VOL. 122, PARTS 1 & 2
29 MAY, 1998

Transactions of the Royal Society of South Australia

Incorporated

Contents

PUBLISHED AND SOLD AT THE SOCIETY'S ROOMS
SOUTH AUSTRALIAN MUSEUM, NORTH TERRACE, ADELAIDE, S.A. 5000

TRANSACTIONS OF THE

ROYAL SOCIETY OF SOUTH AUSTRALIA

INCORPORATED

VOL. 122, PART 1

TRANSACTIONS OF THE

ROYAL SOCIETY OF SOUTH AUSTRALIA INC.

CONTENTS, VOL. 122, 1998

PARTS 1 & 2, 29 MAY, 1998

PARTS 3 & 4, 30 NOVEMBER, 1998

Insert to Transactions of the Royal Society of South Australia, Vol. 122, parts 3 & 4, 30 November, 1998

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Key Words: Sthenurus baileyi sp. nov., Sthenurus antiquus, Sthenurus, Simosthenurus, sthenurine kangaroo, Victoria Fossil Cave, Naracoorte, Brothers Islands, Eyre Peninsula, Pleistocene.

Transactions of the Royal Society of S. Aust. (1998), **122**(1), 1-15.

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by GAVIN J. PRIDEAUX* & RODERICK T. WELLS*

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Sthenurus baileyi sp. nov. is described from Pleistocene deposits of Eyre Peninsula and the southeast of South Australia. The dentary is similar in size and morphology to *S. occidentalis* Glauert, 1910 but the cranium is much less inflated across the frontals and the rostrum less tapered anteriorly. *Sthenurus baileyi* is characterised by very low crowned molars, most similar to *S. cegsal* Pledge, 1992, *S. brachyselenis* Prideaux & Wells, 1997 and *S. antiquus* Bartholomai, 1963. Upper and lower premolars are similar to *S. antiquus* and *S. brownei* Merrilees, 1967. Overall, *S. baileyi* appears most closely related to *S. antiquus* and may represent the most plesiomorphic member of the lineage containing the more brachycephalic sthenurine species.

KEY WORDS: *Sthenurus baileyi* sp. nov., *Sthenurus antiquus*, *Sthenurus*, *Simosthenurus*, sthenurine kangaroo, Victoria Fossil Cave, Naracoorte, Brothers Islands, Eyre Peninsula, Pleistocene.

Introduction

Following its discovery in 1969, the extensive Pleistocene deposit within Victoria Fossil Cave at Naracoorte, South Australia has yielded remains from around one hundred vertebrate species. Included are slightly less than half of the known Pleistocene species of sthenurine kangaroos (subfamily Sthenurinae): *Procoptodon rapha* Owen, 1874, *Sthenurus andersoni* Marcus, 1962, *S. brownei* Merrilees, 1967, *S. gilli* Merrilees, 1965, *S. maddocki* Wells & Murray, 1979, *S. occidentalis* Glauert, 1910, *S. pales* DeVis, 1895 (Wells *et al.* 1984), and a new sthenurine, *S. baileyi* sp. nov. The species is also known from a single specimen collected from an eroded cave on one of the Brothers Islands in Coffin Bay, Eyre Peninsula (Brown 1908; Fig. 1). Williams (1980) identified the cranium and associated dentaries as *Sthenurus* cf. *maddocki*, but it is here designated as the holotype of *S. baileyi* sp. nov. Description of the new species and a consideration of its phylogenetic implications form the subject of this paper.

Materials and Methods

The material is housed in the South Australian Museum, Adelaide (prefix SAMA) and Flinders University (prefix FU). Dental homology follows Flower (1867) and Lucketi (1993). Dental nomenclature follows Tedford & Woodburne (1987), Ride (1993) or is standard. Mensuration follows Tedford (1966) and Wells & Murray (1979). Dental measurements (mm) are provided in Table 1.

Fig. 1. Map of southeastern Australia showing location of deposits yielding *Sthenurus baileyi* sp. nov.

Systematics

Order Diprotodontia Owen, 1866
Suborder Phalangerida Aplin & Archer, 1987
Superfamily Macropodoidea (Gray, 1821)
Family Macropodidae Gray, 1821
Subfamily Sthenurinae (Glauert, 1926)
Genus *Sthenurus* Owen, 1874
Subgenus *?Simosthenurus* Tedford, 1966

Sthenurus (?Simosthenurus) baileyi sp. nov.
(FIGS 1-8)

Holotype: SAMA P13670, partial cranium (with I1-3, dP2, dP3, M1-4, excavated P3; Fig. 2A,B, 3A, 4A,

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TABLE 1. *Cheek tooth dimensions of* Sthenurus baileyi, S. brachyselenis, S. brownei *(eastern form)*, S. cegsai *and* S.antiquus: *mean, standard deviation (parentheses), range (brackets).*

Abbreviations: L= length, AW = width of anterior loph(id); PW = width of posterior loph(id); AH = crown height of anterior loph(id) on buccal side; PH = crown height of posterior loph(id) on buccal side; n = sample size. Note that crown heights are heavily dependent on degree of enamel wear, hence, frequently high standard deviations.

Tooth	Species	L	AW	PW	AH	PH	n
UPPER DENTITION							
dP2	*S. baileyi*	10.5	7.5	10.0	6.2	6.1	1
	S. baileyi TYPE	As above					
	S. brownei (eastern form)	10.9 (0.43) [10.4-11.9]	8.7 (0.40) [8.1-9.5]	10.8 (0.38) [10.4-11.4]	7.0 (0.51) [6.0-8.0]	7.9 (0.60) [6.6-8.7]	15
S. cegsai	-	-	-	-	-	-	
	S. antiquus	-	-	-	-	-	-
dP3	*S. baileyi*	10.6	9.9	10.8	-	-	1
	S. baileyi TYPE	As above					
	S. brownei (eastern form)	11.3 (0.29) [10.6-11.7]	10.7 (0.32) [10.2-11.3]	11.0 (0.37) [10.6-11.8]	5.7 (0.54) [4.8-6.4]	5.9 (0.46) [5.3-6.8]	15
	S. cegsai	9.3	8.6	9.2	6.3	6.3	1
	S. antiquus	-	-	-	-	-	-
P3	*S. baileyi*	17.2 (0.14) [171.-17.3]	9.9 (0.28) [9.7-10.1]	12.9 (0.21) [12.7-13.0]	9.8 (0.28) [9.6-10.0]	9.7 (1.06) [8.9-10.4]	2
	S. baileyi TYPE	17.1	10.1	13.0	10.0	10.4	
	S. brownei (eastern form)	17.1 (0.57) [16.2-18.0]	10.9 (0.68) [9.0-11.8]	13.7 (0.81) [12.1-15.0]	9.8 (0.76) [8.3-11.1]	9.7 (0.78) [8.6-11.3]	21
	S. cegsai	-	-	-	-	-	-
	S. antiquus	14.9	8.3	11.3	8.4	10.1	1
M1	*S. baileyi*	12.3 (0.14) [12.2-12.4]	12.3 (0.21) [12.1-12.4]	12.3 (0.21) [12.1-12.4]	6.3 (0.07) [6.2-6.3]	6.6 (0.42) [6.3-6.9]	2
	S. baileyi TYPE	12.2	12.1	12.1	6.2	6.3	
	S. brownei (eastern form)	12.9 (0.43) [12.2-13.6]	12.4 (0.40) [11.6-13.0]	12.3 (0.34) [11.8-13.1]	6.1 (0.76) [5.0-7.9]	6.5 (0.62) [5.3-8.1]	28
	S. cegsai	-	-	-	-	-	
	S. antiquus	12.4	12.0	12.1	-	-	1
M2	*S. baileyi*	13.8 (0.21) [13.6-13.9]	13.2 (0.21) [13.0-13.3]	13.1 (0.14) [13.0-13.2]	6.9 (0.42) [6.6-7.2]	7.2 (0.35) [6.9-7.4]	2
	S. baileyi TYPE	13.6	13.3	13.0	7.2	7.4	
	S. brownei (eastern form)	14.1 (0.37) [13.2-14.7]	13.6 (0.46) [12.9-14.4]	13.1 (0.43) [12.5-14.3]	6.6 (0.76) [5.3-7.8]	6.9 (0.58) [5.8-8.0]	23
	S. cegsai	-	-	-	-	5.6	1
	S. antiquus	14.9 (0.07) [14.8-14.9]	13.4 (0.14) [13.3-13.5]	13.0 (0.21) [12.8-13.1]	7.2 (1.13) [6.4-8.0]	7.4 (1.34) [6.4-8.3]	2
M3	*S. baileyi*	14.5 (0.00) [14.5]	13.7 (0.21) [13.5-13.8]	12.6 (0.35) [12.8-13.3]	7.0 (0.14) [6.9-7.1]	6.8 (0.28) [6.6-7.0]	2
	S. baileyi TYPE	14.5	13.5	12.8	7.1	6.6	
	S. brownei (eastern form)	14.5 (0.39) [13.7-15.5]	14.0 (0.50) [13.3-14.8]	12.9 (0.54) [12.3-14.5]	6.7 (0.62) [5.4-8.1]	7.0 (0.53) [5.9-8.1]	19
	S. cegsai	13.1 (0.07) [13.0-13.1]	11.5	10.9 (0.14) [10.8-11.0]	5.4 (0.00) [5.4]	5.5 (0.14) [5.4-5.6]	2
	S. antiquus	16.0 (0.35) [15.7-16.2]	13.6 (0.49) [13.2-13.9]	12.9 (0.85) [12.3-13.5]	8.3 (0.35) [8.0-8.5]	8.3 (0.00) [8.5]	2
M4	*S. baileyi*	13.8	13.4	11.3	6.7	6.1	1
	S. baileyi TYPE	As above					
	S. brownei (eastern form)	14.0 (0.43) [13.2-14.5]	12.2 (0.48) [11.3-13.0]	11.2 (0.40) [10.6-12.0]	8.1 (0.62) [7.4-9.6]	7.4 (0.78) [6.5-8.8]	16
	S. cegsai	12.2	11.0	9.5	5.5	5.1	1
	S. antiquus	-	-	-	-	-	-

TABLE 1. – Continued

LOWER DENTITION							
dp2	*S. baileyi*	9.6	7.5	8.9 (0.99) [8.2-9.6]	7.3	6.2 (0.71) [5.7-6.7]	2
	S. baileyi TYPE	9.6	7.5	8.2	7.3	5.7	
	S. brachyselenis	8.1	5.1	6.1	5.7	5.5	1
	S. brownei (eastern form)	9.8 (0.45) [9.2-10.9]	6.5 (0.34) [5.9-7.2]	9.1 (0.36) [8.6-9.7]	7.5 (0.82) [5.8-8.7]	7.1 (0.71) [6.0-8.2]	17
	S. cegsai	-	-	-	-	-	-
	S. antiquus	-	-	-	-	-	-
dp3	*S. baileyi*	9.8 (0.14) [9.7-9.9]	8.9 (0.71) [8.4-9.4]	9.1 (0.28) [8.9-9.3]	6.0	6.0	2
	S. baileyi TYPE	9.9	8.4	8.9	-	-	
	S. brachyselenis	10.2	7.8	8.2	6.2	7.0	1
	S. brownei (eastern form)	10.4 (0.36) [10.0-11.1]	9.2 (0.46) [8.4-10.0]	9.3 (0.31) [8.7-9.8]	7.3 (0.47) [6.6-8.2]	7.2 (0.63) [6.0-8.2]	17
	S. cegsai	-	-	-	-	-	-
	S. antiquus	-	-	-	-	-	-
p3	*S. baileyi*	16.2 (0.78) [15.3-17.8]	8.0 (0.32) [7.7-8.4]	9.7 (0.44) [9.1-10.3]	9.5 (1.04) [7.9-11.0]	9.0 (1.03 [7.3-10.2]	6)
	S. baileyi TYPE	15.3	7.9	9.5	8.9	9.0	
	S. brachyselenis	13.8	6.3	8.0	7.3	6.7	1
	S. brownei (eastern form)	16.2 (0.53) [15.2-17.0]	8.5 (0.34) [8.0-9.5]	10.3 (0.58) [9.4-11.5]	9.9 (0.85) [8.9-11.4]	9.9 (0.83) [8.9-11.3]	19
	S. cegsai	14.8	6.5	7.2	8.3	7.1	1
	S. antiquus	17.6	8.2	10.1	12.2	11.4	1
m1	*S. baileyi*	12.0 (0.41) [11.5-12.5]	10.1 (0.22) [9.9-10.4]	10.1 (0.26) [9.8-10.4]	7.1 (1.01) [6.3-8.5]	7.0 (0.76) [6.3-8.0]	4
	S. baileyi TYPE	12.1	10.0	10.2	6.4	6.5	
	S. brachyselenis	13.9	9.9	10.3	9.3	9.4	1
	S. brownei (eastern form)	13.1 (0.64) [12.1-14.7]	10.4 (0.49) [9.4-12.0]	10.6 (0.43) [9.6-11.5]	8.6 (1.04) [6.4-10.0]	8.7 (1.07) [6.5-10.2]	29
	S. cegsai	10.5	-	-	-	-	1
	S. antiquus	13.8	-	11.0	8.5	8.5	1
m2	*S. baileyi*	13.3 (0.46) [12.8-13.9]	11.4 (0.27) [11.0-11.6]	11.2 (0.41) [10.7-11.7]	8.3 (0.49) [7.8-8.9]	8.4 (0.63) [7.8-9.2]	4
	S. baileyi TYPE	12.8	11.5	11.7	8.0	8.0	
	S. brachyselenis	-	-	-	-	-	-
	S. brownei (eastern form)	14.7 (0.53) [13.8-16.1]	11.4 (0.39) [10.4-12.0]	11.7 (0.33) [11.1-12.2]	9.5 (0.94) [8.2-10.8]	9.5 (0.80) [8.0-11.2]	21
	S. cegsai	12.7	10.8	10.3	5.9	5.9	1
	S. antiquus	15.3 (0.85) [14.7-15.9]	11.9 (0.71) [11.4-12.4]	12.1 (0.78) [11.5-12.6]	10.4	10.4	2
m3	*S. baileyi*	14.1 (0.64) [13.6-15.0]	12.2 (0.37) [11.7-12.6]	11.9 (0.42) [11.4-12.4]	8.2 (0.93) [7.0-8.9]	7.9 (0.71) [6.9-8.4]	4
	S. baileyi TYPE	13.6	12.6	12.4	7.8	7.8	
	S. brachyselenis	-	-	-	-	-	-
	S. brownei (eastern form)	14.9 (0.51) [13.7-15.7]	12.0 (0.43) [11.2-12.9]	12.2 (0.35) [11.4-12.9]	9.3 (0.61) [8.4-10.3]	9.1 (0.73) [7.5-10.4]	21
	S. cegsai	12.8	11.0	10.2	7.0	6.4	1
	S. antiquus	16.0 (0.99) [15.3-16.7]	12.4 (0.42) [12.1-12.7]	12.2 (0.49) [11.8-12.5]	10.5	10.3	2
m4	*S. baileyi*	13.9 (0.11) [13.7-14.0]	12.1 (0.26) [11.8-12.3]	11.1 (0.42) [10.5-11.5]	7.4 (0.43) [7.1-8.0]	7.2 (0.35) [6.9-7.8]	5
	S. baileyi TYPE	13.8	12.2	11.2	7.1	7.1	
	S. brachyselenis	-	-	-	-	-	-
	S. brownei (eastern form)	14.0 (0.43) [13.2-14.5]	12.2 (0.48) [11.3-13.0]	11.2 (0.40) [10.6-12.0]	8.1 (0.62) [7.4-9.6]	7.4 (0.78) [6.5-8.8]	16
	S. cegsai	11.9	10.3	8.6	5.3	5.3	1
	S. antiquus	15.4 (0.49) [15.0-15.7]	12.4 (0.21) [12.2-12.5]	11.0	8.5 (0.35) [8.2-8.7]	7.7 (0.35) [7.4-7.9]	2

5A), left and right dentaries (with i1, dp2, dp3, m1-4, excavated p3; Fig. 3B, 4B, 5C,D), apparently collected from a bone breccia in an eroded cave on the western end of west Brothers Island (34° 35' S, 135° 20' E), Coffin Bay, Eyre Peninsula South Australia (Brown 1908; Williams 1980; Fig. 1). Other mammals from the deposit include *Macropus rufogriseus*, *Potorous platyops*, *Pseudocheirus* sp., *Rattus fuscipes* and *Neophoca cinerea*. A large bird femur previously attributed to *Genyornis newtoni* (Rich 1979) belongs to *Dromaius novaehollandiae* (J. McNamara pers. comm. 1996). Age of type locality is considered Pleistocene because all taxa identified to species are only known from the Quaternary. Similarly, the genus *Sthenurus* appears not to have existed anywhere beyond the late Pleistocene. Details of collection are uncertain but probably retrieved by D. R. George around 1902 (J. McNamara pers. comm. 1996).

Diagnosis

Cranium similar in size to *Sthenurus occidentalis* but frontals less expanded, rostrum shorter and broader, with wider nasals and larger narial aperture. P3 similar to *S. browneí* but with relatively narrow, shallow longitudinal basin and two accessory cuspules anterior to prominent posterobuccal accessory cusp. Upper molars very low crowned, with short precingulum, weak postprotocrista and very well developed postparacrista. Dentary similar in size and morphology to *S. occidentalis* and *S. antiquus* Bartholomai, 1963 but with more posteriorly inflated pterygoid fossa than in any *Sthenurus* species. Posteroventral border of masseteric fossa expanded laterally into wide shelf, similar to *S. cegnai*, *S. gilli* and *S. maddocki*. i1 intermediate between *S. occidentalis* and *S. browneí* in general shape and degree of procumbency. p3 most similar in morphology to *S. antiquus* but lower crowned, with straighter lingual crest. Lower molars very low crowned, with anteroposteriorly short trigonid, well-developed premetacristid, and very reduced cristid obliqua and paracristid producing a morphology closest to *S. cegnai*, *S. antiquus* and *S. brachyselenis* Prideaux & Wells, 1997 but wider relative to length.

Description of holotype

Vertical portion of premaxilla flared dorsally providing elongate contact with nasals. Diastema short, anterior ¼ comprising premaxilla and posterior ¾ maxilla. Incisive foramina long, narrow, anterior border level with posterior extreme of I3 alveolus (Fig. 3A). Rostrum short, tapered anteriorly (Fig. 2A). Buccinator fossa on maxilla rather shallow anteriorly, deeper posteriorly, anterior to zygomatic arch. Masseteric process well-formed, rather narrow, eroded off ventrally on left and right sides. Nasals very broad posteriorly and, although broken anteriorly, clearly short. Nasofrontal suture gently sinusoidal (Fig. 2A). Frontals moderately inflated anteriorly; supraorbital crests only slightly developed (Fig. 2A). Temporal crests moderately developed, not fully convergent upon sagittal suture. Large infraorbital foramen positioned anteroventral and mesial to lachrymal foramen, just below orbital centre. Palatal vacuities extend anteriorly to anterior extreme of M1 (Fig. 3A). Right lateral extremity of broken postpalatine bar level with M4 interloph valley.

I1 crown rather long, moderately wide, with vertical occlusal surface facing posteriorly. I2 very small, splint-like, ⅓ size of I1, I3 high crowned, but quite short anteroposteriorly (Fig. 2B). Small anterolingual lobe evident on I3.

dP2 reminiscent of P3, rounded in general outline, especially lingually, but much shorter relative to width (Fig. 4A). Buccal and lingual crests straight, except for buccal curvature of lingual crest at posterior extremity. Anterior basin small, quite deep and separated from longitudinal basin by low transverse ridgelet. Posterior basin appears to have been relatively large, approx. half size of longitudinal basin.

dP3 completely molariform and similar in general outline to M1, but differs by having lophs orientated obliquely (not perpendicular) to buccal and lingual sides of tooth (Fig. 4A). In addition, precingulum very slight terminating before reaching lingual extreme of tooth. Premetacrista appears well-developed. Protoloph appears to have been very curved, convex anteriorly. No enamel crenulations present in interloph valley; very low, barely detectable postprotocrista positioned just lingual of dP3 midline (Fig. 4A). Postmetaconulecrista curves dorsobuccally from metaconule to meet vertical postmetacrista. Small accessory crest positioned mesial to postmetacrista, slight postlink centrally positioned on posterior metaloph face.

P3 rounded in outline and tapered anteriorly (Fig. 5A). Longitudinal basin shallow. Buccal crest barely exceeding lingual crest in height. Anteriorly, lingual crest begins to run parallel to buccal crest then posterior ⅔ of crest curves out lingually. Small anterior basin present and separated from longitudinal basin by transverse ridge descending from anterior buccal cusp terminating adjacent to anterior lingual cusp. Posterior basin short, well-formed and separated from longitudinal basin by low transverse ridge originating from posterior lingual cusp and orientated obliquely (slightly anterobuccally) to meet low down on buccal crest. Main posterobuccal accessory cusp well-formed, not quite as high as posterior part of buccal crest. Three

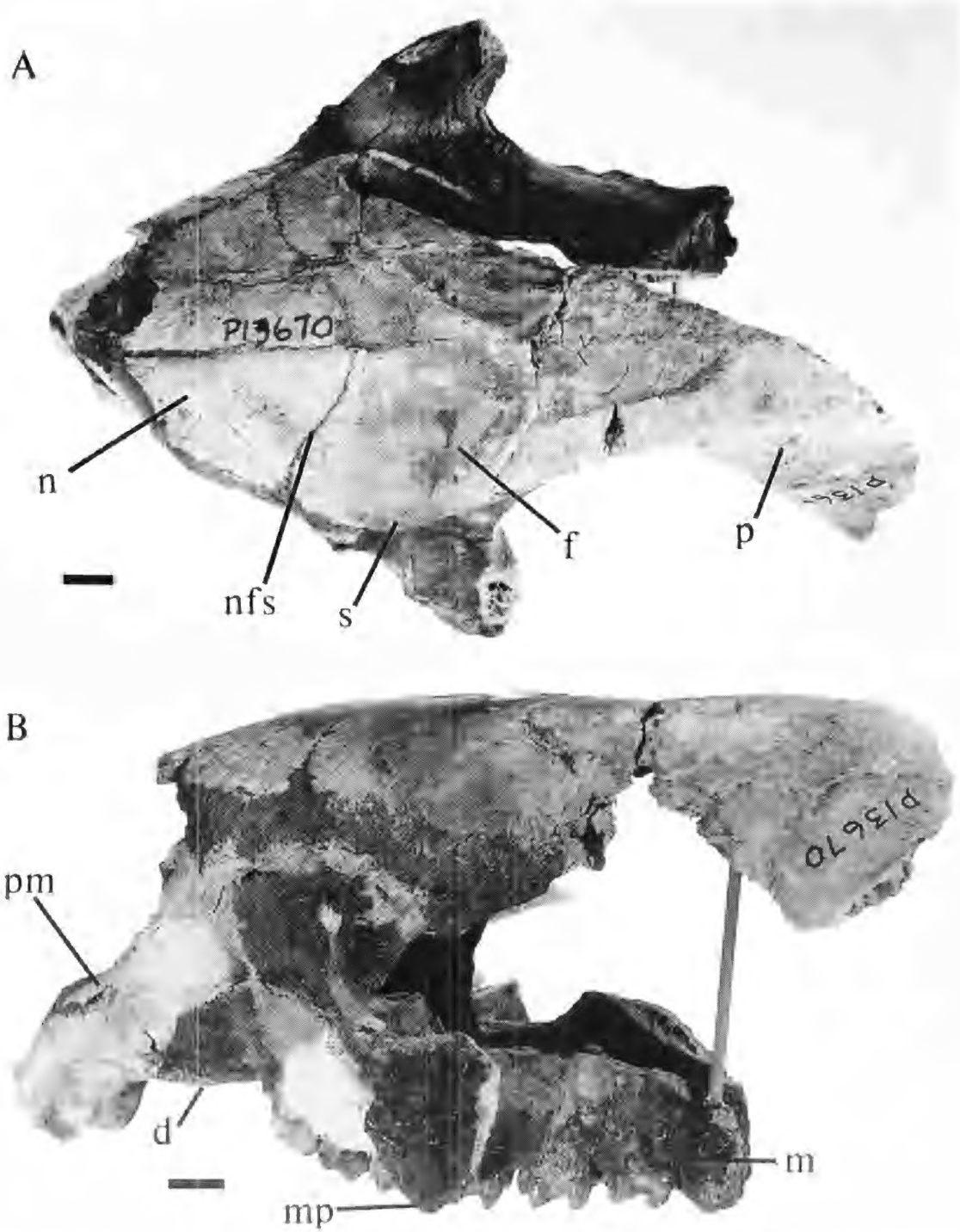

Fig. 2. *Sthenurus bailevi* sp. nov. cranium. A. Holotype (P13670) dorsal view. B. Holotype lateral view. Scale bars = 10 mm. Abbrevs: d = diastema, f = frontal, m = maxilla, mp = masseteric process, n = nasal, nfs = nasofrontal suture, p = parietal, pm = premaxilla, s = supraorbital crest.

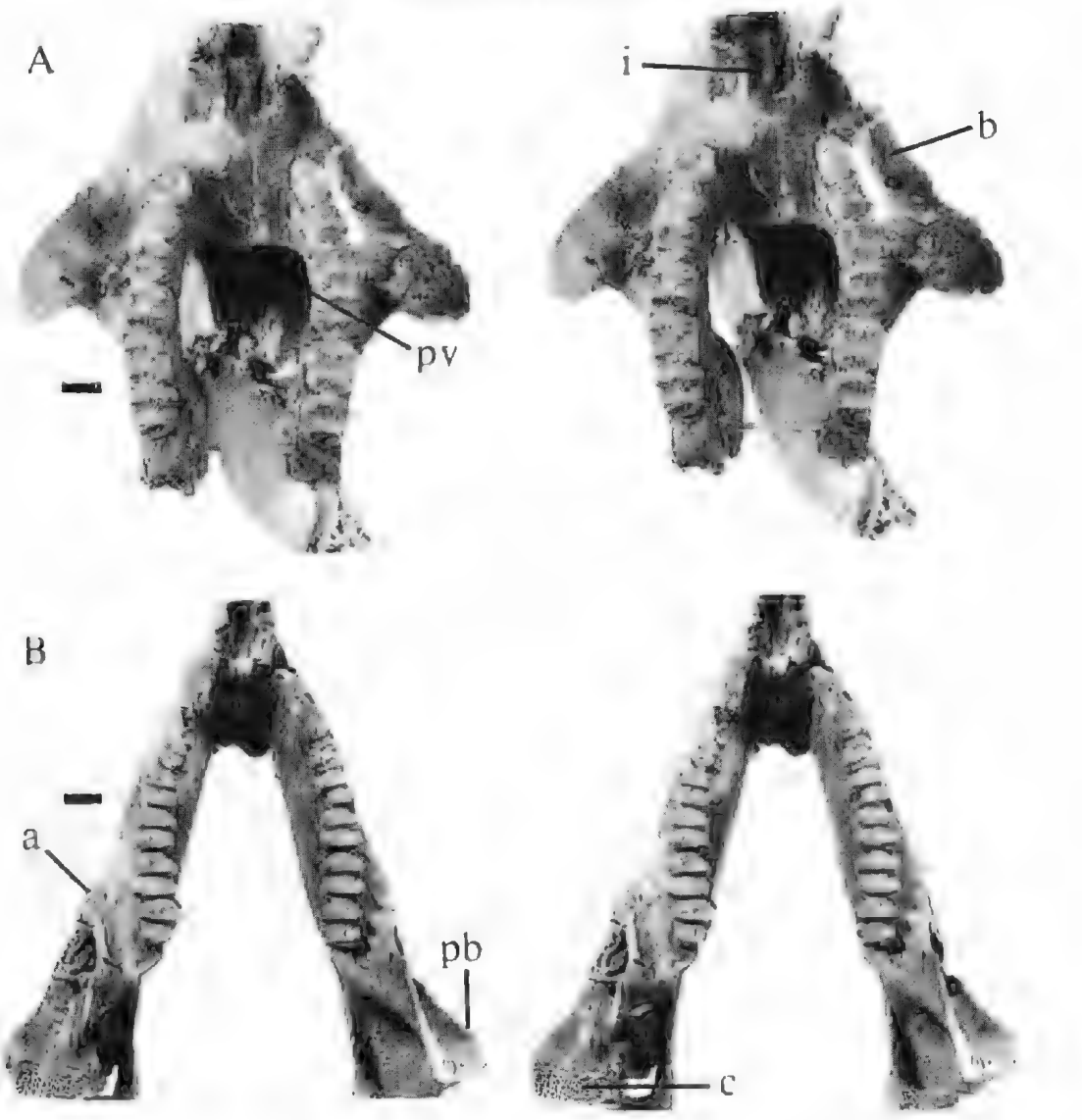

Fig. 3. *Sthenurus baileyi* sp. nov. cranium and dentaries. A, Stereopair of holotype cranium (P13670) palatal view. B Stereopair of holotype dentary occlusal view. Scale bars = 10 mm. Abbrevs: a = anterior root of ascending ramus, b = buccinator fossa on maxilla, c = mandibular condyle, i = incisive foramina, pb = posteroventral border of masseteric fossa, pv = palatal vacuities.

small poorly separated accessory cuspules positioned anterior to main accessory cusp (Fig. 5A).

Upper molars very low crowned, with protoloph equal in width to metaloph in M1-2, but wider in M3-4 (Fig. 4A). Precingulum short, buccal extreme terminating at distinct cuspule, representing either stylar cusp A or B. Slight crest (probable paracrista) connects cuspule posteriorly to paracone. Two to four slight vertical crenulations centrally located on precingulum, with most lingual probably remnant preprotocrista (forelink). Postprotocrista weak, low, ascending buccally across face of protoloph into interloph valley, uniting with vertical crenulation directed posteriorly from mid-point on protoloph. Postparacrista strongly developed, forming buccal border of interloph valley, meeting slight premetacrista on anterior face of metaloph (Fig. 4A) Interloph valley with few very fine to no enamel crenulations. Postmetaconulecrista sweeps across posterior face of metaloph terminating just posterior to end of postmetacrista. Two to three small distinct crenulations enclosed by postmetaconulecrista on metaloph posterior face.

Dentary moderately proportioned, except for

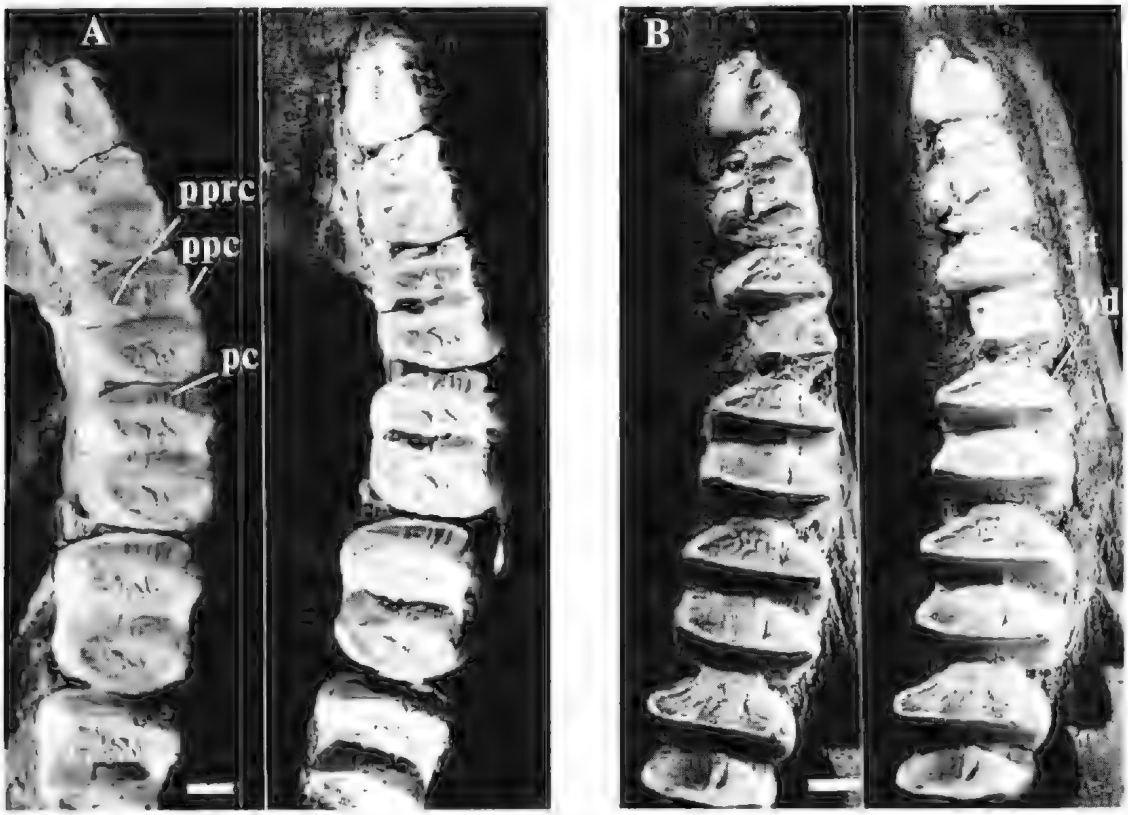

Fig. 4. *Sthenurus baileyi* sp. nov. cheek tooth rows. A. Stereopair of holotype (P13670) left upper cheek tooth row occlusal view. B. Stereopair of holotype (P13670) right lower cheek tooth row occlusal view. Scale bars = 5 mm. Abbrevs: co = cristid obliqua, pc = precingulum, pd = paracristid, ppc = postparacrista, pprc = postprotocrista, t = trigonid.

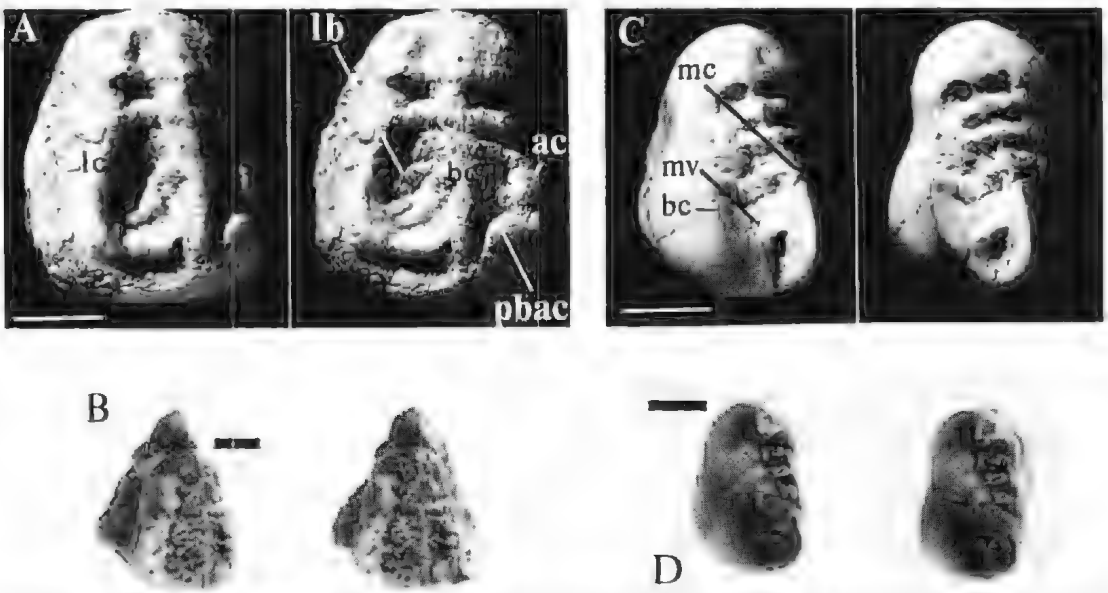

Fig 5. *Sthenurus baileyi* sp. nov. premolars. A. Stereopair of holotype (P13670) left P3 close-up occlusal view. B. Stereopair of paratype (FU0167) left P3 occlusal view. C. Stereopair of holotype left p3 close-up occlusal view. D. Stereopair of holotype left p3 occlusal view. Scale bars = 5 mm. Abbrevs: ac = accessory cuspules, bc = buccal crest, lb = longitudinal basin, lc = lingual crest, mc = main crest, mv = median valley, pbac = posterobuccal accessory cusp.

posteriorly inflated pterygoid fossa and lateral expansion of posteroventral border of masseteric fossa into wide shelf. Ramus moderately deep for width, particularly in region of symphysis. Symphysis gently tapered anteriorly and posteriorly, only extended short way beneath genial pit, below anterior root of dp3. Digastric eminence present but not particularly prominent. Digastric sulcus extending from below anterior extreme of pterygoid fossa to below m2 hypolophid. Diastema short, with median dorsal groove deep, relatively wide. Very shallow buccinator sulcus arises near posterior extreme of diastema, dorsal to large anterior mental foramen. Buccinator sulcus deepens slightly posteriorly, terminates below m1 hypolophid. Posterior mental foramen positioned below m2 hypolophid, half-way between dorsal and ventral borders of ramus.

Anterior root of ascending ramus begins adjacent to m3 hypolophid (Fig. 3B), extending posteriorly to form buccal border of postalveolar fossa. Pterygoid fossa inflated posteriorly, projecting well beyond border of masseteric fossa when viewed laterally. Masseteric fossa deep, due largely to laterally expanded posteroventral border (Fig. 3B). Ventral border of masseteric fossa at same horizontal level as posterior region of buccinator sulcus. Masseteric foramen moderately large, vertical in orientation. Inferior mandibular foramen rather small. At anterior extreme of pterygoid fossa, anteromedial to inferior mandibular foramen, dorsoventrally wide mylohyoid groove present. This appears to have been partially overhung by sharp anterodorsally-directed process at anteromedial border of pterygoid fossa, and similarly-shaped posteroventrally-directed process positioned below posterior extreme of postalveolar fossa. Mandibular condyle moderately large (Fig. 3B). Angular process well-developed, rising dorsally to acute point.

i1 rather short, slender, upturned, with occlusal surface at a horizontal level just above base of cheek teeth crowns. dp2 on both sides of holotype too worn or fragmentary to interpret. Likewise, dp3 very worn, although clearly molariform, possessing low but well-defined para-, premeta-, prehypo- and preento-cristids.

p3 considerably longer than any molar, with main (lingual) crest extending from posterolingual corner to midline of tooth anteriorly (Fig. 5C,D). Three cuspules form anterior part of main crest, with each bearing pair of lateral ridgelets, one descending buccally, one lingually. Buccal ridgelets terminate at low shelf formed by three confluent cuspules, located immediately anterior to buccal crest. Buccal crest straight, short, equal in length to and mirroring shape of posterior part of main crest. Median valley rather narrow, moderately deep. Toward its posterior 1/3, median valley traversed by coarse ridgelet (Fig. 5C,D).

Lower molars very low crowned, with protolophid and hypolophid occlusal surfaces linear and close to parallel. Trigonid very short, with paracristid low and composed of two moieties. Degree of separation of anterior and posterior moieties increases from m1 to m4. Posterior part of paracristid sweeps smoothly anterolingually across protolophid face, terminates on buccal side of anterior part. In more posterior molars, anterior component of paracristid shifted more lingually but posterior extreme remains within buccal 1/3 of anterior protolophid face, originating well below lophid apex. A few fine enamel crenulations arise low down on anterior face of protolophid and descend into trigonid basin. Lingual side of trigonid bordered by well-developed premetacristid, which terminates at paraconid. Precingulid small and positioned anterobuccal to paracristid, extending lingually as very thin peninsula at anterior extreme of molar. Cristid obliqua (prehypocristid) low, similarly developed and aligned in similar position on hypolophid as paracristid on protolophid. Preentocristid very low and barely detectable. Aside from these weakly developed crests, shallow interlophid valley bears no enamel crenulations. Posterior face of hypolophid with low, shallow inflation.

Paratypes: From Victoria Fossil Cave, Naracoorte, South Australia (37° 00' S, 140° 48' E): FU0004, left and right adult dentaries; FU0167, left P3, M1 (P3 in Fig. 5B); FU0168, right p3; FU0294, partial right dentary; SAMA P16531/P16558, left and right adult dentaries (left dentary in Fig. 6A,B); P28282, right juvenile dentary; P28659, right M2, left M3. FU0004, FU0167 and SAMA P28659 may belong to same individual based on proximity in deposit, degree of enamel wear and occlusal fit. Specimens collected by Prideaux, Wells and others. Age of deposit is medial to late Pleistocene (Wells *et al.* 1984; Aylliffe *et al.* in press).

Features not preserved adequately in holotype are described from paratype SAMA P28282.

dp2 equal in length to dp3, very similar in morphology to p3 but wider relative to length. As in p3, three cuspules dominate anterior half of main crest, each with transverse ridgelet on buccal side. Ridgelets likely to have terminated in tiny cuspules like p3, but due to considerable wear sustained have become confluent with buccal crest, conveying an impression of more elongate crest.

Completely molariform, dp3 bears protolophid tapered more toward lophid apex than hypolophid. As with dp2, wear has removed several features. However, cristid obliqua appears more strongly developed than in molars and curved directly from hypoconid apex into interlophid valley, terminating

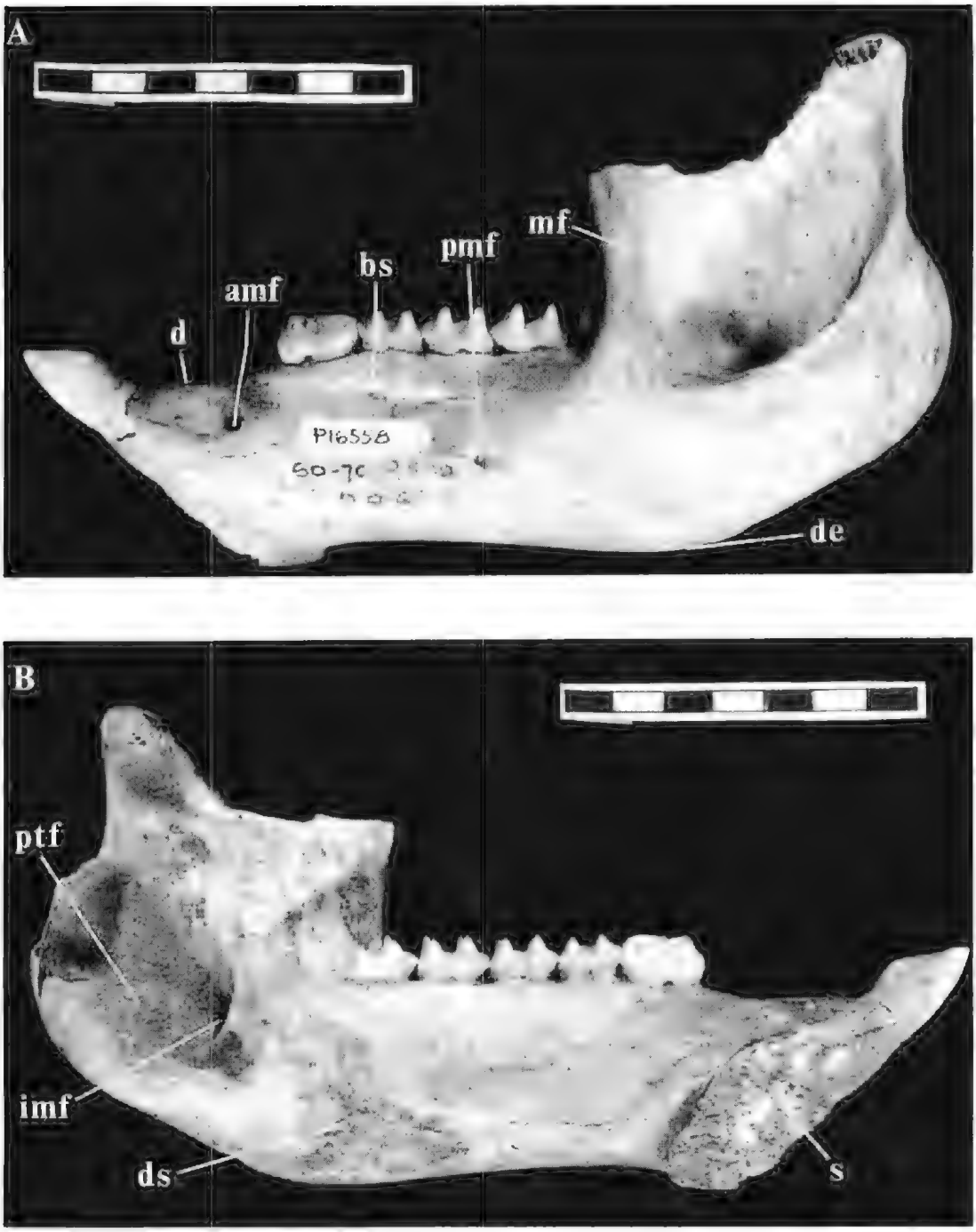

Fig. 6. *Sthenurus baileyi* sp. nov. left dentary. A. Paratype (P16558) lateral view. B. Paratype (P16558) mesial view. Scale bars = 70 mm. Abbrevs: amf = anterior mental foramen, bs = buccinator fossa, d = diastema, de = digastric eminence, ds = digastric sulcus, imf = inferior mandibular foramen, mf = masseteric fossa, pmf = posterior mental foramen, ptf = pterygoid fossa, s = symphysis.

centrally on posterior protolophid face. Very weak precentocristid also present, curving from entoconid into interlophid valley, terminating lingual to cristid obliqua. Enamel crenulations, similar to those on molars, appear to have been present on anterior lophid faces. Slight, rounded posteingulid on posterior face of hypolophid appears confluent with slight postentocristid.

Etymology

Named in honour of Mr Edwin "Ed" Bailey whose efforts over the last 25 years have contributed so much to the success of palaeontological work in the Naracoorte Caves.

Variation

Unfortunately, only one cranium is known of *S. baileyi* sp. nov. and variation within the upper dentition can only be assessed by comparison of P3 and M1-3, which are each represented by two specimens. P3 is very similar in the holotype and FU0167, with the slight occlusal wear in FU0167 responsible for most of the superficial differences between the specimens. In the holotype, P3 is slightly wider anteriorly, both across the whole tooth and the longitudinal basin. The lingual surface of the holotype P3 is slightly more convex and rounded than FU0167. The three cuspules anterior to the main posterobuccal accessory cusp are more separated in FU0167.

Only one slight difference is detectable on comparison of M1-3 of P13670, FU0167 (M1) and P28659 (M2-3). The postparacrista is larger in the holotype. While greater wear sustained by FU0167 and P28659 could account for these differences, consideration of the manner in which teeth occlude suggests that they are more likely to reflect morphological variation.

Complete or partial dentaries are known for five individuals, with three characters clearly variable. Depth and extent of the digastric sulcus is the most variable character. Although deep and extending from the anterior extreme of the pterygoid fossa to below the m2 hypolophid in P13670 and P16531/P16558, the sulcus is much shallower and only extends to below the m4 protolophid in FU0004. In P28282, the digastric sulcus is even shallower, thus negating the diagnostic utility of this character. The degree to which the pterygoid fossa is inflated posteriorly also varies between specimens. Inflation is greatest in P16531/P16558, slightly less in the holotype (P13670), FU0004 and P28282, and least in FU0294. However, it is sufficient in the latter to mark it as a distinctive feature of *S. baileyi*. Dentary depth relative to width is greater in P16531/P16558 (depth to width ratio below m2-3 = 1.791) compared to FU0004 (1.65) and P28282 (1.61). The ratio is lowest in the holotype (1.46). Intraspecific variation in dentary depth relative to width is commonly observed in sthenurine species known from even small sample sizes.

Variation in p3 size is common in all sthenurines, including *S. baileyi*. While most of the paratypes are very similar in size, P16530/P16551 and the holotype are noticeably shorter and narrower. Morphology varies only slightly between individuals, primarily in the form of the buccal crest and minor variation in width of the median valley. The anterior half of the buccal crest in P28282 is slightly higher than the posterior half and curves posterolingually, becoming confluent with a transverse ridgelet which crosses the median valley. This buccal crest morphology is not observed in any of the other specimens, although a very similar transverse ridgelet traverses the median valley in P13670. Apart from this feature, only the relative inflation of the anterior region of the p3 varies slightly. A p3 referrable to *S. baileyi* is also known from Lindsay Hall Cave, near Madura on the Nullarbor Plain, Western Australia but this specimen remains in the private collection of L. Hatcher, Perth. This specimen is inseparable in size and morphology from the South Australian specimens.

There is little variation in both size and morphology of the lower molars, although the premetacristid, paracristid and cristid obliqua of the paratypes are slightly more weakly developed than the holotype and the anterior lophid faces bear more fine enamel crenulations. In addition, the posteingulid is more shelf-like in each of the paratypes than in the holotype, except in FU0294 where there is a larger inflation of the ventrobuccal region of the hypolophid posterior face.

Comparison with other taxa

Cranium. Although P3 was unerupted in the holotype of *S. baileyi* sp. nov., the presence of M4 in occlusion indicates that P3 eruption was imminent. An examination of other species for which a good age series is known, reveals that little change in morphology or size in most aspects of the cranium and dentary occurs from this ontogenetic stage to the stage where P3 is erupted. This means that direct comparisons with older representatives of other taxa are tenable. It is worth noting that the two samples of *S. browneí* and *S. occidentalis* with which *S. baileyi* is compared come from Naracoorte and are considered to represent the eastern forms of both species. Although very similar in overall morphology, they can be distinguished from the topotypic Western Australian samples by their larger overall size and slightly smaller dentition relative to jaw size.

The cranium of *S. baileyi* is very similar in size and brachycephaly to *S. occidentalis*. The premaxillae are also similar in relative size and morphology. Although rostral length of the two species is similar, the buccinator fossa on the side of the maxilla is deeper in *S. occidentalis*. This is coupled with a mesially concave aspect to the edge of the diastema, in contrast to the less distinct edge and shallow buccinator fossa in *S. baileyi*. This condition is more reminiscent of *S. gilli* and *S. andersoni*.

The rostrum of *S. baileyi* does not taper to the same degree anteriorly as *S. occidentalis*, both because the frontals are less expanded and its narial aperture is proportionally larger. Among the *Sthenurus* species for which the splanchnocranium is known, lateral inflation of the frontal region (particularly anteriorly) and formation of supraorbital crests is greatest in *S. maddocki*, *S. occidentalis*, *S. stirlingi* Wells & Tedford, 1995 and *S. brownei*. The frontal region is relatively narrow in *S. gilli*, *S. andersoni* and *S. tindalei* Tedford, 1966. The proportions displayed in *S. baileyi* are intermediate between these two groups, particularly between *S. brownei* and *S. gilli*. However, the nasals of *S. baileyi* are very wide and constitute a greater proportion of the dorsal aspect of the rostrum than any other *Sthenurus* species, except *S. maddocki*. Overall, the short and broad nature of the rostrum is characteristic of *S. baileyi*.

The anterior extent of the palatal vacuities in *S. baileyi* is akin to a number of other species, terminating close to the dP3 metaloph, or what would be close to the posterior extreme of the P3 if it were in occlusion. The masseteric process appears to have been well-developed, allowing for the damage in the holotype, and is intermediate between *S. maddocki* and *S. brownei* in size.

Upper Dentition. In *S. baileyi* sp. nov., the crown of I1 is slightly longer and broader than *S. brownei* and is most similar to *S. occidentalis*. I1 is not as high crowned as that of *S. gilli*, and not as broad as in *S. andersoni*, *S. atlas* (Owen, 1838), *S. tindalei* or *S. pales*. The small, cylindrical I2 is intermediate in size between *S. brownei* and *S. occidentalis*. I3 is most similar in size and general morphology to *S. brownei* but the buccal surface is smooth and flat, not bearing any vertically-orientated undulations. In this respect, *S. baileyi* is similar to *S. occidentalis* and *S. gilli*.

Although slightly shorter and less inflated laterally than in *S. brownei*, dP2 of *S. baileyi* sp. nov. is closest in overall morphology to that species. Orientation of the buccal and lingual crests is also similar but the posterior basin appears to have been larger in *S. baileyi*. P3 of *S. baileyi* is most reminiscent of *S. brownei* and *S. antiquus* in morphology, particularly in the shape and orientation of the buccal and lingual crests and the anterior basin (Fig. 7). However, *S. baileyi* possesses a shallower and narrower longitudinal basin and a prominent posterobuccal accessory cusp with two cuspules anterior to it (Fig. 7). The posterior basin is smaller than in either *S. antiquus* or *S. brownei*. Height of the lingual crest in *S. antiquus* is considerably lower relative to the buccal crest than in either *S. brownei* or *S. baileyi*. In addition, the *S. antiquus* P3 is also smaller relative to the size of the molars. The amount of wear that dP3 has undergone has obliterated several characters useful for comparison. However, the tooth appears to have been generally similar to that of *S. brownei* but with a smaller precingulum, larger premetacrista and many fewer and finer enamel crenulations on the loph faces and interloph valley.

The very low crowned nature of the *S. baileyi* upper molars is only approached among *Sthenurus*, by *S. vegsai*, *S. antiquus* and *S. maddocki*. Similar to *S. vegsai* and *S. antiquus*, there are few crenulations on the loph faces and the interloph valley but the postprotocrista is more weakly developed in *S. baileyi*. The postparacrista is more strongly

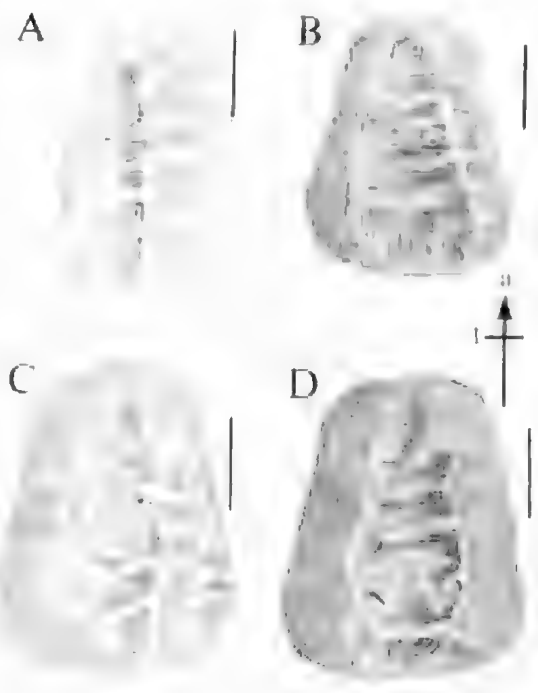

Fig. 7. Comparative sketches of left P3 in occlusal view. A *Hadronomas puckridgei*. B. *Sthenurus antiquus* (posterolingual corner reconstructed – incomplete in actual specimen). C *S. baileyi* sp. nov. D. *S. brownei*. Scale bars = 5 mm. Abbreviations: a = anterior, l = lingual

developed in *S. baileyi* than any other species, including *S. brownei*. The slight nature of the precingulum is similar to that of *S. antiquus*.

Dentary. In general morphology, the dentary of *S. baileyi* sp. nov. is most similar to *S. occidentalis*, *S. antiquus* and *S. gilli*, and to the former two in size. The ramus differs from *S. occidentalis* in the following features: it is slightly narrower for its depth, the symphysis extends only just beneath the genial pit, the i1 and symphysis are slightly more procumbent, the diastema is slightly longer, the digastric sulcus is shallower and less extensive, the posteroventral border of the masseteric fossa is more flared laterally and the pterygoid fossa is more inflated posteriorly. *Sthenurus baileyi* differs from *S. antiquus* in its longer cheek tooth row relative to ramus depth. Morphology of the *S. baileyi* symphysis most resembles that of *S. maddocki*, where the symphysis tapers gently anteriorly and only extends slightly below the genial pit. However, unlike *S. maddocki*, the orientation of i1 closely approximates that of the anteroventral border of the symphysis and in this respect is similar to *S. occidentalis* and *S. brownei*. Morphology of the i1 crown and its degree of procumbency are intermediate between *S. occidentalis* and *S. brownei*. Relative to the length of the ramus, the diastema of *S. baileyi* is proportionally longer than that of *S. occidentalis*, *S. brownei* and *S. gilli*. It is most similar in length to *S. maddocki* but is not convex dorsally as in this species. Depth and extent of the digastric sulcus are similar to, but slightly more pronounced than in *S. maddocki*. The degree of intraspecific variation in depth and extent of the digastric sulcus also seems similar between the two species. Lateral expansion of the posteroventral border of the masseteric fossa into a wide shelf is similar to *S. cegsai*, *S. gilli* and *S. maddocki*. The pterygoid fossa is more inflated posteriorly than any other *Sthenurus* species and in this respect, *S. baileyi* resembles *Procoptodon*.

Size and morphology of dp2 most resembles that of *S. brownei* but is not as narrow anteriorly relative to the posterior part of the tooth. The median valley is also narrower. Superficially, the dp2 buccal crest appears similar in length to that of *S. brownei* but this impression is created because the wear sustained has resulted in the crest becoming confluent with the small cuspules to its anterior. dp3 is also similar in size and morphology to that of *S. brownei*, but the crest oblique mountains contact with the hypoconid apex and there are fewer enamel crenulations on the lophid faces. In these characters the *S. baileyi* dp3 more closely resembles that of *S. occidentalis*.

In morphology, size relative to the molars, and orientation of the main and buccal crests, the *S. baileyi* p3 is similar to that of *S. antiquus* (Fig. 8). It differs by being smaller, lower crowned, slightly more inflated anteriorly and having a straighter main crest orientated from the posterolingual to the anterobuccal corner of the tooth. In *S. antiquus*, the posterior part of the main crest trends anterobuccally then straightens anteriorly along the tooth's midline. The *S. baileyi* p3 shares with *S. brachyselenis* the major features of the main crest and a ridgelet traversing the median valley but is easily distinguished by its larger size, slightly greater width relative to length (ratio 0.55 compared with 0.52) and longer, straighter buccal crest (Fig. 8). In size and general outline, the *S. baileyi* p3 is also similar to *S. brownei* but is lower crowned and bears a considerably shorter buccal crest.

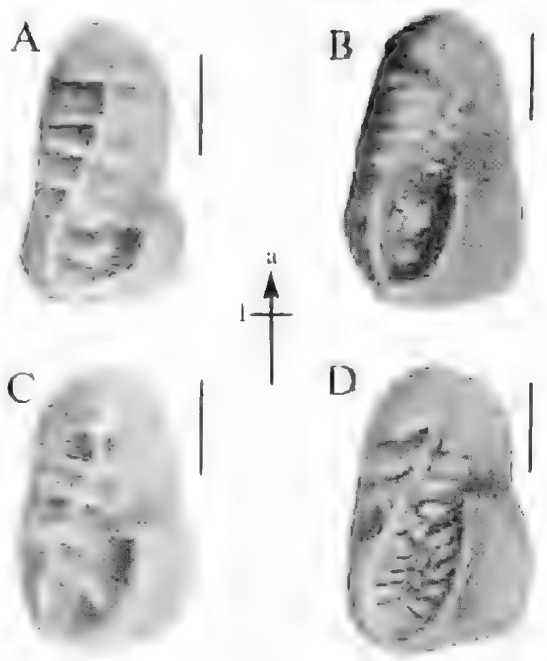

Fig. 8. Comparative sketches of right p3 in occlusal view. A, *Sthenurus brachyselenis*. B, *S. antiquus*. C, *S. baileyi* sp. nov. D, *S. brownei*. Scale bars = 5 mm. Abbreys: a = anterior, l = lingual.

In size and crown height, the lower molars of *S. baileyi* are somewhat similar to those of *S. cegsai* and *S. antiquus*, but are most similar to those of *S. brachyselenis*. They differ from the latter in their greater width relative to length (ratio 0.84 compared with 0.72), in the anterior cingulum not being symmetrically tapered anteriorly and the shelf-like inflation on the posterior face of the hypolophid being much less pronounced. In general, *S. baileyi*, *S. brachyselenis*, *S. cegsai* and *S. antiquus* have relatively smooth lophid faces, with only a few fine enamel crenulations.

Discussion

Sthenurus baileyi sp. nov. retains a suite of craniodental characters that suggest a fairly plesiomorphic position within the genus. Although the deposits from which the species is known are Pleistocene in age, *S. baileyi* is most closely comparable with the Pliocene *S. antiquus* from Chinchilla in southeastern Queensland and *S. brachyscelenis*, a species of uncertain age from Wellington Caves, eastern New South Wales. p3 is very similar to *S. antiquus*, but considerably more derived than *S. brachyscelenis*, given its greater robustness relative to the molars and longer, straighter buccal crest. In *S. brachyscelenis*, p3 is quite narrow and has a short, crescentic buccal crest restricted to its posterobuccal corner, features which are considered plesiomorphic for the genus (Prideaux & Wells 1997). The lower molars are intermediate between *S. brachyscelenis* and *S. antiquus* in general morphology, but, unfortunately, no upper molars for the former are known. However, the upper molars of *S. baileyi* are very similar to those of *S. antiquus*. Based on a comparison of single upper molars, these two species would be difficult to separate. However, P3 is notably more derived in *S. baileyi*, the lingual cingulum having become raised into a crest subequal in height with the buccal crest. In *S. antiquus* it is markedly lower.

Although the only known cranium is incomplete, *S. baileyi* can be clearly distinguished from all species of *Sthenurus* for which the cranium is known. While exhibiting a similar degree of brachycephaly to *S. occidentalis*, *S. baileyi* possesses a shorter, broader rostrum and a less inflated frontal region than any of the other brachycephalic Pleistocene species. Increased inflation of the frontals appears to have co-evolved with increased cheek tooth complexity in the lineage (or possibly lineages) leading to the more brachycephalic (shorter-faced) species, eg. *S. brownei*, *S. occidentalis* and *S. maddocki*. The modest degree of frontal inflation, relatively simple low crowned molars and short buccal crest not joining the main crest anteriorly on p3 provide a conceivable antecedent morphology to these other species.

Unfortunately, only one ramus and one maxilla fragment of *S. antiquus* are known but given the dental similarities between this species and *S. baileyi*, the likelihood may be that these reflect overall cranial similarities. Although the dentary of *S. antiquus* is incomplete, one important difference in the cranium of this species and *S. baileyi* may be indicated by the longer cheek tooth row relative to dentary depth observed in *S. antiquus* (ratio 2.42 compared with 1.85 for *S. baileyi*). This suggests a relatively longer dentary and therefore, a more elongate cranium than for *S. baileyi*. This feature, in conjunction with the slightly higher crowned molars, and more distinct cristid obliqua and paracristid, may make *S. antiquus* a possible structural precursor to the lineage that led to the more dolichocephalic (longer-faced) Pleistocene species. This contention is supported by the fact that the lingual crest of the *S. antiquus* P3 is notably lower than the buccal crest, a feature shared by the more dolichocephalic species. In the more brachycephalic species the crests tend to be subequal in height. Since raising of the lingual cingulum into a crest is a synapomorphy for all sthenurines excluding the plesiomorphic late Miocene *Hadronomas puckridgi* Woodburne, 1967 (Fig. 9), a lower crest may be regarded as a more plesiomorphic condition.

Despite the reliance on relatively limited Pliocene material, the similarities between *S. baileyi* and *S. antiquus* imply a close relationship. They are more derived than *S. regsai* and *S. brachyscelenis* but more plesiomorphic than any described Pleistocene species. Features not shared with each other are either those shared with the more dolichocephalic species in the case of *S. antiquus*, or with the more brachycephalic species in the case of *S. baileyi*. If Tedford's (1966) subgeneric (generic *sensu* Flannery 1983) definitions hold (i.e. *Simosthenurus* = brachycephalic, low-crowned cheek teeth with low links and many coarse enamel crenulations, *Sthenurus sensu stricto* = dolichocephalic, high crowned cheek teeth with strong links and few fine enamel crenulations), then *S. antiquus* may represent the least derived species in the subgenus *Sthenurus*, while *S. baileyi* may fulfil a similar position in *Simosthenurus* (Fig. 9). Because *S. notabilis* Bartholomai, 1963, an apparently derived dolichocephalic species co-occurs with *S. antiquus* in the Pliocene Chinchilla deposit, the divergence of the shorter- and longer-faced sthenurine groups must have occurred much earlier in the Pliocene. Similarly, very derived species co-occur with *S. baileyi* in the Pleistocene, but all that this demonstrates is that *S. antiquus* and *S. baileyi* are structural precursors to the dolichocephalic and brachycephalic lineages, rather than part of their direct ancestry.

So given their verisimilitude, are the differences between *S. baileyi* and *S. antiquus* sufficient to warrant placement in different subgenera? While they do not possess many of the extreme character states Tedford (1966) used to define the subgenera, the question is phylogenetically irrelevant so long as *Simosthenurus* and *Sthenurus* s.s. are monophyletic. The validity of these taxa is currently under investigation by one of us (GJP) and requires some revision, since the number of described sthenurine

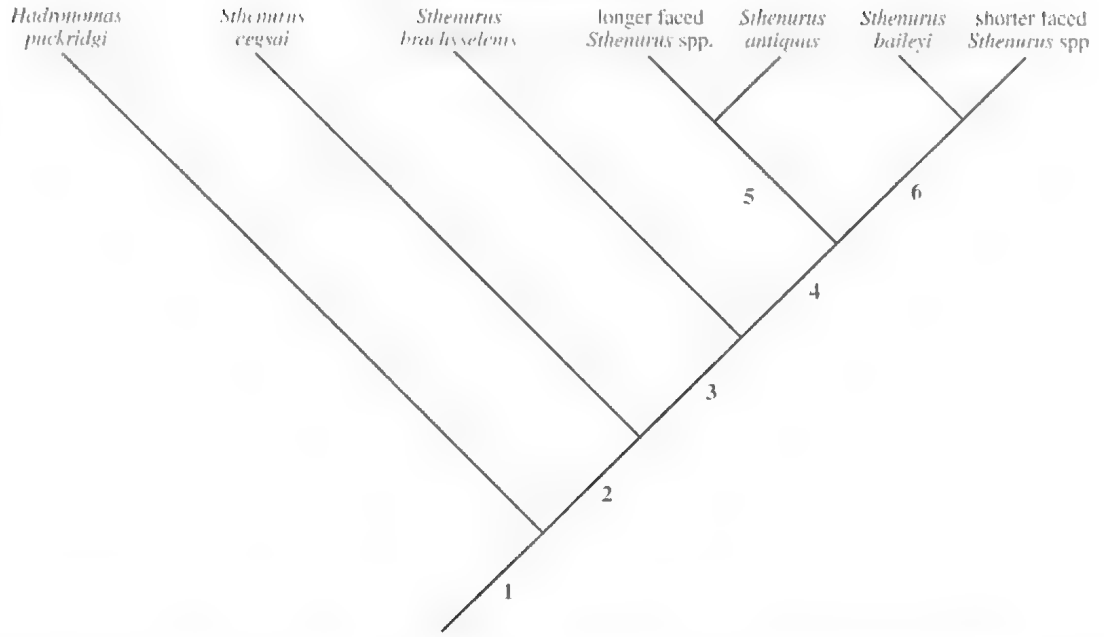

Fig. 9. Possible phylogram of basal relations in the Sthenurinae, based on the following synapomorphies. 1. Cranium relatively large; neurocranium flexed dorsally relative to rostrum; occiput close to vertical, broad and deep with well-developed lambdoid crest; large palatal vacuities, narrow post-palatine bars; deep jugal expansion forming ectoglenoid process; laterally expanded supraorbital crests; ectotympanic thick, wide, cancellous and ventrally-keeled; ascending ramus relatively vertical, with pterygoid fossa elevated and deep; digastric sulcus / eminence well-developed; I2 very small and splint-like; I3 dominated by buccal crest, lingual crest restricted to anterolingual corner; upper incisors form V-shape when viewed ventrally; C1 absent; p3 bears posterobuccal cingulum; molars fairly short relative width and squarish in occlusal view; molar lophs relatively straight and close to parallel; lower molars with posterior face of hypolophid inflated ventrally. 2. Rostrum broad and deep; zygomatic process of squamosal relatively deep; dentaries ankylosed at symphysis; mandibular ramus deep and wide, with depth at symphysis barely shallower than beneath molars; P3 with lingual cingulum raised into crest, separated from buccal or main crest by longitudinal basin traversed by ridgelets; p3 with buccal cingulum raised into crest. 3. p3 with curved buccal crest separated from main crest by wide median valley; p3 widened posteriorly; molars with more fine enamel crenulations. 4. p3 wider overall relative to length, with longer buccal crest; lower molars with cristid obliqua and paracristid shifted more lingually. 5. Cheek tooth row long relative to ramus depth, higher crowned molars, more prominent cristid obliqua and paracristid. 6. Cheek tooth row short relative to ramus depth; brachycephalic; retained lower crowned molars, low cristid obliqua and paracristid.

species has roughly doubled since Tedford's (1966) review. Almost certainly, *S. cegsai* and *S. brachyselenis* have no place within the two subgenera because they lack many of the delimiting character states and appear to be the earliest derivations from the sthenurine lineage, post-*Hadronomas puckridgi* (Fig. 9). We await the discovery of further Pliocene species to confirm exactly where *S. cegsai* and *S. brachyselenis* fit within the sthenurine radiation. As more taxa become available more light will inevitably be thrown on this paramount phase in sthenurine diversification.

Acknowledgments

We thank N. Pledge and J. McNamara (South Australian Museum), R. Molnar (Queensland Museum) and R. Jones (Australian Museum) for the loan of specimens. L. Hatcher loaned the Western Australian specimen for comparison. J. McNamara is sincerely thanked for providing data on the type locality, preparing the holotype and his characteristic perspicacity when commenting on an early draft of this paper. We are also grateful to J. Long and M. Archer for their constructive criticism of the manuscript.

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Appendix

Material used for comparison with *S. bailevi*. See "Introduction" for abbreviations, except AM = Australian Museum, QM = Queensland Museum.

Species	Registration Number	Locality
Sthenurus antiquus	QM F2931, F2973	Chinchilla, Darling Downs, Qld
S. brachyselenis	AM F31026	Wellington Caves, NSW
S. brownei (eastern form)	SAMA P20483, FU 0202, FU 0271	Victoria Fossil Cave, Naracoorte, SA
S. cegsai	SAMA P31800 (holotype)	Corra Lynn Cave, Curramulka, SA
S. gilli	SAMA P16528, P16629, P20797, FU 0246	Victoria Fossil Cave, Naracoorte, SA
S. maddocki	SAMA P16627, P16643, P16673	Victoria Fossil Cave, Naracoorte, SA
S. occidentalis (eastern form)	SAMA P20798, P27799	Victoria Fossil Cave, Naracoorte, SA
S. oreas	QM F2923 (holotype)	Darling Downs, Qld
S. pales	SAMA P27797	Victoria Fossil Cave, Naracoorte, SA

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Collectors were the dominant feeding group across all habitats with the ratios of different Functional Feeding Groups (FFGs) suggesting that Goyder Lagoon is heterotrophic, dependent on allochthonous organic matter as a carbon source.

Multivariate analyses separated temporary from permanent habitats. The prawn *M. australiense*, the yabbie *Cherax destructor* (Clark), the ephemeropteran *Tasmanocoenis arcuata* Alba-Tercedor & Suter and the trichopteran *Ecnomus* sp. dominated at frequently inundated sites whereas infrequently inundated sites were dominated by the notonectid *Enithares* sp., and the corixids *Micronecta* spp.

There were striking differences in assemblages from different sites, even those from the same mesohabitat type (channel, waterhole or billabong). This may reflect different successional trajectories within the assemblage at each site after hydrological isolation. This supports the hypothesis that the variable flows characteristic of Goyder Lagoon are important for maintaining macroinvertebrate diversity.

KEY WORDS: Macroinvertebrates, semi-arid river, functional feeding groups, Goyder Lagoon, variability

Introduction

The establishment and maintenance of specific types of wetlands and wetland processes are controlled, at least in part, by the prevailing hydrological regime (Mitsch & Gosselink 1986). Although it sounds contradictory, wetlands do occur in arid landscapes. Dryland rivers and their associated wetlands have a number of unique hydrological features (Molles & Dahm 1990; Walker *et al.* 1995; Puckridge *et al.* 1998). The dominant hydrological rhythms of dryland rivers are not seasonal or annual but reflect, in part, large weather phenomena such as the El Niño Southern Oscillation (ENSO) (Walker *et al.* 1997). In the Australian arid zone, significant freshwater wetlands are mainly associated with river channels and floodplains and intermittent river flow ensures that these wetlands do not accumulate salt from year to year and become salt lakes (McComb & Lake 1988).

Wetlands are amongst the world's most productive ecosystems. Arid zone wetlands have considerable regional significance for migratory birds (Breen 1991; Kingsford 1995; ANCA 1996). Despite this, their biology is poorly documented, in general (Breen 1991) and almost nothing is known of Australia's arid freshwater wetlands (Puckridge in press).

This study describes the macroinvertebrate assemblage composition at eleven sites within Goyder Lagoon, an arid freshwater wetland on the lower reaches of the Diamantina River, Lake Eyre Basin, South Australia (Fig. 1). The Diamantina River system is one of the major wetland systems in Australia that remains substantially unmodified by water resource development and, as such, is likely to harbour a relatively pristine biota (ANCA 1996). Little, however, is known of the macroinvertebrate fauna of any of the rivers in the central Lake Eyre Basin. Puckridge & Drewien (1988) and Reid & Puckridge (1990) list some of the taxa found in the Coongie Lakes system but there are no published data on the macroinvertebrates of Goyder Lagoon. The highly variable flows in Goyder Lagoon are likely to produce a diversity of habitat types with a range of inundation frequencies and hence a spectrum of different habitats for aquatic invertebrates over time (Boulton in press).

Multivariate analyses were used to identify the environmental variables structuring the assemblages at each site and for different habitat types. The Functional Feeding Group (FFG) composition (Cummins & Klug 1979) of assemblages at each site

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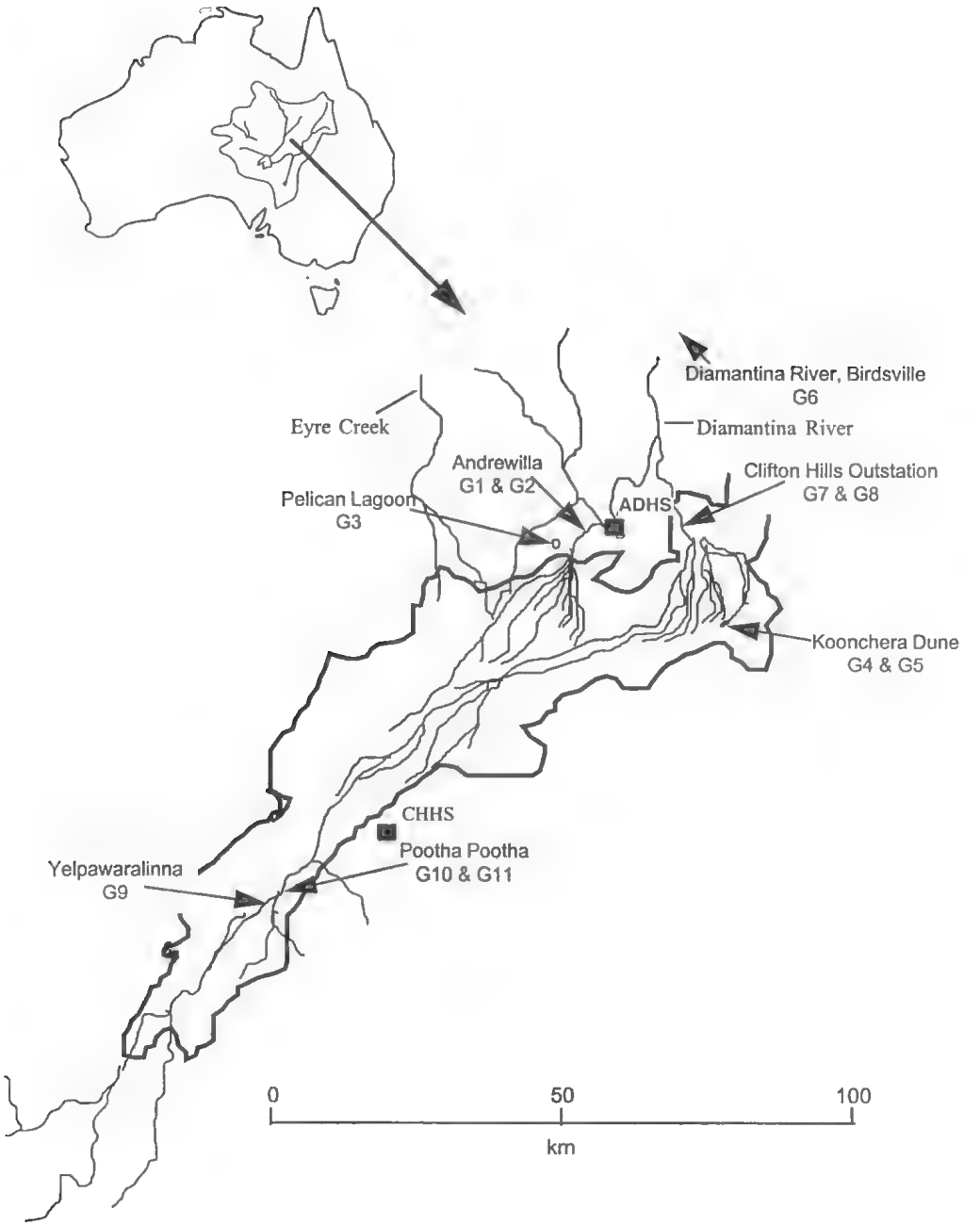

Fig. 1. Position of sampling sites (cf. Table 1) in Goyder Lagoon and on the Diamantina River. The heavy line marks the boundary of Goyder Lagoon. ADHS = Alton Downs Homestead; CHHS = Clifton Hills Homestead.

and in different habitats is explored with ratios of different FFGs used to indicate ecosystem attributes. Attributes such as the relative importance of heterotrophy or autotrophy (suggested by a dominance of either detritivorous collectors or herbivorous scrapers) and the relative amounts of Coarse Particulate Organic Matter (CPOM) and Fine Particulate Organic Matter (FPOM) in transport or in storage (suggested by the presence of filtering collectors or gathering collectors) (see Merritt & Cummins 1996) were examined. Goyder Lagoon may be similar to the Chowilla wetland of the lower River Murray, South Australia, where collectors dominated the assemblage suggesting allochthonous organic carbon was a dominant food source (Boulton & Lloyd 1991).

Materials and Methods

Study area

Goyder Lagoon is a 3030 km² *intermittent* (sensu Comin & Williams 1994) floodplain wetland at the terminus of the Diamantina/Georgina river system which has a catchment area of 365,000 km² (Fig. 1). The Diamantina is one of the most hydrologically variable river systems in the world (Puckridge *et al.* 1998). Goyder Lagoon begins 80 km below the town of Birdsville where the Diamantina River splits into an eastern and a western anabranch. These branches then radiate into a reticulate system of fine channels to form the eastern and western internal deltas. The eastern internal delta is larger and more frequently flooded. Water that makes its way through the maze of Goyder Lagoon drains to Lake Eyre via Warburton Creek. The lagoon is bounded by the dunefields of the Simpson Desert to the west and northwest and by the gibber plains of Sturts Stony Desert to the east.

The survey was conducted during November 1993 when water levels in the lagoon were low, the last major flooding having occurred in mid-1991. All but the deepest waterholes were dry and sampling was therefore confined to these waterbodies. In the period 1985-1993 flows occurred somewhere in the lagoon 9 out of 10 years (Landsat data; South Australian Department for Environment, Heritage and Aboriginal Affairs). Flooding frequency and flood residence times appear, from the Landsat record, to diminish in the lagoon downstream, and in the northern lagoon from east to west. The inundation frequency of each site within the lagoon was ranked using an estimate from the overall gradient in inundation frequency evident in the Landsat record (1986-1993) and checked with local landowners' knowledge.

Sites were chosen to represent a range of hydrological conditions and a spatial distribution along the lagoon's axis (Fig. 1). In order of inundation frequency, sites included:

- the permanent channel of the Diamantina River approximately 1 km downstream from the town of Birdsville (G6),
- the permanent channel of the main (northeastern) branch of the Diamantina in Goyder Lagoon at Clifton Hills Outstation (G7) and a closely associated backwater (G8),
- an isolated waterhole at Andrewilla Station on a semi-permanent segment of the northwestern branch (G2), a closely associated backwater (G1), and a nearby isolated billabong, Pelican Lagoon (G3),
- a deepened but impermanent portion of the reticulate channel system of the eastern delta formed by the intrusion of Koonchera Dune (G4, G5),
- a segment of the less frequently flooded Warburton channel in the southern lagoon, Pootha Pootha Waterhole (G10), and an associated billabong (G11),
- an isolated waterhole on a less frequently flooded anabranch of the Warburton downstream of G10, Yelpawaralinna Waterhole (G9).

Aquatic systems such as Goyder Lagoon can be divided into macro-, meso- and micro-habitats (Walker *et al.* 1995). Using this hierarchical system, Goyder Lagoon is a distinct macrohabitat. Within this macrohabitat exist mesohabitats such as channels, waterholes and billabongs and within these are microhabitats such as emergent and submerged vegetation, submerged wood and other substrata.

In this study four mesohabitat types, channel, waterhole, backwater and billabong were sampled (Table 1). Overall, microhabitats included emergent vegetation such as sedges (*Cyperus* spp.) and semi-aquatic grasses (e.g. *Cynodon* spp.) forming sometimes dense stands along the edges of the waterbodies; aquatic macrophytes (e.g. *Polygonum* sp., *Myriophyllum* spp.), submerged woody debris ('snags') represented by the roots or fallen limbs of trees such as river redgums (*Eucalyptus camaldulensis* Dehnh., var. *obtusa* Blakely) Coolibah (*Eucalyptus coolibah* Blakely & Jacobs ssp. *arida* (Blakely) L. Johnson & K. Hill) and River coobah (*Acacia stenophylla* Cunn. ex Benth.), coarse particulate organic matter such as packs of leaf litter and twigs from riparian vegetation, and unvegetated littoral areas free of vegetation, woody detritus or other cover. The latter were further divided into silt and clay substratum, sandy substratum or rock substratum. Ninety two samples were collected from microhabitats present within the 11 sites (Fig. 1, Table 1).

TABLE 1. *List of sites (and their abbreviations) grouped by mesohabitat.* The number of samples collected from each microhabitat at each site is also given.

Mesohabitat	Site Number	Site Name	Microhabitats	No. Samples
Backwater	G1	Backwater of Andrewilla Waterhole	Leaf litter	4
			Silt	4
	G8	Backwater of Clifton Hills Waterhole	*Polygonum*	3
			Lignum	3
			Silt	3
Waterhole	G2	Andrewilla Waterhole	Rock	4
			Silt	8
	G4	Koonchera Dune Waterhole (eastern portion)	Sand	4
			Silt	4
	G5	Koonchera Dune Waterhole (western portion)	Lignum	4
			Sand	4
			Silt	4
	G7	Clifton Hills Waterhole	*Polygonum*	4
			Lignum	4
			Silt	5
			Snag	3
	G9	Yelpawaralinna Waterhole	Emerg. veg	4
	G10	Pootha Pootha Waterhole	Emerg. veg	3
			Silt	3
Channel	G6	Main channel of Diamantina River (Birdsville)	*Polygonum*	3
			Grass	3
			Rock	4
			Silt	4
Billabong	G3	Pelican Lagoon Billabong	Silt	2
	G11	Small Billabong	Silt	1

Sample collection and processing

Each site was considered a distinct mesohabitat and was stratified into the microhabitats defined above (Table 1). The most prevalent of these were then sampled randomly (Boulton & Lloyd 1991). Macroinvertebrates were collected in replicate samples from each microhabitat by sweeping a 500 µm mesh pond net over 5 m^2 for 20 sec. Samples were preserved in 70% ethanol and later washed through nested sieves (4000, 2000, 1000, 250 µm) and the organisms hand-sorted, enumerated, and identified as far as practicable. Unidentified specimens were recorded as separate taxa (e.g. "tiny Zygoptera"). Each taxon was assigned to one of four broad functional feeding groups (FFGs): collectors, predators and scrapers (Cummins & Klug 1979), with collectors incorporating filterers and gatherers. The assigned FFGs, particularly "collectors", are tentative as the diets of most taxa are unknown; assumptions about diet were therefore based on taxonomic affinities. Classification of taxa into functional feeding groups followed Cummins & Klug (1979), Boulton (1988)[1], Boulton & Lloyd (1991) and Sheldon (1994)[2]. At each sampling site, spot measurements were recorded of depth, Secchi transparency, temperature, dissolved oxygen (YSI oxygen probe) and conductivity (Hanna HI 8733 conductivity meter); salinity was computed from temperature corrected conductivity values using the equations in Williams (1966).

Data analysis

Hierarchical analysis of variance (Underwood 1981) was used to explore patterns in richness and abundance between mesohabitat and microhabitat scales. As the sampling design was unbalanced, subsets of the total dataset were used. Subsets were chosen so there were equal replicates within each level making the design balanced. The following separate analyses were performed:

i. Microhabitats (emergent vegetation, silt) nested within sites (G6, G7, G8, G10).
ii. Microhabitats (lignum, silt) nested within sites (G5, G7, G8).

All analyses were performed in SYSTAT v. 5.03 (Wilkinson 1990). Data were rendered normal by transforming using $\log_{10}(x + 1)$.

[1] BOULTON, A.J. (1988) Composition and Dynamics of Macroinvertebrate Communities in Two Intermittent Streams. PhD thesis, Monash University (unpub.)

[2] SHELDON, F. (1994) Littoral Ecology of a Regulated Dryland River (River Murray, South Australia) with Reference to the Gastropoda. PhD thesis, University of Adelaide (unpub.).

Hierarchical patterns in the data were also explored using multivariate statistics from the PATN software package (Belbin 1993). Multivariate analysis allows patterns between samples to be explored. Two multivariate approaches were used: classification (or derivation of discrete groupings of samples) and ordination (arrangement of samples in a space of a few dimensions). Both techniques arrange samples on the basis of their species composition, with those samples that cluster or group together more likely to be similar in species composition (ter Braak 1987). Data were $\log_{10}(x + 1)$ transformed before analysis and then range standardised as suggested by Belbin (1993); the Bray-Curtis coefficient was used as the measure of dissimilarity between samples. All taxa occurring in one or more samples were retained in the analyses. Flexible-UPGMA was used to cluster the samples, with the ANOSIM procedure (Clarke 1993) used to test for significant clusters of samples at a meso- and microhabitat scale. The SIMPER procedure from the PRIMER software package (Clarke & Warwick 1994) was used to identify the percentage contributions of different taxa to the sample groups. Semi-Strong Hybrid multidimensional scaling (SSH) ordinations were also computed from the Bray-Curtis similarity matrix generated from the transformed and standardised data: settings of 50 iterations and a ratio-ordinal cut value of 0.8 over 100 random starts was used. Solutions were calculated in two, three and four dimensions. The solution presented here had a stress of 0.18. The stress measure gives an indication of the "goodness-of-fit" for the ordination (Kruskal & Wish 1978); an ordination with a good fit for samples within the ordination space has a stress value of less than 0.2. Sample groups from mesohabitats, sites and microhabitats were mapped on to the ordination plots.

Relationships between environmental and community data are usually many, complex and nonlinear (Gauch 1982). One aim of conducting multivariate analyses is to detect major differences in species composition for sample groups which are potentially related to environmental differences (Boulton 1988)[1]. Spearman Rank correlations (Zar 1984) between the physicochemical variables measured in the field and the ordination scores on the SSH axes were calculated to examine relationships between environmental factors and macroinvertebrate assemblage composition.

Results

Environmental conditions

The environmental conditions for all sites are given in Table 2. The Diamantina River carries a high load of very fine suspended sediment with particle diameters of less than 1 μm. This contributed to Secchi depth measurements well below 20 cm at all sites. Salinities were highest at those sites in the centre of the Lagoon which were the most disconnected from any recent flow of water, sites on Andrewilla Station (G1 and G2), at Koonchera Dune (G4 and G5) and Pelican Lagoon Billabong (G3). Pootha Pootha Waterhole (G10) at the southern end of the Lagoon had a lower salinity, probably the result of recent rain. Sites on the main channel of the Diamantina (G6) and Clifton Hills Outstation (G7 and G8) also had relatively low salinities due to a recent small flow through the system. All sites were well oxygenated (near saturation) with instantaneous water temperatures ranging from 20-34° C.

Patterns of richness and abundance

A total of 7,363 individuals from 54 taxa was collected in 92 samples (Appendix). Insects were the dominant group comprising 76% of taxa and 63% of individuals (Fig. 2a). Of the Insecta, the Diptera

TABLE 2. *Environmental conditions measured in the littoral zone of each site in Goyder Lagoon, Diamantina River, South Australia in November 1993.*
Data were not available for sites G6 and G11 - n/a = not available)

Site	Sample Depth (cm)	Salinity (mg l^{-1})	Secchi (cm)	Temp (° C)	Oxygen (% Saturation)
G1	72	309	7.0	20.0	99.0
G2	94	260	6.0	23.0	90.9
G3	50	8265	20.0	34.0	100.0
G4	57	1299	4.0	22.7	93.2
G5	35	2133	4.0	23.7	93.9
G6	n/a	n/a	n/a	n/a	n/a
G7	62	172	3.0	26.0	84.8
G8	74	122	3.0	25.4	76.3
G9	68	769	3.0	23.0	81.6
G10	53	142	2.5	21.6	n/a
G11	n/a	n/a	n/a	n/a	n/a

comprised 39% of taxa and 41% of individuals (Fig. 2b). The prosobranch gastropod *Thiara balonnensis* (Smith) was the most abundant taxon, with the freshwater prawn *Macrobrachium australiense* (Ortmann), the corixids *Micronecta* spp., the predatory chironomid larvae *Coelopynia* sp. and the predatory caddisfly larvae *Oecetis* sp. also common. The prawn *M. australiense* comprised the greatest biomass. Five taxa occurred only once. Observed at Koonchera Dune Waterhole, but not collected, was the freshwater crab *Holthuisiana* (*Austrotelphusa*) *transversa* (Martens).

Both the number of taxa (richness) and the number of individuals (abundance) differed between the mesohabitats (Fig. 3). Backwaters and waterholes had more individuals than the channel or billabongs. However, richness was similar for all mesohabitats. When the mesohabitats were split into sites there were differences between sites from the same mesohabitat. Of the backwaters, G1 had many more individuals and a greater richness than G8. Similar differences occurred between the billabongs G3 and G11 and there was also variation in both richness and abundance for different waterhole sites (Fig. 3). Numbers of taxa and individuals also differed between microhabitats depending upon the site. Large numbers of individuals were found in leaf litter packs in G1 and silt microhabitat from both G4 and G5, fewest individuals were found in snag and silt microhabitats from G7 and the rock microhabitat from G6. Emergent vegetation and submerged areas of lignum contained the greatest number of taxa while the fewest number of taxa were from snag microhabitats.

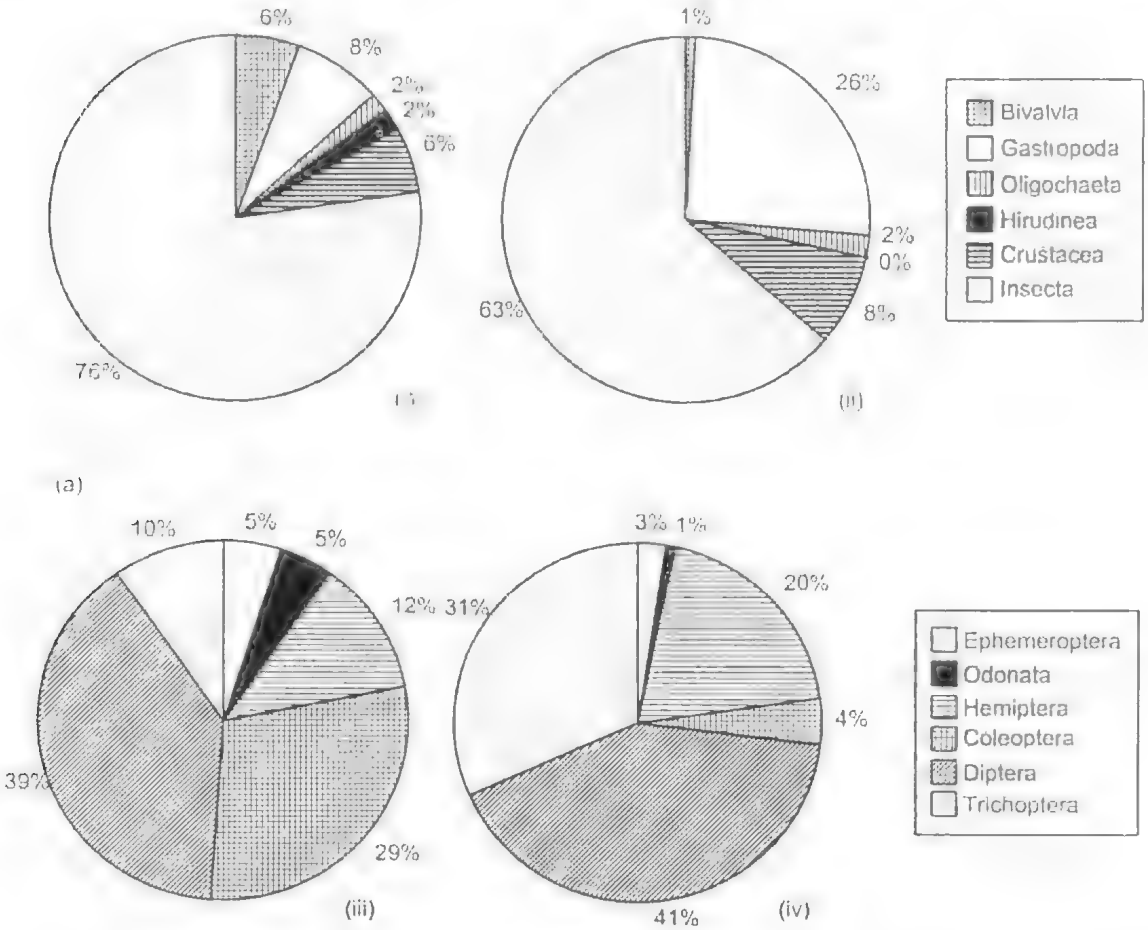

Fig. 2. (a). Percent representation of the major invertebrate groups in samples from all sites within Goyder Lagoon, November 1993, in terms of the number of (i) taxa in each group and (ii) abundance of individuals. (b). Percent representation of the major insect Orders in samples from all sites within Goyder Lagoon, November 1993, in terms of (iii) the number of taxa in each Order and (iv) the abundance of individuals.

Mean numbers of individuals ($F_{3,4}$ = 6.246, p>0.05) did not differ between sites G6, G7, G8 and G10 but mean numbers of taxa ($F_{3,4}$ = 12.178, p<0.01) did with G10 having more taxa than the other sites (Fig. 3). Mean numbers of taxa ($F_{4,16}$ = 0.586, p>0.05) and individuals ($F_{4,16}$ = 1.607, p>0.05) did not differ for emergent vegetation and silt microhabitats nested within these sites. There were also differences in mean number of taxa ($F_{2,3}$= 148.08, p<0.001) and individuals ($F_{2,3}$ = 103.47, p<0.001) between the sites G5, G7 and G8, with G5 having more taxa and individuals than the other sites (Fig. 3). However, again there were no differences for either taxa ($F_{3,16}$ = 0.192, p>0.05) or individuals ($F_{4,16}$ = 0.603, p>0.05) between lignum and silt microhabitats nested within the sites.

Multivariate analysis of samples

UPGMA classification of the sample data indicated two main groups. The majority of samples from the more temporary habitats (G1, G2, G3, G4, G5, G9, G10) formed one group (A-D) while those from more permanent habitats (G6, G7 G8) formed the other (E-H) (Table 3, Fig. 4). The first group (A-D) further split into Group A-B, containing samples from the western anabranch of the lagoon (G1, G2) which is the more frequently inundated of the temporary habitats, one sample from G6 and one from G7, and Group C-D containing samples from the extreme temporary habitats on the lower section of the eastern anabranch and the southern end of the lagoon (G4, G5, G9, G10). The second group separated into Group E-G containing a majority of samples from Clifton Hills Outstation on the upper section of the eastern anabranch (G1 and G8) and Group H containing most of the samples from the permanent channel of the Diamantina River at Birdsville. The single sample from the infrequently inundated billabong associated with Pootha Pootha Waterhole, G11, was an outlier clustering with the more permanent sites in groups A-D.

SIMPER analysis showed that the prawn *Macrobrachium australiense*, the yabbie *Cherax destructor* (Clark), the ephemeropteran nymph *Tasmanocoenis arcuata* Alba-Tercedor & Suter and the trichopteran larvae *Ecnomus* sp. dominated the assemblage in the more frequently inundated sites.

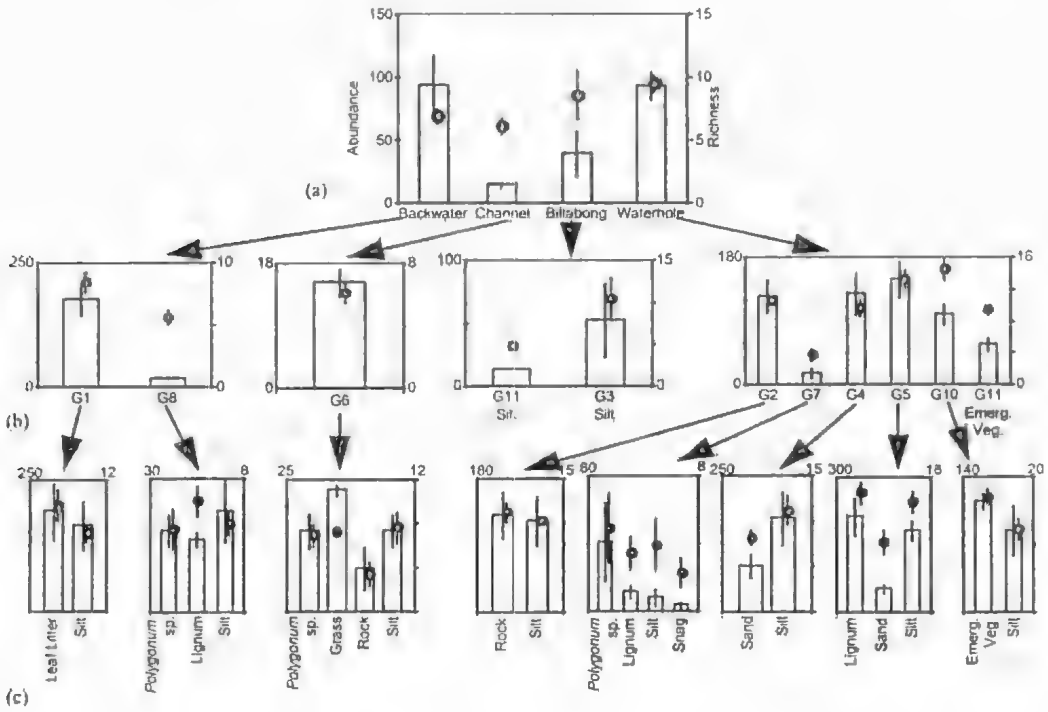

Fig. 3. Mean (±SE) of richness and abundance for each of the three sampling scales. (a). Mesohabitats. (b). Sites within mesohabitats. (c). Microhabitats within sites, collected from Goyder Lagoon, November 1993. Points indicate richness and bars abundance.

TABLE 3. *Flexible-UPGMA groups by site, mesohabitat and microhabitat.*
Those taxa contributing more than 5% to the similarity of the sample groups are also indicated.

UPGMA Group	No. Samples	No. Samples from Sites	No. Samples from Mesohabitats	No. Samples from Microhabitats	Contribution of taxa to sample group (SIMPER) %	
A	21	7 G1 12 G2 1 G6 1 G8	8 Backwater 12 Waterhole 1 Channel	4 Organic Matter 13 Silt 4 Rock	*Thiara balonnensis* *Coelopynia* sp. *Micronecta* spp. *Macrobrachium australiense*	61.5 10.2 10.1 5.2
B	1	1 G7	1 Waterhole	1 *Polygonum*	no taxa	
C	23	2 G3 1 G7 12 G5 8 G4	2 Billabong 21 Waterhole	11 Silt 8 Sand 4 Lignum	*Oecetis* sp. *Coelopynia* sp. *Bezzia* sp.	42.0 24.5 11.9
D	10	4 G9 6 G10	10 Waterhole	4 Grass 3 Sedge 3 Silt	*Enithares* sp. *M. australiense* *Micronecta* spp. *Coelopynia* sp. *Anisops* spp.	37.1 19.8 13.9 6.8 6.4
E	8	1 G1 4 G6 1 G7 2 G8	3 Backwater 4 Channel 1 Waterhole	3 Silt 1 Grass 1 Snag 3 *Polygonum*	*M. australiense* *Austrogomphus australis* *Cherax destructor*	61.5 17.7 7.9
F	22	4 G6 11 G7 6 G8 1 G11	4 Channnel 11 Waterhole 6 Backwater 1 Billabong	1 Rock 2 Snag 7 Lignum 4 *Polygonum* 6 Silt 2 Grass	*M. australiense* *Tasmanocoenis arcuata*	75.6 13.8
G	2	2 G7	2 Waterhole	2 Silt	no taxa	
H	5	5 G6	5 Channel	3 Rock 1 Silt 1 *Polygonum*	*Ecnomus* sp. *M. australiense*	57.6 40.6

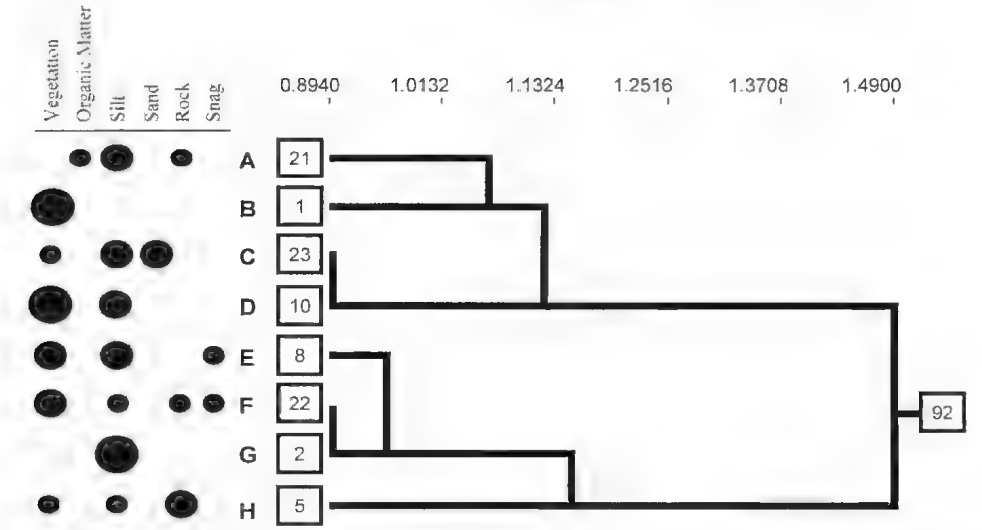

Fig. 4. Flexible-UPGMA dendogram, using Bray-Curtis dissimilarity, of the 92 samples collected from Goyder Lagoon in November 1993. Entities in sample groups A-H are listed in Table 3. A pictorial summary of the microhabitat representation of samples is also given. Large circles depict greater than 70% of the samples from the microhabitat occur in the sample group, medium circles 30-70% and small circles 1-30%.

G6, G7, G8 (Table 3, Fig. 5). The prosobranch gastropod *Thiara balonnensis*, predatory tanypod larvae *Coelopynia* sp. and corixids *Micronecta* spp. dominated samples from sites at Andrewilla (G1, G2) whereas the predatory trichopteran larvae *Oecetis* sp. and *Coelopynia* sp. dominated samples from sites at Koonchera Dune (G4, G5) as well as the temporary billabong G3. The infrequently inundated sites G9 and G10 had an assemblage dominated by the highly mobile predatory hemipteran *Enithares* sp., the prawn *M. australiense* and corixids *Micronecta* spp. (Table 3, Fig. 5).

Ordination highlighted the differences between mesohabitats and between sites. When grouped by mesohabitat, those samples from backwaters were dispersed across Axes 1 and 3 and grouped low on Axis 2 (Fig. 6). Samples from waterholes were dispersed across all three axes whereas samples from channels grouped centrally on Axes 1 and 2 and low on Axis 3. Billabong samples were central on Axes 1 and 3 and grouped high on Axis 2. When samples were grouped according to sampling site, their distribution along Axis 2 reflected the inundation frequency of the site (Fig. 7). Samples from the more permanent sites G6, G7 and G8 grouped low on Axis 2, those from the less frequently inundated G1 and G2 grouped centrally on Axis 2 while those from the more extreme temporary sites G4, G5, G9 and G10 grouped high on Axis 2. Samples showed no distinct groupings according to microhabitat on any of the three axes (Fig. 8).

The ANOSIM procedure suggested differences between groups of samples at each level: significant differences were located between sample groups at a mesohabitat (R=1.118, p<0.001), site (R=1.362, p<0.001) and microhabitat (R=1.079, p<0.001) level.

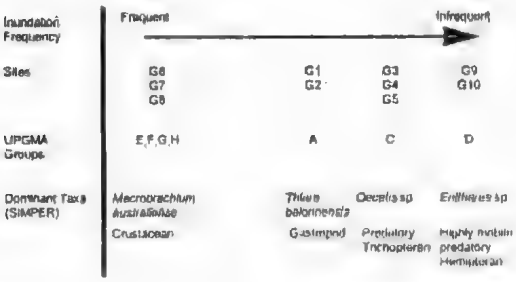

Fig. 5. Sites, UPGMA groups and dominant taxa from SIMPER in relation to inundation frequency. UPGMA group B has been omitted as it contains only one sample and dominant taxa cannot be generated for one sample groups using SIMPER. Also the single sample from site G11 (in UPGMA group F) is omitted as it is an outlier, being an infrequently flooded site that grouped with the frequently flooded sites.

With regard to the instantaneous environmental variables measured, the sample distribution along the first axis of the SSH ordination was significantly correlated with Secchi depth, temperature and oxygen saturation (Table 4). Axis 2 showed significant correlations with salinity, temperature and oxygen saturation and all variables were correlated with sample distribution along Axis 3.

Functional feeding groups

Collectors dominated the invertebrate assemblage of Goyder Lagoon. However, there was considerable variation in the FFG composition of the mesohabitats and of sites within mesohabitats (Fig. 9). Billabongs and waterholes contained similar numbers of collectors and predators. However, collectors dominated the assemblage composition of the backwaters in both richness and abundance. When the FFG composition of individual sites was further

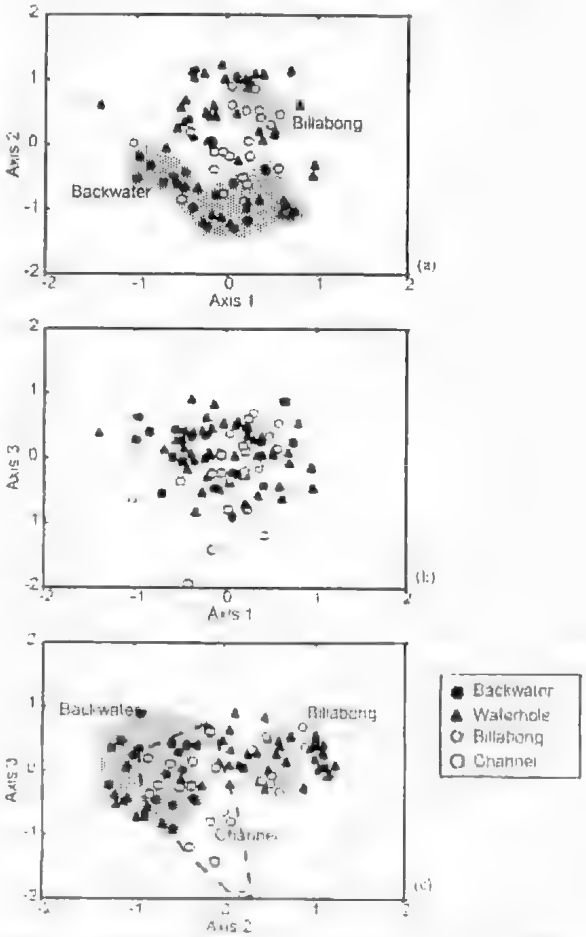

Fig. 6. SSH plot on axes (a) 1 v. 2, (b) 1 v. 3, (c) 2 v. 3 of samples collected from Goyder Lagoon, November 1993. Samples are labelled according to the mesohabitats from which they were collected.

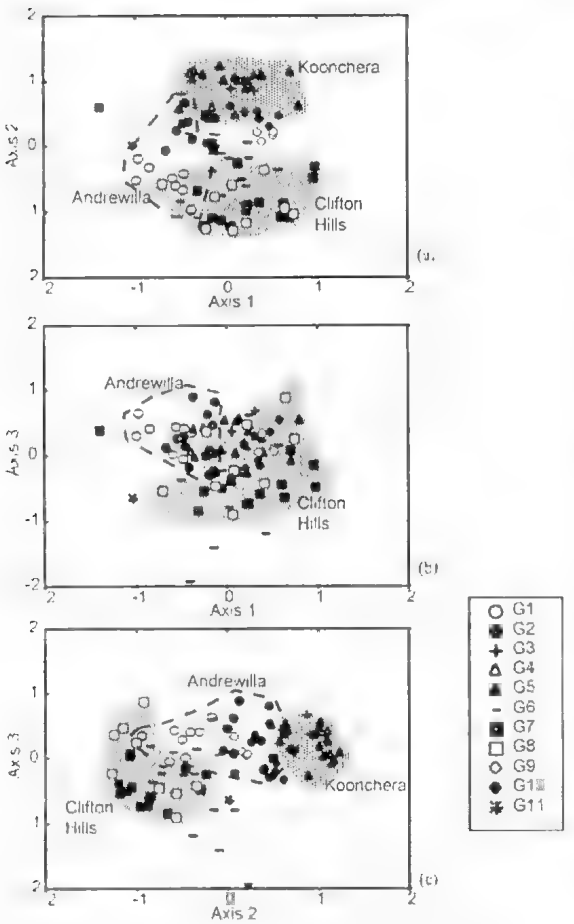

Fig. 7. SSH plot on axes (a) 1 v. 2, (b) 1 v. 3, (c) 2 v. 3 of samples collected from Goyder Lagoon, November 1993. Samples are labelled according to the site from which they were collected.

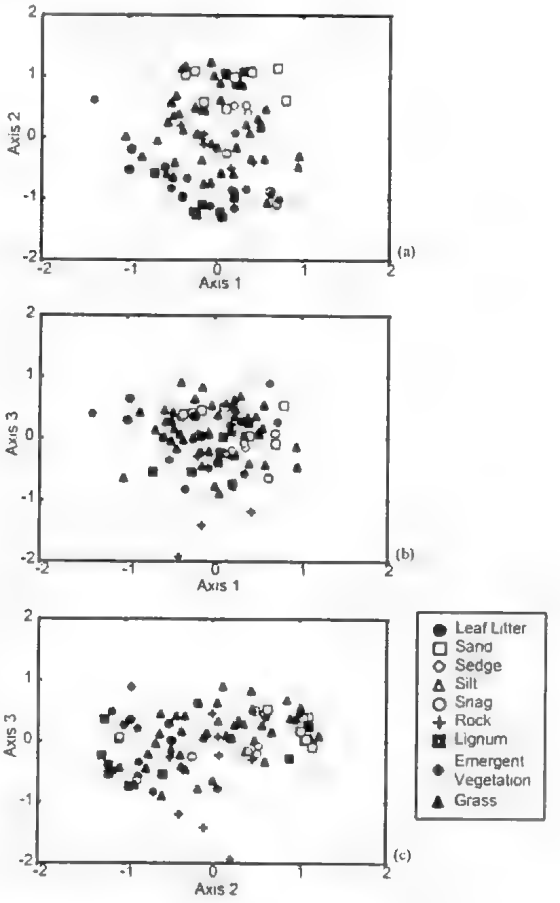

Fig. 8. SSH plot on axes (a) 1 v. 2, (b) 1 v. 3, (c) 2 v. 3 of samples collected from Goyder Lagoon, November 1993. Samples are labelled according to the microhabitat from which they were collected. Emergent vegetation = *Polygonum* sp. and flooded *Cyperus* spp.

TABLE 4. *Spearman Rank correlation coefficients between environmental variables and the sample scores on the first three axes of the SSH of faunal data from all samples collected from habitats in Goyder Lagoon, November 1993.* Significance levels are indicated as follows: ns = not significant; * = $p<0.05$; ** = $p<0.01$; *** = $p<0.001$.

	Axis 1	Axis 2	Axis 3	Salinity	Secchi	Temp
Axis 2	0.032					
	ns					
Axis 3	-0.143	0.324				
	ns	**				
Salinity	-0.071	0.698	0.416			
	ns	***	*			
Secchi	-0.658	0.029	0.375	0.401		
	***	ns	***	***		
Temp	0.394	-0.302	-0.367	-0.237	-0.355	
	***	**	**	*	*	
Dissolved Oxygen	-0.365	0.414	0.409	0.835	0.688	-0.261
	***	***	***	***	***	*

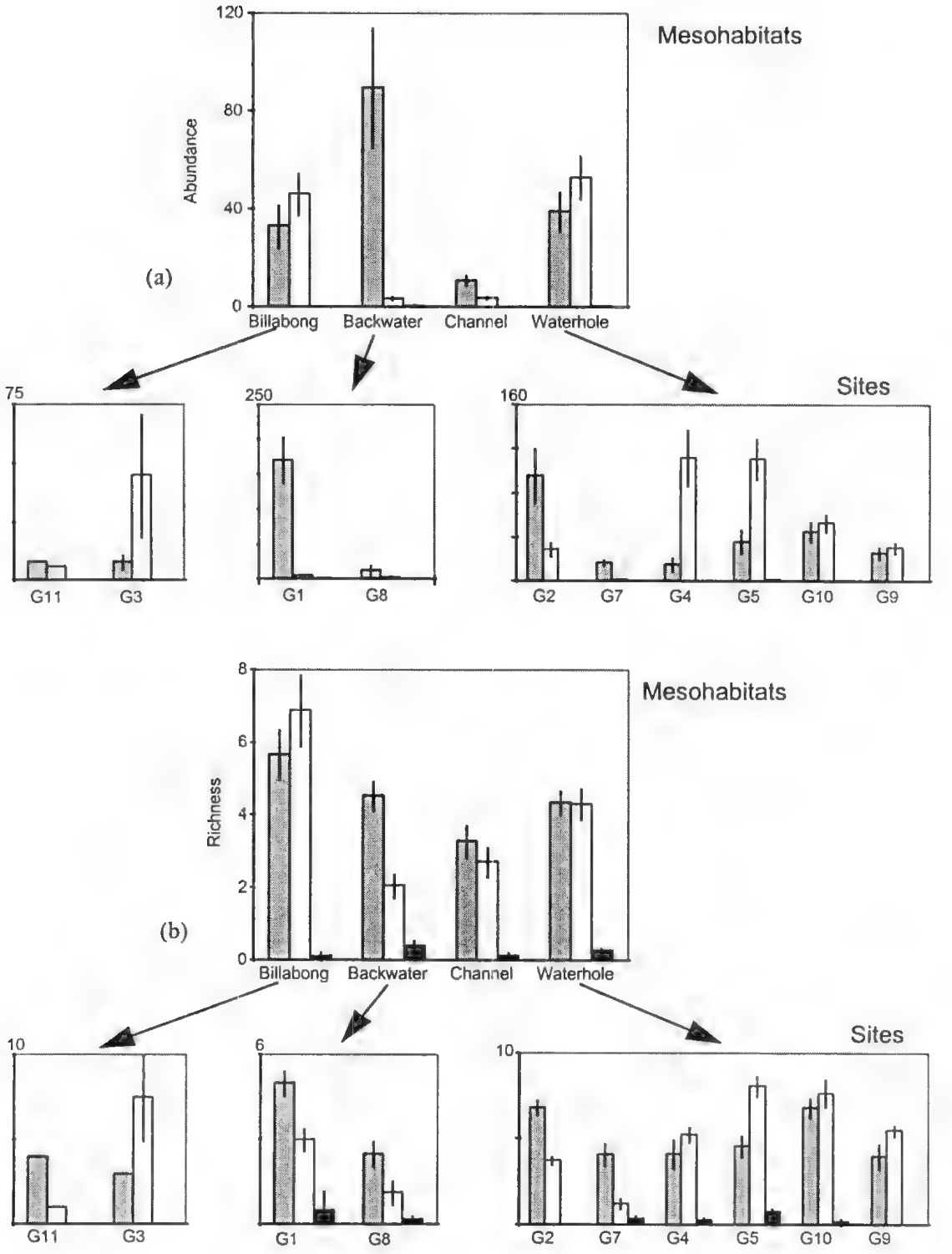

Fig. 9. Mean (±SE) of (a) abundance and (b) richness for collectors (grey bars), predators (white bars) and scrapers (black bars) for mesohabitats and sites within mesohabitats, collected from Goyder Lagoon, November 1993.

TABLE 5. *Functional Feeding Group ratios as indicators of dominant ecosystem processes.* [Auto = autotrophy, Hetero = Heterotrophy; CPOM = Coarse Particulate Organic Matter; FPOM = Fine Particulate Organic Matter; TFPOM = FPOM in transport; BFPOM = FPOM in substrate] (see Merritt & Cummins 1996).

Ecosystem Parameter	Functional Feeding Group Ratios	Calculated Ratio	General Criteria ratio levels	Evaluation
Auto/Hetero	Scrapers to Shredders + Total Collectors	0.21	Autotrophic >0.75	Heterotrophic system, dependent on allochthonous organic matter inputs
CPOM/ FPOM	Shredders to Total Collectors	0	Normal Shredder association linked to functioning riparian system >0.25	No shredders, riparian zone functioning differently from that predicted by Merritt and Cummins.
TFPOM/ BFPOM	Filtering Collectors to Gathering Collectors	0.12	FPOM transport (in suspension) enriched >0.50	low FPOM in transport, high particulate load
Stable Channel	Scrapers + Filtering Collectors to Shredders + Gathering Collectors	0.36	Stable substrates plentiful >0.50	Limited stable substrates, habitats dominated by sand and silt
Top-down control	Predators to Total of all other groups	0.59	Normal predator to prey balance <0.15	Large number of invertebrate predators, reflecting temporary habitats late in succession

explored there were considerable differences among sites even within the same mesohabitat. The backwaters G1 and G8 showed similar patterns with both richness and abundance dominated by collectors. The two billabongs, however, differed with both the richness and abundance of G3 being dominated by predators compared with collectors in G11 (Fig. 4). Variation in FFG composition of assemblages also differed between the different waterhole sites. The more temporary waterholes G4, G5, G9 and G10 were dominated by invertebrate predators whereas the more permanent waterholes G2 and G7 had a larger number of collectors. Overall, there were few scrapers.

Of the total of 54 taxa collected from Goyder Lagoon six were designated as "Scrapers", three as 'Filtering Collectors', 25 as 'Gathering Collectors' and 20 were 'Predators'; no 'Shredders' were collected from Goyder Lagoon (see Appendix). FFG ratios (Merritt & Cummins 1996), calculated using the FFG data indicate that Goyder Lagoon is heterotrophic, has low levels of invertebrate mediated leaf litter breakdown, and the majority of FPOM in the system is in storage (Table 5).

Discussion

Samples taken in November 1993 from habitats in Goyder Lagoon contained a total of 54 macroinvertebrate taxa. Nearly all of these taxa have also been recorded from the Coongie Lakes system (Sheldon unpub.) and from the lower River Murray and Darling River (Sheldon & Walker 1998). However, a striking feature of the Goyder Lagoon assemblage was the presence of a diverse group of Mollusca, including two gastropod taxa, *Notopala sublineata* (Conrad) and *Thiara balonnensis*, that have become extremely rare, if not extinct, in the River Murray and Darling River (Sheldon & Walker 1993a,b).

Collectors were the dominant feeding group across all habitats in Goyder Lagoon. Functional feeding group ratios (Merritt & Cummins 1996) suggest that Goyder Lagoon is heterotrophic and dependent on allochthonous organic matter as a carbon source (Table 5). This is not surprising since aquatic plants were rare within the Lagoon, small stands of the macrophyte *Polygonum* sp., being the most conspicuous. The absence of shredders in the assemblage suggests that for the invertebrates the major allochthonous inputs do not come directly from riparian litter fall but rather from particulate organic matter present as FPOM within the substrate. Decomposing plant material of mostly terrestrial or floodplain origin would therefore form the dominant food source for the aquatic macroinvertebrate food webs. Organic matter of floodplain origin has been found to influence the structure of invertebrate assemblages in other large floodplain river systems (Post & De La Cruz 1977; Cuffney 1988; Perry & Perry 1991; Thorp & Delong 1994; Meyer *et al.* 1997).

All samples were collected when water levels within Goyder Lagoon were low. Low water levels tend to maximise the 'between mesohabitat' differences (i.e. differences between channel, waterhole and billabong). At higher flows, between habitat differences would become increasingly blurred as billabongs and waterholes became part of the channel environment. Although we expected the main differences in assemblage composition to occur between different meso- and microhabitats (regardless of site), there were striking differences in the richness and abundance of macroinvertebrates collected from the different sites, even between sites from the same mesohabitat type (Fig. 3). These differences may reflect different successional trajectories occurring within the assemblage at each site after hydrological isolation (Boulton & Lake 1992). Thus, the recent flooding/drying history of each site may be a significant factor in determining the structure of the assemblage at any time.

Sites, regardless of mesohabitat type, at Andrewilla and Koonchera Dune contained the largest number of individuals and the greatest number of taxa (Fig. 3). These sites are intermediate in the range of flooding frequency (Fig. 5). As flooding is a form of ecological "disturbance" this supports the notion of 'intermediate disturbances' being a driving force in maintaining animal diversity within ecosystems (Ward & Stanford 1983). The sites at Andrewilla Waterhole and Koonchera Dune, falling within this band of intermediate flooding frequency, were characterised by taxa such as the prosobranch gastropod *Thiara balonnensis* and the predatory caddisfly *Oecetis* sp. (Fig. 5). Both these taxa tended to be rare in the more permanent sections of the Lagoon.

Goyder Lagoon is an area of high conservation significance (Morton *et al.* 1995a). It provides habitat for a variety of aquatic and terrestrial organisms in an otherwise arid environment (Morton *et al.* 1995b; ANCA 1996). The macroinvertebrate assemblage, although not unique to Goyder Lagoon, did contain a number of molluscs that are becoming increasingly endangered in other river systems. It is the geomorphology of the Lagoon that gives rise to the different mesohabitat types. Overlying this morphological template is the hydrology of the system. The variable flows characteristic of Goyder Lagoon are intrinsic in maintaining macroinvertebrate diversity. The waters of wetlands in arid regions are increasingly in demand by water resource developers (Walker *et al.* 1997). If Goyder Lagoon is to remain an area of high conservation value then it is imperative that the hydrological diversity characteristic of the system is maintained.

Acknowledgments

This study was conducted as part of the Biological Survey of the Lower Diamantina Floodplain, a joint project of the Conservation Council of South Australia and the South Australian Department of Environment and Planning. The project was funded by the Australian Heritage Commission. We thank R. Molsher, J. Arnold, A. Bingemer and Bunge for collection and sampling sorting assistance and Mr P. Schultz and an anonymous referee for extremely helpful comments.

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Appendix

Species, functional feeding group [FC = filtering collector; GC = gathering collector; S = Scraper; P = Predator] and total abundance for samples collected from habitats in Goyder Lagoon, Diamantina River, November 1993

	Species	FFG	Total
MOLLUSCA			
BIVALVIA			
Sphaeriidae	*Sphaerium* sp.	FC	45
Corbiculidae	*Corbicula australis* (Deshayes)	FC	22
Hyriidae	*Velesunio wilsonii* (Lea)	FC	1
GASTEROPODA			
Ancylidae	*Ferrissia* spp.	S	4
Planorbidae	*Glyuphyysa* sp.	S	21
Viviparidae	*Notopala sublineata* (Conrad)	GC	11
Thiaridae	*Thiara balonnensis* (Smith)	GC	1944

OLIGOCHAETA	Indeterminate spp.	GC	134
HIRUDINEA			
Glossiphoniidae	Indeterminate sp.	P	4
CRUSTACEA			
CONCHOSTRACA			
Cyzicidae	*Cyzicus* sp.	GC	11
DECAPODA			
Palaemonidae	*Macrobrachium australiense* (Ortmann)	GC	556
Parastacidae	*Cherax destructor* (Clark)	GC	22
INSECTA			
EPHEMEROPTERA			
Caenidae	*Tasmanocoenis arcuata* Alba-Tercedor & Suter	GC	117
Baetidae	*Cloeon* sp.	GC	2
ODONATA			
Gomphidae	*Austrogomphus australis* Selys	P	22
Cordulidae	*Hemicordulia tau* Selys	P	16
HEMIPTERA			
Corixidae	*Micronecta* spp	GC	547
	Cymatia sp.	GC	18
Ochteridae	Indeterminate sp.	GC	1
Notonectidae	*Anisops* spp.	P	87
	Enithares sp.	P	261
COLEOPTERA			
Dytiscidae	*Antiporus femoralis* (Boheman)	P	11
	Allodessus sp.	P	48
	Eretes australis Erichson	P	1
	Cybister sp.	P	10
	Rhantus sp.	P	1
	Hyderodes sp.	P	15
	Sternopriscus sp.	P	70
Hydrophilidae	*Enochrus* sp.	S	2
	Berosus sp.	S	3
	Limnoxenus sp.	GC	13
Hydraenidae	*Octhebius* sp.	S	8
	Hydraena sp.	S	5
DIPTERA			
Tipulidae	Indeterminate sp.	P	4
Chironomidae:Tanypodinae	*Ablabesmyia* sp.	P	57
	Coelopynia sp.	P	761
	Procladius sp.	P	260
Chironomidae: Chironominae	*Cladotanytarsus* sp.	GC	14
	Tanytarsus spp.	GC	77
	Chironomus sp.	GC	23
	Chironomus cloacalis Atchley & Martin	GC	17
	Cryptochironomus sp.	GC	15
	Stenochironomus sp.	GC	2
	Parachironomus sp.	GC	181
	Dicrotendipes sp.	GC	21
	Paratendipes sp.	GC	2
Chironomidae: Orthocladinae	*Cricotopus* spp.	GC	11
Ceratopogonidae	*Bezzia* sp.	P	501
Muscidae	Indeterminate sp.	P	1
TRICHOPTERA			
Ecnomidae	*Ecnomus* sp.	P	18
Leptoceridae	*Triplectides australis* Navás	GC	298
	Triplectides elongatus Banks	GC	20
	Oecetis sp	P	1144

BREEDING BIOLOGY OF LITORIA BOOROOLONGENSIS (MOORE, 1961), AND LITORIA LESUEURI (DUMÉRIL & BIBRON, 1841) (ANURA: HYLIDAE) AND COMMENTS ON POPULATION DECLINES OF L. BOOROOLONGENSIS

By Marion Anstis, Ross A. Alford† & Graeme R. Gillespie‡*

Summary

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Key Words: Litoria booroolongensis, Litoria lesueuri, embryology, larval development, habitat, aggregation, population decline.

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The embryonic and larval development of *Litoria booroolongensis* are described and compared to those of the closely related *Litoria lesueuri*. The habitat, behaviour and distribution of each species are compared and indications of marked population declines of *L. booroolongensis* are discussed.

The two species have similar lotic life-histories but some differences occur in body proportions, colour in life, behaviour and habitat. In both species the egg mass is a compact gelatinous clump, typical of frogs breeding in a lotic environment. The tadpoles of both species are adapted to the lotic environment and have streamlined bodies and suctorial mouth-parts. Adult *L. booroolongensis* aggregate throughout the year and are active diurnally in summer.

Key Words: *Litoria booroolongensis*, *Litoria lesueuri*, embryology, larval development, habitat, aggregation, population decline

Introduction

Litoria booroolongensis was first described by Copland (1957), as *Hyla X* Moore, pending the type description (Moore 1961). Moore described it as an "upland species" extending from the Armidale region to the Blue Mountains in NSW, but made no reference to larval development. Anstis (1974) briefly described the tadpole as lotic and suctorial, with a tooth row formula of $^{2}/_{3}$ and numerous oral papillae. The present paper provides a description of embryonic and larval development of *L. booroolongensis*, with comparisons to the similar tadpole of *L. lesueuri*. *Litoria booroolongensis* is associated with flowing streams on the slopes and tablelands of the Great Dividing Range from the Queensland border to the Victorian border (Barker *et al.* 1995), with the type locality (Guy Fawkes Creek near Ebor, NSW) and most records of this species indicating that it commonly occurs above 800 m in the region of the New England Tablelands, NSW (Heatwole *et al.* 1995). The most southern record of this species is from the Tumut River, Kosciusko National Park and it has recently been found in the adjacent Goobarragandra River, east of Tumut NSW (Hunter & Gillespie unpub.). Observations on the current state of populations (particularly in the New England region) are discussed.

Litoria lesueuri (Duméril & Bibron) occurs in eastern Australia from northern Queensland to Victoria and almost certainly involves a complex of sibling species (Moore 1961; Barker *et al.* 1995). The type locality is Port Jackson, NSW. Observations on current population trends at some southern sites are reported. The eggs of the northeastern Queensland form have been described by Richards & Alford (1992) and Barker *et al.* (1995) briefly describe the site of egg deposition by the populations found from southern Queensland to Victoria. The tadpole as found in the Melbourne area has been briefly described by Martin *et al.* (1966). As the distributions of both species overlap in places, a more detailed description of *L. lesueuri* tadpoles from NSW is provided here for the purposes of comparison with *L. booroolongensis* and to assist in distinguishing the species. Distribution maps for both species together with localities studied in the present paper, are presented as Figure 1. Numbered localities on Fig. 1A relate to *L. booroolongensis* and those on Fig. 1B to *L. lesueuri*.

Materials and Methods

Material examined

Litoria booroolongensis larvae: Australian Museum (AM) R119062-64, 119067, 119071, 119073 (Serpentine River, Point Lookout NSW), R119055, 119080, 119083, 119085, 119087, 119088 (larvae from Back Creek, Point Lookout NSW). Embryo/larval descriptions are based on one egg mass from an amplectant pair collected at Serpentine River (near Point Lookout NSW) on 3.xi.1973. The pair was placed in an inflated plastic bag containing stream water, reeds and a rock, until after oviposition. Larvae were maintained for up to three months in containers of 40 cm diameter at water temperatures of 14°–25° C. Only larvae from streams

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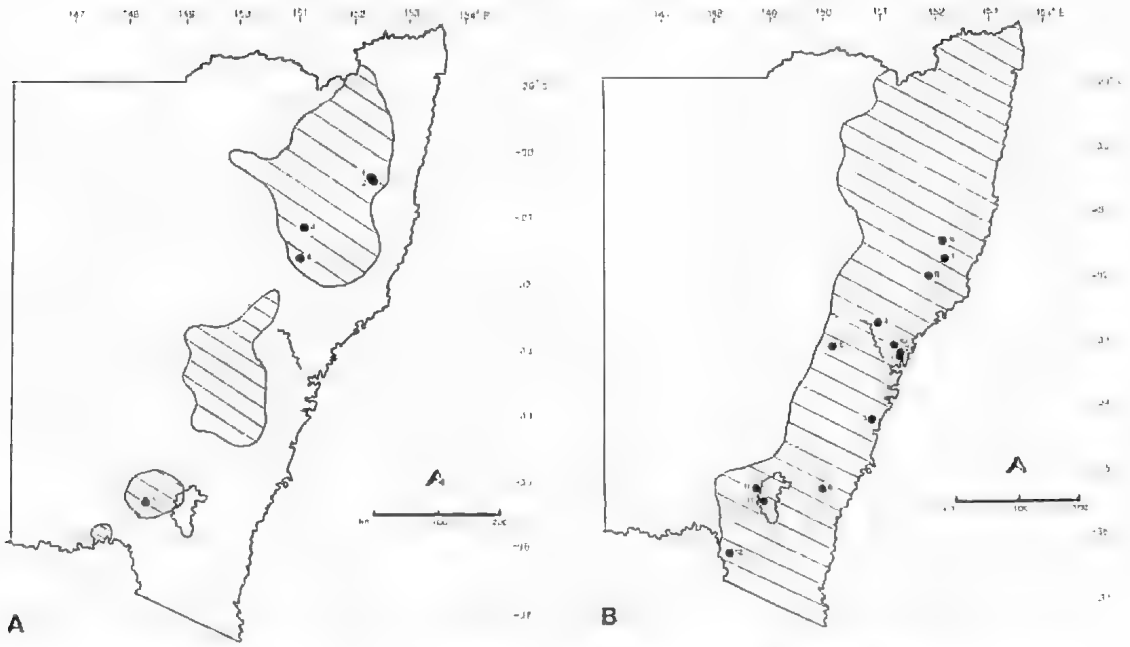


Fig. 1. A. Map of eastern half of NSW showing distribution of *Litoria booroolongensis* (shaded area = AM records; • = localities referred to in present paper). 1. Back Creek, Point Lookout 30° 29' 29" S, 152° 20' 38" E. 2. Serpentine Creek, Point Lookout 30° 28' 26" S, 152° 19' 26" E. 3. Near Tamworth 31° 13' 40" S, 151° 10' 30" E. 4. Isaacs Creek, Timor Caves 31° 41' 40" S, 151° 07' 20" E. 4. Goobarragandra River 35° 24' 02" S, 148° 26' 01" E. Populations no longer exist at localities 1 & 2 (see text). B. Map of eastern half of NSW showing distribution of *Litoria lesueuri* (shaded area = AM records; • = localities referred to in present paper). 1. Ourimbah Creek, 33° 19' 45" S, 151° 21' 38" E. 2. Near Palmdale 33° 18' 17" S, 151° 20' 42" E. 3. Darkes Forest 34° 14' 02" S, 150° 54' 00" E. 4. Darkey Creek near Singleton 32° 43' 36" S, 150° 56' 32" E. 5. Coco Creek E. of Capertee 33° 08' 15" S, 150° 06' 40" E. 6. Mongarlowe River, Braidwood 35° 22' 42" S, 149° 57' 11" E. 7. Dingo Creek, Wingham 31° 49' 50" S, 152° 18' 00" E. 8. Berrico 32° 04' 00" S, 151° 49' 19" E. 9. Tirrill Creek, Bulga State Forest 31° 31' 49" S, 152° 08' 21" E. 10. The Basin, Watagan State Forest 33° 06' 20" S, 151° 13' 41" E. 11. Bogong Creek 36° 21' 30" S, 148° 12' 15" E. 12. Couer River 35° 35' 27" S, 148° 49' 20" E. 13. Goodradigby River 35° 25' 05" S, 148° 44' 40" E. The MacDonald River is shown on both maps.

where *L. lesueuri* does not occur (in the region of the type locality) were included in the study. *Litoria lesueuri* larvae:- NSW localities: AM R119101 - Glen Davis; 119099 - Ourimbah; 119104 - Allens Creek Picton; 119106, 119107 - Dingo Creek near Wingham; 119108 - Berrico Creek, 2 km E. of Berrico; A948 - Watagan State Forest; A724 - Tirrill Creek (collection of M.A.).

Tadpoles were reared to metamorphosis to confirm identity. Embryos and larvae were measured with vernier callipers and an ocular micrometer attached to a Wild M5 stereoscopic microscope. Larvae were observed in the natural environment, then examined while anaesthetized with chlorbutanol. The staging system of Gosner (1960) was used. For *L. booroolongensis*, embryos studied included stages 2 (n = 11), 8 (n = 15), 17 – 18 (n = 9), 19-21 (n = 9), 22 & 25 (n = 8). larval stages included 27 (n = 1), 28 (n = 4), 31 (n = 2), 32 (n = 1), 33 (n = 3), 34 (n = 4), 35 (n = 3), 36 (n = 4), 37 (n = 2), 38 (n = 1), 40 (n = 1), 41 (n = 6) and metamorphs at stage 46 (n = 10). For *L. lesueuri*, larval stages included 25 (n = 3), 27 (n = 1), 31 (n = 2), 32 (n = 1), 34 (n = 1), 35 (n = 3), 36 (n = 2), 37 (n = 4), 38 (n = 1), 39 (n = 2), 41 (n = 2) and metamorphs at stage 46 (n = 7). Illustrations were made with the aid of a drawing tube attached to the microscope. The following abbreviations for all morphometric variables are taken from Anstis (1994).

Lateral view: TL = total length; BL = body length; BD = body depth; BTM = depth of tail musculature at base of tail; TD = maximum tail depth; DF = depth of dorsal fin (in line with TD); VF = depth of ventral fin (in line with TD); TM = depth of tail musculature (in line with TD); SS = snout to spiracle; S-E = tip of snout to anterior rim of eye; S-N = tip of snout to anterior rim of naris; ED = diameter of eye.

Dorsal view: BW = body width; EBW = body width at level of eyes; BTMW = width of tail musculature at base of tail; IO = inter-orbital span; EN = edge of eye to edge of naris; IN = internarial span.

Ventral view: MW = maximum width of oral disc.

The above morphometric variables were $\log_{10}$ transformed prior to statistical analysis. A principal components analysis (PCA) on the covariance matrix of these values was used to reduce the

dimensionality of the data set and remove the effects of overall size (which is extracted as the first component (Marcus 1990)). The scores of each animal on the second and third component (representing shape variables) were plotted in a biplot (Digby & Kempton 1987) in which the scaled coefficients of each variable on the second and third PC axes were overlaid on the data. Examining this plot enabled us to determine whether the species differed in shape, which size-independent shape variable was most important in this discrimination and to postulate which of the original variables contributed most to the score on that variable. We then calculated the slopes and intercepts of the relationship between $\log_{10}$-transformed body length and all other $\log_{10}$-transformed morphometric variables for each species. We used separate analyses of covariance (ANCOVAs) for each morphometric variable to determine whether the slopes and intercepts of the regressions differed significantly between species.

Results

Distribution/habitat

Litoria booroolongensis

A map of the eastern half of NSW shows the general distribution of this species as determined from specimens registered in the Australian Museum and the localities referred to in the present study (1-5, Fig. 1A). Habitats studied were permanent flowing streams running through wet or dry sclerophyll forest, or through semi-cleared grazing land in basalt or granite range country (altitude range 450 -1340 m). Field observations on this species were carried out annually in the summer breeding time of December/January (1965-1974) at Back Creek, Point Lookout NSW (locality 1 Fig. 1A, 30° 29' 29" S, 152° 20' 38" E), Serpentine Creek (locality 2 Fig. 1A; 30° 28' 26' S, 152° 19' 26" E) and other nearby streams at Point Lookout NSW (1250-1340 m). During this period of nine years, numerous tadpoles metamorphs and adults were readily found in the several streams in the Point Lookout and Armidale region. A survey of these same streams in December 1994 revealed no adults or larvae.

The only southern locality surveyed was Goobarragandra River (locality 5 Fig. 1A, 35° 54' 02" S, 148° 26' 01" E) where 13 adults were found on 30.xi.1996 along an 800 m stretch of the river.

Litoria lesueuri

A map of the eastern half of NSW shows the general distribution of this species as determined from specimens registered in the Australian Museum, and a sample of localities studied from 1972-1996 (Fig. 1B, 1-13). Habitats varied from flowing streams to large dams in sandstone, metamorphic or granite country in rain forest, dry sclerophyll forest or heath land (40-1100 m). The frog was encountered in fairly low numbers in recent surveys in most streams in NE Victoria and was absent from several streams where it would be expected to occur, on the basis of habitat and local distribution. Surveys in the Kosciusko National Park in 1996 (Hunter & Gillespie unpub.) found the species to be present in only 15 of 40 likely streams.

Behaviour

Litoria booroolongensis

During summer months in the 1960s-70s, adults were observed basking in the sun on exposed basalt rocks in mid-stream and frequently three or more individuals were found under the same rock within/beside the stream, at the northern Back Creek and at Serpentine Creek. When disturbed, they immediately leapt under the flowing water. Males were observed calling at night while sitting on exposed rocks in shallow, flowing sections of the stream. Six females (four gravid) and seven males (six with nuptial pads) were found by day under stones on pebble banks at the southern Goobarragandra River on 30 November 1996.

Numerous larvae and metamorphs from stages 25-46 were observed at the two northern localities throughout December/January (1965-74). Tadpoles were commonly found on the substrate amongst rocks, in shallow flowing sections of stream including runs and riffles, and in shallow, slowly flowing inlets at the sides of the stream. The tadpoles possessed a number of features typical of species inhabiting the lotic environment, including a suctorial oral disc fully surrounded by three or more rows of papillae, a more streamlined body form (especially the snout), a thicker tail musculature and relatively shallow fins. They were observed adhering to rocks with their suctorial mouths, tails bending in the direction of water flow.

Litoria lesueuri

During winter, adults were found on ridge-tops in forest country away from streams. Adults were usually associated with flowing streams, but also bred in completely isolated streamside pools (ISPs) such as in bedrock shelves, where the water was still. Males were observed calling beside dams in open forest near Durimbah NSW (locality 1 Fig. 1B, 33° 19' 45" S, 151° 21' 38" E). Eggs were found laid in the stream on the edge of runs in slow water, in connected still pools, or in ISPs. At Bogong Creek (locality 11 Fig. 1B, 36° 21' 30" S, 148° 12' 15" E) a series of perched ISPs was consistently selected as breeding sites by several females from 1994 - 1996. In the first year, all but one tadpole from two

clutches survived, in the second year the pools dried up and in the third year, newly-hatched tadpoles could not be found after a high spring flood. No tadpoles have been found in the stream itself in any of these years.

In streams or rivers, tadpoles were most commonly found on the substrate in shallow, slowly flowing sections of streams, segregated back waters with reduced flow and perched rock pools or isolated pools (at times stagnant) beside the stream. They were very agile when disturbed, capable of fast movement darting under rocks or leaf litter. As in *L. booroolongensis*, they possessed a suctorial mouth, shallow fins, thick tail musculature and streamlined body.

Oviposition and embryonic development
Litoria booroolongensis

The mean egg complement of four gravid females examined at Goobarragandra River near Tumut NSW was 1519 (range 1292-1784). A pair of frogs found in amplexus at Serpentine Creek on 3.xi.1973 was first observed at 0740 h sitting in sunlight on an exposed rock in a shallow inlet pool near the edge of the stream. After 10 min they had moved to a rock closer to mid-stream in a shallow, flowing section. The frogs were then collected and placed in a plastic bag, and at 1300 h a single, compact egg mass was found partly adhering to suspended vegetation within the bag. To avoid disturbance during development, eggs were not counted.

Embryos were at stage 2 when a sample was first preserved at 1300 h, three or four hours after eggs were laid. There were two layers of jelly surrounding the embryo. In live embryos the animal pole was dark grey and the vegetal pole grey. The same preserved embryos examined in 1996, had a brown animal pole merging to cream over the vegetal pole. A series of 11 preserved embryos at stage 2 all had a diameter of 1.46 mm. Approximately nine hours after deposition they were at stage 8 and 15 embryos had a mean diameter of 1.5 mm. The blastomeres were more evenly divided in the animal pole than in the vegetal pole. After 36 h embryos were at stages 11 and 12 and after 56 h most were at stage 14. Stages 17-18 (tail-bud).. were reached after 67 h. Nine specimens at these stages ranged from 2.43-3.36 mm (mean 2.96). A typical stage 17 embryo (Fig. 2A), had a rounded snout; prominent V-shaped adhesive organ; stomodaeal pit; small gill-plate bulge; indistinct pronephric swelling; slight optic bulge; indistinct narial pit slightly delineated with pigment, and rudimentary fins along the tail bud. Live embryos at stage 19 were light grey above with a pale grey yolk sac.

Some embryos burst through the capsules during the muscular response in stage 18 but most did not begin hatching until stage 20. An embryo at stage 20 measuring 5.76 mm (Fig. 2B) is described as follows:- snout rounded; two pairs of external gills - two branches on upper pair and 4-5 branches on lower; optic and narial regions partly outlined with small crescent of pigment; adhesive organs well divided – remnant of V-shape below each; numerous fine muscular ridges along tail musculature; stomodaeal pit and fins both deepening. Dorsum grey, yolk sac pale grey in live embryos, and pale brown/yellow brown in preserved specimens.

Live embryos at stages 20 and 21 were grey above with a lighter grey yolk sac and translucent grey fins. Nine specimens at these stages ranged from 4.82 - 5.67 mm (mean 5.43). Hatchlings adhered strongly to the jelly mass. The external gills were visible macroscopically and when fully developed by stage 22, extended about 2/3 the length of the yolk sac.

Eight embryos at early stage 25 ranged from 9.23 - 9.57 mm (mean 9.46) - dorsal pigmentation of larval stages developing; dorsal edge of tail musculature finely edged with melanophores; fins, external body wall and venter clear (in preservative); spiracle and vent tube both functional; jaw sheaths pigmented, but as yet without shape of older larvae; keratinisation incomplete. Tooth rows almost complete except for 3rd lower row, which was beginning to develop in two more advanced larvae at stage 25, measuring 11.5 and 12.15 mm, respectively.

Litoria lesueuri

Most clumps of eggs observed were loosely adhering to rock substrate but some also adhered to bottom sediments or sedges. There was no indication

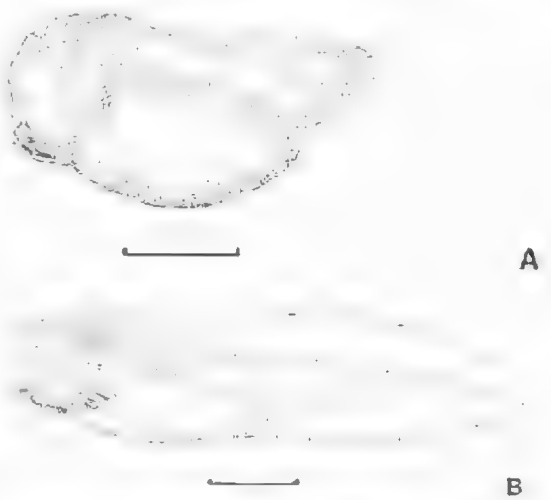


Fig. 2. Embryos of *Litoria booroolongensis*. A. Removed from capsule, stage 17, 3.24 mm. B. Just hatched, stage 20, 5.76 mm. Scale bar = 1 mm. Stages are from Gosner (1960).

of nest-site excavation, as in the north-Queensland form, and 20% of clutches observed were deposited under, or partly under a small rock on the bedrock of the stream. Eggs were laid in a water depth of 10-20 cm. Clutch sizes of 14 egg masses examined in 1995-1996 ranged from 810-3564 (mean 1878). The mean diameter of 10 eggs at stages 3-5 (Gosner 1960) from Goodradigby River (locality 13 Fig. 1B, 35° 25' 05" S, 148° 44' 40" E, was 1.7 mm. No embryos beyond this stage were available for study.

Larvae

Analysis of covariance showed that the two species follow very similar trajectories through larval body sizes and stages (tests for differences in slope and intercept both $p >> 0.05$). The relationships between developmental stage and body size for both species are illustrated in Fig. 3, which makes it clear that they cannot be distinguished on this basis.

The results of the principal components analyses (PCA) are presented in Fig. 4A, with the contributions of each variable to the second and third eigenvectors shown in Table 1. The first (general size) principal component accounted for 87% of the variation in the data set. The second and third (shape) components accounted for 4.4 and 3.7%, respectively. Despite the relatively small proportions of the overall variance accounted for by these components, it is clear from Fig. 4A, that in combination they discriminate very effectively between the two species, indicating that the species

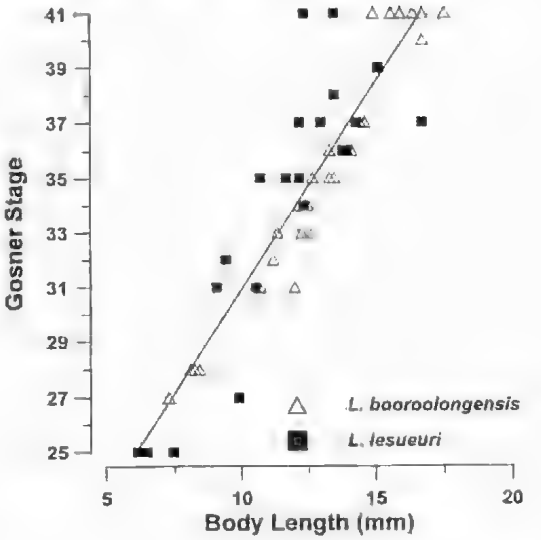
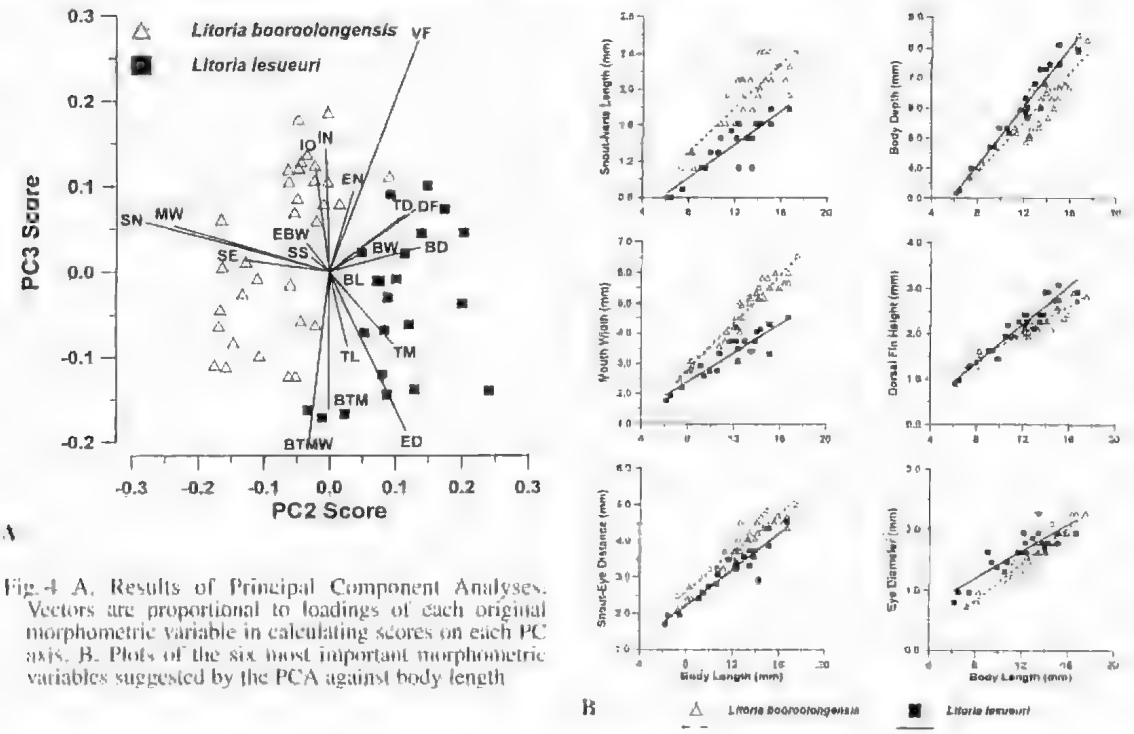


Fig. 3. Gosner (1960) stages plotted against body length for *Litoria booroolongensis* and *Litoria lesueuri*. Line represents pooled regression of stage on length, $y = 1.52 x + 15.77$, $r^2 = 0.84$, $p < 0.0001$.

do differ strongly in shape. Most of the discriminatory power resides in component 2. This means that the morphometric variables responsible for the eigenvector loadings which are most closely aligned with axis 2 of the PCA in the biplot, should be most important in discriminating between the shapes of the two species.

TABLE 1. *Regression of $\log_{10}$ of morphometric variables on $\log_{10}$ of body length for each species, with p-values for significance of differences in slope and intercept between species from an ANCOVA, and eigenvectors for the second and third principal components of $\log_{10}$ transformed morphometric variables.*

	L. booroolongensis		*L. lesueuri*		ANCOVA *p*-values		Principal Component Eigenvectors	
Dependent Variable	Intercept	Slope	Intercept	Slope	Intercept	Slope	PC2	PC3
TL	0.2588	1.1077	0.2801	1.1077	0.0012	1.0000	0.05519	-0.17586
BL	-	-	-	-	-	-	0.03292	-0.03320
BW	0.1078	0.8645	-0.1623	0.9193	0.5654	0.4516	0.11301	0.04901
BD	-0.1623	0.8300	-0.2574	0.9625	0.0001	0.1327	0.27523	0.05558
LBW	0.1376	0.8944	0.1512	0.8838	0.0001	0.8145	0.06823	0.06452
IO	-0.4061	0.8095	-0.8312	1.1647	0.0001	0.0002	0.04259	0.24300
IN	-0.3804	0.5303	-0.9227	1.0063	0.0148	0.0001	-0.01072	0.28724
EN	-0.6254	0.7780	-0.9479	1.0677	0.1942	0.0002	0.07379	0.18867
BFMW	-1.5500	1.7951	-1.0958	1.3810	0.5247	0.0008	-0.06175	-0.39549
BTM	-0.9376	1.2425	-0.6718	1.0097	0.1851	0.0275	-0.00254	-0.32361
TD	-0.1152	0.7760	-0.4368	1.0944	0.0058	0.0001	0.22844	0.13129
DE	-0.6379	0.8747	-0.9954	1.2369	0.0014	0.0002	0.26151	-0.14459
TM	-0.7799	0.9276	-0.8920	1.0579	0.0569	0.3348	0.19223	-0.16840
VE	-0.3627	0.4277	-0.9264	1.0493	0.7292	0.0003	0.26800	0.53630
SS	-0.1476	0.9439	-0.1894	0.9637	0.0016	0.7269	-0.05235	0.03154
ED	-1.2235	1.2728	-0.7270	0.8731	0.0001	0.0004	-0.23216	-0.37399
MW	0.5509	1.1001	-0.4149	0.8719	0.0001	0.0061	-0.47445	0.10678
SE	0.4276	0.9189	-0.4735	0.9108	0.0001	0.9153	-0.26168	0.02676
SN	0.6832	0.8675	-0.7280	0.8072	0.0001	0.5980	0.55849	0.11531



A

B

Fig. 4 A. Results of Principal Component Analyses. Vectors are proportional to loadings of each original morphometric variable in calculating scores on each PC axis. B. Plots of the six most important morphometric variables suggested by the PCA against body length

Figure 4B presents plots of the six most important variables suggested by the PCA against body length. These plots show that the species differ in these characteristics, in the direction indicated by the PCA; *L. booroolongensis* has relatively greater snout-naris length, mouth width, and snout-eye distance and relatively lower body depth, dorsal fin depth and eye diameter than *L. lesueuri* does at each body length.

Litoria booroolongensis

A composite description of tadpoles at stages 25-39 is given, using some anaesthetized specimens still showing colour in life. A tadpole at stage 37 (36.2 mm) from the egg mass laid at Serpentine Creek (locality 2 Fig. 1A) is shown in Fig. 5 A,C.

Dorsal: body ovoid, widest across branchial region; snout broadly rounded; eyes dorso-lateral, positioned almost 1/3 along body length from tip of snout; nares opening antero-laterally; body wall uniform rusty-brown with some darker mottling; darker brown band across urostylar region; brown body colour continues along tail musculature as two longitudinal stripes, becoming lighter towards tail tip; young tadpoles at stages 25-26 dark brown with irregular light grey band just anterior to darker urostylar region; limbs increasingly pigmented after stage 34.

Lateral: body streamlined, snout rounded, elongate; spiracle sinistral, moderately long and broad, tapering slightly from origin to postero-dorsal opening; oral disc directed ventrally; vent tube dextral; body brown with part of golden ventral sheen visible, particularly over branchial region; iris golden; tail musculature thick anteriorly, uniform brown with some darker patches, main anterior blood vessel and crevices between muscular ridges outlined with pigment; fins relatively shallow, dorsal fin rises gradually (or more acutely) to greatest depth at mid-point of tail, or just posterior/anterior to it, ventral fin increases slightly in depth in posterior half, but generally shallower than dorsal fin; fine network of melanophore clusters traced over vascular system on dorsal fin and posterior half of ventral fin (denser beyond stage 30); tail tip rounded.

Ventral: venter with almost uniform copper/gold sheen of iridophores, or patchy sheen with darker areas showing through in between patches. Branchial region densely covered with copper/gold iridophores.

Oral disc (Fig. 6B): oral disc wide, directed ventrally; band of papillae surrounding entire convoluted margin; 2 - 3 rows around anterior, 4 - 6 around lateral and 3 - 4 around posterior margin; inner papillae on posterior margin larger and more widely spaced; papillae diminish in size and increase in number through to outermost row; two complete anterior and three complete posterior rows of labial teeth, all equal in length; jaw sheaths moderately massive, quite heavily keratinised, upper sheath with

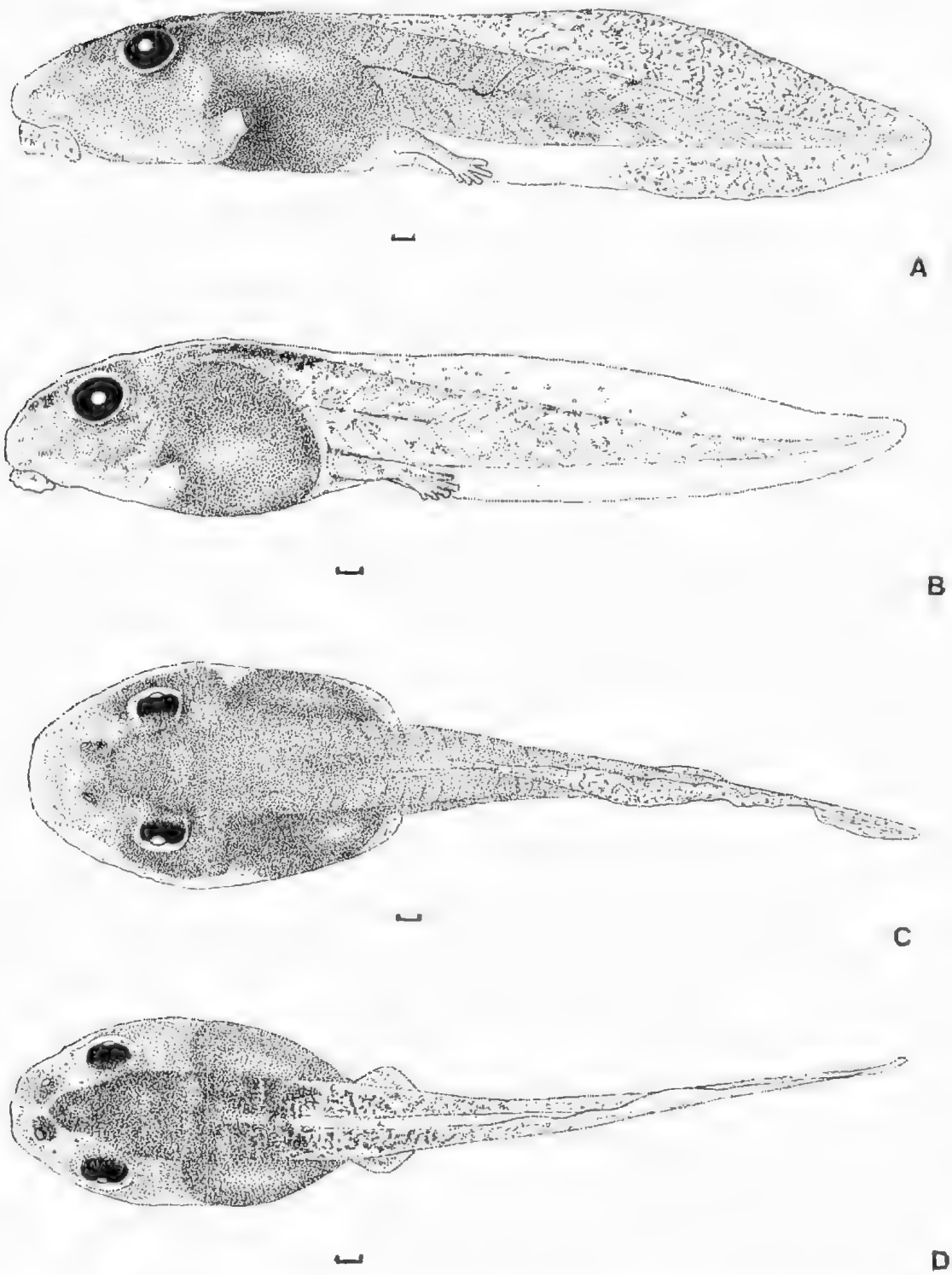


Fig. 5. Larvae of *Litoria booroolongensis* and *Litoria lesueuri*, each at stage 37. A. *L. booroolongensis*, lateral view. B. *L. lesueuri*, lateral view. C. *L. booroolongensis*, dorsal view. D. *L. lesueuri*, dorsal view. Scale bars = 1 mm. Staging system of Gosner (1960).

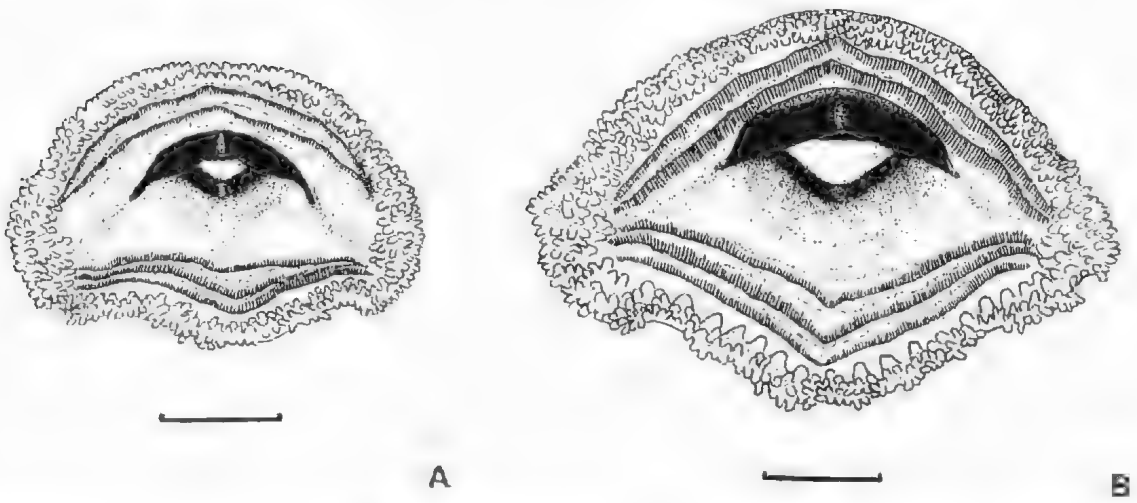


Fig. 6. Oral discs of *Litoria booroolongensis* and *Litoria lesueuri*. A, *L. lesueuri* (locality 10, Fig. 1B, Stage 37). B, *L. booroolongensis* (locality 2, Fig. 1A, Stage 34). Scale bars = 1 mm.

central notch and small underlying keratinised ledge; inner margins of jaw sheaths serrated; ledge partly worn in some individuals and does not appear before stage 28 in specimens examined.

Colour in preserved specimens (composite description, stages 33-39): pigment slightly darker over abdomen, cranial, vertebral and post-narial regions, tail musculature evenly pigmented (dorsal view); abdomen opaque with fine layer of melanophores over snout and branchial region; dermal body wall clear with a few scattered clusters of melanophores; iris black (lateral view); fine dense layer of melanophores over heart, abdomen and just anterior to each gill; intestine visible; tail musculature and limbs unpigmented (ventral view).

Litoria lesueuri

Composite description, live specimens, stages 31-39. A tadpole at stage 37 (33.9 mm) from Watagan State Forest (locality 10 Fig.1B) is shown in Fig. 5 B,D.

Dorsal: body ovoid, widest across abdominal region; snout rounded; eyes dorso-lateral and positioned less than 1/3 along body length from tip of snout; nares open anterolaterally; abdominal, cranial, post-narial regions and eyes appear darker below dermal layer of golden iridophores covering most of dorsum, except for urostylar region, where absence of iridophores creates broad, uniform or broken darker band; body wall sparsely flecked with small clusters of melanophores in some specimens; some brown patches over tail musculature; golden iridophores denser over gills, snout, posterior rim of iris and just anterior to urostylar region; young tadpoles at stages 25-26 with darker dorsum (less iridophores) and contrasting band of pale grey pigment just anterior to darker urostylar region; tail musculature sandy gold, or with slight salmon tinge; dark brown patches scattered along length of tail, especially along anterior half. limbs increasingly pigmented from stage 34.

Lateral: body ovoid; snout rounded; spiracle sinistral, broad at origin tapering towards postero-dorsal opening; oral disc directed ventrally; vent tube dextral; snout appears golden; layer of copper/gold iridophores over majority of iris and lower part of abdomen; clumps of iridophores outline lower edge of each gill, continuing over venter; tail musculature fairly thick anteriorly, some scattered melanophore clusters over all but anterior lower edge; main blood vessels, crevices between muscular ridges pigmented; fins relatively shallow to moderately so, clear, with faint golden hue, fine scattered melanophore clusters over dorsal fin and some dusky pigment over ventral fin, venation unpigmented but visible; dorsal fin rises gradually (or more acutely) to greatest depth anterior to, or at, mid-point of tail; tail tip narrowly rounded.

Ventral: opaque copper/gold sheen over abdomen, heart and some clusters of iridophores over sides of each gill; anterior half of venter otherwise clear; limbs and tail musculature unpigmented.

Oral disc (Fig. 6A): oral disc ventral in direction, fairly wide; band of papillae surrounding entire margin; 2-3 rows fine papillae around anterior, up to six around lateral and 3-4 around posterior margin; innermost row of papillae around the posterior margin very slightly larger; two complete anterior and three complete posterior labial tooth rows, equal in length (P1 row a little shorter in some); jaw

sheaths moderately massive, with degree of keratinisation greater on upper sheath; central notch on upper sheath; in some individuals there is a small underlying keratinised ledge visible, similar to that shown in Fig. 6B for *L. booroolongensis* but less prominent, and absent or worn in others; inner margins of jaw sheaths serrated.

Colour of preserved larvae (composite description stages 31-41): body colour uniform brown over abdomen, cranial, vertebral and post-natial regions, lighter elsewhere; dermal body wall clear, sparsely flecked with small clusters of melanophores in some specimens; some brown patches over tail musculature (dorsal view); abdomen opaque, fine layer of melanophores over gill region, patchy in some specimens, becoming sparser over snout; iris black; fins mostly clear, venation unpigmented but visible (lateral view); fine layer of melanophores around sides of abdomen, intestine visible, rest of venter clear; limbs and tail musculature unpigmented (ventral view).

Metamorphosis

Litoria booroolongensis

Eggs laid on 3.xi.1973 were first metamorphosing from 18.i.1974, after a larval life span of 2½ months. Some were still metamorphosing by 13.ii.1974. Numerous metamorphs were observed annually in December/January at Back Creek and Serpentine Creek during 1965-74. No tadpoles or metamorphs were observed in late autumn at Back Creek on 16.v.1973. Ten newly metamorphosed frogs from Serpentine Creek (stage 46, 1974) ranged from 14.0 - 17.5 mm (mean 15.23).

Litoria lesueuri

Known observation dates for metamorphosis are 7 April 1974 at Coco Creek (locality 5 Fig. 1B, 33° 08' 15" S, 150° 06' 40" E) and 18 January 1977 at Dingo Creek (locality 7 Fig. 1B, 31° 49' 50" S, 152° 18' 00" E). Larval life span is not known. Seven newly metamorphosed frogs (stage 46) from Dingo Creek ranged from 11.7 - 15.0 mm (mean 13.54).

Discussion

Population declines, habitat

While the present known distribution for *Litoria booroolongensis* along the mountain range country in NSW is from the Queensland border to the Victorian border, the distribution and status of *Litoria lesueuri* needs clarification, with a likelihood of two or more species being involved (Moore 1961). Heatwole *et al.* (1995) report *L. booroolongensis* as "widespread" in the New England region but the records they provide are only those of existing Museum specimens spanning "a period from early 20th century to 1990". Furthermore, extensive surveys for regional conservation planning in north-eastern NSW undertaken since 1991 through the eastern escarpment forests around Tenterfield, Armidale and Glen Innes by NSW National Parks & Wildlife Service (NP&WS), have failed to locate this species (H. Hines, Queensland Department of Environment & Heritage pers. comm. 1997). Field observations at Guy Fawkes River and nearby well-known localities where the species was similarly abundant prior to 1980, have indicated few adults over the past 17 years. The species could not be found in recent surveys at Ebor (type locality) and a large number of rivers in the area (M. Mahony, University of Newcastle pers. comm. 1997). Intensive searches during 1995-96 in this area were also to no avail (K. Harris, University of New England pers. comm. 1997).

Surveys since 1992 in upland forests such as Glen Innes, Walcha, Mt Royal, Dorrigo, Tenterfield, Coolah Tops and south to Tumut/Tumbarumba (targeting frogs in areas where *L. booroolongensis* is likely to occur), also resulted in none of this species being found (F. Lemckert, State Forests NSW pers. comm. 1997).

Surveys in the southern region near Tumut NSW by Hunter & Gillespie (unpub.) located only 13 frogs on 30 November 1996, along an 800 m stretch of the Goobarragandra River. Extensive searches along the Tumut River, where *L. booroolongensis* had been recorded in the 1960s and in 1987 failed to locate any evidence of the species (Hunter & Gillespie unpub.).

Examination of over 1,000 specimens of *L. booroolongensis* in the Australian Museum revealed that only five specimens have been collected since 1980; one at Wombeyan Caves (34° 19' S, 149° 59' E), two at Canimbula, Blue Mountains (33° 41' S, 150° 12' E), one at Cox River (33° 28' S, 150° 04' E) and one at the Abercrombie River, Governors Flat (34° 03' S, 149° 31' E), where *L. lesueuri* are sympatric (K. Small, Sydney University pers. comm. 1997). Accordingly, the species has been nominated for inclusion in Part 1 of Schedule 1 (Endangered Species) of the Threatened Species Conservation Act 1995 (TSC).

More studies on current population numbers of *L. booroolongensis* over a much broader range of its distribution are required to assess further the current status of this species, in the light of very significant frog declines in the northern ranges between latitudes 31° 30' S and 29° 30' S (north of the Macdonald River - Fig. 1A). From present indications, the species appears to have disappeared at the very least from its type locality and all known localities in the Armidale/Guyra/Point Lookout

regions where it once was abundant. The only known northern area where adults have been observed is locality 3 (Fig. 1A) near Tamworth (1994) in streams at an altitude of 450–500 m (M. Mahony, University of Newcastle pers. comm. 1997), much lower than the Armidale/Point Lookout region. Further field surveys will need to be undertaken to verify the frog's continued existence here, but if so, this may relate to the data being gathered on frogs in north Queensland which indicate that most declines are amongst upland riparian species above 400 m (Richards *et al.* 1993).

Some observations in southernmost localities near Tumut in 1996 also indicate a distinct drop in frog sightings (Hunter & Gillespie unpub.), suggesting the species is likely to be endangered throughout its general distribution.

Litoria lesueuri

This species has a broader current distribution than *L. booroolongensis*. Barker *et al.* (1995) indicate that at least two species are currently included under *L. lesueuri*, "one confined to northeastern Queensland and the other extending down the coast as far as Victoria."

Comparative population studies on *L. lesueuri* are needed, especially where the ranges of the two species overlap, to determine whether this species is also undergoing a decline in certain localities. Surveys by Hunter & Gillespie in 1996 in Kosciusko National Park NSW showed that the species was present in only 15 out of 40 likely streams, which may indicate a possible decline. While *L. booroolongensis* is restricted to flowing streams generally above about 400 m, *L. lesueuri* can breed in streams, streamside pools and even dams from 1100 m (River Murray and Snowy River, Mt Kosciusko NSW) to 40 m (Ourimbah NSW). This greater versatility of altitude and breeding site selection may have helped more populations remain than for *L. booroolongensis*.

Behaviour

Neither *L. booroolongensis* nor *L. lesueuri* has a vocal sac and each produces a soft, low call of a series of short, repeated notes. Adults are similar morphologically, both breed in association with flowing streams, and have a similar tadpole which is adapted to the lotic environment.

Litoria booroolongensis aggregates under stones in large number during winter. A group of 10 individuals was found under the same stone beside Isaacs Creek NSW (locality 4 Fig. 1A, 31° 41'-40" S. 151° 07' 20" E) on 12.vii.1970, by F. Parker. Populations here were large, with a total of 150 frogs of all size classes observed on 19.vii.1970 during the day, under stones in the creek bed. Males called during the day and night. The aggregation of *L. booroolongensis* under rocks both during colder months and also in the breeding season during spring/summer, has not been reported for other Australian hylid species. Winter aggregation has been reported for *Litoria subglandulosa* (Tyler & Anstis, 1983) (Tyler & Anstis 1975) and for *L. pearsoniana* (Copland, 1960) (McDonald & Davies 1990), but neither species has the same habit of commonly gathering in groups under rocks in the stream environment during its breeding season. *Litoria lesueuri* adults, found on ridge-tops in forest away from the stream during winter, are not known to aggregate. *Litoria booroolongensis* is similar to the stream-dwelling *L. spenceri* (Spencer, 1901) (Watson *et al.* 1991) in its diurnal behaviour, often basking in the sun on very warm rocks in mid-stream. Amplexus and oviposition also occurred diurnally in one observation for *L. booroolongensis*. *Litoria lesueuri* has been observed basking in sun, but not as frequently as has been observed for *L. spenceri* or *L. booroolongensis*.

Oviposition/embryos

The egg mass of *L. booroolongensis* found partly adhering to suspended vegetation in a plastic bag does not give a true indication of the mode of deposition in the natural environment, as the adults had separated and were swimming vigorously within the bag, constantly disturbing the egg mass. Barker *et al.* (1995) reported that the egg mass of *L. booroolongensis* is deposited "among rocks".

While the northeastern Queensland form of *L. lesueuri* lays eggs in a single clump of two or more layers deposited in circular nests excavated in sand at the sides of flowing streams (Richards & Alford 1992), egg masses are also deposited among rocks in streams where the substrate is not sand. The number of eggs in one clutch was estimated by Richards & Alford to be 1200. Two other clutches counted by S. Richards and M.A. at Elphinstone Creek north-Qld on 31.vii.1996, numbered 1,738 and 1,674, respectively. Referring to southern populations, Barker *et al.* (1995) state that several hundred eggs are deposited in a solid gelatinous clump which adheres to submerged rocks or the bottom sediments. We have seen 2-3 masses laid beside each other, partly connected.

Whilst egg deposition sites of the north Queensland form of *L. lesueuri* may be excavated nests in sand bars, eggs of the southern form have only been observed in rocky areas where such excavation is not possible. As frogs have been observed around dams (e.g. at locality 2 Fig. 1B) where no rocks were present, and tadpoles found in sandy streams (localities 1, 3, 5, 10 Fig. 1B), further study of the mode of deposition in the southern form

is needed to determine whether or not nest excavation may occur at suitable sites. The mean egg complement of *L. lesueuri* was greater than in *L. booroolongensis*. Both species have a compact, gelatinous egg mass similar in form to that of other stream-breeding hylid frogs such as *L. pearsoniana* (McDonald & Davies 1990), *L. subglandulosa* (Anstis & Littlejohn 1996), *L. genimaculata* (Horst, 1883) (as *L. eucnemis*, Davies 1989), and *L. spenceri* [1]. The egg mass of *L. lesueuri* is loosely attached to the substrate, while those of *L. subglandulosa*, *L. spenceri* and *L. pearsoniana* adhere more strongly.

Larvae

Although larvae of both species are the same size at any given stage (Fig. 3) and appear superficially similar, they differ considerably in shape. The tadpole of *L. booroolongensis* has a relatively larger, wider oral disc and broader, more elongated, streamlined snout than *L. lesueuri* (Table 1, Figs 4,5). The distances from the tip of the snout to the anterior rim of the eye and to the anterior rim of the naris are relatively greater in *L. booroolongensis* and the body depth, dorsal fin depth and eye diameter are less. The eyes are positioned more medially and directed a little more dorsally. The presence of the small keratinised ledge underneath the central notch of the upper jaw sheath was noted in populations of both species, but not found as consistently nor as prominently in *L. lesueuri*. This feature has not been recorded for larvae of any other Australian frogs. The jaw sheaths are commonly more heavily keratinised in *L. booroolongensis*, but this feature may be variable amongst populations, as has been observed in *L. lesueuri*, and in northern and southern populations of the tadpole of *L. verreauxi* (Duméril, 1853) (Anstis 1976).

[1] Marantelli, G., Gillespie, G. & Pickering, S. (1996) Observations on oviposition sites of the spotted tree frog *Litoria spenceri*. "In the Spotlight" **2**: 12-14.

Acknowledgments

The Australian Museum is acknowledged for the loan of specimens. A grant to M.A. from the Peter Rankin Trust Fund in 1996 has assisted this study, and is gratefully acknowledged. Valuable observations on population declines of *L. booroolongensis* were provided by H. Hines, P. Webber, K. Harris, M. Mahony, F. Lemckert, J. Reesel, K. Thumm and K. Small. Constructive comments on the manuscript were given by S. Richards, F. Parker, M. Mahony, G. Watson and M. Davies.

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TRANSACTIONS OF THE

ROYAL SOCIETY OF SOUTH AUSTRALIA

INCORPORATED

VOL. 122, PART 2

A NEW GENUS AND TWO NEW SPECIES OF GALL MIDGE (DIPTERA: CECIDOMYIIDAE) DAMAGING YOUNG BRANCHES OF EUCALYPTUS SPP. IN SOUTH AUSTRALIA

*By Peter Kolesik**

Summary

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Two new gall midges are described from galls on young branches of two Eucalyptus species in South Australia and a new genus, Okriomyia, is described to contain them. The new genus belongs to the tribe Asphondyliini and the subtribe Schizomyiina. It differs from other Schizomyiina in the shape of the aedeagus, the solid tooth of the gonostylus and the cerci-like female tenth tergite. Okriomyia schwarzi gen. et. sp. nov. was found on Eucalyptus gracilis and O. flabellidentata sp. nov. on E. cosmophylla. Infested branches fracture at the site of the gall as the trees mature. Males, pupae, and larvae of both species and the female of O. schwarzi are described. The new species differ from each other in the morphology of the male genitalia, the pupal face, and the pupal prothoracic spiracle. A key to the Australian genera of the tribe Asphondyliini is given.

Key Words: Gall midge, Cecidomyiidae, Okriomyia schwarzi, Okriomyia flabellidentata, Eucalyptus gracilis, Eucalyptus cosmophylla, South Australia.

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KEY WORDS: Gall midge, Cecidomyiidae, *Okriomyia schwarzi*, *Okriomyia flabellidentata*, *Eucalyptus gracilis*, *Eucalyptus cosmophylla*, South Australia.

Introduction

Eucalyptus, the dominant genus of most Australian woodlands and forests, hosts a whole suite of gall-forming insects, many of them undescribed. The present paper describes two gall midges, new to science, which were found damaging young branches of two eucalypts in South Australia. Galls of *Okriomyia schwarzi* sp. nov. on *Eucalyptus gracilis* F. Muell. (Fig. 1) were found at two localities: Nadda, in the southern part of South Australia near the Victorian border and Forestville, a suburb south-west of Adelaide. Galls of *O. flabellidentata* sp. nov. on *E. cosmophylla* F. Muell. (Fig. 2) were found at Cleland Conservation Park, near Adelaide. The newly-described gall midges were found only in moderate abundance. However, heavy infestations could have the potential to impact seriously on the population dynamics of their hosts, since the infested branches fracture at the site of the galls as the trees mature.

Eucalyptus gracilis is a 3 - 12 m high shrub or tree distributed through the mallee belt of continental southern Australia. It is an arid zone species useful for firewood and erosion control and is highly regarded for honey production (Cunningham *et al.* 1981; Chippendale 1988). It is often used in urban planting.

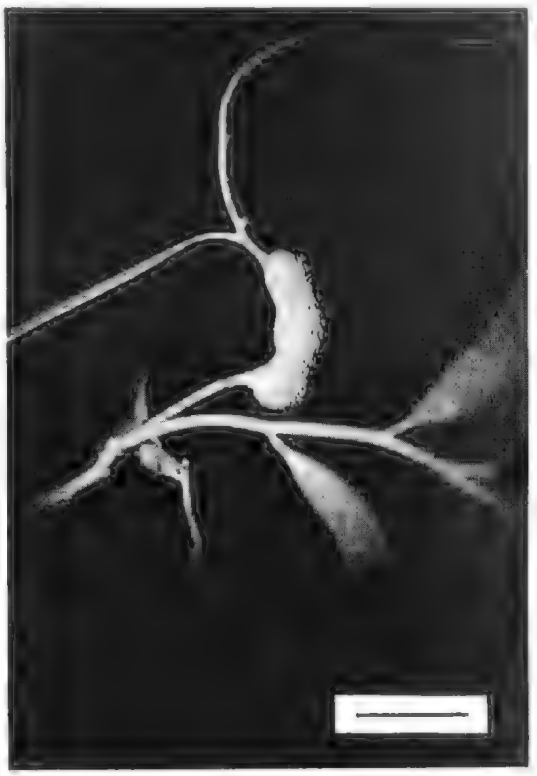

Fig. 1. Gall of *Okriomyia schwarzi* sp. nov. on young branch of *Eucalyptus gracilis*. Scale bar = 20 mm.

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Fig. 2. Gall of *Okriomyia flabellidentana* sp. nov. on young branch of *Eucalyptus cosmophylla*. Scale bar = 20 mm

Eucalyptus cosmophylla is a South Australian shrub or tree, usually 5 - 10 m high, that occurs from the Mount Lofty Range to the Fleurieu Peninsula and Kangaroo Island in open shrubland, low, open forest and heathland near the sea (Chippendale 1988). It is widely used in urban planting.

The new gall midges do not resemble any known genus so a new genus has been erected for them. *Okriomyia* becomes Australia's fourth known genus of the tribe Asphondyliini and the third of Schizomyiina, a subtribe consisting exclusively of genera endemic to Australia. A key to the Australian genera of Asphondyliini is given in the present paper.

Material and Methods

Galls on branches of *Eucalyptus gracilis* were collected at Forestville (19.ii.1993) and Nadda (12.vi.1996). Two, one, three, four and one galls from branches of *E. cosmophylla* were collected at Cleland and Morialta Conservation Parks 27.xi.1992, 23.i.1993, 5. and 12.iii.1995, and 23.ii.1997, respectively. In the laboratory the galls were cut open and the larvae processed in two ways. A small number was preserved in 70% ethanol. A larger number was transferred into rearing pots where the larvae dug themselves into wet sand. Pupation took place in the sand. Several males and females emerged from the galls from *E. gracilis*. Of the galls collected from *E. cosmophylla* adults emerged only from the sample collected on 23.ii.1997 - 12 males and no females. Emerged adults were preserved together with their pupal skins in 70% ethanol. Microscope mounts of the type series were prepared according to the technique outlined by Kolesik (1995a). The type series and other material retained in 70% ethanol, together with dried galls, are deposited in the South Australian Museum, Adelaide [SAMA], the Australian National Insect Collection, Canberra [ANIC] and the State Herbarium of South Australia, Adelaide [SHSA]. Descriptions and measurements refer to the holotypes and paratypes. Terminology of adult morphology follows that of Gagné (1981); larval terminology follows that of Gagne (1989).

Genus *Okriomyia* gen. nov.

Type species: *Okriomyia schwarzi* sp. nov.

Adults

Head. Eye facets hexagonoid, eye bridge 6 - 8 facets long medially. Antenna with 12 flagellomeres, distal ones not shortened. Flagellomeres cylindrical, sessile, first and second not fused, with short setae and bearing low, finely reticulate circumfila. Scape as long as wide, pedicel half as long as wide. Labella hemispherical, each with several setae. Palpus with 4 segments.

Thorax. Wings: R_{5} joining C at apex, slightly bowed anteriorly, Rs absent, R_{1} joining C near mid-length, Cu forked. First tarsomere lacking ventro-distal spine, tarsal claws simple, as long as empodia.

Abdomen. Tergites 1 - 8 with setae evenly distributed, forming dense row posteriorly. Sternum 1 not sclerotized, asetose; sternites 2 - 8 with setae in two separate areas: wide, anterior field and narrow, posterior band. Female abdominal sternite 7 1.5 x sternite 6. Male terminalia: gonocoxite with apico-ventral lobe; gonostylus short and wide, with tooth in form of serrate plate no more strongly pigmented than remainder; cercus bilobed, deeply divided medially, emarginated posteriorly, with several posterior setae; parameres small, setose; hypoproct with posterior margin concave, each lateral lobe with 1 - 2 apical setae; aedeagus comprising two parts: dorsal part robust, conical, ventrally covered with sclerotized villi on apical third, ventral part smooth, thin in lateral view, shallowly emarginated apically in dorso-ventral view, asetose. Female terminalia: ovipositor short, fleshy; tergum 9 and sternum 9 sclerotized; tergum 10 in form of two large, cerci-

like lobes, more sclerotized anteriorly, evenly setose; cerci large, discrete, more sclerotized posteriorly, evenly setose; hypoproct small, bilobed, each lobe with apical seta.

Pupa

Antennal horns strongly pigmented; cephalic swellings, facial protuberances, prothoracic spiracle, dorsal spines of abdomen slightly pigmented; abdominal skin not pigmented. Antennal horns blunt on anterior surface, produced antero-ventrally into an acute ridge. Cephalic sclerite with pair of swellings shorter than antennal horns. Cephalic pair of papillae with long setae. Frons with one or two sclerotized protuberances on each side, one of two lower facial papillae with seta, one of three lateral papillae with seta. Abdominal segments 1 - 7 with pair of setose ventral papillae, 2 pairs of setose pleural papillae, 2 pairs of asetose and pair of setose dorsal papillae. Abdominal segment 8 with pair of ventral papillae, 2 pairs of pleural papillae, pair of dorsal papillae, all setose. Abdominal segments 2 - 8 dorsally with field of strong, one- or two-pointed spines on anterior half.

Larva

Integument covered with tiny, sparse spicules. Head: strongly sclerotized, postero-lateral apodemes longer than head capsule, antennae 2 x longer than basal width. Neck segment with pair of dorsal papillae. Thoracic segments with pair of ventral papillae, 2 pairs of pleural papillae, pair of sternal papillae, 3 pairs of lateral papillae, 2 pairs of dorsal papillae. Spatula bilobed, with shaft. Abdominal segments 1 - 7 with pair of ventral papillae, 2 pairs of pleural papillae, 3 pairs of dorsal papillae. Abdominal segment 8 with pair of ventral papillae, 2 pairs of pleural papillae, pair of dorsal papillae. Terminal segment with pair of anal papillae on short lobes, pair of terminal papillae on prolonged lobes. All papillae asetose.

Etymology

The prefix "Okrio-" is from the Greek *okrios*, meaning roughness, referring to the jagged ventral surface of the aedeagus and distinguishing the new genus from other Schizomyiina. The suffix "-myia" is Greek for fly.

Remarks

Okriomyia gen. nov. belongs to the tribe Asphondyliini on the basis of the following shared apomorphies: the presence of a ventro-apical lobe on the gonocoxite with gonostylus consequently situated dorso-ventrally; the short, quadrate gonostylus, the presence of parameres; and the large female sternite 7 that is 1.5 x as long as sternite 6. The new genus belongs to the subtribe Schizomyiina because it lacks a ventro-apical spine on the first tarsomere, has male parameres, has a short, fleshy ovipositor and the pupal integument is unpigmented. The new genus is unique among the Schizomyiina because of the divided aedeagus, the solid tooth on the gonostylus and the cerci-like female tergum 10. The Australian genus, *Eucinctiformia* Felt, the only other genus associated with galls on *Eucalyptus* spp. (Kolesik 1995a), most closely resembles *Okriomyia* gen. nov. *Okriomyia* shares with *Eucinctiformia* the long lobes on the terminal larval segment and the fleshy ovipositor with divided cerci, which represents the most plesiomorphic ovipositor in Asphondyliini.

The tribe Asphondyliini is known in Australia from 12 species distributed among four genera. *Asphondylia* Loew, a large, cosmopolitan genus, belonging to the subtribe Asphondyliina, contains seven species: *A. anthocercoides* Kolesik (Kolesik *et al.* 1997), *A. dodonaeae* Kolesik (1995c), *A. eucaformis* Kolesik (1997), *A. lilli* Edwards (1916), *A. inflata* Kolesik (1997); *A. loewi* Skuse (1888) and *A. rubicunda* Skuse (1888). The other three genera, all belonging to the subtribe Schizomyiina, are known only from Australia and contain five species: *Eucinctiformia australasiae* Felt (1915), *E. malarski* Kolesik (1995a), *Skusemyia allocasuarinae* Kolesik (1995b) and the new species, *Okriomyia schwarzi* and *O. flabellidentata*.

Key to Australian genera of Asphondyliini

1. First tarsomere with spur; male parameres absent; female with pair of dorsal lobes at base of needle-like ovipositor; pupal skin completely pigmented ..... *Asphondylia*
   First tarsomere without spur; male paramere present; female without pair of dorsal lobes at base of ovipositor or ovipositor not needle-like; pupal skin not pigmented on at least abdomen 2

2. Have terminal female flagellomeres successively and progressively shorter; ovipositor needle-like; male parameres large, as wide as posterior lobes of cerci; pupal cephalic swellings longer than antennal horns ..... *Skusemyia*
   Three terminal female flagellomeres subequal in length; ovipositor short, fleshy, with unfused cerci; male parameres small, much narrower than posterior lobes of cerci; pupal cephalic swellings shorter than antennal horns 3

3. Tooth on gonostylus consisting of several separate teeth; female with pair of small dorsal lobes posterior to eighth tergite; largest dorsal spines on pupa serrated apically ..... *Eucinctiformia*
   Tooth on gonostylus solid, in form of a plate; female without pair of dorsal lobes posterior to eighth tergite; dorsal spines on pupa one- or two-pointed ..... *Okriomyia*

Okriomyia schwarzi sp. nov.
(FIGS 1, 3-6, 10-23, 27-30)

Holotype: ♂, Nadda, South Australia [34° 37' S, 140° 53' E], 13.viii.1996, reared by P. Kolesik from branch gall on *Eucalyptus gracilis* F. Muell., larva collected 12.vii.1996 by J. Schwarz, 121338 [SAMA].
Paratypes: 2 ♂♂, 3 ♀♀, 4 pupal skins [SAMA, 121339-121347], 2 ♂♂, 2 ♀♀, 3 pupal skins [ANIC], same data but emerged 12.-20.viii.1996; 3 larvae [SAMA, 121348-121350], 2 larvae [ANIC], collected with holotype

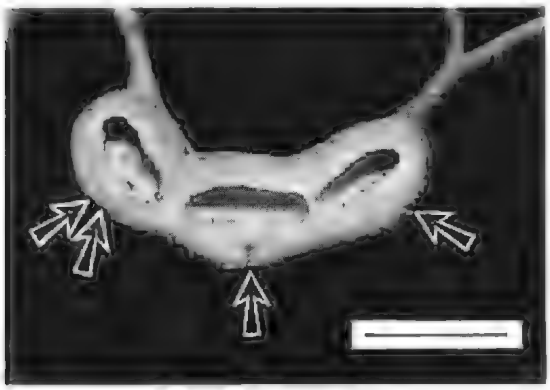


Fig. 3. Gall of *Okriomyia schwarzi* sp. nov. on *Eucalyptus gracilis* - longitudinal section. Arrows mark larval exit holes. Scale bar = 10 mm.

Other material [SAMA]: 4 ♂♂, 24 ♀♀, 23 pupal skins, 3 pupae, same data; 17 larvae, gall, collected with holotype; 2 ♀♀, 2 pupal skins, Forestville, South Australia [34°56' S, 138°36' E], 23.vii.1993, P. Kolesik, reared from branch galls on *E. gracilis*, larvae collected 19.ii.1993; 4 galls, collected with holotype [SHSA].

Description
Male (Figs 4-6, 10-15)
Colour: antennae grey; head black; thorax brown; legs yellow; abdomen with sclerotized parts and setae black, non-sclerotized parts orange. Wing length 2.2 mm (1.9 - 2.5). Genitalia: gonocoxite covered with short setae, with 2 short, thin, posterior, dorso-medial lobes; apico-ventral lobe on gonocoxite long, aciculate; tooth on gonostylus narrow, finely serrated; aedeagus narrow distally in lateral view; hypoproct with large lobes, as long as aedeagus.

Female (Figs 16-20)
Wing length 3.0 mm (2.8 - 3.3). Circumfila on flagellomeres about half density of male ones. Abdominal sternite 7 1.5 x (1.3 -1.6) longer than sternite 6. Setae on cerci 2 x shorter and much denser than on tergite 10. Ovipositor as long as tergites 7 and 8 together. Colour as in male.

Pupa (Figs 21-23)
Colour: Antennal horns brown, cephalic swellings, facial protuberances, prothoracic spiracle, dorsal spines pale brown, abdominal skin grey. Total length 4.3 mm (3.8 - 4.6). Antennal horns 86 µm (77 - 109) long. Cephalic setae 161 µm (138 - 181) long. Cephalic swellings 46 µm (36 - 65) long. Upper face with 2 pairs of sclerotized protuberances, inner pair 51 µm (48 - 54) long, outer pair 30 µm (29 – 38). Setae on lower facial papillae 122 µm (103- 143) long. Prothoracic spiracle with slight, gradual curve, 244 µm (206 - 267) long, trachea ending at apex.

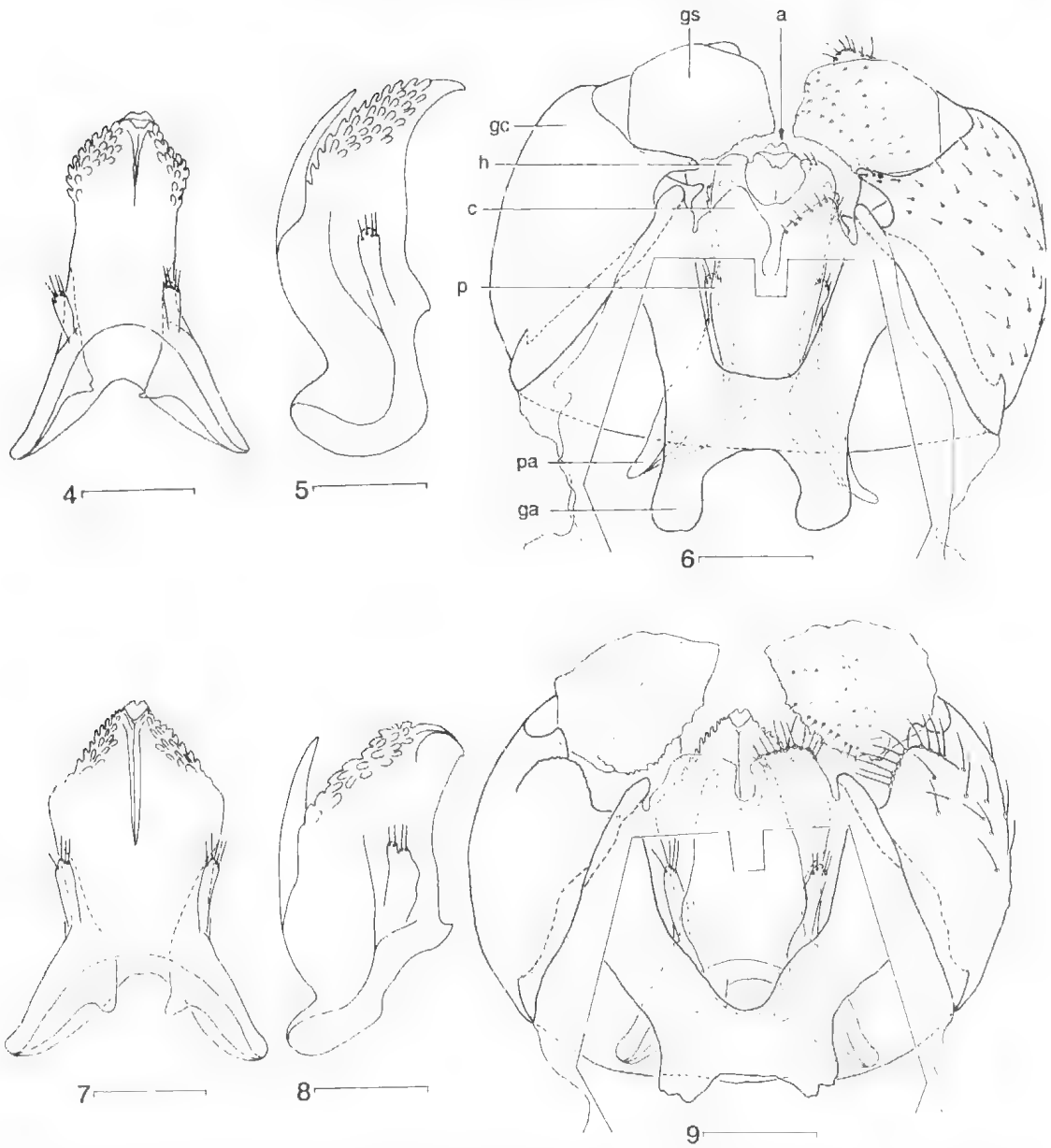
Larva (Figs 27-30)
Colour: pink to orange. Total length 5.9 mm (4.3 - 7.8). Head capsule width at base 92 µm (90 - 94), length 70 µm (63 - 74), length of postero-lateral apodemes 116 µm (110 - 127). Antenna 26 µm (25 - 27) long. Sternal spatula 445 µm (361 - 543) long, with apical enlargement 100 µm (83 - 130) wide, depth of incision 46 µm (29 - 68). Terminal lobes 160 µm (113 - 233) long.

Etymology
The species is named after the collector of the larval stage of the type specimens, Julie Schwarz, Department of Plant Science, University of Adelaide.

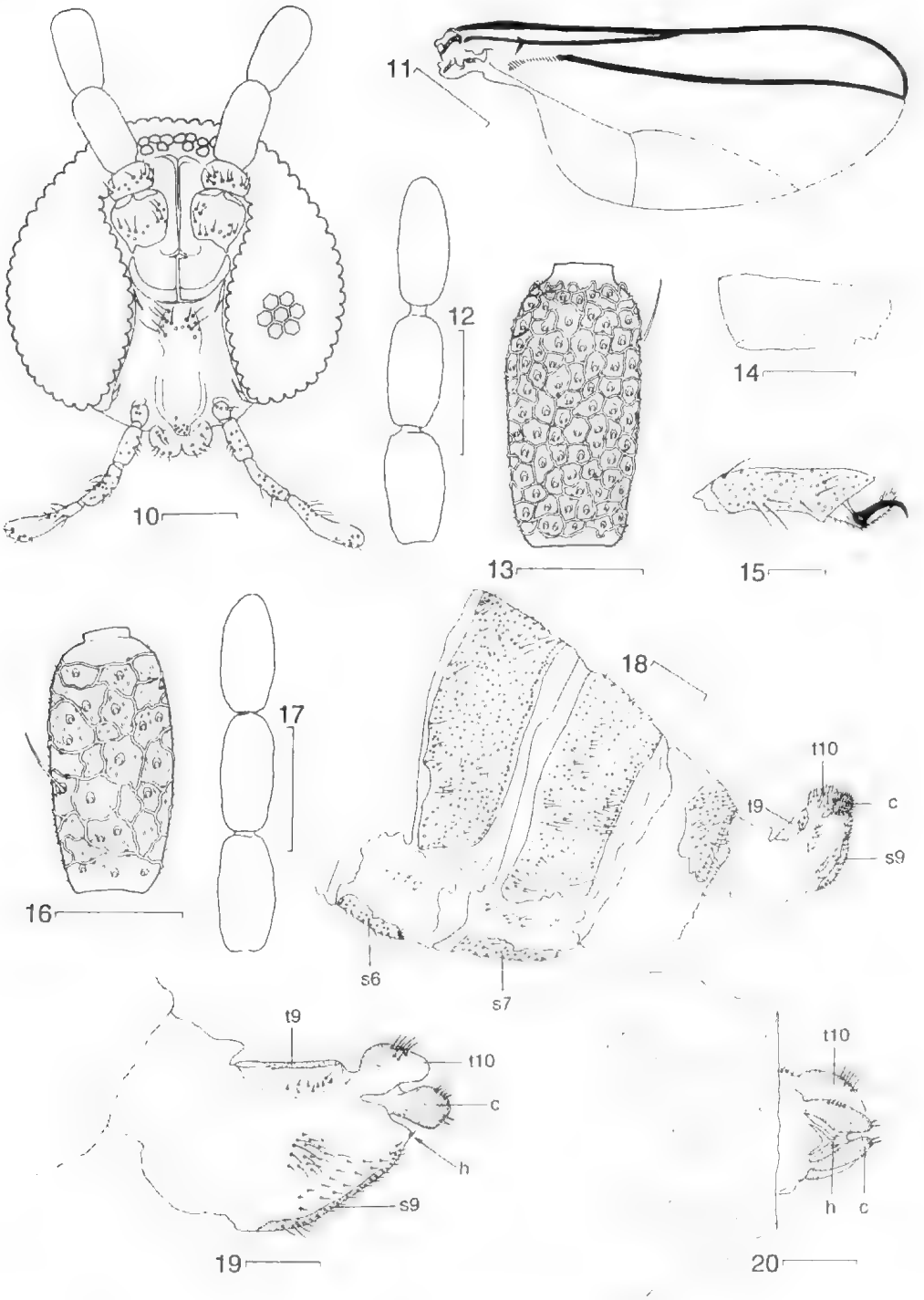
Gall and biology
Young branches of *Eucalyptus gracilis* are swollen to form galls 8 - 20 mm in length and 7 - 9 mm in diameter, with outer walls 1 - 3 mm thick (Fig. 1). The gall outer surface is scabrous, reddish brown in colour. Inside there are 1 - 5 ovoid chambers, each occupied by 1 - 13 larvae. Larval colour may vary from pink to orange between chambers of the same gall but is the same within a chamber. No association between the colour and the age of larvae was apparent. Gall walls contain less woody tissue than unaffected parts of the branch, which results in the gall being springy to the touch and crunchy when cut with a knife. This characteristic is shared with galls of *O. flabellidentata*. When the larvae are fully grown, they leave the galls through one or two circular openings that develop in each chamber (Fig. 3). Pupation takes place in the soil.

Okriomyia flabellidentata sp. nov.
(FIGS 2, 7-9, 24-26, 31-34)

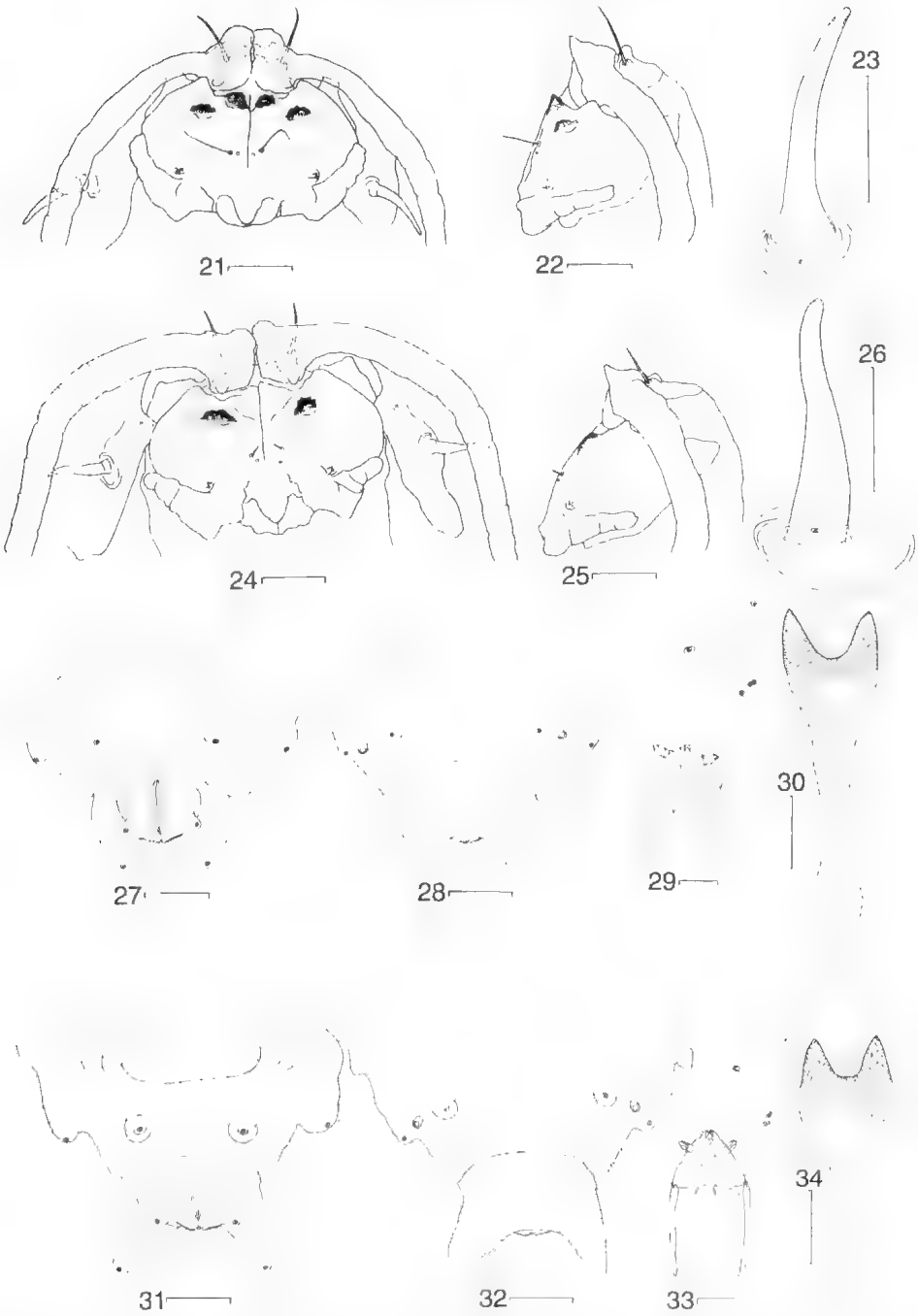
Holotype: ♂, Cleland Conservation Park, South Australia [34° 58' S, 138° 42' E], 15.iii.1997, P. Kolesik, reared from branch gall on *Eucalyptus*



Figs 4-6. Male of *Okriomyia schwarzi* sp. nov. Fig. 4. Aedeagus in frontal view. Fig. 5. Aedeagus in lateral view. Fig. 6. Genitalia in dorsal view (inner part of cerci diagrammatically cut out for better clarity). Figs 7-9. Male of *Okriomyia flabellidentata* sp. nov. Fig. 7. Aedeagus in frontal view. Fig. 8. Aedeagus in lateral view. Fig. 8. Genitalia in dorsal view (inner part of cerci diagrammatically cut out). Scale bars = 100 µm. Abbrev.: a, aedeagus; c, cercus; ga, gonocoxal apodeme; gc, gonocoxite; gs, gonostylus; h, hypoproct; p, paramere; pa, parameral apodeme.



Figs 10-20. *Oktomyia schwarzi* sp. nov. 10-15 male, 16-20 female. Fig. 10. Head in frontal view. Fig. 11. Wing. Fig. 12. Last three flagellomeres. Fig. 13. Sixth flagellomere. Fig. 14. First tarsomere. Fig. 15. Last tarsomere with claw and empodium. Fig. 16. Sixth flagellomere. Fig. 17. Last three flagellomeres. Fig. 18. End of abdomen in lateral view. Fig. 19. Ovipositor in lateral view. Fig. 20. Ovipositor in ventral view. Scale bars = 100 µm 10, 12, 17, 19, 20; 500 µm 11; 50 µm 13-16; 200 µm 18. Abbrev.: c, cercus; h, hypoproct; s, sternite; t, tergite.



Figs 21-23. Pupa of *Okriomyia schwarzi* sp. nov. Fig. 21. Anterior part in dorsal view. Fig. 22. Anterior part in lateral view. Fig. 23. Prothoracic spiracle. Figs 24-26. Pupa of *Okriomyia flabellidentata* sp. nov. Fig. 24. Anterior part in dorsal view. Fig. 25. Anterior part in lateral view. Fig. 26. Prothoracic spiracle. Figs 27-30. Larva of *Okriomyia schwarzi* sp. nov. Fig. 27. Eighth and terminal abdominal segments in ventral view. Fig. 28. Eighth and terminal abdominal segments in dorsal view. Fig. 29. Head in ventral view. Fig. 30. Spatula with adjacent papillae. Figs 31-34. Larva of *Okriomyia flabellidentata* sp. nov. Fig. 31. Eighth and terminal abdominal segments in ventral view. Fig. 32. Eighth and terminal abdominal segments in dorsal view. Fig. 33. Head in ventral view. Fig. 34. Spatula with adjacent papillae. Scale bars = 200 µm 21, 22, 24, 25, 27, 28, 31, 32; 100 µm 23, 26, 30, 34; 50 µm 29, 33.

cosmophylla F. Muell., larva collected 23.ii.1997, I21351 [SAMA].

Paratypes: 2 ♂♂, 3 pupal skins [SAMA, I21352-I21356], 2 ♂♂, 3 pupal skins [ANIC], same data but emerged 15.-17.iii.1997; 3 larvae [SAMA, I21357-I21359], 2 larvae [ANIC], collected with holotype.

Other material [SAMA]: (all collected from branch galls on *E. cosmophylla* by P. Kolesik): 7 ♂♂, 4 pupal skins, same data but emerged 1.-14.iv.1997; 12 larvae, gall collected with holotype; 3 larvae, Morialta Conservation Park [34° 54' S, 138° 44' E], 27.xi.1992; 9 larvae, Cleland Conservation Park, 5. & 12.iii.1995; gall, Cleland Conservation Park, 23.i.1993 [SHSA].

Description

Male (Figs 7-9)

Colour: as in *O. schwarzi*. Wing length 2.9 mm (2.7 – 3.0). Genitalia: gonocoxite covered with long setae, with two short, postero-dorsal lobes, one thin, one wide; apico-ventral lobe on gonocoxite short, rounded; tooth on gonostylus wide, coarsely serrated; aedeagus wide distally in lateral view; hypoproct with thin lobes, much shorter than aedeagus.

Female

Unknown

Pupa (Figs 24-26)

Total length 3.9 mm (3.7 - 4.1). Antennal horns 82 µm (51 - 115) long. Cephalic setae 147 µm (137 - 165) long. Cephalic swellings 25 µm (20 - 29) long. Upper face with pair of sclerotized protuberances, 31 µm (25 - 38) long. Setae on lower facial papillae 38 µm (32 - 45) long. Prothoracic spiracle bowed at distal third, 190 µm (174 - 209) long, trachea ending at apex. Otherwise as in *O. schwarzi*.

Larva (Figs 31-34)

Colour: pink to orange. Total length 4.4 mm (3.7 - 5.0). Head capsule width at base 99 µm (95 - 102), length 76 µm (69 - 81), length of postero-lateral apodemes 125 µm (100 - 141). Antenna 24 µm (24 - 25) long. Sternal spatula 425 µm (398 - 475) long, with apical enlargement 127 µm (108 - 154) wide, depth of incision 54 µm (50 - 59). Terminal lobes 148 µm (121 - 160) long.

Etymology

The name "flabellidentata" is a compound Latin adjective from "flabellum", meaning fan, and "dentatus", meaning toothed, refering to the shape of the tooth on the gonostylus.

Gall and biology

Young branches of *Eucalyptus cosmophylla* are swollen to form galls 10 - 70 mm in length and 10 - 15 mm in diameter, with outer walls 2 - 4 mm thick (Fig. 2). The gall outer surface is smooth to scabrous, green to brown in colour. Inside there are 1 - 4 irregularly-shaped chambers, each occupied by 5 - 15 larvae. Pupation takes place in the soil. The galls remain recognisable on the branches for several years after they have been formed. Many branches later fracture at the site of the gall since the gall tissue is less rigid than that of the tree. The same phenomenon was observed in *O. schwarzi*. The galls of *O. flabellidentata* on *E. cosmophylla* are common in the nature conservation parks around Adelaide.

Remarks

The two new species differ from each other in several characters. The males of *Okrimyia schwarzi* have a narrow tooth on the gonostylus, the hypoproct is as long as the aedeagus, the gonocoxite has two thin, posterior lobes dorso-medially, and the apico-ventral lobe on the gonocoxite is aciculate. The males of *O. flabellidentata* have a wide tooth on the gonostylus, the hypoproct is much shorter than the aedeagus, the gonocoxite has no posterior lobes dorso-medially but has one thin and one wide lobe dorsally, and the apico-ventral lobe on the gonocoxite is short and rounded. The pupae of *O. schwarzi* have two pairs of sclerotized protuberances on the upper face, long setae on the lower facial papillae, and an evenly-bent prothoracic spiracle. The pupae of *O. flabellidentata* have one pair of sclerotized protuberances on the upper face, short setae on the lower facial papillae, and a distally bowed prothoracic spiracle.

That as many as 12 males and no females were reared from the one gall on *Eucalyptus cosmophylla* collected 23.iii.1997 suggests that females of *O. flabellidentata* produce unisexual progeny, a phenomenon found in *Contarinia sorghicola* (Coquillett) (Baxendale & Teetes 1981) and *Cystiphora sonchi* (Bremi) (McClay 1996). In order to verify the production of unisexual progeny in *O. flabellidentata*, and perhaps *O. schwarzi*, more adults have to be reared from separate galls. This may require rearing larvae from a larger number of galls as *O. flabellidentata* seems not to be an easily reared species. From some 150 larvae originating from 10 galls included in this work only the 12 males emerged.

Acknowledgments

The Department of Environment and Natural Resources, South Australia kindly permitted collecting in the Cleland and Morialta Conservation Parks. M. C. O'Leary, State Herbarium of South

Australia Adelaide, courteously identified the host plant species. Special thanks go to J. D. Gray, Department of Horticulture, Viticulture and Oenology University of Adelaide and R. J. Gagné, Systematic Entomology Laboratory USDA Washington DC USA, for commenting on an early draft of the mansucript.

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WITHIN-NEST BEHAVIOUR IN A EUSOCIAL AUSTRALIAN ALLODAPINE BEE EXONEURA (EXONEURELLA) TRIDENTATA HOUSTON (APIDAE: XYLOCOPINAE)

By Zeta Steen & Michael P. Schwarz**

Summary

Steen, Z. & Schwarz, M. P. (1998) Within-nest behaviour in a eusocial Australian allodapine bee Exoneura (Exoneurella) tridentata Houston (Apidae: Xylocopinae). Trans. R. Soc. S. Aust. 122(2), 55-63, 29 May, 1998.

Understanding the processes involved in the evolution of social behaviour has become one of the most challenging areas of modern biology. Since bees and wasps exhibit a variety of social organisations they are particularly useful for addressing social evolutionary questions. Allodapine bees are especially useful for examining social evolution, since species display varying forms of social organisation from solitary to eusocial. This study examines within-nest behaviour of Exoneura (Exoneurella) tridentata, a native Australian allodapine bee. This species has the largest known colony sizes of any allodapine bee and exhibits striking size variation among female nestmates suggesting that sociality may be regarded as highly eusocial.

Key Words: Exoneura tridentata, social behaviour, allodapine bees, aggression.

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by ZETA STEEN[1]* & MICHAEL P. SCHWARZ[1]*

Summary

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KEY WORDS. *Exoneura tridentata*, social behaviour, allodapine bees, aggression

Introduction

The allodapine bees provide opportunities for comparative approaches to the evolution of social behaviour because of the wide range of social organisation within and between species and genera. One small and endemic Australian subgenus *Exoneurella*, contains four species that range from the predominantly solitary *Exoneura lawsoni* Rayment (Michener 1965) to the eusocial *E. tridentata* (Houston 1977; Hurst & Schwarz 1996).

In most comparative studies of insect social evolution there is an implicit assumption that small colony size is associated with flexible and behaviourally mediated reproductive skew. The maintenance of dominance hierarchies via physical agonism is considered a primitive trait (Wilson 1971). Correspondingly, large colony sizes with strong reproductive skew and non-agonistically maintained hierarchies are usually regarded as more derived traits. Wilson (1971) suggested that less sophisticated forms of social organisation would involve physical mechanisms of control such as aggression within a colony, but that this is replaced by "gentle despotism" in more advanced forms of sociality. It is also generally assumed that a high level of behavioural specialisation is a more derived trait and that this can lead to higher levels of colony efficiency (Jeanne 1986). However, the idea that different forms of social organisation can be arranged in a sequence of 'primitive' to 'advanced' has been questioned (Kukuk 1995) but few studies have explicitly investigated whether 'primitive' or 'advanced' forms of sociality within taxa correspond to basal or distal positions within phylogenetic trees.

Exoneura tridentata is an Australian allodapine bee that lives in semi-arid environments. This species has the largest known colony sizes of any allodapine bee and exhibits morphological differentiation between putative castes (Houston 1977, Hurst & Schwarz 1996). Much of the information about social organisation has been inferred from dissection of nest occupants and brief observations of females outside of their nests (Houston 1977; Hurst unpub.). It is suspected that this species exhibits caste differentiation, where large females (termed 'Majors') are queen-like and smaller females ('Minors') act as workers within the colonies (Houston 1977; Hurst 1996). However, within-nest behavioural studies have not been carried out to assess whether these two morphs really are behaviourally distinct. Colony size and the association between morphology and reproductive status suggest that this species more closely approaches the highly eusocial form of organisation characteristic of apine, meliponine and highly eusocial halictine bees, than any other allodapine bee.

This study investigates within-nest behaviour in observation colonies of *E. tridentata*. A repertoire of behaviours is presented here in the form of a behavioural catalogue and compared with other behavioural studies of allodapines. These data will also be used for specific analysis of behavioural specialisation, which will appear in a future series of

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publications. In addition, the idea that morphological caste differentiation and large colony size are associated with low levels of agonism in colony integration is discussed in relation to the social organisation of *E. tridentata*.

Materials and Methods

Study sites

Exoneura tridentata nests were collected from Lake Gilles Conservation Park (136 48' E, 32 54' S) located in the north east of Eyre Peninsula, South Australia. In this area, *E. tridentata* nests were principally in disused beetle burrows excavated in *Acacia papyrocarpa* Benth. (Western Myall) and *Halyctryon oleiofolium* (Desf.). (Bullock Bush). Dead branches of both tree species were examined for nest entrances i.e. the exit holes made by the original beetle occupants. Intact colonies were collected during February 1995. Field collection of nests took place when temperatures were cool (12 C-20 C), to ensure that all occupants were present. Once an entrance hole was located, the branch was removed, entrances were blocked with tissue paper, the branch was placed in a waterproof bag and stored in an insulated container with ice for transport to Flinders University.

At Flinders University the nests were stored in a constant temperature room at approximately 10 C for processing. Nests were opened using a knife and all nest occupants, including brood and nest contents such as pollen, were transferred to a Petri dish. Adults were individually marked using Humbrol™ and Testors™ enamel paints applied to the thorax and metasoma. Bee colonies were then transferred to artificial observation nests.

Artificial nests were similar in design to those described by Schwarz & Overholt (1993) but were made of pine wood instead of balsa. Each nest consisted of a rectangular piece of untreated pine wood 210 x 20 x 15 mm. A groove was gouged into one longitudinal face (5 mm diam x 200 mm length). The groove was smoothed out with a metal rod to remove any splinters of wood. A piece of glass, 210 x 20 mm, was placed flush against the groove and secured at both ends with insulation tape. A black cardboard cover was placed over the glass to exclude light between observation periods.

Observation nests were set up on subhorizontal trays in a shade house at Flinders University. One end of the shade house was open so that bees could forage freely outside. Nest entrances faced the open end of the shade house. A maximum of four nests was placed on each tray with approximately 15 cm between each nest. Observation nests were first placed in the shade house at dusk 5-6 days after collection and opening. This ensured that the bees had approximately 12 hours in the artificial nest to allow their odours to permeate the nest before it was possible for them to leave (the next morning). Sticks were haphazardly placed near nests to act as visual cues for returning bees.

Behavioural observations

Once observation nests were set up bees were allowed to adjust to their new environment for one week before observations began. Data collection involved 'scan' and 'focal' sampling techniques (Altman 1974). Scan sampling involved recording the position of each individual in the observation nest, using a 5 mm scale along the glass and was conducted immediately before and after focal sampling. This was done to determine whether certain bees were spending more time than others in certain areas of the nest, for example, near the entrance or near the brood. Focal sampling involved 2 min observations of each bee in a nest. Nests and individuals were randomly selected each day for order of observations. A headband magnifier (x 5.2 magnification) was used to observe the behaviour of individuals. All behaviours performed in a 2 min period for each individual were recorded into a voice operated recorder. Observations were transcribed on to data sheets at a later date. These behavioural data were used to construct the behavioural catalogue and later to examine behavioural specialisation.

Behavioural observations took place in the afternoon, (1300-1700 h), when temperatures were ≥ 20 C and bees were active. In total, 10 nests were observed with up to four nests being observed in any one session. Table 1 provides information about which nests were observed, when they were observed and how many minutes of observation each bee per nest received. In addition, the numbers of bees that were present for the initial and final observation periods are given.

Results

Field-collected nests

The contents of nests collected in February 1995 are summarised in Table 2. During these sampling periods, colonies used for behavioural observations were rearing brood. In early February colonies contained brood of all developmental stages, i.e. eggs, larvae, prepupae and pupae. By late February female bees in the colonies had almost ceased egg laying and brood mostly comprised larvae, prepupae and pupae. There was a great deal of variation in the number of adult females present in a nest, ranging from 1-18 (Fig. 1).

TABLE 1. *Details for nests of* Exoneura tridentata *observed in this study.*

Nest	First observations	Last observations	Total number of observation periods per nest	Total minutes of observation per bee per nest	Initial no. of Individuals	Final no. of Individuals
1	7 Mar.	14 Apr.	15	30	8	5[a]
6	7 Mar.	14 Apr.	15	30	9	5[a]
9	7 Mar.	14 Apr.	15	30	9	12[b]
12	7 Mar.	14 Apr.	15	30	13	15[b]
3	5 Apr.	4 May	19	38	5	5
4	5 Apr	4 May	19	38	4	5[b]
20	5 Apr	4 May	19	38	4	5[c]
30	26 Apr.	16 May	20	40	6	5[a]
43	26 Apr.	16 May	20	40	3	4[b]
56	29 Apr.	16 May	20	40	4	4

Decreases in the number of indivduals were probably due to death whilst foraging or dispersal to other nests[a]. Increases were due to the addition of newly eclosed bees[b], or intruders which swapped nests[c].

TABLE 2. *Summary of nest contents for colonies of* Exoneura tridentata *collected in February 1995 from Lake Gilles, South Australia.*

Nest contents	Mean value (+ S.E.) for early February (N=24)	Mean value (± S.E.) for late February (N=13)
Eggs	1.21 (0.57)	0.08 (0.08)
Larvae	1.75 (0.63)	0.62 (0.27)
Prepupae	0.67 (0.28)	0.31 (0.13)
Pupae	2.42 (0.72)	2.23 (0.70)
Majors	1.17 (0.16)	1.23 (0.34)
Minors	4.17 (0.83)	4.38 (1.30)
Males	0.33 (0.13)	0.38 (0.21)

Behavioural repertoire

In the following section behaviours observed during the study are presented as a behavioural catalogue. Observed behaviours are classified into four functional groups (often inter-connected or overlapping): (i) self maintenance behaviours, (ii) nest maintenance behaviours, (iii) inter-adult behaviours, and (iv) adult-brood interactions.

SELF MAINTENANCE BEHAVIOURS

INACTIVITY

Bees were recorded as being "inactive" when no other behaviour was being performed. Inactivity often occurred within a behavioural sequence. For example, a bee could stop grooming, be inactive for some time, and then travel forward in the nest. Bees could either be standing 'upright' or they could be lying 'upside down' on the floor of the nest. Maeta *et al.* (1992) included slight movements in their description of a similar behaviour, "Resting". However, in this study bees were only recorded as

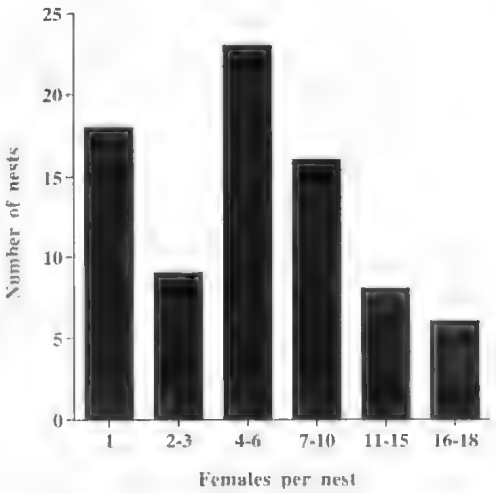

Fig. 1. Histogram of colony sizes (number of females per nest) of *Exoneura tridentata* collected from Lake Gilles South Australia, February 1995

inactive when they were motionless. *Exoneura tridentata* spent a large amount of time inactive. Since inactivity can occur within and between behavioural sequences it is difficult to show numerically the amount of time spent inactive because of the way the data were collected. Generally, though, the bees were more active when temperatures were >20° C and/or when a forager returned.

SELF GROOMING

"Grooming" was observed frequently, and included any activity where the body surface was cleaned. Sequences for cleaning different areas of the body were similar to those reported for *Braunsapis hewitti* Cameron and *Ceratina* spp., (Maeta *et al.* 1992). The most common sequences were: (a) head cleaned by initially wiping a foreleg with the proboscis then foreleg used to wipe the length of the antennae, beginning at the base; foreleg again wiped with the proboscis, followed by the wiping of the head with the forelegs, (b) the metasoma was cleaned by using the tibial spurs on the hindlegs to scrape off dust/pollen, (c) the thorax was cleaned with the mid legs (the metasoma and the thorax were often groomed at the same time with the different legs), (d) the wing surfaces were groomed by dragging the wings under the metasoma with the hind legs, wiping them between the metasoma and hind legs, and then flicking them back into position. Grooming did not occur as one long uninterrupted sequence as has been observed for *B. hewitti* (Maeta *et al.* 1992). Grooming could be brief or last for the whole 2 min observation period.

SLIGHT BODY MOVEMENTS

This was intermittent behaviour which was often observed during long bouts of inactivity, and behaviour comprised slight movements of head, body or legs, which did not involve any other type of behaviour.

TRAVELLING

"Travelling" involved moving forwards or backwards up or down the nest for 1-20 cm. Bees that were travelling were usually very active but the travelling speed varied. Travelling forward often resulted in a bee coming into contact with others and was usually followed by "passing" (see below).

TURNING

"Turning" was used to describe a change of direction in the nest. Turning involved curling the body and somersaulting, resulting in the bee facing the opposite direction. Both Majors and Minors appeared to turn with equal ease. This behaviour occurred anywhere in the nest, unlike that in *Ceratina* spp. which have a turning burrow enlargement near the nest entrance (Maeta *et al.* 1992). Turning often occurred as part of a sequence of behaviours during interactions between individuals, i.e. it could occur during sequences which involved "nudging", "passing" or "avoidance" (see below). If a bee approached but avoided another bee, it might either "travel" up to the bee, and then back away or it might "turn" and "travel" in the opposite direction.

NECTAR DEHYDRATION

Individuals were observed flexing and bending the proboscis and, although droplets of nectar could not be seen with at the magnifications used, it was assumed that they were dehydrating nectar as has been observed in other allodapines after feeding (Michener 1972; Maeta *et al.* 1992). Some bees slowly fully extended and retracted the whole proboscis without bending it. The proboscis was extended and held out for about 20 sec then retracted before being extended again. Some individuals spent the whole two min observation period performing this behaviour.

NEST ABSENTEEISM

When individuals were regularly absent from the nest it was assumed that they were foraging. However, if they were absent for more than 5 observation sessions in a row, it was assumed that they were either dead or had dispersed. Absenteeism (or foraging activity) was only observed when temperatures were ≥ 25° C. Foragers were identified when they were seen returning to the nest. Upon returning, foragers usually worked their way down the nest passing and interacting with other individuals, often having "buccal contact" with other individuals, presumably providing them with nectar (see inter-adult behaviours). Often such a bee would then leave the nest again and return later. Foragers were not observed feeding larvae.

Nest Maintenance Behaviours

GUARDING

A bee was recorded as "guarding" when it occupied the position closest to the nest entrance with its body oriented so that its head was facing away from the entrance. Such a position allows the metasoma to block the nest entrance from intruders, as recorded for other allodapine bees *B. hewitti* (Maeta *et al.* 1992), *B. mista* (Batra *et al.* 1993) and *E. bicolor* (Mehta & Schwarz, 1993). During guarding the bee was inactive either on its back or standing upright. If a bee was closest to and facing the nest entrance, it was not recorded as guarding, since bees in this position would often be in the process of leaving

the nest. Minors were often seen guarding and in some nests, Majors, particularly egg-layers, were not seen to guard at all.

Guarding did not always occur near the nest entrance. In some nests the "guard" was stationed ¼-½ of the way down the nest but was the bee closest to the nest entrance. These guards were sometimes seen to 'patrol' the nest from that section up to the entrance. This involved the bee rapidly "travelling" forward, whilst rapidly antennating ("inspecting") the nest lumen before returning to the guard position. In some nests it also appeared that two individuals would guard alternately or one in front of the other. Although there were times when more than one individual was seen in the guard position, there were individuals who never "guarded". During the study, no other invertebrates were observed entering the nests. Since there was no interference from other invertebrate predators in the captive situation, guarding in this study may not reflect natural behaviour of this species.

INSPECTING

This behaviour involved a bee alternately antennating objects, for example the nest wall or brood. Eggs were frequently antennated in this way. Sometimes bees travelled up and down the nest inspecting the lumen wall. During this behaviour bees moved their heads slightly and rapidly moved antennae.

MOVING DEBRIS

Debris in the nest was moved by passing it under the body with the forelegs to the hind legs then pushing backwards with the hind legs or metasoma. This behaviour was rare (approx. 0.3% of the observation time), since the nests were in hard, fine-grained wood which required little maintenance. Debris observed in the nest included exuviae and, occasionally, dead individuals. "Moving debris" was not usually observed unless temperatures were ≥ 25 C.

INTER-ADULT BEHAVIOURS

AVOIDANCE

"Avoidance", a combination of other behaviours, involved one individual travelling towards another individual and "antennating" either the metasoma or face of that individual and then suddenly backing away or turning and travelling in the opposite direction.

ANTENNAL CONTACT

"Antennal contact" accompanied most inter-adult behaviours. When an individual came in to contact with another individual it either "antennated" the other's metasoma or face. If individuals were face-to-face the two individuals tapped each other's antennae.

PASSING

"Passing" is the exchange of positions by nest mates. Passing occurred when individuals were either facing each other or the "passer" was facing the metasoma of the individual she intended to pass. In each case, individuals oriented themselves venter-to-venter, essentially walking over each other. A pass was either simple or complex. "Simple passing" involved the smooth exchange of positions, with individuals usually flattening their bodies against the nest wall. "Complex passing" involved one individual biting at another individual's body parts, and/or struggling and grasping each other with the legs. Either one or both individuals would bite. Sometimes one individual would bite the other on the ventral side between the metasoma and the thorax, near the articulation between the trochanter and the thorax. Passing sometimes involved brief "buccal contact" between the two individuals, although it was often difficult to determine clearly whether buccal contact had actually occurred. It was not always easy to distinguish between the passer and the "passed", except when one was initially stationary and another was travelling.

BUCCAL CONTACT

Individuals were often observed to touch each other's open mandibles with their own open mandibles; this was termed "buccal contact". When individuals were involved in such interactions, one individual was standing upright and the other was positioned upside down. Individuals also engaged in brief buccal contact during passing. During approximately 5% of buccal contact interactions, nectar flow between the mouth parts of individuals was observed and individuals were observed placing their proboscis between the mandibles of another individual, Proffering of globules of nectar (Melna & Schwarz 1993), was not observed in *E. bidentata*.

NUDGING

"Nudging" involved one individual using its face to nudge or butt the metasoma or face of another individual. The bee that "nudged" was usually upright. Nudging usually resulted in one of the following:

a) The nudged individual turned and the nudger retreated, which sometimes involved the nudged bee opening its mandibles.

b) If nudged from behind, the bee being nudged would sometimes position its antennae laterally (out to the side), then if nudged again it might open its mandibles. This eventually resulted in the bee

turning, investigating the "nudger", and then simple or complex passing and/or buccal contact.
c) The nudged or the nudger passing and "biting" each other.

MANDIBULATING

Mandibulating, i.e. the opening and closing of the mandibles not associated with eating, appeared to occur before biting encounters. In some cases it appeared that mandibulating was a signal that one individual was rejecting an approach from another individual. For example 'A' approached 'B', 'A' nudged 'B', 'B' then opened mandibles, 'A' then retreated. "Biting" encounters sometimes followed. Similarly, if an individual was nudged from behind it sometimes opened its mandibles and/or turned and faced the nudger often opening the mandibles again. In addition, flattening of the antennae laterally often occurred during mandibulating. This sometimes occurred when individuals came face to face or if one was nudged from behind.

BITING

In this study aggressive encounters were observed for *E. tridentata*. These involved biting of mandibles, antennae, neck, legs, the ventral side of the thorax, around the coxae and metasoma. Often when one individual tried to escape from such an encounter the other bee would pull it back using its forelegs. "Biting" encounters were often complex. For example, 'A' used its face to nudge 'B's face. Then one or both bees opened the mandibles and a complicated pass followed. Whilst the bees were venter to venter and struggling (holding each other with legs) one would bite the other on the ventral side of the thorax. After a struggle, the bitten bee was often observed on its back while the biter held the other bee's antennae in its mandibles, in a "tug-of-war" encounter. This tug-of-war could last for 10-20 sec. Following a tug-of-war encounter the individual which had initiated the pass (the biter) sometimes attempted to pass again and often a simple pass would follow.

ADULT-BROOD INTERACTIONS

EXAMINATION OF BROOD

Examination of brood was accomplished with the antennae, and, to a lesser extent, the mouth parts (opening and closing mandibles on the brood). Individuals tapped pupae, larvae or eggs, with each antenna.

NUDGING BROOD

Brood were sometimes nudged before they were moved. This behaviour did not result, however, in the brood appreciably changing position.

MOVING BROOD

Older brood (late instar larvae, prepupae and pupae) were usually moved in a way similar to the way debris was moved in the nest. In *E. tridentata*, similar to *E. bicolor* (P. S. Hurst pers. comm. 1995), the bee initially held the brood with the fore tarsi then passed them under the body and pushed them backwards using the hind legs. Repositioning of brood occurred often within the nests of *E. tridentata*. Sometimes a bee would move each pupa until it reached the end of the nest, then it would move them all back again; seconds later another individual sometimes did the same thing. Some Minors which consistently stayed near the brood were often observed performing this behaviour. In addition, bees sometimes simply handled the pupae with the fore legs but did not actually reposition them.

GROOMING BROOD

Bees occasionally extended the proboscis to the brood or bit gently at the brood with their mandibles; such behaviour was categorised as "grooming brood". This behaviour was rarely observed. Grooming may have occurred during moving or with handling but it was difficult to observe the finer movements of such behaviour because of the speed of movement of the proboscis and the limited magnification.

OVIPOSITION

When "Ovipositing", the female oriented herself so that the head pointed towards the nest entrance. During egg laying bees were observed in one of three positions; ventral surface facing upwards, dorsal surface facing upwards and lateral surface facing upwards. Prior to and during "Oviposition" the sting was extended. Once an egg had been deposited on the floor of the nest, the bee retracted the sting. Approximately 1-6 min passed before the female turned around and inspected the egg with the antennae.

Oviposition occurred close to the nest end (0.5 mm) and was observed for 4 Majors and 1 Minor (5 separate colonies). Individuals took approximately 5-6 min to discharge an egg. However, one Major took 38 min to lay an egg.

Discussion

Behaviour has previously been studied in detail for *B. hewitti* (Maeta *et al.* 1992), *B. nitida*, *B. kallagi* (Batra *et al.* 1993), *Allodape exclusa* (Strand) (Mason 1988) and *E. bicolor* (Melin & Schwarz 1993). *Exoneura tridentata* generally spend a large amount of time inactive, similar to other bees (Maeta *et al.* 1992; Batra *et al.* 1993). Activity tended to be greater on days when the temperatures were above

25 °C. Similarly, when the temperature was warmer bees tended to forage more and, especially after return of a forager to the nest, general activity appeared to increase.

Exoneura tridentata was not observed to exhibit the types of nest maintenance behaviours found in other allodapines, probably due to the hard nature of the nest substrate. Most allodapines excavate their own nests in pithy substrate material, whereas *E. tridentata* do not. Although observation nests provided no opportunity for nest walls to decay during the course of the study, natural nests are also unlikely to require repairs to the nest wall or entrance, since they also occur in fine grained wood. This contrasts with *E. bicolor* which performs various nest maintenance activities such as clearing and lamping (removing loose material from the nest wall and shaping nest lumen), extending the nest lumen (excavating rear of the burrow), collar construction (lamping wood into a collar near nest entrance) and removing debris (wood strands). *Exoneura tridentata* may exhibit nest maintenance activities to a greater degree when new nests are founded and there is a need to remove frass left behind by beetle larvae.

This study is the first to describe egg laying in an *Exoneura* species. Egg laying was only observed during the day, although it may also have occurred at night (observations were only made during the day). Egg laying was similar to that described for *B. mixta* (Batra *et al.* 1993) and *B. hewitti* (Maeta *et al.* 1992). However, two of the three *E. tridentata* majors that were observed ovipositing were rarely or never seen guarding. The third major was seen to guard but she was usually 5 cm from the base of the nest and not near the entrance. This differs from *B. hewitti* (Maeta *et al.* 1992) and *E. bicolor* (Hogendoorn & Schwarz 1998; Bull *et al.* in press) where reproductive dominants are guards. Egg laying in this species appears to be a very slow process compared with other bees (58 sec. *B. hewitti*) (Maeta *et al.* 1992), in terms of both the time taken to deposit an egg and the frequency of egg laying. One female, in particular, spent 38 min depositing an egg which may have been related to the fact that the temperature was low that day (< 20° C), and bees were generally less active at lower temperatures. However, these observations did not cover the period of maximal egg production and should be treated with caution.

Aggressive behaviour has not been reported for other allodapine bees except rarely between *B. mixta* and its social parasite *B. kalinga* (Batra *et al.* 1993) and infrequently for *A. exoloma* and *B. jurcata* (Mason 1988). The agonistic behaviour described for these species mainly consisted of nudging, biting of legs and bodies and blocking passage, but also included stinging (Batra *et al.* 1993; Mason 1988). Agonistic behaviour between a host and its parasite is not uncommon and often results in either host or parasite being removed from the nest (Batra *et al.* 1993). Aggressive interactions are also found in social species of the bee tribes Halictini and Xylocopini (Breed *et al.* 1978; Michener 1990). However, *E. tridentata* was often observed to engage in aggressive encounters which involved a great deal of biting and struggling, with some encounters becoming quite savage. Such encounters were often preceded by nudging and followed by passing. The mandibulating that occurred sometimes, either prior to or in response to nudging and biting, might also be aggressive in nature. Cane & Michener (1983) found that some *Exoneura* spp. produce irritants which elicit vigorous grooming responses in predatory ants. Batra *et al.* (1993) described mandibulating during aggression between *B. mixta* and its social parasite *B. kalinga* and suggested that mandibular secretions were involved. It may therefore be suggested that when *E. tridentata* mandibulate at each other, they also release chemical secretions which may be agonistic or relay information about dominance status.

The agonistic behaviours observed in *E. tridentata* suggest that dominance hierarchies may be present within colonies. It appears that some individuals engage in certain types of behaviour which could be interpreted as assertion of dominance. Bees that are often nudged or bitten and those that exhibit avoidance behaviour may have more subordinate roles in the nest. Differences in the way individuals respond to other individuals in terms of these behaviours may be related to dominance (i.e. when some individuals are nudged they engage in a simple pass, whereas when other individuals are nudged and/or bitten they engage in a complicated pass). Brothers & Michener (1974) found that 'queens' of *Lasioglossum zephyrum* were the maximal nudgers in the colony. They suggested that nudging behaviour indicates dominance similar to that observed in other primitively eusocial wasps and bees. Brothers & Michener (1974) experimentally showed, for *L. zephyrum*, that nudging by the queen plays a role in the division of labour among the workers by inhibiting ovarian development.

During this study guarding behaviour was not the same as that observed in field studies of *E. tridentata*, i.e., with the abdomen curled and used to block the entrance from predators such as ants (Hurst unpub.). This may be related to the fact that there was no predation pressure in the shade house environment, unlike studies on *E. bicolor* conducted in shade houses where ants were a problem (Bull[1]; Hurst[2]). However, females that were guarding were always facing the bottom of the nest which suggests that

they were in a position to block the nest if the need arose.

Trophallaxis is altruistic behaviour; foragers engage in energetically costly and risky behaviour to obtain food which they relinquish to others. Trophallaxis is important in the social organisation of many social insects (Wilson 1971). In allodapines there may be differences in the way in which trophallaxis is performed. *Exoneura bicolor* have been observed to engage in solicitation behaviour before trophallaxis occurs (Melna & Schwarz 1993). Solicitation involved individuals rapidly stroking each other's antennae prior to buccal contact. Trophallaxis in *E. bicolor* can also involve one individual proffering a globule of liquid to another (Melna & Schwarz 1993). Proffering of globules was not observed in *E. tridentata* and if solicitation occurred, it was too fast to be identified. However, it is likely that individuals which engaged in "buccal contact" where nectar flow was observed, were frequently engaging in trophallaxis. Trophallaxis allows females to feed without leaving the nest. The presence of trophallaxis in *E. tridentata* therefore allows behavioural specialisation where only some of the females have to forage and other females can perform other duties in the nest.

Exoneura tridentata exhibits a similar repertoire of behaviours to other allodapines (Maeta *et al.* 1992; Batra *et al.* 1993; Melna & Schwarz 1993). Behaviours recorded in this study, including adult-adult interactions and adult-brood interactions, are all similar to those found for other species, suggesting that such behaviours are likely to be ancestral and that development of novel behavioural elements is not necessary for social organisation to evolve from small family groups to large groups with morphological differentiation among colony members.

However, unlike other allodapines, *E. tridentata* exhibits frequent and overt agonistic behaviours among nest mates. Such agonistic behaviour has often been associated with more primitively social species. According to Wilson's (1971) criteria, *E. tridentata* can be classed as highly eusocial because there is female morphological dimorphism associated with reproductive division of labour. Therefore, *E. tridentata* doesn't conform to Wilson's (1971) suggestion that aggression within a colony can be replaced by "gentle despotism" as sociality involves larger group size and requires a greater degree of integration. Most other highly eusocial species display distinct morphs which are directly associated with discrete behavioural castes, involving minimal or no aggression. Considering the presence of aggressive interactions within *E. tridentata* colonies, it would seem that increased colony size and the development of morphological differentiation among colony members need not be accompanied by decreased levels of overt intra-colony aggression.

Acknowledgments

We would like to thank friends and laboratory members who assisted with field work and N. Bull, S. Reyes, P. Hurst, J. Bird and two anonymous referees for advice on the manuscript. This research was partially funded by grants from the Australian Research Council to M. P. S. Field work was carried out with permission from the South Australian Department of Environment and Natural Resources, permit no. Q23256-03, issued to M. P. S.

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FIELD ECOLOGY AND BEHAVIOUR OF THE EGG PARASITOID TRISSOLCUS BASALIS (WOLLASTON) (HYMENOPTERA: SCELIONIDAE)

By S. A. Field, M. A. Keller* & A. D. Austin**

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Key Words: *Trissolcus basalis*, Scelionidae, egg parasitoid, horehound bug, *Agonoscelis rutila*, egg masses, defensive behaviour.

Introduction

Trissolcus basalis (Wollaston) is a solitary parasitoid of the eggs of the introduced green vegetable bug, *Nezara viridula* (L.) (Hemiptera: Pentatomidae), and a number of other pentatomid species (Cumber 1964), including the native horehound bug, *Agonoscelis rutila* (F.). Since its first importation into Australia in 1933 (Noble 1937), *T. basalis* has been released a number of times (Clarke 1990). Due to its perceived importance as a biocontrol agent worldwide, many aspects of its biology have been documented (e.g. Wilson 1961; Cumber 1964; Powell & Shepard 1982; Bin *et al.* 1986; Volkoff & Colazza 1992; Mattiacci *et al.* 1993).

Although the field ecology of *T. basalis* in Australia is best known from its association with *N. viridula* (e.g. Turner 1983; Clarke 1990), its biology when parasitising *A. rutila*, on the introduced weed horehound, *Marrubium vulgare* (L.), has also been investigated in view of its potential for maintaining parasitoid numbers in cropping areas (Kelly 1987). When feeding on horehound, reproductive maturity of *A. rutila* is dependent upon the availability of flowers, and so both host and parasitoid population dynamics are closely linked to seasonal cycles of plant growth. Although activity and population peaks of both host and parasitoid coincide with the major growth phase of the plant in spring and early summer, neither species appears to enter diapause over winter and a high rate of parasitism (> 70%) is maintained throughout the year (Kelly 1987).

Due to the small size and rapid movement of *T. basalis*, field observations are difficult and data have only been collected from one study on host searching under semi-field conditions (Turner 1983). Oviposition behaviour, exploitation of host egg masses (= patches) and competition have not been studied in the field. This paper reports field data on the ecology and behaviour of *T. basalis* parasitising *A. rutila*, its most common host in the Adelaide region of South Australia (Fig. 1). In spring and summer of 1994-5 and 1995-6, data were collected on the seasonal fluctuations of host plant and host populations, sources of host mortality and behaviour of parasitoids as they exploited, and competed for, masses of host eggs. The purpose of this work was also to provide the foundation for more detailed laboratory-based studies of patch exploitation and defence (Field *et al.* 1997).

Materials and Methods

Host plants and hosts

Data on the ecology and behaviour of *T. basalis* in the field were collected from late October to late March in 1994-5 and 1995-6 in the Brownhill Creek Conservation Park, in the Adelaide foothills. Sampling sites were selected by taking two 50 m transects along random directions through a patch of horehound. The transects were divided into 10 intervals of equal length and a random point was taken along each interval. The nearest horehound plant, or discrete cluster of plants, to each of these points was marked as a sampling site. If stems ceased

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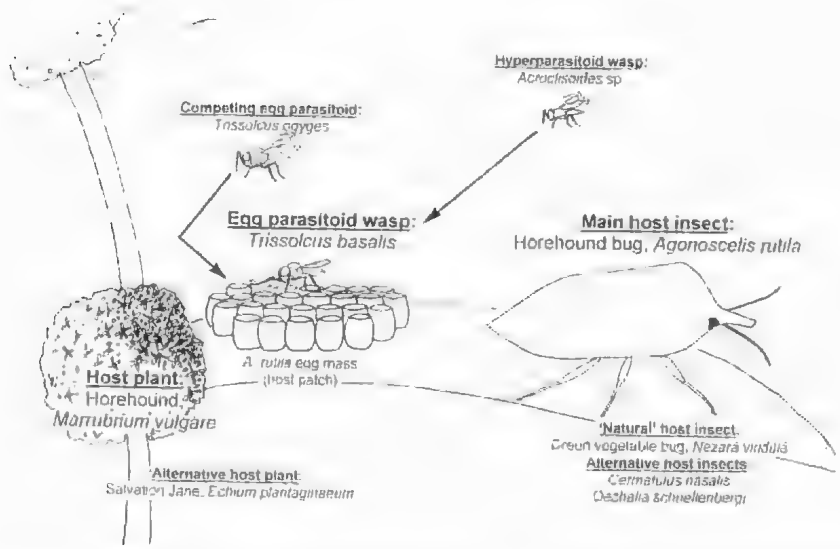

Fig. 1. Summary of the natural history of the *A. rutila* – *T. basalis* system used in this study (see text for description)

to show any green foliage during sampling, the marker was removed and replaced on the nearest stem bearing foliage. When no plants with eight or more stems with green foliage remained, sampling was discontinued. On 21 days between 26 October and 21 March 1994-5, data on host plant and host population, and parasitoid behaviour were collected. The numbers of open flowers on stems were recorded and an index of the *A. rutila* population was obtained by counting the total number of adults on all sample stems at 10.00 a.m.

Parasitoid egg load

The numbers of eggs carried by female parasitoids (n = 31) were assessed by collecting wild *T. basalis* females on seven days between 30 November and 20 December in 1994, and dissecting them in the laboratory. In addition, egg maturation under laboratory conditions was studied by determining parasitoid egg load when females were between one and 10 d old. Prior to dissection, wasps were held individually in vials supplied with honey solution for 1-10 d at 25° C, without ovipositing, before being frozen at -60° C. The metasoma of individual wasps was removed and dissected in a drop of water on a cavity slide and the number of eggs in the ovaries counted.

Behavioural observations

In both years, behavioural observations on parasitoid oviposition behaviour, patch exploitation and competition were made. Host patches were created by glueing 0-1 d old egg masses of laboratory-reared *A. rutila*, each containing between 12 and 24 eggs, on to small squares of green cardboard and stapling them to leaves on randomly chosen sample stems. Patches were laid out between 9.00 a.m. and 2.30 p.m., and the number of female wasps on each egg mass was recorded every 30 min until 6.30 p.m. In 1994, between one and 12 egg masses were observed on each of five days between 26 November and 12 December. In 1995, 16 egg masses were observed on each of eight days between 8 November and 26 December. An index of daily competition for egg masses was obtained by taking the maximum number of wasps observed in any one sample during the day for each egg mass and calculating the mean across all egg masses. To facilitate comparison between data sets for the different years, these means were taken in the period 2.30 p.m. to 6.30 p.m., as some data from 1994 were collected only during these times of day. To compare rates of discovery of egg masses, Kaplan-Meier estimates of survivor functions (Haccou & Meelis 1994) for the time until discovery of egg masses were calculated for data pooled within seasons. The survivor functions plot the cumulative proportion of egg masses discovered as a function of time, and thus provide an estimate of the instantaneous rate of discovery of egg masses.

To observe patch exploitation and defence behaviour in detail, patch visits by single wasps (n = 4), and by pairs of wasps (n = 6) to randomly selected artificial patches were videotaped and converted to behavioural sequence records in the laboratory using a TRS-80 Model 100 portable computer programmed with event recording software (The Observer, Noldus Information

Technology Wageningen The Netherlands). Behaviour was divided into categories representing host examination, oviposition, patch-leaving and, for pairs of females, agonistic behaviour (Field[1]; Field in press). When patch contests between two females occur, one individual (the 'resident') usually establishes dominance and aggressively excludes the other (the 'intruder') (Wilson 1961; Field[1]). The intruder then waits nearby and periodically returns to the egg mass to attempt further oviposition. Where bout length sample sizes permitted ($n > 20$), intruder 'retreat' behaviour (defined as the time between being driven away from the egg mass and returning) was tested for abrupt changes in bout length using a non-parametric multiple change point test (Haccou & Meelis 1994). Where changes were significant at the adjusted levels suggested by Haccou & Meelis (1994), they are illustrated with cumulative bout length plots.

Results

Host plants, hosts, parasitoids and hyperparasitoids

In 1994 and 1995, host plants and host insect populations underwent marked fluctuations. Numbers of flowers peaked in late November, and thereafter declined steadily until mid January (Fig. 2), when all plants showed very little or no green vegetation and no flowers or leaves. Population counts of *A. rutila* decreased in parallel with the decline in plant quality, stabilising at low levels in mid-January (Fig. 2). Adult *A. rutila* also appeared to be susceptible to high temperatures, as many died during a hot, windy spell early in December. The first nymphs appeared at this time, indicating the emergence of the first generation of the season. Numbers of adult *A. rutila* over summer remained much lower than the peaks observed in spring.

Weeds other than horehound, in particular Salvation Jane, *Echium plantagineum* (L.) were also abundant at the field-site in 1995-6, and were utilised for feeding and reproduction by *A. rutila* (Fig. 1). Adults were observed feeding, mating and laying eggs on *E. plantagineum*, although it was unclear whether nymphs were able to complete development solely on this plant. *Trissolcus basalis* were also observed foraging on *E. plantagineum* plants.

Apart from *A. rutila*, other pentatomids occasionally observed on horehound at the study site were *N. viridula*, *Cermatulus nasalis* (Westwood) and *Oechalia schnellenbergi* (Guérin-Méneville) (Fig. 1), all of which have previously been recorded as hosts for *T. basalis*. Eggs of *N. viridula* and *C. nasalis* were not seen but those of *O. schnellenbergi* were collected and both *T. basalis* and *Trissolcus ogyges* (Noble) were reared from them (Fig. 1). *Trissolcus ogyges* did not complete development in *A. rutila* eggs, so *O. schnellenbergi* appears to have been its main host at the site. *Trissolcus ogyges* could be distinguished from *T. basalis* in the field and laboratory by a distinct difference in host marking behaviour. Rather than dragging the ovipositor smoothly over the host egg in a 'figure 8' motion as in *T. basalis* (Wilson 1961; Weber *et al.* 1996), *T. ogyges* moved the ovipositor horizontally across the egg with a 'bouncy, jagged' motion. Females defended egg masses similarly to *T. basalis* and interspecific contests were observed, but not recorded in detail. As one objective of this study was to gauge the overall levels of competition for access to hosts among *T. basalis*, the data presented below include observations in which *T. ogyges* was also present. In 1994, the proportion of total observations in which *T. ogyges* occurred was not recorded but in 1995 it was approximately 10%.

In addition to the primary parasitoids, females of the hyperparasitoid *Acmedisoides* sp. (Girault & Dodd) (Hymenoptera: Pteromalidae) were occasionally observed sitting on egg masses from December 1994 to January 1995 (Fig. 1).

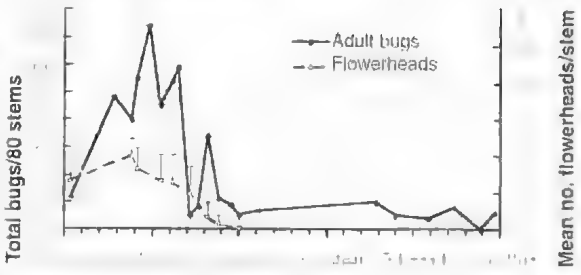

Fig. 2. Numbers of *A. rutila* adults and mean numbers of flowerheads (±1 SD) on horehound stems in 1994-95.

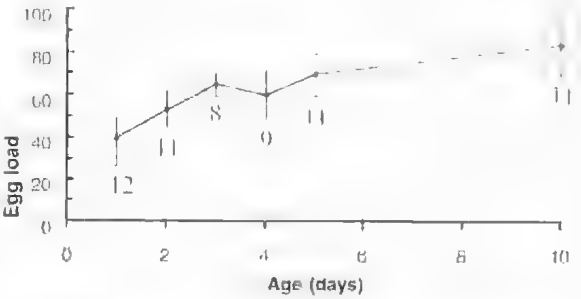

Fig. 3. Mean number of eggs (±1 SD) in the ovaries of female *T. basalis* from 1-10 d after emergence. Numbers below error bars indicate sample sizes.

[1] Field, S. A. (1998) Patch exploitation and defence in the egg parasitoid *Trissolcus basalis* Wollaston (Hymenoptera: Scelionidae). PhD thesis, The University of Adelaide (unpubl.)

Parasitoid egg load

Dissections of laboratory-reared female *T. basalis* revealed that they emerged with a substantial complement of eggs and then slowly matured further eggs over time (Fig. 3), showing that *T. basalis* is a synovigenic species.

Most of the parasitoids collected from the field were carrying substantial numbers of mature eggs (Fig. 4), indicating that egg-limitation was not common in the field at this time. In early November in 1994, three different females that discovered egg masses in the afternoon remained on them overnight, although no intruding conspecifics were observed. Two of these females were dissected and found to have egg loads of one and three eggs, respectively.

Behavioural observations

Parasitoids searched for hosts by flying between horehound stems, and then walking rapidly up and down the stems, palpating the surface with their antennae until they had located an egg mass. While searching a stem, they often passed within a few centimetres of an egg mass without detecting it and so did not appear to be detecting egg masses using visual or chemical cues. Thus, location seemed to be by physical contact. Upon contacting an egg mass, wasps examined only one or a few host eggs, then commenced oviposition (Bin *et al.* 1993). If one or more conspecifics were present, wasps engaged in agonistic behaviour (Wilson 1961).

Competition for egg masses differed widely between the two years (Figs 5,6). In 1994, there was a peak of parasitoid activity on December 2 (Fig. 5). On this date several remarkable observations of parasitoid competition were recorded. In one instance, a maximum of 14 parasitoids was observed simultaneously competing for access to a single egg mass. In another observation, five parasitoids had discovered an egg mass as it was being laid by the female *A. rutila*. They were following the bug, parasitising the eggs immediately they were laid and were fighting each other for possession of the incipient egg mass. Three other cases of immediate patch discoveries were recorded on the same day. *Agonoscelis rutila* showed only rudimentary defensive behaviour, occasionally kicking at the parasitoid but this had no deterrent effect on the *T. basalis*. Instead, the parasitoid sometimes responded by directing its aggressive behaviour toward *A. rutila*.

In contrast to the high peak of competition observed in 1994, competition remained low throughout the entire sampling period in 1995 (Fig. 5). This difference in intensity of parasitoid activity between the two years is also reflected in the time until discovery of patches (Fig. 6). In 1994-95, almost all egg masses were discovered within 7 h of being laid, whereas in 1995-96, the vast majority of egg masses remained undiscovered in the same time period, resulting in a highly significant difference between the two curves (Log-rank test, $\chi^2 = 100.9$, 1 d.f., $p < 0.001$).

Sample sizes for continuous time records of patch exploitation and defence were small and observations were sometimes incomplete, precluding an extensive analysis of the time and sequence structure of behaviour. However, the observations did confirm that the patterns of behaviour seen in previous laboratory studies (Wilson 1961; Cumber 1964) reflected those occurring under field conditions. When alone, wasps successively examined, oviposited in and marked hosts before examining the surrounds of the egg mass and finally leaving. In each of the four observations, self-superparasitism (i.e. double oviposition in the same host egg by the same female parasitoid) did not occur before the egg mass was fully depleted (i.e. all host eggs in the egg mass were parasitised), and only occurred after that in one observation, when the wasp self-superparasitised three times before leaving. Upon depletion of the patch, in two of the four observations wasps embarked on periods of

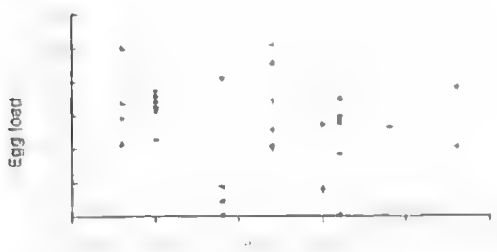

Fig. 4. Mature egg loads of female *T. basalis* collected between 30 November and 20 December in 1994.

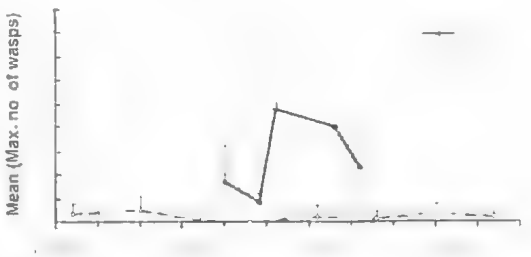

Fig. 5. Comparison of patch competition between years: mean (±1 SD) of maximum number of *T. basalis* on any egg mass.

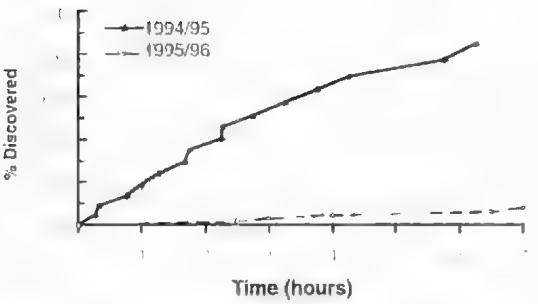

Fig. 6. Comparison of patch discovery times between years for 1994 (26 November–12 December) and 1995 (23 November–14 December).

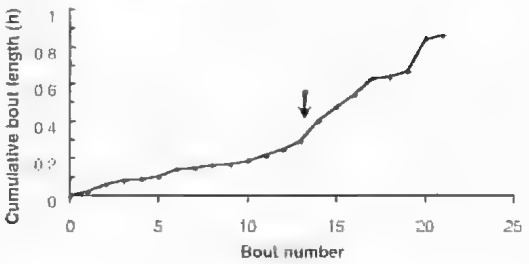

Fig. 7. Cumulative bout length plot for 'retreat' behaviour of the intruder in a pairwise contest, showing a single abrupt increase in bout length (arrow).

'defence' of the egg mass. These defence periods consisted of alternating bouts of 'stationary' behaviour (motionless, sitting on the egg mass) and 'patrolling' behaviour (rapidly darting from one side of the egg mass to the other). This apparently pre-emptive patch defence behaviour continued for approximately 11 min and 2 h 30 min in the two observations, respectively, despite the fact that no competitors were present.

When contests between two individuals occurred, sequences of agonistic behaviour developed. These sequences exhibited the same major characteristics as those observed by Wilson (1961) and Cumber (1964), including the establishment of resident-intruder roles. Fights occurred either on the first encounter, or after a brief period of mutual tolerance. The tendency for individuals to fight appeared to increase after successful completion of one or more ovipositions, although occasionally individuals became aggressive immediately upon arriving at an egg mass, and before examining the host eggs or ovipositing. Following the onset of aggression and role establishment, the intruder usually retreated to the underside of the leaf when attacked by the resident, out of view of the resident (egg masses were always placed on the upper side of the leaf).

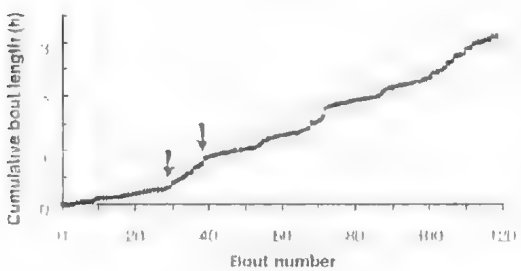

Fig. 8. Cumulative bout length plot for 'retreat' behaviour of intruder in pairwise contest showing two abrupt changes in bout length: first an increase (left arrow), then a decrease (right arrow).

and either sat motionless, groomed, searched the surrounds of the egg mass, or fed on nectar in flowerheads.

In two cases of pairwise contests, abrupt changes in bout length were observed. In the first observation (Fig. 7), the intruder switched from short to long retreat bout lengths, suggesting that it had ceased to compete for possession of the egg mass, and had begun waiting for the resident to leave. In the second observation (Fig. 8), which lasted 36 min longer, the intruder switched twice: first to longer retreat bout lengths, and then back to shorter ones, which were still longer than those in the initial period.

The intensity of bouts of aggression varied widely: from no-contest encounters in which one individual retreated without retaliation, to intense escalated fights, in which individuals locked together and rolled across the leaf for up to 30 s. Although no obvious injuries were observed, sometimes both individuals fell from the leaf, temporarily losing opportunities to exploit the egg mass and leaving it unguarded. Although some individuals recovered their position on the egg mass quite rapidly, others did not return, showing that in addition to the possible risk of injury, engaging in an escalated fight also entailed the risk of permanently losing access to the egg mass.

Conspecific superparasitism (i.e. oviposition in the same host egg previously parasitised once or more by a different female parasitoid) was common, either when wasps visited egg masses sequentially or simultaneously. In one extreme case, a mass of 20 eggs set out on the day of peak competition (December 2) in 1994 received 126 ovipositions over a period of 9 h.

Discussion

The host population observed in this study underwent marked seasonal fluctuations. Populations peaked in spring, but eggs laid by the overwintering population of adults at this time

attracted high levels of predation and parasitism and few nymphs emerged to form the new generation. This mortality, combined with the decline in food availability resulting from the senescence of host plants, led to a sharp decrease in host population levels by the end of the December. Therefore, for the parasitoid there was a peak in absolute numbers of host eggs available for approximately two months from late October to early December. Although depletion of egg reserves in *T. basalis* was rare during this period, it may have had significant effects on foraging behaviour when it occurred, causing wasps to stay longer and guard egg masses, rather than continue foraging.

The occurrence of hyperparasitism by *Acroclisoides* sp. may also have exerted a selective pressure on wasps with low egg load, causing a tendency toward staying and guarding egg masses. *Acroclisoides* sp. has previously been recovered from egg masses of *N. viridula* in eastern Australia by Clarke & Seymour (1992). These authors showed that the species is a hyperparasitoid of *T. basalis*, but suggested it may be only casually associated with *T. basalis*. Clarke & Seymour (1992) did not report which stage of *T. basalis* the hyperparasitoid attacks but in observations made in the present study wasps only sat on the egg masses without probing or ovipositing, suggesting that they may have been waiting for the immature *T. basalis* to reach a later larval stage, or the pupal stage. Attempts to observe behaviour of the *Acroclisoides* sp. and rear it in the laboratory were unsuccessful, as it was only observed a few times in the field and was never recovered from *A. rutila* egg masses.

The frequent occurrence of superparasitism by *T. basalis* in this study provides further evidence that superparasitism is common in nature (Janssen 1989; van Alphen & Visser 1990). Its ecological importance for *T. basalis* is underscored by the finding that the probability of the superparasitising female obtaining offspring from a host is very high if she superparasitises soon after the other female oviposits in the host (Field *et al.* 1997). As this leaves the offspring of the first female to oviposit at substantial risk, the high frequency of occurrence of superparasitism and its high fitness pay-off may have favoured the evolution of patch defence in *T. basalis*, in addition to the fact that egg masses are of a defendable size, as noted by Waage (1982). The drop in the pay-off from superparasitism towards zero after 8 h (Field *et al.* 1997) may explain the observation that females aborted oviposition in an egg mass that had been parasitised as much as 9 h earlier. Still, this raises the question of the mechanism of host discrimination, which needs to be pursued in future studies.

Observations of patch exploitation and defence revealed behaviour patterns similar to those seen in previous laboratory studies (Field[1]) and suggest that behaviour is adapted to high levels of competition. When alone on an egg mass, wasps engaged in extended periods of defensive behaviour, both before and after the egg mass was fully depleted, suggesting a high innate 'expectation' of conspecifics arriving and superparasitising. This behaviour could result from a combination of innate expectation of competition set by natural selection, and a flexible response based on experience from previous egg masses. After resident-intruder roles were established in pairwise contests, intruders showed abrupt increases in periods of retreat behaviour during contests and waited out of vision of residents (under the leaf), suggesting they were waiting for residents to leave the egg mass. Although intruder behaviour was not followed in detail, in the second contest analysed (Fig. 8), it is probable that the first switch resulted from the intruder making an extensive search of the surrounding area to check for other unoccupied egg masses, and the second from its returning to the original patch. Exploring the surroundings for alternative host egg masses to the current one may be particularly important when many individuals are competing for an egg mass and gaining access is difficult, a situation that was frequently observed in times of peak competition. The dynamics of patch defence in such situations involving more than two individuals are complex and difficult to infer from the present study. Although substantial fluctuations in the levels of competition do occur, and competition is sometimes less intense, periods of extreme competition may nevertheless have played an important role in the evolution of foraging behaviour.

The observations made in this study reveal some novel patterns in the agonistic behaviour of *T. basalis* and indicate the appropriate ecological context in which to investigate them further in the laboratory. The factors leading to the onset of aggression and the mechanisms of contest resolution (i.e. establishment of resident-intruder roles) have rarely been studied in parasitoids (but see Petersen & Hardy 1996) and are the subject of current investigation in *T. basalis* (Field & Calbert unpub.). Also, a quantitative analysis of the time-structure of interactions between fighting parasitoids has not previously been attempted, and the present results indicate that this may be both possible and of great interest in *T. basalis*.

Acknowledgments

We wish to thank G. Thomas for the use of his property, G. Calbert for programming the multiple change-point test and L. Mound, M. Kokkinn and J. Bird for criticisms of the manuscript.

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WOODWARDOSTRONGYLUS PETROGALE SP. NOV. (NEMATODA: CLOACINIDAE), FROM THE STOMACHS OF ROCK WALLABIES (PETROGALE SPP.) FROM ARNHEM LAND

*By I. Beveridge**

Summary

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Key Words: Nematoda, marsupials, rock-wallabies, Petrogale, Woodwardostrongylus, new species.

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by I. BEVERIDGE*

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KEY WORDS: Nematoda, marsupials, rock-wallabies, *Petrogale*, *Woodwardostrongylus*, new species.

Introduction

One of the most unusual genera of nematodes occurring in the stomachs of kangaroos and wallabies is the cloacinid genus *Woodwardostrongylus* Wahid, 1964 which is found in tunnels in the superficial squamous epithelium of the stomach and oesophagus rather than in the lumen of the stomach or large intestine or coiled around oesophageal papillae as is the case with most of the other members of the family (Wood 1931; Mawson 1971, 1976; Beveridge & Spratt 1996). Two species are currently known within this genus, the type species, *W. woodwardi* (Wood, 1931) originally described from Woodward's wallaroo, *Macropus robustus woodwardi* Thomas, 1901, from the north of Western Australia (Wood 1931; Wahid 1964), subsequently redescribed from Pearson Island rock wallabies, *Petrogale lateralis pearsoni* (Thomas, 1922) from South Australia (Mawson 1971) and *W. obendorfi* Mawson, 1976 from the whiptailed wallaby, *Macropus parryi* Bennett, 1835 (type host), the wallaroo, *M. robustus robustus* Gould, 1841 and the red-necked wallaby, *M. rufogrisens* (Desmarest, 1817), from north-eastern New South Wales and south-eastern Queensland (Mawson 1976). The latter species was subsequently reported as a common parasite of brush-tailed rock wallabies, members of the *Petrogale penicillata* complex (*P. assimilis* Ramsay, 1877, *P. godmani* Thomas, 1923, *P. herberti* Thomas, 1926, *P. inornata* Gould, 1842, *P. mareeba* Eldridge & Close, 1992, *P. penicillata* (Gray, 1825) and *P. sharmani* Eldridge & Close, 1992) from eastern Queensland by Beveridge *et al.* (1989) and has since been found also in the agile wallaby, *Macropus agilis* (Gould, 1842), and the swamp wallaby, *Wallabia bicolor* (Desmarest, 1804) (see Spratt *et al.* 1991). Spratt *et al.* (1991) listed an additional undescribed species of *Woodwardostrongylus* from the habarlek, *Petrogale concinna* Gould, 1842 and the short-eared rock wallaby, *P. brachyotis* (Gould, 1841), from the Northern Territory. In the present paper, the undescribed species listed by Spratt *et al.* (1991) is described, the diagnostic features of the genus are reassessed and its position within the existing classification is discussed since the genus has in the past been variously allocated to the Strongyloidea (Wahid 1964) and the Trichostrongyloidea (Mawson 1971).

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Materials and Methods

Nematodes were recovered from the preserved carcases of rock wallabies provided by Dr J. E. Nelson, Monash University, Melbourne, Vic. Immediately after shooting, carcases were perfused with 10% formol saline via the left ventricle followed by immersion of the entire carcase in 10% formalin. Nematodes recovered from the gastric mucosa were stored in 70% ethanol and were cleared in lactophenol for examination. Drawings were made with the aid of a drawing tube attached to an Olympus BH microscope. Measurements are presented in mm as the range for 5 specimens followed by the mean in parentheses. To examine the localisation of nematodes within the gastric mucosa, small pieces of parasitised stomach wall were embedded in wax and sections, cut at a thickness of 5 µm, were stained with haematoxylin and eosin. All nematode specimens have been deposited in the South Australian Museum, Adelaide (SAMA).

Woodwardostrongylus petrogale sp. nov.
(FIGS 1-13)

Holotype: ♂ from stomach of *Petrogale concinna*, Arnhem Land NT, 1.xi.1977, coll. J. E. Nelson, SAMA AHC 30592.

Allotype: ♀ same data, SAMA AHC 30593.

Paratypes: 9 ♂♂, 9 ♀♀, same data, SAMA AHC 13790.

Other material examined: from stomach of *Petrogale brachyotis*, Arnhem Land NT, coll. J. E. Nelson, 1.xi.1977: 10 ♂♂, 20 ♀♀, SAMA AHC 14071.

Description

Slender-elongate nematodes, cuticle covered with numerous fine transverse annulations. Mouth opening tiny, dorsoventrally elongate, apparently rigid; lateral margins of mouth opening each with row of four retractile, dome-shaped denticles; additional pair of tiny denticles at dorsal and ventral extremities of each row. Two amphids and four submedian papillae lateral to rows of denticles; nerve tissue extending posteriorly and laterally from sensory papillae. Subcuticular region of anterior extremity heavily sclerotised. Buccal capsule thick walled, with faint transverse striations; anterior part of buccal capsule dorsoventrally elongate in apical views of head, becoming circular posteriorly, buccal capsule supported externally by 10 prominent bands of muscle running from external surface of buccal capsule to longitudinal somatic musculature, two bundles of muscles present dorsally and two ventrally, two thick lateral muscle bundles and four slender submedian bundles. Oesophagus long and slender; corpus cylindrical narrowing slightly to form short isthmus; isthmus merging into elongate bulb. Nerve ring surrounding junction of oesophageal corpus and isthmus; secretory-excretory pore in mid-region of oesophageal bulb; deirid at level of secretory-excretory pore.

Male

Total length 13.1-15.5 (14.0); maximum width 0.17-0.23 (0.20); buccal capsule 0.020-0.037 (0.032) in length, width in lateral views 0.017-0.020 (0.019), in dorso-ventral views 0.010-0.013 (0.012); oesophagus 0.79-0.86 (0.83); nerve ring to anterior end 0.40-0.48 (0.42); secretory-excretory pore to anterior end 0.48-0.57 (0.52); deirid to anterior end 0.60 (0.60).

Bursal lobes short, of approximately equal length; ventral lobes joined ventrally; dorsal lobe small, slightly shorter than lateral lobes, not clearly demarcated from lateral lobes. Ventral rays slender, apposed, reach margin of bursa, externo-lateral ray slightly stouter than other lateral rays, divergent from them, slightly recurved near extremity, not reaching margin of bursa; medio-lateral and ventro-lateral rays slender, apposed, reaching margin of bursa; externo-lateral ray arises from lateral trunk, straight, does not reach margin of bursa. Dorsal ray bifurcates close to origin; branches long, slender, arcuate; secondary division into branchlets occurs near extremity of ray; external branchlets short, directed postero-laterally, do not reach margin of bursa; internal branchlets longer, directed posteriorly, almost reach margin of bursa. Genital cone prominent; anterior lobe large, conical, extends almost to limit of ventral lobes; posterior lip small with pair of prominent posteriorly directed appendages; gubernaculum absent; central cordate and lateral paired elongate thickenings of spicule sheaths present at their junctions; spicules elongate, alate, 0.90-1.07 (0.97) long; anterior extremities irregularly knobbed; distal tips blunt; ala diminishes in width towards spicule tip.

Female

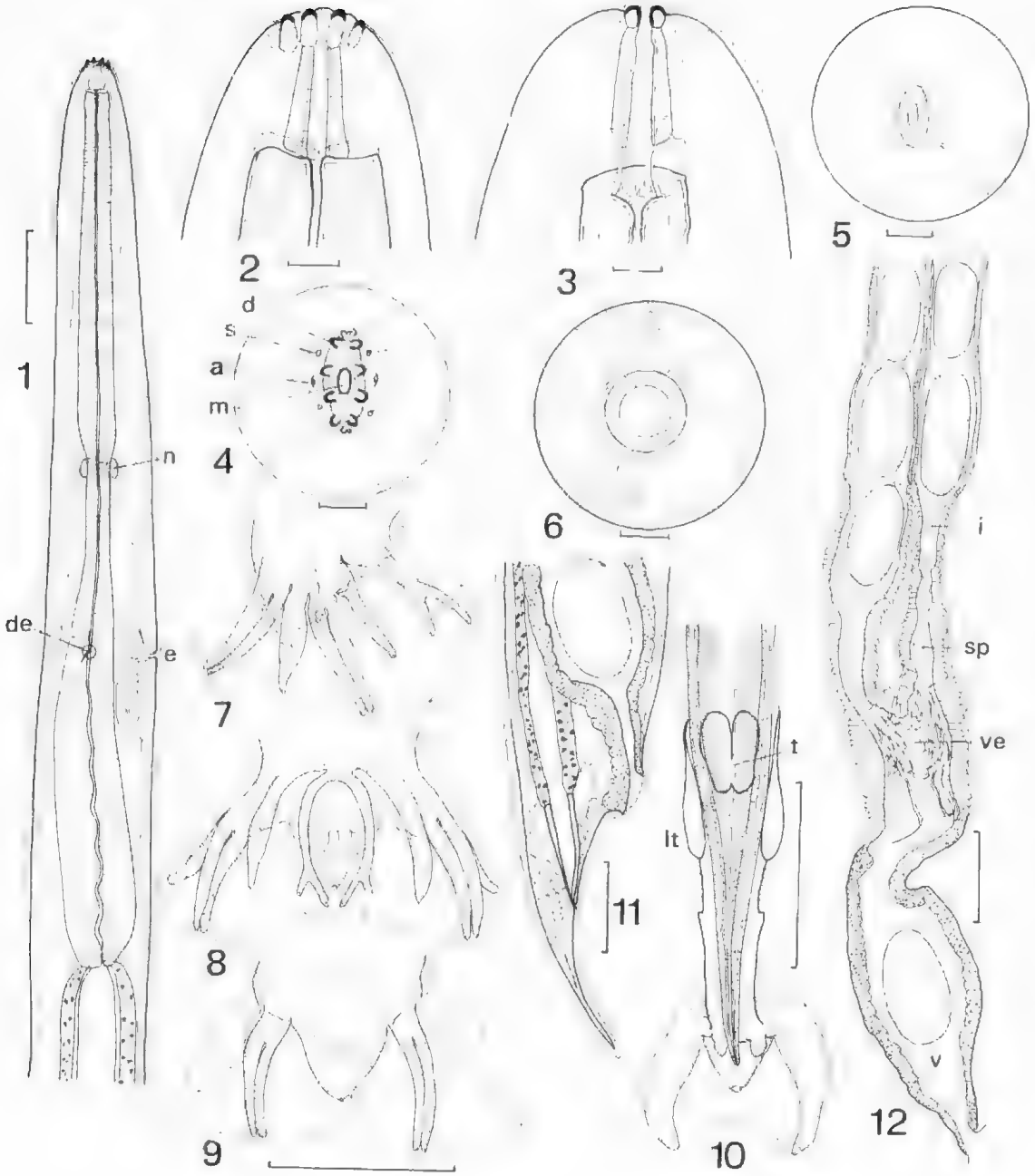
Length 16.4-22.8 (20.1); maximum width 0.18-0.29 (0.27); buccal capsule 0.027-0.034 (0.030) in length, width in lateral views 0.020, in dorso-ventral views 0.010-0.015 (0.013); oesophagus 0.92-1.28 (1.01); nerve ring to anterior end 0.24-0.44 (0.39); secretory-excretory pore to anterior end 0.57-0.65 (0.62); deirid to anterior end 0.58-0.65 (0.62). Tail short, conical 0.11-0.17 (0.15), vulva immediately anterior to anus, 0.23-0.32 (0.26) from posterior end. Vagina short, straight, directed anteriorly, 0.31-0.48 (0.39); vestibule in form of Y, with thick muscular walls, 0.15-0.20 (0.17) long; sphincter and infundibulum of approximately equal lengths, very variable in length, each 0.08-0.25 long; uteri parallel, run anteriorly from infundibula; egg ellipsoidal 0.13-0.14 (0.13) x 0.07-0.09 (0.08).

Localisation within stomach

Nematodes lie in small sinuous tunnels in the superficial layer of the stratified squamous epithelium of the forestomach. Nematodes were not found penetrating as deeply as the *lamina propria* and the presence of the nematodes in the squamous epithelium provoked no inflammatory response. The anterior ends of the nematodes were buried in tunnels while the posterior ends lay free in the gastric lumen.

Discussion

The nematode species described above belongs to the Cloacininae Stossich, 1899 because it possesses a cylindrical buccal capsule, a bursa in which the dorsal lobe has four branches, the externo-dorsal ray arises from the lateral trunk and a cervical groove is



Figs 1-12. *Woodwardostrongylus petrogale* sp. nov. 1. Anterior end, lateral view. 2. Cephalic extremity, lateral view. 3. Cephalic extremity, dorsal view. 4. Cephalic extremity, apical view. 5. Transverse optical section through anterior end of buccal capsule. 6. Transverse optical section through posterior part of buccal capsule showing muscle bands running radially from outer wall of capsule. 7. Bursa, lateral view. 8. Bursa, dorsal view. 9. Bursa, ventral view. 10. Posterior end of male, dorsal view showing spicules and thickenings of spicule sheaths at their junction. 11. Female tail lateral view. 12. Female genital system, lateral view. Scale bars = 0.1 mm 1, 7-12; 0.01 mm 2-6. Legend : a, amphid; d, denticle; de, deirid; e, secretory-excretory pore; i, infundibulum; lt, lateral thickening of spicule sheath; m, mouth opening; n, nerve ring; s, submedian cephalic papilla; sp, sphincter; t, central thickening at junction of spicule sheaths; v, vagina; ve, vestibule.

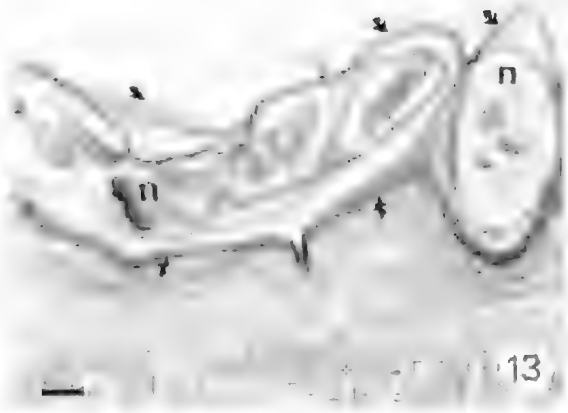


Fig. 13. Histological section of the stomach wall of *Petrogale concinna* showing localisation of *Woodwardostrongylus petrogale* sp. nov. (n) in a superficial squamous epithelial tunnel (arrows) formed by the nematode and the lack of any inflammatory reaction in the epithelium. Scale bar= 0.1 mm.

lacking. It belongs to the genus *Woodwardostrongylus* because it possesses a heavily sclerotised mouth region, a transversely striated buccal capsule and a row of sclerotised denticles on either side of the mouth opening, the latter characteristic being the most obvious feature defining the genus. The specimens described above are distinguishable from *W. woodwardi* and *W. obendorfi* primarily by the number of pairs of sclerotised oral denticles. *Woodwardostrongylus woodwardi* possesses 16 pairs of denticles while *W. obendorfi* possesses six pairs. In all of the specimens from *Petrogale* spp. from Arnhem Land, there are four large pairs of denticles. At each end of the rows of denticles, there is a pair of tiny denticles which has not been included in the determination of the number of pairs of denticles because these denticles are not obvious in lateral views and are only clearly visible in an apical view of the mouth region. The same terminal pairs of tiny denticles are evident in the scanning electron micrograph of the cephalic extremity of *W. obendorfi* published by Mawson (1976, fig.11) although the feature is not mentioned in the description and was not taken into consideration when determining the number of pairs of denticles on each side of the mouth opening. Whether these same terminal pairs of tiny denticles are present in *W. woodwardi* is not known. In addition, the specimens described above differ from congeners in spicule length, being 1.4 mm in *W. woodwardi* (Wood 1931), 1.7–2.1 mm in *W. obendorfi* (see Mawson 1976) compared with 0.90–1.07 mm in the species described above. There is also a corresponding difference in the length of the vagina which is 0.7–1.0 mm long in *W. woodwardi*, 0.8 mm in *W. obendorfi* and 0.31–0.48 mm in the species described here. Therefore, the material from rock wallabies from the Northern Territory is considered to represent a distinct species and the name *Woodwardostrongylus petrogale* sp. nov. is proposed for it, the name being derived from the generic name of the hosts.

In comparing the description of the new species with those of its congeners, several morphological characteristics of the genus warrant comment due to apparent inconsistencies or errors in published descriptions.

The oesophagus is described in the other species as being slender and clavate yet in *W. petrogale* there is a distinct constriction at the level of the nerve ring and the oesophagus is clearly divisible into corpus, isthmus and an elongate bulb. Specimens of *W. obendorfi* were examined and the same subdivisions of the oesophagus are evident although they have not been illustrated or described in the literature. The structure of the oesophagus is of considerable taxonomic significance because it is clavate in genera of the tribe Cloacininea (Stossich, 1899) of the Cloacinidae but is subdivided into corpus, isthmus and bulb in the tribe Pharyngostrongylinea Popova, 1952 into which *Woodwardostrongylus* has been placed (Lichtenfels 1980). The revised interpretation of these morphological characters therefore becomes concordant with the current taxonomic position of the genus.

In the original description of the genus, Wahid (1964, fig. 11) described and illustrated a "gubernaculum" in the type species, *W. woodwardi*. In the original description of the same species, however, Wood (1931) had been much more cautious and had described "an accessory piece ... present as an irregular shaped structure" which "appears to function as a guide for the spicules". Mawson (1976) stated that a gubernaculum was present in *W. obendorfi* but did not illustrate the structure. Durette Desset & Beveridge (1980) illustrated the "gubernaculum" of *W. obendorfi* but it is clear from the illustration that the structure is not a gubernaculum but the cordate thickening at the junction of the spicule sheaths (Beveridge 1982). A gubernaculum is absent in *W. petrogale*, although it does possess a cordate thickening and paired lateral thickenings of the spicule sheaths at their junction in common with all other cloacinids and chabertiids that have been examined for the presence of the structures (Beveridge 1987). It therefore seems most likely that a gubernaculum is absent in this genus and the cordate central thickening at the junction of the spicule sheaths has been mistaken for a gubernaculum in the past. This problem pertains to several genera of the Pharyngostrongylinea and has been discussed in detail by Beveridge (1982).

The morphology of the female genital system has not been described in detail for *W. woodwardi*,

although Mawson (1971) illustrated an essentially Y-shaped ovejector with parallel, amphidelphic uteri in her redescription of this species from rock wallabies from South Australia. The ovejector was described for *W. obendorfi* by Durette-Desset & Beveridge (1980) who illustrated a short Y-shaped vestibule with short sphincters and infundibula and suggested that the morphology of the ovejector was intermediate between that found in the Trichostrongyloidea and the Strongyloidea. Lichtenfels (1980) classified the ovejector of *Woodwardostrongylus* as typically strongyloid and as being Y-shaped superficially, but resembling related genera with I-shaped ovejectors in that the sphincters and infundibula are short. The ovejectors of *W. petrogale* are similar to those of *W. obendorfi* and confirm Lichtenfels' interpretation. Beveridge (1987) illustrated the ovejector of *W. petrogale* (described simply as *Woodwardostrongylus* sp.) and confirmed that it too agreed with the description and allocation suggested by Lichtenfels (1980). The ovejector in this genus is therefore considered to be a modified I-shaped ovejector according to the definitions of Lichtenfels (1980), with the modification probably being a direct result of the slender elongate body structure imposed upon this nematode genus by its localisation within epithelial tunnels of the gastric mucosa.

The systematic position of the genus *Woodwardostrongylus* has been the subject of some uncertainty. The type species was initially described as *Pharyngostrongylus woodwardi*, indicating a close relationship with the genus *Pharyngostrongylus* Yorke & Maplestone, 1926. Walnid (1964) subdivided the genus *Pharyngostrongylus* and erected the new genus *Woodwardostrongylus* for *W. woodwardi* but provided no explanation of its possible relationships with *Pharyngostrongylus*. Mawson (1971) redescribed *P. woodwardi* from rock wallabies and erected the new genus *Cristaecps* which she placed in the trichostrongyloid family Amidostomatidae (Travassos, 1919) based on the papers of Inglis (1965, 1968) dealing with convergence of the cephalic features of nematodes occurring buried in the stomach lining of their hosts and his view that many of the strongylate nematodes of Australian marsupials were members of the trichostrongyloid family Amidostomatidae. Subsequently, in describing *W. obendorfi*, Mawson (1976) recognised the synonymy of *Cristaecps* with *Woodwardostrongylus* but placed *Woodwardostrongylus* within the Amidostomatidae. Durette-Desset & Beveridge (1980) in contrast referred the genus to the Strongyloidea and Lichtenfels (1980) placed the genus in the strongyloid tribe Pharyngostrongylinea characterising the tribe primarily on the basis of a buccal capsule with transverse striations and thereby re-associating *Woodwardostrongylus* with *Pharyngostrongylus*, the genus with which it was first linked by Wood (1931). Beveridge (1982), in a revision of the Pharyngostrongylinea, omitted *Woodwardostrongylus* on the basis of uncertainties as to its affinities. The addition of a new species confirms the characters upon which the genus was erected while providing some modification to the definition of the genus, principally in relationship to the morphology of the oesophagus and ovejector and the absence of a true gubernaculum. The association with members of the Pharyngostrongyloidea is supported on the basis of a transversely striated buccal capsule, although this character occurs also in certain genera of the related tribe Zoniolaiminea (Popova, 1952) (Beveridge 1983). This morphological character appears to be the only feature upon which affinities can be judged because other characteristics of the genus are so highly modified to accommodate its unusual mode of existence within the stomach wall that they are phylogenetically uninformative. Therefore, in view of the lack of evidence to the contrary, and with the limited or even equivocal evidence of associations based on the presence of a striated buccal capsule, it seems reasonable to consider *Woodwardostrongylus* as a highly modified member of the tribe Pharyngostongylinea.

The host and geographical distributions of members of the genus are not yet fully elucidated. On the basis of current evidence, *W. obendorfi* occurs in a variety of rock wallabies, scrub wallabies and kangaroos along the eastern coast of Queensland and New South Wales. *W. woodwardi* is known from kangaroos originating from the northwest of Western Australia (although based on a zoo record from Britain) and from rock wallabies in South Australia, while *W. petrogale* is known from rock wallabies from Arnhem Land in the Northern Territory. The feature common to all members of the genus is that they parasitise rock wallabies but host relationships warrant more thorough investigation before any conclusions can be drawn from this observation.

Acknowledgments

Thanks are due to Dr J. E. Nelson for provision of the parasites upon which this description is based and to Dr D. M. Spratt for reading a draft of the manuscript.

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MESORHABDITIS KINCHEGENSIS SP. NOV. (NEMATODA: RHABDITIDAE) FROM ARID SOIL IN KINCHEGA NATIONAL PARK

*WARWICK L. NICHOLAS**

Summary

Nicholas, W. L. (1998) Mesorhabditis kinchegensis sp. nov. (Nematoda: Rhabditidae) from arid soil in Kinchega National Park. Trans. R. Soc. S. Aust. 122(2), 79-84, 29 May, 1998.

Mesorhabditis kinchegensis sp. nov. was collected in an anhydrobiotic state in dry red sand under a bluebush. Maireana pyrimidata (Benth.) Wilson, 1975. This is not the usual habitat for Mesorhabditis which is commonly associated with rich organic matter. The same species was also found in agricultural soil.

Key Words: Anhydrobiosis, Australia, Mesorhabditis, nematode, soil, taxonomy.

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Mesorhabditis kinchegensis sp. nov. was collected in an anhydrobiotic state in dry red sand under a bluebush *Maireana pyramidata* (Benth.) Wilson, 1975. This is not the usual habitat for *Mesorhabditis* which is commonly associated with rich organic matter. The same species was also found in agricultural soil.

Distinguishing features of this species are that in the male the tips of the long, almost straight, distally fused spicules, are abruptly turned ventrally. The formula for the arrangement of the bursal papillae is (2+5+3) with none of the papillae fused at their bases. In the female the tail is long and pointed so that the distance from the posterior vulva to the anus is about one and a half times the tail length.

KEY WORDS: Anhydrobiosis, Australia, *Mesorhabditis*, nematode, soil, taxonomy.

Introduction

Most species of *Mesorhabditis* have been reported from rich decaying organic matter such as humus, rotting wood or dung. Several species are usually found in close association with insects. Few species have been found in arid habitats. The species described herein was collected in an anhydrobiotic state from dry sandy soil with little organic matter. One other species of *Mesorhabditis*, *M. spiculigera* (Steiner, 1936) Osche, 1952 has been reported to survive anhydrobiosis (Sudhaus 1978).

Osche (1952) subdivided the very large genus *Rhabditis* into seven subgenera, one of which was *Mesorhabditis*, with the type species *Rhabditis spiculigera* Steiner, 1936. The taxonomy of Rhabditidae has been extensively reviewed by Sudhaus (1974, 1976, 1978) who has retained *Mesorhabditis* at subgeneric rank. This view was not supported by Andrassy in his authoritative monograph on the suborder Rhabditina (Andrassy 1983) in which he considered *Mesorhabditis* to be a separate genus within the Mesorhabditinae, a rank accepted in this paper. Sudhaus (1991) was not, however, persuaded by Andrassy's arguments that *Mesorhabditis* has generic ranking. The difference in ranking rests on the taxonomist's inclination towards 'lumping' or 'splitting'.

Within the suborder Rhabditina, the combination of characters that distinguish *Mesorhabditis* are a monodelphic female with the vulva well posterior to the mid-point of the body and a pointed conical tail. The male has long, more or less straight spicules that are distally fused. The male bursa is peloderian with paired bursal papillae arranged in three groups, typically two pre-cloacal, five peri-cloacal and three closer to the tip of the tail, expressed by the bursal formula (2+5+3).

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Material and Methods

Several samples of dry sandy soil were taken with a cylindrical metal corer, 12.5 cm long, 5 cm internal diameter, close to and below a bluebush on 4 November 1984. The samples were placed in plastic bags and returned to the laboratory in Canberra. Ten days later subsamples of 5 g were placed on tissue paper in tap water in Baermann funnels. After 18 h the funnels were drained and the nematodes collected. From one subsample, taken from directly beneath the bluebush, fifteen specimens of a new species of *Mesorhabditis* were found (together with many other nematodes). This species was not found in any of the other samples.

The specimens of *Mesorhabditis* were fixed in 5% formalin and transfered to 5% aqueous glycerol, which was concentrated by evaporation at 40° C, then mounted on slides in anhydrous glycerol with cover slips supported by glass beads and ringed with Glycegel (Gurr). Drawings and measurements were made with a camera lucida attachment on a Zeis Ultraphot microscope.

Type material has been deposited in the National Nematode Collection (ANIC) at the CSIRO Division of Entomology, Canberra ACT.

Mesorhabditis kinchegensis sp. nov.
(FIGS 1-8)

Holotype: ♂ Kinchega National Park, NSW, 4.xi 1984, ANIC Nematode Collection slide 0000005,

specimen 00000007.
Paratypes: 6 ♂♂, 5 ♀♀, Kinchega National Park, 4.xi.1984, ANIC Nematode Collection slides 0000006-12, specimens 00000008-19.

Measurements: Table 1. Measurements in µm.
Description of Holotype male

Body cylindrical, slightly tapered at head, rather bluntly truncated at hind end (Fig. 1), tail short with peloderan bursa (Figs 1,3). Cuticle finely annulated, lateral field appears as three parallel lines beginning in cervical region and extending as far as tail (Fig. 3). Six offset, rounded, clearly separated lips, each bearing a prominent labial papilla (Fig. 5). Buccal cavity cylindrical, without pharyngeal collar, glottis possessing minute denticles, probably two (Fig. 5). Pharynx with strong muscular corpus, slightly expanded at metacorpus, narrow isthmus, surrounded by nerve ring, valved pharyngeal bulb terminating in very short trilobed cardia, surrounded by intestinal tissue (Fig. 2). Secretory-excretory pore, ventral, level with base of isthmus (Fig. 2). Intestine, initially filling pseudocoel, becoming compressed about halfway along body by gonad, followed by rectum opening at cloaca (Fig. 1). Tail short, sharply pointed. Single testis reflexed dorsally, leading to short vesicula seminalis and long vas deferens. Cloaca surrounded by a peloderan bursa with 10 pairs of papillae arranged (2+5+3) (Fig. 3). Bursal papillae not fused at base, short posterior pair curled over. Two long narrow nearly straight spicules, capitulum distinct, distally fused, tips abruptly angled ventrally at about 25° to the main part, just beyond a slight constriction (noteh) (Fig. 4). Gubernaculum a short straight rod. Posterior deirids at level of middle of spicules (Fig. 3).

Paratypes and other males
Measurements: Table 1.

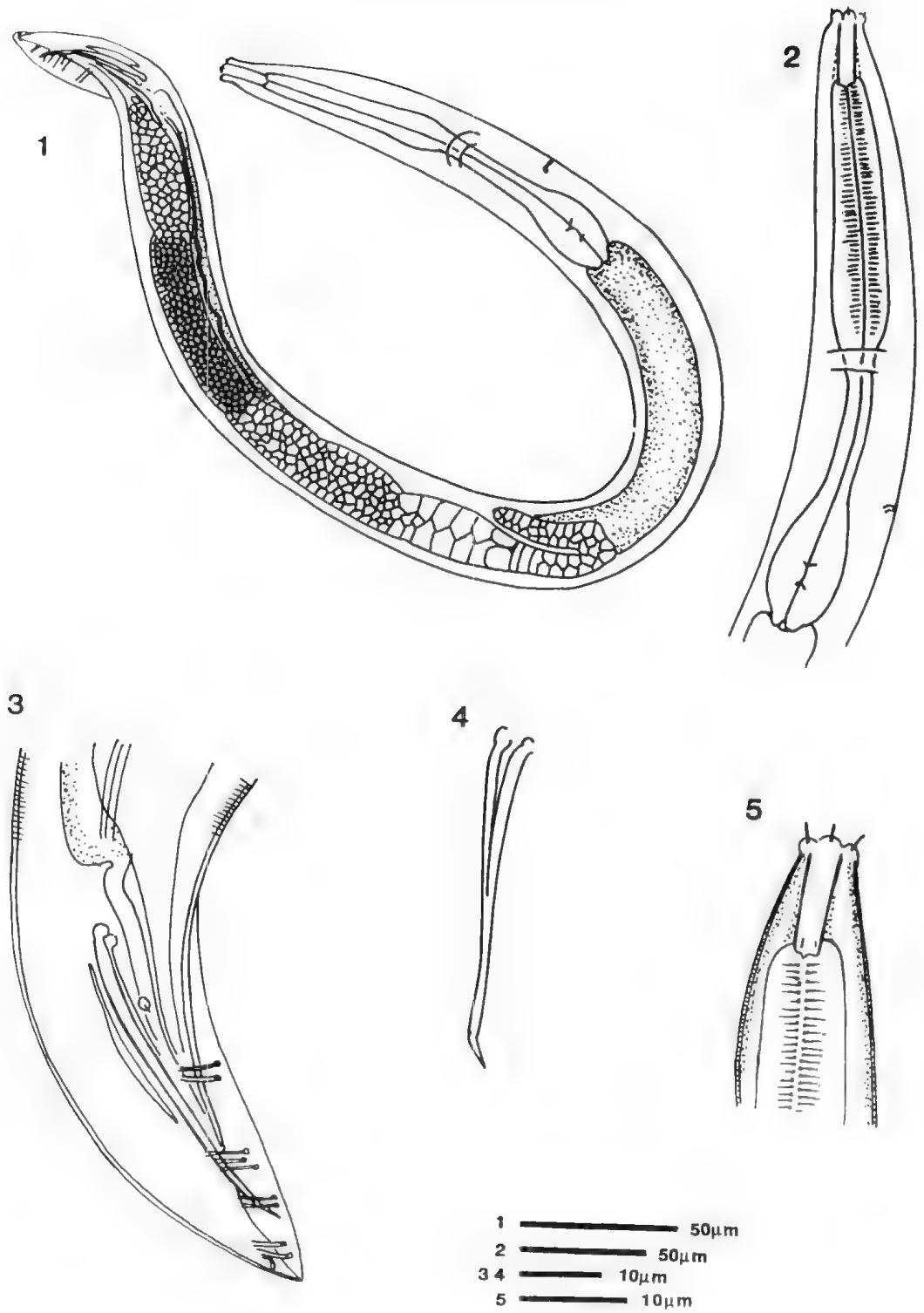
All the male paratypes closely resemble the holotype. The level at which the spicules fuse, about 50% of their length, can only be clearly seen by squashing and rolling the specimen under a cover slip, which renders the specimen useless as a type specimen

Female paratypes
Measurements: Table 1.

Female paratypes closely resemble males (Figs 6,7) except for reproductive organs and tail (Fig. 8). Homodromous ovary reflexed dorsally in mid region of body. Uterus extending to just beyond short vagina and vulva. One paratype female (Figs 6-8) possesses sperm in a short transitional region between ovary and uterus and six developing eggs, about 15 µm in diameter and varying from 15 - 24 µm in length. Amphid fovea, a minute oval slit at base of lateral lips, visible only in this paratype

TABLE 1. *Measurements of* Mesorhabditis kinchegensis *sp.nov.*

Sex/Type	Male/Holo	Male/Para n=6			Female/Para n=5		
		Mean	SD	Range	Mean	SD	Range
Length	524	482	39.30	432-533	543	71.96	467-662
Max. width	28	30	3.83	25-34	30	2.94	23-35
Buccal cavity	15	15	2.37	14-16	15	1.51	14-16
Corpus	61	54	1.27	51-57	58	1.51	56-60
Pharynx	129	126	4.27	119-130	122	6.91	118-128
Head to nerve ring	92	72	11.25	56-86	71	6.22	61-76
Head to secretory/excretory pore	116	92	10.42	77-106	81	20.10	55-103
Head to intestine	142	138	5.01	132-141	135	8.09	131-112
Head to gonad flexure	224	210	19.85	188-245	242	56.69	205-284
Head to vulva	–	-			439	61.96	378-455
Head to anus	490	459	36.91	410-507	493	57.21	355-518
Gonad length	288	278	13.97	268-295	301	134.14	186-535
Rectum length	39	31	4.08	23-34	32	6.10	20-35
Tail	22	23	3.31	18-27	50	14.77	32-76
Vulva to anus		-	-	-	65	7.89	57-76
Spicule	45	46	3.98	41 51	-		
Gubernaculum	16	21	2.56	18-24			
De Man's a	18.7	17	3.06	12.7-18.0	17.9	2.42	15 4-20 7
De Man's b	3.7	4	0.37	3.0-4.1	4.0	0.47	3.3-4.7
De Man's c	23.8	21	2.41	19.2-25 9	11.5	2.41	8.7-14.5
De Man's V%	-	-	-	-	81	2.32	77-82

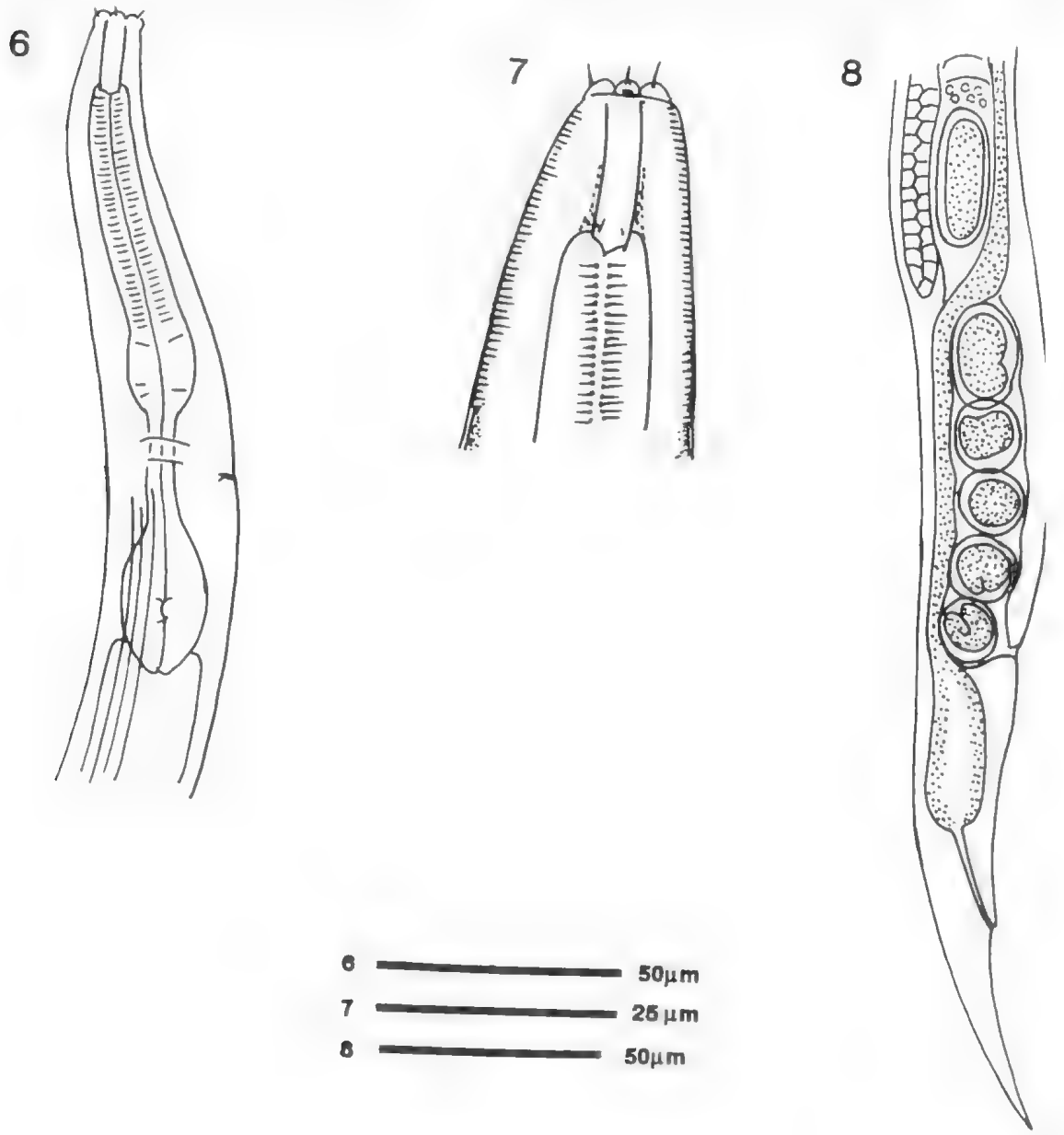


Figs 1-5. Holotype male. 1. Entire male. 2. Cervical region. 3. Cloacal region with spicules, gubernaculum, bursa and bursal papillae and lateral line in lateral view. 4. Spicules orientated to show fusion. 5. Head and buccal cavity.

female (Fig. 7). Tail conical and sharply pointed (Fig. 8). Vulva posterior and distance from vulva to anus about 1.5 x tail length. Lateral line marked by three incisures extending from mid pharyngeal region to caudal region (Fig. 6).

Differential diagnosis.

Mesorhabditis spiculigera (Steiner, 1936) Osche, 1952, is the only other species reported to survive periods in anhydrobiosis (Sudhaus 1978). It has a world-wide distribution and has been reported from New Zealand but not from Australia. It differs from *M. kinchegensis* sp. nov. in possessing a longer narrower buccal cavity, fusion of the bases of bursal rays 4, 5 and 6 and the tips of the spicules, though notched, are not angled ventrally. The ratio of length to width of the buccal cavity in *M. spiculigera* is about 10 : 1 (illustrated by Sudhaus 1974 Fig. 7), whereas in *M. kinchegensis* it is about 4 : 5. Two other species, *M. szunyoghi* Andrassy, 1961 and *M.*



Figs 6-8. Paratype female. 6. Cervical region also showing the three incisures of the lateral line. 7. Head. 8. Posterior body showing reproductive organs.

longespiculosa (Schuurmans Stekhoven, 1915) Dougherty, 1955, also have a notch close to the tip of the spicules, but unlike *M. kinchegensis*, their spicule tips are not angled ventrally beyond the notch.

Andrassy (1983) provides a useful key to the 17 species he recognises, a summary of diagnostic characters and references to taxonomic descriptions. Several species, *M. oschei* (Körner in Osche, 1952) Dougherty, 1955, *M. megachilis* (Sudhaus, 1978) Andrassy, 1983, *M. irregularis* (Körner in Osche, 1952) Dougherty, 1955, *M. szunyoghi*, *M. juglandicola* (Fuchs, 1937) Dougherty, 1955, *M. sudhausi* and *M. inarumensis* (Méyl, 1953) Dougherty, 1955 can be clearly distinguished by having a shorter female tail so that the distance from vulva to anus is much greater than the tail length. In the new species the distance is only about 1.5 x the tail length. A variety of features distinguishes other species from *M. kinchegensis*. In *M. mianki* (Sudhaus, 1978) Andrassy, 1983 the spicules are much shorter (29–36 µm) compared with 41–51 µm in *M. kinchegensis*). The buccal cavity of *M. anisomorpha* (Sudhaus, 1978) Andrassy, 1983 is asymmetric, the pharynx of *M. cranganorensis* (Khera, 1968) Andrassy, 1983 is unusually long, one third of body length. *Mesorhabditis africanus* Andrassy, 1982 has labial papillae curved inwards, *M. altima* (Körner in Osche, 1952) Dougherty, 1955 has pointed lips, *M. tenuispiculum* (Körner in Osche, 1952) Dougherty, 1955, *M. belari* (Nigon, 1949) Dougherty, 1953 and *M. inarumensis* possess only nine bursal rays, the middle group having four instead of the more usual five. In *M. striatica* Dassonville & Heyns, 1984, described by Dassonville & Heyns (1984) after the publication of Andrassy's monograph, the lateral line has five incisures rather than the more typical three, as in *M. kinchegensis*. Sudhaus (1978) has observed aberrations in the tail length and bursal rays of individual specimens but the characters used to distinguish *M. kinchegensis* are consistent in all the type specimens described in this paper.

Habitat

Soil around plant roots. The type specimens were collected in dry sand in an anhydrobiotic state from around the roots of bluebush, *Maireana pyramidata*, in Kinchega National Park, NSW. Three males of the same species were collected by M. Hodda from a field of lupins on The Soil Conservation Experimental Farm at Cowra, NSW. These are in the ANIC collection, Nematode Collection slides 0001290, 0001295 and 0001286 but are not included as paratypes, as they come from a very different habitat and are mounted on slides with several other species of nematodes.

Distribution

At present the species is known from only two localities in New South Wales.

Discussion

The type-specimens of *Mesorhabditis kinchegensis* sp. nov. come from an atypical habitat for *Mesorhabditis*, namely, arid soil with little organic matter in Kinchega National Park, although this species has also been collected from agricultural land. Kinchega National Park has a very irregular annual rainfall, averaging 235 mm, and an annual evaporation rate of 2000 mm. Temperatures reach 49° C in summer and fall to 0° C in winter. Most of the previously described species of *Mesorhabditis* have been found in decomposing organic matter such as mouldy or rotting wood, or humus (Andrassy 1983). Several others have been found in close association with insects such as scarabid beetle larvae. *Mesorhabditis megachilis* was associated with hymenopteran nests (Andrassy 1983). *Mesorhabditis sudhausi* has been reported from soil (Andrassy 1983) and *M. striatica* from fresh water (Dassonville & Heyns 1984). *Mesorhabditis spiculigera*, the other species known to survive in anhydrobiosis, has been found in rotting wood and horse dung. Its dauer larvae were associated with dung beetles (Sudhaus 1978).

Acknowledgments

I am grateful to Ms J. Smith for collecting samples from Kinchega National Park and Dr M. Hodda, for making specimens from CSIRO Nematology collection available for study.

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FIRST QUEENSLAND RECORD OF THE BURROWING FROG CYCLORANA CRYPTOTIS TYLER & MARTIN, 1977 (ANURA: HYLIDAE)

BRIEF COMMUNICATION

Summary

During fauna surveys conducted in Cape Melville National Park (150 km north-west of Cooktown) and adjacent areas, new species and new records of vertebrates and earthworms were obtained[1,2]. Following a thunderstorm on 21.xi. 1995, large numbers of frogs were found in a localised area (14°34′45′′ S, 144°29′50′′ E) approximately 7-9 km west by road of the Wakooka Outstation. A call unfamiliar to me was in the large chorus. Observation revealed a species of burrowing frog of Cyclorana not recorded in Queensland. Thirteen males and one female were collected. The call was recorded, tissues sampled and photographs taken.

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On the basis of morphology and call I tentatively identify the frog as *Cyclorana cryptotis*, a small burrowing frog previously known from northern Western Australia and the Northern Territory.

Individuals conform in colour and appearance to the description of *C. cryptotis* Tyler and Martin, with a highly mottled dorsum of slate grey and salmon with a distinct salmon post-orbital bar (Fig. 1). The appearence is strikingly similar to the photograph in Tyler *et al.* 1982. In preservative, the salmon colouration was lost. The nuptial pads were salmon and faded in preservative. The ventral surface was white and males had a slate throat. The tympanum was covered with skin in all animals. Toes were half-webbed with no expanded terminal discs.

Fig. 1. Male *Cyclorana cryptotis* from west of Wakooka Outstation, Queensland.

The general appearance is of a dumpy and robust frog (Fig. 1). Measurements, following previous methods[4], fall within the range of *C. cryptotis*[4]. Snout-vent length ranges from 35.7-45.9 mm, with the only female measuring 38.1mm. Legs are short (TL/S-V 0.33-0.39) and the eye to naris distance is greater or less than the internarial span (E-N/IN 0.955-1.141) (Table 1).

Frogs were found in temporary, rain-filled pools along a drainage line in low, open woodland on clay soils. The vegetation was dominated by *Melaleuca stenostachya* and *Eucalyptus leptophleba* (Fig. 2). Altitude was 40 ± 10 m.

Call duration was 503 msec with a pulse repetition rate of 113 pulses sec^{-1} and a dominant frequency of 800 Hz. The pulse repetition rate is lower than those males of *C. cryptotis* described in the literature and Lake Argyle area (183-193 pulses sec^{-1}, 26 km NE Lake Argyle Tourist Village[4]; 145-160 pulses sec^{-1}, [G. F. Watson pers. comm. 1997], Lake Argyle; 158 pulses sec^{-1} for holotype, Daly Waters[5]) (Table 2). Temperatures at the calling site were 28.2° C (water) and 27.2° C (air).

Cyclorana cryptotis was calling while floating in water. When the vocal sac inflated the anterior half of the body was lifted. The inflation and deflation of the vocal sac caused the body to rock in a manner similar to *Notaden melanoscaphus* observed elsewhere in Cape York. At other localities in its range *C. cryptotis* usually calls whilst floating in water (G. F. Watson pers. comm. 1997) although the holotype was calling from land (A. A. Martin pers. comm. 1997). The single female was collected floating in the water in axillary amplexus. Two other species of *Cyclorana*, *C. brevipes* and *C. novaehollandiae*, called from the banks of pools whereas *Limnodynastes ornatus* called with *C. cryptotis* in the pools.

The presence of *C. cryptotis* near Wakooka Outstation represents a range extension of 900 km east from previous locality records obtained by Davies, Tyler and Watson at Borroloola, Northern Territory (SAMA R 43702, 16°12' S 136°51' E). The intervening area across the gulf plains has not been extensively sampled and additional populations may be expected. The location of all records for *C. cryptotis* is in a band across northern Australia from Derby, Western Australia to Wakooka Outstation near Cape Melville between 14°30' S and 17°20' S.

Other frogs collected with *C. cryptotis* were : *C. brevipes*, *C. novaehollandiae*, *Litoria alboguttata*, *L. caerulea*, *L. rubella*, *Limnodynastes ornatus*, *Notaden melanoscaphus* and *Uperoleia mimula*.

Voucher specimens of *C. cryptotis* collected at the Wakooka site are in the Atherton office of Department of Environment collection Nos N 30 000, N 72018-20, 72023-25, 72035-36, 72040-44.

TABLE 1. *Morphological measurements of 14* Cyclorana cryptotis *from west of Wakooka Outstation, Queensland.* Abbreviations follow Tyler & Martin (1975).

	SVL	TL/SVL	HW/SVL	HW/TL	ED/HW	E-N/IN
Range	35.7-45.9	0.339-0.39	0.36-0.43	0.923-1.169	0.26-0.343	0.955-1.141
Mean	39.509	0.356	0.386	1.085	0.294	1.065

Fig 2. Habitat of *Cyclorana cryptotis* west of Wakooka Outstation, Queensland. Frogs were calling from the temporary pool.

Morphologically these specimens conform closely with *C. cryptotis*. However in view of the size of its range extension as well as the differences in call structure, the identification should be regarded as provisional until substantiated by biochemical analysis.

Dr M. Davies, University of Adelaide and Dr A. A. Martin, Royal Melbourne Zoological Gardens read an early version of the manuscript and provided helpful comments. Associate Professor G. F. Watson, University of Melbourne provided call analysis data. Field assistance was provided by M. Blackman, Q. Hart and R. Worall. C. Frith supplied the *C. cryptotis* photograph. The referees, Associate Professor M. J. Tyler and Dr A. A. Martin, made significant contributions to the manuscript. All of this assistance is gratefully acknowledged.

TABLE 2. *Call variation within* Cyclorana cryptotis.
Superscript numbers in source column refer to references. W – Water temperature, A – air temperature, at calling sites.

Source & call sample	Locality	Dominent frequency	Call duration (milliseconds)	No. of pulses	Pulse sec	Calls min $^{-1}$	Temperature °C
This paper n=1	Wakooka, Qld	800	503	58	113.3	77.4	28.2 (W)
G. F. Watson (pers. comm. 1997) n=2	Lake Argyle area, WA	920	439-455	65-74	145.8	83.9	
Holotype[3]	Daly Waters, NT	1060	530	-	158	-	24.1 (A)
Tyler *et al*,[4] n=1	Lake Argyle area, WA	850-1100	330-348	61-70	183-193		26.9 (A)

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THE PREVALENCE AND DISTRIBUTION OF NEMATODES IN THE LARGE INTESTINES OF SHEEP IN SOUTH AUSTRALIA

BRIEF COMMUNICATION

Summary

Nematodes from three genera (Trichuris Roederer, 1761, Oesophagostomum Molin, 1861 and Chabertia Railliet & Henry, 1909) have been identified from the large intestine of sheep in Australia[1]. However, there is relatively little information on their distribution and prevalence. Oesophagostomum venulosum (Rudolphi, 1809) and Chabertia ovina (Fabricius, 1788) are believed to be widely distributed, particularly in winter rainfall areas[2,3] and Trichuris ovis (Abildgaard, 1795) and T. skrjabini Baskakov, 1924 are common species in sheep and goats[4].

Transactions of the Royal Society of S. Aust. (1998), **122**(2): 87-88

BRIEF COMMUNICATION

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Nematodes from three genera (*Trichuris* Roederer, 1761, *Oesophagostomum* Molin, 1861 and *Chabertia* Railliet & Henry, 1909) have been identified from the large intestine of sheep in Australia[1]. However, there is relatively little information on their distribution and prevalence. *Oesophagostomum venulosum* (Rudolphi, 1809) and *Chabertia ovina* (Fabricius, 1788) are believed to be widely distributed, particularly in winter rainfall areas[2,3] and *Trichuris ovis* (Abildgaard, 1795) and *T. skrjabini* Baskakov, 1924 are common species in sheep and goats[4].

Beveridge and Ford surveyed the distribution and prevalence in South Australia of the economically important trichostrongyloid nematodes of sheep, which occur in the stomach and small intestine, and reported that some were better adapted to hot dry environments than others[5]; nematodes in the large intestine were identified only incidentally.

In the present study the prevalence and regional distribution of nematodes of the large intestine of sheep in South Australia was determined by examining freshly collected caeca and colons of 313 sheep collected from 116 widely distributed localities (Fig. 1) from 1991-1993. Information on farm management, age, sex or breed of sheep was unavailable and provision for the possibility of seasonal variations in infection was not possible in the collection of material. Intestines were opened, emptied, washed in water and the internal surface was inspected for nematodes which occasionally adhere to the gut wall. A 1/64 subsample of the intestinal contents was examined for immature nematodes using an Olympus stereo-microscope. The remaining contents were washed through a 670 µm sieve. Nematodes were collected, fixed in 10% buffered formalin and cleared in lacto-phenol for identification. Male and female nematodes were identified by comparison with published descriptions of species[3,6,7]. Four nematode species from three genera were found; their prevalence in three rainfall zones is shown in Table 1. Fifty-eight percent of sheep were infected with nematodes. The mean numbers and range of burdens of adult nematodes and the number of localities from which each species was recovered are shown in Table 2.

Trichuris ovis and *T. skrjabini* were common and widely distributed with the latter species more prevalent. Both nematodes occurred in 13% of animals and in 71% of these cases *T. skrjabini* was the predominant species. Significantly fewer *T. ovis* were found in the low rainfall zone (<250 mm) than in areas with higher rainfall ($\chi^2 = 9.1$; $p < 0.02$).

Oesophagostomum venulosum was the most common nematode recovered and was most prevalent in sheep from areas with more than 500 mm of rainfall. Nematodes of all three genera occurred concurrently in only four animals, all from the highest rainfall zone (>500 mm). Fourth stage larvae of *O. venulosum* were the only immature nematodes found; these were present in 38 animals from 24 localities, 17 with an annual rainfall greater than 500mm. Wetter areas of South Australia are apparently more favourable for the transmission of *O. venulosum* than drier areas.

Banks[3] detected *C. ovina* in "notable" numbers in South Australia forty years ago but did not consider it to be important. The influence of highly effective anthelmintics, since their introduction in the 1960s, may have contributed to the current low prevalence of *C. ovina*. *Trichuris* spp. are generally regarded as harmless[1], but have been associated

TABLE 1. *Prevalence (%) according to rainfall of nematodes in the large intestine of sheep in South Australia.*

Parasite	Overall	Rainfall zone 200 - 349mm	350 – 499mm	≥500mm
Trichuris ovis	20	10	22	28
Trichuris skrjabini	32	32	34	28
Oesophagostomum venulosum	33	30	29	59
Chabertia ovina	5	6	4	5

TABLE 2. *The mean number and range of nematode burdens and the number of localities (in 250-349mm (a), 350-499mm (b), >500mm (c) rainfall zones) from which each species was recovered.*

Nematode species	Mean	Range	No. of localities		
			a	b	c
Trichuris ovis	7	0-63	11	13	15
Trichuris skrjabini	7	0-60	20	21	17
Oesophagostomum venulosum	15	0-261	22	20	20
Chabertia ovina	4	0-19	3	6	3

The total localities in each rainfall zone - (a) = 23, (b) = 44 (c) = 49

with deaths of sheep in Australia during drought conditions[8]. *Oesophagostomum venulosum* is non-pathogenic[9]. Immature *C. ovina* cause intestinal damage during their development but adults are less pathogenic[7].

Natural nematode infections in sheep often consist of a mixture of genera and species, some of which appear to have little effect on their own but may contribute to disease caused by more pathogenic species[1]. Although the parasites found in this survey are not considered to be economically important, the data supplement previous records of gastro-intestinal nematodes of sheep in this region of Australia.

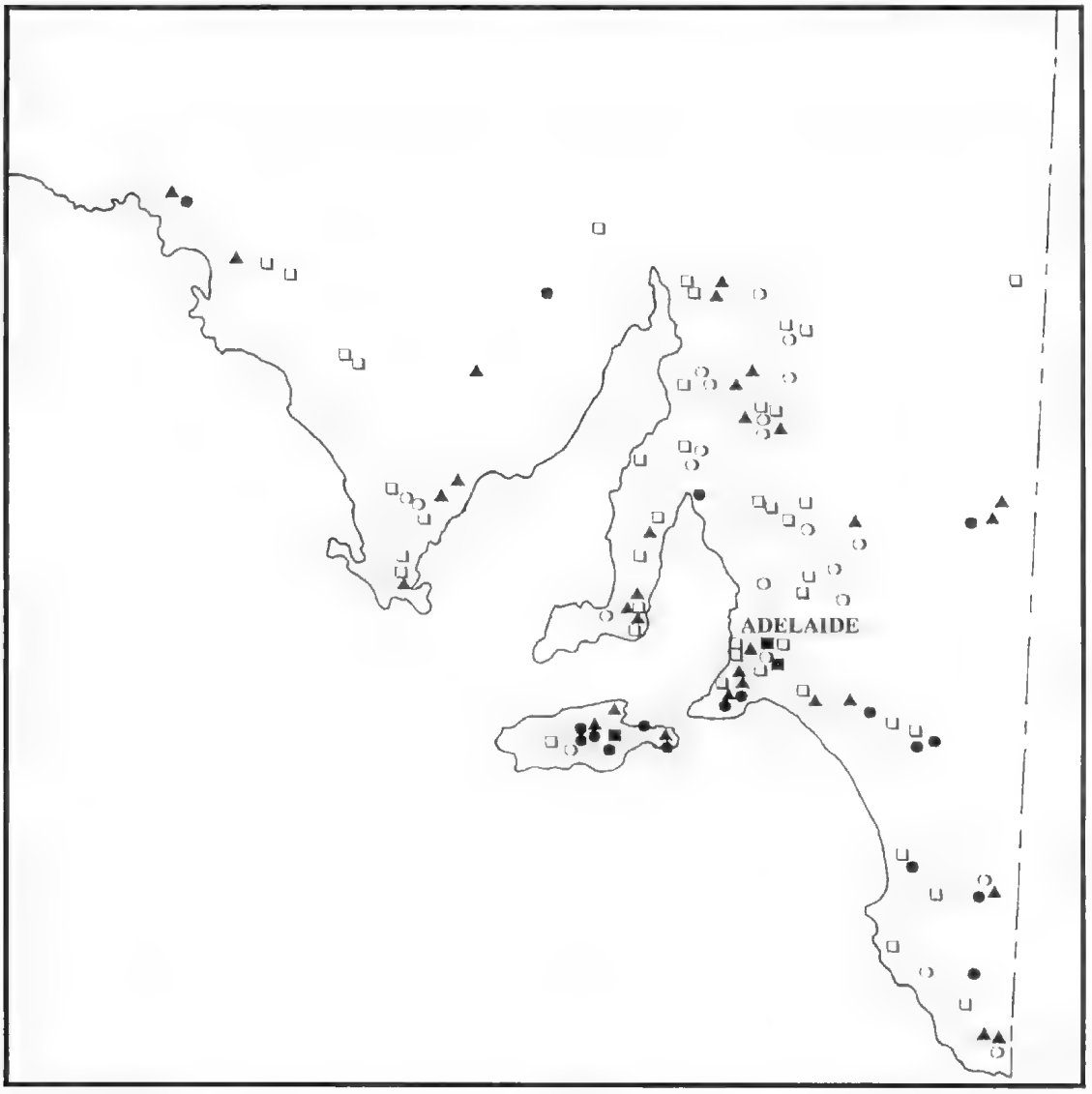

Fig. 1. Distribution of samples examined from sheep in South Australia. One to 4 sheep were examined at each locality. Negative for nematodes ○, one nematode species ⊥, two species ▲, three species ●, four species ■.

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VOL. 122, PARTS 3 & 4
30 NOVEMBER, 1998

Transactions of the Royal Society of South Australia

Incorporated

Contents

PUBLISHED AND SOLD AT THE SOCIETY'S ROOMS
SOUTH AUSTRALIAN MUSEUM, NORTH TERRACE, ADELAIDE, S.A. 5000

TRANSACTIONS OF THE

ROYAL SOCIETY OF SOUTH AUSTRALIA

INCORPORATED

VOL. 122, PART 3

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*By Helene A. Martin**

Summary

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The vegetation of the late Paleocene and middle Eocene was mainly forests with minor herbaceous swamp communities. Gymnosperm pollen dominated the late Paleocene palynofloras and proteaceous taxa were very diverse. Pollen of Cunoniaceae/Elaeocarpaceae is moderately common and there is a wealth of angiosperm pollen. In the mid Eocene, pollen of Araucariaceae, Casuarinaceae and a little *Nothofagus* were dominant and there was a great diversity of angiosperms. The Pliocene-Pleistocene palynofloras have a limited diversity with pollen of the herbaceous/shrubby Cyperaceae, Poaceae, Asteraceae and Chenopodiaceae/Amaranthaceae dominant. Casuarinaceae and Myrtaceae are the only likely trees and there is relatively little pollen of these families, hence the vegetation was open shrublands similar to that found in the region today. There are, however, some disparate taxa in this Pliocene/Pleistocene palynoflora that are unknown in the arid region today.

KEY WORDS: Central Australia, Palynology, Late Cretaceous, Tertiary, Palaeovegetation.

Introduction

This study of the Delhi-Santos-French Petroleum Co. (Aust.) Poonarunna-1 well was undertaken in the hope that it would shed some light on the evolution of the arid flora and vegetation. The location of the well, northeast of Lake Eyre, and within the first sand ridges of the Simpson Desert (Magnier[1]), is strategically placed for this purpose (Fig.1).

Finding preserved pollen in arid/semi-arid regions is a major problem. Preservation requires anaerobic conditions in permanent lakes, swamps, bogs etc. Once the climate becomes dry, these permanently-wet sites disappear. Alternate wetting and drying in seasonal swamps and lakes destroys pollen. Moreover, when pollen is deposited in permanently-wet sites, it must be buried deeply enough to escape the effects of a later fluctuating water table of a future drier climate, if it is to remain preserved. Deep weathering has undoubtedly destroyed much of the pollen record, but where pollen has been preserved, good palynofloras were recovered. This paper documents the pollen species recovered and reports on the palynostratigraphy of the Tertiary and upper Cretaceous sequences intersected in the Poonarunna-1 well

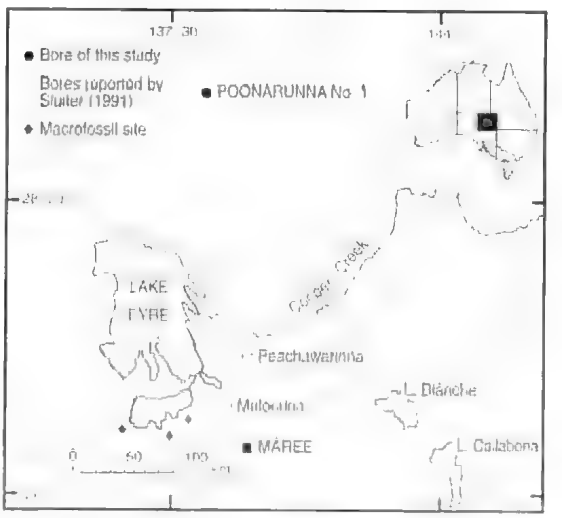

Fig 1. Locality map.

Geology

Poonarunna-1 was sunk to 1,696 m with the intention of exploring the Palaeozoic or Proterozoic basement strata beneath the Permian or Mesozoic

School of Biological Science, University of New South Wales Sydney NSW 2052.

Magnier, P. (1964) Well completion report of Poonarunna No. 1 South Australia (unpubl.).

cover beds. The well established a good reference for Mesozoic studies (Magnier[1]), but there was no interest in the Cainozoic. The present study concentrates on the Tertiary palynostratigraphy but includes the uppermost of the Cretaceous which establishes the Tertiary/Cretaceous boundary.

In the well completion report (Magnier[1]), the following units are defined from the lithology and correlation of gamma-ray logs with supplementary information from sonic logs and resistivity. The Tertiary and Quaternary were defined as consisting of Quaternary sand and alluvium (0-5.5 m) and white dolomitic limestone interbedded with grey marly, sandy clay (5.5-95.4 m). The Late Cretaceous (Cenomanian) (95.4-667.5 m) was defined as the Winton Formation, consisting of alternating grey to dark grey silt, fissile shale and siltstone with disseminated pyrite. The present study records the palynology of the upper 146 m only, i.e. the Cainozoic and the upper part of the Late Cretaceous sequence.

The upper part of the Winton Formation examined in this study is remarkably uniform in appearance. From the palynology, the Cretaceous-Tertiary boundary occurs at about 110 m, and the interval from 95-110 m should be reassigned to the Eyre Formation, since the Winton Formation elsewhere in the Lake Eyre Basin is correlated with the upper *Phimopollenites pannosus* and *Plicatella distocarinata* Zones, of Albian to Cenomanian age (Krieg *et al.* 1991).

The Eyre Formation (Callen *et al.* 1995) is a widespread and distinctive fluvial to fluviolacustrine sand unit, but lithological variations occur in some channel facies. Plant fossils are characteristic and locally abundant. Carbonaceous horizons within the Eyre Formation contain spores, pollen and a few dinoflagellates of late Paleocene to middle Eocene age. The Eyre Formation was deposited in large meandering and braided streams (Krieg *et al.* 1991).

The unit between 5.5 and 95.4 m is correlated with the Etadunna Formation of probable late Oligocene to Pliocene age, but it is most likely largely early Miocene. The Etadunna Formation was deposited in an evaporative flood plain-lacustrine environment, under a climate drier than that of the Eyre Formation (Krieg *et al.* 1991; Callen *et al.* 1995).

Materials and Methods

Only cuttings were available for the present study. The possibility of contamination is greater with cuttings, but with proper drilling and sampling procedures, reliable samples may be obtained. This topic is fully discussed by Martin (1984a). In the present study, the Late Cretaceous assemblages contained very few Tertiary grains and barren samples in the Cainozoic section suggest that contamination is minimal and these samples are reliable.

The samples were treated with hydrochloric and hydrofluoric acids to remove mineral matter. Controlled oxidation with cold Schulze solution and potassium carbonate was used to clear the residues, which were then mounted in glycerine jelly (Brown 1960; Gray 1965).

The palynofloras were assigned to zones using the ranges of diagnostic species. The Tertiary palynofloras were quantified with counts of about 150-200 grains and percentages were based on the total pollen count. The pollen spectra derived from the counts provide a basis for interpretations of the palaeovegetation.

An assessment of the abundance of microscopic carbonised particles in the Tertiary assemblages was made. The formation of these particles is controversial. When they are found in mid-late Tertiary and Quaternary sediments, it is generally accepted that they were formed from burning and are charcoal particles (Luly *et al.* 1980; Martin 1987; Kershaw *et al.* 1991). On the other hand, Schopf (1975) has suggested that black carbonised particles have formed by oxidation at the surface of swamps. However, there have been numerous studies which show that charcoal may be distinguished from other black carbonised material (Scott 1989; Cohen & Spackman 1977; Sander & Gee 1990) and charcoal may be found in sediments of any age.

Palynostratigraphy

Late Cretaceous palynostratigraphy is based on that of Helby *et al.* (1987), the systematic palynology is presented in Appendix 1, the species identified are given in Table 1 and the ranges of diagnostic species in Figure 2.

110-146 m. Plicatella distocarinata *Zone.*
Cenomanian

The assemblages in this zone lack the distinctive *Phyllocladidites mawsonii* and *Proteacidites* spp. of the *P. mawsonii* Zone. *Plicatella distocarinata* and *Trilobosporites trioreticulatus*, whose ranges end within the *P. mawsonii* Zone are present. These assemblages thus fit the *P. distocarinata* Zone of Cenomanian age (Fig. 2). *Amosopollis cruciformis* is usually present in the Cenomanian in the Lake Eyre Basin (N. F. Alley pers. comm. 1995), but it has not been recorded from these assemblages. Burger (1993) reports that *Forumisporis dailyi* has not been recorded from the *P. distocarinata* Zone, but it is present in the sample from 115-119 m of this study (Table 1).

Spores of ferns, lycopods and bryophytes are

TABLE 1. *Late Cretaceous species identified from Poonarunna-1.*
+, present. ++, common.

Depth (m)	110-113	115-119	128-131	134-137	143-146
Spores					
Aequitriradites spinulosus	+				+
A. verrucosus					+
Baculatisporites comaumensis			+	+	+
Balmeisporites glenelgensis	+				
B. holodictyus	+				+
B. tridictyus	+		+		
Camarozonosporites australiensis	+			+	
Ceratosporites equalis	+			+	
Cicatricosisportes sp. of Burger		+			++
Cicatricosisportes spp.		+			+
Clavifera triplex	+			+	
Crybelosporites punctatus	+				
C. striatus			+		
Cyathidites australis	+	+		+	+
C. minor	++	++	++	++	++
Dictyophyllidites sp.	+	+			
Foraminisporis dailyi		+			
F. wonthaggiensis		+	+		+
Foveogleicheniidites confossus			+	+	
Gleicheniidites circinidites	++	+	+	++	+
Laevigatosporites ovatus	++		+	++	
Microfoveolatosporites canaliculatus				+	
Ornamentifera sp. cf. *O. sentosa*			+		
Perotrilites jubatus	+			+	+
Plicatella distocarinata	+	+		+	+
Polycingulatisporites sp.	+				
Reticuloidosporites arcus	+		+	+	
Retitriletes austroclavatidites	+				
Ruffordiaspora australiensis	+		+	+	
R. ludbrookiae	+				
Sestrosporites pseudoalveolatus			+		
Stereisporites antiquasporites		+	+	+	
S. pocockii				+	
Stoverisporites microverrucatus	+	+	+		+
Trilobosporites tribotrys	+				+
T. trioreticulosus	+				+
Triporoletes sp. cf. *T. simplex*		+	+	+	
Gymnosperms					
Alisporites sp. cf. *A. grandis*		+	+	+	+
Araucariacites australis	+	+	+	+	+
Corollina sp. cf. *C. classoides*	+		+	+	+
Ginkgocycadophytus nitidus				+	
Microcachryidites antarcticus	+	+	+	+	+
Podocarpidites ellipticus	+	+	+	+	+
P. exiguus					+
Podosporites sp.					++
Trichotomonosulcites subgranulatus	++	+			
Angiosperms					
Cupuliferoidaepollenites cf. *C. parvulus*					+
Dicopopollis sp.	+				
Foveotetradites fistulosus	+				

TABLE 1 continued...

Depth (m)	110-113	115-119	128-131	134-137	143-146
Liliacidites sp. cf. *L. kaitangataensis*	+				
Liliacidites sp.	+				
Phimopollenites augathellaensis	+		+	+	+
P. pannosus	+		+		+
Senectotetradites varireticulatus	+				
Tricolpites sp. cf. *T. upwasensis*	+				
Algae					
Botryococcus braunii			+		
Homologinella sp.	+				
Lecaniella sp.			+		
Saeptodinium gravattensis	+		+		+
Schizosporis reticulatus		+			+
Acritarch sp. indet.	+				

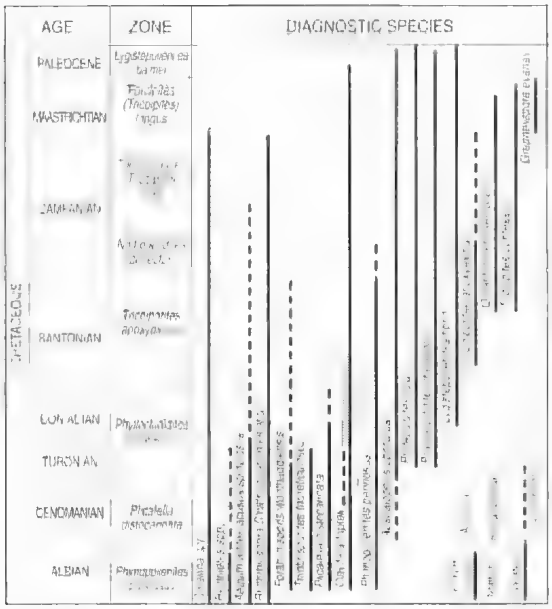

Fig. 2. Ranges of diagnostic Cretaceous species, from Helby *et al.* (1987).

particularly diverse and abundant in this zone. *Cyathidites minor* is very common in all of the samples and *Ruffordiaspora/Cicatricosisporites* spp., *Foraminisporis wonthaggiensis*, *Gleicheniidites circinidites*, *Laevigatosporites ovatus* and *Stereisporites antiquasporites* are sometimes abundant. Gymnosperm pollen is diverse and well represented with *Podosporites* spp. common in some samples. Most of the trees in the palaeovegetation would have been species of gymnosperms. There is a small angiosperm pollen content with *Phimopollenites augathellaensis*, *P. pannosus* and *Foveotetradites fistulosus* being the most common (Table 1). The angiosperm palynoflora may be placed in Suite III, of Late Aptian-Early Cenomanian age (Burger 1990), for it lacks the triporate forms of Suite IV which starts within the Cenomanian (Burger 1993).

The five sequential samples are essentially the same age, but there are quantitative differences. The three oldest assemblages are diverse with a good representation of gymnosperm pollen, but the angiosperm content is restricted in diversity and abundance. The abundance of gymnosperm pollen suggests that forest would have have been a major part of the vegetation. The assemblage at 115-119 m has fewer gymnosperms than the other assemblages and an unusual abundance of *Stereisporites antiquasporites*, with affinities to *Sphagnum*, and *Foraminisporis wonthaggiensis*, similar to the living hepatic *Nothylas bruetelii* (Dettmann 1963). This assemblage suggests that there were extensive bogs or wetlands and fewer forest trees in the immediate vicinity. The uppermost assemblage has a diverse gymnosperm palynoflora, indicating forest similar to that of the oldest assemblages, and an increased angiosperm palynoflora. The megasporangiate water ferns, *Balmeisporites* spp., are also well represented at this level.

The microplankton content of these assemblages is low with only a few forms represented. *Lecaniella* sp. and *Schizosporis reticulatus* have probable affinities with the Zygnemetaceae (Grenfell 1995), a family of filamentous green algae usually found in shallow, flowing fresh water. *Botryococcus braunii* may be found in fresh and brackish water (Pentecost 1984) and *Saeptodinium gravattensis* is a fresh water dinoflagellate (Harris 1973).

TABLE 2. *Tertiary species identified in Poonarunna-1.*
Percentages of total pollen count are given. +, present but not counted in the counts of 150 or more grains.

Depth (m)	6-9	73-76	94-97	97-101	101-104	104-107	107-110
Spores							
Azolla sp.		+					
Camarozonosporites amplus			+	0.6	0.6	+	
C. bullatus				+		+	
Camarozonosporites sp.		1.2					
Ceratosporites equalis		0.6	1.3				
Cyathidites australis		0.6	+	2.4	0.6	1.3	1.3
C. paleospora	1.3	5.4	1.9	3.0	1.9		0.6
C. splendens		+	+	+	+	+	
Dictyophyllidites concavus		8.4	2.6	1.2	1.3	1.3	
Foveotriletes lacunosus				+	0.6		
Gleichenia circinidites		1.8	1.9	1.2	4.5	0.6	5.9
Grapnelispora evansii							+
Laevigatosporites ovatus		1.2	0.6		0.6	3.9	0.6
Polypodiacoisporites sp. cf. *P. retirugatus*		+					
Polypodiidites spp.		0.6			0.6	0.6	
Retitriletes austroclavatidites				0.6		+	
Stereisporites sp.			0.6		1.9	0.6	
Todisporites sp.				+	0.6		
Triletes sp. cf. *T. tuberculiformis*		1.8		+	0.6		0.6
Triporoletes reticulatus	0.7	+					0.6
Verrucosisporites cristatus		+					
Unidentified	0.7			1.2			0.6
Gymnosperms							
Araucariacites australis	1.3	14.4	1.3				0.6
Cupressaceae/Taxodiaceae		0.6	0.6	+	0.6	1.3	0.6
Dacrycarpites australiensis			0.6	2.4		0.6	2.6
Dilwynites granulatus		1.2	1.9	1.2	2.6	+	
D. tuberculatus		0.6	1.3	1.2		0.6	
Lygistepollenites florinii		8.4	7.2	7.3	3.2	2.6	5.9
Microcachryidites antarcticus			1.9	1.2	0.6	2.6	0.6
Phyllocladidites mawsonii		0.6	9.9	10.9	7.7	4.6	3.3
P. reticulosaccatus							+
Podocarpidites spp.	0.7	4.2	24.3	24.2	25.0	24.3	28.1
Trichotomonosulcatus subgranulatus			1.9	3.0	3.8	0.6	0.6
Angiosperms							
Acaciapollenites myriosporites	2.6						
Aglaoridia qualamis						0.6	
Amosopollis dilwynites				+	+		
Arecipites sp. cf. *A. minutiscabratus*				+			+
Australopollis obscurus			5.9	6.0	3.2	2.6	9.1
Beaupreaidites elegansiformis		+					
Chenopodipollis chenopodiaceoides	19.2						
Cunoniaceae (tricolporate)		0.6	3.4	1.2	3.2	6.6	3.9
Cunoniaceae (bicolpate)						3.3	
Cupaneidites orthothechus		0.6					
Cyperaceae	10.6	1.8	1.9	2.4		1.3	0.6
cf. *Dodonaea*	0.7						
Elaeocarpaceae			1.9	1.2		1.3	0.6
Ericipites crassiexinus		1.8	0.6	+			
Gothanipollis bassensis				+			
Graminidites monoporites	7.3						

TABLE 2 continued...

Depth (m)	6-9	73-76	94-97	97-101	101-104	104-107	107-110
Haloragacidites haloragoides	+						
H. harrisii	8.6	12.0	3.9	3.0	3.2	2.0	3.9
Ilexpollenites austroclavatus			0.6	0.6			0.6
Lewalanipollis cf. *L. rectomarginis*				+			
Lewalanipollis cf. *Persoonia*		+					
Liliacidites lanceolatus						+	
Malvaceaerumpollis sp.	0.7						
Malvacipollis diversus		0.6	0.6				
M. subtilis		+					
Milfordia homeopunctata		0.6		+	0.6	1.3	
M. hypolaeniodes		1.8		1.2	0.6	0.6	1.3
Myrtaceidites eucalyptoides	0.7						
M. parvus	0.7	0.6	1.3				
M. verrucosus		+					
Myrtaceae unidentified	3.9	1.8		+	0.6	2.0	
Nothofagidites emarcidus	0.7	9.6					
N. deminutus		+					
N. falcatus		0.6					
N. vansteenisii		0.6					
Nuxipollenites kempii	1.3						
Polyoriticites oblatus			1.8				
Polyporina granulata	1.3						
Propylipollis ivanhoensis			5.3	4.8	1.9	0.6	
P. latrobensis			+				
P. cf. *pseudomoides*				+		+	
P. cf. *P. reticuloscabratus*				+	0.6	+	
Propylipollis sp.			+	+			
Proteacidites adenanthoides			3.3	1.2		0.6	0.6
P. adenanthoides/crassus							0.6
P. angulatus			+	1.2	1.3	2.0	1.3
P. annularis				0.6	0.6		
P. cooksoniae				0.6		+	+
P. crassus			1.3	0.6	0.6		0.6
P. fromensis				0.6	1.3	1.3	1.9
P. grandis					1.3	+	+
P. incurvatus		+					
P. sp. cf. *P. incurvatus*					+		
P. cf. *obscurus*		+					
P. cf. *stipplatus*		0.6	0.6	0.6			0.6
Proteacidites spp.		2.4	1.8	3.0	7.0	3.3	1.9
Quintiniapollis psilatispora			1.9		0.6	0.6	
Rhopites alveolatus		+					
Rhopites sp. cf. *R. alveolatus*							+
Santalumidites cainozoicus		+					
Sapotaceoidaepollenites rotundus							+
Simplicepollis meridianus		0.6		+	0.6		
Simpsonipollis sp.							+
Sparganiaceaepollenites barungensis	0.7	0.6	1.3	+	1.9	2.6	0.6
Tricolpites sp. cf. *T. asperamarginatus*		+					
T. sp. cf. *T. confessus*				+			+
T. sp. cf. *T. discus*		+					
T. phillipsii			+				
T. thomasii		+					
Tricolporites angurium		+					
T. leuros				0.6	0.6	2.0	

TABLE 2 continued...

Depth (m)	6-9	73-76	94-97	97-101	101-104	104-107	107-110
Tricolporites substriatus/T. paenestriatus			2.4				
Tricolporopollenites endobalteus		0.6					
Triorites miniscules							+
Triporopollenites ambiguus		+					
Tubulifloridites antipodica/simplis	27.8						
Unidentified angiosperms	7.9	6.0	2.5	9.1	13.6	15.0	14.3
Algae							
Botryococcus		++	+	+	+		+
Debarya	+						
Morkallacysta pyramidalis							+
Pediastrum	+		+				
Summary of major pollen groups							
Spores	2.0	21.5	9.2	9.7	14.1	11.8	13.7
Gymnosperms	1.4	29.9	51.3	51.5	43.6	37.5	42.5
Casuarinaceae	8.6	12.0	3.9	3.0	3.2	2.0	3.9
Myrtaceae	5.3	2.4	1.3		0.6	2.0	
Cunoniaceae/Elaeocarpaceae			5.4	2.4	6.4	13.2	5.8
Nothofagus		10.8					
'Proteaceae'		3.0	12.8	13.3	12.8	9.2	8.5
Asteraceae	27.8						
Cyperaceae	10.6	1.8	1.9	2.4		1.3	0.6
Poaceae	7.3						
Restionaceae		2.4		1.2	1.3	2.0	1.3
Sparganiaceae	0.7	0.6	1.3		1.9	3.3	0.6
Chenopod type	19.2						

These Cenomanian palynofloras are generally similar to those of Bathurst Island, northern Australia, described by Norvick & Burger (1975), except that the former contains freshwater microplankton whereas the latter has a very diverse marine dinoflagellate flora. Norvick & Burger (1975) illustrate the known occurrences of Cenomanian palynofloras and, except for three non-marine localities in the Eromanga Basin, all the others are around the northern, western and southern periphery of Australia. The stratigraphically important species of the Cenomanian have been studied, but other than this study, the report by Norvick and Burger (1975) is the only Australian report to document all the palynomorphs in Cenomanian assemblages.

Tertiary palynostratigraphy follows Stover and Partridge (1973), Macphail (1996) and studies in Central Australia (Krieg *et al.* 1991; Sluiter 1991; Alley *et al.* 1996; N. F. Alley pers. comm. 1994). The systematic palynology is given in Appendix 2, the species identified in Table 2 and the pollen diagram in Figure 3. The definitions of the pollen groups are given in Table 3.

TABLE 3. *Definition of the major pollen groups used in the pollen diagram, Fig. 3.*
A full list of taxa is presented Appendix 2.

Name on diagram	Taxa included in the group
Spores	All spore taxa
Araucariaceae	*Araucariacites australis*
Podocarps	*Podocarpidites* spp.
Lagarostrobos	*Phyllocladidites mawsonii*
Dacrydium	*Lygistepollenites florinii*
Other gymnosperms	All other taxa under gymnosperms
Cunoniaceae	Cunoniaceae and Elaeocarpaceae
Casuarinaceae	*Haloragacidites harrisii*
Myrtaceae	All species of *Myrtaceidites*
Nothofagus	All species of *Nothofagidites*
'Proteaceae'	All species of *Beaupreaidites, Lewalanipollis, Proteacidites* and *Propylipollis*
'Callitriche'	*Australopollis obscurus*
Cyperaceae	Cyperaceae
Poaceae	*Graminidites monoporites*
Asteraceae	*Tubulifloridites* spp.
Chenopod type	*Chenopodipollis chenopodiaceoides*

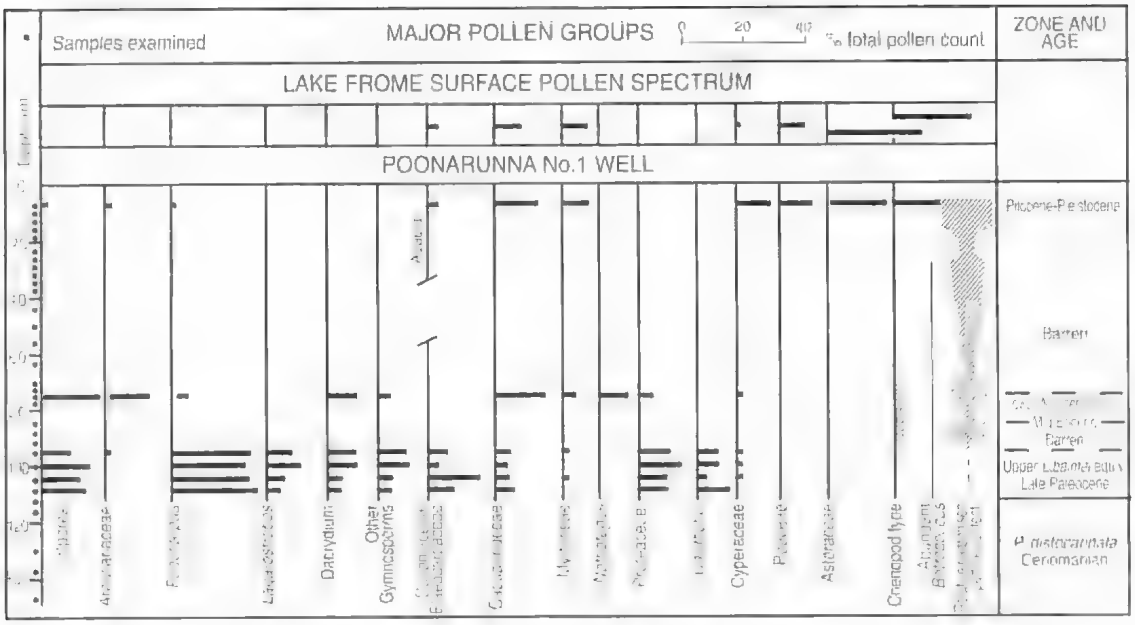

Fig. 3. Pollen diagram. For definitions of the pollen groups, see Table 3. The surface pollen spectrum from Lake Frome (Sluiter & Kershaw 1982) represents the present vegetation and is added for comparison.

94-110 m. Upper Lygistepollenites balmei *Zone equivalent, late Paleocene*

Gymnosperm taxa are diverse and their pollen may constitute more than half the count (Fig. 3, Appendix 3). *Podocarpus* (*Podocarpidites* spp.), is the most common, and *Lagarostrobos* (*Phyllocladidites mawsonii*) is well represented. Pollen from the angiosperm taxa Cunoniaceae/Elaeocarpaceae, Casuarinaceae (*Haloragacidites harrisii*) and Myrtaceae (*Myrtacidites* sp.) is present but that from *Nothofagus* (*Nothofagidites*) has not been detected in this study, although is is usually present but extremely rare in this zone (N. F. Alley, pers. comm. 1994). There is a profusion of the proteaceous taxa *Beauprealites*, *Lewalanipollis*, *Propilypollis* and *Proteacidites* spp., (see Appendix 2) with *Proteacidites adenanthoides*, *P. angulatus*, *P. crassus*, *P. fromensis*, *P. cooksoniae*, *P. leightonii* and *P. reflexus* the most common. Cf. *Cullitricha* (*Australopollis obscurus*), Restionaceae (*Milfordia* spp.) and Cyperaceae (*Cyperaceaepollis* sp.) are present also. There is a number of unidentified angiosperm pollen types present, and while they may not be important for stratigraphic consideration, they indicate a rich and abundant angiosperm element in the late Paleocene. The content of carbonised particles is low.

These assemblages are assigned to the Upper *L. balmei* Zone equivalent. The occurrence of *Gambierina crassa* and *Triporopollenites* cf. *T. confessus*, whose ranges end at the top of the Maastrichtian (Helby *et al.* 1987) is anomalous, but they may be reworked. Other distinctive taxa usually found in the Maastrichtian are lacking and quantitatively, these assemblages are unlike those of the Maastrichtian.

Comparisons

When compared with the *L. balmei* Zone of the Gippsland Basin, the stratigraphic ranges of some diagnostic and characteristic species are not the same in the two regions. For example, *Proteacidites crassus*, *P. leightonii* and *P. reflexus*, present in Poonarunna begin their ranges in the Eocene of the Gippsland Basin and *P. fromensis* in Poonarunna has not been reported from the latter site (Stover & Evans 1973; Stover & Partridge 1973). In contrast, Cunoniaceae, Cyperaceae and *Milfordia hypolaenoides* of this study are not found in the Gippsland Basin. The rich and abundant proteaceous flora are a feature of the assemblages in central Australia but they are 'neither particularly diverse nor particularly common' in those of the Gippsland Basin (Stover & Evans 1973, p. 59). There are similarities, however, in that gymnosperm taxa are diverse and common in both localities, although the nominate species of the zone, *L. balmei*, has not been found in this study. *Phyllocladidites* spp. and *Australopollis obscurus* are characteristic of both regions.

The late Paleocene *L. balmei* Zone is reported from the Southern Monaro in the highlands of southeast Australia (Taylor *et al.* 1990). Gymnosperm pollen

dominates some of the assemblages and *Nothofagus* may be abundant in others. Angiosperm taxa are well represented and the proteaceous element may be relatively abundant in some. *Australopollis obscurus* and species of *Myrtaceidites* have not been recorded from the Monaro, unlike the other late Paleocene localities. Cunoniaceae, Cyperaceae and Restionaceae are lacking, in keeping with other localities in southeast Australia, but in contrast to that of central Australia.

In the Otway Basin, the *Gambierina edwardsii* Zonule (Harris 1971) is late Paleocene in age also (Stover & Partridge 1973). Gymnosperm pollen is abundant and *A. obscurus* is usually present. The proteaceous taxa are well represented in the Otway Basin, but Cunoniaceae, Cyperaceae and Restionaceae have not been recorded.

Sluiter (1991) records late Paleocene palynofloras from the BMR Muloorina 2 bore, southeast of Lake Eyre. The assemblages are dominated by an exceptional abundance (up to 67%) of Cunoniaceae. Gymnosperm pollen is common and *Nothofagus* rare, similar to those of Poonarunna-1, but the proteaceous taxa are not particularly abundant. The late Paleocene-early Eocene suite is similar but with an increase in Myrtaceae, the proteaceous taxa and *Australopollis obscurus*, with an overall decrease in gymnosperm pollen (Sluiter 1991). The palynofloras of these two localities near Lake Eyre are thus very similar, but Poonarunna-1 has much less Cunoniaceae.

76-94 m

Pollen is extremely sparse in this interval and is insufficient for study. *Botryococcus*, however, is sometimes abundant, indicating a fresh-brackish water lake environment. Carbonised particles are present throughout in small amounts but are particularly abundant at the 79-85 m level.

73-76 m. Lower Nothofagidites asperus *Zone equivalent, mid Eocene*

The gymnosperm pollen content is less than that of the *L. balmei* Zone equivalent but is still considerable. Araucariaceae (*Araucariacites australis, Dilwynites granulatus*) and *Dacrydium* (*Lygistepollenites florinii*) are the most abundant in this group. The angiosperm flora is particularly rich with Casuarinaceae (*Haloragacidites harrissii*) and *Nothofagus* (*Nothofagidites* spp.) moderately abundant. The spore content (ferns, bryophytes, lycopods) is moderate. The proteaceous content is restricted in diversity and abundance. The carbonised particle content is low.

This assemblage is similar to that of the mid Eocene unit of Peachawarinna-2 of Lake Eyre Basin (Sluiter 1991). As well as the general characteristics expressed above, Cunoniaceae or Myrtaceae (*Myrtaceidites* spp.) may be common and the proteaceous content may be more diverse in the assemblages of Peachawarinna-2. It also contains species which first appear in the late Eocene Middle *Nothofagidites asperus* Zone of the Gippsland Basin, viz. *Agathoridia qualmis, Proteacidites* cf. *P. stipplatus* and *Tricolpites thomasii* (Stover & Partridge 1973, 1982). However, Sluiter (1991) records all of these species from the mid Eocene unit of Peachawarinna-2.

Assemblages at Nelly Creek, southern Lake Eyre Basin (Alley *et al.* 1996) are dominated by pollen of Casuarinaceae (*Haloragacidites harrissii*) and gymnosperm pollen is relatively common with Araucariaceae (*Araucariacites australis, Dilwynites granulatus*) the most abundant. Angiosperm pollen is well represented and there is a wealth of proteaceous species. Myrtaceae (*Myrtaceidites*) and *Nothofagus* (*Nothofagidites*) are consistently present. *Tricolpites thomasii* and *Proteacidites stipplatus*, with ranges of Lower and Middle *N. asperus* Zone equivalents in central Australia, are present also (Alley *et al.* 1996). The Poonarunna-1 assemblage thus compares well with those from Nelly Creek, with the exception that the proteaceous component is more diverse and abundant in the latter. The Poonarunna-1 assemblage is therefore assigned to the Lower *N. asperus* Zone equivalent of mid Eocene age.

Comparisons

Mid Eocene macrofossil assemblages at Nelly Creek, Poole Creek and in some of the silcrete floras have a number of taxa with botanical affinities in common with the Poonarunna-1 microfossil assemblage, and the general characteristics are similar. Four proteaceous leaf taxa, *Agathis* (Araucariaceae), Podocarpaceae, *Gymnostoma* (Casuarinaceae) and *Myrtciphyllum* (Myrtaceae), are listed (Christophel *et al.* 1992). More detailed comparisons of macro- and microfossil assemblages are not possible because of the difference in provenance, transport and preservation of the plant parts found in the two types of assemblages. Leaf physiognomy yields invaluable evidence about the vegetation and this topic is discussed later.

The Poonarunna-1 assemblage has less *Nothofagus* and more Casuarinaceae when compared with the Lower *Nothofagidites asperus* Zone of the Gippsland Basin (Stover and Partridge 1973, 1982; Partridge 1976). As well, the ranges of many species are not the same in the two localities. The non-woody swamp taxa of Cyperaceae, Restionaceae and Sparganiaceae have not been reported from the Lower *Nothofagidites asperus* Zone of the Gippsland Basin.

This Poonarunna-1 palynoflora is probably time equivalent to the *Proteacidites pachypolus* Zonule of

the Otway Basin in Victoria (Harris 1971) which is rich in *Nothofagus* and proteaceous taxa. Mid Eocene floras are also found in the St Vincent Basin, South Australia, where the palynofloras have an abundance of fern spores but frequencies of gymnosperm, Casuarinaceae and *Nothofagus* pollen are low. There is a diversity of proteaceous and other angiosperm pollen, with no single group dominant (Alley 1987; Alley & Broadbridge 1992).

When the mid Eocene palynoflora at Poonarunna is compared with those of Anglesea (Christophel *et al.* 1987), the latter has more *Nothofagus* and fewer gymnosperms. Palynofloras at Bungonia (Truswell & Owen 1988) also have few gymnosperms when compared with those in Poonarunna.

61-73 m

Pollen was not recovered from this interval but the alga, *Botryococcus*, is present and very abundant from 67-73 m. The 70-73 m level has *Pediastrum* also. These algal species indicate a fresh-brackish water lake environment. The carbonised particle content is low through this interval, except for the 67-70 m level where it is high.

9-61 m

Pollen was not recovered from this interval. Carbonised particles are present throughout, increasing up the section, except for the 16-20 m level where they decrease.

6-9 m, Pliocene–Pleistocene

Asteraceae (*Tubulifloridites* spp.), Poaceae (*Graminidites monoporites*) and the chenopod type (*Chenopodipollis chenopodiaceoides*) make up the bulk of the pollen count; Casuarinaceae (*Haloragacidites harrisii*) and Myrtaceae (*Myrtaceidites* spp.) are present, but gymnosperm pollen and spores are minimal. Carbonised particles are extremely common.

This type of assemblage has not been recorded previously from central Australia and there is no direct means of dating it. The general quantitative aspects of the assemblage suggest a Pleistocene age, based upon experience in southeastern Australia (Martin 1987), but it lacks the distinctive Pleistocene *Tubulifloridites pleistocenicus* (Macphail 1996). *Polyporina granulata* of late Miocene–Pleistocene (Macphail 1996) is present. Frequencies similar to those shown in Fig. 3 may be found in shrublands of arid regions today (Stuiver & Kershaw 1982). When the Poonarunna-1 assemblage is compared with surface samples from shrublands around Lake Frome, it is remarkably similar, except for a greater Cyperaceae pollen content, suggesting that there was more swamp vegetation in the Pliocene–Pleistocene than there is at Lake Frome today.

Tubulifloridites spp. first appear in the mid Miocene of southeastern Australia (Stover & Partridge 1973), but there are numerous reports of these species from the early Miocene and a few from the Oligocene (Muller 1981). My experience has shown that most pollen types are not common in the early part of their ranges, but become more abundant later. At Poonarunna, *Tubulifloridites* is the most abundant group, suggesting a relatively young age, i.e. Pliocene if not Pleistocene.

0-6 m

No pollen was recovered. The charcoal particle content was very high.

Palaeovegetation and palaeoenvironment

The Cenomanian palynofloras are dominated by bryophytes, lycopods, pteridophytes and gymnosperms but the angiosperm content is relatively small and this suggests that the vegetation was mainly forest with gymnosperms forming the major part of the canopy, if not the whole of it. One palynoflora suggests more extensive bogs or wetlands, as discussed previously. These palynofloras predate the appearance of proteaceous and *Nothofagus* pollen types which become a distinctive element in younger palynofloras.

The late Paleocene palynofloras of Poonarunna-1 indicate that the region was mainly forest. The gymnosperms *Podocarpus* (*Podocarpidites* spp.), *Lagarostrobos*, the Huon pine (*Phyllocladidites mawsonii*) and *Dacrydium* (*Lygistepollenites florinii*) were common, and there was a diversity of other gymnosperm taxa, e.g. *Dacrycarpus* (*Dacrycarpites*), *Microcachrys* (*Microcachryidites*), Casuarinaceae (*Haloragacidites harrisii*), *Nothofagus* (*Nothofagidites* spp.), Myrtaceae (*Myrtaceidites* spp.), Cunoniaceae/Elaeocarpaceae were part of the forest canopy, though probably a relatively minor part. There is a wealth of proteaceous pollen types but most of them cannot be identified with living taxa. At least some of them are likely to have been forest trees, similar to the proteaceous trees found in rainforests today. Proteaceous species have a very low pollen representation (Kershaw 1970, 1971, 1976; Martin 1978); hence, these extinct proteaceous taxa were probably far more abundant in the Paleocene vegetation than is suggested by the pollen frequencies. Swamp communities were limited in extent and contained the non-woody taxa cf. '*Callitriche*' (*Australopollis obscurus*) (Macphail 1990), Cyperaceae and Restionaceae. Other angiosperms were diverse (Table 2) and if they were low pollen producers, as is the case with most insect pollinated species, they were probably more abundant than is suggested by the pollen counts.

A fresh water lake environment with copious *Botryococcus* and some *Pediastrum* succeeded the late Paleocene floras, through most of the presumed Eocene. There is, however, insufficient pollen for study through most of the sequence. Within this lake sequence, there is a layer of sediment with a good pollen content, suggesting that the lake had receded from this area and that it had become vegetated. The mid Eocene palynoflora in this layer suggests mainly forests with little non-woody swamp vegetation. Araucariaceae, *Dacrydium*, Casuarinaceae and *Nothofagus* were prominent, the proteaceous content was low at this particular location and there was a great diversity of other angiosperms.

The Pliocene-Pleistocene vegetation was probably open woodland or shrubland, generally similar to that of today in arid and semiarid regions. Trees, if present, were probably Casuarinaceae and Myrtaceae, but both of these families contain shrubby taxa as well as trees. *Acacia* (*Acaciapollenites myriosporites*) is present, and as *Acacia* has a very low pollen representation (Sluiter & Kershaw 1982), it may have been common in the vegetation, similar to that of today. The very low frequencies of Araucariaceae and *Podocarpus* may have resulted from long distance dispersal, or there may have been small, rare stands in the landscape. It is remarkable that a Plio-Pleistocene palynoflora has been preserved at all. A wetter climate and some condition(s) which allowed a more rapid burial of sediment must have prevailed for a brief interval.

If it is accepted that most of the carbonised particles result from burning, then the Tertiary record (Fig. 3) suggests that burning increased during the presumed Neogene, reaching a maximum in the Pliocene/Pleistocene. There was, however, episodic burning in the Eocene. Very few carbonised particles are found in the late Paleocene and Cenomanian palynofloras.

TABLE 4. *Register of illustrated specimens.*

Species	Fig.	Slide No.	England Finder coordinates
CRETACEOUS SPECIES			
Acritarch sp. indet.	10J	3060-3	W43-0
Aequitriradites spinulosus	4A, B	3063-3	O35-0
Aequitriradites verrucosus	4E, F	3064-1	T63-0
Alisporites sp. cf. *A. grandis*	9A	3060-3	K41-2
Araucariacites australis	9B	3064-1	P55-4
Baculatisporites comaumensis	4G	3064-1	J35-1
Balmeisporites glenelgensis	5A	3060-1	O35-0
Balmeisporites holodictyus	4H	3060-3	J51-1
Balmeisporites holodictyus	4I	3064-1	S60-0
Balmeisporites tridictyus	4B, C	3060-1	M34-1
Balmeisporites tridictyus	4D	3062-1	O56-3
Camarozonosporites australiensis	4J	3063-1	P47-2
Camarozonosporites australiensis	4K	3060-3	V33-1
Ceratosporites equalis	5E, F	3062-3	G34-4
Cicatricosisporites sp. of Burger	6C	3064-3	S49-4
Cicatricosisporites sp. of Burger	6D, E	3064-3	R41-0
Clavifera triplex	6J	3063-2	M59-0
Clavifera triplex	6K	3063-1	E29-1
Corollina sp. cf. *C. classoides*	9C	3062-3	V49-0
Crybelosporites punctatus	6L, M	3060-3	G49-0
Crybelosporites punctatus	7C	3060-3	V41-0
Crybelosporites striatus	7A, B	3062-1	R44-0
Cupuliferoidaepollenites cf. *C. parvulus*	9I	3064-1	W32-2
Cyathidites australis	6I	3063-3	S58-1
Cyathidites minor	6H	3061-3	M45-1
Dicopopollis sp.	9M, N	3060-1	J35-1
Dictyophyllidites sp.	6N	3060-3	S45-4
Foveotriletes dailyi	7D	3060-3	T48-1
Foveotriletes wonthaggiensis	6Q	3064-1	W55-1
Foveoglacihenidites confossus	7J, K	3062-3	Q33-0
Foveotetradites fistulosus	10A, B	3060-3	P31-2
Gleicheniidites circinidites	6P	3060-3	S40-2
Horologinella sp.	10L	3063-2	L60-3

TABLE 4 continued...

Species	Fig.	Slide No.	England Finder coordinates
Laevigatosporites ovatus	7G	3060-3	Y42-4
Lecaniella sp.	10C	3063-2	M54-0
Lecaniella sp.	10D, E	3063-3	O60-2
Lecaniella sp.	10F, G	3063-3	F50-0
Lecaniella sp.	10I	3061-1	H36-3
Liliacidites sp. cf. *L. kaitangataensis*	9P	3060-1	S33-0
Liliacidites sp.	9S	3060-1	N29-3
Microcachryidites antarcticus	9D	3060-3	V42-0
Microfoveolatosporites canaliculatus	8K, L	3063-1	Q43-0
Ornamentifera sp. cf. *O. sentosa*	7H, I	3062-1	O53-0
Perotrilites jubatus	7L, M	3064-2	F60-4
Perotrilites jubatus	8C	3064-2	N49-2
Phimopollenites augathellaensis	9O	3060-3	O36-0
Phimopollenites augathellaensis	9Q, R	3064-2	Q52-0
Phimopollenites pannosus	9U	3060-3	O36-3
Phimopollenites pannosus	9V	3060-3	G50-0
Plicatella distocarinata	4C, D	3060 3	N37-4
Podocarpidites ellipticus	9E	3960-3	X43-2
Podocarpidites exiguus	9F	3060-1	M29-4
Podosporites sp.	9H, I	3060-3	X39-4
Podosporites sp.	9J, K	3060-3	Y44-2
Polycingulatisporites sp.	8A, B	3060-3	F54-3
Reticuloidosporites arcus	8G	3063-3	O39-0
Retitriletes austroclavatidites	8D	3060-3	Y45-0
Retitriletes austroclavatidites	8E, F	3060-2	P40-0
Ruffordiaspora australiensis	6A	3063-3	J54-3
Ruffordiaspora ludbrookiae	6B	3060 3	M36-0
Saeptodinium gravattensis	10H	3060-3	Y37-0
Schizosporis reticulatus	10K	3064-3	O40-4
Senectotetradites varireticulatus	9T	3060-1	E40-3
Sestrosporites pseudoalveolatus	6O	3062-3	K41-3
Stereisporites antiquasporites	8N	3061-3	O50-0
Stereisporites antiquasporites	8O	3061-3	H46-3
Stereisporites pocockii	6F, G	3063-1	Q47-0
Stoverisporites microverrucatus	8M	3061-2	O59-0
Trichotomonosulcites subgranulatus	9G	3060-2	U65-0
Tricolporites sp. cf. *T. apoxyexinus*	9X,Y	3060-1	M61-3
Trilobosporites tribotrys	9I	3064-3	H45-0
Trilobosporites trioreticulosus	8H	3060-3	R48-4
Triporoletes sp. cf. *T. simplex*	8J	3060-3	X40-4
TERTIARY SPECIES			
Acaciapollenites myriosporites	13C	2983-1	N34-4
Aglaoridia qualamis	17G	3000-3	P41-2
Amosopollis dilwynites	13E	3057-2	S40-3
Amosopollis dilwynites	13F	3057-1	N36-0
Amosopollis dilwynites	13G	3006-3	D31-0
Araucariacites australis	12I	3000-1	O40-0
Arecipites sp. cf. *A. minutiscabratus*	13D	3006-1	X42-1
Australopollis obscurus	13N,O	3059-2	T55-0
Azolla sp.	11J	3000-2	J45-0
Beaupreaidites elegansiformis	13J, K	3000-2	L45-3
Botryococcus braunii	18B	3000-1	V42-3
Botryococcus braunii	18D	3000-1	V42-1
Camarozomosporites amplus	11A	3006-1	W38-4

TABLE 4 continued...

Species	Fig.	Slide No.	England Finder coordinates
Camarozonosporites amplus	11B	3000-3	O42-1
Camarozonosporites bullatus	11D	3059-2	O40-3
Camarozonosporites sp.	11E, F	3000-2	E47-0
Chenopodipollis chenopodiaceoides	13L	2983-1	Y53-0
Cunoniaceae (tricolporate)	13S, T	3058-3	O41-0
Cunoniaceae (bicolpate)	13U, V	3057-2	T37-1
Cupressaceae/Taxodiaceae	12D	3058-2	S55-3
Cyathidites paleospora	11I	3059-1	O60-2
Cyathidites splendens	11G	3059-1	V45-3
Cyathidites splendens	11H	3059-1	V52-2
Cyperaceaepollis	13M	3000-3	D39-0
Dacrycarpites australiensis	12L	3059-1	S50-0
Dicopopollis sp.	18F	3000-1	Q29-0
Dilwynites granulatus	12J	3000-1	R42-0
Dilwynites granulatus	12K	3006-2	W39-3
Dilwynites granulatus	13A	3006-2	V58-0
Elaeocarpaceae	13Z, AA	3005-1	K39-0
'Ephedra' notensis	13B	3006-2	L33-4
Ericipites crassiexinus	13P, Q	3000-1	R30-0
Gleichenia circinidites	11C	3059-3	L59-2
Gothanipollis bassensis	14A, B	3006-3	W57-1
Grapnelispora evansii	12A	3059-2	Q43-3
Haloragacidites haloragoides	13R	2983-1	O30-2
Haloragacidites harrisii	14G	3000-1	V41-4
Ilexpollenites austroclavatus	14D, E	3059-2	E49-4
Lewalanipollis cf. *L. rectomarginis*	16G	3006-1	F43-4
Lewalanipollis cf. *Persoonia*	15J, K	3000-3	C55-1
Liliacidites lanceolatus	14F	3058-3	V50-0
Lygistepollenites florinii	12G	3059-2	P41-1
Malvacipollis subtilis	14H, I	3000-1	Q28-0
Microcachryidites antarcticus	12N	3059-2	L34-1
Milfordia homeopunctata	14C	3000-1	Q28-0
Milfordia homeopunctata	14J	3000-1	P47-3
Milfordia hypolaeniodes	14K	3006-3	O49-0
Myrtaceidites eucalyptoides	14Q	2983-1	Q33-1
Morkallacysta pyramidalis	18C	3059-2	Q28-1
Myrtaceidites eucalyptoides	14R	2983-1	V41-2
Myrtaceidites verrucosus	14S	3000-1	S40-1
Nothofagidites emarcidus	14L	3000-1	K58-2
Nothofagidites deminutus	14N	3000-3	T48-0
Nothofagidites falcatus	14M	3000-2	P36-4
Nuxipollenites kempii	14O, P	2983-1	J46-1
Pancolpate sp.	18E	2983-1	T39-0
Panporate sp.	18G	2983-1	Q40-1
Pediastrum sp.	18A	3000-1	R53-2
Phyllocladidites mawsonii	12E	3059-3	R43-0
Phyllocladidites reticulosaccatus	12H	3059-2	Q42-4
Podocarpidites exiguus	12M	3059-3	K39-1
Polyorificites oblatus	14BB, CC	3000-1	O59-1
Polypodiaceoisporites sp. cf. *P. retiregatus*	11L, M	2983-1	J43-2
Polyporina granulata	17A, B	2983-1	L46-0
Propylipollis ivanhoensis	14T	3006-3	Q47-3
Propylipollis ivanhoensis	14W	3058-2	Q58-2
Propylipollis latrobensis	14X	3005-1	U40-0
Propylipollis sp. cf. *P. pseudomoides*	16B	3006-2	V64-0

TABLE 4 continued...

Species	Fig.	Slide No.	England Finder coordinates
Propylipollis sp. cf. *P. pseudomoides*	16C	3058-1	S56-4
Propylipollis sp. cf. *P. pseudomoides*	16D	3006-3	Q47-3
Propylipollis sp. cf. *P. reticuloscabratus*	14U	3006-3	S43-3
Propylipollis sp. cf. *P. reticuloscabratus*	14V	3058-1	S56-2
Propylipollis sp.	14Y, Z	3006-1	X39-1
Propylipollis sp.	14AA	3005-1	X43-4
Proteacidites adenanthoides	15A, B	3058-3	O49-2
P. angulatus	15G	3057-1	X57-0
P. angulatus	15H	3059-3	J38-0
P. cooksoniae	16A	3006-2	M50-0
P. crassus	15C, D	3059-3	L59-2
P. fromensis	15E, F	3059-1	O49-2
P. grandis	15I	3059-1	R60-4
P. incurvatus	15N	3000-1	S40-0
P. sp. cf. *P. incurvatus*	16N, O	3057-1	K34-1
P. cf. *obscurus*	16J, K	3006-1	K46-1
P. cf. *stipplatus*	16I	3006-2	S58-0
Proteacidites sp. 1	16E, F	3059-3	Q41-0
Proteacidites sp. 2	16L, M	3006-1	M51-0
Proteacidites sp. 3	16H	3059-3	Q51-2
Quintiniapollis psilatispora	17L	3000-3	C53-4
Retitrileles austroclavatidites	12B,C	3059-3	N59-2
Rhopites alveolatus	17E	3000-1	S40-2
Rhopites sp. cf. *R. alveolatus*	17P, Q	3059-2	U65-2
Santalumidites cainozoicus	17F	3000-1	X44-2
Sapotaceoidaepollenites rotundus	17J, K	3059-2	T62-1
Simplicepollis meridianus	17C, D	3000-1	K54-2
Simpsonipollis sp.	13H, I	3059-2	S27-0
Tricolpites sp. cf. *T. asperamarginatus*	17H, I	3000-1	P50-4
Tricolpites sp. cf. *T. confessus*	17O	3059-2	R41-0
Tricolpites sp. cf. *T. discus*	17M, N	3000-1	Q40-0
Tricolpites phillipsii	17T	3005-1	W43-4
Tricolpites thomasii	17U, V	3000-1	W39-1
Tricolpites sp.	18O, P	3058-2	Q51-2
Tricolporites angurium	17Z	3000-1	P29-2
Tricolporites leuros	17W, X	3005-1	Q46-0
Tricolporites sp. 1	17CC	3058-2	N41-0
Tricolporites sp. 2	17AA, BB	3057-1	T33-4
Tricolporites sp. 3	18I	3058-1	P55-2
Tricolporites sp. 4	18J, K	3058-1	W53-0
Tricolporites sp. 4	18L	3058-2	N42-4
Tricolporites sp. 5	18M, N	3057-1	W33-3
Tricolporopollenites endobalteus	17R, S	3000-1	O62-0
Triletes sp. cf. *T. tuberculiformis*	11K	3000-1	N54-3
Triorites minisculus	18Q	3058-2	S55-3
Triorites sp.	18H	3059-3	T33-3
Triporoletes reticulatus	12F	3059-2	S57-3
Triporopollenites ambiguus	17Y	3000-1	L43-4
Tubulifloridites antipodica/simplis	18R	2983-1	S39-2

The development of the arid flora and vegetation

The aim of this study was to find fossil evidence about the development of the arid flora and vegetation. The late Paleocene-mid Eocene palynofloras described here, with a substantial rainforest element, are clearly not arid adapted. The vegetation, however, grew on the floodplains and depositional basin, and such habitats would not be the first in the landscape to register aridity. Middle Eocene macrofossil assemblages from other localities in the Lake Eyre Basin have some large-leaved taxa, consistent with rainforest, and a variety of smaller leaved taxa, suggesting sclerophyllous vegetation (Christophel *et al.* 1992; Christophel 1994). The vegetation is interpreted as being gallery rainforest along the watercourses and sclerophyllous vegetation, adapted both to low fertility and seasonally dry conditions, in the interfluves. These macrofossil assemblages are unique to central Australia (Greenwood *et al.* 1990; Greenwood 1994).

The interval between the mid Eocene and the Pliocene-Pleistocene did not yield pollen. The Pliocene-Pleistocene assemblage is generally similar to that produced by the extant arid shrublands of Lake Frome (Fig. 3) but contains some disparate elements. *Dodonaea triquetra* (*Nuxipollenites kempii*) is found in this assemblage, but the modern species is restricted to wet sclerophyll forests of the southern half of the east coast of Australia (Martin 1997). *Dodonaea triquetra* is also present in the mid Eocene of the Lake Eyre Basin (Sluiter 1991) and probably became extinct in this region at some time after the Pliocene-Pleistocene.

There have been many studies on the flora of the arid zone that have generated various hypotheses about its origins. As many of the taxa in the arid zone show affinities with related taxa in adjacent regions, most of the hypotheses involve recruitment from the floras surrounding the arid zone (Barlow 1981). Such studies, however, do not reveal taxa which once grew in the arid zone and have become extinct there, such as *Dodonaea triquetra*. The fossil record suggests that the vegetation developed by continuous adaptation of some of the taxa already in the region (by evolution of new species) to a drying environment. Those taxa that could not adapt to the arid environment disappeared from the region.

Acknowledgments

I am indebted to N. F. Alley of the Department of Mines and Energy Resources (formerly the South Australian Department of Mines and Energy) for invaluable assistance with this project which was supported by an Australian Research Grant.

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Appendix 1

Late Cretaceous Systematic Palynology. For the distribution of the species in the bore, see Table 1. For the register of illustrated specimens, see Table 4.

Spores

Genus *Aequitriradites* Delcourt and Sprumont emend. Cookson & Dettmann 1961

Type species: *Aequitriradites dubius* Delcourt & Sprumont emend. Delcourt, Dettman & Hughes 1963

Aequitriradites spinulosus (Cookson & Dettmann) Cookson & Dettmann 1961
FIG. 4A, B

Comments. The spinulose elements over the distal surface are about 1 µm in diameter and the exine 1 µm thick. Compare with *A. verrucosus*. Spore body, 45 µm, overall, 55 µm.

Stratigraphic Range. Early and Middle Cretaceous (Dettmann 1963). *Aequitriradites ascus/spinulosus*, from the *Murospora florida* Zone, late Jurassic, into *Phyllocladidites mawsonii* Zone, Turonian-Coniacian (Helby *et al.* 1987)

Aequitriradites verrucosus (Cookson & Dettmann) Cookson & Dettmann 1961
FIG. 4E, F

Comments. The verrucate elements over the distal surface are 2-3 µm in diameter and the exine 2-36 µm thick. Compare with *A. spinulosus*. Spore body, 48-57 µm, overall, 70-85 µm.

Stratigraphic Range. Widely distributed in south-eastern Australia in the Upper Mesozoic (Dettmann 1963).

Genus *Baculatisporites* Thomson & Pflug 1953

Type species: *Baculatisporites primarius* (Wolff) Thomson & Pflug 1953

Baculatisporites comaumensis (Cookson) Potonié 1956
FIG. 4G

Stratigraphic Range. From the late Jurassic-Early Cretaceous, it is common throughout the Upper Mesozoic (Dettmann 1963).

Genus *Balmeisporites* Cookson & Dettmann 1958

Type species: *Balmeisporites holodictyus* Cookson & Dettmann 1958

Balmeisporites glenelgensis Cookson & Dettmann 1958
FIG. 5A

Comments. This species is similar to *B. holodictyus* but the spore body is larger and the exine thicker. The inner homogenous layer is 5 µm thick on these specimens, compared with 1-2 µm on *B. holodictyus*. Spore body, 162 x 112 µm.

Stratigraphic Range. Within the *Plicatella distocarinatus* Zone, Cenomanian, to within *Tricolpites pachyexinous* Zone, Santonian, of south-eastern Australia (Dettmann & Playford 1969). Cenomanian, possibly Turonian of north-west Australia (Norvick & Burger 1975).

Balmeisporites holodictyus Cookson & Dettmann 1958
FIG. 4H, I

Comments. Most of these large megaspores are broken. The spore exine consists of an inner, homogenous layer 1-2 µm thick and an outer granular layer about 5 µm thick, the latter supporting the muri of the reticulum. Spore body, 97-110 µm equatorial diameter, overall, 137-166 µm x 170-235 µm

Stratigraphic Range. *Cybelosporites striatus* Subzone, Late Aptian-Early Albian, to the lower part of the *Appendicisporites distocarinatus* Zone, Cenomanian (Dettmann & Playford 1969).

Balmeisporites tridictyus Cookson & Dettmann 1958
FIG. 5B-D

Comments. The absence of a reticulum, a thick, inner homogenous layer (5 µm), an outer granular layer, 1-2 µm and the large membranous wing-like outgrowths distinguish this species (Cookson & Dettmann 1958). These specimens show sinuous ridges 4 µm high (arrow), which may anastomose. Spore body, 82-85 x 82-110 µm.

Stratigraphic Range. Aptian-Albian (Cookson & Dettmann 1958; Dettmann 1963). Cenomanian, this study.

Genus *Cumarozonosporites* Pant 1954 ex Potonié 1956 emend. Klaus 1960

Type species: *Rotasporites cretaceous* Weyland & Krieger 1953

Cumarozonosporites australiensis Norvick & Burger 1975
FIG. 4J, K

Comments. The distal surface has coarse rugulae about 3 µm wide, separated by grooves 1 µm wide. On the proximal surface, the pattern is finer and the contact surfaces are almost smooth. This species is smaller than *C. amplus*, 28-57 µm compared with 57-109 µm respectively (Norvick & Burger 1975; Dettmann & Playford 1968). Equatorial diameter, 40-44 µm.

Stratigraphic Range. Albian of the Great Artesian Basin and Albian into Turonian of Northern Australia (Norvick & Burger 1975).

Genus *Ceratosporites* Cookson & Dettmann 1958

Type species: *Ceratosporites equalis* Cookson & Dettmann 1958

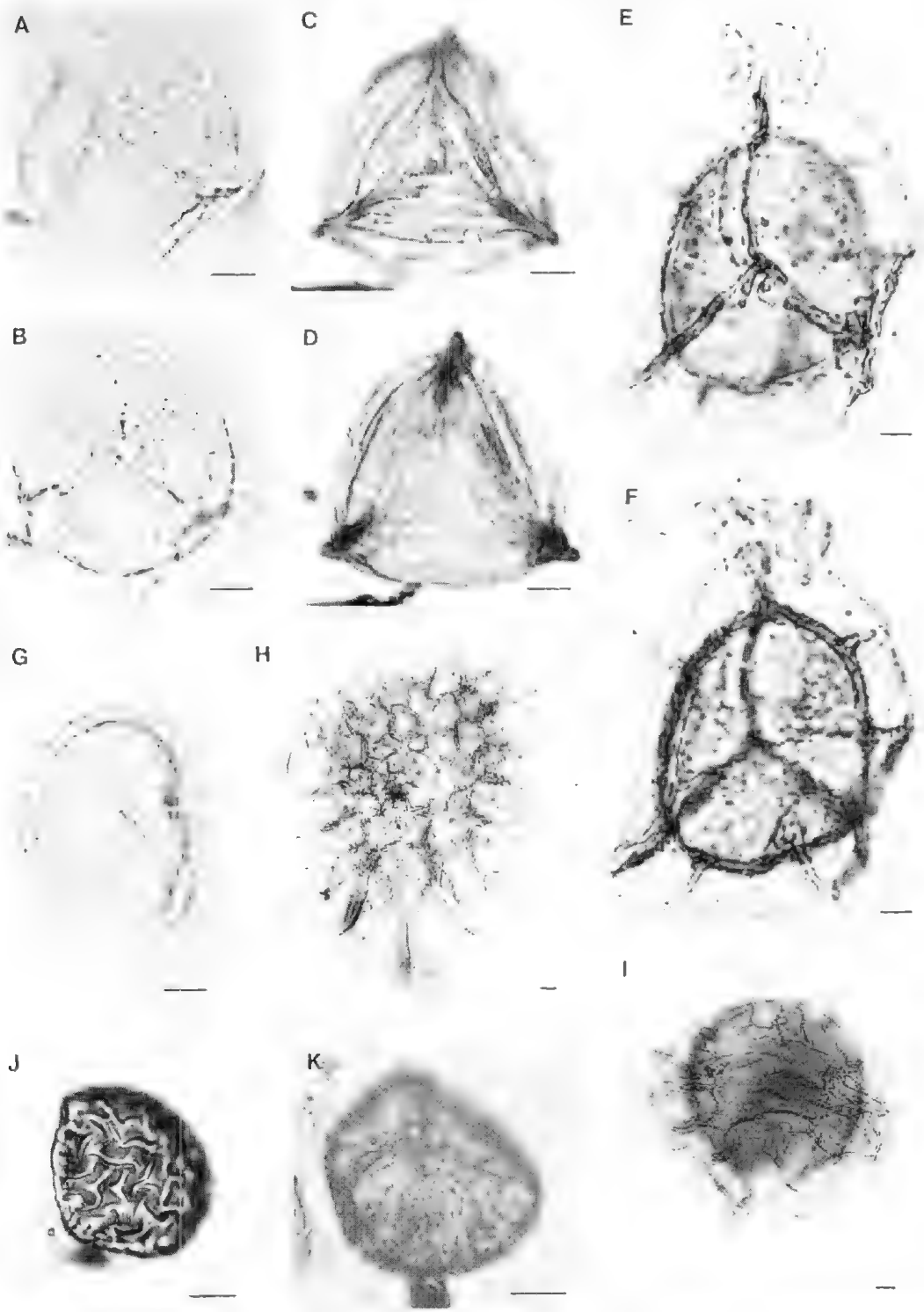

Fig. 4. Cretaceous species. A, B. *Aequitriradites spinulosus*. C, D. *Plicatella distocarinatus*. E, F. *Aequitriradites verrucosus*. G. *Baculatisporites comaumensis*. H, I. *Balmeisporites holodictyus*. J, K. *Camarozonosporites australiensis*. Scale bars = 10 μm.

Ceratosporites equalis Cookson & Dettman 1958
FIG. 5E, F

Stratigraphic Range. From the *Retitriletes watherooensis* Zone, latest Jurassic (Helby *et al.* 1987) through the Paleocene (Harris 1965; this study).

Cicatricosisporites sp. of Norvick & Burger 1975
FIG. 6C-E

Description. Spore trilete, amb triangular, sides slightly convex to deeply concave. Most spores have deeply concave sides, appear 3 lobed and present in equatorial view. Lasurae extend almost to equator, membranous lips 4-5 µm high. Three sets of parallel muri anastomose in radial region of distal surface. Edges of muri irregular or wavy with small foveolae within muri, especially where sets of muri anastomose. Four muri and intervening grooves, 8-10 µm. Equatorial diameter 43-53 µm, polar diameter 35-40 µm.

Comments. This species is distinguished from *Ruffordiaspora australiensis* by the irregular nature of the muri. Norvick & Burger (1975) figure an undescribed species, pl. 20 fig. 3, similar to this one.

Stratigraphic Range. Norvick & Burger (1975) note that their undescribed species in the Cenomanian is characteristic of the Upper Albian in Queensland. Cenomanian, this study.

Genus *Clavifera* Bolkhovitena 1966

Type species: *Clavifera triplex* (Bolkhovitina) Bolkhovitina 1966

Clavifera triplex (Bolkhovitina) Bolkhovitina 1966
FIG. 6J, K

Comments. The distal surface is strongly arched and the proximal pyramidal. The interradial crassitudes are 4-5 µm thick, features which distinguish it from *Gleicheniidites*. Its affinities are with the Gleicheniaceae.

Stratigraphic Range. From within the *Coptospora paradoxa* Zone, Albian, in northern Australia and rare in the *Plicatella dyscrasirinata* Zone, Cenomanian, southeastern Australia, through the *Forcipites longus* Zone, Maastrichtian (Helby *et al.* 1987).

Genus *Crybelosporites* Dettmann 1963

Type species: *Crybelosporites striatus* Cookson & Dettmann 1958

Crybelosporites punctatus Dettmann 1963
FIGS 6L, M, 7C

Overall diameter, 36-55 x 28-48 µm.

Stratigraphic Range. Lower Cretaceous (Dettmann 1963). Cenomanian, this study.

Crybelosporites striatus
(Cookson & Dettman) Dettmann 1963
FIG. 7A, B

Comments. The sclerine is 4-5 µm thick with a homogeneous inner layer 1 µm thick and a ruffled outer layer which is irregularly striate on the proximal side and reticulate on the distal surface. The muri are thin and sinuous, and the lumina 3-4 µm wide. All these features are a good fit with *C. striatus*.

Stratigraphic Range. *Crybelosporites striatus* Zone, into *Clavifera triplex* Zone, Late Aptian into Turonian (Dettmann & Playford 1969). *C. striatus* Zone through *Phimopollenites pannosus* Zone, latest Aptian through Albian of northern Australia and continuing into the *Tubulifloridites lilliei* Zone, early Maastrichtian of southern Australia (Helby *et al.* 1987). Cenomanian of northern Australia (Norvick & Burger 1975; this study).

Genus *Cyathidites* Couper 1953

Type species: *Cyathidites australis* Couper 1953

Cyathidites australis Couper 1953
FIG. 6I

Stratigraphic Range. Common throughout the upper Mesozoic in southeastern Australia (Dettmann 1963). From the Permian (Foster 1979) into the Tertiary (Harris 1965).

Cyathidites minor Couper 1953
FIG. 6H

Comments. Very common in this study.

Stratigraphic Range. From the Jurassic (Dettmann 1963) into the Tertiary (Harris 1965).

Genus *Dictyophyllidites* Couper emend. Dettmann 1963

Type species: *Dictyophyllidites harrisii* Couper 1958

Dictyophyllidites sp.
FIG. 6N

Comments. There is considerable variation in the population assigned to this genus.

Genus *Foraminisporis* Krutzsch 1959

Foraminisporis wonthaggiensis
(Cookson & Dettmann) Dettmann 1963
FIGS 6Q, 7E, F

Stratigraphic Range. From the *Ruffordiaspora australiensis* Zone, earliest Cretaceous, to the *Phyllocladidites mawsonii* Zone, Turonian-Coniacian (Helby *et al.* 1987).

Foraminisporis dailyi
(Cookson & Dettmann) Dettmann 1963
FIG. 7D

Stratigraphic Range. Widely dispersed in the Upper Mesozoic of southeastern Australia (Dettmann 1963).

Genus *Foveogleicheniidites* Norvick & Burger 1975

Type species: *Foveogleicheniidites* (al. *Gleicheniidites*) *confossus* (Hedlund) Norvick & Burger 1975

Foveogleicheniidites confossus
(Hedlund) Norvick & Burger 1975
FIG. 7I, K

Description. Amb triangular with rounded apices, trilete lasurae thin and straight, reaching to apices. Exine 1 µm thick with interradial crassitudes up to 6 µm wide. Foveolae, < 1 µm in diameter, spaced up to 1 µm apart, occur on both surfaces. Equatorial diameter, 30-32 µm.

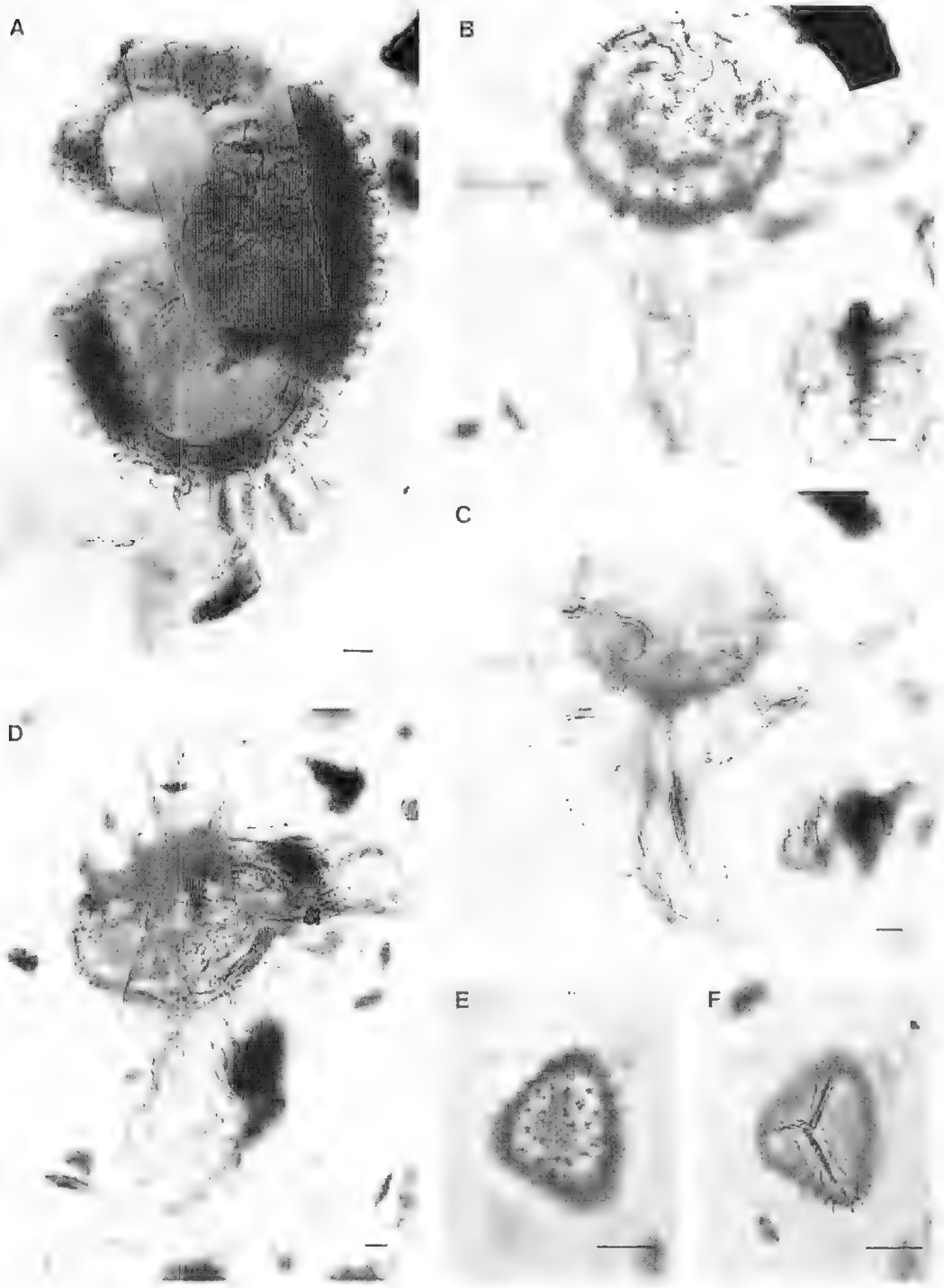

Fig. 5. Cretaceous species continued. A, *Balmeisporites glenelgensis*. B-D, *Balmeisporites tridictyus*. E, F, *Ceratosporites equalis*. Scale bars = 10 μm.

Stratigraphic Range. Cenomanian of northern Australia and sporadically in the Albian of the Great Artesian Basin (Norvick & Burger 1975).

Genus *Gleicheniidites* Ross ex Delcourt & Sprumont, emend. Dettmann 1963

Type species: *Gleicheniidites senonicus* Ross 1949

Gleicheniidites circinidites (Cookson) Dettmann 1963
FIG. 6P

Stratigraphic Range. *Gleicheniidites* spp. first appear in the Early Jurassic (Helby *et al.* 1987). *G. circinidites* is common in Upper Mesozoic sediments of southeastern Australia (Dettmann 1963). It is comparable to *Gleichenia* and ranges through the Tertiary to the present day.

Genus *Laevigatosporites* Ibrahim 1933

Type species: *Laevigatosporites vulgaris* (Ibrahim) Ibrahim 1933

Laevigatosporites ovatus Wilson & Webster 1946
FIG. 7G

Comments. A common and widely distributed species in the Upper Mesozoic (Dettmann 1963; Norvick & Burger 1975) and through the Tertiary. It is very common in some of the samples of this study.

Genus *Microfoveolatosporites* Krutzsch 1959

Type species: *Microfoveolatosporites canaliculatus* Dettmann 1963

Microfoveolatosporites canaliculatus Dettmann 1963
FIG. 8K, L

Stratigraphic Range. Albian of the Great Artesian Basin (Dettmann 1963; Norvick & Burger 1975), Cenomanian of northern Australia (Norvick & Burger 1975) and central Australia (this study).

Genus *Ornamentifera* Bolkhovitina 1966

Type species: *Ornamentifera echinata* (Bolkhovitina) Bolkhovitina 1966

Ornamentifera sp. cf. *O. sentosa*
Dettmann & Playford 1968
FIG. 7H, I

Description. Amb triangular with rounded angles, trilete scar with elevated membranous lips. Interradial crassitudes 16–20 µm long, 5–6 µm wide, bear sinuous rugulae < 1 µm high and 1 µm wide. Rugulae extend over distal surface. Proximal surface patterned with low verrucae. Diameter, 32 µm.

Comments. The rugulate pattern over the crassitudes differs from *O. sentosa* which has crassitudes with serrate margins. The pattern on the distal surface covers the entire surface on this form whereas it is restricted to a triangular area, with the apices in the interradial region on *O. sentosa* (Dettmann & Playford 1968). This specimen is similar to the one figured by Norvick & Burger (1975, pl. 23, fig. 3), without description.

Stratigraphic Range. For *O. sentosa*, within the *Tricolporites apoxyexinus* Zone to within the *Nothofagidites* Microflora, Coniacian to Campanian (Dettmann & Playford 1969). From the *Tricolporites apoxyexinus* Zone through *Forcipites longus* Zone, Santonian through Maastrichtian (Helby *et al.* 1987). *Ornamentifera* cf. *O. sentosa*, Cenomanian (Norvick & Burger 1975; this study).

Genus *Perotrilites* Erdtman ex Couper 1953, emend. Evans 1970

Type species: (designated by Couper 1953) *Perotrilites granulatus* Couper 1953 emend. Evans 1970

Perotrilites jubatus (Dettmann & Playford) Evans 1970
FIGS 7L, M, 8C

Comments. This species is distinctive with two main ridges bearing spinose crests, running more or less parallel to the trilete lasurae on the distal surface ('pseudomuri' of Norvick & Burger 1975). Spore body, 45–58 µm diameter. Zona, 25–30 µm wide.

Stratigraphic Range. *Phimopollenites pannosus* Zone, Late Albian through *Clavifera triplex* Zone, Early Turonian (Dettmann & Playford 1969).

Genus *Plicatella* Maljavkina 1949

Type species: *Plicatella trichacantha* Maljavkina 1949, by subsequent designation of Potonié 1960

Plicatella distocarinata
(Dettmann & Playford) Davies 1985
FIG. 8C, D

Comments. Parallel muri occur on both distal and proximal surface. The three sets of muri run parallel to the equator and on the distal surface, coalesce to form a fin-like projection in the radial region, height 5 µm and projecting 5–8 µm beyond the equator. The muri are 2–4 µm wide and the grooves, 1–3 µm. Equatorial diameter, 53–62 µm.

Stratigraphic Range. From within the *Coptospora paradoxa* Zone to within the *Phyllocladidites mawsonii* Zone, Albian through Turonian, starting earlier in northern Australia than in the southeast (Helby *et al.* 1987).

Genus *Polycingulatisporites* Simoncsics & Kedves emend. Playford & Dettmann 1965

Type species: *Polycingulatisporites circulus* Simoncsics & Kedves 1961

Polycingulatisporites sp.
FIG. 8A, B

Description. Amb subcircular, trilete lasurae have thickened margins, 2–3 µm wide, with regular striations about 2 µm apart. Equatorial thickening 2–3 µm wide, distal surface bears two circular, concentric ridges. Surface is psilate. Diameter, 48 µm.

Comments. A rare species in this study. Species of *Polycingulatisporites* are more typical of the Jurassic, but some may be found in the Cretaceous (Playford & Dettmann 1965, Helby *et al.* 1987).

Genus *Reticuloidosporites* Pflug 1953

Type species: *Reticuloidosporites dentatus* (Pflug) Pflug 1953

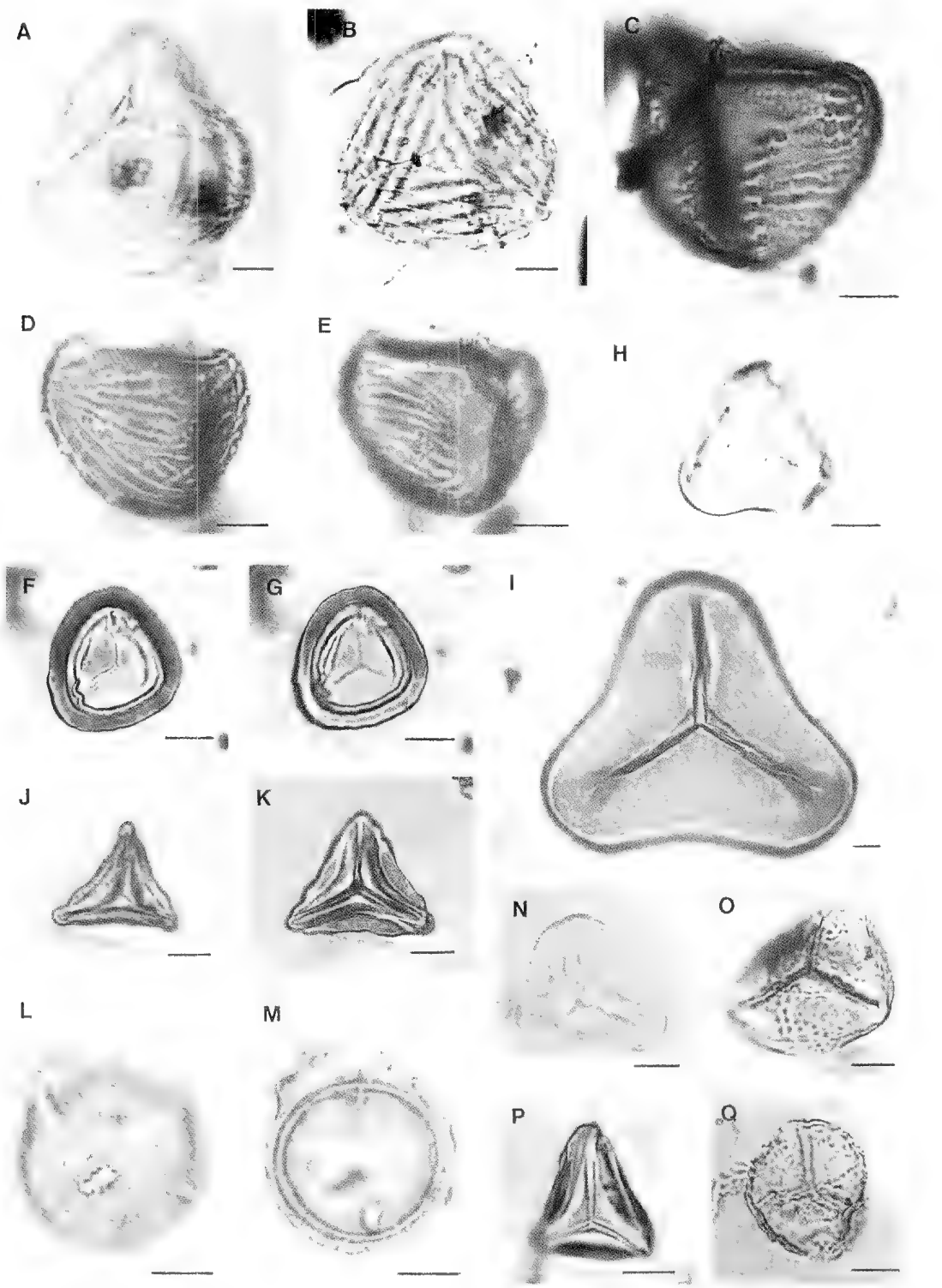

Fig. 6. Cretaceous species continued. A. *Ruffordiaspora australiensis*. B. *Ruffordiaspora ludbrookiae*. C-E. *Cicatricosisporites* sp. of Norvick & Burger. F, G. *Stereisporites pocockii*. H. *Cyathidites minor*. I. *Cyathidites australis*. J, K. *Clavifera triplex*. L, M. *Crybelosporites punctatus*. N. *Dictyophyllidites* sp. O. *Sestrosporites pseudoalveolatus*. P. *Gleicheniidites cercinidites*. Q. *Foraminisporis wonthaggiensis*. Scale bars = 10 μm.

Reticuloidosporites arcuus (Balme) Dettmann 1963
FIG. 8G

Stratigraphic Range. Jurassic and Lower Cretaceous sediments (Dettmann 1963). Cenomanian, this study.

Genus *Retitriletes* van der Hammen ex Pierce emend. Doring, Krutzsch, Mai & Schultz in Krutzsch 1963

Type species: *Retitriletes globosus* Pierce 1961

Remarks. *Lycopodiumsporites* has been restricted to forms with foveo-reticulte sculpture formed by pits closely spaced to form a reticulum. *Retitriletes* accommodates a positive reticulate sculpture formed of raised muri (see the discussion in Backhouse 1978).

Retitriletes austroclavatidites (Cookson) Doring, Krutzsch, Mai & Schultz in Krutzsch 1963
FIG. 8D-F

Stratigraphic Range. Widely distributed in Jurassic and Cretaceous sediments.

Genus *Ruffordiaspora* Dettmann & Clifford 1992

Type species: *Ruffordiaspora* (al. *Mohriaisporites*) *australiensis* (Cookson) Dettmann & Clifford 1992, by subsequent designation of Dettmann & Clifford 1992

Ruffordiaspora australiensis
(Cookson) Dettmann & Clifford 1992
FIG. 6A

Comments. The narrower muri distinguish this species from *R. ludbrookiae*. The muri have straight edges, thus it is distinctive from *Cicatricosisporites* sp. of Norvick & Burger (1975).

Stratigraphic Range. From the *Ruffordiaspora australiensis* Zone, earliest Cretaceous (Helby *et al.* 1987) to *Clavifera triplex* Zone, early Coniacian (Dettmann & Playford 1969).

Ruffordiaspora ludbrookiae
(Dettmann) Dettmann & Clifford 1992
FIG. 6B

Comments. The wider muri distinguish this species from *C. australiensis*.

Stratigraphic Range. From the *Crybelosporites stylosus* Zone, earliest Cretaceous, to the base of the *Coptospora paradoxa* Zone, latest Aptian-earliest Albian (Dettmann & Playford 1969). This species is rare in this study and somewhat corroded; hence it may be re-worked.

Genus *Sestrosporites* Dettmann 1963

Type species: *Cingulatisporites pseudoalveolatus* Couper 1958

Sestrosporites pseudoalveolatus (Couper) Dettmann 1963
FIG. 6O

Diameter, 35 µm.

Stratigraphic Range. Upper Mesozoic of southeast Australia (Dettmann 1963).

Genus *Stereisporites* Pflug 1953

Type species: *Stereisporites stereoides* (Potonié & Venitz) Pflug 1953

Stereisporites antiquasporites (Wilson & Webster) Dettmann 1963
FIG. 8N, O

Comments. Pattern of low verrucae, < 1 µm height, 2-5 µm wide, creates negative reticulum on distal surface. Pattern varies from barely perceptible (Fig. 8O) on small specimens to conspicuous (Fig. 8N), usually on larger specimens. Equatorial diameter, 26-46 µm.

Stratigraphic Range. Mesozoic and Tertiary strata.

Stereisporites pocockii Burger 1980
FIG. 6F, G

Stratigraphic Range. Uncommon in the Early Cretaceous. Similar forms have been found in the Cenomanian (Burger 1980).

Genus *Staverisporites* Norvick & Burger 1975

Type species: *Staverisporites microverrucatus* Norvick & Burger 1975

Staverisporites microverrucatus Norvick & Burger 1975
FIG. 8M

Comments. Crescentic shaped elevations which delimit or partially enclose circular or elliptical shallow depressions are characteristic of the genus. This species differs from *Staverisporites lunaris* (Cookson & Dettmann) Novick & Burger 1975 in that *S. microverrucatus* has microverrucate ornamentation. Diameter, 32-35 µm.

Stratigraphic Range. Cenomanian of Bathurst Island (Norvick & Burger 1975), probably the Albian of the Carpentaria Basin (Burger 1973). Cenomanian of Central Australia (this study).

Genus *Trilobosporites* Pant ex Potonié 1956

Type species: *Trilobosporites hannonicus* (Delcourt & Spumont) Potonié 1956

Trilobosporites tribottrys Dettmann 1963
FIG. 8I

Stratigraphic Range. Lower Cretaceous in the Otway and Great Artesian Basins (Dettmann 1963). Cenomanian, this study.

Trilobosporites trioreticulosus Cookson & Dettmann 1958
FIG. 8H

Stratigraphic Range. From the *Coptospora paradoxa* Zone to within the *Plicatella distocarinata* Zone, latest Aptian into early Cenomanian (Dettmann and Playford 1969). Cenomanian of northern Australia (Norvick & Burger 1975).

Genus *Triporoletes* Mtchedlishvili 1960 emend. Playford 1971

Type species: *Triporoletes singularis* Mtchedlishvili in Mtchedlishvili & Samodovich 1960

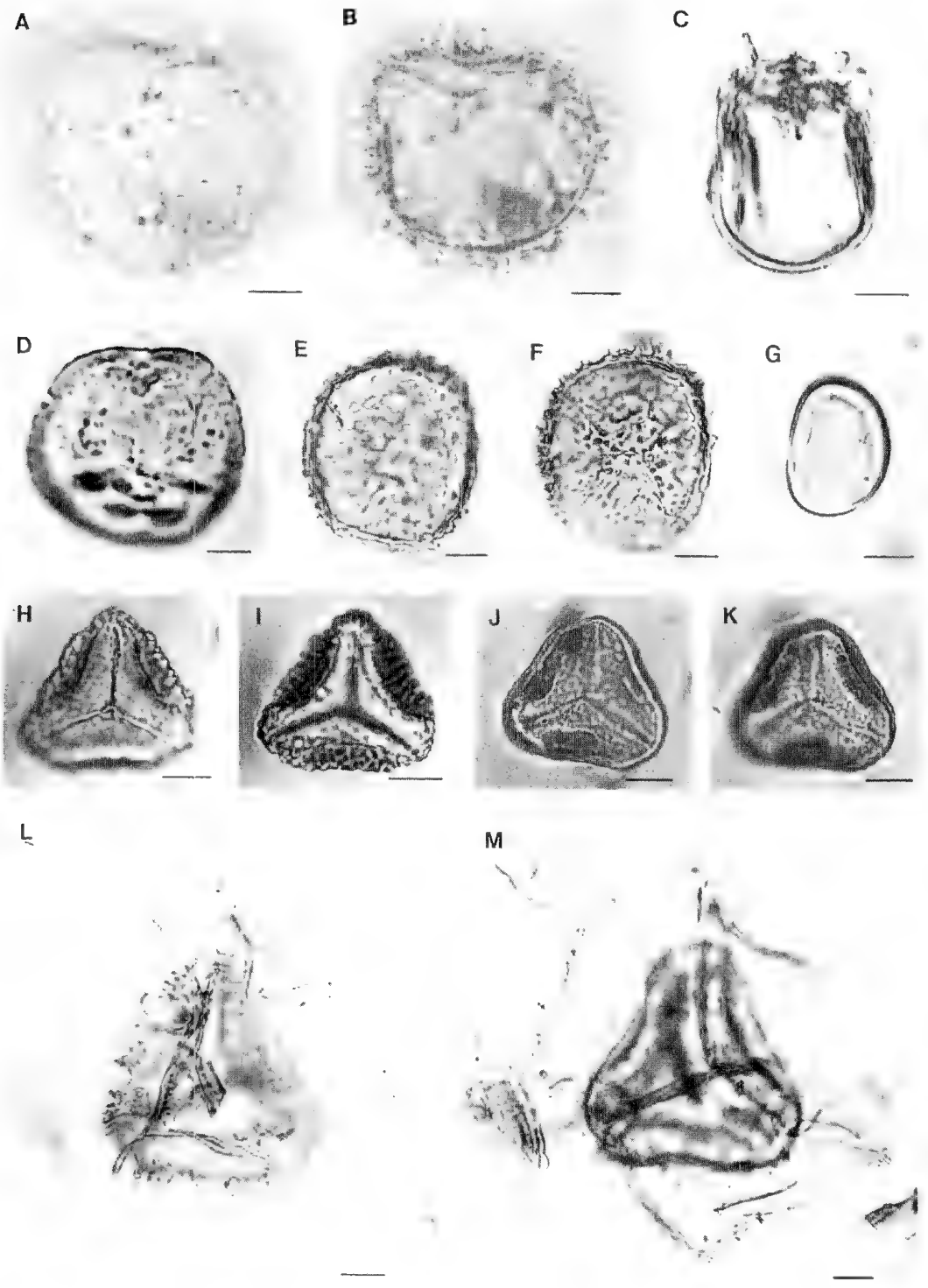

Fig. 7. Cretaceous species continued. A, B. *Crybelosporites striatus*. C. *Crybelosporites punctatus*. D. *Foraminisporis dailyi*. E, F. *Foraminisporis wonthaggiensis*. G. *Laevigatosporites ovatus*. H, I. *Ornamentifera* sp. cf. *O. sentosa*. J, K. *Foveogleicheniidites confossus*. L, M. *Perotriletes jubatus*. Scale bars = 10 μm.

Triporoletes sp. cf. *T. simplex*
(Cookson & Dettmann) Playford 1971
FIG. 8J

Comments. The specimens of this study, when compared with *T. simplex*, have a thinner inner layer of the sclerine, < 1 µm compared with 1.5-2.5 µm and the muroid ridges are more variable when compared with three radially oriented ridges on *T. simplex*. Diameter, 48-56 µm.

Stratigraphic Range. For *T. simplex*, Albian and Aptian (Dettmann 1963). Cenomanian, this sudy.

Gymnosperms

Genus *Alisporites* Daugherty 1941

Type species: *Alisporites opii* Dougherty 1941

Alisporites sp. cf. *A. grandis* (Cookson) Dettmann 1963
FIG. 9A

Comments. The size range of these specimens is rather small when compared with 78-136 x 36-70 µm for *A. grandis*. Overall size, 50-70 x 27-53 µm.

Stratigraphic Range. For *A. grandis*, Upper Jurassic and Lower Cretaceous (Dettmann 1963) into Paleocene (Harris 1965).

Genus *Araucariacites* Cookson ex Couper 1953

Type species: *Araucariacites australis* Cookson 1947, designated by Couper 1953

Araucariacites australis Cookson 1947
FIG. 9B

Stratigraphic Range. Widely distributed in the Upper Mesozoic (Dettmann 1963) and in the Tertiary, to the present day as species of *Araucaria* and *Agathis* (Cookson & Duigan 1951). See also the Tertiary specimens in Fig. 12I, J

Genus *Corallina* Malyavkina emend.
Cornet & Traverse 1975

Selected Synonomy
1953 *Classopollis* Pflug.
For full synotomy, see Cornet and Traverse (1975).

Remarks. *Classopollis* was originally described as tricolporate and the original description of *Corallina* was vague and inadequate. With an emended description of *Corallina*, *Classopollis* becomes a junior synonym

Type species: *Corallina compacta* Malyavkina 1949

Corallina sp. cf. *C. classoides* Pflug emend. Pocock and Jansonius 1961 comb. nov.
FIG. 9C

Comments. Rare at Poonarunna.

Stratigraphic Range. Widely dispersed in Upper Mesozoic sediments (Dettmann 1963). *Corallina* (=*Classopollis*) *simplex* and *Corallina* (=*Classopollis*) spp. are recorded from the Cenomanian of northern Australia (Norvick & Burger 1975). *Corallina* spp. are found from the Upper Triassic-transitional to Lower Jurassic into the Maastrichtian, Upper Cretaceous (Helby *et al.* 1987).

Genus *Microcachryidites* Cookson ex Couper 1953

Type species: *Microcachryidites antarcticus* Cookson 1947

Microcachryidites antarcticus Cookson 1947
FIG. 9D

Stratigraphic Range. Appears first in the *Murospora florida* Zone of the Late Jurassic. It is common through the Early Cretaceous and continues throughout the Cretaceous (Helby *et al.* 1987) and the Tertiary to the present day as the Tasmanian endemic, *Microcachrys tetragona*, (Cookson & Pike 1954a). See also the Tertiary specimen Fig. 12N.

Genus *Podocarpidites* Cookson ex Couper 1953

Type species: *Podocarpidites ellipticus* Cookson 1947

Podocarpidites ellipticus Cookson 1947
FIG. 9E

Stratigraphic Range. Usually abundant in the Jurassic and Cretaceous (Dettmann 1963) and continues through the Tertiary (Harris 1965; Martin 1973a) to the present as *Podocarpus* (*sensu lat.*).

Podocarpidites exiguus Harris 1965
FIG. 9F

Stratigraphic Range. Cenomanian, this study. Paleocene (Harris 1965), cf. *P. exiguus* at Bungonia, NSW, mid Eocene (Truswell & Owen 1988), late Eocene in the Eucla Basin (Milne 1988).

Genus *Podosporites* Rao 1943

Type species: *Podosporites tripakshii* Rao 1943

Podosporites sp.
FIG. 9H, K

Description. Grains trisaccate, outline lenticular to circular, Cappa, 2 µm thick, has fine, uniform reticulum. Cappula psilate, subtriangular. Sacci broadly crescentic with distinct, radially arranged muri within sacci. Muri reticulate at extremities of sacci. Overall size, 22-33 x 30-35 µm, corpus, 25-35 µm, sacci length 20-25 µm, height and width 8-10 µm.

Comparisons. The form is similar to *Podosporites ovatus* Haskell 1968, which, however, has a scabrate cappa, compared with the distinctly reticulate pattern of the specimens in this study. It is also similar to *Podosporites meduus* Haskell 1968 which also has a scabate cappa and irregularly reticulate sacci, when compared with the radial disposition of the muri of the specimens of this study

Comments. Superficially, this species resembles *Lycopodiumsporites florinii* in the pattern within the muri of the sacci, but the dimensions of the sacci are much smaller than those of *L. florinii*

Genus *Trichotomosulcites* Couper 1953 emend
Dettmann 1985

Type species: *Trichotomosulcites subgranulatus* Couper 1953

Trichotomosulcites subgranulatus Couper 1953
FIG. 9G

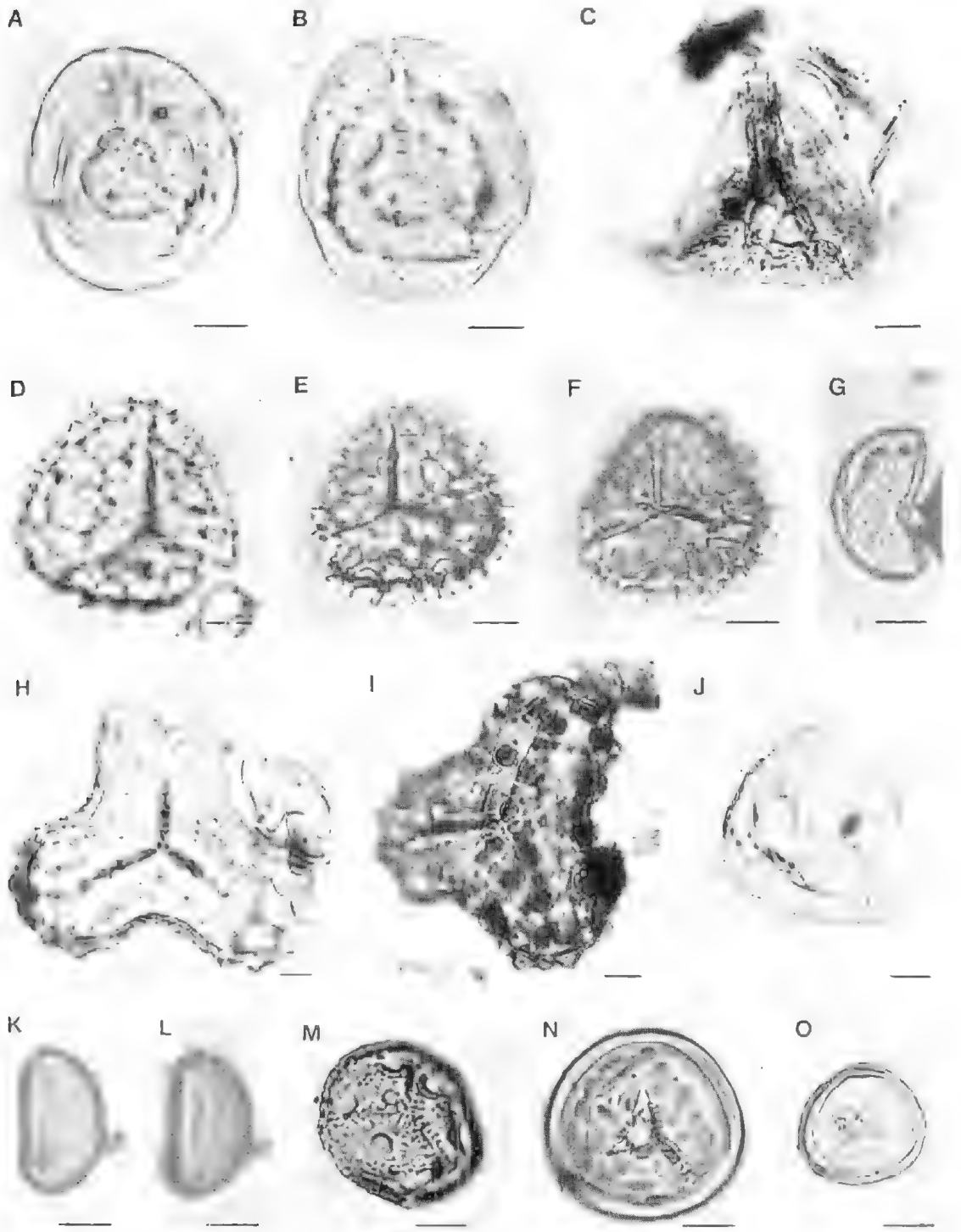

Fig. 8. Cretaceous species continued. A, B. *Polycingulatisporites* sp. C. *Perotrileles jubatus*. D-F. *Retitrileles austroclavatidites*. G. *Reticuloidosporites arcus*. H. *Trilobosporites triorelusosus*. I. *Trilobosporites triobotrys*. J. *Triporoletes* cf. *T. simplex*. K, L. *Microfoveolatosporites canaliculatus*. M. *Stoverisporites microverrucatus*. N, O. *Stereisporites antiquasporites*. Scale bars = 10 μm.

Stratigraphic Range. Early Cretaceous (Dettmann 1963) through the Miocene (Macphail 1996). It is morphologically similar to some modern species of *Phyllocladus*, found in Tasmania, New Zealand and elsewhere (Cookson & Pike 1954a).

Angiosperms

Cupuliferoidaepollenites Thomson & Thiergart 1950

Type species: *Cupuliferoidaepollenites liblarensis* Thomson in Potonié, Thomson & Thiergart 1950

Cupuliferoidaepollenites sp. cf. *C. parvulus*
(Groot & Penny) Dettmann 1973
FIG. 9L

Comments. The grains are prolate, tricolpate with slit-like colpi, exine < 1 µm thick, not clearly differentiated into nexine and sexine, with a scabrate surface. Size, 12 x 10 µm.

Stratigraphic Range. Late Albian, Cenomanian, Turonian in northern Australia (Norvick & Burger 1975; Dettmann 1973).

Dicolpopollis Pflanzl, 1956, emend. Potonié 1966

Type species: *Dicolpopollis kockeli* Pflanzl 1956

Dicolpopollis sp.
FIG. 9M, N

Description. Amb more or less circular, two broad, relatively short colpi. Exine 2 µm thick with thin nexine, robust columellae supporting a reticulum. In polar region, murus plus lumen together measure 1 µm. Lumina larger, up to 2 µm in intercolpal region. Heads of the columellae distinct under reticulum. Size, 31 x 26 µm.

Comments. Norvick & Burger (1975) describe one dicolpate type and figure two additional forms from Bathurst Island. The type described here is different from any of those.

Foveotetradites Singh 1983

Type species: *Foveotetradites fistulosus* (Dettmann) Singh 1983

Foveotetradites fistulosus (Dettmann) Singh 1983
FIG. 10A, B

Size of tetrad, 42-58 µm.

Stratigraphic Range. Cenomanian of northern Australia (Dettman 1973; Norvick & Burger 1975) and central Australia, this study.

Liliacidites Couper 1953

Type species: *Liliacidites kaitangataensis* Couper 1953

Liliacidites sp. cf. *L. kaitangataensis* Couper 1953
FIG. 9P

Size, 42 x 31 µm.

Stratigraphic Range. Cenomanian of Bathurst and Melville Islands (Dettmann 1973; Norvick & Burger 1975) and of central Australia (this study).

Liliacidites sp.
FIG. 9S

Description. Shape oval, monosulcate, sulcus extending length of grain. Exine ≤1 µm, nexine thin, baculate/clavate columellae slender. Surface pattern scabrate. Size, 24 x 17 µm.

Distribution. Rare in the Cenomanian of this study.

Phimopollenites Dettmann 1973

Type species: *Phimopollenites pannosus* (Dettmann & Playford) Dettmann 1973

Phimopollenites augathallaensis (Burger) Dettmann 1973
FIG. 9O, Q, R

Size, 27 x 30-33 µm.

Stratigraphic Range. Albian to Cenomanian (Burger 1970; Dettmann 1973; Norvick & Burger 1975)

Phimopollenites pannosus
(Dettmann & Playford) Dettmann 1973
FIG. 9U, W

Size, 12-15 x 15-20 µm.

Stratigraphic Range. *Phimopollenites pannosus* Zone, Late Albian, through *Tricolporites apoxyexinous* Zone, Santonian (Helby *et al.* 1987).

Senectotetradites Dettmann 1973

Type species: *Senectotetradites varireticulatus* Dettmann 1973

Senectotetradites varireticulatus Dettmann 1973
FIG. 9T

Size of tetrad, 50 x 55 µm.

Stratigraphic Range. Cenomanian of northern Australia (Dettmann 1973; Norvick & Burger 1975) and probably Cenomanian of the Otway Basin (Dettmann 1973). Cenomanian of this study.

Tricolporites Cookson ex Stover & Evans 1973

Type species: *Tricolporites sphaerica* Cookson 1947, designated by Stover & Evans (1973)

Tricolporites sp. cf. *T. apoxyexinus* Partridge 1987
FIG. 9X, Y

Description. Shape almost spherical, long colpi reach almost to poles. Colpi with well defined borders, pores with irregular edges, exine 1 µm thick, with two layers of approximately equal thickness. Surface smooth and faintly scabrate. Size, 14 µm polar diameter x 15 µm equatorial diameter.

Comparisons. The grain of this study is similar to *T. apoxyexinus* but it has a thinner exine and the nexine is relatively thinner than that of *T. apoxyexinus*.

Stratigraphic Range. *T. apoxyexinus*, from the *Tricolporites apoxyexinus* Zone, Santonian, into *Nothofagidites senectus* Zone, Campanian (Helby *et al.* 1987).

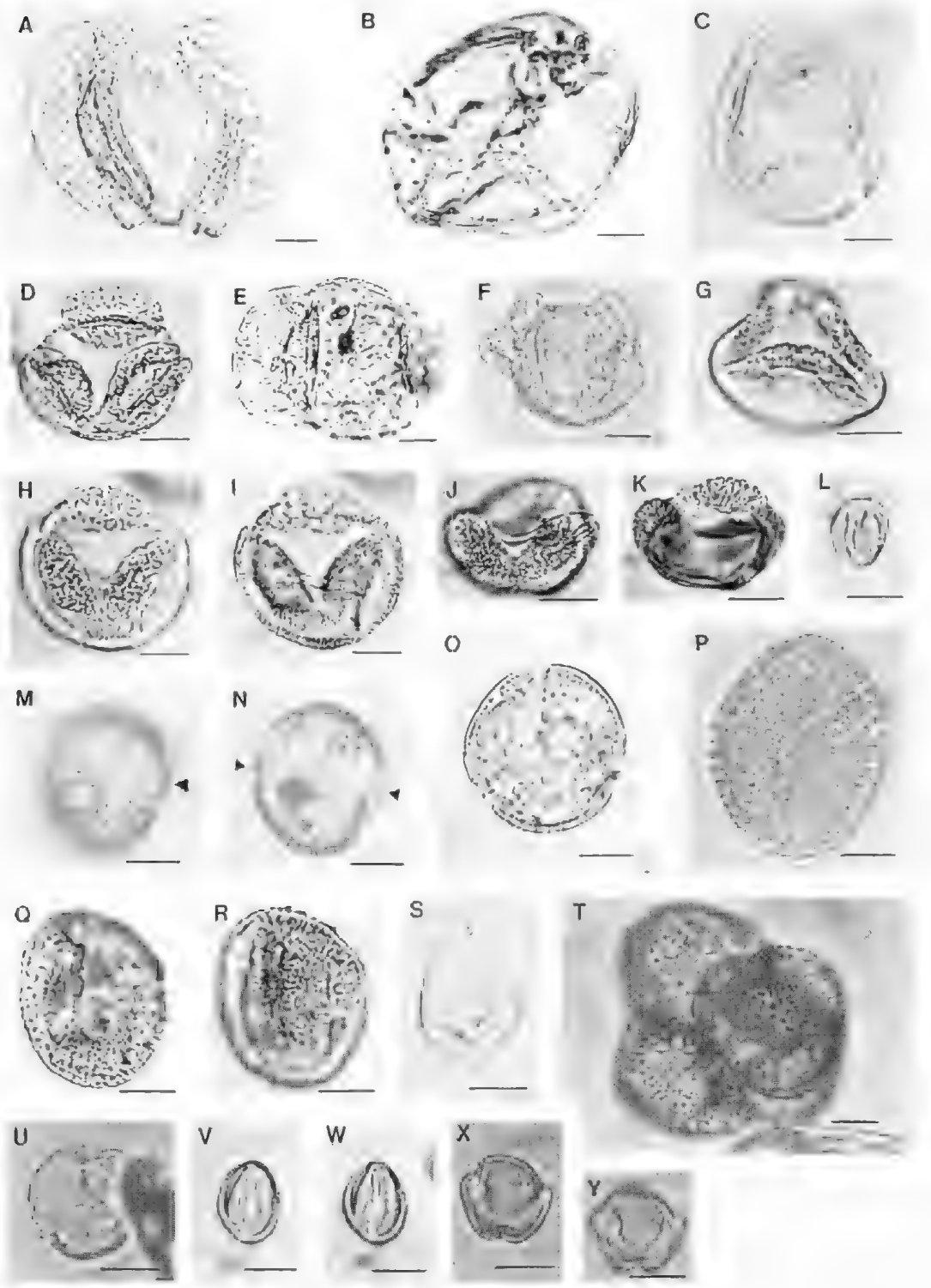

Fig. 9. Cretaceous species continued. A. *Alisporites* sp. cf. *A. grandis*. B. *Araucariacites australis*. C. *Corollina* sp. cf. *C. classoides*. D. *Microcachryidites antarcticus*. E. *Podocarpidites ellipticus*. F. *Podocarpidites exiguus*. G. *Trichotomosulcites subgranulatus*. H-K. *Podosporites* sp. L. *Cupuliferoidaepollenites* sp. cf. *C. parvulus*. M, N. *Dicolpopollis* sp. Arrows indicate colpi. O, Q, R. *Phimopollenites augathellaensis*. P. *Liliacidites* sp. cf. *L. kaitangataensis*. S. *Liliacidites* sp. T. *Senectotetradites varireticulatus*. U-W. *Phimopollenites pannosus*. X, Y. *Tricolporites* sp. cf. *T. apoxyexinous*. Scale bars = 10 μm.

Microplankton

Genus *Horologinella* Cookson & Eisenack 1962

Type species: *Horologinella lineata* Cookson & Eisenack 1962

Horologinella sp.
FIG. 10L

Description. Body rectangular with folds on the surface, corners rounded. Long splits (20-22 µm) extend inwards from concave depressions on shorter sides of rectangle. One pore, 15 x 5 µm, with thickened edge, in central position of one of longer sides. Wall < 1 µm with granular-striate surface pattern. Size, 94 x 82 µm.

Comments. The body does not show any sign of tabulation, but the splits extending from the indentations are characteristic of *Horologinella*. The specimen figured shows openings at the corners of the rectangle, but these are thought to be the result of damage.

Genus *Lecaniella* Cookson & Eisenack 1962

Type species: *Lecaniella margostriata* Cookson & Eisenack 1962

Lecaniella sp.
FIG. 10C-G, I

Description. Cyst spherical, splitting into two halves, halves flattening out to saucer shape. Whole cysts (Fig. 10F, G) rarely seen. Each half has outer marginal zone 5-7 µm wide with radial striations and central rugulate-reticulate area, muri about 1 µm wide, lumina 2 µm. Whole cyst, 39 µm, halves, 28-62 µm.

Comments. The unsplit cyst (Figs 10F, G) and one contracted half (Fig. 10I) show a more distinct striated marginal zone than the other specimens, but this is probably due to the state of contraction. The specimens here differ from *Lecaniella margostriata* which has a much coarser reticulate pattern. *Lecaniella dictyota* Cookson & Eisenack 1962 has a finer reticulate pattern and the radial striations are much coarser than on these specimens.

Lecaniella has probable affinities with the Zygnemataceae (Grenfell 1995). This family of filamentous algae is found mainly in shallow, flowing fresh water.

Genus *Saeptodinium* Harris 1973

Type species: *Saeptodinium gravattensis* Harris 1973

Saeptodinium gravattensis Harris 1973
FIG. 10H.

Comments. Uncommon in Poonarunna-1.

Stratigraphic Range. Paleocene (Harris 1973), Cenomanian, this study.

Genus *Schizosporis* Cookson & Dettmann 1959

Type species: *Schizosporis reticulatus* Cookson & Dettmann 1973

Schizosporis reticulatus Cookson & Dettmann 1973
FIG. 10K

Stratigraphic Range. Widely distributed in the Upper Mesozoic of eastern Australia (Dettmann 1963). Cenomanian of northern Australia (Norvick & Burger 1975) and of this study.

Comment. *Schizosporis reticulatus* has probable affinities with the Zygnemataceae (Grenfell 1994).

Acritarch, sp. indet.
FIG. 10J

Description. Outline broadly elliptical, pylome oval, 15 x 10 µm, near one end. Border of pylome psilate, 1.5 µm wide. Wall two layered, 1 µm thick, with patches of pitted, grooved, verrucate and broad linear thickenings. Size, 105 x 75 µm.

Appendix 2

Tertiary Systematic Palynology. For the distribution of the species in the bore, see Table 2. For the register of illustrated specimens, see Table 4.

Spores

Genus *Azolla* Lam.

Type species: *Azolla filiculoides* Lam.

Azolla sp.
FIG. 11J

Comments. Massulae that have lost all the microspores have been found.

Stratigraphic Range. Probably from the beginning of the Campanian (Hall 1974) to the present. Mid Eocene, this study.

Genus *Camarozonosporites* Pant ex Potonié emend. Klaus 1960

Type species: *Camarozonosporites cretaceus* (Weyland & Krieger) Potonié 1956

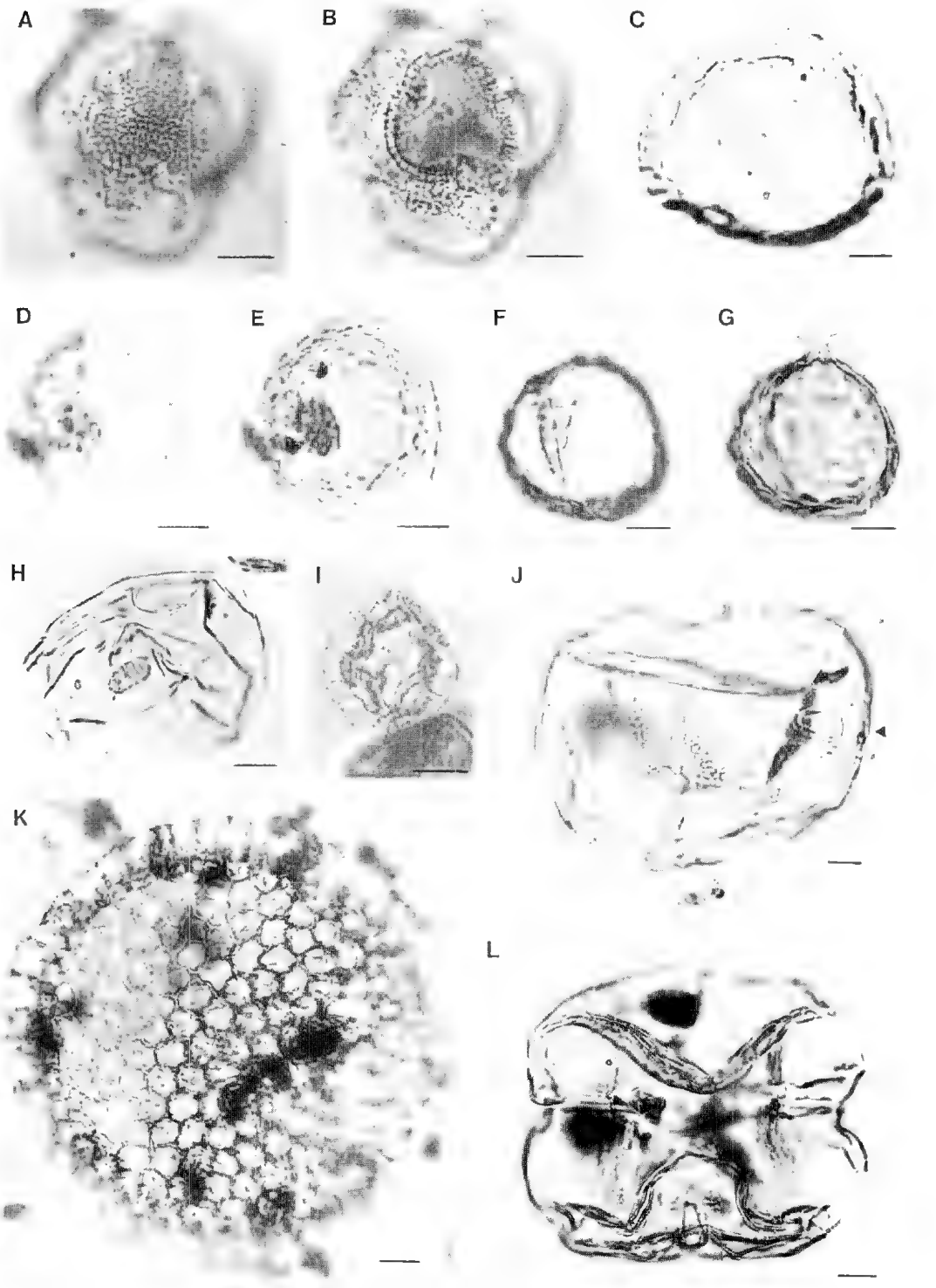

Fig. 10. Cretaceous species continued. A, B. *Foveotetradites fistulosus*. C-G, I. *Lecaniella* sp. C-E, I are half cysts and F-G, a whole cyst with part of the filament attached. H. *Sacptodinium gravattensis*. J. Acritarch sp. indet. Arrow indicates pore. K. *Schizosporis reticulatus*. L. *Horologinella* sp. Scale bars = 10 μm.

Camarozonosporites amplus
(Stanley) Dettmann & Playford 1968
FIG. IIA, B

Stratigraphic Range. Upper Cretaceous and Paleocene (Dettmann & Playford 1968).

Camarozonosporites bullatus Harris 1965
FIG. IID

Comments. The specimen illustrated has narrower crassitudes and is slightly smaller than those described by Harris (1965) and Dettmann & Playford (1968). Size, spore body 28 µm, overall, 43 µm.

Stratigraphic Range. Late Cretaceous (Dettmann & Playford 1968) through Paleocene (Harris 1965)

Camarozonosporites sp.
FIGS IIE, F

Description. Spore trilete, amb circular, lasurae straight, extending about ⅔ of radius. Exine 1-2 µm thick with interradial crassitudes, 4-5 µm thick. Surface pattern of interlocking rugulae 1 µm wide, with lumina 1-2 µm wide and <1 µm high. Equatorial diameter, 35 µm.

Comparisons. The spore is smaller and the pattern much finer than that seen on *Camarozonosporites ohaiensis*.

Distribution. Lower *N. asperus* Zone Equivalent, mid Eocene (this study).

Genus *Cyathidites* Couper 1953

Type species: *Cyathidites australis* Couper 1953

Cyathidites paleospora
(Martin) Alley & Broadbridge 1992
FIG. III

Stratigraphic Range. Throughout the Tertiary. Found in the late Paleocene, mid Eocene and Pliocene-Pleistocene of this study

Cyathidites splendens Harris 1965
FIG. IIG, H

Comments. The scabrate surface pattern is distinctive and becomes etched out on corroded specimens (Fig 11H).

Stratigraphic Range. Late Paleocene and early Eocene (Harris 1965, 1971).

Genus *Gleicheniidites* Ross ex Delcourt & Sprumont emend. Dettmann 1963

Type species: *Gleicheniidites senonicus* Ross 1949

Gleicheniidites circinidites (Cookson) Dettmann 1963
FIG. IIC

Stratigraphic Range. Jurassic (Helby *et al.* 1987) to the present, as the fern *Gleichenia*.

Genus *Grapnelispora* Stover & Partridge 1984

Type species: *Grapnelispora evansii* Stover & Partridge 1984

Grapnelispora evansii Stover & Partridge 1984
FIG. 12A

Comments. This beautifully preserved specimen has 7 appendages, one with a recurved-hook tip and the others with 3-4 short-branched, recurved tips. Endospore 50 µm, overall spore body 70 µm, length of appendages 90-100 µm. It is found in dominantly non marine to marginal marine environments (Stover & Partridge 1984).

Stratigraphic Range. Upper part of the *Forcipites (Tricolpites) longus* Zone, middle to late Maastrichtian, with most occurrences found in the latest Maastrichtian (Stover & Partridge 1984), late Paleocene (this study) possibly reworked.

Genus *Polypodiaceisporites* Potonié 1951

Type species: *Polypodiaceisporites speciosus* Potonié 1934

Polypodiaceisporites sp. cf. *P. retirugatus* Muller 1968
FIGS III,-M

Comments. This specimen is very similar to *Polypodiaceisporites* sp. cf. *P. retirugatus* as described by Truswell *et al.* (1985). It is similar to *Pteris umbrosum* and *Pteris tremula* of the Pteridaceae (Martin & McMinn 1993). Size, 45 µm.

Stratigraphic Range. Late Oligocene to early–mid Miocene (Truswell *et al.* 1985),. late Miocene into Pleistocene (Martin & McMinn 1993). Pliocene-Pleistocene (this study).

Genus *Retitriletes* van der Hammen ex Pierce emend Doring, Krutzsch, Mai and Schultz 1963

Type species: *Retitriletes globosus* Pierce 1961

Retitriletes austroclavatidites
(Cookson) Potonié 1956 comb. nov.
FIG. 12B, C

Description. Lasurae with psilate border up to 3 µm wide, extend ⅔ spore radius. Proximal surface psilate or with faint, radiating ridges. Distal surface reticulum has muri 1 µm high, 0.5 µm wide and lumina 3-7 µm in diameter. Exine 1 µm thick, excluding reticulum. Diameter 30-35 µm.

Stratigraphic Range. Species of *Retitriletes* are significant in the Cretaceous but a few may be found through much of the Tertiary.

Genus *Triletes* Erdtman ex Couper emend. Dettmann 1963

Type species: *Triletes tuberculiformis* Cookson 1947 emend. Dettmann 1963

Triletes sp. cf. *T. tuberculiformis*
Cookson 1947 emend. Dettmann 1963
FIG. IIK

Description. Outline triangular, trilete lasurae extending for most of the radius. Exine 1 µm thick, bearing large verrucae/rugulae, 3 µm high inter-radially, up to 6 µm high at apices. Distal surface pattern coarse rugulate-reticulum, muri 3-5 µm high, lumina about 5 µm diameter. Proximal surface pattern similar but with lower, more widely spaced elements. Size range, 58-64 µm.

Distribution. *L. balmei* Zone Equivalent, late Paleocene and Lower *N. asperus* Zone Equivalent, mid Eocene (this study).

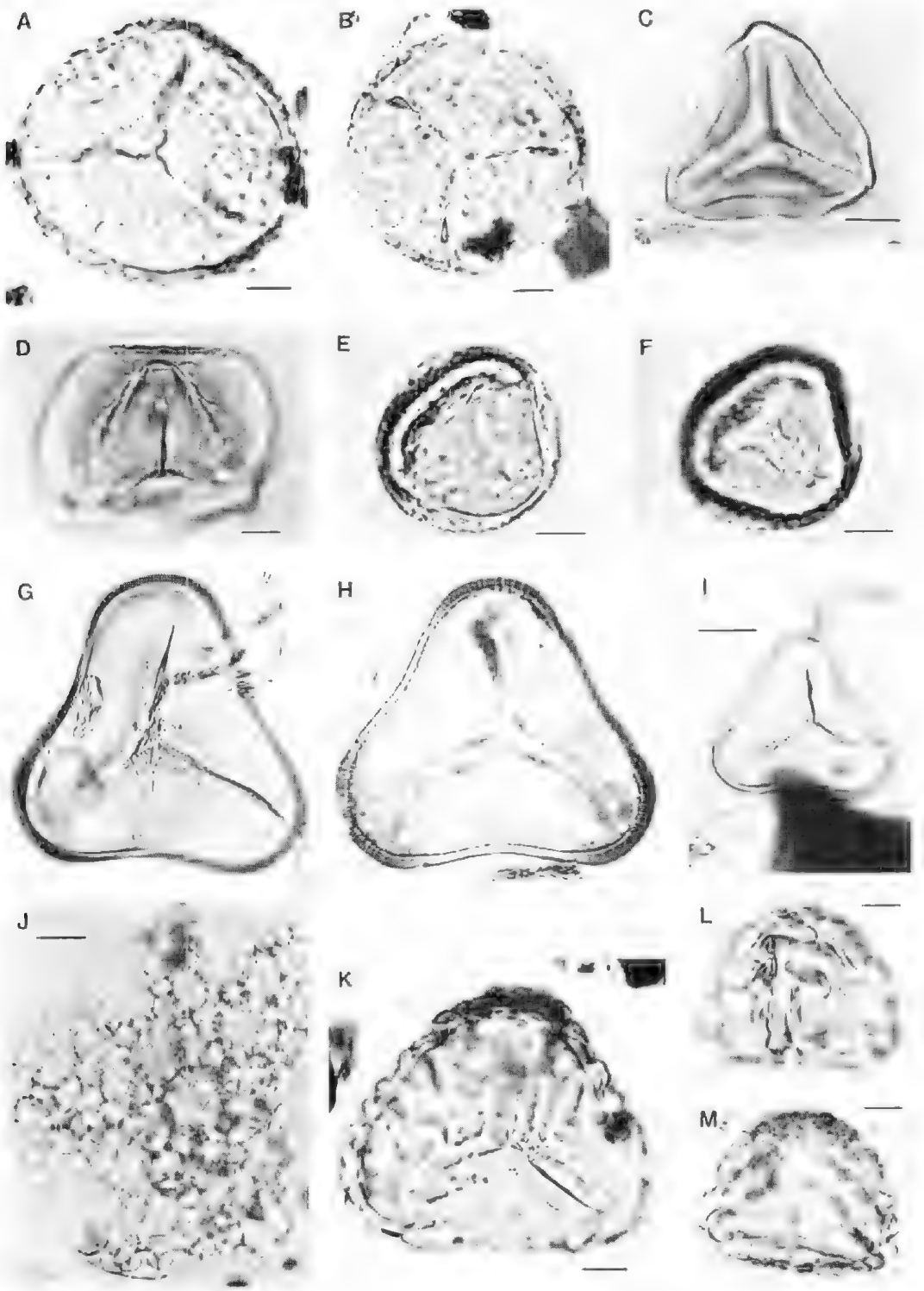

Fig. 11. Tertiary species. A, B, *Camarozonosporites amplus*. C, *Gleicheniidites circinidites*. D, *Camarozonosporites bullatus*. E, F, *Camarozonosporites* sp. H, G, *Cyathidites splendens*. I, *Cyathidites paleospora*. J, *Azolla* sp. K, *Triletes* sp. cf. *T. tuberculiformis*. L, M, *Polypodiaceisporites* sp. cf. *P. retirugatus*. Scale bars = 10 μm.

Genus *Triporoletes* Mtchedlishvili emend. Playford 1971

Type species: *Triporoletes singularis* Mtchedlishvili in Mtchedlishvili & Samoilovich 1960.

Triporoletes reticulatus (Pocock) Playford 1971
FIG. 12F

Stratigraphic Range. Early Cretaceous (Dettmann 1963), Cenomanian (Norvick & Burger 1975), Tertiary (this study).

Gymnosperm pollen

Genus *Araucariacites* Cookson ex Couper 1953

Type species: *Araucariacites australis* Cookson 1947 ex Couper 1953

Araucariacites australis Cookson 1947
FIG. 12I

Stratigraphic Range. See this species in Appendix 1

Cupressaceae Taxodiaceae
FIG. 12D

Stratigraphic Range. Late Paleocene, (this study) to late Tertiary (Martin 1973a) and the present day. Macrofossil studies (Peters & Christophel 1978) show that both of these families predate the Paleocene.

Genus *Dacrycarpites* Cookson & Pike 1953

Type species: *Dacrycarpites australiensis* Cookson & Pike 1953

Dacrycarpites australiensis Cookson & Pike 1953
FIG. 12L

Stratigraphic Range. Late Paleocene (this study) to late Tertiary (Martin 1973a).

Genus *Dilwynites* Harris 1965

Type species: *Dilwynites granulatus* Harris 1965

Dilwynites granulatus Harris 1965
FIGS 12J, K, 13A

Stratigraphic Range. Maastrichtian through Miocene (Stover & Partridge 1973; Partridge 1976).

Genus *Ephedra* L. 1753

Type species: *Ephedra distachya* L. 1753

'Ephedra' notensis Cookson 1956
FIG. 13B

Comments. The fossil is similar to *Ephedra* (Cookson 1956), which, however, is much larger. A very similar pollen morphology is found in the Araceae (Martin 1973a).

Stratigraphic Range. Early Cretaceous to Eocene (Cookson 1956), early Miocene (Martin 1973a, 1984b) in Australia, Miocene in New Zealand (Mildenhall & Pocknall 1989).

Genus *Lygistepollenites* Stover & Evans 1973

Type species: *Lygistepollenites florinii* (Cookson & Pike) Stover & Evans 1973

Lygistepollenites florinii
(Cookson & Pike) Stover & Evans 1973
FIG. 12G

Stratigraphic Range. From within the *Phyllocladidites mawsonii* Zone, the basal portion of Santonian (Helby *et al.* 1987, Fig. 2), widespread throughout the Tertiary, to Pleistocene, about 26,000 years ago on the Atherton Tableland (Kershaw 1985).

Genus *Microcachryidites* Cookson ex Couper 1953

Type species: *Microcachryidites antarcticus* Cookson ex Couper 1953

Microcachryidites antarcticus Cookson ex Couper 1953
FIG. 12N

Comments. See this species in Appendix 1.

Genus *Phyllocladidites* Cookson ex Couper emend. Stover & Evans 1973

Type species: *Phyllocladidites mawsonii* Cookson 1947 ex Couper 1953

Phyllocladidites mawsonii Cookson ex Couper 1953
FIG. 12E

Stratigraphic Range. The base of the *Proteacidites* Superzone, Late Cretaceous (Helby *et al.* 1987, Fig. 2), through most of the Tertiary on mainland Australia, to the present day in Tasmania as *Lagarostrobos franklinii*, the Huon Pine (Playford & Dettmann 1978).

Phyllocladidites reticulosaccatus Harris 1965
FIG. 12H

Stratigraphic Range. Paleocene (Harris 1965; Stover & Partridge 1973)

Genus *Podocarpidites* Cookson ex Couper 1953

Type species: *Podocarpidites ellipticus* Cookson 1947

Podocarpidites exiguus Harris 1965
FIG. 12M

Stratigraphic Range. Cenomanian (this study), Paleocene (Harris 1965), mid Eocene (Truswell & Owen 1988; this study), late Eocene (Milne 1988).

Angiosperm pollen

Genus *Acaciapollenites* (Cookson) Mildenhall emend Mildenhall & Pocknall 1989

Type species: *Acaciapollenites myriosporites* (Cookson) Mildenhall 1972

Acaciapollenites myriosporites
(Cookson) Mildenhall 1972
FIG. 13C

Stratigraphic Range. Late Oligocene (Truswell *et al.* 1985), but usually early Miocene (Stover & Partridge 1973) to present day, as *Acacia*. Found only in the Pliocene Pleistocene of this study.

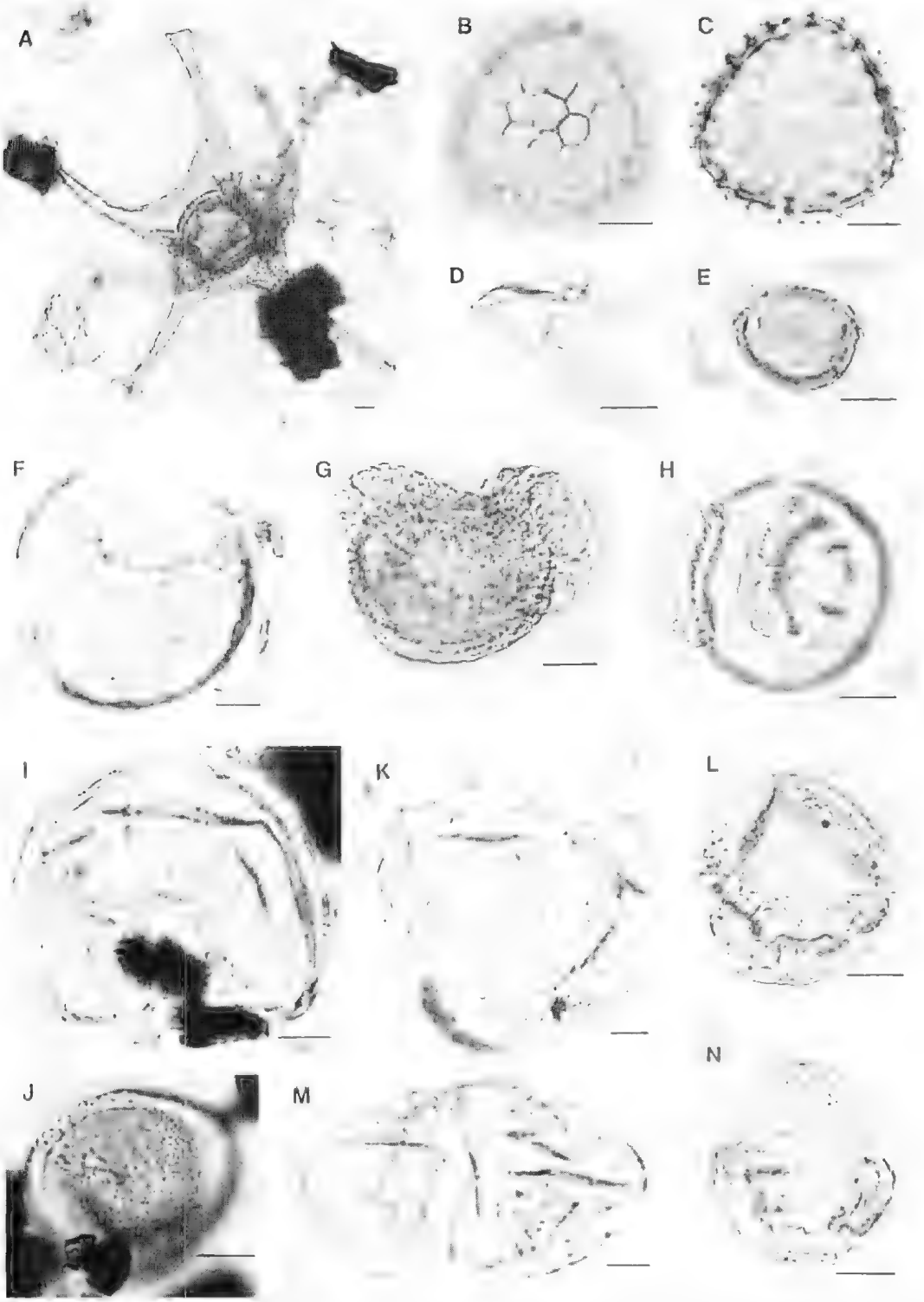

Fig. 12. Tertiary species continued. A. *Grapnelispora evansii*. B, C. *Retitriletes austroclavatatus*. D. Cupressaceae/Taxodiaceae. E. *Phyllocladidites mawsonii*. F. *Triporoletes reticulatus*. G. *Lygistepollenites florinii*. H. *Phyllocladidites reticulosaccatus*. I. *Araucariacites australis*. J, K. *Dilwynites granulatus*. L. *Dacrycarpites australiensis*. M. *Podocarpidites exiguus*. N. *Microcachryidites antarcticus*. Scale bars = 10 μm.

Genus *Aglaoridia* Erdtman 1960
Type species: *Aglaoridia cyclops* Erdtman 1960

Aglaoridia qualumis Partridge in Stover & Partridge 1973
FIG. 17G

Stratigraphic Range. Southeast Australia, mid Eocene to early Oligocene (Stover & Partridge 1973), mid Eocene to early Pliocene (Macphail 1996). Lake Eyre Basin, early-mid Eocene (Sluiter 1991).

Genus *Amosopollis* Cookson & Balme 1962

Type species: *Amosopollis cruciformis* Cookson & Balme 1962

Amosopollis dilwynensis Harris 1972
FIG. 13F-G

Description. Tetrads rhombiodal, usually crumpled to some degree. Each grain has distal sulcus extending most of the diameter of the grain. Exine < 1 µm, psilate with patch of granules < 1 µm diameter over area around sulcus. Some or all of the granules may be missing on less well preserved specimens. Size range, 57-75 µm diameter of tetrad.

Stratigraphic Range. Paleocene (Harris 1972; this study).

Genus *Arecipites* Wodehouse emend. Anderson 1960

Type species: *Arecipites punctatus* Wodehouse ex Potonié 1958

Arecipites sp. cf. *A. minutiscabratus*
(McIntyre) Milne 1988
FIG. 13D

Description. Grain elliptical, monosulcate, sulcus extending most of the length of the grain, ends rounded. Exine 1 µm, tectate with minute perforations, thickness endexine, ectexine approximately equal. Surface finely scabrate, sparse granules ≤ 0.5 µm on distal surface. Size, 25 x 17 µm.

Comments. The sparse granules on the distal surface are not seen on *A. minutiscabratus*.

Stratigraphic Range. For *A. minutiscabratus*, Paleocene (McIntyre 1968), late Eocene (Milne 1988).

Genus *Australopollis* Krutzsch 1966

Type species: *Australopollis obscurus* (Harris) Krutzsch 1966

Australopollis obscurus (Harris) Krutzsh emend.
Stover & Partridge 1973
FIG. 13N, O

Stratigraphic Range. Cenomanian through Paleocene (Helby *et al.* 1987; Stover & Partridge 1973).

Genus *Beaupreaidites* Cookson ex Couper 1953

Type species: *Beaupreaidites elegansiformis* Cookson 1950

Beaupreaidites elegansiformis Cookson 1950
FIG. 13J, K

Stratigraphic Range. Infrequent in the early to late Maastrichtian or earliest Danian in the Otway, Bight and Duntroon Basins (Dettmann & Jarzen 1996) through Miocene (Stover & Partridge 1973). For a full account of its distribution, see Dettmann & Jarzen (1996).

Genus *Chenopodipollis* Krutzsch 1966

Type species: *Chenopodipollis multiplex* (Weyland & Pflug) Krutzsch 1966

Chenopodipollis chenopodiaceoides
(Martin) Truswell *et al.* 1985
FIG. 13L

Stratigraphic Range. Early Oligocene (Macphail & Truswell 1989) to the present in the families Chenopodiaceae and Amaranthaceae. Found only in the Pliocene-Pleistocene of this study.

Cunoniaceae
FIG. 13S-V

Description. Grains bi- or tri-colpate or colporate, finely reticulate, very small, about 10 µm. Tricolporate type (Fig. 13S, T) most common, bicolpate grains (Fig. 13U, V) few. Three fossil types attributed to the family (Luly *et al.* 1980). Size range, 9-11 µm x 7-9 µm.

Comments. Mildenhall & Pocknall (1989) describe *Tricolpites inconspicuous* and attribute it to Cunoniaceae, as well as possibly several other families. The size range, however, is larger, 17-26 µm x 10-18 µm compared with that above; hence this form species is inappropriate for these specimens. Modern species *Callicoma serratifolia* (Fig. 13Y, bicolpate) and *Ceratophyllum virchowii* (Fig. 13W, X, tricolpate) are given for comparison.

Stratigraphic Range. Late Paleocene (Sluiter 1991) to the present in the eastern coastal rainforest, North Queensland to Tasmania.

Genus *Cyperaceaepollis* Krutzsch 1970

Type species: *Cyperaceaepollis neogenicus* Krutzsch 1970

Cyperaceaepollis sp.
FIG. 13M

Comments. The grain is triangular in shape with one pore and a fine scabrate pattern. For descriptions of some modern Cyperaceae pollen types and the variation found in the family, see Tseng-Chieng (1972) and Heusser (1971). Most specimens are folded or crumpled. Size range, 30-37 µm.

Stratigraphic Range. Late Paleocene (Sluiter 1991; Alley *et al.* 1996) to the present as the family Cyperaceae.

Elaeocarpaceae
FIG. 13Z, AA

Comments. The grains are small, tricolporate with thin walls, < 1 µm, with a psilate surface (Luly *et al.* 1980). Because of their small size, they may be difficult to separate from Cunoniaceae. Fig. 13BB is modern *Elaeocarpus reticulatus*. Size, equatorial view, 9 x 5 µm, polar view, 11 µm.

Stratigraphic Range. The same as that of Cunoniaceae.

Genus *Ericipites* Wodehouse 1933

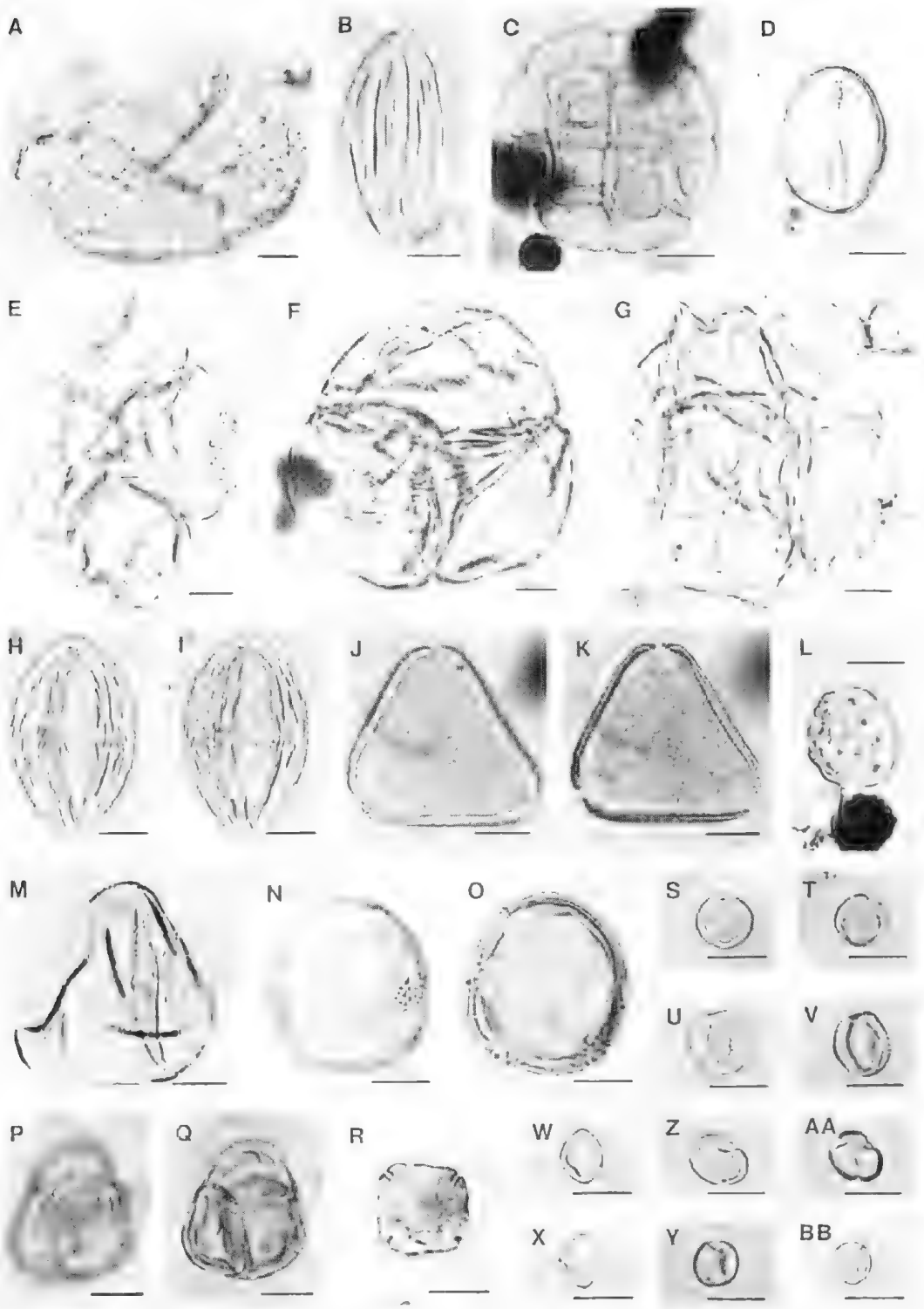

Fig. 13. Tertiary species continued. A. *Dilwynites granulatus*. B. *'Ephedra' notensis*. C. *Acaciapollenites myriosporites*. D. *Steccipites* sp. cf. *A. miautiscabratus*. E, F, G. *Amosopollis dilwynites*. H, I. *Simpsonipollis* sp. J, K. *Beaupreaidites elegansiformis*. L. *Chenopodipollis chenopodiaceoides*. M. *Cyperaceaepollis* sp. N, O. *Australopollis obscurus*. P, Q. *Ericipites scabratus*. R. *Haloragacidites haloragoides*. S, T. Cunoniaceae, tricolporate form. U, V. Cunoniaceae, bicolpate form. W, X. Modern Cunoniaceae, *Ceratopetalum virchowii*, a tricolporate form. Y. Modern Cunoniaceae, *Callicoma serratifolia*, a bicolpate form. Z, AA. Elaeocarpaceae. BB. Modern *Elaeocarpus reticulatus*. Scale bars = 10 μm.

Type species: *Ericipites longistylatus* Wodehouse 1933

Ericipites scabratus Harris 1965
FIG. 13P, Q

Stratigraphic Range. From the late Paleocene in southeastern Australia (Harris 1965), late Paleocene in central Australia (Sluiter 1991).

Genus *Gothanipollis* Krutzsch 1959

Type species: *Gothanipollis gothanii* Krutzsch 1959

Gothanipollis bassensis Stover in Stover & Partridge 1973
FIG. 14A, B

Stratigraphic Range. Middle Eocene to middle Miocene (Stover & Partridge 1973; Macphail & Truswell 1989), late Paleocene (this study).

Genus *Haloragacidites* Couper 1953

Type species: *Haloragacidites triradiatus* Couper 1953

Haloragacidites harrisii (Couper) Harris 1971
FIG. 14G

Comments. The Paleocene specimens are smaller, with pores that hardly protrude when compared with those of the Eocene, but they fit the species well.

Stratigraphic Range. Paleocene (Stover & Partridge 1973) to the present as Casuarinaceae.

Haloragacidites haloragoides Cookson & Pike 1954
FIG. 13R

Stratigraphic Range. Late Miocene (Stover & Partridge 1973) to the present as *Gonocarpus*/*Haloragis* (Cookson & Pike 1954b). It is sometimes recorded in early Miocene and possibly older sediments, e.g. Tulip *et al.* (1982) and Truswell *et al.* (1985). Found only in the Pliocene-Pleistocene of this study.

Genus *Ilexpollenites* Thiergart 1937

Type species: *Ilexpollenites iliacus* (Potonié) Thiergart 1937

Ilexpollenites anguloclavatus McIntyre 1968
FIG. 14D, E

Comments. The size, shape and density of the sculpturing are highly variable (Stover & Partridge 1973). This specimen has relatively small sculpturing. Size, 25 x 19 µm.

Stratigraphic Range. Maastrichtian to Oligocene (Helby *et al.* 1978; Stover & Partridge 1973) in southeastern Australia. The living genus *Ilex* produces this pollen type and is found in northern Australia today (Martin 1977).

Genus *Lewalanipollis* Dettmann & Jarzen 1996

Type species: *Lewalanipollis tycherus* Dettmann & Jarzen 1996

Lewalanipollis sp. cf. *L. rectomarginis* (Cookson) Dettmann & Jarzen 1996
FIG. 16G

Description. Sides straight to slightly concave, pores 9–11 µm diameter. Exine 5 µm thick, thinning considerably towards pores. Nexine 3 µm thick, becoming thinner in zone around pore, with faint channeling. Fine columellae support irregular verrucae up to 5 µm diameter. Surface pattern around pores granular. Size, 55 µm.

Comments. The pattern is similar to that of *L. rectomarginis*, but it lacks the distinctive disaggregation of the nexine around pore of the latter.

Stratigraphic Range. For *L. rectomarginis*, Campanian to Maastrichtian or earliest Danian in the Otway Basin (Dettmann & Jarzen 1996), middle Eocene into late Miocene (Stover & Partridge 1973). cf. *L. rectomarginis*, late Paleocene (this study).

Lewalanipollis sp. cf. *Persoonia*
FIG. 15J, K

Description. Grain irregularly square with 4 pores 5 µm diameter. Exine 1 µm thick with three layers of approximately equal thickness. Middle layer has very fine, hardly distinguishable columellae. Surface pattern very finely scabrate with larger more widely spaced 'granules'. Granules not visible in optical section, hence they may be tiny perforations through tectum. Middle layer of exine thins towards pores. 'Granules' more conspicuous on thinner exine around the pores. Size, 38 µm.

Comments. This type of grain is found in *Persoonia* (Fig. 15L, M), which however, is triangular with 3 pores. Fourporeal grains are sometimes seen in species of Proteaceae. *Conospermum* also has an exine thinning towards the pores but it is much larger and thicker-walled than *Persoonia*.

Distribution. Mid Eocene (this study).

Genus *Lilacidites* Couper 1953
Type species: *Lilacidites kaitangataensis* Couper 1953

Lilacidites lanceolatus Stover in Stover & Partridge 1973
FIG. 14F

Stratigraphic Range. Latest Paleocene through Miocene (Stover & Partridge 1973; Partridge 1976). Late Paleocene (this study)

Genus *Malvacipollis* Harris 1965

Type species: *Malvacipollis diversus* Harris 1965

Malvacipollis subtilis Stover & Partridge 1973
FIG. 14H, I

Comments. The species is described as zoni- or stephanoporate (Harris 1965; Stover & Partridge 1973, respectively) but some of these specimens are panporate.

Stratigraphic Range. Late Paleocene through Miocene (Harris 1965; Stover & Partridge 1973).

Genus *Milfordia* Erdtman 1960

Type species: *Milfordia hypolaenoides* Erdtman 1960

Milfordia homeopunctata
(McIntyre) Partridge in Stover & Partridge 1973
FIG. 14C, J

Comments. This species has the small annulate *Revnia* type of pore. Fig. 14C has a thickened annulus 3 µm wide,

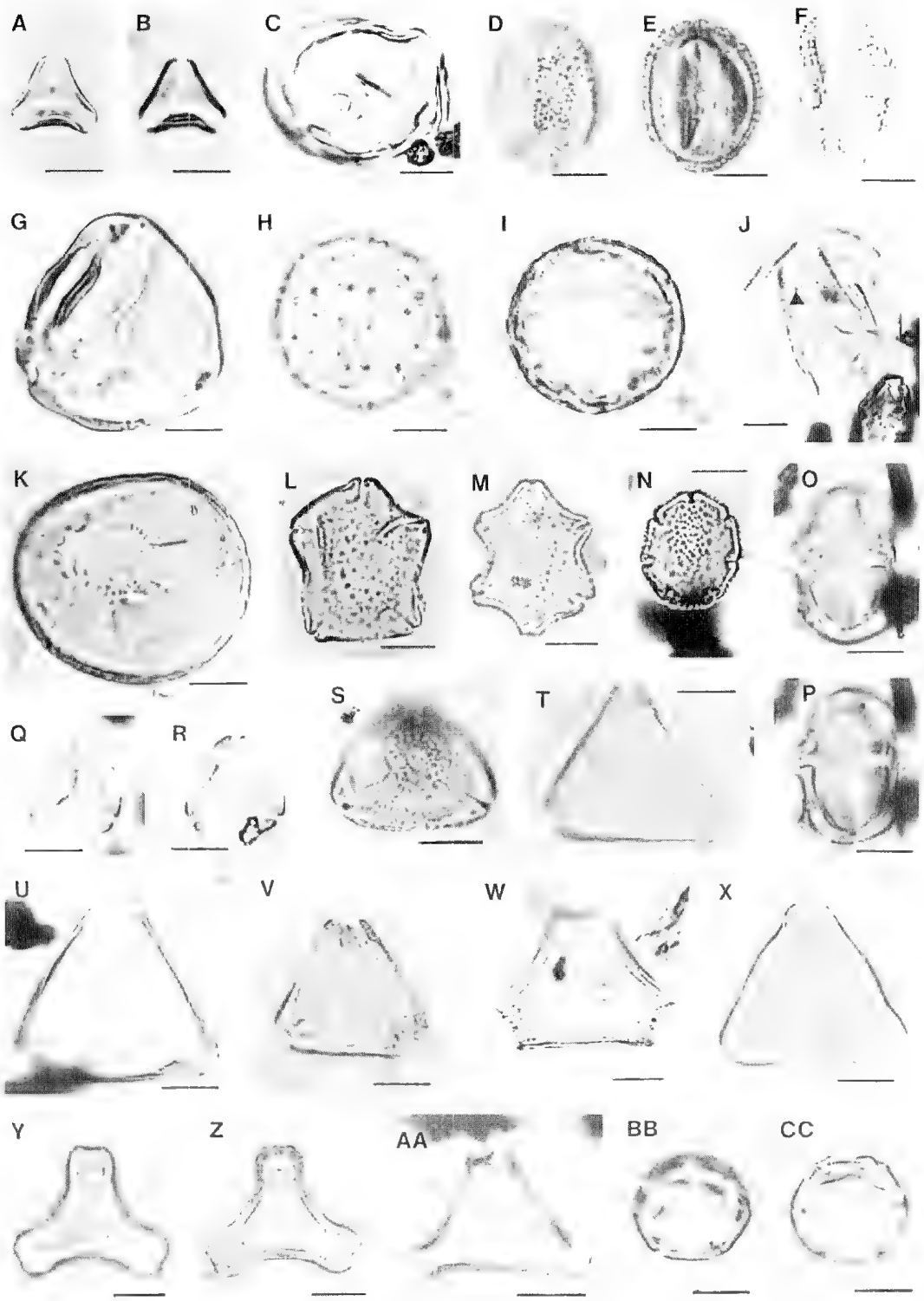

Fig. 14. Tertiary species continued. A, B. *Gothanipollis bassensis*. C, J. *Milfordia homeopunctata*. Arrow indicates pore. D, E. *Ilexpollenites anguloclavatus*. F. *Liliacidites lanceolatus*. G. *Haloragacidites harrisii*. H, I. *Malvacipollis diversus*. K. *Milfordia hypolaenoides*. L. *Nothofagidites emarcidus*. M. *Nothofagidites falcatus*. N. *Nothofagidites deminutus*. O, P. *Nuxipollenites kempii*. Q, R. *Myrtaceidites eucalyptoides*. S. *Myrtaceidites verrucosus*. T, W. *Propylipollis ivanhoensis*. U, V. *Propylipollis* sp. cf. *P. reticuloscabratus*. X. *Propylipollis latrobensis*. Y, Z, AA. *Propylipollis* sp. BB, CC. *Polyorificites oblatus*. Scale bars = 10 μm.

whereas the pore on Fig. 14J (arrow) is not thickened. Size, 34-47 µm.

Stratigraphic Range. Early Eocene through Middle Miocene (Stover & Partridge 1973), late Paleocene (Sluiter 1991).

Milfordia hypolaenoides Erdtman 1960
FIG. 14K

Comments. This species has the distinctive scabrate pattern with larger pits, typical of the family Restionaceae, and a large *Hypolaena* type pore with granules aligned along the margin. Size, 30-40 µm.

Stratigraphic Range. Late Paleocene (this study) to the present.

Genus *Myrtaceidites* Cookson & Pike emend. Potonié 1960

Type species: *Myrtaceidites mesonesus* Cookson & Pike 1954

Myrtaceidites eucalyptoides Cookson & Pike 1954
FIG. 14Q, R

Comments. This pollen type is found in the *Angophora*/bloodwood group of *Eucalyptus*. There are, however five other groups within the genus (Chalson & Martin 1995). Size, 17-19 µm.

Stratigraphic Range. From the early Eocene (Alley *et al.* 1996) to present (Martin 1994). Found only in the Pliocene-Pleistocene of this study. Sluiter (1991) records *Myrtaceidites* spp. through the late Paleocene, early and mid Eocene of the Lake Eyre Basin, but the species are not differentiated.

Myrtaceidites verrucosus
Partridge in Stover & Partridge 1973
FIG. 14S

Stratigraphic Range. Early Eocene through Miocene (Stover & Partridge 1973; Macphail 1996), early Eocene (Sluiter 1991), mid Eocene (this study).

Genus *Nothofagidites* (Erdtman) Potonié 1960

Type species: *Nothofagidites flemingii* (Couper) Potonié 1960

Nothofagidites emarcidus (Cookson) Harris 1965
FIG. 14H.

Stratigraphic Range. Early Eocene through Miocene (Stover & Partridge 1973), mid Eocene, (this study).

Nothofagidites falcatus (Cookson) Stover & Evans 1973
FIG. 14M

Stratigraphic Range. Mid Eocene through mid Miocene (Stover & Partridge 1973).

Nothofagidites deminutus (Cookson) Stover & Evans 1973
FIG. 14N

Comments. The U-shaped colpi with margins narrowly rimmed by inrolled exine and all other features of the morphology fit those of *N. deminutus* (Dettmann & Pocknall 1990). Size, 22-27 µm.

Stratigraphic Range. Early Eocene (Stover & Evans 1973) into early Miocene (Cookson 1959)

Genus *Nuxipollenites* Elsik emend. Frederiksen 1980

Type species: *Nuxipollenites chairbournensis* Elsik 1974

Nuxipollenites kempii sp. nov.
FIG. 14O, P

1976 *Tricolporites* sp. aff. *Diplopeltis* Kemp, p. 113, fig. 4n, v.
1981 *Tricolporites* sp. aff. *Diplopeltis* Bint, p. 286, figs 34, 35.
1985 *Nuxipollenites* sp. Truswell *et al.*, p. 286, fig. 8e, f
1989 *Nuxipollenites* sp. aff. *Diplopeltis* Mildenhall & Pocknall, p. 47, pl. 11 figs 1, 3
1989 *Nuxipollenites* sp. Macphail & Truswell, p. 327, fig. 10 I, J, L.
1994 *Dodonaea triquetra* pollen type Martin, p. 128, fig. 7.11 (a)-(k).

Holotype: Slide AMF 103724, England Finder coordinates J46/1 (Table 4). Grain in equatorial view, 29 x 20 µm. Fig. 14O, P.

Etymology: Named in honour of E. M. Truswell (née Kemp) who first documented this species.

Diagnosis: Grains prolate, tricolporate with protruding pores. Distinctive thickened intercolpal bands meet at the poles. Exine in outline thinner at equator, thicker towards poles, 2 layered with thin columellate layer in between, columellae barely visible. Only the outer layer thickened to produce intercolpal bands.

Description: Grains prolate, poles broadly rounded, tricolporate with long colpi extending almost to poles. Pores 3 x 4 µm protrude, transverse margins thickened. Exine 1-2 µm thick at equator, has two distinct layers with thin, fine-columellate layer between them. Columellae not always visible. Poles 3 µm thick where distinctive thickened intercolpal bands meet. Only outer layer of exine becomes thickened, inner and columellate layer remaining same thickness over whole grain. Surface pattern scabrate. Size range, 29-40 x 15-30 µm, polar x equatorial diameter, respectively (6 specimens).

Comments. Kemp (1976) attributed this pollen type to *Diplopeltis* Endl. (George & Erdtman 1969). Unlike *N. kempii*, the exine over the poles of 4 of the 5 species of *Diplopeltis* is either the same thickness over the whole of the grain or it is thinner than over the rest of the grain. The fifth species has pointed poles where the exine is thicker than the rest of the grain, which otherwise has a uniform thickness. The columellae are well defined in *Diplopeltis* and in some species, extend throughout the thickened part of the exine, unlike *N. kempii*. *Dodonaea triquetra* has very similar thickened intercolpal bands meeting at the poles and a fine, thin columellate layer, like *N. kempii*. The fossil is thus very similar to *D. triquetra* and less like *Diplopeltis*. *Dodonaea triquetra* is the only species in the genus with this pollen morphology, and is found in eucalypt forests on damp sites and in gullies along the southern half of the eastern coastal strip of Australia (Martin 1994, 1997)

Stratigraphic Range. Mid Eocene of central Australia (Kemp 1976; Sluiter 1991) to the present day, on the southern part of the east coast (Martin 1994). Found only in the Pliocene-Pleistocene of this study.

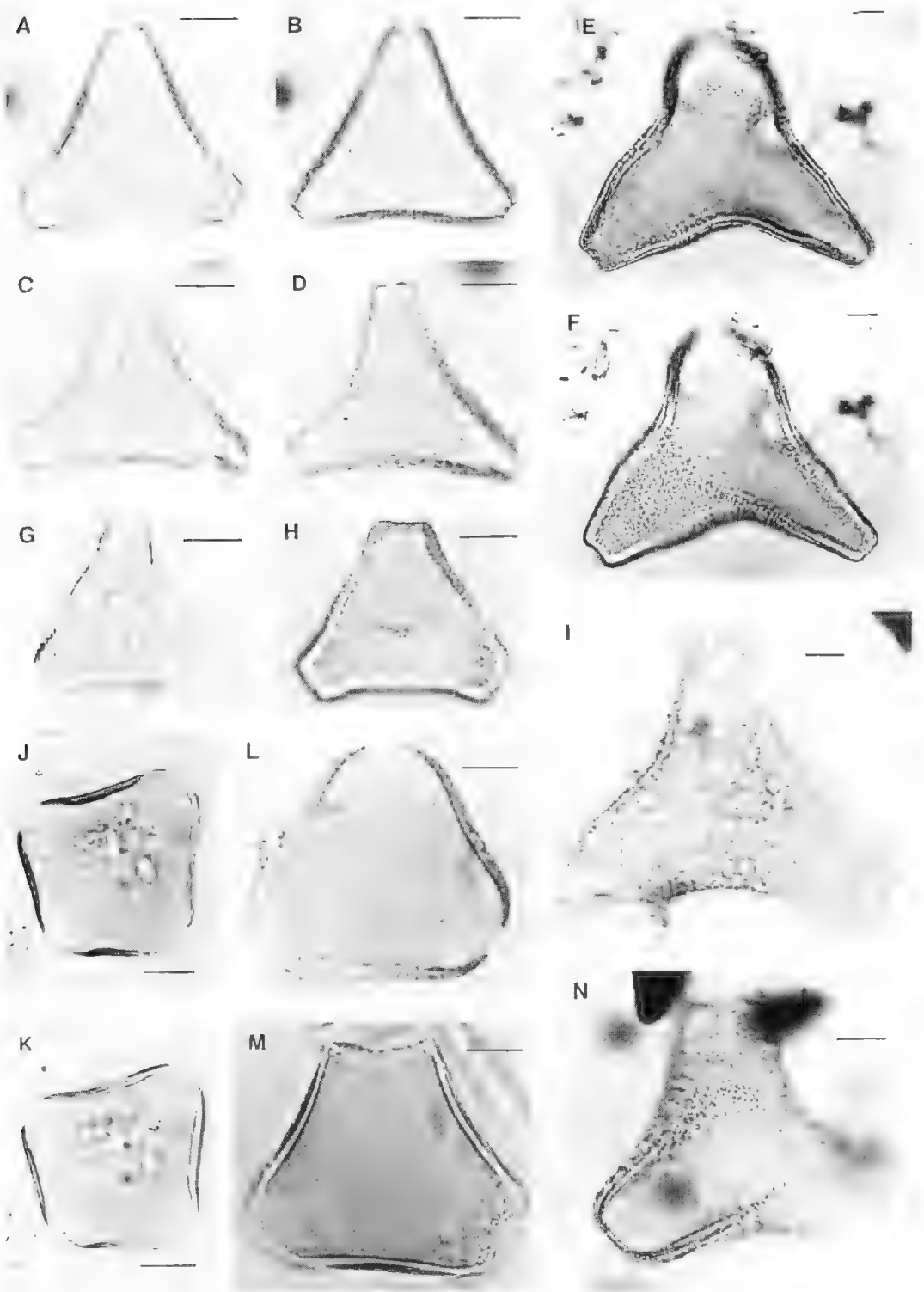

Fig. 15. Tertiary species continued. A, B, *Proteacidites adenanthoides*. C, D, *Proteacidites crassus*. E, F, *Proteacidites fromensis*. G, H, *Proteacidites angulatus*. I, *Proteacidites grandis*. J, K, *Lewalanipollis* sp. cf. *Persoonia*. L, M, Modern *Persoonia laurina*. N, *Proteacidites incurvatus*. Scale bars = 10 μm.

Genus *Polyorificites* Martin 1973a

Type species: *Polyorificites oblatus* Martin 1973a

Polyorificites oblatus Martin 1973a
FIG. 14BB, CC

January 1973a *Polyorificites oblatus* Martin, p. 45, figs 196-198.
May 1973, *Heliciporites astrus* Partridge in Stover & Partridge, p. 271 pl. 26, figs 3-5.

Stratigraphic Range. Early to late Eocene (Stover & Partridge 1973), late Eocene to mid Miocene (Martin 1987), mid Eocene into Pleistocene (Macphail 1996).

Genus *Polyporina* Naumova ex Potonié 1960

Type species: *Polyporina multistigmosa* Naumova ex Potonié 1960

Polyporina granulata Martin 1973a
FIG. 17A, B

Description. Grain spherical, panporate with about 24 pores, 2-3 µm diameter. Exine 2 µm thick, with sexine, columellate layer and tectum of approximately equal thickness. Tectum has numerous perforations 0.5 µm wide, spaced about 1 µm apart. Surface has scattered granules. Similar to some Amaranthaceae. Size, 37 µm.

Stratigraphic Range. Late Miocene into Pleistocene (Macphail 1996). Found only in the Pliocene Pleistocene of this study.

Genus *Propylipollis* Martin & Harris 1974

Type species: *Propylipollis reticuloscabratus* (Harris) Martin & Harris 1974

Propylipollis ivanhoeensis (Martin) Milne 1988
FIG. 14I, W

Description. Sides straight, apices truncate, pores 3-7 µm, usually about 5 µm, nexine and sexine approximately equal thickness, wide very finely columellate layer. Surface pattern finely scabrate with scattered granules and/or foveulae. Pores have well-defined modified zone where surface pattern is more granular and nexine is modified. Size, 23-30 µm.

Comments. These specimens are more variable, especially in size, and in the thickening, than those of the original description (Martin 1973a), e.g. Fig. 14W with a much larger pore. This pollen type is similar to that of species of *Helicia*, *Orites* and *Macadamia* found in east coast rainforests.

Stratigraphic Range. Late Eocene (Milne 1988), late Eocene through Pliocene (Martin 1987), late Paleocene [illegible].

Propylipollis latrobensis (Harris) Martin & Harris 1974
FIG. 14X

Stratigraphic Range. Early to late Eocene (Stover & Partridge 1973), late Paleocene (Harris 1965; this study).

Propylipollis sp. cf. *P. pseudomoides*
(Stover) Dettmann & Jarzen 1996
FIG. 16B-D

Comments. Some specimens, e.g. Fig. 16C, fit the diagnosis, with the exception that tiny columellae may just be visible on the coarsest part of the reticulum and the size range here is a little larger than the 27-36 µm of Stover & Partridge (1973). Others, e.g. Fig. 16B, D, have a pattern that is puncto-reticulate, with the dimensions of the lumina and muri less than 0.5 µm, the lower limit for *P. pseudomoides*. Size, 30-44 µm.

Stratigraphic Range. For *P. pseudomoides*, Campanian-Maastrichtian or earliest Danian of the Otway Basin (Dettmann & Jarzen 1996), elsewhere in southeastern Australia, late Paleocene into Oligocene (Stover & Partridge 1973).

Propylipollis sp. cf. *P. reticuloscabratus*
(Harris) Martin & Harris 1974
FIG. 14U, V

Comments. This form is a delicate version of *P. reticuloscabratus* where the exine is thickened around the pore but not as heavily as those of Harris (1965), and the reticulum is finer. Size, 25-35 µm.

Stratigraphic Range. For *P. reticuloscabratus*, Campanian-Maastrichtian of the Otway Basin (Dettmann & Jarzen 1996), Southeastern Australia, late Paleocene into late Eocene (Harris 1965; Stover & Partridge 1973) cf. *P. reticuloscabratus*, late Paleocene (this study).

Propylipollis sp.
FIG. 14Y, Z, AA

Description. Shape triangular with protruding, domed pores. Exine 1-2 µm, sexine and nexine approximately equal thickness. Irregular, broken reticulate pattern, muri < 1 µm, lumina 1-2 µm. Small columellae may just be visible. Pores 2-3 µm diameter, protrude 2-8 µm. Nexine thins towards pore, base of pore may be marked by a notch or inward protrusion. Size, 20-30 µm.

Comments. The distinctive pore is seen in present day species of *Banksia* and *Grevillea*. The size, however, is much smaller than these living taxa. It is unlike *Proteacidites hakeoides* Couper which is much larger than these specimens and has a coarse-granular pattern (A.R.H. Martin 1973).

Distribution. Late Paleocene (this study).

Genus *Proteacidites* Cookson ex Couper emend.
Martin and Harris 1974

Type species: *Proteacidites adenanthoides* Cookson 1950

Proteacidites sp. cf. *P. adenanthoides* Cookson/*P. crassus*
Cookson complex
FIG. 15X-D

Comments. Cookson (1950) differentiates these two species on (1) the shape (*P. adenanthoides* has straight to slightly concave sides whereas *P. crassus* has very concave sides), (2) the pattern (*P. adenanthoides* has a fine reticulum whereas *P. crassus* has a coarse reticulum) and (3) size, *P. adenanthoides* is smaller, 32-48 µm equatorial diameter whereas *P. crassus* is larger, 58 µm. There are some other minor differences as well. Stover & Partridge (1973) describe a lectotype of *P. adenanthoides* which is much larger (73 µm) than the size range quoted by Cookson

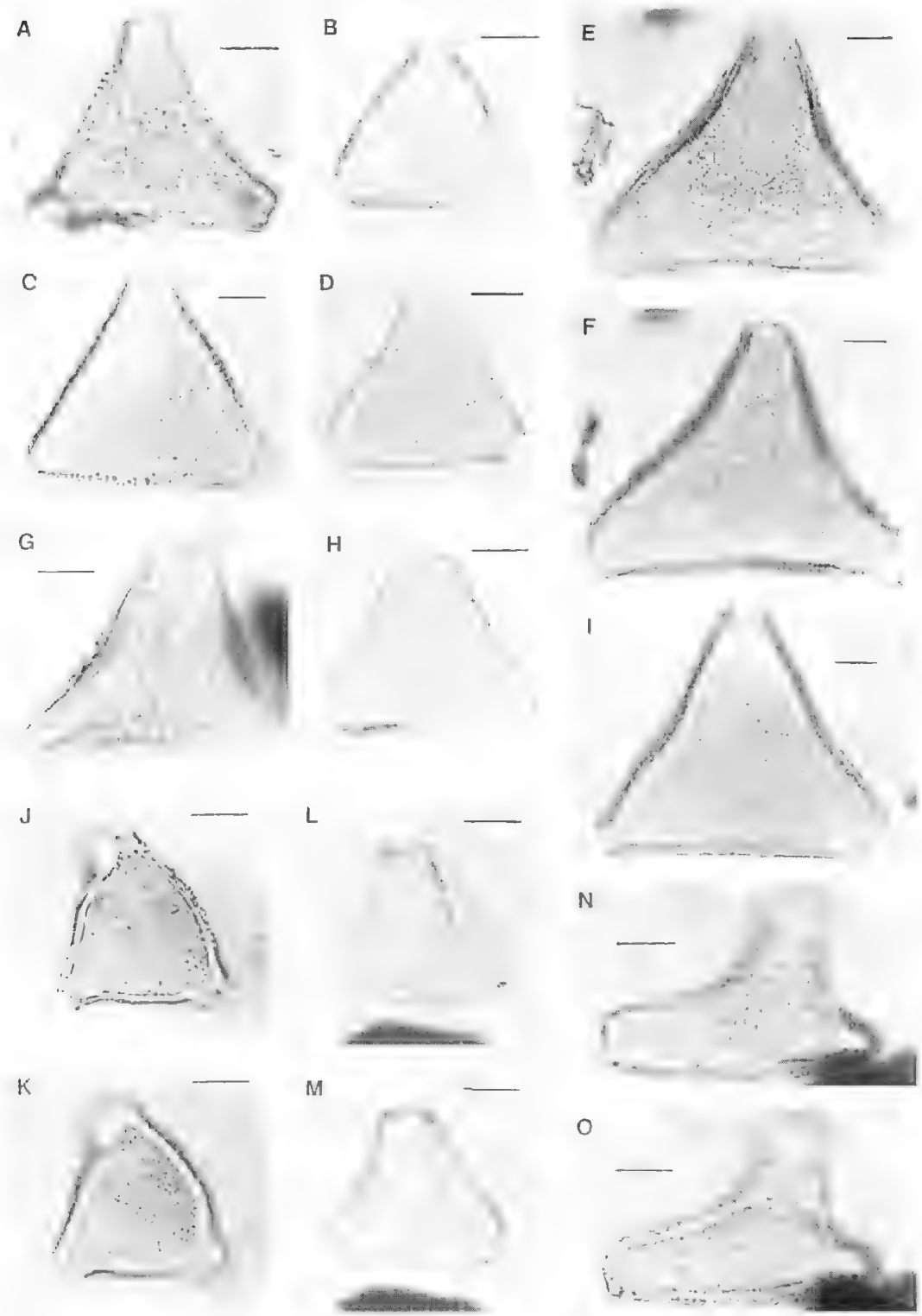

Fig. 16. Tertiary species continued. A, *Proteacidites cooksoniae*. B, C, D, *Propylipollis* cf. *P. pseudomoides*. E, F, *Proteacidites* sp. 1. G, *Lewalanipollis* sp. cf. *L. rectomarginis*. H, *Proteacidites* sp. 3. I, *Proteacidites* cf. *P. stipplatus*. J, K, *Proteacidites* sp. cf. *obscurus*. L, M, *Proteacidites* sp. 2. N, O, *Proteacidites* sp. cf. *P. incurvatus*. Scale bars = 10 μm

(1950). Moreover, Stover & Partridge state that both layers of the exine thin towards the pores whereas Cookson states that the nexine does not thin towards the pores.

The two species as described by Cookson are recognisable in this study, but there are intermediates that are difficult to place in either species. Thinning of the exine towards the pores is rarely seen and is very slight when present. Size range for the complex, 28–45 µm.

Stratigraphic Range. For *P. adenanthoides*, from early Campanian to Eocene in the Otway Basin (Dettmann & Jarzen 1996). For southern Australia, late Paleocene into Oligocene (Stover & Partridge 1973; Milne 1988). For *P. crassus*, middle Campanian-Maastrichtian or earliest Danian in the Otway Basin (Dettmann & Jarzen 1996). For southern Australia, early into late Eocene (Stover & Partridge 1973; Milne 1988). For the complex, late Paleocene (this study).

Proteacidites angulatus Stover in Stover & Partridge 1973
FIG. 15G, H

Comments. These specimens fit the description of *P. angulatus* with the exception that the exine is usually thicker around the pores, whereas in the original description, it may be thinner (Stover & Partridge 1973). The precise amount of thickening, however, is variable. Size range, 28–35 µm.

Stratigraphic Range. Maastrichtian and Paleocene (Stover & Partridge 1973), late Paleocene (this study).

Proteacidites cooksoniae Dettmann & Jarzen 1996
FIG. 16A

Comments. The smaller size differentiates this species from *P. grandis* (Dettmann & Jarzen 1996). Size range, 37–46 µm.

Stratigraphic Range. Campanian-Maastrichtian or earliest Danian in the Otway Basin and possibly Late Cretaceous/Paleocene in the Bight/Duntroon Basin (Dettmann & Jarzen 1996). Late Paleocene (this study).

Proteacidites fromensis Harris 1972
FIG. 15E, F

Comments. These specimens fit the original description well, except that the surface pattern is finely puncto-reticulate, grading to granular around the pores, in contrast to the evenly granular to scabrate pattern of the original description (Harris 1972). Size, 50–71 µm.

Stratigraphic Range. Paleocene (Harris 1972), late Paleocene to mid Eocene (Sluiter 1991), late Paleocene (this study).

Proteacidites grandis Cookson 1950
FIG. 15I

Stratigraphic Range. Late Paleocene to mid Eocene (Stover & Partridge 1973; Partridge 1976), late Paleocene (this study).

Proteacidites incurvatus Cookson 1950
FIG. 15N

Description. Grain anisopolar, sides concave, apices broadly rounded. Pores slightly depressed, 5 µm diameter. Exine 5 µm thick, thinning to 2 µm and curving inwards towards pore. Sexine, nexine approximately equal thickness. Columellae support irregularly-shaped gemmae/verrucae, 2–4 µm diameter, becoming smaller near pore and producing granular pattern near pore. Size, 30–50 µm.

Comments. The morphology fits *P. incurvatus* but this specimen is slightly smaller and thinner walled than the range quoted by Stover & Partridge (1973).

Stratigraphic Range. Late Paleocene through mid Eocene (Stover & Partridge 1973), mid Eocene (this study).

Proteacidites sp. cf. *P. incurvatus* Cookson 1950
FIG. 16N, O

Comments. The morphology is very similar to that of *incurvatus* except that the exine does not thin towards the pore and the gemmae/verrucae are the same size over the grain, with a ring of slightly larger verrucae around the pore. Size, 40 µm.

Distribution. Late Paleocene (this study).

Proteacidites sp. cf. *P. obscurus* Cookson 1950
FIG. 16J, K

Description. Sides straight to convex, pores protruding. Exine 2 µm thick, sexine and nexine more or less equal width, columellae indistinct. Surface pattern verrucate, verrucae 1–2 µm in diameter, but several may be fused into larger sheets, especially over the poles. Nexine broken into coarse granules in zone 2–3 µm around pore. Size, 32 µm.

Comments. The sexine differs from *P. obscurus* which is widely baculate and somewhat reticuloid (Cookson 1950).

Stratigraphic Range. For *P. obscurus*, early Eocene to late Miocene (Stover & Partridge 1973). For *Proteacidites* sp. cf. *P. obscurus*, late Paleocene (this study).

Proteacidites sp. cf. *P. stipplatus*
Partridge in Stover & Partridge 1973
FIG. 16I

Comments. This form fits the description of *P. stipplatus* with the exception that the nexine is slightly thicker around the pore than in the interradial region. It is less like *Proteacidites rectus* Pocknall & Mildenhall 1984, the differences being (1) the grain is much larger, the size given below compared with 32–49 µm for *P. rectus*, (2) the nexine is equal to or slightly thicker than the sexine, whereas it is three times thicker on *P. rectus*, (3) the columellae are very clear, spaced 0.5–1.0 µm apart and the surface uniform and granular, whereas the columellae are faint and the surface scabrate on *P. rectus* (Pocknall & Mildenhall 1984). Size, 60 µm.

Stratigraphic Range. For *P. stipplatus*, mid Eocene into Oligocene (Stover & Partridge 1973) and mid Eocene into mid Miocene (Macphail 1996) in southeastern Australia. For cf. *P. stipplatus*, late Paleocene (this study) and mid Eocene (Sluiter 1991) in the Lake Eyre Basin.

Proteacidites sp. 1
FIG. 16E, F

Description. Sides straight to slightly concave, exine 4 µm thick in interradial region, thinning towards pores. Nexine, sexine approximately equal thickness; tectum incomplete. Columellae produce strong granular surface pattern, pieces of tectum form rugulate-reticulate pattern, rugulae about 2 µm wide, supported by two rows of columellae. Size, 66–83 µm.

Comments. This species differs from *P. frumensis* in that the sides are less concave and it has the rugulate-reticulate surface pattern.

Distribution. Late Paleocene (this study).

Proteacidites sp. 2
FIG. 16L, M

Description. Sides straight to concave, exine 1-2 µm thick, distinct sexine and nexine approximately equal thickness, exine not thinning towards pore. Pores 2-4 µm in diameter, surface pattern finely reticulate. Size, 19-27 µm.

Distribution. Late Paleocene (this study).

Proteacidites sp. 3
FIG. 16H

Description. Grain triangular with straight or slightly concave sides, apices truncate, pores 3-4 µm wide. Exine 1-2 µm thick, with the nexine, columellate layer and sexine of approximately equal widths. The exine may thin slightly towards the pores. Surface pattern finely verrucate in the intercolpal and polar regions and scabrate around the pores. Size, 33 µm

Distribution. Late Paleocene (this study).

Genus *Quintinapollis* Mildenhall & Pocknall 1989

Type species: *Quintinapollis psilatispora* (Martin) Mildenhall & Pocknall 1989

Quintinapollis psilatispora
(Martin) Mildenhall & Pocknall 1989
FIG. 17I.

Comments. These specimens are slightly larger those of the original description, 18 µm of this study compared with a maximum of 15 µm (Martin 1973a) and they lack of the small semi-circular expansion of the end of the colpi seen on the original specimens. These differences are relatively minor and Mildenhall & Pocknall (1989) note similar variation

Stratigraphic Range. In southeastern Australia, late Eocene to the present in east coast rainforests, early Eocene in the Gippsland Basin and mid Eocene to Pleistocene in the inland Murray Basin (Macphail 1996). In the Lake Eyre Basin, mid Eocene (Sluiter 1991) and late Paleocene (this study)

Genus *Rhopites* Wodehouse 1933

Type species: *Rhopites bradleyi* Wodehouse 1933

Rhopites alveolatus (Couper) Pocknall & Crosbie 1982
FIG. 17E

Stratigraphic Range. Mid Eocene to late Pliocene in New Zealand (Pocknall & Crosbie 1982). Oligocene-Miocene in Queensland (Hekel 1972), late Eocene to Pliocene-Pleistocene in southeastern Australia (Macphail & Truswell 1989; Martin 1973a). In the Lake Eyre Basin, late Paleocene-early Eocene (Sluiter 1991), mid Eocene (this study)

Rhopites sp. cf. *R. alveolatus* (Couper)
Pocknall & Crosbie 1982
FIG. 17P, Q

Description. Grain oblate, tricolporate with long colpi, very small apocolpia. Colpi with well defined margins and granular colpal membrane up to 4-5 µm wide at equator. Endopore with thickened transverse margins and capped with raised plug bearing granules. Exine 1-1.5 µm thick with thin nexine and perforate tectum, well defined columellae and reticulate surface pattern, with muri ≤ 0.5 µm, lumina 0.5-1.0 µm. Size, 30 µm polar view, 26-30 µm x 22 µm equatorial view.

Comments. The wide colpal membrane and thickened endopore resemble *R. alveolatus* which, however, has psilate colpi.

Distribution. Late Paleocene (this study)

Genus *Santalumiidites* Cookson & Pike emend.
Potonié 1960

Type species: *Santalumidites cainozoicus* Cookson & Pike 1954

Santalumiidites cainozoicus Cookson & Pike 1954
FIG. 17F

Stratigraphic Range. Southeastern Australia, early Eocene into late Eocene (Stover & Partridge 1973, 1982; Partridge 1976), Lake Eyre Basin, mid Eocene (Sluiter 1991; Alley *et al.* 1996; this study)

Genus *Saputaveoidaepollenites* Potonié Thomson &
Thiergart 1950

Type species: *Saputaveoidaepollenites* (al. *Pollenites*) *manifestus* Potonié 1931

Saputaveoidaepollenites rotundus Harris 1972
FIG. 17J, K

Stratigraphic Range. Southeast Australia, early Eocene through Miocene (Stover & Partridge 1973), mid Eocene to mid Tertiary (Harris 1972), Lake Eyre Basin, late Paleocene (this study), and mid Eocene (Sluiter 1991; Alley *et al.* 1996).

Genus *Simplicepollis* Harris 1965

Type species: *Simplicepollis meridianus* 1965

Simplicepollis meridianus Harris 1965
FIG. 17C, D.

Comments. This planar tetrad is rare when compared with the usual tetrahedral tetrad.

Stratigraphic Range. Southeast Australia, Late Cretaceous into late Eocene (Stover & Partridge 1973). Lake Eyre Basin, late Paleocene-early Eocene (Sluiter 1991), mid Eocene (this study).

Genus *Simpsonipollis* S. K. Srivastava 1975

Type species: *Simpsonipollis mulleusis* S.K. Srivastava 1975

Simpsonipollis sp.
FIG. 13H, I

Comments. The regular striate ridges on top of a perforated tectum place this pollen type in *Simpsonipollis*. The specimen illustrated is 42 µm polar diameter x 26 µm equa-

torial diameter, much larger than *Simpsonipollis mulleri* Kemp in Kemp & Harris 1977 with dimensions of 14-22 µm polar diameter x 10-21 µm equatorial diameter.

Distribution. Late Paleocene.

Genus *Tricolpites* Cookson ex Couper 1953

Type species: *Tricolpites reticulatus* Cookson 1947 (subsequent designation by Couper 1953)

Tricolpites sp. cf. *T. asperamarginis* McIntyre 1968
FIG. 17H, I

Description. Grain oblate, tricolpate with wide, gaping open colpi. Exine 1.5-2 µm in intercolpal region, thinning markedly towards colpi. Nexine thin, collumellate layer thin with distinct columellae, tectum ≥ 1 µm in intercolpal region, surface scabrate. Size, 25-29 µm.

Comments. The exine thinning towards the colpi is not seen on *T. asperamarginis*. The very thick tectum and the exine thinning towards the colpi are not seen on *Tricolpites lilydalei*.

Stratigraphic Range. For *T. asperamarginis*, Paleocene in New Zealand (McIntyre 1968), lower Tertiary to late Miocene in Queensland (Hekel 1972). *Tricolpites* sp. cf. *T. asperamarginis* mid Eocene (this study).

Tricolpites sp. cf. *T. confessus*
Stover in Stover and Partridge 1973
FIG. 17O

Comments. These specimens are very similar to those originally described except that they are slightly larger, the size given below compared with a maximum of 25 µm. The exine is 1-1.5 µm, two layers are distinguishable and the surface is psilate/scabrate whereas the original description states that the layers in the exine are not clearly differentiated. Size, 30-31 µm.

Stratigraphic Range. For *T. confessus*, Santonian to latest Maastrichtian-earliest Paleocene (Helby *et al.* 1987), cf. *T. confessus*, late Paleocene (this study).

Tricolpites sp. cf. *T. discus* Harris in Kemp & Harris 1977
FIG. 17M, N

Comments. This specimen is larger than those described by Harris (in Kemp & Harris 1977), 30 µm equatorial diameter compared with 17-23 µm respectively. The morphological features, however, are very similar.

Stratigraphic Range. For *T. discus*, Paleocene, Ninetyeast Ridge, Indian Ocean (Kemp & Harris 1977) and late Eocene, Eucla Basin (Milne 1988). For *Tricolpites* sp. cf. *T. discus*, mid Eocene (this study).

Tricolpites phillipsii Stover in Stover & Partridge 1973
FIG. 17T

Stratigraphic Range. Southeast Australia, Paleocene into late Eocene (Stover & Partridge 1973, 1982; Partridge 1976). Lake Eyre Basin, early Eocene (Sluiter 1991) and mid Eocene (this study).

Tricolpites thomasii Cookson & Pike 1954
FIG. 17U, V

Stratigraphic Range. Mid and the lower part of the late Eocene (Stover & Partridge 1973, 1982). Lake Eyre Basin, early and mid Eocene (Sluiter 1991), mid and late Eocene (Alley *et al.* 1996), mid Eocene (this study).

Genus *Tricolporites* Cookson ex Stover & Evans 1973

Type species: *Tricolporites sphaericus* Cookson (designated by Stover & Evans 1973)

Tricolporites angurium
Partridge in Stover & Partridge 1973
FIG. 17Z

Comments. These specimens fit the diagnosis except that the generally indistinct ora of the diagnosis are hardly visible here. Size, 31-47 µm x 22-29 µm.

Stratigraphic Range. Southeast Australia, early mid-late Eocene (Stover & Partridge 1973, 1982). Lake Eyre Basin, mid Eocene (Sluiter 1991; this study).

Tricolporites leuros Partridge in Stover & Partridge 1973
FIG. 17W, X

Comments. These specimens fit the diagnosis well, except that on some specimens, the "indistinct ora" cannot be seen at all. On other specimens, the exine in the interradial areas may be 1-1.5 µm thick, compared with 2-4 µm in the diagnosis, and on these, the ora may protrude so that they lack the polygonal outline of the thicker walled specimens. Size, 20-25 µm.

Stratigraphic Range. Southeast Australia, mid Eocene to mid Miocene (Stover & Partridge 1973; Macphail 1996). Lake Eyre Basin, late Paleocene (this study) and mid Eocene (Sluiter 1991; Alley *et al.* 1996).

Genus *Tricolpumpollenites*
Pflug in Thomson & Pflug 1953

Type species: *Tricolpumpollenites dolium* (Potonie) Pflug 1953

Tricolpumpollenites endobalteus McIntyre 1965
FIG. 17R, S

Stratigraphic Range. Southeast Australia, mid Eocene into Pliocene (Martin 1987; Macphail 1996). Lake Eyre Basin, Early-mid Eocene (Sluiter 1991), mid Eocene (this study).

Genus *Triorites* Cookson ex Couper 1953

Type species: *Triorites magnificus* Cookson 1950, designated by Couper 1953

Triorites minisculus McIntyre 1965
FIG. 18Q

Description. Grain triporate, pores 2-3 µm diameter. Exine 1µm thick, two layered, psilate except for faint pattern around pores. Size, 13 µm.

Comments. The morphology of the specimen fits the description of *Triorites minisculus* given by McIntyre (1965).

Stratigraphic Range. New Zealand, Paleocene (McIntyre 1965). Lake Eyre Basin, late Paleocene-early Eocene (Sluiter 1991), late Paleocene (this study).

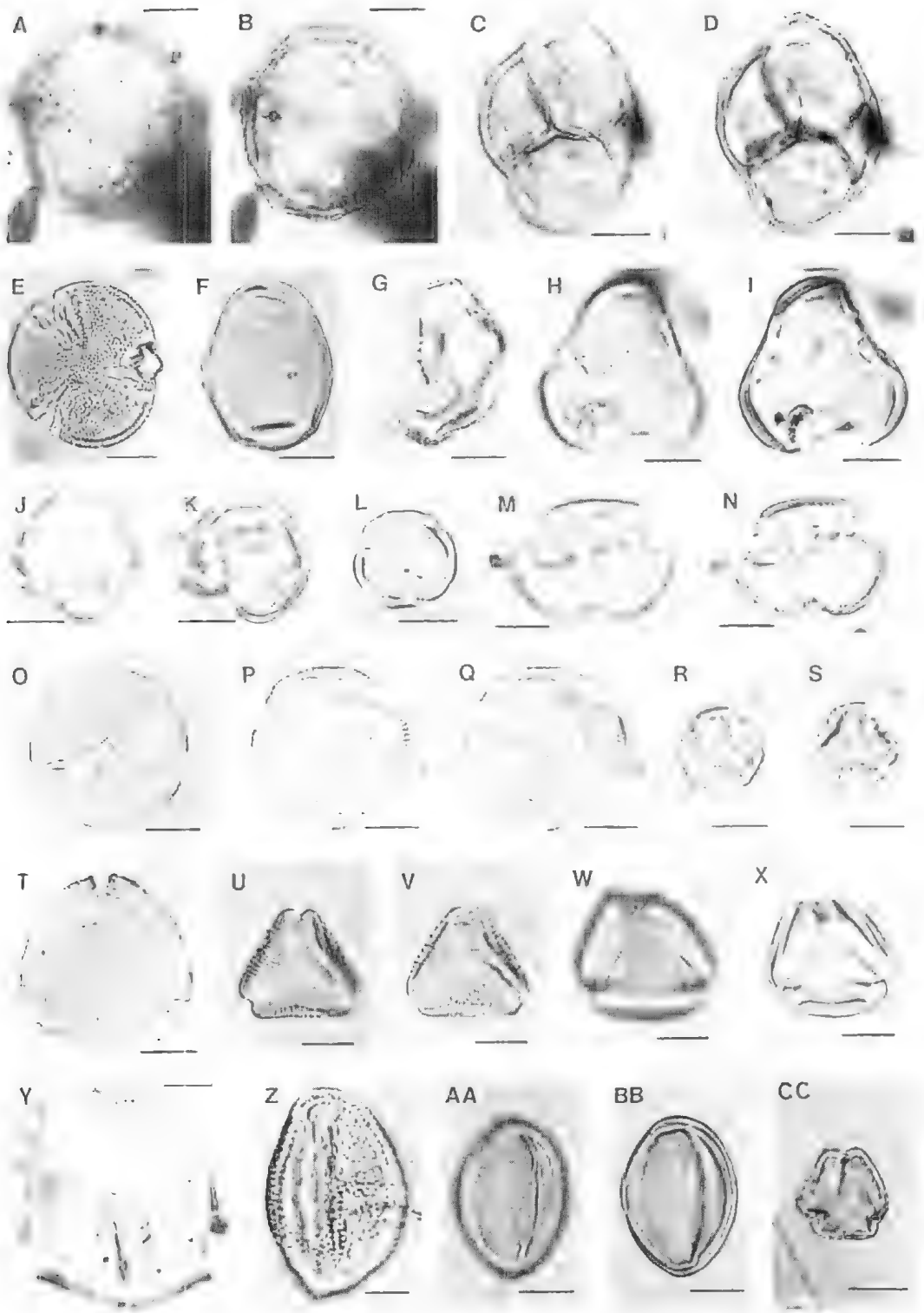

Fig. 17. Tertiary species continued. A, B. *Polysporina granulata*. C, D. *Simplicepollis meridianus*. E. *Rhopites alveolatus*. F. *Santalumidites cainozoicus*. G. *Aglaoridia quatamis*. H, I. *Tricolpites* sp. cf. *T. asperamarginatus*. J, K. *Saponaceoidaepollenites rotundus*. L. *Quintiniapollis psilatispora*. M, N. *Tricolpites* sp. cf. *T. discus*. O. *Tricolpites* sp. cf. *T. confessus*. P, Q. *Rhopites* sp. cf. *R. alveolatus*. R, S. *Tricolporopollenites endobalteus*. T. *Tricolpites phillipsii*. U, V. *Tricolpites thomasii*. W, X. *Tricolporites leuros*. Y. *Triporopollenites ambiguus*. Z. *Tricolporites angurium*. AA, BB. *Tricolporites* sp. 2. CC. *Tricolporites* sp. 1. Scale bars = 10 μm.

Triorites sp.
FIG. 18H

Description. Grain circular, triporate, pores 5 µm wide with ragged margins. Exine 1 µm thick, clearly two layered, with faint scabrate surface pattern. Size, 25-28 µm.

Comments. The morphology of this species is similar to that of some species of Ulmaceae, especially *Aparthes philipensis*. The former, however, has a ragged edge to the pore whereas the latter has a well defined rim. Some species of *Celtis* are similar to the fossil also, e.g. *C. glabra* and *C. occidentalis*, but the latter show distinct columellae and the pore has an annulus.

Distribution. Late Paleocene.

Genus *Triporopollenites* Pflug & Thomson 1953 in Thomson & Pflug 1953

Type species: *Triporopollenites coryloides* Pflug in Thomson & Pflug 1953

Triporopollenites ambiguus
Stover in Stover & Partridge 1973
FIG. 17Y

Stratigraphic Range. Southeast Australia, early Eocene into late Eocene (Stover & Partridge 1973). Murray Basin, mid Eocene into early Miocene (Macphail 1996), mid Eocene (this study).

Genus *Tubulifloridites* Cookson ex Potonié 1960

Type species: *Tubulifloridites antipodica* Cookson, designated by Potonié 1960

Tubulifloridites sp.
FIG. 18R

Stratigraphic Range. *Triporopollenites bellus* Zone, late Miocene (Stover & Partridge 1973) to the present as the daisy family, Asteraceae. Oligocene through Pleistocene (Macphail 1996). Found only in the Plio-Pleistocene of this study.

Unidentified taxa

Dicolpopollis Pflanzl emend. Potonié 1966

Type species: *Dicolpopollis kockelii* Pflanzl 1956, designated by Potonié 1966

Dicolpopollis sp.
FIG. 18F

Description. Grain has two, gaping colpi. Exine, 1 µm thick, has nexine, columellate layer and tectum, all of approximately equal thickness. Surface pattern fine, uniform puncto-reticulum. Size, 40 x 32 µm.

Distribution. Middle Eocene.

Tricolpites sp.
FIG. 18O, P

Description. Grain prolate with broad poles, long colpi with ragged margins. Exine 1 µm thick, two layered with very fine, faint columellae. Surface pattern finely puncto-reticulate. Size, 20 x 16 µm.

Distribution. Late Paleocene.

Tricolporites sp. 1
FIG. 17CC

Description. Grain oblate, tricolporate, distinct thickenings around the pores. Exine 1 µm thick, with two layers approximately equal thickness, no discernible structure. Grain covered with minute coni spaced about 1 µm apart. Size, 15-17 µm, equatorial diameter.

Distribution. Late Paleocene

Tricolporites sp. 2
FIG. 17AA, BB

Description. Grains prolate, tricolporate with long colpi reaching almost to poles, pores indistinct. Exine 1.5-2 µm thick, with nexine, very finely columellate layer and tectum as thick as nexine. Surface extremely fine granular/reticulate pattern with larger (up to 0.5 µm) fovulae through tectum. Size, 26-30 µm x 22 µm.

Distribution. Late Paleocene

Tricolporites sp. 3
FIG. 18I

Description. Grains, prolate, tricolporate with indistinct pores and granules aligned along borders of colpi. Exine, 1-2 µm thick, is thicker over poles, viz. 1 µm in equatorial region, 2 µm over poles. Nexine, very fine columellate layer and tectum of equal thickness. Surface scabrate. Size, 24 x 16 µm.

Distribution. Late Paleocene

Tricolporites sp. 4
FIG. 18J-L

Description. Grains oblate, tricolporate with weakly defined colpi, pores with ragged margins. Exine 0.5-1 µm, no discernible layering on thinner walled specimens, but thicker ones show two layers, thinning towards colpi. Surface faintly scabrate. Size, 12-15 µm.

Distribution. Late Paleocene.

Tricolporites sp. 5
FIG. 18M, N

Description. Grain more or less spherical, tricolporate with smooth colpal membranes, weakly defined pores. Exine 1 µm thick with two equal layers. Sexine reticulate, lumina about 1 µm, muri 0.5 µm in intercolpal areas, becoming very finely puncto-reticulate over poles and towards colpi. Size, 26 µm.

Distribution. Late Paleocene.

Pancolpate sp.
FIG. 18E

Description. Grain presumed originally spherical, now flattened. There are about 16 colpi over surface, arranged to form square or polygonal shapes. Exine 1 µm thick, with thin nexine, distinct columellate layer, thin tectum. Surface has scattered coni, 0.5-1 µm high, spaced about 1-2 µm apart. Size, 58 µm.

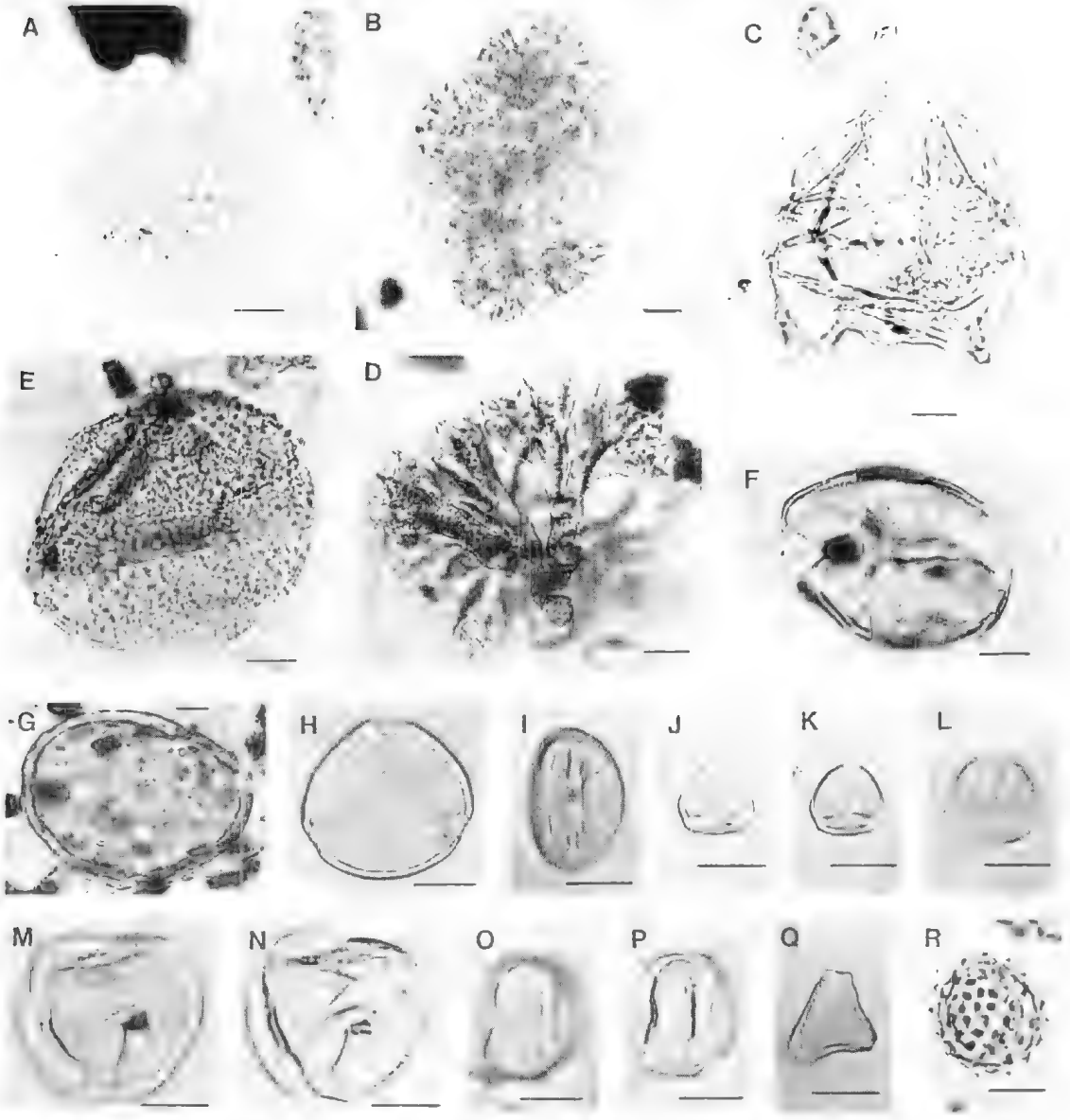

Fig. 18. Tertiary species continued. A, *Pediastrum* sp. B, D, *Botryococcus braunii*. B, Small form. D, Large form. C, *Maltallacysta pyramidalis*. E, Pancolpate sp. F, *Dicolpopollis* sp. G, Panporate sp. H, *Triorites* sp. I, *Tricolporites* sp. 3. J-L, *Tricolporites* sp. 4. M, N, *Tricolporites* sp. 5. O, P, *Tricolpites* sp. Q, *Triorites minisculus*. R, *Tubulifloridites* sp. Scale bars = 10 μm.

Comparisons. This type differs from *Lymingtonia* which has a thicker sexine and a rugulate/verrucate pattern (Pocknall & Mildenhall 1984). Portulacaceae gen. et sp. indet. (Martin 1973b) lacks the coni of this pollen type.

Distribution. Pliocene/Pleistocene.

Panporate sp.
FIG. 18G

Description. Grain is broadly elliptical, panporate, with about 16 pores, 6-8 µm diameter. Exine 3 µm thick, with thin nexine, thick densely columellate layer and thin tectum which has small perforations, < 0.5 µm, spaced 1-3 µm apart. Surface pattern granular. Size, 78 µm.

Distribution. Pliocene/Pleistocene.

Microplankton

Genus *Botryococcus* Kützig

Type species: *Botryococcus braunii* Kützig

Botryococcus braunii Kützig
FIG. 18B, D

Comments. *Botryococcus braunii is* a cosmopolitan and extremely variable species with a number of races. Cookson (1953) remarks that only one race, the small form (Fig. 18B) has been found in Australia. In this form, the algal cells are 4-6 µm in diameter and the colonies are tightly packed. There is also a much larger form (Fig. 18D), where the algal cell is cup-shaped, 10-12 µm deep and 8-9 µm wide at the top and colonies are more or less fan-shaped, branching dichotomously, with the branches 6-9 µm wide. This larger form probably constitutes a separate race (Blackburn 1936). *Botryococcus braunii* usually inhabits freshwater ponds and lakes. Sometimes it may be found in brackish waters and coastal lagoons. It may be extremely prolific and was responsible for boghead coal (Cookson 1953). In the Poonarunna well, *B. braunii* is extremely abundant from 67-91 m.

Stratigraphic Range. Ordovician to the present.

Genus *Morkallacysta* Harris 1973

Type species: *Morkallacysta pyramidalis* Harris 1973

Morkallacysta pyramidalis Harris 1973
FIG. 18C

Comments. This species is rare and the specimens are usually crumpled.

Stratigraphic Range. Paleocene (Harris 1973; this study).

Genus *Pediastrum* Meyen 1829

Type species: *Pediastrum duplex* Meyen 1829

Pediastrum sp.
FIG. 18A

Comments. *Pediastrum* is usually found floating amongst aquatic plants, rarely in deep water. It may be found in lakes and small ponds where the water is rich in nutrients (Pentecost 1984).

Stratigraphic Range. Early Cretaceous to the present (Evitt 1963).

TRANSACTIONS OF THE

ROYAL SOCIETY OF SOUTH AUSTRALIA

INCORPORATED

VOL. 122, PART 4

RHOPALOMYIA LAWRENCIAE, A NEW GALL MIDGE SPECIES (DIPTERA: CECIDOMYIIDAE) DEFORMING LEAVES OF LAWRENCIA SQUAMATA (MALVACEAE) IN SOUTH AUSTRALIA

*By Peter Kolesik**

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Key Words: Gall midge, Cecidomyiidae, Rhopalomyia lawrenciae, Lawrencia squamata, saltmarsh flat, River Murray, South Australia.

Transactions of the Royal Society of S. Aust. (1998), **122**(4), 139-145.

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KEY WORDS: Gall midge, Cecidomyiidae, *Rhopalomyia lawrenciae*, *Lawrencia squamata*, saltmarsh flat, River Murray, South Australia.

Introduction

Lawrencia is an Australian plant genus comprising 12 species of perennial herbs and small shrubs (Jessop 1986). *Lawrencia squamata* Nees in Lehm. is a rigid shrub up to 1 m high, occurring in all mainland states (Jessop 1986). In South Australia, it grows on saltmarsh flats, sand dunes and rocky cliffs along the coast and on sandy soils and marshes inland. The plant forms part of the shore vegetation on the saltmarsh flats in the estuary of the River Murray where in September, 1996, on the south-eastern coast of Hindmarsh Island, many leaves of *L. squamata* were found to be swollen (Fig. 1). The swellings were caused by larvae of an unknown gall midge described here. The new species is placed in *Rhopalomyia*, a large, worldwide genus. The new species becomes the second gall midge described from South Australian saltmarsh flats; the first, *Asphondylia inflata* Kolesik (1997) having been described last year.

Materials and Methods

Branches of *Lawrencia squamata* plants bearing leaf galls were collected on Hindmarsh Island, South Australia on 8 September, 1996. The branches were brought to the laboratory and the galls processed in one of two ways. A small number was dissected and the larvae and pupae were preserved in 70% ethanol. A larger number was left on the branches and kept in plastic bags to develop to adults. Pupation took place within the galls. Emerged adults were preserved in 70% ethanol after their colour had been noted. Canada balsam mounts of type specimens were prepared according to the technique outlined by Kolesik (1995). The type series, and other material retained in 70% ethanol, are deposited in the South Australian Museum, Adelaide [SAMA] and the Australian National Insect Collection, Canberra

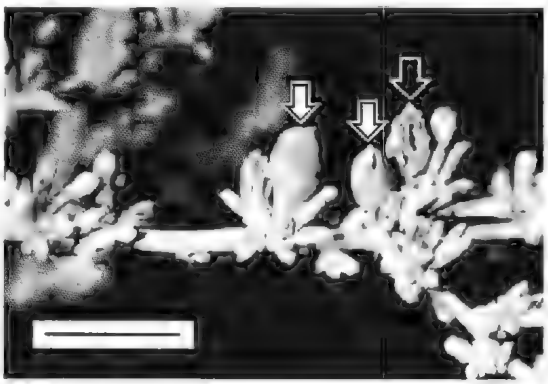

Fig. 1. Galls of *Rhopalomyia lawrenciae* sp. nov. on *Lawrencia squamata*. White arrows mark whole galls, black arrow marks a gall cut open, presumably by birds. Scale bar = 10 mm.

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[ANIC]. A dried sample of an infested plant is deposited in the State Herbarium of South Australia, Adelaide [SHSA]. All measurements refer to the holotype and paratypes. Investigation of the geographic distribution of the new species was based on examining the presence of galls on dried specimens of the host plant deposited in SHSA. The galls were easily recognisable and some still contained pupal skins of the new gall midge.

Genus *Rhopalomyia* Rübsaamen, 1892

Rhopalomyia Rübsaamen, 1892: 370
Type species: *Oligotrophus tanaceticola* Karsch, 1879: VII. Jber. westf. Prov.Ver. Wiss. Kunst: 27 (des. Kieffer, 1896: 89)

Rhopalomyia is a large, worldwide genus of the tribe Oligotrophini with an undivided eighth female abdominal tergite and completely setulose gonostylus. Most of the known species have a one- to three-segmented palpus, and one species, the Australian *R. goodeniae* Kolesik (1996), has a three- or four-segmented palpus.

Rhopalomyia lawrenciae sp. nov.
(FIGS 1-19)

Holotype: ♂, Hindmarsh Island, South Australia [35° 33' S, 138° 53' E], 9.ix.1996, P. Kolesik, reared from a leaf gall on *Lawrencia squamata* Nees in Lehm., gall collected 8.ix.1996, [SAMA, I21394].

Paratypes: 2 ♂♂, 3 ♀♀, 3 pupae [SAMA, I21395-I21401], 2 ♂♂, 2 ♀♀, 2 pupae [ANIC], same data but emerged 8-17.ix.1996; 3 larvae, [SAMA, I21402-I21405], 3 larvae [ANIC], collected with holotype.

Other material: 27 ♂♂, 18 ♀♀, 8 pupae, 11 larvae [SAMA], same data as paratypes; gall, collected with holotype [I21406-I21416, SHSA].

Male (Figs 2-7)

Colour: head and thorax brown, abdomen with sclerotised parts brown and non-sclerotised parts grey.

Head: Antenna: scape broadest distally, as long as distal breadth, 1.5x length pedicel, pedicel broader than long; flagellomeres 13-14 in number, first and second not fused, neck about 1/6 length node; circumfila comprising two transverse and two longitudinal bands. Palpus three-segmented. Eye facets rounded, close together, sparser at vertex, eye bridge 5-6 facets long. Labella roughly hemispherical, laterally with 2-5 setae. Frons with 12-20 setae per side.

Thorax: Wing length 2.2 mm (1.9-2.4, n = 5), width 1.0 mm (0.8-1.1); R_5 same thickness entire length, slightly curved posteriorly, joining C anterior to apex; R_1 joining C near wing mid-length; Sc cell pigmented and together with R_1 and adjacent part of R_5 bearing scales. Claws toothed, empodium as long as claws, pulvilli half length empodium.

Abdomen: All tergites with pair of sensory setae in anterior corners and row of setae posteriorly, tergites 7 and 8 additionally with few setae scattered mesolaterally; sternites 2-8 with pair of sensory setae anteriorly, a row of setae posteriorly and a band of setae mesally. Genitalia: gonocoxites cylindrical, ventral articulation with gonostylus longer than dorsal articulation, setose and setulose; gonostylus about same width entire length, setose and setulose throughout, with strong tooth, comblike distally; cerci separate, setose and setulose; hypoproct bilobed, with one seta apically on each lobe, setulose; parameres setulose, with 6-8 setose apical papillae; aedeagus conical.

Female (Figs 8-13)

Colour: head and thorax brown, abdomen with sclerotised parts brown and non-sclerotised parts red.

Head: Flagellomeres 12-13 in number, terminal ones sometimes fused, neck about 1/10 length node.

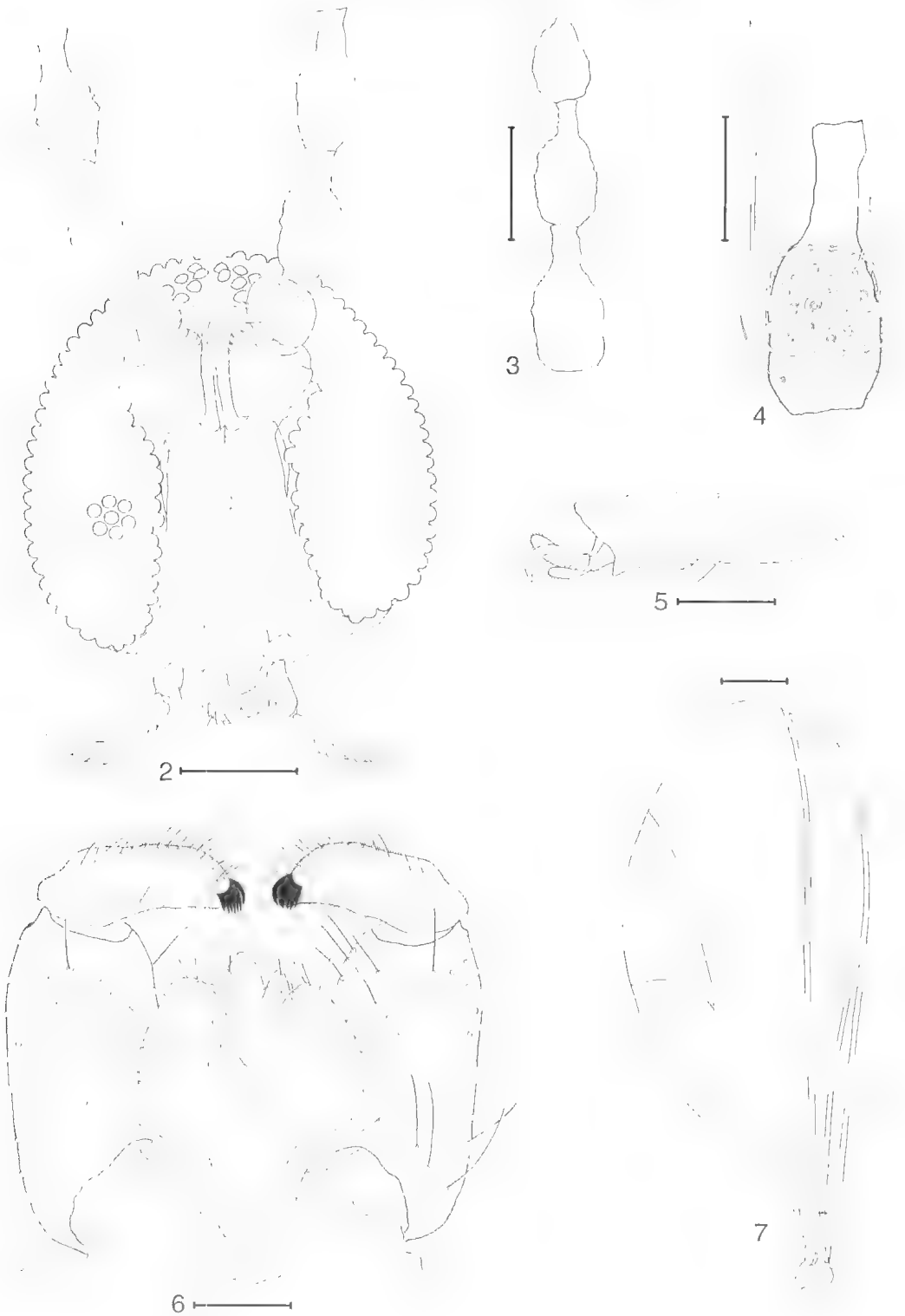
Thorax: Wing length 2.0 mm (1.4-2.3, n = 5), width 0.8 mm (0.6-0.9). Tergite 8 with single pair of sensory setae anteriorly, sclerotisation undivided, in shape of letter "x". Ovipositor: cerci fused into single, terminal spheroid lamella, setose and setulose; hypoproct rounded apically in dorsoventral view, bearing two setae posteriorly, setulose. Other characters as in male.

Pupa (Figs 14-16)

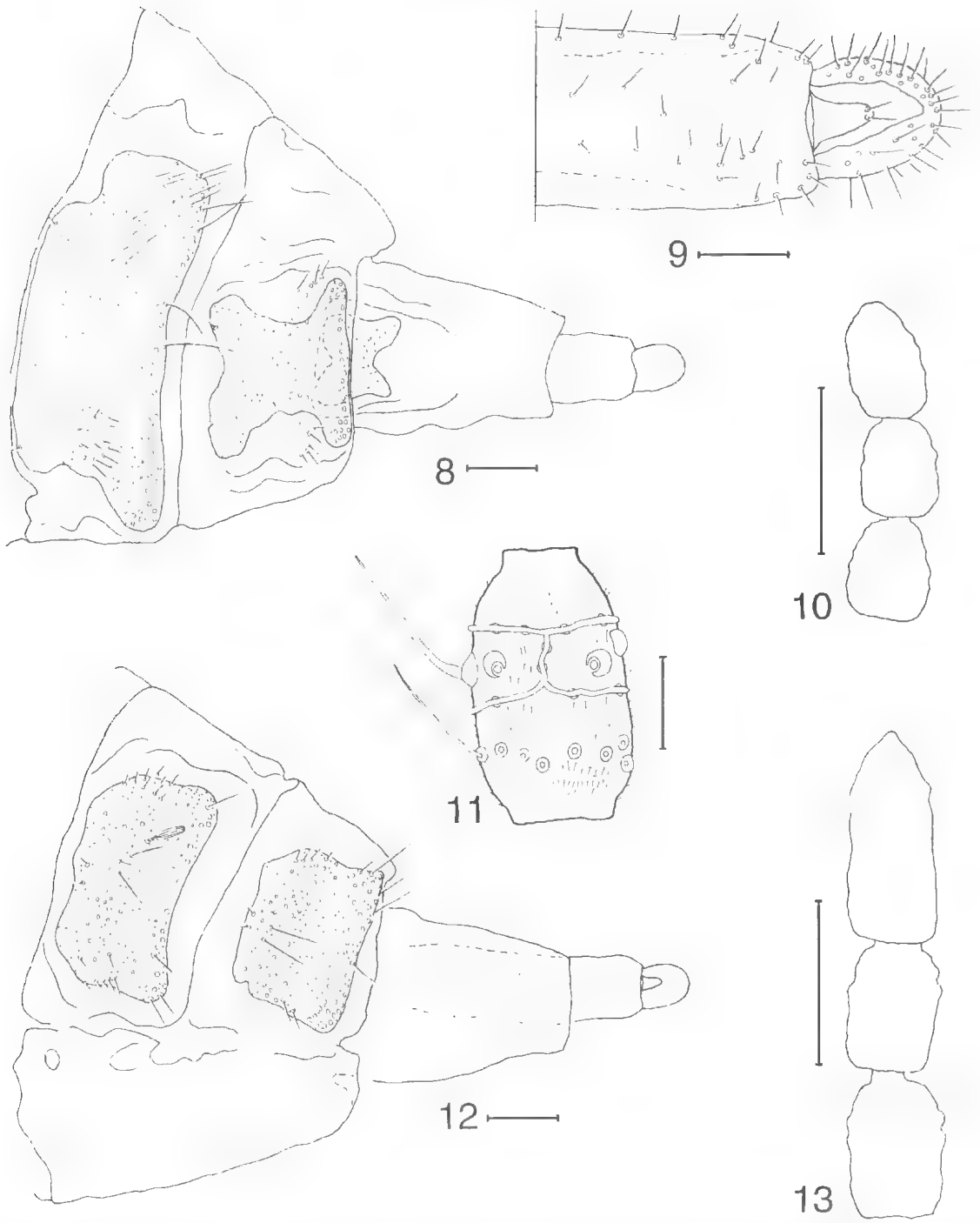
Colour: antennal and frontal horns pigmented, brown, remaining parts unpigmented. Length 2.6 mm (2.5-2.8, n = 5). Antennal horns strong, bifid, 191 µm (172-206) long. Frons on each side: one frontal horn; pair of papillae on lower face, one setose, one asetose; triplet of lateral facial papillae, one setose, two asetose. Prothoracic spiracle with several irregular protuberances apically. Trachea ending between half and distal third of spiracle. Integument of abdominal segments covered with spicules, very dense dorsally, no dorsal spines present.

Last instar larva (Figs 17,18)

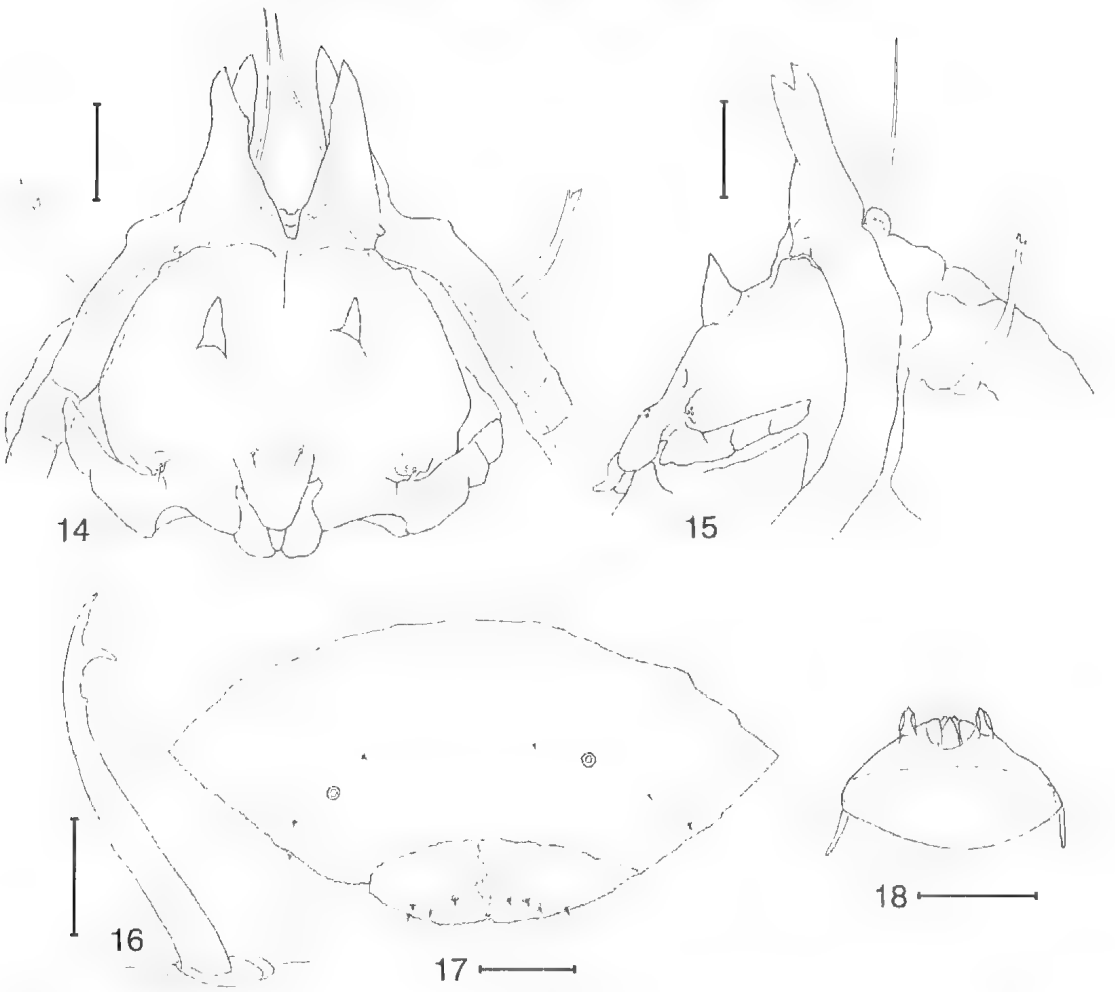
Colour: pinkish red. Length 2.5 mm (2.5-2.6, n = 6). Integument covered with spicules. Head with postero-lateral apodemes shorter than head length. No spatula present. All papillae with short setae. Thoracic and first abdominal segments with pair of ventral papillae, two pairs of pleural papillae, three pairs of dorsal papillae. Abdominal segment 8 with pair of ventral papillae, two pairs of pleural papillae,



Figs 2-7. Male of *Rhopalomyia lawrenciae* sp. nov. 2. Head in frontal view. 3. Last three flagellomeres. 4. Sixth flagellomere. 5. Last tarsomere with claw, empodium, and pulvillus. 6. Genitalia in dorsal view. 7. Wing. Scale bars = 100 μm 2, 3; 50 μm 4-6; 200 μm 7.



Figs 8-13. Female of *Rhopalomyia lawrenciae* sp. nov. 8. Posterior end of abdomen in dorsal view. 9. Posterior end of ovipositor in ventral view. 10. Last three flagellomeres (paratype 121397). 11. Sixth flagellomere. 12. Posterior end of abdomen in ventral view. 13. Last three flagellomeres (paratype 121398). Scale bars = 100 μm 8, 10, 12, 13; 50 μm 9; 25 μm 11.



Figs 14-18. *Rhopalomyia lawrenciae* sp. nov.: 14-16, pupa. 17,18, larva. 14. Anterior part in ventral view. 15. Anterior part in lateral view. 16. Prothoracic spiracle. 17. Two terminal segments in dorsal view. 18. Head capsule. Scale bars = 100 μm 14, 15, 17; 50 μm 16, 18.

pair of dorsal papillae. Terminal segment with four pairs of terminal papillae. Anus ventral.

Etymology

The specific name means "of *Lawrencia*", the host plant.

Gall and biology

Leaves of *Lawrencia squamata* infested by this gall midge are several times larger than normal in volume, 4-6 mm long and 3-4 mm wide (Fig. 1). Each gall contains a chamber occupied by one larva. The chamber wall is lined with a thin, hard, pale-brown layer of tissue at the time the larva is fully-grown.

Pupation takes place inside the gall. The pupa raises two thirds of its body outside the gall before the adult breaks through the anterior end of the pupa. On 8 September, 1996, on the southeastern coast of Hindmarsh Island (Fig. 19), the galls contained larvae and pupae, with the first adults already emerging. On this occasion, the host plants were about 20 cm high and about 50 cm in diameter and approaching the end of flowering. *Lawrencia squamata* accounted for some 10% of the ground covering of the dense, herbal, coastal vegetation at this locality. The population density of the new gall midge was high, comprising up to 10 galls per host plant. Many galls were found cut open, possibly by birds, a phenomenon described for other cecidomyiid galls previously (Struble & Osgood 1976; Tscharntke 1990).

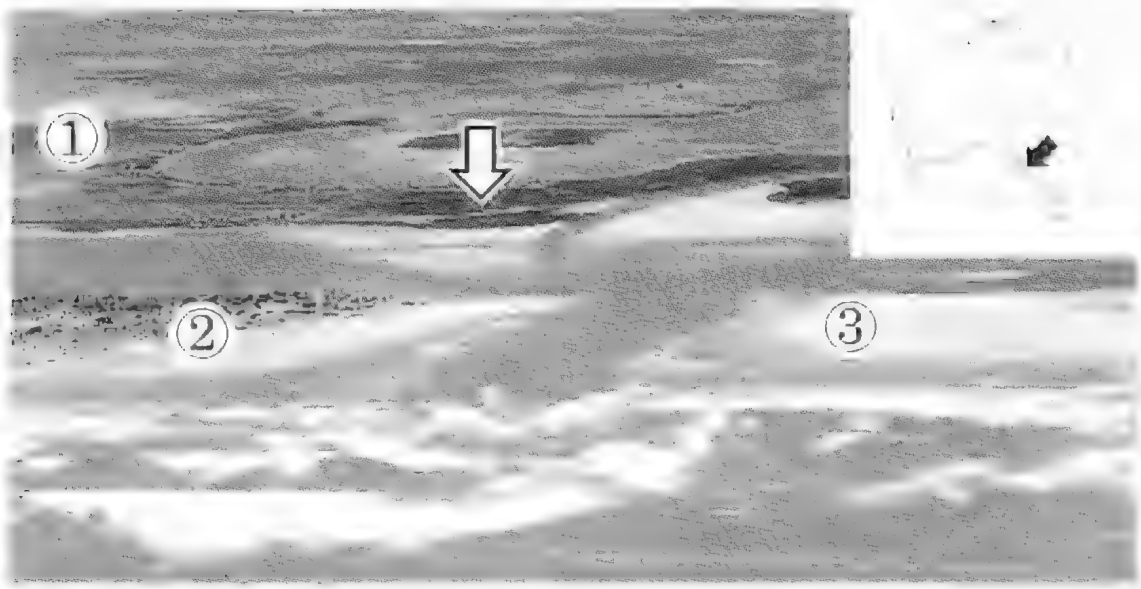


Fig. 19. Hindmarsh Island, South Australia – aerial view of the type locality of *Rhopalomyia lawrenciae* sp. nov. 1 Hindmarsh Island, 2 Sir Richard Peninsula, 3 Youngshusband Peninsula. White arrow marks the type locality.

Leucopsis dreisbachi

Galls of the new gall midge were found on *Lawrencia squamata* plants collected from the following localities in South Australia: N-W of Marla [27° 20' S, 133° 20' E], track to Fisher [31° 20' S, 130° 54' E], 15 km W of Nullarbor [31° 27' S, 130° 44' E], 30 km S of Eyre Highway [31° 47' S, 131° 52' E], 4 km S of Coorabie [31° 56' S, 132° 18' E], Port Lincoln [34° 43' S, 135° 50' E], Threeneard [32° 09' S, 133° 10' E], Smoky Bay [32° 18' S, 133° 50' E], Ayoldet Post Office [32° 22' S, 135° 31' E], Mt Ive Station [32° 25' S, 135° 59' E], Carrieton [32° 26' S, 138° 32' E], Egg Island [32° 28' S, 137° 19' E], Dog Island [32° 29' S, 133° 20' E], 18 km N of Ellison [33° 30' S, 134° 53' E], St Francis Island [32° 31' S, [illegible] E], Middleton Island [32° 47' S, 133° 17' E], Venus Island [32° 53' S, 133° 17' E], Reevesby Island [32° 53' S, 133° 17' E], Redcliffe Smoky Area [32° 43' S, 137° 51' E], Streaky Bay [32° 18' S, 134° 13' E], 6 km E of Cungena [33° 35' S, 140° 05' E], Elliston [33° 39' S, 134° 53' E], Cowell [33° 41' S, 136° 55' E], Burra Creek Plain (18 km N of Mt Mary) [33° 53' S, 139° 26' E], W side of Lake Hamilton [33° 57' S, 135° 16' E], Port Hughes [34° 05' S, 137° 33' E], Mt Mary [34° 06' S, 139° 26' E], Adelaide Outer Harbour [34° 48' S, 138° 30' E], West Cape (Innes National Park) [35° 15' S, 136° 50' E], Minlaton [34° 36' S, 137° 36' E], Port Lincoln [34° 44' S, 135° 52' E], Torrens Island [34° 48' S, 138° 32' E], Port Adelaide [34° 50' S, 138° 30' E], Port Noarlunga [35° 09' S, 138° 29' E], Pondalowie Bay [35° 14' S, 136° 50' E], Hindmarsh Island [35° 31' S, 138° 50' E], Mahnong [35° 31' S, 139° 31' E], 18 km N of Meningie [35° 37' S, 139° 20' E], Vennachar Point (Kangaroo Island) [35° 53' S, 136° 42' E], Cooyong [36° 18' S, 139° 43' E].

The highest abundance of galls was found on plants collected 3.x.1972 by N. M. Wace on the exposed rocky headland of Dog Island where plants were subject to salt spray during storms. The plants from this area which are deposited in SHSA are rigid, dense shrubs, about 100 mm high and 150 mm in diameter, each bearing some 100 galls of the new gall midge. Other localities with a lesser incidence of galls were The Coorong (plants collected 1.x.1961 by M. C. R. Shurrah and Adelaide Outer Harbour (plants collected 7.xi.1971 by A. G. Spooner).

Remarks

Rhopalomyia is a "rangy-tail" genus with most of its species forming galls on plants of the family Asteraceae. There are two distinctive morphological groups in the genus, one contains species that have larvae with spatula absent and pupae with antennal horns present, the other contains species that have larvae with spatula present and pupae with antennal horns absent (Gagne 1994). The new species belongs to the former group. The only other known Australian species, *Rhopalomyia* sp. of Kotejsk (1996), a species deforming stems of *Goodenia lunata* J. Black (Goodeniaceae) in the Lake Eyre region, belongs to the latter group. Both species belong to Sylvén's (1975) biological group V of primary gall inducers with larvae feeding

solitarily and pupation taking place in the gall. The gall of *R. goodeniae* comprises a conglomerate of individual chambers whereas the gall of *R. lawrenciae* sp. nov. consists of a single chamber. Because only these two species of *Rhopalomyia* are known to be native to Australia, it is too early for a general characterisation of the genus on this continent. Below, a key is given to adults of the two native species and *R. californica* Felt, an American species introduced into Australia to control *Baccharis halimifolia* L. (Asteraceae) (McFadyen *et al.*[1]; Gagné & Boldt 1995).

Key to adults of Australian species of *Rhopalomyia*

1. Tarsal claws toothed.....*R. lawrenciae*
   Tarsal claws simple 2
2. Palpus with 3 or 4 segments; length of papillae on male parameres $^1/_5$ - $^1/_2$ paramere width.....*R. goodeniae*
   Palpus with 1 or 2 segments; length of papillae on male parameres about $^1/_{20}$ paramere width.....*R. californica*

Acknowledgments

W. R. Barker and M. C. O'Leary, both of the State Herbarium of South Australia Adelaide, courteously identified the host plant species and assisted in examination of dried host plant specimens, respectively. D. Eastburn, Murray-Darling Basin Commission, kindly gave permission to print the photograph in Figure 19. I thank J. D. Gray, Department of Horticulture, Viticulture and Oenology University of Adelaide, and R. J. Gagné, Systematic Entomology Laboratory USDA Washington DC, for commenting on an early draft of the manuscript.

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DASINEURA WAHLENBERGIAE, A NEW SPECIES OF GALL MIDGE (DIPTERA: CECIDOMYIIDAE) DAMAGING SHOOT TIPS OF WAHLENBERGIA STRICTA (CAMPANULACEAE) IN SOUTH AUSTRALIA

*By Peter Kolesik**

Summary

Kolesik, P. (1998) Dasineura wahlenbergiae, a new species of gall midge (Diptera: Cecidomyiidae) damaging shoot tips of Wahlenbergia stricta (Campanulaceae) in South Australia. Trans. R. Soc. S. Aust. 122(4), 147-151, 30 November, 1998.

A new South Australian gall midge, Dasineura wahlenbergiae, that damages shoot tips of Wahlenbergia stricta (R.Br.) Sweet, a common plant of grassy habitats in Australian and New Zealand, is described. Two leaves of the shoot tip of the host plant are malformed into a globular, hollow, hairy, partially discoloured gall, 2-5 mm in diameter. The male, female, pupa and larva of the new species are described. The new gall midge is the fourth Dasineura species known from Australia.

Key Words: Gall midge, Cecidomyiidae, Dasineura wahlenbergiae sp. nov., Wahlenbergia stricta, South Australia.

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by PETER KOLESIK*

Summary

KOLESIK, P. (1998) *Dasineura wahlenbergiae*, a new species of gall midge (Diptera: Cecidomyiidae) damaging shoot tips of *Wahlenbergia stricta* (Campanulaceae) in South Australia. *Trans. R. Soc. S. Aust.* **122**(4), 147-151, 30 November, 1998.

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KEY WORDS: Gall midge, Cecidomyiidae, *Dasineura wahlenbergiae* sp. nov., *Wahlenbergia stricta*, South Australia.

Introduction

The new gall midge described here was found in malformed shoot tips of the tall blue bell, *Wahlenbergia stricta* (R. Br.) Sweet (Campanulaceae) at Morialta Conservation Park, near Adelaide. *Wahlenbergia stricta* is a perennial herb, 100-900 mm high with large, blue flowers and is common at grassy sites in various vegetation types throughout Australia and New Zealand (Smith 1986). The plants grow on slopes at the Morialta Conservation Park and in the spring the shoot buds of many of them are modified into globular, hairy galls. Some plants have all their shoot tips galled and consequently do not reproduce.

Materials and Methods

Shoot tip galls on *Wahlenbergia stricta* were collected at Morialta Conservation Park on 15 September, 1996 and brought to the laboratory where a few of the galls were peeled open and the developmental stages of the gall inducer examined. Some of the galls contained young larvae, some mature larvae, some cocoons and others were empty. The cocoons contained either larvae or pupae. A small number of the mature larvae was preserved in 70% ethanol. A few cocoons were torn open and the larvae and pupae preserved as above. The majority of the galls was laid on wet sand within a pot to allow them to develop into adults. Pupation took place within the galls. Emerged adults were preserved in 70% ethanol. Canada balsam mounts of the type series were prepared for microscopic examination according to the technique outlined by Kolesik (1995). Measurements refer to the holotype and paratypes. The type specimens, and other material retained in ethanol, are deposited in the South Australian Museum, Adelaide [SAMA], the Australian National Insect Collection, Canberra [ANIC] and the Swedish Museum of Natural History [SMNH]. Dry samples of the galls are deposited in the State Herbarium of South Australia, Adelaide [SHSA].

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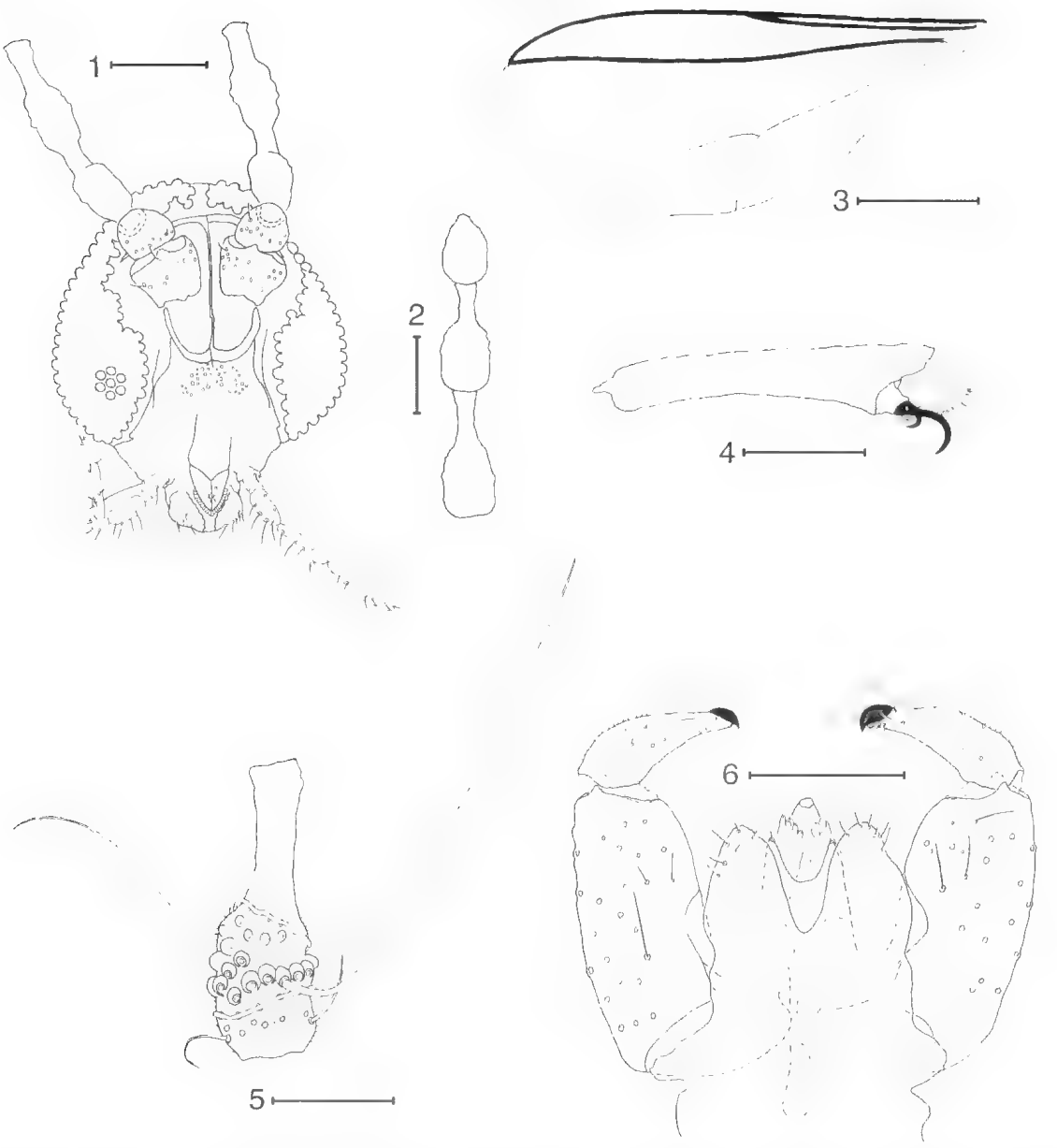
Genus *Dasineura* Rondani, 1840

Dasineura Rondani, 1840: 12 & 17
Proposed type species *Tipula sisymbrii* Schrank, 1803: Gagné *et al.* (1997)

Dasineura is a large, cosmopolitan genus of some 200 species containing Oligotrophini with four-segmented palpi, toothed tarsal claws, an R_5 wing vein that meets C anterior to the wing apex, and the female eighth tergite divided into two longitudinal sclerites.

Dasineura wahlenbergiae sp. nov.
(FIGS 1-15)

Holotype: ♂, Morialta Conservation Park, South Australia [34° 54' S, 138° 44' E], 20.ix.1996, P. Kolesik, reared from a shoot tip gall of *Wahlenbergia stricta* (R. Br.) Sweet collected 15.ix.1996, 12|384 [SAMA].



Figs 1-6. Male of *Dasineura wahlenbergiae* sp. nov. 1. Head in frontal view. 2. Last three flagellomeres. 3. Wing. 4. Last tarsal segment with claw and empodium. 5. Sixth flagellomere. 6. Genitalia in dorsal view. Scale bars = 100 µm 1, 6; 50 µm 2, 4, 5; 500 µm 3.

Paratypes: 3♂ 2♀, 3 pupae [SAMA, I21385-I21390]. 1♂, 2♀ ♂, 2 pupae [all ANIC], same data but emerged 17.-25.ix.1996: 3 larvae [SAMA], 3 larvae [ANIC], collected with holotype.

Other material: 3♂ 4♀ [SMNH], same data as holotype but emerged 20.-25.ix.1996: 37 larvae, 5 pupae within cocoons [SMNH], collected with holotype; gall [SHSA, AD99747199], collected with holotype.

Description

Male (Figs 1-6)

Colour: eyes black; head, thorax and abdomen orange-red; legs, antennae, palpi, setae and scales grey; halteres orange brown.

Head: Antenna: scape square in frontal view, pedicel spheroid; 16 flagellomeres, first and second fused, necks as long or slightly longer than nodes; circumfila comprising two transverse and two longitudinal bands. Palpus four-segmented, segments progressively longer. Eye facets rounded, close together except on vertex where small area of no facets separates the eyes. Labella tapered distally, laterally with 6 setae. Frons with 23-26 setae per side.

Thorax: Wing length 2.1 mm (2.0-2.1, n = 2), width 0.9 mm (0.8-0.9); R_5 joining C anteriorly to apex; R_1 joining C slightly anteriorly to mid-length; Rs not obvious. Claws toothed, empodia as long as claws.

Abdomen: Tergites 1-8 with pair of sensory setae in anterior corners, tergites 1-7 with single setal row posteriorly and scales scattered evenly, tergite 8 in form of narrow, sclerotised, anterior band, without setae. Sternites 2-8 with pair of sensory setae anteriorly, setae in wide band anteriorly and narrower band posteriorly, area between two bands of setae more weakly sclerotised. Genitalia: gonocoxite cylindrical, setose and setulose; gonostylus tapered distally, sparsely setose, setulose basally up to ⅔ of its length ventrally and ½ dorsally, sparsely striate beyond, bearing distal comb; cerci large, each with several setae apically, setulose; hypoproct deeply and widely divided, with one seta on each lobe, setulose; parameres sheathing aedeagus, with subglobular distensions dorso-basally, with 4-5 setose papillae apically; aedeagus long, stout.

Female (Figs 7-10)

Colour: as in male.

Head: 16 flagellomeres, cylindrical, with necks ⅓-½ node's length, circumfila comprising two transverse and two longitudinal bands, distal transverse band with loop, circumfilar attachment points very dense. Labella with 7-10 setae laterally, frons with 22-28 setae laterally.

Thorax: Wing length 2.1 mm (2.0-2.3, n = 5), width 0.8 mm (0.8-0.9).

Abdomen: Tergites 1-8 with pair of sensory setae in anterior corners, tergites 1-7 with single setal row posteriorly and scales scattered evenly, tergite 8 divided into two longitudinal sclerites. Sternites 2-7 with pair of sensory setae anteriorly, setae in wide band anteriorly and narrower band posteriorly, area between two bands of setae more weakly sclerotised, sternite 8 not developed. Ovipositor: protractile, elongate, 0.7 mm (0.6-0.7) long (anterior limit of genital chamber to terminal tip distance), 31% (29-35) of wing length; cerci fused medially into single, prolonged, terminal lamella, setose and setulose; hypoproct with two setae, setulose.

Pupa (Fig. 11)

Colour: antennal horns brown at apex, remaining parts yellow. Length 2.0 mm (1.8-2.1, n = 5). Antennal horns small, pointed. Frons on each side: three frontal papillae two of them setose, asetose one sometimes lacking; three asetose lateral facial papillae. Cephalic papilla with seta 194 µm (189-201) long. Prothoracic spiracle 230 µm (220-244) long, trachea ending at apex. Integument of abdominal segments covered with spiculae slightly longer dorsally, second through seventh abdominal segments with group of dorsal spines on anterior half. First through eighth abdominal segments with two pairs of dorsal asetose papillae, one pair of setose pleural papillae, two pairs of asetose ventral papillae.

Last instar larva (Figs 12-14)

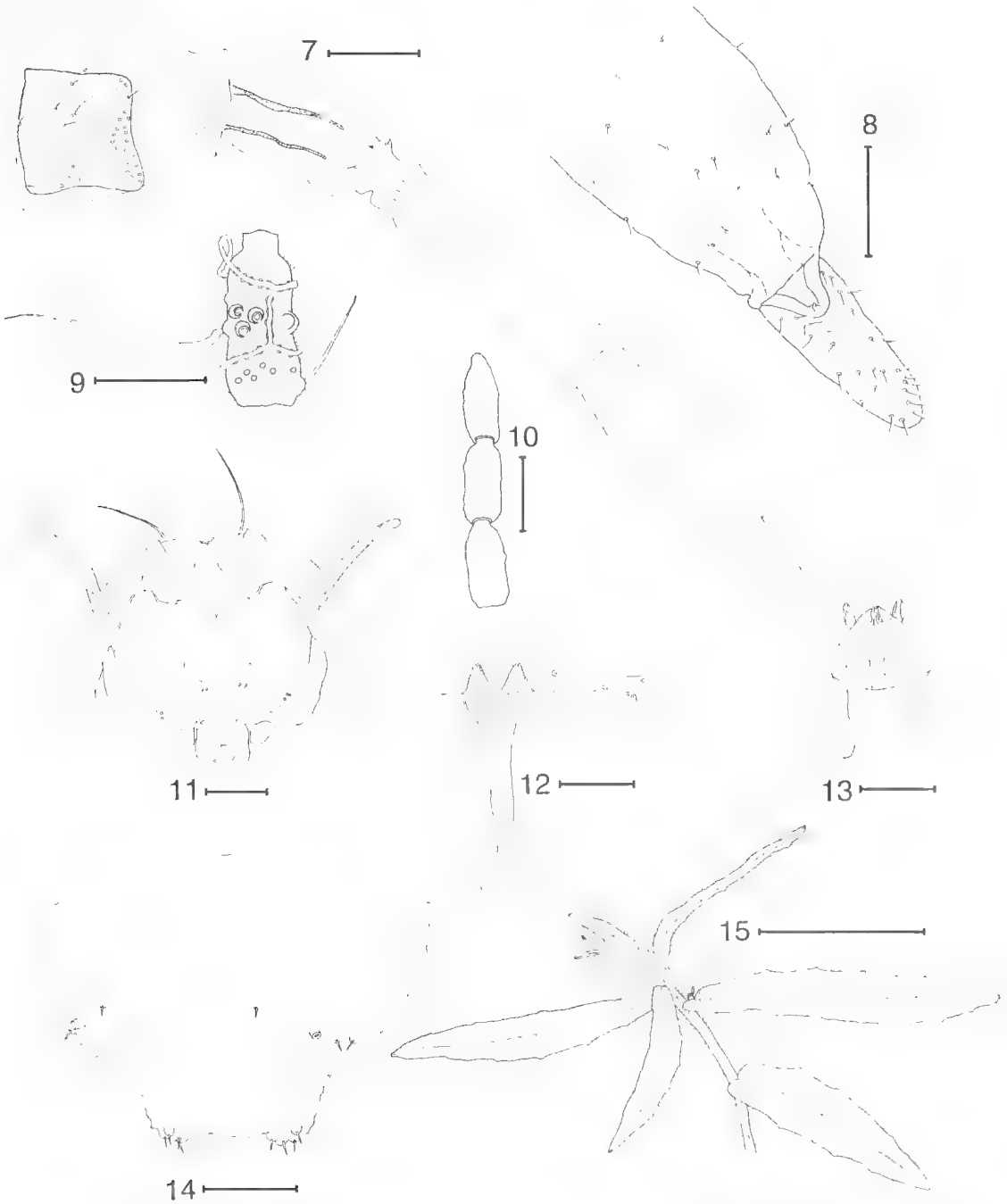
Colour: red. Length 2.4 µm (2.0-2.8, n = 6). Integument covered with rounded plates about 10 µm in diameter, ventrally with several transverse rows of spiculae on anterior half of thoracic and abdominal segments. Head with postero-lateral apodemes as long as head length. Spatula bilobed, with long shaft, length 147 µm (117-169). Papillae characteristic of *Dasineura* larva (Sylvén 1975).

Etymology

The name *wahlenbergiae* is derived from the generic name of the host plant.

Gall and biology

The new gall midge modifies two leaves of the shoot tip of *Wahlenbergia stricta* into a globular, hollow, hairy, partially discoloured gall, 2-5 mm in diameter (Fig. 15). On 15 September, 1997, at Morialta Conservation Park most galls contained mature larvae, but some galls contained young larvae, some cocoons with larvae or pupae within or



Figs 7-15. *Dasineura wahlenbergiae* sp. nov.: 7-10 female, 11 pupa, 12-14 larva, 15 infestation symptoms. 7. Posterior end of abdomen in dorsal view. 8. Posterior end of ovipositor in ventral view. 9. Sixth flagellomere. 10. Last three flagellomeres. 11. Anterior part in ventral view. 12. Spatula with adjacent papillae. 13. Head. 14. Two terminal segments in dorsal view. 15. Gall on *Wahlenbergia stricta* (R. Br.) Sweet. Scale bars = 100 µm 7, 11, 14; 50 µm 8-10, 12, 13; 10 mm 15.

empty cocoons, and others contained no remnants of the gall inducer. Up to 20 larvae were found within a gall. The adults reared in this study originated from larvae pupated within the galls.

Discussion

Dasineura, the largest genus of Cecidomyiidae, comprises species occurring in all zoogeographical regions of the world. Four species are known from Australia: *D. acaciaelongifoliae* (Skuse, 1890) (Gagné & Marohasy 1993) and *D. dielsi* Rübsaamen (1916) which damage flowers of *Acacia longifolia* (Andr.) Wild. (Mimosaceae) and *A. eyclops* Cunn. ex Don respectively, *D. hybanthi* Kolesik & Skuhravá (1997) which is an inquiline in flower galls on *Hybanthus floribundus* (Lindley) Muell. (Violaceae) induced by an unknown gall midge, and the new species described here. *Dasineura wahlenbergiae* sp. nov. belongs to Sylvén's (1975) biological group II of gall midges whose larvae are primary gall inducers, feed gregariously and pupate in both the soil and the plant. The adults of the new species reared in the present study originated from larvae that pupated within galls, but the fact that some galls were found empty with neither cocoon remnants nor parasitoids within suggests that part of the larval population pupates in the soil. This conforms with the behaviour of Sylvén's (1975) biological group II. *Dasineura hybanthi*, the only other Australian species of this genus described in detail, belongs to group III of gall midges whose larvae are inquilines, feed gregariously and pupate in the soil. The new species differs from *D. hybanthi* in several morphological characters. In *D. wahlenbergiae*, the wing vein R_5 is not obvious, the tooth on the tarsal claw is much smaller than the claw, the female flagellomeres are much longer than wide, in the male genitalia the gonostylus is tapered distally, the male cerci and parameres are nearly as long as the aedeagus, and the larva has no medial papillae between the terminal papillae. In *D. hybanthi*, the R_5 is evident, the tooth on the tarsal claw is nearly as large as the claw, the female flagellomeres are as long as wide, in the male genitalia the gonostylus is about the same width through its entire length, the male cerci and parameres are much shorter than the aedeagus, and the larva has several medial setose papillae between the terminal papillae.

Acknowledgments

I am grateful to H. R. Toelken, South Australian State Herbarium for the identification of *Wahlenbergia stricta*. A. Stark, Halle Germany courteously provided a copy of Rübsaamen's paper. Special thanks go to J. D. Gray, Department of Horticulture, Viticulture and Oenology University of Adelaide, R. J. Gagné, Systematic Entomology Laboratory USDA Washington DC, and E. Sylvén, Swedish Museum of Natural History Stockholm for commenting on an early draft of the manuscript

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DEVELOPMENTAL BIOLOGY OF UPEROLEIA TALPA TYLER, DAVIES & MARTIN, 1981 (ANURA: MYOBATRACHIDAE)

By Margaret Davies & Graeme F. Watson†*

Summary

Davies, M. & Watson, G. F. (1998) Developmental biology of Uperoleia talpa Tyler, Davies & Martin, 1981 (Anura: Myobatrachidae). Trans. R. Soc. S. Aust. 122(4), 153-157, 30 November, 1998.

Uperoleia talpa is a small fossorial frog restricted to the southwestern portion of the Kimberley Division of Western Australia. The frog breeds in the monsoonal wet season, and lays clumps of eggs in single capsules in ephemeral ponds. Larvae hatch at stage 19. Later-stage larvae have strongly arched tail fins, a sinistral spiracle, extremely large, cavernous external nares and a larval tooth row formula of two upper and three lower rows of labial teeth. Labial papillae are clearly interrupted both anteriorly and posteriorly. Larval life span is about 71 days. The large and conspicuous external nares have been found in a further five species of Uperoleia and are suggested as a possible diagnostic character for some larvae of the genus.

Key Words: Uperoleia talpa, larvae, embryos, generic character, life history, tadpole, Myobatrachidae.

Transactions of the Royal Society of S. Aust. (1998), **122**(4), 153-157.

DEVELOPMENTAL BIOLOGY OF *UPEROLEIA TALPA* TYLER, DAVIES & MARTIN, 1981 (ANURA:MYOBATRACHIDAE)

by MARGARET DAVIES[1] & GRAEME F. WATSON[2]

Summary

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KEY WORDS: *Uperoleia talpa*, larvae, embryos, generic character, life history, tadpole, Myobatrachidae.

Introduction

Uperoleia Gray, 1841 is a genus of small, burrowing, myobatrachine frogs with a wide-ranging distribution across Australia in areas of poor winter rainfall. Prior to the revision of Tyler *et al.* (1981), the genus comprised three species, but with the description of *Uperoleia altissima* (Davies *et al.* 1993), now includes 24 taxa. However, very little is known of the larval biology of the genus.

Moore (1961) described the larva of *U. marmorata* (now considered to be *U. laevigata* Keferstein, 1867 (Davies & Littlejohn 1986)) whilst Watson & Martin (1973) described the larva of what was thought to be *U. marmorata*, but which is now considered to be a representative of *U. tyleri* (Davies & Littlejohn 1986). Tyler *et al.* (1983) recorded the life history of *U. inundata* Tyler, Davies & Martin, 1981; Davies *et al.* (1986) described the larva of *U. lithomoda* Tyler, Davies & Martin, 1981 and Richards & Alford (1993) provided a description of the larva of *U. minula* Davies, McDonald, Corben & Ingram, 1986. Full life history data of these species are scarce.

Uperoleia talpa Tyler, Davies & Martin, 1981 is a large member of the genus (males 26-40 mm S-V, females 35-38 mm) (Tyler *et al.* 1994), with a restricted distribution in the southwestern portion of the Kimberley Division of Western Australia. The species was originally described from three frogs collected on a very dry night south of Derby (Tyler *et al.* 1981) and the description has been amplified by Davies & Martin (1988), who provided additional morphological, osteological and distributional information and described the call. In early February 1994 we collected amplectant pairs of *U. talpa* the spawn of which we reared to metamorphosis, thus allowing the description of the life history of the species that we report here. We also discuss some features that may aid in generic recognition of larvae.

Materials and Methods

The series of *Uperoleia talpa* was reared from spawn deposited in plastic bags by amplectant pairs collected in the field. Larvae were initially reared in aerated water at ambient temperature in the field before being transported to Adelaide where they were maintained in a constant temperature room at 30 ±1° C in dechlorinated tap water. Larvae were fed on boiled organic lettuce leaves supplemented with commercial goldfish flakes (Biosera). Material was preserved in Tyler's fluid (Tyler 1962) and illustrations were made with the aid of a Wild M8 stereo dissecting microscope with attached camera lucida. Measurements were made using an eyepiece micrometer.

Developmental stages are those of Gosner (1960).

Material examined: Davies collection: *Uperoleia talpa* series; *U. lithomoda* series; *U. altissima* series; *U. inundata* series (basis of data used by Tyler *et al.* 1983); larvae of *Crinia (Ranidella) signifera* (Girard, 1853); *C. (R.) riparia)* (Littlejohn & Martin, 1965); *Pseudophryne* Fitzinger, 1843. Tadpoles of *U. laevigata* were provided by Harold Ehmann and

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tadpoles of *U. russelli* (Loveridge, 1933) were examined in the collection of the University of Michigan, Museum of Zoology, Ann Arbor, Michigan.

Results

Two amplectant pairs of *Uperoleia talpa* were collected at 2345 h on 5.ii.1994 at a site 12.2 km south of the Gibb River Rd turnoff on the road south of Derby in the Kimberley Division of Western Australia (Fig. 1). The night was extremely hot, humid and stormy although no rain fell in the immediate area. Two other species of *Uperoleia* (*U. mjobergi* (Andersson, 1913) and *U. aspera* Tyler, Davies & Martin, 1981) were calling at the same pond. *Uperoleia talpa* was calling from the dry vegetation farthest from the water, *U. mjobergi* was calling from the edge of the water and *U. aspera* was calling from the intermediate areas. The choruses of *U. talpa* and *U. aspera* were substantial, whilst that of *U. mjobergi* was less vigorous. *Litoria rubella* (Gray, 1842) and *Cyclorana australis* (Gray, 1842) were also calling around the pond. When we visited the same site the following evening, there was much less activity with a single *U. talpa* and very few *U. aspera* calling. At that time, newly metamorphosed *C. cryptotis* Tyler & Martin, 1977, *C. longipes* Tyler & Martin, 1977 and *C. australis* were located.

The captive pairs were retained in pond water in inflated plastic bags, supported by icecream containers. The *U. talpa* spawned early on 6.ii.1994. At 0700 on 7.ii.1994, the eggs had reached late gastrula stage 12. A single capsule surrounded the ovum. Mean capsule diameter of six eggs was 1.88 mm (range 1.78-2.04) and the ova had a mean diameter of 1.38 mm (range 1.30-1.60 mm). At 1300 on 7.ii.1994 embryos were at stage 17 (tail bud) (Fig. 2), with the tail being better developed than the head. Hatching (stage 19) was completed by 1115 on 8.ii.1994 (Fig. 3). The newly hatched larvae had no external gills; the eyes were very difficult to detect and the mouth had not perforated; adhesive glands were not pigmented at this stage.

By 0945 on 11.ii.1994, some preserved larvae were already at Stage 25. The spiracle had formed and the adhesive glands were pigmented. There was no keratinisation of the beak or teeth (Fig. 4).

Material preserved on 12.ii.1994 included some larvae still at Stage 22/23 (Fig. 3) in which the nostrils had not perforated although the adhesive glands were pigmented. The spiracle had not formed and although the mouth was perforated there was no keratinisation on the beak or teeth.

Fig. 1. Site at which amplectant pairs of *Uperoleia talpa* were collected, 12.2 km S Gibb River Rd turnoff on Highway 1 south of Derby, WA.

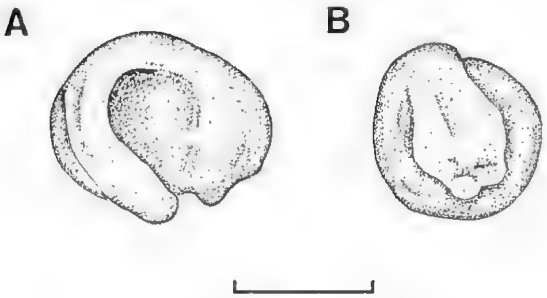

Fig. 2. A. Lateral and B. Dorsal views of Stage 17 (tail bud) embryo of *Uperoleia talpa* at 2200. Scale bar = 1 mm.

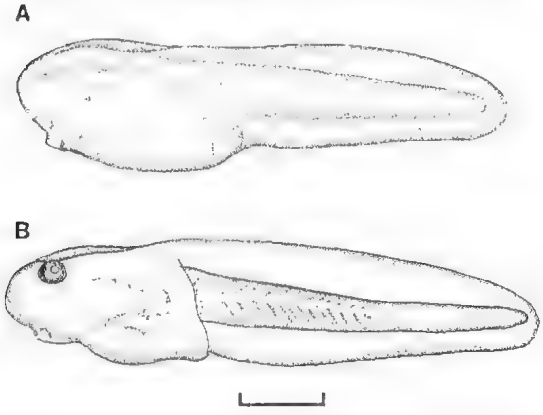

Fig. 3. A. Lateral view of newly hatched larva at Stage 19. B. Lateral view of larva at Stage 22 of *Uperoleia talpa*. Scale bar = 1 mm.

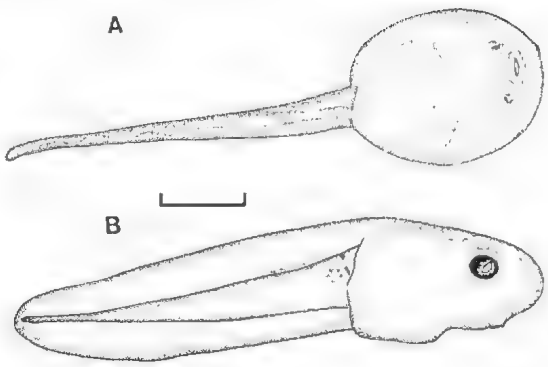

Fig. 4. A. Ventral and B. Lateral views of Stage 25 larva of *Uperoleia talpa*. Scale bar = 1 mm.

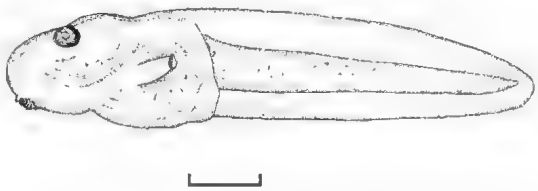

Fig. 5. Lateral view of Stage 25 larva of *Uperoleia talpa*. Scale bar = 1 mm.

TABLE 1. *Measurement (in mm) of body and total length of larvae of* Uperoleia talpa *as mean and range.* N = number of individuals.

	Stage (Gosner 1960)	Body length (mm)	Total length (mm)	N
11.-20.ii.1994	25	4.19	9.66	5
		(3.84-4.64)	(7.84-8.16)	
14.ii.1994	26	3.2	8.0	4
		(3.2 - 3.6)	(7.84-8.16)	
26.ii.1996	27	5.44	12.8 - 13.8	2
2.-29. iii.1994	28	5.46	13.72	7
		(4.8-5.92)	(12.96-14.58)	
6.-29.iii.1994	29	6.46	15.33	5
		(5.44-8.48)	(14.24-17.44)	
29.iii.-13.iv.1994	30	6.99	16.69	3
		(6.08-7.52)	(15.36-17.6)	
13.iv.1994	31	6.08	16.00	1
13.iv.1994	32	7.84-8.64	18.56-21.8	2
13.iv.1994	33	9.28	21.92	1
13.iv.1994	34	8.72	21.8	4
		(8.0-9.28)	(20.32-22.72)	
13.iv.1994	35	9.28-10.4	23.2-26.4	1
13.iv.1994	36	10.72	26.08	3
		(10.24-11.2	(24.8-27.2)	
13.iv.1994	37	9.92-11.2	25.28-26.58	2
13.iv.1994	38	10.8	25.12	1

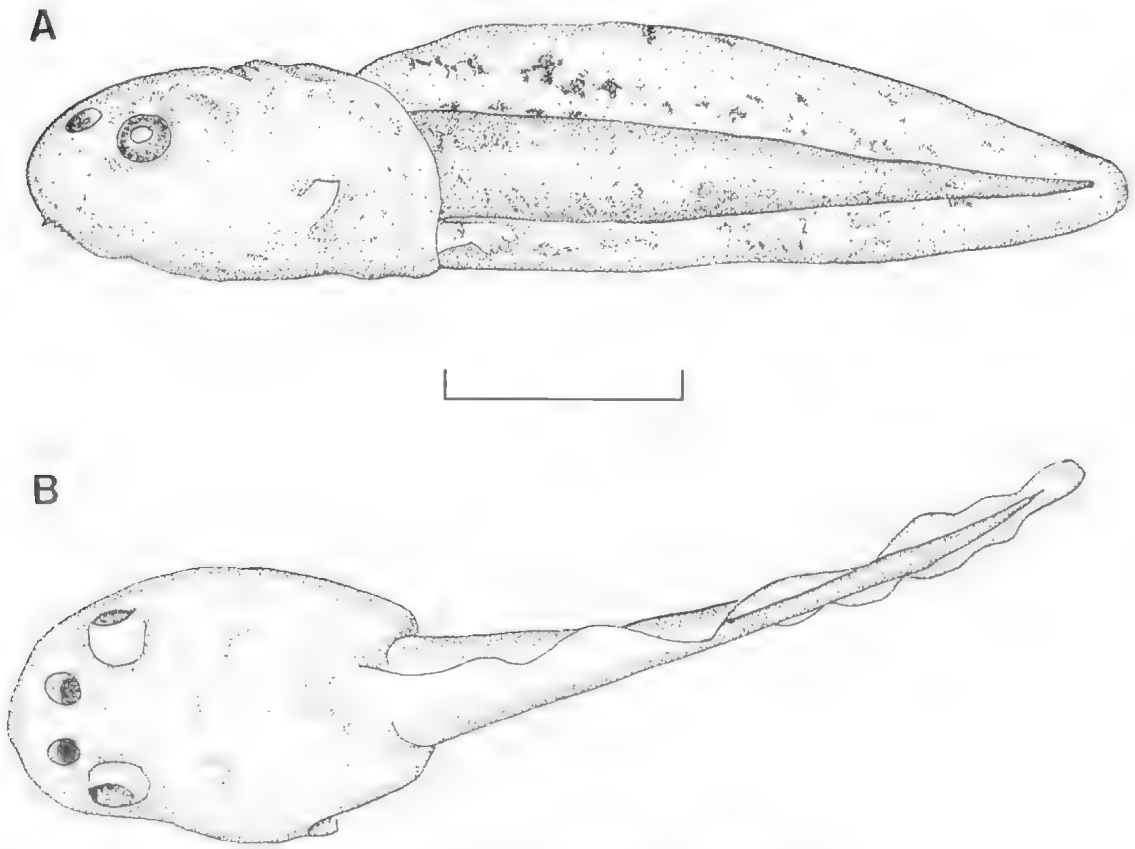

Fig. 6. A, Lateral and B, Dorsal views of Stage 36 larva of *Uperoleia talpa*. Scale bar = 5 mm.

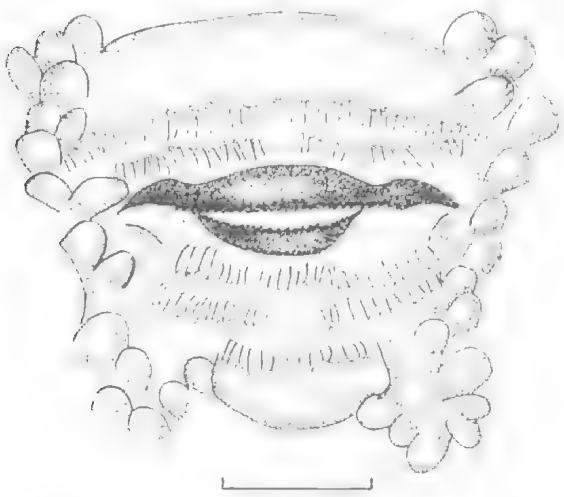

Fig. 7. Oral disc of Stage 36 larva of *Uperoleia talpa*. Scale bar = 1 mm.

Larvae at stage 25 preserved at 1115 on 14.ii.1994 (Fig. 5) had perforated nostrils, which were round, but these were not as conspicuous as is seen at later stages (see below). The horny beak was keratinised and keratinisation of one upper and 2-3 lower rows of labial teeth was beginning. Yolk still remained in the gut, although the cloaca was open dextrally. Larvae remained at stage 25 until after 20.ii.1994, a period of up to 9 days since the onset of this stage.

Measurements of larvae at stages 25-38 of Gosner are given in Table 1

The following description is of a larva at Stage 36 (Fig. 6).

Body ovoid, widest at midpoint of body. Snout evenly rounded in dorsal and lateral view. Nares dorsal and extremely large and cavernous. Eyes moderately conspicuous. Spiracle sinistral, short, opening dorsally and visible when viewed from above. Anal tube broad and dextral to ventral fin. Dorsal fin more strongly arched than ventral fin. Fins rounded terminally. Dorsal fin commencing on posterior part of body, deepest about half way along its length. Ventral fin commencing posteriorly to body, approximately same width along its length. Tail musculature moderately thick, tapering to fine point. Oral disc small and ventral. Labial papillae widely interrupted anteromedially. Also interrupted

posteromedially. Two rows of upper teeth and three rows of lower, the second of which is divided (Fig. 7). Short P3 row supported on flexible flap. Tail musculature and fins moderately heavily suffused with pigment. Small dark-brown islands of pigmentation on the body.

Larvae reached metamorphosis at stage 46 on 15.iv.1994, 71 days after spawning.

Discussion

We have now examined tadpoles of six species of *Uperoleia*, as well as several other myobatrachine species. It is clear that the external nares of many *Uperoleia* larvae are unusually large and cavernous (Fig. 6). Of the species examined, this feature was present in all but *U. inundata*. Richards & Alford (1993) provided measurements of *U. mimula*, but these do not allow a direct comparison of the data we provide here, since diameter in relation to the width of the head could not be ascertained. These authors do not comment on the relative size of the nares.

If, however, the nares are not particularly large, this feature would be useful in separating larvae of *U. mimula* from *U. lithomoda* - a species pair in which the adults are difficult to separate both morphologically, and, at high temperature, by call (K. R. McDonald pers. comm. 1986)

There is no generic tooth row formula for *Uperoleia*. *Uperoleia mimula*, *U. lithomoda* and *U. inundata* share a formula of 2(2)/3 whilst *U. laevigata* has a formula including no undivided rows of 1/3. *Uperoleia talpa* has 2(2)/3(2), whilst that of *U. altissima* is 2(2)/3(1,2) (Davies & McDonald 1998). The dark tail tip recorded by Richards & Alford (1993) in early stage larvae, whilst shared by *U. mimula*, *U. lithomoda*, *U. laevigata* and *U. altissima* (Davies & McDonald 1998), is not present in *U. talpa*. The heavy pigmentation of *U. talpa* larvae is shared by *U. tyleri* (Watson & Martin 1972). The flexible flap supporting P3 labial teeth is recorded in all *Uperoleia* to date, but is not unique to *Uperoleia*, being found in *Crinia (Ranidella) signifera*, *C. (R.) riparia* and as a larger structure in *Pseudophryne* species (Watson & Martin 1973; Davies unpub.). Thus the possibility of using this feature for generic recognition foreshadowed by Richards & Alford (1993), cannot be sustained.

The large nares may be useful in some species assemblages, being absent in only *U. inundata* among the species we have examined to date.

The unusual tail bud stage in which the tail is better developed than the head was noted also by Moore (1961) in *U. laevigata*. This developmental condition merits further investigation

Acknowledgments

Fieldwork was supported by the Australian Research Committee and we thank M. J. Tyler for companionship in the field and the referees for helpful comments

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A NEW SPECIES OF FROG (ANURA: MICROHYLIDAE) FROM CAPE MELVILLE, QUEENSLAND

By Margaret Davies & Keith R. McDonald†*

Summary

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Key Words: Cophixalus zweifeli, new species, osteology, Microhylidae, morphology.

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KEY WORDS: *Cophixalus zweifeli*, new species, osteology, Microhylidae, morphology.

Introduction

Fauna surveys have been conducted in Cape York Peninsula by the Queensland Department of Environment (and its predecessors) since 1975. Information on the vertebrate fauna of the area has been reviewed by Winter & Lethbridge 1995[1] as part of Stage 1 of the Cape York Peninsula Land Use Study. Subsequently fauna and flora surveys in Cape Melville National Park have located significant new records for mammals, reptiles, frogs, earthworms and vegetation types (Stanton 1994[2]; Little & Hall 1996; Stanton & Fell 1996[3]; Jamieson 1997; McDonald 1997, 1998, unpub.). The area of Cape Melville National Park was increased from 36 000 ha to 137 000 ha in 1995, thus incorporating a greater diversity of habitats and an increase in the range of flora and fauna in the park. The new area includes assemblages of topography, geology and vegetation types unique to Cape York (Stanton 1994[2]), so the Cape Melville National Park is an area of proven and potential endemism (Covacevich & Ingram 1978; Stanton & Fell 1996[3]; Jamieson 1997; McDonald 1997).

A large hylid frog (*Litoria andiirmalin* McDonald, 1997) was discovered in boulder fields of the Melville Range. In addition, a second new frog species was located amongst boulders. This species was recognised as a member of Microhylidae, a family well represented in New Guinea but with Australian representatives restricted to the subfamily Genyophryinae in two genera *Cophixalus* and *Sphenophryne*. Australian microhylids are confined to northeast Queensland, with the exception of *Sphenophryne adelphe* Zweifel, 1985, a species found in the north of the Northern Territory (Tyler & Davies 1986). Australian microhylids were reviewed by Zweifel (1985) who recognised 16 species, seven of which he described at that time. Richards *et al.* (1994) described *Cophixalus monticola* from the Carbine Tablelands, northeast Queensland and here we describe a further *Cophixalus* from Cape Melville.

Materials and Methods

The material studied is deposited in the Queensland Museum, Brisbane (QM) and the South Australian Museum, Adelaide (SAMA). Measurements were made with dial calipers reading to 0.01 mm. Measurements taken (in mm) were : tympanum diameter (T), eye to naris distance (EN), eye diameter (E), foot (F), hand (H), head width (HW), head length (HL), internarial span (IN), snout to vent length (SV), tibia length (TL), width of third finger disc and of penultimate phalanx, width of fourth toe disc and of penultimate phalanx, length of hand and length of foot and follow Zweifel (1985) and Tyler (1968). Material was cleared and stained using a modification of the method of Dingerkus & Uhler

Dept of Zoology, University of Adelaide, Australia 5005.
[1] Conservation Strategy Branch, Department of Environment, PO Box 834, Atherton Qld 4883.

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(1977). Description and discussion of osteology follow Zweifel (1985).

Results

The new species is assigned to *Cophixalus* on the basis of the following features: dentaries not in contact; vertebral column procoelous; tongue ½ free behind with no furrow or pouched pocket; maxillae not in contact (relationship with premaxillae indeterminable). This combination of features assigns the species to the Genyophryninae (Zweifel 1971).

In addition, the species lacks procoracoids and clavicles, has a snout that is not narrow or elongate and lacks a hypertrophied serous gland on the snout. The other defining feature of *Cophixalus*, the alary process being typically slender and not merging insensibly into the body of the bone, could not be determined.

Cophixalus zweifeli sp. nov.
(FIGS 1-4)

Holotype: ♀ QM J64888 (formerly QNPWS N29789) Cape Melville National Park, 14° 15' 3" S, 144° 27' 40" E, altitude 60-80 m, 17.ii.1995, Coll. K. R. McDonald and L. A. Jackson.

Paratypes: ♀ SAMA R51080 16.ii.1995, Same location and collectors as holotype; ♀ QM J64889 (formerly (QNPWS N73038) Cape Melville National Park, Permanent Camp Qld (near type locality), altitude 40 m, 14.xii.1995, Coll. J. O'Shea (cleared and stained)

Definition

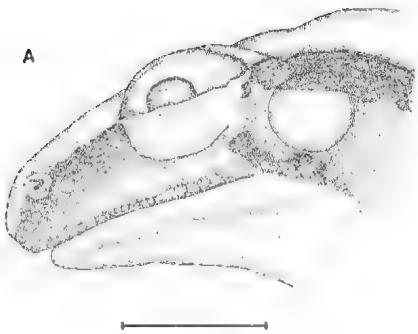
A large species (♀♀ 40.1-45.4 mm SV) with long legs, large finger discs with third finger disc larger than fourth toe disc, an elongate snout; dorsal colouration brown with flame-scarlet axilla, thigh flashes and ventral leg markings.

Description of Holotype

Head slightly narrower than body; legs moderately long (TL/SV 0.51); snout truncate from above, straight and slightly projecting in profile (Figs 1, 2); canthus rostralis straight, loreal region steeply sloping; nares anterolateral on tip of snout; eye to naris distance greater than internarial span (EN/IN = 1.125); eyes moderately large, corneal outline clearly visible from beneath; interorbital width greater than width of upper eyelid. Tympanum large, obscure dorsally, diameter greater than half eye diameter.

Relative lengths of fingers 3>4>2>1, the first slender and approximately half the length of the second (Fig. 3). Discs of fingers 2-4 greatly enlarged and truncate, that of first barely extending beyond width of penultimate phalanx (Fig. 3); subarticular tubercles rounded, moderately prominent. Low

Fig. 1. *Cophixalus zweifeli* sp. nov. in life (SV 41.5 mm).



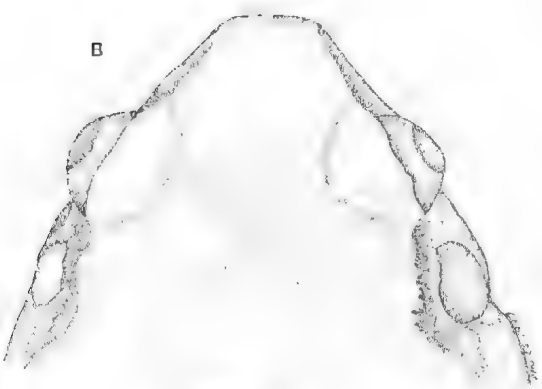


Fig. 2. *Cophixalus zweifeli* sp. nov. A. Lateral and B. Dorsal views of head of holotype (QM J64888). Scale bar = 5 mm.

ovoid inner and outer palmar tubercles. Relative lengths of toes 4>3>5>2>1 (right foot). toe three abnormally short on left foot; length of first toe approximately half that of the second. All toes with enlarged truncate discs with terminal grooves. Discs on first and fifth toes smallest and approximately same size. Toe discs smaller than those of fingers 2-4 (Fig. 3). Subarticular tubercles rounded, moderately prominent. Low elongate inner metatarsal tubercle, no outer metatarsal tubercle.

Dorsal and ventral surfaces smooth.

Colour and pattern: dorsum tan with darker brown pigment spots above insertion of arm, along flanks and superior to inguinal region and along midvertebral region; large faint mark between and posterior to eyes; dark canthal stripe from tip of snout, through nostril and eye and above and slightly posterior to tympanum. Pale crescent along anterior

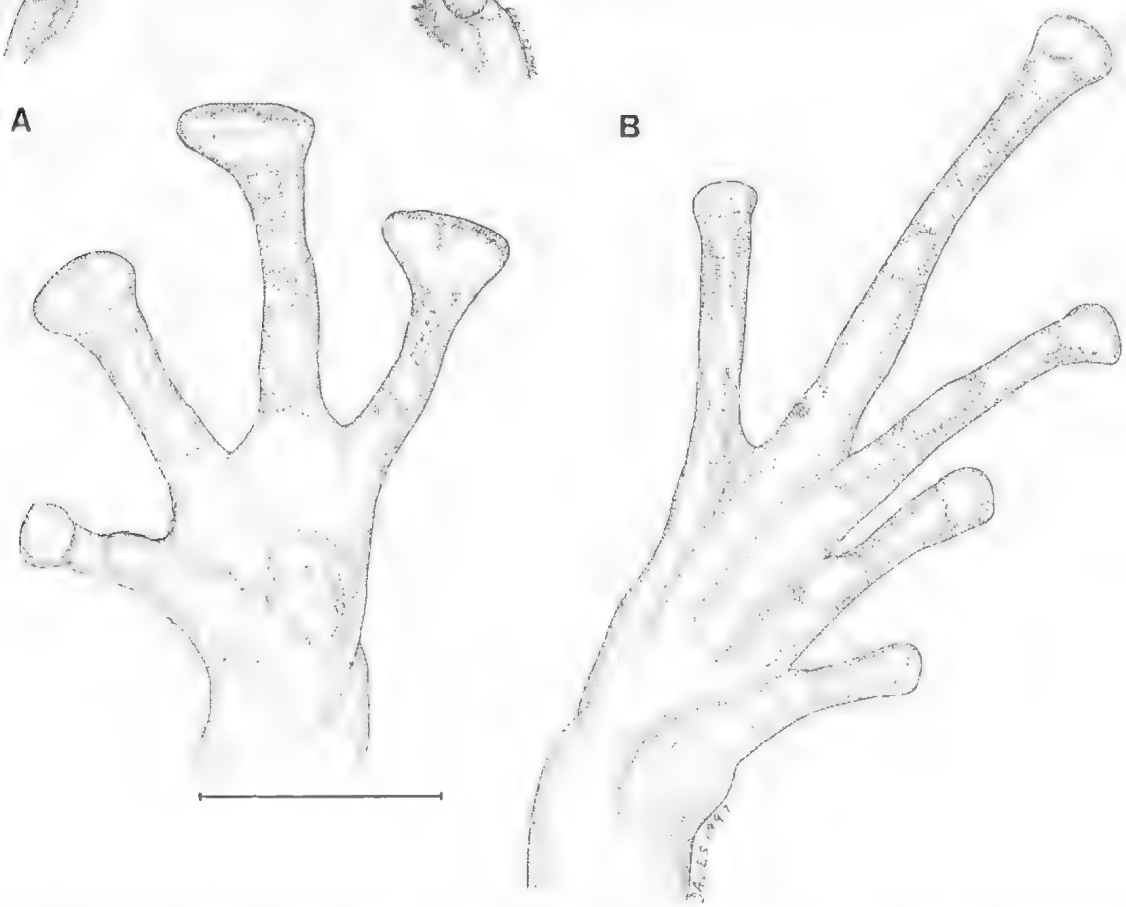


Fig. 3. *Cophixalus zweifeli* sp. nov. A. Palmar view of left hand. B. Plantar view of right foot of holotype (QM J64888). Scale bar = 5 mm.

rim of tympanum and paler stripe along lower rim of eye. Dark brown pigment patches on dorsal surfaces of hand and forelimb. Lesser pigment spots on dorsal surface of foot; dark patches along anterior edge of tibia. Throat very lightly dusted with pigment, more concentrated around margin of jaw and speckled with white.

Measurements

SV 40.1; TL 20.6; HW 13.9; HL 13.4; E 4.5; T 3.1; EN 3.6; IN 3.2; third finger disc 2.2 (penultimate phalanx 1.0); fourth toe disc 1.9 (penultimate phalanx 0.7); hand 11.7; foot 7.3; TL/SV 0.51; HW/SV 0.35; HL/SV 0.33; EN/IN 1.125; HL/HW 0.96; E/SV 0.11; IN/SV 0.08; third finger disc/SV 0.054; fourth toe disc/SV 0.047; hand/SV 0.29; foot/SV 0.45; EN/SV 0.090; T/E 0.69.

Colour in life

Dorsal surface beige when first observed at night, darkening to tan during the day with widely scattered, irregular brown speckles. Brown mottling on arm and thigh dorsal surface. Black canthal streak from snout through eye and above tympanum. Lateral dark brown mottled marking between axilla and groin. Axilla, groin, hidden parts of thigh, ventral tibia and inner half of foot flame scarlet (Smithe 1975). Ventral surface densely mottled light purple on throat and chest becoming more diffuse posteriorly. Ventral surface of femur and arm mottled with brown. Dull yellowish wash on lower third of abdomen and under the femur. Brown ventral surface to hand and foot.

Variation

The two paratypes have the following measurements.

SAMA R51080: SV 41.5; TL 22.2; HW 12.8; HL 14.4; E 5.0; T 3.3; EN 4.0; IN 4.2; third finger disc 2.5 (penultimate phalanx 1.2); fourth toe disc 1.7 (penultimate phalanx 0.6); hand 12.1; foot 19.1; TL/SV 0.54; HW/SV 0.31; HL/SV 0.35; EN/IN 0.95; HL/HW 1.13; E/SV 0.12; IN/SV 0.10; third finger disc/SV 0.06; fourth toe disc/SV 0.04; hand/SV 0.29; foot/SV 0.46; EN/SV 0.096; T/E 0.66. QM I64889. SV 45.4; TL 20.8; HW 14.2; HL 13.0; E 4.1; T 3.4; EN 3.6; IN 3.5; third finger disc 2.45 (penultimate phalanx 1.8); fourth toe disc 1.9 (penultimate phalanx 0.6); hand 10.8; foot 19.5; TL/SV 0.46; HW/SV 0.32; HL/SV 0.31; EN/IN 1.03; HL/HW 0.92; E/SV 0.09; IN/SV 0.077; third finger disc/SV 0.053; fourth toe disc/SV 0.042; hand/SV 0.24; foot/SV 0.43; EN/SV 0.079; T/E 0.83

Dorsal colour is more brown than tan in SAMA R51080 and the markings are more distinct. The ventral surface, in particular at the throat and anterior abdomen, is more heavily and irregularly pigmented with a faint white stripe medially. The undersurface of the thighs is more heavily speckled.

Comparison with other species

Cophixalus zweifeli sp. nov. is a very large species of Australian microhylid comparable only with *C. saxatilis* Zweifel & Parker, 1977. In addition, the third finger disc of the new species is larger than that of the fourth toe, a feature shared by *C. saxatilis* and *C. ornatus* (Fry, 1912). This latter species is smaller than either *C. zweifeli* or *C. saxatilis*. The canthus rostralis is straight in *C. zweifeli* compared with a rounded canthus in *C. saxatilis*. The snout of *C. zweifeli* is longer than that of *C. saxatilis*. The distinctive flame-scarlet colouration on the hidden surfaces of legs is not found in any other *Cophixalus* in Australia. Females of *C. saxatilis* are canary yellow at night, darkening to a light tan during the day. Unpublished data of C. Hoskin from mitochondrial DNA sequences show *C. zweifeli* to be a sister taxon to *C. infacetus* Zweifel, 1985 and in a separate clade from *C. saxatilis*. *Cophixalus infacetus* is a small species (females to 17.6 mm SV) with a rounded canthus rostralis, features not shared by *C. zweifeli*. In life, *C. infacetus* is dark grey on the underside, compared with the purplish colour of the throat and chest of *C. zweifeli*.

Osteology

One paratype was cleared and stained, but unfortunately because of poor preservation, the material did not remain intact throughout the maceration process. However, characteristic and diagnostic features were obtainable.

Skull: The skull is toothless with well-developed and well-ossified nasals and frontoparietals. The quadratojugal articulates with the maxilla. The eleutherognathine condition of the premaxillae, typical of the Genyophryinae, could not be confirmed. The otoccipital region (prootic and exoccipital) is ossified and the bones are closely associated with each other. The vomers have a well developed transverse arm (probable fused vomer and palatine) arising from an expanded area in the midline of the palate, and an anterior arm that passes mesial to and then anterior to the internal nares. The transverse arm reaches the maxillary shelf although remaining tied to the maxilla by cartilage (Fig. 4). The pterygoid is extremely robust.

There is a thickened median portion of the hyoid plate and the posterior cornua have well-developed flanges (Fig. 4).

The pectoral girdle lacks clavicles and a very small medial projection may represent a vestigial omosternum (Fig. 4). Calcification is absent in the mesosternal region.

Presacral vertebrae are non-imbricate. Relative widths of transverse processes are: III>II>IV>I =V=VI=VII=VIII. Vestigial transverse processes are apparent on the urostyle.

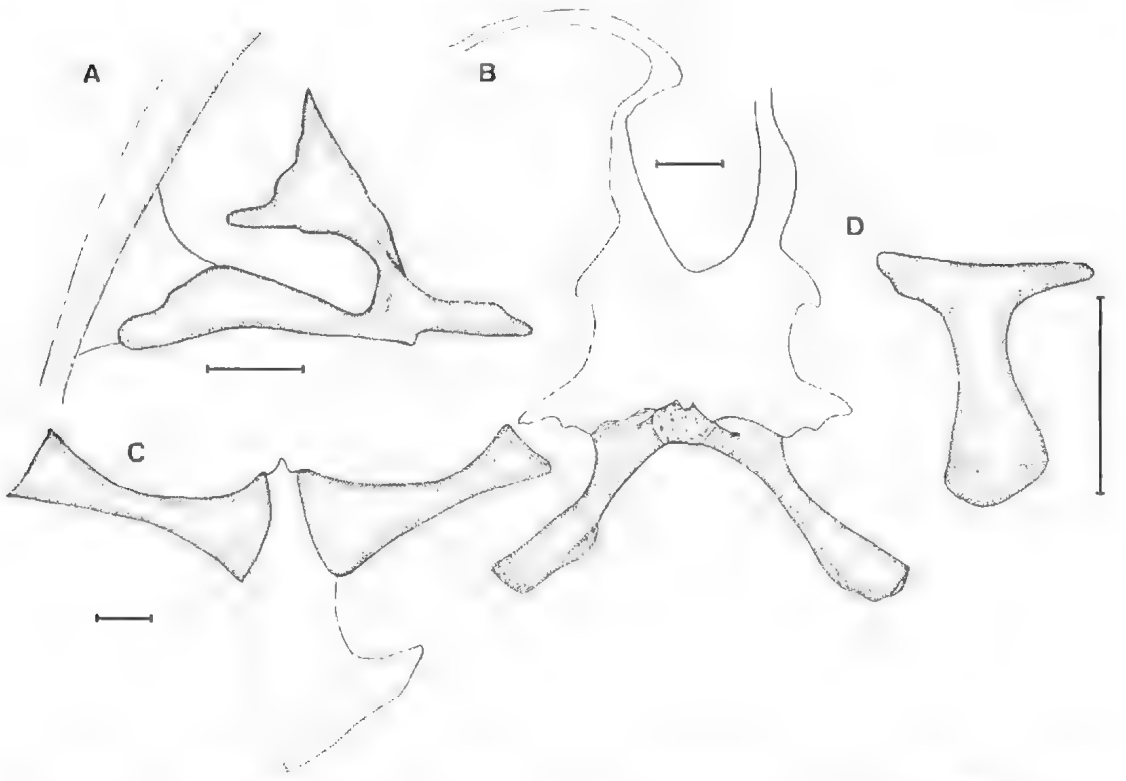


Fig. 4. *Cophixalus zweifeli* sp. nov. A. Right vomerine bone in ventral view. B. Dorsal view of hyoid plate. C. Ventral elements of pectoral girdle. D. Terminal phalanx of finger (Paratype QM J64889). Scale bars = 1 mm.

The tips of the terminal phalanges of the hands and feet are T-shaped (Fig. 4).

Comparison with other species

Zweifel (1985) examined the osteology of 11 species of Australian *Cophixalus* and the current comparison is with these data.

The otoccipital region of *C. zweifeli* is similar to that of *C. saxatilis*, *C. concinnus* Tyler, 1979, and *C. exiguus* Zweifel & Parker, 1969. *Cophixalus infacetus* and *C. hosmeri* Zweifel, 1985 have the ossification of the prootics restricted to buried nubbins, as seen from above. The other species examined by Zweifel have an intermediate condition between these two extremes.

The fused vomers and palatines of *C. zweifeli* approach those of *C. concinnus* in their relationship with the maxillary shelf, whilst the mesial extension approaches that of *C. ornatus*. The anterior portion of the complex approaches that of *C. saxatilis* although it is more robust in *C. zweifeli*.

Zweifel did not recognise characters in the hyoid as being useful in interspecific comparisons.

Some *Cophixalus* (including *C. saxatilis*) have a small cartilaginous protrusion on the anterior ventral midline of the pectoral girdle (? vestigial omosternum). A smaller process is apparent in *C. zweifeli*.

The terminal phalanges lack a median notch found in *C. infacetus*, *C. saxatilis* and *C. ornatus*.

Distribution

The species is known only from the type locality in Cape Melville National Park.

Habitat

The habitat of *C. zweifeli* sp. nov. is restricted to boulder fields of Altanmoui granites (Fig. 5). The holotype and paratype (SAMA 51080) were located at the base of rocks at night near a creek flowing through the rock formation. No calling was heard. Paratype (QM J64889) was found on a rock in a stream flowing out of the boulders.

Etymology

This species is named for Richard G. Zweifel, former Curator of Herpetology at the American Museum of Natural History, New York, whose revision of the Australian microhylids is a standard reference. We honour his contribution to herpetology and his friendship.

Discussion

Morphologically *Cophixalus zweifeli* appears to be a sister species to *C. saxatilis*. Both are large frogs, the largest of any Australian microhylid, and similar in body proportions. The flame-scarlet coloration in the axilla, groin and on the legs is unique to *C. zweifeli*.

In addition to morphological appearance, *C. zweifeli* and *C. saxatilis* utilize similar habitats of granitic boulder fields with patches of closed vegetation in moist pockets (Fig. 5; see Zweifel & Parker 1977, Fig. 7 for the habitat of *C. saxatilis*). This form of habitat is restricted to the Melville Range and Black Mountain in Cape York Peninsula. Similar small areas of just a few hectares are found in numerous locations in eastern Queensland (Stanton 1994). The direct distance from Black Mountain to the Melville Range is 175 km. Rainfall around the Cape Melville Range is estimated to be as high as 2000 mm (some 700 mm higher than the surrounding country) (Stanton 1994).

Notwithstanding the morphological linking of *C. zweifeli* with *C. saxatilis*, Hoskin's data from mitochondrial DNA sequences link the species with *C. infacetus* in a separate clade from *C. saxatilis*. Zweifel (1985) attempted to derive a tree of relationships amongst *Cophixalus* using external morphological characters but found this to be "unsatisfying" (Zweifel 1985 p. 370). Zweifel did not believe that any one of his most parsimonious trees was defensible. Given the non-congruence between morphological and biochemical data indicated here, it is clear that a more robust morphological study using other morphologies than external features is needed as a test of the robustness of the mitochondrial DNA data. If the data are copious, independent and evenly distributed across the branches of the tree, phylogenies from any data set tend to converge (Mishler 1994) and such congruence between trees from different data sets provides strong evidence for any hypothesis of phylogenetic history.

It is clear, however, that whatever the data set used to derive relationships, monophyly of Australian *Cophixalus* first must be demonstrated.

Acknowledgments

We thank L. Jackson and J. O'Shea for field assistance and C. Hoskin for permission to quote unpublished data from his BSc (Hons) thesis and further studies. M. J. Tyler critically read the manuscript. We also thank the referees for constructive suggestions.

Fig. 5. Habitat of rocky boulders in Cape Melville National Park where *Cophixalus zweifeli* sp. nov. is found.

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DEVELOPMENTAL BIOLOGY OF UPEROLEIA ALTISSIMA DAVIES, WATSON, McDONALD, TRENERRY & WERREN, 1993 (ANURA: MYOBATRACHIDAE)

By Margaret Davies & Keith R. McDonald†*

Summary

Davies, M. & McDonald, K. R. (1998) Developmental biology of Uperoleia altissima Davies, Watson, McDonald, Trenerry & Werren, 1993 (Anura: Myobatrachidae). Trans. R. Soc. S. Aust. 122(4), 167-172, 30 November, 1998.

Uperoleia altissima is a small fossorial frog restricted to upland areas in northeast Queensland. The frog breeds in the monsoonal wet season, and lays clumps of eggs that fall to the floor of ephemeral ponds. Larvae hatch at stage 19. Later-stage larvae have moderately strongly arched tail fins, a sinistral spiracle, large, narrow, cavernous, external nares, and a larval tooth-row formula of two upper (second divided) and three lower rows (first and second divided). Labial papillae are strongly interrupted both anteriorly and posteriorly. Later-stage larvae are strongly pigmented although the strongly-pigmented tail tip of earlier larvae is less so. Larval life span is about 39 days in captivity.

Key Words: Uperoleia altissima, larvae, embryos, life history, tadpole, Myobatrachidae.

Transactions of the Royal Society of S. Aust. (1998), **122**(4), 167-172

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by MARGARET DAVIES[1] & KEITH R. McDONALD[2]

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KEY WORDS: *Uperoleia altissima*, larvae, embryos, life history, tadpole, Myobatrachidae

Introduction

Uperoleia altissima Davies, Watson, McDonald, Trenerry & Werren, 1993 is a toothed member of a speciose genus of small fossorial frogs distributed across mainland Australia except for the southwest of the continent. *Uperoleia altissima* is confined to elevated sites on the western Wet Tropics Biogeographic Region (Stanton & Morgan 1977) from Princess Hills, Lumholtz National Park, north to the Windsor Tableland of northeastern Queensland. The species is found in moist eucalypt forests and woodlands above 600 metres. Although described in 1993 from freshly collected material, the species had been collected but not identified previously. Little was known of its breeding biology.

In early February 1997, we encountered a breeding chorus of the frog following heavy rainfall at a site on the Atherton Tablelands. Amplectant pairs which later spawned were collected, and the resultant larvae were reared to metamorphosis.

The description of this life history adds to the scarce data available on life histories of the 24 species of *Uperoleia* (Moore 1961; Watson & Martin 1973; Tyler *et al.* 1983; Davies *et al.* 1986; Richards & Alford 1993; Davies & Watson 1998).

Materials and Methods

The series of *Uperoleia altissima* was obtained from spawn deposited by amplectant adults collected in the field. Larvae were initially reared in aerated water at ambient temperature (water temperature approximately 24° C) in the field before being transported to Adelaide where they were maintained in a constant temperature room at 30 ± 1° C in dechlorinated tap water. Larvae were fed on boiled organic lettuce leaves supplemented with commercial goldfish flakes (Biosera). Material was preserved in Tyler's fluid (Tyler 1962) and illustrations were made with the aid of a Wild M8 stereo dissecting microscope with attached camera lucida. Measurements were taken using an eyepiece micrometer. Developmental stages are those of Gosner (1960).

Results

Four amplectant pairs of *Uperoleia altissima* were collected on 1.ii.1997 at a quarry near Carrington Falls (17° 19' 51" S, 145° 26' 42" E). The site is a quarry with gravel pits some of which have regrowth vegetation. We had visited the site on the previous night after rain, but although *U. altissima* was calling, no breeding was observed. However, *Litoria rubella* (Gray, 1842) was calling and breeding took place later that night. Other species calling when *U. altissima* was breeding included *Crinia remota* (Tyler & Parker, 1974), *L. nasuta* (Gray, 1842), *L. nithi* (DeVis, 1884), *L. fallax* (Peters, 1881) and *Limnodynastes terraereginae* Fry, 1915. The night was humid following torrential rain in the nearby Herberton Range, although rain did not appear to have fallen at the site.

Males were calling from the gravel areas surrounding the temporary pools (Fig. 1), often

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Fig. 1. Calling male *Uperoleia altissima* at Carrington Falls Quarry site (SV approximately 24 mm).

Fig. 2. Amplexant *Uperoleia altissima* at Carrington Falls quarry site (SV of male approximately 24 mm).

facing away from the water toward the surrounding vegetation. Pairs in inguinal amplexus were found moving toward the shallow water (Fig. 2)

The *U. altissima* spawned early on 2.ii.1997. At 1310 on 3.ii.1997, the eggs had reached stage 12, late gastrula. A single capsule surrounded the ovum. Mean capsule diameter of four eggs was 2.27 mm (range 2.22-2.32) and the ova had a mean diameter of 1.36 mm (range 1.32-1.40 mm). At 1300 on 4.ii.1997 embryos were at stage 17 (tail bud) (Fig. 3), with the tail being better developed than the head. Adhesive glands and the stomodaeal pit were prominent. They had reached stage 18 by 5.ii.1997 (Fig. 4). Hatching (stage 19) was completed on 6.ii.1997 (Fig. 4). The newly hatched larvae had no external gills; the eyes were very difficult to detect and the mouth had not perforated; adhesive glands were pigmented at this stage.

By 0900 on 7.ii.1997, some larvae were at stage 20. Adhesive glands were well developed on stalks and both the mouth and the external nares were perforated. Larvae were still at stage 20 at 1140 on 8.ii.1997, the cornea was not transparent, and heavy pigmentation was apparent on the tail fin.

Larvae had reached stage 26 by 1000 on 14.ii.1997. The horny beak was keratinised as were upper and lower labial tooth rows. The adhesive glands were reduced to patches of pigmentation. The nares were large and cavernous and the tip of the tail was particularly heavily pigmented (Fig. 5). Stage 28 was reached by 1100 on 19.ii.1997.

Later-stage larvae lacked the heavily pigmented tail tip.

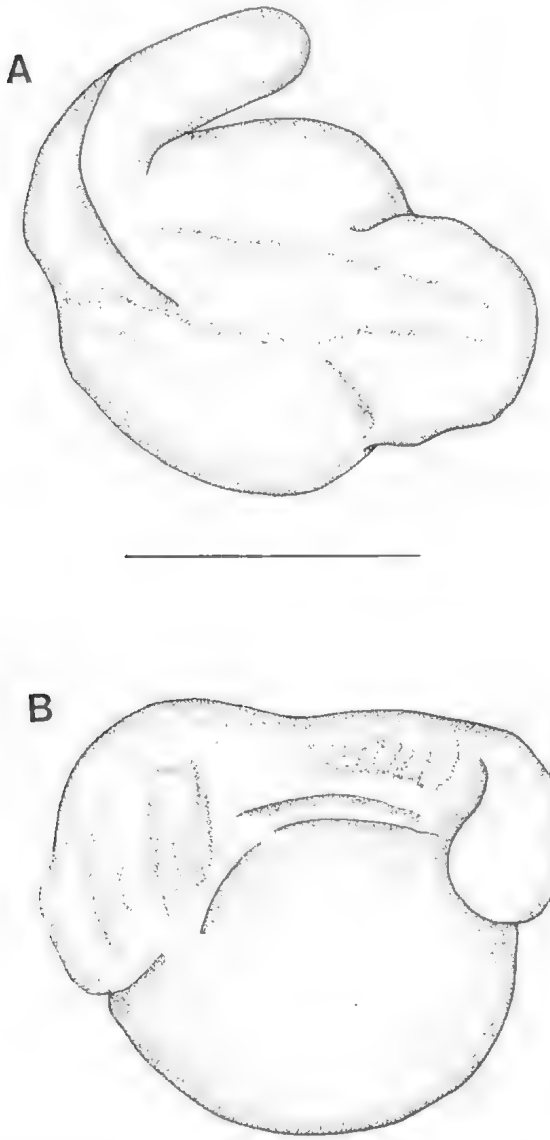

Fig. 3. A. Dorsal. B. Lateral views of Stage 17 (tail bud) embryo of *Uperoleia altissima*. Scale bar = 1 mm.

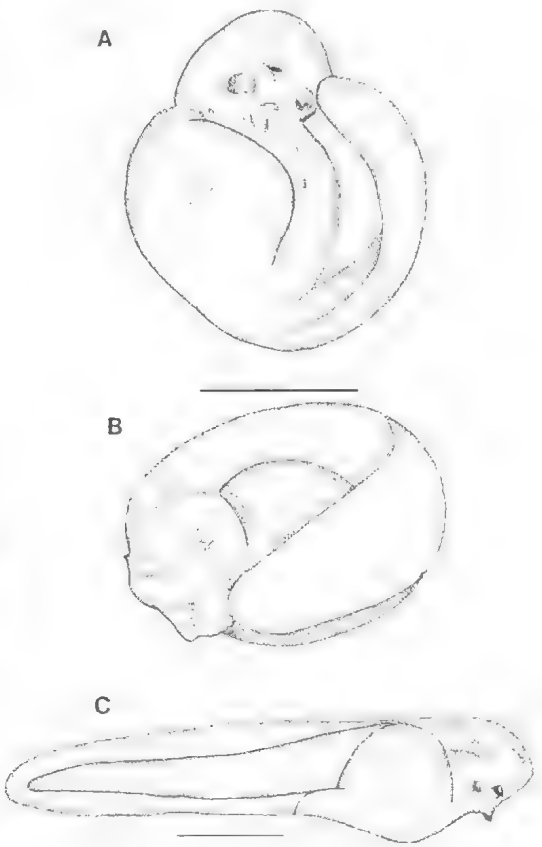

Fig. 4. A. Ventral. B. Lateral views of Stage 18 (muscular response) embryo. C. Lateral view of newly hatched larva of *Uperoleia altissima* at Stage 19. Scale bars = 1 mm.

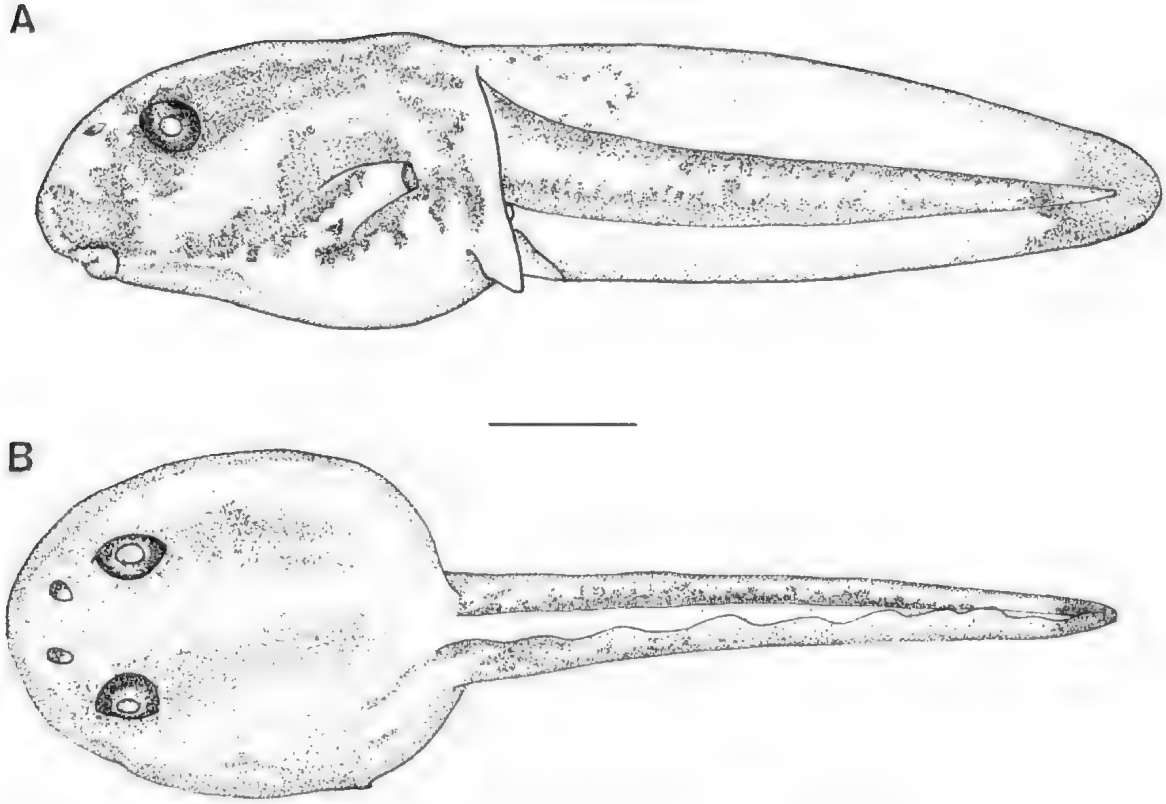

Fig. 5. A. Lateral, B. Dorsal views of Stage 26 larva of *Uperoleia altissima*. Scale bar = 1 mm.

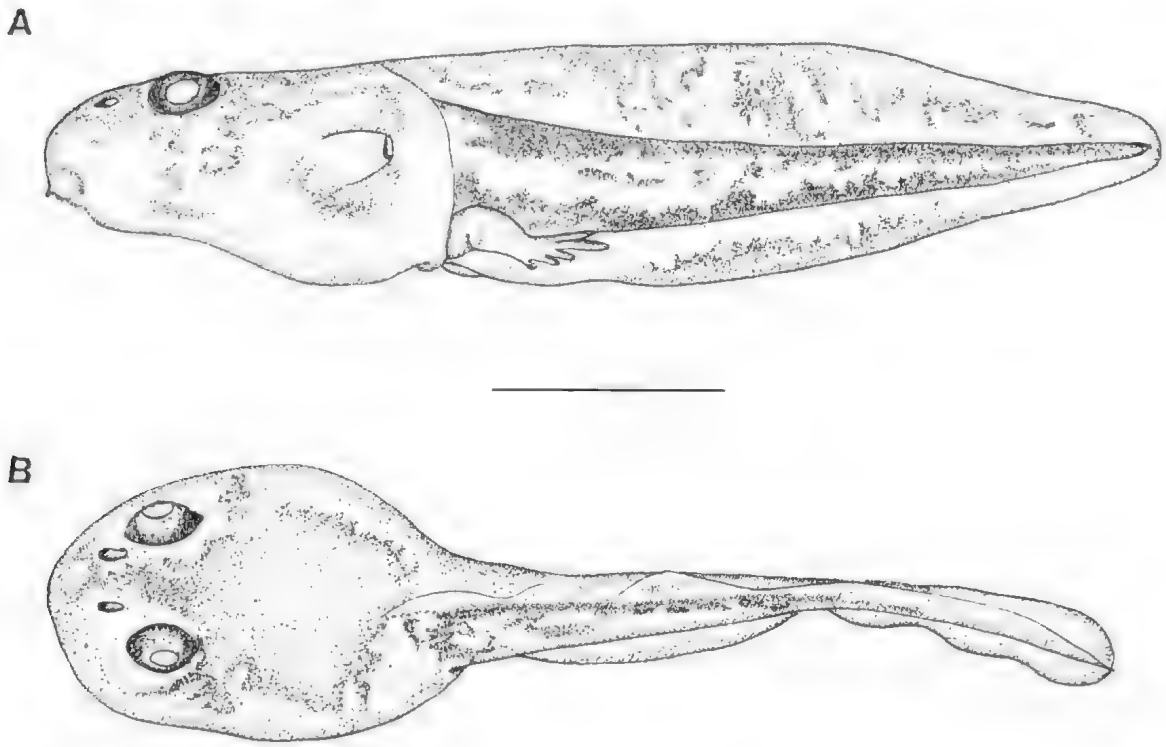

Fig. 6. A. Lateral, B. Dorsal views of Stage 39 larva of *Upendeia altissima*. Scale bar = 5 mm.

TABLE 1. *Measurements (in mm) of body and total length of larvae of* Uperoleia altissima *as mean and range.* N = number of individuals.

Stage (Gosner 1960)	Body length (mm)	Total length (mm)	N
28	6.16	13.68	2
	(6.08-6.24)	(13.12-14.24)	
29	6.83	16.53	3
	(6.36-7.36)	(15.68-17.12)	
30	6.72	16.56	2
	(6.72)	(16.32-16.8)	
32	7.84	19.20	1
35	8.42	19.31	3
	(8.00-8.64	(18.24-20.48)	
36	9.36	23.68	2
	(9.28-9.44)	(23.52-23.84)	
37	9.36	23.68	4
	(9.12-9.60)	(21.92-24.96)	
38	9.09	24.08	6
	(8.64-9.6)	(22.24-25.92)	
39	10.08	26.08	2
	(10.08)	(25.92-26.24)	
40	9.60	25.28	1
41	9.74	26.26	9
	(9.6-10.56)	(25.76-27.36)	
42	10.00		2
	(9.92-10.08)		
43	10.27		7
	(9.6-10.94)		
44	10.24		2
	(10.08-10.40)		
45	10.44		4
	(10.4-10.56)		
46	10.24		2
	(10.08-10.40)		

Measurements of larvae at stages 28-36 are given in Table 1.

The following description is of a larva at Stage 39 (Fig. 6).

Body ovoid, widest at midpoint. Snout evenly rounded in dorsal and lateral view. Nares dorsal, large, narrow and cavernous. Eyes conspicuous. Spiracle sinistral, moderately long, opening posteriorly and scarcely visible when viewed from above. Anal tube broad opening dextral to ventral fin. Dorsal fin more strongly arched than ventral fin. Fins rounded terminally. Dorsal fin commences on posterior part of body and is deepest about halfway along its length. Ventral fin commences posteriorly to body and is deepest about halfway along its length. Tail musculature moderately thick, tapers to point. Oral disc small and ventral. Labial papillae widely interrupted anteromedially; less widely interrupted posteromedially. Two rows of upper teeth, second divided; three lower rows, first and second divided (Fig. 7). Short P3 row supported on flexible flap. Tail musculature and fins heavily suffused with pigment. Dark-brown islands of pigmentation on body.

Larvae reached metamorphosis at stage 46 on 13.ii.1997, 39 days after spawning.

Discussion

The complete larval biologies of *Uperoleia altissima*, *U. inundata* Tyler, Davies & Martin, 1981 (Tyler *et al.* 1983), and *U. talpa* Tyler, Davies & Martin, 1981 (Davies & Watson 1998) are now known as are tadpole morphologies of *U. tyleri* Davies & Littlejohn, 1986 (as *U. marmorata*, Watson & Martin 1973), *U. lithomoda* Tyler, Davies & Martin, 1981 (Davies *et al.* 1986) and *U. minula* Davies, McDonald & Corben, 1986 (Richards & Alford 1993). These latter two species occur in or near geographic locations of *U. altissima*, hence a comparison of their salient features is of value for identification of tadpole assemblages.

Uperoleia minula and *U. lithomoda* share a tooth row formula of 2(2)/3 whilst that of *U. altissima* is

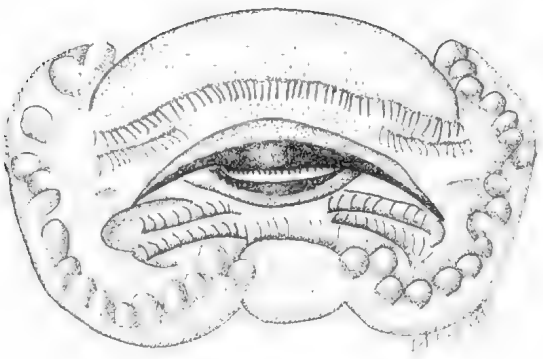

Fig. 7. Oral disc of Stage 37 larva of *Uperoleia altissima*. Scale bar = 1 mm.

2(2)/3(1,2). The flexible flap supporting P3 labial teeth is recorded in all *Uperoleia* to date, but is not unique to *Uperoleia* (Davies & Watson 1998). The dark tail tip in early stages of *U. mimula* recorded by Richards & Alford (1993), is shared by *U. lithomoda* and *U. altissima*. The heavy pigmentation of later *U. altissima* larvae may be greater than the diffuse pigment of *U. lithomoda* and *U. mimula*, and is a feature of other *Uperoleia* (Davies & Watson 1998). There are considerable differences in the length of the spiracle, that of *U. altissima* being intermediate between those of *U. mimula* and *U. lithomoda*.

The unusual tail bud stage in which the tail is better developed than the head was noted also by Moore (1961) in *U. laevigata* Kelerstein, 1867 and Davies & Watson (1998) in *U. talpa*.

Acknowledgments

This research was supported by the Department of Zoology, University of Adelaide and the Queensland Department of Environment and Heritage. We thank M. Tyler for critically reading the manuscript and the referees for their helpful comments.

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CHANGES IN A MANGROVE/SAMPHIRE COMMUNITY, NORTH ARM CREEK, SOUTH AUSTRALIA

*By Peri S. J. Coleman**

Summary

Coleman, P. S. J. (1998) Changes in a Mangrove/Samphire Community, North Arm Creek, South Australia. Trans. R. Soc. S. Aust. 122(4), 173-178, 30 November, 1998.
Use of a computer GIS package to study aerial photographs of North Arm Creek (1979-1993) confirmed previous studies suggesting a landward migration of the grey mangrove, Avicennia marina, but seaward progradation was also apparent. Samphire communities were reduced in area by nearly two-thirds, with the majority of the lost area overgrown by mangroves. At the same time samphires colonised unvegetated areas and some areas previously occupied by mangroves. From 1979-85 the area colonised by samphire was similar to the area lost, but was less from 1985-93. It is suggested that several factors are responsible for the changes in distribution.
Key Words: Avicennia marina, Halosarcia, Sarcocornia, mangrove, samphire, saltmarsh, temporo-spatial change, progradation, colonisation.

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KEY WORDS: *Avicennia marina*, *Halosarcia*, *Sarcocornia*, mangrove, samphire, saltmarsh, tempero-spatial change, progradation, colonisation.

Introduction

North Arm Creek drains from the Wingfield/Dry Creek area of Adelaide northwards into the mangrove zone of Barker Inlet (Fig.1). The zone comprises a seaward fringe of the grey mangrove *Avicennia marina* (Forst) Vierh. var *resinifera* (Forst) Bakh., backed by a salt marsh comprising mixed samphires of the genera *Halosarcia* P. G. Wilson and *Sarcocornia* A. J. Scott. The mangroves and samphires form bands of variable width on both banks of the creek.

The creek has been used for the reception of stormwaters, sewage effluent and trade wastes. The wet coastal ecosystem edging the creek has been considerably modified since European settlement. In the late 1800s seawall embankments were built along the mangrove/samphire interface, and the samphire zone was used as pasturage. Salt production on the eastern side of the creek began in 1934 and progressively much of the low lying area inland of the seawall embankment has been ponded. On the western side of the creek the low lying land behind the seawall became a municipal refuse tip. In the 1970s a series of groynes supporting power pylons was built through the mangrove/samphire zone abutting the creek.

The more recent changes have resulted in changes to the water flows and tidal dynamics in the area. In

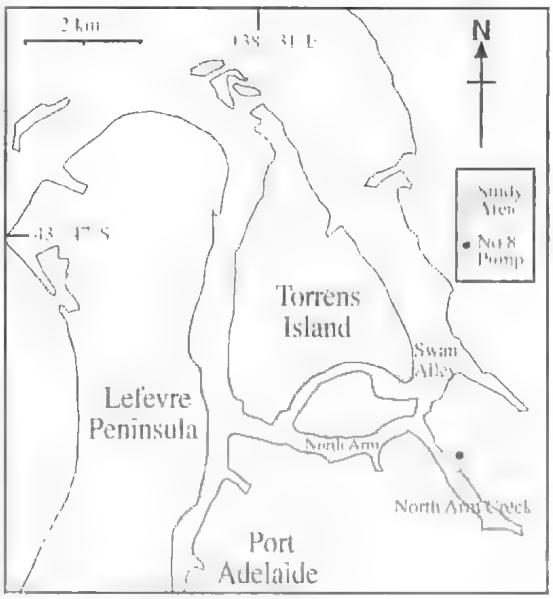


Fig 1. Map of the region.

1986 Bradley[1] recorded large scale dieback of both mangroves and samphires in the vicinity of the power pylon groynes and recent field inspections have revealed that the area is only slowly being recolonised.

Aerial photographs of North Arm Creek, taken between 1949 and 1993, show changes in the mangrove and samphire communities. Some changes are marked, such as areas of dieback, or the inland advance of mangroves. The use of Geographic Information Systems (GIS) technology has allowed a closer look at the changes in one small region of the

Delta Environmental Consulting, 12 Beach Road, St Kilda S. Aust. 5110.

[1] Bradley, P. (1986) Baseline Study and Preliminary Evaluation of ICI Solar Evaporation Ponds' Bitterns Discharge on the Mangrove Community, with Supplement. Report provided to ICI Australia, Adelaide. (Unpubl.)

North Arm Creek coastal wetland, the drainage area of the Dry Creek Saltfields' No. 8 Pump.

The area is bounded on the east by a seawall and on the west by North Arm Creek. Running centrally across the area is a small creek that has been formed by the discharge of bitterns (brine that remains after salt crystallisation is complete) from the saltfields. The No. 8 Pump and its supply drains are clearly visible on aerial photographs.

Previous studies

Burton (1982) studied mangrove development north of Adelaide to the River Light using aerial photographs covering the period from 1935-1982. He noted that the mangrove stands showed different directions of growth at the two extremities of the study zone. Generally the northerly mangroves were prograding (extending seawards) while the southerly mangroves near Swan Alley were retreating inland across the samphire flats. Burton's paper discusses the possible causes of this difference, in particular discussing terrigenous supply and relative sea-level rise (eustatic rise and land subsidence).

During 1985-6 Bradley[1] examined the mangroves in the vicinity of the No. 8 Pump on North Arm Creek. He used visual comparisons of aerial photographs of the area taken in 1979 and 1985. He pegged two transect lines across the area and mapped the distribution, health and age of the vegetation along these. Plastic 30 cm rulers were attached to the transect pegs to determine possible sedimentation patterns. The alignment of the substrate on the rulers was recorded.

A further study of the North Arm Creek to Swan Alley area was undertaken by Blackburn[2] in 1994. He used GIS techniques to ascertain distribution changes within the mangrove and samphire communities. Blackburn[2] did not physically visit the North Arm Creek, but the photographs he examined indicated both landward and seaward progradation of mangroves.

The present study re-examines the area reported by Bradley[1] (Fig. 2). The review of the area combines a GIS analysis of aerial photographs (1949-1993) with a ground survey using Bradley's[1] existing transects. The study was constrained by growth of mangroves making access difficult, loss of some sediment rulers and loss of transect pegs nearer the seaward fringe.

Materials and Methods

Department of Environment and Natural Resources 1:1480 scale enlargements of four aerial survey photographs dated 10 January 1949, 19 March 1979, 18 February 1985 and 8 December 1993 were manually digitised into a form suitable for use in the GIS mapping package TNTmips Lite. The three more recent photographs, dating from 1979 to 1993, were georectified using man-made structures on the neighbouring saltfield as control points, along with isolated mangrove (*A. marina*) trees that were identifiable through the series of photographs. The 1949 photograph shows a landscape so different from the present that georectification could only be accomplished by matching the angles of narrow 'borrow-pits' along the sea-wall, so data from it were only used in a general manner in the present study.

The principal components of the mapped area were defined as mangroves, samphires or neither (water or bare mud). An analysis of the limits of vegetation over each of two periods (1979-1985 and 1985-1993) was undertaken to try to determine what the dynamics of the vegetative change were.

Fieldwork in 1996 included finding the transect pegs placed by Bradley[1] in 1985. The vegetation along the two transects was recorded and its height measured to metres using a measuring tape. Readings were also recorded where sediment rulers were still in place.

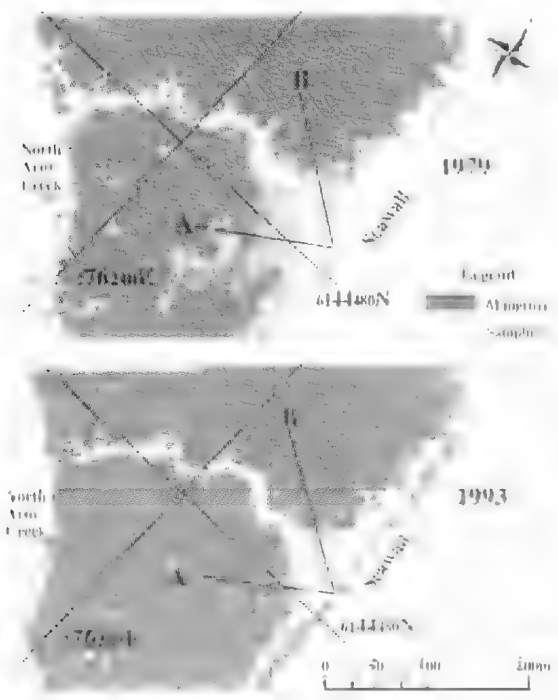


Fig. 2. The study area in 1979 and 1993.

TABLE 1. *General changes in the vegetation, 1979-1993.*

	Mar-'79	Feb-'85	Dec-'93	Change, '79-'93
Mangroves (m²)	73902	78608	88459	+14557
Samphire (m²)	14173	12769	5340	-8833
Vegetative cover (m2)	88075	91377	93799	+5724

TABLE 2. *Change rates of the principal components of the vegetation.*

	Area of each change class of the vegetation (m²)		Annual rate of change	
	1979-1985	1985-1993	1979-1985	1985-1993
Mangrove to mangrove (no change)	69175	76974	-	-
Samphire to mangrove	6202	6098	1034	762
Mangrove to samphire	2913	620	486	78
Neither* to mangrove	3520	3758	587	470
Mangrove to neither*	1240	588	207	74
Neither* to samphire	3876	1163	646	145
Samphire to neither*	1923	3988	321	499
Samphire to samphire (no change)	5993	2650	-	
Vegetative loss	3163	4576	527	572
Vegetative increase	7396	4921	1233	615
Rate of change in total vegetative cover			706	43

* "neither" indicates areas of bare mud or water

Because the *A. marina* trees had grown considerably during the 11 years since the transect pegs were placed, locating the pegs past the 80 m mark on Transect A and the 110 m mark on Transect B might possibly have resulted in damage to the mangal and so no data were collected beyond these points.

Results

Vegetation mapping

A comparison for the period 1979-1993 shows extension of the mangrove canopy, and a reduction in the area covered by samphires, with an overall increase in vegetated area (Table 1). As the study zone is delimited on the landward side by the seawall embankment, the gain must either be the overgrowing of previously bare mud patches, or some seaward accession.

The results of the analysis of the limits of vegetation from 1979-1985 and 1985-1993 are summarised in Table 2.

The largest change over the period was an increase of mangroves at the expense of the samphire community. However, the extension of both mangroves and samphires over bare mud and into water areas is also occurring, along with samphire colonisation of areas previously supporting mangroves. Erosion is occurring in some areas of samphire.

Samphire has given way to mangrove at their interface as the mangrove has extended inland. Almost the entire central samphire zone has been succeeded by mangroves and the trees have also occupied many of the creek lines as well as colonising the bare mud areas along the seawall embankment. Site visits in July and September 1996 revealed juvenile mangroves growing along the No. 8 Pump discharge channel and specimens more than 4 m high growing along the seawall within 40 m of the discharge point.

Some mangrove areas have been replaced by samphire or by bare mud. This has mainly occurred in the southern part of the study area but also along the bitterns discharge creek.

Along the seaward edge, progradation of mangroves is apparent along the entire length of the study zone. The extension is most marked in the southern areas, with a maximum advance of approximately 25-30 m in the 14 years from 1979-1993.

In the northern part of the study zone the seaward progression consisted mainly of infilling the many invaginations and embayments around isolated trees and the advance was between 10 and 15 m. The cause of the slower progradation of mangroves in the northern area is uncertain but the infilling of semi-enclosed areas suggests that low-water flow rates in the sheltered areas were conducive to sediment accretion, whereas the actual seaward fringe may have been exposed to stronger wave action.

The samphire community has also been extending, and has become established on previously bare mud; there are now samphires along the seawall within 15 m

TABLE 3. *Sedimentation readings along the transects.*

Distance along transect	A Transect			B Transect		
	1985 initial reading	1986 reading (change)	1996 reading (change)	1985 initial reading	1986 reading (change)	1996 reading (change)
0 m	5.2	6.3 (-1.1 cm)	na	5.2	6.3 (-1.1 cm)	na
10 m	6.6	8 (-1.4 cm)	3 (+5.0 cm)	4.5	4.6 (-0.1 cm)	7 (-2.4 cm)
20 m	4.3	5.2 (-0.9 cm)	4 (+1.2 cm)	4	3.8 (+0.2 cm)	na
50 m	8	7.5 (+0.5 cm)	na	7	6.2 (+0.8 cm)	na
100 m	6.1	6.1 (no change)	na	6.3	6.3 (no change)	5.5 (+0.8 cm)

Note 1: 1985 & 1986 readings from Bradley (1986)[1].
Note 2: Readings are the alignment of the substrate against 30 cm plastic rulers attached to the transect pegs. Zero is to the top of the ruler.

of the discharge point. As the creeks are being infiltrated by mangroves, new areas for samphire colonisation have appeared. Much of the new growth is along the seawall and to the north of the study area, where the ETSA groyne has altered the tidal circulation.

The bitterns discharge does not appear to have affected growth of samphires negatively, possibly because the species are adapted to surviving in high salinity regimes, but samphire has been eroded away in some areas along the bitterns discharge creek.

Transects

Figure 3 presents the 1985 and 1996 heights of the vegetation along Bradley's[1] existing transects and shows the maturation of young stands of mangroves and the new colonisation (by mangroves and samphire) of areas closer to the discharge point. The 1996 data were collected along the transects in September. The forests are now so dense that accessing the pegs is difficult and so the transects do not continue to the original 150 m point.

Sedimentation

The bitterns discharge creek has formed since the 1949 aerial photograph was taken and Bradley's[1] report expressed some concern that erosion might be occurring in this creek near the discharge point. He examined sedimentation patterns away from the immediate discharge point by attaching plastic rulers to the transect pegs and recording the relative height of the substrate at each location.

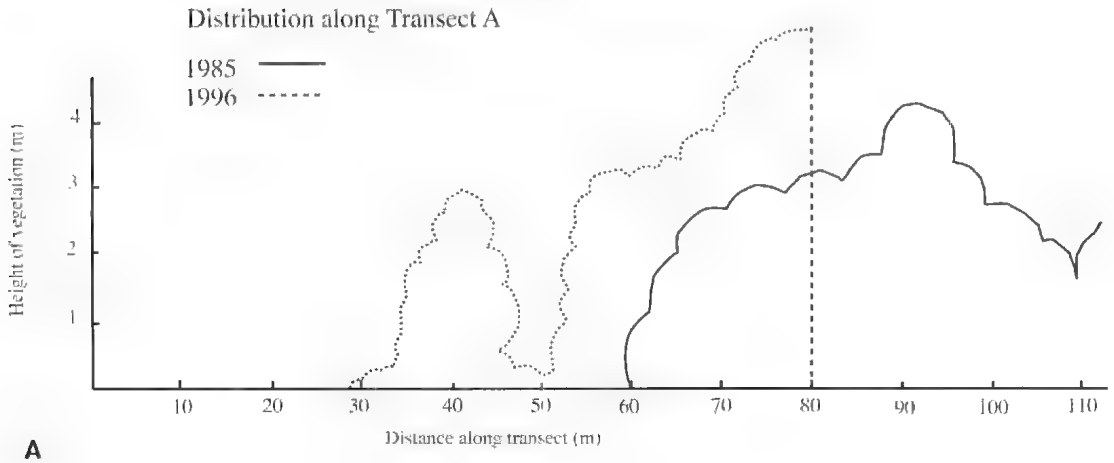
In response to Bradley's[1] finding during the initial observation period (1985-1986) that some erosion was occurring near the discharge point, saltfield personnel deposited concrete blocks in the drain to break up the flow. To determine the types of change that might have been occurring since 1985/86, the rulers were examined in September 1996 where they still existed. The few remaining sediment rulers indicated that the hydrology of the area may have changed. These 1996 readings are presented (Table 3) together with Bradley's[1] 1985 and 1986 readings.

The southern transect (Transect A) shows deposition to have occurred within 10 m of, and possibly closer to, the discharge point. The topography of the transect is smooth, with no creeks crossing it, so sedimentation may be relatively uniform across the area.

The northern transect has several small creeks crossing it, and the erosion/sedimentation pattern is more complex. The lack of rulers makes it difficult to interpret. However, the area closest to the discharge point has eroded somewhat over the last 10 years, forming a creek line. At low tide any discharge follows the existing creeks (slightly to the north before turning westerly), which have become more defined as mangroves have colonised the flats around them. The creek at 60 m is not recorded as having a sediment ruler on Bradley's[1] original sediment table, but a reading of the topographic plan of the transect done in 1985 shows the creek to be about 15 cm deep; the current reading is 14 cm. The ruler on the 100 m transect peg in the main forested area along the northern transect shows a small sediment gain.

Discussion

The detailed GIS study was possible because sufficient markers were visible in aerial photographs



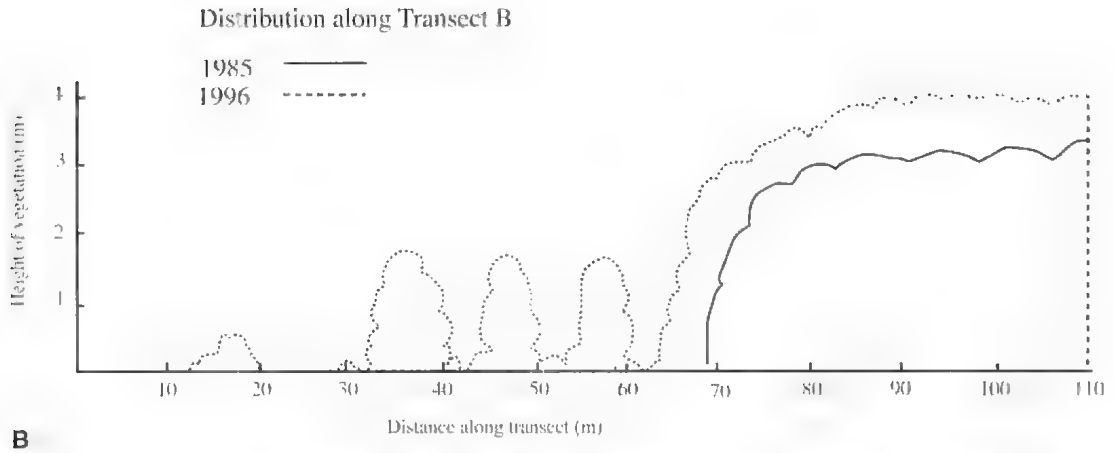


Fig. 3 A. Height distribution of vegetation along Transect A B. Height distribution of vegetation along Transect B.

to allow precise georectification. The 1949 photograph lacked some markers, reducing confidence in the precision of its georectification. However, this earlier photograph provides some insight into changes in vegetation patterns. The main differences include:

1. a larger area of vegetation in 1949 between the seawall and North Arm Creek; mangroves extended further out into the creek,
2. no creek in the location of the current bitterns discharge creek and the land inside the seawall was grazing land,
3. a wide expanse of samphires, with mangroves penetrating from North Arm Creek in towards the seawall along depressions, and
4. areas of mangrove dieback just behind the seaward fringe of mangroves.

The 1949 photograph showed that the mangroves in North Arm Creek were already retreating inland, so the seaward expansion visible in the post-1979 photographs must have started before 1979 but after 1949.

It is postulated that there has been an advance and regression of the mangroves with relatively small changes in water flow patterns. According to Hodgson *et al.* (1966)[3] North Arm Creek received the flow of effluent from the Islington Sewage Farm from 1881 through to the opening of the Bolivar Sewage Treatment Works in the 1960s.

During the operation of the sewage farm, nutrient rich water would have been released into North Arm Creek. The effluent may have supported algal blooms that could have caused the sporadic oxygen depletion in the waters of the creek recorded by Hodgson (1959)[4]. Induced anaerobic conditions are

reported to cause the asphyxiation death of areas of mangroves (Diop *et al.* 1997) and this may explain the areas of dieback visible in the 1949 photograph.

The changes in the mangrove/samphire communities visible in the 1979-1993 photographs confirm previous studies that have suggested that a landward migration of *A. marina* is occurring in the southern reaches of Barker Inlet resulting in a reduction of the area of samphires. However mangroves are also prograding seawards and covering a larger area, suggesting that the growth and distribution pattern is not a response to a single factor.

While land subsidence/sea-level rise (Burton 1982) may be responsible for the landward progradation, it cannot account for simultaneous seaward progradation. Sedimentation readings from the transect rulers indicate that sediment is accumulating over much of the area and that any lowering of the land surface is likely to be a widespread landform settlement (PPK 1992[5]) of the sedimentary coastal deposits rather than a lack of sediment supply or erosion *per se*, except in specific areas such as creek lines and patches of mangrove dieback.

Samphire communities over the period 1979-1993 were reduced in area by nearly $^2/_3$ despite the overall gain in vegetated area. Most of the lost area was overgrown by mangroves. However, the direction of change was not entirely one way, as samphires colonised areas previously occupied by mangroves plus areas of mud/water. During the earlier period, between 1979 and 1985, the area of new samphire growth each year nearly matched the area lost, so that there was an apparent loss of only 200 m^2 of samphire annually. The later period (1985-1993) showed a slowing in newly colonised areas of samphire. Although the area overgrown by mangrove or eroded each year remained about the same as in the earlier period, the rate of loss appeared higher (1000 m^2 annually) because there was little colonisation of new areas by samphire

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NEW SPECIES OF SEURECHINA (NEMATODA: SEURATIDAE) PARASITIC IN DASYURID MARSUPIALS FROM AUSTRALIA

*By L. R. Smales**

Summary

Smales, L. R. (1998) New species of Seurechina (Nematoda: Seuratidae) parasitic in dasyurid marsupials from Australia. Trans. R. Soc. S. Aust. 122(4), 179-184, 30 November, 1998.

Seurechina hobbsi sp. nov. is described from the stomach of Phascogale tapoatafa from Western Australia. It differs from S. chaneeti, the type and only described species, in being a larger worm (6-8 mm compared with 3.1-3.8 mm) with longer spicules (500-630 μm) for S. hobbsi compared with 185 μm for S. chaneeti. Seurechina spratti sp. nov. is described from the stomach and small intestine of Sminthopsis leucopus and Antechinus agilis and is most closely related to S. hobbsi from which it differs in having three lateral papillae extending into the caudal alae rather than two, oval rather than spherical eggs and the absence of a large projecting lip anterior to the vulva.

Key Words: Seurechina, nematodes, Seuratidae, Echinonematinae, Australia, Dasyuridae, marsupials.

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Seurechina hobbsi sp. nov. is described from the stomach of *Phascogale tapoatafa* from Western Australia. It differs from *S. chaneti*, the type and only described species, in being a larger worm (6-8 mm compared with 3.1-3.8 mm) with longer spicules (500-630 µm) for *S. hobbsi* compared with 185 µm for *S. chaneti*. *Seurechina spratti* sp. nov. is described from the stomach and small intestine of *Sminthopsis leucopus* and *Antechinus agilis* and is most closely related to *S. hobbsi* from which it differs in having three lateral papillae extending into the caudal alae rather than two, oval rather than spherical eggs and the absence of a large projecting lip anterior to the vulva.

Key Words: *Seurechina*, nematodes, Seuratidae, Echinonematinae, Australia, Dasyuridae, marsupials.

Introduction

Nematodes of the family Seuratidae are parasites of reptiles, birds, bats, rodents and Australian marsupials (Chabaud 1978). The family includes genera in which the mouth is dorso-ventrally elongated and flanked by paired lips and genera in which the mouth opening is triangular or hexagonal (Inglis 1967). All three genera occurring in Australian marsupials, *Seurechina*, *Inglechina* and *Linstowinema* spp., are contained in the subfamily Echinonematinae Inglis, 1967, characterised by a large mouth opening with no lip lobes, the anterior end of the body being swollen as a cephalic bulb bearing hooks, no pre-cloacal sucker on the male and a cloacal region covered by cuticular granulations. Although originally placed in the Schneidernematidae by Inglis (1967) the affinities of *Linstowinema* Smales, 1997 (formerly *Echinonema* Linstow, 1898 preoccupied) with the larvae of a species of *Seuratum* Hall, 1916 resulted in Quentin (1971) placing the Echinonematinae in the Seuratidae.

The genera *Linstowinema* and *Inglechina* Chabaud, Seureau, Beveridge, Bain & Durette-Desset, 1980, contain species with a triangular mouth opening on a swollen cephalic bulb bearing hooks. The monotypic genus *Seurechina* Chabaud, Seureau, Beveridge, Bain & Durette-Desset, 1980 however, has neither a triangular mouth opening nor a swollen cephalic bulb bearing hooks, although it does have other characteristics of the subfamily.

In this paper, two new species of *Seurechina* are described. The definition of the subfamily Echinonematinae is re-evaluated and the relationships between the genera discussed.

School of Biological and Environmental Sciences, Central Queensland University Rockhampton Qld 4702.

Materials and Methods

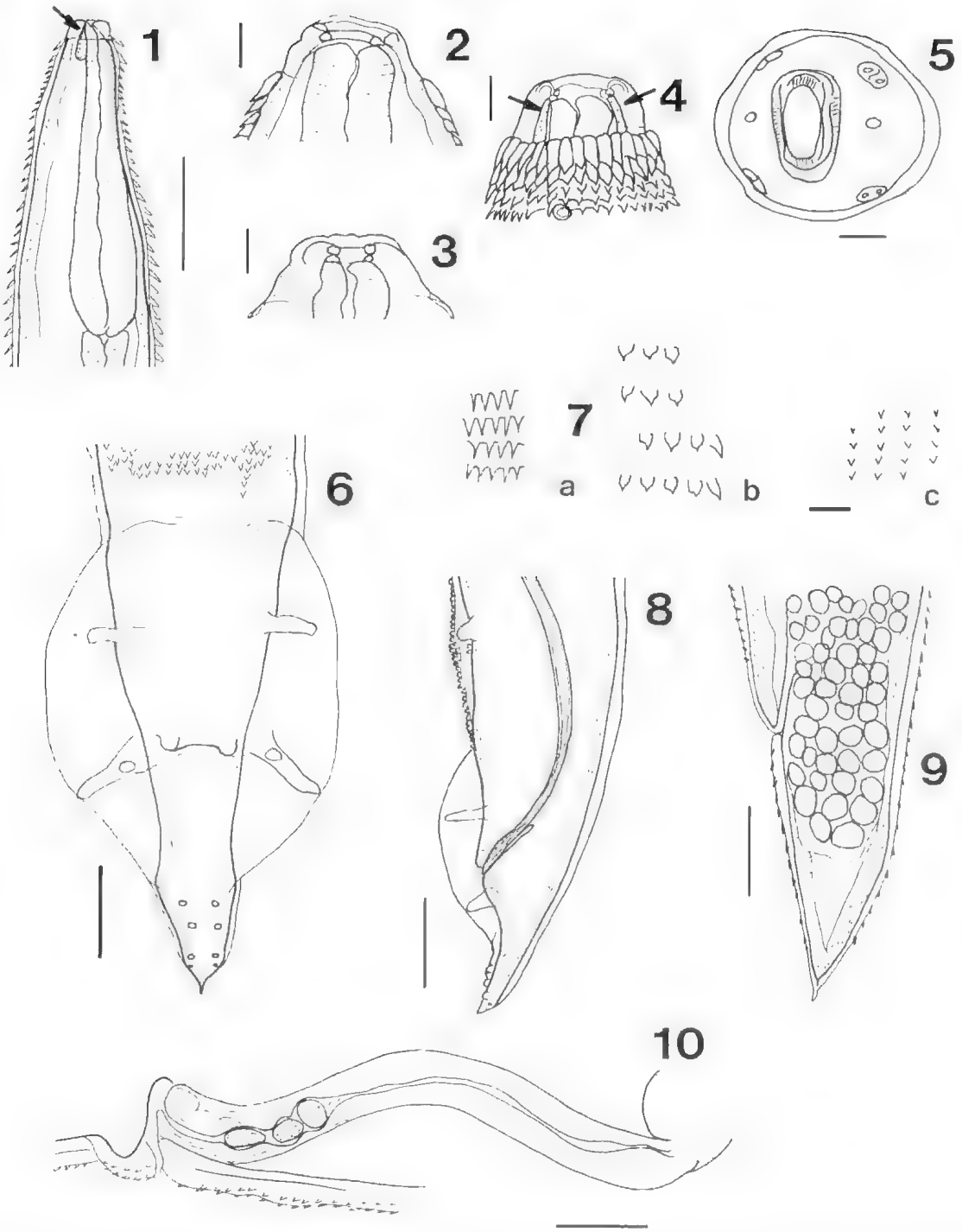
Nematodes collected from *Sminthopsis leucopus* and *Antechinus agilis* were fixed in hot 10% formalin and then stored in 70% ethanol. The preservation history of the specimens from *Phascogale tapoatafa* is unknown although they were stored in 70% ethanol. All nematodes were examined after clearing in lactophenol. Measurements for more than four specimens are given in micrometres, as the range followed by the mean in parentheses, and were made with the aid of an ocular micrometer or drawing tube and map measurer. Drawings were made with the aid of a drawing tube.

Type material has been deposited in the South Australian Museum, Adelaide (SAMA) and voucher specimens are held in the collection of CSIRO Wildlife and Ecology (CSIRO).

Seurechina hobbsi sp. nov.
(FIGS 1-10)

Types: Holotype ♂, allotype ♀, paratypes 4 ♂♂, 17 ♀♀, from stomach of *Phascogale tapoatafa* (Meyer, 1793), Manjimup (34° 15' S, 116° 09' E) WA, June 1992, coll. S. Rhind, SAMA AHC 31262, AHC 31263 and AHC 31264, respectively.

Material examined: From *Phascogale tapoatafa* types.



Figs 1-10. *Seurechina hobbsi* sp. nov. 1. Anterior end optical section, arrow indicating laminae (lateral view). 2. Cephalic end, optical section (lateral view). 3. Cephalic end, optical section (dorsal view). 4. Cephalic end, arrows indicating laminae (lateral view). 5. Cephalic end (*en face* view) 6. Male posterior end (ventral view). 7. Body spines. a. From oesophageal region. b. From mid body region. c. From posterior body region. 8. Male posterior end (lateral view). 9. Female posterior end (lateral view). 10. Vagina (lateral view). Scale bars = 200 µm 1; 10 µm 5; 100 µm 6, 8, 9, 10; 50 µm 7; 25 µm 2, 3, 4.

Description

Small worms, body with fine transverse cuticular annulations. Cephalic extremity without spines, remainder of body with up to 50 rows of spines (mid body of female) at each annulation, extending over ⅔ body dorsally to caudal alae ventrally of male, over entire body of female; spines becoming progressively smaller towards posterior end. Anterior extremity with mouth opening and oral cavity elongated dorso-ventrally, bearing 2 pairs double cephalic papillae, pair amphids; without lips or lip-like structures. Anterior end of oesophagus capped by 2 oval, dorso-ventrally aligned sclerotised rings, enlarged dorsally and ventrally. Oesophagus surrounded at anterior end by 4 pairs laminae 80 long. Oesophagus simple, claviform 1/12-1/13 body length. Nerve ring and secretory-excretory pore not seen, deirids large, conical, at level of 5th row of spines.

Male (n=5 unless otherwise stated) (Figs 1-8)

Length 6.0-7.0 (6.5 mm), width 300-370 (340). Oesophagus 502-569 (536) long. Deirids 77-94 (85) from anterior end. Spicules equal, similar, without alae, 500-630 (590) long, about 1/11 body length. Gubernaculum 50 (n=1) long. Two pairs lateral pre-cloacal papillae, 1 pair extending into lateral alae; 1 pair lateral ad-cloacal papillae extending into lateral alae; 3 pairs post-cloacal papillae, 1 pair phasmids well posterior to cloaca near tail tip. Peri-cloacal papillae not seen. Tail 130-170 (150) long.

Female (n=5 unless otherwise stated) (Figs 9, 10)

Length 7.0-8.0 (7.8 mm), width 510-580 (550). Oesophagus 536-670 (610) long. Deirids not seen. Vagina 550 (n=1) long; vulva opening behind a large projecting lip, 2600-3450 (3000) from anterior end. Monodelphic. Tail 215-280 (255) long. Eggs spherical 40-54 (47) diameter.

Etymology

The species is named after Mr R. Hobbs who has been helpful in providing material for this work.

Remarks

The method of fixation used for this material was not ideal, most specimens being contracted and distorted. It was impossible to determine the number and arrangement of the peri-cloacal papillae on male specimens but lateral pre-, ad- and post-cloacal papillae could be seen. Their number and arrangement are similar to those of the type and only other species, *S. chaneeti*. *Seurechina hobbsi*, 6-8 mm long, is a larger worm than *S. chaneeti*, 3.1-3.8 mm, with longer spicules (500-630 in *S. hobbsi* compared with 185 in *S. chaneeti*). The posterior ventral body spines cover the entire ventral body surface of male *S. hobbsi* whereas those of *S. chaneeti* terminate in two lateral bands (Chabaud *et al.* 1980, Fig. 1j p 430). In *S. hobbsi* the female tail (215-280) is longer than that of *S. chaneeti* (120), the spherical eggs are larger (47 diameter compared with 40x35), the vulva is pre-equatorial compared with a post-equatorial vulva in *S. chaneeti*. *Seurechina hobbsi* is monodelphic, whereas *S. chaneeti* is didelphic.

Seurechina spratti sp. nov
(FIGS 11-19)

Types: Holotype ♂, allotype ♀ from stomach of *Sminthopsis leucopus* (Gray, 1842), Sidlings Swamp South, Timbillica State Forest (37° 18' S, 149° 45' E), NSW, 25.x.83, coll. P. Haycock, SAMA AHC 31265 and AHC 31266, respectively.

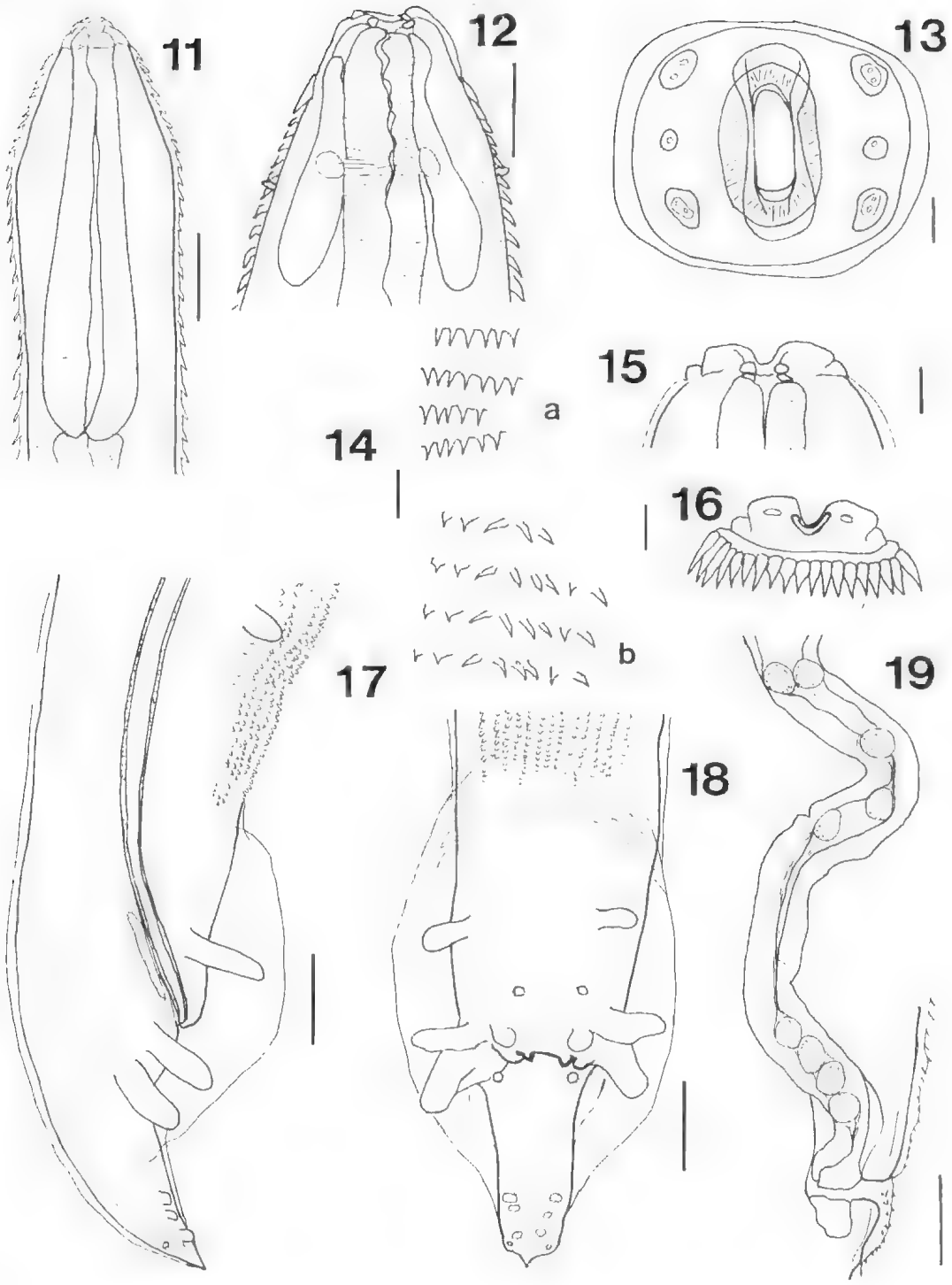
Material examined: From *Sminthopsis leucopus*: NSW, types; From stomach *Antechinus agilis* Dickman, Parnaby, Crowther & King, 1998: 20 ♂♂, 7 ♀♀, Sidlings Swamp North, Timbillica State Forest, NSW, 13.iv.87, 31.iii.88, coll. P. Haycock and B. L. Walter, CSIRO N2841, N2977.

Description

Small worms, body with fine transverse cuticular annulations. Cephalic extremity without spines, remainder of body with up to 46 rows spines (mid body of female) at each annulation, extending over ⅔ body dorsally to caudal alae ventrally, of male, over entire body of female; spines becoming progressively smaller towards posterior end. Anterior extremity with mouth opening and oral cavity elongated dorso-ventrally, bearing 2 pairs double sub-median cephalic papillae, pair lateral amphids; without lips or lip-like structures. Anterior end of oesophagus capped by 2 oval dorso-ventrally aligned sclerotised rings, enlarged dorsally and ventrally. Oesophagus surrounded at anterior end by 4 pairs laminae 110-165 long. Oesophagus simple, clav-iform, 1/10-1/12 body length, nerve ring anterior to deirids, deirids large, conical, at level of about 6th-7th row of spines; secretory-excretory pore not seen.

Male (measurements of holotype followed by measurements of 2 ♂♂ from *A. agilis*) (Figs 11, 12, 14, 17, 18)

Length 4.8, 4.5-6 mm; width 220, 270-340. Oesophagus 470, 355-470 long. Nerve ring 85; deirids 110, 80-110 from anterior end. Spicules equal, similar, without alae, 500, 550-600 long, about 1/9 body length. Gubernaculum not seen in holotype, 50-58 in specimens from *A. agilis*. Two pairs of lateral pre-cloacal papillae: 1 pair extending into lateral alae, 2 pairs lateral ad-cloacal papillae



Figs 11-19. *Seurechina spratti* sp. nov. 11. Anterior end, optical section (lateral view). 12. Cephalic end, optical section (lateral view). 13. Anterior end (*en face* view). 14. Body spines. a. From oesophageal region. b. From mid body region. 15. Cephalic end, optical section (dorsal view). 16. Cephalic end (dorsal view). 17. Male posterior end (lateral view). 18. Male posterior end (ventral view). 19. Vagina (lateral view). Scale bars = 100 μm 11, 19; 50 μm 12, 17, 18; 25 μm 14, 15, 16; 10 μm 13.

extending into lateral alae, 3 pairs peri-cloacal papillae; 3 pairs post-cloacal papillae, 1 pair phasmids well posterior to cloaca near tail tip. Anterior lip of cloaca with swollen lateral edges simulating pair of supplementary papillae. Tail 130, 165-200 long.

Female (measurements of allotype followed by measurements of 7 ♀♀ from *A. agilis*) (Figs 13, 15, 16, 19)

Length 6.8, 6.0 7.0 mm (6.9), width 470, 300-630 (400). Oesophagus 600, 380-570 (485 long). Nerve ring, secretory-excretory pore, deirids not seen. Vagina 340, 450 (n=1) long. Vulva 2950, 2975-3485 (3150) from anterior end. Monodelphic. Tail 240, 190-290 (250) long. Eggs oval 33-53 (47) long by 23-33 (27) wide.

Etymology

The species is named after Dr D. M. Spratt in recognition of his contribution to our understanding of the helminths of dasyurids.

Remarks

The secretory-excretory pore, tiny and concealed between body spines close to the anterior end, is often difficult to detect in echinonematines. In this species, the anterior ends of all worms from *A. agilis* were contracted, to a greater or lesser extent during fixation, obscuring the secretory-excretory pore. This may have occurred because the heads of the worms were embedded in the mucosa at post-mortem examination (D. M. Spratt pers. comm. 1998). Measurements of oesophageal length were also affected by the state of fixation, those of females from *A. agilis* being apparently shorter than that of the female from *S. leucopus*. Other measurements of specimens from the two hosts were consistent with their belonging to a single species.

Seurechina spratti most closely resembles *S. hobbsi* in size, length of spicules, distribution of body spines, position of vulva, being monodelphic and the length of the tail in both the male and female. All of these characters distinguish both *S. hobbsi* and *S. spratti* from *S. chaneti*. *Seurechina spratti* can be readily distinguished from both *S. hobbsi* and *S. chaneti* in having three rather than two large lateral papillae extending into the caudal alae. *Seurechina spratti* has oval eggs whereas those of *S. hobbsi* are spherical. *Seurechina spratti* lacks the large projecting lip anterior to the vulva found in *S. hobbsi*.

Seurechina chaneti was described from *Dasyurus hallucatus* Gould, 1842 from Koolan Island, off the coast of north Western Australia, *S. hobbsi* from *P. tapoatafa* (Meyer), 1793) from the southern mainland of Western Australia and *S. spratti* from *S. leucopus* (Gray, 1842) and *A. agilis* Dickman, Parnaby, Crowther & King, 1998 from southeastern New South Wales near the Victorian border. The differences between *S. chaneti* and the other two species may be explained, at least partly, by geographic separation. The similarities between *S. hobbsi* and *S. spratti* could be the result of a common ancestor in coastal Victoria and/or New South Wales, where the ranges of the three host species overlap (Sumner & Dickman 1998; Soderquist 1995).

Discussion

Inglis (1967) created the subfamily Echinonematinae to accommodate the genus *Echinonema* (sic), and placed it within the Schneidernematidae, rather than the Seuratidae because of its long simple spicules, short gubernaculum and a triradiate mouth opening without lips. The affinity of the Echinonematinae with the Seuratidae was discovered by Quentin (1971) and confirmed by Chabaud *et al.* (1980). They linked the presence of a simple, lipless, triradiate mouth opening, two pairs of doubled, submedian cephalic papillae, a very shallow cheilostome, and characteristic spines on the body cuticle of adults with the Seuratidae, and with larval development in *Seuratum* sp.

When the genus *Seurechina* was erected by Chabaud *et al.* (1980), these authors discussed its lack of cephalic hooks but placed it in the Echinonematinae along with the genera, *Linstowinema* (formerly *Echinonema* preocc.) and *Inglechina*, which also occur in dasyurid hosts. They did not comment upon the fact that *Seurechina* has an oval mouth opening nor upon the significance of the dorso-ventrally elongated cuticular structure between the oesophagus and the mouth opening. At present this chitinous cup, the walls of which are made up of two superimposed rings (Chabaud *et al.* 1980), is not interpreted as part of a cheilostome as defined by Inglis (1967) but rather as associated with an oesophastome. The four pairs of sublateral laminae found in the cephalic hypodermis were noted by Chabaud *et al.* (1980) as appearing to be dilatations of the lateral fields, possibly playing a role in a mechanism to hold the cervical spines steady when they are embedded in the gastric mucosa. These structures have not been found in other echinonematines (Chabaud *et al.* 1980; Smales 1997).

For the time being it is convenient to retain *Seurechina* within the Echinonematinae until the developmental relationships of the mouth, oesophagus and associated structures have been determined. The genus could either be moved to

the Seuratinae on the basis of a bilaterally symmetrical mouth opening, necessitating emendation of the diagnosis of the Echinonematinae to accommodate adult worms with an oval mouth opening, or, alternatively new groupings could be established.

Acknowledgments

I am grateful to R. Hobbs and D. M. Spratt who made available the specimens for this study, and I. Beveridge who criticised an early draft of the manuscript.

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SPIROXYS CHELODINAE BERRY, 1985 (NEMATODA: SPIRUROIDEA) AND CAMALLANUS CHELONIUS BAKER, 1983 (NEMATODA: CAMALLANOIDEA) FROM FRESHWATER TURTLES (PLEURODIRA: CHELIDAE) IN QUEENSLAND, AUSTRALIA

By Meryl A. Ferguson & Lesley R. Smales**

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Key Words. Spiroxys, Camallanus, nematode, freshwater turtles, Pleurodira, Australia.

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Introduction

Two major routes of origin for the nematode parasites of reptiles and amphibians have been suggested (Baker 1984). Groups with sporadic representatives in amphibians and reptiles are considered to have been captured from invertebrates or other vertebrates. The majority of nematodes, however, have evolved with their amphibian and reptilian hosts.

The spirurid family Camallanidae is an example of the first mode of origin. This family is suggested to have evolved in fish in tropical Asia, the region with the greatest diversity and richest camallanid fauna (Stromberg & Crites 1974). Buccal morphology suggests that the sub-family Camallaninae, including the genus *Camallanus* Railliet & Henry, 1915 is the most recently evolved and this is supported by the fact that 43% of *Camallanus* species occur in turtles, frogs and snakes (Stromberg & Crites 1974). In Australia there are no species known from freshwater fish or turtles, although *Serpinema octoroga*tus (Baylis, 1933) Petter, 1979 has been reported from a cryptodiran turtle, *Heosemys grandis*, in Malaysia (Baylis 1933).

The spirurid family Gnathostomidae, including the monogeneric subfamily Spiroxinae, is an example of the second mode of origin, i.e. evolving primarily in amphibians and reptiles (Baker 1984). The genus *Spiroxys* Schneider, 1866 probably originated in the holarctic or oriental regions as parasites of non marine chelonians of the Suborder Cryptodira (Berry 1985). *Spiroxys chelodinae* Berry, 1985 was first recovered from *Chelodina* sp. from Australia (South Australia, New South Wales, Queensland and Western Australia) and New Guinea (Berry 1985).

Extant turtles are grouped into two suborders on the basis of differences in neck vertebrae flexion during head retraction. All Australian turtles are members of the Suborder Pleurodira, a group characterised by sideways flexion of the neck vertebrae, which had a cosmopolitan distribution before the separation of Gondwanaland and Laurasia 120-100 million years ago (mya) (Pough *et al.* 1990). Their modern distribution is restricted to the Pelomedusidae of South Africa, the Podocnemidae of South America and the Chelidae of South America, New Guinea and Australia (Cogger 1996). All remaining freshwater and marine turtles are members of the Suborder Cryptodira, a group characterised by vertical flexion of the neck.

In this study, *S. chelodinae* was found in *Emydura krefftii* Gray in Eastern Australia. *Camallanus cheloniu*s Baker, 1983 is reported for the first time from the pleurodiran turtles *Emydura krefftii*, *Elseya latisternum* Gray, *Chelodina expansa* Gray and *C. longicollis* Shaw from Australia.

Materials and Methods

A total of 86 turtles, 1 *Chelodina expansa*, 8 *Elseya latisternum* and 77 *Emydura krefftii*, was taken from 6 Queensland catchments using a baited crab pot or

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Fig. 1. Distribution of the Nematodes *Camallanus chelonius* and *Spiroxys chelodinae* from *Emydura krefftii*, *Elseya latisternum* and *Chelodina expansa* to all localities sampled in Queensland from May 1994 to Dec 1997. ■ = *Camallanus chelonius*, ▲ = *Spiroxys chelodinae*.

Fig. 2. Photomicrograph of anterior of *Camallanus chelonius* from *Emydura krefftii*. Arrow indicates chitinous buccal ridges. Scale bar = 35 µm.

hland line. The following localities were sampled: Cooktown, 15° 28' S, 145° 15' E (2 *E. latisternum*); Cairns 16° 45' S, 145° 47' E (1 *E. latisternum*, 1 *Em. krefftii*); Townsville 19° 16' S, 146° 49' E (15 *Em. krefftii*); Proserpine 20° 24' S, 148° 35' E (5 *E. latisternum*, 10 *Em. krefftii*); Rockhampton 23° 22' S, 150° 32' E (1 *C. expansa*, 50 *Em. krefftii*) and Bundaberg 24° 52' S, 152° 21' E (1 *Em. krefftii*) (Fig. 1). The turtles were euthanased by cervical injection of at least 2.5 ml of Pentobarbitone sodium (Nembutal ®) per kg of turtle. The turtles were dissected then all organs were examined with the aid of a dissecting microscope. All nematodes found were washed in saline, fixed in near boiling 10% formalin then stored in 70% ethanol. Specimens from the Queensland Museum, Brisbane (QM) from *C. longicollis*, locality unknown (G207571), from *E. latisternum*, Mulgrave River, El Arish and Edmonton, Queensland (G213238, G213239, G213241), and from *Em. krefftii*, Mulgrave River, Queensland (G213240), were also examined for comparative purposes. Specimens for detailed microscopic examination were cleared in lactophenol. All measurements are in µm unless otherwise indicated and were made using an eyepiece micrometer. Voucher specimens, nos G213999-G214004, have been deposited in the Queensland Museum, Brisbane. Ecological terminology conforms to the definitions of Margolis *et al.* (1982).

Results

Adult *Spiroxys chelodinae* were recovered from granulomas in the stomach of 22 of 77 *Em. krefftii* examined (28.6% prevalence), but not from other species examined. Examination showed that the granulomas originated in the mucosal layer, but in some cases had extended into the submucosa and muscularis, and could be seen in the serosa on the external surface of the stomach. Encysted larvae were also found in the intestinal walls, mesenteries and liver, but numbers were not recorded. Adult *Camallanus cheloniis* (Fig. 2) were recovered from the small intestine of 19 of 77 *Em. krefftii* (24.7% prevalence), 7 of 8 *E. latisternum* (87.5% prevalence) and the single *C. expansa* examined. Of 77 specimens examined, 4 *Em. krefftii* were infected

TABLE 1. *Comparative body measurements, in μm unless otherwise stated, of male and female* Spiroxys chelodinae *from* Emydura krefftii *from Rockhampton, Queensland and the paratypes of* S. chelodinae, *(paratype measurements from Berry 1985).*
Means in parenthesis.

	Specimens from *Emydura krefftii*		Paratypes	
	Male n = 5	Female n = 5	Male n = 10	Female n = 10
Total length (mm)	18-25 (21)	18-27 (22)	7.3-27.3	7.9-28.6
Maximum width	429-516 (457)	374-563 (491)	179-545	171-860
Length pseudolabium	36-49.5 (42)	40 (n = 1)	31-65	23-65
Width pseudolabium	83-112 (101)	76 (n = 1)	53-114	44-136
Length muscular pharynx	335-415 (380)	308 (n = 1)	-	-
Length glandular pharynx	2500-3100 (2883)	2300 (n = 1)	-	-
Length pharynx (mm)	3.26 (n = 1)	2.61 (n = 1)	1.53-3.61	1.72-3.59
Nerve ring from anterior	536-714 (609)	489 (n = 1)	332-621	325-643
Secretory-excretory pore from anterior	901-1173 (1037)	-	429-810	410-891
Deirids from anterior	102-1224 (1099)	-	624-1334	644-1312
Length gubernaculum	115-168 (142)	-	108-295	-
Length spicule	1230-1630 (1455)	-	770-2410	-
Length tail	174-201 (189)	235-268 (254)	96-281	121-459

TABLE 2. *Comparative body measurements, in μm unless otherwise stated, of male and female* Camallanus chelonius *from* Elseya latisternum *from Queensland and* C. chelonius *from South Africa (measurements from Baker 1983).*
Means in parenthesis.

	Specimens from Queensland		Specimens from South Africa	
	Male n = 5	Female n = 5	Male n = 4	Female n = 4
Total length (mm)	9-14 (12)	13-24 (18)	10.6-16	17.2-23
Maximum width	181-409 (261)	340-516 (388)	-	-
Length buccal valves	101-127 (119)	134-151 (140)	-	-
Width buccal valves	107-147 (121)	134-168 (151)	-	-
Length muscular pharynx	429-502 (474)	489-594 (550)	506-595	519-575
Length glandular pharynx	608-1020 (822)	884-1054 (949)	838-950	931-1094
Nerve ring from anterior	231-241 (237)	235-288 (270)	219-281	275-281
Secretory - excretory pore from anterior	523 (n = 1)	-	-	
Deirids from anterior	-	663-765 (714)	-	
Vulva from anterior (mm)	-	7-10 (8)	-	8.4-12.4
Length right spicule	450-460 (455)	-	522-572	-
Length left spicule	450-460 (455)	-	325-384	-
Length tail	100-175 (132)	181-261 (214)	135-175	322-428

with both *C. chelonius* and *S. chelodinae*, 15 were infected with *C. chelonius* only (19.5% prevalence) and 18 were infected with *S. chelodinae* only (23.4% prevalence). *Spiroxys chelodinae* was found at Bundaberg, Rockhampton and Townsville only. *Camallanus chelonius* was found at all localities except Bundaberg, but this is probably because only one host specimen was examined at this locality.

Measurements of *S. chelodinae* from this study are in the range reported by Berry (1985) for *S. chelodinae* occurring in *Chelodina* sp. from Western Australia, South Australia, New South Wales, Queensland and Papua New Guinea (Table 1). The quality of the female specimens was such that few measurements could be taken, but no measurements were outside the range reported by Berry (1985).

Specimens of *C. chelonius* from this study conform to the description by Baker (1983) especially regarding buccal valve morphology and the number and arrangement of caudal papillae. The

Fig. 3. Drawing of tip of right spicule of *Camallanus chelonius* from *Emydura krefftii* showing difference from South African specimens of Baker (1983). Scale bar = 25 µm.

measurements of *C. chelonius* (Table 2) conform for the most part to those given by Baker (1983) although there are differences in spicule length (shorter in Queensland specimens) and female tail length (shorter in Queensland specimens). Also the slender, sharply pointed elongate process on the tip of the right spicule as figured by Baker (1983, Fig. 11, p. 163) appears to be shorter in the South African specimens than the Queensland specimens (Fig 3). However, these differences do not appear to be significant enough to propose a new species.

Discussion

Although specimens of *Elseya* and *Emydura* were examined for nematodes by Berry (1985), the sources of these hosts were not given. *Spiroxys chelodinae* was not recovered by Berry in either host genus but has now been found in *Em. krefftii* from Bundaberg, Rockhampton and Townsville. The finding of *S. chelodinae* in *Em. krefftii* in Central and Northern Queensland is a new host and locality record.

This is the first record of *C. chelonius* from Australian turtles. *Camallanus chelonius* has now known been reported from Australian, (this study) and South African (Baker 1984) pleurodiran turtles. The only other report of a camallanid from a pleurodiran turtle is *Serpinema amazonicus* (Riberio, 1941) Petter, 1979 from South America (Riberio 1941). All other *Serpinema* spp. are found in cryptodiran turtles, with each geographical region having its own species (Petter 1979).

Camallanus spp. have large numbers of unseparated buccal ridges (Fig. 2), while *Serpinema* spp. have smaller numbers of distinctly separated buccal ridges. The similarity of spicule morphology and distribution of caudal papillae between *C. chelonius* and *Serpinema* spp., however, indicates a close relationship (Baker 1983). Also, the buccal morphology of *S. amazonicus* and *C. chelonius* has been suggested to be intermediate between *Camallanus* and *Serpinema*. This suggests that *Serpinema* may have evolved first in pleurodirans (Baker 1983). A camallanid ancestor of *S. amazonicus* may have been captured by early cryptodiran turtles and radiated with the major cryptodiran radiation around 120-90 mya (Shaffer *et al.* 1997). The geographical distribution of *Serpinema* in cryptodiran turtles shows that the greatest diversity of fauna is in South and Central America and tropical Asia (Stromberg & Crites 1974). The finding of *S. amazonicus* in South America, an intermediary form between *Camallanus* and *Serpinema*, suggests that South America may have been a point of origin for this genus, which then moved into North America and Asia with its hosts.

The occurrence of *C. chelonius* in both Australian and South African pleurodires suggests that this species originated before the separation of Australia and South Africa, approximately 120-100mya. The close link between South Africa and South America as recently as 90 mya and the similarities between *C. chelonius*, *S. amazonicus* and other *Serpinema* spp. suggest a common origin for these groups.

Acknowledgments

Thanks go to C. J. Parmenter for assistance in turtle collection and identification, and to L. Cannon and K. Sewell of the Queensland Museum for providing access to museum specimens.

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Printed by Graphic Print Group, 10-14 Kingston Avenue, Richmond, S.A. 5033