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BY R. J. SHIEL & W. KOSTE†*

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by R. J. SHIEL* & W. KOSTE†

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KEY WORDS: Rotifera, Australia, taxonomic revision, Trichocercidae, *Ascomorphella*, *Elosa*, *Trichocerca*

Introduction

There are sporadic systematic references to the occurrence of trichocercid rotifers in Australia (cf. Shiel & Koste 1979), however a review comparable to that of Jennings (1903) for North America, or included in Koste (1978) for Europe, is lacking. A thorough global revision of the family using modern techniques (e.g. SEM) is desirable, particularly in view of recent evidence of species-specificity in rotifer trophi (e.g. Markevitch & Kutikova 1990).

Trichocercid rotifers are a common component of plankton and littoral microfaunal communities in most Australian fresh waters. The family includes three genera: *Elosa*, recorded from N.S.W. (Murray 1913b); *Ascomorphella* (*A. volvocicola* often occurs as an inhabitant of *Volvox* colonies in reservoirs (see Ganf *et al.* 1983)) and *Trichocerca*. *Trichocerca* is the most diverse rotifer genus known from Australia (46 taxa recorded). Some species may be found in limno- and river plankton, however they reach their greatest diversity and abundance in littoral (vegetated) margins, especially in billabongs. Up to eight species may coexist in billabongs of the River Murray, where their morphological and/or behavioural adaptations permit effective resource partitioning (Tan & Shiel in press).

This paper follows the format of earlier parts (listed in Koste & Shiel 1990) to review the present status of the family in Australia, including available ecological information. Where type locality information was not available to us, the probable country of origin of the material is given in parentheses. Very little holotype material has been lodged for the Rotifera in general.

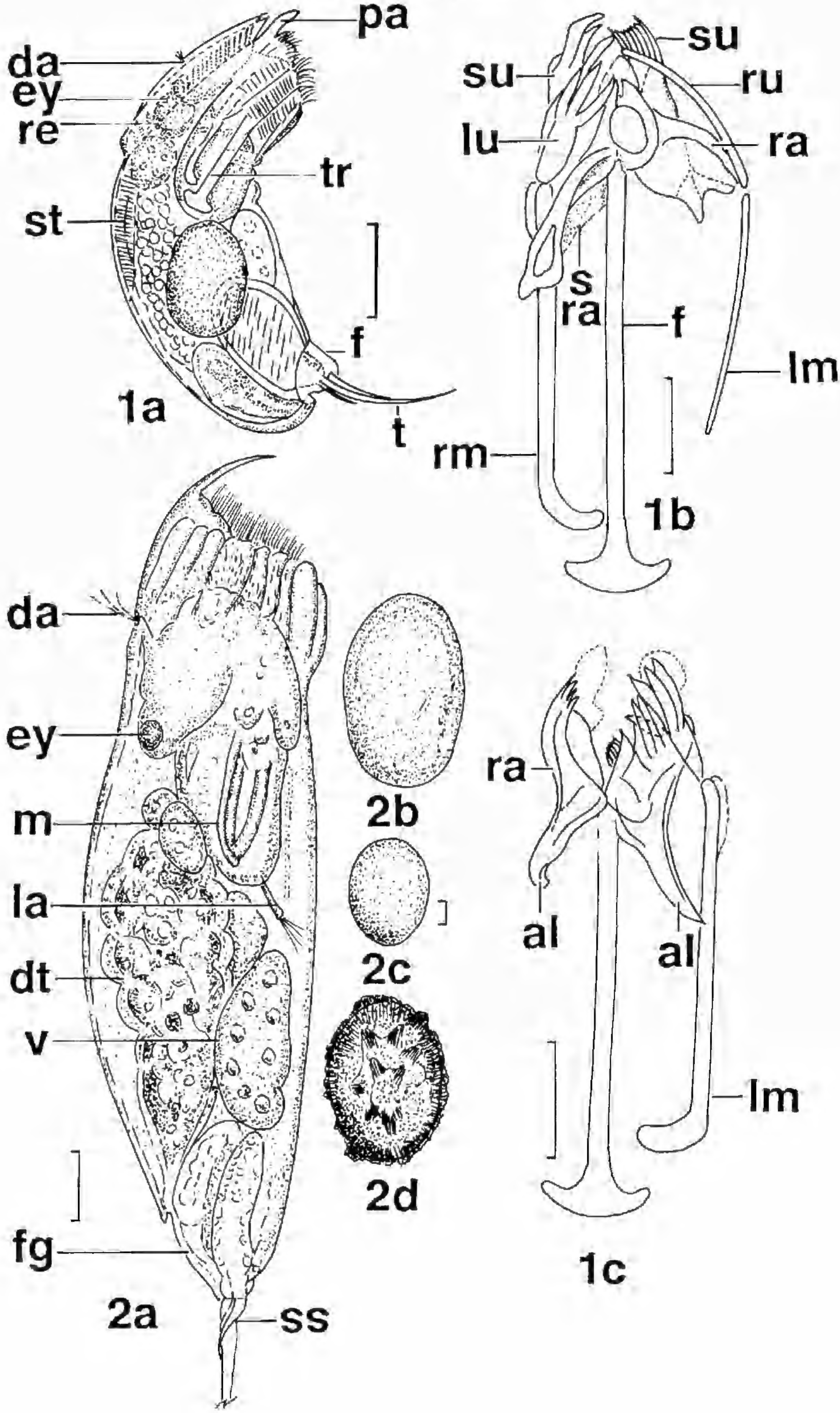
Methods of studying Trichocercidae

Taxonomically significant features of trichocercid rotifers are detailed in Fig. 1. Preserved (contracted) individuals generally can be identified, however contraction of protruding anterior spines, denticles or folds may vary between individuals. To observe palpar organs and sensors on the corona, living specimens are preferable. Trophi examination also is important in species determination (Fig. 1b, c). For example *Trichocerca porcellus* and *T. musculus* have similar morphology, but differ in trophi. The position of the lateral antennae at the front of the striated area is significant. By the addition of Eau de Javelle (KOHCl) or sodium hypochlorite (NaOCl) the animal is spread out and the position of the lateral antenna is momentarily clearer; rapid observation is necessary. Important in trophi analysis are the manubria (particularly terminal morphology), direction of the alulae, number of teeth of unci and rami. Excessive exposure to hypochlorite destroys the trophi — it can be neutralised by dilute acetic acid. Toe and body lengths should be measured. Substyli at the toe bases are sometimes stuck together by excretions from foot glands; in view of apparent variability in number this is unimportant for identification.

Two subgenera of *Trichocerca* are distinguished on toe morphology. *T. (Diurella)* Bory de St Vincent has toes of similar length or right at least ⅓ the length of left; *T. (s. str.)* Lamarck has dissimilar length toes, right never more than ⅓ the length of left. We have combined the subgenera in a single dichotomous key, but for convenience in comparing figured morphology, the two subgenera are treated separately in the systematic section. To date 43 species of *Trichocerca* have been identified from Australia, most from littoral vegetation in billabongs or in the open water of billabongs or lakes and rivers as incursion species from marginal vegetation. *T. similis* occurs commonly in the plankton of Murray-Darling reservoirs and rivers (Shiel *et al.* 1982).

* Murray-Darling Freshwater Research Centre, P.O. Box 921, Albury, N.S.W., 2640 (to whom reprint requests should be addressed).

† Ludwig-Brill Strasse 5, Quakenbrück, D 4570, Federal Republic of Germany.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Abbreviations used in systematic section:

TL = total length; BL = body length; LT/RT = left or right toe; TR = trophi length; F = fulcrum; LM/RM = left or right manubrium; LR/RR = left or right ramus; RE/SE = resting or subitaneous egg.

Family Trichocercidae Remane, 1933

Body ovoid to barrel-shaped *(Elosa, Ascomorphella)*, cylindrical, spindle or sack-shaped *(Trichocerca)*, often asymmetrical as a result of torsion of the body; foot present, short or absent; toes curved or straight, short or long, setae-like, rarely the same length; usually left toe longer; toes may be rudimentary; toe(s) may have substyli; trophi of virgate type, asymmetrical; corona resembles *Notommata* type (cf. Koste & Shiel 1991). Nomenclature follows Koste (1978).

Key to genera

1. Foot present, toes bristle-like, often of considerable length .... *Trichocerca* Lamarck
   Foot absent 2
2. Cuticle soft, toes minute; single cerebral eyespot .... *Ascomorphella* Wisniewski
   Cuticle stiff, toes rudimentary or absent; cerebral and apical eyespots .... *Elosa* Lord

Ascomorphella Wisniewski

Ascomorphella Wisniewski, 1953, p. 340.

Type: Hertwigia volvocicola Plate, 1886. Monotypic genus.

Ascomorphella volvocicola (Plate)
FIGS 2:1, 3

Hertwigia volvocicola Plate, 1886, p. 26, Fig. 17–8.

Ascomorphella volvocicola (Plate) Wisniewski, 1953, p. 340.

Type locality: (Germany).

Holotype: Not designated.

Description: Squat barrel-shaped body; corona *Asplanchna* type, apical field with fingerlike palps between longer cilia; wide lips ventrally between which trophi can be extruded; suture separates head from trunk, trunk with four longitudinal striae dorsally, two ventrally; short diverging striae between both sets; paired lateral antennae, single dorsal antenna; abdomen with small terminal bulge; two foot segments (one in juveniles), with two minute toes; dorsally, small tail overhangs anus; trophi virgate, of *Trichocerca* type; fulcrum long; LR more robust, with pointed, somewhat elevated alula; subunci daggerlike; unci with three pointed teeth; comb-toothed oral plate in front of unci; single medial red cerebral eye; transparent retrocerebral sac; mastax with two asymmetric salivary glands; unciliated gut; gastric glands large; vitellarium with six nucleii; REs brownish with short, thick, slightly curved bristles; male with invaginated dorsal antenna, everted penis, large brain and cerebral eye.

Total length 120–160µm; width to 75µm; trophi 32µm (LM 24µm, RM 18µm, F 18µm, rami 14µm); male 80µm, RE 66µm long.

Distribution: Known from Europe, N. America and N.Z. Obligate parasite of colonial algae *(Volvox, Uroglena)*. Widespread in eastern Australia, reaches high densities during seasonal blooms of *Volvox* in reservoirs and billabongs (cf. Ganf *et al.* 1983). Female eats cells of colony from the inside, leaving distinctive damage (Fig. 3), lays eggs inside colony.

Literature: Koste (1978).

Elosa Lord

Elosa Lord, 1891, p. 323.

Type: Elosa woralli Lord, 1891, p. 323.

Two taxa are referred to *Elosa* by Koste (1978: 409), f. typ. and var. *spinifera* (Wisniewski). It is not evident that differences are more than ecotypic variation. As 'var.' is without formal taxonomic status, on present evidence, *Elosa* appears to be monotypic.

Elosa woralli Lord
FIG. 2:2

Elosa woralli Lord, 1891, p. 323, Fig. 19.

Type locality: (London?)

Holotype: Not designated.

Description: Dorsally rounded to domed, ventrally wider and flat; body broadly elongate oviform; head demarcated by transverse suture; lorica smooth, caudal short spines may be present; on ventral posterior a semicircular or elliptical aperture with foot and toe rudiments; corona with long cilia; 1–2 palps in apical field; trophi asymmetric, virgate, with distally spatulate fulcrum; RM rod-shaped, LM a rod or crooked; LR with horizontal alula, larger than right; suprarami present; gastric glands relatively small; stomach and intestine indistinctly separated; gut generally orange

Fig. 1. Morphological features of trichocercid rotifers and their trophi. 1. *Trichocerca bidens* (Lucks): (a) lateral, swimming (pa palpar organ; da dorsal antenna; ey eye; re retrocerebral organ; tr trophus; st striated field; f foot; t toe); (b) trophus, dorsal, (c) trophus, ventral (su subuncus; lu left uncus; ru right uncus; ra ramus; sra: supraramus, fu fulcrum; lm left manubrium; rm right manubrium; al alula). 2. *T. cylindrica* (Imhof): (a) lateral (la lateral antenna, m mastax; di digestive tract; v vitellarium; fg foot glands, ss substyle); (b) subitaneous egg, (c) male egg; (d) resting egg. After Koste (1978). Scale lines: adult 50µm, trophi and eggs 10µm.

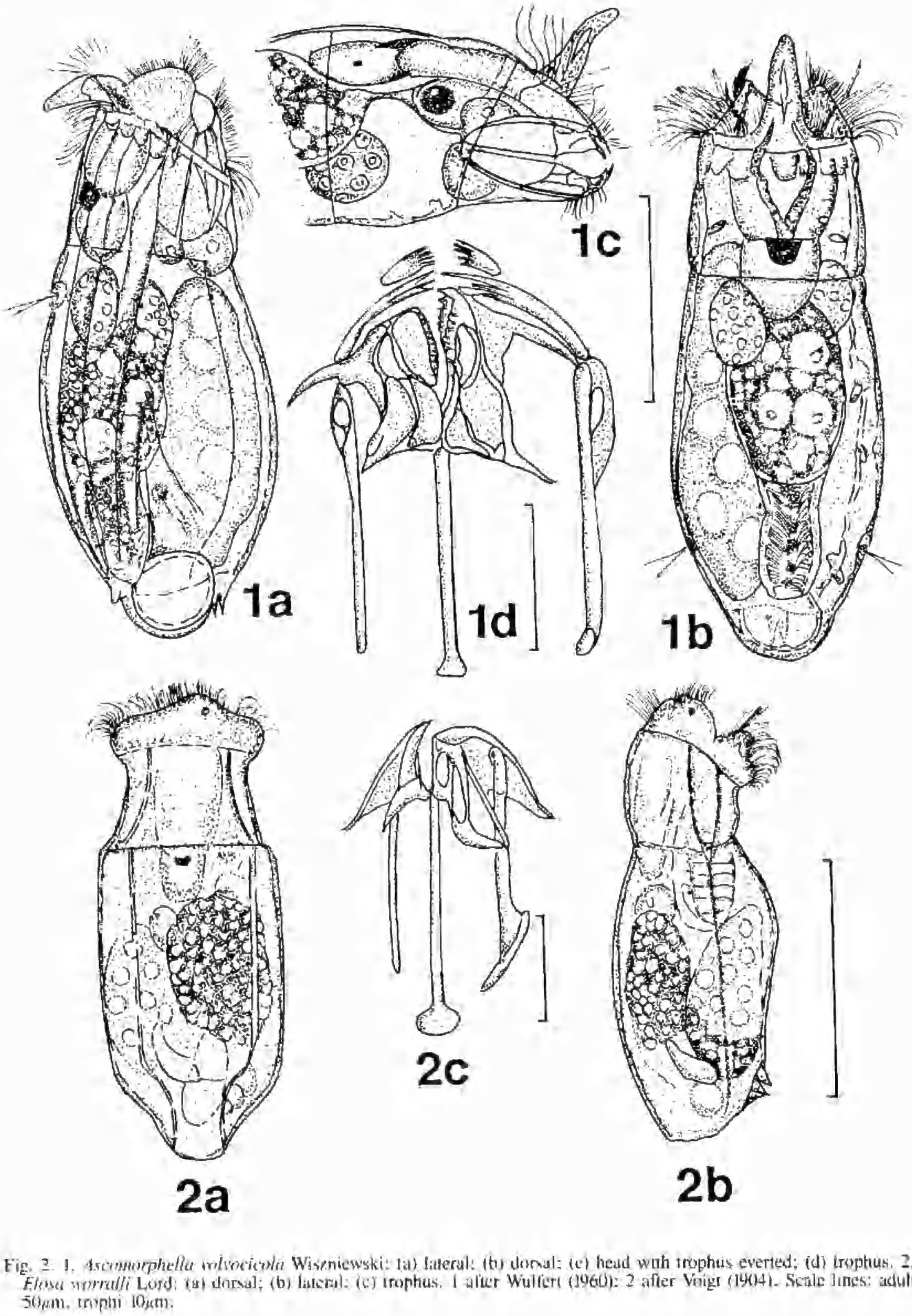


Fig. 2. 1. *Ascomorphella volvocicola* Wiszniewski: (a) lateral; (b) dorsal; (c) head with trophus everted; (d) trophus. 2. *Elosa worralli* Lord: (a) dorsal; (b) lateral; (c) trophus. 1 after Wulfert (1960); 2 after Voigt (1904). Scale lines: adult 50μm, trophi 10μm.

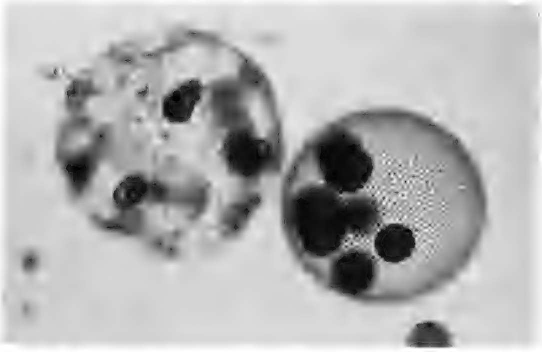


Fig. 3. Colony of *Volvox* showing resident *Ascomorphella volvocicola* and extensive damage to cells.

coloured; vitellarium with eight (10?) nuclei; bladder small; cerebral eyespot to left of brain; second eye displaced to right, lies in ciliary field, near 'brow' border, sometimes lost in separate pigment granules.

Total length 80–100μm (contracted 70μm); width 40μm; trophi 30μm (F 26μm, manubria 25μm, rami 12μm).

Distribution: In wet *Sphagnum*. Reported from Europe, N. America, Australia and N.Z. Not seen in our collections.

Literature: Murray (1913b); Russell (1960).

Trichocerca Lamarck

Trichocerca Lamarck 1801: 394.

Type: Trichocerca rattus (Müller) = *Trichoda rattus* (Müller) 1776, p. 281.

Body elongate or squat, more or less curved, in many species somewhat spiraled, or bent from left (right side concave, left side convex), anterior end of lorica with multiple spines, denticles or folds (particularly conspicuous after contraction of more or less firmly loricate animals); posterior to these may be striated area associated with torsion of body, followed by keel or two ridges; caudally, abdomen projects further on left than right, foot is inserted obliquely; rudimentary RT lies dorsally, LT often well developed ventrally; eye, brain and lateral antennae also asymmetrically placed; elongated mastax strongly asymetrical; rami have complex alulae; subunci have been described in different species; LM always more strongly developed (terminal shape essential for identification); RM mostly rodlike. Salivary glands and retrocerebral organ are described; intestine generally clearly separate from stomach. Excretory system has a few flame cells and protonephridial bladder, which can readily be confused with reservoir of foot glands; ocelli in living animals distinct on or at end of brain; dorsal antennae with short sensory setae (except in *T. cylindrica*). Lateral antennae either at same height in last ⅓ of abdomen, or placed very asymmetrically. *T. cylindrica* has been observed in gelatinous sheath. This pelagic species carries subitaneous and male eggs (both smooth shelled; Fig 1: 2a, b) at end of the abdomen. REs of *T. cylindrica* have blister-like blunt projections of outer shell (Fig. 1: 2c). There is little available information on biology of the different species. They appear to be adapted to specialized niches or their preferred habitat. Planktonic species *T. capucina* and *T. cylindrica* suck out the contents of eggs of planktonic rotifers, eg. *Brachionus* and *Keratella*. Littoral taxa extract contents from algal cells, e.g. *T. longiseta*, common in billabongs, breaks filaments of chlorophyceae (e.g. *Spirogyra*) using its dorsal spine and sucks out cytoplasm contents; *T. similis grandis* takes whole coccoid chlorophytes, e.g. *Gloeocystis*; *T. bidens* has developed a specialized pharyngeal basket to suck contents from desmids (see Pourriot 1970 for other feeding specialties).

Key to species of *Trichocerca* known from Australia

1. Toes of similar length, or RT at least ⅓ length of LT ..... *T.* (*Diurella*)..2
RT considerably reduced, always < ⅓ length of LT ..... *T.* (s. str)..22
2. Lorica anterior margin without projections.....3
Cusps, spines or other projections present.....4
3. Anterior lateral tongue shaped plate present..... *T. vernalis* Hauer (Fig. 8:5)
Lateral plate absent..... *T. collaris* (Rousselet) (Fig. 4:3)
4. Anterior margin with lateral tongue-shaped plate.....5
Lateral plate absent.....6
5. Margin with stubby projections, no spine(s)..... *T. sulcata* Jennings (Fig. 8:1)
Margin with one long spine..... *T. weberi* Jennings (Fig. 8:6)
6. Margin with blunt projections, or blunt projections with two dissimilar length spines.....7
No blunt projections: one or two spines or cusps.....12
7. Margin with blunt projections only.....8
Blunt projections, 2 dissimilar length spines, 8–9 serrations..... *T. rousseleti* (Voigt) (Fig. 7:1)
8. Dorsal keel present.....10
No dorsal keel.....9
9. Toes curved ventrally; LM with distinct single bend..... *T. inermis* (Linder) (Fig. 5:2)
Toes not curved ventrally; LM weakly curved terminally..... *T. ruttneri* (Donner) (Fig. 7:2)
10. Toes curved ventrally; LM with double crook.....11
Toes follow body axis (occasionally lightly curved terminally); LM only weakly bent..... *T. dixon-nuttalli* Jennings (Fig. 4:4)
11. Lower third of body conspicuously narrower; left uncus with several teeth..... *T. brachyura* (Gosse) (Fig. 4:1)
Body not conspicuously narrower; left uncus with single tooth..... *T. cavia* (Gosse) (Fig. 4:2)
12. Lorica anterior margin with single spine.....13
Lorica anterior margin with two spines.....17

13. Spine short (<14μm) 14
Spine long (14–26μm) .... *T. uncinata* (Voigt) (Fig. 8:4)

14. Body long and slender, conspicuously narrower in lower third; LM with single or double bend .. 15
Body not constricted posteriorly, LM weakly bent .... *T. tenuior* (Gosse) (Fig. 8:2)

15. BL > 130μm; toes > 50μm .... *T. tigris* (Müller) (Fig. 8:3)
BL 90–106μm; toes < 35μm 16

16. LM with double bend; left uncus single toothed .... *T. intermedia* (Stenroos) (Fig. 6:1)
LM weakly bent; left uncus with several teeth .... *T. insulana* (Hauer) (Fig. 5:4)

17. Two dissimilar length spines/cusps 18
Two similar length spines/cusps 21

18. Body squat; posterior lorica overhangs foot .. 19
Body long; posterior lorica does not overhang foot 20

19. LT 43–60μm; RT 36–45μm; TR > 50μm .... *T. porcellus* (Gosse) (Fig. 6:4)
LT < 43μm; RT < 35μm; TR < 50μm .... *T. musculus* Hauer (Fig. 6:2)

20. Body conspicuously constricted in lower ⅓; anterior spines different length *T. myersi* (Hauer) (Fig. 6:3)
Body not constricted; spines similar length .... *T. insignis* (Herrick) (Fig. 5:3)

21. Single dorsal keel; posterior lorica projects over foot .... *T. bidens* (Lucks) (Fig. 1:1)
Double keel; posterior margin does not project over foot .... *T. similis* (Wierzejski) (Fig. 7:3)

22. Lorica anterior margin without projections ... 23
Anterior margin with blunt projections, spines or cusps 28

23. Single dorsal keel present 24
Double dorsal keel 25

24. LM with single crook; alula of LR angled about 45° from TR axis ...... *T. rattus* (Müller) (Fig. 13:1)
LM with double crook; alula of LR angled > 45° from TR axis .... *T. flagellata* Hauer (Fig. 10:4)

25. Body tapers in posterior ⅓; toes curved ventrally 26
Body slender or squat, not constricted posteriorly; toes follow body axis 27

26. BL > 190μm; LT > 200μm .... *T. bicristata* (Gosse) (Fig. 9:2)
BL < 190μm; LT < 150μm .... *T. mucosa* (Stokes) (Fig. 12:2)

27. BL > 300μm; LT > 160μm .... *T. elongata* (Gosse) (Fig. 10:3)
BL < 130μm; LT > 150μm (exceeds BL) .... *T. braziliensis* (Murray) (Fig. 9:3)

28. Lorica anterior margin with spine(s) 33
Lorica margin with blunt projections, no spines 29

29. Dorsal keel present .... *T. gracilis* (Tessin) (Fig. 11:1)
Dorsal keel absent 30

30. TL > 180μm; BL > 135μm 31
TL < 180μm; BL < 135μm 32

31. Posterior lorica overhangs foot; LT > 70μm .... *T. agnata* Wulfert (Fig. 9:1)
Posterior lorica without overhang; LT < 70μm .... *T. stylata* (Gosse) (Fig. 13:5)

32. LT > BL (ratio 0.72–0.83) .... *T. mus* Hauer (Fig. 12:3)
LT < BL (ratio 1.8) .... *T. pusilla* Jennings (Fig. 12:4)

33. Anterior margin with single spine 34
Anterior margin with two spines 37

34. TL > 450μm; anterior spine long .... *T. cylindrica* (Imhof) (Fig. 10:2)
TL < 450μm; anterior spine short 35

35. Dorsal posterior lorica projects over foot; RT > 30μm (right : LT ratio < 5.5) .... *T. jenningsi* Voigt (Fig. 11:3)
Posterior lorica does not overhang foot; RT < 30μm (ratio > 5.5) 36

36. TL > 300μm; BL > 200 μm; LT > 100μm .... *T. macera* (Gosse) (Fig. 12:1)
TL < 300μm; BL < 200μm; LT < 100μm .... *T. iernis* (Gosse) (Fig. 11:2)

37. Two dissimilar length spines 38
Two spines and dorsal cowl-like structure .... *T. capucina* Wierzejski & Zacharias (Fig. 9:4)

38. Body constricted in posterior ⅓; posterior overhangs foot; LM weakly curved terminally .... *T. rosea* (Stenroos) (Fig. 13:2)
Body not constricted; no overhang; LM with single crook .... *T. longiseta* (Schrank) (Fig. 11:4)

Trichocerca bidens (Lucks)
FIG. 1: 1

Diurella bidens Lucks, 1912, p. 66, Fig. 12–13.
Trichocerca bidens: Ahlstrom 1938, p. 105, Fig. 9: 8–9.

Type locality: Germany.

Holotype: Not designated.

Description: *T. bidens* has (when contracted) two sharp similar length transversely striated cusps on dorsal lorica margin, with striated area beneath, but no keel; may be three transverse folds in neck region; dorsal antenna in middle of head; lateral antennae at same height on posterior ⅓ abdomen; at base of similar length toes are conspicuous rather long substyli; toes often curved ventrally at tips, or sigmoid. Mastax with dorsal and ventral salivary glands; ganglion with long retrocerebral organs and two subcerebral glands; TR: rami and unci multi-toothed at tips. Larger than, but often confused with *T. cavia* (Fig. 4:2). See also *T. collaris* (Fig. 4:3).

TL 220–240μm (swimming); lorica length 175–205μm; height 65–80μm; toes 52–66μm; TR 65μm; (F 51μm; manubria 42/31).

Distribution: Cosmopolitan, isolated finds in acid waters particularly *Sphagnum*. Rare, Tas., Vic. 13.0–27.0°C, pH 5.4–7.5, DO 9.2 mgl^{-1}, <10 NTU.

Literature: Koste (1978), Berzins (1982), Koste *et al.* (1988).

Trichocerca brachyura (Gosse)
FIG. 4:1

Monocerca brachyura Gosse, 1851, p. 199.
Trichocerca brachyura: Myers 1937, p. 6.

Type locality: England.

Holotype: Not designated.

Description: Body squat, robust; on contraction, anterior margin has stumpy projections on left side, folds on right; toes of similar length or only slightly different; right lateral antenna notably further to rear, left antenna approximately midway between it and dorsal antenna; TR with suprarami; LM with crook. Similarities with *T. cavia* (Fig. 4:2), *T. dixon-nuttalli* (Fig. 4:4), *T. porcellus* (Fig. 6:4) and *T. vernalis* (Fig. 8:5).

BL 73–112μm; toes 23–30/20–23μm; TR to 36μm (in a 33μm TR, LM 26μm; RM 12μm; F 26μm).

Distribution: Cosmopolitan, generally solitary in psammon and littoral of most freshwaters; pH tolerant. Uncommon; probably pancontinental, but not yet recorded from S.A. Occurs in *Myriophyllum* in River Murray billabongs. 10.0–25.0°C, pH 5.76–7.5, 43.5–218.0μS cm⁻¹

Literature: Koste (1978, 1981); Koste *et al.* (1983), Koste & Shiel (1987).

Trichocerca cavia (Hudson & Gosse)
FIG 4:2

Coelopus cavia Hudson & Gosse, 1886, p. 69, Fig. 49:22.
Trichocerca cavia: Myers 1937, p. 6.

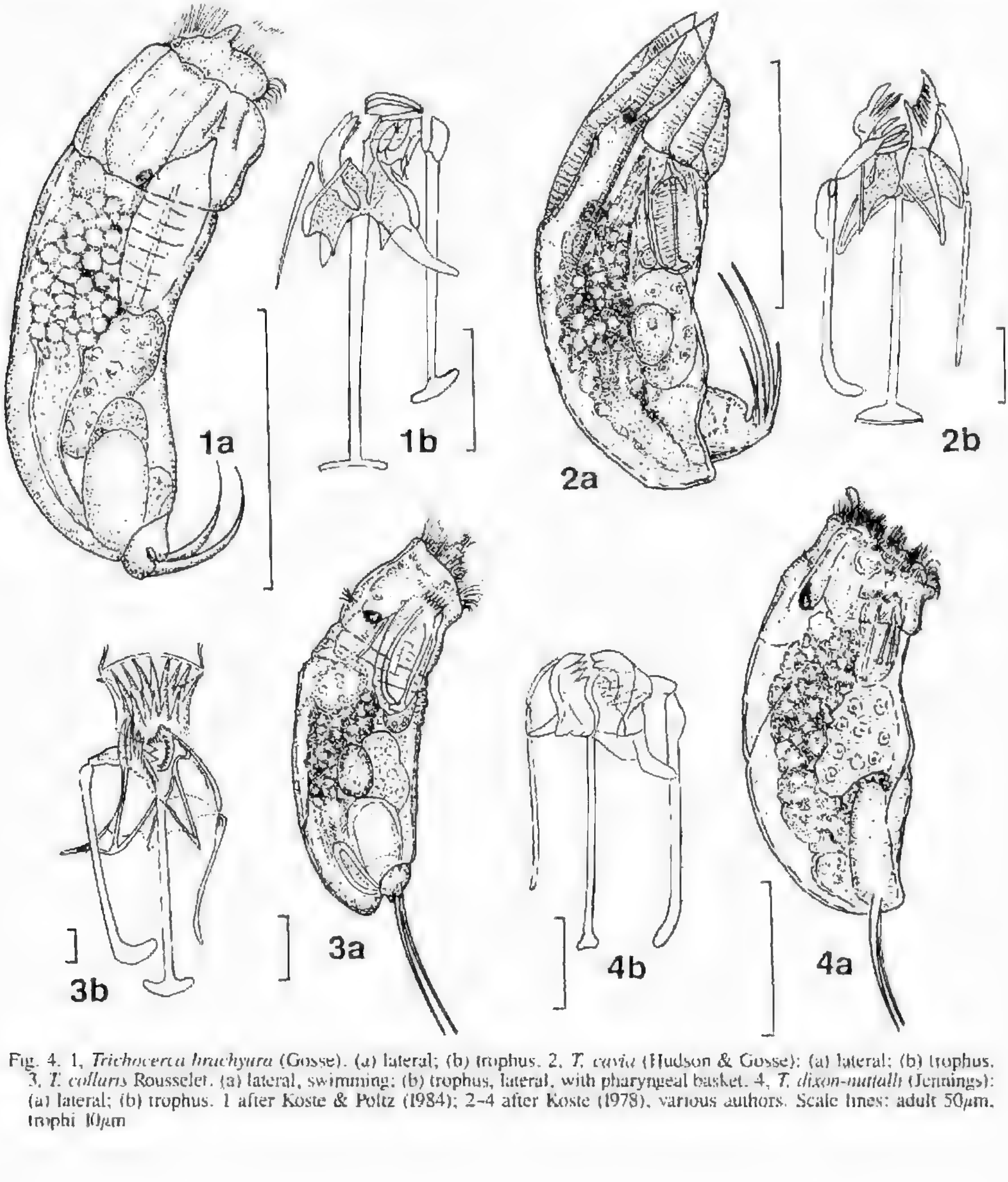


Fig. 4. 1, *Trichocerca brachyura* (Gosse). (a) lateral; (b) trophus. 2, *T. cavia* (Hudson & Gosse): (a) lateral; (b) trophus. 3, *T. collaris* Rousselet. (a) lateral, swimming; (b) trophus, lateral, with pharyngeal basket. 4, *T. dixon-nuttalli* (Jennings): (a) lateral; (b) trophus. 1 after Koste & Poltz (1984); 2–4 after Koste (1978), various authors. Scale lines: adult 50μm, trophi 10μm

Type locality: ". . . near Snaresbrook, Epping Forest", England.
Holotype: Not designated.
Description: Body of contracted animal plump, almost ovoid ("the aspect of a . . . squatting guinea-pig" – P. H. Gosse in Hudson & Gosse 1886); without keel; lorica anterior margin variably smooth and plated (in most cases); seen laterally, these give impression of spines, larger on right, dorsally as pointed projection, reduced on left; foot coniform, small, offset from wide abdomen; lateral antennae at same level; toes of similar length, usually crossed. Resembles *T. bidens* (Fig. 1:1).
BL 97–132μm; TL 30–41μm; TR length 42–48μm.
Distribution: Cosmopolitan, in periphyton in plants of standing waters, pH 5–10, 5.5–19.0°C (Koste 1978). Rare, one record each from N.T., Tas., Vic. 8.5–18.0°C, pH 6.0–7.0, DO 11.0 mgl^{-1}, 70μS cm^{-1}, <1 NTU.
Literature: Koste (1978), Koste & Shiel (1980, 1987).

Trichocerca collaris (Rousselet)
FIG 4:3

Rattulus collaris Rousselet, 1896, p. 266, Fig. 11:1
Trichocerca collaris: Myers 1937, p. 6.
Type locality: England.
Holotype: Not designated.
Description: Lorica smooth to stippled with transverse bulges in neck region; contracted, head projects at acute angle, somewhat tongue-shaped; no dorsal ridges, but a constricted area, dorsal antennae between neck folds in normal position; lateral antennae at approximately same height; TR with crooked fulcrum; winglike suprarami over rami; pharyngeal basket anterior to rami apices; two large palpar organs. Animal can bend sharply forward to poke the toe tips into the mouth area.
BL 204–309μm; toes 90–113μm; TR 80–85μm (F 56μm, LM 63μm).
Distribution: Cosmopolitan in acid waters with *Sphagnum*; eats diatoms and desmids which are not swallowed entirely but fragmented and sucked out. Rare; several records from Tasmania, only one from the mainland (Magela Ck, N.T.), 22.5–24.5°C, pH 5.2–6.3, DO 5.8 mg l^{-1}, 32–59μS cm^{-1}, <1 NTU.
Literature: Koste (1972), Koste & Shiel (1980, 1987).

Trichocerca dixon-nuttalli (Jennings)
FIG 4:4

Diurella dixon-nuttalli Jennings, 1903, p. 318, Fig. 4:40–44.
Trichocerca dixon-nuttalli: Donner 1950, p. 148, Fig. 13
Type locality: Not specified. . . . "common in ponds in England".
Holotype: Not designated
Description: Body cylindrical, tapers posteriorly; head sheath separated by transverse constriction with several longitudinal folds; short dorsal furrows (containing dorsal antennae) correspond to striated area of other species; corona with dorsal palpar organ and several blunt protrusions; lateral antennae asymmetrical in posterior, left further forward than right; LT about half BL, RT ⅔ length of left; TR asymmetrical; right malleus much reduced; left uncus 4-toothed; eyespot at posterior end of brain; resembles *T. brachyura* (Fig. 4:1), *T. ruttneri* (Fig. 7:2), *T. pusilla* (Fig. 12:4) and *T. stylata* (Fig. 13:5). Evidently most closely related to *T. pusilla*.
TL 103–186μm; BL 90–122μm; LT 41–50μm; RT 27–28μm; TR 30–32μm.
Distribution: Probably cosmopolitan on floodplains, inundation zones, periphyton, tychoplankton. Recorded from Qld (Russell 1961). In Jan. 1989 populations were found in several small pools (Solomon's Jewels) and Lake Loane in the Walls of Jerusalem National Park, Tasmania, 23.0°C, pH 6.88–6.99.
Comment: Conspecificity of *Trichocerca inermis* (Linder, 1904) and *T. dixon-nuttalli* has been debated, e.g. Koste (1978), however Hauer (1931) was convinced on the basis of European finds of the former which conformed to Linder's descriptions and not to those of Jennings, that two distinct taxa were involved. *T. inermis* has been distinguished to date only by a shorter right toe.
Literature: Koste *et al.* (1988).

Trichocerca euodonta (Hauer)
FIG 5:1

Diurella euodonta Hauer, 1937, pp. 377–8, Fig. 25a–d.
Trichocerca euodonta: Koste 1978, p. 408; (=*Trichocerca euodonta*, Berzins 1982, p. 7)
Type locality: North Sumatra, Indonesia.
Holotype: Not designated
Description: Body almost cylindrical, *ca.* 4× longer than wide, symmetrically curved, rotated about 90°; strong spine on right side of head, left of which a second, left-curving, wider spine, about 50% its length, is deflected ventrally; a shovel-shaped protrusion of the head margin arises left of the head opening, separated from left anterior spine by a deep notch; single distinct fold on underside of head; well-developed keel slants across back from base of anterior spine, ending at base of foot; head clearly demarcated from rest of body only on underside; foot lies in direction of body axis, almost as long as wide; toes of dissimilar length, weakly curved, widely separate, RT slightly longer than ½ LT; two stylets at base of each toe; TR asymmetric; manubria rod shaped
TL 133μm; LT 62μm; RT 37μm;
Distribution: Known only from North Sumatra and one unconfirmed Australian record from the Moorabool River at Ballan, Vic. (Berzins 1982).
Comments: Hauer's figures and descriptions are reproduced here. The trophi were not figured in the original description. Whether this species or *T. (D.) myersi* (Fig. 8:2), which it resembles and which is

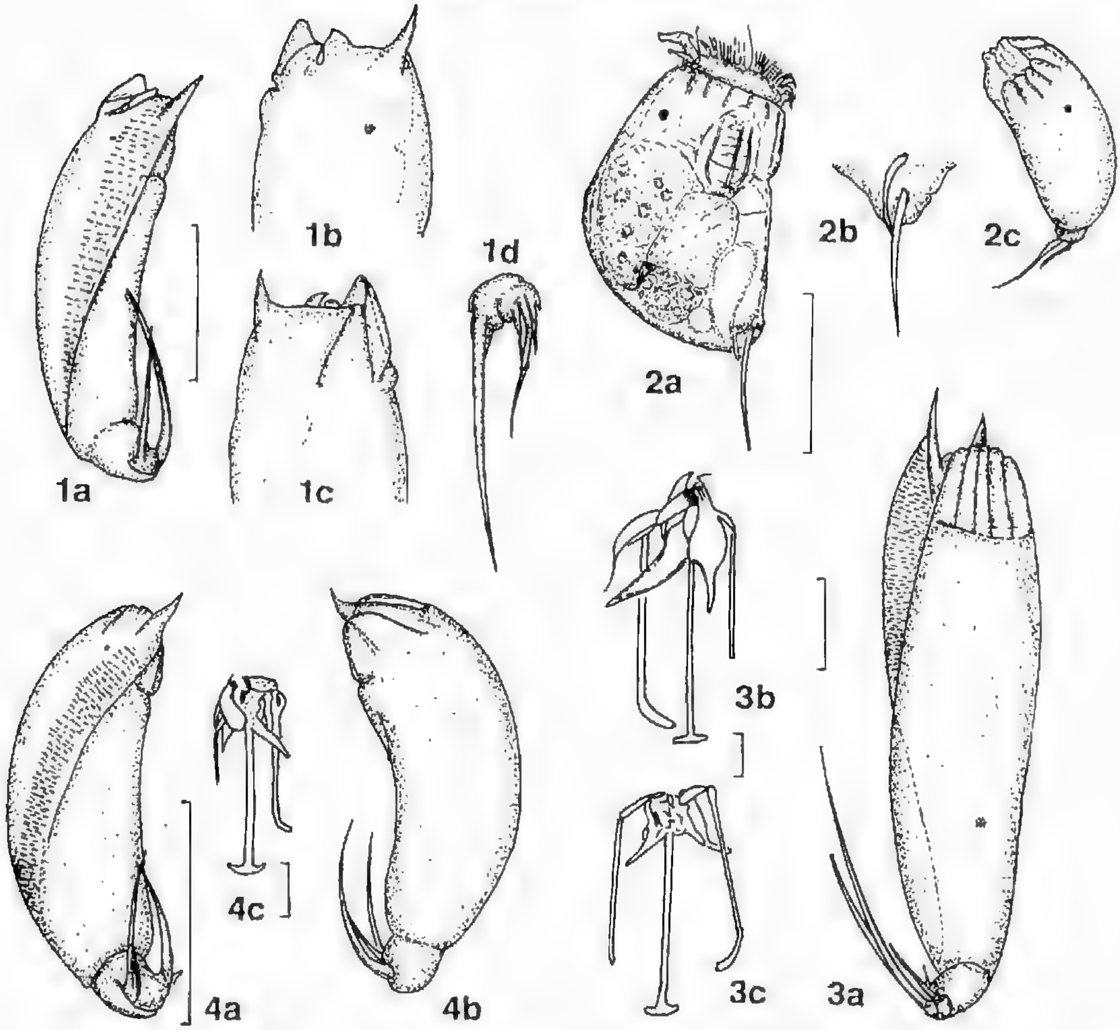


Fig. 5. 1, *Trichocerca euodonta* (Hauer): (a) lateral, contracted; (b) head from right side; (c) head from left side; (d) foot and toes. 2, *T. inermis* (Linder): (a) swimming, lateral; (b) toe; (c) lateral, contracted. 3, *T. insignis* (Herrick): (a) lateral, contracted; (b–c) trophus. 4, *T. insulana* (Hauer): (a–b) lateral, contracted; (c) trophus. 1 after Hauer (1937); 2–4 after Koste (1978) (various authors). Scale lines: adult 50µm, trophi 10µm.

confirmed from Australia (Koste & Shiel 1980), is the record of Berzins, is unresolved. Neither figures nor description were given by Berzins.

Trichocerca gracilis (Tessin)
FIG. 11:1

Acanthodactylus gracilis Tessin, 1890, p. 155, Fig. 2:14.
Trichocerca gracilis: Carlin 1939, p. 36, Fig. 10a.
Type locality: Rostock, Germany.
Holotype: Not designated.
Description: Head defined from trunk by suture; no large teeth on occipital margin; low keel on right side of lorica reaches end of lorica. No trophi description. May be confused with the similar *T. iernis* (Fig. 11:2).

TL 210–227µm; LT 81–90µm; RT 26–30µm.
Distribution: Europe, N. & S. America. Rare, between submerged plants. Single record, Solomon Dam, Palm Island, N. Qld (coll. P. Hawkins).
Literature: Shiel & Koste (1985).

Trichocerca inermis (Linder)
FIG. 5:2

Coelopus inermis Linder, 1904, p. 240, Fig. 4:9.
Trichocerca inermis: Edmondson 1936, p. 219, Fig. 28:10.
Type locality: Lake Bret (Switzerland?).

Holotype: Not designated
Description: Resembles *T. dixon-nuttalli*, *T. pusilla* and *T. stylata*. Stout body; light suture ventrally distinguishes head-sheath; numerous folds in head-sheath on contraction; dorsum may be arched; single palpar organ in ciliary field; LT < ⅓ body length; RT ⅓ LT; trophi not described.

TL 135μm; BL 95μm; LT 30–45μm; RT 12–13μm.
Distribution: Isolated occurrences in lakes, Europe, N. America. Single record, Sheepwash Billabong, Yea, Vic.
Comment: Edmondson (1936) noted that the body is shorter and thicker than that of *T. dixon-nuttalli*. Koste (1978) noted that only the shorter right toe of *inermis* separated the taxa. Until trophi structure are compared, the status of these two taxa is unresolved.

Trichocerca insignis (Herrick)
FIG. 5:3

Diurella insignis Herrick, 1885, p. 50, Fig. 4.
Trichocerca insignis: Edmondson 1936, p. 215

Type locality: U.S.A.
Holotype: Not designated.
Description: Body elongate cylindrical, tapers to foot in posterior ⅓, lorica anterior projections usually of similar length; lorica height:length ca. 1:5; keel begins between anterior teeth and runs to caudal end; palpar organ and two ciliated papillae in apical field; TR: fulcrum distally anchor-shaped, manubria rod-like; LM curved inwards distally; rami and unci with denticles, right lateral antenna at the end of dorsal keel; vitellarium with indentations; on average larger than other species; probably related to *T. myersi* (Fig. 6.3).

TL 320–376μm; BL 200–257μm; LT 90–152μm; RT 50–75μm; TR 62μm (F 48μm; LM 38μm; RM 12μm).
Distribution: Europe, North and South America, New Zealand. In periphyton of standing and flowing water, occasionally in plankton. Pancontinental; rare; 13.5–31.2°C, pH 4.5–8.0, DO 7.4–8.4 mg l^{-1}, 46–400μS cm^{-1}, to 160 NTU.
Literature: Koste (1978), Shiel & Koste (1979), Koste & Shiel (1986).

Trichocerca insulana (Hauer)
FIG. 5:4

Diurella insulana Hauer, 1937, p. 378–9, Fig. 26a–e.
Trichocerca insulana: Carlin 1939, p. 45

Type locality: Moor pool near L. Toba, Sumatra, Indonesia
Holotype: Not designated
Description: Body cylindrical, dorsally humped; prominent anterior margin spine from which long, low keel runs diagonally almost to foot base; toes ca. ⅓ body length, of approximately similar length, set wide apart at their base; fulcrum double-crooked, notably longer than manubria; LM thin, terminally slightly expanded, not crooked; RM shorter than LM, rodlike, more delicate. Resembles *T. tigris* (Fig. 8:3).

BL 92μm; toes 33–35μm; BL including anterior spine 100μm; lateral height 34μm; LT 38μm; RT 35μm;
Distribution: Mud, sand, periphyton; Sweden, Indonesia. Two records: Magela Ck, N.T., L. Dulverton, Tas.; 18.0°C, pH 7.2, 3330μS cm^{-1}
Literature: Koste (1978, 1981), Koste & Shiel (1986).

Trichocerca intermedia (Stenroos)
FIG. 6:1

Coelopus intermedius Stenroos, 1898, p. 150, Fig. 2:10.
Trichocerca intermedia: Edmondson 1936, p. 214
Trichocerca montana Hauer, 1956, p. 308, Fig. 23

Type locality: Finland.
Holotype: Not designated
Description: Small species; body cylindrical; head sheath separated by constriction; when head contracted, nine folds identifiable in head sheath; single tooth at dorsal anterior margin just to right of midline; striated area extends back from base of tooth to dorsal midline; foot very short; toes of equal length; lateral antenna widely separated on dorsum; right in posterior ¼ of abdomen, left in the midline between it and dorsal antenna; whorls is just in front of head constriction; foot gland including reservoir very long; TR notably large.

BL 90–106μm (without toes); toes 23–30μm; TR 33μm (F 25μm; LM 25μm, RM 14/12μm).
Distribution: New Zealand, Europe, North America, between water plants in standing and flowing water. Four widely separated records, probably more widespread; Magela Ck, N.T. (as *T. montana*); Bromfield Swamp, Qld, and two stock dams in southern Tas. (the latter with cyanobacterial blooms) 10.5–17.5°C, 230μS cm^{-1}, 13–110 NTU.
Literature: Koste (1978, 1981), Green (1981), Koste & Shiel (1987).

Trichocerca musculus Hauer
FIG. 6:2

Diurella musculus Hauer, 1936, p. 141, Fig. 2:10.
Trichocerca musculus: Carlin 1939, p. 39.

Type locality: Germany.
Holotype: Not designated.
Description: Body short, squat; head sheath folds project as "corner folds" (two dorsal and one ventral denticulate mucrones); keel striated approximately ½ dorsum length; LT longer than right; crook of LM "shoe last" shaped; suprarami approximately symmetrical.
TL 115–170μm; BL 80–132μm; toes 30–43/25–35μm; mastax 39–43μm;(F 30μm; LM 30μm; right uncus 13μm).
Distribution: Europe, North America; indicator for oligosaprobic water; in periphyton, in pools, lakes, moors. Two records, Mt Kosciusko, N.S.W. and southwest W.A.
Literature: Berzins (1982), Koste *et al.* (1983).

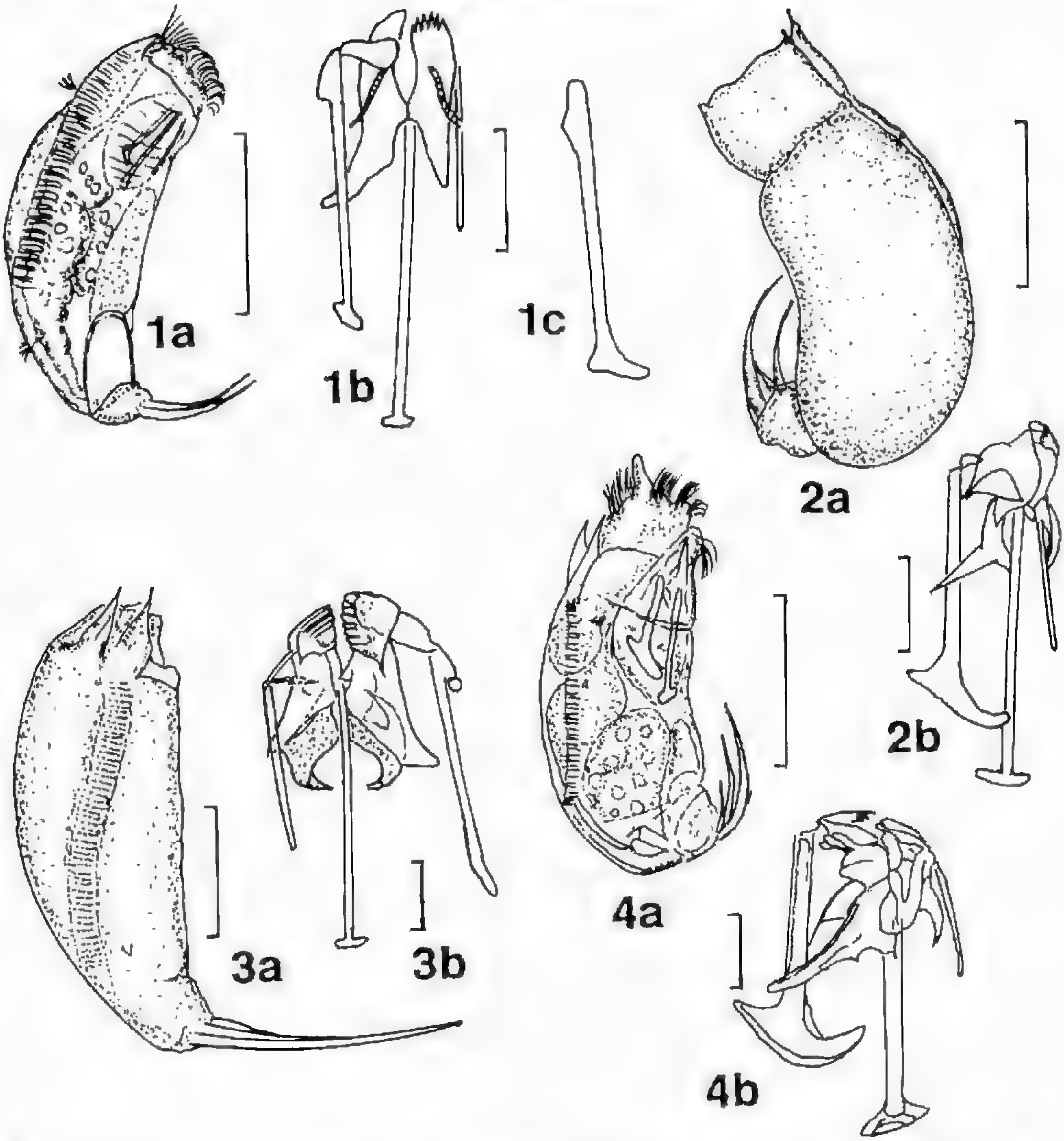


Fig. 6. 1, *Trichocerca intermedia* (Stenroos): (a) swimming, lateral; (b) trophus; (c) left manubrium. 2, *Trichocerca musculus* Hauer: (a) lateral, contracted; (b) trophus. 3, *T. myersi* (Hauer) (a) lateral; (b) trophus. 4, *T. porcellus* (Gosse): (a) swimming, lateral; (b) trophus. After Koste (1978) (various authors). Scale lines: adult 50 μm, trophi 10μm.

Trichocerca myersi (Hauer)

FIG. 6:3

Diurella myersi Hauer, 1931, p. 174, Fig. 2a,b.
Trichocerca myersi: Carlin 1939, p. 44.

Type locality: Germany.

Holotype: Not designated.

Description: Anterior lorica spines (mucrones) very different in length; lorica height:width 1:5; body fusiform, dorsal keel runs almost to height of right lateral antenna (two antennae at different heights); short head sheath, distinctly offset by suture; foot short, somewhat obliquely placed; LT weakly curved, reaching about ½ body length; RT (tightly placed) to left, with substyli often cemented together by foot gland secretion and difficult to see. Trophi: LM robust rod, only weakly curved terminally; suprarami with pincer-like inward-directed apices.

TL 270–310μm; BL 180–210μm; LT 90–102μm; RT 50–57μm; TR 50–61μm; F 36μm; LM 38μm; LR 21μm; RR 21μm; unci 13μm.

Distribution: Probably cosmopolitan, in standing waters, in periphyton of weedy ponds. Jabiluka, N.T., L. St Clair Natl Park, Tas., Moorabool R., Vic.; rare; 10.0–27.0°C, pH 5.4–6.3, DO 5.1 mg l⁻¹, 42μS cm⁻¹.
Literature: Koste (1978), Koste & Shiel (1987).

Trichocerca porcellus (Gosse)
FIG. 6:4

Monocerca porcellus Gosse, 1851, p. 199.
Trichocerca porcellus, Myers 1937, p. 6

Type locality: England.
Holotype: Not designated.
Description: Short, plump, distinctly curved body; head sheath separated by constriction, two anterior dorsal cusps, right one slightly larger; when head slightly contracted, lips of a ventral notch in the lorica margin may protrude as slight "teeth" but are not seen in extended animal; variable height ridge (sometimes absent), striated; extends backwards from the largest tooth; corona with club-shaped palpar organ; foot small, partly enclosed within lorica; two toes, left longer, ca. the same as body width, the right somewhat shorter, usually held against ventral abdomen. Trophi very asymmetrical, LM robust, crooked, RM a slender rod; LR alula much longer than right.

BL 90–115μm; body width 45–48μm; toes 22–42μm; male 56–60μm long, 32–36μm wide (a larger form, f. *uncior* was described by Hauer, 1935).
Distribution: Cosmopolitan, pH 6.0–6.7, 12.1–19.0°C, larger in alkaline than acid waters. Indicator for oligosaphrobic waters; all forms in littoral, in periphyton; occasionally in tychoplankton. May be pancontinental, not yet known from S.A., W.A.; common; 8.0–22.0°C, pH 5.2–7.5, DO 6.1–11.2 mg l⁻¹, 16–1020μS cm⁻¹, <1–120 NTU
Literature: Evans (1951), Green (1981), Koste (1981), Koste & Shiel (1987).

Trichocerca rousseleti (Voigt)
FIG. 7:1

Coelopus rousseleti Voigt, 1902, p. 38.
Trichocerca rousseleti: Ahlstrom 1938, p. 92.

Type locality: Plön, Germany.
Holotype: Not designated.
Description: Squat body with arched dorsum; anterior lorica margin with 8–9 projecting serrations, the dorso-dextral tooth largest; striated area of other species replaced by furrow between dorsal teeth; head clearly distinguished by transverse suture; RT about ½ length of left, slender, easily overlooked. Trophi: manubria of similar length; left uncus with short denticles. May be confused with *T. stylata* (Fig. 13:5).

TL 105–145μm; BL 72–113μm; LT 27–32μm; RT 11–19μm; TR 33μm (F27μm; LM 31μm; RM 27μm); palpar organ to 20μm. SE 46×29μm.
Distribution: Previously known from Palaearctic and Nearctic oligosaprobic waters, with sporadic occurrences in plankton of lakes, where eggs are attached to *Melosira* filaments. Population maxima in spring. Rare, in our collections invariably associated with flowing waters — Darling (N.S.W.), Goulburn (Vic.), Murray (S.A.), with *Melosira* blooms. 14.0–17.9°C, pH 7.0–8.1, DO 8.9–9.8 mg l⁻¹, 47–365μS cm⁻¹, 28–135 NTU.
Literature: Shiel & Koste (1979).

Trichocerca ruttneri (Donner)
FIG. 7:2

Diurella dixon-nuttalli; Hauer 1937/38, p. 309
Trichocerca ruttneri Donner, 1953, p. 19–22, Fig. 1a–d

Type locality: Not specified: lake plankton, Sumatra and Java.
Holotype: Not designated.
Description: Plumper than very similar *T. dixon-nuttalli;* tubular lateral antennae at similar height; dorsal antenna displaced to right; LT slightly sigmoid; one longer substyle, 2× length of others; robust trophi; fulcrum inverted T; manubria of similar length, bent to crooked in distal ⅓; left uncus with four strong teeth.

BL 122–200μm; height 63–82μm; LT 53–85μm; RT 29–40μm; TR 36–43μm.
Distribution: Widespread in tropics, Europe. Known only from dams near Chillagoe, Qld (coll. B.V. Timms).
Literature: Shiel & Koste (1985)

Trichocerca similis (Wierzejski)
FIG. 7:3

Coelopus similis Wierzejski, 1893, p. 406.
Trichocerca similis: Edmondson 1935, p. 303
Trichocerca birostris (Minkiewicz): Koste 1978, p. 393–394, Fig. 136:1b.

Type locality: Galicia, Poland.
Holotype: Not designated.
Description: Fusiform body; head sheath marked by distinct suture(s); two slender, subequal occipital spines somewhat deflected to right, flex with lorica movement, may be bent across head aperture on contraction; may be knob or spinule between spines; two low keels extend back from spines, with narrow transversely striate area between; dorsal antenna in striae field; knoblike left lateral antenna well before midline, right lateral antenna slightly before foot; end of rump overhangs first foot segment; two toes unusually short, unequal; LT ca. ⅙ lorica length, RT shorter; torsion of abdomen has placed RT base above LT, difficult to distinguish separate toes in dorsal view; 1–3 substyli present. Trophi: fulcrum straight, knife-like in lateral view; manubria asymmetrical, left more robust than right; right uncus multi-toothed; retrocerebral organ notably large, may extend beyond midline; bright red cerebral eye; two lateral ocelli visible in living specimens; salivary glands absent

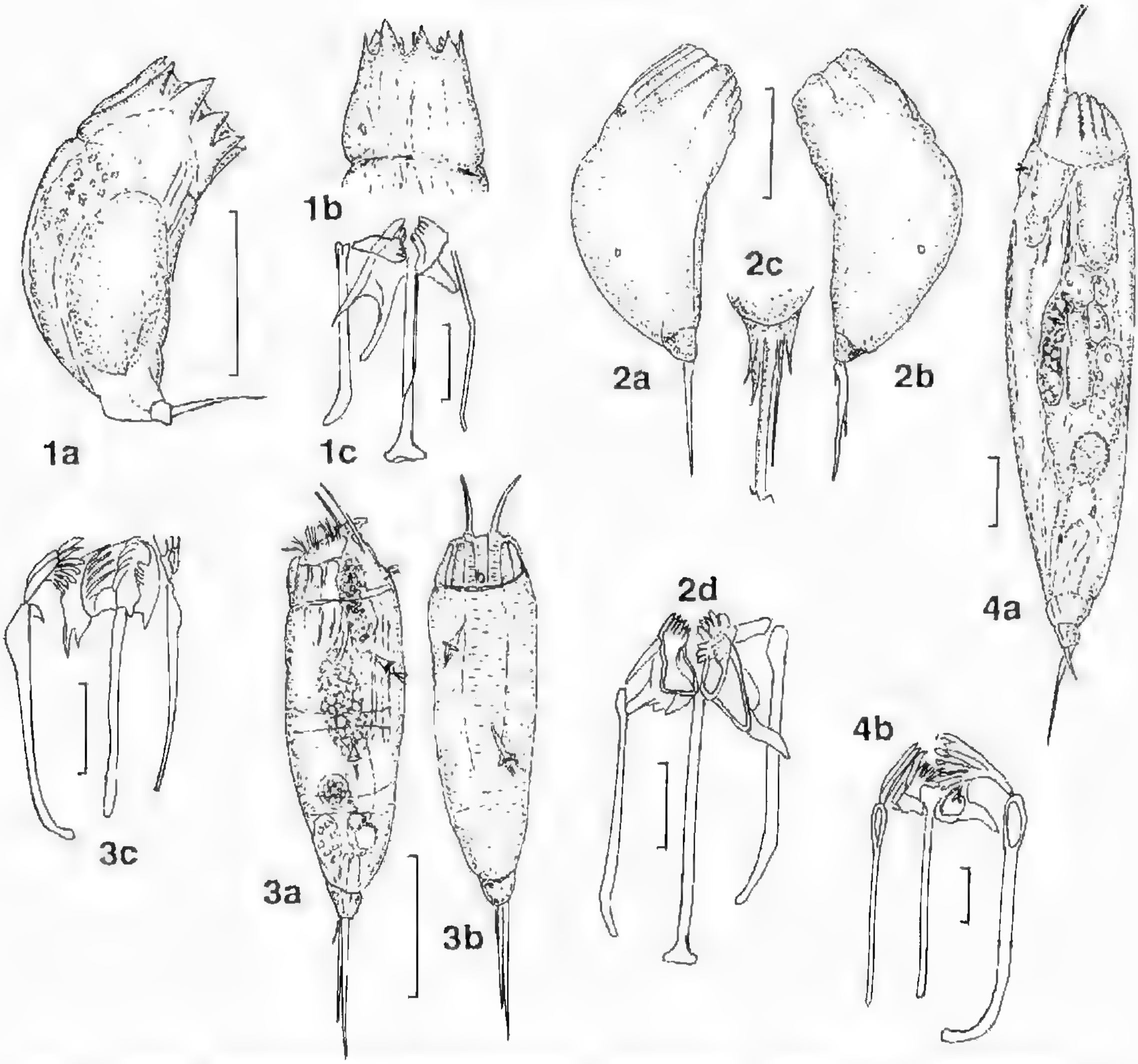


Fig. 7. 1, *Trichocerca rousseleti* (Voigt): (a) lateral, contracted; (b) head margin; (c) trophus. 2, *T. ruttneri* (Donner): (a-b) lateral, contracted; (c) base of toes; (d) trophus. 3. *T. similis* (Wierzejski): (a) swimming, lateral; (b) dorsal, contracted, (c) trophus. 4. *T. similis grandis* Hauer: (a) lateral, contracted; (b) trophus. After Koste (1978) (various authors). Scale lines: adult 50μm, trophi 10μm.

TL 166–300μm; BL to 140μm; LT 50–80μm; RT 30–50μm; TR 30μm (F 21μm, LM/RM 30/24μm); male 68–73μm.

Distribution: Important component of plankton in oligotrophic, humic waters, attaches subitaneous eggs to other plankters. Pancontinental, most common *Trichocerca* in Australian waters, planktonic in lakes, ponds, billabongs, stock dams. Particularly common in humic acid waters in western Tasmania. 7.0–24.5°C, pH 3.9–8.2, DO 5.8–11.6 mg l^{-1}, 31–7000μS cm^{-1}, 0.5–120 NTU.

Comment: A larger form often found with *T. similis* has similar morphology, including occipital spines. It is common in Murray-Darling reservoirs, e.g. L. Hume, L. Dartmouth, where it grazes green algae e.g. *Gloeocystis*. This large form is presently regarded as a ssp., *T. similis grandis* Hauer, 1965 (Fig. 7:4). It is distinguished by larger, more elongate body and relatively shorter toes than the typical form.

TL 400–525μm; LT to 44μm; RT to 28μm.

Distribution: Known from Amazonian floodplain waters. Rare; River Murray billabongs in Victoria.

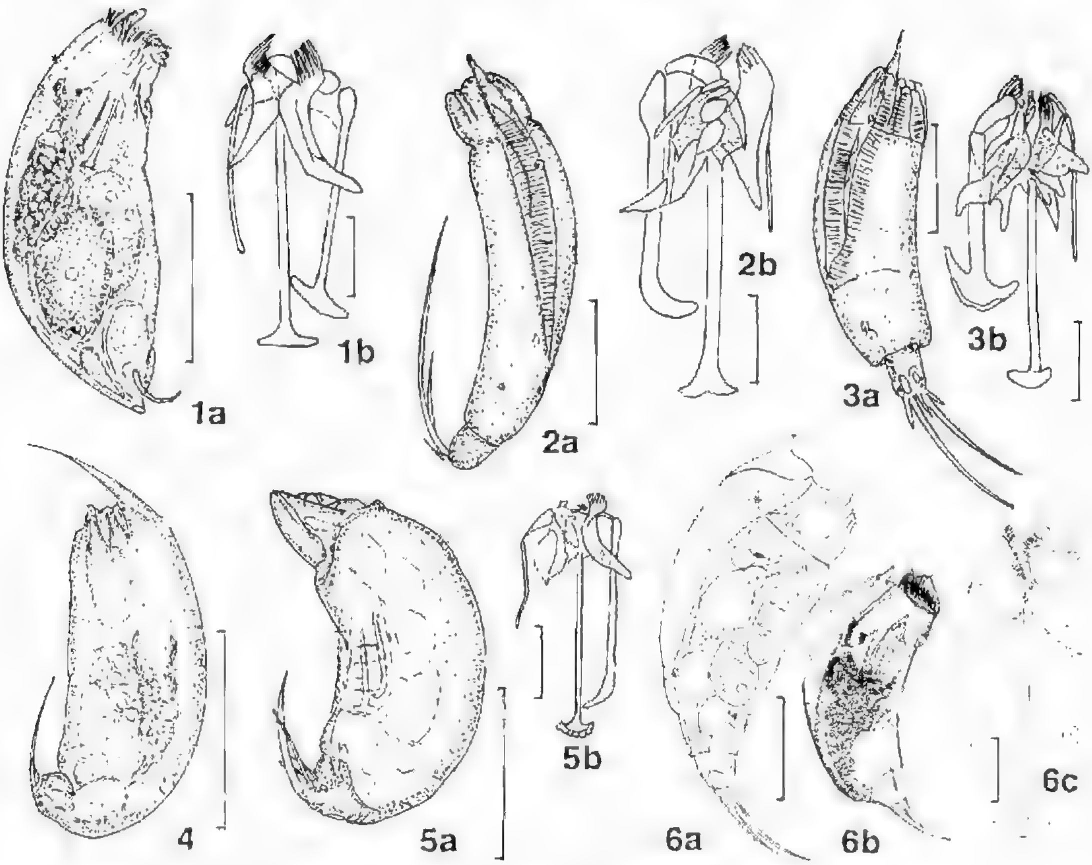


Fig. 8. 1, *Trichocerca sulcata* (Jennings): (a) swimming, lateral; (b) trophus. 2, *Trichocerca tenuior* (Hudson & Gosse): (a) lateral; (b) trophus. 3, *T. tigris* (Muller): (a) lateral, contracted, (b) trophus. 4, *T. uncinata* (Voigt): lateral, contracted 5, *T. vernalis* Hauer, (a) lateral, contracted; (b) trophus. 6, *T. weberi* (Jennings): (a) lateral; (b) s.str., from Tasmania, lateral, (c) trophus. 1, 3–5 after Koste (1978) (various authors); 2 after Koste & Poltz (1984) 6 after Koste *et al.* (1988). Scale lines: adult 50μm, trophi 10μm.

L. Pedder, Tas., probably more widely distributed. 15.5–20.0°C, pH 6.8–7.0, DO 10.8 mg l⁻¹

Literature: Koste (1978), Koste & Shiel (1980, 1987), Koste *et al.* (1988).

Trichocerca sulcata (Jennings)
FIG. 8:1

Rattulus sulcatus Jennings, 1894, p. 20, Fig. 8.
Trichocerca sulcata: Myers 1937, p. 6.

Type locality: L. St Clair, Michigan, U.S.A.

Holotype: Not designated.

Description: Body cylindrical, dorsum arched to form hemisphere; two prominent sutures mark head sheath, which has numerous creases on contraction; two tongue-shaped fleshy projections from anterior margin appear triangular in lateral view, right most obvious; shallow, transversely striate furrow along dorsal median line; foot and short, equal-length toes curved forward under posterior, held adpressed to body; dorsal antenna in median furrow, lateral antennae at similar height on posterior ⅕ of trunk; trophi asymmetrical, robust; fulcrum double crooked; LM reaches end of fulcrum, distally dilated; RM a shorter, slender rod; ramus with enlarged bifurcate alula; brain with honeycombed retrocerebral sac; eyespot at base of brain; foot glands with large mucus reservoirs.

BL 97–132μm; toes 13μm; TR 40–42μm (F 33μm; LM 28μm; RR 16μm). Wulfert (1968) gives BL 200μm; toes to 35μm.

Distribution: Possibly cosmopolitan in periphyton of submerged plants. Recorded by Berzins (1982) from the Avoca River, Vic. No ecological information, not seen in our collections.

Trichocerca tenuior (Hudson & Gosse)
FIG. 8:2

Coelopus tenuior Hudson & Gosse, 1886, p. 68, Fig. 20:19
Trichocerca tenuior: Hauer 1931, p. 179, Fig. 5a

Type locality: No single locality specified. "Woolston: Sutton Park and Coleshill, Birmingham", England.

Holotype: Not designated.

Description: Body elongated, curved, with single acute tooth at right anterior margin of lorica; left of tooth is a low, pleated plate; transversely striated low keel continues obliquely from base of tooth to ca. midline; head sheath marked off by suture, has longitudinal folds when head withdrawn; lateral antennae at different heights, left more anterior; foot short, offset from trunk; toes unequal – left toe ca. half lorica length, slightly curved ventrally, right more delicate, half length of left; substyli present; trophi asymmetrical; fulcrum double crooked; LM almost fulcrum length, distally with 70–80° inward bend; RM fragile straight rod; RR with triangular alula pointing almost at right angles to fulcrum; gut may be orange coloured. *T. tenuior* may be confused with *T. gracilis* (Fig. 11:1), *T. insignis* (Fig. 5:3), *T. intermedia* (Fig. 6:1) and *T. tigris* (Fig. 8:3), can be separated readily by trophi morphology.

BL 125–210μm; height 40–50μm; LT 54–80μm; RT 35–37μm; TR 40–45μm (F 31μm; LM/RM 31/19μm; rami 17/15μm) subitaneous egg 65×38μm.

Distribution: Cosmopolitan in detritus, in algal mats, in periphyton, psammon, occasionally in tychoplankton of still waters or in beach sand of flowing waters, also in moor pools. Rare in mainland samples (Vic.), more common in Tas.: 8.0–22.0°C, pH 6.0–7.0, DO 10.0–11.2 mg l^{-1}, 70–700μS cm^{-1}, 1.7 NTU.

Literature: Koste & Shiel (1987).

Trichocerca tigris (Müller)

FIG. 8:3

Trichoda tigris Müller, 1786, p. 206, Fig. 29:8.

Trichocerca tigris: Voigt 1957, p. 321, Fig. 63:12.

Type locality: Copenhagen, Denmark?

Holotype: Not designated.

Description: Similar morphology to *T. tenuior*, with elongate, curved cylindrical body, single anterior occipital tooth, longitudinally pleated head sheath, oblique low keel arising from base of tooth; differs in usually greater size, more prominent keel, relatively large foot, equal length toes, trophi structure (cf. Figs 8:2b and 8:3b). *T. tigris* has distinctive anchor-shaped manubrium, double crooked fulcrum. May also be confused with *T. insulana*, again readily separated on trophi structure (cf. Figs 5:4, 8:3).

TL 220–300μm; BL 130–200μm; TR to 41μm; toes 50–80μm.

Distribution: Cosmopolitan, isolated occurrences in wide range of water quality, in periphyton and benthos (Koste 1978). Common in billabongs, Vic, Tas.: 16.0–22.0°C, pH 6.4–7.4, 114–274μS cm^{-1}.

Literature: Koste & Shiel (1987).

Trichocerca uncinata (Voigt)

FIG. 8:4

Coelopus uncinatus Voigt, 1902, p. 679.

Trichocerca uncinata: Carlin 1939, p. 43.

Type locality: Plön, Germany.

Holotype: Not designated.

Description: Body short, curved, anterior lorica margin slightly denticulate; acute occipital curved tooth displaced to right of midline; low tongue-shaped plate to left of tooth; ventral striae or pleats run to weak suture separating head-sheath from trunk; short foot with two unequal curved toes; trophi asymmetrical; left uncus club-shaped with several acute teeth, right uncus shorter, plump, bifurcate; large red eyespot.

BL 65–95μm; LT 12–27μm; RT 10–25μm; TR 27μm; occipital tooth 14–27μm.

Distribution: Probably cosmopolitan, in periphyton, algal mats, psammon, tychoplankton of fresh waters. Unconfirmed record from Tabrabucca Creek, Barrington, N.S.W. No ecological information. Not seen in our collections.

Literature: Koste (1978), Berzins (1982).

Trichocerca vernalis Hauer

FIG. 8:5

Trichocerca vernalis Hauer, 1936, p. 334, Fig. 1.

Type locality: Germany.

Holotype: Not designated.

Description: Squat, vaulted to conical body; left anterior margin with large rounded plate, foot and toes curved forward; short diagonal keel from striae field; toes of similar length; trophi strongly asymmetrical; left manubrium robust, with 'hockey-stick' crook, right manubrium a slender fragile rod with median kink; fulcrum double crooked; left uncus with two teeth; subuncus with several (commonly three) fine teeth. Resembles *T. sulcata* (Fig. 8:1), *T. brachyura* (Fig. 4:1), in particular the latter if trophi are left too long in caustic solution – left manubrium may dissolve away to produce the characteristic bend of *vernalis*' LM.

BL 86–138μm; height 51–58μm; LT 26–43μm; RT to 38μm; TR 31–46μm (in TR 45μm), F 32μm, RM 20μm, LM to 34μm).

Distribution: Ephemeral waters in Europe, N America, Indonesia. Rare, billabongs and ephemeral pools, R. Murray and Mitta Mitta R., Vic: 14.0–21.0°C, pH 6.2–6.85, 73–292μS cm^{-1}.

Literature: Berzins (1982).

Trichocerca weberi (Jennings)

FIG. 8:6

Diurella weberi Jennings, 1903, p. 309, Figs. 1:11–14; 13:116–117.

Trichocerca weberi, Edmondson 1935, p. 303.

Type locality: Not specified. Lake Erie and vicinity, Michigan, U.S.A.

Holotype: Not designated.

Description: Body short, curved in arc; head sheath indistinctly marked by suture; broad, rounded projecting plate to left of head aperture; short palpar organ in apical field; single prominent occipital tooth to right of dorsal median line; occasionally a spinule between plate and tooth; high, thin, transversely striated keel from median tooth to ⅔ lorica length; toes of similar length; trophi asymmetrical; LM with distal right-angled bend; RM ca. ½ length of LM, slightly sigmoid rod; suprarami distinctly elongated; toes with three-four inconspicuous substyli. Resembles *T. cavia* (Fig. 4:2) and *T. porcellus* (Fig. 6:4).

BL 95–155μm; height to 50μm, LT 30–54μm; RT to 42μm; occipital spine to 12μm; trophi to 52μm.
Distribution: Probably cosmopolitan, not recorded from Africa (Koste 1978). In periphyton of littoral, also moors. Rare: Qld, Tas., Vic., Tasmanian specimens slightly larger than those of the mainland: LT to 60μm, RT to 50μm. Possibly ecotypic variation.
Literature: Russell (1961), Koste *et al.* (1988).

Trichocerca (s. str.)
Trichocerca agnata Wulfert
FIG. 9:1

Trichocerca agnata Wulfert, 1939, p. 73-75, Fig. 5.
Type locality: "Heykasee bei Koslin". Present Poland
Holotype: Not designated.
Description: Medium slender body with lightly convex dorsum; convex abdomen; 12 somewhat similar large head creases without frontal process (in swimming animals folds not apparent); corona with one palpar organ and two antennae; dorsal antennae in pit, slightly displaced to right; left lateral antenna medial; right antenna at distal end of abdomen; LT straight, about ½ BL, RT <1/5 length of left. TR: LM longer and more strongly built with curved distal end; RM shorter more slender, also curved in at distal end; LR with longer pointed alula; RR weakly developed; suprarami small; F fanned distally.

TL 230μm, BL (contr.) 144μm, LT 73μm, TR 35μm.
Distribution: Europe. Single record from the River Murray at Echuca, Vic. 15.0°C, pH 7.6, DO 9.0 mg l^{-1}.
Literature: Koste (1978), Koste & Shiel (1980).

Trichocerca bicristata (Gosse)
FIG 9:2

Mastigocerca bicristata Gosse, 1887, p. 2, Fig. 5
Trichocerca bicristata: Harring 1913, p. 101.
Type locality: Scotland.
Holotype: Not designated.
Description: Both slender and plump forms known; in corona two stiff projections; in cross section two variable height ridges separated by wide depression run length of dorsum, veering slightly to left; LT with triapical tip, median apex much longer than laterals; lateral antennae at similar height at end of abdomen. TR: both manubria terminally crooked, one side curved, suprarami large; LR occasionally with two-pointed alula. Lorica finely stippled; sometimes red brown coloured; RE with irregular "rodlet" reinforcement between the shells. May be confused with *T. mucosa* (Fig. 12:2), but is larger, with longer, more obvious keel structure.

TL 294–660μm; BL including foot 194–360μm; LT 200–320μm; RT 25–36μm; TR 65–79μm (F 50μm, LM 60μm, RM 50μm, rami 36–50μm, unci 22μm).
Distribution: Cosmopolitan, indicator of oligosaprobic waters; isolated occurrences in littoral in detritus occasionally in tychoplankton. Rare in Murray-Darling Basin, also Cape York, Qld and Kakadu Natl Pk, N.T. 8.0–24.5°C, pH 6.3–8.4, DO 5.3–13.0 mg l^{-1}, 59–575μS cm^{-1}, 23.5–40.0 NTU.
Literature: Colledge (1914), Koste (1981).

Trichocerca braziliensis (Murray)
FIG 9:3

Rattulus braziliensis Murray, 1913a, p. 244, Fig. 10,16a, b
Trichocerca braziliensis, Hauer 1965, p. 375, Fig. 32.
Type locality: Water lily pond, Praca Republica, Rio de Janeiro, Brazil.
Holotype: Not designated.
Description: Short, stout body with distinctive double keel ¼–⅓ length of dorsum; body broadest behind keels, tapers to foot; keels strongly rounded; LT longer than body, continues line of body, with basal sigmoid bend; RT ⅓ length left; TR resembles those of *T. mucosa* and *T. bicristata*, but whereas these taxa have manubria with only a hint of a crook, in *T. braziliensis* both are strongly crooked (Fig. 9:3b); RR with markedly bifurcate alula, LR with single spinelike process.

TL 270–275μm, contracted lorica 120–122μm; keels 38–40μm; LT 150–153μm; RT 33–50μm; substyles ca 10μm; TR 57–60μm (F 40μm; manubria 40 and 24μm; unci 10 and 12μm).
Distribution: Rare; previously recorded only from vegetated waters in South America, to 30.8°C, pH 4.5–6.7 (Koste 1978). Single record, Tasmania, several individuals, from a roadside marsh, Deloraine (22.ix.87). 18°C, pH 6.9, 106.5μS cm^{-1}.
Literature: Hauer (1965), Koste *et al.* (1988).
Comment: Although synonymised with *T. elongata* by Koste (1978), *T. braziliensis*' smaller size, general morphology and specific trophi differences (particularly bifurcate alula of LR and more robust crooked LM) as figured, suggest specific status be retained.

Trichocerca capucina Wierzejski & Zacharias
FIG. 9:4

Mastigocerca capucina Wierzejski & Zacharias, 1893, p. 242, Fig. 13:11–3.
Trichocerca capucina, Harring 1913, p. 102

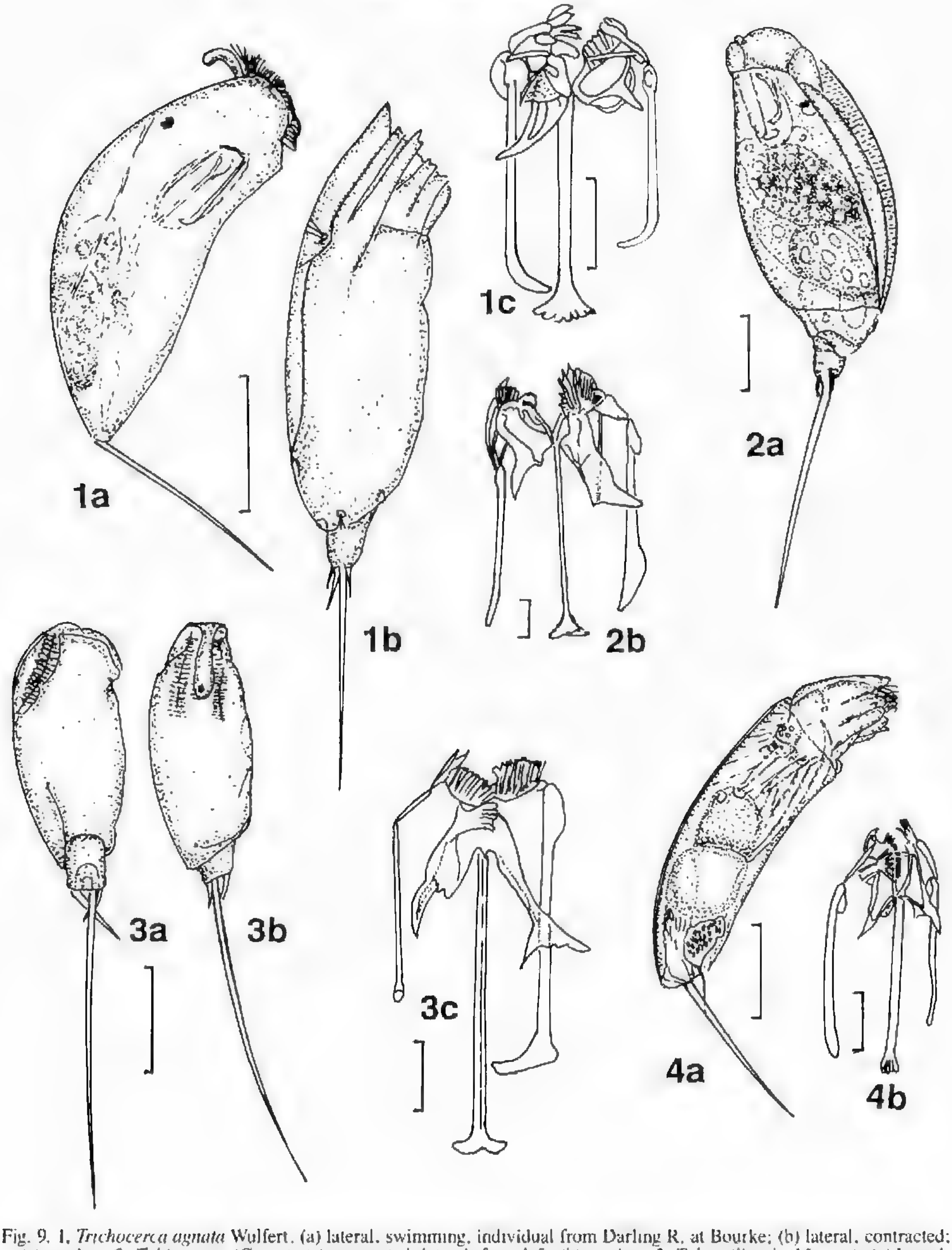


Fig. 9. 1, *Trichocerca agnata* Wulfert. (a) lateral, swimming, individual from Darling R. at Bourke; (b) lateral, contracted; (c) trophus. 2, *T. bicristata* (Gosse): (a) contracted, lateral, from left; (b) trophus. 3, *T. braziliensis* (Murray): (a) lateral; (b) dorsal; (c) trophus. 4, *T. capucina* Wierzejski & Zacharias: (a) lateral, swimming; (b) trophus. 1 b,c after Wulfert (1939); 2 after Wulfert (1956); 3 after Hauer (1965); 4 after Koste (1978). Scale lines, adult 50μm, trophi 10μm.

Type locality: (Germany)

Holotype: Not designated.

Description: Body fusiform; head with 5 palps and two antennae; abdomen cylindrical, slightly curved; cowl-like loricate head with retractible apices (= mucrones?) demarcated from trunk by distinct transverse suture; lateral antennae at similar height; TR almost symmetrical; RM slightly more robust; TR parts relatively fragile; male loricate with large red eyespot and rudimentary toes; RE brown, hard and shelled;

TL 250–430μm; LT 90–125μm; RT 45–48μm; male 90–100μm; RE 108–128 X 80–82μm; SE 86–100 X 68–72μm; male egg 60–64 X 70–80μm.

Distribution: Cosmopolitan, in plankton of lakes, also in moor and athallassic saline waters; attaches its eggs to other rotifers e.g. *Asplanchna*; feeds on eggs of other rotifers, e.g. Keratella, sucking out the contents. Uncommon; N.T., Qld, Tas., Vic. 7.9–24.5°C, pH 5.8–7.3, DO 5.8–9.8 mg l^{-1}, 38–92μS cm^{-1}, 1.0–5.0 NTU.

Literature: Murray (1913a), Koste (1978), Koste & Shiel (1987).

Trichocerca chattoni (Bauchamp)
FIG. 10:1

Rattulus cylindricus var. *chattoni* Beauchamp, 1907, p. 154, 6, Fig. 4.
Trichocerca chattoni: Hauer 1938, p. 563.
Trichocerca cylindrica chattoni: Koste 1978, p. 403.

Type locality: Pond of the Dombes (north of Lyon, France)

Holotype: Not designated.

Description: Body cylindrical; contracted animal has numerous folds in head producing undulate or serrated frontal margin; no pronounced suture at neck, only slight depression; distinctive characteristic single long ventrally curved spine left of dorsal antenna arising from thickened base; TR not described in Koste 1978. Distinguished from *T. cylindrica* by smaller, more squat body, shorter LT, less reduced RT and ratio of right:LT (LT max. 16μm in *T. cylindrica*, <5μm in *T. chattoni*).

TL 300–448μm, LT 115–140μm; RT 24–39μm; anterior spine 26–51μm.

Distribution: Tropical and subtropical waters, Europe, Africa, Indonesia, South America, probably pan-tropical/subtropical. pH 5.7–7.3 to 30.5°C (Koste 1978). Rare, confirmed from ca. 14 localities in the Kimberley, W.A., Magela Ck, N.T. and Cape York, Qld [collections by: P. Hawkins (Townsville), B.V. Timms (Cooranbong) and M.J. Tyler (Adelaide)], 25.0–29.0°C, pH 6.15–7.4, DO 3.7–8.0 mg l^{-1}, 48–245μS cm^{-1}, 0.5–6 NTU. Warm stenotherm? See comment below for *T. cylindrica*.

Literature: Koste & Shiel (1983).

Trichocerca cylindrica (Imhof)
FIG. 10:2

Mastigocerca cylindrica Imhof, 1891, p. 37.
Trichocerca cylindrica: Harring, 1913, p. 102.

Type locality: Lake in the Black Forest (Germany).

Holotype: Not designated.

Description: Elongate, cylindrical body; very fine, ventrally-curved acute spine from median dorsal lorica margin, may be folded down and invisible in contracted animal; longitudinal striae in head region in latter case; short keel and striated field; LT always longer than body; RT reduced to rudimentary short, scaly spine; dorsal antenna long, rigid; left lateral antenna in middle of trunk, right just before foot; TR almost symmetric, but LR more robust; both manubria longer than fulcrum, curved distally, with fenestrated proximal ends (Fig. 10:2b), animal occasionally in gelatinous sheath; eggs carried attached to parent, male toeless, RE in striated gelatinous sheath.

TL 490–796μm; body 225–468μm; LT 190–328μm; RT to 21μm; TR 50μm (F 36μm, manubria 46μm); male 80–90mμm; male egg 52×35μm.

Distribution: Palaearctic and Nearctic lakes, pools and moors. Sudzuki (1967) recorded *T. cylindrica* from L. Sorrell in Tasmania; we subsequently found it in L. Eucumbene, Snowy Mts, and L. Dartmouth, Vic. 12–18.0°C, pH 6.65–7.04, 26–47μS cm^{-1}, DO 7.0 mg l^{-1}.

Comment: Apparently two ecologically, and taxonomically distinct taxa occur in Australia: the larger cool water species, *T. cylindrica*, and the tropical *T. chattoni*. Koste (1978) synonymised the latter with the former (as a var.), but on the basis of apparent ecological and morphological differences we retain the distinction until SEM analysis can clarify the status of both taxa.

Literature: Sudzuki (1967), Koste & Shiel (1980).

Trichocerca elongata (Hudson & Gosse)
FIG. 10:3

Mastigocerca elongata Hudson & Gosse, 1886, p. 62, Fig. 20:8.
Trichocerca elongata: Harring 1913, p. 102.

Type locality: Loch near Dundee, Scotland.

Holotype: Not designated.

Description: Large species, body long and slender; head sheath not marked by constrictions; anterior edge unarmed; short double keel about ⅛ length; dorsal surface striated approximately ⅓ length anterior lorica with median furrow back to dorsal antenna; corona with single palpar organ; lateral antennae at same level although torsion of the body means left antenna is now more ventral and right antenna closer to dorsal line (only one seen in dorsal view); torsion has also moved toe to dorsal (right)/ventral (left) position rather than side by side; LT more than ⅔ lorica length, RT rudimentary; TR asymmetrical, left side more

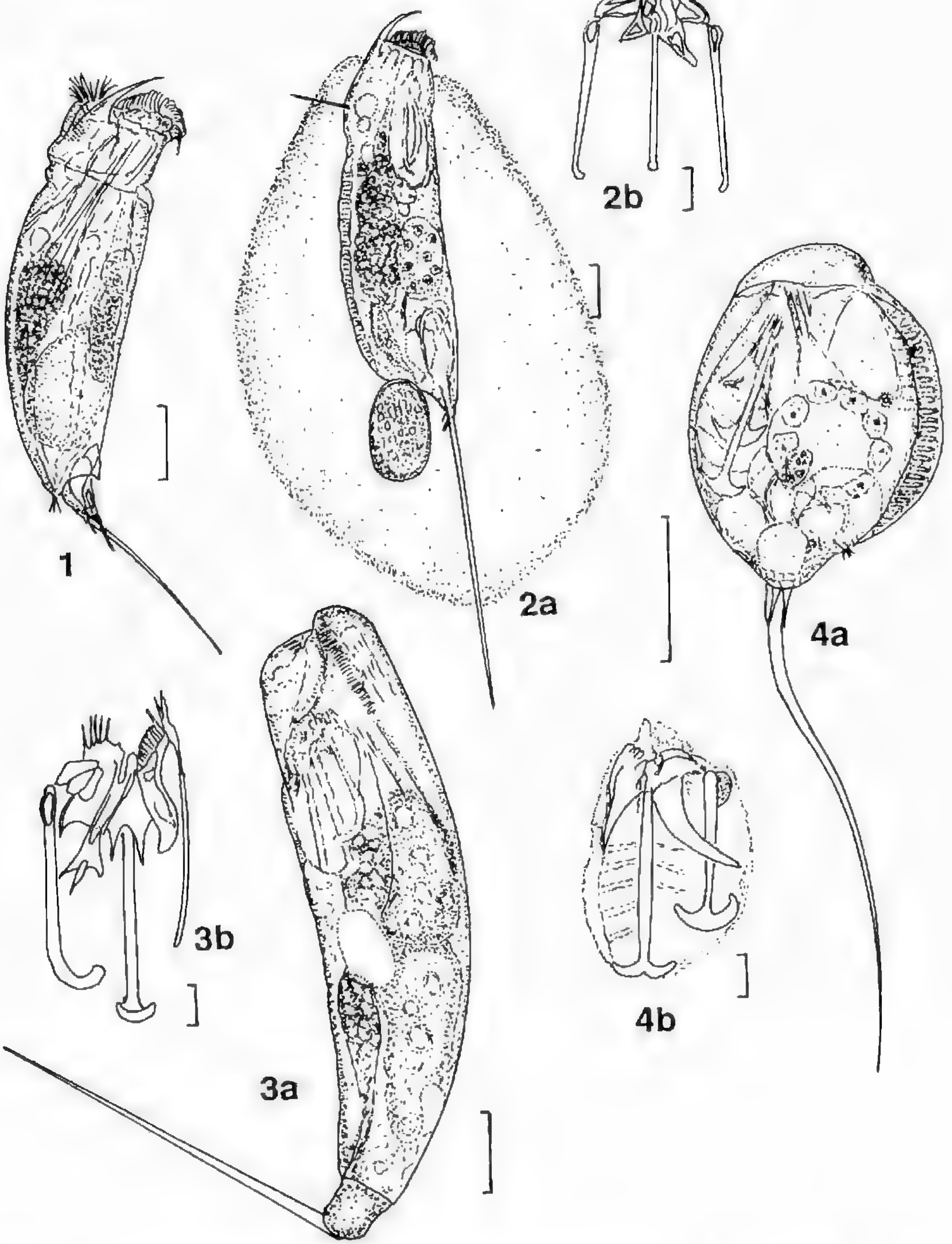


Fig. 10. 1, *Trichocerca chattoni* Beauchamp: lateral, swimming. 2, *T. cylindrica* (Imhof): (a) lateral, in gelatinous sheath; (b) trophus. 3, *T. elongata* (Hudson & Gosse): (a) lateral, contracted; (b) trophus. 4, *T. flagellata* Hauer: (a) lateral; (b) trophus; (c) dorsal. 1a after Beauchamp (1907); 1 after Hauer (1938); 2, 3b, 4b after Koste (1978) (various authors). Scale lines: adult 50μm, trophi 10μm.

developed; LM robust, with strongly curved distal end, fenestrated proximal end; RM a delicate rod; fulcrum double-crooked (inverted T); LR ends in 3-pronged alula (middle spine can be missing); lorica may be reddish-brownish; surface may also appear stippled.

TL 308–810μm; BL 130–460μm; LT 160–350μm; RT 32–56μm; TR 70–80μm; (LM to 63μm; RM 45μm).

Distribution: Cosmopolitan in littoral and tychoplankton of freshwaters. Pancontinental, common in billabongs. 11.6–27.0°C, pH 5.4–7.4, DO 9.1–9.8, 60–1600μS cm⁻¹, <10 NTU.

Literature: Koste (1978), Shiel & Koste (1979).

Trichocerca flagellata Hauer

FIG. 10:4

Trichocerca flagellata Hauer, 1937, p. 284, Fig. 1.

Type locality: Almali Lake, Madras, India.

Holotype: Not designated.

Description: Body compact, ovoid; head sheath indistinctly demarcated; anterior margin raised in a smooth curve on the right side; the rest undulating; medially a smooth notch; keel high-vaulted with wide striated area extends to the beginning of the short foot opening; left lateral antenna somewhat behind the middle of the abdomen; dorsal antenna near beginning of second third of trunk; LT slightly sigmoid; toe length: BL index ca. 1.5; TR robust with strongly crooked fulcrum and LM; brain large with large terminal cerebral eye.

BL 115–128μm; LT 172–173μm; RT 30μm; TR 60–72μm (44μm F; 40μm).

Distribution: Warm stenotherm; India, Malaysia, Amazon. Three localities known: Magela Ck, N.T.; Cape York, Qld and L. Purrumbete, Vic. 18.0°C, pH 6.1, DO 6.7 mg l⁻¹, 63μS cm⁻¹.

Literature: Koste (1978), Koste & Shiel (1980), Green (1981).

Trichocerca iernis (Gosse)

FIG. 11:2

Mastigocerca iernis Gosse, 1887, p. 866, Fig. 15:13

Trichocerca iernis: Harring 1913, p. 103

Type locality: Ireland (lacustrine).

Holotype: Not designated

Description: Body elongate, cylindrical; head sheath separated from trunk by transverse fold; single very small spine on lorica anterior margin; left lateral antenna inserted higher than right; keel with striae runs from anterior margin to end of abdomen; LM not crooked; suprarami small; left uncus bidentate.

TL to 300μm; BL 168–198μm; LT 80–100μm; RT?μm; TR 38–40μm; (F 30μm; LM 27μm; uncus 11μm).

Distribution: Cosmopolitan, between water plants in littoral standing and slowly flowing waters; single unconfirmed report from Yarra River at Warburton, Vic.

Literature: Koste (1978), Berzins (1982).

Trichocerca jenningsi Voigt

FIG. 11:3

Rattulus scipio Jennings, 1903, p. 322, Fig. 5:50–52 (non *Mastigocerca scipio* Hudson & Gosse, 1886, p. 61)

Trichocerca jenningsi Voigt, 1957, p. 321, Fig. 68:8.

Type locality: (U.S.A.)

Holotype: Not designated.

Description: Body elongated, curved with dorsal striated keel rising from anterior lorica, passing across dorsum diagonally right for ca. ¾ body length; keel with tooth at anterior end which may extend beyond lorica margin in contracted individuals; head sheath indistinctly separated, more obvious on ventral side; dorsal antenna at left side of keel; lateral antenna approximately equal height in posterior ¼ of lorica; foot offset from body with posterior dorsal edge of lorica projecting over left side of foot, restricting movement on left side; LT ¾ body length; RT rudimentary; trophi asymetrical; LM long, stout, curved; RM slender straight rod.

TL 320–408μm; LT 120–177μm; RT to 33μm.

Distribution: North America, Europe, Sri Lanka. N.T., Tas.; rare; 29.0°C, pH 6.5, DO 2.9 mg l⁻¹, 28μS cm⁻¹

Literature: Koste (1978), Koste & Shiel (1980).

Trichocerca longiseta (Schrank)

FIG. 11:4

Vaginaria longiseta Schrank, 1802, p. 383, Fig. 2:13.

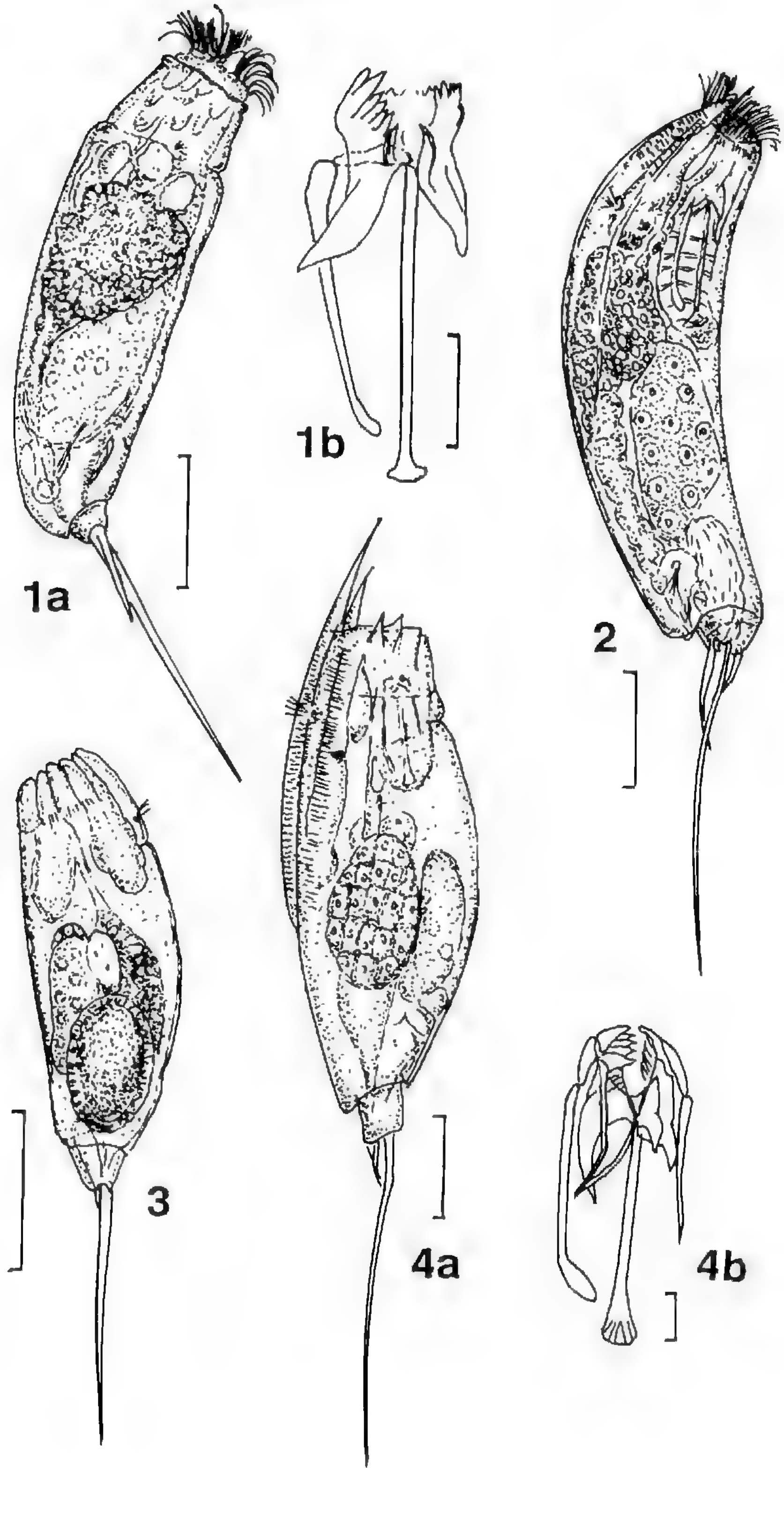
Trichocerca longiseta: Harring 1913, p. 103

Type locality: Germany?

Holotype: Not designated.

Description: Body elongate with two long spines on occipital margin, right almost twice length of left, with two small projections between spines; shallow keel from longest tooth to middle of abdomen, usually with striae; lateral antennae at similar height in posterior ⅓ abdomen; head sheath with longitudinal folds in contracted individuals; in living animals, apical fold has dorsal elongate palpar organ beside a membranelle, ventral to that two ciliated lobes; dorsal antenna beside keel, slightly behind constriction separating head and trunk; LT approximately body length; RT rudimentary. Trophi: Lm long, terminally thickened and curved inwards; LR with long pointed alula; suprarami with characteristic acute apices.

Fig. 11. 1. *Trichocerca gracilis* (Tessin): (a) lateral, swimming, (b) trophus. 2. *T. iernis* (Gosse), lateral, swimming; 3. *T. jenningsi* Voigt. 4. *T. longiseta* (Schrank): (a) lateral, contracted; (b) trophus. After Koste (1978) (various authors). Scale lines: adult 50μm, trophi 10μm.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TL 300–575μm; BL 200–370μm; anterior mucrone 48–55μm; LT 100–225μm; TR 63–84μm; RE 57–68 X 115–127μm.

Distribution: Cosmopolitan in most submerged vegetation zones. Punctures cells of green algal filaments and sucks out cell contents. Widespread, not yet recorded from S.A. or W.A.; common; 8.5–20.0°C, pH 6.3–8.9, DO 7.1–11.2 mg l^{-1}, 16.6–927μS cm^{-1}, 4–28 NTU.

Literature: Koste (1978), Koste & Shiel (1980, 1987).

Trichocerca macera (Hudson & Gosse)
FIG. 12:1

Mastigocerca macera Hudson & Gosse, 1886, p. 61, Fig. 20:12
Trichocerca macera: Harring, 1913, p. 105
Trichocerca fusiformis Levander: Koste 1981, p. 104.

Type locality: England?

Holotype: Not designated.

Description: Elongate fusiform body occasionally curved, dorsal surface more convex than ventral; head sheath marked off by slight constriction; small tooth on anterior margin right of midline; broad area corresponding to location of keel in other species may be noticeable but generally is not; dorsal and lateral antennae of usual appearance; LT straight, ca. ½ lorica length, RT < 1/6 its length; substyli present; when toe bent forward a spur-like point extends backwards from distal end of foot at base of toes, not known for other species; trophi not described.

TL 440μm; BL 278–330μm; LT 112–140μm; RT 18μm.

Distribution: Peaty pond waters, also littoral of larger waters, Europe, North America. Rare: N.T., Qld, Vic.

Literature: Koste (1978), Berzins (1982).

Trichocerca mucosa (Stokes)
FIG. 12:2

Mastigocerca mucosa Stokes, 1896, p. 17, Fig. 7:1.
Trichocerca mucosa: Hauer 1965, p. 377 (=*T. bicristata mucosa* Koste 1978).

Type locality: ". . . a shallow clear-water pool in a rocky wood near Trenton, New Jersey, U.S.A."

Holotype: Not designated

Description: Body, seen laterally broadly oblong; head sheath with constriction; no anterior teeth or spines; deep narrow fold on ventral side when head retracted; two well marked striated dorsal ridges or keels with furrow between them; in swimming animals one club shaped palpar organ on corona, two slender lateral rods; dorsal antenna left of left ridge, in a pit; lateral antenna well behind midline; foot short conical; lorica projects well beyond it on left, restricting toe movement in that direction; LT may reach BL (Jennings 1903:331 noted that the animal often swims with the LT carried against the right side and appears toeless); RT rudimentary indistinguishable from substyli; TR massive, strongly asymmetrical; fulcrum crooked. LM robust, distally curved. RM much smaller, thin rod; LR with long downward curving alula.

TL 300–350μm; BL 180–191μm; LT 120–150μm; TR 63μm (F 43μm; RR 21μm; LR 35μm; RM 37μm; LM 45μm); RE 150 X 130μm;

Distribution: Cosmopolitan/cosmotropical? Early record from Qld, not seen in our collections.

Comment: Koste's (1978) referral of *T. mucosa* to a varietal morph of *T. bicristata* is not justified in view of differences in morphology, in particular of the trophi. Specific status is retained awaiting detailed SEM analysis of the trophi of both taxa.

Literature: Colledge (1911), Koste (1978).

Trichocerca mus Hauer
FIG. 11:3

Trichocerca mus Hauer, 1938, p. 561, Fig. 86.

Type Locality: Tjigombong, Java.

Holotype: Not designated

Description: Body of fully contracted animal egg-shaped; head sheath a series of folds around contracted head opening; head not clearly separated from trunk; no keel, but shallow groove extends dorsally to past midline (no keel); dorsal antennae is in the anterior part of this groove; short, stout foot; LT slightly kinked at the base, about 1.5 times BL; RT about 1/5 length LT; TR??

TL 131μm; BL 50–55μm, LT 60–76μm; RT 16μm.

Distribution; Canada, Java, central America. N.T., Tas., Vic.; rare; 15.0°C, pH 7.4, DO 8.9 mg l^{-1}, 103μS cm^{-1}.

Literature: Koste (1978, 1981), Koste & Shiel (1980).

Trichocerca pusilla (Jennings)
FIG. 12:4

Rattulus pusillus Jennings, 1903, p. 339, Figs. 81–85.
Trichocerca pusilla: Harring 1913, p. 104.

Type locality: U.S.A.

Holotype. Not designated.

Description: Small pyriform to fusiform body [cf. *T. dixon-nuttalli* (Fig. 4:4) and *T. ruttneri* (Fig. 7:2)]; LT in contracted individuals elevated at right-angles; weak longitudinal striae at anterior margin; median groove dorsally; no striated field; bright red eye dorsal to brain; right lateral antenna shortly before foot, left at beginning of last third of body. Trophi: rami with robust, outwardly directed alulae; LM terminally weakly curved. RM shorter, rodlike.

Total length 110–175μm; body length 69–115μm; LT to 63μm; RT to 15μm; trophi 31μm (F 22μm; manubria 21/28μm; left uncus 8μm; rami 6/12μm); male 60μm.

Distribution: Cosmopolitan in plankton of lakes, ponds, also in moors and brackish water. Eggs often fixed to loricae of *Brachionus* species, particularly *B. angularis*. Pancontinental, common in billabongs; 10.5–24.5°C, pH 5.1–8.4, DO 5.8–10.0 mg l^{-1}, 28–725μS cm^{-1}, 6–120 NTU.

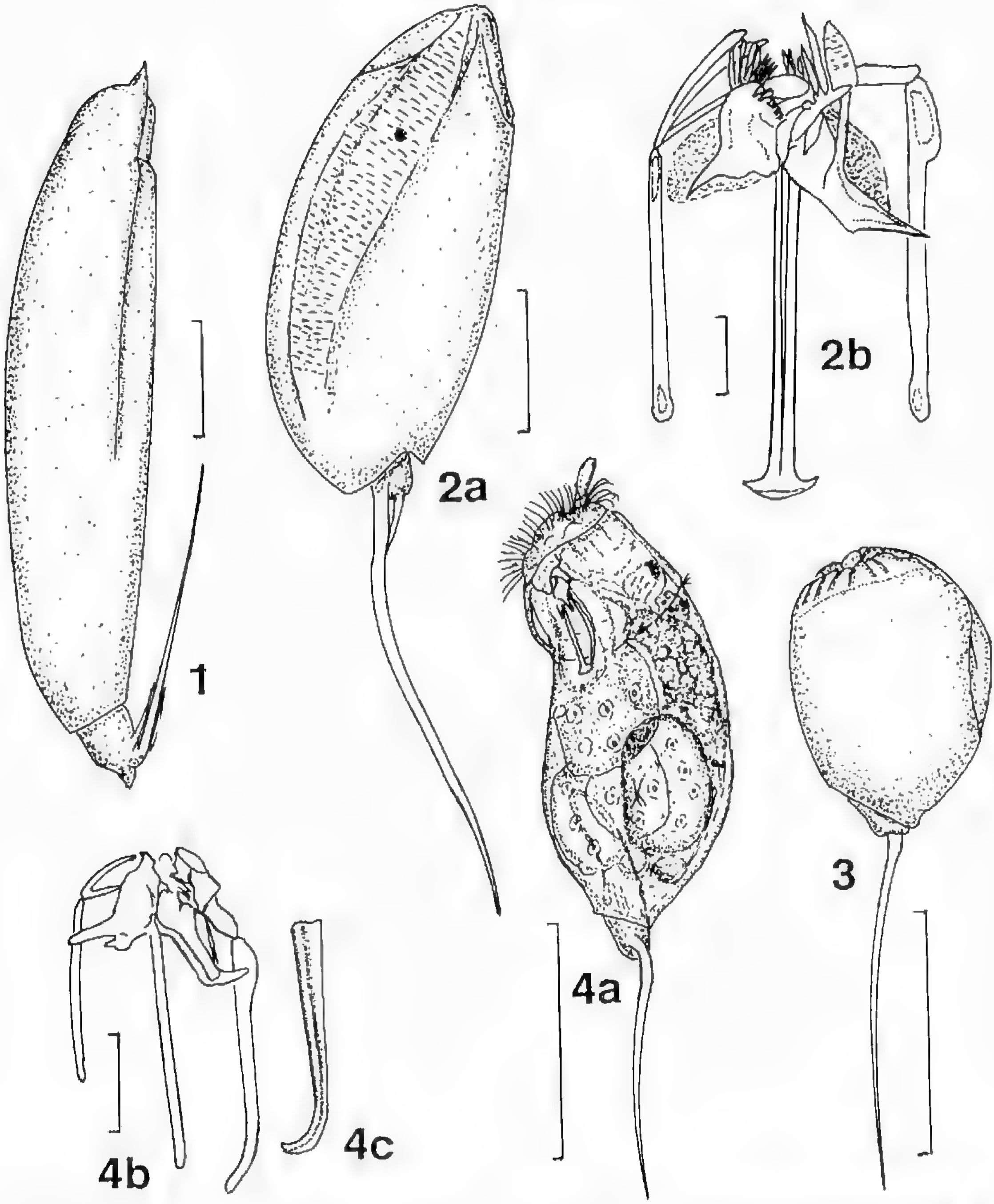
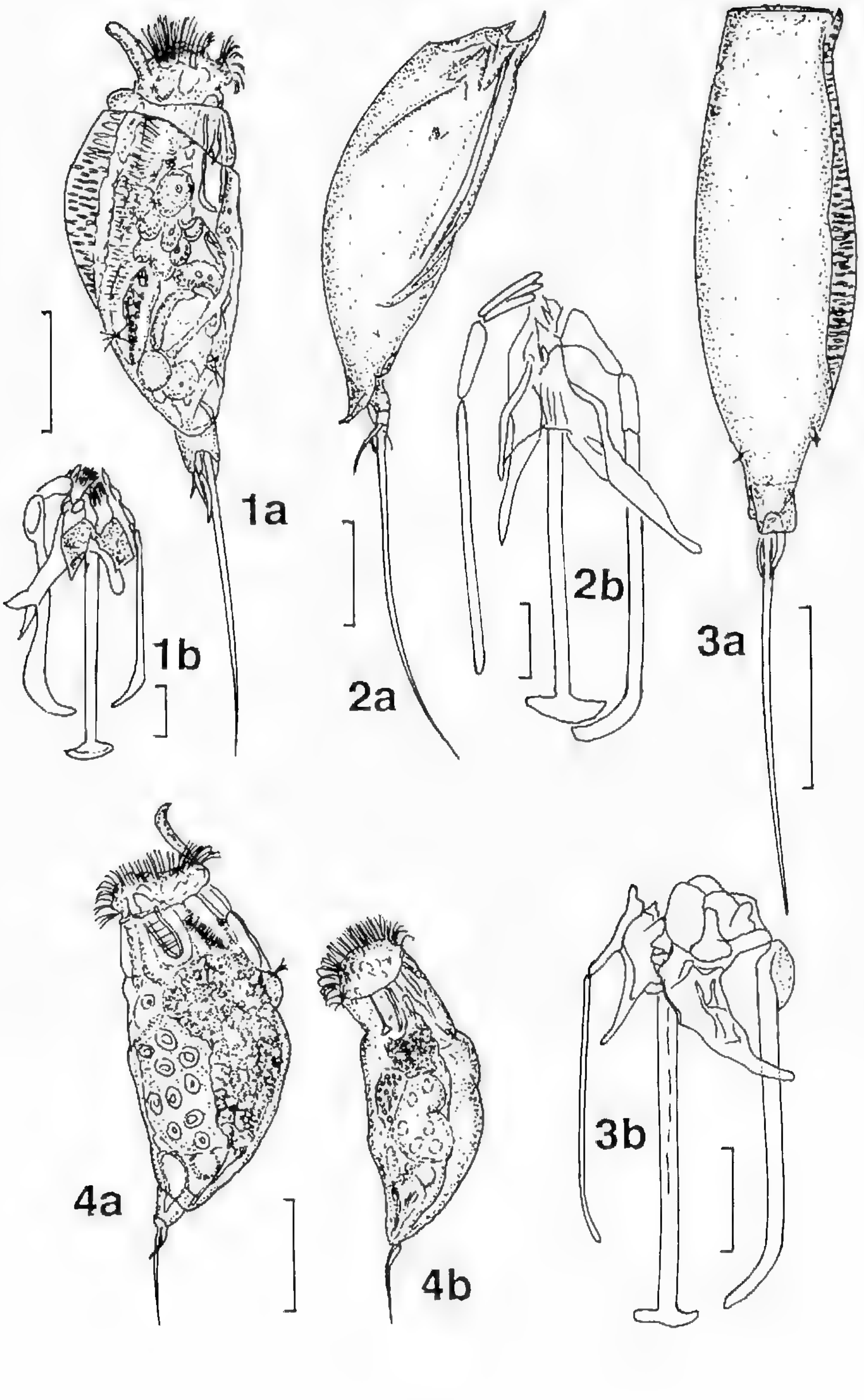


Fig. 12 1, *Trichocerca macera* (Hudson & Gosse): lateral, contracted. 2, *T. mucosa* (Stokes): (a) lateral, contracted; (b) trophus. 3, *T. mus* Hauer: contracted, lateral. 4, *T. pusilla* (Jennings): (a) swimming, lateral, (b) trophus; (c) fulcrum, lateral. After Koste (1978) (various authors). Scale lines: adult 50μm, trophi 10μm.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Literature: Berzins (1953), Koste (1981), Koste & Shiel (1987).

Trichocerca rattus (Müller)
FIG. 13:1

Trichoda rattus Muller, 1776, p. 281.
Trichocerca rattus: Harring 1913, p. 104.

Type locality: Copenhagen, Denmark.

Holotype: Not designated

Description: Lorica with low or medium keel ca. half dorsal length, may be rudimentary; wide striae-field; lateral antennae in posterior trunk region, right higher than left; RT shorter than longest substyle. Trophi: fulcrum an inverted T; both manubria single-crooked, right more delicate, occasionally straight; left alula elongate, bifurcate, deflected ventrally, right alula shorter, more rounded; animal may have reddish patches; red cerebral eye; male toeless.

TL 260–320μm; BL 150–225μm; LT 130–192μm; RT to 20μm; TR 60μm; SE 102×51μm; male 60–70μm.

Distribution: Cosmopolitan, isolated occurrences in littoral of standing and flowing waters, moors and brackish water. Common, widespread in eastern Australia and Tasmania. 8.0–27.0°C, pH 5.4–10.00; DO 6.2–13.0 mg l^{-1}, 15–1080μS cm^{-1}, 3–135 NTU.

Comment: A variant, *T. rattus carinata* (Ehrenberg) differs from *T. rattus s. str.* only by a wider head opening and higher keel; all body measurements and ecological ranges are within those of the typical form. There is no evidence that this is other than an ecotype: it is here synonymised.

Literature: Koste (1978), Shiel & Koste (1979), Koste & Shiel (1986, 1987).

Trichocerca rosea (Stenroos)
FIG. 13:2

Mastigocerca rosea Stenroos, 1898, p. 146
Trichocerca rosea: Fadeev 1927, p. 12, Fig. 2,6–7.

Type locality: Finland.

Holotype: Not designated.

Description. Dorsal margin with acute projection, of variable length, resembles *T. longiseta*; from base of spine, left of dorsal antenna, shallow keel and striated field reach right lateral antenna; left lateral antenna more posterior; retrocerebral organ with sac; sensory papillae in apical field; LT ca. BL. Trophi: fulcrum spatulate distally; LM slightly curved distally.

BL 260–376μm; LT 160–218μm; RT to 40μm.

Distribution: Littoral of lakes, moor pools in Europe, North America, New Zealand. Single record from Tas.: 18.0°C, pH 6.9, 106.5μS cm^{-1}.

Literature: Koste *et al.* (1988).

Trichocerca scipio (Hudson & Gosse)
FIG. 13:3

Mastigocerca scipio Hudson & Gosse 1886, p. 61, Fig 20:11.
Trichocerca scipio: Harring 1913, p. 104
non *Rattulus scipio:* Jennings 1903, p. 322–323, Fig. 5:50–52 (=*T. jenningsi* Voigt, 1957).

Type locality: England, "on water-moss in pools".

Holotype: Not designated.

Description: Body sub-cylindrical, slightly larger at front, thickened, rounded posteriorly; three spines on anterior lorica margin, one occipital, two lateral, each continues as a low ridge onto anterior lorica; long low keel displaced to right; toe half lorica length; substyli ca. ¼ toe length; mastax large, occupying >½ body length; trophi not described; conspicuous crimson cerebral eyespot.

TL to 250μm; BL to 148μm; LT to 80–100μm.

Distribution: England, Europe? Probably littoral in habit, in pools. Recorded from three localities in Tasmania. 16.0–18.0°C, pH 4.9–7.5.

Comment: It is unclear from the literature whether species referred to *T. scipio* are this species or Jennings taxon subsequently described as *T. jenningsi*. Three populations recorded from L. Pedder region, Tasmania resemble the animal described by Hudson & Gosse. 16.0–25.0°C, pH 4.9–7.47.

Literature: Koste *et al.* (1988)

Trichocerca stylata (Gosse)
FIG. 13:5

Monocerca stylata Gosse, 1851, p. 199
Trichocerca stylata: Harring 1913, p. 105.

Type locality: ". . . garden reservoir near London", England.

Holotype: Not designated.

Description: Body irregular in form, plump, gibbous; integument very flexible; contracted animal has blunt, puckered head sheath, marked from trunk by distinct suture; no apparent ridges; lateral antennae in middle of trunk; cerebral eye may be papillate; LT < ⅓ BL, slightly curved; RT rudimentary, ca. ⅓ length of LT, held appressed, easily overlooked; not substyli; trophi asymmetrical.

Fig. 13. 1 *Trichocerca rattus* (Muller): (a) typical form, lateral; (b) trophus; 2. *T. rosea* (Stenroos): (a) lateral, contracted; (b) trophus. 3. *T. scipio* (Hudson & Gosse): (a) lateral, contracted; (b) trophus. 4, *T. stylata* (Gosse): (a–b) swimming, lateral. 1–4 after Koste (1978) (various authors). Scale lines, adult 50μm; trophi 10μm

TL 180–230μm; BL 135–180μm; width 71μm; TR 31–35μm; LT 45–53μm; male 60μm.
Distribution: Cosmopolitan in plankton of lakes and pools, where it attaches its eggs to other planktonic rotifers. Rare: Qld, Tas., Vic. 10.5–25.0°C, pH 7.5–8.4, DO 8.2–10.0 mg l^{-1}, 440–495μS cm^{-1}, 4.5–68.0 NTU.
Literature: Koste (1978), Shiel & Koste (1979).

Other species of Trichocerca

We must stress that the keys above (and in earlier parts of this series) are based on known morphology of rotifers we have identified, or other systematists have recorded, from Australian waters. Collections which contained only single individuals not readily identifiable with known taxa have been excluded. Until more material of these taxa becomes available they cannot be treated adequately. We are aware of at least three *Trichocerca* taxa in local waters which cannot be keyed successfully here. Users of our keys finding animals which do not conform to one or more of the morphological ranges for taxonomically significant features, in particular the trophi, should treat them with caution. Variants from the 'norm' should not be "shoe-horned" into known taxa because they 'look a bit like' the figures in an authoritative text! The wide distribution of such texts, until now northern hemisphere in origin, is the principal reason for the assumed cosmopolitan distribution of many rotifers, and the basis of widespread confusion in the taxonomy of the group.

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SELECTIVITY OF MICROCRUSTACEAN ZOOPLANKTON BY GOLDEN PERCH (*MACQUARIA AMBIGUA*) LARVAE AND FRY IN LABORATORY STUDIES

BY R. J. SHIEL & W. KOSTE†*

Summary

First-feeding golden perch larvae in experimental beakers were able to ingest only the smallest size-class (0.78-0.86mm) *Daphnia.* As the larvae grew the size of prey captured increased. First-feeding larvae preferred the cladocerans, *Daphnia* and *Moina,* to a similar size-class of the calanoid copepod *Boeckella.* Ten to 20 mm golden perch were non-selective for the prey species. while larger fry preferred *Daphnia,* the largest prey. The pattern of predation by larvae and fry changed from gape-limited to size-dependent to large-size selective, consistent with optimal foraging theory. Larval rearing ponds should be managed to provide small cladocerans and nauplii and early stage copepodites for first feeding larvae and larger zooplankters for fry greater than 20 mm.
KEY WORDS: Golden perch, *Macquaria ambigua,* fish larvae, fry, prey. *Moina micrura, Daphnia carinata, Boeckella,* prey preferences, size-selective

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SELECTIVITY OF MICROCRUSTACEAN ZOOPLANKTON BY GOLDEN PERCH (*MACQUARIA AMBIGUA*) LARVAE AND FRY IN LABORATORY STUDIES

by P. T. ARUMUGAM* & M. C. GEDDES†

Summary

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First feeding golden perch larvae in experimental beakers were able to ingest only the smallest size-class (0.78-0.86 mm) *Daphnia*. As the larvae grew the size of prey captured increased. First-feeding larvae preferred the cladocerans, *Daphnia* and *Moina*, to a similar size class of the calanoid copepod *Boeckella*. Ten to 20 mm golden perch were non selective for the prey species, while larger fry preferred *Daphnia*, the largest prey. The pattern of predation by larvae and fry changed from gape-limited to size-dependent to large-size selective, consistent with optimal foraging theory. Larval rearing ponds should be managed to provide small cladocerans and nauplii and early stage copepodites for first feeding larvae and larger zooplankters for fry greater than 20 mm.

KEY WORDS: Golden perch, *Macquaria ambigua*, fish larvae, fry, prey, *Moina micrura*, *Daphnia carinata*, *Boeckella*, prey preferences, size-selective

Introduction

The Australian freshwater fish golden perch, *Macquaria ambigua* (Richardson), is routinely spawned in hatcheries and the larvae reared in earthen ponds which are managed to provide zooplankton forage for the larvae and fry (Rowland 1983, 1986). Some understanding of the diet of larvae and fry in these ponds has been achieved by observing differences between zooplankton communities in enclosures with and without fish (Arumugam & Geddes 1986, 1988), from consideration of mouth gape and feeding behaviour (Arumugam & Geddes 1987) and from analysis of gut contents of larvae and fry (Culver & Geddes in press). However, when studying diet from analysis of gut contents of fish in natural habitats or nursery ponds, size and species preferences of fish fry may be obscured by turbidity (cf. Vinyard & O'Brien 1976; Gardner 1981) and prey availability due to successional or seasonal patterns of species abundance and size fractions (Arumugam & Geddes 1986, 1988). Laboratory studies of the prey preferences of golden perch will provide a better understanding of the diet during their ontogeny, possibly leading to improved pond management strategies. In the laboratory, combinations of selected prey can be presented under standard conditions and the resulting predation can be presented as preference indices.

Laboratory techniques have been used to study prey preferences of many planktivorous freshwater fish (see Lazzaro 1987 for review), but fewer studies have been made on larvae and fry. Confer & Blades (1975) found that the distance of visual perception (reactive distance) of a fish was proportional to the size of the prey. Usually prey size is the major factor in determining preferences (Brooks 1968), but prey preference can be influenced by light intensity (Jacobs 1978), decreasing prey densities (Werner & Hall 1974), escape ability of the prey (Drenner & McComas 1980), prey motion, visual portions of the prey (cf. Zaret 1980), and prey ratios and feeding durations (Gerking & Plantz 1980). In studying prey preference it is necessary to consider both prey size and alternate prey species which have different morphologies and behaviours. Care needs to be given to the density and prey ratios in the feeding experiments.

The objectives of the current study were to determine (i) the size preference and (ii) the preference among some common microcrustaceans species, shown by golden perch (*Macquaria ambigua*) larvae and fry under laboratory conditions. The prey preferences of golden perch larvae and fry would contribute further to an understanding of predation by larval fish and would allow evaluation of different preference models proposed for planktivorous fish larvae (Zaret 1980). Additionally, management options for the improvement of golden perch fry culture could be derived from this study.

Materials and Methods

Laboratory experiments were carried out at the Inland Fisheries Research Station (IFRS), Narrandera, New South Wales, from November to December 1985.

* Centre of Applied Science Studies, Universiti Pertanian Malaysia Campus Bintulu P.S. 396,97008 Bintulu, Sarawak, Malaysia.

† Department of Zoology, University of Adelaide, G.P.O. Box 498, Adelaide, S. Aust. 5001. To whom reprint requests should be directed.

An experimental chamber in which ten replicates could be run simultaneously at 20–22°C was used (Arumugam 1990). The chamber consisted of ten 250 ml beakers arranged in two rows on a platform in a 600 mm × 300 mm × 300 mm glass aquarium which was provided with aeration and sub-gravel filtration. Each beaker had a U-tube connecting the water inside the beaker with the water in the aquarium and maintaining water in the beaker at the 150 ml level. A 60 μm mesh nylon screen covered the end of the U tube inside the beaker to prevent the larvae, fry and prey items from escaping. In each replicate, one larva or fry was placed into each beaker. A water exchange rate of 6 to 10 times hr^{-1} was maintained in each beaker by continuous pumping of water from the aquarium. This water rate ensured that the slower swimming prey were not trapped at the nylon screen.

Fish and zooplankton

Golden perch of approximately 4.6, 10, 20 30 and 38 mm standard length (SL) were used. The 4.6 mm larvae were taken from an aquarium in which the eggs were incubated until the larvae commenced feeding. Fish 10–38 mm were caught from the nursery ponds. One larva or fry of appropriate size was placed into each beaker in the experimental chamber. A plastic tube (diameter: 25 mm, length: 30–40 mm) was provided as a refuge. The larvae and fry used for the feeding trials were not fed during the acclimatization period which was usually less than 18 hours.

The microcrustaceans *Moina micrura*, *Daphnia carinata* and *Boeckella fluvialis* were either collected from the ponds at the station or cultured in the laboratory. The total prey density used in feeding trials was 90 individuals in 150 ml of water (600 individuals/litre). This density was about the maximum of total microcrustaceans recorded in the larval rearing ponds (Culver & Geddes in press).

Prey preference index

The prey preferences of larvae and fry were determined using Manly's index for a case when prey density was limited (Chesson 1983). This Manly-Chesson index takes into account changing prey ratios that may occur during the feeding process if feeding is selective. The index range is 0 to 1.0 and the point of equal preference would be the reciprocal of the number of prey types. In this study, the value is one-third (0.33) since three prey types were used.

Size preferences

Three size-classes of *Daphnia* were used in feeding trials to determine the size preferences of golden perch larvae and fry. *Daphnia* in the small size-class ranged from 0.78 to 1.04 mm, in the medium size-class 2.00 to 3.12 mm, and the large class 3.68 to 5.44 mm; all measured from the tip of the rostrum to the base of the spine (Table 1). Thirty *Daphnia* of each size-class were placed in a holding beaker, swivelled to mix them up and then gently transferred to one of the beakers with a fish of the appropriate size. For a particular size-class of fish, ten feeding trials were run simultaneously, each trial staggered at three to ten minute intervals. For the 4.6 mm larvae, each feeding trial was run for 24 hrs; for the larger larvae and fry, the feeding trial was run for 10 to 35 min depending on the feeding activity; trials were terminated before more than about 30% of the prey were taken. At the end of a feeding trial, the fish was removed and the number of *Daphnia* remaining in each size-class was recorded. For each size-class of fish, the preference index values for each size-class of *Daphnia* were calculated and expressed as means (± standard error).

Species preferences

Moina micrura Kurz, *Daphnia carinata* King and *Boeckella fluvialis* Henry were used to determine the species preferences of golden perch. Thirty individuals of each prey species were used for each feeding trial as described for the size preference experiment. For *D. carinata* length was measured to the base of the spine; for *M. micrura*, total length was measured and for *B. fluvialis* the measurement was of cephalo-thorax length. An attempt was made to present prey of about

TABLE 1. *Length ranges of golden perch (standard length) and of small, medium and large* Daphnia *together with the duration and consumption rates of feeding trials.*

Fish Length (mm)	*Daphnia* Lengths (mm) Small	Medium	Large	Duration	Consumption Rate (Number h^{-1})
4.4–4.8	0.78–0.86	2.80–3.12	4.15–5.23	24h	0.04–0.25
10.0–10.6	0.78–0.86	2.40–2.60	4.15–5.38	5–32 min	2–36
19.5–22.0	0.80–1.04	2.16–2.72	4.52–5.12	10–38 min	15–48
29.0–33.6	0.78–0.86	2.16–2.70	4.22–5.24	10–35 min	8–60
35.2–41.4	0.78–0.86	2.00–2.64	3.68–5.40	15–25 min	82–168

TABLE 2. *Length ranges of golden perch (standard length) and* Moina, Daphnia *and* Boeckella, *together with the duration and consumption rates of feeding trials.*

Fish Length (mm)	Prey Lengths (mm) *Moina micrura*	*Daphnia carinata*	*Boeckella fluvialis*	Duration	Consumption Rate (Number h^{-1})
4.4–4.8	0.35–0.50	0.78–0.86	0.43–0.96	24h	0–0.21
10.0–10.6	0.72–0.88	0.78–0.86	0.96–1.20	2.75–3.5 h	8–17
19.5–22.0	0.88–1.04	1.12–2.16	0.96–1.28	11–39 min	120–480
29.0–33.6	0.80–1.04	1.36–2.56	1.12–1.28	10–34 min	60–240

equal size and of a size appropriate to the different sizes of the fish used in the experiment. Newly hatched *Daphnia* and *Moina* and copepodite stage 3 *Boeckella* were presented to the first-feeding larvae while larger zooplankton were presented to the larger larvae and fry (Table 2). The relative sizes of the three prey species were similar for the 4.6 to 20 mm fry, but for the 30 mm fry, large specimens of the various prey types were used resulting in the length of *Daphnia* being greater than *Boeckella*, which was greater than *Moina*. The first-feeding larvae were allowed to feed for 24 hrs, the 10 mm larvae for about 3 hrs and the larger fry for from 10 to 39 min. (Table 2).

Results

Generally, the larvae and fry responded to the experimental chamber well and fed readily. A few of the 30 and 38 mm fry did not feed within the time duration and were replaced. Two of the 4.6 mm larvae died during feeding trials, with one of them having a *Daphnia* engorged in its throat. Mortality of the prey, monitored by looking for dead zooplankters at the end of each trial, was negligible for experiments up to three hrs duration and was less than 10% over 24 hrs.

The duration of each feeding trial and the consumption rates in the size preference experiment are shown in Table 1, and the relative sizes of the three classes of *Daphnia* are presented in Fig. 1a. The consumption rate increased with the size of the fry. The 4.6 mm larvae ate 1–6 *Daphnia* in 24 hrs, while the 10, 20, 30 and 38 mm golden perch fry ate 2–26 *Daphnia* in 10 to 38 min.

Observations of feeding behaviour were made for all size-classes of fish except for the 4.6 mm larvae which had only a low rate of predation. Most 10 mm larvae initially attacked the large and medium *Daphnia* which, because of their relatively large size, usually escaped. On sighting a small *Daphnia*, the larvae would attack and engulf it with ease; however larvae continued to attack large and medium *Daphnia*. The 20 mm fry would follow a *Daphnia* individual first

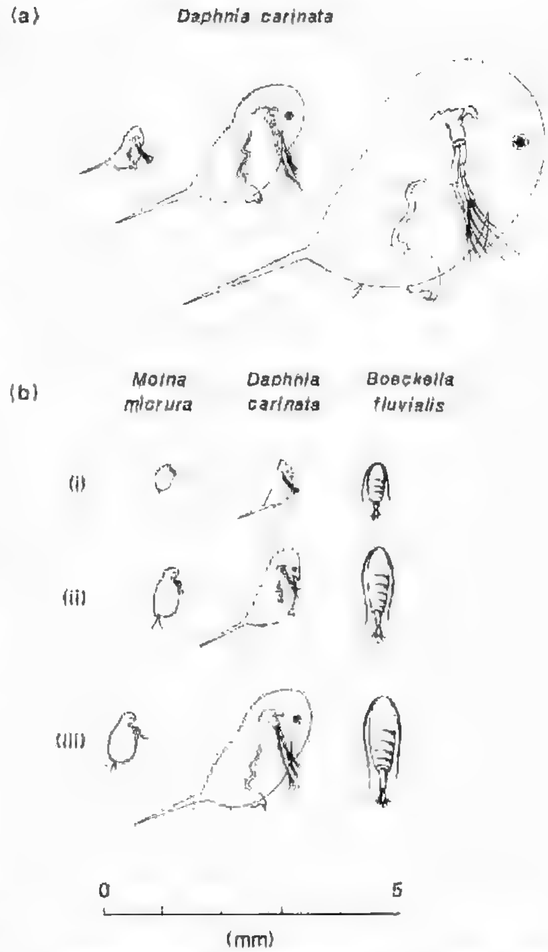

Fig. 1. Relative sizes and morphology of prey used in the golden perch prey preference experiments (all to same scale). (a) Small, medium and large size classes of *Daphnia carinata* used in the size preference experiment. (b) Size classes of *Moina micrura*, *Daphnia carinata* and *Boeckella fluvialis* used in the prey preference experiment for (i) first-feeding golden perch larvae (4.6 mm SL), (ii) 20 mm SL golden perch fry and (iii) 30 mm SL golden perch fry.

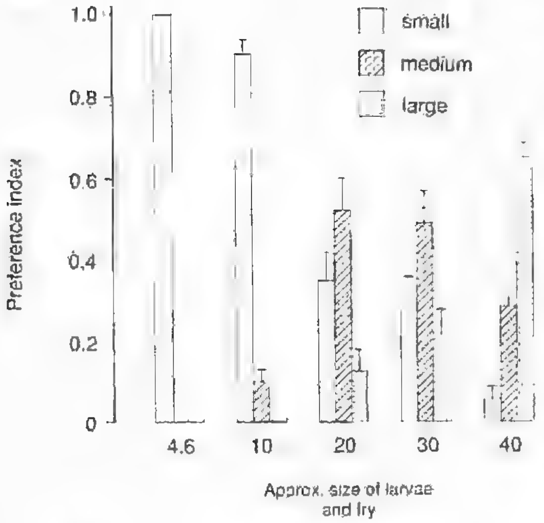

Fig. 2. Preferences for different size classes of *Daphnia carinata* by different size classes of golden perch larvae and fry. (Column represents mean and vertical bar represents a standard error for each mean value.)

before attacking it. In general attacks on large *Daphnia* by these fry were unsuccessful and, with experience fry usually avoided *Daphnia* that were too large. Fry of 30 mm and larger could engulf the whole size range of *Daphnia*.

The preferences by different sizes of golden perch fry for the three size-classes of *Daphnia* are shown in Fig. 2. First-feeding larvae preyed upon only the small *Daphnia*. Preference for the small *Daphnia* decreased with increase in fry size. "Bell-shaped" preference curves, with the middle size-class of prey most preferred, were obtained for the 20 and 30 mm fry. The 38 mm fry preferred the largest *Daphnia* and ate few of the smaller size-classes.

The sizes of the different prey used in the species preference feeding trials for the 4.6 mm larvae and the 20 mm and 30 mm fry are shown in Fig. 1b. The 4.6 mm larvae ate 0–5 prey items in 24 hrs, the 10 mm larvae ate 3–6 prey in about three hrs while fry had a higher consumption rate (Table 2). The 10 mm larvae captured *Moina* and *Daphnia* in one attempt, while some attempts at capturing *Boeckella* were not successful. The 20 and 30 mm fry could capture all three prey species with ease.

The species preferences of golden perch are shown in Fig. 3. The 4.6 mm larvae preferred cladocerans (*Moina* and *Daphnia*) with the preference for *Moina* slightly higher than that for *Daphnia* whereas the copepod *Boeckella* was hardly eaten. The 10 mm and 20 mm fry showed a similar preference for all three species. In these trials, the lengths of the three prey species were similar (Fig. 1b). At 30 mm, the fry preferred *Daphnia* which was the largest of the three prey species (Fig. 1b). The preference for *Moina* decreased with increasing fry size; for calanoids it increased initially and then decreased, and for *Daphnia* it varied initially and then increased with fry size.

Discussion

Most golden perch larvae and fry attacked large *Daphnia* on their first encounter even when they were too large to be engulfed, suggesting that size is an important factor determining prey detection. The bias towards larger prey means that the probability of larger prey species or of larger individuals within a species being eaten is greater (Eggers 1977). However, the prey preference index is determined by a sequence of prey detection, pursuit and capture. Pursuit and capture abilities of the larvae and small fry were limited and so they influenced the preference recorded for *Daphnia* of different sizes. Golden perch larvae at first feed have mouth gapes of only 0.5 mm (Arumugam & Geddes 1987) and so they were able to capture and engulf only

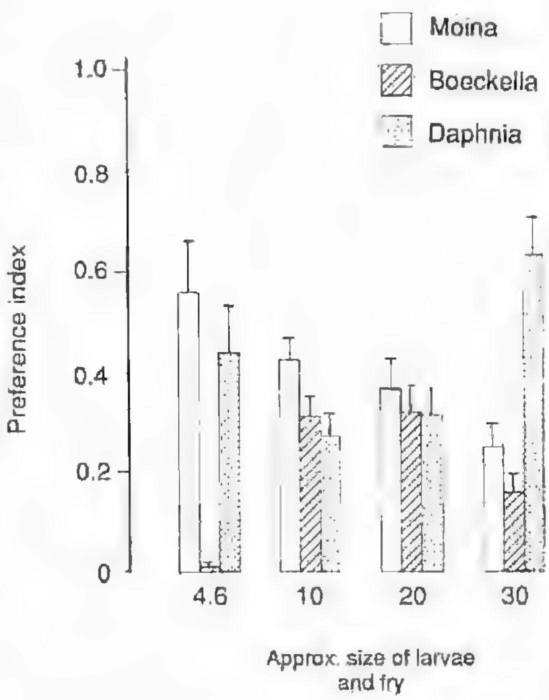

Fig. 3. Preferences for *Moina micrura*, *Daphnia carinata* and *Boeckella fluvialis* by different size classes of golden perch larvae and fry. (Column represents mean and vertical bar represents a standard error for each mean value.)

the smallest size-class of *Daphnia*. The middle size class of *Daphnia* was 2.8 mm long and with a head width of about 1 mm (Fig. 1a), well beyond the mouth gape of the first-feeding larvae. Golden perch larvae are clearly gape limited predators (Zaret 1980). The 10 mm larvae were unable to engulf the largest size-class of *Daphnia* and so they too were gape limited. The 20 and 30 mm fry exhibited a bell shaped size-preference curve, a form associated with size dependent predators (Zaret 1980; Scott & Murdoch 1983). This model of predation is generally associated with invertebrate predators (Scott & Murdoch 1983), but Griffiths (1975) reported low preference values at prey size extremes in fish. Fry of *Perca fluvescens* and *Morone americana* were shown to consistently select smaller *Daphnia* and other zooplankters than they were capable of consuming (Hansen & Wahl 1981; Parrish & Margraf, 1991). Limitations in attack ability of moderate size fry along with the increased evasion ability of larger *Daphnia* would produce a preference for mid-sized *Daphnia*. When golden perch fry were 38 mm long they preferred the largest *Daphnia* and so they were acting as size-selective predators in the way reported for most particulate feeding planktivorous fish (Lazzaro 1987). Golden perch at 38 mm have a mouth gape of just over 5 mm and so they must have been only just able to engulf the largest *Daphnia* which had a length of up to 5.5 mm (not including tail spine) and a head width of about 3.5 mm (Fig. 1b). Thus, as golden perch larvae and fry develop they pass through stages when they are gape-limited predators, size-dependent predators and predators with preference for largest sized prey.

Experiments on prey preference among different prey species can often be confounded by the different sizes of the alternative prey species. The prey presented to golden perch larvae had only a small size range, with the calanoid copepod *Boeckella* intermediate between the cladocerans (Fig. 1), and so the strong preference for cladocerans probably relates to differences in prey behaviour. Cladocerans may be more easily detected because of their contrast, body shape or pattern of movement (Zaret 1980) and/or the calanoid copepods may have been more successful at eluding capture (Confer & Blades 1975; Drenner & McComas 1980). The 10 mm larvae and 20 mm fry had similar preferences for all three species suggesting that capture efficiency had increased and that prey detection was similar for similar-sized prey from different species (Confer & Blades 1975; Vinyard & O'Brien 1976). In the trial with the 30 mm fry, the largest prey species, *Daphnia*, was preferred, suggesting that prey detection was the major determinant of prey preference. Preferences among prey species seems to vary with fish species although generally cladocerans or cyclopoid copepods (Hulbert & Mulla 1981; Meng & Orsi 1991; Parrish & Margraf 1991) seem to be preferred by small fish or fry.

The results of the feeding behaviour and prey preferences experiments provide information that is relevant to management of golden perch larval rearing ponds. First-feeding larvae appear to have a low preference for calanoid copepods compared to cladocerans, presumably because of the higher escape ability of the calanoids. It should be noted that the smallest calanoids used in the present experiments were stage 3 copepodites and it is likely that copepod nauplii and early stage copepodites can be taken by the larvae. Rowland (1986) stated that golden perch larvae feed initially on copepod nauplii, copepodites and small copepods and cladocerans in ponds at IFRS. Inefficiency in the capture of larger calanoids and the limitations imposed by the small mouth gape restricts the range of prey items that can be taken by the larvae, and so pond management needs to ensure abundant small cladocerans and early stage calanoid copepods when larvae are stocked. The possible importance of rotifers as prey for first-feeding larvae also needs to be considered. When golden perch are 10 to 20 mm long they show about equal preference for *Moina*, *Daphnia* and *Boeckella* suggesting that they are generalist zooplanktivores, a good strategy for a species from a complex and unpredictable floodplain-river environment. At 30 mm, fry show a preference for the largest *Daphnia*, whereas some other fish fry apparently select prey that are considerably below the size they are capable of ingesting (Hansen & Wahl 1981; Parrish & Margraf 1991). This rapid development from gape limited predation to selection of the largest prey is consistent with the optimal foraging model proposed by Werner & Hall (1974). Furthermore Mills *et al.* (1989) have shown that growth in age zero *Perca fluvescens* is promoted by the availability of large size prey. Therefore, the management of golden perch rearing ponds should also aim at providing large species of zooplankters for fry 20 mm and larger to maximize growth.

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A NEW SPECIES OF *ACANTHOCEPHALA* FROM THE GREENBACK FLOUNDER, *RHOMBOSOLEA TAPIRINA* GÜNTHER, 1862

BY S. J. EDMONDS & L. R. SMALES***

Summary

Aspersentis minor sp. nov. (Acanthocephala: Heteracanthocephalidae) is described from the small intestine of *Rhombosolea tapirina* Günther, 1862 from Tasmania. Australia. It is distinguished from other species in the genus by the small size of the trunk. proboscis and proboscis hooks.
KEY WORDS: Acanthocephala. *Aspersentis minor* sp. nov.. Australia. *Rhombosolea,* taxonomy.

Transactions of the Royal Society of S. Aust. (1992), 116(1), 35-38.

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Summary

EDMONDS, S. J. & SMALES, L. R. (1992) A new species of Acanthocephala from the greenback flounder *Rhombosolea tapirina* Günther, 1862. *Trans. R. Soc. S. Aust.* 116(1), 35-38, 29 May, 1992.

Aspersentis minor sp. nov. (Acanthocephala: Heteracanthocephalidae) is described from the small intestine of *Rhombosolea tapirina* Gunther, 1862 from Tasmania, Australia. It is distinguished from other species in the genus by the small size of the trunk, proboscis and proboscis hooks.

KEY WORDS: Acanthocephala, *Aspersentis minor* sp. nov., Australia, *Rhombosolea*, taxonomy.

Introduction

About 30 small acanthocephalans were collected from the small intestine of the greenback flounder, *Rhombosolea tapirina* Günther, 1862 in Tasmania by Dr D.L. Obendorf on 16 June 1986. The collection contained only one male. These are considered to be a new species and are described here.

Materials and Methods

Specimens were stained in haematoxylin by conventional methods and mounted in balsam. Illustrations and measurements were made with the aid of an ocular micrometer, drawing tube and measuring wheel. Measurements are given in millimetres unless otherwise stated. Where possible the range of measurements is followed by the mean in parenthesis. Type material has been deposited in the South Australian Museum, Adelaide (SAM).

Systematics

Phylum: Acanthocephala Koelruther, 1771
Class: Palaeacanthocephala Meyer, 1931
Family: Heteracanthocephalidae Petrochenko, 1956
Genus: *Aspersentis* van Cleave, 1929

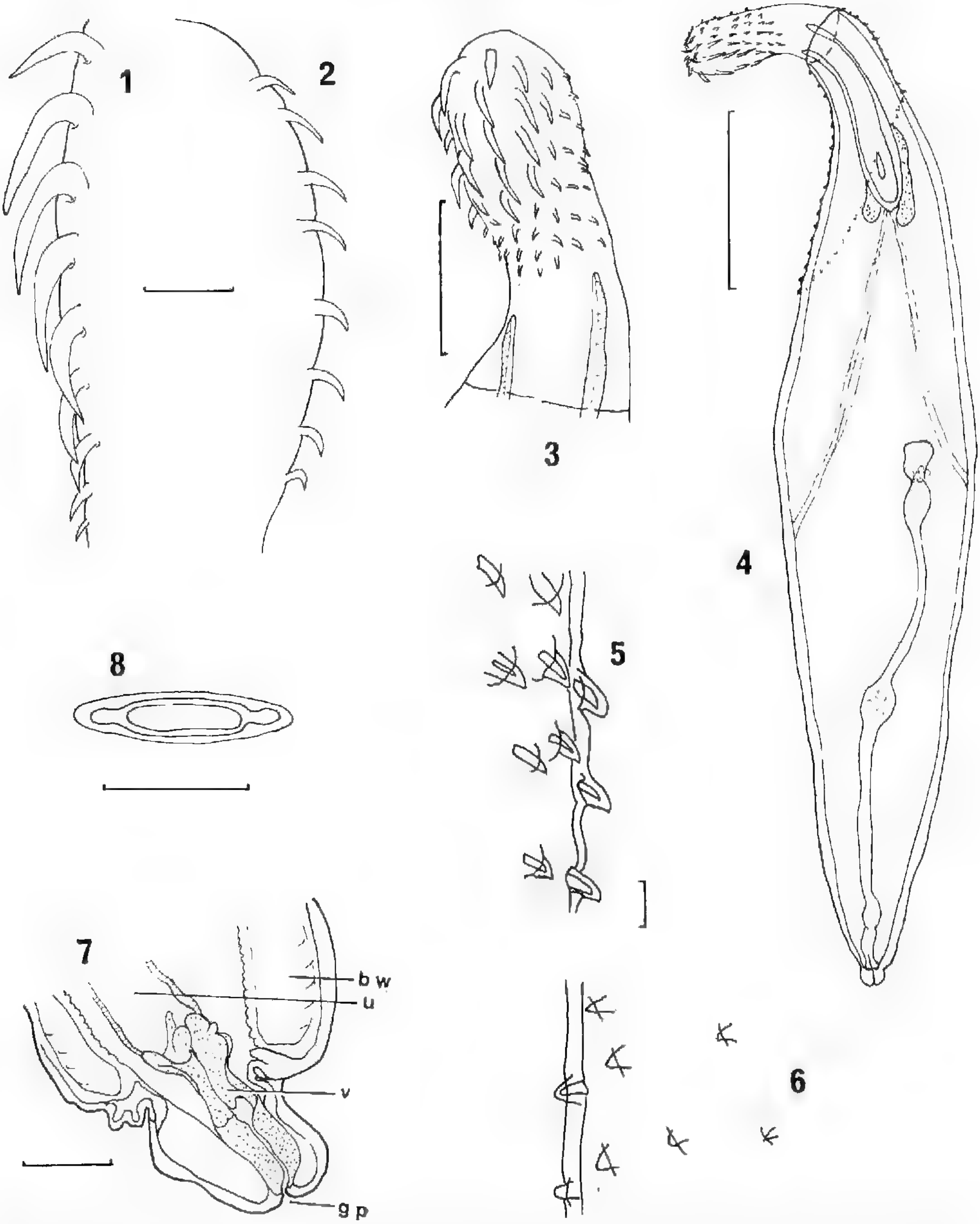
Aspersentis minor sp. nov.
FIGS 1-8

Male (one specimen in poor condition): Trunk spindle-shaped, length 1.6, maximum width in mid trunk region 0.28; anterior region bearing numerous rows of small spines, most noticeable and largest ventrally. Field of spines extends ventrally for about a quarter of body length, but less extensive dorsally. Remainder of trunk, including genital region, without spines. Proboscis (almost completely extended), set at angle to trunk, cylindrical to clavate with armed section 0.23 long and 0.12 wide, bearing 14 rows of 7-8 hooks per row. Dorsal and ventral hooks differ markedly in size and shape, the latter being much larger. Short unarmed, truncated neck about 0.15 long. Two ovoid testes tandemly placed. Cement glands, pyriform and pressed closely together but number not clear. Proboscis receptacle double walled, 0.32 long with ganglion placed near base. Lemnisci about as long as receptacle. Male aperture subterminal.

Female (based on 10 mounted specimens): Trunk spindle-shaped, length 2.4-4.1 (3.2), maximum width 0.37-0.75 (0.54) in mid-trunk region; field of spines extends for about a quarter of body length ventrally, less extensive dorsally, a few tiny cuticular spines present at posterior end of some specimens. Proboscis, placed at slight angle to trunk, cylindrical to clavate 0.24-0.32 (0.26) long × 0.10-0.17 (0.14) wide and armed with 14-15 rows of 7-9 hooks per row. Ventral and dorsally placed hooks differ most noticeably in size and shape (Figs 1,2). Longest ventral hooks (third in row) measure 0.062-0.080 (0.065), longest dorsal hooks 0.030-0.035 (0.032). Unarmed truncated neck 0.15-0.28 long. Receptacle, maximum dimensions 0.52 long × 0.19 wide, double walled, with ganglion lying near its base. Genital complex long, extending in most specimens about half length of trunk. Embryonated eggs, slender 0.068-0.077 (0.071) × 0.012-0.019 (0.015) with prolongations of middle shell. Small terminal papilla (invaginule) present in most specimens. Female aperture almost terminal.

Host: greenback flounder, *Rhombosolea tapirina* Günther, 1862.
Location: small intestine
Locality: Tasmania, Australia
Type specimens: Holotype male: SAM V4150. Paratype female: SAM V4151

* South Australian Museum, North Terrace, Adelaide, S. Aust. 5000
** University College of Central Queensland, Rockhampton, Qld 4702.



Figs 1-8. *Aspersentis minor* sp. nov. ♀ from *Rhombosolea tapirina*. 1. Proboscis hooks, ventral row. 2. Proboscis hooks, dorsal row. 3. Proboscis. 4. Whole mount. 5. Cuticular spines, dorsal surface 6. Cuticular spines, ventral surface 7. Vaginal region extended., 8. Egg. Scale bars: Figs 1, 2, 5 & 6, 50 μm. Fig. 3. 0.2mm. Fig. 4. 0.5mm. Fig. 7, 80mm Abbreviations: b w, body wall; g p, gonopore; u, uterus; v, vagina.

Discussion

The specimens of *Aspersentis minor* sp. nov. most closely resemble *A. austrinus* van Cleave, 1929 from Antarctic fish and subsequently redescribed by Zdzitowiecki (1981) from hosts from the Antarctic and sub-Antarctic islands. *A. austrinus* was also reported by Joyeux & Baer (1954), Edmonds (1955, 1957), Golvan (1969), Zdzitowiecki & Rokosz (1986) and Zdzitowiecki (1990). Similarities include the number of rows of proboscis hooks, which for *A. austrinus* is 13-16 (usually 14) rows of 7-11 hooks and for *A. minor* 14-15 rows of 7-9, and in the size of the embryophores, which for the former is 0.060-0.088 × 0.019-0.025 and for the latter 0.068-0.077 × 0.012-0.019. The specimens differ most notably in the size of the trunk, which is 4.9-8.5 for female *A. austrinus* as compared with 2.4-4.1 for female *A. minor*, the proboscis length, which for the former is 0.51-0.73 and the latter 0.24-0.32, and the length of the largest ventral hook, 0.12-0.15 as compared with 0.06-0.08.

Golvan (1969) considered *Echinorhynchus megarhynchus* (Linstow, 1892) to be a senior synonym of *A. austrinus*, a determination that was followed by Amin (1985) in his classification of the Acanthocephala. Amin, however, appears to have overlooked Zdzitowiecki's (1981) redescription of *A. austrinus* based on more than 1350 specimens collected from South Georgia and the South Shetlands. Zdzitowiecki (1981) concluded that *Echinorhynchus (sensu lato) megarhynchus*, as described by Linstow, was "impossible to identify with any more recently described species". Subsequently Zdzitowiecki & Rokosz (1986), then Zdzitowiecki (1990), on the basis of the re-examination of old material and the collection of new material, confirmed the validity of *A. megarhynchus* (Linstow, 1892) *syn E. megarhynchus* Linstow, 1892 *nec A. megarhynchus sensu* Golvan, 1960. *E. megarhynchus* lacks body or cuticular spines and no asymmetry is described for its proboscis hooks. *A. austrinus* and *A. minor* differ from it in both these characters. *A. minor* also differs from *Heterosentis thecephalus peltorhamphi* (Baylis, 1944), and *H. hureaui* Dollfus, 1964, both of which lack body spines.

In his redescription of *A. austrinus*, Zdzitowiecki (1981) commented on the distribution of spines over the trunk. Because he found specimens in which tiny spines, often embedded in the cuticle, were present either over the middle and/or posterior regions of the trunk as well as larger more obvious spines on the anterior trunk, he accordingly proposed an emendation of the generic diagnosis. The armature on the distal part of the body is particularly difficult to determine, especially if the material is contracted or methods of preparation have rendered spines hard to detect. The specimens of *A. minor* described here were found to have spines over the anterior trunk and sparsely scattered, tiny spines on the posterior of some specimens.

Zdzitowiecki (1981) found considerable differences in the size of specimens from *A. austrinus* populations collected from South Georgia and the South Shetlands. He found that specimens from South Georgia, where water temperatures are higher, were on average 30% larger and their proboscises, receptacles and lemnisci 10-20% larger (Table 1). He suggested that these differences in body dimensions might depend on different environmental conditions, (for example water temperatures) where host populations occur. Similar reasoning cannot be used to explain the difference in size between the Tasmanian and South Georgian specimens since the annual water temperature around Tasmania varies from 10-20°C and around South Georgia from 5-10°C (Plate 3 The Times Atlas of the World), and the Tasmanian specimens are not larger but smaller. They are also smaller than *A. austrinus* described from *Notothenia cyanobrancha* Richardson from Heard Island (Edmonds 1955). Although considerable variation in measurements has been found

TABLE 1 *A comparison of female body measurements of* Aspersentis austrinus *Van Cleave, 1929 from the South Shetlands and South Georgia, and* A. minor *sp. nov. from Tasmania.*

	South Shetlands	South Georgia	Tasmania
trunk length	4.93-6.42(5.79)	6.94-8.54(7.25)	2.3-4.1(3.2)
trunk width	1.16-1.79(1.49)	1.09-2.09(1.73)	0.31-0.95(0.54)
proboscis length	0.51-0.66(0.59)	0.67-0.73(0.70)	0.24-0.32(0.28)
proboscis width	0.29-0.32(0.30)	0.29-0.35(0.32)	0.10-0.17(0.14)
dorsal hook length (maximum)	0.054-0.064(0.060)	0.060-0.065(0.062)	0.03-0.035(0.032)
ventral hook length (maximum)	0.119-0.137(0.126)	0.132-0.149(0.140)	0.062-0.08(0.065)
neck length	0.17-0.03(0.126)	0.22-0.31(0.27)	0.12-0.25
egg	0.060-0.088 ×0.019-0.025	0.071-0.087 ×0.020-0.025	0.068-0.077 ×0.012-0.016
hook disposition	13-16 rows of 7-11 hooks/row		14 rows of 7-9 hooks/row

between populations of *A. austrinus*, measurements of *A. minor* clearly fall outside their range. Moreover the smaller size of *A. minor* goes against the trend, established for *A. austrinus*, that specimens from populations from hosts of warmer waters tend to be larger than specimens from cooler waters. Therefore *A. minor* is considered sufficiently different to be a new species.

A re-examination of *A. austrinus* from Heard Island shows that in addition to the spines on the anterior body surface reported by Edmonds (1955), small spines are also present on some other regions of the trunk, a feature previously overlooked.

Analysis of the ratios of male to female *A. austrinus* sp. (Zdzitowiecki 1981; Zdzitowiecki & Rokosz 1986) has shown that there is both a twofold predominance of females over males and a difference of preferred location in the host, males preferring the posterior half of the small intestine and females the large intestine. A similar difference may explain why the ratio of males to females of *A. minor* collected from the greenback flounder was 1:30.

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TRANSACTIONS OF THE

ROYAL SOCIETY OF SOUTH AUSTRALIA

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VOL. 116, PART 2

NEW RECORDS OF SUBFAMILIES, TRIBES AND GENERA OF BRACONIDAE (INSECTA: HYMENOPTERA) FROM AUSTRALIA, WITH DESCRIPTION OF SEVEN NEW SPECIES

BY A. D. AUSTIN & R. A. WHARTON***

Summary

Three subfamilies of Braconidae are recorded from Australia for the first time with the description of the following new species from Queensland: *Ecnomios stenosoma* sp. nov. (Ecnomiinae), *Histeromerus clavatus* sp. nov. (Histeromerinae), and *Meteoridea anic* sp. nov. (Meteorideinae). The tribe Muesebeckiini is also specifically recorded from Australia for the first time with the description of *Paroligoneurus pallidus* sp. nov. (Ichneutinae) from the Northern Territory, Queensland and New South Wales, as is the genus *Chrysopophthorus* Goidanich, with the description of *C. hageni* sp. nov. (Euphorinae) from South Australia. A new species of the Australian endemic subfamily Mesostoinae from South Australia and Victoria, *Mesostoa kerri* sp. nov., is described, as is a new species of the little-known genus *Calohelcon* Turner (Helconinae) from central Australia, *C. dangerfieldi* sp. nov. The diagnoses, biogeography and biology of these taxa are discussed and notes are provided on the euphorine genus *Stenothremma* Shaw, previously thought to be rare within the Australian fauna. Keys to species are provided for the genera *Histeromerus* Wesmael, *Mesostoa* van Achterberg and *Culohelcon* Turner.
KEY WORDS Hymenoptera, Braconidae, Ecnomiinae, Histeromerinae, Meteorideinae, Euphorinae, Helconinae, Mesostoinae, Ichneutinae, Muesebeckiini, new species.

Transactions of the Royal Society of S. Aust. (1992), 116(2), 41-63.

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Summary

AUSTIN, A. D. & WHARTON, R. A. (1992) New records of subfamilies, tribes and genera of Braconidae (Insecta: Hymenoptera) from Australia, with description of seven new species. *Trans. R. Soc. S. Aust.* 116(2), 41-63, 29 May, 1992.

Three subfamilies of Braconidae are recorded from Australia for the first time with the description of the following new species from Queensland: *Ecnomios stenosoma* sp. nov. (Ecnomiinae), *Histeromerus clavatus* sp. nov. (Histeromerinae), and *Meteoridea anic* sp. nov. (Meteorideinae). The tribe Muesebeckiini is also specifically recorded from Australia for the first time with the description of *Paroligoneurus pallidus* sp. nov. (Ichneutinae) from the Northern Territory, Queensland and New South Wales, as is the genus *Chrysopophthorus* Goidanich, with the description of *C. hageni* sp. nov. (Euphorinae) from South Australia. A new species of the Australian endemic subfamily Mesostoinae from South Australia and Victoria, *Mesostoa kerri* sp. nov., is described, as is a new species of the little known genus *Calohelcon* Turner (Helconinae) from central Australia, *C. dangerfieldi* sp. nov. The diagnoses, biogeography and biology of these taxa are discussed and notes are provided on the euphorine genus *Stenothremma* Shaw, previously thought to be rare within the Australian fauna. Keys to species are provided for the genera *Histeromerus* Wesmael, *Mesostoa* van Achterberg and *Calohelcon* Turner.

KEY WORDS: Hymenoptera, Braconidae, Ecnomiinae, Histeromerinae, Meteorideinae, Euphorinae, Helconinae, Mesostoinae, Ichneutinae, Muesebeckiini, new species.

Introduction

The Braconidae is one of the largest families of parasitic Hymenoptera. Its members are ecto- and endoparasitoids of a wide range of insect hosts, in particular larval stages of Lepidoptera, Coleoptera and Diptera. Although the family has been extensively studied elsewhere, the fauna of Australia remains poorly known, despite the existence of a relatively large number of endemic subfamilies and genera. Indeed, the majority of subfamilies in Australia have not been revised, and most genera and species are known only from their original early descriptions (the majority described prior to the 1920's). Recent taxonomic work undertaken by us on the Microgastrinae and Alysiinae (Austin & Dangerfield 1992; Wharton in prep.) indicates that for these two subfamilies less than 10% of Australian species are described, and this is likely to be the general situation across the whole family. Until the Braconidae are better surveyed at the generic level, questions regarding the evolution and biogeography of the Australian fauna cannot begin to be addressed. Here we make a contribution in this regard by reporting on a number of significant taxa that were discovered when sorting material in major Australian collections, in particular the Australian National Insect Collection, Canberra and the Department of Primary Industries Collection, Brisbane. Seven species are newly described, three representing the first record from Australia of the subfamilies Ecnomiinae, Histeromerinae and Meteorideinae, and one representing the first description of an Australian species from the ichneutine tribe, Muesebeckiini. The relationships, diagnoses and biogeography of all taxa are discussed and notes are provided on their biology where available. Keys to species are provided for the genera *Histeromerus* Wesmael, *Mesostoa* van Achterberg and *Calohelcon* Turner.

Abbreviations for collections are: AEIC, American Entomological Institute, Gainesville; ANIC, Australian National Insect Collection, Canberra; BMNH, The Natural History Museum, London; CNCI, Canadian National Collection, Ottawa; HNHM, Hungarian Natural History Museum, Budapest; QDPI, Queensland Department of Primary Industries, Brisbane; RMNH, Rijksmuseum van Natuurlijke Historie, Leiden; TAMU, Texas A & M University, College Station; USNM, United States National Museum, Washington, D.C.; WARI, Waite Agricultural Research Institute, Adelaide. Terminology for morphology and sculpturing pattern follow Gauld & Bolton (1988) and Wharton (1977, 1986), respectively, while that for venation follows van Achterberg (1979).

* Department of Crop Protection, Waite Campus, University of Adelaide, Glen Osmond, S. Aust. 5064.

** Department of Entomology, Texas A & M University, College Station, TX 77843-2475, USA.

Treatment of species

Subfamily Ecnomiinae van Achterberg

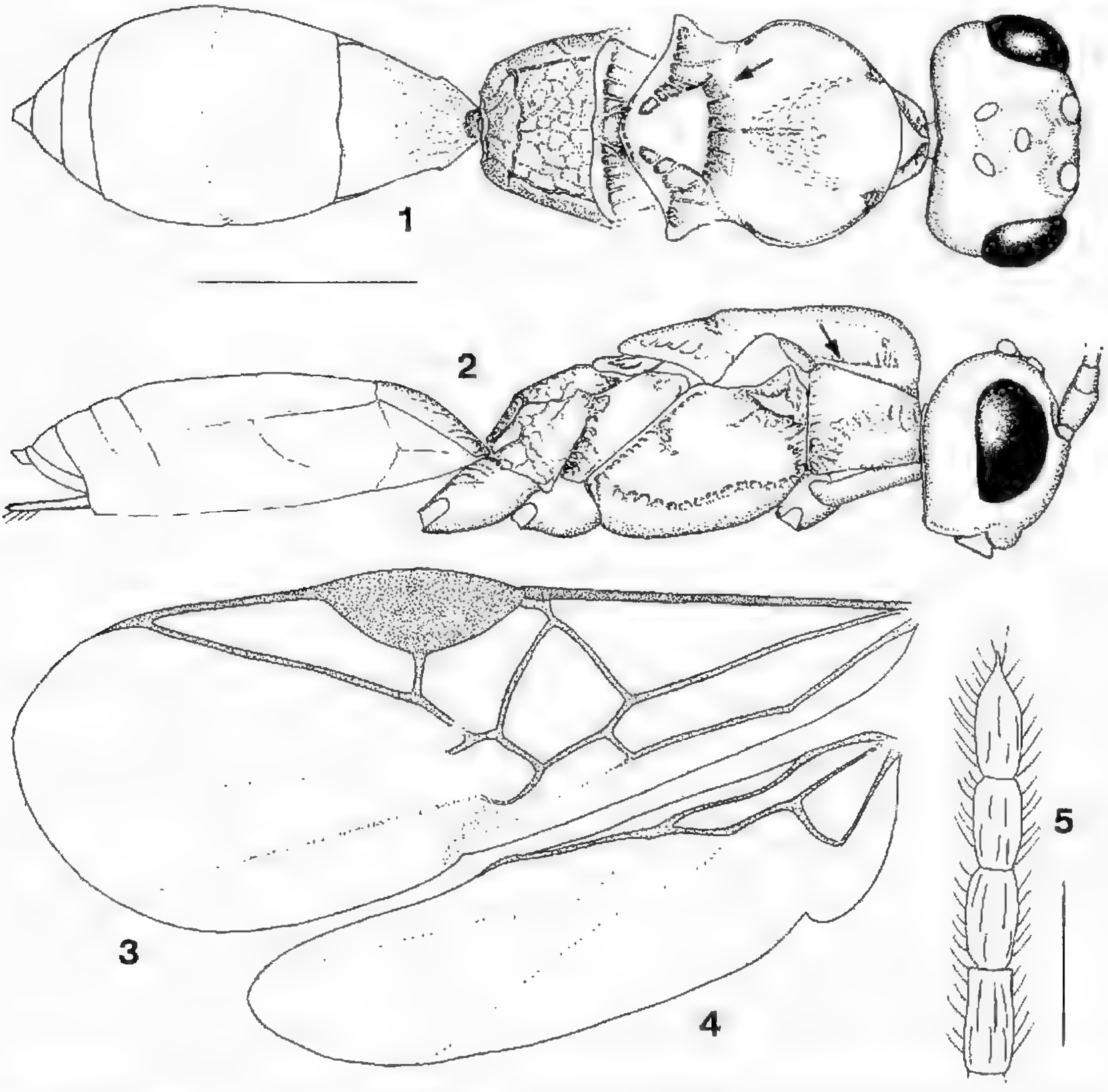
Comments: The systematic position of the only included genus, *Ecnomios* Mason, has been the subject of some debate. Mason (1979) noted its superficial resemblance to Microgastrinae, but excluded it on the basis of the sclerotised distal radial sector of the fore wing and the arrangement of abdominal spiracles. Mason (1979) emphasized seven other characters which suggested a relationship with *Orgilus* Haliday, and thus included *Ecnomios* in the Orgilinae. Van Achterberg (1985, 1988) put *Ecnomios* in its own subfamily, and suggested that it is best placed halfway between Cheloninae and Neoneurinae. Van Achterberg (1985) excluded *Ecnomios* from the Orgilinae because "the Orgilinae lack vein 1-SR of fore wing, have marginal cell long and rather narrow, presence of vein CU1b of fore wing, convex face, large hind coxae, and small plical lobe of hind wing". The face is actually as convex in *Ecnomios* as it is in many *Orgilus*. The remaining features are as suitable for arguing against a relationship between *Ecnomios* and Cheloninae as they are for arguing against the relationship between *Ecnomios* and Orgilinae. Furthermore, *Ecnomios* lacks three of the four synapomorphies proposed by van Achterberg (1984) for the Cheloninae-Microgastrinae lineage. The placement of *Ecnomios* is thus still unsettled, as noted by Quicke & van Achterberg (1990). We prefer to treat it provisionally as intermediate between Orgilinae and the chelonine-microgastrine lineage based largely on wing venation patterns. However, the presence of a transverse postscutellar plate in the species described below opens up the possibility for relationships with the Blacinae and Euphorinae, where similarly reduced venation occurs.

Mason (1979) and van Achterberg (1985) provide detailed lists of characters defining and differentiating *Ecnomios*. The material available to us, representing at least four species, largely conforms with the original description and redescription, but there are important exceptions. The following remarks are therefore provided to supplement previously published information. Maxillary palps are interspecifically variable, either 4- or 5- segmented. Antennal segments are also variable in number both intra- and interspecifically; most flagellomeres have placodes in two ranks, and the apical flagellomere is spinose at the tip. Although van Achterberg (1985) states that the apical antennal segment lacks an apical spine, Mason (1979) correctly notes that it is acutely pointed (Fig. 5), and this is true for all species examined.

Van Achterberg (1985) described the pronotum dorsally as having a large, deep, transverse pronope. However, this is not the same structure as the isolated pit found, for example, in some species of opiines, alysiines, and rogadines. It is actually part of a complex series of pits or depressions forming a crenulate sulcus which separates a weakly raised posterior median area from weakly raised antero-lateral areas (Fig. 1). There is considerable variation in pronotal sculpture and the pattern should prove useful in defining species or species-groups. Both Mason (1979) and van Achterberg (1985) described a conspicuous projection in the middle of the antero-lateral margin of the pronotum (in lateral view). This feature, though very well developed in *E. papuensis* Mason, is weak or virtually absent in some other species, and is thus of questionable value for generic or subfamily characterisation. In *Ecnomios* the "projection" is actually the ventral portion of an indentation in the thin, anterior margin of the pronotum. The occipital carina fits into this indentation when the head is retracted. The structure is thus different in both appearance and function from the angular projection of the margin seen in some species of *Orgilus*.

The carinate antero-lateral margin of the mesonotal disc has some potential for characterising higher taxa if accurately described. Mason (1979) correctly notes its presence in the type species, but van Achterberg (1985) claims that it is absent in front of the tegula. It is well developed and complete from the base of the notauli to well past the tegula in all Australian species we examined (Fig. 2, arrowed). The transscutal articulation (Fig. 1, arrowed) is also distinct along the anterior margin of the scuto-scutellar sulcus in all species, but indistinct laterally. In *E. papuensis*, the scutellum lacks a median postscutellar plate (transverse scutellar depression *sensu* van Achterberg). In the species described below, however, a small one is present similar in shape and position to that in *Sigalphus bicolor* Cresson and some Centistini. The bicarinate median portion of the metanotum is also similar to that of sigalphines and many centistines, but this pattern is repeated in several other braconid subfamilies. A broad propodeal areola is present posteriorly in all species, but variously shaped, and often largely obscured by rugose sculpture. Mason (1979) noted ridges on the dorsal surface of the hind coxa in his description of *E. papuensis*. All species have at least a single ridge in this position, suggesting a synapomorphy for the genus. The venation of the short, broad fore and hind wings (Figs 3, 4) is also diagnostic for *Ecnomios*, has been adequately characterised by previous authors, and is essentially uniform in all species. 1-SR varies in length among species, and its presence may not be sufficiently reliable for subfamilial diagnosis.

The new species described below is a predictable range extension for *Ecnomios* from Papua New Guinea into northern Queensland. We have had an opportunity to examine a single female from Somalia (CNCI)



Figs 1-5 *Ecnomios stenosoma* sp. nov., ♀ holotype. 1, dorsal view of body (transscutal articulation, arrowed); 2, lateral view of body (carinate antero-lateral margin of mesonotal disc, arrowed); 3, fore wing; 4, hind wing, 5, distal flagellomeres of antenna. Scales: Figs 1–4 = 0.5 mm; Fig. 5 = 125 μm.

representing an undescribed species and seven specimens from Queensland and Northern Territory (ANIC), which differ primarily in colour from *E. papuensis* and the species described below. Based on this distribution pattern, *Ecnomios* should eventually be found in India as well as other Indo-Australian localities.

Ecnomios stenosoma sp. nov.
FIGS 1–5

Material examined. Holotype: ♀, ANIC, Queensland, "15 16 S 144 59 E 14 km W by N of Hope Vale Mission Q 7-10 May 1981 I. D. Naumann ex ethanol". Paratypes: Queensland, 3 ♀♀, Rex Range Lookout, via Julatten, 16°30′S, 145°25′E, 9.xi-2.xii.1981, malaise trap (QDPI); 1 ♀, 1 ♂, 15°03′S, 145°09′E, 3 km NE Mt Webb, 1-3.x.1980, J. C. Cardale, ex ethanol, collected at light (ANIC, TAMU); 1 ♂, 15°47′S, 145°14′E, Shiptons Flat, 16-18.v.1981, I. D. Naumann, ex ethanol (WARI); 1 ♂, 17°41′S, 145°26′E, Millstream Falls Nat. Pk, 24-25.v.1980, I. D. Naumann & J. C. Cardale, ex alcohol collection (TAMU).

Female

Head. 1.05-1.15 broader than mesonotum (between tegulae); face 1.45-1.60 × wider than high; malar sulcus restricted to a weak impression extending less than half distance from eye to mandible; malar space about 2 × basal width of mandible; mandibular teeth minute, dorsal tooth nearly 2 × longer than ventral tooth; clypeus with shallow widely spaced punctures; head otherwise largely smooth and polished, with fine hair punctures; ocelli similar to *E. papuensis*, though lateral ocelli slightly more distant from eyes; antenna 28- to 30-segmented.

Mesosoma 1.85-2.05 × longer than high; width between tegula 0.95-1.15 × height; pronotum in dorsal view with thin medially emarginate anterior border and small posterior median plate and transverse crenulate sulcus curving anteriorly in front of median plate; indentation and associated angular protrusion along antero-ventral margin of pronotum weak, barely evident in some specimens; lateral margin of mesonotal disc sharply carinate, the sculpture extending from base of notauli beyond tegula to posterior margin of basal wing pad; disc uniformly and densely short-setose and finely punctate; notauli narrow, very shallow, crenulate-rugulose, converging posteriorly to form a large crescent-shaped, rugulose patch as in *E. papuensis*; apical margin of scutellum sculptured medially (Fig. 1) giving the appearance of a transverse postscutellar plate; scuto-scutellar sulcus, parascutellar fields, metanotum, mesopleuron and metapleuron as in *E. papuensis*, but with slightly weaker sculpture; anterior portion of propodeum rugulose, median longitudinal carina usually absent, lateral longitudinal carinae usually weak, sometimes almost indistinguishable amongst background sculpture, smaller posterior declivous portion more finely sculptured, marked anteriorly by broadly bowed transverse carina; hind coxa shorter than petiole, with a strong diagonal carina dorsally extending nearly from base to apex and with 1-2 shorter weaker carinae adjacent to this.

Fore wing (Fig. 3) As for *E. papuensis* except as follows: 2+3 M variable, short as in *E. papuensis* in one paratype but approximately equal in length to 2SR−M in other specimens; 1SR+M arising from 1−M near parastigma, with 1−SR nearly absent in several specimens; 2−CU1 2.20±0.35 × longer than 3−CU1; 2−1A often represented by a short tubular spur at extreme base, otherwise almost completely indistinguishable.

Metasoma. Petiole with length slightly shorter than (0.75-0.85 ×) apical width; metasoma shape, sculpture, and setal patterns otherwise as in *E. papuensis*.

Colour. Light yellow-brown; ocellar triangle, most of T2+3 and at least apical margins of subsequent terga darker than rest of body; scutellar region often suffused with brown; antenna and apices of 5th tarsal segments brown; mouthparts white, except for tip of mandible which is reddish.

Length. 2.2-2.4 mm.

Male
Essentially as for female except ocellar field and petiole possibly a little broader, but insufficient material for adequate comparison.

Biology. Unknown.

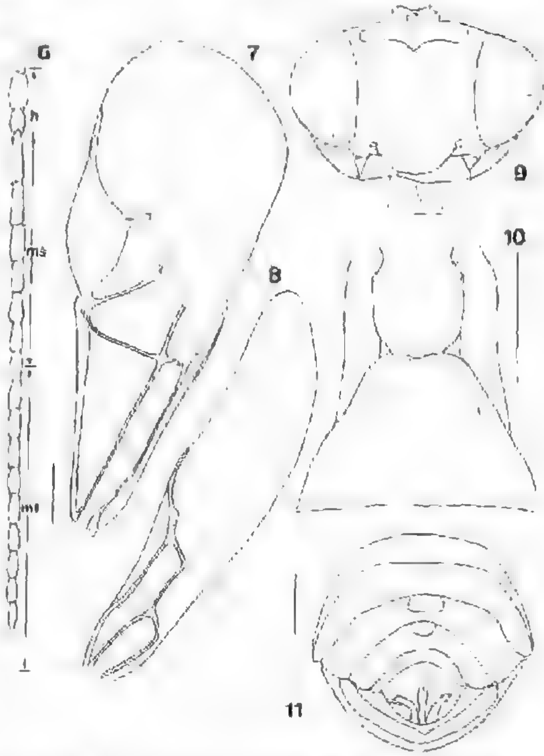
Diagnosis: This species is readily identified on the basis of its pale coloration. Both *E. papuensis* and an undescribed species from Queensland are largely dark brown to black. *E. stenosoma* also has a narrower body, with the head somewhat broader than the mesonotum. The mesonotum is broader than the head in *E. papuensis*.

Subfamily Ichneutinae Foerster
Tribe Muesebeckiini Mason

Comments: Mason (1969) placed this tribe in the Ichneutinae. He included six genera, three of which were transferred from the Microgastrinae. This placement was overlooked by Shenefelt (1973) but accepted by other workers (e.g. Marsh 1979; van Achterberg 1984) except Tobias & Belokobylskij (1981) who later transferred the Muesebeckiini to the Miracinae on the basis of host relationships and similarity in reductions of venation, palp segments, and male genitalia (Tobias 1986; Belokobylskij 1989).

The relationship between *Ichneutes* Nees von Esenbeck and the Muesebeckiini is based largely on the nature of the sharply bent basal vein (1-M) of the fore wing, a feature not shared by other ichneutines such as *Ichneutidea* Ashmead and *Proterops* Wesmael. In *Mirax* Haliday, 1−SR generally forms a sharp angle with the parastigma, but the resemblance between this and the condition in ichneutines is superficial, and does not support the inclusion of Meusebeckiini in Miracinae. Mason (1969) lists six other characteristics shared by *Ichneutes* and Muesebeckiines, but none of these is unique to this clade. The Muesebeckiini lack the most significant synapomorphy of the microgastrine group of subfamilies (to which *Mirax* belongs): the placement of the spiracle in the membranous lateral portion of the first tergum. Additionally, the flagellomeres are not fixed in number as they are in Microgastrinae and Miracinae. On the basis of spiracular placement, we include miracines within the microgastrine group, and place Adeliinae and Ichneutinae (the latter including Muesebeckiini) with the Neoneurinae and Cheloninae as a sister-group of this clade. Meusebeckiines are most readily recognized by the venation pattern of the fore wing (Fig. 7).

The tribe Muesebeckiini is represented in Australia by the widespread genus *Paroligoneurus* Muesebeck. One species is described here, but others will undoubtedly be found with more intensive collecting. As interpreted here, *Paroligoneurus* is a large genus, with numerous undescribed species in the New World. De Saeger (1944), working on the tropical West African fauna, has described the largest number of species, but propodeal differences suggest that at least some of his species belong elsewhere. Nixon (1965) previously noted the occurrence of *Paroligoneurus* in Queensland, but did not describe any species. Risbec (1951) described a species reared from Agromyzidae in Senegal, but this is an opiine. Known hosts of true *Paroligoneurus* are leaf-mining Lepidoptera. Muesebeck (1931) noted the close resemblance between *Oligoneurus* Szépligeti and *Paroligoneurus* in his original description of the latter. He differentiated the two solely on the basis of the relatively bare eyes and reduced number of flagellomeres in *Paroligoneurus*, but noted that *P. johnsoni* Muesebeck had a few scattered eye hairs. Subsequently, De Saeger (1944) described some species of *Paroligoneurus* with scattered eye hairs and Belokobylskij (1986) described a species of *Oligoneurus* with hairy eyes and relatively few (21-23) flagellomeres. Mason (1969) did not discuss either genus when he transferred them to Muesebeckiini, but presented a key to genera in which he separated *Oligoneurus* and *Paroligoneurus* on the basis of whether or not the eyes were hairy. Belokobylskij (1986) noted that previous characterisations were inadequate for distinguishing these two genera. He therefore added a clypeal character, and modified the traditional eye and antennal diagnosis. The moderately hairy eyes of the species described below further emphasize the weakness of this character state for separating *Oligoneurus* and *Paroligoneurus*, and we suggest that it should be abandoned entirely. Although the type species of *Oligoneurus* is very distinctive, with its large size, relatively large number of flagellomeres, carinate propodeum and petiole, and broad second tergum, other species which have been assigned to *Oligoneurus* possess only one or two of these traits, and otherwise resemble the type species of *Paroligoneurus*. A revision of the large Neotropical fauna is needed before the genera can be adequately defined. Until this can be accomplished, we believe that the best character for separating the two is the propodeal sculpture, admittedly a weak feature. The clypeus is evenly rounded in *Oligoneurus concolor* Szépligeti and *P. johnsoni* Muesebeck, and thus cannot be used for separating the two genera. Members of the distinctive Holarctic species-group with medially protruding clypeus more closely resemble *Paroligoneurus* than *Oligoneurus*, based on propodeal sculpture and the shape of tergite 2. The placement of two such species in *Oligoneurus* (Belokobylskij 1986) thus needs to be reassessed.



Figs 6–11. *Paroligoneurus pallidus* sp. nov., ♀ holotype. 6, antenna; 7, fore wing; 8, hind wing; 9, anterior view of head; 10, T1 and T2+3 of metasoma. 11, *Paroligoneurus pallidus* sp. nov., ♂ paratype, postero-dorsal view of metasoma showing medial pit in T6 and T7. Scales: Figs 6-8 = 0.5 mm; Figs 9-11 = 250 μm. Abbreviations for Fig. 6: length of antenna relative to body. h = head; ms = mesosoma; mt = metasoma.

Paroligoneurus pallidus sp. nov.
FIGS 6–11

Material examined. Holotype: ♀, ANIC, Northern Territory "12.06S 133.04E Cooper Ck, 19 km E by S of Mt. Borradaile, N. T. 9-10 Nov 1972 J. C. Cardale". Paratypes: 6 ♀♀, same data as holotype (ANIC, TAMU, WARI); 8 ♀♀, 1 unknown sex, 12°40'S, 132°54'E, Magela Ck, 9 km SSE of Mudginberri H.S., 7-8.xi.1972, J. C. Cardale (ANIC, TAMU, WARI); 1 ♂, 12°27'S, 135°55'E, Ngarradj Warde Djobkeng Kakadu Nat. Pk, 27.vi.1980, I. D. Naumann (ANIC). Queensland: 2 ♀♀, Iron Range, Cape York Pen., 26-31.v.1971, S. R. Monteith (ANIC); 1 ♂, same data except 1-9.vi.1971 (ANIC); 1 ♀, 15°03'S, 145°09'E, 3 km NE Mt Webb 30.iv.-3.v.1981, I. D. Naumann, ex ethanol, collected at light (ANIC); 2 ♂♂, Henrietta Ck, Palmerston Nat. Pk 23.iv.1970, S. R. Curtis (ANIC); 1 ♂, 12°42'S, 143°20'E, 13 km ENE Mt Tozer, 14.vii.1986, J. C. Cardale, at MV light (ANIC); 1 ♂, 15°16'S, 144°59'E, 14km W by N of Hope Vale Mission, 7-10.v.1981, I. D. Naumann, ex ethanol (ANIC).

Female

Head. Frons bare medially, head otherwise densely setose; in dorsal view 2.05-2.20 × wider than maximum length, wider at eyes than at temples, in lateral view eye 2.85-4.05 × longer than temple; height of head between apex of clypeus and base of antenna 1.0-1.2 × narrowest width of face; eyes hairy (Fig. 9); fronto-clypeal suture indistinct, clypeus thus not clearly separated from face; clypeus weakly convex in profile, ventral margin sharp, evenly convex, bearing a line of long erect setae; malar space short, in frontal view distinctly shorter than basal width of mandible; malar suture sharp, deep; antenna 18-segmented, slightly longer than body; flagellum broadest at middle, gradually narrowing apically and basally; first flagellomere 1.20-1.45 × longer than second; fifth flagellomere about 2.5 × longer than mid-width; labial palp 4-segmented, the third segment minute.

Mesosoma. Short and broad, 1.3-1.5 × longer than high, about as wide as high; pronotum laterally often collapsed in dried material, thus giving mesosoma the appearance of being depressed; mesonotal disc weakly convex, nearly flat; scutellum flat; mesonotum densely and uniformly covered with short setae and associated weak punctures, notauli absent externally, but visible internally as thin, dark streaks beneath pale integument; scutellum densely setose laterally, nearly bare medially; propodeum polished, unsculptured, covered with setae, these less densely spaced than on mesonotum; mesopleuron and metapleuron polished, unsculptured; hind femur broad, 2.6-3.0 × longer than mid-width.

Fore wing. Stigma very large, about 2 × longer than broad, roughly 2 × longer than metacarpus; r arising slightly distad of midpoint; fully sclerotised, pigmented portion of weakly curved r about half length of metacarpus, but distinctly longer than pigmented, sclerotised stub of 2−SR+M; anterior portion of basal vein sharply bent distally.

Metasoma. Petiole nearly flat, with very low weak dorsal carinae basad of spiracles, otherwise without sculpture; petiole broadest at spiracles, strongly narrowed towards base and apex, base and apex of approximately equal width, width at spiracles 1.5-1.8 × width at apex, length 1.1-1.5 × width at spiracles; T2 bare, polished, unsculptured, with trapezoidal median sclerite, its apex roughly 2 × wider than its base; T1 and T2 with broad weakly sclerotised areas between median sclerite and laterotergites; hypopygium large, about 2.4-2.5 × longer than petiole, gradually narrowing over posterior half to a weakly pointed apex; ovipositor sheath (total length) nearly 2 × longer than petiole (when dead); visible portion normally slightly longer than petiole, with ventral row of apical setae extending slightly more than half way towards base.

Colour. Yellow to orange; face varying from dark orange to variegated orange and brown; remainder of head and tip of metasoma usually brown; scape and pedicel, usually entire first flagellomere and sometimes base of second flagellomere yellow, remainder of antenna brown; ovipositor sheaths black.

Body length. 1.7-2.1 mm.

Male

As for female except as follows: median flagellomeres more slender, flagellum thus less obviously tapered towards apex, both T6 and T7 with a deep median pit (Fig. 11).

Referred material examined. Queensland, 1 ♀, 1 ♂, Bald Mtn area via Emu Vale (ANIC); 1 ♀, Bramston Beach (ANIC); 2 ♂♂, Brisbane (TAMU); 2 ♀♀, 3 ♂♂, 12 km NW Brisbane, (TAMU); 1 ♂♂, Bunya Mts (ANIC, WARI); 3 ♀♀, Camp Mountain (QDPI); 3 ♂♂, Iron Range (ANIC); 2 ♂♂, Mt Tamborine (QDPI); 2 ♂♂, Paluma Dam (ANIC). New South Wales, 2 ♀♀, Scotts Head, near Warrell Ck (ANIC, WARI).

Biology. Unknown.

Diagnosis. This species is readily recognised by its generally pale coloration, all congeners having distinctly darker bodies. The metacarpus is short relative to *P. johnsoni*, and the transverse radial vein arises nearer the midpoint of the stigma. The venation of *P. pallidus* thus more closely resembles that of the Afrotropical *P. wittei* De Saeger. Additionally, the ovipositor is longer than in all congeneric species. The antennae of the known Afrotropical species are 19- to 20-segmented, but the antennae are 18-segmented in both *P. pallidus* and *P. johnsoni*.

Discussion. The distinctly setose eyes of *P. pallidus* necessitate a clarification of the definition for *Paroligoneurus*. Mason's (1969) use of setose eyes for separating genera in the Muesebeckiini, and especially for separating *Oligoneurus* from *Paroligoneurus*, needs clarification. Nearly all species of *Paroligoneurus* have at least some setae on the eyes, and several short setae are readily visible medially on the eye of *P. johnsoni* the type species. The number, size, and arrangement of setae constitute an important character set for species level discrimination in *Paroligoneurus*. Deep median pits, though not previously described, are found in a number of mueseheckiines. They are usually located on tergites 6 and/or 7, and occur in only males.

The type series of *P. pallidus* has been restricted to the material from Northern Territory and far North Queensland because of colour differences in the material from south-eastern Queensland. The more southerly specimens are generally darker, with most of the metasoma dark brown. However, there is some overlap, and there are insufficient representatives of both sexes from any one locality to adequately assess whether or not males are darker than females.

Subfamily Histeromerinae Fahringer

Comments: The monotypic, *Histeromerus* Wesmael, has been variously treated over the years. Until recently, most 20th century authors placed *Histeromerus* in the Doryctinae due to the presence of stout setae or pegs on the fore tibiae. Fahringer (1930) was the first to isolate it as a separate tribe within the Doryctinae. Van Achterberg (1976) initially transferred *Histeromerus* to the Braconinae, but soon realised that it was misplaced. Van Achterberg (1984) subsequently regarded it as a separate subfamily with a sister group relationship to Ypsistocerinae + Mesostoinae. This placement is based on the shared presence of a flattened petiole, compressed hind femora, and location of the metasomal spiracles in the epipleuron (van Achterberg 1984, 1988). Additionally, the transscutal articulation is absent. In the doryctine *Rhoptrocentrus* Marshall, however, the gaster is similarly shaped, with the spiracles located on the epipleuron. The hind femora are also flattened in *Rhoptrocentrus* (though generally not as much as in *Histeromerus*) and the venation is similar. The petiole shape and absence of the propleural flange, the epicnemial (=prepectal) carina, and the transscutual articulation are thus more useful features for separating *Histeromerus* from doryctines. Additional features are discussed by Quicke & van Achterberg (1990), who consider the Histeromerinae to be one of the most basal groups of Braconidae. The subfamily is readily recognised by the exceptionally long hind basitarsus, oddly shaped head with long temples and very short face, short antennae, and clavate fore tibia with stout setae clustered in a large patch along the dorsal (or outer) surface.

This is the first species of *Histeromerus* described from outside the Holarctic Region.

Key to known species of *Histeromerus*

1. Vein m-cu just antefurcal; fore tibia abruptly widened (Fig. 17) [Australia] . . . . *H. clavatus* sp. nov.
   Vein m-cu postfurcal; fore tibia more gradually enlarged (Figs 18, 19) 2
2. Prosternum yellow; antenna with 15 or fewer segments; small species (about 2.5 mm in length) [Nearctic] . . . . *H. canadensis* Ashmead
   Prosternum brown; antenna with 17-20 segments; larger species (at least 3.0 mm in length) [Palaearctic] . . . *H. mystacinus* Wesmael

Histeromerus clavatus sp. nov.

FIGS 12–17

Holotype: ♀, ANIC, Queensland, "12.43S 143.18E QLD 11 km ENE Mt. Tozer 11-16 July 1986 J. C. Cardale Malaise trap/ethanol".

Female

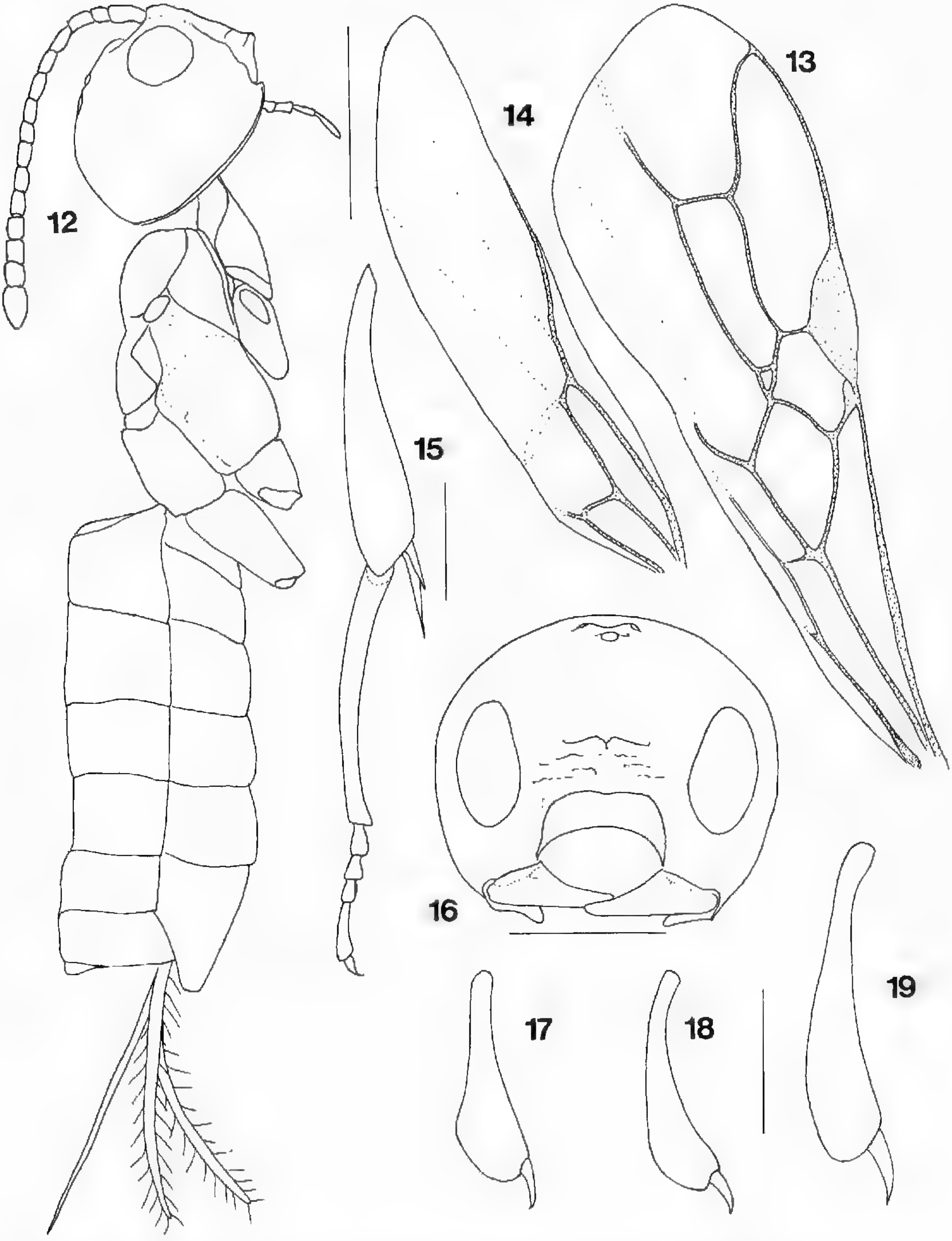
Head. 1.25 × broader than mesonotum (between tegulae); temples typically produced, in dorsal view 2.25 × longer than eye; malar space about half eye height; length of frons (between anterior ocellus and antennal socket) 1.7 × width of ocellar field; frons, vertex, temple and gena unsculptured; setae largely absent on gena, setal bases separated by length of setae on temple and vertex, more closely spaced on frons; face about equal in height to clypeus, about 4.3 × wider than high; face transversely strigose, with row of deep punctures laterally, extending through malar region; clypeus deeply punctate; antenna short, about equal in length to metasoma, 15 segmented; all flagellomeres with multiple placodes; palps 5- and 3-segmented; apical setae on labial palp longer than 3rd segment of palp.

Mesosoma. Pronotum in dorsal view a narrow unsculptured band; pronotum laterally weakly rugulose except along anterior margin; mesonotum without notauli; density of setae on anterior declivity similar to that on frons, less dense on median part of disc and largely absent laterally; scuto-scutellar sulcus unsculptured, without anterior demarcation, the mesonotal disc sloping gradually to form a depression along anterior margin of scutellum; propodeum unsculptured; mesopleuron bulging, strongly convex; subalar depression deep, narrow, unsculptured; mesopleuron lacking crenulate posterior margin; metapleuron weakly wrinkled dorso-posteriorly and ventrally.

Legs. As in other species of *Histeromerus*; hind femur more strongly compressed than mid femur; fore coxae broadly contiguous; hind coxa long, about 0.75 × length of hind femur; outer surface of fore tibia with short thick setae on its apical half; fore femur weakly grooved ventrally for reception of tibia, fore tibia abruptly broadened over apical half (Fig. 17), narrowing slightly from mid tibia to base; hind basitarsus very weakly curved, about 2 × longer than combined length of tarsi 2-5, slightly inflated over basal half.

Wings. Stigma short, broad, nearly hemispherical, about 2.4 × longer than broad; r vertical; 3–SR about 5.6 × longer than r, subequal to SR1; SR1 moderately curved, reaching metacarpus somewhat before wing tip; 2nd submarginal cell broader distally than proximally; m-cu antefurcal by about 0.3 × its length; cu a postfurcal; CU1b completely absent, 1st subdiscal cell thus open at lower distal corner; M+CU1 tubular and pigmented except at extreme base; 1A+2A thickened in region of barely visible 2A; hind wing with 1-M about 1.1 × longer than M–CU; m-cu long, pigmented but spectral; 1r-m shorter than cu-a; R1 of hind wing distinctly shorter than SC+R1.

Metasoma. Petiole nearly flat, without dorsal or lateral carinae and associated pits; ovipositor strongly



Figs 12–19. *Histeromerus clavatus* sp. nov., ♀ holotype. 12, lateral view of body. 13, fore wing, 14, hind wing; 15, hind leg; 16, anterior view of head; 17, fore tibia. 18, *Histeromerus canadensis* Ashmead, ♀, fore tibia. 19, *Histeromerus mystacinus* Wesmael, ♀, fore tibia. Scales: Figs 12–14 = 0.5 mm; Fig. 15 = 375 μm; Figs 16–19 = 250μm.

compressed, blade-like, deeper basally, tapering distally, without obvious teeth; exserted portion about equal in length to mesosoma; ovipositor sheath densely setose, the setae longer than sheath width.

Colour: Dark brown; prosternum, anterior margin of pronotum, palps, first 4 antennal segments (largely), mid and hind coxae, tibiae, and all but extreme tip of tarsi yellow; fore coxae, mesosternum, and femora variously yellow-brown; ovipositor sheath whitish, with apical one-fifth brown; wings hyaline with infumate streak along 1-M; microtrichia on membrane very short and thick, giving wing a spotted appearance. *Body length.* 2.4 mm

Male

Unknown.

Biology: Unknown, but host records of previously described species indicate parasitism of coleopteran larvae in woody stems or bracket fungi.

Diagnosis: This species is most easily identified by its venation, with m-cu entering the first submarginal cell, the 1st subdiscal cell open in the lower distal corner through complete loss of CUlb, and the vertical position of r. Both *H. mystacinus* and *H. canadensis* have m-cu postfurcal, CUlb present at least as a stub, and r inclivous. The Australian species is otherwise very similar to *H. canadensis* and *H. mystacinus*, as noted above in the number of unique features used to define the subfamily. Both *H. clavatus* and *H. canadensis* are small species, with fewer flagellomeres and paler coloration than *H. mystacinus*. The apical setae on the palps are also longer and cu-a is postfurcal in the two smaller species.

Discussion: The holotype has a spurious vein in the second submarginal cell of the fore wing (Fig. 13). Anomalous venation has also been recorded for *H. mystacinus* (Marshall 1885, 1888). Marshall's specimen showed traces of a second recurrent vein (2m-cu), producing a pattern similar to that in *Apozyx* Mason. The latter however, has the petiole and prepectal carina more typical of doryctines than *Histeromerus*.

Subfamily Euphorinae Foerster

Comments: Shaw (1985) has provided substantial support for the clade composed of *Stenothremma* Shaw, *Wesmaelia* Foerster, *Chrysopophthorus* Goidanich, and *Aridelus* Marshall. Although all but *Wesmaelia* are well represented in Australia (Shenefelt 1969; Huddleston 1983; Shaw 1984; this study), *Chrysopophthorus* has not been previously reported from the continent (see Mason 1964), and until recently relatively few *Stenothremma* have been known. Additional information on these genera is presented here.

Stenothremma Shaw
FIG. 24

Comments: Amongst the most commonly encountered members of the Euphorinae in Australian collections are various species of *Stenothremma*. The genus was recently described from Australia and New Caledonia (Shaw 1984), based on three species. However, most Australian species are undescribed (e.g. approximately 20-30 new species in ANIC) and the material at hand considerably broadens the definition originally provided by Shaw (1984, 1985). Since *Stenothremma* is such a prominent member of the Australian euphorine fauna, and because males cannot be readily identified using existing keys, we take this opportunity to present additional morphological data. Hosts for *Stenothremma* are unknown, but two undescribed species (ANIC) have been swept from *Acacia* and *Eucalyptus*, respectively.

Shaw (1984, 1985) places *Stenothremma* within the *Aridelus-Wesmaelia-Chrysopophthorus* lineage, and provides a set of synapomorphies for this group. The most useful of these for identification purposes is the long, almost uniformly narrow (apical width less than 3 × basal width) petiole which is completely fused ventrally from base to apex. This feature, together with the completely developed, tubular SR1+3−Sr and 1−SR+M of the fore wing, are sufficient for placement of all Australian species in this lineage. The median frontal carina, which Shaw (1984) lists as a synapomorphy for this group of genera, is absent in some of the undescribed species of *Stenothremma* and weakly developed in others. It is more strongly developed in larger species.

Some New and Old World tropical species of *Meteorus* Haliday might be confused with members of the *Aridelus* lineage, and care must be taken to avoid this error. In these species, the apex of the petiole is often less than 3 × wider than the base. In all cases, however, the sides of the petiolar tergum are widely separated at least on the apical third. Additionally, as noted by Shaw (1985), the mandibles in *Meteorus* are broadly overlapping relative to the sickle-shaped mandibles of *Stenothremma*. The petiolar and mandibular characters are not always readily visible on pinned specimens. Within the *Aridelus* lineage, *Aridelus* is easily identified on the basis of the reticulate or reticulate-areolate sculpturing of the mesonotum. The mesonotum of *Stenothremma* varies from punctate to finely granular. Both *Wesmaelia* and *Chrysopophthorus* have M+CUI at least partly desclerotised or absent. In all species of *Stenothremma*, M−CUI is tubular throughout, and provides the most readily observed character for separation from these two genera (c.f. Figs 23, 24). Australian species of *Chrysopophthorus* known to us have the basal half of the fore wing yellow, and M+CU1, though appearing weakly developed because of the pale coloration, is actually tubular over its basal and apical quarter, and nebulous only near its mid length. The Australian *Chrysopophthorus* are thus very similar to *Stenothremma*. Shaw (1984, 1985) has emphasised the compressed metasoma in defining *Stenothremma*, but this feature is not useful for males, and varies considerably in dried females, depending on the quality and manner of preservation (e.g. the metasoma of critical-point dried specimens is frequently bloated rather than compressed).

Shaw (1985) provides an excellent character set for analysis of euphorine phylogeny. Shaw's data for *Stenothremma* should be modified as follows, based on material available to us including all undescribed species:

Character 1, ocular setae: present in some species, absent in others.

Character 4, median frontal carina: extending nearly to anterior ocellus in some species, short and weak in others, absent in some.

Character 8, apical flagellomere: pointed in most species examined, but rounded in at least two species.

Character 15, malar suture: present in nearly all species examined, but weak and difficult to see in several.

Character 16, facial setae: variable among species, either obscuring face or not (as noted by Shaw (1984) in his original descriptions of the species, but not reflected in the coding for this character in Shaw (1985)).

Character 17, shape of lower clypeal margin: rounded (strongly convex) in most species, but nearly truncate in at least one species. The medially indented condition given by Shaw (1985) for other members of the *Aridelus* lineage does not hold for two of the Australian *Aridelus* species, and the indentation in the *Chrysopophthorus* species described below is barely perceptible. In these species, the clypeus varies from more or less truncate to convex.

Character 19, maxillary palps: 6-segmented in several of the species examined.

Character 25, legs: the difference between the legs of *Chrysopophthorus* and those of small yellow legged species of *Stenothremma* is very slight.

Character 26, mesonotal sculpture: varies from finely granular to finely punctate. The imbricate microsculpture of the mesosoma which Shaw (1984) noted as an unusual feature characterising *Stenothremma* is absent in a few species.

Character 36, metafemur length/width: short and broad in some species, moderately slender (length 5-6 × maximum width) in others, very long and slender (length greater than 6 × maximum width) in one species; both character states used by Shaw (1985) are therefore applicable.

Character 44, radial cell: the distance between the end of the radius and the wing tip is quite variable, and this variation is not adequately reflected in the character states used by Shaw (1985).

Character 62, tergite 2+3 length: the difference between *Stenothremma* and *Chrysopophthorus* are clearly evident in females, but considerably less so in males.

Character 65, lateral suture between tergites 2–3: this feature is present in at least the Australian species of *Chrysopophthorus*, although usually not as clearly evident as in *Stenothremma*. It is better developed in males than females.

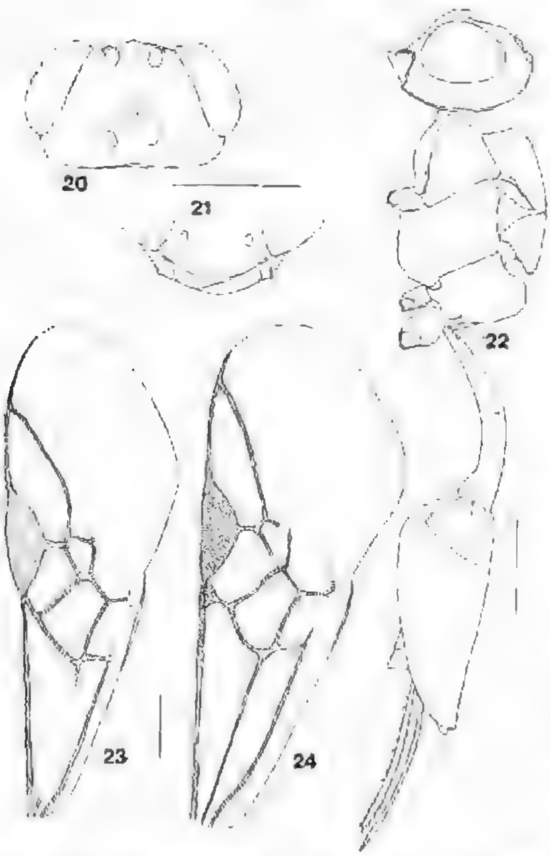
There is little doubt that *Stenothremma* belongs in the *Aridelus* lineage, and although its exact placement therein is now less certain, our analysis does support Shaw's (1984) hypothesis of relationships. Shaw (1985) treats *Stenothremma* as the sister-group of *Wesmaelia*+*Chrysopophthorus*+*Aridelus*. With the new data presented above, we find that two of the five characters supporting the *Wesmaelia*+*Chrysopophthorus*–*Aridelus* clade (numbers 17 and 19) do not hold, and the other three (numbers 62, 63 and 65) form a single character complex associated with terga 2–3. We treat this entire character complex as a cline, with the plesiomorphic state found in *Stenothremma*, and the apomorphic state found in *Aridelus*. The condition in females of *Chrysopophthorus* and *Wesmaelia* is definitely more like *Aridelus* than *Stenothremma*, and supplies the sole supporting feature for the *Wesmaelia* +*Chrysopophthorus*–*Aridelus* clade. The problem of using characters 1 and 36 to unambiguously support the *Wesmaelia*+*Chrysopophthorus* clade leaves the partially desclerotised M+CU1 as its strongest synapomorphy. *Aridelus* has a large number of autapomorphies (Shaw 1985), emphasising its separation from the other genera. However, the relationships among the other three genera are now less clear. Information on the hosts of *Stenothremma* may help solve this problem, for if the hosts are neuropteroid rather than hemipteroid, this would support a *Stenothremma*+ *Chrysopophthorus* clade.

Chrysopophthorus hageni sp. nov.
FIGS 20–23

Material examined: Holotype ♀, ANIC, "SOUTH AUSTRALIA: Adelaide Mar. 11-29, 1990 R. Wharton". Paratypes: 1 ♀, 3 ♂♂, same data as holotype (TAMU, WARI)

Female

Head. Transverse; in dorsal view 1.7 × broader than mid length; 1.4 × broader than mesonotum between



Figs 20–24. *Chrysopophthorus hageni* sp. nov., ♀ holotype. 20, dorsal view of head; 21, anterior view of lower head; 22, lateral view of body; 23, fore wing. 24, *Stenothrema* sp., fore wing. Scales = 0.5 mm

tegulae; eyes bulging, in dorsal view 3.2 × longer than temples; temples convex, receding behind eye, densely covered with short decumbent setae; ocellar field small, widely separated from eye (Fig. 20); posterior ocelli separated by about 2.5 × their diameter; clypeus very broad (Fig. 21); apical margin thin, broadly and weakly truncate medially, very weakly emarginate centrally; smooth, nearly impunctate dorsally, weakly transversely aciculo-punctate along apical margin; face punctate medially, transversely striate just below antennal bases; frons, vertex, and temples punctate; punctures narrowly separated, almost coalescing medially on frons, more widely separated (1–3 × their diameter) on temples and vertex; malar space rugulose; antenna 21-segmented: first flagellomere about 5 × longer than wide; second flagellomere about 4.5 × longer than wide; fifth flagellomere about 1.4 × longer than wide: first flagellomere 2.6 × longer than fifth.

Mesosoma. Pronotum aciculate laterally; mesonotal disc punctate, punctures weak (shallow) and less densely spaced on lateral lobes than on median lobe, more densely spaced medially on anterior declivity than on disc; notauli crenulate, distinct though shallow; narrow anteriorly, converging and broadening posteriorly, the two sides separated posteriorly by a low median ridge; notauli not extending to prescutellar pit; scuto-scutellar sulcus with median ridge only slightly better developed than lateral ridges; scutellum covered with shallow punctures, lateral margins carinate only at extreme base; propodeum uniformly reticulate, without distinct carinae, shallowly excavated; mesopleural disc polished, with diagonal row of scattered punctures, otherwise smooth; precoxal sulcus shallow, punctate and irregularly alveolate.

Fore wing. Second submarginal cell subquadrangular; 2-SR and r-m separated at the radial sector by about 4 × their width; 3-SR nearly equal in length to r.

Metasoma. Petiole as long as mesosoma, 10.2 × longer than width at spiracle, slightly deeper at spiracles than at apex and base, width at spiracle about 1.5 × width at base; petiole without sculpture laterally; ovipositor sheath about 0.8 × length of petiole.

Colour. Yellow-orange; propodeum, metanotum and margins of scutellum variously brown to dark brown; T2 and apical one-quarter of ovipositor sheath dark brown to black; remainder of ovipositor sheath, ovipositor, petiole, legs, most of pronotum, clypeus ventrally, and most of mouthparts (except red mandibular teeth) white to yellow-white; antenna yellow basally, apical seven flagellomeres brown, darkening towards tip; fore wing venation yellow basad of stigma; stigma and veins bordering second submarginal cell brown; base of metacarpus yellow.

Body length. 3.3–3.4 mm.

Male

As for female except as follows: eye smaller, in dorsal view 1.8–1.9 × longer than temple; posterior ocelli separated by about 1.5 × their diameter; antennae 21- to 22-segmented; fifth flagellomere 2.6–2.8 × longer than wide; first flagellomere 1.3–1.6 × longer than fifth; scuto-scutellar sulcus with median ridge distinctly better developed than lateral ridges in 2 of 3 specimens; one male with distinct lateral carinae bordering median excavation of propodeum; 3-SR of fore wing absent or nearly so, the second submarginal cell decidedly petiolate in one specimen; petiole shorter, about 0.8 × length of mesosoma, 6.4–7.7 × longer than width at spiracle.

Referred material examined: A.C.T., 1 ♀, 1 ♂, Canberra (TAMU)

Biology: Unknown. Other members of the genus are parasitoids of adult Chrysopidae.

Diagnosis: This species runs to couplet 5 in Mason's (1964) key to species, based on the broad and very shallowly emarginate clypeus. The distinctive sculpturing of the notauli, the polished median region of the mesopleuron, and the pattern of dark brown markings of the body readily separate this species from all previously described *Chrysopophthorus*. As Mason (1964) notes, *C. orientalis* Mason from Singapore has a number of unusual features. This Australian species shares none of these and is thus not closely related to *C. orientalis*.

Discussion: The two specimens from Canberra closely resemble those from Adelaide, but the female petiole is slightly shorter and the clypeus is more extensively punctate dorsally. We have seen an additional species from Queensland (ANIC), but as it is thus far known only from males, it is not described here. The species is named for Ken Hagen, in recognition of his contributions to chrysopid biology.

Subfamily Mesostoinae van Achterberg

Comments: This small endemic subfamily was previously known from only three species and very little material. Following recognition of the subfamily by van Achterberg (1975) and description of the first species, *Mesostoa compressa* van Achterberg from Perth, Quicke & Huddleston (1989) described a second species from Adelaide, *M. austini* Quicke & Huddleston. These authors also placed Tobias' monospecific subfamily Praonopterinae (Tobias 1988) as a junior synonym of Mesostoinae, but maintained *Praonopterus laevis* Tobias, from Jervis Bay, A.C.T. as a separate genus based primarily on differences in wing venation.

Members of the Mesostoinae show a general resemblance to some cyclostome braconids, particularly certain doryctines, exothecines and hormiines, but they can be usually separated from these taxa by the labrum being only slightly depressed, fore tibia evenly and finely setose, and antennal flagellomeres flattened. However, the species described below brings two of these characters into question, in that the labrum is strongly depressed and oval in shape and the mandibles are curved distally to form a subcyclostome mouth (Fig. 37), and the fore tibia has two rows of spines (Fig. 39). The recognition of these characters for *Mesostoa* requires further interpretation, but may indicate a much closer relationship with the Doryctinae than has previously been postulated (van Achterberg 1984; Quicke & van Achterberg 1990).

Key to known species of *Mesostoa*

1. Occipital carina absent; propodeum smooth, without medial longitudinal strigose sculpturing; scutum with only a trace anteriorly of a medial longitudinal groove [female antenna with 12 flagellomeres] . . . . . . *M. compressa* van Achterberg
   Occipital carina present (Figs 34, 36); propodeum strigose in medial longitudinal line (Figs 31, 33); scutum with almost complete medial longitudinal groove (Figs 30, 32) 2

2. Ovipositor present (Figs 25, 26) (female) 3
   Ovipositor absent (male) 4

3. Antenna with 14 flagellomeres . . . . *M. austini* Quicke & Huddleston
   Antenna with 19 flagellomeres (Fig. 26) . . . . *M. kerri* sp. nov.

4. Posterior half of scutum with some longitudinal rugose striate sculpturing laterally, transscutal articulation present but faint . . . . . . *M. austini* Quicke & Huddleston*
   Posterior half of scutum virtually completely smooth, transscutal articulation absent (Fig. 32) . . . . *M. kerri* sp. nov*

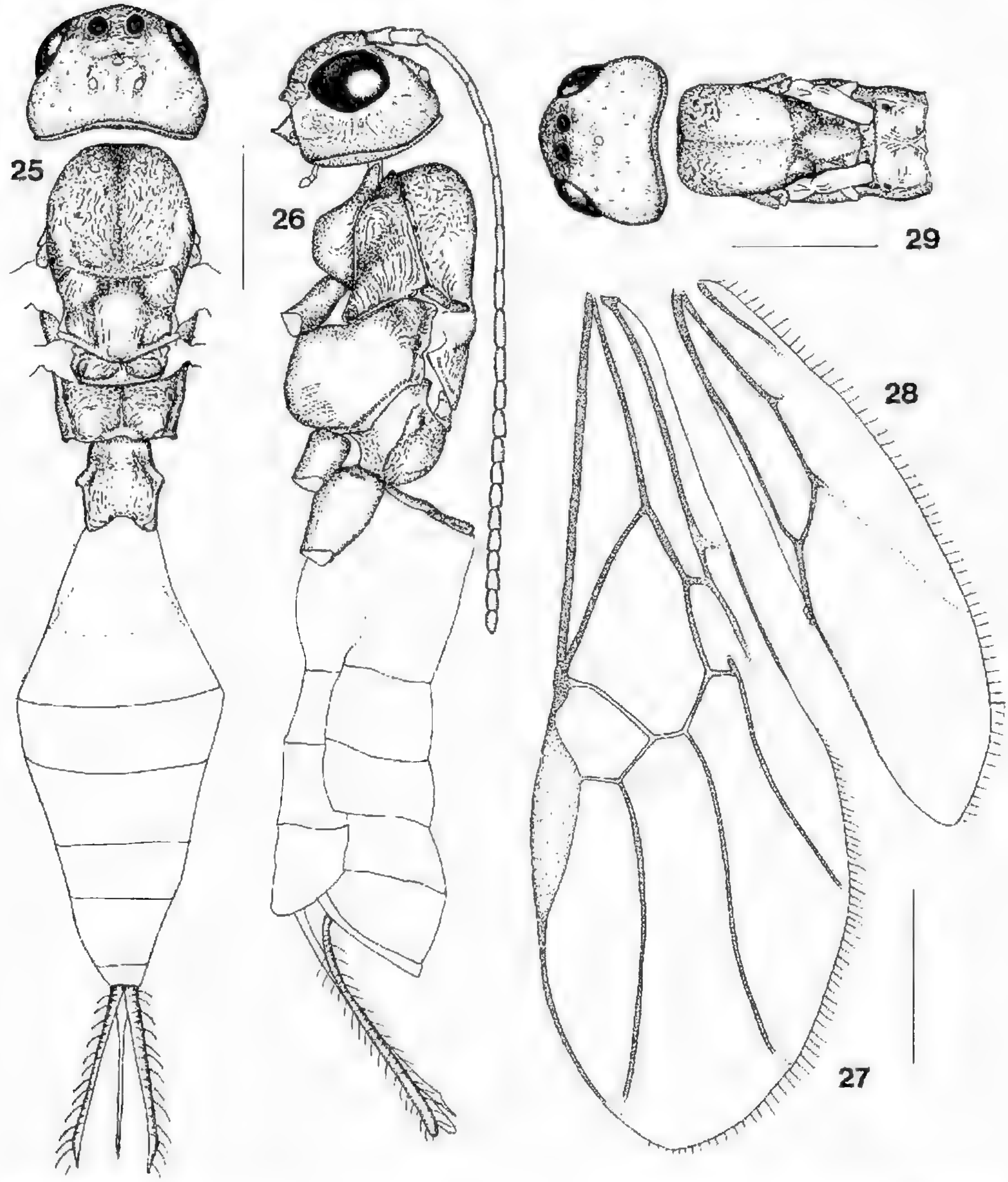
* males of both these two species have 18-19 flagellomeres.

Mesostoa kerri sp. nov.
FIGS 25–40

Material examined. Holotype: ♀, ANIC, South Australia "S. Aust: Reedy Creek, 37.17S, 140.15E, 10th Oct 1991, Austin & Dangerfield ex twig gall of *Banksia marginata*". Paratypes: 52 ♀♀, 34 ♂♂, same data as holotype (2 ♀♀, 2 ♂♂ each in AEIC, ANIC, BMNH, CNCI, HNHM, QDPI, RNMH, USNM; 5 ♀♀, 5 ♂♂ TAMU; 31 ♀♀, 13 ♂♂, 2 of each gold-coated, WARI); 74 ♀♀, 38 ♂♂, S. Aust Reedy Crk., 3.x.1953, emerged from galls on *Banksia* sp., dried from extended alcohol storage (10 ♀♀, 10 ♂♂ TAMU, 64 ♀♀, 28 ♂♂ WARI).

Female

Head. In dorsal view posterior part of head broadly emarginate, distinctly truncate so that angle between vertex and occiput is approximately 90°, occipital carina fine but complete throughout; vertex, temples and frons mostly smooth with very sparse short setae; ocellar triangle obtuse, area within and around triangle faintly strigose; ocelli of equal size; ratio of distance between posterior ocelli to shortest distance to eye margin 0.9:1.1 (Fig. 34); frons broadly depressed; widest part of head behind eyes i.e. temples extending laterally past line of eyes; face and malar region rugose to striate-rugose, with long scattered setae; face evenly convex, ratio of width of face to head (2.0:4.3); ratio of eye height to height of head (measured in midline from margin of labrum) (2.0:3.7); face slightly depressed at epistomal suture so that clypeus protrudes outwards slightly (best seen in antero-lateral view); lower margin of clypeus slightly convex and wrinkled; labrum depressed and oval in shape, mandible curved inwards in distal half to form subcyclostome condition (seen best in antero-ventral view); antenna with 19 flagellomeres, relative lengths of flagellomeres 1-4



Figs 25–29 *Mesostoa kerri* sp. nov., ♀ holotype. 25, dorsal view of body; 26, lateral view of body; 27, fore wing; 28, hind wing; 29, ♂, paratype, dorsal view of head and mesosoma. Scales = 0.5 mm.

(1.5:1.1:1.1:1.1), proximal 6-8 flagellomeres with very sparse setae, more distal flagellomeres becoming progressively more setose; distal 6-7 flagellomeres about 1.5 × longer than wide.

Mesosoma. Moderately dorso-ventrally flattened (seen in lateral view), about 2 × as long as high; scutum narrower than head, as wide as long, medial longitudinal line depressed to form a shallow groove extending almost to posterior margin of scutum, anterior part of groove smooth, posterior part with few fine longitudinal striae merging with surrounding sculpturing; antero-lateral shoulders of scutum finely rugose, posterior margin smooth, rest finely rugose-striate in anterior part, narrowing into fine rugose-punctate tracts posteriorly which indicate position of notauli, outer side of these tracts bordered by smooth strip; whole surface covered with short setae. transscutal articulation distinct (Fig. 30); scuto-scutellar sulcus strongly curved posteriorly and faintly crenulate, this sulcus separating distinct subtriangular axillae; medial scutellum smooth with finely striate lateral borders, virtually hairless and oval in shape; lateral scutellum faintly strigose to smooth; propodeum with percurrent medial longitudinal band of fine strigose sculpturing, postero-lateral corners smooth, rest of propodeum very finely striate to rugose-striate, with some very fine background punctation (Fig. 31); in lateral view pronotum finely rugose medially surrounded by fine striate sculpturing extending to margins; mesopleuron smooth and bare except for rugulose epicnemial area; precoxal sulcus indicated by fine vertical striate sculpturing; metapleuron rugulose on ventral half, smooth dorsally; outer surface of fore tibia with irregular double row of spines (Fig. 39).

Wings. Generally the same as *M. austini* and differing from *M. compressa* in the fore wing as follows: 1−M broadly and faintly sinuate; anterior part of 1−SR+M bent; 2+3−M slightly curved basally; subdiscal cell widening distally.

Metasoma. As long as head and mesosoma combined; petiole (T1) about as long as maximum width across position of spiracles, with fine longitudinal striae. T2+3 the largest tergite, about 0.6 × as long as T4−T7; suture between T2 and T3 indicated by fine transverse line; T2−T5 smooth with single transverse row of fine hairs, ovipositor and sheaths about one-third length of metasoma, sheaths with long sparse setae throughout.

Colour. Head and mesosoma dark brown to black; mandibles yellow with dark tip; legs brown with lighter bands at joints, femora slightly darker; metasoma and ovipositor sheaths dark brown to black with anterior sternites sometimes dark yellow-brown, wings hyaline, stigma pale.

Body length. mean 2.6 mm (range 2.3–2.9, n=15).

Male

Similar to female but differing as follows: length 2.3 (range 1.9–2.7, n=15); posterior ocelli minute (Fig. 36), sometimes absent; antenna with 19-20 flagellomeres; brachypterous (Fig. 29), fore wings rectangular, reaching to anterior margin of propodeum, base of wing darkly sclerotised, rest white in colour, membranous and without venation; hind wing minute, about half length of fore wing; mesosoma generally narrower; scutum broader and more truncate anteriorly, squarish at shoulders, smooth in posterior half; transverse scutellar suture absent (Fig. 32); medial scutellum more elongate; fore tibia without distinct spines on outer surface (Fig. 40); metasoma longer than head + mesosoma (6.0:4.3); T1 broader across position of spiracles than long (2.0:1.4); suture between T2 and T3 complete and membranous, these and other tergites subequal in length; T2–T6 smooth, with a few scattered minute hairs.

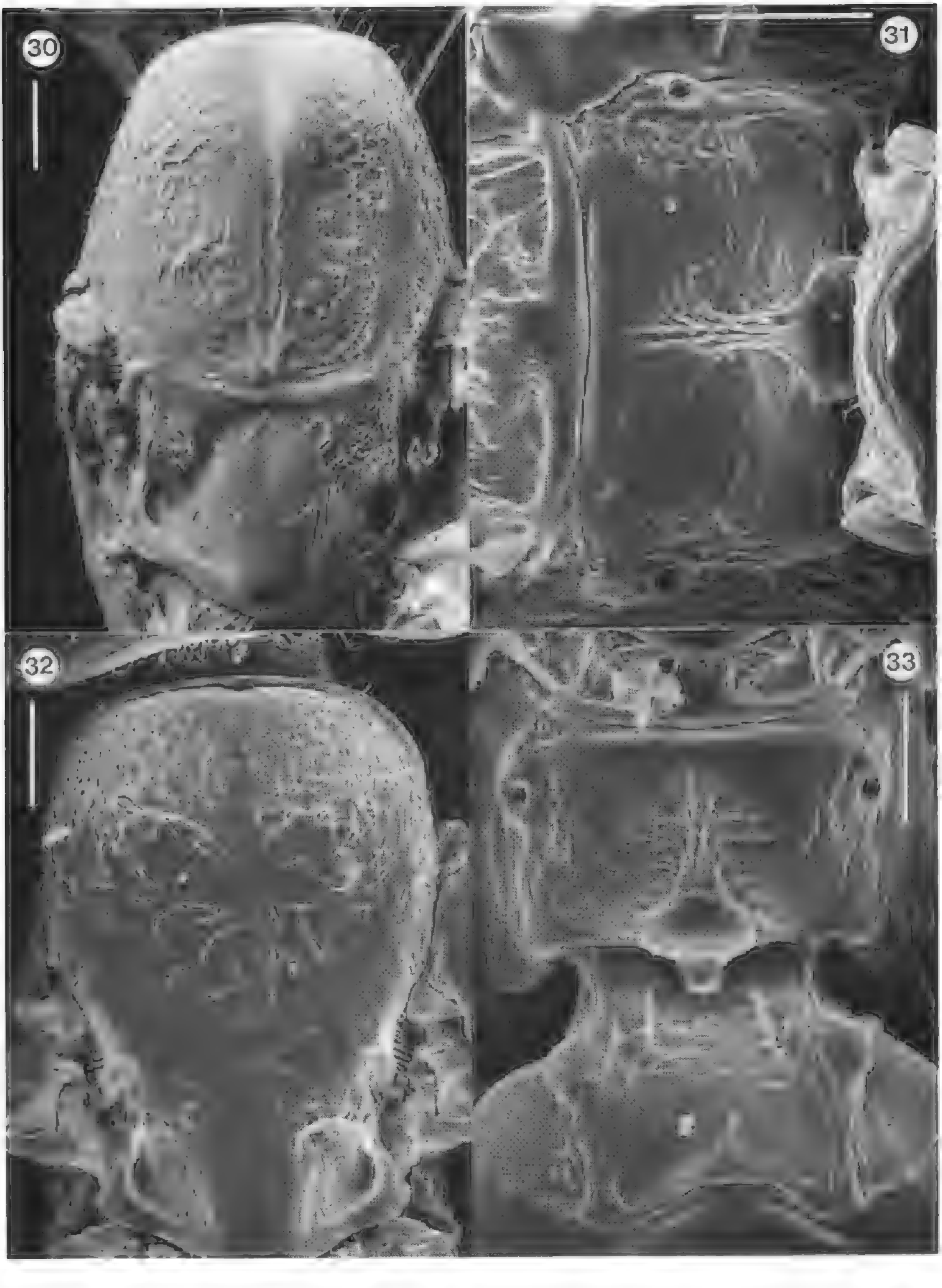
Referred material examined: Victoria, 4 ♀♀, 5 ♂♂, Melbourne, 7.x.1904, *Banksia* galls (BMNH).

Biology: This species is associated with galls on the outer branches of *Banksia marginata*, a relationship with this plant genus that may be general for all *Mesostoa* spp., given that *M. austini* has also been thus reared. However, the exact host is not yet known, but presumably it is the primary gall former or one of the several insects that inhabit *Banksia* galls, such as curculionid beetle larvae.

Discussion: This species is much closer to *M. austini* than it is to *M. compressa*. The latter species has the head and scutum more extensively sculptured with coarser curved striae. The scutum of *M. compressa*, although having the posterio-medial part flattened, lacks a longitudinal groove, the propodeum is smooth, the female antennae only have 12 flagellomeres, and the lateral fields of the scutellum are striate. In comparison, *M. austini* and *M. kerri* generally have the face rugose to rugose-striate and the scutum finely rugose-striate, the scutum with a longitudinal groove, the propodeum medially strigose, the female antennae with a greater number of flagellomeres, and the lateral fields of the scutellum smooth or faintly striate. *M. austini* and *M. kerri* differ substantially only in the number of antennal flagellomeres for the female and more subtly on the degree of sculpturing on the head and scutum, with *M. kerri* generally being less extensively sculptured.

As pointed out by Quicke & Huddleston (1989) the presence or absence of an occipital carina is often used as a primary distinguishing character at the generic level, and in this respect there is some justification for placing *M. austini* and *M. kerri* in a separate genus from *M. compressa*. However, until more material of this rare subfamily becomes available there is little or no advantage in arranging the four known species of Mesostoinae in three separate genera.

This species is named after Professor Allen Kerr, inaugural head of the Department of Crop Protection at the Waite Institute, and one of Australia's leading scientists.



Figs 30–33. *Mesostoa kerri* sp. nov., ♀, paratype. 30, dorsal view of scutum and scutellum; 31, dorsal view of propodeum 32, 33. ♂, paratype. 32, dorsal view of scutum and scutellum; 33, dorsal view of propodeum and T1. Scales = 100 μm

Figs 34–40. *Mesostoa kerri* sp. nov., ♀, paratype. 34, dorsal view of head; 35, anterior view of head. 36, 37, ♂, paratype. 36, dorsal view of head; 37, antero-ventral view of head (N.B. transverse lines on face are due to specimen charging). 38, 39, ♀, paratype. 38, tip of ovipositor; 39, fore tibia. 40, ♂, paratype, fore tibia. Scales: Figs 34–37 = 100 μm; Figs 38–40 = 50 μm.

Subfamily Meteorideinae Capek

Comments: This small subfamily is defined by its biology (gregarious larval-pupal endoparasitoids of Lepidoptera) and highly modified metasoma (Nixon 1941). Capek (1970) separated the nominate genus, *Meteoridea* Ashmead, from the Diospilini on the basis of larval morphology and biology, and placed it in a subfamily of its own. Until recently only two genera had been described, *Meteoridea* and *Benama* Nixon. Shenefelt & Muesebeck (1957) redescribed the previously poorly characterised *Meteoridea*, and synonymised *Benama* with it. This synonymy was accepted by Capek (1970). Van Achterberg (1984), however, implied that the two were distinct, but has since reversed his opinion (van Achterberg 1990). In addition to the Australian species described below, we have examined material of *Meteoridea* from West Africa and North America. In North American material, the median lobe on the apical margin of the clypeus is more tooth-like than in the Australian and West African species. Additionally, the deep basal pits of the petiole (dorsope) are more laterally displaced in North American species, and not visible in dorsal view. However, we do not consider these differences sufficiently clear-cut for separating *Benama* from *Meteoridea*. Van Achterberg (1990) has recently described a third genus of Meteorideinae from New Zealand, *Pronkia* van Achterberg, which has a number of unusual features that align it, at least superficially, with the Agathidinae and Sigalphinae. *Pronkia* differs substantially from *Meteoridea* in that it has a smooth propodeum, dorsope absent, fourth tergite depressed, fore wing vein 1−SR present and vertical, r short, M+CU1 unsclerotised, and hind wing marginal cell slender.

The species of *Meteoridea* described here is the first record for the subfamily from the Australian continent. Although van Achterberg (1984) has previously stated that the Meteorideinae are "restricted to the (sub)tropics," the description of *M. compressiventris* Shenefelt & Muesebeck from Wisconsin, U.S.A. (Shenefelt & Meusebeck 1957) and *P. antefurcalis* van Achterberg from New Zealand, clearly show that the subfamily extends into more temperate regions.

Meteoridea anic sp. nov.
FIGS 41–44

Material examined. Holotype: ♀, ANIC, Queensland, "15.03S 145.09E 3km NE Mt. Webb 1-3 Oct. 1980 Q J. C. Cardale ex ethanol". Paratypes: 3 ♀♀, 15°04'S, 145°07'E, Mt Webb Nat. Pk., 28-30.ix.1980, J. C. Cardale, ex ethanol (ANIC, WARI); 5 ♀♀, 15°17'S, 145°10'E 5km W by N Rounded Hill nr Hope Vale Mission, 7.v.1980, J. C. Cardale, ex ethanol (ANIC, TAMU, WARI); 1 ♀, 1.5 km SE Kuranda, lu 17.v.1980, I. D. Naumann & J. C. Cardale (ANIC).

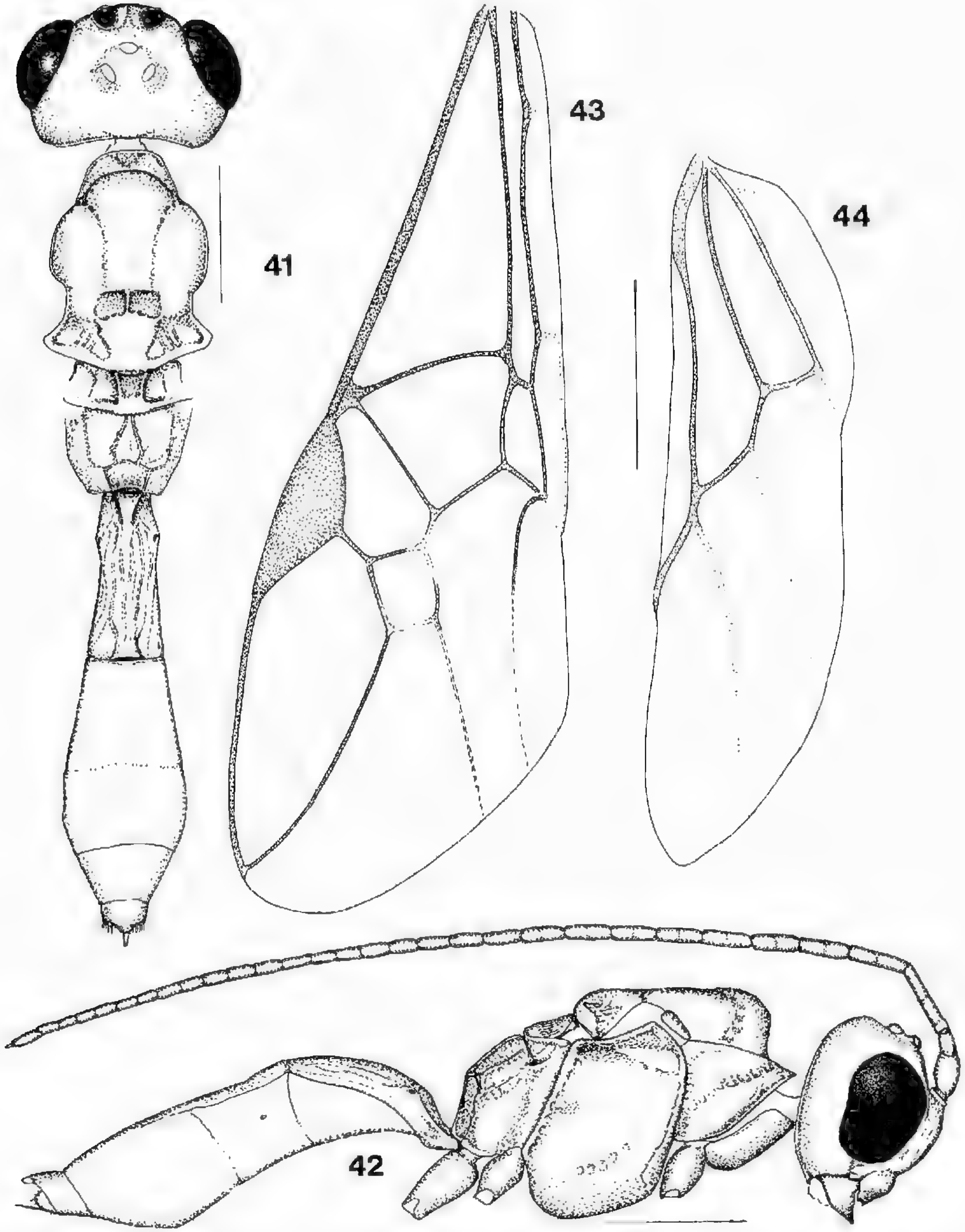
Female

Head. In dorsal view wider than scutum; temples broad; eyes bulbous and glabrous; ocelli forming a compact triangle, distance between posterior ocelli much shorter than distance from them to margin of eye; occiput, vertex, frons and temples smooth and shining, except for few tiny punctures associated with occasional fine setae; head in anterior view almost circular; face strongly convex, with broad medial longitudinal ridge and scattered punctures associated with long fine setae; epistomal suture impressed; clypeus convex with scattered punctures and slightly up turned lower margin; malar space small, margin adjacent to mandible slightly convex; antennal sockets with raised margins; antenna 31-segmented, all flagellomeres longer than wide, reaching as far as posterior edge of metasoma.

Mesosoma. Pronotum with large dorsope, in lateral view with medio-diagonal line crenulate, posterior and ventral margins crenulate; scutum smooth with occasional scattered punctures and associated fine setae; notauli percurrent and crenulate, anterior declivous portions broadly crenulate; transscutal articulation straight; scuto-scutellar sulcus comprising 2 or 3 deep foveae; scutellum convex, smooth and shiny, except for a few scattered punctures and associated long setae; lateral fields of scutellum faintly striate; posterior margin of scutellum smooth though sometimes with faint medial rugosity; metanotum with 2 prominent medial longitudinal carinae and less distinct carinae laterally; propodeal carinae sometimes somewhat irregular but always forming a distinct areola and enclosed lateral and posterior areas which are punctate or rugose-punctate; surface of propodeum and metapleuron covered with long, fine setae; precoxal sulcus and pleural suture faintly crenulate; flange above epicnemial area carinate (see van Achterberg 1979), margined by crenulate or foveolate impressions.

Wings. Fore wing with vein 1−M slightly bowed; r emerging from mid point of stigma; CU1a strongly arched basally; subbasal cell narrowed slightly at middle; subdiscal cell widened distally; hind wing 1−SR and 2−M indicated by short pigmented spurs basally, rest of these veins desclerotised; M+CU 3 × as long as 1−M; 1−1A desclerotised.

Metasoma. Almost as long as head and mesosoma combined; petiole (T1) slightly constricted behind spiracles then widening slightly in posterior half, widest across posterior margin, 2.5 × longer than wide, with distinct antero-lateral pits, dorso-lateral margins distinctly carinate, dorsal surface longitudinally striate with punctate to rugose-punctate background sculpturing; T2 and all other metasomal tergites smooth and shiny with occasional scattered hairs concentrated laterally and on posterior tergites; posterior most tergite somewhat extended distally and



Figs 41–44. *Meteoridea ane* sp. nov., ♀, holotype. 41, dorsal view of body; 42, lateral view of body; 43, fore wing; 44, hind wing. Scales = 0.5 mm.

laterally to form a capsule enclosing ovipositor; ovipositor and sheaths hidden.

Colour: Body including legs uniformly yellow; scape and pedicel yellow, flagellomeres brown; mandibles darkened distally; wings hyaline, venation evenly coloured, stigma translucent yellow-brown.

Male
Unknown.

Biology: Unknown.

Diagnosis: The uniformly yellow body separates this species from all but *M. testacea* (Granger) from Madagascar. It is nearly identical to the latter, differing only in minor sculptural features of the petiole.

Subfamily Helconinae Foerster

Comments: The helconines represent a rather diverse assemblage of taxa which, even in the strict sense (i.e. with the removal of *Cenocoelius* Haliday into a separate subfamily — Szépligeti 1902), may still be polyphyletic or at best paraphyletic (Quicke & van Achterberg 1990). Van Achterberg (1983) recognised four tribes: Helconini Ashmead, Brulleiini van Achterberg, Diospilini Foerster and Brachistini Foerster, all of which are represented in the Australian fauna (Brulleiini only by undescribed species). Of these the Helconini is the most diverse, with four of five recorded genera endemic to Australia. *Helcon* Nees von Esenbeck is virtually cosmopolitan in distribution, while *Austrohelcon* Turner, *Parahelcon* Kokujev, *Trichiohelcon* Turner and *Calohelcon* Turner are known only from mainland Australia and Tasmania. Collectively, they are represented by nine described species, with the first three genera not having been treated since their original descriptions (Kokujev 1901; Turner 1918). *Calohelcon* has recently been redescribed and discussed by Quicke & Holloway (1991). The tribe Helconini has been defined by the presence of the following characters: frons with a medial longitudinal carina (lamella), hind femur rugose ventrally, propodeal spiracle situated medially, and fore wing veins 1−SR and 2A present (van Achterberg 1983). As is true of many of the Australian helconines which have been placed in the Helconini, *Calohelcon* is unusual in several respects. The species of *Calohelcon* and *Trichiohelcon* which we have examined have a very smooth body and so lack a precoxal sulcus and carinate or rugose propodeum. *Calohelcon* is particularly remarkable in that the first metasomal tergite is enlarged so as to appear inflated (Figs 48, 51). Quicke & Holloway (1991) also state that *Calohelcon* has retained a number of plesiomorphic characters, in particular a large number of hamuli, the presence of hind wing vein m-cu, and the presence of a costal cell in the fore wing. Clearly, the definition of Helconini used by van Achterberg (1983) must be reassessed in the light of the Australian fauna, but this cannot be accomplished until the rich helconine fauna of this continent has been more thoroughly described.

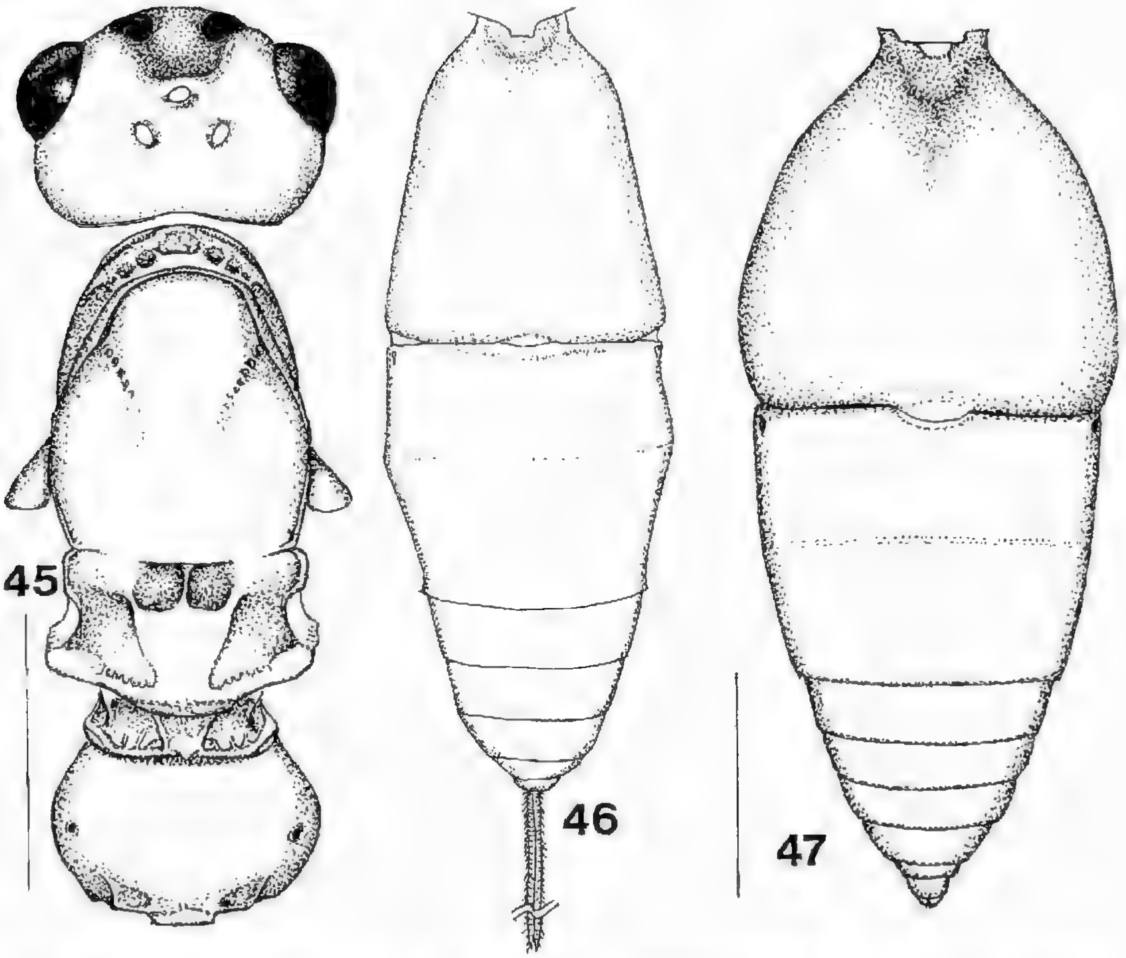
We describe below a third species of *Calohelcon* from central Australia, where the genus has previously been known only from the eastern coastal margin of the continent. The inclusion of this species extends the limits of the genus slightly and requires the diagnosis of *Calohelcon* presented in Quicke & Holloway (1991) to be modified as follows: frons with median longitudinal carina varying from well-developed to reduced or nearly absent; propodeal spiracle circular to slightly elliptical; fore wing with costal cell open for about two-thirds of length of veins C and Sc+R+Rs to almost closed over; hind wing with vein m-cu present or absent; hamuli number variable (5-9); ovipositor as long as or longer than body. *Calohelcon* shares a number of features with *Trichiohelcon*, but is readily separated by the inflated, nearly bare first metasomal tergite.

Host records for the Helconinae show that they have only been reared as endoparasitoids of coleopteran larvae. We treat with scepticism the record for *C. obscuripennis* Turner in Quicke & Holloway (1991) (1 ♀, ANIC — "probing tree trunk with cossid larvae") as evidence that the host biology of this genus departs from that known for other helconine genera. In our experience, *Eucalyptus* and *Acacia* trees can be heavily infested with both coleopteran and lepidopteran larvae, and so observed ovipositor probing is likely to be inaccurate as a method of associating potential hosts.

Key to known species of *Calohelcon*

1 Dorsal surface of T1 in lateral view convexly rounded in anterior part and flattened posteriorly (Fig. 48); ovipositor longer than body; body 8 mm in length or shorter . . . . *C. dangerfieldi* sp. nov.
— Dorsal surface of T1 in lateral view with large hump in anterior half and weakly rounded posteriorly (Fig. 51); ovipositor as long as body; body about 13 mm in length or longer 2

2 Lateral margins of T1 in dorsal view constricted in anterior part; scutum and T5−T9 black, wings yellowish basally, grey-brown apically . . . . . . *C. obscuripennis* Turner
— Lateral margins of T1 in dorsal view only slightly constricted in anterior part; scutum and T5−T9 orange, wings evenly light brown . . . . *C. toddi* Quicke & Holloway



Figs 45–47 *Calohelcon dangerfieldi* sp. nov., ♀ holotype. 45, dorsal view of head and mesosoma; 46, dorsal view of metasoma. 47, ♂, dorsal view of metasoma. Scales: Fig. 45 = 0.8 mm; Figs 46, 47 = 0.75 mm.

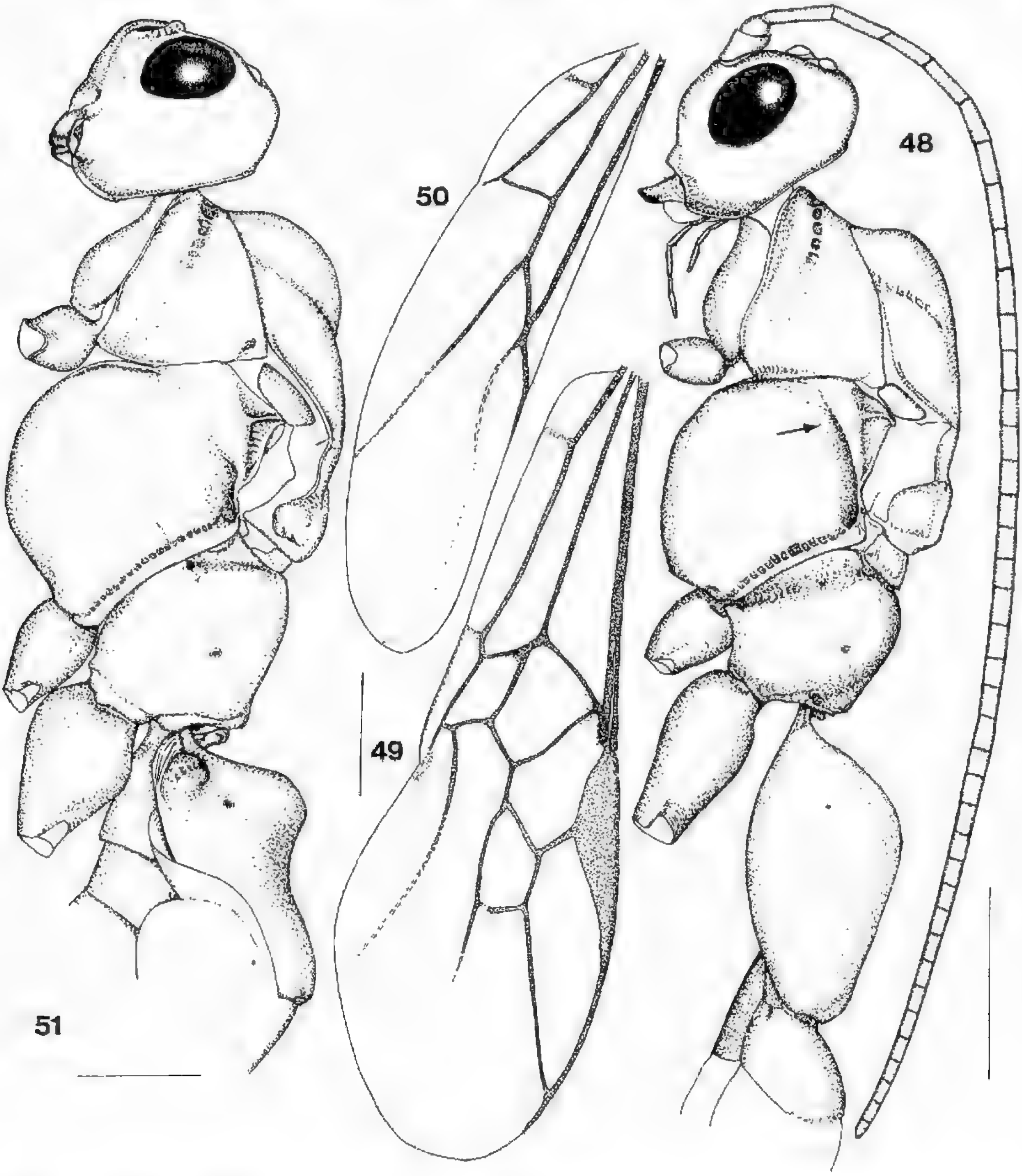
Calohelcon dangerfieldi sp. nov.
FIGS 45–50

Material examined. Holotype: ♀, AEIC, Northern Territory, "Yuenduma N.T., Australia August", no collector or date given.

Female

Head. Completely smooth and shiny; temples and face with minute punctures and associated fine setae; vertex and frons virtually bare; in dorsal view occipital carina angled slightly so as to be obtusely pointed medially; in lateral view occipital carina extending ventrally to meet hypostomal carina; ocelli forming equilateral triangle, distance between posterior ocelli slightly less than distance from them to eye margin (2.0:2.3); in anterior view vertex convexly rounded so that lateral ocelli are above dorsal margin of the eyes; face evenly convex, node between antennal sockets extending dorsally into short faint carina which fades out before reaching frons; eyes more than half height of head (2.5:4.0 — measured in lateral view from vertex to base of mandible); malar sulcus absent; clypeus moderately transverse, slightly less than 2 × wider than long; mandibles short, only overlapping slightly; antennae reaching to about midpoint of T2+T3, 41-segmented

Mesosoma. Slightly narrower than head; pronotum well exposed dorsally, coarsely crenulate around pronope, crenulate line fading on smooth lateral pronotum, latero-anterior margin of pronotum finely crenulate; scutum, scutellum and propodeum smooth and shiny, with a few scattered fine setae; antero-lateral margins of scutum slightly emarginate at point of notauli; notauli crenulate and reaching posteriorly to about middle of scutum; scutellar sulcus developed as 2 deep foveae; flange above epicnemial area carinate



Figs 48–51. *Calohelcon dangerfieldi* sp. nov., ♀ holotype. 48, lateral view of head, mesosoma and anterior metasoma (carinate flange above epicnemial area, arrowed); 49, fore wing; 50, hind wing. 51, *Calohelcon obscuripennis* Turner, ♀, lateral view of head, mesosoma and anterior metasoma. Scales: Figs 48–50 = 1.0 mm; Fig. 51 = 1.5 mm

(Fig. 48, arrowed) and reaching anteriorly to touch dorsal part of prepectal carina.

Wings. Costal cell of fore wing indistinct; m-cu much shorter than 1−M so that discal cell narrows distally; 1−SR+M sinuate; 1−SR very short almost obliterated; 2−SR+M 0.67× as long as 2−SR; 3−SR as long as r-m; SR−1 straight; hind wing without vein m-cu arising from 2−M; R1 with 5 hamuli.

Metasoma. T1 longer than T2+T3, in dorsal view broadening posteriorly, with broad shallow medial longitudinal depression in anterior one third, lateral margins virtually straight, in lateral view convexly rounded in anterior part and flattened posteriorly, lacking large antero-lateral pits; suture between T2 and T3 faint; ovipositor longer than body (7.5:6.0)

Colour. Head, mesosoma including coxae and T2−T8 orange-brown; antennae and legs black; latero-anterior half of pronotum black; propleura yellow-brown; wings evenly and darkly infuscate; T1 white; S1 white with 2 broad dark transverse bands; laterotergites of T2 and T3 and posterior sternites black; ovipositor brown, sheaths black.

Body length. 7.0 mm, not including ovipositor.

Male

As for female except as follows: slightly larger in size, body length 8.0 mm; T1 larger, in dorsal view wider than rest of metasoma, lateral margins rounded; 2−SR+M of fore wing almost as long as 2−SR; costal cell slightly more obvious; flange above epicnemial area not reaching anteriorly as far as dorsal part of prepectal carina, lateral pronotum more extensively black, anterior mesopleuron and distal half of all coxae black.

Biology: Unknown.

Referred material examined: South Australia, 1♂, Dalhousie Springs, 29.x.83, G. A. Holloway (ANIC).

Diagnosis: This species is most easily identified by the shape of T1, the crenulate notauli, lack of medial sculpturing and a carina on the face and frons, shape of the pronotum (in lateral view), fore wing venation, number of hamuli and length of the ovipositor. Although this is the first record of a male for the genus, we have not included the single male specimen in the type series because there is a possibility that the slight differences between the sexes described here are representative of two species, not intraspecific sexual dimorphism. Until more material becomes available this problem will not be satisfactorily resolved.

Etymology: This species is named after Paul Dangerfield in recognition of the illustrations he has prepared for us.

Subfamily Alysiinae Stephens

Comments: In a recently published paper by the authors revising the Australian members of the Tribe Dacnusini (Wharton & Austin 1991), several type-setting errors were overlooked which could result in significant taxonomic confusion. We therefore take this opportunity to correct the most serious of these, as follows: 1) p. 198, line 30, subheading "*Chaenusa nigricapitis*" should read "*Chorebus nigricapitis*"; 2) p. 201, line 50 "1 or 2" should read "1 of 2"; and 3) p. 205, line 17, "*areolis*" should read "*areolaris*".

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AN EOCENE MEGAFOSSIL FROM NELLY CREEK, SOUTH AUSTRALIA

BY D. C. CHRISTOPHEL, L. J. SCRIVEN* & D. R. GREENWOOD***

Summary

Clay from the Eyre Formation in Nelly Creek in far north South Australia contains the first Middle Eocene mummified leaf flora reported from the interior of Australia. The 269 leaves collected are placed in 16 parataxa, with one angiosperm parataxon of unknown affinity providing 64% of the flora. Eleven of the 16 parataxa can be assigned to extant families which include Proteaceae, Myrtaceae, Araucariaceae, Podocarpaceae, Casuarinaceae and Lauraceae. *Myrtaciphyllum eremeaensisi* sp . nov. is formally described.

Comparison with Middle Eocene megafossil floras suggests that the Nelly Creek flora is taxonomically distinct and physiognomically more sclerophyllous than the other south-eastern Australian floras. However. Sampling programs in extant rainforests and other Eocene deposits suggest that the number of parataxa (16) recorded at Nelly Creek from this first collection will likely increase markedly with further collections.

Comparison with the silcrete floras of northern South Australia, in particular the Poole Creek flora. Demonstrates that while some taxa, including a possible Proteaceae infructescence, are common to both deposits, the majority of both floras do not correspond.

KEY WORDS: Fossil, Eocene, Nelly Creek, Silcrete, Myrtaceae.

Transactions of the Royal Society of S. Aust. (1992), 116(2), 65-76.

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Comparison with Middle Eocene megafossil floras suggests that the Nelly Creek flora is taxonomically distinct and physiognomically more sclerophyllous than the other south-eastern Australian floras. However sampling programs in extant rainforests and other Eocene deposits suggest that the number of parataxa (16) recorded at Nelly Creek from this first collection will likely increase markedly with further collections.

Comparison with the silcrete floras of northern South Australia, in particular the Poole Creek flora, demonstrates that while some taxa, including a possible Proteaceae infructescence, are common to both deposits, the majority of both floras do not correspond.

KEY WORDS: Fossil, Eocene, Nelly Creek, Silcrete, Myrtaceae

Introduction

The Middle Eocene flora of Australia is well known from megafossil localities in south-eastern Australia. These include the Anglesea flora (e.g. Christophel 1984; Christophel & Lys 1986; Christophel *et al.* 1987; Hill 1980; Rowett & Christophel 1990), the Golden Grove flora (Barrett & Christophel 1990; Christophel & Greenwood 1989), the Maslin Bay flora (Lange 1970; Christophel & Blackburn 1978; Blackburn 1981) and the Nerriga flora (Hill 1978, 1983). These occur near the coast, with the first three considered to be lowland and the last (Nerriga) to be upland (Fig. 1). All of these floras have been interpreted as representing tropical to sub-tropical (or very warm temperate at the minimal) rainforest communities (Christophel 1989; Christophel & Greenwood 1989) and all contain well preserved, compressed or mummified leaves, allowing maximum potential for interpretation.

A second source of data on Early Tertiary floras in southern Australia comes from the extensive impression and cast floras of interior southern and central Australia, collectively known as the silcrete floras. While known for a relatively long time (Chapman 1937), these floras have not played a major role in interpreting Tertiary vegetation because of the lack of stratigraphic control. More recently, Ambrose *et al.* (1979) suggested an Eocene age for some of these silcretes, including those described by Lange (1978) containing leptospermoid Myrtaceae fruits. Recent work by Greenwood *et al.* (1990[1]) described a flora from the Poole Creek area of South Australia and placed the age as Middle Eocene based on lithostratigraphic correlations. Fossil pollen has not been preserved in these silcretes and hence palynology could not be used to confirm their age.

The discovery in 1986 by R. Callen of fossiliferous clays in northern South Australia which contained well preserved, compressed and mummified leaves and which was interpreted as Middle Eocene (Alley 1989[2]) was important for several reasons. Firstly, it greatly extends the geographic range of well-preserved Middle Eocene megafossil floras. Secondly, it provides biostratigraphically datable evidence for a truly inland, lowland flora of that age, and finally, it provides the possibility of better chronological control over the interpretation of the numerous silcrete floras of the interior (Ambrose *et al.* 1979; Greenwood *et al.* 1990). The aims of this report are therefore to provide a preliminary description of the megafossil flora of Nelly Creek, to formally describe a new species of Myrtaceae from this deposit, and to compare the parataxa from Nelly Creek with the known silcrete elements.

[1] GREENWOOD, D. R., CALLEN, R. A. & ALLEY, N. F. (1990) The correlation and depositional environment of Tertiary strata based on macrofloras in the southern Lake Eyre Basin, South Australia. S.A. Department of Mines and Energy Report 90/15, 1–57, Plates 1-7.

[2] Alley, N. F. (1989) Preliminary Palynological dating of macrofloras from Eyre Formation, Nelly Creek, Lake Eyre Basin. Dept. of Mines and Energy of South Australia Rept Bk No. 89/46

* Department of Botany, University of Adelaide, G.P.O. Box 498, Adelaide, S. Aust. 5001

** Geology Department, University of Saskatchewan Saskatoon, Saskatchewan, Canada S7N 0W0

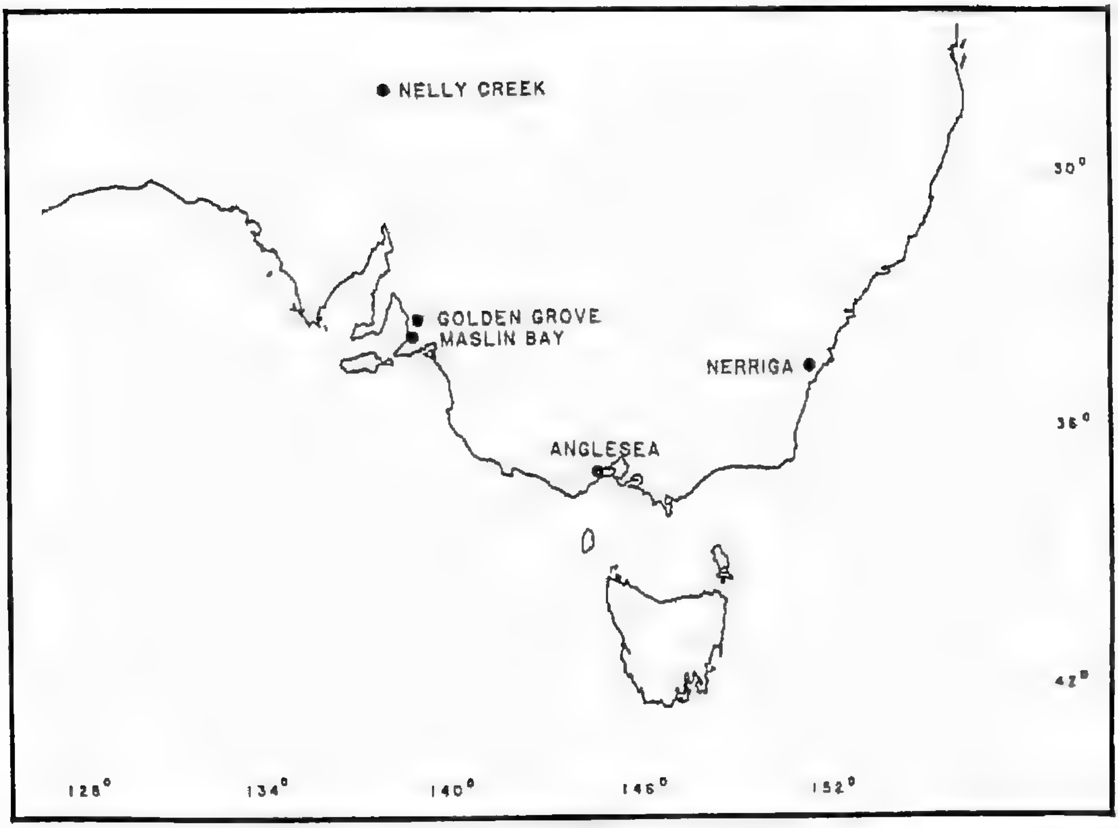


Fig. 1. Map of southeastern Australia showing the location of Nelly Creek and other Middle Eocene plant megafossil localities.

Materials and Methods

The Nelly Creek flora is contained in the Eyre Formation located at 29°19′S, 137°18′E, approximately 1 km south of the southern shore of Lake Eyre South (Fig. 1). The deposit consists of sands, silts and grey, carbonaceous clays forming a portion of the bed of Nelly Creek. Overlying strata consist of partially silicified sediments, disaggregated sands, and a salt-pan crust. The deposit is restricted to the stream bed and is only accessible when little or no water is found in Nelly Creek. The fragility of the material, as well as the terrain and general inaccessibility have severely limited the amount of material collected to date. The extent of the fossiliferous clay horizon outside the stream channel is unknown, although fossiliferous clays have been intersected in a number of bore holes in the region (N. Alley pers. comm.). The width of the deposit within the stream bed is less than 3 metres, and its thickness less than 1 metre.

The high water table and the high salt content of the ground water result in freshly excavated, moist blocks drying quickly with a salt crust. Most southern Australian clays containing mummified leaves can be disaggregated by immersion in approximate 7% w/v H_2O_2 which has been heated. Salt in the Nelly Creek matrix interferes with disaggregation, and maceration is only successful if the blocks have been either presoaked in distilled water to remove some of the salt, or if a detergent such as Quaternary O is added to the maceration mixture. Approximately 40% of the leaves obtained from a given macerate are translucent (Fig. 2, A–C) while other specimens are black/opaque and much more brittle. Leaf remains obtained in this fashion are contained in complete cuticular envelopes and treatment with hot H_2O_2 (e.g. Scriven & Christophel 1990) followed by staining in crystal violet yields clean, easily photographed cuticle specimens. Cuticles from this deposit prepare easily and are in a better state of preservation than those of any other Eocene deposit previously examined by the authors. Two frequent causes of cuticular abrasion or fragility are alkalinity of the matrix (or ground water) and presence of excessive fungal activity during, or prior to, fossilization. Based on the excellent preservation, both of these factors were either absent or minimal during the burial and subsequent fossilization of the Nelly Creek leaves. All specimens figured in this paper

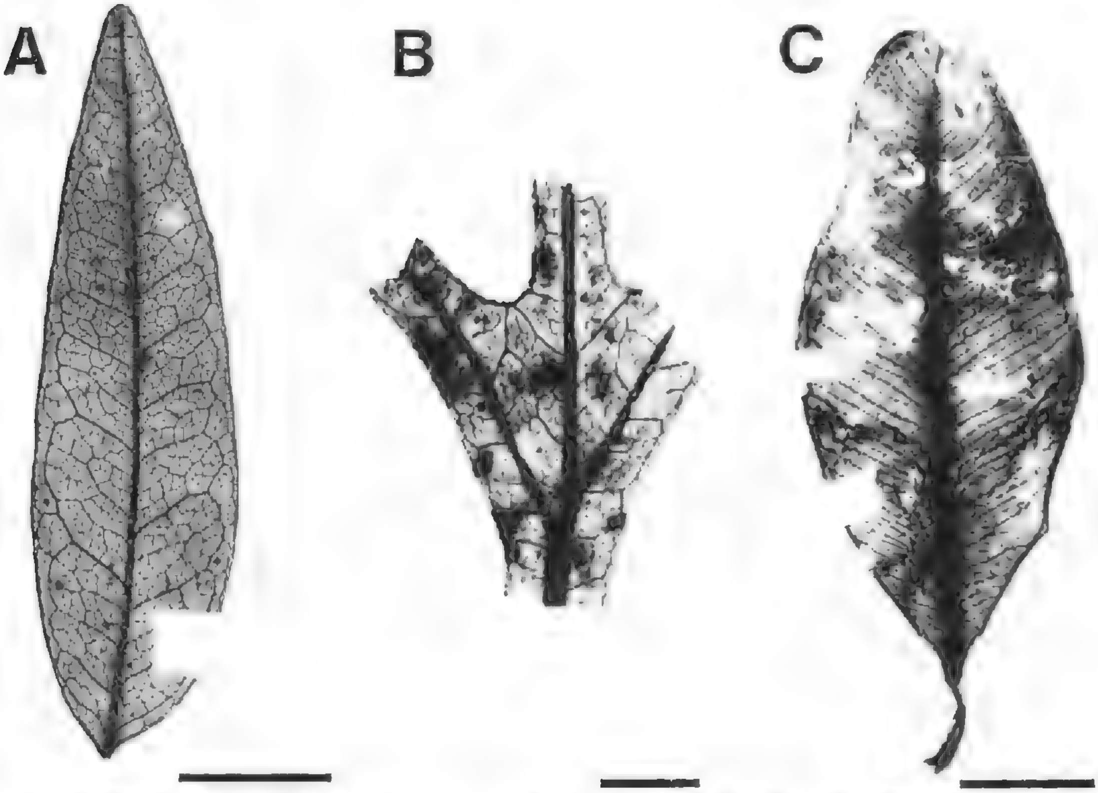


Fig. 2. Selected leaves from Nelly Creek deposit. A = specimen NC1000 and is an example of Parataxon 1 (affinities unknown); B = specimen NC1012 and is an example of Parataxon 2 (Proteaceae); C = NC1017 and is an example of Parataxon 3 (Myrtaceae) — it is the holotype of *Myrtaciphyllum eremaeensis*; Scale bars = 1 cm.

have been mounted in phenol glycerin jelly and are housed permanently in the Palaeobotany Collection, Botany Department, Adelaide University.

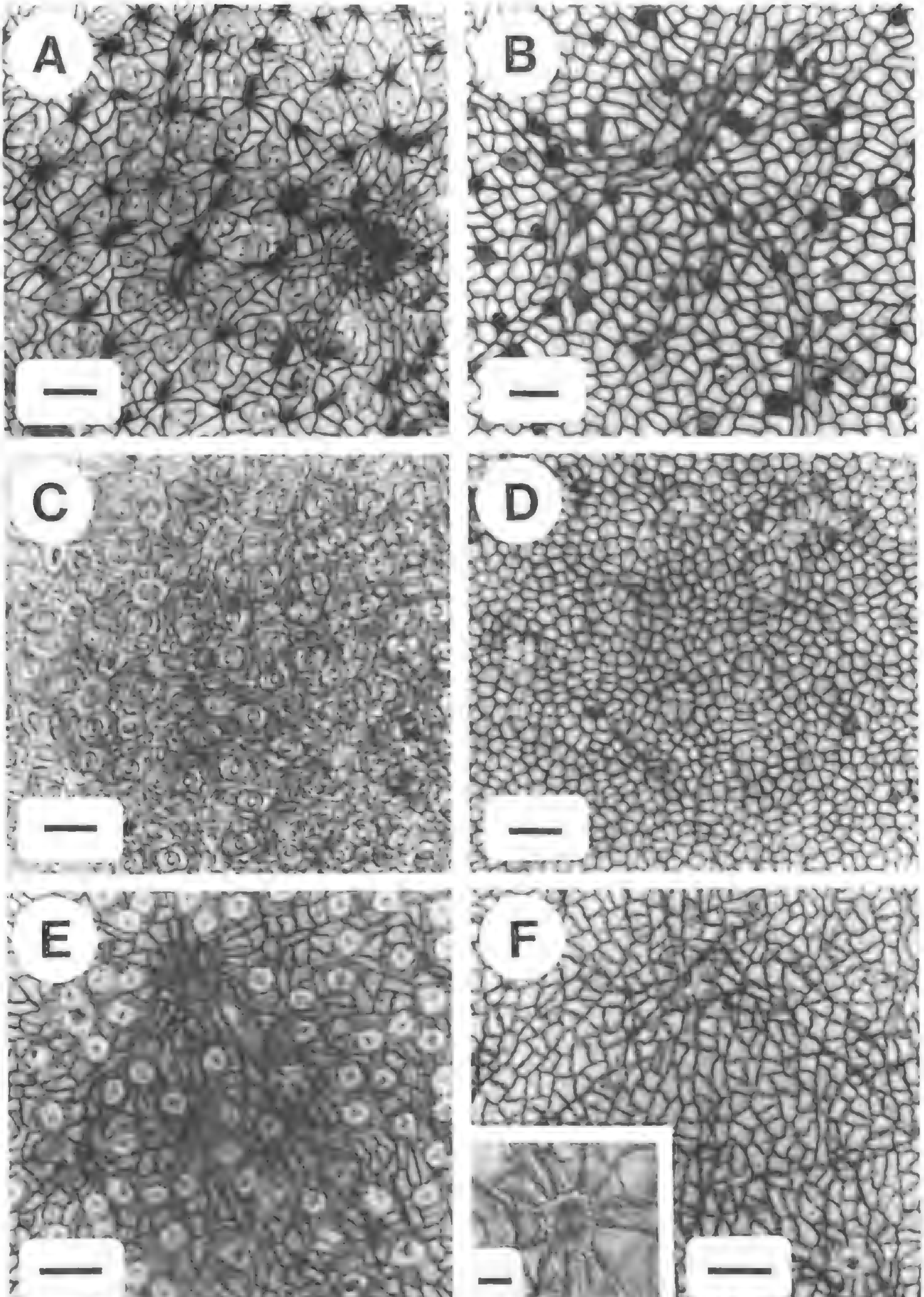
The Middle Eocene age is based on the well preserved pollen flora contained within the sediments (Alley 1989[2]). As he reported, the Nelly Creek palynoflora correlates with the Lower *Nothofagidites asperus* Zone of Stover & Partridge (1973) and with the *Proteacidites pachypolus* Zone of Harris (1971), and the Nelly Creek flora is correlative with the floras at Maslin Bay and Golden Grove.

Floristics of the locality

Collections made by N. F. Alley in 1986 and by the first and third authors and others in 1988 have been macerated to yield a collection of 220 broadleafed specimens (each representing 50% or more of a leaf) and numerous small specimens including *Gymnostoma* (Casuarinaceae) twigs, Podocarpaceae twigs, and various unidentified fruits and seeds. Broken leaves and detrital sievings from the macerations have also been kept for dispersed cuticle analysis.

TABLE 1. *Leaf megafossil composition of the first blocks macerated from the Nelly Creek clay lens.*

Parataxon Number	Number of Specimens (% of the Flora)		Affinities
1	172	(64)	UNKNOWN
2	16	(6)	PROTEACEAE
3	15	(5.5)	*MYRTACIPHYLLUM*
4	3	(1)	*AGATHIS*
5	1	(0.5)	LAURACEAE
6	1	(0.5)	*BRACHYCHITON*
7	2	(1)	PROTEACEAE
8	3	(1)	MONOCOT
9	3	(1)	PROTEACEAE
10	1	(0.5)	UNKNOWN
11	1	(0.5)	UNKNOWN
12	1	(0.5)	PROTEACEAE
13	1	(0.5)	UNKNOWN
14	25	(9)	PODOCARPACEAE
15	14	(5.5)	*GYMNOSTOMA* SP A
16	10	(3)	*GYMNOSTOMA* SP B
TOTAL	269	(100)	


A
B
C
D
E
F

The 220 specimens recovered could be divided into 13 parataxa based on both macromorphological features and cuticular structures (Table 1). The analysis of the material clearly showed a dominance of the sample by one parataxon (Parataxon 1, Fig. 2A, 3A–B). The leaves of Parataxon 1 are generally microphylls with a few being classed as notophylls (*sensu* Webb 1959). All are entire margined and most display apices with a general ovate to elliptical shape. Following the descriptive terminology of Hickey (1979), primary venation of Parataxon 1 is pinnate with brochidodromous secondary venation and reticulate tertiary veins. Generally, five orders of vein branching are present.

The cuticle of Parataxon 1 is hypostomatic with numerous stomates displaying either two or three subsidiary cells. Both abaxial and adaxial surfaces are densely covered with simple, collared trichomes (Fig. 3A–B). This collared appearance could represent torn tissue from glandular apices on the trichomes, but the general excellent preservation of the cuticles and the large number of specimens sampled does not support that hypothesis.

It has not been possible to determine the affinities of this dominant parataxon. Several large Australian rainforest families can be easily recognised by their cuticular structure. Such identifying features have been discussed for the Lauraceae (Hill 1986), Proteaceae (Lange 1970) and Myrtaceae (Christophel & Lys 1986). Therefore, it is possible to eliminate these families in the identification process. However, several other large families, including the Fabaceae, Euphorbiaceae, Sapindaceae and Oleaceae all have taxa with leaves approximating the venation pattern and general macromorphology of the Nelly Creek dominant. It is also possible that the fossil could represent a family or lower level taxon which is now extinct, and thus no reasonable match could be forthcoming.

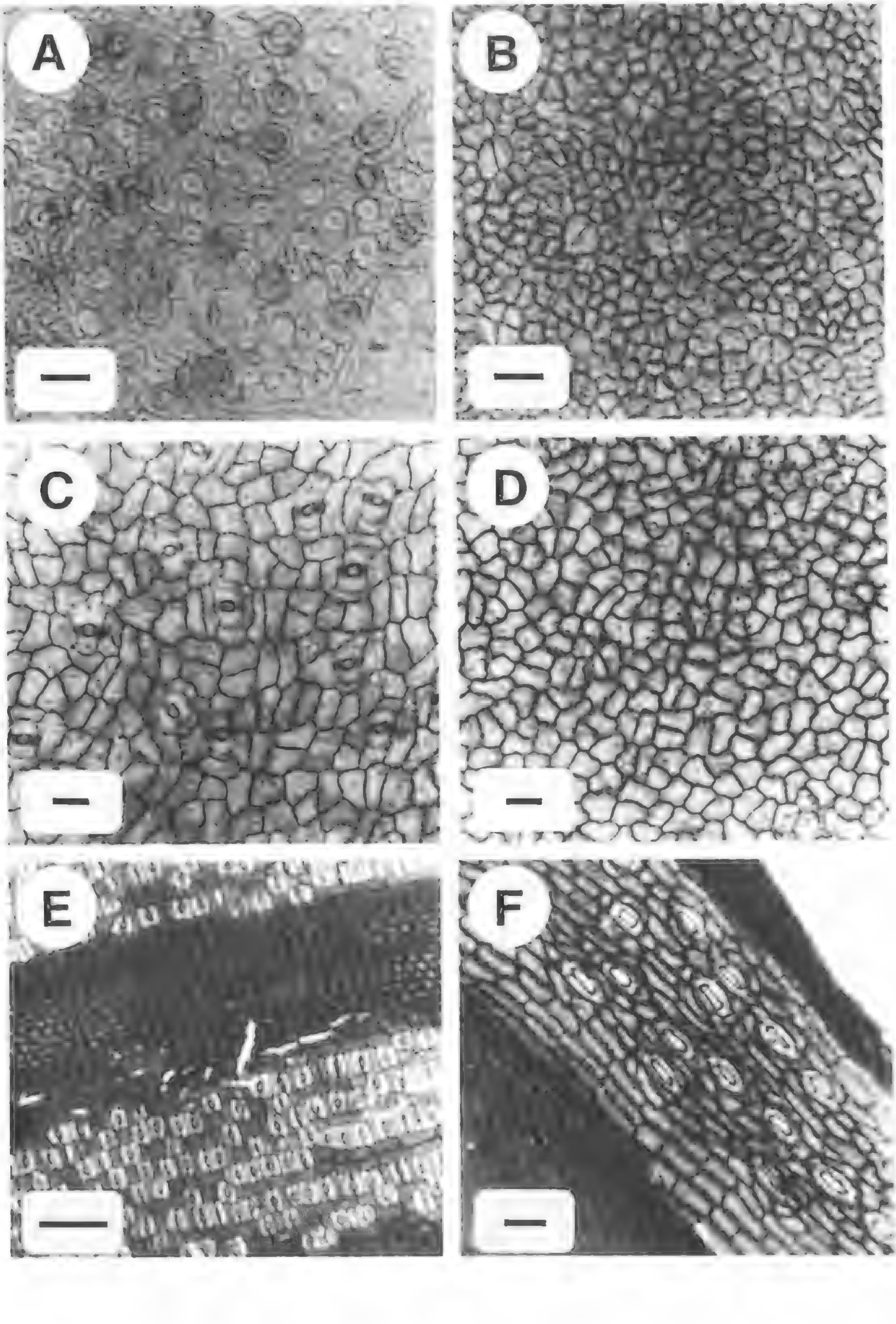
There are twelve other broadleafed parataxa. Parataxon 2 is a lobed, serrate leaf which, while quite large, is very brittle and has not been recovered as a complete leaf (Fig. 2B). It usually occurs as a pinnately lobed specimen with three apparent lobes. These lobes are toothed near their apex. Secondary venation is brochidodromous near the base of each lobe and semicraspedodromous near the apex when teeth are present. Cuticles prepared from these leaves show that the leaf is hypostomatic with numerous stomates on the abaxial surface possessing a paracytic subsidiary cell arrangement (Fig. 3C). This, coupled with the numerous four-celled trichome bases observed on both surfaces of the leaf (Fig. 3C, D), places the parataxon in the Proteaceae. While more detailed comparisons will be required for final identification, preliminary examination indicates a similarity in structure to several species of *Grevillea*.

The vein pattern of Parataxon 3 showing numerous, close spaced, high angle secondary veins forming a distinct intermarginal vein suggests that the parataxon belongs in the Myrtaceae (Fig. 1C). Examination of the cuticle confirms this with the presence of diagnostic lid or capping cells on both surfaces (Fig. 2E, F). This leaf type is one of the most variable in size and shape. However, Christophel & Lys (1986) demonstrated that such interspecific variation is common within the family. They also demonstrated that no obvious foliar character or suite of characters defined genera within the family, and that the capsular fruited taxa and berry fruited taxa often numerically clustered together (were morphologically similar). It is interesting to note that while the Nelly Creek Myrtaceae bear some general similarity to genera of both capsular (e.g. *Lophostemon*) and berry fruited (e.g. *Syzygium*) groups in the family, there is no close similarity to *Eucalyptus*. The Nelly Creek *Myrtaciphyllum* is formally described in the following section. Capsular fruits with likely Myrtaceae affinities have been recovered from a Nelly Creek macerate (Fig. 5C), and will be described when more material becomes available.

The remaining 10 parataxa are all relatively rare in those samples processed to date. All but four are represented by only one specimen. Some of these remaining parataxa are distinctive, and assignable to families, and in some cases genera, so are worth discussing in the overall floristic context of the paper. The first of these broadleafed taxa is assignable to *Agathis* (Araucariaceae) based on general form and cuticular structure (e.g. Hill & Bigwood 1987; Stockey & Ko 1986).

A comparison of all the leaves examined (220 broadleafed and 49 microphyllous) can be seen in Table 1. Parataxon 5 (one specimen) can be placed in the Lauraceae based on the size and nature of the stomatal ledges and also the subsidiary cells (Fig. 4C, D) (Hill 1986). Parataxon 6 (one specimen) can be assigned to *Brachychiton* (Sterculiaceae) based on the hair bases and stomatal arrangement. Because the specimen is fragmentary (one lobe) very little can be said as to its specific affinities. Interestingly, three of the other parataxa (two non-entire and one entire margin) can be placed in the Proteaceae. A final parataxon (Parataxon 8) is represented by three specimens and is clearly a monocotyledon based on the parallel venation and the stomatal type.

Fig. 3. Cuticles of leaves illustrated in Fig. 2. A = abaxial cuticle of NC1000 (Parataxon 1); B = adaxial cuticle of NC1000; C = abaxial cuticle of NC1012 (Parataxon 2); D = adaxial cuticle of NC1012; E = abaxial cuticle of NC1017 (Holotype of *Myrtaciphyllum creekensis*); F = adaxial cuticle of NC1017. Insert for F is an enlarged view of a lid cell. Scale bars = 5 μm except the insert where bar = 2.5 μm.


A
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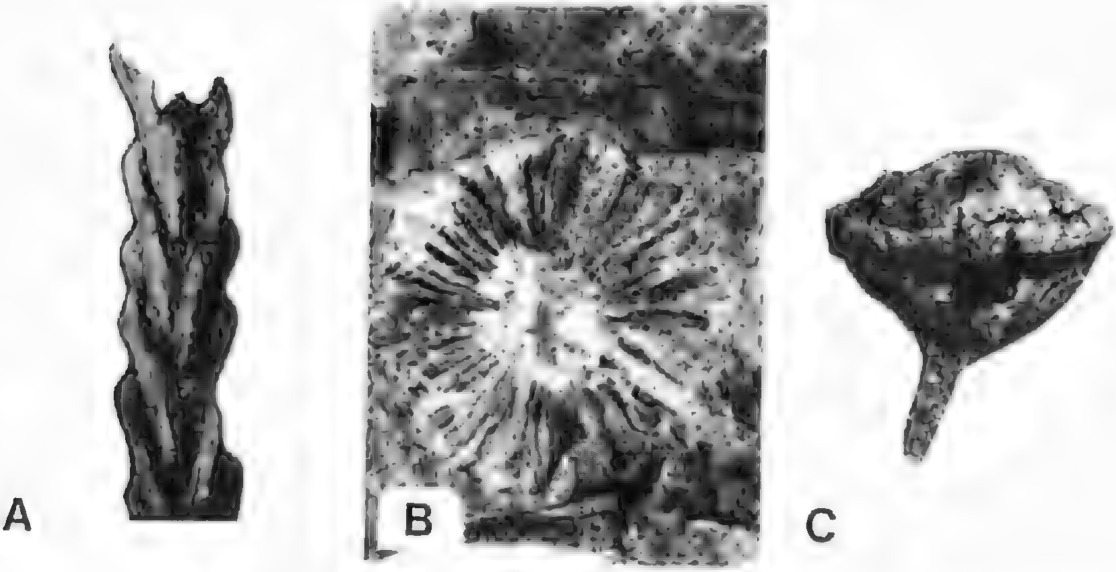

Fig. 5. Miscellaneous structures from the Nelly Creek and Poole Creek deposits; A = NC1501 — twig of Parataxon 14 (Podocarpaceae) from Nelly Creek X8; B = possible Proteaceae infructescence from Poole Creek Silcrete deposit X2; C = NC1500 — leptospermoid fruit (Myrtaceae) from Nelly Creek X10.

In addition to the 13 broadleafed parataxa, three microphyllous parataxa were collected. These include one conifer and two distinct species of *Gymnostoma* (Casuarinaceae). Based on macromorphological features, the conifer could be either Cupressaceae or Podocarpaceae (Fig. 5A). However, the cuticle clearly shows that this parataxon belongs to the Podocarpaceae (Fig. 4F).

Approximately 20 twigs were recovered which were assignable to *Gymnostoma*. It has been shown that cuticle features are distinctive in extant species of this genus (Dilcher *et al.* 1990; Scriven & Christophel 1990), and examination of the Nelly Creek specimens revealed that two species were present. A cuticle of one of the two Nelly Creek types is shown in Fig. 4E. No fertile material has been recovered thus far.

Although the taxonomic study of the flora is preliminary, 12 of the 16 parataxa recognised can be assigned to some formal taxonomic level. This means that at least a very generalized comparison may be made with other floras and with modern vegetation types.

Taxonomic Description

Order: Myrtales
Family: Myrtaceae
Genus: *Myrtaciphyllum* Christophel & Lys, 1986

Myrtaciphyllum eremeaensis sp. nov.
FIGS 2C, 3E–F

Diagnosis

Architectural features: leaf shape elliptic, ovate or obovate. Size range: 3.5–13 cm long by 1.5–4 cm maximum width. Leaf tip acute or attenuate, rarely acuminate. Leaf base acute, rarely obtuse. Primary venation pinnate, secondary veins straight, brochidodromous with a prominent intermarginal vein.

Cuticular features: leaves hypostomatic, stomatal complex anomocytic, with between three and six subsidiary cells (three or four most common). Anticlinal epidermal cell walls angular – straight to slightly curved. Cells of both upper and lower epidermis equal sized; no striations visible on periclinal walls. Simple hairs infrequent (less than three per mm^2) on both surfaces. Hydathodes rare on lower

Fig. 4. Miscellaneous cuticles from Nelly Creek parataxa. A = abaxial cuticle of NC1003 (Parataxon 7 — Proteaceae). B = adaxial cuticle of NC1003; C = abaxial cuticle of NC1011 (Parataxon 5 – Lauraceae); D = adaxial cuticle of NC1011; E = cuticle of NC1301 (*Gymnostoma* sp A – Parataxon 15); F = cuticle of NC1302 (Podocarpaceae — Parataxon 14). Scale bars = 5 μm.

(abaxial) epidermal surface, apparently absent on adaxial (upper) surface. Lid cells numerous on both surfaces with S-shaped to straight sinus showing no beaded thickening or perforations (Fig. 3F-inset). Epidermal cells surrounding lid cells frequently modified into a somewhat radial pattern — particularly on upper epidermis.

Holotype: Specimen NC 1017, housed in the Palaeobotany Collection, Botany Department, Adelaide University, as one mummified leaf and one cuticle slide (NC-C 1017)

Type Locality: Nelly Creek, S.A. (29°19'S, 137°18'E.)

Collector: D. C. Christophel

Etymology: from Eremean, referring to the large, central Australian arid vegetation province used by L. A. S. Johnson and B. Briggs as a distributional region for Australian Myrtaceae and Proteaceae (e.g. Johnson & Briggs 1981). The type locality occurs within this region

Description of Holotype: Collected in 1988. Leaf 51 mm long by 22 mm wide at position of maximum width. Elliptic, symmetrical with attenuate apex (apex angle 35°) and acute base (57°). Secondary veins are straight, average angle 37°.

Cuticle typical for the species. Stomates located on abaxial surface with three to six subsidiary cells. Average length of stomates 20 μm (mean L/W = 1.0). Anticlinal epidermal cell walls angular — straight to slightly curved with no thickening or beading. Cells of both abaxial and adaxial cuticles equal size (mean 20×20 μm — range 15–30 μm). No striations visible on periclinal walls. Simple hairs rare on both surfaces. Large multicellular hair bases present, and no hydathodes visible on sample prepared from holotype.

Lid cells numerous on both surfaces with S-shaped to straight sinuses, showing no beaded thickening or perforations. Epidermal cells surrounding lid cells frequently modified into radial pattern. Lid cell size $= 20 \times 20$ μm. Density of lid cells 12 per 100×100 μm section.

Comparison with other species: The first two species described for the genus could not be distinguished by leaf architectural features, and cuticular characters were used (Christophel & Lys 1986). The same situation applies to *Myrtaciphyllum eremeaensis*, as the specimens included overlap both previously described species in macromorphological and venation features. In cuticular features, however, *M. eremeaensis* is distinct from *M. undulatum* from the Eocene of Anglesea in that it lacks the sinuous anticlinal walls of the epidermal cells exhibited by the latter species. *M. eremensis* differs from *M. douglasii* from Anglesea in having numerous lid cells on both surfaces as compared to a complete lack of lid-cells in the latter species.

Physiognomic Interpretation

Christophel & Greenwood (1989), in discussing litter deposition in Australian rainforests, demonstrated that there was a predictable physiognomic signature for the forest types categorized by Webb (1959). Of the 220 broadleafed specimens recovered from Nelly Creek samples, it is possible to measure (or estimate) the length and maximum width for approximately 160. Results showed that there were no mesophylls present, while approximately 20% of the leaves (40% of taxa) were notophylls and 80% of the leaves (60% of the taxa) were microphylls. The discrepancy between species and total leaves reflects the high frequency of one microphyll parataxon and the attendant rarity of most other parataxa. This single parataxon domination was reflected to a lesser degree in the margin type percentage, with 88% of leaves (75% taxa) entire-margined. If Nelly Creek leaf length, maximum width and position of maximum width are superimposed on the box diagram of physiognomic signatures from Christophel & Greenwood (1988, Fig. 3) it becomes apparent that the Nelly Creek flora does not resemble Golden Grove or Anglesea, having much smaller leaves than either of them. Even remembering the caveat concerning interpretation of small sample numbers, there are several interesting subjective observations that can be coupled with the above physiognomic data. Unlike the other Middle Eocene deposits mentioned earlier, there is no evidence of drip tips in the Nelly Creek flora. Additionally, very few germlings (*sensu* Lange 1976) are present on leaf cuticles, and in general the leaves from Nelly Creek can be considered more sclerophyllous. This includes such features as generally thicker cuticles, denser trichomes, and smaller, more coriaceous or woody leaves. These features would tend to suggest a drier (or certainly more seasonally dry) climate than the other reported Eocene megafossil deposits, or alternatively a much more depauperate soil nutrient level (Beadle 1963).

Comparison with other Eocene Floras

The first impression of the Nelly Creek flora with its total of 16 parataxa is one of clear dominance and low diversity. However, some of this can be most likely attributed to the small sample size and limited portion of the clay lens sampled. For the better known Australian Eocene floras, the diversity is higher. For example, the most thoroughly studied clay lens at Anglesea has over 40 parataxa (Christophel *et al.* 1987), Golden Grove has over 30 parataxa (Barrett & Christophel 1990) and Maslin Bay is estimated at approximately 200 parataxa (Christophel & Blackburn 1976) or perhaps as low as 150 (L. J. Scriven unpubl. data).

TABLE 2. *Leaf litter composition of two one metre square quadrats at Noah Creek.*

Species Present	Quadrat One Leaf Numbers # (%)	Quadrat Two Leaf Numbers # (%)
Ceratopetalum macropetalum	68 (33.5)	58 (29)
Acacia aulacocarpa	29 (14)	23 (11)
Buckinghamia ferruginiflora	21 (10)	30 (15)
Lindsayomyrtus brachyandrus	18 (9)	22 (11)
Medicosma sessiliflora	12 (6)	10 (5)
Choriceras majus	12 (6)	14 (7)
Beilschmiedia oligandra	8 (4)	5 (2.5)
cf. *Diospyros hebecarpa*	8 (4)	7 (3.5)
Dissiliaria laxinervis	6 (3)	7 (3.5)
Euodia hortensis	5 (2)	8 (4)
Xanthostemon chrysanthus	3 (1.5)	0
Franciscodendron laurifolium	3 (1.5)	4 (2)
Orites sp. nov.	2 (1)	1 (0.5)
Syzygium kuranda	2 (1)	1 (0.5)
Sarcopteryx aff. *martyana*	2 (1)	3 (1.5)
Calophyllum australianum	1 (0.5)	0
Syzygium erythrocalyx	1 (0.5)	0
Unknown A	2 (1)	0
Unknown B	1 (0.5)	0
Unknown C	0	4 (2)
Unknown D	0	2 (1)
Unknown E	0	1 (0.5)
Unknown F	0	1 (0.5)
TOTAL TAXA	19	18
TOTAL LEAVES	204 (100)	202 (100)

It is possible to test the relationship between sample size and diversity in both fossil deposits and extant rainforests where the diversity is known. When four random samples of 250 leaves each were taken from the Anglesea lens mentioned above, the mean diversity was 18 ±3 (D. Christophel unpubl. data). Similarly, recent collections from an extant *Gymnostoma* community on a half hectare island in Noah Creek in the Daintree region of north Queensland showed that, although 75 different tree species occurred on the island, two litter samples (containing 200–300 leaves) had a diversity of less than 20 species per sample (Table 2). Therefore, the 16 preliminary parataxa recovered at Nelly Creek could easily represent less than half of the expected total diversity for the fossil flora, and an even smaller fraction of the diversity of the forest from which it was derived.

A more accurate estimation of the diversity of a flora may be had from a study of its dispersed cuticle (Rowett & Christophel 1990). Samples of clay from Nelly Creek had an average diversity of 26 cuticle parataxa, while similar sized samples from Golden Grove yielded 25–32 parataxa (A. Rowett pers. comm.). Rowett reported that the samples were dominated by fragments of Myrtaceae leaves – probably all belonging to *Myrtaciphyllum eremaensis*.

At higher taxonomic levels, the flora has many elements common to other Middle Eocene floras. Golden Grove, Anglesea and Nelly Creek contain abundant (greater than 10%) Myrtaceae leaves. Similarly, Anglesea has approximately the same percentage of the flora made up of Proteaceae species as does Nelly Creek. *Gymnostoma* is found at Nelly Creek, Anglesea, Nerriga and Maslin Bay. *Brachychiton* is known from all of the Eocene localities except Nerriga, and *Agathis* is found at Maslin Bay and Nelly Creek. One interesting floristic difference, however, is in the representation of the Lauraceae. At Maslin Bay, Nerriga, Anglesea and Golden Grove this family is both plentiful and diverse, while at Nelly Creek only one leaf has been recovered. Similarly, the Elaeocarpaceae (aff. *Sloanea/Elaeocarpus*), which is well represented at Anglesea, Golden Grove and Maslin Bay, has not been recovered at Nelly Creek.

At the specific level, the differences are more pronounced. The entire margined microphyll (Parataxon 1) at Nelly Creek is not known from any other locality. Parataxon 2 (lobed Proteaceae) is also absent from all other floras. The two Nelly Creek *Gymnostoma* species are taxonomically distinct from the common species at Anglesea. The Podocarpaceae parataxon at Nelly Creek is different to any reported from the other localities. Comparisons of the *Brachychiton* and *Agathis* species have yet to be made. The Nelly Creek *Myrtaciphyllum* species is definitely different from either species at Anglesea.

While a brief comparison of the foliar physiognomy was made in the preceding section, the generalization can be made that the floristic elements at Anglesea, Golden Grove and Maslin Bay all show more tropical and/or high moisture regime features. These three Middle Eocene deposits all have leaves with drip tips, prolific, high rank germlings, and noticeable quantities of leaves in Webb's (1959) mesophyll size class, in direct contrast to Nelly Creek. Although certain Gondwanic families are shared between Nelly Creek and the other Middle Eocene deposits (e.g. Myrtaceae, Proteaceae, Casuarinaceae, Podocarpaceae), the specific floristic composition and the physiognomic signature is different for Nelly Creek.

Comparison with Silcrete Floras

Early studies of the silcrete deposits of northern South Australia concentrated on the description and evolutionary importance of some of the plants (Chapman 1937; Lange 1978, 1982; Ambrose *et al.* 1979). More recent studies have attempted to address the important aspects of the stratigraphy of the deposits and of their comparative floristics (Greenwood *et al.* 1990). A major problem with these silcrete floras has been the lack of stratigraphic continuity with data strata, and thus the age has been difficult to determine. This has been highlighted by Ambrose *et al.* (1979), where a possible Miocene age is suggested early in the paper and later in the same paper an Eocene age is supported. In their recent studies, Greenwood *et al.* (1990) found that there were two distinct macrofossil floras in the Poole Creek silcrete locality, and based on their taxonomic composition and on the stratigraphy of near-by sedimentary units they determined that one flora was restricted to the upper Eyre Formation (Middle Eocene) and the other to the Etadunna Formation (Oligo-Miocene) sediments. Comparison between the Eyre Formation silcrete flora (Eocene) and the Nelly Creek fossils of palynologically determined Middle Eocene age therefore becomes important.

Preliminary comparisons do not result in the definite conclusion that the Eyre Formation silcretes and the Nelly Creek flora represent the same vegetation. However, some common taxa are present and the comparison most certainly needs to be made more rigourously when additional Nelly Creek material is available. In support of the correlation, *Gymnostoma* is common in the silcrete and at Nelly Creek. However, it commonly occurs as female infructescences in the former and only as vegetative remains in the latter. Until reproductive material is recovered from Nelly Creek, conspecificity cannot be determined. Similarly, a lobed Proteaceae leaf very similar to Nelly Creek Parataxon 2 commonly occurs in the silcretes. Two other parataxa from Nelly Creek, a narrow linear, entire-margined Proteaceae leaf and *Brachychiton* also occur in the silcrete. Again, further studies are required to determine conspecificity — particularly as the Nelly Creek *Brachychiton* is only a single lobe, and hence even a rudimentary character, like the number of lobes present, cannot be compared.

Within the silcretes there also commonly occurs a flattened, woody reproductive structure (Fig. 5B). Based on silcrete impressions alone, the structure has not been identifiable, and has not been recorded from any other published fossil plant locality known to the authors. However, one specimen of this structure has now been recovered from a Nelly Creek macerate. Although the specimen has fragmented, it can be seen that each of the woody wedges consists of two flattened, appressed woody bracts. More detailed study is still required, but it would appear that the structure has some similarity to a Proteaceae cone — e.g. like the flattened infructescence of *Isopogon* or *Dryandra*. In the original paper describing silcrete material, Chapman (1937) figured a specimen and labelled it as a "*Banksia* flowering tip." That specimen, however, does not resemble those discussed here.

Some credence is given to the interpretation of the woody reproductive structures as Banksiae Tribe (Proteaceae) infructescences by the fact that the silcrete floras contain serrate foliage identified by Greenwood *et al.* (1990) as *Banksiaeformis* Hill & Christophel, which could have affinities with *Dryandra*. Unfortunately, no such *Banksiaeformis* leaves have been recovered at Nelly Creek.

Other evidence does not support the correlation. In addition to the common *Banksiaeformis* leaves in the silcretes, other toothed leaves with possible affinities to either the Cunoniaceae or Elaeocarpaceae are reported from there (Greenwood *et al.* 1990) and are missing from Nelly Creek. Of particular interest, the narrow, sometimes falcate Myrtaceae leaves which bear similarity to *Eucalyptus*, while common in the silcretes, are also absent from Nelly Creek. Finally, the dominant, brochidodromous Parataxon 1 from Nelly Creek has not been reported in the silcrete deposits (Greenwood *et al.* 1990).

Physiognomically, the silcretes contain larger leaves than Nelly Creek has thus far yielded, and also a higher percentage of non-entire margined leaves. It is reported (N. F. Alley pers. comm.) that blocks of clay with large leaves peeling off them were unearthed on an early expedition to the locality. Unfortunately these blocks did not survive transport to Adelaide, and our more recent material has not contained such leaves. However, this serves to illustrate the potentially mosaic distribution of taxa within the clay, and also highlights the need for additional collections. It is certainly the case, however, that some of the sclerophyllous nature of the Nelly Creek leaves is mirrored in the portion of the Poole Creek silcrete flora considered by Greenwood *et al.* (1990) to be Middle Eocene.

Discussion

The potential of the Nelly Creek flora to add to our broader knowledge of Middle Eocene Australia floras has been mentioned in the introduction. Examination of that flora more closely has emphasized this importance. Firstly, the preliminary taxonomic assessment has shown that the flora has a very different composition to that of the other well known Australian Middle Eocene macrofossil floras. While some of the major Gondwanic families, including the Proteaceae, Myrtaceae, Casuarinaceae, Podocarpaceae and Araucariaceae are present in all floras of that age, the generic and specific composition of the floras is different. Physiognomically, the Nelly Creek flora is different from the Golden Grove, Anglesea, Maslin Bay and Nerriga floras, being decidedly smaller leafed and lacking the numerous rainforest indicators (driptips etc.) shown by those floras. The inland position of the locality is perhaps responsible for the difference in floristics and physiognomy seen at Nelly Creek, and our overview of Middle Eocene Australia must be tempered accordingly.

The potential importance of the Nelly Creek locality to our understanding of South Australia's silcrete floras must also be emphasized. While the evidence for positive correlation is poor, the presence of certain indicator taxa, such as the disk-shaped woody reproductive structure and the narrow lobed Proteaceae leaf in both deposits and in no others, must certainly be taken as encouragement for further collections and comparisons.

Greenwood *et al.* (1990) suggested that the assumed Eocene elements of the silcrete floras might well represent deciduous seasonal vegetation types mixed with a wetter riparian element such as those associated with monsoonal vine thickets in Queensland today. Such an interpretation for the Nelly Creek locality is consistent with both the known elements of the flora and also the physiognomic interpretation, and a more thorough search of modern forest types of this description will be made in the hope of identifying further elements in the Nelly Creek flora particularly the dominant parataxon.

Acknowledgments

We wish to thank Dr N. F. Alley, S. A. Department of Mines and Energy and Dr A. I. Rowett, Botany Department, Adelaide University, for their assistance in the original collection of material for this study and for critically reading the manuscript. The project was funded by ARC Grant A38931389 to D. C. Christophel.

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THE RESPONSE OF SOIL NEMATODES TO ENVIRONMENT STIMULII IN ARID SOUTH AUSTRALIA

BY JACQUELINE MARY NOBBS

Summary

Transactions of the Royal Society of S. Aust. (1992), 116(2), 77-78.

BRIEF COMMUNICATION

THE RESPONSE OF SOIL NEMATODES TO ENVIRONMENTAL STIMULII IN ARID SOUTH AUSTRALIA

Nematodes are known to form an anhydrobiotic coiled state in response to desiccation in soil[1]. From investigation of nematodes occurring in arid areas (Mojave Desert, Nevada, U.S.A.[2]) the anhydrobiotic state was also found to be represented by "coiling". The activity of nematodes can then be related to form, with "coiled" nematodes being inactive or anhydrobiotic and "straight" nematodes being active. A preliminary study was set up to investigate if "coiling" was a good indicator of nematode activity within arid soils. Also under investigation was the overall effect of environmental stimulii on the different nematode trophic groups.

A site located on Plumbago Station pastoral property (near Yunta, South Australia) was selected for sampling. The vegetation consisted of a low Chenopod shrubland dominated by *Atriplex vesicaria*. Soil samples (n=10) were taken every two months from August 1985 (M2) to October 1986 (M16) to a depth of 25 cm. Nematodes were extracted from 50 ml of soil per sample.

The modified Baermann's funnel technique[3] was used to extract the different nematode trophic groups. After extraction (over a three day period), the nematodes were heat killed and fixed in 2% formalin (40% formaldehyde). The different trophic groups were then counted. The trophic groups consisted of:- omnivores (mainly dorylaims), bacterial feeders (mainly rhabditids), fungal feeders (mainly aphelenchs and tylenchs) and plant parasites (mainly *Tylenchorhynchus tobari* Sauer & Annells, 1981 and *Telotylenchus hastulatus* (Colbran, 1960) Siddiqi, 1963). The extraction efficiency was found to be about 65% and the counts were adjusted accordingly.

Anhydrobiotic ("coiled") and active ("straight") nematodes were extracted using the Hot Formalin method[4]. The method involved killing the nematodes in the soil with hot formalin (90°C), then separating the nematodes from the soil using a solution containing Separan NP - 10[R] (Dow Chemical Ltd) (0.75g/l tap water). The nematodes were then separated into "coiled" and "straight" forms and counted. The extraction efficiency of the Hot Formalin method was found to be about 75% and the counts were adjusted accordingly. Due to loss of material it was not possible to extract nematodes from the August 1985 (M2) and February 1986 (M8) samples using the Hot Formalin method. The Hot Formalin method tended to extract more nematodes than the modified Baermann funnel technique possibly because the Hot Formalin method extracted directly from soil while the modified Baermann's funnel method relied on movement of nematodes into a collecting dish.

As with other arid regions[5], bacterial feeders were the most abundant trophic group found in the samples throughout the sampling period (Fig. 1). The other trophic groups occurred in much lower numbers. From August 1985 (M2) to April 1986 (M10) the total mean number of nematodes extracted was relatively constant, averaging around 200–300. Over the same period the mean number of "coiled" nematodes was much greater than "straight" nematodes (Fig. 2), fluctuating between 300 (M4) and 600 (M6) with the mean number of "straight" nematodes remaining fairly constant throughout.

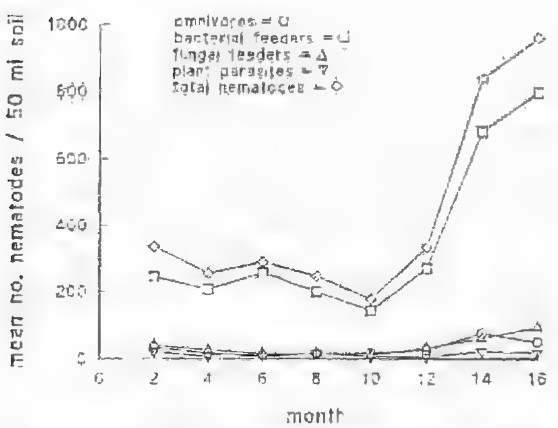

Fig. 1. Mean numbers of omnivores (o), bacterial feeders (□), fungal feeders (Δ), plant parasites (∇) and total nematodes (◇) extracted from 50 ml of soil (n=10) using the modified Baermann's funnel technique from samples collected every two months from August 1985 (2) to October 1986 (16).

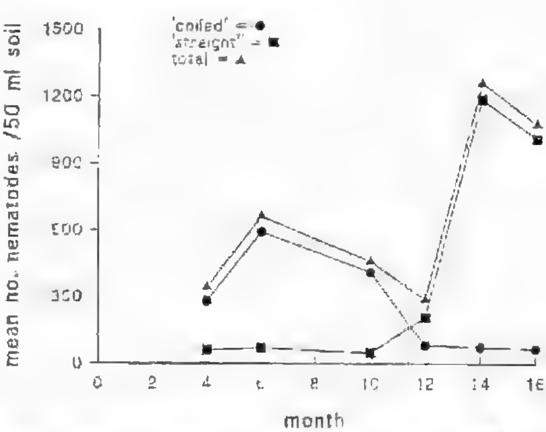

Fig. 2. Mean numbers of "coiled" (●); "straight" (■) and total nematodes (▲) extracted from 50 ml of soil (n=10) using the Hot Formalin method from samples collected every two months from October 1985 (4) to October 1986 (16) excluding February 1986 (8).

However, from June 1986 (M12) to October 1986 (M16) there was an increase in the mean number of all trophic groups (except plant parasites), with the bacterial feeders showing the greatest increase. During the same period there was also a large increase in the mean number of "straight" nematodes with a sharp decrease in numbers of "coiled" nematodes (M12) which remained fairly constant afterwards. The change in form of the nematodes was, therefore, closely correlated with the increase in numbers of nematodes, particularly the bacterial feeders. The change in form and increase in numbers of nematodes could reflect increased activity of the micro-flora within the soil ecosystem.

Rainfall may have been the trigger for the increased activity of the nematodes. The region under study usually has the highest rainfall and lowest temperatures during the months April to October and the driest and hottest months from November to March. Fig. 3 shows the rainfall recorded over the sample period at the homestead of Plumbago Station (about 10 km from the sample site). Over the first 10 months of sampling there were large fluctuations in rainfall while the final six months had a more even distribution. The final month had the highest rainfall of the sampling period. The more sustained period of rainfall over the last six months of sampling was matched with increased numbers of nematodes and increased numbers of "straight" or active nematodes.

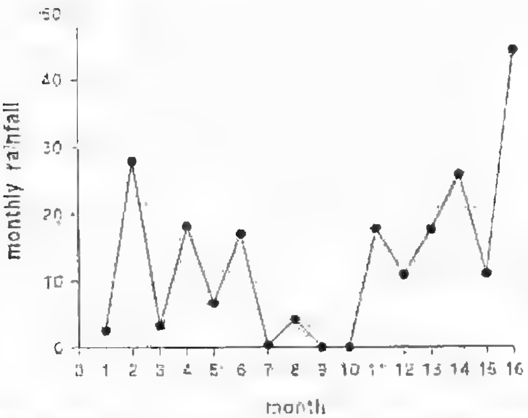

Fig. 3. Monthly rainfall (mm) recorded at Plumbago Station homestead from July 1985 (1) to October 1986 (16).

In other arid areas the activity of the nematodes was found to be exhibited as a "pulse" phenomenon[6], with an environmental "trigger" (i.e. rainfall) causing rapid increase in numbers followed by a rapid decrease when the soil dries out. The bacterial feeders were particularly well adapted to a cycle of dehydration and rehydration. The rapid response of the food source (bacteria) to appropriate environmental stimuli and the short life cycle of the nematodes (in some cases only 6-7 days) allows bacterial feeders to increase in numbers when conditions are favourable. In this study, the environmental "trigger" was found to be rainfall.

Nutrient turnover in soils of other arid regions were found to be influenced by nematodes as consumers of bacteria and yeast (during the first stages of decomposition) and fungi (as decomposition advanced)[7-9]. Further studies on the role of nematodes in nutrient turnover may be helpful when looking at the ecology of arid region soils and may be useful in assessing the impact of overgrazing and mining on soil ecology. Nematodes could be used to monitor levels of microbial activity within the soil as activity of nematodes can be measured through extraction of "coiled" and "straight" forms, which could reflect activity of the food source.

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JACQUELINE MARY NOBBS, CABI Institute of Parasitology, St. Albans, Herts, U.K., AL4 0XU.

CYSTICERI OF *TAENIA HYDATIGENA* (CESTODA: TAENIIDAE) IN AN ENTELLUS LANGUR (*PRESBYTIS ENTELLUS*)

BY MICHAEL O'CALLAGHAN

Summary

Transactions of the Royal Society of S. Aust. (1992), 116(2), 79

BRIEF COMMUNICATION

CYSTICERCI OF *TAENIA HYDATIGENA* (CESTODA: TAENIIDAE) IN AN ENTELLUS LANGUR *(PRESBYTIS ENTELLUS)*

In May 1982 an adult female Entellus langur monkey *(Presbytis entellus)* died at the Adelaide Zoological Gardens following rupture of the uterus in the terminal stages of pregnancy. During autopsy three large cysts 1.7–3.1 cm in diameter were found attached to the greater omentum. Each cyst contained a single cestode cysticercus with a large bladder 1.6 cm in diameter (Fig. 1).

The rostella were dissected from each scolex and mounted *en face* in DeFaure's medium for examination of the rostellar hooks. Each rostellum was armed with 14 large hooks 183–189 μm (mean 188 μm) in length and fourteen small hooks 129–144 μm (mean 132 μm) in length, morphologically resembling those of *Taenia hydatigena*[1] (Figs 2, 3). In addition the size of the hooks conformed to measurements of adult specimens of the same species from dogs in Australia[2] and it was concluded that the cysticerci recovered from the monkey are metacestodes of *Taenia hydatigena*. The scoleces have been deposited in the Australian Helminthological Collection, South Australian Museum (AHC.S 42153).

The metacestode of *T. hydatigena* has an exceptionally wide host range, principally in artiodactyls but occasionally also in perissodactyls, rodents, lagomorphs, marsupials and primates[3,4]. Abuldase (1964) listed species of *Cercopithicus*, *Macacus*, *Papio* and man as hosts of *T. hydatigena*, however his and subsequent reports of this parasite in primates[5,6] do not record *Presbytis* as a host. Cysts from *Macacus cynomolgus* in Vietnam recently described as *T. saigoni* appear to be similar to *T. hydatigena*[7]. Recently, coenuri morphologically similar to *T. multiceps* or *T. serialis* were reported in *Presbytis obscura* raised in captivity in a number of zoos in the U.S.A.[8]

The more familiar langurs belonging to the genus *Presbytis* are from India and Southeast Asia. *P. entellus* (the Hanuman, Sacred or Entellus langur) the largest of the langurs, is native to India, Sri Lanka and Nepal and is known to live close to towns and villages. The langur examined at the Adelaide Zoo was imported from Sri Lanka ten years prior to its death and may have acquired the infection either here or overseas. There was no pathological reaction associated with the presence of the parasite. This finding constitutes a new host record for *T. hydatigena*.

Figs 1-3. 1. Cyst of *Taenia hydatigena* from the greater omentum of *Presbytis entellus*; 2 & 3. rostellar hooks (Bar scale = 0.10 mm).

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MICHAEL O'CALLAGHAN, Central Veterinary Laboratories, Department of Agriculture, GPO Box 1671, Adelaide, S. Aust. 5001 and IAN BEVERIDGE, The University of Melbourne, Veterinary Clinical Centre, Princes Highway, Werribee, Vic. 3030.

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Contents

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VOL. 116, PART 3

WETLANDS OF THE RIVER MURRAY FLOOD PLAIN, SOUTH AUSTRALIA.
1. PRELIMINARY SURVEY OF THE BIOTA AND PHYSICO-CHEMISTRY OF TEN WETLANDS FROM CHOWILLA TO MANNUM.

BY *P. M. GOONAN, J. A. BEER, T. B. THOMPSON & P. J. SUTER**

Summary

Qualitative data were collected on the water chemistry and aquatic invertebrate fauna from ten wetlands between Chowilla and Mannum on the River Murray flood plain in South Australia. Sites were separated into two main groups that corresponded to freshwater wetlands connected to the River Murray, and wetlands with TDS concentrations >1000 mgL^{-1} that were isolated from the main channel. Wetlands with TDS concentrations <l000 mgL^{-1} were generally low in nutrients, and characterized by the dipteran *Cladotanytarsus* sp. and the shrimp *Paratya australiensis.* The more saline wetlands were high in nutrients and characterized by the presence of dipterans such as *Proclaims* sp., Ephydridae and Culicidae.
Phosphate and nitrogen concentrations from most sites exceeded critical levels for eutrophication. Nutrient enrichment was indicated by the high chlorophyll concentrations recorded from most wetlands. These results indicate that nutrient levels entering the flood plain need to be reduced to minimize the risk of nuisance algal blooms during low flow conditions.
KEY WORDS: Wetlands, River Murray, biota, aquatic invertebrates, physico-chemistry. nutrients, salinity, multivariate analysis, South Australia

Transactions of the Royal Society of S. Aust. (1992), 116(3), 81-94.

WETLANDS OF THE RIVER MURRAY FLOOD PLAIN, SOUTH AUSTRALIA. 1. PRELIMINARY SURVEY OF THE BIOTA AND PHYSICO-CHEMISTRY OF TEN WETLANDS FROM CHOWILLA TO MANNUM.

by P. M. GOONAN, J. A. BEER, T. B. THOMPSON & P. J. SUTER*

Summary

GOONAN, P. M., BEER, J. A., THOMPSON, T. B. & SUTER, P. J. (1992) Wetlands of the River Murray flood plain, South Australia. 1. Preliminary survey of the biota and physico-chemistry of ten wetlands from Chowilla to Mannum. *Trans. R. Soc. S. Aust.* 116(3), 81-94, 30 November, 1992.

Qualitative data were collected on the water chemistry and aquatic invertebrate fauna from ten wetlands between Chowilla and Mannum on the River Murray flood plain in South Australia. Sites were separated into two main groups that corresponded to freshwater wetlands connected to the River Murray, and wetlands with TDS concentrations >1000 mgL^{-1} that were isolated from the main channel. Wetlands with TDS concentrations <1000 mgL^{-1} were generally low in nutrients, and characterized by the dipteran *Cladotanytarsus* sp. and the shrimp *Paratya australiensis*. The more saline wetlands were high in nutrients and characterized by the presence of dipterans such as *Procladius* sp., Ephydridae and Culicidae.

Phosphate and nitrogen concentrations from most sites exceeded critical levels for eutrophication. Nutrient enrichment was indicated by the high chlorophyll concentrations recorded from most wetlands. These results indicate that nutrient levels entering the flood plain need to be reduced to minimize the risk of nuisance algal blooms during low flow conditions.

KEY WORDS: Wetlands, River Murray, biota, aquatic invertebrates, physico-chemistry, nutrients, salinity, multivariate analysis, South Australia

Introduction

Over 1600 wetlands are distributed throughout the River Murray flood plain, lower lakes and Coorong in South Australia (Pressey 1986). Whereas many of these were included in a recent survey of River Murray wetlands (Thompson 1986), little has been published on their biota and physico-chemistry. Thompson (1986) provides some information on the water quality and dominant flora and fauna of the 248 wetlands included in his study. Geddes (1984a & b, 1988) gives a detailed account of the limnology of Lake Alexandrina over several years, whereas O'Malley & Sheldon (1990) describe the results of a survey of the biological communities of the Chowilla flood plain. Birds have been described from some areas (Tubbs 1928; Schodde & Glover 1955; Mack 1961; Cox 1973; Simpson 1973a) and Simpson (1973b) discussed the distribution of the mammals, reptiles and amphibians between Mildura and Renmark. Lloyd & Walker (1986) reported the distribution and conservation status of the small freshwater fish throughout the lower River Murray flood plain.

This paper presents the results of a preliminary survey conducted during May-June 1990 on the aquatic invertebrate assemblages and physico-chemistry of 10 wetlands distributed from Chowilla to Mannum. The aims of the survey were to describe and compare the limnology of flood plain wetlands with different hydrology and geomorphology, including anabranches, swamps and lakes. The emphasis of the work was to study the biota and water chemistry of regulated wetlands, focussing on evaporation basins. This survey is part of a larger study which aims to (1) generate a comprehensive baseline and comparative database on the aquatic biota and physico-chemistry of selected wetlands throughout the River Murray flood plain in South Australia, and (2) investigate the effects of various changes in the hydrological management of regulated wetlands.

Materials and Methods

Selection of study sites

The location of study sites was based on those previously investigated by Thomspon (1986) and Lloyd *et al.* (1984)[1] to enable some comparison with the available data from previous surveys. Additional sites were sampled from some wetlands to examine between-site variation.

Pilby Creek was the only wetland included in this survey not previously studied by the above workers. Sites were located on either side of a causeway which restricted water flow, enabling comparison between two sites in close proximity with different hydrology.

Wetlands surveyed

The wetlands sampled in this study were distributed from the Chowilla flood plain to north of Mannum.

* Australian Centre for Water Quality Research, Private Mail Bag, Salisbury, S. Aust. 5108

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TABLE 1. *Location and physical characteristics of the 10 wetlands surveyed along the River Murray flood plain in South Australia during May-June 1990.*

Site No(s)[a]	Wetland	Acronym	Location		Area (ha)	Hydrology and Geomorphology
1,2	Pilby Creek	PILC	33°59′S	140°53′E	5	Permanent flood plain anabranch
3	Clover Lake	CLOL	34°00′S	140°46′E	140	Intermittent flood plain swamp
4	Lake Merreti	LMER	34°01′S	140°45′E	390	Permanent regulated flood plain lake
6, 7	Disher Ck Evap. Basin	DISC	34°14′S	140°42′E	260	Permanent regulated flood plain anabranch
8-10	Katarapko Evap. Basin	KATS, KATN	34°26′S	140°34′E	42,36	Complex of permanent regulated flood plain lakes
11	Berri Evap. Basin	BERB	34°18′S	140°34′E	325	Permanent regulated flood plain swamp
12-15	Ramco Lagoon	RAML	34°10′S	139°55′E	91	Permanent regulated flood plain lake
20, 21	Devon Downs North	DEVD	34°38′S	139°36′E	120	Permanent flood plain lake
19	Wongulla Lagoon	WONL	34°43′S	139°33′E	120	Permanent flood plain swamp
16-18	Lake Carlet	LCAR	34°52′S	139°31′E	330	Permanent flood plain swamp

[a]Site 5 from Lake Woolpolool (34°02′S, 140°43′E) was omitted as samples were not preserved.

Details of the location, area, hydrology and geomorphology are given in Table 1.

The location of sampling sites is shown in Fig. 1. Specific site coordinates and descriptions of the dominant vegetation are given in Appendix 1. Each site was designated with an acronym and number.

Collection and analysis of samples

At each site, the sampling area consisted of a 20 m section of shoreline representative of that part of the wetland. Sites were sampled in May-June 1990 during a rise in the River Murray hydrograph, with a flow of about 30000 ML/D recorded at the S. Aust. border (Unpubl. Murray-Darling Basin Commission records).

Field measurements made at each site were pH (ICI 211 portable pH meter), conductivity (ICI 303 ATC conductivity meter), water temperature, dissolved oxygen (YSI model 58 dissolved oxygen meter), and Secchi disc transparency. Surface water samples were collected and stored in air free, airtight bottles on ice before laboratory analyses for nutrients (nitrogen, phosphorus and carbon fractions), pesticides, and major ions (Ca^{2+}, Mg^{2+}, Na^{+}, K^{+}, CO_3^{2-}, HCO_3^{-}, SO_4^{2-} and Cl^{-}).

Analyses of NH_3, oxidised nitrogen (NO_3-N), dissolved reactive phosphorus (DRP), SO_4^{2-} and Cl^{-} were made using a Skalar automated flow analyser, while HCO_3^{-}, CO_3^{2-} and alkalinity were determined using titration against a HCL standard solution. Total Kjeldahl nitrogen (TKN) and total phosphorus (TP) analyses were made with a Technicon autoanalyser and spectrophotometer. Cations were analysed using a Labtest model V-25 inductively coupled plasma emission spectrometer fitted with a polychromator. Dissolved and total organic carbon were measured with a flame ionization detector. Pesticides were extracted in hexane and analysed using a Varian 3300 gas chromatograph. All procedures are described in detail in two methods manuals produced by the E. & W.S. Department, South Australia[2,3].

Aquatic invertebrates were sampled from the littoral zone at each site using a 30 s sweep sample with a 200 μm mesh dip net. Samples were preserved in 5% formalin and returned to the laboratory for sorting and identification. Invertebrates were identified to the lowest practical taxonomic level using CSIRO (1970), Smith & Kershaw (1979), Williams (1980a), Matthews (1980, 1982), Smirnov & Timms (1983), Wiederholm (1983), Merritt & Cummins (1984), Hawking (1986), and several unpublished keys prepared by one of us (PS). A voucher collection is maintained for all taxa recorded from the River Murray flood plain in South Australia at the E. & W.S. Dept, State Water Laboratory, Bolivar, S. Aust.

Water samples for analysis of chlorophyll were processed in the field by passing a known volume of water through a 1.2 μm Whatman GF/C filter disk. The GF/C filter was placed in a centrifuge tube containing 95% ethanol, which was then wrapped in alfoil and stored on ice. Samples were centrifuged and then analysed in the laboratory using a Pye SP8-100 ultraviolet spectrophotometer at wavelengths of 750, 665 and 649 nm. Chlorophyll *a* and *b* concentrations

[2]Anon (1989) "Analytical Methods Manual — Inorganic Chemistry." (State Water Laboratory, E. & W.S. Dept, S. Aust. S.W.L. Report No. 30.)
[3]Anon (1990) "Analytical Methods Manual — Organic Chemistry." (State Water Laboratory, E. & W.S. Dept, S. Aust. S.W.L. Report No. 32.)

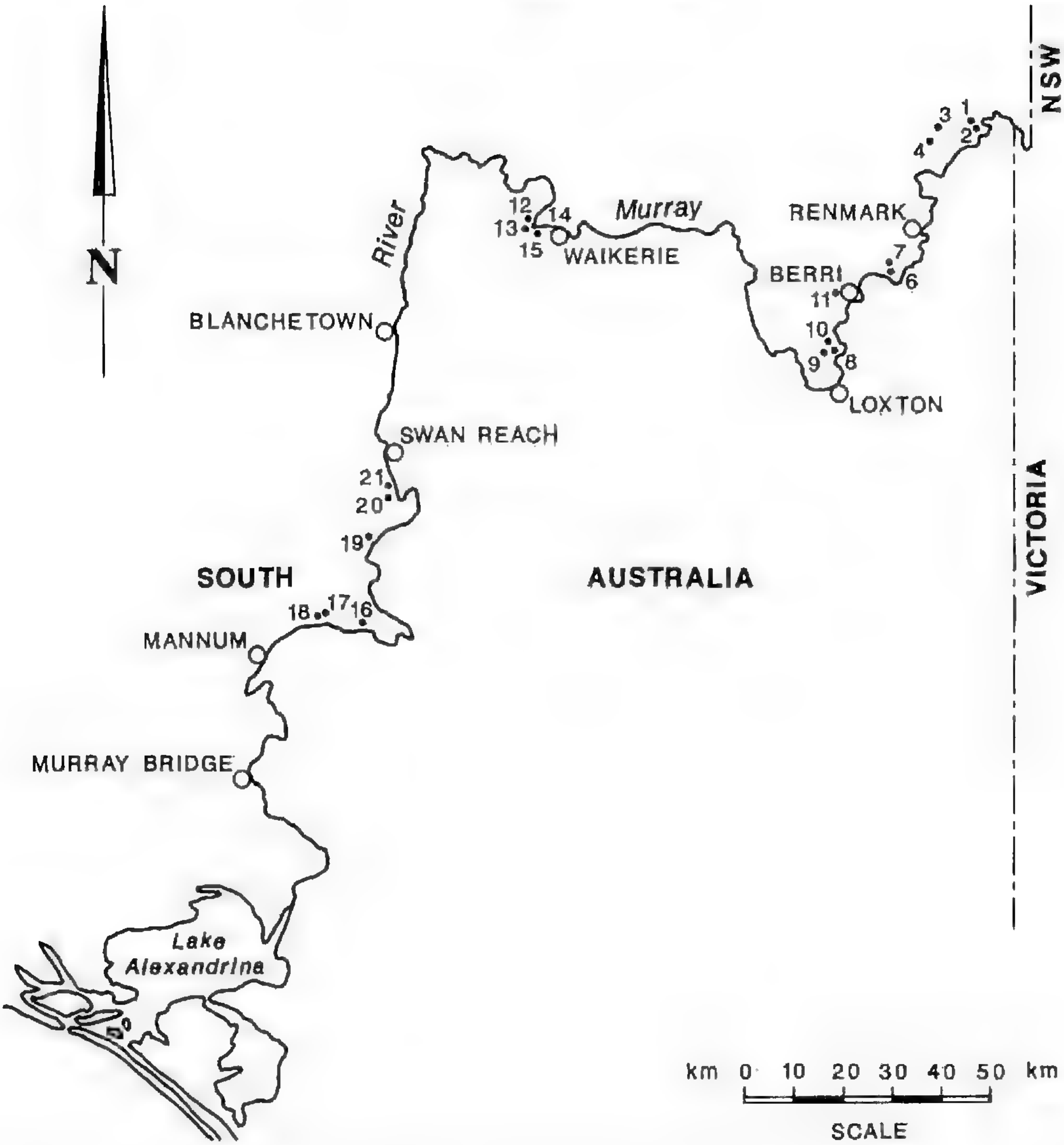

Fig. 1. Map of the River Murray flood plain in South Australia with site locations and numbers.

were calculated using the equations developed by Wintermans & de Mots (1965).

Collections of macrophytes and riparian vegetation were made at each site (see Appendix 1), and representative samples retained as voucher specimens. Identifications were made according to Aston (1973) and Jessop & Toelken (1986).

Data analyses

All biological analyses were based on the presence/absence of the aquatic invertebrates recorded from the 20 sites sampled. The sampling technique used in the survey resulted in the collection of many semi-aquatic and terrestrial species that were associated with vegetation in the littoral zone. These were omitted from the analyses.

Sorensen's index of community similarity (cf. Hellawell 1978) was used to group the sites on the basis of the composition of the fauna at each site. Clustering of sites was summarized in a dendrogram showing the degree of similarity in aquatic invertebrate composition among sites.

TABLE 2. *Physico-chemical features of 18 sites from 10 wetlands surveyed from Chowilla to Mannum in South Australia* (*water depth too shallow to obtain a measurement. – measurement not recorded or analysed. Units in mgL^{-1} unless otherwise indicated)

Site	Water Depth (m)	pH	Conductivity ($\mu S\ cm^{-1}$)	TDS	Dissolved O_2	Secchi Disc (cm)	Water Temp. (°C)	Ammonia	NO_3-N	TKN	DRP	Total P	Total Hardness	Alkalinity	DOC	TOC
PILC 1	0.45	7.3	7870	4400	11.0	35	14.0	0.85	0.01	3.43	0.09	0.44	1181	112	-	
PILC 2	>1.00	7.6	501	280	9.8	40	16.0	0.07	<0.01	1.35	0.04	0.18	109	95		-
CLOL 3	0.08	8.8	4560	2500	9.7	*	15.5	<0.01	<0.01	6.65	0.06	0.91	420	439	63.0	81
LMER 4	0.65	8.0	421	230	9.8	18	15.0	<0.01	0.01	1.10	0.04	0.30	81	71	5.1	9
DISC 6	0.62	7.9	1200	660	9.6	24	15.5	0.05	0.01	0.89	0.04	0.18	-	-	5.2	8
DISC 7	0.80	8.8	4280	2400	9.8	76	14.5	0.01	<0.01	0.95	0.01	0.09	477	71	5.8	8
KATS 8	0.70	9.0	3430	1900	10.2	22	14.5	<0.01	0.02	3.20	0.03	0.22	366	462	16.0	32
KATS 9	0.95	9.1	3430	1900	9.8	20	15.0	<0.01	<0.01	2.90	0.01	0.20	-	-	14.2	36
KATN 10	0.75	9.2	3980	2200	10.0	26	15.0	<0.01	<0.01	2.07	0.02	0.13	372	525	12.1	29
BERB 11	0.05	8.8	39800	25000	7.6	*	17.0	0.16	0.01	9.68	0.05	0.51	1989	379	91.0	108
RAML 12	0.37	7.7	1250	690	9.2	18	17.5	0.09	0.03	1.33	0.02	0.32	-	-	5.4	9
RAML 13	0.30	8.2	12000	6900	8.4	26	18.0	0.09	0.01	3.93	0.02	0.31	978	299	28.0	29
RAML 14	0.38	8.1	12300	7100	9.7	16	17.5	0.04	0.01	4.69	0.04	0.42	-	-	25.0	31
RAML 15	0.30	9.0	11700	6700	9.5	*	12.5	0.43	0.02	4.48	0.08	0.30	1008	296	19.6	24
LCAR 16[a]	1.10	8.1	504	280	10.0	26	13.0	0.01	0.01	0.80	0.02	0.10	95	71	5.9	8
WONL 19	0.45	9.0	1260	700	9.8	28	9.9	0.01	<0.01	1.21	0.01	0.08	183	123	10.6	12
DEVD 20	0.43	7.7	655	360	–	20	13.2	0.07	0.09	1.07	0.02	0.28	125	90	6.3	10
DEVD 21	0.55	8.0	826	450	–	15	13.5	0.01	0.02	1.83	0.01	0.26	145	98	8.8	14

[a]Physico-chemical features not measured at sites 17 and 18 from Lake Carlet.

TABLE 3. *Ionic composition of water samples from 10 wetlands from Chowilla to Mannum in South Australia* (Units in mgL^{-1}).

Site[a]	Ca^{2+}	Mg^{2+}	Na^{-}	K^{+}	CO_3^{2-}	HCO_3^{-}	SO_4^{2-}	Cl^{-}
PILC 1	187	173	1140	11.7	0	137	510	2250
PILC 2	20	14	49	6.0	0	116	20	81
CLOL 3	47	73	792	23.2	36	462	170	1090
LMER 4	15	11	45	4.6	0	86	19	73
DISC 7	61	79	689	12.9	1	85	370	1060
KATS 8	35	68	593	22.9	54	454	200	695
KATN 10	28	74	692	23.6	76	486	290	740
BERB 11	100	423	8760	82.8	1	460	3900	12200
RAML 13	105	174	2130	36.1	0	365	580	3570
RAML 15	110	178	2140	41.5	30	300	630	3480
LCAR 16	16	13	60	4.3	0	87	25	100
WONL 19	26	29	197	7.2	18	114	68	300
DEVD 20	23	16	91	5.7	0	110	32	137
DEVD 21	26	19	116	6.4	0	120	39	180

[a]Analysis of major ions not conducted for DISC6, KATS9, RAML12, RAML14, LCAR17 and LCAR18.

The difference in aquatic invertebrate species composition within and among wetlands was analysed by multivariate procedures. Relationships among sites were examined by the ordination procedure of detrended correspondence analysis (Hill & Gauch 1980; Gauch 1982), using the program DECORANA (Hill 1979a). Salinity measurements were superimposed onto the DECORANA plots to reveal relationships between community composition and salinity (cf. Williams *et al.* 1990). The hierarchical classification procedure of two-way indicator species analysis (Gauch & Whittaker 1981; Gauch 1982), using the program TWINSPAN (Hill 1979b), was carried out to group similar sites together in clusters. Indicator species refer to the preferential taxa used by TWINSPAN to distinguish the clusters. The TWINSPAN program was run using the default options.

The data generated by Thompson (1986) and Lloyd *et al.* (1984)[1] were not included in statistical comparisons with the results from the present survey due to differences in the methods and objectives of each study. Only general trends in the data from these earlier studies are discussed.

Results

Water chemistry

The physico-chemical data are given in Tables 2 and 3. As the preliminary survey consisted of only one sample per site, no data are available concerning fluctuations of the various physico-chemical parameters with season and changes in water level. Consequently, only major trends in the data will be highlighted at this stage.

Ionic concentration

Williams (1967) classified any water with a concentration of total dissolved solids (TDS) greater than 3000 mgL^{-1} as "saline". Based on this definition, Berri Evap. Basin, Ramco Lagoon and Pilby Ck (PILC1) were saline when sampled. Other wetlands to approach this level included Clover Lake, Disher Ck Evap. Basin (DISC7), and Katarapko Evap. Basin. Converting ionic concentrations into ionic equivalents, waters from these wetlands were dominated by sodium and chloride, and had ionic stoichiometries similar to that of seawater (i.e. $Na^+ > Mg^{2+} > Ca^{2+} > K^+$; $Cl^- > SO_4^{2-} > HCO_3^-$). The only deviations in ionic trends among this group of wetlands were Katarapko Evap. Basin and Clover Lake, which had anionic stoichiometries similar to the more freshwater group.

The remaining wetlands had TDS concentrations of less than 1000 mgL^{-1}. Sodium and chloride were also the dominant ions, although they represented smaller fractions of the total cations and anions respectively. Cationic stoichiometry was the same as the more saline wetlands, but the anionic stoichiometry differed in that bicarbonate dominated sulphate ion (i.e. $Cl^- > HCO_3^- > SO_4^{2-} > CO_3^{2-}$).

Ionic composition

An inverse relationship was evident between sodium ion and calcium/magnesium ions, with sodium becoming more dominant with increasing TDS. Potassium ions represented very low fractions of the total cations from all wetlands. The proportion of chloride to total anions increased with increasing TDS, while the proportion of bicarbonate decreased. Sulphate contributed 10-24% of the total anions, with the higher proportions generally being recorded from the more saline wetlands. Carbonate ions were detected from the more alkaline wetlands (pH 8.8-9.4), reflecting the effect of pH on the dissolved CO_2 equilibrium.

Nutrients

Ammonia was present in higher concentrations than NO_3-N at most sites, although at some the concentrations of both forms of dissolved nitrogen were negligible (i.e. <0.01 mgL^{-1}). The highest NH_3 levels were recorded from three of the more saline sites (PILC1, RAML15, BERB11). The highest NO_3-N concentration was recorded at DEVD20, which also had a high NH_3 concentration compared with the other freshwater sites. TKN values were generally higher at the more saline sites, although low concentrations were recorded from Disher Ck Evap. Basin.

DRP levels were relatively low at all wetland sites, but were highest at the more saline sites of PILC1, RAML15, CLOL3 and BERB11. Total phosphorus concentrations showed a similar trend as DRP and TKN levels, with the more saline wetlands generally having higher concentrations of phosphorus than the freshwater wetlands.

Nitrogen was mostly present as organic forms at all wetland sites. It is difficult to comment on phosphorus, however, as only the dissolved fraction of the total reactive phosphorus was measured during this study. Despite this, the DRP results indicate that inorganic phosphorus was a significant contributor to total phosphorus for RAML15, DISC6, and PILC2.

The sites DEVD21, KATS, KATN, DISC7, LCAR and WONL were depleted of both nitrogen and phosphorus in dissolved inorganic forms. The latter three sites also had the lowest TKN and TP concentrations recorded during the survey.

Organic carbon

Concentrations of total organic carbon (TOC) and dissolved organic carbon (DOC) were highest at the

TABLE 4. *Chlorophyll concentrations recorded from 17 sites from Chowilla to Mannum in South Australia.* (Units in μgL^{-1})

Site[a]	Chlorophyll a	Chlorophyll b	Site No.	Chlorophyll a	Chlorophyll b
PILC 1	114.8	31.4	BERB 11	60.0	22.8
PILC 2	17.2	5.8	RAML 12	32.3	7.0
CLOL 3	42.1	10.6	RAML 13	9.8	5.9
LMER 4	27.7	7.6	RAML 14	99.6	37.1
DISC 6	17.1	4.1	RAML 15	255.8	83.8
DISC 7	37.2	16.9	LCAR 16	1.2	0.2
KATS 8	39.1	9.6	DEVD 20	10.8	2.5
KATS 9	69.3	15.8	DEVD 21	3.5	0.6
KATN 10	44.1	9.4			

[a]Data not available for LCAR17, LCAR18 and WONL 19.

TABLE 5. *Occurrence of aquatic invertebrate taxa from 20 sites surveyed from Chowilla to Mannum during May-June 1990.*

Taxon	Occurrence (Site No.)	Total No. of Occurrences
TURBELLARIA	2	1
GASTROPODA		
Unidentified snail	6	1
Potomopyrgus niger	16,18	2
Ferrissia petterdi	4,16,19	3
Physa acuta	4,9,10,12,15,16,17,18,19,20	10
Isidorella newcombi	16	1
BIVALVIA		
Sphaerium tasmanicum	16	1
OLIGOCHAETA	1,2,4,8,12,13,14.15,16,17,19,21	12
CRUSTACEA		
OSTRACODA	2,3,4,6,9,10,11,12,13,14,15,16,17,19,20,21	16
COPEPODA : HARPACTICOIDA		
Atthevella australica	1	1
COPEPODA : CYCLOPOIDA	3,6,7,8,11,13,14,17,18,19,20	11
COPEPODA : CALANOIDA	2,3,4,6,7,8,9,10,11,16,17,18,19,20,21	15
AMPHIPODA		
Afrochiltonia australis	9,11,12,13,14,15,16,19,21	9
ISOPODA		
Austroargathona picta	6	1
CLADOCERA		
Leydigia australis	3	1
Ilyocryptus sp.	17,18	2
Daphnia lumholtzi	2,16	2
D. carinata	1	1
Daphniopsis pusilla	11	1
Ceriodaphnia sp.	17,19	2
DECOPODA		
Macrobrachium australiense	20	1
Paratya australiensis	2,4,6,8,9,10,13,14,16,17,18,19,20,21	14
ARACHNIDA		
HYDRACARINA	4,6,13,15,16,17,18	7
INSECTA		
EPHEMEROPTERA		
Cloeon fluviatile	19	1
Tasmanocoenis tillyardi	9,16	2
ODONATA		
Ischnura heterosticta	4,9,10,16,19	5
Austrolestes sp.	21	1
Juvenile Zygoptera	2	1
HEMIPTERA		
Anisops sp.	3	1
Anisops thienemanni	4,8,9,10,14,19,20	7

Taxon	Occurrence (Site No.)	Total No. of Occurrences
Micronecta robusta + M. gracilis	3,4,6,7,10,11,12,13,14,15,16,18,19,20,21	15
M. annae	16,19	2
Agraptocorixa eurynome	1,3,10,12,13,14,19,20	8
Hydrometra sp.	16	1
Mesovelia sp.	16	1
COLEOPTERA: HYDRAENIDAE		
Ochthebius sp.	12,20	2
COLEOPTERA: HYDROPHILIDAE		
Hydrophilid larvae	4	1
Berosus sp. larvae	3	1
Hydrochus sp.	16	1
Helochares australis	16	1
COLEOPTERA: DYTISCIDAE		
Sternopriscus sp.	3	1
LEPIDOPTERA: PYRALIDAE		
Pyralid larvae	6,15,16,20	4
TRICHOPTERA: LEPTOCERIDAE		
Triplectides sp.	2,4,9,16,21	5
Juvenile leptocerid	18	1
TRICHOPTERA: ECNOMIDAE		
Ecnomus pansus	16	1
TRICHOPTERA: HYDROPTILIDAE		
Hydroptila acinacis	16	1
DIPTERA: CHIRONOMIDAE: TANYPODINAE		
Procladius sp.	1,3,4,6,7,11,12,13,14,19,20	11
DIPTERA: CHIRONOMIDAE: CHIRONOMINAE		
Chironomus cloacalis	15,17,18	3
C. duplex	12,13	2
Dicrotendipes sp.	3,8,9	3
Chironomus tepperi	1,2,4,11,14,15	6
Cladopelma sp.	3	1
Kiefferulus intertinctus	4,10,11,14,20	5
Polypedilum sp.	1,2,18,19	4
P. nubifer	3,4,13,14	4
Parachironomus sp.	4,6,8,9,10,14,19,21	8
Cryptochironomus sp.	3,20	2
Cladotanytarsus sp.	4,8,9,10,16,17,19,20,21	9
Tanytarsus, sp.4	19	1
T. barbitarsus	1,2,4,11,21	5
DIPTERA: CHIRONOMIDAE: ORTHOCLADIINAE		
Corynoneura sp.	4	1
Cricotopus sp.	1,3,4,8,9,10,16,19,21	9
C. albitibia	3,4,8,9,10,16,19,20,21	9
Limnophyes sp.	2,4,16,20	4
Parametriocnemus sp.	4	1
DIPTERA: CERATOPOGONIDAE		
SR[a] sp.1	3,10,11,12,13,15	6
SR sp.6	11,13,14,16,19	5
SR sp.8	3	1
SR sp.16	14	1
SR sp.18	7,13	2
DIPTERA: PSYCHODIDAE	11,12,13,14	4
DIPTERA: STRATIOMYIDAE	4,10,11,14,15,20	6
DIPTERA: TABANIDAE	4	1
DIPTERA: SCIOMYZIDAE	8,16,19	3
DIPTERA: EPHYDRIDAE	1,7,11,12,13,15	6
DIPTERA: MUSCIDAE	4,6,7,14	4
DIPTERA: CULICIDAE	3,10,11,13,14,15,20	7
DIPTERA: DOLICHOPODIDAE	1,13	2

[a]SR – refers to voucher specimens in the collection at the State Water Laboratory, Victoria.

more saline wetlands. The fraction of TOC represented by DOC varied from 39-50% at KATS and KATN to 97% at RAML13.

Pesticides

No pesticides were detected in any of the water samples (detection limit of 0.02 μgL^{-1}).

Chlorophyll concentrations

The concentration of chlorophyll was high at most wetland sites (Table 4), indicating that significant phytoplankton production was occurring during the sampling period. Chlorophyll *a* concentrations varied considerably among wetlands, ranging from 1.2 μgL^{-1} at LCAR16 to 255.8 μgL^{-1} at RAML15. Chlorophyll *b* followed a similar trend.

Chlorophyll concentrations also varied markedly within wetlands. The most noted difference occurred at Ramco Lagoon where chlorophyll *a* ranged from 9.8 μgL^{-1} at the more sheltered western site (RAML13) to 255.8 μgL^{-1} at the exposed, downwind site (RAML15). Similar trends occurred at Pilby Ck, Devon Downs Nth, Katarapko Evap. Basin, and Dishers Ck Evap. Basin, where differences in the morphology of the wetland, water flow, and the dominant wind direction may result in large variations in chlorophyll concentrations within wetlands.

Aquatic invertebrate composition

Seventy-eight aquatic invertebrate taxa were recorded from the 20 sites (Table 5). Insect taxa predominated (69%), and the most diverse component of the fauna were dipterans with 32 species, including 19 species of chironomids. Crustacea contributed 18% and Gastropoda 6% of the total taxa recorded.

Ostracod taxa were the most widespread (16 sites), followed by *Micronecta robusta-M. gracilis* (15), calanoids (15), *Paratya australiensis* (14), oligochaetes (12), cyclopoids (11), *Procladius* sp. (11) and *Physa acuta* (10). In contrast, 31 taxa were recorded from only one site.

The taxonomy for many invertebrate groups is incomplete (Williams 1980b; Campbell 1981; Bennison *et al.* 1989), making it difficult to assign some specimens below the generic or family level. Consequently, not all taxa were identified to species, which underestimates the species composition and richness of some sites.

LCAR16 had the highest species richness with 30 taxa and DISC7 the lowest with 7 taxa. Considerable variation occurred within wetlands, particularly Lake Carlet where 11, 11 and 30 taxa were recorded from the three sites sampled. Of the wetlands that were sampled from more than one site, Lake Carlet was the most diverse with a total of 36 taxa, followed by Ramco Lagoon (29), Devon Downs Nth (25), Katarapko Evap. Basin (23), Pilby Ck (18), and Disher Ck Evap. Basin (14).

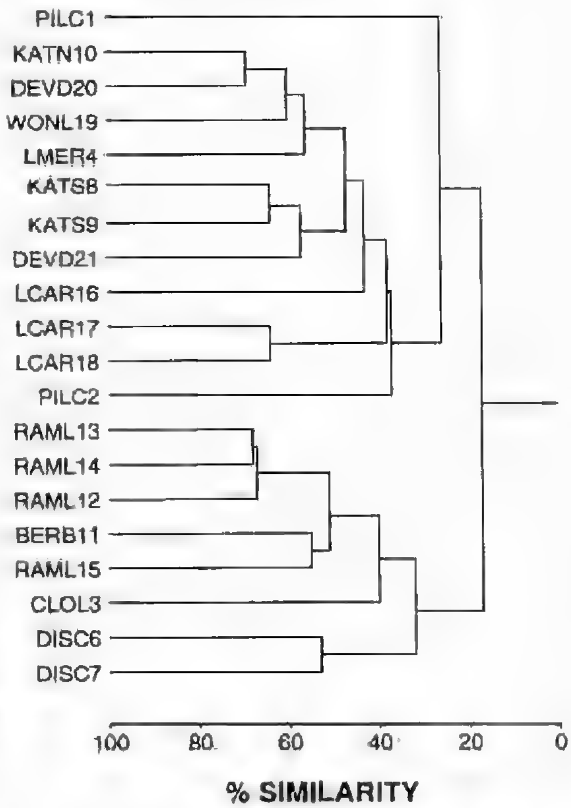

Fig. 2. Dendrogram produced by Sorensen's similarity coefficients of 20 sites based on the aquatic invertebrate data.

Groupings of the sites

Cluster analysis initially separated the sites into two main groups that generally correspond to more saline wetlands with TDS concentrations >1000 mgL^{-1} and less saline wetlands with TDS <1000 mgL^{-1} (Fig. 2). Exceptions included the clustering of the saline anabranch PILC1 and sites from Katarapko Evap. Basin with the freshwater group, and DISC6 and RAML12 with the more saline wetlands.

Within the more saline group, sites from within the same wetland were more similar to each other than sites from different wetlands. In the freshwater group, however, sites from the same wetland did not necessarily cluster together, indicating that some heterogeneity existed within some wetlands (e.g. Devon Downs Nth).

Multivariate analyses

The DECORANA ordinations of the samples are illustrated in Fig. 3, and show the centroids for each

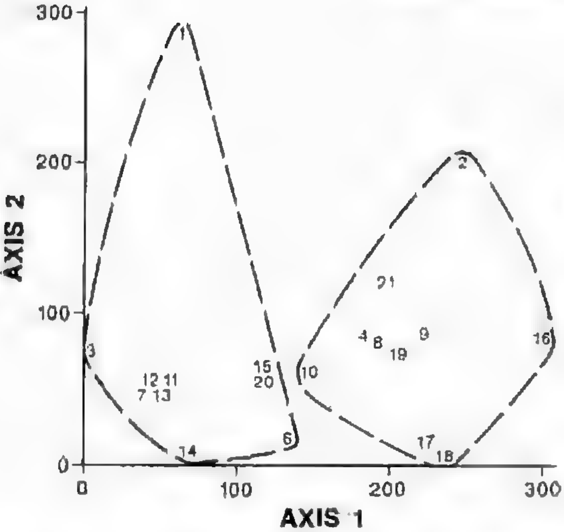

Fig. 3. DECORANA ordination of sites based on the aquatic invertebrate data, with TWINSPAN groups superimposed. (Eigenvalues: Axis 1 = 0.46, Axis 2 = 0.28, Axes in standard deviation units).

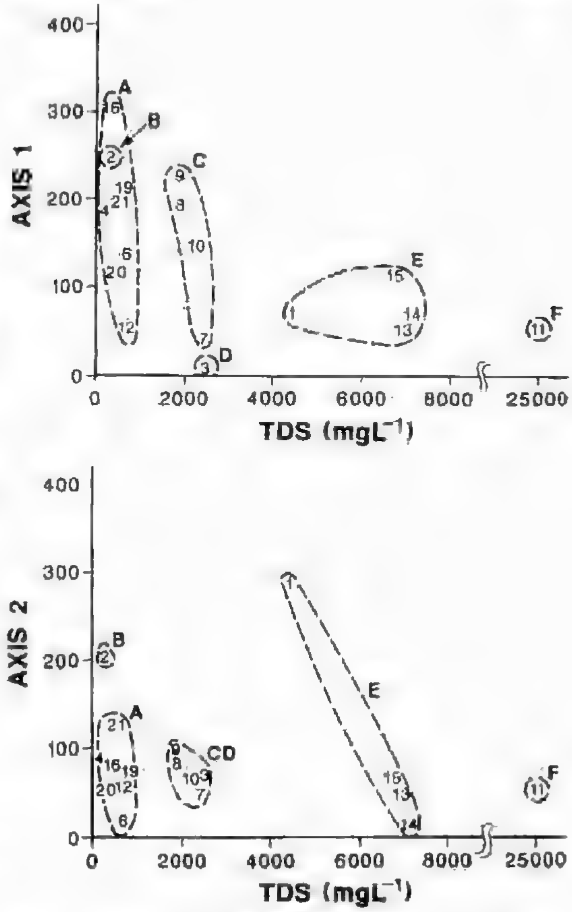

Fig. 4. Scattergram of DECORANA ordination from Fig. 3 showing TDS concentration recorded at each site.
(a) Axis 1 vs TDS (b) Axis 2 vs TDS
The groups enclosed in dotted lines are described in the classification of sites in Table 6. (Ordination axes in standard deviation units, TDS in mgL^{-1}. LCAR 17 and LCAR 18 omitted due to absence of chemical data).

of the 20 sites (i.e. the average score for each axis). Superimposing the TWINSPAN groups onto the ordination plots results in two groups that also correspond to more saline wetlands with TDS concentrations >1000 mgL^{-1} and freshwater wetlands with TDS <1000 mgL^{-1}. This trend was confounded by the inclusion of sites from Katarapko Evap. Basin in the freshwater group, and DISC6, RAML12 and DEVD20 in the more saline group.

The two sites from Pilby Ck were outliers on the ordination analysis and tended to "compress" the other sites on the second ordination axis. Deletion of these sites from subsequent analyses did not alter the orientation or spacing of sites appreciably, so the original results based on all sites are presented herein.

The projection of sites onto the first ordination axis is shown with their TDS concentrations in Fig. 4a. Sites to the left were characterized by having freshwater with TDS <1000 mgL^{-1} and were connected to the River Murray (Table 6). These included the permanent flood plain lakes and swamps, and two sites from regulated wetlands. The freshwater site from Pilby Ck also grouped with the other freshwater wetlands despite being isolated from the main channel when sampled. Sites with TDS concentrations between 1000-2999 mgL^{-1} formed intermediate groups. Katarapko Evap. Basin and Disher Ck Evap. Basin (DISC7) were connected to the River Murray through their regulating structures when surveyed, while Clover Lake was isolated due to its location high on the flood plain. Sites to the right were saline with TDS >3000 mgL^{-1} and were isolated from the River Murray. These included the western reach of Pilby Ck (PILC1) and Ramco Lagoon in one group, and the hyper-saline Berri Evap. Basin in the most extreme group.

The same general pattern resulted when the points from the second ordination axis were plotted against their TDS concentrations (Fig. 4b), although PILC2 split from the other freshwater wetlands, and the two intermediate groups merged together.

Superimposing the nutrient data onto the ordination plots revealed a similar, though less distinct, gradient between wetlands with/without any connection to the River Murray. TP showed increasing concentration with isolation from the River Murray along the first ordination axis, but no interpretable pattern for the second axis. The remaining physico-chemical variables displayed no obvious pattern along either axes.

TABLE 6. *Classification of wetland sites based on their TDS concentration and connection to the River Murray.*

TDS (mgL^{-1})	0 - 999 Fresh Waters	1000 - 2999	3000 - 9999 Saline	10000 > Highly Saline
Connected to River Murray	4,6,12,16,19,20,21 (GROUP A)	7,8,9,10 (GROUP C)	-	-
Isolated from River Murray	2 (GROUP B)	3 (GROUP D)	1,13,14,15 (GROUP E)	11 (GROUP F)

The TWINSPAN classification (Fig. 5) describes a similar pattern to the ordination results and highlights the indicator taxa that are unique to each grouping. The freshwater group was characterized by the dipteran *Cladotanytarsus* sp. and the shrimp *Paratya australiensis*. The more saline group was distinguished by the presence of the dipterans *Procladius* sp., Ephydridae and Culicidae.

Discussion

Water chemistry

Like most inland waterbodies in Australia, all wetlands included in the present study were dominated by sodium and chloride (Williams & Wan 1972). The differences in ionic concentration and dominance between wetlands were largely the result of dilution and concentration. The freshwater group were permanent waterbodies connected to the mainstream, where water level fluctuations are less extreme than in the more saline group of isolated wetlands. The regulated wetlands, ephemeral swamp, and saline reach of the Pilby Ck anabranch had higher salinities due to the effect of evapoconcentration. Seepage of saline groundwater and the inflow of saline irrigation water also added to the high levels of dissolved salts in the evaporation basins and Ramco Lagoon (Unpubl. E. & W.S. Dept. records). Recent and proposed changes in the management of these wetlands by the use of out of the flood plain evaporation basins (e.g. Noora, Stockyard Plains) and groundwater interception schemes, should lead to a reduction in salinity of these wetlands in the long-term. We should note, however, that mean salinity levels would probably need to be reduced to at most 4000 mgL^{-1} before significant changes in the biota of these wetlands would be evident (see Centre for Steam Ecology 1989[4] for references).

Comparison of TP and TKN concentrations recorded in this study (Table 2) with Wetzel's (1975) classification of lake productivity (after Vollenweider 1968), reveal that the 10 wetlands were eutrophic or hyper-eutrophic with respect to TP, and meso-eutrophic or eutrophic with respect to TKN. Levels of DRP and

[4]Centre for Steam Ecology (1989) "Biological Effects of Saline Discharges to Streams and Wetlands." (Chisholm Inst. Tech., Unpubl. Report for Salinity Bureau, Vict.)

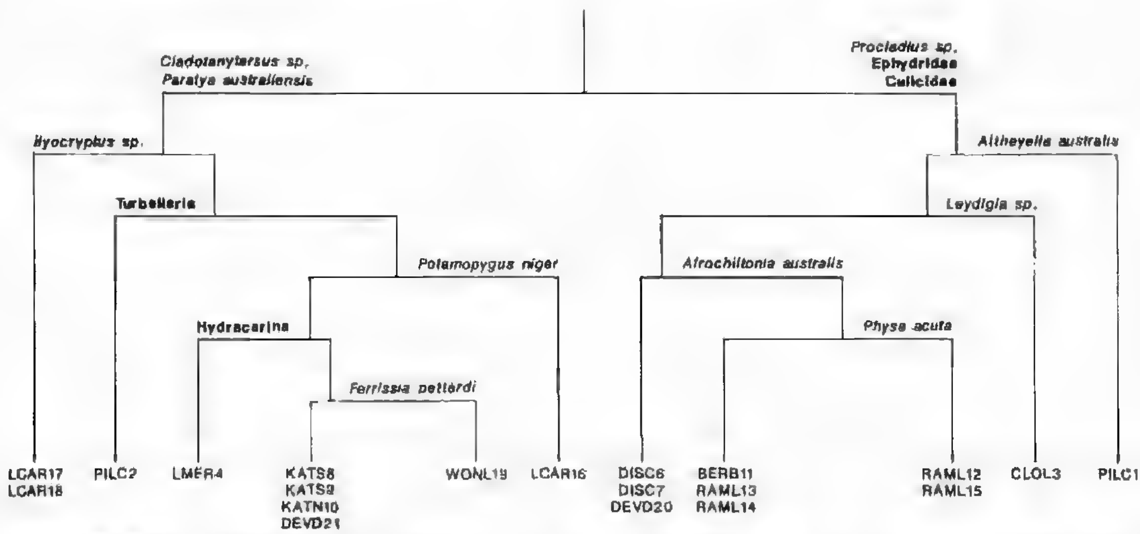

Fig. 5. TWINSPAN classification of sites based on the aquatic invertebrate data. Indicator species names are included with each dichotomy.

NO_3-N, however, were generally low, suggesting that most of the nutrients were in particulate forms that may be unavailable to phytoplankton (Smith 1982; Geddes 1984a).

Nutrient concentrations of the wetlands reflect those in the lower River Murray. Values of TP, DRP, TKN, and NO_3-N were within the ranges reported from Lock 5 to Murray Bridge (MacKay *et al.* 1988) with some exceptions. These included the higher TP concentration from Clover Lake and the higher TKN concentrations from Berri Evap. Basin, Clover Lake, Ramco Lagoon and Katarapko Evap. Basin. These are shallow and/or regulated wetlands subject to considerable evaporation, resulting in high concentrations of nutrients and dissolved salts by evapoconcentration.

Comparison of nutrient levels with other wetlands from the River Murray is difficult as few studies have been published on the chemistry of these waters. Shiel (1980) reported the nutrient concentrations from three billabongs near Wodonga during 1975-77, and found that nitrate varied from 2-685 mg N m^{-3}, and phosphate from 11-624 mg P m^{-3}. Nutrient levels from Lake Alexandrina (Geddes 1984a), Lake Hume and Lake Mulwala (Walker & Hillman 1977; Brymner 1982), Murrumbidgil Swamp and Lake Merrimajeel (Briggs *et al.* 1985) were all within Shiel's ranges. Large fluctuations in nutrient concentrations were recorded from each wetland. In the present study, nitrate and dissolved phosphate concentrations were low compared to Shiel's (1980) values. Low levels of inorganic nitrogen relative to the high TKN concentrations indicate that N was either present in the sediments or had been assimilated by phytoplankton. The high chlorophyll concentrations (Table 4) from most sites support the latter suggestion. Based on Wetzel's (1975) chlorophyll *a* categories, LCAR16, DEVD21, RAML13 and DEVD20 were meso-eutrophic, whereas the other sites were eutrophic. Although meaningful critical concentrations of nutrients have not been defined for Australian waters (Wood 1975; Cullen 1986), the flood plain wetlands included in the present survey were clearly enriched in both N and P. Future work will determine whether the high levels of nutrients and algal biomass are sustained, as this could result in the alteration of phytoplankton communities to favour nuisance species of cyanobacteria (Walker & Hillman 1977).

Aquatic invertebrates

The aquatic invertebrate fauna was diverse (Table 5) considering the small number of samples collected and that sampling occurred during the cool, wet months of May-June. At least 78 taxa were recorded from the 10 wetlands, with insects and crustaceans dominating the invertebrate communities at every site. The majority of insects were dipterans (32 taxa), hemipterans (7) and coleopterans (6). Sites from the permanent freshwater lakes and swamps (LCAR16, LMER4 and WONL9) had the most taxa, while a permanent regulated wetland (DISC7) had the least.

The unpublished database compiled by Thompson (1986) contains remarkably few records of invertebrates and aquatic macrophytes from the wetlands included in his study. This was probably due, in part, to the high flows of very turbid water from the Darling River into the River Murray at the end of 1983 (MacKay *et al.* 1988), resulting in most wetlands being turbid when sampled by Thompson in 1983-4. Apart from noting ostracods from DISC7, no new data could be derived from this database.

Lloyd *et al.* (1984)[1] collected 71 aquatic invertebrate taxa during a 12 month study of the fluctuations in the aquatic invertebrate communities and water chemistry of three wetlands, including Berri and Disher Ck Evap. Basins. Comparison of results from the same time of the year show that the fauna and water chemistry have not changed appreciably at BERB11, while the artificial manipulation of water levels in DISC6 led to a lower salinity and a more diverse fauna in the present study. A total of 28 taxa were found at BERB11 by Lloyd *et al.* (1984)[1], with 12 taxa being recorded during May 1984. The same faunal assemblage was present during May 1990, with the addition of *Afrochiltonia australis*, *Daphniopsis pusilla* and *Micronecta robusta-M. gracilis*. Of the 35 taxa recorded from DISC6 in the earlier work, only four were found during May 1984. In May 1990, 11 species were collected, dominated by crustaceans and dipterans. Future work will determine whether the seasonal trends described by the earlier study are maintained. This will provide a useful means of predicting how conservative are the different parameters that were measured in these evaporation basins, and establish a database upon which any changes in the management of these wetlands can be compared.

Lloyd & Boulton (1990) recorded 96 macroinvertebrate taxa during a recent short-term survey of 13 wetlands from the Chowilla flood plain. Wetlands were sampled as river levels fell in October 1988. As in the present study, most taxa were insects, with dipterans (31 taxa) dominating the fauna. Few crustaceans were collected, partly because a larger meshed dip net was used and did not sample the microcrustaceans. The major difference in the fauna between the two studies was the large number of beetles (22 taxa) recorded by Lloyd & Boulton (1990). Dytiscids and hydrophilids are most commonly collected during spring-summer from most inland waterbodies (Matthews 1980, 1982), with shallow temporary wetlands often having a variety of species (Lloyd & Boulton 1990; pers. obsv.). The timing of our survey may account for the fewer species of beetles recorded.

Comparison of the faunal communities at the 20 sites using DECORANA ordination (Fig. 4 and Table 6) illustrated the importance of connection to the River Murray on both the water chemistry and aquatic invertebrate assemblages. Wetlands/sites with direct connection to the River Murray were characterized by low salinities (TDS concentration <1000 mgL^{-1}), generally low nutrient concentrations, and the presence of the dipteran *Cladotanytarsus* sp. and the shrimp *Paratya australiensis*. Wetlands/sites that were isolated from the main channel formed a second group, characterized by higher salinities (TDS concentration >1000 mgL^{-1}), high nutrient concentrations, and the presence of dipteran larvae such as *Procladius* sp., Ephydridae and Culicidae.

The sites misallocated by the analyses deserve special mention. Hydrological manipulations of three regulated wetlands, prior to the survey, confounded the salinity gradient. Katarapko Evap. Basin, Disher Ck Evap. Basin, and the inlet site at Ramco Lagoon were receiving water from the River Murray when sampled, as their regulating structures had been opened two, seven and 10 days respectively, prior to sampling (Unpubl. E. & W.S. Dept records). Salinity readings from these wetlands indicate that some mixing and dilution had occurred in Katarapko Evap. Basin and Disher Ck Evap. Basin (Unpubl. E. & W.S. Dept records), while little to no flushing had occurred beyond the inlet/outlet site at Ramco Lagoon (Table 2). This appears to have altered the fauna of Katarapko Evap. Basin to resemble a more freshwater assemblage of invertebrates. Sites from Disher Ck Evap. Basin and Ramco Lagoon, however, retained invertebrate assemblages typical of the more saline sites/wetlands.

The high nutrient concentrations recorded at DEVD20 may have contributed to an assemblage of invertebrates typical of saline conditions, despite having a TDS concentration of only 360 mgL^{-1}. This site was heavily grazed by sheep, with the stock having direct access to the waterbody. Biological decomposition of the manure in the water could have produced the high NH_4 concentration, which would then oxidise to NO_3-N by bacterial action (Bayly & Williams 1973).

Sites from Pilby Ck tended to form outlier positions in the data analyses, emphasizing a difference in the fauna from this anabranch compared with the other wetlands. Pilby Ck is a small anabranch in the Chowilla region, characterized by narrow banks with River Red Gums extending over the water. As none of the other wetlands resembled this macrohabitat, the distinctiveness of this wetland within the analyses was not remarkable. The causeway across Pilby Ck has clearly reduced the water quality of the western reach to favour organisms adapted to saline, organically enriched conditions. Placement of a culvert with a regulator under the causeway would provide a simple means of manipulating water levels to reduce the salinity and nutrient concentrations of the western reach.

These are the preliminary results of an ongoing study of the water chemistry and biota of flood plain wetlands in South Australia. They provide an initial database and demonstrate the influence of the River Murray on the water chemistry and aquatic invertebrates of the wetlands sampled. Future work will describe the influence of season, flow and regulation on the limnology of some of these wetlands, and provide guidelines for the management of wetlands throughout the Murray-Darling flood plain.

Acknowledgments

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APPENDIX 1 *Map coordinates and descriptions of the dominant vegetation from the 20 sites surveyed from Chowilla to Mannum in South Australia.*

Site No.	Wetland	Map (1:50000 Topographic Series)	Site Coordinates	Dominant Vegetation
1	Pilby Ck (saline western reach)	CHOWILLA 7030-II & PT.7130-III	489550E, 6239200S	*Eucalyptus camaldulensus* (dead), *Muehlenbeckia florulenta*, *Azolla filiculoides* (dead)
2	Pilby Ck (freshwater eastern reach)	CHOWILLA 7030-II & PT.7131-III	489550E, 6239200S	*E. camaldulensis*, *M. florulenta*, *Typha* sp., *Myriophyllum* sp., *A. filiculoides*
3	Clover Lake	PARINGA 7029-I	478600E, 6237550S	*E. largiflorens*, *Acacia stenophylla*, *Cyperus gymnocaulos*.
4	Lake Merreti	PARINGA 7029-I	477800E, 6234400S	*E. camaldulensis*, *E. largiflorens*, *A. stenophylla*, *M. florulenta*, *C. gymnocaulos*.
6	Disher Ck Evaporation Basin (south of basin)	LOXTON 7029-III	472100E, 6209700S	*E. camaldulensis* (dead), *E. largiflorens*, *M. florulenta*, *Phragmites australis*.
7	Disher Ck Evaporation Basin (middle of basin)	RENMARK 7029-IV	471800E, 6211300S	*E. camaldulensis* (dead), *E. largiflorens*, *M. florulenta*.
8	Katarapko Evaporation Basin (south lagoon)	LOXTON 7029-III	460100E, 6189500S	*E. camaldulensis* (living and dead), *M. florulenta*, *P. australis*, *C. gymnocaulos*.
9	Katarapko Evaporation Basin (south lagoon)	LOXTON 7029-III	460100E, 6190300S	*E. camaldulensis* (living and dead), *M. florulenta*, *P. australis*, *C. gymnocaulos*.
10	Katarapko Evaporation Basin (north lagoon)	LOXTON 7029-III	459900E, 6191000S	*E. camaldulensis* (living and dead), *M. florulenta*, *P. australis*, *C. gymnocaulos*, *Typha* sp.
11	Berri Evaporation Basin	LOXTON 7029-III	460100E, 6205700S	*Suaeda australis*, *Pachycornia* sp., *Bolboshoenus caldwellii*, *C. gymnocaulos*.
12	Ramco Lagoon (inlet/outlet)	CADELL 6829-I	399800E, 6219800S	*P. australis*, *Paspalum vaginatus*
13	Ramco Lagoon (western bank)	CADELL 6829-I	399750E, 6219750S	Bare bank.
14	Ramco Lagoon (eastern bank)	CADELL 6829-I	399900E, 6219750S	*C. gymnocaulos*, *P. vaginatus*
15	Ramco Lagoon (southern bank)	CADELL 6829-I	400900E, 6218500S	*P. australis*, *Paspalum* sp.
16	Lake Carlet (inlet)	CAURNAMONT 6828-III	365500E, 6139900S	*P. australis*, *M. florulenta*, *C. gymnocaulos*, *Schoenoplectus validus*, *Ceratophyllum demersum*, *Vallisneria spiralis*, *Azolla* spp.
17	Lake Carlet (willows near outlet)	MANNUM 6728-II	357600E, 6141800S	*Salix babylonica*.
18	Lake Carlet (pool between willows and R.Murray)	MANNUM 6728-II	357600E, 6141800S	*Typha* sp., *M. florulenta*, *C. gymnocaulos*, *S. validus*, *Triglochin procera*, *Azolla* spp., *C. demersum*.
19	Wongulla Lagoon	SWAN REACH 6828-IV	367400E, 6157100S	*E. camaldulensis*, *Myoporum acuminatum*, *M. florulenta*, *C. gymnocaulos*, *S. validus*, *B. caldwellii*, *Azolla* spp., *V. spiralis*.
20	Devon Downs North Lagoon (southern reach)	SWAN REACH 6828-IV	372150E, 6166100S	*E. camaldulensis*, *M. acuminatum*, *E. largiflorens*, *C. gymnocaulos*.
21	Devon Downs North Lagoon (northern reach)	SWAN REACH 6828-IV	372400E, 6167750S	*M. florulenta*, *E. camaldulensis* (dead), *C. gymnocaulos*, *Eragrostis* sp., *Paspalum* sp.

DISPERSED CUTICULAR FLORAS OF SOUTH AUSTRALIAN TERITARY COALFIELDS, PART 2:LOCHIEL

*BY A. I. ROWETT**

Summary

Dispersed cuticles were recovered from two lithotypes (Facies Ia, IIa) within the G seam of the Kooliata Coal Zone of the Lochiel Coalfield. The floras are distinct. The younger lithotype (IIa) contains a monospecific flora, represented by a robust, coriaceous non-stomatiferous cuticle whereas the older lithotype (la) contains thirty-seven cuticle types. The major contributors are *Agathis* (Araucariaceae) which dominates the flora and Podocarpaceae, Proteaceae and Myrtaceae.
KEY WORDS: Palaeobotany, Tertiary, Eocene, dispersed cuticles, Lochiel, South Australia.

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DISPERSED CUTICULAR FLORAS OF SOUTH AUSTRALIAN TERTIARY COALFIELDS, PART 2: LOCHIEL

by A. I. ROWETT*

Summary

ROWETT, A. I. (1992) The dispersed cuticular floras of South Australian Tertiary Coalfields. Part 2. Lochiel. *Trans. R. Soc. S. Aust.* 116(3), 95-107, 30 November, 1992.

Dispersed cuticles were recovered from two lithotypes (Facies Ia, IIa) within the G seam of the Kooliata Coal Zone of the Lochiel Coalfield. The floras are distinct. The younger lithotype (IIa) contains a monospecific flora, represented by a robust, coriaceous non-stomatiferous cuticle whereas the older lithotype (Ia) contains thirty-seven cuticle types. The major contributors are *Agathis* (Araucariaceae) which dominates the flora and Podocarpaceae, Proteaceae and Myrtaceae.

KEY WORDS: Palaeobotany, Tertiary, Eocene, dispersed cuticles, Lochiel, South Australia.

Introduction

This is the second paper on the dispersed cuticular floras of South Australian Tertiary coalfields and follows the format used in Rowett (1991).

The Lochiel coalfield, located 130 km north of Adelaide (Fig. 1), at the head of the Gulf St Vincent (33°56', 138°10'), is one of five separate lignite deposits within the Northern St Vincent Basin, i.e. the Beaufort, Bowmans, Clinton and Whitwarta deposits. It was first discovered in 1982 by geologists of the Electricity Trust of South Australia.

The Northern St Vincent Basin is characterised by north-south trending faults, considered responsible for controlling Tertiary sedimentation (South Australian Department of Mines and Energy 1987). The Ardrossan and Whitwarta Faults (Fig. 1) delineate the Lochiel deposit in the west and east.

The Lochiel coal-bearing sediments are members of the Clinton Formation which has been subdivided into three units in the northernmost part of the basin, from the base, the Bumbunga Sands, Condowie Silt and Kooliata Coal Zone (ETSA 1988[1]). Small lignite lenses occur in the Bumbunga Sands but are of little economic importance. Three major lignite seams (F, G and H seams) occur in the Kooliata Coal Zone (Kremor & Springbett 1992), which average thicknesses of 2, 6.5 and 2.5 metres respectively. Carbonaceous lacustrine silt, sand and clay of the Condowie Silt separate the Bumbunga lignites from those of the Kooliata Coal Zone. Unconsolidated Oligocene clay, silt and water-saturated sand of the Warrindi and Tarella Silts, ranging in thickness from 20-70 m, unconformably overlie the lignite.

Palynological evidence from these lignites suggests a Late Eocene-Oligocene age (Harris 1965, 1971; Alley & Lindsay 1991 pers. comm.). The palynoflora from the Bumbunga lignite are the time equivalents of the Middle and Upper *Nothofagidites asperus* Zones of Stover & Partridge (1973, 1983), which are Late Eocene to Early Oligocene in age (Kremor & Springbett 1992). The Kooliata lignite is somewhat younger, probably Early Oligocene, and the palynofloras are time equivalent to the Lower *Proteacidites tuberculatus* Zone (Stover & Partridge 1973, 1983).

Materials and Methods

Lignite samples were recovered from a trial pit (Fig. 1) excavated during the initial resource assessment in 1987. Only the lignite seams of the Kooliata Coal Zone were exposed in the pit (Springbett pers. comm.) but limited access (1 hour) to University of Adelaide, Botany Department collectors prevented comprehensive sampling. Sampling was therefore undertaken of those lignite seams noted to contain considerable amounts of heavily carbonised dispersed cuticle and wood fragments. The two samples selected for this study were taken from Facies Ia and IIa of the central G seam (Springbett pers. comm; Fig. 2).

Dispersed cuticles of the Lochiel deposit were processed and analysed using techniques outlined by Christophel *et al.* (1987), Rowett & Christophel (1990) and Rowett (1991).

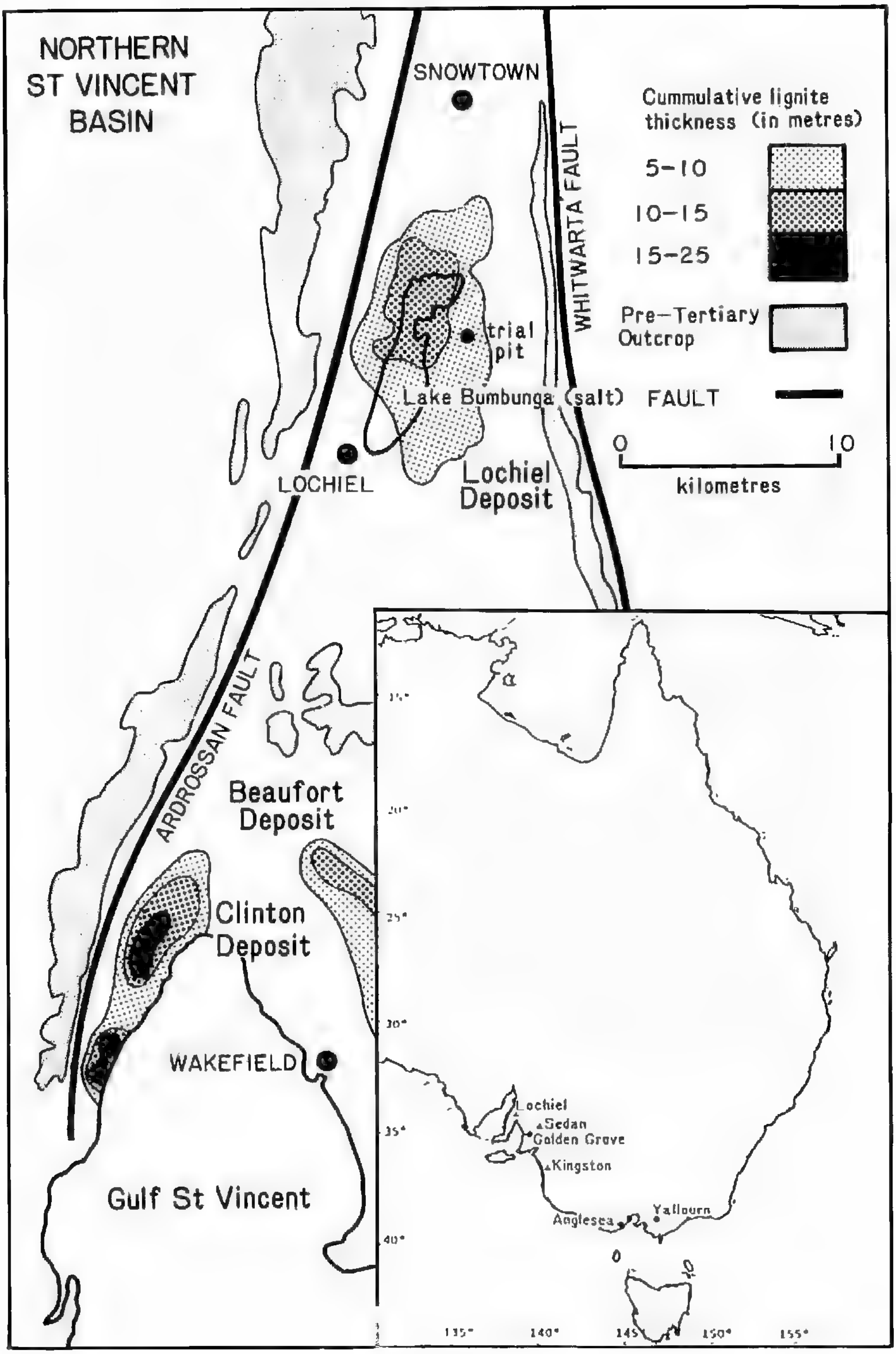
Dispersed Cuticle Flora

Analysis of samples revealed a diverse cuticular flora of 38 parataxa which are unevenly represented in the two facies, i.e. 1 (Facies IIa), 38 (Facies Ia).

The cuticle flora of the upper highly gelified lignite (IIa) consists solely of the parataxon No. AW 007, which is very distinctive despite the absence of stomates. The robust, thick, coriaceous cuticle, sinuous

* Dept of Botany, University of Adelaide, G.P.O. Box 498, Adelaide, S. Aust. 5001.

[1] Figure on page 5 of ETSA 1988, Lochiel report shows E-W stratigraphic cross-section of deposit.


NORTHERN ST VINCENT BASIN
SNOWTOWN
Cummulative lignite thickness (in metres)
5-10
10-15
15-25
Pre-Tertiary Outcrop
FAULT
0
10
kilometres
WHITWARTA FAULT
trial pit
Lake Bumbunga (salt)
LOCHIEL
Lochiel Deposit
ARDROSSAN FAULT
Beaufort Deposit
Clinton Deposit
WAKEFIELD
Gulf St Vincent
Lochiel
Sedan
Golden Grove
Kingston
Anglesea
Yallourn
135°
140°
145°
150°
155°

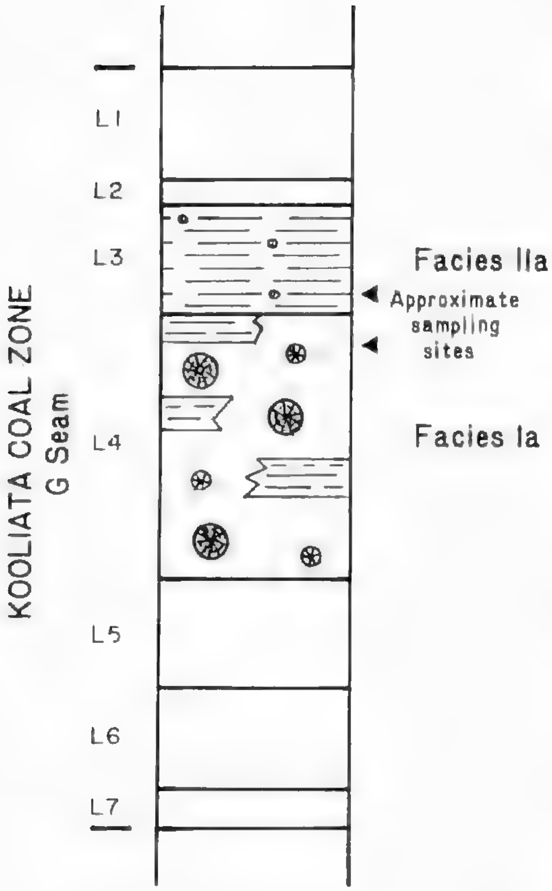


Fig. 2. A simplified lithological column of G seam of the Kooliata Coal Zone showing the seven lenses identified by Springbett (L1-L7) and the approximate location of the samples used in this investigation within Facies Ia and IIa. Facies Ia is an earthy textured coal containing more than 40% relatively ungelified woody material while Facies IIa is a darker fibrous, lignite consisting of gelified twigs. The seam is approximately 6.5 m thick and at a depth of 30 metres.

epidermal cells (types 3-4 of Wilkinson 1979) and distinctive trichome clusters distinguish this cuticle from all stomatiferous parataxa (Fig. 3). This monospecific flora may provide a useful stratigraphic marker in the correlation of the Lochiel lignites. Parataxon No. AW 007 is also present in the underlying facies (Facies Ia).

The lower lignite facies, with an abundance of wood ranging from twigs to large diameter logs, contains a dispersed cuticle flora characterised by a large Araucariaceae component (29.0%) as well as significant Podocarpaceae (15.5%), Myrtaceae (15.2%) and Proteaceae (12.9%) components (Table 1). Unknown cuticle types represent a large percentage of the Lochiel flora (33.5%). Casuarinaceae, Elaeocarpaceae, Lauraceae and Zamiaceae are poorly represented (0.5%, 0.6%, 0.4% and 0.2% respectively).

The Araucariaceae is represented by a single parataxon No. LC 003 (Figs 4-5) with a suggested affinity to the modern *Agathis*. The fragmentary cuticles, a common feature of this locality, makes a more definite identification impossible.

The Podocarpaceae is represented by three parataxa of which No. LC 002 (9.9%) is most abundant (Figs 6-7). Stomates have a variable appearance which makes it difficult to assign the cuticle type to a known podocarp genus. The circular appearance of numerous stomates suggests a possible affinity to *Falcatifolium* (Greenwood 1987). Parataxa Nos. LC 015 and ABP 001 are also common, representing 4.6% and 1.0% respectively. Parataxon No. LC 015 is assigned to *Dacrycarpus* on the basis of smooth-walled epidermal cells and arrangement and cuticular thickening of subsidiary cells (Figs 8-9). Parataxon No. ABP 001 (Figs 10-11) is identified as the cuticle of *Podocarpus platyphyllum* (Greenwood 1987).

The Myrtaceae comprises two cuticle types Nos. LC 001 (12.0%) and LC 011 (3.2%). Both appear

TABLE 1. *The cuticle frequencies (%) of extant plant families represented in the two facies of the central lignite seam of the Lochiel deposit.* Families represented are Podocarpaceae (POD), Araucariaceae (ARAUC), Myrtaceae (MYRT), Elaeocarpaceae (ELAEO), Proteaceae (PROT), Lauraceae (LAUR), Casuarinaceae (CAS), Zamiaceae (ZAM). The OTHERS category represents all other cuticle parataxa whose modern family affinities are unknown.

LOCALITY	POD	ARAUC	MYRT	ELAEO	PROT	LAUR	CAS	ZAM	OTHERS
Lochiel (Facies Ia)	15.5	29.0	15.2	0.6	12.9	0.4	0.5	0.2	25.7
Lochiel (Facies IIa)	–	–	–	–	–	–	–	–	100.0

Fig. 1. Map showing extent and thickness of lignite in the Lochiel deposit and major structural features. 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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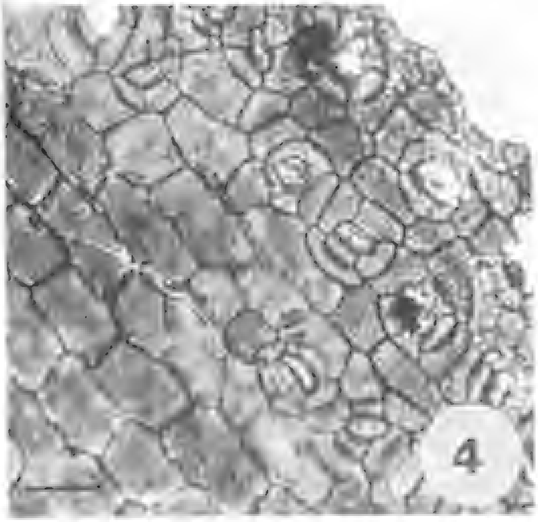
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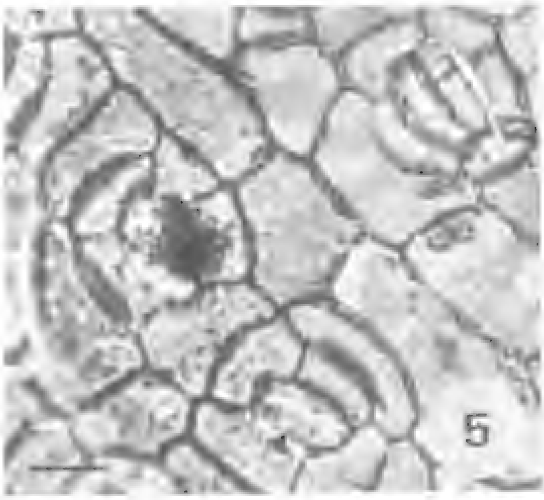
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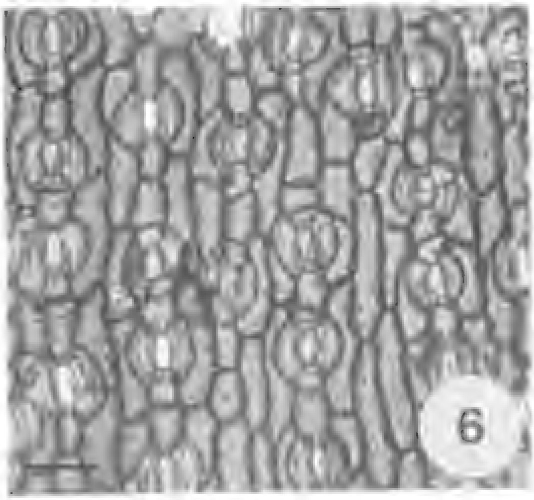
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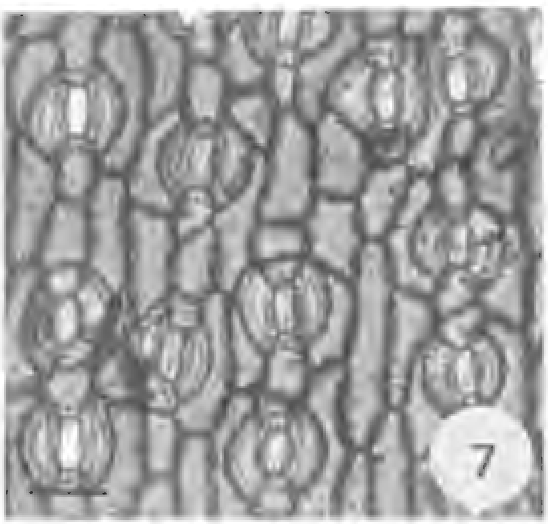
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morphologically similar but can be distinguished on epidermal cell shape, stomatal arrangement and epidermal cell, stomate and oil gland lid cell dimensions. Parataxon No. LC 001 (Figs 12-13) is characterised by rounded to undulate epidermal cells, an anisocytic to staurocytic stomatal arrangement of 3-5 subsidiary cells and lid cells that may be constricted at the sinus. Parataxon No. LC 011 on the other hand, is characterised by undulate to sinuous epidermal cells, a (cyclocytic to) staurocytic stomatal arrangement of 3-6 dark-staining subsidiary cells and large lid cells not constricted at the sinus (Rowett 1991). None of these parataxa are closely comparable with cuticles of the species of *Myrtaciphyllum* described by Christophel & Lys (1986) from Anglesea.

The Proteaceae is a diverse group of nine cuticle types the majority occurring in low frequencies (>0.1%). The most abundant is *Banksieaephyllum* aff. *B. laeve* (5.1%), the same cuticle type that dominated the Late Eocene lignites of the Sedan deposit (Rowett 1991). Two other common cuticle types are parataxa Nos. LC 004 (3.0%) and LC 012 (2.8%), both assigned to *Banksieaephyllum* with the former cuticle type identified as *Banksieaephyllum* aff. *B. fastigatum* Cookson & Duigan (Figs 14-15). The cuticle can be identified by the well-defined areoles, the relatively low frequency of stomata/areole, slightly raised stomata, a pair of poorly defined subsidiary cells surrounded by 3-5 darkly stained epidermal cells and long unicellular trichomes with a poral base. The cuticle of *B. fastigatum* was described by Cookson & Duigan (1950) from the Oligocene brown coals of Yallourn together with five other species of *Banksieaephyllum*, i.e. *B. angustum*, *B. acuminatum*, *B. laeve*, *B. pinnatum* and *B. fastigatum*. The distribution of these species has been discussed by Rowett (1991).

Parataxon No. LC 012 may have an affinity to *B. obovatum* Cookson & Duigan (Figs 16-17). Descriptions of *B. obovatum* and *B. fastigatum* are similar, the distinguishing feature appears to be position of the stomate, i.e., slightly raised in the former and slightly sunken in the latter (Cookson & Duigan 1950). Another cuticle type, parataxon No. LC 013 (Fig. 18), is also assigned to *Banksieaephyllum*. It is possible the parataxon may represent another fragment of *Banksieaephyllum* aff. ?*B. obovatum*.

Casuarinaceae, Elaeocarpaceae, Lauraceae and Zamiaceae are of minor importance in the lower Lochiel flora. Casuarinaceae is represented by *Gymnostoma* (parataxon No. DM 007), which also occurs in the lower lignite seam of the Sedan deposit (Rowett 1991). *Gymnostoma* cuticles at Lochiel indicate that the genus was more widespread during the Late Eocene-Early Oligocene, not restricted to south-eastern Australia as would appear was the case during the Middle Eocene (Christophel 1980; Rowett & Christophel 1990).

Zamiaceae is represented by parataxon No. ABD 002 identified as *Pterostoma* aff ?*P. zamioides* Hill (1980) (Figs 19-20). This tentative association is prompted by the rarity and poor preservation of the Lochiel specimens.

Elaeocarpaceae and Lauraceae are represented by cuticle types ABD 005 and AG 010 (Figs 21-22 and Figs 23-24 respectively).

Dispersed Cuticle Descriptions

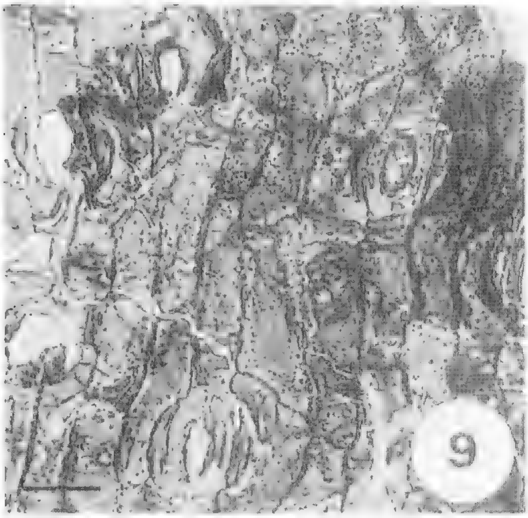
As in Rowett (1991) only parataxa of floristic, stratigraphic and taxonomic significance are described. Some parataxa have been previously identified by the author from other Eocene localities (Rowett & Christophel 1990; Rowett 1991). These and many more are included in the National Energy Research Development and Demonstration Council reference cuticle catalogue of Australian Eocene cuticles types (Rowett in prep[2]). All parataxon numbers are preceded by an abbreviation of the type locality. Terminology used in these descriptions follows that of Rowett (1991) which was derived from Stace (1965), Dilcher (1974) and Wilkinson (1979).

Cuticle Parataxon No. AW 007
FIG 3

Thick, coriaceous cuticle. Non-stomatiferous surface only. Adaxial epidermal cells undulate (type 3-4.

[2] Australian Eocene Dispersed Cuticle Catalogue. Appendix A to ROWETT, A. I., (1990). National Energy Research Development and Demonstration Council. Final Report. No. 3.

Figs 3-8. 3, Parataxon No. AW 007. Non stomatiferous cuticle of unknown affinity. Note heavy cuticular thickening around the trichome base. Scale 1 cm = 70 µm. 4, Parataxon No. LC 003, aff. *Agathis*, Araucariaceae. Shows predominantly obliquely oriented stomates arranged in rows and rounded epidermal cells. Scale 1 cm = 45 µm. 5, Parataxon No. LC 003 aff. *Agathis*, Araucariaceae. Cuticular thickening around stomatal pore could be interpreted as a Florin ring (arrowed). Scale 1 cm = 22 µm. 6, Parataxon No. LC 002. ?*Falcatifolium*, Podocarpaceae. Shows arrangement of stomates in broad bands consisting of long uniseriate rows. Scale 1 cm = 50 µm. 7, Parataxon No. LC 002, ?*Falcatifolium*, Podocarpaceae. Shows stomatal arrangement and a number of circular stomates, which may suggest an affinity to this genus. Scale 1 cm = 40 µm. 8, Parataxon No. LC 015, *Dacrycarpus*, Podocarpaceae. Shows arrangement of stomates. Scale 1 cm = 50 µm.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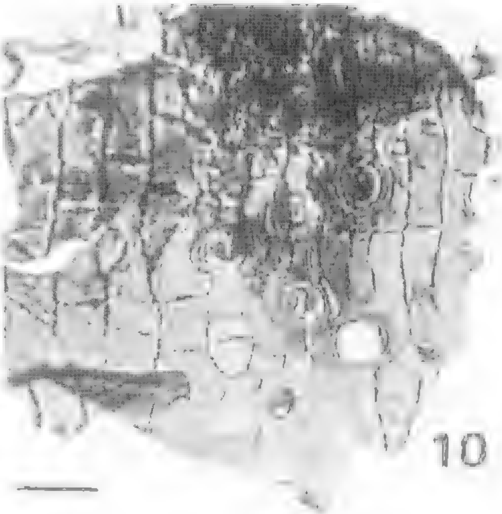
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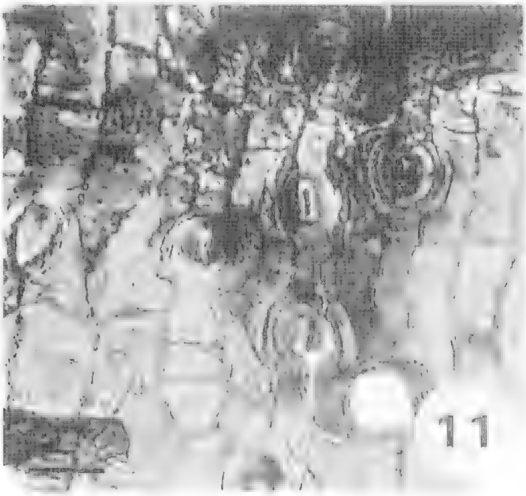
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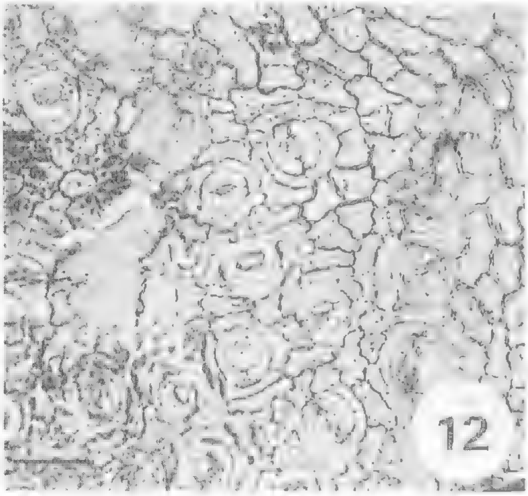
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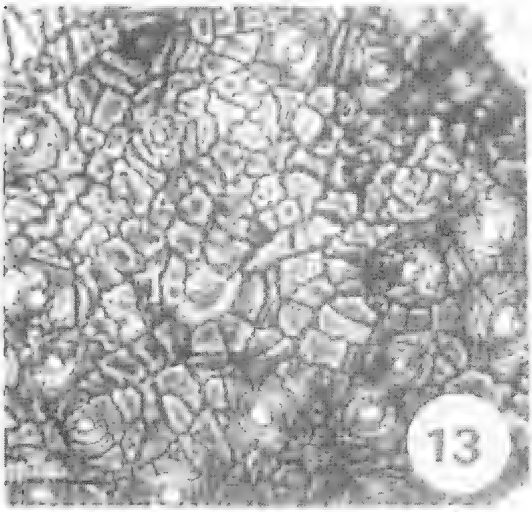
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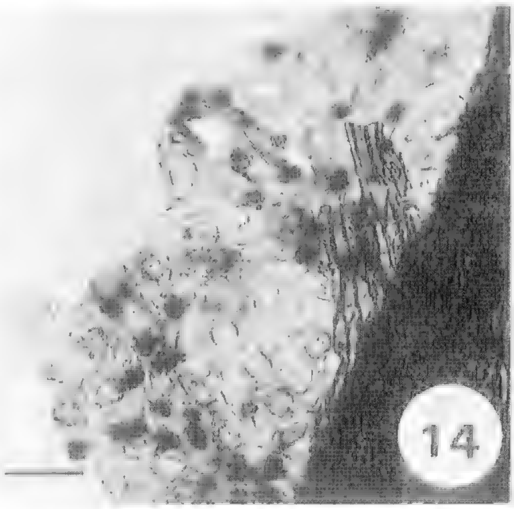
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Wilkinson, 1979). 48-80μm long, 40-68μm wide. Anticlinal wall thin, smooth. Periclinal wall irregularly thickened, granulate to striate. Trichome bases multicellular?, common, uniform distribution, give rise to many single cell trichomes, appear as tufts. Trichomes of variable length, radiate out from centre of base.

Affinity: Unknown.

Cuticle Parataxon No. LC 003
FIGS 4-5

Stomatiferous surface only. Epidermal cells angular to rounded, arranged in longitudinal rows, 24-44μm long, 20-36μm wide. Anticlinal wall irregularly thickened, smooth to beaded. Periclinal wall granulate. Stomata loosely arranged in uniseriate rows, 20-32μm long, 8-16μm wide. Stomatal orientation ranges from parallel, oblique to perpendicular to long axis of epidermal cell rows. Stomatal arrangement tetracytic to cyclocytic. Guard cells sunken. Subsidiary cells 4-5, lateral cells generally larger than polar cells. Anticlinal wall smooth to beaded. Periclinal wall granulate. Guard cell/subsidiary cell wall heavily cutinized, slightly raised. Florin ring evident.

Affinity: The parataxon is assigned to the Araucariaceae. The predominantly oblique orientation of stomata, rounded epidermal cells and uniseriate stomatal rows suggest an affinity with *Agathis* (Cookson & Duigan 1951; Stockey & Taylor 1981; Bigwood & Hill 1985; Hill & Bigwood 1987).

Cuticle Parataxon No. LC 002
FIGS 6-7

Stomatiferous surface only. Epidermal cells angular, arranged in longitudinal rows oriented parallel to vein direction, 32-60μm long, 8-28μm wide. Anticlinal wall irregularly thickened, smooth be beaded. Periclinal wall irregularly thickened, smooth to granulate to pitted. Stomata arranged in uniseriate rows, may be discontinuous, oriented parallel to vein direction, rows grouped in broad bands, 2-4 epidermal cells apart. Stomatal arrangement tetracytic. Guard cells sunken, poral thickening. Outer stomatal ledge, prominent, broad. Florin ring present. Subsidiary cells four (rarely five), polar cells wedge-shaped to rounded (occasionally elongate) rarely shared, lateral cells crescent-shaped. Anticlinal wall irregularly thickened, smooth to beaded, thickening extends along radial walls of polar cells. Periclinal wall irregularly thickened, smooth to granulate.

Affinity: The parataxon is assigned to the Podocarpaceae with a possible affinity to *Falcatifolium* but may equally belong to one of the many extinct Australian Tertiary genera.

Cuticle Parataxon No. LC 015
FIGS 8-9

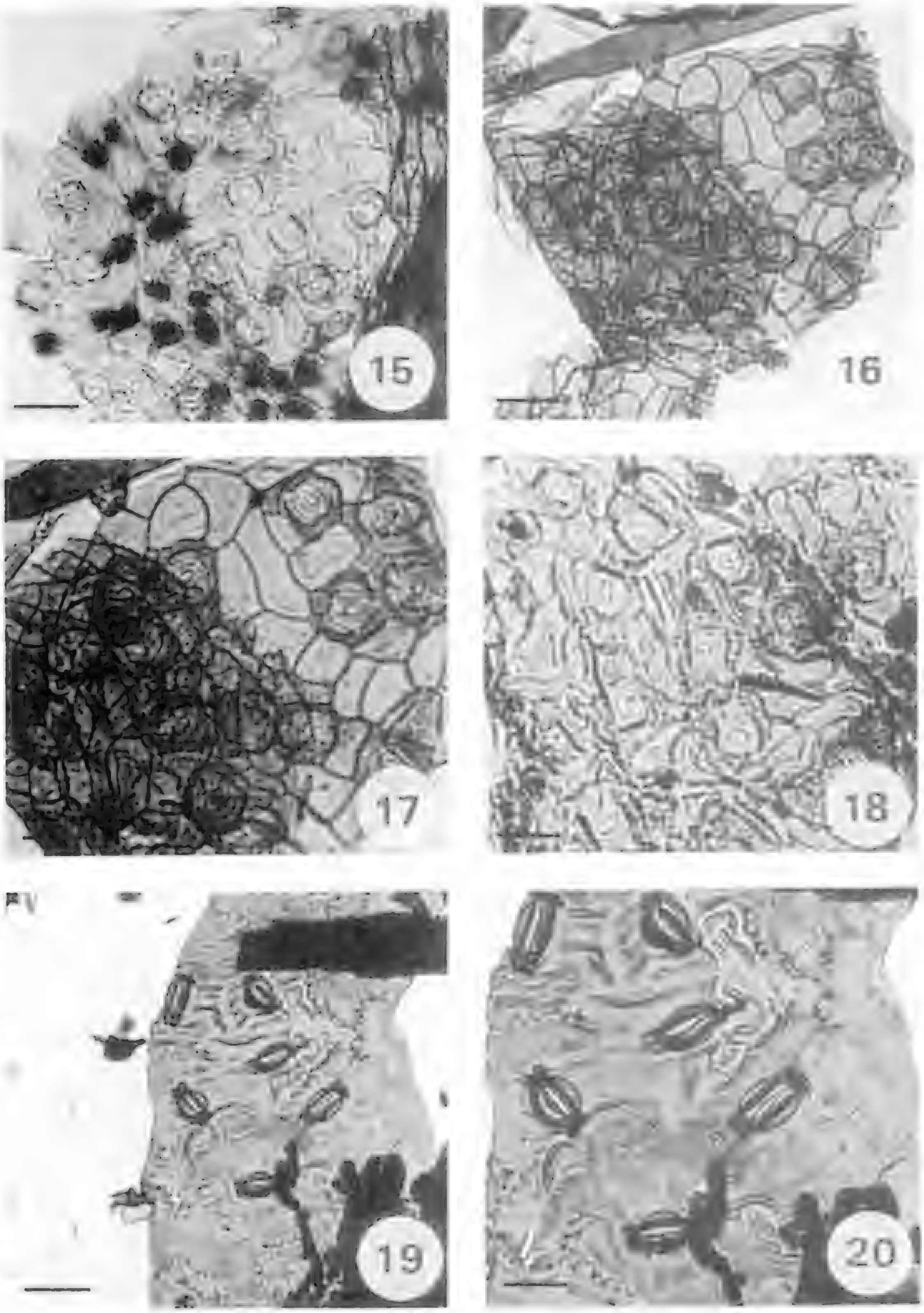
Stomatiferous surface only. Epidermal cells generally rectangular. Cells 25-125μm long, 12.5-27.5μm wide. Anticlinal wall undulate, smooth or showing some buttressed thickening. Periclinal wall irregularly thickened, granulate to striate. Stomata in broad bands, oriented parallel to the long axis of the leaf. Stomatal bands contain on average six uniseriate rows of stomata. Stomata generally separated by more than a single epidermal cell. Stomatal arrangement paratetracytic. Guard cells slightly sunken. Subsidiary cells four (rarely five). Polar cells much smaller than lateral cells. Lateral cells arched. Anticlinal wall rounded, smooth to beaded thickening, occasionally buttressed. Periclinal wall very thick, darker staining. Thickening extends over guard cells. Stomatal ledge evident.

Affinity: The parataxon is assigned to *Dacrycarpus* (Podocarpaceae). Distinguishing features of this cuticle mainly are related to subsidiary cells, i.e. shared polar subsidiary cells, thicker cuticle over the polar subsidiary cells and lateral subsidiary cells that surround the base of the polar subsidiary cells.

Cuticle Parataxon No. ABP 001
FIGS 10-11

Stomatiferous surface only. Epidermal cells rectangular to isodiametric between stomatal rows, becoming elongate over veins, oriented parallel to long axis of the leaf, some groups of cells obliquely oriented to

Figs 9-14. 9, Parataxon No. LC 015. *Dacrycarpus*, Podocarpaceae. Shows elongate polar subsidiary cells and increased thickening of the lateral subsidiary cells within the stomatal arrangement. Scale 1 cm = 37 μm. 10, Parataxon No. ABP 001. *Podocarpus* aff. *P. platyphyllum*, Podocarpaceae. Shows arrangement of stomates in short uniseriate rows. Note beaded thickening on anticlinal walls of epidermal cells and the presence of striations on polar subsidiary cells. Scale 1 cm = 55 μm. 11, Parataxon No. ABP 001, *Podocarpus* aff. *P. platyphyllum*, Podocarpaceae. Shows stomatal arrangement. Note prominent Florin ring surrounding stomate (arrowed). Scale 1 cm = 35 μm. 12, Parataxon No. LC 001. Myrtaceae. Shows sinuous epidermal cells and random arrangement of stomates. Note prominent guard cells and associated T-shaped thickening at the poles. Scale 1 cm = 40 μm. 13, Parataxon No. LC 001. Myrtaceae. Shows an oil gland lid cell (lc), a diagnostic cuticular feature of the family. Scale 1 cm = 40 μm. 14, Parataxon No. LC 004. *Banksieaephyllum* aff. *B. fastigatum*, Proteaceae. Shows small clusters of sunken stomates between prominent veins covered with numerous dark-staining hair bases. Scale 1 cm = 80 μm.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long axis of the leaf, 40-96 μm long, 12-36 μm wide. Anticlinal wall irregularly thickened; beaded to buttressed. Periclinal wall irregularly thickened, strongly striate to reticulate. Stomata in distinct uniseriate rows, oriented parallel to the long axis of the leaf, 92-144 μm long, 24-32 μm wide. Rows 2-6 cells apart. Stomatal arrangement paratetracytic. Subsidiary cells four; lateral subsidiary cells reniform. Anticlinal wall irregularly thickened; smooth to buttressed. Periclinal wall irregularly thickened, smooth to reticulate. Polar subsidiary cells square to rectangular. Anticlinal wall irregularly thickened, smooth to buttressed. Periclinal wall irregularly thickened, reticulate. Polar subsidiary cells may be shared. Florin ring prominent.

Affinity: The parataxon is identical to cuticle described by Greenwood (1987) for the Anglesea fossil species *Podocarpus platyphyllum* (Podocarpaceae). The distinctive beading of the anticlinal walls and striation of the periclinal walls of the epidermal cells are diagnostic of the species. Parataxon No. ABP 002 is therefore identified as *Podocarpus* aff. *P. platyphyllum*.

Cuticle Parataxon No. LC 001
FIGS 12-13

Stomatiferous surface only. Abaxial epidermal cells rounded to undulate (3), becoming elongate over veins, 12-36μm long, 8-20μm wide. Anticlinal wall thin, smooth. Periclinal wall thin, smooth. Stomata randomly oriented, uniform distribution, 20-28μm long, 20-24μm wide, S.I. 11.4. Stomatal arrangement anisocytic to staurocytic. Guard cells not sunken, poral thickening. T-shaped thickening, polar rods present. Outer stomatal ledge prominent, narrow. Subsidiary cells 3-5. Anticlinal wall thin, smooth. Periclinal wall thin, smooth. Hydathodes rare, over veins, dimensions 32μm long, 24μm wide. Oil gland lid cells rare, isodiametric, 32μm in diameter, constricted at sinus. Sinus undulate (single undulation), dark-staining circular region of thickened cuticle centres on sinus. Lid cell surrounded by a cyclocytic arrangement of six modified epidermal cells.

Affinity: The oil gland lid cells and general stomatal morphology (Rowett 1991) confirm affinity of the cuticle parataxon to Myrtaceae.

Cuticle Parataxon No. LC 004
FIGS 14-15

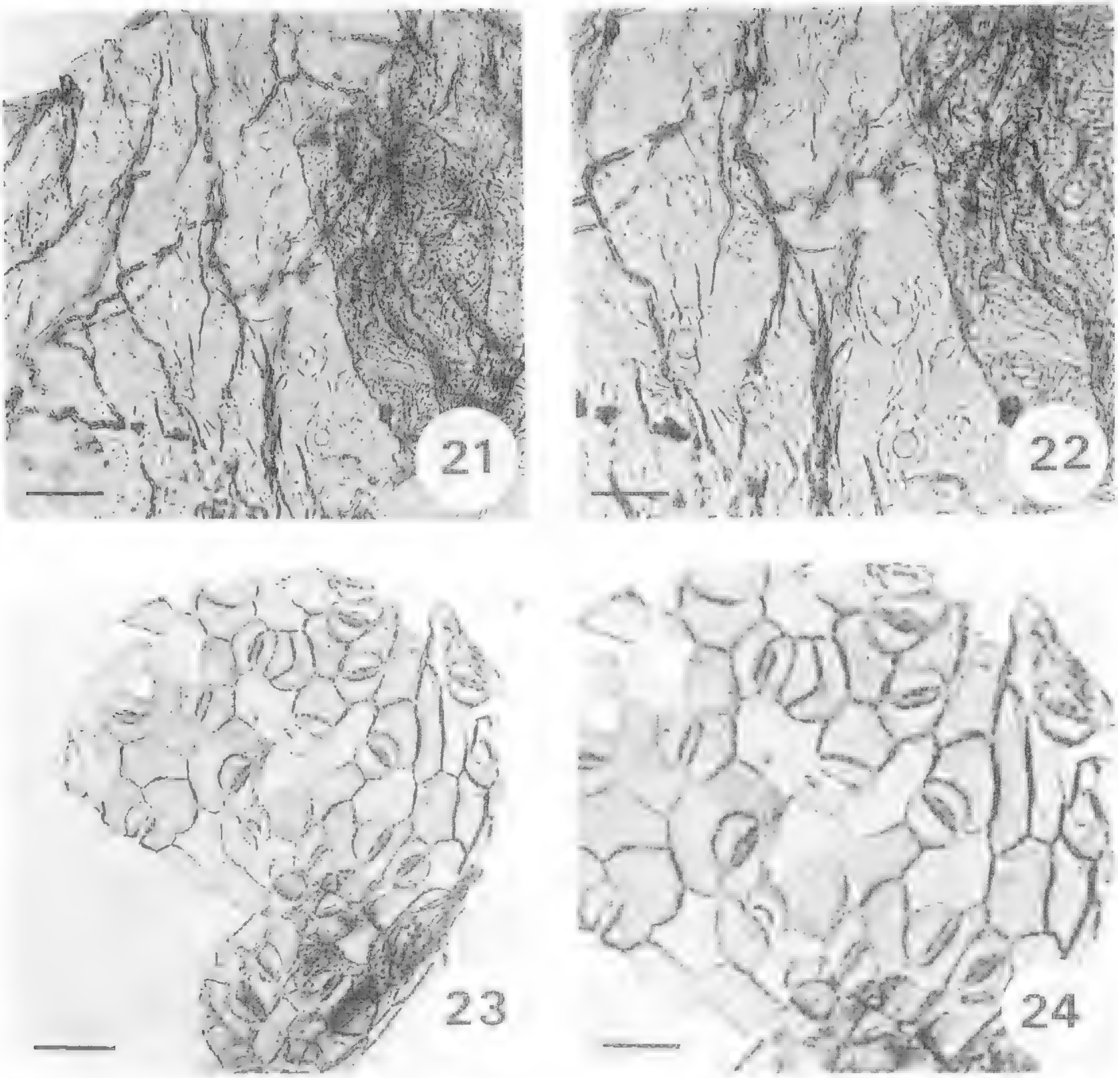
Stomatiferous surface only. Abaxial epidermal cells undulate (3), becoming elongate over veins, 28-40μm long, 16-32μm wide. Anticlinal wall thin, smooth. Periclinal wall irregularly thickened, smooth to finely granulate. Stomata randomly oriented, uniform distribution within well defined areoles, 16-24μm long, 12-16μm wide. Stomatal arrangement brachyparacytic. Guard cells sunken. 3-5 dark-staining, staurocytically arranged epidermal cells surround stomatal apparatus. Raised cuticular folds that encircle and over-arch stomata may be present. Outer stomatal ledge prominent, delicate, narrow. Peristomal rim may be present. Subsidiary cells two, inconspicuous. Anticlinal wall thin, smooth. Periclinal wall irregularly thickened, smooth to granulate. Trichome bases common, over veins, poral, heavily cutinised pore. 4-6 scarcely modified epidermal cells surround pore.

Affinity: The parataxon is assigned to the Proteaceae on the basis of the brachyparacytic stomatal arrangement (Cookson & Pike 1950; Blackburn 1981). The rather inconspicuous, small subsidiary cells encircled by a staurocytic ring of dark-staining epidermal cells, stomatal density and sunken stomata indicate an affinity to *Banksieaephyllum fastigatum* (Cookson & Duigan 1950), i.e. *Banksieaephyllum* aff. *B. fastigatum*.

Cuticle Parataxon No. LC 012
FIGS 16-17

Hypostomatic. Adaxial epidermal cells undulate to sinuous (3-4), becoming elongate over veins, 20-44μm long, 16-40μm wide. Anticlinal wall thin, smooth. Periclinal wall thin, smooth.

Figs 15-20. 15, Parataxon No. LC 004. *Banksieaephyllum* aff. *B. fastigatum*, Proteaceae. Shows prominent guard cells, subsidiary cells are generally inconspicuous. Scale 1 cm = 56 μm. 16, Parataxon No. LC 012. *Banksieaphyllum* aff. *B. obovatum*, Proteaceae. Shows small clusters of raised stomates and simple, poral trichome bases scattered amongst stomates. Scale 1 cm = 44 μm. 17, Parataxon No. LC 012. *Banksieaephyllum* aff. *B. obovatum*, Proteaceae. Shows narrow light areas immediately inside dark staining surrounding cells indicating the position of inconspicuous subsidiary cells. Scale 1 cm = 32 μm. 18, Parataxon No. LC 013. *Banksieaephyllum* aff. ?*B. obovatum*, Proteaceae. Shows raised paracytic stomates and scattered simple, poral trichome bases but the absence of dark staining surrounding cells makes this indentification tentative. Scale 1 cm = 33 μm. 19, Parataxon No. ABD 002. *Pterostoma* aff. ?*P. zamioides*, Zamiaceae. Shows prominent cuticular ridges over the anticlinal wall of sinuous epidermal cells and heavily cutinised stomates grouped in loosely defined bands. Scale 1 cm = 100 μm. 20, Parataxon No. ABD 002. *Pterostoma* aff. ?*P. zamioides*, Zamiaceae. Shows "bon-bon"-like appearance of the prominent outer stomatal ledge. Note irregular distribution and patterning of cuticular ridges on epidermal cells. Scale 1 cm = 53 μm.



Figs 21-24. 21, Parataxon No. ADB 005. Elaeocarpaceae. Shows high degree of ornamentation (fine striations) that characterises this parataxon. Scale 1 cm = 60 μm. 22, Parataxon No. ABD 005. Elaeocarpaceae. Shows guard cells without ornamentation, other than a fine apiculate outer stomatal ledge. Scale 1 cm = 30 μm. 23, Parataxon No. AG 010. Lauraceae. Shows random arrangement of stomates. Scale 1 cm = 40 μm. 24, Parataxon No. AG 010. Lauraceae. Shows paracytic stomates, highlighting the prominent, narrow outer stomatal ledge, and absence of a guard/subsidiary cell wall, all of which are common features of the family. Scale 1 cm = 30 μm.

Abaxial epidermal cells rounded to undulate (3), becoming elongate over veins, 24 - 44μm long, 12-32μm wide. Areoles well-defined. Anticlinal wall thin, smooth. Periclinal wall thin, smooth. Stomata randomly oriented, uniform distribution, 18-20μm long, 14-20μm wide. Stomatal arrangement brachyparacytic. Guard cells not sunken to very slightly raised. Outer stomatal ledge prominent, narrow. Subsidiary cells two. 4-5 dark-staining staurocytically arranged epidermal cells surround stomatal apparatus. Anticlinal wall irregularly thickened, smooth to beaded. Periclinal wall granulate. Trichome bases common, over veins, poral, some thickening around pore, up to six surrounding cells. Trichomes simple, unicellular, acute apex. Small poral trichomes, common within areoles, four radially arranged surrounding cells.

Affinity: The cuticle parataxon has been assigned to the Proteaceae on the basis of the brachyparacytic stomatal arrangement. The rather inconspicuous, small subsidiary cells encircled by a staurocytic ring of dark-staining epidermal cells, stomatal density and raised stomata indicate an affinity to *Banksieaephyllum obovatum* (Cookson & Duigan 1950), i.e. *Banksieaephyllum* aff. *B. obovatum*. The feature that distinguishes this fossil species from the related *B. fastigatum* is the superficial position of the stomata, i.e. they are slightly raised.

Cuticle Parataxon No. ABD 002
FIGS 19-20

Hypostomatic. Adaxial epidermal cells sinuous (8), becoming elongate over veins, 40-72μm long, 32-44μm wide. Anticlinal wall irregularly thickened, smooth to beaded to buttressed. Periclinal wall irregularly thickened, striate to reticulate. Striations follow cell outline. The cuticular ornamentation may obscure cell outline.

Abaxial epidermal cells sinuous (6), becoming elongate over veins, 44-80μm long, 20-40μm wide. Anticlinal wall irregularly thickened, thin, beaded. Beading may appear slightly raised. Periclinal wall irregularly thickened, granulate to striate, reticulate. Stomata randomly oriented, arranged in broad bands between veins. S.I. 27.3. Stomatal arrangement haplocheilic. Guard cells sunken. Subsidiary cells 4-5. Anticlinal wall irregularly thickened, beaded. Periclinal wall irregularly thickened, with prominent striation in radiating pattern. Short cuticular folds common over the entire stomatal region, often associated with the stomata. Outer stomatal ledge prominent, raised over lateral subsidiary cells narrows to produce thin arcs over polar subsidiary cells. Gives outer stomatal ledge a "bon-bon"-like appearance. Often absent from polar subsidiary cells.

Affinity: The cuticle has been assigned to extinct *Pterostoma* (Hill 1980) of the Zamiaceae due to sinuous epidermal cells, cuticular ridges/folds on the abaxial surface and a prominent and distinctive stomatal ledge ("bon-bon"-like appearance). The apparent regular venation pattern of the Lochiel specimens suggests a possible affinity to ?*P. zamioides*.

Cuticle Parataxon No. ABD 005
FIGS 21-22

Stomatiferous surface only. Abaxial epidermal cells rounded to undulate, becoming elongate over veins, 16-28μm long, 8-20μm wide. Anticlinal wall thin, smooth. Periclinal wall irregularly thickened, smooth to striate. Striations obscure most cell detail. Stomata randomly oriented, uniform distribution, 16-24μm long, 16-20μm wide. S.I. 13.5. Stomatal arrangement staurocytic? Guard cells not sunken, polar rods present. Subsidiary cells 4-6? Outer stomatal ledge evident, narrow. T-shaped thickening occasionally present. Hydathodes rare, over veins, 36-44μm long, 20-28μm wide. Striations radiate out from hydathode.

Affinity: The cuticle parataxon is assigned to the Elaeocarpaceae on the basis hydathodes and what appears to be a staurocytic stomatal arrangement.

Cuticle Parataxon No. AG 010
FIGS 23-24

Stomatiferous surface only. Abaxial epidermal cells angular to rounded, becoming elongate over veins, 24-44μm long, 12-28μm wide. Anticlinal wall thin, smooth. Periclinal wall thin, smooth. Stomata 20-24μm long, 20-36μm wide, randomly oriented, uniform distribution. S.I. 11.1. Stomatal arrangement paracytic. Guard cells slightly sunken. Guard cell/subsidiary cell wall absent. Cuticular scales prominent, narrow. Subsidiary cells two. Anticlinal wall thin, smooth. Periclinal wall thin, smooth.

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

Floristic Comparison of Samples

The older lignite flora comprising 38 dispersed cuticle parataxa is characterised by an abundance of Araucariaceae, Podocarpaceae, Myrtaceae and Proteaceae cuticles and minor occurrences (<1%) of Casuarinaceae, Elaeocarparceae, Lauraceae and Zamiaceae cuticles which easily distinguishes it from the younger monospecific flora.

The floristic difference is also reflected in the two lithotypes. The lignite of the older sample (Facies Ia) is defined as an earthy textured coal containing more than 40% relatively ungelified woody material (Springbett 1980 pers. comm.). Facies IIa is a darker fibrous, lignite consisting of gelified twigs (Fig. 2).

Correlation between flora and lithotype indicates that the two floras were deposited in different sedimentary environments, and as the Kooliata Coal Zone consists of peatswamp and lacustrine sand and silt cycles (Kremor & Springbett 1992) the changes in the sedimentary environments are most likely due to fluctuations in water level. The degree of gelification also gives an indication of changes in water levels (Springbett pers. comm.); high degree of gelification — low water level and vice versa.

Comparison with Other Australian Tertiary Deposits

The dispersed cuticle floras of the Lochiel deposit includes parataxa that occur in a number of other

Australian Tertiary deposits. *Banksieaephyllum* aff. *B. laeve*, the principal parataxon of the Sedan lignites is well represented at Lochiel. This expands the known distribution of the species and establishes a floristic link between the Northern St Vincent Basin and Latrobe Valley, from where the type species was originally described. This association is further strengthened by the presence of *Banksieaephyllum* aff. *B. fastigatum* and *Banksieaephyllum* aff. ? *B. obovatum* (Cookson & Duigan 1950) both reported outside the Latrobe Valley for the first time. *Banksieaephyllum obovatum* has also been identified in the Miocene coals at Morwell where it occurs in low frequencies in the medium light coloured coals, the colour values 90-116 (State Electricity Commission of Victoria Coal colour classification scheme, Blackburn 1985[1]). All three cuticle types have affinities to the modern genus *Banksia* (Blackburn 1985[1]; Hill & Christophel 1988).

Parataxon No. LC 011 in both the Lochiel and Sedan deposits has an affinity to the Myrtaceae. It is a minor component in the floras of both localities but is most abundant at Lochiel. The cuticle type has also been identified from the Middle Eocene Maslin Bay sediments.

The occurrence of *Pterostoma* aff. ?*P. zamioides* (parataxon No. ABD 002) at Lochiel is significant in that it represents the first report of *Pterostoma* specimens outside of south-eastern Australia and Tasmania. *Pterostoma* is reported from a number of Tertiary localities, including Anglesea (Eocene, *P. zamioides* Hill 1980), Nerriga (Eocene, *P. anastomosans* Hill 1980) Cethana (Oligocene, Carpenter 1991) and Buckland (Eocene, Carpenter 1991) and has a known stratigraphic range from the Cretaceous to Early Oligocene (Hill pers. comm.). With such a extensive age range for *Pterostoma* parataxon No. ABD 002 is of little biostratigraphic significance.

Similarly, parataxon No. LC 015 with an affinity to *Dacrycarpus*, is of little biostratigraphic importance. *Dacrycarpus* is the most common podocarp genus in Tertiary sediments in south-eastern Australia which is known from numerous deposits ranging in age from Eocene to Oligocene-Miocene (Anglesea, Vegetable Creek, Yallourn, Bacchus Marsh in mainland Australia and Regatta Point, Loch Aver and Cethana in Tasmania) (Hill & Carpenter 1991). Therefore cuticles assigned to *Dacrycarpus* are unsuitable as biostratigraphic indicators. However, indentification of *Dacrycarpus* cuticles at Lochiel does expand our knowledge of the distribution of the genus during the Late Eocene.

There are a number of Anglesea parataxa present in the Lochiel flora, including No. ABP 001 (*Podocarpus aff. P. platyphyllum*), all representatives of the Elaeocarpaceae and Lauraceae and several of the unknown cuticle types.

In conclusion, analysis of the dispersed cuticle floras of Facies Ia and IIa, of the Lochiel lignite show that two distinct floras exist, i.e. the diverse, Araucariaceae-dominated flora of the older ungelified, woody lignite and the monospecific flora (parataxon No. AW 007) of the younger dark, gelified lignite. The lithotype and floral differences between lignites are most likely due to fluctuations in the hydrological cycle; changing from a lacustrine to peatswamp environment. These differences may prove useful in intra-basin correlation.

The dispersed cuticle composition of the Lochiel lignites provides valuable information on the distribution of a number of Tertiary plant taxa, including *Agathis*, *Banksieaephyllum* aff. *B. laeve*, *Banksieaephyllum* aff. *B. fastigatum* and *Banksieaephyllum* aff. ?*B. obovatum*, *Dacrycarpus*, *Gymnostoma*, *Podocarpus platyphyllum* and *Pterostoma*. The presence of the three Latrobe Valley *Banksieaephyllum* species provides a interesting floristic link between the deposits and may be of some biostratigraphic significance. Rowett (1991) discussed this point in relation to *Banksieaephyllum* aff. *B. laeve* at Sedan and concluded that its occurrence could either imply a younger age for the deposit or an extended lower limit to the age of the fossil. These comments could apply to the *Banksieaephyllum* cuticle types of Lochiel. However, as the dispersed cuticle flora is without any known Eocene, Oligocene or Miocene indicators little can be concluded regarding the age of the Lochiel lignites in addition to that provided by palynology.

Acknowledgments

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

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THE MORPHOLOGY OF *NIPPOSTRONGYLUS MAGNUS*, A PARASITE OF NATIVE AUSTRALIAN RODENTS

BY IAN BEVERIDGE & MARIE-CLAUDE DURETTE-DESSET†*

Summary

Nippostrongylus magnus (Mawson) (Nematoda: Trichostrongyloidea) is redescribed from specimens from naturally-infected *Rattus fuscipes* from Blackwood, Victoria and from experimentally infected *R. fuscipes* and *R. norvegicus.* The asymmetry of the bursa, a characteristic of the genus, is matched by asymmetry of the spicules and genital cone. The synlophe is similar to that of *N. brasiliensis* but includes some variable features which appear to be of specific value. The morphological differences in *N. magnus* are discussed in relationship to the estimated period of separation from its congener, *N. brasiliensis.*
KEY WORDS: Nematoda, Trichostrongyloidea, rodents, *Nippostrongylus*

Transactions of the Royal Society of S. Aust. (1992), 116(3), 109-115

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KEY WORDS: Nematoda, Trichostrongyloidea, rodents, *Nippostrongylus*

Introduction

During a study of the helminth parasites of the bush rat, *Rattus fuscipes*, a particular nematode species, *Nippostrongylus magnus* (Mawson) was encountered commonly in the duodenum. The species was described originally by Mawson (1961), although features of the complement of cuticular ridges, the synlophe, were not described. Some features of its synlophe were described by Durette-Desset (1969) and by Lichtenfels (1974), based on a small number of specimens, and in the latter paper their use for taxonomic purposes at the species level was considered. *N. magnus* has never been described in detail, and the use of the synlophe to identify species of *Nippostrongylus* as suggested by Durette-Desset (1970) and Lichtenfels (1974) has not been fully explored.

It was evident therefore that a detailed redescription of the nematode, particularly features of the synlophe, would allow a more definitive assessment of whether it provided useful taxonomic characteristics at the species level, as is the case in other trichostrongyloid genera. It would also provide a basis for subsequent ultrastructural and life-history studies of this parasite.

Materials and Methods

Nematodes were obtained from naturally infected *Rattus fuscipes* collected at Blackwood, Victoria (37°29′S, 144°19′E) and from laboratory raised *R. fuscipes* and *R. norvegicus* which had been infected experimentally with third-stage larvae of the species. Nematodes were collected live, washed in 0.9% saline and fixed in hot 70% ethanol. Additional specimens were fixed in 2.5% glutaraldehyde in phosphate buffer at 4°C and embedded in resin. Sections 1 µm thick were stained with toluidine blue, examined under the light microscope and photographed. Whole specimens were examined using Nomarski interference contrast microscopy after clearing in lactophenol and drawings were made with the aid of a drawing tube attached to an Olympus BH microscope. Apical views and transverse sections of the nematode body were prepared by hand using a cataract scalpel. Morphological terms for the complement of body ridges or synlophe and the numbering system for bursal rays follow Durette-Desset (1971, 1985).

Numbering of synlophe ridges was based on relationship to the axis of orientation of the synlophe as described by Durette-Desset (1971). Ridges dorsal to the axis were numbered from left to right 1, 2, 3 etc.; ridges ventral to the axis were numbered from left to right 1′, 2′, 3′. . . ; etc. Measurements are given in mm as the range followed by the mean of five specimens in parentheses.

Specimens examined have been deposited in the South Australian Museum (SAM), Adelaide.

* Department of Veterinary Science, University of Melbourne, Parkville, Vic. 3052

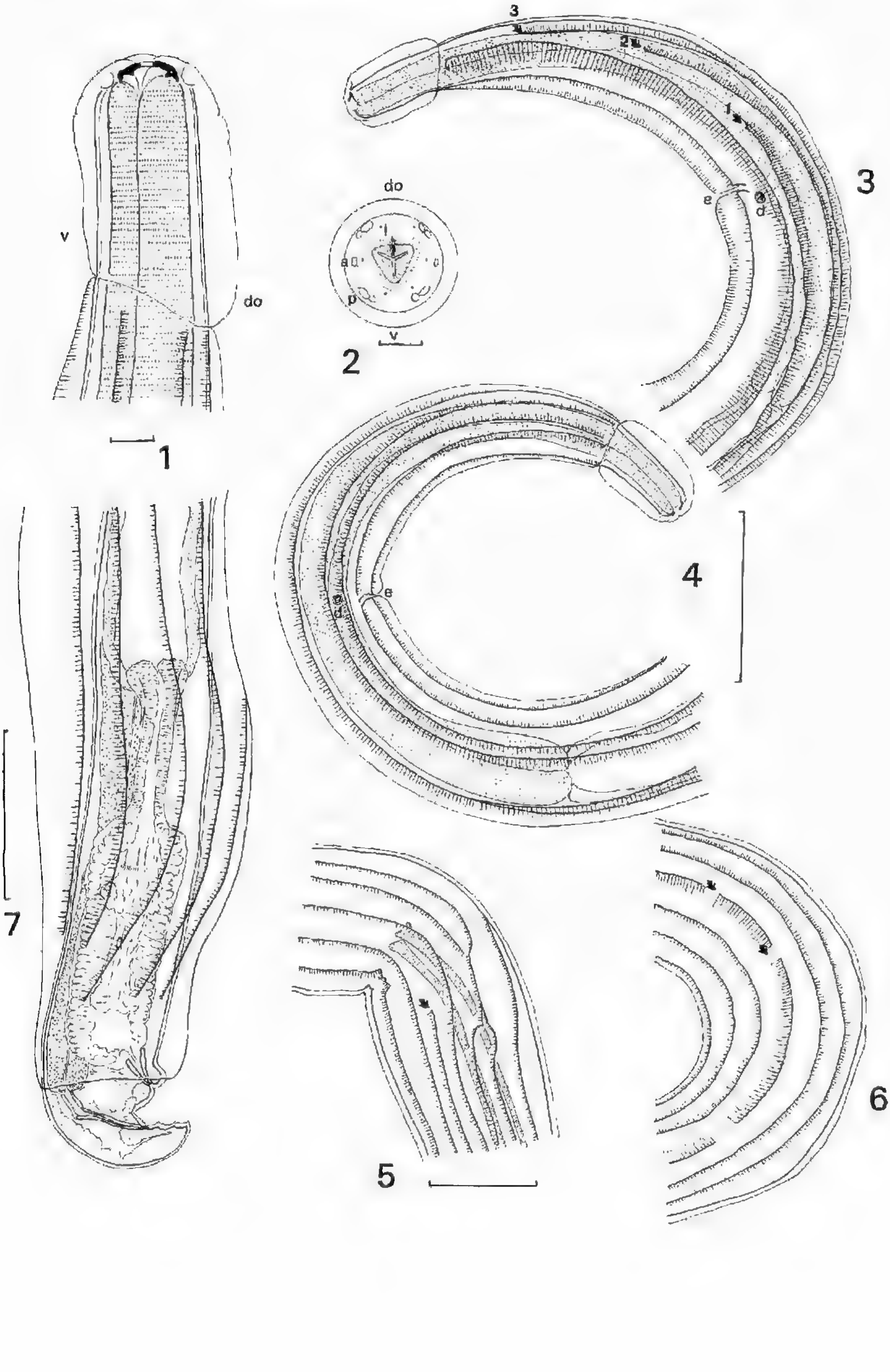
† Biologie parasitaire, Protistologie et Helminthologie, Muséum national d'Histoire naturelle, 61 rue Buffon, Paris, 75005 France.

Nippostrongylus magnus (Mawson)
FIGS 1-20

Austrohelignonema magnum Mawson, 1961, pp. 816-817, figs 46-47, from *Rattus fuscipes*, *R. rattus*, *R. conatus*, *R. norvegicus* and *Melomys cervinipes*; Durette-Desset (1969), p. 737, fig. 3 (as *A. magna* from *Rattus* sp.).

Nippostrongylus magnus, Durette-Desset (1971), p. 818; Lichtenfels (1974), p. 286, (as *N. magna*); Obendorf (1979), p. 868, 896.

Material examined: From *Rattus fuscipes*: natural infections: 20♂♂, 20♀♀, Blackwood, Vic., 3♂♂, 4♀♀, deposited (SAM HC22877); experimental infections: 4♂♂, 2♀♀ (SAM HC22878); From *Rattus norvegicus* experimental infections: 20♂♂ 16♀♀ (SAM HC22875).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Description: Small, sinistrally-coiled nematodes, red in colour when live; prominent slightly asymmetrical cephalic vesicle present, buccal capsule vestigial; mouth opening sub-triangular, surrounded by six tiny labial papillae; four double submedian papillae and paired amphids present, external to labial papillae; oesophagus claviform; nerve ring in mid-oesophageal region; deirids dome-shaped, in region of excretory pore.

Synlophe: composed of 14 ridges in mid-body region; axis of orientation from right-ventral field to left dorsal field, at approximately 60° to sagittal axis (Fig. 15); carene, or cuticular swelling present in left dorsal field between ridges 2' and 4; eight ridges in dorsal field; ridges 1-4 diminishing in size, ridges 5 and 6 larger than 7 and 8; six ridges in dorsal field; ridge 1" very large, dimishing in size to ridge 6; all ridges arise immediately posterior to cephalic vesicle except for ridges 3,2,1 which arise progressively between vesicle and excretory pore, ridges sometimes interrupted in mid-body region, number and orientation of ridges alters in posterior extremity of body.

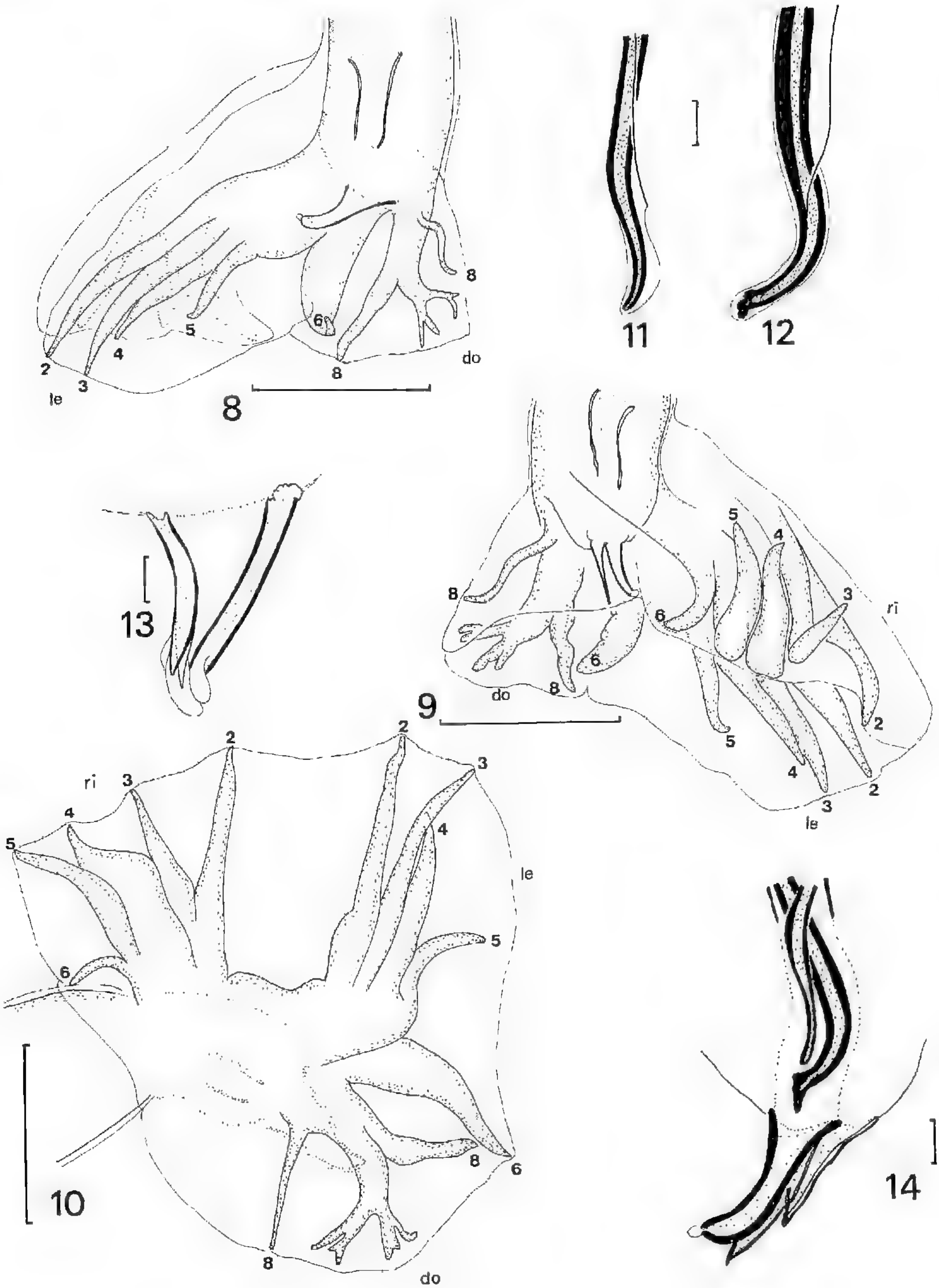
Male. Length 3.3-4.2 (3.7), maximum width 0.10-0.14 (0.11); cephalic vesicle 0.06-0.07 (0.065) long; oesophagus 0.36-0.53 (0.44); nerve ring 0.17 from anterior end; excretory pore 0.25-0.32 (0.28) from anterior end; deirids 0.26-0.32 (0.29) from anterior end; spicules 0.50-0.54 (0.52); gubernaculum 0.05 long. Synlophe: additional ridge arises in right ventral field in region of spicules, between 0.45 and 0.85 from posterior end, immediately anterior to bursa, additional dorsal ridge present, with eight dorsal and eight ventral ridges; ridges reduced in size, orientation barely discernible, ridges of similar size; irregular anastomosing and branching of ridges seen close to bursa. Bursa asymmetrical, right lateral lobe longer than left; dorsal lobe reduced. Dorsal ray with rays 8 arising at different levels; left ray 8 more robust and arising posterior to right; major bifurcation of dorsal ray in posterior third of its length; rays 9 as long as internal rays (10); latter with suggestion of secondary lateral lobe; on left, ray 6 robust, arising close to dorsal trunk, reaching margin of bursa; rays 5 and 4 slender, not reaching margin of bursa, common lateral trunk with prominent bulge at origin of ray 5; rays 3 and 2 elongate, slender, reaching margin of bursa; on right, ray 6 short, slender, arising from lateral trunk; ray 5 slender, reaching margin of bursa; ray 4 extremely robust at base, extremity slender, reaching margin of bursa; rays 3 and 2 slender, reaching margin of bursa. Genital cone prominent, elongate, conical; lightly sclerotised; ventral lobe simple with globoid, non-sclerotised apical appendage; dorsal lobe with two unequal pointed ends, tip surrounded by elongate appendage. Spicules elongate, triquetrous in transverse section; spicule tips dissimilar; tip of left spicule knobbed, with ala arising near tip; tip of right spicule tiny, ala arising at tip; gubernaculum present, lightly sclerotised.

Female. Length 4.6-4.8 (4.7), maximum width in mid-body region 0.12-0.14 (0.13), at posterior extremity 0.14-0.17 (0.15); cephalic vesicle 0.06-0.08 (0.07) long; oesophagus 0.46-0.50 (0.48); nerve ring 0.20 from anterior end; excretory pore 0.26-0.31 (0.29) from anterior end; deirids 0.27-0.31 (0.29) from anterior end; tail 0.03-0.06 (0.05); vulva to posterior end 0.09-0.23 (0.10); egg 0.07-0.08 (0.07) × 0.03-0.05 (0.04). Synlophe: same number of ridges in posterior end of body; ridges become more prominent in region of ovejector, terminate immediately anterior to vulva; ridges of almost equal size, orientation almost lost in posterior region. Posterior extremity of female with swelling of cuticle, variable in shape, often forming sleeve over tip of tail. Tail short, conical, vulva close to anus; monodelphic, ovejector leads to short infundibulum, then into uterus; egg thin-shelled, ellipsoidal.

Discussion

In spite of the fact that the sub-family Nippostrongylinae is cosmopolitan in distribution, and that the type species of *Nippostrongylus*, *N. brasiliensis*, has been widely used as a model in immunological research, few of the species as recognised by Durette-Desset (1970) have been described in detail. Features of the synlophe in the mid-body region have been described for various species by Chabaud & Durette-Desset (1966), Durette-Desset (1969, 1970), Greenberg (1972) and Lichtenfels (1974). Features of the synlophe which might be useful in species separation have been investigated by Lichtenfels (1974) following a detailed examination of the synlophe in laboratory strains of *N. brasiliensis* and limited observations on several additional species. Equally

Figs 1-7 *Nippostrongylus magnus* (Mawson). 1, ♂, cephalic extremity, lateral view, showing asymmetry of cephalic vesicle; 2, apical view of anterior extremity; 3, ♂, anterior end, left side showing origins (arrows) of ridges 1,2 and 3. 4, ♀, anterior end, right side showing origins of ridges at cephalic vesicle; 5, ♂, left view, at level of spicules, 0.5 mm from posterior end, showing origin (arrow) of additional ridge and branching and anastomosing of ridges, 6, mid body region of ♂, left side, showing discontinuities (arrows) in ridge, 7, female tail, right side, showing sleeve formed by cuticle and termination of ridges. Scale lines: Figs 1,2, 0.01 mm; Figs 3-7, 0.1 mm. Legend: a, amphid; d, deirid, do, dorsal; e, excretory pore; l, labial papilla; p, submedian papilla; v, ventral.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detailed studies however have not been made on any congeners. Thus, apart from providing a basis for ultrastructural studies currently underway, the detailed description of *N. magnus* is considered valuable as a comparison with studies already carried out on *N. brasiliensis*.

The asymmetry of the bursa has been noted in each congener. The bursa is best studied in apical or ventral views (Durette-Desset 1985), however, in species of *Nippostrongylus* it is extremely difficult to open the bursa, because of its asymmetry. For this reason, left and right lateral views are provided (Figs 8, 9) as well as an apical view (Fig. 10), which was obtained using a live male specimen prior to fixation. The greatest morphological asymmetry occurs in rays 6 and 8, both of which are much larger on the left side of the bursa than on the right, though ray 4 is larger on the right side. Apart from the bursa itself, the spicules and genital cone also exhibit some degree of asymmetry. The tip of the left spicule is much longer and more complex structurally than that of the right spicule, which terminates in a simple point, paralleling the asymmetry of the bursa. Details of the spicule tips have not been provided for congeners except for the tips of the spicules of *N. brasiliensis* (see Mawson 1961). In the case of the genital cone, the (ventral lobe, bearing papilla 0, is symmetrical, while the dorsal lobe, bearing the paired papillae 7 is asymmetrical, with the right papilla longer and hence more posterior than the left (Figs 13, 14). Comparable morphological details are generally lacking for other species, although the genital cone appears to be asymmetrical also in Fig. 1F of *N. rauschi* (see Chabaud & Durette-Desset 1966). Some of these characters may prove useful as generic criteria when described in all species.

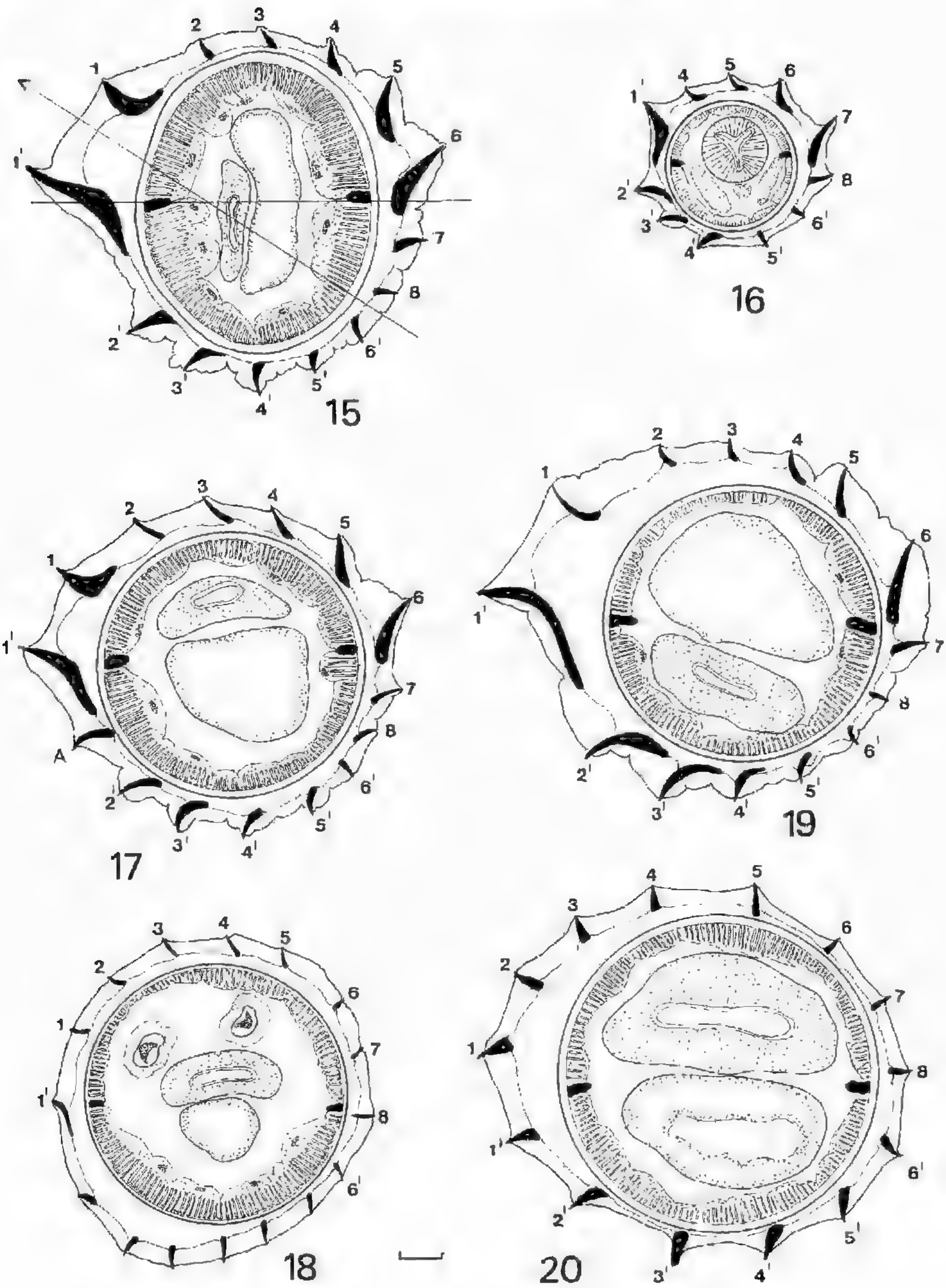
The synlophe is described fully for the first time and confirms the preliminary observations of Durette-Desset (1969) and Lichtenfels (1974). It resembles that of congeners (Chabaud & Durette-Desset 1966; Durette-Desset 1970, 1971; Greenberg 1972) in possessing 14 ridges in the mid-body region with an oblique axis of orientation directed from right-ventral to left-dorsal and a consistent gradient in ridge size. The majority of ridges arise immediately posterior to the cephalic vesicle, with ridges 1,2,3 in the left-dorsal field (ridges 2,3,4 of Lichtenfels 1974) arising immediately anterior to the deirid (1), halfway between deirid and cephalic vesicle (2) and posterior to the vesicle (3). These origins are consistent in males and females and resemble the situation found in *N. brasiliensis* except that in *N. brasiliensis*, ridge 1 arises slightly more posteriorly, at the level of the excretory pore (Lichtenfels 1974). In the posterior region of the male, two additional ridges appear in the left-ventral field, also resembling the arrangement described in *N. brasiliensis* (see Lichtenfels 1974), one about 0.5-0.8 mm from the posterior extremity and a second ridge in the prebursal region. In the posterior region of the female, the number of ridges remains constant, although the ridges become more similar in size and the orientation is more difficult to establish. The extra ridge described in female *N. brasiliensis* by Lichtenfels (1974) is absent in *N. magnus*. Thus the synlophe of *N. magnus* resembles that of *N. brasiliensis* very closely.

The system for numbering ridges employed here differs from that used by Lichtenfels (1974). It attempts to show the axis of orientation and the homology of ridges on either side of the axis. It demonstrates that in both the male and female of *N. magnus*, the asymmetry of ridges and the size gradient are lost in the posterior parts of the body with a symmetrical arrangement of almost equal sized ridges, mostly arranged perpendicular to the body of the nematode. This arrangement would be considered a "hyper-evolved" state in the sense of Durette-Desset (1985). It is of interest that in male *N. magnus*, in the posterior region of the body, not only is there a reduction in size of body ridges and a loss of particular orientation, but also the symmetry of the number of ridges is restored with eight dorsal and eight ventral ridges.

Features of the synlophe of *N. magnus* which might be useful at the specific level are the interruption of ridges in the mid-body region and the irregular branching and anastomosing of ridges in the region of the male bursa, noted by Lichtenfels (1974). In the present study, the interruption of ridges (Fig. 6) occurred in both male and female nematodes, while branching and anastomosing (Fig. 5) was seen in males. Thus Lichtenfels' (1974) observations have been confirmed, but studies of the remaining congeners are required to establish their usefulness.

Lichtenfels (1974) examined specimens of laboratory strains of *N. brasiliensis* adapted to the rat, mouse and hamster and showed that the synlophe was constant, independent of the host species in which the nematode developed. Although much more limited in their extent, the observation that the synlophe of *N. magnus* is identical in specimens from the natural host, *R. fuscipes*, as well as in the laboratory rat, *R. norvegicus*,

Figs 8-14. *Nippostrongylus magnus* (Mawson), male genitalia: 8, bursa, left lateral and dorsal lobes; 9, bursa, right lateral and dorsal lobes; 10, bursa, apical view, left lateral lobe on right hand side; 11, tip of right spicule; 12, tip of left spicule; 13, genital cone, lateral view; 14, genital cone and spicule tips, right ventro-lateral view. Scale lines: Figs 8-10, 0.1 mm; Figs 11-14, 0.01 mm. Figures follow ray numbering system as described by Durette-Desset (1985). Legend: do, dorsal; le, left; ri, right.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adds weight to his conclusions on the stability of synlophe characters in different host species.

The affinities of *N. magnus* with congeners have not been fully investigated. Mawson (1961) considered its differentiation from *N. typicus* (both as species of *Austroheligmonema* Mawson, 1961) based on the shape of the spicules, number of ridges and overall size and from *N. brasiliensis*, due to the greater asymmetry in its bursa, and the form of the dorsal ray. Greenberg (1972) provided a comparative table of measurements of all species, but not of other morphological features. Because of the incomplete nature of the descriptions of several species, comparisons are limited to the synlophe and bursal rays. The synlophe is apparently similar in most species of *Nippostrongylus*, but ridge 1 is substantially larger than ridge 2 in *N. magnus*, the male of *N. typicus*, and *N. rauschi*, with the qualification that *N. rauschi* is described as having 14 ridges, but only 13 are illustrated (Chabaud & Durette-Desset 1966, Fig. 2A). In the case of the dorsal ray of *N. magnus*, the asymmetry of rays 8, with a slender right ray arising before a more robust left ray resembles *N. typicus*, but differs from *N. rauschi*, *N. brasiliensis* and *N. djumachani* which have rays 8 arising symmetrically, though with the left ray more robust than the right, and from *N. rysavyi* in which the left ray 8 arises first and is more slender than the right ray (Erhardova 1959; Mawson 1961; Chabaud & Durette-Desset 1966; Tenora 1969). In *N. witenbergi*, the branching pattern of the dorsal ray resembles that of *N. rysavyi*, but rays 8 are slender (Greenberg 1972).

Thus, *N. magnus* can be differentiated from congeners by several morphological features, in addition to the measurements tabulated by Witenberg (1972), but the features discussed indicate a close relationship with *N. typicus*, also a parasite of endemic Australian rodents.

N. magnus is of biogeographical interest because it is an endemic Australian species occurring in various species of *Rattus* and occasionally in *Melomys cervinipes*. The full host range may be greater than this as a number of endemic rodent species in Australia have not yet been examined for helminth parasites (Mackerras 1958). The endemic species of *Rattus* probably arrived in Australia about one million years ago (Watts & Aslin 1981), hence the morphological differentiation between *N. brasiliensis*/*N. rauschi* and *N. magnus*/*N. typicus* has probably occurred over this same period of time. There are few instances where a time scale can be placed on morphological differentiation between species of parasitic nematodes.

Acknowledgments

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Figs 15-20. *Nippostrongylus magnus* (Mawson), synlophe. 15, male, mid-body region, 1.9 mm from anterior end of 3.3 mm worm with full complement of 14 ridges; arrow indicates axis of orientation of synlophe; 16, male, anterior oesophageal region prior to origin of ridges 2-3; 17, male, 0.85 mm from posterior end showing additional ridge (A); 18, male, immediately anterior to bursa, showing reduced size of ridges and additional ventral ridges; 19, female, mid-body region, with full complement of 14 ridges; 20, female, 0.80 mm from posterior extremity showing reduction in size of ridges but maintenance of same number of ridges. Scale line: 0.01 mm.

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EARLY DEVELOPMENT OF *LIMNODYNASTES* TERRAEREGINAE AND *L. FLETCHERI* (ANURA: LEPTODACTYLIDAE: LIMNODYNASTINAE)

BY *MARGARET DAVIES**

Summary

The development biology of *Limnodynastes terraereginae* and *L. fletcheri* is described. Life history data generally conform with those of congeners in the same species groups. Tadpoles show lentic adaptations and have a generalized body form. At 30°C *L. terraereginae* completed its development in 71 days and *L. fletcheri* in 60 days.
KEY WORDS: Anuran larvae, development, *Limnodynastes terraereginae, Limnodynastes fletcheri,* Limnodynastinae, tadpoles, foam nests.

Transactions of the Royal Society of S. Aust. (1992), 116(4), 117-122.

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DAVIES, M. (1992) Early development of *Limnodynastes terraereginae* and *L. fletcheri* (Anura: Leptodactylidae: Limnodynastinae). *Trans. R. Soc. S. Aust.* 116(4), 117-122, 30 November, 1992.

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KEY WORDS: Anuran larvae, development, *Limnodynastes terraereginae*, *Limnodynastes fletcheri*, Limnodynastinae, tadpoles, foam nests.

Introduction

Limnodynastes Fitzinger comprises 12 species (Tyler 1992) that can be grouped into three morphotypes: burrowing species with short hind limbs and a rotund body, 29-46 mm in body length (two species: *L. ornatus* group), larger burrowing species (52-90 mm length) characterised by well-developed tibial glands (four species: *L. dorsalis* group) and more streamlined non-burrowing species found in marsh and flooded grassland, and ranging from 31-75 mm in body length (six species: *L. tasmaniensis* group) (Tyler *et al.* 1979).

Limnodynastes spp. lay foamy egg masses (but see Roberts & Seymour 1989), but the entire developmental biology has been described only for *L. ornatus* (Tyler *et al.* 1983). Watson & Martin (1973) described tadpoles of *L. interioris*, one of the large burrowing species and examined larvae of *L. dumerilii*, *L. terraereginae*, *L. peroni*, *L. salmini*, *L. tasmaniensis* and *L. fletcheri* to permit a generic definition. However, these authors did not describe these larvae specifically, nor did they provide complete developmental data for *L. interioris*.

Martin (1965) described tadpoles and early stages of *L. dumerilii*, *L. peroni* and *L. tasmaniensis* whilst Tyler *et al.* (1983) described tadpoles of *L. convexiusculus*. Here I describe the developmental biology of *Limnodynastes terraereginae* Fry, (*L. dorsalis* group) and that of *L. fletcheri* Boulenger, (*L. tasmaniensis* group).

Materials and Methods

Spawn of *L. terraereginae* was collected 7 km SW Pentland, Qld and transported to the University of Adelaide after eight days, where it was reared at 30 ±°C in aerated dechlorinated tapwater contained in glass aquaria 25 × 25 × 8 cm.

Spawn of *L. fletcheri* was obtained from individual adults from Deniliquin, N.S.W., that spawned in the laboratory. This material was reared in the same manner.

Developing larvae were fed lightly-boiled, organically-grown mignonette lettuce leaves supplemented with SERA bioflakes pond fish food. Water and food were changed daily.

Samples of eggs, embryos and larvae were collected as shown in Tables 1 and 2 and preserved in Tyler's fixative (Tyler 1962). Cuts were made with a scalpel

TABLE 1. *Dimensions of developmental stages of* Limnodynastes terraereginae.

Age (approx. days, date)	Stage	Body Length $\bar{x}$, range in parentheses	Total Length $\bar{x}$, range in parentheses	n
1 27.i.1991	20	2.37 (2.24-2.4)	5.24 (5.2-5.68)	5
4-17 28.i.1991-12.ii.1991	25	4.19 (2.48-7.2)	11.12 (7.12-19.52)	62
17-22 10.ii.1991-15.ii.1991	26	6.69 (5.6-7.2)	18.08 (15.84-19.52)	10
21-28 14.ii.1991-8.iii.1991	27	9.27 (7.04-11.97	25.15 (18.4-32.13)	14
28 27.ii.1991	28	8.72	34.45	1
55 19.iii.1991	29	11.03 (10.5-11.55)	29.72 (29.4-30.03)	2
28-55 21.ii.1991-19.iii.1991	31	11.07 (8.72-12.45)	35.69 (34.03-38.18)	3
55 19.iii.1991	32	14.12 (13.7-14.53	38.81 (38.18-39.43)	2
50-70 14.iii.1991-7.iv.1991	34	15.13 (14.53-15.8)	42.94 (41.5-44.6)	5
55-70 19.iii.1991-7.iv.1991	36	15.51 (14.0-16.5)	43.77 (39.5-46.7)	7
55-70 19.iii.1991-7.iv.1991	37	15.98 (14.0-17.6)	45.84 (41.7-49.7)	12

* Department of Zoology, University of Adelaide, GPO Box 498, Adelaide, S.A. 5001.

in the presumptive region of the tibial gland of *L. terraereginae* in the metamorphosing specimens.

Measurements of developmental stages were made using an eyepiece micrometer or vernier calipers (reading to 0.05 mm). Illustrations were made with the aid of a Wild M8 stereodissecting microscope and camera lucida.

Developmental stages are those of Gosner (1960).

Results

Limnodynastes terraereginae

Spawn was collected from a heavily-vegetated, deep, roadside depression at approximately 0800 on 26.i.1991. Adults of *L. terraereginae*, had been heard calling at this site the previous night, just before midnight, under an isolated patch of vegetation. The foam nest was large, but an egg count was not obtained, nor were eggs preserved.

At 2130 on 28.i.1991, embryos were at stage 25 (Fig 1). Adhesive glands were reduced to prominent pigment patches. The horny beak and one upper and one lower complete tooth rows were keratinized. The anal opening was median and the spiracle had formed. Embryos remained at stage 25 for a further 24 hr. Feeding had commenced (faeces were in the anal tube). Faint pigmentation was detectable on the adhesive glands. One complete and one divided upper and two complete lower labial tooth rows were keratinized.

Embryos sampled on 30.i.1991 and 1.ii.1991 remained at stage 25. Pigmentation on the adhesive glands was detectable although considerably reduced in the older embryos. Further keratinization of tooth rows was not apparent.

Adhesive gland pigmentation had vanished by 4.ii.1991, although embryos were still at stage 25. The body was more heavily pigmented together with the tail musculature and a lighter dusting on the tail fins. A second divided upper labial tooth row was keratinized.

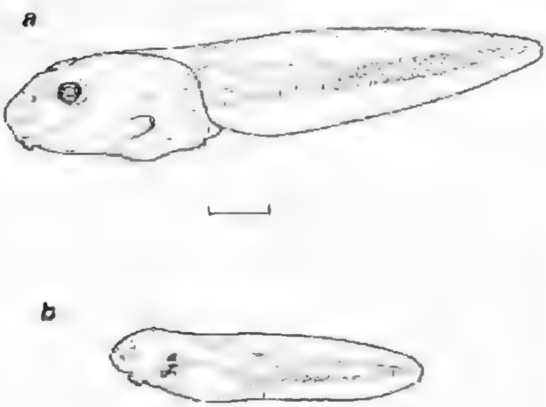

Fig. 1. Embryos of *Limnodynastes terraereginae*: a, Stage 25; b, Stage 20 of hatching. Scale bars = 1 mm

Embryos sampled on 7.ii.1991 remained at stage 25, the only change being an increase in pigmentation particularly on the tail fins. Measurements are given in Table 1.

A single stage 26 larva was sampled on 10.ii.1991 and a second on 12.ii.1991. Pigmentation had increased in these larvae. Stage 27 larvae sampled on 14.ii.1991 had strongly pigmented bodies, tail musculature and tail fins. By 15.ii.1991 stage 27 larvae had a further divided upper and a divided lower tooth row keratinized.

By 21.ii.1991, larvae had reached stage 28 and pigmentation of the body and upper tail musculature had darker pigment patches superimposed over the uniform background. Most of these pigment patches surrounded the neuromasts of the lateral line organs.

By 8.iii.1991, a single stage 31 larva had well-differentiated lateral line organs and the hind limb paddle was pigmented dorsally, extending along the mediolateral surface of the hind limb bud by stage 34. Larvae attained stage 37 by 14.iii.1991.

Measurements of all larvae sampled are given in Table 1.

A larva at stage 36 is shown in Fig. 2. The body is ovoid and widest behind the eyes. The snout is evenly rounded in dorsal and lateral views. The nares are dorsolateral and sessile, opening laterally. The eyes are lateral and relatively large. The spiracle is sinistral, short and ventrolateral with a small orifice directed posterodorsally. It is attached along its medial edge to the body of the larva. It is visible from above and is slightly tapered towards its orifice.

The anal tube is medial and opens at the extremity of the ventral fin. The tail fins are poorly arched and rounded terminally. The dorsal fin commences in the posterior 1/10 of the body, being deepest about halfway along its length. The tail musculature is thick, tapering to a subacuminate terminus.

Tadpoles are moderately heavily pigmented and chocolate markings usually surrounding neuromast cells of the lateral line are superimposed on the background pigmentation. The mouth is ventral and the oral disc is surrounded by lateral and posterior labial papillae interrupted by an anteromedial gap. There are five or six upper and three lower labial tooth rows. The first upper and second and third lower rows remain undivided. The horny beak is moderately robust. The oral disc of a larva at stage 36 is shown in Fig. 3. The first larva reached stage 42 on 2.iv.1991 and stage 46 on 7.iv.1991 having taken a total of 71 days to metamorphose from spawning. Froglets at stage 46 measured 18.00 mm S-V.

Supralabial glands were apparent at stage 42 and although not apparent externally, glandular tissue was detected by eye in cut skin in the region of the presumptive tibial gland.

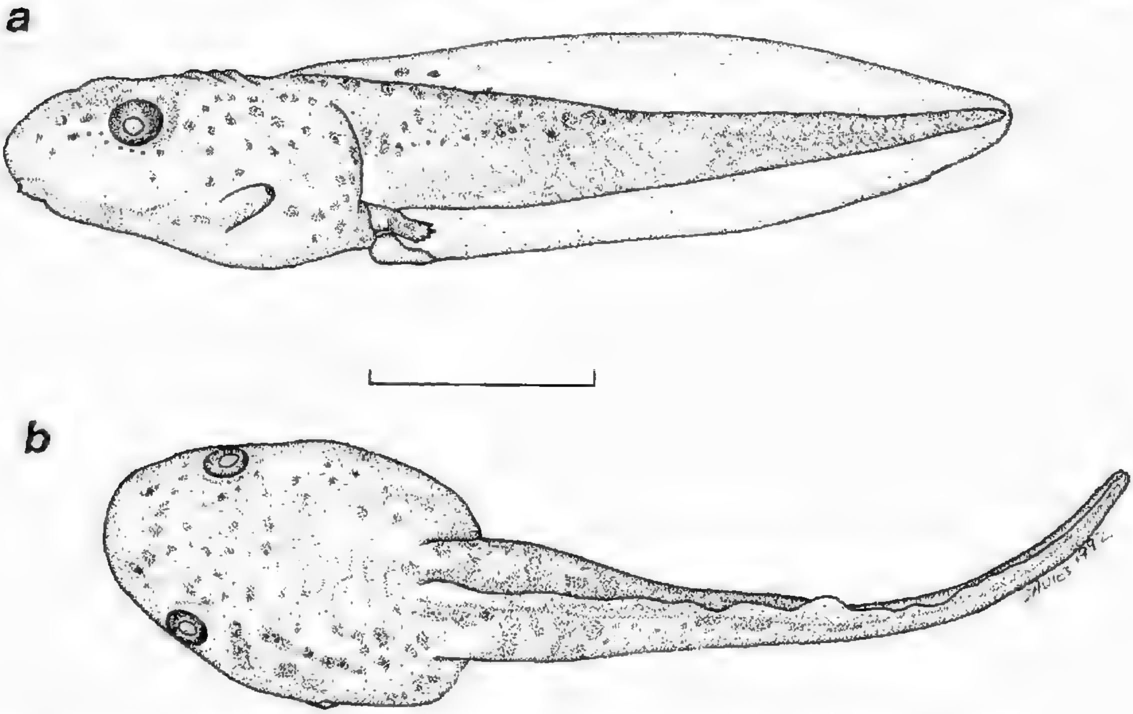

Fig. 2. Larva of *Limnodynastes terraereginae* at Stage 36: a, lateral view; b, dorsal view. Scale bar = 10 mm.

Limnodynastes fletcheri

Spawn was laid in the laboratory in a chamber of recyling, continuously-flowing water described by Chapman (1987). Two spawn clumps deposited overnight on 16/17.xi.1991 and 21/22.xi.1991 respectively were collected. Data are mostly derived from the first clump. Spawn was laid in a foamy nest and twelve eggs from the second clump had a mean diameter of 1.39 mm (range 1.28-1.56). Mean capsule diameter was 1.80 mm (range 1.72-1.88).

Within 24 hours the embryos had reached stage 18 (Fig. 4) and hatched at stage 19, 24 hr later on 20.xi.1991 (Fig. 4). Gills were poorly developed. The mouth was perforated but the nares were not. Tail musculature was poorly delineated.

At 48 hr, the gills had disappeared, but the embryo remained at stage 19.

Embryos reached stage 25 four days after hatching. The anus was median. Slight protrusions of the adhesive glands remained, the base speckled with pigmentation. Over the next three days, the adhesive glands disappeared. The anus moved from a median to a dextral position and the horny beak, together with firstly one and then two upper labial tooth rows and three lower tooth rows, keratinized.

Measurements of stage 25 embryos are given in Table 2 and one is illustrated in Fig. 4.

Stage 26 and 27 larvae were sampled on the seven days after hatching. By stage 27, all tooth rows were keratinized. The body of the larva was irregularly pigmented and a faint dusting of pigment was apparent on the dorsal tail musculature and tail fins.

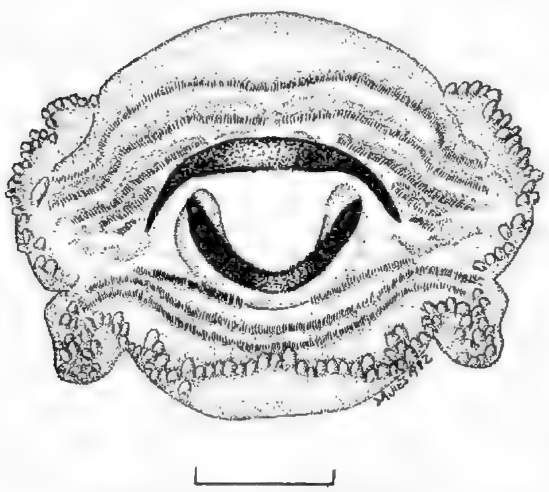

Fig. 3. Oral disc of a larva of *Limnodynastes terraereginae* at Stage 36. Scale bar = 1 mm.

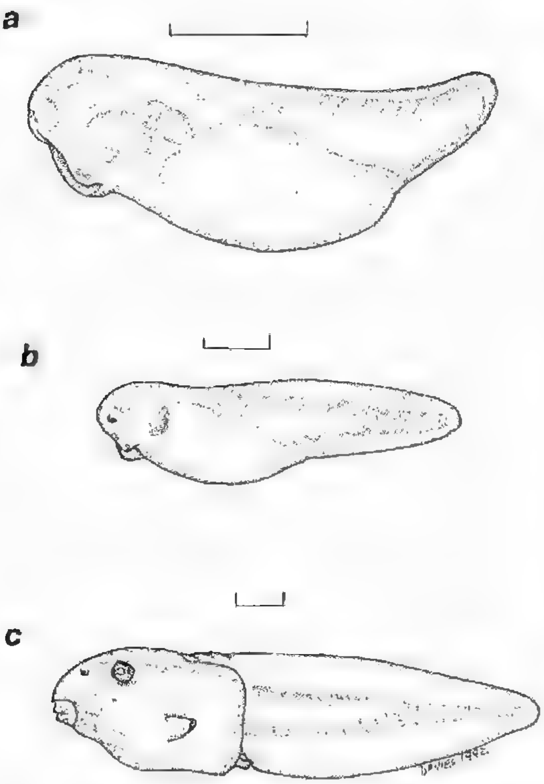

Fig. 4. Embryos of *Limnodynastes fletcheri*: a, Stage 18; b, Stage 19 at hatching; c, Stage 25. Scale bars = 1 mm.

Larvae reached stage 30, 14 days after hatching. The anus was median and patches of chocolate pigmentation were appearing, superimposed over the background coloration of the body and tail. Measurements are given in Table 2.

Larvae reached stage 33 23 days after hatching and stage 35 after 27 days.

A larva at stage 37 is illustrated in Fig. 5. The body is ovoid and widest behind the eyes. The snout is evenly rounded in dorsal view and slightly truncated laterally. The nares are dorsolateral, not elevated, opening anterolaterally. The spiracle is sinistral and relatively short and is visible from above. It is attached to the body wall along its medial edge with the diameter of its orifice being less than the diameter of the tube. The spiracle tapers towards its orifice. The anal tube is median and opens along the ventral edge of the ventral tail fin. The tail fins are arched, the dorsal fin commencing in the posterior 1/10 of the body. Both are deepest approximately half way along their length. The tail fin is slightly rounded at its terminus. Tail musculature is moderately thick, tapering to a point posteriorly. Blotchy chocolate pigmentation on a cream background is located on the tail musculature with weaker melanic patches on the fins. The body is

TABLE 2. *Dimensions of developmental stages of* Limnodynastes fletcheri.

Age (approx. days, date)	Stage	Body Length $\bar{x}$, range in parentheses	Total Length $\bar{x}$, range in parentheses	n
6-11 23.xi.1991-28.xi.1991	25	4.97 (4.0-6.24)	12.49 (9.76-15.2)	27
10-17 27.xi.1991-4.xii.1991	26	7.01 (6.4-8.0)	18.07 (12.0-22.0)	6
10-26 27.xi.1991-13.xii.1991	27	7.25 (6.51-8.61)	19.83 (17.22-23.31)	12
17-26 4.xii.1991-13.xii.1991	28	9.79 (9.13-10.29)	26.48 (24.9-27.46)	3
26 13.xii.1991	29	10.49 (9.96-10.79)	27.73 (26.56-28.59)	4
17-26 4.xii.1991-13.xii.1991	30	11.91 (11.62-12.06)	30.71 (29.88-31.54)	3
47 15.i.1992	31	10.85 (10.3-11.4)	30.85 (30.2-31.5)	2
23-52 9.xii.1991-15.i.1992	32	13.83 (10.8-17.43)	36.96 (27.6-46.07)	18
26-47 13.xii.1991-15.i.1992	33	13.35 (12.0-14.8)	37.20 (34.4-40.26)	10
47-52 11.xii.1991-15.i.1992	34	14.36 (13.1-15.8)	38.83 (34.0-42.0)	14
47-52 8.i.1992-15.i.1992	35	16.23 (15.3-18.0)	44.23 (40.6-48.7)	4
52-70 8.i.1992-26.i.1992	36	17.08 (16.0-18.9)	48.32 (44.2-52.4)	5
70 26.i.1992	37	18.86 (17.5-20.5)	52.24 (48.8-56.0)	13
70 26.i.1992	38	19.0 (18.1-19.9)	57.1 (56.3-57.9)	2
70 26.i.1992	39	22.0	58.5	1
70 26.i.1992	40	24.2	68.5	1
65 21.i.1992	42	22.0	67.9	1
78 3.ii.1992	43	26.1	43.5	1
80 5.ii.1992	43	23.5	60.1	1
74 30.ii.1992	44	22.9	34.8	1
79 4.ii.1992	44	22.5	29.6	1
60 14.i.1992	46	21.2	--	1

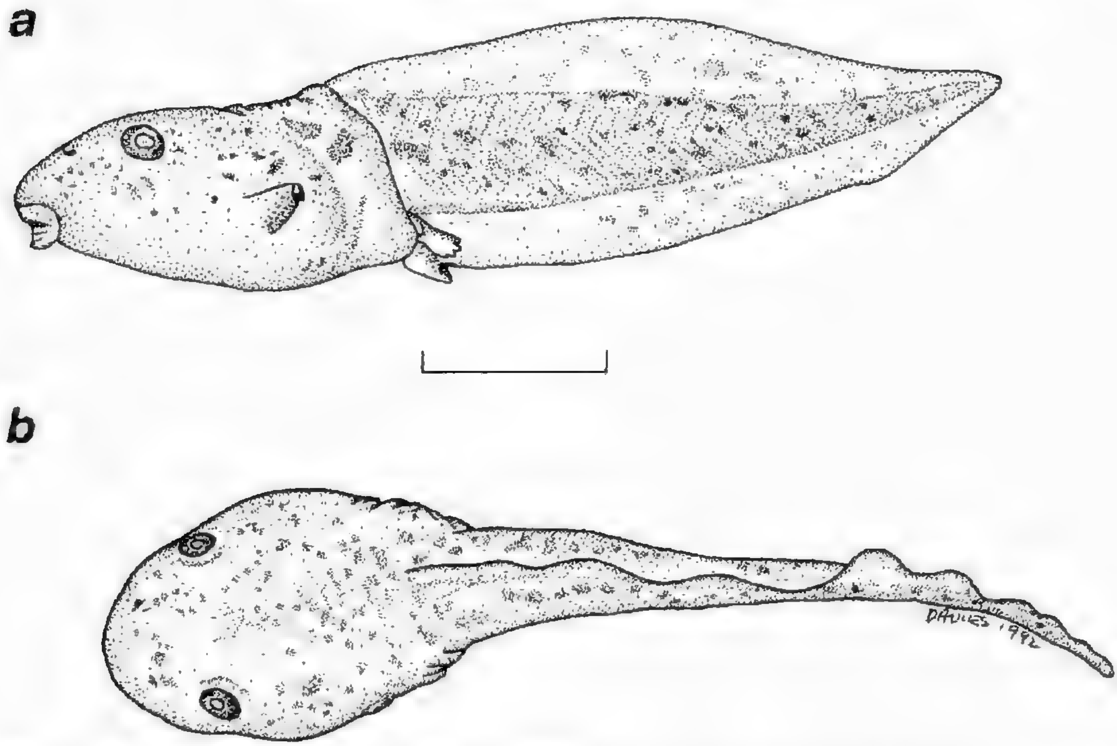

Fig. 5. Larva of *Limnodynastes fletcheri* at Stage 37: a, lateral view; b, dorsal view. Scale bar = 10 mm.

moderately pigmented with a paler cream posterodorsally. Chocolate freckles and smaller blotches are superimposed on the background pigmentation.

The mouth is anteroventral. The oral disc is surrounded laterally by a single row and posteriorly by a double row of labial papillae. Papillae are absent anteromedially. There are three upper and three lower rows of labial teeth. Only those rows adjacent to the beak, which is moderately keratinized, are divided (Fig. 6).

Many of the oral discs examined were abnormal in development with split beaks and incomplete or distorted tooth rows.

Measurements of larvae are provided in Table 2.

By 12.i.1992 a larva had reached stage 42 and by 15.i.1992 it had reached stage 46, 60 days after spawning. Apart from a further three or four individuals, the remainder of the spawn clump did not metamorphose until about 30 days later, i.e., about 10.ii.1992.

Body length at metamorphosis was 21.2 mm.

Discussion

Of the tadpoles of large burrowing species of *Limnodynastes*, only those of *L. interioris* and *L. dumerilii* have been described and illustrated (Watson & Martin 1973; Martin 1965). Larvae of *L. terraereginae* described here have a similar morphology to that of these species although the inner edge of the spiracle may be free in *L. dumerilii* and these larvae are usually darkly pigmented, with older tadpoles being generally lighter (Martin 1965). The

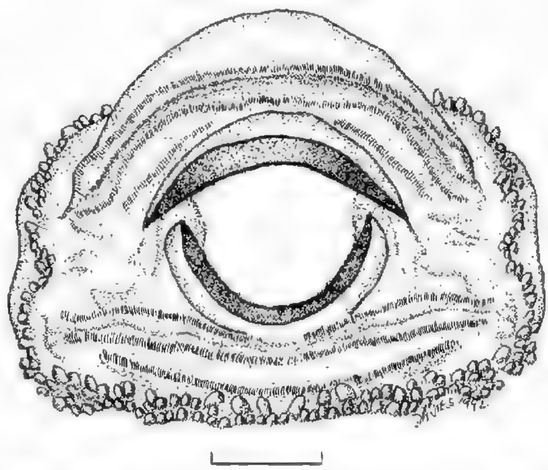

Fig. 6. Oral disc of larva of *Limnodynastes fletcheri* at Stage 37. Scale bar = 1 mm.

general lentic body form of the three species is similar (described as generalized by Watson & Martin 1973).

A tooth row formula of five or six upper and three lower labial tooth rows is consistent within the group and the pattern of labial papillae is common to the three species.

Of the marshy and flooded grassland species, larvae of *L. tasmaniensis* and *L. peroni* have been described by Martin (1965) and those of *L. convexiusculus* by Tyler *et al.* (1983).

Tail fins of these species and of *L. fletcheri* tend to be more strongly arched than those of the *L. dorsalis* group. *L. peroni* has four upper and three lower labial tooth rows, *L. tasmaniensis* have five upper and three lower rows and *L. convexiusculus* has five upper and three lower rows of labial teeth (Martin 1965; Tyler *et al.* 1983). Watson & Martin (1973) recorded at least four and usually five to six rows of upper labial teeth for *L. peroni*, *L. salmini*, *L. tasmaniensis* and *L. fletcheri*.

The presence of only three upper tooth rows in the *L. fletcheri* examined here may be a result of the high proportion of abnormal mouths in the two spawn clumps reared. Only one male was present in the colony of adults from which the spawn was obtained and given that larvae of *L. terraereginae* and *L. salmini* reared under identical conditions did not show the same phenomenon, it is possible that the problem is a genetic one. Ridges lacking in teeth were apparent in the *L. fletcheri* tadpoles and it is possible under other circumstances that tooth rows form on these. It is known that larvae reared in the laboratory tend not to have tooth rows that are as well developed as those that are collected from the field but the deficiency in the rearing methods has not been identified (M. Davies, M. J. Tyler & G. F. Watson unpubl. data).

Whilst recognising the anomaly in the tooth row formula recorded for *L. fletcheri* here, larval characters are consistent with the species groupings based on adult morphology.

Acknowledgments

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A NEW SPECIES OF TRICHOSTRONGYLOID NEMATODE, ODILIA BAINAE, FROM A NATIVE RODENT, RATTUS FUSCIPES (WATERHOUSE)

BY I. BEVERIDGE & M. C. DURETTE-DESSET†*

Summary

Odilia bainae sp. nov. is described from the duodenum of *Rattus fuscipes* (Waterhouse) from Blackwood, Victoria. The new species differs in having shorter spicules than any congener (0.26-0.28 mm), in having a symmetrical bursa and in the number of body ridges.
KEY WORDS: Nematoda, Trichostrongyloidea, *Odilia,* new species, *Rattus.*

Transactions of the Royal Society of S. Aust. (1992), 116(4), 123-128.

A NEW SPECIES OF TRICHOSTRONGYLOID NEMATODE, *ODILIA BAINAE*, FROM A NATIVE RODENT, *RATTUS FUSCIPES* (WATERHOUSE)

by I. BEVERIDGE* & M.-C. DURETTE-DESSET†

Summary

BEVERIDGE, I. & DURETTE-DESSET, M.-C. (1992) A new species of trichostrongyloid nematode, *Odilia bainae*, from a native rodent, *Rattus fuscipes* (Waterhouse). *Trans. R. Soc. S. Aust.* 116(4), 123-128, 30 November, 1992.

Odilia bainae sp. nov. is described from the duodenum of *Rattus fuscipes* (Waterhouse) from Blackwood, Victoria. The new species differs in having shorter spicules than any congener (0.26-0.28 mm), in having a symmetrical bursa and in the number of body ridges.

KEY WORDS: Nematoda, Trichostrongyloidea, *Odilia*, new species, *Rattus*.

Introduction

Very few studies have been undertaken to ascertain the parasite fauna of the various species of the genus *Rattus* endemic in Australia (Mackerras 1958). The most extensive survey to date on the parasites of *Rattus fuscipes* in Victoria (Obendorf 1979) revealed several undescribed species of nematodes including two which were described. A third species, referred to by Obendorf (1979) as "*Longistriata* sp. (undescribed)" was found at a single locality (Blackwood) in Victoria. In this paper, we describe and name the new species as a precursor to studies on its ultrastructure and life history.

Materials and Methods

Nematodes collected from the duodenum of naturally infected *Rattus fuscipes* from Blackwood, Victoria (37°29′S, 144°19′E) were washed in 0.9% saline and fixed live in either hot 70% ethanol or 2.5% glutaraldehyde in phosphate buffer at 4°C. Additional specimens were obtained from laboratory-reared *Rattus fuscipes* infected either orally or subcutaneously with the third-stage larva of the nematode and from laboratory rats *(Rattus norvegicus)* infected via the same routes. Specimens fixed in ethanol were cleared in lactophenol and examined using Nomarski interference microscopy. Drawings and measurements were made using a drawing tube attached to an Olympus BH microscope. Transverse sections of the body of male and female nematodes were prepared using a cataract scalpel and were mounted in lactophenol for examination. An apical view of the cephalic extremity was prepared by the same means. Morphological terms for the body ridges and bursal rays follow Durette-Desset (1985). Ridges dorsal to the axis of orientation of the synlophe were numbered from left to right, 1, 2, 3 . . . etc. while ridges ventral to the axis were numbered from left to right 1^1, 2^1, 3^1 . . . etc. Measurements were made on five male and five female specimens and are presented, in millimetres, as the range followed by the mean in parentheses. Specimens fixed in glutaraldehyde were embedded in resin, sectioned at a thickness of 1 μm, stained with toluidine blue and examined under the light microscope.

Type specimens and specimens from experimental infections have been deposited in the collections of the South Australian Museum (SAM), Adelaide.

Odilia bainae sp. nov.
FIGS 1-18

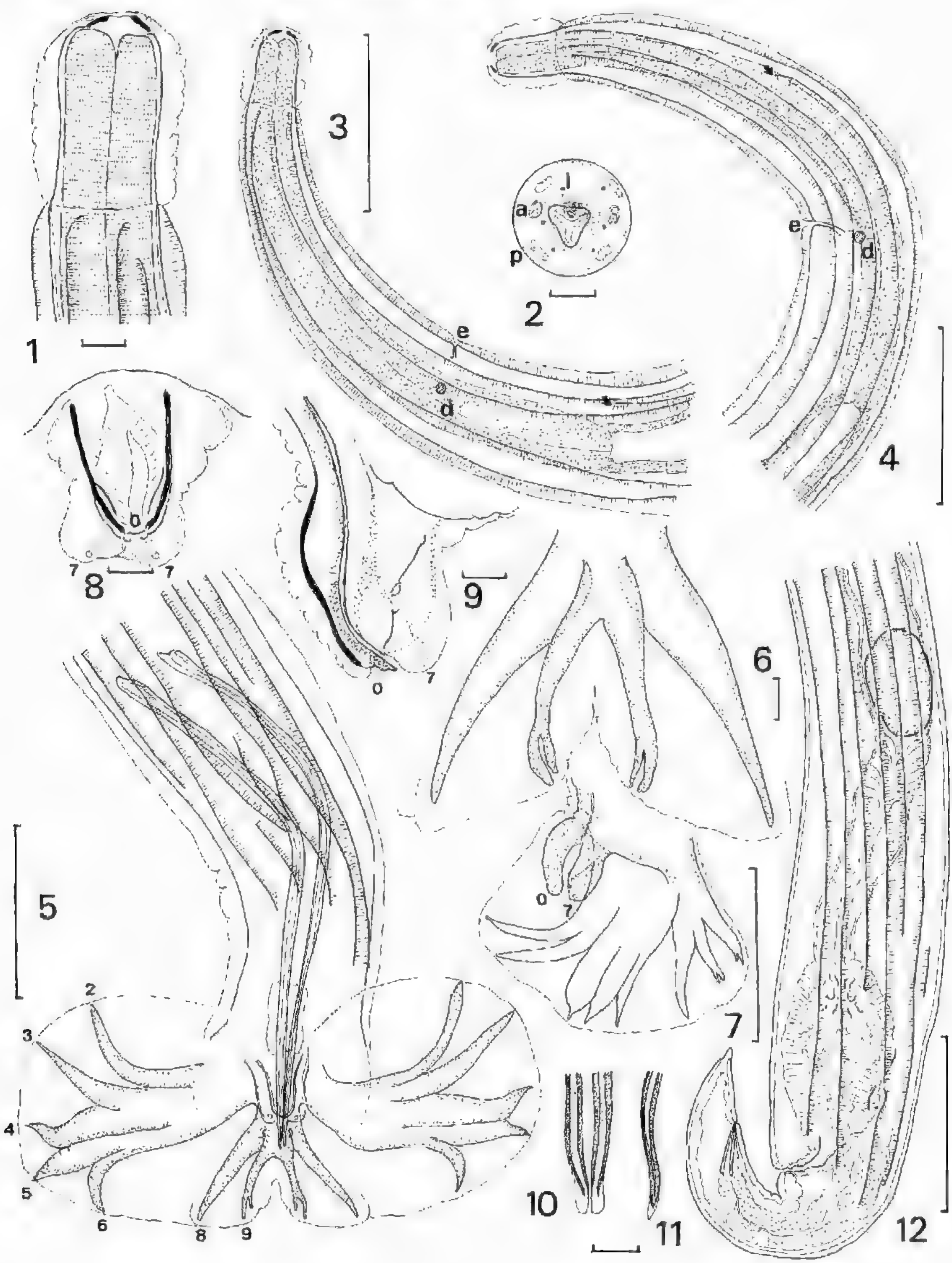
Longistriata sp. (undescribed) of Obendorf (1979).

Types: Holotype male, from duodenum of *Rattus fuscipes* (Waterhouse), Blackwood, Victoria, 15.x.1991, SAM V4181; allotype female, SAM HC22890; paratypes, 12♂♂, 10♀♀, SAM HC22879, 22883.

Material examined: From *R. fuscipes* (natural infection): types; (experimental infections): 26♂♂, 29♀♀ (SAM HC22881). From *R. norvegicus* (experimental infections): 14♂♂, 17♀♀, (SAM HC22875).

Description: Small, sinistrally-coiled nematodes, red in colour when live; prominent cephalic vesicle present, symmetrical in shape; buccal capsule vestigial, teeth absent; mouth opening sub-triangular, surrounded by six tiny labial papillae; four double sub-median papillae and paired amphids present, external to labial papillae; dorsal oesophageal gland small but distinct in apical views of head; oesophagus claviform; nerve ring in mid-oesophageal region; deirids dome-shaped,

* Department of Veterinary Science, University of Melbourne, Parkville, Vic. 3052.
† Biologie parasitaire, Protistologie et Helminthologie, Muséum national d'Histoire naturelle, 61 rue Buffon, 75005 Paris, France.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in region of excretory pore. Synlophe composed of 17 longitudinal ridges in mid-body region: axis of orientation (Fig. 13) from right-ventral field to left-dorsal field at approximately 40° to horizontal: diminutive carène, or cuticular dilation, present on left dorsal aspect between ridges 2' and 5 (Figs 14, 17): nine ridges in dorsal field, ridges 1 to 5 small, ridges 6 and 7 larger, ridges 8 and 9 small; eight ridges in ventral field, ridges 4 and 5 larger than either 1 to 3 or 6 to 8; some variation in relative size of ridges occurs along body of nematode, with ridges 1(1') and 2(2') diminishing in size in mid-body region (for example, compare Figs 13 and 14); most ridges arise immediately posterior to cephalic vesicle, single ridge on left side arises at level of nerve ring; single ridge on right side arises posterior to excretory pore; number and orientation of ridges variable in posterior extremity of body.

Male. Length 3.5-4.1 (3.8), maximum width 0.09-0.10 (0.09); cephalic vesicle 0.04-0.05 (0.05) long; oesophagus 0.31-0.36 (0.34) long; nerve ring 0.16 from anterior extremity; excretory pore 0.23-0.24 (0.23) from anterior extremity; deirids 0.23-0.25 (0.24) from anterior extremity; spicules 0.26-0.28 (0.27) long; gubernaculum lightly sclerotised, visible only in few specimens, 0.05-0.07 (0.06) long. Synlophe: ridges branch and anastomose irregularly in posterior region of body; up to 19 ridges at level of spicules; ridges reduced but relatively uniform in size, most oriented perpendicular to body, synlophe orientation difficult to discern. Bursa symmetrical, dorsal lobe reduced. Dorsal ray symmetrical, divided near origin, terminal subdivisions short, symmetrical; rays 8 arising with dorsal trunk, papillae 8 close to margin of bursa; rays 4, 5, 6 grouped together; ray 6 slender, sharply recurved near extremity; ray 5 robust; ray 4 robust, almost acuminate; rays 2 and 3 slender, reaching margin of bursa. Genital cone extremely prominent, lightly sclerotised; ventral lip conical with single apical papilla, dorsal lobe with paired papillae 7. Spicules elongate, alate, triquetrous in transverse section; similar; tips with slightly expanded flange of clear spicular material in dorso-ventral view; gubernaculum present, very lightly sclerotised, not visible in all specimens.

Female. Length 4.3-4.9 (4.6), maximum width 0.10-0.13 (0.11); cephalic vesicle 0.04-0.06 (0.05) long; oesophagus 0.33-0.44 (0.38); nerve ring 0.19 from anterior extremity; excretory pore 0.23-0.27 (0.25) from anterior extremity; deirids 0.25-0.27 (0.26) from anterior extremity; tail 0.03-0.07 (0.05); vulva to posterior end 0.09-0.17 (0.12), egg 0.07-0.08 (0.08) by 0.04-0.05 (0.05). Monodelphic; infundibulum short; egg thin-shelled, ellipsoidal. Synlophe: Ridges interrupted in posterior part of body, disappear at level of vulva; up to 19 ridges present at level of infundibulum, ridges reduced in size and uniform in size, most oriented perpendicular to body; orientation of synlophe difficult to discern. Tail short, conical; vulva close to anus.

Discussion

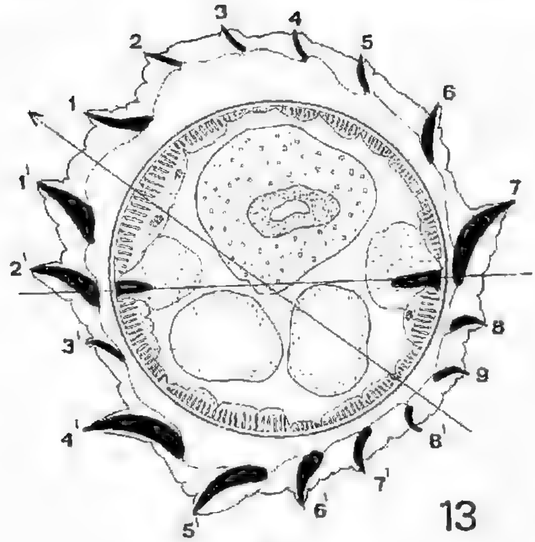
The species described above clearly belongs to the Nippostrongylinae Durette-Desset, 1971 in possessing a synlophe oriented between 45 and 67° from the sagital axis and a latero-median gradient in ridge size. In possessing a carene, or swelling on the left dorsal aspect of the body, with a moderately hypertrophied left lateral ridge and an obvious size difference between the left lateral ridge and the left dorsal ridges, the nematode belongs to one of series of related genera, *Neoheligmonella* Durette-Desset, 1971, *Carolinensis* Travassos, 1937, *Odilia* Durette-Desset, 1973 and *Nippostrongylus* Lane, 1923 (see Durette-Desset 1983). The possession of a dorsal ray divided close to its origin and a common origin for the dorsal and externo-dorsal rays exclude this species from *Neoheligmonella* and *Carolinensis*, while the symmetry of its bursa, and in particular rays 6, exclude it from *Nippostrongylus*. Genera erected since the publication of the key of Durette-Desset (1983), *Malaistrongylus* Ow Yang, Durette-Desset & Ohbayashi, 1983, *Rattustrongylus* Ow Yang, Durette-Desset & Ohbayashi, 1983, and *Sabanema* Ow Yang, Durette-Desset & Ohbayashi, 1983, all differ from the species described above in lacking a hypertrophied left lateral ridge (see Ow Yang *et al.* 1983). The species described above therefore belongs to *Odilia*.

Figs 1-12 *Odilia bainae* sp nov from *Rattus fuscipes*. 1, cephalic extremity, showing cephalic vesicle; 2, apical view of anterior extremity, 3, anterior end, right side, showing origin of ridge (arrow) at level of oesophago-intestinal junction; 4, anterior end, left side, showing origin of ridge (arrow) at mid-oesophageal level; 5, posterior end of male, ventral view, showing irregularities in ridges; 6, dorsal lobe of bursa, dorsal view, 7, lateral view of bursa showing prominent genital cone; 8, genital cone, ventral view, 9, genital cone, lateral view, 10, spicule tips, ventral view, 11, spicule tip, lateral view, 12, tail of female.

Figs 5-9 follow ray numbering system as described by Durette-Desset (1985), 0,7 represent the papillae of the genital cone in the same system.

Legend: a, amphid, d, deirid, e, excretory pore, l, labial papilla, p, submedian papilla.

Scale lines: figs 1, 2, 6, 8-11, 0.01 mm; figs 3-5, 7, 12, 0.1 mm



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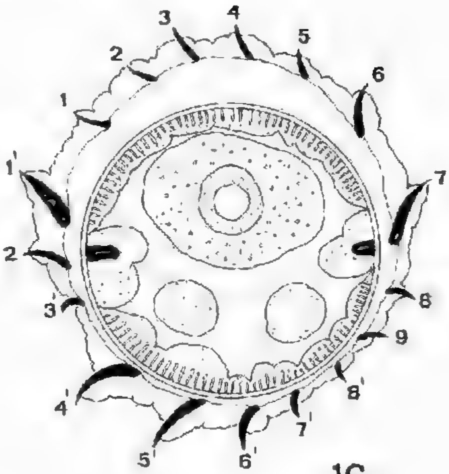

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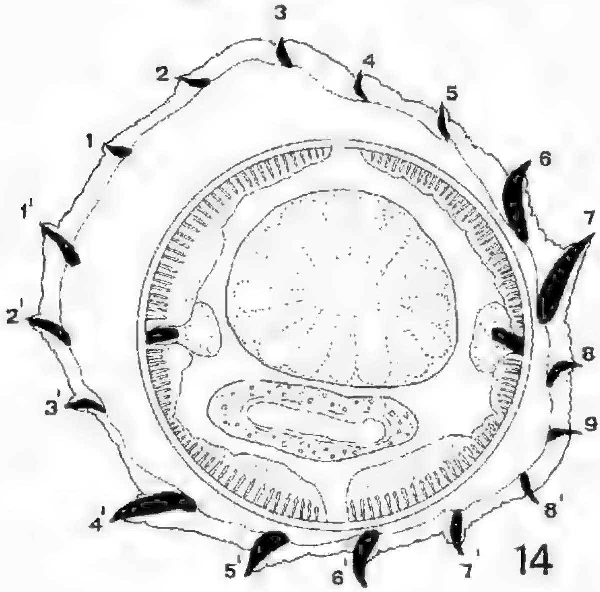

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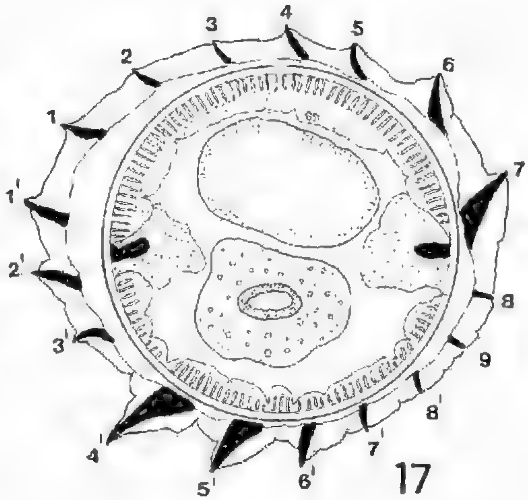

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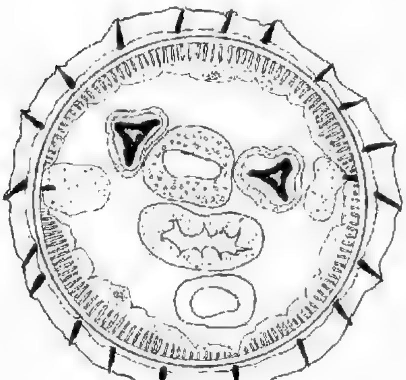

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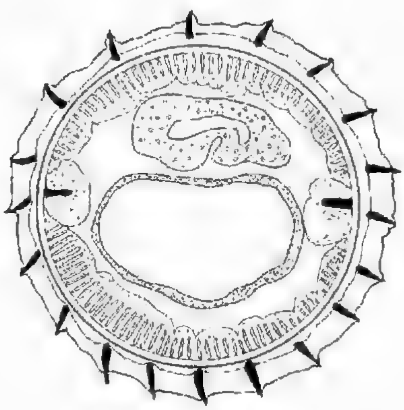

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The genus *Odilia* was established to contain seven species of trichostrongyloid nematodes belonging to the Nippostrongylinae, parasitic in Australian murid rodents. The genus is clearly related to *Nippostrongylus*, which is cosmopolitan in rodents, particularly *Rattus* spp. (see Durette-Desset 1970), *Neoheligmonella* in African murid rodents and *Carolinensis* in holarctic arvicolid and gerbillid rodents, but is distinguished primarily by the characteristic form of the dorsal ray (Durette-Desset 1971) which is deeply divided and arises at the origin of the externodorsal rays. The new species described here was initially identified as "*Longistriata* sp., undescribed" (*sensu* Mawson 1961) by Obendorf (1979). The species described above can be differentiated from all congeners by its extremely short spicules (0.26-0.28 mm). It differs from *O. mackerrasae*, *O. mawsonae*, *O. brachybursa*, *O. polyrhabdote* and *O. emanuelae* in possessing a symmetrical caudal bursa. The remaining species, *O. melomyos* and *O. uromyos* have a symmetrical bursa. The new species also differs from all congeners in which the synlophe has been described in the number of ridges in the mid-body region, 17 in the new species compared with 14 in *O. brachybursa*, 18 in *O. emanuelae*, 16 in *O. mackerrasae*, 15 in *O. melomyos*, 36 in *O. polyrhabdote* and 21 in *O. mawsonae*, although *O. mawsonae* has 17 ridges in the anterior part of the body (Durette-Desset 1969). The number of ridges in *O. uromyos* is not known. Thus the material described confirms the observation of Obendorf (1979) that it is a new species, which we here name *O. bainae*, after Dr Odile Bain, in whose honour the genus was erected.

The presence of an additional species of *Odilia* in an endemic species of *Rattus* is of interest in view of current hypotheses on the evolutionary relationships of the genus. Mawson (1961) observed that the trichostrongyloid genera present in endemic murine rodents, that is the species of *Rattus*, belong primarily to *Nippostrongylus* and *Austroheligmonema* Mawson, 1961, although *Austroheligmonema* is now regarded as a synonym of *Nippostrongylus* (see Durette-Desset 1971). Those nematodes present in the "Old endemic" rodents belonging to the sub-family Hydromyinae were mainly species placed in the genera *Longistriata* Schulz, 1926 and *Heligmonoides* Baylis, 1928, although all of them are now included in a single genus *Odilia*. In a re-examination of the morphology of Australian species by Durette-Desset (1969), a trend in synlophe morphology was observed from species with a carene, hypertrophied left, lateral ridges and a size gradient in ridges from right to left towards synlophes such as that found in *O. polyrhabdote* in which the number of ridges was increased, but their sizes diminished and the distinctive orientation was lost. Because the former type of synlophe occurs in genera such as *Nippostrongylus* which occur in south-east Asia, Durette-Desset (1971, 1985) considered these findings consistent with the hypothesis that the hydromyine rodents reached Australia with nematodes resembling *Nippostrongylus*, and that the genus *Odilia* evolved in isolation in the Hydromyinae. The more recent arrival of species of *Rattus* in Australia about one million years ago (Watts & Aslin 1981) probably introduced or re-introduced *Nippostrongylus*, and lead to the development of the two endemic species, *N. typicus* and *N. magnus* in *Rattus fuscipes*. According to this hypothesis, species of *Odilia* present in endemic Australian *Rattus* spp represent transfers from hydromyine rodents.

With respect to synlophe morphology, the new species fits within the transition series envisaged by Durette-Desset (1969). The number of synlophe ridges (17) is greater than that expected in the supposed ancestral state (14) and although a size gradient in the ridges remains, the carene is not prominent. Two species of *Odilia* occur in *Rattus* species in addition to *O. bainae*, these being *O. emanuelae* in *R. conatus* and *O. polyrhabdote* in *R. fuscipes* (syn *R. assimilis*). In each instance, the species of *Rattus* involved is broadly sympatric with hydromyine rodents, principally *Melomys* spp. (Watts & Aslin 1981) which could have acted as donors in the transfer to *Rattus* spp. At Blackwood, the only known locality for *O. bainae*, no other hydromyine rodents other than the water rat, *Hydromys chrysogaster*, occur. This suggests that *O. bainae* is exclusively a parasite of *Rattus* spp., and that transfer of the species of *R. fuscipes* occurred some time in the past, either when hydromyine rodents occurred in the area, or prior to the extension of *R. fuscipes* into this region. However, of the Australian hydromyine rodents, only the parasites of *Hydromys*, *Uromys* and *Melomys* have thus far been studied, and for many species and genera, there are as yet no records (see Mackerras 1958). Therefore any conclusions on the host or geographic distributions of individual nematode species within them need to be treated with some caution.

Figs 13-18. *Odilia bainae* sp.nov. from *Rattus fuscipes*. Transverse sections at different levels showing synlophe. 13, male, 0.40 mm from anterior end with arrow indicating axis of orientation of synlophe, 14, male, mid-body region, 2.2 mm from anterior end; 15, male, section at level of spicules, 0.26 mm from posterior end, 16, female, 0.40 mm from anterior end; 17, female, mid-body region, 1.4 mm from anterior end; 18, female, 0.20 from posterior end. Scale line: 0.01 mm.

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A DISSECTION METHOD FOR DETERMINING THE GUT CONTENTS OF CALANOID COPEPODS

BY JOHN D. GREEN

Summary

Transactions of the Royal Society of S. Aust. (1992), 116(4), 129-132

BRIEF COMMUNICATION

A DISSECTION METHOD FOR DETERMINING THE GUT CONTENTS OF CALANOID COPEPODS

The examination and recording of gut contents has proved to be a useful aid in the study of the diets of zooplankton. The method cannot give a complete picture of the diet of a particular species as some food items are more delicate than others and are more readily broken during mastication and dissolved by digestive enzymes. However, many algae and animals in the diets of copepods remain sufficiently undamaged, or have adequate identifiable parts that are resistant to enzymatic breakdown, to allow a reasonably good assessment of diet from gut contents analysis [1,2,3,4]. It is preferable to base the analysis on the contents of the fore-gut (Fig. 2), in which much of the ingested material has been less affected by enzymatic action and is less compacted, than on the compacted and well digested bolus in the hind-gut, or the faecal pellets.

It is not a simple matter, however, to dissect out the entire gut contents of a copepod, largely because of the manipulative delicacy required. The contents of the foregut can be particularly difficult to extract in their entirety because of their diffuseness. Those who have used a dissection method may thus choose to remove only the hind gut bolus[5]. The methods most used for examining gut contents avoid direct dissection. In the squash technique, the gut contents are extracted from either live or preserved specimens by pressing down on a coverslip over the animal[1,2,6]. This method has the advantage of both releasing the material in the gut and dispersing it so that individual items may be identified and counted. Another method is to render the whole animal transparent by clearing it in lactic acid[7], or in euparal or canada balsam after passing it through an alcohol series[8]. The drawback here is that the gut contents are not dispersed, and even when the gut boluses can be clearly seen the individual food items are mostly difficult to identify positively or to count. One way of overcoming such difficulties is to place the specimen under a cover slip and erode away most of the tissues with weak sodium hypochlorite[9]. The hypochlorite is then flushed away before the gut contents are oxidised, and it is usually possible to identify many of the individual food items by gently moving the cover slip, which partly redistributes the gut contents. The method has been used successfully in Australia to determine maximum gut food-particle sizes of the copepods *Calamoecia lucasi*, *Boeckella minuta* and *B. triarticulata* in Wallerawang Reservoir[4].

During a study of carnivory by three large omnivorous calanoid copepods (*Boeckella major*, *B. pseudochelae* and *Hemiboeckella searli*) from temporary ponds on the upper River Murray floodplain, we tried all the above methods of gut contents analysis. None of them proved entirely satisfactory, particularly for revealing the remains of animals in the gut contents. This appeared to be mainly due to the large size and thick bodies of the copepods, and because we had available only specimens preserved in 4% formalin and 70% alcohol. The squash method appeared reasonably satisfactory for small specimens, but in larger animals (and particularly those preserved in 4% formalin) the gut contents were often difficult to observe clearly amongst the mass of disrupted exoskeleton and muscle tissue. Clearing in lactic acid was only partly successful. The copepods did not clear very well, again apparently because of their large size. Whenever the food boluses could be seen clearly, animal remains (e.g. cuticle, setae) were difficult or impossible to recognise as they usually were crushed and compacted within the bolus. The hypochlorite erosion method was also not entirely successful. Even though the gut contents could be partly manipulated, the fact that the gut boluses were not fully dispersed made animal material difficult to see. As well, it was found that bubbles of oxygen produced during tissue erosion accumulated within the body and obscured the gut contents, and that care had to be taken to ensure that the gut contents themselves were not oxidised.

In order to overcome these difficulties we developed the following dissection method, which enables the entire gut contents of both small and large copepods to be removed. The contents of both fore- and hind-guts can be cleanly extracted without interference from most surrounding tissues, dispersed, and permanently mounted.

Needles for dissection are made from 2 cm lengths of 0.3 mm tungsten wire, which is rigid enough to allow some pressure to be applied during dissection, and may be sharpened to a fine point. For dissecting large copepods a sharp enough point can be produced with a fine diamond whetstone (e.g. "Ezelap"). For small copepods it is better to produce the desired point by erosion, either in molten $NaNO_2$, heated over a bunsen burner in a crucible[10] or by electrolysis in 10-20% KOH. For electrolysis, the wire is clamped to one terminal of a 6V alternating current electrical circuit (a microscope-illumination transformer is suitable) and dipped into the KOH[11,12]. In either case, the wire is moved in and out of the fluid, and the depth to which the wire is inserted governs whether the resulting point is short and stout or long and slender. The sharpened needle is then mounted in a holder. Satisfactory holders may be made from pin vices (small finger-operated drill holders available from model shops) that have been lengthened, if necessary, by the addition of a section of brass rod (Fig. 1,e). The tungsten needle is bent at a slight angle to the axis of the holder (Fig. 1,tn), to aid keeping the needle parallel to the slide surface during dissection. Jeweller's forceps, with finely sharpened points, are used for transferring copepods, or their parts.

Dissection can be done in water, but it is easier if a more viscous medium is used. Polyvinyl alcohol-lactophenol mountant (PVA)[13] is very suitable as it can be used to make permanent mounts of the gut contents. Lignin pink may be added to the PVA to stain chitin.

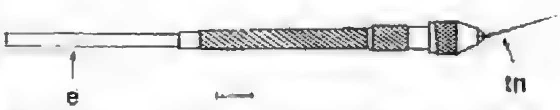


Fig. 1. A dissecting needle, consisting of a pin vice holding a finely pointed tungsten needle (tn). The commercially available pin vice has been extended by the addition of a section of brass rod (e). Scale bar = 1 cm.

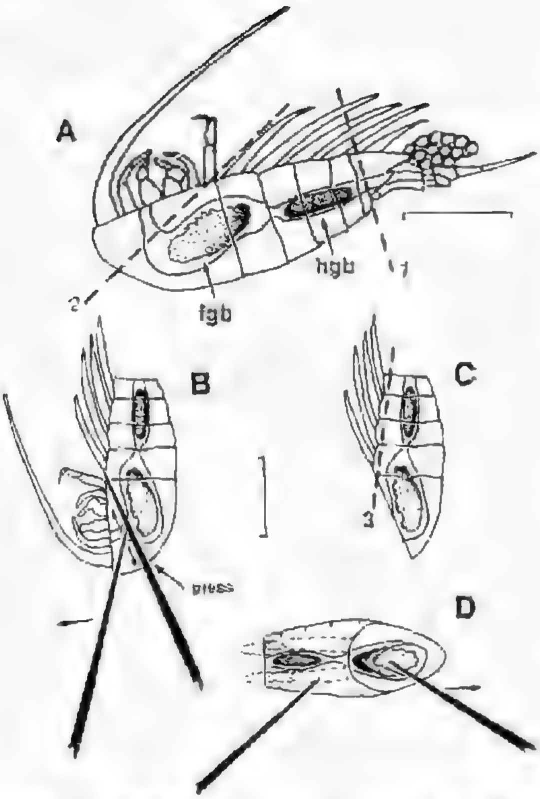


Fig. 2. Dissection of gut contents. Orientation of specimens is that for a right handed person. A. Lateral view of *Boeckella major* showing the fore gut (fgb) and hind gut (hgb) boluses. The first and second dissection cut-lines are shown by dashed lines 1 and 2, respectively. B. Orientation of the copepod and dissection technique for removing the antero-ventral portion of the prosome. The right needle is placed with its point between the maxilliped and first swimming legs and pressed firmly down and held against the slide. Back and forth movements of the left needle then sever the antero-ventral surface, which is pulled away to the left. C. The body ready for transfer to the second drop of PVA. The optional cut-line for removing the remaining ventral surface is shown by a dashed line. D. Extraction of the fore gut contents. The body is held with the left needle while the fore gut bolus is gently pulled out with the right needle. Scale bars = 1 mm.

Using the forceps, two drops of PVA are placed on a slide. The copepod is picked up with the forceps and placed in one drop, in which most of the dissection (i.e. removal of urosome, antero-ventral surface and mouthparts) is done. The body is then transferred to the second drop for the removal, teasing-out and mounting of the gut contents.

Dissection is done using a stereo dissecting microscope at a magnification of ca. 30-40×. The copepod is orientated with its ventral surface partially inclined to the left and away from the dissector, and, for a right-handed person, with its anterior end to the left (Fig. 2a). Firstly the urosome and terminal segment of the prosome are removed by cutting along dashed line 1 (Fig. 2a), and then the antero-ventral surface of the cephalosome plus mouthparts, by cutting along dashed line 2 (Fig. 2a). If desired, the swimming limbs (P1-P4) may also be removed (by cutting along dashed line 3, Fig. 2c). This is not absolutely necessary but may be useful if the ovaries are well developed. Swollen ovarioles make removal of the gut contents difficult, and removal of the swimming limbs and remaining ventral surface usually results in the concomitant removal of much of the ovary tissue.

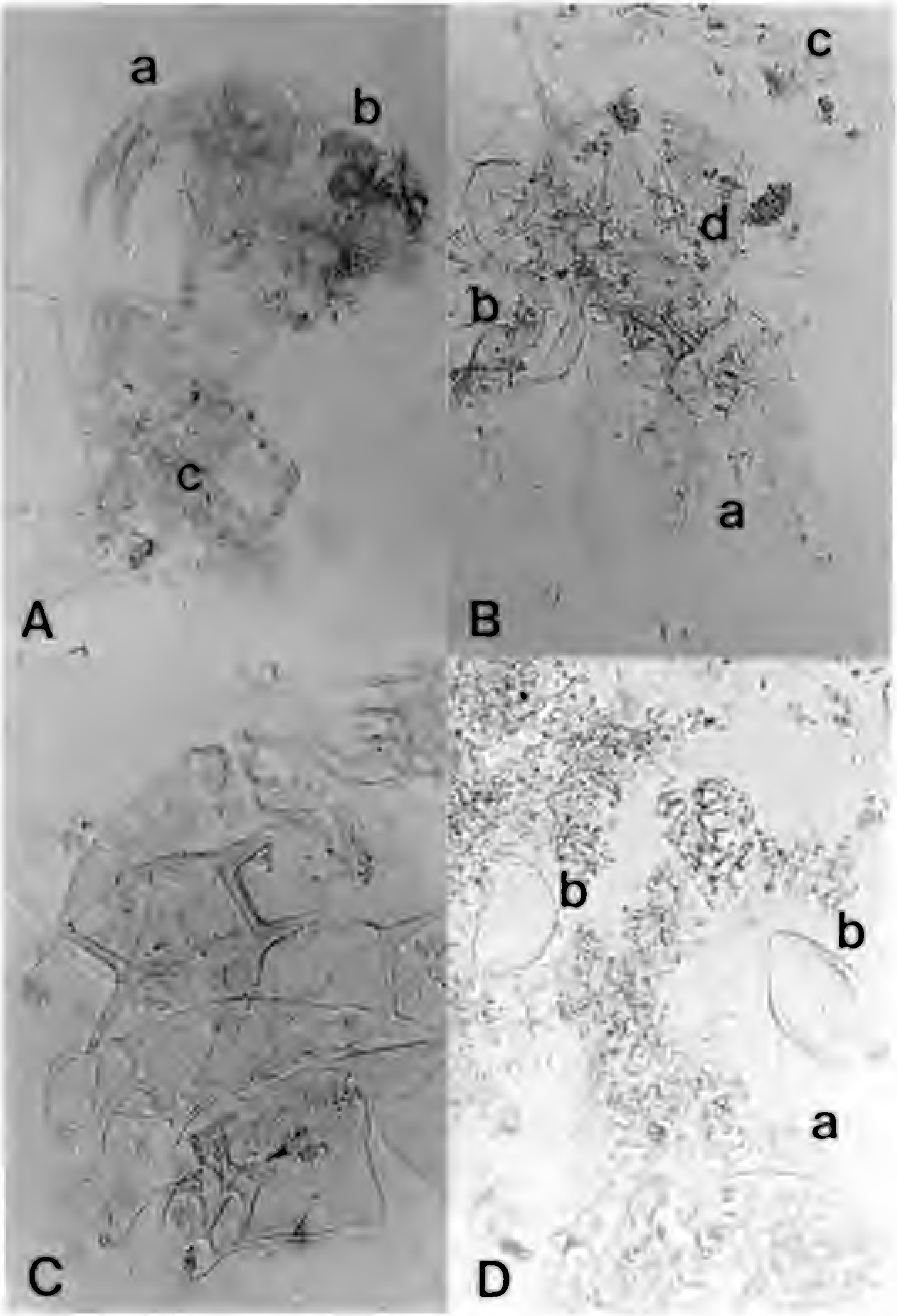
The first cut is made with the animal orientated as shown in Fig. 2a. The body is held with the left needle and the cut made with the right needle by pressing down firmly along line 1, using a forward and backward sawing action of the right needle if necessary. For the second cut, the animal is reorientated to the position shown in Fig. 2b. The animal is held with the left needle (near the base of the first antennae is a suitable point) and the right needle firmly pressed down over the body (Fig. 2b), with the point of the needle between the maxillipeds and first pair of swimming limbs. While the right needle is pressed firmly down against the slide, the antero-ventral surface and mouthparts are severed by back and forth cutting movements by the tip of the left needle (Fig. 2b). The procedure usually pushes the fore-gut bolus slightly dorso-posteriorly towards the rear of the fore gut, and very occasionally may result in the rear-gut bolus being extruded. If this happens, the rear-gut bolus can be retrieved with the forceps and transferred to the second drop of PVA. The body should now look as shown in Fig. 2c. If necessary, the swimming legs may now be removed by cutting along line 3 (Fig. 2c), pressing down on the body with the right needle.

Using the forceps, the body may now be transferred to the second drop of PVA, and held by the left needle with ventral side uppermost and anterior end facing right (Fig. 2d). The fore-gut contents are then carefully scraped out with the right needle (Fig. 2d), the body rotated 180°, and the rear-gut bolus removed in a similar manner. Finally, the body is removed with the forceps and discarded.

The food boluses may now be carefully teased apart with both needles and a small coverslip added. A 10 mm or smaller diameter coverslip is better than the standard 24 mm size, to reduce the area that has to be searched during microscope examination. The gut contents can be fully dispersed by the application of light pressure, and perhaps also small side-to-side movements, to the top of the cover slip with a needle or the forceps.

The gut contents of both small (e.g. *Boeckella symmetrica*, body length ca. 1-1.5 mm) and large (e.g. *B. major*, body length ca. 3-5 mm) freshwater calanoid copepods can be easily extracted using this dissection method. Because both the gut boluses can be extracted and teased apart we found that the

Fig. 3. Photomicrographs of animal remains and algae in dissected gut contents of *Boeckella major*. A. *Daphnia carinata*: a, post-abdomen; b, mandibles; c, cuticle and thoracic limbs. B. a, calanoid copepodite limbs; b, calanoid copepodite mandible; c, calanoid nauplius; d, *Testudinella patina*. C. *Keratella procurva*, trophus arrowed. D. Algae; a, *Staurastrum* sp; b, indet. diatom


a
b
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method reveals animal remains in the gut contents better than the whole-animal squash and clearing techniques mentioned above. It is possible to pick out both very small animal remains (e.g. rotifer trophi, Fig. 3), and the diaphanous cuticular remnants and setae of cladocerans and copepods (Fig. 3). The visibility of cuticular fragments is enhanced by the lignin pink stain in the PVA, and also by the use of Nomarski interference optics. Algae, fungi, detritus and inorganic material in the guts are also clearly visible (Fig. 3). It is possible to make quantitative counts of the gut contents.

Animals preserved in 70% alcohol proved to be easier to dissect than those in 4% formalin. Alcohol preservation results in the dissolution of much of the muscle tissue and the softening of the exoskeleton. The body is thus easier to sever and to manipulate than when preserved in formalin, and there is less tissue "rubbish" in the final gut contents preparation.

The dissected limbs and other body parts remaining in the first drop of PVA can be put to good use. The mouthparts can be dissected off the remnant antero-ventral surface more readily than they can be from the whole animal. To do this, the apodemes at the bases of the mouthparts are anchored solidly against the slide with the left needle, while the mouthparts are easily dissected off with the right needle. Moreover, egg sacs removed with the urosome can be used for clutch-size determinations and measurements of egg size.

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JOHN D. GREEN, Dept of Biological Science, University of Waikato, Private Bag 3105, Hamilton, New Zealand.
RUSSELL J. SHIEL, Murray-Darling Freshwater Research Centre, P.O. Box 921, Albury N.S.W. 2640.

"ROLLERS" AND "CARRIERS": FIELD OBSERVATIONS OF CARRION REMOVAL BY TROGID BEETLES (*OMORGUS STRZELECKENSIS*) IN ARID NORTH-EASTERN SOUTH AUSTRALIA

BY ANDREW J. BOULTON

Summary

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BRIEF COMMUNICATION

"ROLLERS" AND "CARRIERS": FIELD OBSERVATIONS OF CARRION REMOVAL BY TROGID BEETLES (*OMORGUS STRZELECKENSIS*) IN ARID NORTH-EASTERN SOUTH AUSTRALIA

Despite substantial advances in the taxonomy of Australian beetles (Coleoptera)[1], little is known about the biology and ecology of most of our species, especially those considered of little economic significance. Matthews[2] suggested that naturalists can make valuable contributions by investigating and describing aspects of the natural history of beetles. Often such observations are opportunistic and represent situations difficult to replicate in the laboratory. With a minimum of equipment, many useful aspects of behaviour can be noted and simple experiments used to clarify observations.

During a recent limnological field trip to the Coongie Lakes area, an opportunity arose to study groups of carrion beetles (Trogidae) transporting faecal pellets and regurgitated egesta along a sand-dune on the western shore of Lake Goolangirie (26°53'S 140°06'E), 112 km NW of Innamincka, in the Innamincka Regional Reserve. The lake fills as a result of overbank flows in the North-West Branch of Cooper Creek. This lake, and many others nearby, owe their irregular shapes to the extensive dune systems running approximately north-south, and vegetated by an open tall shrubland of *Acacia ligulata* A. Cunn. ex Benth. in the wider swales, a hummock grassland dominated by *Triodia basedowii* E. Pritzel along the major dune systems and sand-hill cane-grass (*Zygochloa paradoxa* (R. Br.)) on the mobile dune crests[3].

The beetles were identified as *Omorgus strzeleckensis* (Blackburn, 1895[4]) described from specimens collected near Lake Callabonna and Strzelecki Creek. The species is widespread throughout mainland Australia, occurring in low rainfall areas of all States except Victoria[5]. It is distinguished from congeners by the combination of shape of the elytral costa and the single large median tooth on the fore tibia. Scholtz[5] noted that specimens had never been collected in January, April, June or December — my observations were made in December (early summer).

Life history data on the Australasian Trogidae are few although some 53 species have been described, of which two are introduced[5]. The only published record of a particular feeding habit appears to be that by Leefmans[6] who reported *O.* (*Trox*) *costatus* living and feeding on bat guano in caves in the Celebes (Sulawesi). In Africa and America, trogid adults and larvae are facultative necrophages and generally appear late in the succession of invasions of carcasses in the arid zones of these continents.

Three broad strategies for coprophagy and necrophagy in arid zones are recognised[7]. The first is to tap the latent moisture of the particle and to breed as quickly as possible before it dries (e.g. dipteran flies, especially calliphorids). Alternatively, the material may be comminuted and buried to conserve its moisture as is the case with dung-beetles (Scarabaeinae). In arid areas, the lack of reliable rain leaves some species of dung-beetles undeterred because they can bury desiccated faecal pellets that rehydrate from soil moisture[7]. Finally, some groups (termites, tenebrionids, trogids) are able to eat dry faeces and mummified carrion. *Omorgus* (*Trox*) spp. can complete their life cycle on only wool clippings or even discarded wool clothing[7].

Omorgus spp. in the Kalahari Desert are morphologically, behaviourally and physiologicaly adapted to survive long periods of aridity interspersed with brief favourable periods when feeding and copulation occur[8]. Adults and larvae quiesce under adverse ambient conditions, renewing activity within hours of amelioration. Immature stages develop rapidly (3–4 weeks[9]) whereas the adult lifespan is long enough to allow overlapping generations. The availability of mummified carcasses of large antelope for several years allows populations to build up below the remains without the risks involved in dispersal to seek food or mates[8].

The following observations were made over two days (10-11.xii.1991). Tracks consisting of numerous small depressions in a band 3-4 cm wide were noticed running east-west along a dune face soon after sunrise (0630 hours) on 10.xii.91. They were made by two beetles carrying a tapered dingo faecal pellet measuring approximately 3cm long and 1 cm in diameter (Table 1). The beetles were moving westward, and a light easterly breeze was blowing when detailed observations commenced at 0645 hr. Subsequently, six other groups of beetles were discovered carrying or rolling egesta from the base of a lone Coolibah tree (*Eucalyptus microtheca* F. von Mueller) growing halfway up the dune face. These groups, noted at about 0700 hr, when the breeze had strengthened slightly and swung to a northerly, were moving southwards and had travelled only several metres.

The most striking feature was the two different modes of carrion transport adopted by the groups of beetles. They either carried or rolled the egesta, depending upon its shape. Irregular pieces of carrion were physically carried upon the backs of the beetles with the load being spread fairly evenly between individuals. The pieces of carrion were stabilized by nodules and grooves on the pronota and elytra of the beetles. More cylindrical pieces were rolled along. Beetles propped their stout forelegs against the carrion or tucked their pronotum under the edge of the particle, lifting their heads while pushing forwards with their middle and hind pairs of legs. Although the beetles were always on the trailing edge of the rolling piece of carrion, they often appeared to push each other forwards and it was not unusual for a beetle to walk over the backs of others to roll the particle.

It is important to distinguish between these two types of carrion transport by trogid beetles and the classification of resource relocation that is frequently applied to the majority of dung beetles. Dung beetles are separated into guilds of tunnellers (paracoprids), dwellers (endocoprids) and rollers (telocoprids)[10,11]. Tunnellers dig burrows immediately below the dung and push pieces of it into the tunnels, dwellers live and feed within the dung heap itself, and rollers make balls of dung that they roll away from the food source and other beetles before concealing them in the soil[12]. In the case of the trogids that I observed, all the beetles would be in the roller guild[11] but exhibit either carrying or rolling behaviour. In dung beetles, the guilds are species specific whereas the modes of particle transport evident in the trogids in my study both occur in the one species.

TABLE 1. *Summary of observations made on seven groups of carrion beetles at Lake Goolangurie. Means (±SEs) are for all groups carrying egesta southwards (group 1 is excluded because it was carrying a faecal pellet west).*

Group	No. of beetles	Size of burden (cm)	Shape	Transport mode	Track length (m)	Mean gradient (%)
1	2	5 × 1	Tapered	Carrier	31	20
2	5	6 × 7	Irregular	Carrier	35	10
3	5	6 × 3	Cylindrical	Roller	28	17
4	3	8 × 2	Irregular	Carrier	28	18
5	3	5 × 2	Irregular	Carrier	40	11
6	3	2 × 2	Cylindrical	Roller	42	7
7	5	9 × 2	Irregular	Carrier	45	7
Mean	4	6 × 3			36.33	11.67
SE	0.45	1.00 × 0.82			2.95	1.96

The inclines up which the carrion was rolled or carried were measured by holding a metre stick horizontally level with one end resting on the track and the stick pointing along the path taken by the beetles. The elevation of the free end of the stick measured the rise (in cm) over 1 m and was expressed as a percentage (Table 1). The maximum incline up which beetles rolled carrion was 30% whereas particles were carried up a slope of 42%. The shape of the carrion particle appeared to determine its mode of transport rather than the slope of the incline or the number of beetles involved (Table 1). In general, there were more beetles associated with larger pieces of carrion but other factors such as particle shape are probably also important. By placing small flags along the tracks at 30 or 60 second intervals and measuring the length of the path, I was able to compare the speeds of carrion transport by the two different modes. At temperatures of 26-28°C and traversing similar terrain, five beetles carrying egesta (Group 2, Table 1) moved faster than a group (3) rolling a smaller piece (Table 1). "Carriers" averaged 0.42 cm.s^{-1} (n = 10 determinations, SE = 0.03) whereas "rollers" moved at 0.28 cm.s^{-1} (n = 9, SE = 0.02).

The pathways were not straight but meandered in a general direction. When the egestum became wedged against a stick or embedded in a hollow, the beetles soon retraced their steps and circling around, tried a slightly new bearing. These circles never exceeded 30 cm in diameter and I only found one piece of carrion that became inextricably trapped in a clump of *Enchylaena tomentosa* R. Br. (Group 5). The following day, this particle was covered in ants and there was no sign of the carrion beetles nearby or buried below.

At times, individual beetles would wander away from the carrion or become dislodged after a particularly vigorous roll. Invariably, they would circle to the downslope side of the carrion and then travel with the wind, moving uphill until they were directly downwind of the particle. Immediately, the beetle would turn towards the carrion and walk in a straight line up to it, even if the particle was out of the direct line of sight due to hollows and sand ripples. I observed this behaviour several times, and successful reunions occurred over distances of 2 m. When a member of the group wandered away or was dislodged, the rest of the group did not alter behaviour and continued moving the egesta.

Beetles were able to sense carrion from a radius of 10-15 cm even if upwind (as "rollers" often were) and moved directly towards the particle. This was confirmed experimentally using both "rollers" and "carriers", and was possibly visual. Shubeck[13] observed that carrion beetles in the family Silphidae could detect odours at distances of approximately 1 m when air movement was negligible but at greater distances (5-75 m), he concluded that orientation to carrion was due to random wandering.

If beetles go to such lengths to transport carrion, do groups exhibit any possessiveness, perhaps defending their particles from other conspecifics? Anecdotal evidence from field observations indicates that inter- and intra-specific competition among dung-beetles can be intense, ranging from direct combat when beetles fight over the possession of dung to scramble competition when the beetles' activity at high densities prevents most individuals acquiring sufficient resources for breeding[14].

What happens if a wandering beetle trying to recover its carrion finds itself downwind of another group's particle and homes in on that. Can a wandering "roller" readily switch to "carrying" if an irregular piece of carrion is encountered? To examine these possibilities, I planned a series of transfers of beetles from one group to another, within and across modes of transport. Touching the beetles caused them to feign death instantly, becoming immobile and tucking their limbs tightly under their body. Thus, it was necessary to allow them to walk onto a strategically placed leaf and then transfer the beetle quickly, placing it just downwind of the carrion in all trials.

In all transfers (n = 5), there was no change in the behaviour of the recipient group and I was unable to detect any physical antagonism. Newcomers often crawled over the carrion for several seconds before joining their fellows either rolling or carrying the particle. I returned all beetles to their original positions at the end of the experiment, where they resumed their behaviour, seemingly unaffected by their brief transfer. Thus, it seems that groups of beetles of this species are not especially protective of their carrion resources. It would be interesting to add beetles continually to a particle to see if intraspecific competition could be induced. Beetles had no apparent difficulty switching modes of transport to match that of their fellows — in no case, did they try to roll a particle that was being carried or *vice versa*. Furthermore, I never observed a group of beetles switch modes of transport in response to a change in grade or substratum particle size.

I also found an eighth group of two beetles rolling a cylindrical piece of egesta (2 × 3 cm) southwards. I sacrificed these two beetles for identification, and with three others, they are lodged in the South Australian Museum (classified with the Trogidae, Dr Eric Matthews, South Australian Museum, pers. comm.)

Could beetles be enticed away from their carrion by another, seemingly palatable piece of egestum, especially given their apparent lack of possessiveness? When this was done, groups of beetles carried or rolled their particles past the new piece, even when it was placed in the path of the group. However, if a single beetle became separated from the group and the particle was placed in its path, the beetle crawled over the carrion in a similar exploratory fashion to that observed earlier and then proceeded to either roll it or to burrow below it.

The morning I made these observations was overcast but sand temperatures rose gradually from 18°C at 0700 hr to 34°C by 1000 hr. By 0900 hr (26°C), Group 1 carrying the dingo faecal pellet to the top of the dune had burrowed below the pellet leaving it exposed. However, sand blown by the wind had half-buried the pellet and completely obliterated the tracks by 1100 hr. At 1115 hr, sand temperature reached 40°C and the other six groups of beetles ceased activity almost instantaneously. The wind had strengthened and air temperature was 35°C. In all cases, beetles either sheltered below the carrion or had burrowed into the sand beneath the particle to a depth of 3-5 cm (n = 3). Observations of depth of burrowing were restricted to groups 2 and 3 ("carriers" and "rollers" respectively). For the rest of the day, the beetles remained inactive.

At 1910 hr, activity around several particles (2, 3, 4, 5 and 7) resumed. Air temperature was 28°C, sand temperature was 27°C, and the wind had dropped. However, humidity was extremely high and intense electrical activity overhead heralded a thunderstorm which broke at about 2000 hr. Up to this time, beetles in groups 2 and 3 had moved their carrion several metres south, and group 4 had carried their particle 12.3 m north. The beetles in group 7 had moved around in a circle (10 cm diameter) surrounding their carrion and then apparently burrowed, leaving pock-marks several mm broad in the ground. Activity ceased completely during the rain from the thunderstorm which effectively ended my observations.

There were no tracks or activity the following morning, which was sunny and 18°C at 0600 hr with a gentle southerly. The rain had soaked to 1.5 cm and although I was able to recover several half-buried, bedraggled pieces of egesta, I was unable to find any beetles even though I destructively excavated each spot where the observations had ceased during the storm. It was not clear whether the egesta had been buried by the beetles or, more likely, wind-blown sand and rain. Presumably, the beetles had either dispersed individually or had carried and buried the carrion in the intervening 10 hours.

Why do these beetles go to such lengths to transport the egesta? One adaptive explanation for this form of behaviour in dung beetles is that the action reduces competition for the resource from rivals of the same species or other species that consume dung[15]. Alcock suggests that had the beetles remained at the site of deposit, the concentration of material might have had a higher probability of attracting vertebrate scavengers or ants that could consume the egesta before the trogids. Possibly, the beetles themselves would then be put at risk as a nearby food resource.

Another explanation has been applied to dung beetles in the tunneller and roller guilds that need to transport the particle from an area where it may have fallen on ground that is unsuitable for burrowing or that is too exposed to harsh ambient conditions[16]. This does not mutually exclude the first hypothesis and may also be a valid explanation for the trogid behaviour observed in the present study. On an unstable sand dune, buried egesta are likely to be exposed by wind whereas in areas stabilised by vegetation, this risk is lessened. Further, local soil moisture is likely to be greater, perhaps enhancing the food quality of the carrion. Relative humidity is an important factor controlling the behaviour of two species of Kalahari *Omorgus*[17]. High relative humidity restricts respiratory water loss, improves food (moist hair and keratin) quality and may compensate for faecal water loss[14]. Perhaps the trogids I observed were transporting their particles long distances until they found clumps of shrubby vegetation where relative humidity and sand stability were high and food quality would be enhanced when the particle was buried. This hypothesis awaits testing.

I am grateful for the coprological encouragement by the other members of the expedition (Fran Sheldon, Philippa Kneebone, Leslie Doddridge, Wendy March and John Slade) and especially the organiser, Jim Puckridge, whose local knowledge and enthusiasm greatly enriched the trip. Dr E. G. Matthews (South Australian Museum) provided keys, encouragement and helpful discussion, Prof. John Alcock (Arizona State University) guided my reading on animal behaviour, and Dr C. H. Scholtz (University of Pretoria, South Africa) kindly sent me reprints of his work on African *Omorgus*. I thank Drs Margaret Davies, Alice Wells and Shelly Barker, Mr Jim Puckridge and James Wallman, and an anonymous referee for comments on an early draft of this manuscript and direction to unfamiliar literature.

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ANDREW J. BOULTON, Dept of Zoology, University of Adelaide GPO Box 498, Adelaide, S. Aust. 5001.

REDEFINITION OF *UPEROLIEA LITTLEJOHNI* DAVIES, MCDONALD & CORBEN (ANURA: LEPTODACTYLIDAE: MYOBATRACHINAE)

BY MARGARET DAVIDS & GRAEME F. WATSON

Summary

Transactions of the Royal Society of S. Aust. (1992), **116**(4), 137-139.

BRIEF COMMUNICATION

REDEFINITION OF *UPEROLEIA LITTLEJOHNI* DAVIES, McDONALD & CORBEN (ANURA: LEPTODACTYLIDAE: MYOBATRACHINAE)

Uperoleia littlejohni was described from preserved material in the collections of the Queensland National Parks & Wildlife Service and the Queensland Museum[1]. For this reason, biological data were absent from the description, as were ephemeral data such as colour in life.

In February 1990 and 1991, we visited Occupation Licence 117, Burra Range, 26.0 km SW Pentland, Qld (20°44'S, 145°14'E), now in the White Mountains National Park, near the type locality of the species. On the first visit we located a single male in extremely dry conditions, but did not obtain further biological data. A second visit coincided with heavy rains, and we located two choruses of *U. littlejohni*, collected specimens and recorded calls. We present those data here.

Material is deposited in the South Australian Museum, Adelaide (SAM) and the University of Adelaide Osteological Collection (UAZ). Methods of measurement and abbreviations in the text follow Tyler (1968)[2]. Selected material was cleared and stained for osteological examination[3,4].

Tape recordings were made using a Sony TCD-5PRO cassette recorder (tape speed 4.76 cm/s) and Beyer M-88 cardioid dynamic microphone. Air wet bulb temperatures (the effective temperature of a frog calling on land) were measured at the calling site of each individual using an electronic thermistor thermometer (Takara Digimulti Model D611). Recordings were analysed on a DSP 5500 digital Sona-Graph (Kay Elemetrics Corp.) using the in-built set-up #10, with playback on a Nakamichi Dragon cassette recorder. Overall variations in tape speed (i.e., from recording to playback) are estimated at less than 0.5%, and the frequency responses of all audio-electronic components are close to linear within the relevant frequency range (based on the manufacturer's specifications).

For each call, three primary attributes were determined: (i) duration, as the interval from the beginning of the first pulse to the end of the last pulse (ms); (ii) number of pulses per note (direct count); and (iii) dominant frequency (Hz), as the maximum value of the spectrum of power between the cursors of the whole note. Two derived attributes were determined: (i) pulse repetition rate (pulses/s), calculated as 1000(n-1 pulses)/duration in ms; and amplitude modulation, calculated by using the only measurable characteristics of envelope amplitude, the maximum amplitude (Y) and the minimum amplitude (Z), according to the formula: % amplitude modulation equals 100(Y-Z)/Y+Z[5]. Levels of resolution were less than 1 ms for temporal aspects, and less than 40 Hz for dominant frequency.

Uperoleia littlejohni Davies, McDonald & Corben

Uperoleia littlejohni Davies, McDonald & Corben, 1986 p.174

Definition: A moderately large species [males 20-32 mm snout-vent length (S-V), females 23-29 mm S-V] lacking maxillary teeth, fingers unwebbed, poorly fringed, basal to no toe webbing, toes fringed; dermal glands prominent; frontoparietal fontanelle moderately extensive; carpus of six elements, anteromedial processes of anterior hyale slender; ilial crest absent; short pulsatile call of eight pulses with a pulse repetition rate of about 131 pulses/s at 26.6°C.

Material examined: UAZ A1712, A1714, A1717, B1713, B1715-6, SAM R39802-9, 26.0 km SW Pentland, Burra Range, 25.i.1991, M. Davies, G. F. Watson, K. R. McDonald; SAM R39801, same locality, 10.ii.1990, M. Davies, K. R. McDonald.

External morphology: Little can be added to the original description other than an increase in the size range of males (Fig. 1).

Colour in life: Dorsum grey with well-defined dark chocolate markings. Prominent tubercles tipped with apricot or cream. Parotoid and inguinal glands buff yellow, supralabial gland cream. Flashes in the inguinal region and the backs of the thigh are chrome orange[6].

Osteology: A further six specimens were examined (three double-stained and three single-stained) but variability was minimal and does not add to the original description.

TABLE 1. *Characteristics of the advertisement calls of three individuals of* Uperoleia littlejohni, *recorded on 25.i.1991, 26 km SW of Pentland, Qld. Patterns of amplitude modulation throughout the calls are shown in Table 2. Effective temperature at the calling sites of each individual (air wet bulb) is also listed.*

Attribute	#1	#2	#3
Temperature (C)	26.2	26.9	26.7
Call duration (ms)	47.92	52.73	60.94
Dominant frequency (Hz)	2080	2080	2040
No. of pulses	8	8	8
Pulse repetition rates (pulses/s)	146.1	132.8	114.9

Call: One call of each of three individuals was analysed, and a summary of the call characteristics is listed in Table 1. The advertisement call of *Uperoleia littlejohni* is a short (mean duration 53.86 ms), partly pulsatile call (mean pulse repetition rate 131.27 pulses/s). The depth of amplitude modulation decreases throughout the call so that individual pulses are difficult to discern, except at the beginning of the call, although may calls also had a distinct final pulse (Fig. 2).

Table 2 shows the changing levels of amplitude modulation in the three calls analysed. To the ear, the call is a sharp loud click, with a pulsatile nature, repeated at a rate of about 20 calls/min. Among other species of *Uperoleia* whose calls have been described, six (*U. aspera*, *U. glandulosa*, *U. lithomoda*, *U. mimula*, *U. minima* and *U. rugosa*) produce "click" calls (short calls of Tyler *et al.* 1981[7]) with the call of *U. aspera* (at 25.6°C; duration 30-35 ms; frequency 2650-2900 Hz; number of pulses 5-6; pulse repetition rate 166.7-171.4 pulses/s[8]) being most similar to that of *U. littlejohni*.

TABLE 2. *Patterns of amplitude modulation (%) throughout calls of three individuals of* Uperoleia littlejohni *recorded on 25.i.1991, 26 km SW of Pentland, Qld.*

Pulse No.	#1	#2	#3
1	95	75	100
2	87	78	90
3	66	31	36
4	15	6	35
5	13	4	19
6	17	42	20
[illegible]	27	28	29
8	38	50	59

Distribution and habitat: The distribution records of *Uperoleia littlejohni* are within the Einasleigh Uplands, northern Desert Uplands, and the north-western Brigalow Biogeographic regions of Queensland[9]. The geology of the collection sites ranges through Quaternary alluvium and colluvial sands, Triassic sandstones, undifferentiated Palaeozoic and Triassic?/Permian granites, and Upper Silurian/Lower Devonian granodiorites. No records are known from the Recent (<3 My. BP), extensive basalts of the McBride Plateau and associated lava flows of the Einasleigh Uplands[10].

Vegetation types at collection sites are predominantly Iron Bark and Bloodwood (sometimes with Box) woodlands and open woodlands with tussock grasses on granites or sandstones

Fig. 1. [illegible]

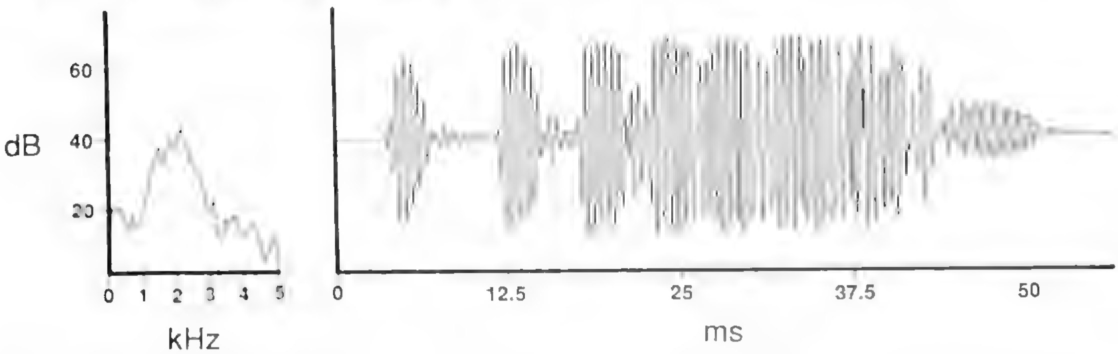

Fig. 2. Power spectrum and wave form of an advertisement call of *Uperoleia littlejohni* recorded on 25.i.1991, 26 km SW of Pentland, Qld, at a wet-bulb air temperature of 26.2°C (#1, Table 1). Note that the ordinate of the wave-form display is not labelled because it depicts a relative linear scale in volts

of the Einasleigh Uplands and northern Desert Uplands[11,12,13]; Lancewood *(Acacia shirleyi)* communities with an understory of Spinifex *(Triodia* sp.) on dissected Warrang sandstone of the Desert Uplands, and the *Eucalyptus populnea* or *E. microtheca* woodlands along drainage lines in the northwestern Brigalow belt.

Altitudes at collection sites range from 150 m at Caerphilly Station (21°03′, 145°, 32′) to approximately 1000 m near Herberton (17°23′, 145°23′), with most records within altitudes of 300-900 m. Rainfall ranges from 480-1150 mm, with most collection locations found within the 500-800 mm rainfall isohyets. Rainfall is strongly seasonal, concentrated in the summer months from December to March [14,15].

The recorded frogs were calling on a steep scree slope, or at the edge of a stream at its base. They were located at the base of, or between, *Triodia* tussocks. A second chorus was found around the edge of a roadside scrape, and individuals were calling at the bases of grass tussocks.

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MARGARET DAVIES, Department of Zoology, University of Adelaide, G.P.O. Box 498, Adelaide, S. Aust. 5001, GRAEME F. WATSON, Department of Zoology, University of Melbourne, Parkville, Vic. 3052 and K. R. McDONALD, Queensland National Parks and Wildlife Service, Pallarenda, Townsville, Qld 4810.

NEW RECORDS OF *MESAPHORURA* (COLLEMBOLA: ONYCHIURIDAE, TULLBERGIINAE) SPECIES FROM AUSTRALIA, MACQUARIE ISLAND AND THE ANTARCTIC

BY P. GREENSLADE

Summary

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BRIEF COMMUNICATION

NEW RECORDS OF *MESAPHORURA* (COLLEMBOLA: ONYCHIURIDAE, TULLBERGIINAE) SPECIES FROM AUSTRALIA, MACQUARIE ISLAND AND THE ANTARCTIC

The Tullbergiinae is a subfamily of strongly reduced Collembola lacking ocelli, pigment and furca, which is adapted for soil living. Within this subfamily the genus *Mesaphorura* currently comprises over 20 described species most of which are only known from the Northern Hemisphere. Specimens belonging to the genus *Mesaphorura* are commonly found in Australia in moist soil under arable and grazing regimes, and also, more rarely, in soils under native vegetation. *Mesaphorura krausbaueri* Börner 1901[1] was recorded from Australia[2-5] and specimens determined as *Mesaphorura* sp. *krausbaueri* group were recorded from southern Australia and Macquarie Island[6]. Three species of *Mesaphorura* already known from Europe have been identified from Australia, and they have all probably been introduced relatively recently with Europeans. All material discussed is deposited in the South Australian Museum collection.

Mesaphorura Börner, 1901

Diagnosis: elongate poduromorph Collembola about 500-600 μm long, lacking ocelli, pigment and furca, and possessing pseudocelli on head, thoracic and abdominal segments with the formula 11/011/00010 or 11/011/10011; antennal III organ normally with two curved cylindrical clubs and two small pegs, only a small cuticular swelling in front of pegs without enlarged granules; ant IV without greatly enlarged sensilla; postantennal organ elongate, consisting of two parallel rows each of 10 to 20 simple elongate vesicles arranged at right angles to longitudinal axis of the organ; abd VI with a pair of crescentic cuticular ridges anteriorly and two posterior anal spines shorter than claw.

*Abbreviations: collectors, KK, K. King, PG, P. Greenslade, HW, H. Womersley.

Key to Australian species (after [7,8,9,10])

1. 3 + 3 median microchaetae in anterior row between a_4 on abd V (a_2 present); a_1 either a micro- or a macrochaeta on abd IV; L_2 present on anal lobes; a_4 of abd V not displaced anteriorly; pseudocelli on thorax close to mid line, behind or between p_3 and p_4 2
   2 + 2 median microchaetae in anterior row between a_4 on abd V (a_2 absent); a_1 a microchaeta on abd IV; L_2 missing on anal lobes; a_4 of abd V displaced anteriorly; pseudocelli of thorax between m_5 and p_5 ... *M. critica*
2. M_5 present on abd IV; long macrochaeta (i.e. a_2 on abd IV) over twice the length of microchaeta (a_1); macrochaeta a_4 on abd V is shorter than macrochaeta p_2; p_1 a macro- and p_2 a microchaeta on abd IV .... *M. macrochaeta*
   M_5 absent on abd IV; macrochaeta (i.e. a_2 on abd IV) only 1.8 times as long than microchaeta (a_1); macrochaeta a_4 on abd V longer than p_2; p_2 a macrochaeta and p_1 a microchaeta on abd IV........ *M. yosiii*

Mesaphorura macrochaeta Rusek

Mesaphorura macrochaeta Rusek 1976 p. 33
FIG. 1

Material examined. **Australian Antarctic Territory,** Mawson Station, pot plant soil (*Coleus, Philodendron?*), January 1989, PG, *ca.* 200 exs; **Macquarie Island,** Isthmus, in greenhouse, soil and moss, 2.xii.86, PG; **New South Wales,** Armidale, Chiswick native pasture, plot 8, 21.viii.78, 26.ii.73, KK, 2 ex; Chiswick improved pasture, ungrazed, 26.ii.72, KK, 2 exs; Cambewarra Ranges, 10 k W of Narooma, leaf litter, Sept 1990, PG, 1 ex; **South Australia,** Mt Lofty Ranges, Bridgewater, Engelbrook Reserve, leaf litter, 16.v.71, PG, 2 exs; Belair, in moss, April 1938, HW, 1 ex; Belair, grass mowings, 27.v.1971, PG, 2 exs; Coorong, Coolatoo, pitfall traps in grass beside road, 28.ix-8.x.75, PG, 1 ex. 15 k N Mt Gambier, *Pinus radiata* leaf litter, 19.v.1975, PG, 2, exs.

Distribution: described from Canada but common in North America and Europe. *Mesaphorura macrochaeta* is abundant in improved pasture in southeastern Australia and has been introduced to an Australian Antarctic Territory Station and to Macquarie Island in imported soil, probably from Tasmania.

Mesaphorura critica Ellis

Mesaphorura critica Ellis 1976 p. 230
FIG. 2

Material examined: **South Australia,** Koonamore Station, 340 km NNE Adelaide, Black Oak Creek, leaf litter, 25.vii.1971, PG, 1 ex.

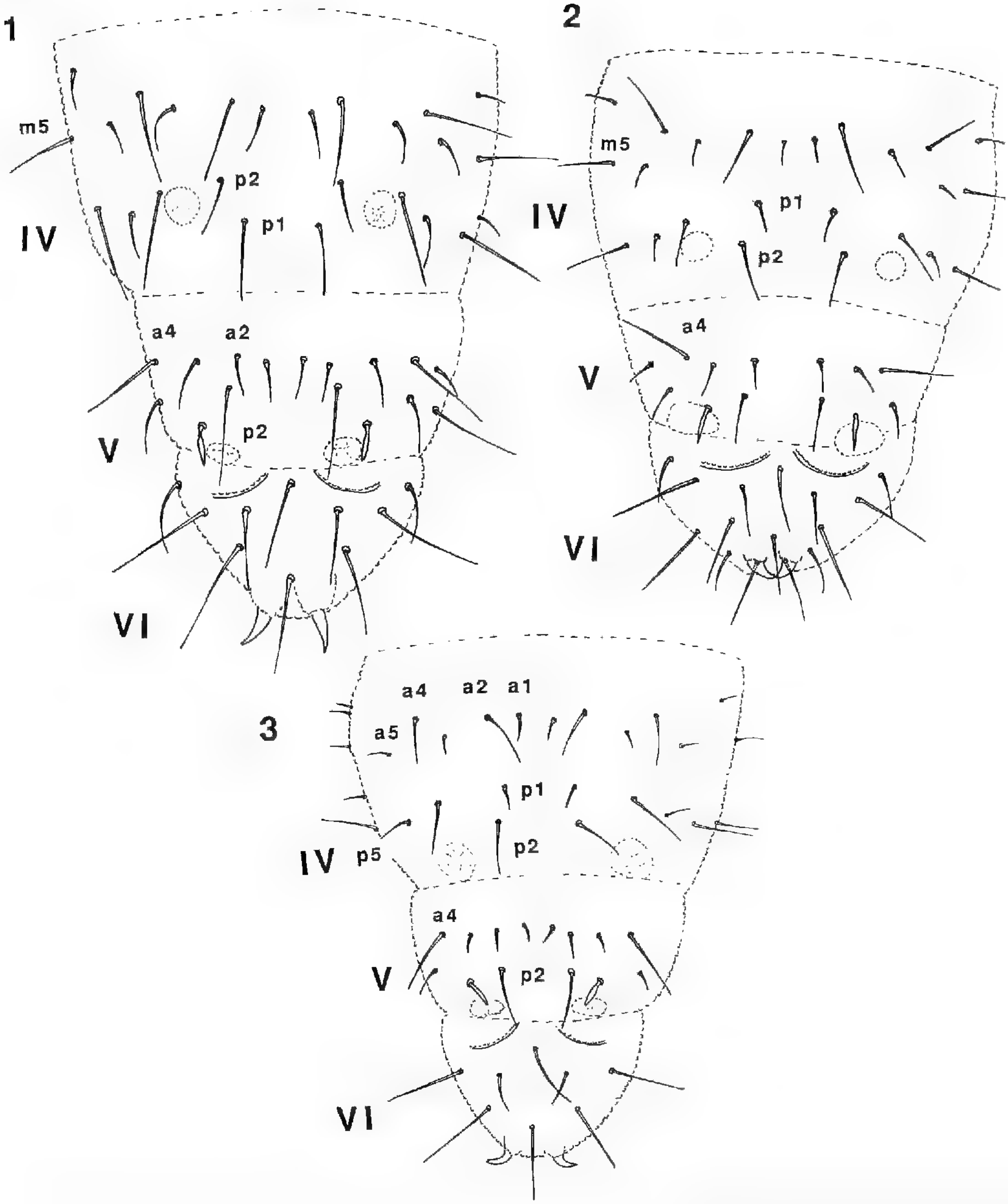
Distribution: previously only known from Europe[11].

Mesaphorura yosiii (Rusek)

Tullbergia yosiii Rusek 1967 p. 191.
FIG. 3

Material examined: **New South Wales,** Armidale, Chiswick native pasture plots, plot 8, 21.viii.78, KK, 2 exs; Chiswick improved pasture, ungrazed plots, 26.ii.72, KK, 1 ex, **Queensland,** 17 km east of Killarney, wet sclerophyll forest, leaf litter, 16.v.76, PG, 1 ex; Great Barrier Reef, Swain's Reef, Frigate Cay, 22.vii.1983, KK, 1 ex; **South Australia,** Koonamore, 340 km NNE Adelaide, Black Oak Creek, leaf litter, 25.vii.73, PG, 2 exs; 10 km N Whyalla, Middleback Stn, under *Casuarina stricta*, 8.x.79, PG, 1 ex

Distribution: Europe, North America, China[12], Australia, New Caledonia[13].



Figs 1-3. 1, *Mesaphorura macrochaetae* Rusek. Dorsal chaetotaxy of abdomen IV-VI. 2. *M. critica* Ellis. Dorsal chaetotaxy of abdomen IV-VI. 3. *M. yosiii* Rusek. Dorsal chaetotaxy of abdomen IV-VI.

Both *M. yosiii* and *M. macrochaeta* are found together in improved pastures in southeastern Australia, generally *M. yosiii* is found on warmer sites and M. macrochaetae in cooler, more southerly regions. Is likely that both were introduced to Australia with Europeans. Morphological differences between the species are given by Rusek[8] and are cited in the key. The specimen from Darlington, Western Australia, determined by Womersley[2] as *M. krausbaueri*, is not in good enough condition to be identified, but other specimens from Belair, South Australia, also determined by Womersley as *M. krausbaueri*, are in fact *M. macrochaeta*. It seems probable that *M. krausbaueri* does not occur in Australia.

All three species are likely to be more widely distributed than these scattered records suggest. In Canadian forests *M. yosiii* and *M. microchaeta* can occur together but have slightly different vertical distributions with *M. macrochaeta* markedly aggregated in the humus layer and upper soil horizon from 0 to 5 cms in depth, and *M. yosiii* concentrated lower in the soil profile and more randomly spaced[14]. In another Canadian forest where *M. macrochaeta* was absent, *M. yosiii* occupied the whole soil profile. This suggests possible competitive exclusion of *M. yosiii* by *M. macrochaeta* on some sites. *Mesaphorura critica* may have been included with the species *M. yosiii* in these ecological studies. In Australia, *M. critica* has been found only under arid native vegetation.

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P. GREENSLADE, c/o CSIRO, Division of Entomology, GPO Box 1700, Canberra, A.C.T. 2601, Australia.

ECOLOGICAL AND BIOLOGICAL NOTES ON THE RARE PLANT *HEMICHROA MESEMBRYANTHEMA* F. MUELL (ARMARANTHACEAE)

BY JOHN L. READ

Summary

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BRIEF COMMUNICATION

ECOLOGICAL AND BIOLOGICAL NOTES ON THE RARE PLANT *HEMICHROA MESEMBRYANTHEMA* F. MUELL (ARMARANTHACEAE)

The succulent shrub, *Hemichroa mesembryanthema*, was described in 1873 after being collected in the previous year by the explorer Ernest Giles in the vicinity of Lake Eyre, South Australia[1]. No further South Australian specimens were collected until 1984 when a specimen was collected from Strangways Springs, 112 years after it was first discovered[2]. It was suggested that the population at Strangways was likely to be the source of the specimen collected by Ernest Giles[2].

In October 1991 the Roxby Downs Field Naturalist Club located *H. mesembryanthema* at the base of Mt Kingston in the Denison ranges, South Australia (28° 02'S, 135° 54'E). A collection was lodged at the State Herbarium of South Australia. A subsequent search of the region by the author in April 1992 revealed that the population of *H. mesembryanthema* was apparently restricted to a small region between the base of Mt Kingston and the Willparoona Springs (Fig. 1). This population is only 5 km from the site of the Peake Overland Telegraph Station which was also visited by Ernest Giles[1], thus casting doubt on the provenance of the original collection. *H. mesembryanthema* has been recorded from eight sites in Queensland and populations apparently intermediate between *H. mesembryanthema* and *H. diandra* have been recorded in Western Australia[3].

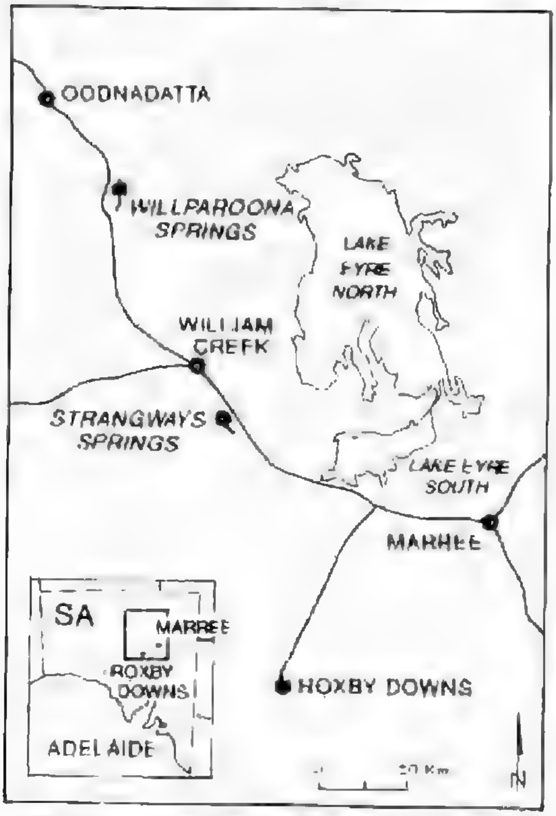

Fig. 1. Major locations mentioned with respect to *Hemichroa mesembryanthema* in South Australia

The Willparoona Springs population of *ca.* 150 mature *Hemichroa mesembryanthema* shrubs was located in a sub-circular patch measuring *ca.* 150 × 160 m. These shrubs were located 120 m from the nearest spring as defined by a bed of *Cyperus gymnocaulos*. The population was growing on powdery saline clay soil (3.14% Cl^-) with a capping of angular feldspar rich granite and quartz gravel, approximately two metres above the spring sediments. Although *H. mesembryanthema* was the tallest shrub in the region, *Halosarcia* spp. dominated the chenopod shrubland. *Atriplex vesicaria*, *Nitraria billardieri*, *Gunniopsis quadrifida* and a *Frankenia* sp. were also present. Two small streams supporting predominantly *Acacia cambagei*, *A. victoriae* and *A. tetragonophylla* divided the population. The remainder of the hillside above the springs was dominated by chenopod shrubland while the majority of the drainage line associated with the springs was unvegetated.

All of the *H. mesembryanthema* bushes appeared to be mature and the largest individual was approximately 0.8 m tall and over 1 m wide. A full description of this species is presented elsewhere[2]. Most of the individuals were flowering in April 1992 and the small white flowers with brilliant red stamens produced a beautiful perfume. Many insects including wasps, butterflies and flies were attracted to these flowers. The wasps, particularly a large black species, were covered with a considerable load of yellow pollen and are probably an important pollinator of *H. mesembryanthema*.

No evidence of browsing was detected on any of the shrubs although cattle, donkeys and rabbits all inhabit the region. This supports the observation that the Strangways population of *H. mesembryanthema* was not touched by either cattle or rabbits[2]. Interestingly it was presumed that *H. mesembryanthema* had been forced to extinction by domestic stock and rabbit grazing[4]. Although introduced herbivore grazing on seedlings cannot be discounted, it is unlikely that the apparent rarity of this species is related to grazing pressure.

The discovery of a further population of *H. mesembryanthema* in close proximity to mound springs raises the possibility that there is some form of assocation between *H. mesembryanthema* and artesian springs. Most vegetation associated with springs grows directly on the vent, tail or seepage zone of the spring. However, it is possible that *H. mesembryanthema* relies on certain edaphic or hydrological properties which are found in a zone at a greater distance from the springs. *H. mesembryanthema* is evidently not obligately tied to springs in all parts of its range since the Queensland collections are from alluvial run on areas in hilly country, or saline areas[3]. The common factor with all of these localities is that they all appear to be confined to comparatively moist regions which suggest that water stress may be limiting.

Although the Willparoona population has significantly increased the recorded South Australian range of *H. mesembryanthema*, this species must still be regarded as rare in South Australia, with only two known populations estimated to comprise a total of less than 1500 plants. The main population at Strangways Springs was under some threat from road building activities[2] and is potentially threatened by off-road driving, since the Oodnadatta track and station tracks pass through it. However, grazing is not believed to be a problem. The Strangways population also appears to have spread to limestone mounds in recent years[7] where it was not observed in 1984[2] or in 1978[5]. Since the discovery of the Queensland populations, the status of the species has been lifted from presumed extinct[4] to "poorly known".

Further research is required on the physiological and ecological requirements of *H. mesembryanthema* to establish a meaningful management plan for this rare species.

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JOHN L. READ, P.O. Box 150, Roxby Downs, S.A. 5725.

EGGS AND INCUBATION IN THE AUSTRALIAN LIZARDS *AMPHIBOLURUS NOBBI* AND *EREMIASCINCUS RICHARDSONI*

BY T. P. MORLEY

Summary

Transactions of the Royal Society of S. Aust. (1992), 116(4), 147-148

BRIEF COMMUNICATION

EGGS AND INCUBATION IN THE AUSTRALIAN LIZARDS *AMPHIBOLURUS NOBBI* AND *EREMIASCINCUS RICHARDSONI*

Reproductive biology, particularly egg-laying, incubation and neonate sizes, is poorly known in Australian lizards[1]. Here I present data on these parameters in the Australian lizards *Amphibolurus nobbi coggeri* and *Eremiascincus richardsoni*.

Amphibolurus nobbi Witten, 1972 includes two subspecies[2], and all available ecological data relate to the nominate subspecies[3,4,5]. No studies have been conducted on *A. n. coggeri*, and in South Australia the species is poorly collected and little known[6]. The Desert Banded Skinks or Sandswimmers (*Eremiascincus* spp.) are distributed over most of arid and semi-arid Australia[7,8], and are abundant in suitable habitats. The biology of the genus is poorly known and accurate reproductive data are only available for oviparous *E. richardsoni* recording its clutch size[1,8]. The accuracy of the available information on *E. fasciolatus* is in doubt, having been reported as a viviparous species[1,8].

Since late 1987, my collections at Swan Reach Conservation Park, and those of Mark Hutchinson in Brookfield Conservation Park have included four gravid *A. nobbi coggeri* (Table 1) and one *Eremiascincus richardsoni*. After collection all females were placed in individual cages, furnished with a hide box and a nest box filled with moist sphagnum moss. Fresh water was available, and a climbing branch provided. Lizards were offered various insects and feeding often occurred until the day before oviposition.

The eggs were marked and measured, with vernier calipers, to the nearest 0.1 mm (Table 2) and were placed on a medium of vermiculite and rainwater (50:50 by weight), in a small plastic container, with 12 small holes drilled into the lid to allow for air exchange. The first two clutches of *A. n. coggeri* eggs were incubated at room temperature (20-34°C). The others, and the *E. richardsoni* eggs, were incubated in a temperature controlled (27-31°C) snake cage. The eggs were checked daily, and the medium sprayed, as necessary, with rainwater that was the same temperature.

Each *A. n. coggeri* laid a clutch of 5-7 eggs (24.xi.1987-10.i.1991) (Table 1). Female SVL and clutch size were not significantly correlated ($r = 0.8465$, $0.1 > P > 0.05$). The nest boxes were not used; all eggs were laid on the floor of the cage. The female *E. richardsoni* (SAM R37015, SVL 90 mm) laid four eggs in the afternoon of 18.xii.1990. These eggs were laid in the sphagnum moss, and each adhered to one other egg in the clutch.

Five *A. n. coggeri* eggs from the second clutch were slightly collapsed and pear shaped (vs. oval) upon laying, and went mouldy during the first week of incubation. These eggs were opened, prior to disposal, to establish fertility. All were infertile. The *A. n. coggeri* eggs maintained in the more controlled environment were more successful in both hatching rate, and a shorter incubation period. All eggs incubated by this method, successfully hatched after $\bar{x} = 47.25 \pm 2.71$ (44-50) days, whereas the eggs in the uncontrolled conditions took $\bar{x} = 62.57 \pm 2.71$ (56-73 days), and two embryos were dead or severely deformed.

On the 27.xii.1990 it was apparent that only two of the *E. richardsoni* eggs (nos. 2 and 3) were fertile. They had increased in size, had a pinkish tinge and blood-vessels were

TABLE 1 *Source and clutch sizes for gravid female* Amphibolurus nobbi coggeri.

Female No.	SVL	Locality	Date Collected	Date Laid	Clutch Size	SAM Reg. No.
1	80	Swan Reach CP	9.x.1987	24.xi.1987	7	–
2	84	Swan Reach CP	9.x.1987	28.xi.1987	7	–
3	74	Swan Reach CP	18.xi.1989	10.i.1990	5	R36316
4	80	Brookfield CP	1.xii.1990	12.xii.1990	5*	R36997
5	69	Ti Tree Well	8.xii.1977		4	R16587

* Two of these eggs were laid in the bag following collection. When discovered they were not viable and were discarded.

TABLE 2. *Egg and neonate sizes in* Eremiascincus richardsoni *and* Amphibolurus nobbi coggeri *expressed as* $\bar{x} \pm SD$ *if appropriate with range in parenthesis.*

Species	Egg Sizes. Length	Egg Sizes. Width	Neonate Sizes SVL	Neonate Sizes TL
E. richardsoni	18.58 (16.5 - 19.5)	9.95 (9.9 - 10.1)	32.5 (31 - 34)	78.5 (77 - 80)
A. n. coggeri	16.0 ± 1.49 (12.1 - 18.3)	9.12 ± 0.3 (8.7 - 9.6)	28.53 ± 0.74 (27 - 30)	80.67 ± 2.97 (76 - 87)

forming on the inside walls. Eggs 1 and 4 had not changed in size or colour, and were thought to be infertile. Measurements of the eggs could not be taken at this stage due to the adherence and shape of the mass. After 36 days incubation, on 23.i.1991 the shell on egg no. 2 had split. This was noticed at 1935 hr, but the lizard did not emerge until 0315 hr the next morning. The shell on egg no. 3 was split at 2020 hr on 23.i.1991 and full emergence occurred at 0922 hr the next day, after 13 hours in the open egg shell. The other two eggs (1 and 4) were mouldy, and were opened before discarding, to confirm them to be infertile. Too few eggs were available to permit opening an egg to determine at what stage of embryonic development this species lays its eggs. The incubation period shown here is similar to that for *Ctenotus taeniolatus*[9], a similar sized skink, whose eggs were laid at stage 30[10]. All neonates were measured at hatching (Table 2).

Most of the *A. n. coggeri* neonates were released at the collection site of their respective parents. The deformed specimen and four neonates were placed in the South Australian Museum (SAM R35843-44, 36318-19 and 37951). The *E. richardsoni* neonates were maintained.

To supplement the observations reported here, specimens held in the South Australian Museum were examined for gravid females. Greer examined all specimens of *Eremiascincus* in State Museum collections prior to 1979[8], therefore only specimens of *Eremiascincus* registered after that year were examined.

Only one specimen of *A. n. coggeri* (R 16587) had oviducal eggs (Table 1). The largest egg in this specimen (16.8 × 8.2 mm) suggests that these eggs were near oviposition. The only data for clutch sizes in *A. nobbi* are related to the nominate subspecies (3-4)[3], which has a smaller clutch size than reported here for *A. n. coggeri* (4-7). This suggests a correlation between female size and clutch size, as *A. n. coggeri* is larger than the nominate race[2]. The clutch size reported here for *A. n. coggeri* is, however, similar to those reported for *A. muricatus* and *A. norrisi* (3-8 and 3-7 respectively)[1], *A. nobbi*'s closest relatives[1,11], and both these species are reported to be larger than *A. n. coggeri* (75 vs 100 and 110 mm SVL respectively)[7].

No further specimens of gravid *E. richardsoni* were found, but two *E. fasciolatus* (R30948 and R36137) were found with well-developed oviducal eggs (5 and 3 respectively). These eggs were surrounded by a thin shell membrane, the appearance of which suggests that the eggs would have been voided.

The egg-laying reported here confirms observations on oviparity in *E. richardsoni*[1,8], and the findings from dissected Museum specimens supports the suggestion that previous reports of viviparity in *E. fasciolatus* may be in error.

The S.A. National Parks & Wildlife Service provided collecting permits. Dr Mark Hutchinson collected two of the specimens on which these observations were made, allowed me to examine Museum specimens and read drafts of the manuscript. Adrienne Edwards provided data for Museum specimens and Brian Miller assisted with weighing the neonates. David Langdon and Ed McAlister read the final drafts of the manuscript, which was typed by Judy Woolman.

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T. P. MORLEY, Royal Zoological Society of S.A., Frome Road, Adelaide, S. Aust. 5000.

RELICTUAL POPULATION OF *TILIQUA SCINCOIDES* (SAURIA: SCINCIDAE) IN NORTH-WESTERN SOUTH AUSTRALIA

BY *G. R. JOHNSTON*

Summary

Transactions of the Royal Society of S. Aust. (1992), 116(4), 149-150

BRIEF COMMUNICATION

RELICTUAL POPULATION OF *TILIQUA SCINCOIDES* (SAURIA : SCINCIDAE) IN NORTH-WESTERN SOUTH AUSTRALIA

The mountain ranges of central Australia are known to provide localised, mesic refugia for several groups of organisms, including plants[1], scorpions[2], frogs[3] and reptiles[4,5]. While some populations isolated in central Australia have diverged considerably and represent endemic species[1,2,4] and others are relictual populations of species occurring in other parts of Australia[3,4], all are of considerable biogeographic interest.

It has long been recognised that some taxa occurring as isolates in central Australia have their closest relatives in the tropical north of Australia and may be relicts of a more tropical climate in the past[1,6]. It is now clear that there are also significant links between the fauna and flora of the central ranges and temperate southern Australia[2,3,5,7].

The scincid lizard, *Tiliqua scincoides*, is one of the most familiar species of reptile in Australia. In South Australia it has hitherto been regarded as an inhabitant of the cool, wet southern areas, extending as a series of relictual populations into the more mesic valleys in the Flinders and Gawler Ranges (Fig. 1). Extralimitally this species occurs in Victoria, eastern New South Wales and Queensland, and the north of the Northern Territory and Western Australia[8].

This paper reports the occurrence of *Tiliqua scincoides* in the arid northwest of South Australia, 740 km NNW of its previously recognised range in this state. Two specimens have been lodged in the South Australian Museum (SAM) to verify this report.

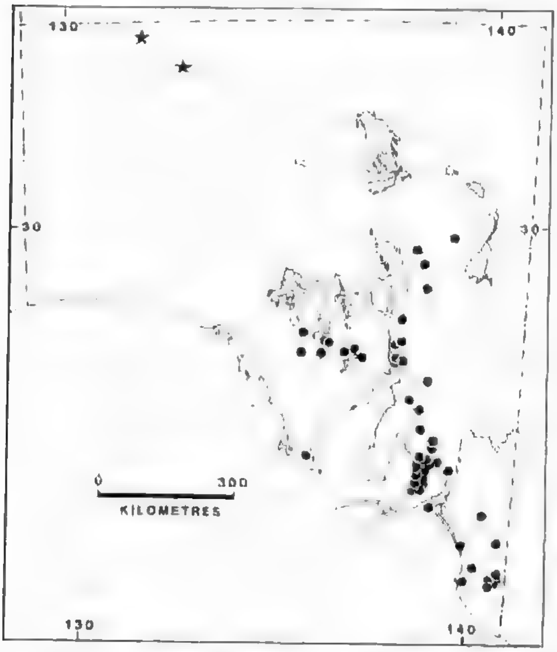

Fig. 1. Distribution of *Tiliqua scincoides* in South Australia. Solid circles denote S.A. Museum specimens. The stars show the new records from Mimili and Pukatja.

One specimen (SAM R33939) was collected at the base of a large granite outcrop close to Mimili (ex Mount Everard Station) (27°01'S, 132°43'E), in the Everard Range on 12.iv.1989. A second specimen (SAM R40230) was collected at Pukatja (ex Ernabella Mission) (26°18'S, 132°08'E) in the Musgrave Range of 20.v.1992. Both specimens were initially sighted basking among rocks and were removed from crevices into which they had moved when disturbed. The rocky outcrops of the Everard and Musgrave Ranges provide localised mesic refugia which are surrounded by harsh, arid sandplains and mulga country. The ranges support very localised, dense stands of *Acacia* and *Ficus*. A further six specimens were observed at Pukatja from 20-25.v.1992. Furthermore, the Aboriginal people who live at Mimili told me that *T. scincoides* is common in the boulders at the bases of the granitic hills in that area[9].

There was no doubt as to the specific identity of these specimens as their anterior temporals were much longer than broad, a diagnostic characteristic of *T. scincoides* in Australia[10]. All other Australian species of *Tiliqua* have fragmented temporal scales. However, both of the specimens collected differed from typical southern South Australian populations of *T. scincoides* in several respects (Fig. 2). They were large animals (SVL = 280 mm, 325 mm), and considerably more robust in body form than southern specimens. The dorsum was pale grey with nine irregular, brown, transverse bands on the body compared with 5-6 bands on the body of other South Australian specimens. Both lacked the distinct black temporal streak typical of other South Australian specimens and the tail was variegated with black and pale grey which tended to form very indistinct bands proximally, whereas *T. scincoides* from elsewhere in South Australia have a series of distinct bands on the tail.

Two other species of *Tiliqua* occur near Mimili and Pukatja[11] and both are known, and distinguished from each other and from *T. scincoides* by local people[9,12]. *Tiliqua multifasciata* occurs in *Triodia* dominated sandy country and is called "Langka". *Tiliqua occipitalis* occurs in mulga country and is called "Ilungkarkara". *Tiliqua scincoides* is called "Illillyarka".

It seems likely that the *T. scincoides* in northwest South Australia are isolated from the rest of that species' range and represent the remnants of a formerly more extensive distribution which may have become restricted by increasing aridity to isolated patches of suitable habitat during the Pleistocene[4,6]. The possibility exists that further isolated populations of *T. scincoides* may be found in other ranges which may provide suitable mesic refugia in the north of the state.

The fact that *T. scincoides* does not occur in the MacDonald Ranges[13] may indicate that this species did not cross the tract of sand plain and dunes between the Musgrave and MacDonald Ranges. Pianka[14] identified this tract of land as a corridor for latitudinal dispersal of sand plain inhabitating reptiles. The same tract may have been a barrier to longitudinal dispersal by at least some animals with different habitat requirements as shown by the occurrence of several species

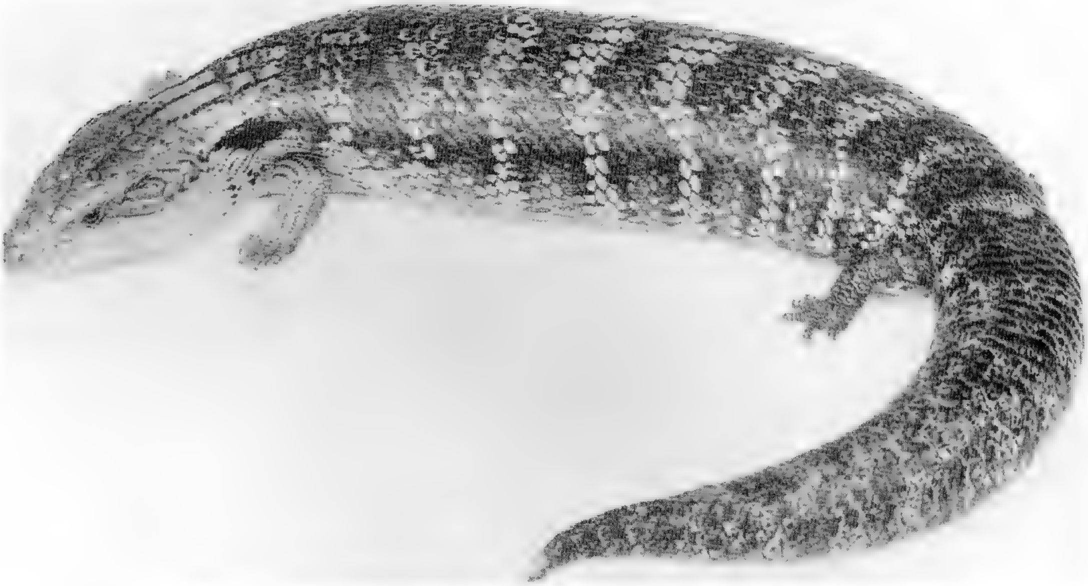

Fig. 2. *Tiliqua scincoides* from Mimili in the Everard Ranges, South Australia (SAM R33939) showing the robust habitus, greater number of bands on the body, indistinct temporal streak and variegated tail which distinguish central Australian specimens from those elsewhere in South Australia. SVL = 325 mm.

which find their geographic limits on either side of it (e.g. *Litoria gilleni, Pseudophryne occidentalis, Ctenotus rufescens, C. caudicinctus*)[8].

The occurrence of *T. scincoides* in central Australia represents a significant range extension for this species and provides further evidence that the mountain ranges of that area provide an important refuge for non-xeric adapted organisms. More importantly, this record represents a most unexpected occurrence of a very familiar species, underscoring our ignorance at a fundamental level about the Australian fauna.

Adrienne Edwards provided data on the distribution of *T. scincoides* in South Australia. Mark Hutchinson made helpful comments on the manuscript. Jenny Wendelbourne and the people of the Mimili and Pukatja communities are thanked for their hospitality.

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G. R. JOHNSTON, School of Biological Sciences, Flinders University of South Australia, G.P.O. Box 2100, Adelaide, S. Aust. 5001.

A NOTE ON *PHASCOLOSOMA TURNERAE* RICE (SIPUNCULA)

BY S. J. EDMONDS

Summary

Transactions of the Royal Society of S. Aust. (1992), **116**(4), 151.

BRIEF COMMUNICATION

A NOTE ON *PHASCOLOSOMA TURNERAE* RICE (SIPUNCULA)

Phascolosoma turnerae Rice, 1985 was described from 104 specimens of a sipunculan found boring into submerged wood and was collected at depths of 1135-1184 m in the Straits of Florida, south of Key West, U.S.A. and also from 366-412 m in the northern area of the Gulf of Mexico, Alabama, U.S.A.[1] This record is the first of a sipunculan living and boring in wood. *P. turnerae* is distinguished from other congeners by the shape of its introvert hooks (Fig. 1), and the structure of its body papillae.

Phascolosoma kapalum Edmonds, 1985 was described from three specimens dredged at 710 m off Sydney, N.S.W., Australia during a cruise of the "Kapala" in 1977[2]. Edmonds in 1985 was unaware of Rice's 1985 species. On comparing material of the two species in 1988, it became clear that *P. turnerae* and *P. kapalum* were conspecific, the latter being a junior synonym. (The date of publication of *P. turnerae* was 20 March 1985 and that of *P. kapalum* was 28 June 1985). No wood, however, was associated with the "Kapala" specimens nor did the collection records report the presence of any at the time of collection. It seems probable, then, that the specimens had been dislodged either during dredging or sorting.

Recently a single specimen of *P. turnerae* was found in some material sent for identification from the Northern Territory Museum, Darwin. The specimen (NTM WS87) was collected during trawling operations of "SOELA" in Queensland waters (17°59.2'S – 17°55.8'S, 147°04.5'E – 147°01.5'E) at 259-260 m by H. Larson, 16.i.1986. The collection label reports that the specimen was collected from "a piece of rotting wood" and a piece of the wood was included in the collecting tube along with the sipunculan.

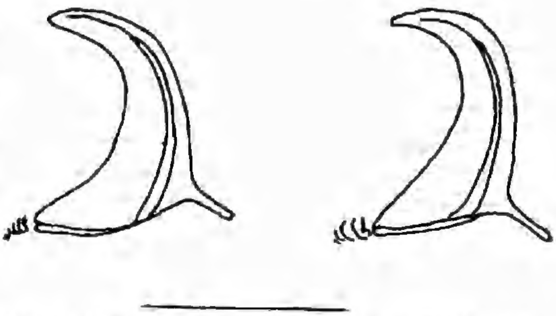

Fig. 1. *Phascolosoma turnerae*, introvert hooks from Queensland specimen (Scale line = 0.05 mm).

The purpose of the present note is threefold: 1. to record the synonymy of *P. turnerae* and *P. kapalum*, the former name having priority, 2. to confirm that *P. turnerae* is associated with submerged wood and 3. to record the wide distribution of *P. turnerae* now reported from the Atlantic Ocean (Straits of Florida and the Gulf of Mexico) and the south-west Pacific Ocean (off Sydney and off the Great Barrier Reef, Australia).

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S. J. EDMONDS, South Australian Museum, North Terrace, Adelaide, S. Aust. 5000.

EARLY HOLOCENE FROGS FROM THE TANTANOOLA CAVE, SOUTH AUSTRALIA

BY MICHAEL J. TYLER, FRED W. ASLIN AND SIMON BRYARS

Summary

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BRIEF COMMUNICATION

EARLY HOLOCENE FROGS FROM THE TANTANOOLA CAVE, SOUTH AUSTRALIA

Five extant species of frogs are represented in the Quaternary record of the southeast of South Australia[1], constituting one of the best known components of the Australian Quaternary frog fauna[2]. Here we report a further site and add one more species.

In 1982 a quantity of fossil vertebrates and invertebrates was recovered from a pocket of sandy clay fill at the entrance to the Tantanoola Tourist Cave at Tantanoola, S.A. The material was uncovered in the process of excavation of the floor of the entrance to permit wheelchair access. Included in the vertebrate material were 185 frog ilia. Here we report the identity of the ilia and place them in the context of the Australian Quaternary record.

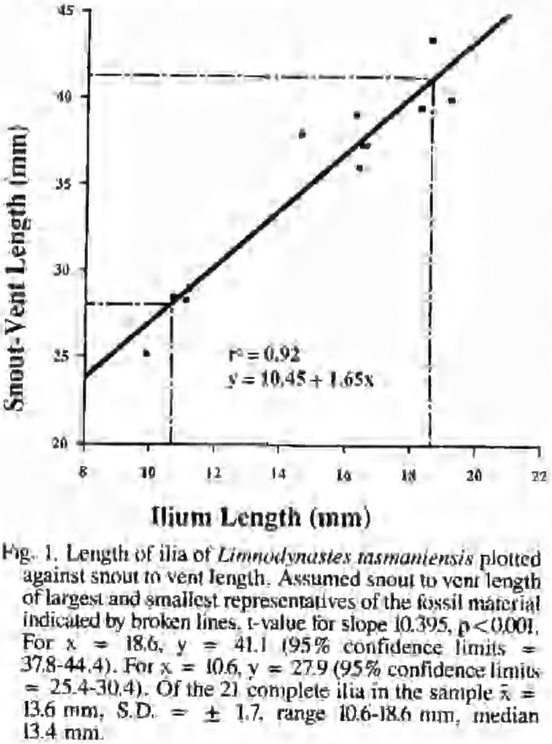

Fig. 1. Length of ilia of *Limnodynastes tasmaniensis* plotted against snout to vent length. Assumed snout to vent length of largest and smallest representatives of the fossil material indicated by broken lines. t-value for slope 10.395, $p<0.001$. For $x = 18.6$, $y = 41.1$ (95% confidence limits = 37.8-44.4). For $x = 10.6$, $y = 27.9$ (95% confidence limits = 25.4-30.4). Of the 21 complete ilia in the sample $\bar{x}$ = 13.6 mm, S.D. = ± 1.7, range 10.6-18.6 mm, median 13.4 mm.

Five species were collected at Tantanoola. They, and the quantities involved are listed in Table 1. From the maximum number of left or of right ilia in each sample it is apparent that a minimum total of 100 individual specimens is included. The very large number of *Limnodynastes tasmaniensis* Günther recovered permits an accurate extrapolation of the size of the individuals compared with modern representatives of the species (Fig. 1). The size ranges of modern individuals are 31.1-39.5 mm (males) and 32.0-47.2 mm (females)[3], hence the fossil material clearly is comparable in size.

The faunal composition is almost identical to that represented at Victoria Cave and Henschke's Quarry Cave near Naracoorte, S.A.[1] *Litoria ewingi*, *Limnodynastes tasmaniensis*, *L. dumerilii* and *Crinia signifera* are common to the three sites. A single *Geocrinia laevis* from Victoria Cave is not represented at Tantanoola, whilst a single *Neobatrachus pictus* at Tantanoola is not represented at the other sites, so increasing to six the number of taxa in the fossil record of the southeast.

TABLE 1: *The frog ilia recovered at Tantanoola Cave**.

Species	Total Ilia	Left Ilia	Right Ilia	Registration Numbers
Limnodynastes tasmaniensis	137	66	71	P32111, P32239
Limnodynastes dumerilii	2	1	1	P32237
Crinia signifera	42	24	18	P32112, P32240
Neobatrachus pictus	1	1	0	P32241
Litoria ewingi	2	0	2	P32238
unidentifiable	1	0	1	
Totals	185	92	93	

*All specimens are deposited in the South Australian Museum.

It has been suggested that the accumulation of so many frogs in cave deposits does not reflect the use of caves as diurnal or seasonal refuges, but rather is a consequence of the disgorgement of pellets by owls which are predators of frogs[1].

The age of the material as determined by C^{14} dating of charcoal is 9860 ± 190 years B.P. The analysis was undertaken by Beta Analytic Inc. (Beta reference 54010; F.W.A. "Area 2").

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[1]**Tyler, M. J.** (1977) Trans. R. Soc. S. Aust. 101 (3), 85-89.
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MICHAEL J. TYLER, Dept of Zoology, University of Adelaide, Box 498 GPO, Adelaide, S. Aust. 5001, FRED W. ASLIN, 29 Elizabeth Street, Mt Gambier, S. Aust. 5290 and SIMON BRYARS, Dept of Zoology, University of Adelaide, Box 498 GPO, Adelaide, S. Aust. 5001.

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