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*BY DENNIS M. OPRESKO* & FREDERICK M. BAYER†*

## Summary

Since 1876, *Dendrobrachia fallax* Brook, an arborescent, noncalcareous anthozoan coelenterate with a spiny, proteinaceous axis, has been assigned to the suborder Antipatharia in spite of such equivocal features as the probable presence of eight pinnately branched tentacles and a solid axial core. In recent years, specimens resembling *D. fallax* have been collected from off the southern coast of Australia and from the Straits of Florida. These specimens represent two new species of *Dendrobrachia* and are here described as *D. paucispina* sp. nov and *D. multispina* sp. nov.

Furthermore, anatomical and histological studies demonstrate that *Dendrobrachia* has characteristic octocorallian features. The solid, noncalcareous axis and absence of calcareous sclerites suggest a relationship with the holaxonian family Chrysogorgiidae, but the distinctive skeletal features warrant retaining the genus in a separate family Dendrobrachiidae.

KEY WORDS: Gorgonacea, Octocorallia, Antipatharia, Chrysogorgiidae, Dendrobrachiidae, *Dendrobrachia*.

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by DENNIS M. OPRESKO* & FREDERICK M. BAYER†

OPRESKO, D. M. & BAYER, F. M. (1991) Rediscovery of the enigmatic coelenterate *Dendrobrachia* (Octocorallia: Gorgonacea), with descriptions of two new species. *Trans. R. Soc. S. Aust.* **115**(1), 1-19, 31 May, 1991.

Since 1876, *Dendrobrachia fallax* Brook, an arborescent, noncalcareous anthozoan coelenterate with a spiny, proteinaceous axis, has been assigned to the suborder Antipatharia in spite of such equivocal features as the probable presence of eight pinnately branched tentacles and a solid axial core. In recent years, specimens resembling *D. fallax* have been collected from off the southern coast of Australia and from the Straits of Florida. These specimens represent two new species of *Dendrobrachia* and are here described as *D. paucispina* sp. nov and *D. multispina* sp. nov. Furthermore, anatomical and histological studies demonstrate that *Dendrobrachia* has characteristic octocorallian features. The solid, noncalcareous axis and absence of calcareous sclerites suggest a relationship with the holaxonian family Chrysogorgiidae, but the distinctive skeletal features warrant retaining the genus in a separate family Dendrobrachiidae.

KEY WORDS: Gorgonacea, Octocorallia, Antipatharia, Chrysogorgiidae, Dendrobrachiidae, *Dendrobrachia*.

## Introduction

On 27 March 1876, at 8°03'S, 14°27'W, off Ascension Island, H.M.S. "Challenger" dredged two specimens of an arborescent coelenterate with spiny proteinaceous axis at station 343 in 425 fathoms of water. These specimens subsequently were described as *Dendrobrachia fallax* by Brook (1889) and assigned to a new family, Dendrobrachiidae, placed in the suborder Antipatharia. The species was taken again in 1901, off the Cape Verdes by the Prince of Monaco, and reported briefly by Thomson (1910), who concurred with Brook in placing it in a special family of Antipatharia.

In spite of their equivocal features — pinnate tentacles probably eight in number, absence of a hollow axial core — the spiny axis and lack of calcareous spicules overrode other considerations and classification of *Dendrobrachia* among the Antipatharia has prevailed until the present.

During 1988 and 1989, Karen Gowlett-Holmes, while aboard trawlers in the Great Australian Bight and farther south off the Continental shelf of Australia, collected a number of deep sea octocorals and antipatharians which were deposited in the South Australian Museum. Along with specimens of *Chrysogorgia* were six colonies also tentatively identified as chrysogorgiid gorgonians. When examined more closely, these were found to resemble Brook's enigmatic *Dendrobrachia fallax*. This new material represents a new species of the genus, and is sufficiently well preserved to permit a more detailed description of the soft anatomy and a reevaluation of the placement of the family Dendrobrachiidae. Also included in this report is a description of a new species of *Dendrobrachia* from the western Atlantic, which is based on one specimen collected from the Straits of Florida.

## Systematics

Subclass Octocorallia
Order Gorgonacea
Suborder Holaxonia
Family Dendrobrachiidae Brook, 1889
Genus *Dendrobrachia* Brook, 1889

*Dendrobrachia* Brook, 1889:159; Hickson, 1895:40; Thomson, 1910:142.

*Type species: Dendrobrachia fallax* Brook, by monotypy.

*Diagnosis:* Arborescent Gorgonacea with purely proteinaceous axis lacking hollow core; axis marked by conspicuous ridges and grooves, with more or less numerous and prominent spines along the summit of the ridges. Polyps and coenosarc without calcareous sclerites.

*Distribution:* Eastern Atlantic Ocean off Ascension and Cape Verde Islands; western Atlantic off Cay Sal, Bahamas; Great Australian Bight. 394-1089 m.

### *Dendrobrachia fallax* Brook
FIGS 1, 2; Table 1

*Dendrobrachia fallax* Brook, 1889:159-160, pl. 10, figs 1-8. Thomson, 1910:142-143.

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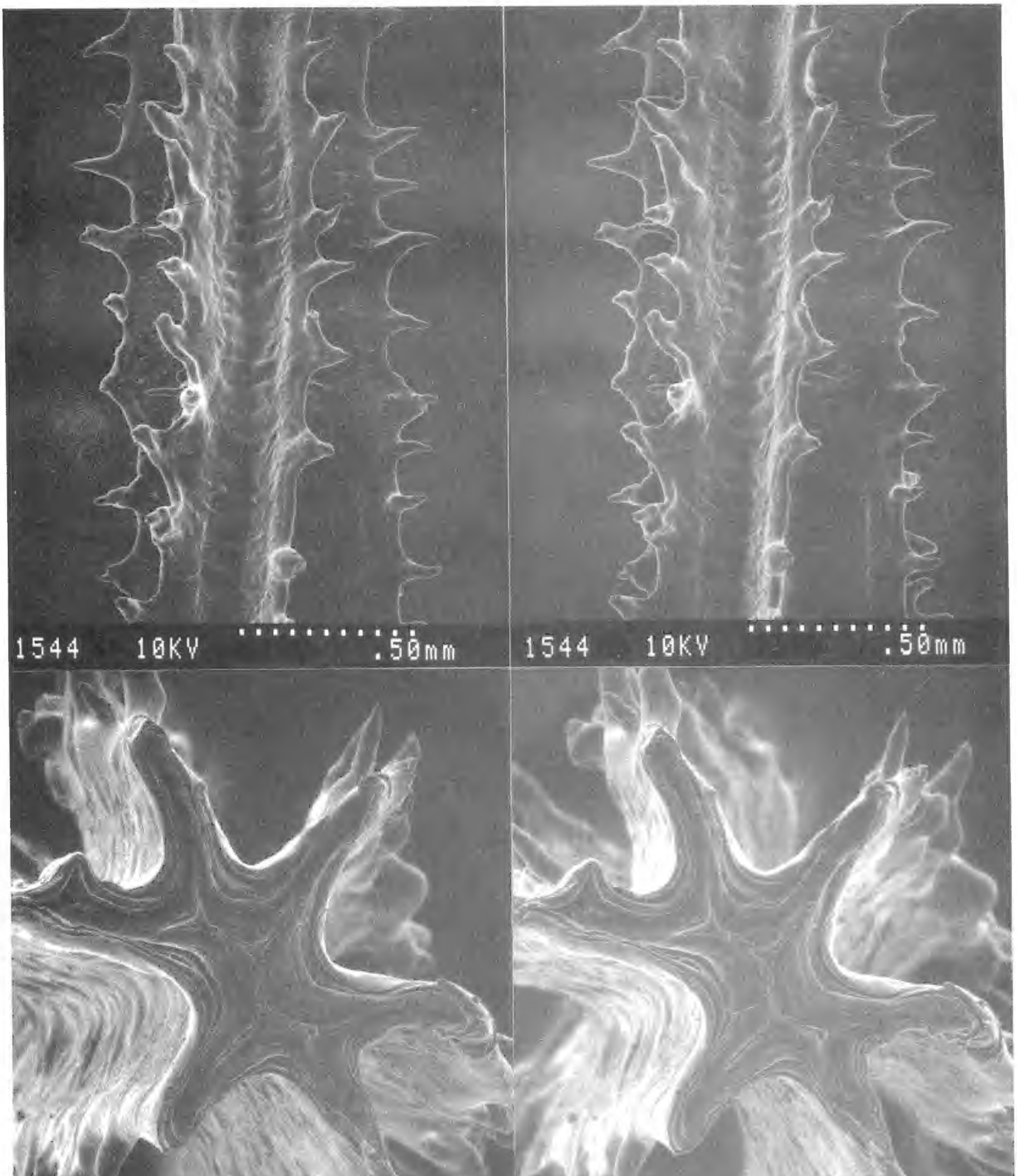


Fig. 1. *Dendrobrachia fallax* Brook, axis. Top, lateral view of terminal twig; bottom, cross section below apex. Stereoscopic pairs, SEM.

*Material Examined:* Type specimens, South Atlantic, off Ascension Island, 8°03′S, 14°27′W, 425 fm (777 m), "Challenger" Expedition, Sta. 343, 27 March 1876, 2 spec. (British Museum (BMNH) 1890.4.9.27).

*Description:* Colony planar, sparsely branched, with some overlapping of adjacent branches; branchlets bilateral, very irregularly alternate, rarely opposite, highest order branchlets mostly 1–3 cm long, occasionally longer, 0.5–0.8 mm in diameter, on average about 1 cm apart on same side of branches. Usually six, occasionally five or seven axial ridges on branchlets, increasing in number on larger branches. Spines present on ridges, one row per ridge; spines variable in size and shape but increasing in size with increasing thickness of branches, 0.2–0.25 mm long on branches about 1 mm in diameter. Polyps placed bilaterally, alternate or in nearly opposite pairs, 3–6 polyps per cm.

*Discussion:* Neither of the type specimens has a basal holdfast and one specimen appears to have been broken off a larger colony. Both specimens are about 20 cm tall and 5–10 cm wide. The basal "stem" diameter is 2 × 2.5 mm in one colony and about 3 mm in the other. Overall, the branching of the colonies is sparse, open, to about the eighth order, and generally in one plane with some overlapping of adjacent branches (see Brook 1899: p. 10, fig. 1). On the central portions of the corallum, the branching is very weakly sympodial in that some of the higher order ramifications become thicker and longer than the branches from which they arise. The branch angles (delineated by the inner or distal side of a branch and the lower order branch from which it arises) are generally greater than 45°. The smallest ramifications of the corallum, the branchlets, occur at all levels of the corallum. They are straight or slightly curved upward, unbranched, about 0.5–0.8 mm in diameter, and usually not more than 3 cm long. They tend to be positioned bilaterally and in a very irregularly alternating pattern along the sides of the branches. The distance between the bases of adjacent branchlets and/or branches on the same side of the lower order ramification from which they arise ranges from about 6–19 mm, and the average distance is 9.4 mm ($n = 24$). The distance between adjacent branchlets and branches on opposite sides of the axis ranges from about 2–17 mm, and the average distance is 6.3 mm ($n = 25$).

At the tips of the smallest branchlets the skeletal axis has six (occasionally five or seven) longitudinal ridges separated by grooves or channels. The ridges do not radiate out from a common central point, but rather appear to develop as bifurcations at the ends of a primary skeletal plate which is narrow and rectangular in cross section. This primary axial structure of branchlets can be seen at the core of the thicker branchlets when viewed in cross section (Fig. 1, bottom).

Extending down from the tips of the branchlets for a distance of about 1–1.5 cm, the ridges remain smooth or possess only small, scattered rounded elevations about 0.05–0.08 mm high. Further down on the branchlets distinct spines develop along the ridges (Fig. 1, top). Although the spines are not strictly uniform in size or shape throughout the corallum, they generally become longer as the diameter of the branchlets and branches increases. Many spines typically have a relatively sharp apex and a flared base (Fig. 2); however, others are more blunt, and some even have a swollen or knob-like apex. On branchlets 0.6–0.8 mm in diameter, the spines are usually 0.10–0.15 mm high; on branches 0.8–1.0 mm in diameter, they are usually 0.15 to 0.20 mm high (but up to 0.25 mm in some places). They are arranged in 5 to 6 rows (one row per skeletal ridge) with 4–5 spines per millimeter in each row. Generally, the ridges remain relatively narrow with a single row of spines. On the thicker branches more longitudinal rows of spines develop. On a branch 1.2 mm in diameter (excluding spines), the spines are about 0.3 mm high, 5–6 rows of spines can be seen in one lateral view, and there are about 3–4 spines per millimeter in each row. The height of the spines near the base of the stem (diameter 2.0 mm) is about 0.5 mm; there are 3–4 spines per millimeter in each row, and about 12 very irregular rows of spines can be seen in one lateral view. The rows are separated by wavy lines of coenenchyme which intersect one another at varying intervals. On the second specimen (basal stem diameter about 3mm), the spines reach a maximum size of about 0.4 mm, and as many as 17 rows of spines can be seen from one aspect. In the illustration given by Brook (1889: pl. 10, fig. 8) there appear to be about 38 or more rows around the entire circumference of a branch from near the base of the corallum.

The polyps arise from the coenenchyme in the grooves formed between the skeletal ridges. Their arrangement on the corallum is not strictly regular, although it is generally bilateral. On some branchlets a regular alternating pattern can be seen with the polyps spaced about 5 mm apart. Occasionally the polyps occur in nearly opposite pairs. In the latter case there can be as many as 6 polyps per centimeter along the branchlets. The condition of the polyps in both specimens is poor and allows for only a rough estimate of their size. They appear to be no taller than about 2–2.5 mm (including tentacles). The body column is about 1.0 mm in length and about 0.5 mm in diameter at the base. As noted by Brook, the polyps do not appear

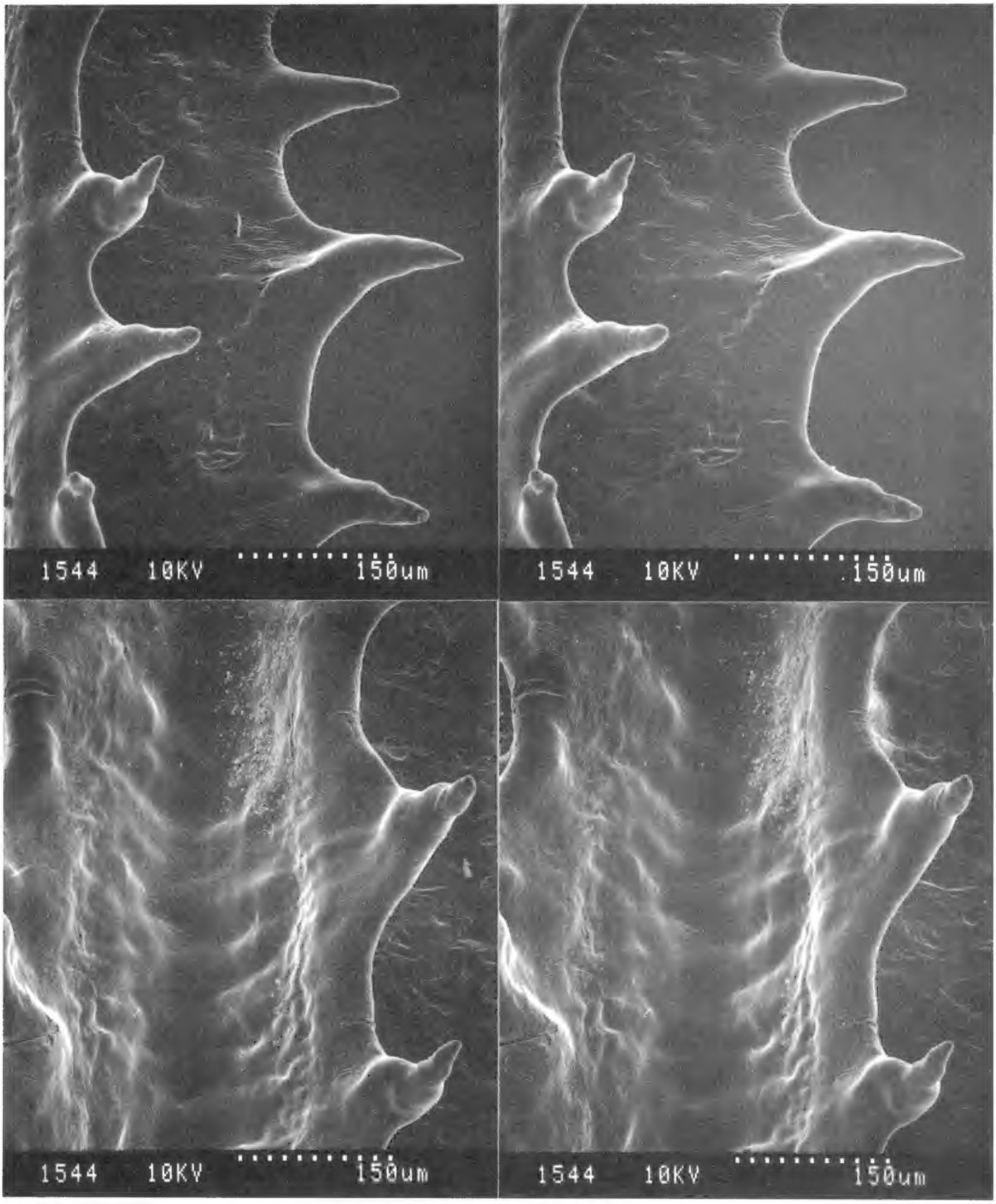


Fig. 2. *Dendrobrachia fallax* Brook, axis. Stereoscopic views of axial spines, SEM.

TABLE 1. *Morphometrics for* Dendrobrachia *spp.*

| Parameter | *fallax* | *paucispina* | *multispina* |
|---|---|---|---|
| Corallum: | | | |
| Stem diam./height (%) | 1.2-1.5 | 1.1-1.7 | 0.7[a] |
| Branchlets: | | | |
| Maximum length[b] (cm) | ca. 3 | ca. 3 | ca. 3 |
| Diameter (mm) | 0.5-0.8 | 0.4-0.8 | 0.4-0.5 |
| Avg dist. apart[c] (mm) | 9.4 | 9.0-9.5 | 13 |
| Axial Ridges: | | | |
| Number on branchlets[d] | 5,*6*,7 | *6*,7,8 | 5 |
| Axial Spines: | | | |
| Number of rows per ridge | 1 | 0-1 | 1-2+ |
| Number per mm per row[d] | 3,4,5 | 3,*4*,5 | *4*,5,6 |
| Height of Spines[e] (mm): | | | |
| Axis diam. ≤0.5 mm | 0.05-0.10 | – | 0.06-0.12 |
| Axis diam. 0.6-0.8 mm | 0.10-0.15 | 0.00-0.07 | 0.10-0.25 |
| Axis diam. 0.8-1.0 mm | 0.15-0.25 | 0.07-0.12 | 0.26-0.32 |
| Axis diam. 1.0-2.0 mm | ca. 0.3 | 0.12-0.18 | 0.25-0.40 |
| Axis diam. >2.0 mm | ca. 0.5 | 0.12-0.25 | – |
| Polyps: | | | |
| Maximum height[f] (mm) | 2.5 | 2.2 | ca. 2.3 |
| Number per cm | 3-6 | 3-6 | 3+ |
| Pairs of pinnules | 6-7[g] | 8-10 | – |

[a] Specimen may be part of a larger colony.
[b] Unbranched branchlets, rarely longer.
[c] On the same side of the axis.
[d] Most common condition italicized.
[e] Height of spines very variable, commonest size ranges shown.
[f] Including tentacles.
[g] As reported by Thomson (1910).

to stand out at right angles to the axis, but rather are inclined distally.

*Remarks:* Thomson (1910) reported that the polyps were often in subopposite pairs, with the pairs spaced at intervals of two lengths or more apart. He also noted that there were six or seven, pairs of pinnules on the tentacles.

*Distribution:* Known from off Ascension Island, 777 m. ("Challenger" Expedition), and from Cape Verde Islands, 394 m.

### *Dendrobrachia paucispina* sp. nov.

FIGS 3-8, 12-13; Table 1

*Material Examined:* Off the southern coast of Western Australia: 125 nautical miles East of Cape Arid, 34°03′S, 125°31′E, 1011-1020 m, F/V "Adelaide Pearl", 31 July 1988, Coll. K. Gowlett-Holmes, K. Olsson, M. Cameron, syntypes: South Australian Museum SAM H715, 1 spec.; USNM 87769, 1 spec.; about 80 nautical miles SW of Pearson Island, 35°04′S, 133°35′E, 900-960 m, F/V "Comet", 13 April 1989, coll. K. Gowlett-Holmes, syntype: SAM H716, 1 spec.; about 100 nautical miles due west of Whidbey Point, 34°49′S, 133°07′E, 884-859 m, F/V "Longva III", coll. K. Gowlett-Holmes, 11 November 1989, syntypes: SAM H728, 1 spec.; USNM 87768, 1 spec.

*Description:* Colony planar, loosely branched, with some overlapping of adjacent branches; branchlets bilateral and very irregularly alternate; highest order branches usually not more than 3 cm long, 0.4-0.8 mm in diameter, on average about 1 cm apart on same side of lower order branches. Six, occasionally seven, rarely eight longitudinal axial ridges on branchlets, increasing in number on thicker branches. Spines sparse, often absent, arranged in one row per axial ridge where present. Spines not uniform in size and shape, but increasing in length on larger branches; about 0.1 mm long on branches 1 mm in diameter. Polyps bilateral, in alternate or subopposite pairs, 3-6 per cm.

*Discussion:* The type series consists of six specimens, all of which are to some degree bent over

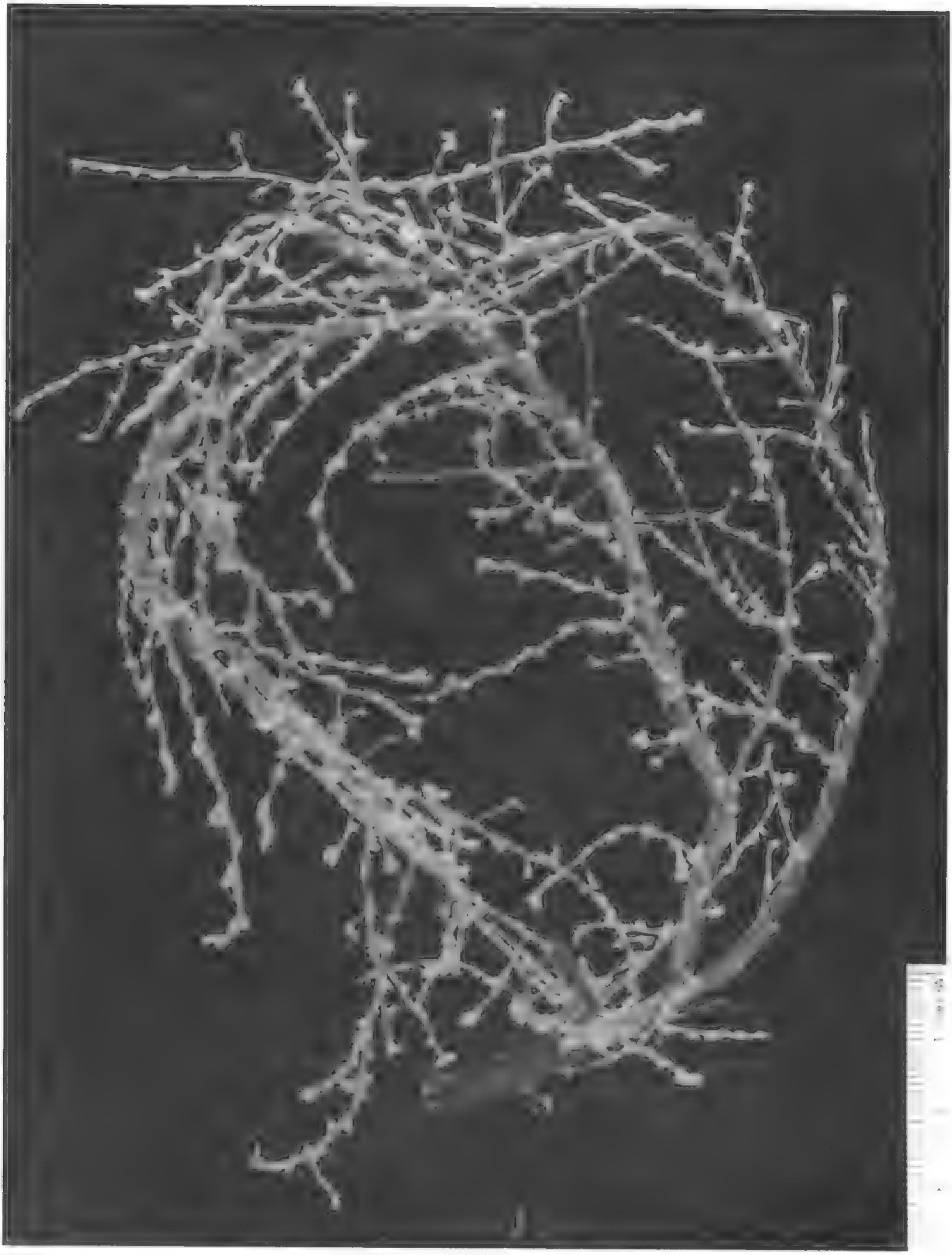


Fig. 3. *Dendrobrachia paucispina* sp. nov. Syntype colony SAM H715.

and twisted in the upper part of the corallum, a condition which may have resulted in part from preservation and storage in small containers. When unfolded into what was probably its natural shape, the largest colony is about 45 cm tall and 15 cm wide, with a basal stem diameter of 7.5 mm. The smallest colony is 15 cm tall and about 7 cm wide, with a basal stem diameter of about 2 mm.

A colony of medium size (SAM H715) is described in detail. This specimen is about 28 cm tall and 6 cm wide, and has a basal stem diameter of 4 × 4.3 mm (Fig. 3). The branching pattern of the corallum is generally planar with some overlapping of adjacent branches. The branching is irregular to about the 9th order. The highest order branching consists of small, relatively thin branchlets arranged in a very loose bilateral and alternating pattern. The smallest unbranched branchlets range in length from 0.4–3.0 cm ($\bar{x}$ = 1.47 cm, n = 23), and they are 0.4–0.6 mm in diameter. The average distance between the bases of adjacent branchlets and/or branches on the same side of a lower order branch is 9.0 mm (range 4–19 mm, n = 30). The average distance between adjacent branchlets and/or branches on opposite sides is 4.8 mm (range 3–8 mm, n = 9). The branch angles (delineated by the distal side of a branch and the lower order branch from which it arises) are generally greater than 45°.

At the tips of the smallest branchlets, the axial skeleton consists of six, occasionally seven, and rarely eight narrow longitudinal ridges separated by deep, u-shaped grooves (Fig. 4, top). The ridges increase in number on the thicker, older parts of the corallum (Fig. 4, bottom), are present on the stem and also faintly visible on the upper part of the holdfast. On branches 2–3 mm in diameter, 12 or more ridges can be seen in one lateral view.

Over most of the corallum, and particularly on branches less than 1 mm in diameter, the skeletal ridges are smooth (Fig. 5, top); however, in some places scattered spines occur in a single row along several of the ridges. On the smaller branchlets they take the form of small rounded elevations (Fig. 5, bottom); on the older branches they are more spine-like (Fig. 6). Where present, the spines occur on only one or a few of the ridges and never on all the ridges around the circumference of the axis. Although quite variable, the height of the spines is generally about 0.07 mm on a branchlet 0.6–0.8 mm in diameter, 0.07–0.12 mm on branches about 0.8–1.0 mm in diameter, and 0.12 to 0.18 mm on branches 1.0–2.0 mm in diameter. There are usually 3–5 spines per millimeter in each row. Spines are also found at the base of several of the small branchlets which arise directly from the stem or thicker branches. In these cases the spines can be 0.25 mm or more in height.

Polyps are present throughout the corallum. They are not arranged in a strictly regular order but are more abundant on the lateral and front sides of the branches (relative to the plane of the corallum). On many of the larger branches a narrow band of coenenchyme without polyps extends down the middle of the posterior side. On the branches the polyps are spaced irregularly (Fig. 7), sometimes unilaterally, and sometimes bilaterally with alternating or opposite pairs. Most polyps are about 5 mm apart, and there can be 3–6 polyps per centimeter depending on whether they are placed singly or in pairs. They are usually inclined distally, often with their adaxial side lying against the axis. The largest polyps are about 2.2 mm tall (including tentacles); the body column is about 1 mm in length (Fig. 8). On several polyps in which the tentacles were adequately expanded, 8–10 pairs of pinnules could be seen on each tentacle.

The remaining specimens in the type series are similar in most morphological features to the one described above. All the colonies have a typical planar branching pattern, with the highest order unbranched branchlets being not more than 3 cm long and spaced about 1 cm apart in a very loose bilateral and alternating fashion. In the larger colonies, there are infrequent fusions of some of the lower-order branches and the larger branches and stem have a distinctive golden, somewhat iridescent sheen.

From specimen to specimen, and even within a single colony — from branch to branch — differences can be seen in the occurrence, size, and density of the axial spines. In the two largest specimens (SAM H728 and USNM 87768), the spines are overall slightly smaller and sparser than those in the described colony. Furthermore, spines are only rarely present on branches of about 2 mm in diameter or more; however, the axial ridges remain distinct and can be seen on both the branches and the stem.

In another specimen (SAM H728, height 30 cm, basal stem diameter about 4 mm) spines are present on all parts of the corallum including the stem and basal plate; however, they are not uniformly distributed, are absent in some places, but present on all the axial ridges in other places. This variability in the occurrence of the axial spines is a characteristic feature of this species.

*Remarks:* Although the general form of the corallum of *D. paucispina* sp. nov. is very similar to that of *D. fallax*, this species can be differentiated on the basis of the very sparse number and relatively smaller size of the axial spines (Table 1). The

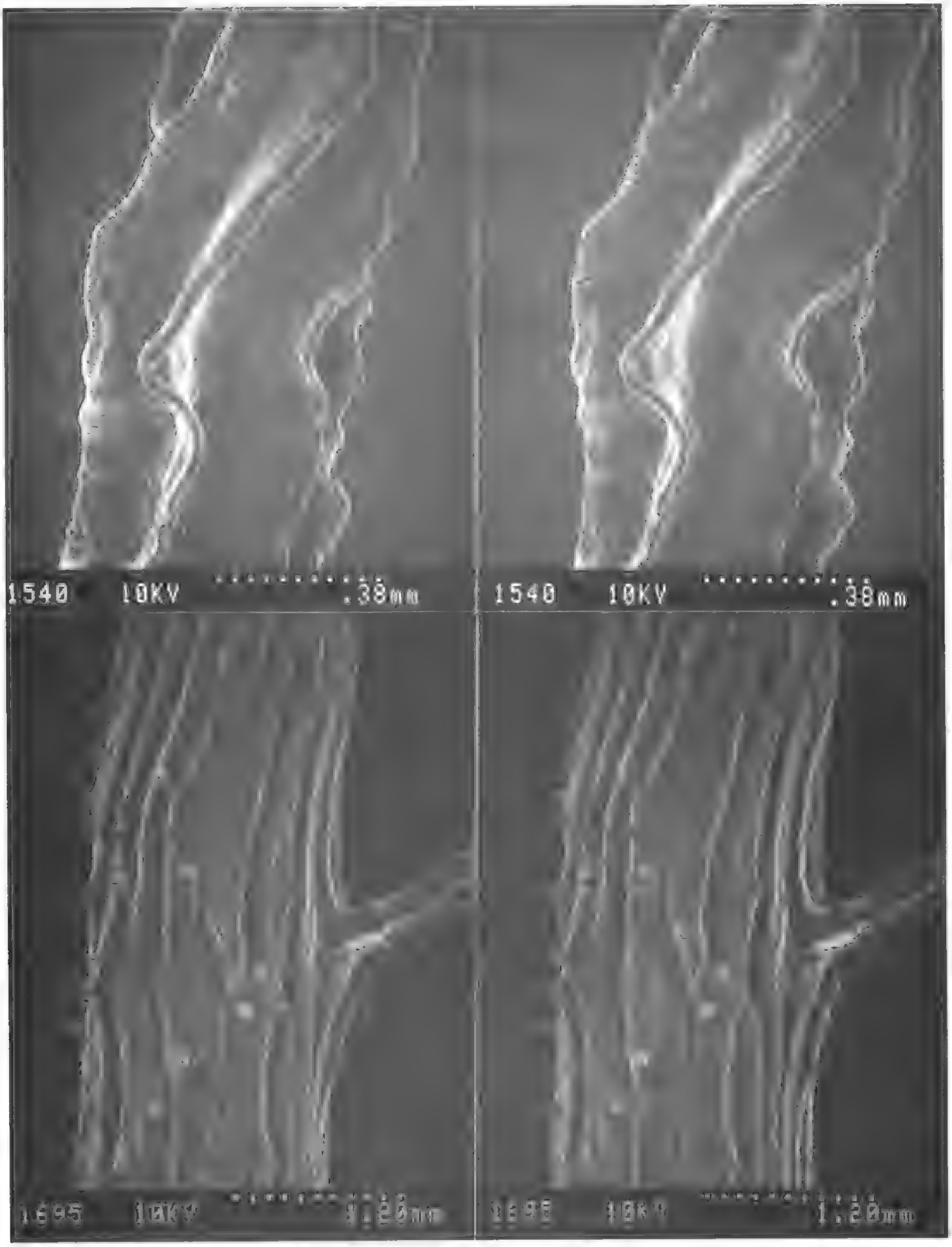


Fig. 4. *Dendrobrachia paucispina* sp. nov., axis. Top, lateral view of terminal twig; bottom, lateral view of larger branch SAM H715. Stereoscopic pairs, SEM.

Fig. 5. *Dendrobrachia paucispina* sp. nov., axis. Lateral views of terminal twigs, SAM H715. Stereoscopic pairs, SEM.

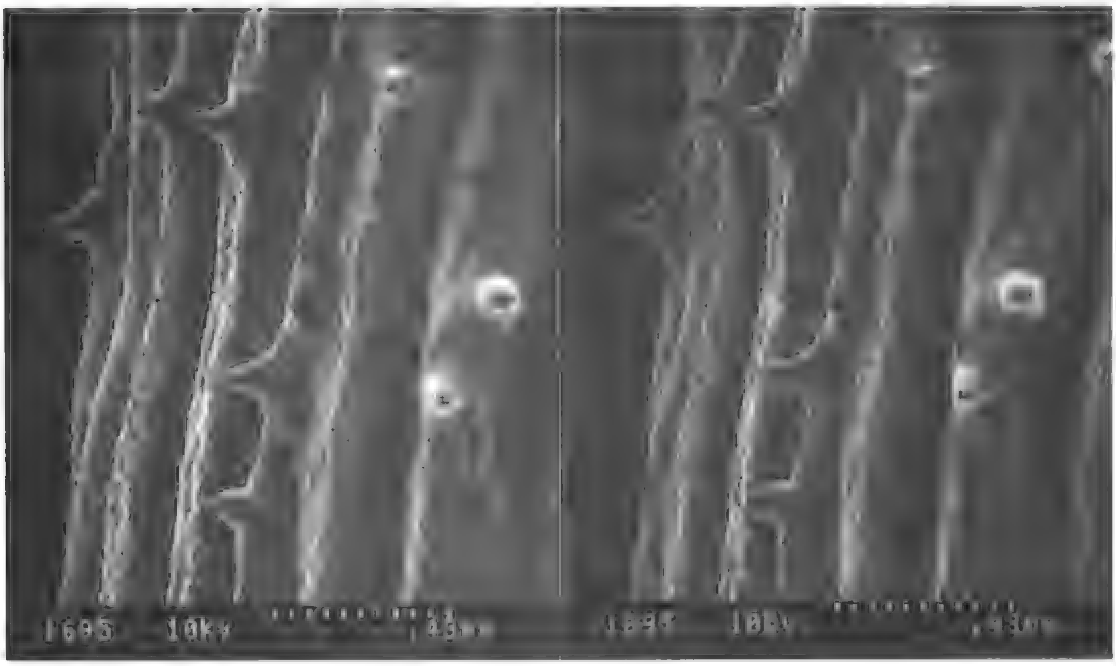


Fig. 6. *Dendrobrachia paucispina* sp. nov., axis. Lateral view of larger branch, SAM H715. Stereoscopic pair, SEM.

complete absence of spines on many parts of the axis is quite distinctive. Where present, and for branches of similar thickness, the spines in this species are only about one-half as large as those in *D. fallax*. Although in both species the smallest branchlets most commonly have six primary axial ridges, in *D. paucispina* sp.nov. there are occasionally seven and sometimes even eight ridges present. In contrast, in *D. fallax* there are occasionally five or seven ridges on the smallest branchlets. The polyps in *D. paucispina* sp. nov. and *D. fallax* appear to be similar in size and number; however, there is some evidence suggesting that the number of pairs of pinnules on the tentacles may be different in the two species. In this species there are eight–ten pairs of pinnules per tentacle. According to Thomson (1910), there are only six–seven pairs per tentacle in *D. fallax*.

*Distribution:* Known only from the Great Australian Bight, 884-1020 m, on the continental slope.

### ***Dendrobrachia multispina*** sp. nov.

FIGS 9–11, Table 1

*Material Examined:* Straits of Florida, west of Cay Sal Bank, Bahamas, 23°51.9′ N, 80°42.7′ W, 1080-1089 m, R/V "Gerda" Sta. 1111, 30 April 1969. Holotype, USNM 87770.

*Description:* Colony planar, very sparsely branched; branchlets bilateral, very irregularly alternate; highest order branchlets usually not more than 3 cm long, 0.4–0.5 mm in diameter, on average 1.3 cm apart on same side of branches. Five longitudinal axial ridges on branchlets. Spines in rows on axial ridges, one row per ridge on smallest branchlets, multiple rows on larger branchlets and branches. Spines not uniform in size or shape, becoming tall and acicular on larger branchlets and branches; about 0.3 mm long on branches about 1 mm in diameter. Polyps mostly bilateral and alternate, 3 per cm.

*Discussion:* The type specimen lacks a basal holdfast and may have been broken off a larger colony. The upper portion of the specimen is bent, perhaps due to preservation (Fig. 9). With the branches straightened and extended vertically, the corallum is about 19 cm high and 7 cm wide. The diameter at the basal end of the "stem" is 1.4 mm. The colony is very sparsely and openly branched in an irregular bilateral fashion. The average distance between the bases of adjacent branchlets and/or branches on the same side of the lower order branches is 13 mm (range 8–21 mm, n = 24). The

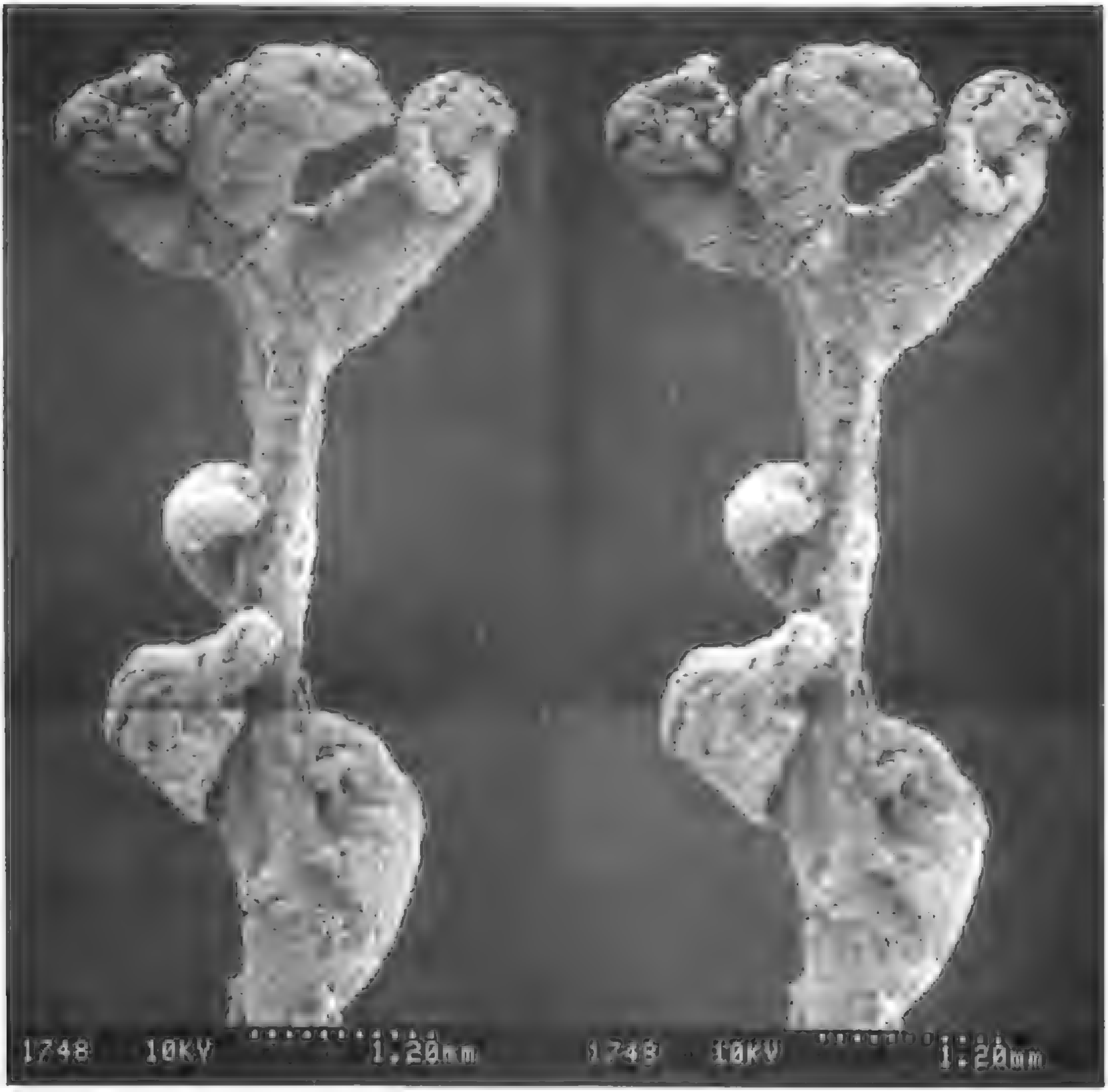


Fig. 7. *Dendrobrachia paucispina* sp. nov. Tip of terminal branch with polyps intact, critical-point dried, SAM H715. Composite stereoscopic pair, SEM.

average distance between adjacent branchlets and/or branches on opposite sides is 6 mm (range 1-16 mm, n = 22). The branch angles are mostly 60° or more. The smallest unbranched branchlets range in length from 0.7–3.1 cm ($\bar{x}$ = 1.5 cm, n = 12) and they are relatively stiff and straight. They are about 0.4-0.5 mm in diameter.

At the tips of the smallest branchlets, the axial skeleton consists of five narrow longitudinal ridges separated by wide v-shaped grooves. For a distance of 0.5–2 cm from the tips of the branchlets the ridges are smooth or have only small irregularly rounded or triangular elevations which are generally not more than 0.07 mm high (Fig. 10). With increasing thickness of the branchlets these develop into spines which eventually become relatively tall and acicular, the ridges become wider and lobe-like, and the grooves become relatively narrow (Fig. 11, top). Multiple rows of spines develop on the surface of the enlarged ridges. In some places two relatively straight rows of spines are positioned along the edges of the ridges adjacent to the grooves with additional irregular rows or scattered spines occurring between the edge rows. Overall, the axis

Fig. 8. *Dendrobrachia paucispina* sp. nov. Single polyp, critical-point dried, SAM H715. Stereoscopic pair, SEM.

becomes quite spinose; however, remnants of the five primary grooves, although quite narrow, remain recognisable, even at the base of the corallum.

The spines are not uniform in size or shape from branchlet to branchlet. They stand out at right angles to the axis and often are slightly crooked. The height of the spines is 0.10-0.25 mm on branchlets 0.6-0.8 mm in diameter (Fig. 11, bottom), 0.26-0.32 on branches about 0.8-1.0 mm in diameter, and up to 0.4 mm on branches 1.0-1.2 mm in diameter. The largest spines are relatively narrow, about 0.05 mm in diameter at their center. There are usually four or five, sometimes six spines per millimeter in each row. Occasionally the spines are slightly more developed at the base of small branchlets arising directly from the stem and thicker branches.

Polyps of this specimen are poorly preserved. They are arranged irregularly, in a somewhat bilateral pattern. There appear to be about 3 per centimeter. The largest polyps are about 2.3 mm tall (including tentacles); the tentacles are about 0.8-1.0 mm long.

*Remarks:* In size and general appearance *D. multispina* sp. nov. is similar to *D. fallax* and *D. paucispina* sp. nov. All have a somewhat planar corallum with rather irregular, but generally bilateral and alternating branching. The branching of the corallum of *D. multispina* sp. nov. is slightly more sparse and open, but this may not be typical, considering that the specimen may only be part of a larger colony. The taxonomic character in which this species differs consistently from the other two species is the greater development of the axial spines. In this species the spines on the larger branchlets and branches develop in multiple rows along the axial ridges, whereas in the other two species there is only one row of spines per ridge. The spines in *D. multispina* sp. nov. are also relatively larger and more crowded together than in the other two species (Table 1). In addition, in *D. multispina* sp. nov. the number of primary skeletal ridges on the branchlets is consistently five throughout the corallum, whereas in *D. fallax* it is usually six, occasionally five or seven, and in *D. paucispina* sp. nov. it is usually six, occasionally seven, and rarely eight.

*Distribution:* Known only from the type locality.

## Anatomy and Histology

Anatomy and histology have not been described for very many species of Octocorallia, and much of the published information deals with a few pennatulacean species. Hickson (1895b) described the anatomy of *Alcyonium digitatum* Linnaeus,

Fig. 9. *Dendrobrachia multispina* sp. nov. Holotype colony, USNM 87770.

Bouillon & Houvenaghel-Crevecoeur (1970) described the anatomy and histology of *Heliopora coerulea* (Pallas), and Bayer & Muzik (1976a) described the general structure of the solitary *Taiaroa tauhou* Bayer & Muzik.

Among the gorgonaceans, the structure of *Pseudoplexaura crassa* Wright & Studer was investigated in considerable detail by Chester (1913), and that of *Plexaura homomalla* (Esper) by Bayer (1974). The anatomy and histology of those species conform in general with those of all other gorgonaceans the structure of which has been described.

The anatomy of the polyps of all monomorphic octocoral species and of the autozooids of dimorphic species is remarkably uniform. As this basic form has been described and illustrated adequately in general treatises (e.g., Hyman 1940; Bayer 1956) as well as in specialized accounts (Hickson 1895b; Chester 1913; Bayer 1974; Bayer *et al.* 1983), it need not be repeated here. The polyps of *Dendrobrachia* conform to the general gorgonacean pattern. Paraffin serial cross-sections of a polyp of *Dendrobrachia paucispina* sp. nov. clearly show that the general form corresponds to the usual gorgonacean pattern, differing in only

Fig. 10. *Dendrobrachia multispina* sp. nov., axis. Lateral views of terminal twig USNM 87770. Stereoscopic pairs, SEM.

minor details. As the specimens were not prepared with anatomical and histological investigation in mind, fixation is adequate only for demonstration of gross anatomy and a very superficial investigation of histology.

From Fig. 12 it is clearly seen that the polyps of *Dendrobrachia* have the usual four couples of complete mesenteries and a single siphonoglyph. The arrangement of longitudinal retractor muscles is, as usual, on the sulcal face of the mesenteries, but the retractors of the asulcal and sulcal mesenteries are relatively weak (at least at the level of the body that was sectioned) and development of mesogloeal plates on the asulacal side of the four lateral mesenteries (Figs 12, 13) is a clear indication that muscle fibers are present on both faces of at least the lateral mesenteries.

The siphonoglyph is well developed and the epithelium of the pharynx at its upper end is thrown into about 10 longitudinal folds, similar to the condition in *Alcyonium* observed by Hickson (1895b). These seem to fade out proximad, where they give way to transverse folding of the pharyngeal wall probably related to shortening of the pharynx resulting from contraction.

The epidermis (Fig. 13) is composed of the usual tall, obconic cover cells (cf. Chester 1913; Bayer 1974), thrown into conspicuous lobes and covered by delicate cuticle, which in many places has been torn off during processing. Nematocysts of unknown type but probably atrichous isorhizas are very widely scattered in the epidermis of the body wall, not densely clustered in batteries as is the case in Antipatharia (van Pesch 1914).

The mesogloea of the body wall of the polyps is unusual in that it appears to consist of two layers, the inner stained pink as usual in haematoxylin-eosin, the outer, somewhat thinner, dark purple. However, as disruption of tissues during the sectioning process separates the two layers here and there, it is more likely that the darkly stained outer layer is, in fact, a basement membrane of the epidermis.

The gastrodermis of the body wall is unusually thick, in some places nearly or quite as thick as the epidermis, and composed of elongate, spindle-shaped cells. In the immediate vicinity of the mesenteries, narrow ridges of mesogloea extend into the gastrodermis, strongly suggesting the presence of longitudinal muscles.

## Affinities within the Octocorallia

It is not insignificant that the curator of invertebrates of the South Australian Museum associated *Dendrobrachia* with *Chrysogorgia*. Often, superficial similarity may reflect more fundamental relationships.

The absence of calcareous sclerites in *Dendrobrachia* eliminates one of the classic characters in gorgonacean classification, leaving only the nature of the axial supporting skeleton as a clue to relationships. Among the gorgonians, only two species of *Trichogorgia* lack sclerites, one of them having been the basis for the genus *Malacogorgia* and family Malacogorgiidae (Hickson 1904). Apart from the complete absence of calcareous skeleton, *Malacogorgia capensis* is identical to *Trichogorgia flexilis* and both have long been placed in the family Chrysogorgiidae on the basis of the typical chrysogorgiid sclerites of *T. flexilis* (Kükenthal 1924; Bayer & Muzik 1976b). *Trichogorgia viola* Deichmann, 1936, from the Gulf of Mexico is morphologically similar and also has sclerites of the chrysogorgiid type. Colonies of *Trichogorgia lyra* Bayer & Muzik, 1976, from the southwestern Caribbean, which are not unlike *Malacogorgia* (=*Trichogorgia*) *capensis* in some respects, like it lack sclerites but have calcareous deposits in the axis.

Gorgonacean families with an unjointed, more or less calcified axial skeleton without a hollow core are Primnoidae, Ellisellidae, Ifalukellidae, and Chrysogorgiidae. Among these, only *Trichogorgia capensis* in the Chrysogorgiidae has an axis devoid of calcareous deposits.

The axis of *Dendrobrachia* lacks calcification as well as a hollow core, thus resembling that of *Malacogorgia* (=*Trichogorgia*) *capensis* and, like it, also lacks sclerites. Some species of *Plumigorgia* are very scantily provided with sclerites of very small size and considerably different from the prevalent chrysogorgiid type, and *Ifalukella yanii* Bayer has so few as to be virtually sclerite-free. However, both genera are inhabitants of shallow, reef-associated waters, and the axis in both develops a strong, even massive, calcareous holdfast. In the case of *Ifalukella*, the holdfast has conspicuous longitudinal grooves and ridges that are sharply serrate or laciniate, but the arborescent part of the axis is only weakly ridged, as in many other gorgonacean genera (Bayer 1955). The holdfast of *Dendrobrachia* is not calcified and forms a minimally spreading encrustation on solid objects.

Anatomically, the polyps of *Dendrobrachia* agree with those of *Chrysogorgia*, *Stephanogorgia*, *Trichogorgia* and *Ifalukella*. Unfortunately, the anatomy and histology of those genera have not been described, but direct comparison with serial sections of *Chrysogorgia elegans* (Verrill), *Stephanogorgia faulkneri* (Bayer), *Trichogorgia lyra* Bayer & Muzik, and *Ifalukella yanii* Bayer reveals similar features.

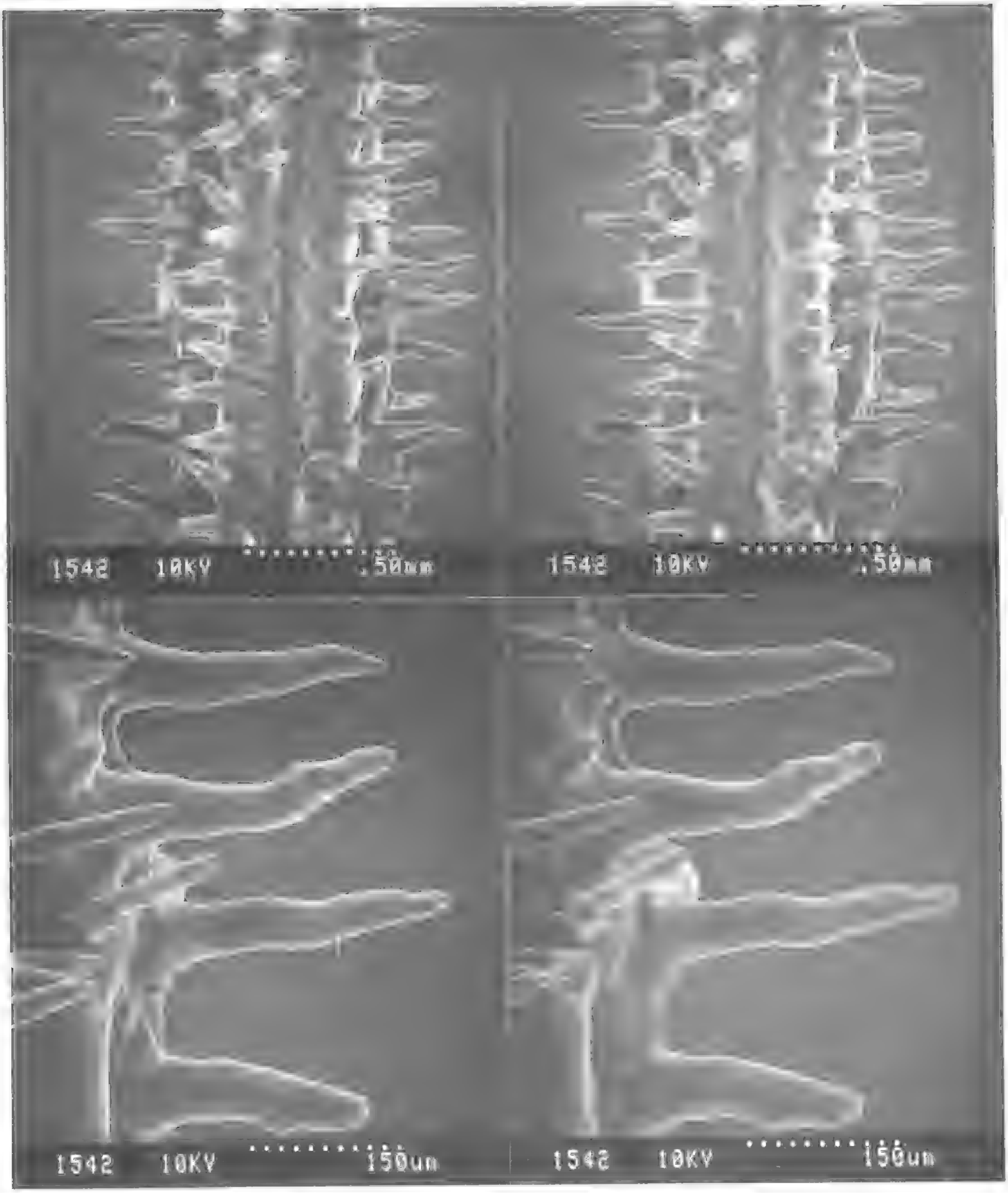


Fig. 11. *Dendrobrachia multispina* sp. nov., axis. Top, lateral view of larger branchlet; bottom, axial spines of same USNM 87770. Stereoscopic pairs, SEM.

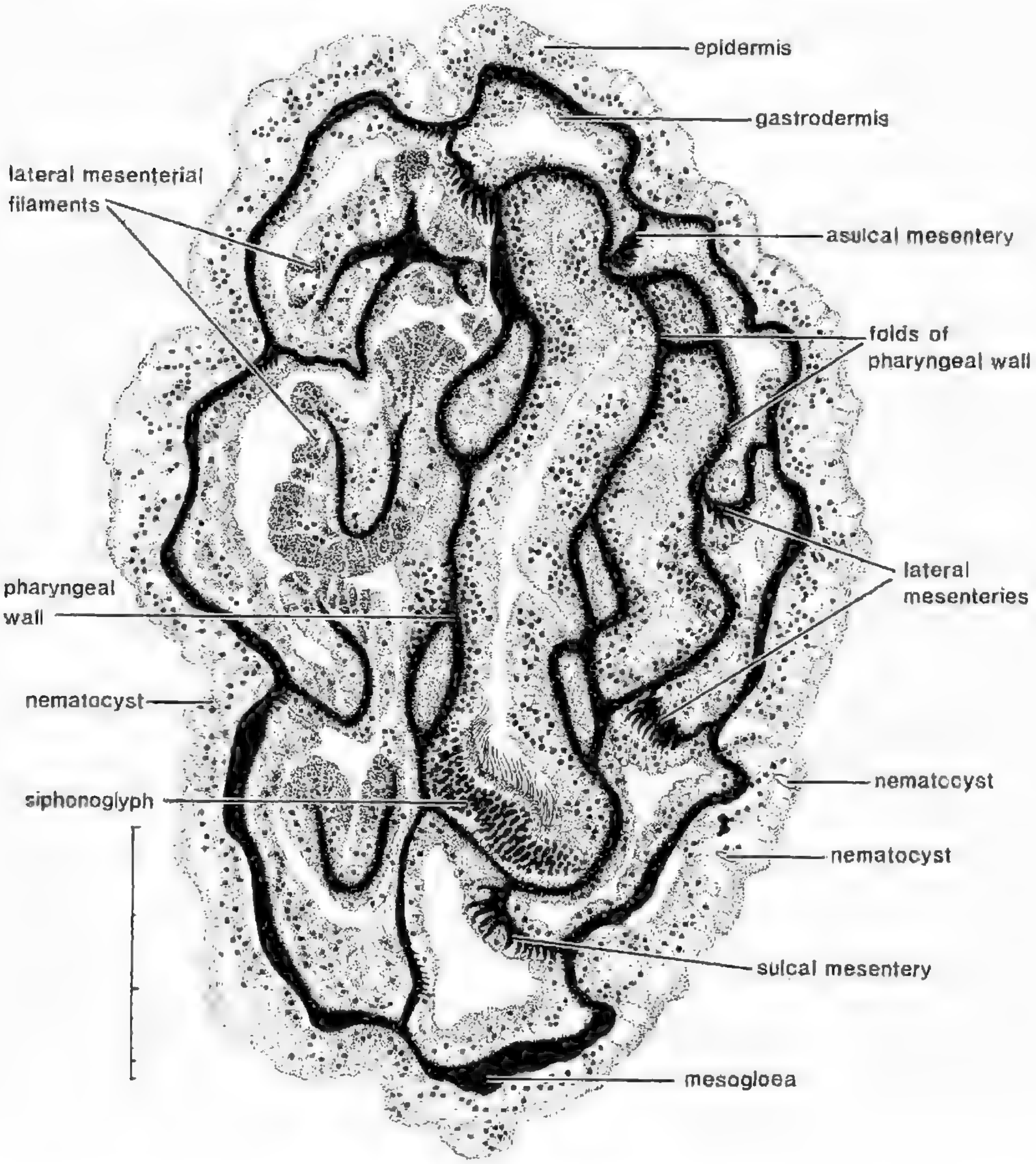
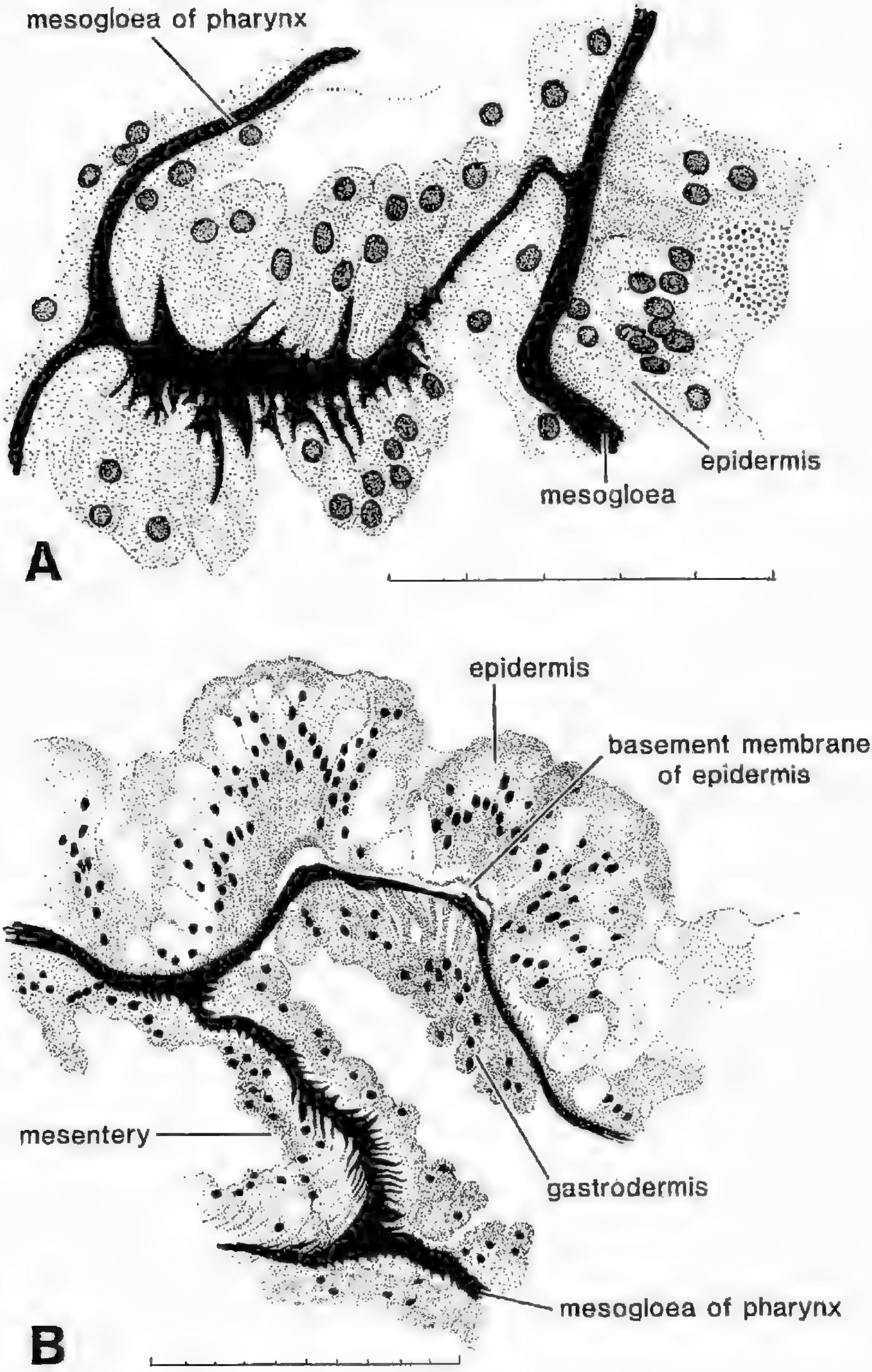


Fig. 12. *Dendrobrachia paucispina* sp. nov. Cross section of polyp, somewhat oblique, at level of pharynx. Scale = 0.15 mm.


mesogloea of pharynx
epidermis
mesogloea
A
epidermis
basement membrane of epidermis
mesentery
gastrodermis
mesogloea of pharynx
B

In spite of the general similarity of the polyps of *Dendrobrachia* with those of the uncalcified species of Chryosogorgiidae, the unique nature of the axial skeleton convinces us that the family Dendrobrachiidae should be maintained, at least until material becomes available for a more comprehensive investigation and comparison of anatomical and histological features of all the species involved.

## Acknowledgments

We would like to thank Mr Shane Parker of the South Australian Museum for providing the specimens of *Dendrobrachia paucispina*, Dr Esther Peters for preparing the histological sections, Ms Cynthia Ahearn for critical-point drying of polyp material for whole mount preparations, and Mr Walter Brown, chief of the SEM laboratory at the U.S. National Museum, for taking the SEM photographs. This work was supported by the Smithsonian Institution, Washington, D.C. and by Oak Ridge National Laboratory, Oak Ridge, Tennessee. The Australian material was collected during the South Australian Museum's continuing deep-sea trawling programme, undertaken with the generous cooperation of the masters and crew of numerous trawlers and research vessels. The specimen of *Dendrobrachia multispina* trawled in the Straits of Florida by R/V "Gerda" was obtained during the DeepSea Biology Programme of the University of Miami, supported by the U.S. National Science Foundation and the National Geographic Society.

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Fig. 13. *Dendrobrachia paucispina* sp. nov., A. Cross section of body wall with mesentery showing longitudinal mesogloeal plates for insertion of retractor muscles on both faces; B. Cross section of body wall showing epidermal lobes and mesentery with longitudinal mesogloeal plates for retractor muscles on both faces. Scale at A = 0.05 mm; scale at B = 0.1 mm.

# THE DISPERSED CUTICULAR FLORAS OF SOUTH AUSTRALIAN TERTIARY COALFIELDS, PART 1: SEDAN

*BY A. I. ROWETT**

## Summary

Dispersed cuticles were recovered from the three seams of the Sedan Coalfield and sixty-two parataxa have been identified. The floras of the two younger lignite seams are distinct from the underlying lignitic clay. The lignites are dominated by Proteaceae cuticle types with one cuticle type, identified as the cuticle of *Banksieaephyllum laeve,* i.e. *Banksieaephyllum* aff. B. *laeve* in abundance. The older lignite seam is distinguished by a large monospecific Myrtaceae component and a cuticle type identified as aff. *Agathis* (Araucariaceae). Other families represented in both seams include the Casuarinaceae, Elaeocarpaceae, Myrtaceae and Podocarpaceae. The flora of the under-lying lignitic clay is dominated by Lauraceae cuticle types.

The presence of *Banksieaephyllum* aff. B. *laeve* in the Sedan lignites suggests either an Oligocene-Miocene age for the lithotype or a longer stratigraphic range (extended lower limit) for the leaf-fossil.

KEY WORDS: Palaeobotany, Tertiary, Eocene, dispersed cuticles, Sedan, South Australia

*Transactions of the Royal Society of S. Aust.* (1991), 115(1), 21-36.

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ROWETT, A. I. (1991) The dispersed cuticular floras of South Australian Tertiary Coalfields, Part 1 Sedan. *Trans. R. Soc. S. Aust.* 115(1), 21–36, 31 May, 1991.

Dispersed cuticles were recovered from the three seams of the Sedan Coalfield and sixty-two parataxa have been identified. The floras of the two younger lignite seams are distinct from the underlying lignitic clay. The lignites are dominated by Proteaceae cuticle types with one cuticle type, identified as the cuticle of *Banksieaephyllum laeve*, i.e. *Banksieaephyllum* aff. *B. laeve* in abundance. The older lignite seam is distinguished by a large monospecific Myrtaceae component and a cuticle type identified as aff. *Agathis* (Araucariaceae). Other families represented in both seams include the Casuarinaceae, Elaeocarpaceae, Myrtaceae and Podocarpaceae. The flora of the under-lying lignitic clay is dominated by Lauraceae cuticle types.

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KEY WORDS: Palaeobotany, Tertiary, Eocene, dispersed cuticles, Sedan, South Australia

## Introduction

There are numerous coalfields found throughout South Australia ranging in age from Permian to Tertiary. The Tertiary deposits represent large resources of low-rank coal (lignite) of Middle to Late Eocene age that are distributed throughout sedimentary basins in the southern part of the State (S.A.D.M.E. 1987). These deposits include the Lochiel, Clinton, Beaufort, Bowmans and Whitwarta deposits of the Northern St Vincent Basin, Kingston in the south-east and the Anna and Sedan deposits on the edge of the Murray Basin. Three of these localities, Sedan, Lochiel and Kingston, are the subject of this study.

Previous dispersed cuticle investigations, the majority of which have been undertaken in the northern hemisphere (e.g. Peters 1963; Schneider 1969; Kovach & Dilcher 1984; Rowett 1986[1]) have revealed that lignites generally contain an abundance of cuticle fragments which can be assigned to either natural or form taxa. These data may subsequently provide information about the source vegetation associated with the formation of the specific lithotype as well as the past environment and climate. Such information is currently being used by the author in the correlation and dating of coal deposits.

The Sedan coalfield is located 75 km northeast of Adelaide (34° 34', 139° 18') on the margin of the Murray Basin, between the Mount Lofty Ranges and the River Murray (Fig. 1). Exploration in the vicinity of the nearby Anna deposit dates back to the 1920's but it was not until 1979 that the Sedan lignite was discovered. The deposit lies in a north-trending trough 5 km wide and 13 km long and comprises two main lignite seams. The upper seam, which is the most economically viable, is continuous and up to 8 m thick. The lower seam is lenticular and averages 5 m in thickness (S.A.D.M.E. 1987). Tertiary foraminiferal biostratigraphy (McGowran 1989) and a preliminary palynological analysis (N.F. Alley, S.A.D.M.E. pers. comm.) have dated the lignites as Late Eocene-Oligocene.

## Materials and Methods

Drill core samples from both seams and the underlying lignitic clay taken from Sedan core CSR CO74B (7.5 cm diameter), housed in the S.A.D.M.E. core library are used in this investigation. Examination of these samples revealed considerable amounts of heavily carbonised dispersed cuticle and wood fragments. Cuticle fragments were extracted from 100g of matrix by modifying the maceration technique outlined by Christophel *et al.* (1987) to include an additional preliminary step whereby the crushed sample is placed in warm Schulze solution for approximately four hours prior to a dilute (50%) hydrogen peroxide solution step. The use of an additional oxidizing step assures the removal of any organic material from the cuticle and makes possible more accurate identifications and descriptions of cuticle types. The cuticle fragments were collected by passing the maceral through a

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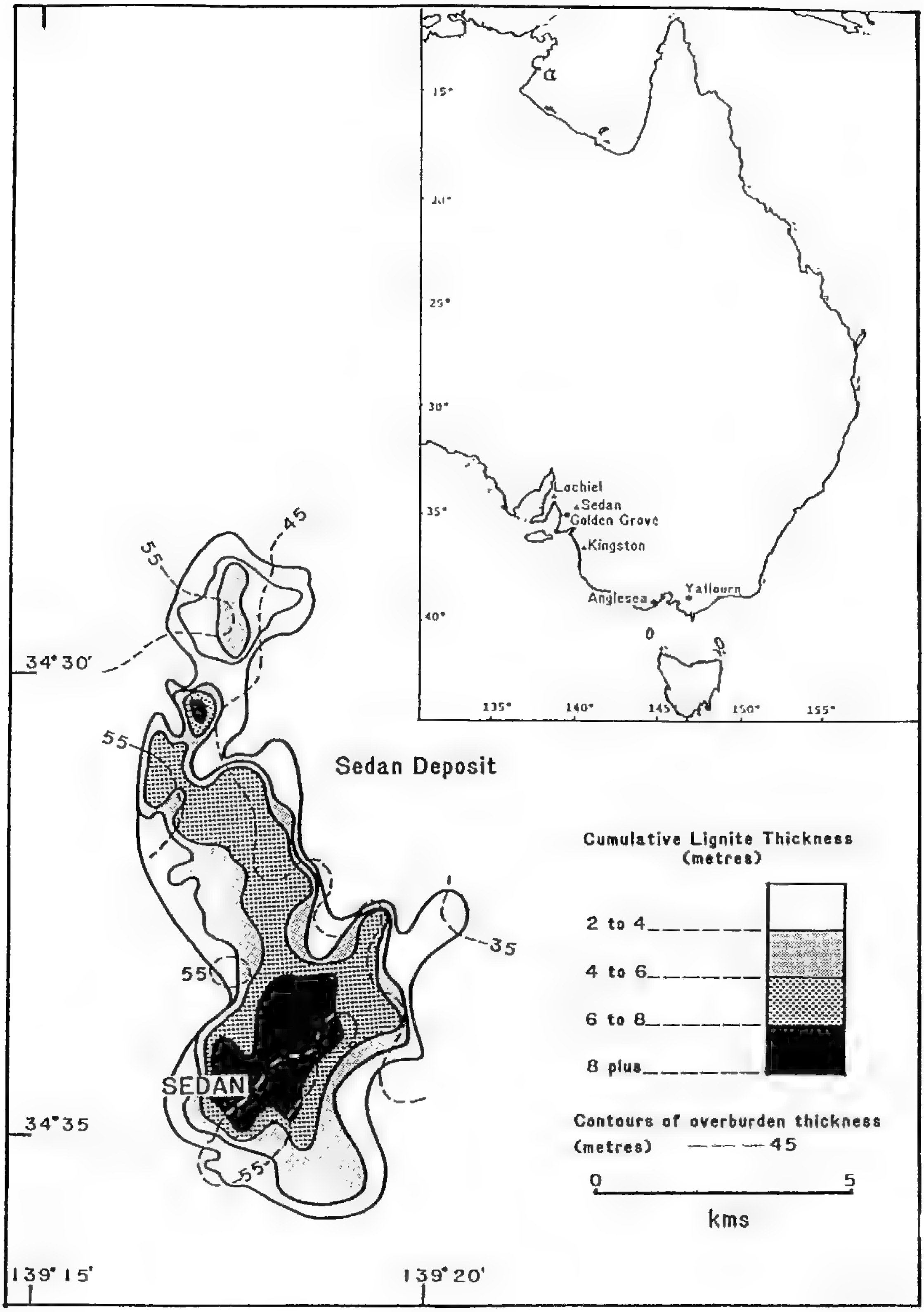
[1] Rowett, A. I. (1986) Megafossil and Microfossil Floras of the Curlew Formation, Queensland. Ph.D. thesis, Botany Dept., University of Adelaide. Unpubl.


Sedan Deposit
Cumulative Lignite Thickness (metres)
2 to 4
4 to 6
6 to 8
8 plus
Contours of overburden thickness (metres) 45
0
5
kms
SEDAN
34°30'
34°35
139°15'
139°20'
55
45
35
Lochiel
Sedan
Golden Grove
Kingston
Anglesea
Yallourn
15°
20°
25°
30°
35°
40°
135°
140°
145°
150°
155°

single fine pore sieve (150 $\mu$m diameter pore). The use of a multiple sieve series was considered unnecessary because of the small range in fragment size; none of the cuticles were greater than 2 mm$^2$. Examination of the cuticles revealed that no single cuticle parataxon was size specific.

Only cuticle types (parataxa) that displayed stomates were considered in the overall analysis as the stomatal features are often diagnostic of a particular plant family, thereby greatly improving the chances of determining the modern affinities of fossil cuticles.

Five replicate samples of 200 cuticle fragments each (Rowett & Christophel 1990) were obtained from core material recovered from three depths, 54.8 m (upper seam), 67.5 m (lower seam) and 75.3 m (lignitic clay). The frequency data presented for both individual parataxa and modern families (i.e. Table 1) is a percentage calculated from the total of the five replicates of each lithotype.

### The Dispersed Cuticle Flora

The three samples that contribute to the Sedan cuticle flora are separated by substantial intervals (approx. 10 m) of barren sediment (K. Wigglesworth, S.A.D.M.E. pers. comm.).

*Lignitic Clay:* The flora of the basal lignitic clay is dominated by the Lauraceae which forms 83.0% of the total cuticle sample (Table 1). This component is particularly diverse, containing 11 parataxa, of which the most frequent are parataxa No. AA 006 (30% of total sample; Figs 4 & 5) and No. S5 005 (19% of total sample; Figs 6 & 7). A number of these Lauraceae parataxa show possible affinities to the extant genera *Endiandra* and *Cryptocarya*. In *Endiandra* the epidermal cells are angular in appearance with irregularly thickened anticlinal walls, stomates are generally elongate with narrow but prominent cuticular scales (eg. No. AA 007, Fig. 2). These scales lie between the sunken guard cells and the overlying subsidiary cells. *Cryptocarya* is generally characterised by epidermal cells with smooth anticlinal walls of uniform thickness. Stomates are generally rounded with prominent reniform cuticular scales. These scales are dark-staining and give a butterfly-like appearance to the stomata (No. AG 005, Fig. 3).

The Myrtaceae component (3.1%) is represented in the flora by the cuticle types No. LC 011 (Figs 8 & 9) and No. S5 004 (Figs 11 & 12), with the latter being the most abundant. The most distinctive cuticular feature of the Myrtaceae is the oil gland lid cell. These cells, which may occur on either/or both cuticular surfaces, are generally isodiametric, divided by a curved to sinuous sinus, surrounded by a number of concentric circles of radially arranged epidermal cells and display some degree of cuticular thickening.

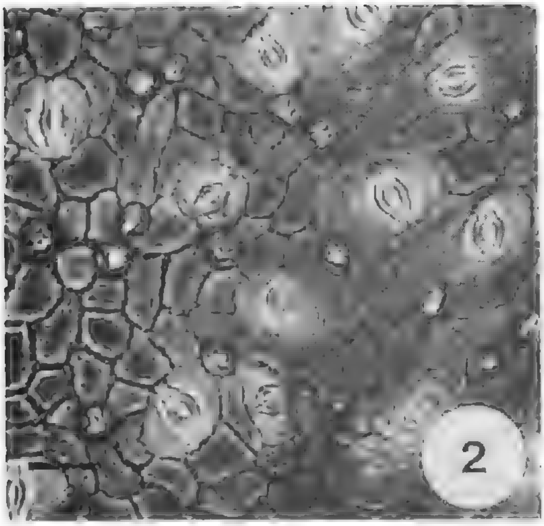
*Falcatifolium* aff. *F. australis* Greenwood (Figs 13 & 14) is the principal contributor to the small Podocarpaceae component (0.8%). The parataxon is suggested as having an affinity to *Falcatifolium australis* on the basis of the circular appearance of the stomata, a feature considered to be distinctive by Greenwood (1987), who first identified the species from the Upper Middle Eocene fossil flora of the Anglesea locality. A very small Proteaceae component (0.2%) is also present in this lithotype.

*Lower Lignite Seam:* The cuticle flora of the lower lignite seam is significantly different from that of the underlying clay. The most obvious differences include the replacement of the Lauraceae as the principal floristic component by the Proteaceae; the

TABLE 1. *The cuticle frequencies (%) of extant plant families represented in the three Sedan lithological units. The families represented are Podocarpaceae (POD), Araucariaceae (ARAUC), Myrtaceae (MYRT), Elaeocarpaceae (ELAEO), Proteaceae (PROT), Lauraceae (LAUR), Casuarinaceae (CAS). The OTHERS category represents all other cuticle parataxa whose modern family affinities are unknown.*

| LOCALITY | POD | ARAUC | MYRT | ELAEO | PROT | LAUR | CAS | OTHERS |
|---|---|---|---|---|---|---|---|---|
| SEDAN 54.68 m | 2.1 | – | 0.4 | 1.3 | 93.0 | 0.7 | 0.1 | 2.2 |
| SEDAN 67.50 m | 3.0 | 2.0 | 14.5 | 9.0 | 40.4 | 0.5 | 0.5 | 29.6 |
| SEDAN 75.30 m | 0.8 | – | 3.1 | 0.4 | 0.2 | 83.0 | – | 12.5 |

Fig. 1. Map showing the extent and thickness of lignite in the Sedan deposit. The town of Sedan is situated above the deposit. Inset: Map of eastern Australia showing the location of the Sedan, Lochiel and Kingston coal localities relative to the Tertiary Megafossil localities of Golden Grove (Eocene), Anglesea (Eocene) and Yallourn (Oligocene)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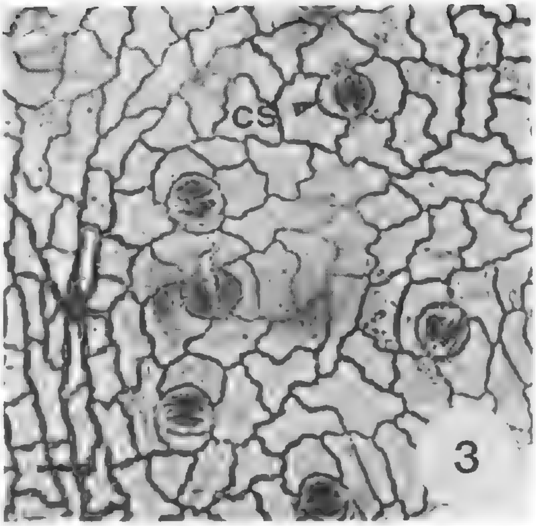
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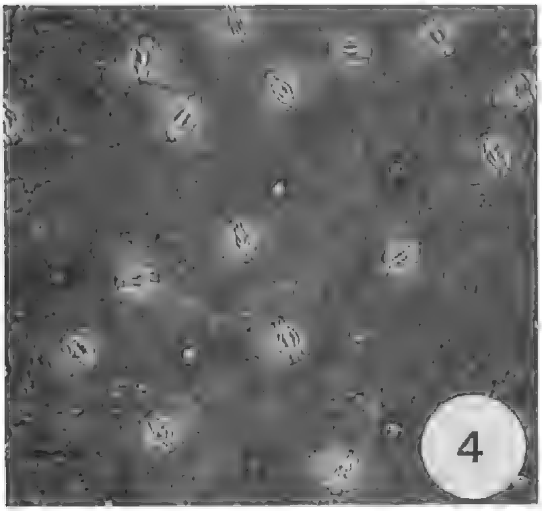
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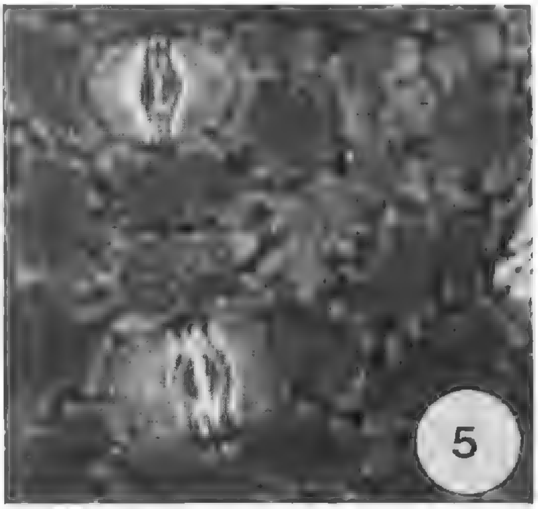
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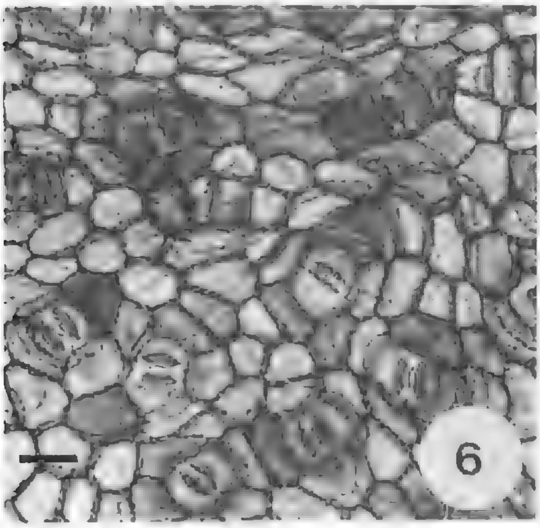
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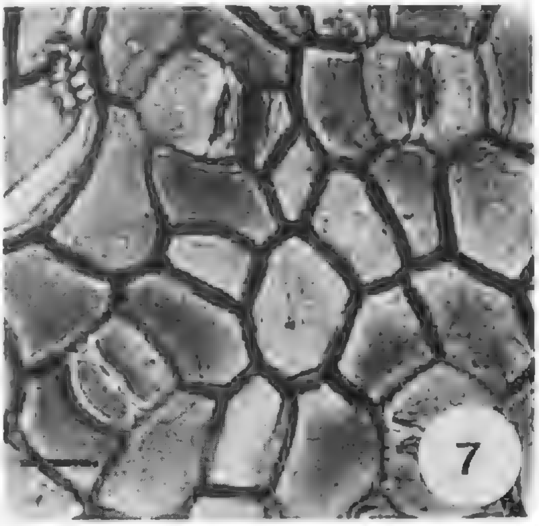
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presence of an Araucariaceae and Casuarinaceae component and increased abundances in the Myrtaceae and Podocarpaceae components. The Elaeocarpaceae is present for the first time.

As stated above, the flora is dominated by the Proteaceae with parataxon No. S1 001 the major contributor. Parataxon No. S1 001 (Figs 17 & 18) has a very distinctive cuticle with slightly raised brachyparacytic stomates, small simple hairs associated with a single epidermal cell which are common over the stomatiferous surface and large multicellular hair bases. These features are characteristic of the cuticle of the fossil leaf genus, *Banksieaephyllum* (Proteaceae). The genus was first used to describe six fossil leaf species, i.e. *B. angustum*, *B. acuminatum*, *B. laeve*, *B. obovatum*, *B. pinnatum* and *B. fastigatum*, with affinities to the modern genera *Banksia* and *Dryandra* (Cookson & Duigan 1950). These leaves were recovered from the Oligocene aged brown coal seam at Yallourn, Victoria. At present eleven species of *Banksieaephyllum* are recognised. These species have all been recovered from southeastern Australian localities ranging from Early Eocene to Early Miocene in age and include, the Middle Eocene Maslin Bay deposit (Blackburn 1981; Hill & Christophel 1988), Early Eocene Deans Marsh, late Middle Eocene Anglesea, Middle Eocene Golden Grove, Late Eocene-Oligocene Cethana, Middle-Late Eocene Loch Aber, Oligocene Pioneer, Oligocene-Early Miocene Loy Yang (Hill & Christophel 1988) and Miocene Morwell (Blackburn 1985[2]). Of the eleven described species, cuticle of *Banksieaephyllum laeve* from the Yallourn Oligocene brown coal flora (Cookson & Duigan 1950) and Miocene flora of the Morwell seam at Morwell most closely resembles parataxon No. S1 001.

The increased Myrtaceae component (14.5%) is represented in the flora by a single parataxon No. S3 001 (Figs 15 & 16). This parataxon only occurs in this lithotype and is distinct from the other Sedan Myrtaceae by the robust nature of the generally larger cuticular features.

The Casuarinaceae component, although a minor contributor to the overall flora, is important in that the presence of the parataxon No. DM 007 (Figs 19 & 20), identified as *Gymnostoma* is the first dispersed cuticle record of the occurrence of this well known Tertiary genus outside of eastern Australia. The cuticle of this parataxon is very distinctive with stomates oriented perpendicular to the longitudinal axis of the epidermal cells. The stomates may have one or two lateral subsidiary cells. The genus was first reported from the Anglesea deposit by Christophel (1980) as a megafossil of the Casuarinaceae, Division Gymnostomae, and has since been discovered in the floras of a number of Tertiary plant fossil localities which range from Middle Eocene to Miocene and include Deans Marsh (Middle Eocene), the Curlew Formation (Middle Eocene), Moranbah (Middle Eocene; Scriven & Christophel 1990), and Yallourn and Morwell open cut mines (Oligocene-Miocene, Blackburn 1985). *Gymnostoma* cone impressions have also been identified in the silcretes of the Eyre Formation (Late Palaeocene-Eocene), Willilinchina Sandstones (Eocene) and Etadunna Formation (Oligo-Miocene) (Greenwood *et al.*[3]).

Parataxon No. AWF 001 (Figs 21 & 22), the sole representative of the Araucariaceae component is only found in this lithotype and may therefore prove to be a useful local stratigraphic indicator. This cuticle type is tentatively assigned to *Agathis* on the basis of the oblique orientation of stomata and the curved to rounded nature of the epidermal cells.

The large Elaeocarpaceae component (9.5%) is represented in this lithotype by two cuticle types Nos. S3 004 (Figs 23 & 24) and S3 005 (Fig. 25), the former being the major contributor with 8.0% of the cuticle sample. Both parataxa occur for the first time in the Sedan deposit. Features of the cuticle which are considered characteristic of the family are the presence of hydathodes (Blackburn 1985), staurocytic stomates and a prominent, narrow outer stomatal ledge which bears small polar extensions, termed an apiculate outer stomatal ledge by Wilkinson (1979).

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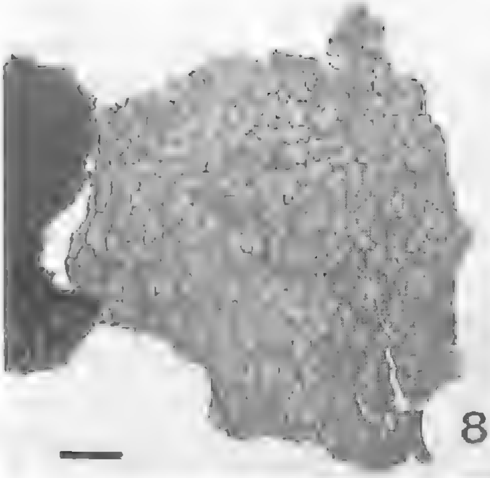
[2] Blackburn, D. T. (1985) Palaeobotany of the Yallourn and Morwell coal seams. Palaeobotany Report No. 3, State Electricity Commission of Victoria. Unpubl.

[3] Greenwood, D. R., Callen, R., & Alley, N. F. (1990) Biostratigraphy of the Cainozoic Macroflora of the southern Eyre Basin in South Australia. Report, South Australian Department of Mines and Energy. Unpubl.

Figs 2–7. 2. Parataxon No. AA 007, aff. *Endiandra*, Lauraceae. The presence of prominent, narrow cuticular scales and angular epidermal cells are features associated with the extant genus. Scale = 20 μm. 3. Parataxon No. AA 005, aff. *Cryptocarya*, Lauraceae. The presence of prominent reniform to crescent-shaped cuticular scales (i.e. cs, arrowed) which give the stomatal apparatus a butterfly like appearance, stomata and undulate epidermal cells are features associated with the extant genus. Scale = 24 μm. 4. Parataxon No. AA 006, Lauraceae, showing stomatiferous surface. Note the sinuous nature of the epidermal cells and poral trichome bases. Scale = 20 μm. 5. Parataxon No. AA 006, Lauraceae, showing the paracytic stomatal arrangement and prominent cuticular scales. Scale = 12 μm. 6. Parataxon No. AA 008 aff. *Cryptocarya*, Lauraceae, showing stomatiferous surface. Note the smooth, uniformly thickened antichinal walls of the epidermal cells. Scale = 20 μm. 7. Parataxon No. AA 008 aff. *Cryptocarya*, Lauraceae showing paracytic stomatal arrangement and crescent shaped to reniform cuticular scales. Scale = 20 μm.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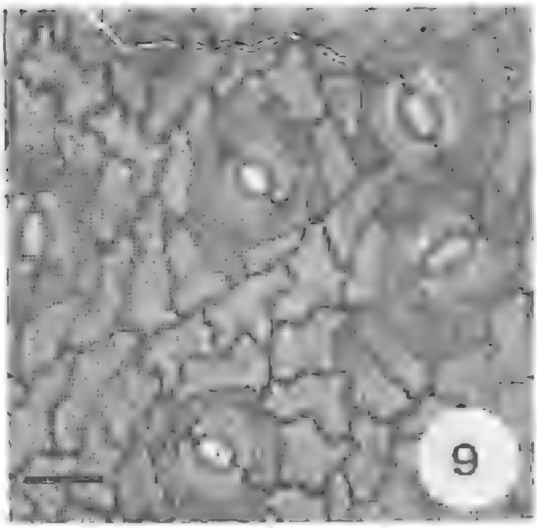
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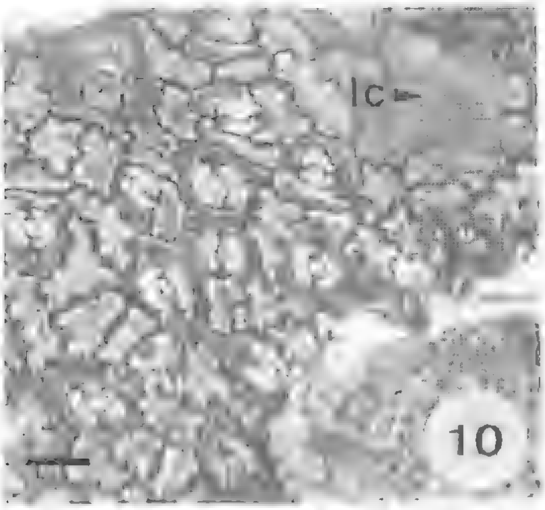

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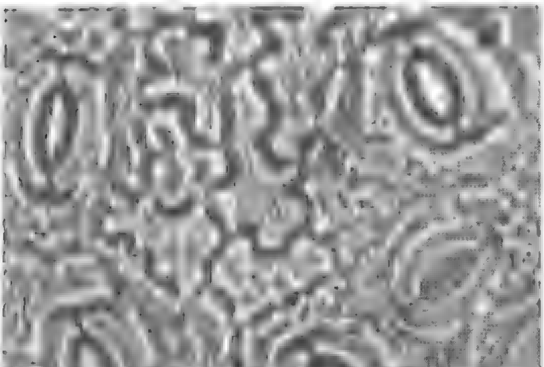
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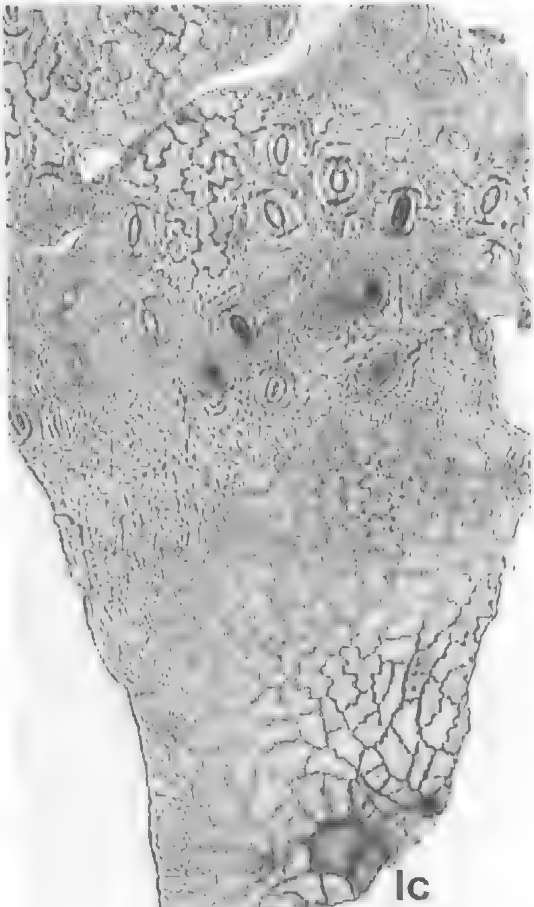

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Although showing an increased abundance (3.0%), with the introduction of parataxon No. LE 009 (Fig. 26), the Podocarpaceae component remains a minor contributor at this depth. Parataxon No. LE 009 is easily distinguished from *Falcatifolium* aff. *F. australis* by the strong buttressing of anticlinal walls of the epidermal cells.

*Upper Lignite Seam:* The upper seam flora, is the most diverse with 30 parataxa represented, the majority of which are recognised as having affinities with the families, Proteaceae, Elaeocarpaceae, Myrtaceae, Podocarpaceae, Lauraceae and Casuarinaceae. The Proteaceae dominates the flora (93.0%) with two parataxa, *Banksieaephyllum* aff. *B. laeve* and parataxon No. S1 003 (Figs 27 & 28), in particular abundance. The only other families of any significance in the flora are the Podocarpaceae and Elaeocarpaceae which record frequencies of 2.1% and 1.3%, respectively. The Podocarpaceae component shows an increased diversity in this seam with six parataxa represented. The parataxa which dominated the component of the other floras, i.e. *Falcatifolium* aff. *F. australis* and parataxon No. LE 009, are again the major contributors in this lithotype. The small Myrtaceae component is marked by the reappearance of parataxon No. LC 011

Four different cuticle types comprise the Elaeocarpaceae component with parataxon No. ALL 011 the most abundant. Cuticles taken from mummified leaves ascribed by Christophel & Greenwood (1987) to *Sloanea/Elaeocarpus* from Golden Grove and leaf type "Serrate 1" described by Christophel *et al.* (1987) from Anglesea are identical to those identified as parataxon No. ALL 011 in the Sedan flora (Fig. 29).

## **Dispersed Cuticle Descriptions**

The dispersed cuticle flora of the Sedan coalfield is represented by 62 cuticle parataxa but for the purpose of this paper only the principle cuticle parataxa, stratigraphically significant parataxa and those with known modern affinities are described here. Several of the parataxa have been previously identified by the author from other Eocene localities. These and many more are included in the NERDDC reference catalogue of Australian Eocene cuticle types. All parataxon numbers are preceded by an abbreviation of the type locality.

The terminology used in the description of the Sedan cuticle parataxa has been derived from that proposed by Stace (1965), Dilcher (1974) and Wilkinson (1980).

### Cuticle Parataxon No. AA 007
### FIG. 2

Only the stomatiferous surface was observed. Epidermal cells angular to rounded (type 1-2, Wilkinson 1979), becoming elongate over the veins. Cells 8-24 μm in length, 6-16 μm in width. Anticlinal wall irregularly thickened, smooth (uniform thickness) to slightly beaded. Periclinal wall irregularly thickened, smooth to finely granulate. Stomata randomly oriented, uniform distribution. Stomata 16-24 μm in length, 6-16 μm in width. Guard cells, sunken, cuticular thickening on poral wall. Cuticular scales (i.e. labelled CS2 on Fig. 1, Hill 1986), prominent, narrow. Stomatal Arrangement paracytic. Stomatal Index (S.I.) 11.4. Subsidiary cells cells 2. Anticlinal wall, thin, smooth. Periclinal wall thin, smooth.

Trichome bases common, uniform distribution, poral, 4-8 radially arranged surrounding cells, cuticular thickening around pore extending along radial wall of surrounding cells giving stellate appearance.

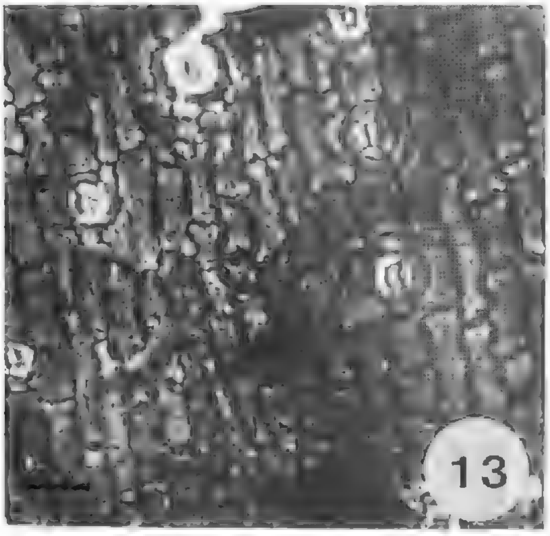
*Affinity:* The parataxon is assigned to the Lauraceae, with a probable affinity to the extant genus *Endiandra*. The modern Australian species of this genus are characterised by predominantly angular epidermal cells with irregularly thickened anticlinal walls, elongate stomates with prominent, though narrow cuticular scales.

### Cuticle Parataxon No. AG 005
### FIG. 3

Only the stomatiferous surface was observed. Epidermal cells undulate to sinuous (type 3-5), becoming elongate over the veins. Cells 20-40 μm in length, 12-20 μm in width. Anticlinal wall thin, smooth. Periclinal wall irregularly thickened, smooth to finely granulate (occasionally finely striate).

Stomata randomly oriented, uniform distribution. Stomata 16-24 μm in length, 12-20 μm in width Guard cells, sunken, cuticular thickening on poral wall. Guard cell/subsidiary cell wall not always

Figs 8-12. 8, Parataxon No. LC 011, Myrtaceae. The dark-staining subsidiary cells and the sinuous nature of the epidermal cells characterise this parataxon. Identical in cuticular morphology to specimens from Lochiel. Scale = 20 μm 9, Parataxon No. LC 011, Myrtaceae, showing staurocytic stomatal arrangement. Scale = 20 μm. 10. Specimen of Parataxon No. LC 011, Myrtaceae from Lochiel, note the same cuticular morphology as the Sedan specimens and the presence of an oil gland lid cell (i.e. lc, arrowed). Scale = 20 μm. 11. Parataxon No. S5 004, Myrtaceae, showing stomatal arrangement. Note the strongly striate periclinal wall of the epidermal cells. Scale = 10 μm 12. Parataxon No. S5 004, Myrtaceae, showing a heavily cutinized oil gland lid cell (lc, arrowed). Scale = 20 μm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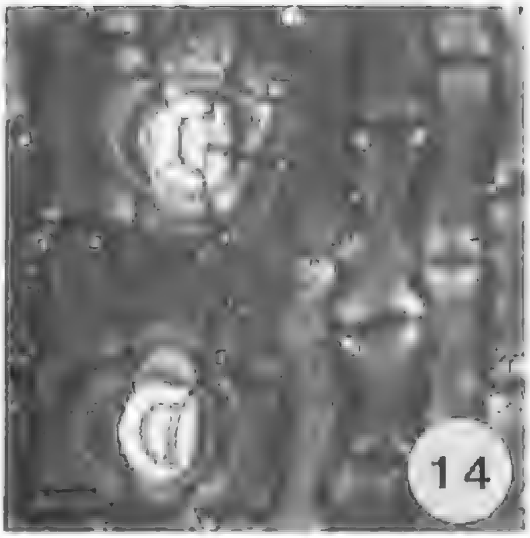
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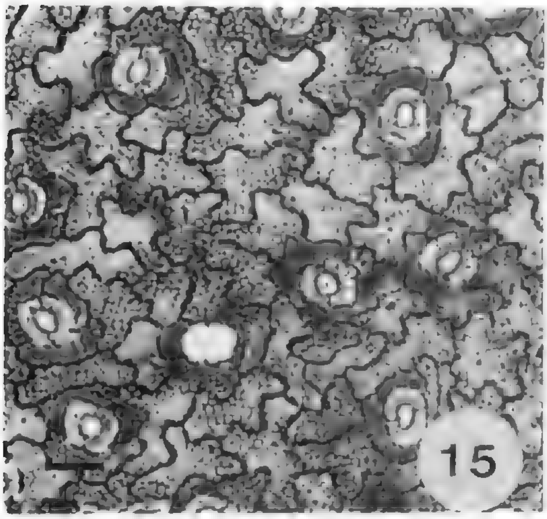
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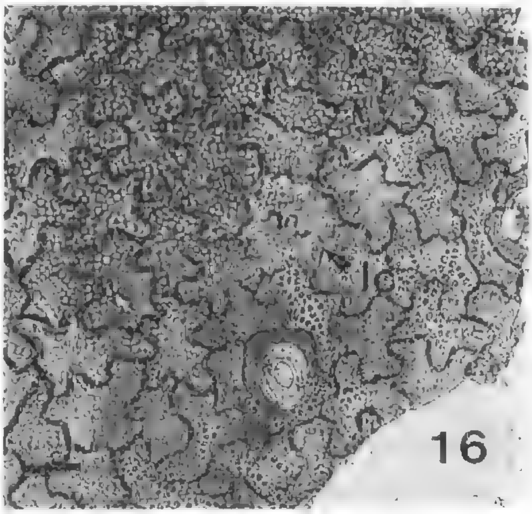
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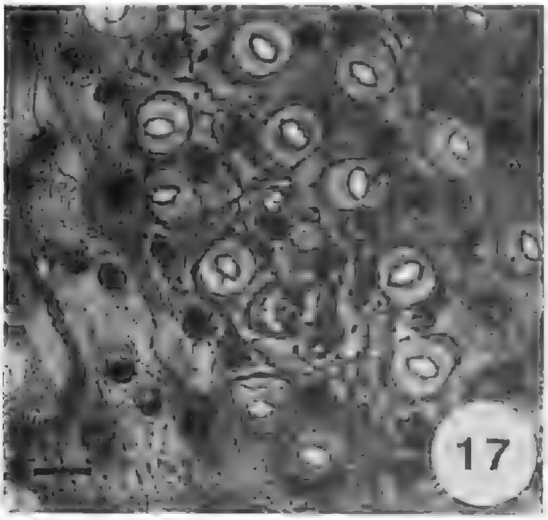
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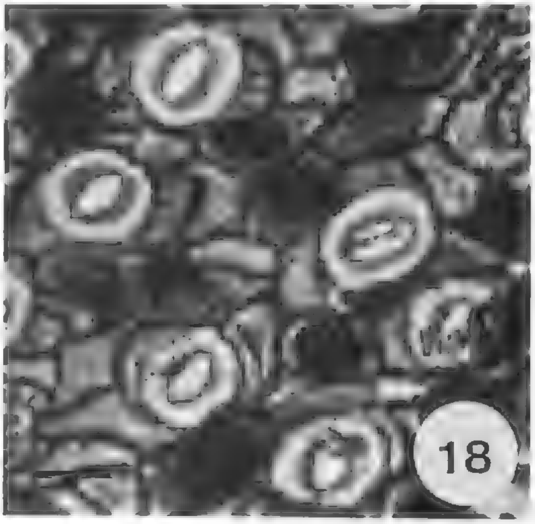
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evident (in which case the stomatal width dimension is taken as a measure across the two subsidiary cells, instead of the usual guard cell width). Cuticular scales, prominent, reniform to crescent-shaped, giving a butterfly-like appearance to the stomate. Stomatal Arrangement paracytic, S.I. 6.2. Subsidiary cells two. Anticlinal wall smooth, thicker than for epidermal cells and raised which produces a cuticular fold that encircles and partially overlies the stomate. Periclinal wall thin, smooth.

Trichome bases common, uniform distribution, poral, 4-8 radially arranged surrounding cells, cuticular thickening around pore.

*Affinity:* The cuticle parataxon is assigned to Lauraceae with a probable affinity to the extant genus *Cryptocarya*. The modern Australian species of this genus are characterised by epidermal cells with smooth anticlinal walls; shape is variable. Stomates are generally rounded with prominent reniform to crescent-shaped cuticular scales which gives a butterfly-like appearance to the stomatal apparatus.

### Cuticle Parataxon No. AA 006
FIGS 4–5

Only the stomatiferous surface was observed. Epidermal cells rounded to sinuous (type 2–5), becoming elongate over the veins. Cells 12–36 μm in length, 8–20 μm in width. Anticlinal wall irregularly thickened, smooth to ridged (Dilcher; 1974). Periclinal wall irregularly thickened, smooth to granulate.

Stomata randomly oriented, uniform distribution. Stomata 16–20 μm in length, 8–10 μm in width. Guard cells, sunken, cuticular thickening on poral wall. Cuticular scales, prominent, narrow. S.I. 9.5. Stomatal Arrangement paracytic. Subsidiary cells 2. Anticlinal wall irregularly thickened, smooth to beaded. Periclinal wall irregularly thickened, smooth to granulate.

Trichome bases common, uniform distribution, poral, 5–6 radially arranged surrounding cells, cuticular thickening around pore.

*Affinity:* The cuticle is assigned to the Lauraceae due to the presence of paracytic stomates and inconspicuous, sunken guard cells.

### Cuticle Parataxon No. S5 005
FIGS 6–7

Only the stomatiferous surface was observed. Epidermal cells angular, becoming elongate over the veins. Areoles are well-defined. Cells 16–32 m in length, 8–20 m in width. Anticlinal wall thin, smooth (occasionally buttressed). Periclinal wall irregularly thickened, smooth to granulate to striate.

Stomata randomly oriented, uniform distribution. Stomata 18–24 m in length, 16–28 m in width. Guard cells, sunken. Guard cell/subsidiary cell wall absent (in which case the stomatal width dimension is taken as a measure across the two subsidiary cells, instead of the usual guard cell width). Cuticular scales, prominent, reniform to crescent-shaped. Stomatal Arrangement paracytic. S.I. 8.6. Subsidiary cells 2. Anticlinal wall thin, smooth. Periclinal wall irregularly thickened, smooth to granulate to finely striate. Striations generally perpendicular to the long axis of the stomate. Epidermal cells that immediately surround the stomate are occasionally dark-staining. Trichome bases are rare, only found over veins. Poral with 4–6 radially arranged surrounding cells. Bases are thickened around the pore.

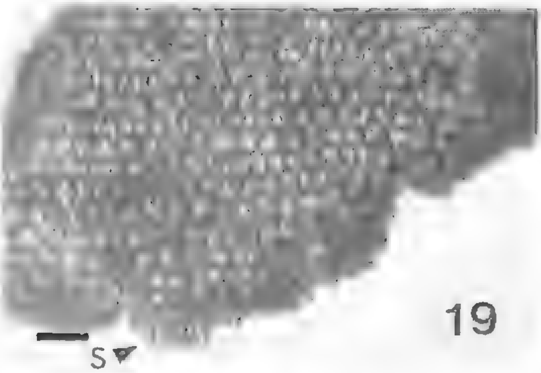
*Affinity:* The cuticle parataxon is assigned to the Lauraceae with a probable affinity to the extant genus *Cryptocarya* due to the presence of epidermal cells with predominantly smooth anticlinal walls and reniform to crescent-shaped cuticular scales.

### Cuticle Parataxon No. LC 011
FIGS 8–9

Only the stomatiferous surface was observed. Epidermal cells undulate to sinuous (type 3–5), becoming elongate over the veins. Cells 16-32 m in length, 10–24 m in width. Anticlinal wall irregularly thickened, smooth to beaded to slightly buttressed. Periclinal wall thin, smooth.

Stomata randomly oriented, uniform distribution. Stomata 16–32 m in length, 16–24 m in width. Guard cells, sunken, T-shaped thickening and polar rods present. Outer stomatal ledge, prominent, narrow. Stomatal Arrangement staurocytic (to cyclocytic). S.I. 10.6. Subsidiary cells 3-6, darker staining. Anticlinal wall irregularly thickened,

Figs 13-18 13. Parataxon No. ABD 001, *Falcatifolium* aff. *F. australis*, Podocarpaceae, showing arrangement of stomata in short uniseriate row. Scale = 32 μm. 14. Parataxon No. ABD 001, *Falcatifolium* aff. *F. australis*, Podocarpaceae. Note the shape of the subsidiary cells and the resultant circular appearance of stomata. Scale = 26 μm. 15. Parataxon No. S3 001, Myrtaceae, showing the stomatiferous surface. Note the dark-staining subsidiary cells. Scale = 30 μm. 16. Parataxon No. S3 001, Myrtaceae, showing an oil gland lid cell (arrowed). Note the sinuous nature of the lid cell sinus. Scale = 30 μm. 17. Parataxon No. S1 001, *Banksieaephyllum* aff. *B. laeve*, Proteaceae, showing the stomatiferous surface. Scale = 20 μm. 18. Parataxon No. S1 001, *Banksieaephyllum* aff. *B. laeve*, Proteaceae, showing the stomatal arrangement. Note the short, cylindrical papillae are present on most epidermal cells. The stomata appear slightly raised above the cuticle surface. Scale = 17 μm.



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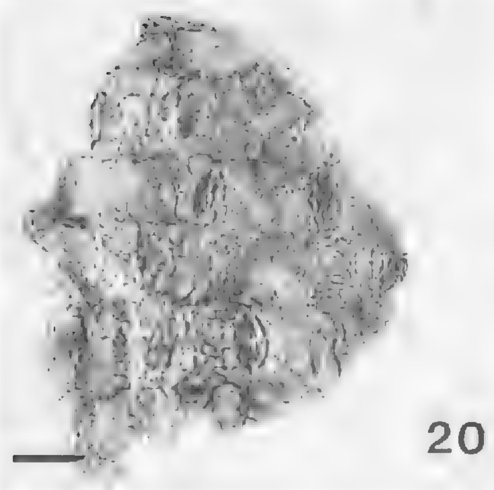

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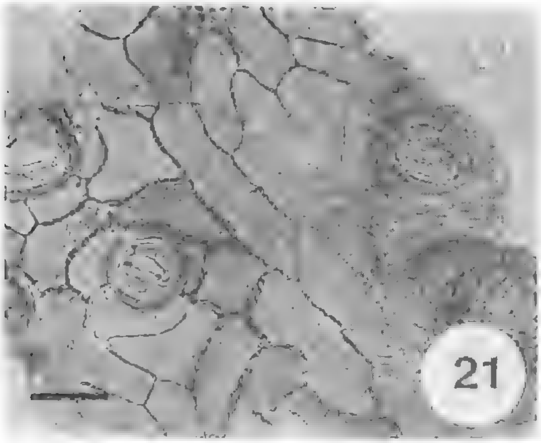

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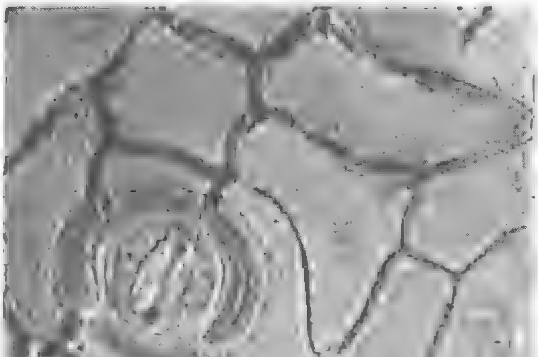

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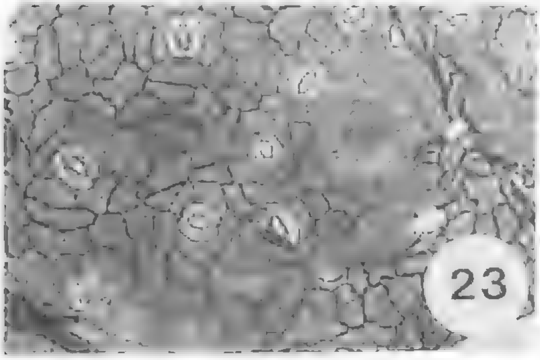

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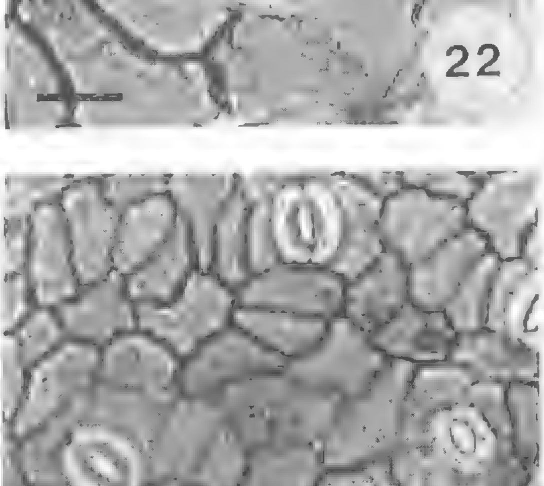

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smooth to beaded. Periclinal wall thin, smooth.
*Affinity:* Myrtaceae. Although oil gland lid cells that are usually found on myrtaceous leaves were not observed on fragments recovered from this locality, the general cuticular morphology is very similar to that of specimens recovered from the Lochiel coalfield (Fig. 10) which are unequivocally Myrtaceae.

### Cuticle Parataxon No. S5 004
### FIGS 11–12

Only the stomatiferous surface was observed. Epidermal cells sinuous (type 4–6). Cells 12–36 µm in length, 10–28 µm in width. Anticlinal wall irregularly thickened, smooth to beaded to ridged. Periclinal wall striate.

Stomata randomly oriented, uniform distribution. Stomata 16–26 µm in length, 12–16 µm in width. Guard cells slightly sunken, T-shaped thickening and polar rods present. Outer stomatal ledge, prominent, narrow. Stomatal Arrangement staurocytic. Subsidiary cells 3–5 more undulate in outline. Anticlinal wall beaded, radial wall often absent or incomplete. Periclinal wall thin, striate. Oil gland lid cells common, prominent, constricted at sinus, sinus straight, dark-staining, thicker cuticle than found over epidermal cells, dimensions 32–44 µm in length, 12–24 µm in width. Lid cell surrounded by a number of circles of radial arranged modified epidermal cells. Striations radiate outwards from lid cell.
*Affinity:* The presence of oil gland lid cells and the general stomatal morphology which includes features like a well-defined, circular guard cell complex and a prominent stomatal ledge, indicate the cuticle is of the Myrtaceae.

### Cuticle Parataxon No. ABD 001
### FIGS 13–14

Only the stomatiferous surface was observed. Epidermal cells angular (predominantly rectangular) arranged in longitudinal rows oriented parallel to the long axis of the leaf. Cells 32–68 µm in length, 20–64 µm in width. Anticlinal wall thin, smooth. Periclinal wall granulate.

Stomata in poorly defined uniseriate rows which suggests the specimen is of the adaxial surface of the leaf. The stomata are oriented parallel to the long axis of the leaf. Stomata 32–44 µm in length, 32–40 µm in width. Guard cells, sunken, poral thickening present. Outer stomatal ledge, prominent, thick, broad with polar extensions over radial anticlinal walls. Florin rings evident. Stomatal arrangement paratetracytic, circular in appearance. Subsidiary cells 4, crescent-shaped lateral cells larger than wedge-shaped polar cells. Anticlinal wall thin, smooth. Periclinal wall irregularly thickened, granulate to striate.
*Affinity:* The cuticle parataxon is assigned to *Falcatifolium* (Podocarpaceae), with a possible affinity to the fossil species *F. australis*. This species was described from the Anglesea deposit by Greenwood (1987) who noted the distinctive circular appearance of the stomata, a feature also exhibited by the Sedan specimens.

### Cuticle Parataxon No. S1 001
### FIGS 17–18

Hypostomatic. Adaxial epidermal cells angular becoming elongate over veins. Cells 20–36 µm in length, 12–28 µm in width. Anticlinal wall thin, smooth. Periclinal wall irregularly thickened, smooth to finely granulate. Trichome bases common, single to multicellular, up to 7 basal cells, heavily cutinized, trichome scar evident.

Cuticle thinner than on adaxial surface. Abaxial epidermal cells (angular to) rounded to undulate (type 3), becoming elongate over veins. Cells 16–40 µm in length, 8–16 µm in width. Anticlinal wall irregularly thickened, smooth to beaded. Periclinal wall irregularly thickened, smooth to papillate. Papillae present on most epidermal cells, short, cylindrical, truncate apex, up to 16 µm in length. Large papillae common, arise from multicellular bases (2-celled), basal cells heavily cutinized, cuticle of papillae also thick, up to 24 µm in length, dome-shaped. Stomata randomly oriented, uniform distribution. S.I. 15.5. Stomata 18–24 µm in length, 12–22 µm in width. Stomatal arrangement brachyparacytic. Guard cells slightly raised, show

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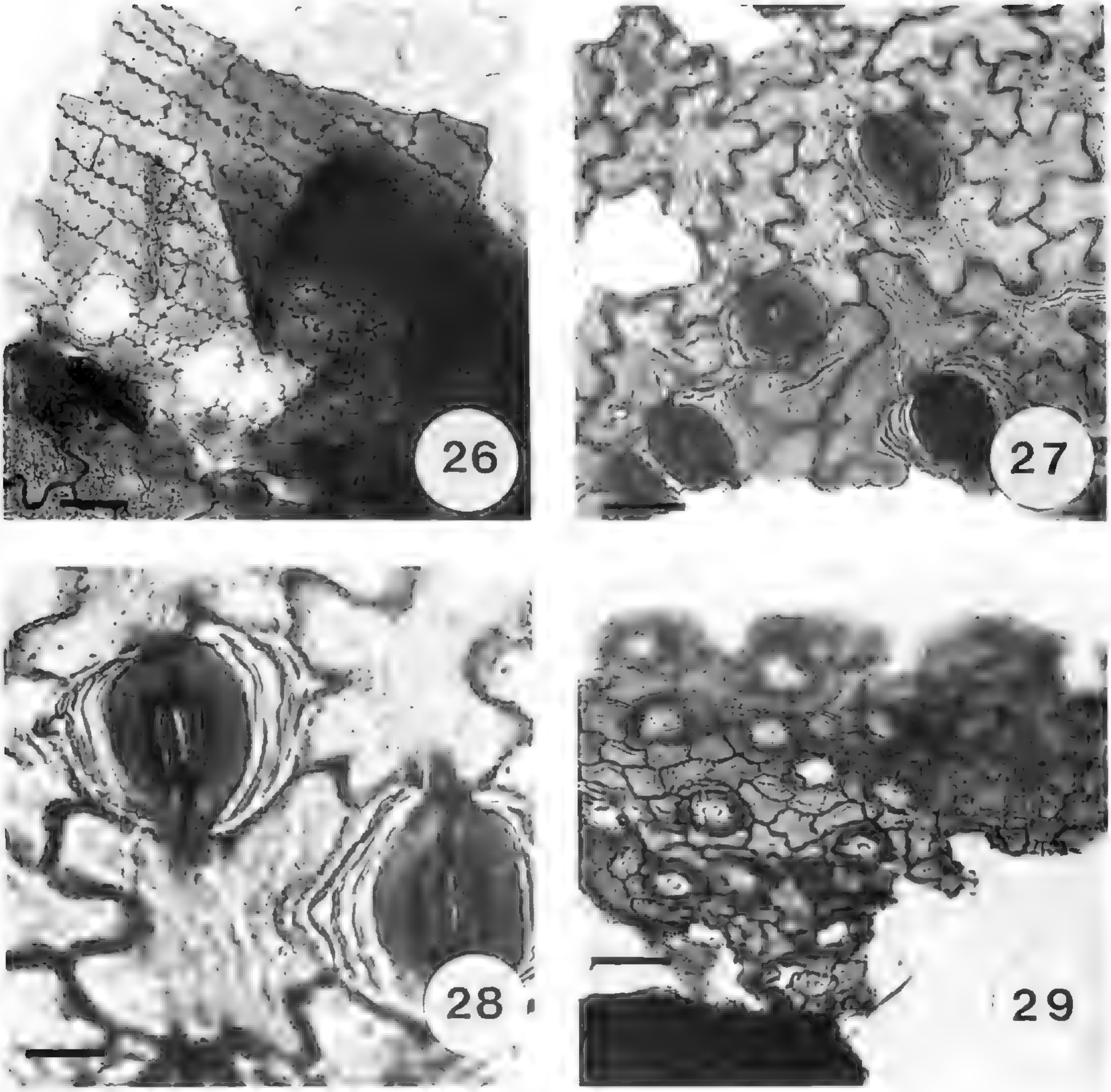
Figs 19–25. 19. Parataxon No. DM 007, *Gymnostoma*, Casuarinaceae. The delicate nature of this cuticle makes recovery difficult and stomates are rarely preserved. Scale = 40 µm. 20. Parataxon No. DM 007, *Gymnostoma*, Casuarinaceae, a slightly better preserved fragment showing a segment of a number of stomatal rows. Note the perpendicular orientation of the stomata relative to the intermediate epidermal cells. Scale = 20 µm. 21. Parataxon No. AWF 001, aff. *Agathis*, Araucariaceae. Note the oblique orientation of the stomates and the prominent Florin rings associated with the stomates. Scale = 40 µm. 22. Parataxon No. AWF 001, aff. *Agathis*, Araucariaceae, showing the stomatal arrangement and the darker staining Florin ring which overlies the subsidiary cells. Scale = 20 µm. 23. Parataxon No. S3 004, Elaeocarpaceae, showing stomatiferous surface. Scale = 20 µm. 24. Parataxon No. S3 004, Elaeocarpaceae, showing the anomocytic and staurocytic stomatal arrangement. Note the apiculate outer stomatal ledge, i.e. ledge with small polar protrusions, on the guard cells. Scale = 20 µm. 25. Parataxon No. S3 005 Elaeocarpaceae, showing the stomatiferous surface, note the staurocytic stomatal arrangement. Scale = 20 µm.



Figs 26-29. 26. Parataxon No. LE 009, Podocarpaceae, showing distinctive buttress thickening of the epidermal cells. Scale = 40 μm. 27. Parataxon No. S1 003, Proteaceae, showing the stomatiferous surface. Note the broad, thick stomatal ledge and prominent T-shaped thickening on the guard cells. Scale = 40 μm. 28. Parataxon No. S1 003, Proteaceae, showing the brachyparacytic stomatal arrangement. Note the prominent striations on the subsidiary cells. Scale = 19 μm. 29. Parataxon No. ALL 011, aff. *Sloanea/Elaeocarpus*, Elaeocarpaceae. The thin guard cells are surrounded by, up to 6, dark staining subsidiary cells. Scale = 32 μm.

slight poral thickening. Subsidiary cells 2. Anticlinal wall thin, smooth. Periclinal wall irregularly thickened, smooth to finely granulate, slightly thicker cuticle, slightly darker staining. Glandular bodies present.

*Affinity:* The cuticle parataxon is assigned to the Proteaceae on the basis of a brachyparacytic stomatal and multicellular trichome base arrangement. The cuticular features are identical to those of the cuticle of the Yallourn open cut fossil *Banksieaephyllum laeve.* The Sedan cuticle type is therefore identified as *Banksieaephyllum* aff. *B. laeve.*

### Cuticle Parataxon No. S3 001
### FIGS 15-16

Only the stomatiferous surface was observed. Epidermal cells undulate (type 3-4). Cells 36-64 μm in length, 12-36 μm in width. Anticlinal wall

irregularly thickened, smooth to beaded. Periclinal wall thin, smooth.
Stomata randomly oriented, uniform distribution. Stomata 20–28 μm in length, 24–28 μm in width. Guard cells not sunken, granulate, small T-shaped thickening present. Outer stomatal ledge prominent, broad, dark-staining. S.I. 14.6. Stomatal arrangement staurocytic. Subsidiary cells 3–5, dark staining. Anticlinal wall irregularly thickened, smooth to beaded. Periclinal wall thick, smooth. Oil gland lid cells rare, isodiametric, slightly constricted at sinus, sinus undulate (2–3 waves), up to 10 scarcely modified to radially arranged surrounding cells, dimensions 32–48 μm in length, 40–48 μm in width.
*Affinity:* The cuticle parataxon has been assigned to the Myrtaceae due to the presence of oil gland lid cells of the type seen on modern members of the family.

### Cuticle Parataxon No. DM 007
FIGS 19–20

Stomatiferous stem/shoot material was observed. Epidermal cells angular (usually hexagonal), arranged in longitudinal rows oriented parallel to the long axis of the shoot/stem. Cells 8–28 μm in length, 16–20 μm in width. Anticlinal wall thin, smooth. Periclinal wall irregularly thickened, smooth to granulate.
Stomata arranged in a uniseriate row near the shoot/stem margin, oriented perpendicular to the long axis of the shoot/stem. Stomata 20–24 μm in length, 8–12 μm in width. Guard cells not sunken. Outer stomatal ledge, prominent, broad, raised. Stomatal Arrangement none to paracytic. Subsidiary cells 0–2. Anticlinal wall, thin, smooth. Periclinal wall irregularly thickened, smooth to granulate.
*Affinity:* The cuticle parataxon has been assigned to *Gymnostoma* (Casuarinaceae) on the basis of predominently angular epidermal cells and the perpendicular orientation of stomates relative to the long axis of the shoot (Dilcher *et al.* 1990).

### Cuticle Parataxon No. AWF 001
FIGS 21–22

Only the stomatiferous surface was observed. Epidermal cells angular to rounded. Cells between stomatal bands are generally arranged in longitudinal rows oriented parallel to the long axis of the leaf. Cells 28–116 μm in length, 16–48 μm in width. Anticlinal wall thin, smooth. Periclinal wall irregularly thickened, smooth to finely granulate.

Stomata arranged in short discontinuous uniseriate rows, oriented obliquely, transverse to parallel to the long axis of the leaf. Stomatal rows separated by 2–5 rows of rectangular epidermal cells, in narrow stomatal bands. Stomata 40–64 μm in length, 20–40 μm in width. Guard cells sunken. Stomatal ledge, prominent, narrow. Guard cell/subsidiary cell wall heavily cutinized, raised. Florin rings evident. Stomatal Arrangement cyclocytic. Subsidiary cells 4–5. Anticlinal wall irregularly thickened, smooth to beaded. Periclinal wall irregularly thickened, granulate to striate.
*Affinity:* The cuticle parataxon has been assigned to the Araucariaceae. The predominantly oblique orientation of the stomata and rounded epidermal cells suggests an affinity to *Agathis* (Cookson & Duigan 1951; Stockey & Taylor 1981; Hill & Bigwood 1985, 1987).

### Cuticle Parataxon No. S3 004
FIGS 23–24

Only the stomatiferous surface was observed. Epidermal cells undulate (type 3). Cells 12–32 μm in length, 8–16 μm in width. Anticlinal wall thin, smooth. Periclinal wall thin, smooth.
Stomata randomly oriented, uniform distribution. Stomata 12–20 μm in length, 12–16 μm in width. Guard cells not sunken. Outer stomatal ledge, prominent, narrow, apiculate. Stomatal Arrangement staurocytic to cyclocytic. Subsidiary cells 3–5. Anticlinal wall, thin, smooth, radial walls may be poorly defined. Periclinal wall thin, smooth. Trichome bases common, over veins, poral, 7 radially arranged surrounding cells, cuticular thickening around pore. Hydathodes rare, over veins.
*Affinity:* The cuticle parataxon is placed in the Elaeocarpaceae due to the presence of hydathodes, an apiculate stomatal ledge and staurocytic stomatal arrangement.

### Cuticle Parataxon No. S3 005
FIG 25

Only the stomatiferous surface was observed. Epidermal cells angular. Cells 10–33 μm in length, 5–23 μm in width. Anticlinal wall thin, smooth. Periclinal wall granulate.
Stomata randomly oriented, uniform distribution. Stomata 12–20 μm in length, 10–15 μm in width. Guard cells, not sunken, T-shaped thickening present. Outer stomatal ledge, prominent, narrow, apiculate. Stomatal Arrangement staurocytic. Subsidiary cells 2–5. Anticlinal wall, thin, smooth. Periclinal wall granulate. Hydathodes rare.
*Affinity:* The cuticle parataxon is placed in the Elaeocarpaceae due to the presence of hydathodes, an apiculate stomatal ledge and staurocytic stomatal arrangement.

### Cuticle Parataxon No. LE 009
### FIG. 26

Only the stomatiferous surface was observed. Epidermal cells rectangular, arranged in longitudinal rows oriented parallel to the long axis of the leaf. Cells 8-36 μm in length, 8-18 μm in width. Anticlinal wall buttressed. Periclinal wall thin, smooth. Stomata arranged in uniseriate rows, often short, occasionally merged, oriented parallel to the long axis of the leaf. Stomata 16–28 μm in length, 12–18 μm in width. Stomatal arrangement paratetracytic. Guard cells sunken. Stomatal ledge prominent, irregularly thickened. Subsidiary cells 4, heavily cutinized, lateral cells larger than polar cells. Polar cells may be shared. Anticlinal wall buttressed. Periclinal wall thick, smooth. Florin ring evident.
*Affinity:* Although very fragmentary the general cuticular morphology of specimens suggests an affinity to the Podocarpaceae.

### Cuticle Parataxon No. S1 003
### FIGS 27–28

Only the stomatal surface was observed. Epidermal cells sinuous (4), 64–104 μm in length, 56-80 μm in width. Anticlinal wall irregularly thickened, smooth to finely beaded to ridged. Periclinal wall granulate. Stomata randomly oriented, uniform distribution. Stomata 36–56 μm in length, 32-38 μm in width. Stomatal arrangement brachyparacytic. Guard cells sunken, broad polar rods, T-shaped thickening and poral thickening present. Outer stomatal ledge prominent, very broad. Subsidiary cells 2. Anticlinal wall beaded. Periclinal wall striate. Trichome bases common, 1-2 basal cells, heavily cutinized, raised anticlinal wall, 6-8 scarcely modified, radially arranged surrounding cells. Striations radiate outwards onto other epidermal cells.
*Affinity:* The cuticle parataxon is assigned to the Proteaceae due to presence of brachyparacytic stomata and multicellular trichome bases.

### Cuticle Parataxon No. AL1 011
### FIG. 29

Only stomatiferous surface observed. Epidermal cells angular to rounded, becoming elongate over veins. Cells 8-40 μm in length, 8-20 μm in width. Anticlinal wall thin, smooth. Periclinal wall thin, smooth. Stomata randomly oriented, uniform distribution within large areoles. Stomata 12–24 μm in length, 12-16 μm in width. S.I. 15.6 Stomatal arrangement actinocytic to staurocytic. Guard cells not to slightly sunken. Subsidiary cells 3–6, darker staining than epidermal cells. Anticlinal wall thin, smooth. Periclinal wall irregularly thickened, smooth to slightly granulate. Outer stomatal ledge prominent, narrow. Polar rods and some T-shaped thickening present on guard cells. Hydathodes rare, over veins, 28–40 μm in length, 16–20 μm in width.
*Affinity:* The cuticle parataxon is placed in the Elaeocarpaceae due to the presence of hydathodes, an apiculate stomatal ledge and staurocytic stomatal arrangement.

## Floristic Comparison of Samples

The floras of each of the three samples possess a number of floristic features that distinguish them from one another. The flora of the upper seam is characterised by the dominance of the Proteaceae component and of one parataxon in particular, No. S1 001 which matches the cuticle of *Banksieaephyllum laeve* (Figs 17 & 18).

The flora of the lower lignite seam has a similar overall composition to that of the younger lignite seam but with a number of differences. These include; 1) the presence of parataxa No. S3 001 and No. AWF 001 both of which are absent from the other floras as well as being the sole contributors to the Myrtaceae and Araucariaceae components respectively. Both parataxa are potentially useful as stratigraphic indicators, at least locally within the depositional basin; 2) an increased abundance of the Podocarpaceae, Myrtaceae, Elaeocarpaceae and Casuarinaceae components which when combined, account for more than 25% of the flora. In no other lithotype do these components attain the same levels of significance either individually or combined.

The flora of the basal clay is easily distinguished from the other Sedan floras by the abundance of Lauraceae parataxa, of which some are related to the extant genera *Endiandra* and *Cryptocarya*, and the minor occurrence of Proteaceae parataxa.

Comparison of the floras of the three lithotypes reveals a distinct floristic difference between the two lignite seams and the basal lignitic clay seam. Both lignite floras are dominated by the Proteaceae with parataxon No. S1 001 the major contributor. The flora of the lignitic clay is very different with the Lauraceae dominating and the Proteaceae reduced to an insignificant level. It is also evident that there is a correlation between the lithotype and dominant floral type, i.e the Proteaceae are associated with the lignite whereas the Lauraceae are associated with the clay.

Examination of modern sedimentary environments has shown that quite different leaf-floras (and by inference, different cuticle floras) are found in separate sedimentary environments (Burnham 1989; Taggart 1988). Within the same stratigraphic sequence these changes in environment may be due to either hydrological succession or climatic changes which subsequently induce changes in the plant community (Luly *et al.* 1980). The correlation between the two lithotypes and the two dispersed cuticle floras therefore indicates that both floras are the product of different sedimentary environments (Taggart 1988); the Lauraceae-dominated lignitic clay and the Proteaceae-dominated lignite. The lignitic clay is likely to have been deposited under open-water conditions, with mainly allochthonous, potentially extra-local (Lauraceae-dominated flora), plant remains, whereas the lignite represents swamp conditions with mainly local deposition (i.e. Proteaceae-dominated flora).

## Comparison with Other Australian Tertiary Deposits

The dispersed cuticle floras of the Sedan deposit include a number of parataxa which are known to occur in other Australian Tertiary deposits. The presence of the very distinctive cuticle of *Banksieaephyllum laeve* in the Sedan lignites, i.e. *Banksieaephyllum* aff. *B. laeve*, would appear to be of some biostratigraphic significance. *B. laeve* has to date only been reported from the Yallourn (Oligocene) and Morwell (Miocene) coal seams of the Latrobe Valley and the Inkerman-Balaklava lignites of the Bowmans deposit, 100 km north of Adelaide (Blackburn 1985). The latter deposit is located a short distance south of the Sedan deposit in the adjoining St Vincent Basin. Although the stratigraphic evidence is limited, it is consistent, with *B. laeve* only being reported from Oligocene-Miocene coals and as one of these coal deposits lies is close vicinity to the Sedan deposit then a younger age could be inferred.

Conversely, based on palynological and micropalaeontological evidence, the presence of *B. laeve* cuticle in the Sedan lignite could imply the leaf fossil has a longer stratigraphic range than previously reported, i.e Late Eocene-Miocene.

The basal lignitic clay is dominated by the Lauraceae, which is of no stratigraphic significance as the family was well represented throughout the Australian Eocene. A comparison of Eocene Lauraceae cuticle types from a number of localities, including Anglesea (Rowett & Christophel 1990) and Nerriga (Hill 1986) has shown that both of the genera identified in this lithotype, i.e. *Cryptocarya* and *Endiandra*, were well represented in terms of species and abundance throughout the period. It should be noted that the lauraceous megafossils of the Nerriga locality were assigned to the form genus *Laurophyllum* by Hill, but affinities to *Endiandra* and *Cryptocarya* were also indicated for a number of these leaf types. It must also be mentioned that the two genera are the major contributors to the modern Australian Lauraceae.

However, the presence of the Lauraceae parataxon No. AA 006 may prove to be an important stratigraphic indicator, based on the author's unpublished information. This parataxon appears to have a restricted distribution, being only recorded in Middle Eocene deposits and reaching maximum abundance in the Upper Middle Eocene. It has not at this present time been identified in Late Eocene or younger sediments.

In conclusion, it is evident from the analysis of the dispersed cuticles of the Sedan coal sequence that 1) two separate dispersed cuticle floras are recognised, i.e. the Lauraceae-dominated flora of the basal lignitic clay and the Proteaceae-dominated flora of the younger lignites; 2) the change in lithotype and flora recognised between the basal clay and lignites may be climatically induced; 3) the key cuticle type *Banksieaephyllum* aff. *B. laeve* recorded at Sedan occurs in younger lignite sequences in the Latrobe Valley (Victoria) and Bowmans deposit (South Australia) suggesting either that the Sedan lignites are younger than indicated by both the micropalaeontology and palynology or that the stratigraphic range (Oligocene-Miocene) of the cuticle type is longer than suggested by the present records.

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# WHALE STRANDINGS IN SOUTH AUSTRALIA (1881-1989)

*BY CATHERINE M. KEMPER & JOHN K. LING**

## Summary

Cetacean strandings were collated from museum records, and published and unpublished sources. The identification of stranded animals was verified in 85% of events by examination of voucher specimens or photographs. Trends in the stranding record were documented, but reasons for strandings were not investigated in detail. From 1881 to 1989, 309 stranding events, involving 24 species, have been recorded in South Australia, while an additional species may have stranded in the State. Stranding events most commonly involved *Tursiops truncatus, Delphinus delphis, Physeter macrocephalus, Caperea marginata, Mesoplodon layardii, Globicephala melas, Kogia breviceps,* and *Balaenoptera acutorostrata.* Strandings were less frequent on the western shores of Gulf St Vincent and Spencer Gulf, possibly because these are protected from strong southwesterly winds. There was a trend towards more frequent events being recorded in January/February and September/October. Some species showed seasonal trends in stranding, possibly related to their migratory patterns or movements inshore/offshore. Eighty-nine percent of stranding events involved single animals; 18% involved groups of two or three animals and **3%** were of four or more. Twenty-eight percent of stranded animals were juveniles. In some species (e.g. *Balaenoptera acutorostrata, Caperea marginata, Globicephala* spp., *Kogia* spp. and other Balaenopteridae), juveniles constituted a high proportion (> 30%). At least 15% of stranding events involved live animals, although more accurate observations and reporting in recent times indicate that live strandings are probably more frequent. There were live strandings of 16 species, including baleen and toothed whales. There was a tendency for large whales to strand more often in a moribund or decaying state than small species. On average, about 20 recorded stranding events have occurred in South Australia each year since 1985.

KEY WORDS; cetaceans, stranding, mass stranding, trends, South Australia.

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## Introduction

Cetacean strandings have captured the attention of humans since Aristotle's time (see Aristotle 335 BC), but only in the last few decades have these events been studied in detail. More recently, trends have been analysed and plausible hypotheses proposed on the possible causes for stranding of live animals (reviewed by Geraci & St Aubin 1979).

There are many possible causes of cetacean strandings, e.g. disease, injury (both natural and anthropogenic), birth difficulties, adverse weather, parasite infections, food supply, old age and toxic pollutants (Geraci & St Aubin 1979). A recent hypothesis suggests that cetaceans may 'make navigational mistakes' if the earth's geomagnetic field is disturbed (Klinowska 1986). Sergeant (1982) concluded that nearly all animals involved in single strandings were diseased or parasitised, but those involved in mass strandings were not.

In Australia, the most detailed accounts of cetacean strandings exist for Tasmania (reviewed by Nicol & Croome 1988). Some published observations are available for Victoria (Wakefield 1967; Warneke 1983, 1988) and the Illawarra district of New South Wales (Robinson 1984). Species recorded in Queensland are discussed in Bryden (1978), Paterson (1986) and Paterson & Van Dyck (1990). Since 1984 all states, but not the Northern Territory, have been reporting strandings to the Australian National Parks & Wildlife Service.

The South Australian Museum has taken a special interest in cetaceans since the mid- to late 1800s (Hale 1956). E. R. Waite, H. M. Hale and, more recently, P. F. Aitken established a stranding reporting and collecting network which provided us with sufficient records to analyse trends. Aitken (1971) published a summary of the 18 species which he regarded as occurring in South Australia, based on strandings or sightings (also summarised by Sergeant 1982). A revised account was presented by Ling & Aitken (1981). Stopp (1984)[1] compiled a detailed account of the locations of many South Australian strandings up to 1984, with some other details for each specimen.

Here we summarise the entire stranding record for South Australia. Trends in strandings are analysed in relation to species composition and abundance, geographic and seasonal distribution, group size of stranded animals, age, and active *vs* passive stranding events. No attempt has been made to investigate or explain the cause of strandings,

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* South Australian Museum, North Terrace, Adelaide, S.A. 5000

[1] Stopp, B. A. (1984) Cetacean strandings in South Australia 1881-1984. Field Study for Associate Diploma in Wildlife and Park Management, South Australian College of Advanced Education.

except in very general terms. Special attention was paid to the possible influences of the unique oceanographic conditions of South Australia on the cetaceans of southern Australian waters.

## Oceanography of the South Australian Coast

The South Australian coast measures approximately 4000 km of which about 1500 km (38%) border two large gulfs, St Vincent and Spencer. Several large bays occur along the seaward coast. The 200-m bathometric contour lies 100–200 km offshore for much of the coast but is closer inshore (50 km) in the southeast of the State. Hence there is a broad continental shelf which, with the exception of Bass Strait, is unique for the southern half of the continent. Deep canyons are found to the southeast of Kangaroo Island and southwest of Ceduna. Annual mean water temperatures in non-gulf waters vary from 15° – 18°C (Radok 1976). Cold oceanic currents generally flow in an easterly direction across southern Australia at rates of 14–25 km per day, except in summer when a westerly eddy is found in the Great Australian Bight region (Federal Department of Transport 1987). A fast (35 km per day) easterly current occurs in the Bight during winter. The Leeuwin current, which originates in the Indian Ocean off Western Australia, brings warm water into the Bight in autumn and winter (Pearce & Cresswell 1985). A surface temperature gradient of up to 5°C may be noted along the southern coast of Western Australia at this time. Little has been documented on gulf and inshore currents in South Australia although studies are in progress (P. Petrusevics pers. comm. 1990)

In South Australia, the prevailing winds are generally southerly or southeasterly in summer and southwesterly or northerly in winter (Climatic Atlas of Australia 1988). There may be some deviation from this pattern in the region of the gulfs. Wind-induced upwelling events are important in the southeast of the State in summer (Lewis 1981; Schahinger 1987). Other areas of upwelling are found off the southwest coast of Kangaroo Island, and between Coffin Bay and Anxious Bay (just south of Streaky Bay) (P. Petrusevics pers. comm. 1990).

Bye (1976) described the gulfs (Spencer Gulf and Gulf St Vincent, separated by Yorke Peninsula) and their associated waters (Investigator Strait and Encounter Bay) as a complex zone of fundamental importance to South Australia's marine environment. (Investigator Strait (north of Kangaroo Island) and Encounter Bay (east of Kangaroo Island) are not considered part of the gulfs, because they are very much influenced by oceanic patterns). Salinity at the head of the gulfs is much higher than at their mouths (for Spencer Gulf as high as 48‰ in the late summer and about 43‰ in late winter (Nunes & Lennon 1986)). Due to the shallowness of the water in the gulfs (<50 m), temperatures range from about 12°C in winter to about 24° in summer (Bye 1976; Nunes & Lennon 1986). Again, there is a north-south gradient. The gulfs are somewhat protected from the full effects of the Southern Ocean by their surrounding land masses.

Another area of interest oceanographically, but about which little is known, is the Head of the Great Australian Bight. In winter, temperatures and salinities are higher than the water to the south (Pearce & Cresswell 1985).

## Materials and Methods

Information on cetacean strandings was gathered from specimens and photographs held in the collections of the South Australian Museum; published records in Aitken (1971), Hale (1931, 1939, 1959, 1962), Ling & Aitken (1981), Stopp (1984), Waite (1919), and newspaper articles; and unpublished records from various sources. No specimens from South Australia exist in the collections of the Western Australian Museum, Australian Museum, or Museum of Victoria. The identifications of all specimens in the South Australian Museum have recently been verified; hence some published observations (e.g. Aitken 1971) may not be consistent with ours. Of the 309 stranding events reported here, 75% are verified with voucher specimens in the South Australian Museum and 10% are verified with photographs alone.

The taxonomy used here is that of Bannister (1988) with the exception of *Globicephala melas* (= *melaena*) (Rice 1989), the placement of *Caperea marginata* in the family Neobalaenidae (Barnes & McLeod 1984) and the use of the specific name *macrocephalus*, not *catodon*, for *Physeter* (see Rice 1989).

A 'stranding', in the present study, is any event involving the beaching or washing up on shore of live or dead cetaceans, as well as observations of dead cetaceans floating offshore. Skeletal material from the coast is included in our definition of stranding (but not dated), except in the case of *Eubalaena australis* near old whaling stations. It is assumed that most museum specimens lacking data were collected as a result of stranding events, although caution was exercised in the cases of *Physeter macrocephalus* and *Eubalaena australis* due to whaling activities. It is possible that some small cetaceans could have been caught accidentally in fishing nets, but this information is not recorded by the Museum. A single *Caperea marginata* (Encounter Bay, September 1887) was caught in a fishing net.

The relative age of individuals was estimated only in those cases where the total length of the animal was known or, in a few cases, was estimated from photographs. Neonates were defined as individuals approximately the length of newborn animals, based on information from other studies (Perrin *et al.* 1984; Ross 1984). Juveniles were defined as being less than, or equal to, a certain proportion of the species' length at physical maturity. These are: 50% (*E. australis, P. macrocephalus, Globicephala* spp., *Grampus griseus*), 55% (*C. marginata*), 60% (Balaenopteridae, *Tursiops truncatus, Delphinus delphis*), 65% (*Kogia* spp.) and 70% (Ziphiidae). These proportions were based on information from several sources (Bryden 1972; Ross 1984; Mead & Potter 1990; Ross pers. comm. 1990).

Where the actual date of stranding was unknown, the month was estimated on the basis of photographs of the animal or a description of its state of decomposition.

The term 'gulfs' refers here only to Gulf St Vincent and Spencer Gulf. The term 'gulfs region' includes Investigator Strait and Backstairs Passage and the north coast of Kangaroo Island.

## Results

### *Species*

Twenty-four species of cetaceans were verified as having stranded along the South Australian coast between 1881 and 1989 (Table 1). There is some uncertainty about the additional species, (*Balaenoptera borealis*) which, although in the South Australian Museum collections, may not have stranded in the State. Recent re-examination of baleen plates (SAM M4829), previously identified as *B. edeni*, resulted in the identification being determined as *B. borealis* (based on characters described by Mead (1977) and Horwood (1987)). However, the plates have no accompanying data and therefore could have been collected elsewhere, or they may not have been from a stranded animal. No species are recorded as stranded in the State based solely on photographs or other reports lacking voucher material (Table 1).

In terms of individuals (but excepting the mass strandings of *Pseudorca crassidens*), the most commonly stranded species were the dolphins, *T. truncatus* and *D. delphis*. These are followed by six species: *Physeter macrocephalus, Caperea marginata, Mesoplodon layardii, Kogia breviceps, Globicephala melas* and *Balaenoptera acutorostrata*, whose status varies depending on whether specimen records lacking vouchers or locality information are included. All have greater than 10 recorded stranding events. *Balaenoptera physalus, Berardius arnuxii* and *Kogia simus* have stranded only once. There is some uncertainty about whether *Tasmacetus shepherdi* has stranded once or twice (G. Ross pers. comm. 1990).

### *Geographic distribution of stranding events*

Stranding events having geographic locality information (238) were not evenly distributed along the South Australian coast (Fig. 1). More strandings occurred in (or were reported from) the Coffin Bay/Port Lincoln and Coorong regions, followed by the eastern side of Gulf St Vincent, the north coast of Kangaroo Island and the Streaky Bay/Ceduna regions. Very few strandings were reported from the western sides of Gulf St Vincent and Spencer Gulf, despite moderate levels of human activity along these coasts. There were few strandings reported in the far west of the State, much of which is lined with inaccessible cliffs and a rocky shore. Forty-six percent of strandings occurred within the gulfs region which includes about 40% of the South Australian coast.

Mass strandings (i.e. more than three individuals) have occurred at six locations (Fig. 1). Five were in the gulfs region. Three locations (north of Adelaide and northeastern Kangaroo Island) were where other live strandings have occurred (Fig. 2).

Active (= live) strandings have been reported less frequently in remote areas than around centres of population, e.g. in the gulfs region (Fig. 2). Nevertheless, it appears that some areas (e.g. Port Lincoln/Coffin Bay, Nepean Bay, eastern Gulf St Vincent, Murray River mouth) are more prone to active strandings than are others.

There are trends in the geographic distribution of stranding events of species or species groups (Figs 3–8). Both *T. truncatus* and *D. delphis* have stranded along much of the coast but concentrations of events exists around Adelaide, Port Lincoln, Nepean Bay and the Murray River mouth (Fig. 3). The two records of *T. truncatus* from Lake Alexandrina (north of the Coorong) were made before the barrages were built in the 1930s. Few dolphin strandings have been recorded from the northern ends of the gulfs. Of the 36 strandings within the gulfs region, more were of *T. truncatus* than *D. delphis* ($P < 0.10$, $\chi^2$ 2.78, 1 d.f.).

Few strandings of *Globicephala macrorhynchus* and *G. melas* were reported in the gulfs region (Fig. 4). The only two records within the gulfs proper being *G. macrorhynchus*; one of these a mass stranding.

TABLE 1. *Stranded cetaceans along the South Australian coast recorded from various sources. South Australian Museum (SAM) specimens with no locality data are in parentheses and are included in the total numbers to their left. Events from other sources includes photographs, published and unpublished records. Total individuals includes specimens plus individuals from other sources. Unidentified records not listed.*

| Family, genus & species | SAM specimens | Events from other sources | Total individuals | Total events |
|---|---|---|---|---|
| BALAENIDAE | | | | |
| *Eubalaena australis* | 7(5) | 0 | 7 | 7 |
| NEOBALAENIDAE | | | | |
| *Caperea marginata* | 27(8) | 2 | 29 | 29 |
| BALAENOPTERIDAE | | | | |
| *Balaenoptera acutorostrata* | 11(2) | 1 | 12 | 12 |
| *B. borealis** | 1(1) | 0 | 1 | 1? |
| *B. edeni* | 6(0) | 1? | 6 | 6 |
| *B. musculus* | 5(1) | 0 | 5 | 5 |
| *B. physalus* | 1(0) | 0 | 1 | 1 |
| *Megaptera novaeangliae* | 4(0) | 1 | 5 | 5 |
| DELPHINIDAE | | | | |
| *Delphinus delphis* | 39(12) | 16 | 60 | 54 |
| *Globicephala* sp. | 0 | 2 | 2 | 2 |
| *G. macrorhynchus* | 10(1) | 0 | 10 | 6 |
| *G. melas* | 11(1) | 4 | 15 | 14 |
| *Grampus griseus* | 2(0) | 2 | 4 | 4 |
| *Orcinus orca* | 3(1) | 0 | 3 | 3 |
| *Pseudorca crassidens* | 2(0) | 0 | c 310 | 2 |
| *Tursiops truncatus* | 71(21) | 12 | 126 | 65 |
| PHYSETERIDAE | | | | |
| *Kogia breviceps* | 20(1) | 1 | 22 | 13 |
| *K. simus* | 1(0) | 0 | 2 | 1 |
| *Physeter macrocephalus* | 26(4) | 8 | 34 | 34 |
| ZIPHIIDAE | | | | |
| *Berardius arnuxii* | 1(0) | 0 | 1 | 1 |
| *Hyperoodon planifrons* | 7(0) | 0 | 7 | 7 |
| *Mesoplodon* sp. | 0 | 5 | 6 | 5 |
| *M. bowdoini* | 2(0) | 0 | 2 | 2 |
| *M. grayi* | 8(0) | 0 | 8 | 8 |
| *M. layardii* | 22(0) | 1 | 24 | 19 |
| *Tasmacetus shepherdi* | 1(0) | 0 | 1 | 1 |
| *Ziphius cavirostris* | 2(0) | 0 | 2 | 2 |
| TOTALS | 290(58) | 56 | 705 | 309 |

* Doubtful S.A. record

Strandings of *C. marginata* have been reported from the Victorian border to Streaky Bay (Fig. 5) although the latter location is unsubstantiated. Sixty-five percent of strandings have occurred in the Port Lincoln and Nepean Bay areas. No strandings have been recorded from well within the gulfs.

Balaenopterids show some interesting trends (Fig. 6). *B. edeni*, with the exception of a dubiously identified specimen from Cape Banks (approx. 38°S), has always stranded well within the gulfs. *B. acutorostrata*, on the other hand, has almost always stranded outside the gulfs and usually in specific areas (e.g. Coffin Bay, Port Lincoln, Nepean Bay and the Coorong). No trends were apparent for other species. The single stranding of a juvenile *B. physalus* occurred at the northern end of Gulf St Vincent.

The numerous strandings of *Physeter macrocephalus* have occurred along almost the entire South Australian coast (Fig. 7). Few have been recorded within the gulfs. The record from Adelaide was a specimen of bones of unknown date, buried in sand in shallow water. No record could be found of a large whale stranding near Adelaide in the past 50 years, so we assume that these bones represent an older stranding event. *Kogia breviceps* has also

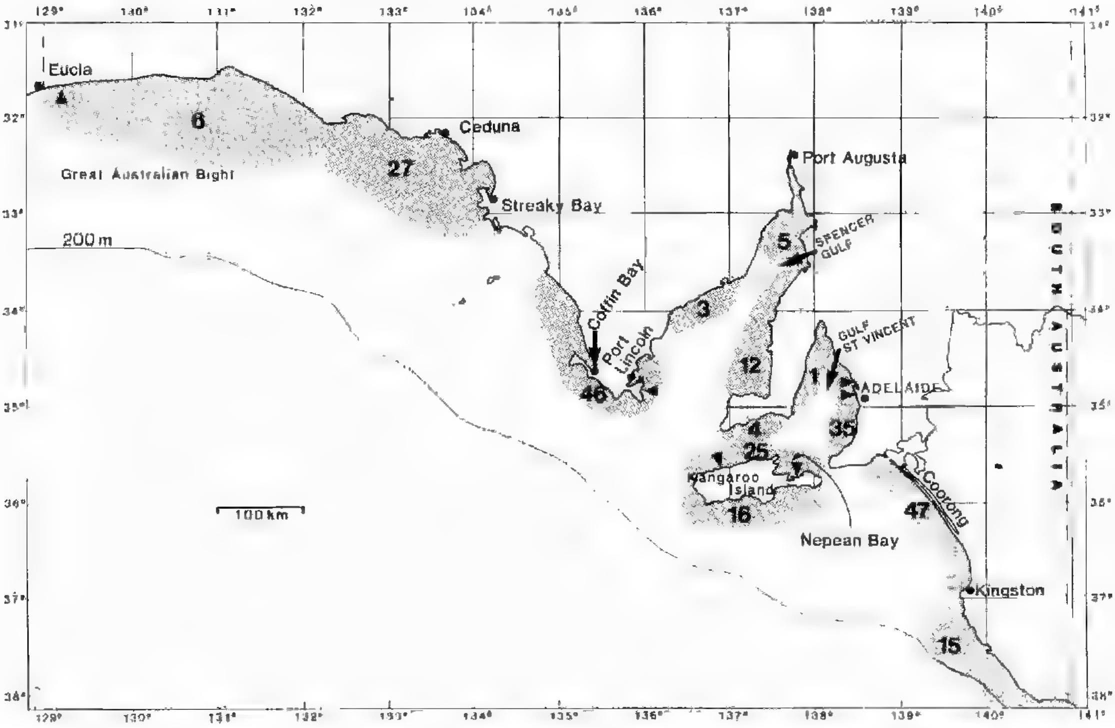

Fig. 1. Geographic distribution and number of reported stranding events in South Australia, 1881–1989. Shaded areas indicate coastline over which events took place. Solid triangles denote mass stranding localities.

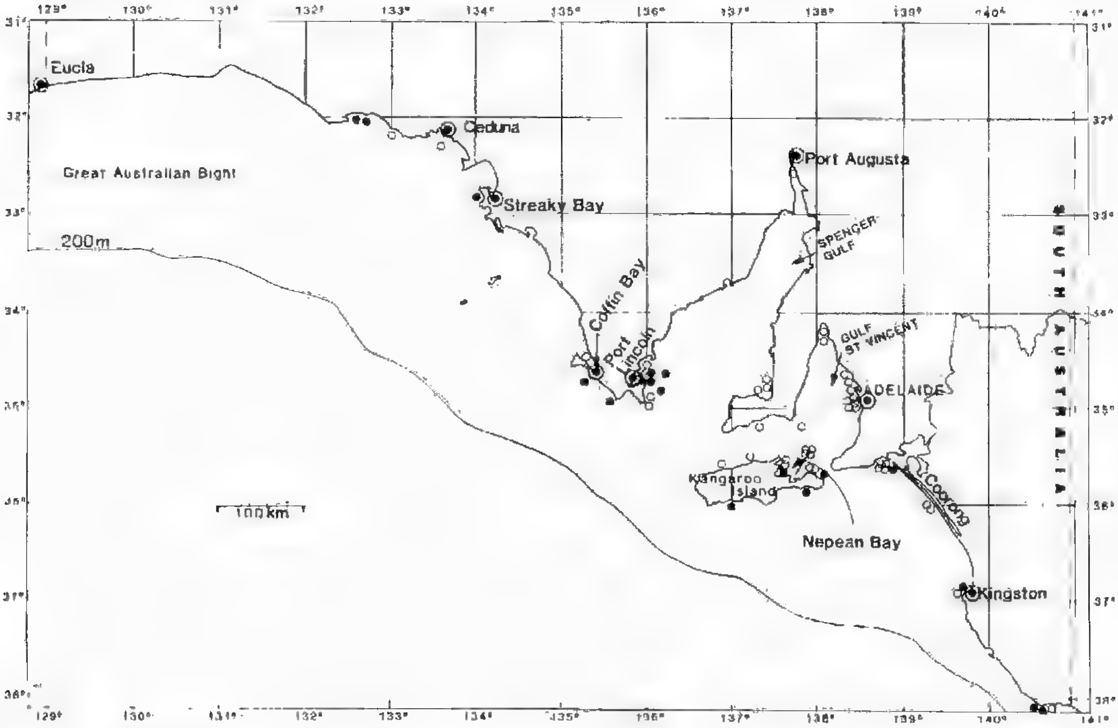

Fig. 2. Geographic distribution of reported active (○) and passive (●) stranding events in South Australia, 1881–1989.

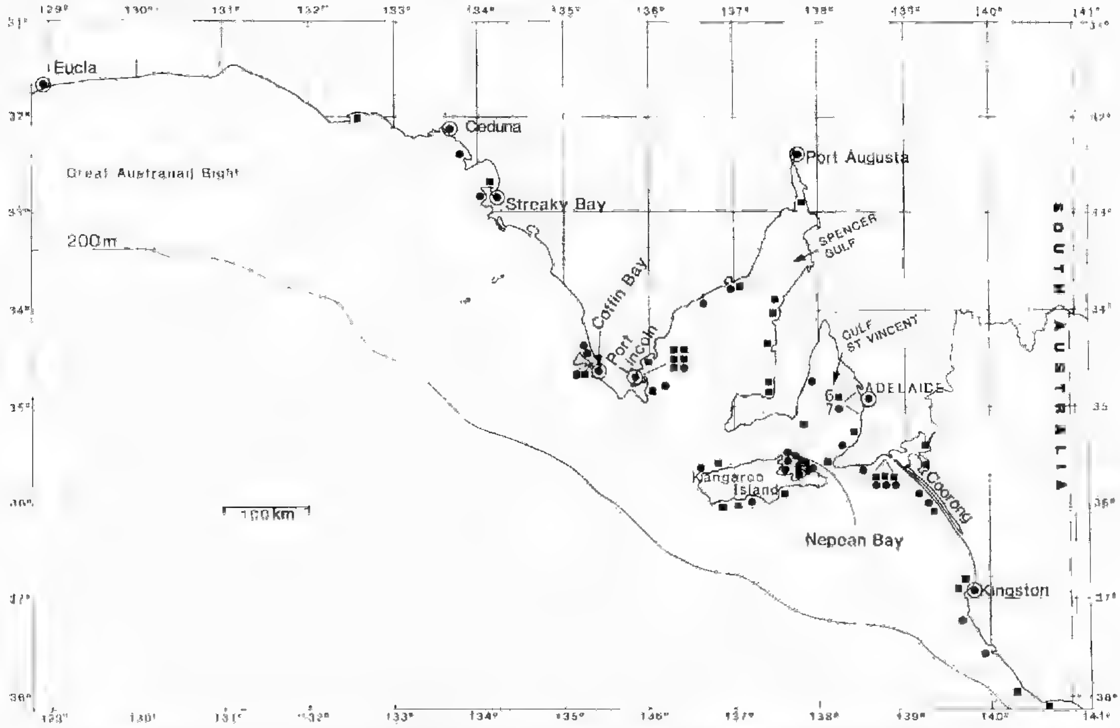

Fig. 3. Geographic distribution of reported dolphin strandings in South Australia, 1881–1989. Each symbol represents a *Delphinus delphis* (●) or *Tursiops truncatus* (■) stranding event.

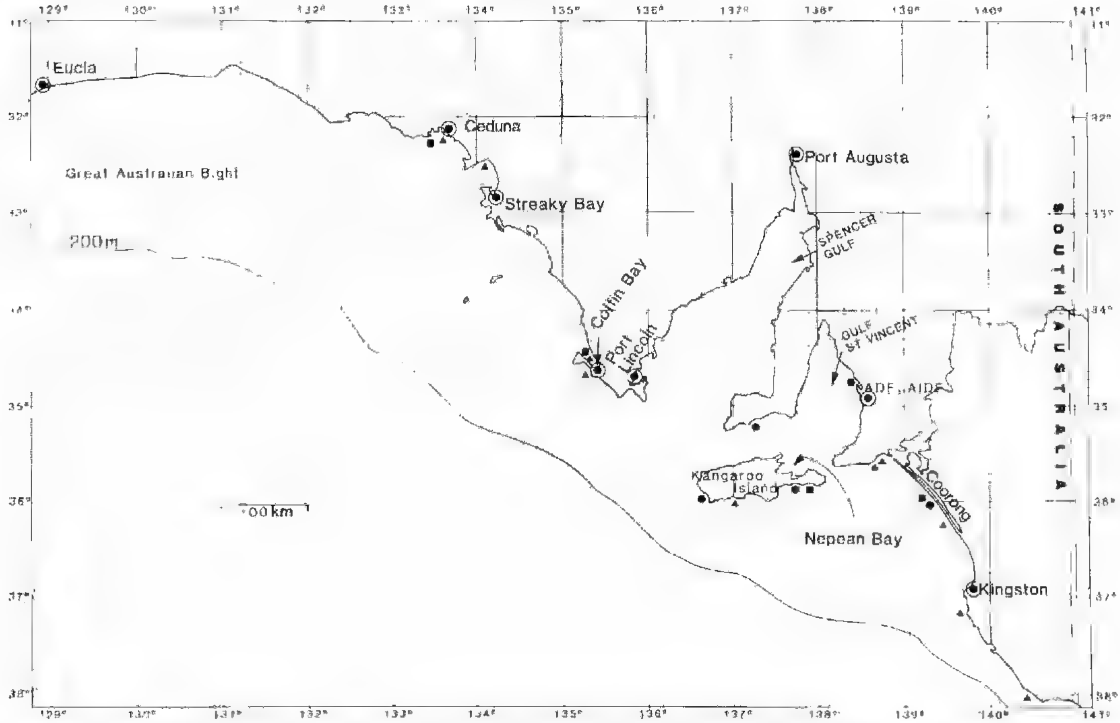

Fig. 4. Geographic distribution of reported pilot whale strandings in South Australia, 1881–1989. Each symbol represents a *Globicephala macrorhynchus* (●), *G. melas* (▲) or *Globicephala* sp. (■) stranding event.

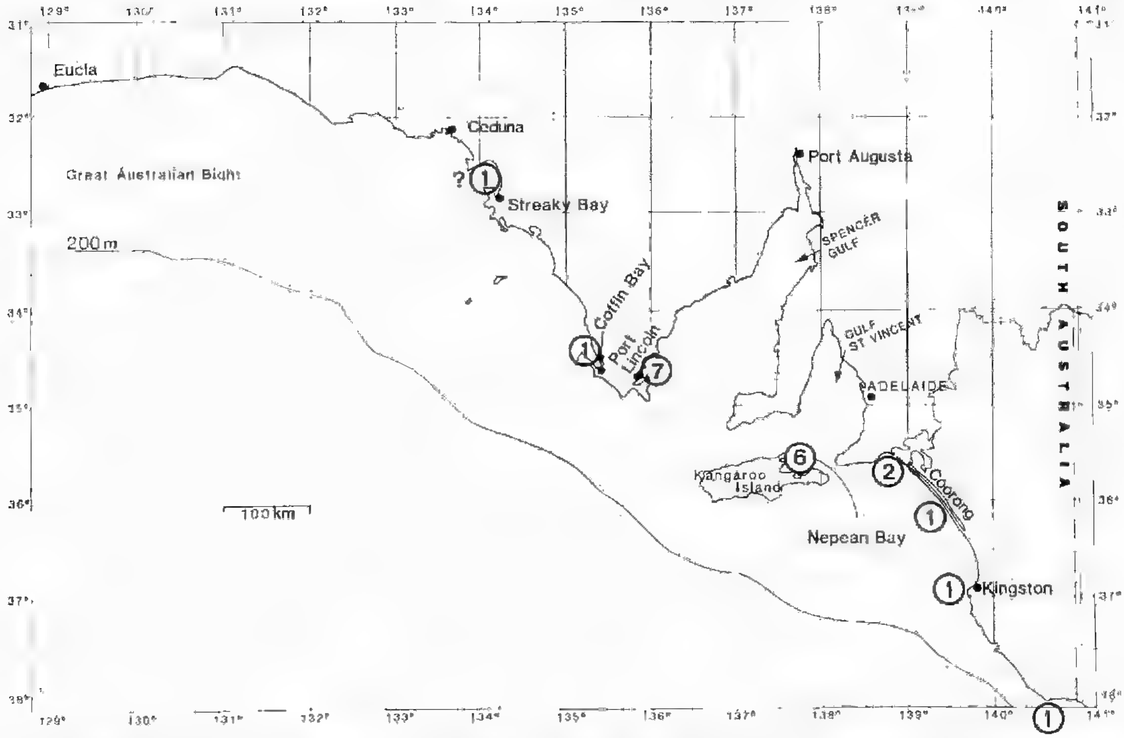

Fig. 5. Geographic distribution of reported strandings of *Caperea marginata* in South Australia, 1881–1989. Numbers in circles represent numbers of events. Streaky Bay stranding is unsubstantiated.

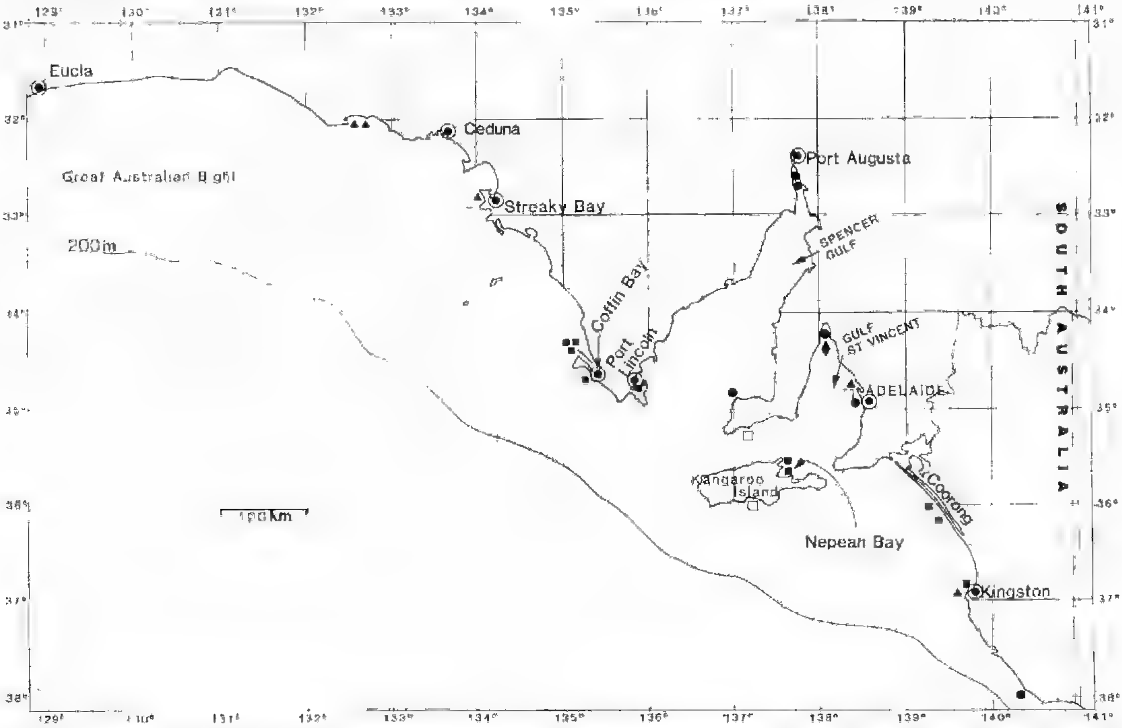

Fig. 6. Geographic distribution of reported strandings of rorquals (Balaenopteridae) in South Australia, 1881–1989. Each symbol represents a *Balaenoptera edeni* (●), *B. musculus* (▲), *B. acutorostrata* (■), *B. physalus* (♦) or *Megaptera novaeangliae* (□) stranding event.

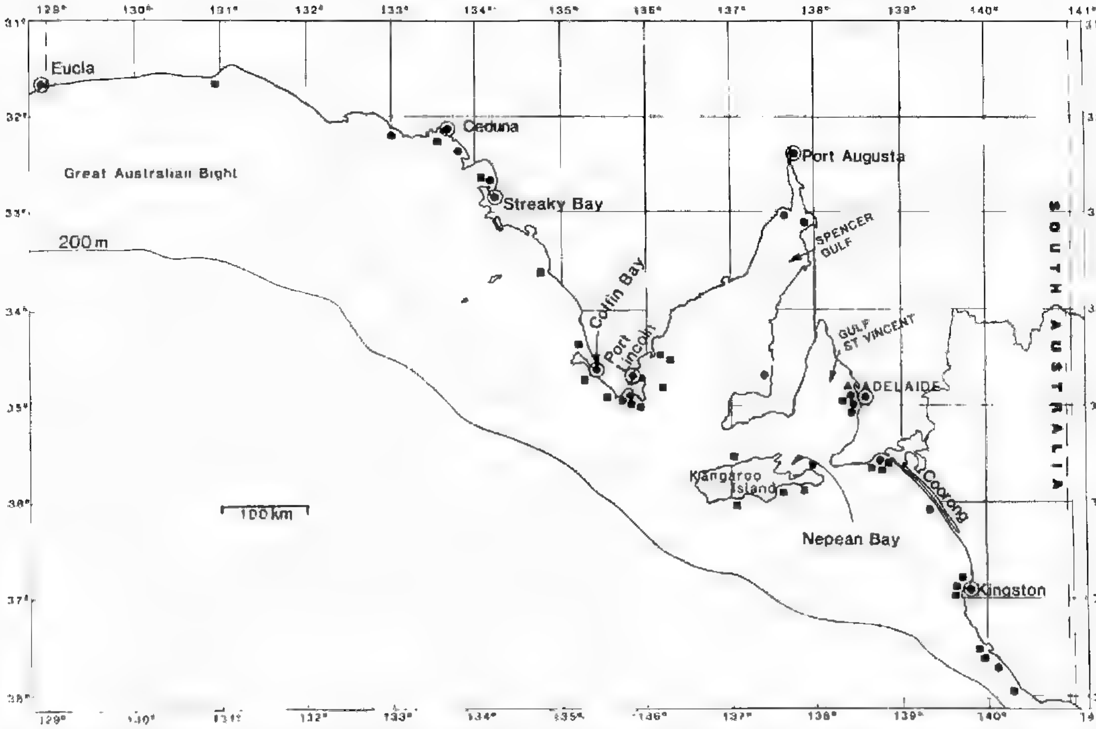

Fig. 7. Geographic distribution of reported strandings of Physeteridae in South Australia, 1881–1989. Each symbol represents a *Kogia simus* (▲), *K. breviceps* (●) or *Physeter macrocephalus* (■) stranding event.

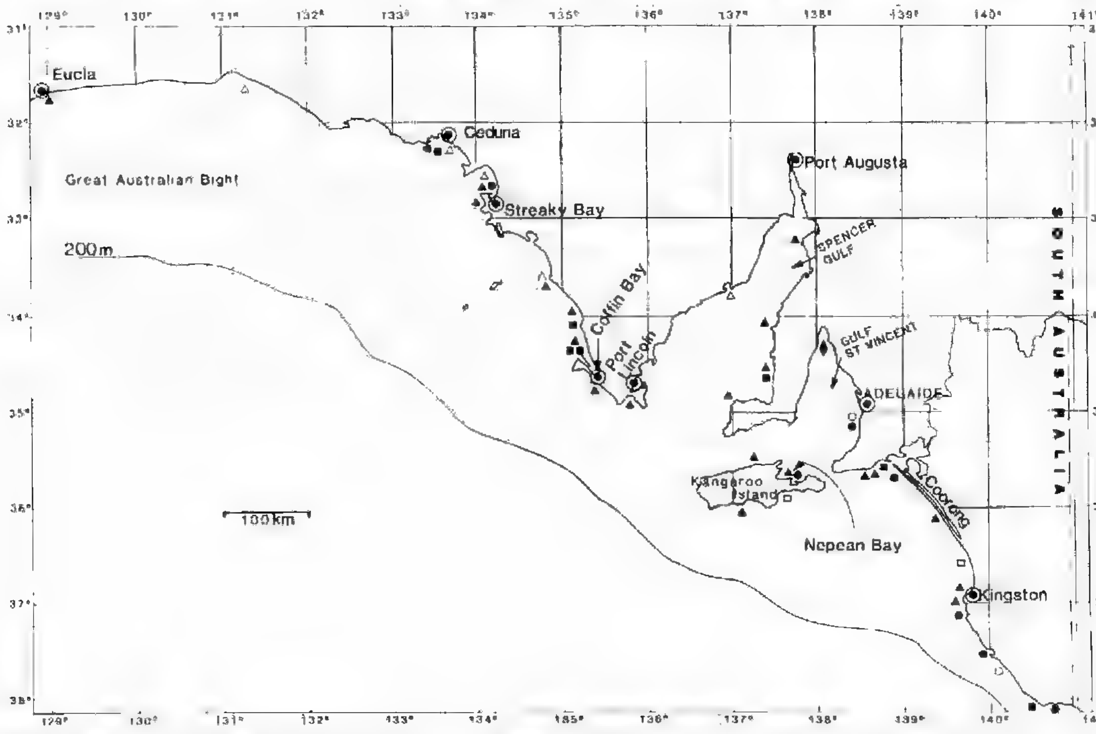

Fig. 8. Geographic distribution of reported beaked whale (Ziphiidae) strandings in South Australia 1881–1989. Each symbol represents a *Berardius arnuxii* (♦), *Ziphius cavirostris* (○), *Hyperoodon planifrons* (■), *Mesoplodon bowdoini* (□), *M. grayi* (●), *M. layardii* (▲), *Mesoplodon* sp. (+) or *Tasmacetus shepherdi* (•) stranding event.

stranded over a wide stretch of the coast, including the gulfs, but none has stranded on Kangaroo Island. The single stranding event of *K. simus* is from Adelaide.

Beaked whale strandings have been recorded along the entire coastline (Fig. 8). Only 25% of the beaked whale stranding events have been within the gulfs region. There are many records from the western side of Eyre Peninsula and along the southeastern coast of the State.

Four species have not been illustrated on the foregoing distribution maps. To our knowledge, *Eubalaena australis* stranded three times during 1881–1990; an adult at Port MacDonnell in the far southeast and two neonates at the Head of the Great Australian Bight. *Grampus griseus* has stranded at four localities: Point Turton (Yorke Peninsula), Coorong, Willson River (Kangaroo Island) and Denial Bay (near Ceduna). The locations of possible *O. orca* strandings have not been reported (see Ling 1991). Mass strandings of *P. crassidens* occurred twice and are discussed under 'Group size of stranded animals'.

*Seasonal trends*

Stranding events (all species combined) were recorded most frequently in January – April and September – October (Fig. 9). However, this trend does not always extend to individual species, or species groups (Figs 10 and 11). Beaked whale and *T. truncatus* strandings were recorded most often in summer (Fig. 10). An increase in rorqual strandings was evident in September (Fig. 11), with six out of the eight being juvenile animals. We have insufficient data on other species, or species groups, to draw conclusions, although there did appear to be slight increases during September – October for *Globicephala* spp., *C. marginata* and *T. truncatus*.

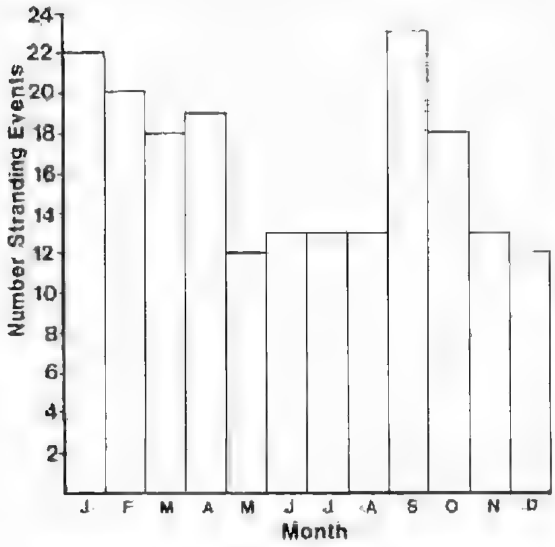

Fig. 9. Month of occurrence of reported stranding events in South Australia, 1881–1989.

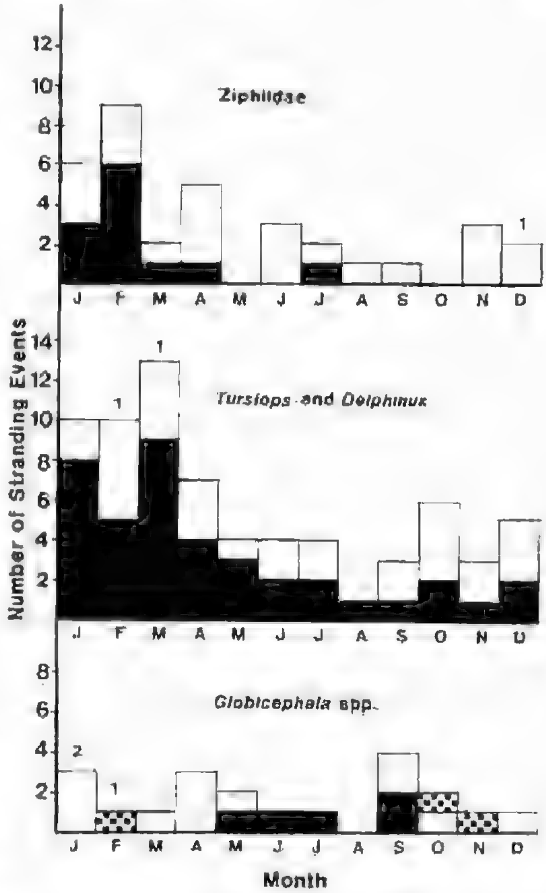

Fig. 10. Month of occurrence of reported stranding events of Ziphiidae, (*Mesoplodon layardii* solid bars), and Delphinidae (*Tursiops truncatus* solid, *Delphinus delphis* open, *G. macrorhynchus* solid, *G. melas*, open, *Globicephala* sp. dotted) in South Australia, 1881–1989. Numbers above bars refer to numbers of neonatal individuals stranded.

Some species appeared to have stranded in specific periods (Figs 10 and 11). *Kogia breviceps* stranded from April to October, mostly between July and October. *Physeter macrocephalus* stranded between July and December. *M. layardii* (January – July) and *G. macrorhynchus* (May – September) have also stranded in somewhat restricted periods, but sample sizes may not be sufficient to be sure of such trends. The stranding of an adult *E. australis* in February is noteworthy, since it is outside the period of sightings of live animals in coastal South Australia and Victoria. The nature of its injuries – almost decapitated (possibly by a large

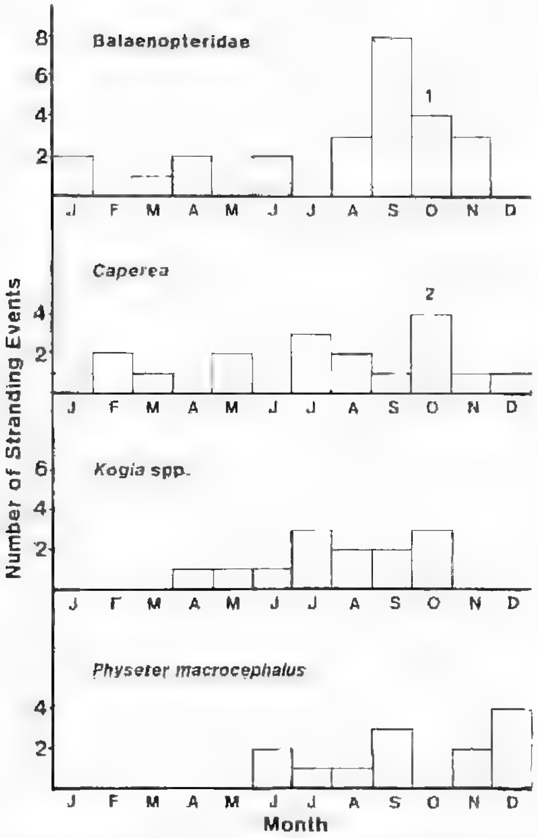

Fig. 11. Month of occurrence of reported stranding events of rorquals (Balaenopteridae), *Caperea marginata*, *Kogia* spp., and *Physeter macrocephalus* in South Australia, 1881–1989. Numbers above bars refer to numbers of neonatal individuals stranded.

ship's propeller) – suggests that it may have died some distance offshore.

Strandings of *T. truncatus* were most frequent in January – March, both within and outside the gulfs (Table 2). Events were recorded throughout the year in both regions, with a possible reduction in July – September outside the gulfs. The pattern for *D. delphis* was similar but there were no strandings recorded in April – June within the gulfs. This could suggest an absence of live *D. delphis* from the gulfs during the autumn quarter.

*Group size of stranded animals*

There were 184 stranding events involving single animals. Fifteen (8%) events had two or three individuals and six (3%) had five or more (Table 3). When two stranded, most of the events were cow/calf associations, especially *Mesoplodon* spp. and *K. breviceps*. Excluded from Table 3 is a possible association between an adult and subadult male *Hyperoodon planifrons* which stranded 60 km and one day apart.

Mass strandings (i.e. more than three individuals) are rare in South Australia. Those that have occurred are described below:

St Kilda (34°45′S, 128°32′E) September 1903

Hale (1931) described briefly the stranding of five *G. melaena* (= *melas*) now identified as *G. macrorhynchus*, in the mud of the St Kilda mangroves. A female stranded first (alive) followed by four males when the tide went out.

Port Prime (34°31′S, 138°18′E) approximately 5 October 1944

Hale (1945, 1959) described the mass stranding of about 250 *P. crassidens* in Gulf St Vincent, north of Adelaide. Approximately 200 stranded (some alive), along the coast of tidal flats in one group, with about 50 others stranding 2.5 km north of the main group and isolated individuals along a 30-km stretch of coast between Port Parham and Port Gawler. Very little biological data were collected or published on the stranded animals which were misidentified as *G. melaena* (= *melas*) at the time of stranding.

Merdayerrah/Eucla (31°41′S, 129°00′E) August 1963

In August 1963, about 59 *P. crassidens* stranded over about eight miles (= 13 km) of sandy beach between Merdayerrah Sandpatch, S.A. and Eucla, W.A. About 12 were on the sandpatch and 47 at Eucla. All were alive or freshly dead when found. Mr H. Gurney (pers. comm. 1989) believes that they stranded at high tide because there were furrows in the sand as if they had been driven up the beach. He recorded males, females and calves but did not count each category. The males were about 20–21 feet (6.4 m) in length and the calves (of varying length), a little less. According to Mr Gurney a storm did not precede the stranding.

TABLE 2. *Stranding events of* Tursiops truncatus *(a) and* Delphinus delphis *(b) which occurred inside and outside Gulf St Vincent and Spencer Gulf during four periods of the year.*

| Location | | Jan – Mar | Apr – June | July – Sept | Oct – Dec |
|---|---|---|---|---|---|
| (a) | Inside gulfs | 9 | 3 | 4 | 2 |
| | Outside gulfs | 9 | 4 | 1 | 4 |
| (b) | Inside gulfs | 5 | 0 | 2 | 4 |
| | Outside gulfs | 7 | 3 | 2 | 4 |

TABLE 3. *South Australian cetacean stranding events involving more than one animal.*

| Species | Number of individuals<br>2 | 3 | 5 | 14–17 | 55 | 60 | c 250 |
|---|---|---|---|---|---|---|---|
| *Delphinus delphis* | 3 | | 1 | | | | |
| *Tursiops truncatus* | 1 | | | 1 | 1 | | |
| *Mesoplodon* sp. | 1 | | | | | | |
| *M. layardii* | 2 | 1 | | | | | |
| *Kogia breviceps* | 4 | | | | | | |
| *K. simus* | 1 | | | | | | |
| *Globicephala melas* | 2 | | | | | | |
| *G. macrorhynchus* | | | 1 | | | | |
| *Pseudorca crassidens* | | | | | | 1 | 1 |

Memory Cove (34°58′S, 136°00′E) 2 May 1977

A school of 55 *T. truncatus* beached on the afternoon of 2 May at Memory Cove, 27 km southeast of Port Lincoln. Thirteen died and local authorities returned the remaining 42 to sea. Twelve of the dead were collected, measured and lodged in the South Australian Museum. Total lengths were 2.29 m – 3.10 m (6 ♀♀, 6 ♂♂). None had food in the stomach and one small male showed evidence of a recent shark attack on his side.

An unsubstantiated report of about 100 dolphins beaching themselves at Louth Bay, 45 km north of Memory Cove on the night of 3 May 1977 was found in P. Aitken's field notes (held in the SAM). Apparently three of these animals died.

American River, Kangaroo Island (35°47′S, 137°46′E) before 22 December 1982

Five male *D. delphis* were found on a rocky beach at American River. Photographs of these animals indicate that they had been dead for a few days when found. American River is at the entrance to Pelican Lagoon, a shallow body of water with a rather restricted entrance. At least five other cetacean strandings have occurred there.

De Mole River, Kangaroo Island (35°42′40″S, 136°46′40″E) 27 April 1985

Between 14 and 17 *T. truncatus* stranded at Snug Cove at the mouth of the De Mole River, on the northwest coast of Kangaroo Island. The sandy beach (200 m wide) and river mouth are very small and form a shallow depression in the cliff-lined coast. The stranding was recorded by a local resident who observed a group of about 80–100 *T. truncatus* swimming offshore at about the time that the stranding occurred. One animal swam in the area for three days after the event. Most stranded animals were about 8–9 feet (2.4–2.7 m) long (D. Seikman pers. comm. 1987).

### *Age of stranded animals*

Overall, 28% of the stranded cetaceans were juvenile, but there was great variation between certain species or species groups. Those having high proportions (>30%) of juveniles were *B. acutorostrata*, *C. marginata*, *Globicephala* spp., other Balaenopteridae and *Kogia* spp. (Table 4). Juvenile *B. acutorostrata* ranged from 3.23–3.96 m (approximately the size at weaning, Jonsgård 1951). Only one physically mature *B. acutorostrata* (9.13 m) and one neonate (2.3 m in October) were recorded. Length at birth has been estimated at about 2 m in *C. marginata*, based on the discovery of what was believed to have been a full-term foetus (McManus *et al.* 1984). Two neonates (2.01 m, which accords with this finding, and 2.10 m) have been recorded in South Australia, both in October (Fig. 11). About 40% of the measured *C. marginata* were roughly half maximum size (6.4 m).

Ziphiids had a low proportion of juveniles (14%), including a neonatal *M. grayi* (2.10 m) that stranded in December (Fig. 10). A stranded neonatal *E. australis* (5.52 m) was found in October. Its state of decomposition suggests it had been dead at least one month and could have been dead for up to four months based on the known calving season for this species in the area (Ling unpublished data). Only 9% of stranded *T. truncatus* were juveniles (Table 4).

TABLE 4. *Relative age of stranded cetaceans in South Australia. Species with insufficient numbers of individuals not included. See text for definition of juvenile length. N = number of individuals for which length recorded.*

| Species | N | % Juvenile |
|---|---|---|
| *Balaenoptera acutorostrata* | 10 | 90 |
| *Caperea marginata* | 16 | 56 |
| *Globicephala* spp. | 17 | 35 |
| Other Balaenopteridae | 12 | 33 |
| *Kogia* spp. | 14 | 31 |
| *Delphinus delphis* | 17 | 18 |
| Ziphiidae | 35 | 14 |
| *Tursiops truncatus* | 32 | 9 |

### *Active and passive strandings*

At least 15% of the recorded stranding events involved live animals (active strandings). In many older stranding records it was not noted whether animals were dead or alive at the time of stranding, so this figure must be considered as minimal. Since 70% of the reported active strandings were after 1970, it is quite likely that more thorough investigations of future strandings (as have been the case in recent years) will result in a higher proportion being recorded as active. Sixteen species, representing all four families occurring in South Australia, are known to have stranded alive (Table 5). Only obviously moribund or decomposed animals were classed as passive stranders and therefore this proportion (6%) of the total number of events is liable to be an underestimate (Table 5). Decomposed carcasses found in remote areas were not added to the passive list unless observers mentioned the carcass having washed up at the time. There was a disproportionate number of large species (e.g. the large mysticetes and *P. macrocephalus*) in this category. (See also Fig. 2 for geographic location of active and passive stranding events.)

TABLE 5. *Cetacean stranding events involving live (active) and obviously dead (passive) cetaceans in South Australia.*

| Species | Number of events<br>Active | <br>Passive |
|---|---|---|
| *Eubalaena australis* | 0 | 1 |
| *Caperea marginata* | 2 | 3 |
| *Balaenoptera acutorostrata* | 3 | 0 |
| *B. edeni* | 2 | 0 |
| *B. musculus* | 0 | 2 |
| *Megaptera novaeangliae* | 0 | 2 |
| *Delphinus delphis* | 5 | 0 |
| *Globicephala macrorhynchus* | 3 | 0 |
| *G. melas* | 1 | 0 |
| *Grampus griseus* | 1 | 0 |
| *Pseudorca crassidens* | 1 | 0 |
| *Tursiops truncatus* | 7 | 0 |
| *Kogia breviceps* | 3 | 0 |
| *K. simus* | 1 | 0 |
| *Physeter macrocephalus* | 3 | 7 |
| *Berardius arnuxii* | 1 | 0 |
| *Hyperoodon planifrons* | 1 | 1 |
| *Mesoplodon* sp. | 1 | 0 |
| *M. grayi* | 1 | 0 |
| *M. layardii* | 5 | 0 |
| Unidentified large whale | 0 | 1 |
| Total | 41 | 17 |

## Discussion

Twenty-five cetacean species have stranded in South Australia. This includes *Mesoplodon hectori* recorded in February 1990 from the Coorong but not the doubtful *B. borealis*. One other species, *Mesoplodon mirus*, has been reportedly sighted (live) in South Australian waters, but without a specimen or photograph to confirm the identity of such a difficult group, the beaked whales, we cannot include this in the State's cetacean fauna. From 19 to 29 species have stranded or are known to occur in other states (Bryden 1978; Paterson 1986; Nicol 1987; Warneke 1988; L. Gibson pers. comm. 1990; J. Bannister pers. comm. 1990). Western Australia has the highest number of species, no doubt because its long coastline includes tropical and temperate waters. South Australia has the next highest, but lacks the tropical dolphins found in Queensland, Western Australian and occasionally New South Wales waters. Australia's cetacean fauna bears a resemblance to that of the southeast coast of southern Africa (Ross 1984). In terms of species composition and in some respects relative abundances in the stranding record, the situation in South Australia is most similar to Victoria and Tasmania. The major differences are many more *C. marginata* and beaked whale (especially *M. layardii*) events in South Australia than in Victoria; and fewer *G. melas*, *P. crassidens* and *Z. cavirostris*; but more *H. planifrons* than in Tasmania. The seventh most frequent strander in South Australia, *K. breviceps*, has not been recorded in Tasmania (Nicol 1987).

The species which occur in South Australia are either cosmopolitan, tropical/subtropical, temperate/subAntarctic or mixed-water in their distribution patterns (Ross 1984). Only *B. edeni* and *G. macrorhynchus* are considered to be tropical/subtropical in nature. The cool waters (15–18°C annual mean) in South Australia would not be expected to support a tropical fauna. However, Gulf St Vincent and Spencer Gulf are appreciably warmer than the waters off the seaward coast in summer. Also, the tropical Leeuwin current, which originates in autumn in the Indian Ocean and dissipates in winter in South Australia, may mix with warm Bight waters and move eastward (Rochford 1986).

All four reliably recorded stranding events of *B. edeni* occurred well within the gulfs (Fig. 6) during April (2), September (1) and November (1). *Balaenoptera edeni* occurs off Western Australia (Chittleborough 1959), but since no sightings of live *B. edeni* have been recorded in South Australia (J. K. Ling unpublished data), it is not known whether this species is resident in the gulfs or simply an occasional visitor. *Globicephala macrorhynchus* has stranded during the winter months inside and outside the gulfs. We suggest that the presence of these species and the frequent strandings and sightings of turtles (A. Edwards pers. comm. 1989) could be related to the Leeuwin current and the warm gulf waters. Zeidler (1989) has suggested that the Leeuwin current may have been responsible for tropical octopus occasionally being recorded in South Australia.

Sergeant (1979) concluded that abundance in the stranding record in most cases reflects the abundance of the free-living population in a particular region. Mead (1979) suggested that *K. breviceps* might be an exception. Other comparable examples are *O. orca*, which occurs in eastern and southern Australia but rarely strands (Bryden 1978; Warneke 1988; Ling 1991; present study), and *E. australis*, which is sighted frequently in coastal waters but also rarely strands. Only five verified strandings of *E. australis* have been reported in South Australia, Victoria and Tasmania (Warneke 1988; present study).

If the stranding record reflects abundance, species that stranded on only one or two occasions (Table 1) may be designated as rare or occasional visitors to South Australian waters. Hence *B. physalus*, *P. crassidens*, *K. simus*, *B. arnuxii*, *M. hectori*, *M. bowdoini*, *T. shepherdi* and *Z. cavirostris* are probably rare here, at least in shallow (<200 m) waters between the continental shelf and the coast. Deep-water and pelagic species such as *P. crassidens* and *Z. cavirostris* (Leatherwood & Reeves 1983; Ross 1984) are frequent stranders in Tasmania (Nicol 1987) and New Zealand (Baker 1983), where deep waters occur closer to shore than in South Australia. The same may apply to *T. shepherdi*: a more common strander in New Zealand (A. Baker pers. comm. 1990) than in Australia. Beaked whales tend to live in deep waters (>200 m) beyond the continental shelf where they feed on deep-water fishes and squid (Ross 1989). They may also feed in areas having underwater canyons (G. Ross pers. comm. 1990) such as the Murray Canyons, southeast of Kangaroo Island, and the canyons southwest of Ceduna (Griffin & McCaskill 1986).

Whether cetacean strandings happen (or are recorded) depends upon many factors including animal movements (seasonal or diurnal), human activity and awareness, the physical environment and the climate. In Tasmania, Nicol (1986) found that cetacean strandings were recorded most frequently in regions with high human activity and a complex coastline. Geraci & St Aubin (1979) concluded that most strandings occur on gently sloping beaches or natural 'traps' in the shoreline.

In South Australia, reported stranding events do not occur evenly along the coast (Fig. 1). They were frequent in regions with large bays (e.g. Coffin Bay/Port Lincoln, Nepean Bay, Streaky Bay) and along westward and southwestward facing coasts (e.g. Coorong, and eastern gulf shores). Observer effort may partly explain these concentrations of reports, because several areas of frequently reported strandings are near cities or are popular with holidaymakers. Reduced observer effort, however, does not account for the small number of reports from the western side of Gulf St Vincent and probably not Spencer Gulf. We believe that prevailing southwesterly winds in winter and spring may contribute to the frequency of strandings along eastern shores (see Fig. 1). Other studies have suggested that adverse weather is associated with strandings (Duguy 1978), but there are few substantiating data (Geraci & St Aubin 1979)

Another important reason for the trends may be that strandings are more frequent where cetacean abundance is high (Sergeant 1979). Presumably abundance is high because productivity of the marine environment is high in some areas, such as where upwelling events occur or deep sea canyons are part of the bottom topography. Upwellings are common summer features in the southeast of South Australia (Lewis 1981; Rochford 1986) and along the coast north of Coffin Bay (P. Petrusivicz pers. comm. 1990). Canyons occur from Kangaroo Island to the Victorian border and in the Great Australian Bight. Some of the areas of high stranding frequency (Fig. 1) can be explained by these oceanographic features.

In South Australia, cetacean stranding events were recorded throughout the year (Fig. 9) with two peaks in frequency; summer and early autumn (January – April), and early spring (September and October). Observer effort would be expected to increase during the summer months, when people spend more time on the beaches and are likely to find stranded animals. Nicol (1986) found that the highest number of strandings in Tasmania was recorded in January and that the winter months of July and August had fewer recorded events. Warneke (1988) also noted that in southeastern Australia more strandings were recorded in summer than in winter. One would expect that in South Australia the stranding frequency of the known migratory species, generally the baleen whales, would increase in winter, but it was spring when many stranded (Fig. 11). It is noteworthy that many of the rorquals that stranded in spring were *B. acutorostrata*, most of which were the size of animals at weaning. Rorquals were absent from the Tasmanian stranding record during the summer months (Nicol 1986).

The early spring peak in the overall record (Fig. 9) cannot be explained by observer effort alone;

wind may be an important factor. Wind velocity and frequency, illustrated in the form of wind roses in the Climatic Atlas of Australia (1988), show an increase in the October quarter for much of coastal South Australia, and coming from a southwesterly direction onto the coast.

Mass strandings are events restricted to the odontocetes (Sergeant 1982) and are most frequently recorded in *Globicephala* spp., *P. crassidens, Lagenorhynchus acutus* and *P. macrocephalus* (Geraci & St Aubin 1979). These are highly social and oceanic species. Mass strandings generally occur where a species is abundant (Sergeant 1982). It is therefore not surprising to find that in South Australia, where shallow waters extend far off the coast and oceanic species would not be expected to occur in large numbers, there have been only six recorded mass stranding events. A similar picture is true for Victoria (seven events: Warneke 1988) and Queensland (two events: Paterson 1986), both with wide continental shelfs. The low number (six; L. Gibson pers. comm. 1990) of mass strandings in New South Wales where waters are deep, may be a reflection of the relatively uncomplicated nature of the coast. In South Australia the species which have mass stranded are *P. crassidens, G. macrorhynchus, T. truncatus* and *D. delphis*.

Overall, the percentage of juveniles which stranded was rather high (28%), a trend also noted by Duguy (1978) in France. Sergeant (1982) concluded that odontocetes have a lower juvenile mortality than mysticetes, probably because of the greater parental care generally associated with odontocete social structure. The present study confirms this, e.g. high juvenile proportions of *C. marginata* and *B. acutorostrata*, but some odontocetes also had about a third juveniles (Table 4). Sergeant (1982) reported that newly weaned and old *B. acutorostrata* strand selectively. In South Australia young *B. acutorostrata*, 3.23–3.96 m in length, have stranded between the months of August and October. This is slightly less than the estimated length at weaning (4.5 m) reported by Lockyer (1984). Births in *B. acutorostrata* in the southern hemisphere are reported to occur in May and June (Lockyer 1984), but in our records one neonatal animal of 2.3 m stranded in South Australia in late September or early October. The body lengths of stranded *C. marginata* (2.01–6.20 m) are more evenly distributed than *B. acutorostrata*, but there is also a tendency for animals to be about the estimated length (*ca* 3.2–3.6 m) at weaning (Ross *et al.* 1975).

In the eastern United States, 17% of the cetacean stranding events involved live animals (Mead 1979). All species with a high incidence of active stranding were offshore forms, *Physeter macrocephalus*, a deep water species, most commonly stranded alive, in contrast to the situation in South Australia and other places (Rice 1989), where single animals are usually dead or moribund. In South Australia, at least 15% of the recorded strandings were active, but recent information suggests a much higher percentage.

The South Australian marine environment is unique: low nutrient levels are offset by upwelling events and proximity to the rich waters south of the Antarctic Convergence; the Indian Ocean influences the oceanographic conditions through several currents; and the gulf waters afford some protection from wind and cold water, at least at some times of year.

It is hoped that additions to the cetacean stranding data base, coupled with a better insight to the State's oceanography, will permit more detailed analysis of the trends identified here and lead to a greater understanding of the biology of the many species of whales that occur in southern Australian waters.

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TRANSACTIONS OF THE

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# RELATIONSHIP OF RESIDUAL HILLS AND SHEET FRACTURES IN THE GAWLER RANGES AND ENVIRONS, SOUTH AUSTRALIA

*BY E. M. CAMPBELL & C. R. TWIDALE**

## Summary

The domical hills developed on silicic volcanic rocks in the Gawler Ranges are typical of many, perhaps most, of their counterparts in other parts of the world, in that they are most satisfactorily explained as etch forms. That is, they are features that have evolved in two stages, the first involving subsurface weathering, the second the stripping of the regolith to expose the bedrock surface beneath. Some of the residual hills developed on granite in the western part of the Ranges, in the Kondoolka and Hiltaba areas, not only differ in morphological detail, but also in their possible mode of origin. Moreover, the region offers evidence relevant to a long-standing debate concerning the origin of sheet fractures.

KEY WORDS: Gawler Ranges, silicic volcanics, granite, sheet structure, bornhardts, etch surface

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## Summary

CAMPBELL, E. M. & TWIDALE, C. R. (1991) Relationship of residual hills and sheet fractures in the Gawler Ranges and environs, South Australia. *Trans. R. Soc. S. Aust.* 115(2), 53-66, 31 May, 1991.

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## Introduction

The Gawler Ranges is a prominent upland located to the north of Eyre Peninsula, in the arid-semiarid interior of South Australia (Fig. 1; Campbell 1990[1]). Developed mainly on the Gawler Range Volcanics of Middle Proterozoic age (Blissett & Radke 1980; Blissett *et al.* 1989[2]), the massif stands highest in the south, where it rises steeply 200-250 m from the piedmont plains to elevations of over 400 m. To the north, hill crests are lower. In the Moonaree area the maximum height above sealevel is 336 m in Bond Hill and Chitanilga Hill, at 317 m above sealevel, is the highest point in the Kokatha region. Here the terrain is also more open, but the transition from hill to plain is everywhere abrupt. For the most part, and especially in the south, the massif comprises ordered rows of domical hills or bornhardts (see Bornhardt 1900; Willis 1934; Twidale 1982a) developed on volcanic rocks.

The Gawler Range Volcanics are crystalline and compact. The rock is physically hard and impermeable. Though well fractured, few of the partings are open and the rock is essentially massive. On the other hand, angular blocks up to 50 cm diameter form a discontinuous veneer on the hillslopes.

The impermeable character of the volcanics enhances the significance of fractures, for it is only by way of such partings that water can penetrate into the rock mass. Three fracture systems, orthogonal, sheet and columnar, crucially influence the morphology of the bornhardts. Each bornhardt is developed on a fracture-defined block of square, rectangular or, more rarely, triangular plan shape (Fig. 2). Each is related to a well-developed, if in places distorted, orthogonal fracture system the components of which trend predominantly northwest-northnorthwest and north-northeast.

In profile the domical shape of the hills is associated with convex-upward sheet structures up to 3 m thick (Fig. 3). In detail, banks of columns defined by polygonal fracture systems, are prominent components of hillslopes (Fig. 4). Some of these columnar joints are due to contraction on cooling but others are of tectonic origin and are related to the regional scale orthogonal systems.

The columnar and orthogonal systems are of considerable antiquity, both predating the Late Proterozoic (Campbell 1990[1]; Campbell & Twidale 1991). The age of the sheet fractures is more difficult to determine but they are probably older than the Beck Surface of Jurassic age (Campbell 1990[1]). Thus the basic morphology of the hills is determined by geological features of great antiquity.

The Gawler Range Volcanics consist predominantly of dacite, rhyodacite and rhyolite that originated as a layered sequence of ashflow deposits or ignimbrites. They were deposited about 1592 Ma. About 1583 Ma they were intruded by the Hiltaba Granite Suite (Fanning *et al.* 1986; Webb *et al.* 1986). The radiometric age determinations obtained from the volcanics and the granite confirm the observed field relations because the former are intruded by the latter. The occurrence of remnants of the volcanics at Mt Cooper, Perfection Well and the Nuyts Archipelago, suggests that the plutonic mass was largely emplaced within the ignimbrite deposit, though much of the original volcanic

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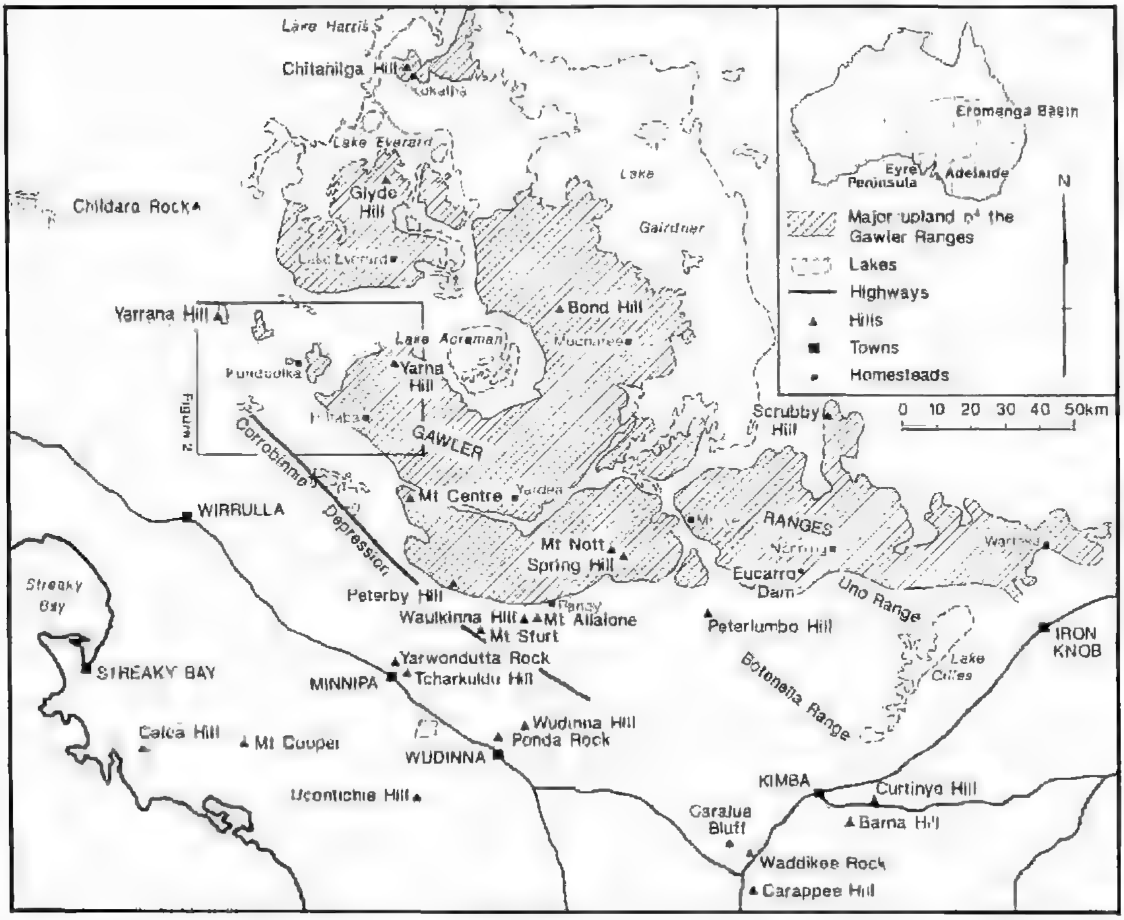

Fig. 1. Location map of the Gawler Ranges, South Australia.

outcrop has been eliminated by weathering and erosion, reducing the original minimum extent from about 80,000 km² to the present 25,000 km² (Blissett 1985).

Within the Ranges the granite is extensively exposed only in the western region around Kondoolka and Hiltaba homesteads and in the north near Kokatha Homestead. In the southwest, the granite was emplaced in a northwest-southeast trending zone extending through Cotton Nob (Fig. 2). The zone of intrusion runs parallel to the fracture-related Corrobinnie Depression (Bourne *et al.* 1974; Binks & Hooper 1984) suggesting that it too may have been developed along a major fracture zone. The contact between the granite and the volcanics is irregular in detail. Patches of volcanic rocks are capriciously distributed on what are essentially granite hillslopes. Some contacts are gently inclined, but most are steep (Fig. 5). A vegetation change commonly accentuates the contrast in rock type, for spinifex is characteristic of the upper slopes of volcanic hills, whereas the vegetation of the granite outcrops is generally dominated by *Acacia tarculensis* — J.M. Black (Whibley 1980) and *Eucalyptus brachycalyx* — Blakely (Jessop & Toelken 1986).

## Origin of the bornhardts

### *Bornhardts developed in Gawler Range Volcanics*

Though all are domical, the bornhardts of the Gawler Ranges, like their counterparts in other areas, vary in their precise form. Individual hills rise to a maximum of 200 m above the adjacent valleys or plains, but low rises only a few metres high are also common. Isolated forms are up to 2 km in diameter, but many bornhardts form interconnected groups that together measure up to 10 km in length (Fig. 6). Typically the bornhardts are rounded or

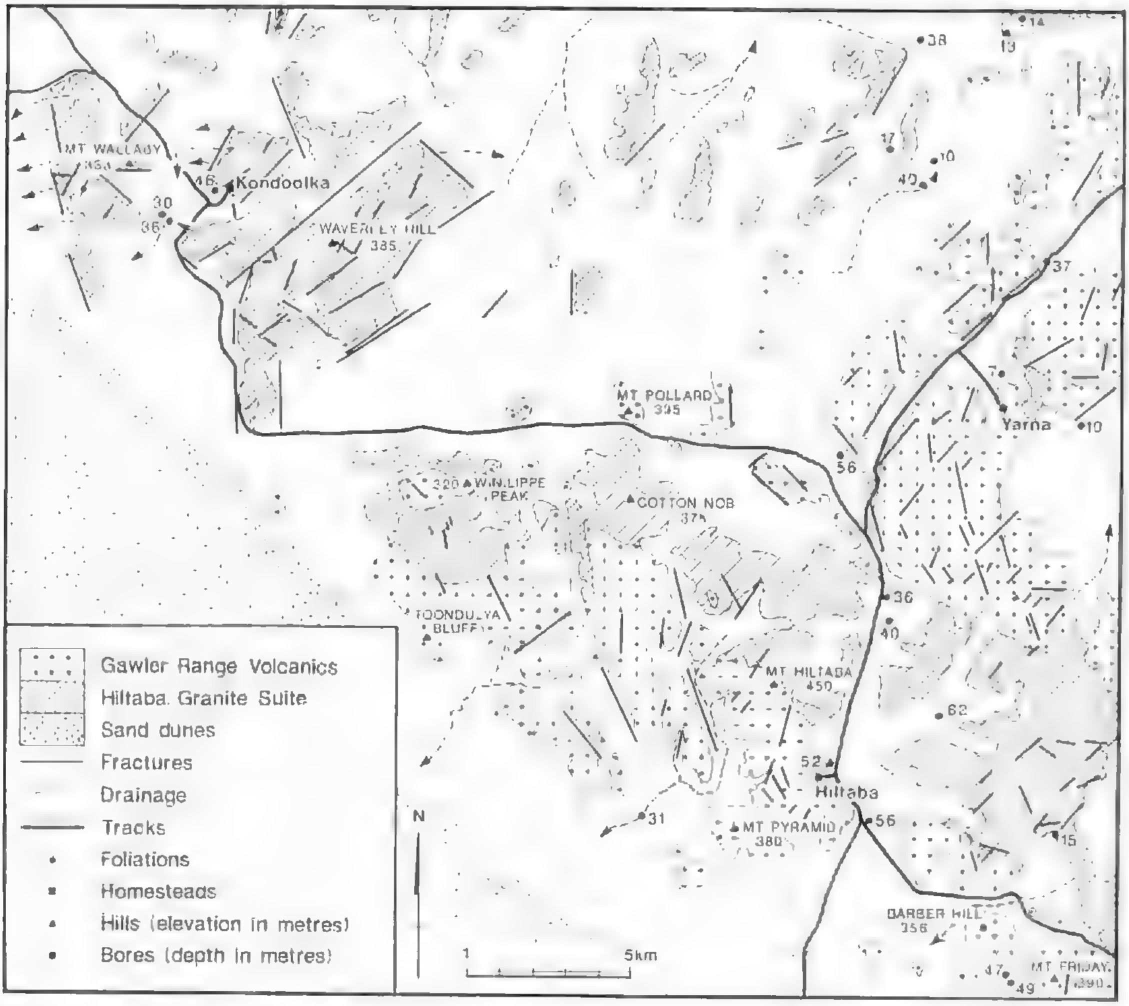

Fig. 2. Plan of the western Gawler Ranges showing the distribution of volcanic and granitic outcrops and inferred fractures.

elliptical in plan, though the linked forms are irregular.

As was recognised by Dickinson (1942) there are prominent bevels preserved on the bedrock crests of many of the bornhardts together forming a summit surface which has been called the Nott Surface (Twidale *et al.* 1976). Most bornhardts are devoid of regolith. Evidence of significant deep weathering of the bedrock occurs only in major valley floors, though the upper slopes of some bornhardts carry patches of a ferruginous rind. The only known remnants of an old regolith, with corestones set in a weathered matrix, are preserved on midslope sites north of Paney Homestead and near Nonning Homestead.

These bornhardts are all probably of etch or two-stage type (Falconer 1911; Linton 1955; Büdel 1957; Twidale 1964, 1982a, 1982b; Campbell 1990[1]). During the Jurassic (and possibly earlier times) the then outcrop of the volcanics was reduced to a surface of low relief beneath which a regolith developed, largely as a result of moisture attack (Fig. 7). The depth of weathering beneath this surface — the Beck Surface — varied, but was deepest along the fractures that define the orthogonal blocks. Then, during the Early Cretaceous, rivers were rejuvenated. The regolith was stripped to expose the weathering front, the Nott Surface. Because of differential weathering, it had been shaped into a series of domical

Fig. 3. Sheet structure coincident with hillslopes in Gawler Range Volcanics, north of Hiltaba Outstation, western Gawler Ranges.

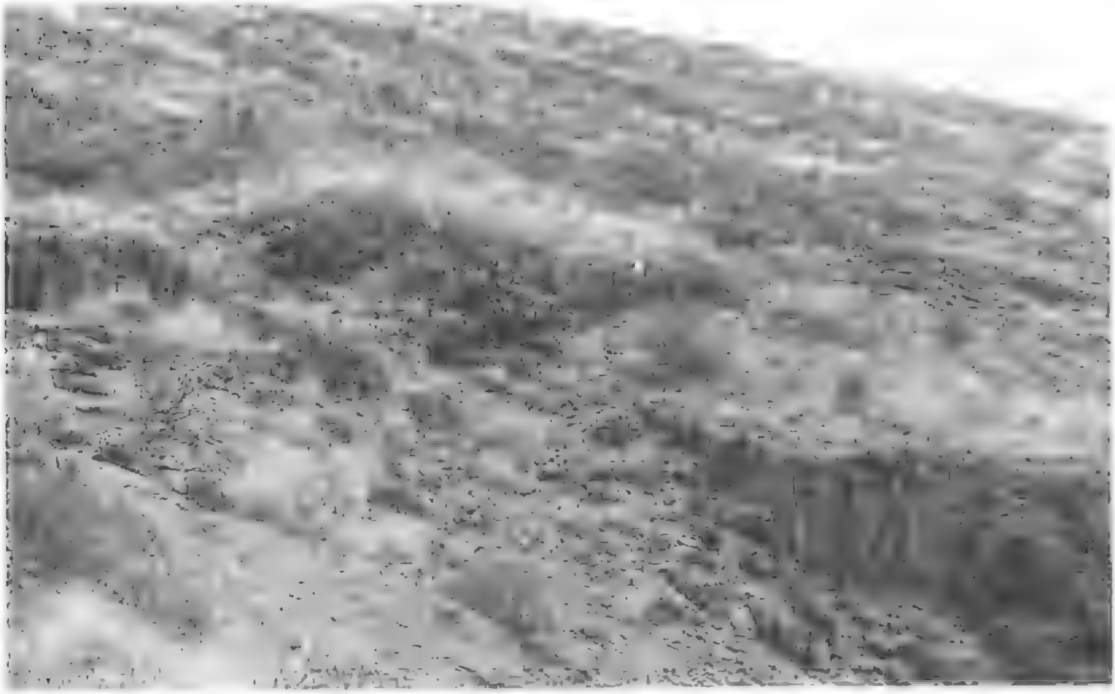

Fig. 4. Banks of columns exposed in lenticular sheet structures, Pancy district, southern Gawler Ranges.

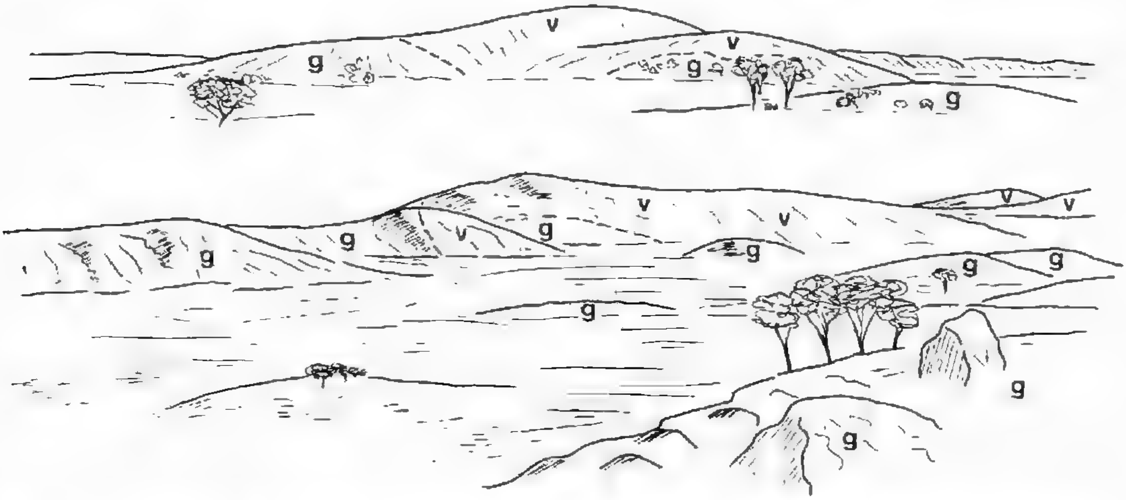

Fig. 5. Sketch showing various examples of the contact of Gawler Range Volcanics with the Hiltaba Granite Suite in the western Gawler Ranges. g = granite, v = volcanic rocks.

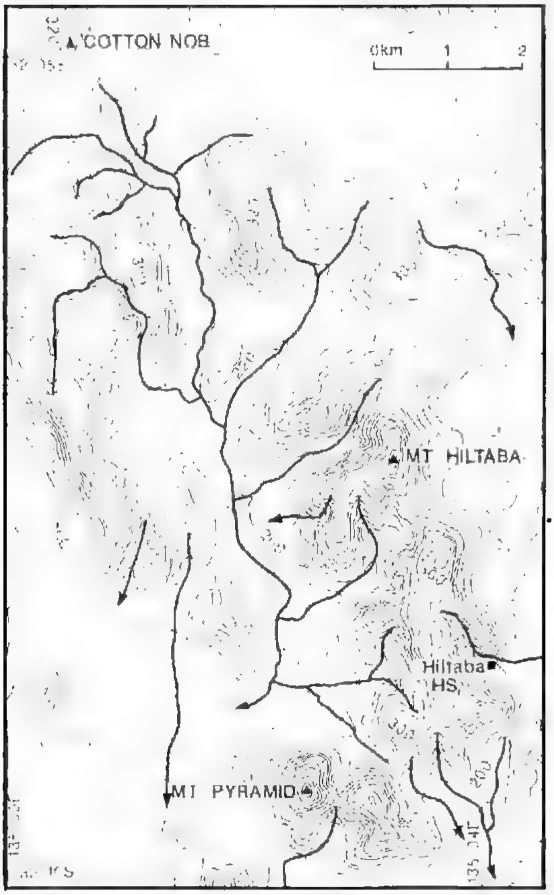

Fig. 6. Contour plan of a group of bornhardts, west of Hiltaba Outstation, western Gawler Ranges (Drawn from South Australia Department of Lands, 1:100,000 Topographic Series, Yartoo sheet).

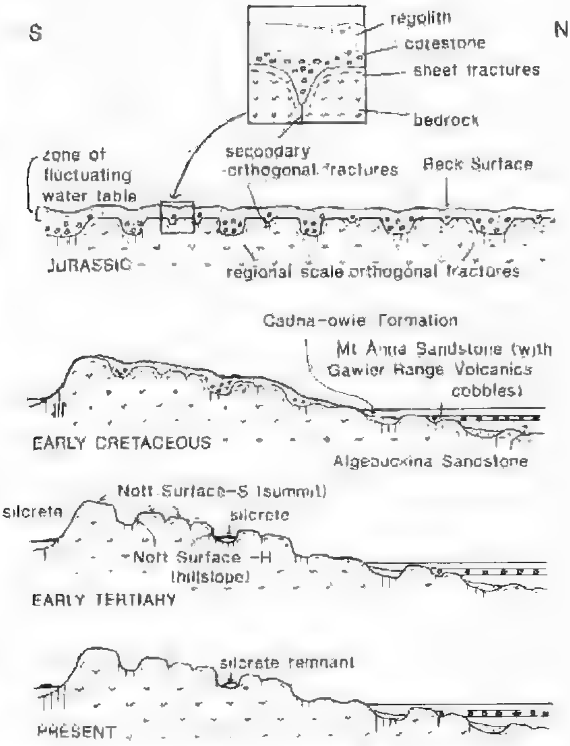

Fig. 7. Sections showing development of the Gawler Ranges from Jurassic times to the present.

protuberances separated by fracture-controlled linear depressions (Wopfner 1969; Campbell 1990[1]; Campbell & Twidale 1991). The landscape revival may have been a consequence of uplift along the Corrobinnie Fault, to give rise to the prominent south-facing escarpment that delimits the Ranges on their southern side; or subsidence of the present Lake Eyre region to produce the Eromanga Basin; or both.

The chronology of events responsible for shaping the volcanic bornhardts is suggested by the relationships between the etch surface in the Gawler Ranges and the stratigraphy of the sedimentary sequences preserved in the Eromanga Basin, located to the north and northwest of the upland. The Mt Anna Sandstone member of the Cadna-owie Formation, of Early Cretaceous (Neocomian-Aptian) age, contains boulders of Gawler Range Volcanics (Wopfner 1969; Wopfner *et. al.* 1970). These boulders are construed as erstwhile corestones formed within the Beck Surface regolith. The boulders low in the Mt Anna Sandstone are more weathered than those above them, consistent with their being derived from the stripping of a regolith. Current directions and thickness measurements also indicate a southerly provenance for the Mt Anna Sandstone (Wopfner 1969). All this suggests that the bornhardts were initiated in the subsurface during Jurassic times and were exposed as landforms during the Early Cretaceous. Thus the Beck Surface beneath which the bornhardts of the Gawler Ranges were initiated, was apparently part of a widely developed middle Mesozoic landscape, remnants of which are found in various parts of central and southern Australia (Twidale & Campbell 1988). That the exposure of the residuals was essentially complete by the Cainozoic is suggested first by the paucity of Tertiary sediments in the Eromanga Basin and of sediments derived from the volcanics in the Eocene and Pliocene formations preserved in the Corrobinnie Depression palaeochannels (Binks & Hooper 1984). Also, silcrete is preserved in valley floors within the Ranges (Hutton *et al.* 1978) and low in the topography, well below the summit surface, marginal to the upland. The silcrete here is probably of Early Tertiary age (Firman 1983) implying that the higher (etch) surface is older.

Such a two-stage mode of development is not unusual. Most bornhardts, though by no means all, evolve in this fashion. Such subsurface weathering demonstrates the primacy of fractures in determining the subterranean penetration of meteoric waters, hence in controlling the pattern of weathering developed, and thus in shaping the bedrock surface and the eventual landform assemblage developed. The Gawler Ranges bornhardts also illustrate the antiquity of elements of the Australian landscape (Twidale 1976; Twidale & Campbell 1988).

### *Bornhardts developed in granite in the southwestern Gawler Ranges.*

In general, the granite exposures stand lower in the landscape than do those of the volcanics. They are more readily weathered than the volcanics. At a regional scale the granites of north and northwestern Eyre Peninsula have been reduced to extensive plains while the Gawler Ranges remain upstanding. This may reflect the lower relative position of the granite, or tectonic uplift of the Gawler Ranges, but the volcanic massif survives essentially intact whereas only small isolated granitic residuals, such as Ucontitchie Hill and Wudinna Hill stand above the level of the plains. In the western Gawler Ranges (Fig. 2) major valleys have been incised in the granite, yet a summit surface of considerable extent, and cut in granite, is preserved around Kondoolka Homestead (Fig. 8). Some higher remnants such as Waverley Hill (385 m) stand almost as high as the most prominent local peaks formed in volcanic rocks.

The preservation of such high granite surfaces needs explanation. There is no evidence of the height to which the granite was emplaced, because the highest peaks, in the Waverley Hill area, do not carry remnants of the volcanic roof that once must have been present. The granite emplacement must have been exposed by the Late Jurassic, since the Nott summit surface is well represented on the granite hills, both in the high plains around Waverley Hill, east of Hiltaba Outstation and in the flattish crests of isolated remnants such as Cotton Nob (375 m). These high remnants owe their elevation to tectonic forces, as they reflect the height of upwelling of the granite magma during its emplacement some 1583 Ma.

Cotton Nob is a nubbin that rises some 50 m from a platform or plinth also eroded in granite and which in turn is bordered by a scarp about 20 m high. Some of the boulders that cover Cotton Nob, including some at the crest, are flared, suggesting that they were once covered by a regolith (Twidale 1962). They, and the stepped morphology of the area as a whole, can be understood in terms of phased or episodic exposure (Twidale & Bourne 1975; Twidale 1982c) and the occurrence of several low hills in the general area and standing some 20 m above the plains or valleys lends support to this interpretation. On the other hand, the granite exposed in the 20 m scarp is, in places, more intensely fractured than is the granite of the nubbin, suggesting that the stepped morphology could be

Fig. 8. Bevelled crests of the bornhardts together form a prominent summit surface, shown here developed on granite east of Kondoolka Homestead, western Gawler Ranges.

a reflection of structural factors, though it is unlikely that fracture density is arranged in concentric patterns as the plinth and boss pattern of topography around Cotton Nob implies.

Mt Wallaby is another high residual of unusual shape and origin. Standing 333 m above sea level and some 130 m above the surrounding plain, Mt Wallaby is a markedly asymmetrical east-west trending ridge of granite (Fig. 9). Its northern slope is gently inclined and boulder-strewn and stands in marked contrast with the bare, precipitous, even overhanging, southern face on which polygonal cracking is well developed. The whole feature, but especially the southern scarp is linear. That it may be related to east-west fractures is also suggested, first by the presence of many prominent latitudinal joints, many of them with associated lineation of the bedrock, and second by the presence, a few hundreds of metres to the east, of two rectilinear east-west drainage lines. In addition, what may have originally been essentially flat-lying joints do, in fact, dip gently northwards. This suggests that Mt Wallaby may be a half horst upthrust at its southern margin.

Most of the granitic bornhardts of the western Gawler Ranges are low domes standing above the valley floors and plains, and there is here good general argument to suggest that they, like their volcanic counterparts in the Gawler Ranges, are two-stage forms. Admittedly there are no exposures like those at Ucontitchie Hill on Eyre Peninsula and elsewhere (see Twidale 1982a) that demonstrate contrasted fracture density between hill and plain. But, whereas the domes are invariably constructed of massive bedrock, the rocks beneath the intervening plains were probably densely fractured since they are altered to depths of up to at least 80 m, and commonly to depths of 40 or 50 m (S.A.D.M.E. borelog information — see Fig. 2).

The valley floor domes are characterised by the presence of numerous boulders, suggesting that the outer shells or sheets of granite have disintegrated. Where domical forms are partially covered by the volcanic host rock, but which can be seen in section (Fig. 5), the outer layers of granite are bouldery. There is no suggestion that the outer boulders represent globules of liquid granite that have migrated into the volcanics (cf Barbeau & Gèze 1957): they are weathering forms. The presence of boulders so close to the contact suggests that the breakdown of sheets takes place beneath the surface, as a result of the infiltration of meteoric

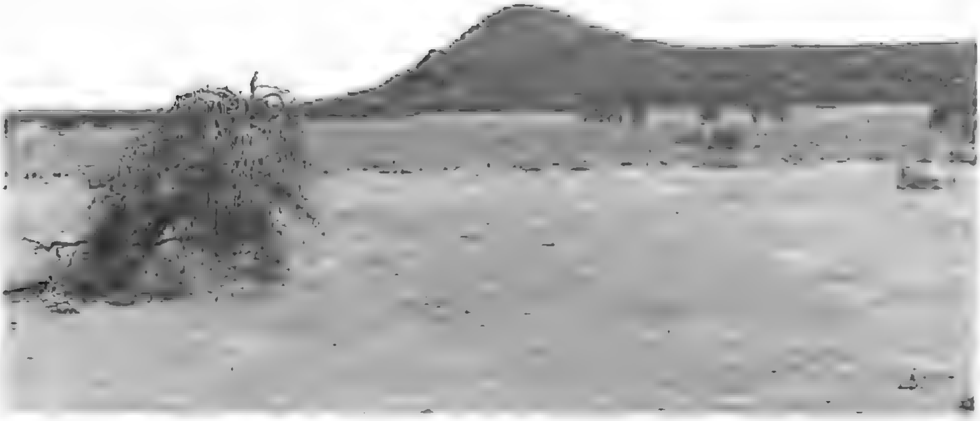

Fig. 9. Mt Wallaby, an asymmetrical granitic residual in the western Gawler Ranges.

waters through the overlying volcanic rocks and into the granite below. This suggestion is sustained by the flared character of some of the boulders (Twidale 1962). On the other hand, the volcanics adjacent to the granite are not themselves notably weathered. Indeed, where the two rock types, volcanic and granitic, are exposed side by side there is no major topographic break between them, though the detailed forms contrast sufficiently for them to be identified from afar (Fig. 5).

The similarity both in shape and in size of the exposed and still partially covered granite rises suggests the possibility that some of the granite hills located close to the volcanic-granite contact may be stocks, bosses or protuberances developed at the margin of the batholith and exposed by the preferential erosion of the overlying host rock (Twidale 1982a, 1982b). Both the exposed residuals and those seen only or partly in section are boulder-strewn nubbins. The exposed and the still-covered appear to display a similar range of size and shape (Fig. 5). In these terms the domes are tectonic forms, i.e. they acquired their essential morphology during intrusion. On the other hand, the volcanics are evidently more resistant to weathering and erosion than is the granite, making it difficult to explain why the host rock should have been weathered and eroded, leaving the granite protuberances intact. Doming and stretching of the volcanics, possibly consequent on the intrusion of the granite, could provide a partial explanation, but the problem essentially remains.

Thus, whereas the bornhardts of the volcanic outcrops of the Gawler Ranges are sensibly uniform in morphology and are all likely of the same origin, the hills of the granitic areas vary in their detailed morphology and, possibly, in their genesis. Some are congeners of the volcanic bornhardts, but others may not be. All however display fracture control in plan.

### *Inselbergs of adjacent areas*

Some volcanic bornhardts within the Gawler Ranges, particularly those located on the margins of the massif, stand in essential isolation and thus can be considered inselbergs – rocky residuals standing abruptly from the level plains around them. Inselbergs are also well represented in the southern piedmont of the Ranges and in the areas west and south of the upland. Indeed, the inselbergs of the southern piedmont like the twin peaks of Mt Sturt, Waulkinna Hill, Peterlumbo Hill and the well named Mt Allalone are of some historical interest for they, together with the scattered volcanic hills of the eastern part of the Gawler Ranges, stimulated Eyre (1845, p. 203) to compare them with 'so many islands in the level waste around them', thus anticipating the now commonly used term 'inselberg'.

The lithology and morphology of these inselbergs varies. Most are granitic in composition though their textures and detailed ages differ from area to area. All, however, are members of the Hiltaba Granite Suite. The hills developed on these materials include such prominent peaks as Wudinna Hill and Ucontitchie Hill as well as low, large-radius domes like Childara Hill, and Polda Rock. Carappee Hill is a prominently stepped gneissic inselberg, and the low domes that comprise Waddikee Rocks are also gneissic. Most are domical but Waulkinna Hill is a nubbin and several others like Ucontitchie Hill carry blocks and boulders.

Isolated elongate residuals, such as Uno Range and Botenella Range composed of sedimentary and metasedimentary rocks are prominent features of the landscape of northern Eyre Peninsula. Some, like Caralue Bluff, have bevelled crests (see also Dickinson 1942). In addition, there are several domical inselbergs also composed of sedimentary material. The areal extent and relief amplitude of these domical forms is similar to that of the volcanic bornhardts of the Gawler Ranges. Mt Allalone, developed on Proterozoic conglomerate, is a low domical hill rising to 342 m above sea level and 120 m above the surrounding plain. Curtinye and Barna hills are composed of Proterozoic quartzite. Curtinye Hill is over 440 m above sea level and rises 110 m above the surrounding gently undulating plain. Approximately 1 km in diameter, it forms part of an ancient fold belt, the sediments of which were highly metamorphosed during the Proterozoic Kimban Orogeny. As a result of this metamorphism, the rocks in Curtinye Hill were altered to quartzites and a schistosity, striking 125° and dipping 80° to the northeast, was developed. The domical form of the hill is only slightly dissected by streams which radiate from the summit. Some have straight sectors which follow the schistosity; others follow the trend of a series of vertical fractures which are predominantly aligned at 55° and 175°. Sheet fractures essentially parallel to the surface of the hill are particularly well exposed on outcrops near the crest and on the eastern slopes (Fig. 10).

Whatever their composition however, the inselberg bornhardts and nubbins on northern Eyre Peninsula are defined by fractures that form orthogonal systems (Fig. 11) and thus reinforce the suggestion (see e.g. Birot 1952; Rognon 1967) that, through the control they exert on the course of weathering, fractures are of prime importance in

Fig. 10. Downslope view on Curtinye Hill, near Kimba, northern Eyre Peninsula, showing sheet fractures parallel to the surface and cutting across near-vertical foliation in the Warrow Quartzite.

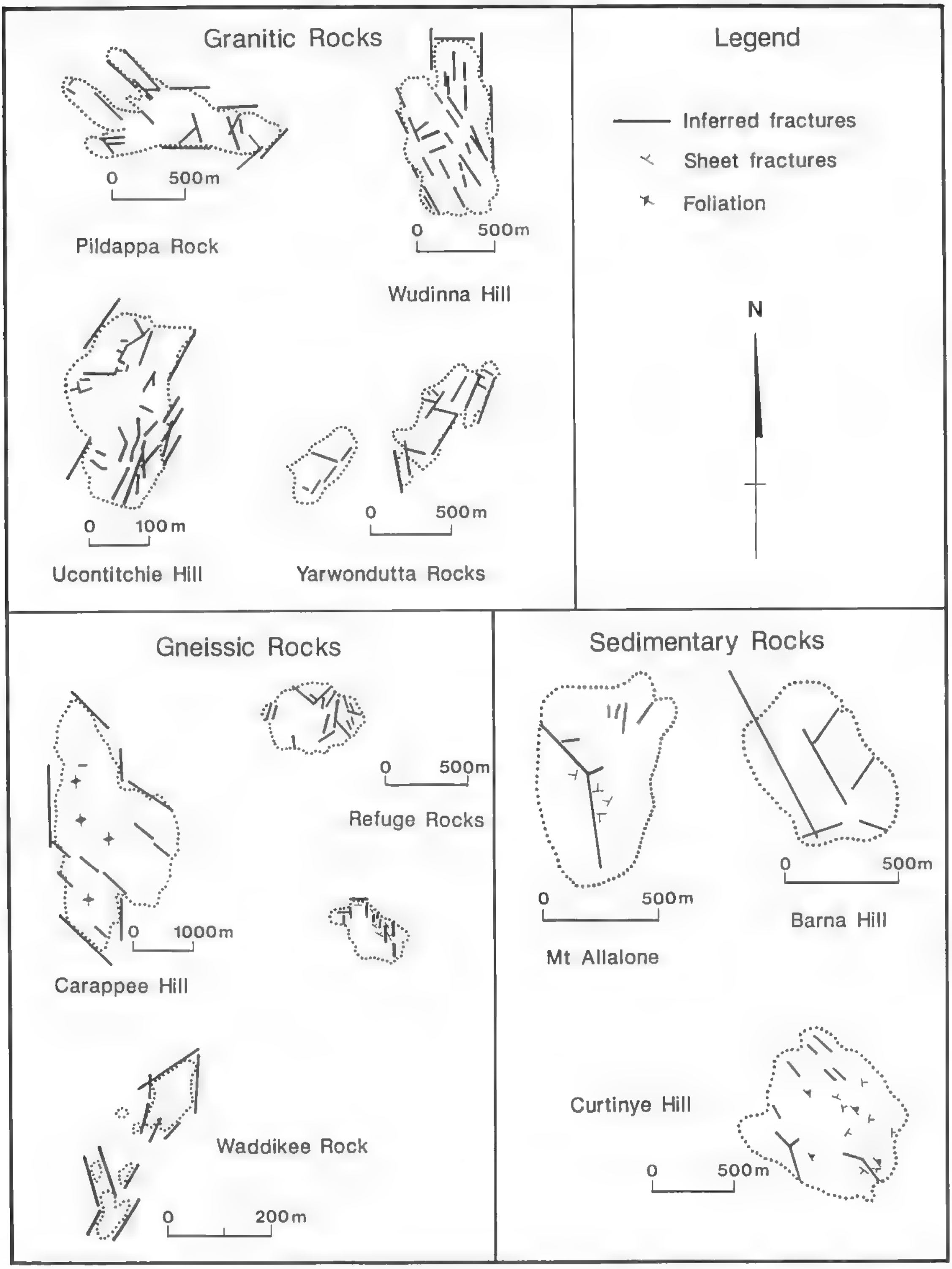

Fig. 11. Prominent orthogonal fracture systems are of prime importance in determining the shape of the inselbergs on Eyre Peninsula.

landform development. The inselbergs of northern Eyre Peninsula are, like their volcanic congeners in the Gawler Ranges, two-stage forms (Twidale 1964, 1982a). The crests of some of the higher forms, residuals like Wudinna Hill, Ucontitchie Hill and Carappee Hill have been putatively dated as late Mesozoic (Twidale & Bourne 1975). If so they are equivalent to the Nott Surface and were initiated by weathering beneath the Beck Surface.

## Implications for explanations of sheet structure

### *Sheet fractures in granitic rocks*

Sheet structure in the granitic rocks, both within the Ranges and to the south on Eyre Peninsula, very much conforms with that described from similar lithological environments the world over. It is well developed and exposed in bornhardts. Flat lying fractures occur wherever granite is exposed, as for instance at Yarwondutta and Calca quarries. In other parts of the world sheet fractures extend to at least 100 m (with no indication of being limited to that depth), but here no such deep exposures are available. The sheet fractures, which take the form of either a single parting or a complex of closely spaced fractures, are commonly disposed convex upwards in the hills. They run parallel to the surface, though some converge to produce wedges. The slabs defined by sheet structure are up to 8 m thick (only about 4 m on Eyre Peninsula), and there is a suggestion that thickness increases with depth. The fractures increase in inclination near major vertical fractures, and cut across lineation, foliation, flow structures and orthogonal joints. Sheet fractures are in some areas older than surficial lamination, but younger than the orthogonal fracture systems.

### *Sheet fractures in volcanic rocks*

In the volcanic areas, hillslopes consist of banks of partially overlapping slabs, that form short, convex-upward bedrock slopes (Fig. 3). They are bounded on their lower sides either by cliffs up to 10 m high in which vertical fractures defining columns are well exposed, or by debris-covered slopes. At and near the summit of the hills the sheet structure is exposed in horizontal benches. In the minor valleys cut in the bornhardts, sheet fractures are generally synformal, though in places, such as near Eucarro Dam, southwest of Nonning Homestead and at Peterby Hill, convex-upward sheet fractures are exposed in the valley floors. In other valleys, however, the sheet factures dip towards the valley axis. The sheet fractures are inclined as much as 40° from the horizontal, but more commonly, within the range 5-20°. Sheet fractures in the Gawler Range Volcanics, unlike those reported from many other areas, tend to divide the rock mass into a series of lenses, each lens being about 4-30 m across and 1-8 m high (Fig. 4). In places the geometry of the sheets is irregular, for example in a valley incised in Peterby Hill swells and depressions that are V-shaped in cross-section reflect the disposition of the sheet fractures. The sheets below, though of similar morphology, are offset with the depressions being located below the swells of the sheet above and the troughs beneath the arches.

The maximum observed thickness of sheets in Gawler Range Volcanics is 3 m. In many exposures, e.g. at Spring Hill, sheets about 1 m thick are underlain by thinner (10 cm) sheets. However, deep exposures are rare. Evidence from the quarry at Mt Cooper suggests that sheet structure may not extend to great depth; although sheets of one metre thickness are present at the surface, sheet structure is not developed in the 10 m or so of rock exposed in the quarry faces.

The surfaces of sheets are essentially fresh, with little or no weathering of the adjacent rock. Polished surfaces, slickensides and the offsetting of columns along sheet fractures at a few sites suggest local lateral dislocation.

Though locally variable, sheet fractures tend to be essentially flat-lying on the crest of the bornhardts and to increase in declination downslope towards the valleys that are associated with the regional and smaller scale orthogonal systems of fractures, suggesting that the sheet structure is either contemporaneous with, or younger than, the orthogonal systems.

Sheet fractures and vertical columnar joints impart a stepped profile to many hill slopes. Some sheet fractures terminate abruptly against the columnar joints, although many merge with the sheet fracture above or below. Sheet fractures transect columnar joints, both of contraction on cooling and of tectonic origin. The sheet fractures must postdate the columns. This relative age is indicated by the offsetting of columns along the sheet fractures.

The sheet structure in the bornhardts developed in Gawler Range Volcanics is not typical of that described from many other areas in that it is associated with columnar joints due to contraction on cooling. The lenticular forms are not typical of sheet structures in general, nor are the evident restriction of the sheet structure to the superficial zones and the presence of thinner sheets beneath thicker ones. The close association of sheet structure with the morphology of the bornhardts is, however, characteristic.

## *Sheet fractures in sedimentary rocks*

Sheet fractures have been described from sandstone in several parts of the world. Bradley (1963), for instance, described thick sheet structures developed in the massive Navajo Sandstone of the Colorado Plateau. Ayers Rock in central Australia is a well known example of an inselberg developed in Cambrian arkose and displaying sheet structure (Twidale 1978). Similarly, sheet fractures are well developed in the domical inselbergs cut in quartzite on northern Eyre Peninsula. Although on Mt Allalone the sheet fractures are apparent on only a few limited outcrops, on Curtinye Hill they are clearly exposed as bare rock outcrops, particularly on the eastern side. The sheet structure cuts across the foliation, and also dips towards the bottom of the minor joint-controlled valleys that score the hill. It is flat lying near the crest, but increases in dip to about 30° further down the slope.

## *Origins of sheet fractures*

Sheet fractures have been explained in many ways. One widely accepted explanation links them with erosional offloading or pressure release. The geometry of the fractures is regarded as consequent upon the form of the land surface. The hypothesis was developed in relation to granitic (Gilbert 1904) and other plutonic rocks that were, it was argued, emplaced deep in the crust, at a depth of several kilometres, but which have been exposed as a result of the erosion of the original superincumbent load. The implied vertical unloading has given rise to radial expansion of which tangential fractures – sheet fractures – are an expression. Though the hypothesis has been criticised (see e.g. Dale 1923; Coates 1964; Twidale 1964, 1973) the offloading, unloading (see e.g. Skinner & Porter 1987) or pressure release hypothesis is still the most favoured explanation of sheet structure. Indeed many geologists refer to sheet fractures as pressure release or offloading joints.

The other generally accepted explanation of sheet fractures involves horizontal compression. There is much evidence and argument to support this suggestion (Merrill 1897; Dale 1923; Twidale 1964, 1973). In particular, many parts of Australia have been shown by direct measurements to be in substantial compressive stress (Moye 1958; Denham *et al.* 1979). Also a suite of minor landforms associated with the release of compressive stress has been described from northwest Eyre Peninsula (Jennings & Twidale 1971; Twidale & Sved 1978; Twidale 1986). In this regard it is notable that within and around the Gawler Ranges sheet structure occurs on bornhardts of various lithologies, including silicic volcanic rocks, which have not been deeply buried. This poses problems for the offloading hypothesis. The orthogonal fractures of the Gawler Ranges are of Proterozoic age. The initiation of the bornhardts at the weathering front did not take place until the early or middle Mesozoic. It is difficult to understand why, given the existence of orthogonal fracture systems, any tendency to radial expansion consequent on unloading was not relieved along partings already in existence rather than through the development of a new set of fractures. It is also questionable whether the pile of volcanic rocks into which the granite of the western Gawler Ranges was intruded was of a sufficient weight to have imposed vertical stresses the relief of which would have produced sheet fractures.

The occurrences of sheet fractures in sedimentary rocks is difficult to explain in terms of the offloading hypothesis where regional and local evidence is suggestive of compression. Curtinye and Barna hills are part of an elongate outcrop of metasedimentary rocks that ought to give rise to strike ridges such as indeed are found on Proterozoic quartzites, for example, in the Botanella Range, in a varied sequence of Proterozoic sedimentary rocks on Eyre Peninsula and in fold mountain belts the world over. Similarly Ayers Rock ought to be a strike ridge; instead there is a bevelled dome. The sheet structure is surely not consequent on the form, as is implied by the offloading hypothesis, for the 'natural' form is a ridge or a range. Cross folding or shearing may be responsible for the stresses which gave rise to sheet structure in Ayers Rock (Twidale 1978) and shearing may have produced the sheet fractures of Curtinye and Barna hills (Fig. 12).

Be that as it may, the sheet fractures of the Navajo Sandstone occur in a different tectonic regime, namely within or close to the Rio Grande (extensional) Rift (Baldridge & Olsen 1989). Convex-upward sheet structure is developed in the Organ Mountains and also in the Rio Grande tensional zone, southern New Mexico (e.g. Seager 1981). These, too, may be interpreted as evidence that sheeting fractures can develop in non-compressional environments. There can be local compression even in a region of extension, just as horsts have been thrust up within tensional rifts. Sheet fractures could, for example, be interpreted as due to upthrust during emplacement of the hot igneous rocks (cf Beche 1839; Whitney 1865; Harris 1888). On balance, however, the offloading hypothesis of sheet fracture formation suggested by Bradley (1963) may be valid in the Navajo Sandstone, though it seems unlikely in the context of the Australian areas discussed.

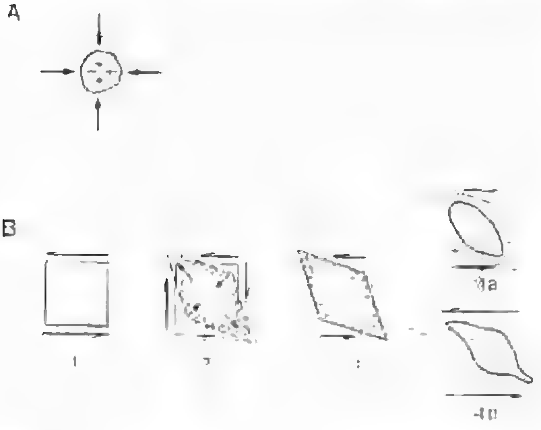

Fig. 12. Cross-folding and shearing, suggested explanations for the stresses which give rise to sheet structure, and hence the domical form of the inselbergs. A – compression, B – shearing.

## Conclusion

The bornhardts developed on volcanic rocks in the Gawler Ranges are features of considerable antiquity that have evolved in two stages, the first involving subsurface differential weathering, the second the stripping of the regolith to expose the bedrock surface beneath. The plan form of the bornhardts is related to complex systems of orthogonal fractures which developed during the Middle Proterozoic. Their domical profile is a result of the development of sheet fractures, which were apparently present prior to a Jurassic period of deep subsurface weathering. The detailed slope morphology of the bornhardts reflects the presence of orthogonal fractures at various scales, of sheet fractures and also of columnar joints due to contraction on cooling of the extrusive mass. The bevelled crests of the bornhardts are part of a summit surface which was exposed by stripping of the regolith in Early Cretaceous times.

In the western Gawler Ranges bornhardts of varied morphology are developed on granite which was intruded into the Gawler Range Volcanics in Middle Proterozoic times. Orthogonal fracture systems and sheet fractures are of fundamental importance in determining the shape of these features. The development of some of these granitic bornhardts may be due to tectonic forces or to structural factors; some may be stocks exposed by erosion of the host rock; most, like their counterparts in the volcanic rocks, are two-stage forms.

The shape of isolated domical inselbergs developed on resistant rocks of varied composition on northwestern Eyre Peninsula is also fracture-controlled. Orthogonal and sheet fractures influenced their morphology. These may also be etch forms.

The residuals of different lithologies present various problems for the offloading hypothesis of sheet fracture formation. Although there is no direct evidence that the sheet structure is due to lateral compression, the confinement of the domes with sheet structures to blocks defined by orthogonal systems, the forms and measurements indicative of crustal compression, and the development of domes in quartzites can all be construed as corroborating this suggestion.

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# DESCRIPTIONS OF THE TADPOLES OF SOME AUSTRALIAN LIMNODYNASTINE LEPTODACTYLID FROGS

BY MARGARET DAVIES*

## Summary

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KEY WORDS: larvae, embryos, *Heleioporus albopunctatus, Neobatrachus centralis, Neobatrachus wilsmorei, Neobatrachus kunapalari, Mixophyes schevilli,* frogs

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## Summary

DAVIES, M. (1991) Descriptions of the tadpoles of some Australian limnodynastine leptodactylid frogs. *Trans. R. Soc. S. Aust.* **115**(2), 67-76, 31 May, 1991.

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## Introduction

Despite considerable advances over the last twenty years, larval forms of many Australian frogs remain unknown. Tyler (1989) documented those for which descriptions have been published, but the breadth of information available for the listed species varies considerably. For instance, some papers provide a composite description of larvae but lack any early developmental data (e.g. Watson & Martin 1973) or illustrations (e.g. Lee 1967): authors rarely have access to complete life history data.

In addition, larvae attributed to species in the early 1960's may be wrongly identified (e.g. larvae of *Neobatrachus pictus* and *N. centralis,* Martin 1965; Watson & Martin 1973). For this reason additional data are necessary to ensure association of larvae with adults of species as currently recognised.

During studies of the ontogeny of bone of limnodynastine leptodactylid frogs, tadpoles of various species have been reared. Some of these have not been described, or have been unreliably associated with adults. Here I provide information on the early development and larvae of *Heleioporus albopunctatus* and on the larvae of *Neobatrachus centralis, N. wilsmorei, N. kunapalari* and *Mixophyes schevilli.*

## Materials and Methods

Material reported here is housed in the Dept of Zoology, University of Adelaide. Larvae were staged according to Gosner (1960). Measurements were made using dial calipers measuring to 0.05 mm or with the aid of an eyepiece micrometer. Measurements taken (in mm) were: total length (TL), body length (BL).

Line drawings were made with the aid of a camera lucida attached to a Wild M8 stereo dissecting microscope. The format of the larval descriptions follows Anstis (1976).

## Results

### *Heleioporus albopunctatus* Gray
FIGS 1-5

The earliest stage available was an embryo within the egg membranes at stage 20 (Fig. 1) which is perched on a large yolk sac around which the tail is wrapped laterally. In five of six embryos the tail is wrapped sinistrally and in the sixth, dextrally. The cornea is not yet transparent but the eye is partially pigmented. External gills are not apparent and ventral adhesive organs cannot be located. The stomodaeal pit has differentiated into a mouth consisting of an upper lip overhanging an unperforated mouth cavity. The olfactory pit also is unperforated. A well-developed orifice (anal opening) is located at the junction of the tail with the body (Fig. 1). The embryo is lightly pigmented with a brilliant yellow yolk sac.

By stage 22 the olfactory pit has become perforated to form the nares. Two upper and two lower tooth rows have begun to keratinize. The tail remains wrapped around the yolk and curved up over the face covering one nostril and the corner of the eye (Fig. 2). The yolk sac shows the beginnings of coiling and the anal opening remains prominent. Blood vessels are present on the tail fins. A yellow spot occurs on the top of the head at the level of the anterior extremities of the eyes. The embryo remains in the egg membrane at this stage. External gills are absent but an aperture is detectable on the left hand side in the usual position of external gills. Ventral adhesive organs also are absent. The embryo is covered with a fine dusting of fine brown pigment.

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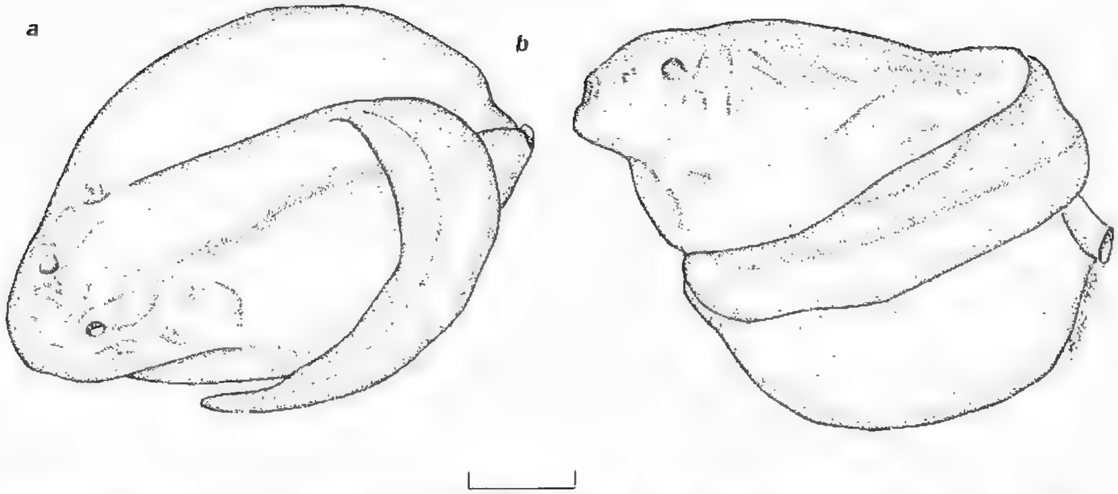

Fig. 1 Embryo of *Heleioporus albopunctatus* at stage 20: a, dorsal and b, lateral views. Scale bar = 1 mm.

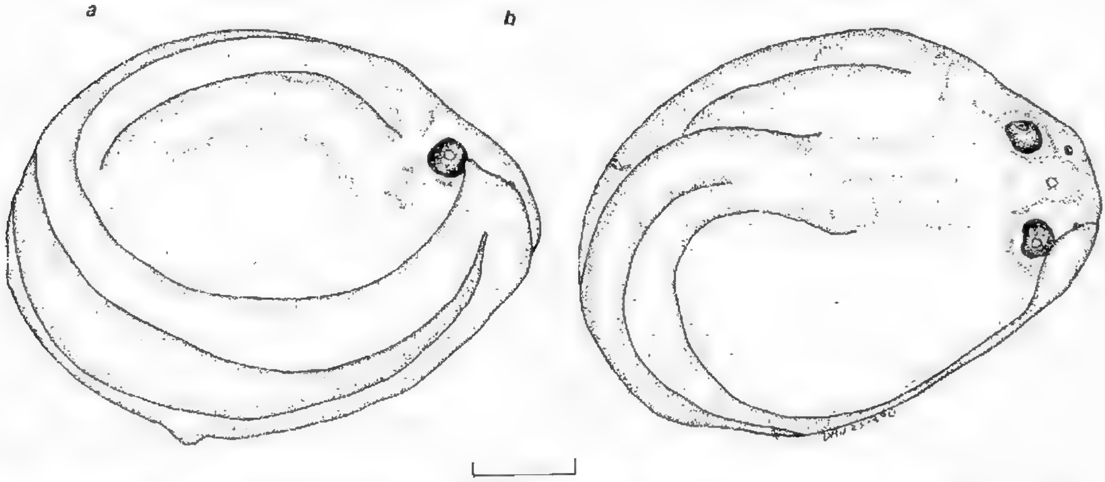

Fig. 2. Embryo of *Heleioporus albopunctatus* at stage 22: a, lateral and b, dorsal views. Scale bar = 1 mm.

By stage 24 the embryos have hatched. The tail is flexed at its tip and the mouth is situated anteroventrally (Fig. 3). Later at this stage the tail loses some of its flexure. The anus is dextral and open. The operculum has closed but the spiracle has not formed.

By stage 25, the mouth is directed anteroventrally. The tail is still very slightly flexed and the spiracle is forming. Coiling of the gut is detectable, but it remains yolk-filled.

At stage 26, the gut appears yolk-filled but is fully coiled. Keratinization is incomplete on the tooth rows but is apparent in some state on all the presumptive mouth structures.

By stage 28 the tadpoles are feeding and the mouth parts are fully formed.

A larva at stage 33 is illustrated in Fig. 4.

The body is elongate and widest at the eyes. The snout is evenly rounded in dorsal view and slopes gently in lateral view. The nares are dorsolateral and sessile. The moderately large eyes are dorsolateral. The spiracle is sinistral, ventrolateral and visible from above. It opens posterodorsally and has a constant diameter along its length. The anal tube is dextral, long and opens about halfway up the ventral fin. The tail fin is not arched and is gently rounded terminally with the dorsal fin extending along the posterior 1/10 of the body and deepest

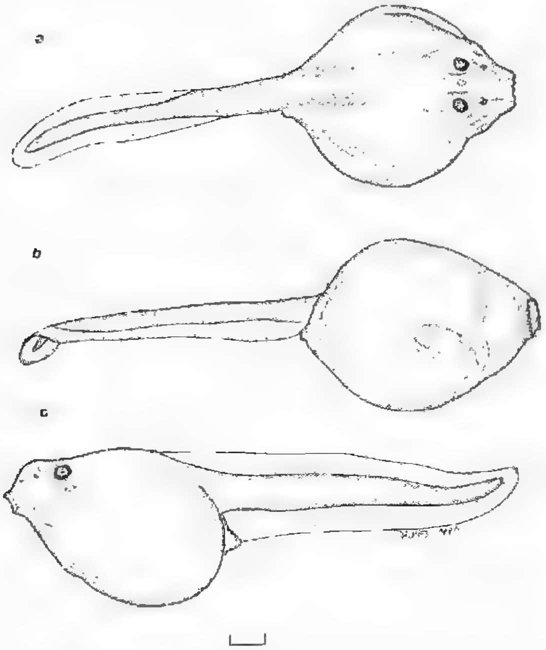

Fig. 3. a, Dorsal, b, ventral and c, lateral views of a larva of *Heleioporus albopunctatus* at stage 24. Scale bar = 1 mm.

approximately halfway along its length. The ventral fin is deepest about 1/3 of the way along its length. Tail musculature is moderately thick and tapers to a fine point posteriorly. The mouth is anteroventral. There are six upper and three lower rows of labial teeth. The second – sixth upper and first lower rows are divided (Fig. 5). The horny beak is of moderate proportions. Tail musculature is pigmented and pigmentation also occurs on the dorsal and ventral fins (Fig. 4).

Meristic data of tadpoles are provided in Table 1.

*Comment:* Lee (1976 p.388) reported that the tooth row formula as recorded here is the "maximal observed" and that variability occurs: "commonly 1 or 2 complete, up to 5 incomplete upper labial tooth rows; 3 lower labial rows, 2 may be incomplete".

The mouth illustrated in Fig. 5 is essentially the same as that illustrated by Watson & Martin (1973) for *H. australiacus.* However the absence of external gills in developing *H. albopunctatus* is not mirrored in *H. australiacus.* Watson & Martin (1973) reported external gills in this species. No comment was made about absence of adhesive organs. Adhesive organs (oral suckers) rapidly disappear after stage 21

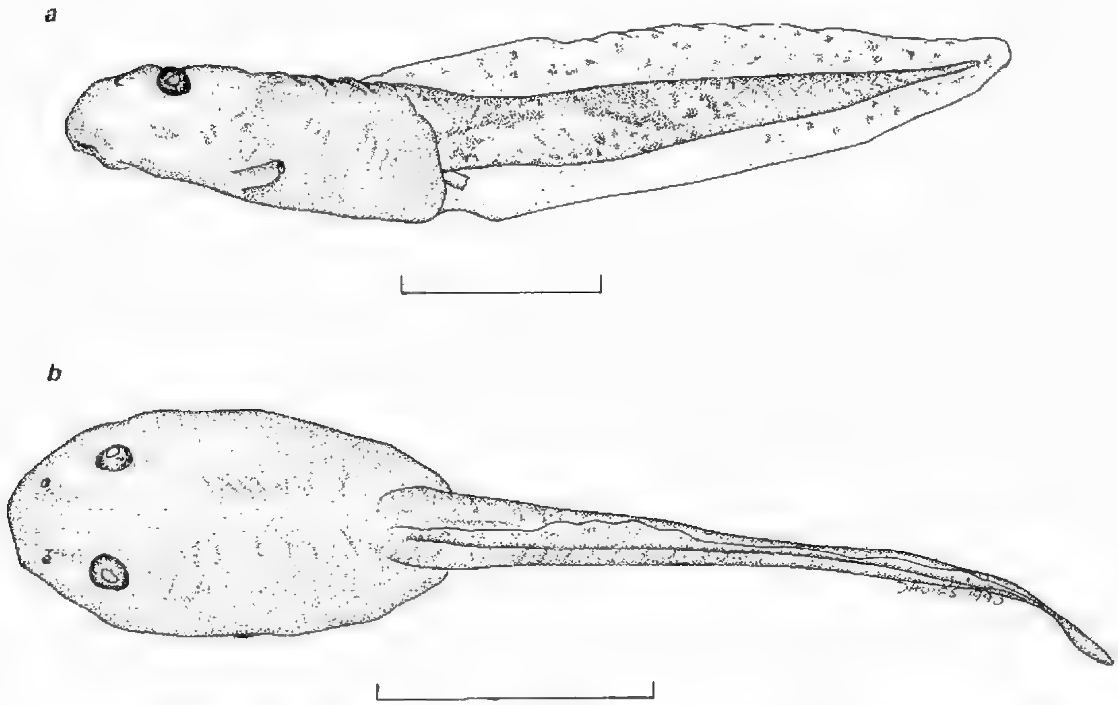

Fig. 4. a, Lateral and b, dorsal views of a larva of *Heleioporus albopunctatus* at stage 33. Scale bar = 10 mm.

TABLE 1. *Measurements (in mm) of tadpoles.*

| Species | Stage | Total length × (range) | Body length × (range) | n |
|---|---|---|---|---|
| *Neobatrachus centralis* | 27 | 23.8 | 9.8 | 1 |
| | 29 | 36.7 | 14.9 | 1 |
| | 32 | 35.5<br>(35.5) | 15.7<br>(15.6–15.8) | 2 |
| | 34 | 37.9<br>(37.6–38.2) | 15.9<br>(15.3 16.5) | 2 |
| | 35 | 37.2 | 17.4 | 1 |
| | 36 | 43.31<br>(33.7–50.7) | 18.97<br>(16.8–23.0) | 14 |
| | 37 | 50.0<br>(48.2–51.8) | 22.7<br>(22.4–23.0) | 2 |
| | 38 | 49.99<br>(46.0–57.1) | 21.46<br>(19.8–25.0) | 9 |
| | 39 | 50.93<br>(49.3–52.3) | 23.19<br>(21.6–23.6) | 4 |
| | 41 | 49.77<br>(45.6–54.5) | 19.58<br>(16.9–21.1) | 12 |
| | 42 | 39.47<br>(35.7–41.7) | 17.23<br>(16.1–18.0) | 3 |
| | 43 | 31.38<br>(22.5–40.7) | 17.66<br>(16.9–19.3) | 8 |
| | 44 | 19.43<br>(15.8–21.6) | 16.95<br>(15.6–20.1) | 6 |
| *N. wilsmorei* | 34 | 49.6 | 19.1 | 1 |
| | 40 | 59.8 | 26.1 | 1 |
| | 41 | 62.9<br>(61.4–64.4) | 26.1<br>(25.7–26.5) | 2 |
| *N. kunapalari* | 36 | 40.7 | 17.1 | 1 |
| *Mixophyes schevilli* | 24 | 98.03<br>(86–116.4) | 34.6<br>(31.1–39.5) | 4 |
| | 25 | 87.53<br>(75.4–107.2) | 30.27<br>(23.3–36.0) | 9 |
| | 31 | 58.4 | 21.5 | 1 |
| | 32 | 59.2 | 21.9 | 1 |
| | 33 | 63.4 | 22.9 | 1 |
| | 33/34 | 66.7 | 23.5 | 1 |
| | 34 | 64.0 | 22.9 | 1 |
| | 35 | 68.25<br>(66.7–70.6) | 25.23<br>(24.6–26.6) | 4 |

TABLE 1. *Measurements (in mm) of tadpoles.* (continued)

| Species | Stage | Total length<br>$\bar{x}$ (range) | Body length<br>$\bar{x}$ (range) | n |
|---|---|---|---|---|
| *Mixophyes* (continued)<br>*schevilli* | 37 | 70.13<br>(67.2–75.0) | 23.63<br>(23.1–24.2) | 3 |
| | 38 | 71.7 | 23.4 | 1 |
| | 39 | 74.45<br>(72.7–76.2) | 21.95<br>(21.2–22.7) | 2 |
| *Heleioporus*<br>*albopunctatus* | 26 | 15.3 | 6.0 | 1 |
| | 27 | 16.4<br>(16.3–16.5) | 6.05<br>(6.0–6.1) | 2 |
| | 28 | 22.6<br>(20.8–24.4) | 8.6<br>(8.0–9.2) | 2 |
| | 29 | 27.0 | 9.2 | 1 |
| | 33 | 40.9 | 14.1 | 1 |
| | 35 | 45.7<br>(42.5–47.4) | 15.43<br>(12.5–17.1) | 3 |
| | 37 | 47.1 | 15.1 | 1 |
| | 38 | 47.25<br>(46.6–47.9) | 17.7<br>(17.5–17.9) | 2 |
| | 41 | 55.9 | 21.2 | 1 |
| | 42 | 44.6 | 18.1 | 1 |
| | 43 | 28.98<br>(23.6–34.40) | 16.55<br>(16.0–17.1) | 2 |
| | 44 | 18.5 | 18.3 | 1 |

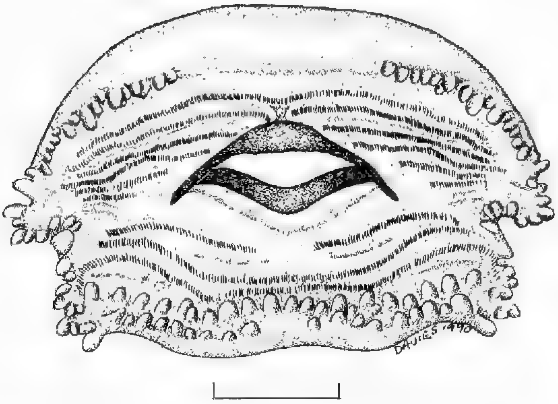

Fig. 5. Oral disc of a larva of *Heleioporus albopunctatus* at stage 33. Scale bar = 1 mm.

(Gosner 1960). The earliest stage examined here is stage 20 and it may be that the structures disappear at an earlier stage in *H. albopunctatus* (the form or oral suckers varies both systematically and ontogenetically (Gosner 1960)).

### *Mixophyes schevilli* Loveridge
### FIGS 6–7

A tadpole at stage 36 is illustrated in Fig. 6. The body is ovoid and widest behind the eyes. The snout is evenly rounded in dorsal and lateral views. The nares are dorsal and sessile, opening laterally. The relatively-large eyes are dorsolateral. The spiracle is sinistral, short and ventrolateral with a large orifice directed posterodorsally, and is not visible from above. The diameter of the spiracular tube is

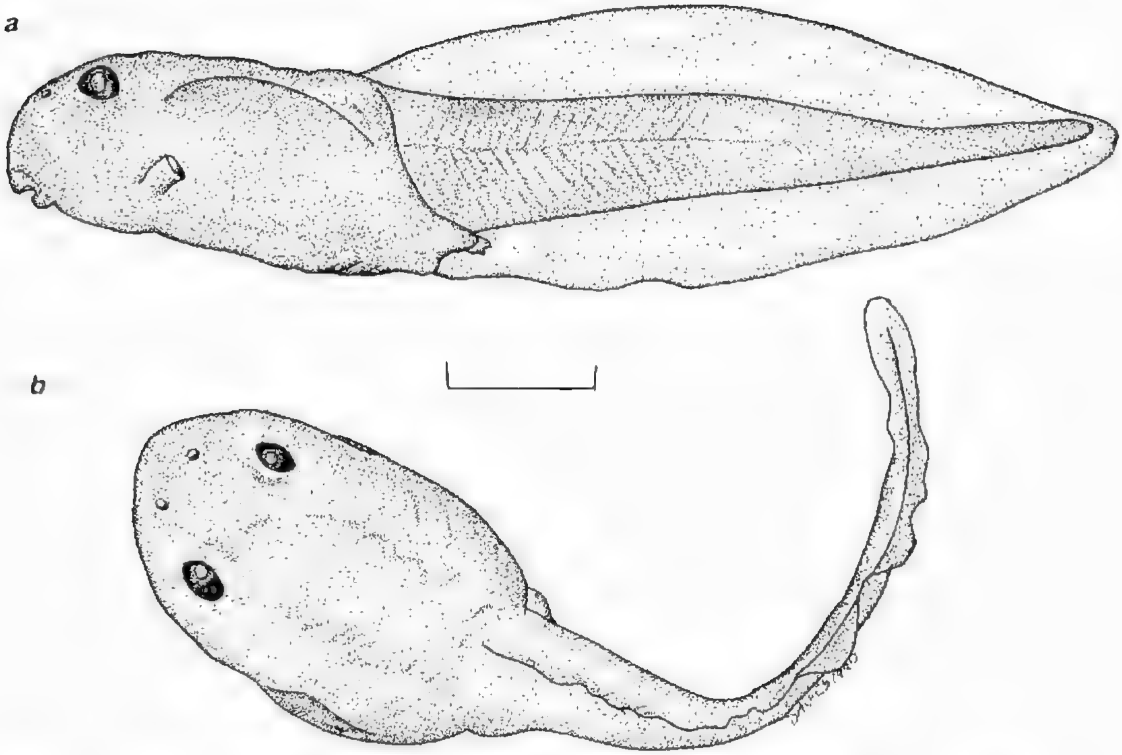

Fig. 6. a, Lateral and b, dorsal views of a larva of *Mixophyes schevilli* at stage 36. Scale bar = 10 mm.

relatively constant along its length. The anal tube is dextral and hidden in a membranous sac which also surrounds the developing hind limbs. At this stage, the feet protrude from the sac. The anus opens about halfway up the ventral fin. The tail fins are arched, the dorsal fin commencing in the posterior 1/10 of the body, being deepest approximately half way along its length. The tail fin is slightly rounded at its terminus. Tail musculature is thick, tapering to a point posteriorly. Tadpoles are heavily pigmented, pigmentation extending over the tail musculature and fins. The mouth is ventral with the oral disc surrounded by a papillary border of moderately fine papillae (Fig. 7). There are six upper and three lower rows of labial teeth and five or six rows occur laterally on each side near the angle of the jaw. All the upper rows except the most anterior are divided. The second and third lower rows are undivided. The horny beak is of relatively fine proportions.

Meristic data on tadpoles of *M. schevilli* are provided in Table 1.

*Comment: M. schevilli* can overwinter as very large tadpoles at stage 25 (Trenerry 1988[1]). This phenomenon is reflected in the mensuration data.

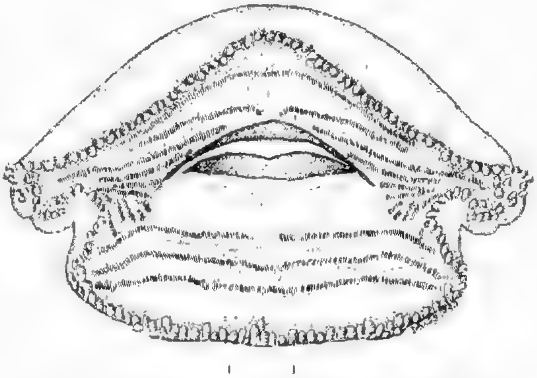

Fig. 7. Oral disc of a larva of *Mixophyes schevilli* at stage 36. Scale bar = 1 mm.

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[1] Trenerry, M. P. (1988) The ecology of tadpoles in a tropical rainforest stream. B.Sc. (Hons) Thesis, Dept of Zoology, James Cook University of North Queensland. Unpubl.

Some of the material measured was reared to metamorphosis in the laboratory whilst the remainder was collected and preserved in the overwintering condition at stage 25.

Tyler (1965) described the oral disc of *M. schevilli* as *Litoria nannotis* (Liem 1974). He recorded six upper and three lower tooth rows, but only three lateral rows of teeth.

Martin (1967) reported six upper, three lower lateral and three lower labial tooth rows with a complete papillary border in *M. fasciolatus* whilst Watson & Martin (1973) recorded six upper, five to six lower lateral and three lower labial tooth rows with a complete papillary border in *M. balbus*. The mouth of this species, illustrated by Watson & Martin (1973, Fig. 4B), is very similar to that of *M. schevilli* reported here. These authors also reported development of the hind limbs in a membranous sac in the early stages. This latter phenomenon presumably is a lotic adaptation shared with other sympatric stream-dwelling species such as *Nyctimystes dayi* and *Litoria nannotis* (Davies & Richards 1990). However, lotic adaptations in *M. schevilli* are not as prominent as those of *M. fasciolatus* (Martin pers. comm.).

### *Neobatrachus wilsmorei* (Parker)
FIGS 8–9

A tadpole at stage 34 is illustrated in Fig. 8. The body is elongately ovoid and widest posterior to the eyes. The snout is slightly truncated in dorsal view and gently sloping in lateral view. The nares are dorsal, sessile and poorly-separated. The relatively-large eyes are dorsolateral. The spiracle, with an attached inner edge, is sinistral, ventrolateral and not visible from above. The spiracular opening is wide; the diameter of the spiracular tube decreases slightly from its origin to its opening. The anal tube is dextral, relatively long and opens about ⅗ of the way down the ventral fin. The tail fins are arched and rounded terminally, the dorsal fin commencing in the posterior ⅛ of the body, being deepest

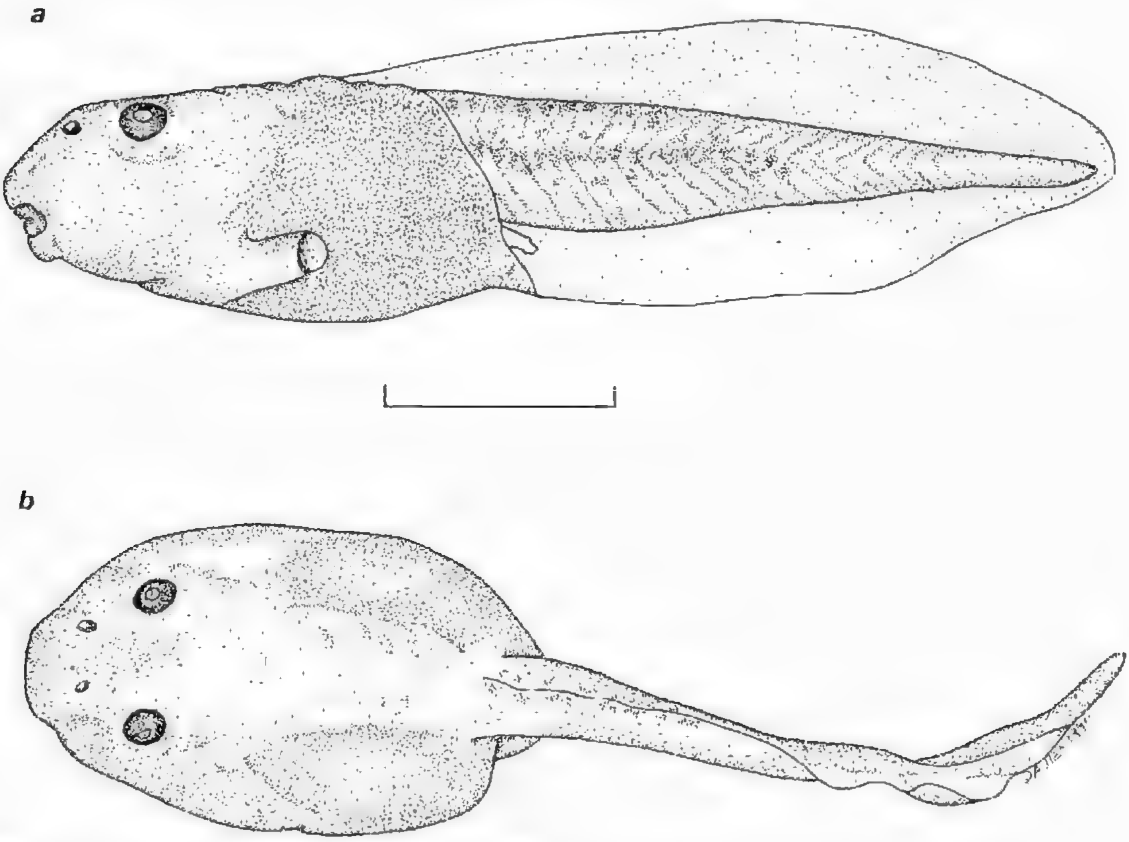

Fig. 8. a, Lateral and b, dorsal views of a larva of *Neobatrachus wilsmorei* at stage 34. Scale bar = 10 mm.

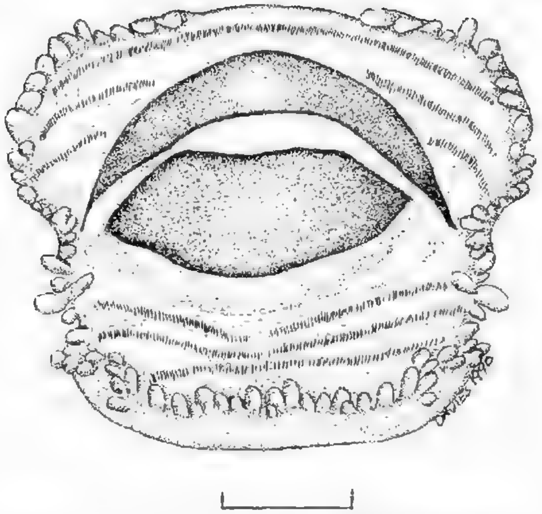

Fig. 9. Oral disc of a larva of *Neobatrachus wilsmorei* at stage 34. Scale bar = 1 mm.

approximately ⅔ along its length. The ventral fin is deepest about halfway along its length. Tail musculature is thick, narrowing to a fine point posteriorly.

The mouth is anteroventral. Labial papillae extend anterolaterally, laterally and posteriorly around the mouth disc with an anterior median gap (Fig. 9). There are three upper and three lower labial tooth rows. The first upper and the second and third lower rows remain undivided. The horny beak is robust.

Tail musculature is finely pigmented as is the dorsal fin. The ventral fin is pigmented only in its posterior third. The head and body are dusted with fine pigment.

Keratin appears on the distal edge of the inner metatarsal tubercle at stage 41.

Measurements of this tadpole are shown in Table 1. A metamorphosing tadpole at stage 45 had a snout-vent length of 20.6 mm.

### *Neobatrachus centralis* (Parker)

### FIGS 10–11

A tadpole at stage 36 is illustrated in Fig. 10. The body is ovoid and widest across its mid region. The snout is evenly rounded in dorsal view and lateral view. The nares are dorsal, sessile and poorly-separated, opening anterolaterally. The relatively large eyes are dorsolateral. The spiracle is sinistral, ventrolateral, not visible from above and with an attached inner edge. The wide orifice opens dorsally and the spiracular tube increases in diameter very slightly from its origin to its opening. The anal tube

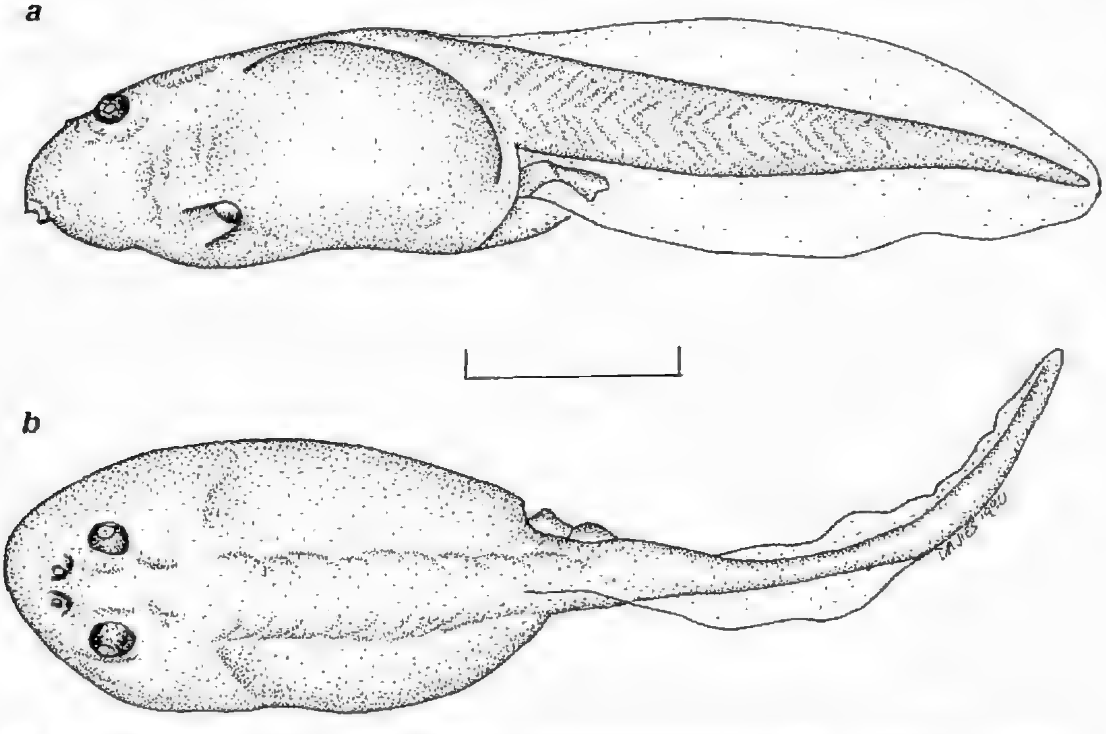

Fig. 10. a, Lateral and b, dorsal views of a larva of *Neobatrachus centralis* at stage 36. Scale bar = 10 mm.

is median and relatively long. The tail fins are arched and rounded terminally, the dorsal fin not extending over the body and deepest approximately halfway along its length. The ventral fin is deepest approximately halfway along its length. Tail musculature is moderately thick narrowing to a point posteriorly. The mouth is anteroventral. Labial papillae extend anterolaterally, laterally and posteriorly around the mouth disc, being interrupted anteriorly. There are four upper and three lower rows of labial teeth (Fig. 11). The first upper and second and third lower rows are undivided.

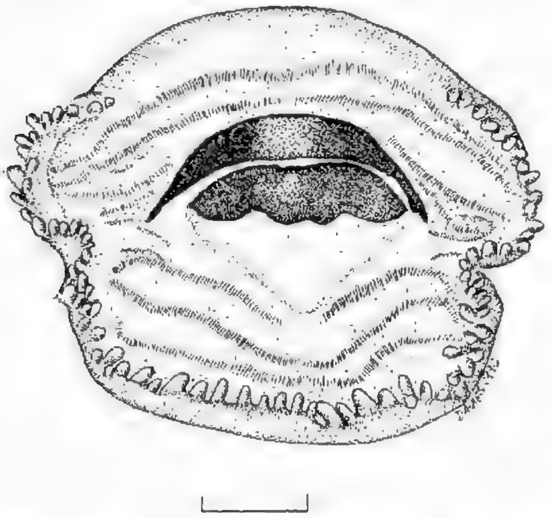

Fig. 11. Oral disc of a larva of *Neobatrachus centralis* at stage 36. Scale bar = 1 mm.

A dark pigment crescent is located around the nares. The remainder of the body is dusted with pigment granules. A very faint dusting of pigment granules covers the tail musculature and the dorsal fin but is absent from the ventral fin.

Earlier stages of *N. centralis* have little or no pigment. Keratin is formed on the distal edge of the inner metatarsal tubercle at stage 41. A metamorphosing individual at stage 45 had a snout-vent length of 14.5 mm. Measurements of *N. centralis* tadpoles are shown in Table 1.

### *Neobatrachus kunapalari* Mahony & Roberts
### FIGS 12–13

A tadpole at stage 36 is illustrated in Fig. 12. The body is ovoid and widest posterior to the eyes. The snout is evenly rounded in dorsal view and gently sloping in lateral view. The nares are dorsal, sedentary and opening anterolaterally. The relatively-large eyes are dorsolateral. The spiracle is sinistral, ventrolateral, not visible from above and with an attached inner edge. It opens dorsally and the tube diameter decreases very slightly along its

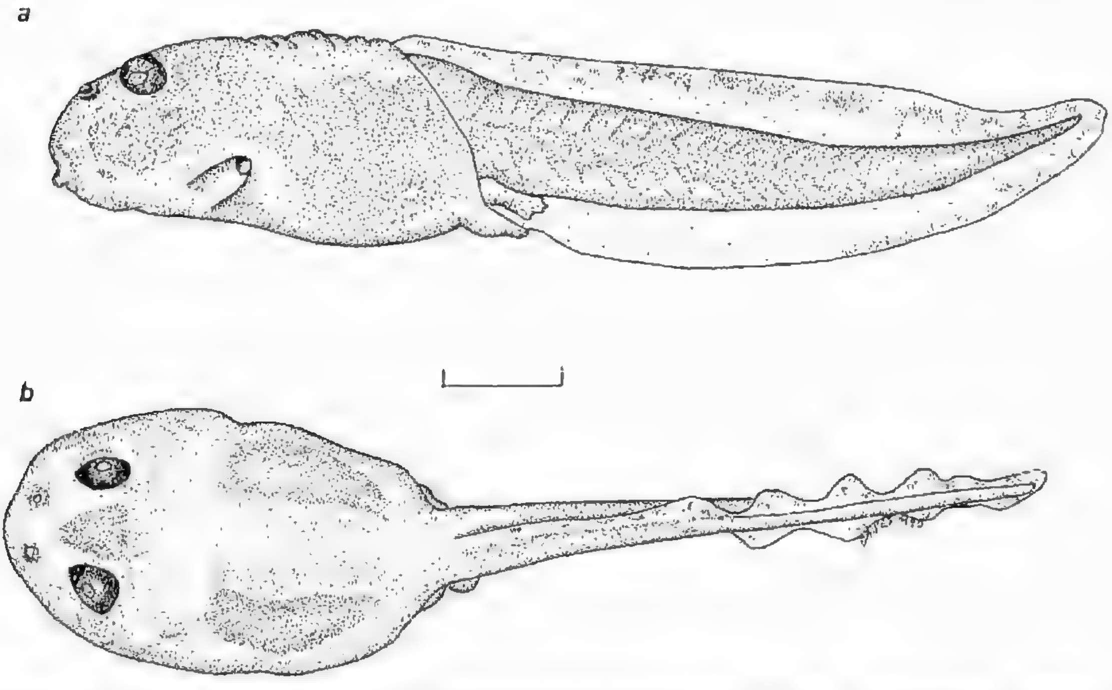

Fig. 12 a, Lateral and b, dorsal views of a larva of *Neobatrachus kunapalari* at stage 36. Scale bar = 10 mm.

length from the origin to the orifice. The anal tube is long, dextral and opens about ⅔ of the way up the ventral fin. The tail fins are poorly-arched and rounded terminally. The dorsal fin does not extend along the body and is deepest about halfway along its length. The ventral fin is deepest about halfway along its length. Tail musculature is moderately thick, narrowing terminally.

The mouth is anteroventral. Labial papillae extend anterolaterally, laterally and posteriorly being interrupted anteromedially (Fig. 13). There are three upper and three lower rows of labial teeth. The third upper and first lower rows are divided. The horny beak is of moderate proportion.

The head and body are heavily dusted with pigment, as are tail fins and tail musculature. A circle of very dark pigment surrounds the nares. The ventral surface is unpigmented.

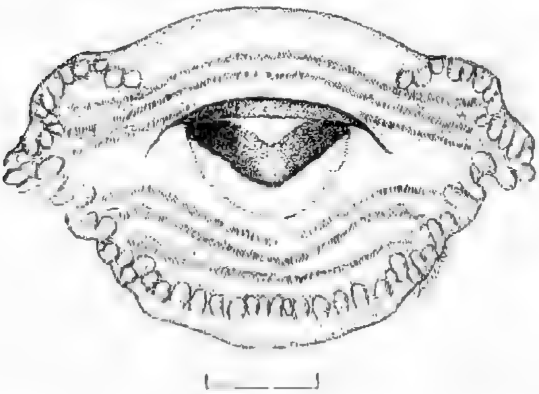

Fig. 13. Oral disc of a larva of *Neobatrachus kunapalari* at stage 36. Scale bar = 1 mm.

*Comment:* More species of *Neobatrachus* have been described or redefined in recent times than of any other limnodynastine genus (Tyler & Ledo 1973; Roberts 1978; Tyler *et al.*, 1981; Mahony & Roberts 1986). For this reason, the data supplied by Martin (1965) for *N. pictus* and by Watson & Martin (1973) for *N. centralis* may have been based on misidentified material. Tyler (1989) reidentified the *N. pictus* of Martin (1965) as *N. sudelli* and a redescription of *N. centralis* is provided here.

*Neobatrachus* tadpoles are known to grow to a very large size in their natural state: Martin (1967) reported tadpoles of 73 mm total length.

*N. centralis* and *N. wilsmorei* are closer to the short body with a strongly arched tail recorded for *N. sudelli* and *N. pictus* by Martin (1965) and Watson & Martin (1973) than is *N. kunapalari* which has a more streamlined body. None of the species examined here has the spiracle free along its inner edge as reported in *N. sudelli* by Martin (1965).

## Acknowledgments

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# PERKINSUS (PROTOZOA: APICOMPLEXA) INFECTIONS IN ABALONE FROM SOUTH AUSTRALIAN WATERS

*BY P. J. O'DONOGHUE*, P. H. PHILLIPS* & S. A. SHEPERD†*

## Summary

A total of 234 abalone were collected from nine sites in South Australian coastal waters and examined for infections with the protozoan parasite *Perkinsus* sp. Infections were detected in ten *Haliotis laevigata* from one location in Gulf St Vincent and in nine *H. rubra* from another location in Spencer Gulf. All infections were characterized by the presence of macroscopic necrotic nodules (0.5-8.0 mm in diameter) in the adductor muscles and mantle. Microscopic examination revealed the nodules to contain variable numbers of host amoebocytes and numerous developmental stages of the parasite, including single ovoid trophozoites (10.0-17.5 μm) and larger rounded schizonts (12.5-35.0 μm) containing vacuolated merozoites. The morphological and ultrastructural characteristics of the parasites were similar to those previously described for *P. olseni.* A total of 240 Pacific oysters *(Crassostrea gigas)* were also examined from four commercial farms in neighbouring coastal waters but no *Perkinsus* infections were detected.

KEY WORDS: Apicomplexa, *Perkinsus,* abalone, *Haliotis,* morphology.

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## Summary

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KEY WORDS: Apicomplexa, *Perkinsus*, abalone, *Haliotis*, morphology.

## Introduction

Two abalone species are fished commercially from South Australian coastal waters; blacklip abalone, *Haliotis rubra* Leach, and greenlip abalone, *H. laevigata* Donovan. Since 1972, licensed divers have reported the occurrence of yellowish pustules in the flesh of *H. rubra* collected near Neptune Island in Spencer Gulf. The pustules render the flesh of the abalone unacceptable for processing and marketing. Microscopic examination revealed the pustules to be caused by a protozoan parasite, *Perkinsus olseni* Lester & Davis, 1981. Only two other *Perkinsus* spp. have been described; *P. marinus* from the American oyster *Crassostrea virginica* (Mackin *et al.* 1950; Perkins 1969) and *P. atlanticus* from the clam *Ruditapes decussatus* (Azevedo 1989). In recent years, local divers have become increasingly concerned with dwindling stocks of *H. laevigata* along the western shore of Gulf St Vincent. *Perkinsus* infections were detected in *H. laevigata* collected from reefs south of Edithburgh (Lester 1986). The present investigation was carried out to determine the geographic extent of *Perkinsus* infections in greenlip and blacklip abalone from South Australian coastal waters, and whether *Perkinsus* infections occur in commercially-farmed Pacific oysters *(Crassostrea gigas)* from neighbouring waters.

## Materials and Methods

Nine sampling sites were selected from the three abalone fishery management zones of S.A. (Fig. 1, Table 1). Licensed divers collected approx. 30 abalone at random from each site between April and October 1986. A Fisheries Officer also collected approx. 60 oysters from each of four commercial oyster farms. The abalone and oysters were fixed by immersion in Davidson's fluid immediately after collection and the species, sex and shell length were

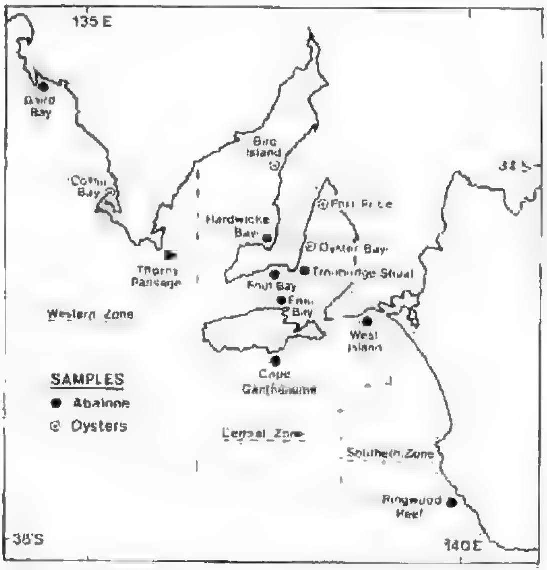

Fig. 1. Locations of sampling sites in South Australian coastal waters from which abalone and oysters were collected.

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recorded in the laboratory following shell removal. The adductor muscles and mantle were examined for macroscopic lesions on all superficial aspects and internally through a series of longitudinal incisions 1 cm apart. Suspicious lesions were excised together with surrounding tissue. Small blocks of mantle, adductor muscle and gonad tissue were also sampled from each abalone and oyster. Tissues were embedded in paraffin wax, sectioned at 5 μm thickness, stained with haematoxylin and eosin and examined by light microscopy at 100–400 × magnification. Tissue blocks found to contain parasites were then processed for electron microscopy by de-paraffinization in xylol containing 2% osmium tetroxide, clearing in propylene oxide and embedding in epoxy resin (TAAB Laboratories). Ultra-thin sections were cut at 75 nm thickness, stained with 6% uranyl acetate and 0.5% lead citrate and examined in a transmission electron microscope (JEM 100 CX, JEOL, Tokyo). Voucher specimens of fixed tissues containing parasites were deposited with the South Australian Museum, Adelaide (SAM E2180 1).

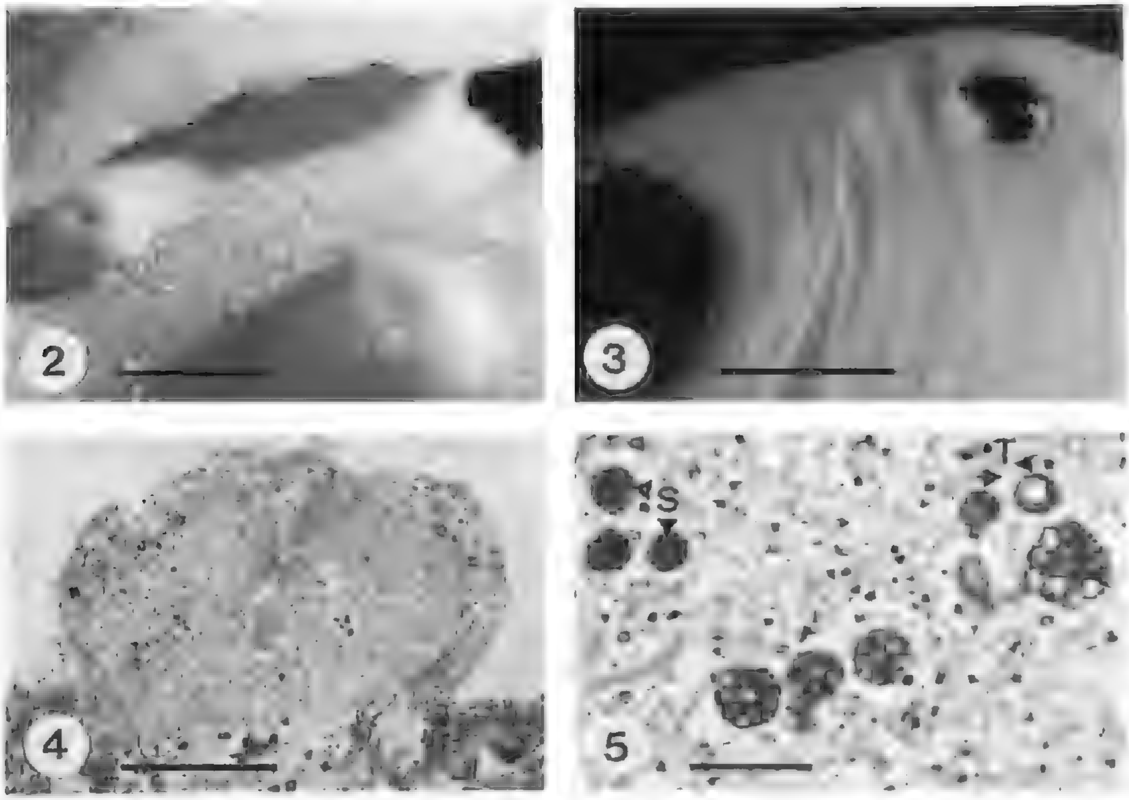
## Results

A total of 125 *Haliotis laevigata* and 109 *H. rubra* were collected from the nine sampling sites. *Perkinsus* infections were detected in ten *H. laevigata* (6 ♂♂, 4 ♀♀) collected from Troubridge Shoal in Gulf St Vincent and in nine *H. rubra* (6 ♂♂, 3 ♀♀) from Thorny Passage in Spencer Gulf (Table 1). Infections were not restricted to any particular size (hence age) group of abalone. Infected *H. laevigata* ranged in size from 8.5–16.0 cm in shell length and infected *H. rubra* from 10.0–16.5 cm. No parasitic infections were detected in any of the 240 Pacific oysters examined.

Infections in abalone were characterized by macroscopic hemispherical blister-like nodules on the superficial aspects of the adductor muscles and mantle (Fig. 2). The nodules were soft and slightly darker in appearance than the surrounding tissue. Larger nodules were found to contain creamy viscous fluid when incised. Ovoid nodules were occasionally detected deeper within the tissues when sectioned (Fig. 3). Infection levels ranged from 1–14

TABLE 1. *Prevalence of* Perkinsus *infections in abalone and oysters from South Australia.*

| Location | Depth (m) | *Haliotis laevigata* (greenlip abalone) |  | *H. rubra* (blacklip abalone) |  | *Crassostrea gigas* (Pacific oyster) |  |
|---|---|---|---|---|---|---|---|
|  |  | No. examined | No. infected | No. examined | No. infected | No. examined | No. infected |
| Baird Bay (33°08′S, 134°16′E) | 10 | 21 | 0 | 23 | 0 | – | – |
| Thorny Passage (34°58′S, 136°04′E) | 5 | 2 | 0 | 16 | 9 | – | – |
| Hardwicke Bay (34°50′S, 137°22′E) | 6 | 16 | 0 | – | – | – | – |
| Foul Bay (35°13′S, 137°15′E) | 20 | 8 | 0 | 2 | 0 | – | – |
| Troubridge Shoal (35°08′S, 137°56′E) | 5 | 30 | 10 | – | – | – | – |
| Emu Bay (35°33′S, 137°34′E) | 15 | 28 | 0 | 1 | 0 |  |  |
| Cape Gantheaume (36°07′S, 137°30′E) | 14 |  | – | 28 | 0 | – | – |
| West Island (35°37′S, 138°35′E) | 10 | 20 | 0 | 15 | 0 | - |  |
| Ringwood Reef (37°38′S, 140°07′E) | 6 |  | – | 24 | 0 | – | – |
| Coffin Bay (34°30′S, 135°18′E) | 1 | – | – | – | – | 51 | 0 |
| Bird Island (33°59′S, 137°33′E) | 1 |  |  | – | – | 52 | 0 |
| Port Price (34°15′S, 138°04′E) | 1 | – | – | – | – | 66 | 0 |
| Oyster Bay (34°52′S, 137°48′E) | 1 | – | – |  |  | 71 | 0 |
| Total |  | 125 | 10<br>(8.0%) | 109 | 9<br>(8.3%) | 240 | 0 |



Figs 2-5. 2. Nodules on surface of adductor muscle of *Haliotis rubra*. Scale bar = 5 mm. 3. Necrotic lesion in adductor muscle of *H. rubra*. Scale bar = 5 mm. 4. Histological section through nodule in adductor muscle of *H. laevigata*. H&E. Scale bar = 0.5 mm. 5. Trophozoites (T) and schizonts (S) of *Perkinsus* within lesion in adductor muscle of *H. laevigata*. H&E. Scale bar = 50 μm.

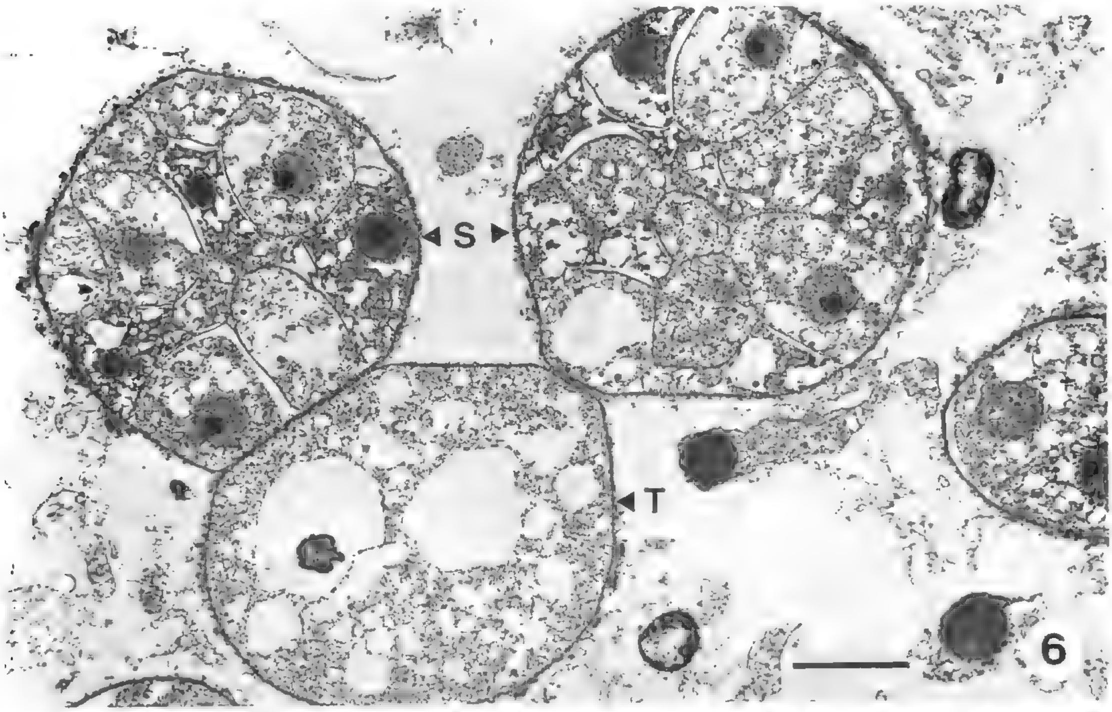
nodules per abalone and the nodules ranged in size from 0.5–8.0 mm in diameter. Those detected in *H. laevigata* and *H. rubra* were similar in location, size, shape and appearance. They were not encapsulated but bound by normal tissues which sometimes contained mild infiltrations of mononuclear inflammatory cells (amoebocytes). The nodules were necrotic and contained variable numbers of amoebocytes together with other host cells. The majority of cells appeared degenerative containing pyknotic nuclei. Connective tissue fibres and occasionally the remnants of muscle fibres were found throughout the lesions forming a loose supporting network. All lesions contained numerous clusters of extracellular basophilic bodies which were identified as various developmental stages of a protozoan parasite (Figs 4, 5). The majority of parasite stages were vacuolated in appearance but some were homogeneous and stained uniformly throughout. Most stages appeared degenerative and morphological integrity was not well preserved within lesions. Nonetheless, two types of parasite developmental stages were evident by light and electron microscopy; unicellular and multicellular forms (Fig. 6).

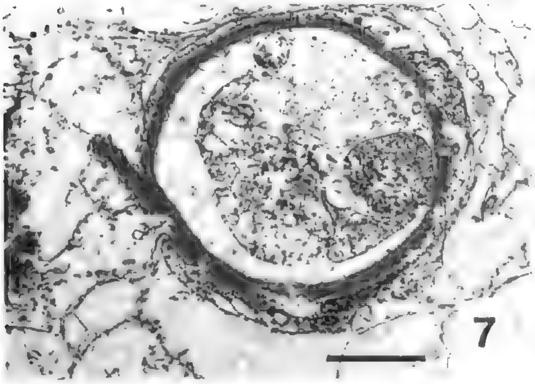
Unicellular stages (termed trophozoites) were found scattered throughout the lesions as individual cells sometimes grouped together in small clusters. They were ovoid in shape measuring from 10.0–17.5 μm in diameter (mean 15.0 μm) and were bounded by a dense wall varying in thickness from 1.5–2.5 μm (Fig. 7). The trophozoites contained a single nucleus with a prominent nucleolus and a highly vacuolated cytoplasm usually containing a large central vacuole measuring from 5–10 μm in diameter. A small dense vacuoplast consisting of eosinophilic granular material was occasionally detected within the central vacuole.

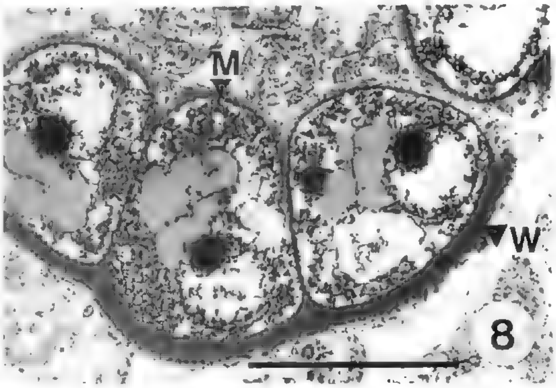
Multicellular stages (termed schizonts) were detected throughout the lesions in distinct clusters (Fig. 8). They were larger in size than the trophozoites measuring from 12.5–35.0 μm in diameter (mean 27.5 μm). They were surrounded by a dense wall (2.0-3.5 μm thick) with an irregular outer margin. The schizonts contained 2-24 rounded cells (termed merozoites) ranging from 5-10 μm in diameter. Each merozoite contained a highly vacuolated cytoplasm and a single nucleus with a prominent nucleolus. Large central vacuoles were not detected in the merozoites nor were vacuoplasts. The majority of schizonts appeared degenerate particularly towards the centre of the lesion.

## Discussion

Identical lesions and parasites detected in *H. laevigata* and *H. rubra* suggests that both abalone species were infected by the same parasite species. This species is similar to *P. olseni* previously reported in blacklip abalone (Lester & Davis 1981). All three parasite developmental stages (trophozoites, schizonts and merozoites) were similar in structure to those previously described although some schizonts appeared larger (mean







Figs 6-8. 6. Electron micrograph of trophozoite (T) and schizonts (S) of *Perkinsus* in adductor muscle of *Haliotis laevigata*. Scale bar = 5 μm. 7. Electron micrograph of *Perkinsus* trophozoite bounded by thick wall. Scale bar = 5μm. 8. Electron micrograph of *Perkinsus* schizont bounded by thick wall (W) and containing several merozoites (M). Scale bar = 5 μm.

diameter of 27.5 µm compared to 15.0 µm) and more mature containing greater numbers of merozoites. However, developing or immature prezoosporangia were not detected and lesions were not surrounded by a loose wall of connective tissue. Despite these differences, the morphological and ultrastructural characteristics of the parasites were considered to be consistent with those of *P. olseni* Lester & Davis, 1981.

Similar developmental stages have been described previously for two other *Perkinsus* spp. Parasites found in the American oyster *C. virginica* were originally described as *Dermocystidium marinum* by Mackin *et al.* (1950) and later as *Labyrinthomyxa marina* by Mackin & Ray (1966). Levine (1978) subsequently renamed the species *Perkinsus marinus* and erected the class Perkinsasida in the phylum Apicomplexa on the basis of the electron microscopic studies of Perkins (1976). This species differs from *P. olseni* in having much smaller trophozoites (3–10 µm in diameter), membranous rather than thickened walls and basophilic rather than eosinophilic vacuoplasts. More recently, thick-walled *Perkinsus*-like trophozoites were found in the gill filaments of the clam *R. decussatus* in Portugal by Comps & Chagot (1987) and Chagot *et al.* (1987). These parasites were cultured in thioglycolate medium to form mature sporangia containing biflagellated zoospores by Azevedo (1989) and were named *P. atlanticus* on the basis of host identity, pathology and zoospore ultrastructure. The dimensions, shape and flagellar organization of the zoospores were more regular than those of *P. marinus* but comparisons with *P. olseni* could not be made because their zoospore ultrastructure has not yet been determined. Several other undescribed *Perkinsus* spp. have been reported in 57 species of molluscs from North America, the Mediterranean and Australia (Andrews 1954; Ray 1954[1]; da Ros & Canzonier 1985; Goggin & Lester 1987) but comparisons could not be made because the only developmental stages reported were large ovoid cells presumed to be prezoosporangia.

Early cross transmission studies suggested that *Perkinsus* spp. may be specific for particular groups of molluscs; *P. marinus* for oysters (lamellibranchs) and *P. olseni* for abalone (gastropods) (Ray 1954[1]; Lester & Davis 1981). However, recent studies have not supported any rigid host specificity for these parasites. *P. olseni* isolated from *H. laevigata* was successfully transmitted to two lamellibranch species (*Pinctada sugillata* and *Anadara trapezia*) and *Perkinsus* spp. isolated from five lamellibranchs (*Anadara trapezia*, *Chama pacificus*, *Tridacna gigas*, *T. crocea* and *T. maxima*) were successfully transmitted to *H. laevigata* (Goggin *et al.* 1989). *P. marinus* has also been transmitted from the oyster *C. virginica* to the pyramidellid gastropod *Boonea impressa* (White *et al.* 1987). These results suggest that *Perkinsus* infections may be transmitted between different mollusc species inhabiting the same waters. No infections were detected in oysters sampled from neighbouring areas in this study but other mollusc species remain to be examined.

Infected *H. rubra* and *H. laevigata* were detected at two different sites located 140 km apart in adjacent Spencer Gulf and Gulf St Vincent. Infections have previously been found in abalone from the same general areas (Lester & Davis 1981; Lester 1986). The reasons for this patchy distribution of infections are not known. The two sites are separated by Yorke Peninsula but both are situated near the mouths of the Gulfs where the same ocean current passes in an easterly direction. However, no infections were detected in abalone sampled from intermediate sites nor from sites located further away in the same current flow. There are also no records of abalone stocks being moved between the two sites of infection. These sites must be regarded as potential point sources of infection and local mollusc populations should be monitored regularly for the spread of infections.

Significant mortalities of *H. laevigata* were first reported along the western coast of Gulf St Vincent in 1980 and further deaths were reported each summer from 1982–1985 (Lewis *et al.* 1987). Abalone had been abundant in this area as far north as Black Point but stocks have now practically disappeared (K.L. Branden pers. comm.). Claims made by divers that mortalities were due to pollution were not substantiated by laboratory investigations for heavy metals, organochlorines, organophosphates and hydrocarbons (Shepherd 1985). Subsequent studies revealed that many abalone in this area were infected with *P. olseni* (Lester 1986) but it is not known whether infections caused the mortalities. The parasite is certainly pathogenic and causes necrotic lesions within host tissues. Mortalities have been observed in experimentally infected *H. rubra* maintained in the laboratory at 20°C whereas those maintained at 15°C recovered from infection (Lester 1986). The continued detection of *Perkinsus* infections in abalone from dieback areas highlights the need for further studies on parasite pathogenicity, transmission and control.

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# DESCRIPTION OF THE MALE OF *TYLENCHORHYNCHUS TOBARI* SAUER & ANNELLS, 1981 AND OBSERVATIONS ON THE MORPHOLOGY AND HOST RANGE OF THE FEMALE IN ARID SOUTH AUSTRALIA

*BY J. M. NOBBS**

## Summary

In a survey of the arid region of South Australia, over 300 sites were found to have *Tyienchorhynchus tobari* Sauer & Annells, 1981. Previously undescribed males of *T. tobari* were identified from only nine sites and are described here. From field observations, plant species of the family Chenopodiaceae were most likely to have *T. tobari* present. This was tested by culturing the nematode on different host plants in the glass-house. It was found that environment affected the morphometrics of different field populations of *T tobari* but not general morphology.

KEY WORDS: *Tyienchorhynchus tobari,* arid South Australia, males, host plant, Nematoda

*Transactions of the Royal Society of S. Aust.* (1991), 115(2), 83-88.

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by J. M. NOBBS*

## Summary

NOBBS, J. M. (1991) Description of the male of *Tylenchorhynchus tobari* Sauer & Annells, 1981 and observations of the morphology and host range of the female in arid South Australia. *Trans. R. Soc. S. Aust.* 115(2), 83-88, 31 May, 1991.

In a survey of the arid region of South Australia, over 300 sites were found to have *Tylenchorhynchus tobari* Sauer & Annells, 1981. Previously undescribed males of *T. tobari* were identified from only nine sites and are described here. From field observations, plant species of the family Chenopodiaceae were most likely to have *T. tobari* present. This was tested by culturing the nematode on different host plants in the glass-house. It was found that environment affected the morphometrics of different field populations of *T. tobari* but not general morphology.

KEY WORDS: *Tylenchorhynchus tobari*, arid South Australia, males, host plant, Nematoda

## Introduction

The arid region of South Australia consists of diverse vegetation and landforms. There is little information on the occurrence and diversity of the plant parasitic nematode fauna within this region. During a survey of the area (Nobbs 1989), one of the most widely distributed plant parasitic nematodes was *Tylenchorhynchus tobari* Sauer & Annells, 1981. The wide distribution of the nematode over a range of environments offered the opportunity to examine the effect of environmental variation on the nematode. This paper examines the effects of environment on female morphometrics and possible hosts among the diverse plant species sampled. Males are described for the first time.

## Methods

### *Extraction of nematodes*

Soil was collected from undisturbed native vegetation which occurred close to the main tracks that run throughout the arid region. Over 300 sites were sampled and the sampled plant species noted. The nematodes were extracted from 50 ml of each soil sample using a modified Baermann funnel (Schindler 1961).

### *Morphology and measurements of* Tylenchorhynchus tobari

To examine the effect of different environments on variation in morphometrics, ten sites were selected from different areas. From each site, ten females were processed through an alcohol series and mounted in glycerol by the wax method (Hooper 1986). Measurements (in mm) of body length, body width, oesophageal length, position of the vulva, tail length, tail width and stylet length were then made under high magnification and the de Man ratios (a, b, c and c′) were calculated. Analysis of variance (ANOVA) was used to determine if there were significant differences in measurements between the ten different populations.

### *Occurrence in the field and in pots*

To determine the most likely host plant of *T. tobari* the number of sites on which a particular plant species occurred was sampled and compared with the actual (or observed) number of sites where that particular plant was sampled and found to have *T. tobari* present. The number of sites where a particular host plant was sampled was used as a percentage of the total sites sampled (expected sites). Using Chi-square analysis (Bailey 1976) the observed number of sites was then compared with the expected number of sites to determine most likely host species. Due to the diversity of the vegetation sites, grouping of the host species was necessary (e.g. Chenopods = plant species of the family Chenopodiaceae).

This information allowed investigation of possible hosts of *T. tobari*. Seeds of native and introduced species including *Atriplex spongiosa*, *A. lindleyi*, *Chenopodium quinoa*, *Lycopersicum esculentum* and *Hordeum vulgare* (cv. Clipper) were surface sterilised (3 min in 1% bleach), pregerminated in a Petri-dish, planted into a 1:4 parts soil to sand mix and inoculated with 50 female *T. tobari*. After two and a half months, the shoots were removed and the roots and soil washed through a set of sieves (500 $\mu$m, 250 $\mu$m and 40 $\mu$m aperture).

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The sediment on the 250 µm and 40 µm sieves was collected and placed in a modified Baermann's funnel for three days. The nematode extract was then counted for *T. tobari*. There were three replicates from each plant species.

## Results

### *Morphometrics of male and female* Tylenchorhynchus tobari *in the arid region of South Australia*

Males of *T. tobari* were identified from nine different sites within the arid region of South Australia (Fig. 1) and mean values ± standard deviations of morphometric measurements for all sites (n = 20 specimens) are presented below. In addition, the same data for a single site (n = 9) near Kingoonya (grid reference 299 180, map KINGOONYA SH53-11 (1 : 250,000) edition 1, series R502, Royal Australian Survey Corps) are provided. The original measurements of Sauer & Annells (1981) for females as well as the grand means of the 10 sites selected are also presented.

Females: original description (Sauer & Annells 1981 (n = 19): Body length = 690 µm (610 – 770); a = 36 (30 – 38); b = 5.0 (4.5 – 6.2); c = 12 (11 – 14); c' = 3.8 (3.1 – 4.4); V = 54 (51 – 54); stylet = 17 – 19 µm. Survey 1983 – 1985 (n = 100) : Body length = 721 ± 62 µm (595 – 900); a = 30.3 ± 3.1 (25.4 – 42.5); b = 5.2 ± 0.5 (4.0 – 7.6); c = 14.0 ± 3.0 (10.6 – 25.1); c' = 3.0 ± 0.8 (1.7 – 4.3); V = 54.4 ± 2.1 (49 – 59); stylet = 17.3 ± 1.4 µm (14 – 21).

Males (Fig. 2) (n = 20) : Body length = 672 ± 18 µm (586 – 752); a = 30.9 ± 1.5 (25.8 – 38.7); b = 5.2 ± 0.2 (4.0 – 5.6); c = 10.8 ± 0.6 (8.5 – 13.2); c' = 3.8 ± 0.2 (2.9 – 4.7); spicule length = 25.5 ± 1.3 µm (19 – 30); gubernaculum = 11.3 ± 2.1 µm (8 – 17); stylet length = 16.7 ± 0.7 µm (14 – 20).

Site near Kingoonya (n = 9) : Body length = 676 ± 26 µm (619 – 727); a = 29.9 ± 0.9 (25.8 – 32.3); b = 5.2 ± 0.2 (4.3 – 5.8); c = 11.7 ± 0.4 (10.4 – 13.2); c' 3.7 ± 0.2 (2.9 – 4.3); spicule length = 25.1 ± 1.1 µm (22 – 28). gubernaculum = 11.2 ± 1.3 µm (8 – 17); stylet length = 17.0 ± 0.7 µm (14 – 18).

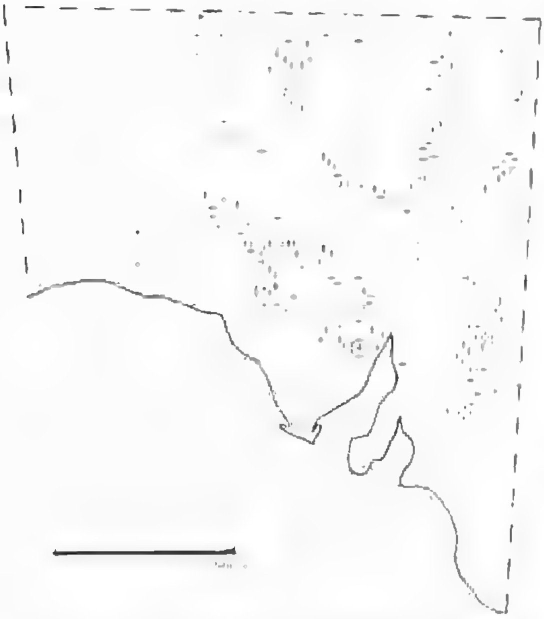

Fig. 1. The distribution of *Tylenchorhynchus tobari* Sauer & Annells, 1981 within the arid region of South Australia. Closed circles are sites from which *T. tobari* was identified; open circles are sites at which males were identified. Sites 1 – 10 were sites from which ten females were measured.

### *Description of the male*

(Fig. 2) Similar to female in anterior region. Lip region offset, 6 – 8 annules, stylet of medium development, with backwardly sloping stylet knobs. Testis single, not reflexed. Tail enveloped by a large, simple, crenate bursa. Spicules distally flanged, terminus narrow, gubernaculum well developed, generally rod-like, protruding. Phasmid easily seen, just anterior to mid-point of tail.

### *Occurrence in the field and in pots*

Chi-square analysis showed that *T. tobari* was found in significantly more sites than expected only where plant species of the family Chenopodiaceae were the most common species (Table 1). Therefore, the most likely preferred host plant is a member of the family Chenopodiaceae. With the pot tests there was some multiplication of *T. tobari* with all the five plant species tested, but *Atriplex spongiosa* had the greatest multiplication rate (Table 2).

### *Analysis of populations*

Although only a small number of females per population were measured, significant differences in morphometrics were observed. Of the characters measured only position of the vulva (V), de Man ratio's a, b, and c' were not significantly different between populations (Table 3). Body length, body width, tail length, tail width, oesophageal length, stylet length and de Man c ratio were all significantly different between naturally occurring populations.

In one population (9), almost all of the observed values were greater than the standard deviation of the grand mean. Few of the other populations had any or more than one value beyond the range of plus or minus the standard deviation. There were no obvious differences in general morphology between specimens collected from the ten sites, so the differences in measurements between the populations are most likely due to environmental effects such as recent rainfall, host species present and soil type rather than species differences.

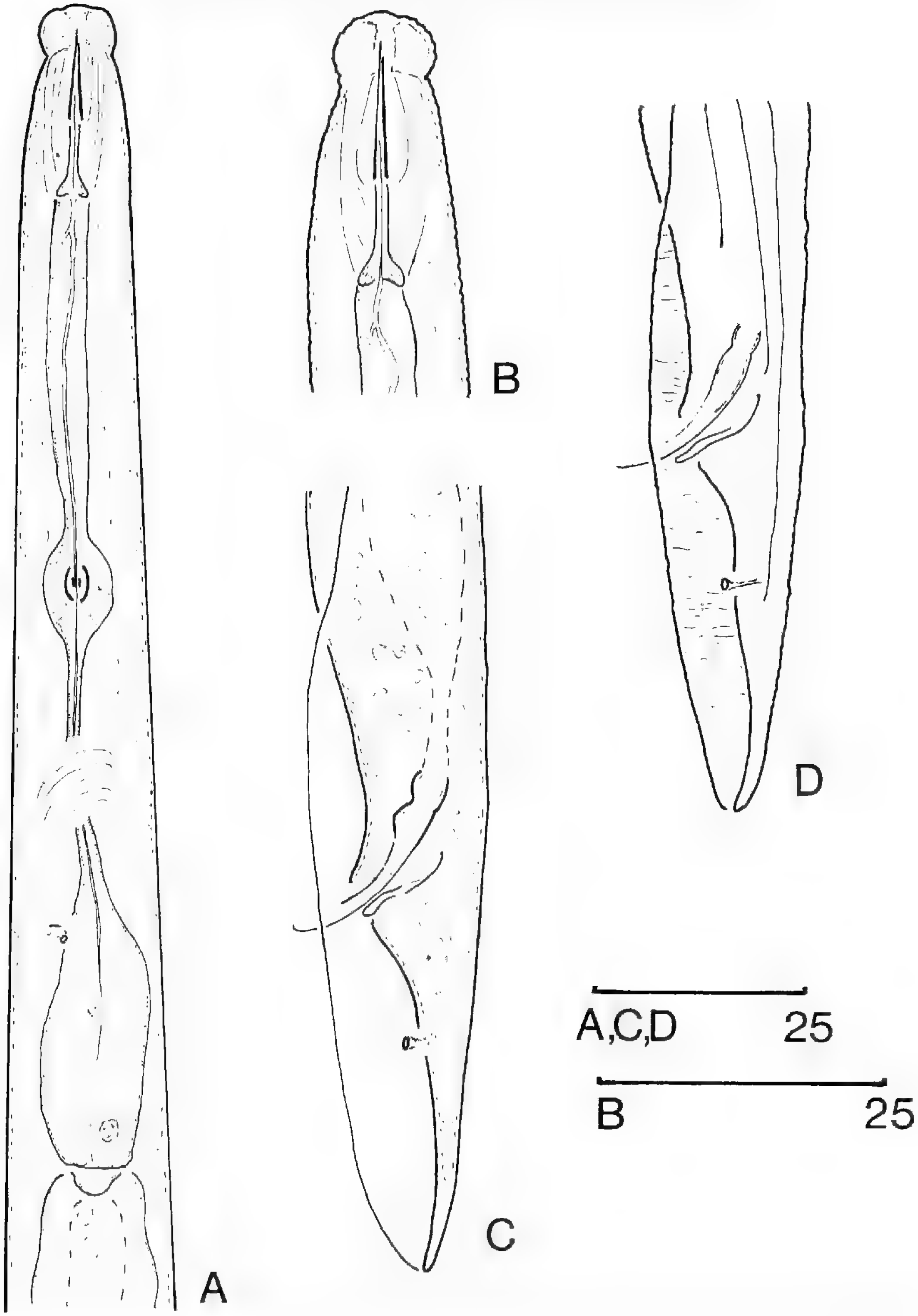

Fig. 2. Morphology of the male of *Tylenchorhynchus tobari* Sauer & Annells, 1981, A – oesophageal region; B – head region; C – shape of tail (internal); D – shape of tail (external). Scale in microns ($\mu$m).

TABLE 1. *The host plant/groups and number of sites where* Tylenchorhynchus tobari *Sauer & Annells, 1981 was collected.*

| Species/groups | Number of Sites Observed | Number of Sites Expected | Chi-square value | | % Total Sites Sampled in Survey 1983-85 |
|---|---|---|---|---|---|
| Chenopods | 140 | 108.5 | 9.14 | ## | 33.5 |
| Ephemerals | 14 | 14.6 | 0.02 | | 4.5 |
| *Eucalyptus* spp. | 27 | 36.6 | 2.52 | | 11.3 |
| *Acacia spp.* | 71 | 76.8 | 0.44 | | 23.7 |
| Grasses | 9 | 15.6 | 2.79 | | 4.8 |
| Shrubs: *(Eremophila, Dodonea, Cassia* sp.) | 16 | 25.6 | 3.60 | | 7.9 |
| Trees: *(Myoporum, Pittosporum, Callitris* sp.) | 24 | 18.8 | 1.44 | | 5.8 |
| *Salicornia* spp. | 8 | 7.8 | 0.01 | | 2.4 |
| Reeds | 0 | 2.9 | 2.90 | | 0.9 |
| *Zygocloea paradoxa* | 15 | 16.8 | 0.19 | | 5.2 |
| Total | 324 | 324.0 | 23.05<br>** | | 100.0 |

** = significantly different, df = 9, P = 0.01, Chi-square analysis.
## = significantly different, df = 1, P = 0.01, Chi-square analysis.
The null hypothesis that there is no difference between the expected numbers of sites from which certain plant species/groups were sampled and the presence of *Tylenchorhynchus tobari* in the soil sample is rejected.
The % total sites indicate the number of samples from which soil was sampled in the period 1983 to 1985 and were used to calculate expected number of sites with *T. tobari.*

TABLE 2. *Final number and multiplication rate of* Tylenchorhynchus tobari *from an initial inoculation of fifty females and sampled after two and a half months. (mean ± standard deviation).*

| Plant species | Mean number | Multiplication rate |
|---|---|---|
| *Atriplex lindleyi* | 212.7<br>*±55.9* | 4.2<br>*±1.12* |
| *A. spongiosa* | 1238.3<br>*±224.6* | 24.8<br>*±4.50* |
| *Hordeum vulgare*<br>(var. Clipper) | 56.0<br>*±17.4* | 1.1<br>*±0.35* |
| *Lycopersicum*<br>*esculentum* | 209.7<br>*±29.7* | 4.2<br>*±0.96* |
| *Chenopodium quinoa* | 499.0<br>*±64.7* | 10.0<br>*±1.29* |

TABLE 3. *Measurements of different populations of* Tylenchorhynchus tobari *from the arid region of South Australia.*

| Population | Body length | Body width | Tail length | Tail width | Length of oesophagus | Length stylet | c ratio |
|---|---|---|---|---|---|---|---|
| 1 | 699.3 | 23.6 | 52.2 | 17.6 | 130.0$^-$ | 17.0 | 13.9 |
| 2 | 699.5 | 23.6 | 56.1 | 17.6 | 135.7 | 17.2 | 12.7 |
| 3 | 716.9 | 23.3 | 49.4 | 16.9 | 145.2 | 16.8 | 14.8 |
| 4 | 725.6 | 23.4 | 47.4$^-$ | 17.3 | 146.2$^-$ | 18.7$^+$ | 15.4 |
| 5 | 701.0 | 24.0 | 55.5 | 18.8$^-$ | 133.9 | 18.0 | 13.5 |
| 6 | 724.2 | 24.1 | 54.5 | 18.6 | 137.0 | 16.2$^-$ | 13.7 |
| 7 # | 734.0 | 23.8 | 58.2$^+$ | 18.3 | 133.3 | 17.4 | 12.7 |
| 8 # | 701.6 | 23.8 | 56.8 | 18.7 | 130.6 | 16.2 | 12.6 |
| 9 | 793.9$^+$ | 27.2$^+$ | 49.6 | 18.3 | 152.1$^+$ | 18.3$^+$ | 16.6$^+$ |
| 10 | 713.4 | 22.8 | 49.9 | 16.8$^-$ | 140.7 | 17.6 | 14.3 |
| Grand Mean | 720.7 | 23.9 | 52.9 | 17.8 | 138.5 | 17.3 | 14.0 |
| + *S.D.* | *61.8* | *2.4* | *8.4* | *1.8* | *11.8* | *1.4* | *3.0* |
| F-value | 2.40<br>** | 2.79<br>** | 2.28<br>** | 2.06<br>** | 3.57<br>** | 4.41<br>*** | 2.12<br>** |

Significant at P = 0.01% level indicated by **; significant at P = 0.001% level indicated by ***; d.f. 9, 86.
Grand mean is calculated from all 100 nematodes measured and includes the standard deviation *(S.D.)* in italics.
# = populations where males were identified.
indicates value less than lowest value of the standard deviation of the grand mean. $^+$ indicates value greater than highest value of the standard deviation of the grand mean.
Measurements are in microns (μm).

## Discussion

Males of *Tylenchorhynchus tobari* were found in only a small number of sites and in low numbers indicating that *T. tobari* may reproduce parthenogenetically. Populations of *T. tobari* from different natural habitats differ significantly in certain morphometric characters. However, the description of a new species is not necessary as the populations are still identifiable morphologically as *T. tobari*. Many workers (Davide 1980; Fortuner 1984a; Fortuner & Queneherve 1980; Kline 1976; Roggen & Asselberg 1971; Townsend & Blakith 1975; Saha & Khan 1988; Singh *et al.* 1985) have looked at the influence of host on morphometrics of different species of nematode. They found that many characters were highly variable between populations and that ratios were of little overall value (except V) in determining species. Fortuner (1984b) suggested that observations of several populations were important in estimating the mean and range of measurements. When identifying species, morphology should always be used with priority over morphometrics as differences in measurements can often be attributed to environmental effects.

*T. tobari* is a migratory ectoparasite and so has a wide host range. In the field the most common plants sampled with *T. tobari* present were of the family Chenopodiaceae. In pot cultures *Atriplex spongiosa* allowed the greatest multiplication. In using a host plant that allows rapid multiplication of *T. tobari*, the host/parasite relationship can be investigated.

## Acknowledgments

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# THE MANGALO METEORITE, A NEW (L6) OLIVINE-HYPERSTHENE CHONDRITE FROM SOUTH AUSTRALIA

*BY MARGARET WALLACE & ALLAN PRING**

## Summary

The Mangalo meteorite is a single stone, which originally weighed 1050 g, and was found near Mangalo (33°34'S 136°39'E) South Australia in 1987. It has been classified as an L6 chondrite, shock facies 'e', and contains olivine ($Fa_{25.2-26.4}$) orthopyroxene ($Fs_{21.4-22.8}$) clinopyroxene ($Wo_{44.7}en_{46.8}fs_{8.5}$), apatite, nickel-iron, troilite and maskelynite. Mineral textures and compositions indicate that Mangalo was a metamorphosed part of the L-planetoid and was heavily shocked before reaching Earth.

KEY WORDS: Mangalo, chondrite, meteorite

*Transactions of the Royal Society of S. Aust.* (1991), 115(2), 89-93.

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## Introduction

The Mangalo meteorite was found by Mr Neil Smith while ploughing on his property at Mangalo near Cowell on the Eyre Peninsula, South Australia (33°34′S, 136°39′E) in June 1987. Mr Smith brought the stone to the attention of two geologists from the South Australian Department of Mines and Energy, who in turn sent it to AMDEL in Adelaide where it was positively identified as a chondritic meteorite. After identification Mr Smith brought the meteorite to the South Australian Museum for detailed examination. No additional material has yet been recovered. In accordance with the guidelines on meteorite nomenclature, the meteorite has been named Mangalo, after the geographical locality closest to its site of discovery.

Mangalo is the forty-fifth meteorite to be found in South Australia and the ninth to be recovered from Eyre Peninsula (see Fig. 1). It does not appear to be related to any of the Eyre Peninsula meteorites (Corbett 1968; Fitzgèrald 1979[1]). Mangalo was found quite close to the site where the Cowell meteorite was found in 1932. The Cowell meteorite is now considered to be part of the Kyancutta fall (Graham *et al.* 1985). It is however an iron and not a stony meteorite (Spencer 1933; Buchwald 1975). South Australia, like Western Australia and the south-west of the United States is a particularly good area for finding meteorites due to its arid conditions and the great age of the land surface (Bevan & Binns 1986, 1989).

The Mangalo meteorite and the Streaky Bay meteorite (Wallace & Pring 1991) are the first new meteorites to be recovered since legislation was enacted in 1980 to protect meteorites found in South Australia. This legislation, in the form of an amendment to the Museum Act, made all meteorites found in South Australia the property of the Museum. Provisions were included in the Act for rewarding the finders of meteorites. In the case of the Mangalo meteorite, the finder, Mr Smith has been presented with a polished piece of the meteorite and a bronze medallion commemorating the meteorite's discovery.

## Physical Description

The meteorite is a five sided sub-rounded stone (11 × 8 × 8 cm) weighing 1050 grams (Fig. 2). The stone is covered in all but one corner with a 1 to

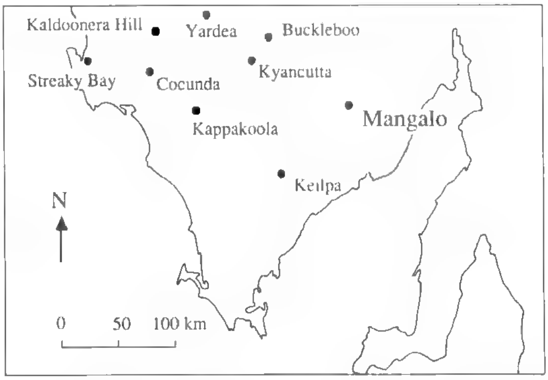

Fig. 1. Map of Eyre Peninsula showing the location of Mangalo and the sites of other meteorite finds on the Peninsula.

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[1] FITZGERALD, M. J. (1979) The Chemistry and Mineralogy of the Meteorites of South Australia and Adjacent Regions. Ph.D. thesis, University of Adelaide. Unpubl.

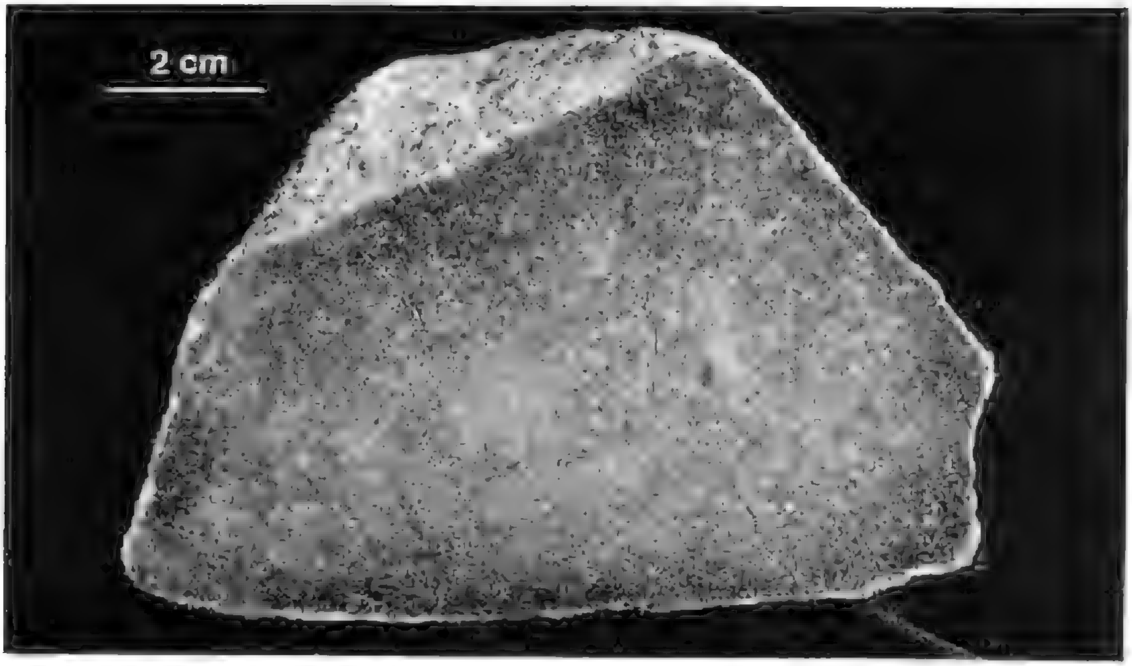

Fig. 2. View of polished slab of the Mangalo meteorite.

2 mm deep well-preserved shiny brownish-black fusion crust, portions of which are gritty with sand grains which may have become attached during weathering. The external appearance of the stone is typical of a chondritic meteorite which has been exposed to the weather for a number of years. The interior of the meteorite is dark green-grey in colour and fine to medium grained. Chondrules (quenched spherical groups of olivine, orthopyroxene and glass) are readily visible especially on polished surfaces. Metals, both kamacite and taenite, occur as finely disseminated grains and stringers, many of which rim chondrules. Silicate minerals are stained brown, probably by terrestrial weathering, and the sample contains several iron oxide filled fractures. The meteorite has been cut and two of the internal surfaces polished. Two polished thin-sections have been made. These were used both in the petrographic examination and in electron microprobe analyses.

## Mineralogy

Compositions of the silicate phases were analyzed with a JEOL electron microprobe at the University of Adelaide. Analyses were made using an accelerating voltage of 15 kV, a sample current of 5 nA, and a beam width of 5 μm. Representative crystal analyses are presented in Table 1.

The meteorite is composed predominantly of olivine and orthopyroxene with minor amounts of clinopyroxene and maskelynite. Microprobe analyses show that the olivine in Mangalo is equilibrated with a mean fayalite content of $Fa_{25.7}$ (10 analyses, range 25.2 to 26.4). The orthopyroxene shows a small variation in chemical composition with a mean ferrosilite content of $Fs_{22.0}$ (10 analyses, range 21.4 to 22.8) and wollastonite content which varies from 1.2 to 1.7 mol% (average = 1.3). The orthopyroxene has a particularly high calcium content which suggests that it equilibrated at high temperatures. Clinopyroxene, which is only abundant and coarse enough for reliable analyses in type 6 chondrites, is homogeneous with an average composition of $Wo_{44.7}En_{46.8}Fs_{8.5}$. Plagioclase crystals normally found in equilibrated chondrites are not present in Mangalo; they have been transformed to the shock produced glass, maskelynite. Accessory minerals include troilite, iron-nickel metal and chlorapatite.

## Chemical Group

Mangalo is an ordinary chondrite, an agglomerate meteorite. This type of meteorite is considered to be compositionally similar to the bulk solar system, less the volatile hydrogen and helium components (Keil 1969). The ordinary chondritic

TABLE 1. *Representative electron microprobe analyses (wt. %) of selected minerals in the Mangalo meteorite*

| | Olivine<br>6 | Orthopyroxene<br>6 | Clinopyroxene<br>3 | Maskelynite<br>6 | Chlorapatite |
|---|---|---|---|---|---|
| $P_2O_5$ | – | – | – | – | 39.71 |
| $SiO_2$ | 37.13 | 54.75 | 53.78 | 66.79 | – |
| $TiO_2$ | – | – | 0.32 | – | – |
| $Al_2O_3$ | – | 0.16 | 0.63 | 21.03 | – |
| $Cr_2O_3$ | – | – | 0.87 | – | – |
| FeO | 23.22 | 14.27 | 5.30 | 0.69 | 2.02 |
| MnO | 0.40 | 0.42 | – | – | – |
| MgO | 38.26 | 28.66 | 16.26 | – | – |
| CaO | – | 0.69 | 21.60 | 2.06 | 50.72 |
| $Na_2O$ | – | – | 0.65 | 5.49 | 0.28 |
| $K_2O$ | – | – | – | 1.11 | – |
| Cl | – | – | – | – | 6.94 |
| Total | 99.00 | 98.94 | 99.43 | 97.18 | 99.68 |
| P | – | – | – | – | 0.958 |
| Si | 0.9827 | 1.9801 | 1.9838 | – | – |
| Ti | – | – | 0.0090 | – | – |
| Al | – | 0.0066 | 0.0276 | – | – |
| Cr | – | – | 0.0254 | – | – |
| Fe | 0.5140 | 0.4328 | 0.1636 | – | 0.0482 |
| Mn | 0.0090 | 0.0130 | – | – | – |
| Mg | 1.5091 | 1.5498 | 0.8941 | – | – |
| Ca | – | 0.0270 | 0.8538 | – | 1.5488 |
| Na | – | – | 0.0467 | – | 0.0157 |
| K | – | – | – | – | |
| Cl | – | – | – | – | 0.3350 |
| Total | 3.0149 | 4.0092 | 4.0041 | – | 2.9058 |
| | Fe# 25.4 | 21.8 | 15.5 | – | – |
| | – | Ca=1.3 | Ca=44.7 | Ca=15.5 | – |
| | – | Mg=77.1 | Mg=46.8 | Na=74.6 | – |
| | – | Fe=21.5 | Fe=8.6 | K=9.9 | – |

meteorites are divided on the basis of the iron content of olivine and orthopyroxene into three chemical groups (H, L, and LL). All the meteorites in any group are believed to have come from the same planetoid from within the asteroid belt (Keil & Fredriksson 1964). The iron content of the olivine and orthopyroxene in Mangalo indicate that it belonged to the L-group of ordinary chondrites (see Fig. 3).

## Petrologic Type

Ordinary chondrites of the same chemical group differ widely in texture and physical history. After the accretion of the planetoid, its components were heated and metamorphosed: chondrules recrystallized, silicate minerals became homogenous and show a narrower variation in composition, and

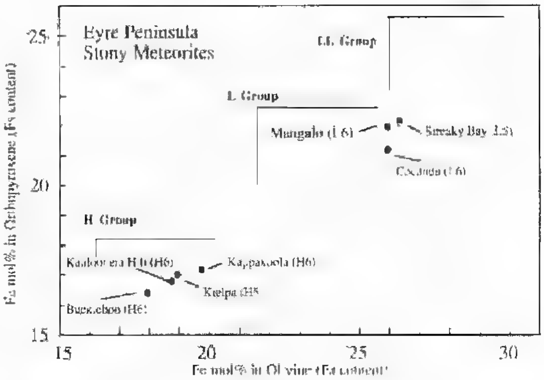

Fig. 3. Iron contents, expressed as mol% Fe in olivine (Fa) and orthopyroxene (Fs) of Eyre Peninsula stony meteorites. Classification groups are from Keil & Fredriksson (1964). Data are from Mason (1974); and Wallace & Pring (1991).

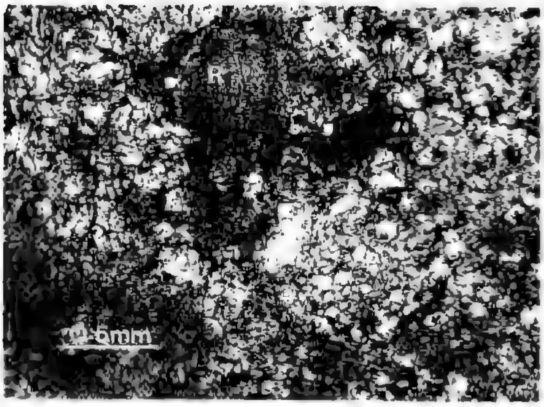

Fig. 4. Thin-section microphotograph of Mangalo meteorite showing a radial pyroxene chondrule (R) and a porphyritic olivine chrondrule (P) in a recrystallized matrix.

plagioclase feldspar crystallized out of the glassy areas. The Mangalo meteorite is a highly equilibrated chondrite and belongs to petrologic type 6 of a six increment scale of the Van Schmus & Wood (1967) classification. In thin-section, the chondrules are easily recognizable, up to 6 mm in diameter, but are well-recrystallized and show poorly delineated boundaries (Fig. 4). The matrix has been recrystallized and now consists of olivine, pyroxenes, and maskelynite (a shock produced glass of plagioclase composition). Silicate mineral chemistry is homogeneous. Temperature calculations using the Wells (1977) and Lindsley (1983) geothermometers based on the calcium content of co-existing pyroxenes indicate that the meteorite has been heated to between 700 and 800°C within its parent body (Fig. 5).

## Shock Effects

Meteorites often record shock features produced by high velocity collisions in space. Shock effects range from fracturing and brecciation to the formation of high pressure minerals and melting. Shock related fracturing is pervasive through Mangalo; the olivine grains show mosaic extinction, and plagioclase has been converted into maskelynite. Mosaic extinction of olivine is characteristic of meteorites which have been shocked to pressures of 150 to 400 kilobars and the conversion of plagioclase to maskelynite suggests shock pressures of about 300 kilobars (Van Schmus & Ribbe 1968; Stöffler *et al.* 1988). Mangalo is therefore a severely shocked meteorite which has suffered from some form of high velocity collision.

Fig. 5. Silicate mineral chemistry in Mangalo meteorite. Isotherms show temperature calculations based on the calcium content of orthopyroxenes and clinopyroxenes (Lindsley 1983).

## Classification

The average compositions of the ferro-magnesian silicates, olivine ($Fa_{24.7}$) and orthopyroxene ($Fs_{22.0}Wo_{1.7}$), show that Mangalo belongs to the L-group of ordinary chondrites (Keil & Fredriksson 1964). The microstructure of Mangalo, which shows recognizable chondrules with indistinct rims in a crystalline matrix, indicates that the meteorite belongs to a high metamorphic grade, petrologic type 6 (Van Schmus & Wood 1967). The wollastonite content of orthopyroxene ranges from 1.2 to 1.7 wt.%, similar to the range found in most L6 chondrites ($Wo_{1.2}$-$Wo_{1.6}$, Scott *et al.* 1986). There have been major alterations to the mineralogy of the meteorite due to preterrestrial shock. Silicate grains are fractured, olivine crystals show mosaic extinction under cross-polarized light, and plagioclase has been converted to maskelynite. This is consistent with a classification of shock facies 'e' (Dodd & Jarosewich 1979).

These observations indicate that Mangalo formed deep within the L-group parent body, which is believed to have been part of the asteroid belt. It was metamorphosed and recrystallized at temperatures between 700 and 800°C (1 to 2 kilobars of pressure) probably within the L-group parent body and was heavily shocked before reaching Earth. The Mangalo meteorite is classified as an L6e chondrite.

## Acknowledgments

We thank Mr Smith for bringing the meteorite to our attention at the South Australian Museum. Gert Horr is thanked for making thin-sections and Jan Forrest for photography. The University of Adelaide is acknowledged for providing access to their electron microprobe facilities housed in its Electron Optical Centre. The project was funded by the Mark Mitchell Foundation.

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# RECENT SIGHTINGS OF KILLER WHALES, *ORCINUS ORCA* (CETACEA:DELPHINIDAE), IN SOUTH AUSTRALIA

*BY JOHN K. LING**

## Summary

Twenty-six sightings of what are believed beyond reasonable doubt to have been killer whales *(Orcinus orca)* were reported between August 1982 and March 1990 in most South Australian coastal waters. The number of whales ranged from one to 52, with singletons and groups of two, three, five and eight whales being the most common social aggregation. Most of the sightings were made between December and June; this may reflect observer effort as much as any seasonal pattern.

KEY WORDS: Killer whale, *Orcinus orca,* Cetacea, sightings, South Australia, social groupings, seasonal occurrences

*Transactions of the Royal Society of S. Aust.* (1991), 115(2), 95-98.

# RECENT SIGHTINGS OF KILLER WHALES, *ORCINUS ORCA* (CETACEA: DELPHINIDAE), IN SOUTH AUSTRALIA

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## Summary

LING, J. K. (1991) Recent sightings of killer whales, *Orcinus orca* (Cetacea: Delphinidae), in South Australia. *Trans. R. Soc. S. Aust.* 115(2), 95-98, 31 May, 1991.

Twenty-six sightings of what are believed beyond reasonable doubt to have been killer whales *(Orcinus orca)* were reported between August 1982 and March 1990 in most South Australian coastal waters. The number of whales ranged from one to 52, with singletons and groups of two, three, five and eight whales being the most common social aggregation. Most of the sightings were made between December and June; this may reflect observer effort as much as any seasonal pattern.

KEY WORDS: Killer whale, *Orcinus orca*, Cetacea, sightings, South Australia, social groupings, seasonal occurrences

### Introduction

The only published record of the Killer Whale *(Orcinus orca)* in South Australia refers to an encounter between 11 Killer Whales and a large whale and calf (apparently Blue Whales, *Balaenoptera musculus*) in the South East of the State (Cotton 1943) (see Table 1). The Killer Whales were furiously attacking the head of the larger whale. This is typical *O. orca* behaviour (Morejohn 1968; Baldridge 1972; Hoyt 1984). Aitken (1971) overlooked this record, although he believed that Killer Whales probably did occur off the South Australian coast.

Since 1982, the South Australian Museum has coordinated a public whale sighting and reporting programme known as "Whale Watch – South Australia". *Orcinus orca* is one of the most distinctive and easily identifiable cetaceans because of its body shape, markings and behaviour. Only one or two diagnostic characters are sufficient for its positive identification. This paper records and analyses sightings of killer whales in South Australian waters resulting from the "Whale Watch" programme.

### Methods

Through extensive media coverage, the public have been encouraged to report sightings to the South Australian Museum of any whales, alive or dead, from around the coast. National Parks and Wildlife Service rangers and Fisheries Department officers have been supplied with *pro formas* designed to enable identification of cetaceans and record pertinent information. Where possible, a follow-up interview is conducted by Museum staff with the observer.

All reports are filed, but only positive identifications have been used here. An identification brochure (Anon 1980) is usually sent to each person following the interview to help maintain interest in the scheme, and to allow further checking of characters useful for identification and follow-up of sightings.

### Results and Discussion

Twenty-six reports of Killer Whales were received between August 1982 and May 1990 (Table 1). In two instances, photographic confirmation was also received (Fig. 1). Killer Whales have been reported for all months except January and October, with most reported sightings occurring between December and June. The preponderance of sightings in the summer to early winter months, may reflect increased numbers of observers, better visibility and calmer weather rather than any actual increase in numbers of Killer Whales in South Australian waters during this period. According to Baker (1983), Killer Whales may calve in autumn or early winter in New Zealand waters. It is known that Killer Whales in other parts of the world move about in response to the movement of food species, e.g. herring in Norway (Christensen 1988). It is possible that their presence in South Australian waters during the summer and autumn months is due to the availability of favoured food items such as fish, squid and seals.

A recent reported sighting involved an encounter with six to eight killer whales near Point Brown in the Far West, by District Fisheries Officer, Bob Spriggs of Ceduna, on 2 March, 1990 (sighting 26). Mr Spriggs observed the whales from a small boat for about two hours. There was one large (ca 10 m) male, four to five whales 4-5 m long and one or two less than 4 m long. They were first seen approximately 1 km north of Point Brown towards which they then headed through foul ground. The

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TABLE 1. *Killer whale sightings in South Australia, 1942 and 1982 – 1990.*

| Sighting No. | Date | Locality | Latitude/ Longitude | No. of whales | Remarks |
|---|---|---|---|---|---|
| 1 | 10 December 1942 | 4 km SE Port MacDonnell | 38°05'S, 140°44'E | 11 | Attacking other whales (Cotton 1943) |
| 2 | August 1982 | Penneshaw, Kangaroo Island | 35°43'S, 137°56'E | 8 | Photographs |
| 3 | April 1983 | South Coast, Kangaroo Island | 37°00'S, 137°00'E | 8 | (= #2?) |
| 4 | 13 December 1983 | Foot of Gulf St. Vincent | 34°33'S, 138°10'E | 3 | 1 adult (?); 2 young (?) |
| 5 | 31 May 1986 | Investigator Strait | 35°27'S, 136°50'E | 1 | F(?) (= #6?) |
| 6 | 1 June 1986 | Cape Jervis | 35°36'S, 138°06'E | 52 | Herding salmon |
| 7 | 1 June 1986 | Goolwa Beach | 35°30'S, 138°47'E | 2 | M + F(?) (= #6?) |
| 8 | 15 June 1986 | Waitpinga Beach | 35°38'S, 138°29'E | 1 | 1 NM offshore (= #6?) |
| 9 | 11 July 1986 | Off Glenelg | 34°53'S, 138°32'E | 1 | 10 km offshore M(?)(= #6?) |
| 10 | 13 February 1987 | Cape Dutton, Kangaroo Island | 35°38'S, 137°90'E | 5 | 3 adults, 2 young |
| 11 | 19 February 1987 | Althorpe Islands | 35°22'S, 136°52'E | 4 | 3 adults, 1 young (= #10?) |
| 12 | 2 November 1987 | Outer Harbor | 34°45'S, 138°29'E | 3 | heading north; 25–30 ft |
| 13 | 14 February 1988 | Brighton North | 35°01'S, 138°31'E | 1 | F (?) |
| 14 | 9 March 1988 | Smoky Bay | 32°18'S, 133°50'E | 5 | 2 Ms + 2 Fs (photographs) |
| 15 | 3 May 1988 | 5-7 km ENE Troubridge Shoal | 35°08'S, 137°48'E | 2 | Attacking other whales |
| 16 | 12 May 1988 | Port Noarlunga | 35°09'S, 138°29'E | 5 | 1 M, 4 Fs |
| 17 | 13 May 1988 | Port Noarlunga | 35°09'S, 138°29'E | ? | Fs(?) heading north (= #16?) |
| 18 | 17 May 1988 | Port Elliot | 35°32'S, 138°41'E | 2 | (= #16?) |
| 19 | 19 May 1988 | 55 km south of Cape du Couedic | 36°34'S, 136°42'E | 24 | (= #16?) |
| 20 | 25 May 1988 | Port Noarlunga jetty | 35°09'S, 138°29'E | ? | (= #16?) |
| 21 | 8 September 1988 | Arno Bay | 33°56'S, 138°35'E | 5 | M, 30 ft; 4 + 20 ft Fs(?) |
| 22 | 19 March 1989 | 15 km west of Rapid Head | 35°31'S, 138°10'E | 3 | 8–10 m long |
| 23 | 28 May 1989 | 2 km south of Fowlers Bay | 32°00'S, 132°27'E | 2 | |
| 24 | 8 December 1989 | 4 km south of Cape Jervis | 35°38'S, 138°06'E | 8-9 | M, 8 m; others, 5-6 m (= #22?) |
| 25 | 27 February 1990 | 15 km NNE of Snug Cove, Kangaroo Island | 35°34'S, 130°52'E | 3 | 2 Ms, 1 F(?) (= #22?) |
| 26 | 2 March 1990 | Point Brown | 32°33'S, 133°51'E | 8 | 1 M, 25–30 ft; Fs 15–20ft (photographs: Fig. 1) |
| 27 | 31 May 1990 | Greenly Island | 34°30'S, 134°45'E | 6–8 | 1 M, 4–5 Fs, 1–2 young (= #26?) |

whales were also seen at one stage to be working in a kind of pack and harassing a Common Dolphin *(Delphinus delphis)*. The latter appeared to be quite frantic in trying to escape from the Killer Whales and was leaping out of the water and somersaulting and cartwheeling in the air. Several of the smaller Killer Whales were also seen leaping into the air and re-entering the water head-first. It is rather remarkable that five Killer Whales were seen (and photographed) in almost the same area on 9 March, 1988 (sighting 14). Although it was not possible to match any photographs to the same whales seen in the two sightings, it is not inconceivable that the same whales were involved on both occasions, and again on 31 May, 1990 at Greenly Island (sighting 27).

Killer Whales are known to form close-knit, highly stable, and probably permanent groups in British Columbia (Ford & Ford 1981). Given that Killer Whales are seen infrequently in South Australian waters, it seems extremely likely that several of the 26 sightings could have been of the same animals or of the same herd. For example, sightings 5, 6 and 7 and possibly sightings 5, 6, 7, 8 and 9; sightings 10 and 11; and sightings 15 to 20 probably included all or some of the same animals. Furthermore, some of the sightings seen in different months or even years could have been of the same whales, e.g. 2 and 3; and 22, 24 and 25, as well as 14 and 26 referred to above. Excluding possible repeat sightings, social groupings were as follows: 1 whale (3); 2 whales (3); 3 whales (4); 5

whales (4); 8 whales (3); 24 whales (1); and 52 whales (1).

Recent Killer Whale sightings in South Australia are not confined to particular areas, but are spread from Goolwa Beach on the south coast to Fowlers Bay in the Far West, and into both gulfs. Indeed, at this stage, it is not possible to nominate any one locality where regular observations might be carried out. Taking Cotton's (1943) report from the South East into account, also means that *Orcinus orca* has been observed over almost the entire South Australian coast. Only sightings from land or boats close to land have been reported to date.

There have been 46 strandings in New Zealand (Baker 1983) and two in Tasmania involving at least three animals (Nicol 1986). Nicol believes that the Killer Whale's predatory lifestyle in and familiarity with inshore waters should include an ability to navigate safely away from hazards that might affect other (particularly oceanic) species and cause them to strand. However, many strandings occur on Vancouver Island, Canada, where large resident and smaller transient populations frequent the waters between Vancouver Island and mainland British Columbia, Canada, and Washington State, USA; despite the Killer Whales' presumed familiarity with the area (Ford & Ford 1981).

There is very little Killer Whale material in the South Australian Museum collections, and associated data are imperfect (Table 2). We have no documented evidence that *Orcinus orca* has ever stranded in South Australia, although the five teeth referred to in Table 2 cannot be discounted entirely as such evidence.

The results presented here emphasise the value of encouraging people to look out for whales and report sightings to the authorities and, in particular, to try and obtain good clear photographs of dorsal fins and other markings by which whales may be identified. Such data will lead to a better understanding of the biology of this spectacular species in South Australian waters.

Fig. 1. Killer Whales, *Orcinus orca*, near Point Brown, South Australia, 2 March 1990. Top, male; centre, male and female; bottom, female. Photographs R. Spriggs.

## Acknowledgments

The interest and cooperation of the many people, particularly Mr Bob Spriggs, who have reported sightings, provided information during interviews, and supplied confirmatory photographs which have made this article possible are gratefully acknowledged. Thanks are also due to Dr Catherine Kemper and Dr Graham Ross for commenting on earlier drafts of the manuscript. Trevor Peters prepared the photographs for publication and Debbie Lowery typed the paper.

TABLE 2. *Orcinus orca* specimens registered in the South Australian Museum

| Reg. No. | Date of registration or collection | Locality | Material/Remarks |
|---|---|---|---|
| M 1590 | 11/9/1922 | "near Mount Lofty Range" | Part skull (specimen lost) |
| M 3224 | ? 1932 | "South Australian beach" | Five teeth |
| M 5345 | ? 1945 | Portland, Victoria | Mandible ramus; no data* |
| M 5649 | ? 1945 | unknown | Part skull (no mandibles); no data* |

*These could be of one and the same animal

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# *CRINIA* TSCHUDI (ANURA: LEPTODACTYLIDAE) FROM THE CAINOZOIC OF QUEENSLAND, WITH THE DESCRIPTION OF A NEW SPECIES

*BY MICHAEL J. TYLER*

## Summary

The leptodactylid frog *Crinia presigngera* sp. nov. is described from a series of Oligo-Miocene sites at Riversleigh Statioin northwest Queensland. This finding represents the first record of the genus *Crinia* from the Tertiary and the first record of fossil material of *Crinia* from Queensland. *Crinia remota* Tyler & Parker is reported from a Quaternary cave deposit at Riversleigh Station.

*KEY WORDS: Crinia,* ilia, Leptodactylidae, Cainozoic, Queensland, Australia

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## Summary

TYLER, M. J. (1991) *Crinia* Tschudi (Anura: Leptodactylidae) from the Cainozoic of Queensland, with the description of a new species. *Trans. R. Soc. S. Aust.* 115(2), 99-101, 31 May 1991.

The leptodactylid frog *Crinia presignifera* sp. nov. is described from a series of Oligo-Miocene sites at Riversleigh Station in northwest Queensland. This finding represents the first record of the genus *Crinia* from the Tertiary and the first record of fossil material of *Crinia* from Queensland. *Crinia remota* Tyler & Parker is reported from a Quaternary cave deposit at Riversleigh Station.

KEY WORDS: *Crinia*, ilia, Leptodactylidae, Cainozoic, Queensland, Australia

## Introduction

The genus *Crinia* Tschudi, including frogs referred to *Ranidella* Girard (according to Heyer *et al.* 1982), is a group of 12 small, ground-dwelling species that live close to water. It is represented in all but the arid, central portion of Australia, and the central coastal area of Western Australia. One species (*C. remota* (Tyler & Parker)) occurs in northern Australia and southern New Guinea.

The genus *Crinia* has been the subject of diverse studies, particularly in the fields of polymorphism and of pre-mating isolating mechanisms. Consequently, published data on this genus are more substantial than those available for any other genus in Australia.

The phylogenetic relationships and the origin of *Crinia* are unclear. Morphological evidence (Heyer & Liem 1976; Davies 1989) suggests a close relationship with *Pseudophryne* Fitzinger and *Uperoleia* Gray.

The current fossil record of *Crinia* consists of the extant species of *C. signifera* Girard, from Pleistocene deposits at Henschke's Cave and Victoria Cave, in the southeast of South Australia (Tyler 1977), and the extant species *C. georgiana* Tschudi from Pleistocene deposits at Skull Cave and Devil's Lair in the extreme southwest of Western Australia (Tyler 1985).

Here I report the first Tertiary record of *Crinia*, and the first Quaternary record of *Crinia* from Queensland. The genus *Crinia* occurs at several Cainozoic sites at Riversleigh Station in northwest Queensland. Previously, two other leptodactylid genera have been reported from that area: *Lechriodus* Boulenger (Tyler 1989) and *Limnodynastes* Fitzinger (Tyler 1990).

## Material and Methods

The material is deposited in the Queensland Museum, Brisbane (QM) and the South Australian Museum, Adelaide (SAM). Letters following the abbreviations are departmental identifications.

Comparative studies were based on the osteological collections at the Department of Zoology, University of Adelaide.

Osteological nomenclature and methods of measurement follow Tyler (1976, 1989).

## Systematics

Family: Leptodactylidae Werner, 1896
Sub-family: Myobatrachinae Schlegel, 1850
Genus: *Crinia* Tschudi, 1838

At the time of the preparation of a description of the ilial characteristics of Australian frogs by Tyler (1976), *Crinia* was considered a monotypic genus, and *Ranidella* distinct from it. The principal morphological features distinguishing *C. georgiana* from the species of *Ranidella* examined (*R. parinsignifera* and *R. signifera*) were considered to be the extent of the dorsal protuberance, and the presence of a very slight longitudinal indentation upon the lateral surface of the ilial shaft of *Crinia* that was absent from the *Ranidella* species (Tyler 1976).

Examination of these particular features in additional species formerly referred to *Ranidella*: *bilingua, deserticola, glauerti, insignifera, pseudinsignifera, remota* and *riparia* indicates that the generic differences proposed by Tyler (1976) cannot be sustained. Nevertheless, and perhaps more significantly, despite its larger adult size, it is evident that *C. georgiana* has a more robust ilium than the species of *Ranidella* so far examined, in which the ilial shaft proportionately is deeper and more substantial than in those species that are now its congeners.

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Diagnostic generic features of *Crinia* are the curved and medio-laterally flattened shaft, lacking a dorsal crest and possessing a very slight medial indentation; large acetabular fossa with a broad peripheral rim; slight development of the ventral acetabular expansion and a subacetabular zone that does not protrude anteriorly. The dorsal acetabular expansion is poorly developed. The dorsal prominence is low and the dorsal protuberance slightly developed.

### *Crinia presignifera* sp. nov.
### FIG. 1A

*Holotype:* QM F17630. A left ilium collected at Wayne's Wok Site, Riversleigh Station, northern Queensland.
*Description of holotype:* Ilial shaft slender and slightly curved. Lacks dorsal crest but with moderately deep, slight lateral concavity along proximal one-third of shaft. Distal end of ilial shaft incomplete inferiorly.

Acetabular fossa large and deep, with prominent, elevated rim. Dorsal margin of acetabular fossa superior to inferior margin of ilial shaft. Pre-acetabular zone evenly rounded, expanding inferiorly into protruding rounded flare of sub-acetabular expansion. Inferior margin of sub-acetabular expansion lacking.

Dorsal acetabular expansion raised slightly.

Dorsal prominence poorly developed. Dorsal protuberance narrowly oval, prominent, projecting laterally.

Length of ilium: 6.3 mm.
*Paratypes:* There are 18 paratypes – Outasite Site: QM F17634–36, 18155, SAM P31230–33; Quentin's Quarry Site: AM F17631; Neville's Garden Site: QM F18156–58, SAM P31234–35; Two Trees Site: QM F17632, SAM P31228; Camel Sputum Site: QM F17633, SAM P31229.

The largest of the specimens in which the ilial shaft is complete measures 7.1 mm. A paratype is shown in Fig. 1.

Throughout the series the dorsal prominence and dorsal protuberance are conspicuous, and the dorsal acetabular expansion is elevated only slightly. The acetabular fossa is consistently large, but the breadth of the adjacent pre-acetabular zone varies from extremely narrow (at its closest proximity to the fossa) to moderately wide. The ventral acetabular expansion is incomplete in most specimens.
*Comparison with other species:* The overall similarity in external morphology of species of *Crinia* (excluding *C. georgiana*) is accompanied by an extreme conservatism in the form of the ilium. Most of the specific characters are slight, when compared with those distinguishing members of other genera e.g. *Limnodynastes* and *Litoria*. Nevertheless one feature distinguishing *C. presignifera* from congeners is the narrow pre-acetabular zone clearly demonstrated by comparison with *C. remota* in Fig. 1. Amongst extant species the one with the narrowest pre-acetabular zone is *C. signifera* but even in that species it is far more substantial than in the new species.

Fig. 1. A. *Crinia presignifera* sp. nov. paratype: QM F17630; B. *Crinia remota* SAM P31236

*Stratigraphy and lithology:* In the Riversleigh Station area Archer, *et al.* (1989) recognised a minimum of five types of Oligo-Miocene carbonates that are rich in bones. The sites bearing *C. presignifera* comprise two sequences of lacustrine carbonates that contain principally non-aquatic local faunas. These collectively are referred to by them as "System B" and "System C".
*Etymology:* In adding pre- (L. *prae*) as a prefix to *signifera* I am alluding to the ancestral nature of the fossil species relative to extant species.

### *Crinia remota* (Tyler & Parker)
### Fig. 1B

*Material:* A single right ilium, SAM P31236 from Carrington Cave, Riversleigh Station, Queensland.
*Descriptive notes:* The ilial shaft is cylindrical and the terminal portion is missing. Existing length 4.6 mm. The superior portion of the dorsal acetabular expansion is missing. The ventral acetabular expansion is broadly expanded.
*Comments: Crinia remota* (Tyler & Parker 1974) was described from southern Papua and is now known to occur also in northern Queensland and the Northern Territory including Melville Island and Groote Eylandt (Tyler *et al.* 1985, in press). The present specimen does not differ from specimens examined and is the first fossil record of the species.

Carrington Cave is situated in a hill adjacent to the Gregory River. The specimen was found near the surface of a vast mound of fragmented bones derived from the excreta of the ghost bat *Macroderma gigas*, and is located approximately 100 m from the entrance to the cave.

The age of the deposit is unknown but it is presumed to be Holocene or Late Pleistocene.

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# A LARGE NEW SPECIES OF *LITORIA* (ANURA: HYLIDAE) FROM THE TERTIARY OF QUEENSLAND

*BY MICHAEL J. TYLER**

## Summary

A new species of large hylid frog of the genus *Litoria* Tschudi is described from a small series of disarticulated, and fragmentary ilia from Tertiary freshwater limestone deposits on Riversleigh Station, Queensland. The species exhibits unique characters in the form of a pair of depressions situated on the ilium, superior to the acetabular fossa, and a horizontal flange projecting mediad from the ilial shaft. *Litoria magna* sp. nov. is the first record of the genus from the Tertiary of Queensland, but several congeners await further study and description.

KEY WORDS: *Litoria,* new species, Tertiary, Riversleigh, Queensland

*Transactions of the Royal Society of S. Aust.* (1991), **115**(2), 103-105.

# A LARGE NEW SPECIES OF *LITORIA* (ANURA: HYLIDAE) FROM THE TERTIARY OF QUEENSLAND

by MICHAEL J. TYLER*

## Summary

TYLER, M. J. (1991) A large new species of *Litoria* (Anura: Hylidae) from the Tertiary of Queensland. *Trans. R. Soc. S. Aust.* **115**(2), 103-105, 31 May, 1991.

A new species of large hylid frog of the genus *Litoria* Tschudi is described from a small series of disarticulated, and fragmentary ilia from Tertiary freshwater limestone deposits on Riversleigh Station, Queensland. The species exhibits unique characters in the form of a pair of depressions situated on the ilium, superior to the acetabular fossa, and a horizontal flange projecting mediad from the ilial shaft.

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KEY WORDS: *Litoria*, new species, Tertiary, Riversleigh, Queensland

## Introduction

Documentation of the rich Tertiary frog fauna from freshwater limestones on Riversleigh Station in northwest Queensland, commenced with the description of a new species of the leptodactylid genus *Lechriodus* Boulenger (Tyler 1989a). Tyler, *et al.* (1990) discuss the significance of the numerical abundance and dominance of that genus amongst the frog fossils recovered.

Two Tertiary species of *Limnodynastes* Fitzinger have been reported from Riversleigh Station (Tyler 1990), but as yet the hylid fauna is unknown.

Here I describe the first of several species of the hylid genus *Litoria* Tschudi. It is represented by a small series of ilia, is distinguished by a suite of unique characters, and is noteworthy for its particularly large size.

## Material and Methods

The material is deposited in museums abbreviated in the text as follows: Queensland Museum, Brisbane - QM; South Australian Museum, Adelaide - SAM. Letters following the abbreviations are departmental identifications.

Comparative studies were based on the osteological collections of the Department of Zoology, University of Adelaide.

Osteological nomenclature follows Tyler (1976), methods of measurement and orientation of specimens follow Tyler (1989a), and stratigraphic interpretation is after Archer *et al.* (1989).

## Systematics

Family: Hylidae Gray, 1825.
Sub-family: Pelodryadinae Günther, 1859.
Genus: *Litoria* Tschudi, 1838.

The diversity in external morphology in this genus is paralleled by the form of the ilium; comparative osteological data for 21 Australopapuan species was presented in tabular form by Tyler (1976). Diagnostic features are the absence of a dorsal crest upon the ilial shaft, and the presence of a shallow, longitudinal groove upon the medial surface of the shaft. The dorsal protuberance and dorsal prominence are not raised much above the superior border of the ilial shaft, but usually are well differentiated.

### ***Litoria magna*** sp. nov.

FIG. 1

*Holotype:* QM F17627. The proximal two-thirds of a right ilium collected at Camel Sputum (C.S.) Site, Riversleigh Station, northwest Queensland.

*Description of holotype:* Ilial shaft curved, deep, robust, cylindrical in section proximally and lacking a dorsal crest (Fig. 1a). Medial surface of shaft with horizontal, superior flange becoming progressively more prominent and rendered more conspicuous by accompanying inferior indentation. At its distal extremity, flange extends from shaft for distance equivalent to depth of shaft (Fig. 1b).

Acetabular fossa large, with narrow but prominent rim. Pre-acetabular zone evenly rounded, with narrow separation from acetabular fossa. Sub-acetabular zone incomplete. Medial surface of acetabular region bears shallow, central cavity ca. 1.0 mm in diameter and 0.7 mm deep.

Dorsal acetabular expansion slightly truncated but apparently poorly developed, being elevated only slightly above level of ilial shaft.

Dorsal prominence and dorsal protuberance poorly developed and replaced by a pair of distinct depressions: one located superior to anterior rim of acetabular fossa, the other superior to the centre of the fossa.

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Fig. 1. Holotype ilium of *Litoria magna* sp. nov. A. Lateral surface; B. medial surface.

Length of ilium 18.7 mm; estimated length of reconstructed complete ilium 25–27 mm.

*Paratypes:* Four incomplete ilia: Camel Sputum Site: QM F17628, SAM P31220-21; Gag Site QM F17629.

*Variation:* Each of the paratypes is an incomplete and variously abraded proximal head of an ilium. Although the ilial shafts terminate at or proximal to the development of the horizontal flange, the conspecificity of the material with the holotype is demonstrated by the presence of a pair of depressions superior to the acetabular fossa. In both SAM P31220 and QM F17628, the anterior of the depressions leads anteriorly to a groove connecting to the superior margin of the shaft.

Paratype QM F17629 is highly silicified, and the elaboration of bone bordering the depressions is suggestive of localised, secondary exostosis.

The paratypes appear to be from individuals that would have been smaller than the holotype and further differ in having a more elevated dorsal acetabular expansion.

The pit reported on the medial surface of the acetabular area of the holotype corresponds to the position of a foramen in QM F17629 and is presumably the effect of artificial enlargement of such a feature.

Paratype SAM P31221 consisted originally of the lateral face of the acetabular region and proximal ilial shaft. This fragile specimen disintegrated into three smaller fragments after it had been drawn. It probably was the corresponding portion of the more complete SAM P31220 which was extracted from the matrix at the same time.

*Comparison with other species:* The presence of a pair of depressions superior to the acetabular fossa, and the horizontal flange upon the ilial shaft distinguish this species from all congeners.

The depth of the ilial shaft of the holotype is indicative of a robust-bodied species, whilst examination of ilia of large species of *Litoria,* including *L. lesueuri* (Duméril & Bibron), *L. caerulea* (White) and *L. infrafrenata* (Günther) suggest that *L. magna* could have been bigger than any extant species, certainly having a snout to vent length of more than 120 mm.

*Stratigraphy and lithology:* Archer, Godthelp, Hand & Megirian (1989) provided a preliminary assessment of the stratigraphy of the major fossil-bearing sedimentary deposits at Riversleigh. The two sites from which *L. magna* has been recovered occur within a series of Oligo-Miocene lacustrine carbonates that range in age from approximately 15 to 25 million years BP. Camel Sputum Site occurs in limestones interpreted to be of early to middle Miocene age (within the Archer *et al.* "System B"), whereas Gag Site occurs in slightly younger middle to early late Miocene limestones (i.e. "System C" deposits).

*Etymology:* Latin *magna:* large, alluding to the size of the fossil species.

## Discussion

*Litoria* is the most speciose genus in Australia and New Guinea, and osteological data have supported the sub-division of the unit into assumed natural groupings of species (Tyler & Davies 1978).

The Tertiary record of *Litoria* is poor. Isolated specimens (*listed* in Tyler 1989b) have not been identified to species. Thus *L. magna* is the first Tertiary member of *Litoria* to be described.

The unique horizontal flange upon the ilial shaft, and the pair of supra-acetabular pits set *L. magna* apart from all extant species, and hence does not appear to be ancestral to any modern species group.

Other species of *Litoria* from Tertiary deposits on Riversleigh Station await description, but none approaches the size of *L. magna.* The large size of *L. magna* is unusual amongst the Tertiary frogs known from Riversleigh Station, for the species there are predominantly small, a feature characteristic, amongst extant frogs, of geographic areas that experience a high rainfall (Tyler 1989b, Fig. 8) and are not exposed to seasonal aridity.

## Acknowledgments

Progress on the elucidation of the Tertiary frog fauna of Riversleigh Station has been supported generously by Professor Michael Archer, Dr Suzanne Hand and Mr Henk Godthelp.

Laboratory studies in Adelaide have been funded by grants from the Australian Research Council. I thank Veronica Ward and Leanne Seller for their invaluable assistance in the sorting and documentation of the material. Research facilities were provided by the University of Adelaide. The provision of gelatin capsules for bone storage by Parke Davis Pty Ltd is gratefully acknowledged.

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# THE DISTRIBUTION OF ECHINOCEPHALUS OVERSTREETI DERDORFF & KO (NEMATODA), A PARASITE OF ELASMOBRANCH FISHES IN AUSTRALIAN WATERS

*BY IAN BEVERIDGE*

## Summary

*Transactions of the Royal Society of S. Aust.* (1991), 115(2), 107.

## BRIEF COMMUNICATION

# THE DISTRIBUTION OF *ECHINOCEPHALUS OVERSTREETI* DEARDORFF & KO (NEMATODA), A PARASITE OF ELASMOBRANCH FISHES IN AUSTRALIAN WATERS

A recent study of the echinocephalid nematode parasites of elasmobranchs from South Australian coastal waters[1] identified the species present as *Echinocephalus overstreeti* Deardorff & Ko, 1983, previously known only from a ray *Taeniura melanospilos* Bleeker from the Marquesas Islands (c. 10°S, 140°E) in the southern Pacific Ocean[2], and since reported from another species of ray, *Urogymnus asperrimus* (Bloch & Schneider), from Eniwetok Atoll (12°N, 164°E) (also spelled Enewetak Atoll) in the Marshall Islands of the eastern Pacific[3].

A number of records exist of *Echinocephalus* sp. from regions of Australia other than South Australia, from molluscs, teleosts, dolphins and turtles[1], but in these cases the species involved could not be determined with certainty, since the reports were based on larval specimens. In addition, adults of a second species, *E. sinensis* Ko, 1975, have been found in a ray, *Dasyatis fluviorum* Ogilby off the southern Queensland coast, and there are no known morphological criteria which reliably distinguish the larvae of the two species[1].

Since the study of *E. overstreeti* in South Australian waters was completed, a further 770 elasmobranchs, covering an additional 72 species, have been examined for parasites, comprising specimens from north-eastern Queensland, the Northern Territory, the north-west and south-west coastal areas of Western Australia and from Tasmania. Detailed records of all elasmobranch hosts examined for parasites have been lodged in the helminthological collections of the South Australian Museum (SAM).

Adult specimens of *E. overstreeti* were recovered from (numbers in parentheses are specimen registration numbers in SAM) 2 of 2 (100%) *Dasyatis sephen* (Forsskål) from Fog Bay, N.T. (HC 17194) and 13 of 15 (87%) at Nickol Bay, W.A. (AHC 17200–17205), from 1 of 12 (8%) *Myliobatis australis* Macleay from Bunbury, W.A. (HC 17208) and 2 of 4 (50%) *Heterodontus portusjacksoni* (Meyer) from Bunbury, W.A. (HC 17252) and 1 of 1 (100%) at Stanley, Tas. (HC 17231).

Larval stages of *Echinocephalus* which could not be identified to species were recovered from one of 10 (10%) *Carcharhinus plumbeus* (Nardo) from Bunbury, W.A. (HC 17216), two of 10 (20%) *Rhynchobatus djiddensis* (Forsskål) from Flat Top Is., Qld (HC 16041, 16042) but in none of 10 of the same species examined in the Northern Territory and Western Australia, from one of 14 (7%) *Himantura uarnak* (Forsskål) from Fog Bay, N.T. (HC 17219), but from none of five *H. uarnak* from Western Australia and Queensland and 1 of 1 (100%) *Aetobatus narinari* (Euphrasen) from Fog Bay, N.T. (HC 17214).

Adult specimens of *E. overstreeti* were thus recovered from elasmobranchs in coastal waters of three of the four states from which fish were examined, inferring an almost circum-continental distribution. Taken together with pre-existing records[1,2,3], the data suggest that *E. overstreeti* is widespread in the Pacific region. *E. sinensis*, described originally from *Aetobatus narinari* Euphrasen from Hong Kong[4] was not encountered in this survey, so the sole record of the species from the Australian region remains that from *D. fluviorum* from Queensland[1].

In spite of the large numbers and wide range of species of elasmobranchs examined, *Echinocephalus* adults and larvae occurred at a much lower overall prevalence (2.9%) than reported earlier for South Australian coastal waters (47.3%). The difference does not reflect the very few heterodontiforms collected outside South Australia, since the respective prevalences when these hosts are removed are 2.5% and 39.8%, but may reflect biases in the other host species sampled.

In South Australian waters, gravid specimens of *E. overstreeti* were found only in *Heterodontus portusjacksoni* (Meyer, 1973)[1]. None of the specimens collected from hosts other than *H. portusjacksoni*, included in this report, were gravid, confirming our earlier observations. However, the type specimens of *E. overstreeti*, collected from the ray *T. melanospilos* were gravid suggesting that heterodontiform sharks are not the only suitable hosts. The state of maturity of the specimens from *U. asperrimus* from Eniwetok Atoll was not reported[3], and no echinocephalids were found in a single *U. asperrimus* examined by us from northern Australian coasts.

Thanks are due to Mr B. G. Robertson who collected the specimens of *Echinocephalus*, and to the Australian Biological Resources Study who financially supported the collecting.

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# REVISED AGE FOR AYERS ROCK AND THE OLGAS

*BY W. K. HARRIS & C. R. TWIDALE*

## Summary

*Transactions of the Royal Society of S. Aust.* (1991), 115(2), 109.

## BRIEF COMMUNICATION

# REVISED AGE FOR AYERS ROCK AND THE OLGAS

In an earlier paper[1], it was deduced that Ayers Rock and the Olgas were already uplands 60-65 My ago, in middle Palaeocene times. It was not suggested, as Ollier[2,3] has claimed with respect to Ayers Rock, that the residual looked "very much as it does today in Palaeocene times . . ."[3] (p. 89). Both residuals are eroded in Cambrian sediments. The steep bounding slopes that give them their dramatic appearance were formed during the later Cainozoic, as a result of scarpfoot subsurface moisture attack[4]. That there were topographic rises on the present upland sites during or by the Early Tertiary was inferred from palaeontological evidence discovered during a programme of drilling instigated during a search for water in the nineteen sixties.

A broad shallow valley cut in the Cambrian sediments has been filled by a maximum of just over 100 m of Cainozoic sediments. The basal sequence is paludal but the sediments include riverine as well as surficial aeolian materials. The present plain surface of low relief is essentially constructional and gives no hint of the bedrock relief below. The suggestion that the ancestral Ayers Rock and the Olgas are of considerable antiquity derives first from the argument that if there were a valley there must have been higher ground on either side, and that the precursors of the modern residuals occupied some of this higher ground; and second from the occurrence near the base of the fill sequence and at depths of 81-84 m of lignites that contain an assemblage of plant remains that was considered to be of middle Palaeocene age. The uplands probably took the form of a soil-covered low dome in the case of Ayers Rock – the present bevelled crest plus a regolithic veneer – and of a complex of low rock domes in the case of The Olgas.

This earlier assignment of a Palaeocene age to the fossil assemblage (from Sample No. S4065) was based on the ranges of several species, in particular, *Herkosporites elliottii* Stover, *Proteacidites angulatus* Stover, *Beaupreaidites elegansiformis* Cookson and *B. verrucosus* Cookson. Elements which are now considered to have a limited Late Cretaceous or Early Tertiary age include *Quadraplanus brossus* Stover and *Tetracolporites verrucosus* Stover. More recently A.D. Partridge has identified fragments of *Grapnelispora evansii* Stover & Partridge (pers. comm. to W.K.H.) in the material. This species has a middle to late Maastrichtian age in Australia and New Zealand[5].

The material was previously equated with the *Gambierina edwardsii* zone (= the *Lygistepollenites balmei* zone). However, an alternative assignment is to the *Tricolpites longus* zone (Maastrichtian to basal Danian[6]) based on the presence of *Q. brossus* and *G. evansii*. The younger Palaeocene element may reflect down-hole contamination.

Since the earlier paper was published, further material from the region has come to hand and has been examined. Bore RN 11577 (lat. 25° 21′ 30″ S, long. 131° 03′ 00″E) yielded a carbonaceous sequence between 67 and 84 m. Palynomorph assemblages recovered from this interval are of Late Eocene age (Upper *Nothofagidites asperus* zone equivalent) indicated by the presence of *Malvacearumpollis* sp., *Quintinia* sp., *Gyrostemon* sp., an abundance of conifer pollen and a low diversity of "proteaceous" pollen.

This evidence, together with that of the original samples, indicates a complex Late Cretaceous and Tertiary depositional history for the valley between Ayers Rock and the Olgas. A similar history occurs in the adjacent Lake Eyre Basin[7] and it is tempting to relate these seemingly sporadic depositional episodes within the craton to regional warping, such as resulted in the disruption of drainage and in the formation of the Amadeus and other basins of internal drainage in Central Australia.

Thus we conclude that there were at least three depositional phases in the area: *viz.* a Late Cretaceous, a possible mid to late Palaeocene and a Late Eocene sequence. The earlier phase implies a slightly older age – by some 5-10 My – for the ancestral Ayers Rock and the Olgas than was previously deduced. Even this slightly older age is a minimum age. The bevelled upper surfaces of Ayers Rock and of the various domes of the Olgas complex may well turn out to be part of the even older Early Cretaceous or even Late Jurassic surface of which remnants remain in the MacDonnell, Flinders and Gawler ranges, and upon which impacted the meteorite responsible for Gosses Bluff[8].

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VOL. 115, PART 3

# ROTIFERA FROM AUSTRALIAN INLAND WATERS. VII. NOTOMMATIDAE (ROTIFERA: MONOGONONTA)

BY *W. KOSTE* & R. J. SHIEL†*

## Summary

Keys are given to 14 genera and 70 species of the Rotifera: Monogononta in the family Notommatidae presently recorded from Australian inland waters. Available distribution data and ecological information are given for *Cephalodella* (26 species), *Dorystoma* (1), *Eosphora* (5), *Eothinia* (1), *Itura* (3), *Monommata* (11), *Notommata* (14). *Pleurotrocha* (1), *Resticula* (3), *Scaridium* (1), *Taphrocampa* (2) and *Tetrasiphon* (1). *Drilophaga* is recorded here for the first time. A record of *Rousseletia* is *incertae sedis.* The genera *Metadiaschiza, Pseudoharringia, Pleurotrochopsis, Sphyrias* and *Tylotrocha* are not recorded from the continent.

KEY WORDS: Rotifera, Australia, taxonomic revision, Notommatidae, *Cephalodella, Dorystoma, Drilophaga, Eosphora, Eothinia, Itura, Monommata, Notommata, Pleurotrocha, Resticula, Rousseletia, Scandium, Taphrocampa, Tetrasiphon*

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# ROTIFERA FROM AUSTRALIAN INLAND WATERS. VII. NOTOMMATIDAE (ROTIFERA: MONOGONONTA)

by W. KOSTE* & R. J. SHIEL†

## Summary

KOSTE, W. & SHIEL, R. J. (1991) Rotifera from Australian inland waters VII. Notommatidae (Rotifera: Monogononta) *Trans. R. Soc. S. Aust.* **115**(3), 111-159, 29 November, 1991.

Keys are given to 14 genera and 70 species of the Rotifera:Monogononta in the family Notommatidae presently recorded from Australian inland waters. Available distribution data and ecological information are given for *Cephalodella* (26 species), *Dorystoma* (1), *Eosphora* (5), *Eothinia* (1), *Itura* (3), *Monommata* (11), *Notommata* (14), *Pleurotrocha* (1), *Resticula* (3), *Scaridium* (1), *Taphrocampa* (2) and *Tetrasiphon* (1). *Drilophaga* is recorded here for the first time. A record of *Rousseletia* is *incertae sedis*. The genera *Metadiaschiza, Pseudoharringia, Pleurotrochopsis, Sphyrias* and *Tylotrocha* are not recorded from the continent.

KEY WORDS: Rotifera, Australia, taxonomic revision, Notommatidae, *Cephalodella, Dorystoma, Drilophaga, Eosphora, Eothinia, Itura, Monommata, Notommata, Pleurotrocha, Resticula, Rousseletia, Scaridium, Taphrocampa, Tetrasiphon*

## Introduction

The purpose of our series of papers has been to document the rotifers recorded from Australia, primarily to provide usable keys to them. We have demonstrated the existence of a diverse Australian rotifer fauna distinct from that of Europe or North America, with >50% of recorded species in some genera endemic. Also, there is marked latitudinal and longitudinal variation in species assemblages. Taxonomic resolution of this component of aquatic systems permits more informed understanding of community ecology in inland waters and, thereby, better interpretation of environmental impacts on water quality.

The taxonomy of the rotifer families we have reviewed to date (see Koste & Shiel 1990b) has been reasonably straightforward. The Notommatidae, in contrast, appears to be the repository of everything not readily placed elsewhere. In their revision of the Wisconsin notommatids, Harring & Myers (1924) noted of the family that "there has been a steady accretion of new species and a periodic shifting of the old ones, until it has become a veritable Serbonian bog, carefully avoided by everybody or, at least, trespassed upon only under compulsion". It seems that time has only compounded the confusion. In the ensuing years some efforts were made to resolve loosely affiliated taxa by erection of new families, e.g. Lindiidae, Dicranophoridae, particularly by Remane (1933). Notwithstanding, the Notommatidae still contains 21 genera in two subfamilies (Koste 1978), with one-third of the genera monospecific, and an extraordinary profusion of 'species' in others [>200 in *Cephalodella* (Ruttner-Kolisko 1974)]. A systematic revision of the family is needed urgently. Given recent technological advances, particularly scanning electron microscopy (SEM) (cf. Koste & Shiel 1990a), resolution of the group is feasible.

Notommatid rotifers are predominantly littoral (epiphytic or epibenthic) in habit, collected in and around vegetation in shallow waters of lake or river margins, in billabongs, and in the roots or scales of floating macrophyte mats. Most are grazers, feeding on detritus, bacteria and epiphytic algae, particularly diatoms. Some taxa are omnivores, taking protozoans and other rotifers, and several species are parasitic on worms or leeches (Pourriot 1965; Koste 1978).

General problems associated with rotifer systematics are more pronounced in the Notommatidae, especially those arising from study of preserved material, sometimes long after collection (cf. Berzins 1982). Animals may be strongly contracted in preservatives, artefacts are produced by distortion, colours of organelles may fade, etc., leading to erroneous observations, incorrect measurements and misidentifications. For these reasons we consider that some of the notommatid taxa reported from Australia probably do not occur here. They may be good endemic species named for the European taxa they most closely resemble, or a known species wrongly identified.

To minimise erroneous identifications, we suggest that live material be examined wherever possible, followed by critical examination of mastax

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morphology, particularly the species-specific sclerotised *trophi* (Fig. 2). Extensive use of trophi morphology has been made in European revisions. General trophi structure was reviewed in Koste & Shiel (1987a), but in view of the difficulty of working with these small structures (some less than 20 µm), we attempted in earlier parts to produce keys to species based on morphometry, e.g. body v. toe length, claw:toe ratios, etc. Unlike most metazoans, rotifers are eutelic (cell numbers constant between generations) with little intraspecific morphological variation, hence comparative measurements of body parts can be used diagnostically. In the Notommatidae, close examination of the trophi is necessary to prevent confusion of closely allied taxa or juveniles of large species with adults of smaller forms.

In this review the format of earlier parts is followed; for convenience, genera and species are treated alphabetically. Keys to rotifer families are included in Koste & Shiel (1987a), which also contains brief descriptions of general morphology. Known distribution and ecological information are given for the species we have encountered. Available type locality and holotype information is included. Where type locality is not known, probable place of origin is given in parentheses; some early authors did not specify origin of material, however we consider it likely that in the late 18th–early 19th century their collections derived from proximal localities.

## Methods

Live animals can be collected with floating or submerged macrophytes from most standing waters. Stems of *Vallisneria, Eleocharis, Myriophyllum,* and other submergents provide rich rotifer assemblages. The floating liverwort, *Ricciocarpus,* or the fern, *Azolla,* usually have diverse rotifer faunas associated with their submerged parts. Whole plants or segments can be examined under LP microscopy and resident rotifers removed by fine pipette onto glass slides for HP microscopy. Animals can be restrained by light pressure of a coverslip (supported on plasticine "feet" or coverslip fragments), or in a purpose-built compression chamber (Martin 1986); all measurements of body morphology can be made on uncontracted individuals. If live material is not available, recently-preserved is preferable to long-preserved.

When all body measurements are taken, preparation of trophi for light microscopy should be made by clearing the animal(s) in sodium hypochlorite; at least several preparations should be made to permit interpretation of the orientation of the minute components. A drop of bleach solution placed beside the coverslip is drawn underneath it by carefully touching lens tissue to the opposite side. The clearing animal should be in view during the process because rapid flow of the bleach may move it or the trophi, and the preparation will be lost. A microscope-mounted video camera is a useful accessory for recording both whole-animal and trophi morphology during this procedure.

Fig. 1. Low vacuum system for mounting rotifers and clearing trophi onto a Nuclepore filter

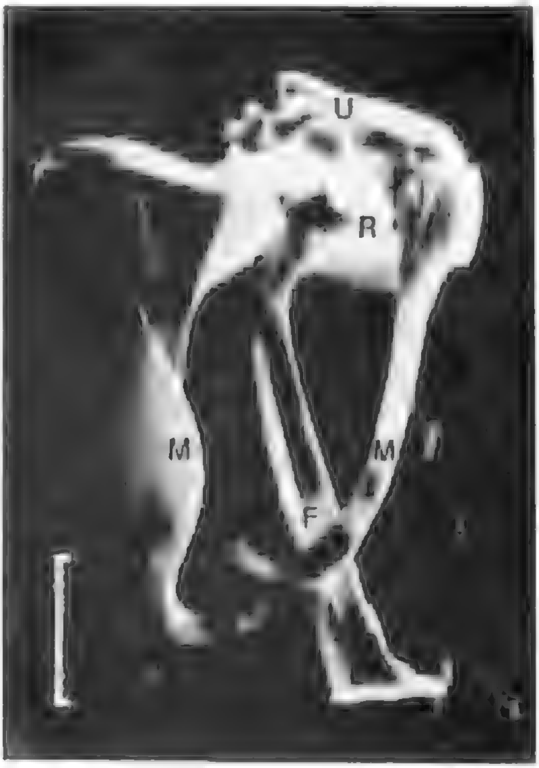


Fig. 2. Trophi of *Notommata copeus* from R. Murray waters, Barmah Forest. F = fulcrum, M. = manubrium, R = Ramus, U = uncus. Cambridge S600 Stereoscan. Scale line 20 µm.

Treatment of trophi for SEM will depend on their robustness; some larger trophi can simply be extracted from cleared animals by micropipette, rinsed through a graded ethanol series and pipetted from the final 100% ethanol or acetone onto a SEM stub (cf. Fig. 1). For more delicate trophi, the system shown in Fig. 2 was adapted from Markevitch & Koreneva (1981). Rotifers removed from field collections are rinsed through filtered water, pipetted in a small drop of water onto a Nuclepore membrane and treated with sodium hypochlorite for 5-10 min. Low vacuum is then applied to remove the hypochlorite solution, the cleared trophi are rinsed gently with distilled water, and the filter is removed and dried over silica gel. Critical point drying is not necessary. If sufficient numbers of animals are used, standard sputter coating with gold/palladium and examination under SEM

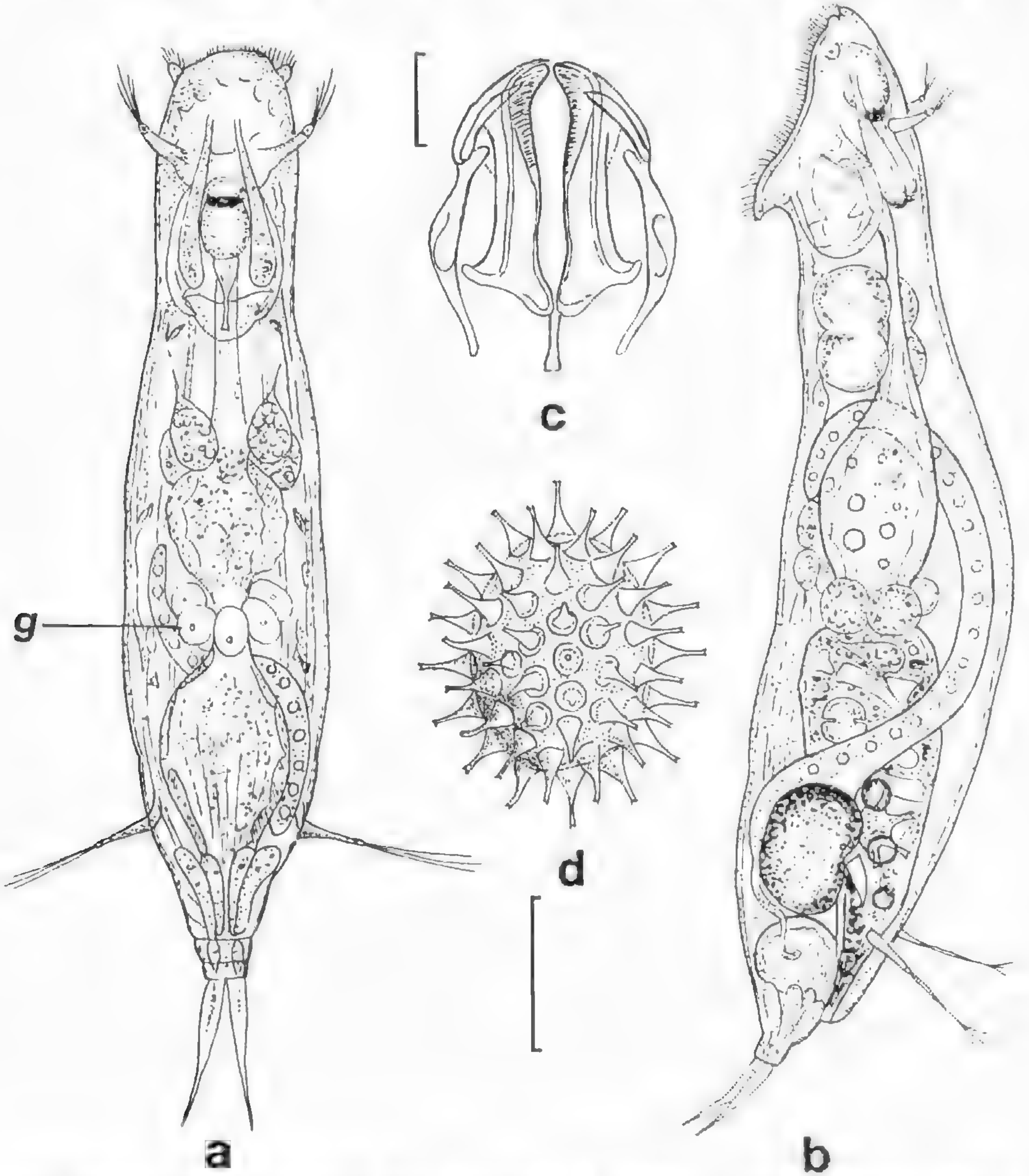


Fig. 3. *Tetrasiphon hydrocora* Ehrenberg: (a) dorsal, swimming (g = glands); (b) lateral, swimming; (c) trophi; (d) resting egg. Scale lines: a, b, d 100 μm; c 20 μm. After Koste (1978).

enables detailed resolution of trophi in different orientations. An alternative method detailed by Kleinow *et al.* (1990) permitted high-resolution micrographs of undistorted trophi preparations of a brachionid species, *Brachionus plicatilis*, but has not yet been used for rotifers with more complex trophi. Further details of trophi ultrastructure are given by Markevitch & Kutikova (1989).

## SYSTEMATICS

### Family Notommatidae Remane

The characteristics of the family were described by, *inter alia*, Harring & Myers (1924), Remane (1933) and Koste (1978). It is a diverse assemblage of illoricate or partly loricate taxa comprising two subfamilies: Tetrasiphoninae (two genera) and Notommatinae (19 genera) separated on the basis of presence (Tetrasiphoninae) or absence (Notommatinae) of a whorl of bulbous glands between the stomach and intestine.

### Subfamily Tetrasiphoninae

Of two described genera, *Repaulina* and *Tetrasiphon*, only *Tetrasiphon* is known from Australia.

### Genus *Tetrasiphon* Ehrenberg

*Tetrasiphon* Ehrenberg, 1840, p. 219. Monotypic genus.

*Type: Tetrasiphon hydrocora* Ehrenberg, 1840 p. 219.

### *Tetrasiphon hydrocora* Ehrenberg

FIGS 3, 4

Syn.: ?*Repaulina dicerea* Berzins, 1960, pp. 1-3.

*Type locality:* Berlin.
*Holotype:* Not designated.
*Description:* Body illoricate, cylindrical to fusiform; no annular ring separating head and trunk, cuticle somewhat stiff; abdomen ends in short stumpy projection over cloaca; foot short, bi-segmented, with two acutely pointed, elongated toes; corona oblique, extended ventrally to elongated 'chin'; tentaculate dorsal paired lateral antennae; lateral antennae towards posterior end of abdomen similarly elongate, with exceptionally long sensory setae; single cerebral eye; trophi with single toothed unci; manubria with complex projections (Fig. 3c); rami long, lyrate, curved dorsally, with pointed alulae; large hypopharynx muscle inserted in mastax wall; adult animal commonly in yellowish gelatinous sheath.

Length 450-1000 μm, toes 60-80 μm; subitaneous egg 140-154x110-115 μm, with curved spinules 45-65 μm long; resting egg 200 x 155 μm; male to 300 μm; male egg 102-126×88-92 μm.

Fig. 4. *Tetrasiphon hydrocora* grazing on *Pleurotaenium*. Tallandoon billabong, Mitta Mitta River, Vic. Kodak T-max, 1/30 sec.

*Ecology:* In *Sphagnum* pools, acid waters in Europe, N. and S. America; billabongs of upper Murray tributaries, N.S.W., Vic.; dune lakes in Tasmania. Specialist grazer on large desmids, e.g. *Cosmarium, Micrasterias, Pleurotaenium* (Fig. 4), *Staurastrum*. During filmed feeding experiments, an individual from a billabong on the Mitta Mitta River at Tallandoon, Vic., ingested 10 *Staurastrum* in 30 min. As the cells passed along the gut they gradually lost colour, the semicell branches were fractured by muscular action, and the fragments were egested.
*Literature:* Pourriot 1965; Koste 1968, 1978.

### Subfamily Notommatinae

The subfamily has 19 named genera, 13 of which are known from Australia. *Metadiaschiza* Fadeev (Fig. 5:1), *Pleurotrochopsis* Berzins (Fig. 5:2), *Pseudoharringia* Fadeev (Fig. 5:3), *Sphyrias* Harring (Fig. 5:4) and *Tylotrocha* Harring & Myers (Fig. 5:5) are not presently recorded here. For further information on them, see Koste (1978). *Drilophaga* is a new record, reported here for the first time. A single report of *Rousseletia* is considered *incertae sedis*.

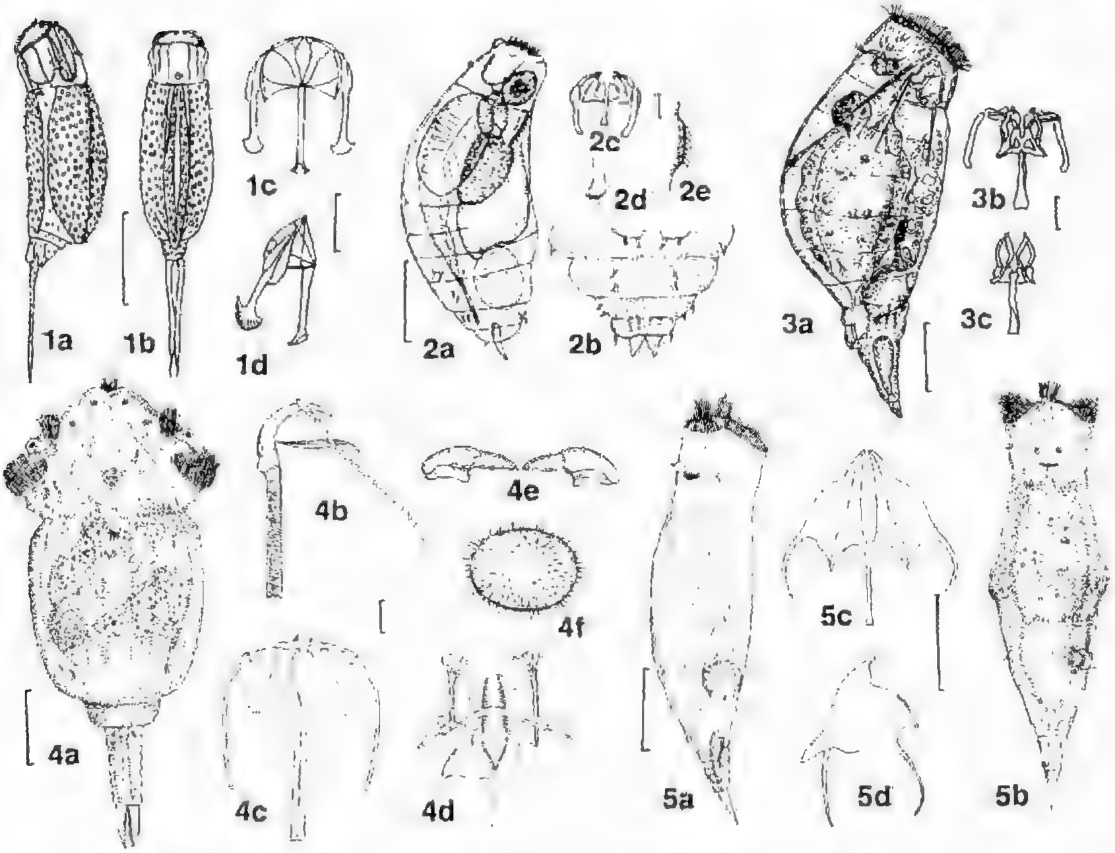


Fig. 5. 1, *Metadiaschiza* Fadeev: (a) lateral; (b) dorsal; (c) trophi ventral; (d) trophi, lateral. 2, *Pleurotrochopsis* Berzins: (a) lateral; (b) posterior abdomen and toes, dorsal; (c) trophi, ventral; (d) distal end of fulcrum; (e) ventral cuticular 'lamella' with hooks. 3. *Pseudoharringia* Fadeev: (a) lateral; (b) trophi, ventral; (c) fulcrum and rami. 4, *Sphyrias* Harring: (a) dorsal; (b) trophi, lateral; (c) trophi ventral; (d) trophi, apical; (e) unci, lateral; (f) resting egg. 5, *Tylotrocha* Harring & Myers: (a) lateral; (b) dorsal; (c) trophi, ventral; (d) trophi, lateral. 1 after Wulfert (1937), 2 after Berzins (1973), 3 after Kutikova (1970), 4 after Koste (1978), 5 after Harring & Myers (1922). Scale lines: adults 50 μm; trophi 10 μm.

## Key to genera of the subfamily Notommatinae

1. Corona on cylindrical extrusion/evagination, with circumapical ciliation (Fig. 14a); annular adhesive organ present; no lateral ciliary auricles; mouth deeply invaginated.....*Drilophaga* Vejdovsky (Fig. 14)
Corona not extruded, may be frontal, oblique or extending ventrally; no adhesive organ; ciliary auricles may be present; mouth not deeply invaginated..................................2
2(1). Vitellarium band or ribbon-shaped..........3
Vitellarium oval or kidney-shaped..........5
3(2). Nuclei arranged linearly......................4
Nuclei irregularly distributed......*Enteroplea* Ehrenberg (Fig. 15:2)
4(3). Eyeless; foot two to three-segmented.......... ...........*Pseudoharringia* Fadeev (Fig. 15:3)
Two frontal eyes on papillae; foot one-segmented with annuli........*Sphyrias* Harring (Fig. 5:4)
5(2). Foot and toes longer than body............6
Foot and toes shorter than body..........7
6(5). Toes of dissimilar length; foot short, mostly 2-, rarely three-segmented...*Monommata* Bartsch (Figs 19, 20)
Toes of similar length; foot 3-segmented and very long.........*Scaridium* Ehrenberg (Fig. 28:1)
7(5). Foot with single toe....*Tylotrocha* Harring & Myers (Fig. 5:5)
Foot with two toes..........................8
8(7). Rump or last foot segment with spine.......9
Rump or last foot segment without spine....10
9(8). Rump with curved spine..................... ......*Dorystoma* Harring & Myers (Fig. 15:1)
Foot-end with short spine.... ....*Rousseletia* Harring (Fig. 29)
10(8). Trunk loricate with 3-5 species-specific cuticular plates............................11
Trunk illoricate..............................12

11(10). 2 dorsolateral plates; 1 granulated ventral plate . . . . . . . . . . . . . . *Cephalodella* Bory de St Vincent (Figs 7-13)
2 dorsoventral, 2 (or 5) ventrolateral plates, also 3 smooth trunk plates present. . . . . . . . . . . . . *Metadiaschiza* Fadeev (Fig. 5:1)
12(10). Cuticle with rows of tiny hooks. . . . . . . . . . . . . . . . . . . . . *Pleurotrochopsis* Berzins (Fig. 5:2)
Cuticle lacking hooks. . . . . . . . . . . . . . . . . . . 13
13(12). Trunk with conspicuous annuli. . .*Taphrocampa* Gosse (Fig. 28:2, 3)
Annuli absent. . . . . . . . . . . . . . . . . . . . . . . . . 14
14(13). One cerebral eye and two widely-separated frontal eyes. . . . . . . . . . . . . . . . . . . . . . . . . . . 15
Cerebral eye absent (or if present, no frontal eyes as above). . . . . . . . . . . . . . . . . . . . . . 17
15(14). Stomach with blind sacs. . . . . . . . . . *Itura* Harring & Myers (Fig. 18)
Stomach without blind sacs . . . . . . . . . . 16
16(15). Mastax with single salivary gland. . . .*Eothinia* Harring & Myers (Fig. 17:2)
Mastax with paired salivary glands. . *Eosphora* Ehrenberg (Figs 16, 17:1)
17(14). Corona displaced ventrally; ciliary auricles generally present. . . . . . . . . . . . . . .*Notommata* Ehrenberg (Figs 21–25)
Corona anterior, no auricles present . . . . . . .18
18(17). Salivary glands symmetrical. . . . .*Pleurotrocha* Berzins (Fig. 26:1)
Salivary glands asymmetrical or rudimentary. . . . *Resticula* Harring & Myers (Figs 27:2-4)

## Genus *Cephalodella* Bory de St Vincent

*Cephalodella* Bory de St Vincent, 1826, p. 43.

*Type: Cercaria catellina* Müller, 1786, p. 130. = *Cephalodella catellina* (Müller).
*Type locality:* Copenhagen.

Fusiform notommatid rotifers of various shapes, from elongate to short and stumpy; occasionally illoricate, but mostly with one or more lorica plates, position of which varies according to species; slight constriction between head and trunk, none between trunk and short foot, which bears two toes; in loricate taxa, dorsal and lateral sulci distinct between plates; corona frontal, oblique, with long marginal cilia and two lateral tufts of long swimming cilia; buccal field lightly ciliated; mastax virgate, with long straight fulcrum, poorly developed rami; retrocerebral organ rudimentary or absent; eyespot cervical, single or paired frontal, or absent.

Of >200 *Cephalodella* species worldwide, Koste (1978) described 132 taxa from Europe. Twenty-four of these, and two endemics, are known from Australia. Other taxa (especially *nomina dubia*) are given by Harring & Myers (1924), who also discuss the confused generic nomenclature.

*Trophi morphology:* In the descriptive section below, we recognize the six trophi types described by Wulfert (1937). In descriptions of trophi structures, we use 'proximal' to refer to the head or anterior end and 'distal' to the tail or posterior end. 'Basal' as used by Wulfert implies proximal.

Type A (Fig. 6:1): fulcrum spatulate distally; rami single, without teeth on inner margin; manubria slender, rodlike, curving inwards in top view, from straight shaft, no basal lamellae or distal dilation of manubria, which form characteristic crescentic shape when closed.

Type B (Fig. 6:2): fulcrum as Type A; inner margin of rami toothed or striated, at times with alulae; manubria with single or bilateral basal lamellae, distally T-shaped (termed 'double-crooked' by Wulfert, referring to a curved shepherd's 'crook'. This implement, and the term, no longer seem to be in common usage). Several species (e.g. *C. eva)* have a spatulate dilation of the manubria ends rather than a free-standing T, but in all other features conform to Type B trophi.

Type C (Fig. 6:3): features distinctive ringlike fenestrations at distal ends of manubria, considered by Wulfert to be derived from double-crooked Type B trophi.

Type D (Fig. 6:4): is most complex, with trophi parts not found in other types. Fulcrum short, dilated distally (also in lateral view), narrower in middle; rami from above widely separated, with comblike teeth on forcipate tips (absent in *stenroosi*); manubria proximally with wide bilateral lamellae, distally with single abrupt inward curve or crook; behind basal expansions, branched structures (subunci) occur; unci single, often with dorsal plate. In some species (*forficula, gigantea, tenuiseta*), a large delicate frontal plate with denticulate margin occurs above rami.

Type E (Fig. 6:5): known only in *C. megalocephala*. Fulcrum not dilated; rami right-angled dorsally (visible in lateral view), closed distally (at fulcrum) and separating proximally; basal lamellae of thin, S-shaped manubria apparently separate.

Type F (Fig. 6:6): recorded only in *C. mira*, which is not known from Australia. This trophus is comprised entirely of delicate rods.

### Key to species of *Cephalodella* recorded from Australian inland waters

1. Ratio total length/toe length <3 . . . . . . . 2
Ratio total length/toe length >3 . . . . . . . 5
2(1). With single or double cerebral eye. . . . . . . 3
Eyeless. . . . . . . . . . . . . . . . . . . . . . . . . . . . 4
3(2). Toes curved dorsally, distinctly segmented. . . . . . . . . . . . . *C. tantilloides* Hauer (Fig. 13:1)

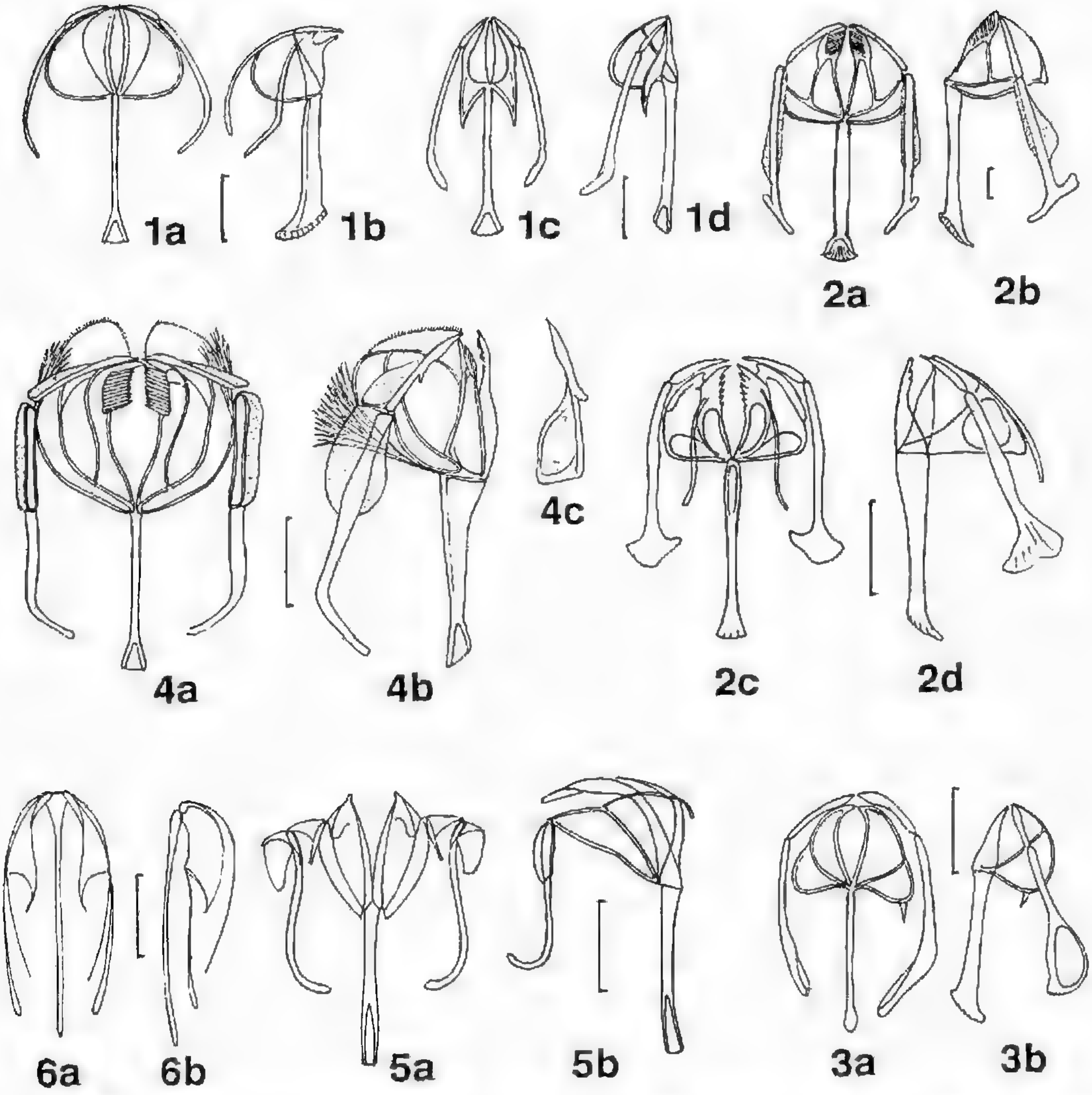


Fig. 6. Trophi types recognized in *Cephalodella* species. 1, Type A: (a) ventral; (b) lateral; (c, d) variant. 2, Type B: (a) ventral; (b) lateral; (c, d) variant. 3, Type C: (a) ventral; (b) lateral. 4, Type D: (a) ventral; (b) lateral, (c) uncus, lateral. 5, Type E: (a) ventral; (b) lateral. 6, Type F: (a) ventral; (b) lateral. After Wulfert (1937). Scale lines 10 μm.

Toes sigmoid in lateral view, not segmented..................*C. nana* Myers (Fig. 12:1)

4(2). Abdomen with hooked caudal projection..................*C. mucronata* Myers (Fig. 11:4)
Without hooked caudal projection..................*C. biungulata* Wulfert (Fig. 7:3)

5.(1). Ratio total length/toe length 3–5..........6
Ratio total length/toe length $>5$..........21

6(2). Toe tips with longitudinal denticle row (2-4) on functionally ventral side........*C. lindamaya* Koste & Shiel (Fig. 11:1)
Toe tips without ventral denticles, but may have median dorsal denticles..................7

7(6). Body $>300$ μm..........................18
Body $<300$ μm..........................8

8(7). Body $>90$ μm, toes $>20$ μm..............9
Body $<90$ μm, toes $\leq 20$ μm.......*C. gisleni* Berzins (Fig. 10:2)

9(8). Toes (straight or curved) taper evenly from base to tip..............................11
Toes with recurved bristle-like tip or obvious segmentation..........................10

10(9). Tips of toes sickle-shaped, recurved..........................*C. apocolea* Myers (Fig. 7:1)

Distal ¼ of toes demarcated by transverse septum into segmented tip .......... *C. intuta* Myers (Fig. 10:5)
11(9). Toes >60 µm .......... 12
Toes <60 µm .......... 13
12(11). Trophi >70 µm .......... *C. gibba* (Ehrenberg) (Fig. 9:6)
Trophi ca. 30 µm .......... *C. tinca* Wulfert (Fig. 13:3)
13(11). Toes 30–60 µm .......... 15
Toes <30 µm .......... 14
14(13). Body <125 µm; toes 20–26 µm; trophi <30 µm .......... *C. exigua* (Gosse) (Fig. 9:3)
Body >125 µm; toes 25–28 µm; trophi 30–34 µm .......... *C. ventripes* Dixon-Nuttall (Fig. 13:4)
15(13). Trophi <30 µm .......... 16
Trophi >30 µm .......... 17
16(15). Paired eyespots with crystalline lens; toes > 1/3 body length .. *C. misgurnus* Wulfert (Fig. 11:3)
No eyespots; toes < 1/3 body length .......... *C. forficata* (Ehrenberg) (Fig. 9:4)
17(15). Single eyespot at posterior end of ganglion; corona with prominent lips; manubria not crooked .......... *C. hoodi* (Gosse) (Fig. 10:4)
Paired frontal eyespots in single capsule; corona without prominent lips; manubria crooked .......... *C. sterea* (Gosse) (Fig. 12:4)
18(7). Toes >100 µm .......... 19
Toes <100 µm .......... 20
19(18). Toes ca. 1/3 body length; trophi >70 µm .......... *C. gibba* (Ehrenberg) (Fig. 10:1)
Toes 1/6 body length; trophi <70 µm .......... *C. panarista* Myers (Fig. 12:2)
20(18). Distinct eyespot; toes 1/5 body length .......... *C. forficula* (Ehrenberg) (Fig. 9:5)
No eyespot, toes ½ body length .......... *C. tenuiseta* (Burn) (Fig. 13:2)
21(2). Toes >20 µm .......... 22
Toes <20 µm .......... *C. catellina* (Muller) (Figs 7:4, 8)
22(21). Body >190 µm .......... 23
Body <190 µm .......... 24
(NB: Occasionally individuals of *C. parasitica* may exceed 190 µm; see species determination.)
23(22). Toes >50 µm (at least 1/3 body length) .......... *C. eva* (Gosse) (Fig. 9:2)
Toes <50 µm, 1/6 body length .......... *C. megalocephala* (Glasscott) (Fig. 11:2)
24(22). Eyespot(s) visible, coloured or colourless ... 25
No eyespot .......... *C. parasitica* (Jennings) (Fig. 12:3)
25(24). Two cerebral eyespots; lorica keeled in dorsal 1/3 .......... *C. euderbyi* Wulfert (Fig. 9:1)
Single eyespot, colourless or coloured; no dorsal keel on posterior lorica .......... 26
26(25). Eyespot reddish; trophi >30 µm .......... *C. auriculata* (Müller) (Fig. 7:2)
Eyespot colourless; trophi <30 µm .......... *C. gracilis* (Ehrenberg) (Fig. 10:3)

### *Cephalodella apocolea* Harring & Myers
### FIG. 7:1

*Cephalodella apocolea* Harring & Myers, 1924, p. 509, Figs 33:1, 2.

*Type locality:* Not specified. ". . . common in weedy ponds and bogs." Vilas and Oneida Counties, Wisconsin, are first localities mentioned by Harring and Myers.
*Holotype:* Not designated, ? Myers Collection, American Museum of Natural History (AMNH), New York.
*Description:* Body transparent, elongate, slightly compressed laterally; plates obvious, with distinct lateral sulci; foot large, robust, with small protruding tail; foot glands large, pyriform; toes set wide apart, straight, ending in recurved, sickle-shaped tips (toes may be crossed in swimming animal); corona oblique, convex, without protruding lips; trophi modified type A, slender, with delicate, curved manubria; fulcrum with slight terminal bend; eyespot absent.

Total length 125–185 µm; trophi 29–33 µm (fulcrum 12–20 µm, manubria 20 µm); toes 32–58 µm.
*Ecology:* In acid-neutral waters on submerged plants, in periphyton, where it feeds on diatoms and unicellular algae. Europe, N. America, New Zealand. pH tolerant. Single record: Magela Creek, N.T. (billabong not named, possibly Mine Valley).
*Literature:* Koste 1981.

### *Cephalodella auriculata* (Müller)
### FIG. 7:2

*Vorticella auriculata* Müller, 1773, p. 111.
*Cephalodella auriculata:* Harring & Myers, 1924, p. 479, Fig. 28:6.
For extensive synonymy see Kutikova (1970: 240), Koste (1978: 366).

*Type locality:* Copenhagen.
*Holotype:* Not designated.
*Description:* Body short, stout; head conspicuously wider than trunk, with small rostrum; lorica rigid, plates distinct; foot very short, toes short (<1/5 length); caudal antennae setae long; mastax large with two round, clear salivary glands; trophi type A, with small, thin mallei, slender recurved manubria, fulcrum long, expanded distally. Resembles *C. ventripes*, but has single red cervical eyespot.

Total length 120–160 µm; trophi 36 µm; toes 22–28 µm; male 95 µm.
*Ecology:* Cosmopolitan in beach sand, in littoral of still and flowing waters, where its main food is phytoflagellates and detritus. Qld, N.T., Tas., Vic., common in R. Murray billabongs. 16.0–22°C, pH 6.4–7.3, 57.3–274 $\mu S\ cm^{-1}$.
*Literature:* Colledge 1914; Koste 1981; Berzins 1982; Koste *et al.* 1988.

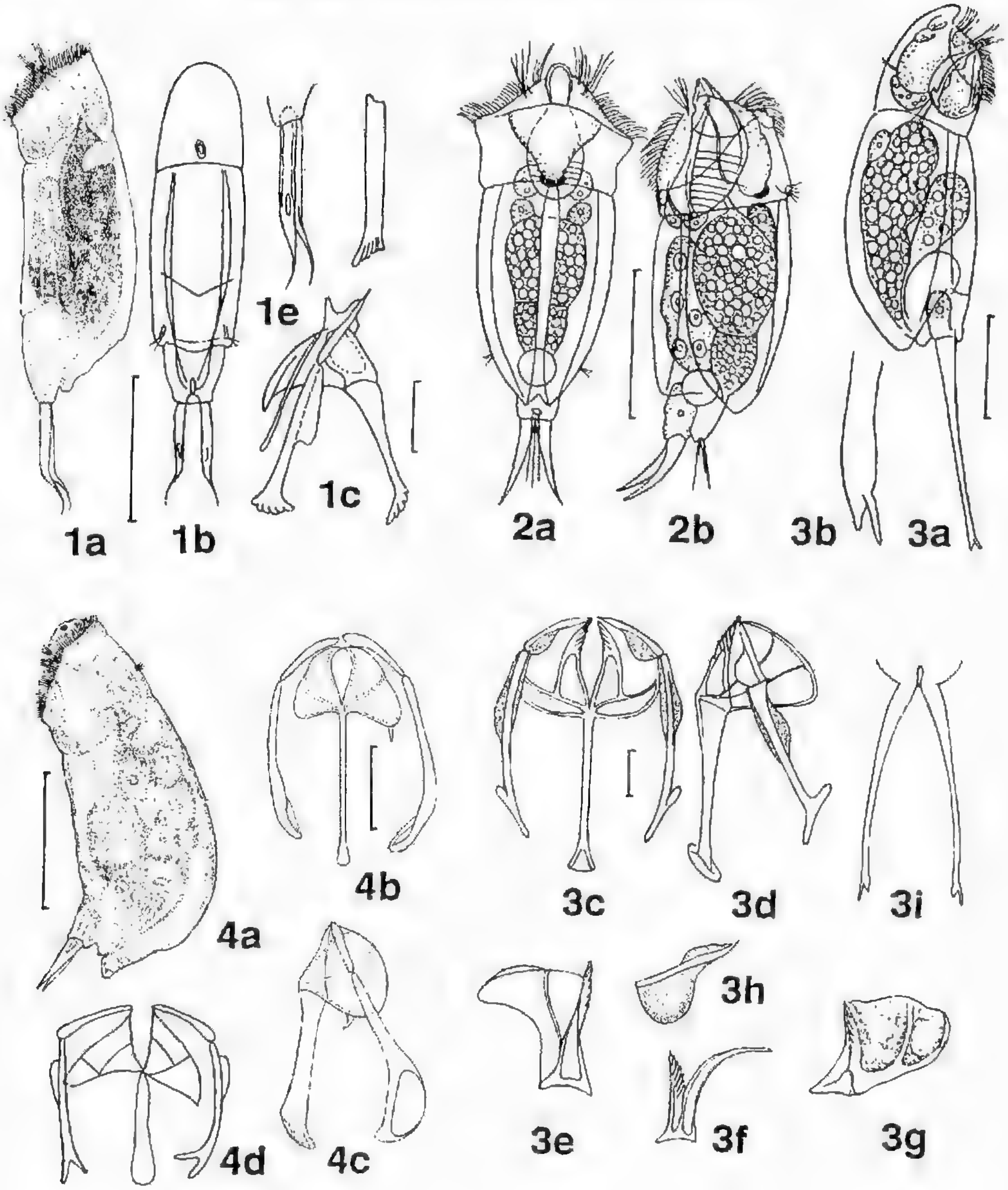


Fig. 7. 1, *Cephalodella apocolea* Myers: (a) lateral; (b) dorsal; (c) trophi, lateral; (d) toe tips, lateral; (e) fulcrum, lateral. 2, *C. auriculata* (Müller): (a) dorsal; (b) lateral; for trophi see Fig. 3:1a, b. 3, *C. biungulata* Wulfert: (a) lateral; (b) toe tip, lateral; (c) trophi, ventral; (d) trophi, lateral; (e) uncus; (f-h) views of ramus; (i) toes, ventral. 4. *C. catellina* (Müller): (a) lateral; (b) trophi, ventral; (c) trophi lateral; (d) trophi of *C. armata* Rudescu. 1, 2 after Wulfert (1940); 3 after Wulfert (1937); 4a–c after Harring & Myers (1924); 4d after Rodewald-Rudescu (1960). Scale lines: adults 50 μm; trophi 10 μm.

### *Cephalodella biungulata* Wulfert
FIG. 7:3

*Cephalodella biungulata* Wulfert, 1937, p. 617–618, Fig. 26.

*Type locality:* (Germany).
*Holotype:* Not designated.
*Description:* Body hyaline, oval, dorsally arched; head short, slightly oblique; abdomen projects over short foot, both covered by dorsal plates; toes long, flexible, >1/3 total length, with distinctive bifurcate tips due to presence of spinule at distal end; mastax lacks salivary glands; trophi of *C. gibba* type (B), with symmetrical rami denticulate on inner margin; manubria double-crooked, with bilateral proximal lamellae (Fig. 7:3c); shaft of uncus with semicircular lamella. Eyes absent. Close to *C. gibba*. Distinguished from it by the lack of eyes, characteristic longer bifurcate toes and trophi differences.

Total length 250–313 µm; toes 88–112 µm; trophi 50–54 µm.
*Ecology:* Rare in littoral/moss of pools and streams in Europe. Several individuals in a collection from the filling Dartmouth reservoir in 1978, probably incursions from a submerged littoral habitat. Not collected subsequently.

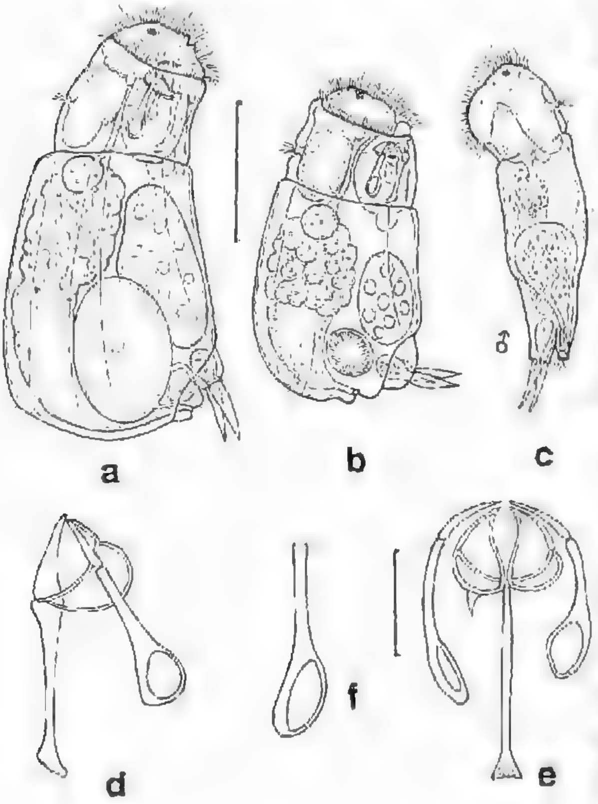


Fig. 8. *Cephalodella catellina* (Muller). (a) lateral; (b) second individual, lateral; (c) male, lateral; (d) trophi, lateral; (e) trophi, ventral; (f) distal end of manubrium. Koste, orig. Scale lines: adult 50 µm; trophi 10 µm

### *Cephalodella catellina* (Müller)
FIGS 7:4, 8

*Cercaria catellina* Müller, 1786, p. 130, Fig. 20:12,13.
*Cephalodella catellina:* Bory de St Vincent, 1826, p. 43.

See Harring & Myers (1924, p. 183–184) and Koste (1978, p. 371) for extensive synonymy.
*Type locality:* Copenhagen.
*Holotype:* Not designated.
*Description:* Body short, stout, bulbous posteriorly; abdomen laterally compressed, with wide lateral sulci separating indistinct lorica plates; foot short, ventral, beneath overhanging 'tail'; toes short, approx. 1/10 body length, thin to conical; mastax with ventral salivary glands (may be absent in small specimens); trophi type C, with long fulcrum slightly expanded distally; manubria rod-shaped, decurved, ending in semicircular dorsal expansion (Fig. 8f). Hooked manubria ends may result from hypochlorite digestion (cf. Fig. 7:4d) (Koste 1978); two separate red frontal eyespots.

Total length 80–160 µm; toes 9–14 µm (18–20 µm in Harring & Myers 1924); trophi 27 µm (45 µm in Harring & Myers); male 140 µm, toes 17 µm.
*Ecology:* Cosmopolitan in fresh to brackish water, occasionally reported in coastal (marine) waters. N.S.W., Tas., Vic. 12.5–23.5°C, pH 4.4–6.8, 69.5–600 µS cm$^{-1}$, 2.9–300 NTU. A parasite of *Volvox* colonies (Europe and North America) is referred to *C. catellina*, *C. catellina volvocicola* (Zawadowsky). It is not recorded from Australia.
*Literature:* Evans 1951; Shiel & Koste 1979; Koste & Shiel 1987b.

### *Cephalodella euderbyi* Wulfert
FIG. 9:1

*Cephalodella euderbyi* Wulfert, 1940, p. 564, Fig. 4.

*Type locality:* Birkhorster Moor (eastern Germany).
*Holotype:* Not designated.
*Description:* Body stout, lightly arched dorsally; head approx. 1/3 body length; corona with slightly protruding lips; posterior dorsal lorica compressed, resembles keel; foot short, almost covered by pointed 'tail'; toes short, approx. 1/5 total length, thin, straight, occasionally slightly recurved; mastax large, with distinct salivary glands; trophi of type A – fulcrum spatulate distally; manubria thin, rodlike, with single crook distally; rami single, with very small alula teeth; two small ruby-red cerebral eyespots.

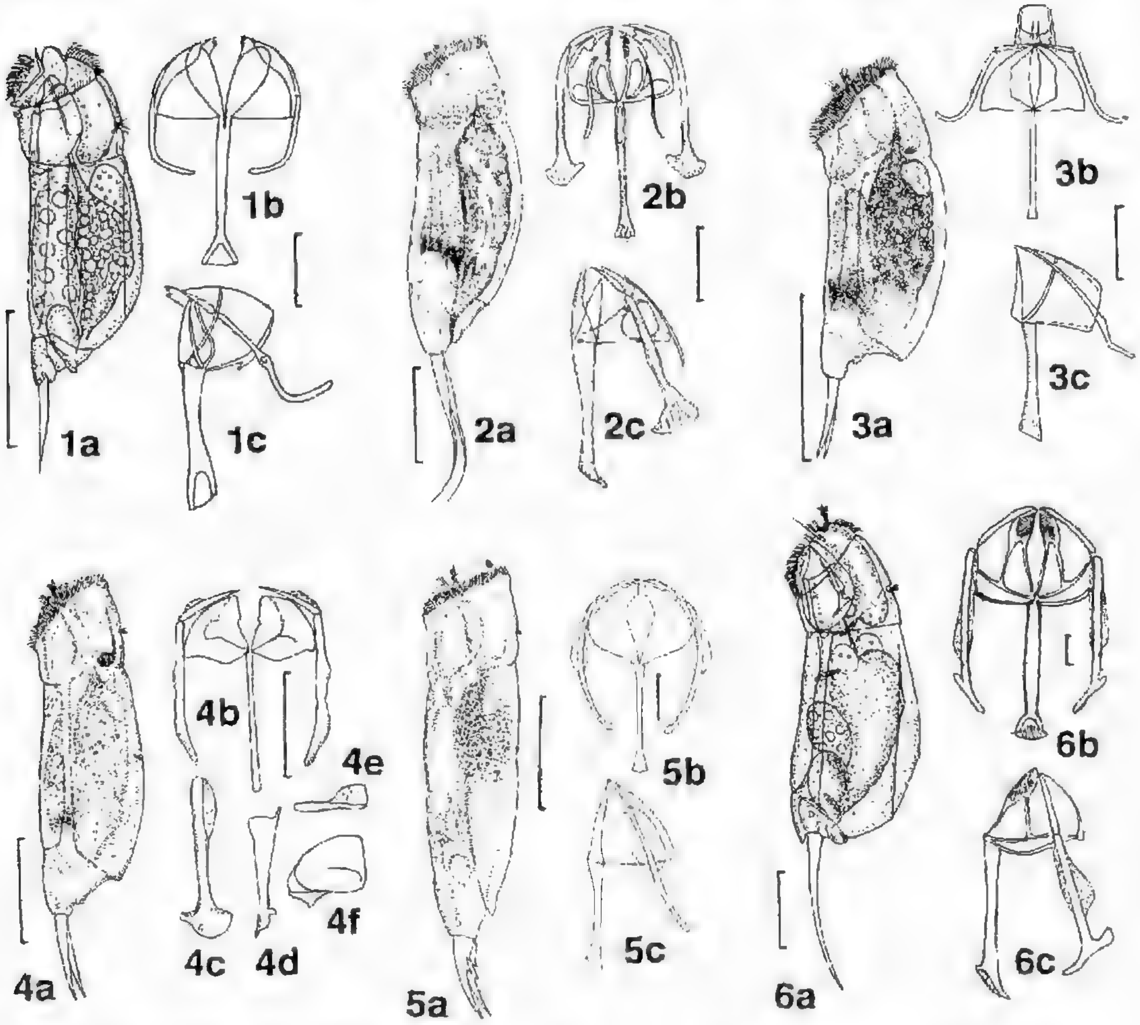


Fig. 9. 1, *Cephalodella euderhyi* Wulfert: (a) lateral; (b) trophi, ventral; (c) trophi, lateral. 2, *C. eva* (Gosse): (a) lateral; (b) trophi, ventral; (c) trophi, lateral. 3, *C. exigua* (Gosse): (a) lateral; (b) trophi, ventral; (c) trophi, lateral. 4, *C. forficata* (Ehrenberg): (a) lateral; (b) trophi, ventral; (c) manubrium, lateral; (d) fulcrum, lateral; (e) uncus; (f) ramus. 5, *C. forficula* (Ehrenberg): (a) lateral; (b) trophi, ventral; (c) trophi, lateral. 6, *C. gibba* Ehrenberg: (a) lateral; (b) trophi, ventral; (c) trophi, lateral. 1, 2b, c, 3c after Wulfert (1940); 2a, 3a, 4a, 5 after Harring & Myers (1924); 3b, 4c-f after Donner (1949); 4b after Wiszniewski (1936); 6 after Wulfert (1937). Scale lines: adults 50 μm; trophi 10 μm.

Total length 150–168 μm; trophi 32 μm; toes 28 μm; male 110 μm; resting egg 53 μm.
*Ecology:* Described from a shallow moor in Germany, where it was noted to graze green algae. Single unverified record from Boar's Lagoon, Vic. Not seen in our material.
*Literature:* Berzins 1982.

### *Cephalodella eva* (Gosse)
FIG. 9:2

*Furcularia eva* Gosse, 1887, p. 864, Fig. 14:9.
*Cephalodella eva:* Harring & Myers, 1924, p. 507.

*Type locality:* (England). "Lacustrine."
*Holotype:* Not designated.

*Description:* Body slender, laterally compressed, dorsally gibbous; head short, broad, neck clearly marked; plates distinct; corona oblique without projecting lips; foot large, with large pyriform foot glands; toes long, approx. 1/2 total length, very slender and generally curved ventrally; trophi type B, with long, strongly crooked manubria; no eyespot or retrocerebral organ.

Total length 190–285 μm; trophi 23–30 μm

(fulcrum 19 μm, manubrium 23 μm, right uncus 11 μm); toes 50–85 μm.
*Ecology:* Cosmopolitan in periphyton, moss, beach sand, moors. Grazes diatoms. Rare, from a billabong near Eildon, Vic.; Tas. 17.9–19.7°C, pH 7.2–7.3, DO 9.2, 87 μS cm$^{-1}$, 0.5 NTU.

### *Cephalodella exigua* (Hudson & Gosse)
FIG. 9:3

*Diaschiza exigua* Hudson & Gosse, 1886, 2, p. 78, Fig. 22:15.
*Cephalodella exigua:* Harring & Myers, 1924, p. 481.

*Type locality:* Cheltenham, England. ". . . window tank."
*Holotype:* Not designated.
*Description:* Body short, stout, appears truncated at posterior end; lateral sulci between lorica plates distinct; neck clearly demarcated; foot small, tubular; toes short, <1/5 body length, tapering gradually to acute tips; salivary glands not described, may be absent; trophi modified type B, fulcrum slightly expanded distally, rami denticulate, manubria strongly curved distally, but two ends do not meet to form the fenestration typical of type C trophi; two red cerebral eyespots; caudal antenna very distinct; male known; resting egg with smooth dark brown shell.

Total length 90–125 μm; toes 20–26 μm; trophi 30 μm; male 74 μm; toes 19 μm.
*Ecology:* Cosmopolitan between water plants, *Sphagnum*. Common in R. Murray (Vic.) billabongs in Spring, Tas. 11.0–13.6°C, pH 6.2–7.4, 220–1900 μS cm$^{-1}$, 2.7–120 NTU.
*Literature:* Berzins 1982; Koste & Shiel 1987b.

### *Cephalodella forficata* (Ehrenberg)
FIG. 9:4

*Notommata forficata* Ehrenberg, 1832, p. 134.
*Cephalodella forficata:* Harring & Myers, 1924, p. 499, Fig. 33:7.

*Type locality:* Berlin.
*Holotype:* Not designated.
*Description:* Body elongate, slender slightly compressed laterally; neck well-marked; lorica plates distinct; sulci narrow, parallel-sided; toes approx 1/4 body length, widely spaced at base, short, stout, taper to acute apices; foot glands large, pyriform; gastric glands large, red-pigmented in older individuals; trophi type B, manubria crooked, eyespot absent.

Total length 148–265 μm; toes 36–58 μm; trophi 16–26 μm.
*Ecology:* Cosmopolitan in vegetation of standing and flowing waters. Rare: N.S.W., Qld., Tas. 16.5–18.5°C, pH 4.8–6.3, 25–100 μS cm$^{-1}$.
*Literature:* Shiel & Koste 1979

### *Cephalodella forficula* (Ehrenberg)
FIG. 9:5

*Distemma forficula* Ehrenberg, 1832, p. 139.
*Cephalodella forficula:* Harring, 1913, p. 29.

*Type locality:* Berlin.
*Holotype:* Not designated.
*Description:* Elongate, spindle-shaped body, slight constriction at neck; integument flexible, without lorica plates; abdomen tapers to ill-defined foot; toes short, stout, recurved, about 1/5 total length; toes have distinctive transverse spicule row (2–4) on dorsal median surface which terminates in a larger spine; mastax with salivary glands; trophi type D, manubria dilated distally, but not crooked, with distinctive oval basal plate; single frontal eyespot; no retrocerebral organ.
*Ecology:* Pancontinental. 12.0–25.0°C, pH 4.8–6.8, 25–440 μS cm$^{-1}$, TDS 19.7 mg l$^{-1}$, 7.3–25 NTU.
*Literature:* Shiel & Koste 1979; Koste & Shiel 1987b.

### *Cephalodella gibba* (Ehrenberg)
FIG. 9:6

*Furcularia gibba* Ehrenberg, 1832, p. 130, Fig. 4:16.
*Cephalodella gibba:* Harring & Myers, 1924, p. 472.

*Type locality:* Berlin.
*Holotype:* Not designated.
*Description:* Body slightly elongated, compressed laterally; gibbous rump; lorica firm with distinct plates; sulci widen slightly posteriorly; toes long, straight or recurved, slender (ca. 1/3 body length); mastax very large; trophi type B; rami with denticulate lamellar combs on inner ventral margins; manubria strongly crooked, shaft with both sides lamellate; no retrocerebral organ; single frontal eyespot.

Total length 250–450 μm; toes 67–150 μm; trophi 70–90 μm.
*Ecology:* Cosmopolitan in littoral of fresh-brackish waters, also in branchial chambers of Crustacea. Eats unicellular algae, flagellates, also carnivorous, particularly on ciliates. Eurytopic, pancontinental in Australia, most common representative of the genus. Abundant in acid waters in Tasmania. 9.5–23.0°C, pH 4.7–7.8, 9.2–700 μS cm$^{-1}$, 1.7–110 NTU.
*Comment:* Several forms (ecotypes or a species complex?) are listed in Koste (1978). Harring & Myers (1924) noted that *C. gibba* is "somewhat variable". A distinctive ssp., *C. gibba microdactyla* Koch-Althaus, 1963 (Fig. 10:1) was recorded from a roadside pool near Scotts Peak Dam, Tas. 18.0°C, pH 6.4, 122 μS cm$^{-1}$. This appears to be a good species, however more detailed comparison of the Tasmanian material with the nominate species is required.

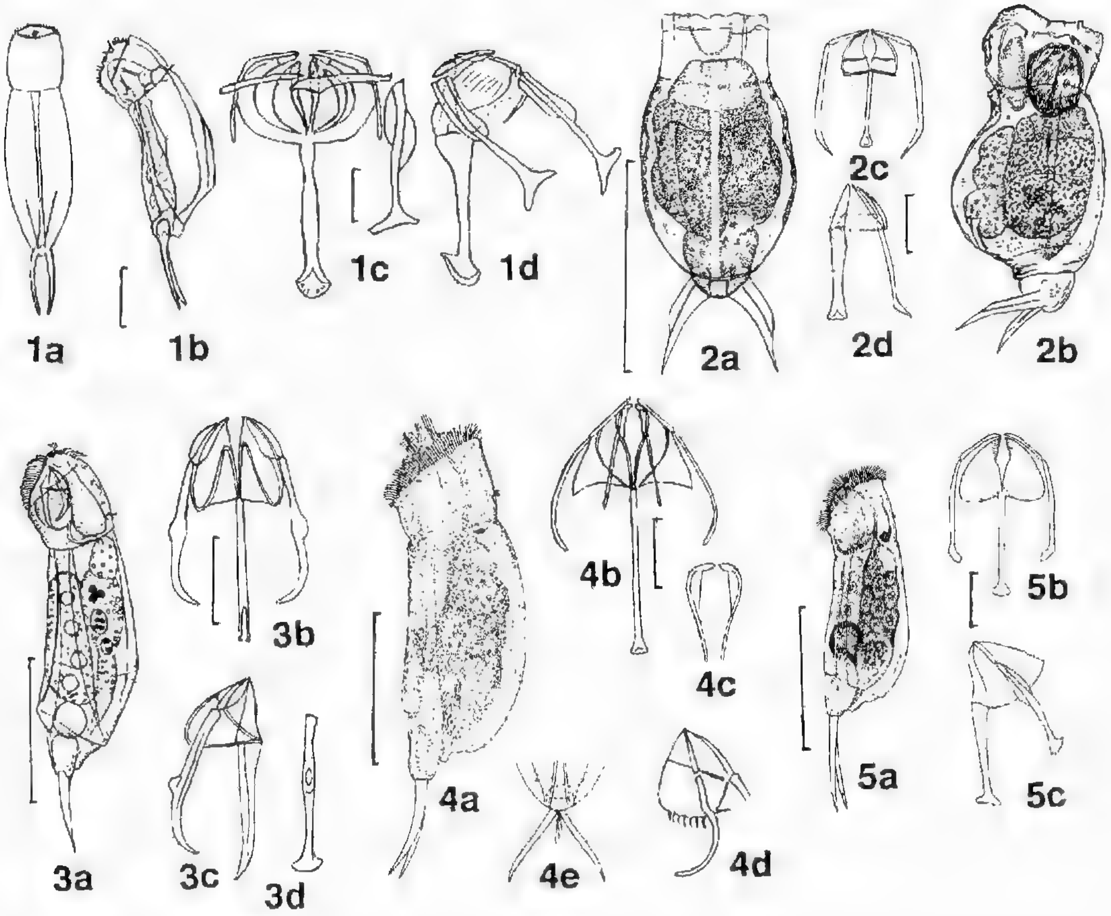


Fig. 10. 1, *Cephalodella gibba microdactyla* Koch-Althaus: (a) dorsal; (b) lateral; (c) trophi, ventral, right manubrium omitted; (c) trophi, lateral. 2, *C. gisleni* Berzins: (a) dorsal; (b) lateral; (c) trophi, ventral: (d) trophi, lateral. 3, *C. gracilis* Ehrenberg: (a) lateral; (b) trophi, ventral; (c) trophi, lateral; (d) manubrium, lateral. 4, *C. hoodi* (Gosse): (a) lateral; (b) trophi, ventral; (c) forcipate rami; (d) trophi, lateral; (e) posterior end and toes. 5, *C. intuta* Myers: (a) lateral; (b) trophi, ventral; (c) trophi, lateral. 1 after Koch-Althaus (1963); 2 after Berzins (1953); 3 after Wulfert (1937); 4a, 5 after Harring & Myers (1924); 4b–e after Donner (1950). Scale lines: adults 50 μm; trophi 10 μm.

*Literature:* Pourriot 1965; Koste 1978; Koste & Shiel 1986, 1987b.

### *Cephalodella gisleni* Berzins
FIG. 10:2

*Cephalodella gisleni* Berzins, 1953, p. 4–6, Figs 1–4.

*Type locality:* Porongorups, W.A.
*Holotype:* Not designated.
*Description:* From Berzins' description of a single contracted individual . . . "Body squat, rounded, with small bulge in dorsal posterior part; ventral margin lightly convex; head very large, almost 1/2 body length, somewhat narrower than body; dorsally a distinct longitudinal sulcus visible; lateral sulci indistinct; cuticle somewhat stiff, enabling head to be seen; dorsal and lateral boundaries of plates obscured, not distinct; animal very hyaline; foot stout, distal, extending slightly over base of toes; toes proximally thickened, compressed dorsoventrally, tapering abruptly in distal 1/3 to sharp points; in dorsoventral view [there is] a very peculiar semicircular deflection of toes; in thickened part of toes is relatively large duct; mastax large, with two salivary glands; trophi symmetric, intermediate between type A (manubria) and type B (rami); fulcrum slender [unusually short for genus], slightly dilated distally; manubria slender, terminally [slightly] crooked; rami wide, of simple construction, without teeth . . . eyes or lenses not observed".

Total length (contracted) 85 µm, body (contracted) 44 µm; head width 40 µm; trophi 20 µm; toes 20 µm; proximal toe thickness 5 µm.
*Ecology:* No ecological information other than that collections came from small alkaline waters or "Brackwasser". A single individual closely resembling Berzins' description was recorded from Salt Creek, near Berri, S. Aust. (19.0°C, pH 7.8, 220 µS cm$^{-1}$, DO 9.2 mgl$^{-1}$, TDS 132 mgl$^{-1}$, 45 NTU) (Shiel & Koste 1979) and another in Ryan's 1 Billabong at Albury (Shiel unpublished).
*Comment:* We regard *C. gisleni* as a valid species on the basis of the distinctive trophi, toes, and other characters described above, despite its description from a single specimen. This species may be more widely distributed across southern Australia than the sparse records indicate.

### *Cephalodella gracilis* (Ehrenberg)
FIG. 10:3

*Furcularia gracilis* Ehrenberg, 1830, p. 130; 1838, p. 421, Fig. 48:6.
*Cephalodella gracilis:* Harring & Myers, 1924, p. 474.

*Type locality:* Berlin.
*Holotype:* Not designated.
*Description:* Short, laterally compressed body, round posteriorly; lorica thin, flexible, plates distinct; sulci narrow, small tail; toes short, ca. 1/5 body length, slender, recurved slightly to acute tips; foot glands moderately large, pyriform; mastax large, trophi (type A) variable (Koste 1978); fulcrum curved, manubria distally crooked or fanlike, denticles may be developed on inside of rami, pseudoallulae symmetric or asymmetric; occasionally a reduced number of nuclei in vitellarium (4–6); single eyespot may be colourless.

Total length 125–150 µm; toes 22–30 µm; trophi 22–27 µm; male 65–75 µm.
*Ecology:* Cosmopolitan in fresh, also in athallassic saline waters. Berzins (1982) noted it was "widespread" in Victoria. We have found *C. gracilis* only twice: a 1987 collection in Tasmania (shallow vegetated pool, Miena-Deloraine road near Golden Valley), and Sept. 1990 in Ryans 2 Billabong, Wodonga, Vic. 16.0–22.0°C, pH 6.4–6.85, 114–292 µS cm$^{-1}$.
*Literature:* Koste *et al.* 1988.

### *Cephalodella hoodi* (Gosse)
FIG. 10:4

*Diaschiza hoodi* Hudson & Gosse, 1886, p. 79, Fig. 22:15.
*Cephalodella hoodi:* Harring & Myers, 1924, p. 482.
*Cephalodella remanei* Wisniewski, 1934, p. 353, Fig. 59:17–21.

*Type locality:* Loch near Dundee, Scotland.
*Holotype:* Not designated.
*Description:* Fusiform body, gibbous dorsally; abdomen unusually elongate, with dorsal plates; foot small, conical; tail prominent; toes short (1/4 total length), stout, decurved, tapering to acute tips; foot glands small, pyriform; corona oblique, with prominent beak-like lips (rostrum); trophi type A, with slender, short, rodlike manubria, curved at end but not crooked; two pleural rods present; rami sometimes with 'pseudoalulae', toothed inner margin; caudal antennae setae long; retrocerebral organ present; eyespot large, at posterior end of cerebral ganglion.

Total length 110–195 µm; toes 32–47 µm; trophi 30–38 µm (fulcrum 16–25 µm, rami 14 µm, manubria 14–20 µm, unci 8 µm); male 110–115 µm.
*Ecology:* Cosmopolitan in fresh and inland saline waters, in beach sand, submerged moss, also in flowing waters. Rare, Gippsland, Vic. and Mt Field Nat. Park, Tas. 16.0°C, pH 7.4 (Shiel & Tan unpublished).
*Literature:* Berzins 1982.

### *Cephalodella intuta* Harring & Myers
FIG. 10:5

*Cephalodella intuta* Harring & Myers, 1924, p. 500–501, Fig. 35:2–5.

*Type locality:* Loon Lake, Vilas County, Wisconsin. "collected among submerged *Sphagnum*."
*Holotype:* Not designated. ?Myers collection. AMNH, N.Y. No. 566 in AMNH is a co-type.
*Description:* Body moderately elongated; head longer dorsally than ventrally, corona markedly oblique; lorica rigid, plates distinct; toes long and slender (1/4 body length), tapering to acute tips with transverse basal septa; mastax large with salivary glands; trophi type B; fulcrum expanded distally; manubria crooked; rami ends strongly toothed; rami with small alulae (easily lost in caustic or bleaching solution used to clear trophi); gastric glands red to red-brown; ducted retrocerebral sac present; no eyespot. May be confused with *C. forficata*, but has relatively longer toes (toe:total length ratio <4 in *C. intuta*, >4 in *C. forficata*).

Total length 115–225 μm; toes 30–60 μm; trophi 30–40 μm.
*Ecology:* Cosmopolitan in standing and flowing fresh waters, in moss and periphyton of submerged vegetation. Rare, N.T., Tas., Vic., 13.0–18.0, pH 4.7–7.8, 42–213 μS cm$^{-1}$.
*Literature:* Koste 1981; Koste & Shiel 1986.

### *Cephalodella lindamaya* Koste & Shiel
FIG. 11:1

*Cephalodella lindamaya* Koste & Shiel, 1986, p. 95–6, Fig. 3–4.

*Type locality:* Stock dam 1 km south of Copping, Tasmania.
*Holotype:* South Australian Museum (SAM) V4019. Coll. R. J. Shiel, 01.xii.1985.
*Description:* Body short, stout; head broad, deflexed; lorica flexible, plates indistinct; toes relatively long (>1/4 body length), basally thickened; terminal claws curved with acute tips, four distinct spinules in row inside claw; mastax large; trophi type B, fulcrum long, narrowest in the centre, flaring at distal end; manubria unusual, terminally crooked, leaf-shaped; rami with denticulate inner margin behind tips, uncus with one tooth and basal lamella; foot glands large, club shaped; eyespot not recorded.

Total length (contracted) 245 μm; toes 68 μm (spinules 4–6 μm); trophi 43 μm (manubria 38 μm, fulcrum 24 μm, unci 17 μm, rami 14 μm.
*Ecology:* Endemic. Known only from acid stock dam at Copping, eastern Tas. 21.7°C, pH <4.0, 80 μS cm$^{-1}$.

### *Cephalodella megalocephala* (Glasscott)
FIG. 11:2

*Furcularia megalocephala* Glasscott, 1893, p. 56, Fig. 4:3.

*Cephalodella megalocephala:* Harring & Myers 1924, p. 494.

*Type locality:* (Ireland).
*Holotype:* Not designated
*Description:* Body stout, dorsally gibbous; head very large, ciliary field extremely oblique; apical field with two large cirri; lorica thin, flexible, plates indistinct; dorsal median sulcus may have convex rather than concave connecting integument (Hauer 1921); foot 2-segmented; toes short (1/6 total length), decurved, sharply pointed; trophi of peculiar type (E): simple rod-shaped fulcrum; manubria two sigmoid curved slender rods; rami appear semicircular from above; unci multi-toothed, rake-like. Sometimes triangular, lamellar, thin epipharynx distinguishable; no eyespot; retrocerebral organ transparent.

Total length 195–210 μm; toes 34–38 μm; trophi 30 μm. Larger forms to 325 μm (Donner 1949) may be ecotypic variants or species complex.
*Ecology:* Cosmopolitan; mud flats, beaches, sand, periphyton of fresh water, margins of flowing water. Feeds on diatoms and Chlorophyceae. Wentworth Falls, N.S.W.; St Marys, Tas., Ryans 2 billabong, Wodonga, Vic. 14–21.0°C, pH 6.2–6.8, 73–351 μS cm$^{-1}$.
*Literature:* Berzins 1982; Koste & Shiel 1986.

### *Cephalodella misgurnus* Wulfert
FIG. 11:3

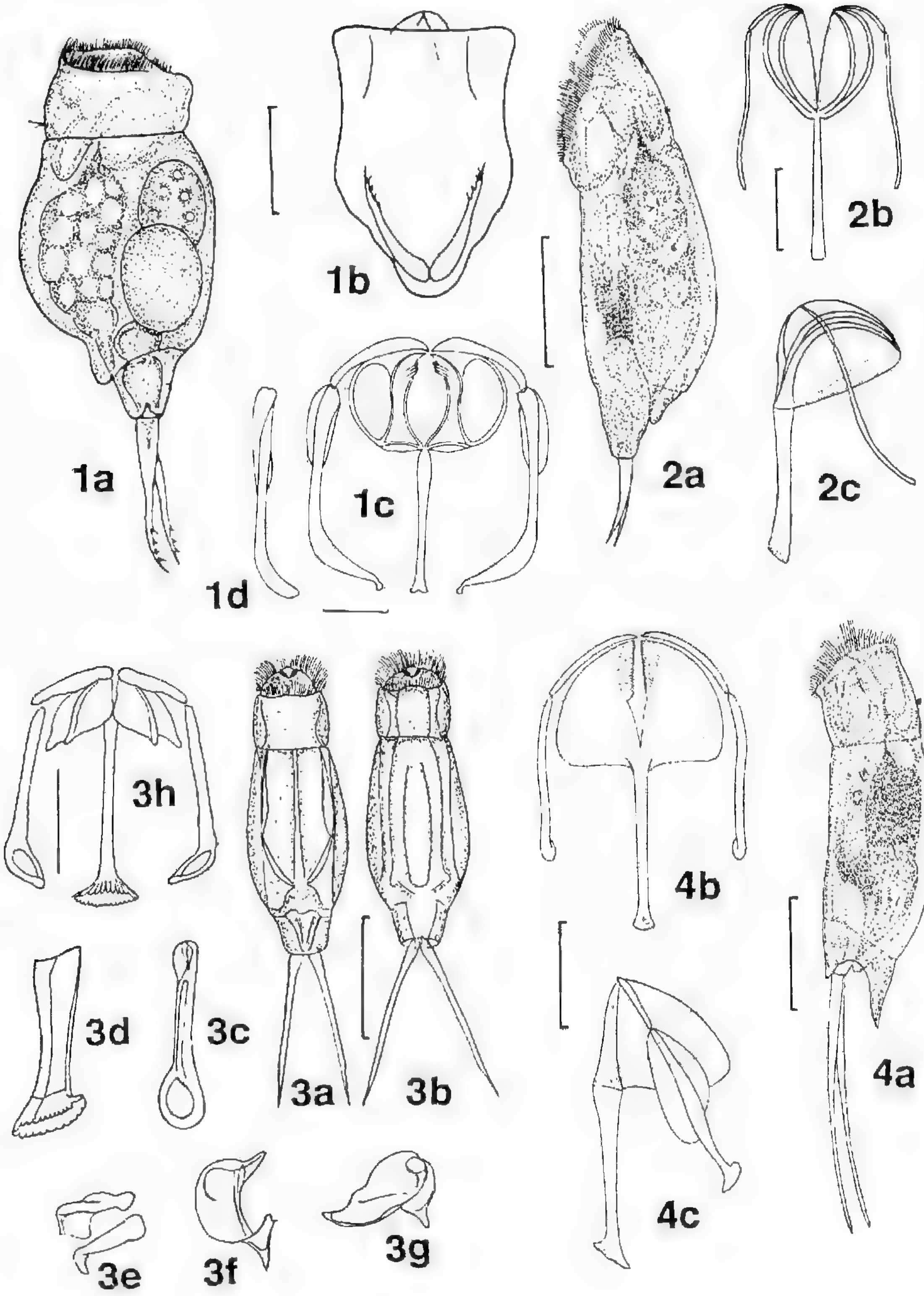
*Cephalodella misgurnus* Wulfert, 1937, p. 620, Fig. 29.

*Type locality:* Single locality not specified. "[ . . . bottom of muddy streams like the Saale and Unstrut . . . ]." (Germany).
*Holotype:* Not designated.
*Description:* Body elongate, widest in posterior third; head and trunk loricate, three large and two smaller plates; neck clearly defined; toes long, ca. 1/3 total length, slightly wider at base, parallel for much of their length, terminating in acute tips; mastax small with two small salivary glands; trophi type C, symmetrical; fulcrum straight, flaring distally, manubria with straight shafts (no lamellae), ending distally in a distinctive open ring; unci robust with quadratic plate on outer half; subcerebral gland present; two frontal eyespots with crystalline lens in common capsule.

Total length 165–190 μm; toes 49–61 μm; trophi 22 μm.
*Ecology:* Europe, recorded in mud, flowing water. Single record, Magela Ck, N.T.
*Literature:* Koste 1981.

### *Cephalodella mucronata* Harring & Myers
FIG. 11:4

*Cephalodella mucronata* Harring & Myers, 1924, p. 510, Fig. 36:2–4.


1a
1b
1c
1d
2a
2b
2c
3h
3a
3b
3d
3c
3e
3f
3g
4b
4a
4c

*Type locality:* Vilas and Oneida Counties, Wisconsin, "in weedy, soft-water ponds."
*Holotype:* Not designated. ?Myers collection, AMNH, NY. No. 252 in AMNH is a co-type.
*Description:* Elongate slender body, with rigid lorica extending beyond end of foot; longitudinal sulci deep; foot sheath has triangular ventral point and dorsal spine, separated by deep, rounded sinus; toes exceptionally long (ca. body length) slender, recurved and pointed; mastax typical for genus: trophi type B; fulcrum long and straight, manubria slender, distally crooked, rami denticulate on inner margin; retrocerebral sac present; no eyespot.

Total length 265–275 $\mu$m; toes 120–140 $\mu$m; trophi 36 $\mu$m.
*Ecology:* Pantropical-pansubtropical warm stenotherm (20–32°C) in shallow vegetated ponds, also New Zealand. Eats diatoms, unicellular algae. Koste (1978) noted that *C. mucronata* also was predatory on bdelloid rotifers. Isolated records from N.S.W., N.T., W.A. Widespread in shallow pools in Tas., where it appears to occupy a greater thermal range than elsewhere: 9.0–29.0°C, pH 3.1–7.6, 11.8–98.3 $\mu$S cm$^{-1}$.
*Literature:* Koste & Shiel 1986.

### *Cephalodella nana* Myers
FIG. 12:1

*Cephalodella nana* Harring & Myers, 1924, p. 491–2, Fig. 1.

*Type locality:* Corduroy Creek, Absecon, New Jersey. "collection in *Sphagnum.*"
*Holotype:* Not designated. ?Myers Collection, AMNH, N.Y.
*Description:* Body short, conical, tapering gradually from corona to base of toes; head large, ca. 1/2 length of body, and wider than abdomen; lorica moderately flexible, plates distinct; toes ca. 1/3 body length, long slender, set wide apart at base with gentle sigmoid curve, tapering to bristle-like apices; foot glands small, pyriform; corona oblique with prominent beaklike lips; mastax very large; trophi type A; fulcrum slightly expanded distally; manubria slender, slightly clubbed and recurved ends but not crooked; salivary glands small; eyespots at posterior end of ganglion; no retrocerebral organ.

Total length 105–160 $\mu$m; toes 35–52 $\mu$m; trophi 30–34 $\mu$m.
*Ecology:* In submerged *Sphagnum* Europe, N. America; recorded from Clunes, Vic. and Little Pine Lagoon, Tas. 8.0°C, pH <5.0, 33 $\mu$S cm$^{-1}$.
*Literature:* Berzins 1982; Koste & Shiel 1987b.

### *Cephalodella panarista* Harring & Myers
FIG. 12:2

*Cephalodella panarista* Harring & Myers, 1924, p. 478–9, Fig. 5–7.

*Type locality:* Four Mile Run, Washington, D.C.
*Holotype:* Not designated. ?Myers collection, AMNH, N.Y.
*Description:* Body large, elongate, slender; dorsal margin curves downwards posteriorly to base of foot; integument very flexible, plates indistinct; toes very long (ca. 1/3 total length), stout and recurved, tapering to acute tips; occasionally a dorsal toothlike spine 1/3 of length along toes; foot glands extremely long, clubbed; mastax large, trophi robust (Type D); fulcrum long, straight slightly expanded posteriorly; manubria short, recurved posteriorly but not crooked; with large basal plate; unci have typical single tooth; eyespot frontal with front part of capsule colourless resembling "lens".

Total length 360–375 $\mu$m; toes 102–105 $\mu$m; trophi 65$\mu$m.
*Ecology:* Rare. N. America, S. E. Europe. Billabongs, Magela Ck N.T., R. Murray N.S.W.
*Literature:* Koste 1978.

### *Cephalodella parasitica* (Jennings)
FIG. 12:3

*Pleurotrocha parasitica* Jennings, 1900, p. 84, Fig. 16:13, 14.
*Cephalodella parasitica:* Harring & Myers, 1924, p. 512.

*Type locality:* Small pool near Lake St. Clair (U.S.A.).
*Holotype:* Not designated.
*Description:* Body fusiform, curved and gibbous dorsally; head unusually long, tapers from neck to corona; integument flexible, no sign of fissured lorica; foot short and conical; toes ca. 1/6 body length, slightly decurved to slightly sigmoid, tapering to acute tips; mastax large with two large salivary glands; trophi type A, with sharply pointed unci and rounded, curved rami which have curved alulae on their outer margins; gastric glands brownish to black; no eyespot.

Total length 110–200 $\mu$m; toes 28–35 $\mu$m; trophi 32 $\mu$m.

Fig. 11 1, *Cephalodella lindamaya* Koste & Shiel: (a) lateral; (b) ventral; (c) trophi; (d) manubrium. 2, *C. megalocephala* (Glasscott): (a) lateral; (b) trophi, ventral; (c) trophi, lateral. 3, *C. misgurnus* Wulfert: (a) dorsal; (b) ventral; (c) manubrium; (d) fulcrum, lateral; (e) two views of uncus; (f, g) two views of ramus; (h) trophi, ventral. 4, *C. mucronata* Myers: (a) lateral; (b) trophi, ventral; (c) trophi, lateral. 1 after Koste & Shiel (1986); 2, 4 after Harring & Myers (1924); 3 after Wulfert (1937). Scale lines: adults 50 $\mu$m; trophi 10 $\mu$m.

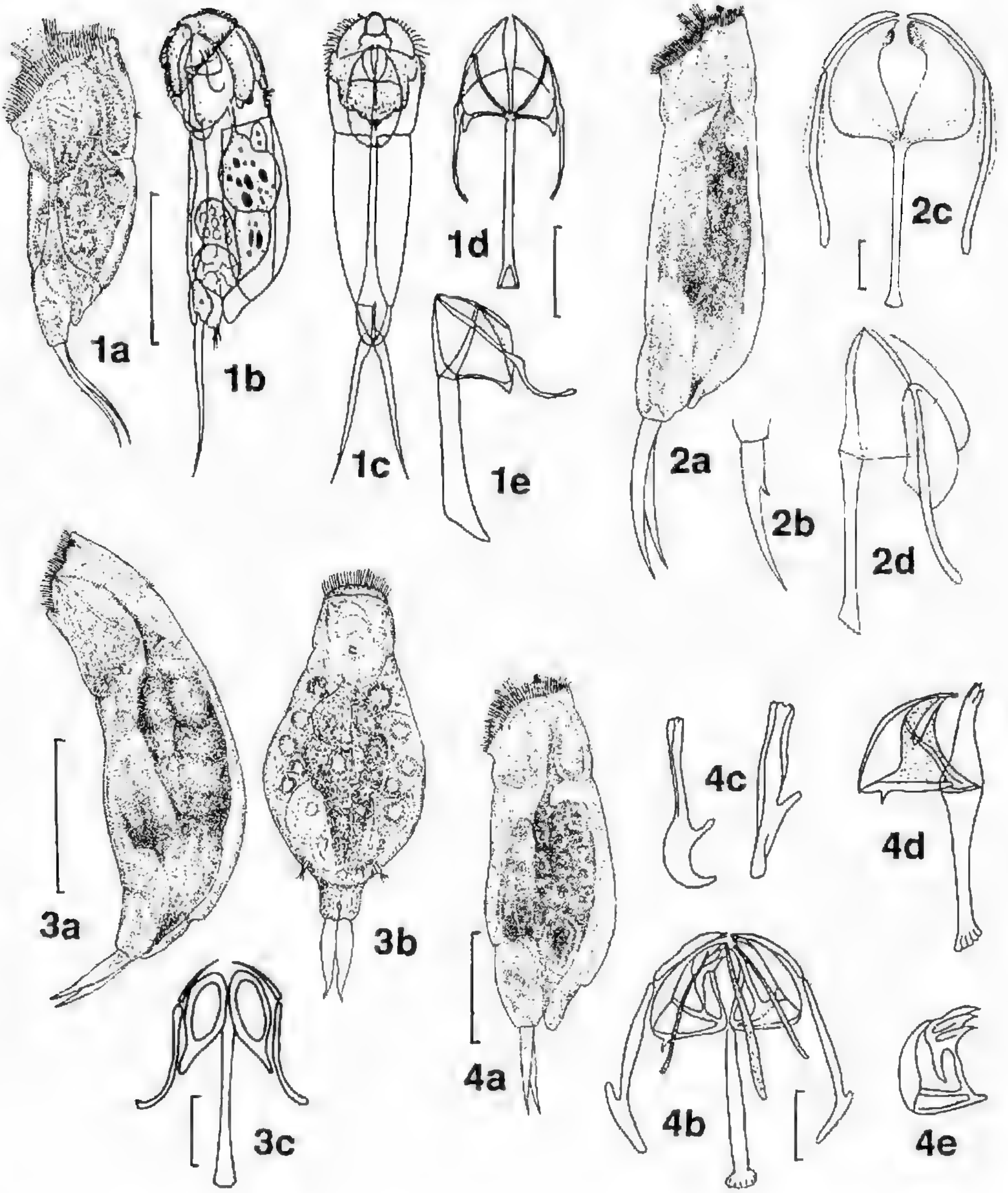


Fig. 12. 1, *Cephalodella nana* Myers: (a, b) lateral; (c) dorsal; (d) trophi, ventral; (e) trophi, lateral. 2, *C. panarista* Myers: (a) lateral; (b) toes, lateral; (c) trophi, ventral; (d) trophi, lateral. 3, *C. parasitica* Jennings: (a) lateral; (b) dorsal; (c) trophi, ventral. 4, *C. sterea* (Gosse): (a) lateral; (b) trophi, ventral; (c) views of manubria; (d) trophi, lateral; (e) uncus. 1a, 2, 3a, 4a after Harring & Myers (1924); 1b–d after Wulfert (1940); 3b Koste orig.; 4b–e after Wulfert (1937). Scale lines: adult 50 µm; trophi 10 µm.

*Ecology:* Europe, N. America, occasionally free-swimming, but more commonly parasitic on oligochaetes (*Chaetogaster, Nais, Stylaria,* etc). Single report from Diggers Ck, Mt Kosciusko. Not seen in our collections.
*Literature:* Koste 1978; Berzins 1982.

### *Cephalodella sterea* (Gosse)
FIG. 12:4

*Furcularia sterea* Gosse, 1887, p. 864, Fig. 14:8
*Cephalodella sterea:* Harring & Myers, 1924, p. 474.

*Type locality:* Rockery pond in the grounds of Watcombe Park near Torquay, England.
*Holotype:* Not designated.
*Description:* Body fusiform; head large; lorica firm, plates well marked; foot large, robust; tail extends beyond distal end of foot; toes short, stout slightly recurved posteriorly, may have slightly undulate margins, generally <1/4 body length; foot glands large and pyriform; mastax large with four small salivary glands; trophi asymmetric type B; manubria strongly crooked; unci with variable inner margin denticulation; rami with three pleural rods; retrocerebral sac present; two red frontal eyespots in single capsule.

Total length 140–250 μm; toes 26–56 μm; trophi 37–39 μm.
*Ecology:* Cosmopolitan, in moss, in mud margins of standing and flowing waters. Rare: N.T., Tas., Vic., 12.0–22.0°C, pH 5.3–6.9, 73–351 μS cm$^{-1}$.
*Literature:* Koste 1981; Koste *et al.* 1988.

### *Cephalodella tantilloides* Hauer
FIG. 13:1

*Cephalodella tantilloides* Hauer, 1935, p. 69, Fig. 9.

*Type locality:* High Moor pond, Black Forest, Germany.
*Holotype:* Not designated.
*Description:* Body squat, vaulted dorsally, abdomen falls sharply to clearly demarcated foot; plates and sulci distinct; dorsal sulcus relatively deep; lateral sulci margin parallel almost to base of toes; toes long (1/3 body length), parallel sided for 3/4 of their length, to a distinctly segmented tip, slightly recurved; toe tips acute; foot glands small; lips project from mouth area; trophi type A; fulcrum dilated distally into a broad plate; rodlike manubria curve upwards; rami with inner denticles; cerebral eye present; retrocerebral sac not recorded.

Total length 104–175 μm; toes 45–56 μm; toe points 14 μm; trophi 34 μm.
*Ecology:* Europe, in *Sphagnum.* Single record, Bromfield Swamp, Qld. No ecological data given.
*Literature:* Green 1981; Koste 1978.

### *Cephalodella tenuiseta* (Burn)
FIG. 13:2

*Furcularia tenuiseta* Burn, 1890, p. 34, text fig.
*Diaschiza tenuiseta:* Dixon-Nuttall & Freeman 1903, p. 138, Fig. 1:2.
*Cephalodella tenuseta:* Harring & Myers, 1924, p. 508.

*Type locality:* (England).
*Holotype:* Not designated.
*Description:* Body elongate, laterally compressed; head large, short; abdomen unusually long, gibbous posteriorly; lorica flexible, plates indistinct; foot short, conical; toes very long (1/2 body length), slender, slightly recurved; mastax large, trophi type D; fulcrum slightly expanded posteriorly, manubria rodlike not crooked; no eyespot.

Total length 205–314 μm (Koste) 380–390 (H&M); toes 59–96 μm (Koste) 120–125 (H&M); trophi 35–39 μm.
*Ecology:* N. America, Europe. Rare: Vic., W.A. 16.0°C, pH 7.1, 264 μS cm$^{-1}$. Eats unicellular green algae and diatoms.
*Literature:* Berzins 1953; Koste 1978.

### *Cephalodella tinca* Wulfert
FIG. 13:3

*Cephalodella tinca* Wulfert, 1937, p. 622, Fig. 31.

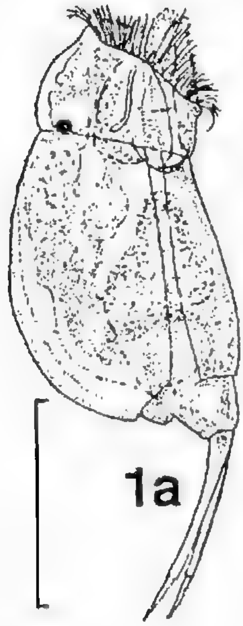
*Type locality:* Drain outflow (Bad Lauchstadt) Germany.
*Holotype:* Not designated.
*Description:* Body elongate, laterally compressed; abdomen slightly bulbous prior to short tail extending beyond foot; plates and sulci distinct; toes relatively short, ca. 1/3 total body length, thickened at base, with slight medial swellings; mastax with two large salivary glands; trophi type D; fulcrum dilated distally, broad-bladed proximally (seen laterally), rodlike viewed apically; manubria with blunt, slightly enlarged tips; paired eyespots in single capsule.

Total length 260–280 μm; trophi 29–31 μm; toes 52–70 μm; male 160 μm; subitaneous egg 60 μm.
*Ecology:* Europe, in drains, decomposing vegetation, manure pits and piggery outflows. Eats diatoms. Rare: Vic. (billagong), Tas. (stock dam) 15.0–19.0°C, pH 4.9–7.1, 264–273 μS cm$^{-1}$, DO 10.3 mg l$^{-1}$.
*Literature:* Koste *et al.* 1988.

### *Cephalodella ventripes* Dixon-Nuttall
FIG. 13:4

*Diaschiza ventripes* Dixon-Nuttall, 1901, p. 25, Fig. 2:1–3.
*Cephalodella ventripes:* Harring & Myers, 1924, p. 484.

*Type locality:* Knowsley Park, Lancashire, England.
*Holotype:* Not designated.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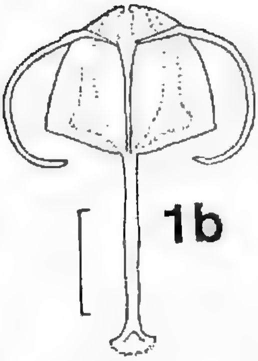
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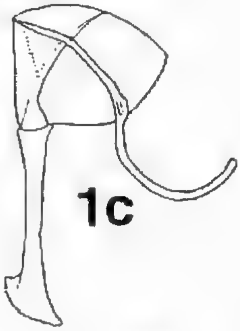
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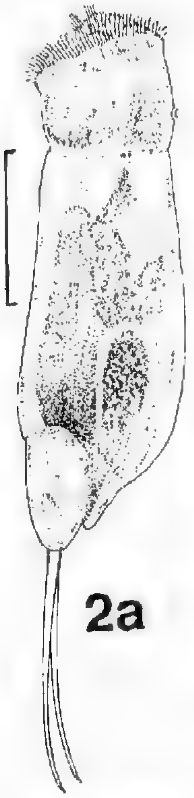
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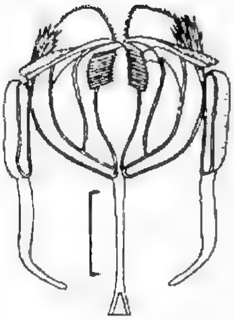
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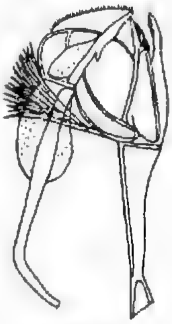
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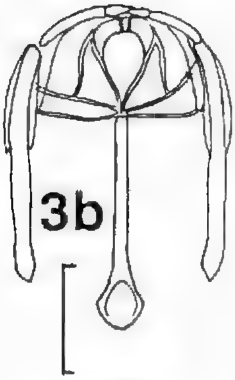
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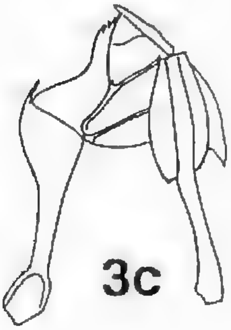
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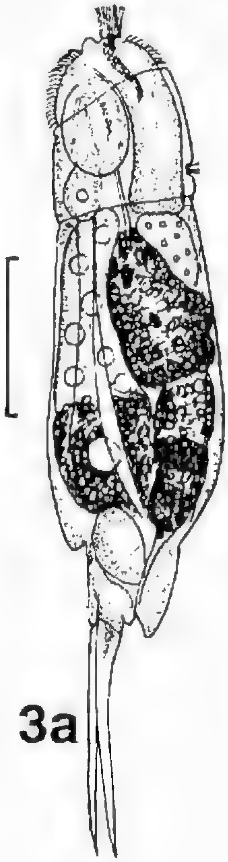
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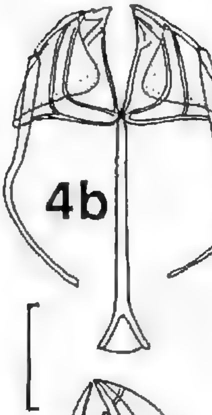
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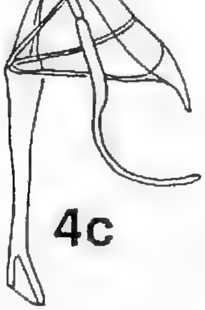
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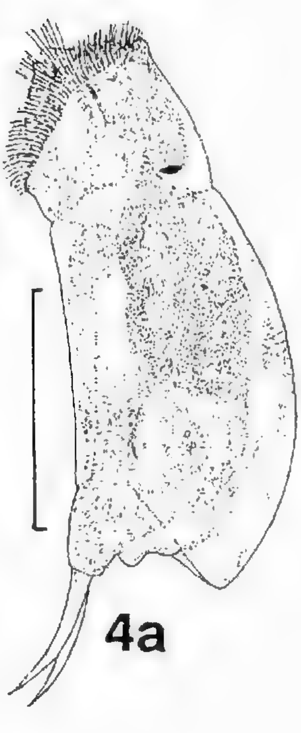
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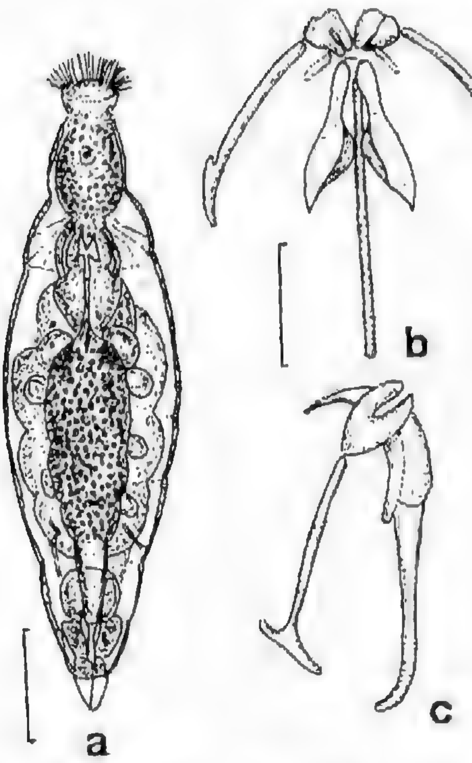


Fig. 14. *Drilophaga bucephalus* Vejdovsky: (a) dorsal; (b) trophi, ventral; (c) trophi, lateral. After Koste (1978). Scale lines: adult 50 µm; trophi 10 µm.

*Description:* Body short, stocky, bulbous dorsally; abdomen may extend beyond distal end of the foot; plates and sulci distinct; dorsal sulcus a distinct V-shaped groove; foot ventral, small; toes short and stout, decurved, ca. 1/5 total length; corona with prominent lips; mastax large; trophi type A; fulcrum dilated distally; distal ends of manubria sickle-shaped, not crooked; double cerebral eye.

Total length 135–140 µm; toes 25–28 µm; trophi 30–34 µm

*Ecology:* In littoral periphyton of most standing fresh waters; N. America, Europe. Uncommon in billabongs of River Murray, N.S.W., Goulburn River, Vic., also dams in northeast Tasmania 13.0–21.0°C, pH 4.8–7.1, 18–351 µS cm$^{-1}$.

*Literature:* Berzins 1982; Koste & Shiel 1987b.

### Genus *Dorystoma* Harring & Myers

*Dorystoma* Harring & Myers, 1922, p. 555. Monotypic genus.

*Type: Proales caudata* Bilfinger, 1894.

### *Dorystoma caudata* (Bilfinger)
FIG. 15:1

*Proales caudata* Bilfinger, 1894, p. 46, Fig. 2:3–4.
*Dorystoma caudata*: Harring & Myers, 1922, p. 555.

*Type locality:* Württemberg, Germany.

*Holotype:* Not designated.

*Description:* Stout, illoricate notommatid rotifer; transparent body, gut may be coloured; corona oblique, with lateral ciliary tufts ('auricles') for swimming; constriction separates head and abdomen; abdomen bulbous, with longitudinal striations; foot short, apparently two-jointed; toes long, pointed, short; at base of foot, bulb above anus carries short spine; gut yellowish, often filled with yellow-gold balls; mastax specialized virgate, with long pharyngeal tube; trophi modified to support mastax walls; specialized piercing epipharynx present; manubria with wide crook; unci absent; single bright red cerebral eyespot, (sometimes absent); dorsal and lateral antennae in pits in cuticle, sensillae distinct; subitaneous egg smooth-shelled.

Total length 130–260 µm; toes 16–22 µm; spine 10–22 µm; trophi 18 µm; pharyngeal tube 22 µm; subitaneous egg 56 × 44 µm.

*Ecology:* Isolated records from periphyton of submerged plants, esp. *Potamogeton, Nuphar,* also in *Sphagnum*. Europe, N. and S. America. Eats algae. Single Australian record: Yarnup Swamp, W.A. 17°C, 1600 µS cm$^{-1}$.

*Literature:* Koste 1978; Koste *et al.* 1983.

### Genus *Drilophaga* Vejdovsky

*Drilophaga* Vejdovsky, 1883, p. 390.

*Type: Drilophaga bucephalus* Vejdovsky, 1883, p. 390, Fig. 1:1–8.

Body slender fusiform; cuticle soft, flexible, with indistinct annuli; head cylindrical, elongate, with simple circumapical ciliation; small tail projects over foot; toes minute, conical, ca. 1/20 body length; foot glands with reservoirs; mastax with two lateral and one posterior salivary glands; trophi with

Fig. 13. 1, *Cephalodella tantilloides* Hauer: (a) lateral; (b) trophi, ventral; (c) trophi, lateral; 2, *C. tenuiseta* (Burn): (a) lateral; (b) trophi, ventral; (c) trophi, lateral; 3, *C. tinca* Wulfert: (a) lateral; (b) trophi, ventral; (c) trophi, lateral; 4, *C. ventripes* Wulfert: (a) lateral; (b) trophi, ventral; (c) trophi, lateral. 1 after Hauer (1935); 2a, 4a after Harring & Myers (1924); 2b–c, 3b–c, 4b–c after Wulfert (1937). Scale lines: adult 50 µm; trophi 10 µm.

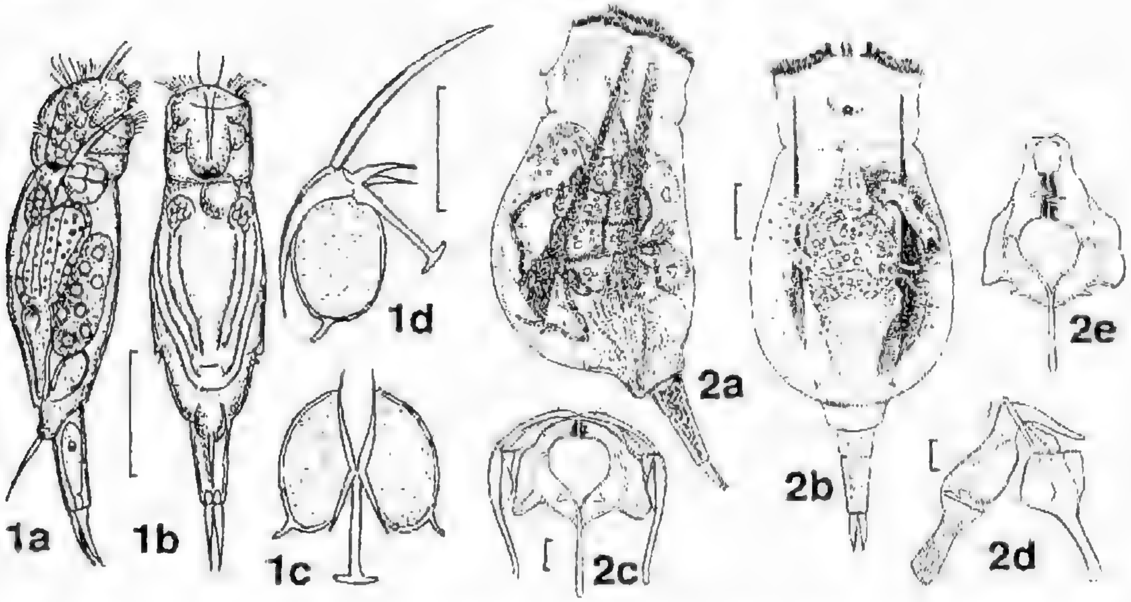


Fig. 15. 1, *Dorystoma caudata* (Bilfinger): (a) lateral; (b) dorsal; (c) trophi, ventral; (d) trophi, lateral. 2, *Enteroplea lacustris* Ehrenberg: (a) lateral; (b) dorsal; (c) trophi, ventral; (d) trophi, lateral; (e) incus, oblique frontal view. 1 after Wulfert (1960); 2 after Harring & Myers (1924). Scale lines: adult 50 µm; trophi 10 µm.

anchor-shaped incus; rami curved inwards; unci short, thick, bidentate; manubria distally crooked; fulcrum long, straight to lightly curved distally; pleural rods present; gastric glands spherical; stomach and intestine separate; vitellarium large; large retrocerebral sac dorsal to ganglion; eyespots absent; dorsal and lateral antennae present, latter projecting from small tubular extensions of integument.

Two other described species were synonymised with *D. bucephalus* (Fig. 14) Koste (1978). *D. bucephalus* is parasitic on the integument of oligochaetes and leeches *(Lumbriculus, Rynchelmis, Stylodrillus, Nais, Herpobdella, Hirudo)* (Koste 1978).

Total length 110–355 µm; toes 6–11 µm; trophi 20–32 µm (unci 8 µm, manubrium 16 µm, fulcrum 25 µm); subitaneous egg 50–62×35–39 µm.

*Comment:* The synonymy of *D. bucephalus*, *D. delagei* Beauchamp and *D. judayi* Harring & Myers requires re-examination. Although Koste (1978) attributed interspecific differences as described and figured to observational errors or preservation artefacts, habit differences were noted by the different authors, i.e., parasitic v. free-swimming *(judayi)*, also differences in morphology, particularly trophi.

A single free-swimming animal identified as *Drilophaga* was collected by WK from Ryan's 2 billabong at Wodonga on Sept. 27, 1990, the first record of the genus from the continent. No oligochaetes or leeches occurred in the sample. The living rotifer was filmed on videotape, but the mastax was lost during clearing, preventing specific determination. Until further material becomes available, we can note only that *Drilophaga* occurs in Australia.

*Literature:* Beauchamp 1904; Harring & Myers 1922.

## Genus *Enteroplea* Ehrenberg

*Enteroplea* Ehrenberg, 1830, p. 46. Monotypic genus.

*Type: Enteroplea lacustris* Ehrenberg, 1830

### *Enteroplea lacustris* Ehrenberg

FIG. 15:2

*Enteroplea lacustris* Ehrenberg, 1830, p. 46.

*Type locality:* Berlin.

*Holotype:* Not designated.

*Description:* Body with wide head, saccate abdomen; foot directed ventrally, three-segmented, offset from body; toes short, laterally barrel-shaped, frontally claw-like; corona an oblique disc circled by ciliary whorl (circumapical band and ventral part of buccal field); dorsal margin of buccal field with type of pseudotrochus made of four closely-situated membranelles; ventrolaterally, beside mouth wide row of membranelles stand on 'pedestal'; inner part of buccal field unciliated; two frontal eyespots on papillae in 'forehead' region; mastax resembles *Eosphora*, with more pronounced seizing function: pincer-like angled rami can be protruded through the mouth opening; inner rami margin with single large tooth, margin finely denticulate before and behind; unci with one main- and one ancillary tooth; no basal apophysis, however, small processes present at insertion point of rami adductor muscle; fulcrum boardlike; two small ventral salivary glands; oesophagus long; stomach rounded, cellular; intestine thin, ropelike. For additional details of internal morphology, see Koste (1978).

Total length 500–600 μm; toes 30–35 μm; trophi 70 μm (fulcrum 21 μm; rami 56 μm; unci 35 μm; incus width 46 μm, length 70 μm) subitaneous egg 155–160×110–130 μm; male 306 μm.
*Ecology:* In shallow pools, ephemeral waters, Europe, E. Asia, N. and S. America. Reported to be carnivorous on other rotifers *(Rhinoglena)* in culture (Pourriot 1965). Recorded by Colledge (1914) from Qld, not found again until Oct. 15–18, 1990, when individuals were identified from submerged scales of *Ricciocarpus natans*, Ryan's 2 billabong, Wodonga (Manuel & Shiel in prep.).
*Literature:* Colledge 1914.

### Genus *Eosphora* Ehrenberg, 1830

*Eosphora* Ehrenberg 1830, p. 47.

*Type locality:* Tobolsk, Siberia.
*Type: Eosphora najas* Ehrenberg, 1830, pp. 47, 84, Fig. 7:3.

Body plump; head and neck distinguished by transverse sutures; abdomen sac-like with rounded or weakly trilobed tail; foot two-, three- or unsegmented; two toes with long foot glands; corona frontal; circumapical band interrupted dorsally; two ciliary bundles laterally; buccal field lightly or non-ciliated; cerebral eye at posterior end of brain (absent in *E. anthadis*); retrocerebral and subcerebral glands present, size and shape variable; mastax three-lobed; unci single toothed, may have small ancillary teeth; rami with symmetric braces, occasionally with strong basal apophyses; at bend of rami teeth on inner margin vary from 1–2 strong to 4–5 smaller teeth in different species; fulcrum wide plank or handle-like; salivary glands differ between species; five of six species are known from Australia.

### Key to species of *Eosphora* recorded from Australian inland waters

1. Foot segmented. . . . . . . . . . . . . . . . . . . . . . . . .2
Foot unsegmented. . . . . . . . . . . . . . . . . . . . . . . .3
2(1). Papilla at base of toes. . . . . . . . . . . . . . . . .*E. najas* Ehrenberg (Fig. 16:3)
No papilla at base of toes. . . . . . . . .*E. ehrenbergi* Weber (Fig. 16:2)
3(1). Obvious cerebral eye present. . . . . . . . . . . . . .4
Cerebral eye absent. . . . . . . . . . . . . . . . . .*E. anthadis* Harring & Myers (Fig. 16:1)
4(3). Trophi length <40 μm. . . . . . . . . . . .*E. thoides* Wulfert (Fig. 17:1)
Trophi length 50 μm. . . . . . . . . . . . . . . . . .*E. thoa* Harring & Myers (Fig. 16:4)

### *Eosphora anthadis* Harring & Myers
FIG. 16:1

*Eosphora anthadis* Harring & Myers, 1922, p. 641, Fig. 58:9–13.

*Type locality:* Not specified ". . . appears to be widely distributed."
*Holotype:* Not designated. ?Myers Coll., AMNH, N.Y.
*Description:* Body broad and robust, ca. three times longer than wide; integument soft, body transparent; stout abdomen tapers from median line to base of broad foot; foot wrinkled but not segmented; toes short, stout (1/20 length), seen dorsally margin almost forms hemisphere; seen laterally, dorso-ventrally flattened, appear as normal conical toes; mastax modified virgate; rami symmetrical with four or five small teeth in median section on each ramus margin; unci with one tooth, small subsquare striated plate at base vestiges of accessory teeth; fulcrum of two plates joined longitudinally to form V; manubrium a straight rod slightly expanded at each end; salivary glands not seen; gastric glands large, elongate, cylindrical, terminating in mucus reservoir at base of toe, retrocerebral sac and two subcerebral glands present; no eyespot.

350–410 μm; toes 16–22 μm; trophi 33–35 μm (fulcrum 20 μm, rami 18 μm, manubria 22 μm).
*Ecology:* In acid waters or mildly saline waters *(Utricularia)* in Europe, N. America, New Zealand, Japan.
*Single Record:* Crackers Swamp, off Brand Hwy, W.A. 20.0°C, 800 μS cm$^{-1}$.
*Literature:* Koste 1978; Koste *et al.* 1983

### *Eosphora ehrenbergi* (Ehrenberg)
FIG. 16:2

*Notommata najas* Ehrenberg, 1832, p. 132.
*Eosphora ehrenbergi:* Weber & Montet 1918, p. 123.

*Type locality:* Berlin.
*Holotype:* Not designated.
*Description:* Body broad, robust, coloured light brown in fresh specimens; integument firm; indistinct transverse folds between head/neck and

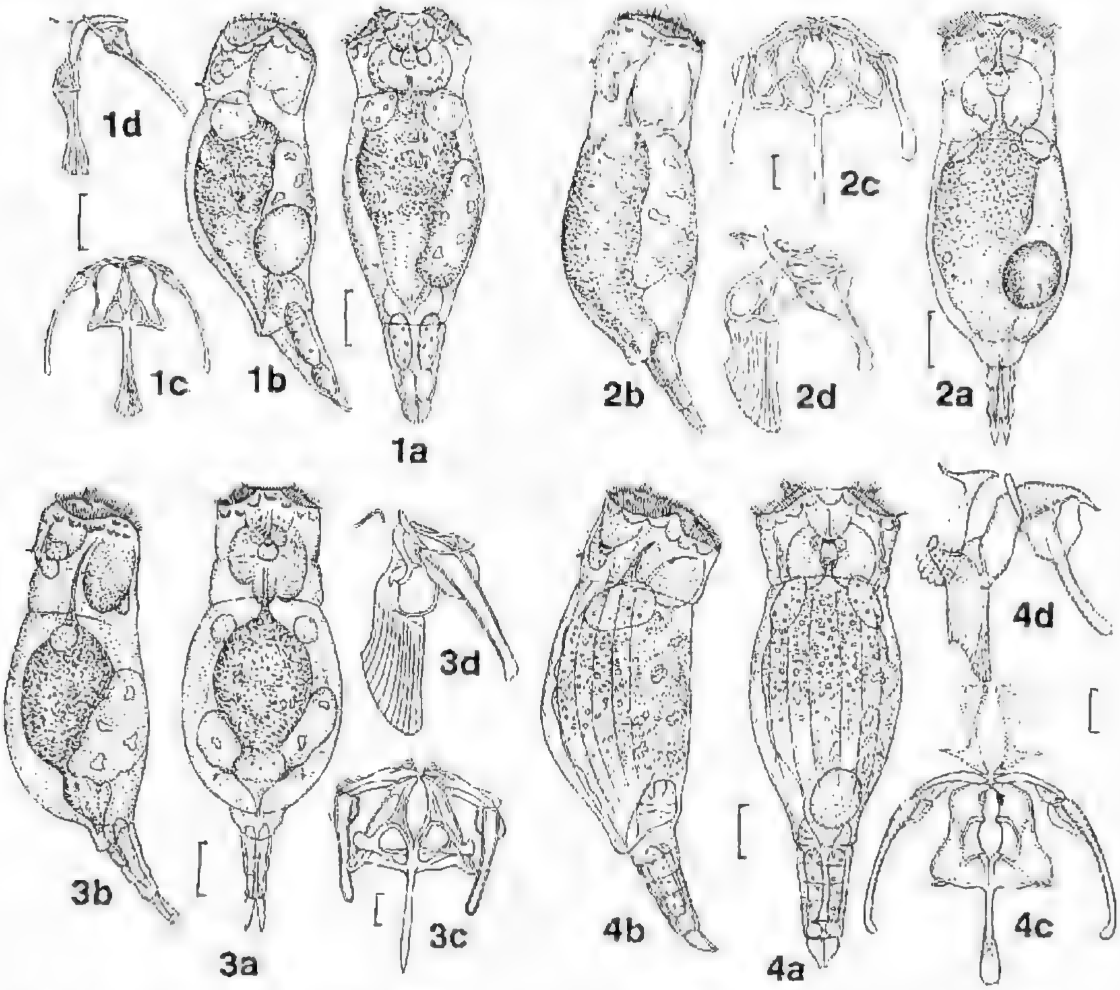


Fig. 16. 1, *Eosphora anthadis* Harring & Myers: (a) dorsal; (b) lateral; (c) trophi, ventral; (d) trophi, lateral. 2, *E. ehrenbergi* Weber: (a) dorsal; (b) lateral; (c) trophi, ventral; (d) trophi, lateral. 3, *E. najas* Ehrenberg: (a) dorsal; (b) lateral; (c) trophi, ventral; (d) trophi, lateral. 4, *E. thoa* Harring & Myers: (a) dorsal; (b) lateral; (c) trophi, ventral; (d) trophi, lateral. 1, 2 after Harring & Myers (1922); 3, 4 after Harring & Myers (1924). Scale lines: adult 50 µm; trophi 10 µm.

neck/abdomen; abdomen rounded posteriorly with short tail (two small lateral lobes); foot long, cylindrical, two-segmented; toes short, acute, conical; virgate trophi adapted for seizing prey; rami approximately triangular, two teeth on each ramus; fulcrum a broad plate with diagonal ventral edge where abductor muscles attach; unci with large subsquare basal plate with strong ventral tooth; manubrium with straight central section, expanded anteriorly into broad triangular plate; two large salivary glands present; foot glands long, without mucus reservoir; retrocerebral sac and two subcerebral glands; eyespot large, dark red, at posterior end of ganglion; hypopharynx muscle rudimentary. Male known.

Total length 350–450 µm; toe length 24–30 µm; trophi 65 µm; male 212 µm.

*Ecology:* Probably cosmopolitan between water plants in fresh to slightly saline water. Single unverified record from Victoria.

*Literature:* Anderson & Shephard 1892; Koste 1978.

### *Eosphora najas* Ehrenberg
FIG. 16:3

*Eosphora najas* Ehrenberg, 1830, pp. 47, 84, Fig. 7:3.

*Type locality:* Tobolsk, Siberia.

*Holotype:* Not designated.

*Description:* Body robust, integument firm, body in fresh material light orange in colour. Head and neck sutures distinct; abdomen broad and oval; tail with larger median lobe, two small lateral lobes; foot indistinctly three-segmented; toes long, straight, slender; mastax modified virgate (for seizing prey); rami triangular in ventral view; left ramus with single large tooth, right with two teeth; rami with finely denticulate dorsal extension; unci small, subsquare basal plate with single clubbed ventral tooth; manubrium broad, lamellate, anteriorly tapering to knobbed posterior end; ventral salivary glands distinct, right longer than left; retrocerebral sac and subcerebral gland as in other species; eyespot at anterior end of ganglion, two (occasionally four) lateral eyespots in small projections of corona.

Length 260–610 μm; toes 26–48 μm; trophi to 80 μm; male to 300 μm; subitaneous egg 140–150×120–130 μm; resting egg 130×170 μm; male egg 100–110×120–130 μm.

*Ecology:* Cosmopolitan in littoral between water plants, preys on rotifers including *Colurella, Lepadella, Lecane, Monostyla* and bdelloids. Early records from Vic. and Qld. In our material, Gwydir R. at Moree, N.S.W. (24.v.78), and recently (30.x.90) in *Myriophyllum* in a flooded roadside marsh, Ryans property, Wodonga, Vic. 13.0–22.5°C, pH 5.97–8.0, DO 8.4 mg $l^{-1}$, 60–400 μS $cm^{-1}$, 160 NTU.

*Literature:* Colledge 1914; Evans 1951; Koste 1978.

### *Eosphora thoa* Harring & Myers
### FIG. 16:4

*Eosphora thoa* Harring & Myers, 1924, p. 523, Fig. 39:1–5

*Type locality:* Cemetery Pond, near Eagle River, Vilas County, Wisconsin.

*Holotype:* Not designated. ?Myers collection, AMNH, N.Y.

*Description:* Body robust, integument flexible, hyaline; head and neck fixed but suture visible between neck and abdomen; abdomen tapers to broad tail; unsegmented conical foot; toes heart shaped in dorsal view; mastax modified virgate; fulcrum short and broad; rami elongate with single blunt tooth on inner edges and posteriorly with ca. 20 denticles; unci with robust clubbed ventral tooth; small retrocerebral sac and two subcerebral glands; large eyespot at posterior end of brain.

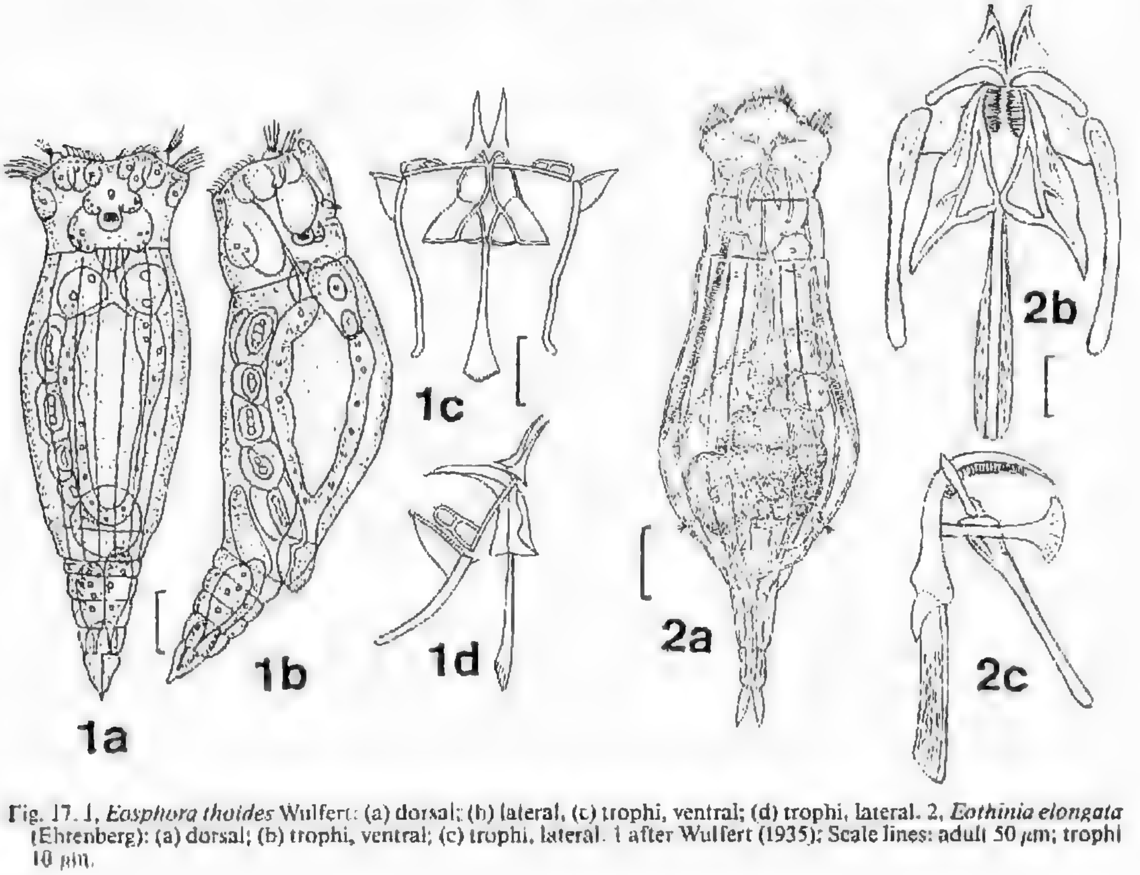


Fig. 17. 1, *Eosphora thoides* Wulfert: (a) dorsal; (b) lateral, (c) trophi, ventral; (d) trophi, lateral. 2, *Eothinia elongata* (Ehrenberg): (a) dorsal; (b) trophi, ventral; (c) trophi, lateral. 1 after Wulfert (1935); Scale lines: adult 50 μm; trophi 10 μm.

Length 300–500 µm; toes 20–35 µm; trophi 50 µm long, 60 µm wide.
*Ecology:* Soft water, N. America. Two records: Forestdale Lagoon, near Perth, W.A. (Coll. J. van Alphen, Murdoch University) and Ryans 2 billabong at Wodonga, Vic. (Coll. J. De Manuel, University of Barcelona). 16.0–24.0°C, pH 6.5–6.7, 263–310 µS cm$^{-1}$.

### *Eosphora thoides* Wulfert
### FIG. 17:1

*Eosphora thoides* Wulfert, 1935, p. 600, Fig. 15a–d.

*Type locality:* Saale River, eastern Germany.
*Holotype:* Not designated.
*Description:* Body resembles *E. thoa* as above; long cilia from lateral margin of head but not auricles *per se;* neck suture distinct; abdomen tapers to wide foot, its greatest width in anterior third; foot 3–4 segmented by light transverse lines; toes appear triangular in dorsal view, conical in lateral view; mastax with lateral salivary glands extends slightly past neck suture; trophi with long, distally widened fulcrum; rami triangular in dorsal view; in lateral view curve downwards at right angle to acute tips; unci with double-looped framework at free end (Fig. 17:1c); manubria slightly asymmetric, with fanlike lamellae at base; bifurcate epipharynx above trophi; foot glands large, right larger than left; mucus reservoir as large as toe present; retrocerebral sac, subcerebral glands and eye as in *E. thoa.*

Body length 460–510 µm; toes 26–35 µm; trophi 37 µm.
*Ecology:* Europe. Two records: billabong of Magela Creek, N.T. (Koste 1981), and margin of L. Mulwala, Vic. (Shiel, unpublished).
*Literature:* Wulfert 1935; Koste 1981.
*Comment:* Wulfert noted the resemblance of *E. thoides* to *E. thoa,* the former is distinguished by the toe morphology, more elongate vitellarium; and above all, differences in trophi structure as described. The animals found in our samples resemble *E. thoides,* however minor differences in trophi structure were noted. Further material is necessary for detailed examination.

### Genus *Eothinia* Harring & Myers

*Eothinia* Harring & Myers, 1922, p. 555.

*Type: Eosphora elongata* Ehrenberg, 1832 = *Eothinia elongata* (Ehrenberg, 1832).
*Type locality:* Berlin.

*Eothinia* was erected by Harring & Myers to accommodate *Eosphora elongata* Ehrenberg, 1832, the mastax of which differed from *Eosphora* but which could not be included in the related genus *Sphyrias* because of other morphological differences.

Body elongate, slender; head and neck clearly marked by transverse sutures; trunk with longitudinal lines tapering to tail of variable form; cuticle very transparent; foot short, 2–3 segmented; two toes and foot gland; corona slightly oblique, with ciliated buccal field and marginal wreath of cilia (reduced dorsally) with two lateral auricle-like curves of strongly developed cilia; mastax virgate; trophi with compact, fine denticles on inner margin of triangular rami; unci generally single-toothed; no preuncial teeth; fulcrum elongate, distally dilated; manubria rod-shaped with triangular-section at proximal end; large retrocerebral and subcerebral glands; cerebral eye and two widely separated frontal eyes. Eight taxa were referred to the genus by Koste (1978); one is known from Australia.

### *Eothinia elongata* (Ehrenberg)
### FIG. 17:2

*Eosphora elongata* Ehrenberg, 1832, p. 140.
*Eothinia elongata:* Harring & Myers 1922, pp. 555, 646–648, Fig. 61:1–5.

*Type locality:* Saale R., eastern Germany.
*Holotype:* Not designated.
*Description:* Transverse folds indistinct; foot longer, 2-segmented; toes straight with conical tips, about 1/10 total length; corona frontal; trophi with triangular rami; symmetrical; inner edges armed with numerous compact denticles; fulcrum of long straight plates fused in a V-shape; distal end of fulcrum finely subdivided; unci single toothed; manubria straight rod-like; two pleural rods pair transversely across mastax for support during pumping action-embedded in mastax walls at dorsal ends of rami (Fig. 17:2c); eyespots at posterior end of brain; two accessory eyespots on corona.

Length 350–510 µm; toes 32–45 µm; trophi 56–69 µm; unci 14 µm; male 150–215 µm; toes 13 µm; spiny subitaneous egg 92×115 µm; spines to 38 µm long.
*Ecology:* Widespread in littoral between water plants. Europe, Asia, N. America. Carnivore of other rotifers, particularly bdelloids. Known only from Ryans billabongs at Wodonga, Vic. 14.0–22.0°C, pH 6.2–7.1, DO 4.1 mg L$^{-1}$, 73–274 µS cm$^{-1}$, 5 NTU.
*Literature:* Koste 1978; Koste & Shiel 1980.

### Genus *Itura* Harring & Myers

*Itura* Harring & Myers, 1928, p. 684.

*Type: Diglena aurita* Ehrenberg, 1830 = *Itura aurita* (Ehrenberg).
*Type locality:* Berlin.

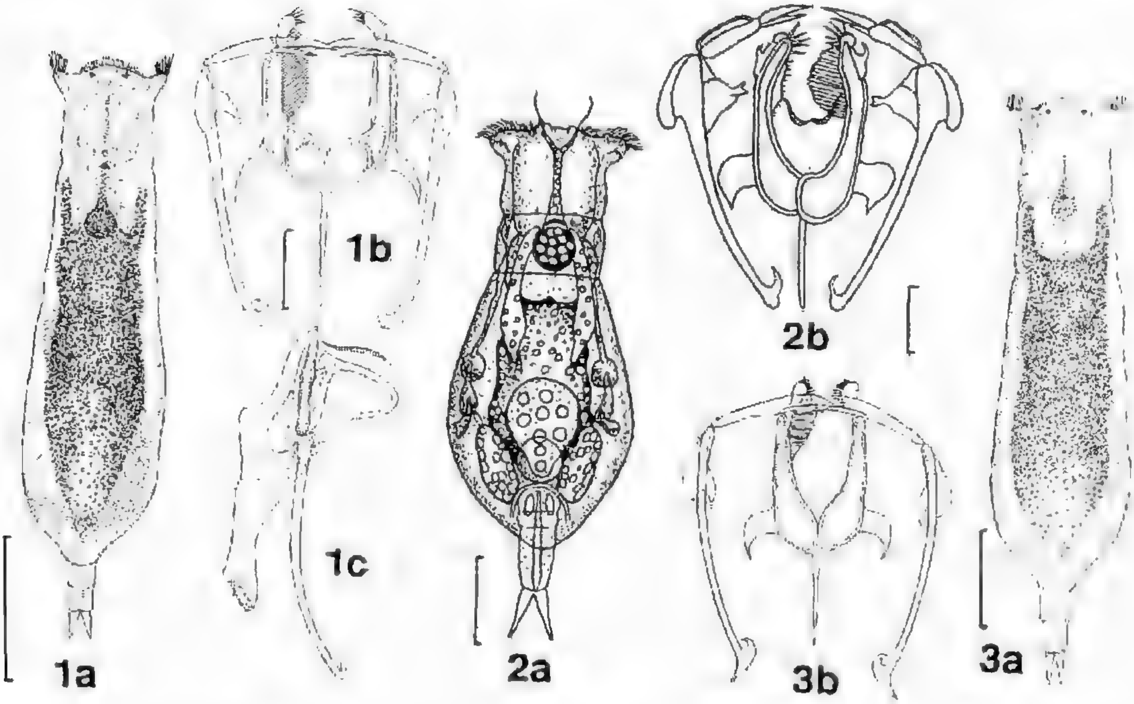


Fig. 18. 1, *Itura aurita* (Ehrenberg): (a) dorsal; (b) trophi, ventral; (c) trophi, lateral. 2, *I. myersi* Wulfert: (a) dorsal; (b) trophi, ventral. 3, *I. viridis* (Stenroos): (a) dorsal; (b) trophi, ventral. 1, 3 after Harring & Myers (1928); 2 after Wulfert (1935). Scale lines: adult 50 μm; trophi 10 μm.

Body elongate, fusiform, gibbous posteriorly; cuticle thin, flexible, body may be green due to symbiotic zoochlorellae; two dorsal transverse sutures separate head and neck; corona with stumpy, non-retractile lateral processes; foot and toes short; one cerebral eye at end of brain; two frontal eyes on apical field, the latter sometimes with speckled pigment flecks; single dorsal antenna; lateral antennae small; retrocerebral sac large; mastax resembles forcipate type of *Dicranophorus* spp., but rami cannot be extended through mouth; unci long, with bifurcate tips and knoblike median swelling; manubria long rods, proximally with small lamellae (dorsal and ventral), distally hooked, crooked or dilated; rami lyrate or forcipate, widely separated, with dorsally curving tips; tips dilated distally, toothed; inner rami margins (one or both sides) with finely striate or smooth lamellae, sometimes also on outer margin; alulae, sometimes asymmetrical, may be present; fulcrum in lateral view hooked or boardlike, frontally rodlike; rudimentary epipharynx and oral plate may be present. Female 180–500 μm. Male known but undescribed. Three species are known from Australia.

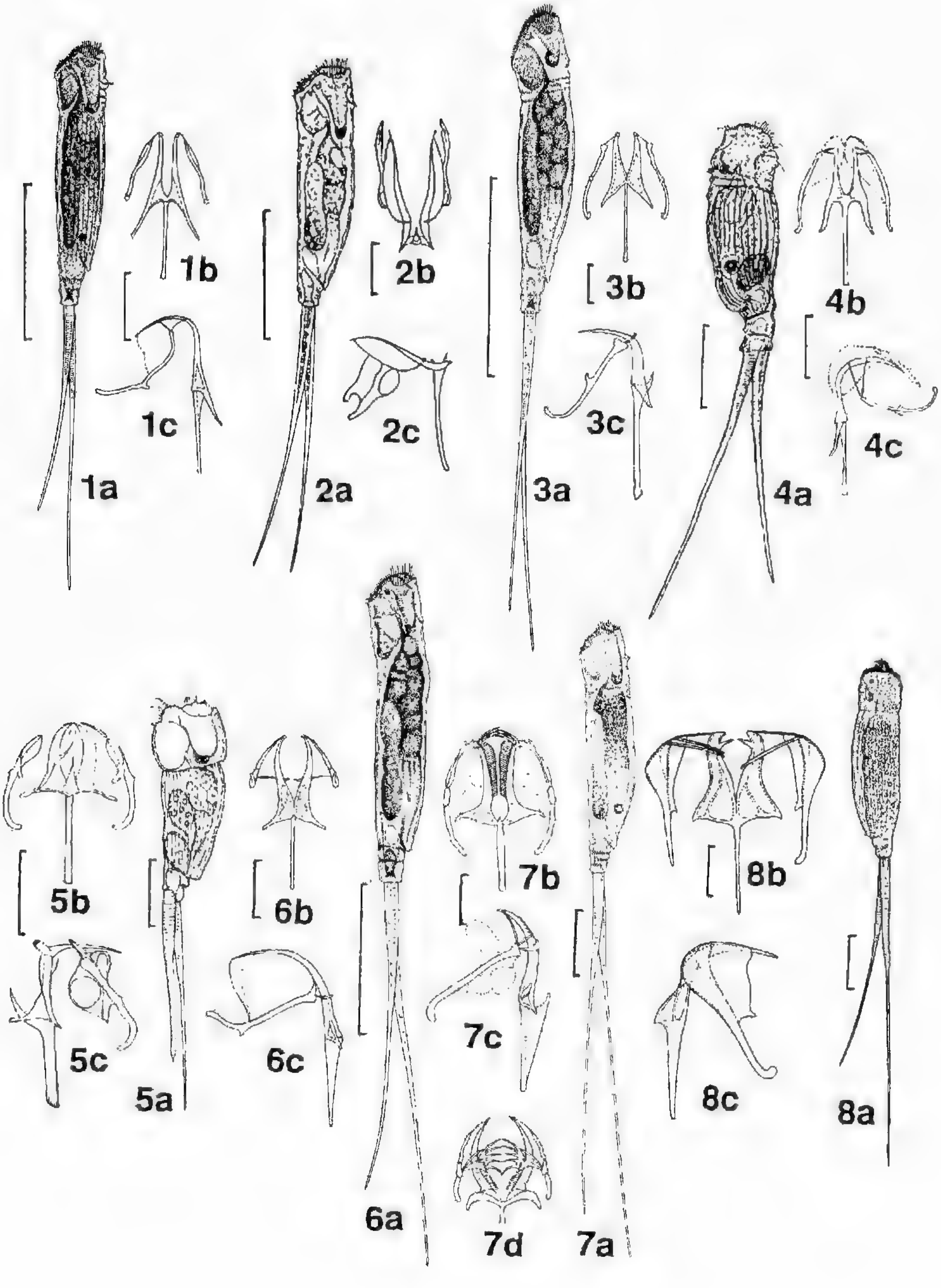
### Key to species of *Itura* recorded from Australian inland waters

1. Rami with asymmetric lamellae on outer border. .............. *I. aurita* (Ehrenberg) (Fig. 18:1)
Rami without lamellary ribs on outer border . . 2
2(1). Subcerebral glands very long .......... *I. myersi* Wulfert (Fig. 18:2)
Subcerebral glands missing or poorly developed. ............... *I. viridis* (Stenroos) (Fig. 18:3)

### *Itura aurita* (Ehrenberg)
FIG. 18:1

*Diglena aurita* Ehrenberg, 1830, p. 16.
*Itura aurita*: Harring & Myers 1928, p. 685.

*Type locality:* Berlin.
*Holotype:* Not designated.
*Description:* Body elongate, fusiform, may be green due to symbiotic zoochlorellae; toes short, conical with obtuse tips; mastax virgate; trophi asymmetric, robust; rami lyrate, knobbed at tip and bearing 5–6 long teeth; inside left ramus has narrow lamella, right ramus has broad denticulate lamella; alulae large, acutely pointed; manubria broadly expanded proximally, abruptly curved distally; gastric glands


1a
1b
1c
2a
2b
2c
3a
3b
3c
4a
4b
4c
5a
5b
5c
6a
6b
6c
7a
7b
7c
7d
8a
8b
8c

absent; retrocerebral sac present; cerebral eye and two frontal eyespots (with lenses) present.

Length 180–220 µm; toes 9–18 µm; trophi 38–45 µm (e.g. fulcrum 20 µm, manubria 30–33 µm, uncus 18 µm).

*Ecology:* In littoral of still and slowly flowing waters; Europe, N. America. Eats euglenoids and other unicellular algae. Early record from Qld. In our material, rare, only in Vic. (billabongs) and Tas. (stock dams). 13.0–18.0°C, pH 4.7–7.7, 42–3330 µS cm⁻¹.

*Literature:* Colledge 1914; Koste & Shiel 1986.

### *Itura myersi* Wulfert
FIG. 18:2

*Itura myersi* Wulfert, 1935, p. 589, Fig. 6a–c.

*Type locality:* Near Halle, eastern Germany.
*Holotype:* Not designated.
*Description:* Variable form, may be broader or narrower than figured; toes short, tapered; frontal eyes with lenses; gut sac glassy green, whereas in other species food balls are brown; long asymmetric subcerebral glands; trophi robust; rami elliptical in outline with inwardly curving tips which carry 5–6 teeth; right ramus with broad denticulate lamella on inner margin, left ramus with narrower finely denticulate lamella; alulae winglike expansion, without sharp points; fulcrum distinctive for species, very short and wide.

Total length 270–406 µm; toes 21–27 µm; (Fulcrum 13–16 µm; rami 27–34 µm; manubria to 33 µm; unci 22 µm.

*Ecology:* Europe, Asia. Eats *Euglena, Scenedesmus, Pediastrum, Trachelomonas.* Single record from an *Eleocharis* bed, Snowdon's Billabong, Wodonga, Vic. 14.7°C, pH 7.1, DO 4.3 mg l⁻¹, 240 µS cm⁻¹, 5 NTU.

*Literature:* Koste 1978; Koste & Shiel 1980.

### *Itura viridis* (Stenroos)
FIG. 18:3

*Eosphora viridis* Stenroos, 1898, 136; Fig. 1:30–32.
*Itura viridis:* Harring & Myers 1928, p. 692, Fig. 24:1–2.

*Type locality:* Lake Nurmijarvi, Finland.
*Holotype:* Not designated.
*Description:* Variable in form, readily confused with congeners; duct of retrocerebral sac much shorter than congeners; rami armed with 12 teeth; right ramus has broad striate, denticulate lamella, left ramus not lamellate; alulae large, broad, pointed posteriorly; fulcrum nearly as long as rami; frontal eyes with large spherical lenses and generally with accessory pigmentation; characteristic straight, narrow, sharply pointed toes; zoochlorellae in gut.

Total length 260–400 µm; toes 16–26 µm; trophi 45–48 µm.

*Ecology:* Littoral, possibly cosmopolitan. Europe, Asia, N. and S. America. Recorded from Trentham, Vic. (Coll. I. J. Powling, Melbourne) and Rapseys 3 stock dam, Wodonga (Coll. F. Dunn, MDFRC). 22°C, pH 6.0, 98.1 µS cm⁻¹.

*Literature:* Koste 1978.

## Genus *Monommata* Bartsch

*Monommata* Bartsch, 1870, p. 344.

*Type: Vorticella longiseta* Müller, 1786 = *Monommata longiseta* (Müller, 1786).
*Type locality:* Copenhagen.

Body cylindrical or fusiform; suture between head and abdomen; cuticle thin, firm, laterally and dorsally with longitudinal striae; foot indistinctly two-jointed; toes extremely long, almost twice body length, right longer than left (with exception of *M. aequalis*); corona slightly oblique, with marginal whorl of cilia and lateral auricle-like tufts of longer cilia for swimming; apical field unciliated, buccal field ciliated; mastax variable, from simple virgate to intermediate between virgate and forcipate type; in former type (Fig. 19:1b), rami lyrate or triangular without inner teeth, manubria simple rods, unci with one weak tooth or reduced to thin lamellar plates (Myers 1930); in intermediate type (Fig. 19:7b), rami lyrate with one or more teeth on inner margin, manubria broad and lamellar at base, unci with three unequal long, slender clubbed teeth; dorsal antennae single or paired on papillae in some species; lateral antennae normal; cerebral eye at posterior end of brain (absent in *M. caeca*). Variations from generic characters are detailed by Koste (1978) and summarised in the species diagnoses below. Eleven species have been recorded from Australia.

### Key to species of *Monommata* recorded from Australian inland waters

1\. Toes of similar length. . . . . . . . . . . . *M. aequalis* Ehrenberg (Fig. 19:2)

Fig. 19. 1, *Monommata actices* Myers: (a) lateral; (b) trophi, ventral; (c) trophi, lateral. 2, *M. aequalis* Ehrenberg: (a) lateral; (b) trophi, ventral; (c) trophi, lateral. 3, *M. aeschyna* Myers: (a) lateral; (b) trophi, ventral; (c) trophi, lateral. 4, *M. arndti* Remane: (a) lateral; (b) trophi, ventral; (c) trophi, lateral. 5, *M. dentata* Wulfert: (a) lateral; (b) trophi, ventral; (c) trophi, lateral. 6, *M. diaphora* Myers: (a) lateral; (b) trophi, ventral; (c) trophi, lateral. 7, *M. grandis* Tessin: (a) lateral; (b) trophi, oblique frontal; (c) trophi, lateral; (d) trophi, dorsal. 8, *M. longiseta* (Müller): (a) lateral; (b) trophi, ventral; (c) trophi, lateral. 1, 3, 6–8 after Myers (1930); 2 after Myers (1937); 4 after Koste (1972); 5 after Wulfert (1940). Scale lines: adult 50 µm; trophi 10 µm.

Toes of dissimilar length.......................2
2(1). Stomach with sacs....................*M. viridis* Myers (Fig. 20:3)
Stomach without sacs.......................3
3(2). Dorsal antenna single.......................5
Dorsal antennae paired.......................4
4(3). Body >200 µm; right:left toe ratio <1.2.......................*M. arndti* Remane (Fig. 19:4)
Body <200 µm; right:left toe ratio >1.2.......................*M. actices* Myers (Fig. 19:1)
5(3). Rami with teeth on inner margin.......................8
Rami without teeth on inner margin.......................6
6(5). Toes <200 µm; trophi 25–35 µm.......................7
Toes >200 µm; trophi <25 µm.....*M. diaphora* Myers (Fig. 19:6)
7(6). Right toe >165 µm; rami lyrate; unci with 5–6 linear teeth..........*M. phoxa* Myers (Fig. 20:2)
Right toe <165 µm; rami triangular; unci single-toothed........*M. aeschyna* Myers (Fig. 19:3)
8(5). Rami with 1–5 inner margin tooth pairs.......9
Rami with 1 or 2 occasionally unpaired inner margin teeth... *M. dentata* Wulfert (Fig. 19:5)
9(8). Unci with plate-like teeth terminally with finger-like extensions....*M. grandis* Tessin (Fig. 19:7)
Unci only with long dagger-like teeth.......10
10(9). Unci teeth paired.......................*M. maculata* Harring & Myers (Fig. 20:1)
Unci teeth single.......................*M. longiseta* (Müller) (Fig. 19:8)

### *Monommata actices* Myers
FIG. 19:1

*Monommata actices* Myers, 1930, pp. 394–5, Figs 4–7.

*Type locality:* Permanent bodies of acid-waters in Atlantic County, New Jersey.
*Holotype:* Not designated. ?Myers Coll., AMNH, N.Y.
*Description:* Body slender, cylindrical, tapering to foot; head clearly separated from trunk by dorsal projections and folds of integument, which is striate; single dorsal antenna tubular, retractile, when extended has papillate base; lateral antennae with two associated round reddish or clear areas in lumbar region; corona oblique, typical; mastax minute, simple virgate; fulcrum long, rodlike; rami slender, lyrate, crooked downward medially; alulae rodlike; unci with two short teeth; pair of thin lamellar plates bounded by dorsal pair of unci teeth; oesophagus short; gastric glands round; no constriction between stomach and intestine; foot glands, bladder and retrocerebral sac small; eyespot at posterior end of ganglion; egg spinulate.

Body length 150–195 µm; trophi 22–24 µm; right toe 200–210 µm; left toe 150–170 µm; subitaneous egg 48×58 µm, spinules 15 µm.
*Ecology:* Europe, N. America, in moor pools and lightly acid waters. Rare, billabong at Jabiluka, N.T.; Goulburn R. billabong at Seymour Vic.; Cradle Mt Nat. Park, Tas. 23.0–25.0°C, pH 5.7–6.2, 48 µS cm$^{-1}$, DO 3.7 mg l$^{-1}$.
*Literature:* Donner 1978; Koste & Shiel; Koste *et al.* 1988.
*Comment:* The single dorsal antenna was considered by Wulfert (1960) to be doubtful; Koste (1978) suggested that paired antennae were overlooked by Myers, and that the appearance of *M. actices* is identical with *M. arndti* Remane. The dimensions given in Koste (1978) are contradictory, and there are differences in the trophi as figured by the two authors. We retain both taxa here until finer resolution of them can be made.

### *Monommata aequalis* Ehrenberg
FIG. 19:2

*Notommata longiseta aequalis* Ehrenberg, 1832, p. 134.
*Monommata aequalis:* Eyferth, 1878, p. 84.

*Type locality:* Berlin.
*Holotype:* Not designated.
*Description:* Long, slender, hyaline body indistinctly demarcated from head; single dorsal antenna; rami lacks inner margin teeth; rami, seen laterally, at right angles to fulcrum; unci uniformly lamellate, fluted or with marginal denticles; fulcrum rodlike; manubria bilaterally lamellate; subcerebral glands absent; toes of equal or similar length; red or yellow-orange vesicles beside intestine.

Total length 200-227 µm; toes 110–120 µm.
*Ecology:* Rare in vegetated waters, Europe, S. America, Early record from Qld. In our Tasmanian collections from Great Lake, Central Plateau 9.0–11.0°C, pH 7.6–7.8, 9.0-13.4 µS cm$^{-1}$.
*Literature:* Koste 1978; Koste *et al.* 1988.

### *Monommata aeschyna* Myers
FIG. 19:3

*Monommata aeschyna* Myers, 1930, p. 387, Fig. 24:4-6.

*Type locality:* Cordoy Creek, Atlantic County, New Jersey.
*Holotype:* Not designated. ?Myers Coll., AMNH, N.Y.
*Description:* Body elongate, fusiform; head demarcated by slight constriction; body tapers gradually to 3-segmented foot from midline; single dorsal antenna on low papilla; mastax virgate, small, simple; fulcrum long, straight, slightly dilated distally; rami triangular, without teeth or denticles; alulae prominent; manubria simple rods, distally curved, with medial blunt tooth-like process dorsally; unci single-toothed; gastric glands, retrocerebral sac small; eyespot on ventral side of ganglion.

Body length 130–150 µm; right toe 150–165 µm; left toe 120-145 µm; trophi 25–35 µm.

*Distribution:* In *Sphagnum,* melt-water pools, Europe, N. America. Rare, billabong at Seymour, Ryans 2 Billabong, Wodonga, Vic., and shallow pools, western Tas. 13.0–27.0°C, pH 5.4–6.9, 25–292 µS cm$^{-1}$, TDS 16.2–21.1 mg l$^{-1}$, 1.1–7.3 NTU.
*Literature:* Koste 1978.

### *Monommata arndti* Remane
FIG. 19:4

*Monommata arndti* Remane, 1933, p. 567–68.

*Type locality:* Moor pool near Kiel, Germany.
*Holotype:* Not designated.
*Description:* Resembles *M. actices.* Paired dorsal antennae also on retractile papillae; lateral antennae tubular; mastax with two paired and one single salivary gland; retrocerebral sac with distinct paired excretory ducts present; two tubular subcerebral glands; gut contents generally yellow-gold; Koste (1978) notes that paired red lumbar bodies develop in response to food intake, and possibly are excretory deposits; ratio of body/toe length changes during development; subitaneous egg spiny, male egg smooth-shelled. Male undescribed.

Length 210–500 µm; right toes to 250 µm; left toe to 210 µm; subitaneous egg 85×75 µm; male egg 48×40 µm.
*Ecology:* Europe. Eats phytoflagellates, e.g. *Synura,* by holding colonies in the corona and sucking cell contents. Single record: billabong of Goulburn R. at Alexandra, Vic. 20.0°C, pH 7.2, DO 9.1 mg l$^{-1}$.
*Literature:* Koste 1972; Koste & Shiel 1980.

### *Monommata dentata* Wulfert
FIG. 19:5

*Monommata dentata* Wulfert, 1940, p. 578, Fig. 22

*Type locality: Sphagnum* pool, Birkhorster Moor, between Scharfenbrück and Neuendorf.
*Holotype:* Not designated.
*Description:* Body squat, glassy; stomach and intestine yellow-grey; right toe shorter than body; coloured vesicles absent, although mastax sometimes contains colourless balls/spheres; single dorsal antenna; trophi structure variable; rami with paired or single (or missing) teeth on inner margin; pleural rod present; unci two-toothed; fulcrum spatulate distally; basal apophysis (medial pointed process on fulcrum) present; manubria bilaterally lamellate, not crooked terminally.

Total length to 400 µm; right toe 115–200 µm; left toe 89–160 µm; trophi length 16–22 µm.
*Ecology:* Previously known only from Europe. Described by Koste (1978) as pH tolerant, eurytherm, oligo-euryhaline. A population closely resembling *M. dentata* was collected from Tasmania (Golden Valley) in 1987, with a second record from Ryans 2 Billabong, Wodonga in Oct. 1990. 15–23.0°C, pH 6.2–6.7, 140–310 µS cm$^{-1}$, 4.0 NTU.
*Literature:* Koste & Shiel 1987b.

### *Monommata diaphora* Myers
FIG. 19:6

*Monommata diaphora* Myers, 1930, p. 388–9, Figs 7–9.

*Type locality:* Acid water of the littoral region of ponds and lakes in Atlantic County, New Jersey.
*Holotype:* Not designated. ?Myers Coll., AMNH, N.Y.
*Description:* Body very long, cyclindrical; characteristic swelling above anterior part of stomach; right toe shorter than body; corona typical; single dorsal antenna; mastax virgate; fulcrum without basal apophysis; rami triangular in ventral view, laterally right-angled, without teeth or denticles; alulae prominent; manubria reduced to simple rods, crooked terminally, attached to rami by thin lamellar plates; unci single toothed; mastax with two large confluent salivary glands; eyespot with lens on ventral side of brain at posterior end; retrocerebral sac with rudimentary excretory duct.

Body length 225 µm; right toe 260 µm; left toe 225 µm; trophi 25 µm.
*Ecology:* Littoral of weakly acid waters (pH 6.2–6.4), southeast Europe, N. America. Single record from Rushy Billabong, R. Murray near Barnawartha, Vic. (Shiel unpubl.).

### *Monommata grandis* Tessin
FIG. 19:7

*Monommata grandis* Tessin, 1890, p. 151, Fig. 3:11–12

*Type locality:* Rostock, eastern Germany.
*Holotype:* Not designated.
*Description:* Body elongate, fusiform; single dorsal antenna on raised prominence; lateral antennae usual; characteristic red pigment spots beneath lateral antennae; foot indistinctly two-jointed; mastax of intermediate type; fulcrum similar length to rami; rami with thin lamellae medially; large basal apophysis; large alulae; inner margins of rami with 25+ comb-like ventral denticles and two pairs of four long, slender opposing oral teeth; each uncus with plate-shaped ventral tooth, ending in five tooth-like projections at tip, and distal rod-like tooth; manubria crooked distally, lamellate proximally; retrocerebral sac small, clearly ducted to corona surface; no subcerebral glands; mastax has confluent salivary glands; eyespot ventral at posterior end of ganglion.

Total length 350–680 µm; body 190–240 µm; right toe 210–470 µm; left toe 150–336 µm.
*Ecology:* Cosmopolitan, rare, generally single finds

in littoral of standing waters in Europe. Rare, Qld, Tas., Vic, 16.7–27.0°C; pH 4.52–7.2; 25.4-60.0 IS cm$^{-1}$; TDS 16.2–24.9 mg l$^{-1}$; 1-9.4 NTU.
*Literature:* Koste & Shiel 1980, 1983, 1987b.

### *Monommata longiseta* (Müller)
FIG. 19:8

*Vorticella longiseta* Müller, 1786, p. 295, Fig. 42: 9–10.
*Monommata longiseta:* Bartsch 1870, p. 344.

*Type locality:* Copenhagen.
*Holotype:* Not designated.
*Description:* Body slender, elongate, with transparent integument marked with closely spaced striae; resembles *M. dentata.* Can be distinguished by trophi differences: rami bent at right angle near mid length, with long slender tooth at angle on each ramus; right uncus has three long slender teeth, left uncus two; fulcrum lacks basal apophysis; manubria broad lamellar proximally, distally rodlike, outward curving; length of toes variable.

Total length 200–250 µm; body length 86–115 µm; right toe 155 µm; left toe 120 µm; trophi 15–16 µm.
*Ecology:* Cosmopolitan in vegetated waters. Earlier records from N.S.W., Qld, Vic. In our material a single record from Scottsdale, Tas. 15.0°C, pH 7.1, 105 µS cm$^{-1}$.
*Comment:* This taxon may not be as widely distributed in Australia (or globally) as the records suggest, because of confusion with other species by earlier authors.
*Literature:* Shiel & Koste 1979; Koste *et al.* 1988.

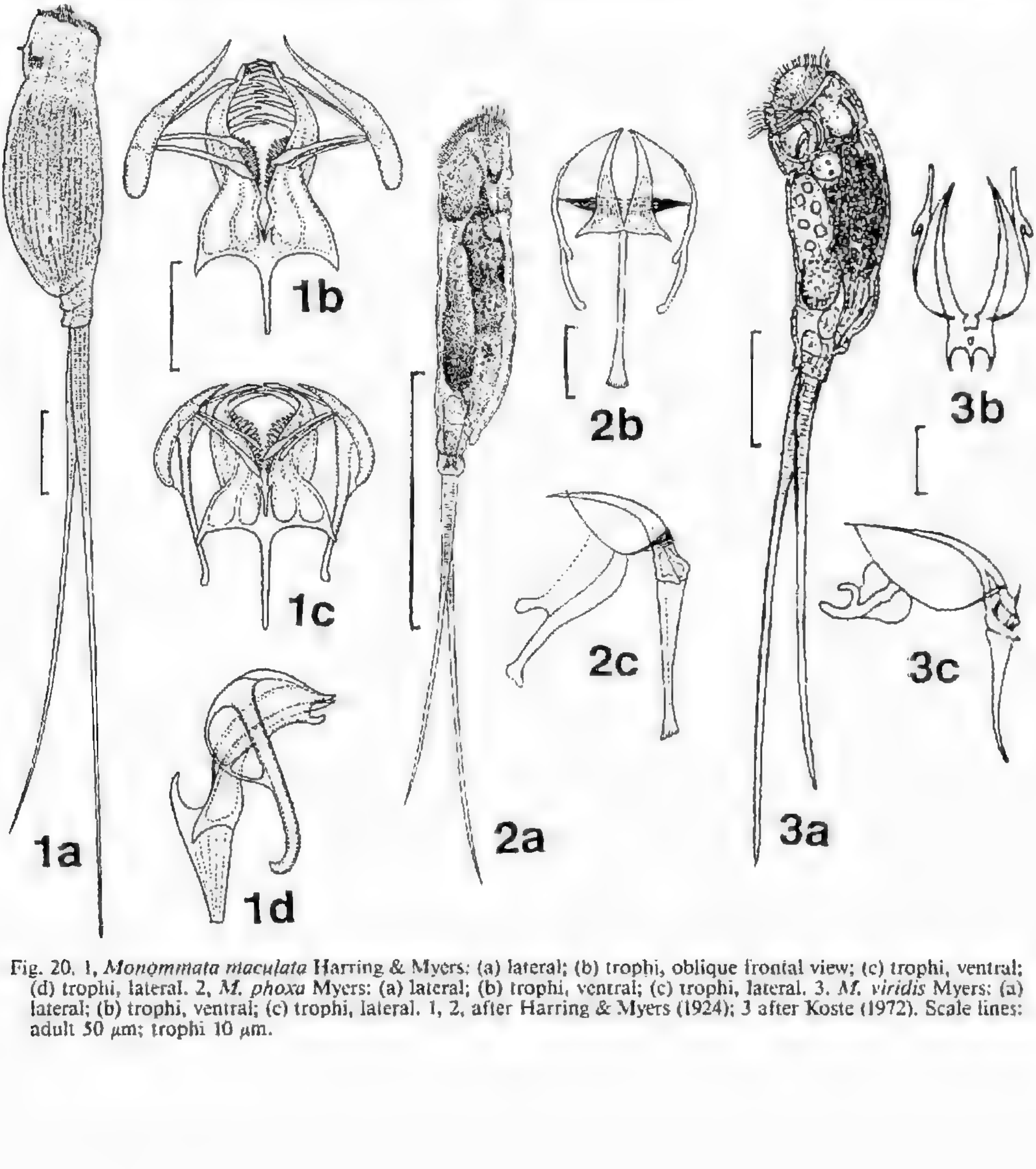


Fig. 20. 1, *Monommata maculata* Harring & Myers: (a) lateral; (b) trophi, oblique frontal view; (c) trophi, ventral; (d) trophi, lateral. 2, *M. phoxa* Myers: (a) lateral; (b) trophi, ventral; (c) trophi, lateral. 3. *M. viridis* Myers: (a) lateral; (b) trophi, ventral; (c) trophi, lateral. 1, 2, after Harring & Myers (1924); 3 after Koste (1972). Scale lines: adult 50 µm; trophi 10 µm.

### *Monommata maculata* Myers
FIG. 20:1

*Monommata grandis* Harring & Myers, 1924, p. 538, Fig. 43: 6-10.
*Monommata maculata* Myers, 1930, p. 385.

*Type locality:* Not specified, ". . . common in weedy ponds . . . ".
*Holotype:* Not designated. ?Myers Coll. AMNH, N.Y.
*Description:* Body slender, elongate; integument striated; foot two-segmented; toes variable, but always unequal; mastax intermediate between virgate and forcipate; fulcrum frontally short, dagger-like, laterally planklike; abnormally large basal apophysis; inner margin of rami with unique, complex denticulation – three groups of teeth: ventral group with 12-14 comb-like teeth; middle oral group with four large curved, pointed interlocking teeth; dorsal group with three long needle-like teeth; unci with three long clubbed teeth; manubrium terminally crooked with ventral strong lamella; retrocerebral sac present.

Total length to 680 μm; right toe 340–470 μm; left toe 270–410 μm; trophi 26–34 μm.
*Ecology:* Europe, Asia, N. and S. America in vegetated waters. N.T., Qld, Tas., W.A. 19.0–27.0°C, pH 5.4–6.9; 25.4–33.5 μS cm$^{-1}$, TDS 16.2–21.4 mg l$^{-1}$, 1.1–2.2 NTU.
*Literature:* Koste 1978; Koste *et al.* 1988.

### *Monommata phoxa* Myers
FIG. 20:2

*Monommata phoxa* Myers, 1930, p. 395-6, Fig. 26: 8-10.

*Type locality:* Acid pond near English Creek, Atlantic County, New Jersey.
*Holotype:* Not designated. ?Myers Coll. AMNH, N.Y.
*Description:* Body long, cylindrical; single minute dorsal antenna; trophi virgate, with long, distally spatulate fulcrum; rami lyrate in ventral view; unci with 5–6 linear teeth; two rods run from bases of teeth to tips of rami, marking limits of two thin lamellar plates resting on sides of rami; manubria with median lobulate projection, distally with slight expansion and outward curve; retrocerebral sac small.

Body length 150 μm; right toe 190 μm; left toe 140 μm; trophi 35 μm.
*Ecology:* Europe, Asia, N. America, ?Africa, in acid moor pools, Tas., Vic. 25.0–27.0°C, pH 5.4–5.8, 25–119 μS cm$^{-1}$, TDS 16.2–76.3 mg l$^{-1}$, 2.0–2.2 NTU
*Literature:* Koste *et al.* 1988.

### *Monommata viridis* Myers
FIG. 20:3

*Monommata viridis* Myers, 1937, p. 10-11, Fig. 12, 19, 21.

*Type locality:* Atlantic County, New Jersey. ". . . in the littoral region among *Sphagnum* in bodies of acid waters."
*Holotype:* Not designated. ?Myers Coll., AMNH, N.Y. Paratype: Cat No. 604, AMNH.
*Description:* Body slender, no constriction behind head; dorsal antenna double papillose projection; stomach ends in four blind sacs; gut contents yellow-green spheres; gastric glands present; mastax modified virgate; fulcrum short, in lateral view curved, tapering; rami slender, lyrate, bent dorsally near mid-length at approximate right angle; dorsal portion has small tooth on inner margin; unci reduced to thin lamellar plates, posterior edges thickened to resemble slightly clubbed teeth; manubria curve dorsally, have small digitiform process near mid length; retrocerebral sac round, clear, ductless.

Total length 382 μm; body length 166 μm; right toe 216 μm; left toe 150 μm; subitaneous egg 65×52 μm.
*Ecology:* Common in *Sphagnum*, pH 4.5–6.5, N. America, Europe. Single record from dune lakes area, western Tas. 17.0°C, pH 3.1, 80.6 μS cm$^{-1}$.
*Literature:* Koste 1978; Koste *et al.* 1988.

## Genus *Notommata* Ehrenberg

*Notommata* Ehrenberg, 1830, p. 46.

*Type: Vorticella aurita* Müller, 1786 = *Notommata aurita* (Müller)
*Type locality:* Copenhagen.

Body cylindrical, spindle-shaped, sac-like, conical, or with lateral alae; neck suture evident; caudal tail usually present; foot short, often 2-segmented, occasionally indistinctly segmented; also rudimentary; with and without caudal sensillae, always with two toes; cuticle generally soft, often with longitudinal striae; corona broadly triangular, displaced ventrally ("*Notommata* type") (Fig. 21:1b), in some species extending into pronounced "chin"; auricles generally large, narrowly to widely separated, retractable; apical field small; mastax virgate; trophi asymmetric in most species; unci often with accessory teeth, occasionally also with rudimentary fulcrum, long and plank-like, straight or curved; pleural rods, epipharynx and oral plates may be present; hypopharynx muscle attached to fulcrum; stomach and intestine separated by weak constriction; retrocerebral organ generally well-developed; protonephridia visible in head- 4–6 pairs of flame cells; cerebral eyespots present or absent;

male not known for all species. Fifty-five *Notommata* species are listed or described in Koste (1978); 12 of these are known from Australia, with two endemic species described subsequently. These are keyed below, however we caution that in view of gross morphological similarities between some taxa, and ready confusion of juveniles of large species with adults of smaller forms, the key can be used reliably only with living adults. For preserved material, and doubtful live material, trophi differences as described and figured enable accurate specific identification.

### Key to species of *Notommata* recorded from Australian inland waters

1\. Cylindrical, fusiform or conical body, without lateral extensions (alae)........2
Body with pronounced alae........ *N. spinata* nov. nom. (Fig. 24:4)

2(1). Rump with projecting digitiform process (Fig. 23:1d)........3
Rump without obvious appendage........4

3(2). Body >500 μm; trophi >80 μm; caudal process with articulated tip, does not reach base of toes ........ *N. copeus* (Ehrenberg) (Fig. 23:1)
Body <200 μm; trophi <30 μm; caudal process not articulated, extends past base of toes ........ *N. tripus* Ehrenberg (Fig. 25:1)

4(2). Caudal 'tail' more or less covering base of foot........5
Rump rounded, with no obvious tail........12

5(4). Toes <10 μm; body vermiform; auricles indistinct ........ *N. contorta* (Stokes) (Fig. 22)
Toes >10 μm; body fusiform or gibbous; auricles distinct........6

6(5). Toes >35 μm........7
Toes <35 μm........8

7(6). Toes 40–42 μm; body <310 μm; trophi 40–45 μm ........ *N. doneta* Harring & Myers (Fig. 23:3)
Toes 35–75 μm; body 300–800 μm; trophi >75 μm ........ *N. pachyura* (Gosse) (Fig. 24:1)

8(6). Trophi <40 μm; toes 16–20 μm; body <350 μm ........ *N. aurita* (Müller) (Fig. 21:1)
Trophi >40 μm; toes 15–35 μm; body 300–750 μm........9

9(8). Mastax large, trophi 100 μm; body 500–750 μm ........ *N. collaris* (Ehrenberg) (Fig. 21:4)
Mastax smaller; trophi <70 μm; body 300–680 μm........10

10(9). Tail with median lobe and two lateral lobes; trophi 45–60 μm........11
Tail rounded; trophi 60–70 μm ........ *N. glyphura* Wulfert (Fig. 23:4)

11(9). Toes 30–35 μm; trophi symmetric, unci single-toothed ........ *N. pseudocerberus* De Beauchamp (Fig. 24:2)
Toes 15–35 μm; trophi asymmetric, unci 3–5-toothed ........ *N. cerberus* (Gosse) (Fig. 21:2)

12(4). Toes 20–30 μm; trophi 30–35 μm ........ *N. cyrtopus* Gosse (Fig. 23:2)
Toes <20 μm; trophi <25 μm........13

13(12). Body 160–200 μm; toes 8–10 μm, trophi 24 μm ........ *N. silpha* (Gosse) (Fig. 24:3)
Body <140 μm; toes 12–16 μm, trophi 20 μm ........ *N. tyleri* Koste *et al.* (Fig. 25:2)

### *Notommata aurita* (Müller)
### FIG. 21:1

*Vorticella aurita* Müller, 1786, p. 288, Fig. 41:1–3.
*Notommata aurita*: Ehrenberg 1830, p. 46.

*Type locality:* Copenhagen.
*Holotype:* Not designated.
*Description:* Body short, stocky, integument transparent, with longitudinal striae; foot 2-segmented, first segment nearly covered by tongue-shaped caudal projection ("tail"); small "peg" between toes; auricles short; corona with well-developed "chin" region; mastax virgate; trophi in ventral view with left ramus more strongly developed; fulcrum long and stout, distal end Y-shaped for attachment of hypopharynx muscle; rami subsquare in ventral view, bent at right angles to anterior point; unci plates with single main tooth, basal plate with 1–2 rudimentary teeth; small preuncial teeth at tip of right uncus; manubria with broad angular anterior plate; triangular oral plate and thin pleural rods present; retrocerebral sac large, spherical, generally opaque; cerebral glands rudimentary; eyespot large, beneath retrocerebral sac, only visible laterally.

Total length 250–350 μm; toes 16–20 μm; trophi 34–36 μm; male 180 μm.
*Ecology:* Cosmopolitan in fresh to brackish water, abundant in spring and autumn in Palaearctic waters; preys on bdelloid and other rotifers as well as algae. Early records from N.S.W., Qld, Vic., recently collected (Sept.–Oct. 1990) in Ryans Billabongs, Wodonga. 13.0–17.0°C, pH 6.85–6.92, 274–292 $\mu S\ cm^{-1}$.
*Literature:* Koste 1978; Shiel & Koste 1979.

### *Notommata cerberus* (Hudson & Gosse)
### FIG. 21:2, 3

*Copeus cerberus* Hudson & Gosse, 1886, p. 34, Fig. 16:3.
*Notommata cerberus*: Beauchamp 1908, p. 401, Fig. 1–3.

*Type locality:* Sandhurst Wood, Berkshire.
*Holotype:* Not designated.
*Description:* Body slender, integument flexible; slight transverse folds between head and neck; tail rounded, with median lobe and rudimentary lateral lobes; foot with two joints; small setose pit in centre of dorsal side of second joint; toes slender pointed, 1/15 total length; corona extends ca. ¼ length of body ventrally; auricles short, with robust cilia tufts; mastax virgate; Y-shaped lamellae at base of

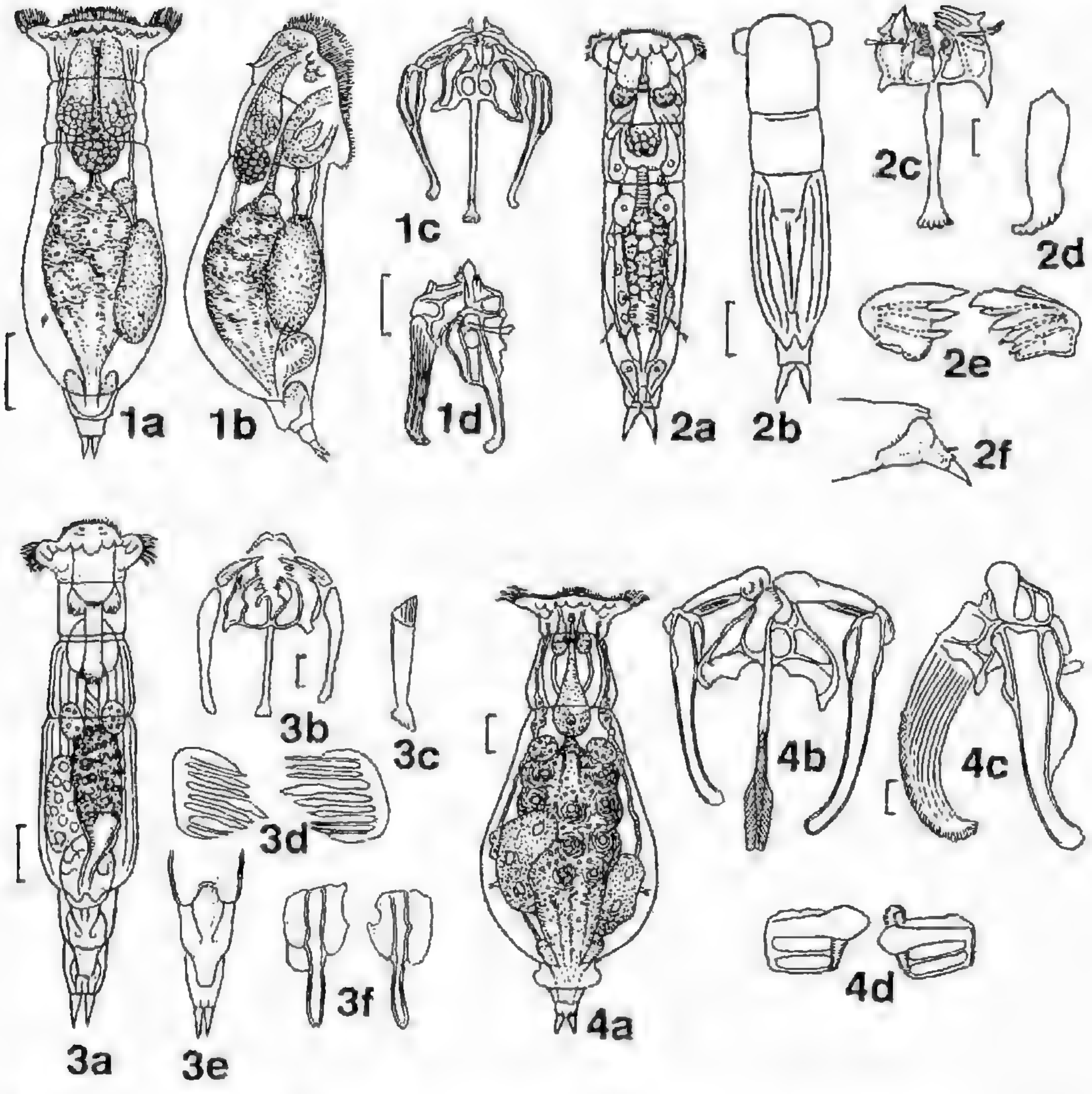


Fig. 21 1, *Notommata aurita* (Müller): (a) dorsal; (b) lateral; (c) trophi, ventral; (d) trophi, lateral. 2, *N. cerberus* (Gosse): (a) dorsal; (b) patterning of integument, dorsal; (c) trophi, ventral, manubria omitted; (d) fulcrum, lateral; (e) unci; (f) foot and toes, lateral. 3, *N. cerberus longinus* Wulfert: (a) dorsal; (b) trophi, ventral; (c) fulcrum, lateral; (d) unci; (e) abdomen, foot and toes, dorsal; (f) manubria. 4, *N. collaris* Ehrenberg: (a) dorsal; (b) trophi, ventral; (c) trophi, lateral; (d) unci. 1, 4 after Harring & Myers (1922); 2 after Wulfert (1940), 3 after Wulfert (1961). Scale lines: adult 50 μm; trophi 10 μm.

fulcrum to which hypopharyngeal muscles attach; rami asymmetric, inner edges striate but not denticulate, outer margin with asymmetric apophyses and short toothed alulae; right more developed than left; pleural rods present; unci plates with 3–5 teeth; ventral main tooth has small accessory teeth; four foot glands, one pair large, one pair small; retrocerebral sac pyriform reaches almost to end of mastax; eyespot large, lenticular.

Total length 300–600 μm; toes 15–35 μm; trophi 46–60 μm (46 μm trophi has 42 μm rami; 32 μm fulcrum; 21μm unci).

*Ecology: Sphagnum*, periphyton, waters in northern hemisphere. Omnivore, eats rotifers, desmids, diatoms, flagellates. Early records from N.S.W., Qld, Vic. Recently collected (Sept. 1990) from a billabong of the Mitta Mitta River at Tallandoon, Vic.

*Literature:* Evans 1951; Shiel & Koste 1979.

*Comment:* A variant described by Wulfert (1961) as *N. cerberus* var. *longinus* occurs in eastern Tasmania. Comparison of the morphological differences shown in Figs 21:2 and 21:3, particularly trophi, suggests that specific status may be warranted. 19.0°C, pH 6.8, 215 $\mu$S cm$^{-1}$.

### *Notommata collaris* Ehrenberg
FIG. 21:4

*Notommata collaris* Ehrenberg, 1832, p. 131, Fig. 4:11.

*Type locality:* Berlin.
*Holotype:* Not designated.
*Description:* Body short, stout, integument 'leathery', transparent; neck long to accommodate large mastax; anterior sutures well marked; abdomen bulges to twice anterior width to rounded posterior with short broad tail which covers ca. ½ of first of two foot joints; toes short, conical about 1/30 total length; auricle ciliation continuous with corona; corona elongate to form prominent post-oral chin; mastax virgate, trophi asymmetric, the largest (in proportion to body) of all *Notommata* spp.; fulcrum with V-shaped lamellae for muscle attachment; right ramus with broad lamellar tooth with denticulate lamellar margin; left ramus excavated; unci with three teeth, only ventral tooth developed; inner unci margin striated; manubria long and broad with wide thin lamella extending nearly to posterior end on dorsal margin; pleural rods present; foot glands slender; retrocerebral sac long, pyriform; eyespot at posterior end of brain.

Length 500–750 $\mu$m; toes 25–32 $\mu$m; trophi 100 $\mu$m; male 240 $\mu$m; resting egg 170×215 (±15)$\mu$m.
*Ecology:* Palaearctic, Nearctic, abundant in dystrophic waters in periphyton. Eats *Closterium* and filamentous algae. N.S.W., N.T.
*Literature:* Shiel & Koste 1979; Koste 1981.

### *Notommata contorta* (Stokes)
FIG. 22

*Diglena contorta* Stokes, 1897, p. 630, Fig. 14:5.
*Notommata contorta:* Harring 1913, p. 78.

*Type locality:* ". . . shallow clear-water pool in a rocky wood near Trenton, New Jersey".
*Holotype:* Not designated.
*Description:* Body elongate-subcylindrical, vermiform, gibbous posteriorly, integument notably flexible; head rounded, convex, with small hook-like proboscis beneath which frontal border is conspicuously emarginate; rump depressed into cylindrical tail overhanging and almost completely surrounding short papillate foot; two small conical divergent toes; buccal field elongate, almost horizontal, extending ventrally ca. 1/3 body length; 'chin' absent; lateral ciliated auricles small, rarely extended; two dorsal and two lateral antennae; small yellowish-orange cerebral eye; retrocerebral sac with bacteroids; subcerebral glands short; trophi simple forcipate; fulcrum long, dagger-like, with basal apophysis and terminal hook-like dorsal curve; unci single-toothed; rami simple, with strong right-angled bend.

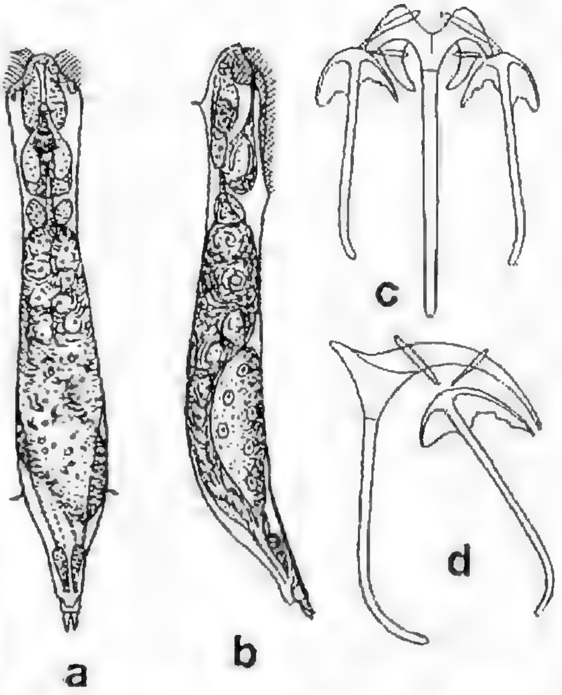


Fig. 22. *Notommata contorta* (Stokes): (a) dorsal; (b) lateral; (c) trophi, ventral; (d) trophi, lateral. After Harring & Myers (1922). Scale lines: adult 50 $\mu$m; trophi 10 $\mu$m.

Total length 206–300 $\mu$m; toes 7–10 $\mu$m; buccal field 83–86 $\mu$m; trophi 17–20 $\mu$m (fulcrum 12 $\mu$m, manubria 13 $\mu$m).
*Ecology:* In acid waters, in periphyton of submerged plants in pools and lakes. Previously known from Palearctic and Nearctic (Koste 1978). First record from Australia 19 Sept. 1990, Ryans 1 Billabong, Wodonga, in *Azolla*. Subsequently also found in nearby Ryans 2 in *Ricciocarpus*. 20.0–22°C, pH 6.39–6.57, 114–274 $\mu$S cm$^{-1}$.

### *Notommata copeus* Ehrenberg
FIGS 2, 23:1

*Notommatus copeus* Ehrenberg, 1834, p. 213.

*Type locality:* Berlin.
*Holotype:* Not designated.
*Description:* Large species, elongate body, truncate posteriorly; anterior sutures distinct; tail a long round, conical projection with articulated tip

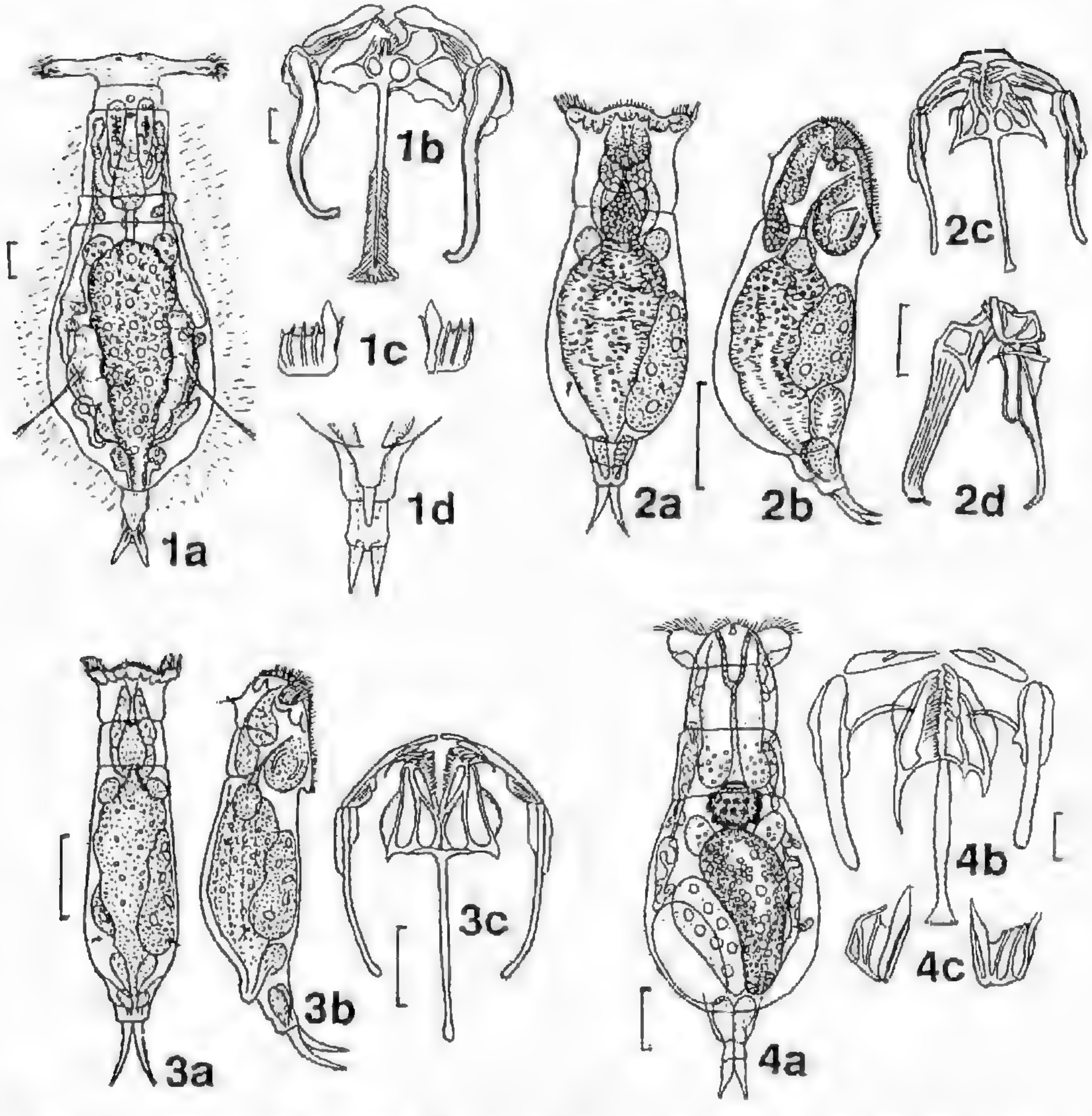


Fig. 23. 1, *Notommata copeus* Ehrenberg: (a) dorsal; (b) trophi, ventral; (c) unci; (d) foot and toes, dorsal. 2, *N. cyrtopus* Gosse: (a) dorsal; (b) lateral; (c) trophi, ventral; (d) trophi, lateral. 3, *N. doneta* Harring & Myers: (a) dorsal; (b) lateral; (c) trophi, ventral. 4, *N. glyphura* Wulfert: (a) dorsal; (b) trophi, ventral; (c) unci. 1a, c, d after Donner (1954); 1b, 2 after Harring & Myers (1922); 3 after Harring & Myers (1924); 4 after Wulfert (1935). Scale lines: adult 50 μm; trophi 10 μm.

segment; foot with two broad segments, with setose papilla at distal end of second joint between toes; toes ca. 1/16 total length, long and slender, slightly decurved; very long ciliary auricles (seldom extended) and exceptionally elongated chin; lateral antennae setae long; mastax virgate, asymmetric, left side more developed; rami triangular with broad lamellar tooth on right ramus, socket on left; left uncus with large ventral tooth and three smaller teeth; right ramus with four undeveloped teeth; manubria and pleural rods as *N. collaris;* retrocerebral sac and subcerebral glands present; eyespot large, at posterior end of brain

Total length 500–1100 μm; toes 40–65 μm; trophi 80–100 μm; male 280–350 μm; toes 36 μm.

*Ecology:* Cosmopolitan in algal-rich standing waters, pH 4–6.5, temp. 15–30°C. Eats filamentous algae *(Spyrogira, Zygnema, Mougeotia);* swallows smaller filaments in short pieces. N.S.W., N.T., Qld, Vic

*Literature:* Shiel & Koste 1979; Koste 1981.

### *Notommata cyrtopus* Hudson & Gosse

FIG. 23:2

*Notommata cyrtopus* Hudson & Gosse, 1886, 2: 22, Fig. 17:7.

*Type locality:* Widcombe Pond, Bath.
*Holotype:* Not designated.
*Description:* Body stout, integument flexible, transparent; single obvious suture between neck/abdomen; abdomen rounded posteriorly without tail; foot 2-segmented; toes long (1/7 total length), curved and tapering; auricles short, ciliation continuous with corona; mastax virgate; trophi slightly asymmetric; fulcrum stout; rami approximately triangular in ventral view; inner edge of right ramus concave, left convex, both denticulate; alulae well-developed; right ramus has four short curved preuncinal teeth at tips, left has five; unci with single main tooth and rudimentary second tooth (two thin slightly curved pleural rods); retrocerebral sac, subcerebral glands and eyespot (at posterior end of brain) present; male known.

Total length 175–250 µm; toes 22–28 µm; trophi 30–35 µm (manubria 18–23 µm, fulcrum 18–21 µm; rami 12–14 µm) male total 139 µm; toes 20 µm.
*Ecology:* Cosmopolitan in periphyton in littoral of flowing and standing waters. Single early record from N.S.W., and a Sept. 1990 record from Ryans 1 Billabong at Wodonga, Vic.
*Literature:* Koste 1978; Shiel & Koste 1979.

### *Notommata doneta* Harring & Myers

FIG. 23:3

*Notommata doneta* Harring & Myers, 1924, p. 448–50, Fig. 22: 1–4.

*Type locality:* Starvation Lake, Vilas County, Wisconsin.
*Holotype:* Not designated. ?Myers Coll., AMNH, N.Y.
*Description:* Body transparent; prominent tail with rounded median lobe; foot with two short joints; toes ca. 1/6 total length; corona extends to small chin; mastax virgate, trophi nearly symmetric; rami broadly triangular in ventral view, armed on inner margins with ca. 12 minute teeth; fulcrum long, slender, slightly curved distally; unci with well developed main tooth and rudimentary second tooth; left uncus with seven small accessory teeth, right uncus with six; manubria long, slender, with small basal plate; pleural rods and two slender epipharyngeal rods present; retrocerebral and subcerebral glands large. Distinguished from close relatives (*aurita, cyrtopus*) by long, peculiar toes.
*Ecology:* In *Sphagnum*, periphyton on submerged plants, Europe, N. America. A notommatid resembling *N. doneta* was collected from a humic pool adjacent to L. Strahan, W. Tas. 14.0°C, pH 5.55.

### *Notommata glyphura* Wulfert

FIG. 23:4

*Notommata glyphura* Wulfert, 1935, p. 590, Fig. 7a–e.

*Type locality:* pools near Merseburg, Germany.
*Holotype:* Not designated.
*Description:* Body with wide, plump abdomen; tail rounded; head and neck clearly defined; foot covered by tail (except distal end of terminal segment); toes straight, tapered to blunt tips; auricle of medium size; corona extends ventrally to form chin; retrocerebral sac brown to black; subcerebral glands long, wide; mastax large; trophi asymmetric; rami with hook-like alulae exceptionally long with inner margin teeth; unci plates with main and three secondary teeth on right uncus fused to rectangular plate; three preuncial teeth in front of main tooth; manubria dilated distally.

Length 325–500 µm; toes 20–24 µm; trophi 60–70 µm; male to 280 µm; resting egg (spiny) 115 × 150 µm.
*Ecology:* Europe, in fresh to brackish water, in littoral standing and flowing waters. Eats algae, rotifers, scavenges dead microcrustacea. Recorded from billabongs of the Goulburn and Murray, Vic. 13.0–17.8°C, pH 6.2–7.2, DO 8.9 mg $l^{-1}$, 74 µS $cm^{-1}$, 8 NTU, also from Nankeen Billabong, Magela Ck, N.T.
*Literature:* Koste 1978, 1981.

### *Notommata pachyura* (Hudson & Gosse)

FIG. 24:1

*Copeus pachyurus* Hudson & Gosse, 1886: 2, p. 31, Fig. 16:4.
*Notommata pachyura*: Harring 1913, p. 79.

*Type locality:* pools, Sandhurst, England.
*Holotype:* Not designated.
*Description:* Body fusiform, transparent; anterior sutures distinct; lobulate tail projects over first foot joint; foot 2-segmented with small papilla between toes; toes long (ca. 1/12 total length), conical; auricles large, stout; post-oral chin prominent; mastax virgate, strongly asymmetric; fulcrum long, stout, posterior cross section Y-shaped; right ramus with broad lamellar tooth, left with socket; alulae large, also asymmetric; unci with one main and four secondary teeth on left, one main and three secondary on right; two sigmoid pleural rods; somewhat quadrangular oral plate present; foot glands long; retrocerebral sac extremely long, clear; subcerebral glands small; large eyespot at posterior end of brain.

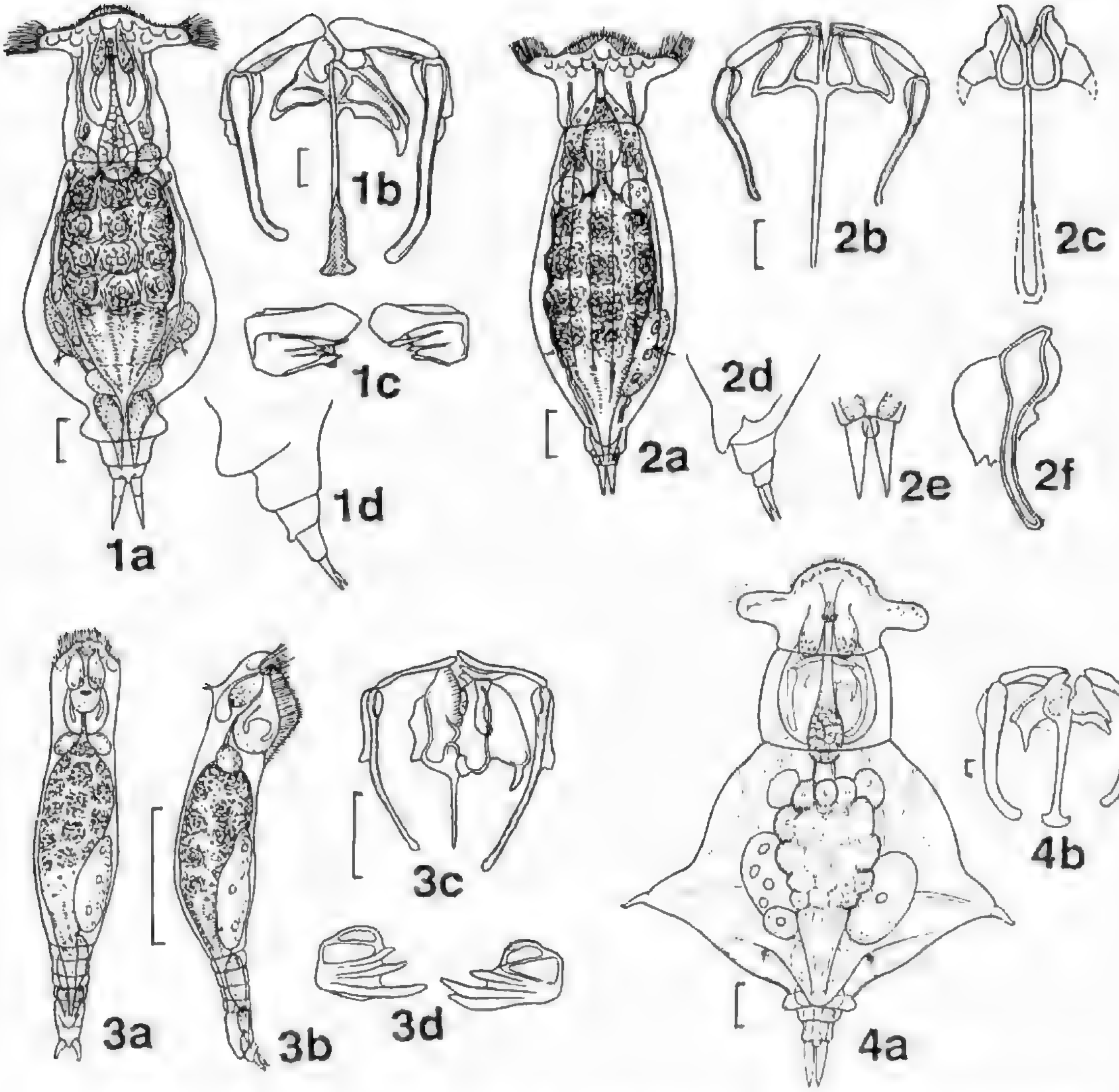


Fig. 24. 1, *Notommata pachyura* (Gosse): (a) dorsal; (b) trophi, ventral; (c) unci; (d) foot and toes, lateral. 2, *N. pseudocerberus* De Beauchamp: (a) dorsal; (b) trophi, ventral; (c) fulcrum & rami, lateral; (d) foot and toes, lateral; (e) toes, dorsal, (f) manubrium. 3. *N. silpha* (Gosse): (a) dorsal; (b) lateral; (c) trophi, ventral; (d) unci. 4, *N. spinata* nom. nov. (a) dorsal; (b) trophi, ventral. 1, 2a, b, d, 3 after Harring & Myers (1922); 2c, e, f after Donner (1954); 4 after Koste (1981). Scale lines: adult 50 μm; trophi 10 μm.

Total length 300–800 μm; toes 35–75 μm; trophi 75–102 μm; male 300 μm.
*Ecology:* Cosmopolitan in aquatic plants of littoral of pools, floodplain waters etc., in *Sphagnum*. Eats desmids, occasionally nematodes and rotifers. Early records from N.S.W., Qld, Vic. In our samples, N.T. and Tas. 14.7°C, pH 6.5, 23.2 μS cm$^{-1}$.
*Literature:* Koste 1978; Koste & Shiel 1986.

### *Notommata pseudocerberus* Beauchamp
### FIG. 24:2

*Notommata pseudocerberus* Beauchamp, 1908, p. 400.

*Type locality:* ?France.
*Holotype:* Not designated.
*Description:* Body slender, integument 'leathery', striated; tail has small tonguelike rounded median

lobe, two lateral lobes; foot two-segmented, toes conical, slender, ca. 1/12 body length; corona extends down ventral side for ca. 1/4 body length; rostrum above mouth, slight chin below; auricles long, robust; mastax virgate, simple; fulcrum long slender; rami broad, lamellate, without denticulation on inner edges; unci with single slender tooth, 4–5 accessory denticles on either side; pleural rods present; salivary glands vestigial; retrocerebral and subcerebral glands large.

Total length 400–680 µm; toes 30–35 µm; trophi 45–56 µm (fulcrum 24–27 µm).

*Ecology:* Cosmopolitan, rare finds in periphyton of littoral, standing and flowing waters. Preys on sessile ciliates. Single record from a stream near Bicheno, Tas. 19.0°C, pH 6.8, 215 µS cm$^{-1}$, 11 NTU.

*Literature:* Koste *et al.* 1988.

### *Notommata silpha* (Gosse)
### FIG. 24:3

*Diglena silpha* Gosse, 1887, p. 2, Fig. 1:2

*Notommata forcipata* In Hudson & Gosse, 1886: 2, p. 23, Fig. 18:1. [non-*N. forcipata* Ehrenberg, 1838].

*Notommata silpha:* Harring 1913, p. 79.

*Type locality:* ". . . the middle of Ireland".

*Holotype:* Not designated.

*Description:* Body elongate, fusiform distally with annular striae; foot rudimentary; toe apices curved lightly inwards and ventrally elevated; evertile ciliated auricles and chin absent; trophi prehensile without sucking function; fulcrum short, ventrally stick-like and laterally plank-like; rami bifurcate, asymmetric (Fig. 24:3c); unci with three large teeth, nearly symmetrical, clubbed at tips; ventral basal lamella of manubria with hood-like process; retrocerebral sac rarely with bacteroids; subcerebral gland absent.

Total length 160–200 µm; toes 8–10 µm; trophi 24 µm.

*Ecology:* Isolated records from Nearctic and Palaearctic in periphyton and in dystrophic waters. Single unconfirmed early record from N.S.W.. Not seen in our material.

*Literature:* Koste 1978; Shiel & Koste 1979.

### *Notommata spinata* nom. nov.
### FIGS 24:4; 25

*Notommata pachyura* f. *triangulata:* Koste 1981, p. 121, Fig. 16a–e, 18.

*non-Copeus triangulatus* Kirkman, 1906, p. 264, Fig. 12:1–2.

*Type locality:* Magela Creek, N.T., Australia.

*Holotype:* Not designated.

*Description:* Body laterally expanded into two distinct alae so that total width is only slightly less than total length (in preserved material alae may

Fig. 25. *Notommata spinata* nom. nov., photomicrograph.

exceed body length due to contraction of head and foot); lateral tips of each ala armed with stout triangular cusp (possibly retractible; partly contracted individuals may have alary tips withdrawn (Fig. 25); no dorsal "hump" (cf. *pachyura*); triangular tail commences at level of lateralantennae, distal end a blunt point at beginning of first foot joint; head and neck sutures distinct; two foot segment; toes conical, long, taper to point; corona ventral, "chin" present; lateral auricles with long swimming cilia; mastax modified virgate; trophi asymmetric; fulcrum expanded into fan at distal end, manubria curved posteriorly, dilated distally; retrocerebral sac long, extending past neck/abdomen suture; pigmented, subcerebral glands large; eyespot hemispherical at posterior of brain.

Total length 600–720 µm; toes 58–60 µm; trophi 140 µm (fulcrum 100 µm; rami 80/60 µm; unci 60/48 µm; manubria 116/100 µm).

*Ecology:* Recorded from billabong of Magela Ck, N.T. A similar form also occurs in W.A. (C.H. Fernando pers. comm.)

*Literature:* Koste 1981.

*Comment:* Koste's (1981) record of this taxon included figures and measurements but no

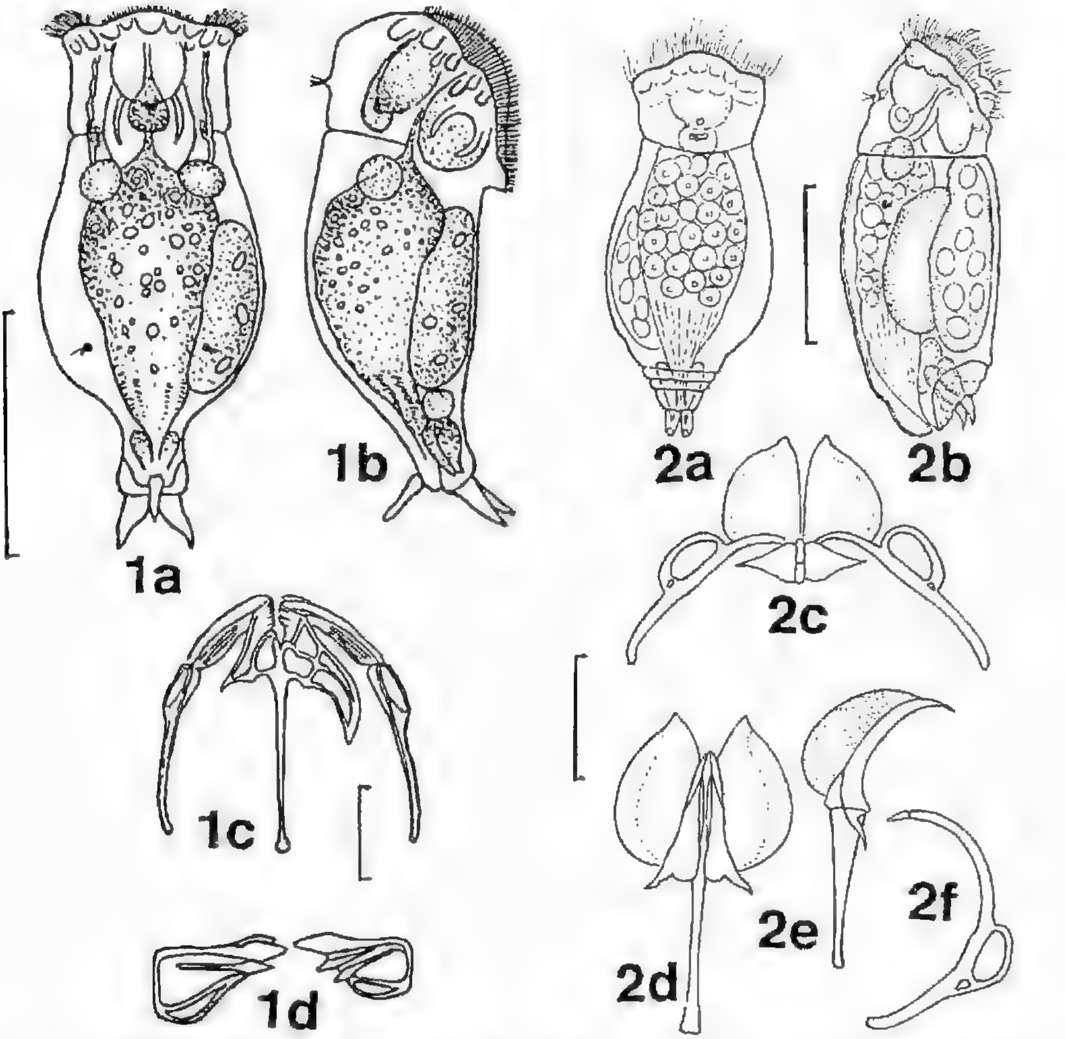


Fig. 26. 1, *Notommata tripus* Ehrenberg: (a) dorsal; (b) lateral; (c) trophi, ventral; (d) unci. 2, *N. tyleri* Koste & Shiel: (a) dorsal; (b) lateral; (c) trophi, ventral; (d) incus; (e) incus, lateral; (f) manubrium, lateral. 1 after Harring & Myers (1922); 2 after Koste & Shiel (1986). Scale lines: adult 50 μm; trophi 10 μm.

description. The above description must be considered provisional until more material is available, however its status as a distinct species rather than a form of *N. pachyura* is justified on the basis of the characteristic alae morphology, particularly the distal tooth, shorter toes, much larger trophi and a differences in trophi morphology. It differs from the winged taxon figured by Harring & Myers 1922: Fig. 43: 1–4 (*Copeus triangulatus* = *Notommata triangulata* (Kirkman, 1906).

*Notommata tripus* Ehrenberg
FIG. 26:1

*Notommata tripus* Ehrenberg, 1838, p. 434, Fig. 1:4.

*Type locality:* Berlin.
*Holotype:* Not designated.

*Description:* Body short, broad; integument rigid, transparent; head and neck form a single segment, dorsally humped; single transverse suture distinct; abdomen rounded posteriorly; projection carries tail and toes, no true foot present; dorsum has keeled appearance due to tapering of top half of abdomen from about 1/3 its length towards tail; rounded tail has spur-like projection with knobbed base, which projects about 1/3–1/2 the length of toes; toes relatively long (1/10 total length), straight, acutely pointed; auricles short, stout, ciliation continuous with corona; mastax virgate, trophi highly asymmetric; rami roughly triangular; right ramus minutely denticulate, left ramus with four blunt teeth; right alula of normal size; left alula hugely developed; unci teeth 3/3, one main tooth; manubria broad triangular lamellate proximally, distally slender curved rods; foot glands large, pyriform; retrocerebral sac almost spherical; eyespot at posterior end of brain.

Total length 150–200 μm; toes 16–20 μm; trophi 26–30 μm; caudal process 16–22 μm.

*Ecology:* Grazer of algae and periphyton, littoral vegetation. Europe, N. America. Rare: N.S.W., N.T., Tas. Vic.; 22.0–24.5°C, pH 5.7–6.4, 45.5–114 μS cm$^{-1}$.

*Literature:* Koste 1978; Koste & Shiel 1986.

### *Notommata tyleri* Koste, Shiel & Tan
FIG. 26:2

*Notommata tyleri* Koste, Shiel & Tan, 1988, p. 125–6, Fig. 15.

*Type locality:* Arthur's Lake, Tasmania, Australia.
*Holotype:* SAM V4110. Collected by R. J. Shiel 22.ix.87.

*Description:* Very small, stout species; body dilated distally to rounded rump; indistinctly segmented lobulate foot with two short, acutely pointed toes; mastax modified virgate; rami strongly convex on outer margins, no inner denticulation; fulcrum straight, spatulate distally; manubria slender, curved, with distinctive median ringlike fenestration; foot glands elongate, club-shaped.

Total length 120–139 μm; toes 12–16 μm; incus 19 μm; subitaneous egg 30–45 × 50–65 μm.

*Ecology:* Endemic. Free-living in Arthurs Lake, Tasmania. 8.0°C, pH 7.7, 17.4 μS cm$^{-1}$.

## Genus *Pleurotrocha* Ehrenberg, 1830

*Pleurotrocha* Ehrenberg 1830, p. 46.

*Type: Pleurotrocha petromyzon* Ehrenberg.
*Type locality:* Berlin.

Notommatid rotifers with short, stout illoricate body; head and neck clearly demarcated; foot long, cylindrical; toes short, conical; corona slightly oblique with ciliated circumapical band and lateral auricle-like tufts of long cilia for swimming; buccal field finely ciliate; mastax virgate, trophi simple; fulcrum long, rod-like; rami curved, triangular, not denticulate; manubria long with reduced basal plate; unci with only single tooth; hypopharynx large; no retrocerebral organ; eyespot single. Fourteen species are referred to this genus (Koste 1978). Only *P. petromyzon* is known from Australia.

### *Pleurotrocha petromyzon* Ehrenberg
FIG. 27:1

*Pleurotrocha petromyzon* Ehrenberg, 1830, p. 46.

*Type locality:* Berlin.
*Holotype:* Not designated.

*Description:* Body short, stout, abdomen wider than head; integument soft, transparent; constriction between neck and abdomen; abdomen pyriform, tapers posteriorly to base of foot; no tail; foot 2-segmented, basal square, distal twice basal segment length; toes short, conical; foot glands long with reservoirs; circumapical band of cilia and two lateral auricle-like tufts; mastax virgate, trophi simple; rami triangular with large rounded alulae; fulcrum very long slender rod, slightly expanded distally; unci triangular plates with one weak ventral and second rudimentary tooth; manubria slightly sigmoid with characteristic lobe projecting ventrally from 1/3 along its length; pleural rods present; no retrocerebral organ; eyespot minute at posterior end of ganglion.

Total length 220–480 μm; toes 20–26 μm; trophi 30–37 μm.

*Ecology:* Mass development after cladoceran "pulses" or in bacteria or protozoa blooms, in a wide range of fresh to brackish waters. Cosmopolitan. Necrophage – cleans out carapaces of dead mites and microcrustacea, also eats sessile ciliates. Rare, N.S.W., Tas., Vic. 12.0–26.0°C, DO 10.4, pH 6.4–7.7, 114–3330 μS cm$^{-1}$.

*Literature:* Evans 1951; Shiel & Koste 1979; Koste & Shiel 1986.

## Genus *Resticula* Harring & Myers

*Resticula* Harring & Myers, 1924, p. 518.

*Type: Furcularia melandocus* Gosse, 1887 = *Resticula melandocus* (Gosse)
*Type locality:* Woolston, England.

Very slender, fusiform illoricate body, tapering gradually from mid-length to base of toes; two toes short, with bulbous enlargement at base containing mucus reservoir; corona frontal or oblique with marginal wreath of short cilia and two lateral auricle-like tufts of long swimming cilia; buccal field ciliated; mastax virgate; fulcrum long, slender; rami triangular, symmetrical with right-angled median bend; unci with single well-developed tooth; epipharynx rudimentary or absent; two salivary glands; retrocerebral organ a small round ductless sac; eyespot a loose aggregation of red pigment granules in vacuoles of sac.

Seven species are recognized by Koste (1978); three of them are known from Australia.

### **Key to species of *Resticula* recorded from Australian inland waters**

1. Foot from end of abdomen to base of toes long (ca. 1/4 total length)........................*R. gelida* (Harring & Myers) (Fig. 27:2)

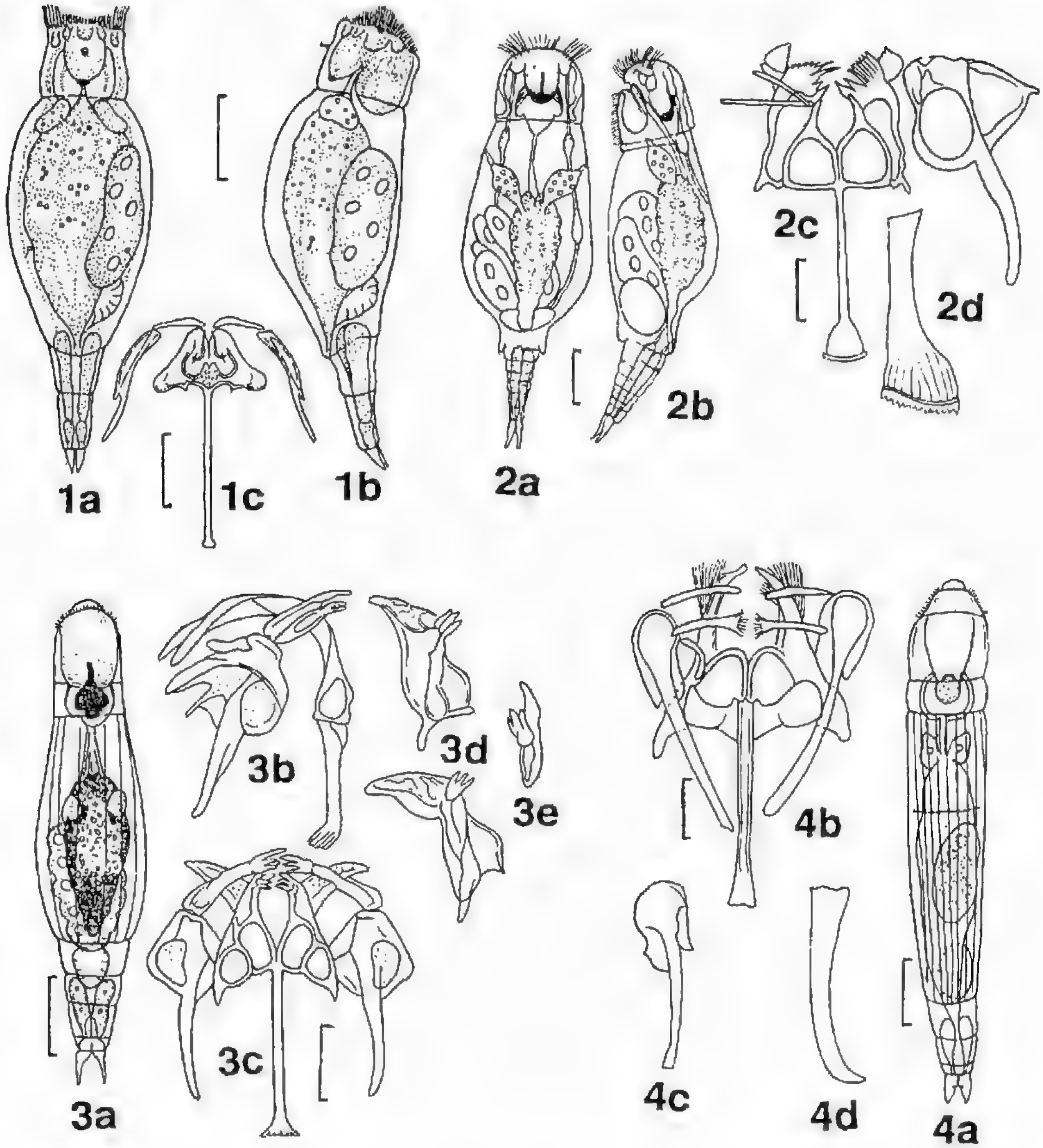


Fig. 27. 1, *Pleurotrocha petromyzon* Ehrenberg: (a) dorsal; (b) lateral; (c) trophi, ventral. 2, *Resticula gelida* Harring & Myers: (a) dorsal; (b) lateral; (c) trophi, ventral, right manubrium omitted; (d) fulcrum, lateral. 3, *R. melandocus* (Gosse): (a) dorsal; (b) trophi, lateral; (c) trophi, ventral; (d) different views of ramus; (e) uncus. 4, *R. nyssa* Harring & Myers: (a) dorsal; (b) trophi, ventral; (c) manubrium; (d) fulcrum. 1 after Harring & Myers (1924); 2 after Wulfert (1935); 3 after Wulfert (1939); 4 after Koch-Althaus (1962). Scale lines: adult 50 μm; trophi 10 μm.

Foot short and indistinct, less than length of toes ........................................ 2

2(1). Eyespot a mass of red pigment granules. ........................................ *R. nyssa* Harring & Myers (Fig. 27:4)

No eyespot discernible.......... *R. melandocus* (Gosse, 1887) (Fig 27:3)

### *Resticula gelida* (Harring & Myers)
FIG. 27:2

*Eosphora gelida* Harring & Myers, 1922, p. 642, Fig. 60:1-6.
*Resticula gelida:* Harring & Myers 1924, p. 519.

*Type locality:* Washington DC.
*Holotype:* Not designated. ?Myers Coll., AMNH, N.Y.
*Description:* Body fusiform; transparent cuticle with variable folding; abdomen occasionally conspicuously wide; head clearly defined; tail rudimentary; foot long (>3× toes), without segments; toes short (1/20 total length) tapering to obtuse tips; corona frontal, circumapical band interrupted dorsally; mastax modified virgate (for seizing prey); rami broad triangular; intricate supporting fenestrated framework of slender, round rods (Fig. 27:2c); fulcrum long and straight, spatulate at distal end for attachment hypopharynx muscle; unci reduced to single slender tooth with three small preuncial teeth on left and two on right; manubrium slender, curving slightly posteriorly with ventral lobe anteriorly and triangular dorsal lobe; retrocerebral organ small, has pigment granules, clustered at posterior end of ganglion where eyespot would be.

Total length 350–600 μm; toes 18–30 μm; trophi 45–75 μm (in 45 μm trophi, fulcrum 26 μm, unci 17 μm; manubria 32 μm); male 150–200 μm.
*Ecology:* Isolated occurrence in periphyton, still and slowly flowing water, Europe and Asia, N. America. Single record, from Yarnup Swamp, W.A. 17.0°C, 1800 μS cm⁻¹.
*Literature:* Koste *et al.* 1983.

### *Resticula melandocus* (Gosse)
FIG. 27:3

*Furcularia melandocus* Gosse, 1887, p. 2, Fig. 1:4.
*Resticula melandocus:* Harring & Myers 1924, p. 518.

*Type locality:* Woolston, England (lacustrine).
*Holotype:* Not designated.
*Description:* Body transparent, variable shape; cuticle thin, with longitudinal striae; foot 3–4 segmented; toes variable, bulbed at base; toe points curve inwards; single salivary gland to right of mastax; unci with single main tooth, left uncus with two preuncial teeth, right uncus with one; rami triangular in ventral view, right angle bend at midpoint toward dorsal surface; two large teeth in each ramus; manubria nearly straight, dorsal and ventral extensions are thin lamellae; pleural rods which support mastax during pumping action embedded in wall of mastax on each side, under upper ends of manubria.

Total length 210–320 μm; toes 25–37 μm; trophi 34–42 μm.
*Ecology:* Cosmopolitan in detritus-rich periphyton. Carnivorous on rotifers (particularly bdelloids) in littoral. Rare, N.T., Qld, Tas, Vic. 22.0–30.9°C, pH 3.4–5.4, DO 4.15 mg l⁻¹, 29.0–59.3 μS cm⁻¹.
*Literature:* Shiel & Koste 1979; Koste & Shiel 1983, 1986.

### *Resticula nyssa* Harring & Myers
FIG. 27:4

*Resticula nyssa* Harring & Myers, 1924, p. 521, Fig. 38: 1-4.

*Type locality:* Atlantic City, New Jersey.
*Holotype:* Not designated.
*Description:* Vermiform with longitudinal and transverse striae, head protrusion anteriorly corresponds to rostrum in other taxa; foot two jointed, very short, broad; toes short, with bulbous basal enlargement and claw-like tip; mastax modified virgate; fulcrum long, spatulate distally; rami triangular with large asymmetric alulae; basal apophysis prominent; three or four small teeth at apex of rami; unci with two teeth each, five accessory teeth on left uncus only; manubria long and slender; pleural rods slender, fibrillate at ends and fused to rami; pedal glands small pyriform; retrocerebral sac but no subcerebral glands; no true eyespot, but mass of red pigment granules occupy portion of sac.

Total length 300–630 μm; toes 14–21 μm; trophi 50–60 μm; male 160 μm.
*Ecology:* Periphyton, Europe, Asia, N. America. Acidophile. Single record: Lake Garcia, western Tas. 0.2.x.87. 17.0°C, pH 4.3, 98.3 μS cm⁻¹, 0.5 NTU, dark, humic water.
*Literature:* Koste 1978; Koste *et al.* 1988.

## Genus *Scaridium* Ehrenberg

*Scaridium* Ehrenberg 1830, p. 47.

*Type:* *Trichoda longicauda* Müller = *Scaridium longicaudum* (Müller).
*Type locality:* Copenhagen.

Body cylindrical or fusiform, partially loricate both dorsally and ventrally; neck behind dorsal antennae also with stiffened cuticle; foot very long, three-segmented, not retractable, with short basal-, long distal-segment; complex internal foot musculature to move very long, straight toes; corona oblique, with perioral buccal field and narrow dorsally-interrupted circumapical ciliation; dorsal and lateral antennae small; eyespot and retrocerebral organ absent; mastax rounded, trophi virgate; unci toothed plates, points offset; manubria widened proximally, hooked distally; fulcrum long, strong, distally spatulate; rami somewhat triangular with alulae, long pointed ends of which curve ventrally; each ramus with a long pointed tooth arising ventrally; epipharynx large, complex, reddish colouration resembles an eyespot; gastric glands large; separate stomach and intestine; male significantly smaller, with much shorter foot and toes, cerebral eye present; subitaneous egg hairy, resting egg spinulate.

Of the two described species, only *S. longicaudum* is known from Australia.

### *Scaridium longicaudum* (Müller)
### FIG. 28:1

*Trichoda longicauda* Müller, 1786, p. 216, Fig. 31:8–10.
*Scaridium longicaudum:* Ehrenberg 1830, p. 47.

*Type locality:* Copenhagen.
*Holotype:* Not designated.
*Description:* As for genus; toes almost as long as foot; unci lamellar plates with acute offset teeth; manubria proximally 'fish-hook' shape, distally almost right angled.

Total length 360–450 μm; foot 118–150 μm; toes 122–145 μm; trophi 48 μm (fulcrum 30 μm; rami 15 μm; manubrium 22 μm; ramus 16 μm); male 150 μm; subitaneous egg 50 μm.

*Ecology:* Cosmopolitan warm stenotherm, pH tolerant, swims slowly between macrophytes in shallow waters. Pancontinental, common in wide range of habitats. 8.0–22°C, pH 7.2–7.4, DO 9.2–9.6 mg $l^{-1}$, 60–1600 μS $cm^{-1}$, 8 NTU.

*Comment:* Distinguished from *Scaridium bostjani* Daems & Dumont (from Nepal) by larger size (>360 μm vs <288 μm) and wide tongue-shaped articulations of the manubria with the unci vs a pointed elongation in the Nepalese species. Detailed analysis of variants reported in the literature is lacking (Koste 1978), however it is likely that these represent more than ecotypic variations, i.e. a complex of species is involved.

## Genus *Taphrocampa* Gosse

*Taphrocampa* Gosse, 1851, p. 199.

*Type: Taphrocampa annulosa* Gosse.
*Type locality:* Leamington, England.

Notommatid rotifers, cylindrical or fusiform body with more or less distinct transverse plicae; corona oblique on anterior surface of head, with lateral ciliated auricle; mastax virgate with asymmetric trophi; fulcrum, long slender; rami approximately hemispherical; manubria long, slender with rudimentary basal plate; unci with 2–3 narrow teeth; well developed hypopharynx muscle; rami with large alulae. Two of the four species listed in Koste (1978) are known from Australia.

### Key to species of *Taphrocampa* recorded from Australian inland waters

1. Body generally <200 μm; toes <15 μm ........ ........................ *T. annulosa* Gosse (Fig. 28:2)
   Body >220 μm; toes >25 μm.......... *T. selenura* Gosse (Fig. 28:3)

### *Taphrocampa annulosa* Gosse
### FIG. 28:2

*Taphrocampa annulosa* Gosse, 1851, p. 199.

*Type locality:* Leamington, England.
*Holotype:* Not designated.
*Description:* Movement sluggish, creeping, gliding; body stocky may be thin when extended; three head "segments"; dorsum of same appearance as *T. selenura;* seen laterally more or less coarsely serrated; ciliary auricles rarely extended; short, indistinct, small tooth on inner margin of left ramus may be present; no basal apophyses.

Total length 130–230 μm; toes 11–15 μm; trophi 25–26 μm.

*Ecology:* Cosmopolitan in detritus rich periphyton (littoral). N.S.W., N.T., Qld, Vic.
*Literature:* Koste 1978, 1981; Shiel & Koste 1979.

### *Taphrocampa selenura* Gosse
### FIG. 28:3

*Taphrocampa selenura* Gosse, 1887, p. 1, Fig. 1:1

*Type locality:* England, not specified. Lacustrine.
*Holotype:* Not designated.
*Description:* Body elongate, cylindrical, tapering to foot; integument "leathery". Dorsally with transverse plications usually 10–12; ventral surface less distinctly plicate; tail separated from abdomen by transverse groove; toes long, tapering, decurved, form semicircle (viewed dorsally); left side of trophi more developed than right; piston muscle attached to end of fulcrum; left ramus with blunt tooth on inner edge, lamellar plate behind this, then two large teeth (Fig. 22:3c), right ramus with eight rudimentary teeth, left uncus with large ventral tooth and smaller second tooth; right uncus one large and two small; manubria have subsquare basal plates with straight posterior branch and terminal expansions.

Total length 220–290 μm; toes 25–33 μm; trophi 36 μm.

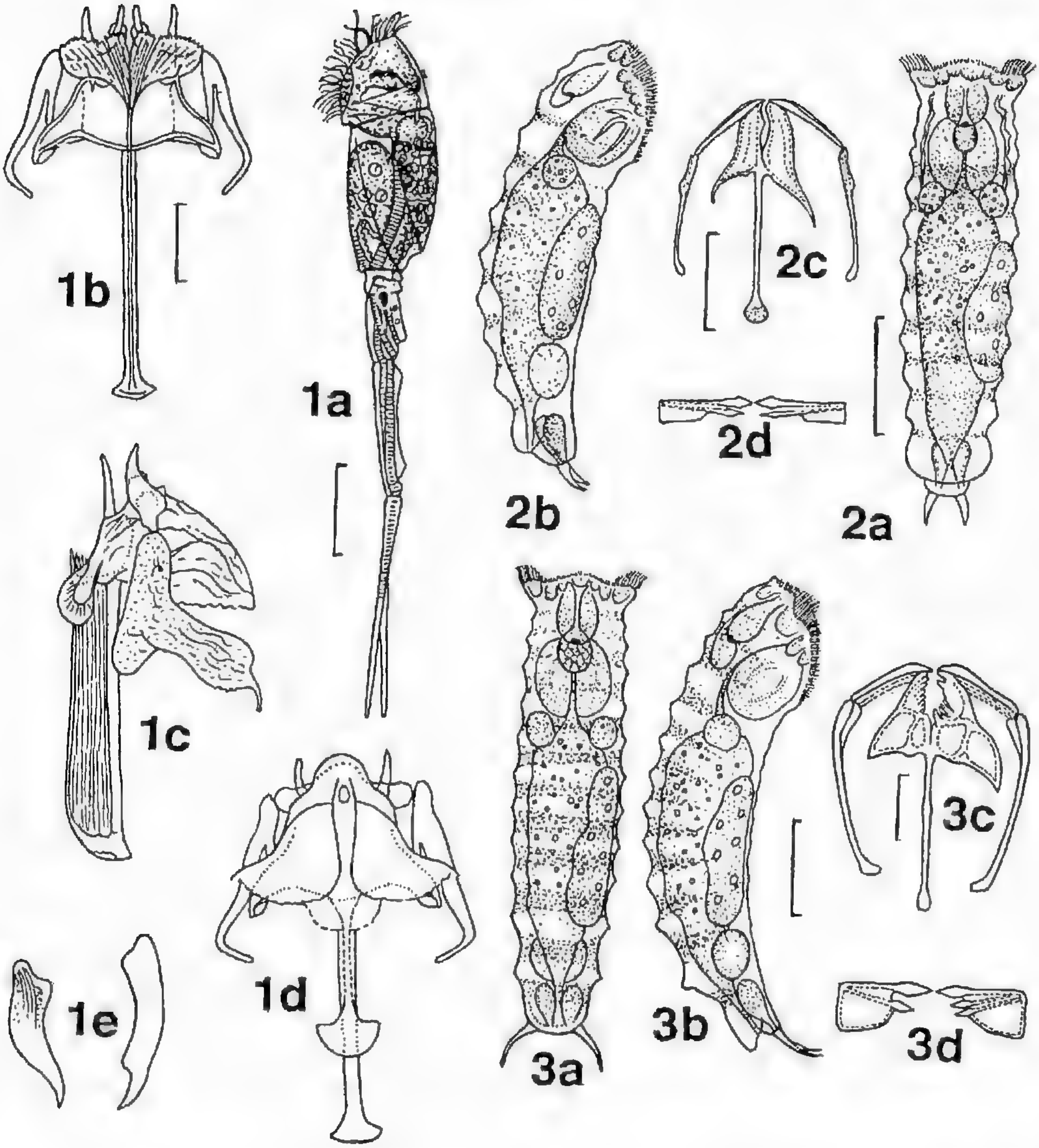


Fig. 28. 1, *Scaridium longicaudum* (Müller): (a) lateral; (b) trophi, ventral; (c) trophi, lateral; (d) trophi, dorsal; (e) two views of uncus. 2, *Taphrocampa annulosa* Gosse: (a) dorsal; (b) lateral; (c) trophi, ventral; (d) unci. 3, *T. selenura* Gosse: (a) dorsal; (b) lateral; (c) trophi, ventral; (d) unci. 1 after Donner (1943); 2, 3 after Harring & Myers (1924). Scale lines: adult 50 μm; trophi 10 μm.

*Ecology:* Cosmopolitan in detritus rich periphyton and eutrophic decomposition areas. Rare, N.S.W., N.T.
*Literature:* Shiel & Koste 1979, Koste 1981.

### Genus *Rousseletia* Harring

*Rousseletia* Harring, 1914, p. 393.

*Type: Rousseletia corniculata* Harring, 1914 (Fig. 29).
*Type locality:* Kenilworth, DC, U.S.A.

Small stout illoricate body; slight constriction between head and abdomen; tail large, collar-like, projects over long foot; foot has dorsal seta, may be broken off; two short conical toes on ventral side of foot tip; corona terminal with circumapical ciliation; two papillae project from unciliated apical plate; buccal field semicircular, ciliated, with mouth near ventral edge; mastax disproportionately large (ca. ⅓ body length), of specialized virgate type; fulcrum spatulate distally; rami large, domed, without marginal denticulation; manubria simple curved rods with ventral spur; unci absent; rod shaped epipharynx present; eyespot large, cervical; retrocerebral sac large, filled with highly refractive granules; large stomach extending to blind sacs on either side of mastax; no intestine; gastric glands small; foot glands club-shaped.

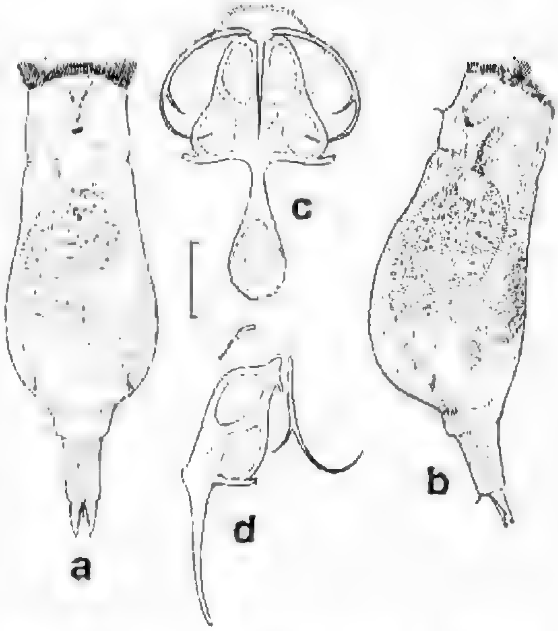


Fig. 29. *Rousseletia corniculata* Harring: (a) dorsal; (b) lateral; (c) trophi, ventral; (d) trophi, lateral. After Harring & Myers (1924). Scale lines: adult 50 μm; trophi 10 μm.

*Rousseletia* is not positively identified from Australia. Sudzuki & Timms (1977) listed a rotifer identified as *Russelletia* [sic] *parroti* Russell from Myall Lake, N.S.W. No description or figures were provided. If this is the rotifer described by Russell (1947), it was referred to the genus *Lindia* (Lindiidae) (see Koste & Shiel 1990b). We regard the record as *incertae sedis*, but include the generic description should the Myall Lake rotifer be encountered again.

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______ (1960) Die Rädertier saurer Gewässer der Dübener Heide. II. Die Rotatorien des Krebsscherentümpels bei Winkelmühle. *Ibid.* **56**, 311–333.

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## Note added in proof

The status of *Lindia parrotti* Russell (see Koste & Shiel 1990b: 141) = *Russelletia parrotti* (Russell) in Sudzuki & Timms (1977) was resolved after this paper was completed. Mr Phil Parr of Levin, N.Z., sent us the photograph of Russell's *Lindia parrotti* missing from our copies of the original description. Mr Jordi De Manuel, University of Barcelona, sent a copy of the description of *Russelletia* Sudzuki (1959), erected to accommodate *L. parrotti*

Mrs La-orsri Sanoamuang, Department of Zoology, University of Canterbury, Christchurch, collected at the type locality (Lake Victoria) a population resembling *parrotti* as figured by Russell, and checked the type collection of the Canterbury Museum for Russell's material. We thank these people for their efforts.

The type material could not be located, but from trophi analysis and comparative photographs of the Lake Victoria rotifers, we consider *Lindia parrotti* a junior synonym of *Proalides tentaculatus* De Beauchamp, 1907.

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# COASTAL ABORIGINAL SHELL MIDDENS AND THEIR PALAEOENVIRONMENTAL SIGNIFICANCE, ROBE RANGE, SOUTH AUSTRALIA

*BY JOHN H. CANN*, PATRICK DE DEKKER** & COLIN V. MURRAY-WALLACE†*

## Summary

Two superposed and stratigraphically distinct shell deposits, located at the seaward edge of Robe Range within Little Dip Conservation Park, southeastern South Australia, are identified as Aboriginal middens. The lower midden consists of *Katelysia* shells and megascopic charcoal, within a terra rossa soil, developed on calcarenite of the Pleistocene Bridgewater Formation. Radiocarbon dates of 8270± 80yr cal B.P. and 7910± 140yr cal B.P. were obtained for charcoal and shell respectively. Amino acid racemisation values confirm an early Holocene age for the *Katelysia* shells and also suggest relatively recent exhumation of the midden materials. The upper midden consists of *Turbo* shells, flint fragments and finely comminuted charcoal within a Holocene sand dune. A radiocarbon date of 470±160yr cal B.P. was obtained for these shells. Amino acid racemisation values confirm that the *Turbo* shells are only slightly older than modern. The midden features, and their established timeframes, together conform to the constraints of the time-cultural archaeostratigraphic Early Horizon and Late Horizon of Aboriginal sites in southeastern South Australia. Accordingly, the middens site is here proposed as a type archaeological locality and type archaeostratigraphic section for the Luebbers Early Horizon and Late Horizon time-cultural units. Shells of the older midden were probably derived from an intertidal marine lagoon that occupied the low lying corridor between the Robe and Woakwine ranges at the culmination of the Holocene transgression. Alternatively, near the peak of Holocene sea level, a similarly protected sandy environment may have hosted *Katelysia* seawards of Robe Range. Shells of the younger midden are equivalent to those extant on the rocky shoreface of Robe Range. The established time difference between the two episodes of human occupation of the site provides a valuable timeframe for Holocene geomorphic changes within the study area.

KEY WORDS: amino acid racemisation, Australian Aborigine, archaeostratigraphy, Early Horizon, Late Horizon, Holocene, Pleistocene, Bridgewater Formation, St Kilda Formation, Glanville Formation, radiocarbon, Mollusca, midden, Robe, Woakwine, South Australia

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CANN, J. H., DE DECKKER, P. & MURRAY-WALLACE, C. V. (1991) Coastal Aboriginal shell middens and their palaeoenvironmental significance, Robe Range, South Australia. *Trans. R. Soc. S. Aust.* 115(4), 161-175, 29 November, 1991.

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KEY WORDS: amino acid racemisation, Australian Aborigine, archaeostratigraphy, Early Horizon, Late Horizon, Holocene, Pleistocene, Bridgewater Formation, St Kilda Formation, Glanville Formation, radiocarbon, Mollusca, midden, Robe, Woakwine, South Australia

## Introduction

This paper is primarily concerned with sediments and landforms that resulted from the Holocene transgression in southeastern South Australia, and with the impact of that transgression on populations of coastal Aboriginal people. The investigation is centred on areas close to the town of Robe and includes the Robe and Woakwine ranges and the low lying inter-dune corridor (Fig. 1). This area is part of the Robe-Naracoorte coastal plain, which provides a unique record of Quaternary sea level changes. Successive high stands of sea level resulted in the construction of beach/dune barrier complexes on a steadily uplifting coastal plain. The result is a series of low altitude ranges, approximately parallel to each other, and to the present coastline, and generally increasing in age landwards.

The Holocene sea transgressed the continental shelf and reached present sea level about 7000yr B.P. Unconsolidated, mostly bioclastic carbonate sands were driven shorewards by the persistent high energy waves of the southern ocean, and redistributed by the wind to form a blanket of transgressive dunes. Sea water flooded the low lying corridor between the late Pleistocene Robe and Woakwine ranges, thus forming a sheltered coastal lagoon. Subsequent coastal sedimentation, upwards shoaling of lagoon sediments and continued uplift of the coastal plain has transformed the lagoon to a series of shallow lakes.

Late Pleistocene populations of Aboriginal people presumably lived on tracts of coastal land that are now inundated by the Holocene sea. Such populations, adapted to a gatherer economy in a coastal regime, would have moved landwards with the Holocene transgression. Thus, the oldest sites of Aboriginal occupation along the coast are contemporary with the peak of Holocene sea level and contain the remains of molluscan fauna harvested from the inter-range lagoon. Younger sites contain shells of molluscs which favour a rocky open ocean shoreface.

The palaeoenvironmental significance of these

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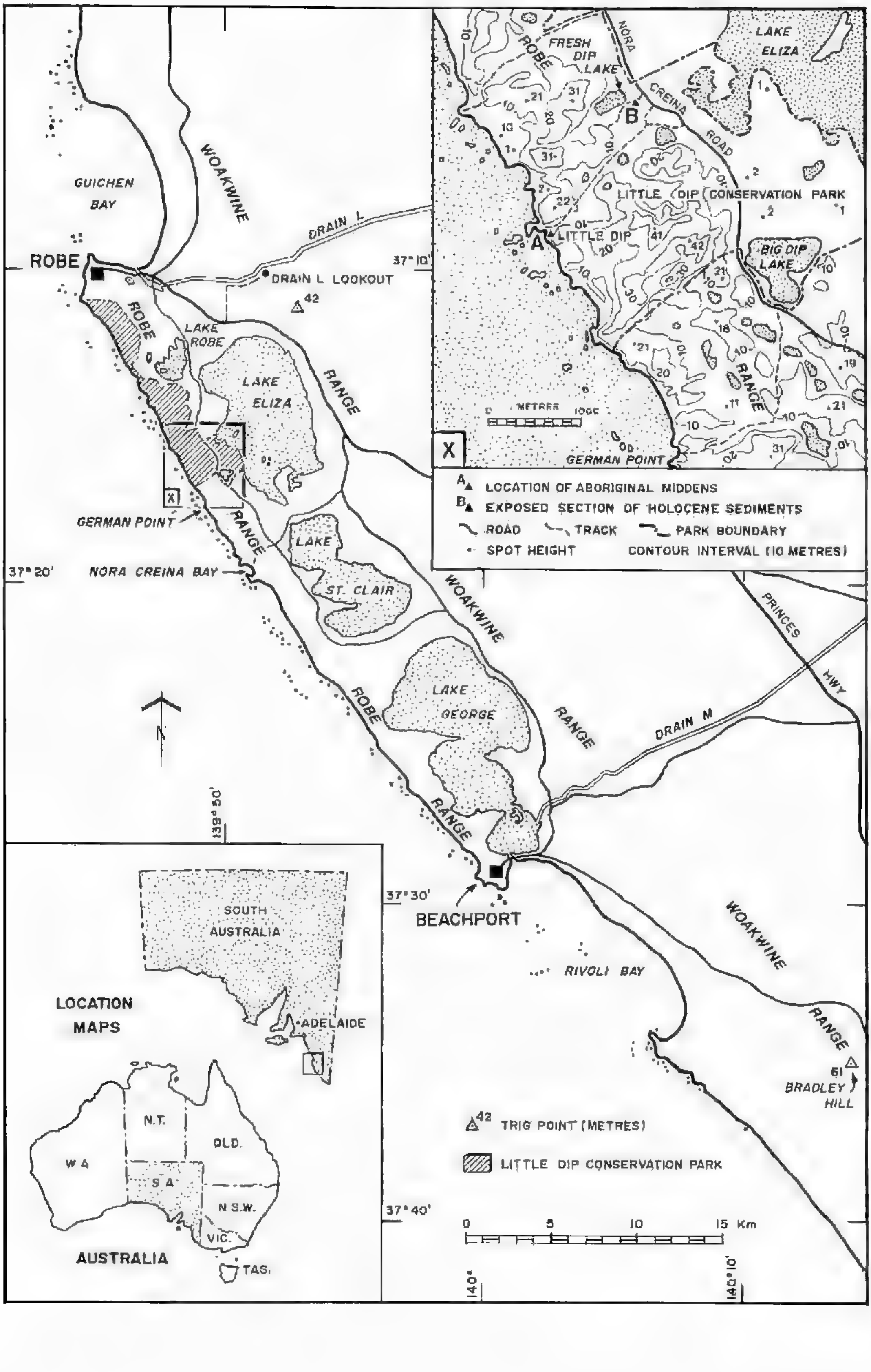
ROBE
GUICHEN BAY
WOAKWINE
DRAIN L
DRAIN L LOOKOUT
37° 10'
42
ROBE
LAKE ROBE
LAKE ELIZA
RANGE
X
GERMAN POINT
RANGE
LAKE ST. CLAIR
37° 20'
NORA CREINA BAY
WOAKWINE
N
ROBE
LAKE GEORGE
RANGE
DRAIN M
PRINCES HWY
RANGE
139° 50'
37° 30'
BEACHPORT
RIVOLI BAY
WOAKWINE
RANGE
61
BRADLEY HILL
37° 40'
42 TRIG POINT (METRES)
LITTLE DIP CONSERVATION PARK
0 5 10 15 Km
140°
140° 10'
LOCATION MAPS
SOUTH AUSTRALIA
ADELAIDE
N.T.
QLD.
W A
S A
N S.W.
VIC.
AUSTRALIA
TAS.
ROBE
FRESH DIP LAKE
NORA CREINA ROAD
LAKE ELIZA
B
LITTLE DIP CONSERVATION PARK
A
LITTLE DIP
BIG DIP LAKE
RANGE
METRES 1000
GERMAN POINT
X
A LOCATION OF ABORIGINAL MIDDENS
B EXPOSED SECTION OF HOLOCENE SEDIMENTS
ROAD
TRACK
PARK BOUNDARY
SPOT HEIGHT
CONTOUR INTERVAL (10 METRES)

middens is evaluated here within a timeframe of radiocarbon and amino acid racemisation (AAR) dates obtained from shells and charcoal.

## Previous investigations

### COASTAL ABORIGINAL OCCUPATION IN SOUTHEASTERN SOUTH AUSTRALIA

A mounting body of archaeological evidence suggests that aboriginal populations were established in southern Australia between 40,000 and 30,000yr B.P. (e.g. Allen 1989; Cosgrove 1989). From approximately 45,000 and 30,000yr B.P. in southern Australia sea levels fluctuated between -30 to -22m (Cann *et al.* 1988, in press). During the last glaciation sea levels were some 130 to 150m below present mean sea level (Chappell 1983; Chappell & Shackleton 1986), while the ensuing transgression reached present sea level 7000 to 6000yr B.P. It has been calculated that Holocene sea levels rose as rapidly as 1.5 to 2.4 cm/yr (Woodroffe *et al.* 1988; Belperio in press). This rise in sea level and the associated environmental changes are likely to have significantly affected those Aboriginal populations, with hunter/gatherer economies, reliant on coastal resources. It has been argued by some that this most recent and extreme rise in sea level would have forced all populations on the now submerged continental shelf to retreat inland (Ross 1985). It is clear that the earliest dates that can be expected for emergent sites of coastal aboriginal occupation in southeastern South Australia will approximate to the peak of the Holocene transgression.

The most comprehensive work detailing early Aboriginal sites in the southeast is that of Luebbers (1978)[1]. The significance of this largely unpublished study can be gauged by the extent to which it has been cited by other researchers (e.g. Pretty *et al.* 1983; Ross 1985; Head 1986; Godfrey 1988, 1989; Egloff *et al.* 1989; Bourman & Murray-Wallace 1990). Luebbers (1978)[1] established a chronology for Aboriginal occupation in the southeast, identifying two discrete episodes of occupation which he termed Early Horizon and Late Horizon. The term "horizon", in this context, is used in a time-cultural sense rather than in reference to the physical materials of the sites.

Aboriginal middens of the Early Horizon occur in terra rossa soils developed on exposed surfaces of late Pleistocene dunes, such as the Robe Range. Luebbers (1978)[1] described material from two such middens, one from Cape Martin and another from Bevilaqua Cliffs, about 5km southeast of Cape Buffon (Fig. 1). The Cape Martin site contained shells of *Katelysia* and *Mytilus*, charcoal and flint tools. Charcoal yielded a radiocarbon date which Luebbers considered questionable. The other site contained 'a small number of nondescript tools' together with shells of *Plebidonax* and charcoal. Dates of 8250±60 and 6350±100yr B.P. were reported for charcoal and shell respectively.

For these sites and another inland, Luebbers (1978)[1] remained unsatisfied with the stratigraphic control and believed it was possible that younger overlying material, perhaps from a more recent occupation, had been incorporated into the lower terra rossa soil. Thus, no specific site was designated as an archaeological type locality for his Early Horizon.

Late Horizon sites occur in unconsolidated sand and in places, such as at Bevilaqua Cliffs, may stratigraphically overlie an Early Horizon site. Luebbers (1978)[1] subdivided his Late Horizon into an Early Phase and a Late Phase. Middens of the Early Phase range in age from 5800 to 1300yr B.P., contain small numbers of tools and 'monospecific deposits of *Plebidonax* or *Brachidontes*'. Middens of the Late Phase are younger than 1300yr B.P., contain numerous flint implements and shells of *Turbo* (= *Subninella*) and other gastropods extant on southern Australian rocky foreshores.

Recent work by Egloff *et al.* (1989) in southeastern South Australia has revealed abundant *Turbo* shells in middens, dated by radiocarbon on charcoal, as old as 2560±120 and 3060±230yr B.P. These dates call into question the Luebbers (1978)[1] subdivision of the Late Horizon time-cultural unit on the basis of the types of shells preserved in coastal middens.

### GEOLOGIC AND GEOMORPHIC FRAMEWORK

The landscape of southeastern South Australia is characterised by a series of low altitude ranges, sub-parallel to each other and to the present coastline. Between Naracoorte and Robe thirteen geomorphically distinct ranges can be identified on the otherwise gently seawards sloping coastal plain (Sprigg 1952; Schwebel 1983). The region has undergone steady regional uplift of about 0.07mm/yr throughout the late Pleistocene (Schwebel 1983; Belperio in press). In general terms, the ranges are geomorphic features associated with palaeoshorelines and they increase in age away from

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[1] Luebbers, R. A. (1978) Meals and menus: a study in prehistoric coastal settlements in South Australia. Ph.D. thesis. A.N.U. Canberra, unpublished.

Fig. 1. Map of study area and surrounding region indicating locations of sites and features referred to in text

Robe towards Naracoorte. The geological origin of these features has been attributed to Quaternary sea level changes (e.g. Tindale 1933; Sprigg 1952; Cook *et al.* 1977; Schwebel 1978[2], 1983; Belperio in press). The ranges were termed 'stranded coastal dunes' by Sprigg (1952), though he recognised that at least some ranges had been constructed during several episodes of marine transgression and that they incorporated sediments of beach, dune and lagoonal palaeoenvironments.

Sediments composing the ranges are predominantly aeolian bioclastic calcarenites with some seaward horizons of shelly limestones in which the fossil molluscs can be associated with rocky foreshore sedimentation. This complex of Pleistocene sediments has been termed the Bridgewater Formation (Boutakoff 1963). Between the ranges closest to the present coastline, sediments are lagoonal and lacustrine bioclastic to muddy limestones. Fossil molluscs in the lagoonal sediments indicate clearly a variety of shallow subtidal and intertidal palaeoenvironments.

In the work reported here, the coastal Robe Range, the adjacent Woakwine Range, and the lagoonal sediments confined by these two features, provide an important geomorphic and palaeoenvironmental framework (Fig. 1).

*Woakwine Range*

The internal structure of Woakwine Range has been exposed in the Drain L and Woakwine cuttings, excavations through the range to effect drainage of wet lands to the northeast. These cuttings reveal a complex Quaternary stratigraphy which resulted from perhaps as many as five separate stands of high sea level. The deposits of each high sea level are separated by conglomerates, soils, calcretes and strong carbonate cementation (Schwebel 1983). Basal transgressive sediments in the Woakwine cutting consist of shelly and pebbly horizons that include flint cobbles, up to 10cm diameter, derived from the underlying Tertiary Gambier Limestone. These are overlain in turn by seaward dipping subtidal sands, beach sediments and landward dipping sands of the transgressive dune facies (Belperio in press).

In the Drain L cutting Sprigg (1952) observed that several exposed planes of marine erosion were immediately overlain by sediments containing 'a typical reef fauna' fossil assemblage (Fig. 2). Blocks of excavated shelly limestone, corresponding to this facies, can be observed today on the roadside overlooking this cutting. Significant faunal components are fossils of abalone and *Turbo* (Fig. 3), species which are characteristic of modern rocky foreshores. Sprigg (1952) deduced that the dune sediments had been substantially lithified during subaerial exposure. Thus they had remained as a coherent geomorphic feature and provided a rocky

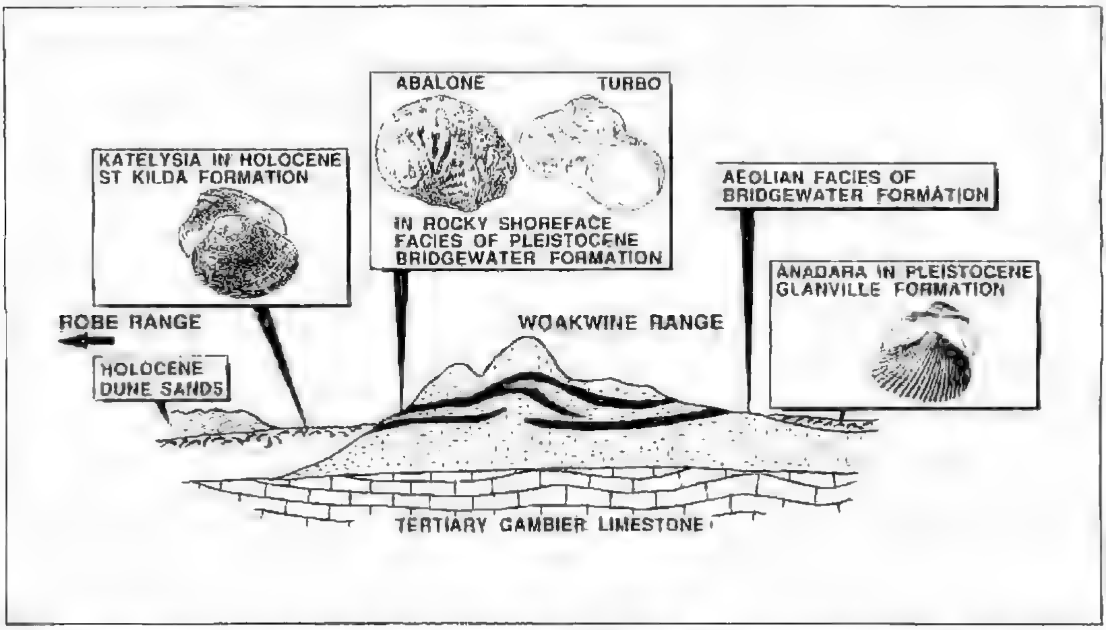

Fig. 2. Diagrammatic section through Woakwine Range (after Sprigg 1952) illustrating stratigraphic distribution of distinctive fossil molluscs. Both *Anadara* and *Katelysia* are characteristic of lagoon facies sediments.

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[2] Schwebel, D. A. (1978) Quaternary stratigraphy of the south east of South Australia. Ph.D. thesis, Flinders University, Adelaide, unpublished.

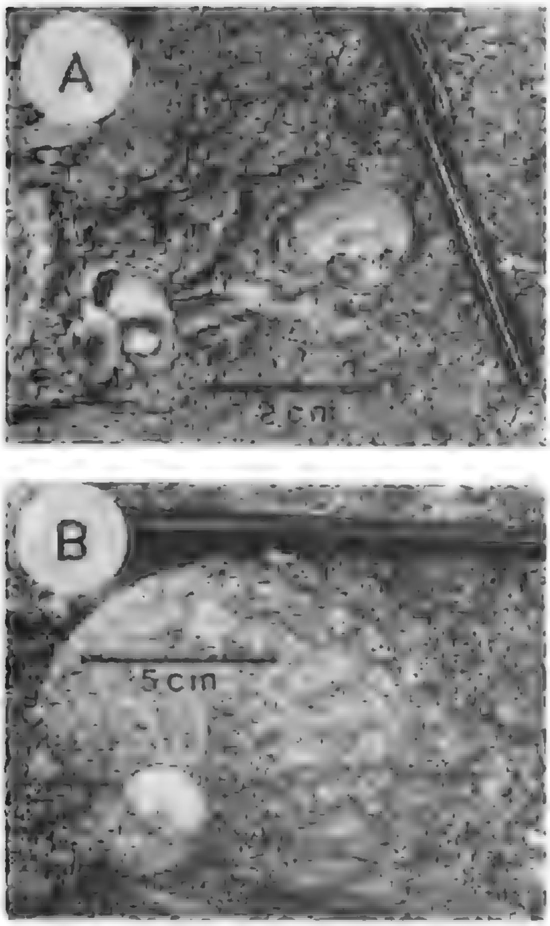


Fig. 3. Fossil gastropods within rocky shoreface facies of the Bridgewater Formation, Drain L cutting, Woakwine Range: A. *Turbo* shell B. Abalone shell.

substrate following marine inundation. On this basis he was able to recognise three episodes of marine regression followed by transgression in the construction of the Woakwine Range.

Fossils of the bivalve *Anadara trapezia* occur in some of the lagoonal sediments onlapping the landward side of Woakwine Range (Fig. 2). This species is characteristic of the late Pleistocene Glanville Formation (Cann 1978; Murray-Wallace *et al.* 1988a) and similiar marine sediments of earlier Pleistocene age (Murray-Wallace *et al.* 1988b).

*Robe Range*

Robe Range is the youngest of the emergent stranded coastal dunes. Within the study area it outcrops as an erosional rocky shoreline with numerous irregular stacks and islands in which aeolian bedding structures are clearly evident (Fig. 4). Basal sediments of this range rest unconformably on Tertiary Gambier Limestone 10-15m below present sea level and there are no horizons of fossiliferous rocky foreshore facies such as were recognised in the Woakwine complex (Sprigg 1952).

Schwebel (1983) identified three stages of development for Robe Range. The late Pleistocene constructional stages were equated with oxygen isotope sub-stages 5c and 5a. Equivalent marine sediments were deposited in Spencer Gulf at sea level maxima of -8m and -14m respectively (Hails *et al.* 1984). The most recent deposition has resulted from the Holocene transgression, during which there was extensive build up of dune sands over the older components of the Robe Range. These Holocene sands remain essentially unlithified.

*Inter-range sedimentation*

Despite the steady regional uplift, maximum sea level of the Holocene transgression was sufficient to flood the low lying corridor between the Robe and Woakwine ranges. Numerous road cuttings and other shallow excavations reveal a wealth of Holocene fossil molluscs characteristic of relatively protected (lagoonal) shallow subtidal and intertidal marine environments (Fig. 5). The floor of Lake Robe (Fig. 1), for example, is littered with the shells of oysters, scallops and cockles, particularly the intertidal *Katelysia*. These richly fossiliferous Holocene sediments belong to the St Kilda Formation, in the sense of Cann & Gostin (1985).

## Present Investigation

The work reported here centres on the Little Dip Conservation Park southeast of Robe (Fig. 1). The area includes coastal exposures of the late Pleistocene Robe Range (Fig. 4) and Holocene shell beds deposited in the low lying areas between the Robe and Woakwine ranges. These features are to a large extent covered by transgressive Holocene sand dunes, some of which are fixed by modern vegetation, while others are little vegetated and subject to present day erosion. The gastropod *Turbo* is extant on the rocky foreshore and its shells are easily collected at the waters edge (Fig. 6).

The Aims of the investigation are three fold:

1. to evaluate critically the cultural-chronostratigraphic concept adopted by Luebbers (1978)[1] within a framework of chronologic, palaeontologic and geomorphic investigation;
2. to propose a type section for the Early Horizon and Late Horizon cutural sites;
3. to document the palaeoenvironmental significance of the type area.

Fig. 4. Erosional rocky shoreface of Robe Range at Little Dip (Location A, Fig. 1).

## Observations and Methods

### ABORIGINAL MIDDENS

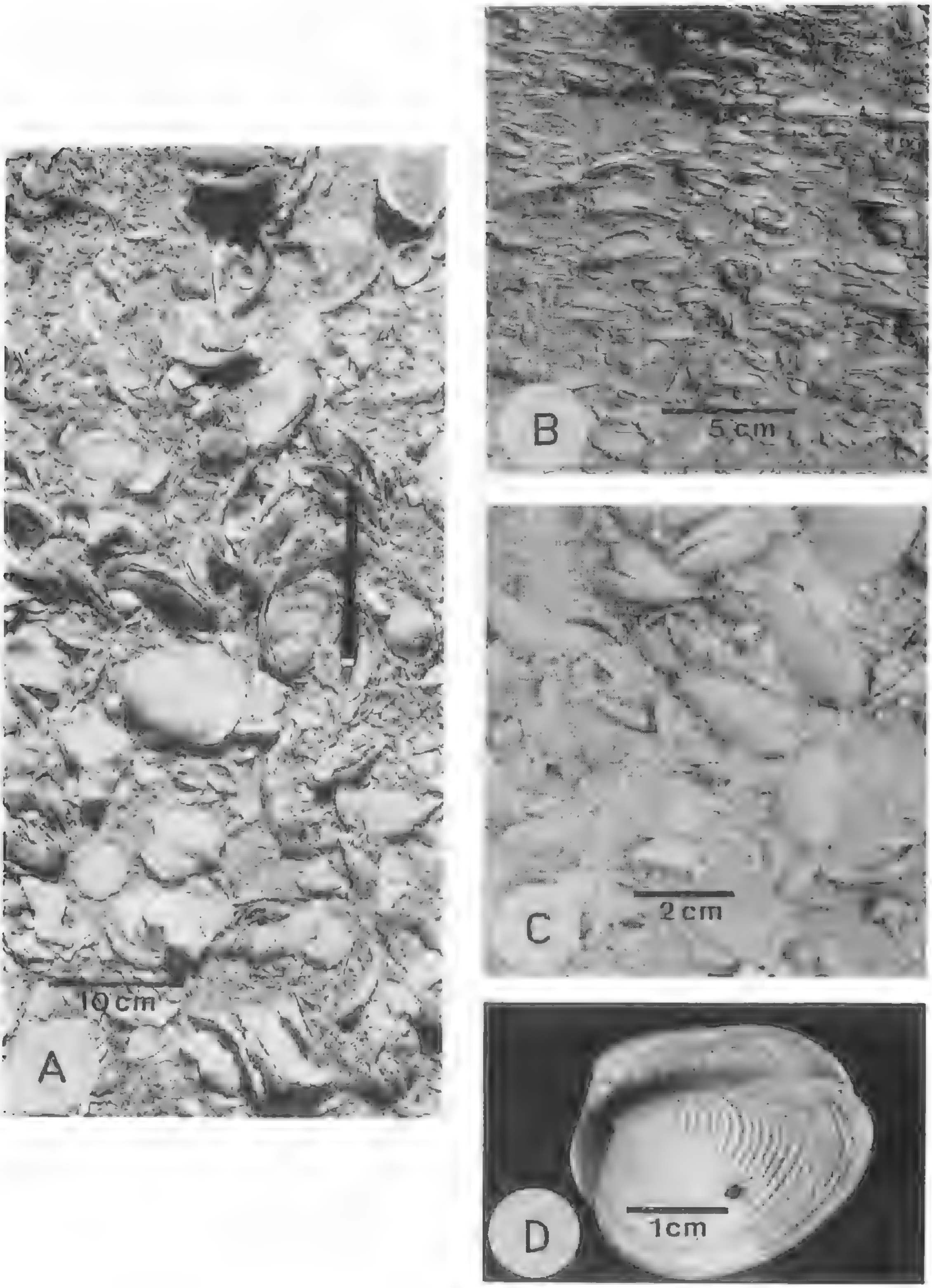
At the study site (Fig. 1, location A) a poorly vegetated coastal dune immediately overlooks the foreshore. The seaward side of this dune has been subjected to wind deflation and a lag deposit of abundant shells and opercula of *Turbo*, together with numerous fragments of flint, litters and surface (Figs 7A, B). Some opercula are chipped or fractured and are more numerous in some areas than others, as if selectively sorted. Above the lag deposit there are numerous conspicuous *Turbo* shells in a greyish, poorly consolidated horizon of the dune (Figs 7A, C). The shell and flint appear to have been derived from this layer which, on field evidence, is interpreted as an Aboriginal midden belonging to the Late Phase of the Late Horizon as defined by Luebbers (1978)[1]. Shell from this midden was taken for radiocarbon and amino acid racemisation dating.

On the landward side of the dune the Holocene sand sharply overlies a well consolidated red-brown terra rossa soil developed on the Bridgewater Formation of the Robe Range (Fig. 8A). Embedded within this palaeosol are numerous shells of the bivalve *Katelysia* and fragments of charcoal (Figs 8B, C; 9A, B). Although no flint fragments were observed, a human origin is also proposed for this material. This assertion is based on the following observations.

a. The shells are disarticulated, lack any preferred orientation and many are severely broken. It is difficult to imagine a natural sedimentary environment that would cause such fracturing of shells, but had they been naturally transported under conditions of high wave or current energy, the shells would have been deposited predominantly convex upwards and tightly imbricated and also show signs of attrition. Such a fabric can be seen in some of the Holocene shell beds between Robe and Woakwine ranges (Fig. 5B). Where shells have not been actively transported their valves usually remain more or less paired (Fig. 5C).

b. Characteristic 'drill' holes, inflicted by predatory gastropods, were not observed in any of the exposed

Fig. 5. Fossil molluscs of Holocene St Kilda Formation between Robe and Woakwine Ranges: A. Oyster shells on the floor of Lake Robe. B. Predominantly shells of *Katelysia*, disarticulated and convex upwards, signifying moderate energy transportation; small roadside excavation, Princes Highway. C. Predominantly shells of *Katelysia*, mostly articulated, signifying little or no transportation. An intertidal environment of deposition is inferred. (Location B, Fig. 1). D. *Katelysia* showing the characteristic "drill" hole inflicted by predatory gastropods. (Location B, Fig. 1).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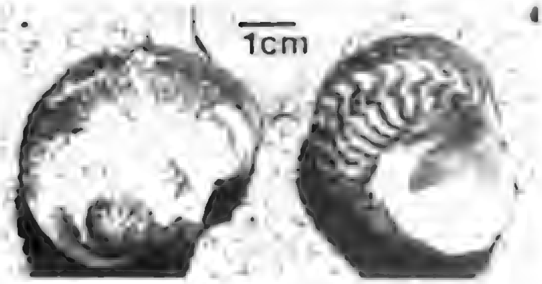


Fig. 6. Shells of *Turbo*, extant on the Rocky foreshore of Robe Range at Little Dip. (Location A, Fig. 1).

*Katelysia* valves, yet within the nearby Holocene shelly sediments such valves with 'drill' holes are numerous (Fig. 5D). Clearly some form of selective process has operated to eliminate bivalves affected by this type of predation. Selection also seems to have favoured larger individuals.

c. Sand enclosed by paired *Katelysia* valves from the Holocene lagoonal sediments was microscopically examined and found to contain species of Foraminifera also known from intertidal sandflats of Gulf St Vincent (Cann & Gostin 1985). Species included *Elphidium crispum, E. macelliforme* and *Miliolinella labiosa.* Gill *et al.*

Fig. 7. A. Lag deposit of *Turbo* shells and flint fragments apparently derived from stratum indicated by arrow. This deposit is interpreted as a Late Horizon Aboriginal midden. (Location A, Fig. 1). B. Flint fragments from the lag deposit. C. *Turbo* shells within the stratum indicated by the arrow in A.

(1991), used the abundance of Foraminifera in a shell deposit at Warrnambool to show that it was a natural estuarine deposit and not of human origin. Microscopic examination of the terra rossa matrix enclosing the *Katelysia* shells revealed no Foraminifera within the deposit under present discussion.

d. Stratigraphic elevation of the *Katelysia* deposit at the crest of Robe Range makes natural sedimentation implausible if these shells are to be correlated with those undisputedly deposited in the Holocene lagoon between Robe and Woakwine ranges. It is also possible that *Katelysia* could have occupied relatively sheltered intertidal seaward environments that probably existed immediately prior to the culmination of the Holocene transgression, a suggestion favoured by Luebbers (pers. comm. 1991).

(Although there is abundant charcoal, both within and surrounding the shell deposit, and unambiguously embedded within the terra rossa soil, there are no clear signs of localisation that might be easily interpreted as camp fires. Thus, for this site, the presence of charcoal does not necessarily, in itself, constitute evidence of human occupation).

Thus the deposit is interpreted as an Aboriginal midden belonging to the Early Horizon as defined by Luebbers (1978)[1]. Shell and charcoal from this midden were taken for radiocarbon assessment. Additional shell was taken for amino acid racemisation dating. Paired *Katelysia* valves from the nearest accessible deposit of Holocene lagoonal sediments (Fig. 1, location B), were taken for comparative AAR dating.

### DATING METHODS: RADIOCARBON DATING

Charcoal and *Katelysia* shell were carefully removed from the terra rossa matrix of the Late Horizon midden and packed in clean plastic bags. Similarly, *Turbo* shells were taken from the Early Horizon midden (Fig. 1, location A). These materials were forwarded to the radiocarbon laboratories of the Australian National University and the University of Sydney for radiocarbon dating. Conventional radiocarbon dating followed the methods of Gupta & Polach (1985).

### DATING METHODS: AMINO ACID RACEMISATION ANALYSES

The following materials were collected for AAR analysis for the purpose of age determination:

a. disarticulated shells of *Katelysia rhytiphora* and *K. scalarina* from the Early Horizon midden (Fig. 1, location A);

b. articulated shells of *K. scalarina* from Holocene lagoon sediments (= St Kilda Formation) within the Robe-Woakwine corridor (Fig. 1, location B);

c. articulated shells of *K. scalarina* from late Pleistocene lagoon sediments (= Glanville Formation) on the landward side of the Woakwine Range, exposed in a small quarry adjacent to Princes Highway;

d. shells of *Turbo* sp. from the Late Horizon midden, and from the immediately adjacent modern shoreface sediments (Fig. 1, location A).

AAR analyses were undertaken on all the collected shell materials. Data obtained from the *Katelysia* shells of the Early Horizon midden were compared and contrasted with the extent of racemisation in specimens obtained from the Holocene and late Pleistocene lagoon sediments. As the nature of racemisation kinetics in *Turbo* spp. shells is not well documented, the significance of AAR analysis of shells from the Late Horizon midden was assessed with reference to data derived from radiocarbon dating of an adjacent midden shell and AAR analysis of modern specimens.

Amino acid analyses were for the 'total acid hydrolysate', complex peptide mixture of varying molecular weights, and followed the methods outlined by Kimber & Griffien (1987). Analyses of the N-pentafluoropropionyl D, L-amino acid 2-propylesters were undertaken using a 25m fused silica Chirasil-L-Val capillary column and Hewlett Packard model 5890A gas chromatograph with a flame ionisation detector and helium carrier gas. The integrity of the analytical procedures undertaken using the AAR technique was evaluated by analysing international interlaboratory comparison samples of Wehmiller (1984a). Results were within two standard deviations of the grand mean of the international comparison.

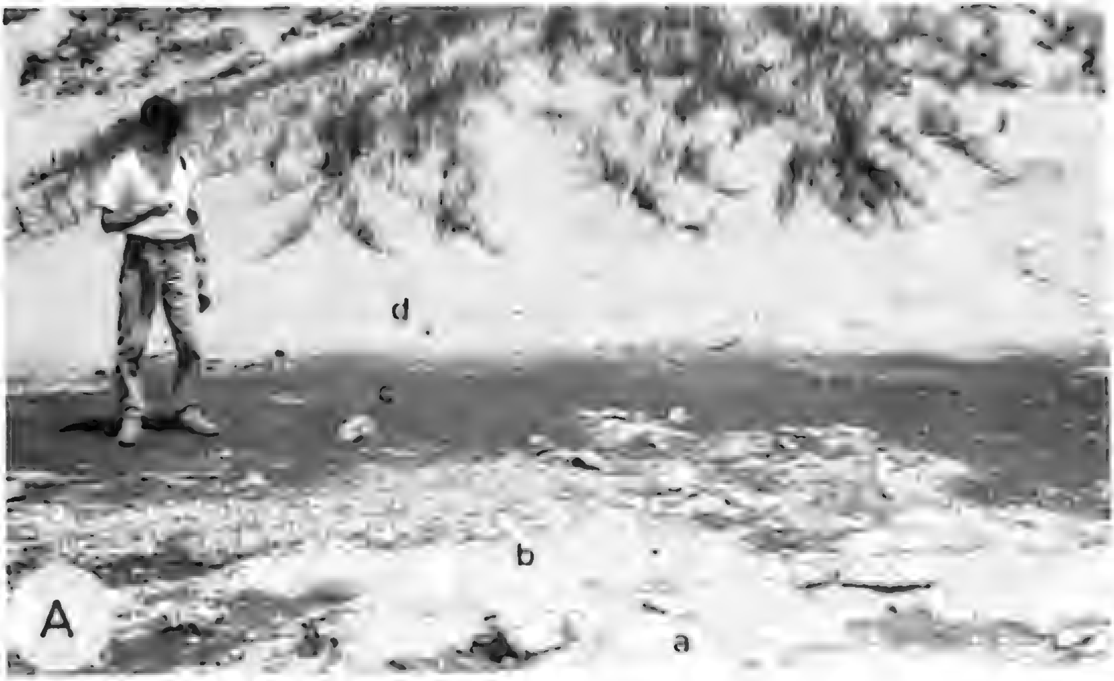
The hinge region of each *Katelysia* shell was analysed as the highest concentration of residual protein occurs within this region. The columella was analysed in the *Turbo* specimens. In excess of 20% by weight for each shell was analysed by AAR to reduce variability which may potentially arise when analysing small fragments (Wehmiller 1984b).

Amino acid D/L ratios were compared with calendric radiocarbon ages (cal B.P.), converted from marine reservoir corrected radiocarbon years (B.P.; Libby half-life) according to the methods outlined by Gillespie & Polach (1979) and Stuiver *et al.* (1986) (Table 1).

## Results

### RADIOCARBON DATES

Charcoal from the Early Horizon midden (lab. code ANU-7448) yielded a radiocarbon age of 8270±80yr cal B.P. *Katelysia* shell, also from the


A
a
b
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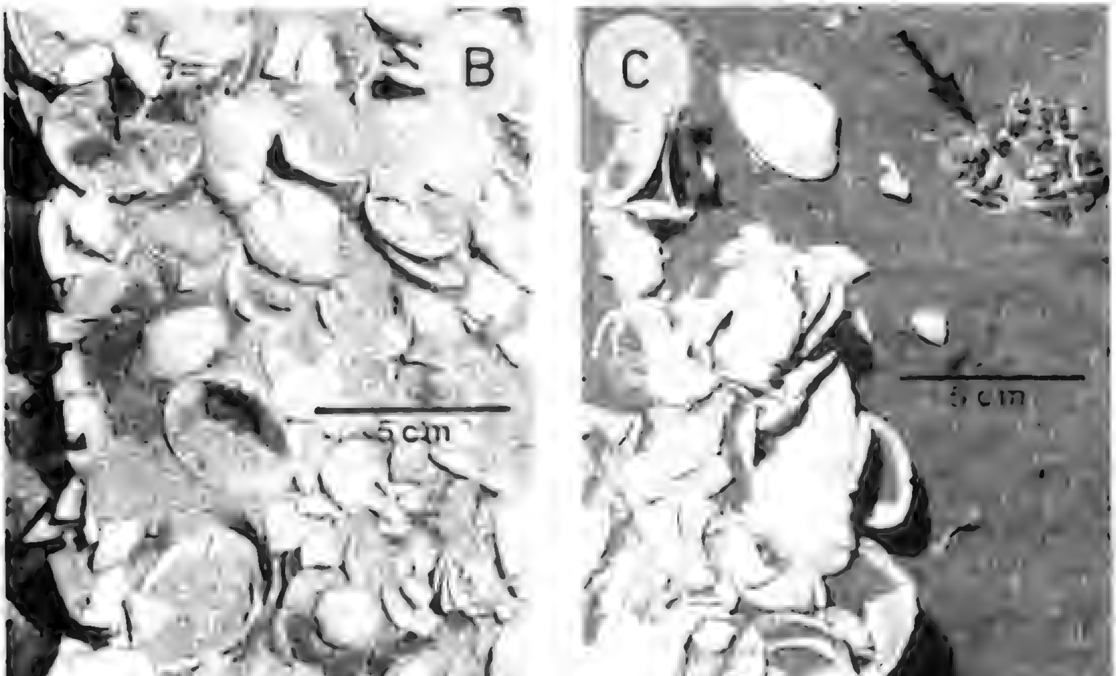
B
5 cm
C
5 cm

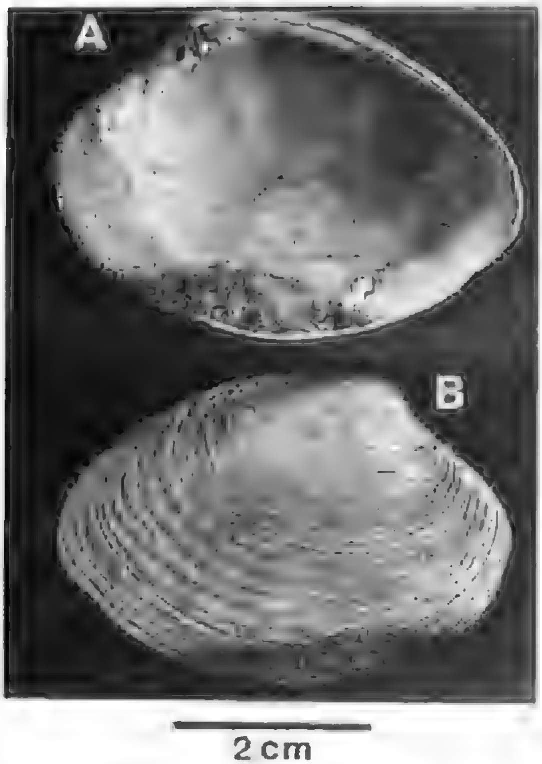

Fig. 9. Selected valve from the Early Horizon midden showing (A) internal and (B) external features of *Katelysia*.

older midden (lab. code SUA-2613), was determined to have a marine reservoir corrected age of 7910±140yr cal B.P. *Turbo* shell from the overlying Late Horizon midden (lab. code ANU-7447) had a radiocarbon age, again corrected for the marine reservoir effect, of 470±160yr cal B.P.

## AMINO ACID RACEMISATION ANALYSES

The relative extent and degree of racemisation for the different amino acides in *Katelysia* spp. and *Turbo* spp. is in accord with other radiocarbon dated Holocene fossils in southern Australia (for example, Murray-Wallace *et al.* 1988c; Murray-Wallace & Bourman 1990) and the theoretically predicted differential rates of amino acid racemisation (Table 1).

The similarity in extent of racemisation of amino acids in *Katelysia scalarina* obtained from lagoonal sediments and molluscs from the Early Horizon midden points to a common age given the assumption that they have experienced equivalent diagenetic temperature histories. The validity of this assumption is strengthened by the close proximity of these two sites. The location of the lagoonal facies close to the feather edge of the Holocene transgressive sediments, which have elsewhere been dated at approximately 7000yr B.P., also points to a common age for these two sites.

A calibrated radiocarbon age of 7910±140yr cal B.P. was obtained on *Katelysia* from the Early Horizon midden (Table 1). These data are significant, for they document Aboriginal coastal occupation during an early transgressive phase of the post glacial Holocene marine transgression. To evaluate the amino acid data of the Early Horizon midden, these results are compared with a sequence of similar age at Smoky Bay, Eyre Peninsula (Table 1). A z-score, according to the methods of Gupta & Polach (1985), indicates that these two calibrated radiocarbon dates are not significantly different at the 5% level (z-score of 1,55). Although contemporary mean annual temperatures (CMAT) between these two sites differ by approximately 2.2°C, it is unlikely that the diagenetic temperature differences will be detected for the Holocene record. In contrast, such temperature differences are significant for last interglacial fossils (for example, Murray-Wallace *et al.* 1991).

The similarity in extent of racemisation for the radiocarbon calibrated Holocene *Katelysia* from Smoky Bay indicates that the *Katelysia* shells of the Early Horizon midden were buried for a significant portion of their diagenetic temperature history. Had the shells been subaerially exposed for much of their diagenetic history, the extent of racemisation of amino acids would be significantly higher (compare Murray-Wallace *et al.* 1988c). The suggestion, independently based on AAR data, that the Early Horizon midden had been buried, then exhumed, is consistent with the geomorphic evidence of the site, that is, recent dune deflation. This clearly represents a novel application of AAR in the recognition of exhumed sequences.

The lower extent of AAR in *Turbo* sp. from the Late Horizon midden, than in *Katelysia* spp. from the Early Horizon midden, is consistent with a younger age, as independently determined by radiocarbon dating. However, as this is the first

Fig. 8 A. Early Horizon Aboriginal midden within terra rossa palaeosol on Bridgewater Formation, Robe Range. (Location A, Fig. 1). a. Karstified rocky outcrop of Bridgewater Formation. b. *Katelysia* shells of the Early Horizon midden. c. Terra rossa palaeosol. d. Holocene sand dune which includes the Late Horizon *Turbo* midden (Fig. 6). Note the sharp contact between this and the underlying terra rossa palaeosol. B. Detail of *Katelysia* shells within the midden. Note that shells are disarticulated, lack preferred orientation and none shows signs of gastropod predation. C. Detail of part of the midden in which charcoal, indicated by arrow, is embedded in the terra rossa palaeosol.

TABLE 1. *Extent of amino acid racemisation ('total acid hydrolysate') in late Quaternary Mollusca from the south east of South Australia.*

| Location/ description | Depth of burial (m) | Species | CMAT+ (°C) | Age PB* & [lab code] | Amino acid D/L ratio# VAL | LEU | ASP | PHE | GLU |
|---|---|---|---|---|---|---|---|---|---|
| Robe Beach | surface | *Turbo* spp. | 14.7 | modern | 0.02 ± 0.001 | 0.02 ± 0.004 | — | 0.03 ± 0.005 | 0.04 ± 0.01 |
| Robe midden (Late Horizon) | surface (exhumed) | *Turbo* spp. | 14.7 | (840 ± 80)<br>470 ± 160<br>[ANU-7447] | 0.04 ± 0.002 | 0.07 ± 0.01 | 0.18 | 0.12 ± 0.002 | 0.09 ± 0.01 |
| Robe midden (Early Horizon) | surface (exhumed) | *Katelysia* spp. | 14.7 | (7480 ± 70)<br>7910 ± 140<br>[SUA-2613] | 0.05 ± 0.01 | 0.09 ± 0.03 | 0.28 ± 0.01 | 0.22 ± 0.02 | 0.11 ± 0.01 |
| Robe/Holocene lagoon facies | 1 | *Katelysia scalarina* | 14.7 | — | 0.06 ± 0.02 | 0.08 ± 0.02 | 0.32 ± 0.01 | 0.16 ± 0.04 | 0.12 ± 0.01 |
| Woakwine Range/ Back barrier lagoon facies | >1 | *Katelysia scalarina* | 14.7 | last interglacial 125 000 | 0.20 ± 0.02 | 0.35 ± 0.01 | 0.54 ± 0.06 | — | 0.31 ± 0.03 |
| Smokey Bay, Eyre Peninsula/coastal sediments[1] | 1.82<br>1.88 - | *Katelysia rhytiphora* | 16.9 | (6940 ± 170)<br>7410 ± 290<br>[CS-450] | 0.08 ± 0.02 | 0.16 ± 0.02 | 0.23 | — | 0.10 ± 0.004 |

\+ C.M.A.T. — Contemporary mean annual temperature (atmospheric).

* Conventional radiocarbon age indicated in parentheses with associated error term (1δ). Marine reservoir corrected sidereal ages without parentheses with 2δ error term. See text for discussion on marine reservoir correction and calibration of radiocarbon ages to sidereal years.

\# amino acids: VAL — valine; LEU — leucine; ASP — aspartic acid; PHE — phenylalanine and GLU — glutamic acid. Error terms indicate analytical precision and intershell amino acid D/L ratio variation (1δ).

[1] data of Murray-Wallace *et al.* (1988c).

AAR analysis on *Turbo* spp. from southern Australia, it is not possible to evaluate critically the relation of the kinetics of racemisation in *Turbo* to the moderate racemisation rates that are characteristic of *Katelysia.* It is likely that racemisation rates vary between bivalves and gastropods, as noted by Miller & Brigham-Grette (1989). However, the small difference in extent of racemisation of amino acids between *Turbo*, of the Late Horizon midden, and *Katelysia*, of the Early Horizon midden, may also point to a history of subaerial exposure for the former.

The extent of amino acid racemisation in *Katelysia scalarina* from the back barrier lagoon facies of the Woakwine Range barrier complex is consistent with other last interglacial Mollusca (Murray-Wallace *et al.* 1988a) and is in accord with a temperature-geographic latitude kinetic model for last interglacial shell taxa in southern Australia (Murray-Wallace *et al.* 1991).

These data assist in constraining the time framework for the Aboriginal coastal occupation of southern Australia.

## Discussion and Conclusions

### THE ARCHAEOLOGICAL SITE: A TYPE LOCALITY

The sharp stratigraphic boundary between the *Katelysia* bearing terra rossa palaeosol of the Bridgewater Formation and the overlying *Turbo* bearing Holocene dune sand is clearly shown in Fig. 7. the palaeosol is well consolidated and has not been contaminated by younger overlying sediment, shells or artifacts.

The two sets of midden materials, as described in this paper, undoubtedly conform to those specified by Luebbers (1978)[1] for his Early Horizon and Late Horizon of aboriginal occupation of southeastern South Australia. Equally, the age determinations of both shells and charcoal, particularly the close agreement of $^{14}C$ and AAR dates, meet the constraints of time applied to this time-cultural classification.

Given that the site meets these tight stratigraphic, archaeological and time constraints, and given that it is located within the boundaries of a National Conservation Park, it is here confidently proposed as a type locality and type section for the time-cultural Early Horizon and Late Horizon of Luebbers (1978)'.

## OTHER ARCHAEOLOGICAL SITES AND POSSIBLE REFERENCE LOCALITIES

It is likely that future investigations will reveal other sites that will equally illustrate, or futher clarify, the Luebbers (1978)' chronology. If appropriate, such sites should be designated as reference localities and reference sections.

In this context, middens within Discovery Bay Coastal Park near Cape Bridgewater in southwestern Victoria seem worthy of further study. Godfrey (1989) differentiated middens in this area into two episodes of occupation, though did not use the Luebbers (1978)' terminology.

The older middens, 8490-3860yr B.P., are in terra rossa soils of the Bridgewater Formation and contain mussel shells of a species no longer extant along the present shore. The younger middens are in unconsolidated sand and contain shells of species, such as *Turbo*, which inhabit the present shoreline, together with numerous flint fragments. Dates of 1050-360yr B.P. were reported by Godfrey (1989) for these younger sites.

### Environmental history of the study area

The following is an account of the interaction of physical and biological processes, from c.125,000yr B.P. to late Holocene, leading to the evolution and early human exploitation of the study environment.

At 125,000yr B.P., oxygen isotope sub-stage 5e, southern Australian sea level was slightly higher than at present. Various estimates place global sea levels at +4 to +6m, but distribution of late Pleistocene Mambray Formation (=Glanville Formation) in northern Spencer Gulf suggests that the 5e sea level was only +1m (Hails *et al.* 1984). At this time, the seaward side of Woakwine Range formed a rocky coastline and the shoreface was inhabited by molluscs favouring such a substrate in a high energy wave regime. Abalone, limpets and *Turbo* were significant faunal elements. Seawater flooded areas landwards of Woakwine Range forming a coastal lagoon, the sheltered waters of which were extensively colonised by molluscs such as *Katelysia* and *Anadara*.

Following marine regression during oxygen isotope sub-stage 5d, at 105,000yr B.P., sub-stage 5c, marine transgression brought palaeo sea level to −8m (Hails *et al.* 1984; Belperio in press). Robe Range stage III sediments accumulated as unconsolidated beach and dune sands (Schwebel 1983).

During isotope sub-stage 5b, the sea receded allowing subaerial diagenesis and at least partial lithification of the carbonate rich sands of the stage III sediments. Protective calcretes developed on exposed surfaces.

At 80,000yr B.P., isotope sub-stage 5a, marine transgression brought sea level to −14m (Hails *et al.* 1984; Belperio in press). Robe Range stage II sediments were deposited at this time. Sea level was not sufficiently high to erode the earlier formed stage III sediments, which were mantled by the dune facies of the stage II transgression.

Following this peak of sea level, the ocean again regressed across the continental shelf and for the remainder of Pleistocene time the shoreline remained seawards of Robe Range. The carbonate sands thus underwent futher extensive diagenesis and consolidation.

Between 45,000 and 30,000yr B.P., oxygen isotope stage 3, there were fluctuations of sea level between −30m and −22m (Cann *et al.* 1988, in press), but these were insufficient to influence Robe Range. Also, by 30,000yr B.P. the base of the range had undergone about 5m of tectonic uplift, futher compounding the impact of the regression. Early humans may have first appeared in southeastern Australia at this time.

From 30,000 to 18,000yr B.P., during oxygen isotope stage 2, the last glacial regression lowered sea level to −130m (Chappell & Shackleton 1986). Aboriginal populations occupied the emergent continental shelf and in coastal areas probably exploited a variety of sea food resources.

At 18,000yr B.P. sea level began to rise, sometimes as rapidly as 2.4cm/yr, totally submerging the continental shelf by 7,000yr B.P. (Belperio in press). Unconsolidated sands were driven shorewards by the rising seas, mantling seaward outcrops of Robe Range stage II and, where exposed, stage III. Sea water flooded the low lying corridor between Robe and Woakwine ranges, providing sheltered shallow subtidal and intertidal environments in which mollusc populations thrived. Aboriginal people occupied Robe Range, open ocean to one side and sheltered lagoon to the other. At the study site they exploited the intertidal cockle *Katelysia*. Elsewhere, for example at Bevilaqua Cliffs to the southeast, ocean beach cockles, *Plebidonax*, were the prime food source.

Bioclastic sedimentation within the shallow Robe-Woakwine marine lagoon was rapid. Sedimentary sections reveal upward shoaling sequences of subtidal oysters overlain by intertidal *Katelysia* and *Anapella*. Shoaling was further facilitated by tectonic uplift of about 0.5m from the time of stabilisation of Holocene sea level to present.

Meanwhile, on the seaward side of Robe Range, sands continued to accumulate. In the absence of any preferred direction of longshore transport

(Sprigg 1952; Bourman & Murray-Wallace 1990), the strong persistent ocean swell (Gostin *et al.* 1988) moved sands onshore from where they were distributed to form a blanket of dunes. Some sands were also redistributed, both up and down the coast, to the protected areas of Guichen Bay, to the northwest, and Rivoli Bay, to the southeast. Sedimentation in these areas effectively isolated the Robe-Woakwine lagoon from futher marine influence.

At the study site, continued onshore and alongshore migration of the Holocene sands once again exposed the older lithified sediments of Robe Range. Their long subaerial emergence through the late Pleistocene had resulted in a high degree of carbonate cementation and they outcropped as a rugged irregular erosional coastline. A marine mollusc fauna, dominated by the large gastropod *Turbo*, became established along this rocky, high wave energy environment. Thus was repeated, on the Holocene shoreface of Robe Range, ecological events that are recorded by the Pleistocene horizons of 'typical reef fauna' (Sprigg 1952) in the Woakwine Range.

For a second time, Aboriginal people occupied the study site and exploited this newly established food resource.

The two middens at the study site therefore reflect profound changes in landscape. The elapsed time between the two periods of human occupation is a valuable clue to the rate of environmental change.

## Conclusions

1. Radiocarbon and AAR dating together confirm an early Holocene age for the Early Horizon Robe Range Aboriginal midden, which is contemporaneous with the culmination of the Holocene transgression. Application of AAR as a palaeothermometer indicates that this early human site has recently been subaerially exposed.
2. This work has demonstrated the importance of an integrated approach to archaeostratigraphic studies through the combined efforts of dating, geomorphology, sedimentology and palaeontology. Such integrated studies can reconcile otherwise seemingly conflicting evidence.
3. The notion of archaeostratigraphic type and reference sections provides a useful approach in the study of Australian prehistory and has potential for wider application.

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# A NEW GENUS AND SPECIES OF PHREATIC AMPHIPOD (CRUSTACEA: AMPHIPODA) BELONGING IN THE "CHILTONIA" GENERIC GROUP, FROM DALHOUSIE SPRINGS, SOUTH AUSTRALIA

*BY* W. ZEILDER*

## Summary

A freshwater amphipod *Phreatochiltonia anophthalma* gen. et sp. nov. is described and illustrated. It is endemic to a few small, cold, artesian springs amongst the Dalhousie Springs complex in the north of South Australia. Unlike species of the closely related genus *Austrochiltonia* the new species seems to be subterranean in habit, is completely white, lacks eyes, and coxa 4 is without a clearly defined posterior excavation. "Chiltonias"generally are considered to be more closely allied to the Hyalellidae than the Ceinidae, and thus transference of chiltonid genera (subfamily Chiltoniinae) to Hyalellidae is recommended.

KEY WORDS: *Phreatochiltonia anophthalma* gen. et sp. nov., new species, amphipod, artesian springs, Australia, taxonomy.

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by W. ZEIDLER*

## Summary

ZEIDLER, W. (1991) A new genus and species of phreatic amphipod (Crustacea: Amphipoda) belonging in the "chiltonia" generic group, from Dalhousie Springs, South Australia. *Trans. R. Soc. S. Aust.* 115(4), 177-187, 29 November, 1991.

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## Introduction

Recent studies of the mound spring fauna of the Great Artesian Basin in South Australia have revealed a diverse endemic fauna (Ponder 1985, 1986; Ponder *et al.* 1989; Zeidler & Ponder 1989). This fauna, components of which are endemic to certain springs or spring groups, is dominated by hydrobiid molluscs (Ponder *et al.* 1989) and crustaceans including amphipods of the genus *Austrochiltonia* Hurley, 1959 (not *Afrochiltonia* K. H. Barnard, 1955 - see Zeidler 1988).

During a recent survey of the fauna of Dalhousie Springs in the extreme north of South Australia (Zeidler & Ponder 1989), we discovered several populations of an undescribed amphipod similar to the *Austrochiltonia* species commonly found in other mound springs, but without eyes. A detailed examination of this species has revealed several characters which preclude it from *Austrochiltonia* or any other allied genus. I therefore propose a new genus to accommodate this new species.

Chiltonias (subfamily Chiltoniinae) also occur in New Zealand (*Chiltonia* Stebbing, 1899) and South Africa (*Afrochiltonia*), but until now no phreatic species have been described, although Williams (1986) reports the probable occurrence of some in Western Australia, from springs and caves near Perth.

The familial placement of chiltonias is briefly reassessed and they are considered to be more closely allied to the Hyalellidae than the Ceinidae, and thus transference of chiltonid genera to Hyalellidae is recommended.

Fig. 1. Location of Dalhousie Springs, South Australia.

## Materials and Methods

Specimens were collected from five rather small, relatively cool, seeps amongst the Dalhousie Springs complex (Fig. 1). The springs are coded following Zeidler & Ponder (1989) (see Fig. 2). Animals were

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TABLE 1. *Temperature measurements, at time of collection, for habitats of* Phreatochiltonia anophthalma *sp. nov and physicochemical data (from Smith 1989) for nearby springs (measured as close as possible to source).*

| Habitat | Temp. Air °C | Temp. Water °C | Nearest Spring | Field Chemistry | | | | | Lab. Chem. | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | Temp. °C | Cond. 25°C Siemens | TDS mg/L | PH | D.O. ppm | TDS mg/l | PH |
| Cb1 | 20 | 20 | None | – | – | – | – | – | – | – |
| Db-la | 22.5 | 22.5 | Db3 | 35 | 1500 | 830 | 7.1 | 0.6 | 901 | 7.6 |
| Nth of E2 | – | – | E2 | 36 | 1600 | 890 | 7.3 | 1.9 | – | – |
| E8 | 22 | 23 | E1 | 29 | 1480 | 820 | 7.7 | 7.5 | 930 | 7.5 |
| Ga4 | 22 | 17 | Ga1 | 32 | 2100 | 1180 | 7.1 | 1.0 | 1220 | 7.0 |
| " | | | Ga3 | 34 | 2120 | 1190 | 7.1 | 2.1 | 1275 | 7.3 |

collected with a small hand sieve or picked off plant debris with forceps, and once, when no surface water was present (at Cb1), two specimens were collected using a household cotton mop placed in a pit dug to water level (approx. 1m). A total of 676 specimens (366 ♀♀, 263 ♂♂, 47 juveniles) were collected and examined.

Physicochemical data for the sites sampled are unavailable because too little surface water was present for meaningful analysis. However, air and water temperatures were measured at the time of collection, and these and physicochemical data for nearby springs are given in Table 1.

Material reported here is deposited in the South Australian Museum, Adelaide (SAM), and the Australian Museum, Sydney (AM). All specimens are preserved in 75% alcohol or 2% formaldehyde/propylene glycol solution. Of the types, only the holotype, allotype and one paratype ♂ have been dissected (partially), with appendages removed from the left hand side of the animal unless indicated otherwise. Dissected appendages are preserved with the carcass or, in the case of the holotype, the mouthparts, pleopods 1–3, and the uropods and telson are mounted in poly-vinyl lactophenol on a microscope slide.

Specimen length is measured along a lateral parabolic line drawn from the anterior extremity of the head through the middle of the body to the posterior limit of the telson.

The thoracic limbs are referred to as gnathopod 1 and 2 followed by pereopods 3–7 to avoid confusion. Size comparisons of gnathopods exclude the coxa and dactyl, and of the pereopods, the coxa, with articles being measured along the middle.

The following abbreviations are used in the text. A1 = first antenna; G1 = gnathopod 1 (first pereopod); G2 = gnathopod 2 (second pereopod); P3–7 = pereopods 3–7; U1-3 = uropods 1–3.

## Systematics

### *Phreatochiltonia* gen. et sp. nov.

Type species: *Phreatochiltonia anophthalma* sp. nov.

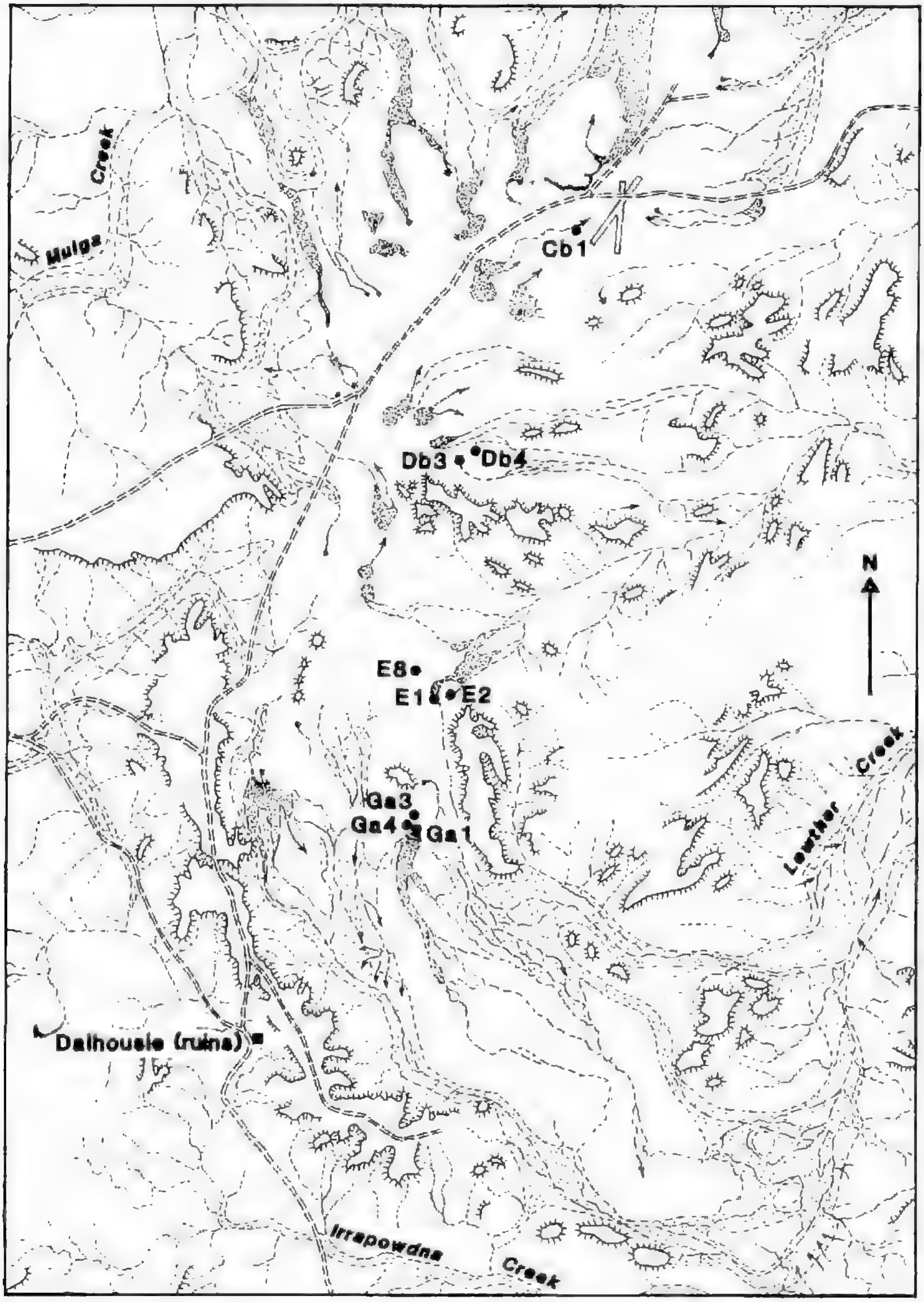
*Diagnostic definition:* Males about ¾ size of females. Eyes absent. Antenna 1 longer than antenna 2, about ⅓ body length; ventral aesthetasc at base of distal three or four (rarely five) flagellar articles. Antenna 2, length almost 0.7× antenna 1; gland cone pressed against head, not readily visible laterally. Maxilla 1 without palp, notched at palp's normal position. Coxae 1–4 deep. Coxa 4 without well-defined posterior excavation; maximum width greater than length (up to 1.25× in female). Gnathopods 1 and 2 subchelate in both sexes; article 6 of gnathopod 2 enlarged in male. Pereopods slender; pereopod 5 distinctly shorter than pereopod 4; pereopod 6 distinctly shorter than pereopod 7. Pleopods unmodified in both sexes. Uropod 3 with single ramus or ramus absent. Telson entire, subrectangular with slightly concave distal margin. Coxal gills on gnathopod 2 to pereopod 6. Oostegites on gnathopod 2 to pereopod 5.

*Etymology:* The generic name, *Phreatochiltonia,* refers to the phreatic habit of the type species, and acknowledges its similarity to *Austrochiltonia.*

## Systematic status of *Phreatochiltonia* gen. nov. and other chiltonid genera.

The new genus clearly belongs to the "chiltonia" generic group (subfamily Chiltoniinae). It is most similar to *Austrochiltonia,* but is readily distinguished from this and the other two chiltonid genera (*Chiltonia* and *Afrochiltonia*) by the following characters: 1) the phreatic habit; 2) the complete lack of eyes; 3) coxa 4 is without well-

Fig. 2. Dalhousie Springs complex showing sites (coded) from which *Phreatochiltonia anophthalma* gen. et sp. nov., has been collected and adjacent springs (referred to in Table 1). Scale = 1:100,000. (Other springs, swamps from springs and creek beds are stippled.) →


Mulga
Creek
Cb1
Db3
Db4
E8
E1
E2
Ga3
Ga4
Ga1
N
Lowther
Creek
Dalhousie (ruins)
Irrapowdna
Creek

defined posterior excavation, and 4) pereopod 5 is distinctly shorter than pereopod 4.

The current familial placement of the chiltonid genera is uncertain. Barnard (1972a) originally placed the chiltonias in his new family, Ceinidae (Barnard 1972b). Bousfield (1982) however, includes the chiltonias in the Hyalellidae, in a brief synopsis of the family, but gives no reasons for this rearrangement; it has thus been ignored or not been accepted (e.g. Zeidler 1988; Barnard & Barnard 1990).

The inclusion of chiltonias in the family Ceinidae by Barnard (1972a) is not altogether satisfactory. They differ from *Ceina* Della Valle, 1893, the type genus, in several key characters; *Ceina* has an aberrant mandibular molar consisting of a long, conical, non-triturative protuberance, and a flat, distinctly cleft telson, whereas chiltonias have a relatively large, triturative mandibular molar, and the telson is curved over the anus and is not cleft except in *Chiltonia mihiwaka* (Chilton, 1898) (for distal ¼). Chiltonias appear to have more in common with *Hyalella* Smith, 1874 and *Allorchestes* Dana, 1849, particularly with respect to the mandible, uropod 3 and the telson. I therefore recommend that the chiltonias, *Afrochiltonia, Austrochiltonia, Chiltonia* and *Phreatochiltonia* gen. nov., be placed in the family Hyalellidae together with *Allorchestes, Hyalella* and *Parhyalella* Kunkel, 1910, subject to a thorough revision of the hyalellids.

## *Phreatochiltonia anophthalma* sp. nov.
FIGS 3–35

*Austrochiltonia* sp. Zeidler, 1989, pp. 83–84, fig. 12.1A.

*Holotype:* SAM C4228. Adult male, South Australia, Dalhousie Springs, from small seep of spring Db4 (Db4a), 26°26′49″S 135°29′15″E, W. Zeidler & K. L. Gowlett-Holmes, 9.vi.1985.

*Allotype:* SAM C4229. Adult female. Collected with holotype.

*Paratypes:* All with same collection data as holotype, except AM specimens collected by W. F. Ponder & D. Winn. AM P40445, 3♀♀, 2♂♂. SAM C4230, 1♂ 3.1 mm. SAM C4231, 136♀♀ (19 ovigerous), 102♂♂, 39 juveniles.

*Other material examined:* All from Dalhousie Springs area (Fig. 2). AM P40446, 1♀, spring Cb1, 26°25′16″S 135°29′52″E, from shallow pool at top of mound, W. F. Ponder, 30.v.1983. SAM C4232, 2♀♀, spring Cb1, from mop trap in pit dug to water level (approx. 1m), W. Zeidler, 14.vi.1985. SAM C4233, 1♂, from small seep of spring Db4 (Db4b), 26°26′49″S 135°29′15″E, W. Zeidler & K. L. Gowlett-Holmes, 9.vi.1985. SAM C4234, 2♀♀ (both ovigerous), from small seep amongst trees (*Melaleuca glomerata*) just north of spring E2, 26°28′30″S 135°29′05″E, W. Zeidler & K. L. Gowlett-Holmes, 8.vi.1985. AM P40447, 23♀♀ (one ovigerous), 38♂♂, spring E8, 26°28′21″S 135°28′52″E, from small seep on north side of mound, W. F. Ponder & D. Winn, 13.vi.1985. SAM C4235, 96♀♀ (33 ovigerous), 92♂♂, spring E8, from small seep on north side of mound, W. Zeidler & K. L. Gowlett-Holmes, 10.vi.1985. AM P40448, 27♀♀ (one ovigerous), 6♂♂, spring Ga4, 26°29′23″S 135°29′10″E, from small seep, W. F. Ponder & D. Winn, 4.vi.1985. SAM C4236, 75♀♀ (20 ovigerous), 20♂♂, 8 juveniles, spring Ga4, from small seep, W. Zeidler & K. L. Gowlett-Holmes, 8.vi.1985.

*Definition:* As for genus with the following additions. Specimens entirely white, relatively small, body length of females up to 4.4 mm, males up to 3.2 mm; relatively robust. Coxal plates 1–3 slightly wider proximally than distally. Oostegites relatively large, that on coxal plate 2 almost as long as gnathopod 2. Uropod 3 a single article.

*Description of holotype:* Male 2.9 mm (Fig. 3). Coxal gills sausage shaped, present from G2 to P6.

Head about as long as deep, length equivalent to first 1–5 pereonites.

Antenna 1 (Fig. 4) about 3× head length; article 1 of peduncle, width 0.6× length and slightly more than 1.5× length article 2, article 3 slightly shorter than article 2; flagellum length almost 1.5× peduncle, of nine articles with one ventral aesthetasc at base of each of last four articles.

Antenna 2 (Fig. 5), article 1 of peduncle as long as wide, article 2 almost twice as long as wide, twice length article 1 and about ⅔ length article 3; flagellum only slightly longer than peduncle, of seven articles.

Upper lip (Fig. 11): slightly wider than long, apically rounded, bearing numerous short setae distally.

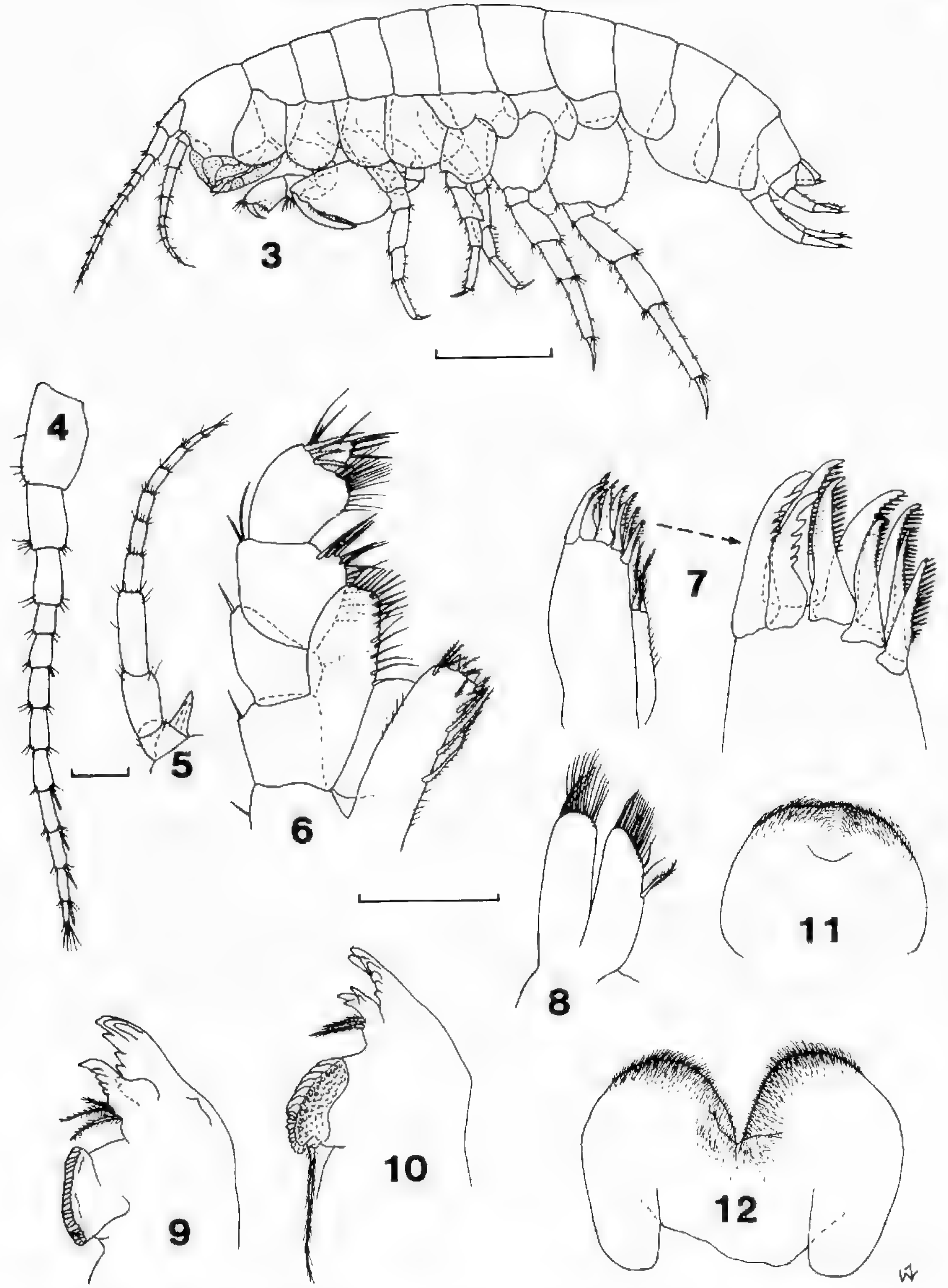
Lower lip (Fig. 12): inner lobes vestigial, outer lobes subovate with setose distal and inner margins.

Mandibles without palp: left (Fig. 9) with incisor of seven teeth plus one tiny protuberance, lacina mobilis of five teeth, spine row of three feathered spines, molar triturative; right (Fig. 10) with incisor of seven teeth, lacina mobilis of four teeth, spine row of two feathered spines, molar triturative with one long feathered seta.

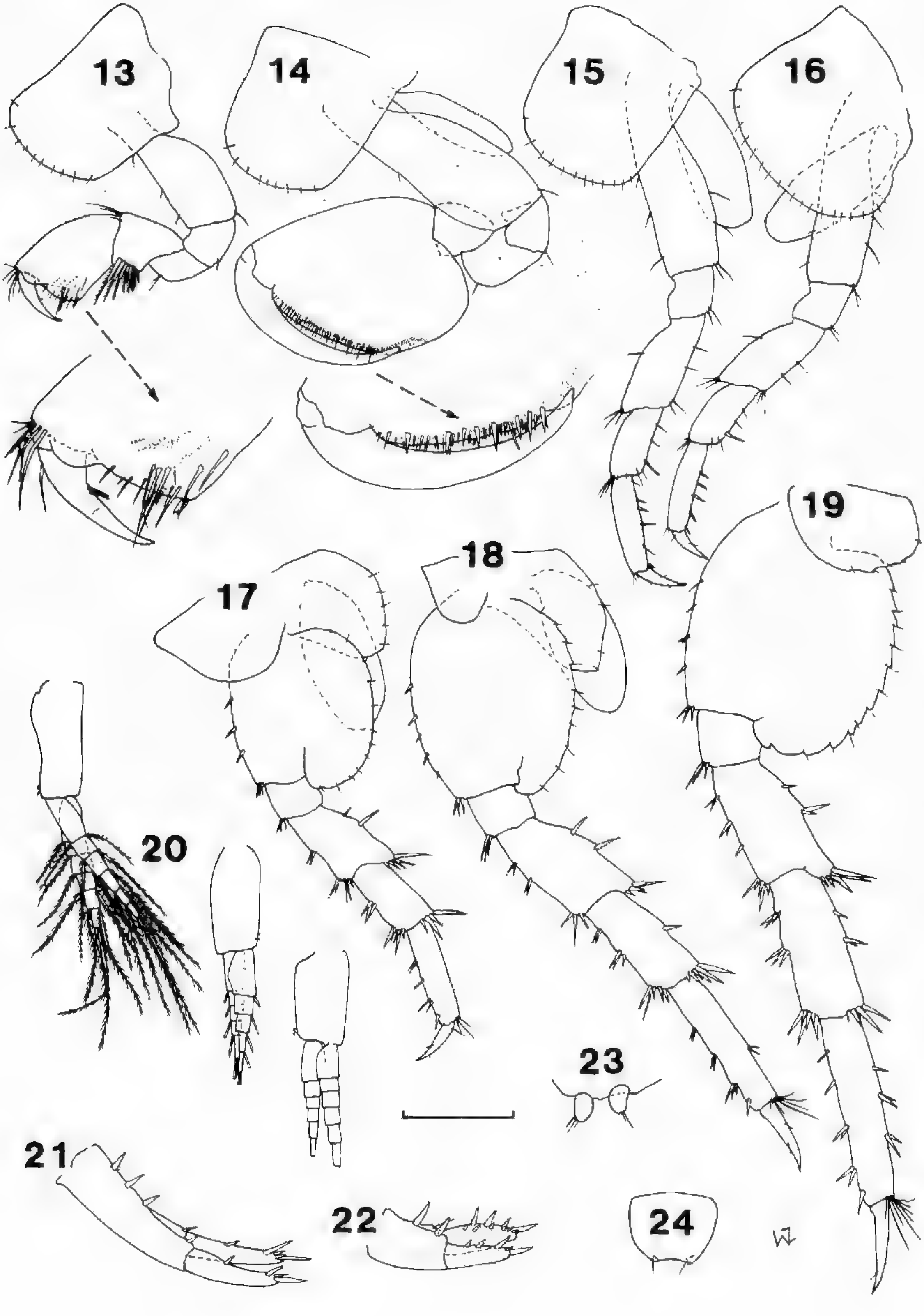
Maxilla 1 (Fig. 7): outer plate with nine comb like spines apically; inner plate very narrow with two feathered spines apically.

Maxilla 2 (Fig. 8): outer plate slightly longer than inner, setal row restricted to apex; inner plate with one large seta on inner margin about 0.6 from base, setal row apically and along inner margin almost to large seta.

Maxilliped (Fig. 6): inner plate reaching extremity of article 1 of palp, rectangular, width about 3× length, with three stout teeth apically, the inner one



Figs 3–12. *Phreatochiltonia anophthalma* gen. et sp. nov., holotype ♂. 3, lateral view; 4, antenna 1; 5, antenna 2; 6, maxilliped; 7, maxilla 1; 8, maxilla 2; 9 & 10, mandible, left & right; 11, upper lip; 12, lower lip. Scale bars = 0.5 & 0.1 mm respectively.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smaller, few feathered setae apically and along inner margin; outer plate ovate, reaching 0.75 along article 2 of palp, slightly wider than inner plate, bearing several setae apically and along about distal ½ inner margin; palp article 1 with oblique distal margin, length outer margin about 2.5× inner; palp article 2 slightly broader than long, slightly expanded distally, as long as outer margin article 1, bearing group of setae on inner distal corner and along distal ⅔ inner margin; palp article 3 about as long as broad, slightly expanded distally, as long as article 2, bearing close-set setae on inner distal corner and for about distal ½ inner margin, several setae on outer distal corner and outer ⅓ distal margin; palp article 4 small, conical, width ⅔ length, slightly less than ½ article 3, four setae terminally; dactyl sharp, slightly longer than article 4.

Gnathopod 1 (Fig. 13): coxa width 0.8× length, slightly longer than article 2, anterodorsal and posterodorsal corners slightly produced, distinctly wider proximally, anterior margin little longer than posterior margin, distal margin evenly rounded with several evenly spaced setae; article 5 length about 1.2× maximum width, posterodorsal lobe with close-set row of eight stout, pectinate spines; article 6 trapezoid, half as long again as article 5, slightly wider distally, width about ⅔ length, posterodistal corner with two stout spines on either side of dactyl, several long setae on anterodistal corner and on posterodistal lobe, several small setae on distal margin; dactyl slightly shorter than width article 6, fitting neatly against palm.

Gnathopod 2 (Fig. 14): length about 1.4× G1; coxal gill length more than 3× width, little shorter than coxa; coxa slightly longer than wide, about 0.8× article 2, distinctly wider proximally, distal margin evenly rounded with several evenly spaced setae; article 4 with right-angled bend; article 5 small, without pectinate spines; article 6 little shorter than article 2, length anterior margin 1.2× maximum width, posteroproximal corner forming rounded lobe, palm oblique with numerous spines of varying lengths on either side of cutting edge followed by shallow groove for tip of dactyl; dactyl claw-like, as long as anterior margin article 6.

Pereopod 3 (Fig. 15): slightly longer than G2; coxal gill length 2.5× width, little shorter than coxa; coxa like that of G2 but slightly larger; article 4 length 2× width, about 0.5× article 2, anterodistal corner produced; article 5 length ⅔ article 4; article 6 about as long as article 4; dactyl length 0.5× article 6; all articles sparsely setose as illustrated.

Pereopod 4 (Fig. 16): slightly shorter than P3, otherwise identical except for coxa; coxa distinctly wider than long, wider distally, anterior margin straight, distal margin evenly rounded extending to small posterodistal lobe, posterior margin with slight indentation but without proximal excavation.

Perepod 5 (Fig. 17): length about 0.9× P4; coxal gill nearly twice as long as wide, as long as article 2; coxa width about 1.5× width article 2, length anterior lobe almost ½ width coxa, length posterior lobe 0.6× width coxa or 0.8× length article 2; article 2 slightly longer than wide with typical expanded posterior margin and posterodistal lobe reaching to about ½ article 3; article 4 length 1.3× width, ½ length article 2, with posterodistal corner produced; article 5 slightly longer than article 4, width about ½ length; article 6 length 1.3× article 5, width ¼ length; dactyl length about ½ article 6; all articles sparsely spinose as illustrated.

Pereopod 6 (Fig. 18): length 1.4× P5; like P5 except for coxa; coxa almost as wide as article 2, length anterior lobe ⅓ article 2, length posterior lobe ⅔ article 2 or 0.8 width coxa.

Pereopod 7 (Fig. 19): longest pereopod, length about 1.2× P6; like P6 except coxa is semi-circular and lacks coxal gill, width 1.4× length, and article 2 posterior margin is distinctly serrated above insertion of setae with acute proximal shoulder.

Pleopods (Fig. 20): all unmodified (c.f. *Chiltonia*).

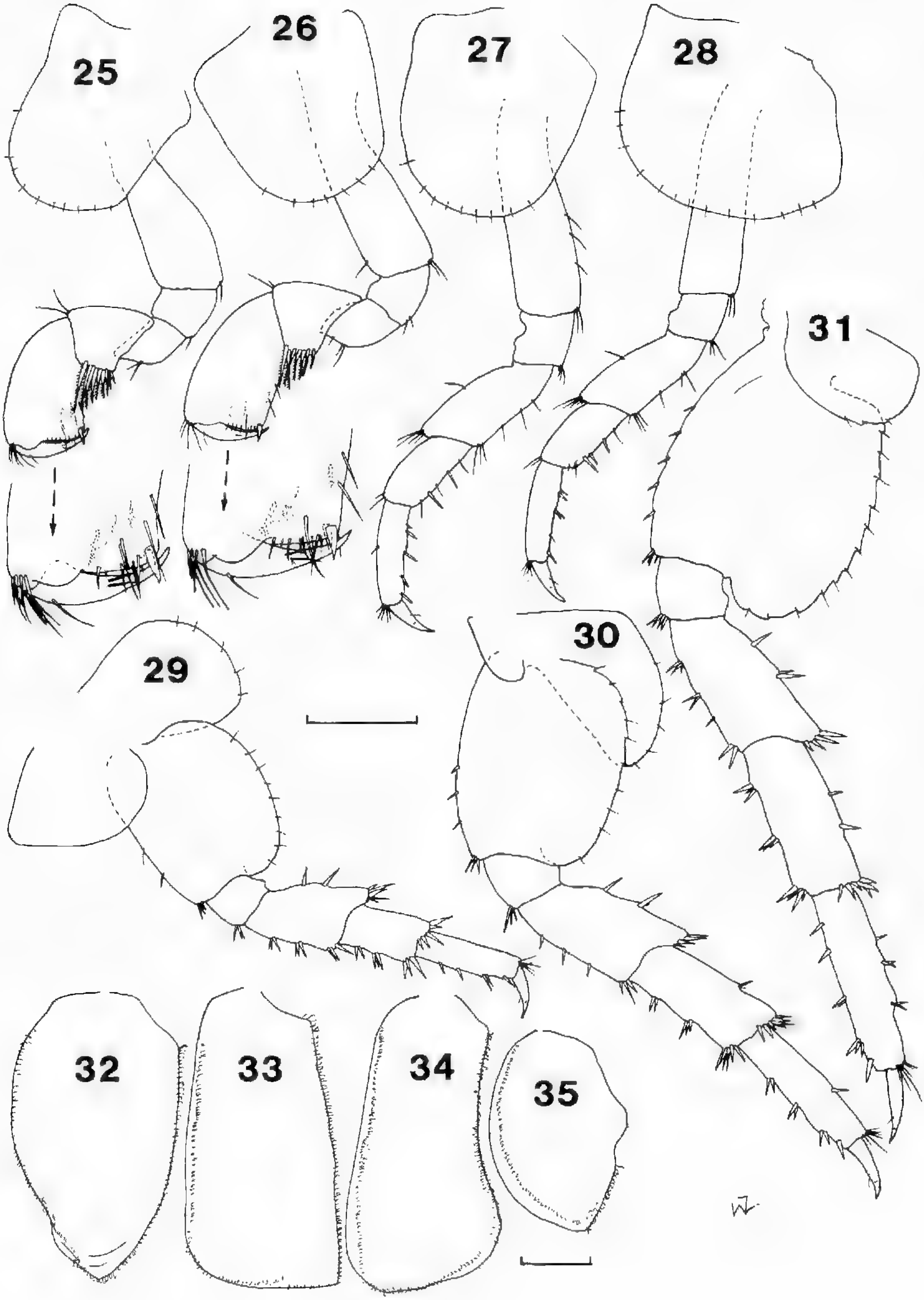
Uropod 1 (Fig. 21): length about 1.8× U2; peduncle with small spine on inner and outer distal corners, and three large spines on dorsal outer margin; rami equal in length, about ⅔ peduncle, outer ramus with two large and one small spine at tip and one large spine medially on dorsal margin; inner ramus with two large and two small spines at tip and one large spine medially on dorsal margin.

Uropod 2 (Fig. 22): peduncle with two large spines on dorsal margin, one medially, the other near distal corner; rami subequal, as long as peduncle, outer ramus with one large spine terminally, one small spine subterminally and three large spines on dorsal margin; inner ramus like outer but in addition a row of five small spines, adjacent to larger spines, on inner dorsal margin.

Uropod 3 (Fig. 23); one-articulate (rami absent), almost ½ length telson, rounded in cross-section with one (right) or two (left) outer and one short inner seta at tip.

Telson (Fig. 24): entire, subrectangular, length about ¾ width, distal margin slightly concave with two small setae at each corner.

Figs 13–24. *Phreatochiltonia anophthalma* gen. et sp. nov., holotype ♂. 13–19, gnathopods 1 & 2, pereopods 3–7; 20, pleopods 1–3 (feathered setae on 2 & 3 not shown); 21–23, uropods 1–3, 24, telson. Scale bar = 0.2 mm.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*Description of allotype:* Female 3.8 mm, ovigerous with 28 eggs in brood-pouch, like male except for the following

Antenna 1: flagellum length 1.6× peduncle, of eight articles with one ventral aesthetase at base of each of last three articles.

Antenna 2: flagellum length slightly more than 1.3× peduncle, of six articles.

Gnathopod 1 (Fig. 25): article 5, posterodistal lobe with close-set row of nine, stout, pectinate spines; article 6 more rectangular, width about 0.6× length, stout spines on posterodistal corner either side of dactyl slightly larger; dactyl a little longer than width article 6.

Gnathopod 2 (Fig. 26): like G1 but length about 1.2× G1, and article 5 posterodistal lobe with close-set row of seven, stout, pectinate spines.

Pereopod 3 (Fig. 27): length about 1.2× G2.

Pereopod 4 (Fig. 28): coxa slightly wider than in male, length only 0.8× width.

Pereopod 5 (Fig. 29): coxa slightly wider than in male, width about 1.8× width article 2; article 2 with small posterodistal lobe; article 4 slightly longer than article 5.

Pereopod 6 (Fig. 30) and pereopod 7 (Fig. 31): as for holotype, but article 2 slightly narrower and with very small posterodistal lobe in P6.

Oostegites (Figs 32–35): on coxae 2–5, all with curled margins and numerous small hooks, together forming tight marsupium. First is heart-shaped, slightly shorter than G2, length 1.8× maximum width; second is trapezoid, length 0.8× P3, 2.7× width proximally and 2× width distally; third is similar to second but with concave posterior margin; fourth is subovate with very convex anterior margin and oblique distal margin, length about 0.6× P5, 1.4× maximum width.

Pleopods, uropods and telson as in holotype.

*Etymology:* The specific name *anophthalma* refers to the absence of eyes.

## Variation

Apart from variations due to size (e.g. number of flagellar articles of antennae), paratypes and other material examined was remarkably similar to either the holotype or allotype. Minor differences noted were as follows. The number of aesthetases on A1 varies with some males having an additional one (five), and some females an additional one (four) or rarely two (five). In the male paratype (SAM C4330) and also the larger male paratype from the AM collections (AM P40445) G2 from the left is noticeably smaller than from the right. In all other specimens homologous pereopods are of similar size. The spination of U1&2 varied slightly with a few specimens with more or less spines (usually only one, at most two). In one specimen (female), from spring E8, U3 from the right is two-articulate (uniramous) as found in *Austrochiltonia australis* (Sayce, 1901). Oostegites of females vary considerably in size, but are expanded, as illustrated, in ovigerous specimens.

The possibility that speciation may have occurred between springs without any obvious morphological changes was considered, and specimens for allozyme electrophoretic analysis were collected from springs Db4 (type locality), E8 and Ga4. A preliminary analysis of this material using methods outlined by Richardson *et al.* (1986) indicated fixed genetic differences of less than 10% (for 16 loci), thus supporting the morphological evidence of one species with little variation. Given these results, a more detailed analysis was considered unnecessary.

## Discussion

The new species described here closely resembles an undescribed species that I have collected from springs scattered throughout the Flinders Ranges in northern South Australia, sympatric with one or more undescribed Crangonyctoid species. However, this other species is not described here as considerably more work is required to determine whether or not one or more species are present.

*Phreatochiltonia anophthalma* has been found only in a few, relatively cold, seeps amongst the 100 or so springs and mounds known as Dalhousie Springs, most of which were sampled in 1985 (Zeidler & Ponder 1989). Many of the active springs at Dalhousie are warm (> 30°C) with large outflows (Smith 1989), and since freshwater amphipods prefer cooler waters (Barnard & Barnard 1983), it is not surprising that no phreatic amphipods were found in these springs. However, a species of *Austrochiltonia* was found in two of these warm springs, but only amongst sedges along the edges of outflows where the water was considerably cooler (Zeidler 1989).

The habitat of *P. anophthalma* is very restricted and animals were seen at the surface, burrowing in and out of the substrate, only near points of water discharge, or were found under plant debris nearby. The species was moderately abundant at most sites except springs Cb1 and E2, which had little or no surface water present. The habitat at the other sites

Figs 25–35. *Phreatochiltonia anophthalma* gen. et sp. nov., allotype ♀. 25–31, gnathopods 1 & 2, pereopods 3–7; 32–35, oostegites from coxa 2–5. Scale bar = 0.2 mm.

was very limited, consisting of small seeps about 3 m long by 20 cm wide, and only a few millimetres deep. At Cb1 one specimen was collected incidently with hydrobiid molluscs in May 1983, from a small shallow pool on the top of the mound. In 1985, this spring was completely dry, but two specimens were collected from a mop trap placed in a hole dug to the water level, adjacent to the mound. This evidence suggests that these amphipods are essentially subterranean in habit and are only seen at the surface when underground water pressure is sufficient to breach the surface of the mound. The notion that these animals, and perhaps others, inhabit the cool interstitial water beneath and between mounds is an interesting prospect that needs further investigation.

Factors that determine the distribution of this species are unknown, but since the habitat appears very limited, it may be more vulnerable to external influences than are the habitats of larger springs. Presence of surface water is probably unnecessary for the survival of the species (e.g. at Cb1), and on a brief visit in April 1986, all habitats had contracted, animals were difficult to collect, and half of the habitat of E8 had dried up. However when surface water is present, they may concentrate at the point of discharge.

Nothing is known about the life history of this species, but of the 366 females collected, 97 were ovigerous, and recently hatched juveniles were common.

One can only speculate as to the evolutionary origin of this species, but its occurrence at Dalhousie Springs on the edge of the Simpson Desert may indicate that it is a descendent of a species which was more widespread during a time when central Australia was much wetter than it is today (Krieg 1989). The phreatic habit having most likely evolved in response to selective pressures in an arid environment.

## Acknowledgments

I am most grateful to Dr W. F. Ponder (AM), who dared to suggest that phreatic amphipods might exist at Dalhousie Springs, and who collected the first specimen in May 1983, provoking a more intensified search in 1985. He is also thanked for his assistance in the field and for collecting more specimens, as is Ms D. Winn (AM). Mrs K. L. Gowlett-Holmes (SAM) assisted greatly with field work and the collection of specimens, and also typed the manuscript. Mr M. Adams, Evolutionary Biology Unit, SAM, conducted the electrophoretic analysis, and his expertise is gratefully acknowledged. I also acknowledge constructive comments of an anonymous referee which markedly improved this paper.

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# *PARAPHAULOPPIA* (ACARIDA: CRYPTOSTIGMATA: ORIBATULIDAE) AND ITS OCCURRENCE IN SOUTH AUSTRALIAN SOILS

*BY D. C. LEE* & C. M. BIRCHBY†*

## Summary

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KEY WORDS: *Paraphauloppia, Paraphauloppia acutinotata, Paraphauloppia globata, Paraphauloppia obtusinotata, Paraphauloppia novazealandica* Hammer, *Paraphauloppia triforata,* new species, Australia, plant litter, soil.

*Transactions of the Royal Society of S. Aust.* (1991), 115(4), 189-198.

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## Summary

LEE, D. C. & BIRCHBY, C. M. (1991) *Paraphauloppia* (Acarida: Cryptostigmata: Oribatulidae) from South Australian soils. *Trans. R. Soc. S. Aust.* 115(4), 189-198, 29 November, 1991.

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KEY WORDS: *Paraphauloppia, Paraphauloppia acutinotata, Paraphauloppia globata, Paraphauloppia obtusinotata, Paraphauloppia novazealandica* Hammer, *Paraphauloppia triforata*, new species, Australia, plant litter, soil.

## Introduction

*Paraphauloppia* Hammer, 1967 is examined as part of a current study of sarcoptiform mites in South Australian soils, sampled from nine florally diverse sites, and for which Lee (1987) provided an introduction to the relevant work on the advanced oribate mites (Planofissurae).

*Paraphauloppia* is allied to *Oribatula* Berlese, 1895, *Phauloppia* Berlese, 1908, *Zygoribatula* Berlese, 1916 and *Jornadia* Wallwork, 1984 within the Oribatulidae Thor, 1929, which is applied here to a taxon approximating to the Oribatulinae of Balogh & Balogh (1984). The Oribatulidae in this restricted sense have been subdivided into the Oribatulinae, Pseudoppiinae Mahunka, 1975 (see Lee 1987) and Fovoribatulinae Lee & Birchby, 1991. The Fovoribatulinae have since been transferred to the Crassoribatulidae, when the latter was newly given family rank (Lee 1991). The original definition of *Paraphauloppia* is modified to accommodate the new species and distinguish it from *Jornadia*, but also to delineate it from similar family-group taxa, because the definition of the Oribatulinae as currently used is unpublished (Lee in prep.). *P. novazealandica* Hammer, 1967 is newly recorded from Australia, and four new species are described from South Australia.

## Materials and Methods

New material examined here, collected by D.C.L., is deposited mostly in the South Australian Museum (SAMA), but also in the British Museum (Natural History) London (BMNH), the Field Museum, Chicago (FMNH) and the New Zealand Arthropod Collection, D.S.I.R., Auckland (NZAC), whilst previously described material is deposited in the Zoological Museum, Copenhagen (ZMC). The morphological notational system follows Lee (1987), the somal chaetotaxy of which is summarized in Figs 5 and 6, with the total setae present in each file (eg. 6Z) indicated by number coming first, whilst a particular seta (eg. Z6) would have the number last. The abbreviations for zoogeographical regions follow Lee (1970, fig. 427). The descriptions of eggs refer to those within the female soma. All material was examined using a Nomarski interference contrast device. All measurements are in micrometres (μm) and were made using an eyepiece micrometer at ×250 magnification.

## Systematics

### *Paraphauloppia* Hammer

*Paraphauloppia* Hammer, 1967, p. 45 (type species by monotypy; *Paraphauloppia novazealandica* Hammer, 1967); Coetzer, 1968, p. 58; Balogh & Balogh, 1984, p. 272; Luxton, 1985, p. 68.

*Definition:* Hysteronotum with 10 pairs (2*J*, 6*Z*, 2*S*) of setae and three or four pairs of multiporose foramina, pteromorphs absent. Dorsosejugal furrow entire (sometimes faint), arched, not extending forward to level of setae *j*2. Proteronotum without translamella, prelamella, sublamella or tutorium, narrow costate lamella (between setae *z*1-*z*2) present. Ventrosejugal apodeme forming single, continuous bar across midsternal line. Coxite seta *IV*1 about level with *JZg*1. Genital shield with three or four pairs of setae. Discidium forms low costate ridge. Femora I and II with five setae (0,2/2,1). Tarsi long (total

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* South Australian Museum, North Terrace, Adelaide, S. Aust., 5000

† State Herbarium, North Terrace, Adelaide, S. Aust., 5000

length of tarsi I, II, III and IV more than 7.5% of idiosomal length) and slim (height less than 33% of length). Pretarsus with three claws, usually lateral claw conspicuously slimmer than central claw (exception *P. triforata* sp. nov., all three claws slim)

*General morphology:* Somal length range for adults: 259–650 (South American species larger, 330–650; South Australian species smaller, 259–365). Somal chaetotaxy: *2j, 2z, 1s; 2J, 6Z, 2S; 3I, 1II, 3III, 3IV*; usually *4JZg* (exception: *P. novazealandica* Hammer, *3JZg*), *1Sg*; *2JZa*, *3Sa*. Leg chaetotaxy (solenidia in parentheses): I – 1, 5, 3(1), 4(2), 20(2); II – 1, 5, 3(1), 4(1), 16(2); III – 2, 3, 1(1), 3(1), 16(2); IV – 1, 2, 2, 3(1), 12. Integument mainly smooth, cerotegument inconspicuous, sometimes (Australian species except *P. novazealandica* Hammer) fine longitudinal lines in coxite region. Hysteronotal setae setose, weakly pilose, seta *z2* clavate or globose. Subpedal and circumpedal ridges merged into single continuous line. Femora lack ventral flanges, femur I without caput collar.

*Distribution:* South America (Nt; Argentine, Bolivia, Chile, Peru), Australia (Au; South Australia) and New Zealand (An; South Island). Within South Australia, *Paraphauloppia* is recorded from four sites each representing a habitat type (mallee-broombush, mallee-heath, savannah woodland, sclerophyll forest) with native vegetation and in a Mediterranean-type climatic region. In South America and New Zealand *Paraphauloppia* occurs in moister, cooler regions. Therefore, despite its absence from the South Australian most southerly, moist, coastal site, *Paraphauloppia* probably also occurs in the moister, temperate environments of Australia.

*Remarks: Paraphauloppia* was considered similar to *Subphauloppia* Hammer, 1967, and so to *Phauloppia* Berlese, 1908, when it was established with one species from New Zealand (An). Now, it could be considered most similar to *Jornadia* Wallwork, 1984, known from North and South America, which differs in having five genital setae. Coetzer (1968) included in *Paraphauloppia* a further eight of Hammer's South American species that had been grouped in either *Oribatula* Berlese, 1895 or *Eporibatula* Sellnick, 1928. One of these species, *P. australis* (Hammer, 1962), has since been mistakenly used (Balogh & Balogh, 1984, fig 70) in order to illustrate *Eporibatula*, despite its being excluded from that genus in the same publication on the basis of having ten pairs of hysteronotal setae. Until the present publication, no other changes have been made to the genus. A paper (Lee 1991) on the higher classification of the Oripodoidea, however, gives more weight to the presence of a central gap in the ventrosejugal apodeme in delineating subfamilies. Consequently, *Diphauloppia* Balogh & Balogh, 1984, *Gerloubia* Coetzer, 1968 and *Subphauloppia* were transferred from the Oribatulinae to the Pseudoppiinae, so that although previously regarded as similar to *Paraphauloppia*, they are now included in another subfamily. Thus *Paraphauloppia* and *Jornadia* are the only oribatuline genera with ten pairs of hysteronotal setae, all the others having 11–14 pairs. *Paraphauloppia cordylinosa* Higgins & Woolley, 1975 is listed in the North American fauna by Marshall *et al* (1987), noting it as a problematic combination; since it has at least 12 hysteronotal setal pairs it is excluded here from *Paraphauloppia*.

South Australian and South American species of *Paraphauloppia* differ. The South American species are larger, except for *P. gracilis* (Hammer, 1958), which is similar to *P. novazealandica* in somal shape, size and form of notal setae, and positioning of notal seta *S5* behind *Z4*. The South American species also have smaller sensory setae (*z2*) and hysteronotal foramina, and lack fine striations on their coxites.

*Paraphauloppia* includes 13 species: *P. altimontana* (Hammer, 1958); *P. acutinotata* sp. nov.; *P. altimontanoides* (Hammer, 1958); *P. australis* (Hammer, 1962); *P. globata* sp. nov.; *P. gracilis* (Hammer, 1958); *P. magniporosa* (Hammer, 1958); *P. morenoi* (Hammer, 1962); *P. novazealandica* Hammer, 1967 (type-species); *P. obtusinotata* sp. nov.; *P. pisacensis* (Hammer, 1961); *P. quadrisetosa* (Hammer, 1961); *P. triforata* sp. nov.

## Key to Australian *Paraphauloppia* species (adults)

1. Hysteronotal setae shorter (*Z3* and *Z4* not reaching *Z2* or *S5*) (Fig. 7). Ventrosejugal apodeme well separated from margin of genital orifice, distance between setae *III1*–*JZg1* at least as great as length of coxite seta *III1* (Fig. 8). . . . . . 2
   Hysteronotal setae longer (*Z3* and *Z4* reaching *Z2* or *S5*) (Fig. 1). Ventrosejugal apodeme abutting onto margin of genital orifice or close to it, distance between setae *III1*–*JZg1* less than length of coxite seta *III1* (Fig. 3). . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 3
2. Larger soma (length > 300 µm). Three pairs of genital setae. Four pairs of hysteronotal foramina. Notal setae *j2* and *Z1* shorter than *Z2* or *Z3*. . . . . . . . . . . . . . . . . . . . . . *P. novazealandica* Hammer, 1967
   Smaller soma (length < 300 µm). Four pairs of genital setae. Three pairs of hysteronotal foramina. Notal setae *j2* and *Z1* longer than *Z2* or *Z3* (Fig. 8). . . . . . . . . . . . . . *P. triforata* sp. nov.
3. Larger soma (length > 350 µm). Hysterosoma subglobular. Hysteronotal setae long (*Z3* length at

least 2× distance *Z3*-*Z2*) (Fig. 2)................................................ *P. globata* sp. nov.
Smaller soma (length < 350 µm). Hysterosoma ovoid. Hysteronotal setae medium length (*Z3* length 1.00×-1.33× distance *Z3* *Z2*) (Fig. 1)..........4

4. Front of rostrum (tooth narrower than long) and hysteronotum (dorsosejugal apodeme adaxial relative to seta *j2*, humeral tectum not obscuring bothridial base) pointed (Fig. 1). Foramen *F4* behind line joining setae *Z4*-*S5*. Major axis of pore *Saf* nearly longitudinal (similar to Fig. 8)................................ *P. acutinotata* sp. nov.
Front of rostrum (tooth as wide as long) and hysteronotum (dorsosejugal apodeme adaxial margin level with seta *j2*, humeral tectum obscuring bothridial base) blunt (Fig. 5). Foramen *F4* in front of line joining setae *Z4*-*S5*. Major axis of pore *Saf* nearly transverse (Fig. 6)....... *P. obtusinotata* sp. nov.

## ***Paraphauloppia acutinotata*** sp. nov.

FIG. 1

*Type material:* Holotype female (SAMA N1990733), plant litter, sparse moss and calcareous sandy soil, under ridge-fruited mallee (*Eucalyptus incrassata*) amongst broombush shrubs (*Melaleuca uncinata*), open scrubland, Ferries-McDonald Reserve (35°15′S, 139°09′E), 20.vi.1974. Paratypes, four ♀♀ (SAMA, N1990734 - N1990737) and four ♂♂ (SAMA, N1990738 - N1990741), same data as holotype.

*Female:* Soma oval, light brown. Idiosomal length, 316 (5, 298-329). Leg lengths (femur-tarsus for 316): I-169, II-142, III-142, IV-180. Tibial maximum heights (for 316): I-17, II-12, III-11, IV-12.

Proteronotum with terminal tooth to rostrum forming narrow point, not as broad as long. Anterior foramen (*F1*) absent. Seta *j2* reaching midway between *j1*-*z1*. Sensory seta (*z2*) clavate, usually with caput longer (over 66% of total setal length) than exposed stalk. Hysteronotum with mainly medium length setae, but some peripheral setae substantially longer, *Z1* usually longer than *z2*, *S6* usually 1.25× length of *Z4*. Seta *S5* well forward so that level with seta *Z4* and foramen *F4* behind line between *Z4*-*S5*.

Idiosternal setae with inconspicuous cilia, long, seta *l2* reaching anterior margin of sternal tectum. Coxite region striated from anterior margin back to seta *Sg1*, posteriorly striae superimposed on weak reticulations. Discidial ridge with straight edge. Slit-like pore *Saf* nearly longitudinal, less than 45° from longitudinal axis. Egg subellipsoidal, exochorion smooth, size 170 × 77 (1), length 52% of somal length, eggs per female – 1 (1).

1

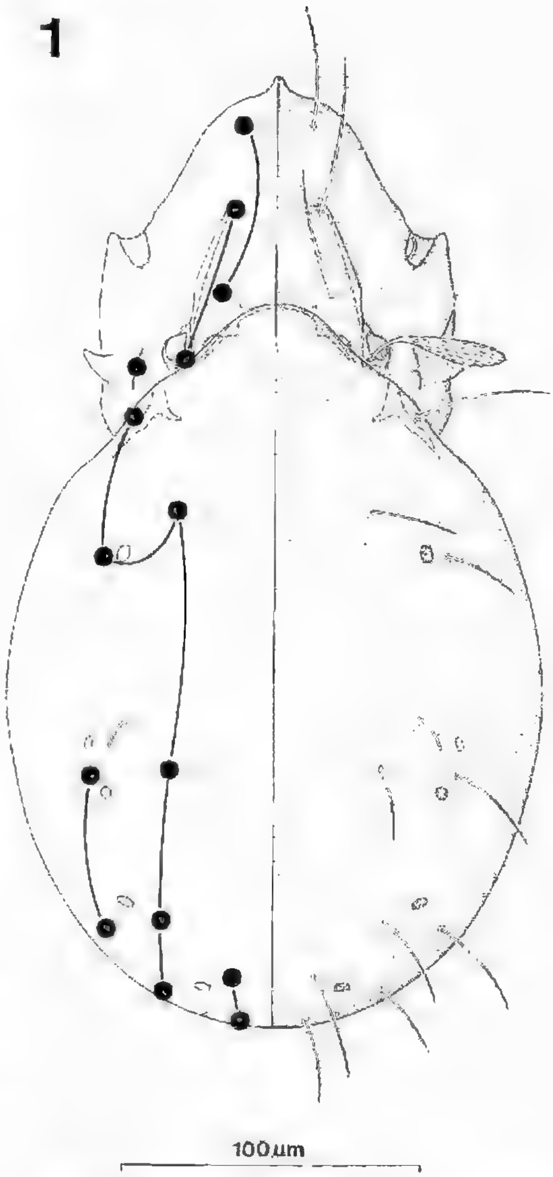
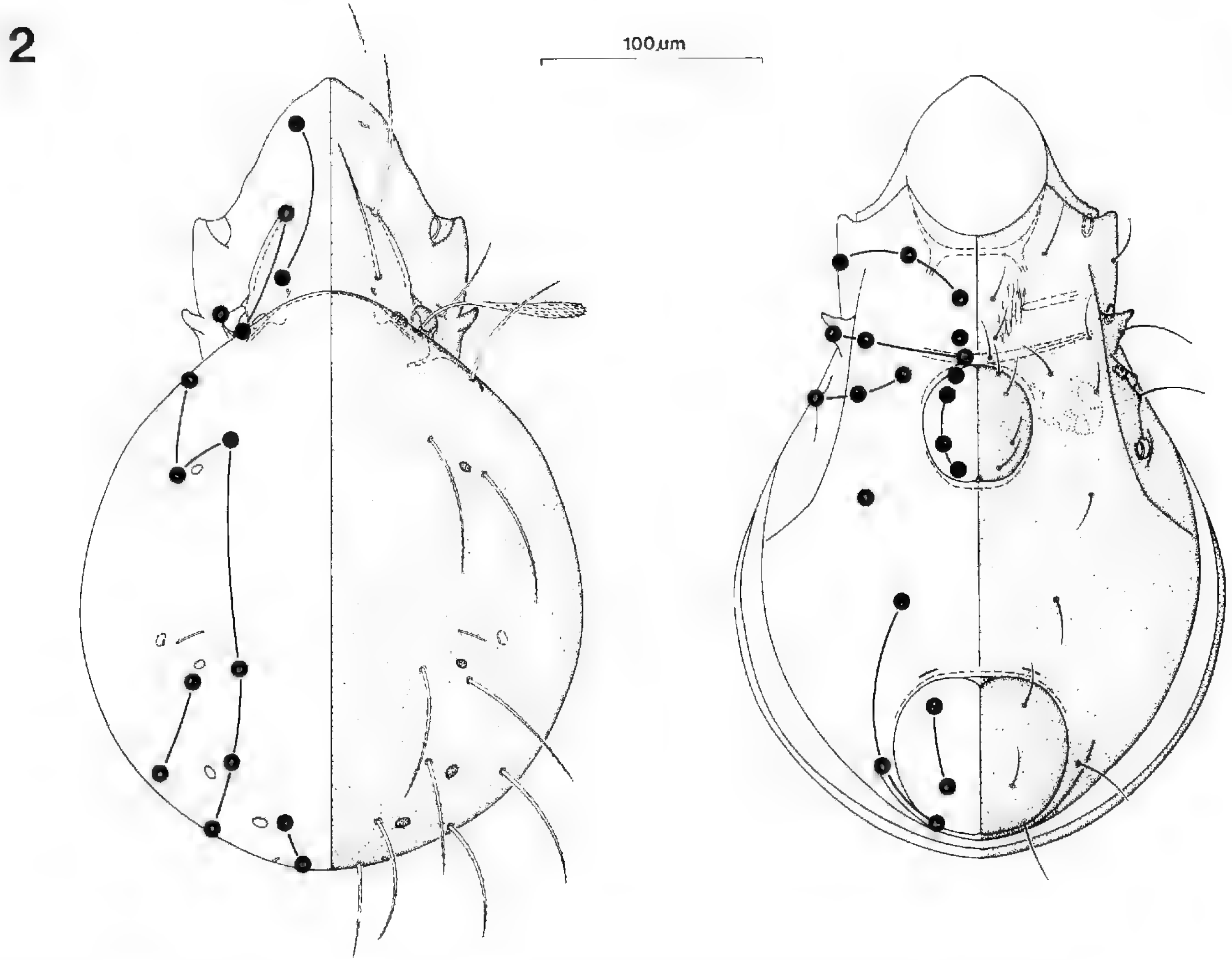


Fig. 1. *Paraphauloppia acutinotata* sp. nov., ♀ notum of soma. For setal notation see Fig. 5.

Legs medium length (mean femur-tarsus length: 50% of somal length) with medium girth (mean maximum tibial height 34% of mean length). Central pretarsal claw with 2× depth of lateral pretarsal claws.

*Male:* Similar to female but idiosoma shorter, mean length, 285 (4, 275-296).

*Remarks:* The specific name *acutinotata* is derived from the Latin for 'pointed' and 'back' and refers



Figs 2–3. *Paraphauloppia globata* sp. nov., ♀ 2, notum of soma. 3, sternum of soma. For setal notation see Figs 5 and 6.

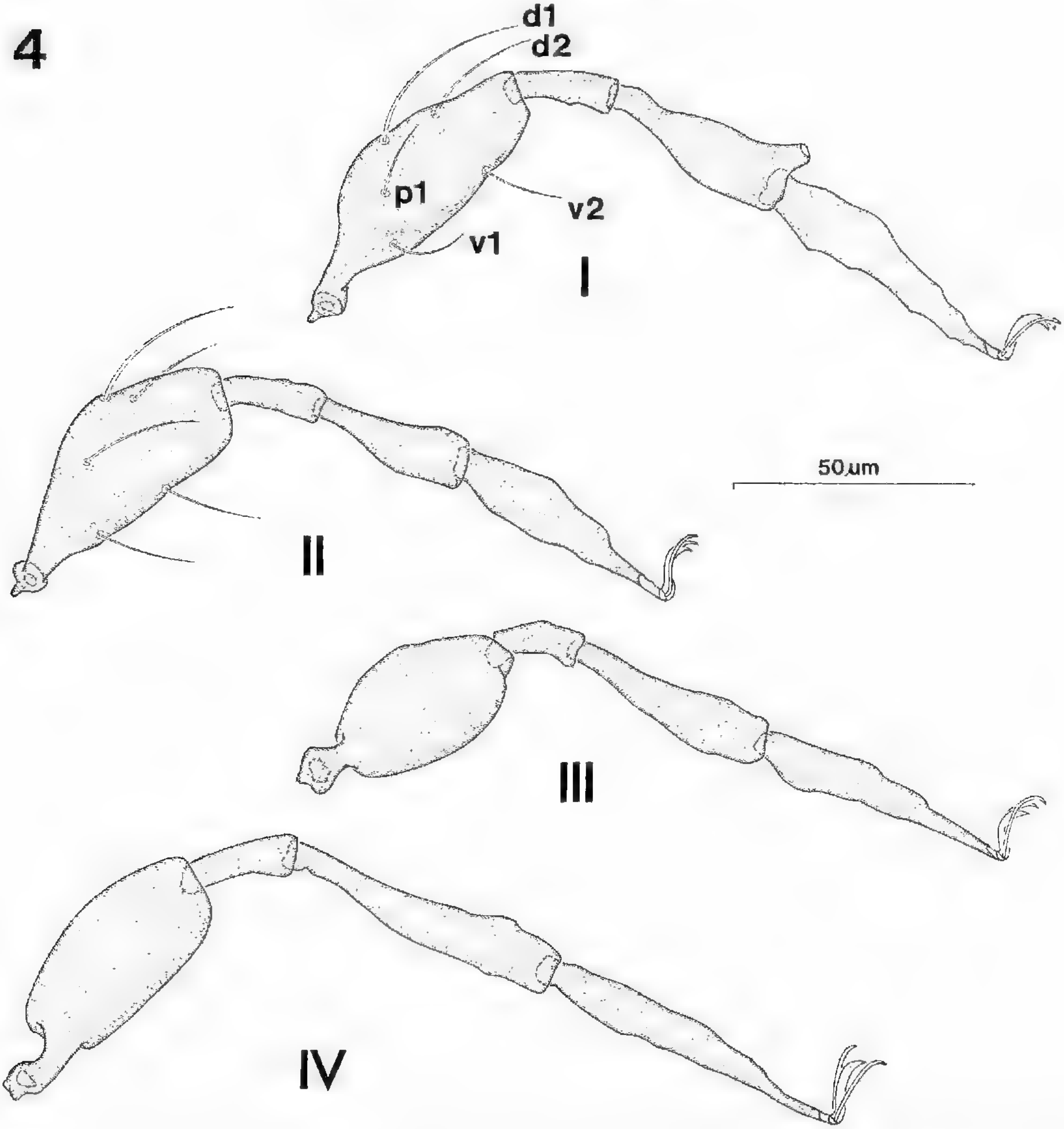


Fig. 4. *Paraphauloppia globata* sp. nov., ♀, posterior aspect of femur-pretarsus of right legs I, II, III and IV. all setae in femora I and II illustrated, d – dorsal, p = posterior, v = ventral.

to the sharp rostral tooth and anterior hysteronotal margin. These distinguish it from the similar *P. obtusinotata*, sp. nov. as do the longitudinal slit-like pore *Saf* and greater length of some peripheral notal setae. *P. acutinotata* and *P. obtusinotata* both have medium sized hysteronotal setae and are distinguishable from the other Australian species which have either clearly longer or shorter relevant setae.

### ***Paraphauloppia globata*** sp. nov.

FIGS 2–4

*Type material:* Holotype female (SAMA N1990742), plant litter, sparse moss and calcareous sandy soil, under ridge-fruited mallee (*Eucalyptus incrassata*) amongst broombush shrubs (*Melaleuca uncinata*), open scrubland, Ferries-McDonald Reserve (35°15′S, 139°09′E), 20.vi.1974. Paratypes, 16 ♀♀

(SAMA, N1990743 – N1990752; 1-BMNH; 1-FMNH; 1-NZAC; 3 lost) and five ♂♂ (SAMA, N1990753 – N1990756; 1 lost), same data as holotype.

*Female:* Soma broadly oval or subspherical in shape, light brown colour. Idiosomal length, 365 (17, 339–365). Leg lengths (femur – tarsus for 365): I–213, II–193, III–188, IV–239. Tibial maximum heights (for 365): I–21, II–16, III–14, IV–16.

Proteronotum with terminal tooth to rostrum forming narrow point, not as broad as long (in Fig. 2 not evident because directed downwards). Anterior foramen (*F1*) absent. Seta *j2* reaching anterior to *z1* to about 0.8× distance between setae *j1* – *z1*. Sensory seta (*z2*) clavate, slim and long, usually with caput subequal in length to exposed stalk. Hysteronotum with long setae, length of setae *Z3* and *Z4* more than 2× distances from *Z2* and *S5* respectively. Seta *S5* nearly far enough forward to be level with seta *Z4*, but foramen *F4* anterior to line between setae *Z4*–*S5*.

Idiosternal setae with minute but noticeable cilia, long seta *I2* reaching anterior margin of sternal tectum. Coxite region with central area striated from anterior margin to seta *III1*, laterally around seta *I2* lines faint and broken up into rows of short striae and dots. Discidial ridge with tubercle bearing seta *IV3*. Slit-like pore *Saf* nearly transverse, more than 45° from longitudinal axis. Egg subellipsoidal, exochorion rugose, mean size 166 × 80 (10), length 47% of somal length, eggs per female – 1 (1), 2 (1), 3 (3) or 4 (2).

Legs long (mean femur-tarsus length: 57% of somal length) and slim (mean maximum tibial height 31% of mean length). Central pretarsal claw with 2× depth of lateral pretarsal claws.

*Male:* Similar to female but idiosoma shorter, mean length 342 (5, 337–347).

*Remarks:* The specific name *globata* is derived from the Latin for 'globe' and refers to the subspherical shape of the hysteronotum. *P. globata* is distinguishable from the other Australian species by this shape, its relatively large size and long notal setae. It is smaller than all but one of the South American species, and differs from them in having such a long clavate sensory seta (*z2*).

### *Paraphauloppia novazealandica* Hammer

*Paraphauloppia novazealandica* Hammer,
1967, p. 45, 46, fig. 59.

*Type material examined:* Of 11 specimens recorded with original description, lectotype ♂ (labelled "type" in vial of alcohol) and four paralectotypes (labelled "paratypes", one ♀ and three ♂♂ on one slide) examined (ZMC), thick moss and bone-dry lichens and *Lycopodium*, open *Manuka* and *Nothofagus* forest, few 100 feet above lake, Lake Rotoiti, South Island, New Zealand, M. Hammer, 1962.

*Female:* Soma oval, straw colour (New Zealand specimens) or light brown (South Australian specimens). Idiosomal length (original description: "about 0.34mm"), 320 (1, New Zealand), 337 (25, Sclerophyll forest, 326–346) or 363 (5, Savannah woodland, 350–370). Leg lengths (femur-tarsus, Sclerophyll forest, for 341): I–170, II–151, III–142, IV–178. Tibial maximum heights (for 341): I–19, II–17, III–12, IV–12.

Proteronotum with terminal tooth to rostrum forming broad point, as broad as long (not illustrated by Hammer, 1967: fig 59). Anterior foramen (*F1* = "ap") small but conspicuous. Short ridge between setae *j2*–*z2* present (New Zealand specimens) or absent (South Australian specimens). Seta *j2* as long as 0.75× distance between setae *j2*–*z1*. Sensory seta (*z2*) globular, with caput subequal to or shorter than exposed stalk, two parts clearly delineated. Anterior hysteronotal margin complete, although faint, recognisable between dorsosejugal apophyses. Hysteronotum with short setae, *Z1*, *Z2* and *Z4* length subequal to distance *Z2*–*Z3*. Seta *S5* well posterior to seta *Z4*, and nearly directly behind it, so foramen *F4* lateral to line between setae *Z4*–*S5*.

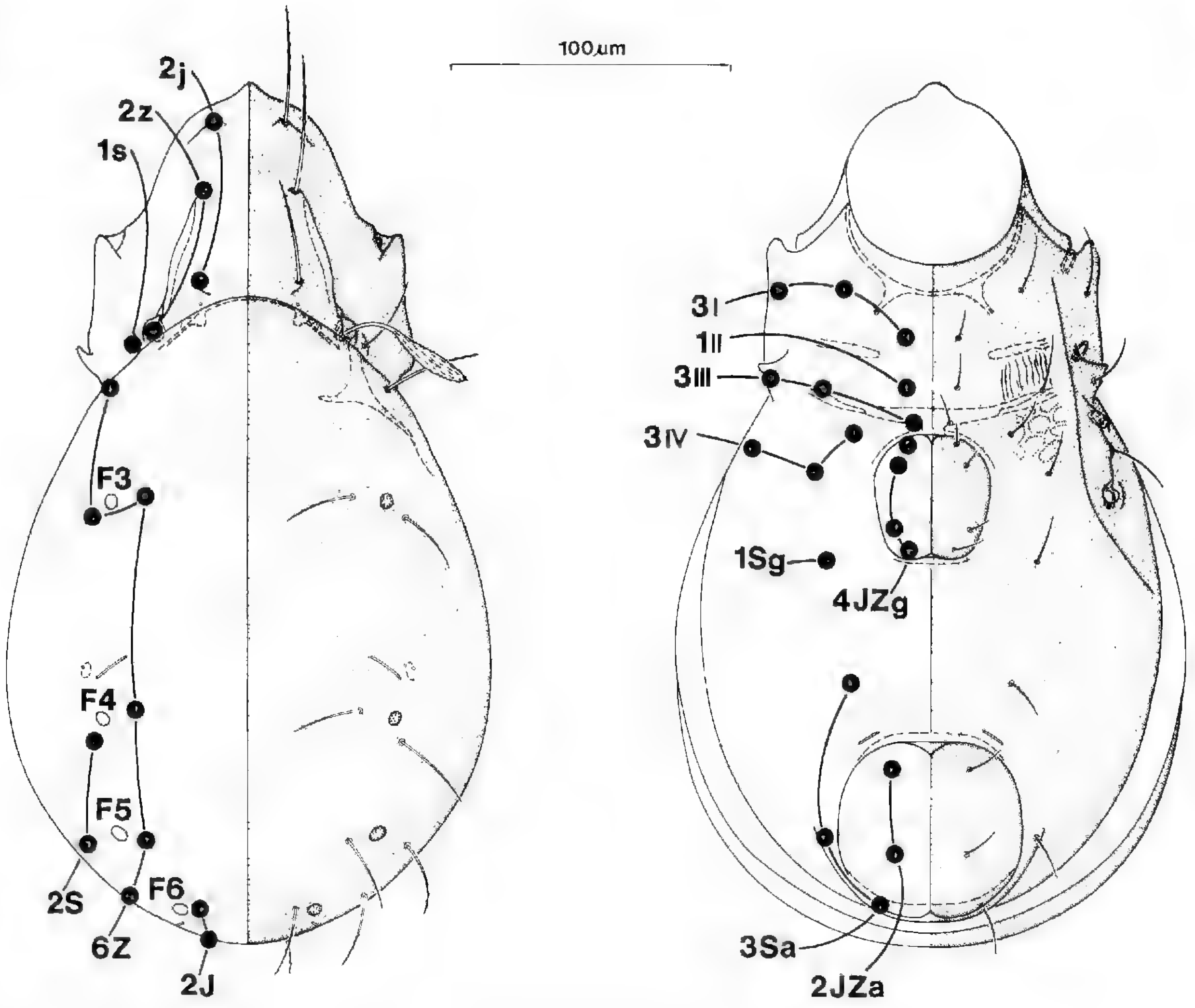
Idiosternal setae with inconspicuous cilia, medium length, seta *I2* not reaching anterior margin of sternal tectum. Coxite region not striated, weak reticulations near midsternum. Apodeme III present, small, thickened fusion to coxite limited to short linear strut or sub-circular tubercle. Discidial ridge with tubercle bearing seta IV3. Slit-like pore *Saf* nearly longitudinal, less than 45° from longitudinal axis. Egg subellipsoidal, exochorion smooth, mean size 145 × 86 (11), length 46% of somal length; eggs per female – 1 (9), 2 (1) or 3 (1).

Legs medium length (mean femur-tarsus length: 47% of somal length) with medium girth (mean maximum tibial height 34% of mean length). Central pretarsal claw with 2× depth of lateral pretarsal claws.

*Male:* Similar to female but idiosoma usually shorter, mean length, 328 (4, types ex New Zealand, 320–334), 323 (25, Sclerophyll forest, 312–336) or 341 (6, Savannah Woodland, 326–355).

*Referred material:* 41 ♀♀ (SAMA N1990939 – N1990945, N1990955 – N1990964, N1990981 – N1990992, 4-BMNH, 4-FMNH, 4-NZAC) and 50 ♂♂ (SAMA N1990934 – N1990938, N1990946 – N1990948, N1990965 – N1990980, N1990993 – N19901006, 4-BMNH, 4-FMNH, 4-NZAC), plant litter, sparse moss and calcareous sandy soil, unde-

5 6



Figs 5-6. *Paraphauloppia obtusinotata* sp. nov., ♀ 5, notum of soma. 6, sternum of soma.

sclerophyllous shrubs amongst messmate stringybark (*Eucalyptus obliqua*), dry sclerophyll forest near summit of Mt Lofty (34°59′S, 138°45′E), Cleland Conservation Park, 9.v.1974. Five ♀♀ (SAMA N1990949 – N1990951, N19901007, N19901008) and six ♂♂ (SAMA N1990952 – N1990954, N19901009 – N19901011), grass, moss, leaf litter and loamy soil under manna gum trees (*Eucalyptus viminalis*), savannah woodland, Chambers Gully (34°58′S, 138°41′E), Cleland Conservation Park, 12.vi.1974.

*Remarks: Paraphauloppia novazealandica* is distinguishable within the genus by the presence of foramen *F1* and only three pairs of *JZg* setae on the genital shields. The South Australian material is more like New Zealand type specimens than the original description indicates, in that the anterior margin of the hysteronotal shield is complete, the notal setae are longer and the rostrum has a tooth. Two small differences, the larger soma and the absence of a short proteronotal ridge on the Australian material, however, suggest that there may be two subspecies present. *P. novazealandica* is superficially similar to *P. obtusinotata* sp. nov., but is distinguished from it and other South Australian species, by its generically unique character states and in having a globular sensory seta and no striae on its coxites. The most similar species to it is *P. gracilis* (Hammer, 1958) from Bolivia, which also shares the positioning of hysteronotal seta *S5*, well separated from *Z4*, but directly behind it.

## ***Paraphauloppia obtusinotata*** sp. nov.
FIGS 5, 6

*Type material:* Holotype ♀ (SAMA N1990757), plant litter, sparse moss and silaceous sandy soil, under sclerophyllous shrubs amongst messmate stringy bark (*Eucalyptus obliqua*), dry sclerophyll forest, near summit of Mt Lofty (34°59′S, 138°45′E), Cleland Conservation Park, 9.v.1974. Paratypes, 105 ♀♀ (SAMA, N1990758 – N1990773 and N1990785 – N1990858; 5–BMNH; 5–FMNH; 5–NZAC) and 101 ♂♂ (SAMA N1990774 – N1990784 and N1990859 – N1990933, 5–BMNH, 5–FMNH, 5–NZAC), same data as holotype.

*Female:* Soma with oval shape and light brown colour. Idiosomal length, 308 (25, 278–329). Leg length (femur-tarsus for 288): I–155, II–149, III–142, IV–168. Tibial maximum heights (for 288): I–19, II–14, III–14, IV–12.

Proteronotum with terminal tooth to rostrum forming broad point, as broad as long. Anterior foramen (*F1*) absent. Seta *j2* length subequal to distance *j2–z1*. Sensory seta (*z2*) clavate, medium size with caput subequal in length to exposed stalk. Hysteronotum with medium length setae, some peripheral setae slightly longer, *Z1* shorter than *z2*, *S6* subequal in length to *Z4*. Seta *S5* posterior to seta *Z4* so foramen *F4* just anterior to line between setae *Z4–S5*.

Idiosternal setae with inconspicuous cilia, long, seta *I2* reaching anterior margin of sternum. Coxite region with striations broken up into short lines or dots, from anterior margin to ventrosejugal apodeme, not superimposed on posterior reticulations. Discidial ridge with tubercle at base of seta IV3. Slit-like pore *Suf* nearly transverse, more than 45° from longitudinal axis. Eggs ellipsoidal, exochorion smooth, mean size 139 × 70, length 48% of somal length, eggs per female – 1 (9), 2 (6) or 3 (2).

Legs long (mean femur-tarsus length: 53% of somal length) with medium girth (mean maximum tibial height 38% of mean length). Central pretarsal claw with 2× depth of lateral pretarsal claws.

*Male:* Similar to female but idiosoma shorter, mean length, 293 (25, 278–293).

*Remarks:* The specific name *obtusinotata* is derived from the Latin words for 'blunt' and 'back' and refers to the broad rostral tooth and rounded anterior hysteronotal margin, which distinguishes it from the similar *P. acutinotata* sp. nov. Other distinguishing characters are the longitudinal slit-like pore *Suf* and the shorter peripheral hysteronotal setae. *P. obtusinotata* and *P. acutinotata* are medium sized amongst other Australian species which have either clearly longer or shorter hysteronotal setae.

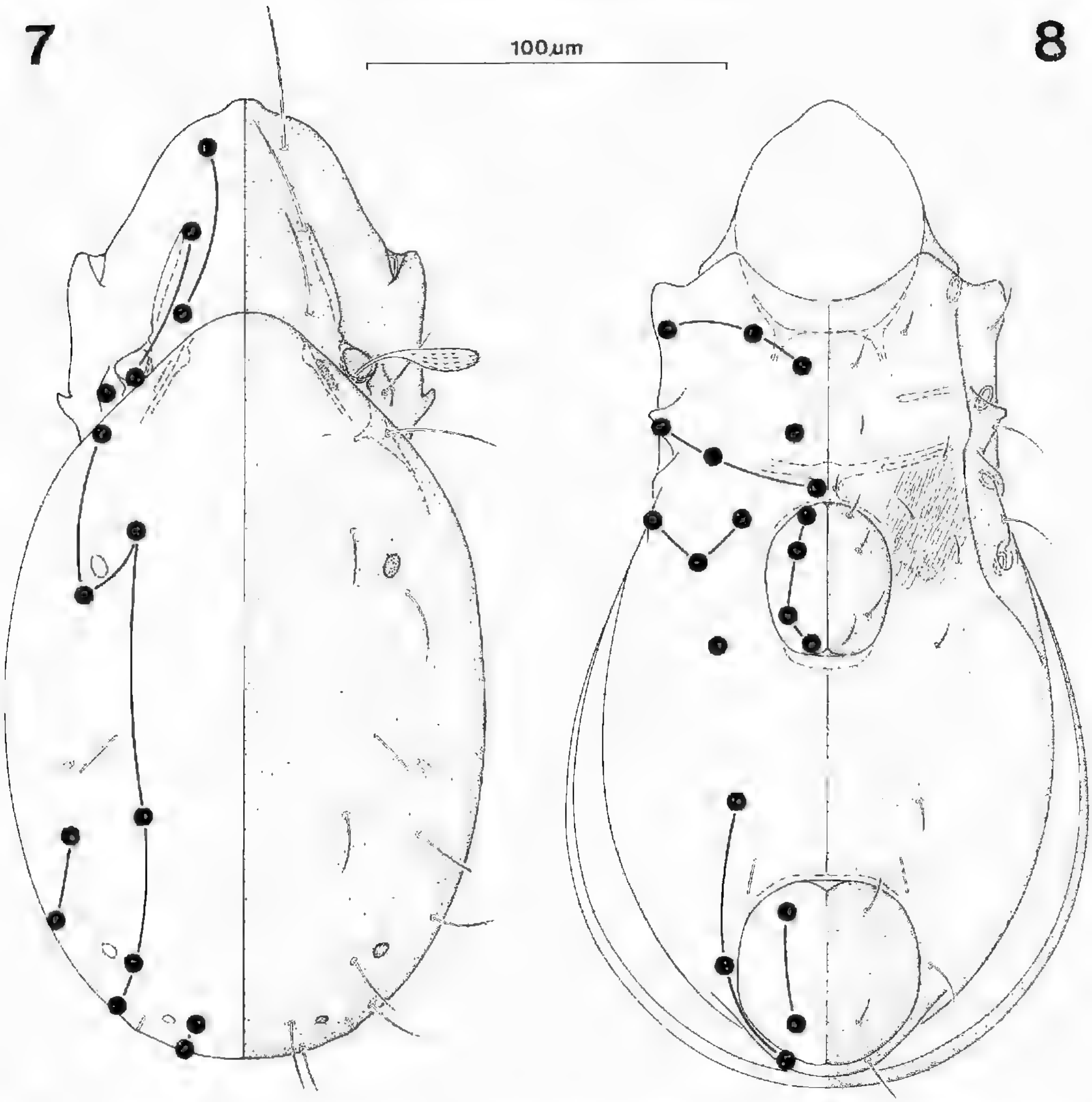
## ***Paraphauloppia triforata*** sp. nov.

FIGS 7, 8

*Type material:* Holotype ♀ (SAMA N19901012), plant litter and calcareous sandy soil, under banksia shrubs (*Banksia ornata*) amongst sclerophyllous shrubs and sparse brown stringy bark mallee (*Eucalyptus baxteri*) on ridge, tall open-shrubland, Tamboore (35°57′S, 140°29′E), 4.vii.1974. Paratypes, 12 ♀♀ (SAMA N19901013 – N19901024) and eight ♂♂ (SAMA N19901025 – N19901032), same data as holotype.

*Female:* Soma narrowly oval, straw colour. Idiosomal length, 279 (13, 270–288). Leg length (femur-tarsus for 278): I–137, II–127, III–108, IV–144. Tibial maximum heights (for 278): I–17, II–12, III–10, IV–10.

Proteronotum with terminal tooth to rostrum forming broad point, as broad as long. Anterior foramen (*F1*) absent. Seta *j2* reaching just beyond seta *z1*. Sensory seta (*z2*) clavate, medium size, caput subequal in length to exposed stalk. Hysteronotum with short setae, *Z3* and *Z4* length less than distance



Figs 7–8. *Paraphauloppia triforata* sp. nov., ♀ 7, notum of soma. 8, sternum of soma. For setal notation see Figs 5 and 6.

from *Z*2 and *S*5 respectively. Seta *S*5 almost level with seta *Z*4, and foramen *F*4 absent.

Idiosternal setae with short, distinct cilia, short seta *I*2 not reaching anterior margin of sternum. Coxite region with striations reaching back posteriorly to seta *IV*2, anterior striae longitudinal, whilst posterior to ventrosejugal apodeme striae angle towards genital shield. Discidial ridge straight. Slit-like pore *Saf* nearly longitudinal, less than 45° from longitudinal axis. Egg subellipsoidal, exochorion smooth, mean size 131 × 66, length 47% of somal length, eggs per female – 1 (4), 2 (3) or 3 (2).

Legs medium length (mean femur-tarsus length: 46% of somal length) with medium girth (mean maximum tibia height 37% of mean length). Central pretarsal claw only slightly greater in depth than lateral pretarsal claws.

*Male:* Similar to female but idiosoma shorter, mean length, 264 (8, 259–270).

*Remarks:* The specific name *triforata* is prefixed by a derivation of the Latin for 'three' and refers to presence of only three pairs of hysteronotal foramina, a state unique in *Paraphauloppia*. *P. triforata* is the smallest member of the genus, and is pale in colour with relatively short legs.

**Acknowledgments**

We are indebted to the Australian Biological Resources study for funding the salary of C.M.B. in a grant to D.C.L., and to Dr Henrick Enghoff (Zoological Museum, Copenhagen) for making available types of the type-species. Thanks are also due to Ms Kirstie Jamieson for the notation and presentation of the figures and Mrs Debbie Lowery and Ms Debbie Van Weenen for typing the manuscript.

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# LAKE FROME (SOUTH AUSTRALIA) ABORIGINAL TRAILS

*BY J. C. MCENTEE**

## Summary

This paper traces a previously unrecorded ceremonial route associated with the Flinders Ranges Aboriginal groups, and their interaction with the people from the Barrier Ranges area in western New South Wales. While most of the groups within the study area culturally practised circumcision, the Wilyakali did not. This cultural difference appeared not to interfere with other activities such as trade in ochre and grindstones or competitive social gatherings. The routes used for the interaction have been interpreted in terms of language and landscape recognition. The nature of the group gatherings has been pieced together with the assistance of the few remaining informants.

KEY WORDS: Lake Frome Plains (South Australia), interaction trails, circumcision, language

*Transactions of the Royal Society of S. Aust.* (1991), 115(4), 199-205

# LAKE FROME (SOUTH AUSTRALIA) ABORIGINAL TRAILS

by J. C. McENTEE*

## Imprimatur

JOHNA-LU IÑA-WAṬAÑA VIPAÑA WAṆḌU YUÑḌ-AÑG-ALU.

Whatever John has put down in this paper is very good. It is all right for anybody to read. I agree with John's use and meaning of the place names which I have learned from my family.

signed: Pearl McKenzie (Pearl McKenzie) 14.xi.90

## Summary

McENTEE, J. C. (1991) Lake Frome (South Australia) Aboriginal trails. *Trans. R. Soc. S. Aust.* 115(4), 199-205, 29 November, 1991.

This paper traces a previously unrecorded ceremonial route associated with the Flinders Ranges Aboriginal groups, and their interaction with the people from the Barrier Ranges area in western New South Wales. While most of the groups within the study area culturally practised circumcision, the Wilyakali did not. This cultural difference appeared not to interfere with other activities such as trade in ochre and grindstones or competitive social gatherings. The routes used for the interaction have been interpreted in terms of language and landscape recognition. The nature of the group gatherings has been pieced together with the assistance of the few remaining informants.

KEY WORDS: Lake Frome Plains (South Australia), interaction trails, circumcision, language

## Introduction

The existing word lists for the complex phonetic system of the ADÑAMAT̃AÑA language contained eighty to one hundred words prior to the work of Schebeck (1974). By the early 1970s it was realized that language use had declined markedly. In response to a special request from John and Pearl McKenzie of Hawker, South Australia, a word list approaching three thousand words was compiled gradually and a pronunciation guide with selective vocabulary was published by McEntee (1976).

The link between general anthropology and Aboriginal language provides the answers to many perplexing questions (McEntee unpublished). In particular, there are several ADÑAMAT̃AÑA language terms connected with mythical storytelling and navigation. For example, the word YAṬA WANDA- meaning 'to tell a story or myth' or literally 'to story tell the land' is derived from the words YAṬA meaning 'ground, country, land', and WANDA- meaning 'to tell a story'. ÑARRU ÑARRU means 'straight to a place', 'as the crow flies', YALPA-RI- means 'to be all in line' and YUWAL-AT̃A- means 'to find one's way across country'.

This paper clarifies these meanings with reference to ceremonial and social interaction among the various groups that lived on and around the Lake Frome Plains (Fig. 1), and to the local importance of landmarks and stories.

Gale (1986) reinforces this view concerning navigation:

> *"Aboriginal people developed a number of ways of depicting the countryside and defining routes to be taken . . . [they] constructed stylised and very practical maps of their environment". (Gale 1986 p. 41)*

Berndt (1987) described mythical ancestral travelling routes and Ngadjuri place names in the north of South Australia and McEntee (unpublished ms.) noted that at various stages, a number of these mythical story lines were placed in remarkably straight lines.

Requests for possible meanings of the Ngadjuri place names in Olary Province, mentioned in Berndt's paper (1987), because of the close relationship with ADÑAMAT̃AÑA, led to the idea of putting together some of the knowledge given by word of mouth by John McKenzie who died in 1986. He was a WIḶARU or fully initiated ADÑAMAT̃AÑA elder who had told the author about some of the interaction between the Flinders Ranges people and those in western New South Wales.

The generally accepted region where groups who did, and did not, practise circumcision shows trails of interaction across the Lake Frome Plains (Figs 1, 2; see also Beckett 1978). It was noted by Dix (1883) that the Boolcoomata people (ie. the Wilyakali) called the groups that practised circumcision Buerndoppa. This term should be compared with Yadliyawarra – Bardnapa, and ADÑAMAT̃AÑA – VAḌN-APA. Since the observation

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* Eridina Station, via Yunta S.Aust. 5440

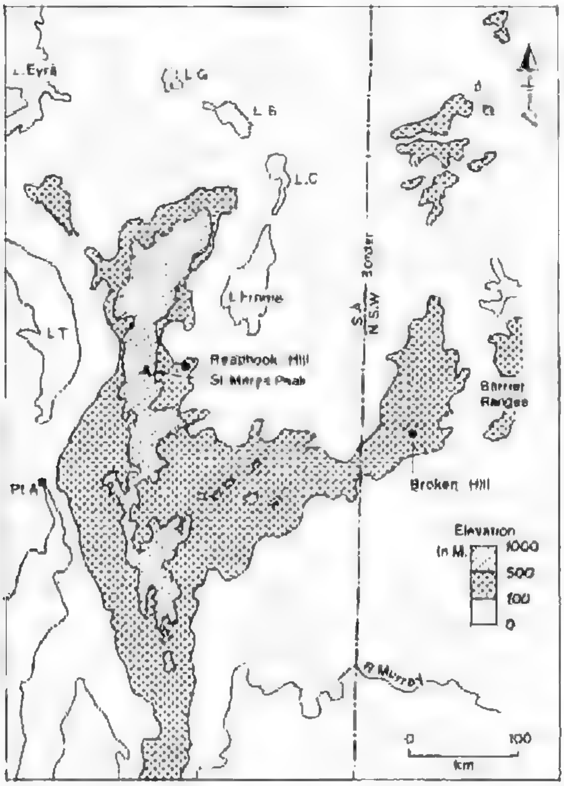

Fig. 1. Study site in the Flinders Ranges, Olary Uplands and Barrier Ranges. L.G. = Lake Gregory; L.B. = Lake Blanche; L.C. = Lake Callabonna; L.T. = Lake Torrens, Pt A = Port Augusta.

by Dix, there had been little investigatory work carried out in the area until that of Beckett (1967) who summarised language and dialect change in groups located in north west New South Wales. Beckett also showed that these groups displayed variations in the fulfilment of initiation requirements (Beckett 1967).

## Informants and the Trails

In the 1880s John McKenzie's father Fred was a lad working on Wirrealpa Station in the Flinders Ranges. In later years he passed on his knowledge to John who over the years retold many of these stories. In an interview in 1984, John described a meeting and a 'challenge match' between neighbouring groups as far off as western New South Wales, which he likened to 'the Olympic Games'. The following is a description by John of this challenge match with waddies, held sometime last century.

> *'There's been a challenge match. Some of the Aborigines from New South Wales, from Milparinka and Wilcannia, had a challenge match. They made a sort of challenge that they were just going to walk to Mt Serle and that the New South Wales people would beat 'em.*
>
> *These New South Wales people came across to challenge the Mt Serle tribe . . . I don't known how many of them . . . quite a mob. They made up their waddies [WIRRI] and they had to go down to Weedna Spring [WIDNA] in Mt Serle country where they held a challenge match to see which side would [win] but the Mt Serle mob won with the waddies they made.'*
> (Lampert Tapes 1984[1])

It is possible, even with sketchy information, to outline the route taken to travel from New South Wales to Mt Serle. One source of material is the legend of the Goanna VAḌNA and the Native Cat IDÑA (Mountford 1937–1941[2]). The legend concerns the illicit relationship between Goanna and Native Cat that caused them to flee from punishment. The story began at Poolamacca in the Barrier Ranges, north of Broken Hill. Goanna and Native Cat were very skilful at hiding and they hurried across the Mundi Mundi plain as they were being pursued by the angry elders of the group. Much of the storyline is lost but the trail would surely include known water sources in this arid plain. The couple reached the vicinity of Billeroo Waterhole on the Billeroo Creek KUMBILAÑA PARI. From there the travellers continued to Coombes Spring YUDLI-WADLU-ÑA meaning 'the bush *Scaevola spinescens* hollow' near the south-east shore of Lake Frome MUNDA (McEntee 1976, 1986). Munda means 'a trap net' in two ways – firstly from the physical shape of the lake and secondly from the fact that if one walks onto the lake there is a possibility of breaking through the salt crust and becoming trapped in the oozy mud. It is unclear whether the storyline goes across the lake but in view of the possibility of becoming trapped, it is likely that the storyline follows the southern shoreline to VUṚA-KARRA-ÑA waterhole in the Big John Creek (Fig. 2). The next place mentioned in the legend is Prism Hill VAḌNA WAḶATI-ÑA meaning 'goanna deep' or 'goanna has dug itself deeply into the ground'. This explains the origin of the large sand dune on the eastern side of Prism Hill. The hill is south of Wertaloona WAṬALU-ÑA meaning 'shadow coming over'. From there the storyline enters the Flinders Ranges to The John waterhole IRRAKA-ÑA. It passes near Mt McKinlay

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[1] Lampert, R. (1984) Unpublished tape recordings, held by collector.

[2] Mountford, C. P. (1937–1941) The Legend of the Native Cat VERLIITATITA and Goanna VARADNA. Research on the Flinders Ranges. Mountford – Sheard Collection, 4 myths, State Library of South Australia. Special Collection unpublished notebooks.

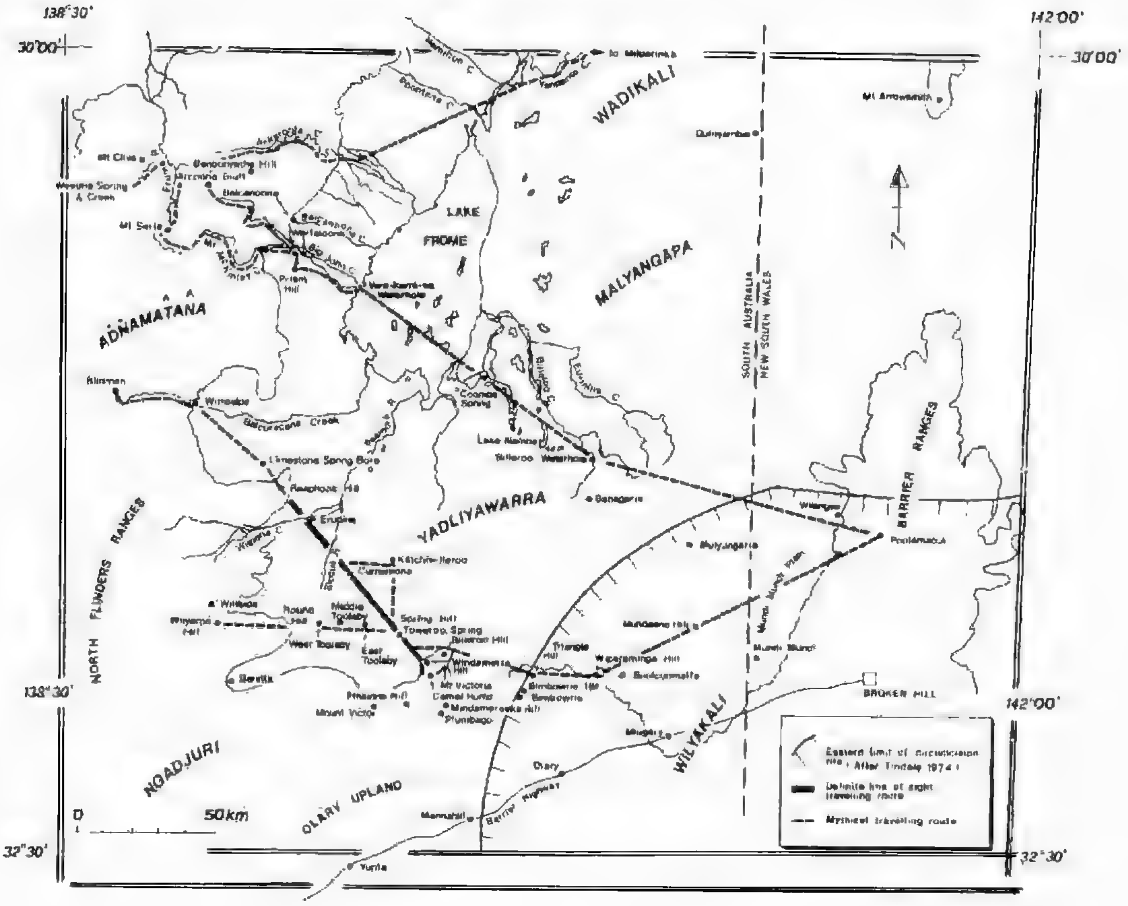

Fig. 2. Map of the Lake Frome Plains and surrounding ranges showing the country occupied by the Aboriginal Groups mentioned in the text and the 'line of sight' trail. The line on the map marking the eastern limit of circumcision is taken from Tindale (1974).

WAYAÑA meaning 'dodge this place' or 'don't go there'. The story ends near Arcoona Bluff ARKUÑA meaning 'red ochre' where Goanna and Native Cat were speared many times at a sandy patch known as YAÑGA-VUTI-VUTI meaning 'dusty liver', because their livers were pounded to dust by the elders as punishment. The spearings are an explanation of the spots on Goannas and Native Cats. From Arcoona Bluff it is not very far to Mt Serle ATU-WAṞAPA-ÑA. It is likely that the people from Milparinka, the Malyangapa group, travelled to Mt Serle via Yandama Creek which enters Lake Callabonna just north of Lake Frome. Once the northern extremity of Lake Frome is reached Mt McKinlay would be visible. The people from the Darling River probably followed the storyline from Poolamacca.

John McKenzie told of another 'challenge match' with the VAWUÑḌI people – likely the Wilyakali group – who travelled across to Blinman from the country around Bimbowrie. These people certainly had ties with Poolamacca, since some years after European settlement the Bimbowrie people returned to their former country at Poolamacca (Mawson & Hossfeld 1926). John McKenzie did not remember much detail about the VAWUÑḌI people, only that they did not practise circumcision. The ADÑAMAṮAÑA term for such groups was YADLARRA. It is of interest to compare this word with 'talara' mentioned by Dix (1883).

The following is a description of a competition using a specially curved throwing club known as the WAVA (Fig. 3b). The WAVA possessed a straight handle and as John described:

> *". . . The point of it had a bit of a curve in it, not a sharp curve, half straight. It had to be levelled off*

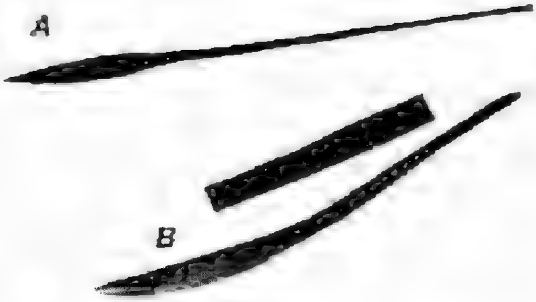

Fig. 3. Aboriginal Throwing Clubs. A = KUKURA, B WAVA. Scale = 30 cms. Photograph courtesy F. Teague.

> *at the point . . . had to put a certain point on it!*
> (Lampert Tapes 1984[1])

There was a second straight piece of green wood, the name of which had been forgotten. This was laid flat on the ground; as opposed to green brush or a bush which was used in another competition where the throwing stick was named KUKURA (Fig. 3a). The men were divided into two teams and took it in turns to throw the WAVA so that the point hit and then ricocheted off the wood lying on the ground until it came to rest with the point of the club facing away from the thrower. If the WAVA landed and came to rest at right angles to the thrower, there was no score. Likewise a foul throw was not counted and that particular competitor could not pick up the WAVA for a second try. The competitors would stand in a line, one behind the other, but alternatively, one team member and then the other team member. Two members of the same team could not stand together. There would be two men from each team standing at the place where the WAVA was going to land, to keep the score. If for example two mates from one team made a mistake like throwing consecutively, the scorekeeper would take away two points. That would contravene the rules.

John McKenzie gave the following account of a WAVA competition as told to him by his father:

> *"From Plamuka [Poolamacca] there was a lot of Aborigines . . . that is like the New South Wales mob. Somehow or other they sent a message like it might be specially two young fellows that go. They would just walk . . . get a bit of tucker to live on in between, to bring the message across. The New South Wales mob sent a message to Blinman, that they [the VAWUNDI] have to come across. Well they came from Plamuka to Wirrealpa, to Blinman. They played there . . . ah played there for about a week and won the game. All the Blinman people had to do was to pay them with rations . . . a bit of flour, tea, sugar, witchetty grubs and cooked meat . . . euro or wallaby."*
> (Lambert Tapes 1984[1])

Before returning to New South Wales they:

> *"Set about arranging the next challenge. The lot from Wirrealpa and Blinman had to go across to Plamuka because the others had come across to Blinman. They sent a message to say there would be another game of WAVA. There was a new horse and cart as a prize at Plamuka. That was the challenge . . . if the Blinman mob could win the game they could take home the horse and cart." [which in fact they did]*
> (Lampert Tapes 1984[1])

The possible route from Blinman to the Plumbago Hills and thence to meet the people at Poolamacca is contained in a fragmentary legend remembered by Pearl and Myra McKenzie, and recorded again by Tunbridge (1988). A family travelled from Blinman to Wirrealpa WIRA-WAḶPA meaning River Red Gum (McEntee 1986). *Eucalyptus camaldulensis* – 'dried vegetable matter' (Fig. 2). From Wirrealpa the line of travel led to Limestone Spring VANḌAIA-ÑA meaning 'hard, precipitated limestone', then through Nob Gap VILI-MAḶKA meaning 'ventral scales of a snake, marks', and then to Tooths Nob Ruins close to Reaphook Hill VILI-WARU-ÑA meaning 'ventral scales of a snake, facing'. This is in reference to the peak of Reaphook Hill which resembles the head and part of the underbelly of a Yellow-faced Whipsnake *Demansia psammophis* or WIPARU. Wiperu also happens to be the Ngadjuri name for Reaphook Hill (Berndt 1987).

From Reaphook Hill the track led to the vicinity of Erudina Station WIRA-VUDNU meaning 'thicket of *E. camaldulensis*.' From Erudina the trail led to the waterhole at Curnamona homestead WIRA-MAḶDA meaning 'clump of *E. camaldulensis*,' referring to the group of trees representing the family waiting at the waterhole, which according to the legend was dry at that time. If the waterhole at Curnamona happened to be dry, there was a chance of finding water by deviating a few kilometres from the straight track to a large swamp known as Katchiwilleroo KAḶDA-WADILU meaning the 'the Emu Bush, *Eremophila duttonii* hollow'. This plant grows around the swamp to this day. This swamp is capable of holding fresh water for twelve months after good rainfall. However, the legend describes the husband leaving his family at Curnamona and heading for Baratta Spring VAṚARIÑA meaning 'playing a joke', where he had to catch a kangaroo to skin to make a waterbag for his perishing family who had travelled in the meantime to Toweroo Spring (Aboriginal word unknown) at Spring Hill. The legend ends with the husband eventually catching up with his family and trying in vain to save them. In times of reasonable rainfall, a more direct route could be taken from Curnamona homestead to Toweroo Spring at Spring Hill. From this place the track could lead to a number of locations on Plumbago, Bimbowrie and Outalpa stations. Billeroo Hill is visible from Spring Hill and shows the way into the granite country where there would be assured water supplies. However the next feature in travelling the straight track from Spring Hill is Windamerta WIÑDAMAṬA meaning '*Tyto alba*, the Barn Owl, thick or stout' (McEntee 1986). The hill certainly looks like the forepart of an owl especially when viewed from the north west. It is uncertain from Berndt's notes whether Windamerta and Windagudna are separate places but Windagudna could possibly refer to the Camel Hump. WIÑDAKUDNA means 'Barn Owl droppings'. On top of Camel Hump is a white outcrop which looks very much as if a legendary owl left droppings at that place. The white outcrop is plainly visible from the north west of Windamerta and an Aboriginal painting site is located at the south western base of Camel Hump. John McKenzie often referred to the Barn Owl as a special bird.

Figs 2 & 4 show the landmarks standing in line of sight. By moving just 1 kilometre to the south west of Curnamona homestead, Spring Hill and Windamerta merge. By moving 1 kilometre to the north east of Curnamona an area of plains country shows between Windamerta and Spring Hill. If the travellers kept Spring Hill in sight from the Reaphook and Curnamona, they would have been assured of arriving at water supplies on the otherwise featureless plain. Conversely, by keeping the Reaphook in sight and the correct shape ( ṄALKA means shape) the reverse trip could be negotiated just as safely. Pearl McKenzie's niece, Myra also told of people who would gather at Willippa and head east, following the low hills to Spring Hill to meet up with the VAWUÑḌI people.

Hardy (1976) mentioned George Dutton who was born at Yancannia, but was brought up by his Malyangapa step-father as being:

> *"more strongly aware of what remained of the old landmarks that had guided his people"*
> (Hardy 1976 p. 202)

Unfortunately the interconnecting knowledge has died with the descendants of the Barrier Ranges people who ventured to the Flinders Ranges.

Two very similar legends concerning "Moon Man" are contained in Isaacs (1980). One version is told by George Dutton (Barkindji Story) and the other is told by May Wilton (AḌNAMAṬAÑA Story). Hercus (1982) recorded an identical southern Baagandji story. Basically the stories describe how a greedy uncle Moon Man with two wives, forbids his nephew to eat emu meat that had been caught during a hunt. The nephew decides to get even with his uncle by tricking the latter into climbing a tree having many witchetty grubs. The nephew keeps blowing on the tree to make it grow taller. He then asks Moon Man to try to touch the sky. As Moon Man grabs at the sky the nephew quickly makes the tree shrink, leaving his uncle stranded in the sky. The nephew then takes off with Moon Man's wives for himself.

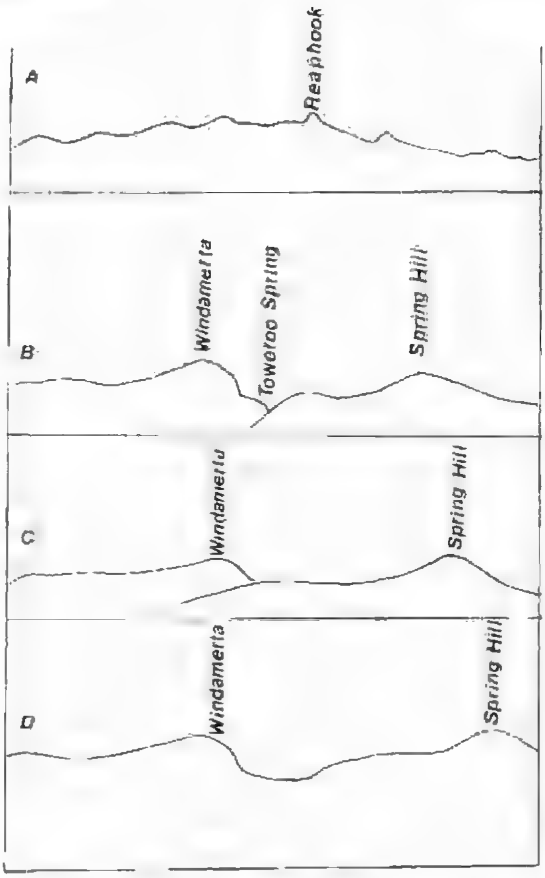

Fig. 4. Silhouettes of the Reaphook, Windamerta, Spring Hill and Toweroo Spring. A. The Reaphook. B. The straight line view from Curnamona Waterhole. C. The view 1 kilometre south west of Curnamona. D. The view 1 kilometre north east of Curnamona. Note that the precise location of Toweroo Spring in Views C and D is difficult to determine.

## Conclusions

These stories, travelling routes and the map show the relationship between country, travel and communication among Aboriginal people in the Flinders Ranges, the Olary Upland and the Barrier Ranges (Fig. 1).

Discussions over the years with John and Pearl McKenzie have shown that links between the people of western New South Wales and the people of the Flinders Ranges were even stronger than the links between the latter and the closely related Kuyani people to the west.

## Acknowledgments

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## Glossary

Many letters in the transcription used by the author for ADÑAMATAÑA words have similar corresponding sounds in English. However consonants with a superinscribed dot are lamino-palatal. Consonants with a subinscribed dot are retroflex and consonants with a superinscribed circumflex are lamino-dental. A bar over N denotes the velar nasal, as 'ng' in sing. The four intervocalic rhotics are transcribed thus: Ḍ and R for the flaps, RR for the trill and Ṛ for the glide. The three vowels A, I and U are similar to Italian in their pronunciation. Verbs appear in 'dictionary form' and therefore end in hyphens.

The words listed are ADÑAMATAÑA words unless otherwise stated.

| | |
|---|---|
| ADNA | stone, rock |
| ARKU | red ochre |
| IḊÑA | Native Cat; most likely *Dasyurus geoffroyi* (Gould, 1840) |
| KAL̇DA | Yadliyawarra word corresponding to ADÑAMATAÑA word AL̇DA '*Eremophila duttonii* F. Muell.', also '*E. freelingii* F. Muell'. |
| KUKLRA | name of straight competition throwing stick (Yadliyawarra ?) |
| KUDNA | Ngadjuri and Yadliyawarra word corresponding to the ADÑAMATAÑA word UDNA 'excrement' |
| KUMBILANA | Yadliyawarra place name, with unknown meaning. Part of Billeroo Creek |
| ÑALKA | shape or form |
| ÑARRU ÑARRU | straight to (a place), direct, express |
| PAṚI | Yadliyawarra - Malyangapa word corresponding to ADÑAMATAÑA word VAṚI 'creek' |
| VADNA | the sand goanna *Varanus gouldii* Gray |
| VADṆ-APA | first stage initiated male person |
| VANDATA | hard, precipitated limestone |
| VAṚARI- | to play a joke or prank |
| VAWUÑDI | appellation for group living around Bimbowrie and eastwards |
| VIPA | 1. ADÑAMATAÑA form of English word 'paper<br>2. May also mean 'thin sheet' as it is contained in the word ARRU VIPA 'cirrus cloud', literally 'grey thin sheet' |
| VILI | ventral scales of a snake |
| VUTI VUTI | dusty, powdered, pulverised |
| VUDNU | thicket of trees |
| VUṚA-KARRA-ÑA | Bottom John Waterhole in the Big John Creek. Possibly derived from VUṚA 'knee' and Yadliyawarra KARRA 'high' cf. ADÑAMATAÑA word ARRA 'high' |
| MATA | thick, stout, large |
| MATA, MATAÑA | plural-person-word attached to nouns, 'group', 'mob', hence ADÑAMATAÑA 'rock group' or 'people of the rocks' |
| MALKA | 1. the mulga tree *Acacia aneura* F. Muell. ex Benth.<br>2. marks |
| MALDA | 1. cheek<br>2. plural-plant-word attached to nouns, 'clump' |
| MUNDA | 1. Lake Frome<br>2. trap net used in hunting |
| YAÑGA | liver |
| YATA | earth, ground, country |
| YADLARRA | term for groups not practising circumcision |
| YALPA-RI- | intransitive verb meaning 'to be stacked', 'to be all in line' |
| YUDLI | the bush *Scaevola spinescens* R.Br. 'Fan Flower'. This word is also pronounced YUḊLI and YUDLI |
| YUNDU | to put down, to place |
| YUWAḶ-ATA- | composite verb meaning 'to find one's way across country' derived from YUWAḶU 'steam' and probably YATA- 'to stretch' |

| | |
|---|---|
| WADLU | Yadliyawarra word for 'hollow' or 'hole' as in waterhole |
| WAṬAT̂I | low down |
| WATALU | shadow coming over |
| WAṆḌU | good |
| WAṆDA- | to tell a story |
| WAVA | name of curved competition throwing stick |
| WAYA | to dodge, to steer clear, avoid |
| WARU | facing, facing towards |
| WAḶPA | dried vegetable matter |
| WIDNA | reeds |
| WIÑDA | the Barn Owl, *Tyto alba* Scopoli |
| WIPA | ant, *Iridomyrmex* spp. |
| WIPAṚU | the Whip Snake, *Demansia psammophis* Schlegel |
| WIRA | the River Red Gum, *Eucalyptus camaldulensis* Dehnh. (1823) |
| WIṚRI | waddy, club with knobbed end |
| WILAṚU | fully initiated male person |

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# A NEW TROMBELLID MITE (ACARINA: TROMBELLIDAE) FROM SOUTH AUSTRALIA

*BY R. V. SOUTHCOTT**

## Summary

*Austrotrombella leprosa* gen. et sp. nov. is described, for the adult and deutonymph, from south-eastern South Australia; the new genus is monotypic. Revised definitions are given for *Parathrombella* Andre, 1958 and *Durenia* Vercammen-Grandjean, 1955. Two species placed by Andre in *Parathrombella* are here reclassified as *Durenia vilhenae* (Andrè), comb. nov., and *D. gracilipalpe* (Andre), comb. nov.

KEY WORDS: Taxonomv. Acarina. Trombellidae. *Austrotrombella,* South Australia, adult, deutonymph. *Durenia, Parathrombella.*

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KEY WORDS: Taxonomy, Acarina, Trombellidae, *Austrotrombella*, South Australia, adult, deutonymph, *Durenia*, *Parathrombella*.

## Introduction

The mite family Trombellidae Thor, 1935, as restricted by Southcott (1986a, 1987), contains three genera known only as adults: *Parathrombella* André, 1958 (Africa), *Neonothrothrombidium* Robaux, 1968 (South America), and *Maiputrombella* Southcott, 1986a (South America). One genus, *Womersleyia* Radford, 1946 (Maldive Islands, southern Asia) is known only from the larva. For *Trombella* Berlese, 1887 (Europe, Africa, Australia) the adult, larval and deutonymphal instars have been described (see Southcott 1986a, b). For *Durenia* Vercammen-Grandjean, 1955 (Africa, South America, south-eastern Asia) the same instars are known (Vercammen-Grandjean, 1955; Robaux, 1968; Vercammen-Grandjean & Audy, 1959). For *Nothrotrombidium* Womersley, 1954 (adult) (Europe, south-eastern Asia, North America) larvae have been described by Feider (1958) and Southcott (1987).

This paper records the discovery of a new genus and species of trombellid, for the adult and deutonymphal instars, from south-eastern South Australia, described here. In consequence generic concepts in the Trombellidae are re-examined, redefinitions offered for *Durenia* and *Parathrombella*, and the reclassification of two species of *Parathrombella* as *Durenia*.

## Materials and Methods

Samples of wet soil with growing grasses and dicotyledonous herbs were collected from a site beneath a stand of *Leptospermum lanigerum* (Aiton) Smith near Robe, South Australia, in March 1990. The site, near a swamp edge, had been studied for four years for life history studies of trombiculid mites. Samples weighing 5-6 kg were placed in six large plastic pots and returned to Mitcham, S.A., where they were placed on a cement patio away from other vegetation and kept moist. At intervals of one month, half the contents of a pot were spread on a coarse wire mesh in a large Berlese funnel, and allowed to dry at ambient temperatures. The arthropod and other fauna were extracted live and examined daily. Among these were three adult and one deutonymphal trombellid mite, of a new genus and species. One adult (the holotype ♀) was alive and active, and an attempt to study its life history was made, by confining it in a tube with some of the site soil; however it died eight days later, without ovipositing. The other three specimens were found dead in the extraction jars, despite daily examinations.

The mites were cleared in 50% lactic acid and mounted in Hoyer's medium (Krantz, 1978). Fig. 1 was taken with a Leica M3 camera with bellows and ring extensions, with a 25 mm lens and flash illumination. All drawings were made with the aid of a camera lucida. All measurements are in micrometres (µm) unless otherwise specified. Setal and other terminology follows Southcott (1986a, b, 1987).

Material is deposited in the South Australian Museum, Adelaide (SAM).

## Genus *Austrotrombella* gen. nov.

*Definition:* Adult: Dorsum of idiosoma with four longitudinal columns of almost contiguous depressions lined with basal plates, heavily sclerotized and sculptured with irregular pits, from rounded to oblong and polygonal, each plate with a smaller more or less central area of much smaller pits. Anteromedian plate single, transverse, with two sensillary pits, well-separated, in its posterior part, each bearing one fine sensillary seta. All dorsal idiosomal plates lack normal setae (scobalae).

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* 2 Taylors Road, Mitcham, S. Aust. 5062.

Crista absent. Two sensory setae on each side, underneath anterior edge of anteromedian plate, the lateral ones resembling the prodorsal sensillary setae. In between the dorsal plates the integument carries simple chitinized structures ('cupolae'), each bearing one strong, simple, pointed seta. Ventral surface with coxae I and II, and III and IV of each side fused in a sclerotized plate; coxae bearing simple, pointed setae. Genital plate triangular, with several rounded pits at anterior and posterior ends of each lateral valve; setation of genital plate reduced. Legs with coarse setae, many robust, lanceolate. Hysterosoma with plates similar to dorsal, asetose, with cupolae on intervening integument.

Eyes apparently 2+2, with outer surfaces somewhat irregular.

Deutonymph: As for adult, but with genital plate reduced, each lateral valve with one large rounded pit at anterior and posterior ends.

Larva: not known.

*Recognition: Austrotrombella* may be separated from other adult (and deutonymphal) Trombellidae by replacing Caption 4 of Southcott (1986a, p. 164) with the following:

4 (3) Four depressions in lateral dorsal idiosomal column . . . . . *Parathrombella* André, 1958
Five or six depressions in lateral dorsal idiosomal column . . . . . . . . . . . . . . . . . 4A
4A (4) Five depressions in lateral dorsal idiosomal column; depressions without setae . . . . . . . . . . . . . . . . . . *Austrotrombella* gen. nov.
Six depressions in lateral dorsal idiosomal column; depressions with normal idiosomal setae (scobalae). . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . *Trombella* Berlese, 1887.

## *Austrotrombella leprosa* gen. et. sp. nov.

FIGS 1, 2, 3A–E, 4A–C

*Holotype:* ♀ SAM N1991112 (adult)
*Paratypes:* SAM N1991113, N1991114 (adults)

*Description of adult* (Figs 1, 2, 3A–*E*): Colour of idiosoma in life reddish brown dorsally, red ventrally, legs and palpi orange-red. Idiosoma oblong; in life 1220 long by 970 wide, total length to tip of chelicerae 1350; after mounting on slide idiosoma 1495 long by 1125 wide, total length 1855.

Details not covered in generic definition: Anteromedian plate transverse, 255 long by 364 wide, wider than two smaller plates immediately posterior; with a large central pit 28 long by 36 wide, lateral to which on each side a sensilligerous pit bearing a filiform seta 130 long; centres of sensilligerous pits 202 apart. Similar seta 145 long originates anterolaterally under anteromedian plate, and medial to this seta another seta 84 long; each seta arises from a small recessed pit. A series of narrow sculptured plates lies laterally along the idiosoma.

Fig. 1. *Austrotrombella leprosa* gen. et sp. nov., adult, holotype, live, dorsal view, from a Kodachrome

Ordinary setae (scobalae) absent from all dorsal and other idiosomal plates, but individual setae set in inter-plate integument, each arising from the summit of a strongly chitinized bell-shaped 'cupola' (see Figs 2, 3A)

Eyes 2+2, with irregular (i.e. non-spherical) external surfaces, set in small ocular plate underlying anteromedian and contiguous anterolateral dorsal plate; strong, pointed seta 102 long on adjacent cupola medial to eyes.

Ventral surface: coxal plates coarsely pitted, bearing simple pointed setae. Genital plate 336 long by 315 wide, each lateral valve bearing three rounded pits at anterior end and six at posterior end (paratype ACB1182 with 7–8 pits at posterior ends). Row of simple pointed setae, 34–50 long along medial edge of each valve, and few similar setae elsewhere on valves (see Fig 3B). No acetabula seen within genital aperture.

Anal plate roughly triangular, with rounded

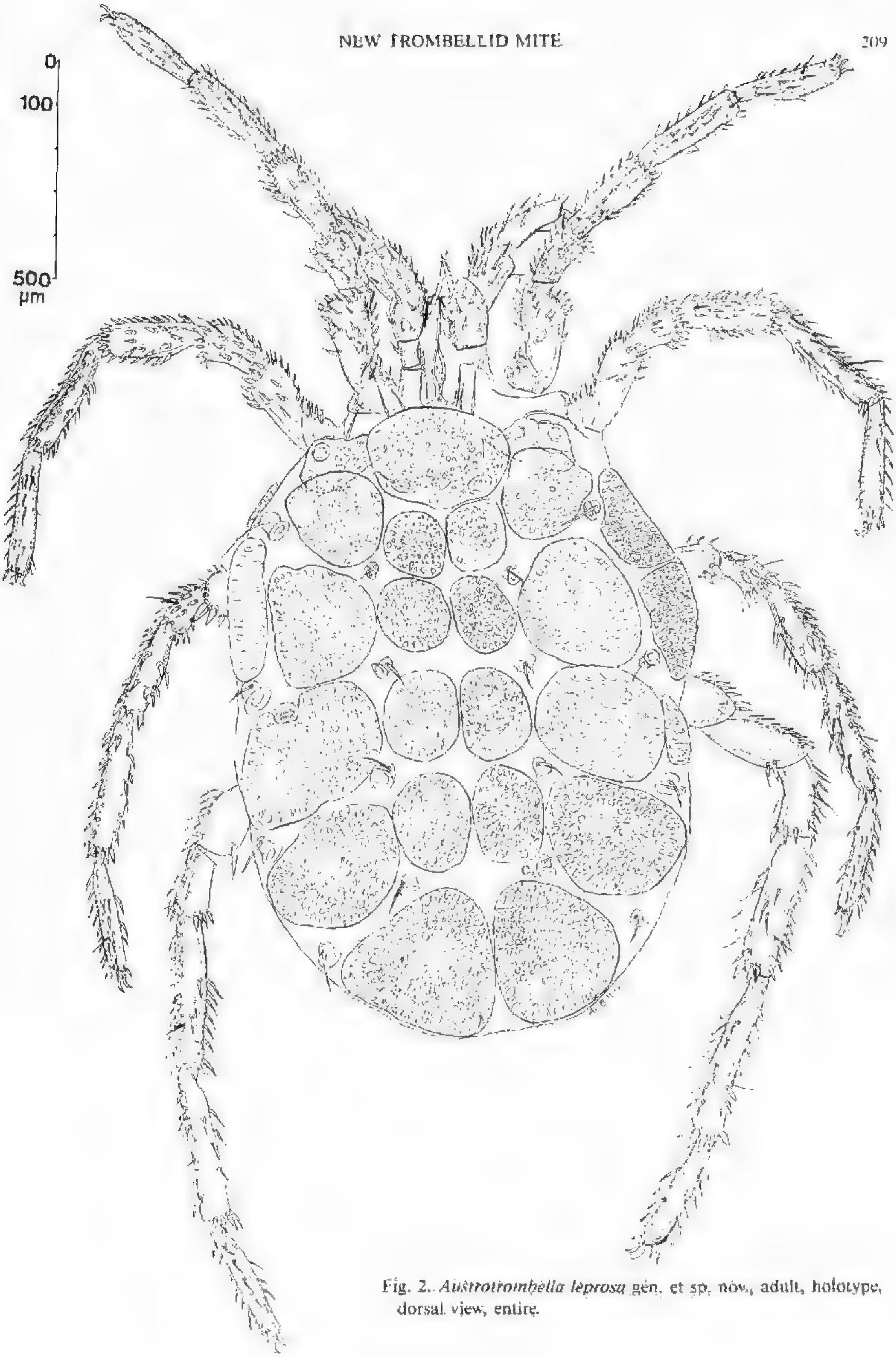

Fig. 2. *Austrotrombella leprosa* gen. et sp. nov., adult, holotype, dorsal view, entire.

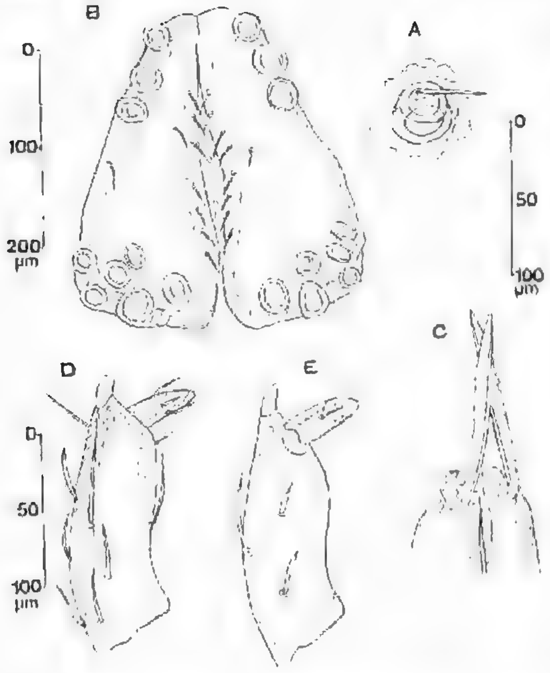

Fig. 3. *Austrotrombella leprosa* gen. et sp. nov., adult, holotype. A. Cupola, bearing seta ('c' in Fig. 1). B External genitalia. C Tip of chelicerae, dorsal. D Palp tibia and tarsus, dorsal. E Same, ventral. (Each to nearest scale).

angles; posterior angle obtuse; length 140, width 235; with pitting as for coxal and hysterosomal plates.

Hysterosoma with symmetrical plates similar to dorsal idiosomal plates, not seen clearly owing to thickness of preparations, but similar to those of deutonymph, *inf.*

Legs robust, lengths (including trochanter to tip of tarsal claws) I 1185, II 1255, III 1260, IV 1695. Legs well provided with coarse, pointed setae, mostly lanceolate to pointed-conical, generally simple, but some of the conical setae with fringing setules. Tarsi, particularly I, with reduced setation, setae mostly simple, lanceolate, pointed; few setae (also on tibiae) slender. Several minute solenoidalae on genua, tibiae and tarsi. Tarsal claws simple, falciform. Leg segmental measurements (genua-tarsi) as in Table 1.

Gnathosoma: cheliceral blades 125 long, pointed, straight, with 12-13 retrorse teeth, more outstanding peripherally. Palpi simplified, particularly tibia and tarsus; general setation similar to that of legs, much reduced on tibia and almost absent on tarsus; tibial claw strong, blunted.

*Description of deutonymph* (from paratype N1991115): (Fig. 4A-C).

Colour and general morphology similar to adult, but less heavily sclerotized. Idiosoma (mounted) 585 long by 405 wide; total length to tip of chelicerae 700. Anteromedian plate of dorsum 150 long by 270 wide, with its sensillary setae c.60 long; centres of sensilla 132 apart.

Eyes apparently 2+2, abortive, corneal surfaces aspherical.

Ventral surface: coxal plates as for adult, with setation of simple pointed hairs, 27–70 long, as figured. External genitalia trapezoidal, 104 long by 86 wide where widest, toward posterior end (Fig. 4B); each valve with one large rounded pit at each (anterior and posterior) end; medial edges of valves with few simple pointed setae 25–36 long. Anal plate obscured in preparation. Hysterosoma with large, pitted plates as figured. Integument between plates with seta-bearing cupolae as figured.

Legs similar to those of adult; lengths (including trochanter to tip of tarsal claws) I 670, II 680, III 665, IV 850. Leg segmental measurements as in Table 1. Leg setation similar to adult.

Gnathosoma: cheliceral blades similar to adult, with c. 13 retrorse teeth. Palpi similar to adult but

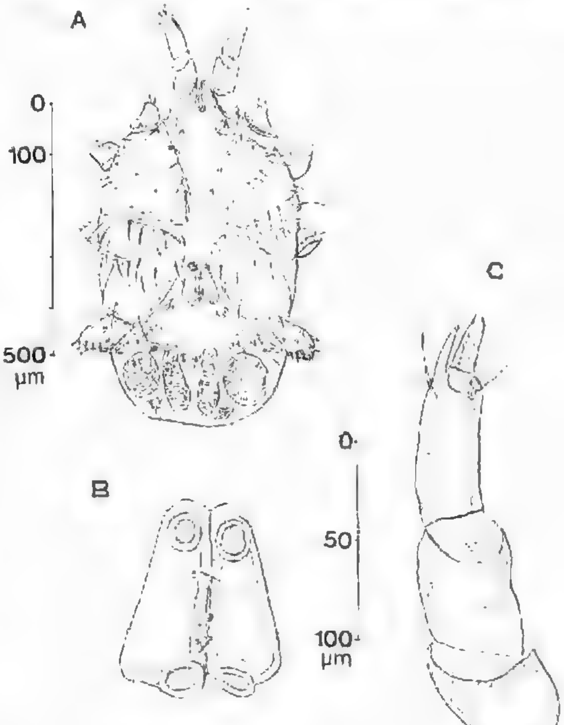

Fig. 4. *Austrotrombella leprosa* gen. et sp. nov., deutonymph, paratype. A Ventral view, legs omitted beyond trochanters. B External genitalia. C Palp, femur to tarsus, ventral. (Each to nearer scale).

TABLE 1. *Leg segmental measurements for* Austrotrombella leprosa *gen. et sp. nov. Data shown as mean ± standard deviation, with the range in parentheses.*

| | Adults | | | Deutonymph |
|---|---|---|---|---|
| | Holotype ACB1132♀ | n | | Paratype ACB1216 |
| GeI | 235 | 3 | 238.7±22.72<br>(218-263) | 125 |
| TiI | 277 | 3 | 277.0±25.00<br>(252-302) | 153 |
| TaI(L) | 258 | 3 | 259.3±19.04<br>(241-279) | 154 |
| TaI(H) | 67 | 3 | 64.3±7.37<br>(56-70) | 36 |
| TiI/GeI | 1.18 | 3 | 1.163±0.0153<br>(1.15-1.18) | 1.22 |
| GeII | 242 | 3 | 249.3±25.79<br>(228-278) | 120 |
| TiII | 308 | 3 | 312.7±33.25<br>(282-348 | 156 |
| TaII(L) | 283 | 3 | 291.0±14.73<br>(282-308) | 168 |
| TaII(H) | 62 | 3 | 61.3±3.055<br>(58-64) | 37 |
| TiII/GeII | 1.27 | 3 | 1.253±0.0153<br>(1.24-1.27) | 1.30 |
| GeIII | 244 | 3 | 249.7±30.89<br>(222-283) | 116 |
| TiIII | 319 | 3 | 328.3±39.83<br>(294-372) | 160 |
| TaIII(L) | 288 | 3 | 294.3±27.06<br>(271-324) | 165 |
| TaIII(H) | 48 | 3 | 48.7±7.02<br>(42-56) | 31 |
| TiIII/GeIII | 1.31 | 3 | 1.313±0.00577<br>(1.31-1.32) | 1.38 |
| GeIV | 382 | 3 | 390.3±56.96<br>(338-451) | 174 |
| TiIV | 369 | 3 | 387.0±51.42<br>(347-445) | 196 |
| TaIV(L) | 309 | 3 | 314.7±22.05<br>(296-339) | 174 |
| TaIV(H) | 43 | 3 | 48.0±9.54<br>(42-59) | 31 |
| TiIV/GeIV | 1.04 | 3 | 1.023±0.0208<br>(1.00-1.04) | 1.13 |

less setose, e.g. palpal tibia with four pointed setae, palpal tarsus with about five flattened, simple setae.

*Material examined:* South Australia: Robe district, Map Reference (Penola 1: 250,000) 283411, in wet, alkaline, shellgrit – containing soil near swamp edge, under a stand of *Leptospermum lanigerum* (Aiton) Smith, collected 22.iii.1990, R. V. Southcott, and successively extracted by drying through Berlese funnels. Holotype SAM N1991112 (ACB 1132) obtained on 2.iv.1990 (adult); died 10.iv.1990. Paratype adults SAM N1991113, N1991114 (ACB 1152, ACB 1182) obtained dead on 5.v.1990 and 12.vi.1990 respectively. Paratype deutonymph SAM N1991115 (ACB 1216) obtained 7.xii.1990.

*Etymology: Austrotrombella* from 'australis' (southern) and 'Australia', and *'Trombella'; leprosa* refers to the appearance in life, as though the dorsum is covered with ulcers.

*Remarks on taxonomy: Austrotrombella* is very distinct from its nearest genera (see the rubrics above). The palp is more obsolete than that in any other described trombellid.

*Remarks on biology:* All specimens came from wet soil. Although the extraction jars were examined daily, only the holotype adult was obtained alive. Evidently this species is sensitive to desiccation.

## Comment on classification of Trombellidae

André (1958) described *Parathrombella* with type species *P. nasuta* André, 1958, and (*l.c.*) two other species from Angola, *P. vilhenae* and *P. gracilipalpe*. From André's descriptions it is clear that the latter two species lack the dorsal plates present in *P. nasuta*, and bear dorsally and anterolaterally on the idiosoma the two small pits which Vercammen-Grandjean (1955) recorded in *Durenia* Vercammen-Grandjean, 1955; they also have similar leg structure to that of *D. bukavuensis* Vercammen-Grandjean, 1955 (Africa) and *D. glandulosa* Robaux, 1968 (South America). These two species of André are here reclassified as *Durenia vilhenae* (André), comb. nov., and *D. gracilipalpe* (André), comb. nov.

The following revised generic definitions are offered:

### *Durenia* Vercammen-Grandjean, 1955

*Definition:* Adult: Trombellidae. Eyes 2+2. Dorsum of idiosoma with two small anterolateral pits, but lacking columns of depressions or depilate areas. Larva: Trombellidae. Eyes 2+2. Pedocoxal setal formula 2, 1, 1. Pedotarsal claws 1, 1, 2. Nasus of dorsal scutum large, triangular, its lateral border continuous with anterolateral border of scutum, with at most only small constriction. Leg tibia III without a large solenoidala.

Type species: *Durenia bukavuensis* Vercammen-Grandjean, 1955.

*Remarks:* *Durenia* is at present known for three African and one South American species in post-larval instars, and (as a larva only) for *D. singaporensis* Vercammen-Grandjean & Audy, 1959 (south-eastern Asia). Larva to deutonymph correlation was established by Vercammen-Grandjean (1955) with the type species.

### *Parathrombella* André, 1958

*Definition:* Adult: Trombellidae. Eyes 1+1. Dorsum of idiosoma with three longitudinal columns of depilate depressions, four in each lateral column. Larva: Not known.

*Remarks:* At present restricted to the type species *P. nasuta* André, from Angola.

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# CRYPTIC SPECIES IN POPULATIONS OF *GLOBOCEPHALOIDES TRIFIDOSPICULARIS* KUNG (NEMATODA: TRICHOSTRONGYLOIDEA), PARASITIC IN MACROPODID MARSUPIALS

*BY D. L. OBENDORF*, I. BEVERIDGE*, & R. H. ANDREWS†*

## Summary

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KEY WORDS: *Globocephaloides; Amphicephaloides; Macropus; Thylogale;* allozyme electrophoresis; cryptic species

*Transactions of the Royal Society of S. Aust.* (1991), 115(4), 213-216.

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OBENDORF, D. L., BEVERIDGE, I. & ANDREWS, R. A. (1991) Cryptic species in populations of *Globocephaloides trifidospicularis* Kung (Nematoda: Trichostrongyloidea) parasitic in macropodid marsupials. *Trans. R. Soc. S. Aust.* 115(4), 213-216, 29 November, 1991.

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## Introduction

*Globocephaloides trifidospicularis* Kung, 1948 is a common duodenal parasite of a number of macropodid marsupial species from south-eastern Australia (Beveridge 1979). Because it feeds on the blood of the host, this nematode species is capable of causing mortality in eastern grey kangaroo (*Macropus giganteus*) populations, particularly in juvenile animals (Arundel *et al.* 1990). In a taxonomic revision of the sub-family Globocephaloidinae, Beveridge (1979) concluded that a single, morphologically variable species occurred in *Macropus giganteus, M. fuliginosus, M. rufogriseus, M. eugenii, M. parryi* and *Wallabia bicolor* in the south-eastern region of the continent.

During an investigation into mortalities in *M. giganteus* on Maria Island, Tasmania (42°38'S, 148°05'E), in which *G. trifidospicularis* was involved, it was observed that *M. rufogriseus*, also parasitised by *Globocephaloides*, remained unaffected (D. L. Obendorf unpubl. data). These observations suggested that the nematodes infecting the two macropodid hosts might belong to different species. The present study aimed to test this hypothesis using the technique of allozyme electrophoresis, a powerful means of testing the existence of sibling species (Richardson *et. al.* 1986).

## Materials and Methods

Specimens of *Globocephaloides* were collected from the duodena of *M. giganteus* from Mt William, Tas. (40°55'S, 148°15'E), and from *M. rufogriseus* from Trevallyn, Tas. (41°27'S, 147°05'E). Nematodes were washed in saline and frozen in the wells of micro-titre plates at -80°C until processing. As an outgroup, specimens of a related genus and species *Amphicephaloides thylogale*, a duodenal parasite of *Thylogale* spp., were utilised; they were derived from *Thylogale billardierii* from the Launceston area, Tas.

Because of their small size, pools of nematodes rather than individuals were examined. Homogenates were prepared by adding an equal volume of homogenising solution (Richardson *et al.* 1986) to thawed samples, sonicating and centrifuging at 5000g for 10 min at 4°C. Electrophoresis was conducted on cellulose acetate ("Cellogel", Chemetron, Milan) according to the methods of Richardson *et al.* (1986).

Forty-five enzymes were screened for suitability as enzyme markers. Thirty-two enzymes showed activity following histochemical staining in at least one sample of either *Globocephaloides* or *Amphicephaloides*. The enzyme names, abbreviations and Enzyme Commission codes (E.C.) for these enzymes are as follows: acid phospbatase (ACP, E.C. 3.1.3.2.), adenosine deaminase (ADA, E.C. 3.5.4.4.), alcohol dehydrogenase (ADH, E.C. 1.1.1.1.), adenylate kinase (AK, E.C. 2.7.4.3), aldolase (ALD, E.C. 4.1.2.13), diaphorase (DIA, E.C. 1.8.1.4), enolase (ENOL, E.C. 4.2.1.11), esterase (EST, E.C. 3.1.1.1), fumarate hydratase (FUM, E.C. 4.2.1.2), guanine deaminase (GDA, E.C. 1.4.1.3), glutamate dehydrogenase (GDH, E.C. 1.4.1.3), aspartate

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aminotransferase (GOT, E.C. 2.6.1.1), glucose-6-phosphate dehydrogenase (G6PD, E.C. 1.1.1.49); glucose phosphate isomerase (GPI, E.C. 5.3.1.9), alanine aminotransferase (GPT, E.C. 2.6.1.2), glutathione reductase (GSR, E.C. 1.6.4.7), hexosaminidase (HEX, E.C. 3.5.1.52), isocitrate dehydrogenase (IDH, E.C. 1.1.1.42), leucine aminopeptidase (LAP, E.C. 3.4.11.1), lactate dehydrogenase (LDH, E.C. 1.1.1.27), malate dehydrogenase (MDH, E.C. 1.1.1.37), mannose-phosphate isomerase (MPI, E.C. 5.3.1.8), purine nucleoside phosphorylase (NP, E.C. 2.4.2.1), peptidase valine-leucine (PEP-A, E.C. 3.4.13.11), peptidase leucine-glycine-glycine (PEP-B, E.C. 3.4.11.4), phosphoglycerate mutase (PGAM, E.C. 5.2.4.1), phosphoglycerate kinase (PGK, E.C. 2.7.2.3), phosphoglucomutase (PGM, E.C. 5.2.4.2), pyruvate kinase (PK, E.C. 2.7.1.40), triose-phosphate isomerase (TPI, E.C. 5.3.11), U.P.D.-glucose pyrophosphorylase (UGPP, E.C. 2.7.7.9) and xanthine oxidase (XO, E.C. 1.1.3.22).

Representative specimens of the two nematode populations from Maria I. were fixed in 10% formalin and cleared in lactophenol for examination. Measurements were made with an ocular micrometer on five male and five female *Globocephaloides* from the two macropodid hosts.

Representative specimens from both hosts from various areas of Tasmania have been deposited in the South Australian Museum: from *M. giganteus* HC 9187, 16572, 16581-3, 16612; from *M. rufogriseus* HC 9164, 10742, 14843-4, 10799, 16440.

## Results

Sufficient staining intensity and resolution for reliable genetic interpretation was observed for 23 enzymes, encoded by a presumptive 24 loci. A further nine enzymes stained but showed sub-optimal activity. Of the 24 enzyme loci scored (Table 1), fixed allelic differences occurred between the two populations of *Globocephaloides* at four loci (*Ada-2, Idh-2, Got, Pep-B*) (17%). Fixed differences between both samples of *Globocephaloides* and *Amphicephaloides* occurred at 14 of the 24 (58%) loci examined (Table 1).

The following enzyme loci were invariant between samples: *Ald, Dia, Gpt, Mdh, Pgam* and *Tpi*.

Detected morphological differences between the two populations of *Globocephaloides* were slight (Table 2). Specimens from *M. giganteus* were marginally longer than those from *M. rufogriseus*, and the females were substantially stouter. The spicules were slightly longer in specimens from *M. giganteus*, but when expressed as a percentage of total body length, were similar to specimens from *M. rufogriseus*. Female nematodes from *M. giganteus* contained substantially more eggs in the anterior and posterior uteri when compared with females from *M. rufogriseus*. In nematodes from *M. giganteus*, there were significantly more eggs in the anterior uterus.

## Discussion

Although allozyme analyses were limited to results obtained from pools of nematodes rather than individuals (because of their small size), fixed allelic differences were found at four of 24 (17%) of the loci examined for the two populations of *Globocephaloides*. Typically, allopatric gene pools having fixed differences at more than 15% of

TABLE 1. *Summary of allelic differences between pools of* Globocephaloides *from* Macropus giganteus *(A) and* Macropus rufogriseus *(B) and pools of* Amphicephaloides thylogale *from* Thylogale billardierii.

| | Enzyme Locus* | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Species | *Acp* | *Ada-1* | *Ada-2* | *Ak* | *Enol* | *Est* | *Fum* | *Gda* | *Got* | *Gpi* | *Gsr* | *Idh* | *Lap* | *Ldh* | *Mpi* | *Pep-A* | *Pep-B* | *Ugpp* |
| *Globocephaloides* A | — | cd‡ | b | a† | d | — | b | — | b | a | a | c | a | b | de | b | c | b |
| *Globocephaloides* B | b | bc | c | a | bd | b | b | c | ac | a | a | b | a | b | de | b | b | b |
| *Amphicephaloides* | a | ab | a | b | ac | a | ab | ac | a | b | b | a | b | a | a/b/c§ | a | a | a |

* Multiple loci are designated numerically according to increasing electrophoretic mobility.

† Alleles are designated alphabetically, where a is the most cathodally migrating allele.

‡ Heterozygosity is represented by the two homologous alleles, ie ab, bc etc.

§ Where electrophoretic patterns did not conform to expectations for heterozygosity (eg MPI, a monomeric enzyme where heterozygotes should be double-banded) samples were depicted as possessing a mixture (/) of allozymes (eg for the monomeric enzyme MPI, the *Amphicephaloides* sample had a mixture of three allozymes a/b/c).

— Staining intensity and resolution was not sufficient to allow unequivocal genetic interpretation

TABLE 2. *Measurements (in millimetres) of* Globocephaloides trifidospicularis *from* Macropus giganteus *and* M. rufogriseus *from Maria I., Tas. (mean of five measurements in parentheses).*

| | *M. giganteus* | *M. rufogriseus* |
|---|---|---|
| Total length ♂ | 9.2-11.1 (10.1) | 7.6-8.6 (8.2) |
| ♀ | 11.1-13.4 (11.8) | 9.9-11.3 (10.7) |
| Maximum width ♀ | 0.38-0.51 (0.45) | 0.23-0.36 (0.30) |
| Spicule length ♂ | 0.54-0.60 (0.56) | 0.43-0.47 (0.45) |
| Spicule length as % of body length | 4.82-6.49 (5.61) | 5.26-5.72 (5.51) |
| No. of eggs in anterior uterus | 92-139 (119) | 13-61 (43) |
| No. of eggs in posterior uterus | 50-132 (103) | 14-68 (47) |

enzyme loci belong to different biological species (see Richardson *et al* 1986). Thus the data presented here suggest that the two populations of *Globocephaloides* examined represent distinct species. However, there is reason to believe that the two nematode taxa are in fact sympatric, even though our samples were not collected at the same site. The two hosts are sympatric over much of their geographical range in Tasmania (Calaby 1983; Kirsch & Poole 1972), and in addition the same two host species on the mainland have a substantial overlap (74%) in diet (Jarman & Phillips 1989). Since *G. trifidospicularis* infects its host orally (Beveridge 1979) the two populations of nematodes in *M. giganteus* and *M. rufogriseus* are essentially sympatric. The morphological differences noted between nematode specimens occurs irrespective of the locality of collection within Tasmania, suggesting that the segregation is by host rather than by geography, and that collecting from any location in Tasmania would yield similar results. In the case of a sympatry, a single fixed allelic difference is sufficient to indicate a lack of gene flow and hence the presence of distinct biological species (Richardson *et al.* 1986). Thus, the demonstration of four fixed allelic differences between these nematode populations would indicate that they belong to distinct biological species. The much greater proportion of fixed differences for both species of *Globocephaloides* and *Amphicephaloides* (58%) supports the generic distinction made between them at the morphological level (Beveridge 1979).

The genetic differences between the two species of *Globocephaloides* are matched by quite minor morphological differences (Table 2). The latter would probably not be considered significant in the absence of genetic data. The difference in absolute size in spicule length is not marked when considered as a percentage of total body length, and in the case of both male and female nematodes, differences in overall body size may have been discounted as being host-induced. Numbers of eggs in the uteri of female worms are not generally considered a reliable taxonomic character in trichostrongyloid genera, and a variety of factors, including exposure to chemicals (Hotson *et al.* 1970), can influence the number of eggs present. This feature as well as differences in egg number between anterior and posterior uteri have, however, been utilised advantageously for taxonomic purposes in the case of the trichostrongyloid nematodes of monotremes (Durette-Desset & Cassone 1983). It appears therefore that in the case of *G. trifidospicularis*, relatively minor morphological differences may indicate the existence of sibling species.

The results presented here raise questions as to the status of records of *G. trifidospicularis* in other macropodid host species. Unsuccessful attempts to infect worm-free *M. eugenii* with *G. trifidospicularis* derived from *M. giganteus* (I. Beveridge unpubl. data), may indicate that the nematode in *M. eugenii* is an independent sibling species. The status of specimens from *M. parryi* and *W. bicolor* also remains to be investigated. The type host of *G. trifidospicularis* is *M. rufogriseus*, the original description being based on specimens obtained from wallabies housed at the Regent's Park Zoo (Kung 1948). Beveridge's (1979) redescription is based on material from *M. giganteus* from Victoria and therefore probably represents an undescribed species. No new names are proposed here, pending the clarification of the status of *G. trifidospicularis*-like nematodes in other macropodid host species.

In northern Australia, *G. trifidospicularis* is replaced by two congeners, *G. affinis* occurring almost exclusively in the black-striped wallaby, *Macropus dorsalis*, and *G. macropodis* occurring in a wide range of host species (Beveridge 1979; Beveridge *et al.* 1984). The results obtained in this study suggest that a similar analysis of *G. macropodis* may be appropriate.

The slight morphological differences observed here between the populations of *Globocephaloides* from *M. giganteus* and *M. rufogriseus*, indicate the care which needs to be taken when morphologically similar parasites from different hosts are assigned to the same taxon. The results have significant practical implications, since in the mortalities observed in *M. giganteus* on Maria I., *M. rufogriseus* was not acting as an alternative or reservoir host for the parasite. Plans to reduce the densities of kangaroos in order to control the adverse effects of this nematode parasite probably do not therefore need to take account of sympatric *M. rufogriseus* populations.

## Acknowledgments

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# A NEW SPECIES OF *ANTECHINIELLA* QUENTIN & BEVERIDGE, 1986 (NEMATODA: ACUARIIDAE) FROM THE AUSTRALIAN WATER RAT, *HYDROMYS CHRYSOGASTER* GEOFFROY, 1804.

*BY LESLEY R. SMALES**

## Summary

*Antechiniella sertatum* sp. nov. (Nematoda) is described from the Australian water rat, *Hydromys chrysogaster* Geoffroy, 1804. *It* differs from its single congener, *A. suffodiax,* in length of body and oesophagus, length and disposition of cordons, length of spicule and proportions of the female tail. The genus is one of only three in the family Acuariidae parasitising mammals. Dietary preferences and feeding habits of the insectivore, dasyurid, procyonid and rodent hosts of these genera may be important factors in host distribution and occurrence of infections.

KEY WORDS: Nematoda, Spirurida, *Antechiniella,* rodent, *Hydromys*

*Transactions of the Royal Society of S. Aust.* (1991), 115(4), 217–220.

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KEY WORDS: Nematoda, Spirurida, *Antechiniella*, rodent, *Hydromys*

## Introduction

Although acuariid nematodes occur principally in birds, a few occur in mammals. These were reviewed by Quentin & Beveridge (1986). They concluded, on the basis of cephalic ontogeny that the three species previously grouped in the genus *Stammerinema* Osche, 1955 (Acuariinae) had different phylogenetic origins. Only the species from holarctic insectivores should remain in the *Stammerinema*, while the species from neotropical procyonids should be referred to the *Skrjabinoclava* Sobolev, 1943 (Acuariinae). The third, from Australian marsupials and rodents, should be referred to a new genus *Antechiniella* to be placed in the Seuratiinae. *A. suffodiax* (Beveridge & Barker, 1975), first described from the Australian marsupial *Antechinus stuartii* Macleay, 1841, was later reported from *Rattus lutreolus* and *R. fuscipes* in Victoria by Obendorf (1979). This was noted by Quentin & Beveridge (1986), but they did not include rodents as hosts in their diagnosis of the genus, nor did they indicate the reasons for this omission. In recent collections of parasites from another rodent, the water rat, *Hydromys chrysogaster* Geoffroy, 1804, a second species of *Antechiniella* has been found.

## Materials and Methods

Nematodes were collected from one water rat from Back Valley, South Australia in August 1988 and from three water rats from the Inman River, S.A., in February 1989. Stomachs were digested in 1% pepsin (pH = 1) at 40°C for up to 2 hours, and the nematodes were dissected free from surrounding gastric tissues. Nematodes were fixed in 70% ethanol, 5% formalin or glacial acetic acid. Additional material, from S.A. and Victoria, held in the Australian Helminthological Collection (AHC), at the South Australian Museum (SAM), lots 1682, 1698, 1764, 4610, 4611, 5326, 14829, was also examined. Only two females and five males remained intact. In addition anterior or posterior ends of some males and females were preserved. Accordingly measurements are from 5–10 male and 2–6 female specimens. Specimens were cleared in lactophenol. Measurements, in µm unless otherwise stated, with the range followed by the mean, were made with the aid of an ocular micrometer, drawing tube and measuring wheel. Illustrations were prepared with the aid of a drawing tube. All specimens have been deposited in the South Australian Museum.

### *Antechiniella sertatum* sp. nov.
### FIGS 1-12

*Etymology:* The specific name *sertatum* is derived from the Latin 'a garland' and refers to the cordons around the anterior end.

*Description:* Seuratiinae. Long worms with anterior half of body considerably dilated. Cuticle thickened irregularly on narrowest mid-section of body adjacent to point of emergence from host stomach wall, leading to slight widening towards posterior end. Two large pseudolabia present; cordons prominent, transversely striated, with deep wide median groove. Cordons anastomosing, extend dorsolaterally and ventrolaterally along pseudolabia and sides of head, extend posteriorly almost to nerve cord, turn towards one another and fuse, recurr to level of distal pharynx. Deirids bicuspid.

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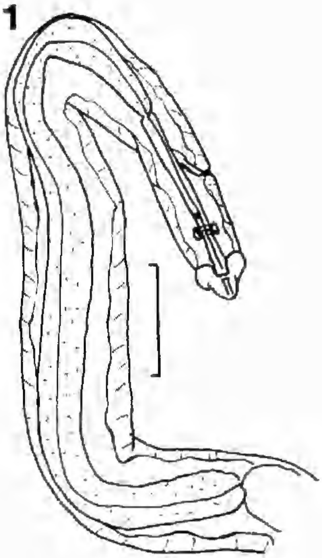

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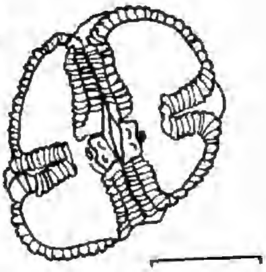

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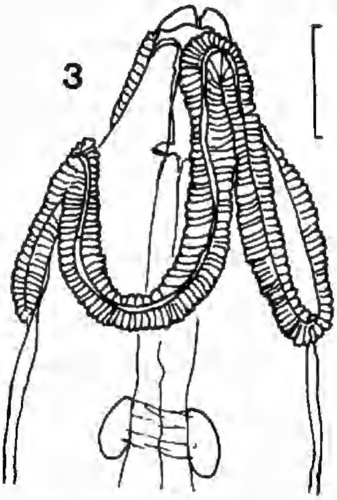

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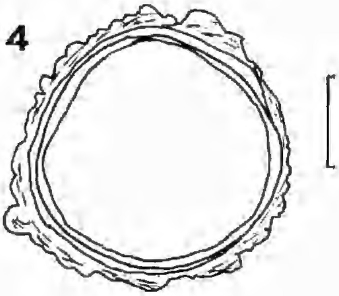

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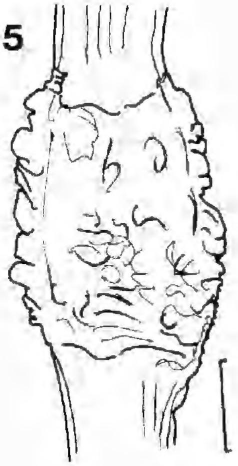

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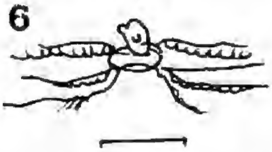

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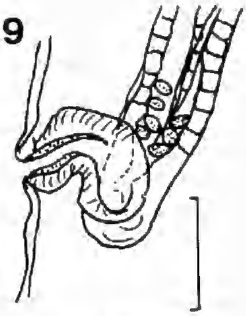

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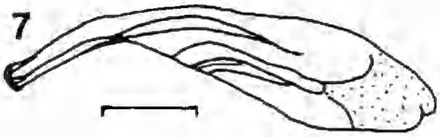

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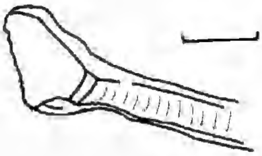

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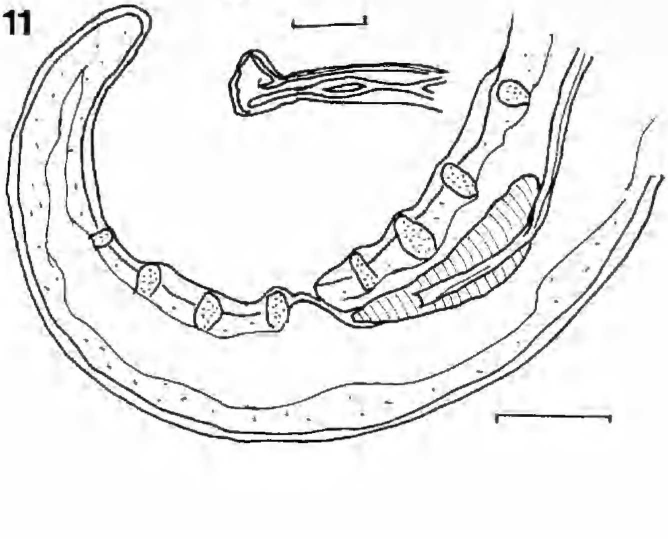

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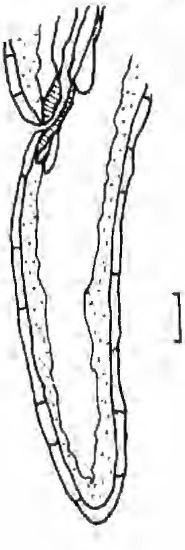

Male: Length 18–38 (31) mm. Maximum width 340–770 (627), minimum width 160–225 (189). Cordons extend 100–240 (189) from anterior end. Pharynx conical, 64–90 (73) long. Anterior muscular oesophagus 500–790 (656) and posterior glandular oesophagus 2880–4000 (3426) long. Nerve ring around muscular oesophagus 220–300 (273) from anterior end, excretory pore 360–550 (478) and deirids 248–380 (333) from anterior end. Left spicule 620–1140 (927) long, flared at proximal end, triangular in section, alae not seen. Right spicule blunt tipped 140–230 (193) long. Four pre-anal and four post-anal pairs of pedunculated papillae present.

Female: Length 30–42 (36)mm. Maximum width 1425–1525 (1475), minimum width 250–275 (263). Cordons extend 260–380 (320) from anterior end. Pharynx conical, 60–100 (92) long. Anterior muscular oesophagus 775–1000 (886) and posterior glandular oesophagus 3250–4325 (3888) long. Nerve ring around muscular oesophagus 310–360 (337) from anterior end, excretory pore 490–720 (605) and deirids 430–540 (485) from anterior end. Vulva situated 7–13.5 (9)mm from posterior end. Vagina vera very short about 250. Tail 268–380 (328) long, tip rounded. Eggs smooth, thick shelled 42.5–47.5 (43.0) × 30.0–32.5 (32.0).

*Type specimens:* Holotype SAM V4148. Allotype, SAM V4149. Paratypes, AHC 18392.

*Type host: Hydromys chrysogaster* Geoffroy, 1804, the water rat.

*Type locality:* Inman River, S.A.

*Site of infection:* Stomach.

## Discussion

This species differs from its congener, *A. suffodiax*, as follows (measurements of males are given unless otherwise stated): greater length of body 18.0–38.0 (31.0)mm compared with 17.2–23.6 (18.9)mm; longer posterior extent, 100–240 (189) as compared with 65–180 (100), and disposition of cordons; and greater length of oesophagus, 500–790 (656) for the muscular portion and 2880–4000 (3426) for the glandular portion as compared with 340–860 (470) and 1200–2500 (2000) respectively; longer left spicule, 620–1140 (927) as compared with 560–860 (700); longer tail of female 268–380 (328), as compared with 170–200 (180) and longer distance from vulva to posterior end, 7.0–13.5 (9)mm compared with 5.0–7.2 (5.8)mm.

Specimens of *Antechiniella* from water rats, held in the AHC, have been variously designated *Spirura* s. l. sp. (Johnson & Mawson 1952) *A. suffodiax* and *Antechiniella* sp. (Smales *et al.* 1990). Some of the specimens were posterior ends of worms associated with fibrous nodules in the stomach wall. Material that consisted only of posterior portions of worms could be identified positively as *A. sertatum* by the length of the spicule, proportions of the female tail, and the presence of irregular cuticular thickening on the mid-body in both sexes. Therefore, all the material from water rats lodged in the AHC is *A. sertatum.*

The appearance of the nodules on the stomach wall was consistent with gross descriptions of nodules given by Beveridge & Barker (1975) for *A. suffodiax*. However the nature of the material, old and inadequately fixed for histological sectioning, precluded a more detailed examination.

Another acuariid *Synhimantus australiensis* (Johnston & Mawson, 1952) also occurs in *H. chrysogaster* and *A. stuartii.* These small worms can readily be distinguished from *A. sertatum* by their size, the disposition of the cordons and the spirally coiled posterior extremity of the male. *S. australiensis* and *A. sertatum* have been recorded from the same localities in S.A. and in *H. chrysogaster* as mixed infections in the same host.

The food preferences of the mammalian hosts of acuariid nematode species appear to be very similar. The insectivores *Antechinus* and *Sorex* will take a variety of arthropods (Herter 1972; Statham 1982), and in the case of *Sorex*, small vertebrates and carrion. *H. chrysogaster* and *Procyon cancrivorus*, the crab eating racoon, are opportunistic predators taking aquatic insects and crustaceans as well as larger animals and fresh carrion (Watts & Aslin 1981; Poglayen-Nenwall 1972). The latter two hosts also demonstrate remarkable similarities in feeding behaviour and food preferences. Both take food from the water and eat it while sitting on the riverbank. "Coon sign", piles of crustacean exoskeleton, left at the feeding sites of *P. cancrivorus* is paralleled by similar midden heaps left by *H. chrysogaster* at its regular feeding sites. These feeding patterns appear to ensure that appropriate intermediate hosts form part of their diet, and may provide an insight into the selective distribution and occurrence of host and parasite.

Since *A. sertatum* is found only in Australian rodents and *A. suffodiax* is found in *R. lutreolus*

Figs 1–12. *Antechiniella sertatum* sp.nov. from stomach of *Hydromys chrysogaster*. 1. Male anterior end, lateral view. 2. Cephalic end, *enface* view. 3. Cephalic end oblique, mainly dorso-ventral view. 4. Transverse section mid body, irregularly thickened cuticle. 5. Mid body region, irregularly thickened cuticle. 6. Deirid. 7. Right spicule, ventral view. 8. Left spicule, proximal end, lateral view. 9. Female, vulval region. 10. Left spicule, distal end, lateral view. 11. Male, posterior end, lateral view. 12. Female posterior end, lateral view. Scale lines: Fig. 1, 0.5mm; Figs 2,3,4,5,11, 80μm; Figs 6,8,10, 25μm; Figs 7,12, 40μm; Fig. 9, 200μm.

and *R. fuscipes* as well as the marsupial *A. stuartii*, the generic diagnosis as given by Quentin & Beveridge (1986) should be expanded to include rodent hosts.

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