MEMOIRS

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PHYLOGENETIC STATUS OF THE IRRAWADDY DOLPHIN *ORCAELLA BREVIROSTRIS* (OWEN IN GRAY): A CLADISTIC ANALYSIS

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Examination of *Orcaella brevirostris* from Queensland has provided new information on colour pattern, external morphometrics, skull morphology, variation in the tympanoperiotic bones and postcranial skeleton. Facial anatomy is described for the first time.

Cladistic analyses, incorporating the new information, investigated the phylogenetic position of *Orcaella*. Our results provide no support for the separation of beluga and narwhal into two different families (Kasuya,1973) nor for the proposal that *Orcaella* and *Delphinapterus* are closely related (Kasuya,1973; Pilleri et al.,1989). The position of delphinoid families in our cladograms is consistent with previous synoptic classifications (Slijper,1962, fig.36; Heyning,1989; Barnes,1990). Our results offer no support for classifications which widely separate delphinids and phocoenids (Shimura & Numachi,1987; Lint et al., 1990; Pilleri et al.,1989).

We suggest that *Orcaella* is a delphinid *sensu lato*. Comparison of characters in the two nearest outgroups (phocoenids and monodontids) suggest *Orcaella* (and other 'blunt-headed' genera) represent the most primitive Delphinidae. However, we cannot rule out the alternative that extensive convergence occurred. Extensive neoteny of the skull in *Orcaella* suggests one means by which the many apparently primitive features could occur.
□ *Cetacea, Orcaella, periotic bone, tympanic bone, facial anatomy, neoteny, cladistics.*

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The phylogenetic status of the Irrawaddy dolphin *Orcaella brevirostris* (Owen in Gray,1866) remains in doubt (Marsh et al.,1989). At least eight taxonomic hypotheses are implied in various proposed classifications (Fig.1). *Orcaella* was initially classified as a porpoise in *Phocoena*. It has also been placed in a more strictly defined Delphinidae (dolphins), Delphinapteridae (with beluga *Delphinapterus leucas* (Pallas,1776)), Monodontidae (with beluga and narwhal *Monodon monoceros* Linnaeus,1758) or in the monotypic Orcellidae.

This paper addresses classification of *Orcaella*. We re-describe the skull, emphasizing neotenic characters which have confounded previous comparisons between *Orcaella* and other odontocetes. We re-examine the tympanoperiotic bones which were poorly known and describe the facial anatomy which was unknown. We assess colour patterns for possible taxonomic characters. New data on external morphometrics and the post-cranial skeleton are presented.

Incorporating this data we evaluate characters that have been used in odontocete classification. Most classifications have been based on one anatomical system (Fraser & Purves,1962; Mead, 1975; Kasuya,1973; Pilleri et al.,1989) and have produced partially conflicting classifications. Only Heyning (1989) used computerized phylogenetic analysis on a range of characters. Although he argued for a phocoenid-delphinid clade, his cladograms left relationships of the Monodontidae, Phocoenidae and Delphinidae unresolved. Gretarsdottir & Arnason (1992) also left the relationship of these 3 families unresolved. de Muizon (1988) examined extant and fossil taxa, using a comprehensive range of characters to produce 4 arrangements of the Monodontidae, Phocoenidae & Albireonidae, Kentriodontidae and Delphinidae, which were still only a subset of the possibilities. We present a cladistic analysis of the Monodontidae, Phocoenidae and Delphinidae *s. l.* Within this context we discuss affinities of *Orcaella*.

MATERIALS

Specimens of *Orcaella* were either found stranded and dead, or recovered after drowning in shark nets near Townsville. Skeletal material
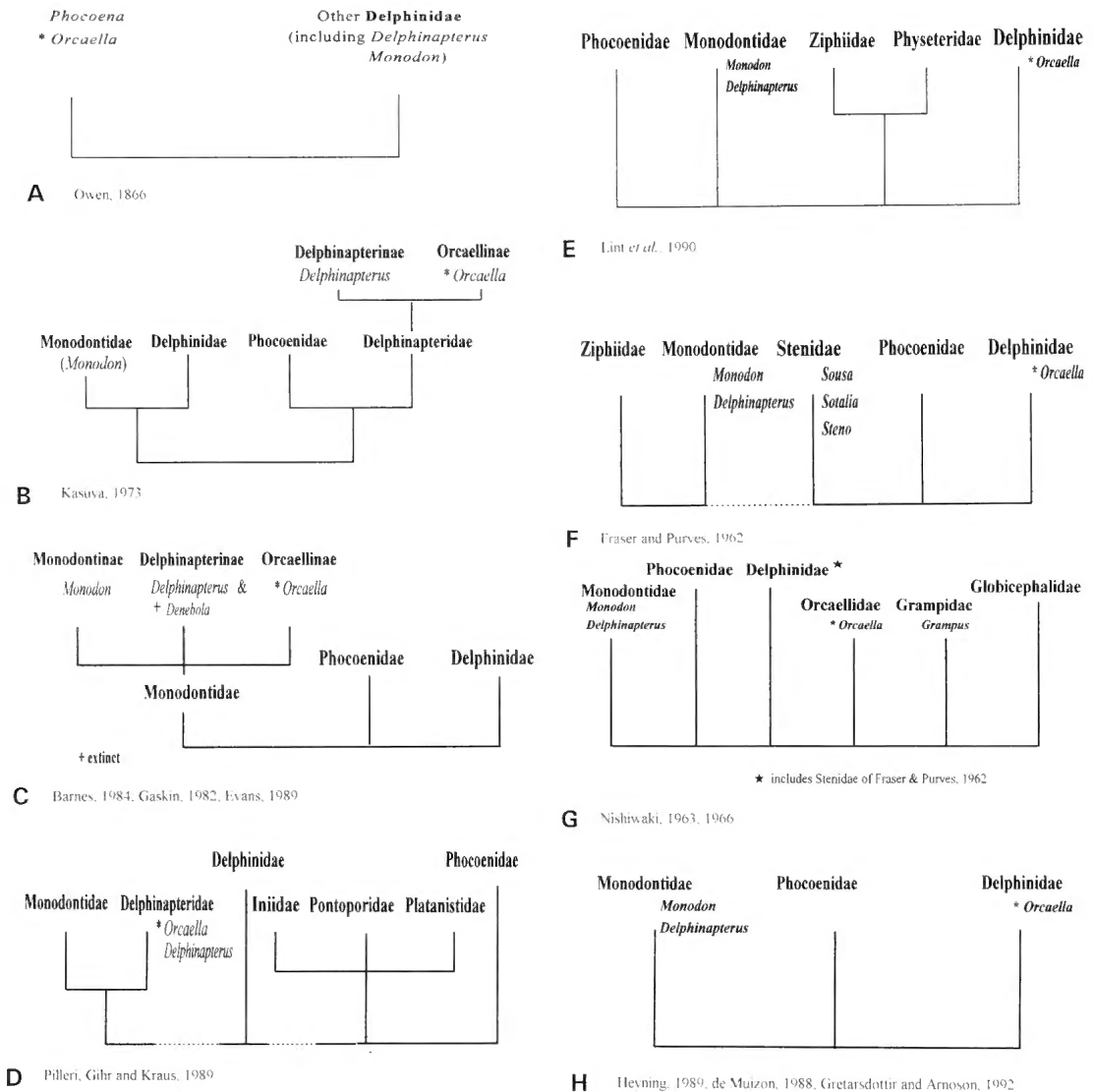
FIG. 1. Taxonomic hypotheses of phylogenetic relationship of *Orcaella* to other toothed whales. A indicates that *Orcaella* was placed within *Phocoena*, which was more broadly defined than at present. The Delphinidae was also more inclusive, containing both the beluga *Delphinapterus* and narwhal *Monodon*. The dashed lines in D separate different lineages as envisioned by Pilleri et al. (1989). The taxonomic relationships in F are derived from the table in Fraser & Purves (1962); the most generalized taxon is Ziphiidae on the left, and increasing specialization is inferred as one moves to the right. The dashed lines indicate a separation of taxa: the Physeteroidea (*Physeter, Kogia*) and Platanistoidea (*Platanista, Inia, Pontoporia, Lipotes*) were interspersed between the Monodontidae and Stenidae. The references indicated in H are only a few of the more recent ones supporting placement of *Orcaella* in the Delphinidae.

is deposited in the Queensland Museum (Paterson, 1986, 1994) (QMJ or QMJM). Most are currently held at the Museum of Tropical Queensland, Townsville; those held in Brisbane are indicated by an asterisk. Specimens collected by James Cook University staff are registered MM or CET, which numbers have been quoted in the literature; these numbers are used particularly when discussing anatomical material. If skeletal material from these specimens has been registered in the Queensland Museum, both the MM and QMJM numbers are listed below. Abbreviations for other collections are: CMN: Canadian Museum of Nature, Ottawa, Ontario, Canada; NSMNH: Nova Scotia Museum of Natural History, Halifax, N.S., Canada; UBC: Dept. Zoology, University of British Columbia, Vancouver, B.C., Canada; VA: Vancouver Aquarium, Vancouver, B.C., Canada. Measurements of beluga and narwhal are of condylobasal length and are approximate.

Orcaella brevirostris (Owen in Gray,1866) Queensland: QMJM4740; QMJM4735 (MM1004); QMJM4700 (MM006); QMJM4704 (MM012); QMJM4708 (MM021); QMJM4709 (MM025); QMJM4712 (MM030); QMJM4714 (MM032); QMJM4721 (MM 061); QMJM4725 (MM081); QMJM4726 (MM082); QMJM4727 (MM088); MM092; MM1003; QMJM11342, QMJM11343; MM1015; MM016.

Phocoenidae

Neophocaena phocaenoides (Cuvier,1829) Saudi Arabia: A. Preen,private collection.

Phocoena phocoena (Linnaeus, 1758) Nova Scotia, Canada: NSMNH973.Z.309.1; NSMNH unregistered, Oct. 26, 1982; NSMNH971.-Z.300.1; NSMNH unregistered, Crescent Beach 1977; NSMNH973.Z.310.1.

Monodontidae

Delphinapterus leucas (Pallas,1776) Quebec, Canada: Trois Pistoiles, May 11, 1983, 573 mm; DL4.85, 400 mm; DL2.86, 468 mm; Northwest Territories, Canada: CMN19556, Collinson Inlet; CMN29997, 548 mm; CMN29998-30000, Belcher I, Hudson Bay, 505, 549 and 552 mm respectively; one unregistered.

Monodon monoceros (Linnaeus,1758) Canada: CMN32278-32280, Baffin I, latter 508 mm; Arctic Biological Station MM65(at CMN); Arctic Biological Station MM66, 580 mm (at CMN); Koluktoo Bay, Baffin I: UBC 9467, 285 mm; Holman I, Northwest Territories: VA, unregistered; VA, unregistered (no data).

Delphinidae

Delphinus delphis Linnaeus, 1758 *QMJM2033, Gold Coast; *QMJM2776, Moreton Bay.

Feresa attenuata Gray, 1874 *QMJM825, Kingscliff, NSW.

Globicephala macrorhynchus Gray, 1846 *QMJM5354; CET1001, Mackay.

Globicephala melas (Traill, 1809) *QMJM4480, Point Lookout; *QMJ15.2104.

Grampus griseus (Cuvier, 1812) *QMJM9542, N. Stradbroke I; *QMJM3858, Moreton I.

Lagenodelphis hosei Fraser, 1956 *QMJM 2749, Fraser I.

Lagenorhynchus acutus (Gray, 1828) NSMNH unregistered.

Lagenorhynchus albirostris (Gray, 1846) NSMNH 72.2.343.8.

Peponocephala electra (Gray,1846) *QMJM2144, Moreton I; *QMJM6577, N. Stradbroke I; *QMJM7854; QMJM4702, Mission Beach; QMJM4730, Crystal Creek, N of Townsville.

Pseudorca crassidens (Owen,1846) *QMJM14210; *QMJM937, Townsville; MM1028.

Sousa chinensis (Osbeck, 1765) QMJM4701, Magnetic I; QMJM4703, Magnetic I; QMJM4711, Townsville; QMJM4717, Magnetic I; QMJM4728; QMJM4731, Pallarenda, Townsville; QMJM4737, Rowes Bay, Townsville.

Stenella attenuata (Gray, 1846) *QMJM6433, Moreton I.

Stenella coeruleoalba (Meyen, 1833) *QMJM3859.

Stenella longirostris (Gray, 1828) QMJM4716, QMJM4718, QMJM4719, all from off Michaelmas Cay, near Cairns.

Tursiops truncatus (Montagu, 1821) *QMJM8859; QMJM4713, juvenile, Magnetic I; QMJM4715, Magnetic I; QMJM4724, Magnetic I; MM91A, Palm I; MM1018.

METHODS

Colour pattern is described from photographs of a captive from Cairns (Dawbin,1972; Leatherwood & Reeves,1983; Mitchell,1975:911); a 1.86m ♀ (MM334) and 2.19m ♀ (MM335) from Cairns; a 2.15m ♀ (MM30), 1.87m ♀ (MM21) and 2.2 m ♀ (MM25) from near Townsville (Talbot & Steene,1984; unpubl. photographs). Based on dentinal layers in teeth, MM25 was estimated at 9 years and MM30 an estimated 8
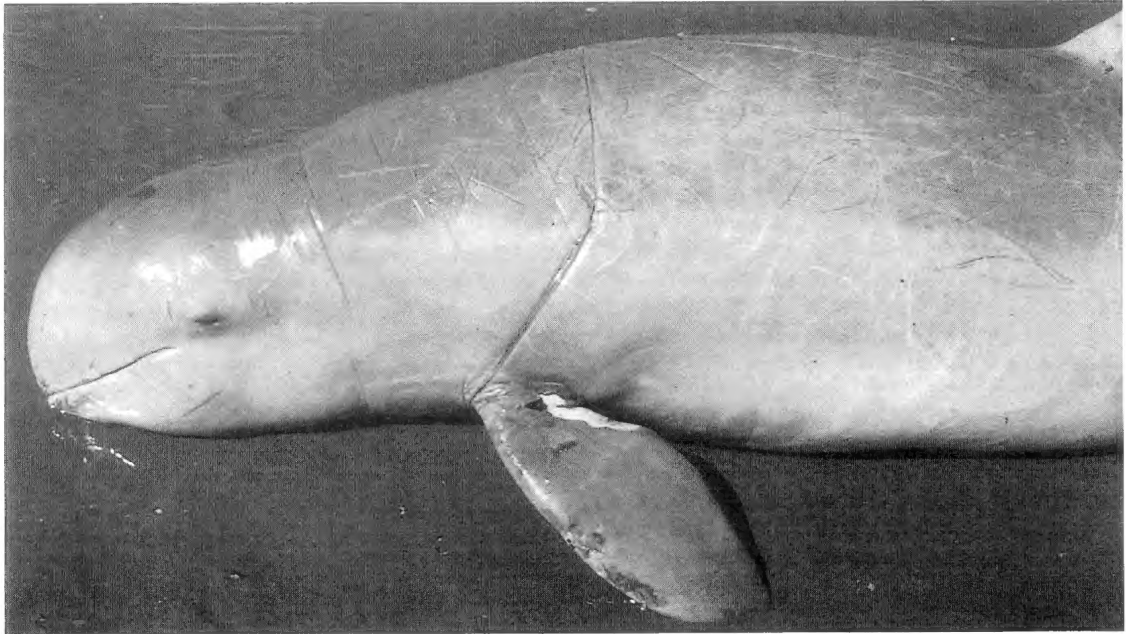
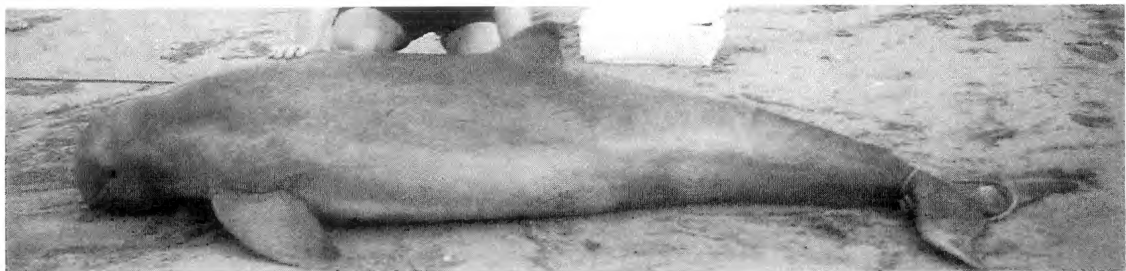FIG. 2. Colour pattern of MM30, a 2.15 m long ♀ from Townsville.

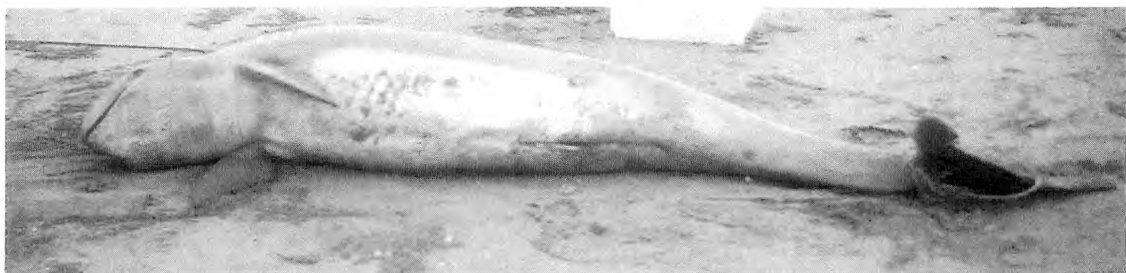FIG. 3. Lateral colour pattern of MM25, a 2.2 m long ♀ from Townsville.

Fig 4. Ventral colour pattern of MM25, a 2.2 m long ♀ from Townsville.

years in age (Heinsohn,1979). Lengths of both animals exceeded the minimum length of confirmed sexually mature ♀♀ in the Queensland population (Marsh et al.,1989); MM335 was pregnant.

Qualitative features of the skull were compared with *Tursiops* (Rommel,1990). Standard skull measurements are as in Perrin (1975).

The angle of the posterior process of the tympanic was determined by temporarily fixing the bulla ventral side upwards on a desk. One arm of a compass was aligned along the meridional axis; the second arm was swung to lie over the lateral edge of the process. The angle so formed was traced onto paper and measured with a protractor.

The periotics were temporarily fixed dorsal side up on the stage of a compound microscope and the positions of the three cochlear apertures drawn using a camera lucida. Care was taken to orient the bulla in the same way to avoid parallax problems. The periotic triangle of Pilleri et al. (1989) was created by drawing lines between outlines of the apertures on the drawing. Angles and lengths of sides of the triangles were determined from the drawings.

Three specimens of *Orcaella* (MM333, 1.34m ♀ from Mackay, MM334, MM335, ♀♀ from Ellis Beach, Cairns) were dissected to examine the upper respiratory tract and facial region. The frozen head of MM334 was sectioned longitudinally on a band saw. The blowhole was set well to the left so the first cut was just to the left of the median line, and the second c.2cm further left. The latter section passed through the tympanoperiotic bones and pterygoid region. Facial musculature was not examined, but the relative proportions of muscle, connective tissue and 'melon' were assessed. The 'melon' was differentiated from connective tissue by its lesser vascularisation (Mead,1975) and the more fatty appearance relative to muscle and connective tissue.

Phylogenetic analyses used Hennig86, version 1.5 (Farris,1988). The implicit enumeration option was chosen to find all of the most parsimonious trees. The implicit enumeration method is time consuming for large data sets so a subset of delphinid genera were analysed. Representatives of most delphinid genera were examined; character states within the genera used to generate the cladograms cover the range of variation within the Delphinidae. Wherever possible, characters were reduced to binary values to avoid some of the problems with multistate characters. All characters were set to non-additive.

In this analysis, only extant families of odontocetes were considered as outgroups, although character states in fossil taxa have been considered in certain cases. We have not examined fossil material, and many features used have not been described in the literature available to us. To include them would result in many missing values, which can cause problems. The Kentriodontidae, which has been considered a potential sister group to delphinids, phocoenids and monodontids, cannot be clearly defined (de Muizon,1988) and may be polyphyletic. de Muizon (1993) considered the peculiar Odobenocetopsidae the sister group to the Monodontidae, but it is so highly modified that it is not relevant to our discussion.

Among extant odontocetes, the river dolphins *Platanista, Lipotes, Inia* and *Pontoporia* are considered the closest living relatives of the Monodontidae-Phocoenidae-Delphinidae (de Muizon,1988; Heyning,1989; Barnes,1990). The first two authors also demonstrated that *Platanista* is separate from the other genera; de Muizon (1990) placed it in a separate superfamily. In the present comparisons, the taxonomic status of the river dolphins can be left unresolved, but *Platanista* was considered separately from *Inia* and *Pontoporia*, and was used as the outgroup.

Character states of features used in this analysis were also determined for *Berardius*, a primitive ziphiid (Moore,1968) and *Physeter*, to determine polarity of characters. In cases where the character was not present in either physeterids or ziphiids, the character state in the fossil taxon Eurhinodelphoidea was considered to help determine the polarity. de Muizon (1990) considered the Eurhinodelphoidea as the sister taxon to Delphinida (his taxon, which encompasses all genera considered here, except *Platanista*). Reasoning in these cases is therefore not that the character is primitive because it occurs in a fossil taxon but because it occurs in a putative sister group, the members of which happen to be all extinct. Polarity decisions for all characters are justified in Appendix 2.

COLOUR PATTERN

RESULTS. A broad grey or blue-grey cape ('spinal field' of Mitchell,1970) extends from the top of the head and back downwards about half the distance to the level of the eye, continuing posteriorly to just behind the base of the dorsal fin, from which it tapers as a wedge along the upper half of the tail stock (captive animal: Daw-
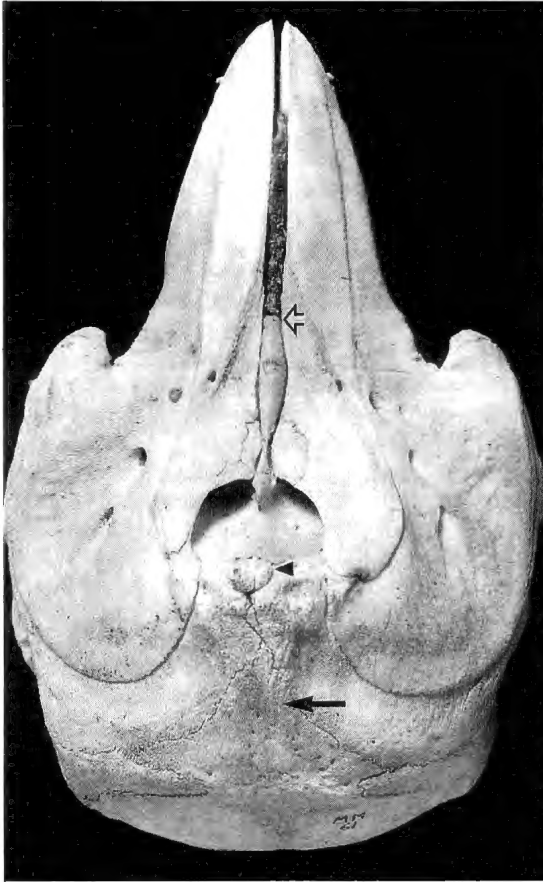
FIG. 5. Dorsal view of QMJM4721, with 312.8 mm condylobasal length and 11.5 dentinal layers. Note broad transverse width of neurocranium; supernumerary bone (triangle) infilling the postnarial fossa; conspicuous triangular interparietal bone (arrow); dorsal extension of parietal bones, posterolateral to the interparietal bone; wide separation of exoccipital and frontal bones; weakly expressed telescoping (wide expanse of frontal bone exposed); prominent spina mesethmoidalis (open arrow); poorly developed nuchal crest.
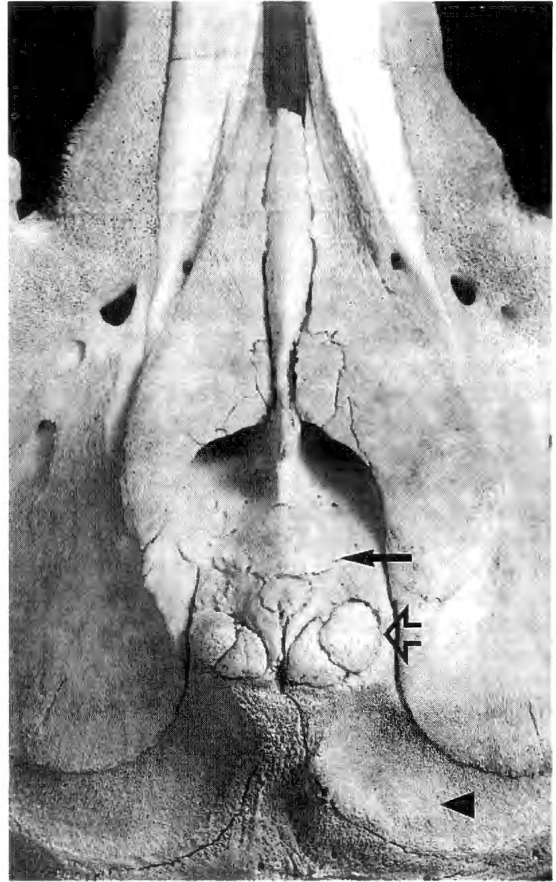
FIG. 6. Dorsal view of QMJM4740. Note triangular area of spongy bone at base of rostrum, extending forward to just in front of spina mesethmoidalis; nodular nasal bones (open arrow); supernumerary bone; poor development of mesethmoid plate (posterior margin indicated by arrow) and consequent exposure of frontal bones anterior to nasal bones; wide exposure of frontal bone (triangle) between the interparietal and maxillary bones.

bin,1972; MM30: Fig. 2; Talbot & Steene, 1984:300; MM25: Fig.3). The dark grey is more extensive on the melon of MM25 than MM30 (Figs 2,3). Grey extends onto the lower jaw and throat region in the captive animal (Leatherwood & Reeves,1983:154) and MM25 (Fig.4) but in the latter, a lighter grey throat patch extends as far back as the axilla of the flippers (Fig.4). The abdominal field from the flipper region to the genital region in MM25 and MM30 (Figs 2,4) is white. The flanks between the dark cape and white abdominal field are light grey to brownish-grey (Talbot & Steene,1984; Figs 2,3); the light grey extends onto the tail stock.

MM334 has the subtle 3-tone pattern, but the dorsal fin on both sides is lighter than the back. This does not appear to be a post-mortem effect.

DISCUSSION. Underwater photographs of *O. brevirostris* from the Mahakan River, Indonesia (Tas'an & Leatherwood,1984; unpubl. photos by Dr. A. Preen) do not show the three tone colour. This may be a real difference, or simply reflect the difficulty in differentiating subtle shading with the rapid loss of contrast underwater.

Anderson (1879, pls 25, 25a) described *O. brevirostris* as 'dark slaty-blue, nearly black, and very little paler on the ventral surface'. It is unclear how long his specimens had been dead; postmortem darkening of cetaceans can be substantial (Pilleri,1976). Anderson (1879) noted that living *O. fluminalis* (=*brevirostris*) were more lightly coloured . The dark grey to black colouration of *Orcaella* needs to be confirmed on living animals.

The subtle 3-tone colouration of Queensland *Orcaella* may be found in juveniles of several dolphin genera, becoming fainter or lost in adults. However, given the sizes and ages of the animals examined, the colour patterns we describe appear to be characteristic of adult animals.

Mitchell (1970) considered the three-tone pattern as the 'common baseline from which to interpret most of the patterns found within the Delphinidae'. Its occurrence in *Orcaella* thus can not be used as evidence for relationship to other delphinid genera. The extension of grey onto the lower jaw and throat in *Orcaella* is similar to the pattern in *Globicephala, Pseudorca, Peponocephala* and *Grampus*. None of the *Orcaella* had a throat chevron, midventral stripe or genital patch as occurs in those genera (Minasian et al., 1987; Mitchell 1970), although MM25 had a vague light grey throat patch similar to a throat chevron. The throat chevron is not restricted to the 'blunt- headed' whales; *Tursiops truncatus* cf *aduncus* may have a distinct throat chevron (G.J.B. Ross pers. comm.). The photographs of *Orcaella* are not of sufficient quality to show unequivocally more specialised features such as spinal blaze, bridles or flipper stripe. In this case, colour pattern is of little taxonomic use.

SKULL

RESULTS

REDESCRIPTION OF SKULL. Values presented below are based on 14 animals from central Queensland, Australia with condylobasal lengths from 297.7–334.8mm and an estimated age (based on dentinal layers) of 3–28 years. An additional skull of a newborn, 232.1mm condylobasal length, was examined for non-mensural characters, but measurements of this specimen were excluded from the descriptive statistics.

Unless otherwise indicated, values are percentages of condylobasal length, based on measurements on the left side of the skull. *Orcaella* has cranial asymmetry as is general in delphinids; this will be considered in detail in a separate publication.

DORSAL ASPECT. The neurocranium is broad (Fig.5), 65.6% (62.6–68.0%) at the postorbital process of the frontal which is usually the widest point of the skull. Zygomatic width is 65.4% (63.2–68.3%).The lacrymal bones extend forward from the maxillary bones to form the lateral border of prominent antorbital notches, 4.0% (2.8–4.5%) deep.

The rostrum is 44.4% (43.2-45.5%)long and 37.6% (34.4–39.8%) wide at the base. Premaxillaries as a percentage of rostrum width are 50.5% (47.0–57.6%) at the base, 62.8% (60.0–65.9%) at 0.25 length, 61.2% (58.1–65.1%) at 0.5 length and 65.0% (56.0–73.1%) at 0.75 length. The spongy, triangular area of the rostrum, bounded laterally by 2 oblique ridges, extends just beyond the proximal quarter of the rostrum (Fig.6).

The premaxillaries continue onto the cranial vault, showing distinct asymmetry at the point of maximum width: the left premaxillary is 4.3% (2.4–5.7%) wide and the right 8.5% (7.6–9.1)% wide at this point. There is a prominent exposure of the frontals between and behind the ascending processes of the maxillaries (Fig. 5).

The vertex is composed mainly of the frontals, with a median suture deflected to the left (Fig.5). It forms an ill-defined ridge running along the body axis between the ascending processes of the maxillaries. The nasal bones are peculiar nodules, often two on each side of the vertex (Fig.6), from 7.3–15.6mm long by 6.4–14.0mm wide. The nasal bones sometimes coalesce, but always retain their nodular appearance (Fig. 7). The postero-medial pair of nasal nodules are at the apex of the vertex while the anterolateral nasal nodules are on the anterior face of the vertex. The anterior face of vertex has a shallow postnarial pit, usually filled in by a supernumerary bone 6.0-22.0mm long by 5.4–17.8mm wide (Figs 5–7).

The mesethmoid plate is generally poorly developed (Figs 5–8), leaving much of the anterior face of the vertex exposed (Figs 6,8). An elongate, shallow fossa occurs laterally in this space, between the apical nasals and the mesethmoid plate (Fig.8). When the mesethmoid plate is more extensive, the fossa excavates its posterolateral margin, leaving a median extension of the plate which reaches back to the supernumery bone on the vertex (Fig.7).

The frontals are always distinctly separated

FIG. 7. Oblique anterodorsal view of vertex, QM JM4714. Note nodular, partially coalesced nasal bones (open arrow); development of mesethmoid plate (posterior margin indicated by triangle); and maxillary intrusions (arrow) along anterior margin of superior nares.

FIG. 8. Dorsal view of QMJM4735. Note poor development of mesethmoid plate (posterior margin indicated by arrow); shallow lateral fossa between mesethmoid plate and depressions for the nasal bones (open arrow); prominent interparietal bone.

from the supraoccipital by prominent dorsal extensions of the parietal bone and a triangular interparietal bone (Figs 5,8).

Anteromedial borders of the superior nares are edged by maxillary intrusions 8.2% (5.8–10.0%) long and 2.4% (1.3-3.5%) wide (Figs 5–8). These intrusions are weakly size dependent (r=0.649 for left maxillary intrusion length vs condylobasal length). A very prominent spina mesethmoidalis extends anterior to the bases of the antorbital notches and widely separates the premaxillaries (Figs 5,6,8). Braincase width is 49.8% (47.0–54.0%) across the parietals and 51.3% (48.2–55.2%) across the squamosals.

LATERAL ASPECT. The skull is deep, 57.2%

(55.3–60.6%) from vertex to the left paroccipital crest.

The orbit is prominent (Fig. 9), 15.8% (15.0–17.1%) between the preorbital and postorbital processes of the frontal bone. The jugal is stout, fitting within a prominent notch on the anterior face of the zygomatic arch. The maxillary bone over the lacrymal and preorbital process of frontal is raised to a variable extent; when it is extensively developed it imparts a concave profile to the supraorbital plate of the maxillary bone.

The temporal fossa is bounded dorsally and posteriorly by a weakly developed temporal crest. The majority of the fossa is bounded medially by parietal and base of the squamosal (Fig.9). The zygomatic arch of the squamosal is prominent, with an extensive mastoid section laterally and a wide post-glenoid space (Fig.9). The paroccipital
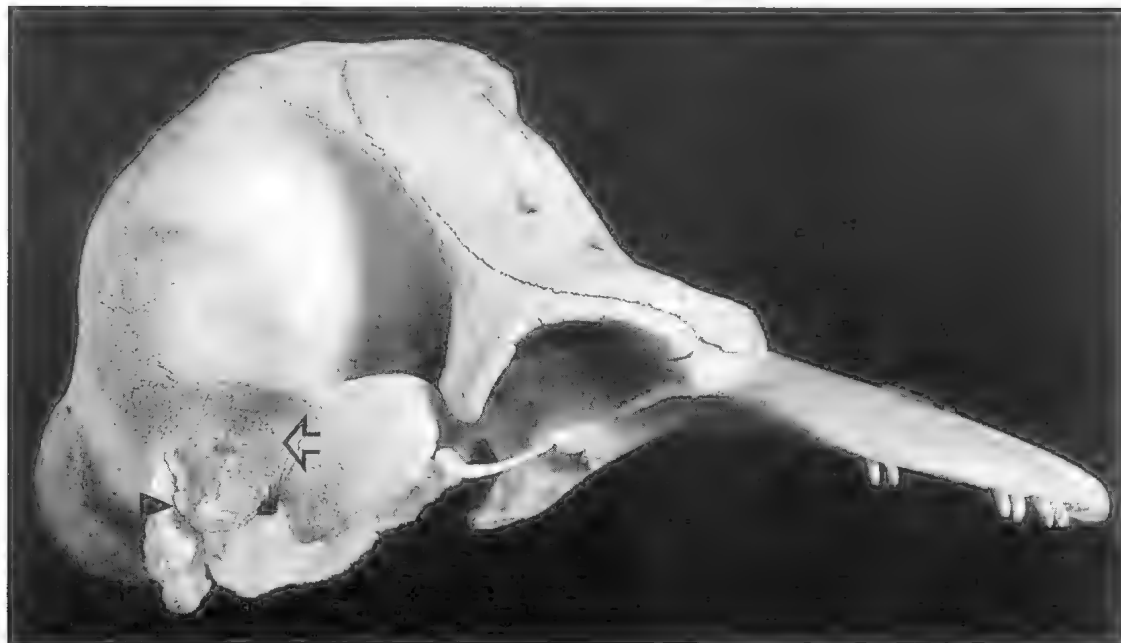
FIG. 9. Lateral view of QMJM4721. Note prominent orbit; robust jugal bone (broken); oblique orientation of occipital condyles; poorly developed temporal crests; ventral orientation of paroccipital process of exoccipital; fissure (triangle) between exoccipital and prominent mastoid portion of zygomatic arch (open arrow).

process of the exoccipital is directed outwards and ventrally, with minimal intrusion anteriorly onto the zygomatic arch. A deep, usually Y-shaped fissure separates the mastoid portion of the squamosal from the paroccipital process of the exoccipital (Fig. 9). The occipital condyles are prominent and directed ventrally at c.45° to the skull axis (Fig.9). Braincase length is 43.1% (42.0–44.9%).

VENTRAL ASPECT. The posterior of the palate contains triangular lateral lobes of the palatine bones, each with a prominent foramen (Fig.10) which forms the anterior end of a channel extendeding dorsally and backwards to the pterygopalatine fossa.

The lateral lobe of the palatines extends posterolaterally as a wing-like process (Figs 10,11) 11.0.% (9.3–12.5%) long along its anterior margin, and underlying an extensive preorbital cavity formed between the maxillaries and presphenoid/frontal bones (Fig.11). This cavity extends dorsally as a lobe, more extensively developed on the right than the left side.

The pterygoid hamuli are distinctly separated by triangular medial lobes of the palatine bones (Figs 10,11). The palatines flank the vomer and spina mesethmoidalis, which is often incomplete-ly covered by the vomer. Sometimes the vomer is visible between the sutures of the palatines and maxillary bones (Fig.12) but in most cases it is indicated only by a pit.

A medial flange extends from the pterygoid hamuli (Figs 10-12), bringing them to within 1.0% (0.6–1.5%) of one another and almost completely covering the inferior nares.

The lacrymal bones are massive (Figs 10,12), 12.4% (10.2–15.0%) long by 14.4% (13.4–15.1%) wide. The frontal bones form a prominent obliquely transverse ridge (Fig. 11) without an optic groove or channel. The optic foramen is incompletely separated from the anterior lacerate foramen by a short vertical bony bridge formed by the fused presphenoid-orbitosphenoid bones. The alisphenoid bone is a prominent plate (Fig. 12), forming the anterior margin of the foramen ovale (posterior margin of foramen provided by an extension of the basioccipital).

The zygomatic arch has an extensive tympanosquamosal recess (Fig. 12). The falciform process is reduced, 3.9% (3.0-5.1%, n=10) long by 3.7% (2.8–4.9%, n=7) wide. It runs parallel to the alisphenoid, rather than ventrally and is not closely associated with the periotic bone. The postglenoid space contains a wide groove for the auditory meatus and a prominent triangular mas-
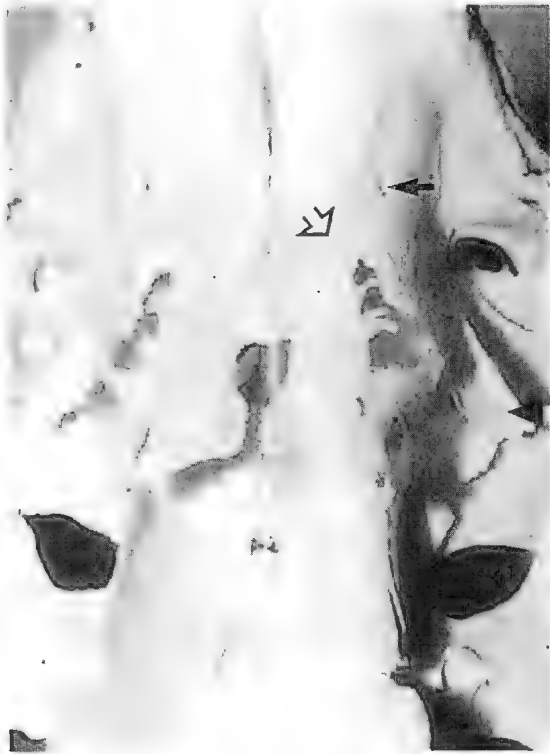
FIG. 10. Ventral view of QMJM4708. Note triangular anterior portion of lateral lobe of palatine, containing palatine foramen (arrow); posterior wing-like extension of lateral lobe of palatine (triangle); complete separation of medial and lateral lobes of palatines by pterygoid (open arrow); separation of pterygoid hamuli by medial lobes of the palatines; medial flanges on pterygoid hamuli.
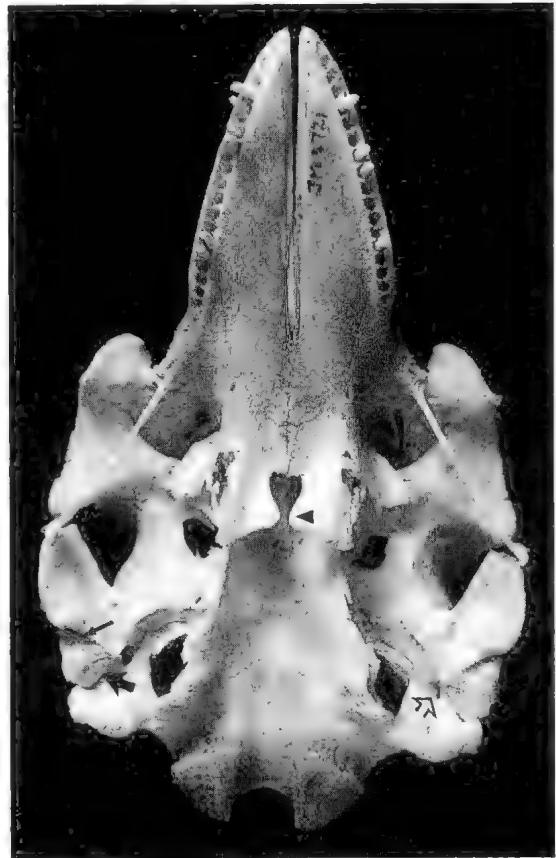

FIG. 11. Ventral view of QMJM4721. Note wing-like posterior extension of lateral lobe of palatine; medial flange of pterygoid hamuli (triangle);transverse frontal ridge anterior to optic channel; large pre-orbital space for dorsal extension of pre-orbital lobe (curved arrow); mastoid pad of zygomatic arch (broad arrow); prominent groove for external auditory meatus (thin arrow); deep pit medial to mastoid pad (open arrow).

toid pad (Figs 11,12), the latter providing articulation for the tympanoperiotic bones. Between the base of the squamosal, just medial to the mastoid, and a ventral extension of the parietal is a deep pit (Figs 11,12). In QM JM4709, this is one end of a channel which opens on the back of the skull in the suture between the squamosal and parietal bones. The cranial hiatus is wide in young animals, but could be completely infilled in older animals.

MANDIBLE (Fig. 13). Mandibles are 76.7% (75.4–78.6%) long, with coronoid depth 23.6% (22.3–25.1%). The mandibular fossa is 32.8% (29.9–35.4%)long, while the mandibular symphysis is 7.7% (5.6–11.4%) long by 8.3% (6.5–9.0%) deep.

Alveolar/tooth counts (mean, rounded to whole number, followed by range in parentheses) are

18 (17–20)/ 18 (16-20) n=14

17 (15–19)/ 17 (16-18) n=13.

Total alveolar/tooth counts are 66–78. Apparently the central teeth erupt first; in MM334 the erupted tooth count is only 15/13 11/14.

COMPARISON WITH TYPE SPECIMEN. Owen's (1866) description of the vertex and the accuracy of his pl.9, fig.2 are confirmed by the holotype (R. Sabin pers comm.; Fig.14). The most significant differences in the vertex, as compared with Australian material, are the 2 elongate antero-posteriorly compressed nasal bones (cf multiple nodular nasal bones) and well-developed mesethmoid plate, abutting on the nasal bones (cf reduced mesethmoid plate).

FIG. 12. Ventral view of QMJM11342. Note vomer insunk between medial lobes of palatine (arrow); incomplete separation of medial and lateral lobes of the palatines; wing-like posterior extension of palatine; medial flange on pterygoid hamuli; prominent alisphenoid; extensive tympano-squamosal recess of zygomatic arch (triangle); mastoid pad and groove for external auditory meatus.

FIG. 14. Dorsal view of BM(NH)1865.4.20.1, holotype of *Orcaella brevirostris.*

FIG. 13. Lateral and medial views of mandible of QMJM4708.

DISCUSSION

NEOTENIC FEATURES OF THE SKULL. Winge (1921) noted that *Orcaella* 'gives the impression of being a dwarf form with noticeably large braincase in proportion to the face'. This appearance is due to massive development of the skull roof. Comparison of newborn and mature *Orcaella* (Fig. 15) with newborn and adult *Peponocephala* (Fig.15) and *Feresa* (Fig.15) show this to be a retained juvenile feature. In all these cases, the interparietals and parietals form major components of the skull roof and much of the frontal bone is exposed in the newborn animal. In adult *Peponocephala* and *Feresa*, the parietals have been excluded from the roof of the skull and the interparietal is reduced or completely obscured by other bones; telescoping of the maxillaries has advanced to cover much of the
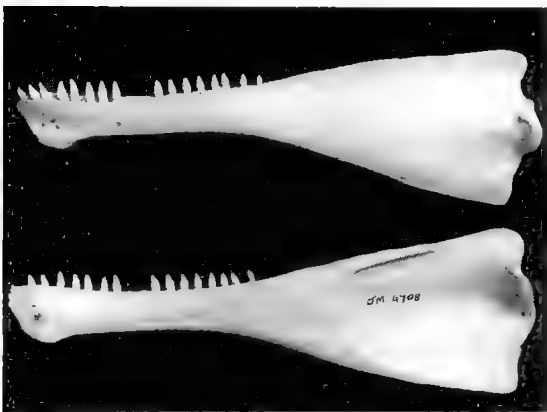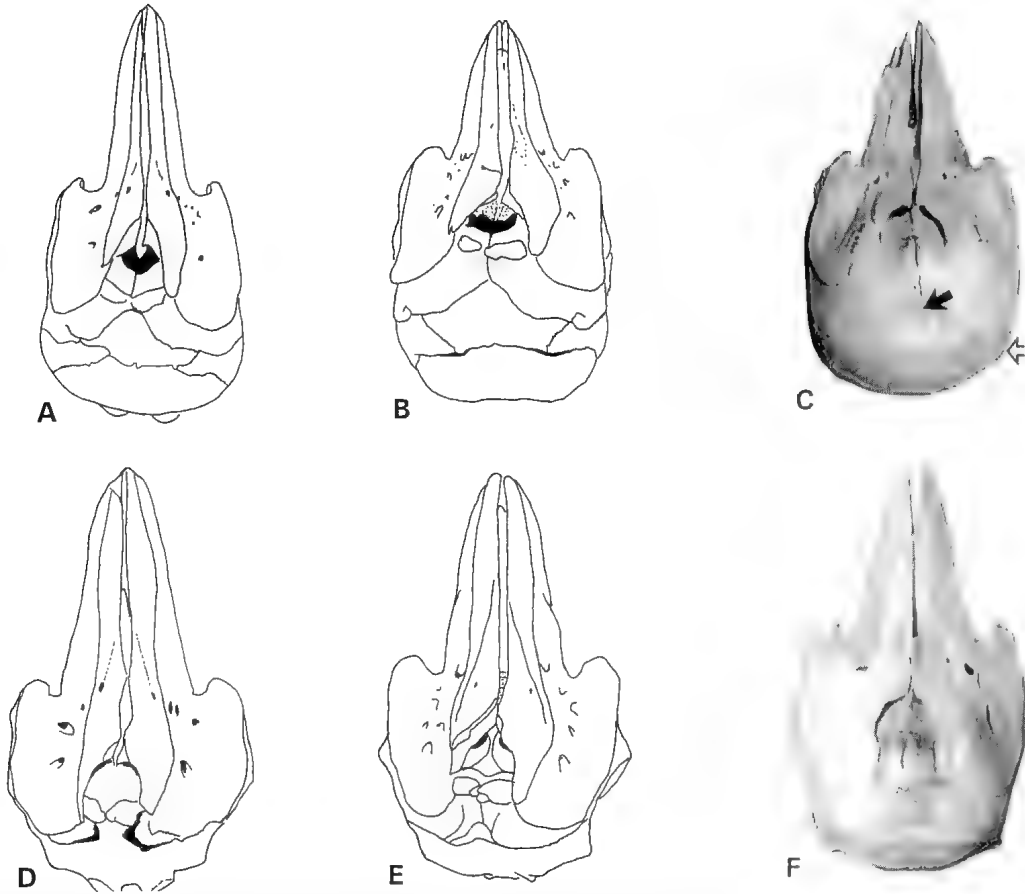
FIG. 15. Neoteny in *Orcaella*. Note similarity in development of interparietal (arrow), dorsal extension of parietal (open arrow), extensive exposure of frontals (weak telescoping of maxillary and premaxillary bones) in the newborn *Peponocephala, Feresa* and *Orcaella* (A,B,C). In adult *Peponocephala* and *Feresa* (D,E) the dorsal exposure of the interparietal is reduced or obliterated; the dorsal extensions of the parietals are similarly overridden; the frontals become covered by the maxillaries and premaxillaries. In contrast, adult *Orcaella* (F) retains juvenile features in the form of extensive dorsal exposure of the interparietal & dorsal extensions of parietals, weak telescoping of skull. *Peponocephala* redrawn from Dawbin et al. (1970), *Feresa* from Perrin & Hubbs (1969). Juvenile *Orcaella* is QMJM11343, a disarticulated skull which was re-assembled; positions of the bones could be determined by their impressions on the braincase.

frontal bone. Similar change with growth is evident in *Pseudorca* (Cowley,1944, pl.1), *Globicephala melas* (Fraser,1950, pl.2), *Monodon* (Eales,1950, fig. 15; van Beneden & Gervais, 1868–1879, pl.45, fig.1) and *Phocoena phocoena* (van Beneden & Gervais,1868-1879, pl.43, fig.5). In adult *Orcaella*, however, dorsal exposure of the interparietal and parietals is maintained, and there is only weak telescoping (Figs 5,14,15; Marsh et al.,1989, fig.3) of the skull, much as in the newborn or juvenile.

This discrepancy between *Orcaella* and other genera can further be demonstrated by comparing proportions of interparietal length and width in

Orcaella and *Pseudorca* of known age. *Orcaella* maintains the proportional length and width of the interparietal in the oldest animals examined (Fig.16). *Pseudorca*, while having a greater dorsal exposure of the interparietal than most odontocetes, shows a significant decrease in interparietal length after two growth laminae and width after 8-14 dentinal laminae (Purves & Pilleri, 1978, fig.16).

Nuchal and temporal crests are poorly defined in *Orcaella*, which is general in juvenile skulls (as in newborn and adult *Pseudorca* (Cowley,1944, pl.1), *Peponocephala* (Dawbin et al.,1970, fig.7) or *Feresa* (Perrin & Hubbs,1969,

fig.4)). Barnes (1985) noted these features as paedomorphic in phocoenids.

Also evident from the growth series of odontocetes is the progressive development of the mesethmoid plate on the front of the braincase. In adult *Orcaella*, the mesethmoid can completely cover the anterior face of the braincase (Fig.14). In Queensland material much of this area is left exposed. The mesethmoid plate is poorly developed in a specimen of *Orcaella* from Melville Bay, Northern Territory (Johnson, 1964, pl.14). Two specimens in the Western Australian Museum also have a poorly developed mesethmoid plate (J.L. Bannister, pers. comm.). This suggests that poor development of the mesethmoid is another retained juvenile feature which may be best expressed in Australian animals. If it were a truly primitive character, one would not expect to see any examples in which the mesethmoid completely covered the front of the braincase.

Telescoping of the skull (Miller,1923) is weak in newborn odontocetes, with the ascending processes of the maxillaries still far forward, leaving a large amount of the frontals exposed. In most genera, telescoping is increasingly expressed in older animals, but in *Orcaella* telescoping resembles that of juvenile odontocetes, with the frontals widely exposed.

The short rostrum of *Orcaella* may be a retained juvenile feature. According to Tomilin (1967), the mean rostrum length as a proportion of condylobasal length for adults and 'young' of *Grampus* were 0.501, 0.457; *Globicephala* 0.507, 0.474; *Pseudorca* 0.481, 0.475; and *Orcinus* 0.500 (adult ♂), 0.471. The mean value for proportion of rostrum length in *Orcaella* (0.444) is thus closer to the values for juveniles of other blunt-headed dolphins (although similar to values for adults of some phocoenids).

Most features listed as neotenic relate to the roof of the braincase. DeBeers (1937 in Pilleri et al., 1982) contrasted the dermal bones of the skull roof and the substitution bones, preformed in cartilage, at the base of the skull. He further noted that it was the dermal bones in which differentiation and growth reflected the growth of the brain, wwhile the bones at the skull base were independent of brain growth. Thus neotenic features should be most obvious in the dorsal aspect of the skull, as documented here for *Orcaella*.

Lloze (1982) documented the os wurmiens ('small supernumerary bones...situated between various bones of the cranium') in *Orcaella*; they also occur on some Queensland specimens. Lloze

suggested that they may be space 'fillers', associated with the growth of the braincase. The braincase is proportionately larger in *Orcaella* than in most odontocetes (Lloze, 1982). An enlarged braincase is generally recognised as a neotenic feature (Gould, 1977) and we suggest it is a retained juvenile feature in *Orcaella*.

Oeschlager (1986) noted a proportional decrease in the mastoid portion of the squamosal with age in *Tursiops* and *Lagenorhynchus*, which suggests that the large postglenoid space in *Orcaella* is a neotenic feature. We think this is unlikely for two reasons. First, a proportional decrease in the mastoid was not obvious in a small series of *Tursiops* skulls available to us. Moreover, the posteroventral orientation of the paroccipital process of the exoccipital in *Orcaella* and the large basicranial space, as well as the extent of the postglenoid space, exceeds that in newborn odontocetes of other delphinoid genera which we have examined, with the exception of *Neophocaena*.

Deflexion of the occipital condyles (Fig.9), otherwise known only in *Neophocaena*, may reflect the enlargement of the braincase, but it probably is not a retained juvenile feature as there is no indication from growth series of *Orcaella* or other genera that the condyles move from a ventral to posterior position.

IMPLICATIONS OF NEOTENY. *Orcaella*'s skull is characterised by large braincase and short rostrum as in Gray's (1866) diagnosis. If these are retained juvenile features as we suggest, then it may not be valid to make comparisons of *Orcaella* with adults of other genera for taxonomic purposes. It is not surprising that published attempts have been equivocal since juvenile skulls of odontocete genera are more similar than are skulls of adults.

de Muizon (1988) placed *Orcaella* in the Globicephaliinae, on dilation of the premaxillae at the tip of the rostrum. However, the premaxillary width of *Orcaella* at 0.75 rostrum length is comparable to that in delphinids (pers. obs.) and is closer to that of juvenile *Globicephala*.

de Muizon (1988) and Barnes (1990) considered a well-developed mesethmoid plate to be diagnostic features of delphinids. Although the *Orcaella* mesethmoid plate can completely fill the posterior border of the nares (Fig.14), it is usually poorly developed in Australian specimens, leaving much of the anterior slope of the vertex exposed. de Muizon (1988) and Barnes (1990) suggested that the greater development of
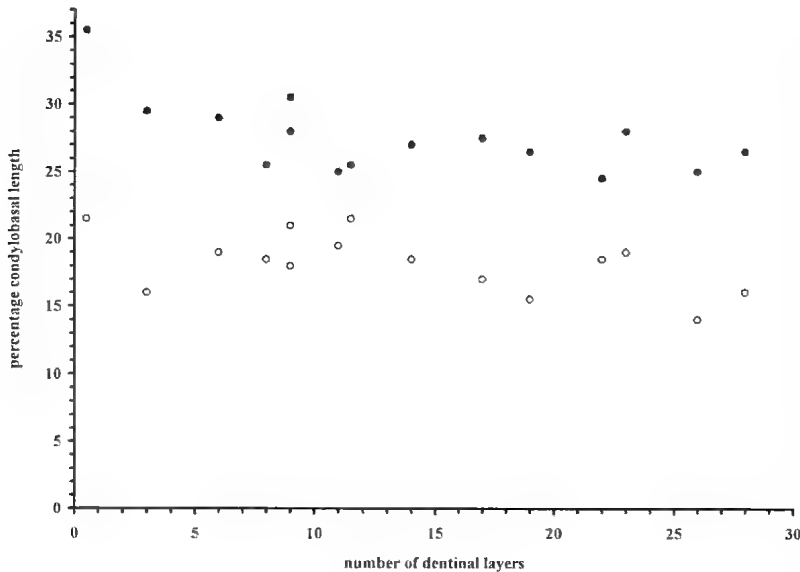
FIG. 16. Variation in width (closed circles) and length (open circles) of interparietal in *Orcaella* as percentage of condylobasal length, compared with age as expressed by dentinal layers in teeth. The newborn animal QMJM11343 was not aged, and is arbitrarily placed at 0.5 years. Note the minimal reduction in both width and length of the interparietal.

the mesethmoid plate pushed the nasals to an apical position on the vertex and resulted in transverse compression of the nasal bones. Despite the weaker development of the mesethmoid plate in our material, the posterior pair of nasal bones of *Orcaella* are apical, so position of the nasals may not be linked to development of the mesethmoid. The nasals are, however, reduced in size, nodular, and not compressed. They differ from the type of *O. brevirostris* (Fig. 14) and from *O. fluminalis* (Anderson, 1879, pl. 42, fig.2). van Beneden & Gervais (1868–1879, pl. 64, fig.2a) illustrated 2 reduced nodular nasals in *Orcaella* from the Mekong River; Lloze (unpubl. MS) also noted that 'the rudimentary nasal bones are formed by two little bones which fuse with advancing age'. Thus reduction of the nasals may be a generic feature, although it seems particularly well shown by Queensland specimens. Reduction of the nasals seems to occur in some *Cephalorhynchus hectori* (van Beneden,1881) (pers. obs.) and Perrin (pers. comm.) noted a *Stenella frontalis* (Cuvier,1829) with two nasals on the right. Perhaps the nodules represent multiple sites of ossification (G.J.B. Ross pers. comm.) which may remain discrete. If so, this could be another neotenic feature.

The postnarial fossa, infilled by a supernumary bone, and shallow lateral fossae on the anterior slope of the vertex have not been described in *Orcaella*, although the former was illustrated by Johnson (1964, pl. 14). This may be because of the greater development of the mesethmoid in animals examined to date from southeast Asia. Postnarial fossae have been described in Kentriodontidae, but these appear to be different from the present case, based on de Muizon (1988, fig.21). The lateral fossae are similar to fossae of phocoenids, *Delphinapterus* and *Monodon* (de Muizon, 1988, fig.25). These fossae in *Orcaella* do not, however, provide evidence for its close relationship to phocoenids or monodontids. Rather, they probably reflect the weak mesethmoid plate in our material, leaving much of the vertex exposed. In a juvenile *Tursiops* (QMJM4713), with the mesethmoid still weakly developed, there are similar shallow imprints or fossae between the mesethmoid plate and nasals.

BASICRANIAL CHARACTERS. Since the basal skull bones are less subject to modification by brain growth, perhaps they offer better characters for assessing relationships of *Orcaella*. Unfortunately, positions of the sphenoidal bones are rarely evident from photographs and we have been able to examine only a limited series of specimens, usually without juveniles.

In ventral view (Figs 10–12), enclosure of the palatine foramen within the triangular lateral lobes of the palatine is characteristic. This appears to be the minor palatine foramen of Evans & Christensen (1979). In sagittal section (Fig.33) the palatine contains a highly vascularised excavation. In *Tursiops* (Rommel, 1990) and in specimens of *Sousa*, *Globicephala*, *Pseudorca*, *Stenella*, *Delphinus*, *Peponocephala*, *Grampus*, and *Feresa* the minor palatine foramen is not visible and there is only the major palatine

TABLE 1. Summary statistics of measurements, based on 21 tympanoperiotic bones from 11 animals. Numbering of characters corresponds to sequence in Appendix 1, which contains full data and details of measurements.

CHARACTER	MEAN	RANGE
(1)Standard length tympanic bone	34.82	33.05-36.50
(2)Tip to posterior end of inner posterior prominence	95.42	93.15–99.71
(3)Distance from posteroventral tip of outer posterior prominence to tip of sigmoid process	62.01	58.07–66.26
(4)Distance from posteroventral tip of outer posterior prominence to conical process	43.95	39.77–47.41
(5)Width bulla at level of sigmoid process	57.80	53.94-60.98
(7)Width across inner and outer posterior prominences	58.81	53.94-62.61
(8)Depth interprominential notch	30.26	22.52-36.19
(10)Width posterior branch of lower tympanic aperture	6.54	5.28-8.89
(13)Standard length periotic bone	35.69	31.00-38.20
(14) Thickness superior process at level of upper tympanic aperture (excluding spongy bone shelf over aequeductus vestibuli)	35.55	31.97-41.38
(15)Width across cochlear portion and superior process at level of tympanic aperture	55.13	49.30-64.09
(19)Length of cochlear portion of periotic	42.65	38.95-46.62
(22)Standard length as percentage of standard length of tympanic bone	102.62	92.00-112.02
(23)separation of foramen singulare and aequeductus Fallopii (n=12)	14.10	9.08-19.01
(25)Anteroposterior length of fundus of the internal auditory meatus	28.75	22.04-38.33
(26)Width of foramen ovale (n=9)	5.55	3.74-7.00
(27) Width of foramen rotundum	8.85	7.54-10.29
(28) Width of head malleus (n=9)	10.86	8.53-12.02

FIG. 17. Diagram of periotic of *Orcaella* in dorsal view showing features of the periotic triangle. Abbreviations: cF=canal for facial nerve (=aquaeductus Fallopi); Av=aquaeductus vestibuli (=ductus endolymphaticus); Ac=aquaeductus cochleae; alpha, beta and gamma indicate angles as defined by Pilleri et al., 1989.

foramen on the suture of the palatine lobe with the maxillaries. However, both foramina may be present in delphinids (Perrin pers. comm.) and their development may be a variable feature.

The lateral and medial lobes of the palatines are widely separated and the maxillary can directly contact the pterygoid hamuli, totally separating the medial and lateral lobes of the palatines (Fig.10). de Muizon (in press) notes that separation of medial and lateral lobes of the palatines is unusual among odontocetes. The separation of the pterygoids in *Orcaella* is by the medial lobes of the palatines, which surround and may override the vomer so that it is no longer visible from
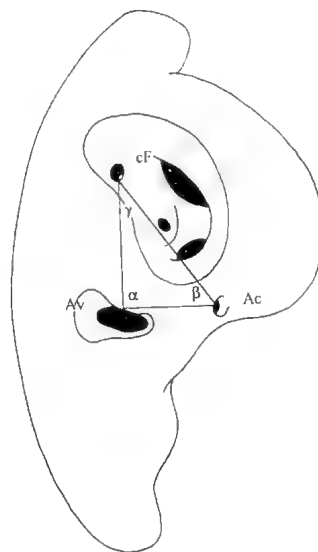
below (but see Fig. 12). This resembles the construction in delphinids such as *Sousa*, *Tursiops* and *Stenella*, and is distinct from other odontocetes with widely separated pterygoids (Pilleri et al., 1982). In phocoenids and *Delphinapterus*, the pterygoid hamuli are relatively small and do not deeply excavate the palatine, so the connection between median and lateral lobes is broad. In the long-snouted dolphins, although the pterygoids deeply excavate the palatines the latter are displaced forward onto the rostrum so that medial and lateral lobes of the palatine remain connected. Partial to complete separation of the lobes can occur in *Grampus* (Tomilin, 1967) and *Feresa* (QMJM825). Perrin (pers. comm.) noted complete separation of the medial and lateral lobes in a juvenile *Globicephala macrorhynchus*; the lobes are also separate in a Southern Hemisphere *G. melas* (QMJ15.2104). This separation may result from deep excavation of the pterygoids abutting onto a shortened rostrum of the skull, but it is not a simple relationship. *Monodon* (Tomilin, 1967; pers. obs.) and the delphinid *Pseudorca* (adult and newborn: Cowley, 1944) have well developed pterygoid hamuli and a short rostrum but the median and lateral lobes of the palatines remain broadly connected.

TABLE 2. Angles of the periotic triangle, measured from camera lucida drawings. Abbreviations: PA, AW: different observers; L=left; R=right; #1, #2: measurements by same observer.

SPECIMEN NUMBER		α	β	γ	γ/β
QMJM4706	L(PA)	91	55.5	33.5	60.4
QMJM4706	(AW)	88	62	30	48.5
QMJM4706	R(AW)	82	63	35	55.6
QMJM4700	L(AW)	80	70	30	42.9
QMJM4700	R(AW)	78	67	35	52.2
QMJM4712	L(PA)#1	89	59	31	52.5
QMJM4712	(PA)#2	84	55.5	40.5	73.0
QMJM4705	L(AW)	86	60	34	56.7
QMJM4705	R(AW)	90	59	31	52.5
QMJM11343	L(AW)	77	66	37	56.1
QMJM11343	R(AW)	77	66	31	56.1
QMJM4704	R(PA)	90	47	43	91.5
QMJM4708	R(AW)	72	54	54	100.0
QMJM4709	L(AW)	78	63	39	61.9
QMJM4709	R(AW)	102	48	30	62.5
QMJM4740	L(PA)	93.5	47	39.5	84.0
QMJM4721	L(PA)	93.5	48.5	38	78.4

TABLE 3. Lengths of sides of the periotic triangle, measured from camera lucida drawings.

SPECIMEN NUMBER		Av-cF	Av-Ac	%Av-Ac/Av-cF
QMJM4709	(AW)	59	40	67.8
QMJM4709		50	36	72.0
QMJM4708	(AW)	39	39	100.0
QMJM4704	(PA)	48	44	91.7
QMJM11343	(AW)	60	40	66.7
QMJM11343		54	37	68.5
QMJM4705	(AW)	61	39	63.9
QMJM4705		55	35	63.6
QMJM4706	(PA)	50	35	70.0
QMJM4706	(AW)	55	32	58.2
QMJM4712	(PA)	48	38	79.2
QMJM4700	(AW)	58	38	65.5
QMJM4700		57	31	54.4
QMJM4740	(PA)	52	45	86.5
QMJM4721	(PA)	49	40	81.6

The posterior wing of the lateral palatine of *Orcaella* is unusual in its separation from the rest of the braincase. A posterior extension of the palatine is found in *Globicephala*, *Feresa*, and *Pseudorca* (Purves & Pilleri, 1978, fig. 18) where it forms a bridge under the optic canal. However, in those genera, the palatine wing is oriented vertically (in adults examined), whereas in *Orcaella* it is parallel with the bones of the basicranium, as a free wing-like structure, which appears to be flattened against the bones of the skull. The basicranium also appears to be flattened. The relatively long paroccipital crest, almost at right angles to the main axis of the skull, creates a very large basicranial space, which may cause a more lateral (flattened) orientation of the bones of the skull base. For instance, the falciform process of *Orcaella* is flattened against the braincase. This differs from the delphinids examined (*Tursiops*, *Sousa*, *Globicephala*, *Pseudorca*, *Stenella*, *Delphinus*, *Peponocephala*, *Grampus*, and *Feresa*) which all have a strong ventral deflexion of the falciform process, curving around the anterior of the periotic bone.

An extensive cavity between the maxillaries and frontal/presphenoid can accommodate a dorsal extension of the preorbital lobe. This feature resembles the extension in phocoenids (Fraser & Purves, 1962). However, there is a similar expansion of the lobe in delphinids such as *Pseudorca*

(pers. obs.) and juvenile *Globicephala macrorhynchus* (Perrin pers. comm.).

The pterygoid hamuli have medial flanges (Figs 10–12) which can almost contact distally although there usually is a distinct gap. The flanges are also visible in a specimen from the Northern Territory (Johnson, 1964, pl.15). This contrasts with the very widely separated pterygoid hamuli, without flanges, in SE Asian specimens (Owen, 1866; Anderson, 1879; Pilleri & Gihr, 1973-1974).

The mastoid portion of the squamosal is well-developed both ventrally and laterally. Ventrally, there is a mastoid pad for attachment of the tympanoperiotic bones (Fig. 11; Owen, 1866, pl. 9, fig. 3; Anderson, 1879, pl. 42, fig. 3) and a conspicuous groove for the external auditory meatus. Laterally, the large lateral rugose mastoid portion of the zygomatic arch may reflect a broad attachment base for the sternomastoid muscles, possibly associated with flexibility of the head. The zygomatic arch of the squamosal is thus well-developed, and intermediate between *Monodon* and *Delphinapterus* on the one hand and phocoenids & delphinids on the other. Thus, contrary to Heyning (1989), *Orcaella* does not show extreme reduction of the zygomatic arch. This reduction of the arch was the only synapomorphy listed by Heyning (1989) for the clade Phocoenidae-Delphinidae. The taxonomic significance of the well-developed arch in *Orcaella* is considered as part of a cladistic analysis of the delphinoid taxa, but note that a relatively well-

FIG. 18. Lateral view of left tympanoperiotic bones, QMJM4709. Note anterior spine of bulla; posterolateral orientation of posterior processes of bulla and periotic (directed towards viewer); triangular depression in front of sigmoid process (open arrow); posterior branch of lower tympanic aperture (triangle); concave ventral margin of bulla, and tubercle on anterior process of periotic (arrow).

developed arch also occurs in *Neophocaena*, within the Phocoenidae (pers. obs.) and in the delphinid *Orcinus* (Heyning, 1989).

The deep, elongate pit between the squamosal and parietal (Fig.11) has been noted by de Muizon (in press) in 'some delphinids'; it occurs in *Sousa chinensis* and in several delphinids (Perrin pers. comm.). It appears to be the channel for a blood vessel which exits on the back of the braincase, between the squamosal and parietal.

CONCLUSIONS. Neotenic features of the skull roof in *Orcaella* include the retained dorsal exposure of the interparietal and dorsal extensions of the parietals, poorly developed telescoping of the skull with large exposure of the frontal bones, and weak development of the mesethmoid plate on the anterior of the cranium (the last character possibly restricted to Australian animals). The relatively large braincase and short rostrum, which substantially affect the appearance of the skull, may also be neotenic features. Retention of juvenile features in *Orcaella* may compromise attempts to establish relationships based on the comparisons of its skull with adults of other genera; it would be more apppropriate to compare it with juveniles of other odontocetes. However, juvenile skulls of various genera are very similar with diagnostic features often only well expressed in adults.

The basicranium may be less subject to neoteny. The skull base of *Orcaella* resembles that of *Pseudorca*, *Globicephala*, *Feresa* and *Grampus* (we have not been able to examine in detail skulls of *Orcinus*). In particular, there is a similar excavation of the palatines by the pterygoid hamuli, which can lead to separation of the medial and lateral lobes of the palatine (shared with *Feresa*, *Globicephala* and *Grampus*); posterior extension of the lateral lobe of the palatine (shared with *Globicephala*,*Feresa*, *Pseudorca*) and a transverse widening of the skull
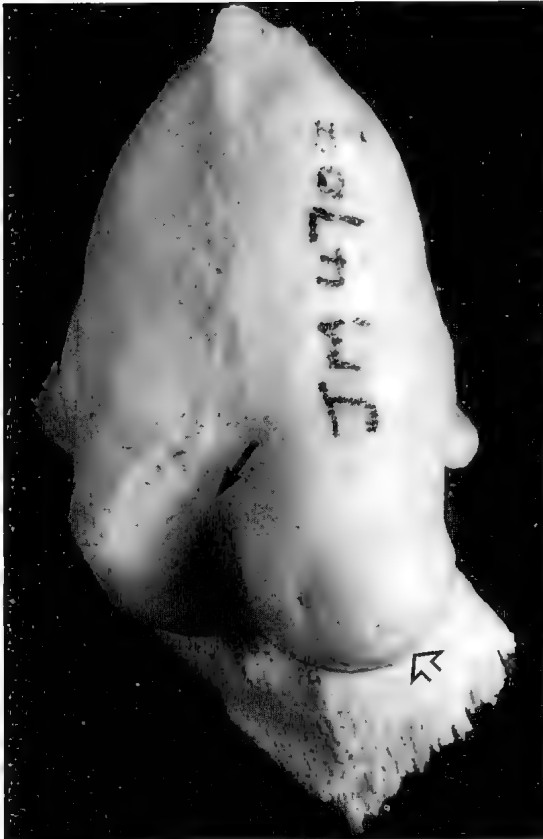
FIG. 19. Ventral view of left bulla, QMJM4709. Note swollen outer posterior prominence (open arrow); deep interprominential notch (arrow); spongy bone along midline of bulla; posterolateral orientation of and spongy bone distally on posterior process.
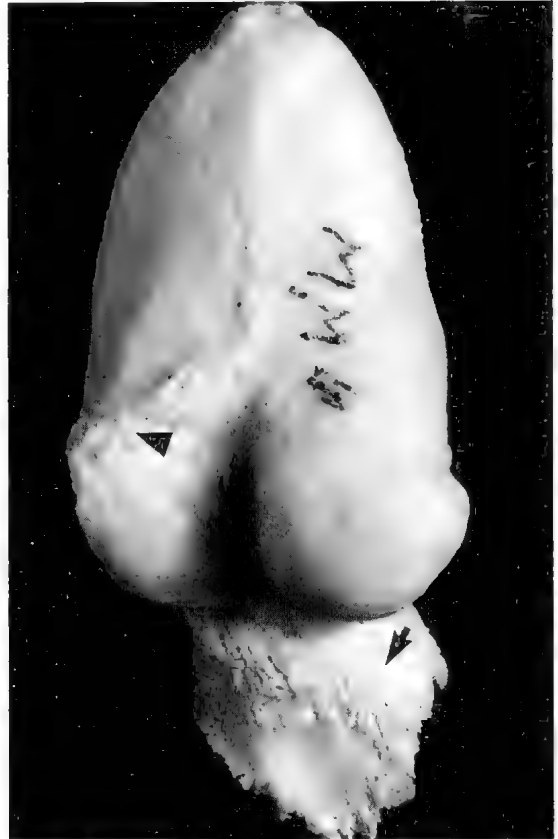

FIG. 20. Ventral view of left bulla, QMJM4700. Note angulate inner posterior prominence (triangle); deep interprominential notch; posterolateral orientation of posterior process (arrow).

(as in *Pseudorca*, *Globicephala*). However excavation of the palatines and orientation of the posterior wings of the lateral palatines may be more similar to juveniles of genera such as *Globicephala* than to adults (i.e. may be neotenous). The cranial sinuses also align *Orcaella* with the bulbous-snouted dolphins (Fraser & Purves, 1962). However, in all these genera the cranial sinuses show few specializations; they may be linked by shared primitive features. A prominent feature is the well-developed zygomatic arch of the squamosal and ventral attachment of the tympanoperiotic bones which sets *Orcaella* apart from delphinids although the arch is similarly developed in *Neophocaena*.

Taxonomic utility of basicranial features needs to be examined further. It has generally proved impossible to demonstrate whether a feature is neotenic or in a generalised, unspecialised state.

One option is to compare a wider range of juvenile delphinid genera than was available to us in this study. Another option is to assess polarity of basicranial features, based on outgroup analyses involving criteria other than cranial morphology. We present such analyses later in this paper.

TYMPANOPERIOTIC BONES
(Table 1; Fig.17; Appendix 1)

TYMPANIC BULLA. Standard length 34.8mm (33.0-36.5). The anterior tip can be drawn out into a spine-like process (Figs 18, 30). The outer posterior prominence is swollen and hemispherical, with no lateral compression (Fig. 19). The inner posterior prominence is sharply angulate (Figs 20, 21); a weak ventral keel extends more than half way to the tip (Fig 20). The interprominential notch is deep (Figs 19,20). There is
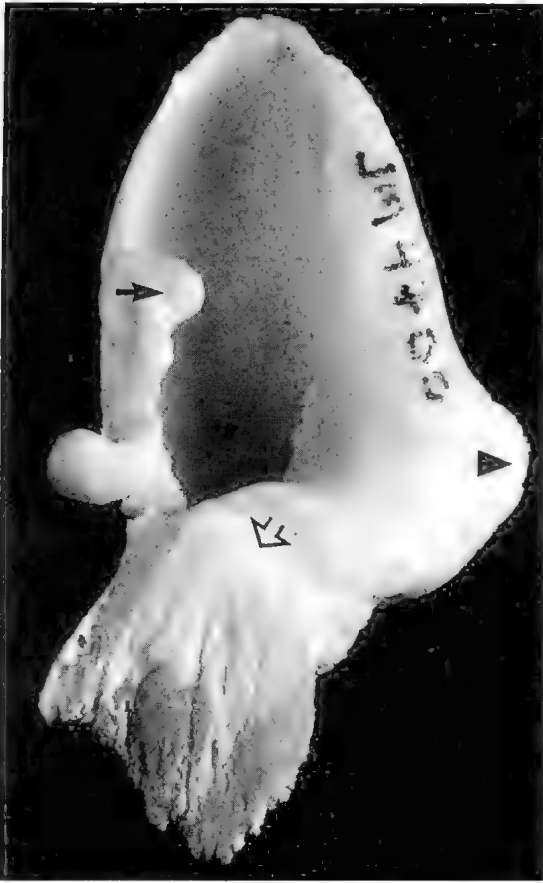
FIG. 21. Dorsal view of left bulla, QMJM4700. Note angulate inner posterior prominence (triangle); prominent accessory ossicle (arrow); ridges and grooves of articular facet (open arrow) which is directed posteriorly (associated with posterior orientation of periotic process).

no median furrow. A spongy, weakly developed ridge extends along the anteromedial border of the interprominential notch, continuing forward to the tip along the midline (Fig. 19). There is no compression: the width of bulla at the level of the sigmoid process is 57.8 (53.9–61.0)% of standard length. The posterior process is well developed, variable in direction from almost posterior to distinctly posterolateral. The mean angle of the lateral margin is 34.9° (17°–47.5° to long axis of bulla) (Figs 18-20). Although the articular facet with the periotic can be more posteriorly oriented (Fig. 21), the posterior process is usually obliquely oriented laterally (Figs 19,26). Distally the posterior process consists of spongy bone (Fig. 19). The facet with the posterior process of the periotic is ridged and grooved (Fig. 21).

In lateral view, the ventral margin is slightly concave (Fig. 18). A deep triangular area anterior to the sigmoid process is bounded on its ventral side by a low, wide ridge which gives rise on its anterior margin to a shallow vertical groove (Fig. 18). The accessory ossicle is prominent (Fig. 21). In medial view, the border of the involucrum is low, not rising anteriorly to form a distinctly curved margin (Fig. 22). The elliptical foramen is closed, but minute perforations are often present in the area usually occupied by the foramen (Fig. 23).

PERIOTIC BONE

DORSAL ASPECT. Standard length 35.7mm (31.0–38.2). Anterior, superior and posterior processes are in a straight line (Fig. 24). The superior process can be directed medially as a shelf of spongy bone, partially hiding the tractus spiralis foraminosus and completely obscuring the internal aperture of the aquaeductus Fallopi (canal for facial nerve) (Fig. 24). A similar medially directed shelf of spongy bone can cover the aperture of the aquaeductus cochleae and aquaeductus vestibuli (ductus endolymphaticus) (Fig. 25). The aquaeductus vestibuli is set at the base of a large funnel-shaped depression bounded by spongy bone (Figs 24,25). The tractus spiralis foraminosus is prominent (Fig. 25). The aquaeductus Fallopi is directed anteriorly at the level of the anteriomost margin of the tractus spiralis foraminosus (Fig. 25). The foramen singulare is at the posterior margin of the tractus spiralis foraminosus and separated from the aquaeductus Fallopi by a long, obliquely oriented crista transversa which has a secondary ridge continuing along the anterior margin of the fundus of the internal auditory meatus.

The posterior process forms an acute backwardly pointing triangle in dorsal view (Figs 24,26; Tables 2,3). At its maximum extent it covers only about 0.75 of the posterior process of the tympanic bulla, and tapers to a tip on the posteromedial side of the process of the bulla (Fig. 26).

LATERAL ASPECT. In external view, the anterior process is square and truncate, directed ventrally where it fuses with the bulla between the accessory ossicle and the sigmoid process (Figs 18,27). A distinct tubercle occurs on the upper half of its anterior face, near the level of the anterior margin of the cochlear portion of the periotic (Figs 18,25).

FIG. 22. Medial view of left bulla, QMJM4700. Note low medial margin of involucrum, not raised anteriorly to form sinusoidal border.

The posterior process bends sharply ventrad, to fuse with the posterior process of the tympanic bulla (Fig. 27). The distal half of the external surface of the posterior process, where it articulates with the squamosal, is spongy bone (Figs 24,26).

In medial view the periotic is oriented obliquely ventrad and is closely apposed to the involucrum of the bulla, although never touching (Fig. 25). The apertures of the aquaeductus vestibuli and aquaeductus cochleae are directed medially, that of the aquaeductus Fallopi anteromedially. The groove for the stapedius muscle is prominent (Fig. 28).

VENTRAL ASPECT. The greatest diameter of the cochlear portion is at right angles to the main axis of the periotic (Fig. 28). On the postero-medial quadrat of the cochlea is an oblique groove which runs obliquely anterior (Fig. 28). It occurs where the periotic is closely apposed to the bulla and may be a channel for a blood vessel (possibly associated with corpus cavernosum; note vascularisation of the region in Fig. 33). The anterior-posterior length of the articular facet (including the basal smooth portion (Fig. 28) and cluding the basal smooth portion (Fig. 28) and

distal spongy portion) is 47.7–54.1% of the periotic length(n=5).

ARTICULATION OF PERIOTIC AND TYM-PANIC BONES. In posterior view, the articulation of the posterior process of the periotic with that of the tympanic is irregular (Fig. 23). The facet for attachment with the mastoid portion of the squamosal is entirely spongy bone (Figs 29,30). Anteriorly, the articulation is between a triangular wedge of the periotic and the squamosal. Posteriorly, the connection is between the the squamosal and the posterior half of the posterior process of the tympanic bone (Figs 23,26).

DISCUSSION

COMPARISONS OF VALUES WITH KASUYA (1973). The morphometrics of this series (Table 1, Appendix 1) generally confirm values presented by Kasuya, based on specimens from unspecified localities held at the United States National Museum and Zoological Survey of India. The bulla is wider across the posterior processes in Queensland specimens. There is a
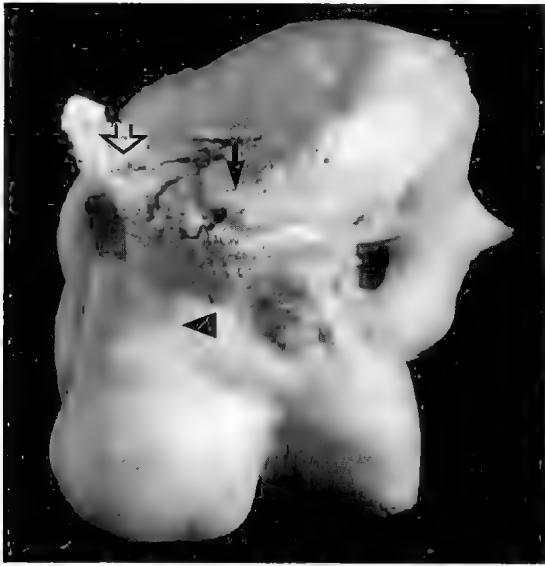
FIG. 23. Posterior view of left tympanoperiotic bones, QMJM4709. Note irregular margin of posterior processes of bulla and periotic; closed elliptical foramen, with a few pores visible (triangle). The open arrow and closed arrow indicate spongy bone of bulla and periotic respectively, which articulates with the mastoid portion of the zygomatic arch.

major discrepancy in the depth of the inter-prominential notch (mean=30.3 in present series vs 11.7 reported by Kasuya). This must involve a difference in measuring technique but the inter-prominential notch is deep in our specimens (Figs 19, 20). Our value for height of the bulla, from sigmoid process to ventral keel, is higher than reported by Kasuya (1973). His measurement was taken obliquely and incorporated not only height but also width of the bulla. Since the latter is wider in our material than reported by Kasuya, our values for 'height' should also be greater.

TAXONOMIC CHARACTERS OF THE TYM-PANOPERIOTIC BONES. Characters used by Kasuya to differentiate the families of delphinoid odontocetes (Table 4) are considered for *Orcaella*: (1) direction of posterior process of bulla. This is not usually posterior as in *Delphinapterus* and the phocoenids, but variable from almost posterior to posterolateral (Figs 19,20), with a mean angle along the lateral margin of approximately 35°. Although the apex of the process is directed posteriorly, the lateral margin is always deflected and the articular facet is usually distinctly posterolateral (Fig. 19). The mean angle of deflection of the posterior process is
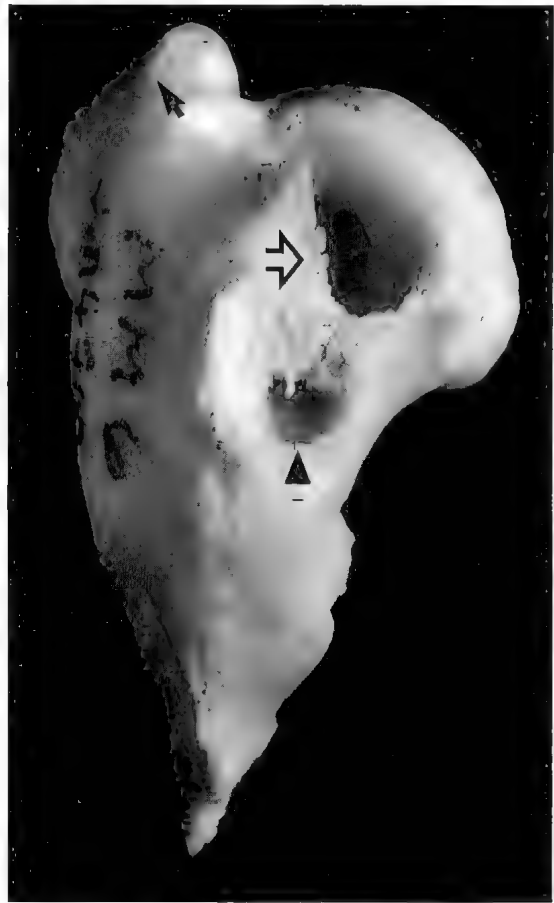

FIG. 24. Dorsal view of left periotic, QMJM4700. Note that anterior (arrow), superior and posterior processes are in line and that the latter is posteriorly directed. Note spongy bone shelf overarching the tractus spiralis foraminosus (open arrow), and wide funnel-like depression, surrounded by spongy bone, which contains the aquaeductus vestibuli (triangle).

comparable to the deflection in delphinids such as *Sousa chinensis* (e.g. 33°, 36.5° in MM1020). The greater variability in the orientation of the posterior process in our series of *Orcaella* brings into question its usefulness as a character to separate families. As such, it weakens the case for linking *Orcaella* and *Delphinapterus* in the Delphinapteridae.

(2) direction of posterior process of periotic. This is directed posteriorly, but the posterior orientation is found not only in *Delphinapterus* but also in phocoenids.

(3) width of posterior branch of lower aperture of tympanic membrane (LTA). Even with our larger series of specimens, there is no overlap in

TABLE 4. Tympanoperiotic characters used by Kasuya (1973) to classify odontocetes. Families are as given by Kasuya (1973). Unless otherwise stated, data for *Orcaella* are from this study; values for other species are from Kasuya (1973).

	Monodontidae *Monodon*	Delphinidae	Delphinapteridae *Delphinapterus*	Phocoenidae	*Orcaella*
direction of posterior process tympanic bulla	lateral	posterolateral to lateral	posterior	posterior	variable, mean = 35° (17°-48°)(this paper)
direction of posterior process of periotic	lateral	posterolateral to lateral	posterior	posterior	posterior
width of posterior branch of lower tympanic aperture	mean = 7.5	means from 2.5 (*Stenella attenuata*) to 7.2 (*Tursiops* cf *gilli*)	mean = 10.8 (10.1 - 11.8)	*Neophocaena* 10.3; *Phocoena* 7.5, 10.6, 10.3; *Phocoenoides* 8.9,10.5	mean = 6.5 (5.4 - 8.9) (this paper)
facet of posterior processes of bulla and periotic	ridged (this paper)	ridged (Yamada in Kasuya 1973)	ridged	smooth	ridged (this paper)
compression of bulla	strongly compressed 39.6 (37.5-41.4)	strongly compressed in *Globicephala* & *Grampus*	not compressed mean = 58.9 (58.0-59.0)	not compressed	not compressed mean = 57.8 (53.9-61.0)
ventral keel	well developed	well developed in Globicephalinae (*sensu* Kasuya)	low	low (in *Phocoena*) to well developed (in *Neophocaena*, *Phocoenoides*)	low
interprominential notch depth	mean = 13.9	mean =10.0 (*Globicephala*) to 16.6 (*Lissodelphis*)	mean=15.1	*Neophocaena* mean=14.1; *Phocoena* mean=14.6, 16.2 *Phocoenoides* mean=17.0, 17.6	mean=11.7 (Kasuya)
anterior spine of tympanic bulla	present	variable, present in *Globicephalinae*	absent	absent	may be present (this paper)
medial margin of involucrum	strongly sinusoidal, high anteriorly	sinusoidal, esp in Globicephalinae	sinusoidal	low, most anterior height in *Neophocaena*	low throughout
elliptical foramen	closed	open in Delphininae,closed in *Globicephala Grampus,Orcinus, Sousa,Sotalia Cephalorhynchus*	closed	closed	closed

ranges of values between *Orcaella* (LTA: 5.3–8.9%) and *Delphinapterus* (LTA: 10.1-11.8%: Kasuya, 1973). This character thus offers no support for linking *Orcaella* and *Delphinapterus* in the Delphinapteridae. Rather, the values for *Orcaella* overlap with both *Monodon* (mean = 7.5%: Kasuya, 1973: Appendix 2) and at least some of the delphinids, such as *Tursiops* (2.2–9.2%: Kasuya, 1973) and *Sousa* (7.3% : Kasuya, 1973). The LTA is wide in *Delphinapterus* and phocoenids where the posterior process of the tympanic is oriented posteriorly. If there is a lateral shift of the process, this must impinge on the LTA which is just anterior to the process. Thus one could expect a narrow LTA in taxa where the posterior process has shifted laterally;

this is as observed. Characters (1) and (3) may thus be linked.

(4) articular facets of posterior processes. These are ridged in *Orcaella* but this is also true in delphinids and *Monodon*, as well as *Delphinapterus*.

(5) compression of bulla. When the width/length ratio was 0.5 or less , Kasuya (1973, fig.75) considered the bulla to show strong lateral compression. Within the Delphinidae of Kasuya, there are genera (e.g. *Globicephala*, *Grampus*) which showed strong compression, while others showed no compression of the bulla. Thus the strong compression of the bulla in *Monodon* but not in *Delphinapterus* can not be used to separate them at family level.

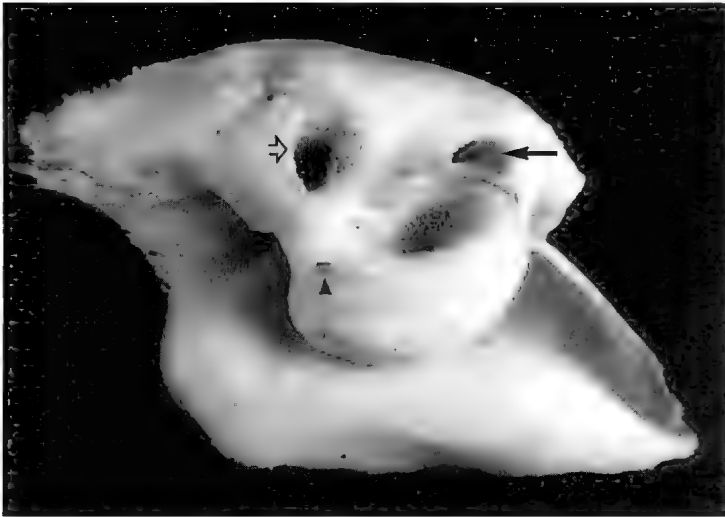(6) development of ventral keel. Kasuya

FIG. 25. Medial view of left tympanoperiotic bones, QMJM4709. Note spongy bone over cF (arrow) and Av (open arrow); position of Ac (triangles); large tractus spiralis foraminosus; tubercle on anterior process of the periotic; close association of cochlear portion of the periotic with medial porion of the bulla.

(1973:54) noted that the development of the ventral keel and the median furrow could be linked with the extent of compression of the bulla. This may also apply to the width of the inter-prominential notch. To the extent that these characters are linked to compression of the bulla, they can not be considered valid family characters.

(7) medial margin of involucrum. The margin is low throughout in *Orcaella*, which contrasts with the sinusoidal form of *Monodon, Delphinapterus* and most delphinids.

The other characters in Table 4 either vary widely within a single family (e.g. closure of elliptical foramen) or are found among several families (anterior spine of bulla) and thus are of limited use in defining families.

PERIOTIC TRIANGLE. Pilleri et al. (1989) defined the periotic triangle, which is formed by connecting the apertures of the canal for the facial nerve (aquaeductus Fallopi), aquaeductus vestibuli and aquaeductus cochleae. They recognized 6 types, including a monodontid triangle in *Monodon, Delphinapterus* and *Orcaella*. The monodontid triangle was defined by (1) apertures of aquaeductus cochleae and aquaeductus vestibuli 'roughly at' the same level, hence angle alpha almost a right angle triangle; (2) distance between the two apertures (AvAc) roughly equal to that between the aquaeductus vestibuli and canal for facial nerve (AvcF); and (3) angles beta and gamma approximately equal (i.e. 45°).

Considering each character of the monodontid triangle:

(1) alpha almost a right angle This was only approximately so for *Delphinapterus* (108°: Pilleri et al., 1989), but more so for *Monodon* (99°,90°,90° Pilleri et al., 1989) and for *Orcaella* (mean=85.4° (72°-102°); Pilleri et al., 1989:

FIG. 26. Dorsal view of left tympanoperiotic bones, QMJM4709. Note posterior orientation of posterior process of periotic; posterolateral orientation of posterior process of tympanic and expanse of spongy bone (arrow) which articulates with the zygomatic arch .
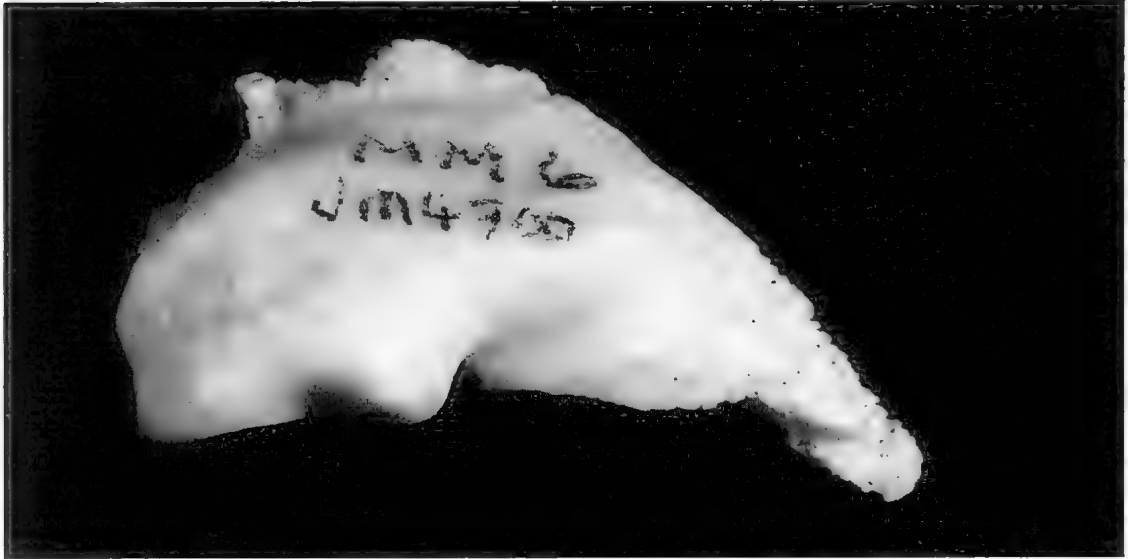
FIG. 27. Lateral view of left periotic, QMJM4700. Note squared off form of anterior process (to the left); ventral deflexion of posterior process to form triangular wedge resting on top of posterior process of tympanic.

86°,84°). However the 'delphinid triangle' is approximately a right angle; the mean value of alpha from Pilleri et al. (1989) for *Monodon* and *Delphinapterus* was 96.8° vs 97.1° for delphinids.

(2) AvAc approximately equal to AvcF, thus AvAc/AvcF approximately equal to 1.0. We had to calculate these figures for *Delphinapterus* and *Monodon* from Pilleri et al. (1989, fig.34). The line from AvAc was equal to that from AvcF in *Delphinapterus* and was about 0.8 of the length of AvcF in *Monodon*. Based on 15 measurements in our series, the line AvAc was about 0.70 (mean=0.73) the length of AvcF, which cannot be considered 'approximately equal'. In our study, there is considerable variation between observers, with the means for two sets of observations as 0.68 (n=10) and 0.82 (n=5); moreover, the range is large (from 0.54-1.00 in the first series; 0.70-0.92 in the second). In defining the 'delphinid' triangle, Pilleri et al. (1989) stated that the line Ac-Av is 'less' than Av-cF. Given the unclear boundaries contrasting this statistic for the 'monodontid' and 'delphinid' triangle,

FIG. 28. Ventral view of left periotic, QMJM4700. Note strong ventral deflexion of anterior process (upper right); great transverse width of cochlear portion; oblique groove on postero-medial border of cochlear portion (open arrow); fenestra ovalis (triangle); prominent groove for stapedial muscle, running obliquely below fenestra ovalis; ridged, compact basal portion of posterior process (arrow).
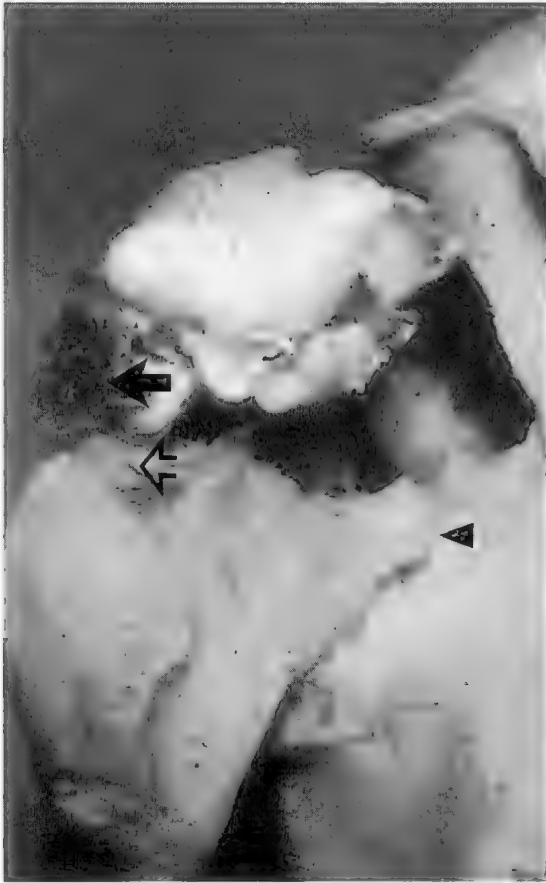
FIG. 29. Oblique ventral view of skull, QMJM4720, incompletely cleaned. Connective tissue (broad arrow) holds tympanoperiotic bones in original, ventral position against mastoid pad (open arrow) of zygomatic arch. Also note falciform process of the zygomatic arch (triangle).
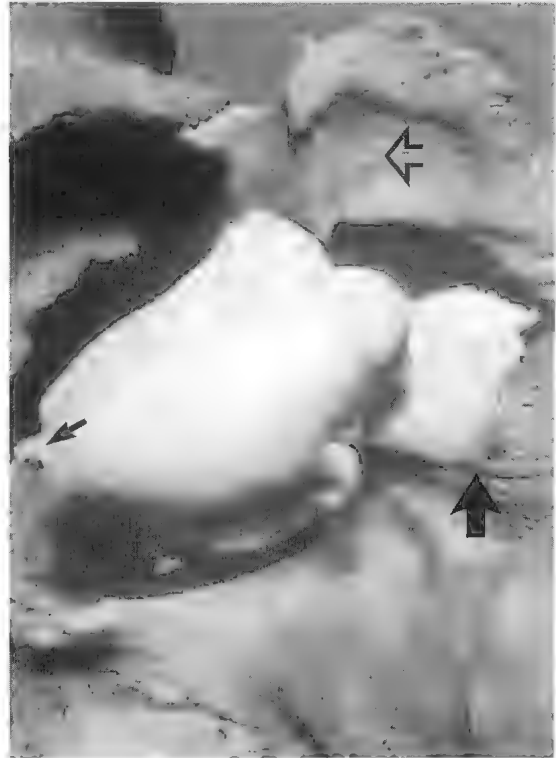

FIG. 30. Oblique ventral view of skull, QMJM4714, with tympanoperiotic bones re-attached against mastoid pad (broad arrow) of zygomatic arch. Note anterior spine of bulla (small arrow); ventral deflexion of paroccipital process of exoccipital, with shallow depression on anterior face (open arrow), and falciform process flattened against the skull base.

and the extensive variability within *Orcaella*, the ratio AvAc/AvcF must be interpreted with caution.

(3) beta and gamma roughly equal; i.e. gamma /beta about 1.0. In measuring periotics of 9 animals, variability and observer bias were extensive. Our mean values (beta 58.3 (47–70); gamma 36.3 (30-54) correspond closely to those of Pilleri et al. (1989): beta 61,62; gamma 33,34. The mean value for beta was much larger than that given by Pilleri et al. (1989) for monodontids (mean=49.5) and delphinids (mean=54.7). The value for gamma was intermediate between that for monodontids (41.9) and delphinids (28.2) (Pilleri et al., 1989, table 16). Given the wide overlap in values (e.g. gamma: *Orcaella* 30-54, *Delphinapterus* and *Monodon* 32-48, delphinids 18-38) the

data provide equivocal support for a relationship between *Orcaella* and monodontids.

The mean of gamma/beta for *Delphinapterus* and *Monodon* is 1.01 (Pilleri et al. (1989)), but our mean for *Orcaella* is 0.64 (n=16). The ratios from Pilleri et al. (1989) are even lower (0.54, 0.55). Again, there is considerable variation within and between observers in our specimens (1st series mean=0.59 (0.43–1.00, n=11); 2nd series mean=0.78 (0.60–0.92, n=5)). However neither our series nor that of Pilleri et al. (1989) can be considered 'approximately the same'.

Variability in monodontid triangle values seem extensive even for *Delphinapterus* and *Monodon*, but our figures and those of Pilleri et al. (1989) for *Orcaella* correspond only poorly to the definition of the monodontid triangle. The closest correspondence is in the angle alpha (mean=85.4° for *Orcaella*, which approximates 90°). However the delphinid triangle is also approximately 90°.
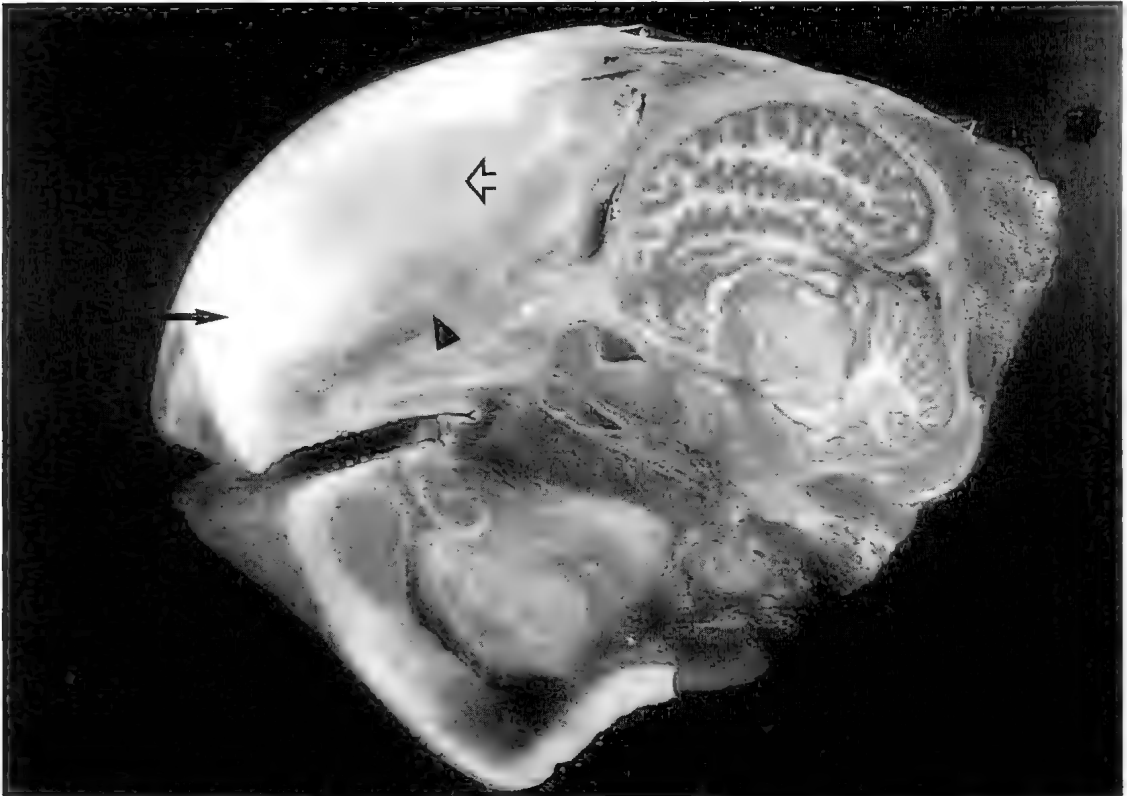
FIG. 31. Near sagittal section of head, MM334, a 1.86m ♀. Note moderate development of melon (open arrow), prominent rostral muscles (triangle), and extent of connective tissue (arrow) at the front of the upper jaw.

Evidence from the so-called monodontid triangle that *Orcaella* is closely related to either *Delphinapterus* or *Monodon* is equivocal at best.

ADDITIONAL CHARACTERS OF PERIOTIC BONES. Details of the tractus spiralis foraminosus, such as a prominent crista transversa, resemble *Neophocaena* and *Pontoporia* (Perrin pers. comm.). The groove in the periotic, which may be the impression of a blood vessel (Fig. 33), has not been described in other odontocetes, and thus can not be used as a taxonomic-character.

ATTACHMENT OF TYMPANOPERIOTIC TO SQUAMOSAL. Kasuya (1973) and Kleinenberg et al. (1969) noted that the periotic of the beluga was firmly sutured to the squamosal; this was considered characteristic of *Delphinapterus* and *Monodon* by Tomilin (1967). Heyning (1989) did not find the periotic sutured to the squamosal in beluga he examined nor is it sutured in beluga and narwhal examined by one of us

(PA). Kasuya (1973) described how the dorsal surface of the periotic is grooved to articulate with the squamosal. We could not confirm the type of articulation in beluga and it is not evident in published photographs where the tympanoperiotics seem to have been re-attached in a variety of orientations. In a juvenile narwhal (UBC9467) the periotic is attached to the squamosal by a thin wedge of the posterior process bounded ventrally by the posterior process of the tympanic. In narwhal and beluga, the main attachment seems to be by the periotic, while in *Orcaella* the attachment is shared between the tympanic and the periotic. The attachment in all three genera appears to be by connective tissue on a mastoid pad on the ventral side of the zygomatic arch within a large post-glenoid space (Figs 29,30); this contrasts with phocoenids and delphinids where the attachment is in a cavity formed by the squamosal, exoccipital and basioccipital (Kasuya 1973; pers. obs.).

Ventral attachment of the tympanoperiotics offers the most convincing evidence that *Orcaella*
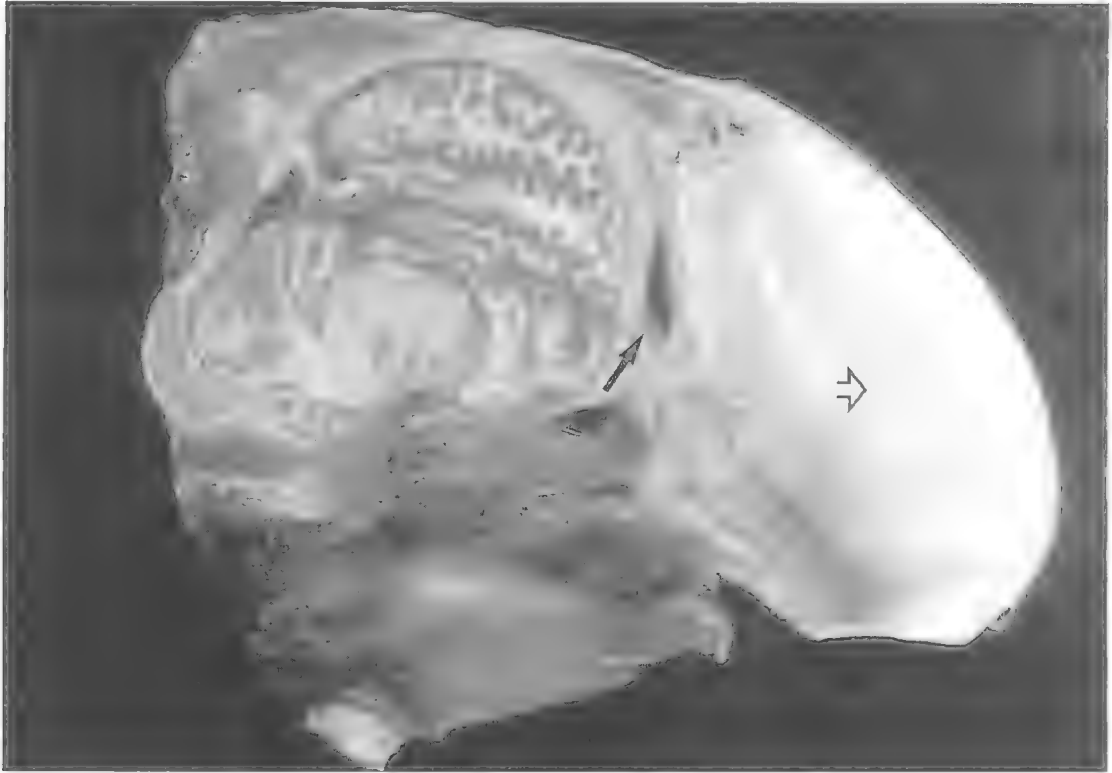
FIG. 32. Opposing section to that in Fig. 31, showing development of melon (open arrow), connective tissue and rostral muscles. Also note partial section of the inferior nares (arrow).

may be related to *Delphinapterus* but the feature is shared with *Monodon* (placed in a separate family by Kasuya) and may be a primitive feature.

CONCLUSIONS. 1. Orientation of the posterior process of the tympanic bulla is variable in *Orcaella*, but the lateral margin is usually deflected approximately 35° from the main axis of the bulla. The deflection of the process is more comparable to delphinids such as *Sousa* than to *Delphinapterus*. A larger series of measurements for the posterior branch of the lower aperture of the tympanic membrane shows that, contrary to Kasuya (1973), it is within the range of delphinids rather than that of beluga. These findings weaken arguments for beluga and *Orcaella* being cofamilial. The other characters (Table 4) provide equivocal evidence for the Delphinapteridae.

2. Linking *Monodon*, *Delphinapterus* and *Orcaella* in one family is inconsistent. Including *Monodon* and *Delphinapterus* in one family implicitly rejects the orientation of the posterior processes of the bulla and periotic, the compres-

sion of the bulla and the width of the posterior branch of the lower tympanic aperture (LTA) as family characters, since they differ between the two genera. However, orientation of the posterior processes and width of the LTA were the main characters used by Kasuya (1973) to unite *Orcaella* and *Delphinapterus* in the Delphinapteridae.

3. Our data and that of Pilleri et al. (1989) on the periotic triangle provide either no support or only equivocal support for linking *Orcaella* with either *Delphinapterus* or *Monodon*.

4. Tympanoperiotics of *Orcaella* are attached by connective tissue to a prominent mastoid pad on the ventral surface of the zygomatic process. A similar ventral connection occurs in *Delphinapterus* and *Monodon*, although there appears to be a greater involvement of the posterior process of the tympanic bulla in the articulation of *Orcaella*. In phocoenids and delphinids the attachment of the posterior processes is within a cavity formed by the squamosal, exoccipital and basioccipital bones.
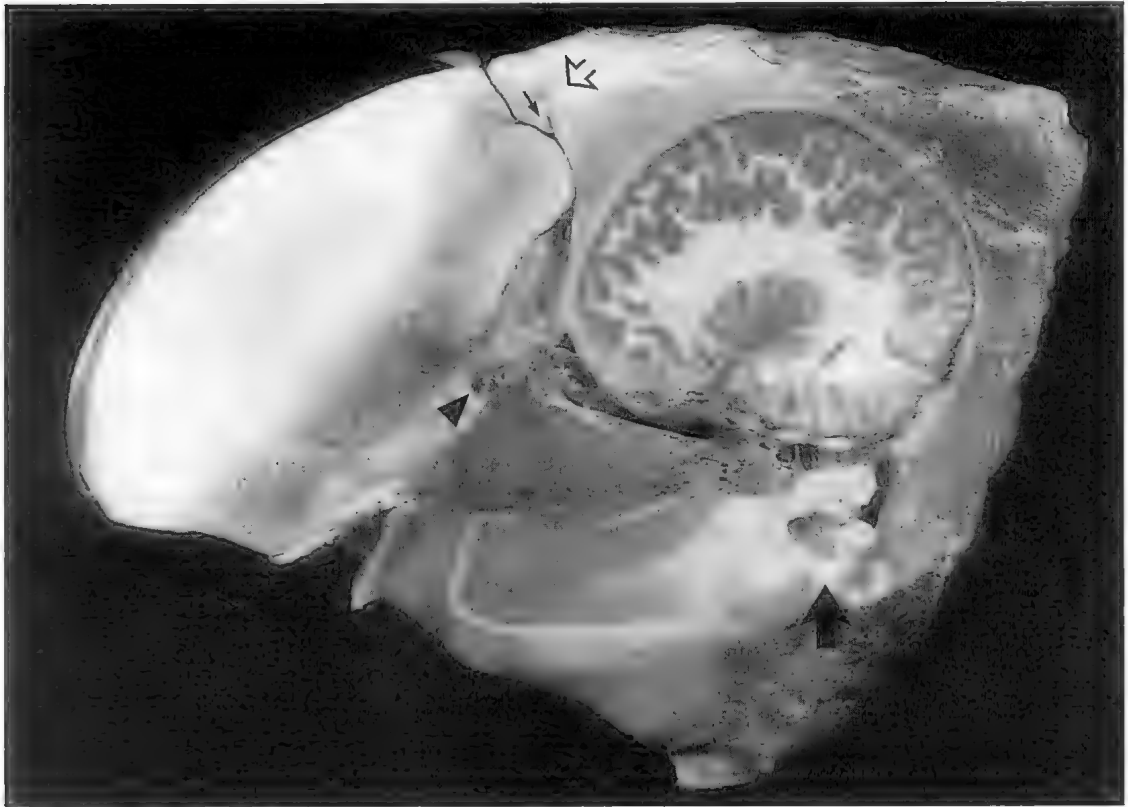
FIG. 33. Section approximately 2 cm left of Fig 32. Note well developed rostral muscles; blowhole ligament with cartilaginous inclusion (small arrow); diagonal membrane (open arrow); vascularised excavation of palatine bones (triangle); tympanoperiotic bones in cross-section (broad arrow) bordered by acoustic fat anteriorly and peribullary sinuses dorsally and posteriorly.

FACIAL ANATOMY

EXTENT OF MELON. MM333 from Mackay has a gape of 130 mm. The anterior boundary of the melon starts about 30 mm behind the tip of the upper jaw; the anterior 30 mm (or c.23% of gape length) is blubber and dense connective tissue. The melon is bordered ventrally by well-developed rostral muscles. The near sagittal sections of MM334 from Ellis Beach (Figs 31–33) show the well-developed rostral muscles and the limited extent of the melon.

Mead (1975) demonstrated that the superficially similar 'bulbous-headed' dolphins are anatomically quite distinct. For instance, *Grampus* has an extensive melon while *Pseudorca* has a preponderance of dense connective tissue in the forehead. *Orcaella* is closest to the generalized delphinid, with neither melon nor connective tissue developed to a high degree. It resembles genera such as *Lagenorhynchus* or even *Tursiops*

as much as it does any of the bulbous headed species.

The bulbous shape of the forehead is one of the reasons for the supposed relationship of *Delphinapterus* and *Orcaella*. Anatomy of the forehead in these two genera is distinct, however, except perhaps for the well-developed rostral musculature (Figs 31-33 for *Orcaella*; Heyning (1989:33) for *Delphinapterus*). There is a conspicuous melon in the beluga, which runs to the front of the forehead (Pilleri et al., 1980, fig.13). The profile of the beluga's forehead is quite malleable and soft. Changes in the forehead are well documented for this species. In contrast, the anterior forehead of *Orcaella* is exclusively dense connective tissue, and it was not possible to deform the profile of the forehead in specimens we examined. Although the 'facial expression' is 'changeable' (Martin,1990), the profile of the head did not vary on captive *Orcaella* observed
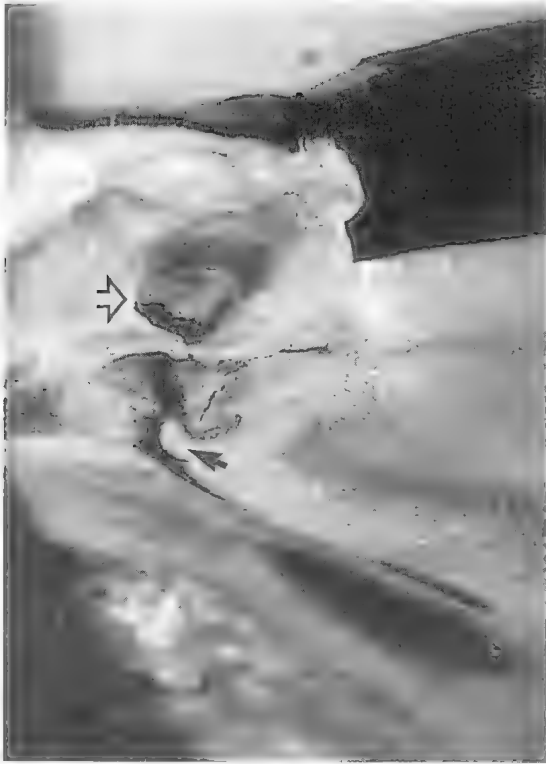
FIG. 34. Oblique dorsal view of section in Fig 32, partially dissected to reveal right vestibular sac (open arrow), with folded walls. Also note lip of the nasal plug (arrow).

FIG. 35. Enlarged view of section in Fig 31. Note muscles around nasal sacs; the darkly pigmented dorsal vestibular sac (small arrow); elongate tubular nasofrontal sac (open arrow); blowhole ligament with cartilage (broad arrow); nasal plug with prominent lip (below blowhole ligament) entering the inferior vestibule; extensive premaxillary sac (triangle).

at the Jaya Ancol Oceanarium (Dr. A. Preen pers. comm.).

Thus the resemblance between *Orcaella* and *Delphinapterus* appears superficial. There is at least as great a similarity between *Orcaella* and the phocoenid *Neophocaena*, which suggests head shape is a shared primitive character.

RESPIRATORY TRACT. The blowhole forms a crescent, with the horns directed anteriorly; its width is 1.5–2.2% of the standard body length. The blowhole is displaced towards the left in MM333, 334.

The spiracular cavity continues ventrally from the blowhole as a transverse slit, which is surrounded by dense connective tissue anterior to the vertex of the skull.

The vestibular sacs extend laterally to posterolaterally from the spiracular cavity. In MM333 they appear to be collapsed and cover less than half the area of the vestibular sacs in the larger MM334. In both specimens, however, the right and left vestibular sacs are approximately equal in size. They are lined with a darkly pigmented epithelium and the walls have slight concentric folds in MM334 (Fig.34) and MM335. The vestibular sacs are connected to the spiracular cavity by a medial ventral slit.

The nasofrontal sacs are immediately below the vestibular sacs. The anterior portion of the nasofrontal sac is tubular; in MM335 the right naso-frontal is 14mm in diameter and the left 10 mm. The anterior portion of the nasofrontal sacs bend posterolaterally, then medially to form a U-shaped tube. The lateral wall of the right nasofrontal sac has a series of perforations and trabeculae, but no extensions from the nasofrontals. The nasofrontal sacs of MM333 are collapsed, about 2.5 mm diameter for the left horn; details are not obvious. In both specimens, the nasofrontal sacs enclose an area comparable to that covered by the vestibular sacs. In MM334, the right nasofrontal sac also has trabeculae.

FIG. 36. Oblique dorsal view of section in Fig. 32. The vestibular sac has been partly removed. The dull probe marks passageway of spiracular cavity from level of vestibular sac to exit between the blowhole ligament (open arrow) and nasal plug (arrow). The pin indicates anterior portion of naso-frontal sac. The lip of the nasal plug has been drawn forward to reveal inferior vestibule. The premaxillary sac (triangle) is also more apparent due to displacement of the nasal plug. There is no indication of posterior septum of blowhole ligament nor posterior nasal sac.

Much of the anterior portion is collapsed and visible in section as a slit (Fig. 35).

In MM335, a probe could be passed from the posterior portion of the nasofrontal sac ventrally to connect with the spiracular cavity; this portion is termed the inferior vestibule (see discussion). The inferior vestibule is bounded anteriorly by the blowhole ligament, which runs laterally on both sides from the nasal septum. In the sagittal section of MM334, the inferior vestibule accommodates the lip of the nasal plug and runs behind the blowhole ligament, apparently in connection with a poorly defined posterior portion of the nasofrontal sac. A small cartilage inclusion is present in the blowhole ligament of MM334 (Figs 35,36). There is no indication of a posterior septum of the blowhole ligament (as defined by Curry, 1992) in any of the specimens examined. The cavity behind the blowhole ligament and connecting with the posterior portion of the nasofrontal sacs is not subdivided by a fold of tissue; i.e. there is no indication of a posterior nasal sac.

The prominent nasal plugs have a conspicuous lateral lip, which fits into the inferior vestibule (Figs 35,36). In MM333, these are 5 mm wide or 19% and 15% of the total width of the left and right nasal plugs respectively. The melon enters the right but not the left nasal plug.

The premaxillary sac is a thin-walled sac with darkly pigmented tissue (Figs 33,35,36). In MM335, the area of the premaxillary sacs is about double (1.7–2.1 times) that of the vestibular sacs. In MM333, in which the vestibular sacs appear collapsed, the premaxillary sacs cover an area about 5–7 times that of the vestibular sacs.

No accessory sacs were found.

Between the inferior vestibule and skull in the sagittal sections of MM334 is a distinct connective tissue sheet which appears to be the diagonal membrane (Fig. 33).

Anderson (1879) noted maxillary (=vestibular) sacs, 'naso-facial' sacs entering the common spiracular cavity and 'large' premaxillary sacs in *Orcaella brevirostris* from India. His description was not detailed enough to compare with more recent studies on the respiratory tract.

Schenkkan (1973), Mead (1975), Heyning (1989) and Heyning & Mead (1990) reviewed the variations in the upper respiratory tract and associated nasal sacs. The cladistic analysis of Heyning (1989) was especially affected by characters of the facial region (24/40 characters), with 11/40 characters referring to the respiratory tract alone. He identified the loss of the 'posterior nasal sac' as a synapomorphy for the Delphinidae. This feature needs to be considered in more detail. The inferior vestibule 'forms a communication between the spiracular cavity and the nasofrontal sac. Hence, if you have both of those features, you, by definition, have the "inferior vestibule"' (Mead pers. comm., 8.3.94). Heyning

TABLE 5. Data for cladograms.

Platanista	0—000000100011010—010020000001000000
Pontoporia	101010000100000101000000020100010100010
Inia	101000000100100101000010021100000100010
Delphinapterus	100010210110000100—111020101110100111
Monodon	100010210110000100—101010111101100111
Phocoena	110110212001100101010000101101110111111
Neophocaena	110110212001100101010010111101110111111
Tursiops	100101211000100101101000001211100101111
Sousa	100111101000100101101000001211100101111
Globicephala	100101212000100101000000001211101101111
Orcaella	100111211000100101000010011111100100111

(1989) used the term 'posterior nasal sac' in its simplest form to refer to a dorsal extension of the inferior vestibule, as in the ziphiid *Mesoplodon* (Heyning, 1989:10). In *Berardius* and *Hyperoodon*, there is a separation of the posterior cavity into an anterior chamber which receives the nasofrontal sac and a caudal chamber which was referred to as the posterior nasal sac. The separation is by a transverse fleshy fold, the 'hintere klappe' of Kukenthal 1893 according to Heyning & Mead (1990). Curry (1992) re-described the facial anatomy of species of *Phocoena* and *Phocoenoides*, and figured a posterior nasal sac separated from the chamber receiving the nasofrontals by an extensive sheet of connective tissue which she referred to as the 'posterior septum of the blowhole ligament'. As a result of the well-developed septum, the upper respiratory tract of phocoenids is well forward of the vertex of the skull. This is shown by diagrams and photographs in Heyning (1989), Curry (1992), Reidenberg & Laitman (1987, fig. 3b) and Schenkkan (1973). This contrasts with the more posterior placement of the upper respiratory tract in delphinids which lack or have a reduced posterior septum (e.g. *Pseudorca* : Mead 1975) and lack a posterior nasal sac (Mead, 1975; Heyning, 1989). The contrast is shown well by comparing the sagittal section of *Phocoena* (Reidenberg & Laitman, 1987, fig. 3b) with *Delphinus, Grampus* and *Globicephala* (Reidenberg & Laitman, 1987, figs 2a,2b,3a), and *Orcaella* (Fig. 31).

In our *Orcaella*, the nasofrontal sacs are clearest in sagittal sections. In all specimens the tubular form of the posterior portion of the nasofrontal sac is ill-defined and there is an extensive connection between it and the inferior vestibule. In this respect, the connection is closer to that illustrated in *Tursiops* by Lawrence & Schevill (1956, fig. 20b) than to Mead's (1975) fig. 4 of the same genus. Sagittal sections of *Orcaella* (Figs 31–33) correspond closely to those in Lawrence & Schevill (1956, figs 3, 4).

Whereas the anatomy of the respiratory tract is well-documented for delphinids (Schenkkan,1973; Mead, 1975), phocoenids (Curry,1992) and ziphiids (Heyning,1989), the situation is less clear in other odontocetes, including the narwhal and beluga. For the former, the only information is a diagram (Huber,1934), which has been discussed by Mead (1975) and Heyning (1989). The occurrence of a posterior nasal sac in narwhal is based on this diagram, even though it is difficult to relate certain other details in the diagram, e.g. the 'lateral sacs' (=vestibular sacs) and the nasofrontals, to the pattern in other odontocetes. The diagrams and description of the respiratory tract of beluga by Kleinenberg et al. (1969) more clearly suggest a posterior nasal sac but again are open to interpretation. Fortunately, Heyning (1989) was able to dissect a beluga and confirmed that the 'inferior vestibule divides dorsally into a rostral nasofrontal sac and caudally into a posterior nasal sac'. The upper respiratory tract appears to be more anteriorly situated in beluga, as in *Phocoena*, if we are interpreting correctly the features in the photograph of a sagittal section (Pilleri et al., 1980, fig. 13). This is consistent with the suggestion above that the anterior position of the respiratory tract is correlated with a posterior nasal sac and well-developed posterior septum. The diagram of the head of a narwhal (Raven & Gregory,1933) also suggests that the respiratory tract is far forward, and Schenkkan (1973), based on Huber's 'very clear diagrams', noted that the blowhole and nasal tract were 'relatively more anteriorly' situated in narwhal than in other odontocetes.

The position of the nasal sacs and upper respiratory tract in our *Orcaella* is consistent with that in delphinids (Lawrence & Schevill, 1956; Mead, 1975) and contrasts strongly with the phocoenid pattern (with a well-developed posterior septum of the blowhole ligament) (Curry, 1992). The orientation of the respiratory tract is not as well documented in monodontids, but appears to be closer to phocoenids and thus differs from what we observed in *Orcaella*. Heyning (1989) noted that in the beluga, the
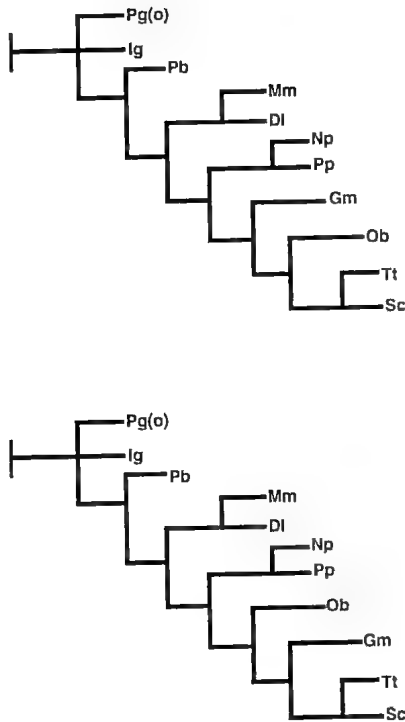
FIG. 37. Analysis One; all characters used. Cladogram length 61; consistency index 70; retention index 75. Abbreviations (for Figs 37-47) are: Pg(o): *Platanista gangetica* (outgroup); Ig: *Inia geoffrensis*; Pb: *Pontoporia blainvillei*; Mm: *Monodon monocerus*; Dl: *Delphinapterus leucas*; Np: *Neophocaena phocaenoides*; Pp: *Phocoena phocoena*; Gm: *Globicephala melas*; Ob: *Orcaella brevirostris*; Tt: *Tursiops truncatus*; Sc: *Sousa chinensis*.

vestibular sacs have apertures on the anterior aspect of the vestibule, as in phocoenids. In our *Orcaella*, the vestibular sac connects with the spiracular cavity by a transverse slit as in *Tursiops* (Lawrence & Schevill, 1956, fig. 20a). Thus, structure of the upper respiratory tract in *Orcaella* is unlike that in either beluga or narwhal.

The balance of evidence suggests that the posterior nasal sac is a feature of ziphiids, beluga & narwhal, and phocoenids but that it is lost in delphinids as indicated by Heyning (1989). This is one of the most soundly based morphological synapomorphies for the Delphinidae. Thus the apparent lack of a posterior nasal sac in *Orcaella* supports its inclusion in the Delphinidae and argues against its close relationship with *Delphinapterus*. The position of the upper respiratory tract in *Orcaella*, close to the vertex of the skull,

is also consistent with the pattern in delphinids. The larger premaxillary sacs relative to vestibular sacs in *Orcaella* is similar to the pattern in delphinids (Schenkkan, 1973). 'Lateral lips on the nasal plugs' was also inferred by Schenkkan (1973) to be a specialised feature, best developed in delphinids; *Orcaella* has well-developed lateral lips on the nasal plugs. However, this feature is inadequately known in other odontocetes, including beluga and narwhal.

The form of the vestibular sacs and, more especially, trabeculae in the right nasofrontal sac of *Orcaella* resemble *Globicephala* (Mead, 1975). The trabeculae in *Globicephala* were considered 'extremely unusual' by Mead, and their occurrence in *Orcaella* and *Globicephala*, along with the bulbous head, suggests a relationship between the two genera. However, the melon structure is different and other criteria need consideration in assessing this relationship.

PHYLOGENETIC ANALYSIS
(Table 5)

RESULTS. In the first analysis all characters were used and treated as non-additive. The two cladograms produced (Fig. 37a,b) link beluga and narwhal as a sister group to *Phocoena, Neophocoena*, the delphinid genera and *Orcaella*. The latter was placed with the delphinid genera, although the two cladograms differed in detail. A comparison of ancestral states in the two cladograms was extracted by option 'hcl' of Hennig86. This shows *Orcaella* linked with *Sousa* and *Tursiops* because only the atlas and axis were fused. *Globicephala* was closer to *Phocoena* and *Neophocoena* as it has at least 3 cervical vertebrae fused. This is a weak character on which to base such a separation, but there is no a priori basis to choose between the cladograms. However, except for the position of *Orcaella* and *Globicephala*, the two cladograms are identical.

In the second analysis, mandibular symphysis length, rostrum length, fusion of cervical vertebrae, presence/absence of olecranon process, roofing of temporal region were masked through option 'cc' because they may be homoplastic. The one cladogram produced (Fig. 38) was identical to Fig. 37b.

As is general practice (Forey et al.,1992), inapplicable values were coded '-, the same as missing values. Platnick et al. (1991) cautioned that while missing and inapplicable values are treated the same computationally, they are logically different (missing values can eventually be coded as
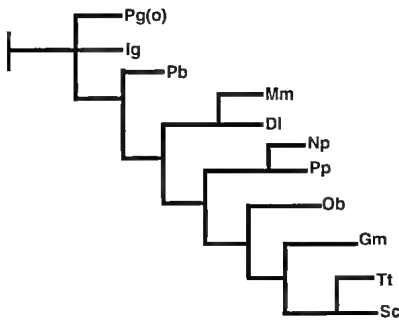
FIG. 38. Analysis 2; characters showing homoplasy masked. Cladogram length 52; consistency index 69; retention index 72.
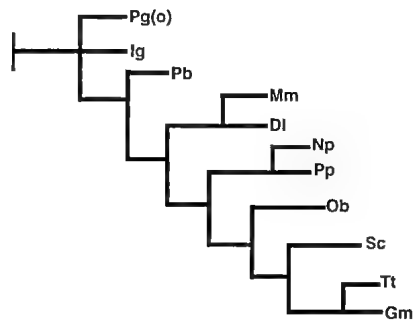
FIG. 39. Analysis 3; characters showing homoplasy and inapplicable characters masked. Cladogram length 48; consistency index 68; retention index 73.

0, 1, etc but there is no way to logically code inapplicable values). They further suggested that cladograms resolved on the basis of inapplicable values may be questionable. In our analysis, this could apply to the subdivision of the pterygoid sinuses, which is a valid character for dolphins and porpoises but inapplicable to monodontids. In analysis 3 homoplastic (as in Analysis 2) and inapplicable characters (relating to subdivision of the pterygoid sinuses) were masked.

In the single cladogram (Fig. 39), *Tursiops* and *Globicephala* were linked, with *Sousa* and *Orcaella* more distantly linked within the terminal cluster of branches. The most important feature is that *Monodon* and *Delphinapterus* were still a group distinct from *Phocoena, Neophocaena, Orcaella* and the delphinid genera. Thus, structure of the other cladograms was not being driven by inapplicable characters. The characters of the pterygoid sinuses were retained in subsequent analyses, because they do allow clearer separation of the delphinid genera without unduly affecting the major branches of the cladogram.

Polarity of a number of the characters is equivocal. In Analysis 4, the homoplastic characters (Analysis 2) and equivocal characters (orbit in front of nares, convex profile of skull, length of zygomatic arch of squamosal, disappearance of superior lamina of pterygoid, orientation of posterior process of periotic, orientation of posterior process of tympanic, form of sigmoid process, presence/-absence of lateral furrow, breadth of lower tympanic aperture, retraction of premaxillaries from nasals,
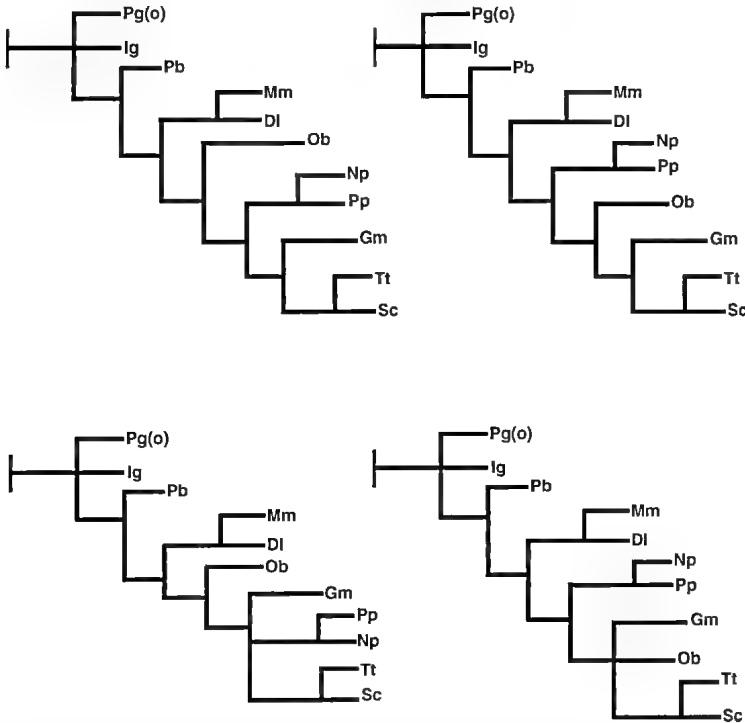

FIG. 40. Analysis 4; characters showing homoplasy or questionable polarity masked. Cladogram length 33; consistency index 69; retention index 68.
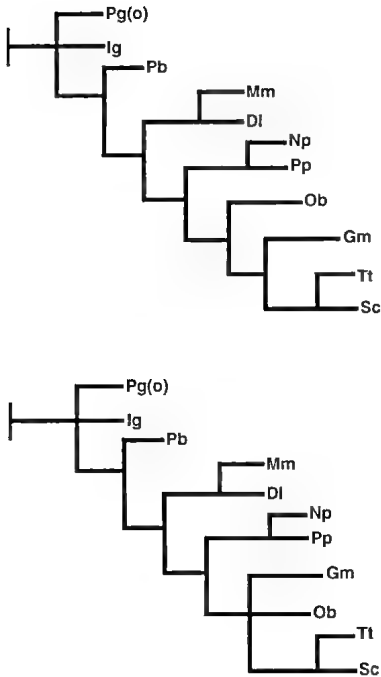
FIG. 41. As in Analysis 4, but with attachment to mastoid pad masked. Cladogram length 31; consistency index 70; retention index 67.

shape of anterior process of periotic) were masked.

In all 4 cladograms produced (Fig. 40A-D), *Monodon* and *Delphinapterus* were separated from *Phocoena, Neophocaena, Orcaella* and the delphinid genera. However, in two cladograms (Fig. 40A,B) *Orcaella* was separated from
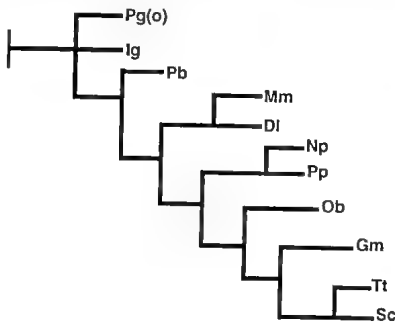

FIG. 42. As in Analysis 4, but with all characters of tympanoperiotic bones retained, despite equivocal polarity. Cladogram length 42; consistency index 69, retention index 71.
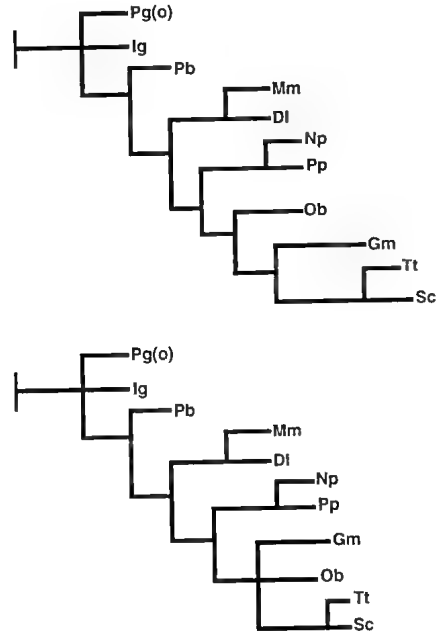
FIG. 43. Analysis 6; characters showing homoplasy and multistate attributes masked. Cladogram length 40; consistency index 75; retention index 78.

Phocoena, Neophocaena and all the delphinids. Analysis of the ancestral states suggested that this is based on the ventral attachment of the tympanoperiotic bones to the mastoid pad of the zygomatic arch. This was confirmed by re-running the analysis with that character masked (Fig. 41A,B) producing two cladograms identical to Fig. 40C,D.

Because of the significance given to the tympanoperiotic bones, Analysis 5 retained tympanoperiotic characters, despite the equivocal polarity. The cladogram (Fig. 42) was identical to Figs 37B,38,40C,41A. Even with all tympanoperiotic characters retained, *Monodon* and *Delphinapterus* are linked, while *Orcaella* is linked with *Phocoena, Neophocoena* and the delphinids.

Coding continuously varying multistate characters (e.g. rostrum length, breadth of lower tympanic aperture) involves a more or less arbitrary decision on where to set the limits of the various categories. This introduces a bias so in Analysis 6 multistate characters were masked. Analysis with characters exhibiting homoplasy and multistate characters masked (i.e. comparable to Analysis 2) produced 2 trees (Fig. 43A,B) with *Monodon* and *Delphinapterus* as a sister group to
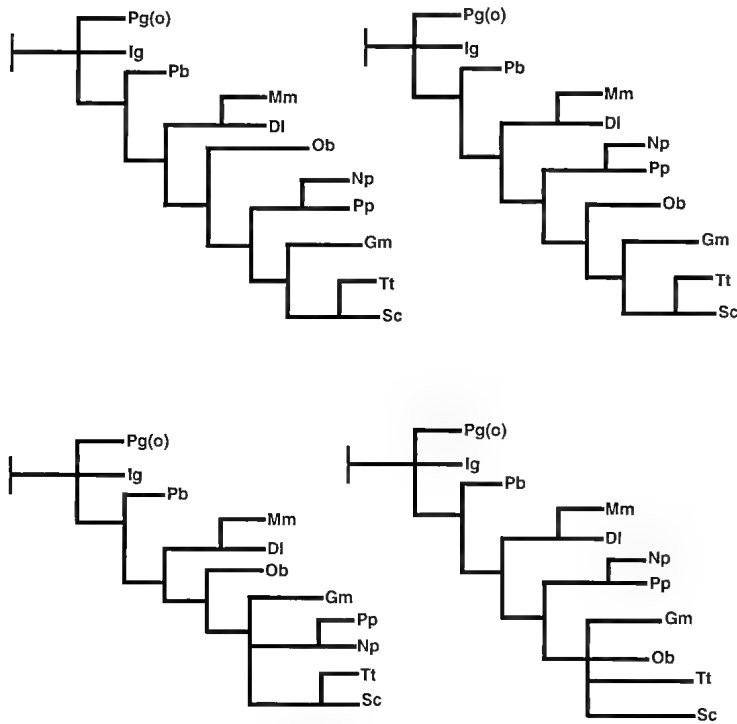
FIG. 44. Analysis 7; characters showing homoplasy or questionable polarity or multistate attributes masked. Cladogram length 30; consistency index 73; retention index 73.

Phocoena, Neophocaena, the delphinids and *Orcaella*. In both cases *Orcaella* was linked with the delphinids as the most derived taxa. This analysis, with a shorter length of 40 (due to fewer attributes), has the highest consistency index (0.75) and retention index (0.78) of all analyses.

In Analysis 7 any multistate characters not already deleted because of homoplasy or questionable polarity were masked. This is comparable to Analysis 4, and produced the same

FIG. 45. Nelson consensus tree based on Analysis 7.

set of cladograms (Fig. 44A-D). The length was shorter (30 vs 33) because of the fewer characters but the consistency and retention indices were lower than in Analysis 6. A Nelson consensus tree was determined using option 'nelsen' of Hennig86 (Fig. 45).

Analysis 7 and Analysis 4 were apparently driven by ventral attachment of the tympanoperiotic in *Orcaella*. Analysis 8 was the same as Analysis 7 except that attachment of the tympanoperiotic bones was also masked. The 2 cladograms (Fig. 46A,B), which were the same as Fig. 41A,B had consistency index (0.75) comparable to Analysis 6, but lower retention index (0.73). The Nelson consensus tree is Fig. 47.

DISCUSSION

TAXONOMIC RELATIONSHIPS OF MONODONTIDAE-PHOCOENIDAE-DELPHINIDAE. The cladograms consistently separated phocoenids and delphinids from the monodontids *Delphinapterus* and *Monodon*, and could even intersperse the phocoenids with the delphinids; this suggests that the phocoenids and
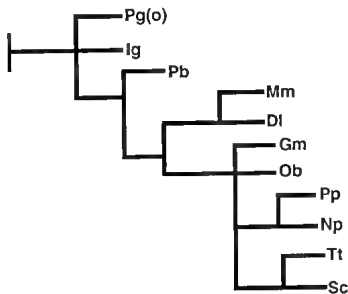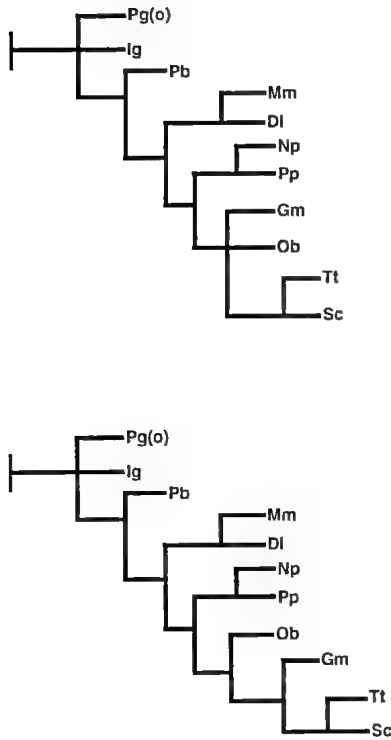
FIG. 46. Analysis 8; as in Analysis 7 but with ventral attachment of the tympanoperiotic bones masked. Cladogram length 28; consistency index 75; retention index 73.

delphinids together form the sister group to the monodontids. This extends previous studies (Heyning, 1989; Gretarsdottir & Arnason, 1992; Milinkovitch et al., 1994) in which the Monodontidae-Phocoenidae-Delphinidae remained an unresolved trichotomy.

We could not demonstrate any synapomorphies for the delphinid–phocoenid clade. Heyning
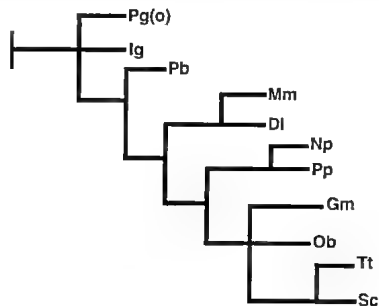

FIG. 47. Nelson consensus tree based on Analysis 8.

(1989) indicated one, 'extreme reduction of zygomatic process of squamosal'. He considered the zygomatic process reduced in *Orcaella,* but we have shown that the zygomatic arch is substantial with a prominent mastoid section and that the mastoid pad provides the attachment point for the tympanoperiotic bones. On this character, *Orcaella* would be excluded from the phocoenid-delphinid clade. This occurred in our cladogram when 'attachment of the tympanoperiotic bones' was not masked. We suggest that form of the zygomatic arch is a reversal and not primitive in *Orcaella*; this is based on a series of synapomorphies it shares with the Delphinidae (Implications for previous classifications, below). Heyning (1989) characterized the zygomatic arch of the delphinid *Orcinus* as 'substantial', an implied reversal which he associated with the handling of large prey by killer whales. The poorly developed mesethmoid plate in *Orcaella* is possibly primitive, linking it more with phocoenids than delphinids. We suggest, however, that the poorly developed mesethmoid plate is a neotenic feature, most apparent in Australian material.

Monodontids and phocoenids have a suite of characters including short rostrum, no beak, short mandibular symphysis, poorly developed mesethmoid plate, widely separated pterygoid hamuli, and relatively unspecialized pre- and post-orbital lobes (especially so in monodontids). As our cladograms suggest that these families are the closest living relatives of delphinids, by outgroup comparison we would expect the features just listed to also occur in the most primitive of the delphinids. This suggests that blunt-headed *Pseudorca, Orcinus, Globicephala* and *Orcaella,* as well as *Cephalorhynchus* (which shows many parallels to phocoenids) are the most primitive delphinids. The alternative suggestion is that long-beaked delphinids such as *Sotalia* and *Sousa* are the most primitive extant delphinids (e.g. Kellogg, 1928; Fraser & Purves, 1962, using the Stenidae) and that the blunt-headed genera are convergent. Three lines of evidence can test the alternatives: (1) molecular data; (2) more extensive fossil material and (3) anatomical studies to determine whether the morphology of blunt-headed odontocetes is homologous. The molecular phylogeny of Milinkovitch et al. (1994, fig.1) is consistent with our cladograms, in that monodontids and phocoenids are separated from the delphinids as potential sister groups. To that extent their results support the possibility that blunt headed dolphins are primitive. Anatomical studies (Mead, 1975; herein)

suggest, however, that the facial anatomy may be quite diverse and non-homologous in 'blunt-headed' dolphins. The anatomy of the facial region is generally considered to reflect adaptations to sound production (Heyning, 1989; Heyning & Mead, 1990) and features of the skull may reflect such modifications. Thus the possibilities of convergence are extensive. The demonstration of neotenic features of the skull in *Orcaella* provides a mechanism whereby more generalized features may be expressed, without implying that the taxon is primitive. The polarity of each character used in classification will therefore have to be examined before the alternative interpretations can be properly evaluated.

IMPLICATIONS FOR PREVIOUS CLASSIFICATIONS. Despite differences between our various analyses, the following were consistent: 1, *Monodon* and *Delphinapterus* were linked; 2, *Orcaella* was not linked with *Delphinapterus* (3) *Phocoena* and *Neophocaena* were linked; 4, *Phocoena, Neophocaena, Orcaella* and the delphinids were the sister group to *Monodon* and *Delphinapterus*; and 5, *Tursiops* and *Sousa* were linked, as the most derived branch.

Fourteen characters were not used (Appendix 2), usually because of insufficient comparative data. Available information for these characters is consistent with the results just outlined, except for the immunological and electrophoretic data of Lint et al. (1990) which is discussed later. The linking of *Tursiops* and *Sousa* may reflect the limited subset of delphinids used and is the most weakly supported of our conclusions. The other results have more general implications for the classifications in Fig. 1:

1. OWEN (1866) (Fig. 1A). *Orcaella* is never linked with *Phocoena* and *Neophocaena* in our cladograms. When Owen described *O. brevi-rostris*, the concept of *Phocoena* was broader than it is today. *Orcaella* has a dorsal extension of the pre-orbital lobe, as in phocoenids. However, this extension was intermediate in development between that in phocoenids and that shown by delphinids such as *Pseudorca* (pers. obs). *Orcaella* has none of the other synapomorphies of phocoenids (e.g., premaxillary boss, spatulate teeth, folded vestibular sacs).

2. KASUYA (1973) (Fig. 1B). *Monodon* and *Delphinapterus* were consistently linked, even when all tympanoperiotic bone characters were included (Fig.41). Our results do not support their family level separation (Kasuya, 1973); they validate Gray's (1821) Monodontidae. This family

ly is as diagnosed by Tomilin (1967, as Delphinapterinae) and Rice (1984), except that the periotic bones do not appear to be fused to the squamosal as stated by the former author. The fossil *Denebola* Barnes, 1984 would also be included in the family, based on the anterior position of its orbits and the extensive border of the nares by the maxillary bones. Other fossils presumed to be monodontids (e.g. in Pilleri et al. 1989) need to be re-evaluated.

Orcaella and the delphinids were linked in our cladograms based on the absence of a posterior nasal sac and the lateral orientation of the posterior process of the tympanic bulla. We have shown elsewhere that characters of the tympano-periotic bones proposed as the basis for the Delphinapteridae by Kasuya (1973) and Pilleri et. al. (1989) are variable or provide only equivocal support. Moreover, *Orcaella* shared none of the synapomorphies identified for *Delphinapterus* (anterolateral margins of superior nares bordered by maxillaries, curvature of flippers & convex profile of skull), nor the undivided cranial sinuses, retention of lateral and superior lamina of the pterygoid bones & anterior position of the orbits with associated prominent palatine bridge under the orbit. Hence we found no support for the Delphinapteridae Kasuya, 1973. Other features used to unite *Orcaella* with *Delphinapterus* appear to be either primitive characters or have proved to be variable when a larger series of specimens were examined. In the first category is the flexibility of the head and cervical sinus, shared not only with beluga but also with river dolphins, such as *Inia*, and *Neophocaena*. Despite statements to the contrary, this flexibility is not associated with separate cervical vertebrae: while these are separate in monodontids and river dolphins, *Orcaella* has the atlas and axis fused as in most delphinids.

The light colour may be a feature of riverine populations, but the Queensland animals at least have a three-tone colour pattern such as in *Tursiops*, rather than the more diffuse pattern of monodontids. The lack of a beak and abbreviate melon are primitive features shared not only with beluga but also phocoenids such as *Neophocaena*. Moreover, the melon in *Orcaella* appears distinct from that in beluga. Similarities in general appearance led Mitchell (1975) to suggest 'a phyletic relationship' between *Orcaella* and 'the Arctic white whale', but we believe that the features are either shared primitive characters or convergent. We similarly suggest that ventral attachment of the tympanoperiotics in *Orcaella*

is a primitive feature shared with monodontids and river dolphins such as *Platanista*, and thus has no taxonomic significance .

Characters which are more variable than originally described include most of the features of the tympanoperiotic bones, such as the posterior orientation of the posterior process of the bulla, width of posterior branch of lower tympanic aperture and the supposedly diagnostic statistics of the periotic triangle. The orientation of the processes and width of the LTA also char-acterize phocoenids, as much as *Delphinapterus*. Our larger series of specimens indicates that an olecranon process is usually present in *Orcaella* (Fig. 48A,B; cf. de Muizon, 1988), as in many delphinids but not *Delphinapterus* or *Monodon* which lack an olecranon process (Tomilin, 1967). The deltoid tuberosity of the humerus is more extended in *Orcaella* than in most delphinids (associated with the greater length of the humerus) but is not as subdistal as in monodon-tids (de Muizon, 1988, fig. 22). It, therefore, provides only equivocal evidence that *Orcaella* is a monodontid (cf. de Muizon, 1988).

Phocoena and *Neophocaena* were consistently linked most closely with *Orcaella* and delphinids *Tursiops*, *Sousa* and *Globicephala*; this does not support wide separation of the Phocoenidae and Delphinidae as in Fig. 1B.

3. BARNES (1984), GASKIN (1982)(Fig. 1C). Both authors linked the phocoenids and del-phinids as in our cladograms. However, their linking *Monodon*, *Delphinapterus* and *Orcaella* in the same family contrasts with our findings. Including *Monodon* and *Delphinapterus* in the same family implicitly rejects the orientation of the posterior processes of the bulla and periotic, the compression of the bulla and the width of the lower tympanic aperture as valid family charac-ters, since these all differ in the two genera. However, orientation of the posterior processes and width of the tympanic aperture were the two main characters used to unite *Orcaella* and *Del-phinapterus* in the Delphinapteridae.

As discussed above, other characters which link these genera are shared primitive features, most of which could be equally used to support a relationship between *Orcaella* and the phocoenids.

Miller (1923) placed *Delphinapterus* and *Monodon* in different subfamilies based on dif-ferences in dentition, the pterygoid hamuli and extent to which the alisphenoid was overspread by the superior lamina of the pterygoids. Except for dentition, these features are not known for *Denebola*, the only other monodontid accepted in this paper. Although *Monodon* and *Delphinap-terus* are distinct, we question the need for sub-family separation.

4. PILLERI et al. (1989) (Fig. 1D). This clas-sification suffers from the same inconsistencies noted in the last section. In addition, the phocoenids and delphinids were widely separated, the former being placed with the river dolphins *Platanista*, *Inia* and *Pontoporia*. None of our cladograms support this classification: phocoenids differ from the river dolphins in profile of the tympanic bulla, shape of the sig-moid process, loss of lateral furrow, symmetry of vestibular sacs, roofing of the temporal region, position of the orbits relative to nares and com-plexity of the cranial sinuses. We consider the delphinids and phocoenids closely related based on morphology (de Muizon, 1988, 1990; Heyn-ing, 1989), and ribosomal DNA (Milinkovitch et al., 1993). This relationship is also consistent with the molecular phylogeny in Milinkovitch et al. (1994), which included the river dolphin *Inia*.

5. LINT et al. (1990) (Fig. 1E). Our results agree with placing *Orcaella* in the Delphinidae. The major discrepancy in their classification is the extreme separation of phocoenids and del-phinids. As indicated in the previous section, this is not supported by any of our cladograms and is inconsistent with most previous classifications. It was based on a combination of immunological and electrophoretic results, the latter incorporat-ing the data of Shimura & Numachi (1987). Shimura & Numachi (1987) used a limited range of species; the ziphiid *Berardius* was the only non-delphinid taxon compared with phocoenids. It is thus possible that ziphiids and phocoenids were linked in the phenogram because they both differed from delphinids, rather than because they were closely related. Even with the extra species considered by Lint et al. (1990), the analysis was biased heavily towards delphinids, which may affect their conclusions on relationships among higher odontocete taxa.

6. FRASER & PURVES (1962) (Fig. 1F). We place *Orcaella* in the Delphinidae, as proposed by Fraser & Purves (1962). There are two aspects of their classification which we would question. The first is the linking of *Sousa*, *Sotalia* and *Steno* in the Stenidae, which is considered a more primi-tive taxon than the Phocoenidae. Grouping *Steno*, *Sotalia* and *Sousa* as the Stenidae (Fraser & Pur-ves, 1962) is based on inconsistent or unclear criteria. The rugose teeth of *Steno*, proposed as a primitive character, is not shared by the other two

genera. The elongate rostrum and elongate mandibular symphysis, appear to be variable features in other odontocete families (Heyning, 1989) and may not be primitive. The length of rostrum appears to be particularly subject to reversals and convergences: a long rostrum occurs not only in less derived taxa such as *Platanista* but in more specialized taxa, such as *Stenella*, which we consider among the most derived of delphinids. Previous authors (Kellogg, 1928) emphasized the resemblance of kentriodontids and long-snouted dolphins such as *Sotalia* (closely related to *Sousa*). In light of the much more primitive form of the kentriodontid skull (e.g. lacking asymmetry), the resemblance may be superficial and dependent on variable features such as rostrum length and length of mandibular symphysis. Fraser & Purves (1962) pointed out the mixture of supposedly primitive characters and an advanced cranial sinus system in *Sotalia* and *Sousa*. We have not examined *Sotalia* but our *Sousa chinensis* skulls suggest close coalescence of pre- and post-orbital lobes to surround the optic nerve, as inferred by Fraser & Purves (1962). In addition, the excavation of the bones in the sphenoidal region of *Sousa* skulls we examined was complex and similar to that in more advanced delphinids such as *Tursiops* and *Stenella*. The consistent grouping of *Tursiops* and *Sousa* as the most derived group in our cladograms further suggests a more derived condition for *Sousa* than recognized in the systems of Kellogg(1928) and Fraser & Purves (1962). We have to recognise the limited range of delphinids considered in our analysis, however, so that our results may be biased.

In most of our cladograms, the phocoenids appeared as less derived than the delphinids. In Figs 40B & 44B the phocoenids were aligned to *Tursiops* and *Sousa*, but the cladogram was unresolved. The more generalized state of phocoenids is further supported by studies of base pair length of repetitive DNA: the phocoenids shared the 1750 base pair length with other taxa such as ziphiids, monodontids, etc whereas the delphinids had a unique base pair length of around 1580. The phocoenids were separated, with monodontids, from the delphinids in the molecular phylogeny of Milinkovitch et al. (1994). The phocoenids, nonetheless, show specializations (e.g. dorsal extensions of the preorbital pterygoid lobe, morphology of the nasal region which was considered by Klima & van Bree (1985) to be more derived in *Phocoena* than in other odontocetes examined). These

specializations may reflect a long period of separation from the delphinids. The large number of synapomorphies for the Phocoenidae suggests it is a conservative body plan, although many of the characters are variably expressed throughout the family (Perrin pers. comm.; Appendix 2). Our results do not support the classification (Fraser & Purves, 1962) which placed the Phocoenidae between the Stenidae (including *Sousa*) and the Delphinidae.

An even greater disparity occurs between our results and the position of the Monodontidae in Fraser & Purves' (1962) classification. They considered the undivided form of the pterygoid sinuses a primary feature and the basis for their Superfamily Monodontoidea. As argued elsewhere, this feature needs to be confirmed by dissection. Beluga and narwhal appear to be more primitive than *Phocoena, Neophocaena* and delphinids (Figs 37–47). However, Fraser & Purves (1962) suggested that they are more primitive than all odontocetes other than ziphiids.

Monodon and *Delphinapterus* are consistently linked with *Phocoena, Neophocaena* and delphinids (Figs 37–47) arguing for their retention within a single taxon, such as the Delphinoidea (Heyning, 1989). Moreover, characters linking monodontids with *Phocoena, Neophocaena* and delphinids are derived features whereas those linking them to river dolphins are primitive or of questionable polarity (e.g. anterior position of orbits). Although Heyning (1989) and de Muizon (1988) did not resolve relationships between monodontids, delphinids and phocoenids, their analyses showed they form the most derived group of living odontocete taxa. Grouping monodontids, phocoenids and delphinids is also supported by some chemical data, such as the distribution of isovaleric acid in acoustic fat (Litchfield et al., 1975; Appendix 2). This grouping was also evident in molecular phylogenies (Milinkovitch et al., 1994). de Muizon (1988) and Heyning (1989) indicated a series of synapomorphies for physeterids and river dolphins (*Platanista, Inia, Pontoporia, Lipotes*), all of which would have to be considered reversals if Fraser & Purves' (1962) position of monodontids was accepted. Our results support de Muizon (1988, 1990) and Heyning (1989), indicating that the undivided pterygoid sinuses must be considered a reversal rather than a primary feature in monodontids. This removes the basis for separating beluga and narwhal in their own superfamily.

7. NISHIWAKI (1963, 1964, 1972) (Fig 1G). Nishiwaki (1963, 1964) proposed the Orcellidae

('Orcaelidae' of Nishiwaki 1972), with: 1, only atlas and axis fused; 2, size less than 12 feet (4 m); 3, no beak and less than 20 teeth in each row of the upper jaw. The first two characters are also consistent with the Delphinidae as defined by Nishiwaki. Although he characterized delphinids as having a distinct beak, he included genera such as *Cephalorhynchus* where the beak is reduced or absent. The only character separating *Orcaella* from delphinids is tooth number, but this seems a questionable basis for family separation given the variability in tooth number within other families (e.g. phocoenids). This character would no longer hold if *Grampus*, put in its own family by Nishiwaki, is considered a delphinid (Mead, 1975). Moreover, fossil *Tursiops* have as few as 14 teeth per side of each jaw (Barnes, 1990).

While we have reservations about the validity of the characters used by Nishiwaki, *Orcaella* does have characters (e.g. attachment of the tympanoperiotics to the mastoid pad of the zygomatic arch, the development of the zygomatic arch) which separate it from the delphinids and phocoenids. These characters could indicate a distinct family for *Orcaella*. We reject this option because *Orcaella* shares several derived features with the Delphinidae, including loss of posterior nasal sac, 1580 bp length of repetitive DNA, maintenance of the right premaxillary close to the nasals, apical position of nasals, development of the mesethmoid plate (de Muizon, 1988; Heyning, 1989; Barnes, 1990; Gretarsdottir & Arnason, 1992), although the last feature may vary between populations. These features imply a commonality of the most recent ancestor. Although some of the cladograms (e.g. Fig. 37B) indicate a basal position among delphinids for *Orcaella*, none suggested that it is a distinct family. The most parsimonious conclusion is that the zygomatic arch and attachment of the tympanoperiotic bones in *Orcaella* are reversals. The other characters which separate *Orcaella* from delphinids are either unique to *Orcaella*, or probably neotenous; in either of these cases they are of no value in assessing relationships between taxa. To emphasize them, rather than evidence for most recent common ancestor, promotes a system based on discordancy, characterised by an ever increasing number of monotypic taxa.

8. SLIJPER (1936), FORDYCE (1984), DE MUIZON (1988), HEYNING (1989), etc. (Fig. 1H). We agree with the 'classic' placement of *Orcaella* in the Delphinidae s.l. *Orcaella* was commonly (Figs 40c, 41a, 43a, 46b) placed as the least derived in the series *Orcaella, Globicephala*

and (*Tursiops* + *Sousa*). However, equally commonly (Figs 40d, 41b, 43b, 46a) there was an unresolved trichotomy of *Orcaella, Globicephala* and (*Tursiops* + *Sousa*). Gray (1866, 1871), Anderson (1879), Fraser & Purves (1962), Mead (1975), de Muizon (1988) and Heyning (1989) placed *Orcaella* with the 'blunt-headed' dolphins such as *Orcinus, Pseudorca* and *Globicephala*. We have indicated skull features (separation of the medial and lateral lobes of the palatines, posterior extension of the lateral lobe of the palatine bone) which link *Orcaella* with the 'blunt-headed' dolphins, especially *Globicephala* and *Pseudorca*. What is unresolved is whether these features are evidence of relationship or whether they are convergent, reflecting shared constraints on morphology (e.g., short rostrum). Fraser & Purves (1962) suggested a series of increasing specialization from *Pseudorca* to *Orcinus, Orcaella, Globicephala* and *Feresa*. This was based on what we consider minor variations in the relative development of the pre- and post-orbital lobes, which have been largely inferred from skulls and not confirmed by dissection. In addition there can be considerable variation in the sinuses within taxa, e.g. *Pseudorca* (Fraser & Purves, 1962; Purves & Pilleri, 1978, fig. 18). *Pseudorca* was apparently placed as most primitive because of the more extensive development of the bony lateral lamina of the sinuses. However, this is formed from the palatine bone, rather than the lateral lobe of the pterygoid bone, as in monodontids and some river dolphins which were considered less derived by Fraser & Purves (1962). The lamina may not be homologous among these genera.

de Muizon (1988) placed *Orcaella* in the Globicephaliinae based on 'dilation of the premaxillae at apex of rostrum'. He illustrated the tip of the snout of *Orcaella*, composed entirely of premaxillae. However, the maxillae do not reach the tip in delphinids such as *Tursiops* or *Sousa* (pers. obs). Moreover, neither the premaxillae nor the rostrum show the broad transverse expansion as in *Pseudorca*, and especially *Globicephala melas*. Premaxillae/rostrum width at 0.75 length in *Orcaella* was 65.0% (56.0%–73.1%), which is comparable to *Lagenorhynchus* (Sergeant & Fisher, 1957) or *Tursiops* (Ross, 1977) in the Delphiniinae *sensu* de Muizon.

Cladograms, which place phocoenids and monodontids as the nearest living relatives of delphinids, suggest by outgroup analysis that features such as short rostrum of skull, widely separated pterygoid hamuli and unspecialized

cranial sinuses are primitive within the delphinids. Similarities of *Orcaella* to phocoenids, especially *Neophocaena*, as well as monodontids, suggests it is one of the most primitive of the delphinids. Dudok van Heel (in Kamminga et al., 1983) suggested that *Orcaella* was one of the 'oldest "modern" species.."forced" inshore by more recent newcomers'. Although we have reservations about invoking competition to explain delphinid distributions, our data are consistent with *Orcaella* being a less derived taxon (at least within the Delphinidae, *s.l.*). Such an interpretation reinforces the generalized nature of genera such as *Cephalorhynchus* (which shows many parallels to phocoenids), as well as *Pseudorca*, *Orcinus* and *Orcaella*. The generalized features in these genera make it difficult to establish natural groupings of such genera based on shared derived features. Moreover, Mead (1975) indicated the wide morphological diversity in the facial anatomy of 'blunt-headed' dolphins which suggests that they may not be a natural group. *Grampus* and *Peponocephala*, in particular, fit poorly with the other genera at least based on the cranial sinus anatomy. Given the generalized and apparently primitive characters which link them, it is difficult to assess whether *Pseudorca*, *Orcinus* and *Globicephala* form a natural grouping, and whether *Orcaella* is related to any of them. *Orcaella*, for instance, has relatively few teeth, but they are not enlarged as in the other genera (e.g. *Pseudorca*, which has enlarged teeth even in the foetus: Pilleri & Purves, 1978, fig. 17).

Cladistic analyses assume that convergence is not so widespread that it masks underlying phylogenetic patterns; by outgroup analysis features of *Orcaella* are assumed to be primitive. The evidence for convergence in toothed whales is overwhelming, however, for characters such as rostrum length and probably mandibular symphysis length. A lack of knowledge of the functional significance of many of the other features used in cetacean classification (e.g. facial anatomy) prevents a balanced consideration of the extent of convergence in delphinids and other odontocetes. Neoteny in *Orcaella* further complicates interpretation; it provides a mechanism whereby apparently primitive features could occur in a more derived species. We conclude that *Orcaella* is not a monodontid or delphinapterid (sensu Kasuya, 1973). The balance of evidence suggests it is a delphinid *s. l.* However, given the ambiguity of characters used to define groupings within the Delphinidae and limitations in the comparative material of delphinids available to us, we did not consider it worthwhile to pursue our cladistic analyses further (e.g. by using different combinations of delphinid genera) in order to place *Orcaella* within the family. Recent DNA studies may provide important new evidence on the relationships of toothed whales. However, rigorous phylogenetic techniques on a wider range of characters than were available for this study, should be rewarding. Such studies will also provide the necessary tests for taxonomic hypotheses generated by DNA and other molecular techniques.

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APPENDIX 1: Measurements of tympano-periotic bones (after Kasuya, 1973). Measurements 1 and 13 in mm. Measurements 2-10 as % of standard length of tympanic bulla. Measurements 14-19, 23-28 as % of standard length of periotic.

TYMPANIC BULLA

1. Standard length of tympanic bulla, distance from anterior tip to posterior end of outer posterior prominence
2. Distance from anterior tip to posterior end of inner posterior prominence
3. Distance from posteroventral tip of outer posterior prominence to tip of sigmoid process
4. Distance from postero-ventral tip of outer posterior prominence to tip of conical process
5. Width of tympanic bulla at level of the sigmoid process
6. Height of tympanic bulla, from tip of sigmoid process to ventral keel
7. Width across inner and outer posterior prominences
8. Greatest depth of interprominential notch
9. Width of upper border of sigmoid process
10. Width of posterior branch of lower tympanic aperture

PERIOTIC

13. Standard length of periotic, from tip of anterior process to posterior end of posterior process, measured on a straight line parallel with cerebral border
14. Thickness of superior process at the level of upper tympanic aperture
15. Width of periotic across cochlear portion and superior process, at the level of upper tympanic aperture
16. Least distance between the margins of the fundus of internal auditory meatus and of aperture of ductus endolymphaticus (aquaeductus vestibuli)
17. Least distance between the margins of the fundus of internal auditory meatus and aperture of aquaeductus cochleae
18. Length of articular facet of the posterior process of periotic for the posterior process of tympanic bulla
19. Anteroposterior diameter of cochlear portion
22. Length of periotic shown by the percentage of length of tympanic bulla
23. Separation of foramen singulare and aquaeductus Fallopi
24. Angle of lateral margin of posterior process of tympanic bulla to sagittal axis

	JM 4700		JM 4705		JM 4709		JM 4712		JM 4720	JM 4721		JM 4725		JM 4726		JM 4734		JM 4735		JM11343	
	L	R	L	R	L	R	L	R	R	L	R	L	R	L	R	L	R	L	R	L	R
1*	34.95	34.80	36.00	36.15	36.25	36.50	33.50	33.70	33.70	35.00	33.85	35.20	35.60	35.20	34.90	34.20	34.35	35.30	35.20	33.05	33.75
2	96.42	99.71	95.56	95.16	95.17	93.15	93.73	96.14	94.66	93.57	94.98	96.73	95.79	92.90	97.28	94.74	97.96	94.33	94.60	96.97	94.37
3	60.37	58.33	63.75	59.06	62.20	62.74	64.18	64.54	63.65	63.14	65.29	59.38	58.57	62.07	61.6	60.53	64.05	58.07	58.52	66.26	65.93
4	43.20	42.67	44.86	44.54	44.83	44.11	47.01	47.03	45.70	42.71	45.79	39.77	41.29	42.33	41.98	42.84	45.85	40.65	41.19	47.20	47.41
5	57.08	57.04	55.83	53.94	57.93	58.08	59.85	60.98	58.01	56.71	58.05	57.24	54.63	59.66	60.03	58.77	57.50	58.07	58.66	57.03	58.67
6	79.11	77.87	75.56	74.69	71.31	69.86	77.01	76.85	77.74	76.14	77.1	72.73	72.61	77.13	77.22	76.32	78.02	72.52	74.57	72.62	72.30
7	62.37	61.35	58.19	53.94	57.52	56.30	61.49	62.01	58.75	57.86	58.94	56.96	55.62	62.35	62.61	60.09	60.55	57.50	58.24	56.58	55.70
8	36.19	34.63	28.19	31.54	27.86	32.6	30.14	29.97	33.53	30.86	32.34	28.69	33.14	31.39	33.95	27.92	28.23	25.78	25.99	29.65	22.52
9	33.05	33.62	20.42	19.36	-	-	-	-	-	20.14	17.28	-	-	22.44	-	20.03	18.78	20.82	19.89	22.09	-
10	5.72	6.75	5.28	6.92	7.45	6.30	6.27	6.97	7.42	5.86	6.2	6.53	6.18	5.68	6.02	6.29	6.4	5.67	7.24	7.26	8.89
13*	37.40	38.20	36.20	36.25	36.90	37.20	35.50	35.70	34.50	38.00	36.90	37.85	37.25	35.10	33.65	35.25	35.15	35.80	33.55	32.1	31.00
14	38.10	34.95	36.74	41.38	34.82	34.41	37.61	34.73	35.51	34.21	32.25	31.97	32.48	37.04	37.30	34.47	35.85	36.03	36.66	33.96	36.07
15	52.54	49.48	56.49	53.24	61.25	54.84	54.08	49.30	49.57	51.84	56.23	52.05	49.93	54.27	57.36	57.87	57.18	55.45	58.42	62.31	64.09
16	7.89	6.41	1.38	6.07	4.34	3.90	6.67	2.52	-	6.45	4.34	5.94	5.1	3.13	3.27	3.26	3.97	7.54	4.62	7.48	9.18
17	6.28	6.54	4.42	4.55	5.69	4.84	5.63	6.16	9.86	4.21	7.72	4.76	5.36	3.56	6.24	5.53	5.69	5.17	6.86	4.67	7.73
18	28.21	27.75	28.18	35.03	-	-	-	-	-	-	-	-	-	-	-	36.31	35.42	37.99	36.07	35.98	-
19	40.11	39.53	45.16	46.62	44.58	42.34	41.13	41.32	42.17	38.95	41.96	39.36	39.73	44.44	44.58	42.98	43.95	42.88	42.03	45.95	46.38
22	107.01	112.02	100.56	100.28	101.79	101.92	105.97	105.93	102.37	108.57	109.01	107.52	104.63	99.71	96.41	103.07	102.32	101.41	95.31	97.12	92.00
23										9.08	16.8	12.68	13.69	15.95	19.01	13.05	11.95	13.83	13.71	15.11	14.49
24	43°	39°	40°	35"	42°	28.5°	47°	34°	25°	33°	17°	43°	43°	32°	41°	40°	27°	33°	19°	47.5°	23.8°
25	25.67	26.57	30.39	27.86	25.20	22.04	25.35	24.93	28.26	26.58	25.54	28.00	27.79	29.63	32.39	33.19	32.57	30.87	28.17	34.42	38.33
26	3.74	4.97	6.22	5.79	-	-	-	-	-	-	-	-	-	-	-	5.53	4.55	6.56	7.00	5.61	-
27	10.29	7.85	7.73	8.69	7.86	9.27	8.17	9.29	7.54	7.89	9.49	8.72	9.13	8.97	9.96	8.37	8.39	9.36	9.99	10.12	-
28	10.29	-	12.02	10.07	-	-	-	-	-	-	-	-	-	-	-	11.49	8.53	11.31	10.73	11.68	11.59

25. Maximum width of fundus of the internal auditory meatus
26. Width of foramen ovale
27. Width of foramen rotundum
28. Width of head of malleus

APPENDIX 2: CHARACTER STATES

1. Vestibular sacs. Heyning (1989) demonstrated that vestibular sacs are a feature of all odontocetes except Physeteridae (including *Kogia*), Ziphiidae and *Platanista*. Schenkkan (1973) described vestibular sacs in ziphiids, but we follow the interpretation by Heyning, who had access to a wider range of material and used supplementary criteria such as position of the sacs relative to muscle layers. Lack of vestibular sacs is primitive by outgroup analysis, as suggested by Heyning (1989).

2. Folded vestibular sacs. This is a specialized feature of the Phocoenidae, as demonstrated by numerous authors. It was coded as - in *Platanista* which lacks vestibular sacs; 0 for those genera with unfolded vestibular sac (primitive condition), and 1 for *Phocoena* and *Neophocaena*, with folded sacs.

3. Hypertrophied right vestibular sac. Schenkkan (1973) and Heyning (1989) noted this specialization of the river dolphins (except *Platanista*). It was coded - for *Platanista* without vestibular sacs, 0 for those with symmetrical sacs (primitive) and 1 for *Inia* and *Pontoporia*.

4. Orbit in front of nares. Miller (1923) noted this feature in *Monodon* and *Delphinapterus*; it occurs in all the river dolphins. It appears to be present in *Physeter* (van Beneden & Gervais 1868-79; Kellogg, 1928), but not in *Kogia simus* (Perrin pers. comm.) It is not so in extant ziphiids, but it is in *Squaloziphius*, which was considered to be a ziphiid by de Muizon (1990) (but see Fordyce & Barnes, 1994).

Miller (1923) noted the posterior opening of the antorbital canal near the anterior of the orbit in delphinids (based on *Delphinus*), as in terrestrial mammals. Since the antorbital canal was more posterior in those species where the orbit was in front of the nares, he argued that this was the specialized condition. However, the posterior opening of the antorbital canal may also be situated more posteriorly relative to the orbits in phocoenids and *Pseudorca*, which do not have the orbits in front of the level of the nares (pers. obs.). This compromises Miller's argument and

the polarity remains equivocal. In the juvenile narwhal UBC 9467, the orbit was already anterior to the nares, so there is no indication of the polarity state from this ontogeny.

Polarity is equivocal based on outgroup analysis, comparative anatomy and ontogeny. The more anterior position of the orbit is considered primitive based on river dolphins and physeterids, and possibly ziphiids (the last based on *Squaloziphius*, which Fordyce & Barnes (1994) considered 'more reminiscent of' the Eurhinodelphidae than Ziphiidae). If they are right, orbit in front of the nares may be a primitive feature by outgroup analysis since the Eurhinodelphoidea is a possible sister group to the Delphinida sensu de Muizon. Coding the anterior position of the orbits as primitive makes the fewest assumptions about the relationships of the river dolphins and monodontids .

5. Separation of pterygoids
Physeter, Berardius and *Platanista* all have medially appressed pterygoids, and by outgroup analysis this is considered the primitive state. Separation of pterygoids is coded as 1.

The palatines and vomer in *Orcaella* resemble those in delphinids where there has been a compression of the palatines and median vomerine spine by the pterygoids. It therefore may not be homologous with the situation in phocoenids, monodontids and some primitive delphinids. All species with widely separated pterygoids are nonetheless scored 1.

6. Posterior nasal sac
We accept Heyning's (1989) argument that a posterior nasal sac is primitive. Its occurrence in the narwhal is from Huber (1934), but Heyning confirmed it in *Delphinapterus*. We have not been able to confirm the loss of this sac in *Sousa*, but it is scored as lacking the sac, as this is a consistent feature of delphinids examined.

7. Mandibular symphysis length
Usually expressed in binary form (short/long) but animals examined fell into 3 ranges: >50% mandible length (in *Physeter* and the river dolphins), 30-50% (*Sousa* and *Steno* (Perrin pers. comm.)) and <30%. The polarity is equivocal by outgroup analysis, as *Physeter* has an elongate mandibular symphysis, but it is shorter (<50%) in *Kogia* and <30% in ziphiids. Coding is 0 =>50%, 1=30-50% and 2=<30%, but since all characters were treated as nonadditive no direction of specialization is implied.
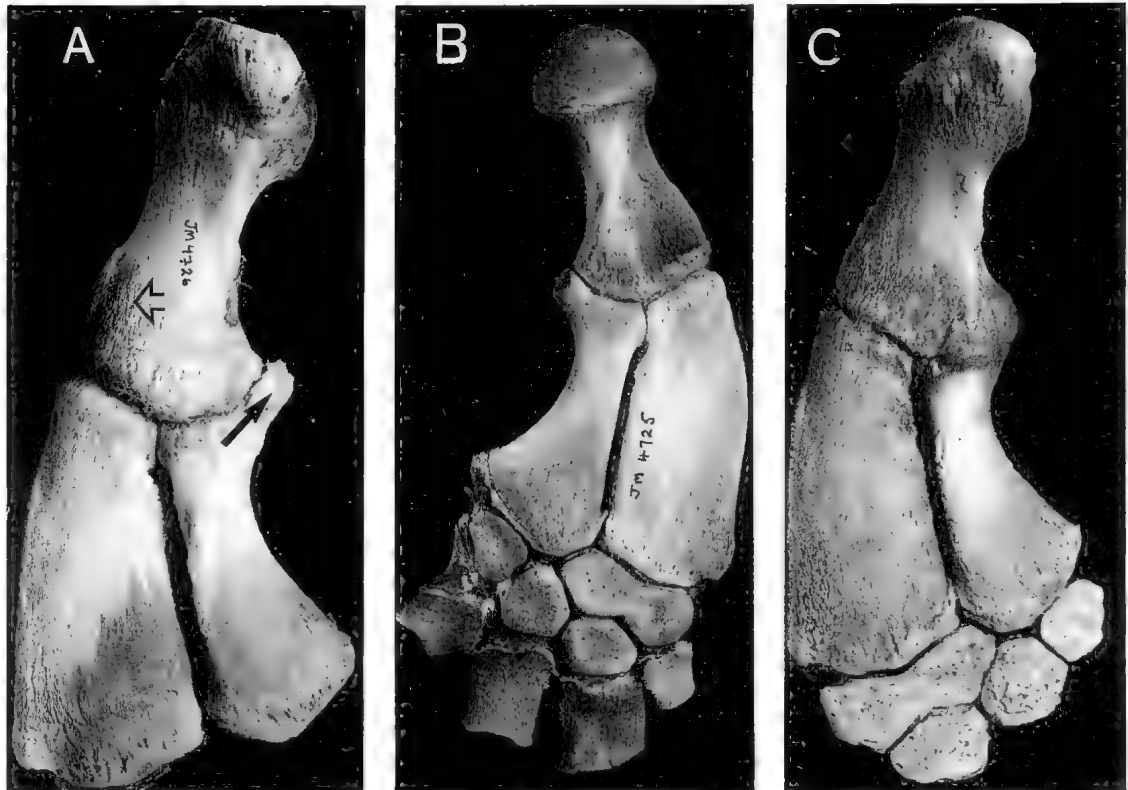
FIG. 48A-C. Variability in development of olecranon process (arrow, in A) in 3 specimens of *Orcaella* from central Queensland. Note the well-developed process in A,B. Also note the elongate deltoid tuberosity of the humerus (open arrow in A).

8. Rostrum length

An elongate rostrum (>60% skull length) was considered primitive, by outgroup analysis. A wide range of fossil odontocetes also have an elongate rostrum. *Neophocaena* has a particularly short rostrum (<40%), while all other genera considered in this study are in the 40-50% range. All are coded 1, however, to reduce the comparisons to binary values. As discussed elsewhere, this feature seems particularly subject to convergences and possible reversals.

9. Atlas and axis separate

The polarity of this character is equivocal by outgroup analysis. *Physeter* has a unique arrangement, where the atlas and axis are separate, but cervicals 2-7 are fused. Extant ziphiids have at least 3 cervicals fused, including the atlas and axis. However, de Muizon (1988) noted that most Mio-Pliocene cetaceans had separate cervicals. This implies that there may have been rever-

sals in some lineages (separate cervicals to partially fused to separate) and thus the character is subject to homoplasy. In the initial analysis, the unfused condition was considered primitive and coded 0 in the analysis. Where only the atlas and axis are fused, the character is coded as 1, while it is 2 for cases when 3 or more cervicals are fused. This extent of fusion of cervical vertebrae has been used (e.g. Nishiwaki, 1963) to define families so it is included as a multistate variable. However, we recognize that the number of fused cervical vertebrae is variable even within a species. Fischer (quoted in Tomilin, 1967) noted that in *Tursiops* there could be fusion of the first two, or the third-fourth and fifth, or even the sixth and seventh cervical vertebrae. Rommel (1990) also noted variability in fusion of the cervicals but attributed at least some of the fusions to pathological conditions. There will also be variability when animals of different ages are compared.

10. Olecranon process

This process on the ulna is considered primitive by outgroup analysis. It is present in ziphiids, although it is less developed in *Berardius* than in *Mesoplodon, Ziphius* and *Hyperoodon* (True, 1910; Tomilin, 1967). It is well-developed in *Physeter*, baleen whales and many fossil taxa. The loss of the olecranon (e.g. in *Delphinapterus, Monodon*: Tomilin, 1967) must then be considered a derived feature. However, the olecranon process appears variable even among the delphinids and phocoenids; this may be another feature subject to reversals, i.e homoplasy.

de Muizon (1988) considered that *Orcaella* lacks an olecranon process, as in monodontids. Our more extensive series of specimens shows that although the process may be obscure (Fig. 48C), it is generally well-developed (Fig. 48A,B). This is not simply an age dependent feature, as specimens with an olecranon process had 9 and 17 dentinal layers in the teeth.

11. Convex facial profile

This is a specialized feature of extant monodontids and some phocoenids (Perrin, pers. comm.). It is considered a derived feature, as by de Muizon(1988), Heyning (1989) and Barnes (1990). de Muizon (1988) and Marsh et al. (1989) noted that *Orcaella* has a concave supracranial profile, as in delphinids, but unlike monodontids. This argument is weakened by lack of a convex facial profile in the fossil monodontid *Denebola brachycephala* Barnes,1984 and juvenile *Monodon*(Eales, 1950; pers. obs. UBC9467). The latter point is relevant, given the retention of numerous juvenile characters in the skull of *Orcaella*.

12. Premaxillary boss

This is generally recognized (e.g. Rice, 1984; Heyning, 1989) as a specialized feature of phocoenids and is so coded.

13. Bony lateral lamina of pterygoid

This is equivocal by outgroup analysis as the Physeterida (Ziphiidae and Physeridae) shows a reduction in the lateral lamina overall. The bony lamina of the pterygoid is present in *Platanista*. Consideration of fossil cetaceans demonstrates a reduction from a bony lamina as the primitive condition to an increasing development of a membranous lamina (Oelschlager, 1990; de Muizon, 1988). More particularly, the bony lamina is found in fossil platanistoids and in the Eurhinodelphoidea (de Muizon, 1988), a possible sister group to the Delphinida. It is coded, with

0 where the bony lamina is well developed and 1 where it is reduced (in *Phocoena,* fide Fraser & Purves (1962) but not confirmed in the small series of *Phocoena* we examined) or absent. This feature may be particularly variable within the phocoenids (Perrin pers. comm.).

14. Pneumatised maxillary crest

This is a specialized feature of *Platanista* and fossil relatives (Heyning,1989; de Muizon,1990).

15. Palatines covered by pterygoids

This is a specialized feature of *Platanista* (Heyning, 1989). It is a special case of the more general trend for separation of the lateral and medial lobes of the palatine by the pterygoid, also seen to a lesser extent in some individuals of *Berardius* and *Kogia* (de Muizon, in press), as well as *Orcaella, Globicephala* and juveniles of other genera, e.g. *Feresa.*

16. Acquisition of lateral lamina of palatine

This character, used to define the Delphinida by de Muizon(1988), is a specialized feature associated with excavation of the palatine by the pterygoids.

17. Nasopharyngeal sac

This is a specialized feature of *Platanista*. No analagous structure has been documented in other odontocetes, although Anderson (1879) noted what he thought was a rudiment of this structure in a foetal *Orcaella*.

18. Pterygoid sinus undivided

Fraser & Purves (1962) illustrated the cranial sinuses in a variety of odontocetes and used the variations in its development as a basis for classification of cetaceans. The undivided sinus was considered a feature of physeterids and ziphiids (including *Berardius*, although that genus was not included in their summary fig. 22) and *Platanista*. This is the primitive condition by outgroup analysis.

Fraser & Purves (1962), de Muizon (1988) and Heyning (1989) noted the undivided pterygoid sinus in *Delphinapterus* and *Monodon*. This condition is even more primitive than that in river dolphins *Inia* and *Pontoporia*, in which there are distinct pre- and post-orbital lobes (Heyning, 1989). It was the basis for placing the monodontids in their own superfamily Monodontoidea (Fraser & Purves, 1962) and presents difficulties in interpretation (de Muizon, 1988; Heyning, 1989). The latter author, while retaining the

monodontids in the superfamily Delphinoidea, commented 'I am perplexed as to how such a primitive air sinus system could have evolved within the Monodontidae'. de Muizon (1990), who considered both fossil and extant taxa, noted that if the condition in monodontids was considered primitive, then reversals would have to be invoked in the Eurhinodelphoids, *Lipotes, Pontoporia, Inia* and the delphinoids. As with all previous authors, we have had access only to skeletal material, and have inferred the air sinus distribution from this. Although the lateral lamina of the pterygoid makes a particularly convincing boundary in *Monodon* (pers. obs.; see also Pilleri et al., 1982, figs 2b, 3), the extent of the lateral lamina in *Delphinapterus* is more variable. *Pseudorca* shows comparable variation in the development of the bony lateral lamina of the palatine. Purves & Pilleri (1978, fig. 18) illustrated considerable variation in the cranial sinuses of *Pseudorca*, apparently associated with the variation in the bony lateral lamina so there may be comparable variation in *Delphinapterus*. In addition, dissections of specimens have not always confirmed the pattern of sinuses inferred by Fraser & Purves (1962) from the skull, e.g. re-examination of *Inia* and *Pontoporia* by Heyning (1989) resulted in different interpretations of the anterior sinus. It is thus highly desirable that the condition of the cranial sinuses in both *Delphinapterus* and *Monodon* be re-examined by dissection of fresh material. In the absence of such information, we accept the undivided condition of the pterygoids in monodontids as suggested by previous workers and supported by our examination of skulls.

19. Coalescence of pre- and post-orbital lobes of pterygoid sinus to surround optic nerve

Fraser & Purves (1962) documented this as a feature of the delphinids such as *Tursiops, Grampus, Stenella,* and *Delphinus.* Based on their work, deMuizon (1988) used the coalescence of the sinuses as the basis for the subfamily Delphininae, within Delphinidae. This is a specialized feature. Coding is - for those genera which have undivided sinus , 0 for well-separated pre- and post-orbital lobes and 1 for coalescence.

20. Dorsal extension of pre-orbital lobe of pterygoid sinus.

This is a specialized feature of the phocoenids (Fraser & Purves, 1962; Heyning, 1989), but is not shown uniformly throughout the family (Perrin, pers. comm.). There is an incipient extension

of this lobe in *Orcaella* (pers. obs.), as already noted by Fraser & Purves (1962) but this is coded as absent in the present analysis, as delphinids such as *Pseudorca* show a similar but less advanced condition. Codes are - for undivided sinus, 0 for limited extension and 1 for well-developed extension of the lobe.

21. Anterior sinus

This is equivocal by outgroup analysis, as the cranial sinus is undivided in ziphiids and physeterids. *Monodon* and *Delphinapterus* would also be coded - as their sinus is undivided. Fraser & Purves (1962) indicated an anterior sinus in *Inia*, based on skull morphology, but Heyning (1989) could not confirm this by dissection. *Inia* is thus coded as 0 (anterior sinus absent) in this analysis. In the absence of contrary information, the configuration indicated by Fraser & Purves (1962) has been accepted. Elongation of the anterior sinus is considered the derived state (Fraser & Purves, 1962).

22. Curvature of flippers

The flippers of mature males of beluga (Vladykov, 1943) and narwhal (Reeves & Tracey, 1980; Martin, 1990) curve upwards at the anterolateral margin. Although this seems a minor character, it is consistent. The deformation of the flipper involves a curvature of the second and third digits (Vladykov, 1943), and may be associated with the relatively larger amount of connective tissue to bone in the flippers of beluga and narwhal than in delphinids. It is a specialized feature of these two genera.

Mature males of both species have a strongly convex posterior edge to the flukes (Vladykov, 1944; Leatherwood & Reeves, 1983); in narwhals the anterior margin may curl forward so that the flukes appear to be 'back to front'. Although there appears to be similar fluke form in the two species, this is not treated as a separate character.

23. Cervical sinus

The indentation of the nape to form a neck-like constriction is a specialized feature, found in *Platanista* (Anderson, 1879), *Inia* (Hoyt, 1984: 68), *Neophocaena* (Hoyt, 1984:75), *Orcaella* and some ziphiids (Perrin pers. comm.).

24. Anterolateral margin of nares formed by maxillaries

This is a specialized feature of extant and fossil monodontids (de Muizon, 1988; Barnes, 1990). de Muizon (1988) pointed out that it is not shared

by *Orcaella,* which has the small maxillary intrusions characteristic of many delphinids.

25. Spatulate teeth

This is a specialized feature of phocoenids (Rice, 1984; Heyning, 1989), but variably developed within the family (Perrin pers. comm.).

26. Length of squamosal

Heyning (1989) considered 2 characters associated with the temporal region: roofing over by the frontal bones and length of the squamosal. The length of the squamosal has generally been considered 'short' or 'long'. Examination of a range of genera (from illustrations in the literature as well as examination of skulls) suggested that they form 3 categories : 0-30%, 30-50% and >50%, which are coded as 0, 1 and 2 respectively. Polarity is equivocal by outgroup analysis: *Physeter* is 1 (Miller, 1923), *Berardius* 0 (Tomilin, 1967) and the river dolphins 2. The character is treated as non-additive so no direction of specialization is implied. Heyning (1989) characterized the zygomatic arch of *Orcaella* as 'extremely reduced', a feature he considered a synapomorphy of the delphinids. However, it is about 35% of the cranial vault length in *Orcaella* (pers. obs.) and 39-42% in *Neophocaena.* This approaches the values for *Monodon* (c. 44%) and is much higher than that for delphinids such as *Tursiops* (21-24%) or *Sousa* (23%). Roofing of the temporal region is discussed later (character 39).

27. Disappearance of superior lamina of pterygoid in orbital region

This is equivocal by outgroup analysis; it was considered an advanced character by Fraser & Purves (1962). This is consistent with the reduction of bony margins to the cranial sinuses as indicated by Oelschlager (1990). de Muizon (1988) noted the strongly developed superior lamina of the pterygoid in Platanistoidea and the Eurhinodelphoidea. The superior lamina is thus considered primitive while its disappearance is treated as the derived condition in this analysis.

28. Orientation of posterior process of periotic

The process is oriented strongly ventrad towards the posterior process of the tympanic or posteriorly, except in delphinids where it is posterolateral to strongly lateral (Kasuya, 1973). The latter is considered specialized (coded 2); ventral orientation (*Platanista*) is coded as 0; posterior orientation as 1.

29. Orientation of posterior process of tympanic

Polarity is equivocal by outgroup analysis; the posterior orientation was considered primitive by Kasuya (1973) and is accepted as such here. We observed the orientation of the process in *Orcaella* to be posterolateral, not posterior as indicated by previous authors (e.g. Kasuya, 1973).

30. Sigmoid process of tympanic bulla

Four forms of the sigmoid process are recognized, based on Kasuya (1973) and Pilleri et al. 1989: square (*Physeter*), flail-shaped (*Berardius*), short (river dolphins) and long & L-shaped (all others). In our analysis, the short sigmoid process of the river dolphins was coded 0 and the L-shaped process 1. No direction of specialization is implied and, in any case, the character reduces to a binary feature in the present analysis.

31. Lateral furrow of tympanic bulla

The polarity of this feature is equivocal by outgroup analysis: it is absent in *Physeter* (and *Kogia*), but present in ziphiids and the river dolphins. It is generally present in fossil odontocetes, including most physeteroids (de Muizon, 1988). It is considered primitive, as by Kasuya (1973).

32. Width of posterior branch, lower tympanic aperture of bulla.

The lower tympanic aperture is not present in physeterids, but is less than 10% standard length of the tympanic bone in *Berardius* and all river dolphins except *Pontoporia.* The branch is over 10% in *Delphinapterus* (Kasuya, 1973, based on very small sample size) and phocoenids. The wide branch is considered a specialization, by outgroup analysis, but this is equivocal (see below). Although boundaries set on continuous variables will always be more or less arbitrary, the value of 10% did appear to be relatively well defined. It also is consistent with use by Kasuya (1973), whose study on tympanoperiotic bones has been very influential. Coding is 0 for < 10% and 1 for >10% standard length of tympanic.

A lateral shift of the posterior process will compress to some extent the posterior branch of the lower tympanic aperture. Thus there may be a purely structural reason for the fact that taxa like phocoenids and beluga, with a posteriorly directed posterior process, have a wide aperture while the delphinids, with postero-lateral to lateral process of the tympanic, have a narrower aperture. Thus this character may not be independent of character 29, and it could be argued that the primitive condition was a wide aperture,

associated with a posteriorly directed process (considered the primitive condition, see character 29).

In *Orcaella* the LTA width is <10% (see section on Tympanoperiotic bones).

33. Compression of bulla

Compression of the bulla (width 50% or less of standard length of tympanic bulla) occurs in *Platanista, Monodon* and *Globicephala*. Lack of compression is considered primitive by outgroup analysis.

34. Sutural connection of tympanoperiotic to skull

Heyning's (1989) interpretation is accepted here. There is a sutural connection in ziphiids and physeterids. This is considered primitive. *Platanista* shows an intermediate condition, with partial fusion to the skull, while all others considered show no sutural connection to the skull. This feature may be subject to some variation within species. Kleinenberg et al. (1964) and Kasuya (1973) reported that the periotic was sutured to the skull in *Delphinapterus*, but neither Heyning (1989) nor we found this to be the case on belugas we examined (see discussion of tympanoperiotic bones for further details).

35. Retraction of premaxillaries from nasals

The anterior retraction of the premaxillaries is a specialized feature of phocoenids (de Muizon, 1988; Heyning, 1989; Barnes, 1990). The river dolphins supposedly show a gradation of lateral retraction of the premaxillaries, but this is not coded here because it is difficult to quantify and appears to overlap with retraction in some delphinids. The general condition in which the left premaxilla is retracted away, while the right premaxilla maintains close contact with the nasals, is considered a feature of the delphinids, as by previous authors (e.g. de Muizon, 1988; Heyning, 1989; Barnes, 1990), but it is variable.

36. position of attachment of tympanoperiotic to skull

In *Delphinapterus, Monodon* and *Orcaella*, the dorsal surface of the posterior processes of periotic and tympanic bones are involved in the connection to the mastoid portion of the squamosal. In the phocoenids, which also have a large mastoid portion of the zygomatic arch, and the delphinids, where the mastoid portion is compressed by the exoccipitals, the processes of the tympanoperiotic join in a cavity formed by the basioccipital, exoccipital and squamosal, more dorsally placed than in the three genera just mentioned. The attachment seems to be a distinctly different form in ziphiids and physeterids, however the more ventral attachment is similar to the situation in *Platanista*. The type of attachment in *Delphinapterus, Monodon* and *Orcaella* is thus considered primitive.

37. Profile of tympanic bulla

de Muizon (1988) and Pilleri et al., (1989) indicate that the bulla in outer lateral view may have a convex or concave profile. The former characterizes Physeteridae, Ziphiidae and all the river dolphins; it is thus primitive by outgroup analysis. Monodontids, phocoenids and delphinids have a concave profile.

38. Shape of anterior process of periotic

de Muizon (1988) listed a square, almost rectangular, profile of the anterior process as a character of the Delphinoidea (Monodontidae, Phocoenidae, Delphinidae) and said that it was a consistently recognizable character. Kasuya (1973), however, was less clear in this separation. He noted that the process was curved and rod-like in *Physeter* and *Platanista*, pyramidal in ziphiids (although elongate in *Berardius*), and flat & rectangular in *Inia, Pontoporia, Delphinapterus* and *Monodon*, phocoenids and delphinids. Kasuya's scheme is used here. There may be some variation, however, in the form of the anterior process in *Monodon*: UBC9467 has an elongate, curved process.

39. Roofing of temporal fossa

The outgroup analysis is equivocal in defining polarity. In *Physeter* and *Berardius* it is roofed over, but in some fossil physeterids (e.g. *Diaphorocetus*: Kellogg, 1928) and various fossil taxa (Agorophiidae, Squalodontidae) as well as *Kogia* (Perrin pers. comm.) and the river dolphins it is open, exposing the wide zygomatic arches. Following Heyning (1989), this is considered the primitive state, with roofing of the temporal region derived. It should be noted that the reason for considering the feature primitive is not because it occurs in a fossil species, but because it is present in at least some representatives of the outgroup, which just happen to be fossil species.

CHARACTERS NOT CONSIDERED

Heyning (1989) included a number of characters specific to ziphiids (e.g. throat grooves,

elevated vertex) or physeterids (e.g. spermaceti organ, distal sac, lack of one nasal bone). Since the inter-relationships of the Physeteridae and Ziphiidae are not under examination, and these characters are irrelevant to the Delphinida (*sensu* de Muizon, 1988), they have not been included. Additional characters not considered are listed below.

1. Bicipital ribs

Slijper (1936, 1962) considered an elevated number of bicipital ribs as a primitive condition. He envisioned that reduction of bicipital ribs was linked to a need for flexibility of the thorax in a diving mammal (Slijper, 1962). This argument is weakened by the finding of Rommel(1990) that the elastic ligaments allowed significant flexure of the bicipital ribs in *Tursiops*. The number of bicipital ribs (7-8/12-13 ribs) in *Orcaella* (see Appendix 4) is higher than in most delphinids, comparable to *Delphinapterus* (8/11-12: Slijper, 1936) but lower than in phocoenids (11/13-14 in *Neophocaena*; 10/12-14 in *Phocoena*: Nishiwaki, 1963). Insufficient information was available to use this character.

2. Lip on nasal plug

Schenkkan (1973) illustrated the increasing development of a lateral lip on the plug from *Kogia, Pontoporia*, ziphiids through to *Phocoena* and delphinids. Insufficient information was available for other genera to use this character. Similarly, there was insufficient information to assess any patterns in the extension of the melon into the right or left nasal plug.

3. Proportion of premaxillary sac to vestibular sac

Schenkkan (1973) documented a gradation from large vestibular sacs in *Pontoporia, Inia* and *Phocoena* to small sacs in *Delphinus* and *Stenella*. Conversely, the premaxillary sacs assumed greater relative importance from the river dolphins to *Delphinus* and *Stenella*. We could not calculate values for monodontids or some of the delphinids not considered by Schenkkan, so have not included the character.

4. Coat of cement on tooth

Lonnberg (1910) contrasted the teeth of *Delphinapterus* with those of *Phocoena, Steno, Globicephala* and *Delphinus*. The former differed from the porpoise and dolphins examined in the strong development of a cement coat, constituting the bulk of the tooth. As pointed out by Lonnberg, a similar tooth structure occurs in *Physeter*, suggesting that this may be the primitive condition. It is not associated with the size of the teeth; *Orcinus* has a typical delphinid tooth.

The cement coat on teeth of *Kogia* may be extensive, building up to form a convex profile to the tooth in old animals of both species in the genus (Ross pers. comm.). Among ziphiids, the situation is more variable: in *Hyperoodon* and *Ziphius* most of the tooth is cement, but dentine predominates in teeth of *Berardius* (Ross pers. comm.). *Platanista* has a substantial cement component in the teeth, but Kasuya (1972) noted that it is distinct from the pattern in *Physeter*. A cement coat extends the entire length of the erupted tusk in *Monodon* (Reeves & Tracey, 1980) but it is unclear if it is as well developed as in *Delphinapterus* or *Physeter*. There were insufficient data to establish polarity of the character, either by outgroup analysis or other arguments. A similar situation exists for accessory cusps, which occur in juvenile *Delphinapterus* (Stewart & Stewart, 1989) and are sporadic in other odontocetes.

5. Phalangeal formula and flipper shape

de Muizon (1988) noted that there is a greater number of phalanges in digits 2 and 3, relative to the other digits in delphinids, whereas there is greater uniformity in monodontids. However, a comparison of phalangeal formula for *Delphinapterus, Monodon* and various dolphins suggest there is considerable overlap. In particular, the formula is similar in *Orcinus* (I:2; II:6-7; III:4-5; IV: 3-4; V: 2-3: Nishiwaki, 1963)to the monodontids (*Monodon*: I:1-2; II: 5-8; III: 4-6; IV:2-4; V: 2-3; *Delphinapterus*: I:1-2; II: 6-9; III: 4-5; IV:2-4; V: 2-4: Nishiwaki, 1963). Eales (1953) noted that phalangeal number decreases with age in the narwhal and beluga; the curvature of the flipper in adult males may be related to this fact. However, it can not be used as a character for the monodontids, as this reduction was also found in *Phocoena* (Eales, 1953). The flipper does tend to be more squared-off in *Physeter*, ziphiids, platanistids and monodontids, than it is in phocoenids and delphinids, but there is variation in form among the latter (e.g. *Orcinus*, a delphinid, has broad paddle-shaped flippers especially developed in the male).

6. Position of delto-pectoral tuberosity

de Muizon(1988) considered the distal position of this tuberosity a feature of delphinids and phocoenids. He further indicated that the tuberosity was subdistal in *Orcaella*, linking it more with the monodontids. On our specimens (Fig. 48 A,B,C), the tuberosity was elongate and, while not distal, it was not as clearly subdistal as figured for *Delphinapterus* and *Monodon* by de Muizon (1988, fig. 22).

TABLE 6. External morphometrics for 22 specimens of *Orcaella brevirostris* from central Queenland. Numbers in the left hand column refer to the following measurements. Values for 2-17 are percentages of total length. 1. Total length (m); 2. Tip of upper jaw to eye; 3. Tip of upper jaw to gape; 4. Tip of upper jaw to ear (auditory meatus); 5. Length eye to ear; 6. Tip of upper jaw to anterior base flipper; 7. Tip of upper jaw to blowhole; 8. Tip of upper jaw to tip of dorsal fin; 9. Tip of upper jaw to umbilicus; 10. Tip of upper jaw to genital aperture (centre); 11. Tip of upper jaw to anus; 12. Length of anterior margin flipper; 13. Length flipper from tip to axilla; 14. Maximum width flipper; 15. Height dorsal fin; 16. Length of dorsal fin base; 17. Width of tail flukes.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1	0.91	1.05	1.34	1.86	1.87	2.11	2.12	2.12	2.12	2.14	2.15	2.15	2.15	2.17	2.19
2	11.54	11.40	9.20	6.70	9.63	7.10	-	6.10	6.10	6.80	7.90	7.00	7.40	5.50	7.30
3	9.34	10.70	7.60	5.60	8.60	6.60	-	4.70	4.30	5.60	7.44	5.60	5.60	4.60	5.00
4	15.71	-	13.30	10.40	-	-	-	7.80	12.30	-	12.10	10.00	11.20	8.80	11.40
5	5.05	-	4.30	-	-	-	-	3.10	6.10	-	3.30	3.49	4.00	3.20	4.10
6	24.73	22.90	23.20	19.60	23.00	17.50	-	18.90	17.90	20.10	19.50	18.60	18.60	16.10	18.30
7	9.78	11.90	11.50	6.10	10.16	7.60	-	3.77	5.70	5.15	6.50	6.50	11.20	8.30	11.40
8	57.14	60.00	58.20	57.50	62.60	-	-	55.20	59.40	54.80	57.00	54.90	58.10	57.60	63.00
9	47.80	48.60	44.50	-	44.90	-	-	-	-	44.50	44.20	42.30	44.70	42.40	-
10	63.19	55.20	60.70	60.50	60.40	-	-	56.60	52.40	-	61.60	54.90	54.40	63.60	54.34
11	65.60	66.70	64.40	64.20	64.20	-	-	66.50	60.80	66.50	66.50	66.50	64.20	67.70	64.80
12	20.33	20.00	17.40	16.40	17.10	17.10	15.10	17.90	15.60	15.90	16.70	18.80	19.80	16.60	16.00
13	18.13	15.90	13.60	12.60	13.90	13.70	12.30	14.40	13.70	15.40	14.90	16.70	16.30	15.20	14.20
14	7.69	7.90	5.80	6.60	6.40	5.90	-	6.80	5.90	7.00	7.20	7.00	7.40	7.40	6.80
15	3.85	5.20	3.70	4.00	4.30	-	-	-	3.80	4.70	4.40	5.10	5.10	5.30	4.60
16	7.69	-	10.10	7.50	9.60	13.30	-	7.60	5.40	9.80	10.20	7.90	7.40	8.10	9.10
17	18.68	27.10	21.40	29.00	25.10	23.70	-	31.60	26.40	33.20	30.20	32.30	30.70	24.90	35.60

7. Impression of 'duplicated apex of nasofrontal sac' on skull

de Muizon (1988) documented fosetta or shallow depressions on the anterior face of the brain case above the nares in phocoenids and monodontids. He considered these the impressions of a duplicated apex of the nasofrontal sacs (apparently the same as the 'posterior nasal sac' of Heyning, 1989). We noticed similar fosetta in *Orcaella* but there was no indication of a posterior nasal sac in our dissections of *Orcaella* (see Facial Anatomy). We therefore reject the occurrence of such fosetta as evidence for a posterior nasal sac.

8. Development of mesethmoid plate and elevation of nasals

de Muizon (1988) and Barnes (1990) linked these two characters, which they considered diagnostic of delphinids. *Orcaella* examined herein have a poorly developed mesethmoid plate, which does not impinge on the reduced nasals. However, the nasals are still elevated on the vertex, suggesting that the characters are not linked. Elevation of the nasals may be a more consistent character for the delphinids, although there are similarities in the position of the nasals in *Monodon, Delphinapterus* and the delphinid

Pseudorca. These characters are supporting features of the delphinids but are not incorporated in the analysis, because of their variability (even between populations of *Orcaella* in the case of the development of mesethmoid plate).

9. Compression of vertebral centra

de Muizon (1988) suggested that delphinids showed a tendency for compression of the vertebral centra. This is linked to higher numbers of vertebrae, and possibly a greater flexibility of the spinal column. Low numbers of vertebrae (under 60) does appear to be a primitive character (see Table in Watson, 1985), but quite unrelated species show elevated numbers of vertebrae (e.g. *Phocoenoides* among phocoenids, *Lissodelphis* and some *Lagenorhynchus* in delphinids). Due to this variability, the feature was not included.

Similarly, de Muizon (1988) suggested that the Phocoenidae and Delphinidae have more elongated transverse processes of the lumbar vertebrae, contrasted with more triangular processes in other Delphinida, such as river dolphins (except *Platanista*) and *Delphinapterus*. However, there again seems to be much variation in delphinids. The transverse processes of a North Atlantic *Globicephala melas* are intermediate between those of *Delphinapterus* and delphinids

TABLE 6 (continued)

	16	17	18	19	20	21	22
1	2.19	2.20	2.22	2.25	2.25	2.26	2.35
2	-	6.40	5.90	8.40	6.20	9.10	6.80
3	-	5.20	4.50	5.80	5.30	7.10	5.10
4	-	12.00	-	10.70	12.00	4.90	10.60
5	-	7.30	-	4.00	-	3.50	3.80
6	19.20	18.20	18.50	19.60	17.30	19.90	19.20
7	-	5.50	5.40	7.10	7.60	11.10	11.50
8	58.50	56.80	56.80	56.00	56.40	53.10	56.60
9	-	42.70	-	-	44.90	36.70	42.60
10	61.60	54.50	-	-	63.10	51.30	53.20
11	64.40	65.20	66.20	-	65.80	54.00	64.70
12	-	19.10	16.70	16.90	17.80	17.30	15.70
13	-	16.10	14.00	16.40	16.00	12.80	14.00
14	-	7.50	5.80	7.10	6.70	6.60	6.20
15	-	4.80	3.60	4.40	4.00	4.40	3.40
16	-	8.20	6.30	8.90	7.10	8.40	7.70
17	28.80	34.00	26.10	29.80	-	24.80	26.00

such as *Lagenorhynchus acutus* with elongate processes (pers. obs.).

10. Palatine bridge under optic channel

de Muizon (1988) considered this a feature of the monodontids; we observed it in beluga and, even more strikingly so, in narwhal but have not used it as a character because posterior development of a palatine wing is not restricted to monodontids. It is equally developed in the delphinid *Pseudorca*, where the lateral boundary is formed exclusively of palatine bone which extends almost to the squamosal. The posterior extension of the palatine, in combination with the more anterior position of the orbit in monodontids, is the basis for the obvious bridge underlying the optic channel in *Delphinapterus* and *Monodon*. It is particularly striking in the latter because of the strong depression of the skull in that genus;this ensures that the palatine wing is closely appressed to the optic channel. *Orcaella* represents the opposite extreme where the posterior extension of the palatine extends outward, well away from the basicranial bones, as a free wing-like structure.

Since we consider the palatine bridge to be associated with the more anterior position of the orbits (character 4), we do not include the palatine bridge as a separate character.

11.   Immunological and electrophoretic distance

Lint et al. (1990) demonstrated a close relationship of *Monodon* with *Delphinapterus*, based on immunological distance; *Orcaella* was well separated from these genera and grouped with the delphinids, *Orcinus* and *Lagenorhynchus. Inia* was closer to the monodontids than delphinids, but was not closely linked to either. These relationships were supported by electrophoretic data, and combined with the latter to give a phylogeny of odontocetes (Lint et al., 1990: fig. 2d) in which delphinids were widely separated from phocoenids. These data have been discussed elsewhere, but were not used in our analysis because there were insufficient data for all species.

12. Base pair length of repetitive DNA

Gretarsdottir & Arnason (1992) compared the base pair lengths of highly repetitive DNA in a variety of odontocetes. Representatives of most families examined, including beluga and narwhal, had a primitive base pair length of about 1750 bp. The delphinids, however, had a bp length of about 1580, while *Orcaella* had a base pair length of 1583.

These data support *Orcaella* being a delphinid, but could not be incorporated in the analysis because comparable data were not available for other species; most importantly there were no data for any of the river dolphins.

13. Isovaleric acid and acoustic fat

Litchfield et al. (1975) compared odontocetes for distribution of lipids in both acoustic (melon and mandible fatty bodies) and non-acoustic (e.g. blubber) tissues. They separated two groups: ziphiids, physeterids and 'Platanistidae' (*Platanista,Inia*) without isovaleric acid in the acoustic tissue, and the Monodontidae, Phocoenidae and Delphinidae with isovaleric acid. They further subdivided the latter group, with delphinids having over 3% of the lipids as waxy esters, while the monodontids and phocoenids had exclusively triglycerides.

Morris (1985) argued that isovaleric acid can not be considered a by- or waste product of standard physiological processes but represents a specialization, produced at considerable physiological cost. Presence of isovaleric acid has been linked to development of the melon, and the function of fat in the melon as an acoustic lens. As pointed out by Litchfield et al (1975), some other mechanism must be used by the river dol-

TABLE 7. External morphometrics for 11 specimens of *Orcaella* from SE Asia. Numbers in the extreme left hand column are measurements, as in Table 6. Specimen numbers 1, 3, 5, 7 & 10 are from Anderson (1879); 2, 6, & 9 from Tas'an et al., 1980; 4, 8 & 11 from Pilleri & Gihr, 1973-1974.

	1	2	3	4	5	6	7	8	9	10	11
1	0.86	1.53	1.80	1.93	2.10	2.11	2.19	2.20	2.20	2.29	2.75
2	-	9.80	-	8.80	-	8.53	-	-	-	-	-
3	6.70	-	8.00	-	7.3	-	5.88	-	-	6.40	-
4	-	14.70	-	-	-	13.30	-	-	-	8.90[9]	-
5	-	2.00	-	-	-	3.30	3.50	-	-	4.20	-
6	23.00	26.80	22.20	21.20	20.00	19.90	-	23.9[8]	-	20.80	38.20[8]
7	-	9.80	12.80	9.80	12.10	9.50	-	-	10.90	11.10	-
8	53.30[1]	54.90	59.20[2]	56.00	55.80[2]	49.30	56.90[4]	57.40[8]	60.40	61.90[2]	66.50[8]
9	49.60	65.40	-	-	-	55.00	-	-	-	-	-
10	62.90	68.60	-	-	-	62.60	-	-	-	58.60	-
11	-	71.90	-	-	-	-	73.20[5]	67.60[8]	-	-	74.50[8]
12	23.70	19.00	22.20	14.50[3]	20.60	11.80	17.40[6]	17.50[3]	-	18.90	15.00[3]
13	-	-	16.20	-	14.50	-	-	-	-	13.00	-
14	-	5.20	8.10	6.20	7.60	9.50	7.03	-	-	-	-
15	-	2.90	3.20	2.30	4.50	2.40	2.40[7]	2.90	3.20	7.0310	2.50
16	-	13.10	7.04	5.70	9.69	10.40	10.40	6.60	-	5.30	6.60
17	-	26.10	28.20	25.40	26.10	30.80	27.90	27.30	29.50	-	23.90

Notes:- 1. to anterior of base; 2. curved along back; 3. unspecified flipper length; 4. to middle of fin; 5. calculated by subtraction of published values; 6. in centre of flipper; 7. 'depth through center'; 8. indirectly calculated; 9. to anterior of eye; 10. 'anterior of base to posterior of tip'.

phins, but distribution of isovaleric acid suggests that it is a derived feature of the more specialized delphinoids. It was not used in the analysis because of missing values for a number of species.

14. Pseudaliid nematode parasites

At least 28 nominal species of pseudaliid nematodes have been reported from the cranial sinuses and respiratory tract of odontocetes and they are perhaps the most promising group of parasites to use in assessing inter-relationships of the hosts.

Except for *Delamurella* Gubanov, 1952 in *Berardius* from the northwest Pacific, pseudaliids are restricted to the Delphinida sensu deMuizon (1988). This record is apparently based on a single report; more information is necessary to evaluate the relationship of *Delamurella* to other pseudaliids.

The phocoenids have the widest range of pseudaliid parasites: *P. phocoena* has 5 species, *Phocoenoides dalli* 6 and *Neophocaena phocaenoides* 5 nominal species, with limited overlap of parasites between host species. *Pseudalius* is apparently restricted to phocoenids (but see anomalous records below). Arnold & Gaskin (1975) maintained *Torynurus* Baylis & Daubney, 1925 distinct from *Pharurus*; at that

time the genera were known from phocoenids (*Phocoena, Phocoenoides*) and monodontids respectively. Descriptions of additional species from *Neophocaena* and *Phocoenoides* (Petter & Pilleri,1982; Kuramochi et al.,1990) have blurred distinctions between these genera. The diagnostic characters of *Pharurus, Torynurus, Stenurus* and *Pseudostenurus* need to be re-evaluated; study of new material of *Pseudostenurus* from *Neophocaena* is crucial to such a review. The species of *Halocercus* in *Phocoenoides* and *Neophocaena* also need review.

If the restricted definition of *Pharurus* as proposed by Arnold & Gaskin (1975) is confirmed, then this genus is restricted to monodontids (*P. pallasi* in *Delphinapterus, P. alatus* in *Monodon*). The other genera reported from monodontids (*Stenurus, Halocercus*) have also been reported in phocoenids and delphinids.

Identifications of pseudaliids in delphinids are often incomplete and poorly documented. *Delphinus delphis* has the largest number (4) of pseudaliid species reported from any delphinid host, all in *Halocercus* or *Skrjabinalius*; some of these species require confirmation. *Halocercus* and *Skrjabinalius* have the widest reported distributions within the Delphinidae, having been

reported from *Delphinus, Stenella, Tursiops, Lagenorhynchus, Sotalia, Sousa, Peponocephala* and *Cephalorhynchus. Skrjabinalius* is known only in the Delphinidae. Distinctions between the species of *Halocercus* in particular are often poorly documented and many records need confirmation. *Stenurus ovatus* has been recorded in *Tursiops* and *Lagenodelphis*, while *S. globicephalae* has been reported from *Globicephala melas, G. macrorhynchus, Lagenorhynchus acutus, Grampus griseus, Peponocephala electra* and *Feresa attenuata*. Unidentified species of *Stenurus* have been reported from *Cephalorhynchus hectori* and *Lissodelphis peronii*. No pseudaliids have been reported from *Orcinus* or *Orcaella*, nor have we found any pseudaliids in the *Orcaella* we necropsied.

Analysis at species level is complicated by the probability of misidentifications in the literature, as noted above. For instance, *Stenurus minor* has been reported from *Delphinapterus leucas, Phocoena phocoena, Phocoenoides dalli* and *Grampus griseus*. The last record is based on a single report by von Linstow (1910). This predates the description of *Stenurus globicephalae*, which is well-known from various blunt-headed genera, including *G. griseus* (Arnold & Gaskin, 1975; paragraph above). Additional questionable or anomalous records include *T. convolutus* and *Pseudalius inflexus* in *Lagenorhynchus acutus* and *Pseudostenurus auditivus* in *Pseudorca*.

Until necessary revision is done on pseudaliids and questionable records evaluated, the distribution of pseudaliid parasites in odontocetes offers little help in assessing inter-relationships of the hosts.

APPENDIX 3:
EXTERNAL MORPHOMETRICS

RESULTS

General features correspond well with descriptions of *Orcaella brevirostris* from Anderson (1879), Lloze (1982) and Marsh et al. (1989).

Among 37 animals from central Queensland, the longest ♂ is 2.70m , the next longest being 2.35m. The longest ♀ is 2.30m; two animals of unknown sex are 2.35 and 2.49m long.

Body proportions are available for a smaller sample (19 animals 1.86-2.35m and 3 animals 0.91-1.34m long). These are compared with measurements in the literature (Tables 6 & 7).

There are anomalous values for animal 21 (Table 6); the measurements are not used in the calculation of the descriptive statistics.

Dimensions of the head (e.g. rostrum to eye, rostrum to flipper, rostrum to gape, rostrum to auditory meatus) are larger in the small animals (0.91-1.34m total length). The only clear sexual dimorphism is in the more posterior position of the genital aperture in ♀♀ (61.6-63.6% total length, plus one anomalous value of 54.9%) than in males (52.4-56.6%). Even with the anomalous value included, the difference is statistically significant (5%, Mann-Whitney U test). There was almost total overlap between sexes for all other characters.

There is considerable variability in the measurement of the dorsal fin base, which is difficult to clearly define. The wide variation in fluke widths may reflect post-mortem shrinkage in some of the stranded animals, as well as errors introduced by calculating total width by extrapolating from one undamaged fluke.

DISCUSSION

Our data and other records (e.g. Pilleri & Gihr, 1973-1974) suggest that ♂♂ grow larger than ♀♀, but the numbers of animals examined is small. More material is necessary to confirm the possible sexual dimorphism in body length.

Morphometrics for 11 SE Asian specimens were collated from the literature (Table 7). For our comparisons, we do not separate *O. 'fluminalis'* and *O. brevirostris*. Smaller animals (0.91-1.34m long) are considered separately.

Animals from Indonesia measured by Tas'an et al. (1980) had much higher values for the measurement 'tip of upper jaw to the umbilicus' than all animals from Queensland. This feature was not routinely measured by other authors, however Lloze (MS) noted that in two specimens 1.9 and 2.0m long from the Mekong, the umbilicus occurs '5-6cm in front of the midlength of the body'. This gives a figure of approximately 47% total length, which is consistent with the Queensland sample. Thus the values reported for Indonesian animals do not necessarily indicate variation between Queensland and SE Asian animals.

Some measurements appear to be taken in different ways. The distance between upper jaw and blowhole will vary according to whether it is taken in a direct line (using calipers) or curved over the body. The measurement of the dorsal fin base also seems to be subject to wide variation. Published values for flipper length (Table 7) were measured along the anterior margin, through the

TABLE 8. Length-weight data for *Orcaella brevirostris*, combining original data from Queensland with literature records. The record from Anderson, 1879 was a near term foetus from India. The records from Tas'an et al., 1980 were consecutive weighings of a captive Indonesian animal. Records of Lloze were from the Mekong River. *= the animal was weighed in pieces, so weight is underestimated.

LENGTH (m)	WEIGHT (kg)	SOURCE
0.86	10.4	Anderson, 1879
0.91	9.9	original
0.96	12.3	Tas'an et al., 1980
1.26	30	Tas'an et al., 1980
1.34	30.9	original
1.53	45	Tas'an et al., 1980
1.90	80	Lloze in Marsh et al., 1989
2.00	87	Lloze in Marsh et al., 1989
2.14	114	*original
2.15	127.9	*original
2.17	190	Marsh et al., 1989
2.25	132.9	*original

centre of the flipper or at an unspecified location. In spite of these inconsistencies, there is general agreement in proportions of animals over 1.86 m long, although the 2.75m male from Thailand (Bonhote in Pilleri & Gihr, 1973-1974) had anomalously high values for rostrum to flipper and rostrum to dorsal fin, as well as a low value for fluke width. Height of the dorsal fin is consistently higher (4.4% (3.4-5.3%), n=18) in Queensland animals, compared with the SE Asian animals (2.9% (2.3-4.5%), n=9); this is highly significant (p =0.002%, Mann-Whitney U test). The 'height' of the dorsal fin in a 2.29 m ♂ (Anderson,1879) was 7.03% (Table 7), however the measurement was taken from the anterior of the base of the fin to the posterior tip of the fin. This implies that it was an oblique measurement, not comparable to the standard height, and the value is not included for comparison. The dorsal fin of Qld animals appears higher, with a more convex anterior margin and shorter base than animals from Kalimantan held at Jaya Ancol Oceanarium (based on photos taken by Dr A. Preen). The posterior margin of the fin of Qld animals is also much straighter (Fig. 3) than the distinctly emarginate border illustrated by Anderson (1879, pl. 25, fig. 4), and is closer to the 2.2 m ♂ *O. 'fluminalis'* illustrated by that author (pl. 25a, fig. 1). In Qld specimens the tip of the fin is usually acute, however it could be rounded as in some SE Asian animals (e.g. Lloze, 1982, Fig. 1).

General accounts (e.g. Morzer-Bruyns, 1971; Sylvestre, 1993) of the Irrawaddy Dolphin give the average weight as 100 kg; Martin (1990) noted that 'typically' weight was 90-150kg. There appear to be very few published values of weights (Table 8). The weights of three animals from Qld between 2.14-2.25m long varied between 114-133kg.

These are underestimates as the animals were weighed in pieces, with loss of body fluids and blood. Another animal 2.17 m long, also weighed in pieces, was reported to weigh 190 kg (Marsh et al., 1989). This value was confirmed from the original data sheets, but in light of other measurements, appears to be too high. More data are needed to provide an accurate length-weight relationship.

APPENDIX 4: POST-CRANIAL SKELETON
AXIAL SKELETON

The vertebral formula for 6 central Qld specimens is C7, T12-13, L9-12, Ca28-30 = 58-60, with 17-20 chevrons and up to two nodules below the caudals. In JM511, there is a small tubercle on the last caudal vertebra; if this represents a fused vertebra the total count becomes 61.

CERVICAL VERTEBRAE (Fig.49)

The first 2 cervical vertebrae are fused. The combined neural processes of C1-C2 are usually bifid at the top (Fig. 49). The transverse processes of C1-C2 are low tubercles, barely extending beyond the condylar facets in anterior view (Fig. 49A). The condylar facets are well separated ventrally.

Diapophyses and parapophyses are developed to a variable degree on cervicals 3-7; in QMJM 4729 (MM92) they are obvious only on cervical 4 (Fig. 49A,B). The last cervical vertebra is distinct in its high neural process, well developed transverse processes and costal facet on the centrum.

THORACIC VERTEBRAE (Fig. 50)

The anterior eight thoracic vertebrae are of similar width; the transverse processes increase in width from T8, with the last thoracic vertebra distinctly wider than the others. On several specimens the anterior border of the transverse processes of the last thoracic vertebra has a distinct antrorse spine (Fig. 50B). In QMJM511, the transverse processes of the last (12th) thoracic vertebra have distinct facets for articulation with the ribs. MM333 has 13 thoracic vertebrae, each with a fossa or swelling of the tip of the transverse processes.

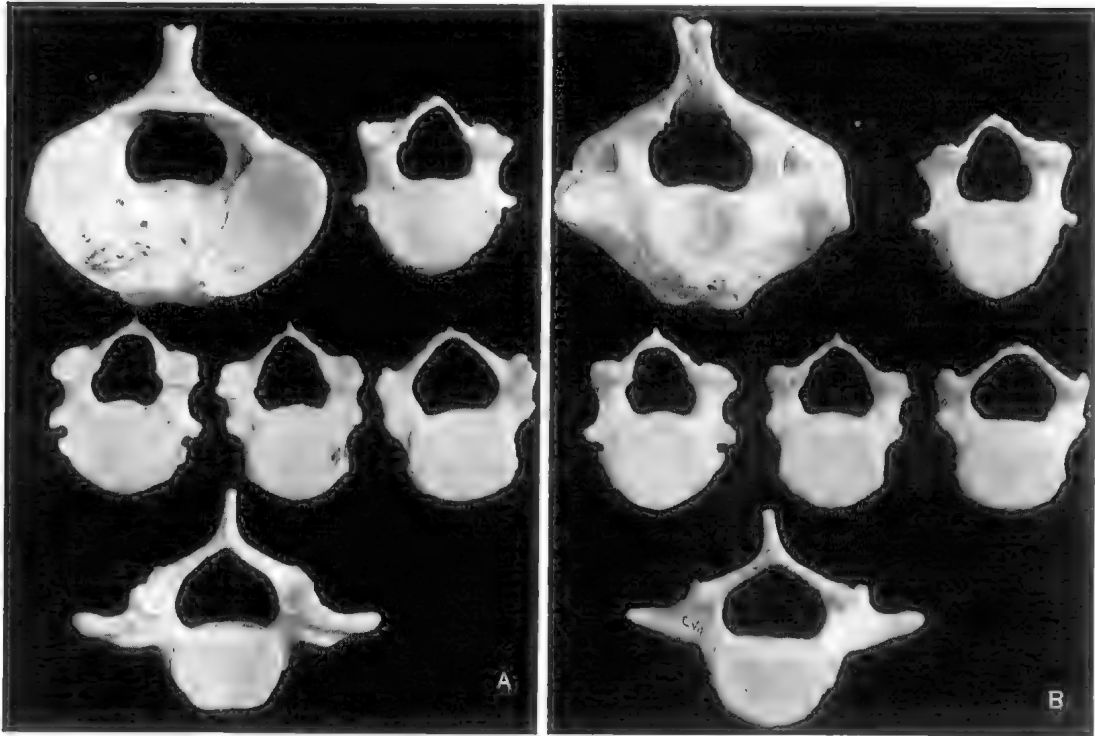The first metapophysis appears on T7-8 ; the

FIG. 49. Cervical vertebrae of QMJM4729, a 2.12 m long ♂. A, Anterior view. B, Posterior view. Note bifid spinous process and poorly developed transverse processes of fused cervicals 1 & 2.

last postzygopophysis on T8-9. The last costal facet is on T7.

LUMBAR VERTEBRAE (Fig. 51)

The transverse and neural processes reach their greatest lengths on lumbars 1-3. In MM16, maximum length of the transverse process is 95mm, that of the neural process 90mm. In QMJM4752 the last 2 lumbars have reduced metapophyses, but they have no mammillary processes or ridges.

CAUDAL VERTEBRAE (Figs 52,53)

The transverse processes are directed anteriorly from Ca2, and by Ca3 the tips of the transverse processes reach in front of the anterior face of the centrum. The greatest widths of the transverse processes are on Ca1-5. From about Ca10, the transverse processes are sharply bent forward (Fig. 52B). The last transverse process is on Ca16-17. The last neural process is on Ca19-21; up to Ca17-18 have metapophyses. In QMJM4729 there is one transitional, globular vertebra and the last 9 caudals are dorsoventrally compressed (Fig. 53A,B); in QMJM511 there are two globular, transitional vertebrae.

CHEVRONS (Fig.54)

QM JM511 has 20 definite chevrons, with possibly a 21st. The next most complete set of chevrons is in MM1015, with 19 chevrons plus 2 small nodules. QMJM4729 and 4752 have 17 chevrons but no nodules.

The first chevron has unfused, asymmetrical arms, with a strongly developed anterior spine and 2 dorsal attachment points on the larger left arm (Fig. 54). In MM334 the chevron is enclosed in thick ligament. The anterior projection and the two dorsal projections are each linked to the posteroventral face of a vertebral centrum; i.e the chevron span three vertebrae. Subsequent chevrons have fused, equilateral arms, presenting more typical Y or V shapes in anterior view.

RIBS

QMJM511, QMJM4752 and MM333 have 13 ribs (one pair reduced in QMJM4752 and
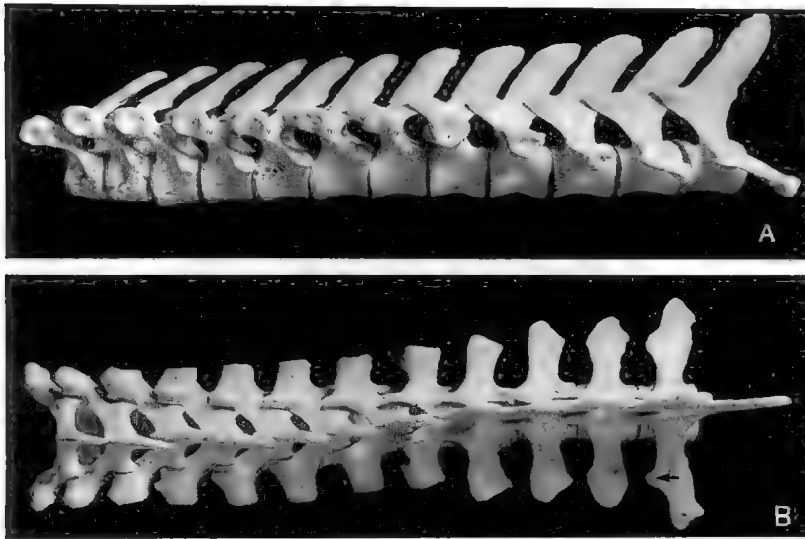
FIG. 50. Thoracic vertebrae of QMJM4729. A, Lateral view. B, Dorsal view. Note antrorse spine (arrow) on transverse process of last thoracic vertebra.
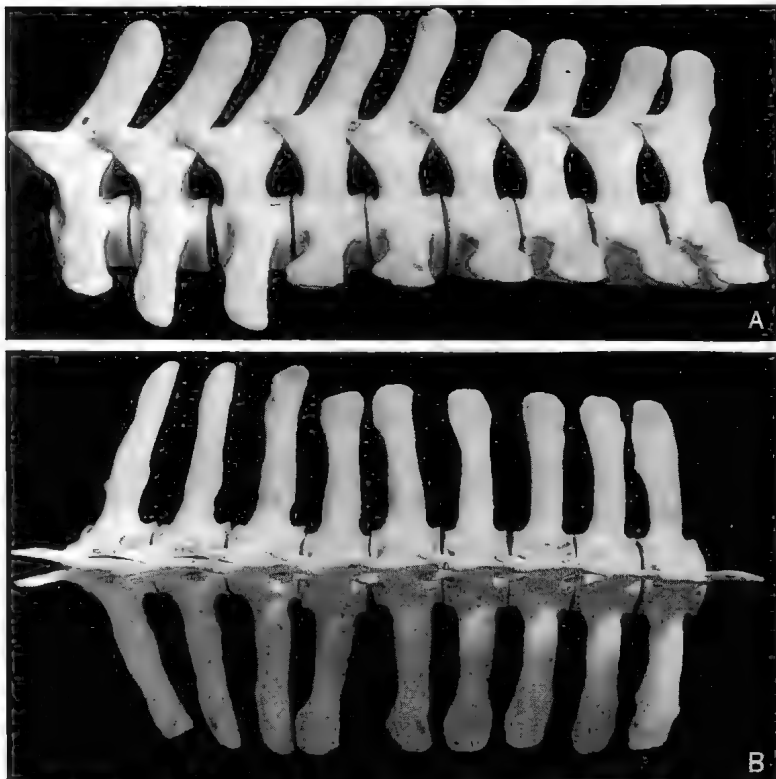
FIG. 51. Lumbar vertebrae of QMJM4729. A, Lateral view. B, Dorsal view. Note the maximum development of transverse processes on anterior lumbar vertebrae.

QMJM511) of which 8 are bicipital. MM1015 and MM92 have 12 ribs, 7 of which are bicipital.

STERNUM (Fig. 55)

The sternum is variable in shape with no apparent sexual dimorphism. A conspicuous foramen is consistently present in the manubrium between the facets for the first two pairs of sternebral ribs. The anterior facets are latero-dorsal in position. In MM1015 there are 5 pairs of articular facets, but 7 pairs of sternebral ribs; the fifth and sixth sternebral ribs articulate with the last facet while the last sternebral rib pair is free.

HYOID APPARATUS (Fig.56)

The fused basi-thyro-hyals form a slender ar-cuate transverse bar with no obvious sexual dimor-phism. The stylohyals are stout, slightly curved and flattened rods.

PELVIC BONES

The small pelvic bones are variable but generally are elongate with a lateral tubercle anteriorly. Not enough material from sexed individuals is avail-able to determine sexual dimorphism. The pelvic bone of MM333 is short and broad, but larger in-dividuals of both sexes have more elongate pelvic bones.

SCAPULA (Fig. 57)

The scapula is distinctly longer than deep, with a distinct anterolateral ridge marking the supraspinatus fossa (terminology from Rommel, 1990), which is 22.3-27.8% of the maxi-mum scapula length. The acromion process is con-

sistently larger than the coracoid process, expanded distally to form a broad triangle, which can have a slightly emarginate or concave distal margin.

FLIPPER BONES

The humerus is elongate (Fig.48). There is a broad, laterally placed humeral condyle and a low medial 'common tubercle'. The delto-pectoral tuberosity on its anterior margin can extend to the distal end but is usually subdistal to the epiphyseal suture (Fig. 48).

The olecranon process is usually prominent (Fig. 48A,B). However, the ulna can become partially fused with the humerus, with no signs of an olecranon process (Fig. 48C). The 5 carpal bones are usually distinct; what appear to be the radiale and intermedium can be fused (Fig. 48).

DISCUSSION

COMPARISONS WITH SOUTHEAST ASIAN ANIMALS

V E R T E B R A L COLUMN. The number of vertebrae from Qld animals is lower than in SE Asian animals (58-60 (61?) vs 62-63).

Anderson (1879:409) gave a formula for *Orcaella* of C7, T12-13, L13-14, Sa2, Ca27-28 = 62-63. For *O. 'fluminalis'* the formula was C7, T13, L16, Ca26 =63 (actually =62, Anderson, 1879:366). Given the variability in published figures (see below) and the limited number of animals examined, it is impossible to assess the significance of these differences. Differences are
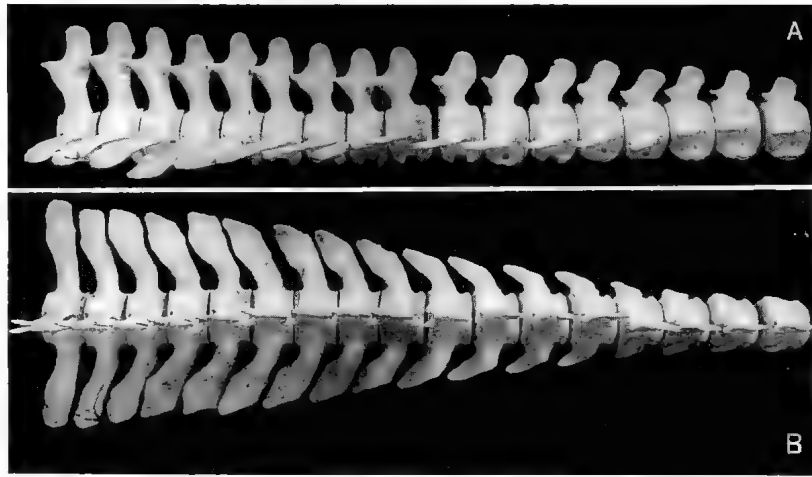
FIG. 52. Anterior caudal vertebrae of QMJM4729. A, Lateral view. B, Dorsal view. Note strong anterior projection of transverse processes.
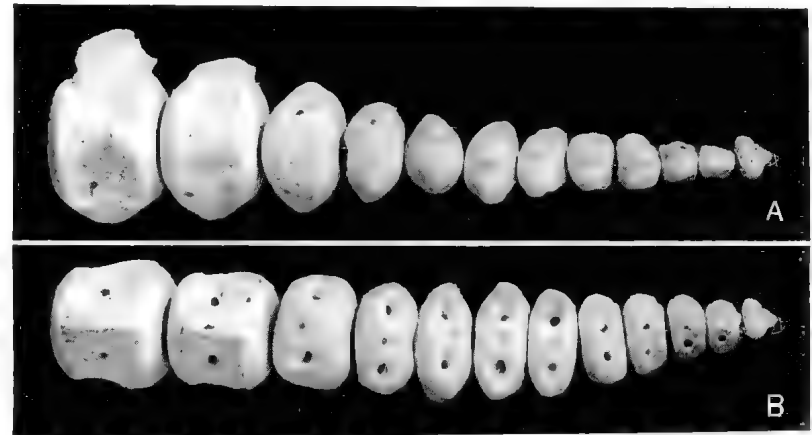
FIG. 53. Posterior caudal vertebrae of QMJM4729. A, Lateral view. B, Dorsal view.
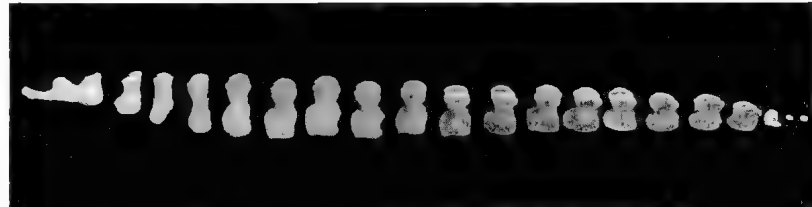
FIG. 54. Chevrons of MM1015, lateral view.

not, however, related simply to differences in the sizes of animals examined. Our specimens are
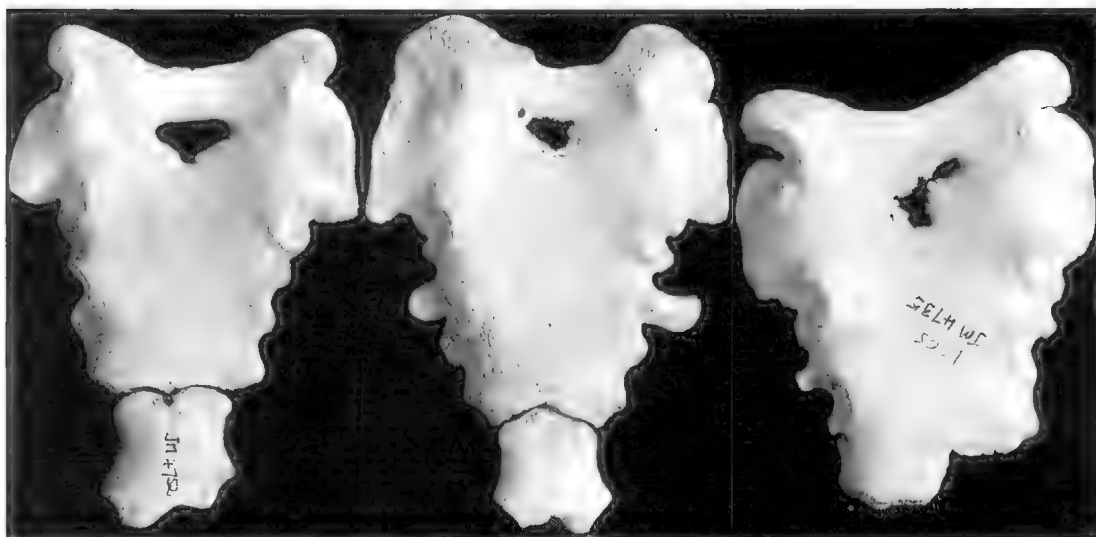
FIG. 55. Dorsal views of sternum from: A, QMJM4752; B, QMJM4729 & C, QMJM4735. Note broadly concave anterior margin, anterior foramen, dorsolateral orientation of facets for anterior sternebrae, and compound nature of sternum (A,B).

1.3-2.4 m long, which overlaps the lengths (1.8-2.3 m) of Anderson's (1879) specimens.

There is difficulty in assessing whether vertebrae are thoracic or lumbar when there are reduced ribs free from the vertebral column. In QMJM511, there are 13 pairs of ribs (last reduced) but only 12 vertebrae with articular facets. Functionally, there are 13 thoracic vertebrae, but only the first 12 would be recognized as thoracic, based on vertebral morphology. We ignored these riblets in the vertebral formula, as did Lloze (in deSmet,1977).

Anderson (1879) noted that sacral vertebrae of *O. brevirostris* have transverse processes, with contracted bases and distal expansions. We do not see this distinction in our material. Sacral ver-

FIG. 56. Fused basi-thyrohyal bones, QMJM4709.

tebrae are not generally recog- nized in cetaceans (deSmet,1977;Rommel,1990).

We follow Rommel (1990) in defining the 1st caudal as that vertebra with a chevron posterior to its centrum (cf deSmet, 1977). This is complicated in *Orcaella* by the elongate, possibly compound, form of the 1st chevron. In MM333 and MM334 which we dissected, the two dorsal projections of the left chevron are each associated with a separate vertebra. In MM334, the anterior projection is also closely associated with a third vertebra. In MM333, the underside of the first centrum is intermediate, lacking the sharp keel typical of lumbar vertebrae and the broad triangular facet for the attachment of chevrons seen on most caudals. In MM334, the vertebra linked with the anterior projection of the first chevron has a sharp keel and would have been classified as lumbar on this basis; the next two vertebrae have broad tubercular facets typical of caudal vertebrae. Only the vertebrae associated with dorsal projections of the chevron are considered as caudal vertebrae.

Anderson (1879:412) noted that in *O. brevirostris* the chevrons begin between the 34th and 35th vertebrae. Using Rommel's (1990) definition, the first caudal vertebra would be the 34th. For *O. 'fluminalis'*, Anderson (1879: 408) noted that chevrons started between the 34th and 35th vertebrae (although elsewhere he gave the position as between L12-13).
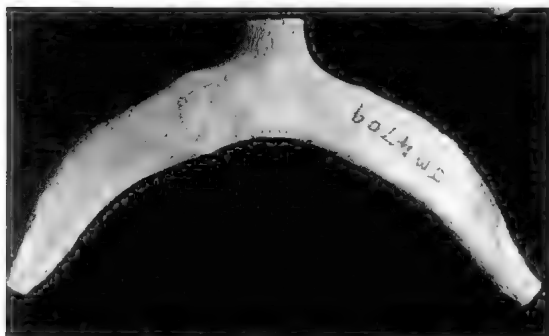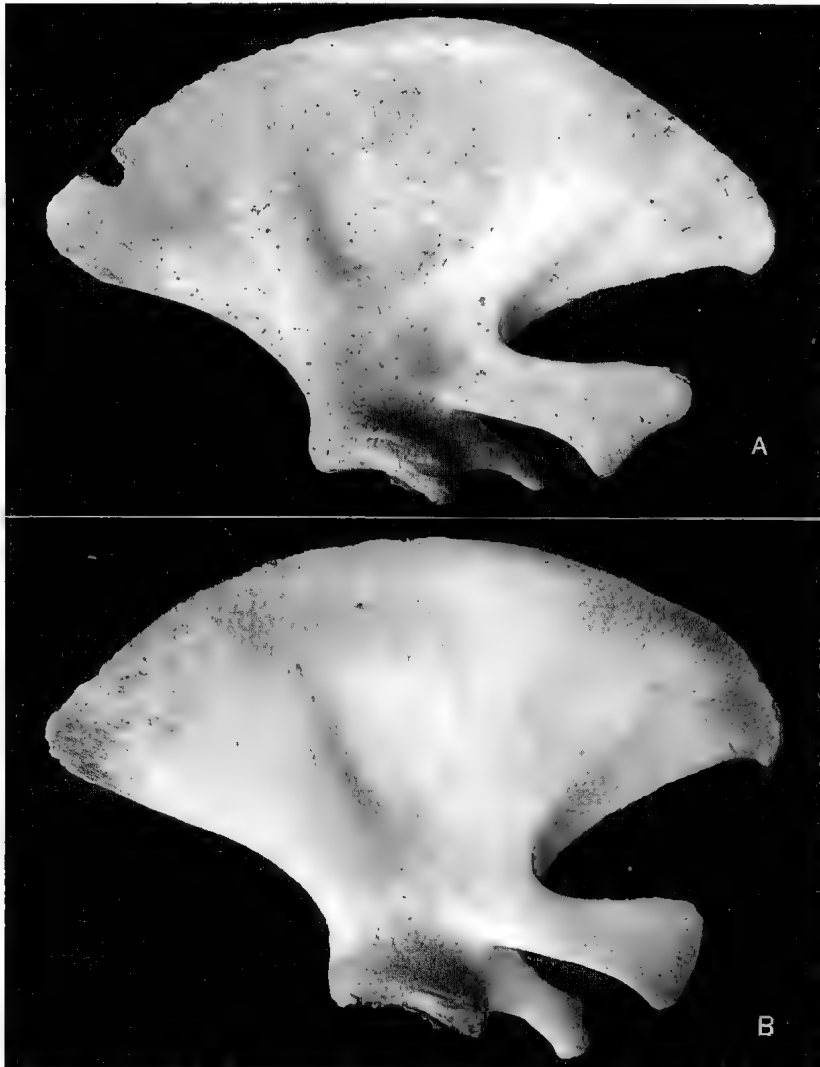
FIG. 57. Lateral view of right scapula. A, QMJM4720. B, QMJM4726. Note well developed acromion process, with triangular distal expansion.

The revised formulae for *O. brevirostris* and *O. 'fluminalis'* would thus be C7, T13, L13, Ca28-29=62-63 and C7,T13, L13, Ca29=62. The formula for an *Orcaella* from the Mekong River was C7, T12, L15, Ca28=62 (de Smet, 1977, adjusted for the difference in defining caudal vertebrae). Lloze (MS, and in Marsh et al., 1989) gave a formula of C7, T13, L16, Ca26-27=62-63.

CHEVRONS

In our material only the first chevron is unfused; Anderson (1879) noted that the first two chevrons are unfused, as are those from chevron 20 posteriorly. Anderson did not describe the shape of the first chevron but noted it articulated 'to the anterior and posterior surfaces of the 34th vertebra'. This implies that there were 2 dorsal projections, as in our material.

RIBS

Anderson (1879), in describing *O. 'fluminalis'*, noted that there were 13 'true' ribs with 'a free floating' rib 'considerably removed from the vertebral column'. In his diagnosis of the genus he noted 12-13 vertebral ribs, with 1-2 free ribs. Both statements imply a total of up to 14 ribs.

Lloze (MS; in deSmet, 1977) also noted 13 pairs of ribs, with a 14th pair free from the vertebral column. MM333 has 13 pairs of ribs, but other Australian specimens have 12 vertebral ribs, sometimes with a 13th free pair of reduced riblets. It is unlikely that the free riblets have been overlooked in those animals where only 12 pairs of ribs were collected.

STERNUM

This is variable (Fig. 55). Our specimens more closely resemble the description and illustration for *O. 'fluminalis'* in Anderson (1879, pl. 43, fig. 10), than *O. brevirostris* (pl. 43, fig. 5). Although Anderson did not illustrate a foramen in the manubrium, he noted it in *O. brevirostris*. None of the sterna illustrated by Anderson or Pilleri & Gihr (1973-1974) are compound, whereas most of Qld specimens have a smaller posterior piece as well as the manubrium (Fig. 55A,B). MM334 has a median slit running from the posterior end to the level of facets for the second pair of sternebral ribs. This is an even more extensive development of the 'deep wide notch' than noted in *O. 'fluminalis'* by Anderson (1879).

PELVIC BONES

The elongate pelvic bones of Qld animals correspond well to the illustration in Anderson (1879, pl. 42, fig. 11). The pelvic bones illustrated by Pilleri & Gihr (1973-1974, pl. 27, fig. 4) appear to be stylohyals.

SCAPULA

The scapula from Qld specimens correspond more to Anderson's (1879, pl. 43, fig. 11) illustration of *O. 'fluminalis'*, but given the variability in our small series there is no basis to separate *O. 'fluminalis'* and *O. brevirostris*. The major distinction in our material from previous descriptions is that the acromion process is generally larger than the coracoid process (Fig. 57) which is opposite to the situation in SE Asian animals (Anderson, 1879; Pilleri & Gihr, 1973-1974, pl. 26).

APPENDIX 5: NOMENCLATURE

The author citation for *O. brevirostris* is generally given as (Gray, 1866). It is generally recognized, however, that the first description of the species was by Sir Richard Owen. This inconsistency is apparent in the synonymy given by Hershkovitz (1966), where in the space of 5 lines the authority was given as '*Orcaella brevirostris* Gray' but the type species was given as '*Orcaella brevirostris* Owen, by monotypy'.

Owen gave an extensive description of the skull of *Phocaena (Orca) brevirostris*, which was read June 20, 1865. The account was not published, however, until the following year. The volume is dated 1869, but independent evidence (Zoological Record 1867) indicates that Owen's article was available in 1866; Johnson (1964) gave the publication date as August 15, 1866. In the meantime (March 1866, according to Johnson (1964)) Gray included an account of '*Orca brevirostris*' in his Catalog of the seals and whales in the British Museum. He attributed *Phocaena (Orca) brevirostris* to the unpublished account by Owen ('Zool. Trans v, ined') and included (also attributed to Owen) an extensive extract of the description and a figure by that worker.

The description and species name were attributed to Owen by Gray. Thus following Ride et al. (1985:91, article 50) and ICZN Recommendation 51B, we consider the appropriate author citation to be *O. brevirostris* (Owen in Gray, 1866).

A NEW SPECIES OF *POMPONATIUS* DISTANT FROM AUSTRALIA
(HEMIPTERA:HETEROPTERA:COREIDAE:ACANTHOCORINI)

H. BRAILOVSKY AND G.B. MONTEITH

The Australian *Pomponatius* Distant is redescribed and the distribution of its type species *P.typicus* Distant is extended to the Northern Territory and to New Guinea. *P. luridus* sp. nov. is described from eastern and northern Australia. Distribution maps and a key are included. Food plants are *Melaleuca* and *Callistemon* (Myrtaceae). □ *Hemiptera, Coreidae, Pomponatius, taxonomy, biological control.*

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Pomponatius Distant, 1904 of the Acanthocorini was described from coastal Queensland and is known only from the type species, *P. typicus* Distant,1904. It has been mentioned as a garden pest, under the common name of the callistemon tip bug, damaging cultivated species of the large Australian native plant genera *Melaleuca* and *Callistemon* (Jones & Elliot, 1986).

Because *Melaleuca quinquenervia* (Cav.) S.T. Blake, has become a severe weed pest of wetlands in Florida (Balciunas, 1990) the United States Department of Agriculture undertook an intensive search among native Australian insects for possible biocontrol agents. This search identified *Pomponatius typicus*, under the common name of the tip wilting bug, as one possible biocontrol agent (Balciunas & Burrows, 1994).

Museum collections were found to contain a second undescribed species of *Pomponatius* which widely overlaps in distribution and food preference with the type species. The new species is described below and the generic range is extended to the Northern Territory and to New Guinea.

The following abbreviations indicate institutions where specimens are deposited or which generously lent material: Australian Biological Control Laboratory, Townsville (ABCL); Australian National Insect Collection, Canberra (ANIC); Museum and Art Gallery of Northern Territory, Darwin (NTM); Department of Primary Industries, Mareeba (MDPI); Department of Primary Industries, Brisbane (QDPI); The Natural History Museum, London (BMNH); California Academy of Sciences, San Francisco (CAS); Canadian National Collections, Ottawa (CNC); Colección Entomológica del Instituto de Biología, Universidad Nacional Autónoma de México (IBUNAM); Australian Museum, Sydney (AMS); Queensland Museum, Brisbane (QM); University of Queensland Insect Collection, Brisbane (UQIC); University of California, Riverside (UCR).

All measurements are in millimetres.

Pomponatius Distant, 1904

Pomponatius Distant, 1904:265.

DESCRIPTION. Body elongate, narrowed posteriorly.

Head. Wider than long across eyes, nearly pentagonal, not produced beyond the antenniferous tubercles and dorsally flat; tylus apically upturned to form a small horn, with apex subacute or truncate; jugum unarmed, thick, apically globose, equal or slightly shorter than tylus; inner margins of antenniferous tubercles with conspicuous and large lobe apically rounded and widely separated; antennal segment I robust, thickest and always longer than head, segments II and III cylindrical, regularly incrassate and segment IV always fusiform or antennal segments I and II regularly incrassate and segment III the thickest and gradually widening; segment IV the shortest, segment III shorter than I and II and segment II usually shorter than I; ocelli sessile; preocellar pit deep; eyes moderately large, semiglobose and sessile or moderately large and compressed at lateral margins; postocular tubercle relatively small; bucculae rounded, short, not extending beyond anterior margin of eyes; rostrum reaching anterior margin or middle
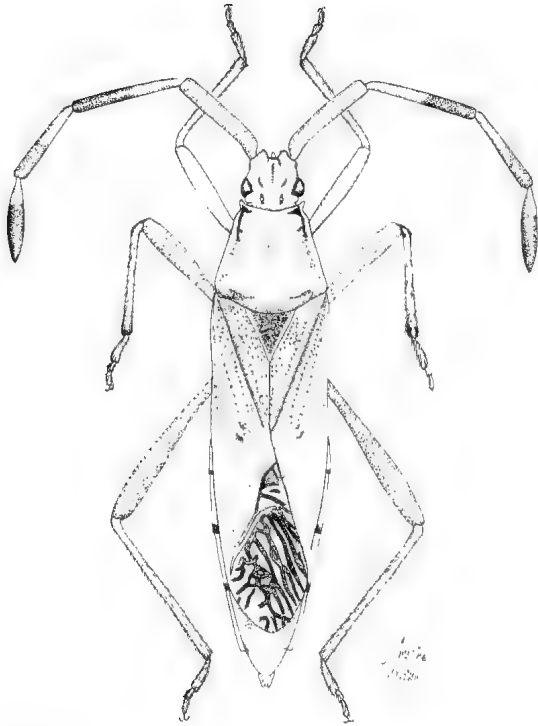
FIG. 1.Dorsal view of *Pomponatius luridus* sp. nov., male, length 11.5mm.

third of mesosternum; rostral segment I the shortest, segment III shorter than I and IV and segment IV the longest or subequal to I; frons with a deep central longitudinal incision.

Thorax. Pronotum trapeziform, wider than long, moderately declivent; collar not clearly marked; frontal angles produced forward as long and broad or produced as medium sized and slender conical projections; anterior margin concavely sinuate; anterolateral margins clearly emarginate or slightly upwardly reflected and nodulose; humeral angles rounded, not expanded and dorsally tuberculate; posterolateral margins slightly concave and smooth; posterior margin expanded on a short lip with the posterior border straight and smooth; calli not elevated, separated along midline by short longitudinal furrow. Anterior lobe of metathoracic peritreme elevated and reniform, posterior lobe sharp, small; mesosternum with a medial groove, extending to anterior third.

Legs. Femora apically incrassate, densely tuberculate and ventrally armed with a distinct tooth near apex; tibiae terete, conspicuously sulcate.

Scutellum. Triangular, longer than wide, flat, transversely striate; apex subacute or truncate.

Hemelytra. Macropterous, almost reaching the apex of the last abdominal segment; costal margin emarginate; apical margin almost straight or clearly sinuate, with inner third concave and outer third straight; apical angle obtuse; hemelytral membrane elongate with several longitudinal veins or small with reticulate venation.

Abdomen. Connexival segments complete, not extended as short spines; abdominal sternite without medial furrow.

Male genitalia. Genital capsule: Posteroventral margin projected in a broad or slender large-sized triangular lobe (Figs. 2F, 2G). Parameres: Body simple and broad or with middle third narrow, neck-like; apical projection with anterior lobe convex and continuous with body and posterior lobe conspicuously curved or dilated and ending in a sharp or blunt short projection (Figs. 2A-E).

Female genitalia. Abdominal sternite VII with plica and fissura; plica triangular, short, reaching anterior third of sternite VII. Genital plate: Gonocoxae I square, shorter than paratergite IX, in caudal view closed, in lateral view slightly convex; paratergite VIII triangular, with spiracle visible; paratergite IX elongate, triangular, larger than paratergite VIII.

DIAGNOSIS. Body elongate and narrowed posteriorly, antennal segments I to III regularly incrassate, antenniferous tubercles with a distinct lobe on the inner margins, posterior margin of pronotum expanded on a short lip and femora apically incrassate with a distinct tooth near apex.

REMARKS. Kumar (1965) studied an undetermined species of *Pomponatius* and described the male and female genitalia as well as the glands associated with the internal male organs.

Pomponatius luridus sp. nov.
(Figs 1,2C-G, 4)

MATERIAL EXAMINED. HOLOTYPE ♂: QMT13987: Central Qld: Mt. Moffatt NP, East Branch, Maranoa R. (Top Moffatt Camp), 26.ix.1986, Monteith, Yeates & Thompson, in QM. PARATYPES: Qld: QMT13988, ♀, same data as holotype (QM); QMT13989, ♀, Levers Plateau, via Rathdowney, 6-ii-1966, F.R. Wylie (QM); QMT13990,♂, Mt Tamborine, 27.x.1957, S. Breeden (QM); ♀, St George, 13.v.1973, J Hodgson (IBUNAM); 1♂3 ♀♀, Indooroopilly, xi.1979, G.Gordh (UCR + IBUNAM); ♂, Einasleigh Riv., 35 m. E. of Georgetown, 31.v.1972, G.B. & S.R. Monteith (UQIC); ♀, 62 km W. Mt Garnet, 31.xii.1978, R.I. Storey, on *Melaleuca* sp.
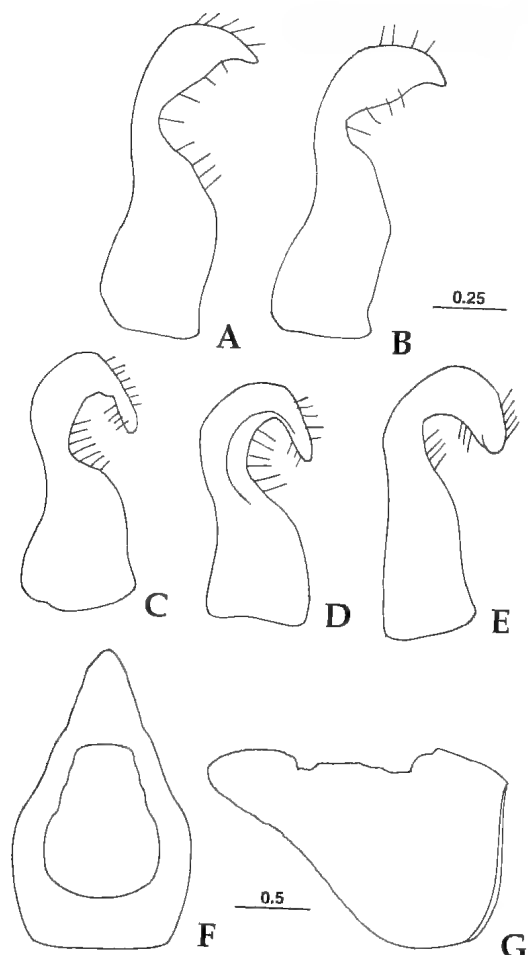
FIG. 2. Male genitalia. A-B, parameres of *Pomponatius typicus* Distant. C-E, parameres of *Pomponatius luridus* sp. nov. F-G, dorsal and lateral views of genital capsule *P. luridus* sp. nov. (Scale lines in mm.)

(MDPI); 1♂ 1 ♀, Biggenden, 12.xii.1971, H. Frauca (ANIC); 1♂ 5♀♀ , Degilbo Ck., Biggenden, 4.xii.1971, H. Frauca (ANIC); 1 ♂, Mullet Ck., 31 mi. N. Bundaberg, 27.iv.1959, T.G. Campbell (ANIC); ♂, Calliope R. Xing, N. of Gladstone, ii.1965, E.J. Reye, on bottle brush (ANIC); ♂, Brisbane, 24.viii. 1976, B.K. Cantrell (QDPI); ♀, Kingaroy, 7. xi.1983, J. Wessels, on *Melaleuca armillaris* (QDPI); 2♂, Stanthorpe, 6.xii.1926 (QDPI); ♀, Indooroopilly, 15.i.1962, J.H. Barrett (QDPI); ♀, James Cook Univ., Townsville, 4.ix.1989, S.J. Newman, on *Callistemon viminalis* (ABCL); ♂, Chelmer, Brisbane, 15.ix.1992, M. Purcell, on *Callistemon viminalis* (ABCL). NSW: ♀, Oatley, 15.vi.1950, Deuquet (AMS); , Enfield, Sydney, E.P. Ramsay (IBUNAM); 2♀♀, Rivertree, 10.viii.1921 (QDPI). NT: ♂, Edith Falls, Katherine Gorge NP, 6.xii.1980, M.B. Malipatil & I. Archibald

(NTM); 1 ♂, No locality, 25.ix.1896, A.L. Schrader (AMS).

DESCRIPTION. MALE. *Dorsal coloration*. Pale yellow, with punctures dark orange and following areas creamy yellow: anterolateral margins of pronotum and apex of scutellum; antennal segment I orange yellow with tubercles reddish, segment II orange yellow with apical third and tubercles reddish, segment III with apical half and apical join pale yellow and basal half including the tubercles dark orange reddish and segment IV pale yellow; following areas black: longitudinal stripe close to the anterior third of anterolateral margins of pronotum, and anterior third of costal margin of corium; connexival segments and abdominal sternite VII pale yellow with punctures dark orange; abdominal segments I to VI bright orange. Ventral coloration: Pale yellow with pink diffuse areas and with following areas black: apex of rostral segment IV, one small discoidal spot on propleura and mesopleura, two longitudinal series of discoidal spots running laterally to the midline on mesosternum and irregular spots on mesocoxa, metacoxa, mesotrochanters and metatrochanters; tubercles of femora black or reddish brown or pale pink.

Structure. Antennal segments I to III regularly incrassate; eyes moderately large, semiglobose, sessile but not compressed at lateral margins. Pronotum: Frontal angles produced forward as long and broad conical projection; anterolateral margins clearly emarginated. Hemelytra: Apical margin clearly sinuate, with inner third concave and outer third straight; hemelytral membrane elongate with several longitudinal veins.

Genital capsule. Posteroventral margin projecting as a large broad triangular lobe (Fig. 2F,G). Parameres (Fig. 2C-E).

FEMALE. *Coloration*. Similar to male. Abdominal segments IV to VII bright orange with two pale brown discoidal or irregular spots, close to the connexival segments; segment VIII dark orange and segment IX dark reddish brown with longitudinal stripe orange, close to midline; connexival segments I to VII pale reddish brown with upper margin mostly pale yellow; connexival segments VIII and IX mostly yellow; abdominal sterna and genital plates pale yellow with following areas black: irregular spots on sterna III to VII and close to midline as well as the internal margin of fissure and the area close to upper margin of plica.

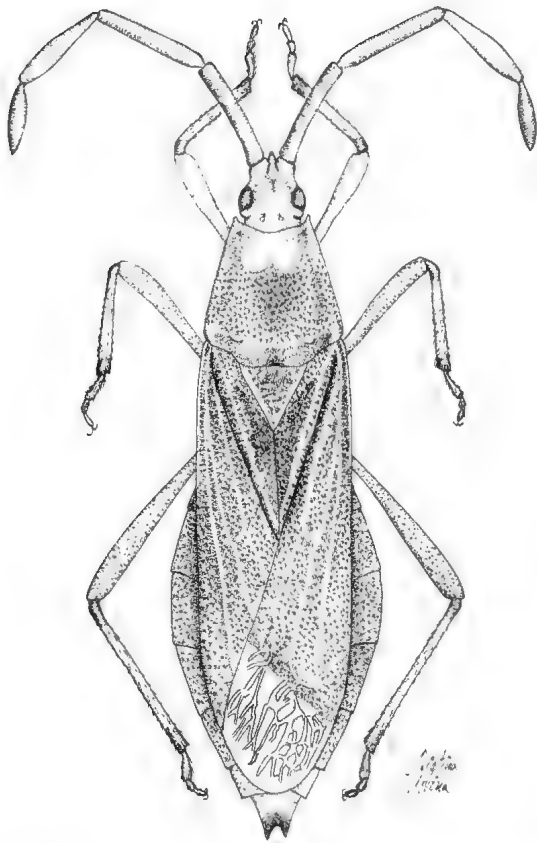VARIATION. 1, Antennal segment IV with dis-

FIG. 3.Dorsal view of *Pomponatius typicus* Distant, female, length 15.1mm.

tal half pale yellow and basal half pale orange yellow. 2, Humeral angles black or dark brown. 3, Endocorium with black discoidal spot somewhat diffuse. 4, Scutellar disc with or without median black stripe. 5, Abdominal sterna and genital plates of female pale yellow, with pale pink marks or with only the internal margins of fissure and the areas close to the plica black. 6, Abdominal segment VIII of female bright orange.

MEASUREMENTS. ♂first, then ♀: Head length: 1.08, 1.32; width across eyes: 1.36, 1.56; interocular space: 0.80, 0.91; interocellar space: 0.25, 0.27; length antennal segments: I, 2.40, 2.72; II, 2.48, 2.64; III, 2.08, 2.24; IV, 2.00, 1.88. Pronotum: Total length: 2.12, 2.76; width across frontal angles: 1.20, 1.44; width across humeral angles: 2.40, 3.08. Hemelytra: Total length of hemelytral membrane: 3.76, 4.40. Scutellar length: 1.00, 1.40; width: 0.92, 1.32. Total body length: 11.52, 14.65.

DISTRIBUTION (Fig. 4). From Sydney along coastal and inland Queensland to the Northern Territory.

FOOD PLANTS. See discussion below.

ETYMOLOGY. Latin *luridus*, pale yellow; for its light coloration.

Pomponatius typicus Distant,1904
(Figs 2A-B, 3, 4)

Pomponatius typicus Distant, 1904: 266.

MATERIAL EXAMINED. NSW: Bulahdelah, 11.xi.1932 (IBUNAM); Hat Head, nr. Kempsey, 3.i.1970 (ANIC). QLD: HOLOTYPE ♀, Townsville (BMNH); Acacia Ridge, 16.i.1973; Lockerbie Area, Cape York, 13- 27.iv.1973; Jardine River road crossing, 16-27.ix.1974; Brisbane, 24.x.1916; Lakefield NP, 75 km N. of Laura, 15-28.vi.1980; Kuranda, 3.x.1920; Nth Keppel Island, track to Mazie Bay, 3.ix.1987 (QM); Archerfield, 19.ix.1964; St Lucia, 6.ix.1965; Bowen, 2.vi.1965; Brisbane, 20.v.1959 (UQIC); Black Mt Rd (Kuranda), 24.i.1970; Cairns, 22.vii-24.xii.1969 (CNC); Townsville 5.ii.1945 (CAS); Watalgan Range, via Rosedale, 6.iv.1974; Baldwin Swamp Fauna Reserve, Bundaberg, 27.xi.1971; Goodwood, Isis Shire, 5.iv. 1974; Gumdale, Brisbane, 11.xi.1968; Ladysmith Yard at Turnoff Lagoon, 18.ix.1930 (ANIC); Bridge Ck, Cook Highway, 29.v.1974, on *Melaleuca*; Kurrimine Beach Rd, 26.vi.1974; Mareeba, 1.ii.1979, at light; Home Hill, 28.vii.1947 (MDPI); Chandler, Brisbane, 29.i.1976, damaging new growth of *Callistemon* sp.; Mareeba, 29.ix.1981; Townsville, viii. 1984, on *Callistemon viminalis*; nr. Gamboola H.S., 23.vii.1982, (QDPI); Coombabah, 14.ii.1990 & 4.ix.1990, on tips of *Melaleuca quinquenervia*; Burpengary, 12.xi.1992, feeds on *M. quinquenervia*; Chelmer, 15.ix.1992, on *M. quinquenervia*; Centenary Park, Cairns, 8.v.1991, tips of *M. quinquenervia*; 16.9 km ESE of Tully, 31.viii.1994 and 2.viii.1994, ex *M. quinquenervia*; same locality, 27.vi.1994, ex *M. dealbata*; 14.3 km S. Tully, 31.viii.1992; 21.8 km S. Tully, 4.xi.1993, ex *M. dealbata*; 15 km ESE Tully, 27.xi.1994, ex *M. quinquenervia*; James Cook Univ., Townsville, 17.iv.1990 & 18.i.1993, feeding on *Callistemon viminalis*; same locality, 4.vii.1991 and 2.ii.1992, ex. *Melaleuca quinquenervia* (ABCL). NT: 48 ml. SW of Daly River, 30.viii.1968; 9 km NE of Mudginbarry HS, 26.v.1973 (ANIC); Wildman River cashew plantation, 17.x.1989, ex adjacent *Melaleuca* regrowth; Mary R., 37 ml. E of Pine Creek, 9.vii.1971; Darwin, 9.viii.1983, ex *Leptospermum* (NTM); Crystal Falls - Biddlecombe Cascades, Nitmiluk NP, 17-18.iii.1995, ex *Melaleuca viridiflora* (QM); Howard River, Darwin, 24.x.1986, ex *Melaleuca nervosa* (ABCL). PNG: Rouku, Morehead River, Western District, PNG, 19.iii-28.v.1962 (ANIC).
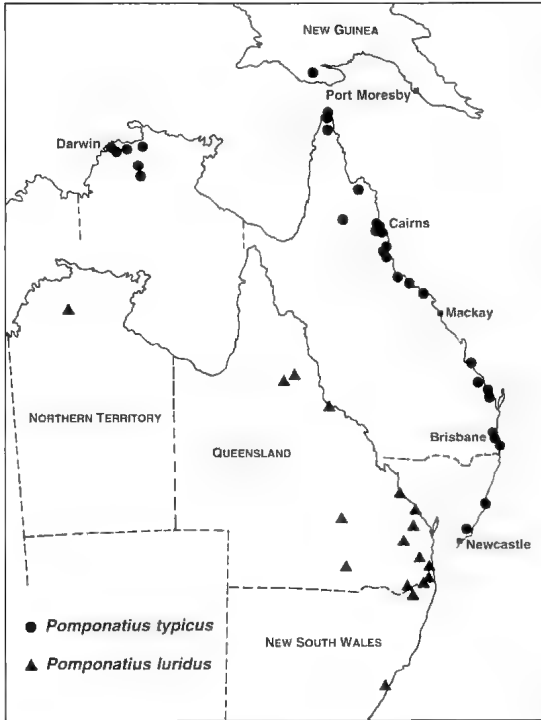
FIG. 4.Distribution map of *Pomponatius* species.

DIAGNOSIS. Antennal segment III gradually widening and uniformly pale orange yellow, hemelytral membrane short, with reticulate venation, anterolateral margins of pronotum slightly reflected, and propleura and mesopleura without black discoidal spot. Genital capsule: Posteroventral margin projected in a large slender triangular lobe. Parameres (Fig. 2A-B).

DISTRIBUTION (Fig. 4). This species was first described from Townsville (Distant, 1904) and later recorded from Rockhampton (Blöte, 1935) and Heathlands in Cape York Peninsula (Cassis, 1993). It is now known to be widespread in Australia from northern NSW along the coast to north Queensland. It is also now recorded from the Northern Territory and New Guinea. Genitalia of specimens from the Northern Territory and southern New Guinea agree with those from eastern Australia.

FOOD PLANT RECORDS

Pomponatius feeds by sucking sap from young stems at the ends of branches, especially when the apical shoot has a flush of soft new growth. Their feeding causes wilting and sometimes death of the terminal shoot and its young leaves. This effect is often useful evidence for locating specimens on plants and has lead to their common name of 'tip wilting bugs'.

All records for *Pomponatius* species are from plants of the Family Myrtaceae, as follows:

Pomponatius luridus – *Melaleuca* sp. (Mt Garnet); *Melaleuca armillaris* (Kingaroy); *Callistemon viminalis* (Townsville, Chelmer); on bottle brush (Calliope R.).

Pomponatius typicus – *Melaleuca quinquenervia* (Coombabah, Burpengary, Chelmer, Cairns, Tully District, Townsville); *Melaleuca dealbata* (Tully district); *Melaleuca viridiflora* (Nitmiluk NP); *Melaleuca nervosa* (Darwin); *Melaleuca* sp. (Cook Highway, Wildman R.); *Callistemon viminalis* (Townsville) *Callistemon* sp. (Chelmer); *Leptospermum* sp. (Darwin).

Almost all records are from the closely related *Melaleuca* and *Callistemon*. The only confirmed *Callistemon* is *C.viminalis* which is sometimes assigned to *Melaleuca*. The only other genera for which records exist are *Leptospermum* (one record from Darwin which may have been a garden plant and for which actual feeding has not been confirmed) and a prolonged infestation of a garden plant of *Calothamnus* in Brisbane by a species of *Pomponatius* which was not identified (GBM obs.). *Calothamnus* is related to *Melaleuca* but is naturally restricted to southwestern Australia beyond the known range of *Pomponatius*.

Circumstantial evidence for *Pomponatius* feeding on other plant species in the form of characteristically damaged growing tips has been noted by the USDA survey staff on *Melaleuca arcana*, *M. argentea*, *M. bracteata* and *Callistemon polandii* (Burrows pers. comm.).

Although both species of *Pomponatius* have been recorded from both *Melaleuca* and *Callistemon* it would appear from inferences which can be drawn from the data that, in the wild, *Pomponatius luridus* is virtually restricted to *Callistemon viminalis*, and *Pomponatius typicus* is similarly restricted to 'paper bark tea trees' of the *M. leucadendra* complex as defined by Blake, 1968. For *P. luridus* the record from *M. armillaris* is from a garden plant outside its natural range while many of the collection localities where plant associations were not recorded are habitats where *C. viminalis* is abundant, e.g. Calliope R., Maranoa R., Degilbo Ck, Mullet Ck. Similarly with *P. typicus* all *Callistemon* records are from unnatural suburban situations, while most natural occurrences of the bug are from habitats where

FIG. 5. A living ♀ of *Pomponatius luridus* sp.nov. on its foodplant *Callistemon viminalis* in Brisbane.

paperbarks predominate. This includes the PNG record.

This apparent food plant dichotomy between the two *Pomponatius* species is suggested as the mechanism which maintains their specific integrity throughout almost identical distributions.

KEY TO THE KNOWN *POMPONATIUS* SPECIES

1. Antennal segment III not noticeably more swollen than II, and bicoloured with apical half paler than basal half; hemelytral membrane elongate, longer than 3.20mm, with several longitudinal veins, and with its basal margin strongly sinuate; dark longitudinal stripes on prosternum about same width as rostrum; apical lobe of paramere not dilated and without a small projection (Figs 2C-E) . . *Pomponatius luridus* sp. nov. (Fig. 1)

Antennal segment III noticeably more swollen than II and not bicoloured; hemelytral membrane short, less than 3.20mm, with reticu-

late venation and with its basal margin uniformly curved; dark longitudinal stripes on prosternum at least twice width of rostrum; apical lobe of each paramere dilated and ending in a sharp or blunt projection (Fig. 2A,B)
. . . . . *Pomponatius typicus* Distant (Fig. 3)

ACKNOWLEDGEMENTS

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REVISION OF THE AUSTRALIAN GENUS *MICROTROPESA* MACQUART
(DIPTERA: TACHINIDAE: TACHININI)

CHRISTOPHER J. BURWELL

The endemic Australian genus *Microtropesa* Macquart is revised and its 14 species keyed. *M. danielsi* sp. nov. and *M. longimentum* sp. nov. are described. *Microtropesa nigricornis* Macquart and *M. intermedia* Malloch are confirmed as valid. *Microtropesa flavitarsis* Malloch is considered a junior synonym of *M. obtusa* (Walker). The female of *M. viridescens* Paramonov and the male of *M. canberrae* Paramonov are described for the first time. The first instar larva of *M. intermedia* and the genitalia of males of most species are figured. □ *Diptera, Tachinidae, Microtropesa, Australia.*

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Australian Tachinini are dominated by the endemic *Microtropesa* Macquart (Crosskey, 1973), specimens of which are up to 16 mm long and often with striking colour patterns on the thorax and abdomen. Malloch (1928, 1929, 1930) described five species and provided a key. Hardy (1939) dealt with a number of species described by earlier authors but omitted by Malloch and synonymised several names (many incorrectly). Hardy incorrectly synonymised *Tasmaniomyia* Townsend with *Microtropesa* (Paramonov, 1951; Crosskey, 1973). Paramonov (1951) described four new species and provided a useful but incomplete key (three species discussed in the text were omitted from the key). Paramonov was unsure of the status of *M. intermedia* but thought it probably conspecific with *M. nigricornis*. These species have been regarded as distinct (Crosskey, 1973; Cantrell & Crosskey, 1989). Paramonov (1951) was also unsure of the identity of two species described by Walker (1853, 1858).

METHODS

Male genitalia were examined by detaching the terminal abdominal segments, immersing them in cold 10% KOH for 24–48 hours, washing in water and dissecting in 70% ethanol. The preparations were stored in glycerol in separate microvials. These were pinned next to the specimen and given duplicate labels.

Drawings of male genitalia and larvae were made with the aid of a compound microscope and drawing tube. Other drawings were prepared using a dissecting microscope and camera lucida.

Measurements of body length were taken from pinned specimens using a micrometer eyepiece.

TERMINOLOGY

Terminology follows Crosskey (1973) and the following abbreviations are used: A1, A2, A3 – 1st, 2nd and 3rd antennal segments; acr, acrostichal seta; dc, dorsocentral seta; fr, frontal seta; ia, intra-alar seta; mm, median marginal seta; ov, outer vertical seta; pfr, parafrontal; pf, parafacial; pro-orb, proclinate orbital seta; prst-acr, presutural acrostichal seta; prst-dc, presutural dorsocentral seta; prst-ia, presutural intra-alar seta; stp, sternopleural seta; St1, St2 - 1st and 2nd abdominal sternites; T1+2, 1st apparent abdominal tergite (= fused 1st and 2nd tergites); T3, T4, T5 – 2nd, 3rd and 4th apparent abdominal tergites. Head height is defined as the vertical dimension of the head, in lateral view, from the ocellar triangle to the peristome (Fig. 1C).

Abbreviations for depositories are as follows: Australian Museum, Sydney (AM); Australian National Insect Collection, Canberra (ANIC); Biological and Chemical Research Institute, Sydney (BCRI); British Museum (Natural History), London (BMNH); Institut für Pflanzenschutzforschung (formerly Deutsches Entomologisches Institut), Eberswalde, Germany (DEI); G. Daniels collection, Brisbane (GD); Muséum National d'Histoire Naturelle, Paris (MNHN); Queensland Department of Primary Industries, Brisbane (QDPI); Queensland Museum, Brisbane (QM); South Australian Museum, Adelaide (SAM); University of Queensland Insect Collec-

tion, Brisbane (UQIC); Western Australian Department of Agriculture, Perth (WADA).

SYSTEMATICS

Order DIPTERA
Family TACHINIDAE
Tribe TACHININI
Microtropesa Macquart, 1846

Microtropesa Macquart, 1846:313; Engel, 1925:344; Malloch, 1928:614; Malloch, 1929:286; Malloch, 1930:99; Hardy, 1939:33; Paramonov 1951:761; Crosskey, 1973:135; Cantrell & Crosskey, 1989:761.
Gerotachina Townsend, 1916:152. Type species *Tachina obtusa* Walker, 1853, by original designation. Synonymy by Hardy, 1939:33.
Tasmaniomyia Townsend, 1916; Hardy, 1939:33 (misidentification).

TYPE SPECIES. *Musca sinuata* Donovan, 1805, by monotypy.

DIAGNOSIS. Eyes bare, pf haired; A2 elongate, almost as long as A3 or longer (Figs 1C,D, 3C, 3G, 4D, 5A); ♀ with 2 pro-orb, absent in ♂; ♂ without ov; palpi normal. Thorax with at least 4+4 dc, 1+2 ia; propleuron haired; 2 or 3 (rarely 4) stp; pleurotergite with long, dense hairs; cell R5 open (Fig. 5B), rarely closed (Fig. 3H). Abdomen wider than thorax, normally subglobose with whitish or grey pollinose markings; T3 with or without mm, if present up to 5 pairs; sternites exposed, often with spiniform setae; aedeagus without epiphallus.

Females differ from males in having wider fore and mid tarsi, shorter claws and a conspicuously wider vertex.

REMARKS. The long, dense hairs on the pleurotergite distinguish *Microtropesa* from all other Tachinini except the New Guinean *Paratropeza* Paramonov, which is distinguished by an inflated abdomen with fused T3 and T4 and deeply excised T5 and by very strong spiniform setae on the abdomen and scutellum.

BIOLOGY. *Microtropesa flaviventris* Malloch parasitises the noctuid moths *Mythimna (Pseudaletia) convecta* (Walker) and *Persectania ewingii* (Westwood) (Crosskey, 1973). Hosts of other species of *Microtropesa* are unknown.

About 70% of specimens of *Microtropesa* in collections are males. This is due in part to the habit of males of some species of frequenting prominent mountain peaks and hilltops. Males of

M. sinuata and *M. violacescens* have been observed resting on the ground in exposed, sunny situations at the summit of hilltops and sometimes on prominent rocky outcrops.

The genus occurs mainly in the southern half of the continent (Fig. 7) with only *M. danielsi* sp. nov. and *M. violacescens* known north of 23°S.

KEY TO SPECIES OF *MICROTROPESA*

1. Mentum of proboscis longer than head height (Fig. 3G); wing with cell R5 closed (Fig. 3H) . . . . *longimentum*
   Mentum of proboscis shorter than head height (Figs 3C, 5A); wing with cell R5 open (Fig. 5B) 2

2. Base of wings with dark brown or black markings; legs black 3
   Base of wings yellowish or orange, without dark brown or black markings; legs with at least femora yellowish or orange 4

3. Hairs on palpi mostly yellow . . . . . *viridescens*
   Hairs on palpi black . . . . *skusei*

4. Dorsal surface of scutellum with yellow or orange-yellow hairs 5
   Dorsal surface of scutellum with black or dark brown hairs 7

5. Pf with black hairs extending below level of vibrissae, at most with a few orange-yellow hairs ventrally near eyes; head, in lateral view, with epistome projecting weakly (Fig. 1C); fr, dc and acr very weak and long, hair-like . *canberrae*
   Pf with black hairs (if present) not extending below level of vibrissae, usually at least ventral third (often much more) of pf with orange-yellow hairs; head, in lateral view, with epistome projecting more strongly (Figs 1D, 5A); fr, dc and acr strong, distinctly bristle-like 6

6. T3 of ♂, from above, with pair of submedian, grey, pollinose, anterior spots, rarely absent in ♀; ♂ with grey, pollinose triangle on T4 about as wide as distance between basal scutellar setae, narrower in ♀; prescutum usually with distinct pattern of whitish pollinose stripes and spots . . . . *sinuata*
   T3 of ♂, from above, without grey, pollinose spots; ♂ with grey, pollinose triangle on T4 about as wide as distance between subapical scutellar setae; prescutum with thin, shifting whitish pollinosity a little thicker surrounding anterior prst-dc; ♀ unknown . . . . . . *danielsi*

7. Dorsal surface of T5 with pair of dark-brown or black, submedian, spots separated from anterior margin and sometimes from similar ventral pair of dark spots by grey pollinosity (T5 often with bases of some setae black) (Fig. 3D) . . . . *latigena*
   · Dorsal surface of T5 without dark-brown or

black spots or if present, spots extend to anterior margin (Fig. 5C) or ventral surface of T5 (Fig. 4C) 8

8. T5 in caudal view with ground colour completely obscured by thick, grey pollinosity . *campbelli*
T5 in caudal view with ground colour not completely obscured by thick, grey pollinosity (eg. Figs 4C, 5C) 9

9. T3 without mm; mesoscutum with uniform, thin, whitish pollinosity 10
T3 with mm; mesoscutum with distinct pattern of whitish, pollinose stripes and/or spots, at least on prescutum 11

10. Ground colour of abdomen yellowish with dark dorsomedial vitta (may cover most of dorsum of abdomen in ♀); pf with black hairs ventrally . . . . *flaviventris*
Ground colour of abdomen red-brown to black; pf with orange-yellow hairs ventrally . . . . *violacescens*

11. Abdomen with whitish, pollinose markings restricted to median triangle or 'V' on T3; T4 and T5 with uniform, orange pollinosity; vertex of ♂ very narrow, distance between eyes about twice width of ocellar triangle . . *ochriventris*
Abdomen with whitish or grey, pollinose markings on T3, T4 and T5; T4 and T5 without orange pollinosity; vertex of ♂ wider, distance between eyes approaching four times width of ocellar triangle 12

12. Thoracic pleura with black hairs restricted to dorsal mesopleuron, remainder with pale, yellow hairs; prescutum with three whitish, pollinose vittae, one median, and two submedian enclosing prst-dc . . . . *obtusa*
Thoracic pleura with black hairs on pleurotergite, sternopleuron and most of mesopleuron; prescutum with median whitish, pollinose vitta, but each submedian vitta replaced by pair of whitish, pollinose spots enclosing anterior and posterior prst-dc 13

13. Pf and genae golden pollinose; ♂ with apex of cerci pointed, surstyli hook-like; ♀ often with dark areas on dorsal T4 and T5 connected . . . . *intermedia*
Pf silver pollinose, genae golden pollinose; ♂ with apex of cerci blunt, surstyli blade-like; ♀ always with dark areas on dorsal T4 and T5 separated by grey pollinosity (Fig. 4C) . . . . *nigricornis*

Microtropesa campbelli Paramonov, 1951
(Fig. 7A)

Microtropesa campbelli Paramonov, 1951:768; Crosskey, 1973:135; Cantrell & Crosskey, 1989:761.

MATERIAL EXAMINED. HOLOTYPE ♀, Blundell's, near Canberra, Australian Capital Territory, 30.ii.1931, T.G. Campbell (ANIC).

DIAGNOSIS. Body length: 10.3 mm. A3 ovoid, orange; pf with black hairs; genae with yellow hairs, except dorsally hairs black; prescutum with pattern of whitish pollinosity (precise pattern obscured by discolouration); wings light grey, bases orange-yellow; ground colour of abdomen yellowish brown except most mesal areas on T3 black; T3 and T4 with thick, grey, pollinose triangles, apex of triangle on T4 very broad enclosing most mesal setae of marginal row; T3 with single pair of weak mm; T5 entirely grey, pollinose with very weak, hair-like setae.

REMARKS. *M. campbelli* is the only species in which T5 is entirely grey pollinose. Only the holotype is known.

Microtropesa canberrae Paramonov, 1951
(Figs 1A-C, 7A)

Microtropesa canberrae Paramonov, 1951:771; Crosskey, 1973:135; Cantrell & Crosskey, 1989:761.

MATERIAL EXAMINED. HOLOTYPE ♀, Black Mountain, Canberra, ACT, 18.v.1942, T.W. Pickard (ANIC). OTHER MATERIAL EXAMINED. NSW: Paddy's R., nr Marulan (1♂, ANIC). S AUST: Talia (1♂, SAM).

DIAGNOSIS. Body length: 11.7-13.3 mm. ♂ cerci and surstyli as in Fig. 3A,B. Fr, dc and acr long, hair-like; very long hairs on pf, genae and thorax; pf with extensive black hairing, extending below level of vibrissae; epistome weakly projecting (Fig. 1C); A3 ovoid, orange; hairs on thoracic pleura almost entirely orange-yellow; hairs on dorsal scutellum orange-yellow; wings grey, bases orange-yellow; ground colour of abdomen reddish-brown to black; T3 with (♂) or without (♀) pair of anterior, submedian grey, pollinose spots; T4 with median, grey, pollinose triangle; T5 grey pollinose except for pair of large dark spots extending on to T4; sternites and inner edges of tergites without pollinosity; T3 without mm; fore tarsi of female wide (cf Fig. 5D).

REMARKS. *M. canberrae, M. sinuata* and *M. danielsi* form a group of very similar species. *M. canberrae* can be distinguished from the latter two species by a weakly projecting epistome (Fig. 1C), parafacials with extensive black hairing, extending below the level of the vibrissae, long
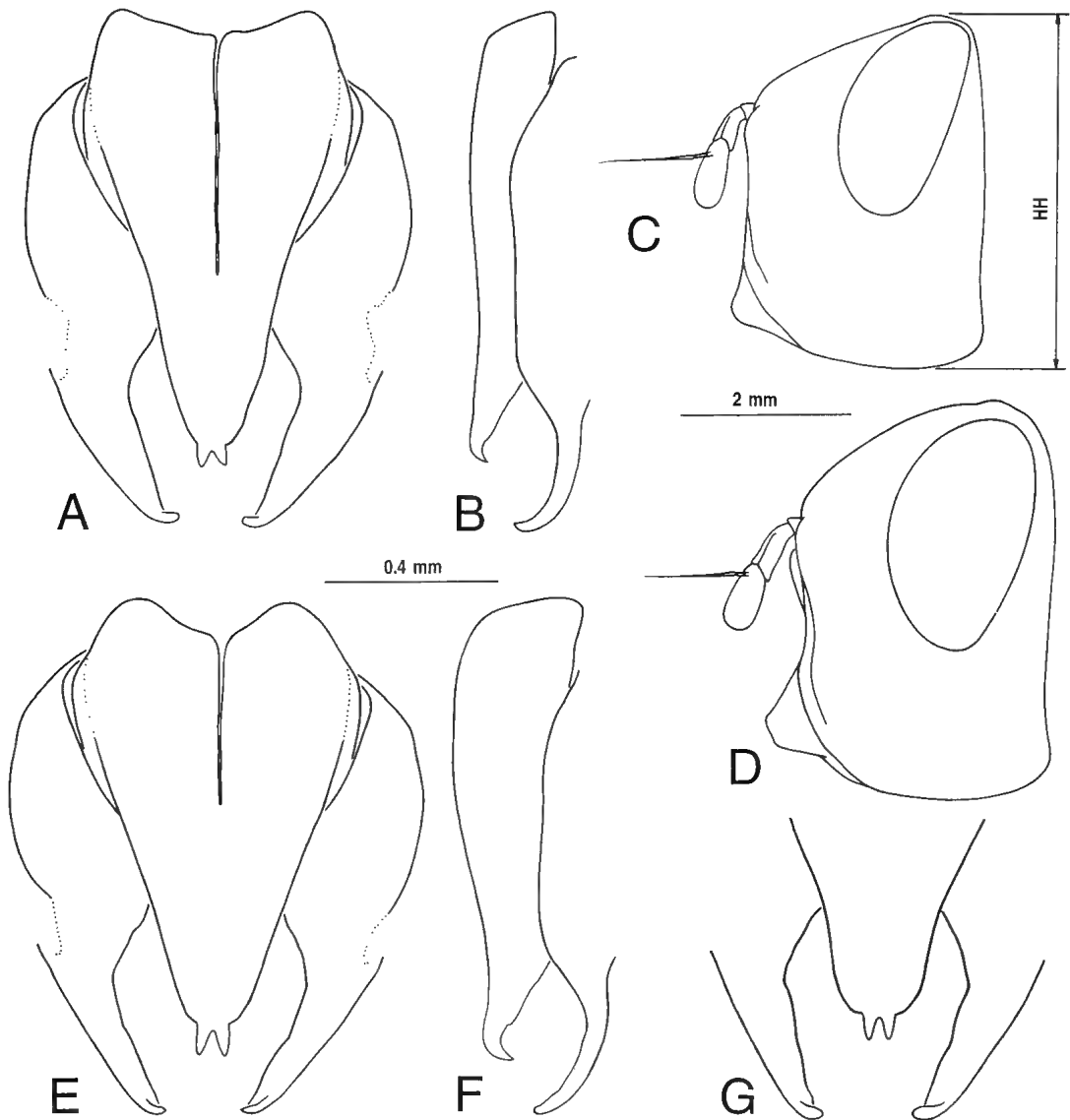
FIG. 1. A-C, *Microtropesa canberrae* (Talia, S.A.); D-G, *M. danielsi* (D-F, 3km NNW Palmer R. crossing, Qld; G, 32 km S Theodore, Qld). A, B, E, F, caudal and lateral views of ♂ cerci and surstyli. C, D, lateral view of ♂ heads, vestiture omitted. G, caudal view of apex of ♂ cerci and surstyli. HH, head height. A, B, E-G to same scale.

and hair-like fr, dc and acr and very long hairs on the parafacials, genae and thorax.

Males, which have not been previously described, are similar to females but differ as follows: vertex narrower; fore and mid tarsi not widened; ground colour of abdominal tergites reddish-brown (black in ♀); T3 with a pair of anterior, submedian, grey, pollinose spots (absent in ♀); median, grey, pollinose triangle on T4

wider. Male terminalia of *M. canberrae* closely resemble those of *M. danielsi*.

Microtropesa danielsi sp. nov.
(Figs 1D-G, 7A)

MATERIAL EXAMINED. HOLOTYPE QM26036, ♂, 3 km NNW Palmer River crossing, 16°04'S., 144°47'E., Queensland, 19.v.1989, G. & A. Daniels

(QM). Terminalia removed and stored in glycerol in microvial pinned next to holotype, with duplicate label. PARATYPES 8 ♂, same data as holotype (one with terminalia removed and stored in glycerol in microvial pinned next to paratype, with duplicate label); 1 ♂, same data as holotype except 6.x.1989, L. Ring; 2 ♂, same data as holotype except 11.ix.1991, R.C. Manskie; 1 ♂, Mt Moffatt Nat. Pk, Mt Moffatt summit, 25°04'S 148°03'E, 23.xi.95; C.J. Burwell (QM26037); 2 ♂, sandstone hilltop 32 km S Theodore, 25° 10'S 150° 00' 4.x.1991, E.G. Daniels (all UQIC unless indicated).

DIAGNOSIS. ♂ cerci and surstyli as in Fig. 1E-G. Pf with extensive yellow hairing; epistome strongly projecting (Fig. 1D); A3 ovoid, orange; hairs on thoracic pleura almost entirely orange-yellow; hairs on dorsal scutellum orange- yellow; mesonotum with thin covering of shifting whitish pollinosity, thicker surrounding anterior prst-dc; wings grey, bases orange-yellow; ground colour of abdomen dark, reddish-brown to black; T3 without grey, pollinose spots; T4 with median, grey, pollinose triangle about as wide as distance between subapical scutellar setae; T5 grey pollinose except for pair of large dark spots extending on to T4; sternites and inner edges of tergites without pollinosity; T3 without mm.

DESCRIPTION. MALE. *Head* (Fig. 1D). ground colour orange-yellow; genae and pf golden pollinose; pfr and sometimes dorsal pf with black hairs, those on rest of pf and genae orange-yellow; A3 orange, ovoid; 1st aristal segment shorter than 2nd, 3rd thickened basally.

Thorax. ground colour of mesoscutum black except posterior yellow intrusion between rows of dc; mesoscutum with thin covering of shifting, whitish pollinosity, thicker surrounding anterior prst-dc in dorsal view; hairs on mesoscutum mainly black, orange-yellow posteriorly; scutellum orange with orange-yellow hairs; hairs on pleura orange-yellow.

Wings. dark grey, bases orange-yellow.

Legs. orange-yellow, tarsi darkened.

Abdomen. ground colour of tergites dark red-brown, black medially; T3 without mm; dorsal surface of T3 immaculate; T4 with median, grey, pollinose triangle about as wide as distance between subapical scutellar setae; T5 grey pollinose except for pair of large dark spots extending onto T4; sternites and inner edges of tergites without pollinosity; hairs on abdomen black except some yellow hairs on ventral T1+2, St1 and St2.

Body length. 10.6–13.0 mm.

FEMALE. Unknown.

REMARKS. *M. canberrae, M. danielsi* and *M. sinuata* form a group of very similar species. *M. danielsi* is most easily distinguished from *M. canberrae* by extensive yellow hairing on the parafacials.

M danielsi is distinguished from most specimens of *M. sinuata* by the thinly pollinose, unpatterned mesonotum. Males of *M. danielsi* differ from males, and most females of *M. sinuata* by the absence of grey, pollinose spots on T3. Males of *M. danielsi* also differ from those of *M. sinuata* by a narrower grey, pollinose triangle on T4 and consistently longer apices of the surstyli (Fig. 1E-G).

ETYMOLOGY. For Greg Daniels, co-collector of the holotype.

Microtropesa flaviventris Malloch, 1930
(Figs 2A,B, 7C)

Microtropesa flaviventris Malloch, 1930:101; Paramonov, 1951:772; Crosskey, 1973:135; Cantrell & Crosskey, 1989:761.

MATERIAL EXAMINED. HOLOTYPE. ♀, Narromine, NSW (ANIC). OTHER MATERIAL EXAMINED. QLD: Taroom (1 ♀, QDPI); Jondaryan (1 ♀, UQIC); Wellcamp (1 ♂, 1 ♀, QDPI); Nobby (1 ♂, QDPI); 16 km N Boonah (1 ♀, QM); 5 km NE Leyburn (1 ♂, QDPI). NSW: nr Bourke (1 ♂, ANIC); 4 mile Ck, W of Wollomombi (1 ♀, ANIC); Bogan R. (1 ♀, ANIC); Mt Boppy, nr Cobar (2 ♂, ANIC); Taree (1 ♀, BCRI); Barrington Tops (1 ♀, ANIC); Round Hill Fauna Reserve (1 ♂, AM); Orange (1 ♀, ANIC); Gosford Dist. (1 ♀, 1 ♂, BCRI); Newbridge (1 ♂, 1 ♀, ANIC, 9 ♂, 6 ♀, BCRI); Penrith (3 ♂, 1 ♀, BCRI); Cowra (1 ♂, BCRI); Sydney (1 ♂, BCRI); Beverly Hills, nr Sydney (1 ♂, AM); Mt Boyce, Blue Mtns (1 ♀, AM); Sutton Forest (1 ♂, BCRI); Berry (1 ♂, BCRI); nr Yass (1 ♂, ANIC); Urana (1 ♀, ANIC); Gevogery [Gerogery?] (1 ♀, ANIC); Albury (1 ♂, BCRI); Mt Gladstone, nr Cooma (1 ♂, ANIC); Nimmitabel (1 ♀, ANIC). ACT: Black Mtn (5 ♂, 1 ♀, ANIC); Canberra (29 ♂, 3 ♀, ANIC); Blundell's, Canberra (1 ♀, ANIC); Mt Gingera (1 ♂, 1 ♀, ANIC). VIC: Strathmerton (1 ♂, ANIC); Hume Weir via Wodonga (1 ♂, UQIC); Alexandra (3 ♀, ANIC); Genoa (3 ♂, ANIC); Ballarat (1 ♂, ANIC); Eagle Point, S of Bairnsdale (1 ♀, ANIC).

DIAGNOSIS. Body length: 8.4–11.4 mm. ♂ cerci and surstyli as in Fig. 2A, B. Hairs on pf black, those on genae mostly pale yellow, sometimes with a few black hairs dorsally; mesonotum in caudal view blue-black with thin covering of whitish pollinosity; wings light grey, almost hyaline, base yellowish; ground colour of abdomen yellowish, excavation of T1+2 blue-
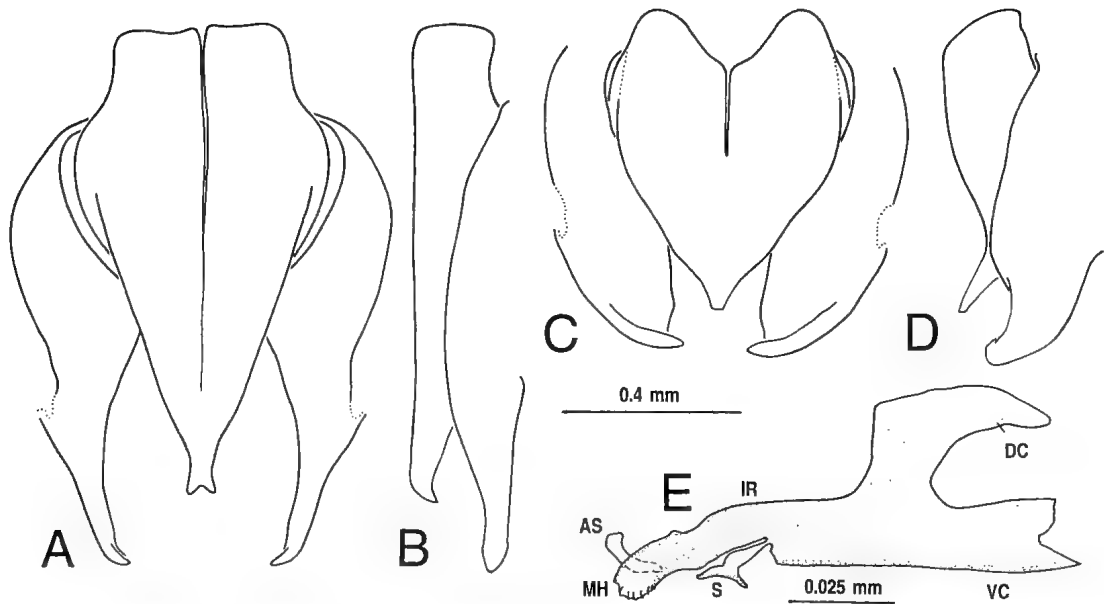
FIG. 2. A, B, *Microtropesa flaviventris*; C-E, *M. intermedia*. A-D, caudal and lateral views of ♂ cerci and surstyli. E, lateral view of cephalopharyngeal skeleton of 1st instar larva. AS, accessory sclerite; DC, dorsal cornu; IR, intermediate region; MH, mouth hook; S, sclerite of salivary gland; VC, ventral cornu. A-D to same scale.

black, continued as dorsomedial vitta extending to T5; T3 and T4 in caudal view each with indistinct, median triangle of thin, whitish pollinosity which hardly obscures ground colour, sometimes only anterior base of triangle present on T3; T5 with extensive thin, whitish pollinosity, sometimes with pair of yellow spots without pollinosity in caudal view; T3 without mm.

REMARKS. *M. flaviventris* most closely resembles *M. obtusa* and *M. ochriventris* from which it can be distinguished by the uniform, thin pollinosity on the mesonotum and the absence of mm on T3. The blue-black, abdominal vitta of *M. flaviventris* is broader in females than males. In females it is about as broad as the distance between the basal scutellar setae, while in males it is, at most, a little wider than the distance between the subapical scutellar setae.

Hardy (1939) incorrectly considered *M. flaviventris* a junior synonym of *M. obtusa*.

Microtropesa intermedia Malloch, 1930
(Figs 2C-E, 7E)

Microtropesa intermedia Malloch, 1930:100; Hardy, 1939:35; Paramonov, 1951:775; Crosskey, 1973:135; Cantrell & Crosskey, 1989:761.

MATERIAL EXAMINED. HOLOTYPE. ♂, Eidsvold, Queensland, 20.iv.1924, Bancroft (ANIC). OTHER MATERIAL EXAMINED. QLD: Yeppoon (1♂, ANIC); Theodore (1♀, UQIC); Electra State Forest, 25 km S Bundaberg (1♂, ANIC); Bluff Ra. foothills, Biggenden (1♀, ANIC); SW Bluff Ra., Biggenden (1♂, ANIC); Rockpool Gorge, Mt Walsh Nat. Pk, Biggenden (2♂, 1♀, ANIC); Coalstoun Lakes, nr Biggenden (3♂, ANIC); S Boolboonda Ra., via Mt Perry (1♀, ANIC); nr Seary's Ck, Cooloola (1♀, QM); Noosa Nat. Pk (1♀, UQIC); Tibrogargan Ck, Glasshouse (1♀, UQIC); Beeberum [Beerburrum?] (1♂, UQIC); Point Lookout, North Stradbroke Is. (1♂, UQIC); Brisbane (1♂, 2♀, QM); St. Lucia, Brisbane (1♂, 1♀, UQIC, 2♀, ANIC); Stradbroke Is. (1♀, QM); Stockyard Ck, SE Capalaba (1♂, UQIC); Sunnybank, Brisbane (2♂, ANIC); 4 km WNW Mt Cotton (1♀, UQIC); The Blunder, Brisbane (1♀, ANIC); 16 km N Boonah (1♀, UQIC); Amiens State Forest, nr Stanthorpe (1♀, UQIC). NSW: Clyde Mtns, nr Braidwood (1♀, ANIC); Alpine Ck, Kiandra (2♀, ANIC). ACT: Canberra (1♂, ANIC); Blundell's (1♂, ANIC); Lees Ck, Brindabella Ra. (1♂, 1♀, AM); Bendora (1♀, ANIC); Mt Gingera (1♂, 3♀, ANIC); Cotter R. (1♂, ANIC). VIC: 2 miles [3.5 km] NW Porepunkah (1♂, ANIC). Tasmania: Rupert Point, Pieman R. (1♂, ANIC); 9 km SE Miena (13♀, UQIC); Derwent Bridge (1♂, ANIC). Other: no data (1♀, QDPI, 1♀, ANIC).
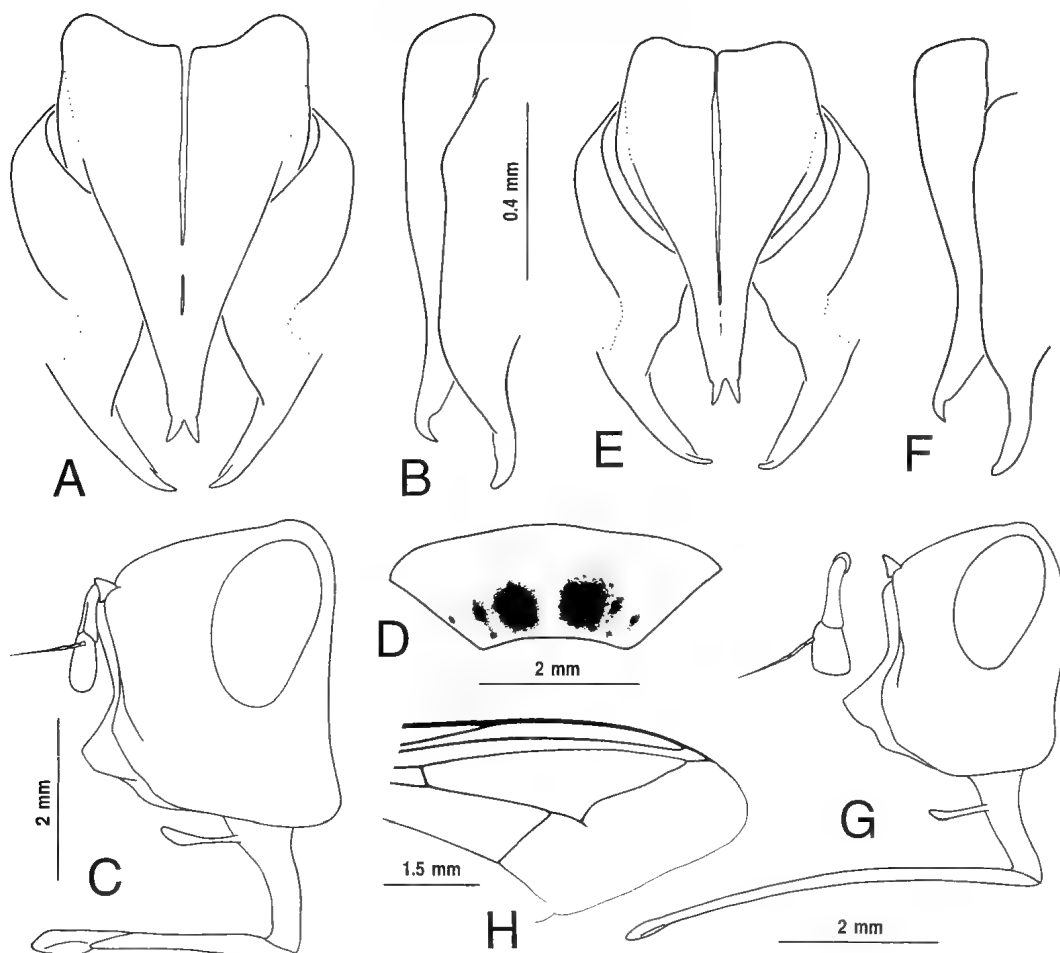
FIG. 3. A-D, *Microtropesa latigena*; E, F, *M.* near *latigena* ; G, H, *M. longimentum* holotype. A, B, E, F, caudal and lateral views of ♂ cerci and surstyli. C, G, lateral view of ♀ heads, vestiture omitted. D, caudal view of 4th apparent abdominal tergite (T5). H, apex of wing.

DIAGNOSIS. Body length 11.7–13.5 mm. ♂ cerci and surstyli as in Fig. 2C,D. Pf and genae golden pollinose; A3 black, base yellow or orange-yellow; mesonotum with bronze reflection and distinct pattern of whitish pollinosity which shifts markedly when viewed dorsally and then caudally; mesonotum with median, pollinose vitta, broken at transverse suture, extending to base of scutellum in most specimens; prescutum, in dorsal view, with a pair of pollinose spots enclosing anterior and posterior setae of each row of prst-dc; wings grey, bases orange-yellow; hairs on ventral surface of basal node of R4+5 black, sometimes with a few yellow hairs; ground colour of T3 and T4 red-brown to black, both with median, grey, pollinose triangles; T5

grey pollinose with pair of large, dark spots; T3 with one or more pairs of mm.

REMARKS. *M. intermedia* is very similar to *M. nigricornis* from which it is best separated by the golden pollinose pf and genae, the bronze reflection and shifting pollinose markings on the mesonotum and the colour of the hairs on the ventral node of R4+5. Some specimens of *M. intermedia* are similar to those of *M. nigricornis* in that the grey, pollinose markings on the abdomen are distinct. However, in other specimens of *M. intermedia* the pollinose triangles on T3 and T4 are thin with poorly defined margins. In addition, some females of *M. intermedia* can be separated from those of *M. nigricornis* by the

dark spots on T5 extending to the anterior margin of the tergite. The male genitalia of *M. intermedia* (Fig. 2C,D) have the apex of the cerci pointed and the surstyli blade-like and differ markedly from those of *M. nigricornis* (Fig. 4A,B).

1st-instar larvae were recovered from the uterus of a female *M. intermedia*. Their banded appearance and strongly arched dorsal cornua of the cephalopharyngeal skeleton resemble the larvae of *Cuphocera* (Tachinini) and the Linnaemyini described by Cantrell (1988). They differ in the distinctly serrate edges of the mouth-hooks (Fig. 2E). Body length: 0.76 mm (n = 10).

Microtropesa latigena Paramonov, 1951
(Figs 3A-D, 7A)

Microtropesa latigena Paramonov, 1951:769; Crosskey, 1973:135; Cantrell & Crosskey, 1989:761.

MATERIAL EXAMINED. HOLOTYPE ♀, Kalgoorlie, WA, August, L.J. Newman (ANIC). OTHER MATERIAL EXAMINED. NSW: Broken Hill (1♂, AM). SAUST: Coonamoree [? Coonamoranie] (1♂, ANIC); Stuart Ra. (1♀, ANIC); 37 miles [60 km] ENE White Well [White Wells] (2♂, ANIC); 19 miles [31 km] ENE Eucla (1♀, ANIC). WA: Mt Squires (1♀, SAM); Nanambinia HS, SW Balladonia (1♀, ANIC).

DIAGNOSIS. Body length: 10.9–12.6 mm. ♂ cerci and surstyli as in Fig. 3A,B. A3 ovoid, brown (darker in ♂), base yellow; pf very wide (Fig. 3C), with black hairs; hairs on genae mostly black; anterior mesonotum with distinct pattern of whitish pollinosity, prescutum with acr enclosed in median, pollinose vitta bordered laterally by pair of black, submedian vittae extending on to scutum, narrowly interrupted at transverse suture; each row of prst dc enclosed in pollinose vitta bordered laterally by black vitta extending on to scutum, broadly interrupted at transverse suture; wings light grey, bases brownish-yellow; ground colour of T3 and T4 in ♀ black, in ♂ reddish-yellow, black medially; T3 and T4 with median, grey, pollinose triangles usually with sharply defined margins; T5 grey, pollinose with pair of small, submedian, black or dark-brown spots posterodorsally (Fig. 3D), often second pair of dark spots posteroventrally; bases of some setae on T5 black; T3 with one or two pairs of mm (weaker in ♂).

REMARKS. A male and female in ANIC from near Alice Springs are similar in most respects to *M. latigena*, to which they key, but the abdominal ground colour of the male is darker, the mm on T3 are extremely weak in the female and absent in the male, the pollinose triangles on T3 and T4 have poorly defined margins and the cerci and surstyli of the male differ slightly (Fig. 3E,F). They probably represent an undescribed species.

Microtropesa longimentum sp. nov.
(Figs 3G,H, 7A)

MATERIAL EXAMINED. HOLOTYPE ♀, Lake Surprise area, Simpson Desert, 135° 5'E., 26° 4'S., S AUST, 13.ix.1971, T.F. Houston (SAM).

The holotype has some setae, hairing and pollinosity abraded, however it differs radically from the other known *Microtropesa* and description is warranted.

DIAGNOSIS. *M. longimentum* is recognisable by its greatly elongated mentum (Fig. 3G) and closed cell R5 in the wing (Fig. 3H).

DESCRIPTION. FEMALE. *Head* (Fig. 3G). Ground colour yellow; viewed laterally, pfr, pf and genae thickly whitish pollinose; pfr with fine black hairs; pf and genae with sparse, strong, black hairs, many seta-like; A3 quadrangular, wider at apex, brownish; 1st aristal segment elongate, almost as long as 2nd; 3rd aristal segment about twice as long as combined length of 1st and 2nd, basal third thickened; proboscis with mentum longer than head height; labellum reduced.

Thorax. Ground colour of mesonotum black, except posterior margin, posterior intrusion between rows of dc and lateral margin enclosing ia yellow; scutellum yellowish; pattern of whitish pollinosity on mesonotum as follows; narrow, median, pollinose vitta between acr; pollinose vitta enclosing each row of prst-dc; prst-ia and presutural seta enclosed in pollinosity; humeral callus pollinose; pollinosity on scutum partially abraded but with large, median patch enclosing both rows of acr; hairs on mesonotum and scutellum black.

Wings (Fig. 3H). Cell R5 closed; wings light grey, bases yellowish-brown.

Legs. Brownish-yellow, apical tarsal segments darkened.

Abdomen. Ground colour of tergites, in dorsal view, shining-black; T3 and T4 each with thick, grey, pollinose, anterior band with median, triangular extension reaching posterior margin; T5 grey pollinose except for pair of large, posterodorsal black spots; venter of abdomen grey pollinose, thin on sternites, yellow ground colour showing through; T3 with pair of very strong mm.
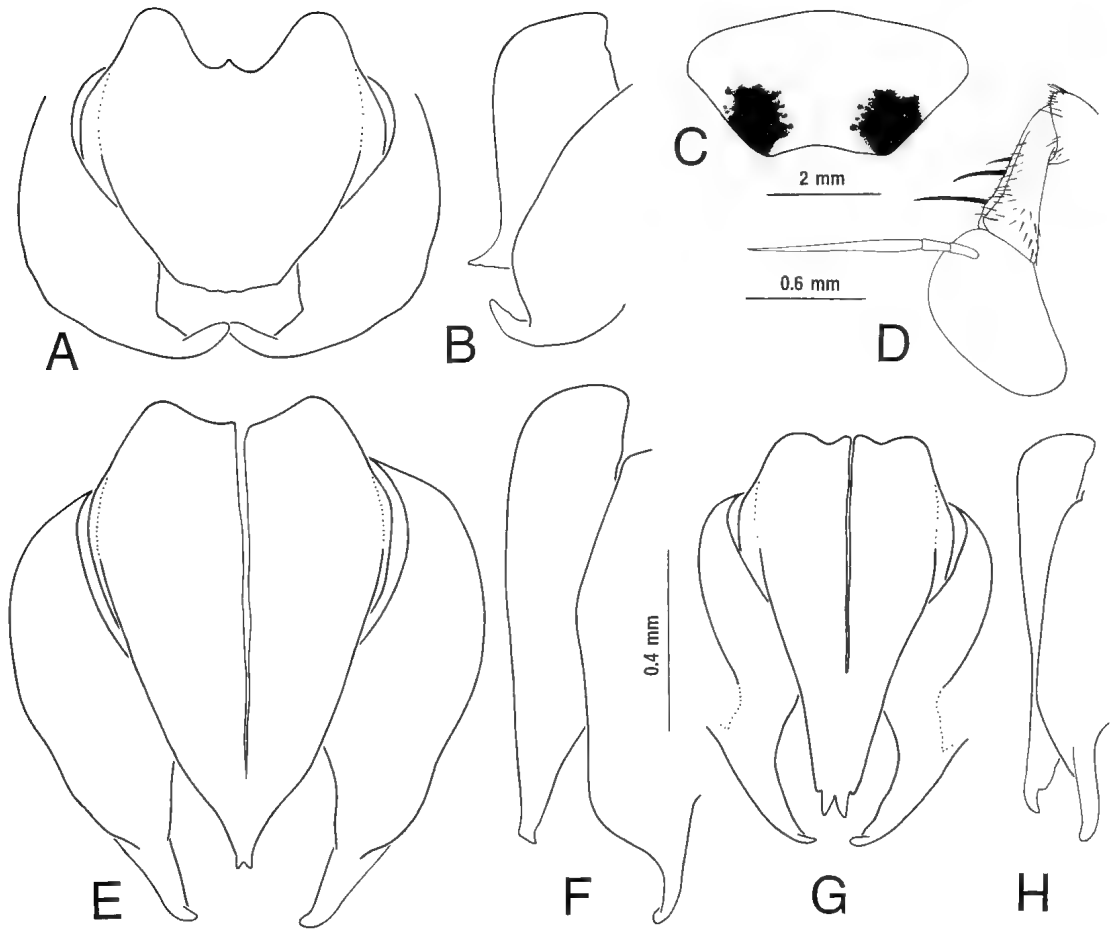
FIG. 4. A-C, *Microtropesa nigricornis*; D-F, *M. obtusa*; G, H, *M. ochriventris*. A, B, E-H, caudal and lateral views of ♂ cerci and surstyli. C, caudal view of 4th apparent abdominal tergite (T5). D, ♂ antenna. A, B, E-H to same scale.

Body length. 10.6 mm.
MALE. Unknown.

ETYMOLOGY. Latin noun in apposition, for the long mentum.

Microtropesa nigricornis Macquart, 1851
(Figs 4A-C, 7F)

Microtropesa nigricornis Macquart, 1851:199, pl. 21, fig. 5; Townsend, 1939:14; Hardy, 1939:35; Engel, 1925:344; Paramonov, 1951:774; Crosskey, 1971:278; Crosskey, 1973:135; Cantrell & Crosskey, 1989:761.

MATERIAL. LECTOTYPE ♂ (designated Crosskey, 1971:278), TAS (MNHN) [not examined but notes on important characters provided by Dr. L. Matile of MNHN]. MATERIAL EXAMINED NSW: Gibraltar Ra. Nat. Pk (2♂, 2♀, UQIC); NE [New England?] Nat. Pk (1♂, ANIC); 6 km NE Bilpin (1♂, AM); 5 km E Bilpin (1♂, 2♀, AM); Jinki Ck, Blue Mtns (1♀, AM); 3 km S Mount Wilson (1♀, AM); Mt Tomah (2♂, AM); 3 miles [5 km] SW Mt Tomah (2♂, AM); Mount Victoria (1♂, ANIC); Hat Hill (10♂, 1♀, AM); Black-heath (1♂, ANIC); Lawson, Blue Mtns (3♂, AM); Goondera Ridge, Royal Nat. Pk (2♀, AM); Clyde Mts, nr Braidwood (1♂, ANIC); Olson's [Olsen's?] Lookout, Snowy Mtns (1♂, ANIC); Sawpit Ck, Mt Kosciusko (1♀, ANIC). ACT: Canberra (1♂, ANIC); Mt Coree (5♂, 1♀, ANIC); Blundell's (1♂, ANIC); Lees Ck, Brindabella Ra. (1♂, 1♀, AM); Mt Franklin (3♂, ANIC). TAS: Granite Point Reserve, Bridport (5♀, UQIC); Mt George (1♂, UQIC); Turners Beach, nr Ulverstone (1♂, UQIC); Don R., nr Don (2♀, UQIC); Hobart (1♂, ANIC); Tasmania (2♂, 1♀, ANIC).

DIAGNOSIS. Body Length 11.8–12.9 mm. ♂ cerci and surstyli as in Fig 4A,B. Pf silver pollinose; genae golden pollinose; A3 black, base yellow or orange-yellow; mesonotum black with distinct pattern of whitish pollinosity which shifts little when viewed dorsally and then caudally; mesonotum with median, pollinose vitta, broken at transverse suture, extending to base of scutellum in most specimens; prescutum with pair of pollinose spots enclosing anterior and posterior setae of each row of prst-dc; wings grey, bases orange-yellow; hairs on ventral surface of basal node of R4+5 yellow, sometimes with a few black hairs; ground colour of T3 and T4 red-brown to black, both with median, grey, pollinose triangles; T5 grey pollinose with pair of large, dark spots; T3 with one or more pairs of mm.

REMARKS. *M. nigricornis* is very similar to *M. intermedia* from which it can be distinguished by the silver pollinose pf, the black mesonotum with stable pollinose markings and the colour of the setae on the ventral surface of the basal node of R4+5. The grey pollinose markings on the abdomen of *M. nigricornis* are always thick with sharply defined margins and the dark spots on T5 are always bordered anteriorly by pollinosity in both sexes (Fig. 4C). Male genitalia of *M. nigricornis* (Fig. 4A,B) have the apex of the cerci blunt and the surstyli hook-like and differ markedly from those of *M. intermedia* (Fig. 2C,D).

Microtropesa obtusa (Walker, 1853)
(Figs 4D-F, 7B)

Tachina obtusa Walker, 1853:274.
Echinomyia stolida Walker, 1858:196. Synonymy by Austen, 1907:330.
Gerotachina obtusa Townsend, 1916:152; Townsend, 1932:40.
Microtropesa flavitarsis Malloch, 1929:288; Malloch, 1930:100; Paramonov, 1951:773; Crosskey, 1973:135; Cantrell & Crosskey, 1989:761. Synonymy by Hardy, 1939:36.
Microtropesa obtusa (Walker); Hardy, 1939:36; Paramonov, 1951:771; Crosskey, 1973:135; Cantrell & Crosskey, 1989:761.

MATERIAL EXAMINED. LECTOTYPE ♀ designated Townsend (1932:40), NSW (BMNH). Holotype of *E. stolida* ♂, NSW (BMNH). Holotype of *M. flavitarsis* ♂, TAS (AM). OTHER MATERIAL EXAMINED. ACT: Canberra (3♂, 3♀, ANIC). S AUST: Roseworthy (1♀, SAM). WA: Kojarena (1♀, ANIC); Geraldton (1♂, 1♀, ANIC); Bunbury (1♂, ANIC, 2♂, WADA).

DIAGNOSIS. Body length: 11.2–12.5 mm. ♂ cerci and surstyli as in Fig. 4E,F. Pf black haired; genae with numerous black hairs dorsally, rest with pale yellow hairs; A3 of ♀ ovoid, of ♂ triangular, produced towards face distally (Fig. 4D); anterior mesonotum with distinct pattern of whitish pollinosity; acr enclosed in median pollinose vitta bordered laterally by pair of black submedian vittae which are narrowly interrupted at transverse suture; each row of prst-dc enclosed in pollinose vitta bordered laterally by black vitta which is broadly interrupted at transverse suture; ground colour of abdomen orange-yellow with black, dorsomedial vitta; T3 and T4 in caudal view each with median triangle of thin, whitish pollinosity which usually obscures ground colour; T5 with pair of large spots without pollinosity in caudal view; T3 with 2-4 pairs of strong mm.

REMARKS. *Microtropesa obtusa* most closely resembles *M. flaviventris* and *M. ochriventris*. The numerous black hairs on the genae, the pattern of pollinose vittae on the mesonotum and the strong mm on T3 distinguish *M. obtusa* from *M. flaviventris*. The pattern of whitish pollinosity on the abdomen, especially T4 and T5 distinguishes *M. obtusa* from *M. ochriventris*.

The triangular A3 of male *M. obtusa* is characteristic.

Microtropesa ochriventris Malloch, 1929
(Figs 4G,H, 7D)

Microtropesa ochriventris Malloch, 1929:287, fig.2; Malloch, 1930:100; Paramonov, 1951:776; Crosskey, 1973:135; Cantrell & Crosskey, 1989:762.

MATERIAL EXAMINED. HOLOTYPE ♀, Allyn Range, Barrington Tops, NSW, February 1925, Sydney University zoological expedition (ANIC). OTHER MATERIAL EXAMINED. QLD: Pomona (1♂, UQIC); Wild Horse Mtn, nr Beerwah (8♂, QDPI); Mt Tibrogargan (1♂, UQIC); Mt Mitchell, nr Aratula (1♂, UQIC). NSW: hilltop, 24 km W Grafton (1♂, UQIC); 25 km W Grafton (1♀, QDPI); Barwick R., NE [New England?] Tableland (1♂, ANIC); Point Lookout, nr Ebor (3♂, ANIC); 12 km SW Ebor (2♀, UQIC); Allyn Ra., Barrington Tops (2♀, ANIC); Hat Hill (1♀, AM); Kuringai [Ku-ring-gai] Chase Nat. Pk (1♀, BCRI); Kanangra Boyd Nat. Pk (1♂, BCRI); Nowra (1♀, ANIC); 9 miles [14.5 km] NW Braidwood (1♀, ANIC); Rutherford Ck, Brown Mtn, nr Nimmitabel (1♀, AM). ACT: Black Mtn Reserve (1♀, ANIC); Canberra (1♂, ANIC); Mt Coree (1♂, ANIC); Lees Ck, Brindabella Ra. (1♂, AM); Mt Gingera (1♀, ANIC). Victoria: Bogong, via Mt Beauty (1♀, UQIC);
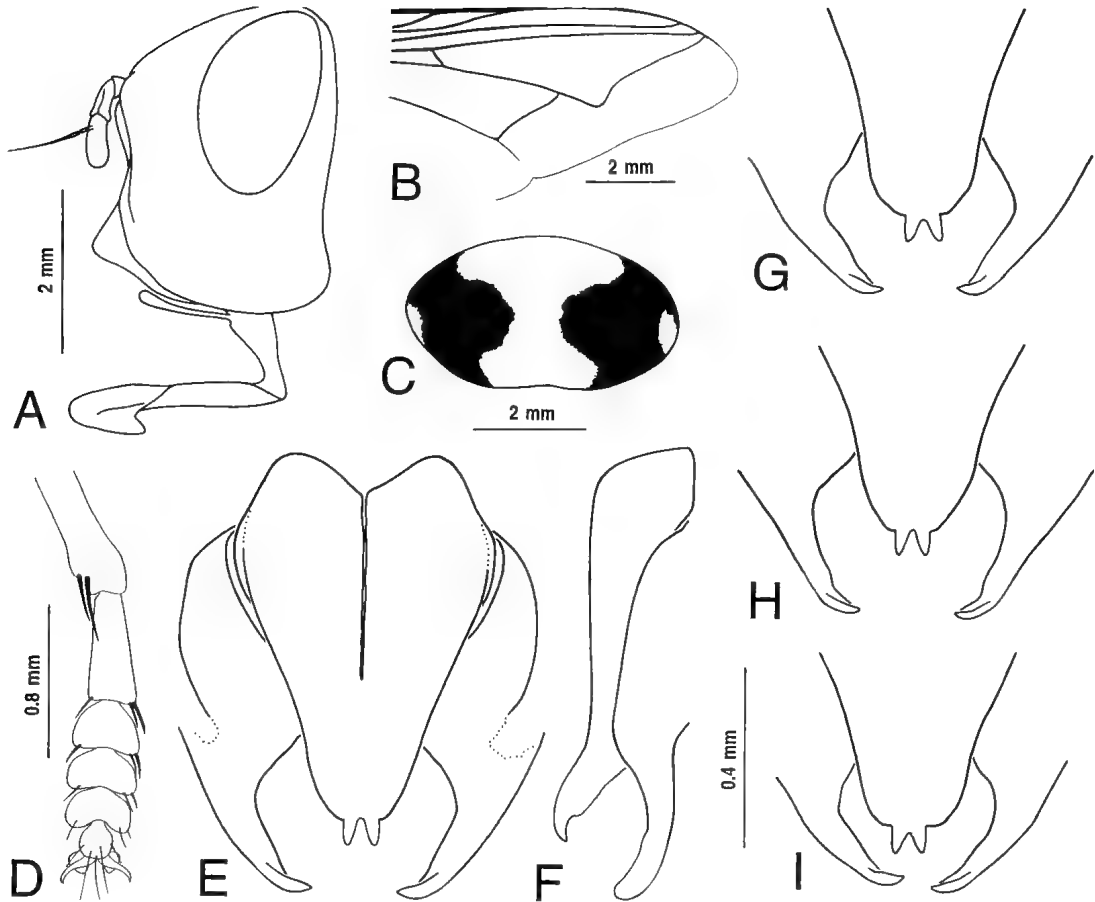
FIG. 5. *Microtropesa sinuata*. (E, F, Mt Tinbeerwah, Qld; G, 25 km W Bridport, Tas.; H, Isla Gorge, Qld; I, Swan R, W.A.). A, lateral view of ♂ head, vestiture omitted. B, apex of wing. C, caudal view of 4th apparent abdominal tergite (T5). D, dorsal view of ♀ fore tarsus. E, F, caudal and lateral view of ♂ cerci and surstyli. G-I, caudal views of apices of ♂ cerci and surstyli. E-I to same scale.

Victoria (1♂, WADA). Tasmania: Strzelecki Peaks, Flinders Is. (1♂, ANIC); Strahan (1♂, ANIC); Hobart (1♀, ANIC). South Australia: 2 km SE of Montacute (1♀, ANIC). Other: Gordon [N.S.W. or Tas.?] (1♀, ANIC).

DIAGNOSIS. Body length 10.7–12.3 mm. ♂ cerci and surstyli as in Fig. 4G,H. Vertex of ♂ very narrow, less than twice width of ocellar triangle; Pf black haired; genae with numerous black hairs dorsally, rest with pale yellow hairs; A3 of ♂ and ♀ ovoid; mesonotum with bronze reflection; anterior mesonotum with distinct pattern of whitish pollinosity; acr enclosed in median pollinose vitta bordered laterally by pair of black submedian vittae which are narrowly interrupted at transverse suture; black submedian vittae coalesce anteriorly; each row of prst-dc enclosed in pollinose vitta bordered laterally by black vitta which is broadly interrupted at transverse suture; ground colour of abdomen orange with black, dorsomedial vitta which is largely obscured by pollinosity; T3 with median triangle or 'V' of whitish pollinosity; rest of abdomen with orange pollinosity (thicker on T5) except for pair of orange spots with black mesal edges on T3; T3 with one or more pairs of mm.

REMARKS. *M. ochriventris* can be separated from the similar *M. flaviventris* and *M. obtusa* by the extensive orange pollinosity on the abdomen. The very narrow vertex of males is characteristic.

Hardy (1939) incorrectly considered *M. ochriventris* a junior synonym of *M. obtusa*.

Microtropesa sinuata (Donovan, 1805)
(Figs 5, 7G)

Musca sinuata Donovan 1805:[166], pl. [41].
Microtropesa sinuata (Donovan); Macquart, 1846:313; Macquart, 1851:199; Engel, 1925:344, fig.B; Townsend, 1932:40; Townsend, 1939:13; Hardy, 1939:34; Paramonov, 1951:776; Crosskey, 1973:135; Cantrell & Crosskey, 1989:762.
Tachina bura Walker, 1849:760. Synonymy by Hardy 1939:34.
Microtropesa ignipennis Brauer, 1899:510 (unavailable name published in synonymy with *sinuata* Donovan, not subsequently made available);Crosskey, 1971:278.
Microtropesa latimana Malloch, 1929:287, fig. 3a; Malloch 1930:100. Synonymy by Hardy 1939:34.
Some early references are given by Hardy (1939:34).

MATERIAL. The holotype of *M. sinuata* is not in London as stated by Townsend (Crosskey, 1971) and is presumed lost. Lectotype of *T. bura* ♂, designated by Crosskey (1973:163), Tasmania, Rev. J. Ewing (BMNH) [examined]. Holotype of *M. latimana* ♀, Queensland (AM) [examined]. OTHER MATERIAL EXAMINED. QLD: Kroombit Tops (2♂, 1♀, UQIC, 1♂, QM); Mt Scoria, 6 km S Thangool (4♂, UQIC); Expedition Ra. (1♂, AM); Marlong Arch, Mt Moffatt Nat. Pk (2♂, QM); Mt Moffatt summit, Mt Moffatt Nat. Pk (4♂, QM); Mt Moffat [Moffatt] Nat. Pk (1♂, UQIC); Isla Gorge Nat. Pk (5♂, UQIC); Mt Woowoonga, 54 miles [87 km] SW Bundaberg (1♂, ANIC); Woowoonga Ra., SW Bundaberg (1♂, ANIC); Bluff Ra., Biggenden (1♂, ANIC); Mt Tinbeerwah, nr Cooroy (2♂, UQIC, 6♂, QDPI); Cooroy (1♂, AM); Beacon Hill, 16 km W Imbil (1♂, UQIC); 16 km SW Kumbia (1♂, UQIC); Sunday Ck Fire Tower, Jimna State Forest (1♂, QM); Yarraman (1♂, UQIC); Wild Horse Mtn, nr Beerburrum (2♂, UQIC); Mt Glorious (1♂, ANIC); Brisbane (6♂, QDPI, 1♂, ANIC); Toowong (1♂, QM); 13 km N Dunwich, North Stradbroke Is. (1♂, UQIC); Flinders Peak (13♂, 4♀, UQIC, 1♂, QM); Mt Edwards, nr Aratula (3♂, UQIC); Bollon (1♂, ANIC); Mt Mitchell, nr Aratula (2♂, UQIC); Miami, G. [Gold] Coast (1♀, UQIC); Mt Greville, nr Aratula (2♂, UQIC); Lamington Nat. Pk (5♂, UQIC); [Lamington?] Nat. Pk (1♀, QM); Amiens, nr Stanthorpe (2♂, AM, 1♀, ANIC); Amiens State Forest (1♂, UQIC); Glen Aplin (3♂, UQIC); Mt Marlay, nr Stanthorpe (1♂, UQIC); Queensland (1♀, AM). NSW: Bald Rock Nat. Pk, 25 km SE Stanthorpe (1♂, UQIC); Gibraltar Ra. Nat. Pk (1♂, 1♀, UQIC); Grafton (2♂, ANIC, 1♂, AM); 24 km W Grafton (1♂, UQIC); 25 km W Grafton (1♂, UQIC, 2♂, QDPI); 15 km W South Grafton (1♂, UQIC); 20 km W South Grafton (1♂, UQIC); 24 km W South Grafton (1♂, UQIC); Mt Kaputar Nat. Pk (2♂, AM); 14 km SW Ebor (1♀, UQIC); New England Nat. Pk (1♂, ANIC); Uralla (1♂, ANIC); Dangar Falls (3♂, ANIC); Warrumbungle Nat. Pk, nr Coonabarabran (1♀, ANIC); Cobar (1♂, UQIC); Mt Boppy, nr Cobar (7♂, ANIC, 1♂,

AM); Mt Gibraltar (1♂, AM); Barrington R. (1♀, ANIC); W end Dilgy Ck Circle Road, N section Barrington Tops State Forest (1♀, AM); Mt Arthur, 3 miles [5 km] W Wellington (1♂, ANIC); Round Hill Fauna Reserve (5♀, AM); Toronto (1♂, UQIC, 2♂, 1♀, ANIC); Orange (1♂, ANIC); Clarence, Blue Mtns (3♀, AM); 3 km NE Bilpin, nr Kurrajong (1♀, AM); nr Mt Bell (1♂, AM); Mt York, Blue Mtns (1♀, AM); Mt Banks, Blue Mtns (1♂, AM); Blackheath (2♀, ANIC); Wentworth Falls (2♀, ANIC); Lindfield (1♀, ANIC); Ashfield (1♀, AM); Baldy Bill Fire Rd, Kanangra Plateau (1♀, AM); Macquarie Fields (1♀, BCRI); Goondera Ridge, Royal Nat. Pk (1♂, AM); Wee Jasper (1♀, ANIC); Clyde Mtns, nr Braidwood (12♂, ANIC); Clyde Mtns, E slope (1♂, ANIC); Talbingo (1♂, ANIC); Durras North (1♂, ANIC); Roseville (1♂, BCRI). ACT: Black Mtn (1♂, ANIC); Canberra (1♂, 1♀, QDPI); Mt Coree (1♀, ANIC); Blundell's (1♀, ANIC); Queanbeyan (1♂, UQIC); Lees Spring, Brindabella Ra. (1♀, ANIC). VIC: Wyperfield Nat. Pk (1♂, AM); Mt William, Grampians (1♂, ANIC); Gisborne (2♂, ANIC, 1♂, QM); Killara (1♂, ANIC); Melbourne (1♂, SAM); Mt Dandenong (1♂, ANIC). TAS: Mt William Nat. Pk (1♂, UQIC); 25 km W Bridport (1♂, UQIC); Lefroy (1♂, SAM); Freycinet Nat. Pk (1♂, ANIC); Tasmania (2♂, 1♀, SAM). South Australia: Sleaford Bay (2♀, ANIC); Mt Lofty (1♂, 1♀, SAM). WA: 6 miles [9.5 km] SW Mullewa (1♀, ANIC); Three Springs (1♀, WADA); Moora (1♂, WADA); Toodyay (1♂, SAM); [?] Cunderdin (1♀, QM); Perth (1♀, ANIC); Crawley, Perth (1♀, ANIC); Swan R. (1♂, 2♀, ANIC); Bedfordale (1♀, WADA); Gleneagle (1♀, WADA); Mt Ragged (1♂, ANIC); 24 miles [39 km] E Pingrup (1♀, ANIC); Margaret R. mouth (1♀, SAM); Stirling Ra. (1♂, WADA); Albany (1♂, ANIC). Other: 1590 (1♂, QDPI); no data (1♀, QM, 1♀, SAM, 1♂, 1♀, QDPI).

DIAGNOSIS. Body length: 10.2–14.6 mm. ♂ cerci and surstyli as in Fig. 5E-I. Pf usually with extensive yellow hairing, rarely with extensive black hairing but never extending below level of vibrissae and at least ventral third of pf with yellow hairs; epistome strongly projecting (Fig. 5A); A3 ovoid, orange; hairs on thoracic pleura almost entirely orange-yellow; hairs on dorsal scutellum orange-yellow; prescutum with whitish pollinosity developed into pattern of stripes and spots; wings grey, bases orange-yellow; ground colour of abdomen dark, reddish-brown to black; T3 usually with pair of anterior, submedian, grey, pollinose spots (rarely absent in ♀); T4 with median, grey, pollinose triangle wider than distance between subapical scutellar setae in ♂; T5 grey pollinose except for pair of large dark spots extending on to T4; sternites and inner edges of tergites without pollinosity; T3 without mm.
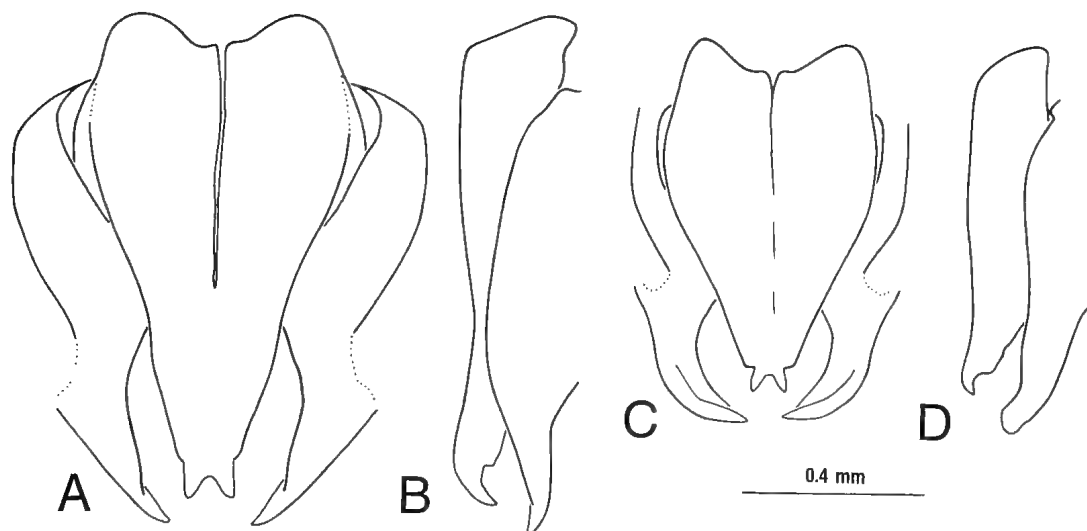
FIG. 6. A, B, *Microtropesa violacescens*; C, D, *M. viridescens*. A-D, caudal and lateral views of ♂ cerci and surstyli.

REMARKS. *M. canberrae, M. danielsi* and *M. sinuata* form a group of very similar species. Most specimens of *M. sinuata* differ from *M. canberrae* by extensive yellow hairing on the parafacials. Rarely the parafacials are black haired as in *M. canberrae*, however, in *M. sinuata* black hairs never extend below the level of the vibrissae.

Most specimens of *M. sinuata* can be separated from *M. danielsi* by the pattern of whitish pollinose spots on the prescutum of the mesonotum. Males and most females of *M. sinuata* differ from males of *M. danielsi* by the pair of anterior, submedian, grey, pollinose spots on T3. Males of *M. sinuata* also differ from those of *M. danielsi* by a wider grey, pollinose triangle on T4 and consistently shorter apices of the surstyli (Fig. 5E-I).

Microtropesa skusei Bergroth, 1894
(Fig. 7B)

Microtropesa skusei Bergroth, 1894:73; Engel, 1925:345; Paramonov, 1951:767; Crosskey, 1973:135; Cantrell & Crosskey, 1989:762.

MATERIAL. HOLOTYPE ♀, Coomooboolaroo, near Duaringa, Queensland (most likely depository Zoological Museum, Helsinki, not located by Crosskey (1973), probably lost).

DIAGNOSIS. As for *M. viridescens* except hairs on palpi black.

REMARKS. Bergroth (1894) described *M. skusei* from one or more females which have not been located. Females of *M. viridescens* match the original description of *M. skusei* except for the hairs on the palps. According to Bergroth (1894) the hairs on the palps of *M. skusei* are black while those on the palps of *M. viridescens* are yellow, occasionally with a few black hairs.

Hardy (1939) incorrectly considered *M. skusei* a junior synonym of *M. sinuata*.

Microtropesa violacescens Enderlein, 1937
(Figs 6A,B, 7B)

Microtropesa violacescens Enderlein, 1937:441; Crosskey, 1973:135; Cantrell & Crosskey, 1989:762.
Microtropesa sinuata; Malloch, 1928:614; Malloch, 1929:287, figs 1, 3b; Malloch, 1930:100.
Microtropesa fallax Hardy, 1939:35; Paramonov, 1951:777. Synonymy by Crosskey, 1973:136.

MATERIAL. Lectotype of *M. violacescens* ♂ (designated Crosskey, 1973:161), Herberton, QLD (DEI) [not examined]. Holotype of *M. fallax* ♀, Brisbane, Queensland [not located, probably lost]. MATERIAL EXAMINED. NT: 7 km NNW Cahills x-ing, E Alligator R. (1♀, ANIC); Manton Dam, 52 km SSE Darwin (1♂, ANIC). QLD: Mt White, Coen (1♂, AM); Cooktown (1♂, ANIC); 12 km N Palmer R. x-ing (1♀, UQIC); 8 km SSW Atherton (7♂, 1♀, UQIC); Bluewater, Paluma Ra., NW Townsville (1♀, UQIC); Biloela (1♂, QDPI); Marlong Arch, Mt Moffatt Nat. Pk (1♂, QM); Mt Moffat [Moffatt] Nat. Pk (1♂, UQIC, 3♂, QM); sandstone hilltop 32 km S Theodore (10♂,
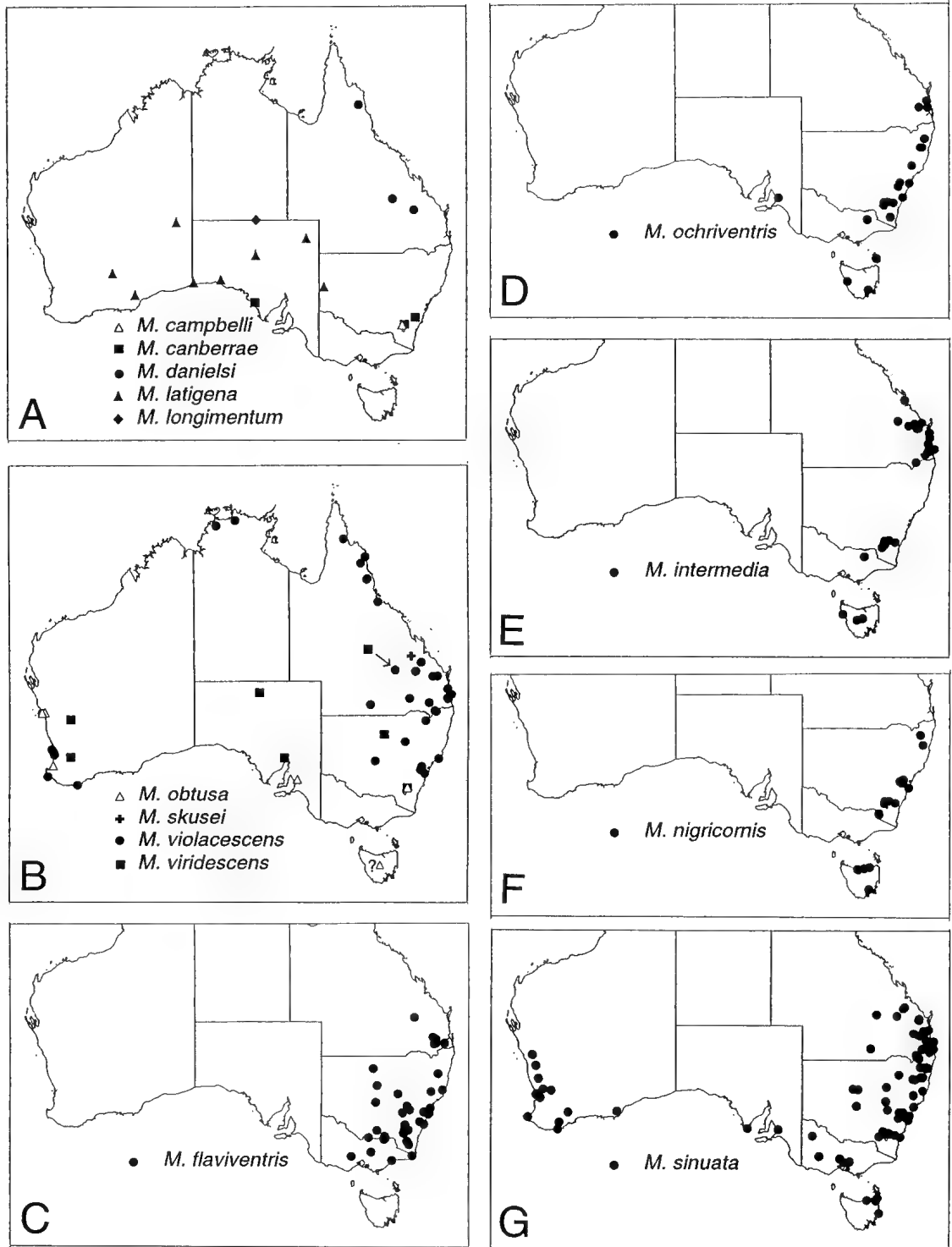
FIG. 7. A-G, Distribution of *Microtropesa* spp. in Australia.

UQIC); Isla Gorge Nat. Pk (1 ♂, UQIC); Mt Walsh Nat. Pk, north peak (1 ♂, ANIC); Bluff Ra. (1 ♂, ANIC); Gayndah (1 ♂, AM); Coast Ra., Biggenden (1 ♂, ANIC); Buderim Mtn, nr Mooloolah (1 ♂, BCRI); Mt Beerwah, via Glasshouse (2 ♂, UQIC); Glasshouse Mtns Lookout (1 ♂, UQIC); Moreton Is. (1 ♂, QM); Brisbane (2 ♀, QM, 2 ♂, QDPI); Palmerston (1 ♀, QDPI); Mt Gravatt (1 ♀, QDPI); Millmerran (2 ♀, ANIC, 1 ♀, UQIC); Cunnamulla (1 ♂, AM); Amiens, nr Stanthorpe (1 ♂, AM); Stanthorpe (1 ♂, QDPI, 1 ♀, UQIC); Palingyard (1 ♀, ANIC). New South Wales: Graman (1 ♂, BCRI); Warrumbungle Nat. Pk (2 ♂, AM); Bogan R. (2 ♀, 6 ♀, ANIC); Stephens Peak (3 ♂, QDPI); Round Hill Fauna Reserve (2 ♂, 1 ♀, AM, 1 ♀, GD); 6 km NE Bilpin, nr Kurrajong (1 ♀, AM); Hazelbrook (1 ♀, ANIC); East Minto (1 ♂, AM). Western Australia: Geraldton (1 ♂, SAM, 1 ♂, WADA, 1 ♂, 1 ♀, ANIC); Rottnest Is. (3 ♂, 1 ♀, ANIC, 1 ♂, 1 ♀, WADA); Garden Is. (1 ♀, ANIC); White Lake, Rockingham (1 ♀, ANIC); Cape Peron, 40 km SW Perth (3 ♂, UQIC); 10 km N Mandurah (4 ♂, UQIC); Augusta (2 ♂, UQIC); King George Sound (2 ♀, AM). Other: no data (1 ♂, 4 ♀, QDPI).

DIAGNOSIS. Body length: 12.0–16.0 mm. ♂ cerci and surstyli as in Fig. 6A, B. A3 ovoid, orange, apex sometimes brown; pf and genae mostly with orange-yellow hairs, those on dorsal pf sometimes black; mesonotum, in dorsal view, with thin covering of whitish pollinosity; dorsal surface of scutellum with black hairs; wings grey, bases orange-yellow; ground colour of abdominal tergites dark, reddish-brown to black (often with bluish reflection); abdomen, in caudal view, usually with grey, pollinose markings as follows; T3 with anterior, pollinose band interrupted medially; T4 with median, pollinose triangle extended laterally as anterior band, T5 with pair of large, dark spots separated from anterior margin by pollinosity; T3 without mm.

REMARKS. In many specimens the grey, pollinose markings on the abdomen are thin and weak and only fully apparent when the abdomen is seen in caudal view. The anterior, pollinose band on T3 can be represented only by a pair of submedian spots, or is rarely absent.

Microtropesa viridescens Paramonov, 1951
(Figs 6C,D, 7B)

Microtropesa viridescens Paramonov, 1951: 765; Crosskey, 1973:135; Cantrell & Crosskey, 1989:762.

MATERIAL EXAMINED. HOLOTYPE ♂, Canberra, ACT, 7.ii.1948, Paramonov (ANIC). OTHER MATERIAL EXAMINED. Queensland: Mt Moffatt

summit, Mt Moffatt Nat. Pk (3 ♂, QM). NSW: Bogan R. (1 ♂, ANIC). S AUST: 5 km SW Mt Sarah HS, N Oodnadatta (1 ♀, ANIC); 20 [miles? = 32 km] SW Port Augusta (1 ♀, ANIC). WA: 15 km NE Mt Singleton (1 ♀, ANIC); Pinjarra (1 ♂, ANIC).

DIAGNOSIS. Body length: 10.8–12.0 mm. ♂ cerci and surstyli as in Fig. 6C, D. Pf and genae with orange-yellow hairs; palpi mostly yellow haired, occasionally with a few black hairs; mesonotum with uniform, thin covering of whitish pollinosity; wings hyaline with black markings at base; ground colour of thoracic pleura, scutellum and abdomen dark-brown or black; legs black; T3, T4 and T5 each with silver, pollinose, anterior band interrupted medially.

REMARKS. Females of *M. viridescens*, which have not been previously described, are similar to males but differ as follows: vertex, fore and mid tarsi wider; mesonotum with coppery-green reflection (greenish in ♂); abdominal ground colour shining black, with bluish (not greenish) reflection.

The only apparent difference between *M. viridescens* and *M. skusei* is the colour of the hairs on the palps. It is likely that *M. viridescens* is a junior synonym of *M. skusei* especially given that *M. viridescens* occurs at Mt Moffatt, about 200 km from the type locality of *M. skusei*.

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GEOMETRICAL STUDY OF A CAST OF *LEPTOPHLOEUM AUSTRALE* (McCOY) WALTON FROM QUEENSLAND

H. TREVOR CLIFFORD

Geometrical study of a cast of *Leptophloeum australe* (McCoy) Walton confirms that during its compression there has been no increase in diameter. □ *Leptophloeum, axis, cast, compression.*

H. Trevor Clifford, Queensland Museum, P.O. Box 3300, South Brisbane, Queensland 4101, Australia; 1 February 1996.

Axial casts of the lepidophyte *Leptophloeum australe* (McCoy) Walton have been recorded in Australia from Queensland (Carruthers, 1872) and Victoria (McCoy, 1874). Herein an additional cast is described from Queensland. The specimen is of particular interest because over most of its surface the outlines of leaf-cushion bases are clearly defined, (Fig. 1) thereby enabling the length of its diameter, prior to compression, to be determined with reasonable accuracy. This length therefore provides a bench mark against which diameters as estimated by other methods may be evaluated.

All methods employed assume the cast to have been cylindrical prior to its compression, a viewpoint justified by the uniformity in size and shape of the leaf-cushions on its surface. Furthermore, the cast was assumed to be elliptical in transverse section which assumption has been confirmed by direct observation. Although casts are often reported to be elliptical in section (Pant & Srivastava, 1995) there appears to be no previous publication in which the contention has been confirmed by a direct comparison of the observed section shape with that of the ellipse calculated from the maximum and minimum widths of the cast.

MATERIAL

The cast (QMF3275) was collected by Leichhardt during his expedition from Moreton Bay to Port Essington and is the only specimen in the Queensland Museum known to have been collected by the explorer whose misfortune it was to lose, by misadventure or necessary abandonment, most of his collections when near to his journey's end (Leichhardt, 1847). The specimen is labelled 'Clarke River' and so most probably has its Provenance in the Clarke River Basin (Draper *et*

al., 1993). Because the cast was collected as a surficial boulder its precise age is not determinable. However, the taxon is well represented by impressions in the Ruxton Formation whose age, based on conodonts, is Late Devonian to Early Carboniferous.

Two available casts (Table 1) are entirely mineral in composition and a thin section of QMF3204 revealed it to be a fine sediment dominated by rock fragments and quartz. Other minerals present are muscovite, orthoclase, plagioclase, sericite and undifferentiated iron oxides. The unabraided condition of the grains and their composition indicates the cast formed in young sediments with a proximal igneous and metamorphic provenance. The cement is dominated by silica and clay with subordinate iron oxides (Alex Cook per. comm.).

RESULTS

From measurements of the specimen (Table 1) it is possible to make several independent estimates of the diameter of the cast before its compression. That the outline of the cast in transverse section approximates closely to an ellipse may be confirmed by reference to Fig. 2 where the ellipse calculated on the basis of the maximum and min-

TABLE 1. Five attributes of two casts of *Leptophloeum australe*.

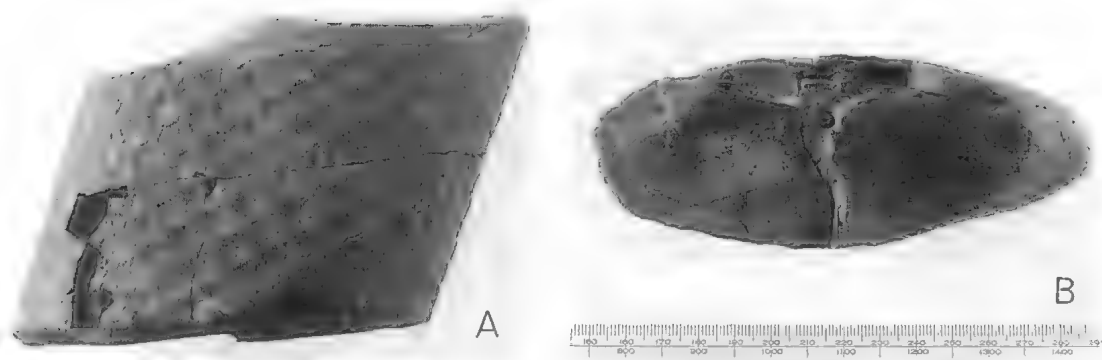| ATTRIBUTE	DIMENSIONs (mm)	
	QMF3275	QMF3204
Perimeter	283	194
Maximum width	117	75
Minimum width	51	47
Leaf-cushion width	13.4	12
No. leaf-cushions encircling axis	25	n.a.

FIG.1. Cast of *Leptophloeum australe* (QMF3275). A, Lateral view. B, End view.

imum widths of the cast is superimposed upon its original outline.

Four approaches to the estimation of the diameter of the cast prior to its compression will now be considered:

1. Perimeter of Cast. If it is assumed that during compression the perimeter of the cast is unchanged the diameter of a circle with the same perimeter is readily calculated (Table 2).

2. Cross Sectional Area of Cast. If the cross sectional area of the cast is unaffected by compression the areas of the elliptical section of the cast and that of its precompression circular section will be the same. Accepting the maximum and minimum width of the cast as axis-lengths the area of the elliptical section may be calculated and from this the diameter of a circle of similar area determined (Table 2).

3. Maximum Width of Cast. Assuming that the vertical compression of a horizontal cylindrical cast may occur without any lateral expansion the maximum width of the cast is the same as the diameter of the uncompressed cast (Table 2).

4. Leaf-cushion number x Leaf-cushion width.

TABLE 2. Four estimates of the diameter of a presumed cylindrical cast of *Leptophloeum australe* as determined from certain attributes of its compressed cast (QMF3275).

BASIS OF ESTIMATE	ESTIMATED CAST DIAMETER (mm)
1. Perimeter	90
2. Cross sectional area	77
3. Maximum width	117
4. Cushion number x cushion width	107

The number of leaf-cushions encircling the cast is half the number of the vertical rows in which they are arranged (Fig. 3). The recognition of these rows is more reliable than that of adjacent leaf-cushion boundaries wherever the surface of the cast is irregular or the leaf-cushions are strongly compressed as in regions of maximum curvature. Therefore, the number of leaf-cushions encircling the cast was determined as half the number of vertical rows of leaf-cushions on the surface of the cast. Multiplication of leaf-cushion number by leaf-cushion width provided a perimeter for the uncompressed cast from which its diameter was calculated (Table 2).

DISCUSSION OF RESULTS

Each of the 4 methods employed provided a different estimate of the diameter of the original cast (Table 2). These differences are readily accounted for if it is assumed that during compression a cylindrical cast was deformed into one elliptical in transverse section, with the major axis of the ellipse being of the same length as the diameter of the cylinder.

Such a situation is illustrated in Fig. 4 where sections of a theoretical cast, prior to and subsequent to its compression, are superimposed. The ellipse is similar to that of Fig. 2 because the lengths of the major and minor axes of the two are the same. Along the perimeter of both the circle and ellipse solid circles mark the positions of leaf-cushion margins. The number of leaf-cushions is the same as that on the cast being studied and their positions on the ellipse are vertical projections of those on the circle. Therefore
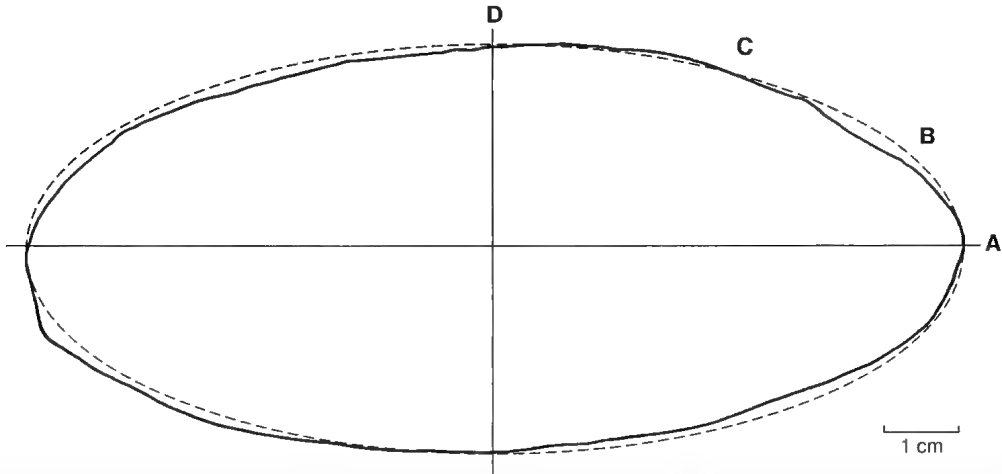
FIG. 2. Outline of cast of *Leptophloeum australe* (QMF3275) with the perimeter of theoretical ellipse superimposed. A-D are places on cast surface at which leaf-cushion widths (Table 3) were measured.

the ellipse may be regarded as a compression of the circle without a change of its diameter.

Both the perimeter and the area of the ellipse will provide measurements which will lead to underestimates of the diameter of the circumscribing circle, and the shorter the minor axis of the ellipse the poorer will be the estimate. Furthermore, of the two parameters under discussion the perimeter of the ellipse will always

provide a closer estimate of the perimeter of the inscribing circle than will the area of the ellipse. This statement is especially true of strongly compressed casts. Towards the limit of compression, as the length of its minor axis approaches zero, the perimeter of an ellipse approaches a value of twice the length of its major axis but the area of the ellipse approaches zero. Hence it is clear that ellipses whose minor axes are short in com-
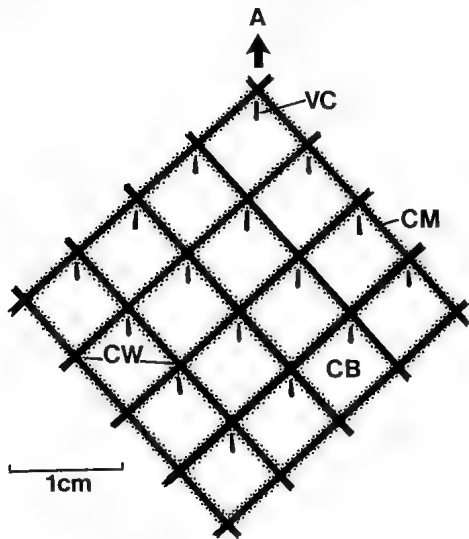
FIG. 3. Semidiagrammatic drawing of the disposition of leaf-cushion outlines on the surface of cast of *Leptophloeum australe* (QMF3275). A= direction of stem apex; CB=leaf-cushion base; CM=leaf-cushion margin; CW=leaf-cushion width; VC=vascular cicatrix..
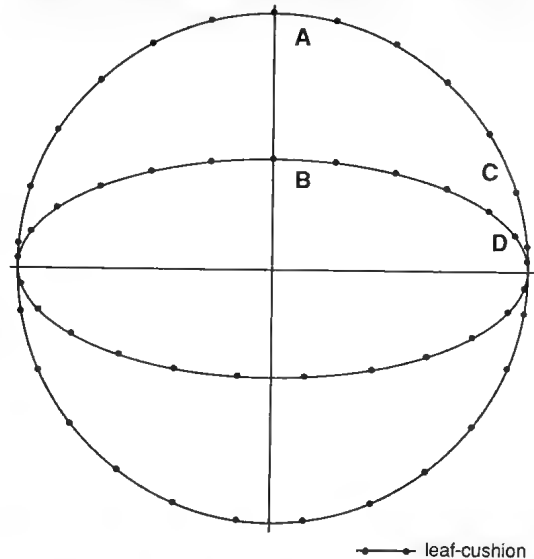
FIG. 4. Transverse sections of 2 theoretical casts on whose perimeters the margins of the leaf-cushion outlines have been marked by solid circles − circle, before compression; ellipse, after compression. The major and minor axes of the ellipse are the same length as in Fig. 2.

TABLE 3. The areas and perimeters of an ellipse with different minor and major axis ratios expressed as proportions of its circumscribing circle.

Length of minor axis Length of major axis	Ellipse as proportion if its circumscribing circle	
	Area	Perimeter
1.0	1.00	1.00
0.9	0.90	0.94
0.8	0.80	0.88
0.7	0.70	0.82
0.6	0.60	0.76
0.5	0.50	0.70

TABLE 4. The widths of leaf-cushion at 4 positions on the surface of a cast of *Leptophloeum australe* (QMF3275) as measured directly and as determined by projection from a circular cast onto one elliptical in transverse section with a major axis the same length as the diameter of the circular cast.

Place on surface (Fig.2)	Leaf-cushion width (mm)	
	Measured	Predicted
A	4.0±0.3	5.5
B	7.2±0.4	8.0
C	11.9±0.2	11.5
D	13.4±0.8	13.5

parison to their major axes provide poor information for predicting the diameter of the circumscribing circle.

However, the situation is different if the length of the minor axis of the ellipse equals or exceeds half the length of the major axis. Over this range of values both the area (exactly) and the perimeter (closely) of the ellipse are linearly related to the area of the circumscribing circle. Whereas for high values of the ratio of the lengths of the minor and major axes, both the perimeter and the area of the ellipse are useful predictors of the diameter of the circumscribing circle, for low values of the ratios neither is useful but the perimeter is the better estimator (Table 3). This observation is confirmed by the estimates of diameter (Table 2).

It is also clear (Fig. 4) that whereas the leaf-cushion bases around the perimeter of the circle are all of the same width their projections on to the ellipse vary in width. Whereas leaf- cushion B (Fig. 4) is almost the same width as that of A, the width of leaf-cushion D is much less than that of C. If the leaf-cushion is bisected by the minor axis of the ellipse its width will be almost exactly that of its width before projection from the circle. Therefore, provided the leaf-cushions measured are situated close to where the minor axis of the ellipse meets its surface their widths combined with their number provide an accurate basis for estimating the diameter of the uncompressed cast.

Because only one cast is available it is not possible to determine whether the diameters of the uncompressed cast as estimated from the maximum width of the compressed cast (117mm) and by the leaf-cushion number x width method (107mm), are statistically different. However, the data indicate that if there has been any lateral spread of the cast during compression the extension has been slight for the ratio of the former to the latter is 1.09 which value is close to unity.

Further support for the view that the width of

the cast has not increased as a result of compression comes from a comparison of the measured and predicted widths of leaf-cushions. Measurements were made on four areas of the cast surface and the predicted widths were taken from similar positions on the ellipse (Fig. 2; Table 4). Standard errors can be attached to the means of the measurements because there are several leaf-cushions available on similar areas of the cast but there is only one predicted value for corresponding parts of the ellipse. Only on the surface of greatest curvature does the predicted value of leaf-cushion width differ significantly from that measured. Such close agreement between the two sets of values is further support for the hypothesis that compression of the cast has occurred without any lateral extension.

Although casts of *Leptophloeum australe* are rare, impressions of their axes are abundant. Most are flat and irregular in outline, but a few are parallel-sided thereby resembling impressions of complete axes. However, it is not reasonable to assume that the impression revealed on a flat surface derives from a whole axis. It may represent any portion of the surface, the remainder of which may be buried in the rock on either side of the plane (along which the rock split) to reveal the impression. Cleavage across a cast near to its surface and parallel to its length would expose impressions with parallel sides but whose widths are much less than the diameter of the cast. That this situation is common is suggested by the many impressions whose leaf-cushion bases have widths typical of casts whose diameters are greater than the width of the impression.

CONCLUSION

Although it has been widely accepted that compression of plant tissues and casts usually occurs, without a concomitant increase in their width at

right angles to the force applied, the process has been subject to little theoretical or experimental study.

Using a series of projections similar to that employed above, Walton (1936) compared the shapes of some solids pre- and post- compression. His approach was qualitative and non-experimental. However, according to Harris (1974: 144) Walton's observations were underpinned by a series of experiments in which he had compressed 'various solid plant organs - plant stems, apples and the like in wet sand in a power press so constructed as to allow surplus water to drain away'. Apples so compressed were converted into hemispheres filled with sand but with their diameters unchanged.

The pioneering study of Walton (1936) has been extended by Harris (1974), Niklas (1978) and Rex & Chaloner (1983). Harris (1974) embedded hollow balls of wax or plastic, in a variety of matrices which were then compressed. After compression the balls were approximately hemispherical and circular in outline. None of the compressions showed any obvious evidence of horizontal extension. Simulated compression studies of Niklas (1978) were quite extensive but, unfortunately, the procedures adopted were not adequately described. However, he demonstrated that whereas hollow and solid, but dehydrated stems compress without lateral extension hydrated solid stems 'show a maximum increase of 10% diameter'. Experimental procedures adopted by Rex & Chaloner (1983) are fully explained and so their results can be critically assessed. Foam rubber was used to represent plant material and saw dust the embedding matrix. Pressure was applied either with a single piston or a parallel system of independent pistons each of which was spring loaded, but with the whole set controlled by a single screw mechanism. After compression, transverse sections of the original cylinders (stems), differed in shape according to the piston system employed. Nonetheless in both systems and for several cylinder diameters the maximum width of the stem following compression was equal to or slightly less than the original diameter. That is, the results are in accord with the predictions of Walton (1936).

It is not possible to compare with certainty the results obtained from the several experimental studies because of the diversity of materials employed and the differences in procedures adopted. Furthermore, these results are not direct-ly comparable with the observational data reported above for none of the experimenters included casts in their studies. Nonetheless, the application of pressure to embedded material did not result in its lateral extension except for one report by Niklas (1978). The similarity of the pre- and post-compressional diameters of the Leichhardt cast (QMF3275) suggest that even when subjected to pressures much greater than those employed in the laboratory plant axes do not expand lateral to the force applied.

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POSSIBLE AFFINITIES BETWEEN *VARANUS GIGANTEUS* AND *MEGALANIA PRISCA*. *Memoirs of the Queensland Museum 39(2):232. 1996:-* Molnar (1990) described two frontals, and a parietal, of a giant Pleistocene varanid at King Creek, eastern Darling Downs. The material was assigned to *Megalania prisca*, the only varanid of comparable size. This identification is probably correct since undoubted remains of *Megalania* occur in the same deposits.

Molnar (1990) noted that the frontals and parietal of the King Creek varanid exhibited many unusual features, which could not be found in any varanid skulls examined, and were thus presumably derived within varanids. Among these features were the prominent sagittal crest along the median suture between the frontals, and the parallel transverse ridges extending at right angles to this crest. Both these features are also found in *Varanus giganteus* (Fig. 1) and are absent in other species of *Varanus* (Molnar, 1990) and in the nearest outgroup taxa, *Lanthanotus* and *Heloderma* (Rieppel, 1980; Pregill et al., 1986; Estes et al., 1988). They are thus derived within *Varanus* suggesting affinities between the King Creek varanid and *V. giganteus*. Molnar (1990) noted that, in the King Creek varanid as in *V. giganteus* (Fig.1), the sagittal crest and parallel transverse ridges were confined to the frontals, and did not extend onto the parietals. This phylogeny is based on very incomplete material and only two characters.

Megalania prisca, Varanus giganteus, V. salvadori and *V. komodoensis* are the 4 largest known varanids (Pianka, 1995). Despite the latter two not being Australian natives, all 4 belong to a discrete radiation of Australian monitors, the '*gouldii* species group' (Baverstock et al.,1993). If *Megalania prisca* has affinities with *V. giganteus* and thus belongs within the *gouldii* species group *Megalania* will have to be synonymised with *Varanus*. Relationships within the *gouldii* species group are not yet well established (Baverstock et al. 1993).: there is a distinct possibility that, when relationships within this radiation are resolved, *V. giganteus, V. salvadori, V. komodoensis,* and *Megalania prisca* will form a clade. If so, this would mean that the four largest varanid species represent a single discrete radiation of giant predatory lizards.

I thank the Australian Research Council for funding, Jenny Clack and Ray Symonds for loan of the figured specimen, and Malcom Ricketts for photography.

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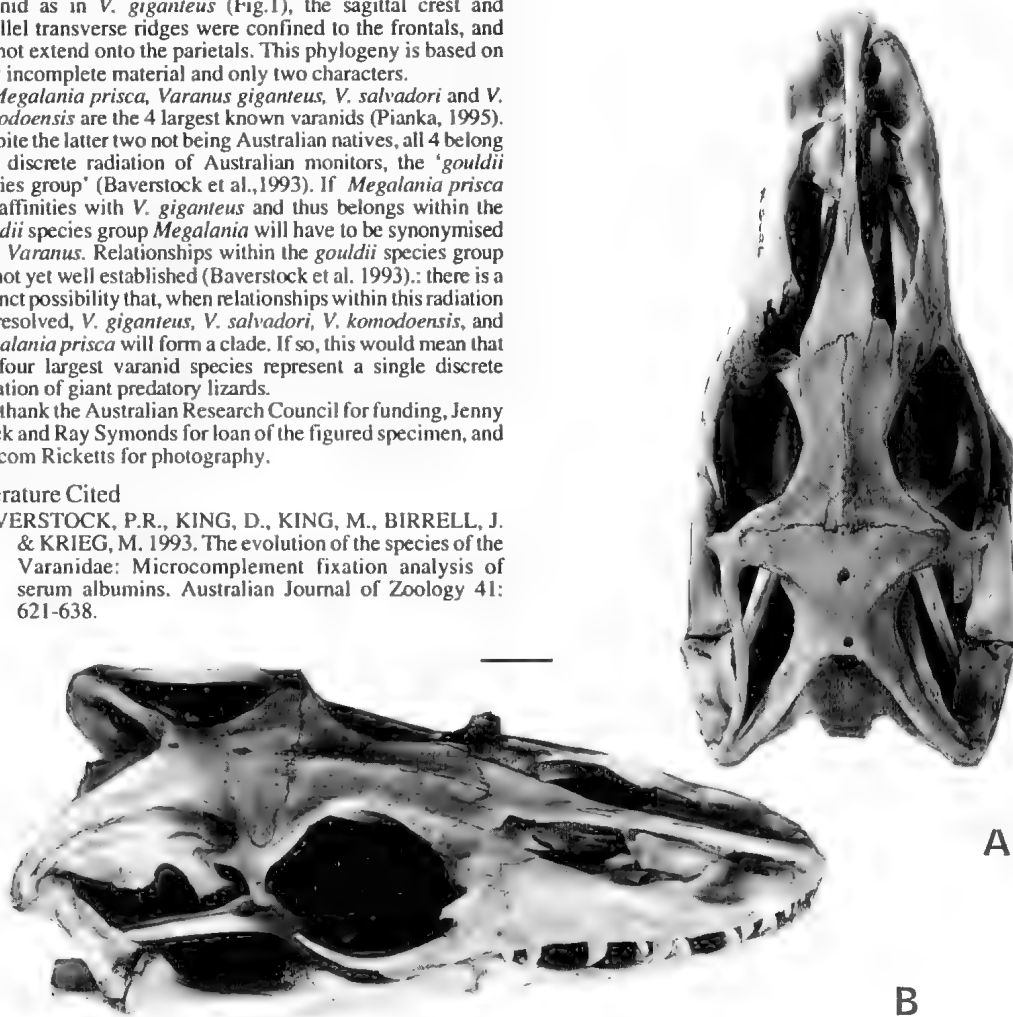

FIG. 1. Skull of *Varanus giganteus* (University Museum of Zoology, Cambridge R9586) in (A) dorsal, and (B) right laterodorsal view, showing the sagittal crest and dermal sculpture on the frontals between the orbits. Scale bar = 3cm.

COGGERIA NAUFRAGUS GEN. ET SP. NOV., A SAND-SWIMMING SKINK FROM FRASER ISLAND, QUEENSLAND

P.J. COUPER, J.A. COVACEVICH, S.P MARSTERSON AND G.M. SHEA

Coggeria naufragus gen. et sp. nov. is a distinct lygosomine in the *Sphenomorphus* group. It has a digital formula of 3/3. A sharp snout and more than 40 lingually-directed maxillary teeth are key distinguishing characters. The new skink is a sand-swimmer, which feeds on worms. It is known only from Fraser Island, SEQ, a World Heritage Site. □*Sphenomorphus group, Scincidae, rainforest species, World Heritage Site, Fraser Is.*

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On Fraser Island in June, 1991, Mike West found a small sand-swimming skink while digging. It was sent to the Queensland Museum for identification. At first glance, the damaged specimen, resembled *Saiphos equalis* (Gray, 1825). Several unsuccessful attempts were made to find more specimens. During summer 1994/95, a party from the Queensland Museum (PJC and JAC) and the Queensland Department of Environment and Heritage (SM, Rod Hobson, Keith Twyford, other staff and volunteers) collected several more specimens.

Like other World Heritage Sites in Queensland, Fraser Is. has been the focus of considerable research and management effort. The island's diverse reptile fauna (Barry & Campbell, 1977; Covacevich & Couper, 1991) in many habitats, including rainforest, was thought to be well known. That a secretive, very distinct skink from Fraser Is. rainforest should be discovered in 1991 indicates that there are still elements of the Queensland reptile fauna about which we know little.

The skink is assigned to the *Sphenomorphus* group within the Lygosominae. The *Sphenomorphus* group has a single frontal bone; palatine bones in contact on the ventral midline; ventrolateral ridges of the frontal each with a short process, and frontal separated from the palatine by an extensive section of prefrontal; nine premaxillary teeth; an open Meckel's groove; iris virtually as dark as pupil; parietal scales in contact behind the interparietal; posteriorlateral edge of each parietal bordered by two temporals and a nuchal, and a greatly enlarged medial pair of preanal scales (Greer, 1970, 1979, 1986a).

MATERIALS AND METHODS

All measurements were taken using Mitutoyo electronic callipers. Supraciliaries, supralabials, infralabials, and subdigital lamellae on the hind toes were counted on both sides. The following meristic characters have been used:- snout-vent length (SVL); axilla to groin (AG); tail length, vent to tip (TL); forelimb, axilla to tip of longest digit (L1); hindlimb, groin to tip of longest digit (L2); forelimb to snout, from axilla to tip of snout (L1-S); head length, tip of snout to posterior margin of parietals (HL); head width, measured level with the posterior margin of the parietals (HW); head depth, measured level with the posterior margin of the parietals (HD); snout, tip to anterior margin of orbit (S); eye to ear-crease, posterior margin of orbit to mid lateral margin of ear-crease (EE). Osteological characters are based largely on a single, cleared and stained specimen, QMJ59670, and supplemented by data (vertebral counts) from X-rays of QMJ57431, 59237, 59312, 59361, 59468-69 and 59671.

SYSTEMATICS
Coggeria gen. nov.

TYPE SPECIES. *Coggeria naufragus* sp. nov.

ETYMOLOGY. For Harold Cogger, former Curator of Reptiles and Deputy Director of the Australian Museum, for his many contributions to knowledge and conservation.

DIAGNOSIS. Elongate body (Fig. 1), reduced limbs (front and rear limb 4.3% and 7.7% of SVL,

FIG. 1. *Coggeria naufragus* gen. et sp. nov.

respectively), snout wedge-shaped in profile (Figs 2,3); nasals slightly enlarged; prefrontals separated; supraoculars 3, first only in contact with frontal; last 2 supraoculars partially separated by a supraciliary; supraciliaries 5, first contacting frontal; supralabials usually 6, fourth below eye; postsupralabial single; ear opening absent; upper secondary temporal overlapped by lower. Osteology: maxilla-frontal contact; pre- and postfrontals in contact above orbit; postorbital absent; distinct narrowing of skull at premaxillary-maxillary junction; maxillary teeth greater than 40, with long axis of tooth running transversely and crowns directed lingually; dentary teeth more than 45; pterygoid teeth absent; presacral vertebrae 47-50; manus lacking intermedium, distal carpals 1 and 5 and metacarpals 1 and 5, and has phalanges reduced to 0.2.3.3.0; pes with astragalus and calcaneum fused, lacking distal tarsals 1 and 5, metatarsals 1 and 5, and with phalanges reduced to 0.2.3.3.0 (Fig. 4); sternal ribs 2; mesosternal ribs 1; ischia forming acute angle at symphysis with shafts paralleling those of pubes. Parietal peritoneum lacking pigment.

Other elongate genera of the *Sphenomorphus* group (*Anomalopus, Calyptotis, Coeranoscincus, Ophioscincus, Saiphos, Lerista*) share some of the apomorphies of *Coggeria* in varying combinations (Table 1). However, many of these apomorphies are associated with burrowing, and may point to parallel evolution rather than close relationships (Greer & Cogger, 1985). Anatomi-

cal variation and phylogenetic relationships in the *Sphenomorphus* group, particularly in the non-Australian members, remain poorly known, and a well-corroborated cladistic phylogeny is not available.

Coggeria shares many apomorphies with *Coeranoscincus* (15; 18) and *Ophioscincus* (17), which are closely associated geographically. However, *Coeranoscincus* differs from *Coggeria* in having: teeth fang-like, posteriorly curved and sharply pointed; snout conical; ischial shaft weakly developed or absent. *Ophioscincus* differs from *Coggeria* in having: supraciliaries 3-4; supralabials 5; limbs 2% of SVL or shorter; phalanges absent on both manus and pes. Tooth shape and a high number of maxillary teeth of *Coggeria* set it apart from *Anomalopus, Calyptotis, Coeranoscincus, Ophioscincus, Saiphos* and *Lerista*, all of which have fewer than 26 maxillary teeth, with a generally upright or posteriorly- curved orientation (Cogger, 1992; Greer,1983, 1986b, 1989; Greer & Cogger, 1985; Storr, 1971).

Coggeria naufragus sp. nov.
(Figs. 1–5)

MATERIAL EXAMINED. HOLOTYPE QMJ59361, E of Central Stn workshop (25°28'42''S, 153°03'21"E) SEQ. PARATYPES QMJ57431, between Leading Hill & Lake Garrawongera, behind Poyungan Valley (25°23'S, 153°05'E); QMJ59237, N of Central Stn workshop (25°28'37"S, 153°03'15"E); QMJ59312,

FIG. 2. *Coggeria naufragus* gen. et sp. nov. showing wedge-shaped snout.

QMJ59468, W of Central Stn workshop (25°28'38"S, 153°03'15"E); QMJ59469, 1km S of Pile Valley, 1.5km E of Central Stn (25°28'56"S, 153°04'20"E); QMJ59670, QMJ59671 Central Stn, E of QDEH workshop (25°28'23"S, 153°03'23"E). OTHER MATERIAL: QMJ60232 (tail only), N of Central Stn workshop (25°28'37"S, 153°03'15"E). All from Fraser Island.

ETYMOLOGY. Latin *naufragus*, castaway, shipwrecked.

DIAGNOSIS. As for genus.

DESCRIPTION. SVL(mm)=62-127 (n=7, mean 98.2). Proportions as % SVL: AG=73.4–76.8 (n=7, mean 75.2); TL=76.5–83.1 (n=3, mean 79.2); L1=3.1–4.3 (n=7, mean 3.8); L2=6.2–7.7 (n=7, mean 6.7); L1-S=20.3–22.7 (n=6, mean 21.4); HL=7.5–9.8 (n=7, mean 8.2); HW=5.3–6.0 (n=6, mean 5.6); HD=4.1–4.5 (n=5, mean 4.4); S=3.3–4.0 (n=7, mean 3.5); EE=4.4–5.6 (n=7, mean 4.9).

Head indistinct from neck; snout wedge-shaped in profile. Nasals large, moderately spaced. Nostril positioned anteroventrally in nasal. Prefrontals large, moderately spaced. Frontal 1.2 times as long as wide; contacting prefrontals, frontonasal, frontoparietals, first supraoculars and first supraciliaries. Frontoparietals paired, in broad contact. Interparietal free, parietal eye present. Parietal scales in broad contact behind the interparietal. Enlarged nuchal scales 4-5 pairs. Two nuchals in direct contact with posterior edge of parietal scales. Loreals 2, first larger. Supralabial scales 6-7 (n=16, mean 6.1); where 6, fourth below eye; where 7, fifth below eye. Postsupralabial single. Infralabials 6. Postmental contacts 2 infralabials on each side. Three pairs of enlarged chin scales; first pair in contact, second pair separated by 1 longitudinal ventral scale row, third pair separated by 3 lon-
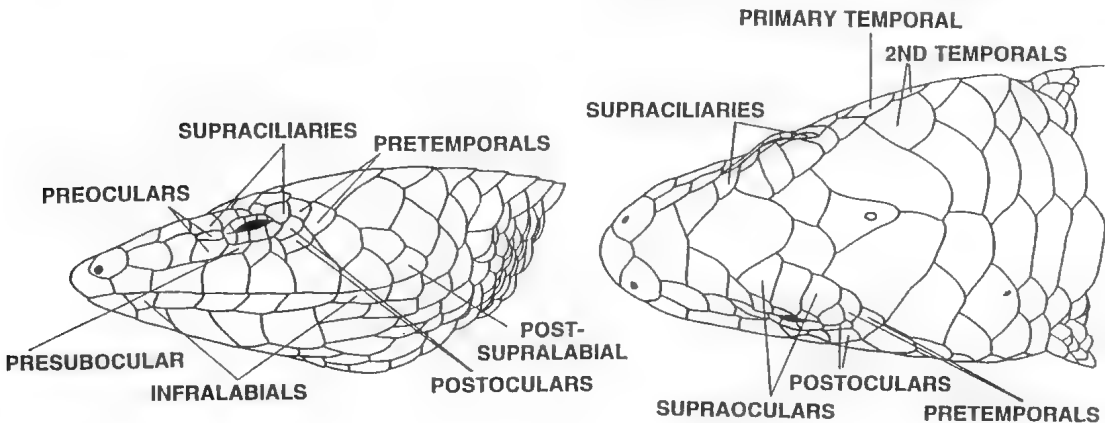
FIG. 3. Head scalation of the holotype (QM J59361) of *Coggeria naufragus* gen. et sp. nov.
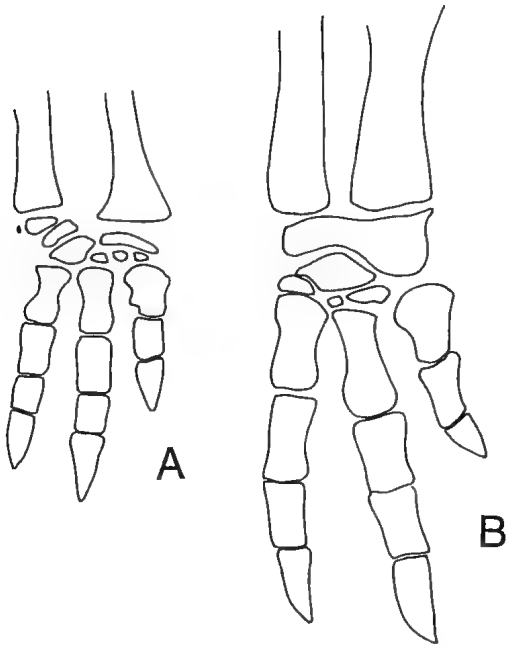
FIG. 4. Number and configuration of the bones in the manus (A) and pes (B) of *C. naufragus*.

gitudinal ventral scale rows (terminology follows Greer, 1989:152). Lower eyelid movable and scaly. Preoculars 2. Presuboculars 1. Suboculars 2. Supraoculars 3. Supraciliaries 5. Postoculars 2. Pretemporals 2. Primary temporals 1. Secondary temporals 2, upper the largest and overlapped by lower. External ear opening completely covered
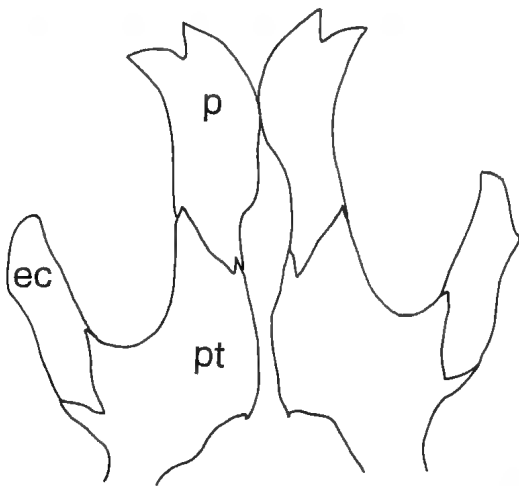
by scaly epidermis, its former position indicated by an elongate, vertically-oriented, shallow depression.

Body elongate, with smooth scalation. Mid-body scale rows, 22-24 (n=8, mean 22.8). Paravertebral scales, from anteriormost nuchal to posterior margin of hindlimb 88-100 (n=7, mean 92.7); slightly enlarged. Number of scales in a direct line between mental and preanal scales 100-111 (n=7, mean 105.9). Medial pair of preanal scales enlarged, overlapping outer preanals. Limbs short, tridactyl. Subdigital lamellae on hindlimb - first toe 2-3 (n= 16, mean 2.3), second toe 3-5 (n=16, mean 3.3), third toe 3-4 (n=16, mean 3.6). Original tail tapered distally, terminating sharply.

Skeletal features. Premaxillary teeth 9 (n=1). Maxillary teeth 43/43 (n=1). Dentary teeth 48/49 (n=1). Frontal single. Vomers fused. Palatines in contact along ventral midline. Palatal rami of pterygoids with slight recurved processes. Ectopterygoid process absent (Fig. 5). Parietal foramen present. Postorbital bone absent. Supraorbital fenestra small, almost obliterated by close apposition of supratemporal arch to parietal. The hyoid apparatus is illustrated in Fig. 6.

Presacral vertebrae 47-50 (n=8). Postsacral vertebrae 45 (n=1). Complete inscriptional chevrons 11 (n=1). Sternal/mesosternal ribs 2/1 (n=1).

Manus comprising radiale, ulnare and pisiform; centrale; distal carpals 2-4; metacarpals 2-4, and phalanges 0.2.3.3.0. Pes comprising fused astragalus and calcaneum; distal tarsals 2–4; metatarsals 2-4; phalanges 0.2.3.3.0. (Fig. 4).

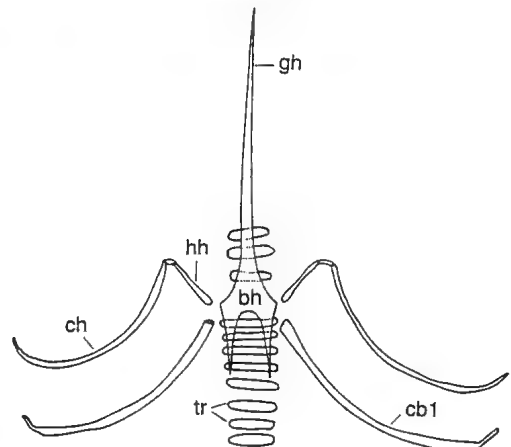FIG. 5. Ectopterygoid, pterygoid and palatine area in *C. naufragus*.

FIG. 6. Hyoid apparatus of *C. naufragus*. bh = basihyal, cb1 = first ceratobranchial, ch = ceratohyal, gh = glossohyal process, hh = hypohyal, tr = tracheal cartilages.

TABLE 1. Character states (derived +, plesiomorphic -) in reduced-limbed genera of the *Sphenomorphus* group. Data for genera other than *Coggeria* are from text and illustrations of Cogger (1992), Greer (1983, 1986b, 1989), Greer & Cogger (1985) and Storr (1971). For other material examined see Appendix 1.

CHARACTER: DERIVED STATE	GENERA						
	Coggeria	*Anomalopus*	*Coerano-scincus*	*Ophio-scincus*	*Saiphos*	*Calyptotis*	*Lerista*
snout profile sharp	+	-	-	-	-	-	+/-
nasal slightly enlarged	+	+	+	+	+	-	+
loreal single	-	+/-	-	+/-	+	+	+/-
prefrontals absent	-	+/-	-	+/-	+	+/-	+/-
supraoculars 3 or less	+	+/-	+	+	-	-	+/-
first supraciliary contacting frontal	+	+/-	+	+	+	+/-	+/-
last 2 supraoculars partially separated by a supraciliary	+	+	+/-	-	-	+/-	+/-
supraciliaries <7	+(5)	+/-(3-7)	+(4-6)	+(3-4)	+/-(5-7)	+/-(6-8)	+(0-6)
supralabials <7	+(6)	+(5-6)	+(6)	+(5)	+(6)	+(6)	+/-(4-7)
supralabial below eye, not 5th	+(4)	+(3-4)	+(4)	+(3)	+(4)	+(4)	+/-(2-5)
postsupralabial single	+	+/-	-	+	-	-	+/-
secondary temporals: lower overlaps upper	+	-	+/-	-	-	+/-	+
ear opening absent	+	+	+	+	+	+/-	-
front limbs ≤20% SVL	+(≤4)	+(≤7)	+(≤7)	+(≤2)	+(≤11)	+/-(≤25)	+/-(≤21)
rear limbs ≤28% SVL	+(≤8)	+(≤9)	+(≤9)	(a) +(≤2)	+(≤14)	+/-(≤33)	+/-(≤33)
midbody scale rows ≤26	+(22-24)	+(18-26)	+/-(23-34)	+(18-24)	+(18-22)	+(18-24)	+(16-24)
nasal-prefrontal bone contact	-	+/-	-	-	-	+	- (b)
pre & postfrontals approach/contact above orbit	+	+	+	+	+	-	+/- (c)
postorbital absent	+	+	+/-	+	+	-	+
ectopterygoid process present	-	+	-	+/-	+	+/- (d)	+ (e)
premaxillary teeth ≤9	-(9)	+(≤7)	+(8)	+/-(≤9)	-(9)	-(9) (f)	+(≤7)
maxillary teeth ≥26	+(43)	-(<15) (g)	-(<26)	-(<21)	-(<21)	-(<20) (h)	-(<15) (c)
dentary teeth ≥26 [i]	+(48-49)	-(<18)	-(<26)	-(<22)	-(<23)	-(<22)	-(<18) (c)
presacral vertebrae >26	+(47-50)	+(≥43)	+(≥52)	+(≥43)	+(38-40)	+/-(26-30)	+(≥31)
sternal ribs <3	+(2)	+/-(≤3)	+(≤2)	+(≤2)	-(3) (j)	-(3) (k)	+/-(≤3) (c)
mesosternal ribs <2	+(1)	+/-(≤2)	+(≤1)	+(≤1)	-(2) (j)	-(2) (k)	+/-(≤2) (c)
ischial & pubic shafts parallel	+	+	(l)	+	- (m)	- (n)	+/- (c)
phalanges (manus), not 23453	+ 02330	+ 02320 01220 00000	+ 02330 00000	+ 00000	+ 02330	+ 23443 23433	+/- 23453 02453 02340 00230 00030 00020 00000
phalanges (pes), not 23454	+ 02330	+ 02200 00000	+ 02330 00000	+ 00000	+ 02330	+ 23453 23443 23444	+/- 23454 02454 02350 00350 00030 00000
parietal peritoneum unpigmented [o]	+	+/-	+	+	-	-	-

Measurements and scale counts for holotype (QMJ59361). SVL=106.5mm; AG=78.4mm; TL =88.5mm; L1=4.6mm; L2=6.8mm; L1-S= 21.6mm; HL=8.4mm; HW=5.7mm; HD= 4.8mm; S=3.5mm; EE=5.6mm. Maximum length of frontal 2.3mm; maximum width of frontal 2.0mm; four pairs of enlarged nuchal scales; supralabial scales 6; Midbody scale rows 22; paravertebral scales 88; number of scales in direct line between the mental and anal shields 100; subdigital lamellae on hindlimb (both sides of body), first toe 2, second toe 3, third toe 3.

Pattern. Dorsum light tan. Some scales with dark brown spots, forming broken, longitudinal lines on body and tail; head with dark brown mottlings. Ventral and lateral surfaces greyish, heavily marked with black flecks; sharply demarcated from dorsum by a dorsolateral row of black spots (1/scale), beginning behind the eye and running the full length of tail. Dorsal scales immediately adjacent to the black dorsolateral zone paler than those of the rest of the dorsum, in juveniles forming a stripe bordering the black dorsolateral zone; stripe less clearly defined in larger animals. Limbs grey, heavily mottled with black.

COMPARISON. *C. naufragus* can be confused with only Australian lygosomines with a digital formula of 3/3 (*Coeranoscincus reticulatus, Hemiergis decresiensis,* southwestern populations of *H. peronii,* some species of *Lerista* and *Saiphos equalis*). *C. naufragus* is separated from *C. reticulatus* by snout shape in profile (sharp vs bluntly conical) and number of maxillary teeth (>40 vs <26); from *H. decresiensis,* southwestern populations of *H. peronii* and *Lerista* spp. by lower eyelid (scaly vs clear window). From *Lerista,* it is further distinguished in lacking an external ear opening; from *Saiphos,* in having prefrontals and 2 loreals (vs 1).

HABITAT. Fossorial species associated with tall forest communities on sandy substrates. The type series was collected from three main vegetation communities: closed *Syncarpia hillii,* Satinay forest (Fig. 7A); mixed *S. hillii* and *Eucalyptus pilularis,* Blackbutt forest (Fig. 7B), and open *E. pilularis* forest (Fig. 7C). The *S. hillii* and mixed *S. hillii / E. pilularis* forests contain a *Backhousia myrtifolia* (Carrol) understorey and *Macrozamia miquelii* (Wild Pineapple) ground cover. The open *E. pilularis* forest has a *Monotoca scoparia* (Prickly Broom Heath) understorey. These forests have a long history of harvest, and mod-

ification by fire. They occur as a broad, broken, central strip on Fraser Is., between latitudes 25°08'–25°44'S, and are illustrated as vegetation types one to four on the Fraser Is. vegetation maps (Department of Forestry 1979, 1985). *C. naufragus* has been collected only between 25°20'–25°30'S. The association between *C. naufragus* and tall forest communities may reflect collecting effort, or population variations between different habitats. For many years, *Anomalopus pluto,* another fossorial skink, was believed to be associated with monsoon forests because this was present at its type locality. Subsequent collections have shown *A. pluto* to occur in a wide variety of vegetation types. Substrate, rather than vegetation type, appears to determine the distribution of *A. pluto* (Couper, 1992).

HABITS. *C. naufragus* is difficult to find during the cooler months and in dry periods. Most individuals (preserved and released) were caught during an extensive pit-trapping programme between 1 December 1994 and 15 March 1995. Surface activity occurs during the summer months in periods of high humidity, or immediately following rain. Most pit-trapped specimens were captured at night. Two specimens have been recorded while digging. The first of these, QMJ57431, was found during winter (13-15 June 1991). The second, a tail only (QMJ60232), was found 20cm below the surface, during an excessively dry period (17 Nov. 1994).

C. naufragus is an adept 'sand-swimmer'. Specimens held briefly in captivity for photography, in sand-filled ice-cream containers, 'disappeared' rapidly, evading capture repeatedly and easily. We surmise that this species is largely subterranean, and that it burrows deeply during cold and dry times.

No data are available on its breeding habits. However, a specimen (TL 80mm, SVL approximately 45mm) is considerably smaller than any specimens in the type series and was considered a juvenile. It was collected 15 August 1995, at Pile Valley, 2km E of the type locality and released.

DIET. Faecal and gut samples from QMJ59670, and a faecal sample from QMJ59671 show that *C. naufragus* is a worm feeder. Both faecal samples contained humus-rich soil (presumed to be worm gut contents), with a few sand grains and numerous oligochaete setae (L. Cannon pers. comm.). The gut sample contained similar
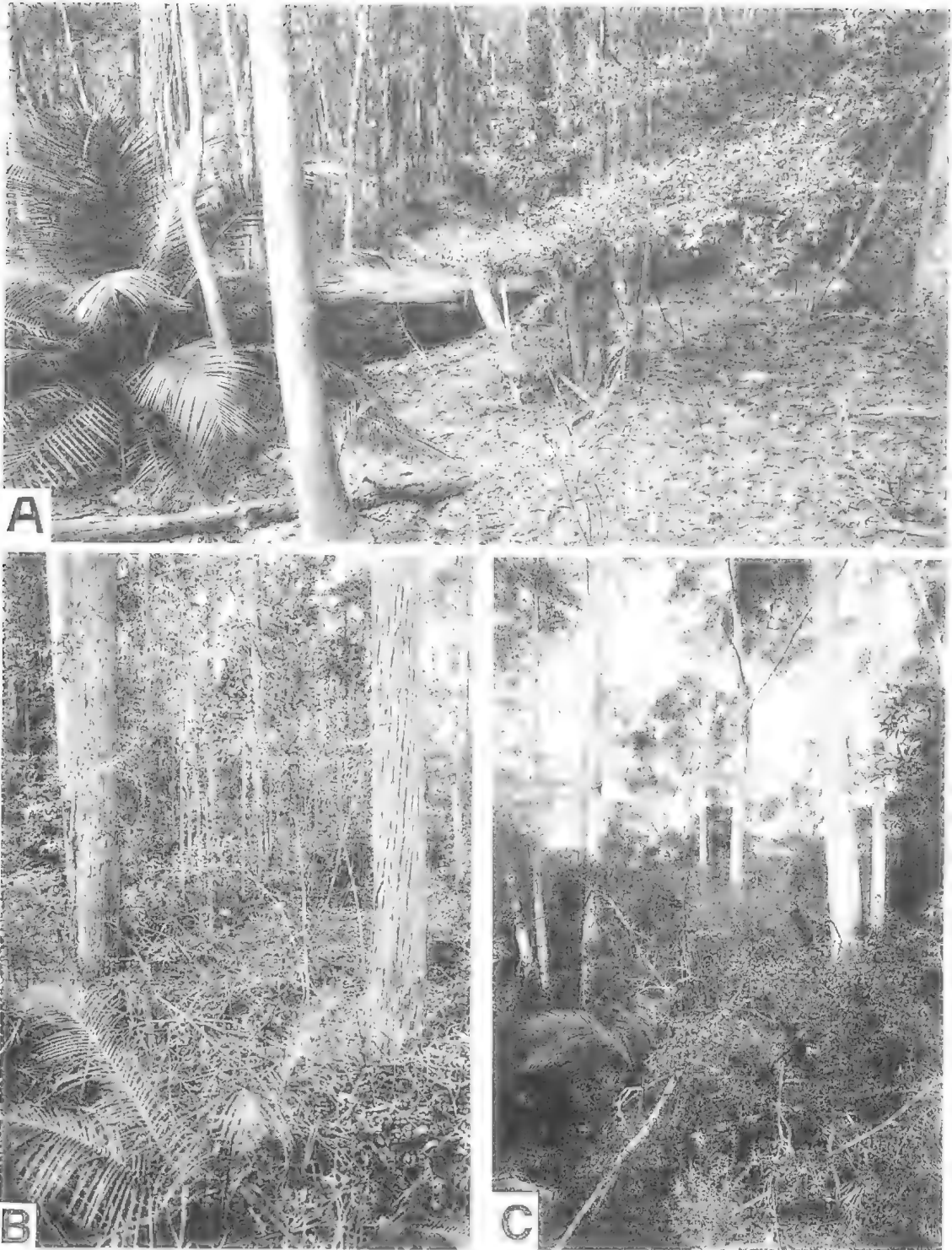
FIG. 7. Vegetation communities with which *C. naufragus* is associated. A, closed *Syncarpia hillii* forest. B, mixed *S. hillii* and *Eucalyptus pilularis* forest. C, open *E. pilularis* forest.

material, with what appeared to be worm dermal tissue.

ACKNOWLEDGEMENTS

We thank Mike West (Fraser Island Safaris) for collecting the first specimen of *C. naufragus,* and bringing it to our attention; Keith Twyford & David Redman (Queensland Department of Environment and Heritage) for supporting our fieldwork and implementing a trapping programme to obtain additional material; the Kingfisher Bay Resort for providing support during the initial search for specimens; Luke Barrowcliffe, Ben Garrett, Rod Hobson, Dan Haipola, Josh Hastings, Celia Jobson, Moyra McRae, Anika Tauchmann, Noel Wedding, Lyn Willsher (Queensland Department of Environment and Heritage staff and volunteers) for patrolling pit traps; Jeff Wright for collecting a road-killed specimen, and for preparing our photographic plates; Mrs K. Reynolds (University of Queensland) for X-raying specimens; Ms H. Janetzki for assisting with the final proof-reading of the manuscript; Ms D. Case for preparing Table 1; Steve Wilson for his valuable advice and Fig. 2 and Lauren Keim for her assistance in the laboratory.

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APPENDIX 1. Specimens examined in preparation of Table 1 and indicated on the table by supercript.

(a) *Ophioscincus truncatus* (QMJ28853, QMJ28620, QMJ40988). (b) *Lerista bougainvillii* (AMR91671, AMR88302), *L. microtis* (AMR47895), *L. lineopunctulata* (AMR64384), *L. labialis* (AMR104024). (c) *Lerista bougainvillii* (AMR91671, AMR88302), *L. microtis* (AMR47895), *L. punctatovittata* (AMR104137), *L. lineopunctulata* (AMR64384), *L. labialis* (AMR104024). (d) *Calyptotis ruficauda* and *C. scutirostrum* after Greer, 1983; *C. temporalis* based on (AMR60765), *C. thorntonensis* based on (AMR56575). (e) *Lerista bougainvillii* (AMR91671, AMR88302), *L. microtis* (AMR47895), *L. punctatovittata* (AMR104137), *L. lineopunctulata* (AMR64384). (f) *Calyptotis ruficauda* and *C. scutirostrum* after Greer, 1983; *C. temporalis* based on AMR60765 and *C. thorntonensis* based on AMR56575. (g) *Anomalopus mackayi* count based on AMR13138. (h) *Calyptotis lepidorostrum* (AMR59246); counts for *C. temporalis* and *C. thorntonensis* inferred from X rays of AM type series. (i) *Anomalopus gowi* (AMR63130), *A. leuckartii* (AMR43949), *A. mackayi* (AMR13138), *A. pluto* (AMR94362), *A. swansoni* (AMR5186), *A. verreauxii* (AMR6437);

Coeranoscincus frontalis (AMR3823), *C. reticulatus* (AMR4795); *Ophioscincus cooloolensis* (QMJ27384), *O. ophioscincus* (AMR47642), *O. truncatus* (AMR866); *Saiphos equalis* (AMR7242); *Calyptotis lepidorostrum* (AMR59246), *C. ruficauda* (AMR52339), *C. scutirostrum* (AMR43061); *C. temporalis* and *C. thorntonensis* (X rays of type series). (j) AMR104138. (k) AM X rays - *Calyptotis lepidorostrum* (AMR90305), *C. scutirostrum* (AMR76120), *C. temporalis* (unregistered), *C. thorntonensis* (AMR56603), and *C. ruficauda* (AMR69547). (l) Not applicable; ischium not projecting in either *Coeranoscincus frontalis* (AMR89278) or *C. reticulatus* (AMR6375). (m) AMR104138. (n) AM specimens: *Calyptotis lepidorostrum* (AMR90305, X ray), *C. ruficauda* (AMR69547), *C. scutirostrum* (AMR76120), *C. temporalis* (X ray), *C. thorntonensis* (AMR56603, X ray). (o) *Anomalopus leuckartii* (QMJ33156), *A. verreauxii* (QMJ57097), *A. brevicollis* (QMJ33122), *A. gowi* (QMJ45361), *A. pluto* (QMJ54040, QMJ54083, QMJ54213), *A. swansoni* (QMJ42773); *Calyptotis lepidorostrum* (QMJ57061), *C. ruficauda* (QMJ26024), *C. scutirostrum* (QMJ30616), *C. temporalis* (QMJ31794), *C. thorntonensis* (QMJ58111); *Saiphos equalis* (QMJ56908).

A BANDY BANDY WITH A DIFFERENCE. *Memoirs of the Queensland Museum 39(2):242:* - The Bandy Bandy, *Vermicella annulata*, is well known for its distinct colour and pattern (Shine, 1980). It is widespread in Queensland (Ingram & Raven, 1991). It is represented in the Queensland Museum by 210 specimens of which 209 are distinctly marked with uniform 'rings' of black and white (Fig.1).

On 26 April, 1995, we found an unusually coloured and patterned bandy bandy on Retro Station, via Capella MEQ (22°51'47"S 147°54'45"E). This specimen, now QMJ 59875 (Fig.2), was under a hollow log in Poplar Box (*Eucalyptus populea*) woodland, with a sparse shrub understorey. The introduced species Buffle Grass (*Cenchrus ciliaris*) and Parthenium Weed (*Parthenium hysterophorus*) were present. The collection site is an 'island' surrounded by paddocks of sunflowers and mung beans.

The specimen (TL 39cm) is unusual in being fawn-grey on black (rather than white on black); having a distinct vertebral stripe on the anterior third of its body (rather than 'rings' only); having a 'broken' vertebral stripe posteriorly connecting sets of 2-4 'rings' (rather than 'rings' only); and in having its venter virtually unmarked by the 'rings' (rather than consistently ringed in white). In other respects (e.g. head shape, scale counts) the specimen is unremarkable (Cogger, 1992).

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A
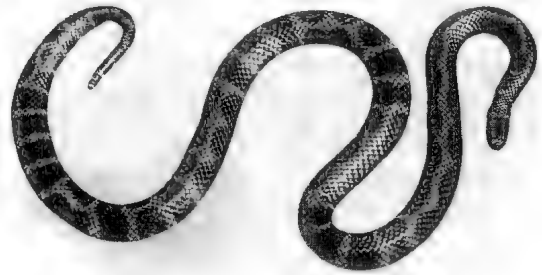
B

Fig.1A, *Vermicella annulata* from Acacia Ridge, Brisbane, SEQ, showing typical, highly distinct, regular black and white colour and pattern. B, *V. annulata*, from Retro Station, via Capella, MEQ, showing unusual colour (fawn-grey on darker grey) and pattern (some longitudinal lines with irregular bands).

ASPIDITES RAMSAYI (BOIDAE) IN THE BRIGALOW BIOGEOGRAPHIC REGION OF QUEENSLAND: OCCURRENCE, CONSERVATION STATUS AND POSSIBLE BILBY ASSOCIATIONS

J.A. COVACEVICH AND P.J. COUPER

Aspidites ramsayi is widespread in central, northwestern, southwestern and parts of eastern Australia. In southwestern Western Australia, an isolated population in what is now 'Wheatbelt' is 'endangered' and A. ramsayi is 'specially protected' under state legislation. In western New South Wales, *A. ramsayi* is 'endangered' at the state level. In the southern Brigalow Biogeographic Region (BBR) of Queensland, it now occurs as an apparently isolated population. Because brigalow habitats are poorly protected in reserves, because much of the habitat of *A. ramsayi* in the BBR is grazed and farmed and because the area is likely to be subjected to further modification, prospects for *A. ramsayi* in the area are poor. Despite the fact that*A. ramsayi* is not accorded special conservation status in Queensland, we contend that this species in the BBR is 'vulnerable'.

The common name 'Bilby Snake' is used for*A. ramsayi* in the Yuleba-Surat area of the BBR. This may point to a former close association there between *A. ramsayi* and the Bilby, *Macrotis lagotis*, an endangered species. □ *Aspidites, Bilby, vulnerable species, endangered species, Brigalow.*

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Aspidites ramsayi (Macleay, 1882) is widespread in arid and semi-arid Australia. It is known from an isolated population in southwestern WA, and from the Broome area, WA, in a broad band across WA, the southern NT, northern SA to southwestern and southern Qld, and western NSW (museum records; Wilson & Knowles, 1988; Cogger, 1992; Cogger et al., 1993; Pearson, 1993; Sadlier, 1994). The isolated population of *A. ramsayi* in southwestern WA is endangered, and is 'close to extinction'... (Cogger et al., 1993). Its range '... now largely coincides with the northeastern wheat belt of Western Australia' (Cogger et al., 1993). There have been two recent (1992, 1996) records from the western edge of the Nullabor Plain (D. Pearson, pers. comm.). Probable reasons for the decline of this population are identified as '... a combination of factors, including clearance of habitat for agriculture and grazing, and crop production.' ... (Cogger et al., 1993). Pearson (1993) suggested that predation by foxes and cats may promote the decline also. In western NSW, *A. ramsayi* is endangered at the state level and is apparently 'lost' from grazing areas; ... 'the most recent sightings ... are from within reserves, so land reservation could have a mitigating effect on the

processes causing the decline. ... (This is) ... a wide-ranging species so habitat fragmentation from clearing and heavy grazing could adversely affect (it).' ... (Sadlier & Pressey, 1993; Sadlier, 1994).

In Queensland, *A. ramsayi* occurs in the dry subtropics, between the Qld-NT and Qld-SA borders, and the Yuleba-St.George areas in south central Qld (Fig.1). In the western part of its range (near Bedourie-Birdsville-Thargomindah), *A. ramsayi* is associated with desert and semi-desert grasslands and chenopod woodlands on red sandy soils and stony downs of the Channel Country Complex (Sattler, 1986). As these areas are sparsely grazed and as there are no firm plans to intensify this land use, no threats to the continued survival of *A. ramsayi* in this part of its range are evident. In the eastern part of its range (Roma-Yuleba-Surat-St. George), *A. ramsayi* occurs on black soils and in stony ridge country, in Brigalow (*Acacia harpophylla*) woodland and grasslands, of the Brigalow Biogeographic Region (Sattler, 1986), and just west of this region. These populations now appear to be isolated from that in the far west of the state, presumably as a result of European land use in the Mitchell Grasslands and Mulga Lands of the in-
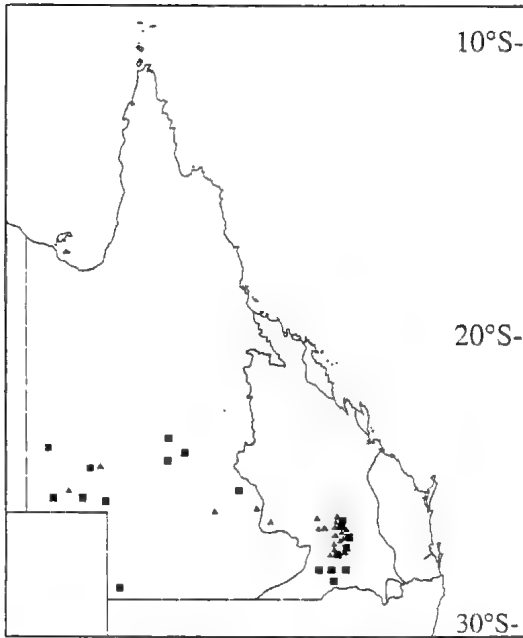
FIG. 1. Queensland showing Brigalow Biogeographic Region and distribution of the Woma/'Bilby Snake', *Aspidites ramsayi*. Squares = museum specimens. Triangles = reliable sight records.

tervening area. Six specimens of *A. ramsayi* have been recorded from the interface of the 'western' and 'eastern' populations: 1915, QMJ944 Avondale Station 23°36'S 143°16'E; 1922, SAMR01101 Minnie Downs 25°02' 145°52'; 1949, QMJ 7454 Jundah 24°05' 143°04'; 1987, sight only, Mariala N.P. 26°05' 145°04' (P.McCrae, pers. comm.); 1995, sight only Morven - Augathella road 26°06'S, 147°14'E, (C.Dollery, pers. comm.); 1 April, 1996, sight only, 20km N Charleville on Augathella road 26°17'146°17' (C. Dollery, pers. comm.). Examination of all Queensland records of *A. ramsayi* suggests that present 'western' and 'eastern' populations were, but are no longer, continuous.

Specimens from western and eastern localities are biochemically indistinct (S. Donellan pers. comm.). Three of these records are between 40 and 80 years old. The remainder are recent, but from very close to the BBR. It seems reasonable to suggest *A. ramsayi* no longer occurs in the 500km stretch between the Betoota (25°42' 140°50') area in the west, and Charleville-Morven-Augathella (26°25'S,147°07'E–25°48'S, 146°35'E) to the east. For conservation, the 'eastern' population of *A. ramsayi* should be con-

sidered virtually confined to the southern BBR and extreme eastern portion of the Mulga Lands.

There are parallels between the populations of *A. ramsayi* in and on the margins of Queensland's BBR and southwestern WA. Both appear to be isolates. Both occur in areas prized for agriculture/grazing. Although much of the natural habitat of *A. ramsayi* in southwestern WA has been cleared, large areas suitable for the species persist in the northern Wheatbelt, and from the eastern edge of the Wheatbelt to the Nullabor Region and the goldfields (D. Pearson pers. comm.) The natural habitat of the south central Qld (i.e. 'eastern') populations of *A. ramsayi* still is subject to grazing and some agriculture, but what appear to be a healthy populations of *A. ramsayi* occurs in the area. Notwithstanding this apparent, current security, there are no grounds for complacency about the status of these populations. Their habitat is not protected in any national parks, although State Forests 328 (Yuleba) and 75, 41, 60 and 48 (in the St George area) are important potential refuges for the species, should plans to expand agriculture in the area proceed.

Several authors have commented in the last decade on the plight of BBR plant communities. All agree that the area has been overcleared and that representation of habitat diversity in reserves is very poor (Sattler & Webster, 1984; Gasteen, 1985; Sattler, 1986, 1993; Davie et al., 1994). The remaining woodland of the Morven-Roma-Yuleba-Surat-St. George area of the BBR where the 'eastern' populations of *A. ramsayi* occur is good grazing land. Much of it has potential for agriculture. If patterns of development elsewhere in the BBR ensue, barring implementation of clearing restrictions currently being discussed (e.g. Central Queensland News 28.04.95), it seems reasonable to suggest *A. ramsayi* should be considered 'at risk' in the region. The potential threat is emphasised by the apparent fate of populations in south-western WA and western NSW.

Our data suggest that *A. ramsayi* in and on the western margins of the BBR of Queensland should be recognized as a 'vulnerable' species (Ingram & Raven, 1991). That is, *A. ramsayi* there is ... 'not presently endangered but at risk over a longer period of time through continued depletion ... largely occur (s) on sites likely to experience changes in land use which would threaten the survival of the species in the wild'. ... (Ingram & Raven, 1991).

BILBY ASSOCIATIONS?

A. ramsayi is known widely by the common name 'Woma' (Wilson & Knowles, 1988; Cogger, 1992); in the Roma-Yuleba-Surat area, it has been known for many years as the 'Bilby Snake'. The name 'Woma' is not in general use in this area (J.Harland, R. Allwood pers. comm., March, 1995).

The Bilby, *Macrotis lagotis* Reid, 1837, is an endangered species, once widely distributed in arid and semi-arid Australia, but now with a restricted range. In Qld, it is confined to a few isolated, small areas of the southwest (Gordon et al., 1990; Southgate, 1990; Department of Environment & Heritage, 1995). The use of the common name 'Bilby Snake' for *A. ramsayi* would be unremarkable if there were not a correlation between the former ranges of both species, including the BBR of Queensland. Distribution maps (Southgate, 1990; Gordon et al., 1990; Ingram & Raven, 1991) for *M. lagotis,* and *A. ramsayi* (Wilson & Knowles, 1988; Ingram & Raven 1991; Cogger, 1992) show that these two species at one time occurred widely, often in the same areas. However, Womas occur in several areas from which Bilbies are not known (e.g. the Pilbara, southern Kimberley, the Gibson Desert west of the Clutterbuck Hills to near Shark Bay in WA, in the area south of Perth, and in much of SA). A Queensland Museum specimen of *M. lagotis,* QMJ90, attests to its presence in the southern BBR. This is a current, but potentially threatened, stronghold of *A. ramsayi*. The *M. lagotis* is from Surat, and was collected in 1912, by H. Donaldson. Local, longtime naturalists do not know now anything of the Bilby in the Yuleba-Surat area beyond the local name, 'Bilby Snake' (R. Allwood, T. Broughton, J. Harland pers. comm., March 1995).

Whether or not there was an association between the Bilby and so called Bilby Snake in this area is uncertain. Womas are known from 'Bilby areas' of Queensland's Channel Country (P. McRae, pers. comm.), but we have no observations of direct association of the two species in the BBR. *A. ramsayi* is known to prey equally on reptiles and mammals (Shine, 1991) and, in the Yuleba-Surat area, to occur on sandy soils and in 'stony country ... and go down sink holes' (R.Allwood pers. comm., March 1995). It does not seem unreasonable to surmise that 'Bilby Snakes' may, at least in this area, have utilized Bilby burrows for shelter, and Bilbies as food, at least enough to have given rise to their local name. Several recently collected (and released), or road-killed specimens of 'Bilby Snakes' in the BBR have been mammal feeders, containing hare and rabbit remains. (R.Allwood, J.Nixon-Smith pers. comm.). With the demise of the Bilby and the rise of rabbits, the snakes may have been forced to prey on common introduced mammals. Many landholders have reported finding 'Bilby Snakes' in and near rabbit warrens recently (C. Eddie pers. comm.).

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LERISTA ALLANAE (SCINCIDAE: LYGOSOMINAE):
60 YEARS FROM EXHIBITION TO EXTINCTION?

J.A. COVACEVICH, P.J. COUPER AND K.R. McDONALD

Lerista allanae (Longman, 1937) is known from 12 specimens collected between 1929 and 1960, from 3 localities (Retro, Logan Downs and Clermont), in a small section of Queensland's central Brigalow Biogeographic Region. The species is/was confined to 'black soil' downs. The area from which *L.allanae* is known has undergone dramatic change since first settlement; it is now farmed or grazed, so little natural vegetation remains.Many searches by specialists have failed to find *L.allanae*. We conclude that *L.allanae* may be extinct, while acknowledging that this is impossible to prove. If it is not extinct, *L.allanae* is critically endangered. Despite its 'obscurity', the possible extinction/endangered status of *L.allanae* is a matter of concern, notwithstanding the extremely high economic value of agriculture in the Brigalow Biogeographic Region. The apparent demise of *L.allanae* may herald loss of other reptile species.

We recommend seeking the co-operation of land holders to protect remnants of natural vegetation in its range; recognising the vital importance of remaining natural grasslands like Gemini National Park; implementing a pit-trapping programme to increase the chance of re-locating the species; and examining the need to protect, at least, the type localities of Brigalow Biogeographic Region species where they still occur. □*Lerista allanae, extinction, endangered species, Brigalow Biogeographic Region.*

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Lerista allanae (Longman, 1937) is a burrowing skink from a small area of Queensland's black soil downs in the Central Brigalow Biogeographic Region. It is known only to taxonomists, and has been collected by, at most, a handful of people, between 1929 and 1960. No photographs are known of *L.allanae* in life.

Thirteen museum specimens comprise the total knowledge base of this species, one of 11 species of Australian reptiles recognised as 'endangered' (Cogger et al., 1993).

SPECIMEN HISTORY

The 13 specimens of *L.allanae* were collected in 3 localities, all in close proximity to one another, in the undulating downs (= gently undulating plains formed on Tertiary basalt, Permian shales, sandstone and unconsolidated sediments of the Oxford Land System) of the central Brigalow Biogeographic Region (J. Mc-Cosker pers. comm.): '20 miles W of Capella' =

Retro Station 22°51'53"S 147°53'43"E*, Aug. 1929+, J.R. Slevin, (AMR13819); 6 Aug. 1929, J.R. Slevin, (CAS77101, 'missing' 14 Feb, 1988); 12 Dec, 1936, J.R. Slevin, (CAS77099); 13 Aug, 1929, J.R. Slevin (CAS77100); Retro Station, Sept, 1936-Nov 1937, Maida (Mrs Percy C.) Allan, (QMJ6180 holotype, QMJ6040, QMJ6179 paratypes, QMJ6238, QMJ6308, QMJ6429, QMJ6430); Logan Downs approx. 22°25'S 147°55'E, 16 Nov, 1948+, H.Womersley, (SAMR2823); Clermont 22°50'S 147°38'E, Jan, 1960+, C.Vallis (QMJ12232), (Couper & Ingram, 1992; Cogger et al., 1993; Shea, 1993; Covacevich & Couper, 1994; J.V. Vindum, pers. comm).

Heber Longman described *Rhodona allanae*, naming it for the collector of the first specimens sent to him. However, nearly a decade earlier, J.R. Slevin from the California Academy of Sciences, had collected specimens of this species.

This material, from '20 miles W of Capella' (=Retro Station) was not included by Longman

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*(Latitude and longitude calculated at Retro homestead, in the absence of precise data on collection locality/ies.
+Date of registration, unless identified as a date of collection. Registration occurs soon after collection, generally.

in his type series. Longman's types (Covacevich & Couper, 1994) were sent to him by Mrs Percy (Maida) Allan, wife of the manager of Retro. The correspondence between Longman and Mrs Allan (Queensland Museum Archives) is a lively record of his excitement at 'the find' on Retro, and her keen interest in natural history. It also sheds some light on the colour of *L.allanae* and on its habitat preferences. (e.g. '...an elongated, *grey, dark - spotted skink*'... in litt., H. Longman to Mrs P.C. Allan, 20 May, 1936; 'This is a *very rare* and interesting lizard, and I hope that other specimens can be obtained and forwarded. It is the first of this particular kind to be obtained in Queensland, and it is probably new to science... in litt., Longman-Allan 10 Sept., 1936; '...In this lot of lizards there is a very good specimen of the elongated one, the 'Retro' lizard, *they are not easy to find*, but have asked the man who brings in new soil for garden to keep a lookout as *they seem to be down a few inches in black soil under tussocks of grass and so far we have had four from that one patch. ...*' in litt., M. Allan to Heber Longman, 18 June, 1937; '... I was particularly pleased to have two additional specimens of the elongated *grey, dark-spotted skink* lizards. These will probably be described as new in the next number of our Memoirs. They are allied in some respects to a North Queensland species named after Sir Hubert Wilkins, and to a West Australian species. Congratulations on this discovery. ...' in litt., Longman to Allan 20 May, 1937).

Longman was keen to exhibit the new reptile. ...'As the type and two paratypes should be preserved downstairs to avoid fading, as far as possible, I hope that you will be able to find other specimens for exhibition and for exchange with one or two other museums.' ... (in litt., Longman to Allan, 18 June, 1937). Specimen QMJ6238, registered 28 June, 1937, was placed on display in the galleries of the Queensland Museum, presumably soon after registration. It was removed from exhibition, faded, but otherwise in good condition, on 18 Aug., 1954.

Data from the registers, correspondence and literature on the habitat of *L.allanae* are scant. Slevin's (1955) description of Retro, from his visit there in 1929 and 1936, '... open grasslands and scattered gum trees with moderately heavy groves of tea tree and an occasional bottle tree. Both black and red soil are in evidence. Though the surrounding country did not look attractive as a collecting ground it proved to be excellent, with a large number of species.' ...; and Mrs Allan's description of the skink's association with 'tus-socks of grass' and being found 'down a few inches in black soil' are all that is known. That four specimens of the 10 known from Retro came from 'one patch', that only 12 have been lodged in museums, and that both Longman and Mrs Allan allude to its 'scarcity' suggest that *L.allanae* may have been always both 'rare' and highly-localized in the black soil downs of the Capella-Clermont area. These data also suggest that the species was difficult to find. The exact collection site for these specimens was not referred to in Longman's description of *L.allanae* (1937), and exact collection sites for the specimens from Logan Downs and Clermont also are imprecise and devoid of habitat notes.

Slevin's collections in 1929 and 1936 suggest that *L. allanae* may have been scarce always. Slevin was a skilfull collector. California Academy of Science records show he collected 1200 reptile specimens of 33 species on his two field trips to Retro. Only three specimens of the then undescribed *L. allanae* were collected.

Reduction in size and intensification of land use on Retro have gone 'hand in hand', since the early 1920's. This pattern, now being implemented more quickly than ever on the central downs of the Brigalow Biogeographic Region, is not new for rich black soil downs in Qld. In southeastern Qld, similar pressures to increase farm produc-tion have resulted in dramatic changes in ver-tebrate and plant species diversity on the Darling Downs (Covacevich unpubl. data; Fensham pers. comm.).

L. ALLANAE VS *L. COLLIVERI*

The recent separation of *L. colliveri* Couper & Ingram, 1992 from *L. allanae* was based on what could be regarded as minor external differences. *Lerista colliveri* was described from 37 spec-imens which had been identified as *L. allanae*. These specimens account for distribution maps (Cogger, 1975, 1979, 1983, 1986, 1992; Ehmann, 1992; Wilson & Knowles, 1988) which suggest that *L. allanae* occurs beyond the Capella-Cler-mont area to the vicinity of Hughenden and the Townsville area.

With Couper & Ingram's (1992) separation of *L. colliveri*, *L. allanae* is again a narrowly-restricted species, which has not been reported or collected since 1960, despite many searches. Comparison of the recent redescription of *L. al-lanae* from the type specimens and of *L. colliveri* (Couper & Ingram, 1992) and the observations of Shea (1993) shows they differ in colour pattern

and in the number of long toe lamellae. In *L. colliveri* the forelimb varies from a nubbin to a style. *L. allanae* has no forelimb.

With these data in mind, we recognise that the differences between *L. allanae* and *L. colliveri* could be seen as too minor to warrant species recognition. If this were so, *L. colliveri* would be treated as a junior synonym of *L. allanae* and, as *colliveri* were collected relatively recently (1977-1985), some of the concern about *L. allanae* would abate.

However, separation of species within *Lerista* from only slight or even without external differences, has well established precedence. Characters used by Greer et al. (1983) to separate *L. cinerea*, *L. storri* and *L. vittata* from one other are also subtle.

In separating *L. emmotti* from *L. punctatovittata* Ingram et al., (1993) identified only one character as diagnostic, a didactyle forelimb vs a monodactyle forelimb or monostylus. Estimates of genetic distance derived from allozyme electrophoresis showed that the two 'forms' warranted recognition as distinct species, despite the fact that development of the toes in degenerate-limbed skinks is highly variable. In other genera also, subtle morphological differences have been used to support species delineations based essentially on allozyme variation (e.g. Daugherty et al., 1990a; Patterson & Daugherty, 1990). Regarding the *Oligosoma nigriplantare* species complex of New Zealand, Daugherty et al. (1990a) observed: 'A clear pattern of genetic and specific divergence is overlain by a highly variable pattern of color and morphological variation, often independent of species boundaries. ...' and that this frustrated traditional taxonomic methods. Another recent New Zealand example highlights the importance of examining the distinctness of *L. allanae* and *L. colliveri*. Daugherty et al. (1990b) analysed the conservation implications of recognising three taxa of tuatara, where only one had been known.

As *L. allanae* has not been collected since 1960, the possibility that genetic distance from *L. colliveri* can be determined from allozyme electrophoresis seems remote. However, given patterns elsewhere; that there are morphological differences between *L. allanae* and *L. colliveri*; and that the two are geographically isolated, we consider *L. allanae* distinct from *L. colliveri*. We also recognise the need for what might be termed 'taxonomic caution' in dealing with potentially endangered taxa; and that ...'Taxonomies are not irrelevant abstractions, but essential foundations of conservation practice' (Daugherty et al., 1990b).

RETRO: SIZE AND LAND USE

Retro was established in or about 1861, from the amalgamation of a series of 'runs' in the Leichhardt Pastoral District. Initially, Retro included close to 400 km² (Queensland Department of Lands, 1866). By the 1880s it extended NE from the Capella-Clermont road, and straddled Retro Ck and its tributaries, (Queensland Department of Lands, 1884) (Fig.1). Through partition and sales, both as a result of government policy and market vagaries, Retro's size has diminished dramatically. By about 1920, a major section of Retro had been excised near the Clermont-Capella road (Queensland Department of Lands, ca. 1920); by the 1940s further excisions on the SE boundary near Abor Ck and on the NE boundary had been made (Queensland Department of Lands, circa 1940s a,b); by 1951, Retro had been reduced to c.72,000 acres (Queensland Department of Lands, 1951). Retro is now a holding of 2208.774 ha. Former 'Retro Station' now forms part of Dakota, Carramah, Meelia, Hazeldene, Weimby Downs, Mt Oscar, Salt Springs, Amatunga, Penaddi, and Grenada holdings (Alick, 1995, map 3).

Intensification and simplification have characterized land use on Retro. It was a sheep station originally. In 1891, 71000 sheep were shorn on the station (L.Vagg pers. comm.). On Retro, and on most other sheep holdings in the Capella area of the black soil central downs, sheep-grazing changed natural pastures to such an extent that 'new' grasses and weeds bearing seeds contaminated 'the clip' beyond use. This forced a change from sheep to cattle grazing in the area (J. McCosker, pers. comm.). Cattle grazing progressively gave way to mixed cattle and grain production, with the availability of machines to hasten clearing and improved grain markets in the 1940s-1950s. In 1951, Retro was held by The Queensland British Food Corporation, and was used primarily for grain production. In 1996, Retro is 'broadscale' farmed, with some irrigation, to produce sunflower seeds, mungbeans and sorghum.

There are no data on early vegetation on Retro, but from the early 1940s (soon after the Allan collections of *L.allanae*), detailed description of Retro's 'natural' vegetation is available. At that time, Retro was primarily a cattle station. The 'Retro Freehold Lands' map, Queensland
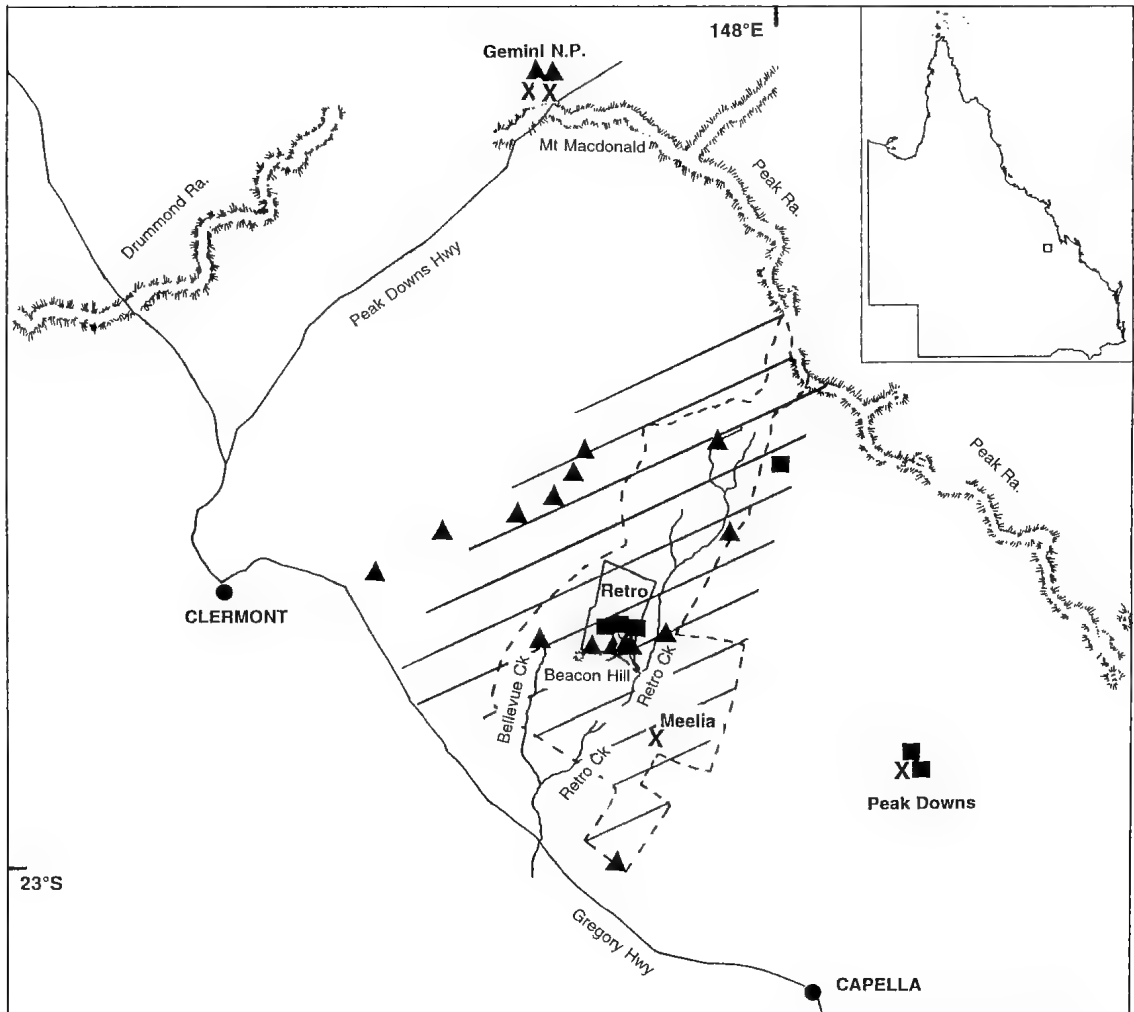
Fig. 1.Retro Station, the type locality of *Lerista allanae*, showing progressive size reduction since the 1860s. (///= approximate extent in the 1860s; ——— = boundary during the 1940s; — = boundary, 1995). Also shown are sites searched in attempts to locate *L. allanae* between 1970 and 1996. (hand collecting, 1970-1994 ■, 1995-1996 ▲; pit-trapping, 1995-1996 x). Two pit-traps and one hand-collecting site for 1996 are not shown. All are on Kevricia, 35km ESE of Capella. 1cm=4.8km.

Department of Lands, c. 1940s describes the country and vegetation from north to south in detail: 'Scattered timber and Stone, Stony Coolibah Ridges, Heavy Scrub with Stony Hills, Some Slope Gullies and Stone, Plain, Ti-tree, Scrubby and Gravelly Ridges, Plain with lightly scattered Bauhinia, Black Soil Fairly Heavy Scrub, Open Tableland Coolibah and Blood-wood, / Open Plain, inter alia' ... Only one tiny area near the homestead, now abandoned, but still standing (Fig.2) was cleared. This is described as 'Old Cultivation'. Retro contains no 'natural' vegetation save for islands of Poplar Box (*Eucalyptus populnea*) woodland with sparse

shrub understorey and open Coolibah (*E. orgadophila*) woodlands. Buffle Grass (*Cenchrus ciliaris*), an introduced pasture grass, and the Parthenium weed (*Parthenium hysterophorus*) are common in areas not under crops.

SEARCHES FOR *L.ALLANAE*, 1968-1995

Between 1968 and 1995 there have been many attempts to find *L.allanae* on Retro, the area formerly part of 'old' Retro, and in 'suitable' habitats nearby. Other reptile specimens have been collected during searches aimed at estab-lishing if *L. allanae* still occurs (Fig.1) . These

Fig. 2.The abandoned homestead Retro Station, a relic of the 19th century, where Maida Allan, who collected the type specimens of *L. allanae*, lived in the 1930s.

searches, which have intensified since 1992, have not been methodical in terms of either seasonal or habitat sampling. However, experienced collectors have searched the area in 'good' reptile times (summer and spring) many times. They have found other burrowing, secretive or elusive, small skinks (e.g. *Lerista fragilis, Anomalopus brevicollis, Glaphyromorphus punctulatus, Menetia greyii* and *M. timlowi*) in the area, but *L.allanae* has not been located. *Lerista* spp. and other burrowing skinks (e.g. *Anomalopus* spp.) are not usually collected by non-specialists. (Since 1985, 125 *Lerista* spp. have been added to Queensland Museum reference holdings. Only seven of these, i.e. 6%, were collected by people other than herpetologists. Numbers for *Anomalopus* spp. are similar, i.e. 8/62, 13%). It is, therefore, not surprising that, despite recent radio and newspaper publicity about *L.allanae*, no specimens have been collected 'accidentally' by 'amateurs'

The Longman-Mrs Allan correspondence had not been used as a basis for target-searching for *L.allanae* prior to 1995. Using Mrs Allan's descriptions; following consultations with Ms J. McCosker (of Department of Environment,

Emerald) regarding soil and vegetation types, especially grasslands; using data from maps of 'old' Retro's boundaries; and bearing the Logan Downs and Clermont collection localities in mind, 4 sites were chosen for intensive *L.allanae* searches, both by hand and using pit traps. Pit-trapping is acknowledged widely to be a reliable way of sampling reptiles, including species often not found by hand- searching (Morton et al., 1988). Many types of fences, traps and designs of pit-traps have been used, with varying success rates. In an arid habitat, it has been shown that . . .'A simple straight line of pit-traps and a drift fence with buckets approximately 7m apart is the most effective . . .' (Hobbs et al., 1994). This method was adopted.

In Gemini National Park, 2 pit-traps lines of 12 buckets each were set at different times, early summer and late summer-early autumn. The first (22°30'25"S 147°51'06"E) was set from 15-21 Feb., 1995; the second (22°29'15" 147°52'14"), from 15-20 April, 1995. Gemini National Park is one of only three small national parks within 100km of Retro. Here, open grasslands, once extensive in the central Brigalow Biogeographic Region, have been protected from invasion by, or

deliberate replacement with, introduced grasses. This is the only such locality in the area. Gemini National Park supports Blue Grass (*Dichanthium sericeum*) Downs, with open-groved *Bauhinia hookeri*, and scattered *Eucalyptus* spp., on dry, cracking, self-mulching, red-black soils. The introduced weed (*Parthenium hysterophorus*) is common on its margins, but has not invaded areas where the native grass is dense. Gemini National Park lies about 30km NW of the former boundary of 'old' Retro. It adjoins Logan Downs, the locality from which the 1948 specimen of *L. allanae* was collected. (Surveys for *L. allanae* were not conducted on Logan Downs because permission to work there could not be obtained). On Meelia, between 21-26 April, 1995, a pit-trap line was set about 8km SE of the old homestead on Retro, at 22°57'12"S, 147°54'30"E. Meelia lies within the boundary of 'old' Retro Station. This site is one of the few, minute remnants of uncleared land remaining in the area. The pit-trap line was set in red-black, cracking clay soil with open-groved *B. hookeri* and some Blue Grass (*D. sericeum*). Much of Meelia has been cleared for, or modified by, cattle grazing but the pit-trap site is grazed only intermittently, and supports native vegetation. Two pit traps were set on Kevricia at 23°14'77"S, 148°16'71"E and 23°14'79"S, 148°16'19"E between 12-16 Feb., 1996. The former (site 1) was set in a 30m wide strip of Brigalow forest on deep, black, cracking soils. It had not been cleared, but was disturbed by cattle and adjoined a ploughed paddock. The latter (site 2), an area of dense Brigalow regrowth, also grazed and trampled by cattle, had been cleared once, in 1981. Kevricia is some 60km from Retro. It was chosen for sampling because of its similarity to some of Retro's former vegetation and because of the scarcity of such habitats in the area. A pit-trap was also set at Peak Downs (22°56'29"S, 148°04'60"E), 12-16 Feb., 1996. This was set in cleared, grassed, black soil adjoining both the old and new homesteads. (Peak Downs was established in the same era as Retro and, like Retro which it once adjoined, has been divided into many small holdings. Like Retro also, Peak Downs was a significant early collecting locality for reptiles (Cogger et al., 1983).

Results of pit-trapping in these sites (Table 2) indicate that burrowing and cryptic reptile species still occur in the area from which *L. allanae* is known.

Further, Queensland Museum register provides a good record of incidental reptile collecting undertaken on and near Retro since 1968. Hand

TABLE 2. Summary of results from six pit-trap lines set in 1995- 1996, at four locations close to Retro, in search of *L. allanae*.

Species	Gemini NP 1	Gemini NP 2	Meelia 1	Kevricia 1	Kevricia 2	Peak Downs 1
Gemmatophora nobbi				+		
Diplodactylus vittatus		+				
D. williamsi					+	
Geyhra catenata	+					
Heteronotia binoei				+	+	
Glaphyromorphus punctulatus	+		+	+		
Lerista fragilis	+			+		
Menetia greyii	+		+	+	+	+
M. timlowi	+					
Carlia pectoralis				+	+	

collections by Queensland Museum staff/colleagues have been made at the following localities (Fig.1): Gibson Downs (22°49'S, 148°12'E); Highland Plains (22°40'S, 148°08'E); 8km from Clermont on Clermont-Mackay road (22°45'S, 147°38'E); Gaylong, via Capella (22°46'S, 148°09'E); 500m ENE of old Corry turnoff (22°45'S, 148°02'); Glencoe Stn (23°08'S, 148°14'E); 8-10km E of Capella at Gregory Mine turnoff (22°58'S, 148°03'E); Retro (22°52'S, 147°54'E); 20km N of Capella on Clermont road (22°59'S, 147°51'E); 17km NW of Capella on Clermont road (23°00'S, 147°54'E); Gemini NP (22°30'25"S, 147°01' 51"E); Mazeppa NP (22°11'51"S, 147°18'48"E); Moonda Siding (22°59'52"S, 147°53'16"E); Peak Ra. NP (22°30'25"S, 147°01'51"E); Huntly Downs (22°52'35"S, 147°07'E); Prairie Stn (23°06'46"S, 147°47'36"E); Meelia (22°57'S, 147°54'); and Peak Downs (22°56'S, 148°04'E).

That *L. allanae* has not been found despite recent pit-trapping and many hand-collecting searches by specialists in the last 28 years does not mean it is extinct. However, as other burrowing species known only to specialists have been found, and as *L. allanae* has not, is reason for concern. It seems reasonable to suggest that, if *L. allanae* survives, the sites on Gemini National Park ('secure' under legislation); Meelia and Kevricia (both freehold) are potential refuges for the species.

L. ALLANAE, POSSIBLY EXTINCT?

Extinction is difficult, if not impossible, to prove. The case of *Tiliqua adelaidensis* parallels that of *L. allanae* in many ways. Both are known from narrowly-restricted localities which have been changed by grazing or farming; both were/are known from only very small series of specimens (20 *T. adelaidensis* vs 13 *L. allanae*); for both, many unsuccessful searches by experienced herpetologists have been undertaken; and both species are secretive. *T.adelaidensis* was classed as 'possibly extinct' or 'extinct' by many authorities (Ehmann, 1982, 1992; Burton et al., 1986; Cogger, 1992; Hutchinson, 1992a,b). On 14 Oct., 1992, 33 years after it had been seen last, a specimen of *T.adelaidensis* was found in the gut of a Brown Snake, *Pseudonaja textilis* (Armstrong & Reid, 1992).

The prospect that *L.allanae* will, like *T.adelaidensis*, be rediscovered is not good. *L.allanae* was collected/seen last in 1960. The three known localities for *L.allanae* have undergone dramatic change, including clearing of forests; replacement of native grasses with introduced species, some of which are aggressive weeds; the replacement of grazing with intensive farming; and heavy use of pesticides to combat insect pests, particularly locust. All will have reduced the species' chances of survival. Thus it does not seem unreasonable to regard *L.allanae* as possibly extinct. *L.allanae* is a secretive species, like all *Lerista* spp., and is unlikely to be collected by farmers or graziers, and sent to a museum for identification, if records for other *Lerista* spp. are any guide; it may have some unusual life habit that has assisted its survival in the face of what appear to be major assaults on its only known habitat; and it is possible that the only known habitat for *L.allanae* may not be its true stronghold. This review confirms that *L. allanae* is, at least, endangered. In any terms it needs urgent conservation attention. *L. allanae* 'fits' almost perfectly the definition of 'endangered' (Cogger et al., 1993): '... Taxa in danger of extinction and whose survival is unlikely if the causal factors continue to operate ... whose numbers have been reduced to a critical level or whose habitats have been so drastically reduced that they are deemed to be in immediate danger of extinction. Also included are taxa that may now be extinct but have definitely been seen in the wild during the past 50 years and have not been subject to thorough searching'... .

So little data are available on *L.allanae* that its critical population level and habitat are unknown, but the area from which it was collected has been drastically altered. It may be extinct now, but has been seen in the last 50 years (last in 1960). It has been subject to many searches, including some that would be termed methodical, if not 'thorough'.

THE IMPORTANCE OF *L.ALLANAE*

If *L.allanae* is extinct, it is the first Australian reptile species to be so since European settlement. This species is neither visible nor 'appealing'. It has no charismatic quality. It has been seen by only a handful of people, and it is poorly known by even specialist naturalists and herpetologists. It has no special status in the area from which it was described.

The reasons usually proposed for striving to maintain biodiversity are that: extinction can disrupt an ecosystem and cause the demise of other species; reduced diversity makes the world less interesting; the present generation has a responsibility to leave a world of maximum diversity = quality, for future generations; we may want properties (e.g. drugs) from species; and species have intrinsic value and a 'right' to exist (Elliot, 1980). The possible extinction of *L. allanae* could not disrupt the modified central downs of the Brigalow Biogeographic Region or cause the extinction of other species. Its possible loss could not be said to diminish seriously the lives of future generations; and its extinction is unlikely to result in the loss of some magical compound for the betterment of mankind. The loss of *L.allanae* may, like the canary in a coal mine, be a warning. Being narrowly restricted, rare and from an area now intensely farmed and grazed, it may be an indicator that other Brigalow species are about to decline. Many other species either confined to or occurring mainly in the Brigalow Biogeographic Region, are already recognised as rare and vulnerable (McDonald et al., 1991), and the conservation status of other Brigalow reptile species is of concern (e.g. *Aspidites ramsayi* after Sadlier, 1994; Sadlier & Pressey, 1994; Covacevich & Couper, this memoir).

Much of Queensland's Brigalow Biogeographic Region is rich grazing and agricultural land. Much of it has already been modified extensively and few reserves have been set aside for the protection of Brigalow communities (e.g. Sattler & Webster, 1984; Gasteen,1985; Sattler, 1986; Davie et al., 1994). It is now well known that nothing, not even stringent habitat protec-

tion, guarantees species protection (e.g. frogs in high altitude rainforests of Queensland; Ingram & McDonald, 1993). However, the corollary seems to be true for the Retro-Clermont-Logan Downs Brigalow habitats. Clearing of native forests comes close to ensuring species loss.

Emerald 65km S of Retro, is the main commercial centre for the central downs. It '... is anticipating an economic boom which will triple the value of production in the area'... which '...has beef cattle, cotton farms, citrus orchards, wheat and sorghum ...(and) coalmines. The key is a $235 million dam ... on the Comet River to provide 1,300,000 megalitres of water for new coalmines and *agricultural expansion.* '... (italics ours), Hay (1995). In the face of such ambitious plans for economic benefits from increased development and clearing in the central downs, whether or not *L.allanae* survives can be seen as trivial. That one cost of such economic benefits could also be the extinction of additional reptile (and other) species, can be seen also as inevitable and trivial. If, however, the pursuit of an ideal - to maintain biodiversity - in the Brigalow Biogeographic Region is worthwhile, the current status of *L.allanae* is not trivial. Rather, it becomes a matter of concern, necessitating, at least, restriction of clearing in the area.

RECOMMENDATIONS

1.Recognise that, inherently, *L.allanae* is worth preserving, if it still exists.

2.Consult with landholders in the Retro-Logan Downs area to encourage their co-operation to protect/preserve remnant stands of native vegetation from cattle, clearing and pest plants.

3.Recognise that Gemini N.P. is the best refuge in which *L.allanae* may still survive. The particular importance of this small park should be recognised, and special effort be directed towards its management (e.g. protection from *Parthenium hysterophorus*, illicit grazing of cattle, fire).

4.Continue efforts, particularly through pit-trapping to locate *L. allanae.* Whether such efforts should be urgent, major, and involve substantial research money and time, is a matter for consideration by protection authorities (i.e. Queensland Department of Environment and the Australian Nature Conservation Agency).

5.Recognise that type localities and habitats of other narrowly restricted species in the Brigalow Biogeographic Region may be altered or threatened by continued development. Where species still occur at their type localities or in small pockets of what may always have been a narrow range and where these areas still support native vegetation, every effort should be made to protect these areas, *at least*, from clearing.

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TWO NEW SPECIES OF FALSE SPIDER CRABS (CRUSTACEA: BRACHYURA: HYMENOSOMATIDAE) FROM NEW CALEDONIA

P.J.F. DAVIE AND B. RICHER DE FORGES

Two new species of Hymenosomatidae are described from estuarine habitats on the west coast of New Caledonia. *Odiomaris estuarius* sp. nov. is most closely allied to the endemic New Caledonian *O. pilosus* (A. Milne Edwards, 1873). *Neorhynchoplax euryrostris* sp. nov. is unique in the genus with its prominent, broad, unilobate rostrum. ☐*Brachyura, Hymenosomatidae, Odiomaris, Neorhynchoplax, New Caledonia.*

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The Hymenosomatidae has been relatively little studied, probably due to their small size and cryptic habit. Lucas (1980) and Lucas & Davie (1982) described 13 species from Australia, indicating that family diversity had probably been seriously underestimated. Ng & Chuang (1996) provided the first overview of the Southeast Asian fauna, recognising 24 species in 10 genera (including 8 new species), making 15 new species described from Southeast Asia since 1988 (Ng, 1988, 1991; Chuang & Ng, 1991). Thus the New Caledonian fauna could be expected to harbour some undescribed species. Ng & Richer de Forges (1996) reviewed the hymenosomatid fauna of New Caledonia, establishing two new genera and describing two new species. During mangrove and intertidal collecting in December 1993 we found 2 new species living under logs and rocks in two estuaries north of Noumea, on the west coast of New Caledonia.

SYSTEMATICS

Abbreviations used in the text are: MNHN, Muséum national d'Histoire naturelle, Paris; QM, Queensland Museum, Brisbane; c.b., carapace breadth; G1, male first gonopod.

Class CRUSTACEA
Order DECAPODA
Suborder BRACHYURA
Family HYMENOSOMATIDAE

Odiomaris estuarius sp. nov.
(Figs 1, 2A, C)

MATERIAL EXAMINED. HOLOTYPE MNHNB 25278, ♂ (4.6 x 4.3 mm), Dumbea estuary, New Caledonia, 8.12.1993, P. Davie & B. Richer de Forges. PARATYPES MNHN-B25275, 4 ♂ (4.7 x 4.4; 4.0 x 3.6; 3.6 x 3.4; 2.7 x 2.7 mm), 4 ♀ (5.4 x 5.0; 4.1 x 3.9; 4.0 x 3.5; 3.8 x 3.4 mm). QMW20576, 5 ♂ (4.8 x 4.4; 4.1 x 3.9; 4.0 x 3.7; 3.0 x 3.0; 2.5 x 2.4 mm), 5 ♀ (6.2 x 5.8; 4.9 x 4.4; 4.3 x 4.0; 3.6 x 3.3; 3.4 x 3.1), same data as holotype.

DESCRIPTION. Carapace subcircular, width 1.0-1.14 (mean=1.08) times length (including rostrum); dorsal carapace surface flat to slightly convex, with gastro-cardiac, cervical and thoracic grooves; thoracic grooves short, angled laterally; anterolateral and posterolateral angles not indicated; carapace rim broad, minutely granular; branchiostegites nearly vertical, sloping out ventrally near last walking legs; rostrum spatulate; eyes prominent, corneas swollen; postocular lobes relatively small in size, not prominent in dorsal view, affording little protection for corneas; lower margin of orbital cup with inner and outer blunt knobs; antennules concealed in dorsal view when flexed; interantennular septum narrow; rostral keel indistinct, rostrum broadly rounded in frontal view; epistome short; upper ridge of pterygostomial region prominent, becoming broken posteriorly, elevated on either side of pterygostomial and branchiostegite junction anterior to cheliped bases; surfaces of pterygostome and branchiostegite granular; Milne-Edwards' apertures normal.

Mouth field wider than long, almost completely filled by 3rd maxillipeds; ischium of 3rd maxillipeds shorter than merus along lateral edge, palp not reaching ischio-merus junction, exopod only visible proximally. Length of chelipeds in available males, and females, subequal to carapace
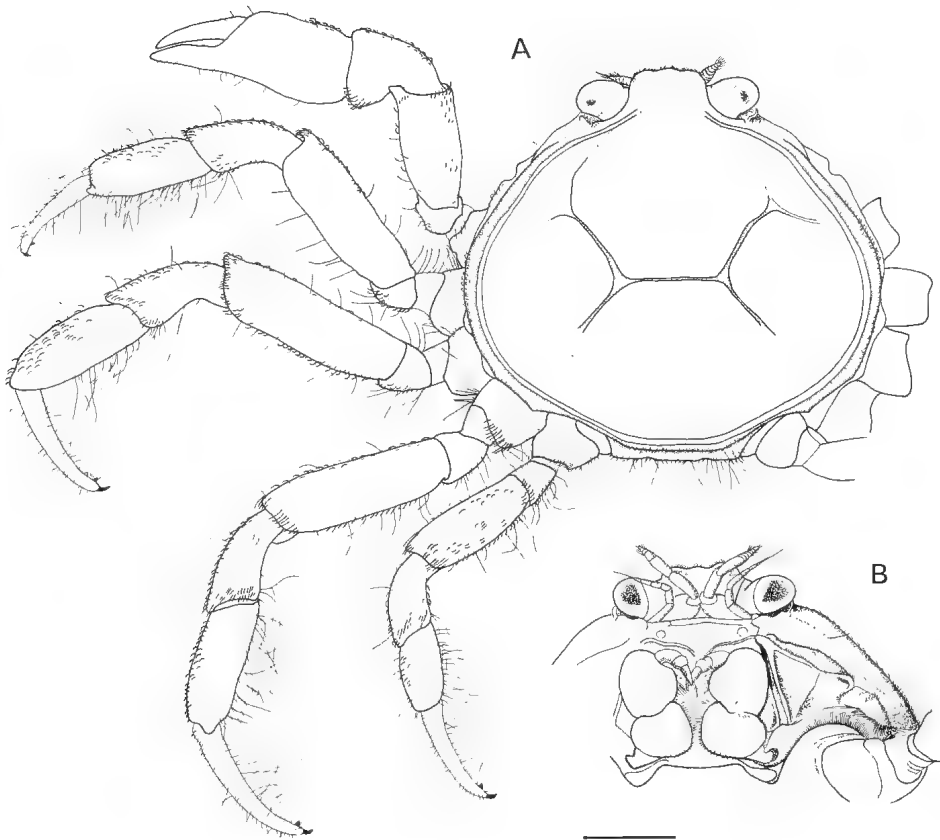
FIG. 1. *Odiomaris estuarius* sp. nov., holotype male. A, dorsal view; B, frontal view. Scale line = 1 mm.

breadth; only slightly stouter than largest walking legs; outer surfaces sparsely setose, and minutely granular; propodus of largest male (holotype) not inflated, similar to females, without ventral keel; fingers curved, without marked proximal gape, cutting margins bearing minute teeth only. Length of walking legs c. 1.4 times carapace width in both males and females, legs moderately thick, dactyli distinctly longer and more slender than propodi, densely setose, slightly curved, with distinct subterminal tooth.

Female abdomen oval, convex, with 2 deep, sinuous, submedial grooves running entire length, defining a convex central region; segments 1-5 progressively longer and broader, with base of telson forming greatest width; telson arcuate, c. 1.75 times longer than segment 5; eggs c. 0.4 mm diameter. Male abdomen with segments 1 and 2 shorter and broader than segments 3-5, segment 3 next shortest, segments 4 and 5 of similar length, tapering to telson, telson bluntly triangular, c. twice length of segment 5; interca-

lated plates laterally at base. Male G1 stout, with 2 distinct distal processes, a longer corneous process and a shorter lobular elongation of stem; conspicuously setose particularly on the disto-abdominal face.

Body coloured light brown (alcohol preserved specimens), often with a thin caked-on layer of very fine sediment; feathered setae, often thick with sediment, around mouth frame, Milne-Edwards' aperture, on walking legs, around edge of female abdomen.

HABITAT. Under logs in estuary.

DISTRIBUTION. Only known from the type locality on the west coast of New Caledonia.

ETYMOLOGY. For its estuarine habitat. Its only congener lives in freshwater.

REMARKS. *Odiomaris* Ng & Richer de Forges, 1996, was erected for a freshwater species from New Caledonia, *O. pilosus* (A. Milne Edwards,
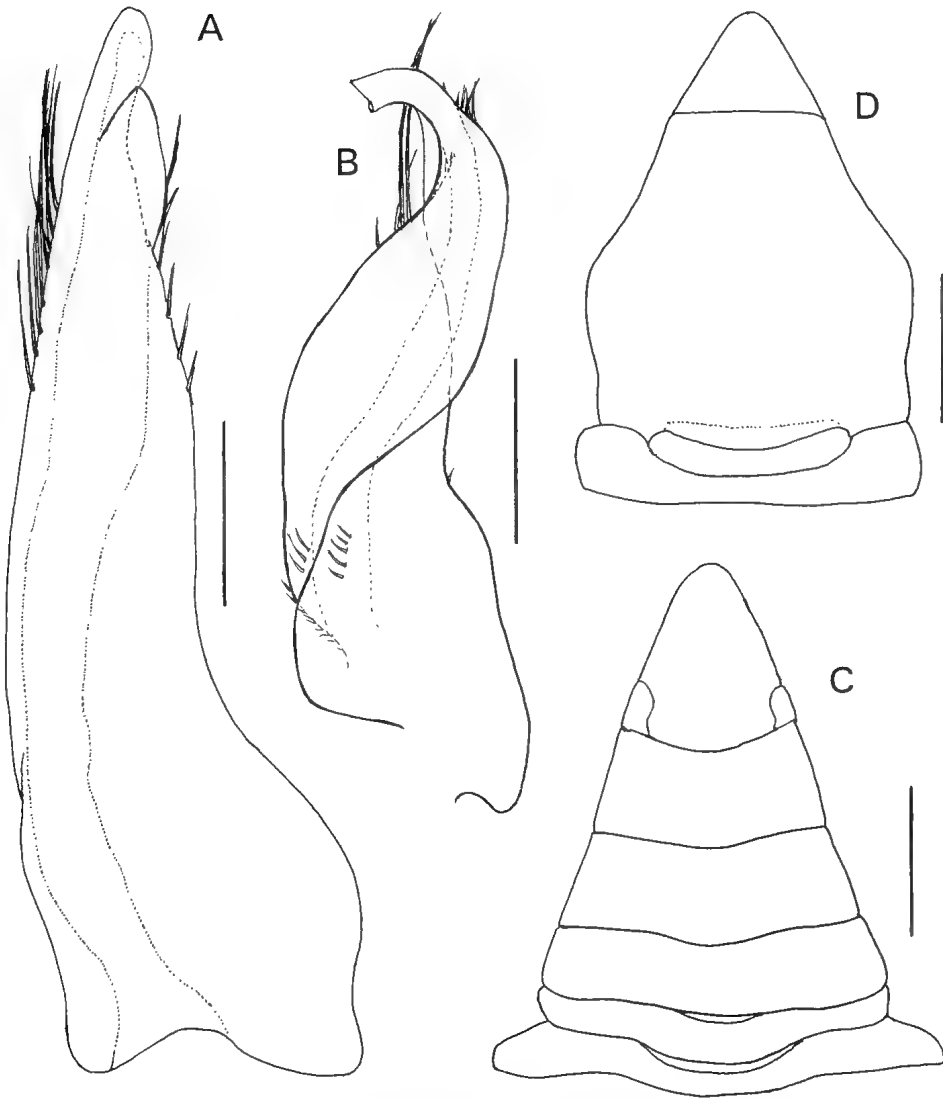
FIG. 2. A, C: *Odiomaris estuarius* sp. nov., holotype, A, first gonopod, C, abdomen. B, D: *Neorhynchoplax euryrostris* sp. nov., holotype, B, first gonopod, D, abdomen. Scale line A, B = 0.2 mm; C, D = 0.5 mm.

1873), which had been included by Lucas (1980) in *Amarinus*. *Odiomaris estuarius* sp. nov. fits well with the generic diagnosis of Ng & Richer de Forges (1996). The two genera appear close but the most important characters separating *Odiomaris* are: 1, G1 more slender, with two distinct distal processes, a longer corneous process and a shorter lobular elongation of the stem; and 2, the elongated triangular telson of the male abdomen which is significantly longer than wide at base (breadth c. 0.9 or less times length); whereas in *Amarinus* the telson is more-or-less

rounded and short, being much wider than long (breadth 1.2 or more times length).

Odiomaris estuarius differs from *O. pilosus* by: 1. The numerous thin spinules (or stiff setae) that cover the carapace margins, rostrum, pterygostomial regions, walking legs and chelipeds, which are so characteristic of *O. pilosus*, are absent; instead the carapace has only soft short fringing setae, and the legs and chelipeds have longer, feathered setae. 2. The rostrum is markedly wider and more spatulate than in *O. pilosus*; also the carapace rim which continues across
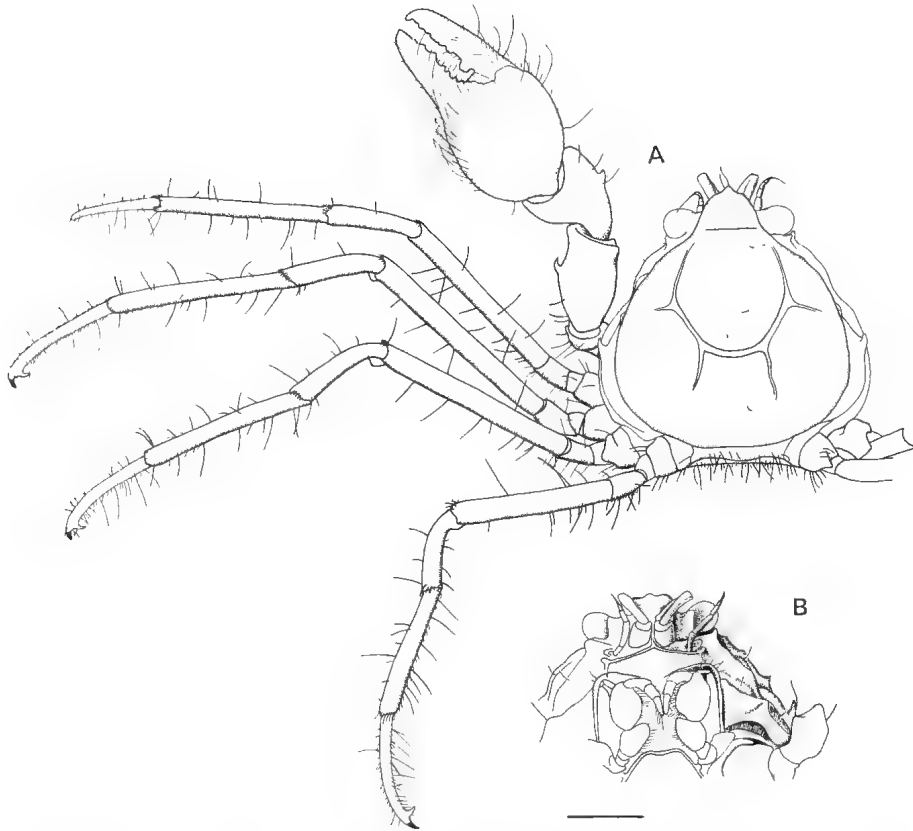
FIG. 3. *Neorhynchoplax euryrostris* sp. nov., holotype male. A, dorsal view; B, frontal view. Scale line = 1 mm.

behind the rostrum, is relatively flat, and does not project forward onto the rostrum as a rounded tongue as it does in *O. pilosus*. Seen in ventral view the rostrum is broad and rounded, and does not form a narrow V-shape as in *O. pilosus*. 3. The eyes are large with the corneas swollen; the postocular lobes are relatively small in size, not prominent in dorsal view, and afford little protection for the corneas. In *O. pilosus* the eyes are relatively smaller and the postocular lobes are prominent and project forward almost as far as the anterior edge of the cornea. 4. The posterior carapace grooves are almost indiscernible on *O. estuarius*, whereas on *O. pilosus* the transverse cardiac-intestinal groove is very distinct, and the cardiac region itself is strongly defined. 5. It seems that *O. estuarius* is a much smaller species (present specimens less than 6.4 mm c.b.) than *O. pilosus* (which from the literature attains at least 18 mm c.b.). The females of *O. estuarius* have a mature abdomen from 5.4 mm, and the males have mature gonopods from as little as 2.5 mm

c.b., although the largest male (4.6 mm) does not yet have inflated chelae.

Neorhynchoplax euryrostris sp. nov.
(Figs 2B, D, 3)

MATERIAL EXAMINED. HOLOTYPE MNHN B25276, ♂ (3.5 x 3.4 mm), Dumbea, New Caledonia, 8.12.1993, P. Davie & B. Richer de Forges. PARATYPES QMW19911, 3 ♀ (3.1 x 2.9; 2.8 x 2.6; 2.8 x 2.6), 1 ♀ (3.0 x 2.8 mm). QMW20573, 1 ♀ (2.0 x 1.8 mm), 2 ovig. ♀ (3.3 x 3.1; 2.7 x 2.6 mm), Le Cap. MNHN-B25277, ♂ (2.7 x 2.7 mm) 3 ovig. ♀ (3.1 x 2.85; 3.3 x 3.1; 2.8 x 2.6 mm), all same data as holotype except as noted.

DESCRIPTION. Carapace width in males subequal to length (including rostrum); slightly wider in females (1.04-1.11 times length). Dorsal surface flattened, with gastric, cardiac and postbranchial regions convex; gastrocardiac, cervical and thoracic grooves well defined; branchiostegites sloping out slightly towards leg

bases; anterolateral margin with two low, blunt, triangular prominences; posterolateral angle with strong, curved, forwardly directed spine; rostrum unilobate, margins moderately converging over posterior two-thirds, more sharply converging anteriorly to prominent acute medial lobe; anterior rostral margin with short, curved fringing setae, and two or more long setae on apex of medial rostral lobe; eyes short, cornea swollen, fully visible in dorsal view; postocular lobes well-formed; antennules longer than rostrum when unflexed, basal segment with blunt lateral lobe bearing setae; interantennular septum a prominent narrow ridge, extending to base of medial rostral lobe; rostral keel clearly defined, rounded; antenna with long, very fine, flagellum; no antennal spine; pterygostomial region with strong dorsal ridge.

Ischium and merus of third maxilliped with strong setae along inner edges, ischium with distinct, acute, anteromedial lobe, palp stout, long, reaching ischio-merus junction, exopodite and epipodite conspicuous. Male chelipeds greater than 1.5 times longer than carapace width, much stouter than walking legs; propodus especially inflated and expanded ventrally; merus with conspicuous spine on outer ventral margin at about distal third, fingers slightly curved, meeting over distal half, small gape proximally; dactyl with large basal molar, and smaller medial tooth; fixed finger with about six small teeth over proximal half, largest medially; outer surface of palm and fingers of holotype male conspicuously setose; largest male with inflated chelae at 3.5 mm carapace width, smaller (2.7 mm) male with claws still immature. Female chelipeds stouter than walking legs but much smaller and less setose than male chelipeds, fingers meeting along most of length, each with row of even low teeth; walking legs long and slender, length of 2nd walking leg c. 2.5 times carapace width, dactyli slender and curved distally, with strong, recurved, subterminal tooth, but otherwise unarmed along ventral edge; walking legs setose, especially on ventral surface of dactylus.

Female abdominosternal region typical of *Neorhynchoplax* species, without pleopods, eggs apparently brooded within abdomen and cephalothorax cavity; segment 1 broad, segment 2 very short, segments 3-5 fused, forming major part of abdomen, telson broad, laterally with prominent, blunt, locking lobes, lateral margins more-or-less straight, a rounded apical lobe differentiated; female genital aperture subovate, with raised broad anterior and outer shoulder,

sited on sternum just posterior to base of cheliped; male abdomen with segments 1 and 2 short, fused article of segments 3-5 expanding moderately to maximum abdomen width then tapering uniformly to telson, telson triangular, apically rounded; G1 little curved, moderately stout, twisted, with a distinct thin terminal portion tapering to a point, and projecting towards sternum, setation as figured.

Body colour light brown to brown (alcohol preserved specimens); short setae on lateral carapace walls, sternum, chelipeds, walking legs and abdomen, with tendency to accumulate silt particles and take on clubbed appearance.

HABITAT. Estuarine to tidal freshwater; in crevices in rotting logs at edge of water at low tide; and under stones in freshwater.

DISTRIBUTION. Only known from the type material from the western coast of New Caledonia.

ETYMOLOGY. For its broad unilobate rostrum.

REMARKS. Ng & Chuang (1996) and Ng & Richer de Forges (1996) restrict *Elamenopsis* A. Milne Edwards, 1873, to only a few species most closely resembling the type, *E. lineatus* A. Milne Edwards, 1873, which is transversely broad with short walking legs, and very different in appearance from *Neorhynchoplax euryrostris* sp. nov. They resurrected *Neorhynchoplax* for the bulk of species included in *Elamenopsis* by Lucas (1980) and subsequent authors. *Neorhynchoplax euryrostris* is easily recognised by the shape of the rostrum. Only 4 species of *Elamenopsis* (*sensu* Lucas, 1980) have a unilobate rostrum *viz. E. lineata* A. Milne Edwards, 1873, *E. inermis* (Takeda & Miyake, 1971), *E. nasalis* (Kemp, 1917) and *E. minima* Lucas & Davie, 1982. Of the three species that properly belong in *Neorhynchoplax*, *E. nasalis* and *E. minima* are very different in having thin spine-like rostrums; and *E. inermis* has only a very short, very narrow, triangular rostrum.

One feature which *Neorhynchoplax euryrostris* and *N. inermis* have in common, which does suggest a close alliance, is the strongly twisted G1, although it differs markedly in detail between the two species.

ACKNOWLEDGEMENTS

is especially thanked for drawing the dorsal and frontal views of the two new species. Peter Ng provided valuable criticism of the manuscript.

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THE HYMENOSOMATIDAE (CRUSTACEA: DECAPODA: BRACHYURA) OF NEW CALEDONIA, WITH DESCRIPTIONS OF TWO NEW GENERA AND TWO NEW SPECIES

P.K.L. NG AND B. RICHER DE FORGES

All 5 previously described species of hymenosomatids were examined. *Micas* gen. nov. is established for *Elamena minuta* A. Milne Edwards, 1873, and *Micas falcipes* sp. nov., whilst *Odiomaris* gen. nov. is established for *Elamena pilosa* A. Milne Edwards, 1873. Specimens previously referred to *E. truncata* (Stimpson, 1858) are here described as *Elamena vesca* sp. nov. □ *Brachyura, Hymenosomatidae, New Caledonia, Indo-West Pacific.*

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Five hymenosomatid crabs have been reported from New Caledonia: *Elamenopsis lineata* A. Milne Edwards, 1873, *Elamena truncata* (Stimpson, 1858), *Halicarcinus minutus* (Milne Edwards, 1873), *Halicarcinus keijibabai* (Takeda & Miyake, 1971) and *Amarinus pilosus* (Milne Edwards, 1873) (Lucas, 1980).

While the first author was revising the hymenosomatids of Southeast Asia (Ng & Chuang, 1996), the second author provided a collection of 6 species of New Caledonian hymenosomatids. The study of this material, as well as the types of *Elamenopsis lineata* and *Elamena minuta*, resulted in a reappraisal of the taxonomy of the New Caledonian Hymenosomatidae. *Halicarcinus minutus* and *Amarinus pilosus* are referred to new genera, *Micas* and *Odiomaris*, respectively. They both differ markedly from *Halicarcinus* White, 1846, and *Amarinus* Lucas, 1980, respectively. A new species of *Micas* is also described. Comparisons with *Elamena truncata* (Stimpson, 1858) from Taiwan also show that *E. truncata* A. Milne Edwards, 1873, is separate. We review the 5 previous species, including necessary new taxa; 2 further New Caledonian species are added by Davie & Richer de Forges (1996).

Specimens examined are deposited in the Queensland Museum (QM), Brisbane, Australia; Muséum national d'histoire naturelle (MNHN) Paris, France; Amsterdam Museum (ZMA), The Netherlands; and Zoological Reference Collection (ZRC), Department of Zoology, National University of Singapore. Measurements provided are of the carapace width and length respectively. G1 and G2=♂ first and second gonopods, respectively. Terminology follows Melrose (1975).

SYSTEMATICS
Class CRUSTACEA
Order BRACHYURA
Family HYMENOSOMATIDAE
Elamenopsis A. Milne Edwards, 1873

Elamenopsis A. Milne Edwards, 1873: 324; Lucas, 1980: 190 (partim).

TYPE SPECIES. *Elamenopsis lineatus* A. Milne Edwards, 1873, by monotypy.

REMARKS. *Elamenopsis* contains *E. lineata* and *E. ariakensis* (Sakai, 1969). Lucas (1980) synonymised *Neorhynchoplax* Sakai, 1938, with *Elamenopsis*. Ng & Chuang (1996) redefined *Elamenopsis*, restricting it to species with a unilobed rostrum, laterally oval carapace and short ambulatory legs; and resurrecting *Neorhynchoplax* Sakai, 1938, for the other *Elamenopsis* species recognised by Lucas (1980).

Elamenopsis lineata A. Milne Edwards, 1873
(Fig. 1)

Elamenopsis lineatus A. Milne Edwards, 1873: 324, pl. 18 fig. 4; Kemp, 1917: 250; Tesch, 1918: 26, pl. 1 fig. 5, 5a-c; Serène & Umali, 1970: 58, pl. 5 fig. 11.
Elamenopsis lineata: Lucas, 1980: 192, figs. 3j, 5j, 8e, 10j; Chuang & Ng, 1994: 87; Ng & Chuang, 1996.

MATERIAL EXAMINED. HOLOTYPE MNHN B651 ♀ (2.6 x 2.0 mm), Dotio, New Caledonia, M. Batema. ZMA uncat., 1 ♂ (3.8 x 2.8 mm), Sulawesi, Indonesia, Siboga Expedition. QM W2341, ♂, 2 ♀, S of Dunwich, SEQ. 15.7.1962, F. Vohra. ZRC 1994.4242, ex. QM W2337, ♂, 2 ♀, S of Dunwich, SEQ, 12.7.1962, F. Vohra.
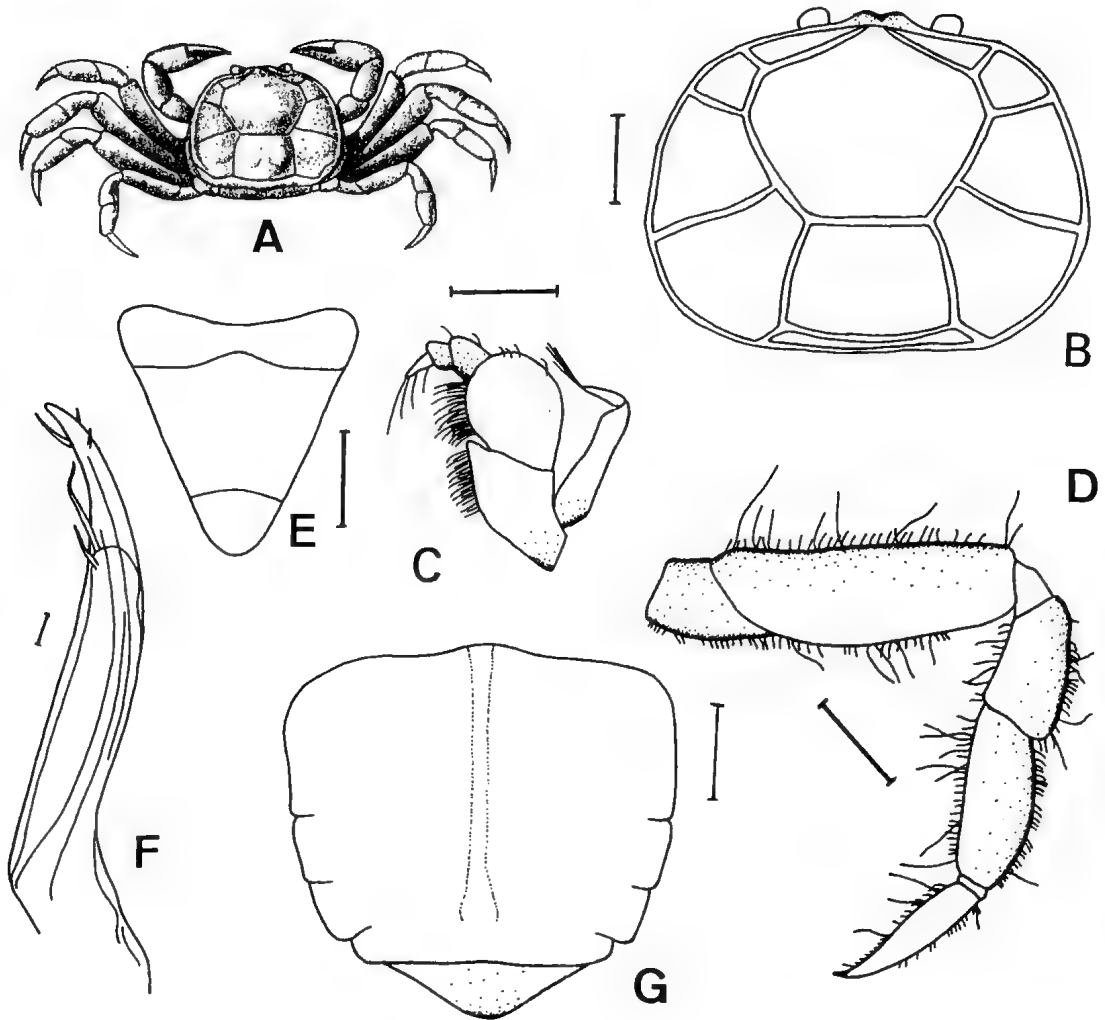
FIG. 1. *Elamenopsis lineata*. A, holotype ♀ (after Milne Edwards, 1873: pl. 18 fig. 4). B, holotype ♀ (MNHN 651), New Caledonia. C-F, ♂ (2.7 x 2.0 mm) (QM W2341) (after Ng & Chuang, 1996). G, ♀ (3.4 x 2.5 mm) (ZRC 1994.4242) (after Ng & Chuang, 1996), Australia. A, overall view. B, dorsal view of carapace. C, left third maxilliped. D, right third ambulatory leg. E, ♂ abdomen. F, left G1. G, ♀ abdomen. Scales: A-F = 0.05 mm. G = 0.5 mm.

REMARKS. This species was treated in detail by Ng & Chuang (1996). Milne Edwards (1873) described it from the Dotio river, New Caledonia, but it has not been reported from there since.

DISTRIBUTION AND HABITAT. New Caledonia, Australia, Sulawesi (Tesch, 1918) and Philippines. Milne Edwards (1873) reported the species from a brackish water habitat while Tesch (1918) reported his specimen from coral reefs, which record was questioned by Lucas (1980) and Ng & Chuang (1996). Lucas (180: 193) noted that the species can be common on muddy substrates in Australia.

Halicarcinus White, 1846

Halicarcinus White, 1846: 178; Lucas, 1980: 176 (complete synonymy).

TYPE SPECIES. *Cancer planatus* Fabricius, 1775, by original designation.

REMARKS. *Halicarcinus minutus* (A. Milne Edwards, 1873)[=*Micas* gen. nov. herein] and *H. keijibabai* (Takeda & Miyake, 1971) have been reported from New Caledonia. Lucas (1980) redefinition of *Halicarcinus* is followed here.

Halicarcinus keijibabai (Takeda & Miyake, 1971)(Fig. 2)

Rhynchoplax keijibabai Takeda & Miyake, 1971: 165, figs 1, 2.
Halicarcinus keijibabai: Lucas, 1980: 164.

MATERIAL EXAMINED. ZRC 1994.4283, ♂, intertidal region, low tide at OUEMO, Nouméa, New Caledonia, 2.7.1992, B. Richer de Forges.

REMARKS. This species was described from New Caledonia (1 ♂ and 1 ♀) (Fig. 2A, B) and has not been reported elsewhere. Our ♂ agrees with Takeda & Miyake's (1971) detailed description and figures. Characters (e.g. G1 and ♂ abdomen) not figured by Takeda & Miyake (1971) are illustrated here. *Halicarcinus keijibabai* is very close to *H. coralicola* (Rathbun) but the postocular tooth is less pronounced, the base of the rostrum is fused with the postocular lobes forming a broad band above the eyestalks, the anterior lateral angle lacks an acute tooth, the subhepatic/pterygostomial regions have only 1 (vs. 3) teeth, and most significantly, the G1 is straighter and not medially curved (Fig. 2G). Other differences in the carapace structure and form of the ambulatory dactylus noted by Takeda & Miyake (1971: 168) however, are subject to variation and cannot be used. Lucas (1980: 164) noted that the medial rostral lobe in *H. coralicola* lacks long terminal setae, but this is incorrect as this character is present in both species.

DISTRIBUTION AND HABITAT. New Caledonia. Under rocks in the intertidal area, in waters no more than 1 m deep. Same habitat for *H. coralicola* in SE Asia and Japan (Chuang & Ng, 1994; Ng & Chuang, 1996).

Micas gen. nov.

TYPE SPECIES. *Elamena minuta* A. Milne Edwards, 1873.

DIAGNOSIS. Carapace rounded; dorsal surface smooth, grooves all well delineated, reaching to lateral margins of carapace; cardiac region with distinct longitudinal groove. Eyes visible dorsally. Rostrum trilobed, lobes short; median lobe may or may not be separated from carapace by crest. Ambulatory legs long, slender; dactylus with 2 subterminal teeth. Male abdominal segments 3 and 4 fused; ♀ abdominal segments 2-5 fused. G1 slender distally, stout basally, twisted medially.

REMARKS. Kemp (1917) commented that *Elamena minuta* should be placed in *Halicarcinus*. It has been collected only twice previously (A. Milne Edwards, 1873; Takeda & Nonumura, 1976) and ♂ ♂ have not been described.

H. minutus has few of the important features of *Halicarcinus*. The complete longitudinal cardiac groove on the carapace is evident in no other hymenosomatid, although *H. hondai* (Takeda & Miyake) has a partial one (Lucas, 1980: 184, fig. 3H). The G1 of *H. minutus* is twisted twice, once medially and again, more strongly 3/4 from the base, with the tip slightly bifurcated. The ambulatory dactyli of *M. minutus* are very elongate, much longer than for other *Halicarcinus* species and have only two subterminal teeth, lacking the series of sharp teeth present on many *Halicarcinus* species (with the exception of the enigmatic *H. filholi* (De Man)). Like most *Elamena*, the ♂ abdomen also has segments 3 and 4 fused, quite unlike most *Halicarcinus* in which all the segments are free. The same is true for the ♀ abdomen, which in *M. minutus* has segments 2-5 completely fused, with no sutures visible (most ♀ ♀ of *Halicarcinus* have all segments free). Unlike both *Halicarcinus* and *Elamena*, the ♂ chelipeds are also short and not elongate. The carapace of *H. minutus* also bears a close resemblance to many species of *Neorhynchoplax* s.s., but the third maxillipeds are quadrate, covering at least 3/4 of the mouthfield.

Micas falcipes sp. nov., is also described from New Caledonia. A NE Australian species, *H. afecundus* Lucas, 1980, is also assigned to *Micas*. It has the same short trilobed rostrum, longitudinal groove on the cardiac region, elongate ambulatory dactyli and ♀ abdominal condition (segments 2-5 fused) as *M. minutus*.

ETYMOLOGY. Latin *mica*, grain; for the small size of the type species. Gender masculine.

Micas minutus (Milne Edwards, 1873) (Fig. 3)

Elamene minuta Milne Edwards, 1873: 324 (partim), pl. 18 fig. 5.
Elamena minuta: Tesch, 1918: 21 (partim).
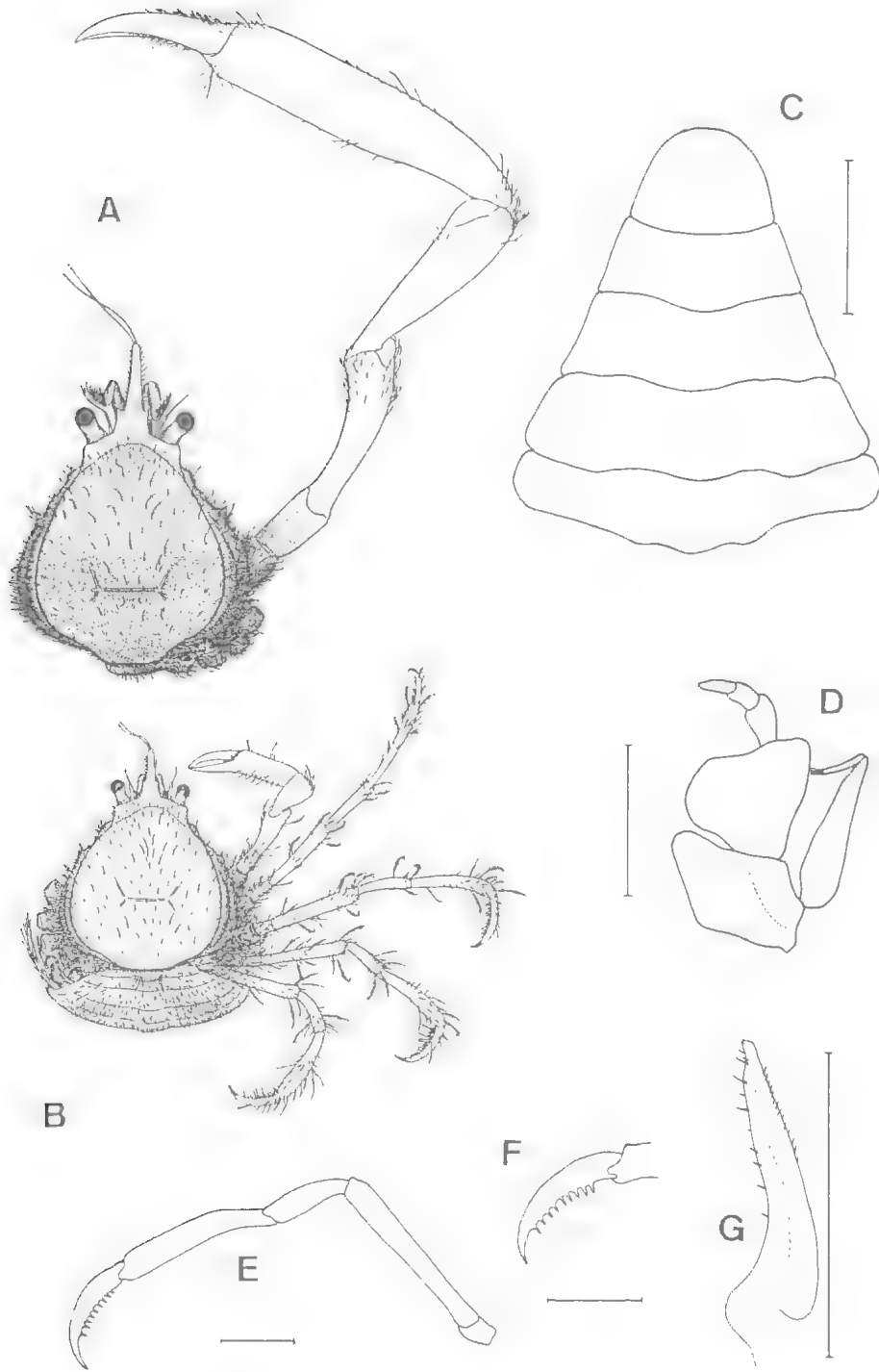*Halicarcinus minutus*: Takeda & Nonumura, 1976: 65,

FIG. 2. *Halicarcinus keijibabai*. A, holotype ♂ (1.7 x 2.0 mm [excluding rostrum]) (after Takeda & Miyake, 1971, fig. 1). B, allotype ♀ (1.7 x 1.8 mm [excluding rostrum]) (after Takeda & Miyake, 1971, fig. 2). C-G, ♂ (2.3 x 2.7 mm) (ZRC 1994.4283), New Caledonia. A, B, overall view. C, ♂ abdomen. D, left third maxilliped. E, left third ambulatory leg. F, left third ambulatory dactylus. G, left G1. Scales = 0.5 mm.
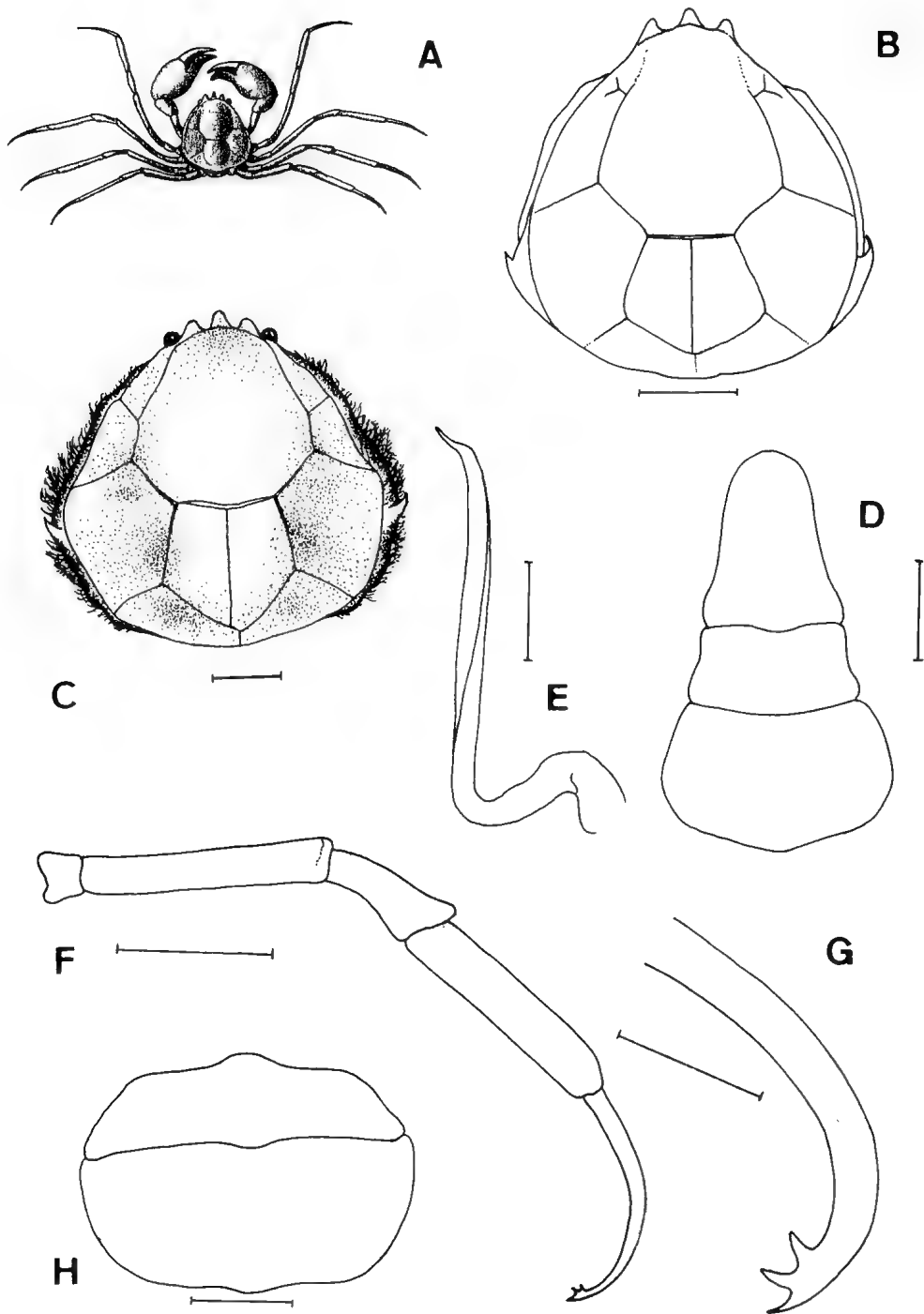
FIG. 3. *Micas minutus*. A, B, D, E, lectotype ♂ (3.4 x 3.5 mm) (MNHN B656Sa) (A, after Milne Edwards, 1873, pl. 18 fig. 5). C, ♀ (after Takeda & Nonumura, 1976, fig. 2). F-H, ♀ (2.9 x 2.6 mm) (ZRC 1994.4250b). A, overall view. B, C, carapace. D, ♂ abdomen. E, left G1. F, right third ambulatory leg. G, left third ambulatory dactylus. H, ♀ abdomen. Scales: B, C, F, H = 1.0 mm. D, G = 0.5 mm. E = 0.25 mm.
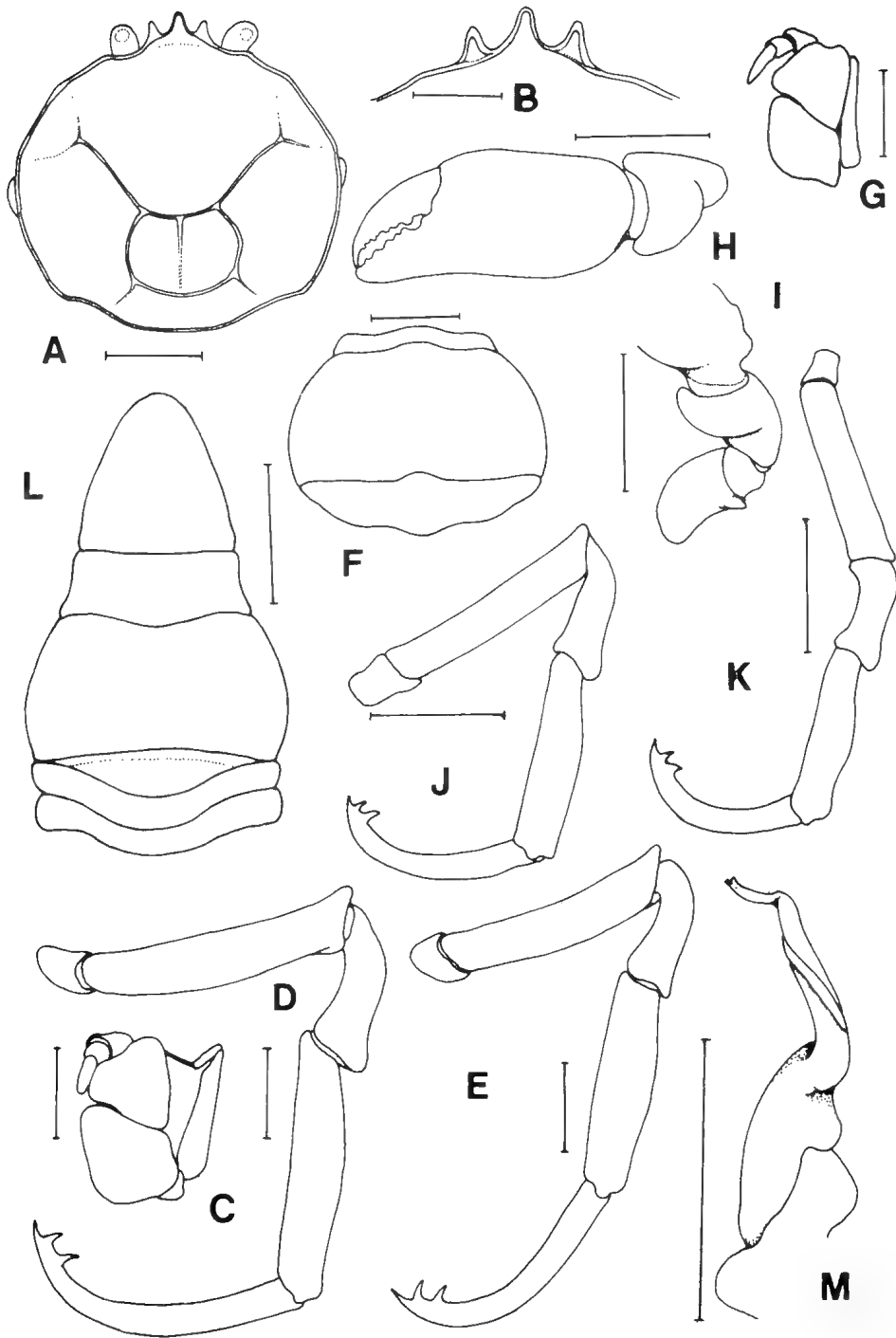
FIG. 4. *Micas falcipes* sp. nov. A-E, paratype ♀ (2.9 x 2.6 mm) (ZRC 1196.477). F, paratype ♀ (3.1 x 2.6 mm) (MNHN B24915b). I-M, paratype ♂ (2.8 x 2.7 mm) (MNHN B24915a). A, carapace. B, rostrum. C, G, left third maxilliped. D, J, right third ambulatory leg. E, K, right fourth ambulatory leg. F, ♀ abdomen. H, left chela. I, carpus and merus of left cheliped. L, ♂ abdomen. M, left G1. Scales: A, F, G, J-M = 1.0 mm. B-E, H, I = 0.5 mm.

fig. 2; Lucas, 1980: 177 (partim); Chuang & Ng, 1994: 88 (partim).

MATERIAL EXAMINED. LECTOTYPE. MNHN-B656Sa, ♂ (3.4 x 3.5 mm), New Caledonia, M. Marie. OTHER MATERIAL: ZRC 1993.6512, ♀ (3.5 x 3.3 mm), ZRC 1994.4250a, ♀ (ovigerous) (4.1 x 3.9 mm), intertidal region, low tide at OUEMO, Nouméa, New Caledonia, 2.7.1992, B. Richer de Forges.

REMARKS. *Elamena minuta* was described briefly by Milne Edwards (1873) and although he did not indicate the number of specimens he had examined, he provided measurement of one specimen 3.0 mm in carapace width (sex not stated). His figure is very schematic and provides almost no information on the carapace lateral margins, third maxillipeds, ambulatory dactylus, abdomen or G1. The condition of the cardiac region and posterior lateral spine was neither figured or mentioned. In the MNHN are three dried specimens which had been labelled as *Elamena minuta*. All were collected by M. Marie and labelled as types. The largest specimen (our lectotype), a ♂ 3.4 by 3.5 mm, carries a label indicating that it was the specimen figured by Milne Edwards. The other two specimens (paralectotypes) belong to *M. falcipes* sp. nov. The lectotype is still in good condition and shows a clearly defined longitudinal groove on the cardiac region and well developed posterior lateral spines.

Takeda & Nonumura (1976: fig. 2) figured a ♀ (Fig. 3B) with a prominent posterior lateral spine; their specimen agrees very well with the lectotype ♂.

DISTRIBUTION AND HABITAT. New Caledonia. Under rocks in the intertidal zone, along the shore or on the fringing reef of small coral islands.

Micas falcipes sp. nov.
(Fig. 4)

Elamene minuta Milne Edwards, 1873: 324 (partim).
Elamena minuta:Tesch, 1918: 21 (partim).
Halicarcinus minutus: Lucas, 1980: 177 (partim);
    Chuang & Ng, 1994: 88 (partim).

MATERIAL EXAMINED. HOLOTYPE MNHMB25300 (ex ZRC 1993.6511), ♂ (3.2 x 3.1 mm), intertidal region, low tide at OUEMO, Nouméa, New Caledonia, 2.7.1992, B. Richer de Forges. PARATYPES ZRC 1994.4250b, ♂ (3.5 x 3.3 mm), ♀ (ovigerous) (2.9 x 2.6 mm), MNHN B24915b, ♂ (2.8 x 2.7 mm), ♀ (3.1 x 2.6 mm), intertidal region, low tide at OUEMO, Nouméa, New Caledonia, 2.7.1992, B.

Richer de Forges. PARATYPE, ZRC 1996.477, ♀ (2.9 x 2.6 mm), station 10, shallow water in bay, OUEMO, Nouméa, New Caledonia, 19.4.1995, B. Richer de Forges. MNHN B656Sb, 2 ♂ (2.5 x 2.3 mm, 2.5 x 2.3 mm), New Caledonia, M.E. Marie.

DESCRIPTION.Carapace width (at posterior pair of angular lobes) greater than length; dorsal surface almost flat, smooth, gastrocardiac grooves deep, distinct; cervical and thoracic grooves shallow; cardiac region with longitudinal groove which is deeper on anterior half; pterygostomian region with low knob. Anterolateral margin with low angle, never spiniform; posterolateral margin gently convex; with distinct, unarmed swelling on posterior lateral angle. Rostrum trilobate, lobes subequal in size; tip of lateral below tip of median lobe; median lobe appears continuous with the dorsal carapace surface, crest separating it from carapace very low. Eyes visible dorsally.

Third maxillipeds almost completely cover mouth field when closed; ischium distinctly shorter than merus along outer lateral edge; inner lateral edge of merus lined with fine setae, inner lateral margins meeting when closed; palp longer than merus; exopod longer than merus, reaching distal edge of merus.

Chelipeds equal, stouter than ambulatory legs; surfaces smooth; fingers c.1/3 length of inflated palm; fingers laterally flattened, slightly curved inwards; cutting edges serrated, with quadrangular tooth at proximal portion of dactylus; tips of fingers sharp, pointed.

Ambulatory legs slender, cross-section of merus subcircular; distal dorsal edge of merus and carpus with well developed but rounded tooth; dorsal margin of propodus convex, median height (measured from dorsal to ventral margins) distinctly higher than distal and proximal heights; margin of dactylus lined with dense, fine setae; strongly curved, tip hooked, with 2 subequal subterminal teeth; subdistal margin smaller and less distinct tooth in between tip and subterminal tooth.

♂ abdomen triangular; segments 3 and 4 completely fused without trace of sutures; all other segments free; telson more than 2 times length of segment 6, lateral margins gently convex. G1 slender, elongate, twisted medially. Female abdomen rounded, segments 2-5 fused, without trace of sutures, telson *c.* half width of fused segments 2-5, lateral margins sinuous; lateral margins of fused segments 2-5 tapering gradually towards segment 1.
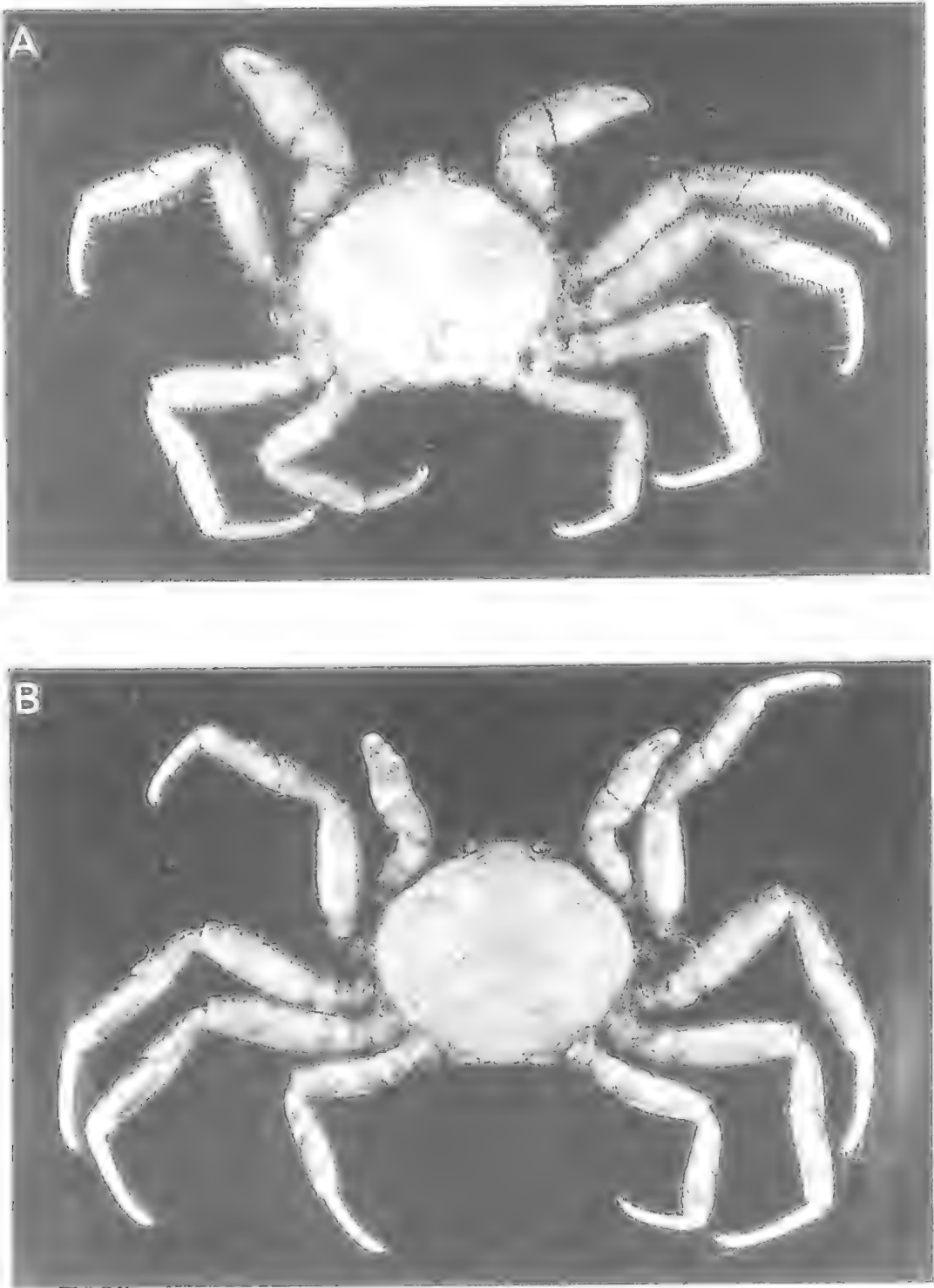
FIG. 5. *Odiomaris pilosus*. A, ♂ (11.8 x 10.1 mm) (ZRC 1994.4251a). B, ♀ (8.8 x 7.8 mm) (ZRC 1994.4251b), New Caledonia.

REMARKS. *Micas falcipes* sp. nov. resembles *M. minutus* but can be separated by: the rounder carapace (mainly because the anterolateral margins are more convex), a posterior lateral swelling (sometimes dentiform, never spiniform), the median rostral lobe continuous with the carapace surface (vs. separated by a crest), the distal angle of the dorsal margin of the ambulatory merus more strongly produced, the dorsal margin of the ambulatory propodus convex, the ambulatory dactyli proportionately stouter and shorter, the ♂ telson proportionately longer, with the lateral margins gently convex and the G1 proportionately shorter. The posterior lateral swelling in *M. falcipes* seems to be reliable in separating *M. minutus. M. minutus* has well-developed, sharp spines, whereas *M. falcipes* is never spiniform.

DISTRIBUTION AND HABITAT. New Caledonia. One specimen was collected under a sponge in 0.2m of water. The others are from shallow waters in the intertidal region. It is typically brown to black in life, with the posterior part of the postbranchial region sometimes white.

ETYMOLOGY. Latin *falx* and *pes*, for the sickle-shaped ambulatory dactylus. A noun in apposition.

Odiomaris gen. nov.

TYPE SPECIES. *Elamena pilosa* Milne Edwards, 1873.

DIAGNOSIS. Carapace laterally oval, distinctly broader than long; grooves on dorsal surface well-defined. Third maxilliped quadrate; anteroexternal angle of merus rounded, not auriculiform; ischium broad, expanded. Ambulatory legs relatively short, dactylus with one weak subterminal tooth. Male abdomen evenly triangular; telson triangular, lateral margins almost straight, base with distinct, movable intercalated plates. G1 relatively slender, distal part with well-developed pectinated process and a smaller, weakly chitinised process.

REMARKS. Lucas (1980) referred *E. pilosa* Milne Edwards, 1873, to *Amarinus* (type *E.* ? *lacustris* Chilton), with all congeners from brackish or freshwater. Lucas (1980: 198) noted that the G1 of *Amarinus* is '... stout, curved at base, otherwise with little curvature, terminal portion with fine setae in tufts or scattered, terminating in one or several lobes'. Holthuis (1968), however, had figured the G1 of *E. pilosa* (as a species of *Halicarcinus*) which is unlike that of any known

Amarinus, being distinctly more slender, the distal part possessing 2 distinct processes. Ten species of *Amarinus* are known (Lucas, 1980; Lucas & Davie, 1982; Ng & Chuang, 1996) and all have very similar G1s, being short and stout.

Comparing *E. pilosa* with *Amarinus* reveals several other differences. In *E. pilosa* the anteroexternal angle of the merus of the third maxilliped is not auriculiform (vs. distinctly auriculiform), the ♂ abdomen is shaped differently, the structure (including the telson with the almost straight lateral margins) being evenly triangular (vs. broadly triangular abdomen, the telson being semicircular), G1 is more slender, the distal part having a well-developed pectinated process and a smaller, weakly chitinised process (vs short, stout and without the two pectinated processes). *E. pilosa* also differs in having the carapace laterally oval (vs. circular to subcircular) and the inner lateral margin of the ischium of the third maxilliped is broad and expanded (vs. narrow). While *E. pilosa* has the intercalated plates at the base of the telson, which is distinctive of *Amarinus* (cf. Lucas, 1980), the differences noted here require generic separation. This decision is further validated by a second species from New Caledonian estuaries (Davie & Richer de Forges, 1996). Intercalated plates on the ♂ telson is a character shared by the closely related *Amarinus*, *Odiomaris*, and the monospecific Australian *Hymenosoma* Lucas, 1980.

In *E. pilosa*, the infraorbital tooth is well-developed and visible in dorsal view, whereas *Amarinus* typically has the infraorbital tooth weak or almost indiscernible, and not visible in dorsal view. Similarly the dorsal carapace grooves of *E. pilosa* are well-defined, with the posterior ones reaching the edge of the carapace, and the intestinal region marked by a short but distinct longitudinal groove. These characters are not considered to be of generic significance as the second species of *Odiomaris* (Davie & Richer de Forges, 1996), does not have a well developed infraorbital tooth, and the dorsal carapace grooves are poorly defined posteriorly, such that there is no obvious longitudinal groove on the intestinal region.

ETYMOLOGY. Latin *odium*, dislike and *maris*, sea; for the type species' freshwater habitats. Gender masculine.
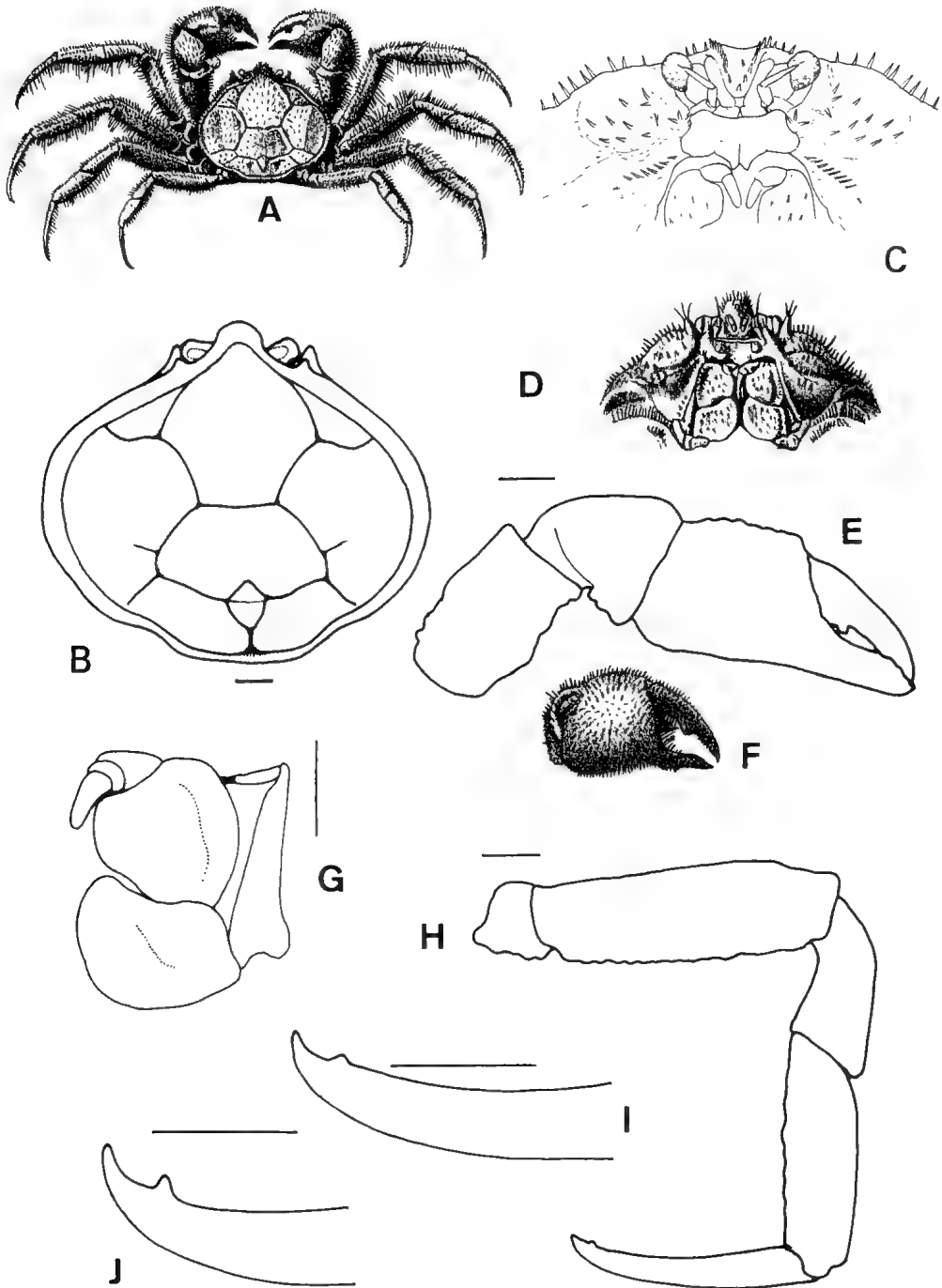
FIG. 6. *Odiomaris pilosus*. A, D, F, ♂ (after Milne Edwards, 1873, pl 18, fig. 6). C (after Holthuis, 1968, fig. 3a). B, E, G-J, ♂ (11.8 x 10.1 mm) (ZRC 1994.4251a). A, overall view. B, dorsal view of carapace. C, frontal view showing epistome. D, front view showing mouthparts. E, right cheliped. F, right chela. G, left third maxilliped. H, right third ambulatory leg. I, right third ambulatory dactylus. J, right fourth ambulatory leg. Scales = 1.0 mm.
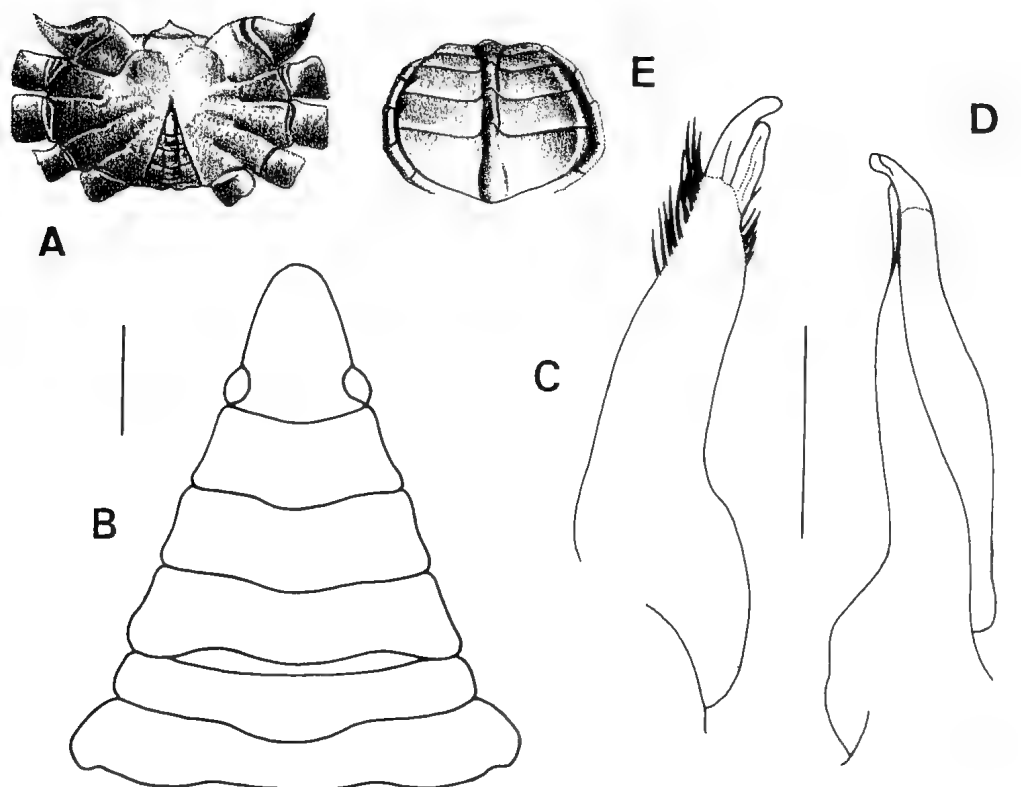
FIG. 7. *Odiomaris pilosus*. A, ♂ (after Milne Edwards, 1873, pl. 18, fig. 6). E, ♀ (after Milne Edwards, 1873, pl. 18, fig. 6). B-D, ♂ (11.8 x 10.1 mm) (ZRC 1994.4251a). A, ♂ sternum and abdomen. B, ♂ abdomen. C, D, left G1. E, ♀ abdomen. C, ventral view. D, dorsal view (setae not drawn). Scales = 1.0 mm.

Odiomaris pilosus (Milne Edwards, 1873)
(Figs 5-7)

Elamene pilosa Milne Edwards, 1873: 322, pl. 18 fig. 6; Kemp, 1917: 247.
Elamena pilosa: Tesch, 1918: 21; Roux, 1926: 229, figs 55, 56.
Halicarcinus pilosus: Holthuis, 1968: 117, fig. 3.
Amarinus pilosus: Lucas, 1980: 198; Chuang & Ng, 1994: 87.

MATERIAL EXAMINED. ZRC 1994.4251, ♂ (11.8 x 10.1 mm), ♀ (8.8 x 7.8 mm), Boghen River, New Caledonia, 17.1.1993, B. Richer de Forges.

REMARKS. This material agrees with the description and figures of Milne Edwards (1873), Roux (1926) and Holthuis (1968). Roux (1926) and Holthuis (1968) described the short and very stiff setae on the carapace as 'spinules/spines', but in our fresh specimens, they were flexible and not stiff. Thus, we refer to them as setae.

Our ♂ was dissected and its gonads preserved in glutaraldehyde for ultramicroscopic study of the sperm.

DISTRIBUTION AND HABITAT. New Caledonia. With *Trigonoplax unguiformis* this is largest of known hymenosomatids. It is common in New Caledonian rivers from the estuary inland for several km, in shallow freshwaters, under or between rocks in areas with rapid currents.

Elamena Milne Edwards, 1837

Elamena vesca sp. nov.
(Fig. 8)

Elamene truncata Milne Edwards, 1873: 323 (junior homonym of *Trigonoplax truncata* Stimpson, 1858).
?*Elamena truncata*: Gordon, 1940: 67, fig. 5; McNeill, 1968: 47; Lucas, 1980: 171, figs 2D, 6D, 8B, 10H.

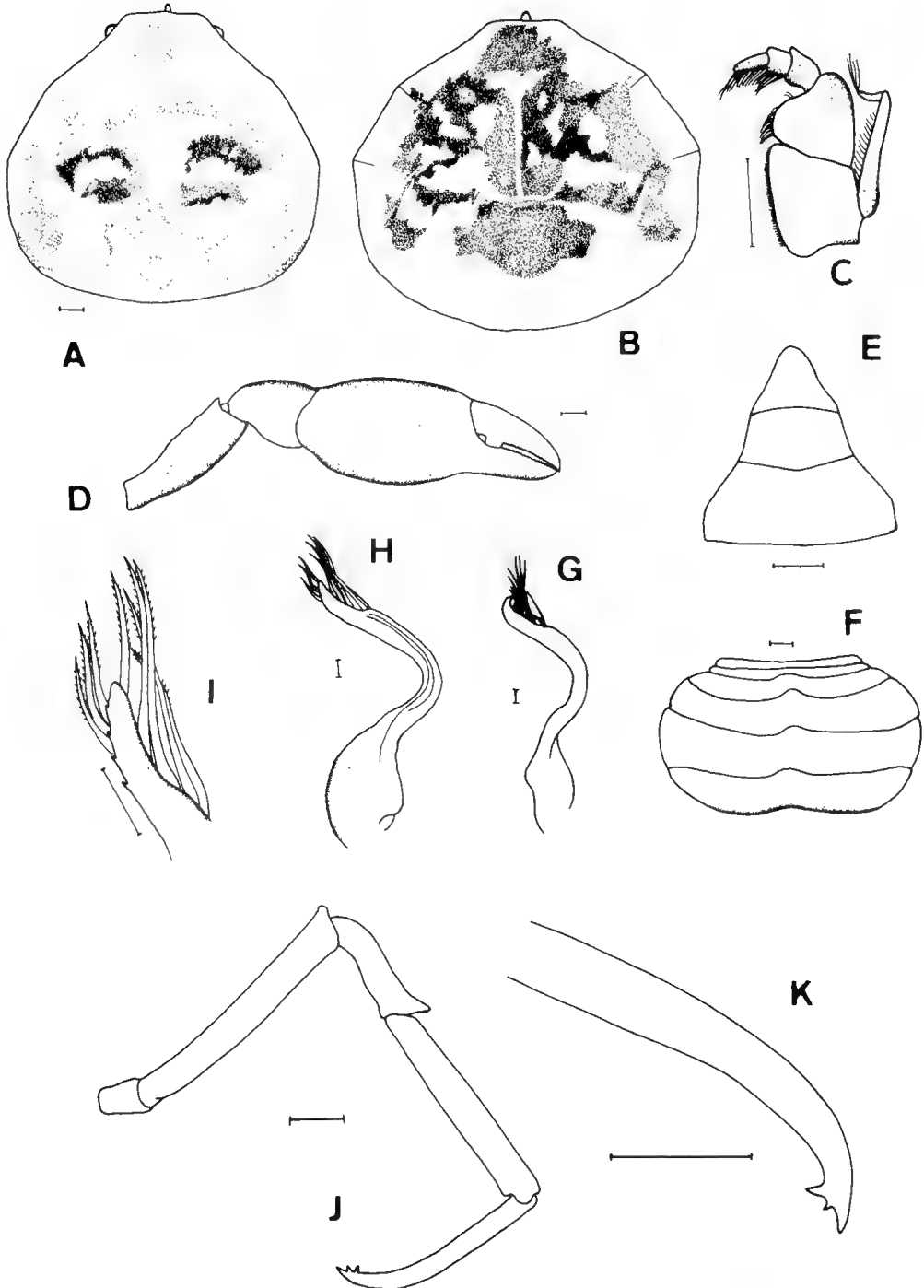MATERIAL EXAMINED. HOLOTYPE MNHNB22843, ♂ (6.0 x 5.4 mm), intertidal region,

FIG. 8. *Elamena vesca* sp. nov. A, C-E, G-I, holotype ♂ (6.0 x 5.4 mm) (MNHN). B, F, paratype ♀ (7.2 x 6.2 mm) (ZRC 1993.6498). paratype ♀ J, K (7.5 x 6.8 mm) (MNHN), New Caledonia. A, B, dorsal view of carapace. C, left third maxilliped. D, ♂ right cheliped. E, ♂ abdomen. F, ♀ abdomen. G, H, left G1. I, G1 apex. J, right third ambulatory leg. K, right ambulatory leg dactylus. Scales: A-I = 0.5 mm. J, K = 1.0 mm.

low tide at OUEMO, Nouméa, New Caledonia, 2.7.1992, B. Richer de Forges. PARATYPES ZRC 1993.6498-6499, ZRC 1994.4285, 4 ♀, MNHN B22844, ♀, same data as holotype; MNHN, 2 ♂, 2 ♀, QM W, 2 ♂, ♀, ZRC 1996.478, 3 ♂, ♀, Nouméa, Anse Vata, New Caledonia, 18.4.1995, B. Richer de Forges.

DESCRIPTION. ♂: Carapace width (at posterior pair of angular lobes) subequal to length; dorsal surface gently convex, smooth with no distinct or very poorly defined cervical, thoracic and gastrocardiac grooves, with dark brown pigmentation sometimes forming 2 eye-like spots; lobules at anterior lateral angle and at pterygostomian region equally rounded; anterolateral and lateral angles poorly defined, rounded. Rostrum truncated with ventral rostral keel partially visible dorsally. Eyes visible dorsally.

Third maxillipeds cover 3/4 of mouth field when closed; ischium shorter than merus along outer lateral edge; dense short setae occupying entire length of inner lateral edge of ischium; inner lateral edge of merus lined with dense setae, longer than that on ischium; inner lateral margins meeting when closed; palp subequal in length with merus; exopod longer than merus, with long setae more sparse than that found on merus lining the inner lateral edge.

Chelipeds equal, stouter than ambulatory legs; surfaces smooth; fingers c.1/3 length of inflated palm; fingers laterally flattened, slightly curved inwards; cutting edges serrated, with quadrangular tooth at proximal portion of dactylus; tips of fingers sharp, pointed.

Ambulatory legs slender, cross-section subcircular; distinct tooth at distal dorsal edge of merus and carpus; dactylus laterally flattened, straight proximally with distal portion more curved with subterminal tooth; tip sharply hooked; smaller and less distinct tooth in between tip and subterminal tooth; ventral edge of dactylus lined with row of short setae; carpus shorter than propodus and merus which is longer than former.

Abdomen triangular, 5-segmented, segments 3 and 4 fused with no distinct suture; all the other intersegmental sutures distinct; width greatest at proximal end of fused segment; telson subequal in length to segment 5; proximal 1/3 length of lateral edge straight, distal 2/3 progressively concave, sides of telson gently concave and tapering rapidly to slightly rounded tip.

G1 slender, strongly curved, tapering gradually to pointed tip; 8 subterminal setae with spinules spanning 1/2 setal length; 4 subterminal, equally spaced protrusions on left side; distal portion slightly curved; middle portion with 90° turn.

♀: Carapace at posterior lateral angle, broader than long; pigmentation much darker and denser with no distinct spots on dorsal surface of carapace, carapace at anterior and posterior angles raised forming slight ridges (in mature ♀). Abdomen with no fused segments, all intersegmental sutures distinct, covers entire sternum, reaching base of legs, broader than long, tip concave (in mature ♀) or slightly pointed (in immature ♀). Cheliped slender, not stouter than ambulatory legs; fingers spatulate, outer cutting edges serrated, tip of fingers sharp.

REMARKS. *Elamena vesca* sp. nov. cannot be separated easily from *E. truncata* unless adult ♂ s are available. Despite many reports of *Elamena truncata* (Stimpson, 1858) in the literature, a clear description is only available from Ng & Chuang (1996). For *E. truncata*, the lateral angles are well marked and distinct, the posterior lateral angle being almost tooth-like, whereas in *E. vesca*, all the angles are more rounded. The fingers of the ♂ chela in *E. vesca* are also proportionately longer than those of *E. truncata*, which has shorter fingers and a more stocky palm. The ambulatory legs of *E. vesca*, especially the dactyli, are also proportionately longer compared to *E. truncata*. The ♂ abdomen of *E. truncata* has a proportionately longer and more rounded telson, and the lateral margins of segment 5 are more strongly concave than in *E. vesca*. The G1s of *E. vesca* and *E. truncata* differ markedly, with that of *E. vesca* being shorter, more strongly bent and the tip curved upwards (almost straight in *E. truncata*) (Ng & Chuang, 1996).

Milne Edwards (1873) described this New Caledonian species as *Elamene truncata*, without figures. He was apparently not aware of Stimpson's (1858) description of *Trigonoplax truncata* from Japan. Kemp (1917: 273) commented '... That both authors have used the same specific name is presumably due to a remarkable coincidence.' The species are in fact different, and Milne Edwards' (1873) name is a junior homonym of Stimpson's. The species is here described as new, using fresh specimens as types.

Australian specimens of *E. truncata* are tentatively referred to *E. vesca* (Ng & Chuang, 1996). The Australian specimens however, differ from *E. vesca* in the ♂ abdomen as well as G1. The ♂ abdomen of '*E. truncata*' of Gordon (1940: 69, fig. 5d) and Lucas (1980: 245, fig. 8B) differ from that of *E. vesca* (Fig. 7E) in having fused segments 3 and 4 longer and the telson longer than segment 5 (subequal in length for *E. vesca*).

Gordon's (1940) ♂ abdomen has a proportionately longer segment 5 and fused segments 3 and 4 compared to that of Lucas (1980). Also the lateral margins of fused segments 3 and 4 are strongly convex in Gordon's figure but only gently convex in Lucas'. The Australian specimens need taxonomic review but are definitely closer to *E. vesca* than *E. truncata* as defined by Ng & Chuang (1996).

DISTRIBUTION AND HABITAT. New Caledonia and possibly Australia. Cryptic, intertidal on rocky shores, in shallow water (about 0.5 m). Our specimens were collected under rocks.

ETYMOLOGY. Latin *vesca*, weak; alluding to the appearance of the species.

ACKNOWLEDGEMENTS

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TWO NEW FRESHWATER CRABS IN *AUSTRALOCARCINUS* DAVIE, WITH REMARKS ON TROGLOPLACINAE GUINOT AND GONEPLACIDAE MACLEAY (CRUSTACEA:DECAPODA:BRACHYURA)

P.J.F. DAVIE & D. GUINOT

Two new species, *A. kanaka* and *A. palauensis*, of the previously monotypic *Australocarcinus* Davie are described from New Caledonia and Palau Islands, respectively. The three species are separated on dentition of the anterolateral margins. Direct development of the young without free-living stages is confirmed for *A. kanaka*. *Australocarcinus* is placed in the previously monotypic almost completely freshwater Trogloplacinae Guinot which is restricted to the tropical West Pacific. Their apparent closest relatives are marine, mostly deepwater Chasmocarcininae Serène (Gonoplacidae). *Trogloplax* has strong troglobitic adaptations and is presumed to have evolved from an *Australocarcinus*-like ancestor. The Trogloplacinae is separated from the Chasmocarcininae by structure of the antennular region, and differences in length and shape of the male gonopods. □ *Brachyura, Goneplacidae, Australoplax, Trogloplax, freshwater.*

P.J.F. Davie, Queensland Museum, P.O. Box 3300, South Brisbane, Queensland 4101, Australia; D. Guinot, Laboratoire de Zoologie (Arthropodes), Muséum national d'Histoire naturelle, 61 rue de Buffon, Paris cedex 05, France; 15 April 1996.

Trogloplax Guinot, 1986, was erected for a freshwater troglobitic crab from New Britain. Its type, *T. joliveti*, has a remarkable appearance, blind, and with many adaptive features for a cave environment. Because of its many peculiar features Guinot (1986) erected the Trogloplacinae, in the Goneplacidae for it.

Australocarcinus Davie, 1988, was established for a north Queensland estuarine species, *A. riparius* Davie, 1988, also peculiar in the combination of morphological characters, in particular the unusual sternal plate, gonopods, and putative direct development of the young.

While *Trogloplax* shared the unusual structure of male sternite 8, its strong troglobitic adaptations made it difficult to be sure if the two genera were closely related. Close comparison shows the 2 genera to be related in the Trogloplacinae. We provide a redefinition of the subfamily and better understanding of its relationships within the Goneplacidae.

Two additional species of *Australocarcinus* are described herein. One comes from a freshwater stream in northern New Caledonia and the second, from Palau, was discovered by P.J.F.D. amongst an unidentified collection of grapsids on loan from the USNM to Michael Türkay at the Senckenberg Museum, Frankfurt. Also a large population of *A. riparius* from a freshwater rainforest stream in north Queensland is reported.

This discovery, the records from freshwater of the New Caledonian species and the confirmation of direct development, show that trogloplacines are a very old freshwater group, probably derived from a marine ancestor, with at least *A. riparius*, showing estuarine tolerance. Jamieson & Guinot (1996) examine the ultrastructure of the spermatozoan of *A. riparius* and discuss possible generic relationships.

Abbreviations used in the text: c.b.=carapace width; G1,G2=male first and second gonopods; MNHN, Muséum national d'Histoire naturelle, Paris; QM, Queensland Museum, Brisbane; SMF, Senckenberg Museum, Frankfurt; USNM, United States National Museum, Washington.

Measurements given in the text are of the carapace breadth (measured at the widest point) followed by length. Leg segments were measured in a straight line to give maximum dorsal length, and so are not always the maximum possible length.

SYSTEMATICS

Family GONEPLACIDAE MacLeay, 1838
subfamily TROGLOPLACINAE Guinot, 1986

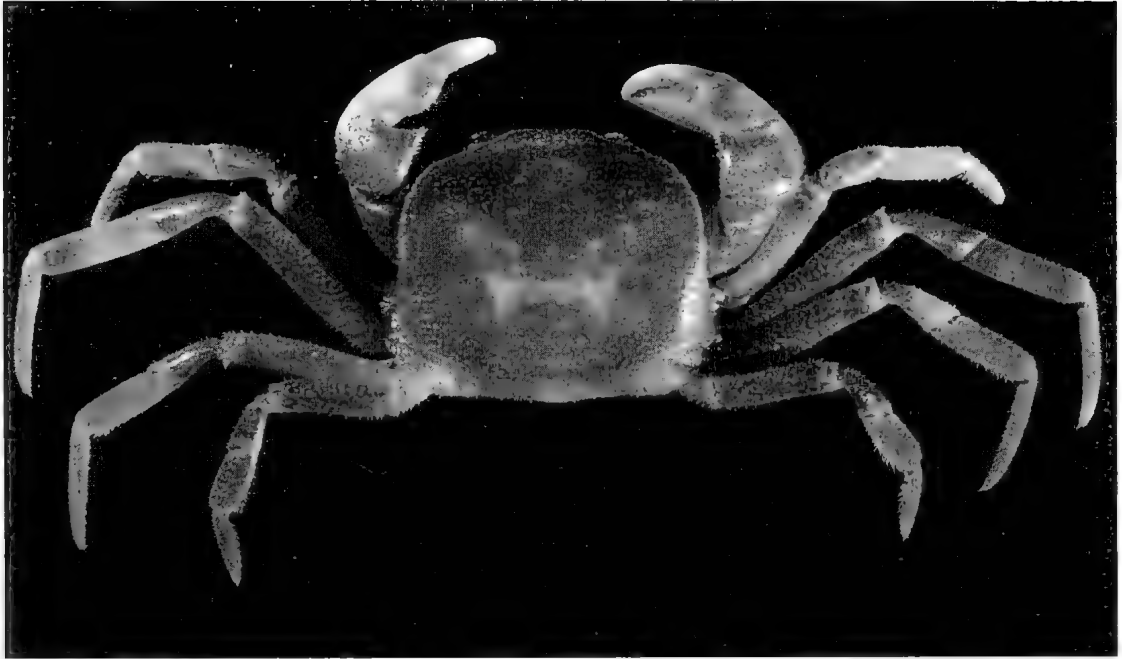Trogloplacinae Guinot, 1986:307; 1987:25; 1988:22; 1994:167; Guinot & Geoffroy, 1987:18.

FIG. 1. *Australocarcinus kanaka* sp. nov., ♀ paratype, 11.1 x 9.5 mm (QMW21389), dorsal view. Scale line in mm.

DIAGNOSIS (emended from Guinot, 1986). Carapace rounded; sometimes poorly calcified; anterolateral margin cristate, entire or toothed; front with or without shallow median indentation, without latero-external notch. Eyes relatively small. Antennules folded completely into fosset. Antenna lying in orbital hiatus. Buccal frame quadrangular; third maxilliped wide, together almost completely closing buccal cavity; exopod broad, with flagellum. Sternal plate very broad, with all sutures interrupted; large part of sternite 8 exposed; a supplementary transverse suture in middle of sternite 8, parallel to suture 7/8, forming a supplementary plate. Sterno-abdominal cavity deep. Male abdomen with segments 3-5 fused. Abdominal locking mechanism in normal position. Vulvae of female very large, occupying position near extremity of sternal suture 5/6. Penis very long, lying in covered channel on sternite 8, only uncovered next to the coxa of P5; finally protruding as long soft papilla. Chelipeds with minor heterochely and heterodonty. G1 stout, moderately tapering, with an apical aperture; G2 about as long as G1, with flagellum about same length as peduncle.

REMARKS. The Trogloplacinae belong to the Heterotremata showing a coxosternal disposition of the male sexual opening (Guinot, 1978, 1979a).

Australocarcinus Davie, 1988

Australocarcinus Davie,1988:259.

TYPE SPECIES. *Australocarcinus riparius* Davie, 1988, by original designation.

DIAGNOSIS. Carapace smooth, glabrous, regions poorly defined; anterolateral margins convex, with or without rounded teeth, posterolateral margins subparallel, posterolateral facet delimited. Frontal margin shallowly sinuous, formed of 2 rounded lobes, moderately deflexed, without preorbital lobes or teeth; fronto-orbital border c. 0.5-0.6 times carapace width. Orbits small, unarmed, with slightly raised rim. Eyestalks short, moveable, with well developed corneas; completely retractable within orbit. Chelae robust, similar but one slightly larger. Legs long, slender, hirsute, second pair longest. Male abdomen with segments 3-5 fused, segment 3 expanded laterally, subequal in width to segment one, neither covering sternum between last pair of legs. Sternal segment 8 in male with a closed, invaginated channel carrying penis, such
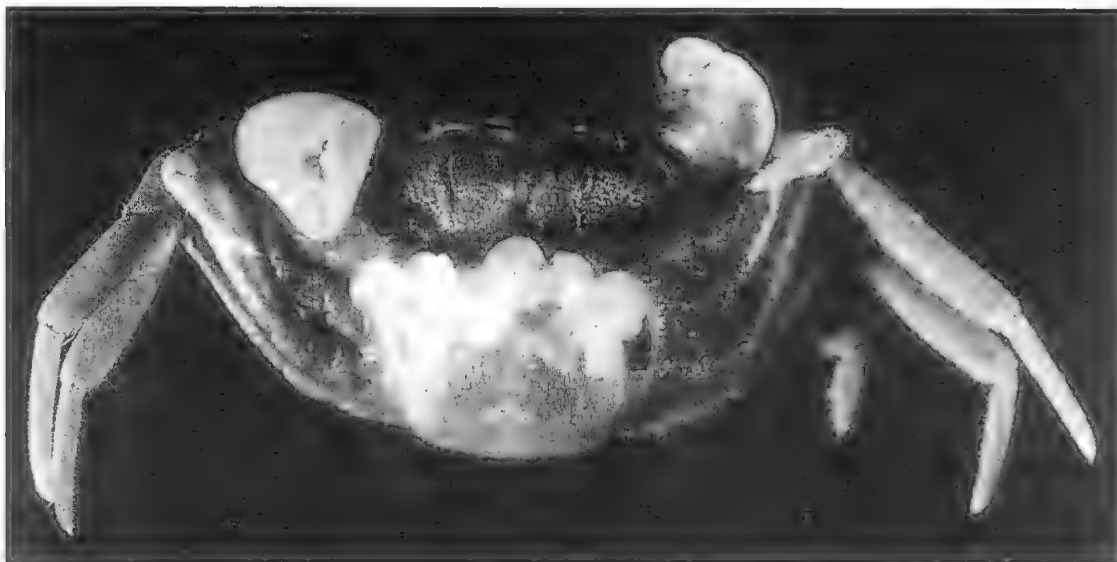
FIG. 2. *Australocarcinus kanaka* sp. nov., ♀ paratype, 11.1 x 9.5 mm (QMW21387), showing hatched megalopae under the abdomen. Scale line in mm.

that appears to be formed of 2 discrete plates; female of normal form. G1 stout, straight, tapering to simple apex; G2 as long as first, slender, narrowed in width over distal half, ending in simple apex.

Australocarcinus riparius Davie, 1988
(Fig. 7)

Australocarcinus riparius Davie, 1988:260, figs 1-3.

MATERIAL EXAMINED. QMW18234, 12♂♂ (8.3x6.7-12.9x10.2 mm), 2♀♀(10.2x8.2, 11.3x 9.5mm), McIvor River at Isabella-McIvor road crossing, 15°07.2'S, 145°04.4'E, freshwater, under rocks in pools in drying river bed, fringing rainforest, DO2 0.9 ppm, altitude c. 30m, 18.11.1992, P. Davie & J. Short.

DESCRIPTION. See Davie (1988).

HABITAT. Freshwater and estuarine. The collection site at the McIvor River, is within rainforest at about 30m altitude, and they were found under rocks in pools in the drying river bed. Previous records were from estuaries where it is apparently common in salinities up to 20 p.p.t. (Davie, 1988).

DISTRIBUTION. This record extends the distribution 400km further north along the eastern Australian coast, from the Murray River, near Cardwell, and Hinchinbrook Island.

Australocarcinus kanaka sp. nov.
(Figs 1-4, 6, 8)

MATERIAL EXAMINED. HOLOTYPE MNHNB25279, ♂ (11.1 x 9.5 mm), Col d'Amoss, near Ouégoa, New Caledonia, in freshwater stream, 100 m altitude, 13.11.1993, R. Raven. PARATYPES QMW21387, ♀ with megalopae (11.1 x 9.5 mm), data as for holotype. QMW21388, ♂ (10.5 x 9.0 mm), 2♀♀ (12.0 x 10.0; 13.1 x 10.8 mm), data as for holotype. QMW21389, ♀ (11.1 x 9.5 mm), ♂ (6.4 x 5.5 mm), Col d'Amoss, near Ouégoa, New Caledonia, in freshwater stream, 100 m altitude, 13.05.1984, G. Monteith and D. Cook. QMW20577, ♂ (3.6 x 3.1 mm), Ouekoula, near Ouémou, upper drainage of the Ouémou River (draining to the west coast), small trickles originating from seeps, 230 m altitude, 13.07.1993, P. Bouchet. MNHN-B25280, 2♀♀ (11.2 x 9.2; 12.4 x 10.4 mm), Pangou, upper drainage of the Ouaième River (draining to the east coast), in wet mosses in splash zone of very small stream forming rapids, 300 m altitude, 13.07.1993, P. Bouchet. MNHNB25281, ♂ (8.7 x 7.3 mm), Ouéné, near Pangou, upper drainage of the Ouaième River, seepage and small trickle, under dense secondary vegetation, 400 m altitude, 14.07.1993, P. Bouchet. MNHNB25282, 3♂♂ (3.5 x 3.0; 4.0 x 3.6; 7.5 x 6.2 mm), 2♀♀ (7.2 x 6.3; 8.4 x 7.2 mm), Koumac, 3 Creeks, New Caledonia.

DESCRIPTION. Carapace subrectangular; greatest width behind exorbital angles; 1.16-1.17 times broader than long. Carapace convex anteriorly, flat from side to side posteriorly, slightly convex anteriorly. Regions poorly defined, cardiac and metagastric regions defined
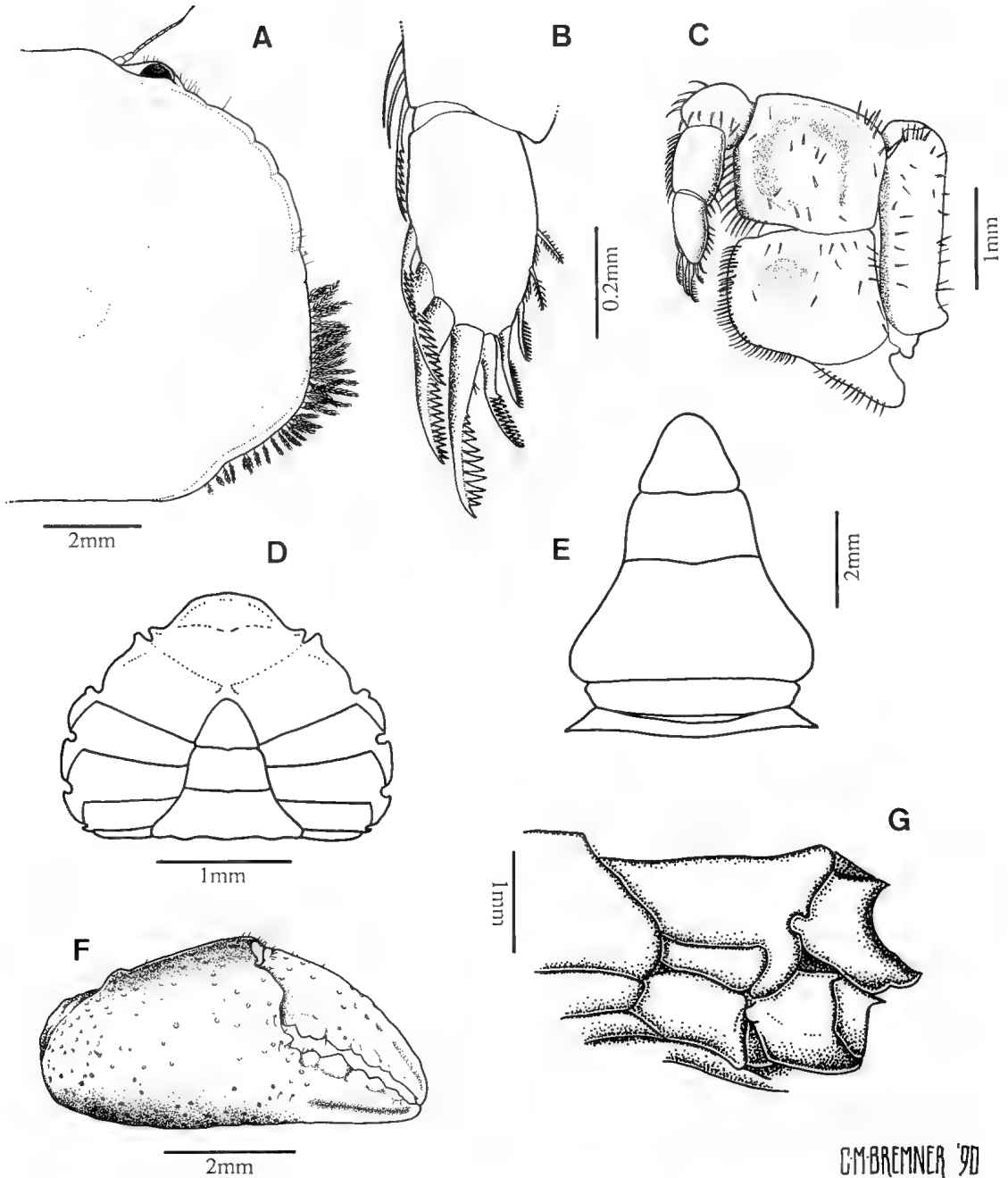
FIG. 3. *Australocarcinus kanaka* sp. nov. A-C, F, ♀ paratype, 11.1 x 9.5 mm. D, E, G, ♂ paratype, 6.4 x 5.5 mm (QMW21389). A, right side of carapace in dorsal view. B, dactylus of third maxilliped showing stout comb-like setae. C, third maxilliped. D, sternum of male. E, male abdomen. F, right chela. G, sternites 7 and 8 of male showing fissure to form a supplementary plate.
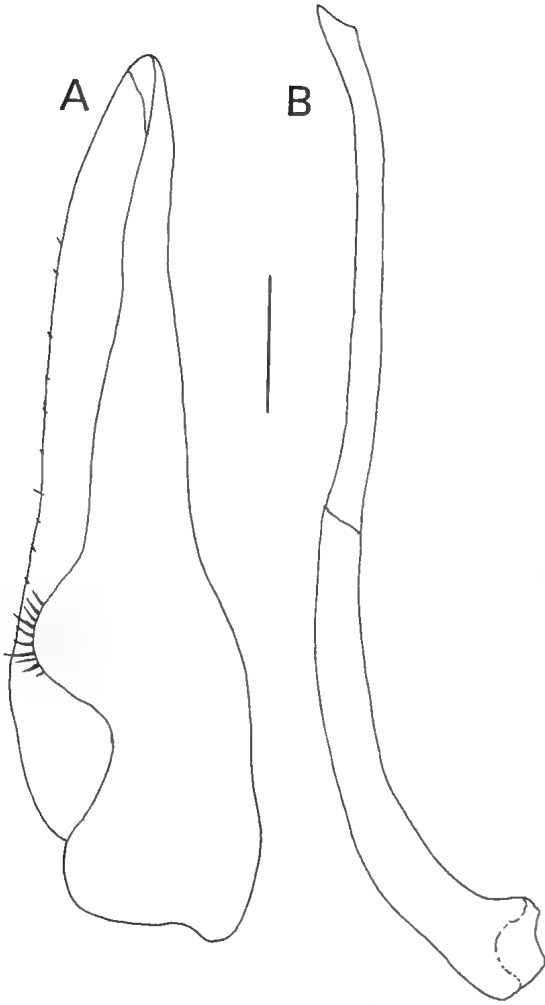
FIG. 4. *Australocarcinus kanaka* sp. nov., ♂ holotype, 11.1 x 9.5 mm, QMW20577. A, gonopod 1. B, gonopod 2. Scale line = 0.5 mm.

by shallow grooves; posterolateral facet delimited from behind last anterolateral tooth. Lateral margins subparallel, or slightly divergent posteriorly; straight. Anterolateral margins regularly convex; cristate; with two teeth behind the exorbital angle. Exorbital angle effaced. First anterolateral tooth blunt, placed about halfway along anterolateral margin. Second anterolateral tooth blunt; similar in size to first in small male but less obvious on holotype. Front moderately deflexed; with or without shallow median emargination; lateral angles rounded; no pre-orbital teeth; lateral margins diverging posteriorly; fronto-orbital border *c.* 0.5 times width. Carapace

surface evenly punctate, smooth, naked, long feathered setae restricted to side walls. Upper orbital border smooth; moderately concave. Lower orbital border straight, slightly concave at inner end; smooth. Inner angle of lower orbital border effaced, reaching about halfway up basal antennal segment; lower orbital border continuous with lower edge of outer orbital tooth as a slightly raised rim. Antennal flagellum entering orbit c.1.5 times length of orbit. Orbital hiatus open. Basal antennal segment short, not touching front; unarmed. Inter-antennular septum narrow.

Third maxilliped with merus and ischium subequal. Merus slightly wider than long; outer margin straight; antero-external angle not produced, broadly rounded; about equal in length to ischium. Suture between merus and ischium horizontal. Ischium quadrate; inner margin smooth. Palp articulating at inner distal margin of merus; relatively long, dactylus armed with long, stout, comb-like bristles apically. Exopod moderately broad.

Chelipeds subequal, right slightly the larger on holotype; large and robust; borders granulate; row of longer feathered setae on anterior and posterior borders; carpus with a broad spine at inner angle. Outer surface of palm smooth, with coarse punctations. Outer surface of palm naked. Inner surface of palm smooth. Immovable finger moderately long; flattened on outer surface; with a broad, shallow, longitudinal groove, bearing close cropped setae; length cutting edge c. 0.4 times length propodus. Ventral border of chela straight. Dorsal surface of dactyl smooth, rounded; distal third of dactyl with broad groove like fixed finger. Fingers pointed, slightly curved inwards; a narrow gape between cutting margins proximally.

Walking legs relatively long, compressed, slender; second pair the longest. Longest leg c. 1.8-1.9 times maximum carapace width. Merus of third leg c. 3.7-4.25 times as long as wide (paratype and holotype respectively); carpus c. 2.7-2.8 times as long as wide; propodus c. 2.5-2.7 times as long as wide; dactylus c. 1.5-1.6 times length of propodus. Dactyli cylindrical, densely covered in felt of setae; terminating in acute chitinous tips. Anterior margin of merus with a subdistal shoulder; unarmed terminally. Leg segments smooth; fringed with short, feathered, setae, longer on infero-distal borders of propodi.

Male abdomen moderately broad; 5 free segments; 3-5 fused; 1 and 3 widest, subequal. First segment not covering entire width of sternum between 4th pereiopods; narrow. Segments 3-5
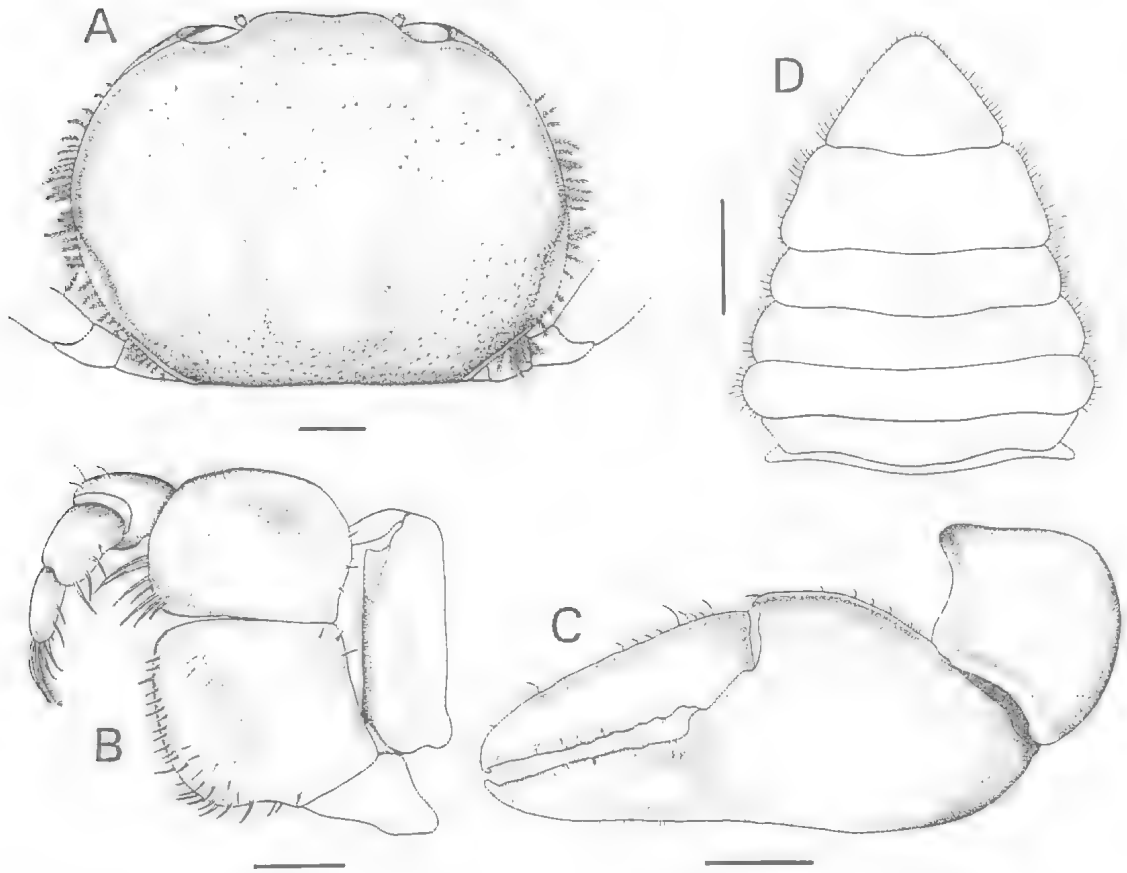
FIG. 5. *Australocarcinus palauensis* sp. nov., ♀ holotype, 7.1 x 5.8 mm (USNM). A. carapace in dorsal view. B, third maxilliped. C, left chela. D, abdomen. Scale line = 1 mm.

tapering, basally bulbous. Segment 6 c. 2 times wider than long. Telson longer than penultimate segment; c. 0.8 times longer than wide; apically rounded. Male gonopods Fig. 4. Sternum broad.

HABITAT. Freshwater habitats - in a freshwater stream; in small trickles originating from seeps; in wet mosses in splash zone of very small stream forming rapids; and in seepage and small trickles under dense secondary vegetation. Recorded up to 400m above sea level.

ETYMOLOGY. A noun in apposition for the native peoples of the islands of the South West Pacific.

Australocarcinus palauensis sp. nov.
(Figs 5, 8)

MATERIAL EXAMINED. HOLOTYPE USNM, ♀

(7.1 x 5.8 mm), Addeido River, in small fast tributary, Babelthuap Id., Palau Islands, 05.03.1946, D.S. Frey.

DESCRIPTION. Carapace subrectangular; greatest width behind exorbital angles; 1.22 times broader than long. Carapace convex anteriorly, flat from side to side but slightly convex towards the margins. Regions poorly defined, cardiac and metagastric regions indistinctly defined; posterolateral facet not defined. Lateral margins subparallel; straight. Anterolateral margins regularly convex; cristate; without teeth. Exorbital angle effaced. Front moderately deflexed; bilobed; lateral angles rounded; no pre-orbital teeth; lateral margins diverging posteriorly; fronto-orbital border c. 0.55 times carapace width. Carapace surface evenly punctate, smooth. Dorsal surface naked, long feathered setae on sidewalls. Upper orbital border smooth; moderately
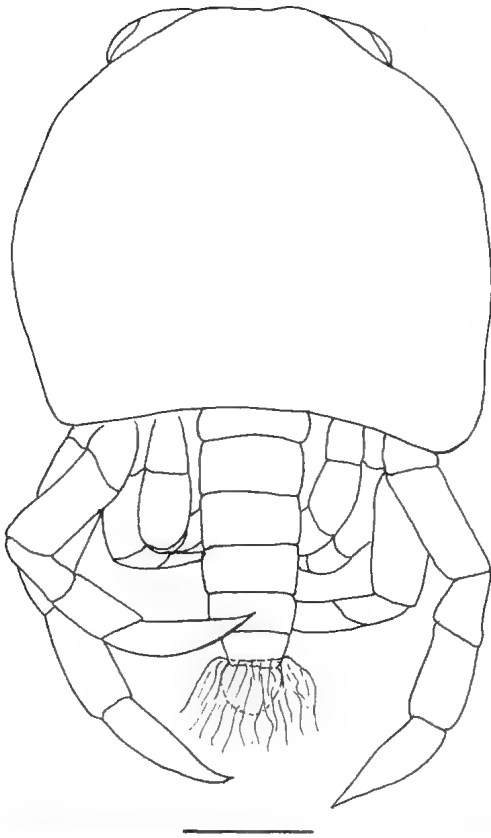
FIG. 6. *Australocarcinus kanaka* sp. nov., megalopa (QMW21387). Pleopodal membrane still attached around base of telson. Scale line = 0.5 mm.

concave. Lower orbital border shallowly sinuous; smooth; inner angle effaced, reaching about halfway up basal antennal segment; continuous with lower edge of outer orbital tooth as a slightly raised rim. Antennal flagellum entering orbit; both flagellums missing. Orbital hiatus open. Basal antennal segment short, not touching front, unarmed. Inter-antennular septum narrow.

Third maxilliped with merus and ischium subequal. Merus wider than long; outer margin slightly convex; antero-external angle not produced, broadly rounded; c. 0.85 times length of ischium. Suture between merus and ischium horizontal. Ischium quadrate; inner margin smooth. Palp articulating at inner distal margin of merus; relatively long, dactylus armed with long, stout, comb-like bristles apically. Exopod moderately broad.

Chelipeds slightly unequal, right slightly the larger; large and robust; borders granulate; row

of long feathered setae on anterior and posterior borders; carpus with a broad, blunt spine at inner angle. Outer surface of palm smooth, with coarse punctations; naked. Inner surface of palm smooth. Immovable finger moderately long, flattened on outer surface; without obvious longitudinal groove. Length cutting edge c.0.4 times length propodus. Ventral border of chela slightly concave at base of fixed finger. Dorsal surface of dactyl smooth, rounded. Fingers pointed; slightly curved inwards; a narrow gape between cutting margins proximally, fingers with teeth poorly differentiated, but large, backwardly directed molar near base of dactyl.

Walking legs relatively long; compressed; slender; second pair the longest, c. 1.8 times maximum carapace width. Merus of third leg c. 3.5 times as long as wide; carpus c. 2.6 times as long as wide; propodus c. 2.4 times as long as wide; dactylus c. 1.4 times length of propodus. Dactyli cylindrical, densely covered in a felt of setae; terminating in acute chitinous tips. Anterior margin of merus with subdistal shoulder; unarmed terminally. Leg segments smooth; fringed with short, feathered setae, longer on infero-distal borders of propodi.

HABITAT. From a fast flowing tributary of the Addeido River suggesting a freshwater habitat.

ETYMOLOGY. For the Palau Islands.

REMARKS ON *AUSTRALOCARCINUS* DAVIE

The three known species are very similar but differ conspicuously by the dentition of the anterolateral margins. *Australocarcinus riparius* has 4 large, prominent blunt teeth; *A. kanaka* has only 2 low, hardly projecting, blunt lobes; and *A. palauensis* has no anterolateral teeth, but simply a continuous crest. The telson of *A. kanaka* is much shorter than on *A. riparius*. *A. riparius* also differs from the other two species by having the outer margin of the merus of maxilliped 3 much more strongly convex.

Davie (1988) speculated that direct development occurred in *A. riparius* because 18 juvenile crabs were collected with the adult female. This reproductive strategy has now been confirmed for *A. kanaka* as one female (QMW21387) has 17 megalopae still attached to its pleopods (Figs 2,6). The megalopae have no obvious yolk reserve. Ovigerous females of *A. riparius* carry about 70 eggs, so there seems to be significant attrition during the developmental stages. The
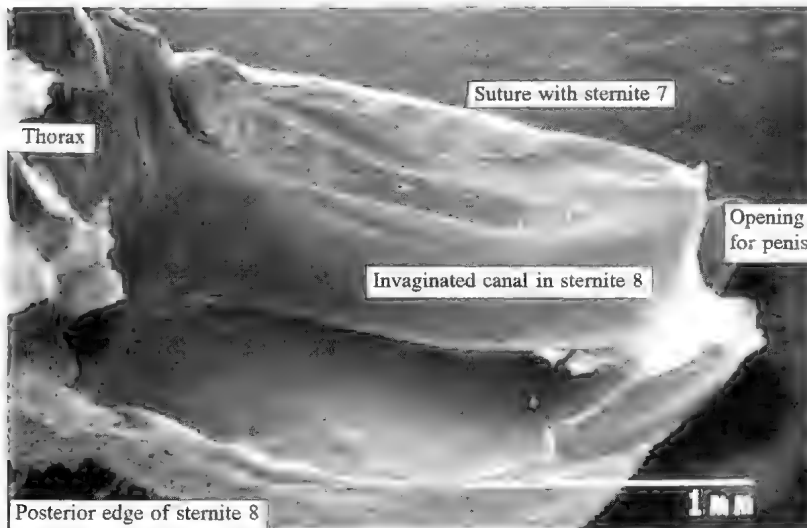
FIG. 7. *Australocarcinus riparius* Davie, 1988 ($\eth$, 11.6 mm c.b., QMW18234), scanning electron micrograph of the inside of sternite 8, showing invaginated channel in which the penis lies.

holotype female of *A. palauensis* also shows large vulval openings and therefore direct development can similarly be inferred for this species.

RELATIONSHIP OF *AUSTRALOCARCINUS* AND *TROGLOPLAX*

Many of the most unusual characteristics of monotypic *Trogloplax* (Guinot, 1986, 1987) (type *T. joliveti*), can be attributed to its cavernicolous adaptations. These are common, to a greater or lesser extent, in all cave dwelling arthropods. They are: 1) the soft, poorly calcified carapace; 2) dorsoventral flattening; 3) the reduced narrow eyestalks with the corneas lacking faceting and pigment (Guinot, 1988, fig. 16A-C); 4) the loss of pigmentation of the carapace and pereiopods; 5) exceptionally elongated and thin pereiopods, especially the ambulatory legs; 6) the two long spines of the chelipeds. (Guinot, 1986:165).

Despite strong superficial differences there are fundamental characters that mark a close relationship between *Trogloplax* and *Australocarcinus*: 1) the carapace lacks setae, is rounded, and the anterolateral borders are anteriorly converging and cristate. 2) the buccal cavity is large and quadrangular. 3) the maxillipeds are short and broad, with the exopods relatively broad and with a flagellum. 4) the sternal plate is broad with the sutures 4/5 to 7/8

interrupted, and with sternite 8 broadly uncovered. 5) the G1 is stout and straight, and with an apical opening. 6) the G2 is subequal in length to G1, and with the two parts (flagellum and peduncle) subequal in length. 7) the male abdomen has segments 3-5 fused. 8) the sterno-abdominal cavity is deep in the male. 9) there is feeble heterochely and feeble heterodonty. 10) the antenullar flagellae fold transversely into fossae under the frontal margin. 11) a sternal crest surrounds the telson of the male. 12) the outer face of sternite 8 is composed of two plates separated by a suture which marks an medial invaginated canal, in which the penis lies.

REMARKS ON THE GONEPLACIDAE

Guinot (1969a,b,c, 1971) showed that the Goneplacidae MacLeay, 1838, *sensu* Balss (1957) constitutes an heterogeneous assemblage, and must be re-appraised. Evolutionary lineages in the family are the goneplacine (=carcinoplacine) line, a pilumnine line, the panopeine line, and the euryplacine line. The Geryonidae were considered very distant from the Goneplacidae. The Rhizopinae Stimpson, 1858, still needs to have some questions resolved. This subfamily may need to be restricted to the type species, *R. gracilipes* Stimpson, 1858, which appears to constitute a separate lineage, a little different from the pilumnine line (*sensu stricto*) because the male G1, while similar, is not of typical pilumnid form with the strongly recurved tip (Guinot, 1969a, fig. 110), but the G2 is effectively the same as in the Pilumnidae. Ng (1987) reviewed the constitution of the Rhizopinae, and it appears that all the genera he included have the G1 with a pilumnine recurved tip, and the short sinuous G2 also typical of pilumnids. We think it possible that the Rhizopinae (*sensu* Ng, 1987) may still be heterogeneous with *Rhizopa* itself forming a separate lineage. If this is so, then the name Typhlocarcinopsinae Rathbun, 1909, is

available for *Typhlocarcinops* and perhaps some other genera. *Typhlocarcinops* has gonopds that are not of the classical pilumnid type (sensu Ng, 1987).

We consider that primitive goneplacid genera of the pilumnine line cannot be separated phylogenetically from the xanthoid Pilumnidae (*Pilumnus*). In the same way the panopeids *Cyrtoplax* Rathbun, 1914, *Tetraplax* Rathbun, 1901, *Glyptoplax* Smith, 1870, and *Cycloplax* Guinot, 1969, etc., cannot be separated phylogenetically from the panopeids like *Panopeus* H. Milne Edwards, 1834, but they form a natural grouping for which the name Eucratopsinae Stimpson, 1871 (= Prionoplacinae Alcock, 1900) may be used.

The Goneplacidae contains the Goneplacinae Miers, 1886, Carcinoplacinae, Miers, 1886, Chasmocarcininae Serène, 1964, Trogloplacinae Guinot, 1986, and the Euryplacinae Stimpson, 1871. Many genera are still not satisfactorily placed in these subfamilies and a revision is urgently needed.

AFFINITIES OF THE TROGLOPLACINAE. The most revealing character in helping to understand the affinities of the Trogloplacinae is the disposition of the penis and gonopore. Typically in coxosternal crabs (*sensu* Guinot, 1978, 1979a), the ejaculatory canal opens on the coxa of P5 and there is a long penis sometimes visible near the aperture on the coxa but with most of its length covered by the complete junction of sternites 7 and 8 and with the distal part long and emerging to enter the base of the G1 (Guinot, 1979a, fig. 51F; 1979b, figs 2,3). Sternite 8 of the Trogloplacinae has an invaginated channel in which the penis lies (Fig. 7).

The Trogloplacinae as Guinot (1986) has already indicated, belongs to the Goneplacidae and is most closely related to the Chasmocarcininae Serène, 1964 (*Chasmocarcinus* Rathbun, 1898) a marine, mostly deepwater group (Serène, 1964a,b). All Chasmocarcininae (*Chasmocarcinus, Camatopsis* Alcock & Anderson, 1899, *Chasmocarcinops* Alcock, 1900, *Hephthopelta* Alcock, 1899, *Scalopidia* Stimpson, 1858) have the penis lying in either an enclosed or open groove in sternite 8 (Felder & Rabelais, 1986), such that sternite 8 has an intercalated plate anteriorly, a fact first observed for *Chasmocarcinus* by Rathbun (1914).

The type species of *Hephthopelta* (*H. lugubris* Alcock) is a female, and not well known, but a new species of *Hephthopelta* we have examined (being described by Davie & Richer de Forges)

has an open suture in sternite 8, such that the penis is visible. Glaessner & Secretan (1987) and Tavares (1992) described exactly such a condition for the fossil American Eocene crab *Falconoplax* Van Straelen, 1933. This genus had been attributed to the 'Tymolinae' by Glaessner (1969)(= Cyclodorippidae), but Tavares (1992) re-attributed this fossil to the Goneplacidae *sensu lato*, agreeing with Van Straelen's (1933) original placement. We believe that *Falconoplax* belongs to the Chasmocarcininae. The first record of a fossil *Chasmocarcinus* was reported from the Eocene of Antarctica, in shallow water sediments (Feldmann & Zinsmeister, 1984).

Serène (1964a), with some reserve, placed *Megaesthesius* Rathbun, 1909, in the Chasmocarcininae. We exclude it from the subfamily but acknowledge its relationships must be investigated further.

In spite of the similarity in the coxosternal plate between the Trogloplacinae and the Chasmocarcininae, there are some notable differences. The major difference is that in the Chasmocarcininae the basal antennular segment is very swollen and completely fills the antennular fosset, such that the flagellum is excluded and cannot be folded. The gonopods of the two subfamilies are similar in that the G1 is stout and tapering and the G2 is long and not sigmoid, however there are also differences. In the Chasmocarcininae the G2 is noticeably shorter than the G1 and the flagellum is short (length varies a little depending on the species). In the Trogloplacinae the G2 is as long or slightly longer than the G1, and the flagellum occupies about half or slightly more of the length.

Considering the close relationships with the exclusively marine Chasmocarcininae, and the presence of at least one estuarine tolerant species in *Australocarcinus*, derivation of the completely freshwater *Trogloplax* from a marine stock is a logical assumption.

BIOGEOGRAPHY. The trogloplacines are so far only known from the western Pacific (Fig. 8). *Trogloplax* occurs in two freshwater subterranean caves on New Britain, PNG (Guinot & Geoffroy, 1987). The two caves are 250 km apart, and the crabs were found 300m into the caves. *Australocarcinus* is now known from three species in north Queensland, New Caledonia, and Palau; it seems probable that other species will be found on the West Pacific Islands. Although little is known of the reproductive patterns of the trogloplacines, Davie's (1988) supposition of direct development for *Australocarcinus riparius*
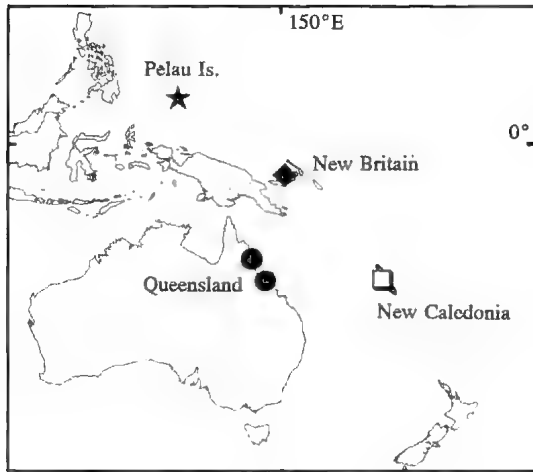
FIG. 8. Distribution of *Australocarcinus* and *Trogloplax*. Star = *A. palauensis* sp. nov.; hollow box = *A. kanaka* sp. nov.; solid circle = *A. riparius* Davie, 1988; diamond = *Trogloplax joliveti* Guinot, 1986.

has been confirmed for *A. kanaka*. If the other species of *Australocarcinus* and *Trogloplax* also have direct development, this should reinforce their allopatric distributions and contribute to small area speciation. One factor which could allow genetic interchange over a limited range is the high salinity tolerance exhibited by *A. riparius*, which allows it to survive under estuarine conditions. Estuarine corridors along the coast between river systems, during flood conditions, could allow dispersal of adults and the maintenance of the species over long distances, as occurs on the NE coast of QLD. Such a dispersal method however is only likely to be of local importance. There seems to be no obvious dispersal or vicariant explanation that conveniently explains the observed distribution patterns of the genera and species of the Trogloplacinae.

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FEEDING HABITS OF THE RING-TAILED GECKO,
CYRTODACTYLUS LOUISIADENSIS. Memoirs of the Queensland Museum 39(2): 288. *1996:-* 'Geckos can be voracious predators and will actively pursue and kill their prey. Generally they attack .... arthropods ... head size governs the size of prey. '... (King & Horner, 1993). Notwithstanding the fact that most Australian geckos are opportunistic arthropod feeders, some supplement their diets with plant exudates (Greer, 1989; Bauer, 1990; Ehmann, 1992; Couper et al., 1995) and a few large species prey also on vertebrates (Bauer & Sadlier, 1994). The following Australian species are known to prey on vertebrates: *Nephrurus asper* (including *N. amyae* and *N. sheai*), *N. deleani, N. laevissimus, N. levis, N. milli, N. stellatus, N. vertebralis, N. wheeleri, Oedura marmorata, O. ocellata, Phyllurus platurus* and *Pseudothecadactylus lindneri* (Bauer, 1990). All are relatively large (maximum SVLs 80-135mm).

Recent observations made near Cooktown, NEQ, show that another large Australian gecko, *Cyrtodactylus louisiadensis* (maximum SVL 130mm, after Couper & Gregson, 1994), feeds on vertebrates. In July, 1994 in a house near Jensen's Crossing, Endeavour R. (15°25'S 145°04'E), a large (exact measurement not recorded), male *C. louisiadensis* was observed stalking, then 'ambushing' a frog (K.J. & M. Jago). The gecko, alerted by the frog's movement, ran quickly down the wall of the house till it was about .3m from the frog (Litoria pallida) on the floor. It then 'jumped' to the floor and ran quickly a few steps to pounce on the frog which was ingested rapidly. Predation by *C. louisiadensis* on *L. pallida* there is apparently a fairly regular event, because it was observed (K.J. & M. Jago) again soon afterwards (September, 1994). On three subsequent occasions, specimens of *L pallida* were placed (K.J. & M. Jago) on the floor about 1m from resting, but alert *C. louisiadensis*, low on the house walls. On all occasions their movement triggered the same 'ambush' and voracious ingestion response by the geckos. In early November, 1995 on the granite boulders of the Black Trevethan Ra. (15°40'S, 145°14'E), a specimen of *C. louisiadensis* (SVL 93.6mm, now QMJ60620) was found (L.R., H.J. & D. Cook) with a struggling specimen of the gecko, *Nactus galgajuga* (SVL 30.8mm, now QMJ61096) in its mouth. The latter had been seized midbody.

As other species of *Cyrtodactylus* (*C. caspius* and *C. cavernicolus*, from Turkestan, and Borneo respectively) are known to prey on vertebrates (Bauer, 1990), it is not surprising that *C. louisiadensis* also does so. However, predation on frogs is unusual amongst Australian geckos, having been reported only once, by *Pseudothecadactylus linderi* (Husband & Irwan, 1995). The stomach contents of all specimens of *C. louisiadensis* in the collection of the Queensland Museum have been examined. They contain only arthropod remains: Class Chilopoda, unidentified (from QMJ38198); Class Arachnida, unidentified (QMJ27083, QMJ53634), *Heteropoda jugulans* (QMJ38330), *Yiinthi chillagoe* (QMJ45365), *Lychas* sp. (QMJ38331), *Liocheles* sp. (QMJ45365); Class Insecta Order Orthoptera, unidentified (QMJ24493), Family ?Gryllacrididae (QMJ27256), Family Stenopelmatidae (QMJ2431, QMJ55367), Family Gryllidae (QMJ2431, QMJ38197), Order Blattodea Family Blattidae *Methana* sp. (QMJ19327), Family Blaberidae *Laxta* sp. (QMJ38197, QMJ38198, QMJ45365), *Calolampra* sp. 1

(QMJ60863, QMJ60865), *Calolampra* sp. 2 (QMJ60328), Order Lepidoptera, unidentified moth (QMJ38198), Order Hymenoptera Family Formicidae *Oecophylla smaragdina* (queens) (QMJ60869), Family Vespidae (QMJ38197), Order Coleoptera, unidentified larva (QMJ30062), Family Tenebrionidae (QMJ30063), Family Elateridae (QMJ60869), Family Curculionidae (QMJ30063), nematode presumed to be a parasite (QMJ48084), unidentified possibly moulted skin (QMJ32323, QMJ52850). This is an unremarkable sample of large, mostly nocturnal, arthropods. Two specimens (from QMJ60863 and QMJ60865 from Peach Ck, McIlwraith Ra. 13°45'30"S 145819'30"E) are interesting. They contain wings and other parts of a very large species of the cockroach genus *Calolampra*. The species is probably undescribed and is rare in collections. It would be expected to be an 'under)bark' species which would forage on trunks of trees. Bauer & Sadlier (1994) discuss the relationship between feeding on vertebrates by *Rhacodactylus auriculatus* and the enlarged, caniniform teeth unique to this species. They conclude that this dentition may reflect the significance of skinks in the diet of this species, and special requirements for subjugation and handling of such prey. The teeth of *C. louisiadensis* are small. However, the anterior maxillary teeth are 'caniniform' and thus well-suited to capturing and holding large arthropods, and to grasping struggling, small vertebrates as the opportunities present.

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ULTRASTRUCTURE OF THE SPERMATOZOON OF *AUSTRALOCARCINUS RIPARIUS* (CRUSTACEA: BRACHYURA: GONOPLACIDAE: TROGLOPLACINAE)

B.G.M. JAMIESON AND D. GUINOT

The spermatozoon of the freshwater crab *Australocarcinus riparius* is heterotreme. However, absence of a recognizable acrosome ray zone is not a general heterotreme feature, though constant for thoracotremes. This zone is also unrecognizable in potamoids and in corystoids. The convex ring at the posterior end of the inner acrosome zone is similar to the xanthid ring, characteristic of the Xanthidae and Panopeidae, but homology is doubtful. Other xanthid features such as the accessory opercular ring and opercular overhang are absent from the sperm of *A. riparius* and relationship with xanthoids is not supported spermatologically. In its pointed shape, the perforatorium resembles that of corystoids but there the operculum is perforate. No special similarities to sperm of potamoids, which similarly have an obligatory freshwater existence at all stages of the life cycle, are apparent. The sperm of *A. riparius* shows no clear affinity with those of any other Heterotremata although confirming its inclusion in that group. In producing more than one spermatozoon per spermatophore, *A. riparius*, having marine relatives, may be less evolved along the path of lecithotrophy than are the potamoids, lacking marine cofamilials. □ *Australocarcinus riparius, Goneplacidae, Trogloplacinae, spermatozoon, lecithotrophy.*

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Davie (1988) described *Australocarcinus riparius* for a curious crab collected from a soft estuarine mud bank of the Murray River, NE Queensland. It has been found living in freshwater in rainforest (Davie & Guinot, 1996). This cryptic crab, excavating its own burrows, is remarkable in having direct development (the ovigerous female has only some 70 large eggs) and maternal care. Davie (1988) assigned it to the marine Goneplacidae. Guinot (1986) described *Trogloplax joliveti* from caves on New Britain. This specialised cavernicolous crab, with loss of pigmentation, thin cuticle, very long legs, and blind, nevertheless is a goneplacid for which Guinot (1986) erected the Trogloplacinae. Davie & Guinot (1996) describe 2 freshwater species of *Australocarcinus* (from New Caledonia and Palau) and show that the Australian epigean *Australocarcinus riparius*) and the insular-subterranean hypogean *Trogloplax* are closely related in the Trogloplacinae. This, incidentally, furnishes additional evidence for the ancient faunal relationship of North Australia and southern Papua-New Guinea/ New Britain.

The Trogloplacinae have pleopod 2 longer than pleopod 1, a very large sternal plate, with all the sutures 4/5 to 7/8 incomplete, and a peculiar plate on sternite 8 which covers the penis at its origin from the coxa of pereiopod 5 (P5) until its final emergence in the middle of the lateral margin of sternite 8. The disposition of the male pores can be considered as coxo-sternal (Guinot, 1978, 1979a, b). The Trogloplacinae fall in that part of Heterotremata possessing a wide thoracic sternum. The Trogloplacinae, which have extant cofamilial marine relatives (Chasmocarciniinae) are derived from a former marine stock. They exemplify how true freshwater crabs (e.g. the potamoids), which lack contemporary marine cofamilials, might have originated from marine precursors during the Tertiary.

Classically the diverse Goneplacidae (Guinot, 1969), are intermediate between xanthids (or related forms) and other crabs such as grapsids.

The sperm of *Australocarcinus* is the first to be investigated in a goneplacid and in a heterotreme with a coxo-sternal disposition of the male genital pore and is here described as a first step in aiding resolution of the relationships within the Goneplacidae.

MATERIALS AND METHODS

COLLECTIONS. The mature male specimen was collected by Peter Davie and John Short from freshwater rainforest habitat in the McIvor River
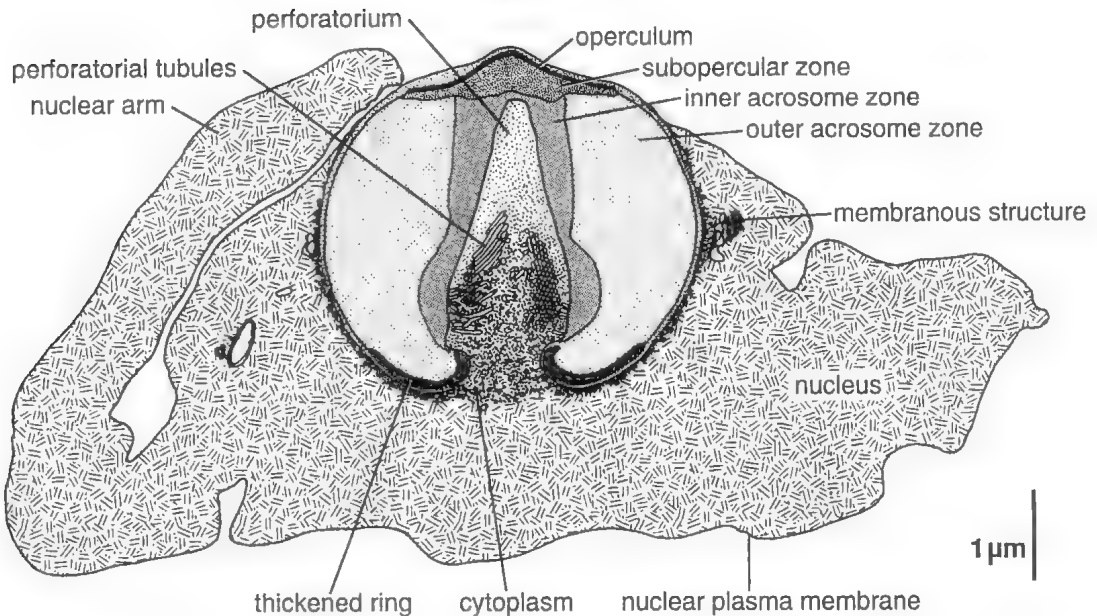
FIG. 1. *Australocarcinus riparius,* Semidiagrammatic sagittal section of a spermatozoon traced from a transmission electron micrograph.

at Isabella-McIvor road crossing, north Queensland in November 1992.

HISTOLOGY. The male reproductive material (both testes including the ducts of the vasa deferentia) was removed from the fresh crab and immediately fixed in cold glutaraldehyde for more than 2 hours at 4°. The gonad tissue was processed in the Zoology Department, The University of Queensland, by the fixation procedure (outlined below) for transmission electron microscopy. This was carried out in a Lynx -el. Microscopy Tissue Processor (Australian Biomedical Corporation, Ltd., Mount Waverley, Victoria, Australia).

Portions of the fixed testis (c.1 mm³) were rinsed in 0.2 M phosphate buffer (pH 7.2) (3 rinses in 15 min), postfixed in phosphate buffered 1% osmium tetroxide for 80 min; similarly washed in buffer and dehydrated through ascending concentrations of ethanol (40-100%). After being infiltrated and embedded in Spurr's epoxy resin, thin sections (500-800 Å thick) were cut on a LKB 2128 UM IV microtome with a diamond knife. Sections were placed on carbon-stabilized colloidin-coated 200 μm mesh copper grids and stained (according to Daddow, 1986) in Reynold's lead citrate for 30 s, rinsed in distilled water, then 6% aqueous uranyl acetate for 1 min,

lead citrate again for 30 s and a final rinse in distilled water. Micrographs were taken on an Hitachi H-300 transmission electron microscope at 80 kV and a JEOL 100-S transmission electron microscope at 60 kV.

RESULTS

For a comparative account and explanation of the various components of the brachyuran spermatozoon see Jamieson (1991a, 1991b, 1994) and the Discussion. The last paper contains a diagram of these components.

GENERAL MORPHOLOGY (Figs 1-3; Table 1). Each of the many spermatophores in the testes contains several to many spermatozoa. As such the spermatophores constitute coenospermia. An acrosome vesicle forms most of the volume. The acrosome is concentrically zoned but lacks the concentric lamellation of thoracotremes; it is capped apically by a dense operculum and is ensheathed in a thin cytoplasm which in turn is embedded in the nucleus. The acrosome vesicle is centrally penetrated by a cylindrical perforatorial column from the posterior end to immediately below the opercular complex. The nuclear material forms several marginal projec-

tions. The subspherical acrosome is typical of the Eubrachyura (Heterotremata + Thoracotremata).

A chromatin-containing posterior median process of the nucleus, seen in homolids, *Ranina* and some majids is absent. The nucleus consists of uncondensed, fibrous chromatin, and forms a cup surrounding the acrosome as in all other brachyurans. A thin layer of cytoplasm which intervenes between nucleus and acrosome as in other brachyurans, forms a small mass containing the centrioles at the posterior end of the perforatorial chamber. Cytoplasmic islets lateral to the acrosome and embedded in the chromatin (Figs 1, 2A, B, 3F) contain lamellae and bodies identifiable by homology with other crabs as degenerating mitochondria, although no cristae have been observed.

ACROSOME. The subspheroidal core of the spermatozoon consists of the concentrically zoned acrosome which is capped by, and includes, the opercular complex (Figs 1, 2A, 3A). The acrosome is invested by an acrosomal membrane underlain by a moderately electron dense sheath, the capsule. The mean length of the acrosome, from the apex of the operculum to the base of the capsule is 3.83 μm (SD=0.10, n=4); the mean width is 4.29 μm (SD=0.09, n=4). The acrosomal membrane and capsule are invaginated to cover an elongate subacrosomal or perforatorial chamber, the contents of which are the perforatorium (Figs 1, 2A, B, 3A-D). The anterior tip of this chamber abuts on the posterior face of the subopercular zone of the opercular complex. The perforatorium has a pronounced anterior taper and has the outline, in longitudinal sagittal section of an elongate triangle with a rounded base (Figs 1, 2A, 3A). It consists of a moderately electron dense matrix and is chiefly remarkable for numerous microtubule-like structures, perforatorial tubules, which appear to arise near, if not from, the posterolateral walls of the perforatorial chamber and extend chiefly anteriorly (Figs 2A, 3A, D). These tubules are closely adpressed to each other and form large bundles in which the tubules, in transverse section (Fig. 3C,E), form a quasi-crystalline array, leaving a narrow central core of the perforatorium of matrix material.

The central, subacrosomal axis of the acrosome formed by the perforatorial chamber is surrounded by a moderately electron dense layer, the inner acrosome zone (Figs 1, 2A, B, 3A-E) which extends from the subopercular zone at the anterior end of the acrosome almost to the

posterior end of the acrosome, reaching the thickened ring. The inner acrosome zone tapers anteriorly, following the outline of the perforatorium. Approximately its posterior 1/3, immediately anterior to the thickened ring, is widened to form a convex ring around the perforatorium (Figs 1, 2A, 3D); the inner acrosome zone, anterior to this ring, narrows so that there is a deep constriction between it and the ring. In some micrographs the convex ring appears to be separate from, although overlapping with, the anterior inner acrosome zone. It is not possible to determine whether the convex ring is the homologue of a xanthid ring. Acrosome ray zone, typical of heterotreme sperm, absent.

An outer acrosome zone (Figs 1, 2A, B, 3A-E) surrounds the inner acrosome zone and the base of the perforatorial chamber, being several times wider than the inner zone. This outer zone extends to the convex margin of the acrosome, being bounded by the capsule. It is uniform in structure and moderately electron dense, though paler than the inner acrosome zone, and, like other heterotreme sperm, does not display the concentric lamellae which are characteristic of thoracotreme sperm.

At the anterior pole of the acrosome, as in all other brachyurans and in paguroids there is a dense circular, imperforate, cap-like operculum (Figs 1, 2A, 3B). In longitudinal section it has an almost flat base and a low triangular anterior surface. Only a very thin layer of the outer, anterior surface is strongly electron dense. The much thicker lower zone is the subopercular zone. The operculum has a mean width of 2.35 μm (SD=0.06, n=4).

Accessory ring, present lateral to the operculum in xanthoids and, though differently orientated, in thoracotremes, is not present nor is there an opercular overhang. Periopercular rim absent.

At the posterior pole of the acrosome (Figs 1, 2A, 3A, D, G, H) the capsule is interrupted, as in all brachyurans, by invagination of the acrosome membrane and capsule as an orifice which opens into the columnar subacrosomal chamber. A thickened ring which is visible on each side of the subacrosomal invagination in most heterotremes and many thoracotremes is strongly developed (Figs 1, 2A, 3A, D). It is more extensive on the posterior, peripheral aspect of the acrosome than where it skirts the inside of the base of the subacrosomal chamber.

CYTOPLASM. The cytoplasm of the sperm forms a thin, scarcely discernible layer of ir-
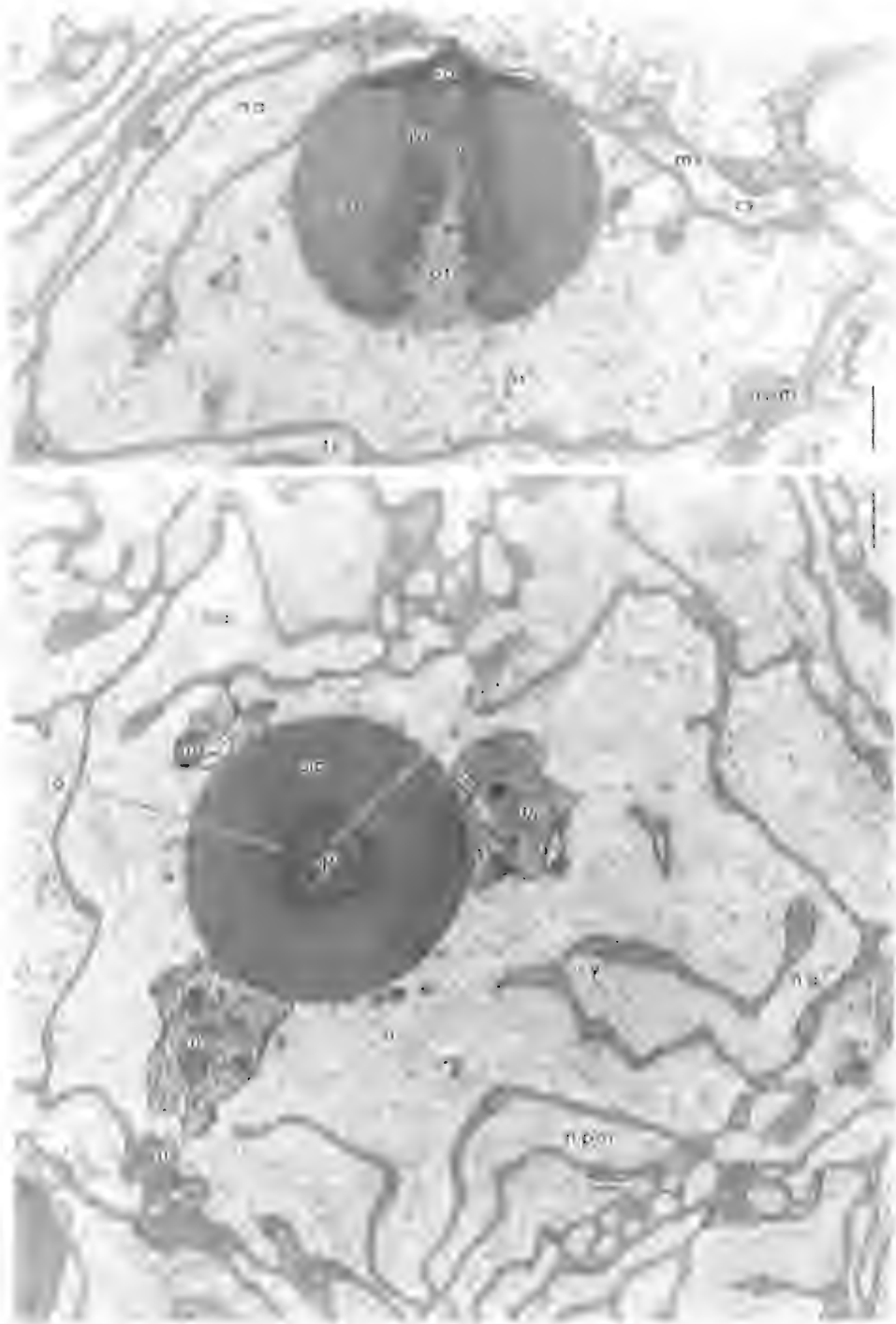
FIG. 2. *Australocarcinus riparius*, transmission electron micrographs of spermatozoa. A, sagittal section. B, transverse section. Abbreviations: ce=centriole; cy=cytoplasm; ia=inner acrosome zone; m=putative degenerating mitochondrion; ms=membranous structure; n=nucleus; na=nuclear arm; npm=nuclear plasma membrane; oa=outer acrosome zone; o=operculum; p=perforatorium; pt=perforatorial tubules; so=subopercular zone; tr=thickened ring.
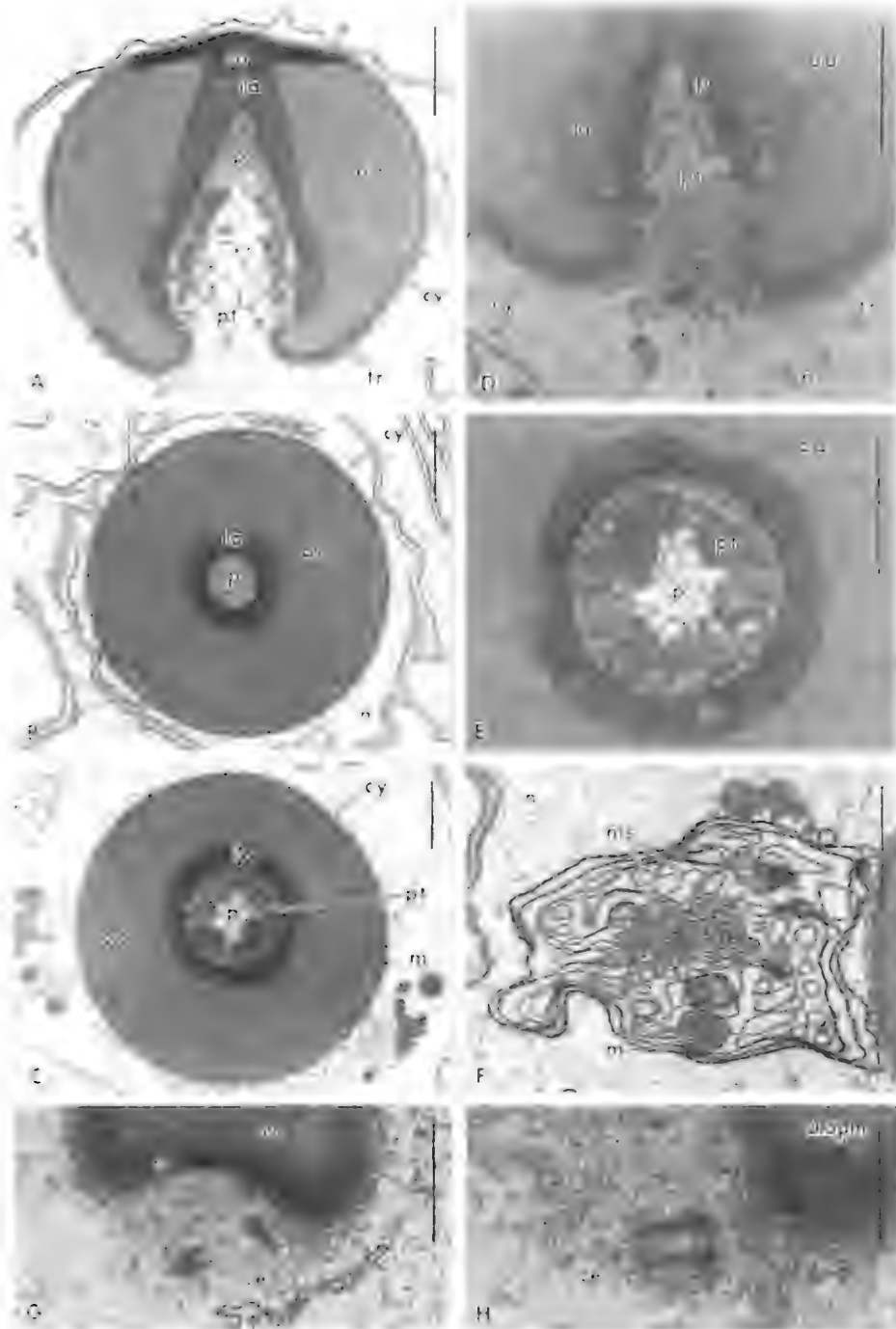
FIG. 3. *Australocarcinus riparius*, transmission electron micrographs of spermatozoa. A, sagittal section (LS). B, transverse section (TS) through the anterior region of the perforatorium. C, TS through the base of the inner acrosome zone proper, showing the quasi-crystalline array of perforatorial tubules. D, LS through the perforatorial invagination, showing the basal origins of the perforatorial tubules. E, TS through the convex ring, showing the quasi-crystalline array of perforatorial tubules. F, TS, showing a large membranous (lamellar) structure. G, Oblique section at the base of the perforatorium, showing two mutually perpendicular centrioles. H, longitudinal section of a centriole. Abbreviations as in Fig. 2.

regular thickness, ensheathing the acrosome excepting its opercular region (Figs 1, 2A, B, 3A, 4A, B). Membrane complexes and putative degenerating mitochondria which extend as islands far into the nucleus material are presumably derived from the cytoplasm but continuity of the large membranous structures of this type (Figs 2B, 3F) with the periacrosomal cytoplasmic layer has not been demonstrated. Periacrosomal cytoplasm is continuous with a mass lying at the posterior pole of the perforatorial chamber and the material within the posterior perforatorial chamber may also be regarded a cytoplasm. No cytoplasm extends into the nuclear arms.

CENTRIOLES. The basal cytoplasm of the perforatorial chamber at the level of the posterior end of the acrosomal capsule contains centrioles (Fig. 3D, G, H). Two centrioles, at right angles (Fig. 3G) are each of normal length (Fig. 3H) and not elongate as in potamoids.

NUCLEUS. As in other brachyurans, the nuclear material is located in the lateral arms and in the cup-shaped structure around both the acrosome and its cytoplasmic sheath. C.1/3 of the length of the spermatozoon consists of the nuclear material which lies posterior to the acrosome (Figs 1, 2A). A nuclear envelope is not present between the chromatin and the periacrosomal cytoplasmic sheath, but some scattered vesicles (Fig. 3G) and components of the membranous structures possibly represent residues of the nuclear envelope.

The external, surface of the cell is bounded by a moderately dense membrane which may represent fused nuclear and plasma membranes, here termed the nuclear plasma membrane (Figs 1, 2A, B, 3A). The general chromatin consists of a diffuse network of electron dense filaments in a pale matrix as in other brachyurans. In longitudinal (Fig. 2A) and transverse sections (Fig. 2B), the nucleus is deeply and irregularly incised by what are presumed to be the bases of the nuclear arms but discrete nuclear arms have not been observed.

DISCUSSION

Varuna litterata and Cardisoma *carnifex* return to brackish or marine water to breed, and during larval growth, and therefore might be expected to differ in fertilization biology from *A. riparius*, which has no marine stages though, as a goneplacid, having extant cofamilial marine relatives. One or other of these species might also differ from freshwater potamoids which have neither marine stages nor contemporary cofamilial marine relatives. Sperm morphology might reflect different fertilization biology while any unusual similarities between the sperm of *Australocarcinus* and potamoids which differed from those of crabs with marine or estuarine stages might be related to the internal physiological environment of nonmarine crabs. However, such correlates, if they exist, are not apparent.

It is presumably coincidental that all 5 genera in Table 1 lack a recognizable acrosome ray zone as, although absence is an unusual feature for heterotremes (in the first 3 genera), absence is an ancestral feature (thoracotreme synapomorphy) in *Varuna* and *Cardisoma*. The acrosome ray zone is absent in all thoracotremes (a predominantly marine group), in which (in contrast with true freshwater crabs) freshwater or terrestrial species always have contemporary relatives in the sea. Absence of the acrosome ray zone in corystoids (pers. obs.), a marine group, as in thoracotremes, suggests that absence cannot simply be attributed to a freshwater existence. Further lack of correlation of absence of an acrosome ray zone with the mode of life is seen in *Varuna litterata*, lacking this zone and reproducing in estuarine and marine conditions whereas *A. riparius*, and the potamoids, also lacking it, reproduce in freshwater. It is difficult to be certain whether acrosome rays are present or absent, as in *Potamonautes perlatus* (Jamieson, 1993).

The convex ring at the posterior end of the inner acrosome zone in *A. riparius* is not seen in other freshwater crabs. It is similar to the xanthid ring, of the Xanthidae and Panopeidae, but homology is doubtful. Other xanthid features such as the accessory opercular ring and the opercular overhang are absent from the sperm of *A. riparius* and relationship with xanthoids cannot be supported spermatologically. In its pointed shape, the perforatorium resembles that of corystoids but there the operculum is perforate.

An opercular perforation in *Potamon*, *Potamonautes* (homoplasic with majids) and in *Cardisoma* (where it is an ancestral, synapomorphic, thoracotreme condition), but not in *Varuna*, or the wholly nonmarine *Australocarcinus*, again cannot be attributed to a nonmarine habitat.

The thickened ring is exceptionally well developed in *Australocarcinus*. Reduction of the thickened ring occurs in *Potamon* and *Potamonautes* and is extreme in grapsids (though moderately developed in *Varuna*) and in *Cardisoma*. Although reduction probably relates to

TABLE 1. Spermatozoal characters of Brachyura as in freshwater (*) and terrestrial crabs (#).

	Australo-carcinus riparius Goneplacidae (This study)	*Potamonautes perlatus* Potamidae (Jamieson, 1993)	*Potamon fluviatile* Potamidae Guinot et al. in press	*Varuna litterata Grapsidae	#Cardisoma carnifex Gecarcinidae
1.Acrosome length/width	0.9	0.9	0.8	0.8	0.9
2.Acrosome zonation	concentric	concentric	concentric	concentric	concentric
3. Operculum	imperforate	imperforate	perforate	imperforate but indented	perforate with apical button
4. Opercular projections into suboperculum	absent	absent	absent	absent	absent
5. Operculum-capsule continuity	discontinuous	discontinuous	discontinuous	discontinuous	discontinuous
6. Operculum thickness	thin	moderate	moderate but thicker	moderate	moderate
7. Opercular width	moderately wide	moderately wide	moderately wide	not wide	extremely wide
8. Periopercular rim	absent	well developed	weakly developed	absent	weak
9. Accessory opercular ring	absent	absent	absent	absent	
10. Subopercular protuberance	absent	absent	absent	absent	absent
11. True acrosome ray zone	absent	presence uncertain	absent	absent	absent
12. Outer acrosome zone	not ragged	not ragged	not ragged	not ragged	not ragged
13. Anterolateral pale zone	absent	absent	absent	absent	absent
14. Flangelike lower zone	absent	absent	absent	absent	absent
15. Xanthid ring	absent?	absent	absent	absent	modified elongate
16. Perforatorium	preequatorial	preequatorial	preequatorial	preequatorial	preequatorial
17. Head of perforations	noncapitate	noncapitate	noncapitate	noncapitate	noncapitate
18. Corrugations of perforatorial chamber	absent	absent	absent	absent	absent
19. Lateral arms	several	several	several	several	several
20. Lateral arms	nuclear only	nuclear only	nuclear only	nuclear only	nuclear only
21. Centrioles	not elongate	elongate	elongate	present	not seen
22. Posterior median process of nucleus	absent	absent	absent	absent	absent
23. Thickened ring	well developed	vestigial	vestigial	present (reduced)	absent
24. Concentric lamellae	absent	absent	absent	lateral vesicle	absent
25. Capsular chambers	absent	absent	absent	absent	absent
26. Capsular projections	absent	absent	absent	absent	absent
27. Capsular flange	absent	absent	absent	absent	absent
28. Spiral acrosome zone	absent	absent	absent	absent	absent
29. Opercular overhang	absent	absent	present?	absent?	present
30. Spermatophores	coenospermia	cleistospermia	cleistospermia	coenospermia	coenospermia

peculiarities of the acrosome reaction (Medina, 1992; Medina & Rodriguez, 1992) it is not a common feature of freshwater crabs.

A. riparius produces large eggs and is suspected to have maternal care but its spermatophores contain several to many spermatozoa, the coenospermial condition. This contrasts with the production of spermatophores with single spermatozoa, cleistospermia, in *Potamon* and *Potamonautes*. This contrast need not invalidate the hypothesis (Guinot et al., in press) that the cleistospermial condition is an adaptation to peculiar features of fertilization biology in potamoids and, particularly, to the large size and

small numbers of eggs, which correlates with their known lecithotrophic, direct development. It was considered possible that sperm from potamoid spermathecae are delivered singly to the eggs. Production of single-sperm spermatophores (cleistospermia) was conjectured to be a device preventing polyspermy in individuals in which wastage of the small numbers of large eggs (and incidentally of spermatozoa) has to be minimized. Possibly *A. riparius*, having marine relatives, is less evolved along the path of lecithotrophy than the potamoids, lacking marine cofamilials.

Sperm of *A. riparius* shows no clear affinity with those of other Heterotremata although confirming its inclusion in that group.

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NEW SPECIES AND RECORDS OF ASTIEAE (ARANEAE: SALTICIDAE) FROM AUSTRALIA AND PAPUA NEW GUINEA

JOANNA GARDZINSKA

Arasia eucalypti sp. nov. and *Helpis minitabunda* (Koch) are first records of each genus from Papua New Guinea. *Helpis gracilis* sp. nov. and *Tauala athertonensis* sp. nov. are described from NEQueensland. □ *Astieae, Arasia, Helpis, Tauala, Australia, Papua New Guinea.*

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Wanless (1988) listed 6 genera of Astieae comprising 32 species, to which Zabka (1995) added monotypic *Megaloastia mainae;* all are of Australian origin. Some genera (*Astia, Helpis, Arasia*) are associated with *Eucalyptus* forests, others (*Sondra, Jacksonoides, Tauala*) are rainforest dwellers. The genera are endemic to Australia except *Helpis* which extends to New Zealand. It is not surprising to find some in Papua New Guinea, an island with a common geological history with Australia, especially in its southern part with similar floristic characteristics (*Eucalyptus* savannah) to NE Australia (Zabka, 1990, 1991, 1993).

MATERIAL AND METHODS

Material from PNG is deposited in the Queensland Museum, Brisbane (QM). Comparative material was borrowed from the Australian Museum, Sydney (AMS). Measurements are in millimetres. The drawings were made using a grid system. Dissected epigynes were digested in lactic acid. Abbreviations used are: AEW=anterior eyes width, ag=accessory gland, AL=abdominal length, CH=cephalothorax height, CL=cephalothorax length, co=copulatory opening, CW=cephalothorax width, e=embolus, EFL=eye field length, fd=fertilisation duct, id=insemination duct, mk=membranous keel, PEW=posterior eyes width, s=spermatheca, sr=seminal reservoir, ta=retrolateral tibial apophysis, tg=tegulum, tl=tegular lobe.

Order ARANEAE
Family SALTICIDAE
Tribe ASTIEAE
Arasia Simon, 1901

Astia Koch, 1880: 1158. (part)

Arasia Simon, 1901: 432, 436-438; Roewer, 1954: 968; Bonnet, 1955: 632; Brignoli, 1983: 626; Wanless, 1988: 81-84, 115-119; Davies & Zabka, 1989: 206, 210.

TYPE SPECIES. *Astia mollicoma* Koch, 1880, by original designation.

Arasia eucalypti sp. nov.
(Figs 1A-E, 2A-D)

MATERIAL EXAMINED. PNG: HOLOTYPE, QMS28896, ♂, National Capital District, Waigani, university campus, under *Eucalyptus* bark, 15.07.1988, D. J. Court, M. Zabka. PARATYPES, QMS28897, ♀, same data except 28.06.1988; QMS28898, 5 ♀, 2 ♂; QMS30725 ♀; QMS30726 ♀, 2 juveniles, same data except 25.06.88-14.09.88; QMS28899 ♀, Central Province, Sinumu Dam., 1.05.88, D.J. Court. QMS30723, ♀, ♂, 2 juveniles, Port Moresby, 25.06.88, D.J. Court, M. Zabka; QMS30724, ♀, ♂, Boroko, 14.09.86, D.J. Court.

DESCRIPTION. Compared to *A. mollicoma* (Fig. 1F), larger, body lighter coloured (Figs 1A, 2A). Tegulum of the palpal organ more robust, seminal reservoir curved, membranous keel accompanying embolus not distinctive (Fig. 1D,E,G,H). Distal part of the insemination ducts in epigynes shorter and wider apart (Fig. 2D,E).

MALE. Cephalothorax (Fig. 1A,B) wide and flat, orange beige with narrow darker margin, covered with scattered stiff brown hairs and white fine marginal hairs. Eyes surroundings black; light guanine spots in the centre of the eye field; eyes fringed by white hairs. Abdomen (Fig. 1A) pale greyish, with pattern of darker markings and white guanine spots, with scattered white and brown hairs. Spinnerets pale grey. Clypeus orange beige with numerous white hairs. Chelicerae of similar colour, plurident, with 3 promarginal and 4 retromarginal teeth (Fig. 1C).
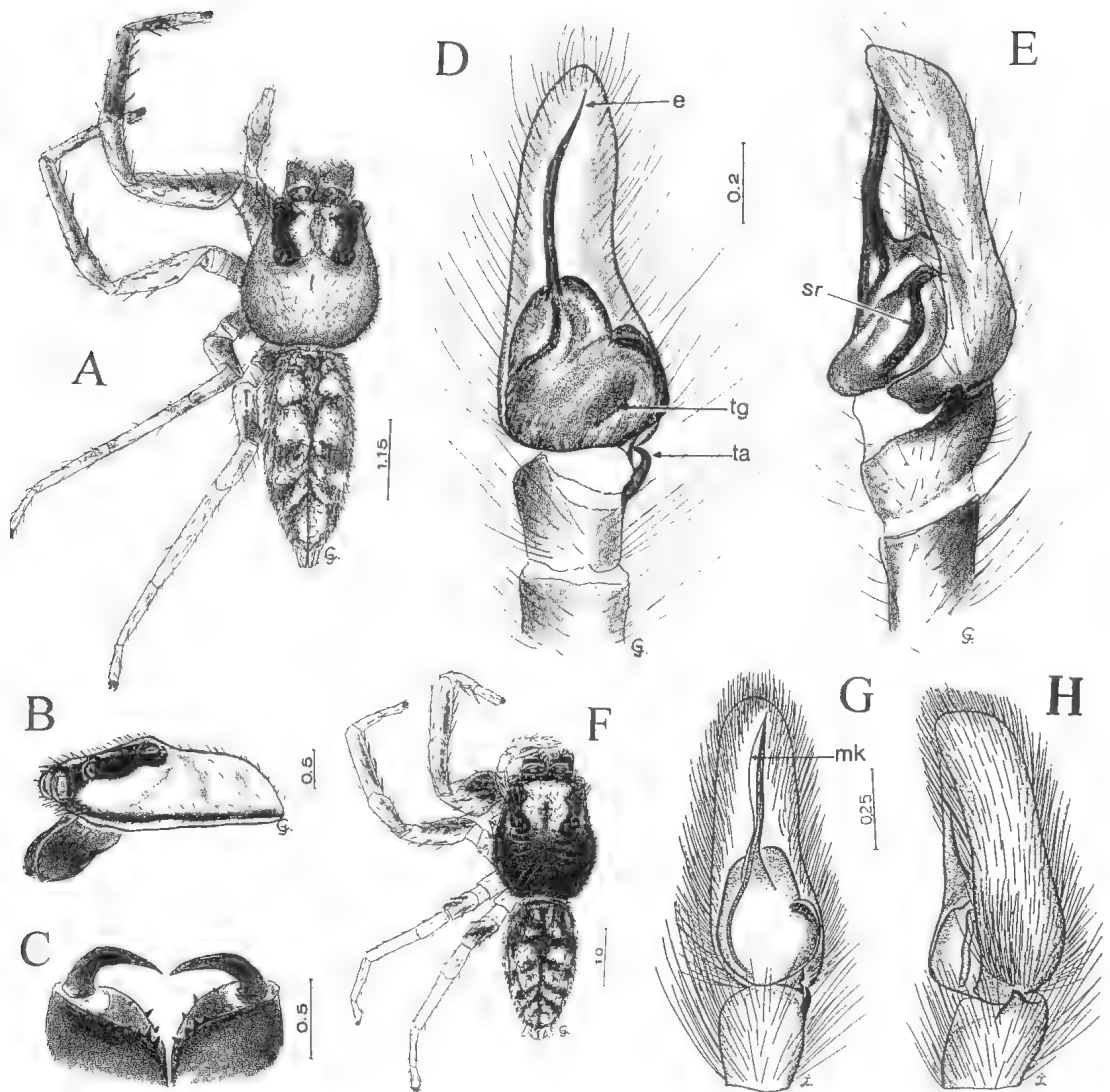
FIG. 1. A-E, *Arasia eucalypti* sp. nov., ♂. A, dorsal view. B, cephalothorax, lateral view. C, cheliceral dentition. D,E, palpal organ, ventral and retrolateral views. F-H, *Arasia mollicoma* (Koch, 1880), ♂. F, dorsal view. G,H, pedipalp in ventral and retrolateral views. (G,H from Davies & Zabka, 1989).

Maxillae and labium orange with lighter tips. Sternum pale yellow with darker margins. Venter yellow-grey. Legs yellowish-orange or pale yellow, anteriors darker, clothed in white and ambery hairs, spines moderately strong; tibia I with 6 prolateral and 6 retrolateral spines, metatarsus I with 3 prolateral and 3 retrolateral spines. Pedipalps yellow with long white and ambery hairs, their structure shown in Fig. 1D,E.

Dimensions. CL 2.70, CW 2.50, CH 0.80, EFL 1.10, AEW 1.60, PEW 1.40, AL 3.90.

FEMALE. Cephalothorax (Fig. 2A) similar in colour and shape to that in the ♂, however, abdomen little darker. Chelicerae robust with 2 or 3 promarginal and 5 retromarginal teeth (Fig. 2B). Legs yellow-orange, darker on tarsi and metatarsi; tibia I with 5 prolateral and 5 or 6 retrolateral spines, metatarsus I with 3 or 4 prolateral and 4 retrolateral spines. Palps yellow with darker tips, clothed in long whitish hairs. Epigyne (Fig. 2C,D) is similar to that in *A. mollicoma* (see arrows on Fig. 2E), except for different course of
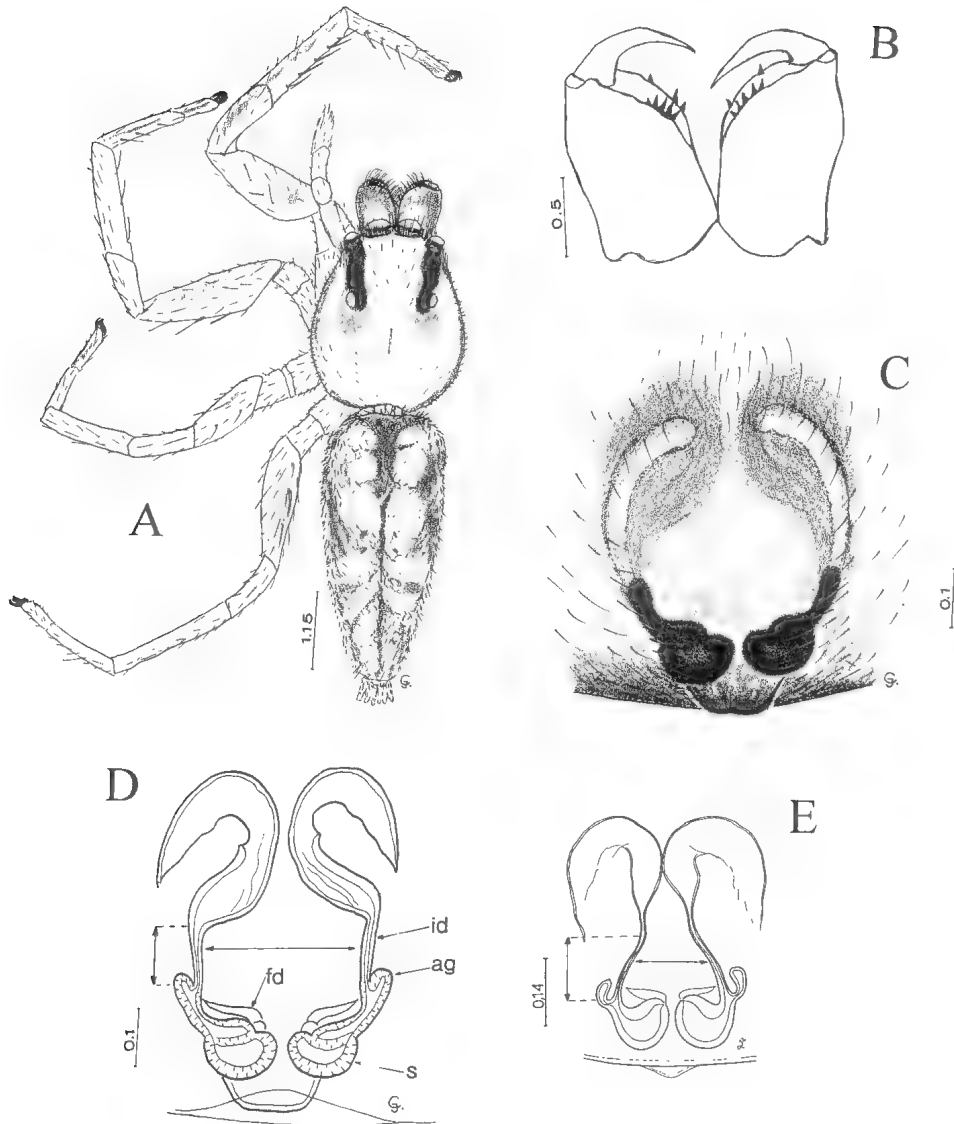
FIG. 2. A-D, *Arasia eucalypti* sp. nov., ♀. A, dorsal view. B, cheliceral teeth. C, epigyne. D, internal structures. E, *Arasia mollicoma*, internal genitalia (E from Davies & Zabka, 1989).

insemination ducts (Proszynski, 1984, 1987; Davies & Zabka, 1989).

Dimensions. CL 3.60, CW 3.30, CH 1.30, EFL 1.40, AEW 2.00, PEW 1.90, AL 6.00.

DISTRIBUTION. Southern PNG, on *Eucalyptus* tree trunks.

Helpis Simon, 1901

Astia Koch, 1880: 1160.(part)

Helpis Simon, 1901: 432, 436-438; Waterhouse, 1912: 125; Neave, 1939:600; Roewer, 1954: 969; Bonnet, 1957: 2150; Brignoli, 1983: 627; Wanless, 1988: 81-84, 94-102; Davies & Zabka, 1989: 206, 212.

TYPE SPECIES. *Astia minitabunda* Koch, by original designation.

Helpis minitabunda (Koch, 1880)
(Figs 3,4,5F)
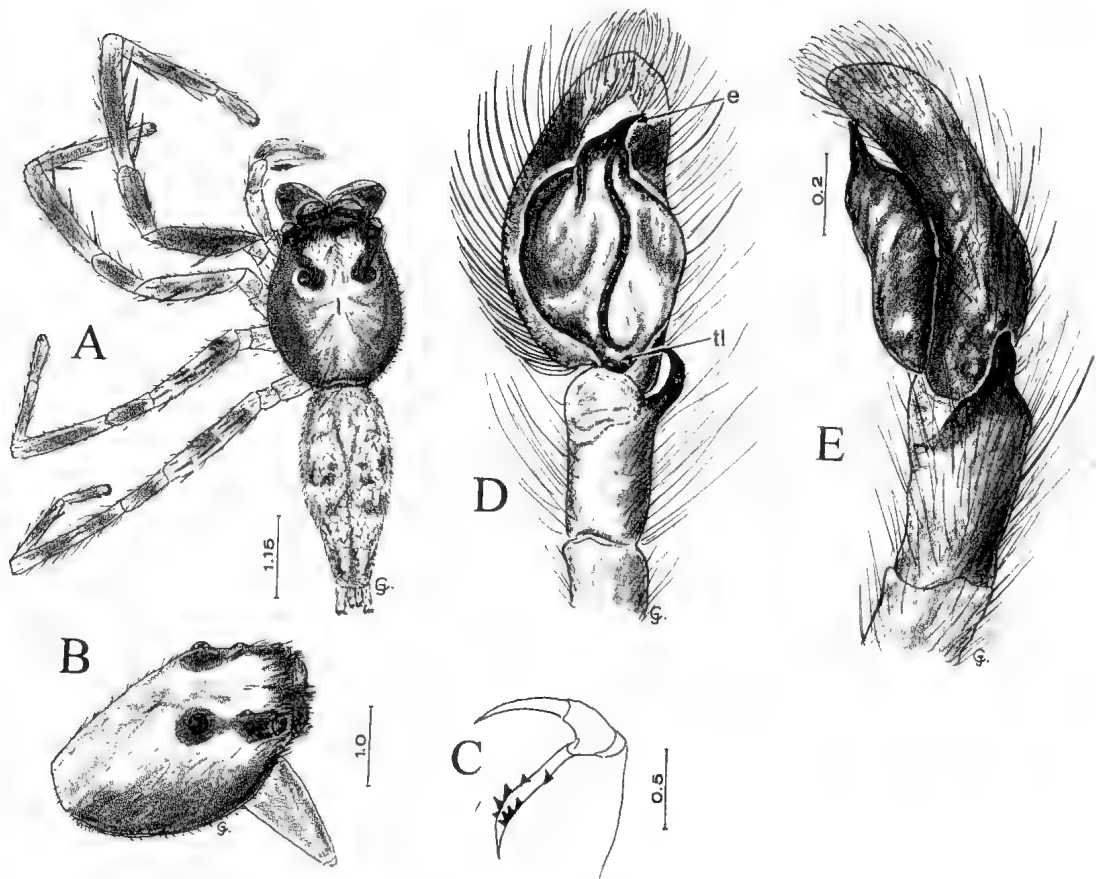
Astia minitabunda Koch, 1880: 1160.

FIG. 3. *Helpis minitabunda* (Koch, 1880), ♂. A, dorsal view. B, cephalothorax, lateral view. C, cheliceral teeth. D,E, pedipalp, ventral and retrolateral views.

Helpis minitabunda Simon, 1901: 431, 432, 436, 438; Rainbow, 1911: 280; Roewer, 1954: 969; Bonnet, 1957: 2151; Proszynski, 1971: 417; Wanless, 1988: 94-98; Davies & Zabka, 1989: 206, 212.

MATERIAL EXAMINED. PNG: QMS28900, 30728, ♂, ♀, Mt. Hagen, Hagen Park Hotel, under *Eucalyptus* bark, 4.07.1986, D.J. Court; QMS28901, ♂, Calanthe, Goroke, Norman Cruttwell's residence, 11.04.87, D.J. Court.

DESCRIPTION. Male. Cephalothorax (Fig. 3A,B) moderately low, pale brown-orange, darker marginally with orange guanine spots in the centre of eye field and scattered whitish and pale brown hairs. Surroundings of eyes black with fine white hairs. Abdomen (Fig. 3A) grey with pattern of white guanine spots and grey-brown markings. Spinnerets grey. Clypeus,

chelicerae (Fig. 3C) and maxillae and labium orange-brown. Sternum pale orange-brown with darker margins. Venter light grey with light spots. First legs orange with brown markings on femora, tibiae and patellae; other legs paler; tibia I with 3 prolateral and 3 retrolateral spines, metatarsus with 2 prolateral and 2 retrolateral ones. Palpal organ (Figs 3D,E).

Dimensions. CL 2.70, CW 2.10, CH 1.40, EFL 1.40, AEW 1.80, PEW 1.60, AL 3.70.

FEMALE. Cephalothorax (Fig. 4A) yellow-brown, paler in the centre; eye region with yellow guanine spots. Surroundings of lateral eyes I, II, and III black with white hairs. Abdomen pale grey with brown and white spots. Clypeus orange brown with rows of white hairs. Chelicerae of similar colour with 5 promarginal and 6 retromar-
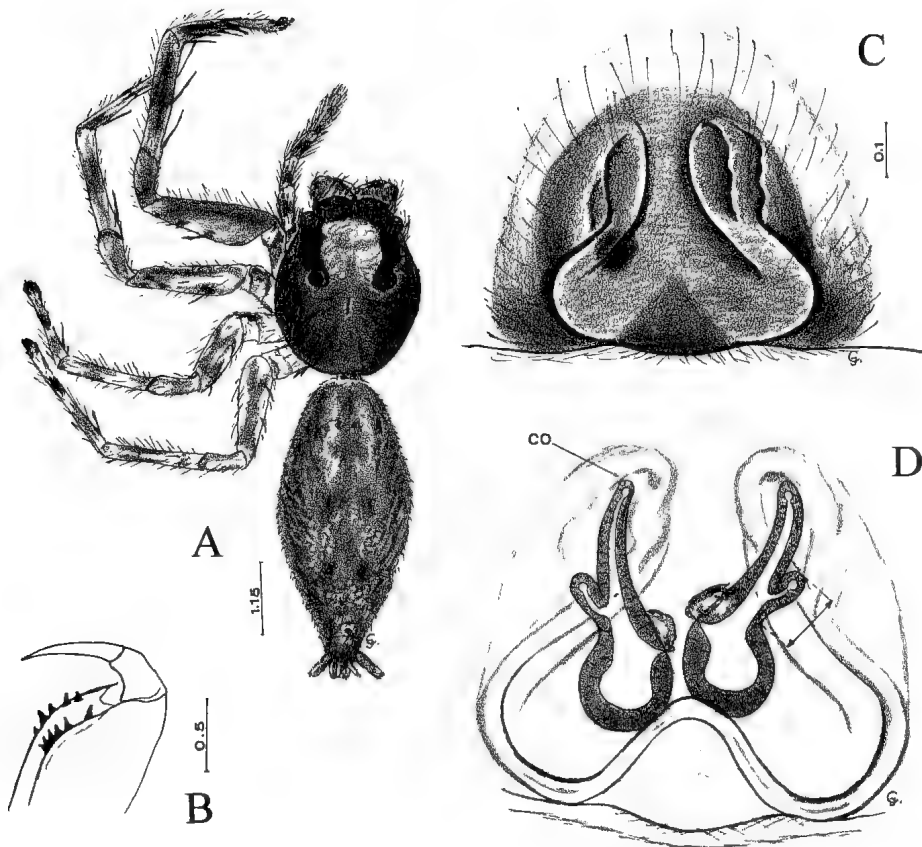
FIG. 4. *Helpis minitabunda* (Koch, 1880), ♀. A, dorsal view. B, cheliceral teeth. C, epigyne. D, internal structures.

ginal teeth (Fig. 4B). Maxillae and labium as in the ♂. Sternum orange-brown. Venter light grey. Legs similar in colour and spination to those in the ♂. Pedipalps generally yellow, darker distally, clothed in white hairs. Epigyne (Fig. 4C,D).

Dimensions. CL 3.80, CW 3.30, CH 1.50, EFL 1.50, AEW 2.20, PEW 2.00, AL 7.20.

COMPARISON. *H. minitabunda* differs from other species by the shape of embolus and tegular lobe in the ♂ palpal organ (Figs 3D,E, 5D,E, G). Accessory glands of the epigyne more distant from the spermathecae (Figs 4D, 6D,E).

DISTRIBUTION. NSW, QLD, TAS, NZ, PNG.

Helpis gracilis sp. nov.
(Figs 5A-E, 6A-D)

MATERIAL EXAMINED. Holotype: ♂, New South Wales, Morton National Park, SW Nowra, Sally Creek Valley, under bark of snow gums, 23.04.1988, M. Zabka. Allotype: ♀, same data. Paratype ♀, same data. All AMS.

DIAGNOSIS. Shape of embolus and tegular lobe distinctive within the genus (Fig. 5D-G). In comparison to *H. minitabunda* the accessory glands more distant from the spermathecae (Figs 4D,6D).

MALE. Cephalothorax (Fig. 5A,B) chestnut-brown with paler median stripe, eye field dark orange. Surroundings of eyes black, covered with brown hairs. Abdomen (Fig. 5A) pale grey, darker laterally, covered with brown hairs. Spinnerets grey. Clypeus orange-brown, fringed by white hairs. Chelicerae relatively long, pale brown, with 5 promarginal and 6 retromarginal teeth (Fig. 5C). Maxillae and labium brown with paler tips, clothed in brown hairs. Sternum orange with narrow darker margins. Venter dark grey. Legs: anteriors orange-brown with brown mark-
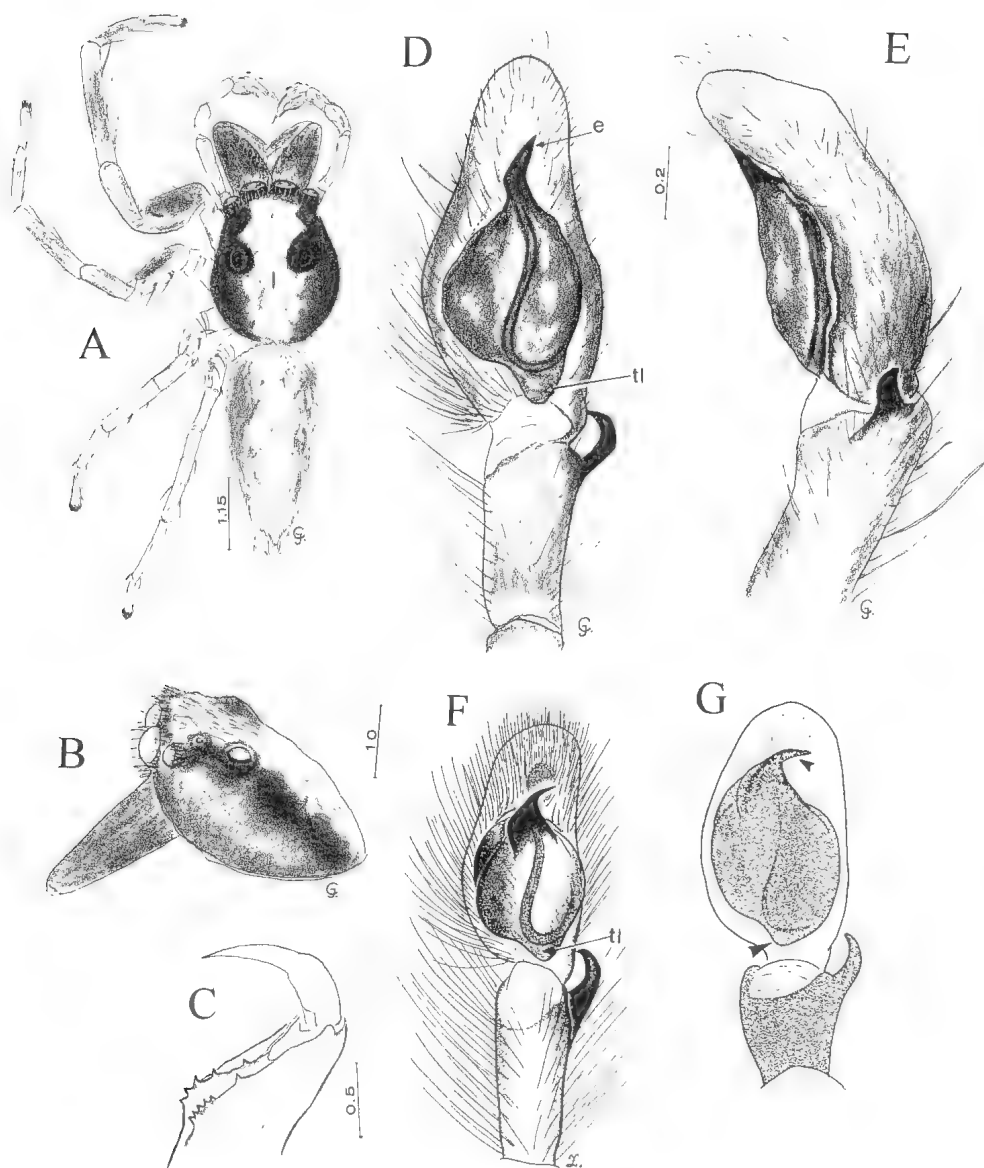
FIG. 5. A-E, *Helpis gracilis* sp. nov., ♂. A, dorsal view. B, cephalothorax, lateral view. C, cheliceral teeth. D,E, pedipalp, ventral and retrolateral views. F, *Helpis minitabunda* (Koch, 1880), pedipalp, ventral view. G, *Helpis occidentalis* (Simon, 1901), pedipalp, ventral view. (F from Davies & Zabka, 1989; G from Wanless, 1988).

ings, especially around the spines, others yellow with brown markings; tibia I with 3 prolateral and 3 retrolateral spines, metatarsus I with 2 prolateral and 2 retrolateral ones. Pedipalps brown-beige with dense, rather long hairs on basal segments (Fig. 5D,E).

Dimensions. CL 3.10, CW 2.75, CH 2.30, EFL 1.40, AEW 2.15, PEW 1.85, AL 4.50.

Female. Cephalothorax (Fig. 6A) orange-beige-brown clothed in short white and brown hairs, with orange spots on the eye field. Surroundings of eyes black. Abdomen pale yellow-grey with pattern of darker spots, covered with brown hairs. Spinnerets pale yellow-grey. Clypeus pale brown with white long hairs. Chelicerae of similar colour, with 4 teeth on
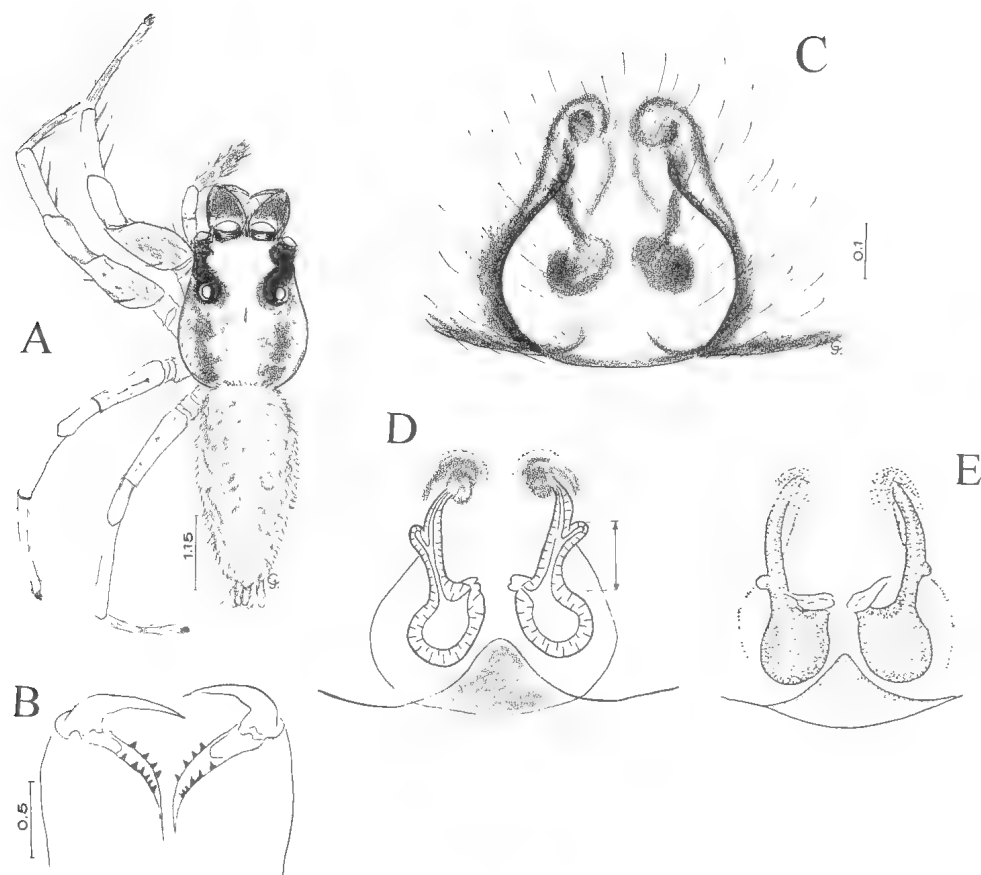
FIG. 6.A-D, *Helpis gracilis* sp. nov., ♀. A, dorsal view. B, cheliceral teeth. C, epigyne. D, internal structures. E, *Helpis occidentalis* (Simon, 1901), internal genitalia.

promargin and 6 on retromargin (Fig. 6B). Maxillae and labium pale brown with pale yellow tips. Sternum light yellow with brown margins. Venter pale yellow-grey, centrally darker. Legs: first pair pale brown-orange with some darker spots, others yellow with brown markings; spination of leg I as in the ♂. Pedipalps yellow, clothed in white hairs. Epigyne (Fig. 6C,D) very similar to *H. occidentalis* (Fig. 6E).

Dimensions. CL 3.40, CW 2.70, CH 1.60, EFL 1.50, AEW 2.20, PEW 1.95, AL 4.65.

DISTRIBUTION. Morton National Park, New South Wales.

Tauala Wanless, 1988

Tauala Wanless, 1988:81-84, 120-133; Davies & Zabka, 1989: 206, 209.

TYPE SPECIES. *Tauala lepidus* Wanless, 1988, by original designation.

Tauala athertonensis sp. nov.
(Fig. 7A-E)

MATERIAL EXAMINED. NE Queensland: Holotype QMS28903, ♀, near Atherton, dry Eucalyptus forest, on grass, 10.11.1987, M. Zabka.

DIAGNOSIS. Course of insemination ducts distinctive (Fig. 7E,F).

DESCRIPTION. Female. Cephalothorax (Fig. 7A,B) beige-brown with scattered short brown hairs and black surroundings of eyes. Abdomen pale grey with pattern of darker spots, clothed in ambery hairs. Spinnerets pale grey. Clypeus orange, edged in short hairs. Chelicerae dark orange with 3 teeth on promargin and 7 on retromargin (Fig. 7C). Maxillae orange-brown
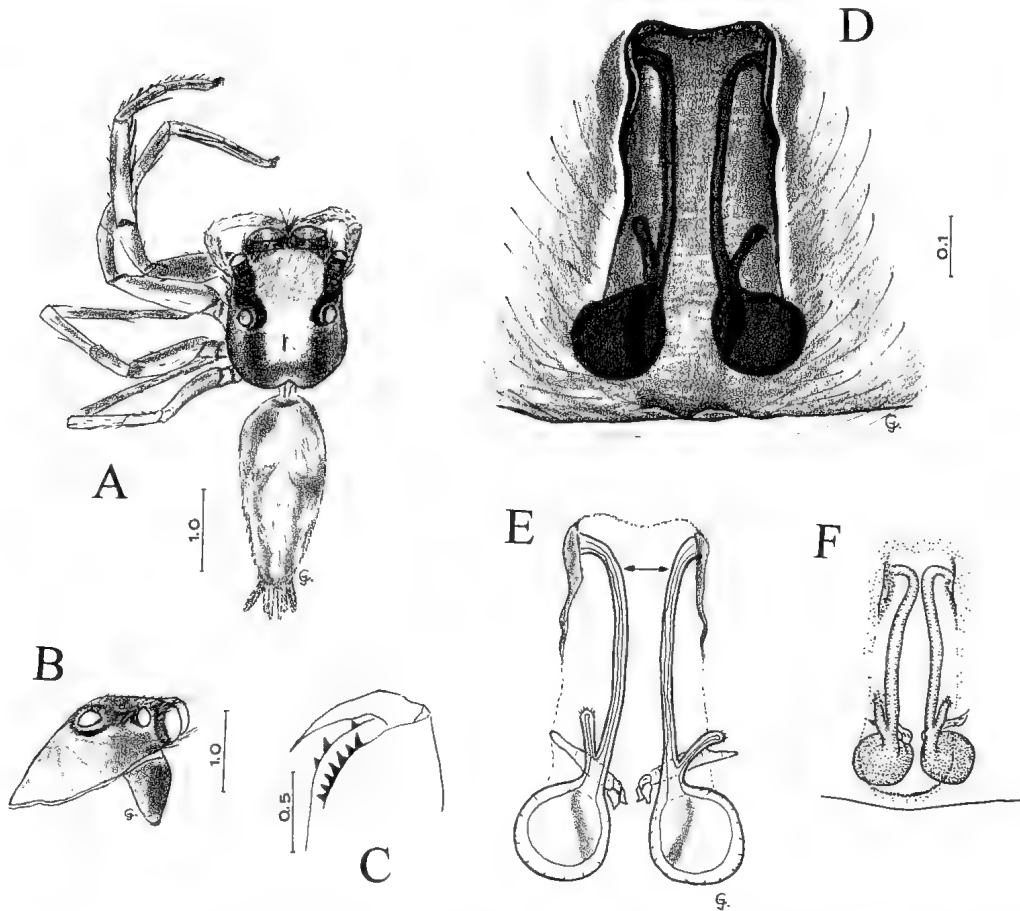
FIG. 7. A-E, *Tauala athertonensis* sp. nov., ♀. A, dorsal view. B, cephalothorax, lateral view. C, cheliceral teeth. D, epigyne. E, internal structures. F, *Tauala alveolatus* (Wanless, 1988), internal genitalia.

with paler inner margins, labium similar, with paler tips. Sternum yellow with darker margins. Legs yellow with brown markings on femora, tibiae and patellae; tarsi and metatarsi darker; tibia I with 4 prolateral and 3 retrolateral spines, metatarsus I with 2 prolateral and 2 retrolateral ones. Pedipalps pale yellow. Epigyne (Fig. 7D,E) with long, narrow insemination ducts, oval spermathecae accompanied by the accessory glands. Diagnostic characters marked with arrows.

Dimensions. CL 1.90, CW 1.50, CH 0.90, EFL

0.90, AEW 1.50, PEW 1.20, AL 2.50.

DISTRIBUTION. Near Atherton, NEQ.

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REPRODUCTIVE CHARACTERISTICS OF FEMALE FROGS FROM MESIC HABITATS IN QUEENSLAND. *Memoirs of the Queensland Museum 39(2): 306. 1996:-* Fecundity has important implications for the life history strategies and population dynamics of all animals, yet few data have been published on the fecundity of Australian frogs (Tyler 1989). Fecundity is herein defined in the strict sense of the word: 'the number of eggs produced by an individual' (Lawrence, 1989). The primary objective of this paper is to present new information on the reproductive characteristics of mesic frogs from eastern Queensland, some of which are now missing or their populations have declined (Ingram & McDonald, 1993; Richards et al., 1993; Hero, 1996). This paper is a supplement to the existing papers relating to fecundity of Australian frogs (reviewed by Tyler, 1989). We present egg counts and mean egg sizes (10 eggs measured / female) from clutches either dissected from museum specimens or layed in captivity. In museum specimens, half of the gonad was removed and the number counted doubled to give the total. Female body size is also provided because it may be an important determinant of fecundity. Specimens were dissected at the Queensland Museum in March 1996 and the museum registration numbers are provided where available.

The results are presented in Table 1. The amphibians exhibit a wide variety of egg numbers and egg diameters. A cursory examination of the data suggests a positive association between body size and egg numbers, however, there is no obvious phylogenetic influence. A thorough examination of these relationships, using a complete data set, is currently in progress.

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Jean-Marc Hero & Sheree Fickling, Wet Tropics Management Authority; Cooperative Research Centre for Tropical Rainforest Ecology and Management; Zoology Department James Cook University, Townsville, Queensland 4811; 6 May 1996

Table 1: Reproductive characteristics of female frogs from mesic habitats in Qld. Mean egg size is from a sample of 10 eggs / female (* indicates n=5 eggs). Measurements in mm. MED=Mean egg diameter

SPECIES	NO. EGGS	M.E.D.	♀ SVL	SOURCE (QMJ)
Hylidae				
Litoria bicolor	220	0.7*	22.6	19502
"	180	-	25.4	38378
L. fallax	574	-	29.1	pers. obs
L. infrafrenata	3364	1.2	96.2	51769
L. lesueuri	1612	1.0	51.05	61731
"	2240	1.5	64.15	61730
L. lorica	<150			36092
L. nannotis	216	1.98	55.5	41298
"	136	2.93	51.75	41301
"	160	-	51.05	30901
L. nyakalensis	86	2.5	32.9	55596
"	90	1.9	37.35	55592
L. revelata	787	-	41.6	pers. obs.
L. rheocola	63	2.6	37.1	32105
"	46	2.4	35.0	25153
L. xanthomera	1598	1.5	54.1	43160
"	1454	1.4	54.2	36006
Myobatrachidae				
Adelotus brevis	216		33.75	28280
"	214	1.5*	35.35	27774
Mixophyes fasciolata	904	2.5	82.6	29256
M. iteratus	4184	1.6	108.4	22951
M. schevilli	422	2.5	84.6	43855
"	538	2.46	88.45	32136
"	318	2.9	79.1	48229
Ranidae				
Rana daemeli	2372	1.4	84.0	26211

A NEW GENUS AND SPECIES OF ANT-ASSOCIATED COCCID (HEMIPTERA: COCCIDAE: MYZOLECANIINAE) FROM *CANTHIUM* LAM. (RUBIACEAE)

PENNY J. GULLAN AND AIMORN C. STEWART

The adult female and first-instar nymph of *Torarchus endocanthium* gen. et sp. nov. (Hemiptera: Coccidae: Myzolecaniinae) from Queensland, is described. This coccid is known only from inside hollow, swollen stems (ant domatia) of plants of the genus *Canthium* Lam. (Rubiaceae), where it lives as a trophobiont in the nests of ants of a *Podomyrma* species (Formicidae: Myrmicinae). The first-instar nymph has typical coccid features, but the adult female is unusual, being distinguished within the Coccidae by its multilocular disc-pores and microducts resembling bilocular pores on the dorsum, and rounded, projecting anal plates on the anterior edge of a setose bulge. ☐ *Coccidae, Formicidae, Rubiaceae, ant-plant association.*

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A new ant-plant association (Monteith, 1989, 1990) from marginal rainforest areas of coastal to central Queensland involves trees of the *Canthium odoratum–C. buxifolium* complex (Rubiaceae) and ants of an undescribed *Podomyrma* species (Formicidae: Myrmicinae). The ant colonies occur within specialised swellings in the living stems (ant domatia) (Fig. 1), which the ants hollow out by perforating the wall and removing the pith. The ants never occur away from their host trees; likewise, the trees are rarely found without these ants. Monteith and co-worker Paul Flower established that the ants obtained their nutrition largely from scale insects, also called coccoids (Hemiptera: Coccoidea), living within the ant domatia (Fig. 1). The feeding stylets of these coccoids presumably tap the phloem of the host plant and the coccoids' excreta, called honeydew, is consumed by the ants. It is not known whether the ants ever eat the coccoids.

These coccoids of *Canthium* belong to two families - the Pseudococcidae (mealybugs) and the Coccidae (soft scale insects or coccids). The mealybugs are *Pseudococcus longispinus* (Targioni Tozzetti) and two undescribed, closely related species, probably belonging to *Crisicoccus* Ferris or *Paracoccus* Ezzat & McConnell. The undescribed mealybug species might be specific to the *Podomyrma-Canthium* association although they belong to a group with no known association with ants, whereas *P. longispinus* is cosmopolitan, polyphagous, and one of the most pestiferous mealybugs in Australia (Williams, 1985; Williams & Watson, 1988). The soft scale

insects belong to an undescribed species of Coccidae with unusual morphology, suggestive of an obligate relationship with the ants. Individual adult coccids have their convex venter closely fitted into pits gnawed by the ants into the inner surface of the domatium. Their dorsum is ridged and covered in setae, and their anal area appears modifed to facilitate honeydew removal by ants. The eversible anal tube is strongly developed and surrounded by a pair of rounded, dorsally projecting anal plates so that the whole complex forms a prominent mound. These coccids have been collected only from ant chambers inside the stems of *Canthium odoratum* (Forster f.) Seemann and may be dependent on this ant-plant association,
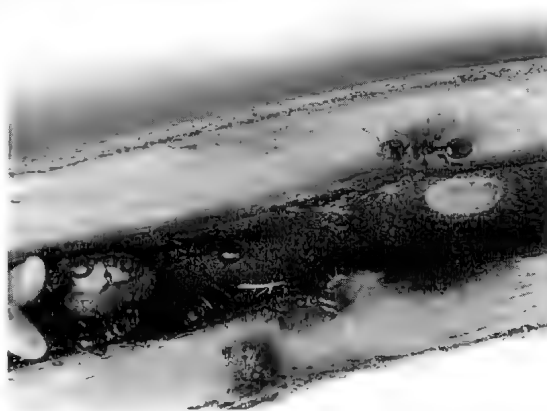

FIG. 1. Sectioned hollow stem of *Canthium odoratum* showing ant workers and larvae (*Podomyrma* sp.) on the right and an adult female of *Torarchus endocanthium* on the left.

although they are not found in all plants that house colonies of *Podomyrma*. To date, the coccids have been collected only in SEQ coastal areas and one more inland site, although the ant-plant association is more widespread. Where coccids are absent, the domatia house mealybugs, often in large numbers and sometimes of more than one of the above species. In older stems, the mealybugs mostly reside in the ant-gnawed pits but may feed anywhere within younger stems. Sometimes domatia house both coccids and mealybugs.

Scale insects have been reported previously from inside the swollen stems of Rubiaceae in Africa (Bequaert, 1922). Those collected with *Crematogaster laurenti* Forel (Formicidae: Myrmicinae) inside hollow stems of *Psydrax subcordata* (DC.) Bridson (formerly *Plectronia laurentii* De Wild.) from Zaire were described as *Hemilecanium recurvatum* by Newstead (1910). This species is morphologically very different from the coccid from *Canthium* in Queensland (types of *H. recurvatum* (BMNH) have been examined) and belongs to a different subfamily. In Australia, no coccids or mealybugs have been reported previously from *Canthium*, although species of *Myzolecanium* Beccari (formerly placed in *Cryptostigma* Ferris; see Qin and Gullan, 1989; Gullan, Buckley & Ward, 1993) and *Alecanopsis* Cockerell (Green, 1924) have been described from ant nests in living hollow stems of other plants. *Alecanopsis* and *Myzolecanium* belong to the same subfamily as the coccids from *Canthium* but are very different morphologically.

This paper describes the coccid from *Canthium*. Features of the adult female place it in the Myzolecaniinae Hodgson, 1994. It is atypical for a coccid in having both multilocular disc-pores and microducts resembling bilocular pores on the dorsum, and in having anal plates which are very rounded and dorsally projecting, together forming a mound when the anal tube is retracted (i.e. when the plates are closed). In most other coccids, each anal plate is triangular, posteriorly directed and lies level with the dorsal surface when the anus is retracted. Furthermore, in this new species the anal area is located on the anterior edge of a prominent bulge which bears very long setae in a central depression. The first-instar nymph is more typically coccid-like (Miller, 1991), except that each stigmatic cleft has only a single stout stigmatic seta. It differs in this regard from known first-instar nymphs of other Myzolecaniinae (Ray & Williams, 1980; Qin & Gullan, 1989; Sheffer & Williams, 1990).

METHODS AND ABBREVIATIONS

Terminology follows Hodgson (1994, 1995). To prepare adult females and nymphs as microscope slide-mounts, body contents were cleared in cold 10% w/v potassium hydroxide (KOH) solution overnight, the cuticle was stained in acid fuchsin in acid alcohol, dehydrated in 3 changes of absolute ethanol and 1 of absolute propan-2-ol and then placed in 3 changes of xylene prior to mounting in Canada balsam. Scale insects were prepared for scanning electron microscopy (SEM) after preservation and storage in 80% ethanol. Each specimen was dehydrated in a graded ethanol series, dewaxed in xylene, rehydrated through a graded ethanol series into distilled water, post-fixed in 1% aqueous osmium tetroxide, washed in distilled water and sonicated briefly to remove any black precipitate, critical point dried, glued onto a metal stub with nail varnish and coated with gold palladium under vacuum. Specimens were then examined and photographed using a Cambridge S360 SEM.

Abbreviations used for the depositories are: ANIC, Australian National Insect Collection, CSIRO, Canberra; BMNH, The Natural History Museum, London; QM, Queensland Museum, Brisbane. Each listed scale insect is mounted on a separate microscope slide, unless otherwise specified.

SYSTEMATICS
Torarchus gen. nov.

TYPE SPECIES. *Torarchus endocanthium* sp. nov.

DIAGNOSIS. Adult female with rounded-elongate elevations on dorsum in a definite arrangement; dorsal cuticle with both multilocular disc-pores and microducts resembling bilocular pores; anal plates rounded and projecting, situated on anterior edge of raised area of cuticle. First-instar nymph of typical coccid form, but with single stout seta per stigmatic cleft. All stages living in hollow stems of host plant attended by ants.

DESCRIPTION. Features believed to be taxonomically significant at generic level are highlighted. The species description provides the best summary of this monotypic taxon.

Adult female broader than long, with a row of rounded-elongate elevations or ridges dorsally on each side of midline, these become less apparent after slide-mounting; setae flagellate, clustered
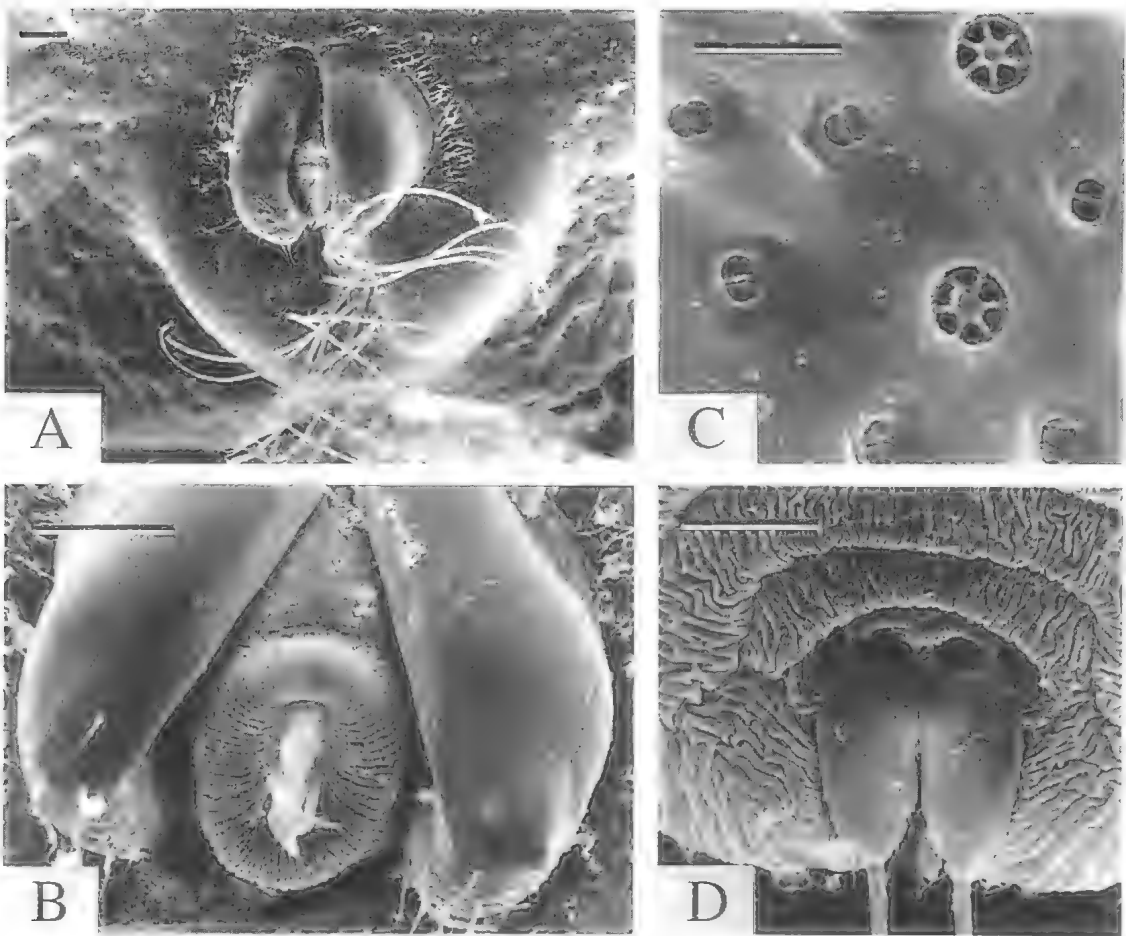
FIG. 2. SEMs of cuticular features of *Torarchus endocanthium*: A, anal area of adult ♀, showing rounded anal plates and long setae on raised area behind anus (scale 50 μm); B, enlargement of anal area of another adult ♀, showing anal plates and partially everted anus (scale 50 μm); C, multilocular disc-pores and openings of microducts on dorsolateral surface of adult ♀ (scale 10 μm); D, dorsal view of anal area of first-instar nymph, showing anal plates and rugose cuticle (scale 25 μm).

dorsally on ridges, in irregular double row marginally and sparsely scattered ventrally, but with a group of very long (1.5-2.5 times length of anal plates), robust setae posterior to anal plates on raised area; dorsal pores of 3 kinds: 1, disc-pores with 4-8 loculi, 2, microducts which resemble bilocular pores when viewed end-on in light microscope (Fig. 3h) and 3, simple pores; dorsal tubular ducts and dorsal tubercles absent; anal plates projecting and lobe-like with cluster of apical setae; spiracles much larger than legs; spiracular disc-pores present in bands between body margin and each spiracle, with 5 loculi; pregenital disc-pores with 5 or 6 loculi; ventral tubular ducts absent but small microducts scat-

tered ventrally; eyespots absent; legs and antennae reduced.

First-instar nymph oval; derm with rugose sculpturing; dorsum lacking setae, pores, ducts and tubercles; anal plates elongate triangular with rounded angles; margin with row of slender setae, each stigmatic cleft with single stout stigmatic seta; venter with few setae on head and thorax, short setae in 2 submarginal rows on abdomen, longer setae in 2 submedial longitudinal rows on abdomen; antennae 6-segmented; legs well developed, fore legs each with single digitule.

COMMENTS. This genus shares several features with others of the Myzolecaniinae; for ex-

ample, *Cyclolecanium* Morrison, *Megasaissetia* Cockerell, *Neolecanium* Parrott and *Pseudophilippia* Cockerell also possess some form of dorsal pore or microduct with a bilocular appearance and that of *N. imbricatum* (Cockerell) even has an inner duct (Hodgson, 1994) similar to that of *T. endocanthium*. The dorsal ridges of *T. endocanthium* are of similar shape but different number and arrangement from those of *Coccus tumuliferus* Morrison (Morrison 1921), which is not a true species of *Coccus* Linnaeus (Coccinae) but undoubtedly a member of the Myzolecaniinae. Furthermore, the anal plates of *C. tumuliferus* are of somewhat similar shape to those of *T. endocanthium* but with different arrangement and number of setae; however, the dorsal pores and setae and ventral ducts of *C. tumuliferus* are very different from those of *T. endocanthium*. The presence of multilocular disc-pores and microducts resembling bilocular pores on the dorsum of *Torarchus* easily distinguishes it from *Akermes* Cockerell, *Alecanopsis* and *Myzolecanium*, which are the other genera of the Myzolecaniinae found in Australia; furthermore, it differs from *Myzolecanium* in having very shallow stigmatic clefts and from *Akermes* and *Alecanopsis* in having no stigmatic setae. *Torarchus* keys out in Hodgson (1994, pp. 91-92) to the couplet containing *Akermes* and *Alecanopsis*, but does not fit the description of either.

ETYMOLOGY. Latin *torus*, round elevation or bulge, Greek *archos*, anus; refers to the shape of the plates surrounding the anus and location of the anal area on a cuticular bulge.

Torarchus endocanthium sp. nov.
(Figs 1-4)

MATERIAL EXAMINED. HOLOTYPE, QMT13986, adult ♀,Qld, Mt Crosby, off Crosby Rd & Bunya St., 27° 32'S, 152° 48'E, 9.iv.1989, P. Flower. PARATYPES adult ♀ ♀ only, QLD: 7 adult ♀ ♀, same data as holotype; 1 adult ♀, 2 slides of first-instar nymphs, Mt Crosby, 18.viii.1988, P. Flower; 1 adult ♀, 1 slide of first-instar nymphs, Mt Moffatt Nat. Park, Kenniff's Lookout, 24° 55'S, 147° 59'E, 13.xii.1987, G. Monteith, G. Thompson & D. Yeates; 7 adult ♀ ♀, 3 immature ♀ ♀, 6 slides of first-instar nymphs, Auburn Gorge, SW Mundubbera, 25° 43'S, 151° 03'E, late March 1989, G. Monteith; 3 adult ♀ ♀, Keysland, 20 km NW of Wondai, late March 1989, G. Monteith.
    Location of paratypes: 4 adult ♀ ♀ and 2 slides of first-instar nymphs in ANIC, 1 adult ♀ in BMNH, remainder in QM (QMT26022-26035).

DIAGNOSIS. As for genus.

DESCRIPTION. Adult ♀ (10 specimens measured). Live material. Body of young ♀ yellow, with sparse coating of white, powdery wax.

Mounted material. Body transversely oval, rounded on each side, 1.3-1.8 times wider than long, rather flattened but with elevated areas on dorsum; stigmatic clefts shallow; anal cleft fused. Length 1.5-2.6 mm, width 2.3-4.4 mm.

Dorsum. Derm membranous except for narrow crescent of sclerotisation around anterior margin of anal plates and light sclerotisation at margin in stigmatic cleft; with 7 radial ridges dorsally on each side of body, forming an elevated submedial area following curve of margin, with anteriormost and posteriormost ridges smallest; a rounded raised area lies posterior to anal plates (Fig. 2A) with central depression marking position of anal cleft. Dorsal setae flagellate, 15-100 μm long in submarginal areas and around anal plates, longer (70-150 μm) medially and clustered on ridges; a group of 13-26 very long (230-500 μm), robust setae posterior to anal plates on raised area. Dorsal pores of 3 kinds: 1, multilocular disc-pores 5.5-7.5 μm in diameter with 4-8 (mostly 6, Figs 2C, 3i) loculi, scattered in marginal and submarginal area; 2, microducts resembling bilocular pores (Figs 2C, 3h), 3-4 μm in greatest dimension, densely distributed over entire dorsum; 3, simple pores (Fig. 3f) 3-4 μm in diameter, scattered over dorsum. Preopercular pores absent. Dorsal tubular ducts absent. Dorsal tubercles absent. Anal plates lobe-like, rounded apically (Figs 2A, 2B, 3d), each 150-210 μm long, 110-150 μm wide when measured in natural position (distortion during mounting common); with 5-6 small setae apically on each plate. Anogenital fold with 2 pairs of setae in hypopygial position, a pair of larger setae at each corner of anterior margin and 1 pair laterally. Anal ring 58-68 μm in diameter, probably with 6 pairs of setae, 65-115 μm long, rather flattened (Fig. 3e), difficult to see when retracted inside anal tube (Fig. 2B).

Margin. Marginal setae flagellate (Fig. 3g), 25-150 μm long, in irregular double row around entire margin except absent in stigmatic clefts and posteriorly where fused anal cleft joins margin. Stigmatic clefts very shallow with small area of light sclerotisation; lacking stigmatic setae. Eyespots apparently absent.
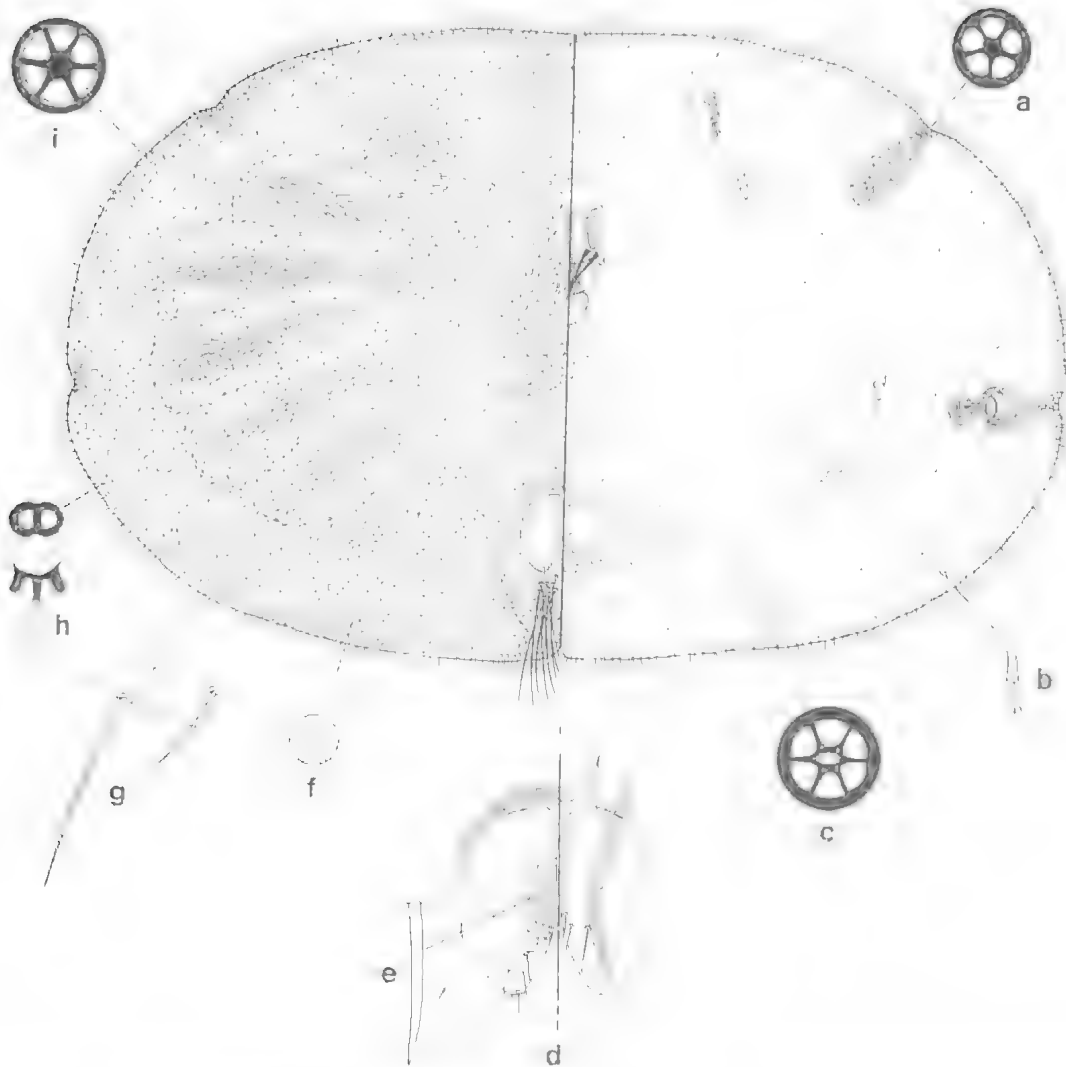
Venter. Derm membranous; only abdominal seg-

FIG. 3. Adult ♀ of *Torarchus endocanthium*. Enlargements: A, quinquelocular disc-pore from stigmatic furrow. B, ventral microduct. C, pregenital disc-pore with 6 loculi. D, anal lobes viewed dorsally (on left) with anal ring and anal ring setae indicated by dashed lines, and ventrally (on right) showing setae and supporting bar of ano-genital fold. E, anal ring seta. F, simple pore. G, marginal setae. H, lateral and end-on views of dorsal microduct. I, multilocular disc-pore.

mentation discernible. Ventral setae flagellate, 15-75 μm long, sparsely scattered. Pregenital disc-pores (Fig. 3c) 8-10 μm in diameter with 5-7 (mostly 5-6) loculi, distributed around vulva on posterior segments and in an irregular line reaching to metathoracic spiracle of each side. Stigmatic furrows each with quinquelocular disc-pores (Fig. 3a), 5-6 μm in diameter, in a band from margin to spiracle. No preantennal pores present. Ventral microducts (Fig. 3b) each with outer ductule 4-5 μm long and inner ductule with

conspicuous innermost end, each microduct appearing as a small slightly oval pore when viewed end-on, scattered throughout venter. Ventral tubular ducts absent. Spiracles well developed, with conspicuous muscle plate to each peritreme; anterior spiracle plus peritreme 150-200 μm long, 110-135 μm wide; posterior spiracle plus peritreme 150-200 μm long, 120-140 μm wide. Legs reduced, each 90-130 μm long, trochanter fused with femur, fusion of tibia and tarsus partial to complete; each claw small, without denticle;
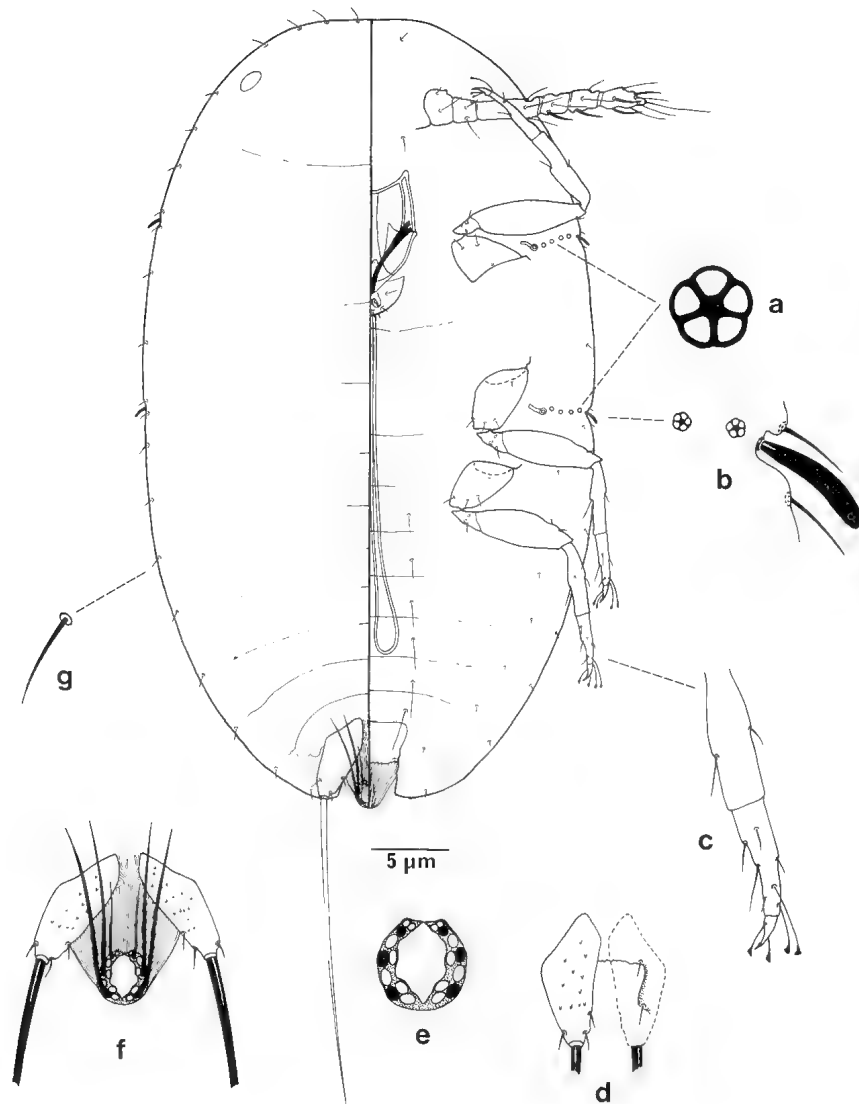
FIG. 4. First-instar nymph of *Torarchus endocanthium*, with anus everted. Enlargements: A, quinquelocular disc-pore from stigmatic furrows. B, stigmatic area with stigmatic seta in cleft, 2 marginal setae and quinquelocular disc-pores. C, apex of hind leg showing digitules. D, dorsal (on left) and ventral (on right) views of anal plates. E, anal ring with setal positions indicated by blackened spots; F, dorsal view of anal lobes and everted anal ring; G, marginal seta.

claw digitules longer than claw but shorter and broader than tarsal digitules; tarsal digitules 22-25 μm long. Antennae reduced, with 5-6 segments at most, segmentation often indistinct; total length 95-150 μm; with fleshy setae 13-25 μm long on apical segments and flagellate setae 15-65 μm long on all segments. Clypeolabral shield 350-390μm long, 270-320μm wide. Labium 1-segmented, 140-150 μm long, c.150 μm wide.

First-instar nymph (10 specimens measured). Mounted material. Body oval, 463-560 μm long, 270-315 μm wide. Derm membranous throughout but with rugose sculpturing dorsally and ventrally, most clearly visible in SEM (Fig. 2D). Segmentation not readily apparent (but obvious in whole nymphs under SEM).

Dorsum. Setae, pores, ducts and tubercles absent.

Anal plates (Fig. 4d) elongate triangular with rounded angles, 40-48 µm long, 15-24 µm wide; anterolateral margin 22-26 µm long, posterolateral margin 25-30 µm long; dorsal surface with scattered microspines. Each plate with 4 dorsal setae, 3 on apex of plate, 1 on mesal margin; median seta on apex robust, 190-225 µm long, about half length of body. Ano-genital fold with 1 pair of anterior margin setae and 1 pair of lateral margin setae. Anal ring (Fig. 4e) approximately circular, 18-22 µm in diameter, with about 14 irregularly shaped pores and 6 setae, 45-68 µm long, with 2 setae distinctly shorter and more slender than other 4 (Fig. 4f).

Margin. Marginal setae (Fig. 4g) 10-15 µm long, slender, tapering to a point, usually curved, pointing in posterior direction, distributed as follows: 8 around head between anterior stigmatic clefts, 4 between each pair of stigmatic clefts, and 18 on abdomen. Stigmatic clefts moderately developed (Fig. 4b), each with single stout stigmatic seta 10-16 µm long, bordered by 2 slender marginal setae, 1 anterior and 1 posterior to each stigmatic seta. Eyespots present just above level of antennal scape.

Venter. Ventral body setae slender, of 2 lengths: submarginal setae short, 2-5 µm long, in 2 longitudinal rows each of 7 on each side of abdomen (2 pairs of setae per segment), 1 seta between anterior and posterior stigmatic clefts and 1 pair at apex of head; submedial setae 20-45 µm long, in 2 longitudinal rows of 6 each on abdomen (1 pair per segment), setae longer posteriorly, and 1 pair between antennae. Spiracles plus peritremes 15-21 µm long, 6-10 µm wide. Stigmatic furrows each with quinquelocular disc-pores (Fig. 4a), 2-3 µm in diameter, in single row; anterior spiracular disc-pore bands each with 4-6 pores; posterior spiracular disc-pore bands each with 4-5 pores. Other pores and ducts absent. Legs well developed, 210-245 µm long, without tibiotarsal sclerotisation or free articulation; 1 or a few flagellate setae on each segment; 2 knobbed claw digitules (Fig. 4c) per leg; 2 knobbed tarsal digitules (Fig. 4c) per leg, except fore legs each with only 1 digitule; tarsal claw with small denticle. Antennae well developed, 6-segmented, 130-160µm long; segment III longest, 33-45 µm; 5 fleshy setae (1 on IV, 1 on V, 3 on VI), 13-25 µm long, and about 15 hair-like setae, 10-53 µm long. Mouthparts with clypeolabral shield 83-90 µm long, 63-77 µm wide; labium 1-segmented,

30-36 µm long, 45-50 µm wide, with 4 pairs of setae; stylets looped, total length 500-660 µm.

COMMENTS. The first-instar nymphs of most Coccidae possess 3 stout stigmatic setae per stigmatic cleft. The nymph of *T. endocanthium* has only one differentiated stigmatic seta per stigmatic cleft (presumably homologous with the median stigmatic seta of other coccids). The 2 slender setae that border each stigmatic seta in nymphs of *T. endocanthium* appear identical to the remainder of the marginal setae but may be homologous with the 2 stout lateral stigmatic setae that normally accompany the longer median stigmatic seta in other coccids.

ETYMOLOGY. Greek *endon*, within or inside, with the name of the host plant *Canthium*.

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THE ATLANTIC-MEDITERRANEAN BIVALVE, *CORBULA GIBBA* (OLIVI) (CORBULIDAE: MYOIDEA) IN PORT PHILLIP BAY, VICTORIA

JOHN M. HEALY AND KEVIN L. LAMPRELL

Established populations of the common European corbulid bivalve, *Corbula (Varicorbula) gibba* (Olivi, 1792) are recorded for the first time from Australia within Port Phillip Bay, Victoria. Aside from a tendency to exhibit pink radiating bands, the Victorian specimens are indistinguishable from typical French and British populations. The species appears to have been introduced to Australia sometime after the mid-1980's, as it was not recorded in benthic surveys of Port Phillip Bay up to 1972 or encountered by local collectors prior to 1983. Although we cannot identify the precise geographical origin of the Victorian population on morphological features, the recent plague-level outbreak of the polychaete *Sabella spallanzanii* in Port Phillip Bay suggests a Mediterranean origin. Presumably this species has been spread via release of ballast water. □ *Corbula gibba, Mollusca, Bivalvia, introduced species.*

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Accidental or in some cases deliberate introduction of foreign marine species, has, and continues to be a serious problem in ports throughout the world. While certain species may be transported as adults attached to ships' hulls, a number of species are apparently being conveyed as larval stages in ballast water (Carlton, 1985, 1987, 1989; Williams et al., 1988; Carlton et al., 1990). To survive such long voyages, these larvae are necessarily hardy and represent species common within their native habitat. The recent plague-proportion spread of the Mediterranean tubiculous polychaete *Sabellaria spallanzanii* throughout Port Phillip Bay – an event now threatening the viability of a major scallop fishery – has highlighted the importance of understanding changes occurring in local shallow water faunas around the Australian coastline. Within the Mollusca, accidentally introduced species of bivalves have in recent years posed a serious challenge to industry and/or the ecological health of marine and freshwater habitats. The fouling damage incurred by the spread of the European ''zebra mussel' *Dreissena polymorpha* throughout the lakes of the United States (Hebert et al., 1989; Topping, 1991) is one notable example of the serious ecological and potential economic impact of an introduced bivalve species.

In recent years authors have documented the sudden appearance of foreign bivalve species in Australian waters including the Japonic mytilids *Musculus imus* (Bartsch) and *Musculista sen-* *housia* (Benson) to Western Australia (Kendrick & Slack-Smith, 1982; Slack-Smith & Brearley, 1987), the Japonic ostreid *Crassostrea gigas* (evidently a deliberate introduction) and the New Zealand venerid *Paphia largilliertii*. During our studies of Australian Corbulidae (basket clams), our attention was drawn to an apparently unknown species from Port Phillip Bay by Mr. R. Burn of the Museum of Victoria. This corbulid had not been taken in two extensive benthic surveys of the bay between 1958 and 1972, nor had it been gathered by local collectors prior to 1983 (R. Burn pers comm.). Thus we suspected an introduced species. We could find no closely comparable Asian or American species. However, there was very close resemblance between the mystery Australian corbulid and the common Atlantic-Mediterranean *Corbula (Varicorbula) gibba* (Olivi, 1792). We illustrate and describe Australian specimens of *C. gibba* and compare them to Atlantic material adding a discussion on the implications of this introduction.

MATERIALS AND METHODS

Australian material (all Port Phillip Bay, Victoria): Hampton Beach - several specimens (coll. G. Macaulay). Mornington (20 miles from Hampton), from mud on the back of scallop trawlers docked on 3 Nov. 1991 (preserved in 10% formalin in sea water; coll. G. Macaulay) (K.Lamprell collection). Southern Port Phillip Survey 1986-1990 Marine Research Group of

Victoria (Museum of Victoria) - Lots NMVF 60444, 60541-60551 all dredged in 6-16m of water.

European material: France: 2 specimens from Bretagne (P. van Pel); England: alcohol-preserved specimens dredged off Shellness, Beer and Milford Haven (all England) (Natural History Museum, London). Ireland: alcohol-preserved specimens dredged off Dublin (Natural History Museum, London).

SYSTEMATICS
Superfamily MYOIDEA
Family CORBULIDAE
Corbula (Varicorbula) gibba Olivi,1792

Corbula nucleus Lamarck,1818.

DESCRIPTION. Shell to length of 13.5 mm, solid, posterior side longer than anterior; right valve much larger and encompassing the left valve marginally, with umbone extending beyond the margin of the left valve; both valves with a well defined postero-umbonal ridge. Sculpture: right valve with well developed, flat, moderately wide, concentric ridges; interstices narrow; left valve with fine, closely set, raised, concentric ridges crossed by several raised, radial ridges which extend from the umbones to the margins. Colour: white, with variable brown or reddish radial rays; internally white or deep purple; periostracum on right valve, thin, light brown, left valve light brown towards the umbones, thick, dark brown, concentric concentric layers marginally.

HABITAT. In sandy mud, obtained from scallop trawlers and by diver in littoral mud and sand.

DISTRIBUTION. Widely distributed throughout the Atlantic Ocean, Mediterranean Sea and extending into the Black Sea (Yonge, 1946; Tebble, 1966; Hrs-Brenko, 1981); Port Phillip Bay, Victoria.

COMPARISONS. We find no characters to separate the Port Phillip Bay specimens from Atlantic and Mediterranean *Corbula gibba*, other than a tendency to reach a smaller size (Fig. 1). Conceivably this could be an environmentally induced effect due to suboptimal nutrient levels or growth conditions. Commonly the Port Philip specimens showed pink-purple colouration on the inside of the valves and/or one or more coloured rays externally, whereas most Atlantic

and Mediterranean material examined showed no or slight traces of colour (some colouration and external coloured rays present in examined material from Bretagne, France). Again this may be due to suboptimal conditions for Port Phillip Bay animals or reflect retention or exaggeration of juvenile colouration. Specimens with no trace of purple colour were also common in the Port Phillip Bay material, and for this reason we do not regard colour differences between Australian and Atlantic material as highly significant (unfortunately very few of the Atlantic and Mediterranean specimens available were of the juvenile size-class).

DISCUSSION. *Corbula (Varicorbula) gibba* has an extensive geographical range in the Atlantic (Norway south to Angola) and the Mediterranean (including the Black Sea [Hrs-Brenko, 1981]). Suter (1913) reported the species (as *C. nucleus*) from the Chatham Islands, east of the South Island of New Zealand, but this needs to be confirmed. In many areas *C. gibba* may be the most abundant subtidal bivalve (for example, off the English coast (Yonge, 1946), some workers in fact using the species for population analyses (Hrs-Brenko, 1981). Corbulid species can survive long periods in the ballast water of ocean going vessels, and then go on to generate heavy or at least significant populations in foreign harbours (e.g. the Chinese corbulid *Potamocorbula amurensis* in San Francisco Harbour - Carlton et al., 1990). It is not possible to identify the precise geographical origin of the Victorian population of *C. gibba* on morphological features. The recent heavy infestation of the Mediterranean tubeworm *Sabella spallanzanii* throughout large areas of Port Phillip Bay does however suggest a possible source (via ballast water) for these bivalves.

Although *Potamocorbula amurensis* is now approaching plague proportions in San Francisco Bay (reaching densities of over 10000/ m2) and out-competing endemic species for settlement space (Carlton et al., 1990; Nichols et al., 1990), there is no direct evidence to suggest that *Corbula gibba* will cause similar problems in Port Phillip Bay. Nevertheless *C. gibba* is known to occur in enormous numbers at certain localities in the Atlantic (>450/m2) and can inhabit a variety of sediment types (coarse sand to fine mud, but preferring sand) and are capable of thriving even in substantially polluted areas (Hrs-Brenko, 1981). For these reasons we feel that the population of *C. gibba* in Port Phillip Bay should continue to be monitored, particularly in relation to
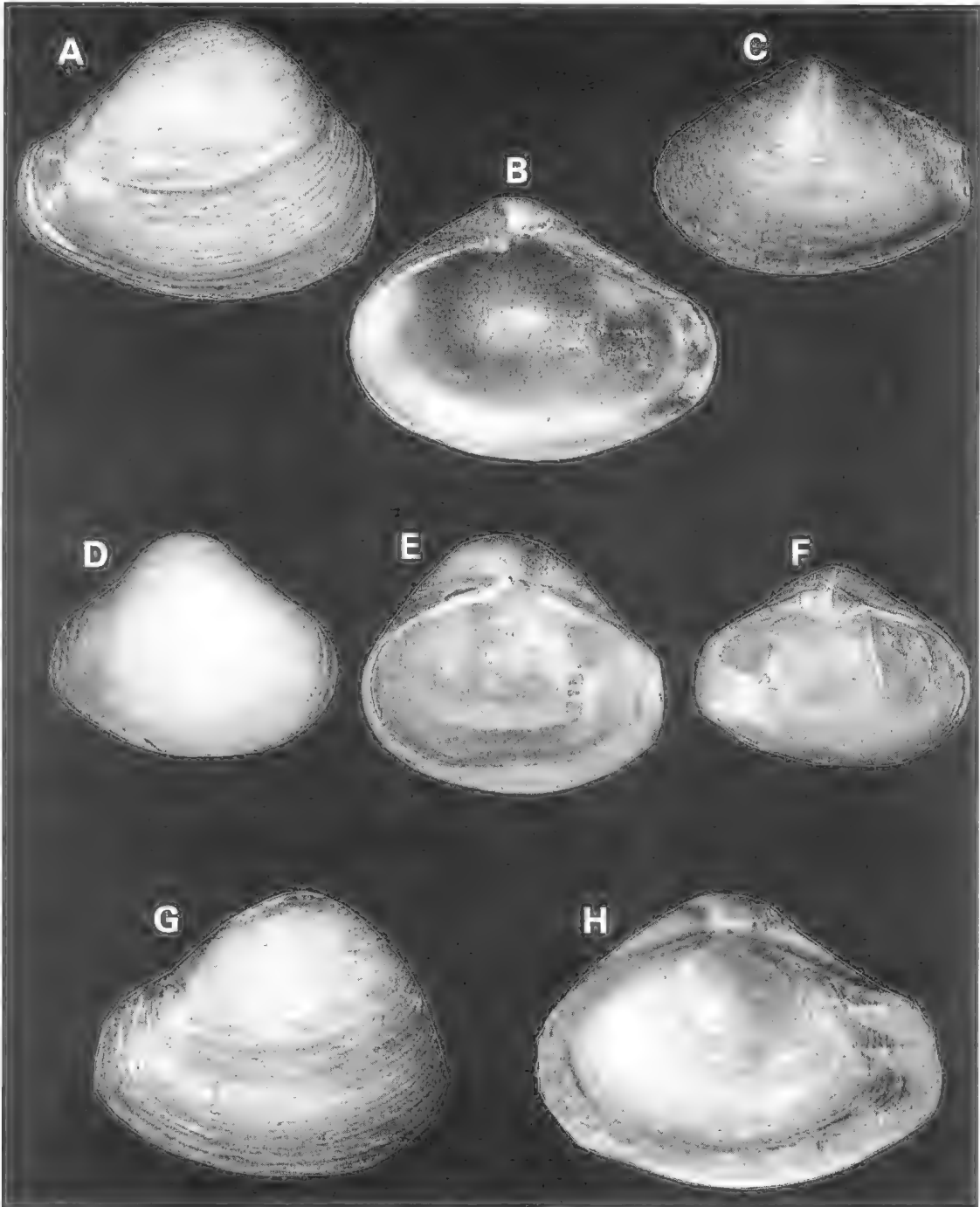
FIG. 1. *Corbula (Varicorbula) gibba* (Olivi, 1792). A-C from silty mud 2-4m, Sandringham Harbour, Port Phillip Bay. D-F, Bretagne, France. G-H, dredged off Shellness, England. A, external view of right valve (valve length 10.8 mm). B, internal view of right valve (valve length 10.8 mm). C, external view of left valve (valve length 9.9 mm). D, external view of right valve (valve length 12.6 mm). E, internal view of right valve (valve length 13.5 mm). F, internal view of left valve (valve length 12.0 mm). G, external view of right valve (valve length 12.5 mm). H, paired valves viewed from left valve (length of right valve 11.5 mm).

the impact of this species on the settlement success of native bivalves within the Bay. Bearing in mind the problems caused by the Asian corbulid *Potamocorbula amurensis* in the San Francisco area, vessels operating out of Port Phillip Bay should not take on ballast water within the Bay. Similarly, the practice of emptying ballast water from foreign vessels in Port Phillip Bay should be discontinued.

ACKNOWLEDGEMENTS

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EVOLUTION AND ZOOGEOGRAPHY OF AUSTRALIAN FRESHWATER TURTLES

BEN MANNING AND CHRISTOPHER P. KOFRON

The contemporary turtle fauna of Australia comprises freshwater and marine species but no terrestrial taxa. The literature on evolution and zoogeography of the Australian freshwater turtles (Chelidae) is reviewed. Because opposing conclusions were reached in several of these studies, we critically examine each of them. We accept the phylogeny of Georges & Adams (1992); *Elseya* and *Emydura* are not synonymous and *Elseya* consists of the *E. dentata* and *E. latisternum* species groups (generically distinct). However, *Pseudemydura umbrina* shares common ancestry with other Australian short-necked turtles and is their extant sister taxon. The *E. latisternum* group is the sister taxon of the non-*Pseudemydura* Australian short-necked turtle genera.

Understanding pre-Cretaceous dispersal of the ancestral lineage on the South American-Antarctic-Australian supercontinent is important for ascertaining relationships among Australian freshwater turtles. Increasing aridification during the Pleistocene, resulting in isolation within river drainages, appears to have augmented allopatric speciation.

We recognize 23 extant species of Australian chelid turtles in 7 genera: *Chelodina expansa, C. longicollis, C. novaeguineae, C. oblonga, C. rugosa, C. steindachneri* and one undescribed species; *Elseya dentata* and 3 undescribed species; *Elseya latisternum* and three undescribed species; *Elusor macrurus; Emydura macquarrii* (inclusive of *E. australis, E. krefftii* and *E. signata*), *E. subglobosa, E. victoriae* and 2 undescribed species; *Pseudemydura umbrina;* and *Rheodytes leukops*. Relationships among genera remain enigmatic. □ *Australia, evolution, turtles, zoogeography.*

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The reptilian order Testudines contains about 257 living species of turtles (Ernst & Barbour, 1989) in two suborders, Cryptodira and Pleurodira. Cryptodira contains 10 families and about 203 species, and Pleurodira two families and about 54 species. Cryptodiran turtles withdraw the head by vertical flexure of the neck into an S, and the pelvic girdle does not attach to the plastron. Pleurodirans withdraw the head by horizontal flexure of the neck, and the pelvic girdle attaches to the plastron. Each suborder is characterised by its own specialised cervical vertebrae.

Although cryptodirans are more derived than pleurodirans, the former did not stem from the latter (Ernst & Barbour, 1989). The earliest fossils of cryptodiran turtles are Middle Jurassic, 50 million years older than the earliest pleurodiran fossils (Legler & Georges, 1993a). However, the fossil record is poor, and pleurodiran turtles probably originated earlier (Gaffney, 1979; Bull & Legler, 1980; Ernst & Barbour, 1989). The two suborders are probably derived from separate ancestral lineages, each of which presumably could

not withdraw the head because of non-specialised cervical vertebrae (Gaffney, 1977).

Pleurodira contains the Pelomedusidae and Chelidae. Pelomedusids inhabit Africa, Madagascar and South America, but previously also Europe, Asia and North America (Frair, 1980). They retain mesoplastral bones in the shell and a squamosal bone in the skull; thus, Pelomedusidae is plesiomorphic to Chelidae (McDowell, 1983), which lacks mesoplastral and squamosal bones.

The contemporary fauna of Australia comprises freshwater and marine turtles, with a complete absence of terrestrial species. The Australian freshwater turtles are pleurodirans of the Chelidae, with exception of one cryptodiran, *Carettochelys insculpta* of the Carettochelydidae. The latter species inhabits northern Australia and New Guinea, and it is the sole extant member of its family. As recently as the Eocene, Carettochelydidae had a broad distribution in the Northern Hemisphere (Legler & Georges, 1993a). The living marine turtles of Australia are cryptodirans of the Cheloniidae and Dermochelyidae.

TABLE 1. Recent primary research papers that recognize the two nominal turtle genera *Elseya* and *Emydura* as separate, or as congeneric

Separate recognition	Congeneric recognition
Cann & Legler (1994)	Gaffney (1991)
White & Archer (1994)	Gaffney, Archer & White (1989)
Georges (1993)	McDowell (1983)
Georges & Adams (1992)	Gaffney (1981)
Legler (1985)	Frair (1980)
Legler (1981)	Gaffney (1979)
Legler & Cann (1980)	Gaffney (1977)
Burbidge, Kirsch & Main (1974)	

Australia was inhabited also by freshwater cryptodirans of the living Trionychidae (Pliocene - Gaffney & Bartholomai, 1979; Willis, 1993), and possibly Emydidae (middle Miocene; Murray & Megirian, 1992). A primitive non-marine cryptodiran was reported from the Early Cretaceous of Victoria (Gaffney et al., 1992), and also primitive terrestrial turtles that are neither cryptodiran or pleurodiran (Rich & Rich, 1989). Australia was inhabited as recently as the Pleistocene by giant horned terrestrial turtles (shells 1.5m length) of the extinct eucryptodiran Meiolaniidae, which also occurred in South America, Madagascar, Lord Howe Island and New Caledonia (Mittermeier, 1984; Archer et al., 1991). The fossil turtles of Australia were reviewed by Gaffney (1981, 1991) and Molnar (1991).

Outside Australia and New Guinea, the Chelidae inhabit only freshwaters east of the Andes in South America (Iverson, 1992), but a fossil specimen was found in Antarctica (Pritchard & Trebbau, 1984). Although chelids are not the dominant turtle family in South America, they are comparable in diversity to those in Australia. Consequently, constructing a phylogeny of freshwater turtles requires understanding of evolutionary relationships between the two geographically distant groups, together with the Pelomedusidae.

Australian chelids separate into two broad morphological and ecological groups (Goode, 1967; Cann, 1978), long-necked species and short-necked species. *Chelodina* contains long-necked species that spear or ambush their food (Pritchard, 1984; Legler & Georges, 1993b). They have 4 claws on the forelimbs, and a neck at least 2/3 the length of the shell (Cogger, 1992), with which they strike out rapidly and capture prey (Legler, 1993). *Elseya, Elusor, Emydura,*

Pseudemydura and *Rheodytes* are short-necked active foragers (Legler & Georges, 1993b; Cann & Legler, 1994). These have 5 claws on the forelimbs, and a neck less than 1/3 the length of the shell (Cogger, 1992).

South American chelids also separate into long-necked sit-and-wait predators and short-necked active foragers (Ernst & Barbour, 1989). Like Australian long-necked *Chelodina*, South American long-necked *Chelus* and *Hydromedusa* have 4 claws on the forelimbs. Also, like Australian short-necked genera, South American short-necked *Phrynops* and *Platemys* have 5 claws on the forelimbs. The questions are posed: How are the geographically-distant Australian and South American chelids related? Are the similar groups a result of ecological convergence, or do they share common ancestry?

Australian chelids are morphologically conservative (Cogger, 1992), which has hindered the recognition of valid taxa and obscured their true relationships. Discoveries of 3 new genera and 11 new species (Legler & Cann, 1980; Georges & Adams, 1992; Cann & Legler, 1994), of which 1 genus and 9 species await description, have made their phylogeny even more enigmatic. Ecologies of most species are poorly known. There is controversy regarding relationships and validity of taxa, especially the nominal genera and species of *Elseya* and *Emydura* (Table 1). The taxonomy is in a state of flux. Cogger (1992) recognized 15 species in 5 genera; Georges & Adams (1992) recognized 23 species in 7 genera.

This paper has 2 purposes; a review of the literature on evolution and zoogeography of Australian freshwater turtles and a review of opposing published conclusions. We recommend acceptance of one of the proposed phylogenies.

EVOLUTION OF THE CHELIDAE

The most important evolutionary and zoogeographic studies of Australian freshwater turtles are by Burbidge et al. (1974), Gaffney (1977), Legler & Cann (1980), Legler (1981), McDowell (1983), Georges & Adams (1992), and Cann & Legler (1994). The zoogeographic background was established by Burbidge et al. (1974), McDowell (1983), and Pritchard & Trebbau (1984). The systematic studies by Legler & Cann (1980), Legler (1981), McDowell (1983), and Cann & Legler (1994) approach an ideal sampling strategy. Georges & Adams (1992) sampled extensively and used sensitive bio-
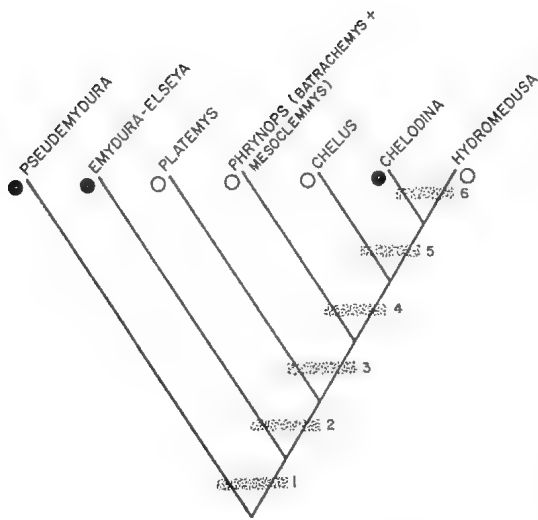
FIG. 1. Relationships within the Chelidae, based upon 26 cranial characters (Gaffney, 1977). Black dots indicate Australian genera, open circles South American genera.

chemical techniques capable of detecting cryptic relationships.

Among the 3 types of systematic methods (evolutionary, phenetic, cladistic), the last has the strongest Popperian scientific basis. Cladistics attempts to test hypotheses by designating characters as either plesiomorphic (ancestral) or derived (descendent). Derived characters shared between taxa are considered evidence of common ancestry unless homoplasy is demonstrated (Hennig,1966; Brooks & McLennan, 1991). The ingroup is the taxon whose evolutionary relationship is being tested. It is compared to a reference taxon, the outgroup, which is usually considered the sister taxon of the ingroup (Brooks & McLennan, 1991). Determination of the outgroup is a crucial and often most subjective decision in cladistics (Hennig, 1966; Maddison et al., 1984).

Gaffney (1977) undertook a cladistic analysis of living chelids using 26 cranial characters (Fig. 1). On the basis of skull simplification, he designated *Emydura* (inclusive of *Elseya*) as the outgroup of all other chelid genera. By assigning equal weight to all character states, Gaffney (1977) assured that all changes had equal probability. The Australian long-necked *Chelodina* were shown to be more closely related to South American long-necked *Chelus* and *Hydromedusa* than to Australian short- necked *Emydura* and *Pseudemydura*. The South American short-neck-

ed *Phrynops* and *Platemys* were positioned between *Chelodina* and the Australian short-necked genera.

Although Gaffney (1977) recognized *Elseya* and *Emydura* as congeneric (as did Frair [1980] and McDowell [1983]), this view is not commonly followed (White & Archer, 1994). However, Gaffney et al. (1989) claimed that the two genera are not adequately diagnosed.

Pseudemydura shares no derived skull characters with either the Australian and South American long-necked turtles or Australian short-necked turtles, but instead posseses 7 unique skull characters (Gaffney, 1977). Gaffney (1977) erected the monogeneric Pseudemydurinae and considered *Pseudemydura* as sister taxon to other chelids. *Pseudemydura* is autapomorphic among chelids in lacking temporal emarginations of the skull (Gaffney et al., 1989), and *P. umbrina* is unique among turtles by its behavior of excavating the egg chamber with forelimbs rather than hindlimbs (Kuchling, 1993). However, several derived characters are shared between *Pseudemydura* and other Australian short-necked turtles, such as reduced neural bones and cornified head scutes (McDowell, 1983). The intergular scute extending posteriorly to separate the humeral scutes was considered unique and derived in *Pseudemydura* (Burbidge et al., 1974), but McDowell (1983) observed it also in *Elseya dentata* and *Emydura australis*. Thus there may be no need for the Pseudemydurinae.

Because changes in chromosome morphology are quantum changes (King, 1985), cladistic analyses using karyotypes are free from problems associated with measuring continuous variables (King, 1985). Mutations detected by G- and C-banding can be treated as analogues of morphological character states (King, 1985). Evolutionary relationships of the cryptodirans were studied in this manner by Bickham & Baker (1976) and Bickham & Carr (1983). Also using G- and C-banding, Bull & Legler (1980) conducted chromosomal studies of 13 of the 14 pleurodiran genera. However, chelids do not respond well to this staining technique and a cladistic analysis was not done.

Even so, Bull & Legler (1980) gave valuable insight into evolution of chelids. For example, the ancestral karyotype is thought to be the one that most species share (King, 1985). The majority of chelids are uniform in number ($2n = 50$) and bands of their chromosomes, which supports the outgroup designation of *Emydura* (and *Elseya*)

FIG. 2. The position of Australia and Antarctica during the mid Cretaceous (after Rich & Rich [1989]). Black areas in Australia indicate the seaway extant during the Cretaceous.

by Gaffney (1977). The Cryptodira existed during the Early Cretaceous. Because the level of chromosomal variation among cryptodiran families is less than that between the two pleurodiran families, pleurodirans probably originated prior to the Cretaceous (Bull & Legler, 1980).

McDowell (1983) used osteological and soft organ characters to study relationships of the Chelidae and Pelomedusidae. He concluded that *Elseya* and *Emydura* were the most pelomedusid-like and, thus, plesiomorphic of the Chelidae, which further supported Gaffney's (1977) outgroup designation. Specifically, *Elseya dentata* has a longitudinal ridge on the maxilla, a character it shares only with the pelomedusid *Podocnemis* of South America.

Frair (1980) conducted a biochemical study of pleurodirans using total protein electrophoresis and immunoelectrophoresis with phenetic analyses, sampling all Chelidae and Pelomedusidae. He confirmed that each family is monophyletic, as first proposed by Gaffney (1975) and supported the arrangement of Gaffney (1979). Frair (1980) also showed the Chelidae to be more closely related to the Madagascan pelomedusid *Erymnochelys* than to the South American pelomedusid *Podocnemis* and *Peltocephalus*. Thus it appears that the lineage giving rise to the

Chelidae occurred in both South America and Africa when joined 115 million years ago. *Erymnochelys madagascariensis* is a relict species (Pritchard & Trebbau, 1984) and is probably most like the ancestral condition.

Pritchard & Trebbau (1984) reviewed earlier zoogeographic hypotheses of the Chelidae, as well as Pelomedusidae and other living and extinct South American turtles. In light of recent geological and evolutionary studies, along with a fossil chelid from Antarctica of Miocene age, they suggested the Chelidae could have originated in Antarctica. Pritchard & Trebbau (1984) argued that passive dispersal across vast stretches of ocean is possible only for terrestrial turtles. Thus an Antarctic landbridge or narrow sea should be considered in zoogeographic hypotheses of Australian and South American chelids (Fig. 2).

The hypothesis that the Australian long-necked turtles (*Chelodina*) did not originate from Australian short-necked turtles (Gaffney, 1977) is supported by recent biochemical data. Georges & Adams (1992) studied the evolutionary relationships of Australian chelids using allozyme electrophoresis (Hillis, 1987). Their extensive data set included 54 independent loci of 277 specimens of all species (except *Pseudemydura umbrina*) from 76 populations through Australia and New Guinea.

Georges & Adams (1992) employed 3 systematic methods. Their phenetic analysis incorporated principal co-ordinates, which gave representations of genetic distance. The cladistic analysis using PAUP (Swofford, 1985) produced unresolved cladograms because only 14 of 54 loci could be used as characters. A parsimony method (Farris, 1972; Baverstock & Schwaner, 1985) using distance-Wagner and Fitch-Margoliash procedures, which are not widely accepted, also produced unresolved cladograms. Although the several generated phylogenies varied, relationships of some taxa remained constant.

Georges & Adams' (1992) results suggest that divergence between the Australian long- and short-necked turtles is about twice that within either of the two groups; and the level of divergence among the short-necked species is substantially greater than that among the long-necked. These results support Gaffney's (1977) phylogeny in which South American genera are intermediates, and short-necked turtles are probably more primitive.

McDowell (1983) presented a simple dispersal theory to explain Gaffney's (1977) results. The

ancestor of *Emydura* entered South America from Australia. The lineage diverged, giving rise to South American short-necked turtles, from which evolved a long-necked form that dispersed back into Australia.

Neural bones are considered an important taxonomic character for chelids. They were reported absent in all living Australian chelids, except *Chelodina oblonga* (Burbidge et al., 1974; McDowell, 1983). Neural bones were reported in South American chelids, which McDowell (1983) considered evidence for convergence of the long-necked condition. However, Rhodin & Mittermeier (1977) reported low frequencies of neural bones in certain populations of both short- and long-necked Australian chelids.

The Australian long-necked *Chelodina oblonga* and South American chelids possess well-developed neural bones, which in *C. oblonga* vary from 5-8 (Burbidge et al., 1974; Rhodin & Mittermeier, 1977). Neural bones (although reduced in size) persist at low frequencies in certain populations of *Elseya latisternum*, an undescribed *Elseya* sp. from the Manning River (NSW), *C. longicollis*, *C. novaeguineae* and *C. siebenrocki*. Of two fossil specimens of *Emydura* from mid- Tertiary deposits in Tasmania, one has one reduced neural bone and the other none (Warren, 1969a). Apparently the character should be assessed as absent/reduced in size, or well developed (Pritchard, 1984).

The fossil record of chelids is poor, beginning in the Early Cretaceous of Victoria (Warren, 1969b) with a specimen identified first as extant *Emydura macquarrii* but later as *Chelycarapookus arcuatus*. It has well-developed neural bones (Burbidge et al., 1974), and is considered ancestral to short-necked turtles in which neural bones are absent or reduced. Early Cretaceous chelid fossils have been found in NSW and in western QLD (a *Chelycarapookus*-like form: R.E. Molnar, pers. comm.).

Chelycarapookus arcuatus was a river-dweller (Molnar, 1991) and probably had a broad distribution in eastern Australia. With vulcanism forming the Great Dividing Range later during the Cretaceous (Galloway & Kemp, 1984), and with increasing aridification during the Pleistocene, the contemporary turtle fauna may have evolved by allopatric speciation.

McDowell's (1983) zoogeographic hypothesis explains certain phylogenetic relationships. The following model is adapted from his, considering that at times Antarctica had a warmer environment. During the Early Cretaceous, the ancestral lineage including *Chelycarapookus* inhabited the southern supercontinent. During the late Eocene, Australia was isolated by sea, with members of the *Chelycarapookus* lineage left in Australia and in the Antarctic-South American landmass. The trend in neural bones in the Australian lineage was for reduction and loss, giving rise to *Elseya, Elusor, Emydura, Pseudemydura* and *Rheodytes*. The South American lineage retained well-developed neural bones, evolving into the South American short-necked and long-necked turtle genera. However, the ancestral lineage of South American long-necked turtles also dispersed back into Australia, giving rise to Australian long-necked turtles. The general trend for neural bones in this group was for reduction and loss, but well- developed neural bones were retained in the immediate lineage to *Chelodina oblonga*. Morphologically and biochemically, *C. oblonga* is plesiomorphic in its genus (Burbidge et al., 1974; Georges & Adams, 1992).

Why did only the ancestral South American long-necked turtle lineage disperse back to Australia from the Antarctic-South American landmass, and not also the ancestral South American short-necked turtle lineage? The answer might be elucidated by examining ecologies of the two groups. Unlike any South American short-necked turtle genus, in addition to inhabiting freshwaters, the South American long-necked *Hydromedusa* also inhabits estuaries (Ernst & Barbour, 1989). Australian long-necked *Chelodina* (*C. longicollis, C. expansa*) has greater resistance to evaporative water loss than Australian short-necked *Emydura* (*E. macquarrii*; Chessman, 1984). *Chelodina* inhabits permanent and temporary freshwaters (Chessman, 1984), and can also tolerate saline waters. During drought, *Chelodina* walks overland and finds other water, or buries into substrate and aestivates (Goode, 1967; Cann, 1978; Grigg et al., 1986). *Chelodina rugosa* can inhabit highly saline ephemeral swamps (Ehmann, 1992), and *C. longicollis* can tolerate brackish water for prolonged periods (Smith, 1993). On the other hand, all Australian and South American short-necked chelids inhabit only permanent freshwaters, except *Pseudemydura* which inhabits ephemeral swamps and aestivates. Thus it appears that the lineage giving rise to Australian long-necked turtles had greater potential for dispersal across land and/or a narrow sea between Australia and the Antarctic-South American landmass.

EVOLUTIONARY RELATIONSHIPS AMONG AUSTRALIAN FRESHWATER TURTLES

In a study of evolutonary relationships of Australian chelids, the ideal sample would include all species; with specimens from throughout a species' range, of various sizes and both sexes to include the variations of geography, ontogeny and sexual dimorphism. Legler & Cann (1980), Legler (1981), McDowell (1983), Georges & Adams (1992), and Cann & Legler (1994) approach this ideal sampling strategy.

Using cladistic analysis of cranial characters, Gaffney (1977) diagnosed distant chelid genera, but he could not separate *Elseya* from *Emydura*. Because the skull and jaw of chelids are probably correlated conservative characters, the data set appears inadequate for diagnosing closely related genera. In addition, the data were from small samples, often single specimens.

Burbidge et al. (1974) diagnosed *Elseya* from *Emydura* on nuchal and intergular scutes: nuchal scute usually absent in *Elseya*, present in *Emydura*; intergular scute smaller and more rectangular in *Elseya*, larger and less rectangular in *Emydura*. *Elseya* was reported to have an elongate snout. However, data for *Elseya* and *Emydura* were from single specimens of *Elseya latisternum* and *Emydura macquarrii*, their sole representatives of the two genera.

Burbidge et al. (1974) also used phenetics to analyze serological data of Australian chelids. The first 3 dimensions of the principal components described 85% of the variation. Among the short-necked turtles, *Elseya dentata* clustered with *Elseya novaeguineae*; *Emydura australis*, *Emydura krefftii* and *Emydura subglobosa* clustered; and the two groups together formed a closely associated group. *Elseya latisternum*, *Emydura macquarrii* and *Pseudemydura umbrina* were outliers; however, after omitting the anti-*Elseya latisternum* data, *Elseya latisternum* clustered with *Elseya dentata* and *Elseya novaeguineae*. The long-necked turtle species (*Chelodina*) clustered together, but with *C. oblonga* an outlier within the genus.

These results showing *P. umbrina* and *C. oblonga* as outliers to the short-necked and long-necked turtles, respectively, are accepted. Their sera react strongly and they have different morphologies. However, the designation of *Elseya latisternum* as an outlier is treated with caution because its serum reacted weakly.

Bull & Legler (1980) reported the short-necked *Elseya*, *Emydura* and *Rheodytes* to have identical karyotypes (2n=50 and gross chromosome morphology), and *Pseudemydura* differed only slightly by having chromosome pairs 6 and 10 acrocentric. Pelomedusid turtles differed greatly, with 2n=26-36 and 5 large macrosomes.

Using total protein electrophoresis, Frair (1980) observed only one type of electrophoretic pattern among two species of *Elseya* and two *Emydura*. The electrophoregrams of *Elseya latisternum* and *Elseya novaeguineae* were similar, but the former longer and with its cathodal line closer to the negative pole. The electrophoregrams of *Emydura signata* and *Emydura subglobosa* were similar to *Elseya novaeguineae*, but the latter slightly more negative. Among *Chelodina*, there were two electrophoretic patterns: 3 anodal lines for *C. longicollis* and *C. novaeguineae*; and 1 for *C. expansa*, *C. rugosa* and *C. siebenrocki*. Observing little variation between *Elseya* and *Emydura* relative to that within *Chelodina*, Frair (1980) recognized *Elseya* and *Emydura* as synonymous.

Frair (1980) concluded the results of Bull & Legler (1980) (similar chromosome numbers and bands of *Elseya* and *Emydura*) supported their synonymy. However the chromosomes of *Pseudemydura umbrina* and *Rheodytes leukops* are also similar in number and bands to *Elseya* and *Emydura*, but *Pseudemydura* and *Rheodytes* are separate genera because of their unique morphologies.

Frair (1980) also used the observations of Webb (1978) on basking of captive Australian turtles to support synonymy of *Elseya* and *Emydura*: *Elseya* and *Emydura* basked regularly, whereas *Chelodina* never basked. However, basking is prevalent in the South American short-necked chelids *Phrynops* and *Platemys* (Lacher et al., 1986; Monteiro & Diefenbach, 1987); in Pelomedusidae (short-necked turtles) (Miller, 1979); and catholically in the suborder Cryptodira (short-necked turtles), especially the Emydidae (Ernst & Barbour, 1989). Because basking behavior is widespread in short-necked turtles, it has little value in supporting synonymy of *Elseya* and *Emydura*. Rather, it probably indicates ecological differences between short-necked and long-necked turtles.

Legler (1981) examined more than 3000 specimens of Australian chelids and considered geographic distributions to elucidate relationships. He stated that *Elseya dentata* (and at least 3 undescribed species) and *Elseya latisternum* (and at least 1 undescribed species) belonged to separate genera, but no diagnoses were presented.
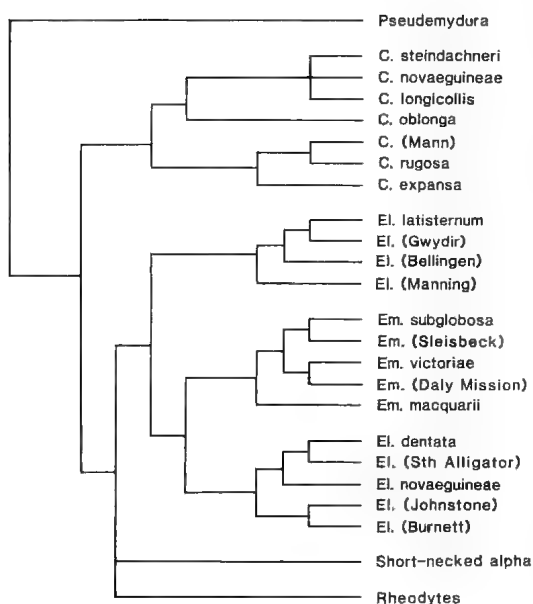
FIG. 3. The phylogeny of Australian freshwater turtles (and *Elseya novaeguineae*), based on allozyme electrophoresis (Georges & Adams, 1992). Short-necked alpha is *Elusor macrurus*.

McDowell (1983) examined at least 5 specimens from various localities of all Australian short-necked turtle species, except *Emydura signata*. Because there were no significant differences among the characters he tested, McDowell (1983) placed *Elseya novaeguineae* in synonymy of *Elseya dentata*; and *Emydura albertisii*, *Emydura krefftii* and *Emydura subglobosa* in synonymy of *Emydura australis*. Also, his results showed *Elseya dentata* (and *Elseya novaeguineae*) to be more closely related to *Emydura australis* than to *Elseya latisternum*, so he recognized *Elseya* and *Emydura* as synonyms. However, the biochemical results of Georges & Adams (1992) argue against these synonymies. In addition, there are pronounced color differences among the nominal species of *Emydura*. In life *Emydura subglobosa*, commonly called the painted turtle, has a crimson plastron and yellow on the face (Legler, 1981). Living *Emydura* sp. (Daly, Nicholson and Roper Rivers) has red on the face and legs, and *Emydura krefftii* yellow across the head (Cann, 1978; Cogger, 1992). But the significance of color pattern in diagnosing short-necked turtles remains unknown.

On allozyme characters, Georges & Adams (1992) could not distinguish between *Emydura*

macquarrii, *E. krefftii* (including Cooper Creek and Fraser Island populations) and *E. signata*, all of which they considered to be *E. macquarrii*. Georges (1993) regarded *E. macquarrii* as polytypic or a species complex, with unresolved systematic positions of distinctive populations in Cooper Creek and Fraser Island and the taxa referred to as *E. krefftii* and *E. signata*.

Although *Elseya latisternum* was an outlier to other *Elseya* species (and *Emydura*), neither Burbidge et al. (1974) nor Frair (1980) suggested that *Elseya* was paraphyletic. In serological studies like Frair's (1980), the variation of electrophoregrams is misconstrued by multiple protein analysis (Baverstock & Schwaner, 1985). However, monovalent techniques with antisera for single proteins are more amenable to genetic interpretation because the strength of cross reaction is directly proportional to differences in the gene locus encoding the protein (Baverstock & Schwaner, 1985). Georges & Adams (1992) considered single locus protein variation and consequently has the same objectivity as monovalent immunological methods.

Georges & Adams' (1992) principal co-ordinates analysis of the first 3 dimensions described 63% of the variation. Australian chelids clustered into 5 groups, which were recognised by Legler (1981). *Elseya novaeguineae*, which McDowell (1983) placed in synonymy of *Elseya dentata*, had a divergence level similar to that of *Elusor* and *Rheodytes* to the *Elseya dentata* group. This species also lost its affinities with the *Elseya dentata* group in higher dimensions.

The highest levels of divergence were within *Elseya* and *Chelodina*; that within *Emydura* was relatively small, suggesting its 5 species are relatively young. Divergence between *Elseya* and *Emydura* was less than that within *Elseya*. The *Elseya dentata* group was closer to *Emydura* than to the *Elseya latisternum* group, which was established also by McDowell (1983). However, instead of recognizing *Elseya* and *Emydura* as congeneric, Georges & Adams (1992) considered the *Elseya latisternum* group to comprise a separate genus, their rationale that synonymization would have to include also *Elusor* and *Rheodytes*. The genetic distances between the provisional genera (*Elseya dentata* group, *Elseya latisternum* group, *Emydura*) are similar to, if not greater than, that between many of the cryptodiran emydid genera, especially the batagurines (Sites et al., 1984).

In regard to Australian long-necked *Chelodina*, the phylogenetic results of Georges & Adams

TABLE 2. Distribution of Australian freshwater turtles (Georges & Adams 1992) and *Elseya novaeguineae*. From Cogger (1992), Ehmann (1992), Georges & Adams (1992), Iverson (1992), Legler & Georges (1993b), Georges (1993). ?=systematic position of the population is unresolved. Zoogeographic regions from Fig. 4

GROUP	SOUTH-WESTERN	WESTERN	CENTRAL	SOUTHEASTERN WESTERN	SOUTHEASTERN EASTERN	EASTERN	NORTHERN WESTERN	NORTHERN EASTERN	NEW GUINEA
Chelodina expansa				*expansa*		*expansa*	*rugosa*		
							sp. (Liverpool + Mann R.)		
Chelodina longicollis		*steindachneri*		*longicollis*			*longicollis*		
					novaeguineae				
Chelodina oblonga	*oblonga*								
Elseya dentata						sp. (Burnett + Fitzroy R.)	sp. (South Alligator R.)	sp. (Johnstone R.)	*novae-guineae*
							dentata		
Elseya latisternum				sp. (Gwydir R.)	*latisternum*				
					sp. (Bellingen R.)				
					sp. (Manning R.)				
Elusor						*macrurus*			
Emydura			? (Cooper C. + Diamantina R.)	*macquarrii*		*krefftii* ?	*victoriae*	*krefftii* ?	
					signata ?			*subglobosa*	
						? (Fraser I.)	sp. (Daly, Mitchell + South Alligator R.)		
							sp. (Daly, Nicholson + Roper R.)		
Pseudemydura	*umbrina*								
Rheodytes						*leukops*			

(1992) aligned with the species groups established by their prinicpal components analysis. In general, their interpretation of relationships agreed with Burbidge et al. (1974) and Legler (1981); however, contrary to Legler (1981), the level of divergence between the *C. expansa* and *C. longicollis* groups did not warrant separate generic recognition.

Georges & Adams (1992) tentatively placed *Elusor* and *Rheodytes* outside the *Elseya dentata, Elseya latisternum* and *Emydura* radiation (Fig. 3). Although the cladograms of Georges & Adams (1992) were unresolved, their phenetic analysis suggests both *Elusor* and *Rheodytes* have their closest affinities with the *Elseya dentata* group. Similarly, the PAUP-generated cladogram of Cann & Legler (1994), based upon 35 morphological and 16 allozyme characters treated equally and compared to *Chelodina* as the outgroup, suggests *Elusor* and *Rheodytes* form the sister group to the *Elseya dentata* group.

Cann & Legler (1994) also performed multi-discriminate analyses with 31 mensural charac-ters from large samples (n=41-1000) of the *Elseya dentata* group, *Elseya latisternum* group, *Elusor*, *Emydura* and *Rheodytes*. The data were treated as percentages of carapace length. In the resulting 3D scatter plots, the groups separated equidistant from each other but with *Emydura* separate from all. Consequently, Cann & Legler (1994) recognized the *Elseya dentata* group, *Elseya latisternum* group, *Elusor* and *Rheodytes* as the *Elseya* group of genera.

The primary weakness of Cann & Legler's (1994) multidiscriminate analysis is that a species' morphology is adaptive to its environment. For example, extrapolation from Cann & Legler (1994) would suggest that Australian short-necked chelids are more closely related to short-necked emydid turtles than to Australian long-necked chelids. Also, sample groups must be of similar sex and age classes to negate sexual and ontogenetic differences in morphology. For example, 90% of Cann & Legler's (1994) sample of *Elusor macrurus* were small juveniles. If this species experiences ontogenetic changes in mor-
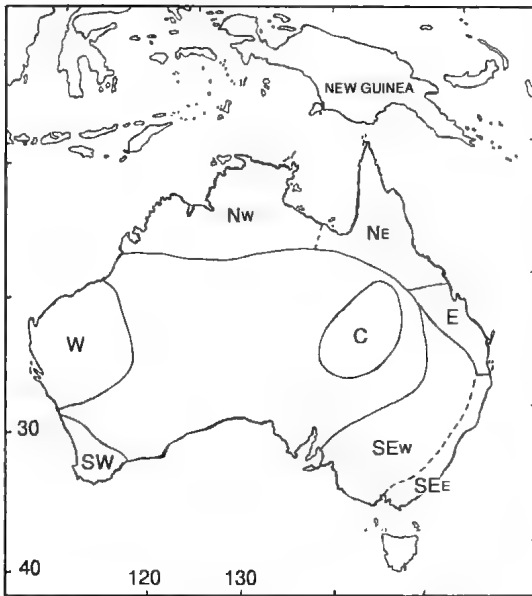
FIG. 4. The zoogeographic regions of Australian freshwater turtles (modified from Burbidge et al., 1974). Species within each region are listed in Table 2.

phology, then comparison against a sample of another species except of similar composition is meaningless.

The relationship of *Pseudemydura umbrina* to other Australian chelids remains obscure. Its endangered status and small population size (Kuchling & DeJose 1989) limit certain avenues of research (e.g. Georges & Adams 1992). Nonetheless, *P. umbrina* shares several derived characters with other Australian short-necked turtles, but none with South American genera or Australian long-necked *Chelodina* (McDowell, 1983). Thus *Pseudemydura* may be the sister taxon to other Australian short- necked turtles.

REPRODUCTIVE PATTERNS OF AUSTRALIAN FRESHWATER TURTLES

Examining the ecology of a species can help elucidate its evolutionary history: knowing functions of structures makes the grading of character states more accurate, and it gives insight into selective pressures for higher or lower rates of speciation (Shine, 1985). Legler (1985) recognized 2 patterns of reproduction among Australian chelids, one having evolved in the tropics and the other in temperate environments.

The two reproductive patterns were defined by egg size and hardness, time of nesting and length of incubation (Legler, 1985). The tropical strategy invoked large hard eggs being deposited during the dry season (winter) with long incubation; and the temperate strategy, smaller flexible eggs deposited in spring or summer with relatively short incubation.

A temperate origin was indicated (Legler, 1985) for the *Elseya latisternum* group (*E. latisternum* and at least 3 undescribed species), *Chelodina longicollis* group (*C. longicollis, C. novaeguineae, C. steindachneri*) and *Emydura*. A tropical origin was indicated for the *Elseya dentata* group (*E. dentata, E. novaeguineae* and two undescribed species) and *C. expansa* group (*C. expansa, C. oblonga, C. rugosa*).

However, the two patterns are not realistic and the criterion for egg hardness was only subjectively defined. For example, the *C. expansa* and *E. dentata* groups lay the largest eggs (Legler, 1985), but these species are the largest Australian freshwater turtles. Also, larger eggs may necessarily be harder because of structural constraints. In cryptodirans there is positive correlation between adult size and egg size; egg size and hatchling size; and for hard shelled eggs, egg size and shell thickness (Ewert, 1979). Also, some tropical species lay soft shelled eggs, and some both hard and soft (Moll & Legler, 1971; Ewert, 1979).

Legler (1985) was selective of data from previous authors, ignoring that which lessened distinction between the two patterns. For example, *C. oblonga* (proposed tropical origin) nests during summer (Burbidge, 1967, 1984) and *C. expansa* (proposed tropical origin) sometimes during autumn (Goode & Russell, 1968; Georges, 1984); and eggs of *C. longicollis* (proposed temperate origin) undergo long incubation, up to 200 days (Cann, 1978). Thus it appears that additional reproductive patterns exist. Also, if the contrasting tropical and temperate environments are strong selective pressures on reproduction, why do some species of each group inhabit the other environment? Within *Emydura* (proposed temperate origin), *E. subglobosa, E. victoriae* and 2 undescribed species inhabit only the tropics; and *E. macquarrii* (inclusive of *E. australis, E. krefftii* and *E. signata*) inhabits both temperate and tropical environments (Cogger, 1992; Iverson, 1992). Georges et al. (1993) previously questioned the fit of Legler's (1985) reproductive patterns to species groups.

However, according to the centre of diversity rule (Ross, 1974), *Emydura* probably evolved in the tropics, and also the *Elseya dentata, C. expansa* (*C. expansa, C. rugosa* and an undescribed

species in the NT, sensu Georges & Adams [1992]) and *C. longicollis* groups. With 3 species in the temperate zone and *Elseya latisternum* inhabiting both temperate and tropical zones, the *E. latisternum* group probably evolved in temperate environments. In addition, the groups for which the centre of diversity rule predicts tropical origins all have representatives and/or closely related species in New Guinea, dispersal northward having been possible by Pleistocene landbridges (Burbidge et al., 1974). On the other hand, the *Elseya latisternum* group (predicted temperate origin), with *E. latisternum* ranging from northern NSW (temperate) to the tip of Cape York Peninsula, has no close relative in New Guinea.

ZOOGEOGRAPHY OF AUSTRALIAN FRESHWATER TURTLES

Zoogeographic regions for Australian freshwater turtles were defined by Burbidge et al. (1974), which in general corresponded to those for freshwater fish (Whitley, 1959). However, we also recognize Central and Eastern zoogeographic regions for freshwater turtles (Fig. 4, Table 2). The Central Region is in the arid zone of interior Australia and contains the Cooper Creek and Diamantina River population of large macrocephalous *Emydura*, which Ehmann (1992) and Legler & Georges (1993b) reported to be an undescribed species. Although Georges & Adams (1992) could not distinguish the population by allozyme electrophoresis from *E. macquarrii*, Georges (1993) regarded it as a distinctive population with unresolved systematic position. The Eastern Region encompasses the Fitzroy, Burnett, Mary and Brisbane river drainages, to which are endemic only an undescribed species of the *Elseya dentata* group (Georges & Adams, 1992), *Elusor macrurus* and *Rheodytes leukops*. Our Central and Eastern regions correspond to Whitley's (1959) Sturtian and Krefftian regions, respectively. Zoogeographic regions for freshwater turtles are almost identical to those for freshwater fish. Also, like some freshwater fish, some freshwater turtles inhabit both northern Australia and southern New Guinea.

The vicariance hypothesis of Burbidge et al. (1974) suggests that ancestors of each species group were distributed widely throughout northern and eastern Australia during the Pleistocene epoch when the climate was cooler and wetter. The existing chelid fauna resulted by allopatric

speciation, directed by isolation of river drainages with increasing aridification.

Southwestern Australia is inhabited by endemic *Chelodina oblonga* and *Pseudemydura umbrina*. This region became isolated by formation of a broad inland sea from the Gulf of Carpentaria to the coast of S AUST during the Early Cretaceous (Rich & Rich, 1989; Fig. 2). Burbidge et al. (1974) proposed that the eastern *Chelodina* ancestor evolved into the form lacking neural bones, and the eastern *Pseudemydura* became extinct. Prior to the Cretaceous sea, *Elseya* and *Emydura* had tropical northern distributions. Later during the Cretaceous the sea receded, leaving a vast waterless desert equally impenetrable. Alternatively, Pritchard & Trebbau (1984) suggested two separate invasions from Antarctica, one each into eastern and western Australia.

The distributions of freshwater turtle and fish species groups support the vicariance hypothesis of Burbidge et al. (1974). The species within each group are largely allopatric, with sympatry between species of different groups (Legler, 1981; Iverson, 1992). In addition, there are fossils and a relict population of *Emydura* in the arid zone of SW QLD and adjacent S AUST (Gaffney, 1979; Ehmann, 1992); and fossils of *Pseudemydura* (early to middle Miocene) from Riversleigh, on the Gulf of Carpentaria (Gaffney et al., 1989).

Burbidge et al. (1974) showed *C. oblonga* to be morphologically and serologically an outlier to other *Chelodina*. Similarly, the phenetic analysis (3D) of Georges & Adams (1992) showed *C. oblonga* to be an outlier within the *C. expansa* group (although this was not maintained at higher dimensions), and their phylogenetic analyses consistently placed *C. oblonga* as pleisiomorphic. These results together with retention of well- developed neural bones (Burbidge et al., 1974) indicate that *C. oblonga* approaches the ancestral condition, further supporting Burbidge's et al. (1974) vicariance hypothesis.

The hypothesis of Burbidge et al. (1974) requires the short-necked turtle genera to have a northern distribution prior to formation of the inland Cretaceous sea. However, the *Elseya latisternum* group probably had a southeastern origin, and thus potential for dispersal into southwestern Australia. The following hypotheses may explain the absence of the *Elseya latisternum* group from southwestern Australia. (1) The *E. latisternum* lineage previously inhabited also southwestern Australia but has since become extinct there. (2) The southern Australian environment during the Cretaceous was not favorable for

dispersal of the *E. latisternum* lineage westward into southwestern Australia. (3) The *E. latisternum* lineage evolved after the Cretaceous, and since then the southern Australian environment has not been favorable for dispersal westward.

Hypotheses (2) and (3) appear most likely because members of the *E. latisternum* group live in the headwaters of rivers, even above major waterfalls in the Great Dividing Range of eastern Australia (Legler, 1981). Low flat land, instead of elevated ranges, between SE and SW Australia may have been a barrier to dispersal of this group. On the other hand, if *Emydura* had a temperate distribution prior to formation of the inland Cretaceous sea, the genus could have dispersed westward into southwestern Australia.

Rheodytes leukops Legler & Cann (1980) and *Elusor macrurus* Cann & Legler (1994) belong to monotypic genera and with highly restricted ranges. *Rheodytes leukops* is endemic to headwaters of the Fitzroy River, E of the Great Dividing Range in central eastern Queensland. The species is highly specialised for inhabiting rapids: it feeds on invertebrates in rapids, and it can obtain all of its oxygen through its enlarged cloacal bursae (Legler & Georges, 1993b). The other short-necked turtles feed in slow-moving or standing water (Legler & Georges, 1993b), and their cloacal bursae are less developed. *Elusor macrurus* is endemic to the Mary River drainage of SE QLD, also E of the Great Dividing Range, and its biology is poorly known (Cann & Legler, 1994)

CONCLUDING STATEMENT

Although we now have a better understanding of Australian chelids, 1 genus and 9 extant species await description (Georges & Adams, 1992), and the systematic positions of several populations of *Emydura* remain unresolved: Cooper Creek, Fraser Island, and the taxa referred to as *E. krefftii* and *E. signata*. Intergeneric relationships remain enigmatic. However, it appears that *Pseudemydura umbrina* shares common ancestry with other Australian short-necked turtles and is their sister taxon. Also, it appears the *Elseya latisternum* group is the sister taxon of the non-*Pseudemydura* short-necked turtles, as suggested by data from Georges & Adams (1992) and Cann & Legler (1994).

ACKNOWLEDGEMENTS

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PERINATAL SKELETAL INJURIES IN TWO BALAENOPTERID WHALES

ROBERT A. PATERSON AND STEPHEN M. VAN DYCK

Two recently born balaenopterid whales (*Balaenoptera acutorostrata* and *Megaptera novaeangliae*) stranded on the coast of southern Queensland exhibited similar pericranial and rib lesions considered to result from compression injury. Birth trauma, perhaps associated with caudal presentation, is considered the most likely cause of the lesions. ☐ *Balaenopterid whales, skeletal injuries, birth trauma.*

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The Queensland Museum (QM) cetacean collection contains skeletal material of 11 juvenile balaenopterids of which 7 are minke whales *Balaenoptera acutorostrata*, 3 are humpback whales *Megaptera novaeangliae* and 1 a blue whale *B.musculus musculus*. Among these, pericranial and rib lesions are evident in 2 very immature specimens, 1 minke whale and 1 humpback whale. This paper describes the pathology and speculates on its cause.

DESCRIPTIONS

QMJM7301. A 2.9 m long ♀ minke whale stranded at the Big Sand Hill, Moreton Island (27°13'S, 153°22'E) on 11.vi.87. Its flipper and body colouration was typical of the diminutive or Type 3 form (Best, 1985) and was illustrated in Paterson (1994). The umbilicus was healed. Superficial 'cookie-cutter' lesions similar to those described in other examples of this species (Williamson, 1975; Arnold et al., 1987) were noted as
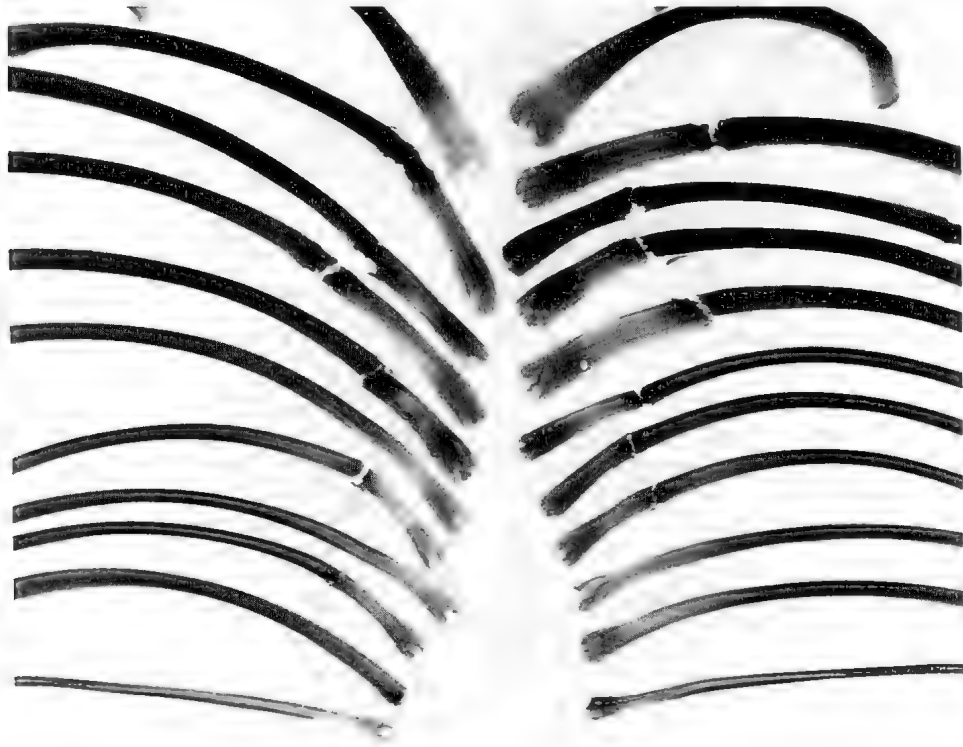

FIG. 1. Minke whale QMJM7301. Radiograph demonstrating numerous bilateral ventral rib fractures. The sternum has not been included.

FIG. 2. Minke whale QMJM7301 (Left). Dorsal view of skull (98cm long) demonstrating periosteal new bone formation on the lateral aspect of the supra-orbital process of the left frontal bone. (Right) Close-up profile view of the same region.

well as predatory rakes near the dorsal fin. Bilateral rib fractures were palpable but there were no wounds or scars superficial to them. Abundant callus (some was lost during preparation) was evident both by direct inspection and radiological examination (Fig. 1). After preparation of the skull a raised area of shell-like ossification 6.0 cm long and 2.5 cm in greatest diameter was noted on the lateral aspect of the supra-orbital process of the left frontal (Fig. 2).

QM JM7303. A 4.2 m long ♂ humpback whale stranded at Moon Point, Fraser Island (25°14'S, 153°00'E) on 17.10.89. It was frozen soon after death and transported to the QM. The umbilicus was healed. Numerous bites and rakes, considered to be due to shark attack, were noted. They included a large fresh right axillary wound. Rib fractures (Fig. 3) were not as severe as those in QMJM7301. During dissection a cystic pericranial lesion measuring 16.0 cm long and 7.0 cm in greatest diameter was noted on the lateral aspect of the supra-orbital process of the right frontal (Fig. 4). There were no soft tissue or cutaneous abnormalities superficial to the lesion. Its raised periosteal edge was biopsied and his-

tological examination (Fig. 5) demonstrated periosteal new bone formation superficial to a sub-periosteal cyst consistent with trauma several weeks prior to death (J. Musgrave pers.comm.).

DISCUSSION

There are very limited data concerning the time and place of birth of Type 3 minke whales. The two smallest examined in South Africa by Best (1985) were 1.92 m and 2.54 m long and they stranded at latitude 34°S in May and July respectively. The former had a raw and completely unhealed umbilicus and was considered to be a very recent live birth (Best, 1985). QMJM7301 was 2.9 m long, and stranding occurred at 27°S in June. Its skeleton was extremely immature compared with the 6 other juvenile minke whale skeletons in the QM collection and this suggests a very young age, probably less than 8 weeks.

There are extensive data concerning the time and place of birth of Southern Hemisphere humpback whales. The modal length at birth is 4.3 m (Chittleborough, 1958) and most births occur in the vicinity of latitude 20°S between late July and mid September (Townsend, 1935; Chittleborough, 1965; Paterson & Paterson, 1989).

FIG. 3. Humpback whale QMJM7303. Radiograph demonstrating healing undisplaced bilateral ventral rib fractures. The sternum has not been included. (The vertical 'tracks' in some ribs on the left of the photograph result from drilling to insert numbering wires).

QMJM7303 was 4.2 m long and stranded at 25°S in October on the western side of Fraser Island, a region frequented by humpback whales during the southern migration (Corkeron et al., 1994). QMJM7303 was probably less than 6 weeks old when it died.

Radiological opinion was sought in an attempt to date the rib fractures. They were considered to have occurred approximately 6-8 weeks before death and were likely to have resulted from compression and not from blunt trauma (J.P. Masel, pers. comm.) The position and extent of the bilateral rib fractures are consistent with compression injury described in human neonates by Caffey (1973). The extensive fractures in QMJM7301 are considered to represent a 'central flail' a term used in human trauma when multiple rib fractures occur on both sides of the sternum

(Hunt & Schwab, 1992). Such an injury in humans is often life-threatening and may require assisted ventilation. However, some healing was evident in the fractures of QMJM7301 and its death was not due to acute chest trauma.

The lateral aspect of the supra-orbital process of the frontal would be susceptible to injury, particularly in an immature animal, if dorsolateral compression occurred. Pericranial injury, similar to that in QMJM7301 and QMJM7303, occurs in c.2% of human neonates and is termed cephalhaematoma. It usually results from cranial moulding during parturition and, as an isolated finding, is not associated with mortality or persistent morbidity (Caffey, 1973). The degree of new bone formation in the pericranial lesion of QMJM7301 (Fig.2) suggests a longer period of survival than QMJM7303 in which new bone
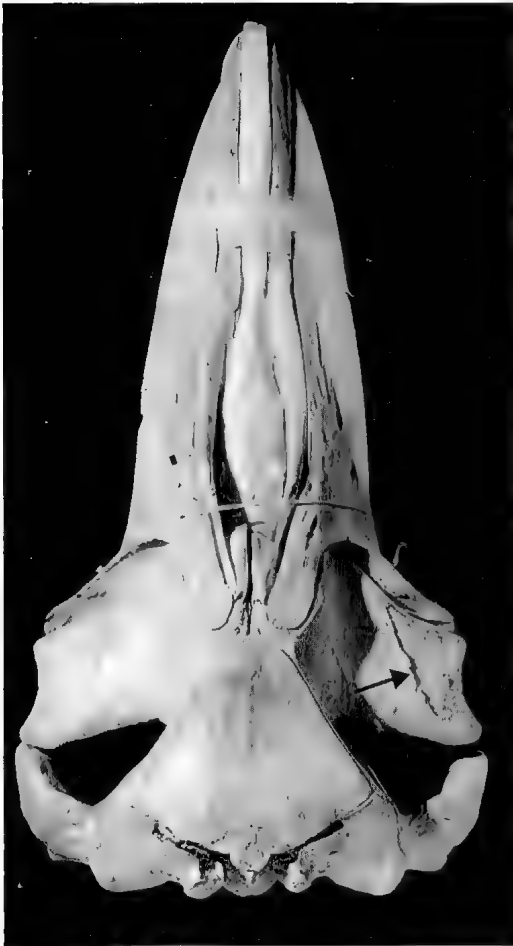
FIG. 4. Humpback whale QMJM7303. Dorsal view of skull (which measures 113cm in length) demonstrating periosteal new bone formation on the lateral aspect of the supra-orbital process of the right frontal bone.

formation was limited to the edge of the lesion (Fig. 4).

Most data concerning foetal presentation and the mechanism of parturition in cetaceans derive from studies of captive odontocetes. Caudal presentation is usual (McBride & Kritzler, 1951; Slijper, 1962), a presentation considered disadvantageous in large domestic animals. Arthur (1964) noted that in such animals the foetus is wedge-shaped when the presentation is cephalic and this serves to progressively dilate the birth canal during its passage, whereas in caudal presentation compression of the foetal abdomen causes expansion of the ribs and the costal arch engages abruptly. Also, the foetal occiput, often

the broadest foetal part, makes an abrupt [pelvic] engagement. Caudal presentation has been noted in a humpback whale (Dunstan, 1957) and such presentation in mysticetes could be associated on occasions with the difficulties described by Arthur (1964), although the pelvic structures of cetaceans and large terrestrial animals differ considerably. Hartley (1983) listed contusions to the cranial periosteum and rib fractures among the postmortem findings in a large series of foal perinatal mortalities.

We conclude on the basis of available evidence that the pericranial and rib injuries in QMJM7301 and QMJM7303 were sustained during parturition. However, it remains conjectural if they contributed to the premature deaths of these whales.

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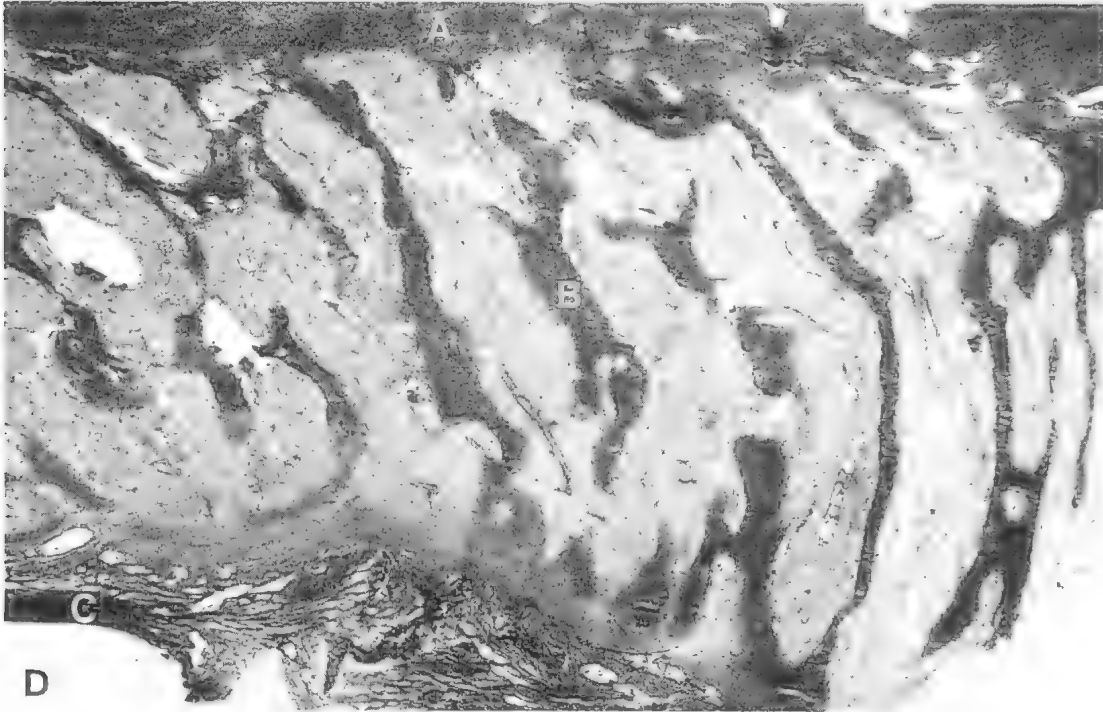
FIG. 5. Humpback whale QMJM7303. Histological section (x100) from edge of supra-orbital lesion demonstrated in Fig. 4. Thickened periosteum (A) is seen superiorly; spicules of vertically arranged osteoid seams (B) with intervening connective tissue are seen centrally and a layer of fibrous tissue (C) lines a sub-periosteal cyst (D) at the lower left of the photograph. The appearances are those of periosteal separation with some new bone formation superficial to a post-traumatic sub-periosteal cyst.

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SURVIVAL OF A LARGE *CROCODYLUS POROSUS* DESPITE SIGNIFICANT LOWER JAW LOSS. *Memoirs of the Queensland Museum 39(2): 338. 1996:-* On 25 May, 1995 a large (SVL 195.5cm; TL 424.5cm), male crocodile (*Crocodylus porosus*) was caught in the Nicholson River, NW Qld (17°44'S, 139°31'E). It was captured in a mesh trap, set under the supervision of the Department of Environment and Heritage. The crocodile had attacked and killed a dog. A significant portion of its dentary, including the symphysis to the region of the 10th and 11th tooth alveoli, had been lost. The right partial dentary, which closed first, was 7.5cm shorter than the left, resulting in an uneven closing of the jaws. The tongue had also been partially amputated, but had healed with a large egg-shaped growth at the anterior edge. This was apparently an area of scar tissue resulting from the trauma or from the inclusion of a bone fragment in surrounding tissue. The tongue appeared to be hypertrophied, probably as a result of its continued involvement in the closing and manipulation of the two dentary fragments. Rather than a normal, flat appearance, buccal edges were greatly enlarged, giving the tongue a pillowed appearance. This crocodile had sustained several other injuries, including scarring on the trunk in front of the hind limbs and amputation of the first and second metatarsals of the right foot. Many teeth were also missing from both lower jaws. (It was not possible to ascertain whether these had fallen out with age or wear, or had been broken during aggressive encounters with other crocodiles).

A wide variety of abnormalities and injuries have been recorded amongst crocodiles (Iordansky, 1973). Some studies of injuries have focussed on particular species (e.g. *Crocodylus niloticus* by Cott, 1961; *C. johnstoni* by Webb & Manolis, 1983 and *C. porosus* by Webb & Messel, 1977). Many injuries sustained by crocodiles result from conflicts related to social behaviour and territoriality. There have been few studies of large crocodiles in the wild. Of 1345 specimens of *C. porosus* examined in one study, only 10 had snout-vent lengths greater than 150cm because, in wild populations, juveniles predominate (Webb & Messel, 1977). The least commonly recorded injuries in large crocodiles are those to the head. They account for only 25% of scarring in large crocodiles (TL >150cm, Webb & Messel, 1977). This is not surprising, because many crocodiles sustaining significant head injuries would die. One example (Webb & Manolis, 1989) was found dead, having lost the dorsal portion of its snout during combat.

The injuries sustained by the Nicholson R. crocodile were significant (Fig. 1). No estimate of when the jaw loss occurred can be made. The specimen was in good condition, with large fat reserves at the base of the tail and neck. It had been known in the area by locals, because of his distinctive head, for at least 18 years. Despite this, there had been no reports of a damaged lower jaw. The crocodile apparently survived largely by exploiting a cattle station rubbish dump where cattle offal, road-killed wallabies and feral pig carcasses were dumped. To do so, it walked close to 50m from the river. It would locate a carcass by smell, and go straight to it, regardless of the difficulty of the terrain. The crocodile would grasp the carcass in its jaws and return to the water by the easiest path, to feed. Abundant tracks indicated that this crocodile actively moved about on land several nights each month.

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Stephen Irwin, Queensland Reptile Park, Glasshouse Mountains Tourist Drive, Beerwah, Queensland 4519, Australia; 23 february 1996.
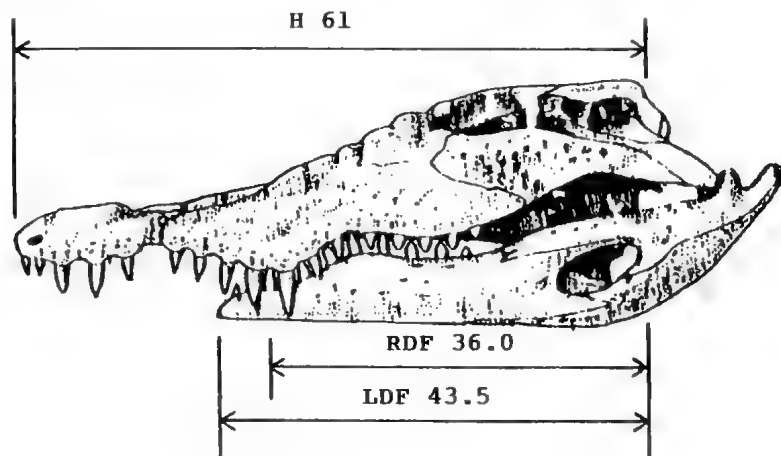

FIG. 1. Lateral view of injury with details of measurements taken at time of capture. Head (H). Left dentary fragment (LDF). Right dentary fragment (RDF). All measurements in centimetres

FOUR NEW RECORDS OF SURGEONFISHES (PERCIFORMES: ACANTHURIDAE) FROM THE GREAT BARRIER REEF

KENDALL D. CLEMENTS AND JOHN E. RANDALL

Four species of surgeonfishes are recorded from the outer Great Barrier Reef for the first time. They are: *Acanthurus maculiceps* (Ahl), *Naso minor* (Smith), *Naso thynnoides* (Valenciennes) and *Ctenochaetus tominiensis* Randall. □ *Great Barrier Reef, surgeonfishes.*

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Four species of surgeonfishes new to Australia were found along the outer shelf reefs of the northern Great Barrier Reef(GBR): *Acanthurus maculiceps* (Ahl), *Naso minor* (Smith), *N. thynnoides* (Valenciennes), and *Ctenochaetus tominiensis* Randall. All except *N. minor* occur around New Guinea (Allen & Swainston 1993; Randall 1994). Prior to this report, 36 species of surgeonfishes were recorded from the GBR and Coral Sea (Randall et al. 1990). The Acanthuridae (surgeonfishes) consists of 73 species, mostly from the Indo-Pacific region. The most distinctive feature of the family is the sharp spine or spines on the caudal peduncle.

SYSTEMATICS

Material is housed in the Australian Museum (AMS), and Bernice P. Bishop Museum (BPBM).

Family ACANTHURIDAE

Acanthurus maculiceps (Ahl, 1923)
(Fig. 1)

Hepatus maculiceps Ahl, 1923:36. (type locality, Talassia, New Britain).

MATERIAL. AMSI37145-001, 213mm SL, No Name Reef (Reef 14-139), 14°38'S, 145°38'E, dense coral growth near reef crest, adjacent to the reef pass, 4m, spear, K.D. Clements, 16 November 1995.

DIAGNOSIS. Dorsal rays IX,25; anal rays III, 23; pectoral rays 17 (including rudimentary uppermost ray); anterior gill rakers 20; posterior gill rakers 22; 14 upper and 18 lower teeth; body moderately deep for genus, depth 2.1 in SL, compressed, width 2.95 in depth; head length 3.3 in SL; dorsal profile of head strongly convex; snout length 4.3 in SL; orbit diameter 4.8 in head length; caudal peduncle depth 8.45 in SL; ninth dorsal spine longest, 6.35 in SL; caudal fin lunate, the caudal concavity 5.3 in SL; caudal spine 3.0 in head length. Stomach thickwalled. Colour in alcohol: dark brown with a horizontal black band (narrowing at each end) at upper end of gill opening from behind eye to 1.5 orbit diameters posterior to gill opening; a narrow black margin at edge of caudal spine socket; numerous faint small pale spots on head; a transverse whitish band on chin; dorsal fin with 9 narrow pale stripes alternating with dark brown, and a narrow black margin; anal, caudal, and pelvic fins dark brown; pectoral fins dark brown, with a pale spot distally on upper half.

REMARKS. This species is known from Christmas Island (Indian Ocean), Ryukyus, Philippines, Indonesia, Palau, Marianas, Marshall Islands, Kiribati, Tuvalu, Samoa, Line Islands, and Caroline Islands (Randall, 1956; Myers, 1989; Jones et al., 1993. It is distinguished from other surgeonfish in colour by a combination of the white caudal spine with a black margin, the patch of yellow on the distal third of the pectoral fin, the black lozenge-shaped mark extending backwards from the upper edge of the operculum, numerous small pale yellow spots on the head, and an irregular white bar at the base of the caudal fin.

Ctenochaetus tominiensis Randall, 1955
(Fig. 2)

Ctenochaetus tominiensis Randall, 1955: 163. (type locality, Gulf of Tomini, Sulawesi).

MATERIAL. BPBM14726, 64.5mm SL, NW side of horseshoe-shaped reef at S boundary of Pandora entrance, 11°30'S, 144°00'E, rich coral bottom, 14m, multiprong spear, R.C. Steene, 20 November 1972.

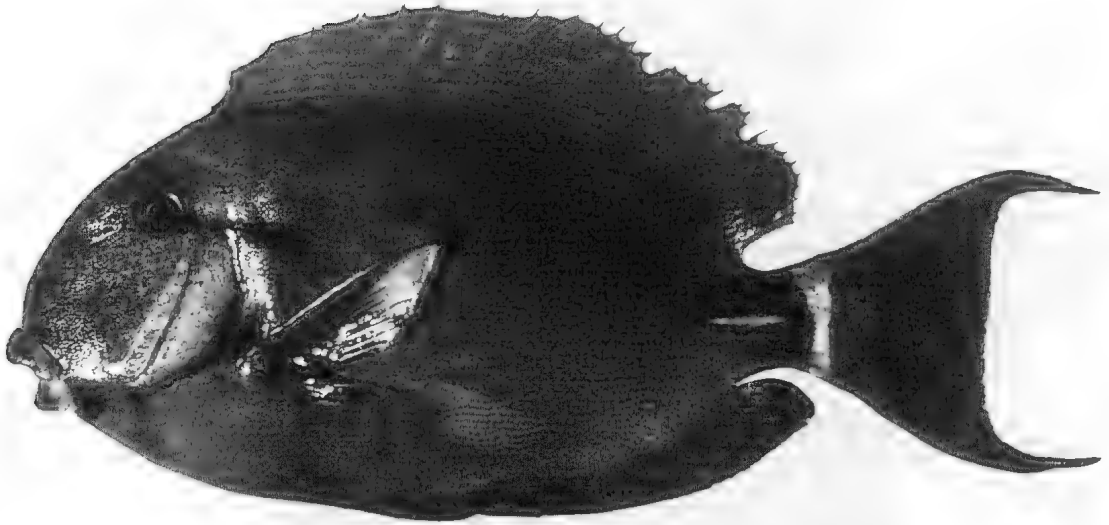DIAGNOSIS. Dorsal rays VIII,26; anal rays

FIG. 1. *Acanthurus maculiceps* (Ahl,1923), AMSI37145-001, No Name Reef, Great Barrier Reef.

FIG. 2. *Ctenochaetus tominiensis* Randall, 1955, BPBM14726, Pandora Reef, Great Barrier Reef.

III,24; pectoral rays 16 (including short splint-like upper ray); anterior gill rakers 20; posterior gill rakers 21; teeth slender and flexible with expanded incurved tips, 25 in upper jaw and 28 in lower; distal half of expanded part of upper teeth smooth-edged, lower half with 3 denticula-

tions; expanded outer part of lower teeth with 3 denticulations (including the tip, much the broadest); edges of lips strongly papillate; body very deep, depth 1.75 in SL, strongly compressed, width 3.1 in depth; head length 3.0 in SL; snout length 4.2 in SL; orbit diameter 5.4 in head length; caudal peduncle depth 9.1 in SL; eighth dorsal spine longest, 5.5 in head length; caudal fin lunate, the caudal concavity 4.2 in SL. Colour in alcohol: head, body and paired fins brown; caudal fin light brown (may be whitish in life); spinous portion of dorsal fin brown, with faint curving oblique pale bands alternating with brown bands, becoming horizontal in outer posterior part of soft portion of fin; soft portion of dorsal and anal fins brown with a broad distal pale zone (bright orange in life) except for a narrow black margin; a black spot at rear base of dorsal fin and a less distinct blackish one at rear base of anal fin; anterior nostril white.

REMARKS. This species is known from Indonesia, Philippines, PNG, and the Solomon Islands. The dorsal and anal softray counts of the GBR specimen are higher than the recorded range (Randall, 1955, table 1), but fin-ray counts of BPBM material are equally high. *C. tominiensis* is distinguished within the genus by the broad orange borders of the soft dorsal and anal fins.

Naso (Axinurus) minor (Smith, 1966)
(Fig.3)

Axinurus minor Smith, 1966:638 (type locality, Pinda Reef, Mozambique).

DIAGNOSIS. See Randall, 1994.

REMARKS. Underwater photographs of this species were taken on the outer reef slope at the north end of No Name Reef (Reef 14-139:

14°38'S, 145°38'E) in 20-30m on 18/1/95, and at the south end of the same reef in 25-30m on 23/1/1995 (Fig. 3). Schools of *N. minor* were observed at the N end of Hick's Reef (Reef 14-086: 14°26'S, 145°28'E), in 15-25m on 24/1/95.

These observations involved schools of 15-20 individuals moving rapidly over the shelf at the base of the escarpment. The schools appeared to move up onto this shelf from deeper water. *N. minor* is common on the seaward side of outer shelf reefs in the northern section of the Great Barrier Reef. The lack of any previous Australian record is probably due to the limited diving on these deepslope habitats, and because *Naso minor* is difficult to approach underwater. We could not collect specimens by spear and our photographs could only be taken from a distance. This species is known from the Philippines, Indonesia, Reunion, and Mozambique (Randall, 1994).

Naso (Axinurus) has a single fixed keel-like spine on each side of the caudal peduncle (Randall, 1994). Other species of *Naso* have two fixed caudal spines. *Naso minor* may be distinguished within the genus by the combination of a single black caudal spine and a bright yellow caudal fin and by the male frequently adopting a distinct countershading pattern (Randall, 1994, pl. 2B).

Naso thynnoides (Valenciennes, 1835)
(Fig.4)

Axinurus thynnoides Cuvier, 1829: 225 (nomen nudum). Valenciennes in Cuvier and Valenciennes, 1835:299, pl. 293 (type locality, Dorey Harbour, New Guinea).

DIAGNOSIS. See Randall, 1994.

REMARKS. Underwater photographs of this species were taken at the north end of Hick's Reef
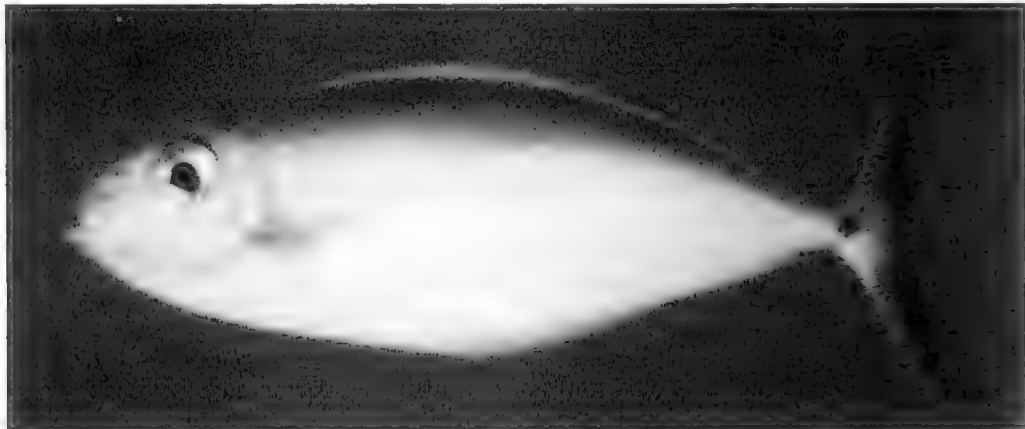

FIG. 3. Underwater photograph of *Naso minor* (Smith, 1966), No Name Reef, Great Barrier Reef.

(Reef 14-086: 14°26'S, 145°28'E) in 15-25m on 24/1/95 and 25/1/1995. On both occasions a group of approximately 6 individuals were moving rapidly over the slope. On the first occasion these fish were schooling with a much larger group of *N. minor*. Attempts to collect specimens by spear were unsuccessful. The N end of Hick's Reef is unusual for outer reefs in the vicinity as the shelf between the base of the escarpment and the outer dropoff is relatively shallow (cf. 20-35 m in other places). We have not seen *N. thynnoides* elsewhere on the GBR.

N. thynnoides may be distinguished within the genus by a single caudal spine and a series of narrow, dark bars on the body (Randall 1994). The caudal fin in the specimens of *N. thynnoides* in our photos is grey, not distinctively yellow as in *N. minor* or blue as in *N. caeruleacauda* (Randall 1994). Colour of *N. thynnoides* photographed at Hick's Reef is very similar to Randall, 1994, pl.1A. It is known from the western Indian Ocean, Philippines, Amami-Oshima Islands, Ryukyu Islands, Indonesia, Solomon Islands, Tuvalu, Caroline Islands, and Maldive Islands (Jones et al., 1991; Randall, 1994).

ACKNOWLEDGEMENTS

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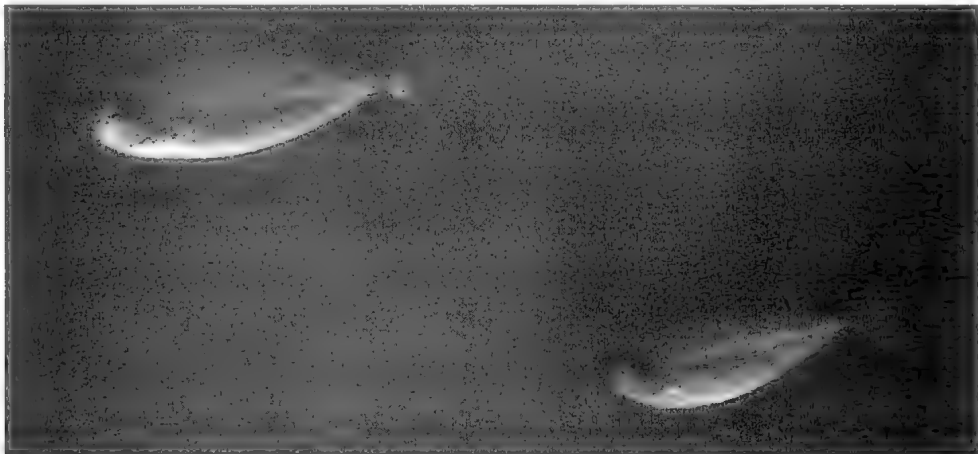

FIG. 4. Underwater photograph of *Naso thynnoides* (Valenciennes, 1835), Hick's Reef, Great Barrier Reef.

NEW LAND SNAILS FROM BOGGOMOSS ENVIRONMENTS IN THE DAWSON VALLEY, SOUTHEASTERN QUEENSLAND (EUPULMONATA: CHAROPIDAE AND CAMAENIDAE)

JOHN STANISIC

Land snails, *Elsothera hewittorum* sp. nov. (Charopidae) and *Adclarkia dawsonensis* gen. et sp. nov. (Camenidae) are described from on and near mound spring environments in the Dawson Valley, southeastern Queensland. These mound springs, locally known as boggomosses, are significant perennially moist habitats, in a predominantly dry environment. Relationships and biogeographic significance of the species are assessed. The roles of the Dawson Valley and the scattered mesic habitats occurring there are examined in regard to past episodes of land snail migration. It is concluded that the boggomosses are central to dispersal of wet-adapted biota in the region. □ *Mollusca, Eupulmonata, Charopidae, Camaenidae, biogeography, boggomosses.*

John Stanisic, Queensland Museum, PO Box 3300, South Brisbane, Queensland 4101, Australia; 25 August 1995.

The Dawson Valley, southeastern Queensland (SEQ) is located in relatively snail-poor countryside. The microphyll vine forests and semi-evergreen vine thickets of the coastal and sub-coastal ranges to the east support some of the richest land snail communities of eastern Australia with up to 40 species recorded at several sites (Stanisic, 1994). However, in southern Queensland land snail diversity decreases rapidly with increased distance from the coast and sites within the Dawson Valley support <10 species.

Climate of the Dawson Valley is sub-humid, being transitional between the eastern humid and western semi-arid regions (Nix, 1977). Rainfall is 600-700mm annually and mesic refugia which are liable to support land snails are scarce. Much of the Dawson Valley has been cleared for cultivation and grazing. In the remaining natural areas, dry open forest and woodland communities, dominated by *Acacia harpophylla* (brigalow), are conspicuous (Johnson, 1984) (Fig. 1C,D). Highly developed rainforest does not occur, but semi-evergreen vine thicket characterised by *Brachychiton rupestre*, is sparsely scattered in the region (Speck, 1968). This vegetation community is usually found on basalt-derived brown and grey-brown loams and clays. Besides well-drained soils, vine thickets also favour the limited rocky outcrops in the area (Fig. 1A,B). These outcrops act as moisture reservoirs and provide protection from fires. Other moist microhabitats are found along drainage lines (Fig. 1F) where weathered alluvium and outcropping Tertiary rocks furnish suitable conditions for the maintenance of small discontinuous pockets of 'rainforest-derived' flora (pers. obs.). In this context new land snails on and around the boggomoss on Mount Rose Station (Fig. 1E), NE of Taroom, Dawson Valley raise interesting questions on significance of scattered mesic refugia to land snail survival in marginally dry areas.

BOGGOMOSSES

The boggomosses are a series of small, elevated peat bogs or swamps scattered among the woodland communities near Taroom, on the Dawson River. They are fed by mound springs which are leakages from aquifers of the Great Artesian Basin (Wilson, 1995). Water forces its way to the surface through faults in the underlying sandstone. Where this water percolates above the ground a unique mesic habitat is formed. Sedges, tall grasses and ferns form a green ground-carpet of vegetation; sometimes an understorey of smaller trees is developed. Large gums are a feature. In many cases the dominant large tree species is *Eucalyptus coolabah* (coolibah) whose size and shallow root system combined with the soft, moist substrate in which it lives, makes it vulnerable to wind damage. Thus a feature of the boggomosses is a large amount of ground-strewn, branch and whole tree debris which provides a diverse array of litter-zone microhabitats. Although a number of the boggomosses have been degraded to varying degrees by stock, and in some instances fire, they are still significant habitats for moisture loving biota.
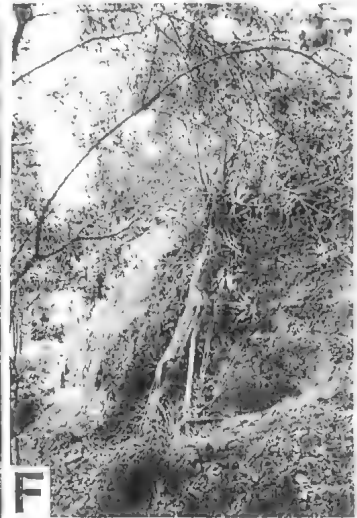
SYSTEMATICS

Class GASTROPODA
Order EUPULMONATA
Suborder STYLOMMATOPHORA
Family CHAROPIDAE

Elsothera Iredale,1933

Elsothera Iredale,1933:53; Iredale,1937a:324 Iredale,
    1937b: 24; Stanisic,1990:160; Smith,1992:187.
 TYPE SPECIES. *Helix sericatula* Pfeiffer,1850; by
original designation.

REMARKS. *Elsothera* is characterised by
species which have strongly, radially ribbed ,
brown to greyish shells (often with darker
periostracal streaks) , with or without an um-
bilicus and with a protoconch that has pre-
dominantly radial ribs and low, moderately
spaced spiral cords. The complex vas deferens/
epiphallus junction, expanded vas deferens and
penis with very enlarged apical bulb and reduced
sheath is a combination of characters peculiar to
Elsothera sensu Stanisic,1990. *Elsothera* pre-
viously extended from SE S AUST into N NSW.
The new species significantly extends the range
of the genus. As presently understood, it is
probably the most ecologically diverse genus of
the Charopidae, inhabiting rainforest, wet and dry
sclerophyll forest, and woodland.

Elsothera hewittorum sp. nov.
(Figs 2A-C; 3A-F; 4A-D)

 ETYMOLOGY. For the Hewitt family, owners of
Mount Rose Station, Taroom.
MATERIAL   EXAMINED.   HOLOTYPE
QMMO56283, Taroom, c.45km NE on Mt Rose Stn,
SEQ (25°27'15"S,150°01'15"E), under log beside
boggomoss, woodland. Collected J.Stanisic, 23 May
1995. Height of shell 2.52mm, diameter 5.21mm, H\D
ratio 0.51, D\U ratio 3.49, whorls 4 3\4. PARATYPES
QMMO56281, 6 specimens, same data as holotype.

DESCRIPTION. Shell (Fig. 2) small, diameter
4.87-5.29mm (mean 5.06mm) with 4 1/2-5 (mean
4 3/4) evenly coiled whorls. Apex and spire
slightly elevated, height of shell 2.27-2.94mm
(mean 2.57mm), SP\BWW ratio 0.10-0.20 (mean
0.13),H/D ratio 0.47-0.61 (mean 0.51).

Fig. 2. A-C, holotype of *Elsothera hewittorum* sp. nov.,
QMMO56283, Mt Rose Stn. Scale line=3mm.

FIG. 1. Vegetation communities in the Taroom area, Dawson Valley, SEQ. A,B, vine thicket on rocky outcrop,
Mt Rose Stn; C, open woodland, Boggomoss Stn; D, brigalow\eucalypt association, Boggomoss Stn; E,
boggomoss, Mt Rose Stn, the type locality of *Adclarkia dawsonensis* sp. nov.; F, remnant vine thicket along
edges of Cabbage Tree Creek, near Taroom.
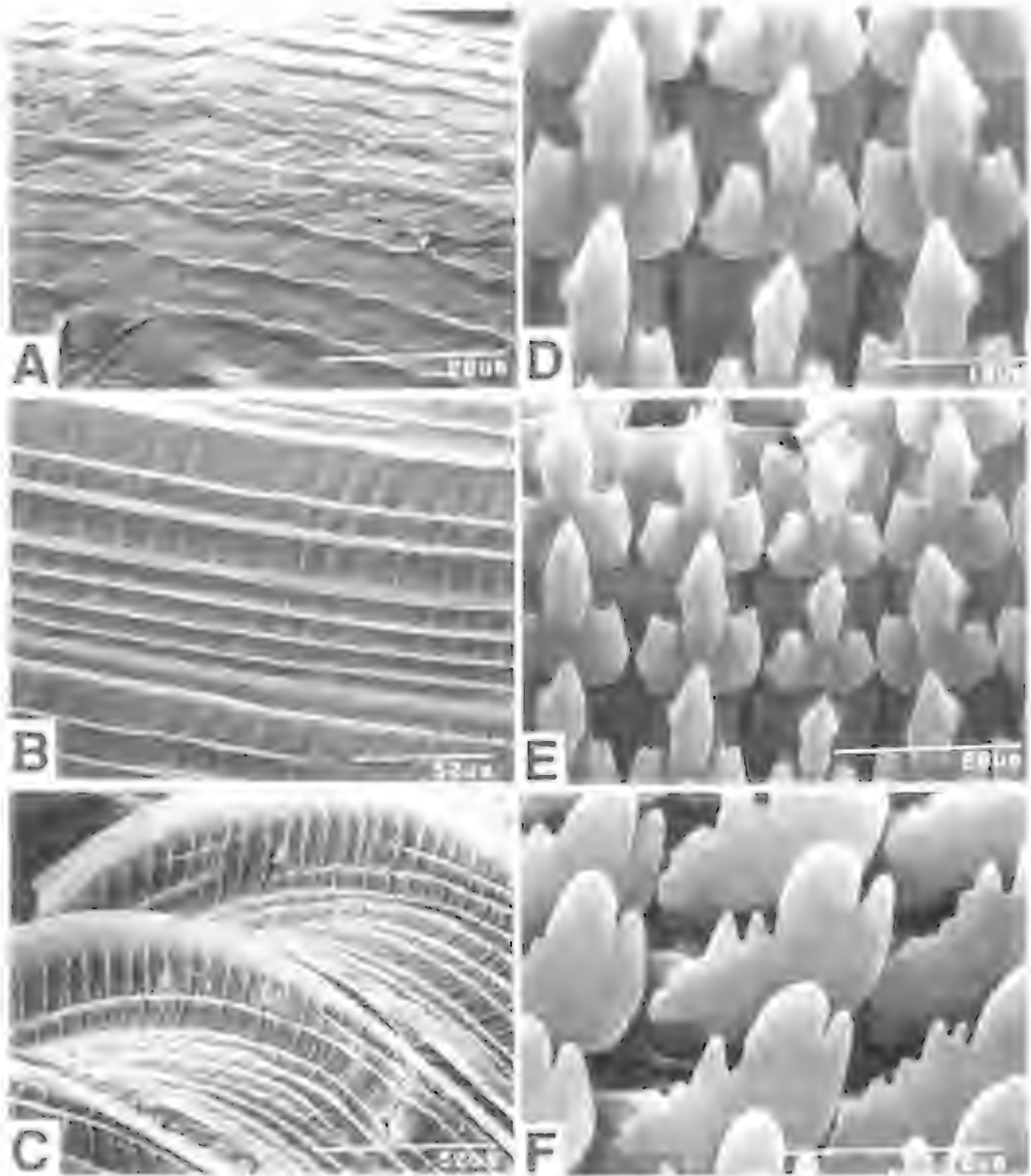
FIG. 3. Shell and radular details of *Elsothera hewittorum* sp. nov. , QMMO56283, holotype, Mt Rose Stn. A, apical sculpture. B, body whorl sculpture. C, close-up of a major rib to show extent of microsculpture. D,E, central and inner lateral teeth. F, marginal teeth. Scale lines as marked.

Protoconch somewhat dull, of 1 1/4 whorls, approximate width 620(m. Apical sculpture (Fig. 3A) of evenly and moderately spaced, fine wavy, spiral cords and weak, slightly curved low radial ridges, mainly on the second half of the protoconch, becoming more pronounced toward the protoconch-teleoconch boundary. Post-nuclear sculpture (Fig. 3B) of crowded, pro-minent, weakly protractively sinuated radial ribs, each with a well developed periostracal blade. Ribs on body whorl 144-176 (mean 157). Micros-culpture (Fig. 3B) of fine radial riblets, 4-8 be-tween each pair of major ribs, and fine, crowded spiral cords; microsculpture continuous on major ribs (Fig. 3C). Umbilicus wide, deep cup-shaped, diameter 1.29-1.64 (mean 1.46mm), D/U ratio
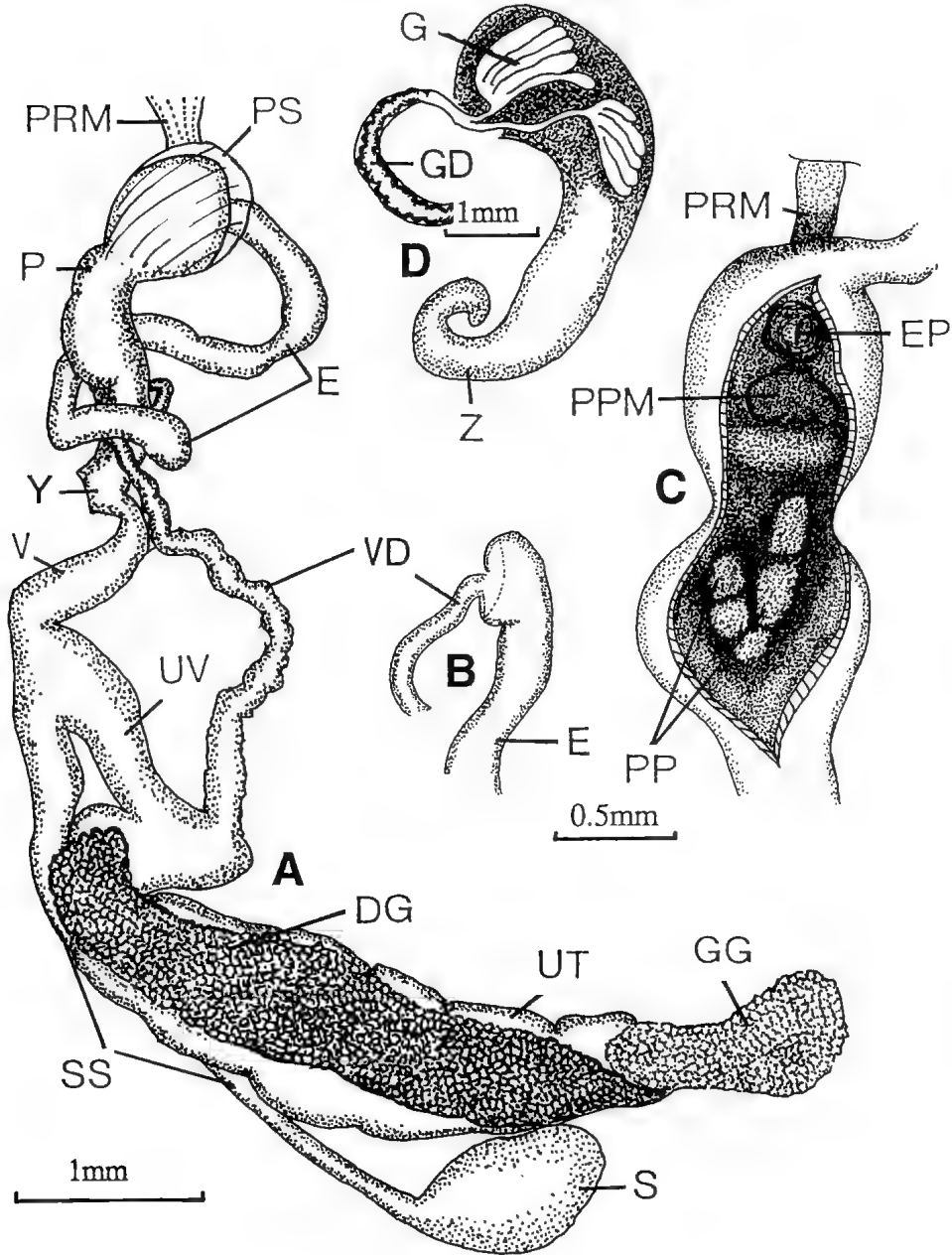
FIG. 4. Reproductive anatomy of *Elsothera hewittorum* sp. nov. , QMMO56283, holotype, Mt Rose Stn. A, reproductive system. B, vas deferens-epiphallus junction. C, penis interior. D, ovotestis. Abbreviations outlined in text. Scale lines as shown.

3.19-3.78 (mean 3.49). Sutures impressed, becoming more so as the last whorl slowly descends. Aperture subcircular, lip simple. Colour of shell greyish-brown with occasional darker periostracal streaks. Based on 5 measured specimens (QMMO56281, QMMO56283).

Penis (P) (Fig. 4A) relatively long, with a prominent apical bulb. Penial sheath (PS) only in the bulb region. Penis internally (Fig.4C) with a

series of low spongy thickenings distally (PPS) and a prominent fleshy, irregularly shaped pilaster proximally (PPM); basal region of penial chamber separated from apical region by a low circular collar-like thickening. Epiphallus (E) long,muscular and twisted about the penis, internally with longitudinal thickenings, entering penis apically through a simple pore (EP). Penial retractor muscle (PRM) attached to penial bulb adjacent to the penis-epiphallus junction.Vas deferens (VD) initially an expanded tube with prominent glandular walls, descending to the peni-oviducal angle, then ascending and twisting about the penis prior to becoming a thin tube and entering the epiphallus through a fleshy, circular collar (Fig.3B). Vagina (V) c.1/2 the length of the penis. Free oviduct (UV) large, swollen. Prostate-uterus (DG\UT) without unusual features. Atrium (Y) short. Spermatheca (S) with an enlarged base, long and thin stalk (SS) and large, ovate head appressed to the surface of the albumen gland (GG). Hermaphroditic duct (GD) typical. Ovotestis (G) (Fig. 3D) two clumps of finger-like alveoli oriented parallel to the plane of coiling and embedded in the apical whorls of the digestive gland (Z). Animal colour grey. Radula (Fig. 3D-F) with tricuspid central and lateral teeth (central slightly smaller) in which the mesocone is long and lanceolate, ecto- and endocones short and acutely pointed; marginal teeth multicuspid due to ectoconal splitting. Based on one dissected specimen (QMMO56281).

COMPARATIVE REMARKS. *Elsothera hewittorum* sp.nov. resembles *E. funerea* (Cox,1868) from NSW (type locality:Mudgee) and *E. nesana* Iredale,1937 (type locality:Port Lincoln, South Australia). [The latter species was considered a synonym of *E. murrayana* (Pfeiffer, 1864) by Smith (1992) but has a tighter coiling pattern and much finer ribbing]. Compared with *E. funerea*, *E. hewittorum* is smaller with less elevated spire and apex, has smaller whorls, finer adult ribbing, larger umbilicus and almost obsolete radial ribs on the the protoconch (Fig. 3A). *E. nesana* has similarly disposed radial ribs but has larger whorls,more prominent radial ribs on the protoconch and a basally flattened body whorl. *E. nautilodea* (Cox,1866) and *E. genithecata* Stanisic,1990 from NE NSW are readily distinguished from the new species by their closed umbilici. *E. sericatula* (Pfeiffer,1850) from central coastal NSW has a closed umbilicus and radial ribs on the entire protoconch. *E. murrayana* has more loosely coiled whorls and widely

spaced bold radial ribs. The combination of very small, brown shell with dense radial ribbing, slightly raised spire and relatively wide umbilicus distinguishes *E. hewittorum* from other land snails of the Dawson Valley.

RANGE AND HABITAT. Known only from the type locality. More westerly species of this complex (*E.funerea, E.nesana, E.murrayana*) inhabit drier woodland environments with a preference for mesic refuges such as rocky outcrops, particularly limestone (Stanisic unpubl. data). *E.hewittorum* has a similar ecologic preference.

REMARKS. Generic assignment of *E. hewittorum* is based on structural similarity of its reproductive system to that of *Elsothera* by Stanisic (1990). However, the anatomical consistency of species of *Elsothera* (Iredale, 1937a,b; Stanisic,1990; Smith, 1992) underpins a wide variation in shell form. Shell shape has a strong ecological correlation (Solem & Climo, 1985; Stanisic,1990) and the variability in this character in *Elsothera* reflects the diverse ecological preferences of its members. *E. hewittorum* is closest to *E. funerea* and *E. nesana* with which it shares a greyish-brown shell with very open umbilicus and apical sculpture of radial ribs and prominent spiral cords. The three species also live in similar habitats.

Family CAMAENIDAE
Subfamily CAMAENINAE

Adclarkia gen. nov.

ETYMOLOGY. For Adam Clark of Taroom.
TYPE SPECIES. *Adclarkia dawsonensis* sp. nov.

DIAGNOSIS. Shell large, relatively thin, with weakly elevated spire and apex, comparatively small umbilicus and weakly reflected lip. Apical sculpture of scattered subcircular pustules. Adult sculpture of very weak radial growth ridges and moderately spaced elongate pustules ; microsculpture of fine periostracal ridgelets. Genitalia elongate,with a long tubular penis, short epiphallic flagellum and proto-sheath enveloping penis, epiphallus and epiphallic flagellum. Penial retractor muscle inserted on epiphallus. Penis internally with prominent pustules and a wrinkled tubular verge with a terminal pore. Head wart present.

COMPARATIVE REMARKS. The shell of

Adclarkia bears little resemblance to other large Queensland camaenids. The relatively thin, almost monochrome shell is in direct contrast to the larger, striped and solid-shelled camaenids of coastal regions. Taxonomic significance of these external differences is supported by the reproductive anatomy, which in *Adclarkia* has numerous irregularities not seen in moist-forest camaenids further east (Solem, 1992a). In particular the proto-sheath and pattern of penial pustules contrasts with the muscular penial sheath and very complicated penial sculpture in *Sphaerospira* Morch, 1867, *Bentosites* Iredale, 1933 and *Hadra* Albers, 1860. *Meridolum* Iredale, 1942 and *Thersites* Pfeiffer, 1842 (see Solem, 1992a) from coastal regions of southern New South Wales and southern Queensland have a protosheath rather than a prominent penial sheath and pustulose penial wall sculpture. However, the shells of these two genera have different form and microsculpture. Only *M.gilberti* (Pfeiffer, 1846) has shell surface pustules but these are round and crowded and lack the periostracal scales of *A. dawsonensis*. *Galadistes* Iredale, 1938 from inland northern New South Wales and *Pallidelix* Iredale, 1933 from the Expedition Range in southern Queensland have yet to be examined anatomically. These genera have pustules on the adult shell but differ in form (circular) from those of *Adclarkia*. They also have quite different shell shape (globose) and apical sculpture (very crowded pustules).

Cupedora Iredale,1933 from eastern South Australia most resembles *Adclarkia* in anatomy and shell. Both genera have a proto-sheath and similar pustulation in the penis. However, in *Cupedora* the pustulations in the penial chamber are largely confined to the upper half with prominent longitudinal ridges in the lower half. In particular the shell sculpture of *Cupedora* (see Solem, 1992a, pl. 26, figs c,d), apart from the shape of the pustules, is very similar to that of *Adclarkia*. Main differences are the the greater calcification in shells of *Cupedora* and their tendency to have reddish chestnut bands in most cases.

Adclarkia dawsonensis sp. nov.
(Figs 5, 6A-C, 7A-H, 8A-D)

ETYMOLOGY. For the Dawson Valley.
MATERIAL EXAMINED. HOLOTYPE QM MO56284, Taroom, c.45km NE, on Mt Rose Stn, SEQ (25°27'15"S, 150°01'15"E), in litter beneath sandpaper fig on boggomoss. Collected by J. Stanisic, J. Johnson, J. Short, 23 May 1995. Height of shell 14.58mm,

FIG. 5. *Adclarkia dawsonensis* sp. nov., QM MO56284, holotype, Mt Rose Stn.

diameter 21.68mm, H\D ratio 0.67, D\U ratio 9.86, whorls 5 1/8. PARATYPES QMMO56280, 4 subadults, 12 juveniles, same data as holotype; QMMO4239, 1 adult, Theodore, Dawson Valley, SEQ, under rubbish in damp situation; QMMO6779, 2 adults, Theodore, Dawson Valley, SEQ, in garden crawling after rain, ex S. McKay; QMMO56289,1 adult, 7 juveniles, same locality as holotype, under logs, C. Eddie, 11 July 1995.

DESCRIPTION. Shell (Fig. 6A-C) comparatively thin, diameter 21.68–25.74mm (mean 23.82mm) with 5 1/8–5 5/8 (mean 5 1/2 whorls. Apex and spire very slightly elevated, height of shell 14.58–16.62mm (mean 15.80mm), H\D ratio 0.65–0.67 (mean 0.67). Apical sculpture (Fig. 7A) of radially disposed, moderately spaced, irregularly elongate pustules. Spire and body whorl with densely scattered, elongate pustules (Fig.7B) and weak, radial growth ridges; in unworn specimens a small periostracal scale sits atop each pustule (Fig. 7C) . Microsculpture of fine, crowded ridgelets (Fig. 7B,C). Shell periphery rounded with last whorl slowly descending. Aperture subcircular. Lip weakly reflected, columellar margin dilated and partially covering the umbilicus. Umbilicus small, width 2.34–3.24mm (mean 2.63mm), D/U 7.15–10.55 (mean 9.26). Shell colour light-brown to greenish-yellow horn, occasionally with a narrow, red subsutural band and a small, red circumumbilical patch; lip white. Based on four measured specimens (QMMO56284, QMMO4239, QMMO6779).

Genitalia (Fig. 8A) with long vagina (V) and short free oviduct (UV). Vagina internally with high, thin, longitudinal pilasters. Spermatheca (S), with stalk swollen basally and head ap-
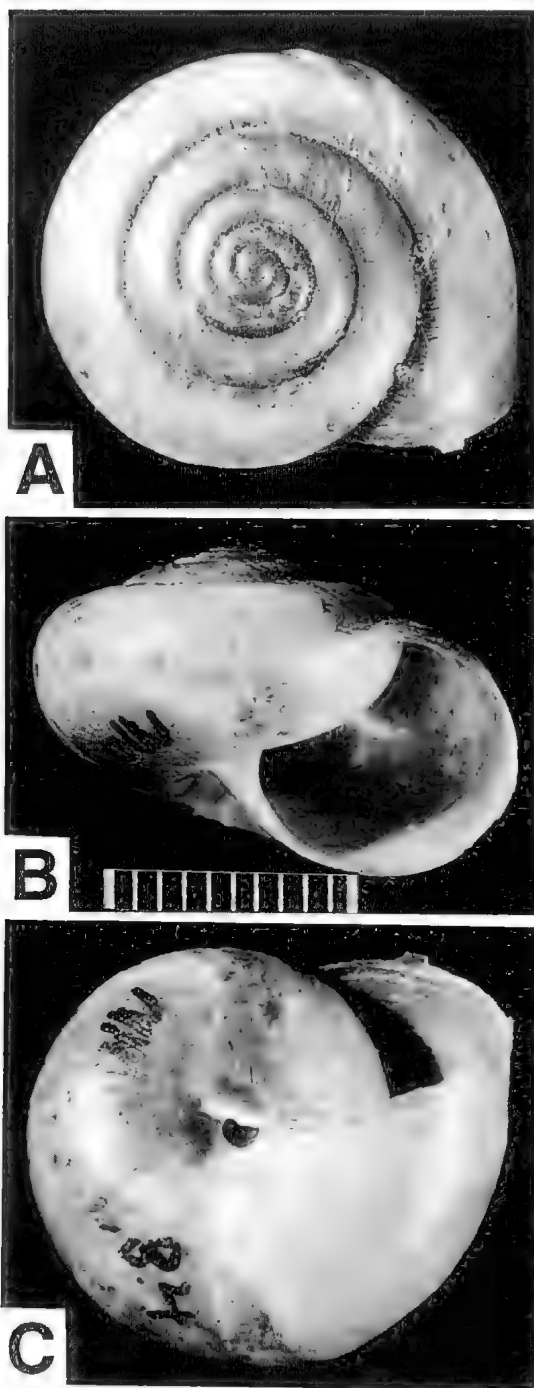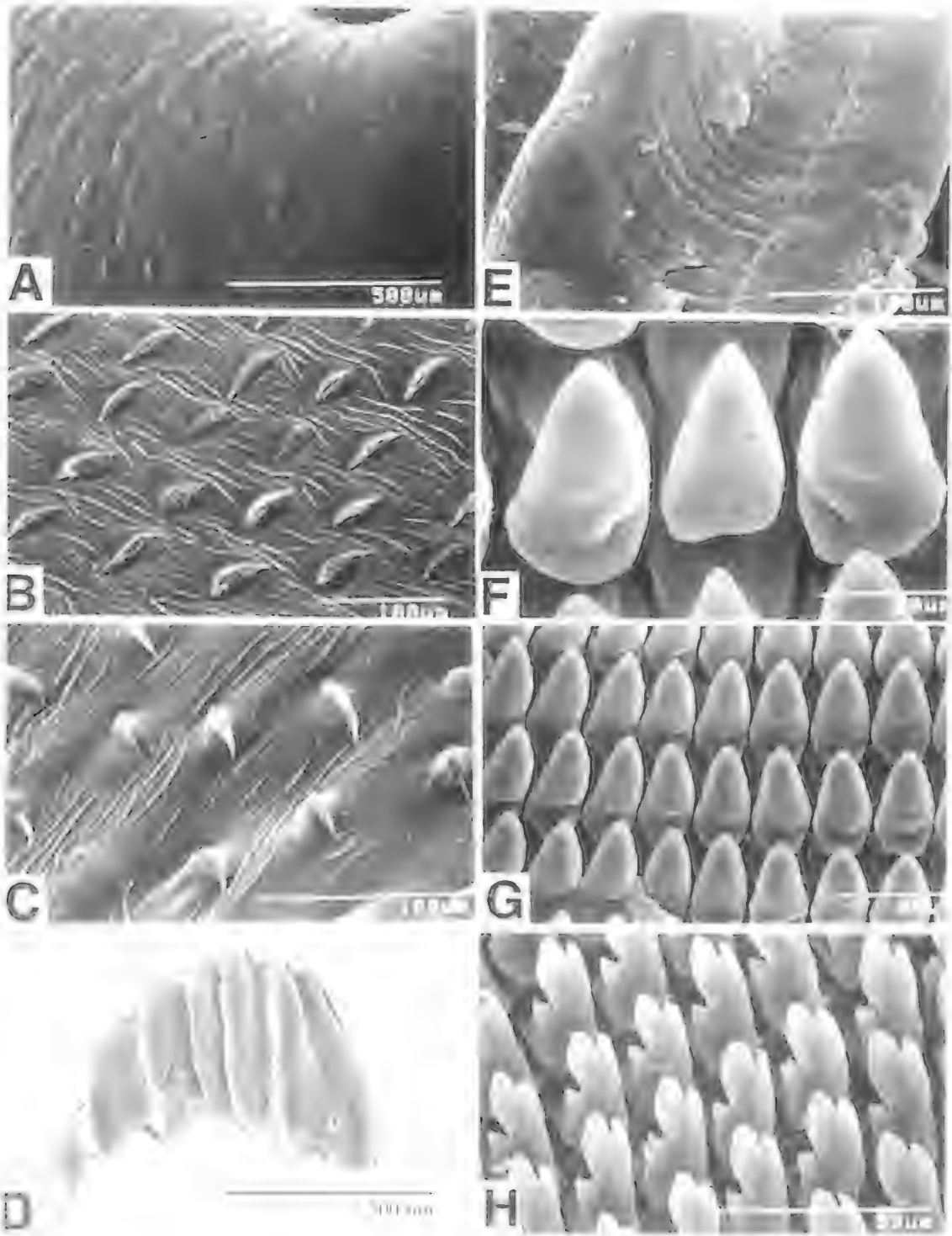
FIG. 6. A-C, Shell of *Adclarkia dawsonensis* sp. nov. QMMO56284, holotype, Mt Rose Stn. Scale in millimetres.

pressed to base of albumen gland (GG). Prostate-uterus (DG\UT) without unusual features. Terminal male genitalia enveloped in a sheath of connective tissue (PS). Penis (P) slightly longer than vagina, muscular; internally (Fig. 8B) with longitudinal rows of elongate pustules (PP) which become more crowded in the lower half of the penis before giving rise to fleshy longitudinal pilasters (PPL) in the lower quarter; apically with a wrinkled, tubular papilla (PV). Epiphallic pore (EP) terminal on the papilla. Epiphallus (E) a reflexed, muscular tube, about half the length of the penis, becoming enlarged about halfway along its length, internally with longitudinal thickenings; a short finger-like flagellum (EF) is located at the epiphallus-vas deferens junction. Vas deferens (VD) a thin tube descending from the prostate-uterus to the peni-oviducal angle, reflexing apicad of the angle. Penial retractor muscle (PRM) inserted on the epiphallus at the point where it reflexes. Talon (GT) short, finger-like, embedded in the surface of the albumen gland. Hermaphroditic duct (GD) weakly convoluted, not swollen. Albumen gland (GG) elongate, rusty-brown. Ovotestis (G) (Fig. 8C) several clumps of long, creamy-coloured, finger-like alveoli, in the apical whorls of the digestive gland (Z). Atrium (Y) without unusual features. Animal colour light brown to white with varying amounts of grey in the neck region, on the sides of the foot and above the tail. Surface of lung-roof and visceral coil with prominent, irregular black pigmentation (Fig. 5). Mantle mustard-orange. Head wart (Fig. 8D) located between the bases of the superior tentacles. Radula (Fig. 7F-H) with basically unicuspid central and lateral teeth, central slightly smaller, with very tiny ectocones situated half-way up the main cusp shaft. Lateral teeth with prominent anterior flare, reduced in central tooth. Lateromarginal teeth tricuspid with endocone located high up on the mesocone. Marginal teeth multicuspid with ectocone splitting into several minor cusps. Jaw (Fig. 7D,E) with several prominent central ribs, considerably reduced on the side and microscopically, transversely striated. Based on one dissected adult (QMMO56284).

FIG. 7. Shell, jaw and radular details of *Adclarkia dawsonensis* sp. nov., QMMO56284, holotype, Mt Rose Stn. A, apical sculpture. B, pustules and fine ridgelets on body whorl. C, body whorl pustules with periostracal scales. D, jaw. E, microsculpture on ribs of jaw. F,G, central and inner lateral teeth. H, marginal teeth. Scale lines as marked.
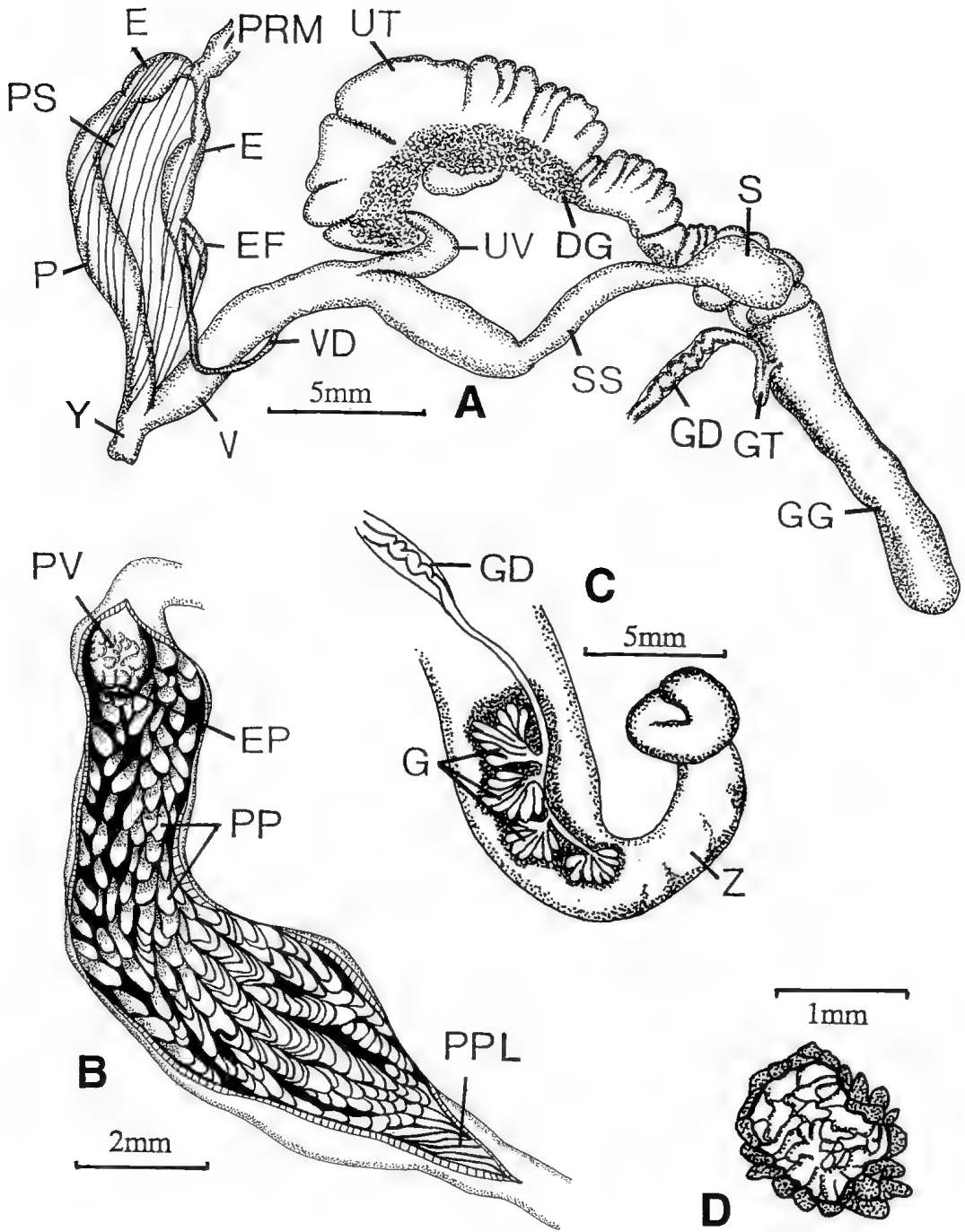
FIG. 8. Reproductive anatomy of *Adclarkia dawsonensis* sp. nov., QMMO56284, holotype, Mt Rose Stn. A, reproductive system. B, penis interior. C, ovotestis. D, head wart. Abbreviations outlined in text. Scale lines as marked.

COMPARATIVE REMARKS. A number of other large camaenids occur in the Dawson Valley. *Sphaerospira mattea* (Iredale, 1933) has a similarly shaped shell but is yellowish-white with several reddish-brown chestnut bands. No surface pustulation is present. The animal is reddish-grey with a red mantle. *Xanthomelon pachystylum* (Pfeiffer, 1845) is much larger than *A.dawsonensis* and has a brownish-yellow, heavy and globose shell without an umbilicus. The animal is light grey in colour and lacks the prominent dark pigmentation of *A. dawsonensis*. However, most confusion is liable to arise through the occurrence of a local, as yet unnamed rhytidid which has a shell of similar size and shape to that of *A.dawsonensis*. This snail is readily recognised by its yellowish, more flattened shell with rather large umbilicus and sculpture of prominent radial ribs.

RANGE AND HABITAT. Taroom to Theodore, in the Dawson Valley. It is a free sealer living in litter and under logs.

REMARKS. Two lots of shells from Theodore (QMMO4239, QMMO6779) have been in the Queensland Museum since the mid-1970's but attempts to find live specimens in the Theodore area have proved fruitless. The thin shell of *A.dawsonensis* indicates that it is not an inhabitant of rock talus but prefers living amongst vegetation and soil (Stanisic pers. obs.). This makes it especially prone to extermination through habitat destruction by fire and land clearing. Considering the degree of habitat modification which has taken place in the Dawson Valley it is possible that the distribution of *A. dawsonensis* is now extremely restricted.

DISCUSSION

The Dawson Valley is depauperate in land snails compared with areas of closed forest further east, yet it would appear that it has played an important part in the past dispersal of terrestrial molluscs now more diverse elsewhere. On the basis of similarities in shell form and reproductive anatomy *E. hewittorum* and *A. dawsonensis* appear related to taxa further south. If this view is supported by much-needed revisionary studies of related taxa in the drier areas of western New South Wales the occurrence of these two species in the Dawson Valley region has interesting biogeographic implications.

Solem (1992b) contended that colonisation of eastern South Australia by the Camaeninae, including *Cupedora*, was from the north through what is now coastal and subcoastal Queensland, and then through New South Wales. Their ancestors came from Papua New Guinea as post-Miocene immigrants (Bishop,1981). Finding a possible relative of this South Australian group of camaenids in the Dawson Valley region lends support to Solem's contention. The thin shell of *A.dawsonensis* would not be unexpected in an ancestor which lived in scattered moist refugia on alluvial flats and along drainage lines. The more complicated penial surface sculpture of *Cupedora* is probably due to sympatric species interactions but nevertheless can be readily derived from the simple pattern of pustules and longitudinal ridges seen in *A. dawsonensis*. *Cupedora* has adapted to living in a restricted moisture regime and is most frequently associated with rocky slopes, crevices and talus. The heavier more robust shell of its members is typical of species with this habitat preference.

E. hewittorum provides additional support for the claim that the Dawson Valley region was an important corridor for snail movement in the past. Apart from the rainforest inhabiting *E. genithecata* there is no other record of the genus in Queensland. Intensive collecting in the Chinchilla area has failed to locate it in that region. This identifies *E. hewittorum* as a northern outlier of a group which has a nearly continuous distribution from northern New South Wales through western Victoria and into eastern South Australia. The Charopidae is a Gondwanan family mainly confined to rainforests (Stanisic, 1990). *Elsothera* is the only group which has managed to diversify into the drier eucalypt forests. Presumably the dispersal was from wetter forests in the east or from ancestors isolated in mesic refugia as rainforests retreated to the coastal mountain ranges. In either case this radiation most probably occurred sometime in the Pliocene when conditions were wetter (Kemp,1981) and were more likely to facilitate the dispersal of these tiny animals. The extensive distribution of the genus suggests an early radiation. The aggressive drying of the Pleistocene (Galloway & Kemp,1981) would have fragmented widespread populations leading to extinctions where mesic refugia did not provide ameliorating microclimates. The close resemblance of *E. hewittorum* to *E. funerea* from northern NSW suggests derivation from a common ancestor and its similarity to *E. nesana* from South Australia attests to the extent of the initial radiation. It is

probably not coincidental that the evolutionary track spanned by these charopids mirrors that of *A. dawsonensis* and *Cupedora*.

Mesic refugia such as those associated with drainage lines in the Dawson Valley have probably played an important part in the endurance of land snails in the region. Their future importance to the survival of wet-adapted biota such as land snails should not be underestimated. The unique, perennially moist boggomosses of Taroom are an integral part of this intricate survival story. It is unlikely that *A. dawsonensis* and *E. hewittorum* are restricted to the boggomoss environment on Mount Rose Stn. *A.dawsonensis* appears to favour drainage lines (Theodore is also on the Dawson River) and is probably spread over the alluvial flats of the Dawson Valley by floods. Following extensive land clearing in the Dawson Valley, opportunistic colonisation of the few remaining mesic refugia such as the boggomosses is now probably an essential part of the long term viability of this species. The single occurrence of *E. hewittorum* makes any speculation about survival in preferred habitat less informative, however, the same general principles of dispersal and colonisation would apply.

The boggomosses, particularly those with structured vegetation communities, form an important part of the scattered archipelago of mesic refugia in the Dawson Valley. Considering the damage which has been caused to these habitats in the past, by both stock and fire, it will be necessary to implement more sympathetic management practices in the future to ensure their continued existence and the survival of the biota which they support.

ACKNOWLEDGEMENTS

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A NEW CAMAENID LAND SNAIL FROM THE WET TROPICS BIOGEOGRAPHIC REGION, NORTHEASTERN QUEENSLAND (EUPULMONATA:CAMAENIDAE)

JOHN STANISIC

A new camaenid land snail, *Monteithosites helicostracum* gen. et sp. nov., is described from the rainforested summits of Bakers Blue Mountain and Hanns Tableland, NE Queensland. These localities are western outliers of the Wet Tropics rainforest massif. The species displays periostracal sculpture and genital anatomy which suggest that its relationships are with camaenids much further to the south. Biogeographic implications of this discovery are discussed. □ *Mollusca, Camaenidae, Wet Tropics, biogeography.*

John Stanisic, Queensland Museum, P.O. Box 3300, South Brisbane, Queensland 4101, Australia; received 20 May 1996.

A number of large-sized camaenid land snails are known from the Wet Tropics region of northeastern Queensland (NEQ). Smith (1992) placed these in *Hadra* Albers, 1860, *Sphaerospira* Morch, 1867, *Spurlingia* Iredale, 1933 and *Jacksonena* Iredale, 1937. *Monteithosites helicostracum* gen. et sp. nov. from the summits of Bakers Blue Mountain (Mtn) and the Hanns Tableland, southwest of Mount Molloy, NEQ is a biogeographically significant addition to this fauna.

Bakers Blue Mtn and the Hanns Tableland (Fig.1) are elevated western outliers of the main Wet Tropics rainforest massif. They are separated from the more expansive Carbine and Windsor Tablelands in the north by the valley of the Mitchell River but are interconnected by a series of low ridges and hills which continue through to the Herberton Range in the south. The lower slopes generally support eucalypt woodland. However the peaks in these outliers exceed 1000m and their summits, where rainfall is adequate, support rainforest. The dominant rainforest type is araucarian notophyll vine forest with austral conifers (*Agathis robusta, Araucaria cunninghamii*) (Tracey, 1982). Floristic relationships of this rainforest appear to be with Mt Lewis in the north (Godwin, 1986). Rainforest on Hanns Tableland is confined to the northern end and to scattered valleys and fireproof niches. The peaks of Bakers Blue Mtn are cooler and wetter than those of the Hanns Tableland and consequently support larger areas of rainforest. Nix (1991) identified these outliers as distinct biogeographic units within the Wet Tropics region.

M.helicostracum gen. et sp. nov. provides important new information on these isolated refugia and their historical relationship to other parts of the Wet Tropics.

SYSTEMATICS

Class GASTROPODA
Order EUPULMONATA
Suborder STYLOMMATOPHORA
Superfamily CAMAENOIDEA
Family CAMAENIDAE

Previous taxonomic studies of the large Camaenidae of the Wet Tropics, NEQ have been largely shell-based. Pilsbry (1894) grouped all these species under *Thersites* Pfeiffer, 1855 in a revision that was partially based on genital anatomy. Iredale (1933, 1937) abandoned Pilsbry's conservative system and introduced a large number of new species and genera, solely on the basis of shell features. Some of these taxa have somewhat doubtful status (Burch, 1976) and have yet to be critically revised. Pace (1901) and Solem (1979) presented anatomical data on the very large *Hadra bipartita* (Ferussac, 1822). Smith (1992) produced an updated but critically untested listing of taxa. Stanisic et al. (1994) produced a preliminary report on the land snails of the Wet Tropics which presented distribution data for a large number of described and undescribed camaenids; the new species described herein was identified as Camaenidae WT 11.

The description of this new land snail has entailed a precursory anatomical examination of several other camaenid species in order to place it in systematic context. These revisionary studies will be more fully pursued elsewhere but do
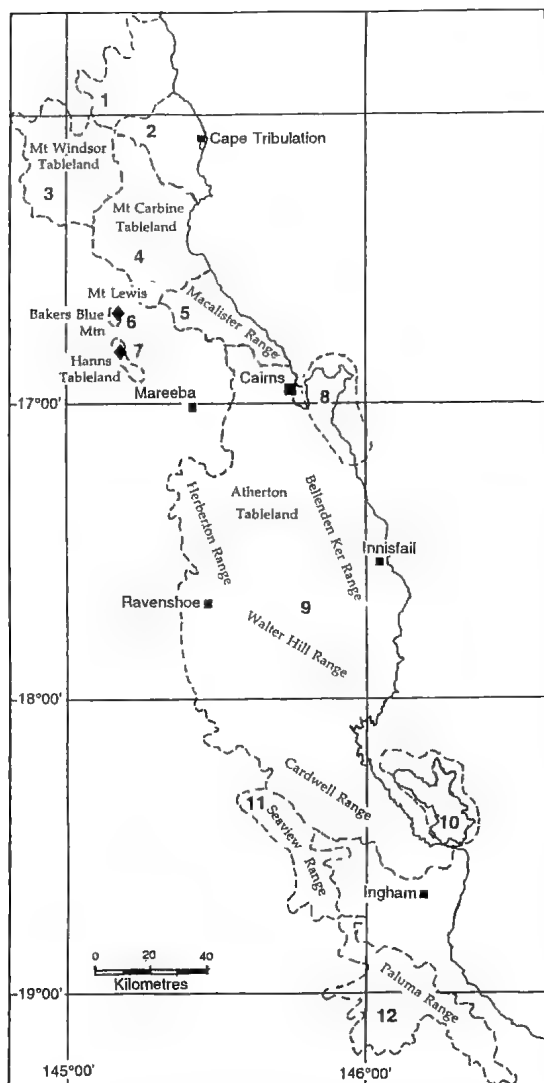
FIG. 1. Distribution of *Monteithosites helicostracum* sp.nov. - ◆ and the biogeographic units of the Wet Tropics (after Nix, 1991). [1, Finnigan; 2, Thornton; 3, Windsor; 4, Carbine; 5. Macalister; 6, Bakers Blue; 7, Hanns; 8, Malbon Thompson; 9, Atherton; 10, Hinchinbrook; 11, Seaview; 12, Paluma].

identify *M. helicostracum* as an unusual member of the Camaenidae of the Wet Tropics.

Monteithosites gen. nov.

ETYMOLOGY. For Dr Geoff Monteith and in reference to the similarity to *Bentosites* from mideastern Queensland (MEQ).

TYPE SPECIES. *Monteithosites helicostracum* sp. nov.

DIAGNOSIS. Shell large (to 33.88mm in diameter), yellow with few to many, dark reddish-brown spiral bands; lip dark brown and reflected. Shell sculpture of very fine, crowded, radial thread-like periostracal wrinkles and prominent, widely spaced spiral periostracal cords. Penis short, stout, with a thick sheath and highly muscularised walls; verge absent. Epiphallus with a weakly expanded ascending arm; entering penis apically through a simple pore. Vas deferens and epiphallus bound to penial sheath. Animal with reddish mantle and tail and dark brown tentacles.

COMPARATIVE REMARKS. The unusual periostracal sculpture readily separates *Monteithosites* from other large camaenids of the Wet Tropics. *Hadra* (sensu Smith, 1992) has bicoloured shells with reduced banding and either almost smooth periostracal sculpture or, in the case of *H. bellendenkerensis* (Brazier, 1875) and *H. beddomae* (Brazier, 1878), fine radial threads with prominent radially disposed, zig-zag periostracal thickenings; *Spurlingia* and *Jacksonena* have comparatively drab shells with strongly rugose sculptures and prominent periostracal scales; *Sphaerospira* Morch, 1867 (sensu Smith, 1992) contains a large number of species with banded shells occurring from SEQ to NEQ and previously included in 5 genera (Iredale, 1937). Unpublished studies by the author suggest that this genus, as defined by Smith (1992), is polyphyletic. A primary division is expressed in animal colour. The greater proportion of species have animals with orange to reddish-orange mantle tissue and tails, and orange to brown tentacles e.g. *S. yulei* (Forbes, 1851) from MEQ. A smaller number have all-over grey to black animals e.g. *S. fraseri* (Griffith & Pidgeon, 1833) from SEQ. The animal of *Monteitosites* bears a strong, external resemblance to the former group particularly those species from MEQ which were previously included in *Bentosites* Iredale, 1933 and *Varohadra* Iredale, 1933 (see Iredale, 1937).

Periostracal sculpture in *Sphaerospira* s.l. varies from a simple microscopic pattern of very fine, crowded, radial periostracal, thread-like wrinkles (*S. yulei*), to one in which these fine wrinkles are supplemented by coarse, wavy or zigzag, radial periostracal ribs (*S. fraseri*) not too dissimilar from those in some *Hadra* spp. The
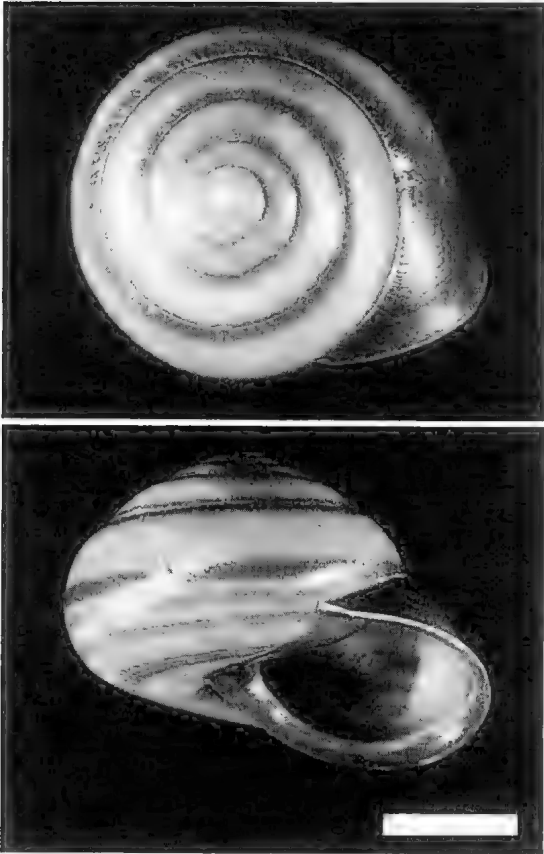
FIG. 2. *Monteithosites helicostracum* sp. nov. Shell of holotype, QMMO57242. Scale line = 10mm.

latter pattern is seen in both black-mantled species (SEQ to NEQ) and red-mantled species from the southern parts of the Wet Tropics (NEQ) only. *Monteithosites* displays yet a third level of variation. However the underlying microsculpture of radial thread-like wrinkles in *Monteithosites* is identical to that in the red-mantled forms from MEQ and NEQ suggesting that the periostracal cords may be merely a functional equivalent of the zigzag to wavy types seen in other hadroid camaenids and of limited value in establishing relationships.

Genital anatomy relates *Monteithosites* to red-mantled *Sphaerospira* s.l. from MEQ and NEQ rather than *Sphaerospira* s.l. from SEQ or *Hadra* from the Wet Tropics. The comparatively weakly muscular epiphallus of *Monteithosites* contrasts with the strongly muscular, elongate condition of *Sphaerospira* s.l.(Solem, 1992) from SEQ and *Hadra* (Solem, 1979). *Hadra* is also characterised by well-developed epiphallic caeca. *S.*

yulei from MEQ has the epiphallus reduced to such an extent that the ascending arm is narrow and barely differentiated from the vas deferens (Solem, 1992); a penial verge and tiny epiphallic flagellum are present. This species also has the simple epiphallic entry and sheath-bound vas deferens of *Monteithosites*. Similar genital anatomy is found in other red-mantled *Sphaerospira* from MEQ and the southern parts of the Wet Tropics. In contrast *S. fraseri* (and other black-mantled species) have a strongly developed epiphallus, no accessory epiphallic structures and usually lack penial verges (Bishop, 1978; Solem, 1992; Stanisic, unpubl.). The penis of *Monteithosites* appears to be highly specialised and finds no correlatives among hitherto illustrated species.

Monteithosites helicostracum sp. nov.
(Figs 2-5)

ETYMOLOGY. Latin *helico*, spiral, referring to the spiral periostracal cords.

MATERIAL EXAMINED. HOLOTYPE QMMO57242, Bakers Blue Mtn, c.17km W Mt Molloy, NEQ (16°42'S, 145°10'E), rainforest, under logs, Collected G.Monteith, D.Cook, 11-12 September, 1981. Height of shell 25.54mm, diameter 33.88mm, H/D ratio 0.754, whorls 6 1/8. PARATYPES QMMO48172, 1 adult, 1 juvenile, same data as holotype; QMMO57240, 1 adult, 1 juvenile, Bakers Blue Mtn, upper slopes, NEQ (16°43'21"S, 145°10'15"E), microphyll vine forest/basalt talus, under logs, J.Stanisic, G.Ingram, 1 Jul 1995; QMMO56834, 7 adults, Hanns Tableland, N end, NEQ (16°49'S, 145°11'E), rainforest, 950-1000m, G.Monteith, G.Thompson, 11-14 Dec 1995. OTHER MATERIAL QMMO48181, 3 juveniles, Bakers Blue Mtn, c.17km W Mt Molloy, NEQ (16°42'S, 145°10'E), rainforest, 800-1000m, ANZSES Expedition, 30 Dec 1989-9 Jan 1990.

DESCRIPTION. Shell (Fig. 2A,B) large, diameter 29.26-33.88mm (mean 31.66mm), with 5 3/4-6 1/8 (mean 5 7/8-) whorls. Apex and spire moderately elevated, height 20.56-25.54mm (mean 22.71mm). H/D ratio 0.699-0.762 (mean 0.727). Protoconch c.1 1/2 whorls. Apical sculpture of crowded, slightly curved, weak radial growth ridges. Spire and body whorl (Fig. 3) with very fine, crowded, radial thread-like periostracal wrinkles and conspicuous, more widely spaced, spiral, coarse, periostracal cords. Umbilicus barely open, covered by the reflection of the collumellar lip. Sutures weakly impressed. Whorls evenly rounded. Last whorl descending rapidly in front.
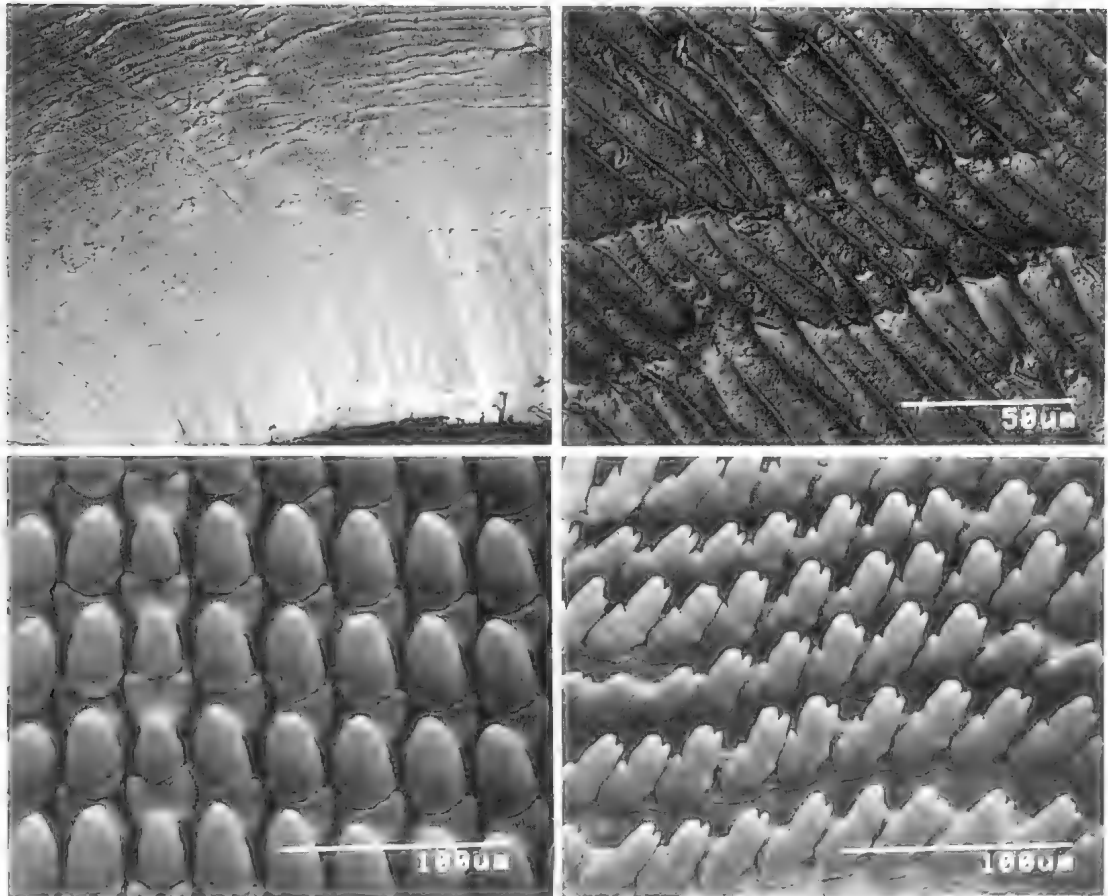
FIG. 3. *Monteithosites helicostracum* sp. nov., QMMO48172. A,B, details of adult shell sculpture; C,D, details of radula. Scale lines as marked.

Aperture lunately ovate; lip strongly reflected. Shell colour yellow-horn with dark reddish-brown spiral bands; subsutural and peripheral bands moderately wide sometimes split into a series of narrower bands; basally a series of narrow bands sometimes coalesced into a single broader band; several narrow intermediate brown bands may also be present. Umbilical chink and lip dark brown. Parietal callus shiny, dark choco-late-brown. Area behind lip with a dark brown suffusion which may extend rearwood for 1/8 whorl. Based on 9 measured adults (QMMO48172, QMMO56834, QMMO57240, QMMO57242).

Genitalia (Fig. 4A) with ovotestis (G, Fig. 4B) comprised of several clumps of finger-like lobes of alveoli lying in the apical whorls of the digestive gland (Z). Hermaphroditic duct (GD) strongly convoluted; talon (GT) short, finger-like. Spermatheca (S) with head lying at the base of the albumen gland (GG); stalk (SS) long, bound to the prostate-uterine surface. Uterus (UT) white, without unusual features; prostate (DG) a series of light brown acini appressed to the uterine surface. Free oviduct (UV) short. Vagina (V) short, about 1/2 length of penis, internally with numerous longitudinal thickenings; spermathe-cal entrance a simple pore. Epiphallus (E) with short thick descending arm and narrow, weakly expanded ascending arm, about 2/5 length of penis, internally with a large longitudinal pilaster; entering penis apically through a simple pore (EP). Ascending arm of epiphallus and vas deferens bound to penial sheath by connective tissue. Vas deferens (VD) a thin tube, barely differentiated from the epiphallus. Penis (P, Fig. 4C) relatively short, stout, strongly muscularised with a thick sheath (PS). Penial wall (PW) ex-tremely thick and penial lumen reduced to a very narrow tube. Internally, penis with a conspicuous,
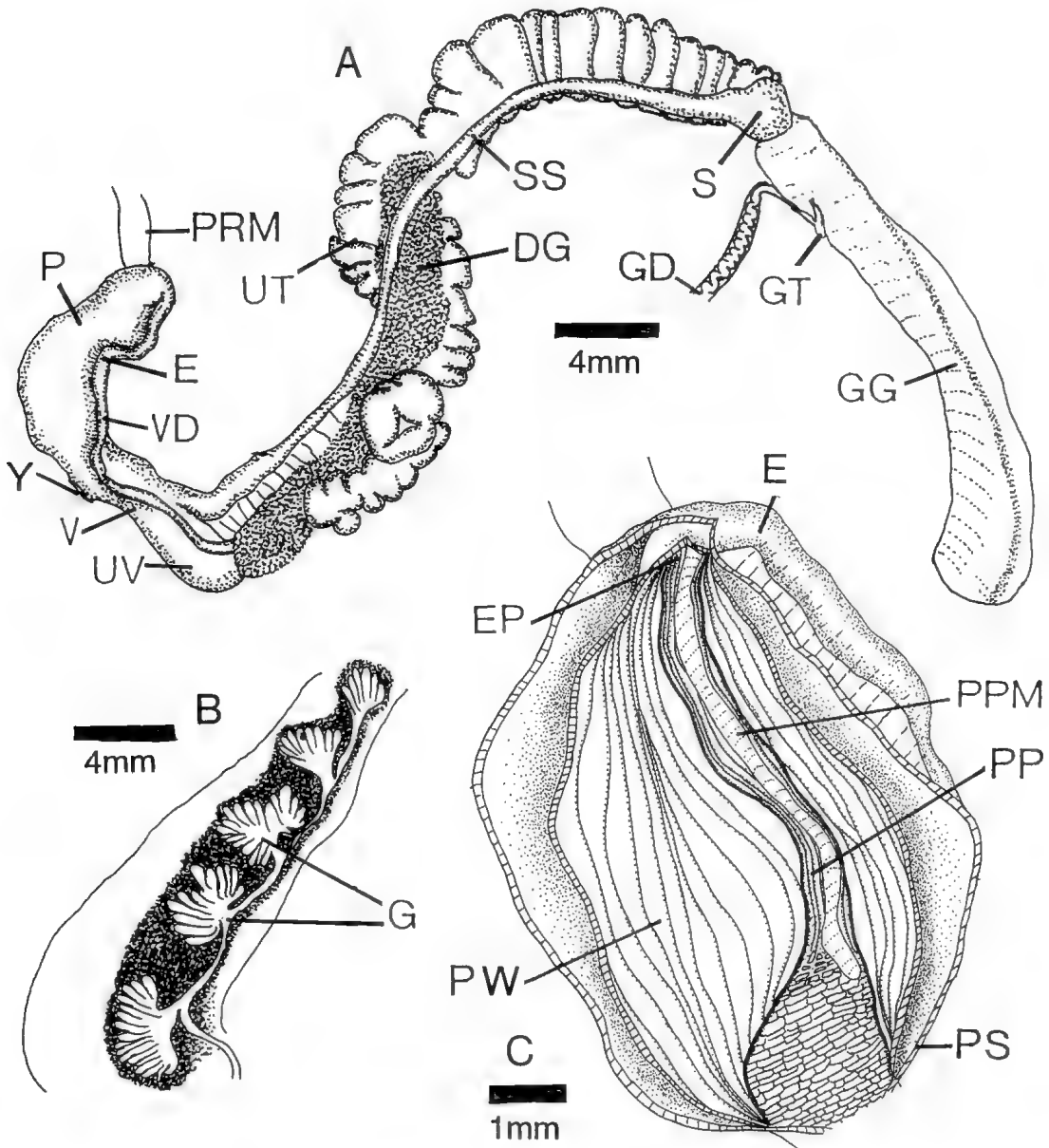
FIG. 4. *Monteithosites helicostracum* sp. nov., QMMO56834. A, genitalia; B, ovotestis; C, details of penis interior. Scale lines as marked.

central longitudinal pilaster (PPM) and several, narrower minor longitudinal pilasters (PP); lower penial chamber with short, rectangular pustules; verge absent. Atrium (Y) very short and without unusual features. Animal (Fig. 5) grey to dark brown with reddish tail and mantle and dark brown tentacles. Head wart present. Radula (Fig. 3B, C) with broadly unicuspid central and lateral teeth, central tooth slightly smaller; anterior flare weak, basal plate prominent. Marginal teeth tricuspid with ectocone low down and endocone high up on mesoconal cutting edge; basal plate and anterior flare reduced. Jaw typically camaenid. Based on two dissected specimens (QMMO57242, QMMO56834).

FIG. 5. *Monteithosites helicostracum* sp. nov., Hanns Tableland, QMMO56683.

COMPARISONS. The shell of *M. helicostracum* comes closest in appearance to that of some *Sphaerospira* (sensu Smith, 1992) from NEQ and MEQ. It resembles *S. saxicola* (Iredale, 1937) from the Bowen area, MEQ which possesses fine thread-like periostracal wrinkles, but lacks any major periostracal elements. Some species in the *S. sardalabiata* (Cox, 1871) complex (sensu Smith, 1992) from the southern parts (Paluma, Seaview and Cardwell Ranges) of the Wet Tropics bear an overall similarity to the new species in size and shape. However, *M.helicostracum* is distinguished from these species by its spiral periostracal cords. *S. sardalabiata* s.l. has coarse, wavy to zigzag, radial periostracal thickenings (Stanisic, unpubl.).

Sphaerospira spp. from NEQ and MEQ also show some anatomical similarity to *M. helicostracum* in reduction of the epiphallus, penial structures, form of the radula (Pilsbry, 1894; Solem, 1992; Stanisic, unpubl.) and animal colour. However the rather unusual penis of *M. helicostracum* distinguishes it from all of these species (Stanisic, unpubl.).

HABITAT AND DISTRIBUTION. Under logs in araucarian notophyll vine forest with austral conifer emergents on Bakers Blue Mtn and Hanns Tableland, NEQ.

REMARKS. The adult periostracal sculpture of coarse spiral cords and the penial specialisation of *M. helicostracum* is a combination of characters not seen in other hadroid camaenids. The periostracal spiral cords may be functionally analagous to the more widely occurring zigzag to wavy variety but the unusual penis is more difficult to correlate. *Sphaerospira rockhamptonensis* (Cox, 1873) from The Caves area, Rockhampton, MEQ has a penis with thick muscular walls and reduced lumen (Stanisic, unpubl.). However this species has a dark-grey to black animal with a greatly enlarged epiphallus and is not closely related. It has a simple periostracal sculpture of very fine wrinkles. An analagous reduction in penial lumen width (in this case caused by a dramatic narrowing of the entire penis) was noted by Solem in *Turgenitubulus pagodula* Solem, 1985, an unrelated camaenid from NW Australia. In this instance more fundamental characters indicated the species' relationship to a widespread genus with otherwise strongly consistent genital anatomy. Similarly the general patterns of shell, animal, and anatomical characters displayed by *M. helicostracum* suggest a relationship with those species with banded shells and orange to red coloured animals from NEQ and MEQ. The simple internal structure of the penial chamber and absence of a verge may be the result of spatial constraints associated with the overall reduction in size of the penial lumen. However, this proposition needs to be more thoroughly tested through a comprehensive revision of all the hadroid camaenids.

DISCUSSION

The relationships of *M. helicostracum* to other hadroid camaenids from eastern Queensland still need to be fully confirmed but appear to rest with a widespread radiation consisting of rainforest-bound species now separated by large tracts of drier countryside. These species are part of *Sphaerospira* s.l. and are characterised by having banded shells and animals with orange to red mantles. In the southern part of the Wet Tropics these species inhabit the drier rainforest between Innisfail and Townsville; in MEQ they occur in drier araucarian vine forests and vine thickets

between Mackay and Bowen; and in SEQ possibly more distantly related species (also with reddish mantles) live in a variety of dry rainforests. These rainforests are peripheral to core wet, upland refugia and presumably land snails in these environments would have been more strongly affected by climatic shifts. The Wet Tropics and MEQ radiations of *Sphaerospira* s.l. are separated by an extensive relatively dry corridor between Bowen and Townsville, NEQ where coastal ranges are absent and orographic rainfall is low (Dick, 1974). In S Queensland a dry corridor in the St Lawrence-Gladstone area separates SEQ and MEQ radiations. Similarly, Bakers Blue Mtn and Hanns Tableland are separated from the main massif of the Wet Tropics by dry valleys and ridges (Nix, 1991). Thus biogeographic interpretation of the history of *M. helicostracum* and its allies would appear to involve climate-induced fragmentation of rainforest communities. This view is supported by Bishop (1981) who suggested that the history of *Sphaerospira* s.l. was intimately linked to the deterioration of the climate and involved subdivision of once more extensive ranges.

It is generally accepted that the Camaenidae are a northerly derived element of the Australian land snail fauna (McMichael & Iredale, 1959; Bishop, 1981; Solem, 1992). In the east, dispersal would have been from the New Guinea region across the Torres Strait following collision of the Australian continental plate with the Asiatic and Pacific Ocean plates (Doutch, 1972). *Sphaerospira* s.l. today extends from the Wet Tropics to northern NSW indicating a long history of dispersal. The moisture dependence and relative low vagility of land snails are important limitations to their dispersal and distribution in eastern Australia (Bishop, 1981; Stanisic, 1994). The present day confinement of these hadroid camaenids to rainforest indicate that tracts of dry sclerophyll forest are effective dispersal barriers. The contraction of rainforest which led to the creation of barriers to their dispersal began in the Miocene with the onset of major aridity episodes (Kemp, 1981). These barriers would have reached their acme in the Plio-Pleistocene when more rapid climatic change isolated mesic communities in montane refugia (Galloway & Kemp, 1981). The effects on *Sphaerospira* s.l. should have been dramatic and it is not surprising that current distribution patterns are complex and that differentiation of the group appears to have occurred on opposite sides of major arid corridors in the St Lawrence-

Gladstone and Bowen-Townsville areas (Bishop, 1981).

M. helicostracum shows a level of differentiation which suggests that its isolation from its allies has been long-term, possibly in the same time frame as the separation of the red-mantled NEQ and MEQ species groups. Recent fluctuations in rainforest distribution (c. 120,000 yBP) within the Wet Tropics (Kershaw, 1981) do not appear to have had an effect on the distribution of *M. helicostracum*. Nix (1991) proposed a possible connection between the Bakers Blue biogeographic unit and other units to the north and east during cool-wet and warm-wet phases of the last 10,000 years, yet *M. helicostracum* remains isolated in the two outliers. Either the proposed connection did not exist or was too brief to allow dispersal of this species.

It is probably significant that *Monteithosites* and its allies are absent from the core of the Wet Tropics. The present day preference of *Sphaerospira* s.l. with reddish to orange coloured animals for drier rainforest types often dominated by hoop-pine (*Araucaria cunninghamii*) (unpubl. data) suggests a disposition for a very particular environmental regime. This is most notable in MEQ and SEQ where araucarian microphyll vine forest is more widespread. *A. cunninghamii* (and its associated dry rainforest type) is relict in NEQ (Tracey, 1982) although it has shown considerable fluctuation in occurrence since the Plio-Pleistocene (Kershaw, 1981).

The absence of *Sphaerospira* s.l. with orange to red-mantled animals from the Atherton biogeographic unit (now dominated by *Hadra* and its allies) and from other moist upland refugia (higher peaks of the Wet Tropics, NEQ and Eungella, MEQ) might indicate that this group only ever occupied marginally wet rainforest types peripheral to the larger massifs. Equally it may indicate displacement from wetter types by the dark animal hadroids which now dominate the truly moist refugia from SEQ to MEQ. Lack of knowledge about the inter-relationships of these species currently makes it difficult to be sure of the accuracy of either alternative. However, some speculation is possible.

The bioclimatic analyses of Kershaw & Nix (1988) support the view that there was no recent connection between Bakers Blue Mtn and Hanns Tableland. In contrast, presence of *M. helicostracum* on both these outliers indicates a past connection which most likely predates the time scale of their analyses. Connections between the outliers and with the Atherton unit in the south

were less likely during recent times but could have been present in the Plio-Pleistocene when araucarian vine forests may have been in comparative ascendency (Kershaw et al., 1991). However, absence of related camaenids from the Herberton Range (a subunit of the Atherton unit) which has summits in excess of 1000m and extensive areas of rainforest, might suggest that the group never colonised this region. These summits should have provided moist refugia during the driest periods of the Plio-Pleistocene. Yet presence of the probable nearest relatives of *M. helicostracum* in the Cardwell, Seaview and Paluma Ranges points to a NW-SE dispersal track on the drier western edge of the Wet Tropics. In these circumstances it is a strong possibility that the suitable dispersal corridors which may have existed on the western edge of the Atherton have been lost since the Miocene. The preference of *M. helicostracum* and its purported allies for a very specific environmental regime which is now restricted in the north would seem to provide support for this proposition. It is possible that the differentiation and speciation within the group needs to be viewed as occurring along very subtle environmental gradients defined by rainforest structural types. A revision of the hadroid camaenids of the Wet Tropics is needed to more fully understand past dispersal routes but indications are that these land snails have the potential to more accurately define current hypotheses.

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FRUIT EATING BY THE GECKO *GEHYRA DUBIA* IN TOWNSVILLE. *Memoirs of the Queensland Museum 39(2): 364. 1996:*-This note describes opportunistic observations of fruit-eating by *G. dubia* occupying a residence in suburban South Townsville. At approximately 1745hr on 14 March 1996 a *G. dubia* was observed feeding on ripe sugar bananas suspended within the residence. Individual bananas had ripened on the bunch and had partially detached, being suspended by one strip of peel only. The ripe flesh was exposed where the skin had given way, and it was on this flesh that the gecko was feeding; tearing large chunks of the fruit off with it's mouth and consuming them. On three subsequent occasions, as the fruit became completely detached from the bunch and was stored on a kitchen table, geckoes were startled from amongst them although fruit consumption was never observed before the gecko(s)? took off in alarm. We do not know if they were the same or different individuals. No invertebrates were seen on the bananas at these times and we suspect that the geckcoes were once again feeding on the fruit.

Greer (1989) summarised published observations of Gecko diet. Non-animal foods variously eaten by *Christinus guentheri*, *C. marmoratus*, *Heteronotia binoei* and *Lepidodactylus lugubris*, include sap, nectar, jam, honey and sugar. Couper et al. (1995) added to the list of sapfeeding Geckos when they described sapfeeding by *Gehyra dubia* in the wild. The only published reference to fruit-eating by an Australian gecko that I am aware of is King & Horner's (1993) observation of *G. australis* feeding on pulpy fruit. As such, this note provides further evidence of fruit-eating by another species of Australian gecko in the wild.

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Scott Burnett & Jacqueline Nolen, 9 Nelson St, South Townsville 4810, Queensland; 23 April 1996.

REVISION OF *AUSTRALOXENELLA* HOWDEN & STOREY IN AUSTRALIA (COLEOPTERA: SCARABAEIDAE: APHODIINAE)

R.I. STOREY & H.F. HOWDEN

Australoxenella Howden & Storey, the only Australian member of the aphodiine tribe Stereomerini, is revised. Eleven species are described of which the following are new: *concinna, kalpara, midgee, mirreen, moogoon, peckorum, teeta, wurrook, zborowskii*. Relationships between species are discussed. Most new specimens were taken in flight interception traps. No information is available on the biology of these suspected termitophiles. ☐ *Coleoptera, Scarabaeidae, Aphodiinae, Australoxenella, taxonomy.*

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Australoxenella Howden & Storey, 1992 was erected for two unusual specimens representing two species of aphodiine Scarabaeidae taken in the far north of the Northern Territory. The Stereomerini was erected for *Australoxenella*, *Bruneixenus* Howden & Storey, and *Stereomera* Arrow and *Termitaxis* Krikken, previously placed in the tribe Rhyparini. Collecting in NT and in Queensland since 1992 has yielded 96 specimens of *Australoxenella*, including nine new species. Most were caught in flight interception traps, although several were from malaise traps and one from a berlesate. Habitat ranged from mixed eucalyptus woodland to dense rainforest. With revision of Australian Aphodiinae in progress (Stebnicka & Howden, 1994, 1995) revision of *Australoxenella* was necessary in light of the new material. Although Howden & Storey (1992) speculated that all Stereomerini were termitophiles, no direct evidence of this life habit in *Australoxenella* has surfaced.

METHODS AND MATERIALS

Terminology follows Howden & Storey (1992). Scale bars on SEM photographs are in millimetres. Collection abbreviations used are: ANIC–Australian National Insect Collection, Canberra, A.C.T.; HAHC–H. & A. Howden Collection, Ottawa, Ontario; ISEA–Institute of Systematics and Evolution of Animals, Cracow, Poland; NTMA–Northern Territory Museum of Arts and Sciences, Darwin; QMBA–Queensland Museum, Brisbane; QPIM–Department of Primary Industries, Mareeba, Queensland; SBPC –S. B. Peck Collection, Ottawa, Ontario.

SYSTEMATICS

Order COLEOPTERA
Family SCARABAEIDAE
Subfamily APHODIINAE

Australoxenella Howden & Storey, 1992

Australoxenella Howden & Storey, 1992:1811.

TYPE SPECIES. *Australoxenella humptydooensis* Howden & Storey, 1992.

DESCRIPTION. *Head.* Dorsally broad, flattened, feebly convex, about twice as wide as long. Clypeus anteriorly with broadly inflexed edge, obtusely angulate medially, nitid. Head dorsally, with distinct median and lateral grooves, length of median groove variable, lateral grooves slightly deeper, c. 1/3 of distance to outer edge of gena, length of lateral grooves variable, lateral grooves slightly convergent anteriorly for apical 1/4–2/3 length; surface of head dorsally, except for grooves, with close, appressed, circular scales giving granulate appearance. Gena not obviously delimited, inner edge indicated by small, nongranulate marking near summit of convex area.

Pronotum. Strongly, irregularly convex with transverse sulcus near middle, extending each side to at least lateral thirds, variable in length, depth and width; area anterior to sulcus with 5 or usually 7 longitudinal grooves, inner 5 grooves variable in depth and width, rounded ridges between grooves variable, inner 2 ridges often elevated and forming rounded prominence just anterior to transverse sulcus; equivalent median surface posterior to sulcus with only trace of

median groove, always strongly convex and more strongly elevated than any other part of dorsum; 3 variable lateral posterior grooves on each side parallel, and extending into sulcus; pronotum laterally with sides almost parallel; anterior angles slightly acute, posterior angles almost 90°, abruptly rounded; pronotal surfaces with close, appressed, circular scales, except grooves and sulcus. Scutellum minute, surface shining.

Elytron. Moderately to strongly ridged on disc, each elytron with sutural and 2–3 lateral intervals elevated with shallow to deep U-shaped depressions between; distinct striae absent or with one stria below feeble humeral umbone, usually merging with lateral bead near middle of lateral edge; epipleuron broadly inflexed, parallel-sided or tapering towards apex, often longitudinally concave near metacoxa; elytral apices not greatly modified, explanate in some species, conjointly broadly rounded; covered by close, appressed, circular scales, density variable, always numerous along crests of ridges and outside fourth ridge, scattered to dense on U-shaped depressions; depressions dull, alutaceous. Metathoracic wings long, functional.

Pygidium. Surface ventral, flattened, wider than long, with broadly rounded apex anterior in position.

Ventral surface. Antenna 9-segmented, club 3-segmented, equal in length to basal 6 segments of antenna combined; area surrounding antenna deeply concave. Mentum medially concave, anterior margin almost straight with small median projection. Maxillary palpus apparently 3-segmented, apical segment lanceolate. Mandibles thin, blade-like. Eye small, somewhat triangular, approximately 10 facets long x 18 wide, not visible dorsally, covered by pronotum when head retracted. Prosternum laterally with alutaceous to subnitid surface, anterior edge near antennae with a raised marginal bead; median prosternal process anteriorly strongly elevated, apex expanded, process posteriorly lanceolate, medially carinate, with obtusely angled sides. Mesosternum moderate in size, triangular, narrowed laterally. Metasternum between mesocoxae narrow, blade-like, posterior to mesocoxae abruptly widened, flat, shallowly concave in posterior median 1/2, anteriorly behind mesocoxae with transverse marginal bead, surface alutaceous to nitid; metacoxae contiguous. Abdomen with 4 (♂) or 5 (♀) segments visible medially, 6 visible laterally, apical segment longer in midline than other segments combined.

Legs. Femora wide, flattened. Protibia with 2

teeth on outer edge, one apical, one subapical, subapical occasionally obsolete. Meso- and meta-tibiae flattened, approximately twice as long as wide; outer narrow edge of each tibia with irregular longitudinal rows of punctures, each puncture with a minute yellowish seta; each tibia with 2 minute apical spurs, may be large setae; small apical setae also present. Protarsus 5-segmented, with several conspicuous setae at ventral apex of each segment; claws normal. Meso - and meta-tarsi 4-segmented, appearing to be 3-segmented, basal segment shorter than second segment; claws reduced in thickness.

KEY TO SPECIES OF *AUSTRALOXENELLA*

1 Pronotum anteriorly with median, longitudinal groove similar in width to groove on each side and nearly as wide as adjacent ridges; anteriorly with ridge on each side of median groove at most only slightly higher than adjacent ridge (Fig. 1A); elytral epipleura nearly constant in width to apices (except *teeta* sp.nov.)
. . . . (Group 1) 2
Pronotum anteriorly with median, longitudinal groove narrow, more so than lateral grooves; anteriorly with ridge on each side of median groove more strongly elevated posteriorly than adjacent outer ridge (Fig. 5C); elytral epipleura noticeably narrowing towards apices.
. . . . (Group 2) 7

2 (1)Each elytron with sutural and three lateral ridges and a single stria in basal outer quarter
. . . . 3
Each elytron with sutural and two lateral ridges, stria in basal outer quarter absent (Fig. 1B); N Qld . . . . *concinna* sp. nov.

3 (2)Pronotal ridges anterior to transverse sulcus lacking clusters of erect spur-like setae 4
Pronotal ridges anterior to transverse sulcus each with four clusters of closely appressed, erect spur-like setae (Fig. 1C); N Qld
. . . . *zborowskii* sp. nov.

4 (3)Pronotum in lateral view with median conical prominence posterior to transverse sulcus much more strongly elevated than area anterior to sulcus; lateral pronotal and elytral margins lacking distinct fringe of yellowish setae 5
Pronotum in lateral view with median conical prominence posterior to transverse sulcus only slightly more elevated than area anterior to sulcus; lateral pronotal and elytral margins with distinct fringe of yellowish setae (Figs 1E, 1F); N Qld . . . . *teeta* sp. nov.

5 (4)Elytron with crests of longitudinal ridges on disc narrow, subacute (Figs 3B, 3D) 6
Elytron with crests of longitudinal ridges on disc

rounded, broad; Bathurst Island, NT
. . . . *A. bathurstensis* Howden & Storey

6 (5) Elytral surface anteriorly between suture and adjacent raised (sutural) ridge with 2 rows of scales; next depression between sutural ridge and first lateral ridge with close, irregular, transverse rows of five scales; narrower species, length to width ratio 2.2:1 (Fig. 3B); NT
. . . . *moogoon* sp. nov.

Elytral surface near base between suture and adjacent raised (sutural) ridge with 3 irregular rows of scales; next depression between sutural ridge and first lateral ridge with close irregular, transverse rows of 6-8 scales; broader species, length to width ratio 2:1 (Fig. 3D); NT
. . . . *wurrook* sp. nov.

7 (1) Pronotum in lateral third posterior to transverse sulcus transversely convex anterior to posterior margin 8

Pronotum in lateral third posterior to narrow transverse sulcus broadly, shallowly concave between sulcus and posterior margin (Fig. 4A); N Qld . . . . *midgee* sp. nov.

8 (7) Posterior prosternal lanceolate process with central carina blade-like, very little expanded at middle (Fig. 2F); elytral U- shaped depressions with regular transverse rows of scales in fine grooves, remaining surface without scales or setae (Fig. 2E); N Qld . . . . . *kalpara* sp. nov.

Posterior prosternal lanceolate process with central carina expanded at middle (Fig. 5E); elytral U-shaped depressions with scales not grouped in transverse rows in fine grooves; NT
. . . . 9

9 (8) Metasternum medially just posterior to mesocoxae with narrow transverse ridge with declivous posterior edge forming anteriorly-directed abrupt, obtuse angle (Fig. 5E); third lateral ridge on each elytron with inner parallel lines of scales 10

Metasternum medially just posterior to mesocoxae with broadened transverse ridge, posterior edge of ridge almost straight or feebly, anteriorly, arcuate medially (Fig. 4E); third lateral ridge on each elytron lacking inner parallel lines of scales (Fig. 4D); NT
. . . . *peckorum* sp.nov.

10 (9) Meso- and meta-femora ventrally with numerous oval, appressed scale-like setae; elytra in lateral view with sutural ridges distinctly arcuately elevated at posterior third (Fig. 5B); NT
. . . . *mirreen* sp. nov.

Meso- and meta-femora ventrally with scale-like setae present only near posterior edges, with scattered, slender setae elsewhere; elytra in lateral view with sutural ridges only feebly arcuately elevated at posterior third (Fig. 5D); NT
. . . . . *A. humptydooensis* Howden & Storey

Australoxenella concinna sp. nov.
(Figs 1A, 1B, 6A)

ETYMOLOGY. For the beautiful appearance.
MATERIAL EXAMINED. HOLOTYPE QMBT 13424 (sex not determined) from 17°24'S, 145°41'E, Westcott Rd, Topaz, Qld, 6.xii.1993-25.ii.1994, Monteith, Cook, Janetzki, RF intercept 680m.

DESCRIPTION. Length 2.9mm, greatest width 2.0mm. Dark reddish brown dorsally and ventrally.

Head. Median groove reaching anterior edge, lateral grooves reaching anterior edge and slightly converging for anterior 1/2; surface of head with small oval-elongate marking above each eye; anterior edge of head between genae with a fringe of short, adjacent, yellowish, flattened setae.

Pronotum. Four central anterior rounded ridges equal in size, none elevated; median, first and second lateral pairs of grooves equal in width and depth, third lateral pair of grooves fine, joining anterior pronotal edge c. 1/3 distance from anterior angles to centre line; posterior median groove not visible in anterior 1/2, adjacent rounded ridges slightly elevated, crest acute, additional fourth pair of lateral grooves present, strong from centre of sculptured area to posterior angles; transverse sulcus strong narrow, running to lateral edge of pronotum, slightly widened posteriorly for inner 1/2; widened area of sulcus bare, anterior edge of sulcus and most grooves with short adjacent yellowish setae, groups of longer similar setae in centre of sculptured area; small clusters of spur-like setae on anterior ridges and posterior prominence, not well developed; lateral pronotal edges from anterior angles to posterior angles with a distinctive fringe of adjacent, yellowish, flattened setae.

Elytron. Broad, flattened, explanate; with sutural and 2 lateral ridges, ridges weakly elevated, shortened, sutural longest c.2/3 length of elytron, second lateral shortest c.1/2 length of elytron; U-shaped depressions very shallow, barely detectable; entire dorsal surface of elytron with close, appressed, circular scales, crest of each ridge with a distinct row of adjacent, appressed, circular scales; lateral margin of elytron with a distinct fringe of adjacent, flattened, yellowish setae, this in the form of a double row on basal 1/6 which could indicate position of a vestigial stria; epipleuron wide, slightly narrowed in apical 1/6, nitid, punctures and setae fine, stronger in apical 1/2.
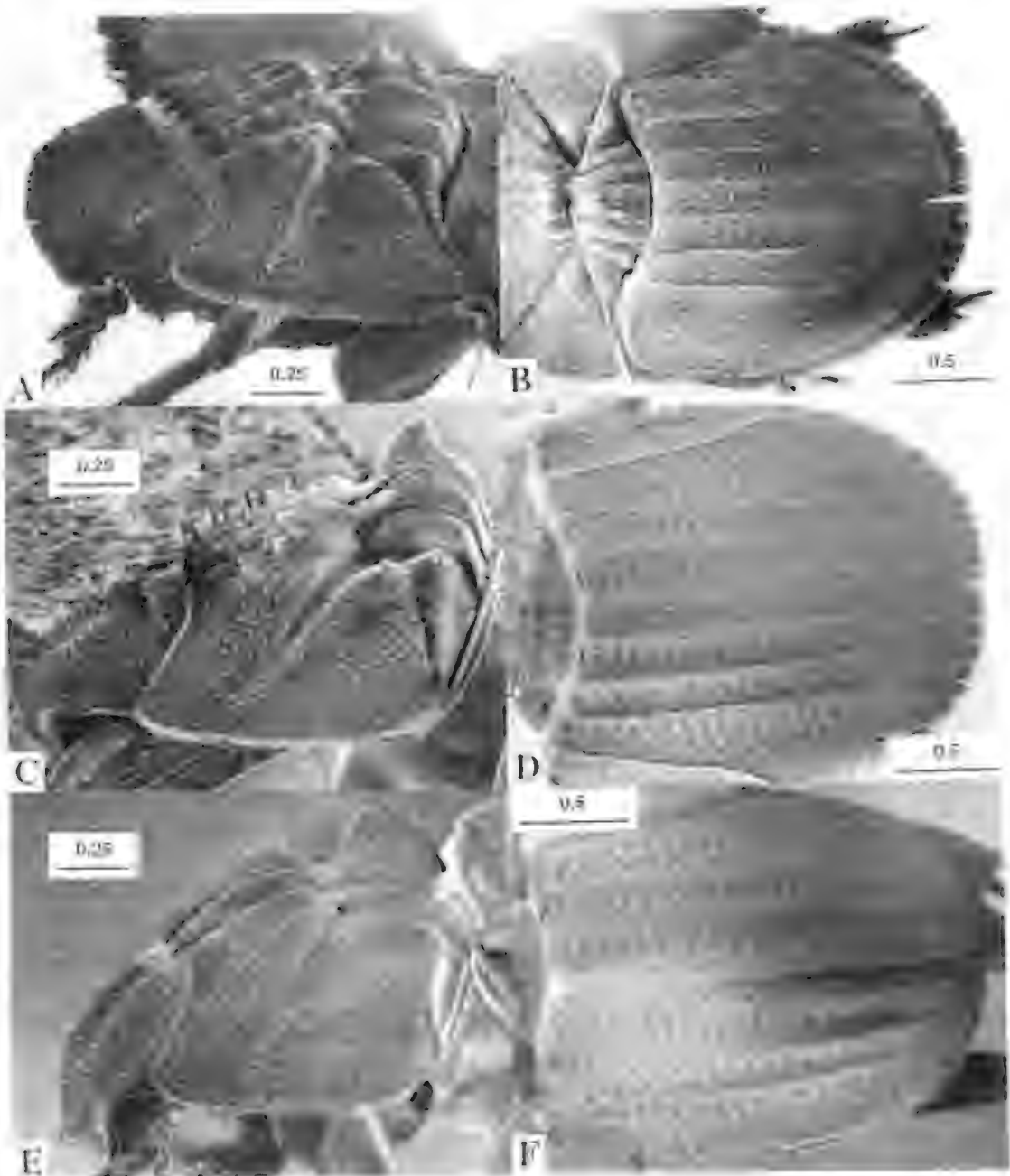
Pygidium. Nitid with small, setate punctures.

FIG.1. A,B, *Australoxenella concinna* sp. nov. A, head and pronotum, lateral view. B, pronotum and elytra, dorsal view. C,D, *Australoxenella zborowskii* sp. nov. C, head and pronotum, lateral view. D, elytra, dorsal view. E,F, *Australoxenella teeta* sp. nov. E, head and pronotum, lateral view. F, elytra, dorsal view.

Ventral surface and legs. Abdominal segments nitid, posterior 1/2 of large segment with small setate punctures; metasternum nitid, central area with small setate punctures; meso- and meta-femora nitid, ventral surfaces with fine setate punctures, more numerous on posterior 1/2; meso- and meta-tibiae nitid, a few fine setate punctures on outer 1/2, lower lateral margin of each metatibia with a row of short, adjacent, flattened setae.

COMMENTS. *Australoxenella concinna* sp. nov. is closest to *A. zborowskii* sp. nov., sharing with it the setal fringes on the pronotum and elytra, and the clusters of spur-like setae on the pronotal sculpturing. It differs from that species in the additional fringe of setae on the anterior margin of the head, the pronotal clusters being not as strongly developed, the elytra having circular scales over the entire surface and the lack of a third lateral pair of elytral ridges. *Australoxenella concinna* is the most southerly species of the genus; it was trapped in dense rainforest (G. Monteith, pers. comm). Several hundred trap-months using flight interception traps by the senior author in many similar Atherton Tablelands sites over many years have failed to capture further specimens.

Australoxenella zborowskii sp. nov.
(Figs 1C, 1D, 6A)

ETYMOLOGY. For Paul Zborowski, collector of several species described in this paper.
MATERIAL EXAMINED. HOLOTYPE ANIC113, sex not determined, from 11° 41'S, 142° 42'E, 14km ENE of Heathlands, Qld, 21.i.-19.ii.1994, P. Zborowski, flight intercept trap.

DESCRIPTION. Length 2.6mm, greatest width 1.4mm. Reddish brown dorsally and ventrally.

Head. Three grooves all reaching anterior edge, lateral grooves converging slightly for apical 1/3 length; surface of head with narrow, elongate, nitid marking above each eye.

Pronotum. Sculptured area anterior to transverse sulcus wider, about 1/2 width of pronotum, grooves strong, intergroove rounded ridges of equal height, not raised around median groove, third lateral pair of grooves weak, almost reaching anterior angles; prominence around median groove posterior to transverse sulcus strong, apex acute, additional fourth pair of lateral grooves present, running from middle portion of sulcus almost to posterior angles; transverse sulcus constant in width, narrowing towards apices, almost reaching lateral edges of pronotum; grooves nitid, middle region of sulcus with prominent yellow setae; pronotal disc with spur-like clusters of erect, yellow setae - four groups on each of the four narrow anterior ridges, five each on adjacent wider ridges, less obvious clusters on posterior central prominence and posterior lateral raised areas; lateral pronotal edges from anterior angles to just past posterior angles each with a distinct fringe of short, adjacent, flattened, yellowish setae.

Elytron. Disc flattened, explanate, ridges not very high and U- shaped depressions shallow; with sutural and three lateral ridges, sutural ridge very slightly stronger, third lateral ridge strong, running from base to c. 3/8 distance along lateral margin of elytron; area of elytron outside stria c.1/2 as wide as in most other species; dorsal surface outside third lateral ridge with close, appressed, circular scales, scales also numerous along remaining margin of elytron and up to apices of elytral ridges, crest of each elytral ridge with a single row of overlapping scales along entire length resulting in a carinate appearance; U-shaped depressions between lateral ridges with regular transverse, single, occasionally double, rows of scales joining ridges; lateral margin of elytron from base to apex with a distinct fringe of short, adjacent, flattened yellowish setae; lateral stria also with a reduced fringe row; epipleuron broad, slightly narrowed at apex, bare, nitid.

Pygidium. Smaller than in other species, with scattered setate punctures.

Ventral surface and legs. Meso- and meta-tibiae with a few minute setate punctures, posterior outer margin with a short setal fringe; ventral surfaces of meso- and meta-femora with scattered, medium, setate punctures.

COMMENTS. This species is known from a single specimen taken in notophyll vine forest in a flight interception trap (P. Zborowski, pers. comm.). Characters separating *A. zborowskii* sp. nov. are discussed under *A. teeta* sp. nov. and *A. concinna* sp. nov. The distinctive pronotal and elytral fringes of flattened setae are found only in three Queensland species, *A. zborowskii*, *A. teeta* and *A. concinna*.

Australoxenella teeta sp. nov.
(Figs 1E, 1F, 6A)

ETYMOLOGY. An Aboriginal word for insect.
MATERIAL EXAMINED. HOLOTYPE ANIC114, sex not determined, from 13° 39'S, 142° 40'E (GPS), 2km N Rokeby, Qld, 15.ii.-18.iii.1994, P. Zborowski & M. Shaw, flight intercept trap.

DESCRIPTION. Length 2.6mm, greatest width 1.3mm. Reddish brown dorsally and ventrally.

Head. Median groove almost reaching anterior edge, lateral grooves slightly shorter and converging for anterior 1/2; surface of head with small elongate, nitid marking above each eye.

Pronotum. Anterior rounded ridges adjacent to median groove weakly elevated posteriorly, third lateral pair of grooves weak, almost straight to
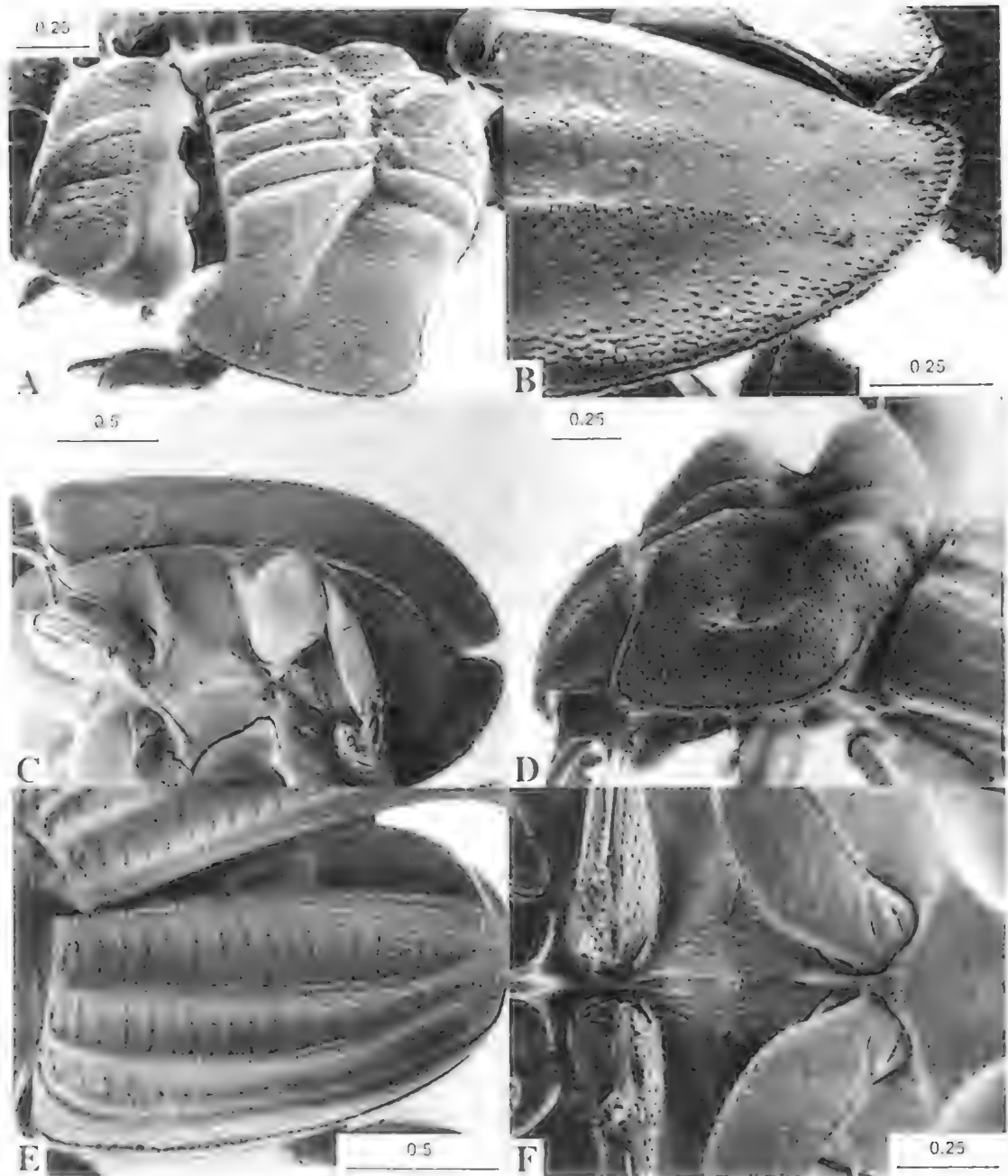
FIG.2. A-C, *Australoxenella bathurstensis* Howden & Storey. A, head and pronotum, dorsolateral view. B, elytral apex, dorsolateral view. C, posterior half, ventral view. D-F, *Australoxenella kalpara* sp. nov. D, head and pronotum, lateral view. E, elytron, dorsal view. F, mesosternum, ventral view. (Figs 2A,B from Howden & Storey, 1992)

anterior angles, ridges adjacent to median groove posterior to transverse sulcus forming an elevated prominence, median groove not visible anterior-

ly, transverse sulcus not widened at apices, sulcus reaching 3/4 distance to lateral edge of pronotum from centre line; sulcus medially and centre of

sculptured area with dense, yellow setae; lateral pronotal edges from anterior angles to just past posterior angles with a distinct fringe of short, adjacent, flattened, yellowish setae.

Elytron. Disc with sutural and three lateral ridges, ridges not strong, sutural ridge most developed, third lateral ridge reduced and meeting margin of elytron about 1/2 distance to apex; lateral stria reaching margin of elytron about 3/8 distance to apex; dorsal surface outside of third lateral ridge with close, appressed, circular scales, crests of other ridges also with scales including a row of adjacent scales on crest of sutural and first lateral, U-shaped depressions between lateral ridges with spaced, transverse, single rows of scales joining ridges, surface dull, bare between; margin of elytron from base to apex with a distinct fringe of short, adjacent, flattened, yellowish setae; epipleuron narrowing only slightly towards apex, surface bare, subnitid.

Pygidium. Nitid with only scattered setate punctures.

Ventral surface and legs. Tibiae wide, flattened, nitid, impunctate on broad surfaces; femora broad, nitid, ventral surfaces of meso- and meta-femora with numerous setate punctures.

COMMENTS. *Australoxenella teeta* sp. nov. was taken in open forest in a flight interception trap set in red earth woodland dominated by *Eucalyptus tetradonta* and *E. mesophila* (P. Zborowski, pers. comm.) The border fringe of flattened setae on the lateral edges of the pronotum and elytra are well developed only in *A. teeta, A. concinna* sp. nov. and *A. zborowskii* sp. nov. All three species are nitid ventrally and have the prominence on the pronotal surface anterior to the transverse sulcus very reduced or absent. *Australoxenella zborowskii* and *A. concinna* have the elytra more explanate, the setal fringes slightly longer, the sculptured area in front of the pronotal transverse sulcus wider and less raised and prominent clusters of spur-like setae on the anterior pronotal ridges, allowing easy separation from *A. teeta.*

Australoxenella bathurstensis Howden & Storey, 1992
(Figs 2A-C, 6B)

Australoxenella bathurstensis Howden & Storey, 1992:1813.
MATERIAL EXAMINED. HOLOTYPE NTMAI287, from Cape Fourcroy, Bathurst Island, NT, 26.x.-3.xi.1979, P. Horner & I. Archibald.

DESCRIPTION. Length 3.2mm, greatest width 1.6mm. Brown dorsally, reddish brown ventrally.

Head. Median groove reaching 3/4 distance to anterior edge, lateral grooves slightly shorter and slightly converging for anterior 1/2; surface of head with narrow, elongate marking above each eye.

Pronotum. Median, first and second lateral pairs of grooves anterior to transverse sulcus strong, equal in depth and width, third lateral pair of grooves fine, joining anterior edge of pronotum c.1/3 distance from anterior angles to centre line, anterior four central ridges strong, rounded, equal in height and width; median groove posterior to transverse sulcus barely visible on posterior half only, first lateral pair stronger, second and third lateral pairs strongest, ridges either side of median groove forming strong prominence, crest rounded; transverse sulcus narrow, barely widened toward centre; area between anterior and posterior sculpturing with groups of appressed, yellow setae.

Elytron. Broad, flattened, explanate; sutural and three lateral ridges not strong, crests low, rounded, third lateral ridge forming lateral margin of elytron just past 1/2 distance to apex; lateral stria joining lateral margin of elytron just before 1/2 distance to apex; close, appressed, circular scales cover surface outside third lateral ridge and along crests of all four ridges, U-shaped depressions with few scattered scales mostly in basal 1/2, surface of depressions dull; epipleuron widened to apex, dull to subnitid on apical 1/3, circular scales along outer margin.

Pygidium. Subnitid with scattered small setate punctures,setae fine, flattened.

Ventral surface and legs. Abdominal segments, metasternum, and meso- and meta- femora subnitid with scattered small punctures each with a fine seta, meso- and meta-tibiae subnitid, with setate punctures only near outer margins.

COMMENTS. *Australoxenella bathurstensis* Howden & Storey can be distinguished from the other species of Group 1 by the form of the elytra, with all ridges low and rounded, with associated scales unordered, and largely bare U-shaped depressions. It is still known only from the holotype.

Australoxenella moogoon sp. nov.
(Figs 3A, 3B, 6B)

ETYMOLOGY. An Aboriginal word for beetle.
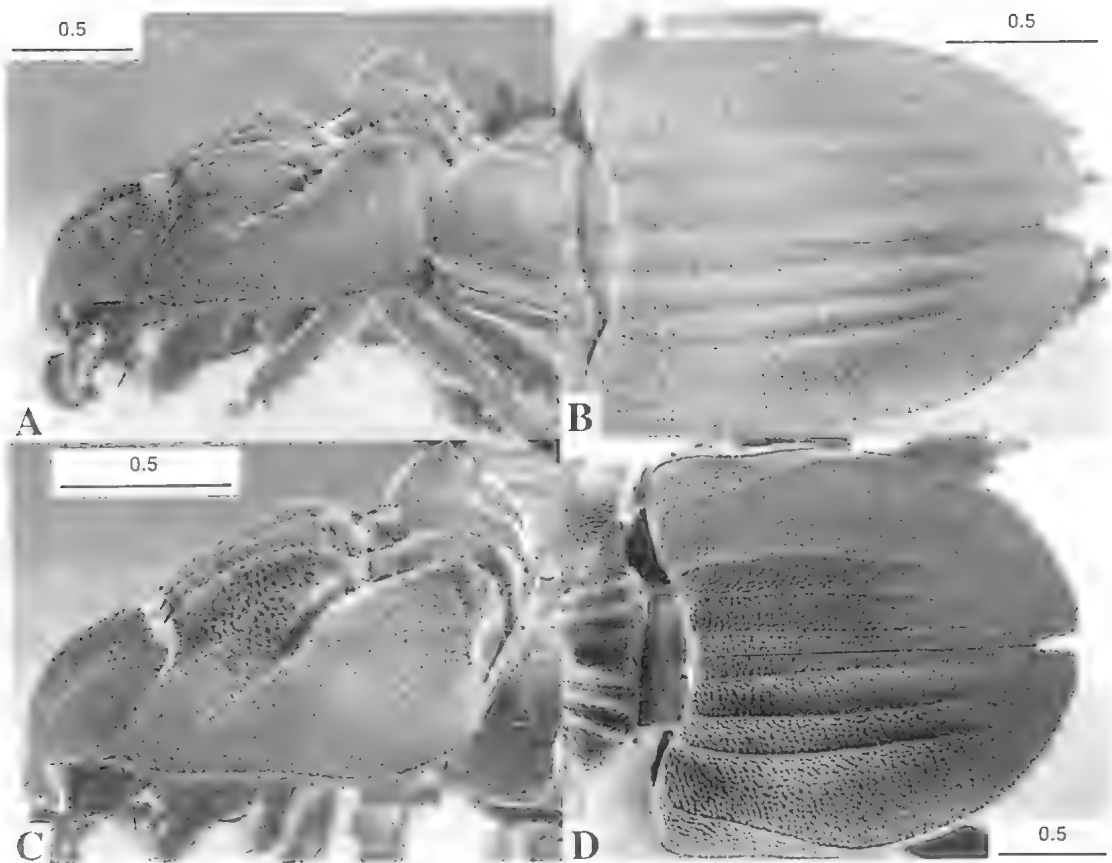MATERIAL EXAMINED. HOLOTYPE ANIC115, sex not determined, from 33km E of Jabiru, Arnhem-

FIG.3. A,B, *Australoxenella moogoon* sp. nov. A, head and pronotum, lateral view. B, elytra, dorsal view. C,D, *Australoxenella wurrook* sp. nov. C, head and pronotum, lateral view. D, elytra, dorsal view.

land, NT, 15-23.xii.1993, S. & J. Peck, 93-130, 5 FITs, Podocarp Canyon, rainforest. PARATYPES (5) in HAHC, QPIM, same data as Holotype.

DESCRIPTION. Length 2.4–2.5mm, greatest width 1.3-1.4mm. Reddish brown dorsally, slightly lighter ventrally.

Head. Median groove almost reaching anterior edge, lateral grooves slightly shorter and slightly converging for anterior 1/2; surface of head with narrow elongate marking above each eye.

Pronotum. Anterior rounded ridges adjacent to median groove only very slightly elevated posteriorly, four ridges and median, first and second lateral pairs of grooves equal in appearance, third lateral pair of grooves fine reaching anterior pronotal edge c.1/3 distance from anterior angles to centre line; ridges either side of median posterior groove forming a subacute prominence, anterior portion of median groove scarcely visible, other grooves strong; transverse

sulcus strong, slightly widened to c.2/3 distance to apices; apical 1/3 of anterior grooves, second and third lateral posterior grooves, widened section of sulcus bare, nitid; apices of both anterior and posterior ridges near centre of pronotum with close, appressed, yellowish setae.

Elytron. Broad, flattened; disc with sutural and three lateral ridges, sutural, first and second lateral ridges similar in development, not strongly raised, third lateral ridge stronger joining lateral margin of elytron c.2/3 distance to apex; lateral stria joining margin of elytron c.1/2 distance to apex; crests along length of all ridges each with single row of adjoining, circular scales, less distinct on third lateral; rest of surface with circular, appressed scales densest outside third lateral ridge, fairly dense inside third lateral towards second lateral ridge, rest of surface with scales most numerous towards crests of ridges; epipleuron wide to apex, subnitid with scales only towards outer margin.

Pygidium. Nitid with scattered, small setate punctures.

Ventral surface and legs. Abdominal segments, metasternum, mid and hind legs nitid, abdominal segments, centre of metasternum and meso- and meta-femora with scattered small, setate punctures.

COMMENTS. *Australoxenella moogoon* sp. nov. is a member of Group 1 species group and does not have a pronotal prominence anterior to the transverse sulcus and has the elytral ridges low and capped with a single row of adjacent circular scales. It is closest to *A. wurrook* sp. nov. and the two species can be separated by characters listed in the key to species. *Australoxenella wurrook* and *A. moogoon* were taken at the same locality and series of flight interception traps but not necessarily in the same trap.

Australoxenella wurrook sp. nov.
(Figs 3C, 3D, 6B)

ETYMOLOGY. An Aboriginal word for flat.
MATERIAL EXAMINED. HOLOTYPE ANIC116, sex not determined, from 33km E of Jabiru, Arnhemland, NT, 15-23.xii.1993, S. & J. Peck, 93-130, 5 FITs, Podocarp Canyon, rainforest. Paratype in HAHC, same data as Holotype.

DESCRIPTION. Length 2.8–3.1mm, greatest width 1.6–1.7mm. Dark reddish brown dorsally, slightly lighter ventrally.

Head. Median groove reaching anterior edge, lateral grooves falling short of anterior edge and slightly converging on anterior 1/3; surface of head with moderately long, narrow marking above each eye; anterior edge of dorsal surface of head with an indistinct fringe of very short flattened setae.

Pronotum. Four central anterior rounded ridges of equal height, median, first and second lateral pairs of grooves of equal width and depth, third lateral pair of grooves fine reaching anterior pronotal edge c.1/3 of distance from anterior angles to centre line; pronotal surface adjacent to posterior median groove elevated, crest of prominence acute, median groove not visible in anterior 1/2, strong in posterior 1/2; transverse sulcus long, narrow, visible for 4/5 distance to lateral pronotal edges, surface of sulcus bare, nitid; pronotal surface except for sulcus and small area between anterior and posterior sculpturing, covered in close, appressed, circular scales, denser in five central anterior grooves, groups of dense, yellowish setae at anterior ends of

posterior grooves; lateral pronotal edges between anterior and posterior angles with indistinct fringe of very short, flattened setae.

Elytron. Wide, flattened, length to width ratio about 2:1; sutural and three lateral ridges visible, not high, sutural ridge not raised near posterior end, equivalent in height to first and second lateral ridges, third lateral ridge weaker, shorter, almost reaching lateral margin of elytron c.3/8 distance to apex then running parallel to margin towards apex; lateral stria strong, short, reaching lateral margin of elytron just before third lateral ridge; entire surface of elytron densely covered with close, appressed, circular scales, these in the form of a single row of adjacent scales along crest of each elytral ridge; epipleuron broad all the way to apex, nitid, with scales only towards outer margin.

Pygidium. Smaller, nitid with scattered setate punctures.

Ventral surface and legs. Ventral surface nitid, last abdominal segment and meso- and meta-femora moderately punctate, punctures with short, fine setae.

COMMENTS. *Australoxenella wurrook* sp. nov. is closest to three new Queensland species, *A. zborowskii* s, *A. concinna*, and *A. teeta*. It lacks the elytral fringes of flattened setae found in the three Queensland species though it does have very short fringes on the anterior of the head and lateral pronotal edges. The circular scales in the U-shaped elytral depressions are not arranged in evenly spaced transverse rows. The pronotal clusters of spur-like setae on *A. zborowskii* and *A. concinna* are absent in *A. wurrook*, and the elytra of *A. teeta* are much less flattened than *A. wurrook*. The two specimens of *A. wurrook* were taken in flight interception traps at Podocarp Canyon near Jabiru, N.T., in rainforest. *A. moogoon* sp. nov. was also taken at this site but not necessarily in the same traps as *A. wurrook*.

Australoxenella midgee sp. nov.
(Figs 4A, 4B, 6A)

ETYMOLOGY. An Aboriginal word for small.
MATERIAL EXAMINED. HOLOTYPE ANIC117, sex not determined, from 11° 51'S, 142° 38'E, 12km SSE of Heathlands, Qld, 16.i.1992, T.A. Weir & I.D. Naumann, Berlesate ANIC 1214 closed forest litter.

DESCRIPTION. Length 2.4mm, greatest width 1.3mm. Dark reddish brown dorsally and ventrally.

Head. Median groove reaching anterior edge,

lateral grooves slightly shorter and slightly converging for anterior 1/2; surface of head with narrow, elongate, nitid marking above each eye.

Pronotum. Anterior rounded ridges adjacent to median groove strongly elevated, the resulting prominence as high as prominence posterior to transverse sulcus, first lateral pair of anterior grooves barely visible, third lateral pair of anterior grooves very weak, meeting anterior pronotal edge c.1/3 distance from anterior angles to centre line; posterior grooves not strong, ridges adjacent to median groove forming an elevated prominence; transverse sulcus not widened at apices; pronotal areas posterior to sulcus and adjacent to median sculpturing depressed, concave, the lateral margins of depressed areas forming costae parallel to lateral pronotal edges.

Elytron. Disc with sutural and three lateral ridges, sutural and third lateral ridges strongest, sutural ridge slightly raised in posterior 1/3; lateral stria not quite reaching lateral margin of elytron c.1/2 distance to apex; dorsal surface outside of third lateral ridge with close, appressed, circular scales, crests of other ridges with similar scales; U-shaped depressions between ridges with regular, transverse, rows of scales joining the ridges, apparently in slight depressions, surface bare, dull between; epipleuron narrowing towards apex, surface dull, bare except with scales along outer margin.

Pygidium. Dull with small dense setate punctures covering entire surface.

Ventral surface and legs. Abdominal segments, legs and centre part of metasternum dull with numerous setate punctures, setae less scale-like than those on dorsal surface; meso- and meta-tibiae and femora less flattened than in other species of the genus.

COMMENTS. *Australoxenella midgee* sp. nov. and *A. kalpara* sp. nov. are the Group 2 Queensland species closest to *A. humptydooensis* Howden and Storey. *Australoxenella midgee* can easily be separated from the latter species by the shape of the pronotum, the transverse rows of scales on the elytral depressions, and narrower tibiae. The only known specimen was taken in a berlesate sample of litter from closed forest.

Australoxenella kalpara sp. nov.
(Figs 2D-F, 6A)

ETYMOLOGY. An Aboriginal word for bed of a river.

MATERIAL EXAMINED. HOLOTYPE ANIC118, sex not determined, from 15° 11'S, 143° 52'E (GPS),

Hann River, Qld, 18.xii.1993- 14.i.1994, P. Zborowski & E.D. Edwards, flight intercept trap.

DESCRIPTION. Length 2.3mm, greatest width 1.2mm. Dark reddish brown dorsally, slightly lighter ventrally.

Head. Median groove almost reaching anterior edge, lateral grooves slightly shorter and slightly converging for anterior 1/2; surface of head with small, narrow, elongate, dull marking above each eye.

Pronotum. Anterior rounded ridges adjacent to median groove strongly elevated, the resulting prominence almost as high as prominence posterior to transverse sulcus, median and first lateral pair of grooves only slighty reduced, third lateral pair of grooves very finely impressed, reaching anterior pronotal edge c. 1/3 distance from anterior angles to centre line; transverse sulcus broad, joined by similar depression running from posterior pronotal edge just outside pronotal sculpturing posterior to sulcus; transverse sulcus and wide grooves from posterior pronotal edge bare, dull, area between two pronotal prominences with close, appressed, yellowish setae.

Elytron. Disc with sutural and three lateral ridges all strong, sutural ridge elevated slightly on posterior 1/3, crest of third lateral ridge with fine groove along inner edge resulting in a doubled appearance; lateral stria strong, meeting lateral margin of elytron c.1/2 distance to apex; crests of sutural, first and second lateral ridges each with single row of adjacent circular scales, additional scattered scales along outer edges of these ridges, close, appressed, circular scales from the third lateral ridge to lateral margin of elytron except along centre of third lateral ridge, just inside the lateral stria and just inside basal 1/4 of margin; U-shaped depressions between ridges with regular transverse rows of adjacent, circular scales, rest of surface bare, dull; epipleuron strongly narrowing towards apex, surface dull, bare except scales along outer margin.

Pygidium. Subnitid with numerous punctures separated by about one diameter, each with a small elongate scale.

Ventral surface and legs. First four abdominal segments and metasternum dull, last visible abdominal segment, meso- and meta-femora and tibiae subnitid; abdominal segments, femora and centre portion of metasternum with scattered, elongate, appressed setae or scales; carinate crest of lanceolate posterior prosternal process not widened near centre.
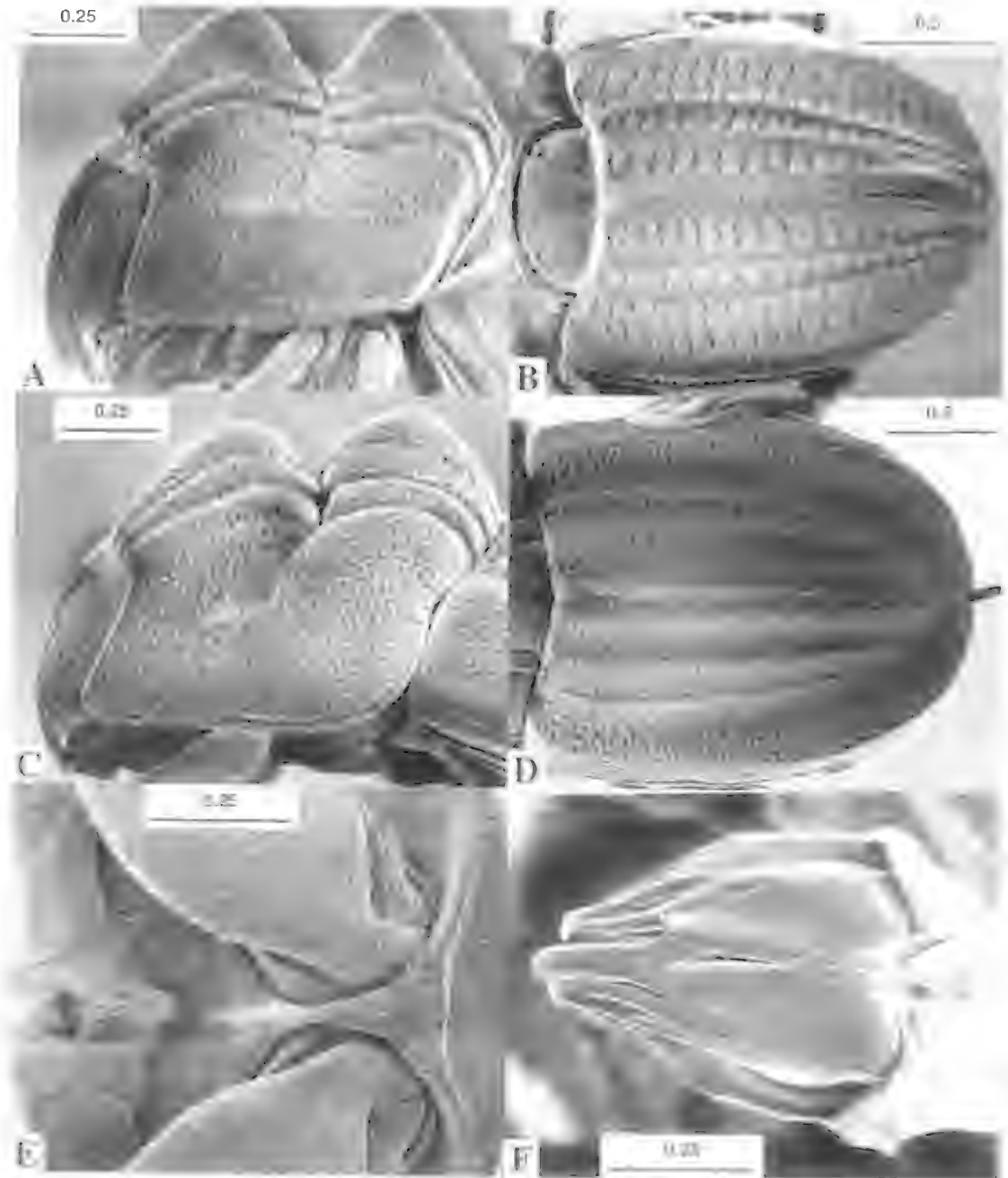
FIG.4. A,B, *Australoxenella midgee* sp. nov. A, head and pronotum, lateral view. B, elytra, dorsal view. C-F, *Australoxenella peckorum* sp. nov. C, head and pronotum, lateral view. D, elytra, dorsal view. E, mesosternum, ventral view. F, male genitalia, dorsal view.

COMMENTS. *Australoxenella kalpara* sp. nov. is closest to *A. midgee* sp. nov., also from Cape York Peninsula. The two species can be separated by pronotal sculpture, reduced punctation on the pygidium in *A. kalpara* and the blade-like shape of the central crest of the prosternal lanceolate process in *A. kalpara*. The habitat was riverine open woodland dominated by *Melaleuca* and *Leptospermum* (P. Zborowski, pers. comm.).

Australoxenella peckorum sp. nov.
(Figs 4C-F, 6B)

ETYMOLOGY. For the collectors of most of the new specimens in this study, Stewart and Jarmila Peck of Ottawa, Canada.

MATERIAL EXAMINED. HOLOTYPE ANIC119, sex not determined, from Kakadu N.P., Kapalga Res. Stn, NT, 11-25.xii.1993, S. & J. Peck, 93-118 FIT eucalypt woodland. PARATYPES same data as Holotype, (10); N.T.: Kakadu N.P., Kapalga Station Gabarlgu, 25. xii.- 7.i.1994, S. & J. Peck, 93-137 FIT rainforest, (2); Kakadu N.P., S. Alligator River, Gungaree rainforest trail, 12-25.xii.1993, S. & J. Peck, 93-120 FIT I, (3), same data except 93-121 FIT II, (5), same data except 25.xii.-6.i.1994, S. & J. Peck, 93-141 FIT I, (1). Paratypes in HAHC, QPIM, NTMA, SBPC.

DESCRIPTION. Length 2.3-3.0mm, greatest width 1.2-1.6mm. Reddish brown dorsally and ventrally.

Head. Median groove reaching or almost reaching anterior edge, lateral grooves reaching 2/3 distance to anterior edge, converging slightly for apical 2/3; surface of head with small elongate marking above each eye.

Pronotum. Anterior rounded ridges adjacent to median groove raised posteriorly to form a prominence almost as high as prominence posterior to transverse sulcus, median and first lateral pairs of grooves reduced, third lateral pair of grooves fine, middle 1/3 often not visible reaching anterior edge of pronotum c.1/3 distance from anterior angles to centre line; posterior prominence strong, apex rounded, median groove weakly visible on posterior half only, first pair of lateral grooves not very deep; transverse sulcus strong, widened almost entire length.

Elytron. Disc with sutural and three lateral ridges, sutural ridge only slightly raised posteriorly, second lateral ridge not strong, third lateral strong reaching almost to apex of elytron, crests of sutural, first and second lateral ridges rounded; lateral stria strong, reaching lateral margin of elytron almost 1/2 distance to apex; close, appressed, circular scales on elytron largely confined to area outside third lateral ridge and near crests of other ridges, U-shaped depressions and area near apex almost bare, dull; epipleuron narrowed towards apex, dull, bare except near outer margin which has close, appressed, circular scales.

Pygidium. Dull with scattered, medium punctures, setae indistinct.

Ventral surface and legs. Abdominal segments dull with scattered, medium-sized punctures, setae indistinct; metasternum dull, punctures and setae of central portion indistinct; meso- and meta-femora with scattered medium-sized setate punctures; metasternum medially just posterior to mesocoxae with broadened transverse ridge, the posterior edge of which is almost straight to feebly, anteriorly, arcuate medially.

Male genitalia as in Fig. 4F.

COMMENTS. The shape of the posterior edge of the transverse ridge of the metasternum which is an almost straight line (instead of an anteriorly directed, abrupt, obtuse angle) allows separation of *A. peckorum* sp. nov. from the other members of Group 2 *Australoxenella* species. The long series was taken at several sites within Kakadu National Park, N.T., using flight interception traps set in eucalyptus woodland and rainforest.

Australoxenella mirreen sp. nov.
(Figs 5A, 5B, 6B)

ETYMOLOGY. An Aboriginal word for south.

MATERIAL EXAMINED. HOLOTYPE ANIC120, sex not determined, from Litchfield N.P., Pethricks Rainforest, NT, 8-30.xii.1993, S. & J. Peck, 93-110 FIT deep rainforest. Paratypes same data as Holotype, (1); N.T.: Litchfield N.P., Wangi Falls, 8- 30.xii.1993, S. & J. Peck, 93-113 FIT deep rainforest, (1). Paratypes in HAHC.

DESCRIPTION. Length 2.4-2.6mm, greatest width 1.3-1.4mm. Dark reddish brown dorsally and ventrally.

Head. Median groove reaching 3/4 distance to anterior edge, lateral grooves slightly shorter and slightly converging for anterior 2/3; surface of head with small oval marking above each eye.

Pronotum. Anterior rounded ridges adjacent to median groove raised posteriorly to form a prominence almost as high as prominence posterior to transverse sulcus, median groove slightly reduced towards apex of prominence, first and second lateral pairs of grooves strong, third lateral pair of grooves finer, reaching anterior pronotal edge c.1/3 distance from anterior angles to centre line; posterior prominence strong, apex rounded, median groove not visible for anterior 1/3, first lateral pair of grooves slightly stronger, second lateral pair stronger still; transverse sulcus strong, widened for most of length.

Elytron. Disc with sutural and three lateral ridges strong, sutural ridge strongly raised posteriorly, three lateral ridges about same height, third lateral ridge slightly longer joining lateral margin of elytron c.4/5 distance to apex;
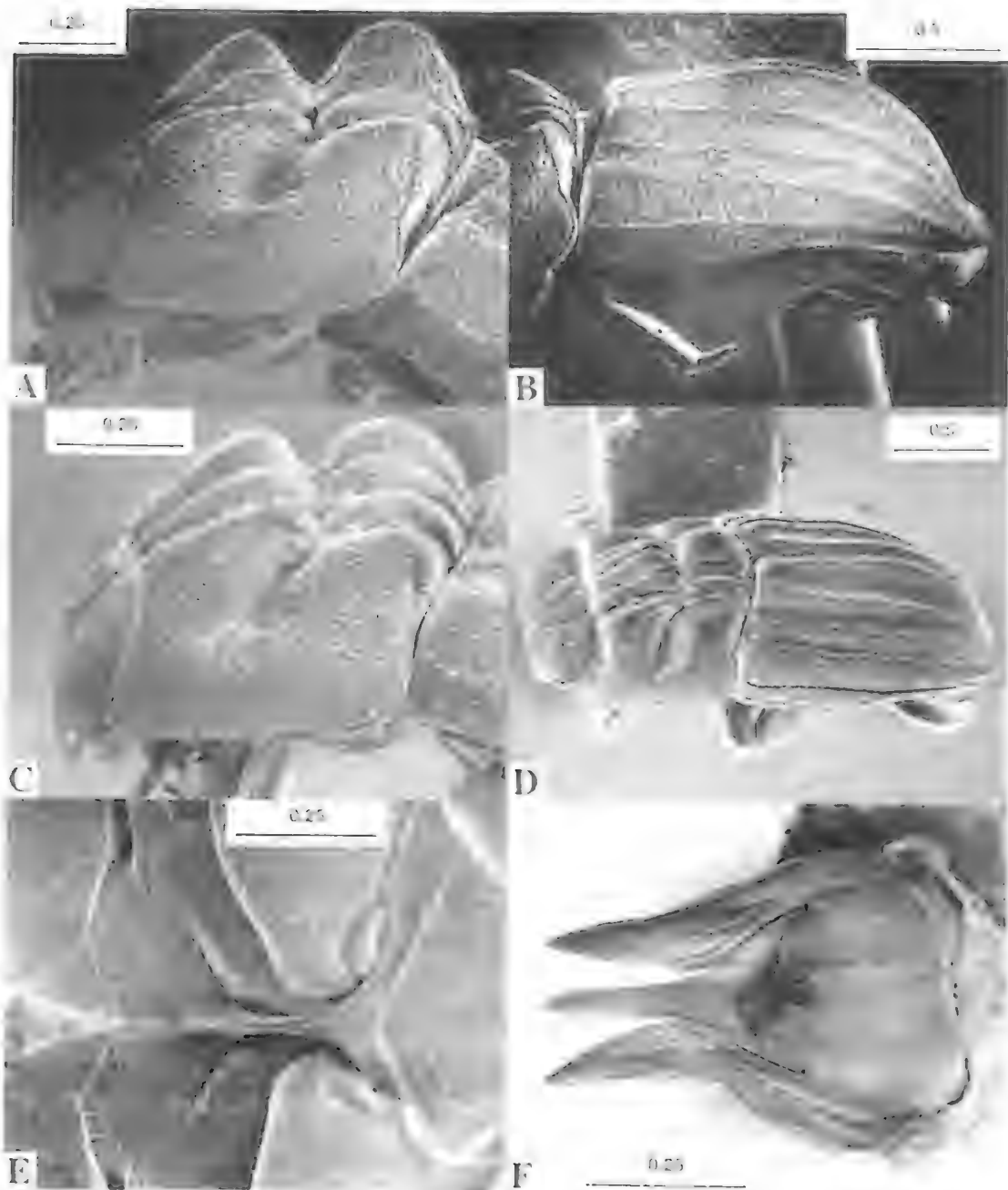
FIG.5. A,B, *Australoxenella mirreen* sp. nov. A, head and pronotum, lateral view. B, elytron, lateral view. C-F, *Australoxenella humptydooensis* Howden & Storey. C, head and pronotum, lateral view. D, dorsolateral view. E, mesosternum, ventral view. F, male genitalia, ventral view. (Fig.5D from Howden & Storey,1992).

lateral stria strong, joining lateral margin of elytron c.2/3 distance to apex; surface outside third lateral ridge and near crests of all ridges with close, appressed, circular scales, these reduced in number in U-shaped depressions and especially near apex; epipleuron narrowed near apex, surface dull bare, except near outer margin which has close, appressed, circular scales.

Pygidium. Dull with indistinct scattered setate punctures.

Ventral surface and legs. Abdominal segments dull with indistinct scattered setate punctures; metasternum dull, centre portion with indistinct setate punctures; meso- and meta- femora dull with scattered setate punctures.

COMMENTS. *Australoxenella mirreen* sp. nov., from Litchfield National Park, west of Adelaide River, is similar to *A. humptydooensis* from the Darwin area. The two species are separable with difficulty by the characters mentioned in the key to species.

Australoxenella humptydooensis Howden & Storey, 1992
(Figs 5C-F, 6B)

Australoxenella humptydooensis Howden & Storey 1992:1813.
MATERIAL EXAMINED. HOLOTYPE QMBAT12146, 6km E Humpty Doo, 6-19.x.1990, R.I. Storey, at U.V. light. Other material (51): N.T.: Darwin, CSIRO McMillans Rd, 1-25.xii.1993, S. & J. Peck, mixed eucalypt woodland 93-87 FIT, (40), same data except 25.xii-10.i.1994, mix. euc. woodlot 93-148 FIT, (3); 50km S Darwin, Berry Spg.Pk, 4-27.xii.1993, S. & J. Peck, 93-99 rainforest malaise, (7), same data except 27.xii.-3.i.1994, 93-154 rainforest FIT, (1). Specimens in ANIC, HAHC, ISEA, QPIM, QMBA, SBPC.

DESCRIPTION. Length 2.2–2.6mm, greatest width 1.1–1.4mm. Dark reddish brown dorsally and ventrally.

Head. Median groove reaching close to anterior edge, lateral grooves slightly shorter and slightly converging for anterior 1/2; surface of head with small oval-elongate marking above each eye.

Pronotum. Median anterior groove slightly reduced, especially posteriorly, apical 1/2 of third lateral pair of grooves fine, joining anterior pronotal edge c.1/3 distance from apical angles to centre line, two median anterior, rounded ridges raised posteriorly to form a prominence, not as high as prominence posterior to transverse sulcus; median groove posterior to sulcus fine, sometimes not visible in anterior 1/2, rounded ridges either side of median groove expanded to form a prominence, with crest rounded; transverse sulcus deep, widened posteriorly for c.3/4 length.

Elytron. Disc with sutural and three lateral ridges, sutural ridge slightly raised in middle 1/3, first lateral ridge strong, basal 1/2 highest, second lateral ridge weaker, third lateral ridge weak,

joining lateral margin of elytron c.4/5 distance to apex; lateral stria reaching margin of elytron c.1/2 distance to apex; close, appressed, circular scales on surface of elytron outside of third lateral ridge, just inside third lateral ridge except for a fine, bare groove on basal 1/2, second lateral ridge rounded with scales on outside, inside bare with fine groove, crest of first lateral ridge rounded with scales over most of length, a slight inner groove on apical 1/3, sutural ridge rounded with scales over entire length. U-shaped depressions and apex of elytron dull with only scattered scales; epipleuron wide, narrowing towards apex, dull with scales along outer margin.

Pygidium. Subnitid with scattered small punctures each with a short appressed, elongate scale.

Ventral surface and legs. Abdominal segments, metasternum, and mid and hind legs subnitid, femora, centre of metasternum and abdominal segments with scattered fine punctures, each with a short, appressed, flattened seta, more scale-like on abdominal segments and apical margins of metafemora.

Male genitalia as in Fig. 5F.

COMMENTS. *Australoxenella humptydooensis* is closest to *A. mirreen* which was taken slightly south of the former, in Litchfield National Park. *Australoxenella humptydooensis* was taken in numbers using both flight interception and malaise traps, in open and closed forest habitats.

DISCUSSION The 11 species of *Australoxenella* fall into two groups separated in the first couplet of the key. Group 1 consists of *A. bathurstensis*, *A. zborowskii*, *A. concinna*, *A. teeta*, *A. wurrook*, and *A. moogoon* . All have the sculptured area of the pronotum in front of the transverse sulcus of a constant height with the centre five grooves of equal depth and the four ridges of equal height; all but *A. teeta* have the elytral epipleura wide to the apex; the epipleura are subnitid to nitid in all species; in *A. zborowskii*, *A. concinna*, *A. wurrook* and *A. moogoon* the elytra are relatively broad, the ridges and U-shaped depressions not strongly developed, and the crest of each ridge is marked by a distinctive single row of adjacent circular scales. Group 2, containing *A. midgee*, *A. kalpara*, *A. peckorum*, *A. mirreen* and *A. humptydooensis*, always has the middle two anterior pronotal ridges developed into a prominence similar to the posterior prominence but lower; the elytral epipleura are always distinctly narrowed towards the apex and not strongly nitid; the elytra are more convex in cross
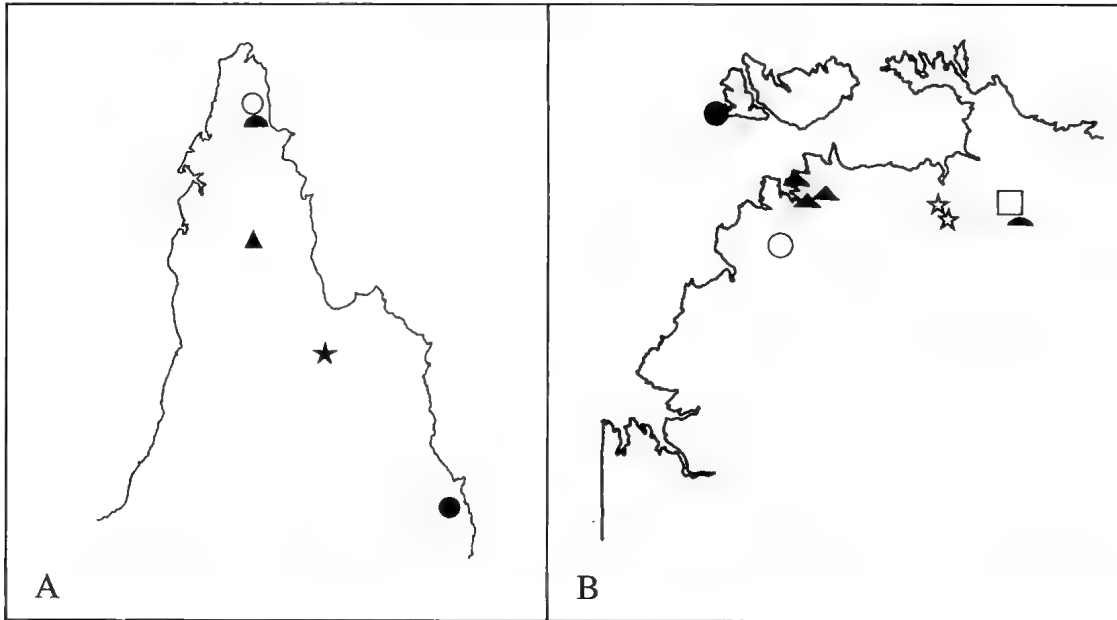
FIG.6. Distribution of *Australoxenella* spp. A, North Queensland: (●) *A. concinna* sp. nov.; (○) *A. zborowskii* sp. nov.; (solid semicircle) *A. midgee* sp. nov.; (★) *A. kalpara* sp. nov.; (▲) *A. teeta* sp. nov. B, Northern Territory; (●) *A. bathurstensis* Howden and Storey; (□) *A. wurrook* sp. nov.; (solid semicircle) *A. moogoon* sp. nov.; (☆) *A. peckorum* sp. nov.; (○) *A. mirreen* sp. nov.; (▲) *A. humptydooensis* Howden and Storey.

section and the ridges and U-shaped depressions more strongly developed; the crests of the elytral ridges usually do not have a distinctive row of adjacent circular scales. Both species groups occur in N.T. and Qld.

The following are comments on characters employed by Howden & Storey (1992): 17. Absence of striae. *Australoxenella* was rated apomorphic (striae absent) in this character despite all but one of the new species and the two original species having an elytral feature which was thought to be a 'stria'. The exact derivation of this stria-like feature is unknown.

18. Less than five abdominal segments at mid-line. The abdominal segments in *Australoxenella* are greatly compacted and reduced at the mid-line (except the large last visible segment), and discerning the exact number is difficult. The number varies with sex, four in males and five in females.

Except for these features, all new species otherwise agree with the character-states table for *Australoxenella* of Howden & Storey (1992). Bordat & Howden (1995) described three new genera in the tribe from Borneo and discussed the phylogeny of the Stereomerini, removing the South American *Termitaxis* Krikken.

Specimens of *Australoxenella* have been taken in closed (rainforest) and open forest situations (c.1/3 in the former). Six species were taken only in closed forest, two only in open forest, two in both, with no information available for one species. Both habitat types produced specimens in N.T. and Qld. As most specimens were obtained using flight interception traps, it would seem that collection site data reflect habitat preferences of the beetles. There was some evidence in the long N.T. series that catches were higher in traps where some odour of decay was evident, the traps having been run for several weeks.

Australoxenella is still rare in collections. Six species are only represented by the holotype. However, the long series of *A. humptydooensis* and *A. peckorum* indicate that at least these species can be common under some circumstances.

There is no information available on the biology of *Australoxenella*. Howden & Storey (1992) speculated that all Stereomerini were termitophiles and the unusual morphology, specialised pronotal setae in some species and rarity all point to the genus being inquiline. The only direct evidence of termite species being the hosts, was that the only known South American specimen of the tribe, the holotype of *Termitaxis holmgreni* Krikken was taken in the nest of a termite (Krikken, 1970). Bordat & Howden (1995) suggested

that *Termitaxis* should be removed from Stereomerini until the holotype could be closely examined. Though some work has been undertaken investigating termite nests and their associated fauna in tropical areas of Australia, no *Australoxenella* specimens have been found.

ACKNOWLEDGEMENTS

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A NEW SPECIES OF *SCHIZOTREMA* (CUMACEA: NANNASTACIDAE) FROM MORETON BAY, QUEENSLAND

D.J. TAFE AND J.G. GREENWOOD

Both sexes of *Schizotrema nudum* sp. nov. are described and figured. It differs from other species of the genus in lacking spines on the carapace and on the dorsal surface of the abdomen. The species also differs from the closely related *S. leopardinum* Hale, in the relative lengths of exopod and endopod of the uropod. Eleven species are now known in this genus. Five (*S. aculeatum* Hale, *S. depressum* Calman, *S. leopardinum* Hale, *S. nudum* sp. nov. and *S. resimum* Hale) occur in Australian waters. □ *Crustacea, Cumacea, Nannastacidae, Australia, Schizotrema*.

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During a study of cumaceans in Moreton Bay, on the central east coast of Australia, a new species of *Schizotrema* Calman, 1911 was captured. The genus is one of 18 in the Nannastacidae. *Schizotrema* is differentiated from the closely related *Schizocuma* by the pseudorostrum which forms widely spaced inhalent siphons.

All specimens were taken using a sledge-mounted net of 500 μm mesh towed within 0.4m of the substratum at night. Although 700 samples were collected from 40 sites widely distributed within the Bay region only three specimens of the new species were taken, and all came from the same location. One specimen of *Schizotrema aculeatum* Hale, 1945, was also taken from the same location. A male and female of the new species were dissected, drawn and described and the other male used for S.E.M. study. Descriptions were carried out with reference to Felgenhauer (1992), Hale (1936, 1945, 1949), Jones (1963) and Watling (1989). In descriptions of appendages lateral refers to that margin of the appendage facing the lateral body surface and medial refers to that margin directed toward the midline of the body. Long plumose natatory setae on thoracic appendages have been truncated in some figures

SYSTEMATICS
Class CRUSTACEA
Subclass MALACOSTRACA
Superorder PERACARIDA
Order CUMACEA

Family NANNASTACIDAE
Schizotrema Calman, 1911

Schizotrema Calman, 1911:360; Stebbing, 1913:165.

DIAGNOSIS. Anterolateral angle of carapace well developed; eyes divided into two separate groups; pseudorostrum forming two widely separated inhalent siphons; second to fifth pereionites well developed, usually with plate-like lateral extensions; no pleopods and no free telson.

Eleven species are now known in this genus. Five (*S. aculeatum* Hale, *S. depressum* Calman, *S. leopardinum* Hale, *S. nudum* sp. nov. and *S. resimum* Hale) occur in Australian waters and only *S. aculeatum* Hale and *S. nudum* sp. nov. are known from Moreton Bay.

KEY TO SPECIES OF *SCHIZOTREMA*
(Adapted from Hale 1949)

1. Carapace broad and depressed. Peduncle of uropod longer than telsonic somite
 . . . . *depressum* Calman
 Carapace not or little depressed. Peduncle of uropod much shorter than telsonic somite . . 2

2. Exopod of uropod at least 0.3 times as long as endopod (not including terminal spines) 3
 Exopod of uropod at most 0.25 times as long as endopod 9

3. Last pedigerous and first pleon somite each with one pair of outstanding dorsal spines 4
 Such somites with clumps of small spines or no spines 5

4. Spines on carapace aculeate . . *aculeatum* Hale

Spines on carapace spatulate . . . *sakaii* Gamo

5. Anterolateral angle of carapace produced as a
   stout cylindrical process 6
   Anterolateral angle of carapace not produced as a
   stout cylindrical process 7

6. Telsonic somite wider than long in dorsal view
   . . . . *bifrons* Calman
   Telsonic somite longer than wide in dorsal view
   . . . . *atlanticum* Bacescu & Muradian

7. Uropod with spine of exopod not quite reaching
   distal end of endopod (excluding terminal spine)
   . . . . *macrodactylus* Fage
   Uropod with spine of exopod clearly reaching
   beyond distal end of endopod (excluding ter-
   minal spine) 8

8. Surface of carapace with reticulate pattern of in-
   dentations; anterolateral corner of carapace an-
   gular and without spine . . . . *nudum* sp. nov.
   Surface of carapace for the most part smooth;
   anterolateral angle of carapace produced as a
   slender spine . . . . *sordidum* Calman

9. Carapace with dorsal and lateral spines
   . . . . *resimum* Hale
   Carapace not spiny 10

10. Carapace with mottled colour pattern, and with
    anterolateral angle broad, not at all down-bent
    . . . . *leopardinum* Hale
    Carapace without mottled colour pattern, and
    with anterolateral angle produced and strongly
    down-bent . . . . *bidens* Fage

Schizotrema nudum sp. nov.
(Figs 1-4)

MATERIAL EXAMINED. HOLOTYPE
QMW20468, adult (S.L., 1.6 mm), perm. slide mount,
Horseshoe Bay, Peel Island, 27°30'S, 153°22'E, site
31, D. Tafe, 17.6.1990, 2-3 m, sand, 34 p.p.t. salinity,
19°C water temperature. PARATYPES QMW20469,
ovig. (S.L., 1.4mm), same data as holotype, perm. slide
mount; QMW20470, adult (S.L., 1.7 mm), S.E.M.
mount, site 34, otherwise same data as holotype.

DESCRIPTION OF MALE. Standard length 1.6
mm, (measured from anterior end of pseudo-
rostrum to posterior end of telsonic somite, ex-
cluding spines and setae). Cuticle well calcified.
Carapace with reticulate pattern of indentations;
last three pedigerous and first three abdominal
somites with paired dorsal nodules but without
obvious spines (Fig. 1A, B). Carapace twice as
long as combined length of exposed pedigerous
somites, almost 1/3 total length of animal;
posterior margin of carapace slightly raised dor-
sally, produced posteriorly to cover whole of first
pedigerous somite and dorsum of second;
anterolateral corner of carapace angular and

devoid of spines. Two prominent ocular regions
located anteriorly on dorsolateral margins, each
composed of 3 separate, hemispherical lenses
(Fig. 1C, D).

Pleural parts of second to fifth pedigerous
somites expanded (Fig. 1D); pleural region of
second pedigerous somite almost as wide as
carapace, 3-5 gradually decreasing in width; ab-
dominal somites not expanded laterally. Dorsal
region of telsonic somite flattened, approximate-
ly as wide as long, and longer than peduncles of
uropods (Fig. 1E).

First antenna (Fig. 2A) with first segment of
peduncle longer than second and third segments
together, three large setae distolaterally, row of
short, simple setae laterally; second segment with
two large setae distolaterally, tubercle with one
plumose and two simple setae distomedially;
third segment subequal in length to second, bear-
ing 1 simple and 2 plumose setae distomedially,
and accessory flagellum distolaterally; accessory
flagellum bearing 4-5 simple setae; main flagel-
lum 3-segmented, first and second segments
slender and subequal in length, third smaller, with
2 long, annulated aesthetascs terminally and 2-3
fine setae subterminally.

Second antenna (Fig. 2B) with 3 short proximal
segments; fourth segment longer than combined
1-3. Third and fourth segments with lateral mar-
gins setose. Flagellum elongate, multiarticulate.

Mandible (Fig. 2C) molar process cylindrical
with flattened masticating surface. Incisor with
3-4 teeth on inner edge; lacinia mobilis present
on left mandible only; row of 5-6 closely spaced
stiff setae on inner margin of mandible between
distal teeth and molar process.

First maxilla (Fig. 2D) with 2 well developed
terminal endites carrying at their distal ends a
number of hamate setae; larger lobe with 7-9
setae, smaller 3-4 setae, with longest proximal,
slender and pappose. Appendage with backward-
ly directed endopodite posteriorly; palp unilobed,
with 2 long, slender setae, each with fine setules
almost invisible at x400.

First maxilliped (Fig. 2E) basis with a row of
slender simple setae medially and a hamate seta
distomedially. Endopod 4-segmented; first seg-
ment short, with 3 setae distomedially; second
segment rectangular with scattered setae; third
segment shorter and narrower, with 3 strong dis-
tal setae one of which is long and serrulate, lateral
margin of segment convex, with simple setae;
fourth segment circular, with 2 fine subterminal
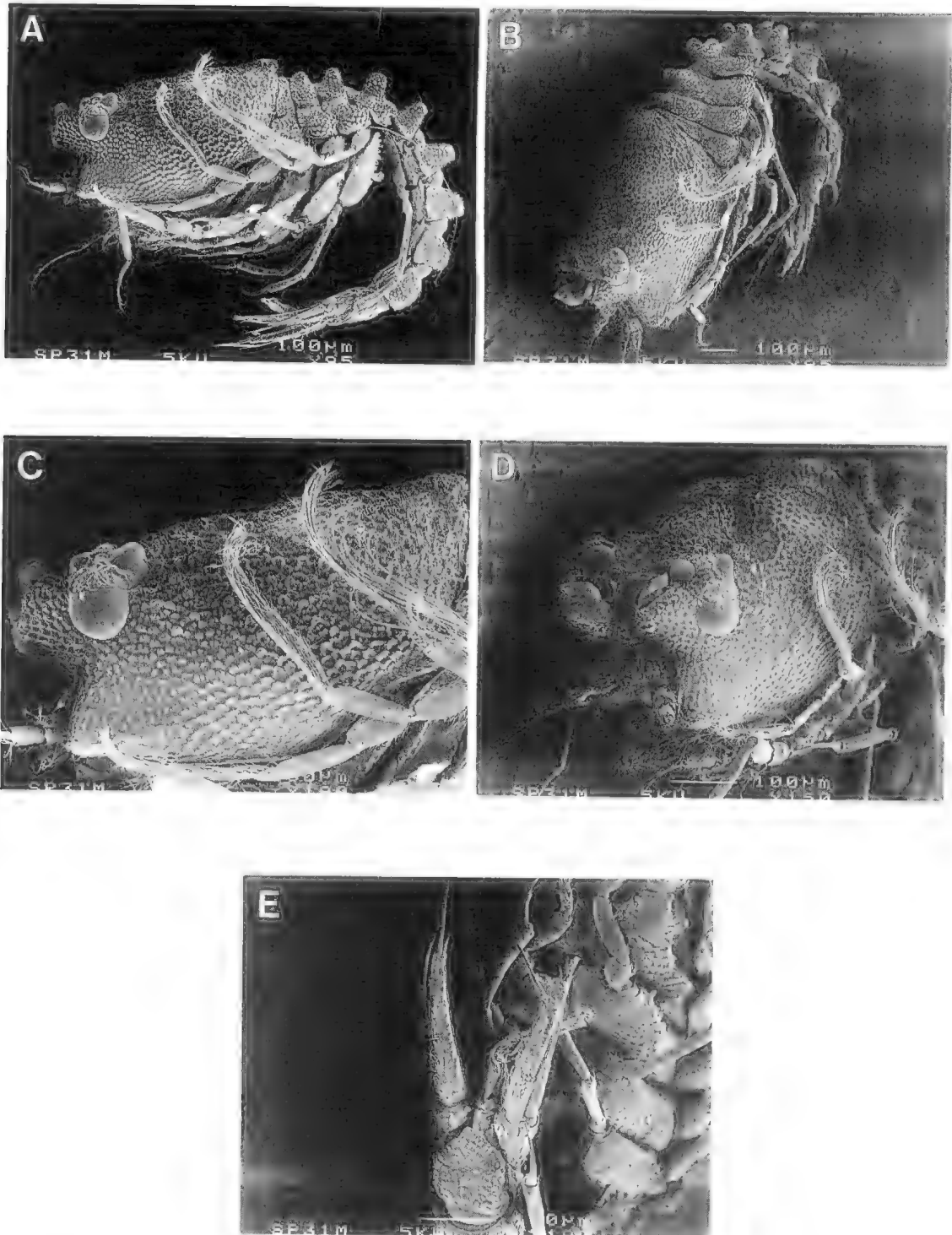setae.

Second maxilliped (Fig. 2F) basis subequal in

FIG. 1. *Schizotrema nudum* sp. nov., adult male. A, lateral view. B, dorsolateral view. C, carapace, lateral view. D, carapace, anterolateral view. E, telsonic somite and uropods, dorsal view. SEMs with JEOL 6400. Scale bars = 100μm
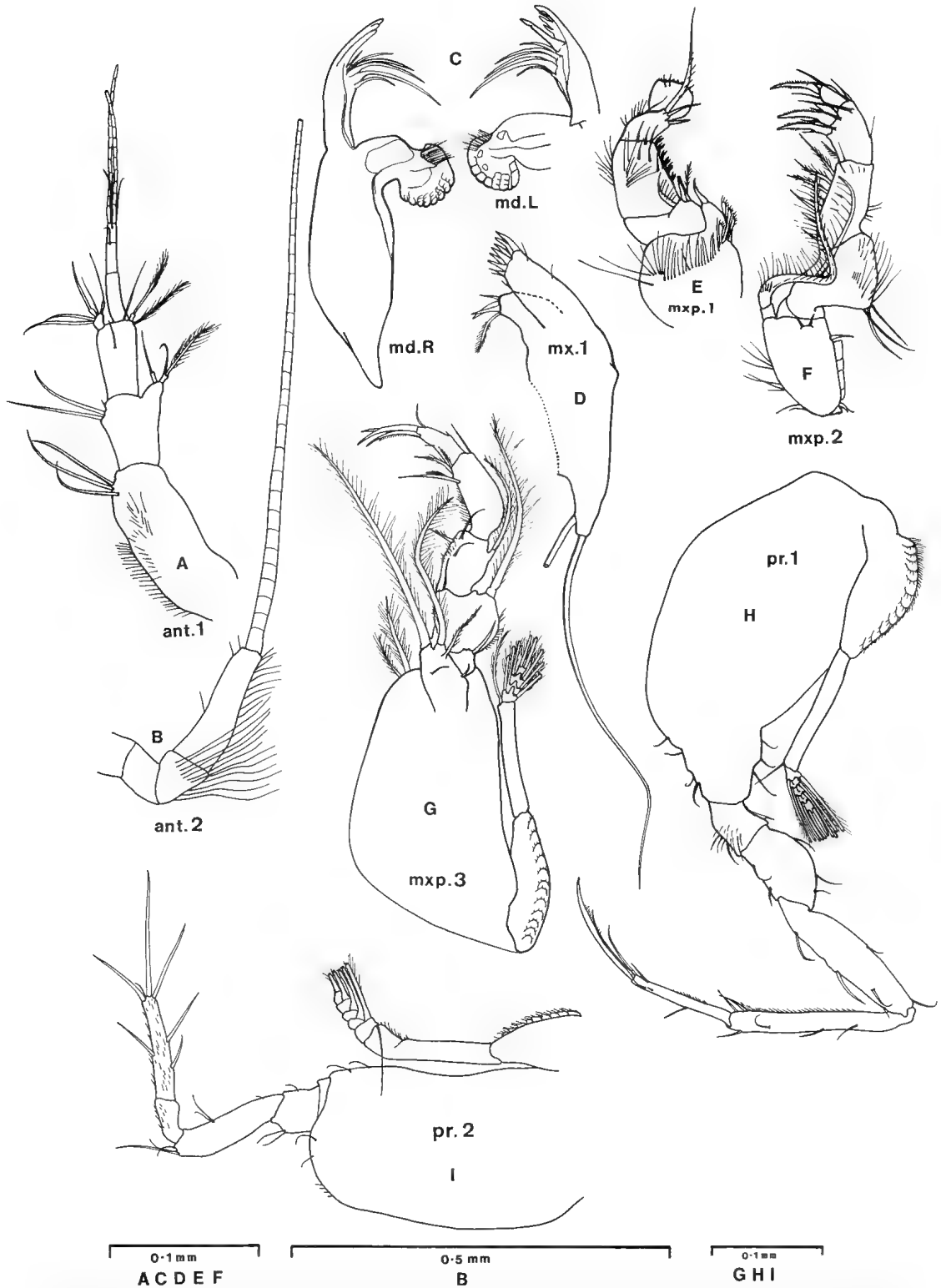
FIG. 2. *Schizotrema nudum* sp. nov., adult male. A, first antenna. B, second antenna. C, right mandible and portion of left mandible. D, first maxilla. E, first maxilliped. F, second maxilliped. G, third maxilliped. H, first pereiopod. I, second pereiopod.

length to merus, long, plumose seta distomedially, setae on medial margin and ridge on lateral margin; ischium extremely short, without setae; merus geniculate, expanded centrolaterally, prominence bearing several long setae distolaterally, single large plumose seta arising from the central anteromedial surface; carpus slightly shorter than merus, longer than propodus, with row of plumose setae along medial margin, scattered simple setae on lateral surface; propodus almost as wide as long, with 3 stout serrulate setae distally, with 3-4 slender setae subdistally; dactylus short with strong terminal seta.

Third maxilliped (Fig. 2G) basis inflated, subequal in length to rest of limb; laterodistal lobe with 2 stout and 1 fine plumose setae, two plumose setae on distomedial region of basis; ischium of endopod reduced, with simple seta distolaterally; merus broad with a stout, plumose seta distolaterally, row of short setae on convex lateral margin; carpus subequal in length to merus but narrower, long plumose seta laterally, scattered short setae distomedially; propodus longer than merus, carpus, and dactylus, simple seta distolaterally, 3 plumose setae distally; dactylus slender with 3 stout, curved terminal setae and 1 slender curved subterminal seta, 1 medial and 2 lateral simple setae. Exopod with basal segment bearing 12 ridges with microspines, following segment naked and elongate, 4 short distal segments each bearing 1 pair of long plumose setae.

First pereiopod (Fig. 2H) with inflated basis and 5 endopod segments. Endopod longer than basis, terminal segments progressively longer from ischium to propodus, dactylus shorter than propodus and subequal in length to terminal seta; setae on all segments (except terminal seta) short and simple; propodus and dactylus with rows of fine setae on medial margins; terminal seta of dactylus slightly curved with setules on distal medial margin, 2 smaller terminal setae and 2 subterminal setae. Exopod with 2 basal segments of similar length, first broad and fringed laterally bearing 12 ridges with microspines; second naked and elongate; segments 3-7 reduced in length, each bearing a pair of long, plumose setae.

Second pereiopod (Fig. 2I) basis inflated, as long as rest of limb. Endopodal ischium reduced; carpus subequal in length to dactylus, twice as long as merus and propodus; terminal dactylar seta straight and longer than segment, 2 shorter terminal setae, 1 lateral and 2 medial setae; surface of dactylus and propodus covered with microspines. Exopod with 2 subequal proximal segments, first bearing 12 ridges with

microspines laterally; segments 3-7 very reduced, each bearing a pair of long, plumose setae.

Third pereiopod (Fig. 3A) endopod segments slender, together at least 1.5 times as long as inflated basis. Endopodal carpus longer than other segments, almost twice combined length of ischium and merus; dactylus arcuate, bearing 2 setae. Exopod with 2 subequal proximal segments, first bearing 10 ridges with microspines laterally; segments 3-7 very reduced, each bearing a pair of long, plumose setae.

Fourth pereiopod (Fig. 3B) similar to third except terminal 5 segments of endopod together twice as long as inflated basis; exopod with 2 subequal proximal segments, first naked and second bearing 7 pairs of minute ridges with microspines; 4 reduced terminal segments each bearing a pair of long, plumose setae.

Fifth pereiopod (Fig. 3C), with slender basis and terminal segments, without exopod. Carpus longer than other segments, 1.5 times length of propodus and twice combined length of ischium and merus; dactylus arcuate as with third and fourth pereiopods.

Telsonic somite (Figs 1E, 3D) as wide as long, with 6 scattered setae on each side of the dorsum but without spines. Dorsal profile as figured.

Peduncle of uropod (Figs 1E, 3D) with lateral margin 0.6 times length of telsonic somite, 0.4 times length of endopod exclusive of its terminal spine. Exopod at least as long as peduncle and 0.45 length of endopod, with its long terminal seta reaching nearly to midlength of terminal endopod seta; 1 short distolateral terminal exopod seta. Terminal seta of endopod about half as long as ramus, with subterminal lateral setule; 2-3 short distomedial endopod setae. Medial margin of endopod serrate, with microspines.

DESCRIPTION OF FEMALE. Standard Length: 1.4 mm. Cuticle well calcified. Carapace and abdominal somites with reticulate pattern of indentations and paired dorsal nodules as in male.

First antenna (Fig. 3E) with first segment of peduncle longer than combined length of segments 2+3, 3 long setae distomedially, row of fine setae medially; second segment with 2 long setae distomedially, tubercle with 3 simple setae distolaterally; third segment subequal in length to second, with accessory flagellum bearing 3-4 setae; main flagellum 3-segmented with 2 annulated aesthetascs and 1 long seta mounted terminally; combined length longer than 3 segments of peduncle.

Mandible (Fig. 3F) molar process cylindrical with flattened masticating surface. Distal end with 4 teeth on inner edge; lacinia mobilis on left mandible only; row of 5 closely packed spines on inner margin of mandible between distal teeth and molar process.

First maxilla (Fig. 4A) with 2 well-developed terminal endites bearing several hamate setae; larger lobe with 8 distal setae and a subterminal seta laterally; smaller lobe with 4 distal setae, longest one proximal, slender and plumose. Posteriorly appendage with a backwardly directed endopodite; unilobed palp with 2 slender distal setae.

Second maxilla (Fig. 4B) with 3 lobes, all with setae along distal margins; largest, most distal lobe with 13-14 setae, longest one plumose; smaller inner lobe with 11-12 simple setae, outer lobe with 6-7 delicate, inwardly directed setae.

First maxilliped (Fig. 4C) basis with row of simple setae laterally and stout setae medially; endopod 4-segmented, first segment short, with one long plumose seta and 2 stout setae medially; second segment rectangular, with hamate setae medially and slender setae laterally; third segment narrow, with 3 strong distal setae, one long and plumose; lateral margin of third segment convex, with simple setae; fourth segment circular, with 2 fine subterminal setae.

Second maxilliped (Fig. 4D) basis longer than merus and ischium combined, long plumose seta distomedially; row of short setae medially and short simple seta distolaterally; ischium rudimentary and naked; merus geniculate, lateral margin convex, with several fine setae, single large plumose seta arising from the central anteromedial surface; carpus longer than merus and propodus, with 4 large plumose setae and numerous simple setae medially, row of simple setae midlaterally; propodus almost as wide as long, 3 strong, serrulate and 5-6 slender setae distally, directed medially, medial margin with rounded setuled lobe, 3 midlateral setae; dactylus slender, shorter than propodus, directed medially with strong terminal spine. Exopod with 5 long, plumose setae.

Third maxilliped (Fig. 4E) basis as long as next 3 segments combined, tubercle with 2 long plumose setae distolaterally, 2 plumose setae distomedially; ischium short with plumose seta distomedially; merus longer than ischium but shorter than carpus, plumose seta distolaterally and small simple seta distomedially; carpus shorter than propodus, plumose seta distolaterally, 3-4 small setae distomedially; propodus nar-

row proximally, lateral margin convex, three slender plumose setae distomedially, row of short setae on medial margin, 3-4 short setae on distal margin; dactylus slender, twice as long as wide, with 2 large curved terminal setae and 2-3 smaller subterminal setae. Exopod with 2 proximal segments subequal in length; 2 reduced terminal segments each bearing a pair of long plumose setae.

First pereiopod (Fig. 4F) basis inflated; 5 slender endopod segments; ischium subequal in length to merus with 1 medial and 2 lateral setae; merus with 3 setae on convex lateral margin and 2 on medial margin; carpus twice length of merus with 2 lateral and 3 medial setae; propodus subequal in length to carpus and at least 1.5 times as long as dactylus, 4 setae laterally and 2 distomedially, row of fine setae along medial margin; dactylus slender, with curved terminal seta as long as dactylus, 2 shorter slender terminal setae and 2 subterminal setae. Exopod with 2 proximal segments subequal in length; 3 reduced terminal segments each bearing a pair of long plumose setae.

Second pereiopod (Fig. 4G) basis inflated, longer than segments 1-4 of endopod, scattered simple setae only; ischium reduced and naked; merus longer than ischium and propodus but shorter than carpus and dactylus, 3 lateral and 2 medial setae; carpus subequal in length to dactylus, twice as long as propodus, 1 long and 2 short distolateral setae, row of fine lateral setae; propodus short with row of fine lateral setae; dactylus twice as long as propodus with major terminal seta straight and longer than segment, 2 shorter terminal setae, surface of dactylus covered with microspines. Exopod with 2 proximal segments subequal in length, 2 reduced terminal segments each bearing a pair of long, plumose setae.

Perciopods 3-5 (Fig. 4H-J) with slender basis and 5 slender endopod segments; dactylus arcuate with seta on inner margin; carpus longer than propodus and nearly twice as long as merus and ischium together; no exopod.

Telsonic somite (Fig. 4K) as wide as long, with 9-10 short setae on dorsal surface, with 2 slender setae distomedially.

Peduncle of uropod (Fig. 4K) with outer margin more than half as long as telsonic somite (0.65X) and half as long as endopod exclusive of its terminal seta, 1 slender distomedial seta; exopod shorter than peduncle and about 1/3 as long as endopod, with its stout terminal seta reaching beyond the distal end of endopod segment, 2

pr. 3

A

pr. 4

B

pr. 5

C

Ur

D

E

ant. 1

md. R

md. L
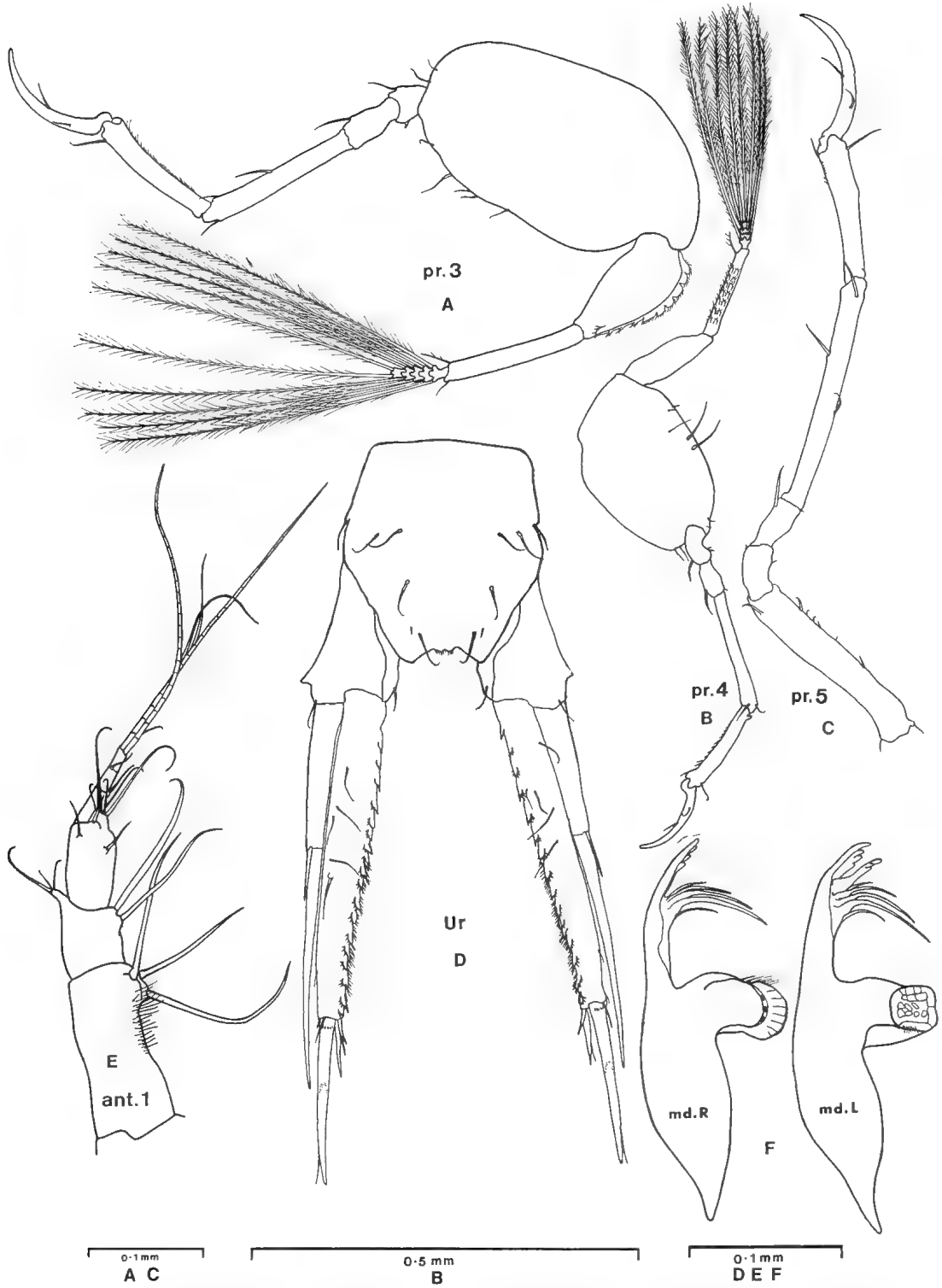
F

0·1 mm
A C

0·5 mm
B

0·1 mm
D E F

FIG. 3. *Schizotrema nudum* sp. nov. A-D, adult male. A, third pereiopod. B, fourth pereiopod. C, fifth pereiopod. D, telsonic somite and uropods. E,F, ovigerous female. E, first antenna. F, right and left mandibles.
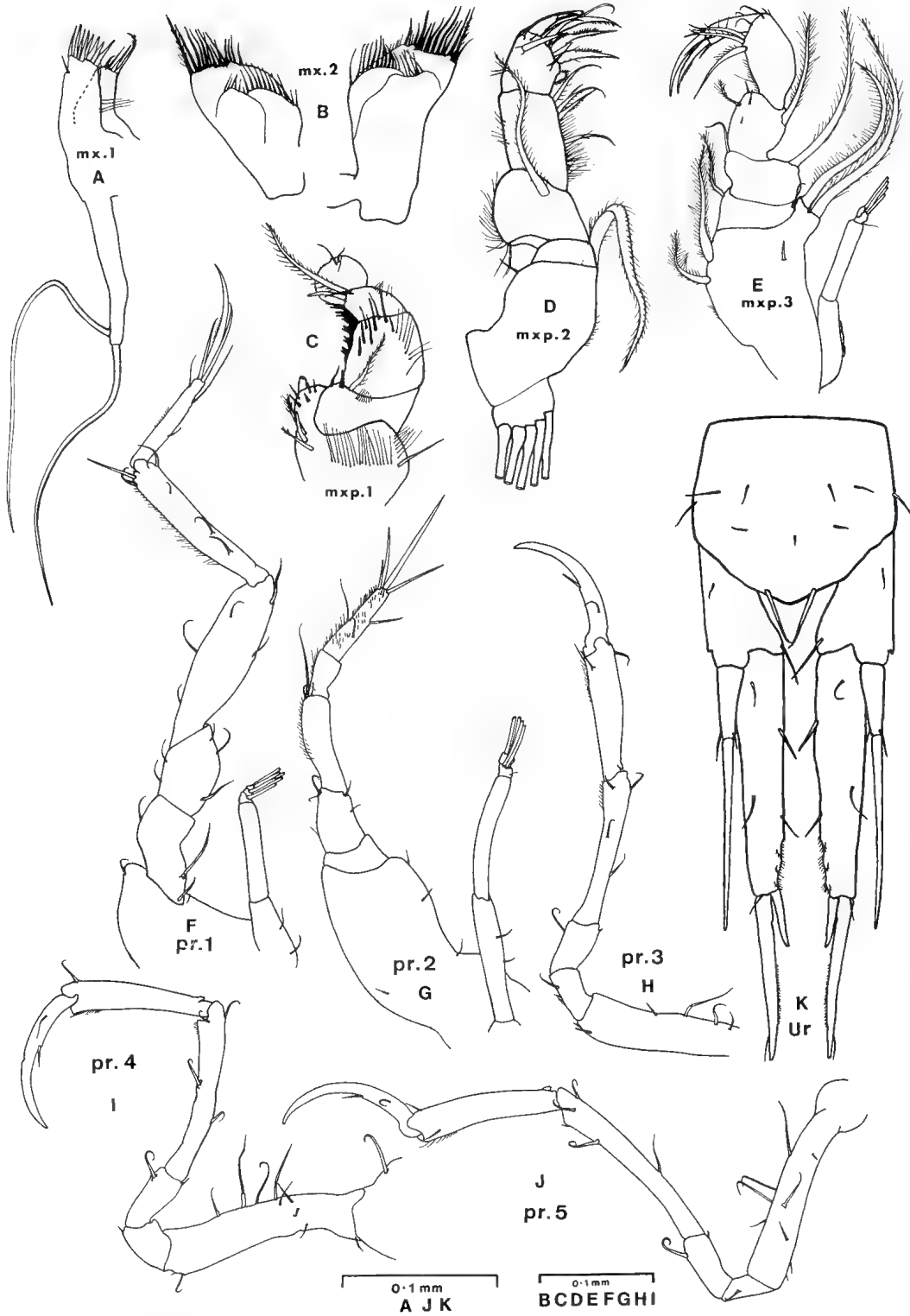
FIG. 4. *Schizotrema nudum* sp. nov., ovigerous female. A, first maxilla. B, second maxilla. C, first maxilliped.
D, second maxilliped. E, third maxilliped. F, first pereiopod. G, second pereiopod. H, third pereiopod. I, fourth
pereiopod. J, fifth pereiopod. K, telsonic somite and uropods.

small subterminal setae; endopod with 2 stout terminal setae, the outer one 2/3 as long as the ramus and 3 times as long as the inner one, bearing a long subterminal setule laterally and row of microspines medially, 1 fine terminal seta, 2 dorsolateral and 2 dorsomedial setae, and 3 distomedial ridges bearing microspines.

DISCUSSION. *Schizotrema nudum* sp. nov. is distinguished within the genus by its lack of spines on the general surface of carapace and abdomen, and by the paired nodules on the dorsal surfaces of most free somites of the pereion and pleon. The uropods also distinguish *S. nudum* from other Australian species. *Schizotrema nudum* id distinguished from *S. aculeatum, S. bifrons* and *S. sakai* which have on spination alone. The latter three species have characteristic spines on the carapace and free somites. Specimens of *S. aculeatum* were also taken at night in Horseshoe Bay.

Like *S. nudum, S. leopardinum* is completely devoid of stout spines on the cuticle. However, the relative proportions of the rami of the uropod enable the two species to be easily distinguished. The female of *S. leopardinum* has not been described but the male uropod has an exopod only 0.25x the length of the endopod, compared to 0.45x in *S. nudum*. Also the differences in colour and surface texture make the two species readily distinguishable. The bold pigment patches of *S. leopardinum* persist even in spirit preserved material (Hale, 1949).

Schizotrema resimum is distinguished from *S. nudum* by its smaller size, conspicuous body spination and very small exopod on the uropod. The dorsum of its carapace exhibits rather large spines, many of which bear a brush of minute setae distally.

Schizotrema depressum exhibits a broad, depressed carapace which distinguishes it from *S. nudum* and all other members of the genus (Hale, 1949).

The new species was compared with type material of *S. aculeatum* and *S. leopardinum*, and non-type material of *S. depressum*, all in the South Australian Museum.

ETYMOLOGY. Latin *nudum* naked; referring to the lack of conspicuous body spines and striking colour patterns.

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REPTILE DIVERSITY IN A *CALLITRIS* FOREST IN CENTRAL QUEENSLAND'S BRIGALOW BELT. *Memoirs of the Queensland Museum* 39(2) 390. 1996:- The clearing of much of Queensland's Brigalow Biogeographic Region for agriculture and grazing has been well documented (Sattler & Webster, 1984; Gasteen, 1985), but the effects of this on animal diversity and populations is unknown. To date no comprehensive review of distribution and status of the Brigalow Biogeographic Region's reptile species has been completed, although such a study is current (Covacevich, Couper & McDonald pers.comm.). To further that work I monitored, a long term pit trap to assess reptile species diversity in a small, relatively untouched forest near Emerald, MEQ.

The study site (23°40'S, 148°06'E) is 100m from the full supply level of Fairbairn Dam. It was maintained by staff of the Camp Fairbairn Outdoor Education Centre of the Queensland Education Department, with assistance from visiting school children. The trap design followed Hobbs et.al. (1994). Twelve buckets were set in a N-S line, over 50m. The study site was located in sand amongst *Callitris columellaris*, with scattered pockets of *Cassia ovata*.

The study was conducted over 199 days, from April till December 1995; specimens were collected on 72 days over 4 seasons. 170 specimens of 24 species were collected. 23 voucher specimens have been lodged in the Queensland Museum reference collection (QMJ61410-61412, 61423, 61426, 61436-61441, 61444-61454, 61459). Most reptile activity occurred during October, November and May. In these months 77.5% of the specimens were trapped (Fig 1).

The following species were collected during the study: *Diplodactylus conspicillatus* x7, *D. steindachneri* x17, *D. taenicauda* x7, *D. vittatus* x11, *Heteronotia binoei* x12, *Nephrurus asper* x3, *Lialis burtonis* x3, *Carlia munda* x1, *C. pectoralis* x7, *Cryptoblepharus carnabyi* x27, *Ctenotus robustus* x6, *C. strauchii* x13, *C.taeniolatus* x13, *Lerista fragilis* x3, *L. punctatovittata* x9, *Menetia greyii* x2, *Morethia boulengeri* x13, *M. taeniopleura* x3, *Varanus tristis* x1, *Ramphotyphlops* sp. x4, *Demansia psammophis* x1, *Rhinoplocephalus boschmai* x1, *Simoselaps australis* x2, *Vermicella annulata* x1. In addition to reptiles the following were collected (and released) from the pit trap: spiders; scorpions; centipedes; millipedes; bush cockroaches; frogs (*Limnodynastes ornatus*); mammals (*Tachyglossus aculeatus*, *Pseudomys delicatulus*).

Construction of the Fairbairn Dam commenced in 1968 and was completed in December 1972. It flooded c.16000ha of native forests, most of which had been grazed or modified. Native forests bounding its waters are now virtually the only non-agricultural land in the Emerald district. That 24 species of small reptiles were found in this small patch of *Callitris* forest in a 9 month period suggests that the diversity of small reptiles has been maintained, despite considerable modification of habitat. It also highlights the value of pit-trapping in surveys. I have been based at Fairbairn Dam for 5 years, and spend some time everyday in the field. Prior to this study, only 7 reptile species had been recorded incidentally in the Outdoor Education Centre's lease, an area of 19 ha. No methodical

hand collecting or searching for reptiles had been undertaken.

No significant range extensions for reptiles were made. However, the study confirms *D. taenicauda*, *C. pectoralis*, *C. taeniolatus and M. taeniopleura* near the limit of their range in the Emerald area (Covacevich & Couper, 1991). Two species on this site are of special conservation concern currently. *D. taenicauda* and *V. annulata* are classified 'rare or insufficiently known' by Cogger et. al. (1993).

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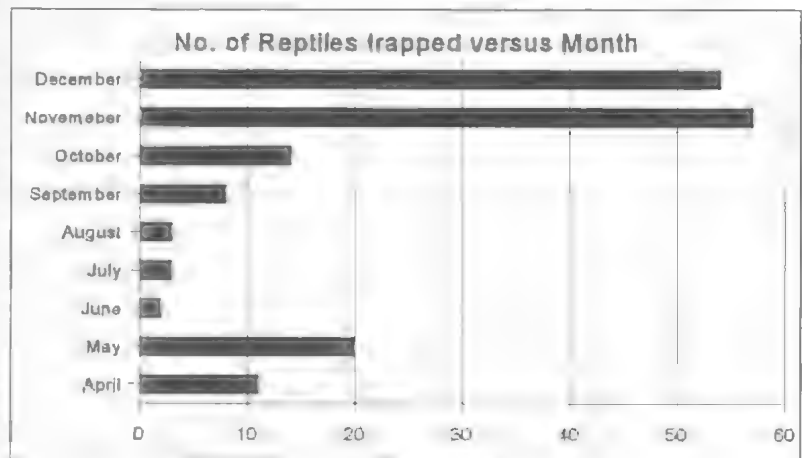*Russell Deer, Camp Fairbairn Outdoor Education Centre, Box 419, Emerald, Queensland 4720, Australia; 20 April 1996.*

Fig.1. Number of specimens trapped per month

THE BODOTRIIDAE (CRUSTACEA: CUMACEA) OF MORETON BAY, QUEENSLAND

D.J. TAFE AND J.G. GREENWOOD

Of 29 species of the Bodotriidae (Cumacea) collected from 40 sites in Moreton Bay (1989-1993) 22 are new records for the region and 18 are new species. Of the new species 5 are left in open nomenclature because insufficient material is available on which to base a description. The ♀ of *Glyphocuma halei*, previously unknown, is also described. Keys are given to the subfamilies, genera and species of Bodotriidae from Moreton Bay. The keys to species of *Cyclaspis*, *Glyphocuma*, and *Leptocuma*, are broadened to include all Australian species. Where a high degree of sexual dimorphism exists within species, such as those in the genus *Glyphocuma*, separate keys to the sexes are constructed. □ *Crustacea. Moreton Bay, Australia, Peracarida, Zooplankton.*

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This is the first major taxonomic investigation of Cumacea in Queensland waters. Isolated or small collections have been studied in works by Hale (1944a,b, 1948, 1949a), Stephenson *et al.* (1978) and Stephenson (1980a,b). The most significant taxonomic works on Australian Cumacea were published between 1928 and 1953 by H.M. Hale. In 1953 he listed 160 species from the W, S and E coasts of Australia.

The Bodotriidae is more diverse than all other families (94 species) in Australian waters (Bacescu, 1988, 1990, 1992b). *Cyclaspis* is by far the most species rich genus and its genetic centre is in the Australasian region (Bacescu, 1992b). The Nannastacidae (45 species) and Gynodiastylidae (36 species) are also well represented around the Australian coastline, while the Diastylidae (15 species), Leuconidae (2 species) and Lampropidae (2 species) are poorly represented. Highest diversity in all families occurs on the Pacific Coast, particularly near rivers, while the S coast has the fewest species (Hale, 1953a).

Five families of Cumacea are represented in the species which have previously been collected from Moreton Bay. They are the Bodotriidae, Nannastacidae, Gynodiastylidae, Diastylidae and Leuconidae. The Bodotriidae is most diverse, as in other areas around Australia (Hale, 1953a). Its dominant genus is *Cyclaspis*. Sixteen bodotriid species were recorded for Queensland waters by Hale between 1928 and 1951. Greenwood & Johnston (1967) added one and Stephenson *et al.* (1978), Stephenson (1980a,b), Bacescu (1990, 1992b) added 6 more. This paper describes fur-

ther new species, and summarises the distribution of bodotriid species in Moreton Bay (Figs 1, 2).

Sexual differences within a species include sculpturing and armature of the body, and the number of spine-like setae and fine setae on appendages. They also include more basic differences which enable greater swimming capacity in the male and a *marsupium* in the ♀ (Jones, 1963).

Specimens described were collected between 1989 and 1993. 787 plankton samples were taken from 40 sites (Fig. 1). Most were taken by sledge-net sampler (approx. 85% at all sites), some by plankton net (approx. 10% at sites 28, 29, 31), and the remainder by re-entry tray (sites 28, 32) and light-trap (site 24).

Two methods of specimen preparation for the SEM were trialled, using ♀♀ of *Bodotria armata* sp. nov. (Fig. 8). The freeze-substitution method (right hand side) eliminated the problem of salt crystallisation and therefore proved to be the most satisfactory method of SEM preparation (Tafe,1995).

Measurements of somites and segments are taken along midlines of the entire sections, not just the exposed portions. Length measurements of whole specimens are recorded as standard lengths, measured from the anterior end of the pseudorostrum to the posterior end of the telsonic somite, excluding spine-like setae and fine setae.

TERMINOLOGY. Terminology (Fig. 3) follows the more recent works on the group (e.g., Day, 1975, 1978a,b, 1980; Watling, 1989, 1991a,b; Felgenhauer, 1992; Roccatagliata, 1989, 1993).

FIG. 1. Satellite photograph of Moreton Bay showing sampling locations (supplied courtesy Ross Quinn through Sunmap, from Landsat imagery, Australian Centre for Remote Sensing, Canberra).

FIG. 2. Map of part of Moreton Bay showing sampling locations in upper Pumicestone Passage (from Queensland Boating Safety Chart, Harbours and Marine, Brisbane).
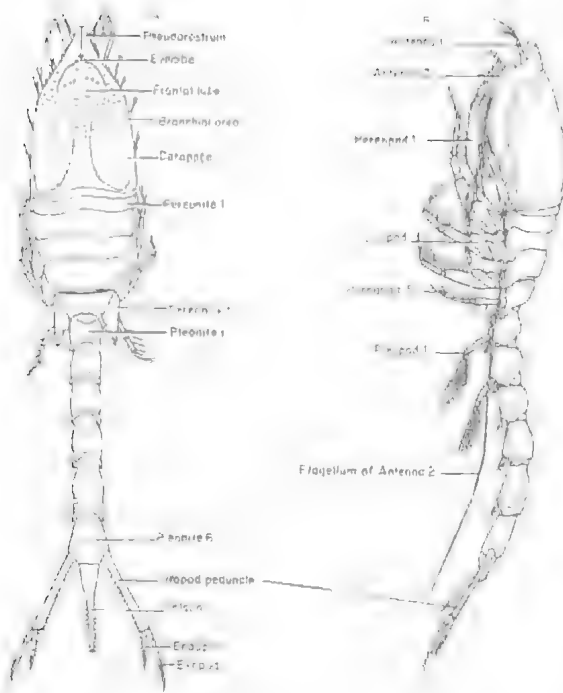
FIG. 3. *Diastylis rathkei*. A, ♀ in dorsal view. B, adult ♂ in lateral view (after Sars, 1900).

As compared to older papers pereiopod replaces peracopod, segment replaces joint, pereionite replaces pedigerous somite or thoracic somite, pleonite replaces pleon somite or abdominal somite and telsonic somite replaces anal or sixth pleon somite. In descriptions of carapace features, such as ridges and tubercles, the terminology employed by Hale (1944a:66) has been retained. In descriptions of appendages and their setation, Watling (1989) and Felgenhauer (1992) are followed. In relation to appendages lateral refers to that margin/border of the appendage facing the lateral body surface and medial refers to that margin directed toward the midline of the body.

The classification of substratum given in the distribution section of each species follows the U.S. Department of Agriculture (USDA) classification of grain sizes [i.e. coarse sand (2,000-1,000 μm), medium sand (1,000-500μm), fine sand (500-125μm), coarse silt (125-63μm) silt/mud (63-2μm)], as given in Gee & Bauder (1986) and Giere et al. (1988). Geographic areas of the Australian marine environment are shown on Fig. 4. The classification of abundance is: uncommon= individuals taken in total of all samples; common=10-100 individuals; very common= 100-1,000; abundant=1,000 individuals.

ABBREVIATIONS. Abbreviations used include: L.V. (lateral view), D.V. (dorsal view), V.V. (ventral view), D.L.V. (dorsolateral view), V.L.V. (ventrolateral view), A.L.V. (anterolateral view), P.L.V. (posterolateral view), SEM (scanning electron microscope), PSM (permanent slide mount), S.L. (standard length), QM (Queensland Museum), AM (Australian Museum), SAM (South Australian Museum).

RESULTS

Eight genera and 29 species (18 new) of Bodotriidae were taken from Moreton Bay. Thirteen of those species are described, the remaining five species lacking sufficient specimens to enable full descriptions. The previously undescribed ♀ of *Glyphocuma halei* Greenwood & Johnston is described. Twenty-two of the 29 species are new records for Moreton Bay.

Taxonomic keys are either updated to include the new species, or newly constructed where necessary. The keys to species of *Cyclaspis*, *Glyphocuma* and *Leptocuma* are extended to include all known Australian species (Indo-Australasian species in the case of *Cyclaspis*). Where a high degree of sexual dimorphism exists (e.g., in *Glyphocuma*), keys to the sexes are kept separate.

Adults of *Cyclaspis ornosculpta* sp. nov. exhibit a high degree of sexual dimorphism, typical for members of the *exsculpta* group. Changes to morphology during the development of *C. ornosculpta* sp. nov. are documented for both sexes.

KEY TO THE FAMILIES OF CUMACEA IN MORETON BAY
(Adapted from Hale, 1946a; Jones, 1963, 1976)

1. No independent telson. Endopod of uropod with 1 or 2 segments 2
   Telson present. Endopod of uropod with 2 or 3 segments 3

2. In both sexes the last 4 pairs of pereiopods either without exopods or with very small rudimentary exopods. ♂ with 5 pairs of pleopods . . . . Bodotriidae
   In the ♀ at most the last 3 pairs of pereiopods without exopods, in male only the last. ♂ with 0 or 2 pairs of pleopods 4

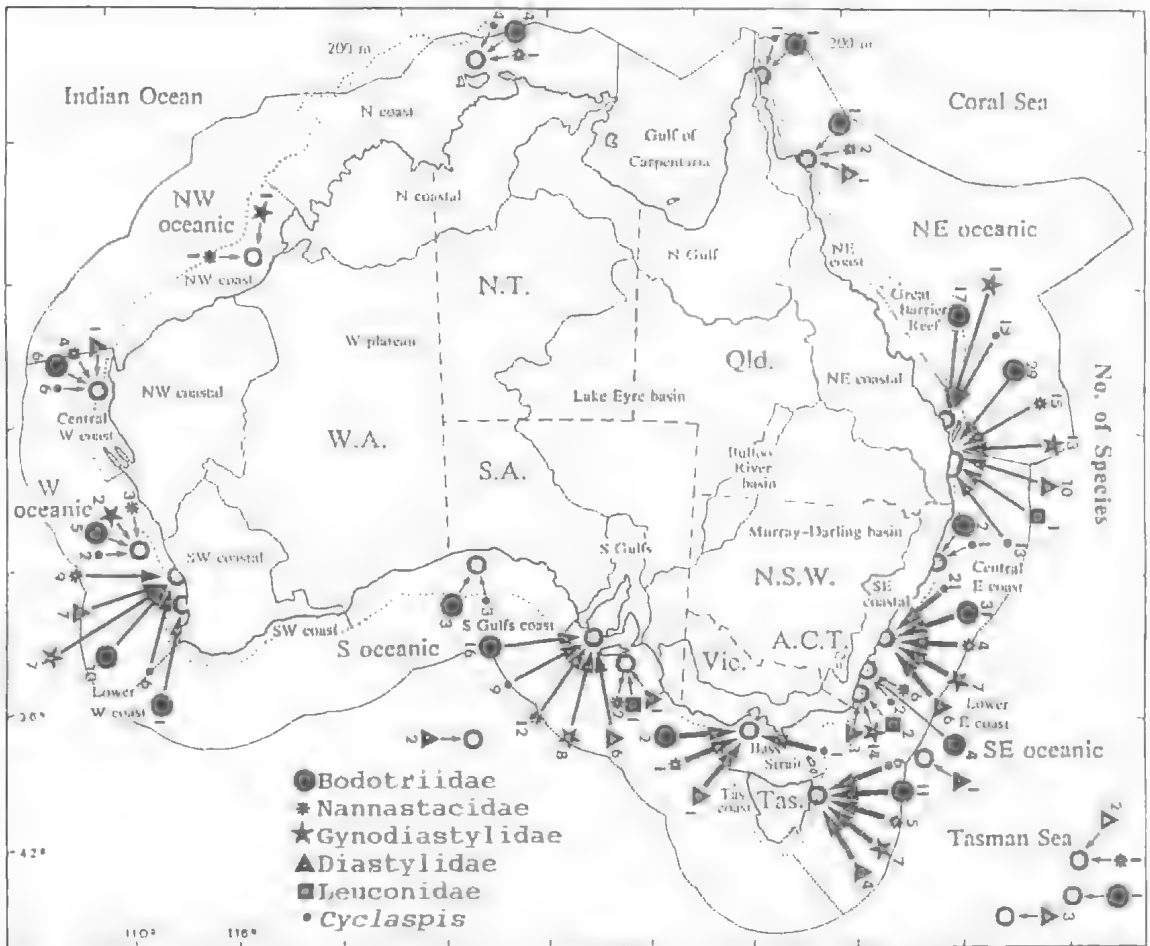3. ♂ with one or two pairs of pleopods. ♀ third maxi-

FIG. 4. States, standard drainage divisions, coastal zones within the 200m bathymetric contour, and the 200 nautical mile Australian fishing zones (courtesy Crustacean Section, Australian Museum).

lliped with exopod (except *Paradiastylis*)
. . . . Diastylidae
♂ with no trace of pleopods. ♀ third maxilliped
lacks exopod . . . . Gynodiastylidae

4.Endopod of uropod 1-segmented. ♀ has last 3
pairs of pereiopods without exopods, in ♂ only
last pair. ♂ without pleopods
. . . . Nannastacidae
Endopod of uropod 2-segmented. ♀ has last 2
pairs of pereiopods without exopods, in ♂ only
last pair. ♂ with 2 pairs of pleopods
. . . . Leuconidae

Family BODOTRIIDAE T. Scott, 1901 emend.
Kurian, 1951

DIAGNOSIS. No free telson. Pleopods in males
only, with an outer process on endopod, usually
5 pairs, occasionally 2 or 3 pairs. Mandibles
narrow at base. Endopod of uropod 1- or 2-seg-
mented.

REMARKS. The family is distinguished from the
Diastylidae and Gynodiastylidae by the lack of an
independent telson, and from the Nannastacidae
and Leuconidae by the 5 pairs of pleopods in the
male (except for the Mancocuminae which are
not known from Australian waters). There are at
least 317 species of Bodotriidae described
worldwide, 94 of which occur in Australian
waters (including the new species described
below). Australian species are distributed
amongst the genera as follows: *Bodotria*, 4;
Cyclaspis, 58; *Eocuma*, 1; *Iphinoe*, 1; *Gaus-
sicuma*, 1; *Gephyrocuma*, 4; *Glyphocuma*, 6;
Leptocuma, 10; *Picrocuma*, 3; *Pomacuma*, 3;
Sympodomma, 2; *Zenocuma*, 1.

The family is divided into 3 subfamilies; the
Bodotriinae Scott, 1901, have exopodites on only
the first pair of pereiopods, the Vaunthomp-
soniinae Sars, 1878 have exopodites on at least
the first 2 pairs of pereiopods; the Mancocuminae

Watling, 1977 have exopodites on at least the first 3 pairs of pereiopods.

KEY TO SUBFAMILIES AND GENERA OF AUSTRALIAN BODOTRIIDAE
(Adapted from Jones, 1976 and Hale, 1944b)

1. Exopods on first pereiopods only   . Bodotriinae.2
   Well developed or rudimentary exopods on at
   least first to third pereiopods
   . . . . Vaunthompsoniinae.5

2. Five free pereionites. Endopod of uropod 2-seg-
   mented . . . . *Iphinoe* Bate
   Four free pereionites. Endopod of uropod 1 or 2-
   segmented 3

3. Carapace with strong lateral ridges separating dor-
   sal from lateral regions throughout length
   . . . . *Bodotria* Goodsir
   Carapace without strong lateral ridges separating
   dorsal from lateral regions throughout length   4

4. Uropods with peduncle more than half the length
   of the rami. Carapace without lateral horns. En-
   dopod of uropod 1-segmented . *Cyclaspis* Sars
   Peduncle less than half the length of the rami.
   Carapace with lateral horns. Endopod of uropod
   2-segmented . . . . *Eocuma* Marcusen.

5. First pereiopods with joints curiously expanded   6
   First pereiopods not so modified   8

6. First antenna strongly geniculate, with joints of
   peduncle sub-globose . . *Gephyrocuma* Hale
   First antenna not strongly geniculate, joints not at
   all globose   7

7. Telsonic somite well produced posteriorly. Basis
   of first pereiopod with distal lobe
   . . . . *Pomacuma* Hale
   Telsonic somite subtruncate, scarcely produced
   posteriorly. Basis of first pereiopod with no dis-
   tal lobe . . . . *Zenocuma* Hale

8. Second pereiopod with a distal brush of setae on
   propodus and dactylus, but no spine-like setae
   . . . . *Leptocuma* Sars
   Second pereiopod without brushes of setae on ter-
   minal segments but with spine-like setae on at
   least dactylus   9

9. Dorsal plate of telsonic somite subtruncate
   posteriorly and not at all produced between
   bases of uropods   10
   Dorsal plate of telsonic somite rounded or an-
   gular posteriorly and produced between bases of
   uropods   11

10. Dorsal plate of telsonic somite truncate posterior-
    ly. Endopod of pleopods with narrow external
    process . . . . *Cumopsis* Sars
    Dorsal plate of telsonic somite excavated
    posteriorly. Endopod of pleopods without exter-
    nal process . . . . *Heterocuma* Miers

11. Third maxilliped with merus much longer than is-

chium but shorter than carpus
   . . . . *Vaunthompsonia* Bate
   Third maxilliped with merus subequal in length
   to ischium and carpus   12

12. Ocular lobe present   13
    Ocular lobe absent   14

13. Fourth pereiopod of male with exopod
    . . . . *Glyphocuma* Hale
    Fourth pereiopod of male without exopod
    . . . . *Sympodomma* Stebbing

14. Pseudorostral lobes meeting in front of ocular
    lobe. Anal portion of telsonic somite much
    shorter than rest of somite . *Bathycuma* Hansen
    Pseudorostral lobes not meeting in front of ocular
    lobe. Anal portion of telsonic somite as long as
    rest of somite . . . . . . *Gaussicuma* Zimmer

Subfamily BODOTRIINAE Scott, 1901

DIAGNOSIS. Exopods present on first pair of pereiopods; first pereionite usually concealed; endopod of uropod often undivided.

Bodotria Goodsir, 1843

DIAGNOSIS. Cuticle strongly calcified. Carapace with strong lateral ridges separating dorsal from lateral regions throughout length. First pereionite not visible in dorsal view, second is long. In both sexes only first pereiopod with exopod. Second pereiopod basis and ischium not distinctly separated. Endopod of uropod one or 2-segmented, with distal segment always shorter.

Bodotria maculosa Hale, 1944
(Figs 5A-F, 6A,C,E)

Bodotria maculosa Hale, 1944b:226, figs 1,2. Hale, 1949a:107, fig. 1.

MATERIAL EXAMINED. HOLOTYPE SAMC2365, adult ♂, 4.2mm long, Dangerous Reef, Spencer Gulf; PARATYPES SAMC2448, ♂, 3.5mm long, off Port Hacking, NSW, 50 m, on sand; AM unreg., Lizard Island, Qld; QMW20471, ovig. ♀, S.L. 2.9mm, SEM mount, Horseshoe Bay, 27°30'S, 153°21'E, site 31, D. Tafe, 11 Oct. 1990, 2-3m, sand, 35.5ppt salinity, 24.5°C water temperature.

DIAGNOSIS. Carapace with median dorsal ridge; lateral carina prominent, below which is secondary carina which curves up posteriorly to meet primary lateral carina; dorsal surface with coarse squamose-reticulate patterning formed by large, shallow pits; line of shallow pits immedi-ately above secondary lateral carina. Antennal notch deep and narrow. Pseudorostral lobes wide, truncate anteriorly, and reach apex of ocular lobe.
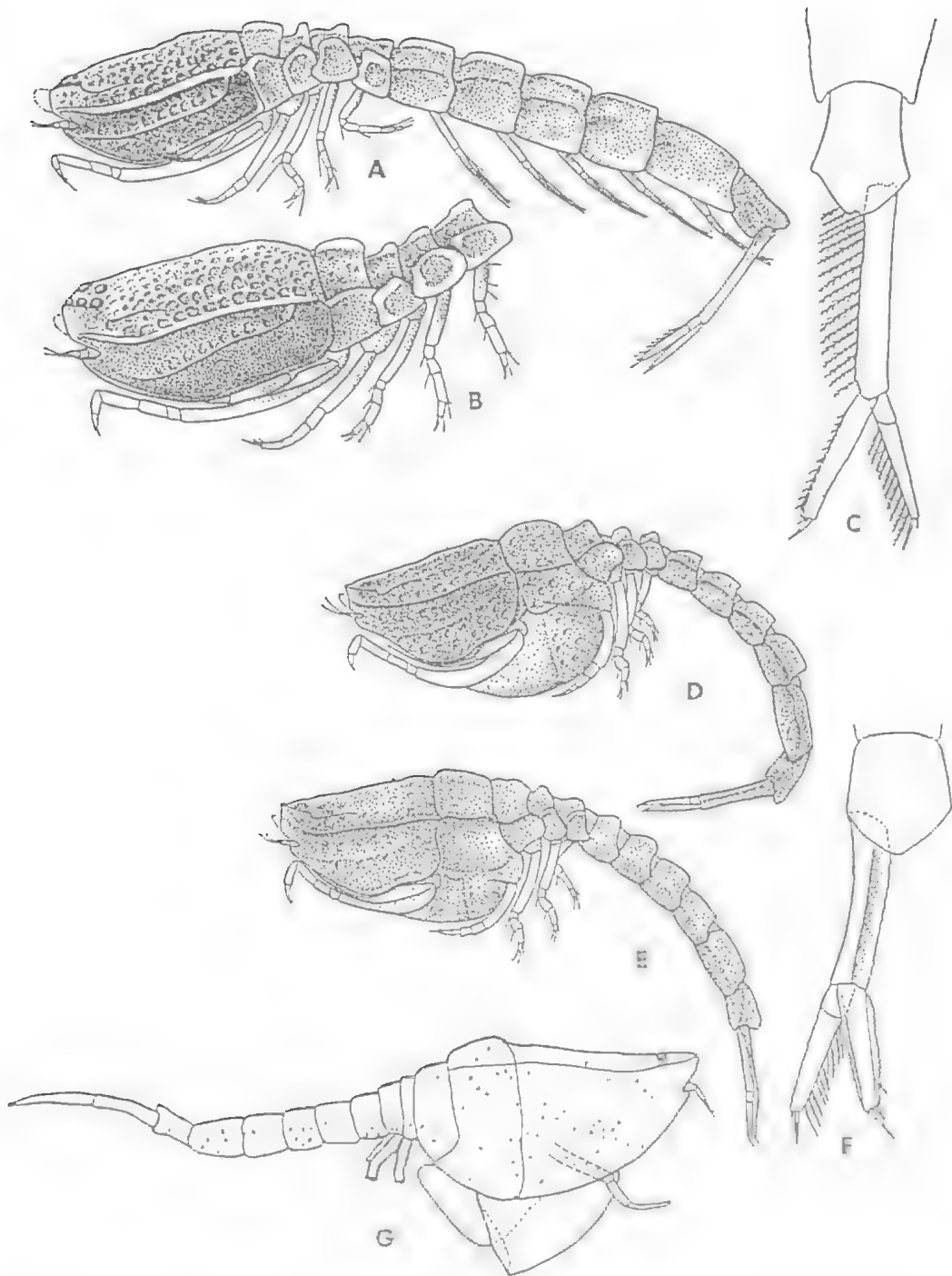
FIG. 5. A-F, *Bodotria maculosa*. A-C, ♂ ♂. A, form from SA, LV. B, form from NSW, LV . C, telsonic somite and uropod of S.A. form, DV. (A-C after Hale, 1944b). D-F, gravid ♀ ♀. D, form from Western Australia, LV. E, form without lateral carina on pleon, from WA, LV. F, telsonic somite and uropod of latter WA form, DV. (D-F after Hale, 1949a). G, *Bodotria* sp. nov. 2, gravid ♀, LV.
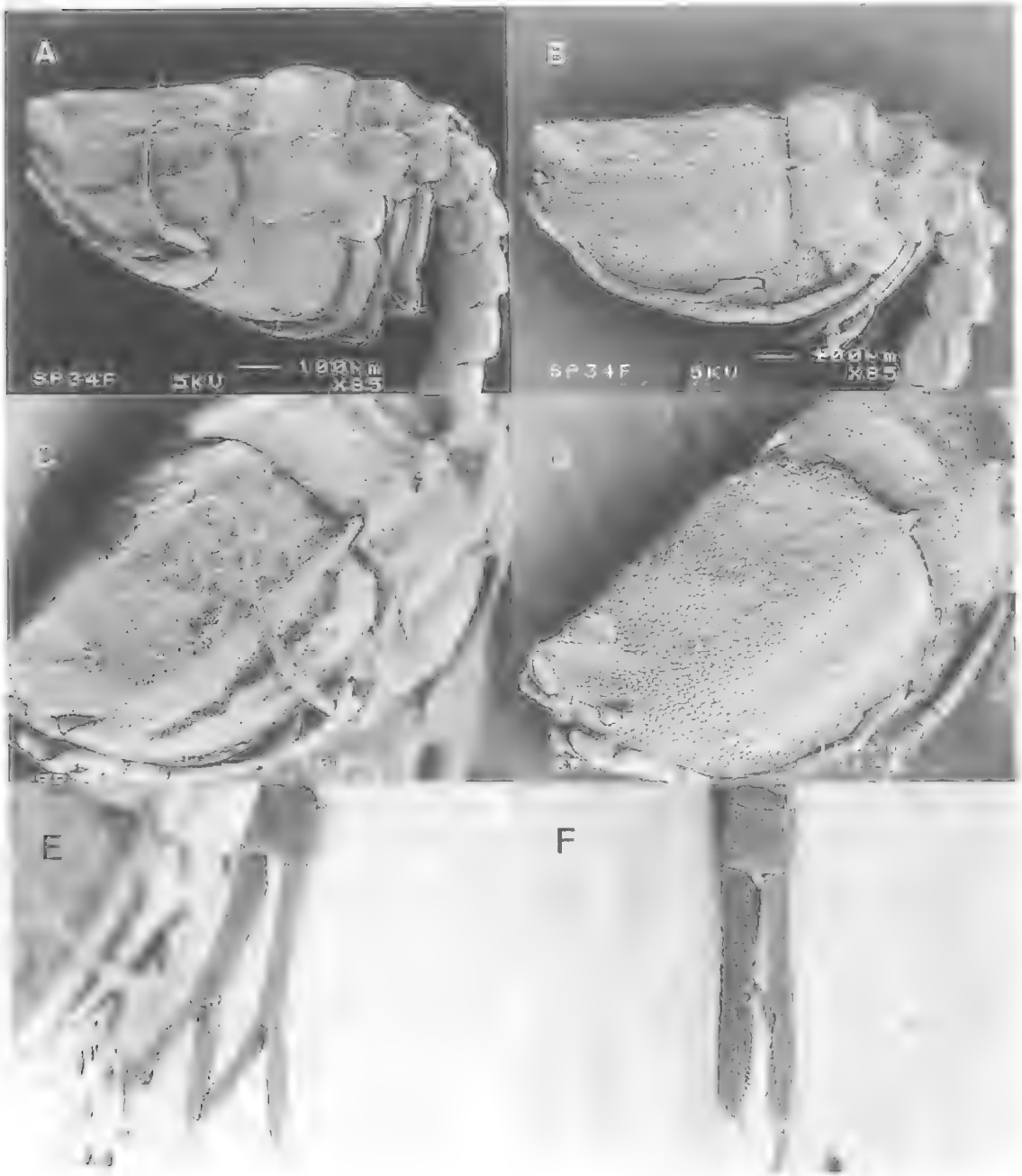
FIG. 6. A, *Bodotria maculosa* Hale ♀ carapace LV, shows squamose-reticulate patterning on carapace and absence of lateral carinae on pleonites. B, *Bodotria armata* sp. nov. ♀ carapace LV, shows lateral carinae on pleonites and absence of squamose-reticulate patterning on carapace. C, *Bodotria maculosa* Hale ♀ carapace DLV, shows prominent lateral carina. D, *Bodotria armata* sp. nov. ♀ carapace DLV, shows overlapping scales and absence of lateral carina. E, *Bodotria maculosa* Hale ♀ uropods VV, shows relatively long, cylindrical peduncles. F, *Bodotria armata* sp. nov. ♀ uropods VV, shows relatively short, angular edged peduncles.

Colour. Orange or brown with numerous black chromatophores dotted over entire body.

S.L. Adult ♂ 3.5-4.5mm. Adult ♀ 2.9-3.1mm.

HABITAT AND DISTRIBUTION. On sand: 2-50m depth. Central and Lower East Coast, S. Gulfs Coast, Central and Lower West Coast (Fig. 4).

REMARKS. *Bodotria maculosa* resembles *B. arenosa* Goodsir, 1843 and *B. pumilio* Zimmer, 1921 (=*B. similis* Calman,1907), but is easily distinguished by the elevated dorsal carinae of the last 3 pedigerous somites (Fig. 5A,D). It is further distinguished from *B. arenosa* by the wider carapace in dorsal view, and the relatively shorter peduncle of the uropod (Figs 5C,F, 6E); from *B. pumilio* by the larger adult size (*pumilio* 2-2.25mm). The Moreton Bay specimen agrees closely with the type series and with the Lizard Island specimens.

Hale noted considerable variation in the sculpture of the carapace and size range of adults (1944b;226). He described two males, one from NSW (Fig. 5A) and 1 from SA (Fig.5B). The NSW form is smaller, has more pronounced squamose pitting of the carapace, and has more slender thoracic appendages with longer spine-like setae and fine setae. Two ♀♀ forms were described from WA (Hale,1949a). One form exhibits strong lateral carinae on the pereionites and pleonites (Fig. 5D) while in the other form such carinae are totally lacking (Fig. 5E). When both forms are adult as these are, such differences indicate that more than one species may be involved. Hale designated a type for both the SA and NSW forms so it will be necessary to erect a lectotype for the SA form to be the true *B. maculosa* should further studies conclusively separate the SA, WA and NSW forms as separate species.

Hale's figure (1949a, fig. 1B). of pereiopod 4 is probably incorrectly labelled and should read 'prp.5', since his own drawings of the whole specimen show long basal segments on pereiopods 1-4.

Bodotria armata sp. nov.
(Figs 6B,D,F, 7-11)

MATERIAL EXAMINED. HOLOTYPE QMW20472 adult ♂ (S.L. 3.2mm), PSM #53, Horseshoe Bay, 27°30'S, 153°21'E, site 31, D. Tafe, 11 Oct. 1990, 2-3m, sand, 35.5 ppt salinity, 24.5°C water temperature. PARATYPES QMW20473 ovig. ♀, allotype, S.L. 2.9mm, PSM #54, same data as holotype;

QMW20474 adult ♂, S.L. 3.0mm, PSM #51, same data as holotype; QMW20475 ovig. ♀, S.L. 2.7mm, PSM #52, same data as holotype; QMW20476 ovig. ♀ S.L. 2.6mm, SEM mount, same location as holotype, 7 April 1991; QMW20477 adult ♂, S.L. 3.1mm, SEM mount, same location as holotype, 7 April 1991; QMW20478 adult ♂, S.L. 3.0mm, PSM #27, same location as holotype, 4 Feb. 1993; QMW20479 ovig. ♀, S.L. 2.4mm, PSM #28, same location as holotype, 4 Feb. 1993.

DESCRIPTION. MALE. Integument calcified, covered with small, rounded overlapping scales. Carapace 0.25 S.L.; with strong median dorsal ridge, almost straight in lateral view; lateral ridges prominent, extending length of carapace; carapace 0.74 as wide as long, lateral margins rounded in dorsal view. Antennal notch deep and narrow. Pseudorostral lobes wide, joining anteriorly to ocular lobe which is as wide as long (Fig.7A-G). Pereionite 1 almost fully concealed. Pereionite 2 as long as fourth or fifth, longer than third; second to fifth pereionites with strong median dorsal and lateral ridges (Fig. 7C,D,G). Pleon robust and tapering in dorsal view; all five pleonites with median dorsal ridges but without defined lateral ridges; first 4 pleonites and telsonic somite subequal in length, fifth pleonite 1.5 times as long as fourth (Fig. 7A-C,E,F,H). Telsonic somite projecting posteriorly over bases of uropods. Posterior margin rounded with median notch in dorsal view (Figs 7B,E,H, 8). First antenna 3-segmented with terminal segmented flagellum; first segment geniculate, longer than next two segments combined; second segment shorter and stouter than third, with two fine setae distomedially, one distolaterally; third segment with three fine distolateral setae; first segment of flagellum twice as long as second, with three proximolateral setae; second segment with two aesetascs and two fine setae distally (Fig. 8A). Third maxilliped as in *B. maculosa*. First pereiopod with carpus reaching level of antennal tooth of carapace; basis c.0.5 as long again as rest of appendage, distal margin not produced, with 2 slender setae; ischium very short, c. 0.33 as long as merus, both segments devoid of long setae; carpus longer than merus and more than twice as long as propodus, which is subequal in length to dactylus; dactylus with 3-4 slender setae distally and strong terminal spine-like seta, subequal in length to segment; all segments of endopod with short spine-like setae on posterior surface; Exopod well developed; 2 slender proximal segments and 5 short distal segments; all segments except basal segment with 2 long setae distally
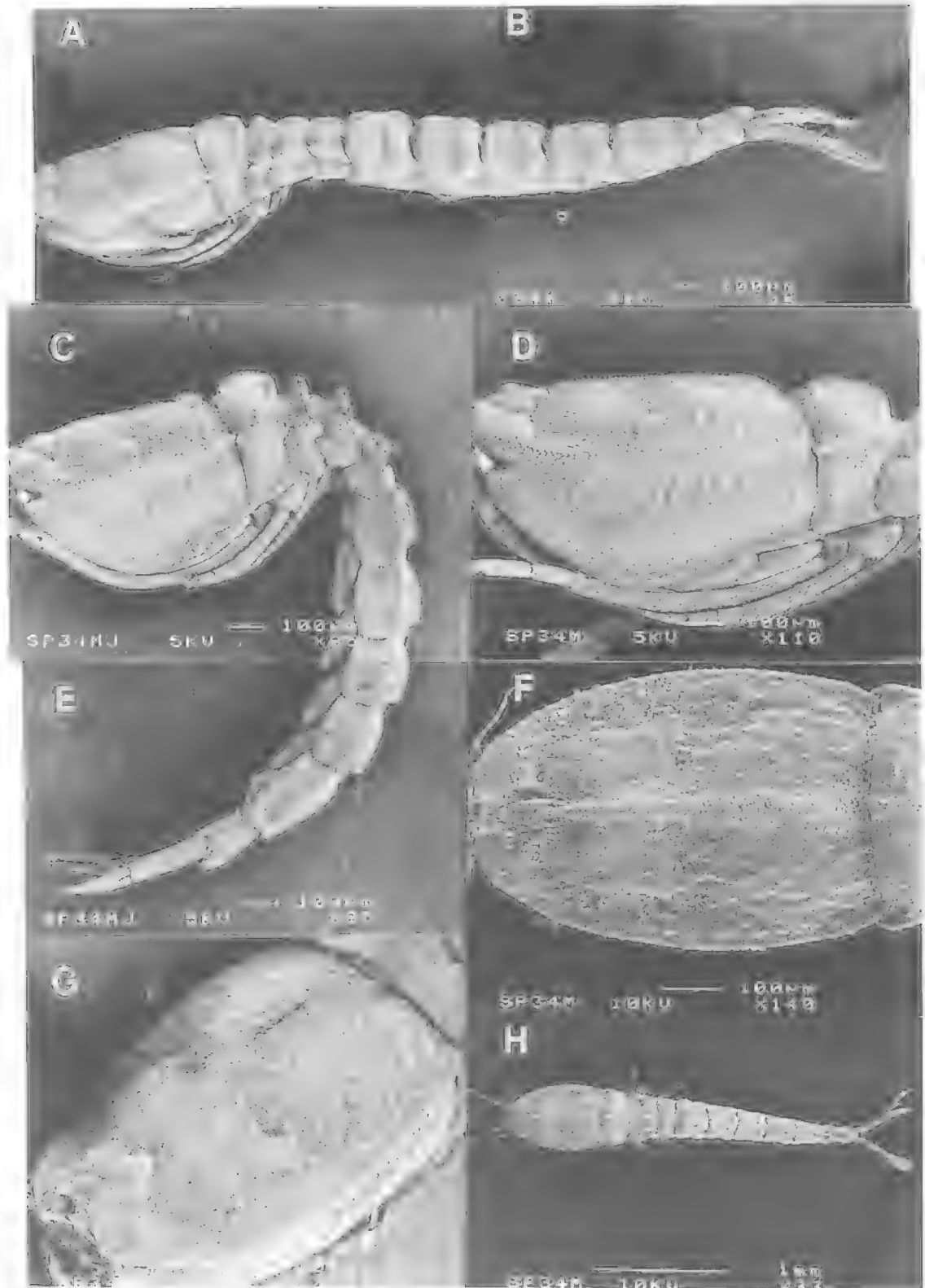
(Fig. 10A). Pereiopods 2-5 5-segmented (excluding coxa), ischium not separated from basis; carpus and dactylus subequal in length; terminal spine-like seta longer than dactylus; small scattered setae on all segments (Fig. 10B-E). Pereiopod 2 with basal segment slightly longer than combined length of remaining segments, with 4-5 plumose setae and brush of small setae on lateral margin; merus subequal in length to carpus and twice as long as propodus; carpus and dactylus each with three strong spine-like setae distally (Fig. 10B). Pereiopod 3 with basis longer than combined length of remaining segments; merus shorter than each of remaining segments, with 2 long setae distally; carpus shorter than propodus, with one long seta distally; propodus with spine-like seta distally, extending to distal margin of dactylus, which itself bears two terminal spine-like setae subequal in length (Fig. 10C). Pereiopod 4 with basis almost as long as remaining segments combined, with proximolateral seta, distolateral seta and lateral brush of fine setae; merus 0.5 as long as carpus, with 2 distolateral setae; carpus shorter than propodus, with distolateral seta; propodus with proximolateral seta and distomedial spine-like seta, extending to distal margin of dactylus; dactylus with 2 terminal spine-like setae subequal in length (Fig. 10D). Pereiopod 5 with basis much shorter than remaining segments combined, with distolateral seta; merus shorter than carpus, with distolateral seta; carpus shorter than propodus, with distolateral seta; propodus with distomedial spine-like seta, extending to distal margin of dactylus, which itself bears two terminal spine-like setae subequal in length (Fig. 10E). Peduncle of uropod 1.6 times as long as telsonic somite, lined with plumose setae on whole length of inner margin; endopod single-jointed, slightly longer than telsonic somite or exopod, with 9-10 truncated spine-like setae on inner margin, a short subterminal and long terminal spine-like seta; inner and outer margins more or less serrate; exopod with 11-12 plumose setae on inner margin, long terminal spine-like seta and short terminal simple seta (Fig. 8B,C).

FEMALE. Integument calcified and covered with

FIG. 8. *Bodotria armata* sp. nov., holotype adult ♂. A, first antenna. B, uropod, DV. C, rami of uropod, DV.

small, rounded overlapping scales, as in the male (Fig.6B,D). Carapace more than 0.25 S.L.; with strong median dorsal and lateral ridges, as in male; carapace 0.85 as wide as long, lateral margins rounded in dorsal view. Antennal notch and pseudorostral lobes as in ♂ (Figs 6B,D, 9B,D,H). First pereionite almost fully concealed by second, which is longer than pereionites 3-5; all visible pereionites have strong median dorsal and lateral ridges, the dorsal ridges being distinctly keel-like (Figs 6B,D, 9B). Pleon robust, all 5 pleonites with median dorsal ridge and first 3 with defined lateral ridges; first 4 pleonites and telsonic somite subequal in length, fifth pleonite 1.5 times as long

FIG. 7. *Bodotria armata* sp. nov. ♂. A,B, whole mount adult LV, shows relative lengths of carapace and somites. C,E, whole mount subadult LV, shows pronounced dorsal lobes of pereionites, lateral carinae on pleonites and mild lateral carinae on pleonites 3-5. D, carapace adult LV, shows almost straight dorsal edge, overlapping scales and absence of lateral carina. F, carapace adult DV, shows maximum width in mid-region of carapace and median dorsal ridge extending over full length. G, carapace adult DLV, shows dorsal ridge extending over full length and absence of squamose-reticulate patterning. H, whole mount adult DV, shows median dorsal ridge extending continuously along carapace, pereion and pleon.
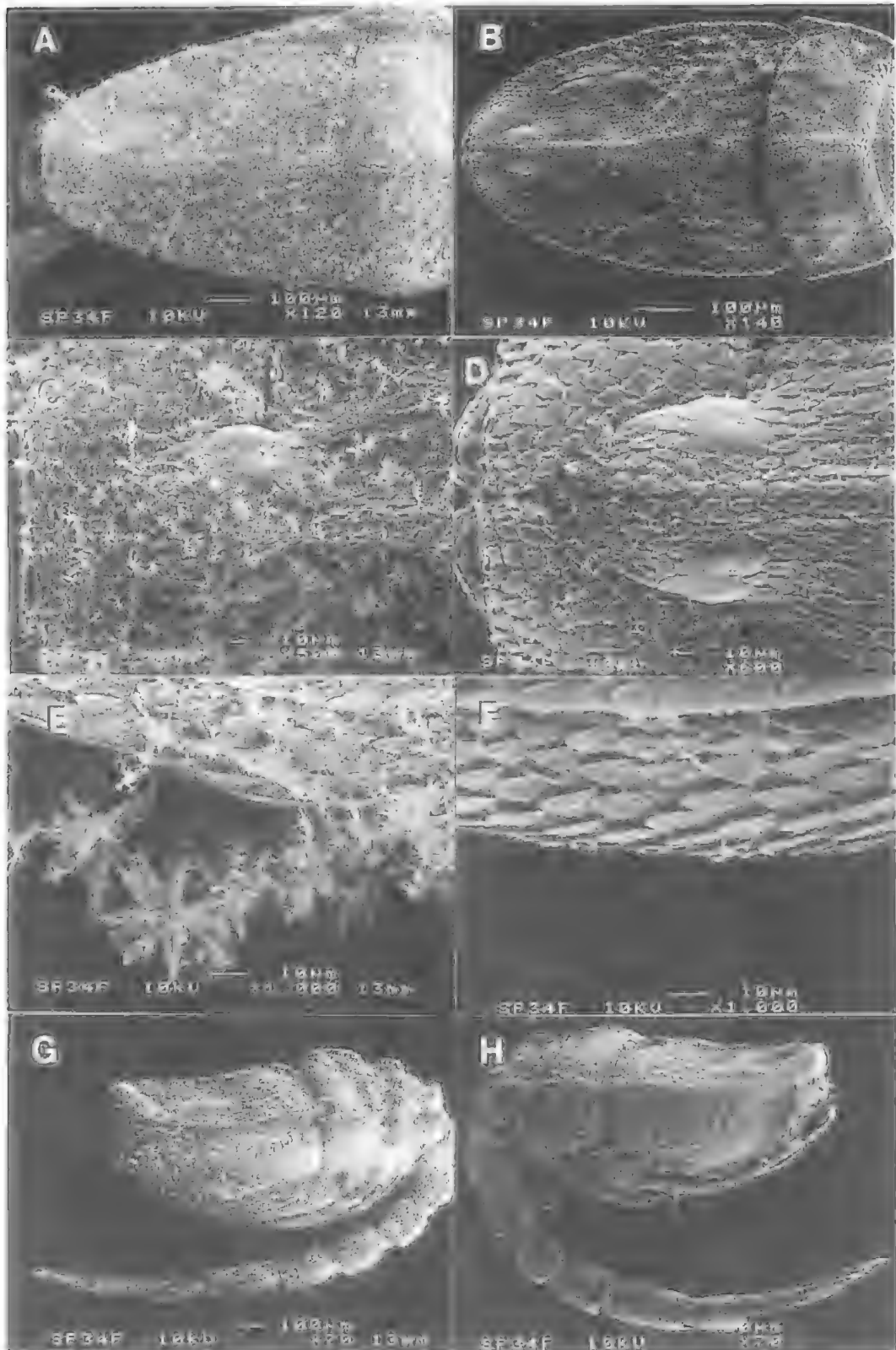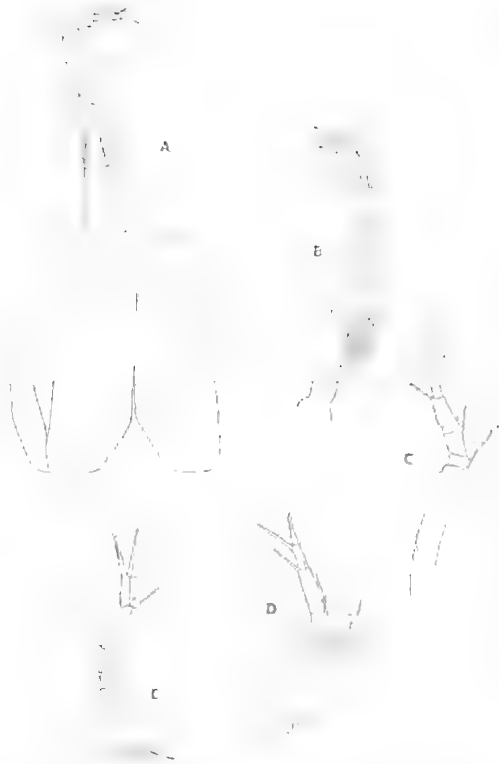
FIG. 10. *Bodotria armata* sp. nov., holotype adult ♂. A, first pereiopod. B, second pereiopod. C, third pereiopod. D, fourth pereiopod. E, fifth pereiopod.

as fourth (Figs 6B, 9H). Telsonic somite projecting posteriorly over bases of uropods (Fig. 11B). First antenna 3-segmented with terminal segmented flagellum, as in male. Third maxilliped, first, third and fifth pereiopods as in male. Basis of second pereiopod has only 2 plumose setae, carpus only with 2 distal spine-like setae. Basis of fourth pereiopod much longer than remaining segments combined (Fig. 11A). Peduncle of uropod 1.5 times as long as telsonic somite, without plumose setae on inner margin but with small scattered setae on posterior surface; endopod single-jointed, slightly longer than telsonic somite and exopod, with 1 spine-like seta and 6-8 short simple setae on inner margin, a short subterminal and long terminal spine-like seta;

inner and outer margins more or less serrate; exopod with 11 plumose setae on inner margin, long terminal spine-like seta and short terminal seta (Figs 6F, 11B,C).

Colour. Orange or brown with numerous black chromatophores in both sexes.

S.L. Adult ♂ 3.0-3.2mm. Adult ♀ 2.4-2.9mm.

HABITAT AND DISTRIBUTION. On sand; 2-4m; sites 15, 30, 31, 34 and 35. Both sexes are abundant at site 31, and at times outnumber all other cumacean species.

REMARKS. *Bodotria armata* resembles *B. maculosa* but is distinguished by the lack of squamose-reticulate patterning on the carapace. Also the scales of the carapace are more pronounced (Figs 6D, 7D, 9D), and the overall size is smaller (0.7x in compared specimens) than that of *B. maculosa*. Minor differences in the ♀ include relatively short, angular uropodal peduncles and lateral carinae on the pleonites (Fig.6). Minor differences in the ♂ include second segment of first antenna shorter than third; dactylus of first pereiopod subequal in length to propodus; terminal spine-like seta of second pereiopod longer than dactylus; uropod with 1-2 fewer inner marginal spine-like setae.

The fourth pereiopod of the ♀ has a much longer basis than *B. maculosa* (Hale, 1949a, fig. 1B). While *B. armata* differs from both forms of *B. maculosa* described by Hale it more closely resembles the NSW form.

ETYMOLOGY. Latin *armata*, armour; for the armour-like overlapping scales on the carapace.

Bodotria sp. nov. 1
(Fig. 5G)

MATERIAL. QMW20480 ovig. (S.L. 2.2mm), in 70% ethanol, site 31, D. Tafe, 11 Oct. 1990, 2-3m, sand, 35.5 ppt salinity, 24.5°C water temperature; specimen poorly preserved.

Colour. Whitish with scattered black pigment spots.

S.L. Adult ♀ 2.2mm.

HABITAT AND DISTRIBUTION. On sand; 3m; 2 ♀ ♀ from site 31, Moreton Bay.

FIG. 9. *Bodotria armata* sp. nov. ♀. A, carapace DV, shows encrusting salt crystals. B, carapace DV, shows surface free of salt crystals. C, ocular lobe DV, shows obscured ocular region. D, ocular lobe DV, overlapping scales of ocular region visible. E, lower carapace LV, shows clinging salt crystals. F, lower carapace LV, shows overlapping scales of lower carapace. G, whole mount LV, shows salt crystals over whole body surface. H, whole mount LV, shows clean body surface with dimpled texture of carapace fully visible.

FIG. 11. *Bodotria armata* sp. nov., allotype ovig. ♀. A, fourth pereiopod. B, uropod, DV. C, rami of uropod, DV.

REMARKS. *Bodotria* sp. nov. 1 cannot be adequately described until more specimens are secured. The species resembles *B. armata* sp. nov. but the carapace is shorter, broader in dorsal view and not strongly calcified (Fig. 5G); the scales on the carapace are not pronounced, the colouration of the carapace is whitish with scattered black pigment spots, even after being preserved in 70% ethanol for two years (cf brownish without pigment spots in *B. armata*), and the uropods are more delicate.

Cyclaspis Sars, 1865

DIAGNOSIS. Cuticle strongly calcified. First pereionite seldom visible in dorsal view. Articular pegs nearly always present on sides of pleonites. Only first pereiopods bear exopod. ♂ with 5 pairs of pleopods. Peduncle of uropods never much shorter than rami; endopod 1-segmented.

REMARKS. 93 species world wide (Bacescu, 1988); found in all oceans, though most species (60%) inhabit shallow water (10-50m) in temperate latitudes of Southern Hemisphere.

KEY TO INDO-AUSTRALASIAN SPECIES OF *CYCLASPIS*
(Adapted from Hale, 1944a)

SECTION 1

Sides of carapace without ridges or tubercles in either sex.

Viewed from above the lateral contour of the carapace is always evenly curved. Carapace usually smooth except for the reticulate patterning, but sometimes slightly roughened owing to granules or pits.

1. Front margin of carapace with an acute, forwardly directed spine on each side, below antennal angle . . . . *caprella* Hale
   No spines at front of carapace 2

2. Pseudorostral lobes meeting for an appreciable distance in front of ocular lobe . . *(picta* group) 3
   Pseudorostral lobes barely or not meeting in front of ocular lobe . . . . *(levis* group) 11

3. Carapace smooth and delicate, with fine median dorsal ridge for full length of carapace 4
   Carapace not as above 5

4. Carapace with a low median dorsal projection at posterior end. Rami of uropod subequal in length . . . . *gibba* Hale
   Carapace with smooth dorsal profile throughout length. Exopod of uropod distinctly longer than endopod . . . . sp. nov. 2

5. Carapace with many longitudinal rows of minute granules. Peduncle of uropod not longer than telsonic somite . . . . *costata* Calman
   Carapace smooth. Peduncle of uropod much longer than telsonic somite 6

6. Both rami of uropod with at least one articulated terminal spine-like seta 7
   Both rami of uropod without terminal spine-like setae 8

FIG. 12. *Cyclaspis cretata* Hale ♂. A, whole mounts LV and DV, shows relative lengths of carapace and somites. B, whole mounts (part) DLV, shows carapace and pereionites with dorsal carinae. C, carapace LV, shows antennal notch, depth and length of carapace. D, carapace DLV, shows median dorsal ridge on anterior half. E, carapace DV, shows cretations, apertures and ocular region. F, carapace (dorsal region) DV, detail of apertures in mid-dorsal region. G, Pereionites DV, shows brush of setae on margin of third pereionite. H, uropods DV, shows relative lengths of peduncle and rami.
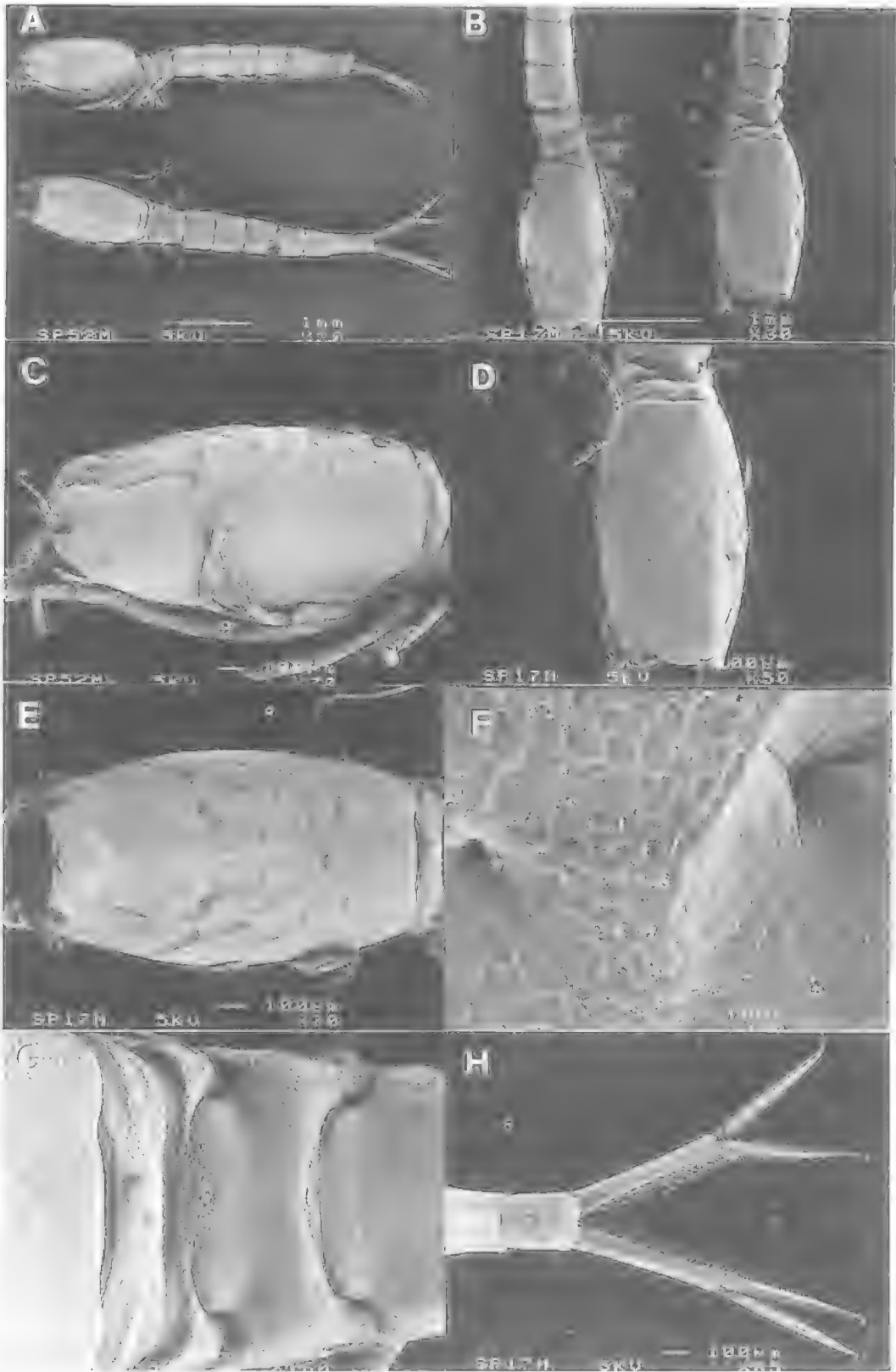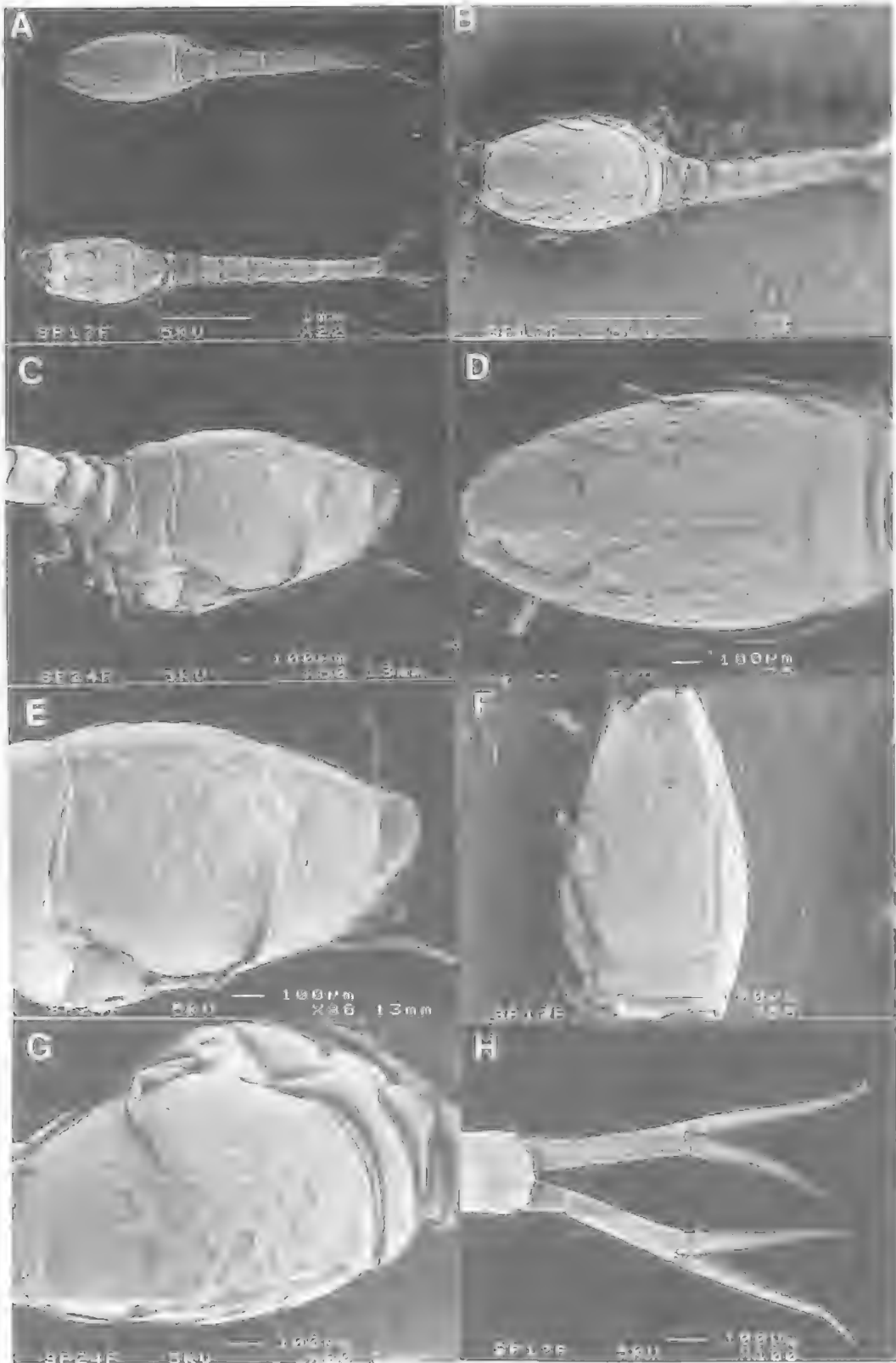
7. First pereiopod short, with carpus not reaching
level of antennal tooth. Rami of uropod barely
half as long as peduncle, exopod with 2 outer
marginal spine-like setae . . . . . *picta* Calman
First pereiopod long, with carpus reaching level
of antennal tooth. Rami of uropod about 2/3 as
long as peduncle, exopod with 2 outer marginal
spine-like setae . . . . sp. nov. 1

8. Exopod bears a mucrone. Carpus of first
pereiopod 1/3 as long again as propodus
. . . . *lucida* Hale
Exopod without mucrone. Carpus of first
pereiopod not longer than propodus 9

9. Peduncle of uropod shorter than exopod. Terminal
spine-like seta of second pereiopod at least 1/3
as long again as dactylus . . . *daviei* sp. nov.
Peduncle of exopod subequal or longer than ex-
opod. Terminal spine-like seta of second
pereiopod subequal in length to dactylus . . 10

10. Setae of third to fifth pereiopods long; 5 on car-
pus, the longest reaching for nearly half of their
length beyond tip of dactylus . . . *mollis* Hale
Setae of third to fifth pereiopods short; 3 on car-
pus, none reaching beyond tip of dactylus
. . . . *fulgida* Hale

11. Endopod of uropod with at least 1 articulated ter-
minal spine-like seta or mucrone. Carapace
heavily calcified and pitted
. . . . *alveosculpta* sp. nov. ♂
Endopod of uropod with apex acute and without
articulated terminal spine-like setae or
mucrones. Carapace not heavily calcified or
pitted 12

12. Exopod of uropod with apex acute and lacking
terminal mucrones 13
Exopod of uropod with one or more articulated
terminal mucrones 30

13. Carapace with numerous fine longitudinal striae
. . . . *strigilis* Hale
Carapace without longitudinal striae 14

14. Carapace with a low median dorsal projection at
posterior end 15
Carapace without median dorsal projection at
posterior end 16

15. Carapace with median dorsal ridge distinct for
whole length and with a conspicuous pit on each
side alongside posterior median projection.
Peduncle of uropod longer than rami
. . . . *sheardi* Hale
Carapace with median dorsal ridge obsolete for
posterior half of length; no conspicuous pits at
posterior end. Peduncle of uropod shorter than
rami . . . . *mjobergi* Zimmer

16. Carapace not globose, somewhat laterally com-
pressed in both sexes. Uropods slender, the
peduncle longer than the telsonic somite . . 17
Carapace globose in both sexes. Uropods stout,

the peduncle shorter than, or barely as long as,
telsonic somite 26

17. Propodus of first pereiopods almost as long as
merus and carpus together 18
Propodus of first pereiopods subequal in length
to carpus 19

18. Inner margin of endopod of uropod with a row of
setae, followed by 7- 8 slender spine-like setae
(adult ♂) . . . . *levis* Thomson
Inner margin of endopod of uropod with 3 to 6
proximal spine-like setae, followed by a row of
15-23 shorter spine-like setae (both sexes)
. . . . *cretata* Hale

19. Carapace roughened with fine granules
. . . . *granulosa* Hale
Carapace not as above 20

20. Carapace with two mid-dorsal depressions, one
either side of dorsal ridge
. . . . *andersoni* sp. nov.
Carapace not as above. 21

21. Carapace somewhat compressed laterally with
strong dorsomedial ridge throughout length and
no other ridges 22
Carapace not as above 23

22. Peduncle of uropod shorter than rami. First
pereiopod with group of spine-like setae (♂) or
fine setae (♀) on medial bulge of basis. S.L.
4-6mm . . . . *sallai* sp. nov.
Peduncle of uropod longer than rami. First
pereiopod without group of spine-like setae (♂)
or fine setae (♂) on medial bulge of basis. S.L.
2-4mm . . . . *cooki* sp. nov.

23. Basis of first pereiopods with a large apical tooth-
like projection, reaching to distal margin of
ischium 24
Basis of first pereiopods without large apical
tooth 25

24. Rami of uropod longer than peduncle (subadult
♂) . . . . *formosae* Zimmer
Rami of uropod equal in length to peduncle
(ovigerous ♂) . . . . *herdmani* Calman

25. Peduncle of uropod longer than rami. S.L. <6mm
. . . . *concinna* Hale
Peduncle of uropod shorter than rami. S.L.>8mm
. . . . *candidoides* Bacescu

26. Size small, ovigerous ♀ 3.5mm. Ocular lobe di-
lated anteriorly, with prominent circular dark len-
ses . . . . *pusilla* Sars
Size large, ovigerous ♀ 7mm or more. Ocular
lobe not dilated anteriorly but somewhat trian-
gular, with lenses pale and elongate 27

27. Carapace overhanging second pereionite
posteriorly. Third to fifth pereiopods with long
setae . . . . *globosa* Hale
Carapace not overhanging second pereionite
posteriorly. Pereiopods 3-5 with short setae
. . . . 28

28.Carapace coarsely pitted, slightly rugose. Pleon robust. Dactylus of pereiopod 2 with longest terminal spine-like seta shorter than propodus and dactylus together . . . . *clarki* Hale
Carapace smooth or with extremely fine reticulation. Pleon slender. Dactylus of pereiopod 2 with longest terminal spine-like seta as long as propodus and dactylus together 29

29.Optic lobe extends in front of pseudorostral lobes. Peduncle of uropod has setae on inner margin . . . . *stocki* Bacescu
Optic lobe does not extend in front of pseudorostral lobes. Peduncle of uropod is devoid of setae on inner margin . . . . *pinguis* Hale

30.Peduncle of uropods less than 1.5 times as long as telsonic segment and subequal to rami. Exopod with at least 2 elongate unequal mucrones at distal end 31
Peduncle of uropods about twice as long as telsonic segment and longer than rami. Exopod with 1 or 2 short mucrones or spine-like setae at distal end (less than 4x as long as broad) . . 32

31.Exopod of uropod with two unequal mucrones at distal end; ♂ with spine-like setae on basis of first pereiopod; ♀ uropod without setae on inner margin of exopod . . . . *sublevis* Hale
Exopod of uropod with 3 unequal mucrones at distal end; ♂ without spine-like setae on basis of first pereiopod; ♀ uropod with setae on inner margin of exopod . . . . *tranteri* sp. nov.

32.Exopod of uropod with one or more mucrones 33
Exopod of uropod with one or more spine-like setae 34

33.Peduncle of uropod at most half as long again as rami. Endopod of uropod has proximal half of inner margin naked or with plumose setae (adult ♂) . . . . *pura* Hale
Peduncle of uropod 2/3 as long again as rami. Endopod of uropod has 5-6 short spine-like setae on proximal half of inner margin (adult ♂) . . . . *nitida* Hale

34.Basis of first pereiopods only 3/4 as long as rest of limb, with a long apical tooth, reaching distal margin of ischium . . . . . . *hornelli* Calman
Basis of first pereiopods subequal in length to rest of limb, with apical tooth short, reaching only mid length of ischium . . . . . *cottoni* Hale

SECTION 2

Sides of carapace never smooth, but with ridges or tubercles, or both. Viewed from above the lateral contour of the carapae, owing to the sculpture, is rarely evenly curved, particularly in the ♀.

1.Sides of carapace almost smooth, with no anterolateral tubercle, ridge or other projection below pseudorostral suture 2
Sides of carapace never almost smooth, with at least one anterolateral tubercle, ridge or tooth-like projection below pseudorostral suture . . 6

2.Carapace with a prominent mid-dorsal tooth over base of ocular lobe . . . . . *uniplicata* Calman
Carapace with no dorsal tooth 3

3.A slight but obvious incision in dorsal margin of carapace at middle of length. Exopod of uropod with no apical spine-like seta, but with mucrone . . . . *sabulosa* Hale
No incision in dorsal margin of carapace at middle of length. Exopod of uropod with slender apical spine-like seta 4

4.Two ridges on each side of carapace. Propodus of first pereiopods subequal in length to dactylus . . . . *argus* Zimmer
One ridge on each side of carapace. Propodus of first pereiopods much longer than dactylus . . 5

5.Carapace with posterior transverse ridge faint, short and confined to posterior half of carapace. . . . . *thomsoni* Calman
Carapace without posterior transverse ridge but with fine ridge curving obliquely forwards from median dorsal ridge to antero-inferior margin . . . . *spilotes* Hale

6.Carapace fully encircled by a collar-like ridge . . . . *cingulata* Calman
Carapace not encircled by a collar-like ridge . 7

7.A quadrilateral area on each side of carapace, defined by ridges or tubercles (distinct and depressed in ♀, often indistinct in ♂) . . . . (*exsculpta* group) 8
No quadrilateral area on side of carapace . . 26

8.Carapace with anterior transverse ridge crossing dorsal midline (distinct in ♀, often indistinct in ♂) 9
Carapace with anterior transverse ridge not crossing dorsal midline 23

9.Posterior transverse ridge of carapace with 2-3 distinct branching ridges. Propodus of pereiopod 1 as long as combined length of ischium, merus and carpus . . . . *indoaustralica* Bacescu
Posterior transverse ridge of carapace without distinct branching ridges. Propodus of pereiopod 1 not as long as combined length of ischium, merus and carpus 10

10.Carapace heavily calcified and composed of a reticulate network of deep craters . . . . *agrenosculpta* sp. nov.
Carapace may be heavily calcified and even pitted but not composed of reticulate network of deep craters 11

11.Post-ocular tubercle on midline of carapace, immediately in front of anterior transverse ridge. Surface of carapace studded with blunt spines anteriorly . . . . *tribulis* Hale
No post-ocular tubercle or blunt spines on anterior of carapace 12

12. Texture of carapace scale-like. Peduncle of uropod much longer than rami, more than twice as long in subadult ♀ . . . . *bovis* Hale
    Texture of carapace pitted. Peduncle of uropod subequal in length to rami 13

13. Carapace with reticulate pattern of shallow rounded pits 14
    Carapace with honeycomb structure of deep angular pits 19

14. Carapace with two lateral carinae running forwards from anterior transverse ridge to front margin of carapace . . . . *exsculpta* Sars
    Carapace without such carinae 15

15. Carapace with median dorsal ridge produced posteriorly as keel-like lobe with notch
    . . . . *alveosculpta* sp. nov.
    Carapace with median dorsal ridge produced posteriorly as rounded keel-like lobe without notch 16

16. Dorsolateral carinae present between two transverse ridges of carapace 17
    No dorsolateral ridges between transverse ridges
    18

17. Transverse ridges of carapace with denticulations. S.L. 9-11mm . . . . . *prolifica* Bâcescu
    Transverse ridges of carapace smooth. S.L. 4-6mm . . . . *ornosculpta* sp. nov.

18. Dactylus of first pereiopod at least - as long as propodus . . . . *candida* Zimmer
    Dactylus of first pereiopod less than 2/3 as long as propodus . . . . *usitata* Hale

19. Carapace with pits separated by thick walls
    . . . . *chaunosculpta* sp. nov.
    Carapace with pits separated by network of thin walls 20

20. Longitudinal ridge runs obliquely from below antennal tooth almost to end of carapace
    . . . . *mawsonae* Hale
    No such ridge 21

21. Carapace with median dorsal keel forming 3 lobes posteriorly; posterior transverse ridge rising on either side of median notch into laminar tooth with sharp apex bending forward and downward . . . . *persculpta* Calman
    Carapace with median dorsal keel forming 1 lobe posteriorly; posterior transverse ridge rising on either side of median line to form blunt forwardly directed tooth 22

22. Carapace with small posterolateral lobes either side of median dorsal lobe; exopod of uropod without setae . . . . . . *supersculpta* Zimmer
    Carapace without posterolateral lobes either side of median dorsal lobe; exopod of uropod with setae . . . . *agrenosculpta* sp. nov.

23. Cephalothorax and pleon covered with small spine-like setae; no ridges on back or sides of carapace . . . . *aspera* Hale
    Cephalothorax and pleon not covered with small spine-like setae; well defined ridges on sides of carapace 24

24. Posterior transverse ridge crosses dorsal midline
    . . . . *australis* Sars
    Posterior transverse ridge does not cross dorsal midline 25

25. Quadrangular area on side of carapace with 4 prominent tubercles . . . . . . *elegans* Calman
    Quadrangular area on side of carapace with 1 or 2 prominent tubercles . . . . . . *similis* Calman

26. Carapace with tubercles or ridges posterior to the anterolateral tubercles 27
    Carapace without tubercles or ridges posterior to the anterolateral tubercles 32

27. Side of carapace with 3 obliquely transverse carinae 28
    Side of carapace with 1 transverse curved carina or none 30

28. Carapace with reticulate pattern of deep angular pits . . . . *mawsonae* Hale
    Carapace without deep angular pits 29

29. Carapace with mid-dorsal projection at hinder margin . . . . *triplicata* Calman
    Carapace without mid-dorsal projection at hinder margin . . . . *sibogae* Calman

30. Carapace covered in minute sparse spinules with a well marked spinose median dorsal ridge for whole length; on each side are four rounded tubercles; short ridge leading back from antennal notch (♂) . . . . *cana* Hale
    Carapace not as above; longitudinal ridge running from antennal tooth to about middle of carapace length 30

31. Dorsum of carapace, as seen from side, rising abruptly to an angular peak at middle of length
    . . . . *simula* Hale
    Dorsum of carapace smoothly rounded
    . . . . *coelebs* Calman

FIG. 13. *Cyclaspis cretata* Hale ♀. A, whole mounts DV, shows relative lengths of carapace and somites. B, whole mount DV, shows carapace, pereionites and pleonites with median dorsal carinae. C, carapace DLV, shows articular peg and median dorsal carina of first pleonite. D, carapace DV, shows ocular region, apertures and absence of setae on margin of third pereionite. E, carapace DLV, shows median dorsal ridge on anterior half and median dorsal depression on posterior half. F, carapace DLV, shows apertures in the bases of both anterior cretations and collar-like first pereionite. G, carapace DLV, shows anterior cretations with apertures and posterior cretations without apertures. H, uropods DV, shows relative lengths of peduncle and rami.
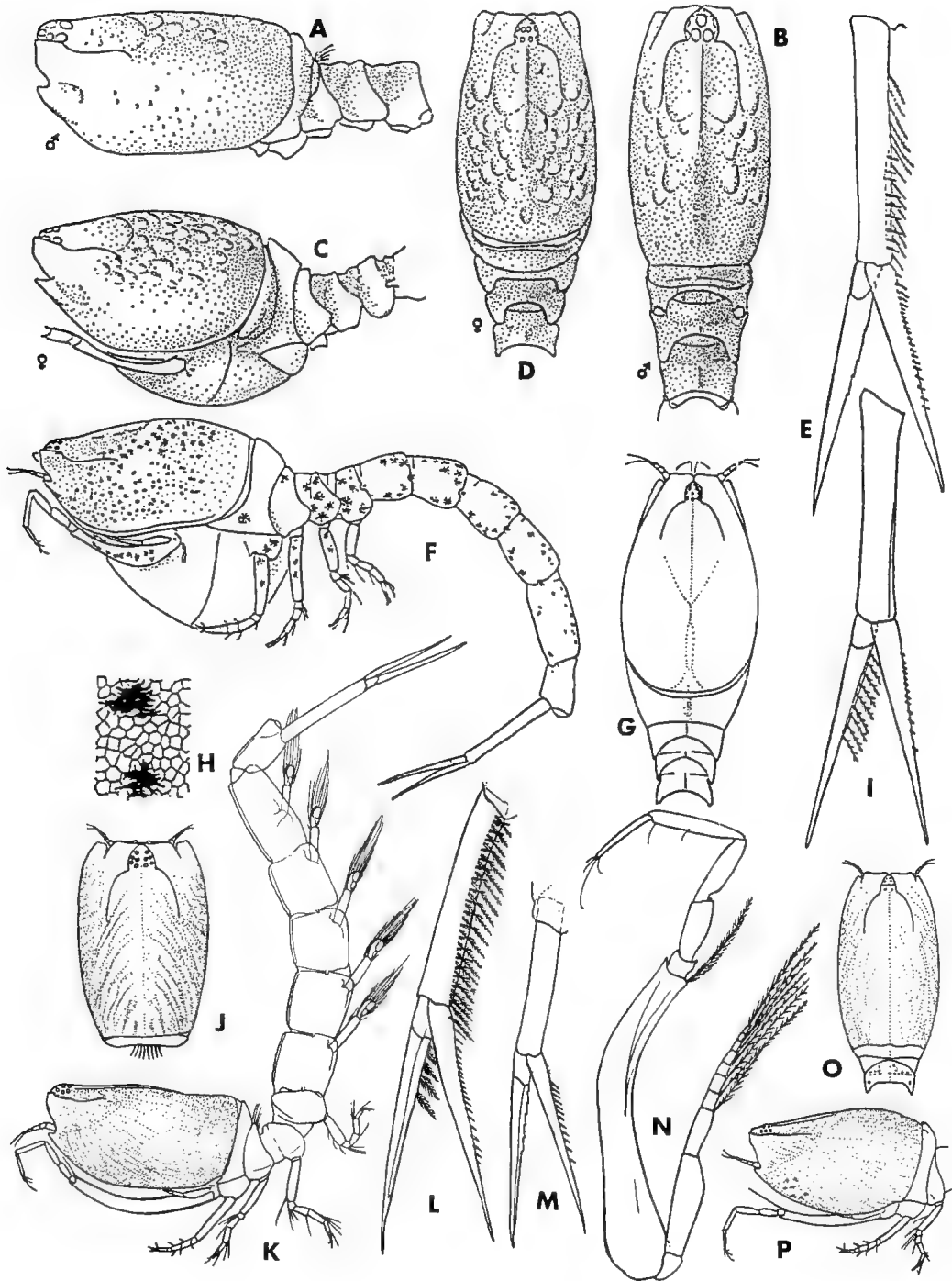
FIG. 14. *Cyclaspis* species. A-E, *Cyclaspis cretata*. A, adult ♂, cephalothorax, LV. B, ♂, DV. C, gravid ♀, cephalothorax, LV. D, DV. (A-D after Hale, 1948). E, paratype ♂ uropod. F-I, *Cyclaspis fulgida*, type ♀. F, LV. G, cephalothorax, DV. H, chromatophores of integument. I, uropod, DV. J-P, *Cyclaspis strigilis*. J-L, type ♂. J, cephalothorax, DV. K, LV. L, uropod, DV. M-P, paratype ♀. M, uropod, DV. N, first pereiopod. O, cephalothorax, DV. P, cephalothorax, LV (E-P after Hale, 1944a).

FIG. 15. *Cyclaspis usitata* gravid ♀. A, first antenna. B, mandible. C, pereiopod 4. D, first maxilla. E, second maxilla. F, uropods, DV. G, rami of uropod, DV.

32. Ocular lobe narrow, much longer than wide. Pereiopod 1 with dactylus about as long as carpus
. . . . *munda* Hale
Ocular lobe as wide as long, much longer than wide. Pereiopod 1 with dactylus less than half as long as carpus . . . . *pruinosa* Hale

Cyclaspis cretata Hale, 1944
(Figs 12, 13, 14A-E)

Cyclaspis cretata Hale, 1944a:91, figs 19,20. Hale, 1948:4, fig. 2.
Cyclaspis ? cretata Stephenson et al., 1978:210.

MATERIAL EXAMINED. HOLOTYPE SAMC2418 ♂ (6mm long), Cronulla, NSW. 2.5m, K. Sheard, submarine light, Sept. 1942. PARATYPES SAMC2366, C2368, C2370, C2371 ♂, ♀, 4.2-5.3mm long, Spencer Gulf, SA, 6m, K. Sheard, Feb. 1941. OTHER MATERIAL QMW20481 adult ♂, S.L. 4.6mm, SEM mount, Rainbow Channel, site 26, 27°27'S, 153°23'E, D. Tafe, 16 Feb. 1989, 6m, on sand,

34 ppt salinity, 25°C water temperature; QMW20482 adult ♀, S.L. 4.2mm, SEM mount, same data as above; QMW20483 adult ♂, S.L. 4.5mm, PSM #41, Horseshoe Bay, site 31, 27°30'S, 153°21'E, D. Tafe, 14 Aug. 1991, 2-3m, on sand, 27.2 ppt salinity, 16.5°C water temperature.

Colour. Whitish with faint brown mottling; sparse black chromatophores sometimes present on carapace and abdomen.

S.L. Adult ♂ 4.2-6.0mm. Adult ♀ 4.0-5.3mm.

HABITAT AND DISTRIBUTION. On sand often around coral reefs; 2-25 m; from S. Gulfs Coast and Lower West Coast (Fig. 4). NSW: Cronulla. SA: Kangaroo Is. Memory Cove, Spencer Gulf (Hale, 1944a). QLD: Sandy Cape, Noosa River, off Moreton Island (Hale, 1948), Moreton Bay (common in sandy areas). WA: Rottnest Island, Shark Bay, South Passage, Thomson Bay, Abrolhos Islands, Turtle Bay, off Walabi Island and Andaman Island (Hale, 1948).

REMARKS. Moreton Bay specimens matched Hale's type specimens but are slightly smaller than his NSW and SA specimens. Both sexes are distinguished from other species by the pattern of pitting on the posterior dorsal surface of the carapace (Figs 12A-F, 13A-G, 14A-D). ♂ ♂ and ♀ ♀ s have 4 depressions in the mid-dorsal region of the carapace, located in the bases of the anterior pits (Figs 12D-F, 13D-G). ♂ ♂ have a tuft of short setae on the dorsum of the third percionite (Figs 12G, 14A), which is not present on the ♀ (Figs 13C-F, 14C). The uropods of the Moreton Bay ♂ ♂ (Fig. 12H) are identical to those figured by Hale (Fig. 14E). The uropods of the ♀ have not been previously figured; those shown here (Fig. 13H) match the original description.

Cyclaspis fulgida Hale, 1944
(Fig. 14F-I)

Cyclaspis fulgida Hale, 1944a:80, figs 9,10. Hale, 1948:24, fig. 13. Hale, 1953a:72.

MATERIAL EXAMINED. HOLOTYPE SAMC2424, ovig. ♀, length 5.75mm, K. Sheard, submarine light, Sept. 1942, 2,5m, Cronulla, NSW. OTHER MATERIAL QMW20484, adult ♂, S.L. 3.9mm, PSM #55, Horseshoe Bay, site 31, 27°30'S, 153°21'E, D. Tafe, 13 Aug. 1990, 2-3m, on sand, 27 ppt salinity, 16.5°C water temperature.

Colour. Whitish, sooty black chromatophores sometimes present on carapace, pereiopods and abdomen.

S.L. Adult ♂ 3.9-5.5mm. Adult ♀ 5.75mm.

FIG. 16. *Cyclaspis usitata* subadult ♂. A, first pereiopod. B, second pereiopod. C, uropods, DV.

HABITAT AND DISTRIBUTION. On sand; 2-5m; Central East Coast, Lower East Coast, and Lower West Coast (Fig. 4). NSW: Cronulla (Hale, 1944a). WA: Garden Island, Careening Bay (Hale, 1948). Qld: Moreton Bay (Hale, 1948).

REMARKS. Moreton Bay specimens match Hale's type specimens from Cronulla. The cuticle is smooth and scarcely calcified and the carapace ovoid in dorsal view. It has a shallow lateral depression on each side of a low median dorsal ridge, which continues towards the posterior as a faint double ridge. The ocular lobe is prominent and slightly elevated. The pseudorostral lobes meet in front of the ocular lobe. The colour of the

cuticle is white with scattered, sooty black chromatophores. This species resembles *C. mollis* but the ocular lobe is more prominent, the basis of the first pereiopod has a well developed distomedial tooth and the endopod of the uropod has 13 (cf. 8) medial spine-like setae (Fig. 14I). Common in Moreton Bay.

Cyclaspis strigilis Hale, 1944
(Fig. 14J-P)

Cyclaspis strigilis Hale, 1944a:83, figs 11-14.

MATERIAL EXAMINED. SAMC2412-2413 ♂, ♀, off Fraser Island, Qld, 24°20'S, 153°02'E. ('Warreen' Mar. 1938); AMP22642 ♂, ♀, North Head, Sydney; QMW20485 ovig. ♀, S.L. 4.7mm, PSM #20, Pumicestone Passage, site #12, 26°49'S, 153°8'E, J. Greenwood, 26 Jan 1990, 2m, on sand, 34.9 ppt salinity, 27.3°C water temperature.
Colour. Colourless to whitish, with a few brown chromatophores on carapace, pereiopods and abdomen.
S.L. Adult ♂ 4.4mm. Adult ♀ 3.6-4.7mm.

HABITAT AND DISTRIBUTION. On sand; 1-7m; NE and Central E Coast. Qld: Fraser Island area (Hale, 1944a), Moreton Bay.

REMARKS. ♀ first pereiopod of Moreton Bay specimen with inner apical angle of basis rounded rather than pointed as shown by Hale (Fig. 9N). S.L. of Moreton Bay specimen is 30% larger than the type specimen. Otherwise the specimen agrees exactly with the original description.

Cyclaspis usitata Hale, 1932
(Figs 15, 16)

Cyclaspis usitata Hale, 1932:549, fig.1; Hale, 1944a:122, figs 43,44.

MATERIAL EXAMINED. HOLOTYPE SAMC1841, ♀, S.L. 10mm, St. Vincent Gulf, SA. OTHER MATERIAL AMG917, ♀; QMW20486 ovig. ♀, S.L. 6mm, PSM #12, Pumicestone Passage, site #12, 26°49'S, 153°8'E, J. Greenwood, Mar. 1992, 2 m, on sand, 35.4 ppt salinity, 24.5°C water temperature;

FIG. 17. *Cyclaspis alveosculpta* sp. nov. ♂. A, whole mount LV, shows relative lengths of carapace and somites. Also shows affects of partial digestion in fish. B, carapace LV, shows shape of carapace in lateral view. C, Anterior carapace LV, shows reduction of anterior transverse ridge and pattern of pits in integument. D, carapace ALV, shows reduction of anterior and posterior transverse ridges and position of ocular lobe. E, carapace LV, detail of integument showing reticulate pattern of scales. F-H, *Cyclaspis cooki* sp. nov. ♀ F, carapace LV, shows delicate, finely reticulate integument and prominent sub-acute antennal tooth. G, Pleonites 1-3 LV, shows articular notches and median dorsal ridge. H, Pleonites 1-3 DLV, shows fine median dorsal ridge of pleon.
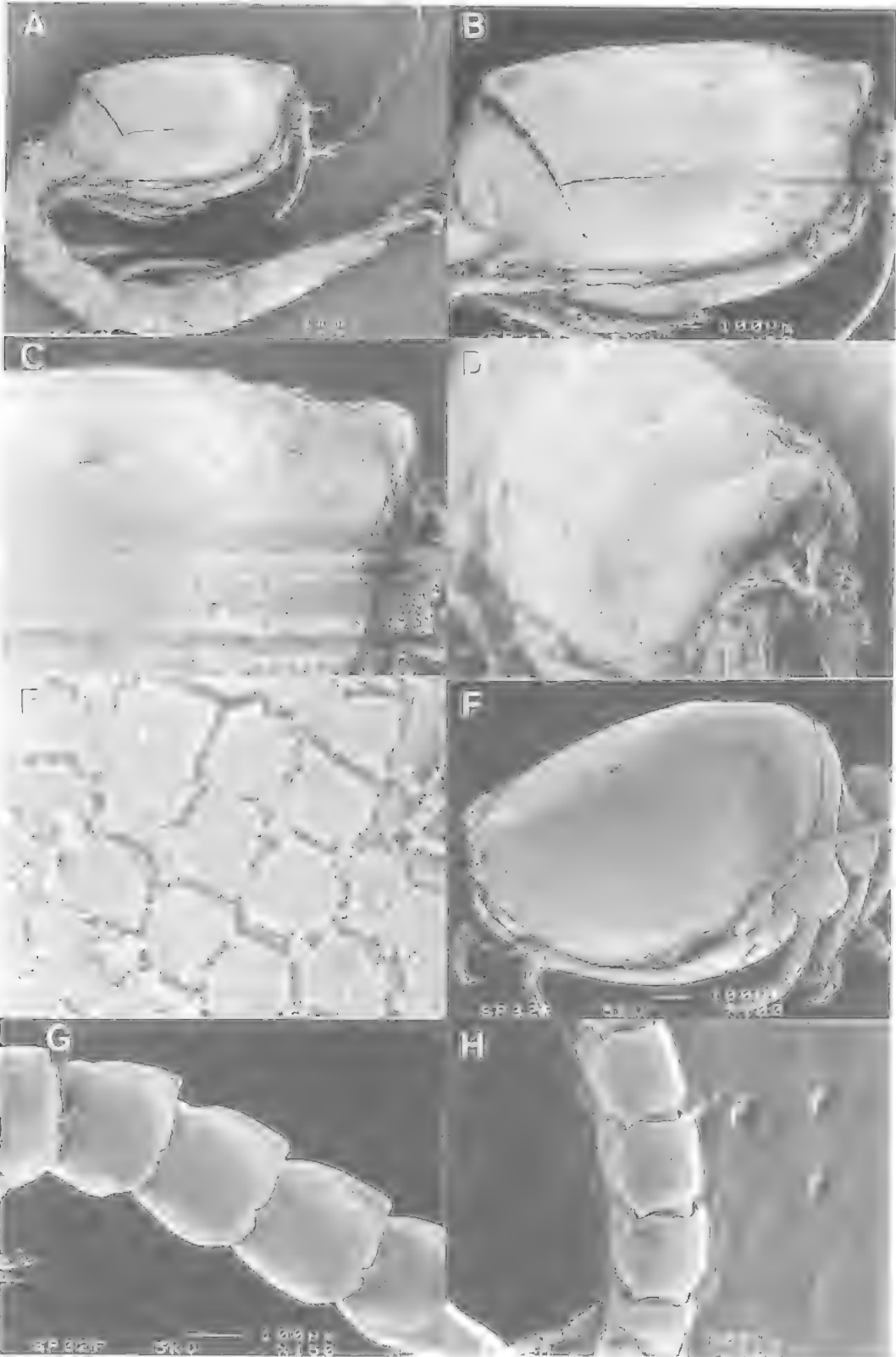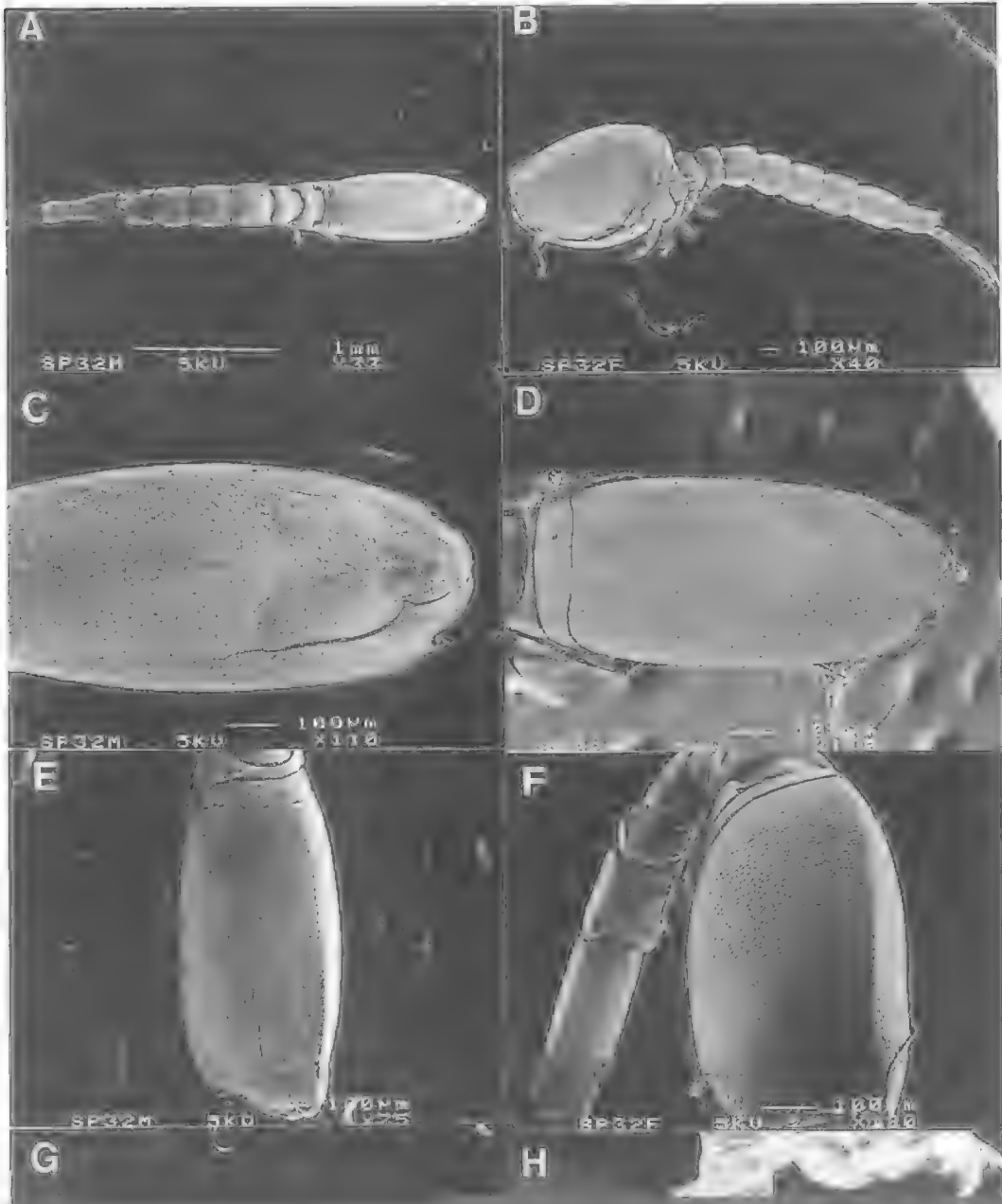
QMW20487 sub-adult , S.L. 5.4mm, PSM #42, Pumicestone Passage, same data as above; QMW20488, sub-adult ♂, S.L. 6mm, PSM #14, off Macleay Island, 27°36'S, 153°22'E, D. Tafe, 9 Nov. 1989, 1.5 m, on fine sand, 34 ppt salinity, 25°C water temperature.

Colour. Whitish to yellow.

S.L. Adult ♂: 6-8mm, Adult ♀: 5-9mm.

HABITAT AND DISTRIBUTION. On sand; 1-7m; S Gulfs Coast, Lower and Central E Coast. SA: St. Vincent Gulf. NSW: Jervis Bay (Hale, 1944a). Qld: Moreton Bay.

REMARKS. The Moreton Bay form is smaller than the SA and NSW forms but similar in size to the WA form. The first antenna, fourth pereiopod and uropod of the ♀ (Fig.15) match those of Hale (1944a:123). The ♂ has not as yet been described. The subadult ♂ from Moreton Bay cannot be described as the ♂ of the species, considering the extent of morphological change which occurs in all members of the *exsculpta* group during maturation. Hale (1948) suggested that *C. mjobergi* Zimmer may well be the ♂ of *C. usitata.* Certainly the description of *C. mjobergi* (♂) given by Zimmer (1921) closely resembles the above subadult ♂ of *C. usitata* (♂), however, the length of the former species (type) is recorded as 14mm. Smaller specimens (8-9mm) of *C. mjobergi* (♂) from St. Vincent Gulf (Hale, 1944a: 88), differ in segmentation and setation of the pereiopods to the above subadult ♂ of *C. usitata* (Fig. 16).

Hale (1944a:122) recorded a large number of ♀♀ of *C. usitata*, c.7mm in length, from Brighton, SA. He also recorded an ovigerous ♀, 6mm long, from Shark Bay, WA (1948:41). The types of *C. candida* and *C. mjobergi* (Zimmer,1921), both appear to be too large (12.5 and 14mm respectively) to be considered the ♂ of *C. usitata.*

Cyclaspis cooki sp. nov.
(Figs 17F,G,H, 18-20)

MATERIAL EXAMINED. HOLOTYPE QMW20520, adult ♂, S.L. 5mm, PSM #48, Pumicestone Passage, site 12, 26°49'S, 153°8'E, J. Greenwood,
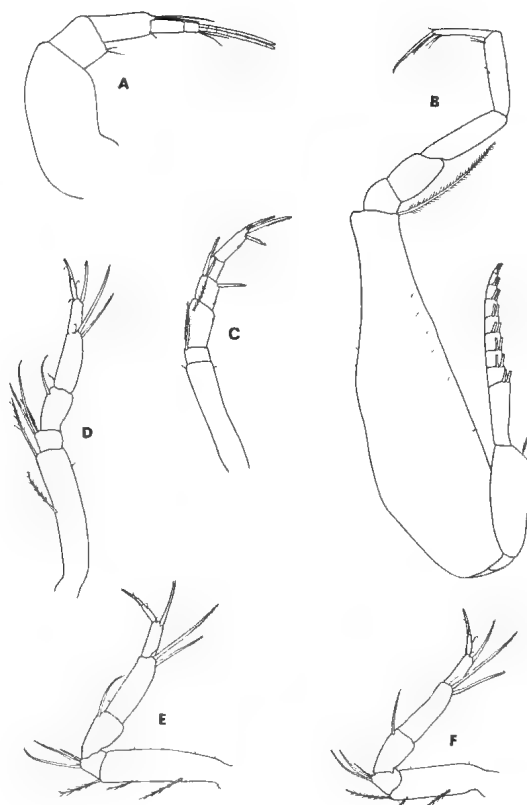
FIG. 19. *Cyclaspis cooki* sp. nov. A-B, holotype adult ♂. A, first antenna. B, first pereiopod. C, second pereiopod. D, third pereiopod. E, fourth pereiopod. F, fifth pereiopod.

4 May 1990, 2m, coarse sand, 33.3 ppt salinity, 23.5°C water temperature. PARATYPES QMW20521, ovig. ♀, allotype, S.L. 2.5mm, PSM #47, same data as holotype; QMW20522, adult ♂, S.L. 3.06mm, SEM mount, off Coochiemudlo Island, site 35, 5m, sand, 27°34'S, 153°21'E, D.Tafe, 17 June 1990, 34 ppt salinity, 18°C water temperature; QMW20523, adult ♀, S.L. 2.4mm, SEM mount, same data as above.

DESCRIPTION. MALE. Integument lightly calcified, delicate and easily broken, even when freshly caught; finely reticulate and sparsely pitted (Fig. 18A,C,E). Carapace length 0.32 S.L. and 0.48 as wide as long in dorsal view, with

FIG. 18. *Cyclaspis cooki* sp. nov. A, ♂ DV, shows relative lengths of carapace and somites. B, ♀ LV, shows relative lengths of carapace and somites. C, ♂ carapace DV, shows shape and texture of carapace. D, ♀ carapace DV, shows shape and texture of carapace. E, ♂ carapace DLV, shows strong median dorsal ridge extending throughout. F, ♀ carapace DLV, shows strong median dorsal ridge extending throughout. G, ♂ uropods DV, shows relative lengths of peduncle and rami. H, ♀ uropods VV, shows relative lengths of peduncle and rami.

FIG. 20. *Cyclaspis cooki* sp. nov. A-B, holotype adult ♂. A, uropods and telsonic somite, DV. B, rami of uropod, DV. C-D, allotype ovig. ♀. C, uropods and telsonic somite, DV. D, rami of uropod, DV.

strong median dorsal ridge throughout length, lateral margins evenly rounded, dorsal edge slightly arched, pseudorostral lobes barely reaching apex of ocular lobe; sides of carapace devoid of ridges or sculpture; antennal notch moderate and visible in dorsal view; antennal tooth subacute, no antennal ridge; pseudorostral lobes wide, joining just anterior to ocular lobe which is almost as wide as long, rounded, with 9 lenses, 3 central surrounded by 6 outer lenses (Fig. 18C,E). Pereion 0.48 as long as carapace; first pereionite fully concealed; second pereionite a narrow collar posterior to carapace; lateral section shorter than each of remaining 3 overlapping pereionites (Fig. 18A,E).

Pleon robust with median dorsal ridge and well-developed lateral articular processes; first 4 pleonites subequal in length, fifth pleonite 1.3 times as long as fourth (Fig. 18A). First antenna 3-segmented with terminal segmented flagellum; first segment somewhat geniculate, longer than second and third segments combined; second segment 0.9 times third segment, with 2 fine setae distolaterally; third segment with 2 slender setae distomedially and one distolaterally; first segment of flagellum twice as long as second, which has 2 aestetascs and 2 fine setae distally (Fig. 19). All pereiopods 7-segmented, with terminal spine-like setae longer than dactylus, except in first pereiopod; some spine-like setae have rows of fine spinules distally (Fig. 19). First pereiopod with basis 1.2 times length of remaining segments combined, with plumose seta distolaterally; ischium 0.6 times length of merus which is 0.7 times length of carpus; carpus subequal in length to propodus, which is 1.4 times length of dactylus, with 1 medial and 2 distal setae; dactylus with 2 slender terminal spine-like setae, 1 almost as long as itself, 1 terminal seta and 2 stout subterminal setae; exopod well developed, wide proximal segment with 1 short plumose seta distolaterally and 8 shorter distal segments, each with 2 long setae (Fig. 19). Second pereiopod with basis 0.8 times length of remaining segments combined, with minute distomedial and distolateral setae; ischium 0.4 times length of merus, with plumose seta distomedially; merus 1.7 times length of carpus, with plumose seta distomedially; carpus 1.4 times length of propodus, with 2 spine-like setae distomedially and 1 spine-like seta distolaterally; propodus 0.5 times length of dactylus, which has 2 terminal spine-like setas, one slightly longer than itself, 1 small terminal seta and 1 subterminal spine-like seta (Fig. 19). Third to fifth pereiopods with merus longer than ischium, carpus as long as combined length of propodus and dactylus, the longer of which is propodus; basis with 1-3 plumose setae medially; ischium with 3 setae distomedially; merus with seta distomedially; carpus with 2 spine-like setae and 1 fine seta distolaterally; propodus with spine-like seta and minute seta distally; dactylus

FIG. 21. *Cyclaspis tranteri* sp. nov. ♂. A,B, whole mount LV, shows relative lengths of carapace and somites. C, carapace LV, shows subacute antennal tooth and first pereiopod. D, carapace DV, shows maximum width in mid-region and median dorsal ridge visible along anterior 2/3 of carapace. E, carapace LV, shows fine reticulate pattern of pits, and relative length and depth of carapace. F, Pereiopods LV, shows very long basal segment of second pereiopod. G, uropods DV, shows relative lengths of peduncle and rami H, Distal end of exopod DV, shows two setose terminal mucrones and one small curved terminal seta.
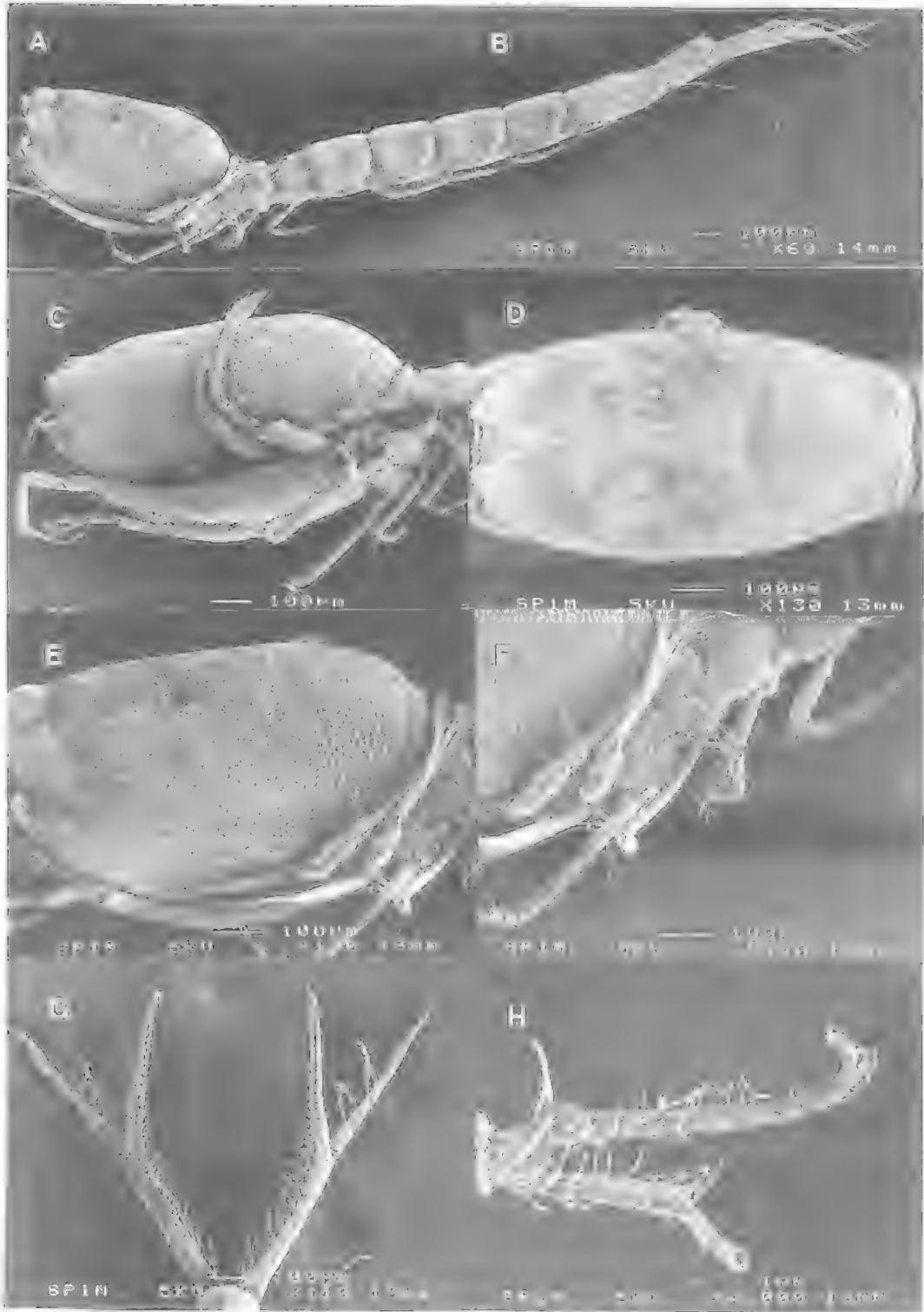
FIG. 22. *Cyclaspis tranteri* sp. nov. ♂. A, distal end of exopod of uropod DV, shows two setose terminal mucrones at apex of exopod. B-D, distal end of exopod of uropod (part) DV. E, distal end of exopod of uropod (part) DV, detail of mucrones showing convoluted appearance of each shaft distally and fibrous appearance of setules.

with terminal spine-like seta, terminal seta and subterminal seta (Fig. 19D-F). Third pereiopod with basis slightly shorter than remaining segments combined; ischium 0.4 times length of merus; merus 0.7 times length of carpus; propodus 1.7 times length of dactylus (Fig. 19D). Fourth pereiopod with basis 0.7 times length of remaining segments combined; ischium 0.4 times length of merus; merus 0.65 times length of carpus; propodus 1.7 times length of dactylus (Fig. 19E). Fifth pereiopod with basis 0.5 times length of remaining segments combined; ischium 0.4 times length of merus; merus 0.7 times length of carpus; propodus 1.7 times length of dactylus (Fig. 19F). Peduncle of uropod 1.8 times as long as telsonic somite, lined with 14-15 plumose setae on inner margin; endopod 0.9 times as long as peduncle, subequal in length to exopod, with 6 slender spine-like setae and 11-12 stout spine-like setae on proximal 3/4 of inner margin, apex pointed, without spine-like setae or mucrones; exopod with 6-8 plumose setae on proximal 2/3 of inner margin, apex pointed, without spine-like setae or mucrones (Fig. 19A,B).

OVIGEROUS FEMALE. Integument lightly calcified, finely reticulate and sparsely pitted, as in ♂ (Fig. 18B,D,F). Carapace length 0.35 S.L. with strong median dorsal ridge and sides devoid of ridges or sculpture, as in ♂; width 0.48 times length in dorsal view; antennal tooth subacute and extending to anterior extremity of carapace; ocular lobe and pseudorostral lobes as in ♂ (Figs 17F, 18D,F). Pereion 0.4 times as long as carapace. First pereionite fully concealed by second, both produced ventrally to form the marsupium; pereionites with dorsal ridge, dorsolateral margin of fifth with articulation notch (Fig. 18B). Pleon robust, all five pleonites with dorsal ridge and lateral articulation notches; first 4 pleonites and telsonic somite subequal in length, fifth pleonite 1.5 times as long as fourth (Figs 17G,H, 18B). Telsonic somite projecting posteriorly over bases of uropods (Figs 18B, 20C). First antenna 3-segmented with terminal segmented flagellum, as in ♂. Pereiopods as in ♂ except: merus of second pereiopod has stout spine-like seta distolaterally; carpus of third to fifth pereiopods each have 3 distal spine-like setae rather than 2 spine-like setae and 1 minute seta. Peduncle of uropod 1.6 times as long as telsonic somite, without plumose setae on inner margin; endopod 0.75 times as long as peduncle, subequal in length to exopod, with 5 spine-like setae on proximal 2/3 of inner margin, apex

pointed, without spine-like setae or mucrones; exopod with 2 plumose setae on proximal 1/3 of inner margin, apex pointed, without spine-like setae or mucrones (Fig. 20C,D).

Colour. Cream with small black chromatophores speckled on carapace and abdomen.

S.L. Adult ♂ 3.0-3.5mm. Adult ♀ 2.4-2.5mm.

HABITAT AND DISTRIBUTION. Medium and coarse sand; 1-5m water depth; sites 12, 34, 35 in Moreton Bay.

REMARKS. *Cyclaspis cooki* resembles *C. pura* Hale from S Aust and *C. juxta* Hale from WA, but the rami of the uropods are longer relative to the peduncle and the setation of the pereiopods and uropods is different (Figs 19, 20). Both sexes are common in Moreton Bay.

ETYMOLOGY. For Steve Cook, Queensland Museum, who collected the types.

Cyclaspis tranteri sp. nov.
(Figs 21-23, 24I,J, 25)

MATERIAL EXAMINED. HOLOTYPE QMW20489, adult ♂, S.L. 2.7mm, PSM #3; PARATYPES QMW20490, ovig. ♀, allotype, S.L. 2.45mm, PSM #2, same data as holotype; QMW20491, adult ♂, S.L. 2.5mm, PSM #4; QMW20492, adult ♀, S.L. 2.5mm, PSM #1; QMW20493, adult ♂, S.L. 2.6mm, SEM mount; QMW20494, ovig. ♀, S.L. 2.4mm, SEM mount; all types from Raby Bay, site 32, 27°30'S, 153°18'E, D. Tafe, 22 July 1989, 5m, sandy mud, 34 ppt salinity, 24.8°C water temperature, same data as holotype

DESCRIPTION. MALE. Integument thin and almost membranous, with fine reticulate pattern of pits (Fig.21A-E). Carapace 0.27 S.L. twice as long as deep; in profile the dorsal margin evenly curved except for the protruding ocular lobe, with mild post-ocular depression; median dorsal ridge is visible along anterior 2/3 of carapace; in dorsal view carapace is widest in mid-region and tapers slightly towards the front and rear; antennal notch widely open, antennal tooth subacute and visible in dorsal view, no antennal ridge; pseudorostral lobes tapering anteriorly and joining just below ocular lobe (Fig. 21D), join not visible in dorsal view; ocular lobe as wide as long, rounded with distinct corneal lenses, and located at anterior extremity of carapace (Figs 21C-E, 24A,E,I). Pereion 0.55 times as long as carapace; first pereionite fully concealed; second pereionite forming a narrow collar posterior to carapace; as
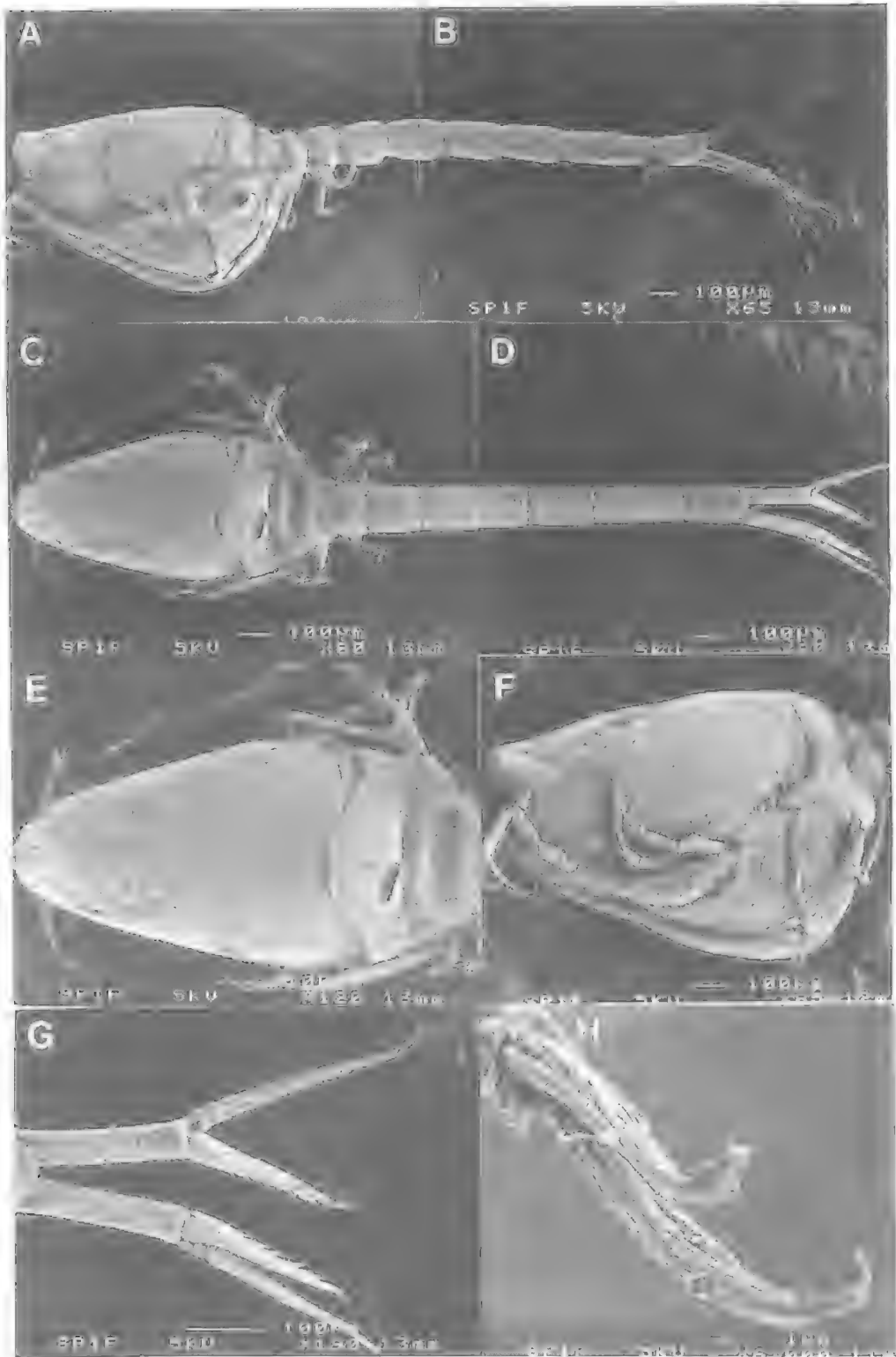
long as third but shorter than fourth and fifth pereionites (Figs 21C,D, 24A,E,I). Pleon slender and long, no dorsal or lateral ridges; first 4 pleonites subequal in length, each with small lateral articular notches; fifth pleonite 1.5 times as long as fourth (Fig. 21A,B). Telsonic somite subequal in length to fourth pleonite, with posterodorsal projection (Figs 21B, 24F, 25B). First antenna as in *C. sublevis*. Second antenna with flagellum reaching to posterior end of peduncle of uropod (Fig. 21B). All pereiopods 7-segmented, with terminal spine-like setae longer than dactylus. First pereiopod with carpus reaching beyond level of antennal tooth; length of basis 1.2 times rest of appendage, with distomedial margin produced into blunt tooth and with plumose distolateral seta; ischium 0.5 times length of merus which is 0.6 times length of carpus; carpus 0.9 times length of propodus and subequal in length to dactylus; propodus 1.1 times length of dactylus, with 2 medial and 2 distomedial setae; dactylus with 2 slender spine-like setae and 1 seta terminally, 1 spine-like seta and 1 seta subterminally and 1 seta on medial margin; exopod well-developed, very broad proximal segment bearing plumose seta distally, and 8 short distal segments, each with 2 long, plumose setae (Figs 21C, 24A,H, 25A). Second pereiopod as in *C. sublevis* except that terminal spine-like seta is distinctly longer (1.3 times) than dactylus and basis is c. twice length of remaining segments combined (Fig. 21A,F). Pereiopods 3-5 as in *C. sublevis*. Peduncle of uropod 1.3 times length of telsonic somite, with 20-21 plumose setae on
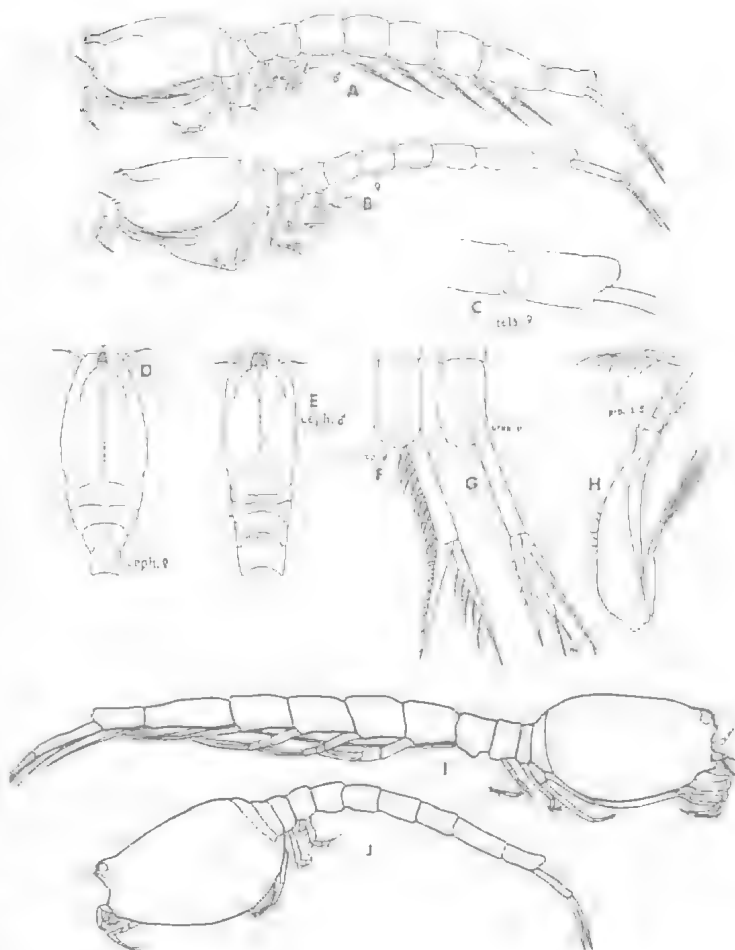
FIG. 24. *Cyclaspis* species. A-H, *Cyclaspis sublevis*. A, type ♂, LV. B, type ovig. ♀, LV. C, telsonic somite of ♀, LV. D, ♀ cephalothorax, DV. E, ♂ cephalothorax, DV. F, ♂ uropod and telsonic somite, DV. G, ♀ uropod and telsonic somite, and m, mucrones of exopod. H, ♂ first pereiopod. (A-H, after Hale, 1948). I-J, *Cyclaspis tranteri* sp. nov. I, adult ♂, LV. J, ovig. ♀, LV.

inner margin in 2 rows; endopod subequal in length to peduncle and 0.95 times length of exopod, with 4 plumose spine-like setae and 11 naked spine-like setae on inner margin, and with 2 minute spine-like setae close to the acute distal end; exopod with 5 plumose setae on inner margin, 2 elongate unequal terminal mucrones (setae) and 1 minute curved terminal seta (Figs 21G,H, 22, 24F, 25B,C).

FIG. 23. *Cyclaspis tranteri* sp. nov. ♀. A, whole mount LV, shows relative lengths of carapace and somites. C, whole mount DV, shows bulbous carapace and slender pleon. E, carapace DV, shows maximum width in posterior region and fine reticulate pattern of pits. F, carapace LV, shows relative length and depth of carapace. G, uropods DV, shows relative lengths of peduncle and rami. H, Distal end exopod of uropod DV, shows two terminal setose mucrones and one small non-setose (convoluted) seta.

OVIGEROUS FEMALE. Integument thin and almost membranous, with fine reticulate pattern of pits, as in ♂ (Fig. 23A-E). Carapace 0.29 S.L. almost as deep as long; in profile the dorsal margin has a slight even curve except for the protruding ocular lobe; dorsal ridge is barely visible along anterior 1/2 of carapace; in dorsal view carapace is widest in posterior 1/2 and tapers anteriorly; antennal notch less widely open than in ♂; antennal tooth subacute, no antennal ridge; pseudorostral lobes tapering anteriorly and joining just below ocular lobe (Figs 23A-F, 24B,D,J). Pereion 0.6 times as long as carapace; first pereionite narrow but visible; second pereionite meets carapace dorsally and continues smooth curve of dorsal profile; pereionites 3-5 taper posteriorly in dorsal view (Fig. 23A-F). Pleon very slender, no dorsal or lateral ridges; first 4 pleonites subequal in length, each with minute lateral notches; fifth pleonite 1.4 times as long as fourth (Figs 23A-D, 24B,J). Telsonic somite subequal in length to fourth pleonite and 0.7 times length of fifth pleonite, with posterodorsal projection (Figs 23B,D, 24C). First antenna as in ♂. Segmentation of pereiopods as in ♂; endopod of first pereiopod without distal tooth and exopod with slender basis (Fig. 15D); setation of pereiopods 2-5 as in ♂. Peduncle of uropod 1.3 times length of telsonic somite, without setae on inner margin; endopod 1.1 times length of peduncle, 0.9 times length of exopod, with 4-7 naked spine-like setae on inner margin and 2 minute spine-like setae close to the acute distal end; exopod with 3-4 plumose setae on inner margin, 2 elongate unequal terminal mucrones (setae) and 1 minute curved terminal seta (Figs 23G,H, 24G, 25E,F).

Colour. Cream and translucent.
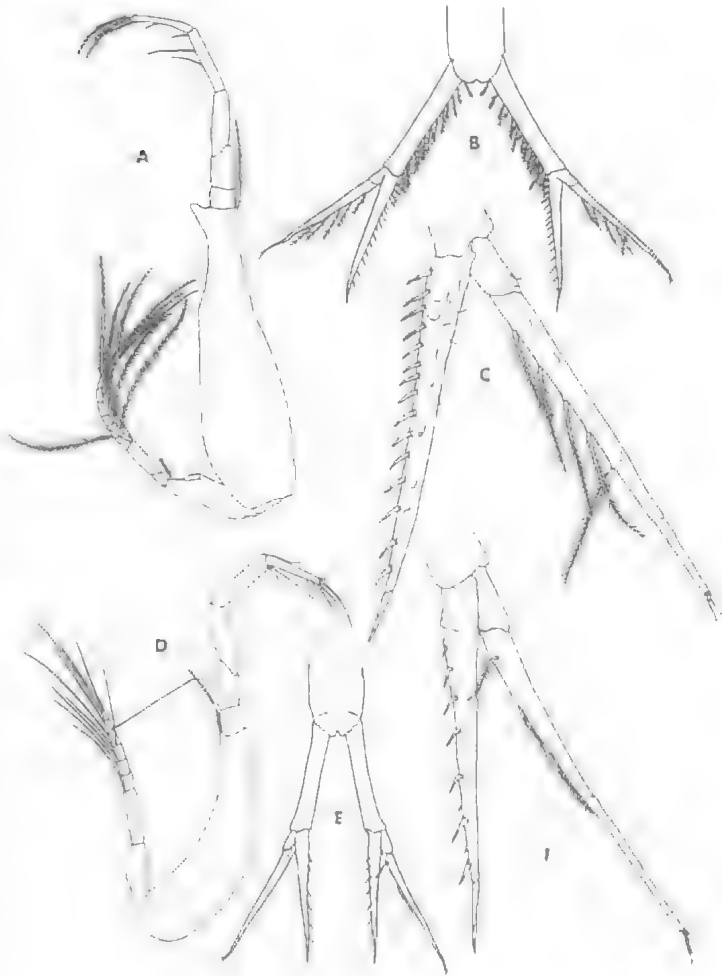
FIG. 25. *Cyclaspis tranteri* sp. nov. A-C, holotype adult ♂. A, first pereiopod. B, uropods, DV. C, rami of uropod, DV. D-F, allotype ovig. ♀. D, first pereiopod. E, uropods, DV. F, rami of uropod.

S.L. Adult ♂ 2.4-2.7mm. Adult ♀ 2.3-2.5mm.

HABITAT AND DISTRIBUTION. In 4-7m over silt and fine sand; Raby Bay, off Cleveland Point.

REMARKS. *C. tranteri* closely resembles *C. sublevis* Hale from Broome, WA, and the Hawkesbury River, NSW (AMP28613). However, the new species has 3 mucrones on the exopod of the uropod, rather than 2 mucrones, and a long terminal spine-like seta (longer than dactylus) on the second pereiopod. In addition the ♂ has no spine-like setae on the medial bulge of the first

TABLE 1. Uropod spination of *C. sublevis* and *C. tranteri*.

	C. sublevis		C. tranteri	
	♂ C2997	♀ C2998	♂♂	♀♀
Peduncle setae	19	6	20-21	5
Endopod spines	15	6	14-15	4-7
Exopod setae	5	0	5-6	3-4
Exopod mucrones	2	2	3	3

pereiopod. The standard lengths of both ♂s and ♀s are, on average, 8 to 10% smaller than *C. sublevis*. Spination of uropods compares with that of *C. sublevis* (Hale, 1948:10, figs 5, 6) (Table 1)

The 2 larger mucrones are setose filaments (Fig. 22). The third naked and smaller filament is present in both sexes (Figs 21H, 23H).

C. sublevis belongs to the *levis* group and most closely resembles the much larger New Zealand *C. calmani* Hale (=*levis* Calman not Thomson) (Hale,1948), but in *C. calmani* the basis of the first pereiopod has no distal tooth and the rami of the uropod are relatively shorter. There remains confusion as to whether *C. levis* Thomson and *C. calmani* Hale are two separate species or variations within the one species.

Thomson's original description and figures of *C. levis* had a number of inaccuracracies (Calman,1907; Hale,1944a; Jones,1963) wit the major points of confusion being relative proportions of segments of the first pereiopods and presence or absence of terminal spine-like setae on the rami of the uropods. Hale (1944a) concluded that the differences between Thomson's and Calman's specimens were consistent, in spite of the confusion, and erected a new species, *C. calmani*, which he thought was related to both *C. levis* and *C. sublevis*. In the key we follow Bacescu (1988) in synonymising *calmani* and *levis*.

Specimens of *C. tranteri* can be distinguished from *C. sublevis* by the setae on the inner margin of the exopod of the uropod in the ♀ and by structural differences of the first pereiopod in the ♂. They include the absence of spine-like setae on the basal segment of the endopod and a broad basal segment on the exopod. These 2 species are distinguished within the genus by the proportion and spination of the uropod. Also the slender dactylus of pereiopods 3-5 separates *C. tranteri* and *C. sublevis* within the *levis* group. *C. tranteri* was abundant over sandy mud.

ETYMOLOGY. For David Tranter, for his contribution to zooplankton research in Australia.

Cyclaspis ornosculpta sp. nov.
(Figs 26-30)

MATERIAL EXAMINED. HOLOTYPE QMW20495, adult ♂, S.L. 5.04mm, PSM #57, Pumicestone Passage, site 5, 26°52'S, 153°7'E, J. Greenwood, 28 Jan 1991, 3m, sand, 36 ppt salinity, 31°C water temperature. PARATYPES. QMW20496, ovig. ♀, allotype, S.L. 4.76mm, PSM #58, Pumicestone Passage, site 3, 26°54'S, 153°5'E, otherwise same data as holotype; QMW20497, adult ♂, S.L. 4.3mm, SEM mount, same data as holotype; QMW20498, ovig. ♀, S.L. 4.25mm, SEM mount, same data as holotype.

DESCRIPTION. MALE. Integument calcified, with reticulate pattern of shallow pitting (Fig. 26A-D). Carapace 0.3 S.L. twice as long as deep; in profile the dorsal margin is slightly convex with mild post-ocular depression; median dorsal ridge is visible along length of carapace and pronounced on anterior half; in dorsal view carapace is widest in region of anterior transverse

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(captions for two following pages)

FIG. 26. *Cyclaspis ornosculpta* sp. nov. ♂. A, whole mount (part) DV. B, whole mount (part) DV, shows relative lengths of carapace and somites. C, whole mount (part) LV. D, whole mount (part) LV shows lateral articulation notches of pleonites. E, Anterior carapace A.DV shows ocular lobe and reticulate pattern of pits. F, carapace LV shows reduced anterior and posterior transverse ridges. quadrilateral area barely discernible. G, carapace DV shows median dorsal ridge along length. H, uropods DV shows relative lengths of peduncle and rami.

FIG. 27. *Cyclaspis ornosculpta* sp. nov. A, carapace adult ♂ LV, shows reduced sculpture. B, carapace ovigerous ♀ LV, shows accentuated sculpture. C, carapace adult ♂ DLV, shows reduced sculpture. D, carapace ovigerous ♀ DLV shows accentuated sculpture. E, carapace late subadult ♂ DLV, shows slightly reduced sculpture. F, carapace late subadult ♀ DLV shows retention of sculpture. G, carapace early subadult ♂ DLV, shows moderate sculpture. H, carapace early subadult ♀ DLV, shows moderate sculpture.
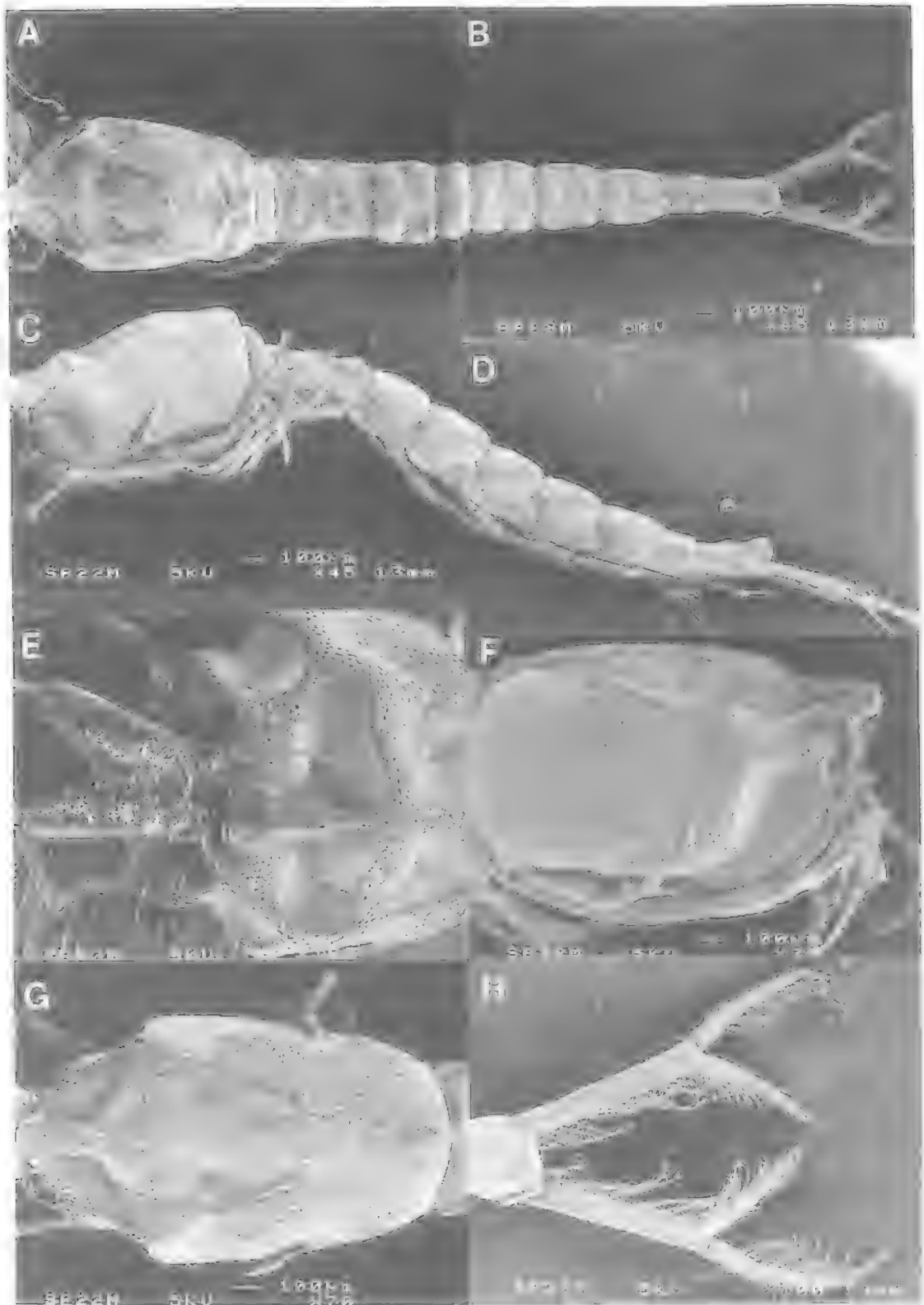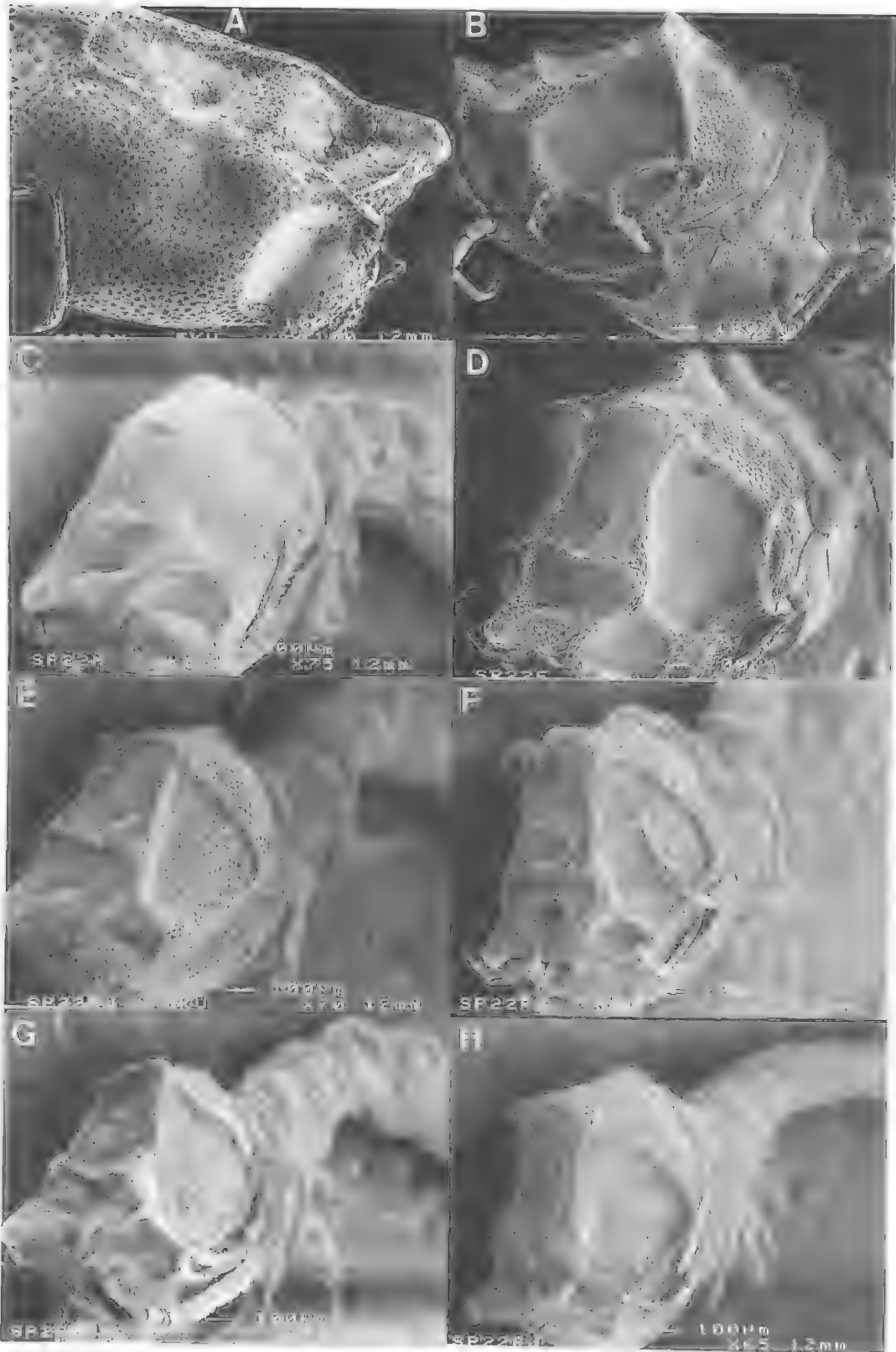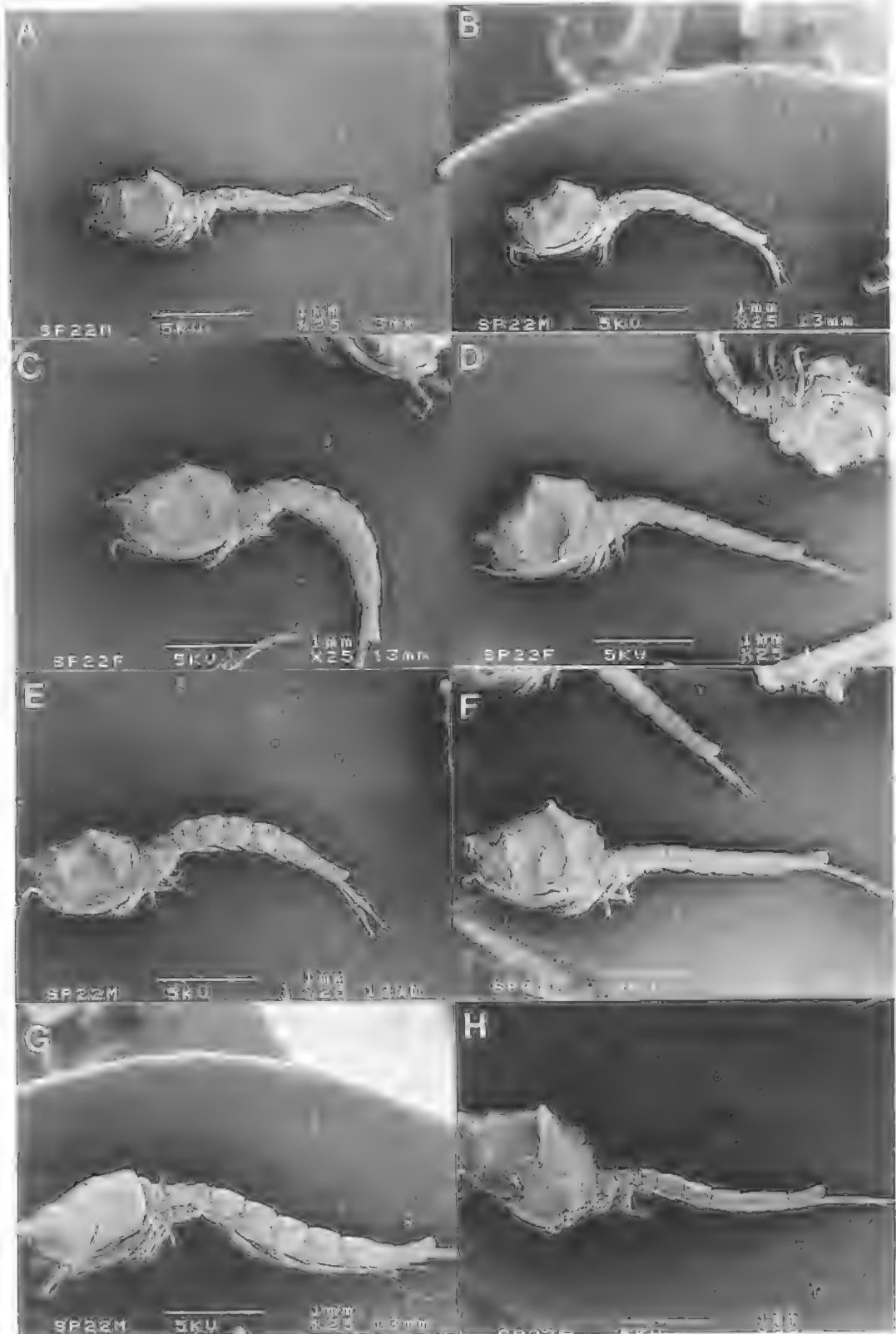
ridge; in lateral view posterior transverse ridge visible only as fine line behind slightly depressed quadrilateral area; antennal notch a short groove;antennal tooth subacute, no antennal ridge; pseudorostral lobes tapering anteriorly and joining just below ocular lobe, join not visible in dorsal view; ocular lobe as wide as long, rounded, and located at anterior extremity of carapace (Fig. 26E-G). Pereion 0.5 times as long as carapace; first pereionite fully concealed; second pereionite forms a narrow collar posterior to carapace, as long as third but shorter than pereionites 4 and 5; tufts of short setae on posterodorsal margins of last 3 pereionites (Fig. 26A-D). Pleon robust, no dorsal ridges; first four pleonites subequal in length, each with lateral notch in posterior margin and oblique carina extending anteriorly and ventrally from notch; fifth pleonite 1.6 times as long as fourth, with 5 short spine-like setae on posterodorsal margin (Fig. 26A-D). Telsonic somite shorter than fifth pleonite and longer than fourth, with posterodorsal projection (Fig. 26B,D). First antenna 3-segmented with terminal segmented flagellum; first segment somewhat geniculate, longer than second and third segments combined; second segment subequal in length to third, with fine seta distomedially; third segment with 2 terminal and 2 subterminal setae; first segment of flagellum 1.6 times as long as second, which bears 2 aesthetascs and 2 fine setae distally (Fig. 29A). All pereiopods with terminal spine-like setae longer than dactylus; first and third to fifth pereiopods 7-segmented, second 6-segmented since ischium is fused with basis. Pereiopod 1 with carpus reaching beyond level of antennal tooth; length of basis 1.1 times rest of appendage, distal margin not produced, with plumose distomedial seta and numerous small lateral setae; ischium 0.9 times length of merus, with plumose distomedial seta; merus 0.6 times as long as carpus, with small distolateral projection; carpus subequal in length to propodus which is 1.2 times·length of dactylus, with group of 5 distomedial setae; dactylus with 2 slender spine-like setae and 1 seta terminally, and 5 setae along medial margin; exopod well-developed, slender proximal segment with 3-4 short setae distolaterally and 8 short distal segments, each with 2 long setae (Fig. 29B). Pereiopod 2 with fused
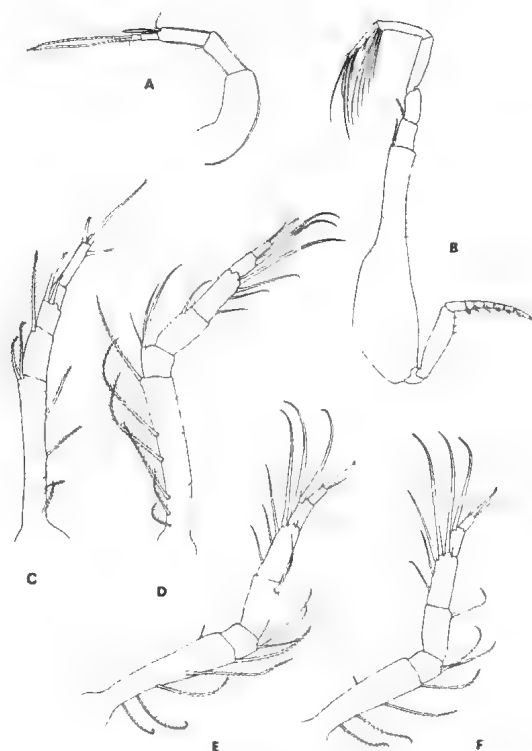
FIG. 29. *Cyclaspis ornosculpta* sp. nov. holotype adult ♂. A, first antenna. B, pereiopod 1. C, pereiopod 2. D, pereiopod 3. E, pereiopod 4. F, pereiopod 5.

basis and ischium (join barely discernible) slightly longer than combined length of remaining segments, with 4 plumose setae laterally and 2 plumose setae distomedially; merus 1.8 times length of carpus, with plumose seta distomedially; carpus 1.2 times length of propodus, with 2 strong spine-like setae and rounded process distally; dactylus 2.3 times length of propodus, with 1 long and 2 short spine-like setae distally, each with a subterminal seta (Fig. 29C). Pereiopods 3-5 with merus longer than ischium, propodus longer than dactylus and carpus longer than combined length of propodus and dactylus; basis with 4-6 plumose setae medially; ischium with 3 setae distomedially; merus with seta distomedially; carpus with 3 setae laterally and 2 spine-like setae distolaterally; propodus with spine-like seta dis-

FIG. 28. *Cyclaspis ornosculpta* sp. nov. A, juvenile ♂ LV,. B, juvenile ♀ LV,. Sexes indistinguishable on external morphology. C, early subadult ♂ LV. D, early subadult ♀ LV. Pleopods developing in ♂, transverse ridges developing in ♀. E, Late subadult ♂ LV. F, Late subadult ♀ LV, Posterior transverse ridge higher in ♀. pleon slender in ♀, robust in ♂. G, ♂ LV. H, Ovigerous ♀ LV. Pleopods and second antennae fully developed in ♂, marsupium developed in ♀. sculpture of carapace reduced in ♂, accentuated in ♀.
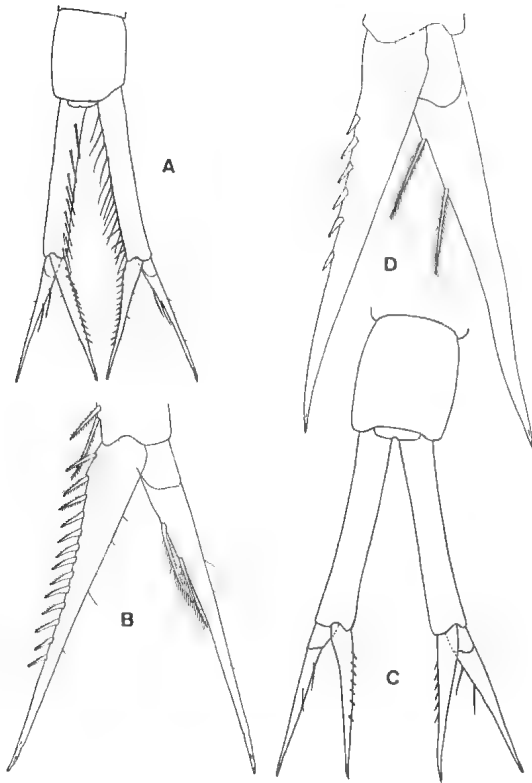
FIG. 30. *Cyclaspis ornosculpta* sp. nov. A-B, holotype ♂. A, uropods and telsonic somite, DV. B, rami of uropod, DV. C-D, allotype ovig. ♀. C, uropods and telsonic somite, DV. B, rami of uropod, DV.
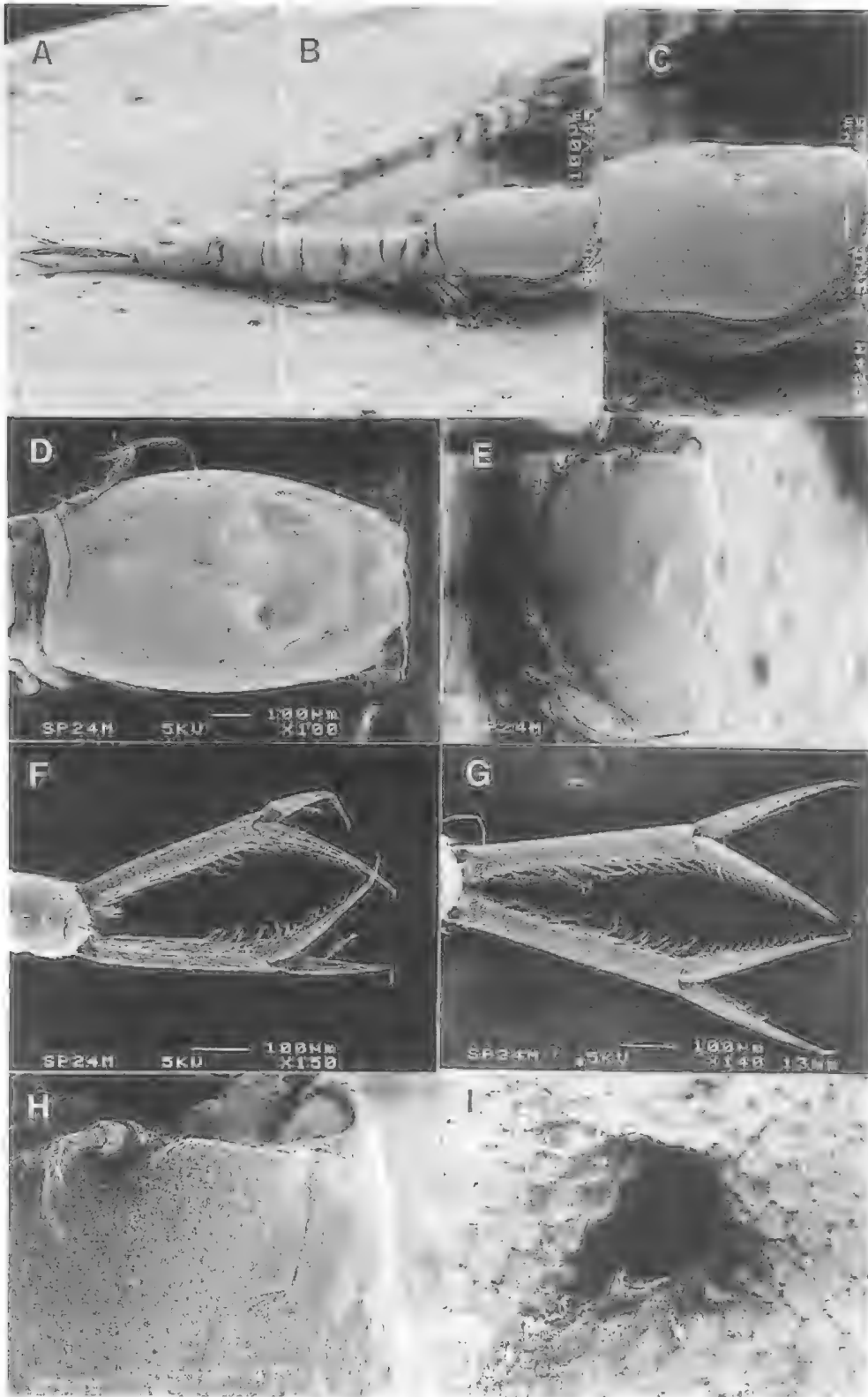
tolaterally; dactylus with terminal spine-like seta and 1-2 terminal setae; some spine-like setae have rows of fine spinules distally (Fig. 29D-F). Pereiopod 3 with basis subequal in length to remaining segments combined; ischium 0.6 times length of merus; merus 0.9 times length of carpus, with distomedial seta; propodus 1.3 times length of dactylus (Fig. 29D). Pereiopod 4 with basis 0.8 times length of remaining segments combined; ischium 0.4 times length of merus which is 0.9 times length of carpus; propodus 1.3 times length of dactylus (Fig. 29E). Pereiopod 5 with basis 0.7 times length of remaining segments combined; ischium 0.5 times length of merus which is 0.9 times length of carpus; propodus 1.5 times length of dactylus (Fig. 29F). Peduncle of uropod subequal in length to telsonic somite, with 15-16 plumose setae on inner margin; endopod 0.8 times length of peduncle and 0.95 times length of exopod, with 12 plumose setae and 6-7 short spine-like setae on inner margin, apex pointed, with serrate inner edge, outer margin with 3 plumose setae; exopod with 12 plumose setae on inner margin, 1 long terminal spine-like seta and 2 minute terminal setae, outer margin with row of fine setae (Figs 26H, 30A,B).

OVIGEROUS FEMALE. Integument calcified, with reticulate pattern of shallow pitting on raised areas of carapace and abdomen (Fig. 27B,H). Carapace 0.35 S.L. almost as deep as long; in profile the dorsal margin is raised in regions of transverse ridges and depressed in postocular region; median dorsal ridge is strong and visible along length of carapace, forming rounded process at posterior extremity; in dorsal view carapace is widest in region of posterior transverse ridge; anterior and posterior transverse ridges and dorso- and inferolateral ridges well developed; depressed quadrilateral region well defined by ridges; antennal notch, antennal tooth and pseudorostral lobes as in ♂ (Figs 27B,D, 28H). Pereion 0.5 times as long as carapace; first pereionite almost fully concealed; second perionite with rounded dorsal projection, pereionites 3-5 with low dorsal profile and tapering posteriorly (Figs 27B, 28H). Pleon robust but much more slender than in ♂, no dorsal or lateral ridges; first 4 pleonites subequal in length, each with lateral articulation notches; fifth pleonite 1.7 times as long as fourth, with 4 short spine-like setae on posterodorsal margin (Figs 27B, 28H). Telsonic somite shorter than fifth pleonite and longer than fourth, with posterodorsal projection (Figs 28H, 30C). First antenna as in ♂. All pereiopods with terminal spine-like setae longer than dactylus; first and third to fifth pereiopods 7-segmented, second 6-segmented as in ♂. Segmentation of pereiopods same as in ♂; carpus of pereiopods 3-5 with 2 rather than 3 setae laterally. Peduncle of uropod subequal in length to telsonic somite, with 9-10 plumose setae on inner margin; endopod 0.8 times length of peduncle, 0.95 times length of exopod, with 2 plumose setae on proximal 1/2 of inner margin, apex bluntly pointed, with serrate inner edge, inner and outer margins with fine scale-like teeth; exopod with 8-10 plumose setae on inner margin, long terminal spine-like seta and minute terminal seta, outer margin with scale-like teeth and scattered fine setae (Fig. 30C,D).

Colour. Cream to brown, black

chromatophores dotted on carapace and abdomen.

S.L. Adult ♂ 4.3-5.0mm. Adult ♀ 4.3-4.8mm.

HABITAT AND DISTRIBUTION. Most common over silt and fine sand but were also present over medium and coarse sand in summer in 1-9m of water; 12 sites in Pumicestone Passage, sites 21 and 36. Their occurrence in sledge net samples was highly seasonal, with peak abundances in summer.

REMARKS. *Cyclaspis ornosculpta* exhibits sexual dimorphism in the adult similar to that in *C. elegans* Calman, 1907 which species it resembles but can be readily distinguished from by the 2 transverse ridges on the carapace in dorsal view. While early juvenile stages of ♂ ♂ and ♀ ♀ of the new species are alike, late juveniles and adults are readily separated by the pleopods in the ♂ and ornate carapace sculpture in the ♀.

Adult ♂s have well-developed second antennae and 5 pairs of pleopods, typical of ♂ ♂ of the Bodotriidae (Fig. 26C,D). The heavily sculptured appearance of the carapace of the adult ♀ is absent in the adult ♂ (Fig. 27A-D). The quadrilateral area of the adult ♂ is not distinctly recessed like that of the ♀ and the posterior transverse ridge is barely visible.

Late subadult ♂ ♂ have partially developed pleopods and reduced sculpturing of the carapace compared to late subadult ♀ ♀ (Fig. 27E,F). The postocular depression of the dorsal median ridge is more acute in the ♀, as is the height of the posterior transverse ridge. Both features are most highly developed in the adult ♀. Early subadult ♂ ♂ and ♀ ♀ cannot be distinguished on external morphology until pleopods begin to develop in the ♂ (Fig. 27G,H).

Comparison of the developmental stages of both sexes (Fig. 28) shows the gradual development of sexual dimorphism. The sex of juveniles is indistinguishable on external morphology alone (Fig. 28A,B) but early subadult ♂ ♂ can be distinguished from ♀ ♀ by having a more robust abdomen and the appearance of pleopod buds (Fig. 28C,D). The quadrilateral areas of both sexes become more developed at this stage. Late subadult ♂ ♂ exhibit a slight reduction in the definition of the quadrilateral area and transverse processes while the reverse occurs in late subadult ♀ ♀ (Fig.28E,F). The most marked changes occur in the final stage of development when the carapace of the ♂ elongates and simultaneously

FIG. 31. *Cyclaspis andersoni* sp. nov. holotype ♂. A, first antenna. B, pereiopod 1. C, pereiopod 2. D, pereiopod 3. E, pereiopod 4. F, pereiopod 5.

loses definition of the quadrilateral area and transverse processes. The ♀, on the other hand, develops calcified posterolateral tubercles and a posterior tubercle along the median dorsal ridge. The dorsal margin of the second pereionite also becomes elevated as a tubercle. The postocular depression becomes more acute in the ♀ and develops into an angular kink in some postovigerous ♀ ♀. In contrast the post-ocular depression in the ♂ remains mildly concave and may even flatten out slightly. The carapace of the ♂, like that of the ♀, calcifies on maturity Fig. 28G,H).

Calman (1907) noted that the subadult ♂ of *C. elegans* more closely resembles the adult ♀ than it does when full grown. It appears from his description and figures that development follows a similar pattern to that of *C. ornosculpta*.

ETYMOLOGY. Orno-, a contraction of ornate, and the *exsculpta* species group to which it belongs.

FIG. 32. *Cyclaspis andersoni* sp. nov. A-B, holotype
♂. A, uropods and telsonic somite, DV. B, rami of
uropod, DV. C-D, allotype ovig. ♀. C, uropods and
telsonic somite, DV. B, rami of uropod, DV.

Cyclaspis andersoni sp. nov.
(Figs31-35)

MATERIAL EXAMINED. HOLOTYPE
QMW20499, adult ♂, S.L. 2.9mm, PSM #23,
Pumicestone Passage, site 10, 26°50'S, 153°7'E, J.
Greenwood, 26 Feb 1991, 2m, sand, 34 ppt salinity,
27.2°C water temperature. PARATYPES
QMW20500, ovig. ♀, allotype, S.L. 3.5mm, PSM #56,
Horseshoe Bay, 27°30'S, 153°21'E, D. Tafe, 2-3m,
sand, 13 Aug. 1990, 27.2 ppt salinity, 16.5°C water
temperature; QMW20501, adult ♂, S.L. 2.8mm, SEM
mount, off Dunwich, 27°29'S, 153°22'E, D. Tafe, 4m,
sand, 17 April 1990, 33 ppt salinity, 26.5°C water

temperature; QMW20502, ovig. ♀, S.L. 2.3mm, SEM
mount, same data as above; QMW20503, adult ♂, S.L.
2.85mm, in 70% ethanol, Pumicestone Passage, site 10,
26°50'S, 153°7'E, J. Greenwood, 25 Jan 1990, 2m,
sand, 34.9 ppt salinity, 27.3°C water temperature;
QMW20504, ovig. ♀, S.L. 2.4mm, in 70% ethanol,
same data as above.

DESCRIPTION. MALE.Integument thin, lightly
calcified, with small, even reticulate patterning
(Fig. 33A-E). Carapace 0.33 S.L. with mild
median dorsal ridge on anterior 1/2 and median
dorsal recess on posterior 1/2; curvature of
carapace is smooth, without lateral ridges, but
with middorsal depressions either side of the
median dorsal ridge; carapace 0.65 as wide as
long, lateral margins evenly curved in dorsal
view; antennal notch a short, shallow groove;
antennal tooth subacute, no antennal ridge; pseu-
dorostral lobes wide, joining just anterior to
ocular lobe which is as wide as long, rounded,
with five lenses (Fig. 33A- E,H). Pereion 0.45 as
long as carapace; first pereionite partially con-
cealed by second, which forms a narrow collar
posterior to carapace, shorter than each of
remaining 3 pereionites which are overlapping,
with low dorsal profile; tuft of very short setae on
posterodorsal margin of third pereionite (Fig.
33B,D). Pleon robust, no dorsal or lateral ridges;
first 4 pleonites subequal in length with small
lateral articulation notches; fifth pleonite 1.5
times as long as fourth (Fig. 33A,B). Telsonic
somite shorter than fifth pleonite and subequal in
length to fourth, with posterodorsal projection
and shallow dorsal notch (Fig. 33A,F). First an-
tenna 3-segmented with terminal segmented
flagellum; segment 1 geniculate, longer than seg-
ments 2+3; segment 2 longer than 3, with fine seta
distomedially; segment 2 with 2 thick and 2 thin
setae distolaterally, and 1 fine seta distomedially;
segment 1 of flagellum slender and 4 times as
long as second which has 2 aesthetascs and 2 fine
setae distally (Fig. 31A). All pereiopods 7-seg-
mented, with terminal spine-like setae longer
than dactylus. Pereiopod 1 with carpus reaching
beyond level of antennal tooth; length of basis 1.5
times rest of appendage, rounded tooth and
plumose seta on distal margin; ischium 0.3 times

FIG. 33. A-H *Cyclaspis andersoni* sp. nov. ♂. A, B, whole mount LV, shows relative lengths of carapace and
somites. C, carapace LV, shows mid-dorsal indentations either side of median dorsal ridge. D, carapace DV,
shows ocular lobe, collar-like second pereionite and maximum width of carapace in mid-region. E, carapace
DLV, shows median dorsal ridge on anterior half and median dorsal recess on posterior 1/2 of carapace. F,
uropods DV, shows posterodorsal projection and shallow dorsal notch on telsonic somite. G, uropods DV,
shows relative lengths of peduncle and rami. H, anterior carapace DLV, detail of antennal notch and ocular
lobe. I, *Cyclaspis alveosculpta* sp. nov. ♂ DV, shows aperture in dorsum of carapace.

length of merus which is subequal in length to carpus; propodus 1.4 times length of dactylus, with 1 medial and 2 distal setae; dactylus with 2 slender terminal spine-like setae, 1 longer than itself, and 2 stout subterminal setae (Fig. 31B). Pereiopod 2 with division between basal segment and ischium barely visible; basis 0.9 times length of remaining segments combined, with small distomedial seta; ischium 0.3 times length of merus, with plumose seta distomedially; merus 1.7 times length of carpus, with plumose seta distomedially and stout spine-like seta distolaterally; carpus 1.2 times length of propodus, with spine-like seta distomedially and spine-like seta distolaterally; propodus 0.65 times length of dactylus, with small distomedial seta; dactylus slender with 2 terminal spine-like setae, 1 longer than itself, 1 small terminal seta and 1 subterminal spine-like seta (Fig. 31C). Pereiopods 3-5 with merus longer than ischium and propodus longer than dactylus; basis with 2-4 plumose setae medially; ischium with 3 setae distomedially; merus with seta distomedially; carpus with 3 spine-like setae distolaterally; propodus with spine-like seta and minute seta distally; dactylus with terminal spine-like seta, terminal seta and subterminal seta; some spine-like setae have rows of fine spinules distally (Fig. 31D-F). Pereiopod 3 with basis subequal in length to remaining segments combined; ischium 0.65 times length of merus which is 0.65 times length of carpus; propodus 1.3 times length of dactylus (Fig. 31D). Pereiopod 5 with basis 0.7 times length of remaining segments combined; ischium 0.5 times length of merus which is 0.6 times length of carpus; propodus 1.2 times length of dactylus (Fig. 31E). Pereiopod 5 with basis 0.5 times length of remaining segments combined; ischium 0.7 times length of merus which is 0.55 times length of carpus; propodus 1.6 times length of dactylus (Fig. 31F). Peduncle of uropod 1.8 times as long as telsonic somite, lined with 16 plumose setae on inner margin; endopod 0.75 times as long as peduncle and 0.95 times as long as exopod, with 12-13 spine-like setae on proximal 2/3 of inner margin and 2-4 fine setae on outer margin, apex pointed, with 2 minute subterminal spine-like setae; exopod with 2 plumose setae on proximal 1/3 of inner margin and 2-3 fine setae on outer margin, apex pointed, with 3 minute subterminal spine-like setae (Fig. 33F,G, 32A,B).

OVIGEROUS FEMALE. Integument lightly calcified and covered with fine reticulate pattern, as in the ♂ (Fig. 34A-E). Carapace 0.29 S.L. with strong median dorsal ridge on anterior 1/2 and dorsal groove on posterior 1/2; middorsal depressions either side of ridge; carapace 0.68 as wide as long, lateral margins evenly curved in dorsal view; depth 0.8 times length of carapace in lateral view; antennal notch and pseudorostral lobes as in ♂ (Fig. 34A-E). Pereion 0.44 times as long as carapace; pereionite 1 almost concealed by second, both produced ventrally to form the marsupium; pereionites 3-5 short, without ridges, and tapering in dorsal view; fifth with lateral articulation notch (Fig. 34A,B). Pleon robust and subcylindrical, devoid of dorsal or lateral ridges; first 4 pleonites subequal in length with lateral articulation notches; fifth pleonite 1.5 times fourth with rounded lateral process overlapping telsonic somite (Fig.34A,B). Telsonic somite 0.55 times fifth pleonite, posterodorsal projection and shallow middorsal notch (Fig. 34F-H). First antenna 3-segmented with terminal segmented flagellum, as in ♂. Pereiopods 1-5 as in ♂ except ischium of 3-5 have 4 rather than 3 setae distally. Peduncle of uropod 1.6 times as long as telsonic somite, without plumose setae on inner margin; endopod 0.75 times as long as peduncle and 0.95 times as long as exopod, with 6-7 spine-like setae on proximal 2/3 of inner margin, apex with fine point and 2 minute subterminal spine-like setae; exopod with 2 plumose setae on proximal 1/3 of inner margin, apex with fine point and 2 minute subterminal spine-like setae (Fig. 32C,D, 34F-H).

Colour. Cream with black chromatophores dotted on carapace and abdomen.

S.L. Adult ♂ 2.8-2.9mm. Adult ♀ 2.3- 3.5mm.

HABITAT AND DISTRIBUTION. Most commonly over silt and fine sand but were also over medium and coarse sand in summer in 1-5mm of

FIG. 34. *Cyclaspis andersoni* sp. nov. A,B, whole mount, ovigerous ♀, LV, shows relative lengths of carapace and somites. C, whole mounts ♂ (left) and ♀ (right), LV, shows relative sizes of both sexes. D, carapace ovigerous ♀ LV, shows relative length and depth. E, carapace ovigerous ♀ DLV, shows median dorsal ridge on anterior half and median dorsal recess on posterior 1/2. F, uropods second ovigerous ♀ DV, shows posterodorsal projection and shallow dorsal notch bearing 2 minute apertures on telsonic somite. G, uropods ovigerous ♀ VV, shows relative lengths of peduncle and rami. H, uropods third ovigerous ♀ DV, shows posterodorsal projection and shallow dorsal notch bearing 2 minute apertures on telsonic somite.
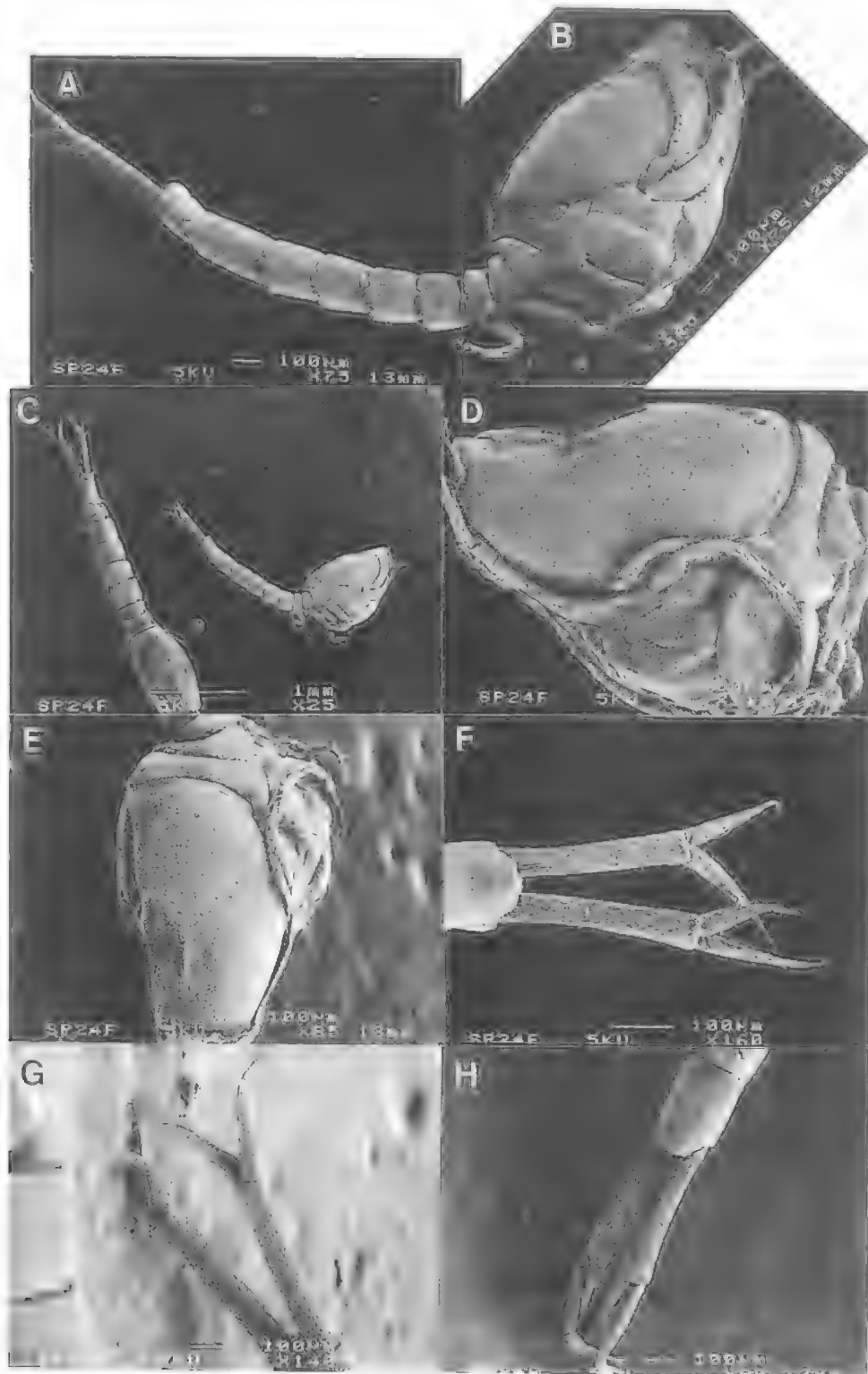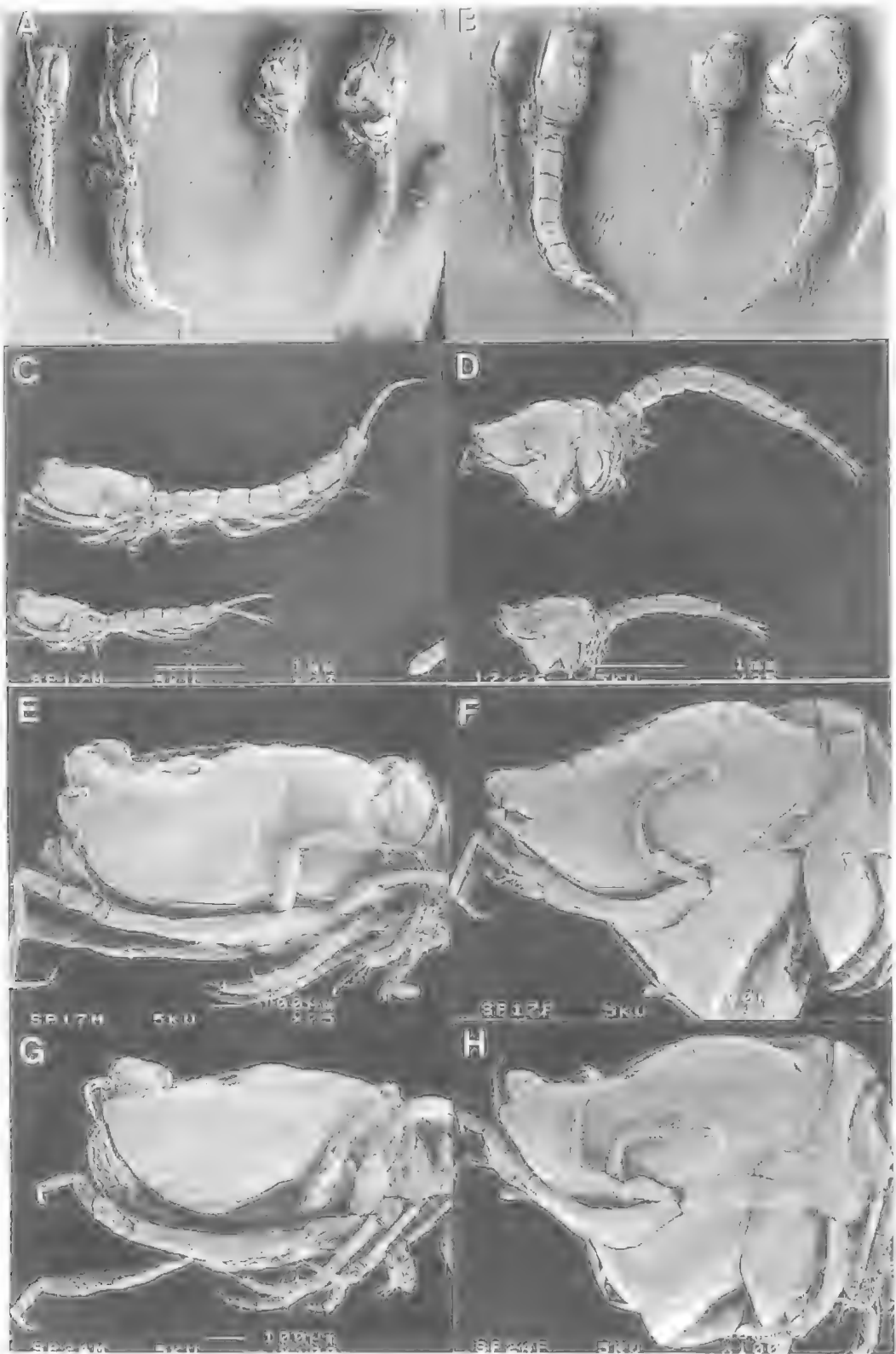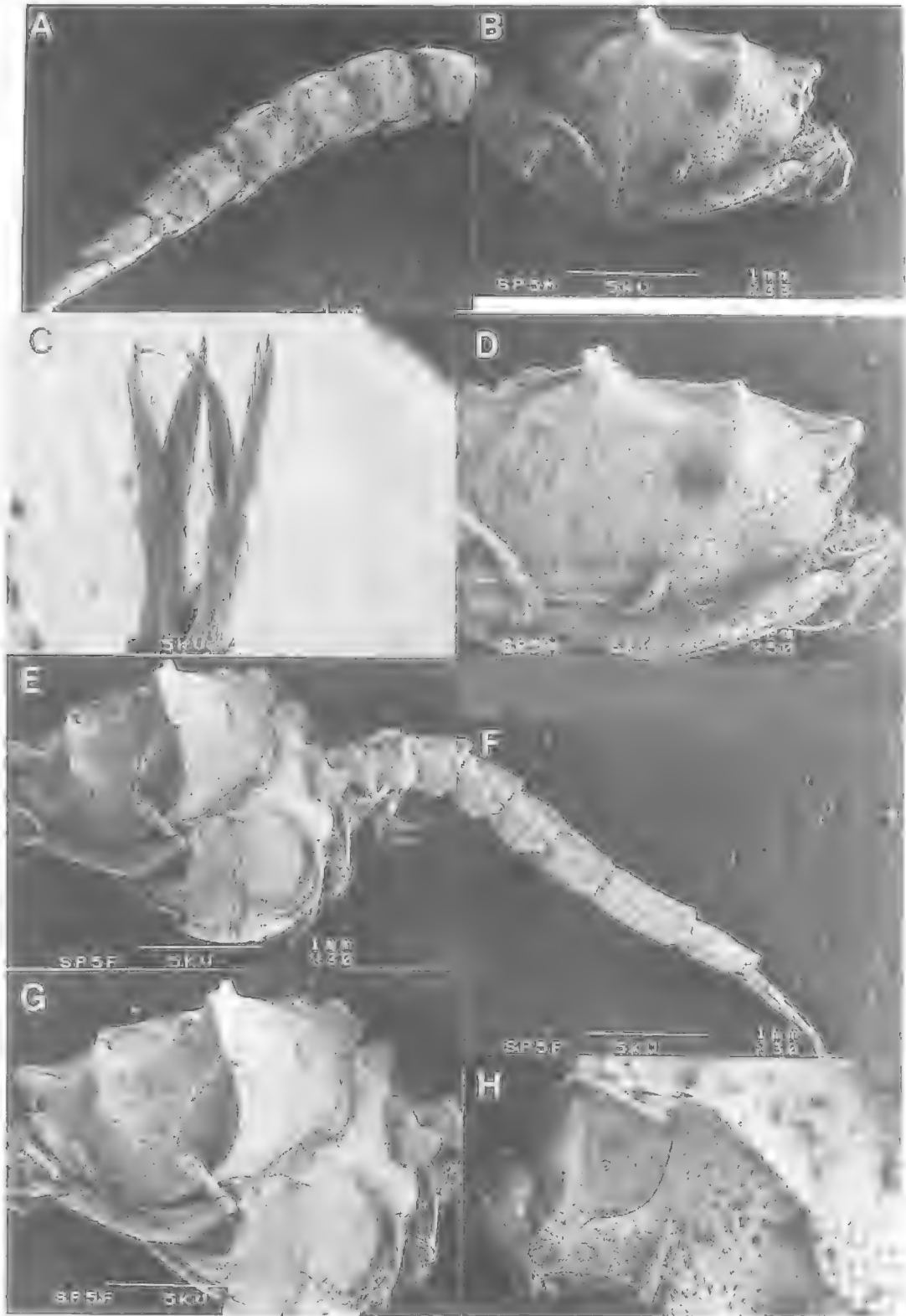
TABLE 2. Setation of ♂ uropods of *C. andersoni* and *C. nitida*.

	C. andersoni sp. nov. (Fig. 33G)	*C. nitida* (Hale, 1944a)
Peduncle setation	16 long	13 long, 5 short
Endopod setation	12-13 spine-setae	7 spine-setae
Exopod setation	2 long	7 long
Exopod term. mucrones	0 mucrones	2 mucrones

water; sites 1-3, 5, 6, 8-12, 15, 26, 28, 31, 33, 34, 35, and 37.

REMARKS. *Cyclaspis andersoni* is related to *C. nitida* Hale, recorded from NSW and WA. The main differences are in carapace shape and setation of the uropods. Hale (1944a) described the ♂ only of *C. nitida* so only the ♂ of *C. andersoni* can be compared. Both sexes of *C. andersoni* have middorsal depressions either side of the midline, behind which the midline is recessed (Figs 33E, 34E). *C. nitida* has a thin longitudinal median dorsal ridge the length of the carapace and shows no indication of middorsal depressions (Hale, 1944a:110). The ocular lobe in *C. andersoni* has 5 lenses (Fig. 33D) compared to 11 in *C. nitida*. Both species have a fine reticulate patterning over the carapace, with black pigment spots, but the new species has a concentration of black spots on the middorsal region of the carapace and their setation differs (Table 2). The differences in the uropods alone distinguish the species. The uropods of the ♀ of *C. andersoni* lack spines compared to the ♂ (Fig. 34F-H).

Cyclaspis andersoni can be distinguished from *C. cretata* Hale and *C. strigilis* Hale, two related species found in SE QLD, by the patterning of the carapace and overall body size. *C. andersoni* is much smaller than *C. cretata* (Fig. 35A-D) and *C. strigilis*. The carapace has a more granular surface texture than *C. cretata* (Fig. 35E-H) which species has a squamose reticulate pattern-ing on the posterodorsal region (Fig. 35E,F), while *C. strigilis* has numerous oblique striae on the dorsal and lateral surfaces. *C. andersoni* differs from both of the latter species in having relatively short uropodal rami (Fig 35C,D). *Cyclaspis andersoni* was the second most abundant cumacean species taken by sledge-net at sites 10-12.

SEM photographs of cumaceans vary in quality depending on the fragility of the specimen (degree of calcification), the state of preservation and the method used for SEM preparation. Specimens shown in figs 33 and 34 were freshly caught and transferred live to liquid nitrogen, using the freeze-substitution method (Tafe, 1995). Specimens in Fig. 35 all suffered some degree of shrinkage during critical point drying.

ETYMOLOGY. For Prof Don Anderson, Sydney University.

Cyclaspis alveosculpta sp. nov.
(Figs 17A-E, 33I, 36-39, 70E-G)

MATERIAL EXAMINED. HOLOTYPE QMW20505, adult ♂, S.L. 7.5mm, PSM #61, Middle Banks, 27°12'S, 153°18'E, S. Cook, Sept. 1972, 8m, sand, 35 p.p.t. salinity, 23°C water temperature. PARATYPES QMW8536, ovig. ♀, allotype, S.L. 7.2mm, same data as holotype; QMW20506, ovig. ♀, S.L. 6.8mm, SEM mount, Horseshoe Bay, site 31, 27°30'S, 153°21'E, D. Tafe, 17 April 1990, 3 m, sand, 33 p.p.t. salinity, 25°C water temperature; QMW20507, subadult ♂, S.L. 6mm, SEM mount, same data as above; QMW20508, ovig. ♀, S.L. 7mm, PSM #11, Raby Bay, 27°30'S, 153°18'E, D. Tafe, 9 Nov. 1989, 5 m, sandy mud, 35 p.p.t. salinity, 25°C water temperature, QMW20509, adult ♂, S.L. 7.8mm, PSM #66, same data as holotype; QMW20510, 2 adults ♂, S.L. 7.4, 7.5mm, PSM #60, off Goat Island, 27°31'S, 153°22'E, D. Tafe, 17 April 1990, from guts of Apogonidae; QMW20511, subadult ♂, S.L. 7.2mm, PSM #59, Raby Bay, 27°30'S, 153°18'E, D. Tafe, 22 July 1989.

(captions for figures on previous two pages)

FIG. 35. A, VLV, left to right, *andersoni* ♂, *cretata* ♂, *andersoni* ♀, *cretata* ♀. B, DLV, left to right, *andersoni* ♂, *cretata* ♂, *andersoni* ♀, *cretata* ♀. C, C. *cretata* ♂ (top); *andersoni* ♂ (bottom) LV. D, C. *cretata* ♀ (top); *andersoni* ♀ (bottom) LV. comparison of ovigerous ♀ in lateral view. E,F, C. *cretata* sp. nov. LV. E, ♂ carapace, shows smooth texture of integument. F, ♀ carapace shows smooth texture with cretations. G,H, C. *andersoni* sp. nov., carapace, LV, shows small, even reticulate patterning of integument. G, ♂. H, ♀.

FIG. 36. *Cyclaspis alveosculpta* sp. nov. A,B, subadult ♂, LV, shows reduced transverse ridges (cf ♀) and partially developed pleopods. C, uropods of subadult ♂ VV, shows relative lengths of peduncle and rami. D, carapace of subadult ♂ LV, shows pitting of integument and posterodorsal lobes. E,F, ovigerous ♀, LV, shows relative lengths of carapace and somites. G, carapace of ovigerous ♀ LV, shows relative length and depth of carapace, and shape of posterodorsal lobes. H, Anterior carapace ALV, shows reticulate pattern of pitting and anterior position of ocular lobe.

DESCRIPTION. MALE. Integument strongly calcified with pattern of shallow pitting (Figs 17A-E, 37). Carapace 0.3 S.L., 1.75 times as long as deep, without defined anterior and posterior transverse ridges though both regions are slightly raised on lateral surfaces; median dorsal ridge pronounced throughout carapace length and smoothly convex in profile, with slight postocular depression; antennal notch a short groove; antennal tooth subacute, no antennal ridge; pseudorostral lobes tapering anteriorly and joining just below ocular lobe, join not visible in dorsal view; ocular lobe at anterior extremity of carapace; posterior extremity with small dorsal lobe, not raised above line of dorsum (Fig. 37C). Subadult ♂ ♂ with anterior and posterior transverse ridges well defined and median dorsal ridge produced posteriorly to form 2 raised, plate-like lobes (Fig. 17A-D). Pereion 0.5 as long as carapace; first pereionite concealed by second, which is partially fused with carapace, dorsal profile that of carapace; dorsal profile of remaining pereionites continuous with pleon, fourth and fifth with lateral articulation notches (Fig. 37C). Pleon robust, median dorsal line visible on last two pleonites; each pleonite with lateral articulation notches, first four pleonites subequal in length, fifth 1.6 times as long as fourth (Fig. 37C). Telsonic somite shorter than pleonite 5 and longer than 4, with posterodorsal projection (Fig. 37A,D). First antenna 3-segmented with terminal segmented flagellum. All pereiopods 7-segmented. Pereiopod 1 with carpus reaching beyond level of antennal tooth; length of basis subequal to rest of appendage, with 20-30 stout
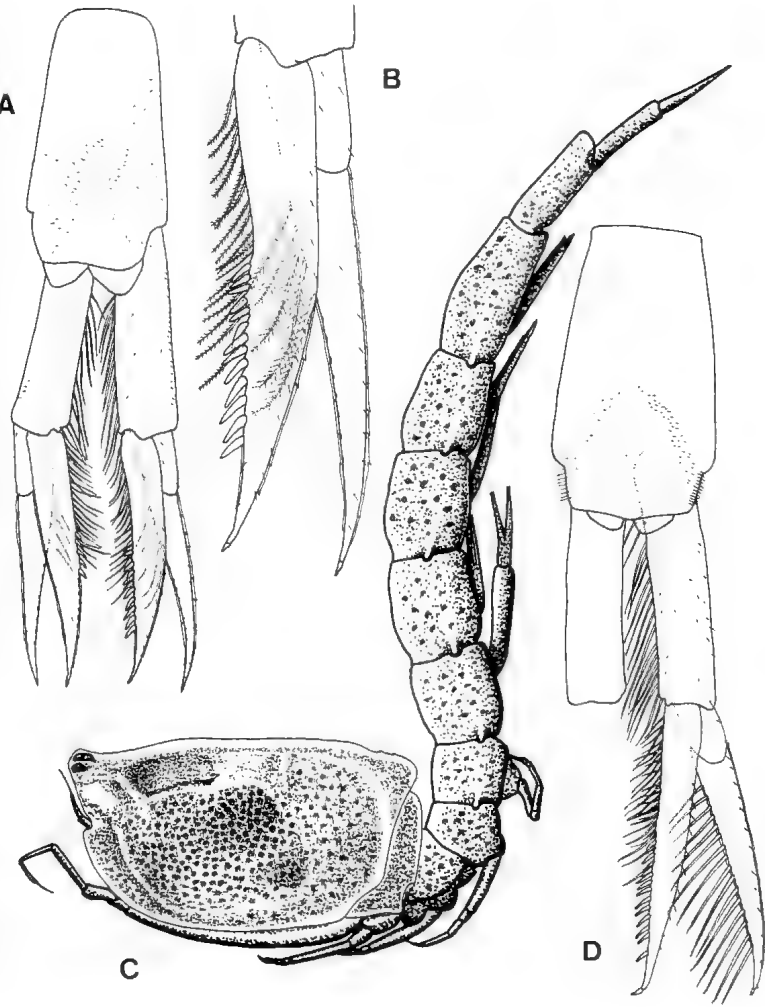
FIG. 37. *Cyclaspis alveosculpta* sp. nov. ♂. A,B, paratype ♂ (removed from gut of *Leiognathus moretoniensis* Ogilby). A, uropods and telsonic somite, DV (some inner marginal spines and setae missing). B, rami of uropod, DV. C,D, holotype ♂. C, LV. D, uropod and telsonic somite, DV.

spine-like setae on proximomedial bulge, 2 plumose distal setae and numerous fine lateral setae; ischium 0.8 times length of merus; merus 0.5 times as long as carpus; carpus 0.9 times length of propodus, with 2 fine medial setae; propodus with 2 distomedial and 4 short medial setae; dactylus 0.85 times length of propodus, with 2 slender spine-like setae and 1 fine seta terminally, 1 spine-like seta and 1 fine seta subterminally and 5 setae along medial margin; exopod well-developed, enlarged proximal segment with 3-4 short setae distolaterally and 8 short distal segments, each with 2 long setae (Fig. 38A). Second pereiopod with basis 0.75 times
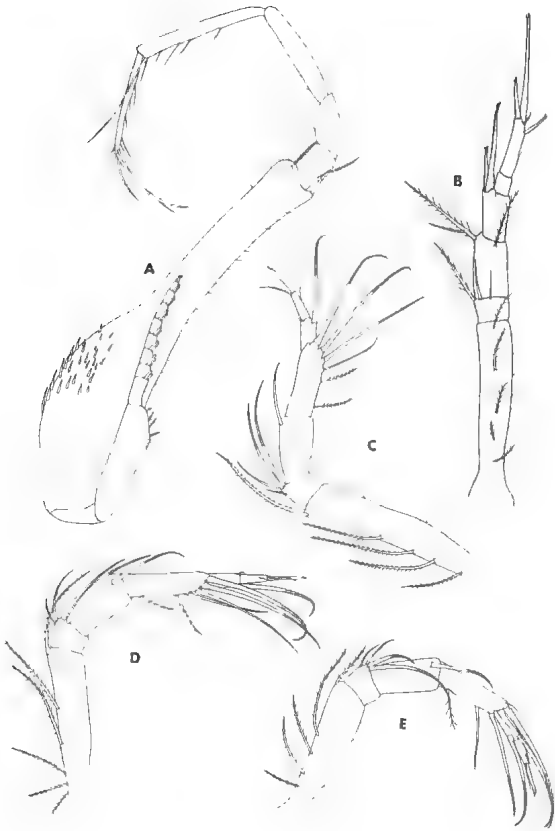
FIG. 38. *Cyclaspis alveosculpta* sp. nov. holotype ♂,
A, pereiopod 1. B, pereiopod 2. C, pereiopod 3. D,
pereiopod 4. E, pereiopod 5.

combined length of remaining segments, with 4
plumose setae laterally and 1 distolaterally; is-
chium 0.3 times length of merus, with 3 setae
distomedially; merus as long as combined length
of carpus and propodus, with 1 plumose seta
distomedially and 1 distolaterally; carpus twice
as long as propodus, with 2 strong spine-like setae
and rounded process distally; dactylus 3 times
length of propodus, with 2 terminal spine-like
setae (one at least 1.7 times longer than itself),
one subterminal spine-like seta and one subter-
minal seta (Fig. 38B). Pereiopods 3-5 with merus
longer than ischium, carpus longer than merus,
propodus longer than dactylus and terminal
spine-like seta longer than dactylus; basis with
4-6 plumose setae medially; ischium with 4 setae
distomedially; merus with seta distomedially;
carpus with 2-3 setae laterally and 3 spine- like
setae distolaterally; propodus with spine-like seta
and minute seta distally; dactylus with terminal
spine-like seta longer than itself, terminal seta

and subterminal seta; some spine-like setae have
rows of fine spinules distally (Fig. 38C- E).
Pereiopod 3 with basis 0.8 times length of
remaining segments combined; ischium 0.4 times
length of merus which is 0.8 times length of
carpus; propodus 1.2 times length of dactylus
(Fig. 38C). Pereiopod 4 with basis 0.7 times
length of remaining segments combined; ischium
0.35 times length of merus which is 0.8 times
length of carpus; propodus 1.2 times length of
dactylus (Fig. 38D). Pereiopod 5 with basis 0.65
times length of remaining segments combined;
ischium 0.35 times length of merus which is 0.9
times length of carpus; propodus 1.2 times length
of dactylus (Fig. 38E). Peduncle of uropod 0.8
times length of telsonic somite, with plumose
setae lining whole inner margin (15-22 setae in
fully mature adult); endopod 1.2 times length of
peduncle, subequal to length of exopod, with
17-30 plumose setae (2 rows) and 10-15 short
spine-like setae on inner margin, apex channelled
and slightly curved inwards, with subterminal
constriction; exopod with 12-16 plumose setae on
inner margin, apex channelled and slightly
curved inwards, with subterminal constriction.
Fine scattered setae on telsonic somite, peduncle
and rami (Fig. 37). Subadult ♂ uropod with
shorter peduncle with fewer setae and endopod
with shorter setae and spine-like setae (Fig. 36C,
39A).

OVIGEROUS FEMALE. Integument strongly cal-
cified with pattern of shallow pitting, as in ♂ (Fig.
36E-H). Carapace length 0.32 S.L. as long as
deep including marsupium, with strong anterior
and posterior transverse ridges; in profile median
dorsal ridge is slightly convex with postocular
depression and raised areas in regions of
transverse ridges; median dorsal ridge is
produced posteriorly to form notched, plate-like
lobe; antennal notch a short groove; antennal
tooth subacute; pseudorostral lobes tapering
anteriorly and joining just below ocular lobe, join
not visible in dorsal view; ocular lobe at anterior
extremity of carapace (Fig. 36E-H). Pereion 0.5
times as long as carapace. First pereionite a nar-
row band, visible in lateral view; pereionites 1
and 2 produced ventrally to form the marsupium,
second also produced dorsally to form plate-like
lobe; pereionites 3 and 4 with lateral overlapping
lobes; fifth with lateral articulation notches and
well-developed dorsolateral carinae (Fig. 36E-
H). Pleon robust, all 5 pleonites with dorsolateral
carinae and lateral articulation notches; first 4
pleonites and telsonic somite subequal in length,

fifth pleonite 1.6 times as long as fourth (Fig. 36F). Telsonic somite projecting posteriorly over bases of uropods (Figs 36F, 39D). First antenna 3-segmented with terminal segmented flagellum, as in ♂. Pereiopods as in ♂ except: basis of first pereiopod with only 1 stout spine-like seta on reduced medial bulge, basis of exopod also has reduced bulge compared to ♂; carpus of second pereiopod has only 1 strong spine-like seta distally; ischium of pereiopods 3-5 with only 3 distal setae, carpus with only 1-2 lateral setae (Fig. 39B,C). Peduncle of uropod 0.7 times as long as telsonic somite, with 6-7 plumose setae on inner margin; endopod 1.4 times as long as peduncle, subequal in length to exopod, with row of minute scales and spine-like setae on inner margin, apex channelled with subterminal constriction; exopod with 8-9 plumose setae on inner margin, apex channelled with subterminal constriction (Fig. 39D).

Colour. Cream to fawn.

S.L. Adult ♂ 7.2-7.8mm. Adult ♀ 7.0-7.5mm.

HABITAT AND DISTRIBUTION. Most commonly over medium and coarse sand in 1-5m of water; sites 11, 12, 15, 26, 30, 31, 32 and 36.

REMARKS. *Cyclaspis alveosculpta* closely resembles *C. usitata* Hale, from NSW and S AUST. The most obvious differences relate to the ridges and tubercles of the carapace. Also the dactylus of pereiopods 1 and 2 are relatively longer in *C. alveosculpta* and the ♂ has many more spine-like setae on the basis of the first pereiopod. Hale (1932:550; 1944a:123) only described and figured the ♀ of *C. usitata* though he later suggested (Hale, 1948:40) it to be the ♀ of *C. mjobergi*, described by Zimmer (1921) from ♂♂ only. It is obvious that the posterior transverse ridge and posterior dorsomedial tubercle of the adult ♀ of *C. usitata* are poorly developed compared those of *C. alveosculpta*. The posterior median dorsal ridge of the carapace is raised in the adult ♂ of *C. mjobergi* but not in *C. alveosculpta*. The dactylus of pereiopod 1 is less than 2/3 as long as the propodus in *C. usitata* and *C. mjobergi* but at least 2/3 as long in *C. alveosculpta*.

Cyclaspis alveosculpta superficially resembles *C. munda* Hale from southern NSW, but differs in having spine-like setae on the basis of pereiopod 1 and a very long terminal spine-like seta on pereiopod 2. Roccatagliata (1989) described *C. sculptilis* from Brazil, which resembles *C. alveosculpta*, but the location and
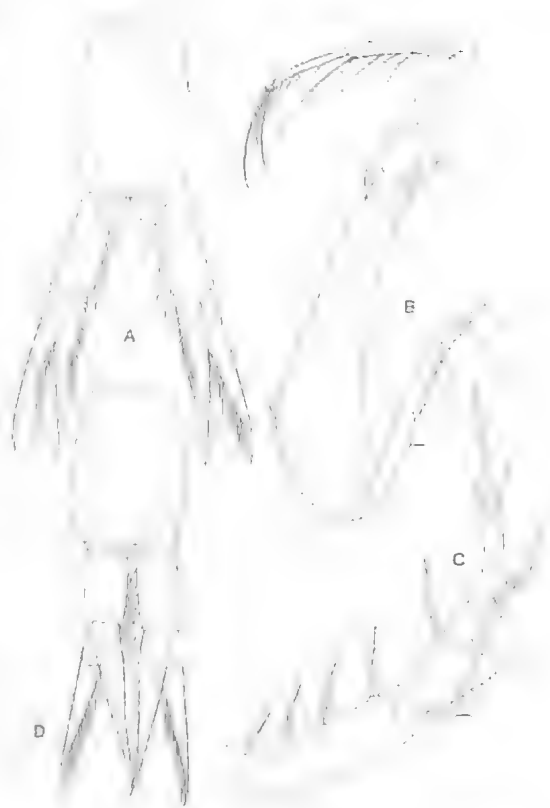
FIG. 39. *Cyclaspis alveosculpta* sp. nov. A, uropods and telsonic somite of subadult ♂, DV. B-D, paratype ovig. ♀. B, pereiopod 1. C, pereiopod 2. D, uropods and telsonic somite, DV.

definition of the posterior transverse ridges on the carapace are different.

♂ and ♀ of *C. alveosculpta* were recorded in the same area, both strongly calcified with reticulate pitting of the carapace. The carapace of the subadult ♂ has similar sculpture to the adult ♀ (Fig. 70E-G), but loses it during the last stage of development (cf. *C. ornosculpta*, Fig. 27). All adults and subadults have 2 dorsal depressions, behind the anterior transverse ridge of the carapace on either side of the median ridge (Figs 33I, 70E,G).

8 adult ♂♂ of *C. alveosculpta* were taken from gut contents of fish (*Leiognathus moretoniensis*, Apogonidae) trawled (17 April 1990) between sites 30 and 31, depth 5-15 m, on sand (S.L. fish 2-7cm). Some setae and spine-like setae have been broken off the uropodal rami (Fig. 37A,B) during the digestive process.
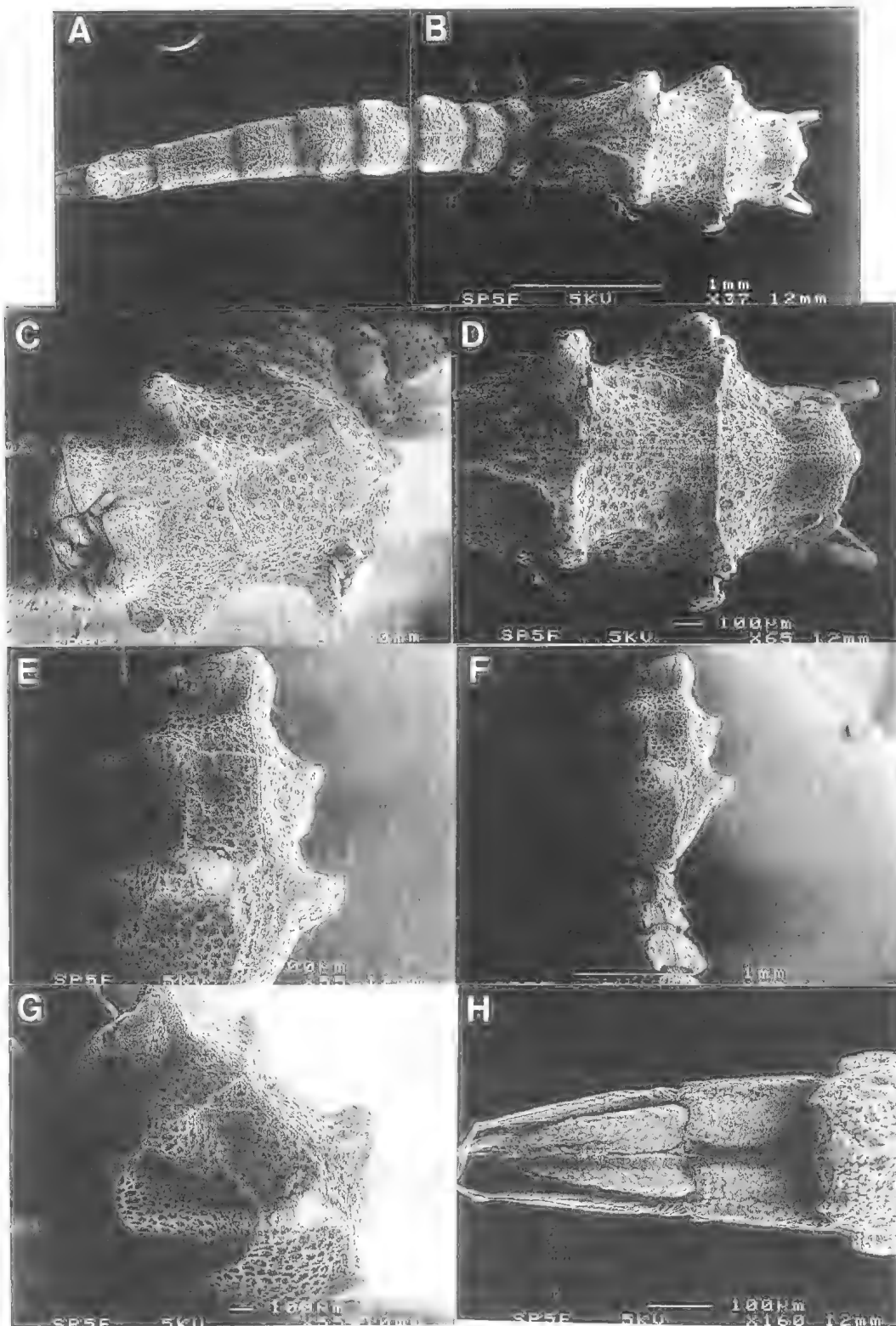
ETYMOLOGY. Latin *alveus*, pit, and *exsculpta* species group.

Cyclaspis chaunosculpta sp. nov.
(Figs 40-43)

MATERIAL EXAMINED. HOLOTYPE QMW20512, adult ♂, S.L. 10.32mm, PSM #65, Middle Banks, 27°12'S, 153°18'E, S. Cook, Sept. 1972, 8m, sand, 35 p.p.t. salinity, 23°C water temperature. PARATYPES QMW20513, ovig. ♀, allotype, S.L. 9.5mm, PSM #63, same data as holotype; QMW20514, subadult ♂, S.L. 5.2mm, SEM mount, Horseshoe Bay, site 31, 27°30'S, 153°21'E, D. Tafe, 17 April 1990, 2-3 m, sand, 33 p.p.t. salinity, 25°C water temperature. QMW8536, 3 adult ♀ ♀, S.L. 9.0-9.7mm, same data as holotype.

DESCRIPTION. MALE. Integument strongly calcified with pattern of pitting which resembles the porous structure of a sponge (Fig. 41A). Carapace 0.3 S.L. depth 0.55 times length, with poorly defined anterior and posterior transverse ridges; profile of median dorsal ridge may be slightly raised in vicinity of both transverse ridges, with shallow post-ocular depression and small posterior lobe; antennal notch a short groove; antennal tooth subacute, no antennal ridge; pseudorostral lobes tapering anteriorly and joining just below ocular lobe, join not visible in dorsal view; ocular lobe at anterior extremity of carapace (Fig. 41A). Pereion 0.65 as long as carapace; pereionite 1 concealed; pereionite 2 without dorsal lobe; pereionites 3-5 with dorsolateral carinae, tufts of setae on posterodorsal margins and dorsal profile continuous with that of pleon; third and fourth with posterolateral overlapping lobes and fifth with lateral articulation notch (Fig. 41A). Pleon robust; each pleonite with lateral articulation notches, first 4 pleonites with dorsolateral carinae and subequal in length, fifth 1.45 times as long as fourth (Fig. 41A). Telsonic somite 0.66 times length of fifth pleonite and subequal to fourth, with swollen posterodorsal projection (Fig. 41A). First antenna 3-segmented with terminal segmented flagellum. All perciopods 7-segmented. Perciopod 1 with carpus reaching beyond level of antennal tooth; basis

FIG. 41. *Cyclaspis chaunosculpta* sp. nov. type specimens. A, holotype ♂, LV. B, allotype ovig. ♀, LV.

1.1 times rest of appendage, with 20-25 stout spine-like setae on pronounced proximomedial bulge, 2 plumose distal setae and rounded distal lobe which extends at least 1/3 length of ischium; ischium 0.6 times length of merus, which is 0.6 times length of carpus; carpus 0.8 times length of propodus; propodus with 3 distomedial and 5 short medial setae; dactylus 0.55 times length of propodus, with 2 slender spine-like setae and 1 fine seta terminally, 1 spine-like seta and 3 fine seta subterminally and 3 setae along medial margin; exopod well developed, proximal segment with distal bulge bearing 3-4 short plumose setae,

FIG. 40. *Cyclaspis chaunosculpta* sp. nov. subadult ♂. A,B, whole mount DV, shows relative lengths of carapace and somites. C, carapace ALV, shows anterior position of ocular lobe and shape of antennal notch. D, carapace DV, shows maximum width in region of anterior transverse ridge, integument strongly calcified with pattern of pitting (resembles porous structure of sponge). E, carapace PLV, shows structure of posterior transverse ridge. F, carapace and Pereion PLV, shows dorsolateral projections of pereion. G, carapace DLV, shows median dorsal ridge and anterior and posterior transverse ridges. H, Uropod DV, shows relative lengths of peduncle and rami.
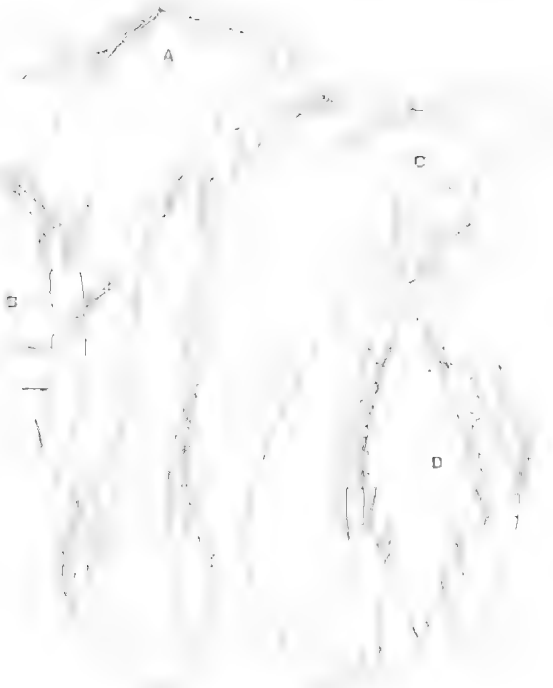
FIG. 42. *Cyclaspis chaunosculpta* sp. nov., A,B, holotype adult ♂. A, pereiopod 1. B, pereiopod 2. C,D, allotype, ovig. ♀. C, pereiopod 1. D, pereiopod 2.

8 short distal segments, each with two long setae (Figs 41A, 42A). Pereiopod 2 same as *C. alveosculpta* except ischium has 2 setae distomedially, dactylus is 2.5 times length of propodus and main dactylar spine-like seta is 1.4 times dactylus (Fig. 42B). Pereiopods 3-5 same as *C. alveosculpta* except basis has 3-5 plumose setae medially and dactylar spine-like seta is 0.9 times length of dactylus. Uropod same as *C. alveosculpta* except peduncle of uropod 0.7 times length of telsonic somite, with 16- 18 setae lining inner margin, endopod 1.3 times length of peduncle, with 30-40 plumose setae (2 rows) and 9-11 short spine-like setae on inner margin, apex finely channelled and incurved, with subterminal constriction; exopod with 12-14 plumose setae on inner margin, apex finely channelled and incurved (Fig. 43A-C).

OVIGEROUS FEMALE. Integument strongly calcified with pattern of deep pitting, as in ♂ (Fig. 41B). Carapace length 0.3 S.L. as deep as long including marsupium, with strong anterior and posterior transverse ridges; in profile median dorsal ridge is convex with postocular depression
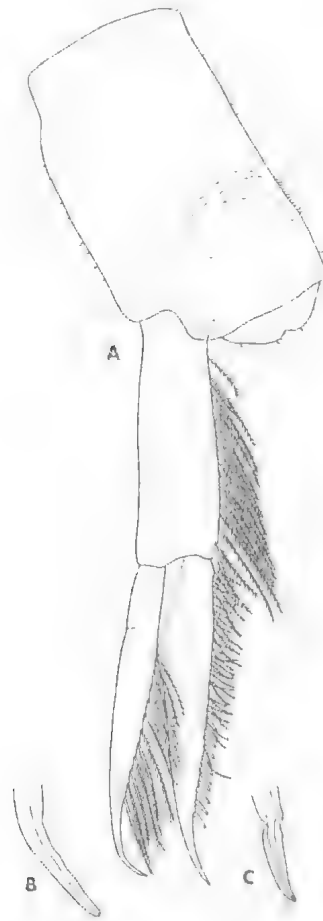
FIG. 43. *Cyclaspis chaunosculpta* sp. nov. holotype ♂. A, uropod and telsonic somite, DLV. B, distal end of exopod. C, distal end of endopod.

and raised areas in regions of transverse ridges; median dorsal ridge produced posteriorly to form rounded plate-like lobe almost as high as median dorsal hump; antennal notch, antennal tooth, pseudorostral lobes and ocular lobe as ♂ (Fig. 41B). Pereion 0.5 times as long as carapace; pereionite 1 a narrow band, visible in lateral view; pereionites 1 and 2 produced ventrally to form marsupium, second also produced dorsally to form plate-like lobe; pereionites 3-5 with dorsolateral carinae, tufts of setae on posterodorsal margins and dorsal profile continuous with that of pleon; pereionites 3 and 4 with posterolateral overlapping lobes and fifth with lateral articulation notch (Fig. 41B). Pleon robust, first 4 pleonites subequal in length, with dorsolateral carinae and lateral articulation notches; fifth pleonite 1.5 times as long as fourth; telsonic

somite projecting posteriorly over bases of uropods (Fig. 41B). First antenna 3-segmented with terminal segmented flagellum, as in ♂. Pereiopods as in ♂ except: basis of pereiopod 1 without enlarged distal lobe or spine-like setae on reduced medial bulge; carpus of pereiopod 2 has 1 strong and 1 weak spine-like seta distally; ischium of pereiopods 3-5 with 3-4 distal setae, carpus has only 1-2 lateral setae in addition to 3 distal spine-like setae (Fig. 42C,D). Uropod same as ♀ of *C. alveosculpta*, except exopod has 11-12 plumose setae on inner margin.

Colour. Cream.

S.L. Adult ♂ 10.3mm. Adult ♀ 9.0-9.7mm.

HABITAT AND DISTRIBUTION. Most common over medium and coarse sand in 1-5m of water; Middle Banks and Horseshoe Bay in Moreton Bay.

REMARKS. *Cyclaspis chaunosculpta* closely resembles *C. supersculpta* Zimmer, 1921, from NW Australia. Both species have a reticulate pattern of deep pits on the carapace and abdominal segments; however, *C. supersculpta* also has lateral bulges either side of the median dorsal ridge at the posterior extremity of the carapace. There is no sign of such bulges in juvenile or adult specimens of the new species. Close examination of the holotype of *C. supersculpta* shows that the posterolateral projection on the fifth pleonite is only about half as long as shown by Zimmer (1921, fig. 8). The size of this projection is similar to that of the new species. *C. chaunosculpta* also has more strongly developed transverse ridges than *C. supersculpta*. A comparison of ♀ juveniles of both species (Fig. 43D,E) shows these differences in carapace structure. The subadult ♂ of *C. chaunosculpta* has strong transverse ridges on the carapace, unlike the adult ♂ (Fig. 40).

C. chaunosculpta also resembles *C. aspera* Hale, which has been recorded off Coffs Harbour, NSW. The most obvious differences relate to the absence, in *C. chaunosculpta*, of spinules on carapace and somites. Also the anterior transverse ridge is wider than the posterior one in dorsal view, whereas in *C. aspera* the posterior ridge is wider (Hale, 1944a:125, figs 45-46).

C. chaunosculpta can be distinguished from *C. candida* and *C. mjobergi* by the shorter peduncle of the uropod relative to its rami. It also differs from the latter species in lacking small tubercles on the middorsal region of the carapace (Zimmer, 1921).

C. chaunosculpta can be distinguished from *C. alveosculpta* by the deeper, sponge-like pitting of the carapace, shorter dactylar spine-like seta of the second pereiopod and larger overall size.

ETYMOLOGY. Greek *chaunos*, porous, sponge-like and the *exsculpta* species group.

Cyclaspis agrenosculpta sp. nov.
(Figs 44-47)

MATERIAL EXAMINED. HOLOTYPE QMW20516, adult ♂, S.L. 10.8mm, PSM #62, Middle Banks, 27°12'S, 153°18'E, S. Cook, Sept. 1972, 8m, sand, 35 p.p.t. salinity, 23°C water temperature. PARATYPES QMW20517, ovig. ♀, allotype, S.L. 9.8mm, PSM #64, same data as holotype; QMW20518, subadult ♀, S.L. 7.4mm, SEM mount, Horseshoe Bay, site 31, 27° 30'S, 153° 21'E, D. Tafe, 10 Jan. 1993, 2-3m, sand, 34 ppt salinity, 26°C water temperature.

DESCRIPTION. MALE. Integument strongly calcified with a network of angular pits interspersed by thin calcified ridges (Fig. 45A). Carapace 0.29 S.L. 1.95 times as long as deep, with poorly defined anterior and posterior transverse ridges; profile of median dorsal ridge almost straight, with slight postocular depression and slight posterior hump; antennal notch a short groove; antennal tooth rounded, no antennal ridge; pseudorostral lobes tapering anteriorly and joining just below ocular lobe, join not visible in dorsal view; ocular lobe at anterior extremity of carapace (Fig. 45A). Pereion 0.6 as long as carapace; pereionite 1 fully concealed; pereionite 2 forming a collar behind carapace with dorsal lobe as high as dorsum of carapace; pereionites 3-5 with dorsolateral carinae, tufts of setae on posterodorsal margins and dorsal profile continuous with that of pleon; third and fourth with posterolateral overlapping lobes and fifth with lateral articulation notch and raised dorsum (Fig. 45A). Pleon very robust and calcified; each pleonite with lateral articulation notches and dorsolateral carinae, first 4 subequal in length, fifth 1.6 times as long as fourth (Fig. 45A). Telsonic somite 0.66 times length of fifth pleonite and subequal to fourth, with small mid-dorsal hump and posterodorsal projection (Fig. 45A). First antenna 3-segmented with terminal segmented flagellum; first segment somewhat geniculate. All pereiopods 7-segmented. First pereiopod with carpus reaching beyond level of antennal tooth; length of basis 1.4 times rest of appendage, with 17-19 spine-like setae and small protrusion on pronounced proximomedial bulge, 2 plumose distal setae and rounded distal lobe extending 1/4
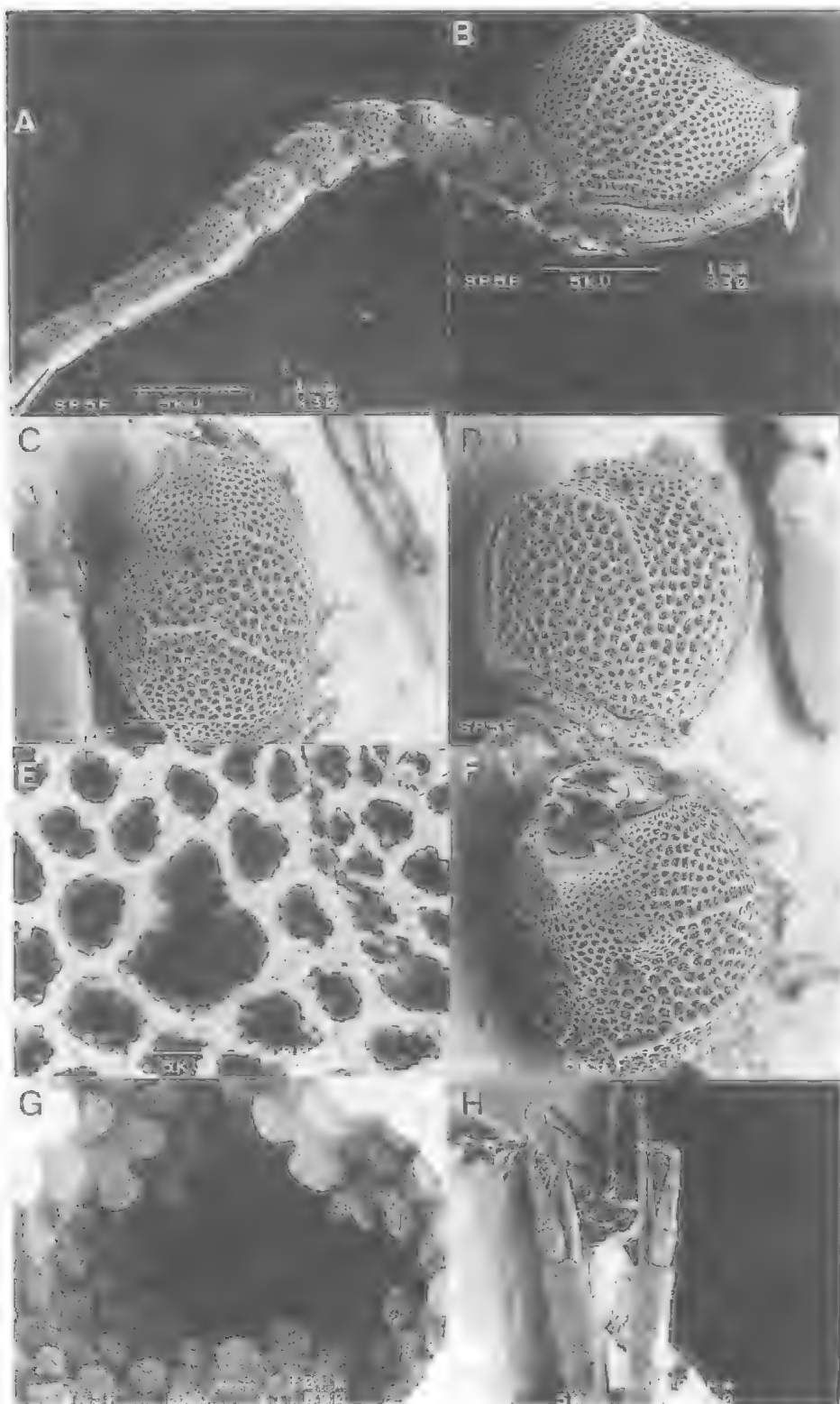
length of ischium; ischium 0.8 times length of merus, which is 0.55 times length of carpus; carpus 0.9 times length of propodus; propodus with 2 slender spine-like setae and 2 setae distomedially; dactylus 0.65 times length of propodus, with 2 slender spine-like setae and 1 fine seta terminally, 1 spine-like seta and 3 fine seta subterminally and 1 seta along medial margin; exopod well-developed, proximal segment with distal bulge bearing 5-6 short plumose setae, 8 short distal segments, each with 2 long setae (Fig. 46A). Pereiopod 2 same as *C. alveosculpta* except ischium has 2 distal setae, smaller of the two carpal spine-like setae reaches distal end of dactylus, dactylus is 2.3 times length of propodus and main dactylar spine-like seta is 1.1 times dactylus (Fig. 46B). Pereiopods 3-5 same as *C. alveosculpta* except basis has 3-7 plumose setae medially, carpus has 1 lateral seta in addition to 3 distal spine-like setae and dactylar spine-like seta is 0.75- 0.85 times length of dactylus. Peduncle of uropod 1.2 times length of telsonic somite (Fig. 45A), with plumose setae lining whole inner margin (26-30 setae in fully mature adult); endopod 0.9 times length of peduncle or exopod, with 25-30 plumose setae (2 rows) and 18 short spine-like setae on inner margin, apex bluntly pointed with subterminal constriction; exopod with 18-20 plumose setae on inner margin, apex channelled, slightly curved inwards (Fig. 47A).

OVIGEROUS FEMALE. Integument strongly calcified with a network of angular pits interspersed by thin calcified ridges, as in ♂ (Fig. 45B). Carapace length 0.3 S.L. almost as deep as long including marsupium, with strong anterior and posterior transverse ridges; in profile median dorsal ridge is slightly concave between transverse ridges and slightly convex behind posterior transverse ridge, with postocular depression and small raised lobe at posterior extremity; antennal notch a short groove; antennal tooth subacute, no antennal ridge; pseudorostral lobes and ocular lobe as in ♂ (Fig. 45B). Pereion 0.6 times as long as carapace; pereionite 1 a narrow band, visible in lateral view; pereionites 1 and 2 produced

FIG. 45. *Cyclaspis agrenosculpta* sp. nov. types. A, holotype ♂, LV. B, allotype ovig. ♀, LV.

ventrally to form the marsupium, second also produced dorsally to form plate-like lobe almost as high as preceding lobe; fifth with lateral articulation notches and welldeveloped dorsolateral carinae (Fig. 45B). Pleon heavily calcified but slender, all 5 pleonites with dorsolateral carinae; first 4 pleonites subequal in length, with lateral articulation notches; fifth pleonite 1.6 times as long as fourth (Fig. 45B). Telsonic somite 0.66 times length of pleonite 5 and subequal to fourth, with small middorsal hump and posterodorsal projection, as in ♂ (Fig. 45B). First antenna 3-segmented with terminal

FIG. 44. *Cyclaspis agrenosculpta* sp. nov. subadult ♀. A,B, whole mount LV, shows relative lengths of carapace and somites. C, carapace DLV, shows structure of anterior and posterior transverse ridges, aperture located behind anterior ridge. D, carapace PLV, shows recessed median dorsal ridge between posterior transverse ridge and posterior of carapace. E, Structure of carapace DV, shows dorsal aperture and network of calcified pits interspersed by thin chitinised ridges. F, carapace ADV, shows ocular lobe at anterior extremity and profile of posterior transverse ridge. G, Detail of dorsal aperture DV, shows aperture lined with numerous plate-like lobes. H, uropods VV, shows relative lengths of peduncle and rami.
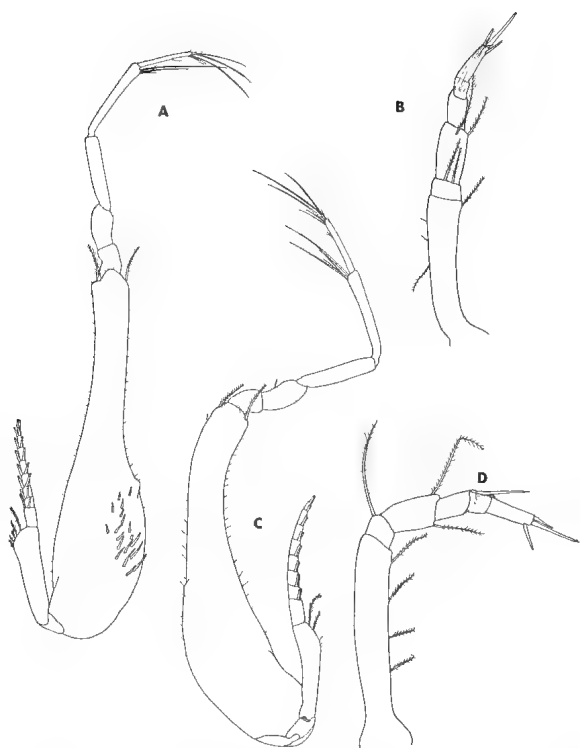
FIG. 46. *Cyclaspis agrenosculpta* sp. nov., A,B, holotype ♂. A, pereiopod 1. B, pereiopod 2. C-D, allotype ovig. ♀. C, pereiopod 1. D, pereiopod 2.

segmented flagellum, as in ♂. Pereiopods as in ♂ except: basis of first pereiopod without enlarged distal lobe or spine-like setae on reduced medial bulge, though protrusion is present on bulge; carpus of pereiopod 2 has 1 strong and 1 weak spine-like seta distally; pereiopods 3-5 with basis with 4-8 medial setae, carpus with 2-3 lateral setae and dactylar spine-like seta 0.83-0.93 times length of dactylus (Fig. 46C,D). Peduncle of uropod 1.1 times as long as telsonic somite, with 7-9 plumose setae on inner margin; endopod sub-equal in length to peduncle and 0.9 times length of exopod, with a single spine-like seta on middle of inner margin, apex bluntly pointed; exopod with 16-17 plumose setae on inner margin, apex channelled and slightly curved inwards (Fig. 47B).

Colour. Cream.

S.L. Adult ♂ 10.8mm. Adult ♀ 9.8mm.

HABITAT AND DISTRIBUTION. Most common over medium and coarse sand in 1-10m of water; from Middle Banks and Horseshoe Bay, Moreton Bay; uncommon on the western but common on the eastern side of Moreton Bay.
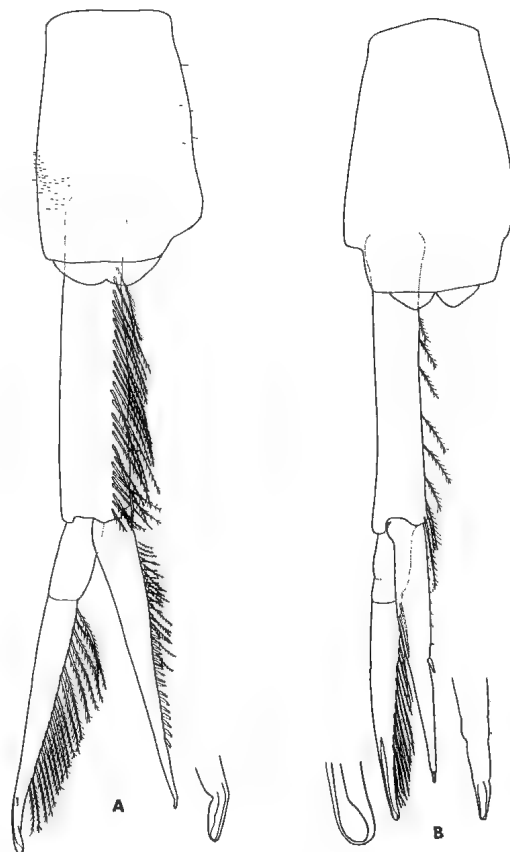
FIG. 47. *Cyclaspis agrenosculpta* sp. nov., A, uropod and telsonic somite of holotype ♂, DV, and distal end of endopod. B, uropod and telsonic somite of allotype ovig. ♀, DV, and distal ends of both rami.

REMARKS. *C. agrenosculpta* resembles *C. australis* Sars (1887:12, pl. 1, figs 1-20) from VIC and *C. tribulis* Hale (1928:34, figs 3,4) and *C. mawsonae* Hale (1944a:119) from S AUST. However, the new species is distinguished from all 3 by the pattern of deep, rectangular pits on the carapace. Stephenson et al. (1978:208, 1980:259; Bacescu, 1988:69 recorded *C. agrenosculpta* ♀♀ as *C. tribulis*. amd ♂♂ as *C. mawsonae* (Stephenson et al., 1978:210; Bacescu, 1988:61). *C. tribulis* and *C. mawsonae* are not known in QLD contrary to Bacescu (1988). Two depressions are located in the dorsal surface of the carapace of *C. agrenosculpta*, roughly in the same positions as for *C. alveosculpta* (Fig. 44C-G). The subadult ♀ of *C. agrenosculpta* closely resembles the adult except for the transverse ridges of the carapace, which are not as well

developed (Fig. 44A,B). The uropod of the subadult ♀ is basically the same as in the adult except for the slightly shorter peduncle and smaller inner marginal spine-like seta of the endopod.

Cyclaspis agrenosculpta most closely resembles *C. chaunosculpta* sp. nov., taken from the same area. They can be readily distinguished by the sculpture pattern of the carapace and the relative peduncle length of the uropod.

Cyclaspis agrenosculpta can be distinguished from *C. candida* and *C. mjobergi* by the height and shape of the second pereionite. It also differs from the latter species in lacking small tubercles on the mid-dorsal region of the carapace (Zimmer, 1921).

ETYMOLOGY. Greek *agrenon*, net, and the *exsculpta* species group.

Cyclaspis daviei sp. nov.
(Figs 48-50)

MATERIAL EXAMINED. HOLOTYPE QMW20521, ovig. ♀, S.L. 3.0mm, PSM #19, Horseshoe Bay, site 31, 27°30'S, 153°21'E, D. Tafe, 4 Feb. 1993, 2-3m, sand, 34 *p.p.t.* salinity, 26°C water temperature. QMW20522, ovig. ♀, S.L. 2.6mm, in 70% ethanol, same data as above; QMW20523, ovig. ♀, S.L. 2.5mm, in 70% ethanol, same data as above.

DESCRIPTION. OVIGEROUS FEMALE. Integument thin, lightly calcified, with small, even reticulate patterning (Fig. 48A). Carapace 0.33 S.L. with mild median dorsal ridge on anterior 1/2 and median dorsal recess on posterior 1/2; curvature of carapace is smooth, without lateral ridges; carapace 0.65 as wide as long, lateral margins slightly rounded in dorsal view. Antennal notch a short, shallow groove; antennal tooth subacute, no antennal ridge. Pseudorostral lobes wide, joining just anterior to ocular lobe which is as wide as long, rounded, with 11 lenses (Fig. 48A). Pereion 0.5 times length of carapace; pereionite
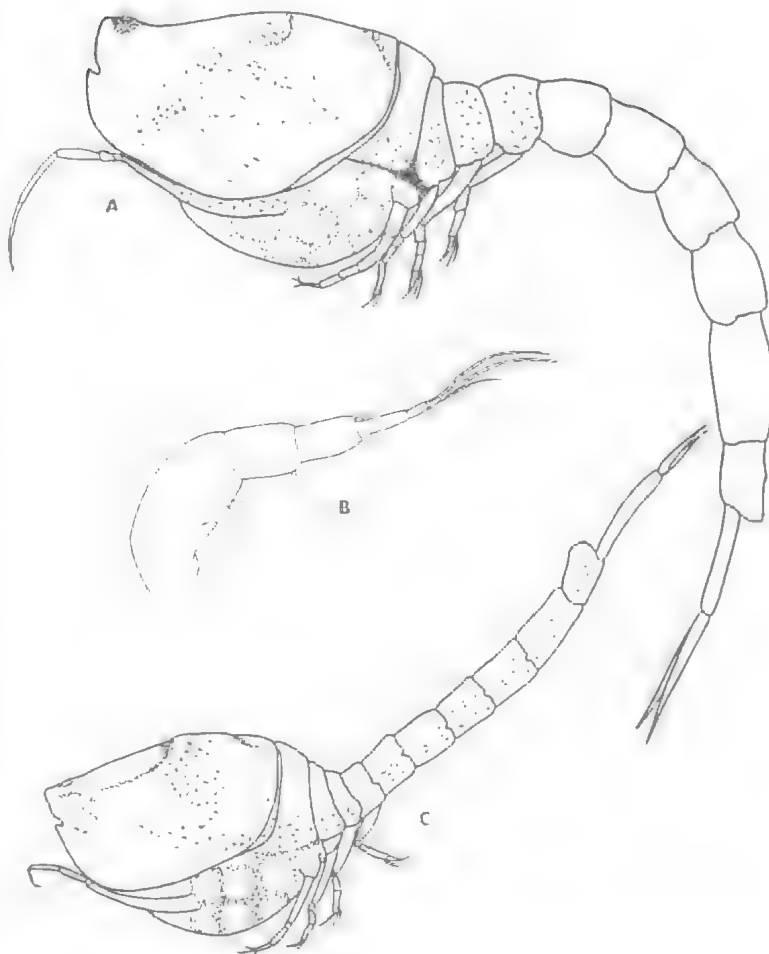
FIG. 48. A,B, *Cyclaspis daviei* sp. nov. paratype ovig. ♀. A, LV. B, first antenna. C, *Cyclaspis andersoni* sp. nov. paratype ovig. ♀, LV.

1 fully concealed by second, which forms a narrow collar posterior to carapace; shorter than each of remaining 3 pereionites which are overlapping (Fig. 48A). Pleon robust, no dorsal or lateral ridges; first 4 pleonites subequal in length, fifth pleonite 1.5 times as long as fourth (Fig. 48A). Telsonic somite shorter than fourth pleonite, with posterodorsal projection. First antenna 3-segmented with terminal segmented flagellum, first segment somewhat geniculate, longer than second and third segments combined; second segment longer than third, with 3 small setae distomedially; third segment with 2 small setae distolaterally and 1 fine seta distomedially; first segment of flagellum 2.5 times as long as second, which bears 2 aesthetascs and 2 fine setae distally (Fig. 48B). All pereiopods 7-segmented, with

FIG. 49. *Cyclaspis daviei* sp. nov. holotype ♀. A, pereiopod 1. B, pereiopod 2. C, pereiopod 3. D, pereiopod 4. E, pereiopod 5.

terminal spine-like seta longer than dactylus, except for first pereiopod (Fig. 49). Pereiopod 1 with carpus reaching beyond level of antennal tooth; length of basis 0.8 times rest of appendage; ischium 0.6 times length of merus which is 0.7 times length of carpus and with small distal process; carpus 0.7 times length of propodus which has 2 small distal setae; dactylus 0.7 times length of propodus with 2 slender terminal spine-like setae, 1 almost as long as itself, and 2 terminal setae (Fig. 49A). Pereiopod 2 with basis subequal in length to that of remaining segments combined, with rows of small setae along medial and distal margins; ischium 0.4 times length of merus, with plumose seta distomedially; merus 1.4 times length of carpus, with plumose seta distomedially and spine-like seta distolaterally; carpus 1.3 times length of propodus, with spine-like seta distomedially and spine-like seta distolaterally; propodus 0.5 times length of dactylus which is slender with 2 terminal spine-like setae, the longer one 1.4 times longer than itself, 2 small

terminal seta and 1 subterminal spine-like seta (Fig. 49B). Pereiopods 3-5 with merus twice as long as ischium and propodus at least 1.6 times as long as dactylus; basis with seta distomedially; ischium with 2 setae distomedially; merus with seta distomedially; carpus with 1-2 spine-like setae distolaterally, small seta distomedially and small seta proximomedially; propodus with spine-like seta and minute seta distally; dactylus with terminal spine-like seta, terminal seta and subterminal seta (Fig. 49C-E). Pereiopod 3 with basis 0.95 times length of remaining segments combined; ischium 0.5 times length of merus which is 0.75 times length of carpus; propodus 1.6 times length of dactylus (Fig. 49C). Pereiopod 4 with basis 0.7 times length of remaining segments combined; ischium 0.5 times length of merus which is 0.9 times length of carpus; propodus 1.7 times length of dactylus (Fig. 49D). Pereiopod 5 with basis 0.6 times length of remaining segments combined; ischium 0.5 times length of merus which is 0.7 times length of carpus; propodus 1.6 times length of dactylus (Fig. 49E). Peduncle of uropod 1.2 times length of telsonic somite, without plumose setae on inner margin; endopod 1.1 times as long as

FIG. 50. *Cyclaspis daviei* sp. nov. holotype ♀. A, uropods and telsonic somite, DV. B, rami of uropod, DV.

peduncle and 0.95 times as long as exopod, with 10-11 short spine-like setae on proximal 2/3 of inner margin and 4-5 short setae on dorsal surface, apex pointed, with 2 minute subterminal spine-like setae; exopod with 5 plumose setae on proximal 1/2 of inner margin and 3-4 short setae on dorsal surface, apex pointed, with 2 minute subterminal spine-like setae (Fig. 50).

Colour. White, translucent with many black chromatophores on carapace and abdomen.

S.L. Adult ♀ 3.0mm.

HABITAT AND DISTRIBUTION. Most common over fine sand in 1-5m of water; from sites 12 and 31 in Moreton Bay.

REMARKS. *C. daviei* most closely resembles *C. andersoni* but can easily be distinguished by the peduncle of the uropod, which is shorter than the rami. Also the dactylus on pereiopod 2 is longer, the setation of the ischium of pereiopods 3-5 is different, as is the setation of the uropodal rami, and there are no indentations on the middorsal region of the carapace.

ETYMOLOGY. For Peter Davie, Queensland Museum.

Cyclaspis sallai sp. nov.
(Figs 51-53)

MATERIAL EXAMINED. HOLOTYPE QMW20524, adult ♂, S.L. 5.2mm, PSM #49, Pumicestone Passage, site 12, 26°49'S, 153°8'E, J. Greenwood, 24 April 1990, 2m, coarse sand, 30.8 ppt salinity, 18.7°C water temperature. PARATYPE QMW20525, ovig. ♀, allotype, S.L. 4.5mm, PSM #50, same data as holotype.

DESCRIPTION. MALE. Integument smooth and calcified, with minute scattered spine-like setae
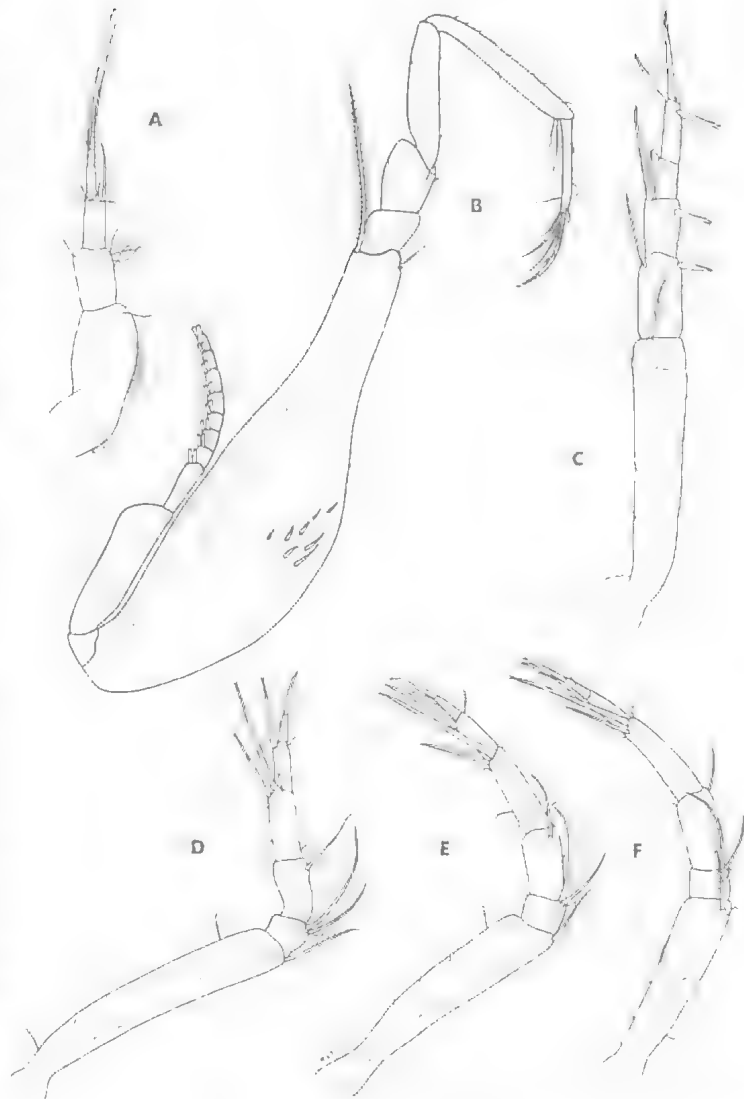
FIG. 51. *Cyclaspis sallai* sp. nov. holotype ♂. A, first antenna. B, pereiopod 1, C, pereiopod 2. D, pereiopod 3. E, pereiopod 4. F, pereiopod 5.

on surface. Carapace resembles that of *Cyclaspis cooki* except ocular lobe has 10 lenses, 4 central and 6 outer. Pereion 0.5 same as in *C. cooki*. Pleon robust and same as in *C. cooki* except fifth pleonite 1.4 times as long as fourth. First antenna 3-segmented with terminal segmented flagellum; first segment somewhat geniculate, longer than second and third segments combined, with rows of fine setae on anterior (medial) surface; second segment 1.2 times third segment, with 4 fine setae distomedially and 2 setae distolaterally; third seg-

FIG. 52. *Cyclaspis sallai* sp. nov. holotype ♂. A, uropods and telsonic somite, DV. B, rami of uropod, DV.

ment with 3 slender setae distomedially and 2 distolaterally; first segment of flagellum twice as long as second, which has two aesthetascs and 2 fine setae distally (Fig. 51A). All pereiopods 7-segmented, with terminal spine-like setae at least as long as dactylus; some spine-like setae have rows of fine spinules distally (Fig. 51B-F). Pereiopod 1 with basis 1.1 times length of remaining segments combined, with simple seta distomedially, plumose seta disto-laterally, and clump of 8 stout spine-like setae on bulge of medial region; ischium 0.65 times length of merus which is 0.5 times length of carpus; carpus 0.8 times length of propodus, which is 1.7 times length of dactylus, with 1 medial and 2 distal setae; dactylus with 2 slender terminal spine-like setae, one as long as itself, 2 terminal setae and stout subterminal seta; exopod well developed.

wide proximal segment, 8 shorter distal segments, each with two long setae (Fig. 51B). Pereiopod 2 with basis 0.8 times length of remaining segments combined, with small distomedial and distolateral setae; ischium 0.4 times length of merus, with plumose seta distomedially; merus 1.4 times length of carpus, with plumose seta distomedially and stout spine-like seta distolaterally; carpus 1.4 times length of propodus, with 2 spine-like setae distomedially and spine-like seta distolaterally; propodus 0.6 times length of dactylus, with fine seta distomedially; dactylus has 2 terminal spine-like setae, the longer one 1.4 times longer than itself, 2 small terminal setae and 1 subterminal spine-like seta; all segments have fine scattered setae (Fig. 51C). Pereiopods 3-5 with merus longer than ischium, carpus as long as combined length of propodus and dactylus, the longer of which is propodus; basis with 1 seta distomedially and fine scattered setae on surface; ischium with 2 long and 1 minute setae distomedially; merus with seta distomedially; carpus with 2 spine-like setae and 1 fine seta distolaterally; propodus with spine-like seta and minute seta distally; dactylus with terminal spine-like seta, terminal seta and subterminal seta (Fig. 51D-F). Pereiopod 3 with basis 1.1 times length of remaining segments combined; ischium 0.5 times length of merus which is 0.8 times length of carpus; propodus 1.7 times length of dactylus (Fig. 51D). Pereiopod 4 with basis 0.95 times length of remaining segments combined; ischium 0.5 times length of merus which is 0.8 times length of carpus; propodus 1.8 times length of dactylus (Fig. 51E). Pereiopod 5 with basis 0.6 times length of remaining segments combined; ischium 0.4 times length of merus which is 0.8 times length of carpus; propodus 1.8 times length of dactylus (Fig. 51F). Peduncle of uropod 1.1 times as long as telsonic somite, lined with 21-22 plumose setae on inner margin (15-16 long, 6-7 short); endopod 1.1 times as long as peduncle, subequal in length to exopod, with 6-7 slender spine-like setae and 10-11 stout spine-like setae on proximal 2/3 of inner margin, the most distal stout spine-like seta being well spaced from the others; apex pointed, without spine-like setae or mucrones; exopod with 6 plumose setae on proximal 2/3 of inner margin, apex pointed, without spine-like setae or mucrones; fine scattered setae on surfaces of telsonic somite, peduncle and rami (Fig. 52A,B).

OVIGEROUS FEMALE. Integument smooth, lightly calcified, with minute scattered setae on carapace

and pleon, as in ♂. Carapace length 0.35 S.L. without distinct dorsal or lateral carinae; width 0.48 times length in dorsal view; antennal tooth subacute and extending to anterior extremity of carapace; ocular lobe and pseudorostral lobes as in ♂. Pereion 0.4 times as long as carapace. Pereionite 1 fully concealed by second, both produced ventrally to form the marsupium; pereionites with dorsal ridge, dorsolateral margin of fifth with articulation notch. Pleon robust, all five pleonites with dorsal ridge and lateral articulation notches; first 4 pleonites and telsonic somite subequal in length, fifth pleonite 1.5 times as long as fourth. Telsonic somite projecting posteriorly over bases of uropods. First antenna 3-segmented with terminal segmented flagellum; first segment geniculate, as in ♂. Pereiopods as in ♂ except: pereiopod 1 has smaller spine-like setae on medial region of basis and 6 reduced terminal segments (rather than 7) on the exopod; carpus of pereiopod 2 has 1 (rather than 2) spine-like setae distomedially (Fig. 53A). Peduncle of uropod 1.3 times as long as telsonic somite, without plumose setae on inner margin; endopod at least as long as peduncle and subequal in length to exopod, with 2 minute setae and 6 stout spine-like setae on proximal two-thirds of inner margin, the most distal stout spine-like seta being well spaced from the others; apex pointed, without spine-like setae or mucrones; exopod with 5 plumose setae on proximal two-thirds of inner margin, apex pointed, without spine-like setae or mucrones; fine scattered setae on surfaces of telsonic somite, peduncle and rami, as in ♂ (Fig. 53B,C).

Colour. White to fawn with small black chromatophores speckled on carapace and abdomen.

S.L. Adult ♂ 5.2mm. Adult ♀ 4.5mm.

HABITAT AND DISTRIBUTION. Most common over medium and coarse sand in 1-4m of water; from sites 11 and 12 in Moreton Bay. Both sexes are common in Pumicestone Passage, Moreton Bay.

REMARKS. *C. sallai* most closely resembles type specimens of *C. cooki*; however, *C. sallai* is 50% larger, more robust, with a covering of fine setae on the pereiopods and uropods. Pereiopod 1 also has spine-like setae on the medial bulge of the basis and a relatively short dactylus, pereiopod 2 has a strong distal spine-like seta on the merus and a relatively short dactylus, and the uropod has rami at least as long as the peduncle.
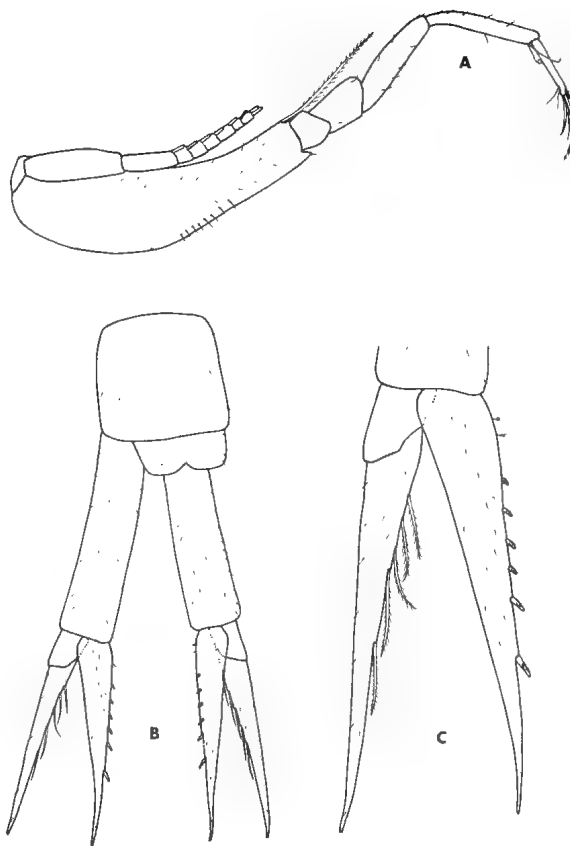
FIG. 53. *Cyclaspis sallai* sp. nov. allotype ovig. ♀. A, pereiopods 1. B, uropods and telsonic somite, DV. C, rami of uropod, DV.

Cyclaspis sallai resembles *C. juxta* Hale from S AUST, but the rami of the uropod are much longer relative to the peduncle, and the setation of the uropod is different. The basis of pereiopod 1 has an angular projection on the distomedial margin which may appear rounded or pointed, depending on the orientation of the appendage.

ETYMOLOGY. For Michael Salla, who assisted in the field.

Cyclaspis sp. nov. 1
(Fig. 54A,B)

MATERIAL EXAMINED. QMW20515, ovig. ♀, S.L. 1.9mm, in 70% ethanol, off Dunwich, site 28, 27°29'S, 153°22'E, D. Tafe, 20 May 1989, 4 m, sand, 34 p.p.t. salinity, 24°C water temperature; uncommon.

REMARKS. Further specimens are required in order to describe the species. *Cyclaspis* sp. nov.

FIG. 54. *Cyclaspis* species. A-B, *Cyclaspis* sp. nov. 1, gravid ♀. A, LV. B, uropods, telsonic somite and pleonite 5, DV. C-E, *Cyclaspis* sp. nov. 2. C, ovig. ♀, LV. D, subadult ♀, LV. E, uropod of ovig. ♀, DV.

1 superficially resembles *C. strigilis* Hale and *C. fulgida* Hale, respectively from Fraser Island, Qld, and Cronulla, NSW. However, it is easily distinguished by terminal spine-like setae on the endopod and exopod of the uropod. Also the carapace does not exhibit the reticulate pattern of sooty black chromatophores, typical of *C. fulgida*, or the numerous oblique striae, typical of *C. strigilis*.

The dorsal line of the carapace of the new species is almost straight in lateral view. The ocular lobe is slightly raised, similar to that of *C. stocki* (Bacescu, 1990), and the pseudorostrum is curiously upturned as 2 pointed filaments (Fig.

54A). Pleonite 5 is 1.5 times the length of pleonite 6 (telsonic somite) and subequal in length to the peduncle of the uropod; the peduncle has 6 short medial spine-like setae and the endopod has 6 medial and 3 terminal spine-like setae. The endopod is subequal in length to the exopod and distinctly shorter than the peduncle (Fig. 54B).

Cyclaspis sp. nov. 2
(Fig. 54C-E)

MATERIAL EXAMINED. QMW20519, ovig. ♀, S.L. 2.7mm, in 70% ethanol, off Coochiemudlo Island, site 34, 27°32'S, 153°20'E, D. Tafe, 17 June 1990, 4m, sand, 35 p.p.t. salinity, 18°C water temperature. QMW20520, subadult ♀, S.L. 2.6mm, same data as above; uncommon.

REMARKS. Further specimens are required to describe this species. *Cyclaspis* sp. nov. 2 resembles *C. gibba* Hale (1944a:75, figs 4-5) from Jibbon, NSW. Both species are of similar length (2.6-3.0mm), both have a smooth finely reticulate, ovoid shaped carapace with delicate median dorsal ridge, large antennal notch and subacute antennal tooth. However, adult and subadult ♀♀ of *C. gibba* have more prominent ocular lobes in lateral view than *C.* sp. nov. 2. Setation of the uropods is similar in both species but the exopods are longer, relative to the endopods, in *C.* sp. nov. 2 (Fig. 35E).

Eocuma Marcusen, 1894

Cyclaspis Kossman, 1880:88.
Eocuma Marcusen, 1894:170. Day, 1978a:168.

DIAGNOSIS. Cuticle strongly calcified and brittle, carapace with lateral horns, at least in ♀. First pereionite and sometimes second firmly united with carapace. Basis of first pereiopod prolonged distomedially. Second pereiopod with basis and ischium fused. Uropods with peduncle much shorter than rami; inner ramus 1-segmented. Genus includes 23 species worldwide, most of which inhabit warm, shallow (5-50m) waters. Only *E. agrion* has been recorded from Australian waters.

FIG. 55. *Eocuma agrion* Zimmer ♂. A,B, whole mount LV, shows relative lengths of carapace and somites. C, carapace LV, shows curved dorsal profile of carapace. D, anterior carapace LV, shows unusual pseudorostral region. E, carapace DV, shows reticulate pattern of shallow pits and well developed lateral horns. F, lateral horn on carapace LV, shows scale-like surface texture of horn. G, anterior carapace DV, shows wide ocular lobe and pseudorostral projection. H, uropod LV, shows very short peduncle relative to rami.
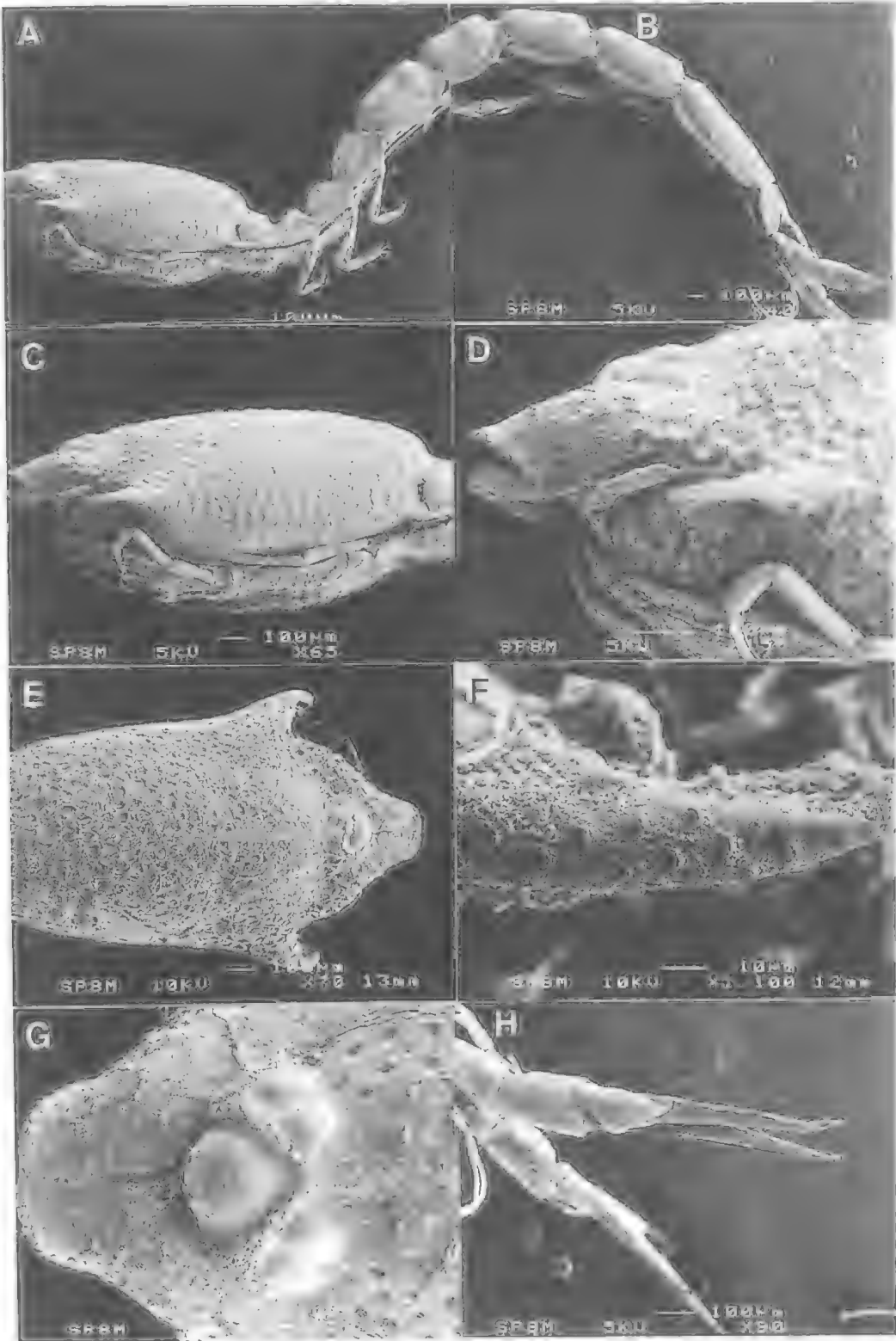
Eocuma agrion Zimmer, 1914
(Figs 55, 56A-C)

Eocuma agrion Zimmer, 1914:176, figs 1-2, Hale, 1944b:229, figs 3-4, Hale, 1949a:109, Stephenson et al., 1978:208.

MATERIAL EXAMINED. QMW20526, adult ♂, S.L. 6.1mm, SEM mount, Horseshoe Bay, site 31, 27°30'S, 153°21'E, D. Tafe, 11 Oct 1990, 4m, sand, 35.5 ppt salinity, 24.5°C water temperature, QMW20527, adult ♂, S.L. 6.3mm, in 70% ethanol, same data as above. QMW20528, subadult ♀, S.L. 5.9mm, SEM mount, same data as above. QMW20529, subadult ♀, S.L. 5.7mm, in 70% ethanol, same data as above.

DISTRIBUTION. Known from Central East Coast, Lower East Coast and Lower West Coast (Fig. 4). QLD: Moreton Bay (Hale, 1949a); sites 15, 26, 28, 31, and 33, Moreton Bay (herein). NSW: Cronulla (Hale, 1944b), WA: Fremantle, Herald Bight and Broadhurst Bight in Shark Bay, Onslow, Dampier Archipelago, Garden Island (Hale, 1944b, 1949a). Common in Moreton Bay. ♂♂ are taken far more commonly in light-trap samples than ♀♀.

REMARKS. Moreton Bay specimens match *E. agrion* in the very long and flexible pleon (Fig. 55A,B). Living specimens are yellowish with a reticulate pattern of pitting on the carapace (Fig. 55C,D,E). The ocular lobe is much wider than long, with 1 large anterior lens and 4 smaller posterior lenses (Figs 55G, 56A). The carapace has large lateral horns in both sexes (Figs 55F, 56A,C). The uropods are held wide apart and the rami of each are also spread (Figs 55, 56B).

Subfamily VAUNTHOMPSONIINAE Sars, 1878

DIAGNOSIS. Exopods on at least first 3 pairs of pereiopods. Always 5 pereionites exposed and endopod of uropod 2-segmented. Second antenna of ♀ often 3-segmented and in most genera third segment is distinct.

Gephyrocuma Hale, 1936

Gephyrocuma Hale, 1936b:412. Hale, 1944b:247.

DIAGNOSIS. Ocular lobe wide and not distinctly separated from frontal lobe, lenses very large. Antennal notch so widely open that no distinct incision or antennal angle is evident. Pleon reduced, at most 2/3 as long as carapace in ♂, shorter in ♀. First antenna strongly geniculate, with segments of peduncle globose. Basis of third maxillipeds without external apical lobe but with very large inner lobe. Basis of pereiopod 1 distinctly twisted, with no distal inner lobe. Exopods of pereiopods 1 and 2 well-developed, rudimentary on 3 and 4. Uropods with short peduncle and with endopod 2- segmented, the first segment much longer than the second.

REMARKS. Four species are known from Australia: *G. pala* from Gulf St. Vincent, SA; *G. repandum* from Cronulla, NSW and Careening Bay, WA; *G. simile* from Shark Bay, WA; and *G.* sp. nov. 1 from Moreton Bay.

KEY TO THE AUSTRALIAN SPECIES OF *GEPHYROCUMA*
(Adapted from Hale, 1944b)

1. Exopod of third pereiopod 1-segmented . . . 2
   Exopod of third pereiopod 2-segmented 3

2. Second endopod segment of uropod with six inner spine-like setae in ♂, none in ♀
   . . . . *repandum* Hale
   Second endopod segment of uropod with one inner spine-like seta in ♂ and ♀ . . . sp. nov. 1

3. Pleon at most barely longer than pereionites together. First segment of endopod of uropod less than twice as long as second . . . *pala* Hale
   Pleon at least half as long again as pereionites together. First segment of endopod of uropod at least 4 times as long as second . . . *simile* Hale

Gephyrocuma repandum Hale, 1944
(Figs 56D-H, 57H)

Gephyrocuma repanda Hale, 1944b:248, figs 15, 16, 17B. Hale, 1949a:110, figs 2, 3.

MATERIAL EXAMINED. QMW20530, adult ♂, S.L. 2.3mm, SEM mount, Pumicestone Passage, site 12, 26°49'S, 153°08'E, J. Greenwood, 14 Mar 1991, 2m, sand, 34.2 ppt salinity, 27.0°C water temperature, QMW20531, adult ♂, S.L. 2.2mm, in 70% ethanol, same data as above. QMW20532, adult ♀, S.L. 1.9mm,

FIG. 56. *Eocuma* and *Gephyrocuma* species. A-C, *Eocuma agrion*, ♂. A, anterior portion of carapace, DV. B, LV. C, cephalothorax, DV. D-H, *Gephyrocuma repandum*. D, type ♂, LV. E, paratype ♂ uropod, DV and Ei, terminal spines of endopod F, ovig. ♀, LV. G, ♀ uropod, DV. H, ovig. ♀ cephalothorax, DV. I-J, *Gephyrocuma similis*. I, type ♂ uropod, DV and Ii, distal segment of endopod J, type ovig. ♀ uropod, DV. (A-E, Hale, 1944b. F-J, Hale, 1949a).
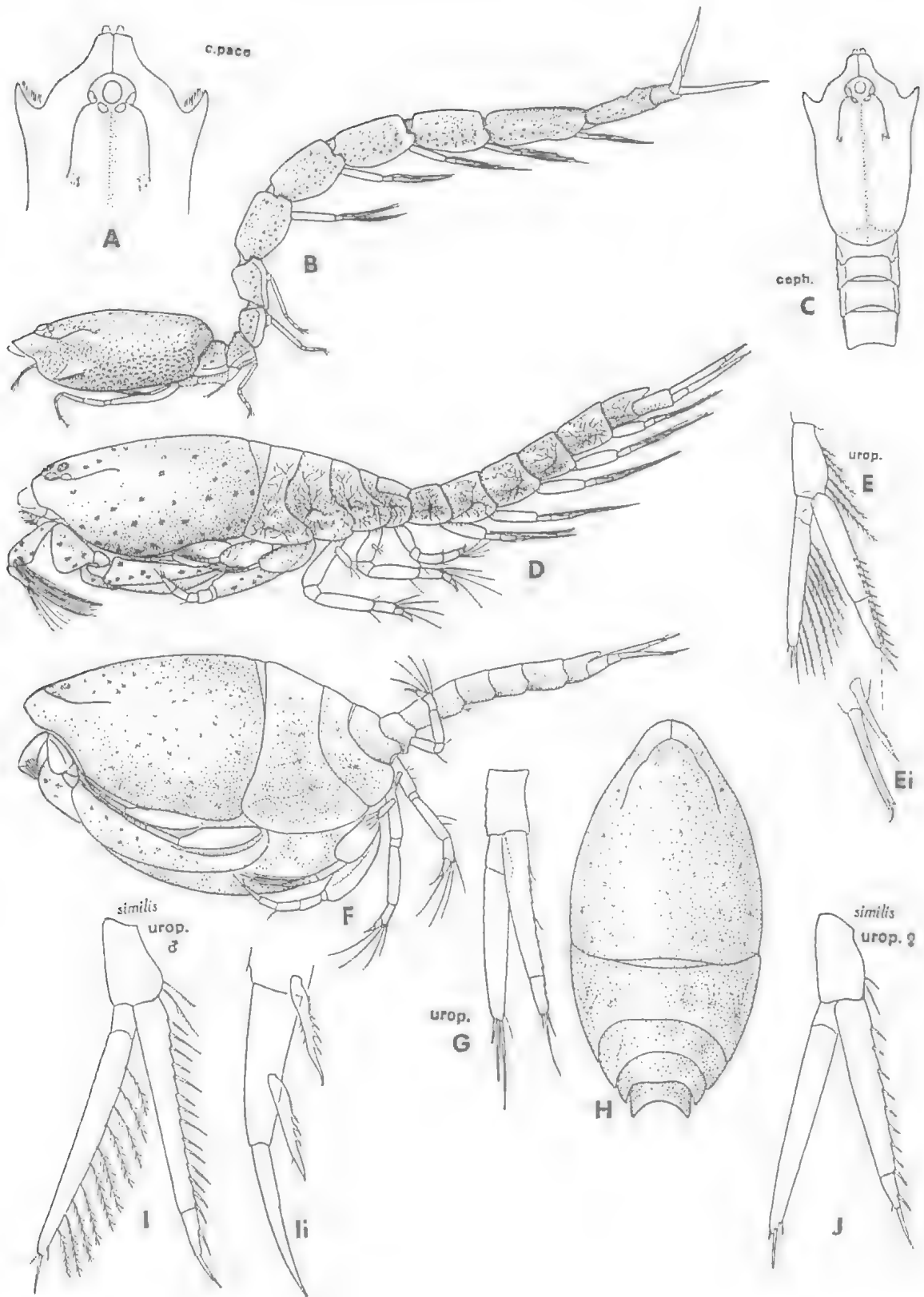
SEM mount, same data as above. QMW20533, adult ♀, S.L. 2.0mm, in 70% ethanol, same data as above.

DISTRIBUTION. Lower and Central East Coast and Lower West Coast (Fig. 4). NSW: Cronulla (Hale, 1944b). Qld: sites 6-9, 10-12 and 31 in Moreton Bay. WA: Garden Island (Hale, 1949a).

REMARKS. Moreton Bay specimens match *G. repandum* from Cronulla, NSW; cuticle thin and smooth with blackish chromatophores (Fig. 56D,F); carapace with dorsal margin evenly and slightly convex; ocular lobe much broader than long (Fig. 56D,F,H); pedigerous somites all exposed, together 2/3 as long as carapace (Fig. 56D,F); pleon more than 2/3 as long as cephalothorax (Fig. 57H); exopod of third pereiopod 1-segmented (Fig. 56D,F); ♂ uropods stout, peduncle only c.1/2 as long as exopod, with a row of long plumose setae on inner margin; endopod a little longer than exopod, segment 1 with spinules on inner margin, segment 2 with inner row of 6 stout spine-like setae and 1 terminal spine-like seta; exopod with 8-10 long plumose setae on inner margin and 3 unequal terminal spine-like setae (Fig. 36E); ♀ uropods stout, peduncle shorter than in ♂, with no long inner setae; endopod with denticles but no spine-like setae on inner margin; exopod with 1 inner seta and 3 terminal spine-like setae (Fig. 36G). *G. repandum* was taken in relatively large numbers throughout the year at sites 10, 11 and 12, in combination with *G. barbarae*. It is the most abundant cumacean recorded at site 12 in Pumicestone Passage.

Gephyrocuma sp, nov. 1
(Figs 57A-G, 70H)

MATERIAL EXAMINED. QMW20534, adult ♂, S.L. 1.8mm, SEM mount, Pumicestone Passage, site 12, 26°49'S, 153°08'E, J. Greenwood, 4 May 1990, 2m, coarse sand, 33.3 ppt salinity, 23.5°C water temperature. QMW20535, adult ♀, S.L. 1.5mm, data same as above.

REMARKS. Further specimens are required to describe the species. *Gephyrocuma* sp. nov. 1 resembles *G. repandum* Hale and *G. similis* but differs in shape of pereiopod 1, maxillipeds 3 and setation of the uropods (Fig. 57A-D,G). The merus and carpus of maxilliped 3 much more robust than in *G. repandum* and the uropods are devoid of plumose setae (Fig. 57E,G). The endopod and exopod are more robust than in *G. repandum* (Fig. 56E,G) and *G. similis* (Fig. 56I,J), the endopod of both ♂ and ♀ have 5-6 short inner spine-like setae on the first segment, 1 on the second and 1 terminal; exopod with no inner spine-like setae and 3 unequal terminal spine-like setae (Fig. 57D,G). The carapace is covered with a reticulate pattern of crescent shaped scales, between which are scattered pits with short sensory filaments (Figs 57F, 70H).

Glyphocuma Hale, 1944

Glyphocuma Hale, 1944b:268.

GENOTYPE. *Sympodomma bakeri* Hale, 1936a:397.

DIAGNOSIS. Pseudorostral lobes not extending in front of ocular lobe, which is narrow. Basis of maxilliped 3 with large external laterodistal lobe, dentate on medial edge and reaching distal end of merus. ♂ with exopods on pereiopods 1-4, those of fourth pair sometimes small. Female with exopods on pereiopods 1-3 only. First antenna with accessory flagellum 2-segmented. Second antenna of ♀ 3-segmented, with conical distal segment distinct. Mandibles elongate, with long row of spine-like setae (up to 20). Telsonic somite produced posteriorly, its apex rounded and slightly excavate.

REMARKS. This genus is close to *Sympodomma* but differs in having an exopod on the fourth pereiopod of the ♂, and in having the merus of maxilliped 3 less expanded externally. It resembles *Heterocuma* but in that genus the crest of the carapace is not incised in the ♀. Maxilliped 3 of *Glyphocuma* has the carpus widened as in *Cyclaspis*, the terminal segment of the second antenna of the ♀ is tiny, the telsonic somite is very different, and the segments of the flagellum of the ♂ second antenna are extremely short.

Glyphocuma contains 5 species, all of which

FIG. 57. A-G, *Gephyrocuma* sp. nov. 1. A, ♂, LV shows relative lengths of carapace and somites. B, ♂ LV shows relative lengths of carapace and somites. C, ♂ DV shows maximum width in anterior region of carapace, tapers posteriorly D, ♀, DV, shows maximum width in posterior region of carapace. E, ♂, VLV shows robust third maxillipeds F, ♂, DV, detail of integument of carapace showing crescent shaped scales and minute filaments. G, ♂ uropod, DV, shows robust, sparsely spinuled rami. H, *Gephyrocuma repandum* Hale ♂ VLV shows numerous setae on pereiopods and rami of uropods.
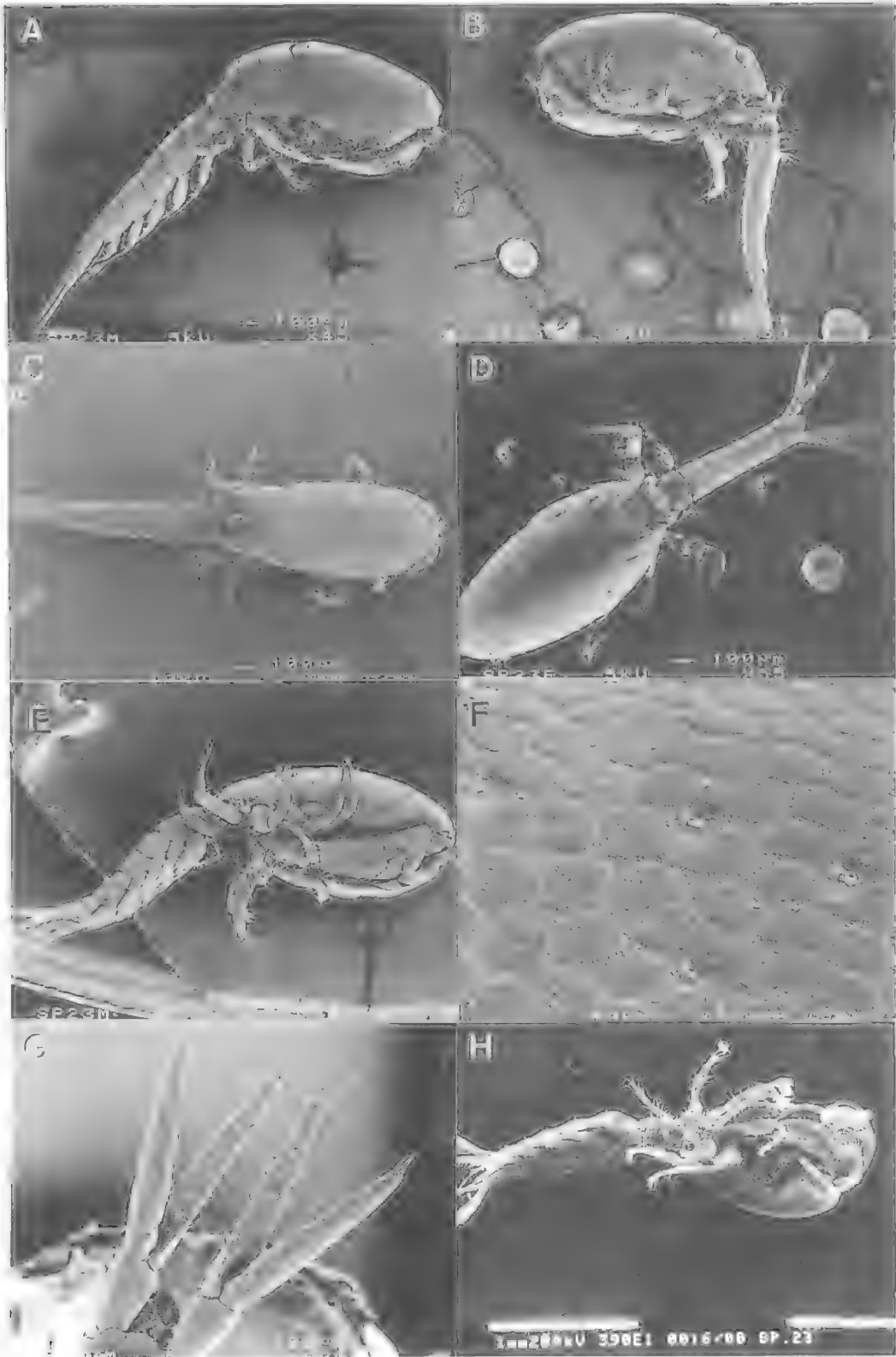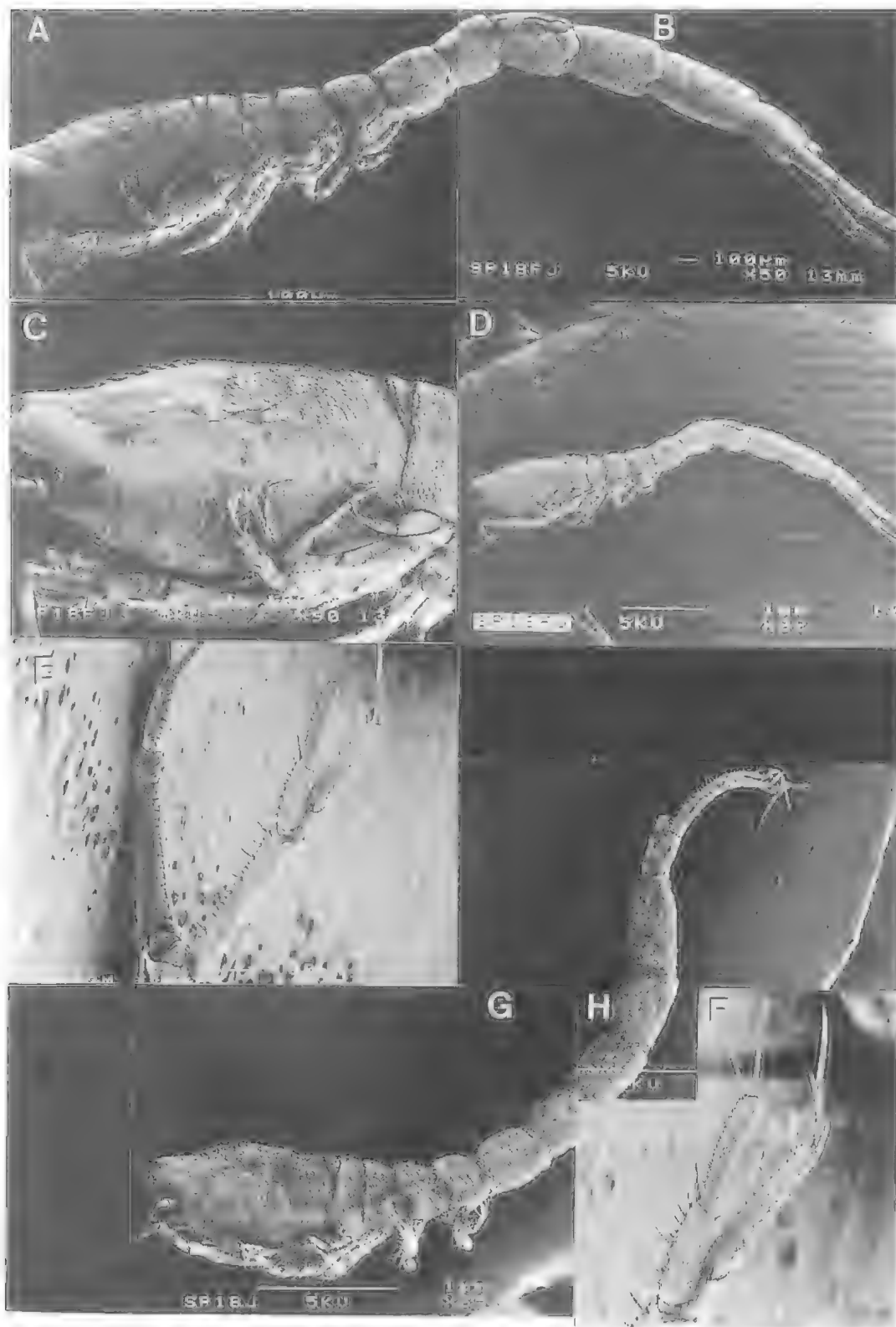
are Australian and two of which (*G. halei, G. serventyi*) have been previously recorded from Queensland.

SEXUAL DIMORPHISM. The ovigerous ♀ and immature ♂ have crest of the carapace finely or coarsely serrate, or incised with resultant angular projections, or strongly ridged. Adult ♂s have the armature of the dorsum obliterated and the antennal notch widely open. They also have the anterolateral portion of pereionite 4 developed as a lobe which may overlap pereionite 3.

KEY TO AUSTRALIAN FEMALES OF *GLYPHOCUMA*
(Adapted from Hale, 1944b)

1. Anterior half of crest of carapace cut into 6 or more small teeth 2
   Anterior half of crest of carapace smooth or with 1 or 2 incisions, but no teeth 3

2. Carapace twice as long as deep, with dorsal teeth inconspicuous; antennal notch narrow; ocular lobe projecting well beyond pseudorostral lobes and with corneal lenses not confined to anterior portion . . . . *bakeri* (Hale)
   Carapace less than twice as long as deep, with dorsal teeth large; antennal notch wide; ocular lobe not projecting beyond pseudorostral lobes and with small corneal lenses restricted to anterior portion . . . . *dentatum* Hale

3. Anterior half of crest of carapace smooth. Exopod of uropod with at least 10 plumose setae on inner margin . . *halei* Greenwood & Johnston
   Anterior half of crest of carapace with 1 or 2 incisions. Exopod of uropod with at most 6 plumose on inner margin 4

4. Carapace slender, with 2 dorsomedial incisions, the second with 2 or 3 denticles; ocular lobe narrow, more than twice as long as wide, apically rounded in dorsal view . . . . . *inaequale* Hale
   Carapace robust, with 1 dorsomedial incision and 2 or 3 denticles; ocular lobe as wide as long, apically angular in dorsal view
   . . . . *serventyi* Hale

KEY TO AUSTRALIAN MALES OF *GLYPHOCUMA*
(Adapted from Hale, 1944b)

1. Body slender, the carapace more than twice as long as deep 2

Body robust, the carapace less than twice as long as deep 4

2. Exopod of uropod without spine-like setae on lateral margin. Exopod of fourth perciopod with flagellum 2-segmented . . . . . *bakeri* Hale
   Exopod of uropod with spine-like setae on lateral margin. Exopod of fourth pereiopod with flagellum 4- or 5-segmented 3

3. Dorsal edge of carapace smooth; exopod of fourth pereiopod with flagellum 4-segmented
   . . . . *halei* Greenwood & Johnston
   Dorsal edge of carapace sinuate; exopod of fourth pereiopod with flagellum 5-segmented
   . . . . *inaequale* Hale

4. Ocular lobe narrow, more than twice as long as wide, with corneal lenses confined to anterior end which is rounded . . . . . . *dentatum* Hale
   Ocular lobe as wide as long, with corneal lenses reaching to posterior end which is angular
   . . . . *serventyi* Hale

Glyphocuma dentatum Hale, 1944
(Figs 58A-D, 59A-G)

Glyphocuma dentatum Hale, 1944b:273, Figs 33, 34.

MATERIAL EXAMINED. QMW20536, subadult ♀, S.L. 4mm, SEM mount, Horseshoe Bay, site 31, 27° 30'S, 153°21'E, D. Tafe, 7 April 1991, sand, 3m, 33.2 ppt salinity, 24.8°C water temperature; QMW20537, subadult ♂, S.L. 5.5mm, in 70% ethanol, data same as above.

DISTRIBUTION. Lower and Central East Coast (Fig. 4). NSW: Port Hacking, Ulladulla, Eden, 46-100m; on mud (Hale,1944b). Qld: sites 28, 31 and 36 in Moreton Bay.

REMARKS. Moreton Bay specimens match *G. dentatum* from Port Hacking, NSW. The degree of dentation of the dorsal edge of the carapace was found to be variable (Figs 58A-D, 59A-G). Common in parts of Moreton Bay.

Glyphocuma halei Greenwood & Johnston, 1967
(Figs 58E-F, 60)

Glyphocuma halei Greenwood & Johnston, 1967:93. figs 1-2.

MATERIAL EXAMINED. PARATYPES

FIG. 58. A-D, *Glyphocuma dentatum* ♀. A,B, LV, shows relative lengths of carapace and somites. C, carapace LV, shows 7 slender teeth on dorsal margin. D, whole mount LV, shows anterior end of carapace. E-H, *Glyphocuma halei* ♀. E, uropods DLV, shows relative lengths of peduncle and rami. F, uropod rami DLV, shows spination of rami. G,H, subadult LV, shows smooth dorsum of carapace and relative lengths of segments.
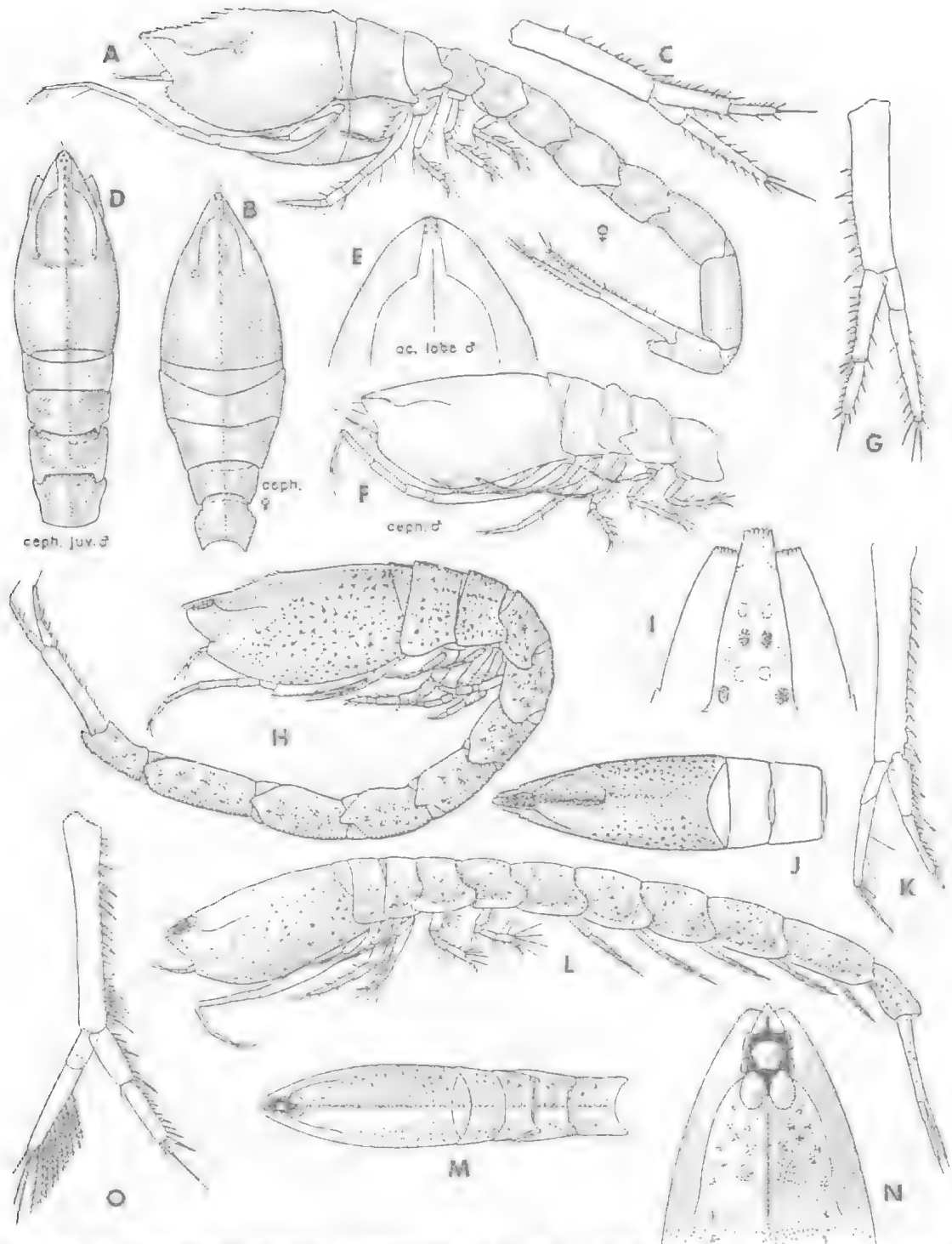
FIG. 59. A-G, *Glyphocuma dentatum*. A, holotype ovig. ♀, LV. B, ♀ cephalothorax, DV. C, paratype ♀ uropod. D, juvenile ♂ cephalothorax, DV. E, allotype ♂ ocular lobe, DV. F, allotype ♂ cephalothorax, LV. G, subadult ♂ uropod. H-O, *Glyphocuma bakeri*. H-K, type ♀. H, LV. I, ocular lobe, DV. J, cephalothorax, DV. K, uropod. L-O, ♂. L, LV. M, cephalothorax, DV. N, ocular lobe, DV. O, uropod. (A-G and L-O, Hale, 1944b. H-K, Hale, 1936a).

QMW20538, adult ♀, allotype, S.L. 10mm, in 70% ethanol, Horseshoe Bay, site 31, 27°30'S, 153°21'E, D. Tafe, 7 April 1991, sand, 3m, 33.2 ppt salinity, 24.8°C water temperature; QMW20539, subadult ♀, S.L. 5,6mm, SEM mount, off Macleay Island, site 36, 27°36'S, 153°22'E, D. Tafe, 8 Nov. 1989, sand/silt. 2m, 33.2 ppt salinity, 26.8°C water temperature; QMW20540, adult ♂, S.L. 11mm, in 70% ethanol, off Coochiemudlo Island, site 34, 27°32'S, 153°20'E, D. Tafe, 17 June 1990, sand, 5m, 34.8 ppt salinity, 18.8°C water temperature; QMW20541, subadult ♂, S.L. 8.5mm, in 70% ethanol, data same as above.

DESCRIPTION. FEMALE. Integument calcified with fine granular texture (Fig. 58G,H). Carapace length 0.25 S.L. with strong median dorsal ridge, the anterior 1/2 of which bears fine crenulations though the dorsal profile is smooth and slightly arched, sides devoid of ridges or sculpture, as in ♂; depth 0.57 times length in lateral view; antennal notch widely open; ocular lobe and pseudorostral lobes as in ♂ (Figs 58G,H, 60F). Pereion 0.86 times as long as carapace. Pereionite 1 visible only above lateral midline; pereionites without lateral ridges, posterolateral margin of pereionite 5 produced as lobe which overlaps pleonite 1, as in ♂ (Fig. 58G,H). Pleon robust, all 5 pleonites without lateral ridges or lateral articulation notches; first 4 pleonites and telsonic somite subequal in length, fifth pleonite 1.35 times as long as fourth (Fig. 58G,H). Telsonic somite projecting posteriorly over bases of uropods (Figs 58H, 60G). First antenna 3-segmented with terminal segmented flagellum; first segment geniculate, as in ♂. Pereiopods as in ♂. Peduncle of uropod 1.2 times as long as telsonic somite, with 14-16 naked spine-like setae along length of inner margin; endopod 0.75 times as long as peduncle and 0.9 times as long as exopod, with 9-11 spine-like setae on inner margin and 1 spine-like seta on
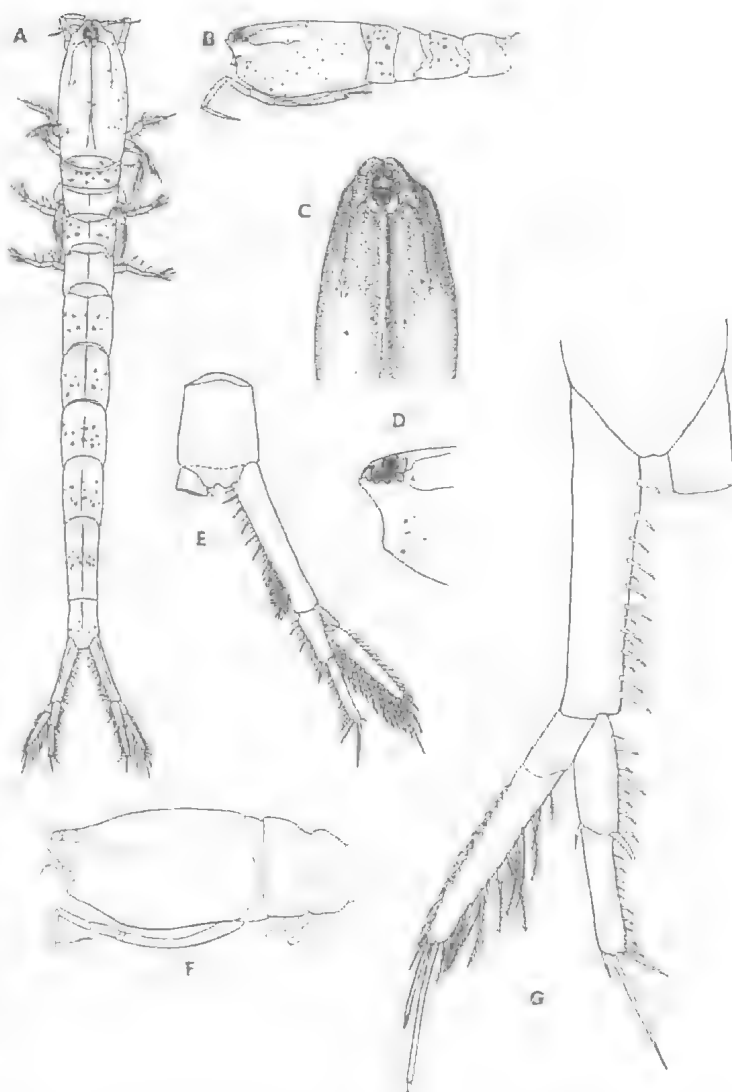
FIG. 60. *Glyphocuma halei*. A-E, ♂. A, DV. B, cephalothorax, LV. C, carapace, DV. D, anterior of carapace, LV. E, uropod and telsonic somite, DV. (All after Greenwood & Johnston, 1967). F-G, ♀. F, cephalothorax, LV. G, uropod, DV.

outer margin of proximal segment, 10-11 spine-like setae on inner margin of distal segment and 3 terminal spine-like setae, the longest of which is as long as the segment; distal segment slightly longer than proximal segment as in ♂; exopod with 11-13 plumose setae on inner margin, 12-14 spine-like setae on outer margin and 3 terminal spine-like setae, the longest of which is at least 1/2 as long as exopod; terminal spine-like setae

of endopod and exopod bear tiny mucrones at apex (Figs 58E,F, 60G).

Colour. Cream with scattered brown chromatophores on carapace and abdomen.

S.L. Adult ♂ 9-11mm. Adult ♀ 10mm.

HABITAT AND DISTRIBUTION. Most common over medium and coarse sand in 1–4m of water; from Central East Coast (Fig. 4). Qld: Waterloo Bay in Moreton Bay (Greenwood & Johnston, 1967); sites 12, 31, 34 and 36 in Moreton Bay.

REMARKS. ♂ specimens matched *G. halei* from the same region. ♀♀ have not previously been found. The adult ♀ from Moreton Bay resembles ♀s of *G. dentatum* from Port Hacking, NSW, but differs in the structure and setation of the uropods (Figs 58E,F, 59C, 60G). In ♂♂ and the adult ♀ of *G. halei* the distal endopod segment of the uropod is longer than the proximal segment (Fig. 60E,G), whereas in *G. dentatum* it is shorter (Fig. 59C,G).

G. halei also resembles *G. bakeri*, however, both sexes of *G. halei* bear at least 12 outer spine-like setae on the exopod of the uropod. The same segment in *G. bakeri* has no outer spine-like setae (Fig. 59K,O). Also, as noted by Greenwood & Johnston (1967:98), the rami of the uropod are relatively longer in *G. halei*, and the exopod of the fourth pereiopod has 4 segments in *G. halei*, 2 in *G. bakeri*. The general body shape of *G. halei* is very similar to *G. bakeri* in lateral view (Fig. 59H,L), but the carapace is not as slender in dorsal view (Fig. 59I,J,M,N).

The uropods of the *G. halei* ♀ carry terminal spine-like setae on the endopod and exopod, each of which bear distinct terminal spinules (Fig. 60G). Spinules are not present on the terminal spine-like setae of ♀ uropods of *G. dentatum* or *G. bakeri* (Fig. 37C,K).

Leptocuma Sars, 1873

Leptocuma Sars, 1873:24. Hale, 1936b: 409. Hale, 1944b:251.

DIAGNOSIS. Pseudorostral lobes extend in front of ocular lobe, not meeting; mandible robust,

with at least 9 spine-like setae; basis of the maxilliped 3 not produced distally; pereiopod 2 with brush of distal setae on the propodus and dactylus, but no spine-like setae; antenna 1 with accessory flagellum 1-segmented; telsonic somite produced posteriorly with apex angular; maxilliped 3 with ischium short and merus not as long as carpus; ocular lobe wide, moderate or large in size; second antenna of ♂ with segments of flagellum elongate; pereionite 3 of ♀ produced forward on each side to form lobe overlapping pereionite 2; anterolateral parts of pereionite 4 of ♂ similarly expanded to override pereionite 3.

REMARKS. The genotype, *L. kinbergii*, was described from the ♀, taken in the South Atlantic off South America. Only two other species have since been recorded from the Americas, *L. forsmani* Zimmer,1943 and *L. patagonicum* Roccatagliata,1993. Hale (1944b) described 2 Australian species, *L. pulleini* (QLD, NSW, SA) and *L. sheardi* (SA); ♂♂ of these 2 species have 5 pairs of pleopods and the exopod of pereiopod 4 is rudimentary, as in the ♀. Hale described *L. intermedium* (NSW), *L. nichollsi* (WA), *L. obstipum* (NSW), *L. serriferum* (NSW, WA) and *L. vicarium* (NSW) from Australia. The American species were keyed out by Roccatagliata (1993). The Australian species fall into two well defined groups.

KEY TO AUSTRALIAN SPECIES OF *LEPTOCUMA*
(Adapted from Hale, 1944b)

1. First pereiopod with a prominent simple spine-like seta on distomedial margin of basis, preceded by several shorter spine-like setae, and with a well-developed brush of setae at distal end of propodus. Setae of pereiopods 3-5 very numerous. Uropod with first segment of endopod shorter, or barely longer, than second. Over 13mm in length 2
   Pereiopod 1 with a serrate spine-like seta on distomedial margin of basis, preceded by 1 longer spine-like seta, also serrate; with sparse setae at distal end of propodus. Setae of pereiopods 3-5 not very numerous. Uropod with first segment of endopod much longer than second. Less than 8mm in length 3

FIG. 61. *Leptocuma barbatae* sp. nov. ♂. A,B, whole mount LV, shows relative lengths of carapace and somites. C, whole mount LV, shows relative lengths of telsonic somite and pleonite 5. D, whole mount DV, shows width tapering from carapace to telsonic somite. E, carapace and pereionites 1-3 DV, shows maximum width in mid-region of carapace. F, carapace and pereionites 1-3 LV, shows relative length and depth of carapace. G, uropods DV, shows relative lengths of peduncle and rami. H, Pereionites 2-3 LV, shows slender spines on anterolateral margins of pereionites 2-3.
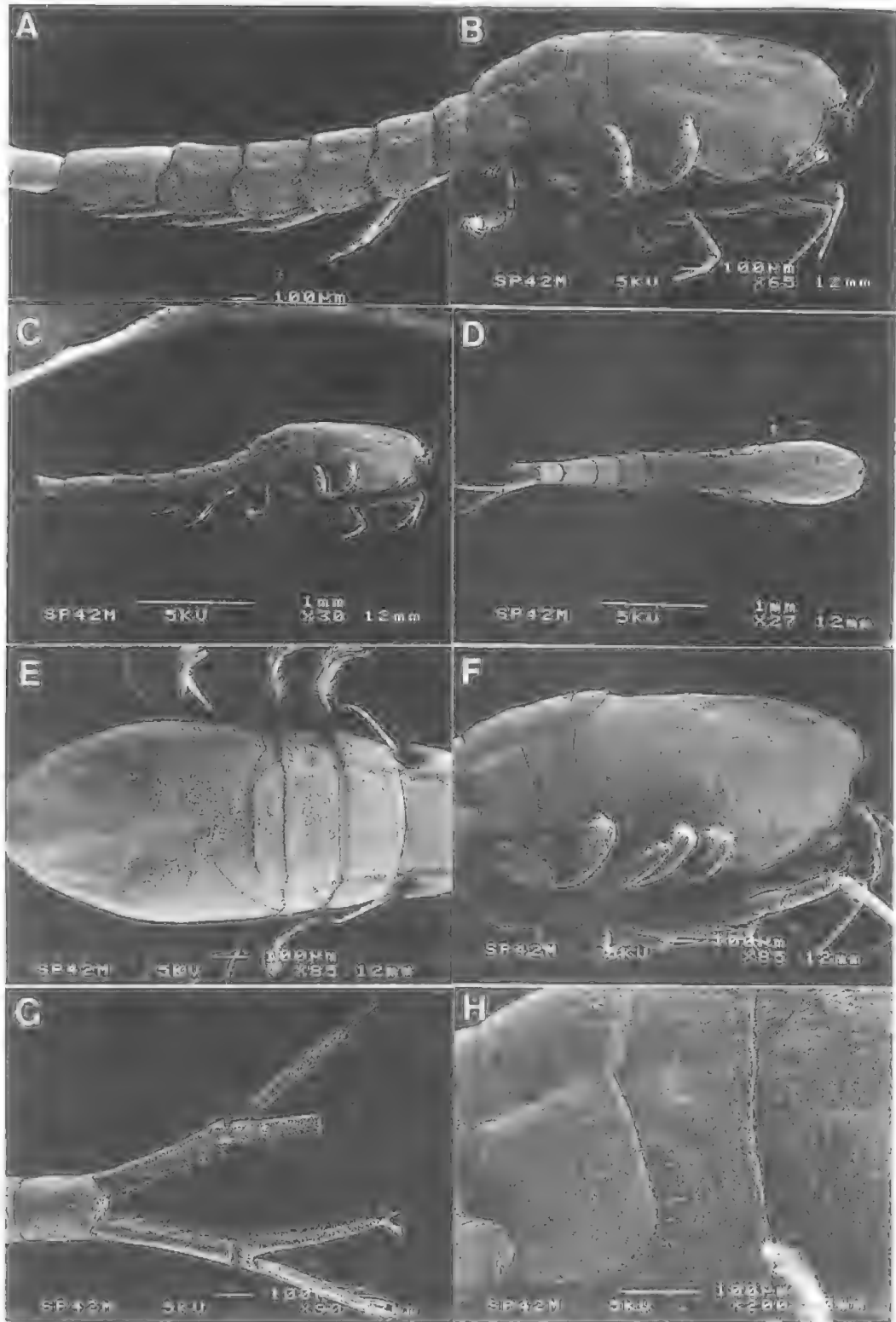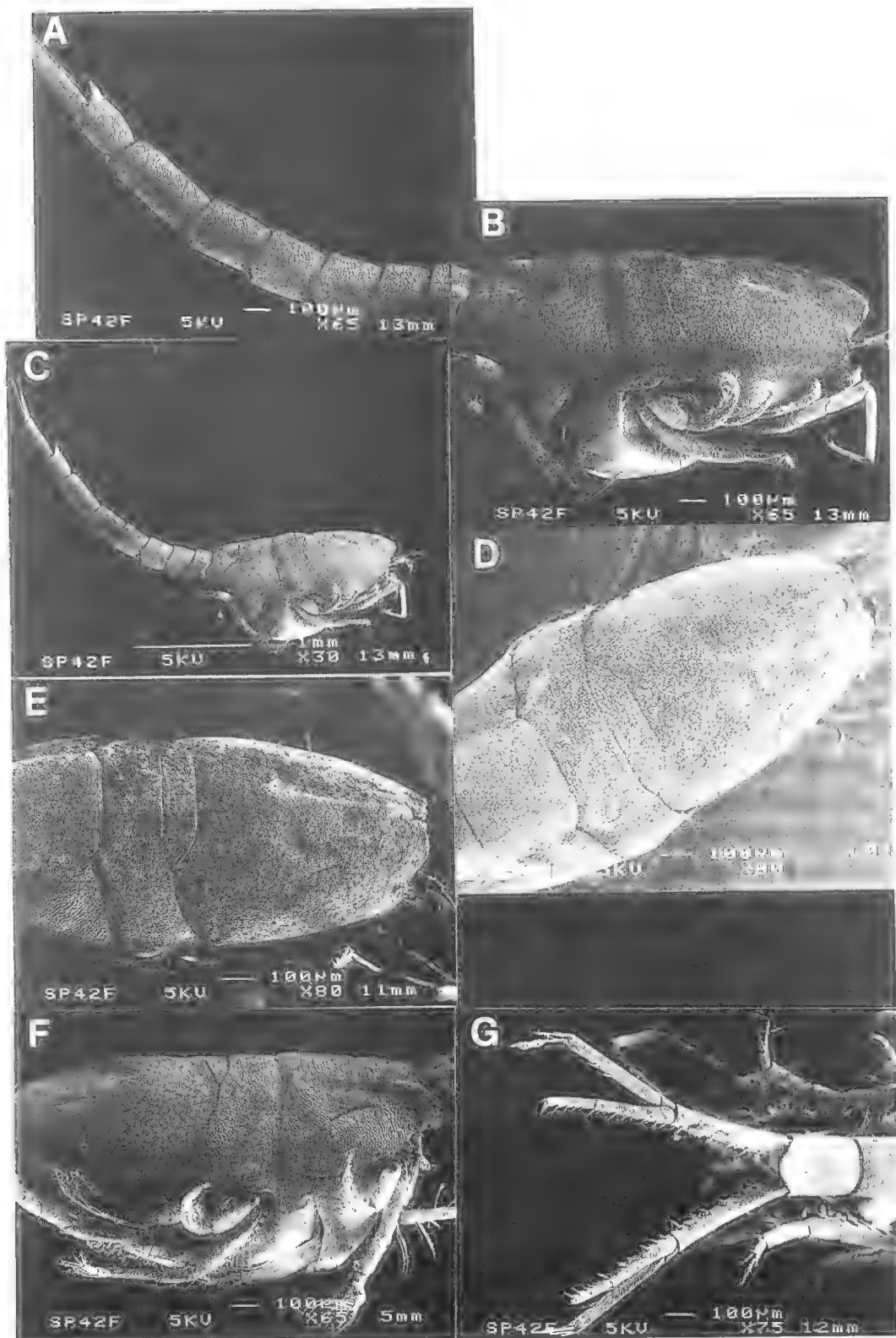
2. Second pereiopod with carpus 2/3 as long again
as merus . . . . *pulleini* Hale
Second pereiopod with carpus subequal in length
to merus . . . . *vicarium* Hale

3. Carapace with strong median dorsal ridge extend-
ing from ocular lobe almost to first pedigerous
somite 4
Carapace with at most scarcely distinguishable
median dorsal ridge 5

4. Anterolateral margins of pereionites 2 and 3 with a
row of spine-like setae. Pereiopod 1 has 2 con-
spicuous serrate spine-like setae on distomedial
margin . . . . *kennedyi* sp. nov.
Anterolateral margins of pereionites 2 and 3
without spine-like setae. First pereiopod has 4
conspicuous serrate spine-like setas on dis-
tomedial margin . . . . *nichollsi* Hale

5. Dorsal margins of pereionites undulating in lateral
view, One of the terminal spine-like setae of en-
dopod of uropod geniculate (♀) or hooked (♂).
Pleon with obvious lateral and dorsal carinae
. . . . *obstipum* Hale
Dorsal margins of pereionites smooth. Terminal
spine-like setae of endopod of uropod straight or
barely curved. Pleon smooth or with scarcely dis-
tinguishable traces of carinae 6

6. Size under 5mm. Uropod with second segment of
endopod much more than half length of first   7
Size about 7mm. Uropod with second segment of
endopod about half length of first 8

7. Anterolateral margins of second and third
pedigerous segments with row of short spine-
like setae . . . . *barbarae* sp. nov.
Anterolateral margins of second and third
pedigerous segments without spine-like setae
. . . . *serriferum* Hale

8. First pereiopod with propodus much longer than
dactylus. Second pereiopod with propodus and
dactylus subequal in length . . . *sheardi* Hale
First pereiopod with propodus scarcely longer
than dactylus. Second pereiopod with dactylus
fully 1/3 as long again as propodus
. . . . *intermedium* Hale

Leptocuma barbarae sp. nov.
(Figs 61-64)

MATERIAL EXAMINED. HOLOTYPE
QMW20542, adult ♂, S.L. 3.3mm, PSM #16, Horse-
shoe Bay, site 31, 27°30'S, 153°21'E, D. Tafe, 4 Feb.

1993, 3m, sand, 34.2 ppt salinity, 26°C water tempera-
ture. PARATYPES QMW20543, ovig. ♀, allotype,
S.L. 3.6mm, PSM #17, same data as holotype;
QMW20544, adult ♂, S.L. 3.6mm, PSM #43, Tan-
galooma, site 15, 27°11'S, 153°19'E, D. Greenwood,
14 April 1990, 8m, sand, 35.5 ppt salinity, 24°C water
temperature; QMW20545, ovig. ♀, S.L. 3.7mm, PSM
#44, same data as above; QMW20546, ovig. ♀, S.L.
3.5mm, PSM #18, same data as holotype; QMW20547,
adult ♂, S.L. 3.2mm, SEM mount, Horseshoe Bay, site
31, D. Tafe, 7 April 1991, 2m, sand, 33.2 ppt salinity,
25.5°C water temperature; QMW20548, ovig. ♀, S.L.
3.1mm, SEM mount, same data as above.

DESCRIPTION. MALE. Integument lightly cal-
cified, with fine granular texture (Fig. 61A,B).
Carapace length 0.26 S.L. and depth 0.6 times
length in lateral view with lateral margins evenly
rounded; dorsal edge slightly arched; mild
median dorsal ridge present on anterior 1/2 of
carapace; lateral surfaces devoid of ridges or
sculpture; greatest width at middle of length in
dorsal view; antennal notch a shallow concavity,
no antennal tooth or antennal ridge; pseudorostral
lobes wide, extending anteriorly beyond ocular
lobe which is wider than long (Fig. 61A-F).
Pereion robust, 0.9 times length of carapace; sides
of pereionite 1 concealed by pereionite 2, which
bears 7-8 slender spine-like setae on anterolateral
margin; pereionite 3 overlaps second laterally
and also bears 7-8 spine-like setae on
anterolateral margin; pereionite 4 overlaps third
and fifth laterally, and bears 4-5 spine-like setae
on each of overlapping lobes; pereionite 5 over-
laps pleonite 1 laterally and bears 4-5 spine-like
setae on overlapping lobe; dorsolateral carinae
pereionites 3-5 (Fig. 61A-F,H). Pleon and tel-
sonic somite 0.5 S.L. without dorsal or dor-
solateral carinae; first 4 pleonites subequal in
length, each with posterolateral overlapping
lobes bearing 4-5 small spine-like setae; fifth
pleonite 1.3 times as long as fourth. Telsonic
somite subequal in length to fourth pleonite, with
posterodorsal projection which is U-shaped in
dorsal view (Fig. 61A-D,G). First antenna as in
L. serriferum except peduncle has tuft of about 12
fine setae proximally, third segment has group of
7 setae distally, all of which extend beyond first
segment of flagellum. Mandible as in *L. ser-*

FIG. 62. *Leptocuma barbarae* sp. nov. ovig. ♀. A,B, whole mount LV, shows relative lengths of carapace and
somites. C, whole mount LV, shows relative lengths of telsonic somite and peduncle of uropod. D, carapace
and pereionites 1-3 DV, shows maximum width of carapace in posterior region, median dorsal ridge barely
visible, granular texture. E, carapace and pereionites 1-3 DLV, shows median dorsal ridge visible on anterior
half of carapace. F, carapace and pereionites 1-4 LV, shows lateral lobes of pereionite 5 overlapping pereionites
2 and 4, slender spines on anterolateral margins of pereionites 2-3. G, uropods DV, shows spination relative
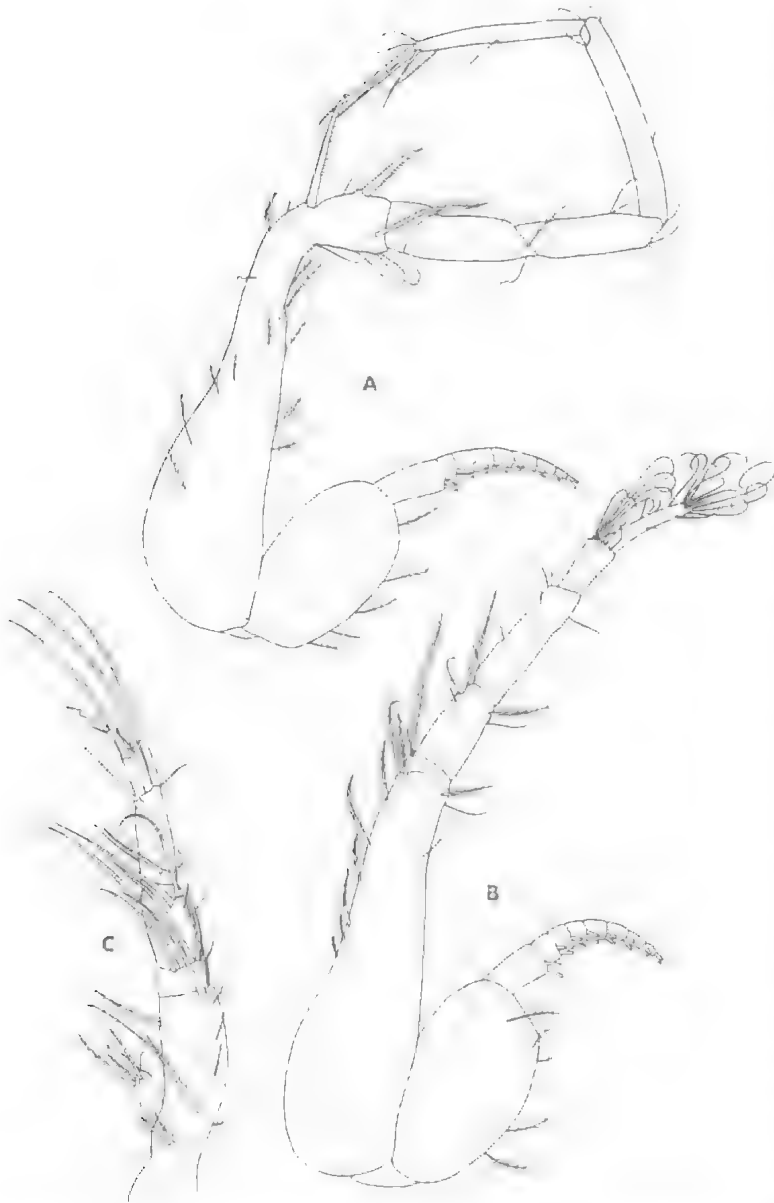lengths of peduncle and rami.

FIG. 63. *Leptocuma barbarae* sp. nov. holotype adult ♂. A, pereiopod 1. B, pereiopod 2. C, pereiopod 4.

medial margin of basis are plumose, propodus is 0.8 times length of dactylus and has 8 medial setae (Fig. 63B). Pereiopods 3-5 with merus longer than ischium, carpus slightly longer than merus and longer than combined length of propodus and dactylus; propodus twice length of dactylus; dactylar spine-like seta at least 1.5 times length of dactylus; basis with 2 setae distally, 2-3 medially and 2-3 laterally; ischium with 2-3 spine-like setae and 2-3 setae distally; merus with 1-2 spine-like setae distally and 1-2 setae medially; carpus with 2-3 spine-like setae distally and 1-2 setae laterally; propodus with spine-like seta and minute seta distally; dactylus with terminal spine-like seta, terminal seta and subterminal seta. Exopod of pereiopod 3 well-developed with bulbous basis, like those of pereiopods 1 and 2; exopod of pereiopod 4 rudimentary and 1-segmented. Pereiopod 4 as in *L. serriferum* except basis of endopod has 3 medial and 2 lateral setae (Fig. 63C). Peduncle of uropod 1.35 times length of telsonic somite, lined with 18-19 spinose spine-like setae (2 rows) on inner margin; endopod subequal in length to peduncle and to exopod, with 15-16 spinose spine-like setae on inner margin of proximal segment, 5-6 sp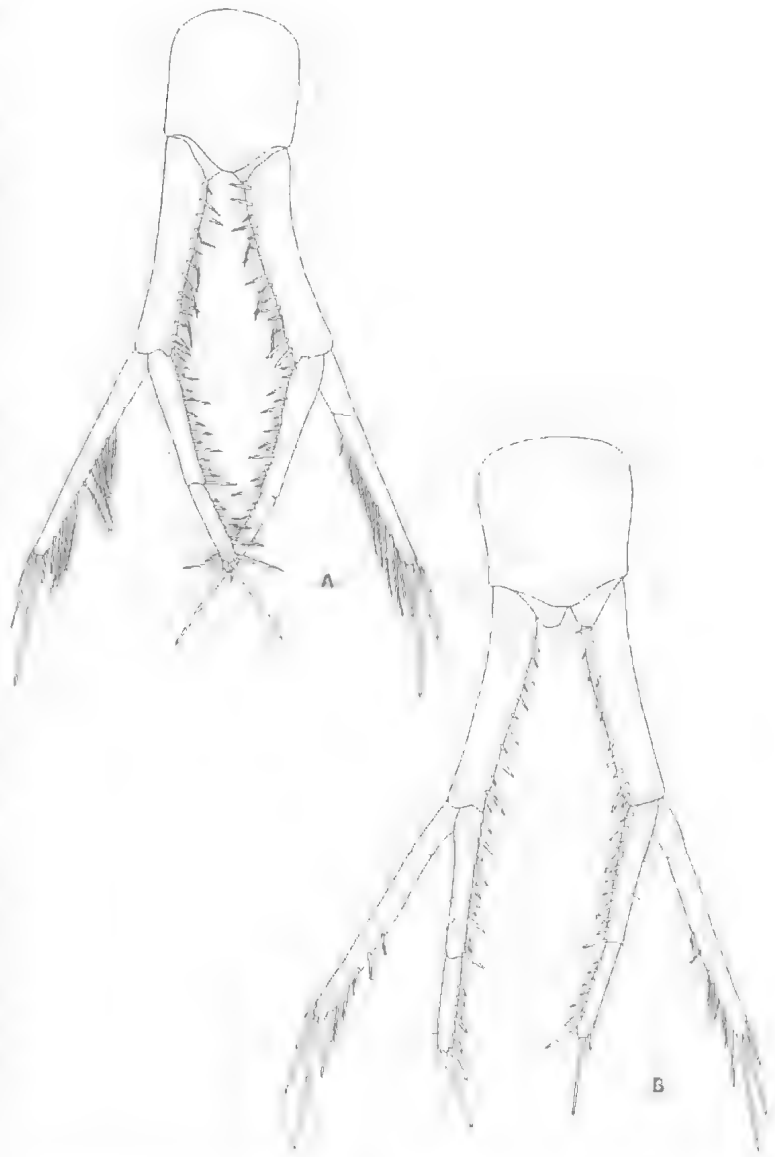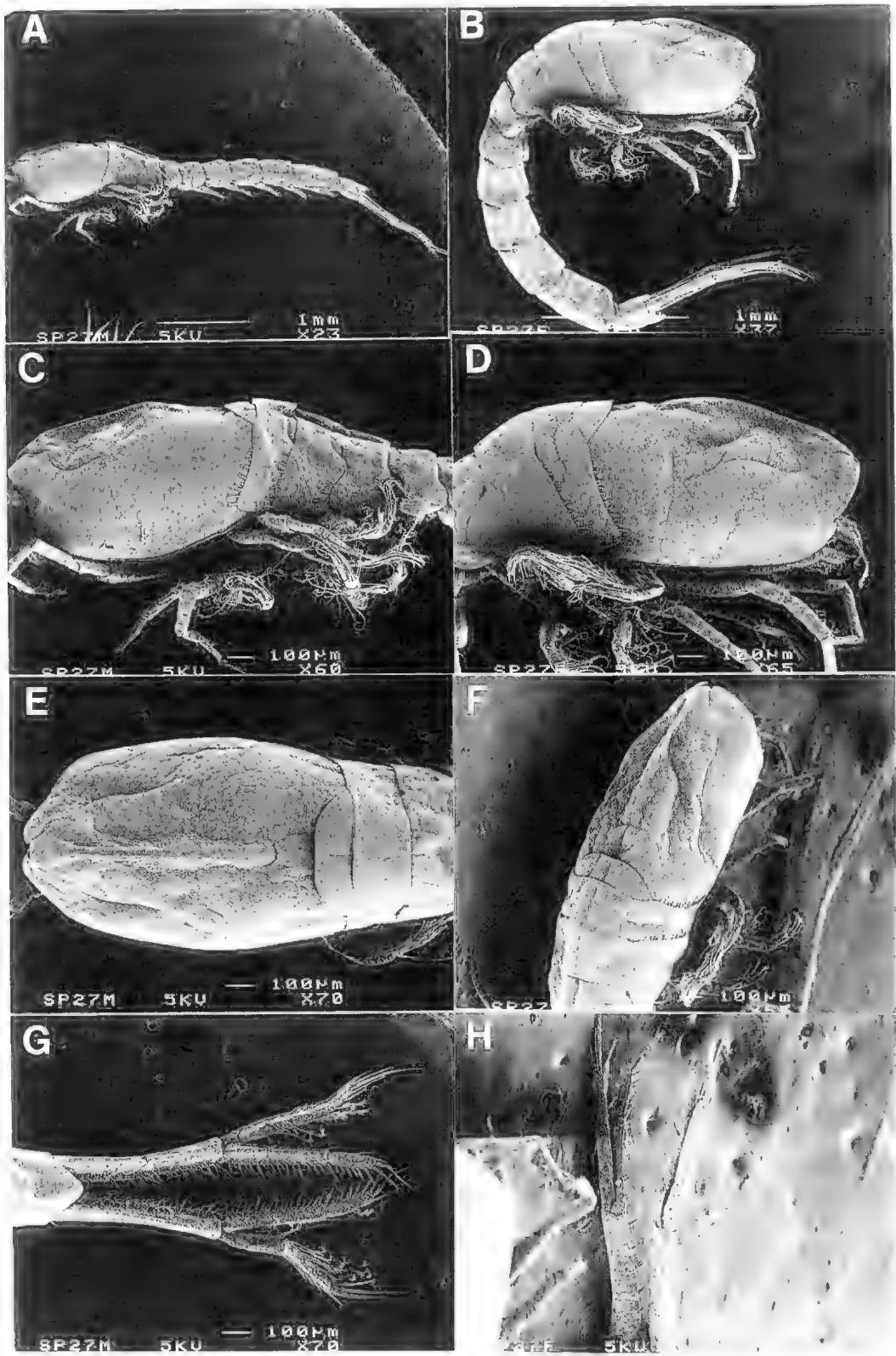inose spine-like setae on inner margin of distal segment (increasing in length distally) and 3 terminal spine-like setae, the longest of which is subequal in length to distal segment, distal segment 0.6 times length of proximal segment; dorsal surface of both endopodal segments bear numerous fine setae; exopod with 9-10 plumose setae and 2 slender spine-like setae along inner margin, outer margin with short subterminal spine-like seta, 3 terminal spine-like setae, the longest of which is 0.5 times length of exopod; terminal and subterminal

riferum except there are 10-11 (rather than 12) spine-like setae. Third maxilliped as in *L. serriferum* except setae along medial margin of basis are all plumose and of similar length. All pereiopods 7-segmented (Fig. 63). Pereiopod 1 as in *L. serriferum* except dactylus is 0.82 times length of propodus and dactylar spine-like seta is 0.72 times length of dactylus (Fig. 63A). Pereiopod 2 as in *L. serriferum* except setae on

spine-like setae of both rami bear minute apical setae; (Figs 61G, 64A).

OVIGEROUS FEMALE. Integument lightly calcified, with fine granular texture, as in ♂ (Fig. 62A-E). Carapace length 0.24 S.L. and depth 0.8 times length in lateral view with lateral margins evenly rounded; dorsal edge slightly arched; median dorsal ridge is obsolete on posterior 1/2 and barely visible on anterior 1/2; lateral surfaces devoid of ridges or sculpture; greatest width at posterior of length in dorsal view; antennal notch a shallow concavity, no antennal tooth or antennal ridge; pseudorostral lobes wide, extending anteriorly beyond ocular lobe which is wider than long (Fig. 62A-E). Pereion robust, 1.25 times length of carapace; sides of pereionite 1 concealed by pereionite 2, which bears 7-8 slender spine-like setae on anterolateral margin; pereionite 3 overlaps second and fourth laterally and bears 9-11 spine-like setae on anterolateral margin; pereionite 4 overlaps fifth laterally and fifth overlaps pleonite 1 laterally; dorsolateral carinae pereionites 3-5 (Fig. 62A-F). Pleon and telsonic somite 0.48 S.L. without dorsal or dorsolateral carinae; first 4 pleonites subequal in length, each subcylindrical with V-shaped posterolateral margins; fifth pleonite 1.5 times as long as fourth. Telsonic somite subequal in length to fourth pleonite, with posterodorsal projection which is U-shaped in dorsal view (Fig. 62B,C,G). First

FIG. 64. *Leptocuma barbarae* sp. nov. A, uropods and telsonic somite of holotype ♂, DV. B, uropods and telsonic somite of allotype ovig. ♀, DV.

antenna and mandible as in *L. serriferum* except mandible has 10-11 (rather than 12) spine-like setae. Third maxilliped as in *L. serriferum* except setae along medial margin of basis all plumose and of similar length. Pereiopod 1 as in *L. serriferum* except dactylus 0.82 times length of propodus; dactylar spine-like seta 0.58 times length of dactylus. Pereiopod 2 as in *L. serriferum* except propodus with group of 10 (rather than 5)

distal setae. Pereiopods 3-5 as in *L. serriferum* except basis of fourth with 4 medial and 4 lateral setae. Peduncle of uropod 1.3 times length of telsonic somite, lined with 10-12 spine-like setae on inner margin; endopod 1.2 times length of peduncle and subequal in length to exopod, with 11-15 spine-like setae on inner margin of proximal segment, 5-7 spine-like setae on inner margin of distal segment, 3 terminal spine-like

setae, the longest of which is at least 0.75 times length of distal segment, distal segment at least 0.5 times length of proximal segment; dorsal surface of both endopodal segments bear numerous fine setae; exopod with 5-7 short setae and 2 slender spine-like setae on distal half of inner margin, short subterminal spine-like seta on outer margin, 3 terminal spine-like setae, the longest of which is 0.5 times length of exopod; terminal and subterminal spine-like setae of both rami bear minute apical setae (Fig. 62G, 64B).

Colour. Pale yellow with conspicuous blackish chromatophores which may appear as dark bands on carapace.

S.L. Adult ♂ 3.2-3.5mm. Adult ♀ 3.1-3.6mm.

HABITAT AND DISTRIBUTION. Most commonly over medium and coarse sand in 1-8m of water; from sites 15, 28, 30, 31, 34, and 35 in Moreton Bay. In late summer *L. barbarae* predominated in the water column at night at site 31.

REMARKS. The Moreton Bay specimens resemble *L. serriferum* from Cronulla, NSW but differ in the spination of pereionites, pleonites and uropods. Fresh specimens of both *L. barbarae* and *L. serriferum* (Hale, 1944b:261) are coloured pale yellow with conspicuous blackish chromatophores, which in *L. barbarae* may appear as bands on the carapace. The most striking difference between the two species is the presence, in *L. barbarae*, of short spine-like setae on the anterolateral margins of pereionites 2 and 3 and on the posterolateral margins of pleonites 1-4. The spination of the ♀ uropod is also reduced compared to *L. serriferum* (Table 3)

The standard length of *L. barbarae* (♀: 3.6mm, ♂: 3.4mm) is a little smaller than *L. serriferum* (♀: 4.4mm, ♂: 4.2mm).

ETYMOLOGY. For Barbara Koh, who assisted in the field.

Leptocuma kennedyi sp. nov
(Figs 65-67)

MATERIAL EXAMINED. HOLOTYPE

TABLE 3. ♀ uropod setation of *L. serriferum* and *L. barbarae*.

	L. serriferum	*L. barbarae*
Peduncle spination	15	10-12
Endopod 1 spination	18	11-15
Endopod 2 spination	11	5-7

QMW20549, adult ♂, S.L. 4.3mm, SEM mount, Tangalooma, site 15, 27°11'S, 153°19'E, D. Greenwood, 14 April 1990, 8m, sand, 35.5 ppt salinity, 24°C water temperature. PARATYPES: QMW20550, ovig. ♀, allotype, S.L. 4.2mm, SEM mount, same data as above; QMW20551, adult ♂, S.L. 3.5mm, PSM #15, Horseshoe Bay, site 31, 27°30'S, 153°21'E, D. Tafe, 4 Feb. 1993, 3 m, sand, 34.2 ppt salinity, 26°C water temperature.

DESCRIPTION. MALE. Integument lightly calcified, finely granular and sparsely pitted with minute indentations (Fig. 65A,C). Carapace length 0.26 S.L. and depth 0.6 times length in lateral view with lateral margins evenly rounded; dorsal edge slightly arched and sinuate; dorsum with strong median ridge throughout length; lateral surfaces devoid of ridges or sculpture; greatest width at middle of length in dorsal view; antennal notch a moderate concavity, no antennal tooth or antennal ridge; pseudorostral lobes wide, extending anteriorly beyond ocular lobe which is wider than long (Fig. 65A,C,E). Pereion robust, 0.9 times length of carapace; sides of pereionite 1 concealed by pereionite 2, which bears 9 slender spine-like setae on anterolateral margin; pereionite 3 overlaps second laterally and bears 7-8 spine-like setae on anterolateral margin; pereionite 4 overlaps third and fifth laterally, and bears 3-4 spine-like setae on anterolateral margin; pereionite 5 overlaps first pleonite laterally (Fig. 65A,C). Pleon and telsonic somite 0.5 S.L. with faint dorsolateral carinae; first 4 pleonites subequal in length, each with poorly developed posterolateral overlapping lobes; fifth pleonite 1.6 times as long as fourth. Telsonic somite subequal in length to fourth pleonite, with posterodorsal projection which is V-shaped in dorsal view (Fig. 65A,G). First antenna as in *L.*

FIG. 65. *Leptocuma kennedyi* sp. nov. A, whole mount ♂ LV, shows relative lengths of carapace and somites. B, whole mount ♀ LV, shows relative lengths of carapace and somites. C, carapace and pereionites 1-5 ♂ LV, shows relative length and depth of carapace, slender spines on anterolateral margins of pereionites 1-3. D, carapace and pereionites 1-3 ♀ LV, shows relative length and depth of carapace, slender spines visible on anterolateral margins of pereionites 1-2. E, carapace and pereionites 1-3 ♂ DV, shows strong median dorsal ridge and sparse pitting of carapace. F, carapace and pereionites 1-3 ♀ DLV, shows strong median dorsal ridge and sparse pitting of carapace. G, Uropod ♂ DV, shows relative lengths of peduncle and rami. H, Uropod ♀ VV, shows relative lengths of peduncle and rami.
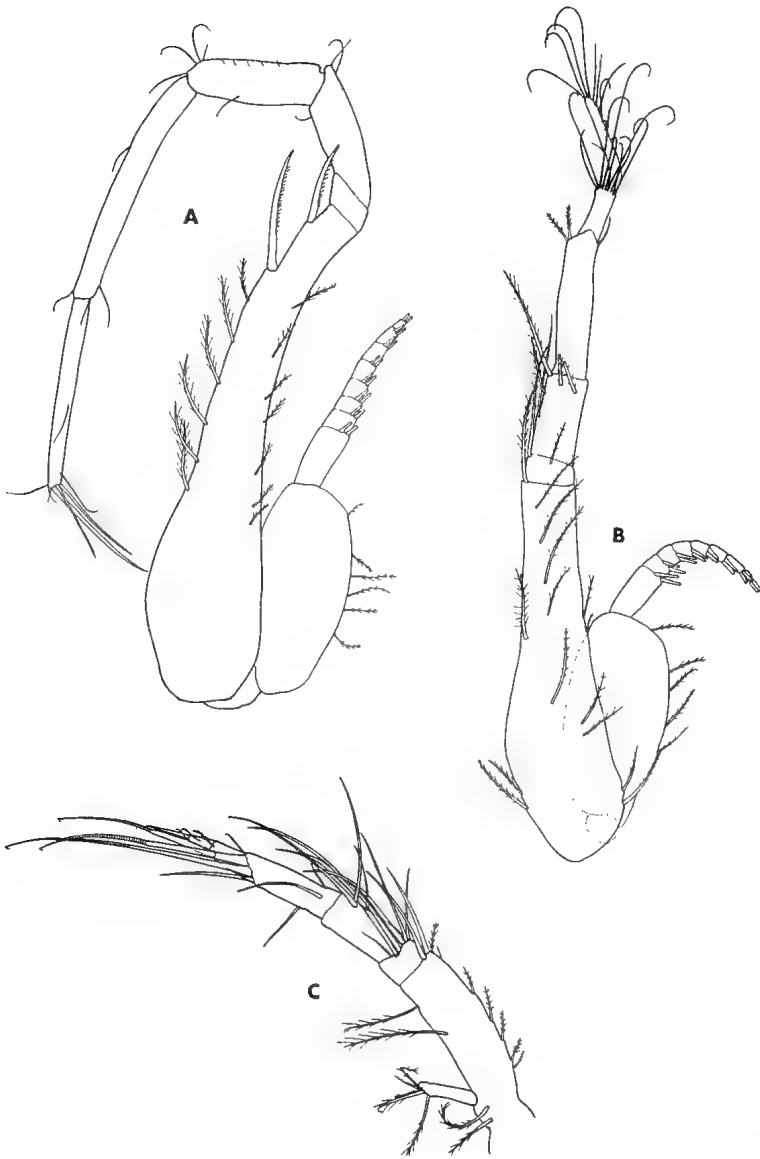
FIG. 66. *Leptocuma kennedyi* sp. nov. paratype ♂. A, pereiopod 1. B, pereiopod 2. C, pereiopod 4.

0.66 times length of dactylus (Fig. 66A). Pereiopod 2 as in *L. serriferum* except setae on medial margin of basis plumose, propodus 0.6 times length of dactylus and with 8 distal setae (Fig. 66B). Pereiopods 3-5 with merus longer than ischium, carpus slightly longer than merus and longer than combined length of propodus and dactylus; propodus twice length of dactylus; dactylar spine-like seta at least 1.5 times length of dactylus; basis with 2 setae distally, 2-3 medially and 2-3 laterally; ischium with 2-3 spine-like setae and 2-3 setae distally; merus with 1-2 spine-like setae distally and 1-2 setae medially; carpus with 2-3 spine-like setae distally and 1-2 setae laterally; propodus with spine-like seta and minute seta distally; dactylus with terminal spine-like seta, terminal seta and subterminal seta. Peduncle of uropod 1.5 times length of telsonic somite, lined with 20-22 spinose spine-like setae (2 rows) on inner margin; endopod subequal in length to peduncle and to exopod, with 14-16 spinose spine-like setae on inner margin of proximal segment, 5-6 spinose spine-like setae on inner margin (increasing in length distally) of distal segment, 3 terminal spine-like setae, the longest of which is subequal in length to distal segment; distal segment 0.6 times length of proximal segment; dorsal surface of both endopodal segments bear numerous fine setae; exopod with 6 plumose setae and 2 slender spine-like setae along inner margin, outer margin with 7 short spine-like setae, 3 terminal spine-like setae, the longest of which is 1/3 the length of exopod; outer edge spine-like setae of exopod and terminal spine-like setae of both rami bear minute apical setae (Fig. 65G, 67A,B).

serriferum except peduncle has tuft of about 20 fine setae proximally, third segment has group of 5 setae distally all of which extend beyond first segment of flagellum. Mandible as in *L. serriferum* except there are 10-11 (rather than 12) spine-like setae. Third maxilliped as in *L. serriferum* except setae along medial margin of basis are all plumose and of similar length. Pereiopod 1 as in *L. serriferum* except dactylus is 0.78 times length of propodus and dactylar spine-like seta

OVIGEROUS FEMALE. Integument lightly cal-
cified, finely granular and sparsely pitted with
minute indentations, as in ♂ (Fig. 65B,D).
Carapace length 0.24 S.L. and depth 0.63 times
length in lateral view with lateral margins evenly
rounded; dorsal edge slightly arched and sinuate;
strong median dorsal ridge on anterior 3/4 of
dorsum; lateral surfaces devoid of ridges or sculp-
ture; greatest width at posterior of length in dorsal
view (Fig.Pl 25F); antennal notch very small and
subacute; pseudorostral lobes wide, extending
anteriorly beyond ocular lobe which as wide as
long (Fig. 65B,D,F). Pereion robust, 1.1 times
length of carapace; sides of pereionite 1 con-
cealed by second pereionite, which bears 14-15
slender spine- like setae on anterolateral margin;
pereionite 3 overlaps second and fourth laterally
and bears 9-11 spine-like setae on anterolateral
margin and 1-2 on posterolateral margin;
pereionite 4 overlaps fifth laterally and fifth over-
laps first pleonite laterally; no dorsolateral
carinae on pereionites (Fig. 65B,D,F). Pleon and
telsonic somite 0.49 S.L. with faint dorsolateral
carinae; first 4 pleonites subequal in length, each
subcylindrical with small nipple-like projections
on posterolateral margins; fifth pleonite 1.6 times
as long as fourth. Telsonic somite subequal in
length to fourth pleonite, with posterodorsal
projection which is V-shaped in dorsal view (Fig.
65B,H). Peduncle of uropod 1.3 times length of
telsonic somite, lined with 5-6 spine-like setae on
inner margin; endopod 1.1 times length of
peduncle and subequal in length to exopod, with
10-11 spine-like setae on inner margin of
proximal segment, 4-5 spine-like setae on inner
margin of distal segment, 3 terminal spine-like
setae, the longest of which is as long as distal
segment, distal segment 0.5 times length of
proximal segment; dorsal surface of both en-
dopodal segments with numerous fine setae; ex-
opod with up to 5 short setae and 2 slender spine-
like setae on distal half of inner margin, short
subterminal spine-like seta on outer margin, 3
terminal spine-like setae, the longest of which is
0.5 times length of exopod; terminal and subter-
minal spine-like setae of both rami bear minute
apical setae (Fig. 65B,H).

Colour. White with small blackish
chromatophores dotted on carapace and pereion.

S.L. Adult ♂ 4.3mm. Adult ♀ 4.2mm.

HABITAT AND DISTRIBUTION. Most com-
mon over medium and coarse sand in 1-8m of
water; sites 15, 28, 31 and 34 in Moreton Bay.
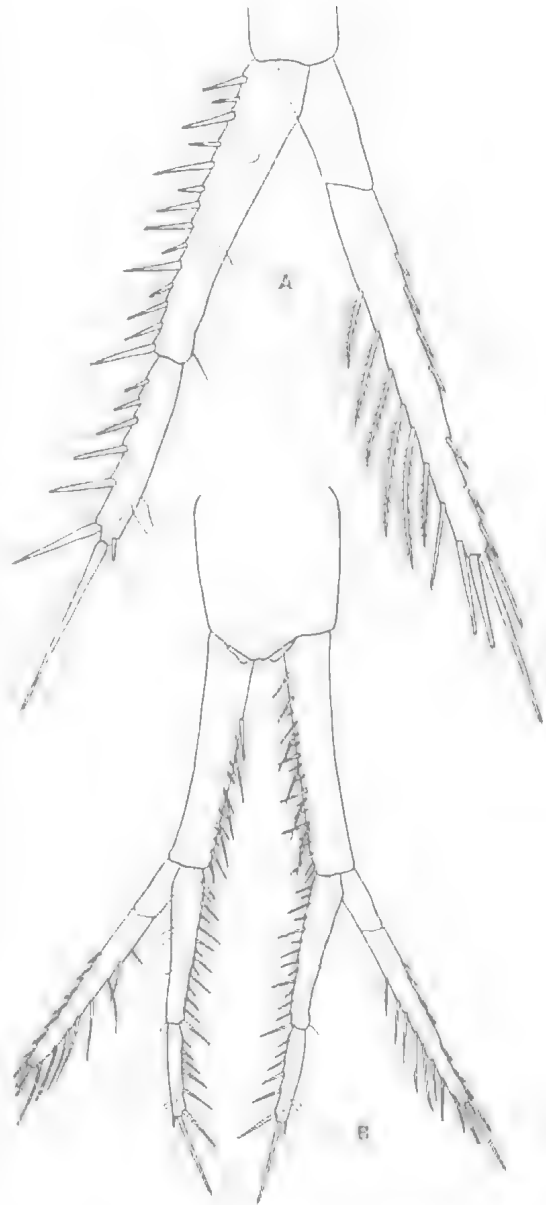
FIG. 67. *Leptocuma kennedyi* sp. nov. paratype adult
♂. A, rami of uropod, DV. B, uropods and telsonic
somite, DV.

REMARKS. *Leptocuma kennedyi* most closely
resembles *L. nichollsi* but has rows of spine-like
setae on the anterolateral margins of pereionites
2 and 3. Also the first endopodal segment of the
uropod is fully twice as long as the second and

has up to 18 inner marginal spine-like setae (cf. 1.5X with 9 spine-like setae in *L. nichollsi*; Hale, 1949a:117).

L. kennedyi is larger than *L. barbarae* and smaller than *L. intermedia*. It also differs from the above two species in having a strong median dorsal ridge, extending from the ocular lobe almost to the first pereionite. Like *L. barbarae* it has a row of short spine-like setae in both sexes on the anterolateral margins of pereionites 2 and 3. Unlike *L. barbarae* (Fig. 61G, 62G) the expod of the ♂ uropod has a row of outer spine-like setae (Fig. 65G). Like *L. intermedia* the body is large and tapering from carapace to telsonic somite. However, the second endopod segment of the uropod (♂s only) of *L. kennedyi* is relatively longer than that of *L. intermedia* (Hale, 1944b:265).

ETYMOLOGY. For John Kennedy, Queenslan Museum, who assisted in the field.

Picrocuma Hale, 1936

Picrocuma Hale, 1936b:415. Hale, 1945c:177.

DIAGNOSIS. Pseudorostral lobes meeting in front of wide ocular lobe. First antenna with 3-segmented peduncle and rudimentary accessory flagellum. Mandible with spine-like seta row, only 4-5 spine-like setae; incisor portion greatly elongated, with cutting edge tridentate. Third maxilliped with exopod and similar to first pereiopod; basis not produced apically. Pereiopods 1-3 with well-developed exopods in ♀. Uropod of both sexes with endopod 1-segmented. Pereionite 2 longer than others.

GENOTYPE. *Picrocuma poecilotum.*

REMARKS. Salient features of genus are structure of mandible and unspecialised third maxilliped.

Picrocuma poecilotum Hale, 1936
(Fig. 68)

Picrocuma poecilotum Hale, 1936b:415, figs 7a-c, 8a-i. Hale, 1945a:178, figs 22, 23.

MATERIAL EXAMINED. SAMC2006, ovig. ♀, holotype, S.L. 1.9mm, Wynyard, Fossil Reef, Tasmania, on stones, Hale, 1936b. OTHER MATERIAL QMW20552, adult ♂, S.L. 1.3mm, in 70% ethanol, Tangalooma, site 15, 27°11'S, 153°19'E, D. Greenwood, 14 April 1990, 8m, sand, 35.5 ppt salinity, 24°C water temperature; QMW20553, adult ♀, S.L. 1.2mm, in 70% ethanol, same data as above; QMW20554, adult ♂, S.L. 1.4mm, SEM mount, same data as above; QMW20555, adult ♀, S.L. 1.3mm, SEM mount, same data as above.

DISTRIBUTION. North East Coast, Central East Coast, Tasmanian Coast and S. Gulfs Coast (Fig. 4). QLD: Lizard Is., Myora Bight in Moreton Bay, on sand (Hale, 1945a:180); sites 15, 28, and 31 in Moreton Bay. Tas: Wynyard, Fossil Reef, on stones (Hale, 1936b:417). SA: Sellicks Beach, Gulf St. Vincent, on stones (Hale, 1936b:417).

REMARKS. *P. poecilotum* from Moreton Bay matches the types (SAMC2006) from Tasmania. Standard lengths of adult and subadult ♀♀ are 1.3 and 0.95mm respectively, smaller than those from Tasmania (Hale,1936b).

Both sexes are described (♀ Hale,1936b; ♂ Hale,1945a). Hale expressed some uncertainty about the fact that adult ♀♀ could be up to 40% larger than adult ♂♂, and that ♀♀ from Moreton Bay have the carapace less swollen than the type ♀. He also pointed out (1936b:417) that, although the species was by far the commonest cumacean at Sellicks Beach, SA, all were immature. The ♀s he examined from Moreton Bay had 'the carapace less swollen than in the type' (Hale,1945a:180), and the ♂ lacked sensory filaments on the first antenna that occurred on the same appendage of immature ♂ specimens from SA. It appears that he has combined two species into his description of *P. poecilotum*, the ♂ being of a different species. Both species commonly occur in parts of Moreton Bay. *P. poecilotum* (Fig. 68) has a shorter, more anteriorly tapering carapace, longer uropodal peduncles and deeper textured integument than *P. crudgingtoni* (Fig. 69).

FIG. 68. *Picrocuma poecilotum* Hale. A,B, whole mount ♀, showing relative lengths of carapace and somites. A, LV. B, DV. C, carapace and pereion ♀ LV, shows arched dorsum and relative lengths of pereionites. D, carapace and pereion ♀ ALV, shows arched dorsum and anteriorly tapering pseudorostral lobes. E, whole mount ♂ DV, shows relative lengths of carapace and somites. F, uropods ♂ DV, shows relative lengths of telsonic somite, peduncle and rami. G, uropods ♀ DV, shows relative lengths of telsonic somite, peduncle and rami. H, uropod rami ♀ DV, shows spination and surface texture of rami.
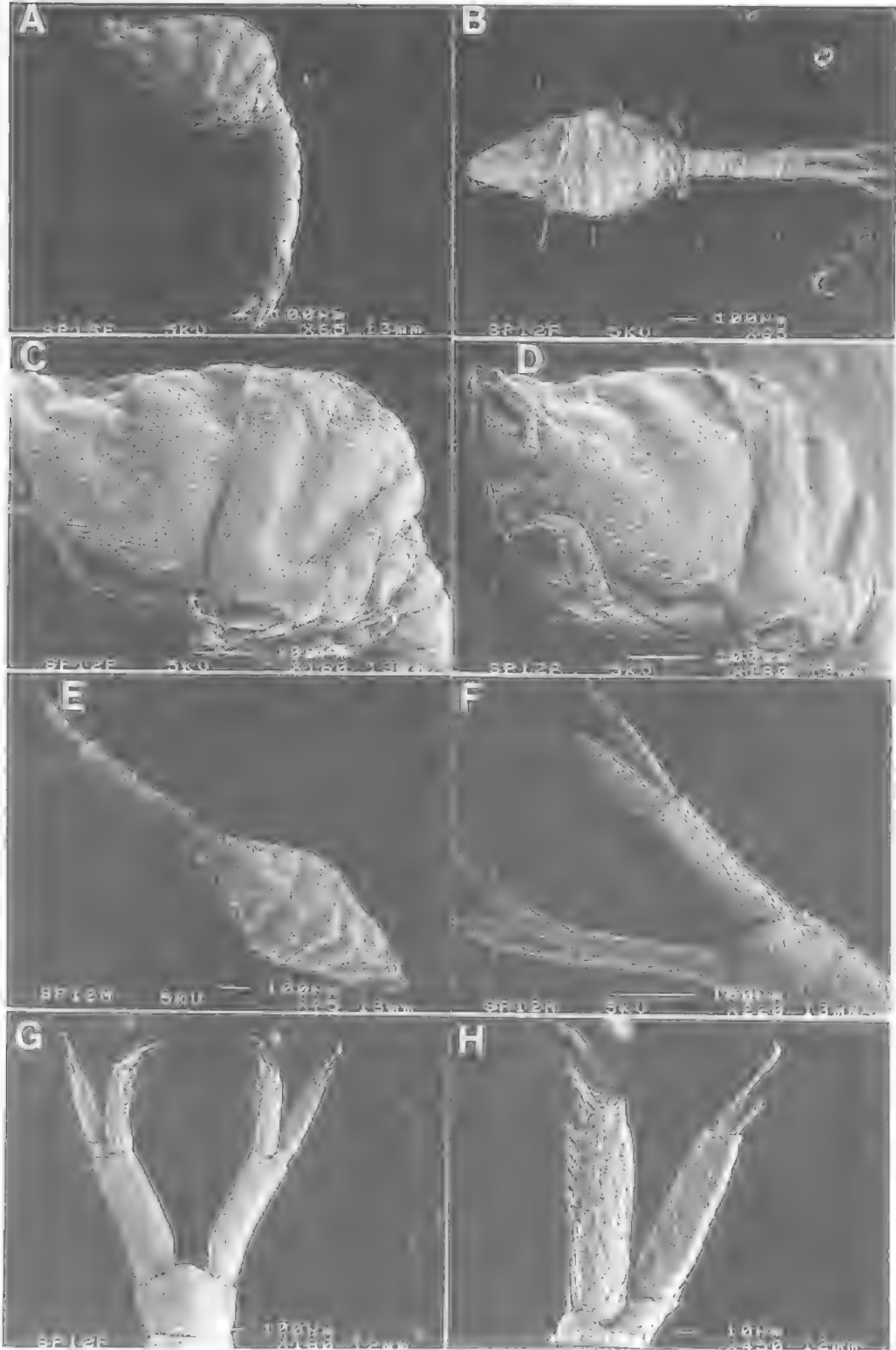
Picrocuma crudgingtoni sp. nov.
(Fig. 69)

MATERIAL EXAMINED. HOLOTYPE QMW20556, adult ♂, S.L. 1.1mm, in 70% ethanol, Hays Inlet, site 17, 27°17'S, 153°09'E, D. Tafe, 12 Oct. 1989, 2m, silt, 33 ppt salinity, 24°C water temperature. PARATYPES QMW20557, ovig. ♀, allotype, S.L. 1.3mm, in 70% ethanol, same data as holotype; QMW20558, adult ♂, S.L. 1.2mm, SEM mount, Pumicestone Passage, site 1, 26°55'S, 153°05'E, J. Greenwood, 14 Dec. 1990, 1.2m, silt, 33.5 ppt salinity, 29°C water temperature; QMW20559, adult ♀, S.L. 1.2mm, in 70% ethanol, same data as above.

DESCRIPTION. MALE. Integument lightly calcified, composed of triangular, overlapping scales giving a smooth appearance (Fig. 69). Carapace 0.3 S.L. and 0.6 times as wide as long in dorsal view with lateral margins evenly rounded, widest at midlength; depth 0.5 times length in lateral view with dorsum smoothly arched, no median dorsal or lateral carinae; antennal notch shallow, no antennal tooth or ridge; pseudorostral lobes wide, roundly truncate, joining for a distance in front of ocular lobe equal to 0.15 times length of carapace; ocular lobe twice as wide as long (Fig. 69A-E). Percion 0.9 times length of carapace; 5 percionites exposed, first narrows laterally, second is longest, twice as long as third or fourth, fifth longer than fourth, third to fifth tapering in dorsal view (Fig. 69A-E). Pleon and telsonic somite 0.45 S.L. and 1.5 times length of carapace; robust structure, no median dorsal or lateral carinae; no lateral articular processes; first 4 pleonites increasing slightly in length, fifth pleonite 1.5 times as long as fourth; telsonic somite 1.3 times wider than long, posteriorly rounded and slightly produced (Fig. 69A-F). First antenna as in ♂ of *P. poecilotum*, 3-segmented with terminal flagellum; first segment somewhat geniculate, as long as second and third segments combined; second segment subequal in length to third, which bears a group of short setae distally; flagellum segment with a group of 7 sensory filaments distally. All pereiopods 7-segmented, except pereiopod 2 which has no distinct ischium. Structure of pereiopods as in ♂ of *P. poecilotum*

(Hale, 1945a, p.179). Peduncle of uropod 1.4 times length of telsonic somite, very broad, its width 0.45 times its length, and without spination; rami short and robust; endopod 0.85 times length of peduncle and slightly longer than exopod, with 5-6 inner marginal and 2 unequal terminal spine-like setae, the longer 0.35 times ramus length; exopod with 2 unequal terminal spine-like setae, the longer 0.4 times ramus length (Fig. 69F,H).

OVIGEROUS FEMALE. Integument lightly calcified, composed of smooth triangular, overlapping scales, as in ♂.

Carapace length 0.25 S.L. and 0.7 times as wide as long in dorsal view with lateral margins evenly rounded and widest at posterior of length; depth 0.6 times length in lateral view with dorsum smoothly arched, no median dorsal or lateral carinae; antennal notch shallow, no antennal tooth or ridge; pseudorostral lobes wide, roundly truncate, joining for a distance in front of ocular lobe equal to 0.2 times length of carapace; ocular lobe and pseudorostral lobes as in ♂. Percion as long as carapace; 5 percionites exposed, first narrows laterally, second is longest, twice as long as third or fourth, fifth longer than fourth, third to fifth tapering in dorsal view. Pleon and telsonic somite 0.5 S.L. and 1.7 times length of carapace; robust structure, no median dorsal or lateral carinae; no lateral articular processes; first 4 pleonites increasing slightly in length, fifth pleonite 1.5 times as long as fourth; telsonic somite 1.3 times wider than long, posteriorly rounded and slightly produced. First antenna 3-segmented, with terminal flagellum; first segment somewhat geniculate, as long as second and third segments combined; second segment subequal in length to third, which bears a group of short setae distally; flagellum with a group of 7 sensory filaments distally. Pereiopods 7- segmented, except pereiopod 2 which has no distinct ischium. Structure of pereiopods same as in ♂. Uropod as in ♂ except peduncle is 1.3 times length of telsonic somite and inner margin of endopod has 3 spine-like setae.

Colour. White with mottled brown chromatophores.

FIG. 69. *Picrocuma crudgingtoni* sp. nov. ♂. A, whole mounts DV & LV. B, whole mount LV, shows relative lengths of carapace and somites. C, whole mount DV, shows body tapering from mid-region of carapace to pleonite 4. D, carapace and percionites 1-5 LV, shows dorsum smoothly arched dorsum, shallow antennal notch and absence of lateral carinae. E, carapace and percionites 1-4 DV, shows relative lengths of percionites in dorsal view and absence of median dorsal ridge. F, uropod DV, shows relative lengths and widths of telsonic somite, peduncle and rami. G, anterior carapace DV, shows pseudorostral lobes wide, roundly truncate, joining for a distance in front of ocular lobe. H, uropod rami DV, shows spination and texture of rami.
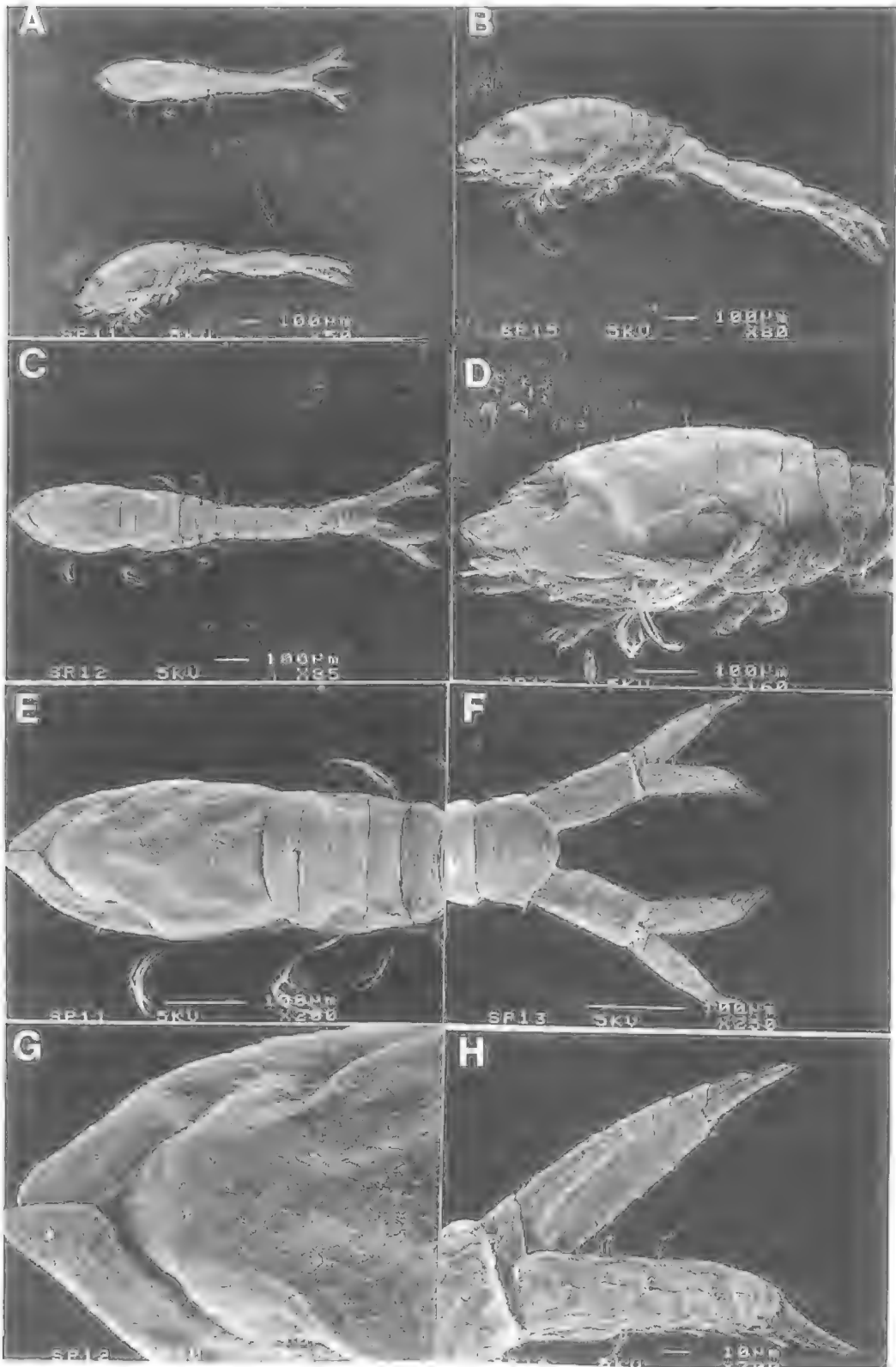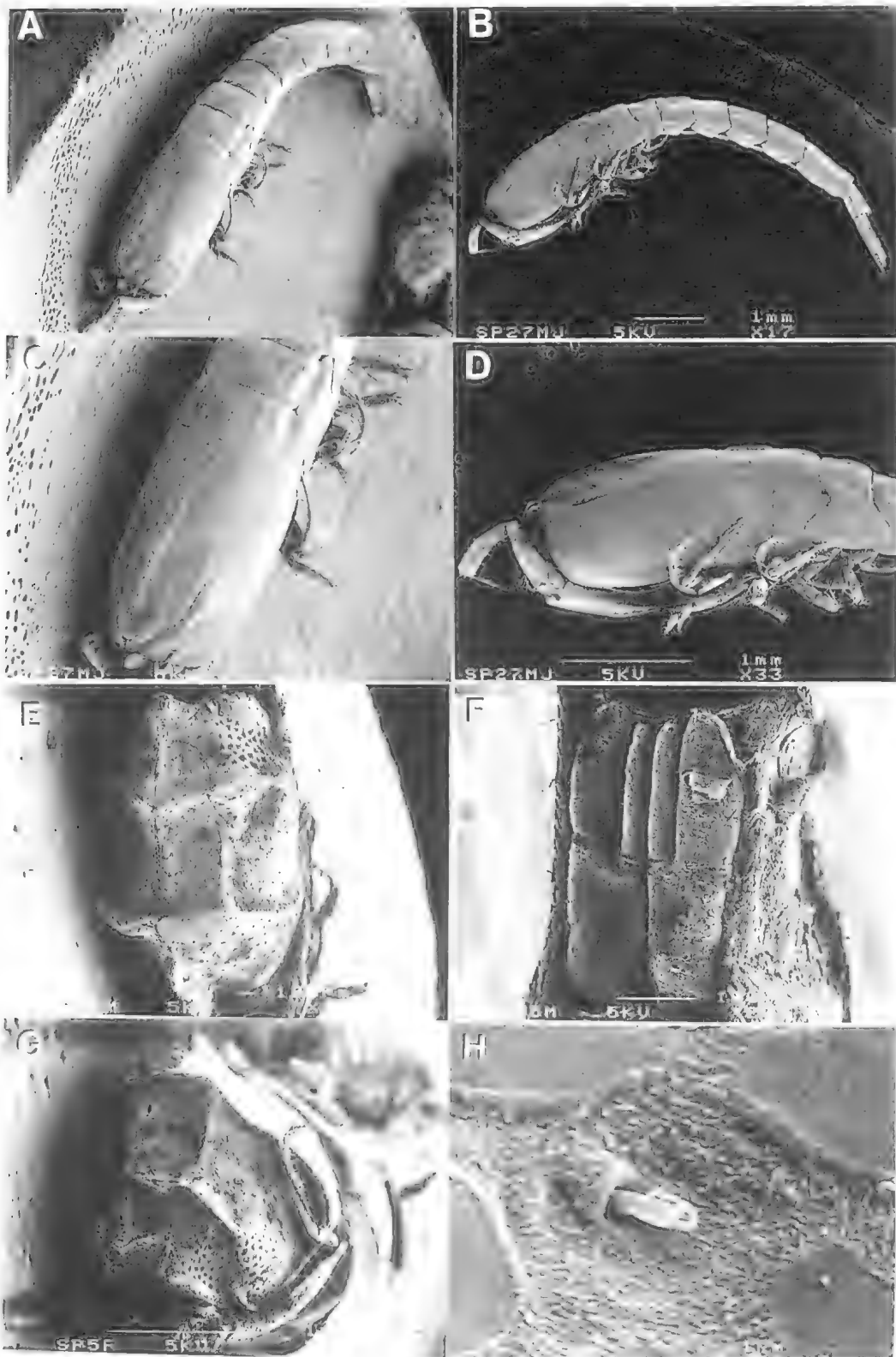
S.L. Adult ♂ 1.0-1.2mm. Adult ♀ 1.1-1.3mm.

HABITAT AND DISTRIBUTION. Most common over fine sand in 1-4m of water; from all sites in Pumicestone Passage, and sites 16, 17, and 31 in Moreton Bay; abundant at sites 1, 2, 3, 9, 10, and 11 in Pumicestone Passage.

REMARKS. *P. crudgingtoni* resembles *P. poecilotum*, but lacks the acutely pointed carapace and pronounced dorsal hump. The hump is located in the region of pereionite 2 of the latter species, which is three times longer than pereionite 3 and half as long as the carapace (Fig. 68C,D). In *P. crudgingtoni* it is only twice as long as pereionite 3 and 1/4 as long as the carapace; the peduncle of the uropod is about twice as long as wide (Fig. 69F), compared to at least three times as long as wide for *P. poecilotum* (Fig. 68F,G). The armature of the uropodal endopod is also different in the new species.

The carapace of *P. crudgingtoni* has a smooth appearance, being composed of flattened triangular, overlapping scales (Fig. 69G). In contrast the carapace of *P. poecilotum* is composed of rounded, overlapping scales giving a roughened, pebbled appearance (Fig. 68C,D).

P. crudgingtoni has a small, streamlined but robust exoskeleton which, like that of *P. poecilotum*, is well adapted to living amongst sand grains in areas subject to currents or wave action. Both species are very common in silt/fine sand areas of Moreton Bay subject to tidal currents.

ETYMOLOGY. For Robert Crudgington, who assisted in the field.

Pomacuma Hale, 1944

Pomacuma Hale, 1944b:241.

GENOTYPE. *Pomacuma cognata* Hale, 1944b.

DIAGNOSIS. FEMALE. Carapace with pseudorostral lobes extending in front of moderately large ocular lobe and meeting in midline; antennal notch closed but not fused. Five pereionites exposed; first pereionite short. Pleon longer than carapace and pereion combined; telsonic somite well produced posteriorly with distal margin rounded. Third maxilliped with well-developed exopod. First 3 pereiopods with well-developed exopods; pereiopod 4 with rudimentary 1-segmented exopod bearing few setae. Basis of pereiopod 1 widened distally with large lobe on distal end; lobe produced to articulation of ischium and merus. Carpus of pereiopod 2 much shorter than merus. Endopod of uropod 2-segmented, distal segment very short; medial margin of exopod with plumose setae.

MALE. Second antenna reaching to end of pleon. Thoracic exopods as in ♀. Five pairs of pleopods.

REMARKS. This genus is related to *Zenocuma* but differs in structure of basis of third maxilliped and first pereiopod, and in pseudorostrum and telsonic somite. Two species of *Pomacuma* have been previously recorded off eastern Australia.

KEY TO AUSTRALIAN SPECIES OF *POMACUMA*

1. Pleon ridged 2
   Pleon not ridged . . . . *australiae* (Zimmer)

2. Sides of carapace tapering anteriorly in dorsal view. Pereionite 4 with only posterior overlapping lobe in lateral view . . . *cognatum* Hale
   Sides of carapace almost parallel in dorsal view. Pereionite 4 with anterior and posterior overlapping lobes in lateral view . . . . sp. nov. 1

Pomacuma australiae (Zimmer, 1921)
(Fig. 71A-D)

Vaunthompsonia australiae Zimmer, 1921:4, figs 1-7.
Leptocuma australiae; Hale, 1936b:408.
Pomacuma australiae Hale, 1944b:244, figs 12-14. Hale, 1949a:110.

MATERIAL EXAMINED. SAMC2480,3 ♂, ♀, S.L. 8.7-9.0mm, Fraser Island, Qld (Hale,1944b);

FIG. 70. A-D, *Pomacuma* sp. nov. 1. A, ♂ DLV, whole mount shows dorsal and lateral carinae extending along pereion and pleon. B, ♂ LV, whole mount showing relative lengths of carapace and somites. C, ♂ DLV, carapace truncate anteriorly and almost parallel sided; median dorsal ridge pronounced. D, ♂ LV, carapace and pereionites 1-4 showing basis of pereiopod 1 widened distally, pereiopod 4 with lateral lobes which overlap pereiopods 3 and 5. E-G, *Cyclaspis alveosculpta* sp. nov. E, subadult ♂ DLV, showing strong transverse ridges and reticulate pattern of pitting. F, subadult ♂ VV, pleonite 5 showing immature pleopod 5. G, subadult ♂ ALV, showing high arches of posterior transverse ridge, and strong median dorsal and dorso lateral ridges. H, *Gephyrocuma* sp. nov. 1, ♂, DV, detail of integument anterolaterally showing a sensory filament, protruding from between cuticular plates.
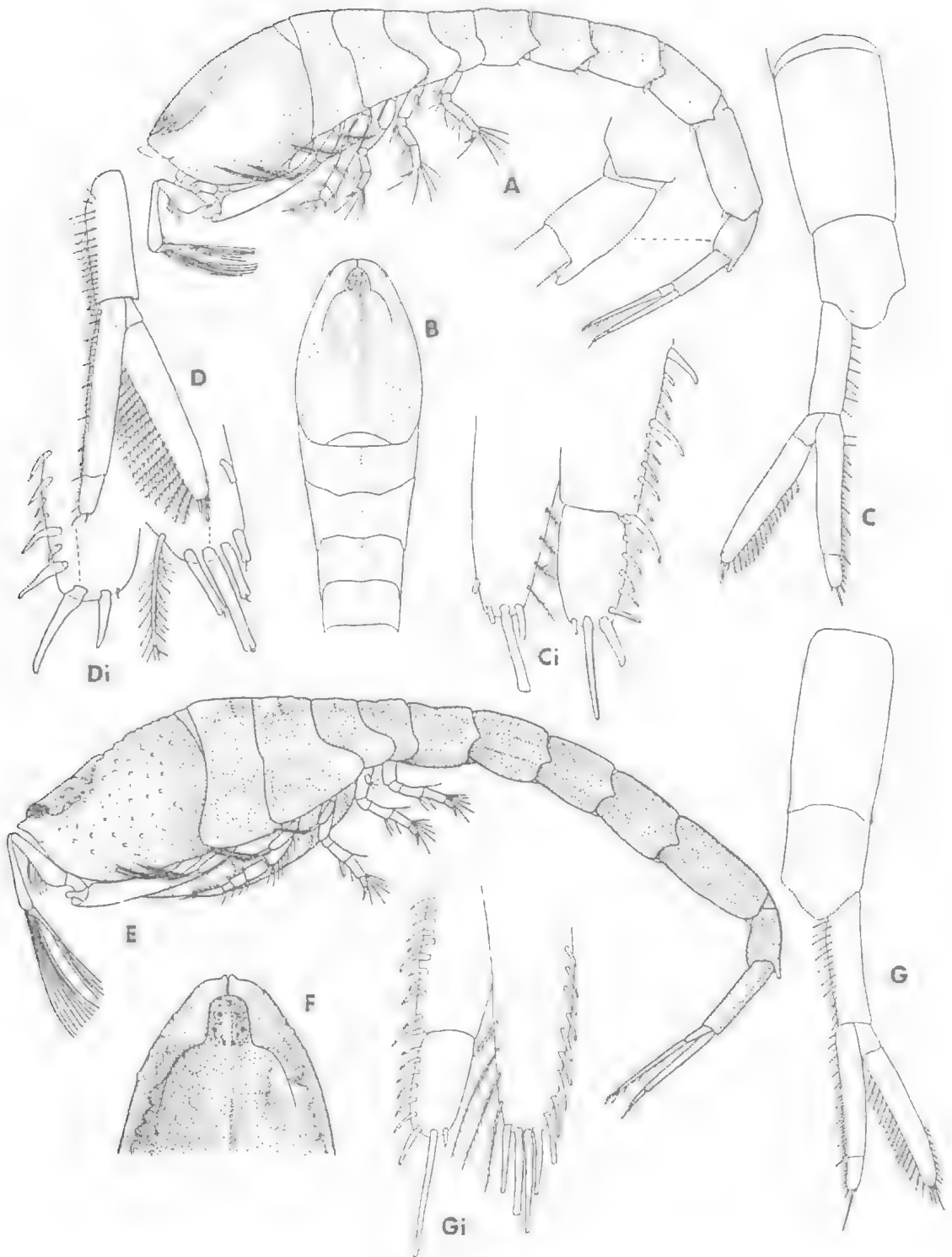
FIG. 71. A-D, *Pomacuma australiae*. A-C, ♀. A, LV. B, cephalothorax, DV. C, uropod, DV. Ci, distal ends of rami. D, ♂ uropod, DV. Di, distal ends of rami. E-G, *Pomacuma cognatum*, E-G, type ovig. ♀. E, LV. F, anterior portion of carapace, DV. G, uropod, DV. Gi, distal ends of rami. (All after Hale, 1944b).

QMW20560, adult ♂, S.L. 8.5mm, in 70% ethanol, off Coochiemudlo Island, site 34, 27°32'S, 153°20'E, D Tafe, 17 June 1990, 7.5m, silt, 33 ppt salinity, 20°C water temperature. QMW20561, adult ♀, S.L. 8.1mm, in 70% ethanol, data as above.

DISTRIBUTION. Central and Lower East Coast, Central and Lower West Coast (Fig.4). Qld: Fraser Island (Hale, 1944b:246); sites 31 and 34 in Moreton Bay. NSW: Jibbon, Wata Mooli, Eden, Ulladulla (Hale, 1944b:246). WA: Cape Jaubert, Shark Bay (Zimmer, 1921:4).Uncommon in Moreton Bay.

REMARKS. Moreton Bay specimens match the types. Two adults and a juvenile were taken by sledge-net during the day and are slightly smaller but otherwise the same as those described by Hale (Fig. 43A-G). The standard length of the ♂ is 8.5mm (cf Hale, 1944b: 9.0mm) and the ♀ is 8.1mm (cf Hale,1944b: 8.7mm).

Pomacuma sp. nov. 1
(Fig. 70A-D)

MATERIAL EXAMINED. QMW20562, subadult ♂, S.L. 4.7mm, SEM mount, Raby Bay, site 32, 27° 30'S, 153° 18'E, D. Tafe, 17 June 1990, 1300 hours, sledgenet, 5m, sandy mud, 33.8 ppt salinity, 18.7°C water temperature. Uncommon.

REMARKS. Further specimens are required to describe the species. The Moreton Bay specimen is subadult but totally unlike any other species of *Pomacuma* described to date. It bears little resemblance to the other two Australian species, *P. australiae* and *P. cognatum*. *P. cognatum* was recorded from the same region by Stephenson et al. (1978) and Stephenson (1980b); the anterolateral angle of its carapace is quite different to that of *Pomacuma* sp. nov. 1. The carapace of the new species has a strong median dorsal ridge extending from the ocular lobe almost to the first pereionite (Fig. 71C). The ocular lobe is wider than long with pseudorostral lobes meeting in front of it. Pereionites 2-4 are virtually as wide as the carapace in dorsal view (Fig. 70C). The pereionites and pleonites have obvious lateral and dorsal carinae (Fig. 70A-D). The uropod has a peduncle at least twice as long as the rami. The anterolateral margins of pereionites 2 and 3 are without spine-like setae. Pereiopod 1 robust with the basis widened distally and extending to the anterolateral curvature of the carapace; it bears a forwardly directed lobe on the distal end, typical of the genus.

DISCUSSION

This study shows the Bodotriidae to be the dominant family in Moreton Bay, both in terms of the number of species and the abundance of individuals. This is consistent with findings on the E, W and S coasts of Australia. Hale (1937, 1943, 1945b, 1953a) stated that, with regard to the number of species, the bodotriids outnumber the other families on the Indian Ocean and southern Australian coasts, but on the Pacific side the diastylids are equally well represented. However, his Diastylidae included the Gynodiastylidae. There is little doubt the Bodotriidae is the most diverse family on the Pacific coast of Australia.

The Bodotriidae is represented by 59 species off the Pacific coast at latitudes of less than 35°S, compared to 19 species in the Southern Ocean (Bacescu, 1988). It appears from cumacean records in other parts of the world (Sars, 1865; Calman, 1904, 1907, 1911, 1912; Zimmer, 1921; Stebbing, 1912, 1913; Bacescu, 1988; Day, 1975, 1978a; Ledoyer, 1993) that the family is negatively amphipolar. No species of Bodotriidae are yet known from latitudes greater than 70° and only 6% of records are from latitudes greater than 50° (Day, 1978a,b). Brandt (1993) and Ledoyer (1993) showed that cumaceans are abundant on the sea floor in both Arctic and Antarctic seas. Ledoyer (1993) recorded population densities of

74 individuals per cubic metre in the Weddell Sea between depths of 200-1200m; however, he did not record any bodotriids.

Endemism is very high within the Bodotriidae. Less than half (42%) of the 81 species recorded around the Australian coastline occur in waters of more than one coastal zone (Fig. 4), and only 17% are recorded in both Indian and Pacific Oceans (Bacescu, 1988). The two subfamilies of Bodotriidae recorded in Australian waters are disproportionately represented. The Bodotriinae exhibit a much higher diversity of species (54 species) and a much higher rate of occurrence than do the Vaunthompsoniinae (27 species), largely due to the high diversity of *Cyclaspis*.

The greatest worldwide diversification of species within the Bodotriidae occurs in southern tropical and temperate latitudes (Day, 1975, 1978a). If it were not for the large number of species of *Cyclaspis* in Australasia, the Bodotriinae would be a mainly tropical group. The Vaunthompsoniinae is mainly a temperate

group, with 48% of species occurring between 20° and 50°S (Day, 1978a).

The vast majority of known species (87%) of Bodotriidae are from depths of less than 200 metres, indicating that the family belongs predominantly to the shelf fauna. A number of new species of Bodotriidae and other families have been recorded from depths greater than 200m (Jones & Sanders, 1972; Day, 1978a; Gamo, 1989; Roccatagliata 1989; Jones, 1990; Watling, 1991a,b; Roccatagliata & Heard, 1992; Roccatagliata, 1993), indicating that the apparent lack of deep water species is at least partly due to scarcity of collecting.

In South African waters the numbers of individuals are highest within the Bodotriinae but diversity within this subfamily is much lower than in Australia (Day, 1978a). The ecological reasons for this difference is not clear, but the immediate cause, according to Day (1978a), is the effective colonisation of South African coastal waters by just a few species. *Iphinoe africana* and *I. stebbingi* account for over half the individuals of the Bodotriinae taken from around South Africa, with a further 10

species of this genus being recorded from the region. In Australia *Iphinoe* has not gained as great a foothold, the only recorded species being *I. pellucida*, off NSW and Tasmania.

Cyclaspis has been highly successful in colonising Australian coastal waters. It accounts for 60% of bodotriid species, and is widespread in its distribution. Hale (1953a) found that *Cyclaspis* individuals were the most abundant in light-trap catches off Garden Island, W.A. He encountered them everywhere where there was a sandy substratum. Bacescescu (1990, 1992b) described 4 new species of *Cyclaspis* from the northern waters of Australia. In the present study *Cyclaspis* predominated in catches over sand and silt/mud substrata, but *Nannastacus* was more common in seagrass beds (Hale, 1949b, 1953a). Males of both of these genera by far outnumbered ♀♀ in Hale's light-trap catches, as in the present sledge-net catches. It appears that ♂♂ of these two genera are much more active in the water column at night than are ♀♀.

Some species of Bodotriidae were highly restricted in their geographical distributions within Moreton Bay. *Gephyrocuma repandum*, the most abundant species by far at the northern entrance to Pumicestone Passage, was not recorded elsewhere in Moreton Bay or in the upper estuary. *Leptocuma barbarae*, the most abundant species in Horseshoe Bay, was not

recorded 8km to the W in Raby Bay. *Cyclaspis tranteri* the most abundant species in Raby Bay, was not recorded in Horseshoe Bay even though over 200 samples were taken there spanning all seasons. Such findings lend support to the view that cumaceans generally have restricted dispersal patterns compared to other peracarids.

The richest areas of those sampled in Moreton Bay were generally the shallow water, marine areas with sandy substrata. High numbers of individuals were consistently taken after sunset in such areas, using a sledge-net sampler at times of slack tide. Despite this the single largest sample was taken at slack high water over a mud substratum. This was an unusually large haul (87 cumaceans per m^{-3}) for the middle of the day. It was mainly due to a swarm of *Cyclaspis tranteri* which accounted for 92% of cumacean numbers taken. Even more unusual was the fact that the haul was taken over a mud substratum. Repeated samplings at the same location (site 32) on other occasions failed to yield numbers of such magnitude. Similar sledge-net hauls over sandy substrata often yielded catches of at least 50 cumaceans per m^3, when taken at night on a slack tide.

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ANNUAL PATTERN OF ACTIVITY OF THE BROWN TREE SNAKE (*BOIGA IRREGULARIS*) IN SOUTHEASTERN QUEENSLAND

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Dates of collection of *Boiga irregularis* from SE Queensland in the Queensland Museum indicate adult snakes were most commonly collected in January, February and March, the warmest and wettest months. Juvenile snakes were less numerous than adults, but were represented in all months of the year, with peaks in January and April. Few females were collected during final stages of egg development, and few gravid females are represented. These observations support field observations that suggest adults are most active in the warm, wet summer months and that females are relatively inactive during late ovarian development and when gravid. □ *Seasonality, Reptilia, Colubridae, Boiga, introduced species, Queensland.*

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The activity of reptilian species may be confined to certain months of the year. In tropical regions, where temperatures are relatively warm and stable throughout the year, many species are active all year round. However, some reptiles in these areas have depressed activity during the tropical 'winter'. This is believed to be a consequence of the low levels of humidity related to the dry season, rather than a consequence of temperature (Shine, 1991a). Even in temperate regions, high humidity seems to stimulate greater snake movement. The apparent relations of snake activity to seasonal changes in temperature and rainfall have prompted this investigation into the annual activity cycle of the arboreal brown tree snake, *Boiga irregularis*, in SE Queensland.

B. irregularis is a colubrid from coastal Australia, Papua New Guinea and islands in NW Melanesia and Indonesia (Cogger, 1992). On Guam (13°N), where it has been introduced, the snake causes a major impact on the power supply of the island by climbing on electrical wires and producing electrical shorts (Fritts et al., 1984). The Naval Public Works Command maintain a log of these occurrences, which has allowed evaluation of activity patterns of the snakes over several years. The seasonal incidence of *B. irregularis* is linked with monthly rainfall similar to other arboreal tropical snakes (Henderson et al., 1978). Peak activity occurs in May, June and July, the months that generally show an increase in rainfall after 7 months of steadily declining precipitation (Fritts et al., 1984).

Although activity of *B. irregularis* in Australasia has not been documented it has been inferred from study of its reproductive habits (Shine, 1991b; Whittier & Limpus, 1996). During late spring and summer *B. irregularis* is encountered in SE Qld, including urban areas. However, in the winter it is more secretive. Being nocturnal and arboreal means that the behaviour of *B. irregularis* is likely to be strongly influenced by seasonal changes in the weather. It is a thermoconformer during its activity period.

To observe general fluctuations in *B. irregularis*' annual activity pattern, snakes were examined from the Queensland Museum (Appendix 1). This study was based around the general premise that the seasonal distribution of the species in the museum's collection is representative of the abundance of *B. irregularis* in natural populations. Therefore, fluctuations in the number of museum specimens over the year would indicate changing activity levels of the snake. Collections of *B. irregularis* from PNG and the wet tropics of Australia differ in being collected as biased samples on specific field trips. SE Qld specimens have been obtained generally from casual encounters, usually by the general public (J. Covacevich, pers. comm.). In the Queensland Museum's collection, reliable collection dates (as opposed to registration dates) began in the 1970's.

Observations of *B. irregularis* and by inference its activity level changes through the year (Figs 1-2). Adult snakes (>75cm) are most numerous in January, February and March. These months are both the warmest and wettest (Fig. 3). Adult snakes are least frequent during May-September, the cooler, drier months of the year. Numbers of
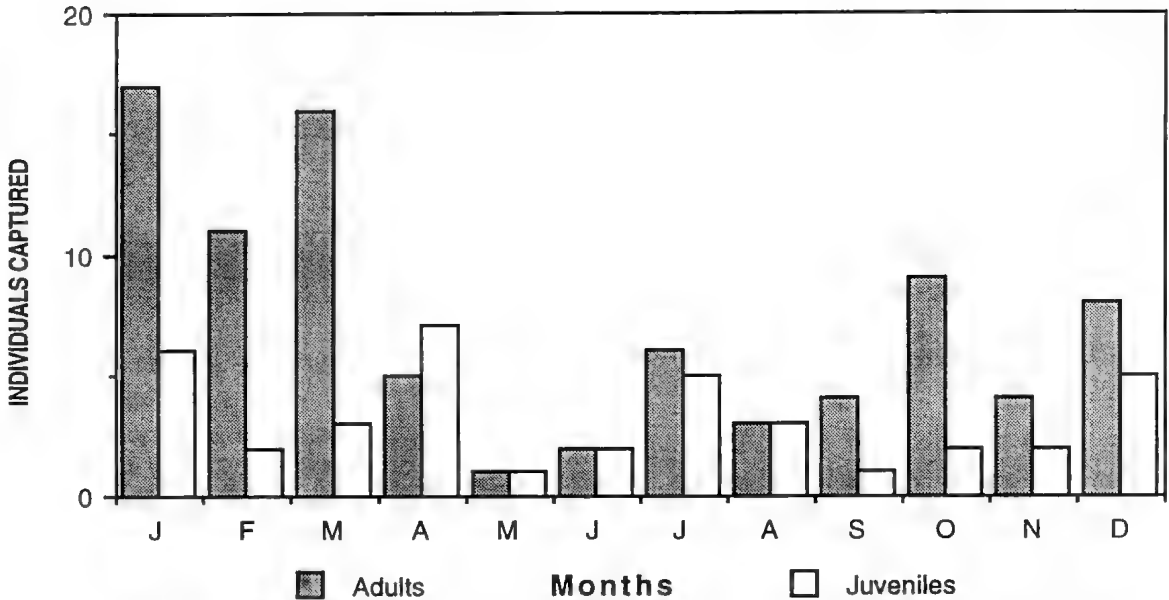
FIG. 1. Monthly incidence of adult and juvenile specimens of *Boiga irregularis* from SE Qld.

snakes only start to significantly increase in October, the first month of increased precipitation after 7 months of steadily declining rainfall. Temperatures begin their upward turn in September, a month earlier than the end of the dry season.

Juvenile snakes (<75cm) are less numerous than adults, however juveniles experience less of a decline in activity over winter, relative to their numbers (Fig 1). They persist at a more or less stable level throughout the year, although are most abundant in January and April.

Males are always more common than females in all months of the year (Fig.2). Both sexes experience declines in activity during April-September, however male snakes appear to emerge prior to females; greater numbers of males are found in October but greater numbers of females are found in December. Females also are under-represented in February, and are found in higher numbers in late summer/autumn in March and April.

Seasonal fluctuations in the activity of *B. irregularis* in SE Qld appear linked with temperature and rainfall. When minimum temperatures fall below 15°C, snakes reduce their level of activity. These minimum temperatures represent the night time temperatures that occur when these nocturnal snakes are foraging and moving about. Although temperatures begin to increase in September, no significant increase in snake activity is observed until October. This may be due to the snake's minimum temperature threshold; that is, the need for temperatures above 15°C to stimulate activity. Otherwise, the onset of rains in October may explain appearance of snakes in this month.

Sexual differences in activity levels of this snake tend to skew the sex ratio of captured snakes. This is probably due to the more secretive nature of females, especially those in the final stages of egg development (September-December) and egg laying (particularly February). Males also tend to be more active in searching for mates and as a consequence may travel further distances than females and appear more active. The large increase in male activity in October may reflect this, as October is the time when spring matings are known to occur (Whittier & Limpus, 1996).

The temporary disappearance of females in the population during February is likely to be due to the occurrence of egg laying during this month. Females must be clandestine at this time, as very few are captured with enlarged ovulated follicles (from 227). Following egg laying, females may
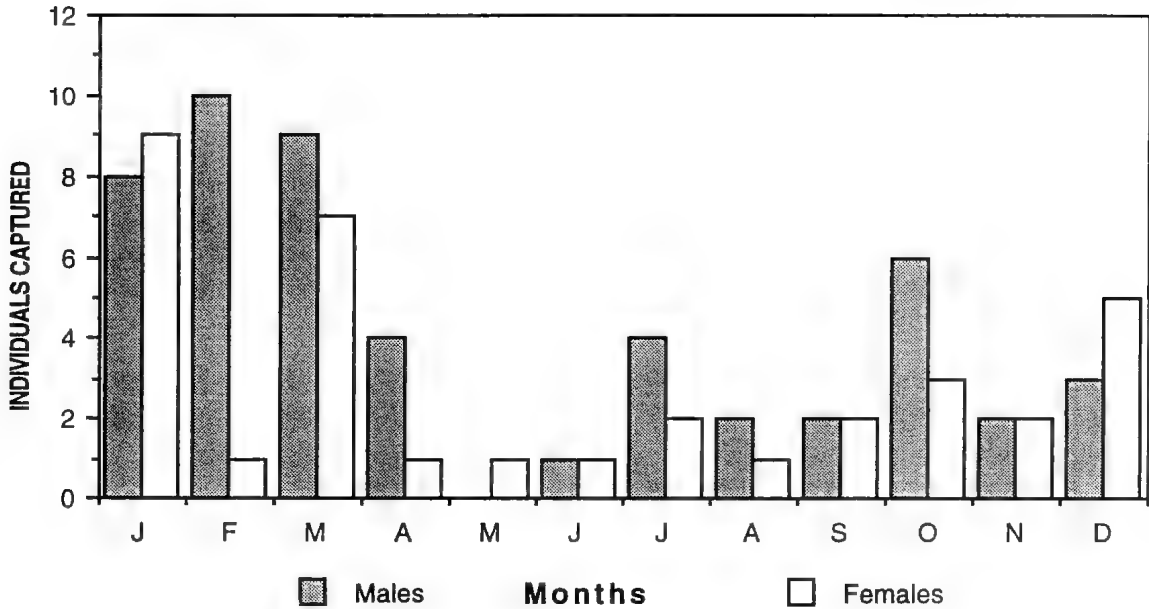
FIG. 2. Monthly incidence of male and female specimens of *Boiga irregularis* from SE Qld.

become active again, feeding to gain fat stores for winter dormancy. Similar observations of inactivity in gravid females have been made in Guam (R.T. Mason pers. comm.)

As incubation takes a minimum of 65 days in *B. irregularis* (Shine, 1991b), the small increase in juveniles in May could represent the emergence of hatchlings. These juveniles must grow and maintain themselves in the months following hatching and, as this does not occur until autumn, it explains the persistence of juveniles over the winter months.

The increase in acquisitions during July is misleading as it is caused by a group of 3 adult males and 2 juvenile males found in a winter aggregation. They were among 30-40 specimens of *B. irregularis, Dendrephalis punctulatus* and *Morelia spilota variegata* (Covacevich & Limpus, 1973). This winter aggregation of mixed species appeared not to be associated with breeding but with thermoregulatory behaviour (Covacevich & Limpus, 1973).

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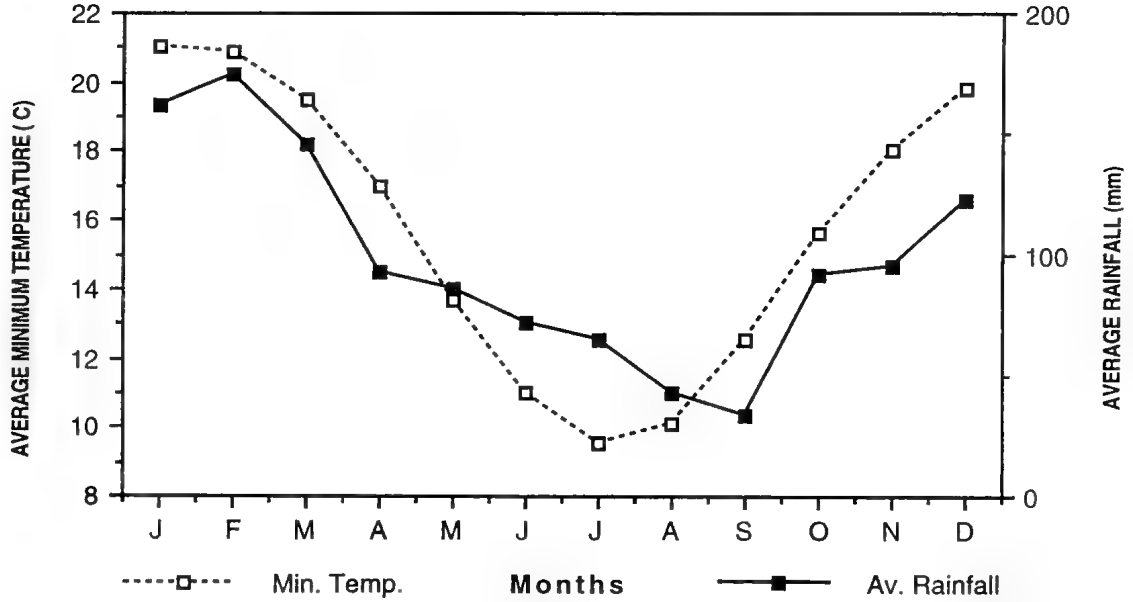
FIG. 3. Monthly mean minimum temperature (°C) and mean rainfall (mm) for Brisbane.

APPENDIX 1. Queensland Museum specimens of *Boiga irregularis* examined for this study.

QMJ11181; QMJ11269; QMJ11337; QMJ11495; QMJ11577; QMJ13512; QMJ14315; QMJ14503; QMJ14744; QMJ15554-QMJ15557; QMJ16104; QMJ16105; QMJ17518; QMJ17702; QMJ18101; QMJ18532; QMJ20295; QMJ22175; QMJ22412-QMJ22417; QMJ22461; QMJ22619; QMJ22622; QMJ22716; QMJ23163; QMJ23774; QMJ25382; QMJ25523; QMJ26906; QMJ28388; QMJ28392; QMJ28393; QMJ28477; QMJ28865; QMJ29007; QMJ30284; QMJ30960; QMJ30963; QMJ30965; QMJ31853; QMJ32238; QMJ32247; QMJ32266; QMJ35332; QMJ36056; QMJ36100; QMJ36754; QMJ36961; QMJ37146; QMJ37174; QMJ38166; QMJ40003; QMJ40278; QMJ40292; QMJ40293; QMJ40936; QMJ40949; QMJ41383; QMJ41393; QMJ41394; QMJ41506; QMJ43868; QMJ44240; QMJ46579; QMJ46860; QMJ47015; QMJ47312-QMJ47314; QMJ47320; QMJ47384; QMJ47396; QMJ47920; QMJ48104; QMJ48121; QMJ48128; QMJ48582; QMJ48599; QMJ48606; QMJ49851; QMJ49894; QMJ49906.

NEPHRURUS ASPER (SQUAMATA: GEKKONIDAE): SPERM STORAGE AND OTHER REPRODUCTIVE DATA. *Memoirs of the Queensland Museum 39(2): 487. 1996:*- Data on size at maturity, sexual dimorphism and seasonal reproductive patterns for *Nephrurus* species were provided by How et al. (1990). They examined over 1000 specimens, of which 70 were assigned to *N. asper*. This taxon has since been shown to be a composite of three species, *N. asper* Günther, *N. amyae* Couper and *N. sheai* Couper (Couper & Gregson, 1994).

The *N. asper* specimens examined by How et al. were from the collections of the Western Australian, South Australian and Northern Territory Museums, and are largely *N. amyae* and *N. sheai* (Couper & Gregson, 1994). Similarly, reproductive records for *N. asper* (Gow, 1979; Bedford & Christian, 1993) also relate to *N. sheai* and *N. amyae*, respectively, based on locality. Wagner & Lazik (1996) provided reproductive data for *N. asper* and *N. levis*. From their account it remains unclear whether their *N. asper* colony contains *N. asper* s.s., the recently described taxa (Couper & Gregson, 1994), hybrids, or a composite of two/three prickly knob-tail species.

N. asper s.s. is confined to Qld (Couper & Gregson, 1994). Two specimens collected on 25 April 1995 from Dipperu National Park (21°53'53"S, 148°43'03"E), 130km from the type locality, provide knowledge of reproduction in *N. asper*. The following observations confirm repetitive clutches for this species (found in other *Nephrurus* species by How et al., 1990, based on the simultaneous presence of oviducal eggs and yolking ovarian follicles, and in '*N. asper*' and *N. levis* by Wagner & Lazik (1996) and record sperm storage for the first time (previously inferred for only *N. milii* by How et al. (1990), on the basis of asynchrony between peak testis size and vitellogenesis).

The Dipperu specimens were transferred to Brisbane and housed in a glass tank (76 x 30cm). The two geckos avoided contact, and always used separate sheltering sites. The female appeared to be dominant and would frequently displace the male from his sheltering site, forcing him to seek alternate cover. The close confinement of these geckos was evidently stressful to the male, which was found dead on 6 Sept. 1995 (QMJ60375). On the morning of 4 Dec. 1995, the female remained in the open during daylight hours, and excavated a cavity in the moist soil surrounding the water bowl. Two eggs were laid. These were immediately removed and placed in moist vermiculite. The female retreated to cover when the eggs were removed, but emerged at night to fill in the nest hole and excavate an extensive cavity beneath a paving stone in the corner of her tank. The eggs measured 31.03x17.17mm (QMJ61614) and 30.04x17.18mm. Only the second of these survived incubation to hatch on the 28 March, 1996. Incubation took 115 days at a max/min temperature range of 31°-21°C. The hatchling measured 46.29mm (SVL) and weighed 3.2g. On the afternoon of 26 Jan. 1995, the female laid a second clutch of two eggs. These also were transferred to moist vermiculite for incubation. The second clutch of eggs was smaller than the first, measuring 26.68x15.64mm and 26.21x15.10mm and weighing 3.7g and 3.3g, respectively. The female weighed 28.5g after the eggs were layed. The relative clutch mass (RCM (1) after Greer, 1989) equalled 24.6%. The second clutch hatched on 2 June 1996. Incubation took 129/130 days at the same max/min temperature range as that for the first clutch. The hatchlings measured 44.76mm and 46.40mm (SVL) and weighed 2.5g and 3.0g, respectively.

These observations provide data on egg and hatchling sizes, and incubation period for *N. asper*. The recorded RCM (1) for *N. asper* (24.6%) corresponds closely with that of *N. amyae* (24.8%, Bedford & Christian, 1993). Given that the male *N. asper* died 140 days before the female produced her second clutch of eggs, it is apparent that females of this species have the ability to store sperm. As the male was obviously stressed, and actively avoided the female, it seems likely that the female was already carrying sperm from a copulation prior to her capture (277+ days prior to laying the second clutch of eggs).

The specimens on which these observations are based were collected during a survey of reptiles of the Brigalow Biogeographic Region in Queensland for the Endangered Species Program of the Australian Nature Conservation Agency, Canberra. I thank Jeanette Covacevich and Glenn Shea for suggesting improvements to the manuscript.

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CONTENTS (*continued*)

NOTES

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