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BY RICHARD J. F. JENKINS

Summary

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by Richard J. F. Jenkins*

Summary

Jenkins, R. J. F. (1977).—A new fossil homolid crab (Decapoda, Brachyura), middle Tertiary, southeastern Australia. *Trans. R. Soc. S. Aust.* 101(1), 1–10, 28 February, 1977.

Two new fossil decapod localities are reported in, respectively, the Oligocene and Miocene of the Mount Gambier area, and a new species of homolid crab, *Paromola pritchardi* sp. nov., is described from fragmentary remains collected at the older of these occurrences. The description of this form provides an opportunity for a review of the genus.

Introduction

In 1953 Professor M. F. Glaessner discovered fossil decapod remains in the Gambier Limestone (Sprigg 1952) near Mount Gambier, South Australia (Fig. 1). A second discovery of fossil decapods in the same formation, and also near Mount Gambier, was made in 1955 by Dr Mary Wade. The Gambier Limestone is of Late Eocene to Miocene age and occurs within the Gambier Embayment, a deep tectonic-sedimentary depression which forms the western part of the Otway Basin in southeastern Australia (Ludbrook 1969). The formation reaches a thickness in excess of 150 m; it consists largely of the fragmented remains of bryozoans and often includes abundant foraminifers (Ludbrook 1961, 1969; Abele 1967).

The discovery made by Glaessner is in the row of building stone quarries on sections 26, 28, 29, 30, 144 and 145, hundred of Blanche, 12 km west of Mount Gambier. Foraminiferal assemblages collected from section 28 and studied by McGowran (1970)[1] and myself suggest a dating within the *Globigerina labiacrassata* zone of Ludbrook & Lindsay (1969) or approximately Zone P. 19/20 of Blow (1970). With reference to Berggren (1972), this is late Early Oligocene. Coccolith studies made on the same samples by Mr S. Shafic were also suggestive of a late Early Oligocene

or late Rupelian age (R. J. F. Jenkins 1974). The fossil decapods from this locality are the richest and most diverse assemblage yet known from the Palaeogene of Australia. Either Glaessner or I[2] have identified representatives of *Pagurus* Fabricius *Trizopagurus* Forest, *Munida* Leach, *Dynomene* Latreille, *Paromola* Wood-Mason & Alcock, *Ebalia* Leach, *Lyreidus* de Haan, *Leptomithrax* Miers, *Tutankhamen* Rathbun, *Ovalipes* Rathbun, *Nectocarcinus* A. Milne-Edwards, *Pseudocarcinus* H. Milne-Edwards, *Carcinoplax* H. Milne-Edwards, and *Homoioplax* Rathbun. Three other unidentified genera are also present.

The decapod remains occur most numerously in the interval of well bedded, coarse grained, pink and yellow, bryozoal limestone which immediately overlies the homogeneous, even grained, white bryozoal limestone cut for building blocks. These limestones are part of the "middle member" of the Gambier Limestone (McGowran 1973).

The occurrence discovered by Dr Wade is in the quarries on sections 601 and 606, hundred of Blanche, 7 km south of Mount Gambier. Foraminiferal studies made by McGowran[1] indicate an age within the later part of the the *Globigerina woodi woodi* zone of Ludbrook & Lindsay (1969) or the *Globigerina woodi connecta* zone of D. G. Jenkins (1967); these

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[1] McGowran, B. (1970).—Age of six samples of Gambier Limestone. Unpublished Geol. Survey Report, Dept Mines, S. Aust. (455), 1–8.

[2] Jenkins, R. J. F. (1972)—Australian fossil decapod Crustacea: faunal and environmental changes. Ph.D. thesis.
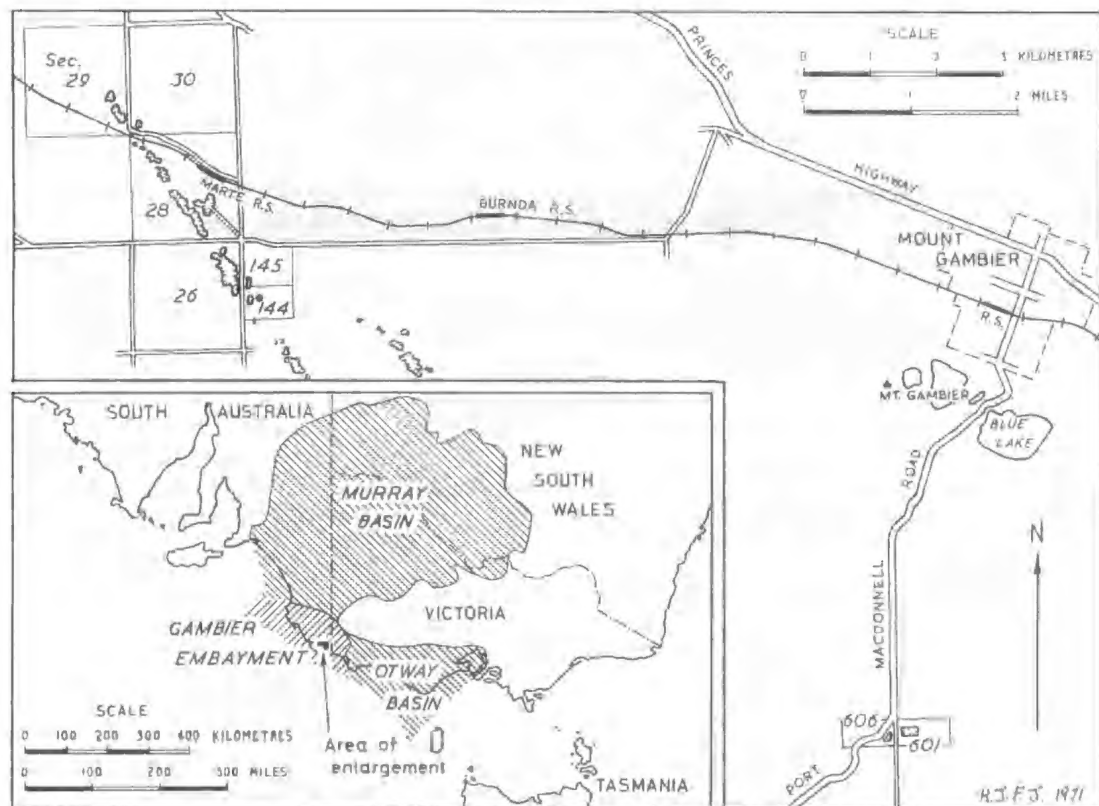
Fig. 1. Southeastern Australia and the Mount Gambier area. The fossil decapod occurrences described are in the quarries on the numbered sections shown on the map of the Mount Gambier area.

datings are in the vicinity of the lower part of Zone N.6 of Blow (1969), or middle Early Miocene. The decapod fauna is less prolific than at the first locality; it includes representatives of *Axius* Leach, *Paguristes* Dana, *Paromola, Lyreidus, Ovalipes* and *Nectocarcinus* and an unidentified parthenopid.

The crabs mostly occur in the fine grained bryozoal limestone at the bottom of the quarries. Two fragments identified as *Paromola* cf. *pritchardi* are from section 606, one from uncertain level and the other in coarse grained bryozoal limestone from probably high in the exposure. The rocks in the quarries are part of the upper member of the Gambier Limestone.

The repository of the fossil specimens studied is the palaeontological collection of the South Australian Museum (catalogue numbers prefixed "P" in the text). Observations were also made on dried specimens of the extant *Paro-*

mola petterdi (Grant 1905) in the collection of the South Australian Museum (numbers prefixed "C").

Systematics

Order Decapoda
  Infraorder Brachyura
    Section Dromiacea
      Superfamily Homoloidea
        Family Homolidae White, 1847

Type-genus: *Homola* Leach, 1815.

Remarks: Workers such as Ihle (1913), Gordon (1950), and Williamson (1965) have concluded from neontological studies that the division between the Latreilliidae (type-genus *Latreillia* P. Roux, 1830) and the Homolidae is less clear than previously supposed and unite these two families. This unity is rejected by Wright & Collins (1972) on palaeontological grounds; they consider that one of the most important diagnostic features of the Homolidae

Footnote added in proof: The following publication was not seen.
    Serene, R. & Lohavanijaya, P. (1973).—The Brachyura (Crustacea: Decapoda) collected by the Naga Expedition, including a review of the Homolidae. *Naga Rep.* 4(4), 1-187.

is the presence of dorsal *lineae homolicae*, and indicate that these structures are absent in *Latreillia* and not present in other Cretaceous forms which they refer to the Latreilliidae. They conclude that the Homolidae and Latreilliidae "have probably been independent stocks since Upper Jurassic times, albeit developing to some extent in parallel". This viewpoint is accepted herein.

Wright & Collins (1972, p. 31) consider that *Latreillopsis* Henderson, 1888, which does have *lineae*, is probably not allied to *Latreillia*, but is a homolid.

Genus *Paromola* Wood-Mason & Alcock, 1891

Type species: *Dorippe cuvieri* Risso, 1816, by monotypy.

Paromola Wood-Mason & Alcock, 1891: 267; Rathbun, 1937: 68; Bouvier, 1940: 190; Gordon, 1950: 222; Griffin, 1965: 86 (but not the new species thereunder described); Alvarez, 1968: 301.

Homola (Paromola) Alcock, 1899: 156; 1901: 64; Ihle, 1913: 69 (in key); Sakai, 1936: 47.

Thelxiope (Moloha) Barnard, 1946: 371; 1950: 341.

Diagnosis: Carapace urn-shaped or subrectangular, longer than broad, widest across branchial regions; rostrum a simple spine flanked on either side by a single supraorbital spine (occasionally with small side branches) of equal or greater size; *lineae homolicae* conspicuous, well inside lateral margins; surface usually granulate with scattered spinules, spines and tubercles, smooth in one extant species. Merus of third maxilliped elongate with a dentate prominence or a spine near middle of length of outer margin; inner margin of joint usually denticulate. Meri of pereiopods usually spinose along their length. Palms of

chelae of 1st pair of pereiopods smooth or granulate. Extant species with 13–14 gills plus 5–6 epipods.

Remarks: In the literature *Paromola* has often been confused with two other genera of homolids, *Homola* Leach, 1815 (= *Thelxiope* Rafinesque, 1814) and *Latreillopsis* Henderson, 1888. These genera all have an urn-shaped or sub-rectangular carapace and slender, elongate pereiopods.

In *Paromola* and *Homola* the meri of the pereiopods are spinose. The branchial formula of extant species of *Homola* is 13–14 gills + 6 epipods, similar to or little different from that in *Paromola* (see Bouvier 1940, p. 191–193; and Gordon 1950, p. 220–221). Differences between the two are indicated in Table 1.

The extant, New Zealand *Paromola spinimana* Griffin, 1965, which has two prominent spines above each orbit, a conspicuous spine on each epigastric region, and the palms of the chelipeds spinose, is referable to *Homola*.

The genus *Latreillopsis* has as its type-species the extant, Indo-West-Pacific *Latreillopsis bispinosa* Henderson, 1888. This, and a second living species, the Japanese *Latreillopsis laciniata* Sakai, 1936, are distinguished from *Paromola* by their branchial formula of 10 gills plus four epipods (Gordon 1950, p. 220). However the gill structure is not preserved in fossils. External morphological differences between these two species and members of *Paromola* are given in Table 2.

The following previously described extant species have been included in *Paromola* or appear referable to this genus:

Paromola cuvieri (Risso 1816)

Mediterranean (excluding the Adriatic) and eastern Atlantic, from Angola, Cape Bojador and the Azores north to Cork, the Shetland Is.

TABLE I

Summary of differences distinguishing Paromola *Wood-Mason & Alcock, 1891, from* Homola *Leach, 1865.*

Character	Homola	Paromola
Supraorbital spines	Two spines project above each orbit, a lateral rostral spine near base of rostrum, and a second spine more lateral	A single spine projects above each orbit
Rostrum	Usually bidentate, less commonly single	Invariably single
Epigastric tubercles or spines	A prominent tubercle or spine is situated on each epigastric region behind lateral rostral spine	Epigastric regions usually without conspicuous tubercles or spines
Chelae of 1st pair of pereiopods	Palms usually spinose	Palms either smooth or bearing pointed granules

TABLE 2

Summary of external skeletal differences distinguishing Paromola *from* Latreillopsis

Character	Latreillopsis	Paromola
Surface of carapace	Upper surface wrinkled with few distinct tubercles	Usually spinose with granules and pointed tubercles between
Width of carapace	Apparently mature individuals widest across hepatic regions, which are very swollen	Except in juveniles, carapace widest across branchial regions
Third maxilliped	Merus quadrate in shape; both merus and ischium without spines	Merus elongate, with dentate prominence or spine about midway along its outer margin; external distal angle of ischium sometimes produced to a spine; inner margin of both joints usually denticulate
1st pair of pereiopods (chelipeds)	Merus bearing only a terminal spine	Merus spinose along length in most species

and west coast of Norway; 150-1320 m, rarely in shallower waters.

Paromola profundorum (Alcock & Anderson 1899)

Travancore coast of India; 786 m. Maldive area; 256 m Eastern coast of Africa; 1362 m.

Paromola petterdi (Grant 1905)

Figs 3I & 4G–H.

Paromola petterdi—Gordon, 1950: 220.

Southern and southeastern Australia, from near Grafton south to Bruny I., Tasmania, and west to Eucla; 9I–1460 m. North Island of New Zealand from the Cavalli Is. to Banks Peninsula; 183-541 m. The specimen photographed, ♂, C 83, is from 32 km S.W. of Cape Everard, Victoria, at a depth of 164 m.

Paromola rathbuni Porter, 1908

Isla de Mas-Afuera, Juan Fernández, Chile.

Latreillopsis multispinosa Ihle, 1912

Latreillopsis multispinosa Ihle, 1912: 78, pl. 4, figs 19–21. Kei Is.; 204 m

This species is referable to *Paromola* because of the numerous long spines on its carapace and the form of the third maxillipeds, which have an elongate merus with a lateral spine and a terminal spine on the ischium. It markedly resembles and is evidently a near relative of *Paromola acutispina* (Sakai 1962) from Japan.

Paromola japonica Parisi, 1915

[= *Latreillopsis hawaiiensis* Edmondson, 1932] Japan: Tanega Shima I., Izu Peninsula, Sagami Bay; 183–392 m. Hawaii; 55 m. According to Sakai (1936) the species inhabits a rocky bottom.

Paromola alcocki (Stebbing 1920)

[Apparently = *Latreillopsis major* Kubo, 1936; ? = *Homola (Parhomola) majora* Edmondson, 1951.]

Southern Africa: Algoa Bay, South Africa; Mozambique; 73–312 m. Maldive area; 229 m. Japan [*Paromola major* (Kubo)]: Izu Peninsula, Sagami Bay, Tokyo Bay; 100–200 m. ?Hawaii [*Homola (Parhomola) majora* Edmondson]; 12-107 m. The Japanese form inhabits a muddy bottom (Sakai 1936).

Paromola faxoni (Schmitt 1921)

Off San Diego, California; 122–370 m. A remarkable photograph of this species in its natural environment at a depth of 370 m (Church 1971, p. 113) shows the subchelate hind limbs holding a piece of sponge above the back of the animal.

Paromola macrochira Sakai, 1962

Japan: Tosa Bay and Kii Peninsula.

Homola (Moloha) acutispinosa Sakai, 1962

Homola (Moloha) acutispinosa Sakai, 1962: 147, pl. 4 fig. 4.

Japan: Tosa Bay.

Characters of this species which indicate that it is referable to *Paromola* are the single large spine above each orbit, single rostrum, absence of epigastric spines and the smooth palms of the chelipeds.

One previously described fossil species can probable be referred to *Paromola*:

Homolopsis japonicus Yokoyama, 1911

Homolopsis japonicus Yokoyama, 1911: 12, pl. 3, fig. 4.

Paleocene or Eocene: Miike Coalfield, Japan.

The single median portion of a carapace from which this species was described unfortunately has the frontoorbital region damaged, but closely resembles *P. pritchardi* and *P. petterdi* in the shape of the other regions and in the positioning of the major tubercles.

The modern species belonging to *Paromola* can be divided into three informal species-groups which may be characterized as follows:

1. *P. cuvieri* group. Carapace more or less covered by granules and spinules and bearing short to moderately long spines on lateral and anterior-dorsal aspects. Palms of chelipeds smooth or bearing pointed granules, particularly in mature individuals. *P. cuvieri, P. petterdi, P. rathbuni, P. japonica, P. alcocki, P. faxoni, P. macrochira.*

2. *P. profundorum* group. Carapace mainly smooth, with one hepatic spine and one denticle on branchial margin. Palms of chelipeds smooth. *P. profundorum.*

3. *P. multispinosa* group. Carapace bearing elongate spines, between which it is mainly smooth. Palms of chelipeds smooth. *P. multispinosa, P. acutispinosa.*

The early Tertiary *Paromola japonicus* (Yokoyama) is a fossil member of the *P. cuvieri* group.

Paromola pritchardi sp. nov.
Figs 2, 3A–G, & 4A–E

Name: Named after Pritchards Quarry, on section 28, hundred of Blanche, South Australia.

Material: Seventeen incomplete specimens of various parts of the carapace and four specimens of isolated abdominal tergites, Holotype, P15631. Median part of carapace with rostrum and supraorbital spines lacking.

Occurrence: Gambier Limestone in quarries on sections 26, 28 and 30, hundred of Blanche.

Age: Late Early Oligocene.

Description: Carapace subrectangular, gently convex above, extremely deep in lateral aspect; regions well marked, delimited and subdivided by moderately deep grooves; greater part of surface covered by variably sized granules and spinules, nine short spines on dorsum in advance of cervical groove, lateral aspects of carapace ornamented by short spines and blunt spinules. Portion of carapace between *lineae homolicae* 1.5 times as long as wide, broadest across mesobranchial regions.

Rostrum a single, forwardly directed, slender spine about a sixth length of carapace, slightly deflexed basally, smoothly upcurved distally.
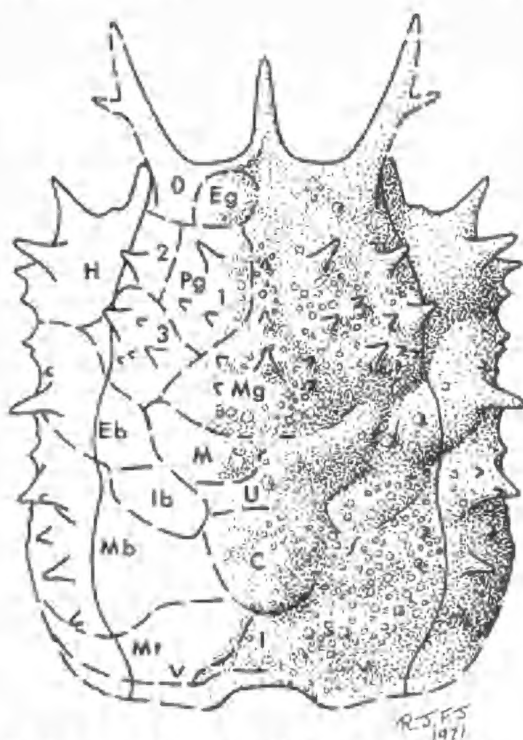

Fig. 2. *Paromola pritchardi* sp. nov., reconstruction of carapace; lettering indicates regions: O, supraorbital; Eg, epigastric; Pg, protogastric; 1, anteromedial lobe; 2, anterolateral lobe; 3, posterolateral lobe; H, hepatic; Mg, mesogastric; M, metagastric; Eb, epibranchial; Ib, inner-branchial lobe; U, urogastric; C, cardiac; Mb, mesobranchial; Mt, metabranchial; I, intestinal. Approximately x3.

Orbits forwardly directed and with a large supraorbital spine above; inner part of supraorbital margin smoothly concave and with a narrow border; supraorbital spine directed obliquely upwards, forwards and slightly outwards, about twice length of rostrum, with a lateral spinule at about half length; a short spine on lower corner of lateral margin of orbit.

Epigastric regions relatively small, slightly raised, with only a few granules. Protogastric regions each subdivided into three lobes by an oblique Y-shaped groove; anteromedial lobe with a central spine and two spinules on posterior part; anterolateral lobe with a single prominent spine; posterolateral lobe with a prominent spine on lateral aspect, a lesser spine on inner portion, and several small spinules between. Hepatic regions strongly inflated, bearing a crescentic row of four acute spines on anterolateral aspect and a group of spinules behind. Mesogastric region with a median spine

set at centre of a circlet of five, or a triangular arrangement of three small spinules; a pair of granulate ridges adjacent to posterior margin of region. Cervical groove strongly impressed, containing slit-like posterior gastric pits at .50–.52 length of carapace. Metagastric region in form of two oblique, elongated, granulate lobes and with a pair of more prominent granules positioned submedially. Urogastric region saddle-shaped, its lateral margins marked by two incised, crescentic grooves. Cardiac region moderately inflated, subtriangular, with three prominences, two side by side before and one behind. Intestinal region depressed, progressively broadened rearwards. Epibranchial regions obliquely elongated, with a spine just outside *lineae homolicae* and an irregular line of spinules on lateral aspect. Inner-branchial lobes on either side of urogastric region obliquely elongated and with one more prominent granule. Branchiocardiac groove well marked. Mesobranchial regions gently inflated, each with a line of at least three short spines just outside *lineae homolicae*, most anterior of these spines the largest and situated on a slight ridge behind lateral portion of branchiocardiac groove. Metabranchial regions relatively small, two-lobed, with a spinule on posterolateral portion of inner lobe. Subbranchial margin with a narrow border. Posterior margin fairly wide, raised, with median third indented.

A spinule at anterolateral corner of buccal frame.

Muscle attachment scars only faintly marked on interior surface of carapace except for the two small depressions forming the gastric apodemes.

Third and fifth segments of male abdomen each with a prominent median lobe and a spinule at centre of each of the lateral lobes. Fifth segment subrectangular, with posterior angles slightly produced; median lobe apparently bearing a few scattered granules and with a spinule on anterior portion; lateral lobes obliquely sulcate and apparently ornamented by coarse granules.

Fourth segment of female abdomen with the lateral lobes slightly inflated and curved downwards (if abdomen was straightened behind crab) and the surface nearly smooth except for a few, scattered weak granules; an obscure tubercle on anterior portion of median lobe.

Measurements: Holotype (P15631), length of carapace excluding rostrum, 18 mm; width of median part of carapace between *lineae homolicae* at level of mesobranchial regions, 12 mm. Paratype (P15632), length of carapace excluding rostrum, 23 mm; length of rostrum (incomplete), 3.6 mm; width of median part of carapace between *lineae homolicae* at level of mesobranchial regions, 16 mm. The largest individual known is represented by an incomplete carapace (paratype P15638) approximately 1.3 times the size of that of P15632.

Remarks: The precise arrangement of the minor spinules on the carapace of *P. pritchardi* is very variable and the relief of the regions also varies slightly in different specimens.

P. pritchardi belongs to the *P. cuvieri* species-group and closely resembles *P. petterdi* and *P. alcocki*. It seems slightly more similar to *P. petterdi* than to *P. alcocki*, but is possibly ancestral to both. It differs from *P. petterdi* in the more rectangular shape of its carapace, its more upturned rostrum, and in the less pronounced sculpture of the mesobranchial regions. The posterior gastric pits are situated at about .50–.52 the length of the carapace in *P. pritchardi*, but at about .41–.43 the length in *P. petterdi*. As well, the fossil species has a prominent spine on the anterolateral lobe of the protogastric regions, while only a small tubercle is situated in this position in *P. petterdi*.

The fossil species differs from *P. alcocki* again in its more rectangular carapace, and in having longer supraorbital spines and many fewer spinules present on the branchial regions. *P. alcocki* has the posterior gastric pits situated at about .43 the length of the carapace.

P. pritchardi apparently differs from the Eocene or Paleocene *Paromola japonicus*

Fig. 3. A-G—*Paromola pritchardi* sp. nov. A, holotype, P15631, median part of carapace, dorsal view, x3; B, paratype, P15632, median part of carapace, dorsal view, x2.5; C-D, paratype, P15637, lateral part of carapace, with spinule(s) on lower corner of lateral margin of orbit, left side, C, dorsal view, x3, D, lateral view, x3; E-F, paratype, P15636, fragment broken from lateral part of carapace, left side, E, dorsal view, x3, F, lateral view, x3; G, paratype, P15639, fragmentary remains of median part of carapace with rostrum and one supraorbital spine present, view of interior surface, x2.
H—*Paromola* cf. *pritchardi* P15806, fragment of median part of carapace, view of interior surface, x2½.
I—*Paromola petterdi* (Grant 1905). Specimen C83, ♂, dorsal view, x1.4.
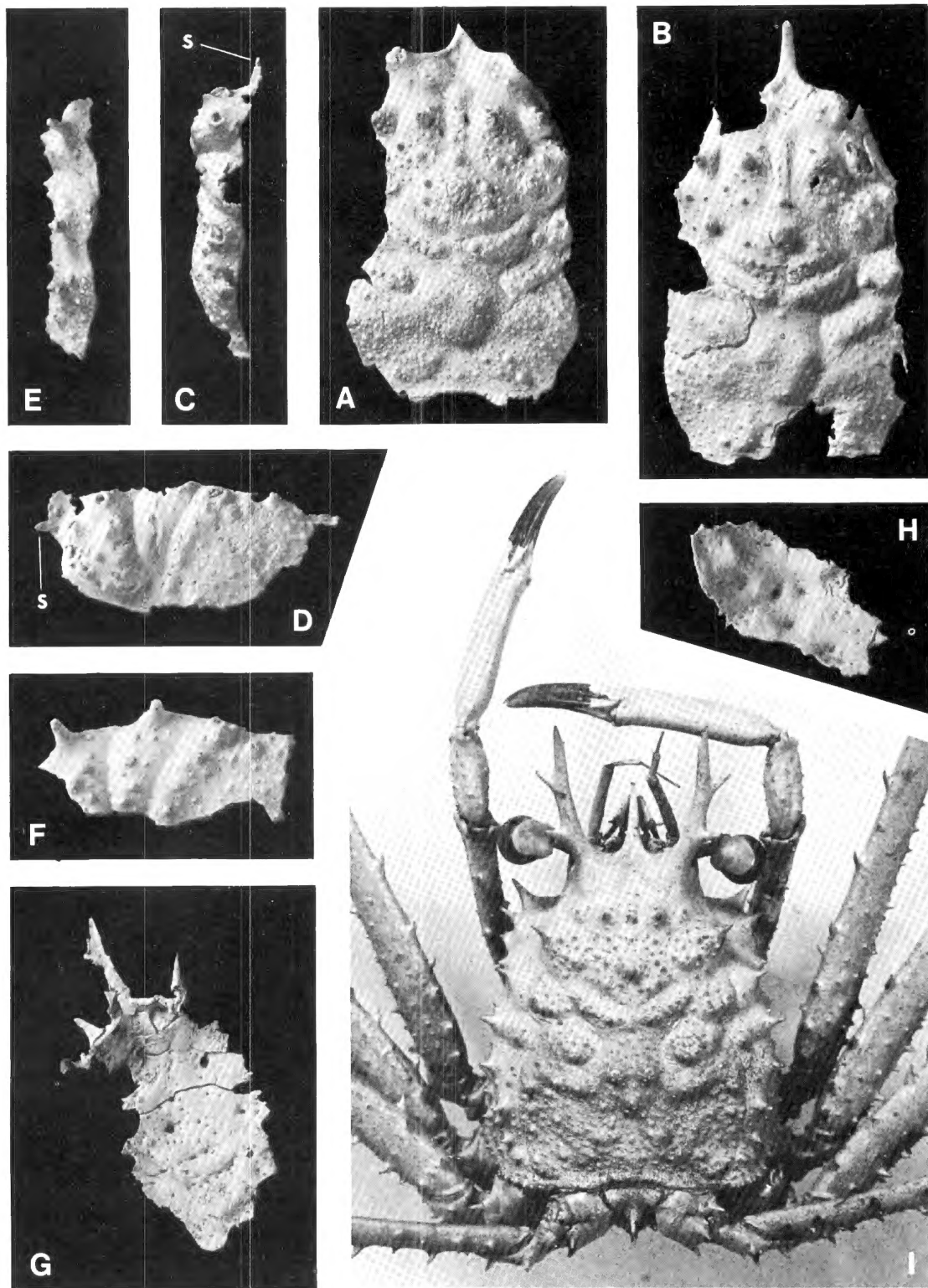
(Yokoyama) in lacking a distinct transverse ridge over the anterior part of each meso-branchial region and in bearing several additional spines. The differences which occur between *P. japonicus* and *P. pritchardi*, and between these fossils and the modern species, *P. petterdi* and *P. alcocki*, seem relatively minor and are indicative of an extremely slow rate of evolutionary change. If this rate of change is at all comparable to rates of evolutionary change experienced by *Paromola* prior to the Eocene or Paleocene, then the genus may date from a much earlier time, probably from within the Mesozoic. The fossil record of the Homolidae extends back to the Late Jurassic (Glaessner 1969). None of the other fossil genera of homolids yet described appears likely to be the direct ancestor of *Paromola*.

Paromola cf. pritchardi
Figs 3H & 4F

Material: A fragment of the median part of a carapace, P15806, and a fragment of the lateral part of a carapace, P15805.

Occurrence: Both specimens from Gambier Limestone in quarry on section 606, hundred of Blanche; P15806 from a loose piece of rock 3.5 m below the ground surface.

Age: Middle Early Miocene.

Measurements: P15806, width of median part of carapace between *lineae homolicae*, approximately 13 mm. P15805, height of lateral part of carapace approximately 8 mm.

Remarks: These remains are too fragmentary to be positively identified to the level of species, but in all features closely resemble the corresponding parts of *P. pritchardi*.

Palaeoecology

The abundance of planktonic foraminifers in the Gambier Limestone (though not at the fossil decapod locality 12 km west of Mount Gambier) is indicative of an open marine environment of deposition (Ludbrook 1961). The scarcity of terrigenous detritus in the formation, particularly the middle member, shows that it accumulated in very clear waters. Slender branching forms of bryozoans comprise the major component of the limestone (Abele 1967). In the present day seas of southern Australia, living bryozoans abound at depths of 90–220 m, and their remains are accumulating as sediments over wide areas of the continental shelf and the upper part of the continental slope (Conolly & von der Borch 1967; Wass, Conolly & MacIntyre 1970). Many of these sediments strikingly resemble those composing the Gambier Limestone in the kinds of bryozoans present, the proportions of foraminifers and other skeletal remains (such as molluscs, echinoids, and serpulid worms), their degree of sorting, and in the associated sedimentary structures (current ripples and mounds). It seems reasonable to suppose that the Gambier Limestone is a fossil equivalent of these deposits and that it formed in waters of comparable depth (approximately 90 to 220 m). This view contrasts to some degree with that of Abele (1967) who noted that the shape of certain foraminifers present in the formation is characteristic of forms which live attached to seaweed. He inferred that deposition occurred between approximately 40 and 100 m depth.

The range of depth of deposition suggested above overlaps the depth range in which the extant species of *Paromola* are most frequently recorded, between approximately 100 and 500 m. Thus *P. pritchardi* probably lived at similar depths as modern members of the genus. The living species to which the other fossil decapods known from the Gambier Limestone are most closely allied, also occur typically on the outer part of the continental shelf or on the upper part of the continental slope. Photographs of the sea bottom in the areas just mentioned (Conolly & von der Borch 1967; Wass, Conolly & MacIntyre, 1970) show living bryozoans occurring in forests and associated with sponges, or more sparsely distributed on open areas of sediment. *Paromola* seems well adapted to live in bryozoan forests, its long

Fig. 4. A-E—*Paromola pritchardi* sp. nov. A, paratype, P15643, hepatic region of carapace, right side, with a spinule(s) on the part of the margin corresponding to the anterolateral corner of the buccal frame, lateral view, x2.5; B, paratype, P15635, incomplete lateral part of carapace, right side, lateral view, x3; C, paratype ♂, P15640, tergite of third segment of abdomen, view of interior surface (top anterior), x6; D, paratype ♂, P15641, tergite of fifth segment of abdomen, view of interior surface (top anterior), x3; E, paratype ♀, P15634, tergite of fourth segment of abdomen, external surface (top anterior), x2.5.
F—*Paromola* cf. *pritchardi* P15805, fragment of lateral part of carapace, left side, lateral view, x3.5.
G-H—*Paromola petterdi* (Grant, 1905). Specimen C83, ♂, G, anterior-ventral aspect, x6, H, dorsal view, x2.5.
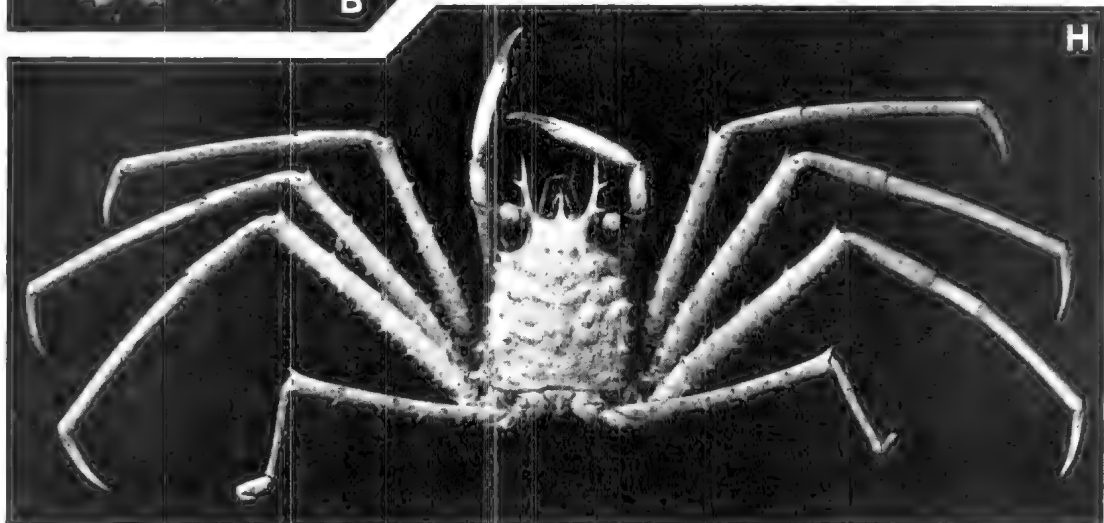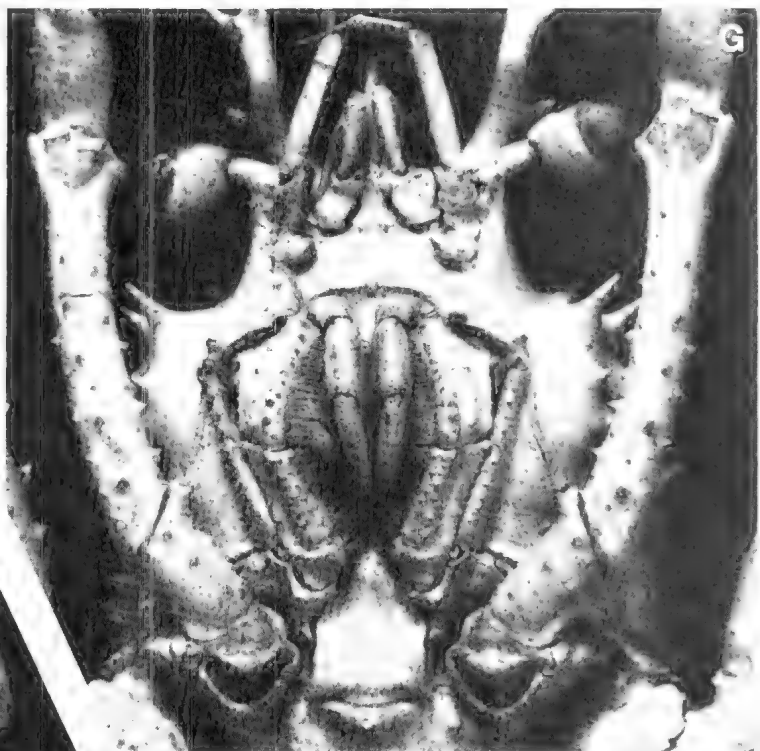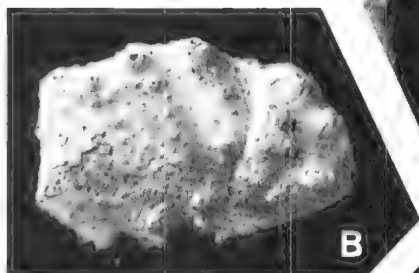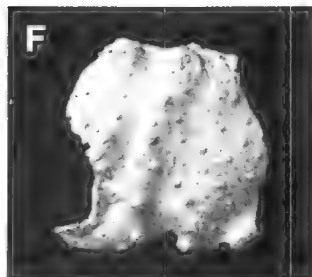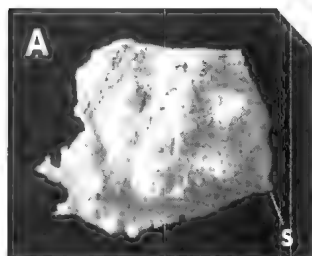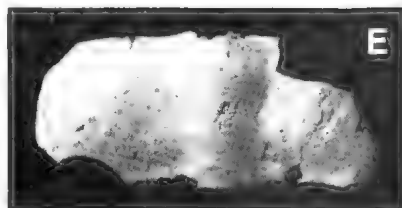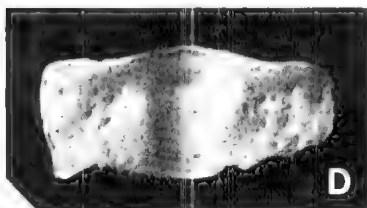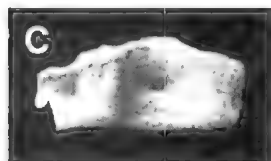
legs and high stance (Church 1971: fig. on p. 113) probably enabling it to step over the bryozoans.

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ASTRAEUS (COLEOPTRA: BUPRESTIDAE): A DESCRIPTION OF THREE NEW SPECIES AND NEW LOCALITY RECORDS

BY S. BARKER

Summary

Three new species of the Australian buprestid genus Astraeus are described, and new data on the distribution of several species are presented.

ASTRAEUS (COLEOPTERA: BUPRESTIDAE): A DESCRIPTION OF THREE NEW SPECIES AND NEW LOCALITY RECORDS

by S. BARKER*

Summary

BARKER, S. (1977).—*Astraeus* (Coleoptera: Buprestidae): a description of three new species and new locality records. *Trans. R. Soc. S. Aust.* **101**(1), 11-14, 28 February, 1977.

Three new species of the Australian buprestid genus *Astraeus* are described, and new data on the distribution of several species are presented.

Introduction

Following my review of the genus *Astraeus* (Barker 1975) more material is available including three undescribed species and several range extensions. I have also referred to the work of Cobos (1955, 1973) who placed *Astraeus* close to the newly defined tribe ACHERUSINI Cobos, which ocurs in South America, whereas I followed Carter (1929) in placing *Astraeus* in the BUPRESTINI.

As yet no information is available in the literature on the life history of *Astraeus*, because apart from the knowledge that the larvae are trunk and root borers and that many feed on *Casuarina* species, little is known of the biology of *Astraeus*.

All specimens referred to are lodged in the collection of the South Australian Museum.

New Locality Records

Astraeus (Depollus) irregularis van de Poll

3 ♂ & 1 ♀ 19 km E of Kimba, S. Aust. on *Casuarina helmsi, S. Barker*, 29.i.1976.

This is the first record of the species and subgenus outside Western Australia to which I stated it was confined (Barker 1975, p. 107).

Astraeus (Astraeus) obscurus Barker

4 ♂ & 1 ♀ 19 km E of Kimba, S. Aust. on *Casuarina helmsi, S. Barker*, 12.xii.1975; 3 ♂ & 2 ♀ Pindar Mill, Tallering Stn, Pindar, W.A. on *Casuarina dielsiana, S. Barker*, 27.xii.1975.

This extends the range by approx. 500 km N and 1,300 km E.

Astraeus (Astraeus) smythi Barker

5 ♂ & 2 ♀ 4 km west of Glasshouse Mountains, Qld, on *Casuarina littoralis, S. Barker*, 5.xi.1975.

Astraeus (Astraeus) watsoni Barker

FIG. 4A

1 ♂, Badjaling, W.A. on *Casuarina huegelliana, S. Barker*, 20.xii.1975.

Size. Male 10.9 x 3.9 mm.

General remarks. A. watsoni was described from female specimens. A male is now available and its genitalia is figured below. On the basis of external features and shape of male genitalia this species shows closest affinity with *A. macmillani, A. carnabyi, A. badeni, A. jansoni, A. oberthuri* and *A. carteri*.

New Species

Astraeus (Astraeus) mourangeensis sp. nov.

FIGS 1, 4B

Types.

Holotype: ♂ 4 km SW Mourangee Stn, Edungalba, Qld on *Casuarina* sp., *E.E. & S. Adams*, 26.xii.1974, SAM I 20 985.

Allotype: ♀ 4 km SW Mourangee Stn, Edungalba, Qld on *Casuarina* sp., *E.E. & S. Adams*, 26.xii.1974, SAM I 20 986.

Colour.

Male. Head blue-green at the apex, dark blue at the base and sides with golden reflections. Antennae blue-green with golden reflections. Pronotum turquoise at the sides with golden reflections, dark blue in the middle with purple reflections. Elytra black with blue reflections, each elytron with the following yellow markings: a basal spot; a clubbed-shaped fascia before the middle covering the humeral fold and running towards the suture but not touch-

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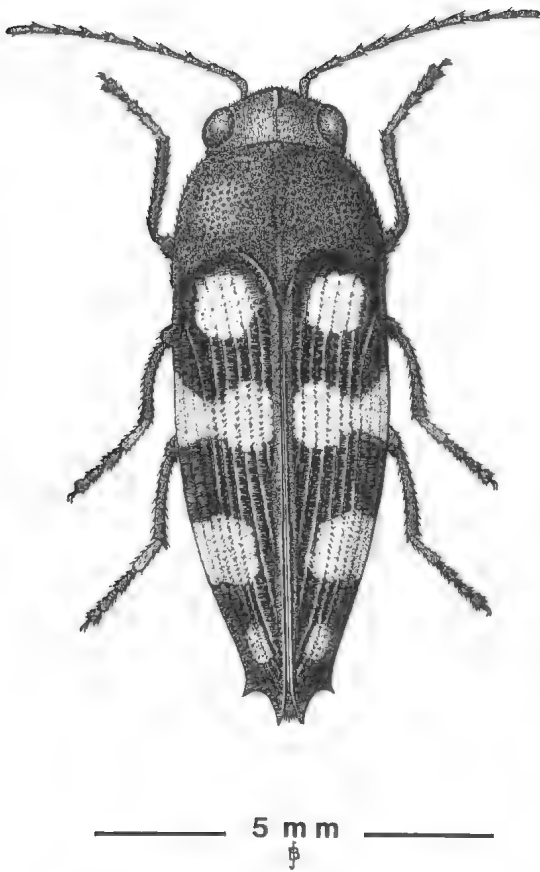
5 m m

Fig. 1. *Astraeus mourangeensis* sp. nov.

ing it; a fascia after the middle touching the margin but not reaching the suture; a preapical spot. Undersurface dark metallic blue with blue reflections; 1st tarsal segment testaceous with dark brown tips; 2nd, 3rd and 4th tarsal segments dark brown with metallic blue reflections on the supper surface; hairs silver.

Female. Head black with blue and purple reflections. Antennae black with purple reflections. Pronotum black with purple reflections in the middle, blue and purple reflections at the sides. Elytra as in the male except that the first fascia is broken to form two spots. Undersurface black with purple reflections. Legs: femur and tibia black with purple reflections; tarsi as in the male; hairs silver.

Shape and sculpture. Head with even, shallow punctures; a thin median keel; hairy. Pronotum with shallow even punctures; with a thin median longitudinal glabrous line which extends forwards from the basal crypt but does not reach the middle, from its end a wide

shallow depression extends forwards almost to the anterior margin; rounded at the sides from the base, tapered before the middle to the apex; apical edge rounded and projecting forwards in the middle; hairy. Elytra costate, the intervals flat; slightly concave at the sides from the base to before the middle then rounded and tapered to the marginal spine which is sharp but barely curved; humeral fold well developed, angled. Undersurface evenly punctured, the punctures shallow in the middle, slightly larger and deeper at the sides; sparsely haired. Overall the body shape is long and narrow.

Size. Male 6.6 x 2.7 mm.
          Female 8.0 x 2.9 mm.

Distribution. Queensland.

General remarks. On the basis of external morphology and shape of male genitalia this species shows closest affinity with *A. mastersi* and *A. samouelli*. *A. mourangeensis* differs from these species; in outline being comparatively narrower; in colour of the head and pronotum; in that only part of the first tarsal segment is testaceous.

Specimens examined. Types only.

Astraeus (Astraeus) blackdownsensis sp. nov.
FIG. 2

Type.
    Holotype: ♀ Blackdowns Tableland Forestry Reserve, Qld on *Casuarina inophloia*, 3.xi.1975, *E.E. Adams & S. Barker.* SAM I 20 987.

Colour.
Female. Head blue-green. Antennae black with green and blue reflections. Pronotum with a heart-shaped dark purple mark in the centre, green at the anterior margins, blue laterally. Elytra black with the following yellow markings on each elytron: a basal spot; a spot before the middle near the suture but not touching it; a fascia after the middle not touching the suture or lateral margin; a small preapical spot; on the margin a spot near the shoulder covering the humeral fold, midway between this spot and the fascia there is a laterally elongate mark commencing at the margin and extending for four intervals between the costae. Undersurface: prosternum metallic blue-green, remaining undersurface and legs metallic blue; hairs silver.

Shape and sculpture. Head uniformly and shallowly punctured; with a median longitudinal keel; hairy. Pronotum with shallow punctures in the middle, deeper and closer at the sides; a broad median longitudinal impressed line clearly defined at the apex run-

5 mm
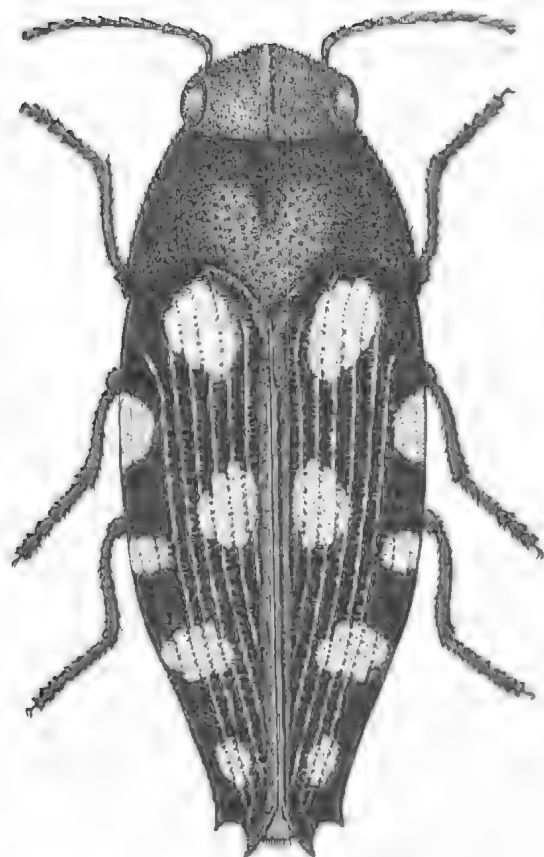
Fig. 2. *Astraeus blackdownsensis* sp. nov.

nlng ⅔ of the distance to the base; at the sides rounded and tapered from base to apex; hairy. Elytra costate, the intervals flat but slightly wrinkled; sides parallel to before the middle then gently rounded and tapered to the apex; marginal and sutural spines sharp and moderately well-developed; humeral fold moderately developed and angled. Undersurface evenly, shallowly but closely punctured; hairy.

Size. Female 10.1 x 3.8 mm.

Distribution. Queensland.

General remarks. The elytral pattern is similar to *A. watsoni* but the species differs being smaller, the elytral intervals are wrinkled and the body is comparatively hairless. It also differs in colour.

Specimens examined. Type only.

Astraeus (Astraeus) crockeri sp. nov.

FIGS 3, 4C

Types.

Holotype: ♂ Juranda rockhole 106 km S Balladonia, W.A. on *Callitris preissii*, 15.xii.1975, S. *Barker*. SAM I 20 988.

Allotype: ♀ Juranda rockhole 106 km S Balladonia, W.A. on *Callitris preissii*, 9.xii.1974, S. *Barker*. SAM I 20 989.

Paratypes: 5 ♂ & 5 ♀ Juranda rockhole 106 km S Balladonia, W.A. on *Callitris preissii*, 9.xii.1974 & 15.xii.1975, S. *Barker*.

Colour. Head and pronotum metallic purple. Antennae black with blue reflections. Elytra black with purple reflections, each elytron with the following yellow markings: a basal spot; before the middle a fascia covering the humeral fold, concave towards the base and running close to the suture but not touching it; after the middle a fascia commencing on the margin concave towards the apex running towards the suture but not reaching it. Undersurface purple. Legs with blue and purple reflections. Hairs silver.

5 mm

Fig. 3. *Astraeus crockeri* sp. nov

L_1mm_」

Fig. 4. Outline diagram of dorsal surface of parameres of male *Astraeus* (*Astraeus*) species A: *A. watsoni;* B: *A. mourangeensis;* C: *A. crockeri.*

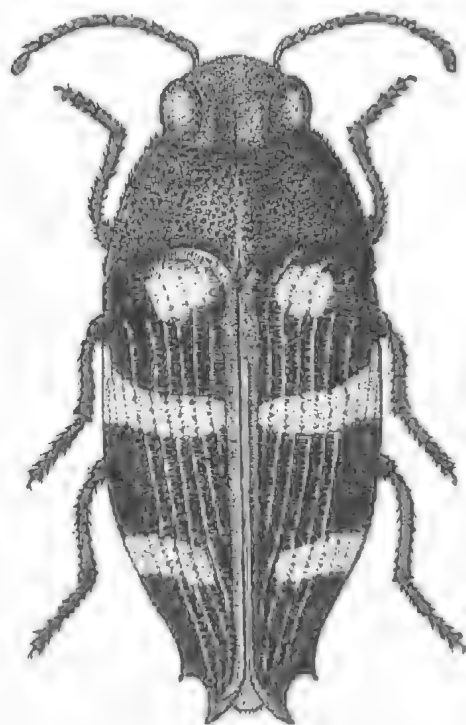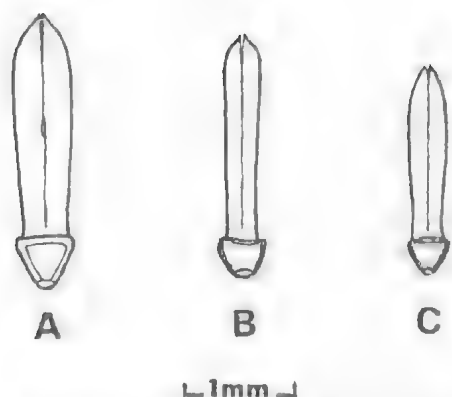*General remarks.* On external characters this species shows closest affinity with *A. badeni,* although male genitalia are similar in shape to those of *A. fraseriensis.* It differs from *A. badeni* in being smaller in size, the intervals between the costae on the elytra are smooth hence the elytra are shinier than in *A. badeni* in which the costal intervals are wrinkled. Also the humeral fold is better developed as are the marginal spines. The colour also differs. In the specimens of *A. crockeri* I have examined, none has a preapical spot on each elytron although in *A. badeni* this is a variable character. Named after Mrs A. E. Crocker.

With the addition of the above new species the key to *Astraeus* (sensu stricto) (Barker 1975, pp. 114, 115) needs the following modifications. Add under the appropriate couplet—

6. Only 1st tarsal segment testaceous .... *mourangeensis* sp. nov.
11. Head green, pronotum with heart-shaped purple mark in centre, green in front, blue at sides .... *blackdownsensis* sp. nov.
21. Humeral fold moderately developed and angled* .... *crockeri* sp. nov.
* See Barker (1975) Fig. 1.

Shape and sculpture. Head with shallow even punctures, no median keel, slightly excavated between the eyes, hairy. Pronotum with shallow even punctures, basal crypt very elongate and with a short impressed line projecting forwards from it and continuous with the basal end of a median longitudinal glabrous line which does not reach the anterior margin; at the sides rounded and tapered from base to apex; hairy. Elytra costate, the intervals flat; more or less parallel-sided from the base to the middle then rounded and tapered to the strongly developed marginal spine, sutural spine well developed; humeral fold moderately developed and angled. Undersurface shallowly but evenly punctured; hairy. Overall the body shape is rounded when seen from above.

Size. Males 6.4 ± 0.2 x 2.8 ± 0.1 mm (6). Females 6.8 ± 0.1 x 2.9 ± 0.1 mm (6).

Distribution. Southeast Western Australia.

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EUCALYPTUS CYANOPHYLLA, A NEW SPECIES FROM SOUTH AUSTRALIA AND VICTORIA

BY *M. I. H. BROOKER*

Summary

A new species of mallee eucalypt, belonging to series DUMOSAE, and distributed in the Murray Mallee region of South Australia and northwestern Victoria, is described and figured, and its affinities discussed.

EUCALYPTUS CYANOPHYLLA, A NEW SPECIES FROM SOUTH AUSTRALIA AND VICTORIA

by M. I. H. Brooker*

Summary

Brooker, M. I. H. (1977).—*Eucalyptus cyanophylla*, a new species from South Australia and Victoria. *Trans. R. Soc. S. Aust.* 101(1), 15-18, 28 February, 1977.

A new species of mallee eucalypt, belonging to series DUMOSAE, and distributed in the Murray Mallee region of South Australia and northwestern Victoria, is described and figured, and its affinities discussed.

Description

Eucalyptus cyanophylla Brooker sp. nov. (SLE:H).[1] Figs 1-3.

Eucalypto dumoso A.Cunn. ex Schau. affinis a qua foliis latioribus et schistacioribus, alabastris et fructibus grossioribus, et florescentia differt.

Frutex "mallee" ad 6 m altus, cortice basin versus fibroso, supra laevi. Glandulae oleosae in medulla. Lignotuberium formans. Cotyledones reniformes. Folia plantulae petiolata, lanceolata vel ovata, 1-6 x 0.4-3 cm. Folia juvenilia petiolata, ovata, atroviridia, 7-12 x 4-7 cm. Folia adulta petiolata, lato-lanceolata, schistacea vel glauca, 10-16 x 2-3 cm. Inflorescentiae axillares 7(11)-florae. Pedunculi crassi, 0.5-1.2 cm longi. Alabastra breviter pedicellata vel subsessilia, 0.8-1.3 x 0.5-0.8 cm. Hypanthium cylindricum vel obconicum, rugosum vel costatum. Operculum hemisphaericum vel turbinatum, costatum. Filamenta in alabastro primum erecta demum inflexa. Antherae oblongae vel obovatae, sub-basiflxae, versatiles, in rimis longitudinalibus dehiscentes. Loculi 4-5. Ovula verticaliter 4-seriata. Fructus cylindrica vel obconica, 0.7-1 x 0.7-0.9 cm, rugosa vel costata. Discus declivis. Valvae non-exsertae. Semina rufa, nitentia, reticulo non-profundo.

Holotypus ca. 3 km northeast of Berri, South Australia (34°15'S, 140°37'E) *B. Copley* 3799, 5.viii.1972 (AD). Isotypus: FRI.

A species with affinity to *E. dumosa* A Cunn. ex Schau. but differing in the broader, bluer leaves, coarser buds and fruits, and in the flowering time (late summer-autumn for *E. dumosa;* winter-spring for *E. cyanophylla*).

A *mallee* to 6 m tall with grey-brown, fibrous bark towards the base, smooth above. Oil glands in pith. Capable of forming lignotubers.

Cotyledons reniform. Seedling leaves petiolate, lanceolate to ovate, 1-6 x 0.4-3 cm. Juvenile leaves petiolate, ovate, dark green, 7-12 x 4-7 cm. Adult leaves petiolate, broad-lanceolate, bluish grey to glaucous, 10-16 x 2-3 cm.

Inflorescences axillary of 7(11) buds. Peduncles thick, 0.5-1.2 cm long. Buds shortly pedicellate to subsessile, 0.8-1.3 x 0.5-0.8 cm. Hypanthium cylindrical or obconical, rugose or ribbed. Operculum hemispherical or turbinate, ribbed. Filaments in bud at first erect then inflexed. Anthers oblong to obovate, sub-basifixed, versatile, opening in longitudinal slits. Locules 4-5. Ovules in 4 vertical rows.

Fruit cylindrical or obconical, 0.7-1 x 0.7-0.9 cm, rugose or ribbed. Disc sloping inwards. Valves to rim level.

Seed red-brown, lustrous, with a shallow reticulum.

Collections examined: South Australia—Overland Corner, 2.xii.1913. J. B. Cleland (NSW); Alawoona, Dec. 1913, J. B. Cleland (AD); Morgan-Renmark, July 1914, W. Gill (NSW); Berri, Jan. 1921, J. B. Cleland (AD); Mindarie, 5.iv.1947, C. D. Boomsma (Woods & Forests Dept Adelaide, FRI); Berri, 20.x.1962, B. Dangerfield (AD); adjacent to northwest corner of Berri Irrigation Area, 11.x.1965. D. E. Symon 3789 (NSW); Winkie, Dalziel Rd, 23.xii.1967, B. Copley 1672 (AD, FRI); Renmark-Berri, 18.viii.1968, L A. S. Johnson (NSW 47194); 20 km from Barmera towards Overland Corner, 27.viii.1968, M. E. Phillips (NSW); 1 km N of Alawoona, 6.vi.1970, G. W. Anderson (AD); Overland Corner, 13.vi.1970, A G Spooner (AD); Berri, July 1970, F. van der Sommen (FRI); 25.9 km E of Waikerie on road to Kingston, 3.iv.1975, M. I. H. Brooker 4905 (FRI, AD, MEL, NSW, PERTH); 24 km W of Karoonda, 24.vii.1975, F. van der Sommen (NSW).

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[1] Code derived from Pryor & Johnson (1971).

Fig. 1. *Eucalyptus cyanophylla* sp. nov. A—Seedling, x .9. B, C—Buds and fruits from type, x .9. D, E Buds and fruit from Berri, July 1970, F. van der Sommen, x .9. F—Adult leaves, x .6.
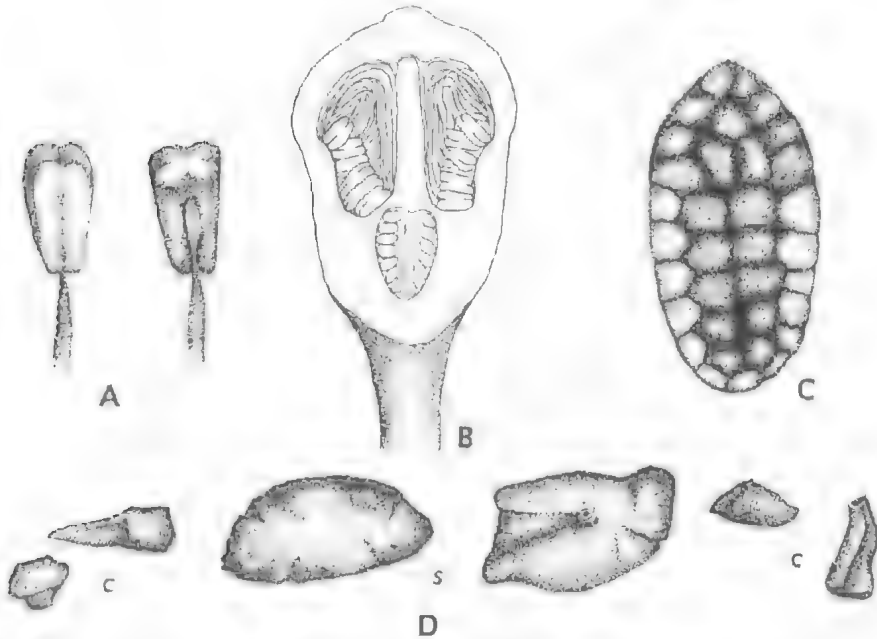
Fig. 2. *Eucalyptus cyanophylla* sp. nov. A—Anthers, x 15. B—Bud section, x 3. C—Ovules, x 14, D—Seed(s) and chaff (c), x 15.
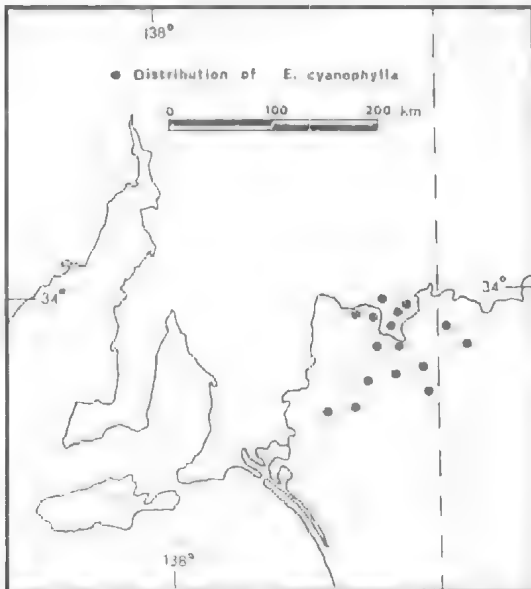
Fig. 3. Distribution of *Eucalyptus cyanophylla* sp. nov.

Victoria—6.4 km S of Meringur, Apr. 1971, H. Gorge (NSW); ca. 2 km E of state border between Renmark and Mildura, 3.iv.1975, M. I. H. Brooker 4904 (FRI, MEL, AD, NSW, K).

Discussion

Eucalyptus cyanophylla is the species of the Murray Mallee of South Australia and of northwestern Victoria (Fig. 3) which has been incorrectly referred to as *E. pileata* Blakely by Burbidge (1947), Black (1952), and Willis (1972). The type of *E. pileata* is from Desmond, Western Australia and the typical form extends eastwards as far as southern and western Eyre Peninsula in South Australia. Related forms on Yorke Peninsula should be interpreted as intergrades between *E. pileata* to the west and *E. dumosa* and *E. anceps* (Maid.) Blakely to the east. *E. pileata* differs strikingly from *E. cyanophylla* in the narrower, bright green, glossy leaves which are often held more or less erect on the branchlets.

Both *E. pileata* and *E. cyanophylla* belong in the series DUMOSAE (Pryor & Johnson 1971) which is segregated in the proposed subgenus *Symphyomyrtus* by the association of several constant features, viz., reniform cotyledons; strict inflection of the staminal filaments each of which bears fertile, versatile anthers; glandular pith; placentae with four vertical rows of ovular structures; and lustrous, reddish seed with a shallow reticulum. These characters have been discussed by Carr & Carr (1969) and Brooker (1971, 1972).

The species name is given for the conspicuously blue-grey leaves which distinguish it from *E. dumosa* and other mallees growing

near or within its area of distribution. Willis (1972) commented on the "silver aspect" of the trees so noticeable in the field.

My observations agree with those of Mr C. D. Boomsma (pers. comm.) that *E. dumosa* does not ocur within the area of distribution although it overlaps along the margins as might be expected.

Key

A revision of part of Black's Key (1952, pp. 616–617) for the South Australian species of the section DUMARIA (Pryor & Johnson 1971) is as follows:

CC.[1] Leaves alternate, thick and stiff.

  DD. Seed reddish-brown, lustrous with a shallow reticulum.

    EE. Buds and fruit quite sessile, hypanthium not wholly tapering if at all .. *E. conglobata*

    EE. Buds and fruit subsessile to pedicellate, hypanthium tapering.

      FF. Leaves green, more or less glossy.

        GG. Buds and fruit more or less sessile, operculum conical to hemispherical, smooth or ribbed .... *E. anceps*

        GG. buds and fruit pedicellate, operculum beaked or hemispherical, usually prominently ribbed .... *E. pileata*

      FF. Leaves grey-green or bluish gray, dull.

        HH. Leaves grey-green, 1–2 cm wide, Flowering in late sumer and autumn .... *E. dumosa*

        HH. Leaves bluish grey 2–3 cm wide. Flowering in winter and spring .... *E. cyanophylla*

  DD. Seed grey and deeply pitted; or blackish-grey, more or less smooth on the dorsal side and with sharp ribs on the ventral side.

    II. Seed grey and deeply pitted.

      JJ. Operculum flattened-hemispherical, as wide or wider than the hypanthium, hypanthium not conspicuously ribbed .... *E. concinna*

      JJ. Operculum obtusely conical or hemispherical and pointed, rarely as wide as, usually narrower than the hypanthium, hypanthium obscurely or conspicuously ribbed.

        KK. Fruit small, to 0.5 cm diameter, leaves narrow lanceolate .... *E. brachycalyx*[2]

        KK. Fruit larger, more than 0.6 cm diameter, leaves lanceolate .... *E. rugosa*

    II. Seed blackish-grey, more or less smooth on the dorsal side and with sharp ribs on the ventral side.

      LL. Fruit barrel-shaped, 1.5–2 cm long, pedicellate, smooth or with shallow ribbing; fruiting peduncle reflexed or rarely erect . *E. pimpiniana*

      LL: Fruit cylindrical or urceolate, 1–2 cm long, pedicellate or sessile, smooth, shallowly or coarsely ribbed; fruiting peduncle reflexed or erect.

        MM. Fruit pedicellate, cylindrical or urceolate, 1–1.5 cm long, smooth or shallowly ribbed; fruiting peduncle erect or reflexed .... *E. incrassata*[3]

        MM. Fruit pedicellate or sessile, cylindrical, 1.5–2 cm long, coarsely ribbed; peduncle erect .... *E. angulosa*

CC.[1] Leaves opposite, glaucous, mostly connate at base. .... *E. gamophylla*

[1] CC only, as in Black (1952).

[2] *E. brachycalyx* and *E. rugosa* are intergrading species. *E. rugosa* is usually coastal and is more robust in leaves, buds and fruit.

[3] *E. incrassata* and *E. angulosa* are intergrading species. *E. angulosa* is usually coastal and is more robust in leaves, buds and fruit.

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THE GENUS CYCLOSTRONGYLUS JOHNSTON & MAWSON (NEMATODA: TRICHONEMATIDAE)

BY PATRICIA M. MAAWSON

Summary

Cyclostrongylus is redefined. The type species of the genus Oesophagonastes (O. gallardi), is a synonym of C. wallabiae, so this genus falls and its species are transferred to Cyclostrongylus. Cyclostrongylus spp. Considered valid are C. wallabiae (type sp.), C. gallardi, C. kartana (s. O. kartana), C. leptos (s. O. leptos) and C. parma (s. O. parma). Of the three other species formerly assigned to Cyclostrongylus, C. clelandi belongs to another genus, C. dissimilus belongs to Macropostrongyloides, and C. medioannulatus (of which no specimen can be found) is regarded as sp. inq.

THE GENUS *CYCLOSTRONGYLUS* JOHNSTON & MAWSON (NEMATODA: TRICHONEMATIDAE)

by Patricia M. Mawson*

Summary

Mawson, P. M (1977).—The genus *Cyclostrongylus* Johnston & Mawson (Nematoda: Tricho-nematidae). *Trans. R. Soc. S. Aust.* **101**(1), 19-20, 28 February, 1977.

Cyclostrongylus is redefined. The type species of the genus *Oesophagonastes* (*O. gallardi*), is a synonym of *C. wallabiae*, so this genus falls and its species are transferred to *Cyclostrongylus*. *Cyclostrongylus* spp. considered valid are *C. wallabiae* (type sp.), *C. gallardi*, *C. kartana* (s. *O. kartana*), *C. leptos* (s. *O. leptos*) and *C. parma* (s. *O. parma*). Of the three other species formerly assigned to *Cyclostrongylus*, *C. clelandi* belongs to another genus, *C. dissimilis* belongs to *Macropostrongyloides*, and *C. medioannulatus* (of which no specimen can be found) is regarded as *sp. inq.*

Introduction

The genus *Cyclostrongylus* was erected in 1939 to include four species, *C. wallabiae*, *C. clelandi*, *C. gallardi* and, doubtfully, *C. dissimilis*. *C. medioannulatus* was added by Johnston & Mawson (1940). These species were similar in having a cuticular collar around the anterior end, a deep buccal cavity and, in the first three, an oesophagus of distinctive shape. The walls of the buccal cavity showed different degrees of thickening.

The types of these species, and fresh material of *C. dissimilis* and *C. clelandi*, have been examined, and it is now possible to clarify the position of the genus.

Results

The most striking fact emerging from this study is that the type species of *Cyclostrongylus* (*C. wallabiae*) is identical with the type species of *Oesophagonastes*, *O. gallardi* (Johnston & Mawson 1942), described from the same host species and from a relatively close locality in New South Wales. *Oesophagonastes* now becomes a synonym of *Cyclostrongylus*, and the species assigned to *Oesophagonastes* must be transferred to *Cyclostrongylus*.

Some of the species originally placed in *Cyclostrongylus* vary considerably from the type, and are not now considered as valid species of the genus. These are:

C. clelandi in which the shape of the oesophagus and of the cephalic papillae are quite different, and in which the walls of the buccal cavity do not appear to be sclerotized at all. A new genus will be necessary for this species (in preparation).

C. dissimilis described from a single damaged male specimen is now referred to *Macropostrongyloides* because of the shape of the oesophagus, tail, and bursa. It differs from other *M.* spp. in having very long spicules. The specimen was apparently moribund when collected, and the buccal capsule is atypical. Several specimens of *Macropostrongyloides* have recently been found in which the buccal capsule is in a similar condition.

In the case of *C. medioannulatus*, the specimen labelled as type is a female *Rugopharynx australis*, obviously placed in the tube in error. No representative of *C. medioannulatus* has been found, and the species must be regarded as *species inquirendum*.

A revised diagnosis of *Cyclostrongylus* and a key to the valid species follows.

Trichonematidae: Small worms, anterior end with more or less well developed cuticular collar pierced by amphids and cephalic papillae; well developed usually transversely striated buccal capsule; oesophagus with anterior cylindrical part followed by constriction surrounded by nerve ring, before terminal bulb; cervical

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papillae setiform, near nerve ring. Male: bursa not deeply lobed, externo-dorsal ray arising separately or with laterals, dorsal ray bifurcate each branch giving off a lateral stem. Female: tail more or less conical, vulva near anus.

Parasites of stomach or oesophagus of macropod marsupials. Type species *C. wallabiae* Johnston & Mawson, 1939 (syn. *Pharyngostrongylus gallardi* Johnston & Mawson, 1942; *Spirostrongylus gallardi*: Mawson, 1955; *Oesophagonastes gallardi*: Mawson, 1965). From *Macropus bicolor*, N.S.W.

Other species:

C. gallardi Johnston & Mawson, 1939. From *M. rufogriseus*, N.S.W.

C. kartana (Mawson 1955), (syn. *Spirostrongylus kartana; Oesophagonastes kartana*: Mawson, 1965). From *M. eugenii*, S. Aust., and *M. rufogriseus*, Qld.

C. leptos (Mawson 1965), (syn. *Oesophagonastes leptos*). From *Macropus dorsalis*, Qld.

C. parma (Johnston & Mawson 1939), syn. *Pharyngostrongylus parma; Spirostrongylus parma*: Mawson, 1955; *Oesophagonastes parma*: Mawson, 1965. From *Macropus parma*, N.S.W.

This genus differs from *Rugopharynx* Mönnig mainly in the presence of a cuticular collar, in the shape of the oesophagus, and in the shape and character of the bursa.

Key to species of *Cyclostrongylus*

1. Buccal capsule wall wider anteriorly than posteriorly 2
   Wall of buccal capsule not markedly wider anteriorly 4
2. Cuticular collar not well developed .... *C. parma*
   Cuticular collar well developed 3
3. Buccal capsule short, about equal to its external diameter at anterior end .... *C. wallabiae*
   Buccal capsule long, at least twice external diameter at anterior end .... *C. kartana*
4. Cuticular collar well developed; buccal capsule wider than long .... *C. gallardi*
   Cuticular collar not well developed; buccal capsule wider than long .... *C. leptos*

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REVISION OF THE AUSTRALIAN TERTIARY SPECIES ASCRIBED TO LIMATULA WOOD (MOLLUSCA, BIVALVIA)

BY M. F. BUONAIUTO

Summary

Limatula crebresquamata Tate (Late Eocene-Miocene) and Limatula jeffreysiana Tate (early Miocene) are revised. The Late Eocene L. margaritata sp. nov. and the Pliocene L. ludbrookae sp. nov. have hitherto been mistaken for L. jeffreysiana. The Early Pliocene L. subnodulosa Tate is shown to be a synonym of Limea (Gemellima) austrina Tate. A brief discussion and revision of the Tortachilla Limestone is given and a new procedure for S.E.M. photography is described.

REVISION OF THE AUSTRALIAN TERTIARY SPECIES ASCRIBED TO *LIMATULA* WOOD (MOLLUSCA, BIVALVIA)

by M. F. BUONAIUTO[*]

Summary

BUONAIUTO, M. F. (1977).—Revision of the Australian Tertiary species ascribed to *Limatula* Wood (Mollusca, Bivalvia) *Trans. R. Soc. S. Aust.* **101**(1), 21-33, 28 February, 1976.

Limatula crebresquamata Tate (Late Eocene-Miocene) and *Limatula jeffreysiana* Tate (Early Miocene) are revised. The Late Eocene *L. margaritata* sp. nov. and the Pliocene *L. ludbrookae* sp. nov. have hitherto been mistaken for *L. jeffreysiana*. The Early Pliocene *L. subnodulosa* Tate is shown to be a synonym of *Limea (Gemellima) austrina* Tate. A brief discussion and revision of the Tortachilla Limestone is given and a new procedure for S.E.M. photography is described.

Introduction

Hitherto only three fossil species of *Limatula* Wood were known or recognized in the Australian Tertiary: *L. jeffreysiana* (Tate), now known to be Early Miocene in age, the Late Oligocene-Early Miocene *L. crebresquamata* Tate, and the Early Pliocene *Limatula subnodulosa* Tate, here believed to be a worn specimen of *Limea (Gemellima) austrina* Tate. Observations made during a current revision of the Eocene Molluscan faunas have revealed that two specimens of the series of *L. jeffreysiana* borne on the tablet SAM T972 from Tate's collection, represent two other species: the Late Eocene *L. margaritata* sp. nov. (T972-M) and the Pliocene *L. ludbrookae* sp. nov. (T972-D).

The material here examined is in the Tate Collection and Mollusc Collection housed in the South Australian Museum (SAM), which remains the property of the Department of Geology and Mineralogy, University of Adelaide.

Optimal S.E.M. results were obtained by pre-treating the specimens by exposure to osmium-tetraoxide vapour for twelve hours, followed by coating with carbon and gold-palladium. Carbon or silver dag or tragacanth glue did not influence the results, and problems of high charging were eliminated other than where there was imperfect specimen-stub connection or coating. It produced excellent resolution even of very tough surfaces at high magnifications, and represents an extreme simplification of Robertson's (1971) technique.

Systematic descriptions

CLASS	BIVALVIA Linné, 1758
SUBCLASS	PTERIOMORPHIA Beurlen, 1944
ORDER	PTERIOIDA Newell, 1965
SUBORDER	PTERIINA Newell, 1965
SUPER-FAMILY	LIMACEA Rafinesque, 1815
FAMILY	LIMIDAE Rafinesque, 1815
GENUS	*Limatula* Wood, 1839

Diagnosis. Shell small, oval, higher than long, inflated, without umbonal ridges; auricles small, subequal; margins not gaping; hinge edentulous; ornaments of primary radial riblets and secondary concentric costellae, more conspicuous on the dorsal and ventral regions; concentric ornaments can develop into primary in the anterior and posterior regions; median sulcus can occur (after Cox & Hertlein, 1969, p. N389).

Limatula margaritata sp. nov.
FIGS 1, 6-9

Derivation of name. From the Latin *margaritatus*, beaded, because of its beaded ribs.

Holotype. SAM P18343, figs 6-7, 9.

Type-formation. Tortachilla Limestone, Late Eocene.

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Type-locality. Maslin Bay, Willunga Sub-Basin, St Vincent Basin.

Material. 172 specimens (21 RV, 22 LV, 129 VV) generally very badly preserved; the topotype SAM T972-M from Tate's collection.

Description. Shell small, oval, higher than long, inflated, slightly inequilateral; umbo central, inflated with little protruding orthogyrate beaks. Margins: anterior and posterior subelliptical, winged; ventral very elliptical. Margin connections: postero-ventral imperceptible; antero-ventral rounded, angular. Auricles small, subequal, longer than high, with protruding ends. Longitudinal shell section convex with maximum at the posterior ridge. Regions: anterior flatter and steep; posterior convex and steep; dorsal and ventral more convex and steeper to the ventral margin. Commissure region crenulate. Cardinal area narrow and rather long, resilifer deep, hinge edentulous.

Ornament. About 40 radial triangular costae with narrow trapezoid trough-shaped interspaces, wider to the anterior and posterior regions. The costae fade to the auricles; marked concentric grooves separating concentric weak costellae; the costellae thicken to the auricles. Costa-costella intersections bear triangular beads. Auricles with concentric costellae and growth lines.

Observations. This form was included by Tate in *L. jeffreysiana* which is Miocene. A topotype is mounted on the tablet SAM T972 labelled *Limatula jeffreysiana* (Tate). Distinctive differences between the species are tabulated in the comparative synopsis in Table 1. The holotype, although rather juvenile, was chosen because it is the only specimen in a good state of preservation, and has a sure stratigraphic location.

Stratigraphic range. Tortachilla Limestone to Blanche Point Transitional Marls (lowermost member of Blanche Point Marls); Late Eocene.

Limatula jeffreysiana (Tate, 1885)
FIGS 1-5

1877 *Lima (Limatula) subauriculata* Tenison Woods, p. 113 (*non* Montfort). 1885a *Lima jeffreysiana* Tate, p. 208 (*nom. nud.*). 1885a *Lima subauriculata*: Tate, p. 213 (*non* Montfort). 1885b *Lima jeffreysiana* Tate, p. 230. 1886 *Lima (Limatula) jeffreysiana*: Tate, p. 119, pl. 4, fig. 8 (pars).

1896 *Limatula jeffreysiana*: Pritchard, p. 128. 1897 *Lima (Limatula) jeffreysiana*: Harris, p. 311. 1899 *Lima (Limatula) jeffreysiana*: Tate, p. 273. 1924 *Lima jeffreysiana: Marwick*, p. 323.

Material. 11 specimens (4 LV + 5 RV + 1 BV) generally well preserved. (SAM T972 A-C, E-L; Coll. Tate.)

Description. Like *L. margaritata.* Differs from it by greater height, less inflation, narrower ventral margin, by longer and narrow ears with more protruding ends.

Ornament. 34-37 triangular thin radial ribs, more spiny on the ventral region, with broad concave to flattened interspaces, narrower on the dorso-ventral region, broader to the anterior and posterior, where ribs fade to the auricles. Very fine growth lines; broadly interspaced concentric costellae, more marked in the anterior and posterior regions. Auricles with concentric costellae. Median radial sulcus shallow and observable only in younger specimens.

Observations. The tablet SAM T972 bears specimens of *L. jeffreysiana* (Tate), together with specimens here described as *L. margaritata* sp. nov. (T972-M) and *L. ludbrookae* sp. nov. (T972-D).

Tenison Woods referred the species to the living *L. subauriculata* (Montfort, *non* Montagu). Tate (1885a, 1885b) distinguished it as a new fossil species and remarked its close affinity with the living *L. strangei* Sowerby (MacPherson & Gabriel 1962, p. 308, fig. 3501; Cotton & Godfrey 1938, p. 108, fig. 97; this study, fig. 20-26). Later, Tate (1899) also referred to *L. jeffreysiana* a New Zealand fossil form, mistaken for the living *L. bullata* Born (Hutton 1873, p. 33). Marwick (1924, p. 323) separated the New Zealand form, that was later named by Finlay *L. maoria* (Finlay 1927, p. 454, figs 104-6). The holotype has not been located; it does not appear to be in the Tasmanian Museum, Hobart (Ludbrook 1967). The two specimens found in Tate's collection are both juveniles and one (T972-L) is broken. Hence, it is here considered inappropriate to choose one of them as neotype.

Distribution. Table Cape, Bass Basin (type); Muddy Creek, "Murray River" Snapper Point, Blanchetown, "Spring Creek". Other localities

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Fig. 1. Tablet SAM T972 (Coll. Tate) bearing specimens of *L. jeffreysiana* (Tate). T972-D: a paratype of *L. ludbrookae* sp. nov.; T972-M: a topotype of *L. margaritata* sp. nov. (x 1.1).
Figs 2-5. *Limatula jeffreysiana* (Tate), plesiotype (SAM T972-A), LV, Muddy Creek; (2) dorsal view (x 2); (3) ornaments, particular from ventral region (x 4); (4) anterior auricle (x 9.3); (5) umbonal region and posterior auricle (x 3.8).
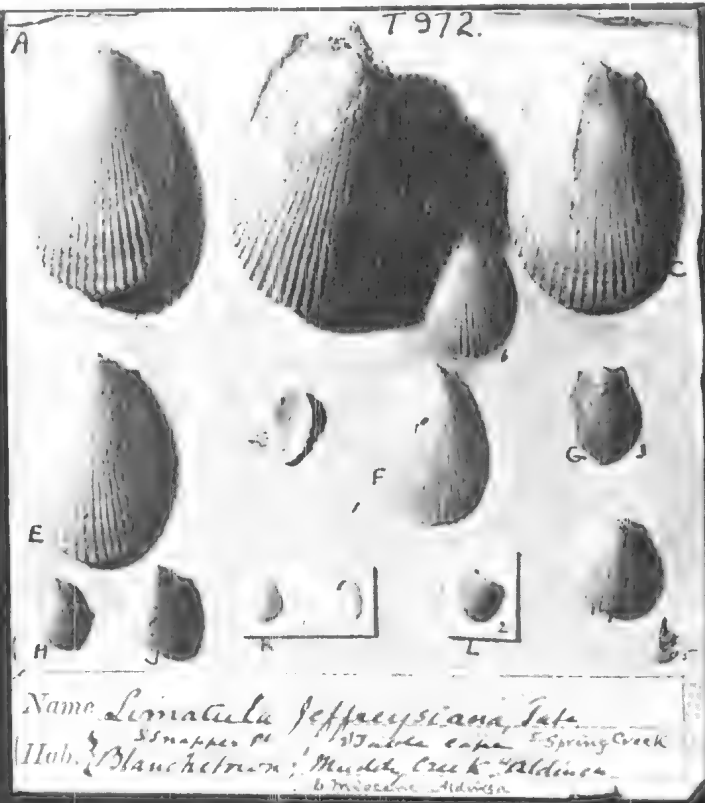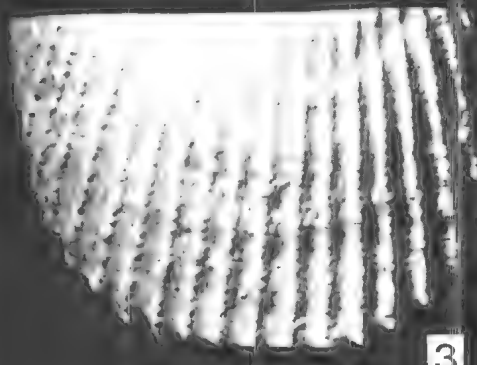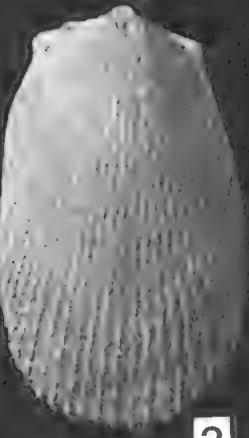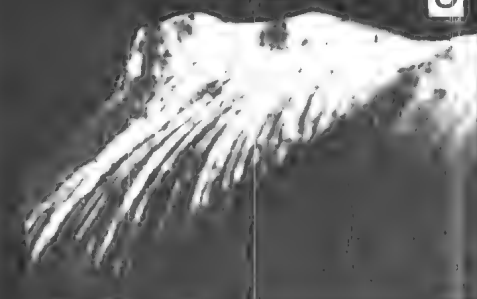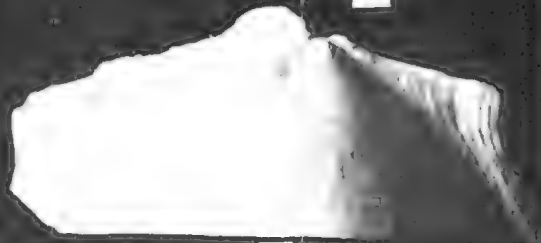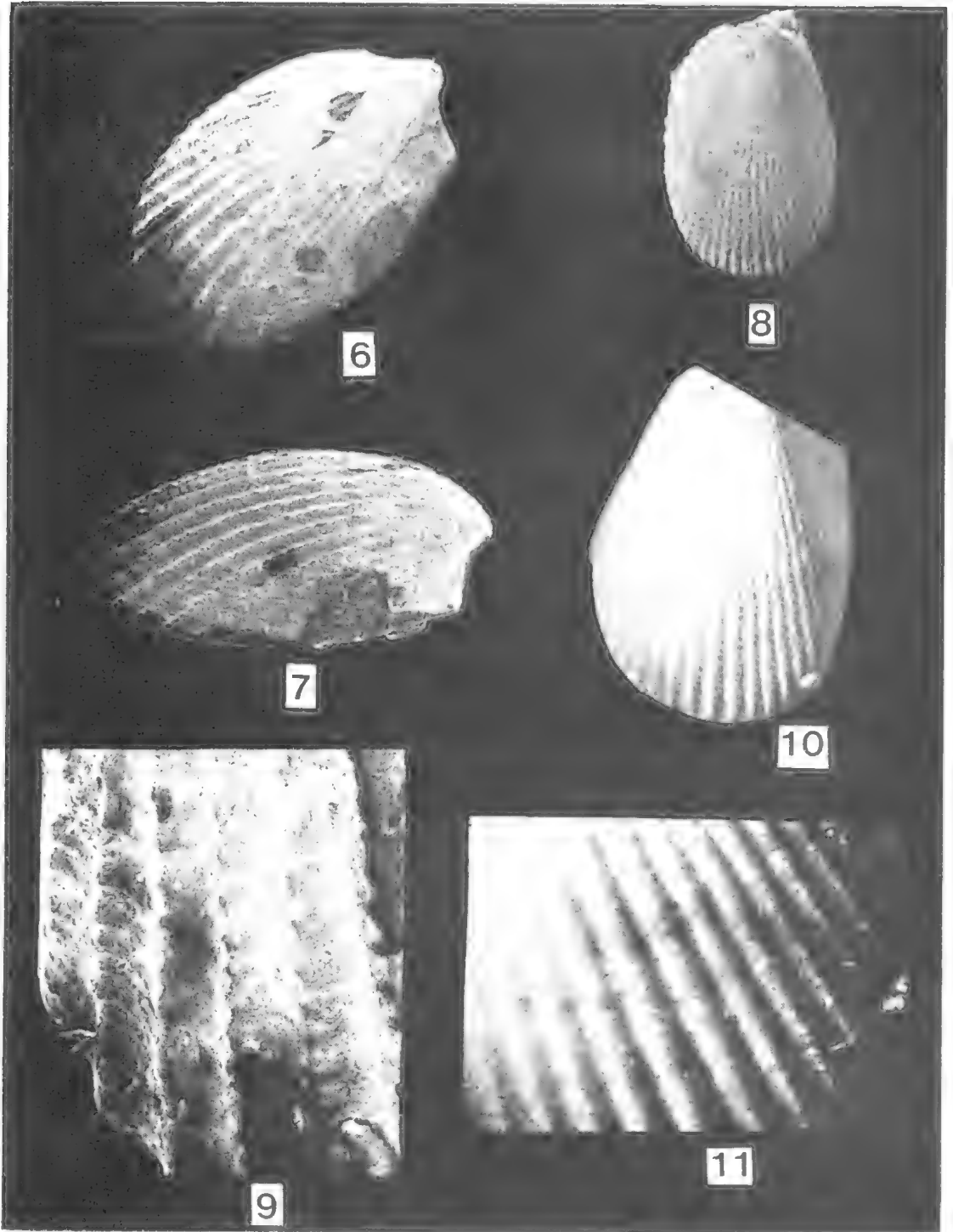
Figs 6-9. *Limatula margaritata* sp. nov., Maslin Bay; (6) Holotype, SAM P18343, RV, antero-dorsal
view (x 14); (7) holotype, anterior view (x 15); (8) topotype, SAM T972-M (x 3.6); (9)
ornaments, particular from holotype's postero-ventral region (x 44).
Figs 10-11. *Limatula ludbrookae* sp. nov.; SAM T972-D, Aldinga; (10) dorso-ventral view (x 6);
(11) ornaments, particular from ventral region (x 16.2).
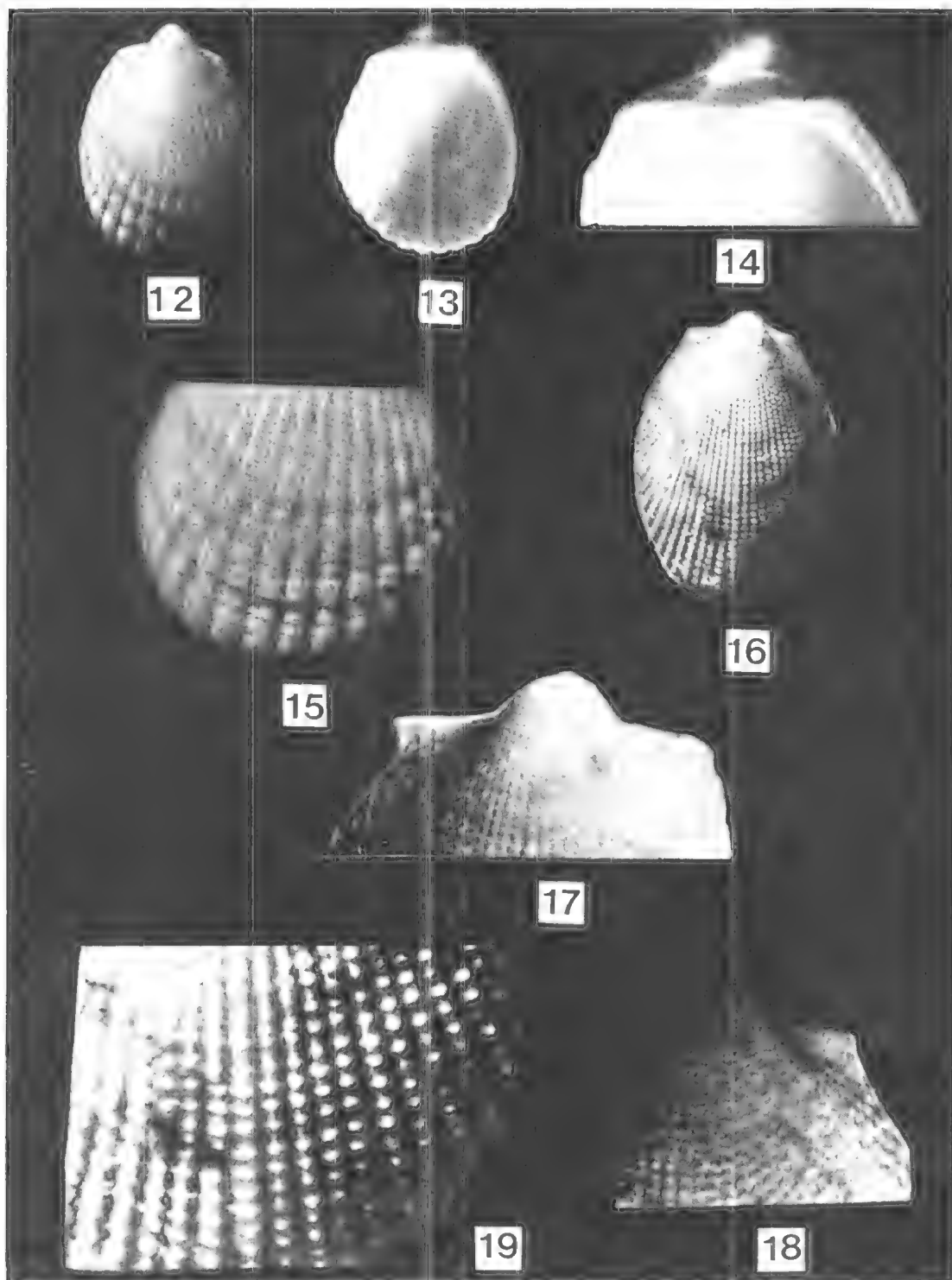
Figs 12-15. *Limea (Gemellima) austrina* Tate, holotype of *Limatula subnodulosa* Tate, SAM T1799, Muddy Creek; (12) dorsal view (x 8); (13) interior view (x 8); (14) hinge and cardinal area (x 17); (15) ornaments, particular from dorsoventral region (x 20 c).

Figs 16-19. *Limatula crebresquamata* Tate, holotype, SAM T978-A, "Spring Creek"; (16) dorsal view (x 3.75); (17) umbo and anterior auricle (x 11.25); (18) posterior auricle (x 11.25); (19) ornaments, particular from dorso-ventral region (x 15).
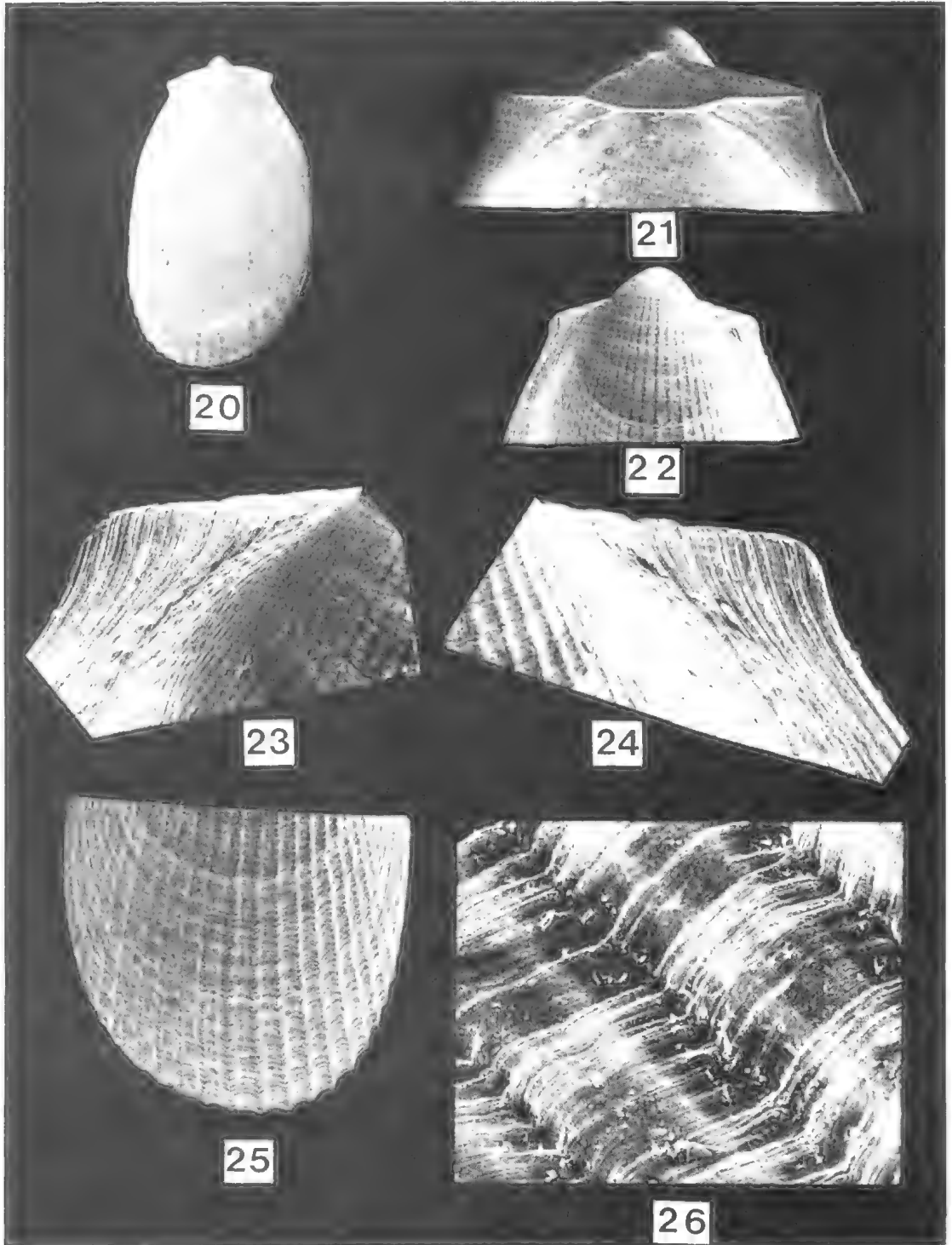
Figs 20-26. *Limatula strangei* (Sowerby); (20) type figured by Cotton & Godfrey, SAM 15145, Hardwicke Bay, South Australia, LV (x 1.2); (21) hinge and cardinal area, specimen SAM D9431-B (Coll. Verco) (x 15); (22) dorso-umbonal region, SAM D15146-A (x 10); (23) posterior auricle, SAM D15146-A (x 40); (24) anterior auricle, SAM D15146-A (x 40); (25) ventral region, SAM D15146-A (x 10); (26) ornaments, particular from the dorsoventral region, SAM D15146-A (x 80).

TABLE 1

Comparative synopsis of morphological characteristics

Species	Outline	Inflation	Radial Interspaces	Radial Ribs	Concentric Ornaments	Radial Ribs on Anterior and Posterior Region	Ears Triangular Subequal	Age
Limatula margaritata sp. nov.	oval, rather short	more inflated	shallow narrower, ⋃-shaped, wider to the anterior and posterior	40 broad, triangular, beaded	fine, roundish costellae separated by grooves	fading but still perceptible	longer, narrower with protruding ends and fine concentric costellae	LATE EOCENE
Limatula crebresquamata Tate	oval to subtrigonal, shorter	very inflated	deep, narrower, ⋁-shaped slightly broader	44 very high, thin, in some places dichotomous bearing chevron shaped scales	growth lines and scales	well marked	long and narrow with protruding ends and concentric costellae	LATE OLIGOCENE-EARLY MIOCENE
Limatula jeffreysiana Tate	oval, high	less inflated	broader, shallow, concave to flattened, wider to the anterior and posterior	34-37 rather fine, triangular more spiny to the ventral region	very fine growth lines with broadly interspaced costellae	fading but from perceptible to more marked	longer, narrower with protruding ends and concentric costellae	EARLY-MIDDLE MIOCENE
Limatula ludbrookae sp. nov.	oval, rather short	more inflated	narrower, deep, ⋃-shaped wider to the anterior and posterior	30 broad, triangular with rare very short and small spines on ventral	flat, fine costellae separated by shallow, broad grooves	more fading	shorter, narrow, with protruding ends and very fine growth lines	LATE PLIOCENE

quoted by Dennant & Kitson (1903) are here omitted because specimens from those localities were not available for checking.

Stratigraphic range. As known at present, Early to Middle Miocene (Quilty 1966; Ludbrook 1973).

Limatula ludbrookae sp. nov.
FIGS 1, 10-11, 27-35

Derivation of name. From Nelly Hooper Ludbrook of Adelaide for her devotion to Palaeontology.

Holotype. SAM P18360, figs 27-28.

Type-formation. Dry Creek Sands (Late Pliocene, Yatalan).

Type-locality. Salisbury Bore, 1942, hd. Munno Para, sec. 4000, at 100 m depth.

Material. 10 specimens from Salisbury Bore (6 LV + 3 RV + 1 VV); 1 LV specimen from Tate Collection (SAM T872-D). Two broken specimens from Abattoirs Bore.

Description. Shell oval, auriculated, very high and narrow, very inflated, sub-inequilateral; umbones with small protruding and prosocline beaks. Non-gaping margins; anterodorsal and posterodorsal represented by two subequal auricles, longer than high; anterior subelliptical very long; posterior very long, slightly more elliptical; ventral very elliptical. Margin connections: anterior-anterodorsal and posterior-posterodorsal angular and concave; others imperceptible.

Longitudinal shell section subtrapezoidal, very convex. Regions: anterior and posterior very declivous, subconvex; dorsoventral convex, more gently declivous. Connections between the regions imperceptible. Cardinal area broad, longer than high, horizontally striated; resilifer triangular, broad, rather deep with curved margins. Hinge edentulous. Inner septum below the cardinal plate. Interior with marked median rib and fine regular striae. Monomyarian, posterior scar at high middle posterior position near to the median rib. Pallial line marked. Commissure region smooth except on ventral margin where it is highly crenulated.

Ornament. 29 triangular radial costae with broader trapezoidal interspaces. From the beak

to the ventral margin a marked broad median sulcus. Fine concentric growth lines; fine growth rugae in adult-senile stage. At costa-line/ruga intersections short spines. On the anterior and posterior region, the costae fade abruptly and the growth lines and rugae predominate. Auricles with concentric growth lines and rugae.

Observations. This form was initially mistaken by Tate for *L. jeffreysiana*. The juvenile SAM T972-D from Aldinga is broken at the umbo and is the only specimen available from outcrop. A search in the uncatalogued part of Tate's collection still kept in the Department of Geology and Mineralogy of the University of Adelaide, led to the discovery of 8 juveniles, 1 adult, and 1 senile specimen from Salisbury Bore. These specimens corroborate the distinction of this form from *L. jeffreysiana* on the basis of rib and interspace shape and shell geometry. The senile was chosen as holotype because of its perfect preservation. The specimen of *L. jeffreysiana* (Tate) reported by Reynolds (1953) in the Pliocene of Aldinga should be more probably referred to *L. ludbrookae*.

Distribution. St Vincent Basin: Aldinga Bay, Hallett Cove Sandstone; Abattoirs Bore, Salisbury Bore (type), Dry Creek Sands.

Stratigraphic range. Yatalan (Late Pliocene).

Limatula crebresquamata (Tate 1899)
FIGS 16-19

1899 *Lima (Limatula) crebresquamata* Tate, p. 274.

Material. Three specimens borne on the tablet SAM T978 (3 LV): T978-A, the holotype broken and glued up on the antero-ventral region; T978-B, well preserved, juvenile; T978-C, broken, with the dorsal region, the umbo and the auricles missing.

Description. Like the above described species, but differs by a shorter oval to subtrigonal outline, more inflation, and the occurrence of ribs on the anterior and posterior regions. Cardinal area narrow, longer than high, horizontally striated; resilifer triangular, concave, rather deep. Hinge edentulous. Interior with marked radial ribs and narrower interspaces. Pallial line and adductor scar imperceptible. Commis-

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Figs 27-34. *L. ludbrookae* sp. nov., Salisbury Bore; (27) Holotype (SAM P18360) dorsal view (x 2.2), (28) holotype, interior (x 2.2); (29) paratype (SAM P18360) A/1 V, dorsal view (x 9); (30) Paratype (SAM P18360B), LV, interior view (x 9); (31) paratype (SAM P18360A) anterior auricle (x 35); (32) paratype A, posterior auricle (x 37), (33) paratype B, cardinal area (x 27); (34) paratype A, particular median sulcus (x 72)
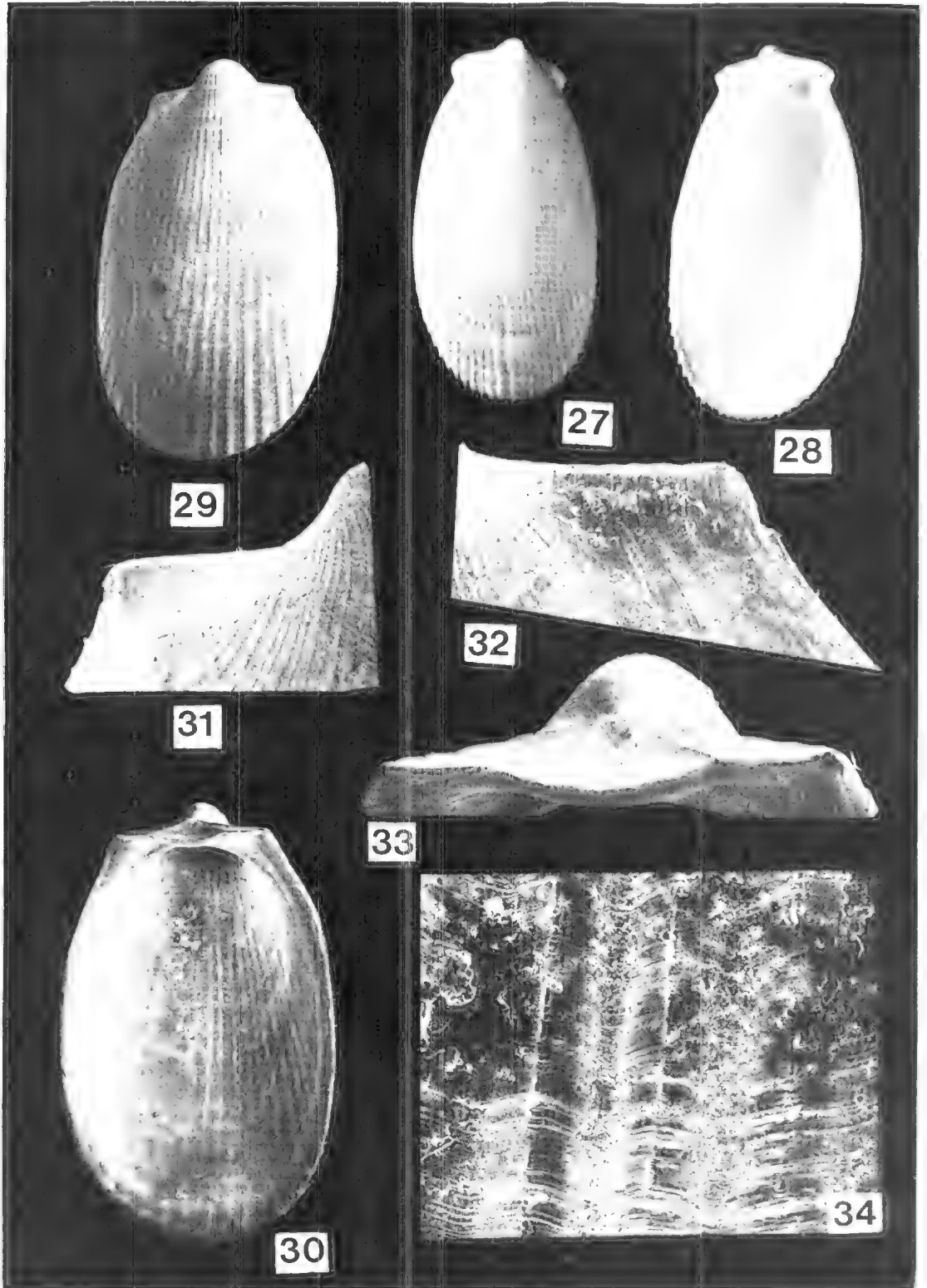
sure region smooth, except the ventral heavily crenulated.

Ornament. 44 ribs, very high, thin, in some places dichotomous, bearing wide, thick, chevron-shaped concentric scales, separated by regular rather broad concentric furrows. Radial interspaces U-shaped, narrower in the dorsoventral region, increasing in width to the anterior and posterior auricles.

Observations. The morphology of this form agrees with the diagnosis of *Limatula* Wood of Cox & Hertlein (1969, p. N389), except in the strong radial ribbing of the anterior and posterior regions. The median sulcus is obscured by the heavy costae and squamae, revealed only by the inner median sulcus. An inner ridge just below the cardinal area may represent an embryonic septum as in *L. ludbrookae.*

Localities. "Spring Creek" (Tate 1899), Bird Rock, Torquay (Fleming, in litt. 1974).

Stratigraphic range. Late Oligocene-?Early Miocene (Janjukian-Longfordian).

Observations. Neither the holotype nor paratypes were figured.

GENUS *Limea* Bronn, 1831.

SUBGENUS *Gemellima* Iredale, 1929.

Limea (Gemellima) austrina Tate, 1887
FIGS 12-15, 36-41

1887 *Limea austrina* Tate, p. 73, pl. 4, fig. 7. 1899 *Limatula subnodulosa* Tate, p. 273. 1907 *Limaea austrina*-Verco, p. 315. 1929 *Gemellima austrina*—Iredale, p. 166. 1938 *Gemellima austrina* —Cotton & Godfrey, p. 107, fig. 93.

Material. 1 specimen (LV) (SAM T1799), the holotype of *L. nodulosa* Tate; several hundred specimens (SAM Lot T17).

Description. Shell small, thick, trigonal, slightly higher than long, slightly inequilateral, very inflated; umbo inflated with central orthogyrate beaks protruding a little. Margins: anterior subelliptical; posterior elliptical, both winged; ventral very elliptical. Margin connections: broadly angular; the antero-ventral rounded. Ears triangular, very narrow, and subequal.

Longitudinal shell section very convex. Regions: anterior and posterior very steep; dorsal declivous; ventral very steep. Cardinal area longer than high; resilifer triangular broad, concave, and shallow; hinge with very

fine vertical teeth; monomyarian with orbicular adductor scar high in the posterior region; pallial line imperceptible or not easily distinguishable from other concentric grooves in the shell interior; commissure region heavily crenulated.

Ornament. Outer: 25 radial large massive protruding ribs with narrower deep U-shaped interspaces; fine regularly interspaced concentric costellae; rib-costellae intersections producing short subtriangular spines; irregularly interspaced broad concentric constrictions. Ears bearing only concentric costellae. *Inner:* fine radial grooves corresponding to the outer ribs; irregular concentric grooves corresponding to the outer concentric constrictions.

Observations. The rediscovered holotype of *Limatula subnodulosa* Tate, 1899 is just a worn and polished fossil specimen of *Limea (Gemellima) austrina* Tate, 1887.

Investigations on several hundred specimens of a sample from Investigator Strait, 36.6 m depth, showed that as soon as the disarticulated valves lose the ligamentary organic matter, their hinge, composed of very fine vertical teeth, is abraded very easily; if the abrasion go further, the crenulated commissure region can be practically smoothed out and the spines on the ribs reduced to blunt nodules or worn out too.

This can explain Tate's erroneous determination. Instituting *Limatula subnodulosa* he remarked that the shell displays *Limea* characteristics, and, although he suspected it was reworked, he did not consider the possibility that it could be actually a worn specimen of *Limea. Limea (Gemellima) austrina* is the type species of *Gemellima* Iredale, considered by Newell (1969) a subgenus of *Limea* Bronn.

Study of the above-mentioned sample indicated two main morphs connected by transitional forms. One is shorter and longer, less inflated, with broader interspaces between ribs. The other is higher and narrower, more inflated, with narrower interspaces (*subnodulosa* type).

Environmental observations. Limea (Gemellima) austrina was dredged in S.A. waters at 14.6-366.0 m, alive from 27.45-40.3 m; the optimum depth for populations seems to be 36.6 m (Verco 1907).

Fig. 35. *L. ludbrookae* sp. nov. paratype B, prodissoconch (x 135).

Figs 36-41. *Limea (Gemellima) austrina* Tate, Investigator Strait. (36) LV, juvenile, dorsal view (x 9.5); (37) LV, worn juvenile, dorsal view (x 9.5); (38) worn hinge (x 18); (39) hinge (x 18); (40) particular posterior hinge (x 36); (41) particular dorso-ventral ornaments (x 18).
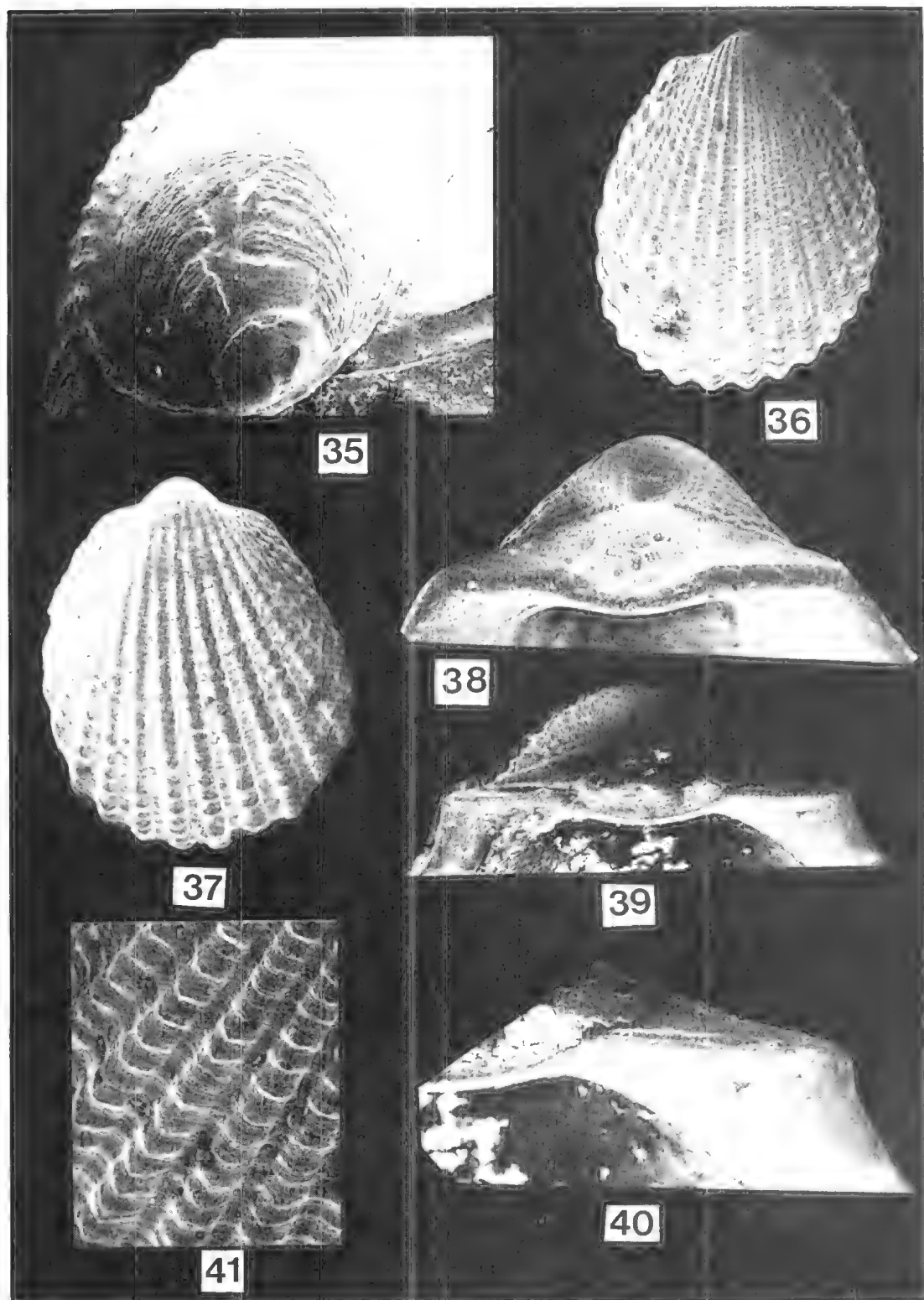
Distribution. Spencer Gulf and Gulf St Vincent, recent deposits; Muddy Creek, Grange Burn Coquina; Otway Basin; Limestone Creek, W. Victoria (*fide* Dennant).

Stratigraphic range. Early Pliocene (Kalimnan)-Holocene.

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Appendix

Stratigraphical observations on Tortachilla Limestone Reynolds, 1953 (Lower Aldingan Stage)

A study of the lithostratigraphy of the fossiliferous Eocene beds at Maslin Bay will be presented elsewhere. Meanwhile a summary is necessary for adequate stratigraphic characterization of *Limatula* and other molluscs.

The Tortachilla Limestone (Reynolds 1953) considered by Ludbrook & Lindsay (1966) and Ludbrook (1973) to be the lowest rock unit in the stratotype for the Aldingan stage (Late Eocene), displays erosional unconformities. The major unconformity (Jenkins 1974, figs 1, 3) separating the lower member (Polyzoal Limestone Member of Reynolds) from the upper one (Blanche Point Glauconitic Limestone Member of Reynolds), is a deeply pitted erosional surface on the topmost limestone in the Polyzoal Limestone. The abundant subvertical pits are filled by the glauconitic sands, in places cemented by sparite, of the Blanche Point Glauconitic Limestone Member. By analogy with the studies of Jaanusson (1961 p. 232 *et seq.*), Krawiec (1971), pp. 128-31), and chiefly by Guilcher (1953) and Wentworth (1939) this unconformity could be interpreted as produced by sub-aerial dissolution of the emergent limestone. i.e. karst. The constant widespread occurrence of the pits can be explained in the negligible slope of the formation at the time of emergence, thus preventing the accumulation of beach deposits thick enough to protect the limestone from the action of erosive and dissolutive agents.

The discovery of this karst surface leads to a stratigraphic revision of the Tortachilla Limestone, restricting the formation to its previous lower member and referring the Glauconitic Limestone Member to the Blanche Point Transitional Marls, to which it belongs in a new episode of sedimentation. The record of this karst surface is the evidence of a lacuna that covered a span of time still unascertainable but longer, however, than has been considered until now.

A precise correlation of the Tortachilla Limestone in terms of planktonic foraminiferal zone is not yet possible.

S. Shafik (pers. comm. 1974) stated "the ranges of the few calcareous nannofossils extracted from Tortachilla Limestone are confined mainly to the Middle to Late Eocene".

McGowran & Lindsay (pers. comm. 1974-5) and Ludbrook (1973) support a probable early Late Eocene age for this formation. Lindsay (1969) considered the undifferentiated deposits of Tortachilla Limestone (or its equivalent) and Blanche Point Transitional Marls, in the Adelaide Plains Sub-basin to be early in the Late Eocene.

At present, the only two biostratigraphic controls on the older part of the section at Maslin Bay are:

— the microfloral asemblage occurring in North Maslin Sands and belonging to the *Proteacidites confragosus* zone, earliest Middle Eocene in age McGowran, Harris, & Lindsay 1970), but possibly latest Early Eocene (McGowran pers. comm 1975).

— The *Hantkenina primitiva* sub-zone occurring in the Transitional Marls at Maslin Bay, southward of "Uncle Tom's Cabin", 80-115 cm above the described karst surface and estimated to be Mid-Late Eocene in age (McGowran, Lindsay & Harris 1971).

DISTRIBUTION AND SEDIMENTS OF MANGROVE FORESTS IN SOUTH AUSTRALIA

BY A. J. BUTLER, A. M. DEPERS, S. C. MCKILLUP AND D. P. THOMAS

Summary

A survey of forests of the mangrove Avicennia marina in South Australia was conducted in summer, 1974-75. This paper describes the distribution of the forests and contains detailed maps of the major stands. Smear slides of the sediments have been examined and on this basis two geographically distinct types are identified. The dynamic relationship between the sediments and the organisms growing within them is discussed. Extinct mangrove swamps at three sites are described and the past distribution of mangroves is discussed. Finally we comment on the composition of the communities of organisms in South Australian mangrove swamps.

DISTRIBUTION AND SEDIMENTS OF MANGROVE FORESTS IN SOUTH AUSTRALIA

by A. J. Butler,[*] A. M. Depers,[†] S. C. McKillup[‡] and D. P. Thomas[‡]

Summary

Butler, A. J., Depers, A. M., McKillup, S. C. and Thomas, D. P. (1977).—Distribution and sediments of mangrove forests in South Australia. *Trans. R. Soc. S. Aust.* **101**(1), 35-44, 28 February, 1977.

A survey of forests of the mangrove *Avicennia marina* in South Australia was conducted in summer, 1974-75. This paper describes the distribution of the forests and contains detailed maps of the major stands. Smear slides of the sediments have been examined and on this basis two geographically distinct types are identified. The dynamic relationship between the sediments and the organisms growing within them is discussed. Extinct mangrove swamps at three sites are described and the past distribution of mangroves is discussed. Finally we comment on the composition of the communities of organisms in South Australian mangrove swamps.

Introduction

Mangrove forests are most complex and luxuriant in the wet tropics of the Indo-West-Pacific region (Macnae 1968), but extend onto desert shores and to latitudes at high as that of Westernport Bay, Victoria (38°22'). South of the Queensland/New South Wales border there are only two species of mangroves, *Avicennia marina* and *Aegiceras corniculatum*, and south of Sydney there is only *Avicennia marina* (Forsk.) Vierh. (Macnae 1966). The stands of this species at Westernport Bay, Victoria, are the southern-most mangroves in the world.

In South Australia, the flora and fauna of mangroves are briefly mentioned by Womersley & Edmonds (1958). Wester (1967)[1] surveyed the distribution of mangroves throughout South Australia using both aerial photographs and inspections on the ground. There is evidence that the South Australian mangroves have been more extensive than they are today; Cotton (1949) reported the exposure of an old man-grove mud-flat under the sand of the beach at Glenelg and he suggested that mangroves lived "until a comparatively short time ago" as far south as Port Noarlunga.

It has frequently been argued that South Australian mangrove forests are important communities in a number of ways, for example in the support of fisheries and the stabilization of sediments, and for these and other reasons steps have been taken to conserve them.[2] Whilst it is clear that mangroves in various places in the world have such functions it is now obvious that "mangrove forests" occur in widely varying conditions and vary considerably in their composition and functioning (Davis 1940, Thom 1967, Bird 1971, Carlton 1974, Lugo & Snedaker 1974, Walsh *et al.* 1975[3]). Thus it is desirable to obtain information, in South Australia, about the dynamics of mangrove ecosystems here.

This paper is merely a preliminary step towards such knowledge. It is based on a survey[2] with the following aims: to check the distribution of mangroves in South Australia and

to record as well as possible their biota, the nature of the sediments in which they grow, the condition of each forest in terms such as the health of the trees and whether the sediment be accreting or eroding, the types of communities to landward and seaward, and human activities in and near mangrove forests. In general, it was beyond the scope of the project to seek explanations for our observations. This paper records the distribution of mangrove forests in South Australia at that time, observations on the sediments, notes on past distribution and brief comments on the composition of mangrove communities. More detailed biological and general notes will be published elsewhere.

Methods

During the summer of 1974–75 almost all stands of mangroves in the State were visited at least once; selected areas were re-visited for more detailed inspection. On these trips we were guided by copies of Wester's[1] maps, and aerial photographs[4] of most of the mangrove stands.

In addition to stands recorded by Wester, we visited several areas where they might have been anticipated to occur. For each location, map accuracy was checked against the 1972 aerial photographs and also by ground surveys. Notes were made of human activities, and of the types of habitats lying to landward and to seaward of the mangroves. Special note was taken of the health and size distributions of the trees, the extent of leaf-damage, and apparent sedimentary processes at each area.

Sediment samples were collected and stored in polyethylene containers. Preliminary tests for carbonate content were made in the field using dilute hydrochloric acid. In the laboratory, smears of the samples were mounted on microscope slides in Caedex resin and examined by transmitted light at a maximum of 400X magnification. Surface scrapes and the sediment smears were examined for the presence of microflora (diatoms, blue-green algae, other algae), and collections of animals were taken at each site.

Observations and Discussion

DISTRIBUTION

Stands of *Avicennia marina* occur at the locations shown in Figure 1. All are in sheltered

sites as noted by Womersley & Edmonds (1958). The most extensive stands (Figs 2–8) are near Ceduna on north western Eyre Peninsula, at Franklin Harbour on Spencer Gulf, around the heads of both Gulfs, and near both Port Pirie and Port Adelaide.[5] We found no evidence to extend the past distribution of mangroves any further south than the stand at Glenelg reported by Cotton (1949).

SEDIMENTS

Generally the South Australian mangroves grow in carbonate-rich sediments, but the percentage carbonate varies considerably, both within and between mangrove communities.

In a mangrove community the seaward side is flanked by extensive intertidal shell-grit sands with or without seagrasses (e.g. *Heterozostera* or *Posidonia*) whilst to landward the mangroves are flanked by samphires and occasionally by extensive supratidal lagoons. Beach ridges of shell-grit and dead *Posidonia* are commonly found here, marking the position of a previous coastline, prior to large sealevel changes.

Sediment types

The mangrove sediments were classified according to depositional texture using Dunham's (1962) classification.

Two different types of mangrove sediments could be distinguished on the basis of grainsize. One, a wackestone-packstone-boundstone, is confined to Eyre Peninsula; the second, a boundstone, is found in northern and eastern Spencer Gulf and Gulf St Vincent.

(1) The wackestone - packstone - boundstone type of sediment was found in all the areas on Eyre Peninsula, from south of Whyalla to Davenport Creek. We shall refer to this as the "West Coast" type. It generally has particles in the clay to medium sand size category (Folk 1974, p. 25). Boundstone sediments are usually found within the mangroves away from tidal channels and creeks. They are covered by a mat of blue-green algae that binds the top 2–5 cm of sediment together. Laminae of such algae can be found in long-established sediments. The boundstone consists dominantly of clay to silt sized particles. The wackestone-packstone sediments are usually found closer to the main tidal channels where coarser particles of silt to sand size are introduced during the tides.
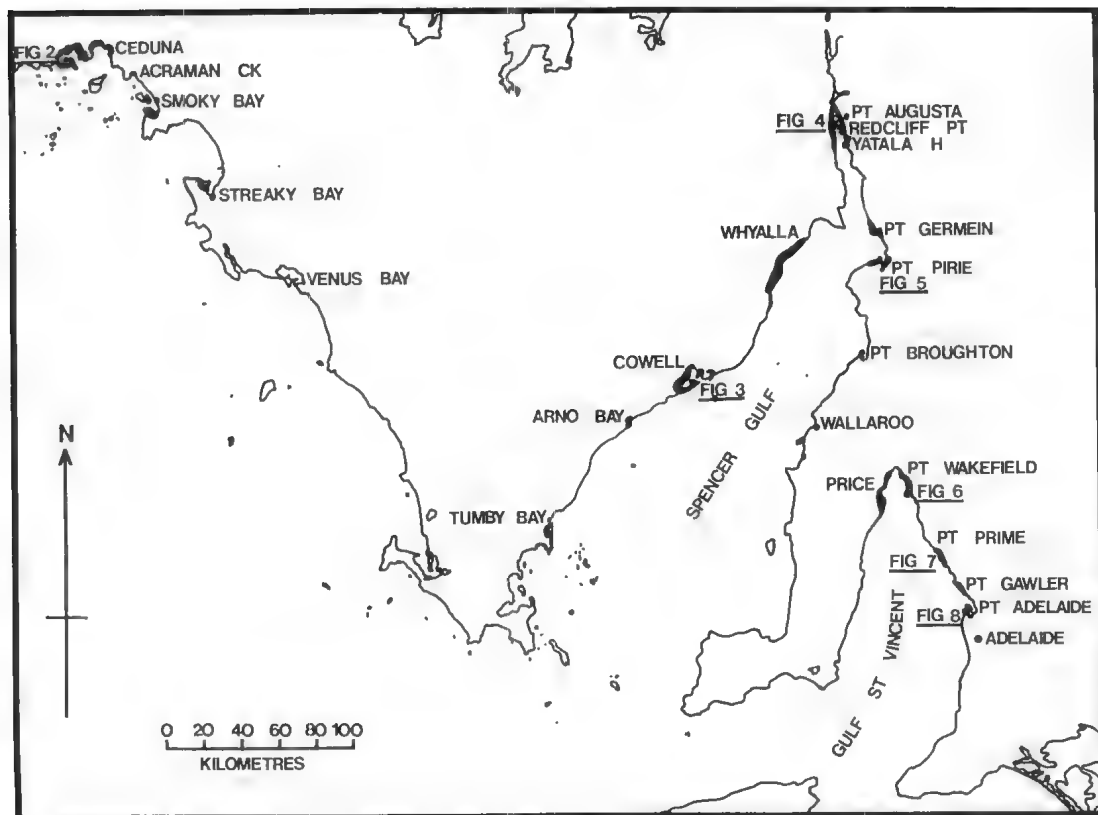
Fig. 1. Distribution of stands of *Avicennia marina* in South Australia, showing locations of stands mapped in Figs 2–8.

They contain a lower percentage of clay sized particles, partly attributable to the winnowing effect of the tides; the tidal waters suspend the the fine material and whilst in suspension it is carried to the backwaters of the mangrove community where it is deposited.

The "West Coast" sediments consist dominantly of quartz, carbonate clay, algal and shell fragments, foraminifera and diatoms. Most of the quartz is rounded to sub-rounded, with some particles subangular (Powers 1953). The percentage of organic carbon, mainly decomposing mangrove and seagrass leaves, varies greatly with location within a given mangrove community, with depth in the sediment and between communities. Minor constituents are echinoid spines, aragonite rosettes and needles, sponge spicules (silica), radiolarian tests (opaline silica) and minerals from the hinterland (e.g. amphiboles and feldspars).

Due to the low-energy depositional environment in which these sediments are found, it is deduced that the quartz is introduced from the extensive beaches and sand-dunes in or near the mangrove stands. These are, or were, environments of much higher energy. The quartz-grains are introduced into the mangrove community either by long-shore drift in the beach environment and then via tidal water, or else by saltation from the surrounding sand-dunes.

Other constituents in the sediments find their way into the mangrove communities via tidal channels, or live and die on the sediments and hence are incorporated (e.g. diatoms).

(2) The boundstone sediments found in Spencer Gulf north and east of Whyalla and in Gulf St Vincent, will be referred to as the "Gulf" type. The particles are predominantly of clay to fine silt size, although there is local variability. These sediments too are covered by an algal mat. The major constituents are similar to those of the "West Coast" sediments. However, the quartz grains are rounded to sub-rounded and clear, whereas in "West Coast" sediments they usually have rutile and tourmaline needle inclusions. Some minor constituents, especially radiolarian tests and sponge spicules,
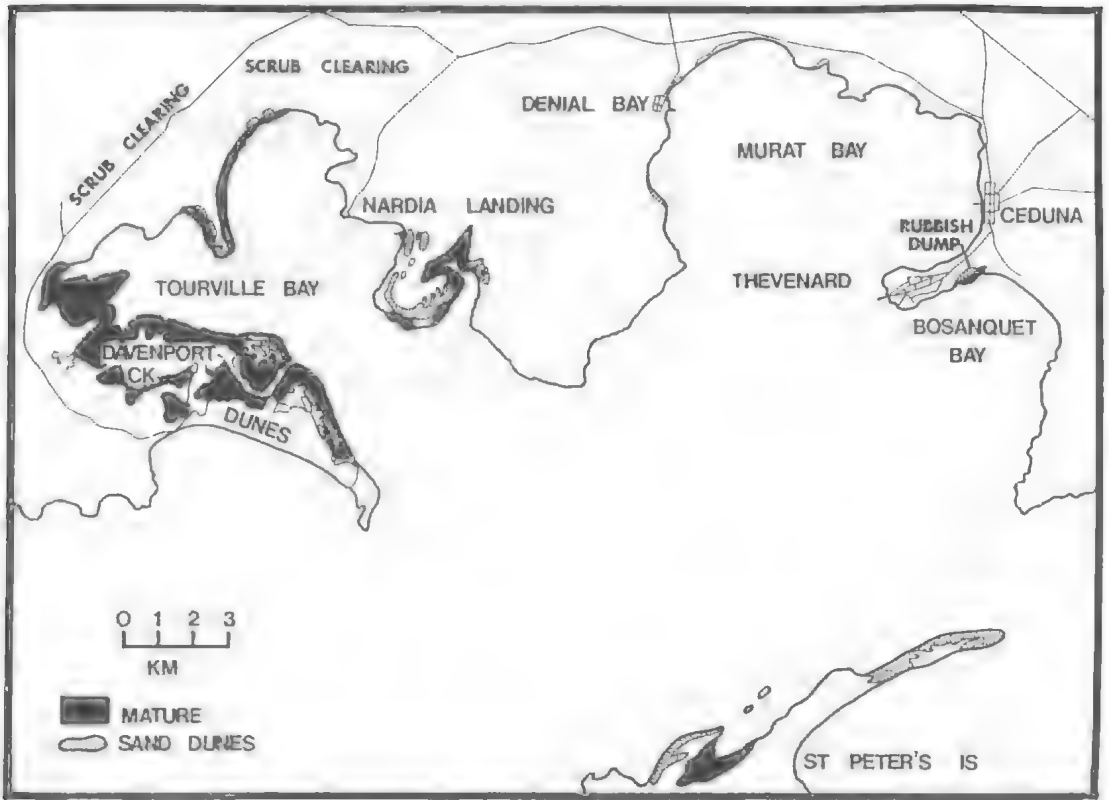
Fig. 2. Davenport Creek, on the west coast.
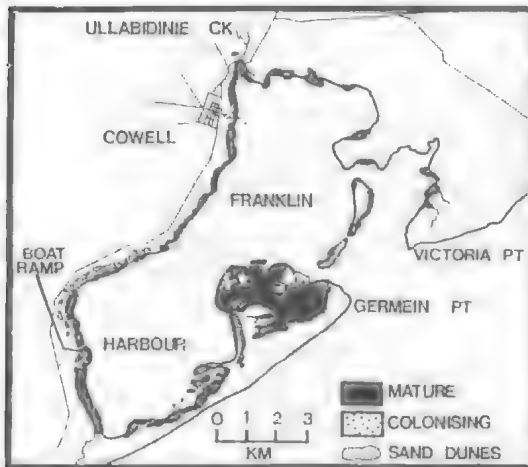
Fig. 3. Franklin Harbour, Spencer Gulf.

are absent. The lack of minerals such as amphiboles and feldspars, like the lack of inclusions in quartz grains, results from the absence of significant metamorphic rock sources in the hinterland of the "Gulf" areas. By comparison, the hinterland of the "West Coast" areas contains a variety of metamorphic sources (Glaessner & Parkin 1958).

Areas studied in more detail

(1) At Port Gawler in Gulf St Vincent (Fig. 7), very rapid sedimentation, with a consequent relative drop in sea-level, has left a very thick pile of sediment in which the present well-established mangroves grow. Deep tidal channels supply the area with seawater. Near the present beach a new mangrove colony has become established, and from a series of aerial photographs it is clear that the lower-tide region of the beach has been progressively colonized within the last 10 years.

Statistics from the smear slide results (Table 1) show certain trends from colonizing mangroves to mature stands. Generally, quartz content decreases as does the grain size of quartz (from medium sand size to fine silt size), carbonate clay increases, the contents of algal and shell fragments decrease along with their grain size (medium sand size to medium silt size), and organic carbon increases. Clearly the trends are not statistically significant in several cases, because of wide variability. However, it was

Fig. 4. Northern Spencer Gulf.

Fig. 5. Port Pirie, Spencer Gulf.
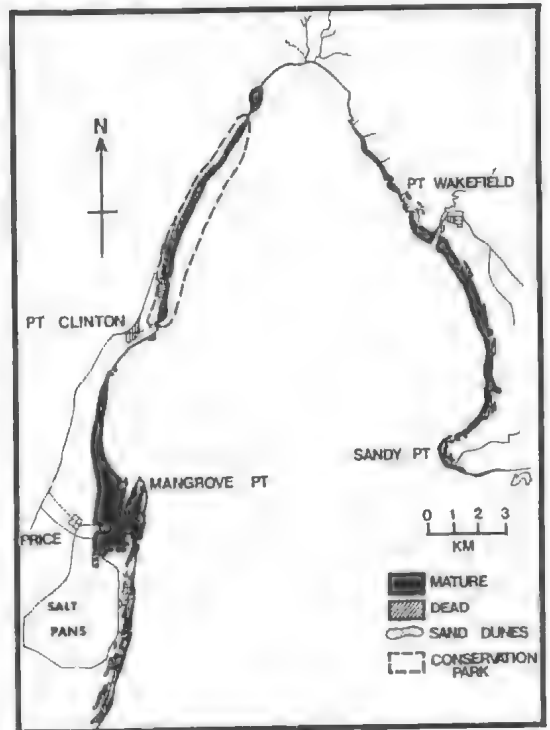
Fig. 6. Northern Gulf St Vincent.

not possible to obtain more data and it seems unwarranted to carry out a more complete statistical analysis of these data. The apparent trends suggest that as mangroves begin to colonize, usually in a shell-grit grainstone of fine sand size, the stabilizing effect of the trees and pneumatophores allows sedimentation of much smaller particles to commence. The final result is an algal-covered fine-grained sediment. The depositional texture of the sediments changes from grainstone to wackestone-packstone then to boundstone. A major factor in these changes would appear to be the activity of species of the blue green alga *Oscillatoria* and the golden brown alga *Vaucheria*.

All of the mangrove sediments are underlain by a coarse grainstone composed of shell fragments from gastropods, bivalves and forams. The influence of this layer is not known, but we suggest that it is important in the growth of the mangroves. Being a coarse

TABLE 1

Statistics from examination of smear slides of sediments from S.A. mangroves

PORT GAWLER

Type of colony	No. of samples		Quartz	Clay	Algal + shell fragments	Forams	Aragonite	Org C	Diatoms	Others
Juveniles up to 50 cm high	10	Mean	37.00	14.90	42.30	1.50	0.20	2.70	1.40	0.00
		S.D.	8.13	7.59	11.18	0.71	0.42	3.05	1.43	0.00
Saplings up to 2 m high	5	Mean	37.00	8.60	45.60	4.00	2.00	2.01	0.80	0.00
		S.D.	13.51	9.24	2.88	3.67	1.73	2.73	0.84	0.00
Mature trees 2 m and more	12	Mean	30.00	28.33	24.58	1.27	0.42	13.75	2.09	0.00
		S.D.	13.98	18.56	13.65	0.37	0.66	9.32	2.02	0.00

DAVENPORT CREEK-CEDUNA

Type of colony	No. of samples		Quartz	Clay	Algal + shell fragments	Forams	Aragonite	Org C	Diatoms	Others
Juveniles up to 50 cm	2	Mean	5.00	27.50	59.00	1.00	0.51	3.50	3.50	0.00
		S.D.	0.00	3.54	2.83	0.00	0.70	2.12	2.12	0.00
Trees 2 m and more	27	Mean	25.00	22.74	34.45	1.82	1.12	12.22	1.78	1.30
		S.D.	22.63	15.67	27.46	1.84	1.74	12.92	1.88	2.30

layer it is also very porous and permeable, so that seawater can move through it freely. This may be important in the functioning of the soil ecosystem and in the nutrient-balance of the trees.

Within the mangrove stands deep burrowing by the crab *Helograpsus haswellianus* (Whitelegge) and other organisms, especially various polychaete worms, bioturbate the sediment extensively. The result is that the algal laminations are destroyed and a mottled texture is commonly found in cross-sections of the sediment. Through these crab holes the water is able to permeate.

(2) In the Davenport Creek area near Ceduna (Fig. 2) extensive, mobile, carbonate-rich sand-dunes are present. These are very coarse-grained (medium sand to coarse sand size) and are composed of about 95% shell fragments and 5% rounded to sub-rounded medium sand size quartz. The prevailing southwesterly wind blows the dunes directly onto the mangrove community to the north-east of the beach, and the mangroves are gradually dying near the sand-dunes due to the "blanketing" movement of the dunes. Not far from its mouth the tidal channel called "Davenport Creek" has cut through the highly organic mud of a former mangrove forest which appears to have been killed by saltation with marine sand.

The mangrove sediments from Davenport Creek are rich in carbonate and quartz (Table 1). Except for the variation in organic carbon the changes from colonizing to mature stands are less clear, but we assume that a process like that described in (1) above occurs here. The sediments here are much coarser-grained than at Port Gawler, and again a coarse grainstone underlies the mangrove sediments.

In the tidal channels, extensive burrowing by polychaete worms has left a mound-covered terrace, not seen in any of the other areas studied, but the crab *Helograpsus* is rare; this seems to be general for "West Coast" sediments.

Within the mangroves are to be found a series of stranded beach ridges (probably cheniers). Since these represent previous shore-lines (the ridges are built up during storms and contain extensive beds of dead *Posidonia* sp.) we infer that this area has been subjected to a number of sea-level changes. There are three such ridges visible and probably several more buried under the dunes. They are grainstones composed of coarse gastropod-bivalve-shell fragments, now overlain by a soil profile supporting small bushes and grasses. Similar stranded beach ridges are found in the other mangrove areas (e.g. Yatala Harbour, Port Pirie, Port Gawler).

(3) Yatala Harbour, south of Red Cliff Point in Spencer Gulf (Fig. 4) was studied in detail prior to this survey.[6] This area exemplifies the "Gulf" type of sediment described above.

[6] Depers, A. M. (1974).—Sedimentary facies at Yatala Harbour and a geochemical comparison with Port Pirie sediments, Spencer Gulf, S.A. B.Sc. (Hons.) thesis, University of Adelaide. Unpublished.
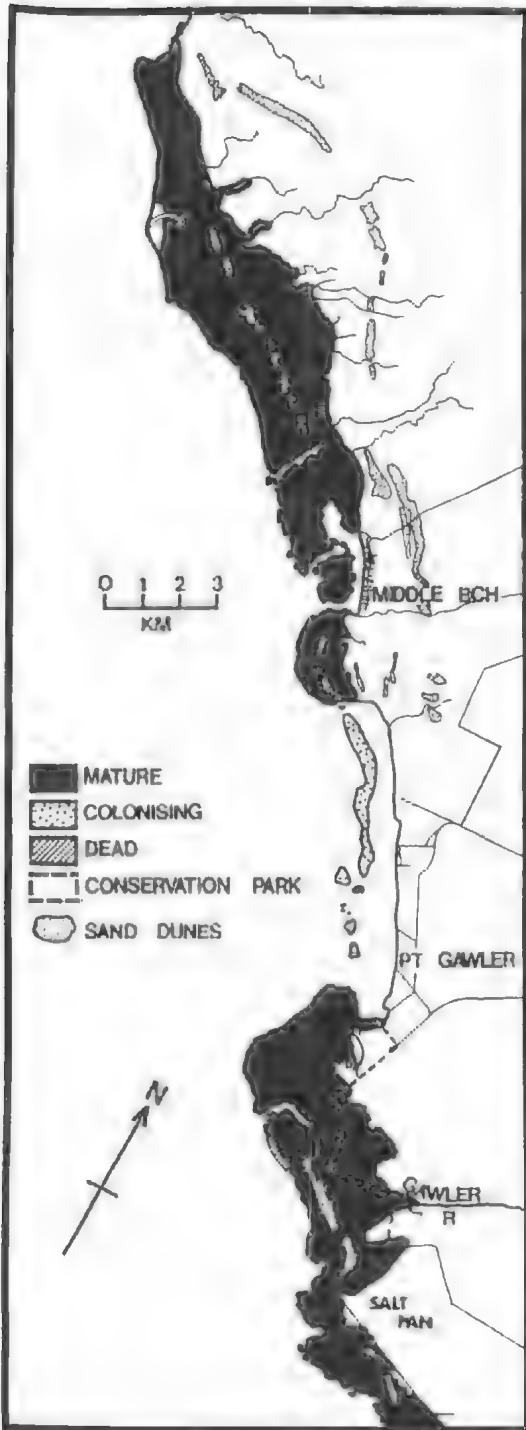
Fig. 7. Middle Beach and Port Gawler, Gulf St Vincent.
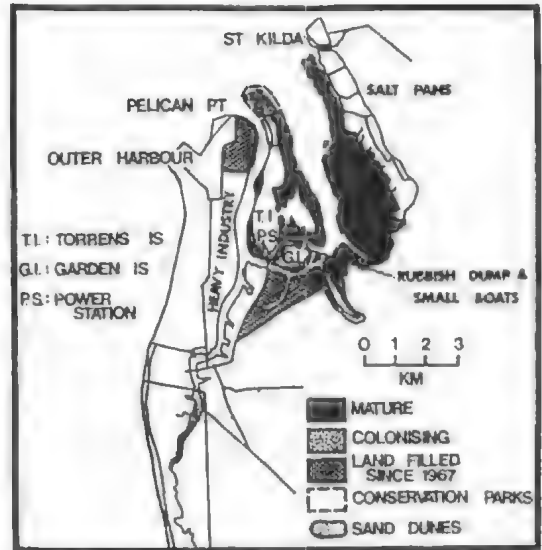
Fig. 8. Port Adelaide, Gulf St Vincent.

A thin sequence of Holocene sediments occurs in a prograding carbonate shoreline. To seaward, the area is flanked by shell-grit grain-stones and *Heterozostera* seagrass banks; in deeper water are banks of *Posidonia* seagrass. On the landward side are extensive supratidal carbonate lagoons and samphires.

The mangroves grow in grey sediments consisting of from 60% to 100% carbonate mud as estimated by areas on smear slides. Terrigenous clay can be as high as 35% and organic matter up to 20%. Smear slides of the sediments show that the carbonate is dominantly precipitated calcite rhombs (45–87%) with minor aragonite rosettes ($\leqslant 1\%$) and some dolomite rhombs ($\leqslant 1\%$). The remainder of the carbonate fraction (6–30%) consists of mainly algal fragments and smaller amounts of foraminifera, echinoid spines and bryozoan fragments. Most of the particles are clay to medium silt sized. Quartz grains are generally rounded to sub-rounded, with the occasional angular grain present. Similar sediments have also been found at Port Pirie.

The algal mats which grow on bare mud and hold the surface sediments together are partially laminated in section. Subaerial exposure causes them to crack and curl. The mud crab *Helograpsus* plays an important role in bioturbating the sediment. The tidal channels are large and usually contain water at low tide. Some of the channels are very rich in decaying organic matter, especially masses of dead leaves of *Posidonia* sp., and smell strongly of hydrogen sulphide. In one channel, 12 cm of solid

black peat was found. The tidal channels commonly contain a channel-lag wackestone, consisting of a concentration of bivalve and gastropod shells.

Extinct Mangrove Stands

Extinct mangrove stands have been recorded at Glenelg (Cotton 1949), at Webb Beach near Parham, and at Davenport Creek (above). We examined only one, Baker's Creek at Webb Beach, in any detail. Here we found two well-preserved platforms of sediment bound by algal mats, one overlying the other with about 15 cm of shell fragment grainstone between them.

Dead tree stumps lie within the platforms. Smear slides showed that the sediments are similar in composition to those found in other areas. Both are carbonate-rich; they are extremely rich in organic carbon, and this is true of all the extinct stands we have seen. Probably the algal layer protects the sediment and, because it does not break apart, decomposition is extremely slow.

There is some evidence of considerable sea-level changes in this area (S. Curr. pers. comm.; Ward & Jessup 1965) and the presence of two mud platforms one above the other may also indicate such changes. But the evidence from the extinct mangrove platforms is not conclusive, because mangroves can live over a range of altitudes in the intertidal zone (Butler unpubl.).

To the south of the extinct stand is a small stand of living mangroves in a tidal channel relatively protected from the dominant sea swell.

The deaths of the two Webb Beach stands seem likely to be the result of encroachment of shell-grit facies over the mangrove boundstone. Extensive dunes on the landward side also could have had an effect on the mangroves.

Sedimentary Dynamics—Conclusion

Within the mangrove community, a dynamic relationship exists between the sediment and the plants growing in and on it. Some sediment must be present for colonization by the plants, but once they have colonized rootlets, pneumatophores and algal mats stabilize the sediment; algal mats facilitate the entrapment and precipitation of carbonate grains (Bathurst 1971; Carlton 1974; Gebelein 1969; Neumann et al. 1970; Scoffin 1970). This relationship is a delicate one, as each supports the other.

It is clear that the persistence of a mangrove forest depends greatly on sedimentary processes. There are places (e.g. Port Clinton)

where erosion of the sediment is leaving the trees without support and they are dying without replacement. In others (e.g. part of Davenport Creek) saltation or encroachment by dunes is killing the forests; it appears that in some such cases mature trees survive but seedlings cannot establish, so that the forest eventually disappears. We cannot cite clear cases of the opposite, where death of mangroves results in erosion of the sediment, but it is possible.

EXTINCT MANGROVE FORESTS, AND NOTES ON HISTORY

We have found sheets of mangrove mud containing dead stumps at Davenport Creek, west of Ceduna, and at Webb Beach, Gulf St Vincent. Cotton (1949) reported such a mudflat briefly exposed at Glenelg, and suggested "from faunal studies" that mangroves existed "until a comparatively short time ago" as far south as Port Noarlunga.

Cotton postulated that mangroves are gradually retreating northwards in Gulf St Vincent. Independently of that, he also suggested because some of the mollusc shells in the mud were larger than present-day specimens that when the forest at Glenelg flourished conditions were a little warmer than at present. We have found, in conversation, a popular local belief that mangroves are retreating northwards because conditions are becoming cooler, so that they cannot survive further south. We do not think this is the best interpretation of the facts.

The distribution of the known extinct stands is not consistent with a simple retreat up the Gulf. Cotton postulated that the mangrove forest at Glenelg was contemporary with the red sand-dunes which lay behind the recent, white dunes and that it flourished 1000–3000 years ago, finally being killed by "sand-silting".

As noted above, we think that the death or reduction of forests in several areas can be explained in terms of sedimentary processes—encroachment by dunes, saltation or erosion.

It is beyond the scope of this paper to discuss broad patterns of changes in sea level, climate, wind, wave and current patterns and coastal morphology into which these cases might fit, but we think it is clearly not a simple case of mangroves retreating north as the climate cools. That would be inconsistent with the fact that they occur much further south at Westernport Bay, Victoria. Rather, we see mangroves as living in very dynamic sediments with

siltation, saltation and erosion taking place in different stands according to the local conditions at this time.

We have also encountered a "popular belief" that mangroves were much more extensive in South Australia on the arrival of white settlers than they are now, for example, that they occupied the beach at Glenelg and occurred at Port Noarlunga. It is said they were cleared because people feared malaria. This belief may be accounted for by a misreading of Cotton's (1949) paper, by a misidentification of the plants, or by its being true. We decided to find what we could from the writings of early settlers.

Cotton (1949) noted that "a sketch of (the Glenelg) area by Colonel Light in about 1835 depicts the beach pretty well as at present". Light (1839; also quoted by Bull 1884) gave a bearing and latitude which clearly placed him off Outer Harbour when he noted "to the northward and eastward mangroves growing to the water's edge". These must have been the mangroves of Torrens Island, St Kilda and northwards to Port Gawler. At another time sailing northward along Holdfast Bay he recorded "hard sandy beach the whole way".

Certainly extensive areas of tidal swamps in the Port Adelaide region and to the south have been filled.[1] Much of this has been done within recent memory, but the beach at Glenelg was not created in this way; the mangroves there appear to have been buried more than 130 years ago. We cannot be sure about Port Noarlunga.

COMMUNITIES OF ORGANISMS IN S.A. MANGROVE SWAMPS

Lists of flora and fauna collected will be presented elsewhere but the following remarks based on those lists are worth recording here.

We found no trends across the State that would be interesting biogeographically; rather,

any of the species could be expected if conditions were appropriate. This is not surprising, as all the mangrove forests fall within the Flindersian Province defined by Womersley & Edmonds (1958). By definition, *Avicennia* was always present; most commonly there was an extensive saltmarsh to landward, dominated by *Salicornia* or with *Salicornia* and *Arthrocnemum* codominant, and bare mud flats or seagrass beds usually lay to seaward of the mangroves. The fauna varied between sites.

It does not appear that there is a unique assemblage of organisms which might be called a "typical South Australian mangrove community", i.e. an assemblage of species which nearly always occur together. Even the animal species most commonly associated with mangroves, such as the crab *Helograpsus haswellianus* and the snail *Bembicium auratum*, are sometimes rare or absent, and they do occur commonly in the absence of mangroves.

These observations indicate that the distribution and abundance of species in the tidal swamps depends primarily on the requirements of the individual species, and on factors such as substrate type and height of sediment above mean sea level, rather than on the presence of the mangrove itself. This is in general agreement with the conclusions of Clarke & Hannon (1971) on plant zonation in tidal swamps in the Sydney district, and of Macnae (1968) on the distribution of animals within mangrove forests.

All areas of mangroves in South Australia have features in common, because *Avicennia marina* has certain requirements (Clarke & Hannon 1967, 1969, 1970, 1971; Farrell & Ashton 1974[2]). But the mangrove is flexible in its requirements and in most respects it appears to have wide tolerances. This is reflected in the variable communities of organisms that live with it.

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[1] Mangroves to the south of North Arm, and along creeks south of the docks at Port Adelaide, can be seen in 1935 aerial photographs held by the Geography Dept., University of Adelaide. (RAAF aerial photography Eden Area (Adelaide Survey) (9-11-35) Frames 03894,5,7,8,9 and 03918, 19,20.) Most of these have been filled, thus they are absent from our Fig. 8. Fig. 8 shows those filled since 1967.

[2] Farrell, M. J. & Ashton, D. H. (1974). Environmental factors affecting the growth and establishment of mangroves in Westernport Bay (Report to Westernport Bay Environmental Study, Melbourne, November 1974).

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THE AGE OF AYERS ROCK AND THE OLGAS, CENTRAL AUSTRALIA

BY C. R. TWINDALE AND W. K. HARRIS

Summary

Large areas of the desert plains of the southwestern part of the Amadeus Basin, central Australia, are underlain by Cainozoic terrestrial deposits which rest on an irregular land surface eroded in folded Proterozoic and Cambrian strata. This pre Cainozoic surface embraces the broad massifs now surmounted by the Olgas and Ayers Rock, and the broad bedrock depression separating the two, as well as many minor valleys and hills. The main depression is part of an ancient valley system which drained to the southwest.

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by C. R. TWIDALE* and W. K. HARRIS†

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TWIDALE, C. R. & HARRIS, W. K. (1977).—The age of Ayers Rock and the Olgas, central Australia. *Trans. R. Soc. S. Aust.* **101**(1), 45-50, 28 February, 1977.

Large areas of the desert plains of the southwestern part of the Amadeus Basin, central Australia, are underlain by Cainozoic terrestrial deposits which rest on an irregular land surface eroded in folded Proterozoic and Cambrian strata. This pre-Cainozoic surface embraces the broad massifs now surmounted by the Olgas and Ayers Rock, and the broad bedrock depression separating the two, as well as many minor valleys and hills. The main depression is part of an ancient valley system which drained to the southwest.

The lower parts of the old landscape have been buried by lacustrine, alluvial and aeolian sediments. The age of the basal Cainozoic strata deposited in the lower parts of the old relief provides a minimum age for the erosional surface including the upland precursors of the contemporary inselbergs, though it is emphasised that the present steep-sided morphology of these bornhardts is a comparatively recent development.

Palynological evidence from carbonaceous sediments lying directly on the old land surface indicates a Middle Paleocene age. Thus the Olgas and Ayers Rock viewed as upland masses cannot be younger than this, and probably evolved during the later Cretaceous. They were upland remnants standing above a late Cretaceous surface of low relief that extended over wide areas of central Australia, the northern Flinders Ranges and northwest Queensland

Introduction

Since their discovery by Europeans just over a hundred years ago (Gosse 1874, Giles 1875, 1889), Ayers Rock and the Olgas complex have fascinated earth scientists and the lay public alike. Both uplands are bornhardts or domed inselbergs (Figs 1 and 2). Ayers Rock is a single, isolated, monolithic dome that stands 877 m above sealevel and 340–350 m above the surrounding desert plains (Fig. 3). The Olgas, on the other hand, consist of a group of topographic domes of varied morphology, some being hemispherical, others towers with rounded crests, and yet others are the *pitons émoussées* or bevelled towers of the French literature (e.g. Mainguet 1972). The highest, Mt Olga itself, rises 1,069 m above sealevel and 500–550 m above the plain level. Both inselbergs are noteworthy by virtue of their size alone, but they gain further dramatic impact from their splendid isolation, from the steepness and intricate etching of their bounding slopes and their consequent abrupt rise from the surrounding essentially flat desert plains, and from the marked contrast between the latter and these towering red massifs.

From a geomorphological point of view the bornhardts are unusual in that they are both eroded from folded sedimentary formations. Bornhardts developed in granitic rocks are fairly commonplace and widely distributed (see Wilhelmy 1958; Twidale 1971, 1976a) but Ayers Rock has been sculptured from very steeply dipping Cambrian arkose, and the Olgas group from the moderately dipping, massive and coarse Mount Currie Conglomerate of the same age (Tate & Watt 1896, Joklik 1952, Forman 1966, Wells *et al.* 1970), deposited in the piedmont of the Musgrave Block, and within the intracratonic Amadeus Basin (Fig. 2).

The processes responsible for shaping these spectacular landforms have been discussed elsewhere (Twidale 1977, Twidale & Bourne 1977). However the age of the inselbergs as topographic forms, as of any landforms, is critical, for this provides a framework for the climatic and tectonic conditions under which the features evolved, and an essential perspec-

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Fig. 1. Oblique aerial view from the southeast of Ayers Rock (foreground) and the Olgas in the distance. Note the steep dip of the strata in Ayers Rock, the flat desert plains, and the approximate location of bore G 394855-44 (circled). (S. Aust. Tourist Bureau.)

tive when problems of survival are contemplated (Twidale 1976b).

Geomorphological setting

Drilling has confirmed inferences drawn from their morphology, namely that the plains that surround the two residuals are depositional. They are underlain by Cainozoic sequences comprising lacustrine, alluvial and aeolian beds, the thickness of which varies. Though the plains surface slopes gently down from west to east and displays only minor local relief amplitude due to the development of dune ridges on the one hand and playa depressions on the other, the surface underlying the terrestrial deposits and eroded in folded Proterozoic and Cambrian beds is irregular. To the west and north of Ayers Rock, for instance, fresh arkose is nowhere more than a few metres beneath the surface (Fig. 3) and there are indeed outcrops of fresh arkose not only in the northern piedmont zone but also 700-800 m west of the base of the Rock. Immediately to the south of the inselberg the Cainozoic cover is more substantial (20-35 m) but about 300 m south of the cliff line it suddenly thickens as it passes over a (?) fault-line scarp separating the arkose from the older Proterozoic strata. The surface cut in the older rocks is here irregular, the Cainozoic being commonly 70–90 m thick but bores have penetrated through 181 m without entering the Proterozoic (Fig. 3).

To the west of the Olgas the Cainozoic cover is thin, and there are many outcrops of the Mount Currie Conglomerate in the form of low domes and platforms. To the east the younger sequence is thin near the dome complex (Fig. 3) but its thickness increases to the east where it buries a broad depression which is more than 100 m deep and is believed to be part of an old valley system draining to the southwest (R. E. Read, pers. comm.). This depression separates the broad platforms or massifs surmounted by the two bornhardts. Thus the Cainozoic sequence has inundated the lower parts of an irregular land surface cut in the Proterozoic and Cambrian sediments. As there was a broad valley depression prior to their deposition, it follows that the two adjacent higher massifs also predate the deposition; and though there is reason to believe that neither
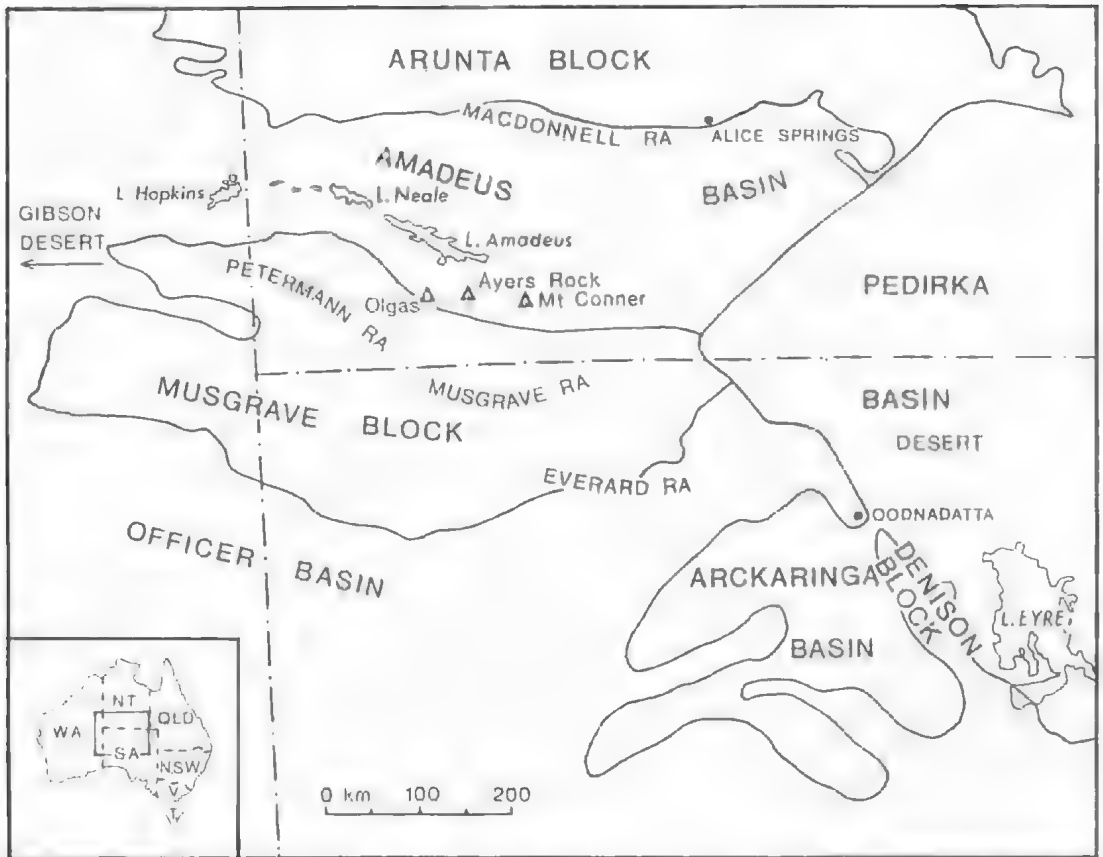
Fig. 2. Generalised tectonic map of southwestern part of the Northern Territory showing locations mentioned in text.

Ayers Rock nor the Olgas were then as steep sided and of such dramatic appearance as they now are (Twidale 1977), there must have been ancestral uplands in the same locations. Thus the age of the basal Cainozoic provides a minimum age for these residuals. Bremer (1965) surmised that Ayers Rock is of some antiquity but was unable to cite any specific evidence on the point.

Age of the basal tertiary strata

According to Wells *et al.* (1970) the Cainozoic sequence of the southwestern part of the Amadeus Basin includes lacustrine strata of early Tertiary age, but they were unable to be more exact. In a general way, however, their estimate is borne out by the fact that some of the Cainozoic beds have been duricrusted, both ferruginous (laterite) and siliceous (silcrete) carapaces having been developed in the course of prolonged deep weathering. The silcrete of central Australia is generally considered to have formed during the early-middle Tertiary, reaching its climax in the Miocene (Wopfner & Twidale 1967, Wopfner *et al.* 1974) so that the lake sediments beneath these duricrusts appear in general to be of early Tertiary age.

Fortunately it is now possible to give a more precise age for the basal Tertiary sediments. Lignites resting directly on the old land surface eroded in the folded Proterozoic and Cambrian rocks occur in four bores near Ayers Rock and the Olgas (Fig. 3). A sample (S.A. Dept. Mines Sample No. S4065) of one lignite from bore G394855-44 located in the broad valley between the Olgas and Ayers Rock (Fig. 3), and from a depth of 81–84 m beneath the surface, contains a diverse palynomorph assemblage, which includes the following stratigraphically useful species: *Anacolosidites acutullus* Cookson & Pike, *Beaupreaidites elegansiformis* Cookson, *B. verrucosus* Cookson, *Camarozonosporites bullatus* Harris, *Cyathi-*
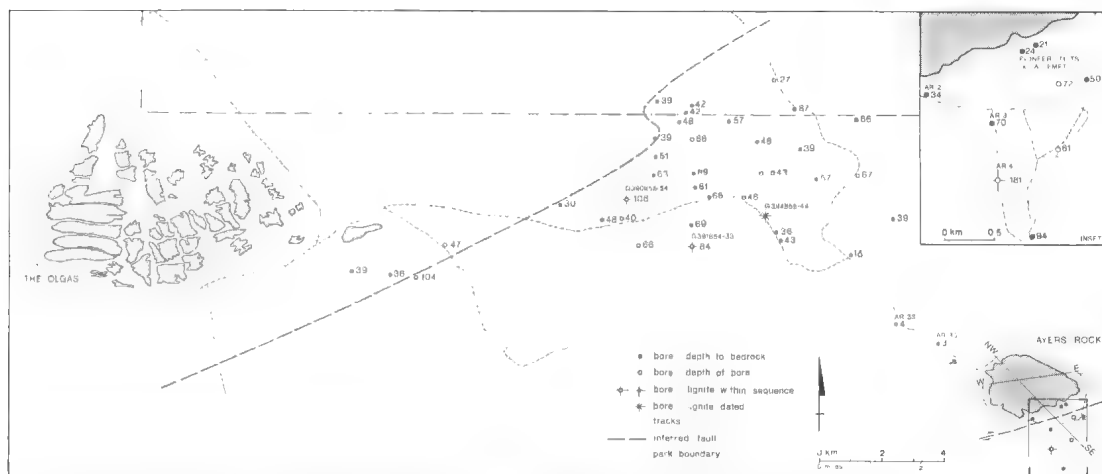
Fig. 3. Drilling sites in the Ayers Rock and Olgas region. Depth to Proterozoic or Cambrian bedrock in metres. Bores with lignite starred. Position of G 394855-44 shown. (After Water Resources Branch, Dept of Northern Territory, Alice Springs).
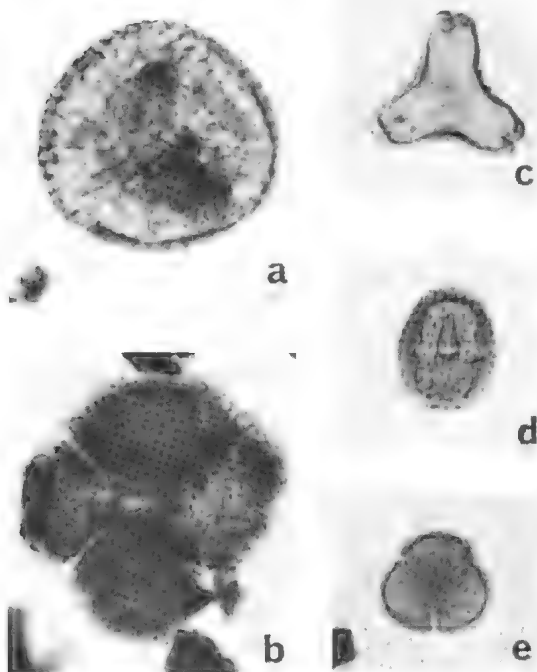
Fig. 4. Spores from carbonaceous sediment from depth of 81-84 m in bore G 394855-44. a *Latrobosporites ohaiensis* (Couper) Stover, b *Quadraplanus brossius* Stover, c *Gambierina rudata* Stover, d *Tetracolporites verrucosus* Stover, e *Tricolpites reticulatus* Cookson. All x500.

dites splendens Harris, *Ephedripites notensis* Cookson, *Gambierina rudata* Stover, *Gephyrapollenites wahooensis* Stover, *Herko-*

sporites elliottii Stover, *Krauselisporites papillatus* Harris, *Proteacidites angulatus* Stover, *P. fromensis* Harris, *P. kopiensis* Harris, *Quadraplanus brossius* Stover, *Tetracolporites verrucosus* Stover and *Tricolpites reticulatus* Cookson. These species and other elements not reported herein have features in common with southern Australian Paleocene spore-pollen assemblages. Biostratigraphic schemes for the early Tertiary have been proposed for the Gippsland Basin by Stover & Partridge (1973) and for the Otway Basin by Harris (1971). More recently these schemes have been extended from the coastal basins to the continental basins of South Australia (Wopfner *et al.* 1974). Paleocene sediments of the Eyre Formation in the Eromanga Basin contain palynomorph assemblages closely similar to that described here.

The absence of the nominate zone species which characterise the biostratigraphic zones of Harris (1971) and Stover & Partridge (1973) does not preclude correlation and whilst there are significant differences between this assemblage and those of both the Otway and Gippsland basins, there are, nevertheless, many elements in common. In particular *Camarozonosporites bullatus*, *Gambierina rudata* and *Krauselisporites papillatus* are late Cretaceous to Middle Paleocene forms, *Herkosporites elliottii* and *Proteacidites angulatus* commence their stratigraphic range in the Middle Paleocene, *Tetracolporites verrucosus* is an Early to Middle Paleocene form and *Quadraplanus brossius* is restricted to the Early Paleocene of the Gippsland Basin. *Anacolosidites acutullus,*

Beaupreaidites elegansiformis and *B. verrucosus* appear later in the Paleocene or Early Eocene of the Gippsland Basin but *A. acutullus* occurs in the Middle to Late Paleocene of the Otway Basin.

The weight of evidence thus favours a Middle Paleocene age for the assemblage which correlates with the *Gambierina edwardsii* zone in the Otway Basin and the *Lygistepollenites balmei* zone in the Gippsland Basin. This is supported by the absence of the younger *Malvacipollis diversus* Harris and the older elements such as *Tricolpites longus* Stover. The assemblage differs from the correlatives of the *Gambierina edwardsii* zone in the Eyre Formation in the very rare occurrence of *Nothofagidites* spp. and absence of *Australopollis obscurus* Harris. Kemp's (1976) assemblages from Central Australia are younger and quite distinct. There are no indications of marine influence and abundance of conifer pollen of the *Microcachrys* and *Podocarpus* types indicates high rainfall.

A systematic account and a full discussion on the implication of this assemblage will be presented elsewhere.

Conclusion

As the lignites resting on the old land surface cut in Proterozoic and Cambrian sediments are of Paleocene age the old landscape including the precursors of the present Ayers Rock and the Olgas cannot be younger than Paleocene in age. They may thus be part of the late Cretaceous land surface described from other parts of central Australia (Mabbutt 1965) and from other areas marginal to the Great Artesian Basin (Woodard 1955, Twidale 1956, 1966, 1969, 1976b, Twidale, Bourne & Smith 1976), and contemporary with the crests of the higher granite inselbergs on Eyre Peninsula (Twidale & Bourne 1975).

Acknowledgments

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TRANSACTIONS OF THE
ROYAL SOCIETY
OF SOUTH AUSTRALIA
INCORPORATED

CONTENTS

REVISION OF THE GENUS MACROPOSTRONGYLUS AND DESCRIPTIONS OF THREE NEW GENERA: POPOVASTRONGYLUS, DORCOPSINEMA, AND ARUNDELIA (NEMATODA: TRICHONEMATIDAE)

BY *Patricia M. Mawson*

Summary

The genus Macropostrongylus is redefined and revised. Species retained in the genus are M. macropostrongylus, M. macrostomata, M. yorkei, M. lesouefi, and M. irma. New genera are proposed: Popovastrongylus for M. wallabiae, M. pearsoni, and M. irma n.sp.; Dorcopsinema for M. dorcopsis; Arundelia for M. dissimilis. M. australis, M. cornutus, and M. minor are referred to Cloacina; M. labiatus to Zoniolaimus, and M. baylisi to Macropostrongyloides. The genus Gelanostrongylus is suppressed. Cloacina daveyi nom.nov. is proposed for C. australis Johnston & Mawson nec C. australis (Yorke & Maplestone).

REVISION OF THE GENUS *MACROPOSTRONGYLUS* AND DESCRIPTIONS OF THREE NEW GENERA: *POPOVASTRONGYLUS*, *DORCOPSINEMA*, AND *ARUNDELIA* (NEMATODA: TRICHONEMATIDAE)

by Patricia M. Mawson*

Summary

Mawson, P. M. (1977) Revision of the genus *Macropostrongylus* and descriptions of three new genera: *Popovastrongylus*, *Dorcopsinema*, and *Arundelia* (Nematoda: Trichonematidae). *Trans. R. Soc. S. Aust.* **101**(2), 51-62, 31 May, 1977.

The genus *Macropostrongylus* is redefined and revised. Species retained in the genus are *M. macropostrongylus*, *M. macrostoma*, *M. yorkei*, *M. lesouefi*, and *M. irma*. New genera are proposed: *Popovastrongylus* for *M. wallabiae*, *M. pearsoni*, and *M. irma* n.sp.; *Dorcopsinema* for *M. dorcopsis*; *Arundelia* for *M. dissimilis*. *M. australis*, *M. cornutus*, and *M. minor* are referred to *Cloacina*; *M. labiatus* to *Zoniolaimus*, and *M. baylisi* to *Macropostrongyloides*. The genus *Gelanostrongylus* is suppressed. *Cloacina daveyi* nom.nov. is proposed for *C. australis* Johnston & Mawson nec *C. australis* (Yorke & Maplestone).

Introduction

As a result of the availability of new collections of nematodes from kangaroos and wallabies it is now possible to revise some descriptions, in particular those of species attributed to *Macropostrongylus* Yorke & Maplestone. Where possible comparison has been made with type material, and a complete revision of the genus has been undertaken. New species undoubtedly await description, as the parasites of macropod marsupials, especially those in western and northern parts of Australia, have seldom been collected systematically. It is hoped that the present work will aid future studies.

Most measurements of specimens have been omitted from descriptions, they are available on request from the author or Librarian.

Historical

Although it has not been possible to examine the type material of *M. macropostrongylus* and *M. australis*, the species for which the genus *Macropostrongylus* was erected by Yorke & Maplestone (1926), specimens so identified by Baylis (1934) have been studied. The species are re-described from this material and from specimens from the same host (*M. agilis*) from Papua. The revised generic diagnosis is given

below. From Yorke & Maplestone's figures *M. australis* appears referable to *Cloacina* Linstow 1898; the specimens identified by Baylis are certainly *Cloacina* sp. As *C. australis* (Yorke & Maplestone) predates *C. australis* Johnston & Mawson (1938), a new name must be given to the latter, and *C. daveyi* is proposed.

Baylis (1927) added *M. yorkei* to the genus; this is redescribed below from the type host.

The paratype material of four new species assigned to *Macropostrongylus* by Davey & Wood (1938) has been re-examined. *M. cornutus*† and *M. minor* belong to *Cloacina*, as was suggested from a study of the figures by Johnston & Mawson (1939). *M. labiatus* belongs to the genus *Zoniolaimus*, close to *Z. setifera* Cobb, 1898. *M. macrostoma*, partially described below is a true *Macropostrongylus*.

Paratype material of *M. dorcopsis* Baylis, 1940, from a wallaby in New Guinea has been examined, and is considered so different from *Macropostrongylus* spp. as to necessitate the erection of a new genus, *Dorcopsinema*, described below.

Johnston & Mawson in several papers (1939, 1940) added five species: *M. dissimilis*, *M. irma*, *M. lesouefi*, *M. pearsoni*, and *M. wallabiae*. Of these, *M. dissimilis* is referred to

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† *M. cornutus* has recently been described by Mawson (in press).

Arundelia n.g., *M. wallabiae* and *M. pearsoni* to *Popovastrongylus* n.g., and the others retained in *Macropostrongylus*.

Yamaguti (1961) placed *M. lasiorhini* Mawson, 1955, from a wombat, as the type of *Macropostrongyloides*. *Macropostrongylus baylisi* Wood, 1930, is now transferred to this genus.

Macropostrongylus macropostrongylus was described as having a leaf crown. Popova (1952) erected a new genus *Gelanostrongylus* for species which had been assigned to *Macropostrongylus* but in which the leaf crown is absent. She placed the following species in the new genus; *M. macrostoma* (type species), *M. dissimilis, M. labiatus, M. irma, M. lesouefi, M. wallabiae*, and *M. dorcopsis*. However, the morphology of *M. macrostoma* is essentially similar to that of *M. macropostrongylus*, and therefore *Gelanostrongylus* cannot stand. However it certainly appears that there are two distinct groups of species left in *Macropostrongylus*, even after those belonging to other genera, as noted above, are excepted. The species *M. macropostrongylus, M. macrostoma, M. lesouefi, M. yorkei* and *M. irma* form a natural group, as do *M. wallabiae* and *M. pearsoni*. A new genus, *Popovastrongylus*, is now proposed for the latter group.

In *Macropostrongylus* the perioral cuticle forms eight lobes, the buccal capsule is ridged longitudinally and ends anteriorly in eight small projections, and the oesophagus is more or less cylindrical ending in an elongate bulb. In *Popovastrongylus* the perioral cuticle continues into the buccal cavity without forming lobes, the buccal capsule is more or less cylindrical (or oval in section) without ridges and without anterior projections, and the oesophagus is relatively shorter, narrows suddenly in its posterior half, and ends in a bulb. *Macropostrongyloides* is distinguished from *Macropostrongylus* by the presence in the buccal capsule of four large teeth, by the shape of the oesophagus, and by the position of the externo-dorsal ray, which rises from the dorsal ray. *Macropostrongylus* spp. and *Popovastrongylus* spp. occur in the stomach of the host; *Macropostrongyloides* spp. in the large intestine.

Macropostrongylus Yorke & Maplestone

Generic diagnosis (revised):

Trichonematidae:

Anterior end with four submedian setigerous papillae and two lateral elevations bearing amphids; buccal capsule and mouth more or less laterally compressed; perioral cuticle forming eight lobes; buccal capsule folded longitudinally into eight ridges which, variously thickened, project anteriorly under the cuticular lobes; oesophagus long, slender, with oval terminal bulb. Male: dorsal lobe of bursa longer than laterals, ventral lobes distinct from laterals and more or less joined ventrally; externo-dorsal rays arising separately or with laterals, dorsal ray bifurcating before mid-length, each branch giving off a lateral branch; spicules alate; gubernaculum present. Female: Tail short, conical, vulva near anus. Parasites of the stomach of macropod marsupials. Type species: *M. macropostrongylus*. other species; *M. macrostoma; M. yorkei; M. lesouefi; M. irma*.

In *Macropostrongylus* the anterior end is simple, without a collar roll. A slightly raised ridge surrounds the cephalic papillae. The submedian papillae, usually setigerous, and the lateral elevations are more or less prominent. Lateral compression of the mouth and buccal capsule, but not of the entire lateral end, is variable. Anteriorly the eight longitudinal ridges of the buccal capsule project as lobes but these are covered by the corresponding cuticular perioral lobe, forming structures which are apparently erectile (Fig. 2), and the buccal capsule varies in shape with this, giving a more or less open mouth. The lobes thus form a sort of leaf crown, but one quite distinct in appearance from that in *Cloacina* and *Murshidia* though both are formed from the peribuccal and perioral cuticle.

Macropostrongylus macropostrongylus Yorke & Maplestone

FIGS 1–7

Yorke & Maplestone, 1926, from *Macropus* sp., Qld.
Baylis, 1934 p. 129, from *M. agilis*, Qld.
Johnston & Mawson, 1939 p. 143, *M. agilis, M. wellsbyi*, Qld, 1939 p. 209, *M. agilis*, Qld.

Figs 1-7. *Macropostrongylus macropostrongylus.* 1. median view of head; 2. lateral view of head, with mouth widely opened; 3. en face view of head, 4. oesophageal region; 5. bursa; 6. dorsal ray. 7. posterior end of female; Figs 1-3 to same scale. Figs 4, 5, and 7 to same scale. Figs 4, 7, 6 to same scale. Figs. 8-12. *Macropostrongylus macrostoma*. 8. anterior end; 9. anterior end en face; 10. oesophageal region; 11. bursa, 12. posterior end of female. Figs 8 and 11 to same scale.
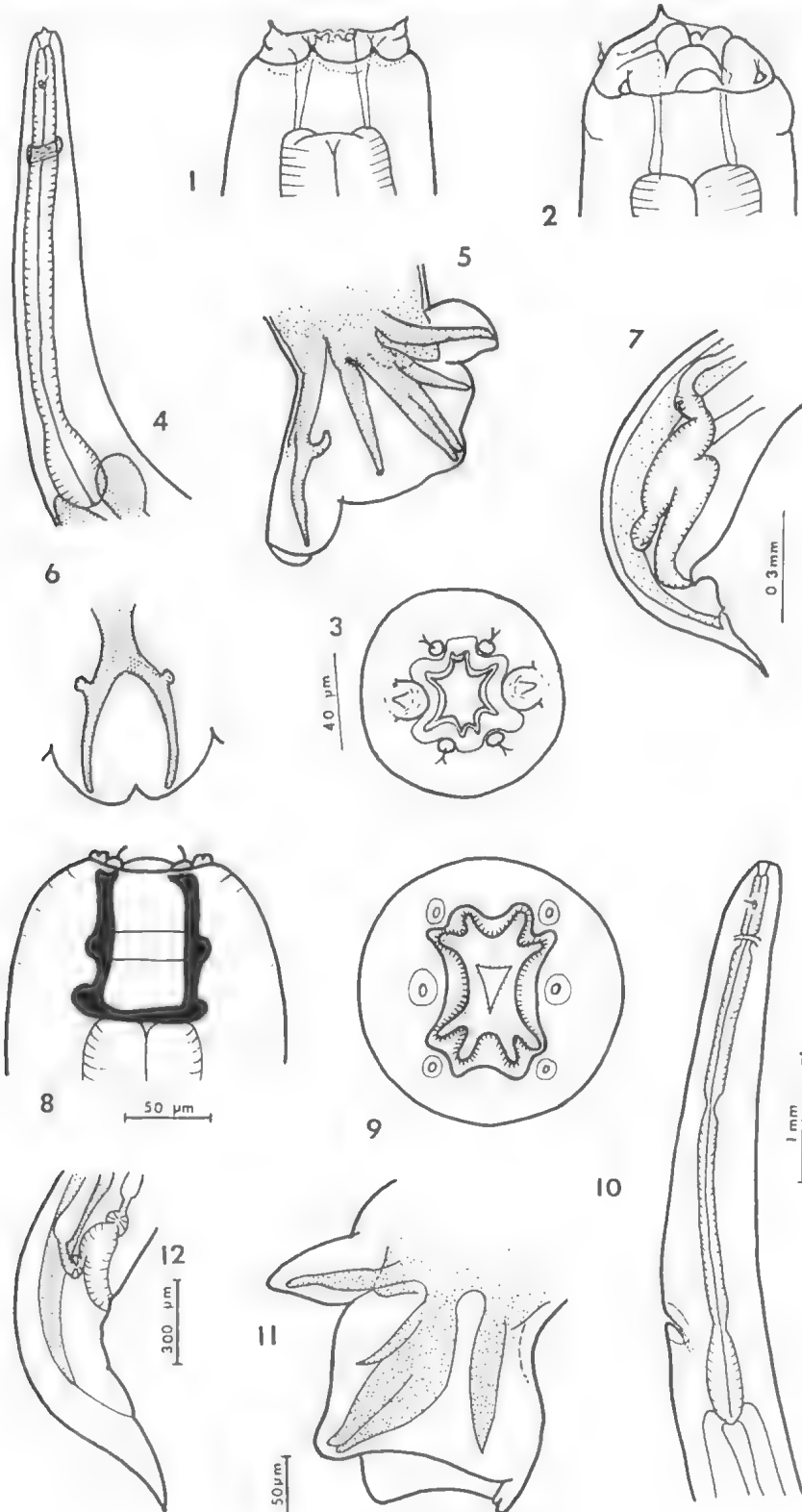
FIGS 1-12

Host and locality: *M. agilis*, from Weam, Papua New Guinea (BBM-NG-50820, BBM-NG-50798); *Thylogale brunii*, from Weam, Papua New Guinea (BBM-NG-50850)

The specimens from Papua New Guinea are shorter than those originally described, but they agree generally with them, and with those identified by Baylis (Yeerongpilly N5.28.1.2) and others recorded by Johnston & Mawson. Some redescription of the anterior end can now be made. (Figures were drawn from Papua New Guinea material from *M. agilis*.)

Amphids lie on apices of two prominent lateral elevations. Buccal capsule, somewhat laterally compressed, is not strongly chitinised; the two largest of the longitudinal ridges are lateral, and the two smallest dorsal and ventral. Ratio length: spicule length 3.0–3.6, and of length: oesophagus 3.3–4.2.

Cervical papillae thread-like, about twice the length of buccal capsule from anterior end. Egg c.a. 80 x 40 μm.

Macropostrongylus macrostoma Davey & Wood
FIGS 8–12, 47

Davey & Wood, 1938 p. 261, from *Macropus robustus*, Queensland.
Macropostrongylus yorkei (*non* Baylis): Johnston & Mawson, 1939 p. 143, p.p., from *M. parryi*
Gelanostrongylus macrostoma: Popova, 1952 p. 176.

The paratype material of this species has been examined and figured.

The anterior end is similar to that of *M. macropostrongylus*. The main differences between these species are
1. Buccal capsule longer and more strongly chitinised in *M. macrostoma*, and its anterior projections more strongly developed and reinforced by extra sclerotisation in the form of an encircling belt at about its midlength, and by a thickening around base, greater dorsally.
2. Oesophagus swollen in middle third of its length in *M. macrostoma*; not swollen in *M. macropostrongylus*.
3. Form of the dorsal ray differs.
4. In *M. macropostrongylus* distance between vulva and anus is less than tail length; in *M. macrostoma* it is distinctly greater.

Macropostrongylus yorkei Baylis
FIGS 13–19, 51

Baylis, 1927 p. 215, from *Macropus* sp., Townsville, Qld; 1934 p. 129, from *M. agilis*, Burketown, Qld.
Johnston & Mawson, 1939 p. 143; 1939 p. 209, from *M. agilis*, Qld.

Host and locality: *Macropus agilis* (stomach), Tipperary Stn, N.T.

The material identified by Johnston & Mawson is scanty and in poor condition. That reported from *M. parryi* by Johnston & Mawson (1939) is now referred to *M. macrostoma* (q.v.), and the single female worm from *M. wellsbyi* (now *Wallabia bicolor wellsbyi*), probably belongs to an as yet undescribed genus. The type and paratypes have not been seen. The following partial redescription is based on some recently collected specimens of *M. agilis*.

Length of male, 6.5–8.6 mm, of female 14.2–20.5. Anterior end outlined by a low ridge, oval in *en face* view, with the long axis dorsoventral. Within this, submedian cephalic papillae and amphids are on slightly raised cuticular swellings. Buccal capsule more rounded-triangular than oval at its base, the longitudinal ridges developing in its anterior half and surrounded near base by a sclerotised ring. The whole area inside the anterior ridge probably eversible. Eversion is associated with an upthrust of the anterior end of the oesophagus, while the buccal capsule appears to widen, so becoming a longer oval in transverse section (Fig. 14).

Oesophagus long (body length: oesophagus 3.6–4.3 in male, 5.8–6.2 in female), more or less cylindrical anterior to spindle-shaped terminal bulb. Nerve ring surrounds oesophagus at about a third to a quarter of its length from head in male, less in female; thread-like cervical papillae lie about half way between anterior end and nerve ring, and excretory pore close to posterior end of oesophagus. Tips of spicules enlarged and alate. Ratio length: spicule 10.9–14.0. Eggs measure 95–110 x 53–55 μm.

The species is most like *M. macrostoma*, differing chiefly in the size and form of the buccal capsule.

Macropostrongylus lesouefi Johnston & Mawson
FIGS 20–24

Macropostrongylus lesouefi Johnston & Mawson, 1939 p. 525, from *Macropus rufogrisea*, Sydney Zoological Gardens.
Gelanostrongylus lesouefi: Popova, 1952, p. 769.

No fresh material of this species is available. The type and paratype material have been examined, and some redescription is possible.

The species is distinguished by the very prominent lateral cuticular elevations, bearing at their apices the openings of the amphids. Buccal capsule laterally compressed only in some
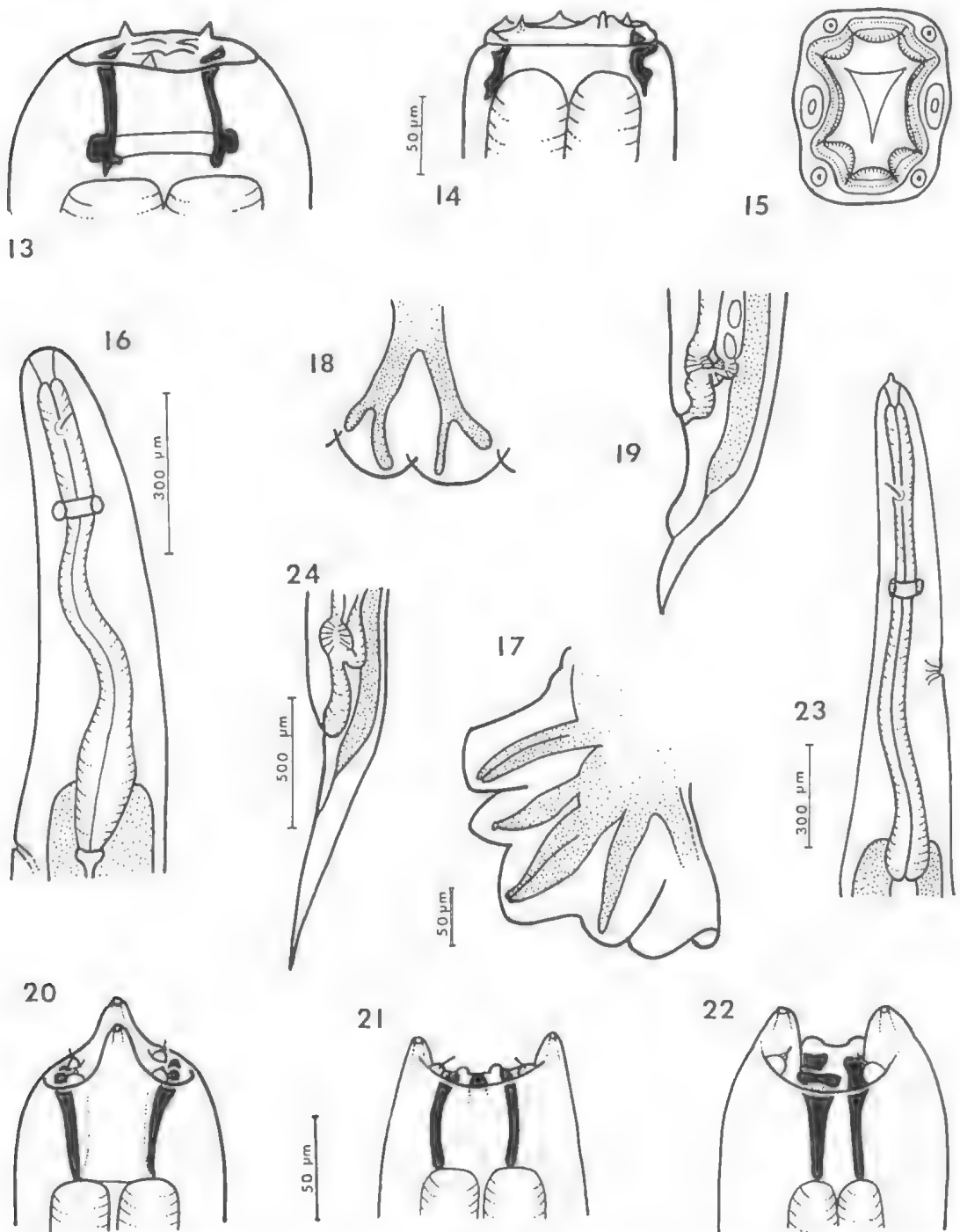
FIGS 13-24

Figs 13-19. *Macropostrongylus yorkei*. 13. head of male; 14. head of female, in mouth wide open position; 15. head, en face; 16. oesophageal region; 17. lateral view of bursa; 18. dorsal ray; 19. posterior end of female. Figs 20-24. *Macropostrongylus lesouefi*. 20. anterior end, lateral view; 21 and 22. anterior end in dorsal view, with mouth in closed and open positions, respectively; 23. oesophageal region; 24. tail of female. Figs 13-15 to same scale. Figs 17-18 to same scale. Figs 19 and 23 to same scale. Figs 20-22 to same scale.

specimens, suggesting that this is a movement connected with feeding. Anterior projections of the capsule strongly developed, those in dorsal and ventral positions directed outwards.

Oesophagus long and more or less cylindrical, with elongate terminal bulb. Nerve ring further back than in other species, almost at the end of the anterior half of the oesophagus. Excretory pore just behind nerve ring; cervical papillae half way between nerve ring and head. In the only specimen in which the spicules are intact, they measure 480 μm.

Anus of female closer to vulva than to posterior end of body; vagina short. Eggs 145–155 x 70–75 μm.

Macropostrongylus irma Johnston & Mawson

Johnston & Mawson, 1940 p. 363, from *Macropus irma*, W.A.
Gelanostrongylus irma: Popova, 1952 p. 769

These specimens are immature, probably fourth stage larvae, as the vulva is not patent. Two referred to as "females differing somewhat" are in fact fourth stage larval males. This species should perhaps be declared a *nomen nudum*, but it may be possible to recognise it should fresh material become available from the same host species. For the time being it is retained.

Key to species of *Macropostrongylus* (excluding *M. irma*).

1. Amphids on very prominent cuticular elevations 2

   Elevations bearing amphids not higher than submedian papillae 3

2. Nerve ring about ⅓ length of oesophagus from head; lateral branches leave dorsal ray immediately after its bifurcation .... *M. macropostrongylus*

   Nerve ring at nearly ½ length of oesophagus from head; lateral branches leave dorsal ray near edge of bursa .... *M. lesouefi*

3. Buccal capsule longer than its width .... *M. macrostoma*

   Buccal capsule not longer than its width ...... *M. yorkei*

Popovastrongylus n.gen.

Syn. *Macropostrongylus* Yorke & Maplestone p.p.

Trichonematidae: Anterior end with cuticular collar bearing four setigerous submedian papillae and two amphids; buccal capsule and mouth opening circular to oval; extension of perioral cuticle lines buccal cavity and may project as shelf inside it; buccal capsule thickest in its midlength, anterior border without projections; oesophagus cylindrical

anteriorly, usually narrowing abruptly in second half, ending in bulb. Male: spicules alate, gubernaculum present; bursal lobes distinct, ventrals not joined, ventral rays separate from laterals, externo-dorsals arise with laterals, dorsal ray bifurcate, each branch with shorter lateral off-shoot. Female: tail long, vulva near anus. Parasites of the stomach of macropod marsupials.

Type species: *P. wallabiae*, syn. *Macropostrongylus wallabiae* Johnston & Mawson, 1939.

Other species: *P. pearsoni*, syn *Macropostrongylus pearsoni* Johnston & Mawson, 1940; *P. irma*, n.sp.

Popovastrongylus wallabiae (Johnston & Mawson)

FIGS 25–30, 49

Macropostrongylus wallabiae Johnston & Mawson, 1939 p. 526, from *Wallabia bicolor* (*M. ualabatus*) from N.S.W.
Gelanostrongylus wallabiae: Popova, 1952 p. 785.

Host and locality: *Macropus rufogriseus*, Logan Village, Qld; Launceston, Tas.

Collections of this species from three hosts in the same area in Queensland and in one from Tasmania permit an elaboration of the original description, in regard to head structure and shape of the dorsal ray.

The small anterior collar is less obvious in some specimens than in others, as it appears partly retractable. In the type specimens a narrow shelf is present towards the anterior end of the buccal cavity, but this is not clear in all specimens. Figs 25–30 were drawn from the type specimens. In the new material from *M. rufogrisea* the eggs measure 105 x 50 μm. The length:spicule ratio is 9.0.

Popovastrongylus pearsoni (Johnston & Mawson)

FIGS 31–33, 48

Macropostrongylus pearsoni Johnston & Mawson, 1940 p. 95; Mawson, 1971, 171; from *Petrogale penicillata pearsoni* from Pearson I., S. Aust.

Host and locality: *Macropus eugenii*, Kangaroo I., S. Aust.; *Macropus rufogriseus* from Launceston, Tasmania.

Popovastrongylus pearsoni was redescribed by Mawson (1971). It is similar in many features to *P. wallabiae*, particularly in the structure of the head. As both species have now been identified from the same host species in Tasmania (though not as yet from the same host specimen) the main features distinguishing them are given:
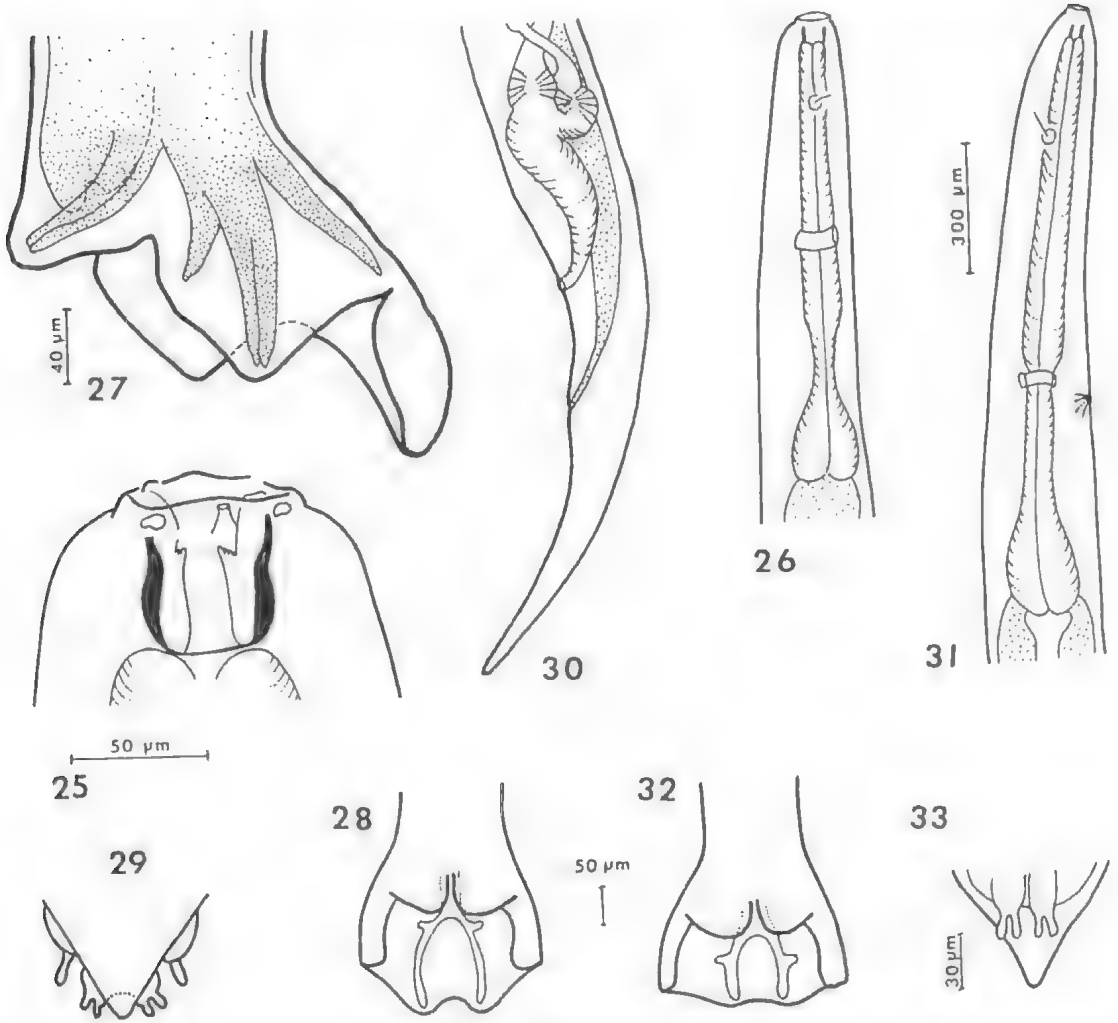
FIGS 25-33

Figs 25-30. *Popovastrongylus wallabiae*. 25. Head; 26. oesophageal region; 27 and 28. bursa, lateral and ventral views; 29. genital cone, ventral view; 30, posterior end of female. Figs 31-33. *Popovastrongylus pearsoni*. 31, oesophageal region; 32, bursa; 33, genital cone, dorsal view. Figs 26, 30 and 31 to same scale. Figs 28 and 32 to same scale. Figs 29 and 33 to same scale.

1. In *P. wallabiae* terminal bulb of oesophagus is spherical; in *P. pearsoni* it is more oval.
2. In *P. wallabiae* nerve ring surrounds oesophagus well in front of the point where it narrows, in *P. pearsoni* it lies at this point.
3. Dorsal lobe of bursa is much longer than lateral lobes in *P. wallabiae*, but about the same length in *P. pearsoni*.
4. Shape of the dorsal ray differs (Figs 28, 32).
5. Appendages of the dorsal lip of the cloaca, on the genital cone, differ (Figs 29, 33).
6. Spicules rather shorter in relation to body length in *P. wallabiae*.

Popovastrongylus irma n.sp.

FIGS 34–40, 50

Host and locality: *Macropus irma* (stomach), from Perth, W.A.

Males 8.7–10.1 mm long, females 11.1–13.0 mm. The cephalic papillae, borne on a well developed cuticular collar, are not prominent. The buccal capsule, its base thickened by an outer sclerotised ring, is a little more oval than circular in transverse section, with the long axis not exactly dorso-ventral; it lacks an internal shelf.

The oesophageal bulb is slightly elongate. Ratio length: oesophagus is 7.2–8.4 in male, 7.8–9.1 in female. Nerve ring surrounds oesophagus at the point of narrowing, and excretory pore is behind this; the thread-like cervical papillae lie shortly behind anterior end.

Spicules alate and end in a rounded tip, without enlargement; ratio length: spicule is 6.7–8.6. Bursa voluminous, all lobes of more or less even length; ventral lobes joined. Genital cone bears two small bilobed processes on dorsal lip of cloaca. Bursal rays are shown in Figs 37, 38.

The female has an unusual constriction between the vulva and the anus; in older females the body is markedly swollen in the region of the vagina, as far back as this constriction. Tail conical, ending in a point. Eggs absent in all specimens.

This species is distinguished from *P. wallabiae* and *P. pearsoni* chiefly by the absence of a "shelf" in the buccal cavity and by the shape of the dorsal ray.

Key to species of *Popovastrongylus*:

1. Nerve ring surrounds oesophagus distinctly anterior to its narrowing . . . . . *P. wallabiae*
   Nerve ring surrounds oesophagus at point of narrowing   2
2. Lining of buccal capsule forms distinct "shelf" . . . *P. pearsoni*
   Lining of buccal capsule without "shelf"
                                                                 P. irma

Arundelia n.gen.

Trichonematidae: Cloacininae: Small worms with heavily ringed cuticle; anterior end with small cuticular collar, four small, bipartite, submedian, cephalic papillae; external leaf crown of 6 elements; lips absent; buccal capsule short, stoutly built, circular in transverse section; base of buccal cavity with large hollow oesophageal projection, associated with dorsal duct in oesophagus; oesophagus widening posteriorly but without bulb. Male: bursa short, wide; ventral rays arising together, ventro- and medio-laterals arise together, postero-lateral and externo-dorsals arise separately; dorsal ray

shown in the E.S. Micrographs (Fig. 52). They bifurcates twice, spicule stoutly built, alate; gubernaculum and telamon present. Female: vulva close to anus. Parasites of the stomach of macropod marsupials.

Type species: *A. dissimilis*, syn. *Macropostrongylus dissimilis* Johnston & Mawson, 1939.

A small dorsal tooth associated with an oesophageal duct has been described in the buccal capsule in *Cloacina dahli* Linstow, 1898 and in *C. mundayi* Mawson, 1972, but in *Cloacina* an internal leaf crown, arising from the buccal capsule, is present.

In *Popovastrongylus* species the buccal capsule is oval to circular in section and a leaf crown is absent, but there is a cuticular lining inside the buccal capsule, no tooth in the buccal cavity, and the oesophagus is quite a different shape. In *Macropostrongylus* the shape of the buccal capsule is quite different.

Arundelia dissimilis (Johnston & Mawson) n.comb.

FIGS 41–44, 52

Macropostrongylus dissimilis Johnston & Mawson, 1939 p. 526, from *Wallabia bicolor* (*M. wallabatus*), N.S.W.

Host and localities: *Wallabia bicolor*, from Keyneton, Bemm River, Yarra Valley, and Dartmouth, Victoria.

This species is apparently a relatively common though not numerous parasite of *Wallabia bicolor*, and has not been found in any other macropod. Details of the buccal capsule are visible in the fresh material so the description can now be amended. Measurements of the specimens are similar to those of the original description.

Cuticle strongly ringed; body widest in posterior half, tapering slowly to head, very rapidly behind vulva, and very little to bursa. A low, thick cuticular collar anteriorly bears submedian papillae and unobtrusive, slit-like, amphid openings. Mouth circular without lips. Six short, triangular, cuticular projections around mouth not easily seen in side view but

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Figs 34-40. *Popovastrongylus irma*. 34, head; 35, head with buccal capsule dorsoventrally compressed; 36, oesophageal region; 37-38, bursa in lateral and dorsal views; 39 and 40. Posterior ends of younger and older females, respectively. Figs 34 and 35 to same scale. Figs 37 and 38 to same scale. Figs 39 and 40 to same scale. Figs 41-44. *Arundelia dissimilis*. 41-43. Head, in lateral, dorsal and en face views respectively; 44, oesophageal region. Figs 42-43 to same scale. Figs 45-46. *Dorcopsinema dorcopsis*. 45. Head of male, antero-lateral view; 46, head of female, sub-lateral view.
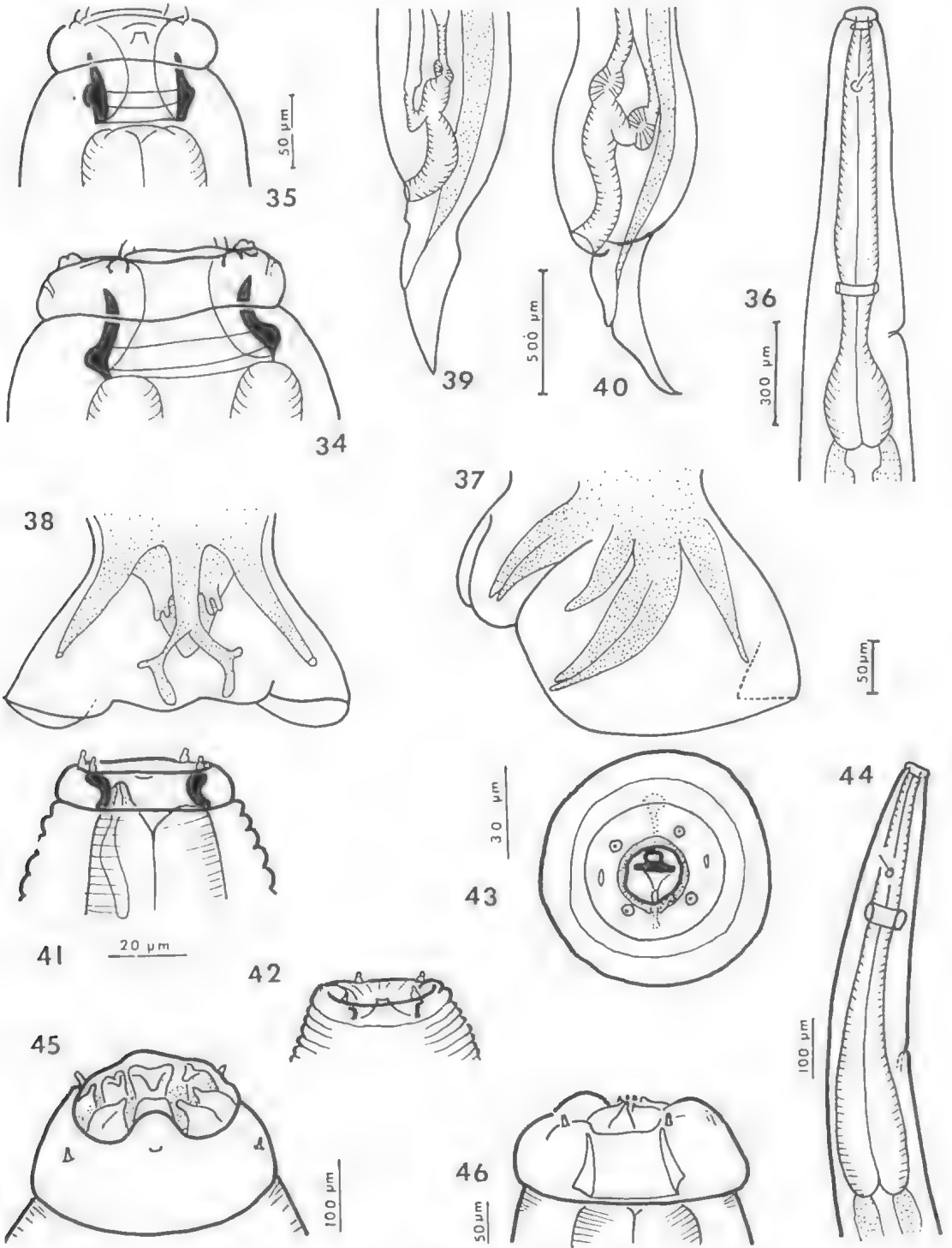
FIGS 34-46
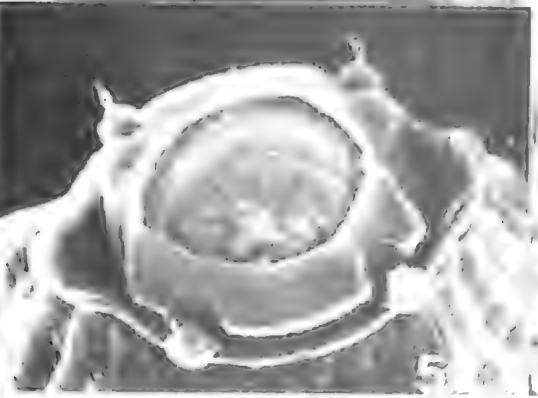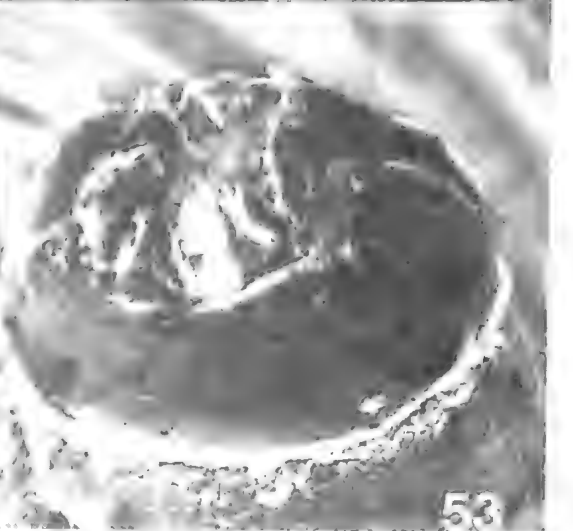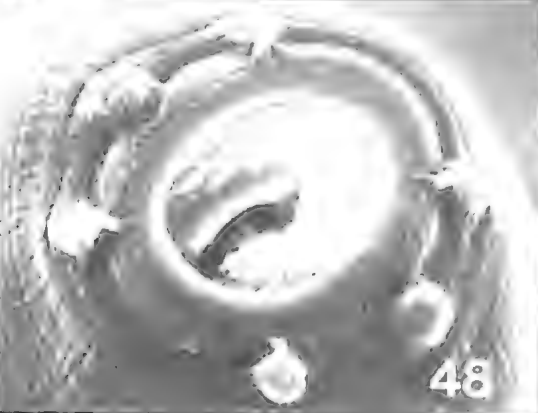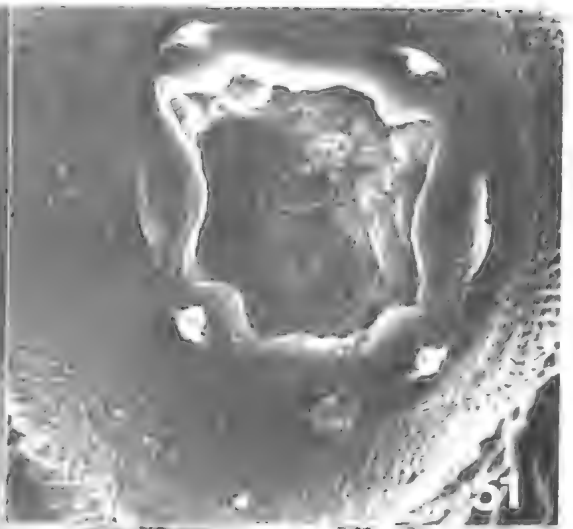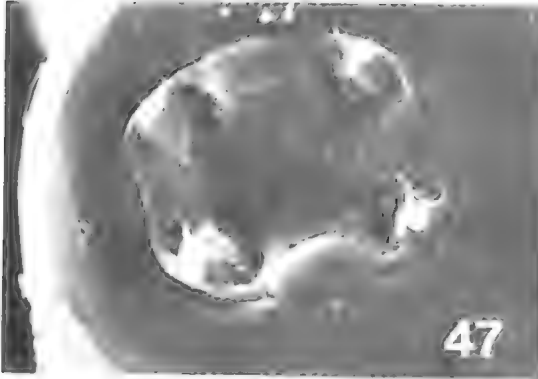
FIGS 47-53

form a sort of leaf crown but do not appear to arise from the buccal capsule as do the elements of the leaf crown in *Cloacina* species. Buccal capsule, circular in transverse sections, shallow, but with thick walls. Large, conical, chitinised structure rises dorsally in buccal cavity from anterior end of oesophagus; this is hollow, open at apex, and connected at its base with a duct in dorsal wall of oesophagus. In *en face* view, a ventral thickening and groove in the capsule wall is associated with a similar but smaller duct from oesophagus, which has not been seen in any side view of the anterior end.

Oesophagus cylindrical in its anterior third, at end of which lies the nerve ring, and then widens gradually to its posterior end. No terminal bulb. Thread-like cervical papillae lie anterior to nerve ring; excretory pore at about three-quarters length of oesophagus from anterior end.

Size of eggs in the vagina, and newly laid in the vaginal extrusion, is 130–132 x 65–70 μm, much greater than in original material (possibly measured in the uterus).

Dorcopsinema n.gen.

Trichonematidae: Zoniolaiminae: Large worms; anterior end with wide collar bearing cephalic papillae and amphids, perioral cuticle forming eight lip-like processes; buccal capsule lightly chitinised, more or less cylindrical; oesophagus long, cylindrical. Male: spicules alate, long; bursa entire, dorsal lobe long, ventral rays arising together, externo-dorsal arising with laterals, dorsal ray bifurcating and with two lateral branches from point of bifurcation. Female: tail conical, vulva shortly in front of anus. Parasites of macropod marsupials.

Type species: *D. dorcopsis* (Baylis), syn. *Macropostrongylus dorcopsis* Baylis, 1940.

The structure of the head does not closely resemble that of any other species. The lip-like processes around the mouth are very like those of *Labiostrongylus* and *Zoniolaimus* but the cephalic papillae are borne on the collar. In *Z. labiatus* Johnston & Mawson (1939) there is a collar around the anterior end bearing the cephalic papillae, and surrounding the "lips", but the oesophagus ends in a bulb.

Dorcopsinema dorcopsis (Baylis) n.comb.

FIGS 45–46, 53

Macropostrongylus dorcopsis Baylis, 1940, p. 313, from *Dorcopsis mulleri* (*D. veterum*) from Papua New Guinea.

A male and a female paratype have been examined. The presence of a very thick collar, the structure of the buccal capsule (no longitudinal ridges, no anterior projections) and the shape of the oesophagus differentiate the species from those of *Macropostrongylus*.

The "tooth-like processes" around the mouth "like a leaf crown" described by Baylis are in fact not thin and chitinised like teeth (or a leaf crown) but are more like fleshy lobes, with broad bases, mucronate at the free ends and grooved on their outer surfaces. In the male these processes are almost closed over the mouth and in the female are drawn back in a "mouth open" position (Figs 45, 46). As described by Baylis, the anterior end is surrounded by a wide collar on which are the small pointed submedian papillae and the amphids.

Fig. 47. *Macropostrongylus macrostoma* (x404); Fig. 48. *Papostrongylus labiatus* (x600); Fig. 49. *P. pearsoni* (x600); Fig. 50. *P. irma* (x600); Fig. 51. *M. yorkei* (x404); Fig. 52. *Arundella dissimilis* (x1,500); Fig. 53. *Dorcopsinema dorcopsis* (x240)

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SHORE PLATFORMS AND SEALEVEL CHANGES IN THE GULF REGIONS OF SOUTH AUSTRALIA

BY C. R. TWIDALE, JENNIFER A. BOURNE AND NICHOLAS TWIDALE

Summary

The platforms that occur along the shores of Kangaroo Island and the Gulfs region of South Australia are developed in Precambrian crystalline rocks, Palaeozic sedimentary strata and Pleistocene dune calcarenite. Evidence from these areas suggests that many platforms cut in granite and gneiss are etch surfaces, or weathering fronts developed in late Pliocene and early Pleistocene times, exposed by erosion in Recent times, and only fortuitously situated within the present tidal or spray zone. Elsewhere the unconformity between crystalline rock and aeolinate has been revealed by marine processes. Contemporary platforms cut across the structure of contorted sediments and of the aeolinate are widespread and occur as much as 8 m above present sealevel. Since they must postdate the aeolinate which is regarded as of last-glacial age, they attest to considerable erosion in a short time. Only on the coast of Kangaroo Island is there unequivocal evidence of an earlier and higher stand of the sea 5-6 m above present sealevel.

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Summary

Twidale, C. R., Bourne, J. A. & Twidale, N. (1977) Shore platform and sealevel changes in the Gulfs region of South Australia. *Trans. R. Soc. S. Aust.* **101**(2), 63-74, 31 May, 1977

The platforms that occur along the shores of Kangaroo Island and the Gulfs region of South Australia are developed in Precambrian crystalline rocks, Palaeozoic sedimentary strata and Pleistocene dune calcarenite. Evidence from these areas suggests that many platforms cut in granite and gneiss are etch surfaces, or weathering fronts developed in late Pliocene and early Pleistocene times, exposed by erosion in Recent times, and only fortuitously situated within the present tidal or spray zone. Elsewhere the unconformity between crystalline rock and aeolianite has been revealed by marine processes. Contemporary platforms cut across the structure of contorted sediments and of the aeolianite are widespread and occur as much as 8 m above present sealevel. Since they must postdate the aeolianite which is regarded as of last-glacial age, they attest to considerable erosion in a short time. Only on the coast of Kangaroo Island is there unequivocal evidence of an earlier and higher stand of the sea 5-6 m above present sealevel.

Introduction

Several of the shore platforms that occur on the coasts of western and southern Eyre Peninsula, and Kangaroo Island (Fig. 1) are anomalous, albeit in different ways.

In each of these areas Precambrian crystalline rocks (granite and gneiss) or Cambrian sediments, metasediments (mainly schists), and granites are exposed from beneath the widespread Pleistocene dune calcarenite. The latter is commonly referred to as aeolianite (Crocker 1946a) for it was deposited in coastal dunes and subsequently lithified through secondary calcification. The old dunes are extensively preserved in coastal areas of Western Australia, South Australia and Victoria. They stand up to 50 m above sealevel and as has long been appreciated the rock extends well below present sealevel at many places (Tate 1879; Sprigg 1961; Cooney 1965); for example, it is recorded that aeolianite rests on bedrock of probable Precambrian age at a depth of some 61 m just east of Elliston.[1]

There is thus no doubt that the aeolianite is related to a glacial phase or phases of the Pleistocene but there is as yet no more precise age determination. Many relic soil profiles are revealed within the aeolianite sequences in cliff sections but the permeability of the old dune rock is such that water readily infiltrates into the mass, and weathering and soil formation are rapid. Despite appearances to the contrary the building of the dunes and the deposition of the aeolianite probably did not occupy a long period of time. As Fairbridge & Teichert (1952) state of the Western Australian aeolianite dunes "the periods of soil formation were not of long duration and . . . the dune developments were in rapid sequence". The dune calcarenite exposed in the areas under investigation was probably all deposited in a single glacial phase. Certainly there is no evidence of cut and fill, such as might be expected had the dune rock presently exposed been built up in the course of several glacial periods and subjected to dissection during sub-

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[1] R. G. Shepherd (1962) Report on groundwater prospects, Hundred of Ward, Elliston Police Station. *Geol. Surv. S. Aust. Rept. Bk.* 58/32.
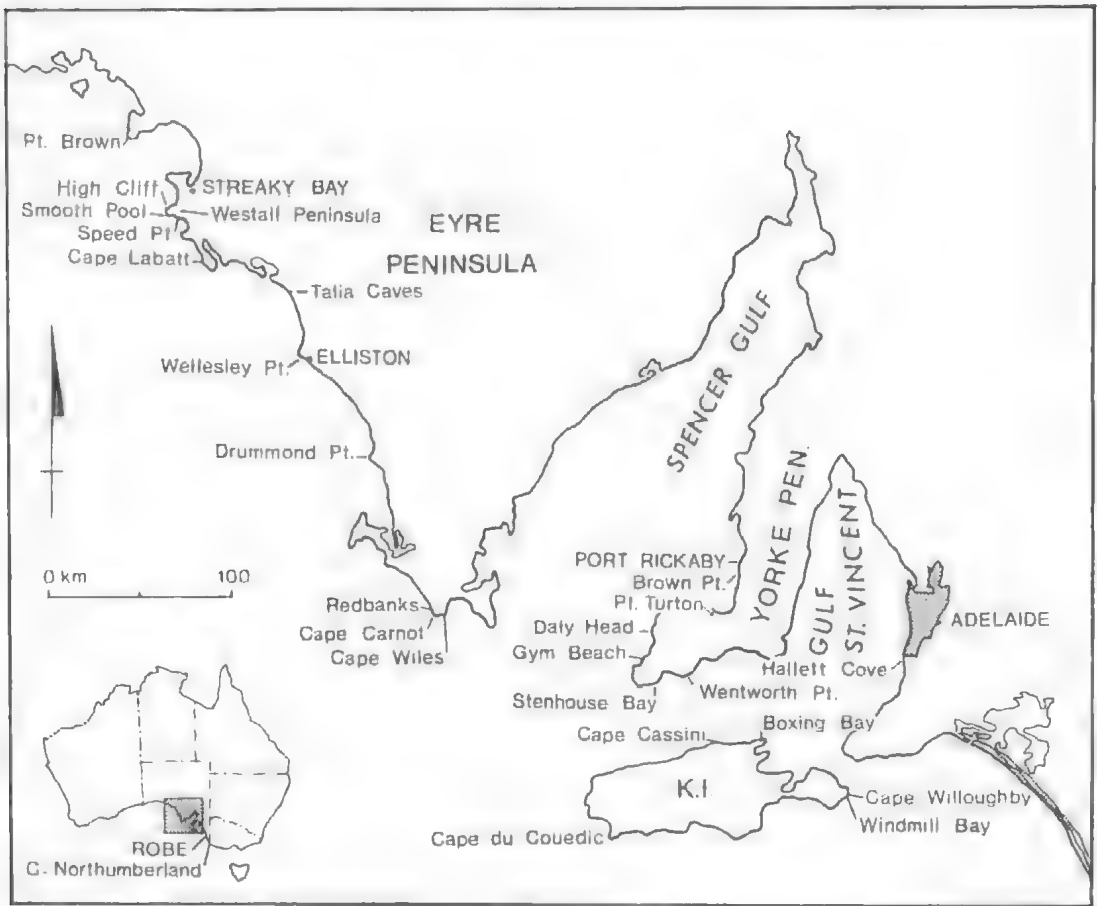
Fig. 1. Location map.

sequent periods of glacial low sealevel, and to planation during the interglacial high stands of the sea.

But which glacial phase: the last, the first, or some intermediate phase? There is no direct evidence on this point. On the other hand there is nothing to show that the aeolianite so widely exposed on the South Australian coast is not all related to the last glacial (Wisconsin) period of low sealevel. And there are several inferences to suggest that they are. For instance, if the dunes predate the Wisconsin they ought, judging from the rate of postglacial erosion, to be more extensively baselevelled than they now are. There ought to be signs of interglacial high stands of the sea imprinted on the dunes, and of these there is no indication. If it is argued that the evidence has been destroyed by erosion, again, why have the dunes survived at all? And if the dunes are of great antiquity why were they not deeply eroded during the Pleistocene glacial low sea-

levels? Further reference is made to some of these arguments below, but the aeolianite is taken to be of late Wisconsin age in the areas under discussion.

The shore platforms of the coastal sectors under consideration are developed in both the older crystalline and sedimentary rocks and the younger aeolianite. They pose several problems.

Platforms developed in fresh granitic bedrock

According to Jutson (1940) and Hills (1949; 1971), shore platforms are poorly developed in fresh granitic bedrock, yet along considerable sectors of the west coast of Eyre Peninsula which is exposed to westerlies sweeping in off the Bight, shore platforms are commonly developed in granite and in places extend some 200 m from the base of the cliffs. How have they formed and in what way, if at all, are they related to the contemporary sea-level?

DRUMMOND POINT

a.

WELLESLEY POINT

b.

Fig. 2a. Diagrammatic composite section at Drummond Point. The tiny remnant of calcrete on the isolated hill (left) is developed on aeolianite.

Fig. 2b. Section of the aeolianite cliffs at Wellesley Point (see also Fig. 7b).

1. Point Brown, northwestern Eyre Peninsula

Point Brown (Fig. 1) is typical of several sites on the west coast of Eyre Peninsula in that Pleistocene aeolianite clearly overlies granite; but this locality, and that at Drummond Point (see below), together provide the clearest evidence concerning the probable origin of the granitic shore platforms.

The granite is even grained but coarsely granular. It is gneissic in places and there are veins of aplite and quartz, but most of the exposure is of the coarse-grained "sugary" granite. This is not fresh for it is iron-stained and disintegrates when hit with a heavy hammer; but it is cohesive and by no means friable. Some of the granite exposures are bouldery, and concentric zones of flaking are preserved around some of the boulders, suggesting that they are corestones or kernels (see Scrivenor 1931; Larsen 1948; Linton 1955; Twidale 1971). But elsewhere the surface of the granite, though criss-crossed by joint crevices and clefts, is essentially even, and though in detail composed of many individual joint blocks, forms a platform that in places extends as much as 30 m from the base of the cliffs.

However, both on Point Brown itself and on the next headland to the south a regolith of weathered granite separates the fresh

granite from the aeolian calcarenite. This weathering profile must have developed beneath a near-stable surface of low relief. Regional considerations suggest that it was the late Pliocene-Pleistocene Koongawa Surface (Twidale, Bourne & Smith 1976). The weathering profile, 2–4 m thick, is mottled red, yellow, white and grey, but the granular texture is retained and the joints remain clearly discernible. The regolith is obviously being eroded by wave action and by pool weathering; there are undercut visors on the seaward-facing bluffs, and alveolar forms and weather pits are commonplace. The stripping of this regolith has exposed the former limit of weathering—the weathering front of Mabbutt (1961a). The weathering front is, as might be anticipated, irregular because of the deeper penetration of water and alteration along and near joint planes. Hence, in some places, corestones are exposed but where the front is even platforms are revealed. In other words the platforms are etch surfaces (see Wayland 1934; Mabbutt 1961b; Twidale 1976).

2. Drummond Point, southwestern Eyre Peninsula

At Drummond Point (Fig. 1), Precambrian gneisses with well developed steeply dipping lineation are exposed beneath the dune cal-

carenite that forms the upper half or three-quarters of the high cliffs (Figs 2a and 3a). The unconformity between the Precambrian and Pleistocene rocks is irregular, but, though eroded, is nevertheless expressed in many places as a gently sloping bench standing well above high tide level[2] but within the spray zone (Fig. 2a). A narrow platform serrated in profile has developed at about mid-tide level but there is another prominent flat located at, or more commonly just above, high tide level. It is everywhere coincident in elevation with the weathering front, the junction between the intrinsically fresh gneisses below and the weathered rock above.

The coastal exposures at Drummond Point suggest very strongly that the high level platform, standing 6 m above the intertidal platform which is located at about mid-tide level, is of etch character. Here perhaps even more clearly than at Point Brown is the nature of some of the platforms revealed: the comparatively high platform at Drummond Point (and the mid- to high-tide platforms at Smooth Pool, Cape Labatt and Talia Caves—see below) are etch surfaces and they have no significance so far as former stands of the sea are concerned. They have developed only because the weathering front happens to be located within the tidal and spray zone of contemporary sealevel.

The weathered gneiss consists of quartz grains and fragments set in a matrix of kaolinised material, and with abundant iron oxides. There is, however, no sign of a ferruginous capping or horizon within the gneiss; rather are there patches of iron discolouration following lineation within the regolith. Whether there was originally a ferruginous carapace that has been destroyed by chemical attack following burial by the aeolianite is not known (cf. Twidale & Bourne 1975).

However, though particularly well displayed there, Drummond Point is not the only site where there is evidence of the etch character of some of the platforms cut in pre-aeolianite crystalline and, in one instance, sedimentary rocks.

3. *Westall Peninsula, northwestern Eyre Peninsula*

The term Westall Peninsula is used of the complex promontory that lies to the west and southwest of Streaky Bay (formerly Flinders)

Fig. 3a. Part of Drummond Point, showing calcarenite overlying gneiss. A—calcarenite; B—gneiss exposed in platforms.

Fig. 3b. Smooth Pool showing the calcarenite cliffs, the massive joint blocks exposed in the granite platform, and the many granite boulders and cobbles, which were originally corestones.

Fig. 3c. Granite platform at Smooth Pool showing large joint blocks, the one in the foreground displaying raised rim and saucer-shaped depression.

[2] The evidence of jetsam on beaches, distribution of lichens, etc. at particular sites has been taken in preference to theoretically derived tidal ranges. Thus "high tide level" implies "near the top of the evidenced tidal range".
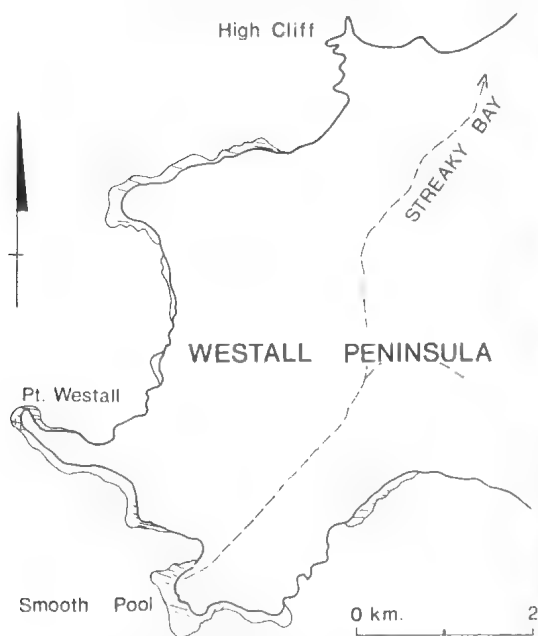
Fig. 4. Westall Peninsula showing the extent of the shore platforms cut in granite and gneiss. Major joint trends are shown.

township. Most of the exposures, notably in the 60–70 m high cliffs, are of aeolianite but over long sectors granite and granite gneiss are exposed at and near present sealevel. At *High Cliff*, located 14 km southwest of Streaky Bay, strong structural control is evident in the platform. The bedrock is subdivided into massive slabs by prominent joints which dip 2° seawards. However, despite the many minor joint-block "cuestas" developed in the massive granite slabs, the outcrop has been eroded and overall the granite forms a platform extending as much as 80 m beyond the base of the aeolianite cliffs, though with clefts well developed along joints.

The granite outcrops at *Smooth Pool* have also been eroded to form a platform which slopes gently ($\frac{1}{2}$°) westwards from the base of the aeolianite cliffs (Figs 3b and 4). At low tide the platform extends about 200 m from the base of the cliffs, but at high tide is covered by the sea. Over wide areas it is coincident with horizontal or sub-horizontal joints but in many places the surface transects the joint blocks, so that there are innumerable minor platforms within the larger feature.

In detail the blocks that comprise the platform display a varied morphology. Some have slightly raised rims, and are in consequence distinctly saucer-shaped (Fig. 3c). Others are
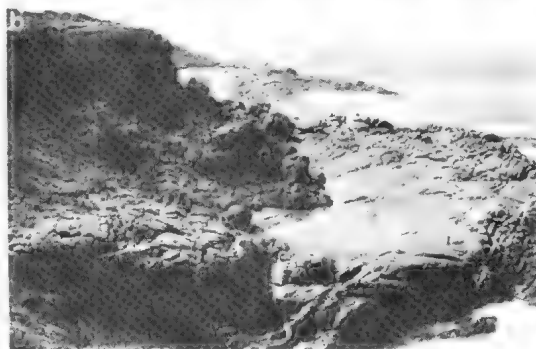
Fig. 5a. Flared slope of granite boulder at Smooth Pool.
Fig. 5b. Granite platform cut in granite at Wentworth Point, Yorke Peninsula. It stands below the unconformity between the calcarenite above and the granite below but the platform seen in the middle distance is essentially coincident with the unconformity.
Fig. 5c. Calcified grus with granite boulders set in it at Wentworth Point.

slightly humped with broad rises a few centimetres amplitude standing above the general level of the edges of the platforms. Some display both saucers and humps. The joint-controlled margins of the blocks are uniformly steep and some are slightly concave. There are

many loose-rounded boulders (diameter 50 cm and less) strewn over the platform and also, particularly in the region close to cliff-foot, many larger joint blocks are rooted in the platforms. Some of the latter are distinctly flared (Fig. 5a). One block has been eroded to form a platform on the landward side and the hump standing above it is slightly flared so that the total effect is that of an elephant rock (Twidale & Bourne 1976).

The platform can be traced continuously round the Peninsula at approximately the same elevation for several kilometres. The unconformity between the crystalline rocks and the overlying limestone is obscured by the coarse blocky rubble that has fallen and accumulated at the base of the cliffs, but to judge from the upper limits of fixed gneiss and granite boulders in the cliff-foot region it occurs 1–2 m above the present high tide limit.

On Westall Peninsula, evidence of the etch origin of the wide platform is fragmentary and difficult to find. However, at one site at Smooth Pool there is a patch of weathered granite, mottled in red and yellow preserved beneath the bouldery granite and blocky aeolianite rubble. This and the many loose boulders suggest that there was at one time a regolith comprising corestones set in a matrix of grus over the fresh rock. Wave action must have stripped all but one small remnant of the grus away though many of the corestones remain as boulders. The flared margins of fixed boulders and of joint blocks are in these terms due to subsurface weathering (Twidale 1962).

This interpretation is corroborated by the character of the unconformity between granite and aeolianite exposed on a minor headland about one kilometre south of Smooth Pool. Here there is abundant calcified grus—granite boulders, fragments and rock particles set in a lime matrix, preserved in joints in the fresh granite. Some 2 m above the intertidal platform cut in granite there is a platform in aeolianite consisting largely of coalesced pools in the flat floors of which granite is exposed.

At *Cape Labatt* remarkably smooth platforms in granite and developed on massive joint blocks are exposed in the intertidal zone at the base of the high aeolianite cliffs, but no remnants of a former regolith have been found there.

4. *Talia Caves, western Eyre Peninsula*

The *Talia Caves* area provides the only exposure of a gently dipping conglomeratic sandstone of possible Mesozoic age (Smith &

Kamerling 1969). A platform eroded across the tilted sedimentary layers is developed close to high tide level. A thin layer of quartz particles set in a lime matrix intervenes between the aeolianite and the still massive sandstone. As the platform here corresponds in elevation with the base of this impregnated and cemented skeletal soil, an etch origin is again indicated.

5. *Cape Carnot, southern Eyre Peninsula*

Platforms cut in crystalline rocks are exposed at the base of towering aeolianite cliffs and apparently emerge from beneath these Pleistocene deposits at several sites in the Cape Wiles-Cape Carnot area of southern Eyre Peninsula; but they are inaccessible. However, at Cape Carnot and in a sector extending a few kilometres northwards the coast is less forbidding and the origin of the platforms can be investigated. Platforms in gneiss are swept by the highest tides at Cape Carnot itself, but only a few score metres to the north, a regolith is preserved beneath aeolianite the base of which stands some 3–4 m above high tide level. This section strongly suggests that the shore platforms are etch surfaces from which both calcarenite and regolith have been stripped. At Redbanks, a few kilometres further to the north, the same relationship obtains between high platforms in fresh gneiss and regolith preserved beneath the aeolianite, the regolith again occurring 3–4 m above high tide level. The regolith is only 2–3 m thick and is ferruginous. It is not a laterite for there is no distinct horizon development; this regolith, like those described from Point Brown and Drummond Point is most likely related to the Koongawa Surface of late Pliocene and Pleistocene age (Twidale, Bourne & Smith 1976).

6. *Wentworth Point, southern Yorke Peninsula*

In the rocky cliffs of Wentworth Point, on southern Yorke Peninsula, both aeolianite and granite are displayed. The unconformity between the two, which in general occurs about half way up the cliffs, is irregular in some sectors but remarkably horizontal and smooth elsewhere. A regolith up to 2 m thick is preserved in places, though whether the weathering to which it is related dates from before the deposition of the dune sand, or whether it has developed subsequent to the burial of the granite is not clear. Nor is there unequivocal evidence as to the nature of the surface cut in granite. Is it of epigene origin, and if so is it related to the Koongawa Surface

WENTWORTH POINT

aeolianite

aeolianite blocks

notch at water level
step near pool surface

rampart

3m

mean sea level

salt crystals in joint clefts

a.

aeolianite

WINDMILL BAY

corestones in grus

stack

high tide level

platform

5-6m.

3m.

beach boulders with lichen

boulder beach

mean sea level

b.
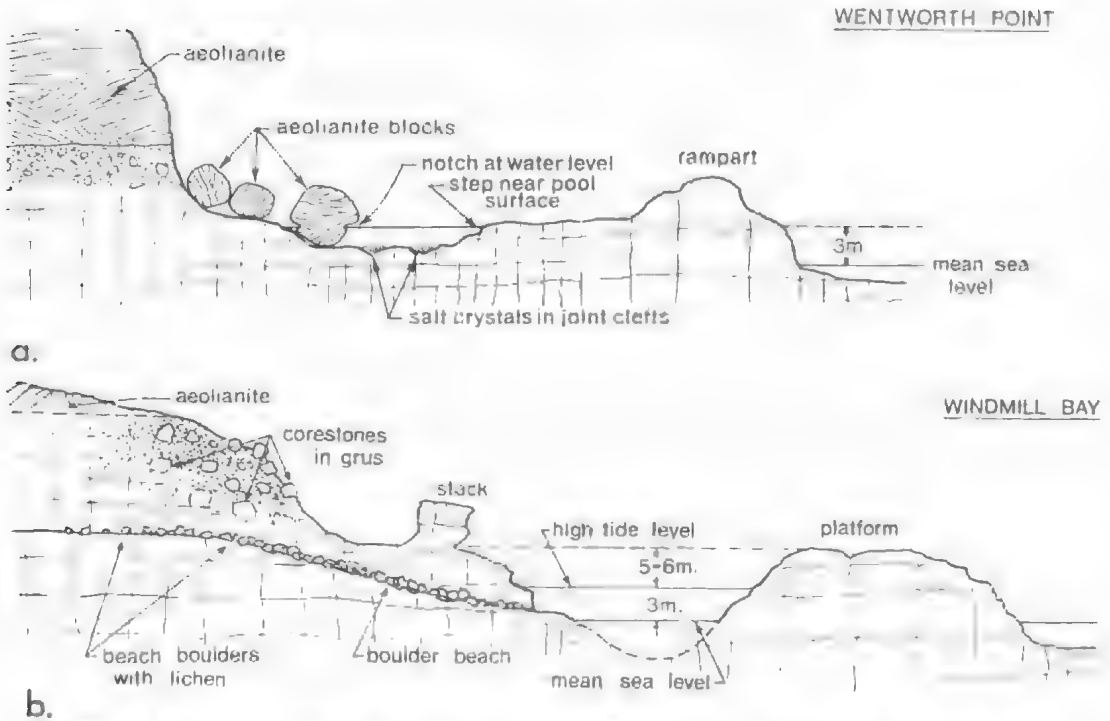
Fig. 6a. Section through granite platform and cliff at Wentworth Point shown in Fig. 5b.
Fig. 6b. Composition section of Windmill Bay showing raised platform raised stack and raised beach.

and associated period of weathering? Or is it an earlier Pleistocene shore profile, including a small platform, which has been preserved and weathered by virtue of the aeolianite cover? The answers to these questions are not apparent.

The granite surface has been cut into a blocky cliff the upper part of which, just below the unconformity, is intensely weathered, but which is quite fresh below this 2 m thick zone (Fig. 6a). The bluff gives way to an essentially smooth platform, with pools, and protected on the outer side by a blocky rampart. The platform is at or just above high tide level on one headland but occurs a few metres higher on others in the locality (Fig. 5b). All, however, are in the spray zone. At some sites calcified grus and corestones are preserved (Fig. 5c), and aeolianite remains in one of several joint controlled *lapiés* developed on the sheer face of a massive block of granite gneiss. Thus although it can be argued that there has been modification of the granite surface since the deposition and stripping of the aeolianite—and the development of solution notches up to 15 cm deep in the limestone blocks that have tumbled into pools on the platforms attest to

this—it is also clear that some, at any rate, of the granite relief essentially predates the aeolianite.

But the problem of the origin of the platforms and associated features is not resolved: are they epigene or marine? If the former one would expect the usual assemblage of flared slopes, widespread *Rillen* and platforms; the flared backing slopes are absent suggesting that the assemblage may be coastal, but the evidence is not wholly convincing.

Modern platforms and the so-called "ten-foot" stand of the sea

Shore platforms are developed within the present tidal range in the aeolianite, and in the various crystalline and sedimentary rocks of Precambrian and Cambrian age. Some developed in older rocks are not evidently coincident with the weathering front and so differ from those earlier discussed in that they cannot be explained as etch forms. The platforms cut in aeolianite must post-date the material in which they are cut. Those eroded in crystalline and Precambrian sedimentary rocks are either related to modern sea level or they predate the aeolianite and have recently been
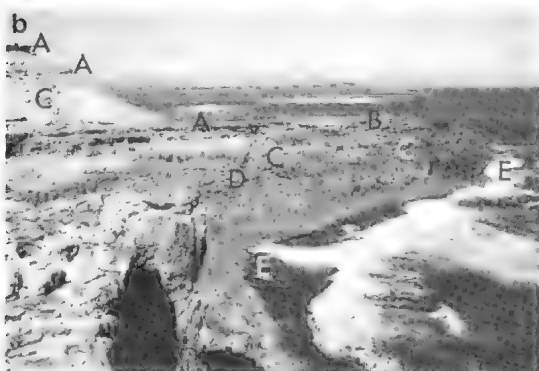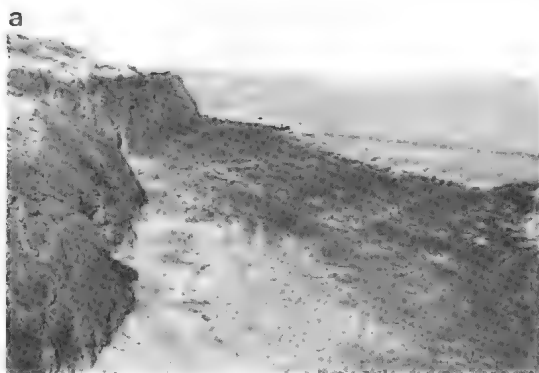
Fig. 7a. Shore platform eroded in dipping Pre-cambrian siltstone at Hallett Cove.

Fig. 7b. Platforms in aeolianite at Wellesley Point. A—calcrete horizons; B—platform eroded below calcrete; C—cliffs; D—spray pool platform (+ 3 m); E—inter-tidal platform. B, D and E transect the cross-bedding.

Fig. 7c. The "10-foot" platform developed in oolitic Pleistocene limestone at Gym Beach, Yorke Peninsula.

exhumed. But if the latter suggestion is correct they must predate the last glacial. Why were they not undercut and cliffed by the sea, and dissected by streams during times of low (glacial) sea level?

Most of the areas considered here are lacking in surface streams due to the perviousness and permeability of the calcarenite but in times past the granitic and gneissic hinterlands would surely have generated surface drainage. Comparisons with the Hallett Cove area seem to be apposite. Here several small streams drain the area immediately back from the cliffs. Waterfall Creek is one of the larger, and it debouches on to the northern end of the shore platform. Now if the platform (Fig. 7a) predates the last glacial, surely the Creek would have cut a valley below it. It has not, and it can only be surmised that the platform is related to the present stand of the sea. Similar arguments apply to the other intertidal platforms on Yorke and Eyre peninsulas. The normal platforms are of Holocene age and they are related to the contemporary sea level; the dunes are late Wisconsin in age.

If the platforms cut in crystalline rocks are of postglacial age, they are contemporary with those eroded in aeolianite. The platforms in aeolianite are widespread but achieve the greatest widths (i.e. development in a direction normal to the coast) in sheltered situations. For example in an unnamed bay behind Speed Point northwestern Eyre Peninsula, the shore platform in aeolianite (Fig. 8a) is about 30 m wide. That developed at the head of Stenhouse Bay, on southern Yorke Peninsula, is 20 m across, in contrast with the 1–3 m widths observed on promontories and headlands. In each case the platforms transect the variable cross-bedding of the aeolianite and so are erosional: they are not the structural benches or ledges of Jutson (1939) and Hills (1971). The contemporary platforms eroded in crystallines are about 10 m wide at most though the platform cut in dipping Precambrian sediments at Hallett Cove (Fig. 1) near Adelaide, extends 30 m from the base of the cliff (Fig. 7a). All these platforms argue considerable rates of erosion in postglacial time. They are extending inland as a result of attack at the cliff base, but they themselves are suffering undermining by wave attack at the outer edge and also by the development of pits (cf Jutson 1949a; Sprigg 1952). But they have all been eroded during the past 6,000–7,000 years, the maximum estimate allowed for postglacial time (see Fairbridge 1961; Curray 1965; Shepard & Curray 1967).

These intertidal platforms pose another difficulty, for some workers take each individual platform to represent a separate and distinct

Fig. 8a. Shore platform in calcarenite in sheltered bay behind Speed Point. Note raised rim of outer edge of platform.

Fig. 8b. Platforms in aeolianite on the exposed coast at Speed Point showing the narrow intertidal feature and the high platform, the so-called "10-foot" platform, cutting away the bedding in the aeolianite. Note the line of debris on the beach in the foreground at the same elevation as the high platform.

stand of the sea (e.g. Teichert 1947). Others consider that whole flights of platforms are developing simultaneously in relation to the contemporary sealevel, and believe that a similar multiplicity of platforms evolved in relation to former stands of the sea (e.g. Jutson 1930, 1949b; Hills 1949).

The question is complicated by structure, for on many coasts lithological differences, and bedding, have been exploited by marine agents to produce benches or flats at different levels. For instance at Daly Head, on the "toe" of Yorke Peninsula, the platform developed in biotite schists is 1–2 m lower than that evolved on the adjacent aplite. Again, both at Wellesley Point near Elliston and at Robe, in the Southeast district (Fig. 1) a calcrete formed at the surface of an ancient dune finds expression in a distinct bench the elevation of which changes parallel to the coast, simulating as it does the slope of the former dune. These are coastal ledges in the terminology of Hills (1971). Jutson (1930, 1939) and Bird & Dent (1966) have cited other examples of structural control.

Nonetheless, when structural effects are fully accounted for there remains within the present tidal zone a multiplicity of platforms extending through a considerable vertical range and clearly cut across the local cross-bedding in the aeolianite, and across jointing and foliation in crystalline rocks. Many platforms have developed within the spray zone as a result of pool weathering (see Wentworth 1938, 1939; Hills 1949; Kaye 1959). Such flights of platforms are especially well displayed on the aeolianite: there are for example, three such at Cape Wellesley which faces the Great Australian Bight (Figs 2b and 7b). Each of these is currently suffering alteration, the lower one
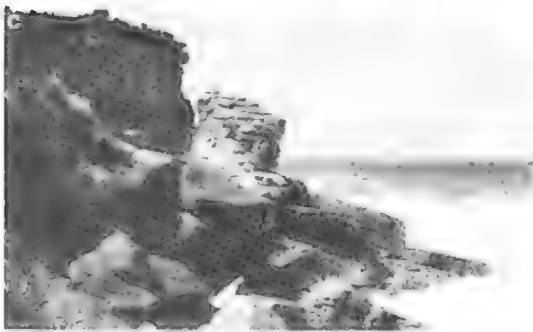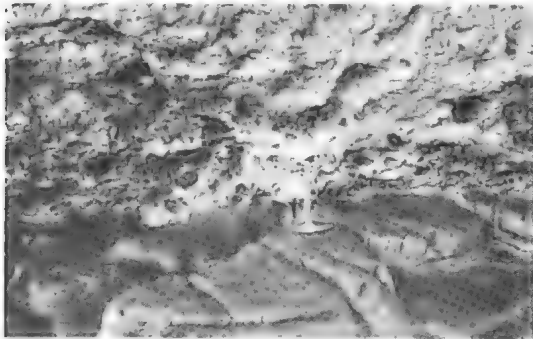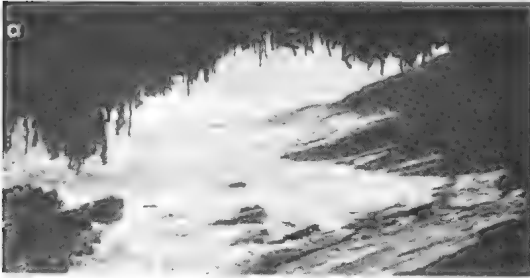
Fig. 9a. General view of Admiral Arch showing the dipping Cambrian schists below and the aeolianite, with stalactites, above.

Fig. 9b. Unconformity between schists and aeolianite with schist cobbles and boulders embedded in the base of the dune rock.

Fig. 9c. Raised stack in granite at Windmill Bay.

by wave attack, the second by rapid alteration of wetting and drying, the higher by occasional wetting and drying by rains and by spray. However, the presence of sand, shells, and salt crystals in pools on the highest platform shows that they receive spray from time to time.

Thus platforms appear to be developing at the present time in a range that extends up to 8 m above present high tide level. But what, then, of the so-called "ten-foot" level, of Recent but relic age, advocated by some workers, for example Crocker (1946b)?

The problem is very well illustrated at Speed Point, on the northwest coast of Eyre Peninsula. There, on the open coast as well as on the shores of the sheltered inlet platforms are well developed at about mid-tide level but there is also a prominent platform preserved on low calcarenite promontories on the exposed coast (Fig. 8b). However, the head of the steeply sloping beach is level with that of the platforms which stand 3 m (10 feet) above the mid-tide platform. The presence of debris at the beach head shows that waves reach to that elevation so that at least occasionally the high platforms are affected by wave action; and they are certainly within reach of spray.

At Brown Point, Crocker's (1946b) type section on the western shore of Yorke Peninsula, the evidence for the ten-foot platform being wholly a relic form is equally unconvincing. The platform extends only 2–3 m back from the cliff edge. Solution hollows and pools attest the effectiveness of spray water in weathering the limestone and though the platform is clearly being undermined and destroyed by wave action it is equally obvious that the platform is also extending and being smoothed by pool weathering.

Similar situations obtain at Port Rickaby, Point Turton (Clark 1928) and Gym Beach (Fig. 7c), all on Yorke Peninsula (Fig. 1), and at Cape Northumberland in the Lower Southeast to name four examples. Are these 3 m platforms relict or modern? There are three possibilities:

1. That they are relict features, date from early Recent times and are now essentially being destroyed, but simultaneously are suffering planation by pool weathering.
2. That they are contemporary forms which are due to pool weathering, but which are at the same time being undermined by wave attack, illustrating that different marine processes act at different levels.
3. That some of the 3 m platforms are relict and others modern.

The evidence favours the second of these possibilities.

Evidence of higher stands of the sea

Is there then, any definite evidence of higher stands of the sea in the area under discussion?

Cambrian Kanmantoo schists that are extensively exposed in the cliffs and platforms of the north coast of Kangaroo Island also occur at the western extremity, near Cape du Couedic. At *Admiral Arch* the schists occur beneath the

Pleistocene aeolianite in the coastal cliffs and in the lower part of the natural arch (Fig. 9a and b). The bay heads between promontories are occupied by shingle beaches composed of the boulders and cobbles of the Kanmantoo schist. Within the arch a former cobble and shingle beach is preserved at the unconformity between dipping schist and limestone (Fig. 9b). It stands 5–6 m above high tide level and the present shingle beaches, and surely indicates the stand of the sea previous to the deposition of the calcarenite dunes, probably during the last glacial.

Windmill Bay is located near Cape Willoughby on the southeastern coast of Kangaroo Island (Fig. 1). In the Bay itself there is a coarse beach of granite boulders (Fig. 6b) some of which are fitted (Hills 1970). These extend 5–6 m up the slope beyond the present beach. Those on the slope are covered with an orange lichen (*Xanthoria ectanea* (ACH) RAS ex R. FILSON) and are scattered over the surface.

The boulders are probably former corestones derived from the weathered granite that is seen in cliff sections a few metres to the southeast and which probably underlies the slope behind the beach. But in front of the rocky coast backed by the granite cliffs is a platform standing 5–6 m above high tide level, and on it an old stack with a notch on its seaward side also 5–6 m above sealevel (Fig. 9c). There is no aeolianite exposed in the cliff but it rests on the granite in the hill immediately to the north.

Some evidence of a similar pre-aeolianite platform standing 3–4 m above present sealevel occurs on the north coast of Kangaroo Island at Boxing Bay and Cape Cassini, where aeolianite rests unconformably on a surface eroded in folded Cambrian quartzites. The surface at and adjacent to Boxing Bay may be a shore platform of pre-aeolianite age and that around Cape Cassini could be a combination of shore platform and coastal plain of similar age. If so both planate features stand 3–4 m above present high tide level and represent a former sealevel of that order.

Conclusions

The evidence from western Eyre Peninsula and southern Yorke Peninsula suggests that many of the platforms cut in granite and gneiss are etch surfaces, or exposed weathering fronts which fortuitously lie within the present tidal or spray zone. Shore platforms cut in fresh granite are of limited extent, as postulated by Jutson and Hills.

Those granite platforms that occur at mid tide level, as at Smooth Pool, are not indicative of a pre-aeolianite stand of the sea similar to the contemporary sealevel. And those that stand at high-tide level, or a few metres above it do not represent a former higher stand of the sea. Pre-aeolianite regoliths preserved on southern Eyre Peninsula may be related to the same baselevel or sealevel to which the epigene surfaces were graded.

These remarks apply equally to the benches essentially associated with the unconformity between the Pleistocene aeolianite and the older rocks. Thus the extent and perfection of the granite and gneiss platforms is due to the effectiveness of weathering in earlier times. The only granite platforms possibly due to contemporary marine processes are at Wentworth Point on southern Yorke Peninsula, and even there the evidence is equivocal.

Of those platforms cut in aeolianite and in older, folded, sediments and due wholly to marine processes, many occur within the modern tidal or spray zone, and are developing simultaneously at the present time. The so-called ten-foot platform may be a relic feature which is suffering modification at present; but there is evidence that it too is a contemporary form. Finally there is evidence of a stand of the sea 5–6 m higher than present dating from pre-aeolianite (probably pre late Wisconsin) times, and no indication of significant tectonism having affected Kangaroo Island in the time interval that has elapsed between the formation of the now raised beaches and other coastal forms and the present.

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REVISION OF THE COMPOSITE SPECIES LIMA BASSI TENISON WOODS (MOLLUSCA, BIVALVIA)

BY M. F. BUONAIUTO

Summary

The composite species Lima Bassi Tenison Woods is revised. Among the forms referred to Lima bassi (ranging from late Eocene to Pliocene), four species are recognized: the Late Eocene L. maslinensis sp. nov., the early Miocene L. bassi s. str., the Middle Miocene (Batesfordian) L. morganensis sp. nov., and the Late Pliocene L. elianae. A neotype and paraneotypes of Lima bassi from the type-locality are established.

REVISION OF THE COMPOSITE SPECIES *LIMA BASSI* TENISON WOODS (MOLLUSCA, BIVALVIA)

by M. F. Buonaiuto*

Summary

Buonaiuto, M. F. (1977) Revision of the composite species *Lima bassi* Tenison Woods Mollusca, Bivalvia). *Trans. R. Soc. S. Aust.* **101**(3), 75-83, 31 May, 1977.

The composite species *Lima bassi* Tenison Woods is revised. Among the forms referred to *Lima bassi* (ranging from Late Eocene to Pliocene), four species are recognized: the Late Eocene *L. maslinensis* sp. nov., the Early Miocene *L. bassi* s. str., the Middle Miocene (Batesfordian) *L. morganensis* sp. nov., and the Late Pliocene *L. elianae*. A neotype and paraneotypes of *Lima bassi* from the type-locality are established.

Introduction

During the present revision of the Eocene Mollusca from the type section of the Aldingan stage, different species revealed themselves as composite: *Lima bassi* Tenison Woods is one of them. Past authors grouped at least three distinct forms in it: the Longfordian *Lima bassi*, the Late Eocene *L. maslinensis* sp. nov., the Batesfordian *L. morganensis* sp. nov., and a fourth Pliocene form *L. elianae* from Dry Creek Sands.

Apart from the revision of *Lima bassi* and the description of three new taxa, it is necessary to establish a neotype and paraneotypes of *L. bassi*. Since Ludbrook (1967) revised the Johnston and Wood's types, it is common knowledge that many of these types were lost during the first half of this century. The holotype of *Lima bassi* is one of them.

Although authors quote several localities, the only localities considered here are those from which the specimens examined were obtained. *Definitions of the parameters here measured* (after Cox, Nuttall & Trueman, *in* Moore 1969).

Ht —height of valve distance between two planes, parallel to cardinal axis, perpendicular to commissure plane, and tangent to umbonal and ventral ends of valve.

Lt —length of valve as distance between 2 planes perpendicular to cardinal axis and tangent to anterior and posterior ends of valve.

Lpa—length of posterior auricle, as distance between two planes tangent to beak and to posterior end of auricle and normal to cardinal axis.

Laa—length of anterior auricle, analogously defined as the above parameters.

Lca—length of cardinal area as distance between two planes tangent to auricles' ends and perpendicular to cardinal axis.

Hr —height of resilifer as distance between two parallel planes, parallel to cardinal axis, and tangent to its upper and lower ends.

Lr —length of resilifer, as distance between two planes, perpendicular to cardinal axis, and tangent to its anterior and posterior ends.

Ts —thickness of valve, as distance between two parallel planes: former tangent to commissure line, and latter tangent to outer valve surface.

Hca—height of cardinal area, as distance between two planes parallel to cardinal axis and tangent to its upper and lower ends.

Tca—distance between two parallel planes: former tangent to beak; latter tangent to commissure line.

Standard ratios were calculated. The ratio $Tca/Ht = Tg\hat{a}$ represents the tangent of the angle â between the geometric generating curve as defined by Raup (1966) after Stasek (1966) where the biological generating curve coincides with the growing edge of the valve, and the geometric generating curve is the intersection of the valve with a plane containing the coiling axis and tangent to the ventral end of the biological curve. The angle â determines the degree of maximum opening breadth between valves.

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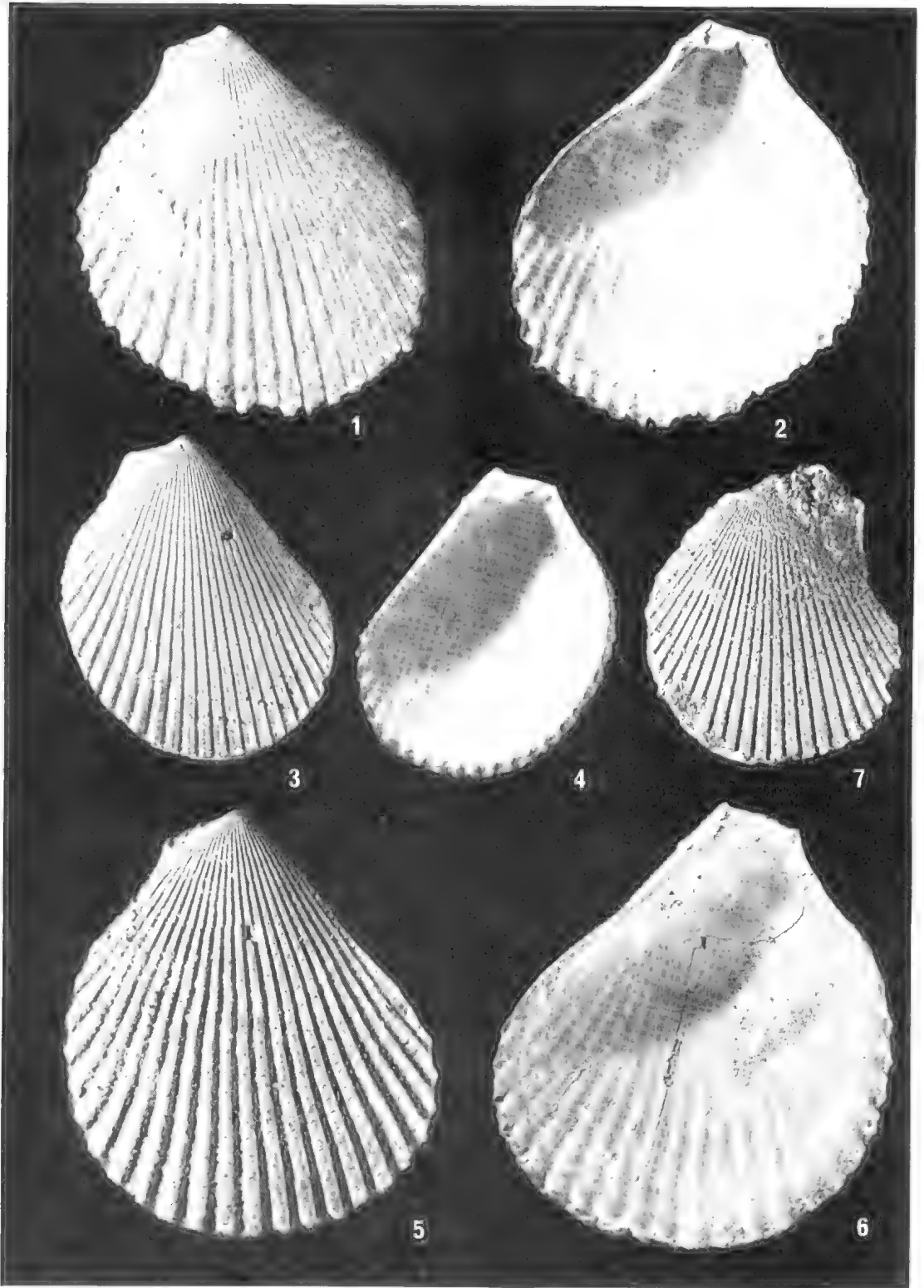
FIGS 1–7

Collections. SAM: South Australian Museum. GSSA: Geological Survey of South Australia.

Systematic descriptions

CLASS: BIVALVIA Linné, 1758

SUBCLASS: PTERIOMORPHIA Beurlen, 1944

ORDER: PTERIOIDA Newell, 1965

SUBORDER: PTERIINA Newell, 1965

SUPERFAMILY: LIMACEA Rafinesque, 1815

FAMILY: LIMIDAE Rafinesque, 1815

GENUS: *Lima* Bruguière, 1797

SUBGENUS: *Lima* s.str.

Lima (Lima) bassi Tenison Woods, 1877

FIGS 1–2, 11–13, 17–24

1877 *Lima bassi* Tenison Woods, p. 112. 1886 *Lima bassi*—Tate, p. 117 (*pars*). 1955 *Lima bassi*—Ludbrook, p. 35 (*pars*).

Neotype: RV senile, figs 1–2 (SAM 18343/1).

Paraneotypes: 6 RV, 2 LV adults, figs 17–24, (SAM P18343/2–8).

Stratigraphic location: Freestone Cove Sandstone (Longfordian).

Type locality: Table Cape, Tasmania, Bass Basin (Freestone Cove).

Description: Shell rather thin, subtrigonal, very inequilateral, little inflated, higher than long; umbones with acute small prosogyrate beaks. Margins: antero- and postero-dorsal straight, the latter longer; anterior very long, concave; posterior very long, concave near the umbo, convex and very elliptical to the ventral; ventral very elliptical. Margin connections: antero-dorsal–anterior and posterodorsal–posterior very angular; anterior/ and posterior–ventral imperceptible. Auricles triangular, small, the anterior reduced. Longitudinal shell section regularly but weakly convex. Regions: posterior and dorsoventral convex and gently declivous; anterior convex and gently declivous to the dorsum, subconcave and vertical at the margin. Region connections: imperceptible; the two different parts of the anterior by a sharp rim.

Cardinal area narrow, triangular; resilifer broad, triangular, concave. Hinge taxodont with two small longitudinal teeth on the auricles. Interior radially ribbed; pallial line imperceptible; monomyarian with posterior adductor scar faint, rather high and marginal, 8-shaped, broader in the upper part. Commissure region crenulated except near the hinge.

Ornament: Prominent scaly radial ribs with equal U-shaped interspaces. Between the interspaces concentric flat microcostae; in juvenile–adult the anteriors and the posteriors convergent to the dorsoventral where they overlap with a shagreen pattern; in adult regularly concentric microcostae; in seniles very fine growth lines only.

Anterior marginal region concentric costae and weak radial ribs.

Auricles: anterior strong concentric costae; posterior with strong radial ribs.

Dimensions (mm): (see Table 1).

Observations: Tate commented on differences among specimens from Table Cape, Morgan, Aldinga and Adelaide. On the basis of concentric microornaments he distinguished from *L. bassi* s. str. a var. *A* for the specimens from Morgan, and a var. *B* for the specimens from Aldinga and Adelaide Bore. These varieties are here raised to species as *L. morganensis* and *L. maslinensis* respectively.

Paraneotype 2 displays in neanic-juvenile stages concentric microornament similar to that of *L. maslinensis*, abruptly passing to the regular concentric microornament. In adult senile stages secondary radial microriblets can develop in some interspaces. The other paraneotypes display variability in Ht/Lt ratio and in morphology (Figs 17–22). In reference to the type-locality, Johnston (1877) quoted a *Lima squamosa* in the "Crassatella Beds". Further, Johnston listed *L. bassi = L. squamosa* Lamarck. Banks (in Gill 1962) revised and redefined Johnston's "Crassatella Beds" as the Freestone Cove Sandstone, attributing to it a Late Oligocene age. Quilty (1966) and Ludbrook (1967, 1973) gave evidence of a Longfordian age for Table Cape Group of which the Freestone Cove Sandstone is part, on the basis of both benthonic and plantonic fora-

Figs 1-2. *Lima bassi*, neotype, Freestone Cove, Longfordian: (1) dorsal view; (2) interior view (x1.15). Figs 3-4 *L. morganensis* sp. nov., Batesfordian. (3) holotype (GSSA M 3138), near Morgan, dorsal view (x2.2); (4) paratype (SAM T982 E), Murray Cliffs, interior view (x2.55). Figs 5-7 *L. maslinensis* sp. nov. Adelaide (Kent Town) Bore, Aldingan; (5) holotype, dorsal view (x2.2); (6) holotype, interior view (x2.2). Paratype (SAM P 18344), Maslin Bay; (7) dorsal view (x2.2).
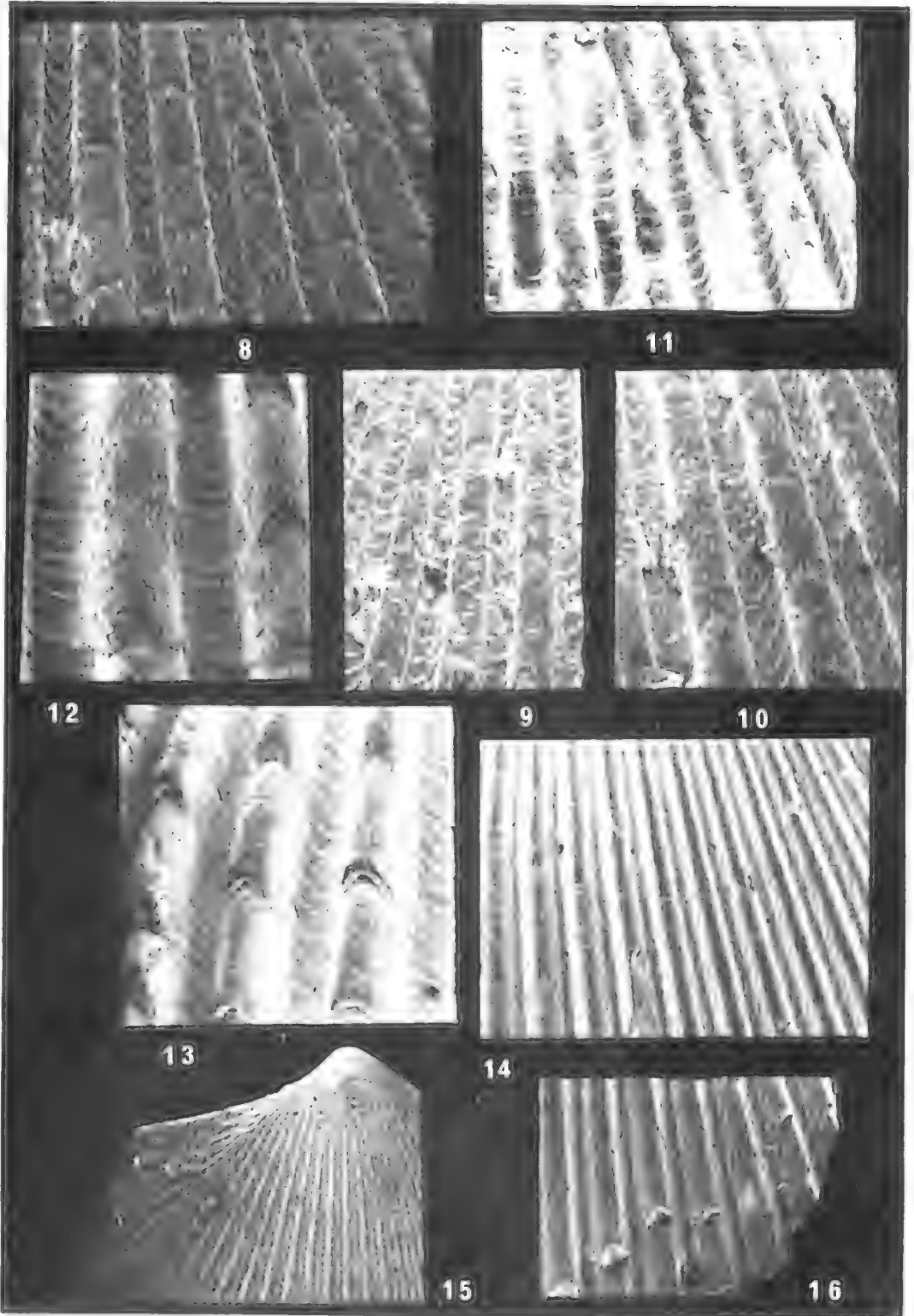
FIGS 8–16

TABLE 1
Dimensions (in mm) and ratios of *Lima bassi*

Specimens	Ht	Lt	Lpa	Laa	Hr	Lr	Ts	Tca	Lca	Hca	â
Neotype	53.01	45.85	7.60	4.80	3.80	4.30	7.95	1.50	12.40	2.90	1°37'
Paraneotype 1	23.50	19.35	2.75	2.45	2.10	1.90	3.10	0.75	5.15	1.45	1°49'
Paraneotype 2	27.15	—	4.60	2.90	2.20	1.70	4.55	1.35	7.50	1.95	2°50'
Paraneotype 3	38.27	32.90	5.25	3.70	3.50	3.00	7.35	1.20	8.95	2.60	1°47'
Paraneotype 4	28.80	22.95	3.75	2.45	2.05	2.45	4.90	0.85	6.70	1.60	1°41'

Specimens	Lt/Ht	Laa/Lpa	Laa/Lca	Lpa/Lca	Lr/Hr	Ts/Lt	Ts/Ht	Tgâ = Tca/Ht	Hca/Lca
Neotype	.8659	.6316	.3879	.6129	1.1316	.1734	.1500	.02830	.2339
Paraneotype 1	.8234	.8910	.4785	.5371	.9048	.1602	.1319	.03191	.2832
Paraneotype 2	—	.6304	.3867	.6133	1.2941	—	.1676	.04972	.2600
Paraneotype 3	.8601	.7048	.4134	.5866	.8571	.2234	.1921	.03137	.2905
Paraneotype 4	.7969	.6533	.3657	.5597	1.1951	.2135	.1701	.02951	.2388

minifera. Hutton (1887) synonymized *L. bassi* with *L. colorata* Hutton, 1873 (Boreham 1965) because "Mr Woods' name stands as mine is incorrect". Later authors such as Suter (1914) accepted Hutton's name. Probably after Hutton, Tate (1899) quoted *L. bassi* occurring also in New Zealand. Finlay (1924) quoted *L. colorata* as one of the New Zealand species corresponding to *L. bassi*. However, an Awamoan senile specimen of *L. colorata* from Otago, in the Department of Geology and Mineralogy at the University of Adelaide, displays specific differences as trapezoidal-shaped broad radial ribs with broader interspaces, as only fine growth lines in juvenile stages and also radial oblique, very fine striations in adult and senile stages.

Lima maslinensis sp. nov.
FIGS 5–10

1886 *Lima bassi* var. *B* Tate, p. 117, pl. 8, fig. 1a–c.

Derivation of Name: From Maslin Bay, locality of the lowest recorded occurrence of this form.

Holotype: T983D, holotype of var. *B*, figs 5–6.

Paratypes: T983 A–C, E.

Type Locality: Old E & W. Dept Kent Town Bore, Hd Adelaide, sect. NE Parklands No. 13

Stratigraphic Range: Aldingan (Late Eocene) (Ludbrook 1973)

Collections: SAM T983 A–E, P18344.

Material: 26 specimens (8 LV, 4 RV, 14 VV) badly preserved; 5 specimens from Tate's Collection (2RV, 3LV)

Description: As *L. bassi*. Differences: stronger teeth, the anteriors longer, the posterior triangular.

Ornament: Primary radial scaly costae with rectangular section and with equal U-shaped interspaces. In the interspaces, fine flat transverse microcostae in the anterior and posterior regions, convergent to the dorso-umbonal; in the dorsoventral region the microcostae overlap with a shagreen pattern. Anterior marginal region with numerous fainter radial spiny ribs.

Auricles: anterior with concentric costae; posterior with concentric costae and faint spiny radials.

Dimensions (mm):
T983 D—Ht, 37.5; Lt, 25.45; Lpa, 4.70; Laa, 3.55; Hr, 2.30; Lr, 2.90; Ts, 5.65; Tca, 1.45; Hca, 2.70; Lca, 8.25.

Ratios: T983 D—Lt/Ht, .6876; Laa/Lpa, .7553; Laa/Lca, .4303; Lpa/Lca, .5697; Lr/Hr, 1.2609; Ts/Lt, .2220; Ts/Ht, .1507; Tgâ = Tca/Ht, .03866; Hca/Lca, .3273.

Observations. Tate initially separated this form from *Lima bassi* Tenison Woods as var. *B*. Teeth, microcostal pattern, posterior auricle and anterior marginal ornaments distinguish this form at specific level from *L. bassi*.

Tate's holotype of the variety is here chosen as the holotype of *L. maslinensis*, although from it is the subsurface and broken into two neat pieces, it is the only well preserved specimen.

Distribution. St Vincent Basin: Adelaide Plains Sub-Basin, Kent Town Bore; Willunga Sub-Basin, Maslin Bay.

Figs 8-10 *L. maslinensis* sp. nov.: (8) anterior ventral ornament (x13); (9) posterior ventral ornaments (x12); (10) dorsoventral ornaments (x12). Figs 11-13. *Lima bassi*, paraneotype 8, Freestone Cove, ornament: (11) anterior ventral (x13); (12) dorsoventral (x13); (13) posterior ventral (x12). Figs 14-16. *Lima morganensis* sp. nov., holotype, ornaments; (14) dorsoventral (x10); (15) juvenile dorsoventral and posterior auricle (x9.5); (16) anterior ventral (x9.5).
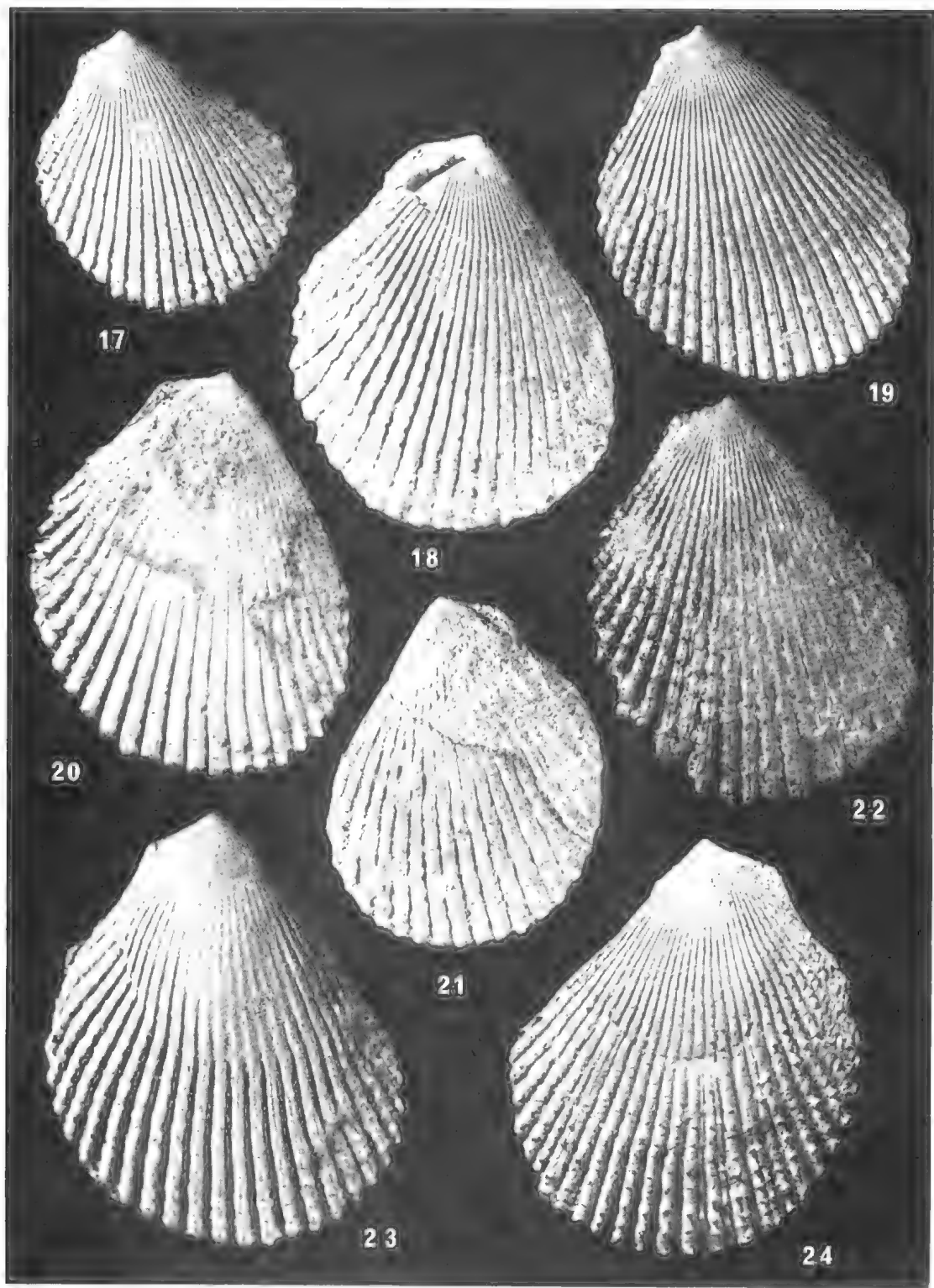
FIGS 17–24

Lima morganensis sp. nov.

FIGS 3–4, 14–16

1886 *Lima bassii* var. *A* Tate, p. 117, pl. 5, fig. 8a–b. ?1897 *Lima bassii* Harris, p. 310 (*non* Tenison Woods).

Derivation of Name: From Morgan, the town nearby, after which Morgan Limestone was named.

Holotype: GSSA M3138, fig. 3.

Paratypes: T982 A–L, fig. 4.

Stratigraphic Location: Cadell Marls Lens (Batesfordian) (Ludbrook 1973).

Type-Locality: 6.4 km S of Morgan, type section of Cadell Marl, section G, Hd Cadell (Ludbrook 1961).

Material: 11 specimens from Tate's collection (7 RV, 4 LV); 1 RV from GSSA Collection (Holotype).

Description. As *L. bassi*.

Ornament: Primary radial subtriangular scaly ribs with equal V-shaped interspaces; long very inclined chevron-shaped microriblets covering ribs and interspaces, with their head on the ribs orientated to the umbo. Posterior auricle with more marked concentric costae and weak spiny radial ribs. Anterior auricle with concentric costae and weak beaded radial ribs.

Dimensions (mm):

T982 A—Ht, 32.20; Lt, 26.00; Lpa, 5.55; Laa, 3.85; Hr, —; Lr, —; Ts, 4.70; Tca, 1.35; Lca, 9.40; Hca, 2.10; $\hat{a}$, 1°24'. T982 E—Ht, 20.50; Lt, 15.25; Lpa, 3.60; Laa, 2.70; Hr, 2.20; Lr, 1.50; Ts, —; Tca, —; Lca, 6.30; Hca, 1.95; $\hat{a}$, —.

Ratios:

T982 A—Lt/Ht, .8074; Laa/Lpa, .6937; Laa/Lca, .4085; Lpa/Lca, .5904; Lr/Hr, —; Ts/Lt, .1808; Ts/Ht, .1460; tg$\hat{a}$ = Tca/Ht, .04192; Hca/Lca, .2234. T982 E—Lt/Ht, .7439; Laa/Lpa, .7500; Laa/Lca, .4286; Lpa/Lca, .5714; Lr/Hr, .6818; Ts/Lt, —; Ts/Ht, —; tg$\hat{a}$ = Tca/Ht, —; Hca/Lca, .3095.

Observations. Tate initially distinguished this form as a variety of *Lima bassi* Tenison Woods. Shape of the ribs and interspaces ornaments of posterior auricle, anterior marginal region and interspaces and radial costae separate this form from *L. bassi*.

The specimen T982 A is the holotype of Tate's var. *A*. The original illustration of Fig. 8a is inverted. The specimen from GSSA Collection was chosen as holotype because of its good topographic and stratigraphic location.

Lima elianae sp. nov.

FIGS 28–31

1955 *Lima bassi*—Ludbrook, p. 36 (pars).

Derivation of Name: After Dott. Eliana Garbarino (Mrs Buonaiuto), the author's mother.

Holotype: GSSA M 2384, figs 25–26.

Paratypes: GSSA M 158, figs 28–31; SAM P19210, Fig. 27.

Type-Locality: Observation Bore D, hd Port Adelaide, St Kilda, 81.38–83.5 m depth.

Type-Formation: Dry Creek Sands, Yatalan.

Material: The holotype (LV) and an adult (SAM P 19210) with damaged margins and a specimen (GSSA M 159) with the ventral part broken.

Description. As *L. bassi*.

Ornament: Primary radial subquadrangular costae with equal U-shaped interspaces; in neanic stage prominent concentric microcostae. In the adult stage short chevron-shaped concentric microcostae with the head to the ventral in the interspaces; the V-microcostae can be substituted by narrow belts of normal concentric microcostae, meanwhile in the senile stage they are entirely substituted by fine growth rugae and fine radial oblique microplicae

Observations. The specimen of *L. elianae* from Abattoirs Bore is that quoted by Woods (1931) as *Austrolima bassi*. The form referred by Tate (1890) to *L. bassi* from Dry Creek Bore is at present unlocated but almost certainly belongs to *L. elianae*.

Unfortunately the only three specimens available are both from bores and both damaged. The senile from Observation Bore is chosen as holotype because it is the only one with a sure stratigraphic location.

L. elianae, *L. bassi*, and *L. maslinensis* are all characterized by subquadrangular radial costae and chevron-shaped concentric microcostae. They might represent a lineage, but the material available is inadequate to be certain.

Figs 17-24. *Lima bassi*, paraneotypes, Freestone Cove; (17) Paraneotype 3 (x1.15); (18) Paraneotype 7 (x1.7); (19) Paraneotype 1 (x2.4); (20) Paraneotype 6 (x2.1); (21) Paraneotype 5 (x1.15); (22) Paraneotype 4 (x2.2); (23) Paraneotype 8 (x2.2); (24) Paraneotype 2 (x2.4).
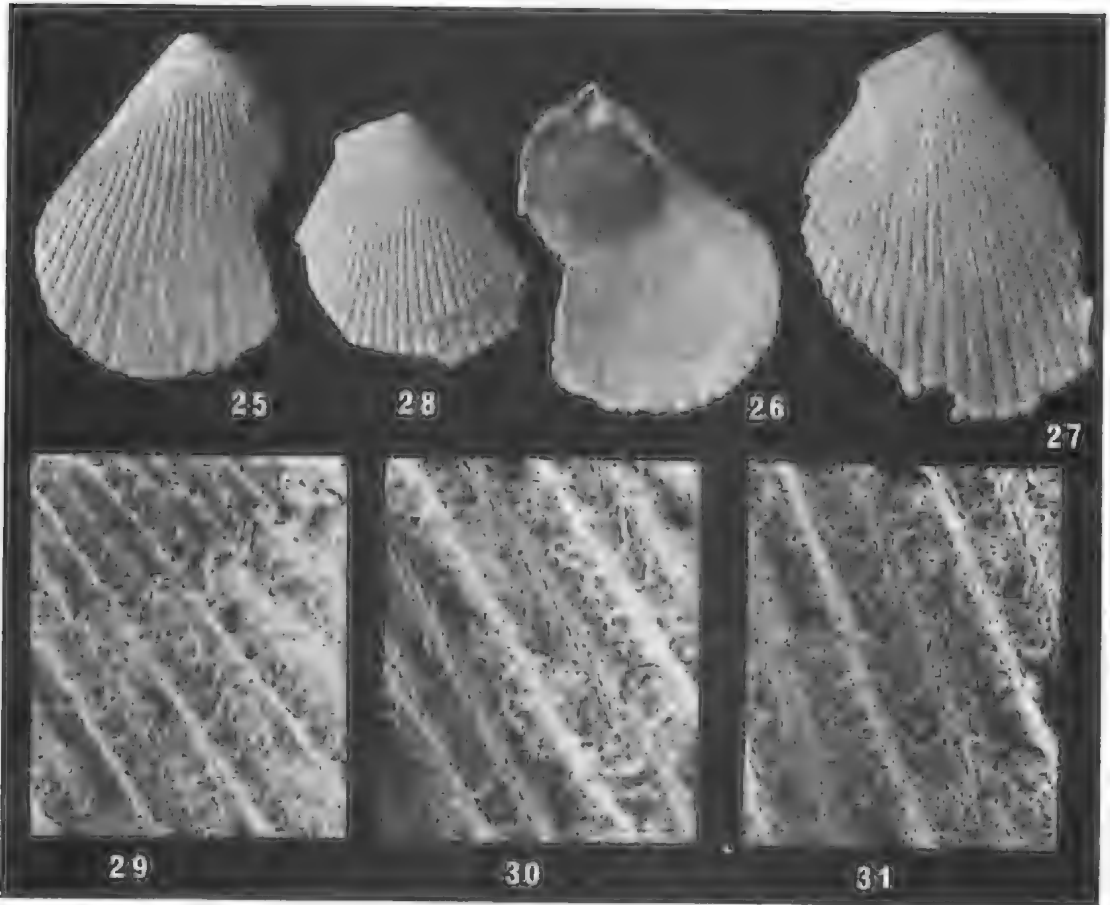
FIGS 25–31

Figs 25-26. *Lima elianae* sp. nov., holotype: (GSSA M 2384), Observation Bore D, Late Pliocene, views (x1.0); (25) dorsal; (26) interior. Fig. 27. *Lima elianae* sp. nov. paratype (SAM P 19210), Abbattoirs Bore, Late Pliocene, dorsal view (x1.4). Figs 28-31. *Lima elianae* sp. nov., paratype (GSSA M 159), Munno Para Bore, Late Pliocene; (28) dorsal view (x1.95). Ornament: (29) dorsal juvenile transitional to adult, (30) dorsal, adult; (31) anterior, adult.

Other Localities: Adelaide Plains Sub-Basin. Abattoirs Bore; bore hd. Munno Para, Sect. 4251, 72.5–78.0 m depth.

Stratigraphic Range: Yatalan (Late Pliocene).

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PLEISTOCENE FROGS FROM CAVES AT NARACOORTE, SOUTH AUSTRALIA

BY M. J. TYLER

Summary

Pleistocene cave deposits at Naracoorte, South Australia, have yielded 166 frog ilia assigned to five species (two questionably) now found in southeastern Australia. They represent the first Pleistocene frogs known in Australia. The significance of the absence of any member of the Litoria aurea species complex in the Naracoorte Pleistocene fauna is discussed.

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Summary

Tyler, M. J. (1977) Pleistocene frogs from caves at Naracoorte, South Australia. *Trans. R. Soc. S. Aust.* 101(3), 85-89, 31 May, 1977.

Pleistocene cave deposits at Naracoorte, South Australia, have yielded 166 frog ilia assigned to five species (two questionably) now found in southeastern Australia. They represent the first Pleistocene frogs known in Australia. The significance of the absence of any member of the *Litoria aurea* species complex in the Naracoorte Pleistocene fauna is discussed.

Introduction

It is generally accepted that glacial periods during the Pleistocene were associated with moist climatic conditions. For the frogs of Australia these moist periods provided the opportunity for them to colonise or cross formerly arid areas and, as a result of eustatic changes, reach previously isolated islands on the exposed continental shelf.

Until recently there have been no known fossil frogs in Australia, and the solitary species recorded (*Australobatrachus ilius* Tyler) is of mid-Miocene age (Tyler 1974, 1976). Therefore, to date, information about the frog fauna during the glacial periods has been interpreted from current geographic distributions and from deduced patterns of speciation.

In late 1974 and early 1975 Dr R .T. Wells permitted me to examine boxes of sievings from Victoria Cave at Naracoorte, South Australia. The site had provided vast quantities of late Pleistocene vertebrates reported by Smith (1971, 1972), Van Tets (1974), Van Tets & Smith (1974) and by Wells (1975). The existing frog fauna within and surrounding the Naracoorte area is well known (Tyler 1966; Woodruffe & Tyler 1968), and the site was therefore ideal for an intensive search for fossil frogs of limited antiquity.

The material provided by Dr Wells was examined for the presence of ilia: bones previously demonstrated to be of considerable value in the identification of genera and species, and previously surveyed to establish the characteristics of Australian species (Tyler 1976).

Following the recovery of numerous ilia in the Victoria Cave deposit, additional specimens were obtained from the adjacent locality of Henschke's Quarry Cave. Subsequently Mr N. Pledge located further specimens from Henschke's Quarry Cave sievings.

In reporting the nature, extent and identity of the material obtained, the object is to establish the existence of the first known Pleistocene frog fauna in Australia, and to explore the palaeoclimatic and biogeographic implications of its nature.

Methods

Descriptions of the Victoria Cave site and of the techniques used for separating the fossils from the silt appear in Smith (1971) and Wells (1975). Rapid isolation of the ilia from the bone fragments and particulate matter involved the establishment of a search image. In practice the only macroscopic confusion was with some small vertebrate ribs.

As yet in Henschke's Quarry Cave only fossil birds have been reported (Van Tets 1974).

Descriptive terminology of the ilium is that of Tyler (1976). With the object of extrapolating the size of the donor animals from the ilial fragments, various measurements were recorded of bones from existing species. As a result an association was found to exist between the body length, and the distance separating the anterior limit of the dorsal acetabular expansion from the inferior limit of the ventral acetabular expansion (DAE-VAE) as depicted in Figure 1.

All fossil material reported here has been deposited in the South Australian Museum, and

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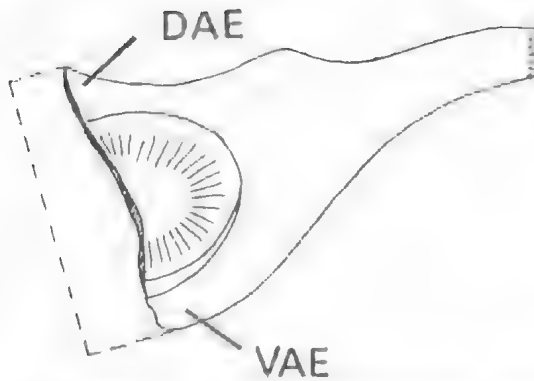
Fig. 1. Acetabular portion of generalised frog ilium illustrating measurement of span between dorsal acetabular expansion (DAE) and ventral acetabular expansion (VAE).

the registration numbers are those of its Palaeontology Department.

Fossil fauna
Family HYLIDAE
Litoria ewingi (Duméril & Bibron)

Henschke's Quarry Cave: P. 18878, P. 19505, 2 left ilia; P. 18940, P. 19504, 3 right ilia.
Victoria Cave: P. 16801, 21 left ilia; P. 16802, 12 right ilia.

The ventral acetabular expansion forms a characteristically thin but exceptionally well developed plate, approximately equidistant from the acetabular margin throughout its length. The dorsal acetabular expansion of this species is of moderate height; the dorsal protuberance is small but usually quite distinct from the dorsal prominence as a laterally disposed projection (Fig. 2c).

The size of the fossils appears to be well within the range of modern individuals from the same locality. In each fossil specimen the ilial shaft is incomplete to a greater or lesser extent.

The maximum DAE-VAE distance is 2.8 mm which, as demonstrated in Table 1, can be equated with a snout to vent length of 35 mm. Such a body size is well within the range of modern individuals from this area, and is the mean for adult males in southern Victoria (Watson, Loftus-Hills & Littlejohn 1971).

Family LEPTODACTYLIDAE
Limnodynastes tasmaniensis Gunther

Henschke's Quarry Cave: P. 19506, 1 left ilium; P. 18853, 18939, 2 right ilia.

TABLE 1

Comparison of measurements of the largest fossil Litoria ewingi with modern representatives.

	DAE-VAE distance	ilial shaft length	snout-vent length
fossil	2.8 mm	10.6 mm (incomplete)	235 mm
modern	2.2 mm	12.3 mm	33 mm
modern	2.8 mm	13.7 mm	35 mm
modern	2.7 mm	13.4 mm	35 mm

Victoria Cave: P. 16803, 14 left ilia; P. 16804, 8 right ilia.

The ilium of this species is characterized by the following combination of features: the sigmoidal margin of the ventral acetabular fossa; a moderate to poorly developed, and pointed, dorsal acetabular expansion; an oval shaped dorsal protuberance inclined anteriorly at an angle of 45° to the superior margin of the ilial shaft, and a slight longitudinal indentation on the lateral surface of the distal half of the ilial shaft (Figs 2f and 3a).

The fossil ilia are rather small in comparison with modern representatives of adults of this species. To a certain extent the range of adult size varies from locality to locality and the extremes derived from the data of Moore (1961) and Littlejohn (1963) are: males 31.7–39.5 mm; females 32.2–43.3 mm. Of seven adult specimens dissected by me the snout to vent lengths are 31.0–35.8 mm, and so situated within the lower portion of the adult size range. The DAE-VAE span for these same seven specimens are 4.0–4.7 mm (mean 4.4 mm). The DAE-VAE span in 17 fossils is 2.5–3.8 mm (mean 3.0 mm), indicating that the fossil frogs were considerably smaller than modern adults.

Limnodynastes sp. cf. *L. dumerili* (Peters)

Victoria Cave: P. 16805, 15 left ilia; P. 16806, 22 right ilia.

Uncertainty about the identity of this material exists because of problems associated with distinguishing *L. dumerili* ilia from those of *L. peroni*. In each species the dorsal prominence and dorsal protuberance exhibit a degree of variation not observed in any other species of Australian frogs. In its simplest form the dorsal protuberance can consist of a slightly raised projection with an obtusely angled superior margin (Fig. 2b). At the other extreme of its development the prominence takes the form of an anteriorly inclined hook (Fig. 2a). Between these two extremes there exists every conceivable intermediate stage.
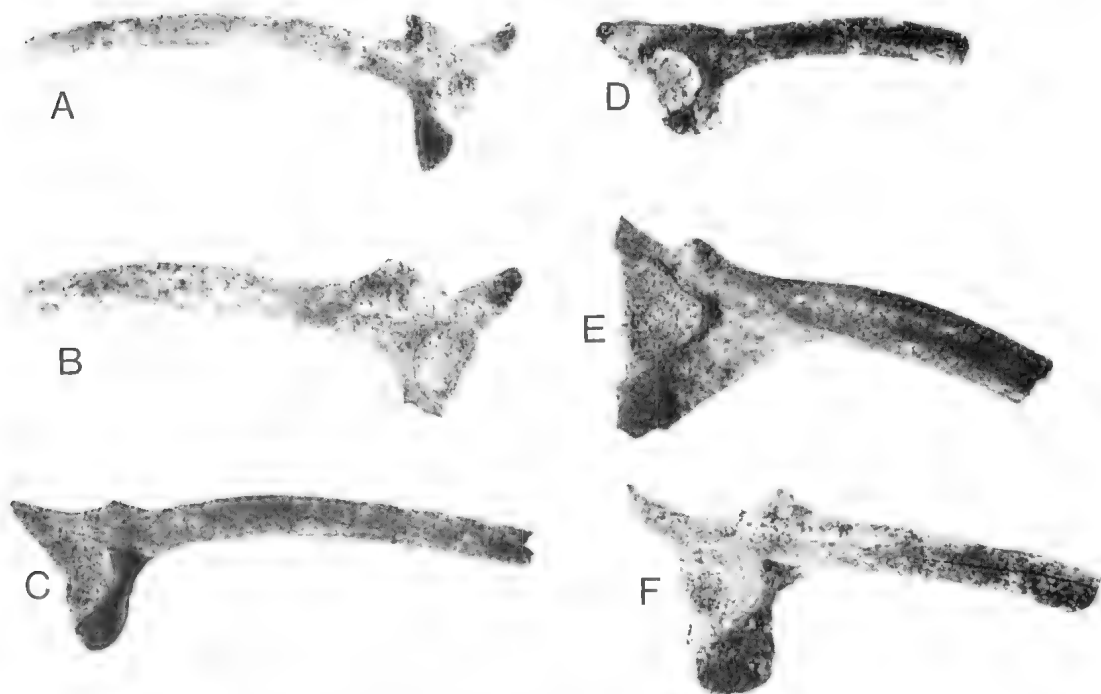
Fig. 2. Fossil ilia from Victoria Cave, Naracoorte. a and b *Limnodynastes* sp. cf. *L. dumerili*, P. 16805; c *Ranidella signifera*, P. 16808; d *Geocrinia* sp. cf. *G. laevis*, P. 16809; e *Litoria ewingi*, P. 16802; f *Limnodynastes tasmaniensis*, P. 16804.
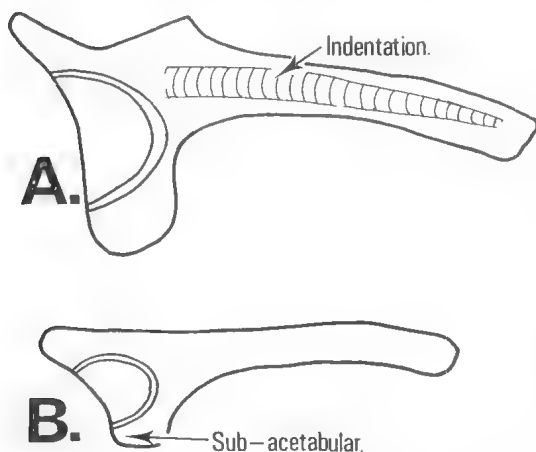
Fig. 3. Features of ilia. A. *Limnodynastes tasmaniensis* showing lateral indentation. B. *Geocrinia* sp. cf. *G. laevis* indicating reduced subacetabular zone.

The highest DAE-VAE distance in the fossils is 7.7 mm and five others exceed 6.5 mm. The minimal ratio of snout to vent length/DAE-VAE distance in the extant material examined is 8.9, placing the minimal extrapolated snout to vent length of the largest fossil individual at about 68 mm.

In the light of numerous differences in other osteological features, in gross morphology and external features, the extent of similarity between the ilia of *L. dumerili* and *L. peroni* is surprising. Until such time that other means are found for distinguishing the ilia of these species the identity of the present material will remain uncertain.

Ranidella signifera Girard

Henschke's Quarry Cave: P. 18936, 1 left ilium; P. 18935, 1 right ilium; P. 18851, 2 right ilia; P. 18934, 2 left ilia; P. 18933, 2 right ilia; P. 18852, 1 left ilium; P. 18932, 4 left ilia; P. 18931, 2 right ilia; P. 19501, 3 right ilia; P. 19502, 2 right ilia; P. 19503, 2 left ilia.

Victoria Cave: P. 16807, 15 left ilia; P. 16808, 17 right ilia.

As can be seen in Fig. 2c the ilium of *R. signifera* is characterised by a comparatively broad acetabular fossa and a sigmoidal shaped anterior margin of the ventral acetabular expansion. In addition the dorsal acetabular expansion and dorsal prominence are both quite pronounced.

The maximum ilial shaft length in the fossil material is 11.4 mm. In modern representatives

this size is attained by individuals approximately 31 mm long, approximating the maximum body length reached by this species.

Geocrinia sp. cf. G. laevis (Gunther)

Victoria Cave: P. 16809, 1 right ilium.

The short and relatively broad ilial shaft and very poorly developed dorsal prominence are features common to Geocrinia and Crinia species. However, Geocrinia is set apart by moderate development of the preacetabular portion of the ventral acetabular expansion, and poor development of the subacetabular portion (Figs 2d and 3b). Geocrinia laevis is the only species available for comparison and the fossil agrees with that species in most respects. Bearing in mind the striking similarity of habitus between G. laevis and G. victoriana, and the genuinely close relationship of these species, it is unlikely that the ilia will differ substantially from one another.

The fossil appears to have a complete shaft and the total length is 4.9 mm. This is considerably less than those of the modern ilia examined and indicates a subadult individual approximately 15 mm in body length.

Discussion

The age of the Henschke's Cave material is at least 32,000 B.P. (N. Pledge, pers. comm.). Preliminary dating of apatite and collagen from the Victoria Cave deposits is equivocal as the deposit may be beyond the range of C14 dating. A more accurate age estimation awaits the completion of detailed C14 and stratigraphic studies (R. T. Wells, pers. comm.).

Evidence of a close relationship between elements of the frog fauna of southeastern and southwestern Australia has been explained as reflecting migration of existing species or their ancestral stocks during the optimal Pleistocene glacial periods (Littlejohn 1967). The fossil Naracoorte fauna therefore assumes importance in terms of acting as a sample of a population of a southern Australian species, conceivably occurring at a time when the last glacial migration may not have reached its maximal geographic limits.

One unexpected deficiency in the Naracoorte fossil fauna is Litoria raniformis (Keferstein) or any other species of the L. aurea (Lesson) species complex as defined by Tyler & Davies[1]. The deficiency is quite genuine, for the ilia and

other bones of L. raniformis are large (ilial shaft length up to 33 mm) and they exhibit a number of features distinguishing the species from all other sympatric species in South Australia. Thus there is no possibility that its presence could have evaded detection during the sorting procedures.

The absence of L. raniformis is an anomaly because it currently extends from New South Wales to the southeast of South Australia including the Naracoorte area. The L. aurea species complex is now well established with four species in southeastern and two species in southwestern Australia[1]. Although the marked level of divergence in the now allopatric species can be attributed to migration from the southeast to the southwest in a penultimate or earlier glacial migration, there has been no suggestion that representation of the complex in southeastern Australia has been other than continuous.

Certainly L. raniformis has existed in at least part of southeastern Australia for 12,000 years because the species occurs in Tasmania, and this is the period of the most recent isolation of Tasmania from the mainland (Littlejohn & Martin 1974). To what extent the maximum duration of colonisation of the southeast can be gauged is uncertain, but there is evidence that the existing boundaries of its distribution are far from being static. For example, Tyler & Roberts (1973) report the recent introduction and subsequent establishment of the species at several locations in the Mt Lofty Ranges, and subsequently it has been found at other "new" adjacent localities near Adelaide. The ease with which it is now colonising this new territory indicates that it is unlikely that the species has existed there previously and has since been displaced, unless extinction can be considered a possibility.

It would therefore appear that the species may not have existed in the extreme southeast 32,000 years ago, but entered the area between that date and 12,000 years ago. Since 12,000 B.P. dispersal westward within the southeast has conceivably been inhibited by arid conditions.

In the light of the above absence of L. raniformis in the Naracoorte fossil fauna, the presence there of Limnodynastes tasmaniensis is particularly perplexing. This species occurs in

[1] In a manuscript on species groups in Litoria. The L. aurea complex currently comprises L. aurea, L. raniformis, L. moorei (Copland), L. alboguttata (Gunther), L. cyclorhynchus (Boulenger), and L. flavipunctata Courtice & Grigg.

southeastern Australia and its western geographic limit is Eyre Peninsula of South Australia. It does not occur in southwestern Australia nor is there a closely related species there. Thus it would appear that *L. tasmaniensis* existed in the southeast at a time when the hypothetical mesic communication to the southwest existed, but did not traverse the communication and thus failed to penetrate the southwest. The presence of *Litoria ewingi* in the deposits is equally surprising in view of its absence from southwestern Australia.

Two of the other species identified in the Naracoorte fauna exist in the vicinity today: *Litoria ewingi* and *Limnodynastes* cf. *dumerili* (Tyler 1966). The third is *Geocrinia laevis* which is limited in South Australia to the extreme lower southeast, and does not now extend as far north as Naracoorte. However, Beck (1975) postulates that there have been substantial withdrawals of the geographic range of this species following trends towards aridity and also as a result of drainage and clearing of vegetation.

In the case of other small vertebrates at Victoria Cave, Smith (1971, 1972) has suggested that they were brought into the cave by predators such as owls. Frogs can form a substantial portion of the diet of some owls so that this interpretation applies equally well to the frog material. However, three species live in the caves at the present time: *Litoria aurea*, *Limnodynastes dumerili* and *L. tasmaniensis*.

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DISTRIBUTION OF INTRODUCED LAND-SNAILS ON YORKE PENINSULA, SOUTH AUSTRALIA

BY A. J. BUTLER AND C. MURPHY

Summary

In three consecutive years surveys for five species of introduced terrestial pulmonates and one native species were conducted on a grid of sampling-points approximately 8 km apart covering the whole of York Peninsula. Sampling in the different years was done by different observers and, despite some technical difficulties, they agree on broad patterns of distribution. Those patterns differ greatly from the results of a survey conducted in 1965. The results, especially possible interactions between species and the spread of Theba pisana, are discussed.

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by A. J. BUTLER* and C. MURPHY†

Summary

BUTLER, A. J. and MURPHY, C. (1977) Distribution of introduced land-snails on Yorke Peninsula, South Australia. *Trans. R. Soc. S. Aust.* **101**(4), 91-98, 31 May, 1977.

In three consecutive years surveys for five species of introduced terrestrial pulmonates and one native species were conducted on a grid of sampling-points approximately 8 km apart covering the whole of Yorke Peninsula. Sampling in the different years was done by different observers and, despite some technical difficulties, they agree on broad patterns of distribution. Those patterns differ greatly from the results of a survey conducted in 1965. The results, especially possible interactions between species and the spread of *Theba pisana*, are discussed.

Introduction

Ten species of terrestrial snails have been introduced into South Australia since colonisation. Pomeroy & Laws (1967) examined the earliest records and concluded that, although exact times of arrival and origins were difficult to ascertain, it was probable that at least four species came from the Mediterranean region. This paper concerns the distribution on Yorke Peninsula of five of these species, *Helicella virgata, H. neglecta, Cochlicella acuta, C. ventrosa* and *Theba pisana* as well as that of the native snail, *Austrosuccinea australis*.

Pomeroy & Laws (1967) summarised available information about the distributions of introduced snails in South Australia at that time. Their information on distributions on Yorke Peninsula came from two kinds of source. For *C. acuta, C. ventrosa* and *T. pisana* they present spot records from South Australian Museum collections and their own collections. For *H. virgata* and *H. neglecta* they present the results of their own survey in which roadsides were examined on a grid of points about 8 km apart, covering the entire Peninsula. At these points ratings were assigned to the abundance of snails. The survey was conducted during summer.

In their findings are two major points to be compared with the results of the present survey: *T. pisana* was recorded from only two sites, Corny Point and Edithburgh; the distribu-

tions of *H. virgata* and *H. neglecta* were almost mutually exclusive. *H. neglecta* occupied the "foot" and "ankle" of the Peninsula, being especially abundant along the north coast of the "foot" from Corny Point to Pt Turton, whilst *H. virgata* occupied the upper "leg" being most abundant around Wallaroo and Moonta. A small gap between the two was noted in the region of Minlaton.

Pomeroy & Laws (1967) record evidence that *H. neglecta* was contracting its range (having formerly occurred as far north as Moonta and perhaps over much of the Peninsula although the records are unreliable), whilst *H. virgata* was expanding its range but . . . "one can only speculate as to whether the two events are related". They also suggest that *T. pisana* had reached its 1967 distribution rather rapidly. Further, they present observations over two years on the numbers of *T. pisana* and *H. virgata* in two quadrats at Outer Harbour and Pt Adelaide from which they suggest *T. pisana* may have been increasing whilst *H. virgata* was decreasing in numbers.

Lim & Jenkins (1972) carried out a survey for *T. pisana* and *H. virgata* in the southeast of South Australia because the former presents an economic problem there. They also noted the known distribution of *T. pisana* throughout the State. On Yorke Peninsula they found it at two more sites than did Pomeroy & Laws (1967). Lim & Jenkins (1972) also noted that in the

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southeast *T. pisana* and *H. virgata* tended not to occur at high densities together.

It was therefore of both theoretical and practical interest to re-examine the distributions of introduced snails on Yorke Peninsula. Theoretically, because Pomeroy & Laws (1967) raise interesting ecological questions. They suggest *T. pisana* may replace *H. virgata* by competition for food; and if *H. virgata* is indeed expanding its range whilst *H. neglecta* is contracting at about the same rate, the mechanism is by no means obvious.

The study was also of practical interest because *T. pisana* is a costly pest in other parts of the world (Pomeroy & Laws 1967; Rimes 1968; Nevo & Bar 1976) and is already a nuisance in the southeast of South Australia (Lim & Jenkins 1972). Its expansion in this State is therefore a cause for concern.

This paper presents the results of surveys carried out from 1973 to 1975 on Yorke Peninsula. The grid of sampling points was similar to that used by Pomeroy[1] and Pomeroy & Laws (1967) but the procedure for assigning ratings was a little different. The surveys were not designed to explain the changes in distribution but we make some comments on them.

Methods

Sampling points were chosen in the manner of Pomeroy & Laws (1967). Sites were on roadsides since these provide a favourable habitat for snails and are readily accessible for observation.

Roads approximately parallel to each other and 8 km apart were plotted on large-scale maps and sampling points ("stops") were chosen at 8 km intervals along them (Fig. 1). The detailed laying-out was done independently in 1973 and 1974. In 1975 the 1974 layout was available in detail and it was followed again except for the addition of some extra stops. Nevertheless, due to random error in odometer readings, 1975 stops do not correspond precisely with 1974 stops. Thus all four surveys have the same basic plan but do not in general incorporate exactly the same sampling sites. A standard procedure was used for assigning a rating to the abundance of snails at each stop, on a scale from 0 (no snails) to 4 (over 150 snails/m²). A separate rating was assigned for each of the six species. The data on abundance are available from the authors, but only "presence-or-absence" records are presented here.

The fieldwork was done by a different pair of observers in each of the three years (see Acknowledgments). Each pair of workers examined museum specimens and literature in order to learn to identify snails and practised the technique of estimating abundance so that the observers were accurately "calibrated" before each survey began. These preparations were made independently by the three pairs of observers. In general, specimens were not collected, but a set of voucher specimens was taken from selected stops in August 1976 by A. Butler; these have been lodged in the South Australian Museum.

Although in 1973 a watch was kept for snails between sampling points where ratings of 0 had been recorded, as done by Pomeroy & Laws (1967), this was subsequently discontinued. Several species were very small, well-camouflaged and usually hidden in vegetation or under rocks. Also, careful inspection was needed to distinguish between the two *Helicella* species. Moreover, numbers at a particular site will vary greatly with the seasons (Pomeroy & Laws 1967; Pomeroy 1969) because of both population fluctuations (Pomeroy 1969) and movement (Hodson[2]). Snails also bury themselves (Pomeroy[1]). Therefore our results are presented not as maps of continuous distribution but as a large set of point observations.

The survey of Pomeroy & Laws (1967) was conducted in summer when snails are mostly dormant (Pomeroy 1968; Hodson[2]) and *Heli-*

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FIGS 1-10

Fig. 1 Sampling-points on Yorke Peninsula. Figs 2-10. Records of snails in each of the three years (summer and winter records pooled). Excepting a few sites (with subscript A in Fig. 1) added in 1975, all sites shown there were visited each year. Thus, the absence of a spot on the map in Figs 2-10 indicates a negative record for the corresponding site. 2. *Helicella virgata*, 1973. 3. *H. virgata*, 1974. 4. *H. virgata*, 1975. 5. *H. neglecta*, 1973. 6. *H. neglecta*, 1974; 7. *H. neglecta*, 1975; 8. *Theba pisana*, 1973; 9. *T. pisana*, 1974; 10. *T. pisana*, 1975.
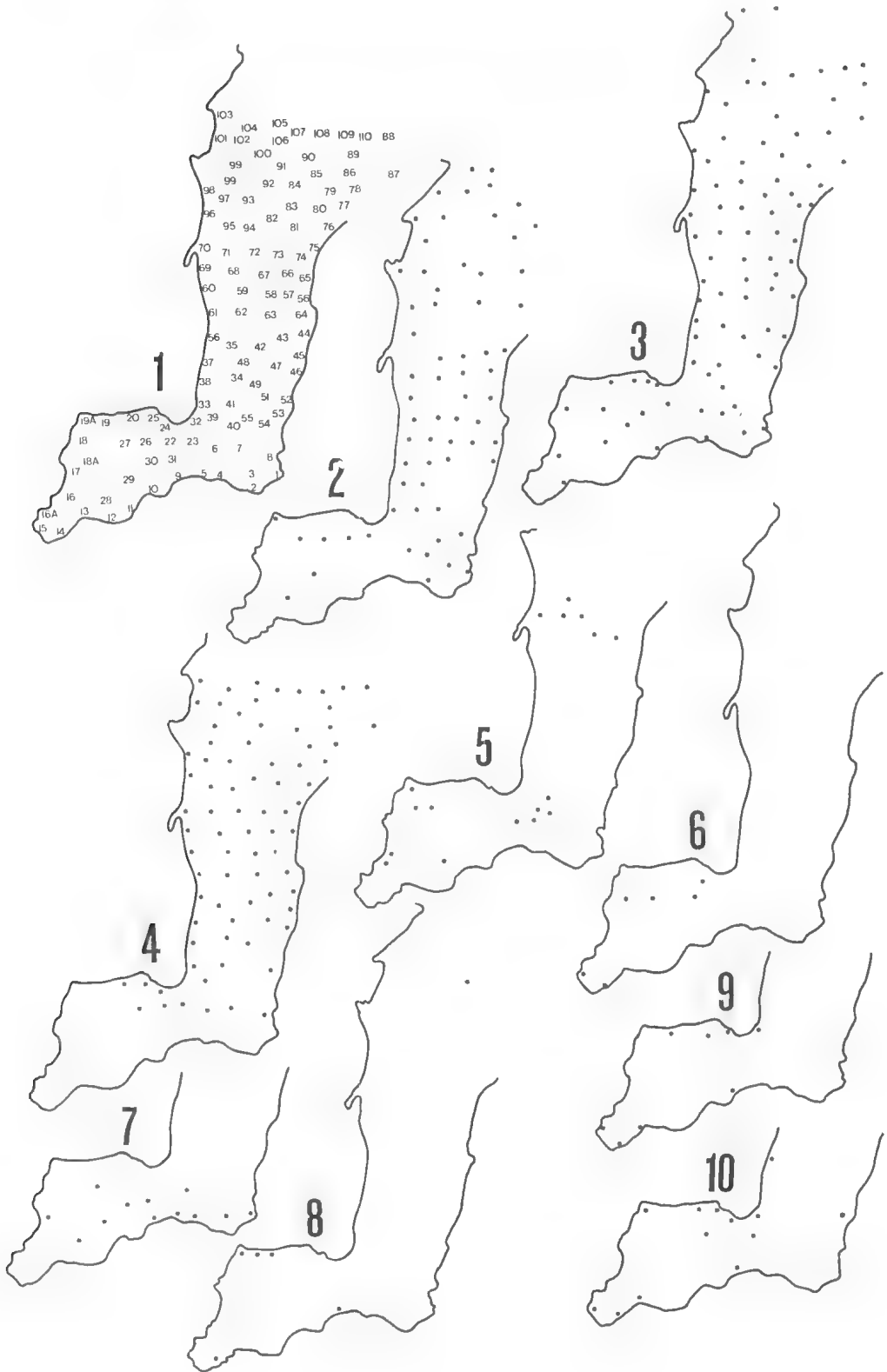
cella might be more conspicuous (although this depends greatly upon the kinds of sites available for aestivation). Our 1973 survey was conducted in winter. The 1974 and 1975 surveys were done in both summer (February) and winter (July). Within one year the sampling sites were the same in the two seasons.

At each site vegetation-type was briefly noted.

Results

The results are shown in Figures 2–19. Each spot represents a non-zero rating. Spots on the 1973 maps represent observations in summer; a spot on a 1974 or 1975 map represents a recording in summer, winter or both. This has been done to facilitate discussion of broad patterns. Separate summer and winter results, and the actual ratings, are available from the authors.

Discussion

Several technical points must be made. It is sometimes difficult to distinguish *H. virgata* from *H. neglecta* on shell morphology alone and it is valuable that the three pairs of observers learned, from literature and South Australian Museum specimens, to distinguish the species. Thus although some errors of identification may have been made in the field, there is unlikely to be a systematic bias due to "cultural transmission" amongst the teams. The 1973 workers collected some doubtful specimens for later confirmation by dissection. Voucher specimens collected by A.J.B. in August 1976 from points 104, 72, 41, 7, 6, 23, 22, 26, 20, 17 and 28 have been deposited in the South Australian Museum.

Because there are likely to be wide fluctuations with season in both numbers and conspicuousness of snails, for numerical comparisons Pomeroy & Laws' (1967) summer results should be compared primarily with our summer results. Similarly our 1973 survey should be compared with the winter results of 1974, 1975. However in this paper we have pooled our summer and winter results, and we discuss only broad patterns.

Pomeroy[1] surveyed systematically, in the way we did, only for the two *Helicella* species. The information presented by Pomeroy & Laws (1967) on other species is based on museum records and spot records by the authors and must not be discussed as complete maps of distribution.

Finally we note that all of the sampling sites were on roadsides. It must be remembered that these sites are especially vulnerable to human influence such as clearing, dumping, spraying for weed control and ploughing for firebreaks. Thus we must assume that to the natural fluctuations which occur in snail populations (Pomeroy & Laws 1967; Pomeroy[1]) is added an unknown variability from year to year. This could include the founding of new populations (Pomeroy & Laws 1967; Pomeroy 1967) as well as the changes of habitats from favourable to unfavourable or vice-versa.

Austrosuccinea australis

This native snail seems to be low in numbers throughout the Peninsula (Figs 17–19). It was scarce in 1973 but nevertheless was recorded at 14 sites. In 1974 it was not observed at all and in 1975 it was found at one site in winter. Perhaps its range is contracting, but given the technical points above, we cannot conclude so with any confidence.

Cochlicella spp.

Pomeroy & Laws (1967) recorded *C. ventrosa* at Corny Point. As noted above this is not strong evidence that this snail was absent at all other points. Our results (Figs 15–17) show it in more localities, with a suggestion that it may be increasing (compare Figs 16, 17). Almost all our records of *C. ventrosa* were in winter, perhaps part of the reason why they recorded it at only one place.

C. acuta was recorded at nine sites on the "foot" and "lower leg" by Pomeroy & Laws (1967). Our results do not show it outside this general area, but there is some suggestion that it is "filling-in" its area of distribution. (Compare Figs 11–13). As with *C. ventrosa*, however, we must not make too much of small differences between years but the independence of our three surveys gives us confidence that *C. acuta* is widespread over southern Yorke Peninsula whereas *C. ventrosa* occurs in isolated pockets scattered over the Peninsula.

Helicella spp.

The changes in the distributions of the two *Helicella* species can be followed from the sum-

FIGS 11-19

Details as for Figs 2-10. 11. *Cochlicella acuta*, 1973; 12, *C. acuta*, 1974; 13, *C. acuta*, 1975; 14. *C. ventrosa*, 1973; 15. *C. ventrosa*, 1974; 16. *C. ventrosa*, 1975; 17. *Austrosuccinea australis*, 1973; 18. *A. australis*, 1974; 19. *A. australis*, 1975.

NO
RECORDINGS
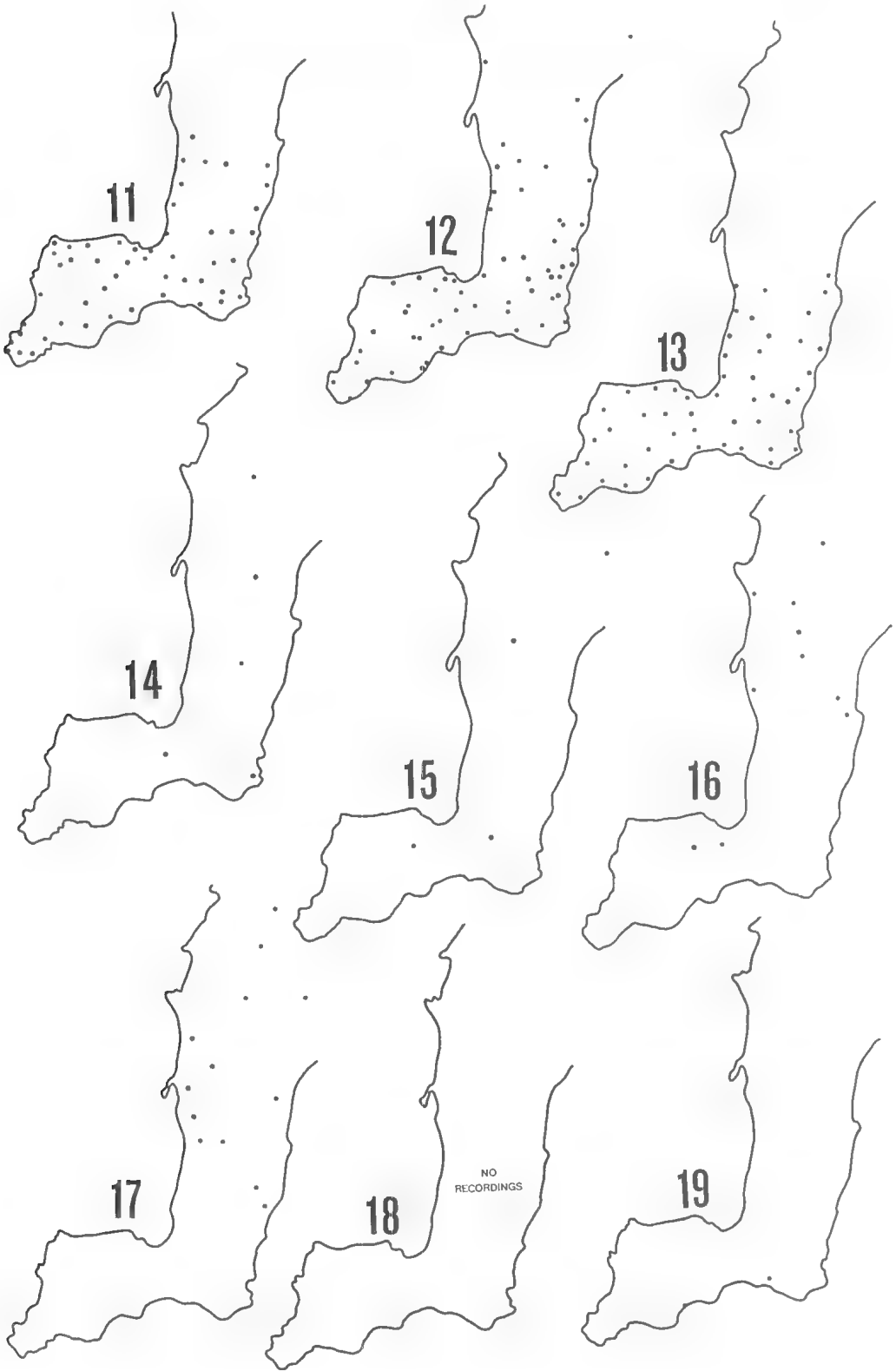
mer of 1954–55, Prof. H. G. Andrewartha (pers. comm.) made a tour of the Peninsula during that summer on which he observed *Helicella virgata* aestivating in great numbers on fenceposts in the vicinity of Wallaroo. Despite a search of about two days in travelling southwards down the Peninsula he found no more *H. virgata* beyond a few miles south of Wallaroo; in fact, he found no snails at all until south of Minlaton. He did find dense populations of *H. neglecta* in the southern part of the Peninsula where it had been known to have been present for the past 64 years.

In 1967 Pomeroy & Laws recorded *H. virgata* extending southwards almost as far as Minlaton (see Introduction).

By 1973 (Figs 2, 5) the distribution of *H. neglecta* was much contracted and that of *H. virgata* greatly extended from those reported by Pomeroy & Laws (1967). Given the independence of the three surveys this difference is very convincing. It is far too great to be accounted for by year-to-year fluctuations and different observers in the three years agree over the broad pattern; *H. virgata* is widespread over the Peninsula including most of the "foot" where Pomeroy & Laws (1967) recorded it at only two locations; *H. neglecta* has contracted to small areas in the "root", although the pocket near Moonta, shown by them may still exist (Fig. 5). On this point, however, note the difficulty in identification discussed above; we must concern ourselves in this paper with broad patterns which were observed by three independent teams of observers, and the northern records of *H. neglecta* in Fig. 5 were not repeated by the 1974 and 1975 teams.

We must again be cautious in interpreting year-to-year differences. *H. neglecta* may be continuing to contract (compare Fig. 5 with Fig. 6); in 1974 (Fig. 7) more sites were examined and this accounts for some of the additional records. *H. virgata* may have filled in some areas within its overall range (Figs 2–4), but this has occurred in areas where Pomeroy & Laws (1967) found it to be very abundant and so may be regarded as part of a fluctuation in numbers.

We note in passing that on a brief visit to a few stops in August 1976 essentially the same pattern was found as in 1975 except that no live specimens of *H. neglecta* were taken. This species was expected, at least in low numbers, at sites 6, 28 and 17 but only dead shells were found there.

Theba pisana

This snail is scarce on much of the Peninsula but appears to be spreading. Cotton (1949) does not record it on the Peninsula at all. According to Pomeroy & Laws (1967) it was then known from two sites only, Corny Point and Edithburgh. Lim & Jenkins (1972) gave four sites on the Peninsula, adding one near Stenhouse Bay and another near Pt Vincent. Such point records do not convincingly indicate a spread, but on our surveys *T. pisana* was found at six sites in 1973, eight in 1974 and 13 in 1975 (Figs 8–10) and its numbers at some of these new sites were high.

Further, the number of "point records" continues to increase. By the end of 1975, the Department of Agriculture had records of *T. pisana* from Ardrossan, Pine Point, Edithburgh, Warooka, the coastal dunes 4 km due north of Warooka, Point Turton, Hardwicke Bay, Brentwood, Port Minlacowie and Port Victoria (P. R. Birks, pers. comm.).

The expansion of *T. pisana* has occurred mostly along coastal areas of the lower Peninsula. Since the coastal dunes have until recently been nearly inaccessible by road much of this expansion may depend largely on the snails' own locomotion. However, Pomeroy & Laws (1967) thought that man was an important dispersal agent for *H. virgata*, and this is almost certain to be true of *Theba* now. P. R. Birks states that *Theba* is now present at "almost every crossroad between Minlaton and Brentwood". Snails are likely to become established at crossroads because people park cars there, having previously parked at centres of dense snail populations. (Many of our sampling sites were not at crossroads.)

Interactions between species

Pomeroy & Laws (1967) noted almost mutually exclusive distributions for *H. virgata* and *H. neglecta* and suggested that *H. neglecta* was contracting and *H. virgata* expanding its range. Our results seem to confirm this, but there is no longer a "confrontation" between the two distributions. *H. neglecta* now occurs in pockets within the range of *H. virgata* and there is one site (No. 6 on Fig. 1) where both have been recorded. However, there are places where *H. neglecta* has disappeared but *H. virgata* has never been recorded. Thus the hypothesis that *H. virgata* is displacing *H. neglecta* can, at best, be only part of the story. We can guess at various environmental changes which may be responsible, but have no tests. Moreover, in our

three surveys and that of Pomeroy & Laws (1967) no relationship could be found between vegetation-type and the snails present.

An interaction may also be occurring between *T. pisana* and *H. virgata*. Numbers of *T. pisana* at sites on the southern Peninsula have increased from 1973 to 1975 whilst *H. virgata* may have contracted there (compare Figs 9 and 10 with Figs 3 and 4). Again not too much can be made of year-to-year differences and there are sites where *H. virgata* has decreased but *T. pisana* has never been recorded. Nevertheless the hypothesis of some direct interaction bears closer consideration here (sites 20, 24, 25, 32, 39). Moreover Pomeroy & Laws (1967) presented data from Outer Harbour showing a slight trend for *T. pisana* to increase and *H. virgata* to decrease in numbers over two years in the same area and Lim & Jenkins (1972) found that in the southeast of South Australia the two species tend not to occur together in high densities.

Pomeroy & Laws (1967) tentatively interpret their observations at Outer Harbour in terms of competition for food. However there is some evidence (Butler 1976) that at least in one area, *H. virgata* may not be short of food in an absolute sense (Andrewartha & Browning 1961). On the other hand it is known for certain aquatic pulmonates that large numbers of snails can inhibit one another's growth, survival and reproduction even in the presence of abundant food (Thomas & Benjamin 1974; Thomas *et al.* 1974). Such an effect could occur in terrestrial snails, possibly through soiling of the food and substrate with excreta, or slime-trails, and may allow *T. pisana* to replace *H. virgata*. Critical experiments will however be needed to discriminate between possibilities.

Polymorphism in shell banding

During the 1975 survey it was noted that three inland populations of *T. pisana* were all monomorphic for unbanded shells whereas the coastal dune populations were polymorphic for shell banding. Vegetation inland was lower, mostly grass; coastal vegetation was more dense, and mostly low bushes. This difference in morph frequencies was not noted in *H. virgata* or *H. neglecta*, all populations of which were polymorphic. Roberts[1] found a similar situation in *H. virgata* at Semaphore Park ex-

cept that inland populations contained the banded morph in low frequency (less than 5%).

There are many suggestions in the literature that genetic changes are important in the dynamics of populations of animals including snails (for review see Williamson 1972). Thus, especially in view of the suggestion of Baverstock[2] that food may be one of the factors influencing morph-frequencies in *H. virgata*, it may be instructive to consider morph-frequencies in examining both the distribution of snails on the Peninsula and the hypothesis of competitive displacement.

Economic importance

The *Helicella* species constitute only a minor economic problem, although not negligible (Pomeroy & Laws 1967; Birks pers. comm.). Where their numbers aestivating on stalks are high enough to foul grain, they can be controlled with a carbamate bait or by using a special outrigger on the harvester (Rimes 1968; Lim & Jenkins 1972). *T. pisana*, on the other hand, not only may cause the same problem but can also damage lucerne and has been reported as doing so in the southeast of this State.

Both *Cochlicella ventrosa* and *Theba pisana* have been causing significant fouling of grain on Yorke Peninsula in the last few years, and in 1976 the Department of Agriculture and Fisheries received its first report (from near Port Lincoln on Eyre Peninsula) of *Theba* actually eating barley plants and causing considerable damage especially to young seedlings (P. Birks, pers. comm.). Our records suggest that this snail is spreading, and so it is potentially a serious pest on the Peninsula.

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NESTING BIOLOGY OF THREE ALLODAPINE BEES IN THE SUBGENUS EXONEURELLA MICHENER (HYMENOPTERA: ANTHOPHORIDAE)

BY T. F. HOUSTON

Summary

Results of a detailed study of nest populations of Exoneura (Exoneurella) tridentata are presented with less complete observations of E. (E.) eremophila and E. (E.) setosa. These species rear their larvae progressively in open burrows in dead plant stems, tridentata in ready-hollowed woody twigs, eremophila and setosa in pithy herbaceous stems. E. tridentata exhibits small semisocial colonies with queen and worker castes. The castes are dramatically morphologically dissimilar, the large-bodied queens appearing flightless and restricted to nests. By contrast, colonies of eremophila and setosa are basically subsocial. The subsocial condition in these species may be derived from a semisocial condition and possibly associated with life in rapidly perishable stems.

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Houston, T. F. (1977) Nesting biology of three allodapine bees in the subgenus *Exoneurella* Michener (Hymenoptera: Anthophoridae). *Trans. R. Soc. S. Aust.* **101**(4), 99-113, 31 May, 1977.

Results of a detailed study of nest populations of *Exoneura (Exoneurella) tridentata* are presented with less complete observations of *E. (E.) eremophila* and *E. (E.) setosa*. These species rear their larvae progressively in open burrows in dead plant stems, *tridentata* in ready-hollowed woody twigs, *eremophila* and *setosa* in pithy herbaceous stems. *E. tridentata* exhibits small semisocial colonies with queen and worker castes. The castes are dramatically morphologically dissimilar, the large-bodied queens appearing flightless and restricted to nests. By contrast, colonies of *eremophila* and *setosa* are basically subsocial. The subsocial condition in these species may be derived from a semisocial condition and possibly associated with life in rapidly perishable stems.

An unidentified encyrtid wasp, reared from pupae of *tridentata*, was found in association with the bees.

Introduction

The bulk of this paper presents the results of a study of the nesting biology of *Exoneura tridentata*. The remainder presents less complete data on the biologies of *E. eremophila* and *E. setosa*. These three species were described only recently (Houston 1976) and nothing hitherto has been recorded of their bionomics. With *E. lawsoni* Rayment, they comprise the subgenus *Exoneurella* (sometimes accorded generic status) and belong to the group of bees termed allodapines (after *Allodape*). A general account of the biology of allodapine bees is given by Michener (1974). Most species make their homes in burrows in pithy stems or twigs or in dead wood. They construct no cells but raise their immatures together in the common nest chamber. Usually the larvae are fed progressively to maturity by the adult females. Most allodapines display primitive social behaviour in at least part of their life cycle, two or more females occupying one nest and exhibiting division of labour. One female functions as an egg layer (or queen) and seldom forages, while one or more other females with undeveloped ovaries function as workers, foraging and tending the brood.

Michener (1964) considered *E. lawsoni* to be essentially 'solitary' (really subsocial) although several other species of *Exoneura* are semisocial (Michener 1965). He postulated that the 'solitary' habits of *E. lawsoni* were probably derived from a semisocial condition and not primitive. The new information on close relatives of *E. lawsoni* presented below is considered in relation to this problem.

The study of *E. tridentata* was prompted by discovery of the first nests which contained relatively huge females amongst normal-sized individuals (cf. Figs 1A, 1B). Female size variation and allometry in this species is described by Houston (1976). Such variation is absent from other *Exoneurella*

Exoneura tridentata Houston

Methods

All nest material was collected from north-eastern Eyre Peninsula, S. Aust., and the greater part of it from the Lake Gilles National Park, 110 km SW of Port Augusta. Nest collection was carried out during early morning, late evening or during cool rainy periods when all occupants should have been present.

* South Australian Museum, North Tce, Adelaide, S. Aust. 5000.
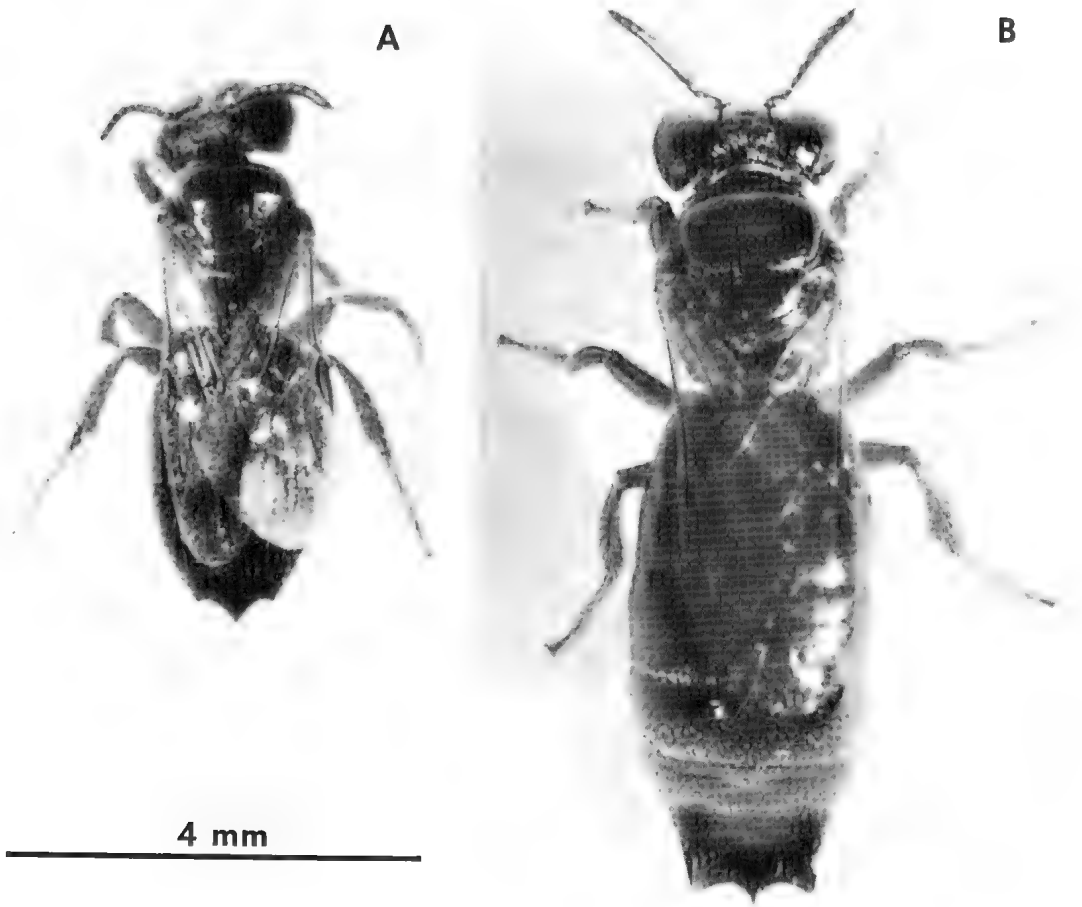
Fig. 1. Females of *Exoneura tridentata* (both to same scale). A. Small minor (pinned). B. Large major (live).

Nest contents were observed alive and then preserved as soon as practicable after collection in 70% ethyl alcohol.

Adult females were measured, examined for wing wear and most were dissected to determine ovary condition and whether or not mating had occurred. Wing wear was rated 0 (margins entire), 1 (one to three nicks), 2 (four to ten nicks), 3 (over ten nicks), 4 (badly tattered). Ovary size was rated 1 (ovaries tiny, slender and borne on long oviducal stalks), 2 (slightly enlarged), 3 (moderately enlarged), 4 (large, at least one ovum near egg size). The length of the largest ovum of each female was also measured.

General observations

Nests

Adults of *E. tridentata* utilise ready made burrows in dead woody twigs or branches of standing trees for both shelter and brood rearing. The term 'nest' is used below to denote burrows used for brood rearing. Shelters are virtually identical except that they are not always cleared of debris, especially when occupied solely by males.

Except for one nest in a branch of native pine (*Callitris* sp.), all occupied tunnels were in dead twigs and branches of Bullock Bush (*Heterodendrum oleaefolium* Desf.), a common small tree of semi-arid southern Australia.

The lower branches of the trees are commonly dead and prone to attack by beetle larvae which bore through the centres of the twigs. Searches of other shrubs and trees revealed very few hollows which the bees might utilise.

Occupied tunnels were 0.6–2.0 m above ground, 2–4 mm in diameter and 25–628 mm in length (most were shorter than 100 mm). They were inclined at various angles from horizontal to about 45° from vertical. Their entrances were either terminal in the ends of broken twigs or lateral but none opened directly upwards so that rain might enter. Entrances were unmodified, showing no traces of the collars of compacted plant material that characterise nests of most other allodapines.

Some tunnels with lateral entrances were double-ended and the bees occupied just one or both ends. In one case (nests 26, 27, Table 1) it appeared that two independent nests had been established in opposite ends of a common burrow.

All nests collected in December and October contained an amorphous patch of dry pollen covering the wall of one side between the brood and the entrance. The patches varied from the merest smear to thick masses up to 30 mm long. Some were composed of one kind of pollen, others of two or more kinds. The quantity of pollen in some nests leaves little doubt that the bees had been accumulating it as a food store and had not simply deposited it accidentally while preparing provisions for the larvae.

Nests collected at other times lacked fresh pollen stores, although a few contained old mould-encrusted ones. The absence of pollen stores from these nests cannot be attributed to lack of flowers for they occurred in abundance at the time of collection. More probably the limited fine weather suitable for foraging was insufficient to allow accumulation of surplus pollen.

Immatures

A description of the immature stages is given by Houston (1976). All occurred loosely within the tunnels. Eggs usually lay crisscrossed or jumbled in the closed ends regardless of the inclination of the tunnels. First and second instar larvae which remain partially enclosed in their chorions were found near the closed ends of the tunnels often amongst eggs. Later instars and pupae were arranged in order of increasing age towards and facing the nest entrances.

A few 3rd and 4th instars were found feeding on moist pollen masses adhering to their venters. However, most larvae were without food, probably because weather conditions at and preceding nest collection were not conducive to flight and food gathering.

The durations of immature stages were not determined. The numbers of each stage found in nests are listed in Table 1.

Eggs exhibited considerable size variation even within nests. A pronounced seasonal shift in average egg size was also noted (Fig 2) so that the size/frequency distributions of the June and October samples barely overlap. The cause of this shift is unknown.

Parasites

The only organism found associated with nest colonies of *E. tridentata* was an unidentified species of minute encyrtid wasp. Larvae of the wasp developed within the bodies of young bee pupae, completely consuming all tissue except the cuticle. Parasitised pupae eventually became filled with numerous wasp larvae which pupated within the host cuticle. Adult parasites emerged through holes chewed through the cuticle.

Of 74 bee pupae collected in December, 39 (53%) were killed by encyrtids, both sexes being equally affected. As no pupae were found in other nest samples the period of activity of the parasite was not determined.

Food sources

E. tridentata is polylectic and has been found collecting pollen from *Amyema*, *Eremophila*, *Eucalyptus* and *Melaleuca*.

Colony composition

A colony may be defined as the living inhabitants of a single nest. The composition of each colony found is shown in Table 1. The smallest of these colonies comprised a lone female with one egg (nest 36). Most nests, however, contained two or more adult females, a maximum of 20 occurring in nest 42. This nest also contained an adult male and 46 immatures (mostly eggs) making it one of the most populous found.

As mentioned above, some tunnels with lateral entrances were double-ended. In one such case, 2 separate colonies (nests 26, 27) were recognised, separate groups of adults and immatures occupying opposite ends of the tunnel. In a second case (nest 22), adults occupied both ends while immatures occurred only at one end. This group was treated arbitrarily as a single colony.
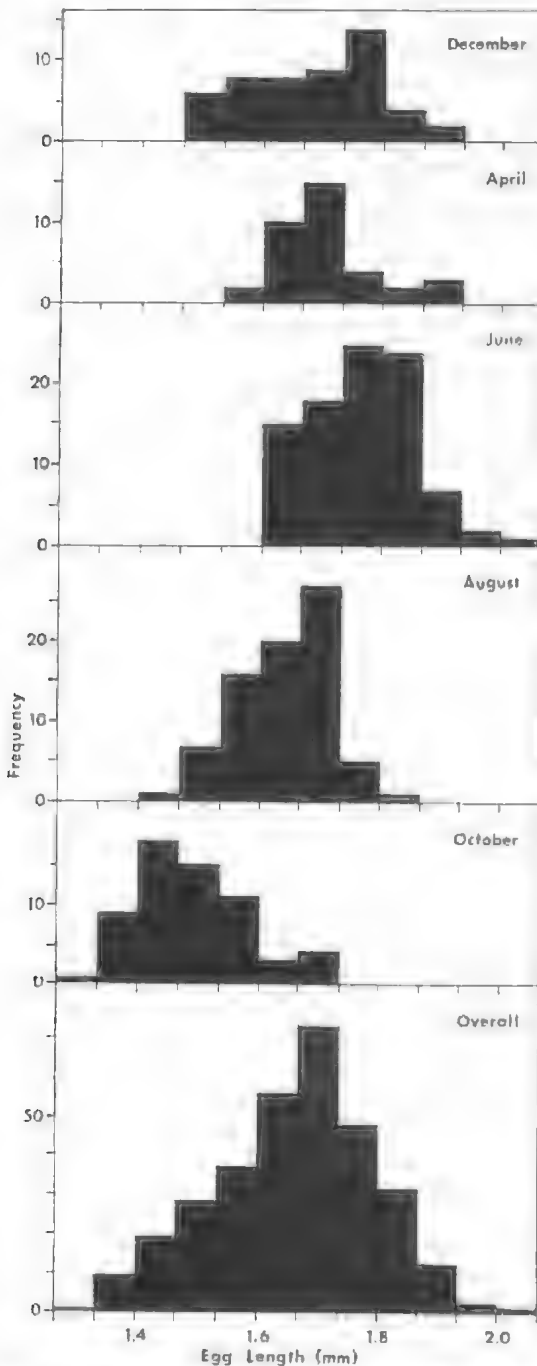
Fig. 2. *Exoneura tridentata*. Histograms showing egg size frequency distributions for different nest samples.

Nest data reveal that brood rearing and production of both sexes occur year round. Eggs, larvae and adults of both sexes were

present in all samples. As pupae occurred only in the December sample, one might suspect that eggs and larvae collected in the relatively cool inclement months of April-September were dormant. However, some adults in the June sample were teneral and had obviously just emerged from pupae. Additionally, some adult females in all samples had ova of or near egg size.

Every nest contained one or more eggs so that egg production must occur intermittently throughout the life of a colony. Were it otherwise, eggs would not be expected in nests with advanced progeny. With such continuous egg production, larval hatching should also occur continuously so that there ought to be no intermediate age gaps in series of immatures. However, it will be seen from Table 1 that many series do have intermediate gaps (e.g. nests 2–4, 8, 26). The rarity of 1st instars is particularly obvious but might be explained by their brief duration (1st instars are non-feeding). The absence of later instars must be attributed to mortality. Perhaps adults occasionally eat eggs or young larvae: eating of eggs has been reported amongst allodapines by Michener (1974, p. 186).

Adult females greatly outnumbered adult males in nests. Males from nests showed little or no wing wear and presumably leave their natal nests while young. Many males were found singly or two or three together in twigs which did not appear to have served as nests. Of the pupae found, 56 were females and 18 were males suggesting a sex ratio of about 3:1.

Colony development appeared to be more or less synchronous. All 10 nests in the December sample contained pupae while none did in other samples. Nests of the April and August samples contained eggs but most lacked larvae. Such synchronisation is unexpected in a species breeding year round and obviously some environmental factor(s) regulates the breeding cycle. Winter cold cannot be the factor in view of the winter breeding. More probably it is the lack of suitable flowers at one or more times of the year which halts breeding and results in synchronisation.

Within single colonies adult females showed marked variation in size, age (as judged by wing wear) and ovarian condition; some were fertilized, others not. The data obtained from examination of females are too numerous to be tabled individually and are summarised and analysed in the following two sections.*

* Copies of the data are obtainable from the author or the Librarian.

TABLE 1

Exoneura tridentata. Contents of nest twigs collected at different times. Larvae were sorted into stadia (stadium i — prepupa). Numbers in the column on the extreme right assign each colony to one of the categories in Table 2. † *indicates pupal series affected by encyrtids.*

| Date of collection	Nest no.	Eggs	Larvae					Pupae		Adults		Pollen store	Colony category
			i	ii	iii	iv	v	♀	♂	♀	♂		
19.iv.1971	1	4	—	—	—	—	—	—	—	14	1	—	II
	2	1	—	—	1	2	3	1	—	6	—	+	IV
	3	5	—	—	1	1	—	6†	—	4	3	+	III
	4	6	—	—	1	—	2	3	—	2	1	+	III
	5	2	—	1	1	1	—	3	1	5	1	+	II
30-31.xii.1973	6	2	—	1	2	—	2	2†	2†	3	—	+	II
	7	11	—	1	1	4	2	18†	5†	9	—	+	IV
	8	1	—	—	—	—	1	3	3	3	2	+	V
	9	12	—	2	2	6	2	13	2	13	1	+	IV
	10	4	—	1	1	—	—	6†	4†	5	2	+	III
	11	4	—	2	1	1	2	—	1	3	2	+	II
	12	4	—	—	—	—	—	—	—	5	—	—	V
	13	4	—	—	—	—	—	—	—	7	—	—	II
	14	4	—	1	—	2	—	—	—	15	1	—	III
	15	3	—	—	—	—	—	—	—	6	1	—	IV
	16	2	—	—	—	—	—	—	—	2	—	—	V
11-16.iv.1974	17	2	—	—	—	—	—	—	—	4	—	—	III
	18	10	—	—	—	—	—	—	—	5	2	—	II
	19	1	—	—	—	—	—	—	—	5	—	—	V
	20	10	—	1	—	1	—	—	—	10	—	—	IV
	21	8	—	—	—	—	—	—	—	4	—	—	III
	22	7	—	—	—	—	—	—	—	13	—	—	IV
	23	23	—	6	—	—	—	—	—	15	2	—	III
	24	13	3	1	—	—	—	—	—	10	—	—	V
	25	9	—	—	—	—	—	—	—	6	—	—	V
14-17.vi.1974	26	5	—	—	—	4	—	—	—	8	3	—	V
	27	27	1	6	6	12	—	—	—	9	7	—	III
	28	16	—	3	—	1	—	—	—	6	2	—	III
	29	2	—	—	—	—	—	—	—	2	—	—	VI
	30	2	—	—	—	—	—	—	—	1	—	—	VI
	31	20	—	2	—	—	—	—	—	14	—	—	III
	32	2	—	1	—	—	—	—	—	2	—	—	III
	33	14	—	1	—	—	—	—	—	7	2	—	III
29.viii-	34	5	—	—	—	—	—	—	—	3	—	—	II
1.ix.1974	35	4	—	—	—	—	—	—	—	1	—	—	I
	36	1	—	—	—	—	—	—	—	1	—	—	I
	37	11	—	1	—	—	—	—	—	4	1	—	III
	38	8	—	1	1	1	—	—	—	3	—	—	V
	39	5	—	—	—	—	—	—	—	2	—	—	V
	40	5	—	—	—	—	—	—	—	2	—	—	III
	41	8	—	2	1	1	—	—	—	5	2	+	IV
27.x.1974	42	32	—	5	3	6	—	—	—	20	1	+	III
	43	2	—	2	1	—	—	—	—	1	—	+	I
	44	23	—	4	3	2	—	—	—	10	—	+	V

Evidence of female castes

In many colonies one adult female was conspicuously larger than the remainder. In some other nests the females were more graded in size but smaller females outnumbered the larger ones. The size/frequency distribution of twig inhabiting females is strongly skewed (Fig. 3) reflecting the relative abundance of the smaller size classes.

As explained by Houston (1976) females exhibit allometry where the metasoma is proportionately greater in large females than in small ones (cf. Figs 1A, 1B). This difference may be quantified by the 'metasomal index': the ratio of the distance between the lateral projections of the 6th metasomal tergum to the head width. The frequency distribution of metasomal indices (Fig. 4) is distinctly bimodal. Thus two
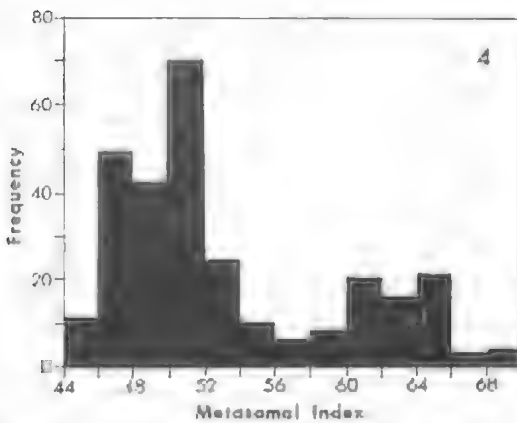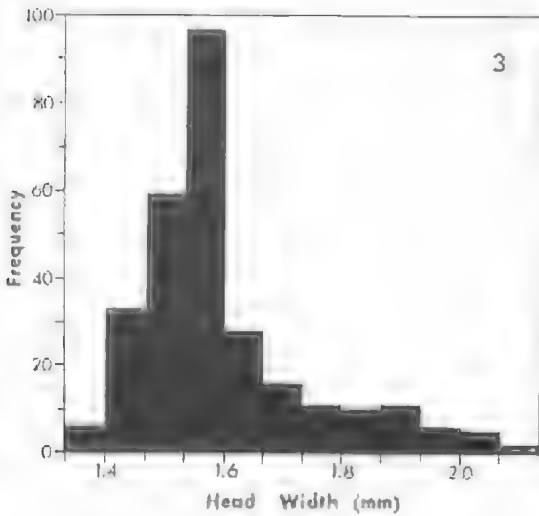
Figs 3, 4. *Exoneura tridentata*. Fig. 3.—Histogram showing strongly skewed frequency distribution of adult female head widths. Fig. 4.—Histogram showing bimodal frequency distribution of metasomal indices of adult females.

partially distinct morphs may be recognized, termed here 'minors' (metasomal index 57 or less) and 'majors' (metasomal index 58 or more).

Majors made up 25% of the total sample of females. In individual samples the percentages were: December, 27%; April, 23%; June, 31%; August, 23% and October, 22%.

The ovaries of most females taken from twigs were examined. Those rated 1 (tiny with stalk-like oviducts) were considered inactive while those rated 2–4 (small to large) were considered active. The relationship between ovarian activity and metasomal index (Fig. 5) suggests that ovarian activity is more frequent

amongst majors than minors. However, the differences between size classes might be due to differences in the proportion of newly emerged females in each sample. Very young females would tend to have undeveloped ovaries. Thus females were sorted into minors and majors for separate analysis. The relationship of ovarian activity to age (as judged by wing wear) in the two groups is shown in Figs 6, 7. Sample numbers for older (more worn) classes were low but approximately half the older minors had inactive ovaries (Fig. 6), whereas all older majors had active ovaries (Fig. 7). Thus there is a real and highly significant correlation between size (or metasomal index) and frequency of ovarian development.

Data obtained on the presence or absence of sperm in the spermathecae of adult females were similarly analysed (Figs 8–10) and there is a distinct correlation between size (or metasomal index) and the frequency of mating.

As Figures 5 and 8 both suggest that a fairly abrupt change in the tendency to possess developing ovaries and to mate occurs around a metasomal index of 56–58, majors and minors may be distinguished on physiological and behavioural grounds as well as morphology.

A further inference which could be drawn from Figs 6, 7, 9 and 10 is that females of higher metasomal index are generally longer-lived than those of lower index: sample numbers above the histograms show there were more older females (wing wear 2–4) amongst majors than amongst minors, despite the fact that there were only about one fifth as many young females (wing wear 0–1). It could also be inferred that majors suffer more rapid wing wear than minors.

Twenty-two females were collected at flowers and all were minors, the largest having a head width of 1.67 mm and a metasomal index of 56. The fact that no major was found outside a nest could perhaps be explained statistically (low frequency and small sample size). However, other observations suggest that majors are sedentary. The long ungainly bodies and relatively short wings of majors appear unsuited to prolonged flight and my observations suggest they may even be incapable of short flights. While opening nests in a closed tent I found that minors were quick to take flight when exposed and would fly to the windows. Majors never attempted to fly but persistently attempted to crawl under cover. When forced to fall, majors did attempt to fly but
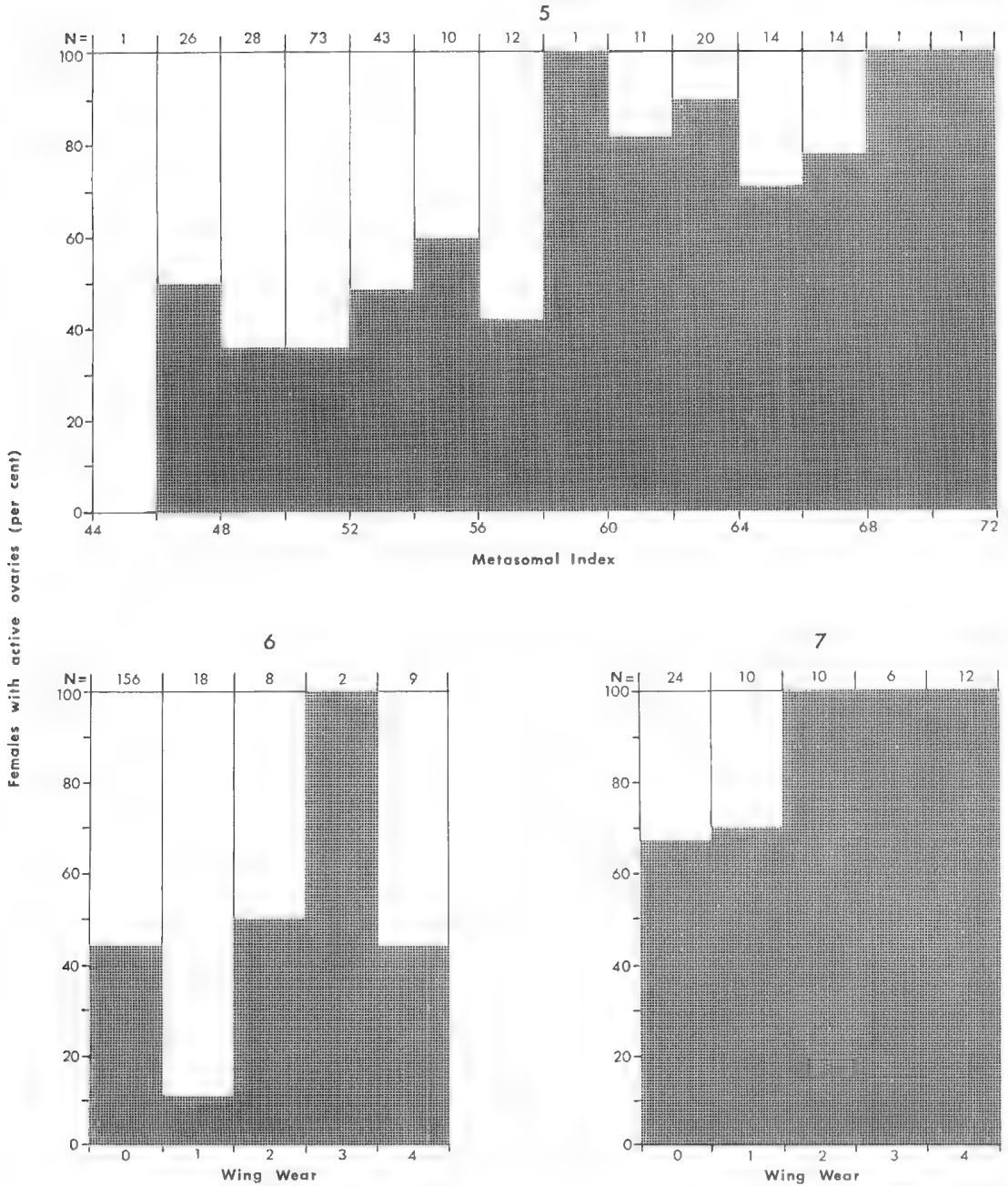
Figs 5-7. *Exoneura tridentata*. Histograms showing relationships between frequency of developed ovaries in females of nest populations and (Fig. 5) metasomal index, (Fig. 6) degree of wing wear in minors and (Fig. 7) degree of wing wear in majors. Sample numbers (N) for each class interval are recorded above each figure.

managed no more than steep descents to the floor. They were apparently unable to fly upwards as did minors under the same conditions.

The relatively high incidence of wing wear among majors seems inconsistent with seden-tary habits, for wear is usually attributed to damage during flight. Evidence that wear must occur other than in flight was found in majors whose wings were reduced well beyond the point where they could have sustained even the briefest flight (Fig. 11). Perhaps wear
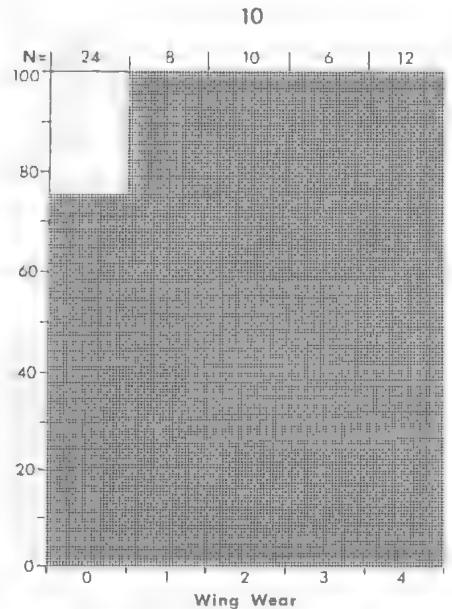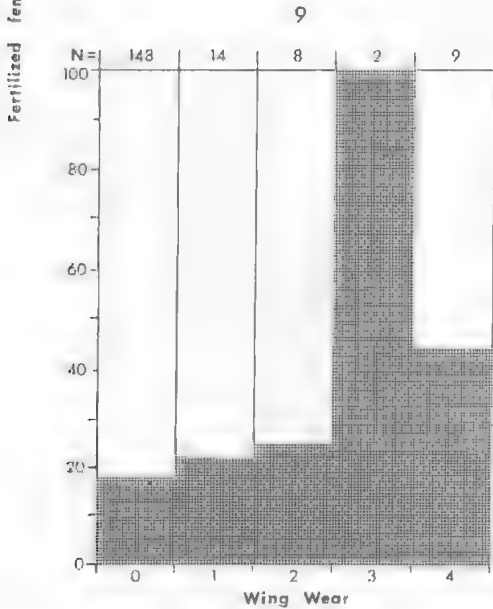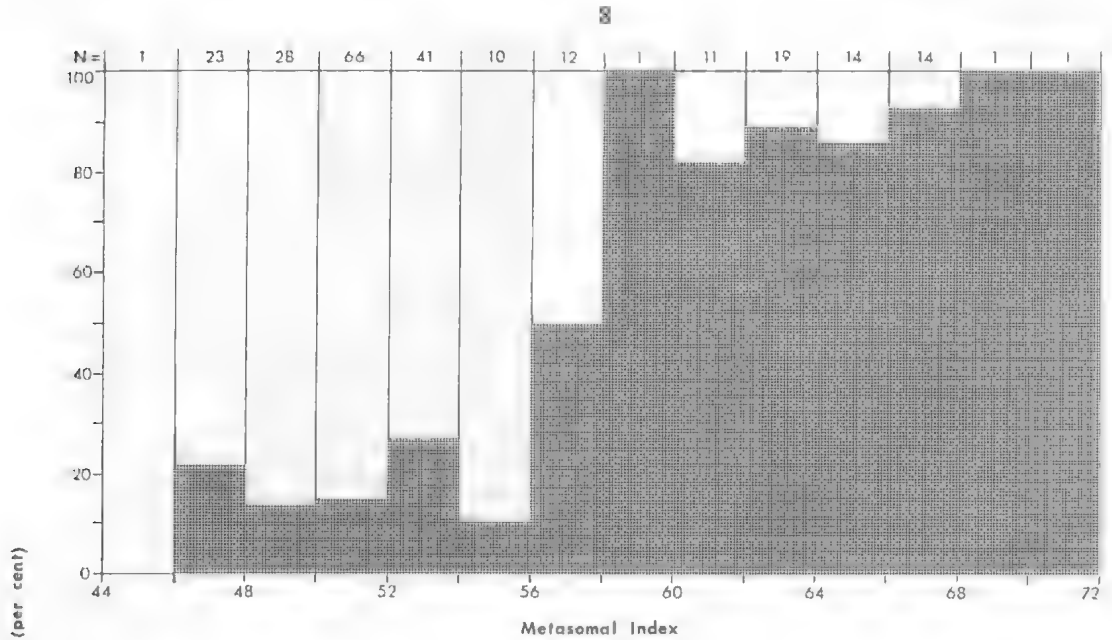
Figs 8-10. *Exoneura tridentata*. Histograms showing relationships between frequency of mated females in nest populations and (Fig. 8) metasomal index, (Fig. 9) degree of wing wear in minors and (Fig. 10) degree of wing wear in majors. Sample numbers (N) for each class interval are recorded above each figure.

results from females scrambling one over the other, somersaulting within narrow tunnels or defending their nests against enemies.

Evidence of the existence of a worker caste was provided by 5 pollen-carrying minors col-

lected at flowers, all of which were unworn and had tiny ovaries. All but one was unmated.

To summarise, the available evidence points to the existence of two female morphs amongst nest populations. There are relatively few inter-
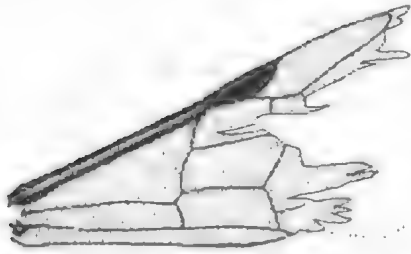
Fig. 11. Tattered right forewing of a large major of *Exoneura tridentata* (dotted line indicates missing portion).

mediates and the morphs differ in their tendency to mate and produce eggs. Majors, characterised by a head width of 1.67 mm and metasomal indices less than 58, function (at least in some cases) as infertile workers, although up to half of them may mate and/or produce eggs.

Colony development

Direct evidence of how new colonies are founded was sought by placing 200 artificial nest sites in the study area in June. These consisted of slender pieces of wood drilled at one or both ends and wired horizontally to the lower branches of *Heterodendrum* shrubs. Unfortunately, when collected six weeks later, none was utilised by the bees although many had been occupied by spiders and ants. Consequently, only indirect evidence of the manner of nest establishment is available.

New nests are probably established by solitary fertile minors. Four nests with single females and immatures were found (nos. 30, 35, 36, 43). All females were mated, had small ovaries and entire to moderately worn wing margins. Two were minors but the others were majors, a fact which appears to conflict with earlier evidence of sedentary habits in majors. However, the tunnels containing the majors were old and stained with pollen, indicating previous use as nests. The only immatures present were a few eggs. Consequently, the two majors may have remained from earlier broods now dispersed and larvae hatching from their eggs would have perished of starvation. The female of nest 43, a minor, must have entered a new tunnel, laid eggs and foraged for food: spots of pollen were present on the walls and one larva had reached the 3rd instar.

If new nests are established by solitary females, and if these females survive until emergence of their adult progeny, we should expect to find nests containing one very worn

female (founder) and one or more unworn adults (progeny). In fact, 22 such nests were collected. Seven of the presumed founders were minors but 15 were majors, once again apparently conflicting with the concept of flightless majors. All of the presumed founders were fertilized and all but two had medium to large ovaries. The exceptions had tiny, apparently depleted ovaries. The presumed daughters ranged from callows to slightly worn, fully matured individuals. Most were unmated and possessed tiny ovaries but a few had medium to large ovaries and/or sperm in the spermatheca.

All of the above 22 nests contained eggs and the ovaries of several presumed founders contained ova of egg size. Thus, it seems that mothers continue to lay in the presence of their adult offspring.

One nest (no. 23) contained 14 adult females with little or no wing wear (some were callows) and the dry carcase of a very worn minor, presumably the colony founder. Another eight nests contained groups of 2–10 unworn or little worn females and early immatures. Evidently these nests contained groups of sisters remaining after their mothers had perished.

Groups of young sisters usually included one or more majors and several minors. Majors (except callows) were usually mated and had medium to large ovaries but minors were more variable. Dissections showed that two or more majors and sometimes minors in a group may carry egg-sized ova and probably oviposit together in their natal nests. Since no female examined had more than four ova near egg size (few had more than two), large clusters of eggs most probably arise only where two or more females are laying together. For example, nest 44 which contained 23 eggs had three fertile majors with medium to large ovaries.

Undoubtedly, some females in groups of young sisters disperse to establish new nests but there is evidence that others remain together in small colonies: seven nests each contained two or three very worn females along with newly emerged adults. In each case, one female was a major, fertilised and with enlarged ovaries, the other one or two being unmated and (except one) with undeveloped ovaries. In these colonies, the majors must have functioned as egg layers, the minors as workers. The newly emerged adults in such nests had presumably been reared by the worn

Category	Frequency	% of total
I. A solitary female	4	9
II. One very worn minor and one or more unworn or slightly worn females	7	16
III. One very worn major and one or more unworn or slightly worn females	13	14
IV. Two or more very worn females and one or more unworn or slightly worn females	7	16
V. Two to several unworn or slightly worn females only	10	23
VI. Other	1	2

individuals. In most cases, the eggs in each of the nests could only have been laid by the worn majors, but in a few nests one or two of the young females had enlarged ovaries and may have oviposited.

If the belief that majors are sedentary and cannot forage for pollen and nectar is correct, the 15 colonies each containing a single worn major with one or more unworn females appear anomalous. However, the young females (plus males and immatures) may have been reared by worker-like females which died when the young began reaching adulthood and which were survived by their longer-lived major sisters. Brood care may have become the responsibility of the newly emerged females.

In 14 groups of newly emerged sisters there were up to 5 (mean 2.5) majors per group. If majors cannot disperse by flight, one would expect to find groups of old worn majors in at least some nests. However, amongst the nests examined, not one contained more than a single worn major. Either the concept of sedentary majors is incorrect or there is some process by which all but one major is eventually eliminated from groups of sisters. If this process took the form of physical contests, it could explain the existence of female allometry. As explained by Houston (1976), the metasoma of relatively large females is more heavily chitinised, more muscular and more scoop-like at the apex than that of smaller females. Larger females thus appear to be better equipped for posteriorly directed combat than smaller ones (these modifications should also be of benefit in nest defence: if majors remain in nests while minors forage, they would

bear a greater share of the burden of defence of the colony against intruding ants and other depredators and it is the usual mode of defence of allodapines to block their nest entrances with the dorsoapical surface of the metasoma). Obviously, direct observation of living colonies is required to see if majors really do engage in physical elimination contests.

The categories to which nests were assigned according to their female contents are listed in Table 2 with indications of relative frequency. In Table 1 each nest is assigned to one of these categories as indicated by the numbers in the last column.

Finally, it remains to mention 14 female-inhabited twigs which contained no immatures. Interpretation is difficult. Seven twigs contained solitary minors which were relatively unworn, mated, had small to large ovaries and which may have been about to found new colonies. The remaining seven twigs contained 2–6 adult females. Two each contained a pair of very worn individuals that could have functioned as egg-layer and worker and may have survived after departure of their offspring. The other five twigs contained unworn females (three included majors) which may have been reared in the twigs, for the walls were dark-stained and showed traces of pollen.

While many aspects remain uncertain, the course of colony development envisaged may be summarised as follows. New nest sites are sought out and occupied by relatively young mated minors with enlarging ovaries. Each female begins to produce eggs intermittently and when larvae emerge she forages and feeds them progressively. She continues to lay even when most of her offspring have reached adulthood. Amongst the brood are males, and minor and major females. For a time, mother and adult offspring may cohabit, some or all of the daughters mating and eventually contributing eggs to the colony. Some minors fail to mate and to develop enlarged ovaries and function as workers tending the combined brood. Eventually the mother dies and the males and most females disperse to other twigs. However, one major and one or more minors remain, functioning as queen and workers, respectively. They do not perish until second generation adults emerge and assume care of the immatures. Once again, the young adults may contribute eggs to the colony before most disperse leaving one major and one or two worker-like minors to tend and protect the immatures.

In all probability, the allometry of adult females is trophically controlled as in other insects, those individuals receiving relatively larger amounts of food as larvae developing into relatively larger adults with certain features exaggerated. This being so, one might expect that generations raised during periods of food abundance might contain a relatively higher proportion of major females than generations raised during periods of food scarcity. However, the facts do not support this expectation: pollen accumulation in December and October nests was taken as a sign of food abundance preceding their collection but the highest percentage of majors occurred in the June sample, the nests of which (and the preceding April sample) lacked pollen stores. Therefore, some social mechanism must control the minor/major ratio.

Exoneura eremophila Houston

Nests of this tiny arid-land bee were collected and examined in haste during the course of other work in southwestern Queensland and northeastern South Australia and the account to follow is based on my rather meagre field notes. Dissection of females was not possible so that data on mating and ovary condition are not available.

A total of 45 nests and shelters of this species were found in dead dry hollowed stems of herbaceous plants. Most occupied stems of *Crotalaria cunninghamii* R. Br. (Fabaceae) and *Myriocephalus stuartii* (FvM.) (Compositae), while a few were in unidentified stems. All nests were within 30 cm of the ground.

In most cases, the bees had burrowed into the soft pith exposed at the broken ends of upright or oblique stems. However, some individuals had utilised naturally hollowed stems, and barricades of pith particles formed the bottoms of the occupied sections of tunnel. Hollows containing immatures ranged in depth from 25–190 mm (mean = 81.5, N = 40). Entrances were circular and of slightly smaller diameter than the tunnels lower down (e.g. 2.0 mm compared to 2.5 mm). None possessed a constructed "collar" of the kind so typical of nests of *Exoneura* s. str. and *Braunsapis* but two entrances were narrowed by small crescents of compacted pith particles.

Immatures

The disposition of immatures in the tunnels was generally as described for *E. tridentata* and the numbers found in each nest are listed in

TABLE 3

Exoneura eremophila. *Numbers of adults and immatures taken from stems with collection data and tunnel lengths.*

Collection data	Stem no.	Tunnel length mm	Eggs	Lar- vae	Pupae	Adults ♀	Adults ♂
LOT 1	1	74	3	—	—	1	—
13 km NE	2	190	6	—	—	—	—
of Windorah,	3	118	4	4	—	1	—
Qld,	4	97	1	6	—	1	—
18.viii.1968,	5	62	4	—	—	1	—
Collected at	6	100	6	—	—	1	—
midday	7	145	5	7	—	—	—
LOT 2	8	103	—	—	—	1	—
Same Loc.	9	90	7	—	—	1	1
19.viii.1968,	10	67	1	—	—	1	—
Collected in	11	30	4	1	—	1	—
cool early	12	8+2	—	—	—	1	—
morning	13	44	3	—	—	1	—
LOT 3	14	78	1	1	—	1	—
5 km W of	15	25	—	1	1	—	2
Windorah,	16	67	4	5	—	—	—
Qld,	17	43	—	13	—	—	2
17.iv.1969,	18	78	—	2	—	—	—
Collected in	19	35	—	6	—	—	—
mid-morning	20	53	2	10	—	—	1
	21	84	—	10	1	3	1
	22	61	—	—	—	1	—
LOT 4	23	—	—	—	—	1	—
New	24	135	2	17	2	5	1
Kalamurina	25	116	1	5	4	3	5
H.S., S.	26	96	3	—	—	1	—
Aust.,	27	68	6	1	—	1	—
10.iii.1972,	28	61	5	6	1	1	5
Collected	29	53	8	—	—	1	—
in cool early	30	95	11	6	8	3	—
morning	31	80	20	1	2	3	—
	32	71	4	—	—	1	—
	33	57	6	—	—	1	—
	34	113	4	14	4	4	2
	35	60	5	4	1	1	2
	36	101	12	9	3	3	2
	37	44	5	4	—	1	4
	38	120	12	9	6	3	2
	39	69	7	7	6	1	2
	40	162	13	19	9	7	4
	41	35	—	—	—	—	1
	42	66	8	—	—	1	1
	43	69	9	3	—	1	—
	44	56	6	3	—	1	4
	45	85	8	3	—	1	1

Table 3. The immature stages are described by Houston (1976).

Food sources

E. eremophila is a polylectic species and has been observed collecting pollen from *Calandrinia*, *Eremophila*, *Goodenia*, *Hakea*, *Helichrysum*, *Myriocephalus*, *Scaevola* and *Wahlenbergia*.

Colony composition and development

Nest collection data and the number of occupants of each are provided in Table 3. Nests were collected in four lots, the 1st and 3rd when conditions suited adult flight and some occupants were out. However, lots 2 and 4 were collected in cool early mornings so that all adult occupants should have been present.

The August sample (lots 1 and 2) was comprised chiefly of single female nests with eggs. Four nests also contained larvae of various ages, some of them defaecating. Two stems (nos 8, 12) contained females but no immatures and were probably under excavation. The highest number of progeny was 12 in nest 7.

Most nests in the April sample (lot 3) lacked adult females which must have been foraging at the time of collection. As the highest number of progeny in any nest was 13 (nest 17), it is probable that all nests had been founded by single females. Three females occupied nest 21 but, as a dark female pupa was also present, any or all of them may have been newly emerged daughters of the founder. Eight nests contained larvae but only 3 had eggs as well, suggesting that egg production ceases after a short period of laying. The burrow of stem 22 was obviously under excavation when found.

The origin of the males in the April nests remains uncertain.

The 23 nests in the March sample (lot 4) were generally more populous than the others and their occupants more diversified. Fourteen contained single adult females but eight each contained 3–7 females. In these nests, the presence of pupae suggests that at least some females may have been newly emerged. However, the presence of relatively large numbers of immatures in some nests with several females and age gaps in some series of immatures suggests that 2 or more females had contributed to the brood.

The nests of lot 4 may be considered in three groups. The ten nests of the first group (nos 26, 27, 29, 32, 33, 37, 42–45) were much like those of lots 1–3, each having a single adult female (and males in some) with up to 12 immatures which were all either eggs or larvae. Three nests of the second group (nos 28, 35, 39) also had a single adult female each (and males) with immatures. However, the immatures of each nest included eggs, larvae and pupae and totalled 20 in nest 39. All stadia were represented in two nests, suggesting continuous and prolonged egg production but in

nest 35 an age gap existed and all larvae were mature. In the third group, eight nests (nos 24, 25, 30, 31, 34, 36, 38, 40) each contained from 3–7 adult females (and males in some) with eggs, larvae (or pre-pupae) and pupae. In all but one nest, immatures totalled 21–41 and must surely have been derived from more than one mother (note especially the 20 eggs of nest 31). A conspicuous age gap (the absence of 3–4 consecutive larval stadia) was noted in three nests and a moderate gap (two consecutive larval stadia absent) in two others. All stadia were present in the remaining three nests.

Without data on degree of wing wear, ovary condition and spermathecal content it is difficult to interpret the relationships of females in the nests found. However, from the observations made one could speculate that colony development proceeds along the following lines: new colonies in some cases may be founded by solitary females each laying up to 12 eggs then ceasing while they rear the emergent larvae. The immatures of such a nest would not span all stages (as in lots 1–3). In other cases, founding females may oviposit intermittently over long periods, sometimes with temporary halts, producing series of immatures spanning all or most stages. Young adult females emerging at intervals in these nests may oviposit, too, so maintaining a more or less continuous series of immatures. Whether such colonies are communal with each sister partaking of foraging and brood care or semisocial with division of labour can only be revealed by further studies.

Male behaviour

Many dozens of males of this species were observed in flight near nests on Kalamurina Station, S. Aust., during midmorning of 10.iii.1972. Each bee flew erratically about 30 cm above ground amongst the many dead *Myriocephalus* stems and frequently hovered about a nest entrance before moving on. *Wahlenbergia* flowers growing in profusion nearby were visited only occasionally by the males.

Presumably these males were awaiting the emergence of virgin females from nests, but no encounters between the two sexes were observed.

Exoneura setosa Houston

Observations of the nesting biology of this species were made during 1965 in coastal dunes at North Glenelg and West Beach, S. Aust.

Nests were collected primarily as a source of live stages for morphological studies and many data now desired were not recorded. However, the available information provides a reasonably clear picture of the life cycle of the species.

The dates of collection of inhabited stems and the numbers of inhabitants are provided in Table 4. Stems 12–24 were collected in cold weather unsuitable for adult flight. However, the remainder were taken at times when some adults may have been absent on foraging trips.

Nests

All colonies and sheltering adults were found in dead dry pithy stems of herbaceous plants and grasses. Most nests were in stems of *Euphorbia*, *Geranium* and *Foeniculum*. Nest burrows had apparently been excavated by the females or, in the case of naturally hollowed stems, had been refined by the removal of irregularities and debris. The bees entered the stems at broken ends and burrowed down their lengths. The burrows were 1.5–2.0 mm in diameter and 35–95 mm deep. Their entrances were circular and showed no traces of any special structures. Occupied stems were variously inclined from vertical to almost horizontal. All were less than 1 m above ground and most below 30 cm.

Immatures

The disposition of the immatures in nest burrows was generally as described for *E. tridentata*. The immature stages were described by Houston (1976).

Food sources

This species, like the preceding two, is polylectic. Pollen taken from nests was derived from *Cakile*, *Geranium*, *Reichardia* and *Wahlenbergia*.

Colony composition and development

As will be seen from Table 4, seven nests (nos 1, 2, 4, 6, 7, 9, 11) each contained a single adult female with 2–9 immatures. Three other nests (nos 3, 5, 8) each contained 2–4 adult females with 3–6 immatures. However, as each of the latter nests also contained pupae and two contained adult males, probably all but one female in each were newly emerged progeny. Assuming this to be so, the total progeny in each nest would have been 9, 7 and 9 respectively. Thus a single female may produce up to 9 offspring.

Females must produce a batch of eggs within a relatively short period and cease laying as the first larvae eclose for, although immatures

TABLE 4

Exoneura setosa. *Numbers of adults and immatures taken from stems at West Beach, Adelaide, S. Aust.*

Date of collection	Stem no.	Eggs	Larvae	Pre-pupae	Pupae	Adults ♀	Adults ♂
5.ii.1965	1	—	6	2	1	1	—
11.ii.1965	2	8	1	—	—	1	—
16.ii.1965	3	—	—	1	3	4	2
	4	—	4	1	2	1	1
	5	—	4	1	1	2	—
	6	—	1	—	1	1	—
	7	—	3	1	—	1	—
10.iii.1965	8	—	—	—	3	3	4
	9	—	2	—	—	1	—
	10	—	—	—	—	2	2
	11	—	1	1	—	1	—
5.iv.1965	12	—	—	—	—	4	—
	13	—	2	—	—	9	5
	14	—	—	—	—	7	5
	15	—	—	—	—	2	1
	16	—	—	—	—	1	1
	17	—	—	—	1	1	—
12.vii.1965	18	—	—	—	—	1	—
	19	—	—	—	—	5	8
	20	—	1	—	—	10	5
	21	—	—	—	—	1	5
	22	—	—	—	—	4	3
18.viii.1965	23	—	—	—	—	1	—
14.ix.1965	24	—	—	—	—	4	—
31.x.1965	25	7	—	—	—	2	1
	26	—	—	—	—	—	1
	27	6	—	—	—	—	1

within individual nests were graded in age, no nest had the full range of immatures.

No nest provides definite evidence of brood rearing by more than a single female. Although nest 26 contained two adult females, a male and seven eggs, there was nothing to suggest that these adults were more than siblings remaining in their natal nest; one female may have been founding a new colony and the other adults may soon have dispersed.

While brood rearing was evident in stems collected in February, March and October, those collected in April and July appeared to contain overwintering groups of adults of both sexes and a few residual immatures (the larvae of nest 13 were shrivelled). All adults from these overwintering groups had unworn wings and fresh body pubescence. Seven females (from nests 16, 18, 19) were dissected and proved to have empty spermathecae and slender undeveloped ovaries.

Most overwintering adults were taken from old nest stems but some occupied rough

natural hollows. Because four overwintering groups (nests 13, 14, 19, 20) each contained 12–15 individuals and no brood nest contained more than nine progeny, one would doubt that they represent family groups alone. Evidence of gregariousness amongst unrelated overwintering adults was obtained using artificial nests. These consisted of *Foeniculum* stems into which glass tubes of 2 mm bore had been inserted and split stems where a clear celluloid strip formed one side of a burrow. Fifty such nests were placed in the study area but only two were utilized as shelters by solitary females. However, in August, three groups of adults found in natural nests were transferred to artificial observation nests. Two groups (10 ♀, 5♂ and 1♀, 4♂) gradually dispersed during September. However, the third group (4, ♀, 3♂) had increased by two individuals after several days and by four more after two weeks. The 13 adults remained together through September and yellow pollen stains within the tunnel entrance testified to foraging activities by at least one member. By late November most individuals had gone but two live and two dead bees remained.

Five females found sheltering in stems 23 and 24 in August and September were dissected. All had mated but their ovaries were small and no ova were near egg size.

A total of 105 adults were collected from stems and comprised 63 females and 42 males, suggesting a sex ratio of approximately 3:2.

To summarise, nests of *E. setosa* appear to be founded and maintained by solitary females which may each produce up to nine offspring. Adults of both sexes and occasional immatures overwinter in old nests or congregate in naturally hollow stems in groups of up to 15 individuals. Females overwinter as virgins but mate during the spring and eventually establish new nests.

Discussion

Details of the nesting biology of *Exoneura lawsoni* have been provided by Michener (1964). At the time of his study, *E. setosa* had not been recognised as a separate species and some lowland nest samples may have belonged to this species. However, Professor Michener advises me that the bulk of his material, if not all, was *E. lawsoni*.

All *Exoneurella* are typical of allodapines in rearing their larvae in open tunnels in plant stems. However, their nests are characterised by the consistent absence of constructed entrance collars. Three species (*eremophila*, *lawsoni* and *setosa*) excavate nest burrows in dead pithy stems of herbs and normally the entrances are narrower than the remainder of the tunnels. The tiny body size of these species is perhaps an adaptation to life in slender stems. *E. tridentata*, by contrast, utilises ready-made burrows in dead woody twigs of standing trees and shrubs. Both these methods are employed by other *Exoneura*: most members of the subgenus *Exoneura* which have been studied burrow in pithy stems (Michener 1965) but some species will occupy trap nests; members of the subgenus *Brevineura* habitually utilize existing woody hollows (personal observations).

Like *Exoneura* s. str., *Exoneurella* lay their eggs freely in the burrows rather than attaching them to the walls with adhesive secretion as do *Brevineura*. The duration of oviposition varies amongst the species, being restricted to the early phase of colony establishment in *setosa* but occurring continuously in *lawsoni* and *tridentata*. In *eremophila* oviposition may occur continuously or be interrupted.

Middle larvae and older immatures are moved about by the bees and arranged linearly in approximate order of ages as in most other allodapines. Feeding is progressive and, in keeping with the year-round activity of adults, all species are polylectic.

Exoneurella appear to be relatively free from pathogens, the only one known being an encyrtid which was reared from summer pupae of *tridentata*.

Brood rearing in *lawsoni* and *setosa* ceases during winter when the populations consist largely of adult males and females (unmated). Mating and nest establishment resume in middle or late spring. In *tridentata*, which occupies a rather more temperate habitat than the preceding two species, brood rearing occurs year round (possibly with brief halts during flowerless periods). The situation in *eremophila* is unknown.

The four species exhibit pronounced differences in their degree of sociality. Both *lawsoni* and *setosa* appear to be almost totally subsocial, each nest being founded and maintained by a single female. At most, a female may care for her immature siblings after demise of her mother. *E. eremophila*, too, is basically subsocial but evidence was found that two or more females may occasionally oviposit and rear brood together in a common burrow. By contrast, *tridentata* develops semisocial colonies

and has morphologically distinct castes. While subsocial colonies may be founded by solitary females, they later become semisocial with two or three sisters functioning as queen and workers. The social structure of *tridentata* is generally similar to that of members of the subgenus *Exoneura* (especially *E. variabilis*) studied by Michener (1965) and various other allodapines (Michener 1974). However, *tridentata* is outstanding amongst its relatives in respect of caste differences. In the majority of social allodapines the castes are indistinguishable morphologically, differing only in the functions they perform and in the states of their ovaries and spermathecae. Queens of *Exoneura variabilis* average larger than their worker sisters. In *tridentata* the size differences are accentuated and accompanied by allometry (Houston 1976). In addition, queens of *tridentata* appear to be flightless and are confined to nests.

The biological characteristics of the four species of *Exoneurella* reflect their relationships as determined on morphological grounds; *tridentata* stands out from the other three and shows some similarities to *Exoneura* s. str.

Michener (1964) noted a seasonal variation in sex ratio of *E. lawsoni* which he felt was inappropriate to a strictly subsocial species and possibly a residual characteristic from a more social ancestor. The discovery of *tridentata* and its social habits supports this idea.

The loss of semisociality in *Exoneurella* may be associated with the use of rapidly perishable pithy stems of annual or ephemeral herbs. Since such stems may only be suitable for occupation for several months, groups of siblings would be forced to disperse to new sites far more often than if living in durable woody twigs. Thus the opportunities for formation of semisocial groups in old nests would be diminished and strictly subsocial behaviour would be favoured.

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TRANSACTIONS OF THE

ROYAL SOCIETY

OF SOUTH AUSTRALIA

INCORPORATED

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DICROCOELIID TREMATODES FROM AUSTRALIAN HOSTS

BY L. MADELINE ANGEL AND J. C. PEARSON

Summary

Eleven species of dicrocoeliids belonging to five genera are described; nine are new. Brachylecithum comprises seven species (six of which are named) separately by size, width/length ratio, acetabulum position and egg size. Skrjabinosomum is represented by three species, two of which are named. Lutztrema and Pancreatrema have one new species each. Proacetabulorchis is recorded from Australia.

DICROCOELIID TREMATODES FROM AUSTRALIAN HOSTS

by L. Madeline Angel* and J. C. Pearson†

Summary

Angel, L. Madeline and Pearson, J. C. (1977) Dicrocoeliid trematodes from Australian hosts. Trans. R. Soc. S. Aust. **101**(5), 115-132, 31 August, 1977.

Eleven species of dicrocoeliids belonging to five genera are described; nine are new. *Brachylecithum* comprises seven species (six of which are named) separated by size, width/length ratio, acetabulum position and egg size. *Skrjabinosomum* is represented by three species, two of which are named. *Lutztrema* and *Pancreatrema* have one new species each. *Proacetabulorchis dogieli* is recorded from Australia.

Introduction

Sandars (1958) described *Platynosomum australiense* (syn. *Zonorchis australiensis*) from Australian marsupials, and listed seven other dicrocoeliids recorded from Australian reptile and bird hosts. Of these, *Paradistomum crucifer* (Nicoll), originally described from *Delma fraseri*, has since been recorded from four other lizards (Angel & Mawson 1968). The only other dicrocoeliids recorded from Australia are *Platynotrema biliosum* Nicoll from *Burhinus magnirostris* (syn. *B. grallarius*) and *Threskiornis molucca* (syn. *Ibis molucca*), *P. jecoris* Nicoll from *B. magnirostris*, and *Athesmia* sp from *Rattus norvegicus* (Munday 1966).

We now add five new species of *Brachylecithum*, one unnamed *Brachylecithum* species, two new species and an unnamed species of *Skrjabinosomum*, a new species each of *Lutztrema* and *Pancreatrema* and *Proacetabulorchis dogieli* Belopolskaja & Bychovskaja-Pavlovskaja.

All of the hosts of trematodes recorded in this paper are native to Australia; only *Petrochelidon nigricans* is migratory, and *Ardea novaehollandiae*, though it has no regular migration, sometimes occurs outside Australia.

The food of the definitive hosts of *Brachylecithum* species is given as indications of the possible intermediate hosts. Information on food was obtained from Cleland (1910), Cleland, Maiden, Froggatt, Ferguson & Musson (1918), Leach (1958), and from dissection records of the Department of Zoology, University of Adelaide. Where the life cycles of dicrocoeliids are known, the first intermediate host is a terrestrial gastropod, and the second, an insect, arachnid or terrestrial isopod.

All drawings were done with the aid of a camera lucida. Where measurements are given, the mean is in brackets after the range.

Holotypes and paratypes are deposited in the South Australian Museum (SAM). Type material and slides of other specimens mentioned are deposited in the former University of Adelaide Helminthological Collection (now located in the South Australian Museum) and in the second author's collection. Additional measurements from the type and other hosts are available from the authors on request. Measurements of suckers are means.

LIST OF PARASITES, ARRANGED WITH THEIR HOSTS

Mammals.
> *Rattus fuscipes* (Waterhouse). *Brachylecithum insulare* n.sp. *Hydromys chrysogaster* Geoffroy. *Brachylecithum hydromyos* n.sp.

Birds.
> Ciconiiformes: Ardeidae.
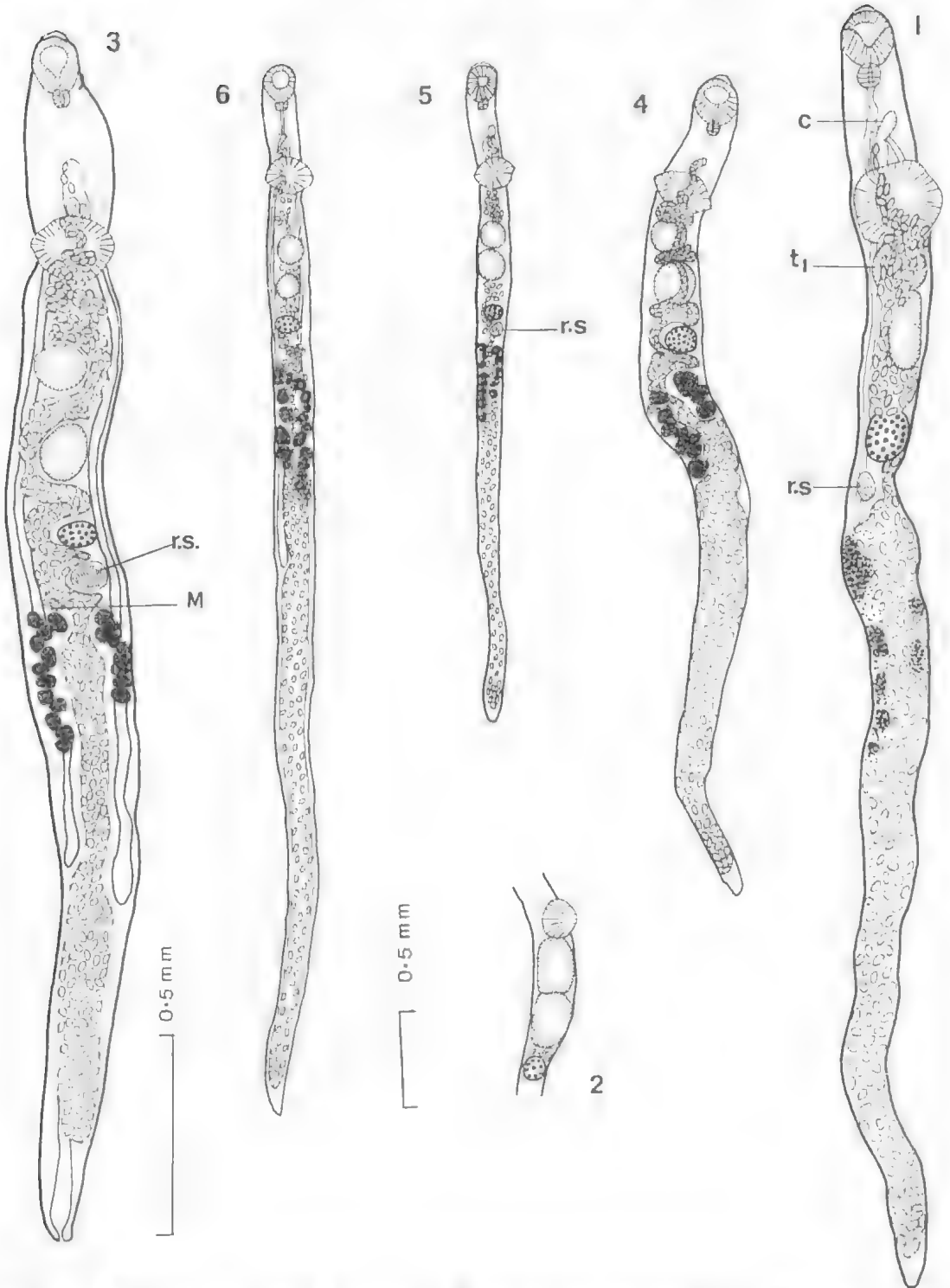> > *Ardea novaehollandiae* Latham. *Proacetabulorchis dogieli* Belopolskaja & Bychovskaja-Pavlovskaja.
> Gruiformes: Turnicidae.
> > *Turnix castanota* (Gould). *Skrjabinosomum mawsoni* n.sp.

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Caprimulgiformes: Podargidae.
  Podargus strigoides (Latham). *Brachyleci-thum podargi* n.sp.
Coraciiformes: Alcedinidae.
  Dacelo novaeguineae (Hermann). *Brachy-lecithum dacelonis* n.sp.
Passeriformes: Hirundinidae.
  Petrochelidon nigricans (Vieillot). *Brachy-lecithum parvum* (Johnston).
Passeriformes: Timaliidae.
  Pomatostomus superciliosus (Vigors & Horsfield). *Skrjabinosomum pomatostomi* n.sp.
Passeriformes: Muscicapidae.
  Microeca leucophaea (Latham). *Skrjabinosomum* sp.
Passeriformes: Meliphagidae.
  Meliphaga ornata (Gould). *Pancreatrema meliphagae* n.sp. *Manorina flavigula* (Gould). *Skrjabinosomum mawsoni* n.sp.
Passeriformes: Cracticidae.
  Cracticus torquatus (Latham). *Brachyleci-thum latius* n.sp. *Gymnorhina hypoleuca* (Gould). *Brachylecithum latius* n.sp., *Brachylecithum* sp.
Passeriformes: Ptilonorhynchidae.
  Ailuroedus crassirostris (Paykull). *Lutz-trema ailuroedi* n.sp.
Passeriformes: Corvidae.
  Corvus coronoides Vigors & Horsfield. *Brachylecithum latius* n.sp.
  Corvus mellori Mathews. *Brachylecithum parvum* (Johnston).
Reptiles.
  Amphibolurus fionni Proctor. *Brachyleci-thum insulare* n.sp.

BRACHYLECITHUM Shtrom

Denton (1945) stated that *Brachylecithum* spp. were very delicate worms that showed considerable morphological variation as a result of host, habitat, age and hereditary factors [sic] and because of different methods of handling. He also noted that essential taxonomic characters were lacking for many species which were inadequately described, or described from poor material. The genus then contained 35 species and subspecies. The number is now over eighty and the observations of Denton still apply. It seems certain that when a thorough revision is made many species will be found to be synonymous. In the meantime it is not possible to compare adequately the Australian species with all previously recorded species. We have compared our species with any which occur in birds of the same or closely related genera. In other

parts of the world. Since only three species have been recorded previously from mammals, we have compared *B. insulare* n.sp. and *B. hydromyos* n.sp. with all three.

Brachylecithum and *Lyperosomum* are very similar genera which have caused taxonomists confusion. From the diagnoses of Skrjabin & Evranova (1953) after Shtrom (1940) and of Yamaguti (1971), it seems that the only consistent character used to separate them is the vitellaria, consisting of a small number of large follicles, occupying a small part of the body length in *Brachylecithum*, and in *Lyperosomum* of numerous small follicles occupying a greater distance in relation to body length.

Yamaguti separated *Brachylecithum* into two subgenera, *Brachylecithum* and *Brachyleci-tholdes* on the presence or absence of the uterus between the testes and between the testes and ovary. This is a character which varies in specimens from one host (compare Figs 1 and 2), so that we have not used it. Further, the size and even the shape of the testes and, to a lesser extent, of the ovary, vary from one specimen to another. Both characters may depend on the maturity of the trematode or on its state of extension when fixed.

Specific characters used are size, width/length ratio, position of acetabulum, presence or absence of papillae on surface of body, and size of eggs. In view of the variability of acetabular shape we have not considered it advisable to compare sucker ratios.

Key to Australian species of *Brachylecithum*

1. Width/length ratio of body greater than 1/9
   .... *B. latius*
   Width/length ratio of body less than 1/9 ... 2
2. Width/length ratio of body between 1/10 and 1/23 3
   Width/length ratio of body between 1/24 and 1/30 5
3. Acetabulum between anterior 1/4–1/5 of body; without papillae on body surface; eggs 36 x 20 μm .... *B. hydromyos*
   Acetabulum within anterior 1/5 of body 4
4. Acetabulum between anterior 1/5–1/6 of body; without papillae on body surface; eggs 43 x 22 μm .... *B. insulare*
   Acetabulum between anterior 1/6–1/7 of body; with papillae on body surface; eggs 39 x 23 μm
   .... *B. parvum*
5. Acetabulum between anterior 1/4–1/6 of body; with papillae on body surface; eggs 39 x 24 μm
   .... *B. dacelonis*
   Acetabulum between anterior 1/7–1/10 of body; without papillae on body surface; eggs 47 x 24 μm .... *B. podargi*

Characters from the type host in all cases.

Figs 1–6. 1. *Brachylecithum insulare* Holotype; 2. *B. insulare* Paratype SAM V77; arrangement of testes and ovary in specimen with comparatively few eggs; 3. *B. hydromyos* Holotype; 4. *B. parvum* from *Petrochelidon nigricans*; 5. *B. dacelonis* Holotype; 6. *B. podargi* Holotype (Figs 1 and 3 to same scale; Figs 2, 4-6 to same scale). ABBREVIATIONS: a, acetabulum; c, cirrus; e.b, excretory bladder; i, intestinal caecum; M. Mehlis' gland; o, ovary; oo, ootype; r.s, receptaculum seminis; t, testis; t1, t2, anterior, posterior testis.

The eggs measured in this study have been the largest mature specimens from balsam mounts. For eggs of *Brachylecithum parvum* (Johnston), Johnston's measurements are used, as the eggs in his slides are now unsuitable for accurate measurement.

Generic diagnosis: *Dicrocoeliidae, Dicrocoeliinae.* Body slender, filiform or lanceolate, flat or cylindrical; maximum width/length ratio not less than 1:45; with pre-oral lobe. Body surface with or without spines or papillae. Suckers usually subequal, not far apart. Caeca not reaching to hind end of body. Testes tandem or sometimes diagonal, contiguous or separate, immediately or a little posterior to acetabulum, occasionally underlying latter. Cirrus pouch pre-acetabular. Ovary round or oval, slightly behind testes. Vitellaria post-ovarian, commencing near ovary, limited in extent, consisting of small number of large follicles.

Parasitic in liver, gall bladder, pancreas or intestine of birds, mammals and reptiles.

Only three species of *Brachylecithum* have been described previously from Australia (Johnston 1917). Johnston assigned them to *Lyperosomum,* but Skrjabin & Evranova (1953) and Yamaguti (1971) placed all three in *Brachylecithum.* The species are *B. parvum* from *Strepera versicolor, B. megastomum* from *Sterna bergii* and *B. harrisoni* from *Ninox novaeseelandiae* (syn. *N. boobook*). We have examined the types of these species. In addition, in T. Harvey Johnston's collection is a slide of *B. parvum* and two of *B. megastomum* with S. J. Johnston's name, and other particulars on each showing them to be from S. J. Johnston's original material, as well as a mounted specimen complete, except for oral sucker and a small part of the anterior end, which bears a Zoological Laboratory, University of Sydney, label written in T. H. Johnston's hand "? *Lyperosomum,* Boobook owl". We have compared measurements of all of these, and find it impossible to differentiate between the three species. There is some variation between individuals of each species, such as the presence of coils of the uterus between the gonads. The specimen of *B. harrisoni* designated as type is incomplete and is in three pieces; the anterior end (oral sucker to beginning of vitellaria) is not a good preparation, the gonads being largely, and the acetabulum partly, obscured by eggs. S. J. Johnston stated that *B. harrisoni* was closely related to *B. parvum*—"indeed, all three species are closely related to one another". With the material

available to us, we hesitate to synonymise these three species.

Brachylecithum parvum (Johnston)
FIG. 4

Lyperosomum parvum Johnston, 1917. from *Strepera versicolor,* N.S.W.

Brachylecithum parvum: Skrjabin & Evranova, 1953.

Host. Petrochelidon nigricans.

Location in host. Liver and gall bladder.

Locality. Mannum, S. Aust., February 1972.

Incidence. 1 of 2 birds from same locality at same time.

Food of host includes insects.

Slides deposited. SAM V85, V86. Identification based on seven balsam mounts. Other specimens too twisted or broken to be of any use.

Host. Corvus mellori.

Location in host. Bile duct and/or gall bladder

Locality. Tas., September 1969.

Incidence. 29 specimens, in one of 48 birds from Tas. (24 in July 1967, 24 in September 1969), in none of 9 *Corvus mellori* from S. Aust., 1966–1970.

Food of host includes insects.

Slides deposited. SAM V87, V88. Identification based on 10 balsam mounts

Since *B. parvum* has priority in Johnston's (1917) paper, we have named the present species, *B. parvum.*

At first examination it appears that acetabulum shape might distinguish specimens from *Petrochelidon* and *Corvus.* Johnston described the suckers of *B. parvum* as "rather longer than broad". In a slide in T. H. Johnston's collection labelled "*Lyperosomum ?parvum, Strepera versicolor*", thought to be one of S. J. Johnston's preparations, the acetabulum measures $200 \mu m \times 282 \mu m$ and shows, on one side, a lateral projection which is a feature in some of the species described here.

In each of four specimens from *Petrochelidon* in which both dimensions can be measured, the acetabulum is distinctly wider than long, and comes to a point on each side (Fig. 4). In 6 of 7 specimens from *Corvus mellori* the acetabulum is longer than broad; in the seventh, length and breadth are equal; in an eighth, mounted partly laterally, there are indications of the lateral projections. We conclude that acetabular shape is variable, depending perhaps on the muscular contraction of the organ, and also on the mounting of the specimen.

The type of *B. parvum* shows papillae on the surface of the body, which were not mentioned by Johnston. They are pointed or

(mostly) rounded; about 13 μm across the base and 8 μm above the surface of the body. They may be present in the acetabular region, but occur only very occasionally anterior to it. Posterior to the acetabulum they are about 25 μm apart, in the vitelline region about 53 μm apart, diminishing to the posterior end.

Papillae similar in size and shape, and also limited to the acetabular and post-acetabular region, are present on the types of *B. megastomum* and *B. harrisoni*. They are present in some specimens from *Petrochelidon nigricans*, but not in the specimens from *Corvus mellori*, which are not so well preserved.

Petrochelidon nigricans, although migratory, breeds in Australia and is found in winter only in New Guinea and the southwest Pacific, from which areas *Brachylecithum* spp. have not been recorded. *Corvus mellori* is restricted to Australia.

Brachylecithum insulare n.sp.
FIGS 1–2

Hosts. *Rattus fuscipes* (type host), *Amphibolurus fionni.*

Location in host. Gall bladder and bile ducts.

Locality. Pearson Island, S. Aust.

Incidence. 1 of 4 rats (January 1969), 2 of 9 rats (February 1973); many trematodes in each infected rat. 2 of 11 lizards (January 1969).

Holotype. SAM V76.

Paratypes. SAM V77, V78, V79.

Other slides deposited. SAM V80, V81.

Pearson Island is remote and only occasionally visited by biologists. Some trematodes, fixed in the field by a colleague in 1969, were recorded as "elongate dicrocoeliids" from *Rattus fuscipes* and *Amphibolurus fionni* by Mawson (1971).

The following description is based on sections of 4 worms (1969, 1973) and on 9 whole specimens from *Rattus fuscipes* (collected in February, 1973 and frozen before dissection). The trematodes (including the holotype and paratypes) were stained in Ehrlich's haematoxylin and examined in cedarwood oil, and later made into permanent mounts. The measurements of these did not differ significantly from the measurements made in cedarwood oil.

Description

Body long, narrow, approximately cylindrical; mostly uniform throughout length, but occasionally wider; rounded anteriorly, slightly tapered posteriorly. Length, 2.8–3.6 mm; width or depth/length ratio 1:17–1:21 (1:19).

(23 balsam mounts of trematodes fixed in the field in 1969 (on slides without pressure) measured 2.0–4.8 mm (2.92); the greatest width (0.36 mm) was in a specimen 2.24 mm long).

No papillae on body surface.

Acetabulum (198 x 208 μm) situated approximately in first fifth of body, larger than oral sucker (141 x 129 μm), wider than body. Ratio of width of oral sucker to width of acetabulum 1:1.5.

Pharynx almost spherical. Oesophagus and alimentary caeca poorly stained, indistinct. Oesophagus 45–110 μm long. Caeca 2, up to 26 μm wide, close to each other dorsal to acetabulum, then diverging laterally; terminating past the ovary, probably near posterior vitellaria.

Testes large, tandem, contiguous or nearly so; anterior testis close to or overlapping posterior border of acetabulum; shape often almost rectangular with rounded corners; posterior testis sometimes much elongated. Cirrus pouch arises dorsal to, and close to anterior border of, acetabulum; encloses coiled seminal vesicle. Pars prostatica absent. Cirrus muscular, about 24 μm wide, with rounded end, often protruding from genital pore, which lies medially, nearer to acetabulum than to pharynx.

Ovary rounded, entire. Receptaculum seminis large, longitudinally oval, close to posterior border of ovary. Laurer's canal not seen. Vitellaria forming approximately eight irregular lobes on both sides of body; limited to area posterior to ovary, extending to distance of 0.88–1.45 mm from end of body.

Uterus occupying all of body posterior to ovary, then passing anteriorly and dorsally, with a few coils between ovary and second testis, sometimes between testes and between first testis and acetabulum; opening at genital pore with male duct. Eggs numerous; brown; oval, often flattened along one side.

Excretory pore apparently terminal, with two wide arms extending well up length of body.

The specimens from *Amphibolurus fionni* differ from those from *Rattus fuscipes* in the relatively greater thickness and shorter length. The width/length ratio of 9 specimens from *R. fuscipes* averaged 1:19 and of 9 from *A. fionni* 1:13. However, a tenth from *A. fionni* measured 3.6 mm by .136 μm deep (1:26) i.e. almost as long as, and narrower than the longest of the 9 from *R. fuscipes*. The relationships and measurements of the organs do not

appear to differ significantly. (Although the testes are in general smaller in specimens from *A. fionni* this is not regarded a significant character). Nearly all the specimens from *A. fionni* are lateral mounts, and the acetabulum could not be compared easily with that from the specimens from *R. fuscipes;* but in two spirit specimens from *A. fionni* the acetabulum was wider than the body, measuring 187 x 197 μm in the first, and 134 x 150 μm in the second. Twenty eggs from specimens from each of the two hosts averaged the same width (22 μm) but were 46 μm long in the specimens from *A. fionni* and 43 μm in those from *R. fuscipes.* Although it is possible (because of the differing width/length ratios) that the trematodes from the two hosts belong to distinct species, we assign the form from *A. fionni* to *Brachylecithum insulare.* The hosts live in close proximity on a small island. The snail host for the trematodes is not known, but it seems certain that ants act as second intermediate host for those from *A. fionni.* Smyth (1971) stated that *A. fionni* appeared to feed exclusively on small ants (*Iridomyrmex*). Although we have no information on the feeding habits of *R. fuscipes,* Smyth (pers. comm.) stated that ants are so numerous on Pearson Island he considered it impossible for any animal on the island to avoid ingesting them.

B. insulare is closely related to S. J. Johnston's three Australian species; the only features by which *B. insulare* can be distinguished are the size of the eggs (slightly longer and relatively narrower in *B. insulare*) and the absence of papillae on surface of body in *B. insulare.*

It is possible that life-history studies may be necessary to determine the relationship of these species. Two complete life-histories have been described—that of *B. americanum* Denton, which uses chrysomelid beetles as second intermediate hosts (Denton 1945), and that of *B. mosquense* (Skrjabin & Isaichikov), which uses ants (*Camponotus herculeanus*) (Carney 1967). Gabrion & Ormières (1973) reported metacercariae of *Brachylecithum* sp. in *Phalangium opilio* in France, but it seems unlikely that arachnids are involved in the life cycles of the four species here.

Of the bird hosts of *Brachylecithum parvum, B. megastomum* and *B. harrisoni, Strepera versicolor* is the only one known to eat ants, though it also includes beetles in its diet. *Sterna bergii* might be expected to feed exclusively on fish, but dissection records show that "beetle grubs" have been found in the stomach. *Ninox novaeseelandiae* eats beetles as well as other insects, spiders, etc., and could possibly ingest night-working ants (e.g. "meat ants" on carrion). We suggest that *B. megastomum* and *B. harrisoni* may use beetle larvae as second intermediate hosts, while *B. insulare* almost certainly uses ants. *B. parvum* could use either.

Brachylecithum has not previously been recorded from reptiles; only three species have been described from mammals. *B. aetechini* Dollfus from *Erinaceus algirus* from Morocco, *B. rodentini* Agapova, from *Clethrionomys rufocanus* from Kazakhstan and *B. taiwanense* Fischthal & Kuntz from *Hipposideros armiger terasensis* from Taiwan. A fourth, unnamed species was reported from *Blarina brevicauda* from N. Carolina by Miller, Price & Wilson (1974). *B. insulare* from *Rattus fuscipes* differs from *B. aetechini* in: smaller size (length, 2.0–4.8 mm in *B. insulare,* 4.6–6.0 mm in *B. aetechini*); ovary separated from second testis, while in *B. aetechini* the ovary is in contact, or almost, with this organ; testes in tandem, while in *B. aetechini* they are slightly diagonal; and in the egg length/breadth ratio, approximately 2:1 in *B. insulare,* 3:2 in *B. aetechini.*

B. insulare differs from *B. rodentini* (Agapova's paper not seen; data in Skrjabin (1970)) in its smaller size (length 2.0–4.8 mm in *B. insulare,* 5.0–6.5 mm in *B. rodentini*). It probably differs in width/length ratio, which was not given for *B. rodentini* but, from the measurements, appears to be from 1:10–1:12, and in *B. insulare* from *Rattus fuscipes* is 1:17–1:21. The acetabulum of *B. rodentini* is further forward; from the measurements, it lies in the anterior eighth to the anterior eleventh of the body, while in *B. insulare* it is in the anterior fifth. The vitelline fields are relatively smaller in *B. rodentini* and one side is said to be at a higher level than the other. Finally, the eggs are shorter in *B. rodentini* (36 x 23 μm), than in *B. insulare* (43 x 22 μm from *Rattus fuscipes*).

B. insulare differs from *B. taiwanense* (described from a single specimen) in: body shape (slightly tapered posteriorly in former, with rounded end in latter); width/length ratio, (1:19 in *B. insulare,* 1:13 in *B. taiwanense*); both suckers larger and oral sucker relatively smaller than acetabulum in *B. insulare* (oral sucker/acetabulum length ratio 1:1.4 in *B. insulare,* 1:1.14 in *B. taiwanense,* width ratio 1:1.6 in *B. insulare,* 1:1.45 in *B. taiwanense*); ovary shape, rounded in *B.*

insulare, much wider than long in *B. taiwanense*; and in its larger eggs (43 μm x 22 μm in *B. insulare*, 35 μm x 19 μm in *B. taiwanense*.

B. insulare is the only trematode found in *R. fuscipes* and *A. fionni* from Pearson Island. The only other trematode found in a lizard from the island was *Paradistomum crucifer* (Nicoll), from the gall bladder of *Phyllodactylus marmoratus* (Mawson 1971). *B. insulare* was not found in other lizards examined, i.e. 6 *P. marmoratus* Gray, 5 *Lerista tetradactyla* (Lucas & Frost), 2 *Hemiergis peronii* (Fitzinger) and 1 *Morethia obscura* Storr (Mawson 1971).

Brachylecithum hydromyos n.sp.

FIG. 3

Host. Hydromys chrysogaster.

Locality. Lily Creek, Cairns, Qld, 14.ii.1975. (Coll. C. M. Weaver).

Location in host. Pancreatic ducts.

Incidence. More than 35 specimens in 1 of 3 rats from Cairns. In none of 49 hosts from S. Aust., or in two from Vict.

Food of host mostly fish, molluscs, crustaceans, but insect remains found in several rats.

Holotype. SAM V82.

Paratypes. SAM V83, V84.

The worms were recovered live, in good condition, and were in two distinct sizes, apparently representing different age groups. Of the 14 larger worms, only 4 were completely intact after removal. The description is based on whole mounts of these four and of six of the smaller (though egg-bearing) worms. Measurements given (range or means) are for the four larger specimens. The width/length ratio and the position of the acetabulum in relation to length of body, were similar in both sizes.

Description

Body sub-cylindrical, with prominent preoral lobe and acetabulum. Length, 1.8–3.4 mm. Greatest width from level of first testis to ovary; width/length ratio 1:12. (Depth approximately three-fifths width). Without papillae on body surface. Acetabulum (153 x 176 μm), aproximately in first fifth of body, rounded, with very slight projections on each side, protruding from body. Ratio of width of oral sucker to width of acetabulum approximately 1.0:1.4. Oral sucker (133 x 119 μm) rounded, pharynx slightly wider than long;

oesophagus short, caeca passing almost immediately to sides of body; caeca obvious, up to 58 μm wide, terminating about 900 μm from end of body.

Testes rounded, in tandem or very slightly diagonal, separated from acetabulum and from each other by uterus. Cirrus pouch begins near antero-dorsal border of acetabulum. Genital pore in region of caecal bifurcation.

Ovary transversely oval; submedian, lying in first half of body. Receptaculum seminis large, with oval or irregular outline, up to 130 x 90 μm. Vitellaria consisting of 8–12 well-defined lobes (approximately 47 x 42 μm), in a compact row on each side of body, near sides of body. Uterus confined to inter-caecal area; posterior to caeca occupying all of body.

Excretory pore terminal; excretory bladder overlaps ends of caeca.

B. hydromyos differs from *B. insulare* from *Rattus fuscipes* in its relatively broader body, oval rather than rounded ovary, smaller and rounded testes; in the first testis being further separated from the acetabulum and the two testes always separated from each other; vitellaria much more prominent, not obscured by uterus and noticeably less in extent than in *B. insulare*; and in having smaller eggs (mean, 36 x 20 μm in *B. hydromyos*, 43 x 22 μm in *B. insulare*). The food of *Hydromys chrysogaster* (a water rat) and *Rattus fuscipes* is very different, and it is unlikely that *H. chrysogaster* would eat many ants.

B. hydromyos resembles *B. aetechini* in width/length ratio and in position of acetabulum, but differs from it in overall size, 1.8–3.4 mm (4.6–6.0 mm) and egg size, 36 x 20 μm (47 x 32 μm). *B. hydromyos* has a similar width/length ratio to *B. rodentini*, but is smaller, 1.8–3.4 mm (5.0–6.5 mm), and differs from the latter: in the more backward position of its acetabulum; in the testes being separated from the acetabulum and from each other (in *B. rodentini* the testes are almost contiguous and the anterior one underlies the posterior border of the acetabulum); the vitelline follicles are more, 8–12 (6–8), and the vitellaria and ovary are further back in the body. *B. hydromyos* resembles *B. taiwanense* in width/length ratio and position of acetabulum, but is apparently smaller, 1.8–3.4 mm for 10 specimens (3.6 for 1 specimen), its suckers are relatively smaller and the testes are separated from the acetabulum (but contiguous with it in *B. taiwanense*).

Brachylecithum dacelonis n.sp.

FIG. 5

Host. [1]*Dacelo novaeguineae.*

Location in host. Liver.

Locality. Bridgewater, S. Aust., July 1973.

Incidence. 1 of 9 birds from S. Aust.; none of 4 from N.S.W.; neither of 2 from Tas.

Food of host includes beetles, other insects, and spiders.

Holotype. SAM V89.

Paratypes. SAM V90, V91.

Description based on 10 balsam mounts of specimens recovered alive.

Description

Body slender, cylindrical, narrowing from ovary to posterior end. Length 2.9–3.5 mm, width or depth/length ratio 1:24–1:29 (1:26). Conical papillae (10 μm across base, 8 μm high, approximately 50 μm apart) on body surface from acetabulum to ovary, diminishing in number posteriorly. Acetabulum (176 x 152 μm) slightly larger than oral sucker (167 x 145 μm), situated approximately in anterior fifth of body, wider than long, with a blunt point on each side. Pharynx mostly wider than long, sometimes round; oesophagus bifurcating near genital pore; caeca end posterior to vitellaria, at about one quarter to one third of body length from posterior end.

Testes oval to rectangular with rounded corners, tandem, close together. Cirrus pouch arises between anterior edge and anterior third of acetabulum. Cirrus up to 80 μm long x 45 μm near base. Genital pore nearer to acetabulum than to oral sucker. Ovary round or slightly wider than long, median, close to second testis, in anterior two-fifths of body. Receptaculum seminis large, loosely coiled, about 105 x 65 μm. Vitellaria consisting of 7–11 compact follicles (up to 60 x 53 μm) on each side of body.

B. dacelonis is close to *B. parvum*, but differs primarily in width/length ratio. Both of Johnston's specimens of *B. parvum* are mounted on their sides, and the depth/length ratios (measured by us) are 1:12 and 1:20, whereas width/length ratio of 7 specimens of *B. dacelonis* is from 1:24–1:29. They are noticeably more slender worms than *B. parvum*. Corresponding with the lesser width in *B. dacelonis*, the suckers, pharynx and gonads are smaller than those of *B. parvum*.

Other species recorded from alcedine birds are: *B. halcyonis* (Yamaguti) from *Halcyon coromanda major* from Japan, *B. andamanensis* Soota, Srivastava & Ghosh (in Soota et al. 1973) from *Halcyon chloris* from the Andaman Islands, *B. palawanense* Fischthal & Kuntz from *H. chloris collaris* and *Ceyx rufidorfus rufidorfus* from the Philippines, and *B. sabahense* Fischthal & Kuntz from *H. chloris* from Sabah.

B. dacelonis differs from all of these in: narrower body (w/l ratio 1:24–1:29); (*B. halcyonis* (1:17–1:20) approaches this most nearly, the other three species are 1:10, 1:9–1:12, 1:8–1:9 respectively (our calculations)) and in size or relative dimensions of eggs (*B. dacelonis* 39 x 24 μm, *B. halcyonis* 42 x 21–22 μm, *B. andamanensis* 63–90 x 12–16 μm, *B. palawanense* 32 x 18 μm, *B. sabahense* 35 x 19 μm). It differs further: from *B. halcyonis* in its smaller size 2.9–3.5 mm (5.1–5.2 mm) and the acetabulum being further back, 1:4–1:6 body length (1:7) and from *B. sabahense* in lacking a constriction of the body at the acetabular level.

Brachylecithum podargi n.sp.

FIG. 6

Host. *Podargus strigoides.*

Location in host. Bile ducts.

Locality. Moggill, Qld, 26.v.1970. Brisbane, Qld, 6.xi.1962.

Incidence. 2 birds from Qld. None of 11 birds from S. Aust. and N.T.

Food of host includes beetles, other insects, and spiders.

Holotype. SAM V92.

Paratypes. SAM V93, V94, V95.

Description based on 10 balsam mounts of mature specimens from Moggill. Immature specimens from Brisbane were also examined.

Description

Body elongate, 4.3–5.8 mm; forebody slightly narrower than hindbody; hindbody fairly uniform in width to behind vitellaria, then narrowing gradually. Width or depth/length ratio 1:24–1:30 (1:28). Without papillae on body surface. Acetabulum (199 x 154 μm), approximately in anterior eighth of body, larger than oral sucker (172 x 155 μm), slightly wider than body, wider than long, sometimes coming to blunt point on each side. Pharynx almost spherical; oesophagus bifurcating about midway between suckers; caeca dor-

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[1] Despite its specific name *D. novaeguineae* does not occur outside Australia.

sal, ending near posterior border of vitellaria.
(In 5.0 mm specimen caeca ending 2.4 mm and
2.6 mm from hind end of body).

Testes rounded, contiguous or not, slightly
larger than ovary; anterior testis somewhat
posterior to acetabulum. Cirrus pouch arises
dorsal to anterior quarter of acetabulum;
seminal vesicle coiled; genital pore midway
between oral sucker and acetabulum, or
slightly nearer to latter.

Ovary, close to or separated from posterior
testis, situated in anterior two sevenths to one
fifth of body. Receptaculum seminis large, post-
ovarian. Vitellaria consisting of 7–13 follicles
(up to 82 x 82 μm and 94 x 59 μm) on each
side of body, post-ovarian. Uterus and male
duct opening side by side at genital pore. Mean
egg size 47 x 24 μm.

B. podargi differs from *B. dacelonis* in its
greater size, the more anterior position of its
acetabulum, and in the longer eggs. It differs
from *B. harrisoni* (from *Ninox novaesee-
landiae*, another night-flying bird, which may
eat the same foods as *Podargus strigoides*) in
the larger eggs, and the absence of papillae
from the body surface.

The only *Brachylecithum* sp. previously
recorded from the Caprimulgiformes is
Brachylecithum transversogenitalis sylvestris
Semenov from *Caprimulgus europaeus*. From
the measurements and figure given by Skrjabin
& Evranova (1953), this species differs from
B. podargi in its shorter, much wider body
(width/length ratio 1:8) and smaller eggs (26–
33 x 16 μm).

Brachylecithum latius n.sp.

FIG. 11

Type host. Cracticus torquatus.

Location in host. Gall bladder.

Locality. Cowell, S. Aust., 27.v.1965.

Incidence. 1 of 5 birds from S. Aust.

*Food of host includes beetles, ants and other
insects.*

Holotype. SAM V102

Paratypes. SAM V103, V104, V105.

*Other hosts. Corvus coronoides; liver; Port Augusta,
S. Aust., 20.ix.1965, 1 of 4 birds from S. Aust.
Food includes beetles and other insects. Slide
deposited SAM V106. Gymnorhina hypoleuca,
gall bladder; Adelaide suburb, S. Aust.,
15.ii.1974, 1 of 68 birds from S. Aust., none
of 16 from A.C.T., or 1 from N.T. Slide
deposited SAM V107. Food of G. hypoleuca
includes beetles, ants, other insects and spiders.*

Description based on balsam mounts of 7
worms in quite good condition. Those from
Corvus coronoides and *Gymnorhina hypoleuca*
are also in good condition, but in the whole
mounts the eggs are mostly filled with air, and
are black.

Description

Body (3.5–6.5 x 0.54–1.26 mm) lanceolate,
widest anteriorly, at level of first or second
testis. No spines or papillae present on surface
of body.

Acetabulum (447 x 588 μm) larger than
oral sucker (259 x 259 μm), weakly muscular,
wider than long, situated close to anterior end
of body. Oral sucker rounded, well-developed.
Pharynx rounded; oesophagus short, caeca two
(only visible to level of mid-acetabulum).

Testes large, contiguous; roughly triangu-
lar, rectangular or oval; tandem to diagonal;
anterior testis underlying posterior half of
acetabulum. Cirrus pouch overlaps anterior
part of acetabulum; cirrus 260 μm long, regu-
lar in width, 33 μm. Genital pore at caecal
bifurcation, slightly nearer to acetabulum than
to oral sucker.

Ovary oval with long axis across width of
worm; generally contiguous with second testis,
to right or left of body. Mehlis' gland posterior
and oblique, to ovary. Receptaculum seminis
not obvious. Vitellaria of quite large follicles,
limited in extent, reaching anteriorly near level
of ovary. Uterus very extensive, generally
obscuring most of acetabulum and sometimes
of vitellaria. Eggs approximately 47 x 31 μm.

The specimens from *Corvus coronoides*
show some differences from those from the
type host, probably attributable to immaturity.
Thus, the uterus is less extensive, and does not
so completely (if at all) obscure the acetabu-
lum; the testes are in general smaller, do not
underlie the acetabulum; and are always at
least slightly diagonal. The acetabulum is
further forward in worms from *Cracticus tor-
quatus* than in those from *Corvus coronoides*,
but the bodies of some of the worms are slightly
contracted anteriorly. We consider that to use
this character would involve comparing worms
obtained alive and fixed under the same con-
ditions. The acetabulum appears relatively
greater in width in worms from the type host,
but in the smallest (in which it is not obscured
by eggs) it is 365 x 412 μm, conforming to
the more nearly round shape in worms from
C. coronoides. (In worms from *C. coronoides*
the acetabulum comes to a blunt point on each
side; a character obscured by eggs in worms

from the type host. The size of the oral sucker may distinguish worms from the two hosts; but although the mean size of the organ in worms from *Cracticus torquatus* is 259 x 259 μm, in the largest worm from this host the oral sucker is 365 x 376 μm, in comparison with the largest, 388 x 353 μm, from *Corvus coronoides*. The eggs in worms from *Cracticus torquatus* are relatively wider than in those from *Corvus coronoides* and *Gymnorhina hypoleuca*, but this character is not sufficient to place the worms in separate species.

We have placed the species in *Brachylecithum* because it resembles this genus more than other related genera as defined by Yagamuti (1971). Although it resembles *Brachydistomum* in shape and some other respects, it is distinguished by the weakly developed acetabulum ("very prominent" in *Brachydistomum*).

Brachylecithum latius differs from congeners described here (including the unnamed species from the intestine of *Gymnorhina hypoleuca*) in body shape and width/length ratio (never more than 1:8.3 in *B. latius;* never less than 1:11 in the other species).

Of all described species of *Brachylecithum* (we have not seen the description of *B. riparia* Erkulov), *B. latius* most closely resembles *B. attenuatum parinum* Oshmarin from *Parus palustris,* Maritime Province, U.S.S.R. in shape and general appearance. However, it is larger (2.8 x 0.4 mm) and the eggs are smaller (reaching 58 x 29 μm in *B. attenuatum parinum*).

Brachylecithum sp.

Host. Gymnorhina hypoleuca.

Location in host. Intestine.

Locality. Encounter Bay, S. Aust. January, 1966.

Incidence. 1 of 68 *Gymnorhina* spp. from S. Aust.; none of 16 from A.C.T. or 1 from N.T.

Food of host includes beetles, ants, other insects, and spiders. Two slides (one of a single specimen in four pieces, a second with two whole worms and the anterior half of a third), University of Adelaide Helminthological Collection.

Two complete worms, one broken worm and the anterior half of a fourth were found. Although in poor condition, they were stained and mounted. Although the caeca are not visible the worms are referred to *Brachylecithum.*

Description

Long, narrow, cylindrical or sub-cylindrical worms (2.9–4.2 mm). Width/length ratio 1:21. No papillae seen on body surface. Not possible to measure testes and ovary but gonads apparently in tandem, situated quite close to acetabulum. Anterior margin of vitellaria 442 μm from acetabulum in each of 3 specimens. Vitellaria, about seven, generally compact, follicles (about 66 x 37 μm in size) on each side of body.

The condition of these worms does not allow a proper comparison with other species. It is probably close to *B. parvum,* the type host of which belongs to the same family as *Gymnorhina,* although it appears likely that the width/length ratio is less than in *B. parvum.* In a broken specimen the ratio of depth behind the acetabulum to the sum of the lengths of the four pieces was 1:35.

SKRJABINOSOMUM Evranova

Generic diagnosis: Dicrocoeliidae, Dicrocoeliinae. Body surface without papillae. Exceptionally long, slender; maximum width to length ratio not greater than 1:45. Pre-oral lobe; pharynx, short oesophagus, elongated caeca, posterior extent of which not traced. Acetabulum near to and larger than oral sucker. Testes elongate oval, separated from acetabulum, lying at end of anterior third or in middle third of body; in tandem, separated from each other and from ovary by uterus. Ovary round or oval. Vitellaria in post-ovarian lateral fields. Genital pore medial, pre-acetabular. Parasitic in liver, ?intestine of birds.

Skrjabinosomum differs from *Brachylecithum* in its greatly elongated narrow body, and displacement posteriorly of the reproductive organs from the acetabulum. *Brachylecithum lobatum* (Railliet) has the smallest width/length ratio known to us from previous descriptions of Dicrocoeliinae: 1:35–1:40, our calculations, from measurements given by Skrjabin & Evranova (1953). To separate the two genera, we have given the maximum width/length ratio of *Brachylecithum* as not less than, and of *Skrjabinosomum* as not greater than, 1:45. This figure may have to be adjusted in the future.
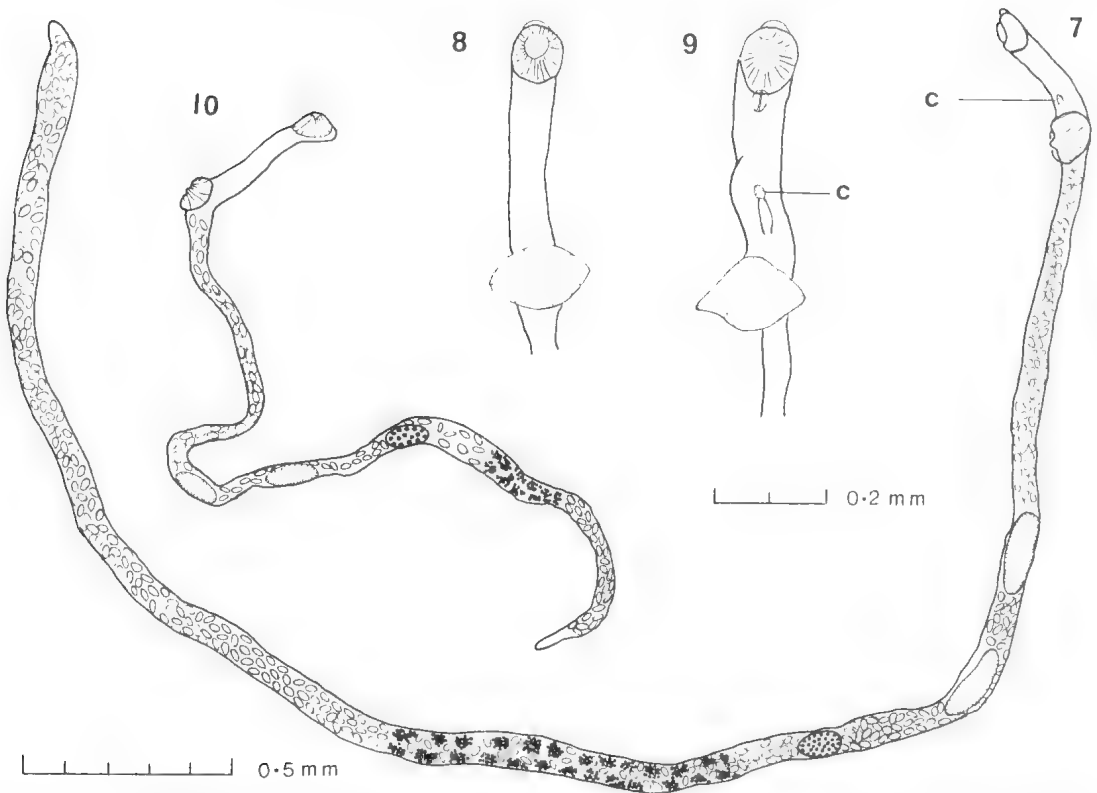
Skrjabinosomum mawsoni n.sp.
FIGS 7–9

Type host. Manorina flavigula.

Location in host. Liver.

Locality. Port Augusta, S. Aust. May, 1965.

Incidence. 1 of 8 birds from S. Aust. and N.T. dissected 1965–1967.

Food of host includes beetles, ants and other insects.

Figs 7–10. 7. *Skrjabinosomum mawsoni* Holotype; 8. *S. mawsoni* Paratype; acetabulum; 9. *S. mawsoni* from *Turnix castanota;* acetabulum; 10. *S. pomatostomi* Holotype. (Figs 7, 10 to same scale; Figs 8, 9 to same scale).

Holotype. SAM V96 (lateral mount), with *paratype* (dorsal mount, complete but for oral sucker) on one slide.

Paratype. SAM V97.

Other slide deposited. SAM V98.

Other host. Turnix castanota. Cowell, S. Aust., 26.v.1965. In 1 of 2 birds collected together. (One complete; one complete except for first testis and anterior end; and four pieces). *From* liver. *Food of host* includes "heavy" insects.

Description based on whole mounts of 5 complete and 3 almost complete specimens, with 17 pieces of several other specimens from the type host.

Description

Body (4.0–5.4 mm) very long, narrow, cylindrical or sub-cylindrical. Width/length ratio 1:85-1:115 (1:102). Papillae not seen on surface of body. Acetabulum (131 x 129 μm), situated approximately in anterior twelfth of body, a little larger than oral sucker (103 x 89 μm); not strongly muscular, wider than body and approximately diamond-shaped; in lateral mounts margin folded irregularly. Oral sucker

more muscular than acetabulum. Pharynx not clearly seen in most specimens; oesophagus and alimentary caeca not seen. (In specimen from *Turnix castanota,* pharynx obvious and part of oesophagus seen).

Testes elongate oval; situated well posterior to acetabulum; tandem. Cirrus pouch mostly anterior to acetabulum; cirrus with bluntly rounded end; genital pore nearer to acetabulum than to oral sucker. Ovary oval, smaller than testes. Ovary and testes more or less well separated from each other, probably depending on state of elongation of worm, by uterine coils. Vitellaria, beginning near posterior border of ovary, consisting of variously sized groups of small follicles; largely obscured by eggs; up to 800 μm in extent. Uterus, with many eggs, occupying all of hindbody not filled by gonads and vitellaria.

S. porrectum (Braun) from *Halcyon saurophaga,* New Guinea, and *S. elongatum* Yadav from *Sterna aurantia,* India, are the only species previously described in the genus. *S. mawsoni* shows a close resemblance to *S. por-*

rectum in general appearance, though it is much smaller. Travassos (1944) who reproduced Braun's (1902) measurements and figures, referred to the great elongation of the body of *S. porrectum*, and said that careful examination of Braun's figures gave a clear impression of material preserved in the early stages of decomposition. The widening of the body shown in the anterior third is almost certainly distorted. The length was 17 mm; maximum width was given as 0.57 mm (width/length ratio 1:30), width at posterior end 0.2 mm (1:85). From Travassos' fig. 3 we estimate the probable maximum width as 0.28 mm (ratio 1:60).

S. mawsoni differs from *S. porrectum* in: size (4–5 mm, 17 mm respectively); width/length ratio (1:85–115, 1:60); acetabulum not so near anterior end (forebody/total length ratio 1:12, 1:22); ovary (oval, spherical); testes further forward (in anterior third, middle third); eggs smaller (32 x 19 μm, 37–41 x 23 μm).

We have not seen the description of *S. elongatum*.

Skrjabinosomum pomatostomi n.sp.
FIG. 10

Host. Pomatostomus superciliosus.

Location in host. Liver.

Locality. The Bunkers, Flinders Ranges, S. Aust. 22.vii.1965.

Incidence. 1 of 35 birds, from S. Aust. and N.T., 1938–1969 (10 of which were from the Bunkers, July, 1965).

Food of host includes beetles and other insects.

Holotype. SAM V99, with six pieces of *paratype* on same slide. Two other slides, one with two twisted specimens and several pieces of no value (paratype SAM V100) the other with only anterior end (paratype SAM V101).

One entire trematode and a number of pieces of at least three others were recovered. All specimens were rather sticky. SAM V101 (anterior end only) was studied first in glycerine. Thus measurements of the suckers from the ventral and lateral aspect were taken. Description based on all available material.

Description

Body elongate (2.4 mm), narrowly cylindrical or sub-cylindrical, with pre-oral lobe. Papillae not seen on surface of body. Acetabulum (115 x 181 μm) not strongly muscular, diamond-shaped and transversely elongate in ventral view, probably a little larger than oral sucker (97 x 94 μm), lying between anterior sixth and seventh of body in holotype. Pharynx present; oesophagus and alimentary caeca not seen. Testes oval, situated well back from acetabulum, in tandem. Testes and ovary separated from each other by uterus. Ovary closer to posterior end of body than to acetabulum. Vitellaria not in well-defined follicles.

In *S. pomatostomi* the sizes of the organs and the distance of the acetabulum from the anterior end of the body, the distance of the first testis from the acetabulum, and the relationship of testes, ovary and vitellaria to each other are similar to these features in *S. mawsoni*. However, the much shorter distance from the ovary to the hind end of the body in *S. pomatostomi* makes the relative positions of the organs in body length distinctly different in the two species. In the five complete specimens of *S. mawsoni* from *Manorina flavigula* the ratio of length of body posterior to ovary to total body length is 10:17, 18, 18, 19 and 19; in a sixth specimen, the length of which can be estimated closely (lacking only the oral sucker), the ratio is 10:20; in the only complete specimen from *Turnix castanota* the ratio is 10:21. In *S. pomatostomi* it is 10:30.

Corresponding with the shortening of the hindbody in *S. pomatostomi* the acetabulum lies relatively further back, the vitellaria are shorter and nearer to the posterior end of the body, and the uterus and number of eggs are much reduced.

It appears that the acetabulum of *S. pomatostomi* is larger than that of *S. mawsoni* from *Manorina flavigula* (though the same size as in *S. mawsoni* from *Turnix castanota*). However, the acetabulum in both species is not strongly muscular and its outline is variable (probably depending on the position in which it is mounted). The natural shape of the acetabulum appears to be angular, with the margin coming to a point on each side of the body. When such a specimen can be measured in this position its width is maximal. The depth is probably a better indication of the size of the acetabulum. The width of the eggs (31 x 16 μm) is less in *S. pomatostomi* than in *S. mawsoni*.

It is possible that *S. pomatostomi* is a young form of *S. mawsoni* in which the hind end of the body has not reached its full length, the uterus and the vitellaria being not yet fully developed. But although the proportions of this part of the body are so markedly different, the size of the gonads (and presumably their maturity) is much the same in the worms from the two hosts. We regard *S. pomatostomi* a dis-

tinct species, characterised by the close proximity of the ovary to the hind end of the body.

S. pomatostomi differs from *S. porrectum* in size (2.4 mm, 17 mm respectively); in the more backward position of the acetabulum (forebody/hindbody 1:6–7, 1:22). In having an oval ovary, situated at 2/3 of body length (round, at midlength in *S. porrectum*), and in egg size (31 x 16 μm, 37–41 x 23 μm).

Skrjabinosomum sp.

Host. Microeca leucophaea.
Location in host. Liver.
Locality. Port Augusta, S. Aust. September, 1965.
Incidence. 1 of 11 birds from various localities (3 near Port Augusta) in S. Aust. and N.T., 1958–65.
Food of host includes beetles and other insects. Slide (with 5 pieces) deposited in University of Adelaide Helminthological Collection.

Five pieces of a very long, narrow trematode were stained and mounted on one slide. The worm was incomplete, and lacked hind end and oral sucker. The acetabulum, mounted in lateral view, is 76 μm high by about 39 μm deep. The testes are obviously situated well posterior to the acetabulum. Vitellaria show in two pieces; they consist of small follicles in large groups, not sharply demarcated, and occupy a length of at least 506 μm. Ten eggs measure 28–33 μm x 13–18 μm (30 x 14 μm).

The worm is similar to the elongate species *S. mawsoni* and *S. pomatostomi* and may be conspecific with one of them.

LUTZTREMA Travassos

Generic diagnosis. Dicrocoeliidae, Dicrocoeliinae. Body elongate or relatively broad, with pre-oral lobe. Body surface with or without papillae or spines. Acetabulum larger than oral sucker or suckers sometimes equal. Single caecum, or with one of caeca rudimentary and not extending beyond acetabulum; caecum relatively long, median, in form of zigzag. Genital pore about half-way between suckers. Testes post-acetabular or almost acetabular, tandem or diagonal. Ovary post-testicular. Vitelline follicles large, post-ovarian, lateral, sometimes converging anteriorly. Uterus occupying most of hindbody, with coils between ovary and testes. Parasitic in liver and gall bladder of birds and mammals.

Lutztrema ailuroedi n.sp.
FIGS 12–14

Host. Ailuroedus crassirostris.
Locality. Mt Glorious, Qld, 16.i.1957, 30.i.1957 (collected K. E. Webber), 29.x.1962.

Location in host. Bile duct and at mouth of gall bladder.
Incidence. From 7 to many specimens, in all 5 green catbirds examined.
Holotype. SAM V108.
Paratypes. SAM V109, V110, V111.

Description based on live worms and on balsam mounts of 8 whole worms and 3 anterior ends (16.i.1957). Measurements of worms from two collections, 29.x.1962 (2 birds) and 30.i.1957, with some additional information on these whole mounts.

Description

Body elongate, almost cylindrical; forebody much narrower, bent back dorsally from protruding acetabulum; in whole mounts width generally slightly greater at level of vitellaria. Length 3.30–4.28 mm (3.80), width 0.221–0.272 mm (0.238) for 5 worms, depth 0.214 mm for 3 worms. Ratio of width to length 1:14–1:18. (In 2 hosts collected 29.x.1962, 8 mature trematodes measure 2.89–4.18 mm (3.30), and in one host collected 30.i.1957, 7 worms are 2.10–2.92 mm (2.60). Papillae scattered over length of body; most numerous on preoral lobe.

Suckers forming deep cups. Acetabulum larger than oral sucker, in anterior seventh to anterior fifth of body; 141–200 μm (176) long x 153–188 μm (172) wide, and (in 3 specimens) 165–200 μm (188) deep. Oral sucker 106–129 μm (114) long x 94–100 μm (96) wide, and (in 3 specimens) 94 μm deep. Sucker ratio (using mean diameters of length and width, in five specimens) 1:1.5–1:1.7). Pharynx 39–50 μm (47) x 53–63 μm (57) and (3 specimens) 55–60 μm (59) deep. Caecum (dorsal to cirrus sac and to middle or side of acetabulum, sinuous dorsal to and between testes, dorsal to ovary and excretory bladder, ending less than half way from ovary to posterior end.

Excretory pore terminal. Excretory bladder I-shaped, in young specimens reaching nearly to ootype; common collecting tubules arising from anterior end of bladder; at level between testes giving off anterior and posterior collecting tubules. Excretory formula 2[(2 + 2 + 2) + (2 + 2 + 2)].

Testes tandem, round to elongate oval, 153–235 μm (191) long x 129–188 μm (162) wide, and (in 3 specimens) 141–153 μm (149) deep. Anterior testis separated from acetabulum by 119–306 μm. Testes contiguous or up to 85 μm apart. Seminal vesicle coiled. Cirrus sac
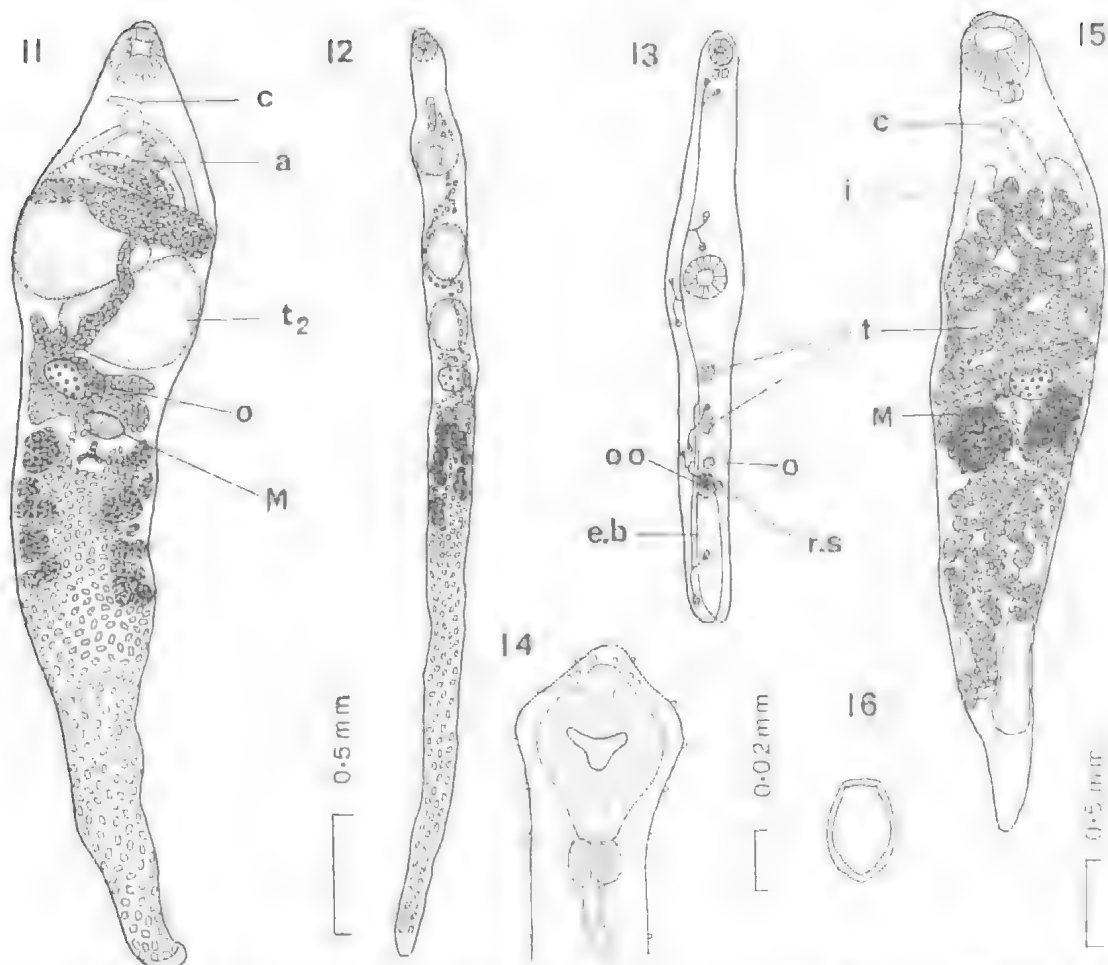
Figs 11–16. 11. *Brachylecithum latius* Holotype, dorsal view; 12. *Lutztrema ailuroedi* Holotype; 13. *L. ailuroedi* Sketch, of young specimen; 14. *L. ailuroedi* Sketch, anterior end showing papillae; 15. *Pancreatrema meliphagae* Holotype; 16. *P. meliphagae* Egg. (Figs 11, 15 to same scale.)

immediately anterior to acetabulum, about 158 x 53 μm. Genital pore about midway between suckers.

Ovary in anterior third to two-fifths of body, submedian, round or transversely oval, 88–118 μm (102) x 112–141 μm (129) and 106–123 μm (118) deep; separated from posterior testis by 34–136 μm. Receptaculum seminis up to 79 x 68 μm. Vitellaria composed of 8–10 large (up to 121 x 60 μm) follicles on each side of body. Vitelline fields 318–447 μm (376) long, from 34–136 μm posterior to ovary. Uterus occupying all of hindbody posterior to vitellaria, then passing forwards dorsal to and between ovary and posterior testis, posterior and anterior testes, anterior testis and acetabulum; travelling dorsal to cirrus sac and opening immediately anterior to cirrus at genital pore. Eggs 32–39 μm (35) by 21–23 μm (22); when new laid hatching in water; miracidium swimming actively.

The character which distinguishes *Lutztrema* from the closely related genera *Brachylecithum* and *Lyperosomum* is the alimentary system, in which there is a single caecum, or with one of the two caeca rudimentary; the main caecum is relatively long, median and in the form of a zigzag. Probably because the alimentary system was not described in the original descriptions, a number of species ascribed to *Lutztrema* have subsequently been referred to other genera (generally to *Brachylecithum*). Yamaguti (1971) listed 11 species from birds and one from a mammal; he did not mention the species *L. heterocaraxi* Bisseru, *L. singhi* Bano, *L.*

stunkardi Bano or L. vitelloconfluentum Ali, Deshmukh & Karyakarte. No further species have been described to date. Most of the above 16 species have relatively broad bodies, short behind the vitellaria, and L. ailuroedi differs from them in this and in other features. Its body width/length ratio is closest to that of L. microstomum Denton & Byrd (from Cyanocitta cristata Linn.), L. singhi Bano (from Corvus splendens (Kreillot)) and L. heterocoraxi Bisseru (from Heterocorax capensis capensis Sharpe). From the ranges of width and length given for the first two species, we estimate the width/length ratio of L. microstomum to vary from 1:11–1:16, and of L. singhi from 1:10–1:13. The measurements given of one specimen of L. heterocoraxi (presumably the holotype) show a ratio of 1:16.

The most notable difference between L. ailuroedi and L. microstomum is in the position of the acetabulum (situated "about one-tenth of body length from anterior end" in L. microstomum, and between the anterior seventh and fifth in L. ailuroedi). Other differences are: the body behind the vitellaria (as shown in the figure) is relatively longer in L. microstomum; in L. ailuroedi, the testes are round or elongate oval and lie in tandem, while in L. microstomum they are rounded to transversely oval and situated slightly obliquely; in L. microstomum the ratio of the diameter of oral sucker to acetabulum is 1:1.75–1:2.80, but in L. ailuroedi, 1:1.5–1:1.7. The eggs of L. microstomum may be slightly shorter (29–35 μm long, 19–24 μm wide). Laurer's canal was not observed in L. ailuroedi, but with these exceptions, this species agrees very closely with the description of L. microstomum.

Apart from its relatively narrower body, L. ailuroedi differs from L. singhi in having scattered papillae on body surface (L. singhi is covered with minute spines); eggs (32–39 μm) are slightly longer (30–36 μm in L. singhi); vitellaria ending somewhat nearer hind end of body; testes in tandem (somewhat oblique in L. singhi). Bano gives the position of the acetabulum as "posterior region of anterior third of body", but from the figure of the type, it is in the anterior fifth (in L. ailuroedi, anterior seventh to fifth).

L. ailuroedi appears to be close to L. heterocoraxi, but differs chiefly in the sucker ratio (1:1.5–1:1.7 in former, 1:2 in latter) and in egg size (35 x 22 μm in former, 39 x 26 μm in latter). The absolute sizes of the suckers appear to be greater in L. heterocoraxi, the

acetabulum is slightly further back (in anterior fifth of body in L. heterocoraxi, between anterior seventh and fifth in L. ailuroedi) and the maximum width of the body is at the acetabulum in L. heterocoraxi; at the vitellaria in L. ailuroedi.

PANCREATREMA Oshmarin

Generic diagnosis. Dicrocoeliidae. Body flattened fusiform, with pre-oral lobe. Oral sucker moderately large, acetabulum lacking. Pharynx, short oesophagus, two caeca, Testes small, rounded, symmetrical, pre-equatorial; genital pore post-pharyngeal or post-bifurcal. Ovary round, submedian, in equatorial region. Vitellaria forming rather compact clusters on each side, close to posterior border of ovary. Uterus extensive but not in the extremities of body.

Parasitic in bile or pancreatic ducts of birds.

Pancreatrema meliphagae n.sp.
FIGS 15–16

Host. Meliphaga ornata.

Locality. Blanchetown, S. Aust. April, 1965.

Location in host. "Probably from bile duct".

Incidence. 1 specimen from 1 of 8 birds.

Holotype. SAM V112.

Description of holotype.

Flattened fusiform worm, 4.35 x 0.85 mm. Greatest width just anterior to testes. Oral sucker 400 x 388 μm; pharynx 118 x 118 μm; oesophagus short; two caeca, apparently terminating near posterior end of body. Acetabulum not seen. Testes entire, pre-equatorial, symmetrical, partly obscured by uterus; right testis about 176 x 200 μm, left testis about 165 x 188 μm. Ovary round, entire, 235 μm in diameter, submedian, just pre-equatorial. Genital pore apparently nearer to pharynx than to caecal bifurcation. Vitellaria in compact clusters; on left side reaching mid-ovarian level, contiguous with ovary. on right side post-ovarian; left cluster 376 x 282 μm; right cluster 470 x 400 μm. Uterus extensive, but not obscuring most of organs. Eggs (Fig. 16) plump, somewhat flattened at opercular end with slight shoulders at rim of operculum, slightly pointed at other end; 34–36 μm x 19–22 μm (average of ten, 34 x 21 μm).

In another specimen of Meliphaga ornata (from Cowell, S. Aust. May, 1965), about 10 trematodes in very poor condition were recovered from the bile duct or liver. It is not possible to identify these specimens definitely, but it is thought likely that they belong to Pancreatrema. They appear to be similar to P.

meliphagae in size and shape, and the eggs have the characteristic appearance of those of *P. meliphagae*, though they are slightly larger (35–42 μm long x 22–26 μm wide (40 x 24 μm)). Six oral suckers, taking stain only faintly, measure 176–212 μm long x 176–235 μm wide (193 x 207 μm), and one pharynx measures 59 x 59 μm.

Pancreatrema disacetabulum Oshmarin from *Eurystomus orientalis* from Russia, including the Primorskii Krai, is the only previously described species, but Lalitha & Alwar (1960) recorded *Pancreatrema* sp. from *Anas boschas domesticus* in Madras.

P. meliphagae differs from *P. disacetabulum* in its more slender shape (width/length ratio 1:5 in former, 1:3 in latter) in the slightly more forward position of the ovary, in the apparently more forward position of the genital pore, and in the size of the eggs (34 x 21 μm in *P. meliphagae*, 62 x 42 μm in *P. disacetabulum*). The eggs, although more pointed at one end in *P. meliphagae*, have the same general appearance in the two species. Measurements of the organs are much the same, except that the largest vitelline field in *P. disacetabulum* is almost twice the length of that in *P. meliphagae*. *P. disacetabulum* was found in the pancreas of *Eurystomus orientalis*; *P. meliphagae* was thought to be from the bile duct of its host.

Proacetabulorchis dogieli Belopolskaja & Bychovskaja-Pavlovskaja

Host. Ardea novaehollandiae.
Localities. Brisbane, Qld, 1.ix.1965 (21 specimens). Deception Bay, Qld, 15.viii.1961 (1 specimen; collected G. Monteith).
Location in host. Bile ducts.
Incidence. 2 of 2 birds from Qld, none of 14 birds from S. Aust.
Slides deposited. SAM V113, V114.

Description based on 9 stained mounts and 9 specimens in glycerine. (Measurements from stained mounts). The specimen from Deception Bay is much larger than the others, and measurements for it are given separately.

Description.

Body flat, elongate; width generally uniform, slightly greater behind acetabulum, generally behind mid-body. Length 3.4–4.2 mm (3.8), width 544–816 μm (646). Width/length ratio 1:4.8–1:6.9 On body surface, papillae, 18 μm across base, as close as 26 μm apart in preacetabular region, much sparser posteriorly (not apparent in all specimens). Suckers rounded, approximately equal. Oral sucker 329–435 μm

(366) long x 294–388 μm (341) wide. Acetabulum, in anterior third of body, 318–412 μm (355) in diameter. Pharynx rounded, 94–112 μm (99) long x 88–118 μm (101) wide. Oesophagus, slightly contracted, 106–223 μm (141) long. Caeca extending to distance 510–816 μm (595) from end of body.

Excretory pore terminal; main stem of bladder bifurcating just posterior to ovary; excretory arms extending to level of pharynx.

Testes 94–212 μm (169) long x 118–247 μm (147) wide; contiguous, generally diagonal. (In 18 specimens, testes of 11 diagonal, 2 approaching tandem, 4 approaching symmetrical, 1 symmetrical). Anterior testis on right or left side; posterior testis slightly dorsal to anterior rim of acetabulum or slightly anterior to latter. Seminal vesicle internal; cirrus in one specimen 176 x 59 μm, with flattened end. Genital pore in region of caecal bifurcation, generally very slightly posterior to latter.

Ovary rounded, 71–153 μm (98) x 82–165 μm (109), median, near mid-length of body. Mehlis' gland somewhat diffuse, posterior and partly lateral to ovary. Receptaculum seminis large, rounded (in four specimens, 165–176 μm (174) x 141–164 (154)), abutting posterior lateral border of ovary.

Vitelline fields mostly extracaecal, from 680–1428 μm (1075) long, sometimes reaching acetabular level anteriorly; posteriorly reaching, approximately, posterior third of body. Follicles up to 82 x 33 μm, mostly in single or double row on each side.

Uterus intercaecal; posterior to caeca spreading out to sides and end of body. Ascending uterus passing dorsal to acetabulum and to testes, to genital pore. Eggs 29–32 μm (30) x 18–22 μm (20).

Specimen from Deception Bay: Length 7.2 mm, width 0.95 mm, width/length ratio 1:7.5. No papillae on surface. Oral sucker 447 x 494 μm, acetabulum 529 x 529 μm. Pharynx 141 x 129 μm, oesophagus 318 μm; caeca ending 1.19 mm from posterior end. Testes diagonal; anterior testis (on left), 517 x 270 μm; posterior, 435 x 282 μm. Cirrus 247 x 59 μm. Ovary 188 x 176 μm. Vitelline fields 2.18 and 2.07 mm, reaching to 2.21 mm from posterior end of body. Eggs 28–31 μm (30) x 17–20 μm (18).

Discussion

Three species have been assigned to the genus: *P. prashadi* Gogate, *P. dogieli* Belopolskaja & Bychovskaja-Pavlovskaja and *P. strigosus* Sudarikov & Pavlov but only *dogieli*

agrees with Australian specimens in a sucker ratio approximately 1:1.

We have been unable to consult Belopolskaja and Bychovskaja-Pavlovskaja's description of *Proacetabulorchis dogieli*. Skrjabin (1970) (who followed Bychovskaja-Pavlovskaja (1962) in including the species in *Platynotrema* Nicoll) gave a figure, presumably from Belopolskaja and Bychovskaja-Pavlovskaja (1954), and a description of the species according to Belopolskaja (1954). We have compared our specimens with a further description by Bychovskaja-Pavlovskaja (1954) and with the figure and description in Skrjabin (1970), and conclude that they are conspecific. (Although in the figures given by these authors the vitelline fields appear to be shorter than in our specimens, in the measurements given in Skrjabin (1970) they are comparable with ours). Belopolskaja and Bychovskaja-Pavlovskaja's original specimens were from *Numenius arquatus* and *N. madagascariensis*

from Siberia. Fischthal & Kuntz (1974) gave a description of *P. dogieli* from the mangrove heron, *Butorides striatus*, from Sabah, with a discussion of the species. They noted variation in the relative positions of the testes, which were somewhat diagonal in most of their specimens but were frequently symmetrical. As mentioned in our description, the testes in worms from one individual host varied from symmetrical to almost tandem.

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A NEW SPECIES OF LARGE, GREEN TREE FROG FROM NORTHERN WESTERN AUSTRALIA

BY M. J. TYLER, MARGARET DAVIES AND A. A. MARTIN

Summary

A new species of large, green tree frog of the genus Litoria is described from the vicinity of Kununurra in northern Western Australia. Details of external morphology are supplemented by a study of radiographic plates. The new species is most closely related to L. caerulea and lives sympatrically with it.

A NEW SPECIES OF LARGE, GREEN TREE FROG FROM NORTHERN WESTERN AUSTRALIA

by M. J. Tyler,* Margaret Davies* and A. A. Martin†

Summary

Tyler, M. J., Davies, Margaret & Martin, A. A. (1977) A new species of large, green tree frog from northern Western Australia. *Trans. R. Soc. S. Aust.* **101**(5), 133-138, 31 August 1977.

A new species of large, green tree frog of the genus *Litoria* is described from the vicinity of Kununurra in northern Western Australia. Details of external morphology are supplemented by a study of radiographic plates. The new species is most closely related to *L. caerulea* and lives sympatrically with it.

Introduction

The green hylid tree frogs of Australia range in size from the predominantly Papuan *Litoria infrafrenata* (Günther), attaining a maximum size of 135 mm, to small and delicate species such as *L. fallax* (Peters) and *L. bicolor* (Gray), adult as small as 23 mm. The conspicuous nature of these green animals renders them particularly highly disposed to being collected by herpetologists, leading to the reasonable assumption that this group of Australian frogs should be well established and taxonomically stable.

In the course of a visit to northern Western Australia in February 1977, we collected representatives of an hitherto undescribed green hylid, readily distinguished by several features of its gross morphology, but with distinct affinities with *L. caerulea*. Subsequently additional preserved specimens were provided by the Western Australian Museum (WAM). Here we describe this new species, compare it with *L. caerulea* and discuss the significance of this discovery.

Methods of measurements follow Tyler (1968). X-ray illustrations were obtained by the Rank Xerography process employing positive mode. Direct comparisons were made between X-ray prints of the holotype of the new species and X-ray prints and dried osteological material of *L. caerulea*.

Litoria splendida sp. nov.

FIGS 1, 3, 4

Holotype: WAM R56840. An adult female collected at Lake Argyle Tourist Village, Kimberley Division, northern Western Australia, by a joint University of Adelaide and University of Melbourne field party on 22.ii.1977.

Definition: The characteristic features of this species are its very large size (males and females *ca* 100 mm S–V length); possession of a vast and bulbous gland on the entire dorsal surface of the head; relatively short and slightly webbed fingers with prominent terminal discs; brilliant green dorsal colouration bearing sulphur spots, and its orange flanks (Fig. 1).

Description of Holotype: Head considerably broader than long (HL/HW 0.85), its length equivalent to one-third of body length (HL/S–V 0.33). Entire dorsal cranial surface obscured by a dermal gland raised approximately 5 mm above surface. Snout not prominent, truncated when viewed from above and in profile. Nostrils more lateral than superior; their distance from end of snout considerably less than that from eye. Distance between eye and naris greater than internarial span (E–N/IN 1.18). Canthus rostralis slightly defined and gently rounded. Eye relatively inconspicuous, its diameter less than eye to naris distance. Tym-

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panum visible and inclined medially at 45°; diameter equivalent to eye diameter.

Vomerine teeth on short, posteriorly directed, triangular elevations between and posterior to choanae. Tongue extremely broad.

Fingers short and equipped with broad lateral fringes; in decreasing order of length 3>4>2>1. Webbing between fingers only basal. Terminal discs extremely broad and extending considerably beyond margin of lateral fringes. Subarticular and palmar tubercles prominent.

Hind limbs rather short (TL/S-V 0.48). Toes in decreasing order of length 4>5 = 3>2>1. Webbing reaches half way up penultimate phalanx on 5 and base of penultimate phalanx of 4. Subarticular tubercles prominent. Very large oval inner and small rounded outer metatarsal tubercles.

In addition to cranial gland, skin modified in following ways: (1) poorly developed dermal ridge on posterior margin of forearm; (2) ventral surfaces of body and femora uniformly granular.

In preservative dorsal surface of head, body and portions of limbs hidden at rest in a living frog are dull slate blue. Dorsum of body liberally spotted with very small white areas. Dorsal surface of third and fourth fingers, and third, fourth and fifth toes, anterior and posterior surfaces of thighs and almost entire ventral surface very pale cream.

In life dorsum dark lime green bearing numerous small sulphur yellow spots, each of which has a dark border. First two fingers, first three toes, groin and back of thighs brilliant orange. Ventrally white, with pale green mandibular border.

This female specimen has a few very small pigmented ova and the oviducts are convoluted only posteriorly.

Dimensions of Holotype: S-V 100.7 mm; TL 48.0 mm; HL 33.4 mm; HW 39.2 mm; E-N 8.6 mm; IN 7.3 mm; E 7.7 mm; T 7.8 mm.

Variation

There are six paratypes all taken in northern W.A.: WAM R26818, Old Napier Downs Cave, Napier Downs, Napier Range, A. M. Douglas and G. W. Kendrick 8.vii.66; R44601-02, spillway at northern boundary of Lake Argyle, Western Australian Museum survey 11.ii.72 and 20.i.72; R47231, Prince Regent River National Park, Western Australian Museum survey 17.vii.74; R56779, Kimbolton

Spring, Kimbolton Stn, W, H. Butler 26.vi.76; R56780 Drysdale River National Park, Western Australian Museum survey 13.viii.76.

The snout to vent length range is 90.2–106.3 mm; the largest of these is a female containing numerous small pigmented ova.

In their gross morphology the paratypes differ from the holotype only slightly. All exhibit an extremely prominent supracranial gland, sometimes extending anteriorly beyond the anterior tip of the snout, and also overlapping the tympanum. The head is consistently broader than long (HL/HW 0.85-0.95), whilst the HL/S-V ratio is 0.32-0.37. Similarly the E-N/IN range is comparable to that of the holotype (1.00-1.23). The limbs are consistently rather short (TL/S-V 0.46-0.50).

All specimens exhibit numerous, small, white spots on the dorsum.

Comparison with other species

(a) *External morphology*

Within the Australo-Papuan region there are several large tree frogs that are predominantly green in life. Of the species restricted to New Guinea, *L. splendida* may be distinguished from *L. graminea* by its slightly broader head (HL/HW 0.85-0.95 in *L. splendida*; 0.90-1.03 in *L. graminea*), shorter hind limbs (TL/SV 0.46-0.50 in *L. splendida*; 0.56-0.60 in *L. graminea*), less extensively webbed fingers (approximately one-half webbed in *L. splendida* but reaching the discs of all fingers in *L. graminea*); *L. graminea* lacks the supracranial gland of *L. splendida* and is probably smaller (males of *L. graminea* are only up to 65 mm in length).

Litoria infrafrenata is a predominantly Papuan species known in Australia only from the Cape York Peninsula in Queensland. Its size overlaps that of *L. splendida*, but it is a shallower bodied creature, always exhibiting a brilliant white mandibular stripe. The head is structurally quite different, tending to be flattened with a prominent and concave facial shelf. In contrast, *L. splendida* has a high head and the prominent supracranial gland is totally lacking in the former species. The hind limbs of *L. splendida* are slightly shorter, TL/S-V 0.46-0.50 as opposed to 0.51-0.63 in *L. infrafrenata*.

Litoria splendida is most closely related to *L. caerulea* (Fig. 2) and occurs sympatrically with it. The size and general habitus of the two species are similar. They differ principally in

Fig. 1. Adult individual of *Litoria splendida*.

Fig. 2. Adult individual of *Litoria caerulea*.

Fig. 3. Distribution of *Litoria splendida* (solid circles) and the Australian portion of the geographic range of *L. caerulea* (stippled).

colouration, dermal gland development and in behaviour (see discussion). *L. caerulea* occupies a large area of the Australian continent (Fig. 3) and is somewhat variable in its colouration throughout its range. Central Australian individuals commonly have large white spots and patches on their bodies and are referred to *L. gilleni* by some authors (e.g. Cogger 1975). In the northern part of the Northern Territory and Western Australia (including the type locality of *L. splendida*), individuals are usually a pale yellowish green; elsewhere the dorsum ranges from dark green to olive. However, the distinctions between *L. splendida* and *L. caerulea* remain conspicuous. *L. caerulea* lacks the brilliant yellow markings found on the thigh, groin and hand of *L. splendida* and lacks the small sulphur spots commonly occurring in the new species. *L. caerulea* is otherwise unique amongst Australian hylids in exhibiting a parotoid gland but it lacks any comparable glandular tissue on the dorsum of the skull.

Osteological features of the two species are listed below.

(b) *Comparative osteology of L. splendida and L. caerulea*

Recognising that a close relationship exists between *L. splendida* and *L. caerulea* we undertook a detailed comparison of a number of osteological features: *L. splendida* is shown in Figure 4.

1. *Skull*

(a) Shape: the shape of the skull of *L. splendida* differs from that of of *L. caerulea* in that it is narrower and less blunt.

(b) Nasals: the shape of the nasals and their relationship with the sphenethmoid are difficult to determine from X-ray photography. It is known that in *L. caerulea* the well-developed nasals are narrowly separated medially by the sphenethmoid with which they articulate and overlap extensively (Tyler & Davies[1]).

(c) Frontoparietals: a supraorbital frontoparietal flange is present in both species, similar to that found in *L. infrafrenata* (Davies in press) but in *L. caerulea* this is developed to a lesser extent than in *L. splendida* and *L. infrafrenata*.

(d) Frontoparietal fontanelle: this is moderately sized and ovoid in both *L. splendida* and *L. caerulea*.

(e) Squamosals: the otic rami of the squamosals do not overlap the crista parotica in either species.

(f) Otoccipital region: the lateral extremities of this region are cartilaginous in both species.

(g) Pterygoid: the well developed pterygoids do not articulate with the otic capsule in either species.

(h) Quadratojugal: the quadratojugal is well developed in both *L. splendida* and *L. caerulea*.

(i) Prevomers: the alae of the prevomers are developed to differing degrees in *L. splendida* and *L. caerulea*. Those of *L. splendida* are elongate and extend almost to the level of the palatal shelf of the maxillaries, whereas those of *L. caerulea* are short and barely reach the level of the extremities of the supraorbital frontoparietal flange.

(j) Palatine processes of premaxillaries: in *L. caerulea*, these processes abut along their medial extremities, whilst in *L. splendida* there is no medial articulation.

2. *Vertebral column*

(a) Sacral diapophyses: the sacral diapophyses are poorly expanded in *L. splendida* and moderately expanded in *L. caerulea*.

(b) Ilia: the ilia extend anteriorly to the sacral diapophyses in both species.

(c) Transverse processes of posterior presacral vertebrae: in *L. splendida* these are equal and

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[1] Tyler, M. J. & Davies, M. (in manuscript) Species group within the Australopapuan hylid frog genus *Litoria* Tschudi.
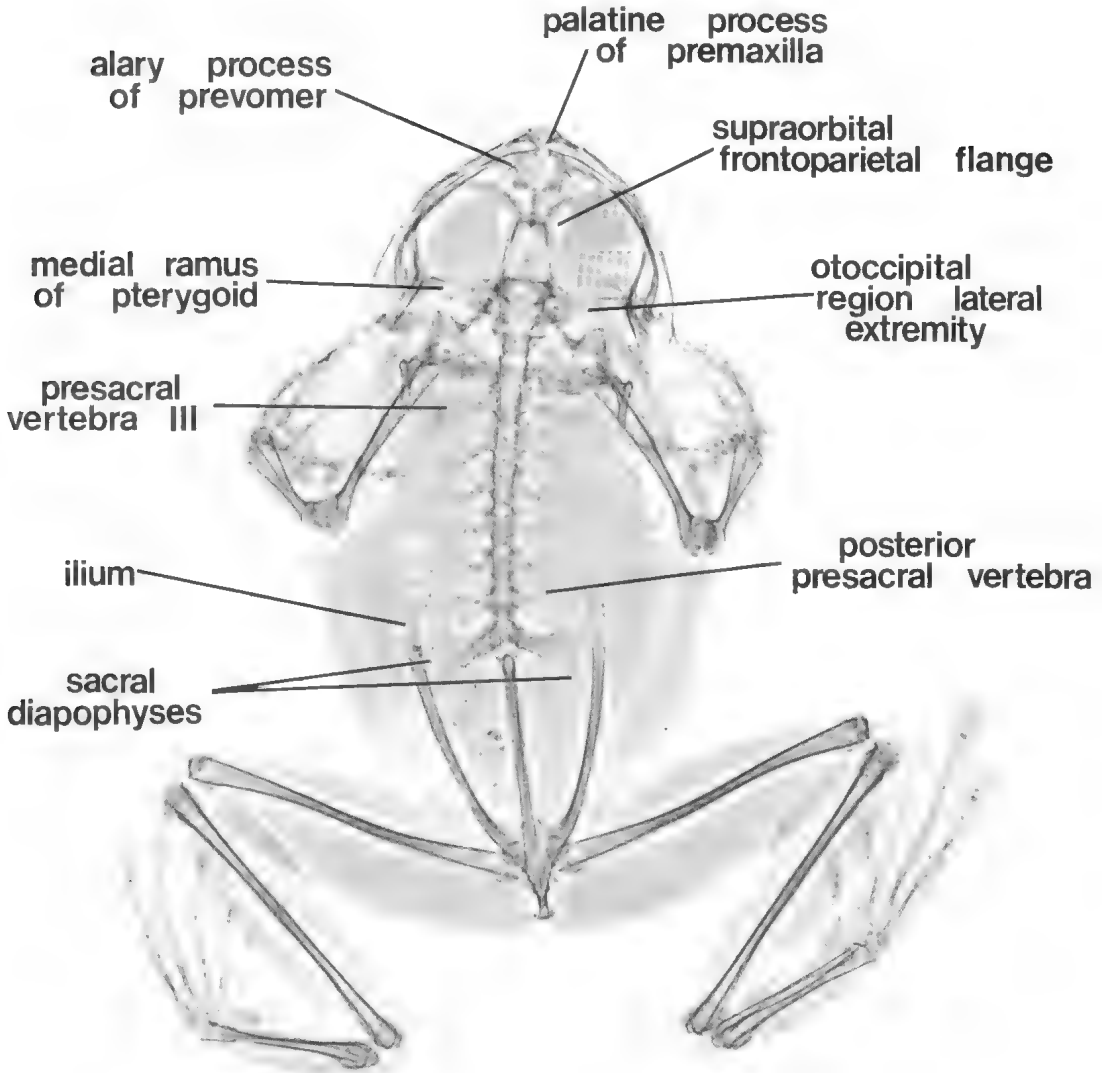
Fig. 4. X-ray print of *Litoria splendida* (Holotype: WAM R56640).

directed slightly anteriorly, whereas in *L. caerulea* the processes are subequal and are directed anteriorly at a slightly more acute angle.

(d) Transverse processes of presacral vertebrae III: these are equal in width to the sacral diapophyses in *L. caerulea,* but narrower than the width of the sacral diapophyses in *L. splendida.*

Habitat

The specimens collected by us were taken in artificial situations such as upon bitumen roads at night following torrential rains. How-

ever it is clear that such a large frog would require a summer retreat to avoid very high temperatures. Two of the paratypes were collected within caves: R26818 at Old Napier Downs Cave, and R44600 at a site 8 km N of Lake Argyle. Similarly R27231 was taken in a ledge in a sandstone gorge.

Litoria splendida is evidently adept at surviving in areas of low rainfall, so paralleling the habits of *L. caerulea.* In the vicinity of the type locality the vegetation is predominantly scattered scrub of sparse, low-growing eucalypts with pockets of *Pandanus.* Soils range there from sand to clay. The area receives an average rainfall of 50–75 mm from

monsoonal rains between December and March.

Litoria splendida is commensal with man and the species is well known to inhabitants at Lake Argyle and at Kununurra. In common with *L. caerulea* it inhabits bathrooms, toilets and other such sites where there is water. The holotype was taken at night on the floor of an ablution block.

Distribution

As demonstrated in Figure 3 all of the localities at which this species has been taken occur in the extreme northwestern and peripheral portion of Australia.

Discussion

As indicated above, the new species is phylogenetically very closely related to *L. caerulea*. The supracranial gland seems to represent hypertrophied parotoid glands that have increased in extent as well as mass, thus becoming a single unified gland.

In captivity, behavioural differences between the species have been noted. Whereas *L. caerulea* tends to become a rather sedentary creature in captivity, *L. splendida* after three months is exceptionally active and avoids attempts to handle it.

In finding such a large and spectacular creature in 1977, we are led to the conclusion that the extent of sampling of the Australian lower vertebrate fauna is highly deficient.

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ON THE MANUS AND PES OF THYLACOLEO CARNIFEX OWEN (MARSUPIALIA)

BY *R. T. WELLS AND B. NICHOL*

Summary

An articulated left and right manus and a partially disarticulated left pes of the cave lion Thylacoleo carnifex were recovered recently from a Pleistocene cave deposit at Naracoorte, South Australia. The structure of the manus and pes is described. The manus is digitigrade with limited flexion in digits II, III. IV and V. Digit I is extremely robust, bears a large hooded ungual crest and is pseudopposable to a spatulate pisiform. The pes is plantigrade with major part of the weight transferred through the astragalus to the calcaneum. Analysis of the structure of the pes indicates syndactyly and the presence of a divergent hallux. The manus and pes show structural affinities with the arboreal phalangerids.

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by R. T. WELLS* and B. NICHOL*

Summary

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An articulated left and right manus and a partially disarticulated left pes of the cave lion *Thylacoleo carnifex* were recovered recently from a Pleistocene cave deposit at Naracoorte, South Australia. The structure of the manus and pes is described. The manus is digitigrade with limited flexion in digits II, III, IV and V. Digit I is extremely robust, bears a large hooded ungual crest and is pseudopposable to a spatulate pisiform. The pes is plantigrade with major part of the weight transferred through the astragalus to the calcaneum. Analysis of the structure of the pes indicates syndactyly and the presence of a divergent hallux. The manus and pes show structural affinities with the arboreal phalangerids.

Introduction

Thylacoleo carnifex Owen (1859), the "flesh eating marsupial lion", was described from skull fragments from a late Pleistocene deposit at Lake Colangulac, Victoria. Although the tooth formula of such thylacoleonids is typically phalangeroid, the animals are characterised by development of exceedingly large sectorial upper and lower third premolars, large conical upper and lower first incisors and a marked reduction in the remaining incisors, canines and molars. The niche occupied by *T. carnifex* therefore has been the subject of considerable speculation (vide Gill 1954; Finch 1971). However recent studies of jaw mechanics (Finch 1971) tend to support Owen's conjecture that it was a large carnivore.

Finch (1971) made a preliminary analysis of the skeleton and suggested that the relatively long fore-limb may be used to strike at prey in a fashion similar to that of *Sarcophilus*. This suggestion relied partly upon her interpretation of the paw as a strong and heavy structure in which the digits could not be widely separated. However the structure of the pes was unknown to her, as the major portions of the hind feet are missing from all the skeletal material previously reported. The following is a preliminary description of the general morphology and arrangement of the bones of the manus and pes of this enigmatic animal.

Materials and methods

During excavations at Victoria Cave, Naracoorte, numerous skeletal elements of *Thylacoleo* were collected including the articulated right and left manus with portions of the forelimb in association. The specimens were held together by a patina of calcite. In the laboratory the left manus was partially cleaned, but left in its fused state; the right manus was carefully disassembled, each element cleaned and then reassembled (Fig. 1). In the course of preparation of the right manus the cuneiform and pisiform of the left manus were recovered from the sediment.

All specimens removed from the Victoria Cave deposit are allotted numbers indicating their positions in a three-dimensional grid (Wells 1975). During the sorting of bone material, portions of a disarticulated left pes bearing similar grid reference numbers were recovered. This partial pes (Fig. 3) is not referable to any extant marsupial, nor could it be attributed to any extinct form for which the foot structure is known. The calcaneum is consistent with one recovered with skeletons from James Quarry, Naracoorte (M. Plane, pers. comm.). The close proximity of *Thylacoleo*

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P 16679

Fig. 1. Assembled right manus (P16679) of *T. carnifex*. The 5th medial phalange, cuneiform and pisiform are missing from this specimen.

tibia and fibula, and similarity in proportions to the manus, suggest that it is indeed the pes of *Thylacoleo*.

The following specimens and casts of the assembled right manus and left pes are lodged at the South Australian Museum:

P16678: left manus including fused carpus P16678a, cuneiform P16678b, pisiform P16678c, fused metacarpus P16678d, fused proximal and medial phalanges. P16678e, distal phalanges P16678f.

P16679: right manus including scapholunar P16679a, trapezium P16679b, trapezoides P16679c, magnum P16679d, unciform P16679e, metacarpals I to V P16679f, g, h, i, j respectively, proximal phalanges I to V P16679k, l, m, n, p respectively, medial phalanges II to IV P16679q, r, s respectively and distal phalanges I to V P16679u, v, w, x, y respectively and sesamoids P16679z.

P16680: left pes including astragalus P16680a, calcaneum P16680b, cuboid P16680c, navicular P16680d, metatarsals II, III, IV V P16680e, f, g, h respectively

General description of the manus

The manus of *Thylacoleo* includes the carpus, metacarpus, phalanges and certain sesamoids associated with them (Figs 2A, B). The carpus is composed of seven bones arranged in two transverse rows. Articulating with the distal row of carpals are five metacarpals. Four of the five metacarpals are closely apposed, and each bears three phalanges. Metacarpals II–V show little lateral mobility, whereas the first (which is considerably shorter and more robust) bears only two stout phalanges. The distal phalange of the first digit bears an extremely large ungual crest and ungual process, suggesting the presence of a large recurved claw or unguis. Unlike digits II to V, the first is capable of considerable divergence as well as flexion. It appears to be opposable to a broad spatulate pisiform rather than to the remaining digits.

Carpus: In *Thylacoleo* there has been a loss and fusion of carpal elements to produce two rows which have a transverse convex cranial outline and a concave caudal one.

The proximal row is composed of three elements, the scapholunar (a fusion of scaphoid and the lunar) the cuneiform and a sesamoid, the pisiform. The scapholunar articulates with the distal end of the radius and bears on the trapezoides, trapezium and portion of the medial face of the magnum. The cuneiform, or ulnar carpal is greatly reduced. In comparison with most mammals it is a small, wedge-shaped bone concave on the proximal surface for receipt of the styloid process of the ulnar, and convex on the distal surface where it inserts in a basin in the unciform. It broadens caudally and bears a facet on the proximal surface at the point of attachment of the pisiform. The pisiform is short, broad and dorso-ventrally flattened and slightly expanded distally.

The distal rows of carpals is composed of: trapezium, trapezoides, magnum and unciform. The trapezium (carpale 1) is a small flattened bone in the form of a partial helix. It articulates laterally with the trapezoides and distally with the first metacarpal; the proximal end inserts in a notch in the palmar face of the scapholunar. Small rotations of the trapezium about its articulation with adjacent carpal bones result in considerable lateral-medial displacement of the first digit.

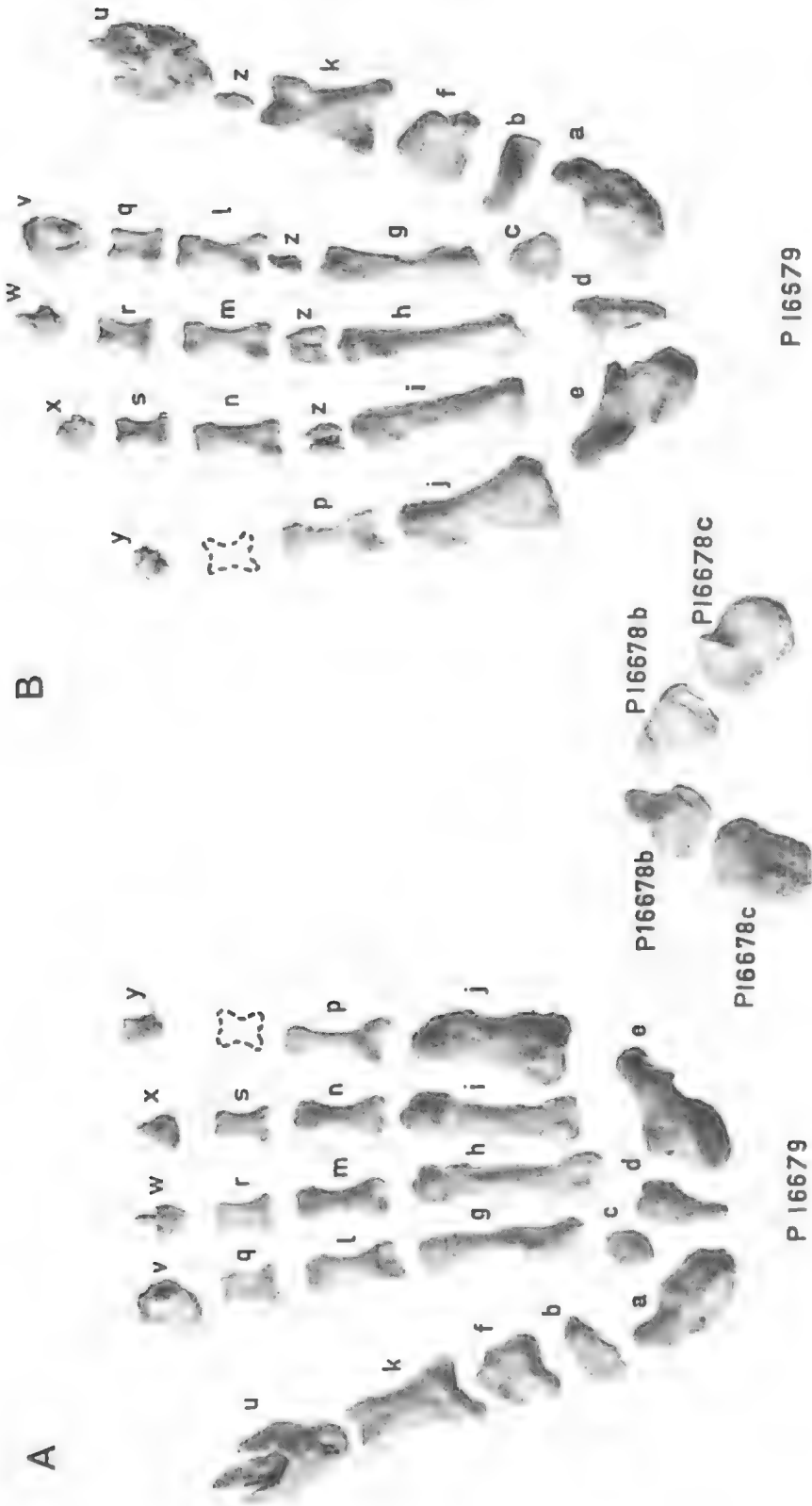The trapezoides (carpale 2) is a small wedge shaped, proximo-distally compressed bone the

Fig. 2. Elements of the right manus and cuneiform and pisiform of the left manus of *T. carnifex* (A) dorsal view (B) palmar view. a, scapholunar; b, trapezium; c, trapezoides; d, magnum; e, unciform; f, g, h, i, j, metacarpals I-V resp.; k, l, m, n, p, proximal phalanges I-V resp.: q, r, s, t, medial phalanges I-IV resp.; u, v, w, x, y, distal phalanges I-V resp.; z, sesamoids.
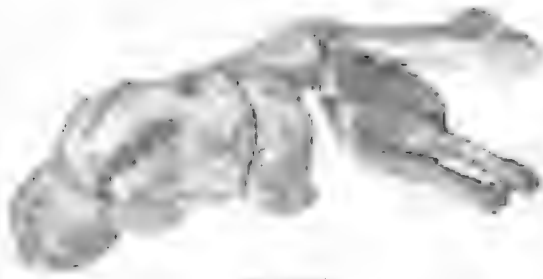
P16680

Fig. 3. Dorsal view of the partial left pes (P16680) of *T. carnifex*. The cuneiforms, metatarsal I, portion of metatarsal IV and the phalanges are missing from this specimen.

ventral face of which is approximately triangular in outline. It articulates proximally with scapholunar, medially with the trapezium, distally with metacarpal II and laterally with the magnum. The magnum (carpale 3) forms a triangular wedge between the scapholunar and the unciform which bear on it medially and laterally respectively. It has a narrow medially-laterally flattened palmar projection. It bears distally mainly on the third metacarpal with a small portion bearing on the oblique lateral projection of metacarpal II.

The unciform (carpale 4) is the largest bone in the carpus, its lateral aspect is convex and extends down in a continuous curve behind the fifth metacarpal. A depression in the middle of the proximal face receives the distal portion of the cuneiform. The convex palmar face of this bone bears facets which articulate with metacarpals IV to V and the lateral face of the magnum.

Metacarpus: There are five metacarpals here numbered I to V from the medial to the lateral side. Metacarpal I is exceedingly robust, being almost twice the cross-sectional area of the remaining four metacarpals, yet only one-third as long. The expanded head of metacarpal I articulates proximally with the distal end of the trapezium and at its furthermost lateral displacement contacts the medial face of metacarpal II close to its proximal end.

Distally the axis of articulation of metacarpal I with the proximal phalanx is rotated medially approximately 30° to the axis of articulation with the trapezium. Metacarpals II, III, IV are closely apposed slender bones, medially-laterally flattened and rectangular in cross section. Metacarpal II is slightly shorter than III and IV which are of almost equal length. The proximal ends of these bones are

expanded and displaced laterally; the shape of the articulating facets restricting movement to the dorso-ventral plane. Metacarpal II bears proximo-medially on the trapezoides and to a lesser degree proximo-laterally on the magnum. Metacarpal III bears proximo-laterally on the lateral face of the magnum while metacarpal IV inserts proximally in a notch in the unciform.

Metacarpal V differs from II, III and IV in the possession of a pronounced lateral flange, and lacks the expansion and lateral displacement of the proximal end; the articulating facet suggesting a small degree of lateral-medial rotation in addition to the dorso-ventral.

Phalanges: Digit I composed of a proximal and distal phalanx is extremely robust, the proximal portion being approximately 3X the cross-sectional area and 1.5X the length of the adjacent proximal phalanges. The distal phalanx bears a large ungual crest and ungual process. Digits II to V, although containing a medial as well as a proximal and distal segment, are overall slightly shorter than those of digit I. All the distal segments bear the sheathing base of small hooded claws. The ungual process of these segments is relatively long and slender and is less recurved than that of digit I

Sesamoid bones: On the palmar surface of the metacarpophalangeal joint of digits III and IV are two sesamoid bones articulating primarily with the head of each metacarpal, and secondarily with the palmar tubercles of each proximal phalanx. A single sesamoid was found associated with the metacarpophalangeal joint of digit II; the small sesamoid found adhering to the proximo-distal phalangeal joint of digit I is probably the other element in this pair.

The mechanism of the grasp in the manus

The relationship between articulating facets was used to determine the range of movement between adjacent bones. A lateral view of the range of movements in digits II, III, IV and V is depicted in Fig. 4 — in the extended position (A) and flexed (B). The distal phalanges are prevented from opposing the palm by restricted movement at the metacarpo-phalangeal joint and to a lesser extent at the proximo-medial phalangeal joint.

In dorsal view, with digits extended (Fig. 5), the extreme divergence of digit I and the slight divergence of digit V contrasts markedly with the close apposition of digits II, III and IV

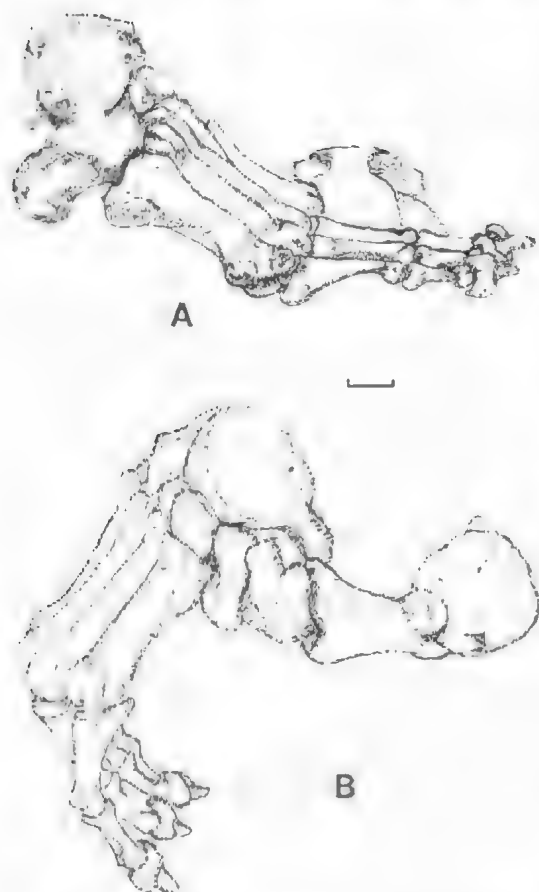The range of latero-medial movement in digit I, and its relationship to the pisiform, is

Tarsus: The tarsus normally consists of seven tarsal bones arranged in two rows with a central bone, the navicular, between. The proximal row consists of the astragalus and calcaneum. In *Thylacoleo* the tibia and fibula articulate only with the astragalus which is the second largest bone in the tarsus. It articulates proximally with the tibia and fibula, distally with the navicular and ventrally with the calcaneum and the proximal dorsal surface of the cuboid. The proximal surface of the main body of the astragalus bears a shallow trochlea groove which articulates with the distal process of the tibia, an oblique lateral facet articulates with the lateral malleolus of the fibula. The astragalus articulates with the calcaneum by two distinct facets, a lateral concave one and a medial convex one. The distal portion, (head of the astragalus) bears a large convex, rounded facet which articulates with the navicular.

The calcaneum is the largest and longest bone of the tarsus. It bears two facets on the

Fig. 4. (A) Lateral view of the right manus of *T. carnifex* with digits fully extended;
(B) Medial view of the right manus of *T. carnifex* with digits fully flexed.

also shown in Fig. 5. Flexion of digit I and the pisiform would bring them into close opposition and it is suggested that this is the primary grasping movement. With the digits in their most divergent position it can be seen that the plane of the grasp is almost at 90° to the remaining digits. A similar grasp is found in the brushtailed possum *Trichosurus vulpecula* (Breeden & Breeden 1970).

Description of the pes

The skeleton of the pes in mammals is composed of the tarsus, metatarsus, phalanges and associated sesamoids. The following bones are missing from the partial pes recovered from the Victoria Cave: the cuneiform bones of the distal row of the tarsus, the first metatarsal, all the phalanges and any associated sesamoids, Fig. 6A, B.

Fig. 5. Dorsal view of the right manus of *T. carnifex* showing digits II to V fully extended with digit I flexed. The outline of the cuneiform and pisiform was produced from a mirror image of those from the right manus.
Inset—depicts dorsal view of digit I in extended position.
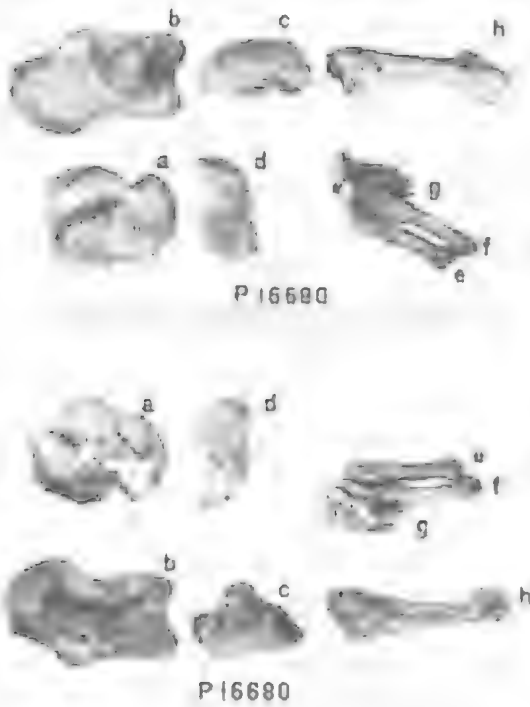
P 16680

P 16680

Fig. 6. Elements of the left pes of *T. carnifex* upper = dorsal view; lower = ventral view. a, astragalus; b, calcaneum; c, cuboid; d, navicular; e, f, g, h, metatarsals II, III, IV, V.

proximal surface which articulate with those on the distal surface of the astragalus to form a stable interlocking joint. The calcaneal tuberosity is short, robust and slightly flared caudally. The distal surface of the calcaneum is deeply grooved dorso-ventrally where it articulates with the proximal surface of the cuboid. The navicular is the central bone in the tarsus, it articulates proximally by way of a large concave latero-medial facet with the astragalus, ventrally by way of a small concave facet with the cuboid and distally by way of a large latero-medial convex facet with the missing cuneiforms. A pronounced tuberosity on the distal medial surface may articulate with the proximal portion of the missing medial cuneiform. The remaining tarsal bone, the cuboid, appears to be as long as the combined length of the navicular and the missing cuneiforms. It articulates proximally by way of a long narrow facet with the dorso-ventral groove in the distal face of the calcaneum. Two small facets occur on the dorsal surface; the larger proximal one articulates with the astragalus while the smaller anterior one presum-

ably articulates with the missing lateral cuneiform. It bears a small plantar process. The distal end forms a large slightly recurved oval surface which for 4/5th of its length articulates with the proximal surface of metatarsal V and for 1/5th with the lateral portion of the proximal surface of metatarsal IV.

Metatarsus: Metatarsals II, III and the proximal portion of IV were found fused together and in the vicinity of metatarsal V. A latero-medial section through the assembled metatarsals has a convex dorsal outline and concave ventral one (Fig. 7).

The structure of metatarsal I is unknown, but the presence of a medial distal tuberosity on the navicular is suggestive of a divergent hallux comparable to *Trichosurus*. Metatarsals II and III are relatively short and slender bones, their close apposition and general form is similar to that of the syndactylous toes in *Trichosurus*. The size of the proximal portion remaining of metatarsal IV and its relationship to metatarsals III and V indicate that it may have been the longest of the three. The lateral half of the proximal facet on metatarsal IV articulates with the dorsal 1/5th of the distal facet of the cuboid. A small proximo-lateral facet articulates with the proximo-medial face of metatarsal V. Metatarsal V is the most robust of all four. It bears pronounced tuberosities on the proximal and distal latero-ventral surfaces. A large proximal facet articulates with the cuboid, while a small ventro-medial facet articulates with metatarsal IV.

In *Thylacoleo* the greater part of the body weight supported by the hind limbs is transferred from the astragalus onto the calcaneum and portion of the cuboid. The surface area of articulation of the calcaneum with the distal tarsals is 20% larger than that of the astragalus suggesting a distribution of weight through these elements to the metatarsals in the ratio 3:2. The larger portion of the weight is borne

Fig. 7. Distal view of proximal surface of metatarsals 2, 3, 4 and 5.

by metatarsal V and a small portion of IV,
while the remaining 40% is borne by digits I,
II, III and a portion of IV. However the
slender nature of metatarsals II and III, and
the presence of a pronounced medial tuberosity
on the navicular, suggests that much of this
load is borne by a robust divergent hallux.

The shallow trochlea groove, the plantigrade
nature of the stance (Fig. 3), the apparent syn-
dactyly of digits II and III and the inferred
presence of a large divergent pollex are charac-
teristics which in Australian marsupials
resemble most closely the pes of phalangerids.

Discussion

The digits of the hands of most mammals
diverge when extended, and converge when
flexed (Haines 1958). Such hands are con-
sidered suitable for scrambling over rough
ground and, if clawed, to climbing; however
they appear unsuitable for gripping branches of
trees unless used in a clasping manner as is the
case with *Didelphis virginiana* (Haines 1958)
Cartmill (1974) examined the non-primate
arboreal sciurids, and concluded that in the
structure of the hand the arboreal genera were
distinguishable from the terrestrial forms only
by their longer 4th digits and carpal pads and
sharper, more recurved claws. Bishop (1964)
found little anatomical difference in the hands
of terrestrial and arboreal carnivores.

Animals which climb by grasping branches
e.g many primate species, usually have prehen-
sile hands. If carpo-metacarpal movement is
restricted to one plane, the divergent thumb is
classified by Napier (1961) as pseudo-oppos-
able but opposable if the thumb can rotate
about the carpo-metacarpal joint so as to
oppose the remaining digits.

In primates the degree of curvature of the
carpal arch is related to the extent of opposa-
bility of the thumb and to the size and func-
tional nature of the long flexors of the digits.
These lie in a tunnel formed by the carpal arch
and the flexor retinaculum which binds the two
sides of the arch together (Napier 1961). A
deeply curved carpal arch is characteristic of
animals in which flexing of the digits plays a
major role in locomotion and is likely to be
similarly deepened and strengthened to match
the exerted stresses of clasping during climbing.

The manus of *Thylacoleo* exhibits several
paradoxical features. (a) Digit I is capable of
wide divergence, and is pseudo-opposable yet
digits II, III and IV show little divergence or
convergence; (b) Digit V could diverge

TABLE 1

*Habit and digital formula of the manus of some mar-
supials*

Habit	Species	Digital formula of manus
Arboreal	*Phascolarctos cinereus*	4>3>2,>5>1
Arboreal	*Pseudocheirus peregrinus*	
Arboreal	*Acrobates pygmaeus*	
Arboreal	*Cercartetus concinnus*	
Arboreal	*Petaurus breviceps*	4>5>3>2>1
"	*Thylacoleo carnifex*	1>4>2,3>5>1
Arboreal	*Trichosurus vulpecula*	
Arboreal/Terrestrial	*Dasycercus cristicauda*	
Arboreal		
Terrestrial	*Dasyurus viverrinus*	
Arboreal/Terrestrial	*Antechinus flavipes*	
Arboreal/Terrestrial	*Sminthopsis crassicaudata*	
Terrestrial	*Vombatus ursinus*	
Terrestrial	*Macropus eugenii*	
Terrestrial	*M. giganteus*	
Terrestrial	*Thylacinus cynocephalus*	
Terrestrial	*Sarcophilus harrisii*	
Terrestrial	*Isoodon obesulus*	3>2>4>5>1
Terrestrial	*Macrotis lagotis*	

slightly; (c) All digits are clawed, the ungual
crest on digit I being extremely robust and
recurved while those on the remaining digits
are small and slender with little recurvature;
(d) the carpal arch is deep and robust yet the
digits with the exception of I, are capable of
only limited palmar flexion.

Finch (1971) suggests that compared with
other marsupials *Thylacoleo* has relatively long
limbs, and that the almost equal length of fore
and hind limbs implies a cursorial mode of
locomotion. However she also notes that the
scansorial (*Trichosurus*) and koala (*Phasco-
larctos*) have "fairly long fore limbs" but have,
in contrast to *Thylacoleo*, mobile digits on the
forepaws which enables the animal to maintain
a firm grasp of the branch of a tree. From our
analysis of the manus of *Thylacoleo* we con-
clude that, in spite of the limited convergence
in digits II, III and IV the animal does indeed
have an efficient and powerful grasping
mechanism in the opposition of digit I to the
pisiform. Furthermore although the manus
would adopt a digitigrade stance on a horizon-
tal surface it would be ideally adapted to a
climbing grasp. Tree frogs of the family
Hylidae illustrate this point very well. How-
ever as pointed out by Bishop (1964) there is
little anatomical difference in the hands of ter-
restrial and arboreal carnivores, a hand well

adapted to a climbing grasp could equally well be adapted to holding prey or both. The structure of the hind foot of *Thylacoleo* suggests a plantigrade stance when on a horizontal surface. Due to the absence of the cuneiforms and digit I of the pes, speculations about its functions are less meaningful, nonetheless it is remarkably similar in form and structure to the pes of the brushtailed possum (*Trichosurus*) which is used mainly in a clasping manner. The slender nature of metatarsals II and III and their close apposition is strongly indicative of syndactyly and is consistent with its proposed phalangeroid ancestry.

Table I lists the digital formulae of a range of marsupials. The truly arboreal forms among the phalangeridae all have the typically long 4th digit similar to Cartmill's (1974) arboreal sciurids. The digital formula for the manus of *Thylacoleo* is similar to a large range of semi-arboreal marsupicarnivores and terrestrial herbivores.

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SALT CRUST SOLUTION DURING FILLINGS OF LAKE EYRE

BY J. A. DULHUNTY

Summary

Investigations of solution of salt crust during the minor (1973) and major (1974) fillings of Lake Eyre were carried out in relation to water depth, salinity layering and wave action. When water depth exceeded half the maximum wavelength of surface waves, a saturated brine layer formed over residual salt crusts and retarded solution. Following the filling in February 1974, a large area of the thickest crust in central Madigan Gulf survived to the end of 1975 or early 1976, when water level fell to less than half maximum wavelength, and the residual crust dissolved; the thickest part of the Belt Bay crust survived until after September 1974 but dissolved by August 1975; in Jackboot Bay the thickest crust dissolved by September 1974.

SALT CRUST SOLUTION DURING FILLINGS OF LAKE EYRE

by J. A. DULHUNTY[*]

Summary

DULHUNTY, J. A. (1977) Salt crust solution during fillings of Lake Eyre. *Trans. R. Soc. S. Aust.* **101**(6), 147-151, 31 August, 1977.

Investigations of solution of salt crust during the minor (1973) and major (1974) fillings of Lake Eyre were carried out in relation to water depth, salinity layering and wave action. When water depth exceeded half the maximum wavelength of surface waves, a saturated brine layer formed over residual salt crusts and retarded solution. Following the filling in February 1974, a large area of the thickest crust in central Madigan Gulf survived to the end of 1975 or early 1976, when water level fell to less than half maximum wavelength, and the residual crust dissolved; the thickest part of the Belt Bay crust survived until after September 1974 but dissolved by August 1975; in Jackboot Bay the thickest crust dissolved by September 1974.

Introduction

Salt crusts, up to 46 cm thick, rest on Quaternary sediments in the southern bays of Lake Eyre North (Bonython 1956; Dulhunty 1974). Small inflows of river water covering parts of the lake bed, termed minor fillings, frequently dissolve some of the salt, but it is soon redeposited by rapid evaporation. On widely spaced occasions, as in 1949 and 1974, sufficient water enters the lake to cover the whole of its bed and dissolve all the salt crusts. On such occasions, referred to as major fillings, it has been assumed that the salt crusts rapidly dissolve; newly introduced sediments are deposited, and then new salt crusts reform on top of the sediments as brines evaporate. However, no precise or quantitative investigations have previously been made on the solution of salt during fillings of the lake, although redeposition of salt after the 1949 filling was described by Bonython & Mason (1953), and Bonython (1956).

The distribution and thickness of salt crusts in the southern bays of Lake Eyre North, were surveyed under dry lake conditions in 1972 (Dulhunty 1974). In 1973 a minor filling of the lake occurred when a limited quantity of water entered from the Warburton River during May, June and July. It flowed to the south-western corner of the lake filling Jackboot and Belt Bays, where solution of salt was examined in July 1973. By late December 1973 the whole

of the water had evaporated and the dissolved salt was redeposited, and the lake had returned to a dry condition, as reported by Mr M. O. Hughes of Muloorina Station.

Early in 1974 Lake Eyre filled to the greatest known depth since European settlement, and possibly for 500 years (Dulhunty 1975). The lake commenced to fill early in February 1974 and remained full throughout 1975 and 1976 during which time the solution of salt was investigated in relation to water depth, salinity layering and wave action; results are recorded in this paper.

Methods of investigation

Areas of undissolved salt crust were found by probing the lake bottom with a long pole from a boat. Where salt crust was present the pole hit its surface with a resounding impact and tended to bounce. Where it was absent, the pole penetrated the soft silt which had underlain the crust before it dissolved. This provided a simple, reliable and positive test for presence or absence of salt crust beneath lake waters. Areas of residual crust were mapped by running pole tests at intervals along pre-determined lines, and plotting results.

The thickness of a residual salt crust was measured by boring from a boat anchored by three radially disposed concrete blocks.

A 15 mm wood-boring auger was attached to lengths of 12.5 mm water pipe, screwed

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together so as to extend about 1 m above the surface of the water when the auger rested on the salt crust. A wood-boring brace was attached to the upper end of the piping. A long pole was then lowered vertically to rest on the salt beside the auger, and the position of a mark near the top of the boring pipe was noted on a scale attached to the pole. The auger was then rotated by means of the brace, and the depth penetrated into the salt by each rotation was measured on the pole scale as the pipe moved down. When the auger reached the base of the salt crust and broke through into the soft underlying silt, the depth of penetration measured gave the thickness of the crust.

Water samples for salinity determinations were collected at different depths by lowering the weighted end of 12.5 mm hose to the required level and then slowly pumping water up through the hose to remove that taken in during the lowering. Further water from the required level was then pumped slowly into a sample bottle. Densities of the water samples were measured very accurately, and their salinities, in terms of grams of Lake Eyre salts per litre of solution, were determined from density-salinity relations previously established by solution of known weights of Lake Eyre salts in water, and by gravimetric measurement of total dissolved solids per litre of Lake Eyre brines.

Results

Major Filling, 1974

The dry lake bed survey of salt crust thickness and distribution (Dulhunty 1974) was carried out about 18 months before the major filling commenced in February 1974. This provided an excellent basis of pre-filling control data for investigation of the progressive solution of salt crusts which occupied almost two years.

The principal investigations were carried out in Madigan Gulf where the largest and thickest salt crust occurred before the filling. Dulhunty (1974) termed the place of thickest salt and lowest height value 'Centre Point' and noted it to be about 10 km southerly from the point of thickest salt and lowest height recorded by Bonython (1956).

At various stages throughout the investigation, salinities were determined for water from the surface and at different depths, as shown in Figs 1B and 1C. The 12 values shown along the salinity curve in Fig. 1B are measured values. Five were obtained from water samples

collected in Level Post Bay (2 in March 1974, 1 in December 1974 and 2 in March and April 1975), and the other 7 were from samples collected at Centre Point. The steep salinity gradient in bottom waters overlying residual salt crust, illustrated in Fig. 1C, was obtained by measurement of salinities in samples collected from bottom waters at Centre Point and along line A–B in Fig. 1A, during July 1974. Residual salt crust thicknesses shown along the salt crust thickness curve in Fig. 1B, were measured by borings at Centre Point, at stages during progressive solution of the crust.

The curve for water depth in Fig. 1B represents the mean of a large number of gauge board readings in Level Post Bay and soundings at Centre Point. The depth values shown along the curve are mean values at different places to facilitate reading of the diagram. The fall of about 0.4 m between November 1975 and March 1976, is based on interpolation between readings in October 1975 and April 1976. Unfortunately no readings were made between these dates, but the level must have fallen, as a result of evaporation, by at least as much as it did during the same period in 1974–75 (see Fig. 1B). No water entered the lake during either of these summer periods. Also observations of shoreline wave cut features, beneath water level later in 1976, indicated that the lake had fallen to a level equivalent to a depth of about 3.2 m at Centre Point. Therefore a fall to this depth is believed to have occurred early in February 1976. An appreciable volume of water entered the lake from the Macumba and Neales Rivers and Frome Creek late in February 1976, raising lake water towards the levels measured in April, May and June of that year.

The margin of the original salt crust before the 1974 filling, is shown in Fig. 1A extending almost to the shorelines of Madigan Gulf. To the northwest the salt crust thinned out and disappeared where the Gulf opened on to the Slush Zone of very thin discontinuous salt overlying soft mud and slush extending across the full width of the lake (Dulhunty 1974).

It had been generally assumed that the salt crusts of Lake Eyre rapidly passed into solution as soon as a volume of water in excess of that which would have been sufficient to dissolve all the salt, entered the lake. The 1974 filling of Lake Eyre North commenced in February, and after six months filling with a volume of water far in excess of that neces-
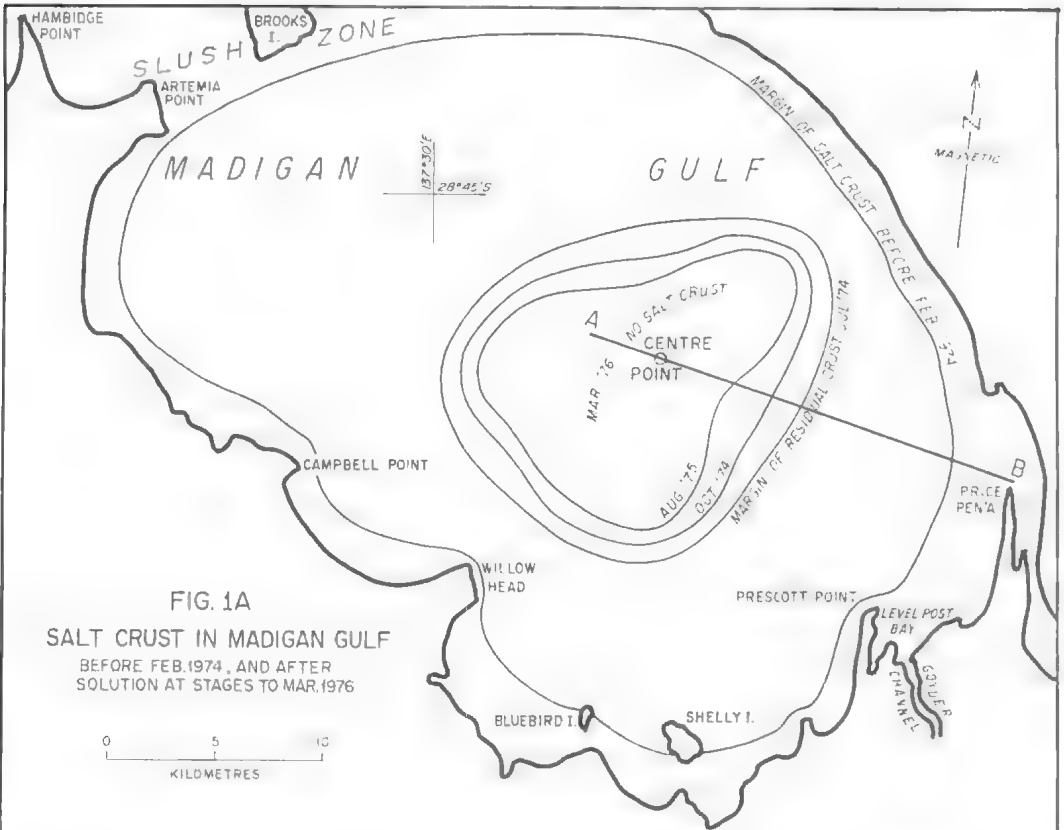
FIG. 1A

SALT CRUST IN MADIGAN GULF

BEFORE FEB.1974 , AND AFTER
SOLUTION AT STAGES TO MAR.1976

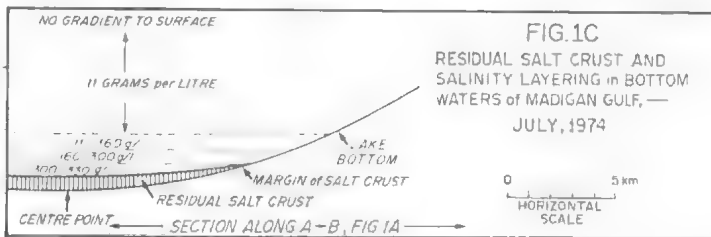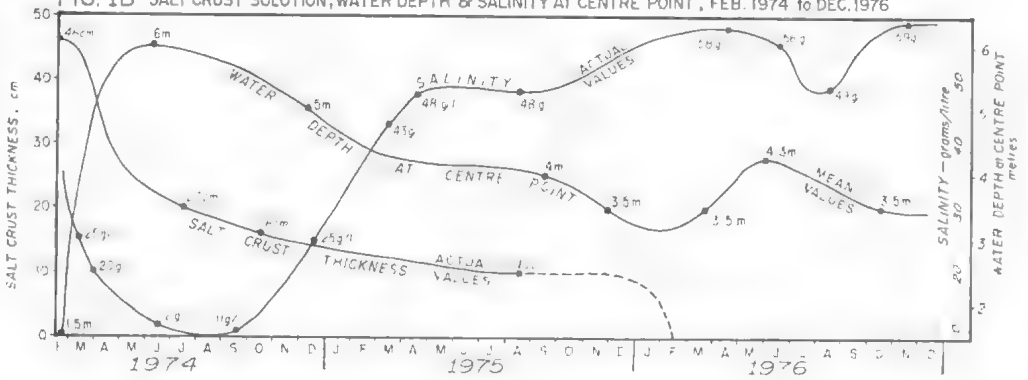FIG. 1B SALT CRUST SOLUTION, WATER DEPTH & SALINITY AT CENTRE POINT , FEB. 1974 to DEC.1976

FIG.1C

RESIDUAL SALT CRUST AND
SALINITY LAYERING in BOTTOM
WATERS of MADIGAN GULF,—
JULY, 1974

Fig. 1. Relations of salt solutions to water depth and salinity in Madigan Gulf.

sary to dissolve all the salt, a residual area of crust remained undissolved in the central area of Madigan Gulf. Its margin, determined by pole test survey in July 1974, was as shown in Fig. 1A. Further surveys in October 1974 and August 1975 showed progressive, but slowing solution of the residual crust to the positions shown in Fig. 1A. Pole tests by R. Clarke and M. Atkinson in August 1976 and by the author in November 1976, established that the whole of the residual crust had gone into solution.

Measurements of salinity at different depths, in July 1974, established a saturated brine layer from 10 to 20 cm deep on the solution surface of the salt crust. Above the brine layer, there existed relatively high salinity water up to 50 cm deep with a high salinity gradient. The saturated brine layer did not extend more than 1 km, and the overlying high salinity water more than 5 km beyond the edge of the salt (Fig. 1C). Away from the area of residual salt crust, where salt had been completely dissolved, the lake waters exhibited very little, if any, salinity gradient, and no saturated brine or high salinity water existed on the bottom.

The bottom saturated brine layers were always almost opaque black in colour, rich in dissolved hydrogen sulphide, and carried finely divided organic debris and clay which appeared to be almost colloidal, but could be separated by filtration

Minor Filling, 1973

The minor filling of Lake Eyre during May, June and July 1973 covered Belt and Jackboot Bays and an area west of Hunt Peninsula to a level of −13.6 m A.H.D. It gave maximum water depths of 1.58 m to the base of salt crusts in Belt Bay and 1.43 m in Jackboot Bay. Some water, when aided by westerly winds, flowed east round Hambidge Point into Madigan Gulf covering parts of its bed to depths of less than 0.5 m.

During July 1973, pole test surveys for salt in Jackboot and Belt Bays indicated the presence of relatively large areas of residual salt crusts beneath the water cover, where the thickest crusts were found in 1972 (Dulhunty 1974) and the deepest water occurred in 1973. Thicknesses of residual crusts were measured by boring and water samples were collected for salinity determinations. Approximately one third of the original thickness of crusts had been dissolved by late July 1973, under the

conditions which existed during the filling, producing salinities of 186 and 235 g/l in Belt and Jackboot Bays, respectively. The small amount of water which reached Madigan Gulf covered part of the salt crust in central areas of the Gulf and extended almost to Willow Head. Measurements 3 km northeast of Willow Head showed that about 12 mm of crust had been dissolved by the end of July when water salinity reached saturation at about 325 g/l.

Salt solution in Jackboot and Belt Bays, 1974–75

Only limited opportunity was available for investigation of salt crust solution in Jackboot and Belt Bays during the 1974 filling. Surveys of these bays were made early in September 1974, to ascertain the extent to which salt solution had occurred. Pole test traverses in Belt Bay indicated a roughly circular residual area of salt crust, about 2.5 km in diameter, where the thickest salt occurred in 1972, immediately to the northwest of a silcrete island situated 1.5 km west of Bonython Head. At a point 0.4 km west of the southern tip of the island, water depth was 5.8 m, salt thickness was 6 cm where it had been originally 29 cm, upper water salinity was 9.4 g/l and a gradient from 11 to 325 g/l occurred in 1 m of bottom water lying on the salt crust. This indicated a layer of saturated brine on the solution surface of the salt crust as in Madigan Gulf, and the 23 cm of salt dissolved was slightly less, but comparable with the 29 cm dissolved in Madigan Gulf by early September 1974. A pole test for salt immediately west of the silcrete island in Belt Bay, by R. Clark, and A. & M. Atkinson in August 1975, indicated that the crust had completely dissolved, and a surface water sample collected at the same time gave a salinity of 29.2 g/l.

In Jackboot Bay it was found that the main salt crust had dissolved by early September 1974, with only occasional small patches of salt remaining on the bottom. Maximum water depth was 5.75 m and salinity of upper water was 11.8 g/l with a gradient from 13.4 to 15.0 g/l in 1.0 m of bottom water, where the salt crust had originally been 23 cm thick. This means that solution of 23 cm of salt had occurred in Jackboot Bay, as in Belt Bay, and that it had just removed all the main crust. No bottom brine layer was found in September 1974, due possibly to the small area of thick crust in Jackboot Bay, or dispersion after solution of the salt.

Conclusions

Salt crust solution in Madigan Gulf, 1974–76

It was evident that the saturated brine layer and overlying high salinity water regulated rate of solution of the crust. Where water depth was appreciably less than half the wavelength of wind waves on the surface, disturbance from wave action would have been sufficient to prevent the formation of a brine layer, and salt crust would have dissolved. At depths considerably in excess of half the wavelength, disturbance of bottom water would have been negligible and a brine layer could have formed over the salt. During the strongest winds experienced on the lake, wavelengths of 8 m were measured suggesting that salt crusts at depths of less than 4 m would dissolve relatively quickly, but at greater depths they could be protected by overlying brine layers. Therefore the history of salt crust solution in Madigan Gulf during the 1974 filling, appears evident from relations between salinity, water depth and rate of solution of salt illustrated in Fig. 1B.

With early vigorous inflow of relatively shallow water across the lake bed during February and March 1974, solution of salt was very active. Crust thickness was quickly reduced from its original thickness of 46 cm at Centre Point, to about 28 cm, producing water salinities in excess of 30 g/l. Water depth increased rapidly until the end of May, reaching its maximum of 6 m in early June 1974.

Depths in excess of half the maximum wavelength of wind waves were soon established. With lack of wave disturbance in bottom waters, brine layers commenced to form on the residual salt crust, slowing down rate of solution. This, and dilution of upper waters by enormous volumes of fresh water, reduced salinity of the upper waters to as low as 10 g/l in August. From September 1974 to October 1975, water depth and salinity increased, and the rate of salt solution slowed down and almost ceased by September 1975. Water level continued to fall reaching a depth of less than half the maximum wavelength during October where it remained until April 1976. In August 1976 no salt crust remained, and it is believed that it finally dissolved during the period from October 1975 to March 1976, as illustrated in Fig. 1C.

Acknowledgments

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BONYTHON, C. W. & MASON, B. (1953) The filling and drying of Lake Eyre. *Geogr. J.*, **119**(3), 321-330.

DULHUNTY, J. A. (1974) Salt crust thickness and lake bed conditions in southern areas of Lake Eyre North. *Trans. R. Soc. S. Aust.*, **98**(3), 125-133.

DULHUNTY, J. A. (1975) Shoreline shingle terraces and prehistoric fillings of Lake Eyre. *Ibid.* **99**(4), 183-188.

COORONGITE, BALKASHITE AND RELATED SUBSTANCES – AN ANNOTATED BIBLIOGRAPHY

BY R. F. CANE

Summary

A resurgence of interest in coorongite has been occasioned by the search for renewable hydrocarbon energy sources. Coorongite is a biogenic polymer originating in profuse blooms of an aberrant alga, Botryococcus braunii (Kutzing). B. braunii can exist in three physiological states, two of which produce large quantities of polyene hydrocarbons. On the death of the colony, the hydrocarbon metabolites oxidize and polymerize into a dark coloured rubbery mass, called coorongite, from which a hydrocarbon oil can be obtained by pyrolysis.

COORONGITE, BALKASHITE AND RELATED SUBSTANCES—AN ANNOTATED BIBLIOGRAPHY

by R. F. Cane*

Summary

CANE, R. F. (1977) Coorongite, balkashite and related substances—an annotated bibliography. *Trans. R. Soc. S. Aust.* 101(6), 153-164, 31 August, 1977.

A resurgence of interest in coorongite has been occasioned by the search for renewable hydrocarbon energy sources. Coorongite is a biogenic polymer originating in profuse blooms of an aberrant alga, *Botryococcus braunii* (Kutzing). *B. braunii* can exist in three physiological states, two of which produce large quantities of polyene hydrocarbons. On the death of the colony, the hydrocarbon metabolites oxidize and polymerize into a dark coloured rubbery mass, called coorongite, from which a hydrocarbon oil can be obtained by pyrolysis.

The lack of a comprehensive bibliography on coorongite and related bio-elaterites has been felt by workers in this field. The present survey, which covers the period 1866-1976, makes good this deficiency.

Introduction

For more than a century it has been recognised that algae provide useful information on the genesis of petroleum. Increasing appreciation of this fact, together with advances in the techniques of analytical chemistry, has resulted in the chemistry of algae becoming an important study for organic geochemists. One outcome of these researches has been a much better knowledge of the geochemical processes which occur during the diagenesis of earth hydrocarbons.

In addition to biologically derived liquid petroleum, there are other types of hydrocarbon deposit which have received recent attention. These may be arranged into three groups, namely:

(i) material resulting from the alteration of petroleum to yield brittle, largely insoluble solids such as wurtzilite, grahamite and gilsonite;
(ii) abiotic hydrocarbons;
(iii) polymeric hydrocarbons arising from extant algae.

The purpose of this paper is to review the literature of the polymeric group and to present a bibliography of an important South Australian representative called coorongite.

Coorongite is a naturally occurring rubbery polymer arising from a specific alga and, like balkashite from Kazakh (Siberia), has its genesis in prodigious blooms of an atypical colonial alga, *Botryococcus braunii*. There are only three known representatives of this type of substance, all of which are of the same algal origin and, presumably, have the same chemical composition, but only coorongite has been fully examined. These representatives and their main habitats are:

(i) Coorongite—The Coorong (South Australia);
(ii) Balkashite—Lake Balkash (Siberia);
(iii) N'Hangellite—Lake N'Hangella (East Africa).

There are dubious reports of other occurrences but these have not been authenticated.

Until a decade ago, the problem of the chemical composition of coorongite had received only scant attention because it had been tacitly assumed that the work of Stadnikov (1929 *et seq*) and others had established the nature of the "algal oil". The availability of gas chromatography and computerized mass spectrometry has now shown that the previous assumptions were wrong and, over the last few years, there have been important publications on this topic. As recently as 1976, it has been suggested (Hillen 1976) that the alga should be fully investigated as a possible future source of hydrocarbon energy.

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Because of the present interest in hydrocarbon-producing algae, it was decided to collect together all reliable information on the nature of coorongite and related materials, with particular refence to the role of B. braunii in the formation of such bio-elaterites. It is inevitable that some citations will provide only passing reference but, for completeness, such material has been included. References dealing with Botryococcus purely from the viewpoint of taxonomy or algology have been excluded unless the text has some direct bearing on coorongite and its allies.

History of Coorongite

Although coorongite was reported in 1852 (see Scrutton 1874—Suppl.), the first description was that given by Francis (1866—Suppl.), followed by an initial scientific report by Dyer (1872). Prior to these dates, the only interest in coorongite (balkashite) had been as a source of fuel by the Khugese tribe of Turkestan (Morgan 1921). Some aboriginal tribes of South Australia had occasionally burned coorongite to provide light.

Because of the appearance of coorongite and its burning characteristics, Dyer (1872) believed that it might be of mineral origin and hence indicate the presence of underlying mineral oil. Arguments over the origin of coorongite were to extend over the next half century (Colyer 1974). If of mineral origin, it was argued, it was likely that "millions of tons" of petroleum was underlying the Coorong. If it were a vegetal growth, it could be grown to produce much oil, so it was said. Early chemical analyses showed that the pyrolysate of coorongite was largely unsaponifiable. This information was used by the "mineral oil" protagonists as evidence of the relation of coorongite to petroleum. More reliable work by Boodle (1907) and later by Cuming (1902) showed that samples of coorongite did contain appreciable saponifiable matter and the field observations of Broughton (1920) left no doubt of the vegetal origin of coorongite and of its mode of formation.

After the establishment of the origin of coorongite, the assumption that the "algal" oil was fatty ester remained the consensus for nearly half a century. Scientific opinion was strengthened by the comprehensive botanical papers of Blackburn (1936) and Temperley (1936), and the extensive organic geochemical studies of Stadnikov & Weizmann (1929) and Stadnikov (1930). In order to provide a suit-able model for his studies of the origin of coorongite and torbanite, Cane (1967) used elaeostearic acid for the synthesis of "synthetic" coorongite, basing his premise on the assumption that the decarboxylated dimer ($C_{31}H_{58}$) was the main "building block". His hypothesis was reasonably satisfactory but there were still unexplained features. Later, Maxwell et al. (1968) using computerized mass spectrometry, showed that the algal lipid matter (of the orange form of the alga) was not fatty ester, as previously supposed, but two isomeric polyene hydrocarbons ($C_{34}H_{58}$) which they called botryococcene and isobotryococcene. At that stage it seemed obvious that botryococcene polymer was the matrix of coorongite. Further work by Cane & Albion (1973) led to the conclusion that coorongite originated, not from the botryococcenes, but from alkadiene hydrocarbons produced from the green form of the alga although botryococcene has a small but still important role. Later work has shown that the nature of coorongite varies more widely than previously supposed and that the composition can be dependent on the ecological conditions during formation. Post-depositional changes are also important. Nevertheless, it is now clearly established that coorongite is essentially a hydrocarbon polymer arising directly by algal metabolism.

The nature of Botryococcus braunii

Botryococcus braunii is an ubiquitous alga distributed from the tropical to temperate climates in many parts of the world. As well as having a wide geographical occurrence, B. braunii occurs, as fossil forms, in many geological eras as far back as the Ordovician, indeed, as Dulhunty (1944) writes "that organic evolution should have allowed the organism to remain unchanged over the immense length of time since the Permian coal measures were laid down, is extraordinary". The alga also occurs in a fossilised condition in the Kukkersite oil shale of Estonia, and as the main contributor to the torbanites of New South Wales, Scotland and South Africa. Fossil B. braunii has been found in English and American peats, in the mud of glacial lakes, in carbonaceous clays, and in some recent carbonate rocks. In extant form it is usually found in fresh-water areas ranging in size from small ponds to lakes although it can also be found in brackish swamps, bogs and even in salt water. Under, as yet, undefined conditions, B. braunii "blooms" to yield large areas of a float-

ing mass of colonies which, on drying at shore lines, have been reported as being of hundred of square metres in extent and up to several centimetres thick. The dried material after some oxidation and ageing is called coorongite.

The ubiquity of *B. braunii* has given rise to some confusion because algologists at various places have not recognised the genus with which they were working. Thus, the species has been "rediscovered" under the generic names of *Pila, Reinschia* and *Elaeophyton*. The family affiliation of the genus has also been controversial, however, the work of Belcher & Fogg (1955) using phytochemical criteria, has placed the genus unequivocally in the *Chlorophyceae*.

Botryococcus braunii exists in three distinct growth states (Belcher (1968), Brown, Knights & Conway (1969)), each with quite different lipid composition. The three states are:

(a) a green coloured, thin cell-walled rapid growth stage. The hydrocarbon metabolite consists of about 30% of straight chain C_{27}-C_{31} dienes;

(b) an orange coloured thick walled resting stage. The hydrocarbons are largely branched chain C_{34} polyenes.

Both forms are colonial, and

(c) a single celled dark green dormant variety containing little hydrocarbons.

The morphology of *B. braunii* has been well documented, the classical contribution being the collaborative papers by Blackburn (1936) and Temperly (1936). These authors showed, beyond doubt, that torbanite and boghead coals had a common origin in vast growths of this alga and that the lipid matter of the algal cups provided the monomer for the organic matter of the minerals. The first instance of the recognition of *B. braunii* as the oil forming alga of these rocks was by Zalessky (1926), although, earlier, he had believed the alga belonged to the genus *Pila* (Zalessky 1914). Zalessky's research was mainly concerned with the identification of the organic matter of Estonian oil shale and like others, later, he recognised that balkashite (coorongite) was the "peat stage" in the diagenesis of algal organic rocks. Both Zalessky (1926) and Stadnikov (1930) believed that the "oil" of this alga was fatty matter and this opinion remained unchallenged until Maxwell's (1968) work in the last decade.

Utilization of Coorongite

It was mentioned in the Introduction that the burning of coorongite has been used by primitive people as a source of heat and light. The substance burns very readily and it has been stated that the infrequent and sporadic finding of coorongite is caused by the destruction of previous deposits by bushfires. In early newspapers, one reads of layers of coorongite ash many inches thick (there may be an element of imagination in this).

After the establishment of the origin of coorongite and the death of the "mineral oil" theory, from time to time it has been suggested that this material might provide a renewable source of energy in the form of liquid or solid fuel. The cultivation of the alga was suggested by Basedow (1925—Suppl.) and Sir Douglas Mawson is believed to have put forward a scheme at the 17th ANZAAS Congress in Adelaide. At the 47th ANZAAS meeting in Hobart, Hillen (1976) presented a case for the further study of *E. braunii* as a renewable hydrocarbon source and a potential fuel supply.

Bibliography

The bibliography has been compiled from first-hand study of all references except one of Zalessky's papers. In general, the verbal tense of the abstract is the present, except where the past tense more suits the original publication.

A BIBLIOGRAPHY OF COORONGITE AND COGNATE SUBSTANCES

containing abstracts of papers and occasional notes

BELCHER, J. H. (1968) Notes on the Physiology of *Botryococcus braunii* (Kutzing). *Arch. Mikrobiol.* 61, 335-346.

A study on the growth of *Botryococcus* under varying conditions. The rate of early growth is exponential and the green colonies are heavier than water. After a few weeks a stationary phase is reached at which the colonies are red and floating; when subcultured, they revert to the green phase. Under non-bloom conditions growth is slow and large irregular colonies are formed. The paper discusses the effect of the environment on the chemical composition of the alga. The rubbery substance found in lakes in Australia, Africa and Siberia is a by-product of this alga. These deposits remain on the edge of lakes and are the result of hydrocarbon residues left behind on the death of the organism.

BELCHER, J. H. & FOGG, G. E. (1955) Biochemical Evidence of the Affinities of *Botryococcus*. *New Phytol.* 54(1), 81-83.

The paper points out the uncertainties in assigning the taxonomic position of *Botryococcus*. Extracts of *B. braunii* were chromatographed and the eluents examined spectrographically. The absorption spectra and other phytochemical criteria show "clearly that the genus should be placed in the *Chlorophyceae*".

BLACKBURN, K. B. (1936) *Botryococcus* and the Algal Coals. Part I—A reinvestigation of the alga *Botryococcus braunii* (Kutzing). *Trans. R. Soc. Edin.* 58(3), 841-854.

This is Part 1 of the classical paper dealing with the role of *Botryococcus* in the formation of balkashite, coorongite and boghead coals. This paper traces the confusion of early workers regarding the taxonomy of the genus and notes how these misconceptions lead to misnomers. The algal morphology is treated in some detail including a discussion on the cell anatomy. Comment is made that the lipids of coorongite are very unstable and that widely different analytical results may be obtained depending on the age of the sample. The material of the cell wall is chemically highly unsaturated but, on exposure to air, the lipid matter becomes more inert and insoluble. This very thorough paper laid the groundwork in this field for the next three decades.

BOODLE, L. A. (1907) N'Hangellite and Coorongite. *Bull. Misc. Inf. R. bot. Gdns Kew* 5, 146-151.

A description of the occurrence and nature of a gelatinous deposit found near Lake N'hangella in East Africa. Examination of specimens showed conclusively that the rubbery material originated in algal growth. It was suggested that the alga belonged "almost certainly to the blue green algae". Although chemical data are not given, a separate description and examination of coorongite (based partially on Dyer's observations) left no doubt that both coorongite and n'hangellite had a common origin and diagenesis.

Boodle expresses indecision as to how the "mucilage" of the alga became transformed into "material showing the characters of bitumen" but assumes extensive chemical change with loss of oxygen. He notes that n'hangellite is directly comparable to certain organic minerals and mentions a likely connection with the kerosene shales (of N.S.W.).

BROUGHTON, A. C. (1920) Coorongite. *Trans. R. Soc. S. Aust.* 44, 386.

This short note occurs in "Miscellania" and consists of only two paragraphs. The note provides a first-hand description, one of the few, of the actual formation of coorongite from the green alga in The Coorong. In view of the uniqueness of this information, portions of the submission are quoted verbatim: "a thick scum, like green paint, is forming. This scum is drying on the water in places to a semi-elastic substance, forming around reeds . . . Like green paint, a quarter of an inch thick, it covers hundreds of square yards of water, and as it drys it forms a skin like linseed oil drying on an overturned mass of paint. This skin in places is yards in area." "Today it is there in thousands of gallons. It is coorongite in process of formation . Every stage from the green, liquid, paint-like substance to the tough, elastic, sand-containing coorongite may be observed. Scooped with the hand from the surface of the lake this substance, within a few minutes, changes before the eyes from a green liquid, which drops from the fingers, to a brown, plastic solid. Large areas are now drying in sheets of coorongite."

BROWN, A. C., KNIGHTS, B. A. & CONWAY, E. (1969) Hydrocarbon Content and its Relationship to Physiological State in the Green Alga, *Botryococcus braunii*. *Phytochem.* 8, 543-547.

Botryococcus is a peculiar alga characterised by the production of hydrocarbons which vary in composition with its three physiological states. The green active-growth form contains three homologous series of alkadienes in the C_{27}-C_{31} range, substantially of straight chain configuration with the general formula C_nH_{2n-2} where n = 27, 29, and 31. There is a second series, C_nH_{2n-4}, where, largely, n = 29. The brown resting stage contains large amounts of highly unsaturated botryococcenes, which may be up to 86% of the dry weight of the colony. The dark-green large cell final stage has little hydrocarbon content. The chemical interrelationship of the stages is uncertain as the botryococcene producing stage reverts to diene production when subcultured. The paper establishes the main chemistry of each stage and shows that the hydrocarbon content varies with growing conditions.

BROWN, H. Y. L. (1908) *Rec. Mines S. Aust.* 4, 350-351.

This annual report contains a short review on the occurrence of coorongite and the presence of mineral oil. It records that coorongite "is

an indiarubber material" found near Salt Creek which empties into The Coorong. After an examination of two bores in the area, the Government Geologist dismisses any likelihood of petroleum being found in the Coorong area.

BURGESS, J. D. (1975) *Botryococcus* Occurrence as an Aid in interpreting Paleoenvironments. Abstract only in *Geosci. Man* **11**, 154.

The full paper is a useful study of the morphology of *Botryococcus* as an indicator in determining the water environment during sedimentation processes. The occurrence of coorongite is discussed in the light of likely environmental conditions during the bloom stages. It appears that the main criterion in determining whether the thin wall or the thick wall stage is predominant is whether the alga is inhabiting fresh or brackish waters.

CANE, R. F. (1967) The Constitution and Synthesis of Oil Shale. *Proc. 7th World Petrol. Congr.* (Mexico) **3**, 681-689 (Elsevier: Barking).

Although this paper is concerned with the origin of oil shale kerogen, the sections entitled "The Nature of Coorongite" and "Polymerisation of Fatty Oils" describe the likely reactions leading to the formation of coorongite. Coorongite analyses and its infrared spectrum are published. The important contribution made by this paper was the hypothesis that the coorongite (and kerogen) unit was a $C_{34}H_{58}$ polyene hydrocarbon. This unit was believed to be a dimer of a decarboxylated trienoic C_{18} acid. Later work showed that coorongite arises directly from algal hydrocarbons and not from an acid alkyl chain. The $C_{34}H_{58}$ molecule corresponds exactly in the same elemental composition as the dimer postulated in this paper.

CANE, R. F. (1969) Coorongite and the Genesis of Oil Shale. *Geochim. cosmochim. Acta* **33**, 257-265

The history and occurrence of coorongite are reviewed. A theory is put forward that coorongite consists largely of a polymer of "hydrocarbon chains containing some unsaturation". Carboxylic groups occur at chain terminations and the non-polar end of the hydrocarbon chain appears to contain a diene structure. Ether cross-linkages are an important feature of the macromolecule. The molecular weight of the monomer (or the dimer) is about 430. Coorongite mass spectra showed a range of aliphatics. Alkaline permanganate oxidation produced a waxy solid with properties corresponding to fatty acids of high molecular weight.

CANE, R. F. & ALBION, P. R. (1971) The Phytochemical History of Torbanites. *Proc. R. Soc. N.S.W.* **104**, 31-37.

The paper shows that the phytochemistry of *Botryococcus* leads to an explanation of the formation of coorongite. The alga is exceptional in that it produces large quantities of unsaturated hydrocarbons which can be either branched or straight chain, depending on the physiological state. This state appears to depend on food reserves and environmental conditions. Coorongite undoubtedly arises from the polymerisation and oxidation of algal hydrocarbons. Spectral studies leave considerable doubt as to the number of methyl groups attached to the carbon chain "back bone" of coorongite. Some alkyl aromatic structures seem to occur in coorongite in addition to hydroxyl and carbonyl groups.

CANE, R. F. & ALBION, P. R. (1973) The Organic Geochemistry of Torbanite Precursors. *Geochim. cosmochim. Acta* **37**, 1543-1549.

This paper extends the work of Cane who had suggested that the building block of coorongite was a decarboxylated polyene acid corresponding to $C_{30}H_{58}$. Recent research had shown that the alga produces $C_{34}H_{58}$ directly and not from carboxylic acid. Further work, using mathematically derived data from proton resonance spectra indicates that long chain dienes from the green form of *Botryococcus* are the precursors to coorongite rather than the highly branched botryococcenes. The orange form of *Botryococcus* produces botryococcenes and these, in turn, form "botryococcus rubber" but not coorongite. The opinion is put forward that, in the field, there may be some contribution from branched chain hydrocarbons as well as carboxylic acids. Post-depositional microbial transformations also occur.

CARNE, J. E. (1903) The Kerosene Shale Deposits of N.S.W. *Mem. geol. Surv. N.S.W.*, 333.

This monograph is devoted to an exhaustive study of the occurrence and nature of the N.S.W. oil shales. The author quotes earlier opinions that there is no real evidence of flow oil in The Coorong. Reference is made to coorongite (p. 109 and p. 302) in connection with other possible oil sources in Australia. There is little additional pertinent information.

COTYER, F. (1974) Fools Gold. *Petrol. Gaz., Melb.* **18**, 58-63.

The text provides no scientific information but the general historical survey is of much interest. The article gives the history of

coorongite from its discovery in 1852. The paper traces the vicissitudes in belief of the interconnection between coorongite and flow oil and the endeavours of early entrepeneurs to raise share capital to drill for oil. Mention is made of previous ideas regarding the cultivation of algae as oil producers.

CONACHER, H. R. J. (1938) Coorongite and its Occurrence. *In* A. E. Dunstan (Ed.) *"Oil Shale and Cannel Coal"*, 42-49 (Institute of Petroleum: London)

The writer reviews the literature, pointing out that, because of the sporadic occurrence of coorongite, definitive information on the occurrence of deposits is lacking. Conacher visited The Coorong in 1935 and, although he was unsuccessful in observing coorongite in the natural state, he provides a very good description of its habitat. The article points out that coorongite is also found in Western Australia and discusses the environmental conditions which appear to favour the growth of the alga.

Cox, R. E., BURLINGAME, A. L., WILSON, D. M., EGLINTON, G. & MAXWELL, J. R. (1973) Botryococcene—a Tetramethylated Acyclic Triterpenoid of Algal Origin. *J. Chem. Soc.* D. 284-285.

As a result of the use of ^{13}C nuclear mass resonance spectroscopy, with pulsed Fourier transform operation, a structural formula of botryococcene is suggested. It appears that botryococcene contains eight methyl, eight saturated and five unsaturated methylene, five saturated and three unsaturated methine carbon atoms. One saturated and four unsaturated quaternary carbons were also identified.

CUMING, A. C. (1902) Coorongite—A South Australian Elaterite, *Proc. R. Soc. Vict.* 15. (n.s.) (2), 134-140.

The paper gives a general description of coorongite and provides references to its early history and discovery. Cuming's investigations showed that this substance could be separated into two portions depending on solubility in carbon bisulphide. The soluble portion was a wax-like solid, from the general properties and chemical analysis of which the formula $(C_{10}H_{18}O)_x$, with x about 8, was assigned. The insoluble portion, amounting to about three-quarters of the sample, was given the elemental formula $C_{10}H_{20}O_2$. As the solubles were readily oxidised, Cuming suggested (quite correctly) that the soluble portion may become insoluble by the combined effects of ageing and oxidation. Ash analysis showed that coorongite was not of animal origin.

CUMING, A. C. (1903) Coorongite, A South Australian Elaterite. *Chem. News* (London) 87, 306-308.

A recast of the previous reference in an abbreviated form.

DAVID, T. W. E. (1890) Note on the Origin of "Kerosene" Shale. *Proc. Linn. Soc. N.S.W.* 4(2), 483-500.

This paper, devoted to the origin of the torbanites of N.S.W. mentions the coorongite theory of biogenesis of oil shale. This is a most important paper as in it David initiates his algal theory of origin of oil shales. Microscopical evidence on the origin of coorongite strongly points to a vegetative source but David leaves the matter undecided. He points out that, if allowance is made for the elimination of oxygen, there are some striking points of resemblance between the chemistry of coorongite and the "kerosene" oil shales of Australia. The coorongite studies represent only a small portion of the work.

DOUGLAS, A. G., DOURAGHI-ZADEH, K., EGLINTON, G. (1969) The Fatty Acids of the alga *Botryococcus braunii*, *Phytochem.* 8, 285-293.

The orange resting stage was purified, the lipid extract hydrolysed and the methyl esters examined by gas/liquid chromatography. The extract was shown to contain a variety of monocarboxylic acids ranging from C_{14} to C_{30} with appreciable amounts of palmitic, oleic and octacosenic acids. The total fatty acids of the alga are in relatively small amounts. A "synthetic coorongite" derived from botryococcene "rubber" was shown to contain traces of various carboxylic acids.

DOUGLAS, A. G., EGLINTON, G., MAXWELL, J. R (1969) The Hydrocarbons of Coorongite. *Geochim. cosmochim. Acta* 33, 569-577.

A brief survey of the literature is given followed by experimental data on the composition of coorongite extracts. The hydrocarbon distribution ranged from C_{14} to C_{27} and consisted of alkanes, terminal alkenes and some aromatic constituents. The fatty acids ranged from $n-C_{14}$ to $n-C_{34}$ with marked even/odd preference and major components at $n-C_{16}$, $n-C_{18}$. The C_{18} isoprenoids contained phytane and pristane, but no botryococcenes. No n-alkanes were detected in the orange bloom state of *Botryococcus*. The paper shows that hydrocarbons amounted to 0.53% of the sample. As the extract amounted to 50% of the sample it is unfortunate that no attempt was made to characterise the whole extract.

DULHUNTY, J. A. (1944) Origin of the N.S.W. Torbanites. *Proc. Linn. Soc. N.S.W.* **69**, 26-48.

The section (p. 31) entitled "Coorongite and its relation to Torbanite" gives a short account of previous work and describes samples collected by the writer. Dulhunty defines coorongite as the "peat-stage" in the formation of torbanite and gives convincing reasons to support his argument. The properties of torbanite and coorongite are compared and discussed.

DYER, W. T. THISTLETON (1872) On a Substance Known as Australian Caoutchouc. *J. Bot., Lond.* **10**, 103-106.

This paper provides the first reliable description of coorongite. The paper states "It consists of sheet-like masses—more than one inch thick and is confined to a depressed portion of the district, the bottom of which is sandy and grass covered . . . or on the sides of island-like elevations". Dyer quotes examinations by various workers which revealed "a granular and cellular structure". The suggestion is put forward that it might be a cryptogamic plant but this is then discounted because of the inexplicably small amount of oxygen. Dyer states, prophetically, that coorongite "is practically a hydrocarbon" and that the origin of the substance is likely to cause a great controversy.

GELPI, E., ORÓ, J., SCHNEIDER, H. J. & BENNETT, E. O. (1968) Olefins of High Molecular Weight in Two Microscopic Algae. *Science, N.Y.* **161**, 700-702.

Laboratory cultures of *B. braunii* have been shown to contain alkenes with carbon numbers ranging from C_{17} to C_{33} with one, two and three double bonds. The C_{27}, C_{29} and C_{31} diolefins were predominant and hydrocarbon distribution was similar to that of the kerogen of certain oil shales.

DE HAUTPICK, E. (1923) Coorongite, A Petroleum Product. *Min. J., Lond.*, **142**, 575.

A short contribution discussing the origin, occurrence and properties of coorongite. The writer errs in dismissing its vegetal origin on the basis of growth. This paper illustrates the conceptual difficulties of early investigators who could not reconcile a "pure" hydrocarbon being produced by algae. Unsaponifiable oils were considered part of the mineral kingdom and therefore must indicate the possible presence of petroleum. His report to The Coorong Oil Company (14 pp., issued June 19, 1923 Adelaide) further elaborates on the alleged interconnection between coorongite and the occurrence of petroleum. De Hautpick urges further boring in the Coorong area.

DE HAUTPICK, E. (1926) Note sur le minéral bitumeneux dit "Coorongite" et sur son témoignage de la formation du pétrole. *Bull. Soc. géol Fr.* **26**(4), 61-66.

The writer reviews previous work and mentions there are many previous papers including a bibliography by L. Wahtall (the present reviewer can find no record—R.F.C.). Mention is made that coorongite appears to have been transported from where it was formed. It is stated that the formation of this "migratory" mineral has been recorded only in 1865 and 1920, after heavy rain. The paper gives the physical properties of coorongite and notes that, on destructive distillation, the material yields a whole series of "petroleum" products, none of which are saponifiable to any extent. Although coorongite is of vegetative origin, de Hautpick reaches the conclusion that "here is the true source rocks of petroleum", i.e. oil globules inside vegetation. This paper again illustrates the enigma facing early workers who couldn't reconcile the non-saponifiable "fats" of coorongite with its plant origin.

This is an important paper but it is particularly unfortunate that no literature references are provided. It might be mentioned, *inter alia*, that Captain Hautpick was associated with early share raising efforts in connection with coorongite and petroleum in South Australia.

HILLEN, L. W. (1976) Prospects for Liquid Hydrocarbon Fuels from Solar Energy via the Alga *Botryococcus braunii*. 47th ANZAAS Conference (Hobart) May 1976.

This paper reviews the occurrence of coorongite and states that there are four well documented areas on the coastal sandy lowlands of Australia where this deposit is found. A study of the growth of coorongite suggests that this alga has potentialities as an energy source, however, the large water areas required for commercial production would present difficulty in any large scale undertaking.

JACKSON, I. R. (1872) Coorongite or Mineral Caoutchouc of South Australia. *Pharm. J.* **31**, 763-4 & 785.

Portion of the paper is based on the earlier observations of Francis (1866—Suppl.) regarding the occurrence and probable nature of coorongite. Jackson found coorongite to be "resolvable into two educts: (1) soft semi-

fluid like balsam . . . resembling vegetable wax, and (2) a tough pulverulent substance . . . (like) . . . a modified form of cellulose".

KNIGHTS, B. A., BROWN, A. C., CONWAY, E., & MIDDLEDITCH, B. S. (1970) Hydrocarbons from the Green Form of the Freshwater Alga *Botryococcus braunii. Phytochem.* 9, 1317-1324.

Botryococcus braunii occurs in two distinct forms, the brown resting stage containing up to 70% of its dry weight of two isomeric hydrocarbons. The green exponential growth form is shown to contain about 20% diene hydrocarbons in the C_{27}-C_{31} range. Ozonolysis, gas chromatography and mass spectral data showed that the diene compounds had the general formula

$$CH_2{:}CH.(CH_2)_n.CH{:}CH.(CH_2)_{14}.CH_3$$

where n = 17, 19, and 15, in order of abundance. The disubstituted double bond is *cis* form, in the same position as in oleic acid.

LITINSKY, L. L. (1921) Balkash "Sapropelite", *Petroleum* (Berlin) 17, 437-440.

Sapropelite from Lake Balkash is a dark coloured substance alleged to be produced by the alga *B. braunii*. It burns with a sooty yellow flame with a peculiar odour. The newly formed sapropelite is green but quickly changes to a yellow brown viscous mass which can be cut by a knife. Organic solvents may be used to separate the material into a hard paraffinic wax-like substance which may amount to 42% of the raw material. Destructive distillation gives a series of hydrocarbon fractions. Even when kept for five years there is no change in its physical properties.

MAXWELL, J. R., DOUGLAS, A. G., EGLINTON, G., & McCORMICK, A. (1968) The Botryococcenes—Hydrocarbons of Novel structure from the Alga *Botryococcus braunii* Kutzing. *Phytochem.* 7, 2157-2171.

The nature, occurrence, and previous work on *B. braunii* are discussed. Early analyses showed a high lipid content containing a large amount of unsaponifiable matter. By the application of column chromatography, mass and infra-red spectroscopy it has been shown that the oily matter is not fatty ester as previously believed. The lipids consist largely of two polyene hydrocarbons of novel structure, which have been called botryococcene and isobotryococcene. The elemental composition corresponds to $C_{34}H_{58}$. Infra-red spectra show the presence of exomethylene and vinyl groups together with much unsaturation. High resolution spectroscopy indicate two terminal vinyl groups, six methyl groups, and perhaps four exomethylene groups. A suggested structure is put forward. The behaviour of the dead algal colonies and the formation of coorongite can well be explained in terms of these hydrocarbons.

The paper presents entirely new evidence on the composition of coorongite and marked the end of the Stadnikov/Cane fatty acid theory.

MAWSON, D. (1938) Further Discoveries of Sapropelic Deposits in The Coorong Region of South Australia. *Oil Shale and Cannel Coal*, 50-52 (Institute of Petroleum: London).

The geological and topological features of The Coorong area are given and observations made on the flora of the saline lagoons. It is stated that the locality is famous for the occurrence of coorongite. Apart from a useful discussion on the area's geology, little pertinent information is presented on coorongite.

MORGAN, R. J. (1921) The Occurence of Coorongite in Central Asia. *Chem. Engng. & Min. Rev.* 348, July 5, 1921.

This paper gives an interesting description of the balkashite area in Siberia. Balkashite is found in Lake Ala-Kool which is a saline extension of the fresh-water Lake Balkash. Coorongite (balkashite) occurs above and at the shore margin. It is a yellowish spongy material which burns with a smoky flame with a disagreeable odour. The deposits vary from 2 feet to 10 feet in width and from thin sheets up to 2" thick. Balkashite is always mixed with algal remains and other general sapropel. Morgan states that the alga grows prolifically at the margin of the lagoon but only in shallow water and preferably where there is some surface disturbance, such as that caused by breezes. He states that balkashite is never found in the main lake and it is interesting to note (R.F.C.) that coorongite has never been recorded as growing in The Coorong itself. Similar deposits have been observed in Turkestan and elsewhere in Siberia.

REDWOOD, B. (1907) Report on a Sample of N'hangellite from Inhambane, Portuguese East Africa. *Bull. Misc. Inf. R. bot. Gdns Kew* 5, 151-153.

A short description of N'hangellite together with proximate analyses. Redwood showed that destructive distillation produced, in addition to an aqueous phase and coke, an oily product resembling mineral oil. The elemental analyses showed figures comparable to those of coorongite and that the two deposits are similar products of the same origin.

SIMPSON, E. S. (1926) Coorongite. *Rep. Dep. Mines, West. Aust*, 234-235.

Coorongite has been found in many localities near the South Coast of Western Australia. Sheets of coorongite, up to one inch thick, have been gathered from a swamp at Martagullup. Dr Simpson, the government analyst, dismisses any connection between the occurrences of coorongite and petroleum. He points out that oily liquids can be obtained by the distillation of "almost any organic substance from coal to cucumbers".

STADNIKOV, G. L., & WEIZMANN, A. O. (1929) Transformation of Fatty Acids During Geological Periods III. *Brennst.-Chem*, 10, 401-403.

Extracts of boghead coal were shown to consist mainly of polymers of unsaturated fatty acids. Such fatty acids are shown to be the parent substances of both coorongite and balkashite. Analysis has shown that coorongite has a high content of saponifiable and unsaponifiable organic acids. Polymerisation in coorongite is not extensive enough to make it totally insoluble.

STADNIKOV, G. L. (1930) Die Entstehung von Kohle und Erdöl—Die Umwandlung der organischen Substanz im Laufe der geologischen Zeitperioden. *Schr. Geb. Brennstoffgeol*. 254 pp. (Enke: Stuttgart).

Sections of the book discuss the oxidation and polymerisation of fatty acids into rubber-like materials. The author outlines the role of coorongite and balkashite in the formation of boghead coal. Investigations show that balkashite is not a wax or of mineral origin but an algal byproduct (wrongly termed *Elaeophyton coorongianum*) derived from fatty matter. Coorongite is similar in constitution and both can be separated into soluble and insoluble portions. The solubles are a thick yellow oil whereas the residue is a rubbery solid. Stadnikov did a great deal of fundamental work showing that oxidation and polymerisation of unsaturated fatty acids could give rise to either rubbers or brittle solids. His hypothesis of the decarboxylation of an acid to yield hydrocarbons was well supported by existing evidence. Recent results, showing that hydrocarbons were the direct algal metabolites, were possible only after the perfection of vapour chromatography. Stadnikov ascribes somewhat different diagnetic routes to coorongite and balkashite depending on conditions of sedimentation and on the ratio of aerobic to anaerobic environments.

STADNIKOV, G. L., & VOZZHINSKA, Z. I. (1930) Transformation of Fatty Acids during Geological Periods IV. *Brennst.- Chem* 11, 414-416.

Balkashite, like coorongite is derived from *Botryococcus braunii* and the remnants of algae can be easily distinguished in samples of both deposits. Fresh balkashite oxidises in the atmosphere and undergoes a slow hardening process. Some fatty acids also show a great tendency to polymerise to insoluble rubber-like materials. Microscopic examination of bogheads and Moscow cannel coal also shows evidence of algal origin.

TEMPERLEY, B. N. (1936) *Botryococcus* and the Algal Coals. Part II. The Boghead Controversy and the Morphology of the Boghead Algae. *Trans. R. Soc. Edin*, 58(3), 855-868.

The second part of this paper (see Blackburn 1936) deals with the interrelationships between *Botryococcus braunii*, coorongite and torbanite. The morphology and mode of reproduction of the alga are discussed and illustrated with diagrams and photomicrographs. Temperley states that, in coorongite, the characteristic cup-in-cup structure has coalesced into a structureless rubbery mass. The important conclusions of this paper laid the groundwork for most later research on the phytochemistry of algal oil shales and showed that the "yellow bodies" of Scottish boghead and the torbanite of N.S.W. were, in fact, remains of *Botryococcus*. The paper also discusses the vegetal origin of coorongite and its close relationship with balkashite.

THIESSEN, R. (1925) Origin of Boghead Coals. *Prof. Pap. U.S. geol. Surv*, 132, 121-135.

This publication deals largely with the origin of the kerogen of bogheads and torbanites. A section (pp. 127-130) is specifically devoted to coorongite, its history, occurrence and composition. Thiessen failed to recognise the genus but applied a new name of *Elaeophyton coorongiana*. Samples from The Coorong were examined and described. Data on the chemical properties of coorongite are given including elemental and proximate analyses. Thiessen believed that it was the oil in the cell wall of the living plant which provides the "yellow bodies" of boghead coal and the matrix of coorongite.

TRAVERSE, A. (1955) Occurrence of the Oil Forming Alga *Botryococcus* in Lignites and other Tertiary Sediments. *Micropal*. 1, 343-350.

Although balkashite and coorongite receive only a mention, the paper presents a good review of (the ubiquity) of the occurrence of

Botryococcus and its role in organic rich deposits. Traverse pre-empts the later discovery that the alga itself may give rise to hydrocarbons. The author also states that other fossil genera described in the literature are often varieties of *Botryococcus* and that it occurs in a wide variety of geological ages and geographical situations.

WARD, L. K. (1913) The possibilities of the Discovery of Petroleum on Kangaroo Island and the Western Coast of Eyre's Peninsula. *Bull. geol. Surv. S. Aust.* 2, 15-20.

The history of coorongite is given and previous investigations are discussed. The opinion is put forward that coorongite is not a petroleum product and analyses would indicate a hydrocarbon-like material of unsaturated nature. Coorongite occurs on the northwestern shore of Murrays Lagoon on Kangaroo Island where a scum is to be found on banks below flood level. The deposits are associated with much vegetal detritus. It is believed that coorongite might be an oxidized product of "some pre-existing hydrocarbon". At the time of publication, this paper was the best general survey and the references are nearly complete. A bibliography is given.

WARD, L. K. (1915) The Supposed Oil Bearing Areas of South Australia. *Bull. geol. Surv. S. Aust.* 4, 36-37.

Section 3 of this publication discusses the alleged connection between coorongite and petroleum. Coorongite is found on the shores of Murrays Lagoon (Kangaroo Island) and close to the Coorong area. It is found a "few feet down on old shores on which sand and debris has subsequently collected" or at the surface on banks associated with ponds after wet seasons. The paper gives a good description of the occurrence of coorongite and asserts that all facts predicate against its being associated with petroleum seepages.
The opinion is put forward that coorongite originates from lowly vegetable organisms which grow on the lagoons and that it has a genesis similar to N'hangellite (see ref. Boodle, 1907).

WARD, L. K. (1916) A Review of Mining Operations in the State of South Australia. Issue No. 24, p. 43, Department of Mines (Govt Printer: Adelaide).

The report emphasises the falsehood of associating coorongite with the occurrence of petroleum. The report goes on to state that pieces of coorongite which were placed "on the crests of calcareous sand dunes . . . (was)

regarded as evidence that the material was deliberately placed there with fraudulent intent".

WARD, L. K. (1944) Search for Oil in South Australia. *Bull. geol. Surv. S Aust.* 22.

There is a short reference to coorongite (p. 12) in the discussion of the occurrence of petroleum in South Australia. A review is given (p. 17) of the prospecting boreholes which were put down in The Coorong in the belief of the association between mineral oil and coorongite.

WILSON, R. C. (1926) Reported oil at Kenderup. *Rep. Dep. Mines West. Aust.*, p. 78.

Mr. Wilson visited Lake Martagallup at the request of local residents and collected pieces of coorongite "about the size of dinner plates" at the edges of the lake from shorelines which have now dried up.

ZALESSKY, M. D. (1914) On the Nature of *Pila*, the Yellow Bodies of Boghead and on Sapropel of the Ala-Kool of Lake Balkash. *Bull. Comité Géol. St Petersbourg* 33(248), 495-507.

The paper supports the opinion that the "yellow bodies" of bogheads were not algal in origin but highly sculptured walls of the spores of cryptogams. At that time there was confusion between the genus *Pila* and the alga of balkashite. Zalessky records that, along the Ala-Kool, this alga comes to the surface of the water and it contains a considerable amount of oil. Decomposition of the alga on the shores of the lake generates much hydrogen sulphide while the green plant residue changes to a brownish rubber-like mass.

ZALESSKY, M. D. (1917) On Some Sapropelic Fossils. *C. r. & Bull. Soc. géol. Fr.* 4th Series, 17, 373-379.

Because of further work, Zalessky believed that Estonian kukkersite is an oil shale derived from *Botryococcus*. This alga is similar to that found growing in Lakes Bieloe and Kolomenskoe in the Tver district of Siberia. The sapropelite is also found in the Ala-Kool gulf of Lake Balkash. In Lake Bieloe, areas up to nine metres square are covered with a type of rubber humic jelly. This sapropel has been used as a source of ammonia for agricultural applications. Other more mature forms of the sapropelite are found in the Kamenkarita valleys in Siberia and known as Kouswvriaslo.

ZALESSKY, M. D. (1926) Sur les nouvelles Algues découvertes dans le Sapropélogène du Lac Beloe et sur une Algue sapropélogène. *Revue gén. Bot.* **38**, 31-42.

A description is given of the deposits at Lake Balkash. The deposits are formed by the coalescence of vast numbers of the colonial alga *B. braunii*, which later dry on the shores of the lake. The deposits are very thick and resist decay. Zalessky gives a description of the variety of *Botryococcus* inhabiting the Siberian lakes. Zalessky shows that the alga has various forms depending on the ecological and environmental conditions.

Supplementary chronological bibliography

Although not always of scientific merit, early references to the heated controversy over the origin of coorongite are included in this survey. The violent arguments arose because of difference of opinion as to whether coorongite was of mineral or of plant origin. If the former, it was alleged that the discovery of a large petroleum deposit could not be discounted. If, on the other hand, the substance was a vegetative growth, then it was said it should be possible to cultivate the plant and harvest the "oil". It is interesting to note that this latter possibility has been recently put forward (Hillen 1976).

As it proved difficult to ascertain the author of some newspaper articles, a selection of the main contributions is set down in chronological order.

FRANCIS, G. (1866) The Substance found near The Coorong. *The S. Aust. Register* S.5.66.

This well presented letter (p. 3, col. 3) gives a general description of coorongite including a reliable examination of its physical properties and chemical reactions. Francis states that all evidence points to a vegetative origin as, under the microscope, coorongite has a cellular structure. Francis considers it "to be neither caoutchouc, elastic bitumen, asphalt or petroleum but a peculiar fungoid growth and that it has no connection with coal or any other combustible mineral". The information in this early article is remarkably true and, although no quantitative data are provided, the qualitative observations are largely still valid. The writer suggests that the substance probably has some financial value if sufficient quantity were available.

MUECKE (1869a) *The Adelaide Observer* 3.7.69.

A letter (p. 6, col. 7) decrying any possibility of a connection between coorongite and petro-

leum. Dr Muecke stated that coorongite has been found on the top of recent sands and shelly limestones and that it never had any connection with the underlying strata. He suggested that coorongite arose from allies of the the grass trees because of its resinous and inflammable nature. "The damp yellow juice exudes from the knot and bottom stalks during the summer heat and flows on the sand where it becomes hard, as every caoutchouc does."

MUECKE (1869b) Caoutchouc. *The S. Aust. Register* 31.7.69.

A further letter (p. 3, col. 8) in reply to another letter reaffirming his opinion on the vegetal origin of coorongite and stating that, under no circumstances, can coorongite be regarded as of mineral origin—see also The Adelaide Observer 7.8.69 (p. 13, col. 5).

ANON (1871) *The S. Aust. Register* 29.8.71.

The article (p. 2, col. 4) contains reproductions of letters from J. Hooker of Kew Gardens and from M. J. Berkeley regarding a substance called "mineral gamboge" which is believed to be a "collemal" in an imperfect state. The general opinion was that the material (coorongite) is of vegetal origin but no firm views are given.

ANON (1871) A Singular Vegetable Formation. *The Advertiser* 29.8.71.

An article (p. 2, col. 5) concerning the dichotomy of opinion on the origin of coorongite, pointing out that a "good deal of money" had been spent in the belief that "mineral gamboge" was an indication of petroleum. Samples had been sent to Kew Gardens and examined by M. J. Berkeley. Berkeley's opinion was that the substance (coorongite) was "a collemal in an imperfect state and a thin slice shows necklaces of gonidia". The famous Dr Hooker, who had written to Adelaide "sets the matter at rest", i.e. coorongite belonged to the vegetable kingdom.
A similar article also appears in *The S. Aust. Register* of 29.8.1871 (see above).

F.V. (Initials only) (1871) Coorongite—Vegetable or Not? *S. Aust. Express & Telegraph* 1.9.71.

A letter (p. 3, col. 1) in reply to the previous abstract. F.V. affirms that the descriptions given can only be applied to globules of mineral oil which are dispersed in water. "The evidence is conclusive that fixed petroleum oil floating on water . . . forms a coat of varnish

or gum more or less thick according to the accidents of position". F.V. appears as a strong adherant of the "mineral oil" theory.
This letter also appears in *The Adelaide Observer* of 1.9.1871 (p. 3).

WHITTELL, H. A. (1871) *The Adelaide Observer* 30.9.71.

A reply to the previous reference, which agrees that coorongite has an organic structure, but, stating that microscope thin section views cannot be explained in terms of the plant origin suggested by M. J. Berkeley. Further, any suggestion of coorongite being a lichen is dismissed on account of the occurrence of diatoms embedded in the matrix.

SCRUTTON, T. U. (1874) Petroleum or Coal in S. Aust. *The S. Aust. Chronicle & Weekly Mail* Suppl. to issue of 21.2.74.

This article reports an address by T. U. Scrutton (p. 1, cols 1-4) to the S.A. Chamber of Manufacturers extolling the many virtues of petroleum whilst calling for further investments in oil drilling. Scrutton refers to the value of coorongite (which he confuses with elaterite) and completely dismisses any possibility of its plant origin. He states that, because of the high oil yield from coorongite on heating, it is likely that, in the past, "millions of tons of oil have been projected from subterranean sources" and it only needs money to find it. Many aspects of the report had no substantial basis at the time, and subsequent efforts have shown that they were

erroneous. Nevertheless, some interesting information on the early discovery of coorongite is given as well as descriptions of the area. The address by Mr Scrutton was also reported in *The South Australian Register* of 16.2.74 (pp. 5 and 6). The report was also issued as a separate pamhplet under the same title.

BASEDOW, H. (1925) *The Adelaide Observer* 14.8.25.

A contribution stating that authorities in the United States had confirmed that coorongite "consists in part of vegetable organism which is oil bearing". Basedow explains that he had grown the alga under laboratory conditions and "the little plants developed so plentifully that the material grew up the sides and neck of the bottle . . . If this can be done on a small scale, why not apply it to the large?" He further states that the material "could be as valuable to the State as a gusher of liquid oil" but no one seems to have given credence to his suggestion.

Acknowledgments

TRANSACTIONS OF THE
ROYAL SOCIETY
OF SOUTH AUSTRALIA
INCORPORATED

CONTENTS

EARLY TERTIARY CYCLAMMINA AND HAPLOPHRAGMOIDES (FORAMINIFERIDA: LITUOLIDAE) IN SOUTHERN AUSTRALIA

BY N. H. LUDBROOK

Summary

The genus Cyclammina is represented in southern Australian Tertiary deposits by five species whose internal and external morphologies are described: C. complanata Chapman, C. otwayensis n.sp. and C. paupera Chapman, which are restricted to sediments of Palaeocene to Middle Eocene age, and C. incisa (Stache) and C. rotundata Chapman & Crespin, which usually occur together over a wide geographical range and have a long stratigraphic range from Palaeocene to Early Miocene. Their palaeogeographical and palaeoecological significance and their stratigraphic utility are discussed.

EARLY TERTIARY *CYCLAMMINA* AND *HAPLOPHRAGMOIDES* (FORAMINIFERIDA:LITUOLIDAE) IN SOUTHERN AUSTRALIA

by N. H. LUDBROOK

Summary

LUDBROOK, N. H. (1977)—Early Tertiary *Cyclammina* and *Haplophragmoides* (Foraminiferida: Lituolidae) in southern Australia. *Trans. R. Soc. S. Aust.* **101**(7), 165-197, 30 November, 1977.

The genus *Cyclammina* is represented in southern Australian Tertiary deposits by five species whose internal and external morphologies are described: *C. complanata* Chapman, *C. otwayensis* n.sp. and *C. paupera* Chapman, which are restricted to sediments of Palaeocene to Middle Eocene age, and *C. incisa* (Stache) and *C. rotundata* Chapman & Crespin, which usually occur together over a wide geographical range and have a long stratigraphic range from Palaeocene to Early Miocene. Their palaeogeographical and palaeoecological significance and their stratigraphic utility are discussed.

A species of *Haplophragmoides* occurring in Late Cretaceous assemblages and with *Cyclammina* in the Palaeocene is described as *Haplophragmoides taylori* n.sp.

Introduction

Since it was first recognised by Chapman (1904) in ochreous brown clay from Brown's Creek in Victoria, the genus *Cyclammina* has occupied a prominent place in the literature on early Tertiary sediments of southern Australia. It occurs abundantly and in some parts of the sequence, particularly in the Gambier Embayment of the Otway Basin and in the Torquay Basin, is the dominant and, apart from marine dinoflagellates, almost the only marine microfossil occurring in Palaeocene and Eocene paralic silts and sands. In the past, its stratigraphic potential was discounted and only superficial attention was paid to its internal structure. Knowledge of the internal structure of *Cyclammina* species has been greatly advanced by the work of Bronnimann (1951), Voloshinova & Budasheva (1961), Serova (1964) and Banner (1966, 1970).

The present paper is designed to vindicate the early work of Chapman in correctly recognising the genus *Cyclammina*, separable into several species, and to support the conclusions of Taylor (1965) that the species in the Otway Basin have stratigraphic value. Glaessner's view (1951) that *Cyclammina* was not a reliable index fossil appears to have prompted Baker (1953) and Harris (1965) to discount its stratigraphic potential. Taylor's contention that arenaceous forms previously assigned to *Cyclammina* are, in fact, *Haplophragmoides*, is shown to be based on a misunderstanding of the internal morphology of the species and to have been influenced by bathymetric and ecological interpretations.

Five species of *Cyclammina* are recognised: *C. complanata* Chapman, *C. incisa* (Stache), *C. otwayensis* n.sp., *C. paupera* Chapman and *C. rotundata* Chapman & Crespin. A species described by Taylor as *Haplophragmoides* sp. B was correctly placed in *Haplophragmoides*. It occurs in the Late Cretaceous with a small benthonic assemblage and in Palaeocene assemblages with *Cyclammina*, and is here named and described as *Haplophragmoides taylori* n.sp.

Abbreviations used are as follows:

S.A.D.M.	Department of Mines, South Australia
E.&W.S.	Engineering and Water Supply Department, South Australia
V.M.D.	Mines Department, Victoria
B.P.N.L.	Beach Petroleum No Liability
O.D.N.L.	Oil Development No Liability
P.A.C.	Point Addis Company
S.E.O.S.	South East Oil Syndicate
CPC	Commonwealth Palaeontological Collection, Canberra
GSSA	Geological Survey of South Australia Collection

GSM   Geological Survey of Victoria Collection

NMV   National Museum of Victoria Collection

WAM   Western Australian Museum Collection

NZGS   Geological Survey of New Zealand Collection

Historical records of *Cyclammina* in southern Australia

Chapman (1904) recorded *Haplophragmium latidorsatum* (Bornemann), *H. glomeratum* Brady and *H. canariense* (d'Orbigny)—and described *Cyclammina complanata* and *C. paupera*—from Brown's Creek. His sample was collected by Kitson from a locality between Rotten Point and the mouth of the Johanna River 13.6 km northwest of Cape Otway, Port Campbell Embayment of the Otway Basin, in the lower 1.3 m of the Johanna River Sands (see map and section, Carter 1958, p. 8). In the section exposed between Rotten Point and Brown's Creek described as Section 28 by Raggatt and Crespin (1955, p. 134), the lowest 25.6 m (84 feet) comprise the Rotten Point Sands, and the overlying 24.4 m (80 feet) the Johanna River Sands (Carter 1958, p. 10) from the 0.6 m (2 feet) bed of "grey to purplish-brown shale with *Cyclammina*" of which Chapman's material is presumed to have been collected (Carter 1958, p. 10; Taylor 1965, p. 151).

Taylor (1965, p. 157) considered that the presence of *C. complanata* and *C. paupera* gave evidence of a Palaeocene age for the lower part of the Johanna River Sands, and, while this is possible, there is no firm supporting evidence, and the age could be somewhat younger. Some support for an age younger than Palaeocene is given by Harris's (1971, p. 83) recognition of his *Proteacidites pachypolus* Zonule (Middle Eocene, P10 to P13 of Blow, 1969) (McGowran *et al.* 1971, Enclosure 14.1) in dark purple to black carbonaceous silts, sands and clays he referred to the Johanna River Sands, without identifying the sediments with those described by Carter (1958). Harris reported that derived Palaeocene species were also present. However, preservation of the *Cyclammina* spp. described by Chapman (1904) is such that it is unlikely that they were derived from older sediments.

Chapman's figured specimens (1904, pl. 22) are, with one exception, mounted on NMV Slide P26049; they are clearly identifiable from Chapman's figures. The specimen figured as *Haplophragmium canariense* (d'Orbigny) (pl. 22, fig. 2) is however, not on the slide: the specimen on square 2 is not *"H. canariense"*, as indicated on the slide, but a distorted juvenile of *Cyclammina complanata*.

Chapman & Crespin (1930) described *Cyclammina rotundata* and *C. longicompressa* from subsurface micaceous marls (Micaceous Marl Member of Carter 1964, pp. 22, 58, Table 1) now renamed the Metung Marl Member (Hocking 1976, p. 259) of the Lakes Entrance Formation. The association of *Cyclammina* species with *Victoriella conoidea* and *Almaena gippslandica* (Carter 1964, pp. 22, 56) establishes an Oligocene to Early Miocene age (Janjukian Stage) for the unit, *Globigerina euapertura* zone of Ludbrook & Lindsay (1969) equivalent to P21 (=N2) to N4 of Blow (1969).

Chapman & Crespin (1932) recorded *Cyclammina incisa* (Stache) from the same unit.

Parr (1938) briefly described *Cyclammina incisa* (Stache) from sediments he believed to be of Late Eocene age from deep borings in King's Park, Perth, but which are now defined as the King's Park Shale, of Palaeocene age (McGowran 1964).

Singleton (1941) erected the Anglesean Stage for "the interval of time represented by the deposition of the dark-coloured sands with *Cyclammina* of cliff sections between Anglesea and Point Addis", which he considered to be of Oligocene age. However, Singleton (p. 13 and correlation chart) correlated other not necessarily contemporaneous *Cyclammina*-bearing carbonaceous sands with those at Anglesea.

Crespin (1943) recorded in detail the distribution and stratigraphic range of *Cyclammina incisa, C. rotundata* and *C. longicompressa* (= *C. incisa*) in subsurface sediments of the Gippsland Basin, *Cyclammina incisa* being selected as the zone fossil for the Janjukian Lakes Entrance Formation in which it was said to be persistent (Crespin 1943, pp. 8, 10, 13, 78, Table 1).

Crespin (1950, p. 72, pl. 10, figs 3, 4, 5a, b) described species occurring in the stratotype Anglesean at Demon's Bluff. The specimen figured as *C. paupera* (pl. 10, fig. 4) appears to be an immature *C. incisa*, and not *C. paupera* as interpreted by Taylor (1965, p. 151, fig. 4 (1a, b)) and in the present paper.

Baker (1953) recorded *Cyclammina* from the Princetown Member of the Dilwyn Forma-

TABLE 1.
Analysis of specimens measured

Species	Specimens	Chambers in last whorl	Diameter	Average diameter	Thickness	Average thickness	Ratio diameter: thickness	Percentage of total							Remarks
								6–7	8	9	10	11	12	12+	
C. complanata	54	7–16	0.45–3.75	1.08	0.15–1.12	0.39	2.8:1	1.85	1.85	16.66	18.20	26.00	20.40	14.82	96% have 9 or more chambers
C. incisa	390	7–15	0.28–3.00	1.15	0.15–1.75	0.54	2.13:1	5.64	14.87	26.41	26.15	11.80	8.20	6.92	79% have 8–11 chambers
C. otwayensis	172 (+480)	7–11	0.35–0.80	0.64	0.15–0.50	0.30	2:1	16.30	29.70	39.50	10.50	4.00	—	—	69% have 8–9 chambers
C. paupera	52	7–11	0.33–0.75	0.52	0.12–0.25	0.20	2.6:1	3.85	26.92	32.69	28.84	5.77	1.92	—	88% have 8–10 chambers
C. rotunda	93	6–13	0.50–2.12	1.13	0.30–1.50	0.73	1.55:1	11.83	23.66	24.73	18.28	6.45	11.93	3.22	85% have 8–11 chambers
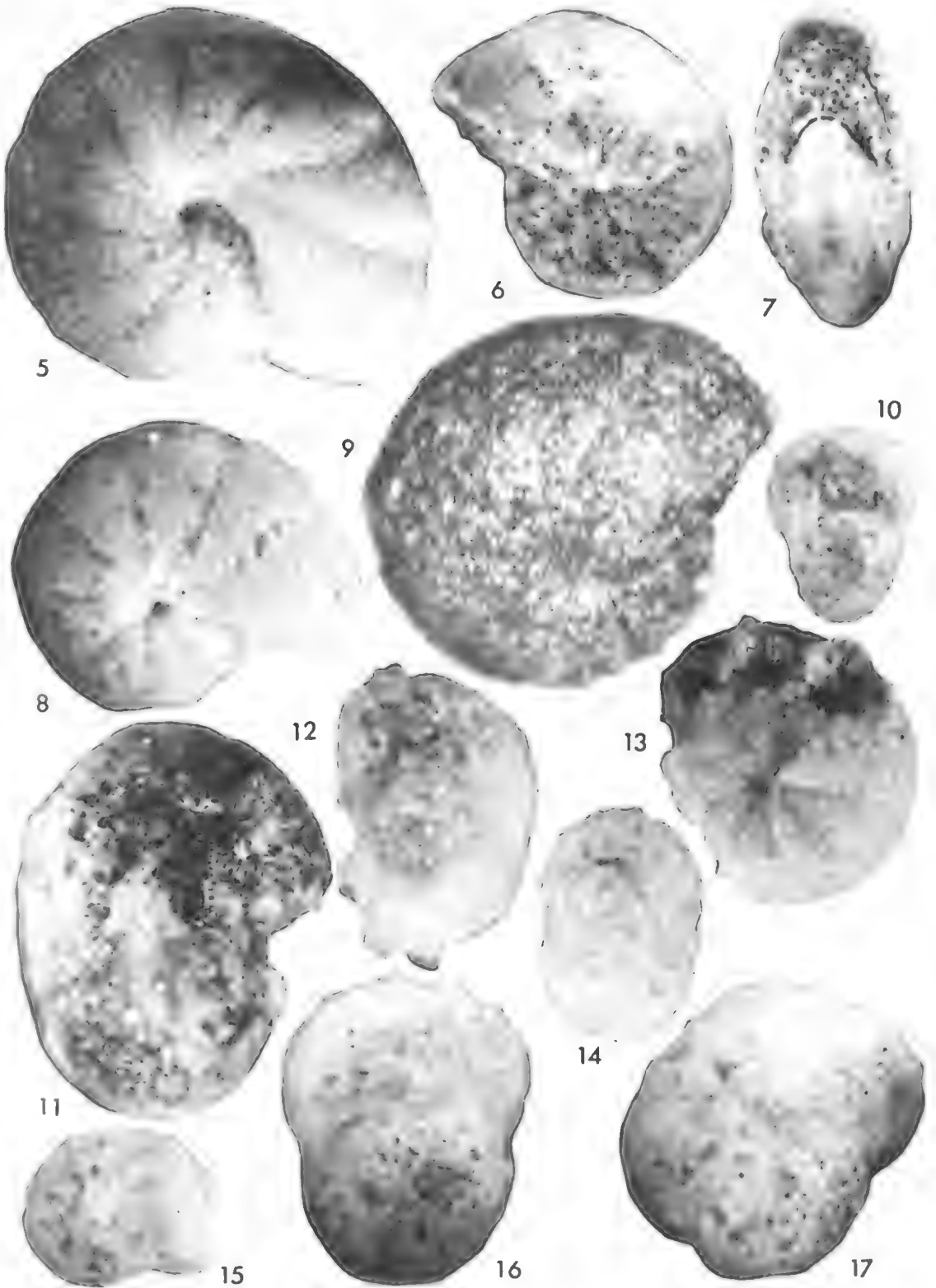
tion. According to Harris (1965, p. 78) palynological evidence indicated a Late Palaeocene age for this member, and the possibility of the microfloral zonule present in the upper part of the Dilwyn Formation being as young as Early Eocene was not excluded (Taylor in Singleton 1968, 1973, p. 116); Harris 1971, pp. 70, 78; Taylor 1971, p. 226). The Princetown Member contains *Planorotalites* cf. *pseudomenardii* (Taylor in Singleton 1968, 1973, p. 116) and a latest Palaeocene to Early Eocene age (latest P6 to P7) is indicated (McGowran et al. 1971, Enclosure 14.1).

Raggatt & Crespin (1955) defined the Demon's Bluff Formation in which *Cyclammina* was the dominant and abundant form in exposures of the formation between Torquay and Eastern View in the Torquay Basin.

From palynological data presented by Harris (1971, pp. 72, 84), the microflora of the Demon's Bluff Formation falls within his *Triorites magnificus* zonule, which in its full range is equivalent to upper *Globigerapsis index index* to "*Turborotalia*" *aculeata* planktonic foraminiferal zones of Ludbrook and Lindsay (1969) corresponding to P13 to P16 of Blow (1969) and of late Middle to Late Eocene age (McGowran et al. 1971, Enclosure 14.1). Singleton's (1968, 1973, p. 116) chart would indicate a Late Eocene age, P16 to P17, and Abele et al. (1976, p. 232) a Late Eocene to Early Oligocene age for the Anglesea Member.

Ludbrook (1963) reported *Cyclammina* as being well-represented in the early Tertiary of the Gambier Embayment.

Taylor (1965) in studies of subsurface sediments of the Port Campbell Embayment, claimed that the genus had been misinterpreted

and that apparent labyrinthic internal structures were not primary morphological features but the result of replacement of agglutinating cement by pyrite, and that quartz plucking was responsible for a cancellate appearance of the wall surface (Taylor 1965, p. 9). Using evidence that the living *Cyclammina cancellata* Brady was restricted to depths greater than 200 metres and that the *Cyclammina*-bearing sediments of the Otway Basin were laid down under fairly shallow shelf to estuarine conditions, so that the presence of *Cyclammina* in the Dilwyn Formation would be contrary to environmental interpretations (p. 158), Taylor transferred the species previously recorded in *Cyclammina* to *Haplophragmoides*. Unfortunately, Taylor's reclassification was accepted by other workers such as McGowran (1965, p. 18), Singleton (1968, 1973, p. 117), Banner (1970, p. 277) and Harris (1971, pp. 80, 83, 84), and the significance of *Cyclammina* in the Australian early Tertiary was temporarily placed in abeyance. Taylor, however, demonstrated mainly from subsurface sections that the *Cyclammina* ("*Haplophragmoides*") species had characteristic stratigraphic ranges. In this he is supported in the present paper.

Ludbrook (1971) asserted that the species were correctly placed in *Cyclammina* by previous authors. McGowran (1973) recorded a *Cyclammina* facies in the Lacepede Formation. Lindsay & Bonnett (1973) recorded and figured "*Cyclammina*" cf. *incisa* from subsurface sediments of Oligocene age in the Waikerie area of the Murray Basin.

Cockbain (1974) described and figured, including a thin section, *Cyclammina incisa* from the Late Eocene Pallinup Siltstone, Plantagenet Group, southwestern Australia.

PLATE 1

Figs 5-8, 13. *Cyclammina incisa* (Stache). Fig. 5—GSSA Ff597, O.D.N.L. Mt Salt No. 1, 939-942 m, Dartmoor Formation, Palaeocene to Early Eocene, X46. Fig. 6—GSSA Ff596, E. & W.S. Kingston No. 3, 65.2–69.2 m, Lacepede Formation, Late Eocene, umbilical view, X30. Fig. 7 —GSSA Ff596, E. & W.S. Kingston No. 3, 65.2–69.2 m, Lacepede Formation, Late Eocene, apertural view, X30. Fig. 8—GSSA Ff595, O.D.N.L. Mt Salt No. 1, 777-780 m, Dartmoor Formation, Palaeocene to Early Eocene, X50. Fig. 13—GSSA Ff603, O.D.N.L. Mt Salt No. 1, 750-753 m, Dartmoor Formation, Palaeocene to Early Eocene, natural dissection, view into chamber lumina showing hypodermal alveolae in walls of two chambers, X46.

Figs 9-12, 14-17. *Cyclammina rotundata* Chapman & Crespin. Fig. 9—GSSA Ff613, O.D.N.L. Mt Salt No. 1, 966-969 m, Dartmoor Formation, Palaeocene to Early Eocene, X50. Fig. 10—GSSA Ff612, B.P.N.L. Geltwood Beach No. 1, 454 m, Tartwaup Formation, Middle Eocene, X30. Fig. 11—GSSA Ff616c, Demon's Bluff Formation, Demon's Bluff, Late Eocene, showing very small areal apertures on the left side, X50. Fig. 12—GSSA Ff616b, Demon's Bluff Formation, Late Eocene, showing slight lip on aperture, X50. Fig. 14—GSSA Ff611, S.A.D.M. Waikerie Bore 28W, 146.3–147.8 m, Ettrick Formation, Oligocene, juvenile specimen showing short open aperture, X50. Fig 15—GSSA Ff612, B.P.N.L. Geltwood Beach No. 1, 454 m, Tartwaup Formation, Middle Eocene, umbilical view, X30. Fig. 16—GSSA Ff612, apertural view, X50. Fig. 17—GSSA Ff612, umbilical view, X50.

TABLE 2.

Measurements of specimens sectioned

Reg. No. GSSA	Number whorls	Chambers in last whorl	Diameter Thickness mm	Diameter mm	Diameter initial chambers mm	Whorls in initial chambers	Wall thickness mm	Interseptal width of chamber mm	Last chamber lumen mm	Septal wall thickness mm	Mega- or micro- spheric	Vertical or equatorial section	Locality (see Fig.1)	depth m
C. complanata														
Ff619	3	15	1.00	2.88	1.25	2	0.38–0.5	0.10	0.75	0.60	micro-	E	15 cavings	651–653
Ff620			0.50	1.50			0.25					V	15 cavings	654–655
Ff623			0.75	1.96			0.25		0.50			V	15	411–415
Ff626	2½	10	0.30	0.75	0.75	2½	0.08	poor specimen, juvenile				E	17	881–884
Ff627	?4	11	0.30	0.70	0.70	3–4	0.10	0.05	0.30	0.05		E	17	881–884
Ff628	2	9	0.30	0.88	0.88	2		0.13	0.13	0.10	micro-	E	17	911–914
Ff629	3	11	0.25	0.75	0.75	3		poorly preserved, juvenile				E	17	914–917
Ff630	3	9	0.25	0.66	0.66	3		poorly preserved, juvenile				E	17	914–917
Ff631	2	11	0.50	1.00	1.00	2	0.13	0.13	0.13	0.05		E	17	917–920
Ff645	3½	13	0.50	1.12	1.00	3	0.13	0.03	0.13	0.13	?mega-	E	17	930–933
C. incisa														
Ff621	4	11		2.00	1.00	3	0.20	0.13	0.38	0.13	micro-	E	15	411–415
Ff632	?3	?11	0.80	1.75	1.00	2		poorly preserved			micro-	E	16	274–277
Ff633	4	15	1.25	2.88	1.50	3	0.45	0.20	0.35	0.13	micro-	E	4	
Ff634		13	1.75	2.75			0.38					V	4	
Ff635	4	15		2.55	1.0	3	0.60	0.20	0.38	0.20	micro-	E	5	
Ff641		10	1.12	1.75			poorly preserved juvenile				?micro-	E	3	
Ff642	3	8	0.37	0.75	0.75	3					?	E	3	
Ff643				1.25			0.25		0.60	0.08	mega-	V	1	
Ff644	2	11		1.12			0.20	0.10	0.18	0.18	micro-	E	5	
Ff646	4	13		2.33	1.13	3	0.38	0.13	0.33		micro-	E	4	
C. otwayensis														
Ff636		11	0.29	0.62	0.62		0.05 (1), 0.05 (2)	0.10	0.13	0.03	micro-	V	21	298.7
Ff637	3	9	0.35	0.62		3		poorly preserved			?	E	21	298.7
Ff647				0.80				poorly preserved				E	21	298.7
Ff648	2½	9		0.60	0.60	2½	0.05	0.13	0.10	0.04	mega-	E	21	298.7
C. paupera														
Ff649	4	8		0.55	0.04	2	0.03	0.15	0.13	0.03	micro-	E	21	298.7
C. rotundata														
Ff624			0.62	0.93	1.00	?3	0.25	poorly preserved				E	5	
Ff625	3	?11		1.75			0.60					E	5	
Ff638	4	11	0.75	1.25	0.62	3	0.25	0.13	0.18	0.10	micro-	E	15	262–265
Ff639		?11	1.12	1.66			0.25 (3)					V	8	12–21

(1), (2), (3) Thickness epidermis 0.025 mm.
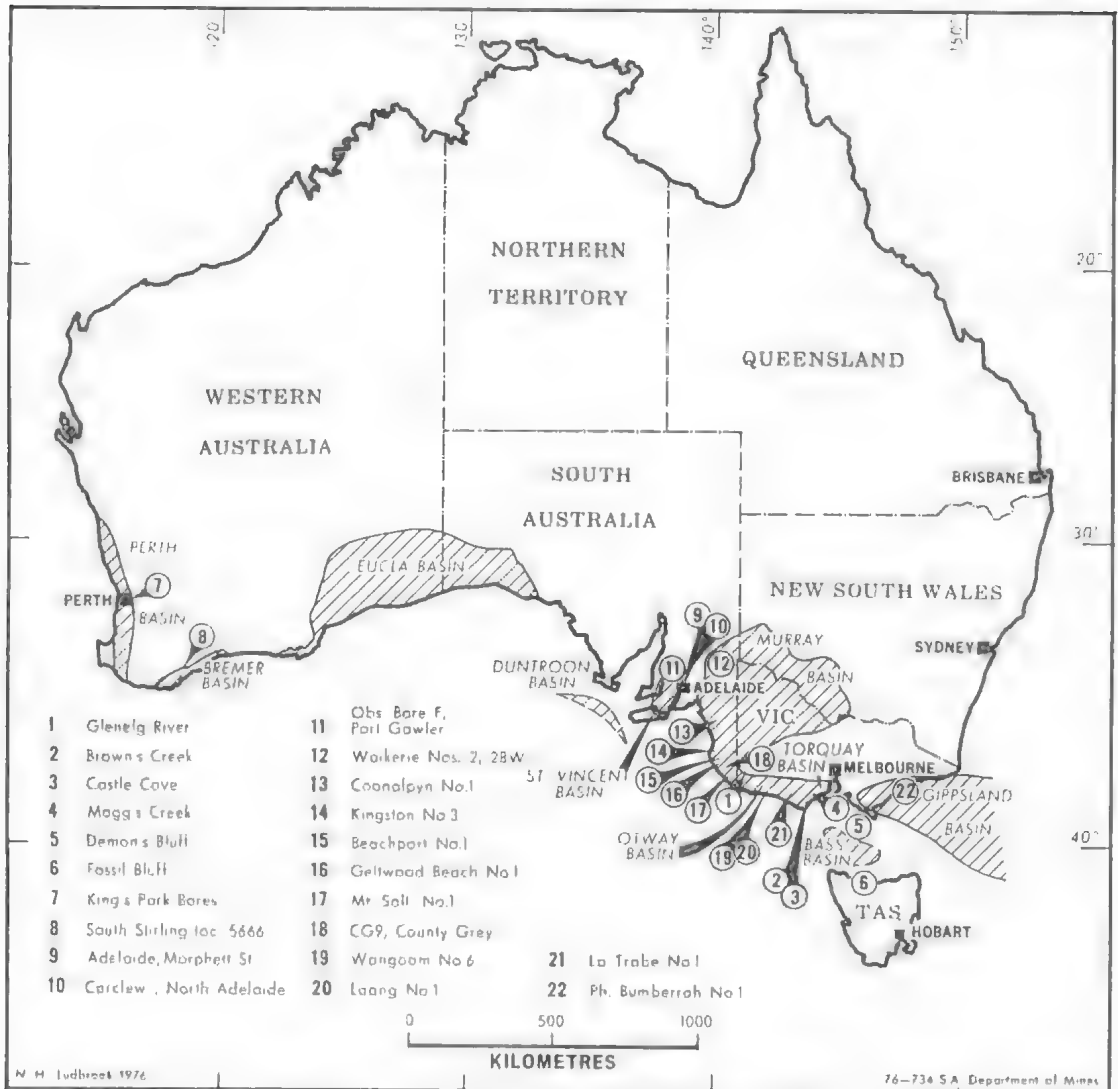
Figure 1. Map showing *Cyclammina* localities.

and recognised the pertinence of Robinson's (1970) observations to the apparent discrepancy between records of *Cyclammina* in early Tertiary shallow water deposits and the predominantly deep water depth range of the genus.

Quilty (1974) briefly described and figured, including a thin section, *Cyclammina* cf. *incisa* from Fossil Bluff, south of Table Cape, Tasmania.

### Source of material

Details of the localities shown in Figure 1 are as follows:

Outcrops

1. *Glenelg River*, 2.4 km downstream from Killara Bridge, 14 km SW of Casterton, HAMILTON 1:250 000 geological map sheet, 37°39'56"S, 141°17'23"E, Gambier Embayment, Otway Basin, base of Dartmoor Formation, Palaeocene to Early Eocene (see *Casterton* 1:63 360 geological map sheet).

2. *Brown's Creek*, between Rotten Point and mouth of Johanna River, 13.6 km NW of Cape Otway, COLAC 1:250 000 geological map sheet, 38°46'22"S, 143°23'14"E, Port Campbell Embayment, Otway Basin, base of Johanna River Sands, ?Palaeocene to Early Eocene (section described by Raggatt & Crespin 1955, p. 134).
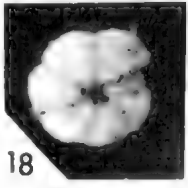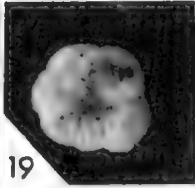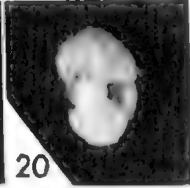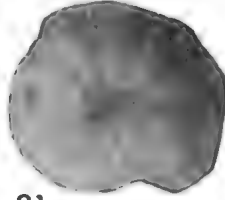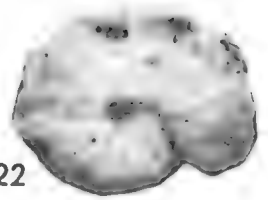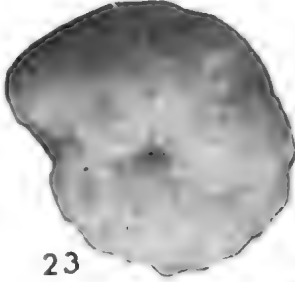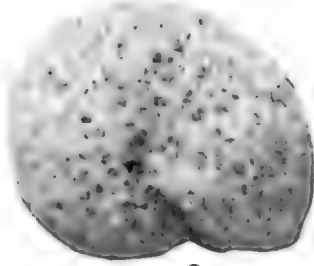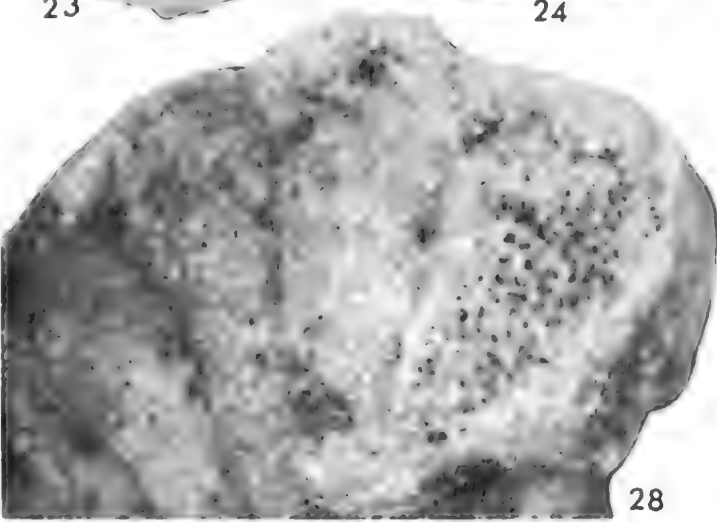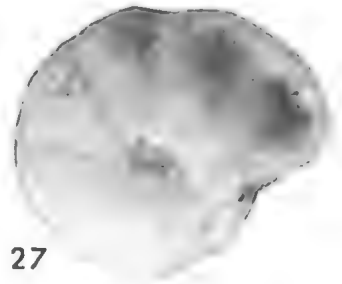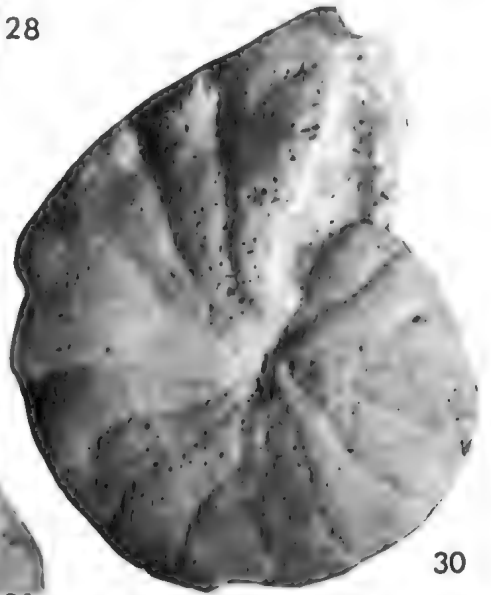
3, *Castle Cove*, 10 km NW of Cape Otway, COLAC 1:250 000 geological map sheet, 38°47'18"S, 143°26'35"E, Port Campbell Embayment, Otway Basin, Johanna River Sands, ?Middle to Late Eocene (see Carter 1958, p., 13; Abele et al. 1976, p. 224).

4. *Mogg's Creek*, 4 km E of Eastern View, QUEENSCLIFF 1:250 000 geological map sheet, 38°28'15"S, 144°04'19"E, Torquay Basin, Demon's Bluff Formation, Late Eocene (section described by Raggatt & Crespin 1955, p. 108).

5. *Demon's Bluff, Anglesea*, QUEENSCLIFF 1:250 000 geological map sheet, 38°24'36"S, 144°11'39"E, Torquay Basin, Anglesea Member, Demon's Bluff Formation, Late Eocene (section described by Raggatt & Crespin 1955, pp. 113-117).

6. *Fossil Bluff, Table Cape*, BURNIE 1:250 000 geological map sheet, 40°58'55"S, 145°44'54"E, Bass Basin, Freestone Cove Sandstone, Table Cape Group, Early Miocene N4/5 (Quilty 1974, p. 33).

Boreholes and Wells

7. *King's Park Bores 1 and 2*, Perth, PERTH 1:250 000 geological map sheet, 31°58'S, 115°50'E, Perth Basin, King's Park Shale, Palaeocene (McGowran 1964).

8. *South Stirling*, Water Bore, Plantagenet Location 5666, near South Stirling, 20 km S of Stirling Range, MOUNT BARKER 1:250 000 map sheet, 34°36'S, 118°08'20"E, at 12-21 m depth, Bremer Basin, Pallinup Siltstone, Plantagenet Group, Late Eocene (Cockbain 1974).

9. S.A.D.M. *Adelaide*, New Morphett Street and Victoria Bridges, Bore 11, Adelaide Railway Station 25-25.6 m; Bore 12, south bank Torrens Lake 16.76-17 m; ADELAIDE 1:250 000 map sheet, 34°55'41"S, 138°35'02"E, St Vincent Basin, Adelaide Plains Sub-Basin, undifferentiated Tortachilla Limestone-Blanche Point Transitional Marl, Late Eocene (Lindsay 1969, pp. 54, 59).

10. S.A.D.M. "*Carclew*", *North Adelaide*, section TA749, hundred of Yatala, ADELAIDE 1:250 000 geological map sheet, 34°55'24"S, 138°35'02"E, 19.8-19.9 m, St Vincent Basin, Adelaide Plains Sub-Basin, Blanche Point Banded Marl, Late Eocene (Lindsay 1969, pp. 53, 58).

11. S.A.D.M. *Observation Bore F, Port Gawler*, T/A, hundred of Port Gawler, ADELAIDE 1:250 000 geological map sheet, 34°45'49"S, 138°27'E, 253-254.5 m, St Vincent Basin, Adelaide Plains Sub-Basin, Blanche Point Banded Marl, Late Eocene (Lindsay 1969, pp. 52, 55).

12. S.A.D.M. *Waikerie* Bore 2, section 692, hundred of Waikerie, 3.6 km SSW of Waikerie, 149 m; Bore 28W, section 553, hundred of Waikerie, 2.5 km southwest of Waikerie, 146-148 m. RENMARK 1:250 000 geological map sheet, 34°13'18"S, 139°57'30"E, Murray Basin, "glauconitic clay unit", Ettrick Formation, Oligocene (Lindsay & Bonnett 1973).

13. E. & W.S. *Coonalpyn No. 1*, section 56, hundred of Coneybeer, PINNAROO 1:250 000 geological map sheet, 35°41'05"S, 139°49'53"E, 69-71 m, 105-107 m, Murray Basin, Buccleuch Beds, A, B, Late Eocene (Ludbrook 1961, pp. 16, 17).

14. E. & W.S. *Kingston No. 3*, section 374, hundred of Lacepede, NARACOORTE 1:250 000 geological map sheet, 36°50'S, 137°51'E, 65.2-69.2 m, Gambier Embayment, Otway Basin, Lacepede Formation, Late Eocene (Ludbrook 1971, pp. 56, 58).

PLATE 2

Figs 18-20. *Haplophragmoides taylori* n.sp. Fig. 18—Holotype GSM 64829 (1), La Trobe No. 1 Well, 292.61 m, Dilwyn Formation, Palaeocene to Early Eocene, X48. Fig. 19—Paratype GSM 64829 (5) Wangoom No. 6, Core 12, 596-601 m, Dilwyn Formation, ?Early Eocene, umbilical view, X48. Fig. 20—Paratype GSM 64829 (5), apertural view, X48.

Figs 21, 22, 26, 27. *Cyclammina puupera* Chapman. Fig. 21—Topotype GSM 64828 (13), Brown's Creek, base of Johanna River Sands, ?Palaeocene to Early Eocene, X50. Fig. 22—GSSA Ff607 V.M.D, La Trobe No. 1, Core at 298.7 m, Dilwyn Formation, Palaeocene to Early Eocene, umbilical view, X50. Fig. 26—GSSA Ff616, V.M.D, La Trobe No. 1, Core at 298.7 m, Dilwyn Formation, Palaeocene to Early Eocene, apertural view, X90. Fig. 27—GSSA Ff650, O.D.N.L, Mt Salt No. 1, 954-957 m, Dartmoor Formation, Palaeocene to Early Eocene, X90.

Figs 23-25. *Cyclammina otwayensis* n.sp. Fig. 23—Holotype GSSA Ff608, Glenelg River, base of Dartmoor Formation, Palaeocene to Early Eocene, X50. Fig. 24—Paratype GSSA Ff609, V.M.D, La Trobe No. 1, Core at 298.7 m, Dilwyn Formation, Palaeocene to Early Eocene, X50. Fig. 25—Paratype GSSA Ff610, V.M.D, La Trobe No. 1, Core at 298.7 m, Dilwyn Formation, Palaeocene to Early Eocene, X50.

Figs 28-30. *Cyclammina complanata* Chapman. Fig. 28—GSSA Ff593, S.E.O.S. Beachport No. 1, 602-604 m, ?cavings from Dartmoor Formation, Palaeocene, showing appearance of distal ends of alveolae as seen through the epidermis and after erosion of epidermis, X40. Fig. 29—GSSA Ff594, S.E.O.S. Beachport No 1, 661-663 m, ?cavings from Dartmoor Formation, Palaeocene, showing areal apertures and thin fine-grained epidermis with distal ends of alveolae exposed by erosion of epidermis, X37. Fig. 30—GSSA Ff594, X26.
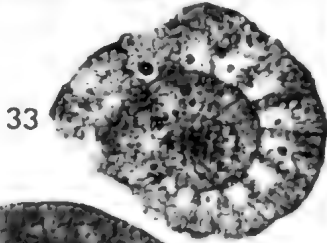
TABLE 3

Stratigraphic distribution and faunal association of *Cyclammina* species.

Species	Size	Chambers	PALAEOCENE TO EARLY EOCENE						MIDDLE TO LATE EOCENE					OLIGOCENE			MIOCENE
			A	B	C	D	E	F	G	H	I	J	K	L	M	N	O
C. complanata	large	15-16	—	X,b	—	X	—	—	—	—	—	—	—	—	—	—	—
C. incisa	large	8-11	?	X	X,p,b	—	X	—	X,a	X,p,b	X,p,b	—	X,p,b	X	X,p,b	X,p,b	X,p,b
C. otwayensis	small	8-9	X,a	X	—	D	—	X	—	—	—	—	—	—	—	—	—
C. paupera	small	8-10	X,a	X	—	X	—	—	—	—	—	—	—	—	—	—	—
C. rotundata	large	8-11	X	X	—	—	X	—	X,a	—	X,p,b	X,p,b	—	X	X,p,b	X,p,b	?

A. Dilwyn Formation
B. Dartmoor Formation
C. King's Park Shale
D. Johanna River Sands at Brown's Creek
E. Johanna River Sands at Castle Cove
F. Burrungule Member, Tartwaup Formation
G. Demon's Bluff Formation
H. Lacepede Formation

I. Gambier Limestone
J. Tortachilla Limestone—Blance Point Marls
K. Buccleuch Beds, A, B
L. Pallinup Siltstone
M. Ettrick Formation
N. Lakes Entrance Formation
O. Freestone Cove Sandstone

X. *Cyclammina*
a. agglutinated foraminifers
p. planktonic foraminifers
b. benthonic foraminifers

Figure 2. Correlation of *Cyclammina*-bearing formations in southern Australia.
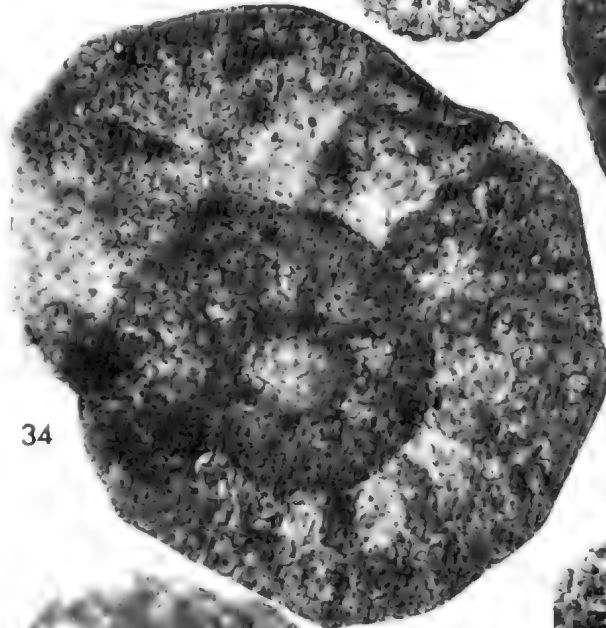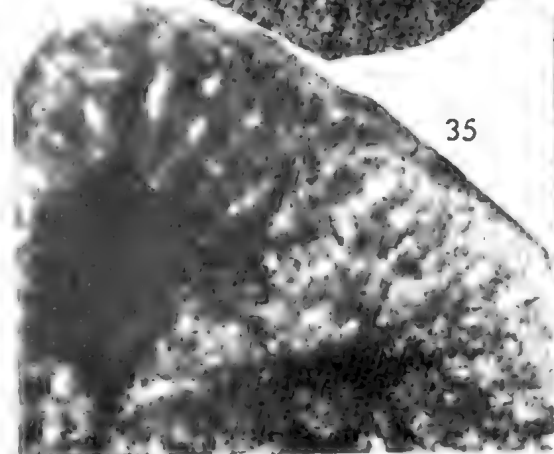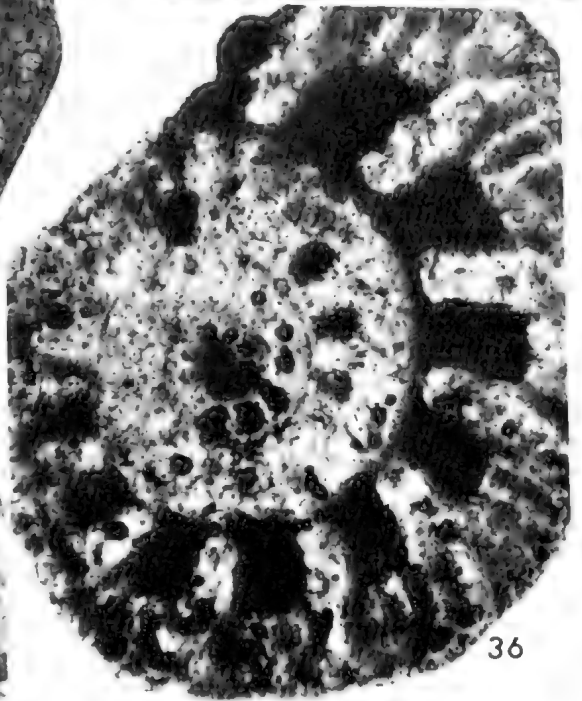
15. S.E.O.S. *Beachport No. 1*, section 20, hundred of Lake George, PENOLA 1:250 000 geological map sheet, 37°26′55″S, 140°02′15″E, Gambier Embayment, Otway Basin; 238–240 m Gambier Limestone, Late Eocene; 259–271 m Lacepede Formation, Late Eocene; 311–417 m Tartwaup Formation, Middle Eocene; 543–546 m Dartmoor Formation, Palaeocene to Early Eocene; 602–663 m ?cavings from overlying Dartmoor Formation (Ludbrook, 1971, pp. 52, 56).

16. B.P.N.I. *Geltwood Beach No. 1*, section 157, hundred of Mayurra, PENOLA 1:250 000 geological mapsheet, 37°39′44″S, 140°14′35″E, Gambier Embayment, Otway Basin; 238–277 m Gambier Limestone, late Eocene; 454 m Tartwaup Formation, Middle Eocene (Ludbrook 1971, pp. 52, 56).

17. O.D.N.L. *Mt Salt No. 1*, section 783, hundred of MacDonnell, PENOLA 1:250 000 geological map sheet, 37°57′25″S, 140°37′43″E, Gambier Embayment, Otway Basin, 585–954 m Dartmoor Formation, Palaeocene to Early Eocene; 954–972 m Bahgallah Formation, Palaeocene (Ludbrook 1971, pp 52, 56).

18. S.A.M.D. *C G.9*, County Grey lignite investigations, section 819, hundred of Young PENOLA 1:250 000 geological map sheet, 37°44′49″S, 140°37′54″E, Gambier Embayment, Otway Basin, 28.96–29.26 m, Burrungule Member, Tartwaup Formation, Middle Eocene (Harris 1966, p. 2, 1971, p. 81).

19. V.M.D. *Wangoom No. 6*, Warrnambool, water exploration bore, PORTLAND 1:250 000 geological map sheet, 38°23′S, 142°29′18″E, Tyrendarra Embayment, Otway Basin, Core 12, 596–601 m Dilwyn Formation, ?Early Eocene (Glenie 1971, Enclosure 13.6).

20. V.M.D. *Laang No. 1*, 28 km east of Warrnambool, water exploration bore, COLAC 1:250 000 geological map sheet, 38°23′S, 142°48′33″E, Tyrendarra Embayment, Otway Basin, Core 12, 654–656 m, Nirranda Sub-Group, Narrawaturk Marl, Late Eocene (Taylor 1965, fig. 5, p. 155; Glenie 1971, Enclosure 13.2).

21. V.M.D. *La Trobe No. 1* Princetown, COLAC 1:250 000 geological map sheet, 38°41′49″S, 143°10′49″E, Port Campbell Embayment, Otway Basin, 292.6–298.7 m Dilwyn Formation, Palaeo-

cene to Early Eocene (Taylor 1965, Fig. 5, p. 155; Glenie 1971, Enclosure 13.2).

22. P.A.C. *No. 1 Bore Parish of Bumberrah*, Metung, BAIRNSDALE 1:250 000 geological map sheet, 37°53′34″S, 147°50′14″E, Gippsland Basin, 394.7 m Lakes Entrance Formation, Oligocene.

Stratigraphic utility

Allowing for differences in nomenclature and taxonomic interpretation, Table 3 gives support to the data presented by Taylor (1965, p. 155, fig. 5). Palaeocene to Middle Eocene faunas are represented by three species: *C. complanata*, *C. otwayensis* and *C. paupera*. These species are not found in Late Eocene to Miocene sediments where only the long-ranging *C. incisa* and *C. rotundata* occur.

The stratigraphic relationships of the *Cyclammina*-bearing formations are shown in Figure 2. For the Otway Basin, the chart has been considerably simplified and for the Aire District slightly modified from those presented by Abele et al. (1976) which should be consulted for greater detail and for illustration of the diachronous relationships between most of the formations. The position of the Glen Aire Clay approximates to that expressed by Ludbrook & Lindsay (1969, p. 371). The name "Knight" (Sprigg 1952; Sprigg & Boutakoff 1953) has been retained for the Group of Early Tertiary non-marine and paralic sediments of the Gambier Embayment, in conformity with its continued use by the South Australian Department of Mines in hydrogeological studies of the Embayment and its use by most authors (Kenley, Rochow, Ludbrook, Taylor) in the Bulletin on the Otway Basin (Wopfner & Douglas 1971) and on the geological maps accompanying the Bulletin. It is beyond the scope of the present paper to disentangle the nomenclatural priorities of the units comprising the Knight and Wangerrip (Baker 1950) Groups which have already been discussed at some length by Kenley (1971), Glenie (1971)

PLATE 3

Figs 31–35. *Cyclammina incisa* (Stache). Fig. 31—GSSA Ff621, Demon's Bluff Formation, Demon's Bluff, Late Eocene, microspheric specimen equatorial section, X30. Fig. 42—GSSA Ff621, enlargement of part of last whorl showing hypodermal and septal alveolae, X75. Fig. 33—GSSA Ff633, Demon's Bluff Formation, Mogg's Creek, Late Eocene, microspheric specimen, equatorial section, X13. Fig. 34—GSSA Ff644, Demon's Bluff Formation, Demon's Bluff, Late Eocene microspheric specimenn equatorial section, X75. Fig 35 GSSA Ff632, B.P.N.I., Geltwood Beach No. 1 274–277 m, base of Gambier Limestone, Late Eocene, part of 2 chambers of collapsed specimen, equatorial section, X75.

Fig. 36 *Cyclammina rotundata* Chapman & Crespin (?*C. incisa* (Stache). GSSA Ff638, S.E.O.S. Beachport No. 1, 262–265 m, Lacepede Formation, Late Eocene, microspheric specimen, equatorial section, X75.
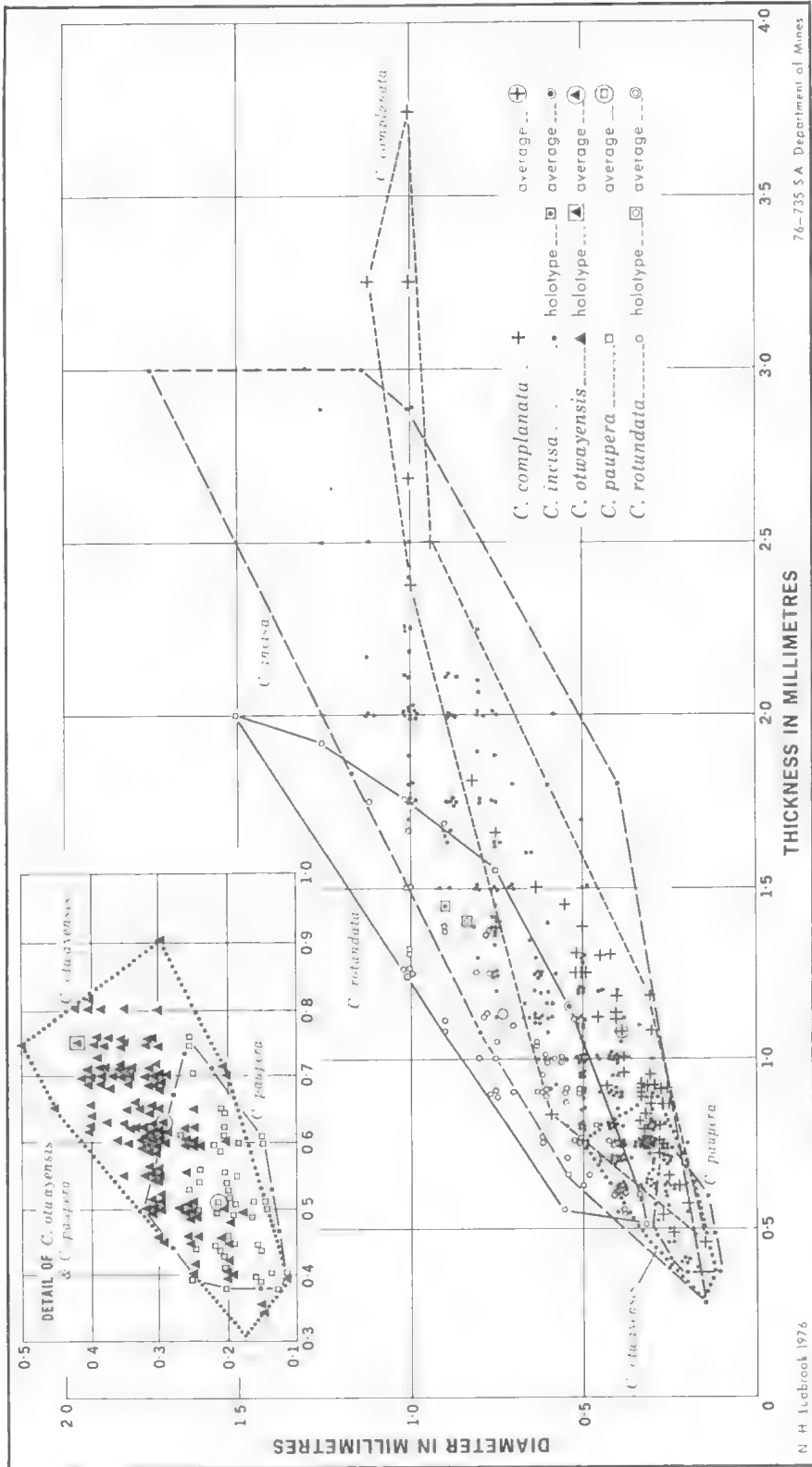
Figure 3. Scatter diagram of dimensions (diameter/thickness) of *Cyclammina* spp.

and Abele et al. (1976). Until the lithological and palaeontological relationships of all the units of the two groups are fully defined, it seems desirable to retain the nomenclature current for the Gambier and Port Campbell Embayments as shown in Figure 2.

Sectioning techniques

On the whole, specimens of *Cyclammina* from the southern Australian Tertiary are abundant and reasonably well-preserved. Distortion is relatively uncommon, and, apart from pyrite infilling, most tests have not been subjected to chemical action such as the secondary silicification described by Serova (1964). They are, nonetheless, difficult to section since the original cementing material was very thin, apparently organic (see pl. 4, fig. 43), and usually not preserved at all, particularly in outcrop specimens. Great care has to be exercised to avoid quickly reducing the specimen to an unrecognisable mass of quartz grains.

Serova (1964) distinguished between half sections or "grinds" (shlifovaniya) achieved by grinding down to the equatorial plane so that the internal structures are viewed in direct light (see Serova 1964, pls. 2 and 3), and thin sections (shlify) completed in the normal way by turning the specimen over and grinding the other side, the result being viewed by transmitted light (see Serova pls. 4 to 7).

Taylor's figures (1965, p. 146, fig. 2) were drawn from dissected specimens (b) or "grinds" (a, c, d, "thick sections" of Taylor). No thin sections were cut.

The first problem encountered in sectioning is to keep the specimens intact and to prevent the agglutinated quartz grains from dispersing during the grinding process. Sectioning was done under the microscope, using one ground glass slide, with or without grinding powder, to grind the specimen mounted in Lakeside Cement on the other. The specimen was kept under constant observation during grinding, and at the first sign of a break through the cement to the test wall, the slide was reheated and the cement redistributed over the specimen by fine needle, filling any exposed cavities. This method of recementation was continued throughout the sectioning process, and turning the specimen over for grinding was done while the specimen was completely immersed in the heated mounting medium. At no stage was grinding done on uncemented test wall or on empty chamber lumina. Any surplus cement was removed when sectioning was completed

and a drop of Xam placed on the specimen before covering with the cover slip. The most successful sections were those of specimens in which the organic lining of the chambers and alveolae were preserved (pl. 4, fig. 43) or where the chamber lumina and alveolae had been filled with pyrite and organic material (pl. 4, figs 37–42). No distorted specimens were used.

Morphology

Species show a wide range of development from the quite simple to non-alveolar structure of *Cyclammina paupera* to the highly-developed alveolar structure of *C. complanata*. Both of these extremes are present in Palaeocene sediments, and the only evidence of evolutionary development is that both the simple and the highly-developed forms do not persist beyond the Middle Eocene. The internal structures become clear only when thin sections are cut, though SEM photographs are valuable aids. Externally, species can be quite difficult to separate, as they almost all appear to intergrade. Considered at the adult well-developed end of the dimensional range, species are fairly readily separated from one another, but some populations contain a high percentage of immature individuals which, without the aid of thin sections, are specifically identifiable with only a mild degree of confidence. The overlap of species determined on their external features and plotted according to their relative dimensions (diameter/thickness) is clear from Figure 3, and the overlap of three of the species when the average diameter of the measured specimens is plotted against the number of chambers in the last whorl (Fig. 4).

Overlap is particularly the case with *C. incisa* and *C. rotundata*, which invariably occur together, and with *C. complanata* and *C. incisa*, which frequently occur together. As specimens identified as *C. incisa* occur over the whole stratigraphic range (Palaeocene to Miocene) of fossil *Cyclammina* in southern Australia and it is not practicable to cut thin sections to confirm the identity of all the specimens, its range may perhaps be open to question; the species has a known range of Eocene and Oligocene in New Zealand (Hornibrook 1971). *C. incisa* has been described as a "common Oligo-Miocene species of the circum-Pacific region" (Chang 1953) and recorded by several authors from the northern Pacific margin (Asano 1951, p. 6, figs 18, 19; Voloshinova & Budasheva 1961, p. 207, pl. 10, figs 1a, 1b, 3a, 4a,
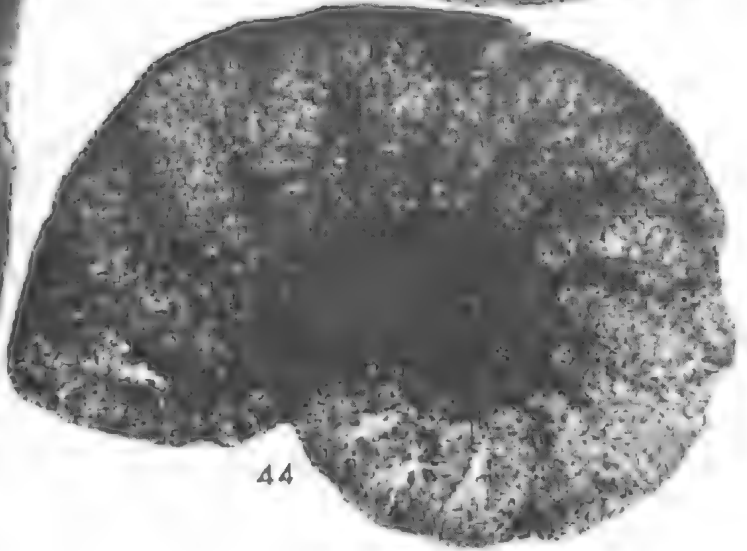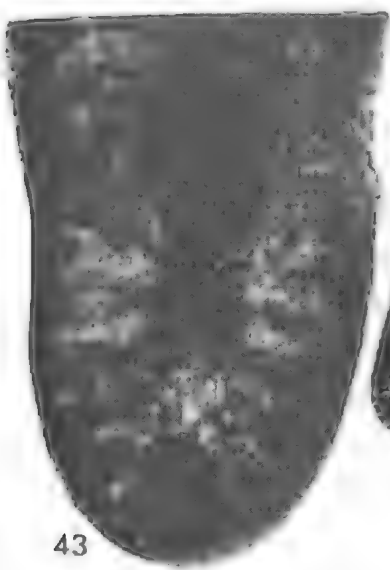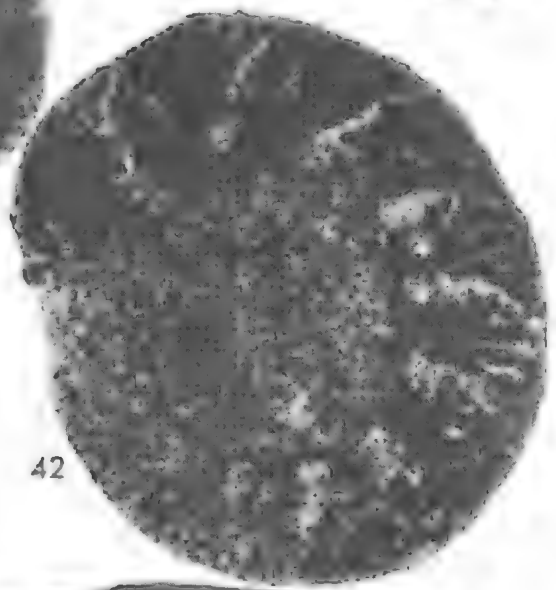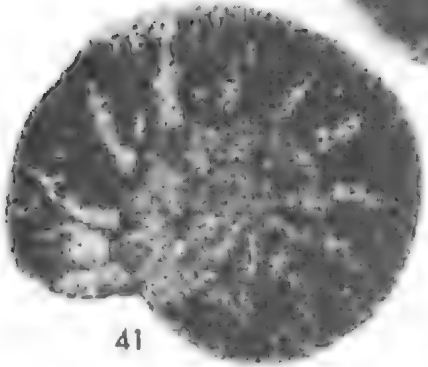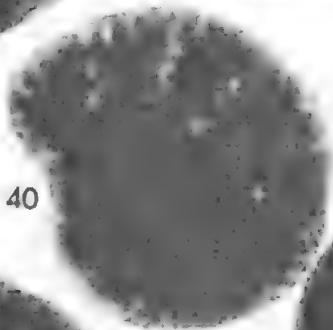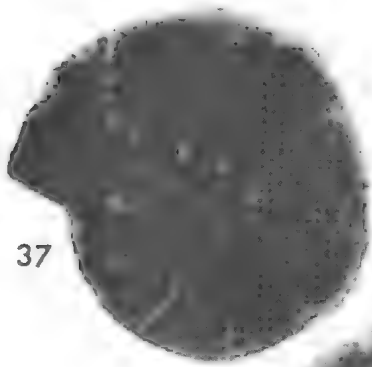
4b; Chang 1953, p. 34, pl. 3, figs 3–10; Chang 1956, pl. 1, figs 6–8), but it has not been possible in the present study to confirm these records.

Diagnostic external characters

Measurable parameters are tabulated in Table 1 and shown graphically in Figures 3 and 4. The 172 specimens of *C. otwayensis* measured are representative of some 600 individuals all of approximately the same dimensions.

C. complanata has a large, flattened, discoidal test, partly evolute, with 15 to 16 chambers in the last whorl of the fully-grown adult and slightly sinuate sutures. It has a thin epidermis through which the alveolar hypodermal structure appears as a fine punctate to vermiform pattern (pl. 2, figs 28, 29). The apertural face is high, laterally flattened, with large supplementary apertures (pl. 2, figs 29, 30).

C. incisa when fully developed and undistorted has a moderately large biconvex involute test compressed at the periphery with 11 to 12 chambers in the last whorl, straight sutures, and a fine-grained epidermis with scattered large quartz grains. The apertural face is moderately high and covered with coarse quartz grains. Supplementary areal apertures are sometimes visible between the grains (pl. 1, fig. 7, pl. 6, figs 47–49).

C. otwayensis is a small, biconvex, rather inflated species with usually 8 to 9 chambers in the last whorl, a thin epidermis through which the distal ends of the alveolae are visible in 2 or 3 radiating series in each chamber. The apertural face is a fairly high rounded arch; small supplementary areal apertures are sometimes visible.

C. paupera is conspicuous in a population as a small, flattened, biconvex, commonly collapsed pauperate test with 8 to 10 chambers in the last whorl and a very fine-grained chamber wall. Alveolae are visible through the epidermis in the holotype and topotypes, but more commonly the alveolar hypodermis appears not to have developed (pl. 4, fig. 37). It would appear to be a primitive type of *Cyclammina* similar to the small species close to *C. elegans* figured by Banner (1970, pl. 13, figs 1, 1a), notable for the absence of a supra-apertural zone.

C. rotundata is a large, inflated species, with a coarse-grained chamber wall and 8 to 11 chambers in the last whorl of the fully-grown adult. The apertural face is a low broad arch at all stages of development (pl. 1, figs 10, 11, 12, 14, 16); areal apertures are frequently visible between the the coarse quartz grains which cover the face (pl. 1, fig. 11).

Diagnostic internal characters

Parameters measurable from thin sections are shown in Table 2.

Almost the complete range of morphological variation illustrated by Banner (1970, pl. 13) is present in the five species. The structure of the hypodermis of southern Australian *Cyclammina* is alveolar, as described for the type species *Cyclammina cancellata* Brady by authors such as Bronnimann (1951), Serova (1964) and Banner (1970), and not labyrinthic as the genus has been conventionally described (e.g. by Loeblich and Tappan 1964). The septal walls are perforated by septal areal

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PLATE 4

Fig. 37. *Cyclammina paupera* Chapman. GSSA Ff649, V.M.D. La Trobe No. 1, 298.7 m Dilwyn Formation. Palaeocene to Early Eocene, microspheric specimen; the black areas are pyrite. X75.

Figs 38–40. *Cyclammina otwayensis* n.sp. Fig. 38—GSSA Ff648, V.M.D. La Trobe No. 1, 298.7 m, Dilwyn Formation. Palaeocene to Early Eocene, megaspheric specimen; black areas pyrite, X75. Fig. 39—GSSA Ff636, V.M.D. La Trobe No. 1, 298.7 m, Dilwyn Formation, Palaeocene to Early Eocene, vertical section; black areas pyrite, X75. Fig. 40—GSSA Ff637, V.M.D. La Trobe No. 1, 298.7 m, Dilwyn Formation, Palaeocene to Early Eocene, microspheric specimen; black areas pyrite, X75.

Figs 41–44. *Cyclammina complanata* Chapman. Fig. 41, GSSA Ff627, O.D.N.L. Mt Salt No. 1, 881–884 m, Dartmoor Formation, Palaeocene to Early Eocene, juvenile specimen; black areas pyrite, X75. Fig. 42—GSSA Ff631, O.D.N.L. Mt Salt No. 1, 917-920 m, Dartmoor Formation, Palaeocene to Early Eocene, juvenile, X75. Fig. 43—GSSA Ff623, S.E.O.S. Beachport No. 1, 411-414 m, Tartwaup Formation, Middle Eocene, part of vertical section showing organic lining of alveolae, some pyrite in lumina and openings of alveolae into chamber lumina, but alveolae mostly free of pyrite, X75. Fig. 44—GSSA Ff619, S.E.O.S. Beachport No. 1, 651–652 m, ?cavings from Dartmoor Formation, Palaeocene, microspheric specimen, equatorial section, alveolae mostly free of pyrite which is in the form of scattered small grains and one small aggregate indicated by the black patch between the tenth and eleventh chambers of the last whorl. X30.
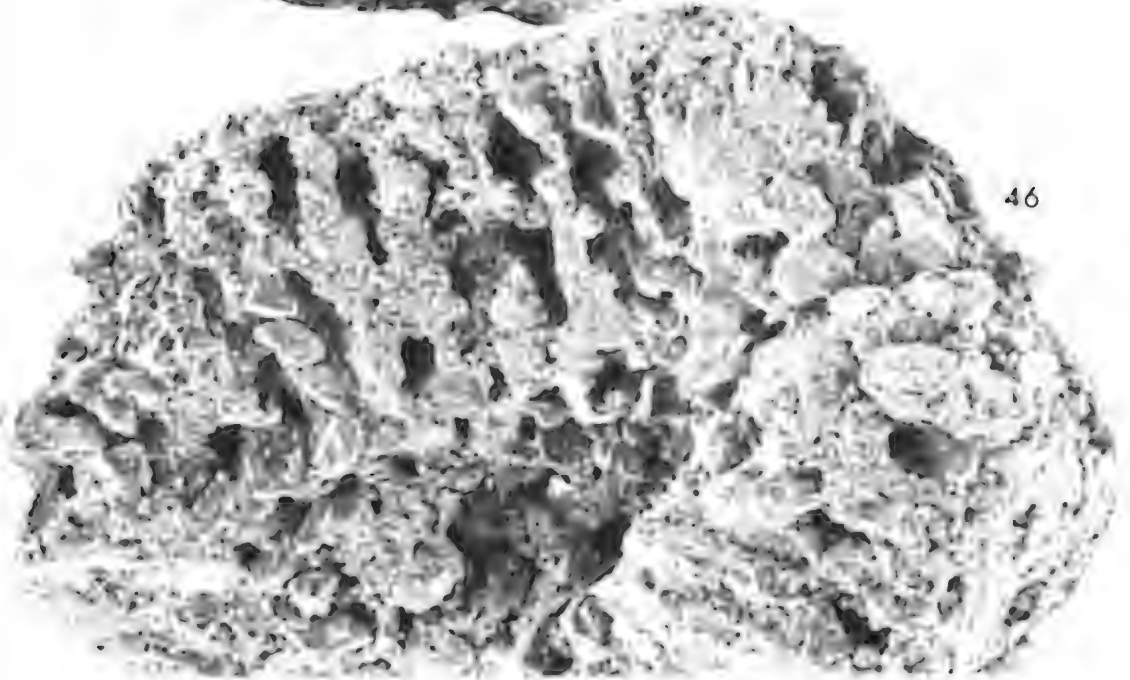
apertures (pl. 3, fig. 32) similar to those illustrated for *Cyclammina* cf. *elegans* Cushman & Jarvis (Banner 1970, pl. 13, fig. 1a).

Each species has a distinctive alveolar pattern when fully developed, although there is the same range of intergradation as that presented by the external features.

C. paupera is a primitive type with a thin epidermis and a simple alveolar or non-alveolar hypodermis: the chamber lumina are widely open and in successive whorls are only slightly, if at all, offset as shown in equatorial section where the overall pattern is of unbroken radii (pl. 4, fig. 37). *C. paupera* appears to be of the type of *Cyclammina* cf. *elegans* Cushman & Jarvis as illustrated by Banner (1970, pl. 13, figs 1, 1a).

C. incisa is similar in structure to the type species *C. cancellata* Brady. The chamber lumina are widely open, separated by rather massive septal walls about equal in width to the interseptal width of the chamber lumina (pl. 3, figs 31–34 and Cockbain 1974, fig. 67C). The alveolar pattern of the hypodermis is somewhat more advanced than that of *C. cancellata*, consisting of simple, more-or-less parallel tubes opening into the chamber lumina (pl. 3, fig. 33; pl. 5, fig. 46; pl. 7, fig. 50) and tending to bifurcate beneath the epidermis (pl. 3, fig. 32). The alveolae, chamber, lumina and septal areal apertures are lined with organic material (pl. 3, fig. 32), which, it is assumed, acted also as cement in the chamber and septal walls.

C. rotundata appears to be a variant of *C. incisa* characterized by the development of very thick walls and reduced chamber lumina. In fully developed specimens the alveolae are fine, thin, more or less parallel tubes.

C. otwayensis has a relatively simple pattern, with alveolae radiating from the chamber lumina in series of 2 or 3 per chamber and bifurcating below the relatively thick, simple epidermis (pl. 4, figs 38, 40).

C. complanata is a highly complex form, with thin epidermis, thick alveolar hypodermis, thick septal walls penetrated by areal apertures and much reduced chamber lumina. The alveo-

lae are lined with pseudochitin (pl. 4, figs 43, 44).

The nature of the organic cement is not known for any species. Staining did not reveal any calcite, as also found by Murray (1973a), and pyrite is present as an infilling of the chamber lumina and alveolae. Hedley (1963) described the cement of living agglutinated foraminifers as an acid mucopolysaccharide with organically bound iron, the cement being reinforced in *Cyclammina* by incorporating ferric iron. The presence of iron in any cement surviving the processes of fossilization could not be confirmed.

Palaeogeographical and palaeoecological interpretations

Sediments containing *Cyclammina* along the margin of southern Australia were deposited mainly during the early stages of the final separation of Australia from Antarctica and the development of the Southeast Indian (Southern) Ocean. Rifting was preceded by the extrusion during the Middle Jurassic of tholeiitic dolerites and basalts in Tasmania, Antarctica and Kangaroo Island (McDougall & Wellman 1976). The Otway Basin was initiated in the Late Jurassic or Early Cretaceous by the opening of a long, deep trough ("Otway Rift Valley" of Griffiths 1971, p. 77) into which a great thickness of non-marine clastic sediments, mainly feldspathic and lithic greywackes, was deposited. This was followed by continued subsidence and sporadic marine incursions in the Gambier and Port Campbell Embayments during the Late Cretaceous and Palaeocene and into the Eocene.

According to Weissel & Hayes (1972), the oldest lineation identified in the Southeast Indian (Southern) Ocean is anomaly 21, the age of which is 54 m.y. B.P. or anomaly 22 (56.5 m.y. B.P.), so that the formation of the normal oceanic crust which recorded the magnetic lineations began in the Late Palaeocene to Early Eocene about 55 million years ago.

Rifting and later patterns of sedimentation were diachronous events progressive from west to east (Griffiths 1971, p. 77). Limited marine

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PLATE 5

Fig. 45. *Cyclammina incisa* (Stache), NZGS F101071, King's Park Bore No. 2, King's Park Shale, Palaeocene, X65.

Fig. 46. *Cyclammina incisa* (Stache), NZGS F100894, Demon's Bluff, Demon's Bluff Formation, Late Eocene, section through chamber wall and chamber lumen, X155.
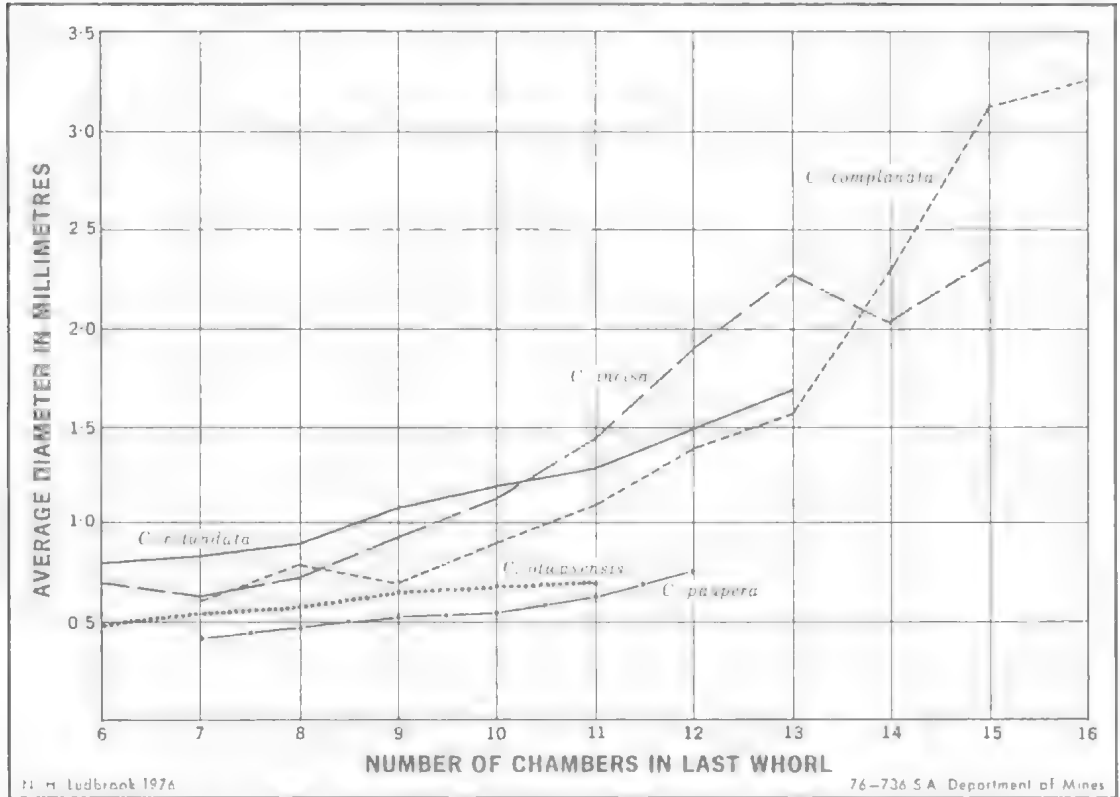
Figure 4. Relationship of number of chambers in last whorl and average diameter.

influence from the west was experienced during the Late Cretaceous, when the sea entered the western part of the Eucla Basin (Ludbrook 1958), the Duntroon Basin (Boeuf & Doust 1975) and the Otway Basin (Taylor 1964, 1971; Ludbrook 1971).

The Eucla Basin experienced an open sea environment during the Middle Eocene when carbonate sediments containing abundant planktonic foraminifers were deposited (Ludbrook 1963, 1969, McGowran & Lindsay 1969). Middle Eocene sediments in the Gambier Embayment of the Otway Basin, as exemplified by the Burrungule Member of the Tartwaup Formation, are paralic, highly carbonaceous clays and silts with sporadic planktonic foraminifers (Ludbrook 1971, p. 57) and also *Cyclammina otwayensis*. Open sea conditions reached the Port Campbell Embayment in the Late Eocene and the Torquay Basin shortly before the beginning of the Oligocene (Abele et al. 1976). Carbonate sedimentation began in the St Vincent Basin in the Late Eocene. The full extent of the easterly transgression did not affect most of the Murray

Basin and the Bass and Gippsland Basins until the Oligocene to Early Miocene (see also Deighton et al. 1976, figs. 9–14).

Cyclammina flourished in the period when the Southeast Indian (Southern) Ocean was passing through the immature ocean phase; that is, in the period between the sporadic marine ingressions of the Late Cretaceous and the easterly spread of carbonate sedimentation extending into the Early Miocene.

The occurrence of *Cyclammina* spp. in southern Australia may be compared with that of *C. cancellata* described by Akers (1954) from the Louisiana Miocene where the species occurs in certain zones with planktonic foraminifers and abundantly in other zones to the exclusion of other foraminifers. Studying living *C. cancellata* from the Peru-Chile Trench, Theyer (1971a) observed that small and comparatively wide forms occur between 500 and 1000 m, with temperatures above 3° to 4°C. larger and proportionately narrow forms live at between 1000 and about 2500 m, below the permanent thermocline and in the oxygen minimum zone with oxygen content below 3 ml/l;

specimens living in deeper waters of more than 3000 m with temperatures below 2°C and oxygen values above 3 ml/l decrease slightly in diameter but widen considerably.

Gregarious in habit, is is found most abundantly as a "one-genus" assemblage (Akers 1954), or with almost all other genera excluded, in Palaeocene to Early Eocene paralic sediments of the Dilwyn Formation of the Port Campbell Embayment, Knight Group of the Gambier Embayment, and in the Late Eocene to Oligocene, Demon's Bluff Formation of the Torquay Basin. In the St. Vincent, Murray, Bass and Gippsland Basins it is associated with the early stages of the diachronous marine transgressions of the Late Eocene, Oligocene and Early Miocene. The sediments in which it is abundant and almost exclusive are usually highly carbonaceous; those in which it is associated with other benthonic foraminifers are frequently glauconitic. They are all assumed to have been deposited in shallow water, though palaeobathymetric studies have not been done in any detail.

It was this apparently anomalous habitat for what has been accepted as a deep-water genus (Brady 1884; Akers 1954; Theyer 1971a, b; Boltovskoy & Wright 1976) that Taylor (1965) found difficult to accept. The living *Cyclammina cancellata* is widely distributed in oceanic waters off the continental shelves at depths between 114 and 5800 m, with a temperature range between 11.6° at depths 278 and 882 m and 1.2° at depth 5800 m in the North Pacific Ocean (Akers 1954). It does not occur in Antarctic waters (Theyer, 1971a). The only species living in Australian waters is *C. tasmanica* Parr, recovered from depths 155 and 172 m in bryozoal mud off Maria Island and at 128 m off northeastern Tasmania on the continental shelf (Parr 1950). These are shallow occurrences compared with depths of from 393 to 1718 m for the widely distributed *C. orbicularis* Brady and *C. pusilla* Brady dredged by B.A.N.Z. Antarctic Expedition (1929–1931) as well as by earlier "Challenger", Deutsche Sudpolar and "Scotia" Expeditions (Parr 1950, p. 273).

According to Theyer (1971b), *C. orbicularis* is the most characteristic index of lower bathyal to upper bathyal zones in the Pacific-Antarctic Basin. Abundant specimens begin to appear at approximately 1800 m and its lower depth limit normally lies between 3500 and 4000 m. *C. pusilla*, which is an index of abyssal depths, becomes significant at 3000–3500 m and disappears between 4500 and 5000 m. It undergoes size changes which probably parallel those of *C. cancellata* in the Peru-Chile Trench area.

While the bathymetry of the *Cyclammina* bearing sediments, particularly in the Otway Basin, and the younger occurrences in the St. Vincent and Murray Basins remains to be studied, some broad interpretations of a limited area, based on microfaunas (Taylor 1971, figs 10–5 to 10–14) and computer-derived reconstructions of the continental margin based on quantitative seafloor spreading data (Deighton et al. 1976) have been made. It is, however, not possible to compare the patterns of bathymetric distribution of southern Australian *Cyclammina* species with that described by Robinson (1970) for Late Miocene to Holocene species in the Gulf of Mexico. Robinson's (Fig. 8) distribution patterns show that the bathymetric distribution of *Cyclammina* spp. decreased from a dominant abundance in the outer neritic–upper bathyal zone, between 137 and 384 m depth, during the Late Miocene-Early Pliocene to a normal distribution of rare but persistent examples from the lower bathyal zone (500 to 2000 m) in the Early Pleistocene.

The relevance of Robinson's studies is to dispel the conviction that the presence of *Cyclammina* is indicative of deepwater sedimentation and to emphasise that the use of generic distributions in palaeoecological interpretations must be made with caution, particularly if the abundance of the generic group differs markedly through time (Robinson 1970). Robinson also noted that, at the generic level, specimens associated with neritic assemblages are usually smaller, lighter in colour, coarser-grained, and with fewer chambers than those associated with bathyal assemblages. In the opinion of Murray (1973b) deepwater forms of *Cyclammina* are larger than the shallow water representatives. Boltovskoy & Wright (1976) show the depth distribution of *Cyclammina* as from the outer shelf to the abyssal zone. Quoting Sigal (1952), Pokorny (1958) and Bettenstaedt (1962), they state that genera such as *Haplophragmoides*, *Trochammina*, *Cyclammina* and *Bathysiphon* require little oxygen to survive.

The distribution and faunal associations of southern Australian species are shown in Table 3. Neritic assemblages in which *Cyclammina* is associated with planktonic and benthonic, other than agglutinated, forms occur principally in Late Eocene or younger sediments. The two species represented in these assemblages, *C.*
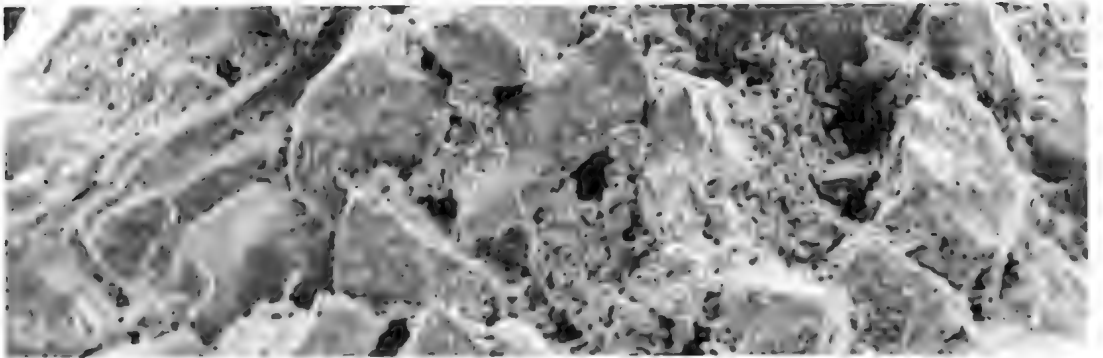
47
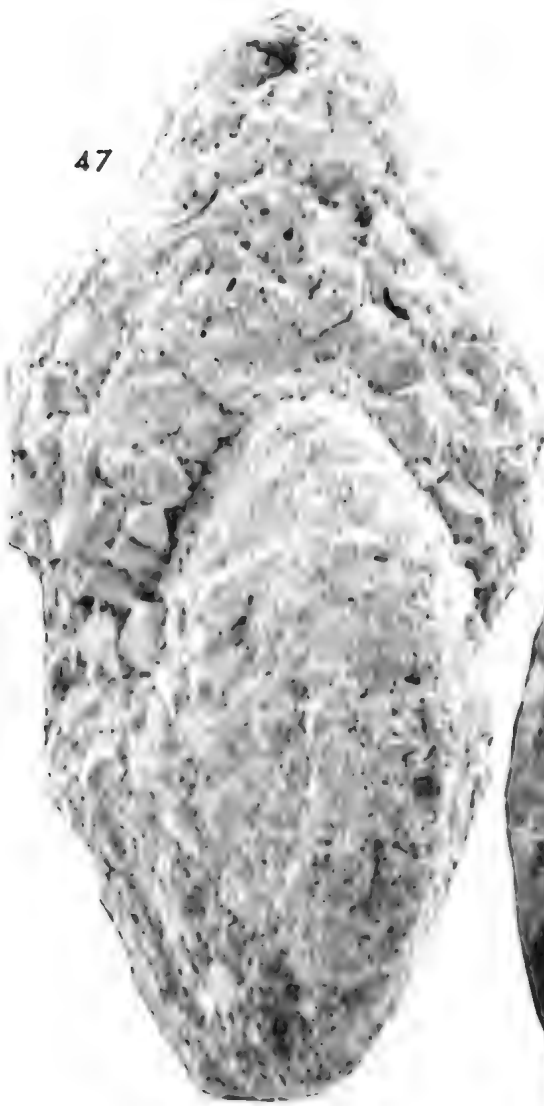
48
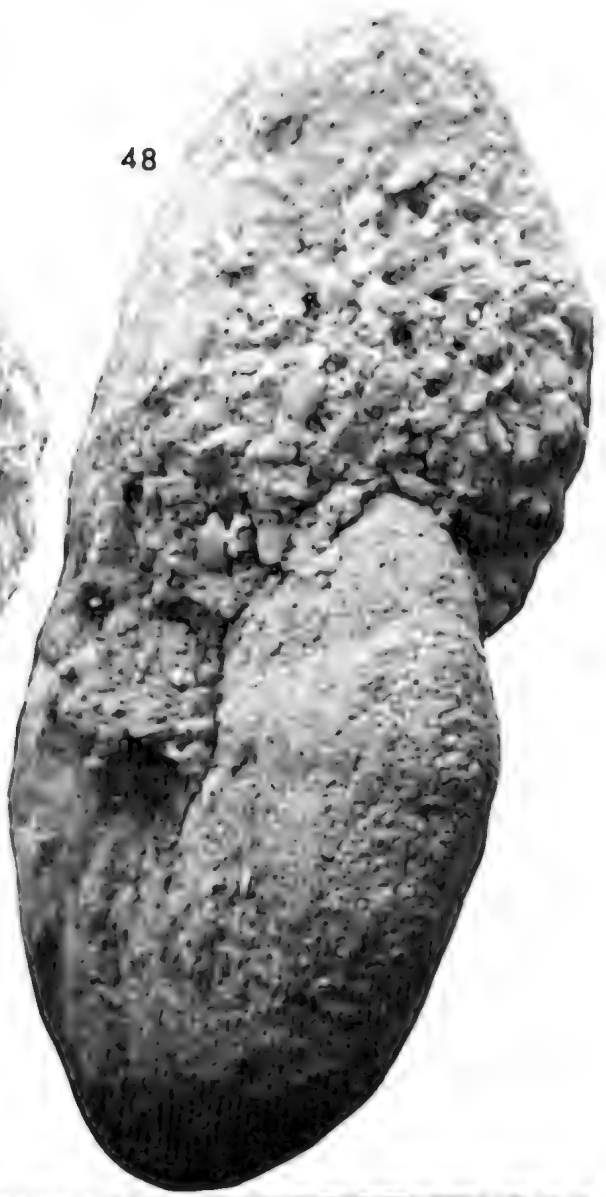
49

incisa and *C. rotundata*, are in general moderately large to large coarse-grained species, the greater proportion of which have relatively few chambers (see Table 3 and Fig. 4). The small fine-grained species *C. otwayensis* and *C. paupera* with fewer chambers and the large complex, fine-grained species *C. complanata* with more numerous chambers are restricted to Palaeocene to Middle Eocene paralic silts and sandy clays which, in the Wangerrip Group at least, are of shallow water origin (Baker 1950). Compared with the neritic assemblages the associated microfaunas are poor.

The largest examples of *C. complanata* were recovered from the Dartmoor Formation intersected in S.E.O.S. Beachport No. 1 Well and from outcrops on Glenelg River. Consistently large examples of *C. incisa* were collected from the Demon's Bluff Formation at Mogg's Creek. There are no data to suggest that these are deepwater representatives of those occurring at other localities.

Systematic descriptions

Order FORAMINIFERIDA Eichwald, 1830

Suborder TEXTULARIINA Delage & Hérouard, 1896

Superfamily LITUOLACEA de Blainville, 1825

Family LITUOLIDAE de Blainville, 1825

Subfamily HAPLOPHRAGMOIDINAE Mayne, 1952

Genus HAPLOPHRAGMOIDES Cushman, 1910

Haplophragmoides taylori n.sp.

PL. 2, FIGS 18-20

Haplophragmoides sp. B. Taylor, 1964: pl. 59, fig. 4; Taylor, 1965: 151, fig. 4 (3a, b).

Holotype: GSM 64829 (1); figured paratypes GSM 64829 (5).

Type locality: V.M.D. La Trobe No. 1 Well, Princetown, 38°41'49"S, 143°10'24"E, COLAC 1:250 000 geological map sheet, Core 53B at 292.61 m, Dilwyn Formation, Palaeocene to Early Eocene.

Material: 244 specimens of which 13 were measured as typical; the holotype and 6 paratypes from V.M.D. Wangoom No. 6, Core 12, 596–601 m, Dilwyn Formation, ?Early Eocene; 48 paratypes O.D.N.L. Mt Salt No. 1 509–590 m, Dartmoor Formation, Palaeocene to Early Eocene; 186 specimens ODNL Mt Salt No. 1, 1533–3061 m Sherbrook Group, Late Cretaceous.

Description: Test small, inflated, umbilicate, involute to slightly evolute, with 6 to 7 chambers in the last whorl, sutures straight, deeply incised, periphery lobulate, umbilicus deep and broad.

Wall finely agglutinated. Apertural face broad, high, aperture an interiomarginal slit without lip or with a slight lip.

Dimensions: Holotype diameter 0.35, thickness 0.20 mm; average of 13 uncollapsed specimens diameter 0.35; thickness 0.23 mm.

Remarks: Taylor (1964, p. 564; 1965, p. 151) described this distinctive small species of *Haplophragmoides*, which is common in Late Cretaceous sediments and occurs also in the Palaeocene of both the Port Campbell and Gambier Embayments of the Otway Basin. It is named in his honour.

Distribution: Otway Basin, Port Campbell and Gambier Embayments — Sherbrook Group, Belfast Mudstone and Paaratte Formations and their equivalents, Late Cretaceous (Turonian-Santonian (Taylor 1964)); Wangerrip Group, Dilwyn Formation, and Knight Group, Dartmoor Formation (Late Palaeocene to Early Eocene).

Subfamily CYCLAMMININAE Marie, 1941

Genus CYCLAMMINA Brady, 1879

Cyclammina complanata Chapman

PL. 2, FIGS 28-30; PL. 4, FIGS 41-44

Cyclammina complanata Chapman, 1904: 228, pl. 22, fig. 7.

Holotype: NMV Slide P26049 No. 6.

Type locality: Brown's Creek, between Rotten Point and mouth of Johanna River, 13.6 km NW of Cape Otway, 38°46'22"S, 143°23'14"E,

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PLATE 6

Figs 47, 49, *Cyclammina incisa* (Stache), NZGS F100894, Demon's Bluff, Demon's Bluff Formation, Late Eocene, apertural view showing areal apertures; 1, X65; 3, enlargement of centre of apertural face, X240.

Fig. 48, *Cyclammina incisa* (Stache), NZGS F100937, Demon's Bluff, Demon's Bluff Formation, Late Eocene, apertural view showing areal apertures and coarse grains on apertural face, X34,

base of Johanna River Sands, ?Palaeocene to Early Eocene.

Material: 101 specimens of which 54 were measured and 8 sectioned. From outcrop—Glenelg River (7); from boreholes—O.D.N.I., Mt Salt No. 1, 585–954 m (84); S.E.O.S. Beachport No. 1, 408–603 m (9); B.P.N.L. Geltwood Beach No. 1, 579 m (1).

Description: Test large, composed mainly of quartz grains, planispiral, flattened, discoidal, partially evolute, with 2 whorls in the megaspheric form and 3 to 4 in the microspheric form; chambers 6 to 16, but 15 or 16 in the fully-grown adult, periphery narrowly rounded, very slightly lobulate, umbilicus well-defined, shallow, sutures incised, sinuate.

Wall agglutinated, thick, epidermis thin, smoothly finished, imperforate; hypodermis thick, alveolar, with a series of parallel alveolae distal to the septal wall but branching from the chamber lumen, all alveolae bifurcating just below the epidermis which they do not penetrate; the distal ends of the alveolae can be seen through the translucent epidermis as a fine punctate pattern or when they have been exposed by erosion of the epidermis.

Septal wall thick, arcuate, thickness as much as 6 times the interseptal width of the chamber lumen at its maximum width in equatorial section; in section each septal wall showing at least 7 more or less parallel alveolae extending from the supplementary apertures.

Chamber lumen much reduced, curved, both chamber lumina and alveolae lined with pseudochitin ("tectin", a combination of protein and carbohydrate (Hyman 1940)).

Apertural face high, more or less flattened laterally and rounded at the periphery, covered with fine quartz grains and with conspicuous supplementary areal apertures, each surrounded by a rim. Aperture an interiomarginal slit at the base of the apertural face.

Dimensions. Holotype diameter 2.0 mm. Of 54 specimens measured, diameter 0.45 to 3.75, average 1.08; thickness 0.18 to 1.12 mm, average 0.39 mm; average ratio diameter : thickness 2.8:1

Remarks: This is a rare species, occurring only from the Palaeocene to ?Early Eocene in the Otway Basin. It is a complex form of *Cyclammina* with greatly reduced chamber lumina and an extensive alveolar pattern similar to that of the *Cyclammina pilvoensis* Voloshinova & Budasheva group (see Banner 1970, pl. 3, figs 11, 12; pl. 13, figs 5–7) and *Cyclammina*

aff. *tani* Ishizaki (Banner 1970, pl. 13, figs 3, 4). From its external features it is obviously very close to *Cyclammina* sp. of Chang from the Shihliufeng sandy shale of the Liuchungchi oilfield, Taiwan (Chang 1956, pl. 1, figs 1–3).

Distribution: Otway Basin—Dartmoor Formation (Palaeocene to Early Eocene) and lower part of Johanna River Sands (?Late Palaeocene to Early Eocene).

Cyclammina incisa (Stache)

PL. 1, FIGS 5–8, 13; PL. 3, FIGS 31–35; ?FIG. 36; PL. 5, FIGS 45, 46; PL. 6, FIGS 47–49; PL. 7, FIGS 50–51; PL. 8, FIGS 52–53.

Haplophragmium incisum Stache, 1864: 165, pl. 21, fig. 1.

Haplophragmium maoricum Stache, 1864: 166, pl. 21, fig. 2.

Cyclammina paupera Chapman, 1904: 229 (in part). Crespin, 1950: 72, pl. 10, fig. 4 (not *C. paupera* Chapman, 1904, *sensu stricto*). Raggatt & Crespin, 1955: pl. 7, fig. 4 (not *C. paupera* Chapman, 1904, *sensu stricto*).

Cyclammina incisa (Stache) Chapman, 1926: 29, pl. 2, fig. 1. Chapman & Crespin, 1932: 14, pl. 15, fig. 6. Parr, 1938: 89, text fig. 1. Crespin, 1950: 72, pl. 10, fig. 3. Raggatt & Crespin, 1955: pl. 7, fig. 3. Hornibrook, 1961: 30; Hornibrook, 1971: 34, text fig. 9, pl. 6, figs. 88–91. Cockbain, 1974: 107, figs. 67A,B,C.

Haplophragmium canariense Chapman, 1926: 28, pl. 2, fig. 2 (not *Nonionina canariensis* d'Orbigny, 1839).

Cyclammina longicompressa Chapman & Crespin, 1930: 97, pl. 5, figs 3, 4.

Haplophragmoides cf. *incisa* (Stache) Taylor, 1965: 150, figs 2d, 3 (3a,b, 4a,b).

Haplophragmoides cf. *paupera* Taylor, 1965: 151, fig. 4 (2a, 2b) (not *Cyclammina paupera* Chapman, 1904).

"*Cyclammina*" cf. *incisa* (Stache) Lindsay & Bonnett, 1973: 33, pl. 1, fig. 4.

Cyclammina cf. *incisa* (Stache) Quilty, 1974, p. 33, pl. 1, figs 1–3 (in part).

Holotype: Slide 64. Naturhistorisches Museum, Vienna (Hornibrook 1971, p. 25).

Type locality: Grid reference N64/483465 (1948 ed.) Department of Lands and Survey, NZMS 1, Te Kopapa Point, Raglan Harbour (Whaingaroa), North Island, New Zealand, Whaingaroa Siltstone, Whaingaroan (Early Oligocene) (Hornibrook 1971, text fig. 1, pp. 9–10).

Material: 702 specimens, of which 390 were measured and 10 sectioned, from the following localities: Outcrops—topotypes, Raglan Harbour (18), Demon's Bluff (98), Mogg's Creek

(68), Castle Cove (76), Fossil Bluff (1), Abbotsford, New Zealand (2). Boreholes— O.D.N.L. Mt Salt No. 1, 719-1115 m (295); O.D.N.L. Mt Salt Structure Hole No. 1, 226-229 m (1); S.E.O.S. Beachport No. 1, 241-271 m (16); B.P.N.L. Geltwood Beach No. 1, 238-277 m (3); E. & W.S. Kingston No. 3, 65-69 m (2); E. & W.S. Coonalpyn No. 1 69-70 m, 105-107 m (2); S.A.M.D. Waikerie No. 2, 149-152 m (20); S.A.M.D. Waikerie No. 28W, 146-148 m (1); Water Bore Plantagenet 5666, South Stirling 11.88-21.03 m (92), King's Park No. 2, 216-219 m (4); Parish of Bumberrah (Melung), 394.7 m (3)

Description: Adult test of moderate to large size, composed mainly of quartz grains, with usually 4 whorls in the microspheric form, 2 in the megaspheric form; 7 to 15 chambers in the last whorl, planispiral, biconvex, involute, more or less compressed at the periphery which is very slightly lobulate, depressed around the rather shallow umbilicus, sutures incised, straight to slightly sinuate.

Wall finely agglutinated, thick, epidermis thin, fine-grained, smoothly finished in fine sediment but varying according to the coarseness of the matrix, of uniform texture but for scattered large quartz grains, imperforate; hypodermis thick, coarse-grained, coarsely alveolar, not labyrinthic, the alveolae consisting of relatively simple tubes with a single conspicuous opening into the chamber lumen and bifurcating just below the epidermis, which they do not penetrate. The distal ends of the alveolae are frequently seen through the translucent epidermis of well-preserved specimens. Alveolae lined with organic material (pseudochitin or "tectin", a combination of protein and carbohydrate (Hyman 1940)), and the test is probably held together with organic cement.

Apertural face moderately rounded to roundly ogival, covered with coarse quartz grains between which fine supplementary areal apertures are sometimes visible. Aperture an interiomarginal narrow slit at the base of the apertural face.

Septal wall thick, about as wide as the interseptal width of the chamber lumina, occasionally perforated by the areal apertures.

Dimensions: Holotype, diameter 1.44 mm, thickness 0.90 mm (Hornibrook 1971). Of 390 specimens measured, diameter 0.28 to 3.0 mm, megaspheric 1.12 mm, average 1.15 mm; thickness 0.15 to 1.75 mm, average 0.54

mm; average ratio diameter - thickness 2.13:1. Diameter of early chambers 1.0 to 1.5 mm (microspheric). Number of whorls in early chambers (microspheric form) 3.

Remarks: *C. incisa* is a ubiquitous and long-ranging species with considerable variation in shape from fairly flat, mostly due to compression, with a diameter : thickness ratio of 4.5:1, to the robust form with a ratio of 1.6:1. Most of the topotypes from Raglan Harbour kindly lent by the New Zealand Geological Survey are rather flattened as compared with the holotype and matched topotype (Hornibrook 1971, p. 35, pl. 6, figs 88, 91). The specimen NZGS Reg. No. FP2078 sectioned by Hornibrook (1971, text fig. 9) appears to be a megaspheric form in which the chamber lumina have collapsed, as Hornibrook suggested. The same type of alveolar pattern is shown in the section of the relatively poorly preserved megaspheric specimen GSSA Ff632 (pl. 3, fig. 35) and in *C. praecancellata* Voloshinova as figured by Voloshinova & Budasheva 1961, pl. 15, figs 4, 5 and Muylaert 1966, pl 42, figs 1-6. Well-preserved specimens (pl. 3, figs 31-33) clearly show an alveolar pattern and relative disposal of chamber lumina and septal wall of the same type as that of *C.* aff. *praecancellata* Voloshinova of Muylaert (1966, pl. 41, figs 1-7; pl 42, figs 7-9; pl. 43, fig. 1). The section of *C. praecancellata* illustrated by Cicha & Zapletalova (1966, pl. 38, fig. 3c) shows a considerable reduction of the chamber lumina and more complex alveolar structure which is not readily comparable with that of *C. incisa.*

The record of the species in the Late Cretaceous Curdies Formation (Ludbrook 1971, fig. 3.3) is based on probable contamination of cuttings in Mt Salt No. 1 Well from the overlying Dartmoor Formation.

Distribution: Widespread in southern Australia and New Zealand from Late Palaeocene to Early Miocene.

**Cyclammina otwayensis n.sp.**

Pl. 2, FIGS 23-25; Pl. 4, FIGS 38-40

Haplophragmoides canariense Chapman, 1904: 228, pl. 22, fig. 2 (not *Nonionina canariensis* d'Orbigny, 1839).

Haplophragmoides complanata Taylor, 1965: 148, figs 2 (a-c), 3(1). (2) not *Cyclammina complanata* Chapman, 1904).
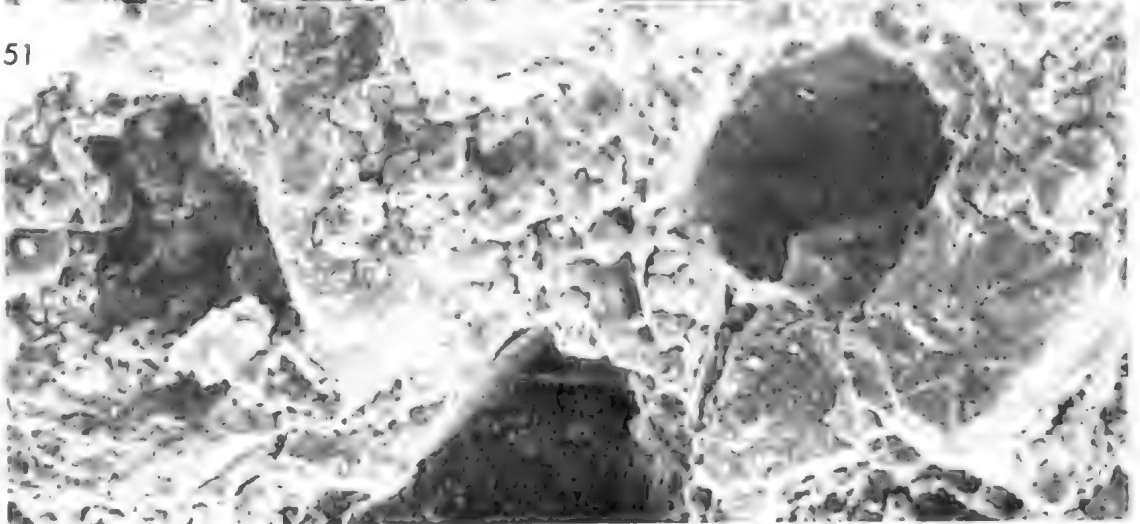
Holotype: GSSA Ff608, figured paratypes GSSA Ff609, Ff610,

Type locality: Glenelg River, Victoria, 2.4 km downstream from Killara Bridge, 14 km SW
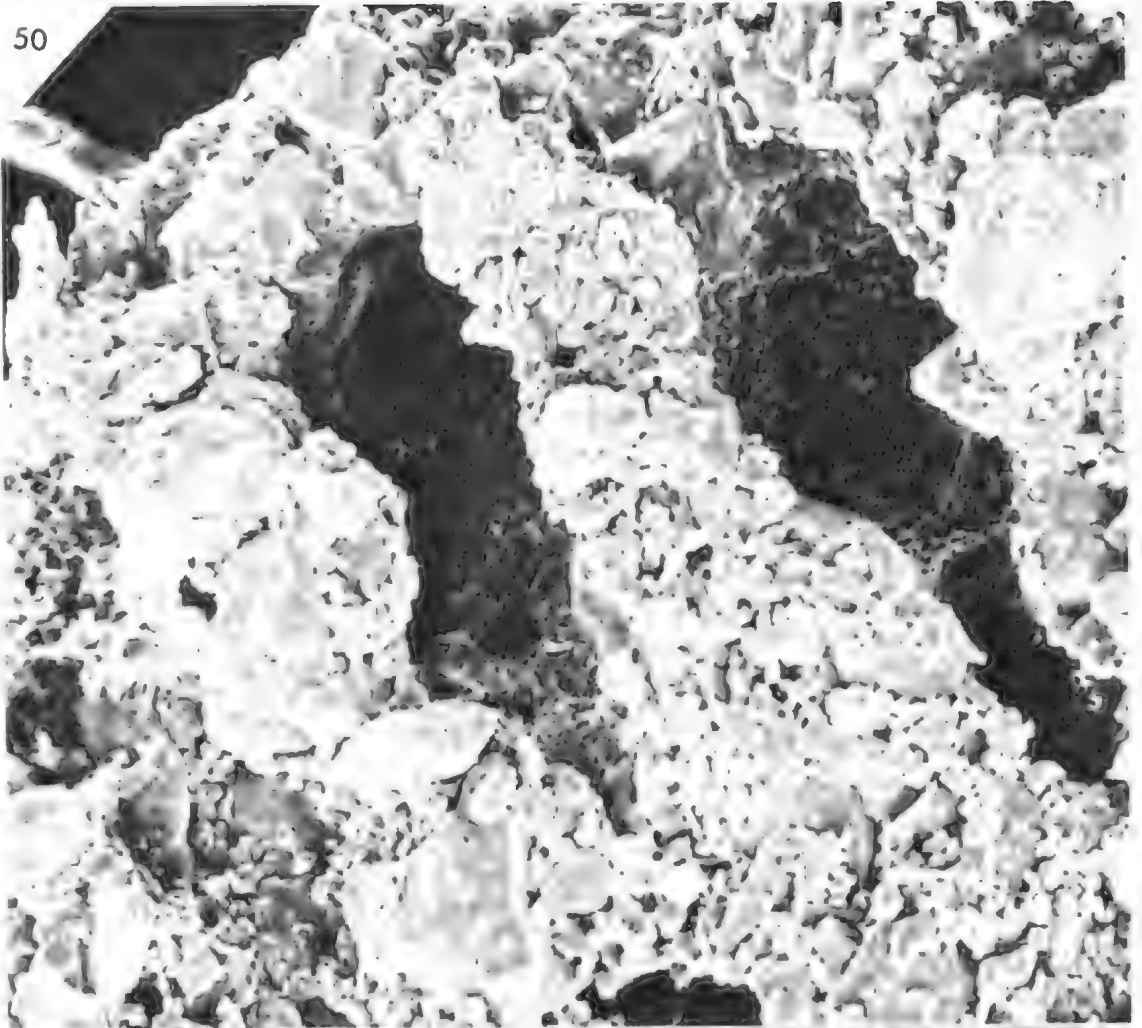
of Casterton, HAMILTON 1:250 000 geological map sheet, 37°39'56"S, 141°17'23"E, Gambier Embayment, Otway Basin, Dartmoor Formation, Palaeocene to Early Eocene.

Material: The holotype, figured paratypes and approximately 650 paratypes, of which 172 were measured and 4 sectioned, from: Outcrops—Brown's Creek (5), Glenelg River (43); Boreholes—V.M.D. La Trobe No. 1 at 298.7 m (500); S.A.M.D. C.G.9, County Grey, 28.96–29.26 m (63); O.D.N.L. Mt Salt No. 1, 585–960 (cavings 1039–1058 m) (23); S.E.O.S. Beachport No. 1, 311–546 m (25).

Description: Adult test small, moderately inflated, composed mainly of fine quartz grains with scattered medium grains which have a tendency to be arranged radially, planispiral, biconvex, involute, with 3 whorls in the microspheric form, 2½ in the megaspheric form, 7 to 11 chambers in the last whorl, but usually 8 to 9 in the adult form, sutures moderately well-defined, not incised, straight; periphery rounded, only slightly or not lobulate, umbilicus well-defined and relatively deep.

Wall rather loosely agglutinated, thin, with very little cementing material, epidermis relatively thick, smooth or roughly finished according to the coarseness of the grains of the enclosing sediment, imperforate; hypodermis thin, simply perforated by conspicuous alveolae having a large opening into the chamber lumen and branching distally from the chamber lumen to the epidermis which they do not penetrate but through which the distal ends can be seen in 2 or 3 radiating series per chamber. Septal wall moderately thin and occasionally punctured by the supplementary apertures. Apertural face a moderately high rounded arch covered with medium quartz grains between which very small supplementary areal apertures are occasionally visible.

Aperture a well-defined interiomarginal slit at the base of the apertural face, sometimes with a slight lip on the absutural side.

Chamber lumen widely open.

Dimensions: Holotype Ff608, diameter 0.75, thickness 0.41 mm; paratype Ff609, diameter 0.85, thickness 0.42 mm; paratype Ff610, diameter 0.80, thickness 0.40 mm. Of 172 specimens measured, diameter 0.35 to 0.90 mm, average 0.64 mm; thickness 0.12 to 0.42, average 0.30 mm; average ratio diameter : thickness 2:1.

Remarks: Chapman (1904) identified this species as *Haplophragmium canariense* (d'Orbigny) (= *Nonionina canariensis* d'Orbigny, the type species of *Haplophragmoides* Cushman, 1910) and figured a specimen (pl. 22, fig. 2) which suggests the presence of alveolae below the epidermis. The figured specimen is, unfortunately, not the one now on Chapman's slide NMV P26049, but on square 33 of a slide GSM 64828 with mounted specimens from Chapman's material very kindly made available by D. J. Taylor, there are four specimens almost identical with the one figured by Chapman. These belong to *Cyclammina* as the open ends of alveolae can be seen on the inside of the chamber wall of one partially dissected specimen. Taylor (1965, p. 157) appears to have overlooked Chapman's separation of the species from *C. complanata* and interpreted the specimens on square 33 (GSM 64828) as *Haplophragmoides complanata*. He figured as "preservation stages" (p. 146, fig. 2a, b, c) three specimens from La Trobe No. 1 Bore at 298.7 m, which are here reinterpreted after examination of the specimens as an ontogenetic series of *C. otwayensis*. GSM 60464 (Fig. 2a) is a half section or "grind" of a pyrite-filled immature specimen; GSM 60465 (Fig. 2b) is a partly dissected specimen showing the open chamber lumina and relatively simple alveolar hypodermis; and GSM 60466 (Fig. 2c) is a half section or "grind" of a pyrite-filled specimen on the reverse side of which the alveolar openings beneath the epidermis are visible. GSM 60466 is similar to the specimen GSSA Ff609 figured on plate 2, figure 24.

The holotype is a rather coarse-grained specimen selected from a sample taken from

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PLATE 7

Fig. 50 *Cyclammina incisa* (Stache), NZGS F100894. Demon's Bluff, Demon's Bluff Formation, Late Eocene, longitudinal view of alveolae from chamber lumen through hypodermis to epidermis, X550.

Fig. 51. *Cyclammina incisa* (Stache), NZGS F100937. Demon's Bluff, Demon's Bluff Formation, Late Eocene, distal ends of alveolae viewed from exterior through ruptured epidermis, X650.
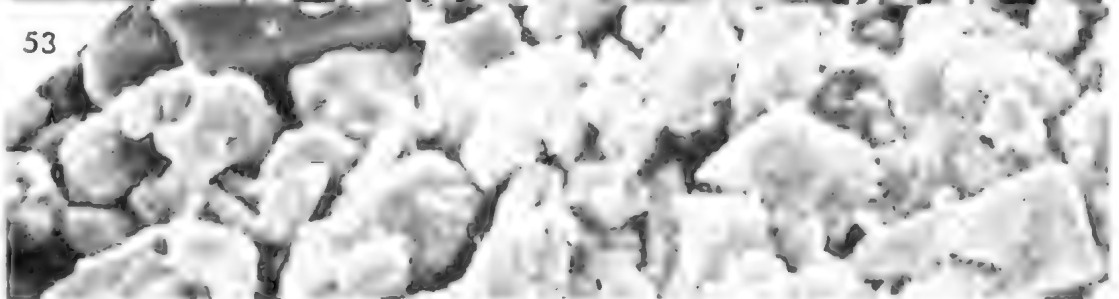
the Dartmoor Formation on Glenelg River because of the accessibility of the outcropping material. The species is very abundant in the Palaeocene to Early Eocene of the Dilwyn Formation in La Trobe No. 1 Bore, and common in the type section (Bore CG9) of the Burrungule Member of the Tartwaup Formation.

The specific name is taken from the Otway Basin to which it is restricted on present knowledge.

Distribution: Otway Basin–Dilwyn and Dartmoor Formations (Palaeocene to Early Eocene) and lower part of Johanna River Sands (?Palaeocene to Early Eocene); Burrungule Member of Tartwaup Formation (Middle Eocene).

Cyclammina paupera Chapman
PL. 2, FIGS 21, 22, 26, 27; PL. 4, FIG. 37

Cyclammina paupera Chapman, 1904: 229, pl. 22, fig. 6.
Haplophragmoides paupera (Chapman) Taylor, 1965: 151, fig. 4 (1a,b) (not *Cyclammina paupera* Crespin, 1950:72, pl. 10, fig. 4).

Holotype: NMV Slide P26049 No. 5.

Type locality: Brown's Creek, between Rotten Point and mouth of Johanna River, 13.6 km NW of Cape Otway, 38°46′22″S, 143°23′14″E, base of Johanna River Sands, ?Palaeocene to Early Eocene.

Material: 86 specimens of which 52 were measured. From outcrops—Brown's Creek (3), Glenelg River (7); from boreholes—V.M.D. La Trobe No. 1 293–299 m (63), V.M.D Wangoom No. 6. 596–600 m (9), O.D.N.I.. Mt Salt No. 1, 902–957 m (63).

Description: Adult test small, planispiral, flatly biconvex, involute or slightly evolute, composed of fine quartz grains, compressed towards the periphery which is acute, rounded or slightly lobulate; umbilicus well-defined, deep. Six to twelve chambers in the last whorl, but usually 8 to 10 in the adult form; sutures incised, straight or slightly arcuate.

Wall finely agglutinated, thin, epidermis very thin, with fine alveolae visible through the translucent epidermis when the specimen is wet, otherwise apparently absent or poorly developed. Septal wall thin. Chamber lumen widely open, subtrapezoidal in section, each chamber tends to be set almost above the corresponding chamber of the previous whorl, so that both chambers and septa appear in equatorial section as unbroken radii (pl. 4, fig. 37).

Apertural face high, narrow, subtriangular, covered with fine quartz grains; aperture a very narrow interiomarginal slit at the base of the apertural face, without lip.

Dimensions: Holotype diameter 1.08 mm. Of 52 specimens measured diameter 0.37 to 1.08, average 0.52 mm; thickness 0.12 to 0.25, average 0.20; average ratio diameter : thickness 2.6:1.

Remarks: In texture of the epidermis, in size and general shape, *C. paupera* may be compared with *C. grangei* Finlay, which has a similar stratigraphical range of Late Palaeocene to Middle Eocene (Hornibrook 1968, p. 48). *C. paupera* is flatter and less elevated around the umbilicus, and in *C. grangei* the alveolar pattern as indicated by the distal ends of the alveolae visible through the siliceous wall is much coarser and more strongly developed.

The specimen (CPC 645) figured by Crespin (1950, pl. 10, fig. 4) is a rather deflated example of *C. incisa*, not unlike topotypes from Raglan Harbour. The specimen figured as *Haplophragmoides* sp. A (Taylor, 1964, p. 563, pl. 9, fig. 3) and placed in synonymy with *Cyclammina paupera* (Taylor, 1965, p. 151) appears to be a *Haplophragmoides* and not *C. paupera*, the occurrence of which in the Late Cretaceous has not been confirmed.

Distribution: Otway Basin–Dilwyn and Dartmoor Formations (Palaeocene to Early Eocene) and lower part of Johanna River Sands (?Palaeocene to Early Eocene).

Cyclammina rotundata Chapman & Crespin
PL. 1, FIGS 9–12, 14–17; ?PL. 3, FIG. 36

Haplophragmium latidorsatum Chapman, 1904: 227, pl. 22, fig. 1 (not *Nonionina latidorsata* Bornemann).
Cyclammina rotundata Chapman & Crespin, 1930: 96, pl. 5, figs 1, 2. Crespin, 1950: 72, pl. 10, figs 5a, 5b. Raggatt & Crespin, 1955: pl 7, figs 5a, 5b.

PLATE 8

Fig. 52. *Cyclammina incisa* (Stache), NZGS F100937 Demon's Bluff, Demon's Bluff Formation, Late Eocene, alveolae viewed from chamber lumen, X650.
Fig. 53. *Cyclammina incisa* (Stache), NZGS F100937 Demon's Bluff, Demon's Bluff Formation, Late Eocene, epidermis, X2500.

Haplophragmoides rotundata (Chapman & Crespin) Taylor, 1965: 153, fig. 4 (4a, b).

Cyclammina cf. *incisa* (Stache) Quilty, 1974: 33, pl. 1, figs 1–3 (in part at least).

Holotype: CPC 14.

Type locality: No. 1 Bore Parish of Bumberrah, Metung, Victoria, BAIRNSDALE 1:250 000 geological map sheet, 37°53′34″S, 147°50′14″E, at 394.7 m depth, Gippsland Basin, Lakes Entrance Formation, Oligocene.

Material: The holotype and 107 specimens of which 93 were measured and 5 sectioned. From outcrops—Demon's Bluff (4), Castle Cove (5). From boreholes—O.D.N.L. Mt Salt No. 1 908–1015 m (22), S.E.O.S. Beachport No. 1 238–271 m (41); New Morphett Street and Victoria Bridges, Adelaide, Bore 11 25–25.6 m (2), Bore 12 20.1–20.4 m (1), Bore 14 16.7–17.0 m (2); "Carelew" Bore 2 19.8–19.9 m (1), Observation Bore F, Port Gawler, 253–254.5 m (2), Waikerie Bore 28W, 146 m (15), Plantagenet Location 5666, South Stirling, 11.88–21.03 m (33).

Description: Adult test of moderate to large size, inflated, planispiral, biconvex, involute, composed mainly of coarse quartz grains, with 4 whorls in the microspheric form, 6 to 12, rarely 13, chambers in the last whorl, periphery rounded, umbilicus scarcely or not depressed, sutures poorly defined, straight.

Wall agglutinated, thick, epidermis thin and usually coarsely finished with numerous agglutinated coarse grains, imperforate; hypodermis thick, coarse-grained, alveolar, with a pattern of fine roughly parallel alveolae with only a slight tendency to bifurcate distally beneath the epidermis. The distal ends of the alveolae are not usually visible through the epidermis. Septal wall thick, chamber lumen much reduced.

Apertural face a low arch covered with coarse quartz grains between which small supplementary areal apertures are frequently visible. Aperture a slit at the base of the apertural face, short and well open in immature specimens.

Dimensions: Holotype diameter 1.4, thickness 0.82 mm. Of 93 specimens measured, diameter 0.5 to 2.12 mm, average 1.13 mm; thickness 0.30 to 1.50 mm, average 0.73 mm. Average ratio diameter : thickness 1.55:1.0.

Remarks: The specimen figures as *Haplophragmoides* sp. C. (Taylor 1964, p. 564, pl 79, fig. 5) and placed in synonymy with *Cyclammina rotundata* (Taylor 1965, p. 153) appears to be a *Haplophragmoides* and not *C rotundata*, the occurrence of which in the Late Cretaceous has not been confirmed. The record of the species in the Late Cretaceous Curdies Formation (Ludbrook 1971, fig. 3.3) is based on probable contamination of cuttings in Mt Salt No. 1 Well from the overlying Dartmoor Formation.

Distribution: Widespread in Australia and New Zealand, associated with *C. incisa*, from Late Palaeocene to Oligocene and possibly Early Miocene.

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A NEW SPECIES OF DIPORIPHORA FROM SOUTH AUSTRALIA AND GEOGRAPHIC VARIATION IN D. WINNECKEI LUCAS & FROST (LACERTILIA: AGAMIDAE)

BY *Terry F. Houston*

Summary

A new species of dragon lizard, Diporiphora linga, is described from western South Australia. It is closely related to D. winnecki and, in order to facilitate comparison, the geographic variation of winnecki is briefly reviewed with the recognition of two distinct races. Notes on the habitats of the two species are included.

A NEW SPECIES OF *DIPORIPHORA* FROM SOUTH AUSTRALIA AND GEOGRAPHIC VARIATION IN *D. WINNECKEI* LUCAS & FROST (LACERTILIA: AGAMIDAE)

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Summary

Houston, T. F. (1977) A new species of *Diporiphora* from South Australia and geographic variation in *D. winneckei* Lucas & Frost (Lacertilia: Agamidae). *Trans. R. Soc. S. Aust.* **101**(8), 199-205, 30 November, 1977.

A new species of dragon lizard, *Diporiphora linga*, is described from western South Australia. It is closely related to *D. winneckei* and, in order to facilitate comparison, the geographic variation of *winneckei* is briefly reviewed with the recognition of two distinct races. Notes on the habitats of the two species are included.

Introduction

Specimens of an undescribed species of *Diporiphora* Gray were first collected in 1921 at Immarna, S.A., on the Transcontinental Rail Line and were identified as *D. australis* (Steindachner) by Kinghorn (1924). These specimens were apparently the basis of Cogger's (1975) record of *D. reginae* Glauert from western S.A. Storr (1974) referred other specimens of the species to *D. winneckei*.

My recognition of the new species followed extensive field studies when many live specimens were examined, from a study of specimens of *D. reginae*, most of the '*winneckei*' listed by Storr (1974) and additional material in the Australian and South Australian Museums. These studies also revealed that *winneckei* comprises at least two geographic races and these are briefly defined in order to allow comparison with the new species.

The following abbreviations of the names of institutions or collections are used:

AEG   Allen E. Greer collection (presently in AM)

AM   Australian Museum, Sydney

SAM   South Australian Museum, Adelaide

WAM   Western Australian Museum, Perth

Diporiphora winneckei Lucas & Frost
FIGS 1–5

TYPICAL EASTERN RACE

Diporiphora winneckei was described from Charlotte Waters, Northern Territory, a locality near the S.A. border on the western fringe of the Simpson Desert. All specimens examined by me from the Lake Eyre and Lake Torrens Basins (i.e. east of broken line A, Fig. 1) agree with the descriptions and figure of Lucas & Frost (1895, 1896) and represent a discrete race.

Features distinguishing this race from western populations are: no pre-anal pores in either sex; gular area with three bold longitudinal stripes, the median stripe continuous with a pair of stripes extending down the chest and belly (Fig. 2), the stripes grey in males and either yellow or grey and yellow in females; head with dark dorsal markings (Fig. 3).

Variation is slight. The lizards all appear extremely slender, almost emaciated. The gular fold is weakly developed and sometimes absent medially.

At each of several localities where I collected specimens the lizards were on sand ridges in or near bushes of Sandhill Canegrass (*Zygochloa paradoxa*). This leafless plant has wiry tangled stems and grows in hummocks almost exclusively on sand ridges. Its range includes the Simpson Desert and bordering areas, and extends south to Port Augusta and east to the Darling River, New South Wales. Thus the known distribution of typical *winneckei* corresponds approximately to the range of the canegrass.

WESTERN POPULATIONS

Specimens of *winneckei* from western N.T. and the Northwest and Eastern Divisions of

* South Australian Museum, North Tce, Adelaide, S. Aust. 5000.

Fig. 1. Known distribution of *Diporiphora linga*, *D. winneckei* and some specimens of doubtful identity. Solid symbols = specimens examined, open circles = literature records. See text for further explanation.

Western Australia (see Fig. 1) differ from those of the typical race as follows: 1–2 pairs of pre-anal pores in both sexes (though weak—rarely absent—in females); gular area with 4–5 narrow longitudinal grey stripes (Figs 4, 5).

These western *winneckei* are far more variable than the eastern race and, as I have only examined preserved material, I have preferred not to formally establish a new race at this time.

While the majority of specimens have the same extremely attenuated form of the typical race, some are outstanding in being more robust with thicker necks and larger heads. To quantify robustness in preserved, often distorted specimens is very difficult, but the ratio of head width to head length provides an approximation. It was found that the frequency distribution of this ratio was normal, so that the robust and very slender specimens connect
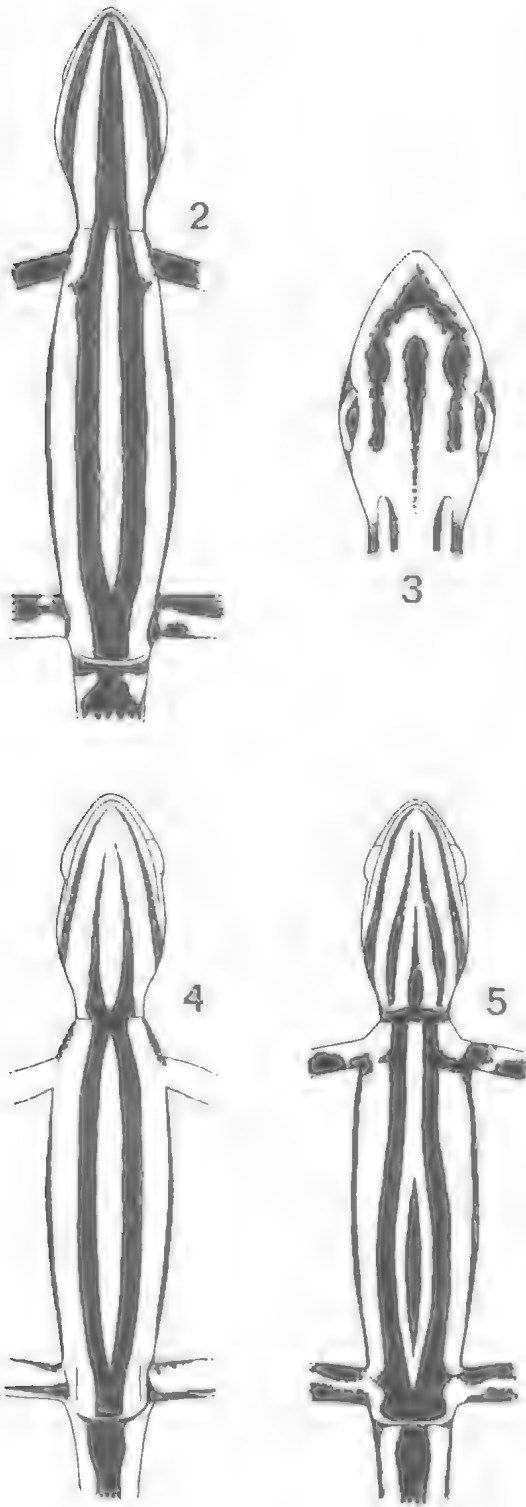
through an unbroken series of intermediates, the latter forming the bulk of the population. Additionally, the unusually robust specimens come from widely scattered localities on the Pilbara coastal plain, the Hamersley Plateau and the eastern desert of W.A.

The gular fold is also subject to variation, being strongly developed in the majority of specimens but occasionally feeble medially or absent. Absence of the gular fold occurred in specimens from across the range of the race (except on the Hamersley Plateau) but occurred more frequently in specimens from the Pilbara coastal plain. Development of the fold also appears to be independent of robustness.

The vertebral stripe (usually distinct and grey) is occasionally buff brown, faint or obscure, or divided medially. The ventral stripes had faded in many specimens but their number (4 or 5) on the gular area appeared to be independent of locality.

Some variation may have resulted from preservation. For example the gular area, or the whole ventral surface of some specimens, had a satin-like sheen and a few had dark dorsolateral stripes instead of the usual pale stripes.

One specimen (WAM R30433) from 16 km S of Port Hedland combined characteristics of the two races: the gular area had three bold stripes as in the eastern race but two pre-anal pores were present.

Although I have no personal observations of the habitat of this race, notes accompanying many specimens reveal that they were caught amongst porcupine grass (*Triodia* spp.) on sand dunes and sandy flats.

Specimens examined

The material listed by Storr (1974) from the collections of SAM and WAM plus the additional specimens listed below.

Typical eastern race: Northern Territory: Charlotte Waters, AM 2143–5. South Australia: 44 km WSW of Anna Creek HS, SAM R14522A–E; 7.5 km ENE of Bopeechee Rail Siding, SAM R13947A–C; Hunt Peninsula, Lake Eyre North, SAM R14643; shore of Lake Eyre, Muloorina Stn, SAM R14796; 22 km WNW of Moralana HS, SAM R14529; 5.5 km WNW of Myrtle Springs

Figs 2-5. Patterning in *Diporiphora winneckei* (in life, the areas shown in solid black are either grey or yellow). 2, ventral pattern of typical eastern race; 3, dorsal head pattern of same; 4, 5, two variations of ventral pattern in western race.
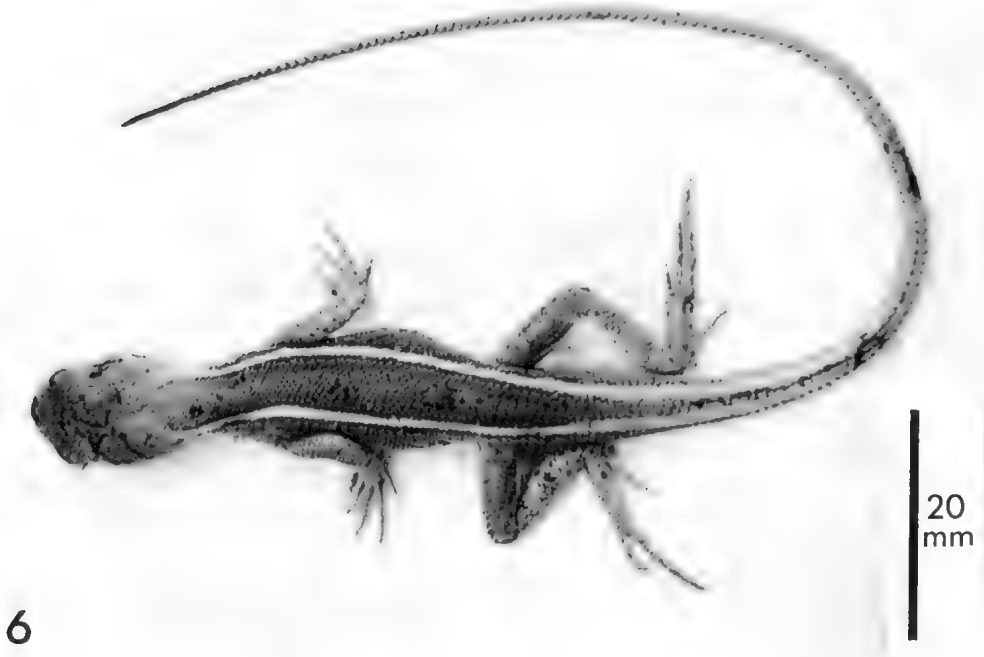
Figs 6–7. *Diporiphora linga:* 6, adult male (black speckling on body is an artefact); 7, adult female in life.

HS, SAM R14532; 10 km ENE of Stuart Creek
HS, SAM R14530 A–E.

Western race: Northern Territory: 62 km W of
Ayers Rock, AEG 311, 342; 62 and 82 km NW
of Chilla Well, AEG 203, 235; 13 km W of Mt
Olga, AM 49711; Palm Valley, SAM R5047; 1.6
km W of Refridgerator Bore, SAM R11168.
Western Australia: Marandoo, Mt Bruce, WAM
R52703, R52737–8; 59 km N of Neale Junction,
AEG 456; Nita Downs Stn, WAM R51996,
R52009, R52011; Well 38, Canning Stock Route,
WAM R44196.

Specimens excluded from D. winneckei

Amongst the specimens which Storr (1974)
listed under *winneckei* were several from the
Kimberley Division of W.A. and from Joanna
Spring. The localities of these specimens lie
above broken line B in Fig. 1. Having
examined these and additional specimens from
nearby localities I feel that they are more
likely to represent an isolate of *D. bilineata*
Gray than of *winneckei*. They differ from *win-
neckei* as follows: gular fold consistently
absent; gular scales mucronate; gular area with
5 or 6 dark longitudinal stripes and chest and
belly with 4 dark longitudinal stripes (faint or
absent in many specimens); a dusky grey or
black area above insertion of fore limb; dorsal
pattern, especially dark cross bars, strongly
developed in some individuals, virtually absent
in others.

Typical and western *winneckei* occasionally
lack the gular fold but never exhibit blackish
patches above the fore limbs. However, such
patches are characteristic of other species (e.g.
lalliae and *bennettii*).

The specimens of this unplaced form which
I have examined are the following (all in
WAM unless indicated otherwise): Beagle Bay
Mission, R46463; 81 miles (130 km) E of
Broome, R36336; Derby (and 'presumably
Derby'), R20262–4, R20317–29, R26834,
R46661; Indujan Creek, La Grange, R27638;
Joanna Spring, SAM R1430 A–B, R14621; La
Grange, R46216; Point Coulomb, R40266.

Diporiphora linga n. sp.

FIGS 6, 7

Holotype: ♂, SAM R15020F, 23 km N of
Koonibba Mission, S. Aust., 31°42'S,
133°26'E, 11–13.xi.1975, collected amongst
tussocks of *Triodia* by C. & T. Houston, A.
Edwards and J. Herridge.

Diagnosis: Morphologically and chromatically
much like *D. winneckei* differing as follows.
Males always and females usually with pre-anal

pores (absent in typical *winneckei*); back with-
out a greyish vertebral stripe and its dark cross
bands reduced to irregular spots along dorso-
lateral stripes or virtually absent; ventral sur-
faces never longitudinally striped, white to
pale grey often with weak ocelli on belly and
base of tail; males with bright pink flanks and
rump during spring (no similar coloration
recorded in *winneckei*); form more robust than
typical *winneckei* with thicker neck and fatter
body; tail, on average, relatively slightly shorter
(c.f. 227% to 253% of SVL). Also very like
D. reginae but of smaller size and not quite as
robust, lacking femoral pores, dorsal scales
more weakly keeled and not mucronate, belly
usually ocellate and pink wash of spring males
extending along full length of flanks, not just
on sides of tail base.

Description

Small dragon lizards reaching a maximum
snout-vent length (SVL) of 51 mm in males
and 61 mm in females; maximum total length
195 mm; form slender (Figs 6, 7).

Relative dimensions (expressed as %). Head
length: SVL, 25–37 (mean 30, n = 49); hind
limb length: SVL, 58–86 (mean 73, n = 47);
tail length: SVL, 165–271 (mean 227, n =
47); head width: head length (measured from
tip of snout to angle of jaw), 58–89 (mean 68,
n = 48).

Dimensions of holotype (in mm): SVL, 48;
head length, 16; head width, 10; tail length,
106; hind limb length, 36.

No nuchal or dorsal crests, nor post-
auricular folds or spines but gular and scapular
folds well-developed; dorsal scales longi-
tudinally keeled but not mucronate; scales of
back homogeneous, the keel lines more or less
parallel or weakly converging posteriorly;
scales of flanks weakly keeled to almost
smooth, the keel lines nearer forelimbs con-
verging with dorsolateral stripes but parallel to
them further back; chin and gular scales vir-
tually smooth; chest and belly scales weakly
longitudinally keeled and apically mucronate;
23–30 (mean 26, n = 48) subdigital lamellae
on 4th toe; usually 2 pairs of pre-anal pores,
occasionally 1 or 3 pairs, rarely absent; no
femoral pores.

Coloration of female: Dorsal ground colour
pale buff, greyish brown or olive brown; head
patternless dorsally; a whitish stripe from eye
to top of ear margined above and below with
dark brown; a narrow dark brown line from
eye extending forwards to snout through

nostril; upper and lower lips whitish; no verte-
bral stripe; a pair of narrow white or yellow
dorsolateral stripes extending along back from
nape, converging on base of tail and continuing
for 1/3 to ¼ its length before merging into
ground coloration; usually 6–9 irregular dark
brown spots along inner edge of each dorso-
lateral stripe on back, merging on base of tail
to form a dark line separating the pale dorso-
lateral stripes; usually corresponding but
smaller spots on flanks below dorsolateral
stripes; an irregular pale midlateral stripe often
present; flanks speckled with dark brown and
dappled with whitish spots; limbs uniform
above or brown-speckled; gular area usually
white; belly and lower half of tail base white to
pale grey, commonly with dark-edged white
flecks or distinct ocelli.

Coloration of male: Similar to that of female
except that dark spots along dorsolateral
stripes are reduced or obscure; in spring a dif-
fuse bright pink wash extends from shoulders
along flanks to sides of tail and onto region of
rump and thighs, and dorsolateral stripes
become rich yellow.

Habitat: The lizards inhabit *Triodia* hum-
mocks in mallee *Eucalyptus* covered sand-
dunes. They regularly bask in the crowns of
the bushes and retreat into the dense growth if
disturbed. Most specimens have been encoun-
tered on the slopes of dunes but a few were
observed on hard sand flats between dunes.

Distribution: Throughout a belt of sandridge
country extending from near Maralinga,
through Ooldea, south-eastwards almost as far
as Wirrulla and the Gawler Ranges on northern
Eyre Peninsula, S.A. (Fig. 1).

Etymology: The specific epithet is a Pitjantjat-
jara aboriginal word meaning "little lizard" and
is used as a noun in apposition.

Specimens examined (all localities in S.A.):
Paratypes: 22 km E of Barton Rail Siding
(30°34'S, 132°52'E), SAM R14978 A–I; Bates
(19 km W of Barton), SAM R14855; 121 km N
of Ceduna, SAM R14459 A–B; Immarna (or 407
miles, E–W line), AM 54626-7; 7 km W of
Immarna Rail Siding (30°29'S, 132°05'E), SAM
R14998 A–L; same data as holotype, SAM
R15020 A–F, G, H; 6.7 km SW of turn-off to Lake
Everard HS on Wirrulla-Kingoonya road, AEG
631; Maralinga bomb site, SAM R14447; S of Mt
Finke (31°40'S, 133°58'E and 31°15'S, 134°00'E),
SAM R15600-1; Watson (obviously in error),
SAM R10822-6; 28–29 km NE of Wirrulla, SAM
R15174, R15208 A–G, R15220; 23 miles (37 km)
ENE of Wirrulla, WAM R24529-30.

Discussion

The relative structural homogeneity of
Diporiphora species requires that maximum
use be made of colour patterning (including
ventral patterning and transient sexual colours)
for the purposes of their separation. However,
because of the tendency of parts of the pattern-
ing to fade after preservation it is highly
desirable that any further taxonomic studies of
the genus be based on field studies of live speci-
mens.

While my studies of preserved material could
find no basis for separation of western *win-
neckei* into two or more races, more specimens
are required, especially from the Hamersley
Plateau, to provide a clearer picture of varia-
tion. More material is also required from the
central southern region of N.T. to show how
closely the ranges of the eastern and western
races approach each other.

Several species of *Diporiphora* are now
known to be closely associated with hummock
grasses: *reginae, lalliae, linga* and western *win-
neckei* with *Triodia* and typical *winneckei* with
Zygochloa. This pronounced habitat specificity
has doubtlessly played a major role in evolu-
tion of the species. Populations of *linga* are
isolated from those of other hummock-dwelling
species by extensive tracts of unsuitable habitat.
In the west is the Nullarbor Plain and across
the north are vast areas of mulga/tussock grass
and chenopod shrub habitats. The ventral pat-
terning differences between the two races of
winneckei are probably related to differences in
the plants inhabited. The ventral striping
probably serves to camouflage the lizards while
they are perched amongst the straight leaves
or stems of the grasses and fewer bolder stripes
in the eastern race would suite the coarser more
open growth of *Zygochloa* whereas more
numerous narrower stripes in the western race
would suit the finer denser growth of *Triodia.*

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