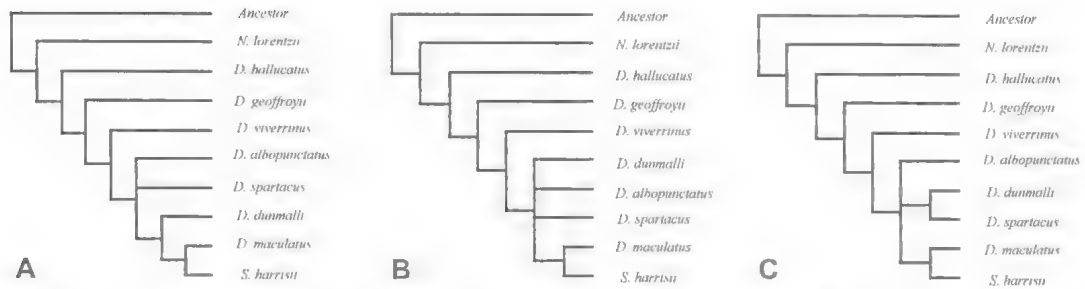


FIG. 2. Three most parsimonious trees (A, B, C) of 39 steps produced using PAUP 3.1.1 for seven species of *Dasyurus*, *Neophascogale lorentzii* and *Sarcophilus harrisii*. Analysis used DELTRAN optimisation and the branch and bound search option. Strict majority-rule consensus produced a tree identical to tree C.

b) Wroe & Mackness (1998) and Van Dyck (1987) score *Dasyurus hallucatus* as showing plesiomorphic phallic morphology. However, Archer (1974) and Woolley & Webb (1977) note that an erectile organ is present in *D. hallucatus*. Indeed, Archer (1974) describes it as identical to that of *D. geoffroyi*.

c) Historically, a number of morphologists have argued for the recognition of possible monophyly for *D. maculatus* and *Sarcophilus harrisii* (see Ride, 1964; Archer, 1982). Some, but not all, recent molecular-based studies have supported this contention (Krajewski et al., 1994, 1997). Also, some molecular investigations have suggested that phascosoricines (sensu Archer, 1982) represent the sister clade to *Dasyurus* and *Sarcophilus*. Consequently, we have included both *S. harrisii* and *Neophascogale lorentzii* in the re-analysis of data presented by Wroe & Mackness (1998).

d) Characters 12 and 17 in the analysis by Wroe & Mackness (1998) are unambiguously correlated. Consequently, we have removed character 12. Re-running the analysis produced 3 most parsimonious trees of 39 steps with uninformative characters excluded: CI = 0.806, HI = 0.194, RI = 0.875 and RC = 0.718 (Fig. 3). In all 3 trees, *D. dunmalli* formed a monophyletic clade with *D. albopunctatus*, *D. spartacus*, *D. maculatus* and *Sarcophilus harrisii*. This group was united by the following synapomorphies: premolars large, ovate in occlusal view (C 5); hypertrophy of M2 trigonid relative to talonid (C 14); and intermediate reduction of the metaconid (C 15). In one of these trees (C), a special relationship was evident between *D. dunmalli* and *D. spartacus*. In another (A), *D. dunmalli* appeared as the sister taxon to *D. maculatus* + *Sarcophilus harrisii*. Curiously, in neither case was the monophyly of *Dasyurus dunmalli* with either of these clades supported by any

TABLE 1. Characters and character states used in phylogenetic analysis with '0' = plesiomorphic, '1' = apomorphic and '?' = missing.

1. Diastema between I¹⁻². 0, present; 1, absent.
2. I¹ morphology. 0, hypsodont relative to I²; 1, not hypsodont relative to I².
3. Shape of incisor row. 0, V-shaped; 1, U-shaped; 2, straight.
4. C₁ morphology. 0, proportionate to uppers. 1 not proportionate.
5. Premolar morphology. 0, premolars narrow and small in occlusal view; 1, large and ovate in occlusal view.
6. Premolar occlusion (ordered). 0, shear past each other in occlusion; 1, do not shear past one another in occlusion.
7. P₃ retained/lost. 0, retained; 1, lost.
8. M₃ postmetacrista/paracristid length (ordered). 0, shorter than in M₂; 1, about equal to M₂; 2, clearly longer than in M₂.
9. Position of metacone relative to styler cusp D on M¹. 0, perpendicular relative to st D; 1, not perpendicular (i.e., posterobuccal).
10. Paracone morphology (ordered). 0, unreduced; 1, intermediate; 2, greatly reduced.
11. Distance between metacone and styler cusp B (ordered). 0, not approximated; 1, intermediate; 2, approximated.
12. Molar shape. 0, not bulbous; 1, bulbous.
13. Posterior cingulid. 0, well developed; 1, reduced or lost.
14. M₂ trigonid vs talonid length. 0, trigonid equal to or less than talonid in length; 1, trigonid > in length than talonid.
15. Metaconid size (ordered). 0, unreduced; 1, intermediate; 2, greatly reduced.
16. M₄ morphology. 0, entoconid present; 1, entoconid absent.
17. Skull height. 0, low; 1, high.
18. Rostrum beneath lachrymals. 0, not broad; 1, broad.
19. Penis morphology. 0, simple; 1, complex.
20. Hallux morphology (ordered). 0, present; 1, reduced; 2, absent.
21. Hind foot morphology. 0, pes short and broad; 1, elongate.
22. Lower incisor row. 0, V-shaped; 1, straight.

TABLE 2. Taxon/character matrix based on the distribution of 22 characters using the 7 species of *Dasyurus*, as well as *Neophascogale lorentzii* and *Sarcophilus harrisi*. Modified from Wroe & Mackness (1998).

Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
ancestor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Neophascogale lorentzii</i>	1	1	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Dasyurus hallucatus</i>	0	0	0	0	0	1	1	0	0	1	0	0	1	0	0	1	0	0	1	0	0	0
<i>Dasyurus viverrinus</i>	1	1	1	1	0	1	1	0	0	1	0	0	1	0	0	1	0	0	1	0	0	0
<i>Dasyurus dunmalli</i>	?	?	?	1	1	?	0	?	?	?	?	0	0	1	2	?	?	?	?	?	?	0
<i>Dasyurus albopunctatus</i>	1	1	1	1	1	2	1	2	1	2	1	0	1	1	2	1	0	0	1	1	0	0
<i>Dasyurus spartacus</i>	1	1	1	1	1	2	1	2	1	2	1	0	1	1	2	1	1	1	1	1	0	0
<i>Dasyurus geoffroii</i>	0	0	1	1	0	2	1	1	1	2	1	0	1	0	1	0	1	1	0	0	0	0
<i>Dasyurus maculatus</i>	1	1	2	1	1	2	1	3	1	2	2	1	0	1	3	0	0	0	1	1	0	1
<i>Sarcophilus harrisi</i>	1	1	2	1	1	2	1	3	1	2	2	1	1	1	3	0	0	0	1	1	0	1

synapomorphy. A third tree (B) also treated *D. dunmalli*, *D. spartacus*, *D. albopunctatus*, *D. maculatus* and *Sarcophilus harrisi* as monophyletic, but within this clade, only the position of *S. harrisi* and *Dasyurus maculatus* as sister taxa was resolved. A strict majority-rule consensus produced a phylogeny identical to this third tree. In all trees, a special relationship between *Sarcophilus harrisi* and *Dasyurus maculatus* was supported by the following synapomorphies: development of a straight upper incisor row (C3); marked elongation of the M3 postmetacrista/paracristid relative to that of M2 (C8); approximation of styler cusp D and the metacone (C11); development of bulbous molars (C12); development of greatly reduced metaconids (C15) and the development of a linear lower incisor row (C22).

In our view, these results provide no support for the existence of a special relationship between *D. maculatus* and *D. dunmalli* as postulated by Wroe & Mackness (1998). Moreover, although on the face of it, the results of this analysis seemingly provide equivocal support for the monophyly of either *D. dunmalli* + *D. spartacus* or *D. dunmalli* + *D. maculatus* + *Sarcophilus harrisi*, the absence of potential synapomorphies uniting either clade provides no real foundation on which to base these phylogenies.

Consequently, we consider the position of *D. dunmalli* unresolved within a clade inclusive of *D. albopunctatus*, *D. spartacus*, *D. maculatus* and *Sarcophilus harrisi*. In this regard, both the present

study and those of Van Dyck (1987) and Wroe & Mackness (1998) largely concur, excepting the placement of *S. harrisi*, which was not included in the latter two studies. Support for the monophyly of *S. harrisi* and *Dasyurus maculatus* will require further testing using an expanded taxon/character matrix for corroboration.

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TABLE 3. Dental measurements (mm) of QM F3357. l = anteroposterior length; w = maximum width (premolars); w1 = maximum transverse dimension of trigonid; w2 = maximum transverse dimension of talonid.

Taxon	QMF No.	P ₂		P ₃		M ₁			M ₂		
		l	w	l	w	l	w1	w2	l	w1	w2
<i>D. dunmalli</i>	3357	4.3	2.4		2.0	1.8	5.4	2.7	3.1		6.7

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