

Transactions of the Royal Society of South Australia Incorporated

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**A REVISION OF THE ECHINONEMATINAE
(NEMATODA: SEURATIDAE) FROM BANDICOOTS
(MARSUPIALIA:PERAMELIDAE)**

*By LESLEY R. SMALES**

Summary

Smales, L. R. (1997) A revision of the Echinonematinae (Nematoda: Seuratidae) from bandicoots (Marsupialia:Peramelidae). Trans. R. Soc. S. Aust. 121(1), 1-27, 30 May, 1997.

The name Echinonema being preoccupied the genus here designated Linstowinema (nom. nov.) is redescribed. The type species *L. cinctum* comb. nov. is synonymous with *E. meridionalis* (sic) Chabaud, Seureau, Beveridge, Bain & Durette-Desset, 1980 but not with *E. cinctum* sensu Inglis, 1967, sensu Chabaud, Seureau, Beveridge, Bain & Durette-Desset, 1980. *L. warringtoni* sp. nov. is established for *E. cinctum* sensu Yorke & Maplestone, 1926 and sensu Chabaud, Seureau, Beveridge, Bain & Durette-Desset, 1980. *Linstowinema inglisi* comb. nov. is synonymous with *E. cinctum* sensu Inglis, 1967 and *E. inglisi* sensu Chabaud, Seureau, Beveridge, Bain & Durette-Desset, 1980 and is redescribed and four new species *L. latens* sp. nov., *L. tasmaniense* sp. nov., *L. maplestonei* sp. nov. and *L. peramelis* sp. nov. are described. Key Words: Linstowinema, Nematoda, Echinonematinae, Isoodon, Perameles, bandicoots, Marsupialia.

A REVISION OF THE ECHINONEMATINAE (NEMATODA:SEURATIDAE) FROM BANDICOOTS (MARSUPIALIA:PERAMELIDAE)

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The name *Echinonema* being preoccupied the genus here designated *Linstowinema* (nom. nov.) is redescribed. The type species *L. cinctum* comb. nov. is synonymous with *E. mefitalensis* (sic) Chabaud, Seureau, Beveridge, Bain & Durette-Desset, 1980 but not with *E. cinctum* sensu Inglis, 1967, sensu Chabaud, Seureau, Beveridge, Bain & Durette-Desset, 1980. *L. warringtoni* sp. nov. is established for *E. cinctum* sensu Yorke & Maplestone, 1926 and sensu Chabaud, Seureau, Beveridge, Bain & Durette-Desset, 1980. *Linstowinema inglisi* comb. nov. is synonymous with *E. cinctum* sensu Inglis, 1967 and *E. inglisi* sensu Chabaud, Seureau, Beveridge, Bain & Durette-Desset, 1980 and is redescribed and four new species *L. lotens* sp. nov., *L. tasmanienne* sp. nov., *L. maplestonei* sp. nov. and *L. peramelis* sp. nov. are described. All seven species can be differentiated as follows: *L. cinctum*, 14-18 rows of body hooks with undulating edges, oesophagus terminating at the level of the 8th-11th row; *L. warringtoni*, 9-13 rows of body hooks with undulating edges, oesophagus terminating at the level of the 9th-13th row; *L. inglisi*, 10-14 rows of body hooks with undulating edges, oesophagus terminating at the level of the 8th-9th row; *L. lotens*, 9-11 rows of body hooks with undulating edges, oesophagus terminating posteriorly to the 11th row; *L. tasmanienne*, 13-15 rows hooks without undulating edges, oesophagus terminating at the level of the 8th-10th row; *L. maplestonei*, 12-13 rows of body hooks without undulating edges, oesophagus terminating posteriorly to 13th row of hooks; *L. peramelis*, 11-12 rows of body hooks without undulating edges, oesophagus terminating at level of the 12th row. A key to the species is given. *Linstowinema cinctum* occurs in *Isodon obesulus*, *I. macrourus*, *Perameles nasuta* and *P. gunnii*; *L. inglisi* and *L. tasmanienne* only in *I. obesulus*; *L. lotens* only in *I. macrourus*; *L. warringtoni* in *I. macrourus*, *I. obesulus*, *I. viratus* and *P. nasuta*; *L. maplestonei* in *I. macrourus* and *P. nasuta* and *L. peramelis* only in *P. hogganville*.

KEY WORDS: *Linstowinema*, Nematoda, Echinonematinae, *Isodon*, *Perameles*, bandicoots, Marsupialia.

Introduction

When Linstow (1898a) described a thorny headed nematode occurring in a bandicoot host, he called it *Hoplocephalus cinctus*. He subsequently found that *Hoplocephalus* was preoccupied so he renamed the genus *Echinonema* later in the same year (Linstow 1898b). *Echinonema* has continued to be used for the genus until the present. *Echinonema* also is preoccupied, however, having been used previously for a genus of sponges by Carter in 1881; I now propose the name *Linstowinema* nom. nov.

The bandicoot host originally was identified as *Perameles obesulus*. Linstow (1898a) described and figured a nematode with seventeen rows of hooks on the cuticular dilation of the oesophageal region of the body and oesophagus terminating on a level with the 9th row of hooks. Yorke & Maplestone (1926) described a nematode with 12-13 rows of body hooks and a relatively short oesophagus which they identified as "*E. cinctum*". They neither gave measurements nor provided a figure to show the relationship between the posterior end of the oesophagus and the rows of body hooks of their

specimens. Yorke & Maplestone (1926) assigned the type and, at that time only species, *L. cinctum* (Linstow, 1898), to the spirurid family Rictulariidae. Later Johnston & Mawson (1939) reported *L. cinctum* from a native cat, *Dasyurus viverrinus*, near Sydney and re-evaluated the available information on the host species. They concluded that Linstow's original description was based on material collected from *Isodon obesulus* (Shaw, 1797) from the Upper Burnett River in Queensland while Yorke & Maplestone's redescription was based on material from a bandicoot, possibly *I. macrourus* (Gould, 1842), collected in the vicinity of Townsville. Johnston & Mawson (1939) further concluded that both Linstow (1898a) and Yorke & Maplestone (1926) were describing material from the same host, namely, *I. macrourus*. Since *I. obesulus* does not occur in the Burnett River region (Braithwaite 1955) but *I. macrourus* does (Gordon 1955), this would seem to be a reasonable conclusion.

The first confirmed record of *Linstowinema* from the bandicoot genus *Perameles* Geoffroy, 1803 is by Johnston & Mawson (1940) from *P. nasuta* Geoffroy, 1804 collected near Sydney. These authors noted differences in the male tail of the specimens they examined, from earlier descriptions by Linstow (1898a) and Yorke & Maplestone (1926) but, nevertheless, assigned the specimens to *L. cinctum*.

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Of the differences noted by Johnston & Mawson (1940), the number of papillae on the male tail is problematic as neither they, Linstow (1898a) nor Yorke & Maplestone (1926) described the number and placement of papillae found on other specimens of *Linstowinema*. The expansion of the male body around the cloacal region described and figured by Johnston & Mawson (1940) is also a significant structure. Although not mentioned by Linstow (1898a), Yorke & Maplestone (1926) or Chabaud *et al.* (1980) in their descriptions of *L. cinctum*, it is comparable to the male tail described by Chabaud *et al.* (1980) for *Echinonema* sp. (*sic*) occurring in *P. nasuta* from an unknown locality.

No further work was done on the genus until Inglis (1967) re-examined the relationships of the superfamily Scutarioidea. He redescribed *L. cinctum* from material collected from *I. obesulus* near Perth and placed the sole genus within a new subfamily, the Echinonematinae, located within the scutarioid family Schneidernematidae on the basis of the form of the mouth opening, distribution of cephalic papillae, long spicules and short gubernaculum. Subsequently, the affinities of the genus were clarified by Quentin (1970) and the Echinonematinae included within the Scutarioidae.

Chabaud *et al.* (1980) re-examined all the available material, established two new genera, *Seurechina* Chabaud, Seureau, Beveridge, Bain & Durette-Desset, 1980 and *Inglechina* Chabaud, Seureau, Beveridge, Bain & Durette-Desset, 1980 for worms from dasyurid marsupials and redefined *Echinonema* (now *Linstowinema*) and *E. cinctum* (*sic*) Linstow, 1898 *nee* Inglis, 1967. In their description of *L. cinctum* they noted difficulties in interpreting Linstow's original figure of 1898a, but decided that an oesophagus 1.8 mm long agreed with their definition of a "long" oesophagus, that is, one terminating at the level of the most posterior body hooks. Linstow's (1898a) figure clearly shows the oesophagus terminating at the level of the 9th of 17 rows of body hooks. Chabaud *et al.* (1980) also described three new species, namely, *E. edmondsi* (*sic*) from a dasyurid, *E. meridionalis* (*sic*) from *I. obesulus* and *E. inglisi* (*sic*) = *E. cinctum sensu* Inglis, 1967 also from *I. obesulus*. These authors also indicated that there were possibly additional species from the bandicoot genus *Perameles* but they had insufficient material for detailed descriptions.

The bandicoots (subfamily Peramelinae) are rabbit-sized omnivorous marsupials with long pointed heads and compact bodies. They forage by digging conical holes with their short forelimbs and explore these holes with their pointed snouts (Gordon & Hulbert 1989). *Perameles nasuta*, the long nosed bandicoot, is found along the east coast of Australia, from rainforest in the north through

wetland and dry woodland to areas with little ground cover in the south (Stoddart 1995). Its distribution overlaps with *I. macrourus*, the northern brown bandicoot which is found on the east coast, north of the Hawkesbury River and across the Northern Territory to the north of Western Australia, in areas of low ground cover including grassland, woodland and open forest (Gordon 1995). To the south, the distribution of *P. nasuta* overlaps that of *I. obesulus*, the southern brown bandicoot which is found across southern Australia in Western Australia, South Australia and Victoria, southern coastal New South Wales and Tasmania and prefers sandy soils with scrubby vegetation or low ground cover that are burnt out from time to time (Braithwaite 1995). The eastern barred bandicoot, *P. gunnii* Gray, 1838, now restricted to Tasmania, where its distribution overlaps with that of *I. obesulus*, and a few relict colonies in southern western Victoria, prefers open grassland, but may also forage in scrub and heathland (Seebeck 1995). The western barred bandicoot *P. bougainville* Quoy & Gaimard, 1824, now existing only on Bernier and Dorre Islands Shark Bay, Western Australia was previously found across much of the southern half of Australia (Friend & Burbidge 1995). The only other bandicoot species still extant, *L. uiratus*, the golden bandicoot, now survives only on Barron and Middle Islands off the coast of Western Australia, the north western Kimberley region and sub-humid parts of the Northern Territory, having been previously recorded from a much wider range of habitats (McKenzie *et al.* 1995).

In this study, all the available records and material collected from peramelids, including material dissected from hosts held in museum collections as well as five caught bandicoots, have been examined. This has provided sufficient material to reassess the taxonomic characters available to use for species discrimination, redesignate and redescribe the type species *L. cinctum* (Linstow, 1898) comb. nov. = *E. meridionalis* (*sic*) Chabaud, Seureau, Beveridge, Bain & Durette-Desset, 1980, redescribe and name *L. warrigami* sp. nov. = *E. cinctum sensu* Yorke & Maplestone, 1926; *sensu* Chabaud, Seureau, Beveridge, Bain & Durette-Desset, 1980 and *L. inglisi* Chabaud, Seureau, Beveridge, Bain & Durette-Desset, 1982 and distinguish the four additional new species from bandicoots that are described below.

Materials and Methods

Material and dissection records from 213 bandicoots were examined. This material was derived from three sources. Firstly, the gastrointestinal tracts of 56 bandicoots, collected between

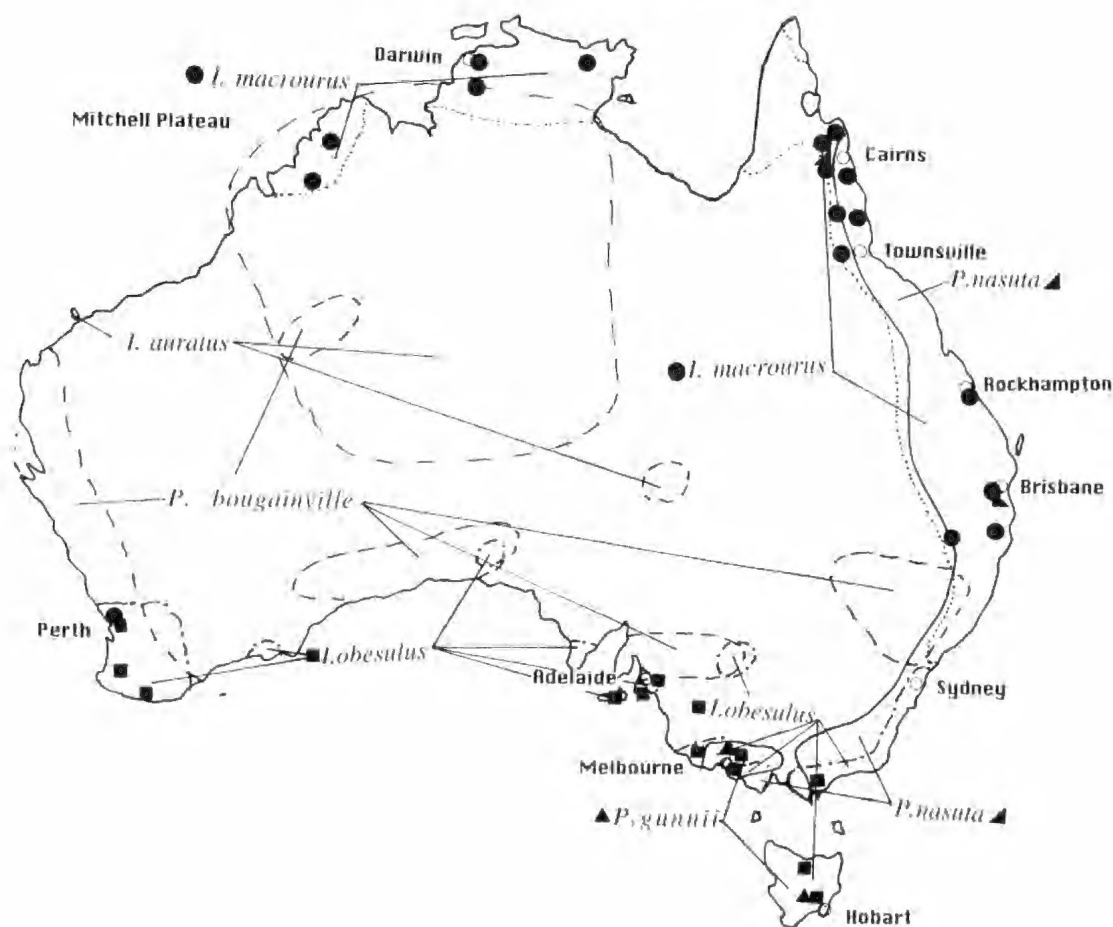


Fig. 1. Present and former distributions of Australian bandicoots (after Gordon & Hulbert 1989). The symbols indicate the localities where bandicoots were collected between 1989 and 1996. *Isodon auratus*, *I. macrourus*, ● *I. obesulus*, ■ *Perameles bougainville*, ▲ *P. gunnii*, ▲ *P. nasuta*, ▲.

1905 and 1988 and deposited in either the South Australian Museum (SAMA) or The Museum of Victoria (VM), were examined. These animals had probably been fixed in 5-10% formalin before being stored in 70% ethanol. The nematodes dissected from these hosts were stored in 70% ethanol. Secondly, 79 animals were either collected as fresh road kills or trapped alive, in spring-loaded wire box traps baited with peanut butter or a peanut butter, honey and oats mixture, between 1989 and 1996. The trapped animals were killed by intraperitoneal inoculation of euthanasia solution pentobarbitone sodium (Nembutal®). The digestive tract of each animal was examined under a dissecting microscope and any nematodes found were washed in normal saline, fixed in glacial acetic acid or hot or cold 10% formalin then stored in 70% ethanol. All the

available specimens of *Linstowinema* held in the Queensland Museum (QM), the Australian Helminthological collection of the SAMA (AHC), the Western Australian Museum (WAM), the CSIRO Division of Wildlife and Ecology (CSIRO) and The Natural History Museum, London (BM(NH)) were also examined. The preservation history of material from the former institutions is largely unknown but probably it was fixed in ethanol or formalin. Material from the CSIRO collection was fixed in hot 10% formalin. All material is now stored in 70% ethanol.

Specimens were examined from all the extant bandicoot species (number of bandicoots in parentheses) from 81 localities across Australia: *Isodon auratus* (5), *I. macrourus* (81), *I. obesulus* (85), *Perameles bougainville* (13), *P. gunnii* (6), *P. nasuta* (14), bandicoot, no species given (9). Host

TABLE 1. Distribution of bandicoot species examined for *Linshawinema* species by State or Territory. Where no specific locality has been given in the dissection record the location is listed as Australia.

Abbreviations: A, Australia; WA, Western Australia; NT, Northern Territory; SA, South Australia including Kangaroo Island and Franklin Island; Q, Queensland; NSW, New South Wales; V, Victoria; T, Tasmania.

Species	Location							
	A	WA	NT	SA	Q	NSW	V	T
<i>Isodon auratus</i>	2	-	3	-	-	-	-	-
<i>I. macrourus</i>	2	2	13	-	50	14	-	-
<i>I. obesulus</i>	2	19	-	30	-	9	13	12
<i>Perameles bongainville</i>	13	-	-	-	-	-	-	-
<i>P. gunnii</i>	-	-	-	-	-	-	2	4
<i>P. nasuta</i>	1	-	-	-	7	4	2	-
bandicoot	1	-	-	-	8	-	-	-
	21	21	16	30	65	27	17	16

distributions and the locations of the 79 animals collected since 1980 are given in Fig. 1. Details of all the localities where specimens were collected are listed in the descriptions of species given below. Latitudes and longitudes are provided for all localities that are listed in the Australian Gazetteer. The location, by state, of all hosts species examined, is given in Table 1.

Specimens were examined after clearing in lactophenol or beechwood creosote. Measurements were made with the aid of an ocular micrometer or drawing tube and map measurer. Measurements are given in μm , as a range from 10 specimens followed by the mean in parentheses, unless otherwise stated. All the new material has been deposited in the AHC.

Comments on taxonomic characters

Prior to 1980 only one species was recognized in the genus *Linshawinema* i.e. *Echinonema cinctum*. Then Chabaud *et al.* (1980) described four species, three from peramelid hosts and one from the dasyurid, *Dasyurus hallucatus* Gould, 1842. The species occurring in the dasyurid was distinguished from the others by having the first row of cephalic hooks longer than the second. The three species from bandicoots were differentiated from each other on the basis of the arrangement of hooks and spines on the body, the relative sizes and positions of papillae on the cloacal region, the relationship between the ventral spines and pre-cloacal papillae, the extent of small cuticular bosses surrounding the cloaca, the number of papillae on the tail of the male and the length of the oesophagus relative to the hooks on the dilated cuticular part of the anterior body associated with the region of the oesophagus.

Although Chabaud *et al.* (1980) recorded all the sensory organs on the male tail tip as pairs of papillae

Inglis (1967) had noted pairs of papillae and a pair of phasmids. Thus Inglis (1967) reported 3 pairs of papillae and a pair of phasmids on the tip of the tail of *Echinonema cinctum* (*sic*) and Chabaud *et al.* (1980) reported 4 pairs of papillae for the same species. Spicule morphology is uniform across the genus, differing only in total length and proportion of body length.

Chabaud *et al.* (1980) described the oesophagus as either "long", extending to the level of the last row of the body hooks or "short", terminating within the dilated cuticular region. Detailed examination of specimens for this study has shown that, although the termination of the oesophagus relative to the surrounding hooks is consistent within each species, the actual length of the oesophagus and its relationship to the body hooks may be difficult to determine. Specimens that are not completely straightened prior to or during fixation are problematic. It is difficult to tell the extent to which the oesophagus may have contracted into the neck region and the cuticle surrounding the oesophagus may also be contracted. Furthermore, the range of lengths of the oesophagus within populations of a species can also be quite variable, depending on the sizes and maturity of the worms being measured.

Both spines and hooks originate in the cuticle, but spines in this context, are defined as being small to tiny and rootless, whereas hooks consist of a thorn and a root anchoring the thorn within the cuticle. The smallest hooks may be only slightly larger than the largest spines. The relative lengths of the three rows of hooks on the cephalic bulb is a consistent character, but the dimensions of the hooks may vary markedly between individuals of the same species from the same individual host. Therefore hook dimensions are not useful for discriminating between species. The dimensions of the cephalic bulb are also

unreliable because of the potential variation caused by the extent of relaxation of the specimens prior to fixation and the method of fixation. Other consistent characters at the species level, however, are the number of rows of hooks on the dilated anterior body and the morphology of these hooks. In some species the roots of the hooks have undulating lateral edges giving them a "frilly" appearance; in others, the edges of the hooks are more or less plain.

Key to the species of *Linstowinema*

1. 1st row of cephalic hooks longer than 2nd row; parasites of dasyurids *L. edmondsi*
2nd row of cephalic hooks longer than 1st row; parasites of bandicoots (2)
2. Body hooks without undulating edges (3)
Body hooks with undulating edges (6)
3. Oesophagus terminates posterior to hooks on cuticular dilation of oesophageal region; male with 4 pairs of papillae, 1 pair of phasmids on tail tip (4)
Oesophagus terminates at or anterior to posterior row of body hooks on cuticular dilation of oesophageal region; male with 3 pairs of papillae, 1 pair of phasmids on tail tip (5)
4. Male with 8-10, female with 10-12 body hooks; male with 6 pairs cloacal papillae all same size, body spines extend along 90% of dorsal surface terminate at level of most anterior pair of lateral pre-cloacal papillae on ventral surface *L. latens*
Male with 11-13, female with 12-13 body hooks; male with 6 pairs of cloacal papillae, 1 pair lateral ad-cloacal papillae larger than other 5 pairs; body spines extend along 75% of dorsal surface terminate markedly anterior to cloacal papillae on ventral surface *L. maplestoni*
5. Male with ala-like expansions of body surrounding cloaca; with 6 pairs of cloacal papillae, 3 pairs of lateral cloacal papillae larger than 3 pairs of ventral cloacal papillae, spicule length about $\frac{1}{9}$ of body length; female with tail longer than 700 *L. tasmanianse*
Male without ala-like expansions of body, with 7 pairs cloacal papillae all same size, spicule length about $\frac{1}{16}$ of body length; female with tail shorter than 500 *L. perameles*
6. Male with 13-16, female with 14-18 rows of body hooks; male with ala-like expansions of body surrounding cloaca, body spines terminate at level of most anterior pair of lateral pre-cloacal papillae on ventral surface *L. cinctum*

Male with 9-12, female with 11-14 rows of body hooks; male without ala-like expansions of body surrounding cloaca, body spines terminate markedly anterior to cloacal papillae on ventral surface (7)

7. Male with oesophagus shorter than 1570, female with oesophagus shorter than 1850, male with 6 pairs of cloacal papillae, pair of lateral ad-cloacal papillae larger than other 5 pairs, 3 pairs of papillae, 1 pair of phasmids on tail tip, spicule length about $\frac{1}{15}$ of body length; female with tail shorter than 940 *L. inglisii*
Male with oesophagus longer than 1570, female with oesophagus longer than 1860; male with 6 pairs of cloacal papillae all same size, 4 pairs of papillae, 1 pair of phasmids on tail tip, spicule length about $\frac{1}{20}$ of body length; female with tail longer than 980 *L. warpingtoni*

Systematics

Order Ascaridida

Super family Securatoidea

Family Securidae

Subfamily Echinomematinae

Genus *Linstowinema* nom. nov.

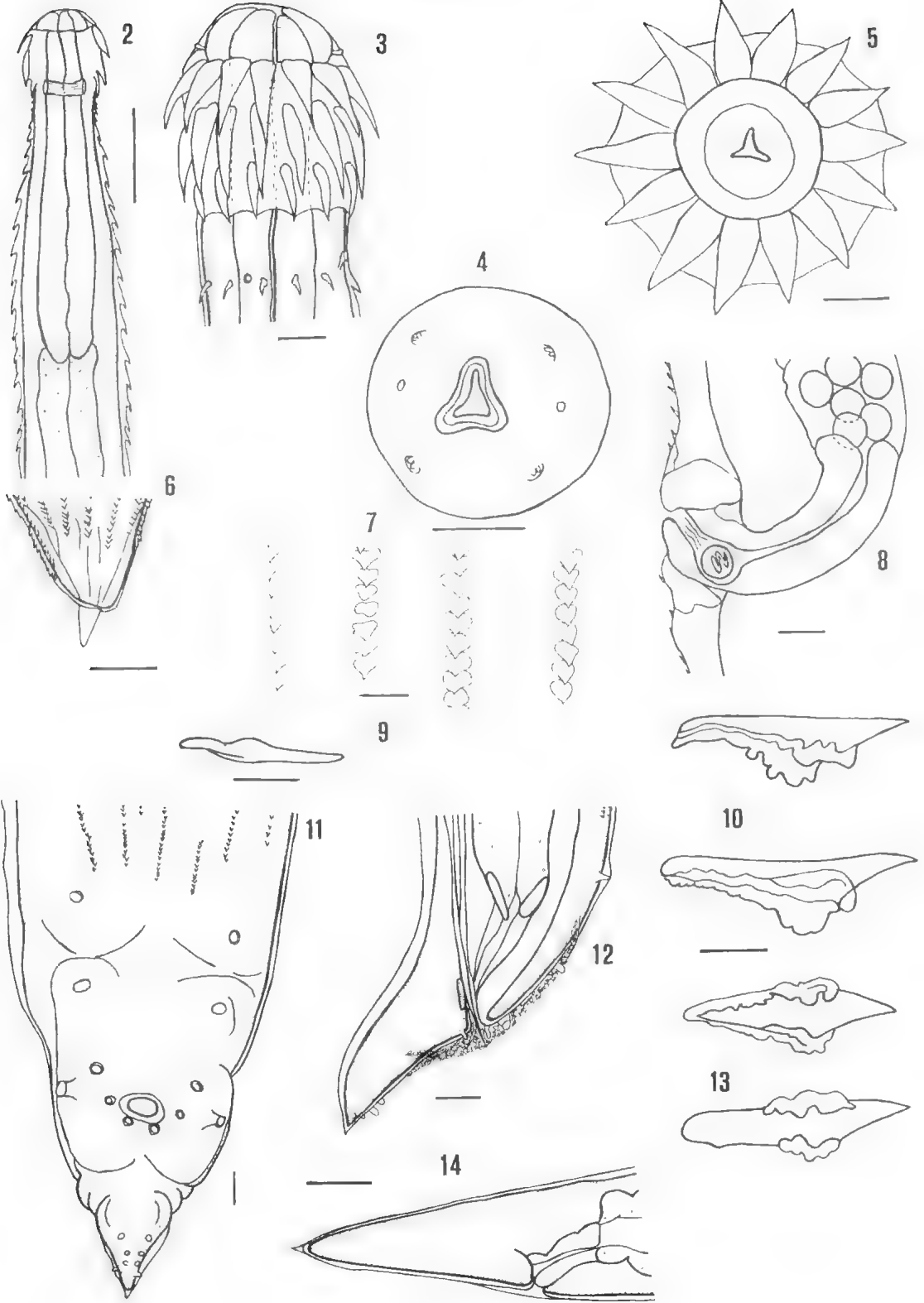
Type species: Linstowinema cinctum (Linstow, 1898) comb. nov.

Synonyms: *Hoplocephalus cinctus* Linstow, 1898, *Echinomema meridionalis* Chabaud, Seureau, Beveridge, Bain & Durette-Desset, 1980 *nee* *Echinomema cinctum sensu* Yorke & Maplestone, 1926; Inglis, 1967; Chabaud, Seureau, Bain & Durette-Desset, 1980 (in part).

Linstowinema (nom. nov.)

Generic diagnosis

Anterior end with cephalic bulb bearing 3 rows of 14-16 files of large hooks. Mouth opening triangular in outline, without lips or lip-like structures, with 4 pairs double cephalic papillae, 1 pair amphids, inner circle of sense organs on edge of mouth (see Inglis, 1967, Figs 6, 7). Neck with 2-11 rows of very tiny spines, 8-18 rows of 14-16 hooks surround an anterior cuticular dilation, associated with oesophageal region. Body with numerous rows of spines, number of files of spines increasing progressively towards mid body, decreasing towards posterior, continuing to caudal tip of female, terminating at about $\frac{1}{3}$ of length dorsally, anterior to cloaca ventrally on male. Short oesophagus simple, club shaped, surrounded by nerve ring at level of cephalic bulb. Deirids simple, conical, at level of 1st row of cervical hooks. Spicules long, equal, identical; small gubernaculum present. Vulva at mid-



region of body; monodelphic ovejector directed anteriorly. Parasites of Australian dasyurid and peramelid marsupials.

Linstowinema cinctum (Linstow, 1898) comb. nov.
(FIGS 2-14)

Synonyms: *Hoplocephalus cinctus* Linstow, 1898a: pp. 469-471, Figs 3-11. *Echinonema meridionalis* Chabaud, Seureau, Beveridge, Bain & Durette-Desset, 1980: pp. 436-438, Figs 4, 5A, D; Spratt, Beveridge & Walter, 1991: p. 26. *Echinonema cincta* Linstow, 1898b: p. 672; Johnson & Mawson, 1940: pp. 473-474, Fig 25; *nec* Yorke & Maplestone, 1926; *nec* Inglis, 1967; *nec* Chabaud, Seureau, Beveridge, Bain & Durette-Desset, 1980. *Echinonema cincta* Mackerras, Mackerras & Sanders, 1953: p. 62. *Echinonema* sp. 2. Chabaud, Seureau, Beveridge, Bain & Durette-Desset, 1980: p. 438, Fig. 5C, F; Spratt, Beveridge & Walter, 1991: pp. 23, 24 (in part).

Material examined

From *Isoodon obesulus* New South Wales: 1♀, fragment Lismore, (28° 49'S, 153° 16'E), April, 1965, AHC 4413. 4♂♂, Timbillica State Forest, (37° 19'S, 149° 43'E), 15.xii.1978, CSIRO N733; 14♂♂, 19♀♀, Sidlings Swamp North, Timbillica State Forest, (37° 17'S, 149° 45'E), 19.vii.1994, 17.iii.1994, 20.vii.1994, 23.iii.1994, CSIRO N4213, N4074, N4228, N4075; 85♂♂, 88♀♀, Sidlings Swamp South, Timbillica State Forest, (37° 18'S, 149° 45'E), 14.vii.1994, 20.vii.1994, CSIRO N4212, N4230.

From Victoria: 2♂♂, 14♀♀, Melbourne, (37° 47'S, 136° 59'E), 9.ix.1991, AHC 30292; 2♀♀, Monash University, (37° 47'S, 136° 59'E), no date, AHC 30293, 30294; 2♂♂, 2♀♀, Gorge Forest Road, (38° 21'S, 141° 36'E), Sept. 1962, AHC 30296; 2♂♂, 11♀♀, 7 fragments, no locality, no date, AHC 30295, 30298.

From South Australia: 1♂, 8♀♀, 6 anterior ends, Waitpinga, (32° 36'S, 138° 32'E), no date, AHC 4460; 3♂♂ 7♀♀, Scott Creek, (35° 04'S, 138° 42'E), 5.x.1992, AHC 30291; 3♂♂, 3♀♀, Myponga, (35° 23'S, 138° 28'E), May 1966, AHC 4446; Kangaroo Island, South Australia: 1♂, 2♀♀, Cape Willoughby, (35° 51'S 138° 08'E) 13.x.1990, AHC 30301; 2♀♀, Seal Bay, (36° 00'S, 137° 20'E), 4.i.1987, AHC 30304; 2♂♂, 2♀♀, Binowie, (37°

47'S, 136° 59'E), 5.viii.1987, AHC 30303.

From *Perameles gunnii* Tasmania: 6♂♂, 14♀♀, 4 fragments, Grove, (42° 59'S, 147° 07'E), AHC 30025; 3♂♂, 4♀♀, Kingston, (42° 59'S, 147° 18'E), 11.vii.1992, AHC 30056, 30057, 30058.

From *Perameles nasuta*: Queensland: 2♀♀, Wongabel State Forest, (17° 20'S, 145° 30'E) 9.vii.1982, CSIRO N1753; 1♀, Mt Nebo Road, (27° 23'S, 152° 47'E) 11.viii.1993, AHC 30316. New South Wales: 1♂, Epping, (33° 46'S, 151° 05'E), 11.viii.1993, AHC 30316; 1♂ Epping, (33° 46'S, 151° 05'E), 14.vii.1933, QM GL 12048; 3♂♂, 2♀♀, Sydney, (33° 50'S, 151° 15'E), no collection data, AHC 1820; 1♀, Nudgee State Forest, (37° 26'S, 149° 54'E), 13.ii.1978, CSIRO N493.

Description

Cephalic bulb with 3 rows of 14 (male) or 16 (female) files of hooks. 2nd row longest. 3rd row shortest (Fig. 3); neck with 5-9 rows of tiny spines; cuticular dilation of oesophageal region bearing 13-18 rows of 14 (male) (Fig. 2) or 16 (female) files of body hooks; 1st and last rows smallest, 4th-7th rows largest; roots of hooks with undulating edges (Figs 10, 13); remainder of body with up to 36 (male) or 54 (female) small spines at each annulation, over whole body of female; extending over $\frac{3}{4}$ of dorsal surface, terminating about 400 anterior to cloaca, almost reaching level of anterior pair of caudal papillae, on ventral surface of male body (Fig. 7). Oesophagus simple, club shaped, terminating about level with 8th - 11th row of hooks, within the anterior cuticular dilation; $\frac{1}{8}$ to $\frac{1}{10}$ body length (Fig. 2). Nerve ring surrounding oesophagus within cephalic bulb; secretory-excretory pore in neck; deirids conical, at level of 1st row of body hooks.

Male: Length 12-22 (14.8) mm, width 460-730 (600). Cephalic bulb 260-490 (395) long by 325-420 (380) wide; cephalic hooks 1st row 145-225 (170), 2nd row 170-235 (200), 3rd row 104-145 (130) long. Oesophagus 1445-2040 (1790) long, cuticular dilation bearing 13-16 rows body hooks. Deirids 520-630 (590), nerve ring 320-420 (375), secretory-excretory pore 500-530 (550) (n=3) from anterior end. Spicules equal, similar, without alae, 935-1150 (1035) long, about $\frac{1}{14}$ body length. Gubernaculum short, simple, subtriangular 60-63 (n=5) long (Fig. 9). Nine pairs caudal papillae: 3 pairs ventral and immediately pre-, ad- and post-cloacal respectively,

Figs 2-14. *Linstowinema cinctum* (Linstow, 1898). 2. Anterior end, optical section (lateral view). 3. Cephalic end (lateral view). 4. Cephalic end (*en face* view). 5. Cephalic end male, optical section at level of first row of hooks (*en face* view). 6. Female tail tip (lateral view). 7. Male posterior body spines (ventral view). 8. Vagina (lateral view). 9. Gubernaculum (lateral view). 10. Body hooks (lateral view). 11. Male tail (ventral view). 12. Male tail (lateral view). 13. Body hooks (lateral view). 14. Female tail (lateral view). Scale bars = 500 µm 2; 100 µm 3, 4, 5; 50 µm 6, 8, 11, 12; 25 µm 7, 9, 10, 13; 250 µm 14.

1 pair lateral ad-cloacal, 2 pairs lateral pre-cloacal; all same size, 3 pairs papillae, pair phasmids well posterior to cloaca, near tail tip (Fig. 11). Cloacal region with small cuticular bosses; ala-like expansion of body anterior and posterior to cloaca (Fig. 11). Tail 310-450 (365) long (Fig. 12).

Female: Length 16-22 (20) mm, width 800-1035 (880). Cephalic bulb 455-580 (505) long by 455-600 (500) wide; cephalic hooks 1st row 180-235 (210), 2nd row 220-265 (245), 3rd row 130-180 (155) long. Oesophagus 1785-2125 (1900) long; cuticular dilation bearing 14-18 rows body hooks. Deirids 150-780 (625), nerve ring 440-520 (470), secretory-excretory pore 520, 585 (n=2) from anterior end. Vulva 7140-10370 (8830) from anterior end (Fig. 8). Vagina about 300 long (n=1). Tail 985-1120 (1050) long (Figs 6, 14). Eggs ovoid, 45-54 (48) long by 36-51 (43) wide.

Type host

Perameles nasuta Geoffroy, 1801

Type locality

Sydney, Australia

Site in host

Small intestine

Type specimen

Neotype AHC 1820

Remarks

The present location of the material described by Linstow as *Hoplocephalus* then renamed *Echinonema* is unknown. Yorke & Maplestone (1926) and Chabaud *et al.* (1980) neither gave a location for the type material nor indicated whether they had examined it. Linstow was working in Göttingen in 1898 but neither *Echinonema* nor *Hoplocephalus* is listed under specimens held in the Zoologisches Museum der Humboldt Universität, Berlin. This Museum does, however, list holdings of other type specimens from Linstow. The specimens are not held in the parasite collections of the BM (NH), the International Institute of Parasitology, St Albans, or the US National Museum Parasite Collection in Beltsville.

The type host was given by Linstow (1898a) as *Perameles obesulus*, one of two bandicoot species collected by Richard Semon. These species were identified by Romer (1901), using the catalogue of Thomas (1888) in the British Museum, as *Perameles obesulus*, from Burnett River and *P. macrura* from Cooktown, with measurements being given for *P. macrura*. *Perameles macrura* is formally listed as a synonym of *Isodon macrourus* (Mahoney & Ride

1988) but *P. obesulus* is not. This is surprising because the taxonomic status of *P. obesulus* was discussed by Mackerras & Mackerras (1960) who indicated that *Perameles obesula* = *Didelphis obesula* = *Isodon obesulus*, but that since the northern limit of distribution of *Isodon obesulus* is near Sydney, bandicoots recorded as *I. obesulus* from Queensland should be referred to as *I. macrourus*, the species occurring from north Queensland to northern New South Wales.

Yorke & Maplestone (1926) list the type host as *Perameles obesula*. Johnston & Mawson (1939) decided that since Yorke & Maplestone had drawn an original figure their material came from Townsville in northern Queensland and stated that Linstow's material from *Isodon obesulus* came from Upper Burnett River also in Queensland. On that basis, Chabaud *et al.* (1980) concluded that the host of both the Linstow material and the Yorke & Maplestone material was *Isodon macrourus*, the northern brown and not *I. obesulus*, the southern brown bandicoot.

This does not, however, explain why Romer (1901) in his identification of the bandicoots collected by Semon lists them as two separate species rather than as *Perameles macrura* now *Isodon macrourus*. The catalogue of Thomas (1888) however, does list *P. nasuta*, so the Upper Burnett River bandicoots were probably *I. macrourus*.

Chabaud *et al.* (1980) noted that 1.8 mm, the measurement given for the length of the oesophagus by Linstow (1898a), was similar to measurements of specimens examined by them that had been collected from *I. macrourus* from northern New South Wales through to northern Queensland. In particular, these specimens had the oesophagus terminating at about the level of the posterior end of the cuticular dilation, a character they described as a "long oesophagus". Yorke & Maplestone (1926) did not indicate the length of the oesophagus relative to the rows of body hooks on the cuticular dilation but they described 12 or 13 "circles" of 14 to 16 rows of hooks. Two specimens collected by Nicoll in 1915, currently held in the BM(NH), which could possibly be the material described by Yorke & Maplestone (1926) and redescribed below also have the "long oesophagus" described by Chabaud *et al.* (1980). The specimens described by Linstow (1898a) are drawn and labelled as having 17 "circles" of hooks with the oesophagus terminating at the level of the 9th row of hooks. These characters are consistent, not with *E. cinereum sensu* Chabaud *et al.* (1980) but with specimens described by Chabaud *et al.* (1980) as *E. meridionalis*, occurring in the southern brown bandicoot *Isodon obesulus* collected in South Australia.

In a re-examination of the material described by Chabaud *et al.* (1980) as *E. meridionalis*, together

with specimens collected from long-nosed and barred bandicoots for this study, it was found that all specimens had 14-18 rows of body hooks and the oesophagus terminated at the level of the 8th-11th row of hooks. Measurements of the oesophagus ranged from 1445 to 2040 for males and 1785 to 2125 for females, also consistent with the measurements given by Linstow (1898a).

Johnston & Mawson (1940) described three females and two males obtained from the intestine of the long nosed bandicoot *P. nasuta* collected in Sydney and attributed these to *E. cinctum*. They described and figured differences in the male tail, namely an expansion of the body surrounding the cloaca, similar to, but not transparent, as are caudal alae Chabaud *et al.* (1980) figured the posterior end of a male which they designated *Echinonema* sp. 2 from *P. nasuta* registered in the AHC as 1820. They commented that their specimens were comparable with those described by Johnston & Mawson (1940). Neither group described the anterior ends of the worms they examined. The only material registered in the SAMA which might be the original Johnston & Mawson specimens is AHC 1820. The morphology of the anterior ends of these worms, 13-18 body hooks, the oesophagus terminating level with the 9th-11th row of hooks, is consistent with *E. meridionalis sensu* Chabaud, Seureau, Beveridge, Bain & Durette-Desset, 1980.

Chabaud *et al.* (1980) did not comment on the presence or absence of an expansion to the cloaca on their specimens but contrast *E. meridionalis* with *Echinonema* sp. 2 (see Chabaud *et al.* 1980, p. 438, Fig. 5) stating that *Echinonema* sp. 2, was comparable with the Johnston & Mawson (1940) description.

A re examination of all the available specimens of *E. meridionalis* (*sic*) and *Echinonema* sp. 2 (*sic*) has failed to show any significant differences between them. Such differences as do exist can be attributed to the fact that Chabaud *et al.* (1980) were dealing with a mixed infection of two species, namely *L. cinctum* and *L. warringtoni* (described below) occurring in the material collected from Waitpinga and Myponga. The male *L. cinctum* in this population were at the small end of the size range and oesophageal length varies with worm length and maturity.

The description by Linstow (1898a) of *H. cinctus* is congruent with the revised description of material designated *E. meridionalis* by Chabaud *et al.* (1980). The description by Yorke & Maplesone (1926) of specimens from *L. macrurus* and identified as *E. cinctus*, is congruent with *E. cinctum sensu* Chabaud, Seureau, Beveridge, Bain & Durette-Desset, 1980 *non* Linstow, 1898. Therefore, I designate a specimen from AHC 1820 as the neotype of *L. cinctum*.

Linstowinema cinctum (Linstow, 1898) most closely resembles *L. inglisi* (re-described below) in that the oesophagus is relatively short in relation to the number of rows of hooks, ending within the cuticular dilation. The males of both species have 3 pairs of caudal papillae and spicules $\frac{1}{10}$ - $\frac{1}{15}$ body length. *Linstowinema cinctum* can be distinguished from *L. inglisi* in having 13-16 (male) and 14-18 (female) body hooks compared with 10-12 and 12-14 in *L. inglisi*. Although the oesophagus is relatively short it is, however, longer than in *L. inglisi*, being $\frac{1}{6}$ body length in male *L. cinctum* compared with $\frac{1}{10}$ body length in *L. inglisi*. The pair of lateral ad-cloacal papillae is no larger than the other pairs of ventral papillae in *L. cinctum* but is larger in *L. inglisi* (see Inglis 1967 Fig. 9). The ala-like expansion of the body surrounding the cloaca of *L. cinctum* is not found on *L. inglisi* (see Inglis 1967 Fig. 9). The body spines of *L. cinctum* only cover $\frac{1}{2}$ of the dorsal body surface but cover $\frac{3}{4}$ of the dorsal body surface of *L. inglisi*. Eggs of *L. cinctum* differ from those of all other species in that they are ovoid rather than almost spherical.

The material from *L. obesulus* from South Australia described by Chabaud *et al.* (1980) as *L. meridionalis* was found to be a mixed infection of *L. cinctum*, females with up to 18 rows of body hooks, oesophagus terminating at about the level of the 9th-11th row) and *L. warringtoni* (females with up to 13 rows of body hooks, the oesophagus terminating about the level of the 10th-13th row) described below. A comparison of the measurements given by Chabaud *et al.* (1980) and the specimens examined for this study reveal that the males they measured were smaller in size, the oesophagus, spicules and tail were shorter than in the specimens examined for this study. The females, however, were within the same size range as for this study and the comparative measurements are more consistent.

The material dissected from the southern brown bandicoot collected at Scott Creek included some females up to 36 mm long. These were larger than the specimens from South Australia studied by Chabaud *et al.* (1980), (up to 27 mm long), from eastern barred bandicoots from Tasmania, (up to 22 mm long), and from long-nosed bandicoots from Tasmania, (30-32 mm long). Other variations observed between female specimens collected in different hosts and localities in the present study and those of Chabaud *et al.* (1980) included the oesophagus longest in southern brown bandicoots from Scott Creek (1853-2380), and shortest in southern barred bandicoots from Myponga and Waitpinga (1100); the tail longest in eastern brown bandicoots from Tasmania (986-1122) and shortest in southern brown bandicoots from Scott Creek (884-986), and the vulva slightly more posterior

(10,030-14,450) in southern brown bandicoots from Scott Creek than in eastern barred bandicoots from Tasmania (7140-10,370) or southern brown bandicoots from Waitpinga (10,800). The eggs from the Scott Creek specimens were smaller than those from Waitpinga or Tasmania, being 33 by 36, 32 by 45, and 43 by 48 respectively. These differences could be either variations between populations within the species, or the result of contraction during fixation.

Linstowinema cinctum, originally described as occurring in *P. obesula* (srs) from Queensland is now recorded as also occurring in *L. obesulus*, *P. nusula* and *P. ginnii*. The geographical range now includes Victoria, New South Wales, South Australia, including Kangaroo Island, and Tasmania as well as northern and southern Queensland. The record of *L. cinctum* in *L. obesulus* from Lismore, New South Wales, AHC 4413 is a dubious host record because the southern brown bandicoot is not found nearly as far north as Lismore (Braithwaite 1995). In all probability the host was *L. macrurus*.

Linstowinema warringtoni sp. nov.
(FIGS 15-24)

Synonyms: *Echinonema cincta* sensu Yorke & Maplestone, 1926: pp. 347-348 *new* Linstow, 1898; *new* Inglis, 1967; sensu Munday & Green, 1972: p. 10 (in part); sensu Chabaud Seureau, Beveridge, Bain & Durelle-Desset, 1980: p. 435-436 (in part); sensu Spratt, Beveridge & Waller, 1991: p. 25 (in part). *Echinonema emman* sensu Johnston & Mason, 1952: p. 33

Material examined

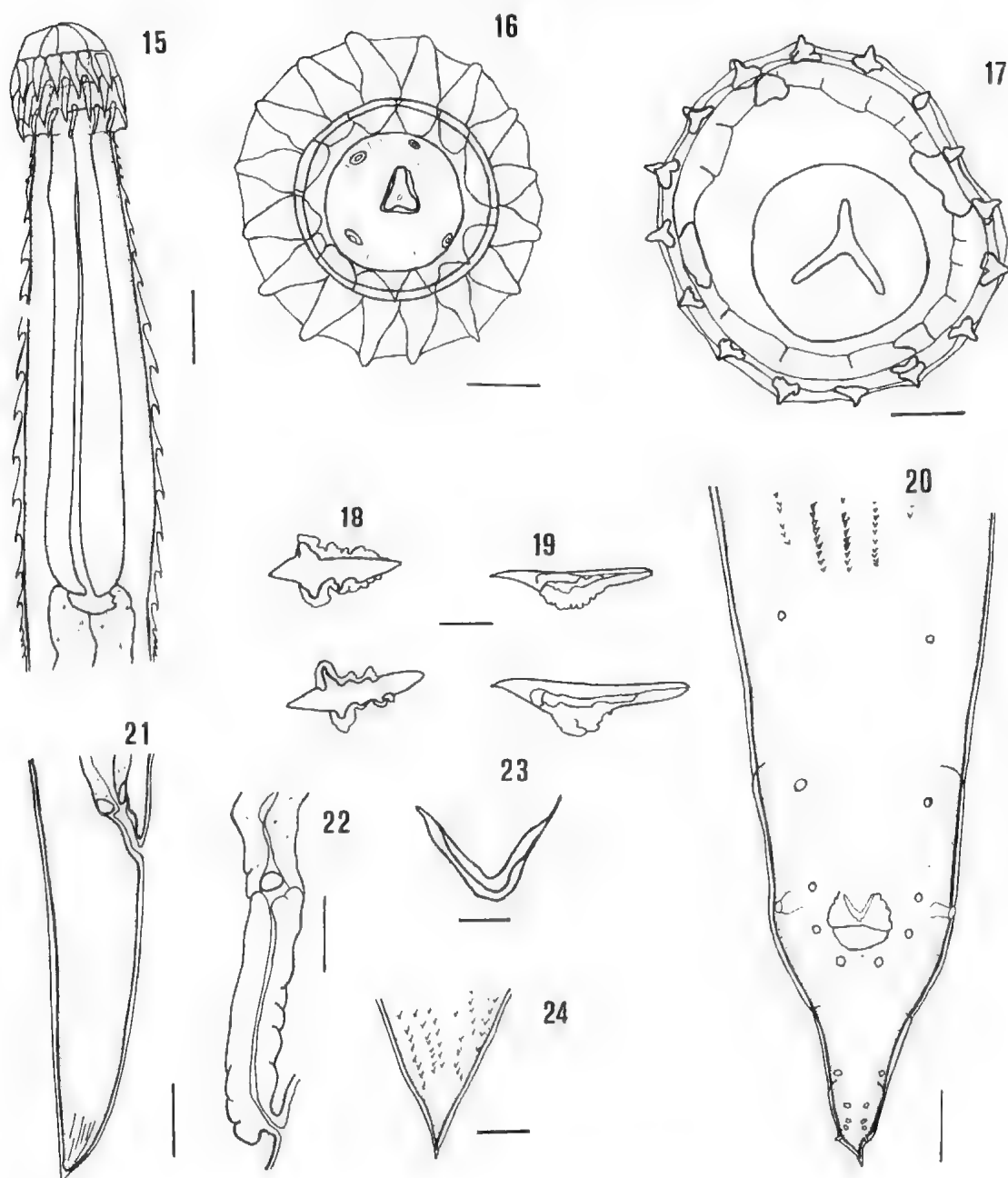
From *Isodon auratus*: 1♂, 1♀, no collection data, AHC 30319.

From *Isodon macrurus* Queensland: 1♂, 1♀, Rollingsstone, (19° 03'S, 146° 24'E), 24.i.1915; BM (NH) 1950 12.6.165-166; Mossman to Damtree Road, (16° 15'S, 145° 19'E), 2.xi.1991, AHC 30275: 221♂♂, 269♀♀, Mossman, (16° 28'S, 142° 23'E), 17.ii.1958, 5.ii.1958, 4.iii.1958 12.viii.1958, 12.ii.1958, 20.ii.1958, 9.ii.1958, QM GL14351, GL14361, GL14363, GL14364, GL14365, GL14366, GL14370, GL14372, GL14373, GL14377, GL14381, GL14383; 2♂♂, 4♀♀, Cairns to Mossman Road, (16° 55'S, 145° 46'E), 2.xi.1991, AHC 30274; 2♂♂, Gillies Highway near Lake Barrine, (17° 15'S, 145° 38'E), 29.x.1991, AHC 30279; 6♂♂, 11♀♀, Atherton, (17° 16'S, 145° 29'E), 25.v.1982, CSIRO N1610; 8♂♂, 11♀♀, Yungaburra to Atherton Road, (17° 16'S, 145° 35'E), 29.x.1991, AHC 30278; 7♂♂, 11♀♀, Miriwinji, (17° 24'S, 145° 55'E), 25.ix.1957, QM GL14368, 181♂♂, 189♀♀, Darudgee (17° 29'S 146° 00'E), 20.ii.1959, QM GL12653, GL4367;

8♂♂, 7♀♀, Millaa Millaa to Innisfail Road, (17° 31'S, 145° 37'E), 31.x.1991, AHC 30276; 76♂♂, 133♀♀, Innisfail, (17° 32'S, 146° 01'E), 16.vi.1959, 5.x.1953, 20.vii.1956, 27.vii.1956, 6.vii.1956, 19.vi.1957, 18.ii.1960, AHC 4528, QM GL14357, GL14360, GL14376, GL14378, GL14379, GL14382; 7♂♂, 3♀♀, Atherton to Ravenshoe Road, (17° 36'S, 145° 29'E), 31.x.1991, AHC 30277; 1♂, 4♀♀, Ingham, (18° 39'S, 146° 10'E), 31.x.1991, AHC 30280; 2♂♂, 6♀♀, Palmerston Highway, 29.v.1959, QM GL14369; 7♀♀, 60km south of Proserpine, (20° 14'S, 152° 35'E) AHC 30266; 3♀♀, Rockhampton to Yeppoon Road (23° 08'S, 150° 44'E), 16.viii.1990, 3.vii.1992, AHC 30271, 30267; 3♀♀, Yeppoon to Emu Park Road, (23° 10'S, 150° 46'E), 16.ix.1990, AHC 30270; 4♂♂, 15♀♀, Rockhampton to Emu Park Road, (23° 13'S, 150° 50'E) 17.iii.1992, AHC 30272; 1♂, 2♀♀, Rockhampton to Keppel Sands Road, (23° 20'S, 150° 48'E), 18.vii.1992, AHC 30268; 6♀♀, Mt Glorious, (27° 21'S, 152° 54'E) 27.x.1955, QM GL14359; 69♂♂, 120♀♀, Ashgrove, (27° 27'S, 153° 02'E), 27.i.1956, QM GL14347; 120♂♂, 203♀♀, Paddington, Brisbane, (27° 28'S, 153° 01'E), 25.viii.1955, 21.x.1955, 14.ix.1955, AHC 4371, QM GL14350, GL14371; 29♂♂, 55♀♀, Brisbane, (27° 28'S, 153° 01'E), 28.ix.1954, QM GL14340, GL14380; 7♂♂, 18♀♀, Moggill, (27° 29'S, 152° 54'E), 12.x.1967, CSIRO N157; 2♂♂, 2♀♀, Mt Nebo, (27° 33'S, 152° 57'E), 1.x.1954, 23.viii.1993, QM GL14359, AHC 30317, 30818; 8♂♂, 13♀♀, Brookfield, (27° 30'S, 152° 55'E), 20.v.1973, 19.v.1967, AHC 19367, CSIRO N151; 13♂♂, 21♀♀, Rocklea Crossing, 19.v.1967, CSIRO N152; New South Wales: 1♀, no other data, AHC 4462; No locality given: 97♂♂, 171♀♀, 8.iii.1938, 29.x.1954, 15.x.1954, 28.ix.1954, 22.ii.1956, 12.iii.1958, QM GL14345, GL14346, GL14352, GL14353, GL14354, GL14355, GL14362.

From *Isodon obesulus* New South Wales: 1♂, Sidlings Swamp North, Timbillica State Forest, (37° 17'S, 149° 45'E), 20.vii.1994, CSIRO N4228. Victoria: 11♂♂, 10♀♀, no collection data, AHC 4461, AHC 30297; 6♂♂, 3♀♀, Halls Gap (37° 08'S, 142° 31'E), no date, AHC 30297; 3♂♂, 3♀♀, Mourn Reservoir Grampians, (37° 14'S, 142° 30'E), no date, AHC 30299. South Australia: 3♀♀, Myponga, (35° 23'S, 138° 28'E), no date, AHC 4446; 3♀♀, anterior end, Waitpinga, (35° 36'S, 138° 32'E), no date, AHC 4460. Kangaroo Island, South Australia: 9♀♀, 1♂, Vivonne Bay, (25° 59'S, 137° 13'E), 1.v.1988, AHC 30302; 16♂♂, 39♀♀, Pandanus, (35° 47'S, 137° 16'E), 3.xi.1986, AHC 30307; 16♀♀, 28♀♀, Binnowie, (37° 47'S, 136° 59'E), 5.viii.1987, AHC 30303.

From *Perameles nasuti* Queensland: 1♂, 3♀♀, Mareeba, (17° 00'S, 145° 26'E) 29.x.1991, AHC 30036.



Figs 15-24. *Linstowinema warringtoni* sp. nov. 15. Anterior end, (lateral view). 16. Cephalic end female, optical section at level of first row of cephalic hooks (*en face* view). 17. Female, hand cut transverse section through body hooks on cuticular dilation. 18. Body hooks (dorsal view). 19. Body hooks (lateral view). 20. Male tail (ventral view). 21. Female tail (lateral view). 22. Vagina (lateral view). 23. Gubernaculum (ventral view). 24. Female tail tip (lateral view). Scale bars = 200 μ m 15, 21; 100 μ m 16, 17, 18, 19, 20, 22, 24; 50 μ m 23.

Description

Cephalic bulb with 3 rows of 14 (male) or 16 (female) files of hooks (Fig. 16), 2nd row longest, 3rd row shortest; neck with 3-7 rows tiny spines; cuticular dilation of oesophageal region bearing 9-13 rows of 14 (male) or 16 (female) files of body hooks (Fig. 17), 1st and last rows smallest, 6th - 8th rows largest, roots of hooks with undulating edges (Figs 18, 19); remainder of body with up to 48 (male) or 54 (female) small spines at each annulation, over whole body of female; extending over $\frac{1}{5}$ of dorsal surface, terminating about 500, anterior to cloaca, not reaching level of most anterior pair of caudal papillae, on ventral surface of male body (Fig. 20). Oesophagus, $\frac{1}{10}$ - $\frac{1}{16}$ body length, simple, club-shaped; terminating at level of 9th-13th row of body hooks (Fig. 15) near posterior end of anterior cuticular dilation. Nerve ring surrounding oesophagus within cephalic bulb; secretory-excretory pore in neck; deirids conical, at level of 1st row of body hooks.

Male: Length 15-20 (17.5) mm, width 450-750 (565). Cephalic bulb 270-340 (295) long by 270-320 (295) wide; cephalic hooks 1st row 140-170 (155), 2nd row 160-190 (175), 3rd row 100-130 (110) long. Oesophagus 1575-1925 (1743) long, cuticular dilation bearing 9-11 rows of body hooks, deirids 490-550 (530); secretory-excretory pore 360 (n=1); nerve ring 310 (n=1) from anterior end. Spicules similar, equal, without alae, 690-1090 (850) long, about $\frac{1}{16}$ body length. Gubernaculum short, simple, sub triangular, 50-75 (n=5) long (Fig. 23). Ten pairs caudal papillae; 3 pairs ventral and immediately pre-, ad- and post-cloacal respectively, 1 pair lateral ad-cloacal, 2 pairs lateral pre-cloacal, all same size; 4 pairs papillae, pair phasmids posterior to cloaca near tail tip (Fig. 20). Cloacal region with small cuticular bosses, ala-like expansions absent. Tail 330-430 (390) long.

Female: Length 32-41 (38) mm, width 720-990 (840). Cephalic bulb 350-390 (370) long by 350-400 (280) wide; bearing 3 rows of hooks, 1st row 170-200 (185), 2nd row 180-230 (195), 3rd row 120-150 (130) long. Oesophagus 1870-2500 (2280) long, cuticular dilation bearing 11-13 rows of body hooks. Deirids 580-700 (670); secretory-excretory pore 370-400 (390); nerve ring 300-360 (330) from anterior end. Vulva 12.5-15.6 (14.2) mm from anterior end (Fig. 22). Tail 1000-1900 (1265) long (Figs 21, 24). Vagina about 300 long (n=1). Eggs almost spherical 30-44 (38) by 33-52 (40).

Etymology

This species is named after Warrington Yorke who with P. A. Mapleston carried out much of the early work on this genus.

Type locality

Townsville, Queensland, Australia

Type host

Isodon macrourus (Gould, 1842)

Site in host

Small intestine

Type specimen

Neotype BM (NM) 1950. 12.6. 165

Remarks

The two worms, 13, 12, BM (NH) 1950. 12.6.165-166 from *Perameles obesula* collected by Nicoll in 1915 in Queensland are the only specimens registered in Australian or United Kingdom parasite collections which could be the material described by Yorke & Mapleston (1926). On examination these worms were found to have the 11 (male) and 13 (female) body hooks described by Yorke & Mapleston (1926) for *Echinomema cineta* and to have the "long" oesophagus and all the other characters attributed to *E. cineta* by Chabaud *et al.* (1980). I therefore designate the male specimen of BM (NH) 1950. 12.6.165-166 as the neotype.

All the specimens identified in this study as *L. warringtoni* conformed to the description given by Chabaud *et al.* (1980) of *L. cineta*. *Larsonium warringtoni* sp. nov. differs from all other species in the genus in having up to 9-11 rows of hooks (male) or 11-13 (female) on the oesophageal cuticular dilation and a "long" oesophagus, that is, the oesophagus terminates at or near the final row of body hooks. Male *L. warringtoni* can be distinguished from *L. cineta* by the combination of characters at the posterior end, i.e., the terminating ventral body spines do not extend to the most anterior pair of papillae in *L. warringtoni* but do in *L. cineta*, the distance between spines and cloaca is 500 μ m not 400 as in *L. cineta*, the limited extent of cuticular bosses surrounding the cloaca in *L. warringtoni* compared with *L. cineta*. *L. warringtoni* does not have an ala-like expansion surrounding the cloaca but *L. cineta* does, and four pairs of papillae not three on the tail tip. The spicules of *L. warringtoni* $\frac{1}{16}$ body length are shorter than those of *L. cineta* $\frac{1}{16}$ body length. The eggs of *L. warringtoni* are almost spherical but those of *L. cineta* are ovoid.

Chabaud *et al.* (1980) in their description of *L. cineta* (*sic*) indicated that they had studied numerous specimens from a range of localities including Woolwonga and Darwin in the Northern Territory. A re-examination of the material from the Northern Territory has shown that it represents a new

species of *Linstowinema*, *L. latens*, described below. The measurements and figures of specimens reported by Chabaud *et al.* (1980) however, are congruent with *L. warringtoni* rather than those of *L. latens*.

Spratt *et al.* (1991) noted that there were no records of helminth parasites from *I. auratus* the golden bandicoot. The finding of *L. warringtoni* in one of five golden bandicoots dissected for this study is therefore the first record of a helminth from this host.

Material registered in the QM as GL14345, 14346, 14352, 14353, 14354, 14355, 14362 was collected by Dr M. J. Mackerras. Therefore although no locality was given these specimens are probably from Queensland.

The finding of *L. warringtoni* in *I. obesulus* is also a new host record. The specimens from Waitpinga, Myponga, Timbillica State Forest and in two of the hosts from Kangaroo Island were found in mixed infections with *L. cinctum*. The geographic distribution of *L. warringtoni* therefore has been shown, in this study, to extend from northern Queensland down the east coast of New South Wales to Victoria, South Australia and offshore to Kangaroo Island. A larger number of *I. obesulus* from the southern states needs to be examined before geographic distributions can be fully mapped. Populations of bandicoots in NSW, Vic. and SA, now have patchy distributions over a reduced range (Braithwaite 1995) and attempts to collect additional specimens of *I. obesulus* for parasitological examination have been unsuccessful to date. Further work on the southern geographic distribution of *L. warringtoni* will be problematic, as bandicoots become more difficult to collect.

The specimens of *L. warringtoni* found in a single *P. nasuta* suggest either a natural low prevalence of infection, or an occasional, incidental infection of this host.

Linstowinema latens sp.nov.
(FIGS 25-36)

Synonym: *Echinonema cinctum sensu* Chabaud, Seureau, Beveridge, Bain & Durette-Desset, 1980: pp. 435-436 (in part); *sensu* Spratt, Beveridge & Walter, 1991: p. 25 (in part).

Material examined

Type material: Holotype ♂, allotype ♀, from *Isoodon macrourus*, Walsh Point, (15° 08'S, 125° 46'E), Mitchell Plateau, Western Australia, 22.vii.1982; AHC 30322, 30323, 43♂♂, 65♀♀, paratypes AHC 13028, WAM 110-83, 116-83.

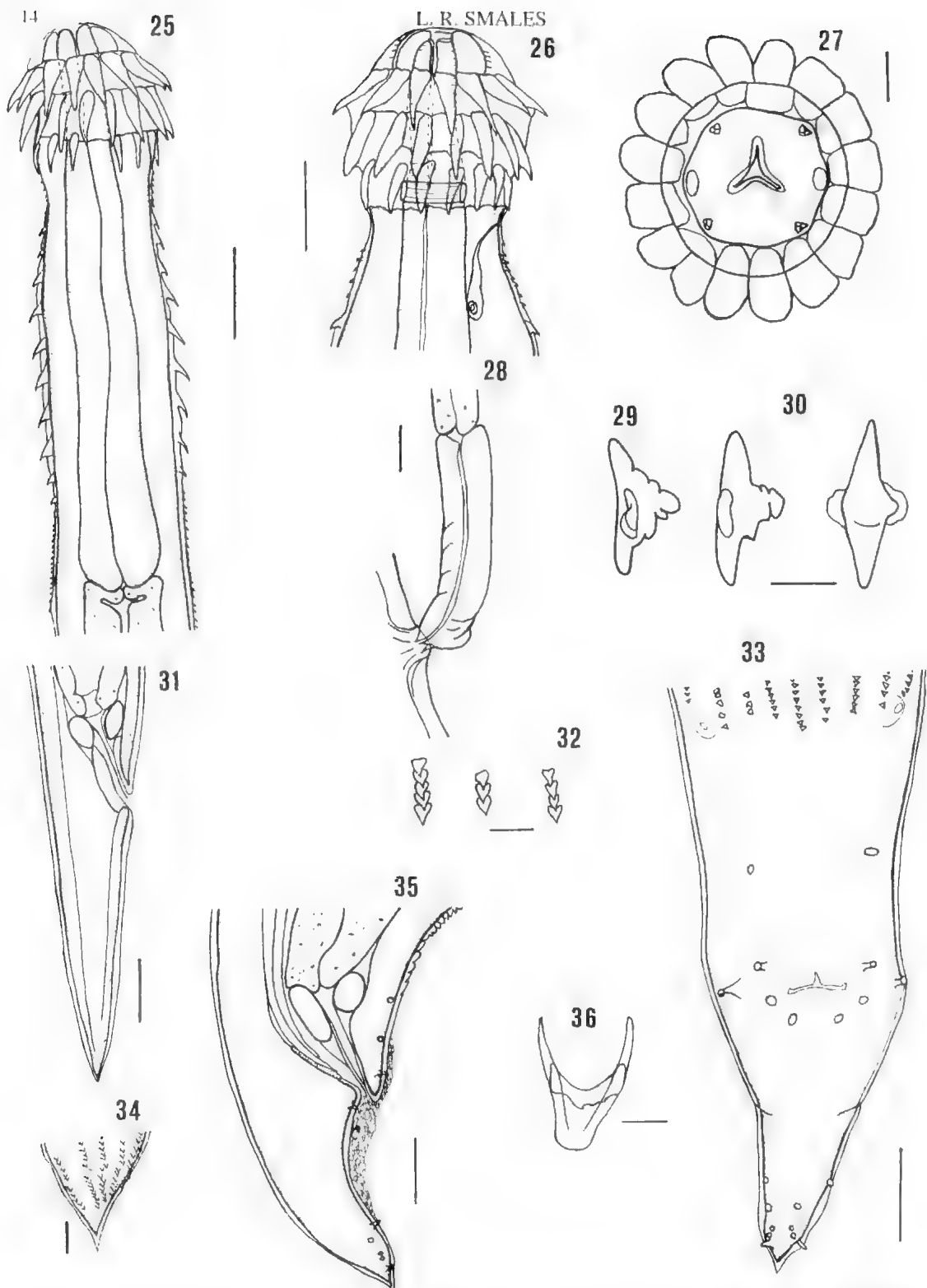
Other material: From *Isoodon macrourus* Western Australia: 1♂, 4♀♀, Mt Hart, Kimberley Ranges,

(16° 48'S, 124° 55'E), 22.x.1993, 24.x.1993, AHC 30289, 30290, Northern Territory: 16♂♂, 18♀♀, Darwin, (12° 27'S, 130° 50'E), no date, 19.vi.1993, 27.vi.1995, 28.vi.1995, AHC 4703, 30287, CSIRO N4413, N4414; 7♂♂, 7♀♀, near Byers Rd, Stuart Highway turnoff, (12° 30'S, 130° 50'E), 18.vi.1993, AHC 30284, 30285; 7♂♂, 10♀♀, Adelaide River, Arnhem Highway, (12° 28'S, 131° 14'E), 20.vi.1993, AHC 30288; 13♂♂, 12♀♀, Bees Creek, off Stuart Highway, (12° 35'S, 131° 04'E), 17.vi.1993, AHC 30286; 11♂♂, 8♀♀, Jabiluka, August 1979, AHC 6421; 3♀♀, Woolwonga, (12° 45'S, 132° 39'E), 19.x.1972, CSIRO N159, Queensland: 6♂♂, 11♀♀, Atherton (17° 15'S, 145° 29'E), 25.v.1928, CSIRO N1610; 11♂♂, 14♀♀, 14km north of Atherton (17° 15'S 145° 29'E), 15.iii.1982, N1532; 19♂♂, 12♀♀, Yungaburra to Atherton Rd, (17° 15'S 145° 30'E), 29.x.1991, 1.xi.1991, AHC 30278, 30281; 1♂, Gillies Highway near Lake Barrine (17° 16'S, 145° 35'E), 29.x.1991, AHC 30279; 6♂♂, 8♀♀, Gillies Highway near Yungaburra, (17° 16'S, 145° 35'E), 29.x.1991, AHC 30283; 23♂♂, 116♀♀, Mareeba to Kuranda Rd (17° 00'S, 145° 26'E), 2.xi.1991, AHC 30282.

Description

Cephalic bulb with 3 rows of 14 (male) or 16 (female) files of hooks, 2nd row longest, 3rd row shortest (Figs 26, 27); neck with 2-9 rows tiny spines; cuticular dilation of oesophageal region bearing 14 (male) or 16 (female) files of body hooks, first and last rows very small, 6th - 7th rows largest; roots of hooks without undulating edges (Figs 29, 30); remainder of body with up to 44 (male) or 60 (female) small spines at each annulation, over whole body of female; extending over $\frac{9}{10}$ of dorsal body surface, terminating about 300-400 anterior to cloaca, level with anterior pair of caudal papillae, on ventral surface of male body (Figs 32, 33). Oesophagus $\frac{1}{10}$ - $\frac{1}{11}$ (male) $\frac{1}{15}$ - $\frac{1}{16}$ (female) body length, simple, club-shaped, terminating posterior to the oesophageal cuticular dilation (Fig. 25). Nerve ring surrounding oesophagus within cephalic bulb, secretory-excretory pore in neck, deirids conical, at level of first row of body hooks.

Male: (measurements of specimens from Western Australia, followed by measurements of specimens from Northern Territory). Length 15-18 (16), 15-21 (18.5) mm, width 425-625 (490), 515-715 (600). Cephalic bulb 280-350 (325) long by 280-380 (340) wide, 275-435 (350) long by 290-385 (340) wide; cephalic hooks, 1st row 150-180 (152), 105-165 (140), 2nd row 160-190 (168), 125-195 (155), 3rd row 100-110 (108), 72-117 (94) long (Fig. 26). Oesophagus 1200-1825 (1555), 1325-1990 (1715) long, cuticular dilation bearing 8-10 rows body hooks. Deirids 540-690 (610), 390-650 (530);



Figs 25-36. *Linstowinema latens* sp. nov. 25. Anterior end, (lateral view). 26. Cephalic bulb (lateral view). 27. Cephalic end female, optical section at level of first row of hooks (*en face* view). 28. Vagina (lateral view). 29. Body hooks (lateral view). 30. Body hook (dorsal view). 31. Female tail (lateral view). 32. Male posterior body spines (ventral view). 33. Male tail (ventral view). 34. Female tail tip (lateral view). 35. Male tail (lateral view). 36. Gubernaculum (ventral view). Scale bars = 200 μ m 25, 26; 50 μ m 27; 100 μ m 28, 31, 33, 35; 25 μ m 29, 30, 32, 34, 36.

secretory-excretory pore not seen, 230-495 (365); nerve ring 300 (n=1), 225-365 (275) from anterior end, Spicules equal similar, without alae, 830-1090 (995), 830-1100 (1005) long, about $\frac{1}{16}$ to $\frac{1}{18}$ body length. Gubernaculum short, simple, sub-triangular, 61-68 (n=3), 66-79 (n=5) long (Fig. 36). 10 pairs caudal papillae; 3 pairs ventral and immediately pre-, ad- and post-cloacal respectively, 1 pair lateral ad-cloacal 2 pairs lateral pre-cloacal, all same size; 4 pairs papillae, pair phasmids, ala-like expansions absent posterior to cloaca, near tail tip (Fig. 33). Cloacal region with small cuticular bosses, ala-like expansions absent. Tail 250-340 (310), 255-320 (305) long (Fig. 35).

Female: Length 20-38 (30), 25-41 (30) mm, width 420-750 (590), 665-1175 (840). Cephalic bulb 300-380 (350), 230-510 (385) long by 350-500 (385), 375-530 (430) wide; bearing 3 rows of hooks, 1st row 160-190 (175), 135-190 (155), 2nd row 170-190 (180), 140-195 (170), 3rd row 100-120 (110), 90-135 (110) long. Oesophagus 1450-2075 (1790), 1565-2430 (1970) long; cuticular dilation bearing 9-12 body hooks. Deirids 600-700 (660), 325-770 (495); secretory-excretory pore not seen, 295-590 (420); nerve ring not seen, 205-405 (355) (n=5) from anterior end (Fig. 28). Vulva 9.2-14.7 (11.8), 9.2-17.2 (11.9) mm from anterior end. Vagina about 115 (n=2). Eggs almost spherical 36-60 (50), 33-42 (35) by 33-39 (34). Tail 790-1210 (980), 920-1615 (1160) long (Figs 31, 34).

Etymology

The species name is derived from the Latin *latens* meaning hidden, since it was not found when the material was first examined.

Type host

Isodon macrourus (Gould, 1842)

Type locality

Mitchell Plateau, Western Australia, Australia

Site in host

Small intestine

Type specimens

Holotype male, AHC 30322, allotype female, AHC 30323, paratypes AHC 13028

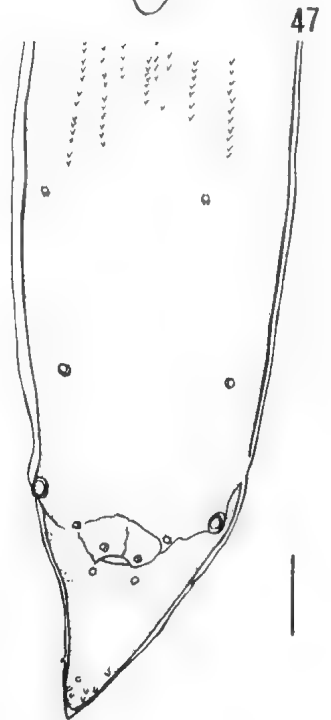
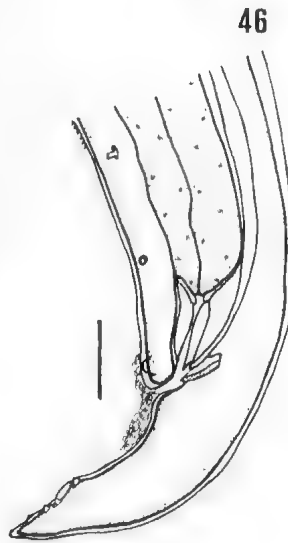
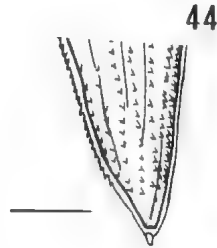
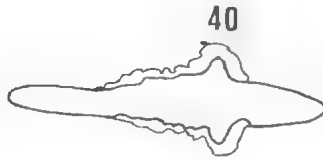
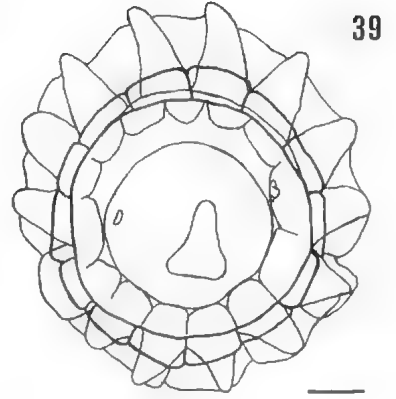
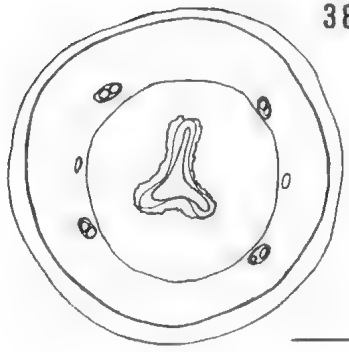
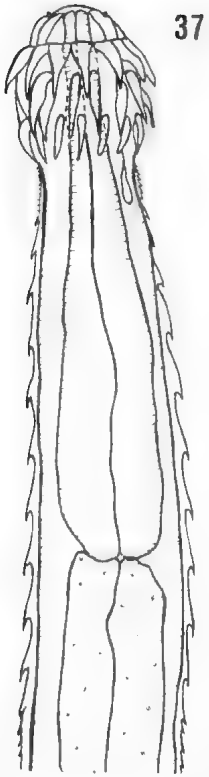
Remarks

Linstowinema latens sp. nov. resembles *L. warringtoni*, also occurring in *I. macrourus*, in being of similar size, (males 15-21 mm in *L. latens* compared with 15-20 mm long in *L. warringtoni*),

having the oesophagus of similar length (1575-1925 in *L. latens* compared with 1200-1825 in *L. warringtoni* males) and four pairs of papillae on the male tail. The oesophagus in *L. latens*, however, terminates posteriorly to the hooks surrounding the oesophageal region whereas that of *L. warringtoni* terminates at about the level of the 9th-13th row of hooks. *L. latens* has 8-10 (male) or 9-12 (female) rows of hooks, roots without undulating edges, while *L. warringtoni* has 9-11 (male) or 11-13 (female) rows of hooks, with roots having undulating edges on the dilated cuticular region. The body spines on the dorsal surface of male *L. latens* extend further towards the posterior end, (about $\frac{9}{10}$ of the body), than on *L. warringtoni* (about $\frac{1}{5}$ of the body). Ventrally the body spines extend to the same level as the most anterior pair of caudal papillae on *L. latens*, but do not on *L. warringtoni*. The male tail is longer in *L. warringtoni* (330-430) than in *L. latens* (250-340). The vagina of *L. latens* (115) is shorter than that of *L. warringtoni* (300).

Specimens were found in *I. macrourus* from northern Western Australia, the Northern Territory and northern Queensland. The population of northern brown bandicoots in Western Australia is isolated from that of the Northern Territory and Queensland (Gordon 1995), but measurements of worms from hosts occurring in the Kimberley, Western Australia, are consistent with those from Darwin, Northern Territory. The only morphological difference observed between these populations was that the first row of cephalic hooks of the Kimberley specimens was almost as long as the second row, 150-180, compared with 160-196 in males, but in the Darwin specimens the difference in length between the two rows of hooks was more marked, 105-163, compared with 126-195. This difference is not considered to be significant and as the Queensland worms were similar to those from the Northern Territory, the material from all three localities is considered to be conspecific.

The northern brown bandicoots collected from northern Queensland were infected with *L. warringtoni*, 8 hosts, *L. latens*, 4 hosts, or both species, 3 hosts. Chabaud *et al.* (1980) identified all the material they examined from the Northern Territory and northern Queensland as *L. cinetum*, now *L. warringtoni*. It is not possible to determine from their paper which, if any, specimens from northern Queensland, presently lodged in the QM, SAMA or CSIRO collections, they examined. The specimens they examined from Woolyonga and Darwin in the Northern Territory have been re-examined for this study, and are all *latens*. The Queensland material examined by Chabaud *et al.* (1980) could have been either *L. warringtoni*, *L. latens*, or both.



Linstowninema inglisi (Chabaud, Seureau, Beveridge, Bain & Durette-Desset, 1980)
comb. nov
(Figs 37-47)

Synonymy: *Echinonema vinetum* sensu Inglis, 1967: pp. 122, 128, 131-133, Figs 8-10, *Echinonema inglisi* Chabaud, Seureau, Beveridge, Bain & Durette-Desset, 1980: pp. 437-438; Spratt, Beveridge & Walter, 1991: p. 26.

Material examined

From *Isodon obesulus* Western Australia: 4♂♂, 3♀♀, Murdoch, (31° 57'S, 115° 51'E), 27.v.1981, AHC 8901; 40♂♂, 106♀♀, Perth, (31° 57', 115° 51'E), Jan. 1993, 9.i.1993, 5.ii.1993, 1993, AHC 30257, 30258, 30259, 30260, 30262, 30263, 30264, 30265; 11♂♂, 44♀♀, Wattle Grove (32° 02'S, 116° 00'E), 5.v.1966, BM (NH) 1967.616-626, WAM 25-70; 10♂♂, 10♀♀, Glen Forest, 10.viii.66, AHC 29760, BM (NH) 1967.473-523; 4♂♂, 10♀♀, Forrestdale, 15.xii.1978, AHC 8885; 40♂♂, 10♀♀, Jarrahdale, (32° 30'S, 16° 07'E), 28.x.1993, AHC 30261; 4♂♂, 8♀♀, Albany, (35° 00'S, 117° 52'E), 18.xi.1994, 19.xi.1994, CSIRO N4242, N4243; 19♂♂, 32♀♀, Manjimup, (35° 15'S, 116° 09'E), 27.vi.1993, 16.ix.1993, AHC 30255, 30256; 62♂♂, 155♀♀, no locality given, 22.x.1977, AHC 8888

Description

Cephalic bulb with 3 rows of 14 (male) (Figs 38, 39) or 16 (female) files of hooks 2nd row longest, 3rd row shortest; neck with 5-11 rows tiny spines; cuticular dilation of oesophageal region bearing 10-14 rows, 14 (male) or 16 (female) files of body hooks, 1st and last rows smallest, 7th - 9th rows hooks largest (Figs 3, 7); roots of hooks with undulating edges (Figs 40, 41). Remainder of body with up to 35 (male), or 45 (female) small spines at each annulation, over whole body of female, extending to 400 µm from tail tip on dorsal surface and about 300-500 anterior to cloaca, not extending to anterior pair of caudal papillae, on ventral surface of male body (Fig. 47). Oesophagus $1/11$ (male) to $1/4$ (female) body length, simple, club-shaped, terminating level with 8th-9th row of hooks. Nerve ring surrounding oesophagus within cephalic bulb, secretory-excretory pore in neck, deirids conical, at level of 1st row of body hooks.

Male: Length 11-18 (15) mm, width 325-625 (540). Cephalic bulb 266-325 (272) long by 247-350 (309) wide; cephalic hooks, 1st row 140-180 (155), 2nd row 160-200 (180), 3rd row 115-140 (125) long (Figs 3, 7). Oesophagus 1120-1565 (1400) long; cuticular dilation bearing 10-12 rows body hooks, Deirids 410-650 (520); secretory-excretory pore not seen; nerve ring 312 ($n=1$) from anterior end. Spicules similar, equal, without alae 700-1200 (985) long, about $1/4$ body length. Gubernaculum short, sub-triangular, 50-58 ($n=5$) long (Fig. 45). Nine pairs caudal papillae: 3 pairs ventral and immediately pre-, ad- and post-cloacal; 1 large pair lateral, ad-cloacal, 2 pairs lateral, pre-cloacal, 3 pairs papillae, pair phasmids well posterior to cloaca, near tail tip (Fig. 47). Cloacal region with small cuticular bosses, ala-like extensions of body absent. Tail 150-350 (265) long (Fig. 46).

Female: Length 15-30 (24) mm, width 560-935 (700). Cephalic bulb 312-357 (334) long by 293-422 (334) wide; cephalic hooks, 1st row 155-195 (180), 2nd row 180-235 (205), 3rd row 115-150 (125) long. Oesophagus 1385-1835 (1655) long; cuticular dilation bearing 12-14 rows body hooks, Deirids 485-570 (545); secretory-excretory pore 390 ($n=1$) from anterior end; nerve ring not seen. Vulva 9.8-10.2 mm ($n=3$) (Fig. 43) from anterior end. Vagina about 350 ($n=1$). Eggs almost spherical 40-48 (44) by 36-45 (40). Tail 610-920 (730) long (Figs 42, 44)

Type host

Isodon obesulus (Shaw, 1797)

Type locality

Wattle Grove, near Perth, Western Australia, Australia

Site in host

Small intestine

Type specimen

Neotype BM(NH) 1967.616

Remarks

Material from *I. obesulus* from Wattle Grove, collected on 5.v.1966 and identified by Inglis is

Figs 37-47. *Linstowninema inglisi* (Chabaud, Seureau, Beveridge, Bain & Durette-Desset, 1980). 37. Anterior end, (lateral view). 38. Cephalic end (*en face* view). 39. Cephalic end male, optical section at level of first row of hooks (*en face* view). 40. Body hook (dorsal view). 41. Body hook (lateral view). 42. Female tail (lateral view). 43. Vagina (lateral view). 44. Female tail tip (lateral view). 45. Gubernaculum (ventral view). 46. Male tail (lateral view). 47. Male tail (ventral view). Scale bars = 200 µm 37, 42; 50 µm 38, 39, 43, 44; 100 µm 40, 41, 46, 47; 25 µm 45.

deposited in the WAM and BM (NH). This appears to be the material described as *E. cinctum* by Inglis (1967). I therefore designate a specimen from BM (NH) 1967, 616-626 as the neotype.

Linstowinema inglisi (Chabaud, Seureau, Beveridge, Bain & Durette-Desset, 1980) can be distinguished from *L. warringtoni* and *L. latens* in having the oesophagus terminating within the anterior cuticular dilation. *Linstowinema inglisi* has 10-12 (male) and 12-14 (female) rows of body hooks compared with 9-11 and 11-13 rows for *L. warringtoni* and 8-10 and 9-12 rows for *L. latens*. The spicules of *L. inglisi* ($1/3$ body length) are relatively longer than for *L. warringtoni* ($1/50$ body length) and *L. latens* ($1/12$ body length). The male tail of *L. inglisi* also differs from both *L. warringtoni* and *L. latens* in being shorter (150-350 (265) compared with 330-130 (390) and 250-340 (307) respectively and in having only 3 pairs of papillae rather than 4. The female tail is also shorter (610-920 (730)) in *L. inglisi* compared with *L. warringtoni* and *L. latens* (1000-1900 (1265)) and 790-1615 (1070), respectively.

The pair of lateral papillae level with the cloacal opening is more prominent than the other pairs of papillae surrounding and anterior to the cloaca of *L. inglisi*. In this respect, *L. inglisi* resembles *L. edmondsi* from dasyurid marsupials but *L. inglisi* differs from *L. edmondsi* in having the 2nd, not the 1st row of cephalic hooks the longest. *Linstowinema edmondsi* occurs in *Dasyurus hallucatus* from the Northern Territory while *L. inglisi* occurs in *L. obesulus* from southern Western Australia.

Linstowinema inglisi can be distinguished from *L. cinctum*, which also occurs in *L. obesulus* and has the oesophagus terminating within the cuticular dilation of the oesophageal region at about the 9th row of hooks, by the number of rows of body-hooks, 10-12 (male) and 12-14 (female) compared with 13-16 and 14-18 in *L. cinctum*. The differences between *L. cinctum* and *L. inglisi* are discussed in detail under *L. cinctum*.

The measurements of *L. inglisi* from this study are congruent with those given by Inglis (1967). Any differences between the two sets of measurements are because Inglis (1967) measured smaller worms, 3.29-11.39 for the males compared with 11-18 in this study and 10.1-18.4 for the females compared with 15-30 in this study. Chabaud *et al.* (1980) described

L. inglisi males as having spines covering only 7% of the body dorsally. A careful examination of specimens for this study, however, has shown that the dorsal spines, although tiny, extend along about 20% of body, that is, further towards the tail tip than do the ventral spines.

Linstowinema inglisi has been found only in *L. obesulus* from the south of Western Australia.

***Linstowinema tasmaniense* sp. nov.**
(FIGS 48-61)

Synonyms: *Echinonema cinctum* *sensu* Munday & Green, 1972: p. 10 (in part). *Echinonema inglisi* *sensu* Spratt, Beveridge & Walter, 1991: p. 26 (in part). *Echinonema* sp.1 Chabaud, Seureau, Beveridge, Bain & Durette-Desset 1980: p. 453; Spratt, Beveridge & Walter, 1991: p. 26.

Material examined

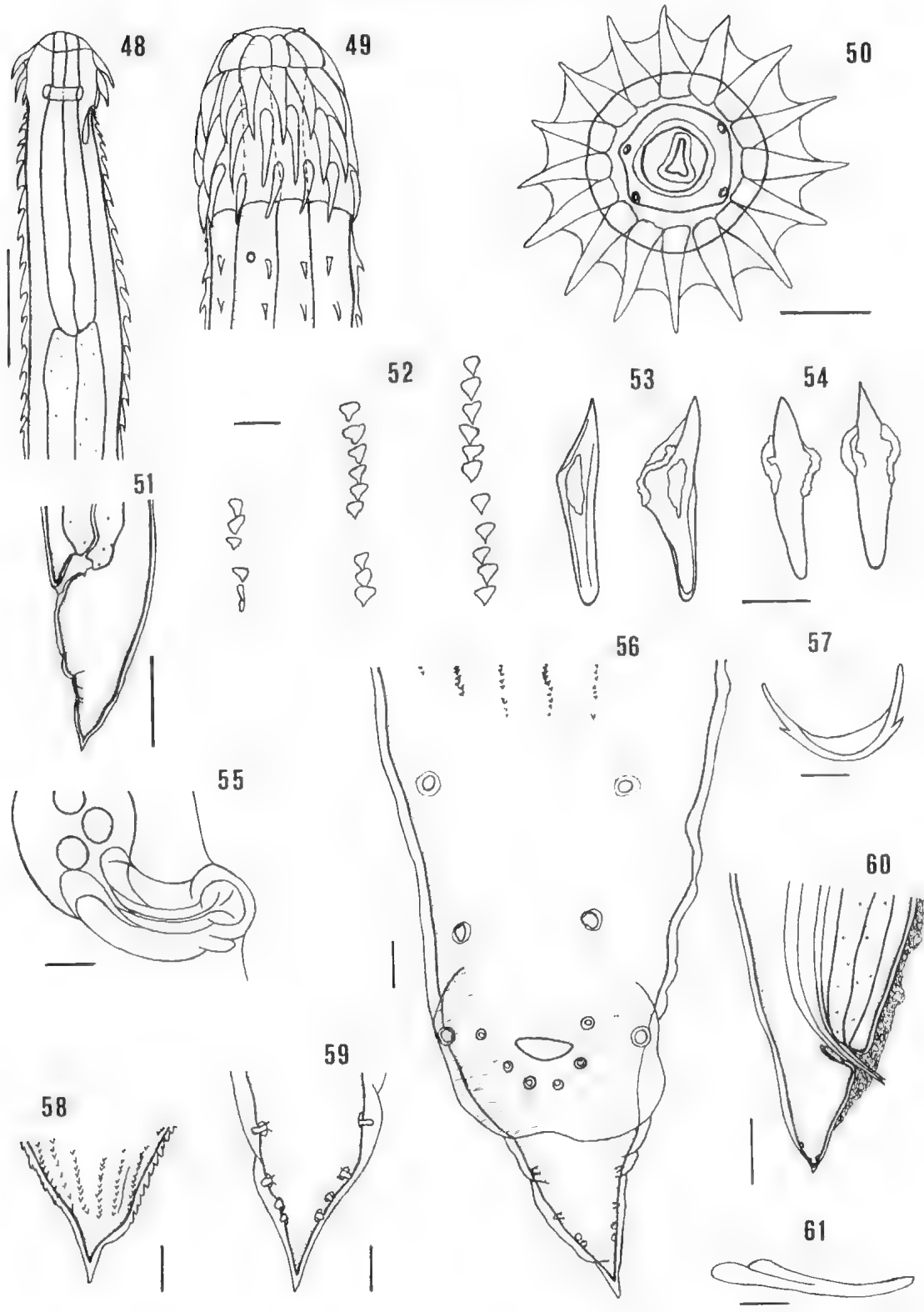
Type material: Holotype ♂, allotype ♀, from *Isodon obesulus*, Kingston (42° 59'S, 147° 18'E), Tasmania, 11.vii.1992, AHC 30320, 30321. Paratypes 12♂♂, 11♀♀, AHC 30310, 30311.

Other material: From *Isodon obesulus* South Australia, Kangaroo Island: 12♂♂, 4♀♀, Vivonne Bay, (35° 59'S, 137° 13'E), no date, i.v.1988, AHC 4458, 30302; 13♂♂, 24♀♀, Hundred of Gosse, June 1983, AHC 30305; 8♂♂, 17♀♀, Karatta, (35° 59'S, 136° 56'E), Sept. 1983, AHC 30306; 13♂♂, 15♀♀, Paardana, (35° 47'S, 137° 16'E), 12.iv.1991, 3.xi.1986, AHC 30308, 30307; 1♂, 1♀, Seal Bay, (36° 00'S, 137° 20'E), 4.i.1987, AHC 30304. Tasmania: 5♂♂, 15♀♀, Beaconsfield, (41° 12'S, 146° 49'E), 1991, AHC 30315; 3♂♂, Glengarry, (41° 21'S, 146° 52'E), 1992, AHC 30309; 1♀, Hobart, (42° 53'S, 147° 19'E), 25.vi.1982, CSIRO N1674; 7♂♂, 8♀♀, Gog Range, (42° 59'S, 147° 18'E), 8.vii.1992, AHC 30308; 8♂♂, 13♀♀, Margate tip, (43° 02'S, 147° 16'E), 10.iii.1993, AHC 30312; 1♂, Upper Dromedary, no date given, AHC 4530; 12♂♂, 19♀♀, no collection data, AHC 30313, 30314.

Description

Cephalic bulb with 3 rows of 14 (male) or 16 (female) (Figs 49, 50) files of hooks. 2nd row longest, 3rd row shortest (Fig. 49); neck with 5-8 rows tiny

(Figs 48-61). *Linstowinema tasmaniense* sp. nov. 48. Anterior end, optical section (lateral view). 49. Cephalic bulb (lateral view). 50. Cephalic end female, optical section at level of first row of hooks (*en face* view). 51. Female tail (lateral view). 52. Male posterior body spines (ventral view). 53. Body hooks (lateral view). 54. Body hooks (dorsal view). 55. Vagina (lateral view). 56. Male tail (ventral view). 57. Gubernaculum (ventral view). 58. Female tail tip (lateral view). 59. Male tail tip (ventral view). 60. Male tail tip (ventral view). 61. Gubernaculum (lateral view). Scale bars = 500 µm 48, 51; 200 µm 49, 60; 100 µm 50, 50 µm 52, 53, 54, 55, 56; 25 µm 57, 58, 59; 12 µm 61.



spines; cuticular dilation of oesophageal region bearing 13-15 rows of 14 (male) or 16 (female) files of body hooks 1st and last rows smallest, 9th 10th rows largest; roots of hooks without undulating edges (Figs 53, 54); remainder of body with up to 46 (male) or 66 (female) small spines at each annulation, over whole body of female, extending over $\frac{2}{3}$ of dorsal surface, terminating about 350 anterior to cloaca, not reaching level of most anterior pair of caudal papillae, on ventral surface of male body (Fig. 56). Oesophagus about $\frac{1}{10}$ - $\frac{1}{11}$ body length, simple, club-shaped, terminating at level of 8th-10th row of body hooks (Fig. 48). Nerve ring surrounding oesophagus within cephalic bulb; secretory-excretory pore in neck; deirids conical, at level of 1st row of body hooks.

Male. Length 11-14 (12.6) mm, width 455-715 (605). Cephalic bulb 215-295 (255) long by 270-390 (325) wide; bearing 3 rows of hooks, 1st row 140-195 (170), 2nd row 175-225 (200), 3rd row 105-130 (120) long (Fig. 49). Oesophagus 1105-1580 (1360) long; cuticular dilation bearing 12-13 rows of body hooks; deirids 355-480 (430), secretory-excretory pore 300-440 (365) ($n=6$); nerve ring 240-300 (280) ($n=4$) from anterior end. Spicules similar, equal, without alae 720-1030 (890) long, about $\frac{1}{14}$ body length. Gubernaculum short, simple, subtriangular, 50-55 ($n=3$) long (Figs. 57, 61). Ten pairs caudal papillae: 3 pairs ventral and immediately pre-, ad- and post-cloacal respectively, 1 pair lateral ad-cloacal, 2 pairs lateral pre-cloacal (Fig. 56); 3 lateral pairs larger (Fig. 56); 3 pairs papillae, pair phasmids posterior to cloaca, near tail tip (Fig. 59). Cloacal region with small cuticular bosses; ala-like expansion of body surrounding cloaca. Tail 235-325 (285) long (Fig. 60).

Female. Length 19-22 (21) mm, width 815-1155 (965). Cephalic bulb 195-325 (255) long by 370-505 (460) wide; bearing 3 rows of hooks, 1st row 190-210 (205), 2nd row 220-265 (245), 3rd row 125-170 (150) long. Oesophagus 1445-1990 (1615) long, cuticular dilation bearing 14-15 rows body hooks. Deirids 355-450 (405); secretory-excretory pore 375 ($n=1$) from anterior end; nerve ring not seen. Vulva 5525-7600 (6500) ($n=3$) long (Fig. 55). Vagina 175 ($n=1$) long. Tail 715-935 (810) long (Figs 51, 58). Eggs almost spherical 36-48 (42) by 33-45 (38).

Remarks

Linstowinema tasmanienne sp. nov. resembles *L. inglisi* and *L. cinctum*, also occurring in *L. obesulus* and having three pairs of papillae on the male tail and the oesophagus terminating within the cuticular dilation of the oesophageal region, at about the 8th-11th row of hooks. *Linstowinema tasmanienne* can be differentiated from *L. inglisi* in having 12-13

(male) and 14-15 (female) rows of body hooks without undulating edges, compared with 10-12 (male) and 12-14 (female) rows of body hooks with undulating edges and from *L. cinctum* which has 13-16 (male) and 14-18 (female) rows of body hooks with undulating edges. *Linstowinema tasmanienne* further differs from *L. inglisi* in having all three pairs of papillae lateral and anterior to the cloaca, larger than those surrounding the cloaca, and in having the cloacal region with ala-like extensions of the body. *Linstowinema inglisi* has only one pair of larger lateral ad-cloacal papillae and does not have the ala-like extensions. *Linstowinema cinctum*, which does have ala-like extensions of the body, has ventral body spines extending to the level of the most anterior pair of lateral caudal papillae but *L. tasmanienne* does not. *Linstowinema cinctum* has all six pairs of papillae lateral and anterior to the cloaca the same size but *L. tasmanienne* has the three lateral pairs larger. The gubernaculum is more U-shaped in ventral view in *L. tasmanienne* than in *L. inglisi* or *L. cinctum*. Female *L. tasmanienne* have a shorter tail 715-935 (810) than *L. cinctum* 986-1132 (1050). The oesophagus is about $\frac{1}{10}$ body length in *L. tasmanienne* males compared with $\frac{1}{8}$ in *L. cinctum* and $\frac{1}{11}$ in *L. inglisi*. The vulva is closer to the anterior end in *L. tasmanienne*, about 0.6 mm compared with 1.0 mm in *L. inglisi* and 1.2 mm in *L. cinctum*. The vagina of *L. tasmanienne*, 175, is shorter than in *L. cinctum* 300 and *L. inglisi* 350.

Chabaud *et al.* (1980) figured the tail of a male specimen, registered as AHC 4530, from *L. obesulus*, Upper Dromedary, Tasmania. There is now only one damaged male specimen in the bottle available for comparison, but such characters as can be seen, and the drawings of Chabaud *et al.* (1980) (Fig. 5 B, E, p. 438), are consistent with *L. tasmanienne*.

Linstowinema tasmanienne appears to have a geographic range which extends across Tasmania and Kangaroo Island. Three hosts from Kangaroo Island were infected with two species of *Linstowinema*, one with *L. cinctum* and *L. tasmanienne*, and two with *L. waringtoni* and *L. tasmanienne*. This suggests past links between Kangaroo Island hosts, mainland Australian hosts and Tasmanian hosts.

Etymology

The species is named according to a label found in AHC 1820, "*E. cinctum tasmaniensis*", here determined to be *L. cinctum*, which had apparently been written by Chabaud *et al.* when preparing their paper of 1980.

Type locality

Kingston, Tasmania, Australia

Type host

Isodon obesulus (Shaw, 1797)

Site in host

Small intestine

Type specimens

Holotype male, AHC 30320, allotype female, AHC 30321, paratypes AHC 30310

Linstowinema peramelis sp. nov.
(FIGS 62-66)

Synonym: *Echinonema cinctum sensu* Spratl.
Beveridge & Walters 1991: p. 22.

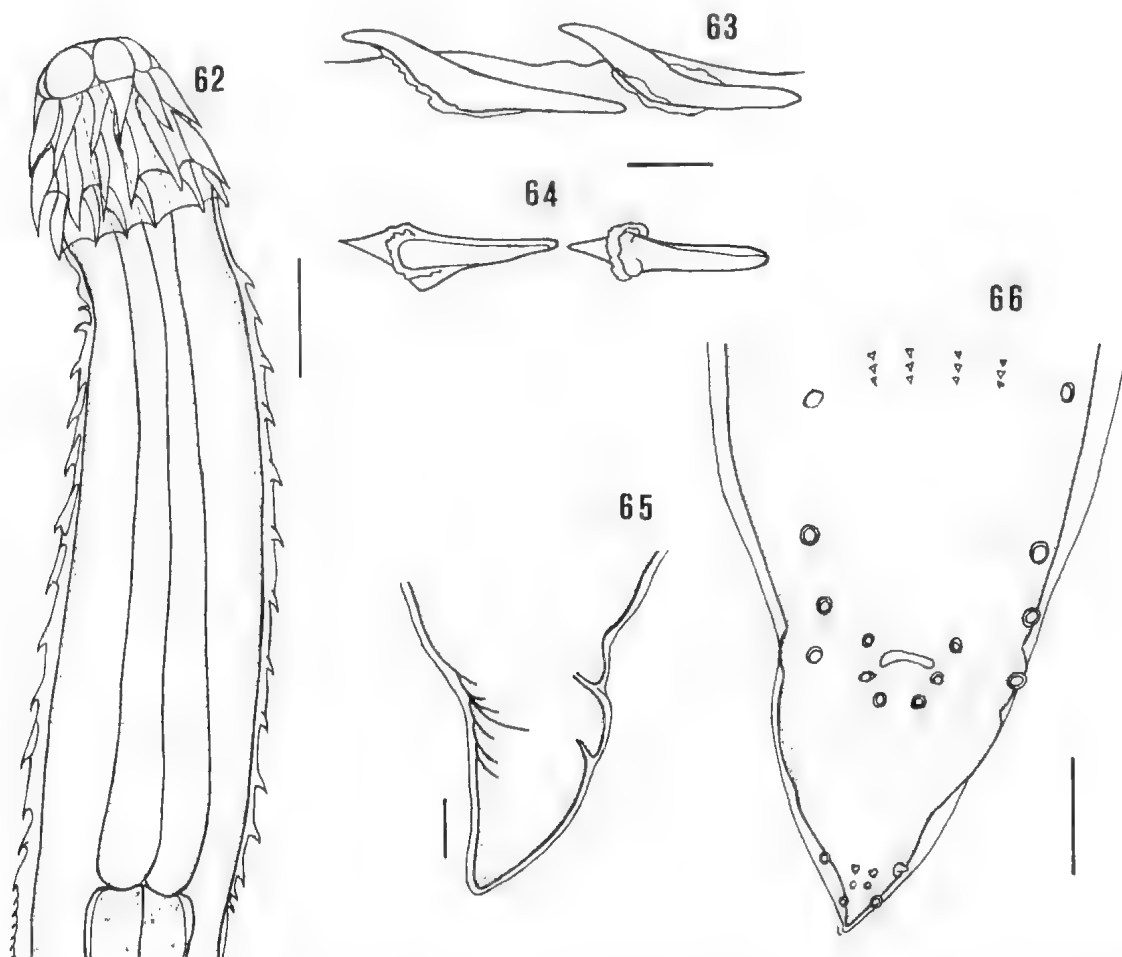
Material examined

Type material: Holotype ♂, AHC 30023, allotype ♀, AHC 30097, from *Perameles bougainville*.

Other material: From *Perameles bougainville* 1 ♂, 1 ♀, 1 anterior end, 1 posterior end, no collection data, AHC 30055, 30054, 30053; 1 ♂, 1 ♀, 3 anterior ends, 2 posterior ends, no collection data, AHC 4522; 2 ♂♂, 1 ♀, captive, University Adelaide, no date, AHC 13928.

Description

Cephalic bulb with 3 rows of 15 (male) or 16 (female) files of hooks, 2nd row longest, 3rd row much the smallest (Fig. 62); neck with about 6 rows



Figs 62-66. *Linstowinema peramelis* sp. nov. 62. Anterior end (lateral view). 63. Body hooks (lateral view). 64. Body hooks (dorsal view). 65. Female tail (lateral view). 66. Male tail (ventral view). Scale bars = 200 µm 62; 25 µm 63, 64; 100 µm 65, 66.

tiny spines; cuticular dilation of oesophageal region bearing 10-12 rows, 14 (male) or 16 (female) files of body hooks, first and last rows smallest, 6th-8th rows largest, roots of hooks without undulating edges (Figs 63, 64); remainder of body with a row of small spines in each cuticular annulation (numbers of spines not counted), over whole body of female; extending over $\frac{1}{4}$ dorsal surface, terminating about 300 anterior to cloaca ventrally, reaching level of most anterior pair of caudal papillae, on ventral surface of male body (Fig. 66). Oesophagus simple club-shaped, about $\frac{1}{10}$ - $\frac{1}{8}$ body length, terminating at 11th-12th row of hooks (Fig. 62). Secretory-excretory pore, detritus and nerve ring not seen.

Male: ($n=2$). Length 9, 9 mm, width 475, 475. Cephalic bulb 235, 325 long by 234, 267 wide, cephalic hooks 1st row 123, 129, 2nd row 117, 150, 3rd row 75, 93 long. Oesophagus 795, 970 long, cuticular dilation bearing 11-12 rows body hooks. Spicules similar, equal, without alae, 950, 1050 long, about $\frac{1}{10}$ body length. Gubernaculum short, simple, sub-triangular, 11 pairs caudal papillae; 3 pairs ventral and immediately pre-, sub- and post-cloacal respectively, 1 pair lateral ad-cloacal, 3 pairs lateral pre-cloacal; 7 anterior pairs all about same size; 3 pairs papillae, pair phasmids well posterior to cloaca, near tail tip (Fig. 66). Cloacal region with small cuticular bosses, ala-like expansion absent. Tail 210, 240 long.

Female: ($n=2$). Length 11 mm, width 520. Cephalic hooks 1st row 260, 135, 2nd row 140, 260, 3rd row 78, 140. Oesophagus 1190, 1250 long; cuticular dilation bearing 10-12 rows body hooks. Tail 460 long (Fig. 65). Vulva not seen. Eggs more or less spherical, 51-57 by 60-63.

Remarks

Although there was only a small number of specimens and they were all in poor condition, significant differences between these specimens and other species of *Linstowinema* could be found. Although elements such as the vulva could not be seen, the worms appeared to be mature, having fertilized eggs *in vitro*. Since *P. bougainville* is now extinct on mainland Australia and fully protected on the islands in Shark Bay Western Australia, it is unlikely that any more specimens will become available. Accordingly, this somewhat incomplete description is presented as the best possible of the species under the circumstances. *Linstowinema peramelis* sp. nov. most closely resembles *L. warringtoni* and the species that have been distinguished in the discussion of *L. warringtoni*, in that there are no more than 11-12 (male) and 10-12 (female) rows of body hooks compared with 9-11 (male) and 11-13 (female) and the oesophagus is

relatively long, extending to the 11th or 12th row of body hooks. The two species can be differentiated by size. *Linstowinema warringtoni* males, 15-20 mm, and females, 32-41 mm, are much larger worms than *L. peramelis*, 9 and 11 mm, respectively. *Linstowinema peramelis* has plain edges on the roots of its body hooks but *L. warringtoni* has undulating edges. The numbers and arrangement of papillae on the posterior end of the male are also different. *Linstowinema peramelis* is the only species of *Linstowinema* with four pairs of papillae lateral and anterior to the cloaca; all other species have three. The spicules of *L. peramelis* (950-1050, $\frac{1}{10}$ body length), are relatively longer than those of *L. warringtoni* (690-1090, $\frac{1}{20}$ body length). *Linstowinema peramelis* has three pairs of papillae near the caudal tip but *L. warringtoni* has five. The tail of *L. peramelis* (210, 240 (male), 160 (female)), is shorter than that of *L. warringtoni* (330-420 and 1000-1900). The eggs of *L. peramelis* (51-57 by 60-63) are larger than those of *L. warringtoni* (30-44 by 33-48).

Linstowinema peramelis is similar to *L. inglesi* and *L. cucutum*, in having three pairs of caudal papillae. It can be differentiated from these two species in having a relatively long oesophagus, terminating at the level of the posterior rows of hooks on the cuticular dilation of the oesophageal region, and not within it, and in having up to 12 rows of body hooks without undulating edges compared with *L. inglesi*, up to 14, and *L. cucutum*, up to 18 rows of body hooks with undulating edges.

Linstowinema peramelis resembles *L. tasmanianse* in having four pairs of caudal papillae near the caudal tip and body hooks without undulating edges, but differs from *L. tasmanianse* in having the oesophagus terminating at the end of the cuticular dilation and not within it, up to 12 rows of body hooks rather than 15 and larger eggs, 51-57 by 60-63, compared with 36-48 by 33-45.

Although the third row of cephalic hooks is relatively much smaller than the first and second rows in *L. peramelis* than in other species of *Linstowinema*, the cephalic hook sizes vary greatly between individuals and so this may not be a consistent character.

The eight *P. bougainville*, dissected to provide *L. peramelis* for this study (three of which were infected), were all registered in the SAMA in 1936, but no other collection data were given in the museum register. The collection data for AHC 4522 and 13928 are equally sparse, the information on the labels giving only the locality as possibly South Australia and captive in the Zoology Department of the University of Adelaide. Examination of the AHC records indicates that five additional bandicoots were dissected for helminths, two of which were infected with *L. peramelis*. This suggests that the prevalence

of infection in *P. bougainville* by *L. peramelis* was about 38%.

Etymology

The specific name is taken from the label of AHC 4522, the material, originally registered as *Echinonema cinerum perameles*, here determined to be *L. peramelis*.

Type locality

Unknown, Australia

Type host

Perameles bougainville Quoy & Gaimard, 1824

Site in host

Small intestine

Type specimens

Holotype male, AHC 30023, allotype female, AHC 30097

Linstowinema maplestoni sp. nov.

(FIGS 67-78)

Material examined

Type material: Holotype ♂, allotype ♀, from *Perameles nasuta* Dinger Creek, (17° 26'S, 146° 00'E), Queensland, 11.v.60, AHC 30094, 30095; Paratypes 4 ♂♂, 1 ♀, 2 anterior ends, 1 ♂ posterior end QM 14363/1, AHC 19763.

Other material: From *Perameles nasuta* Queensland; 2♀♀, no locality given, 5.ix.57, QM GL 14457, 1♂, 2♀♀, 1♂ fragment, Innisfail, (17° 32'S, 146° 01'E), 15.xii.59, QM GL 14356; 2♂♂, 2♀♀, southern Queensland, no date, AHC 1726.

From *Isodon macrourus* Queensland; 2♀♀, Mossman, (16° 28'S, 142° 23'E), 4.iii.1958, QM GL 14363/2; 2♂♂, 2♀♀, Innisfail, (17° 32'S, 146° 01'E), 22.vi.79, AHC 1726; 1♂, Brisbane, (27° 28'S, 151° 01'E), no date, AHC 1738; 5♂♂, 1♀, 1 anterior end, Puddington, (27° 28'S, 153° 01'E), Aug. 1955, AHC 4371; from bandicoot, no collection data, 3♀♀, AHC 19667.

Description

Cephalic bulb with three rows of 14 (male) (Fig. 69) or 16 (female) files of large hooks, 2nd row largest 3rd row smallest (Fig. 68); neck with 5-8 rows of tiny spines; cuticular dilation of oesophageal region bearing 11-13 rows of 14 (male) or 16 (female) files of body hooks, first and last 2 rows smallest, 7th - 9th rows largest; roots of hooks without undulations (Figs 72, 73), remainder of body with a row of up to 42 (male) or 50 (female) small spines at each annulation (Fig. 71), over whole body of female,

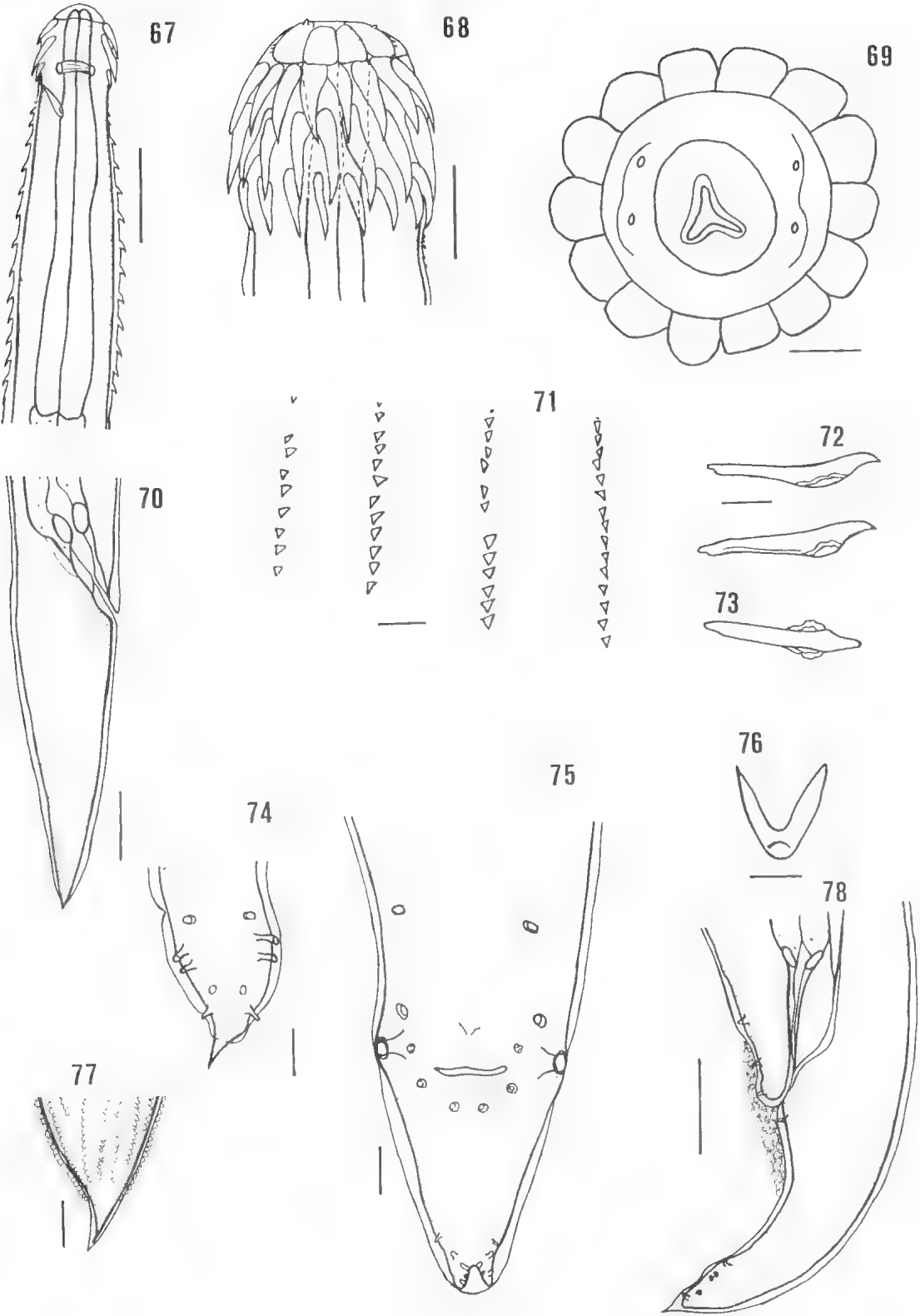
extending over $\frac{1}{2}$ dorsal surface, terminating about 400 anterior to cloaca on ventral surface of male body. Oesophagus simple, club shaped about $\frac{1}{10}$ - $\frac{1}{6}$ body length terminating posterior to oesophageal cuticular dilation (Fig. 67). Nerve ring surrounding oesophagus within cephalic bulb; secretory-excretory pore in neck; deirids conical, at level of 1st row of body hooks.

Male: Length 13-23 (17.5) mm, width 475-560 (550). Cephalic bulb 285-350 (335) long by 260-310 (290) wide; cephalic hooks 1st row 117-150 (130), 2nd row 140-175 (160), 3rd row 90-130 (120) long. Oesophagus 1360-2210 (1809) long; cuticular dilation bearing 11-13 rows body hooks. Deirids 405-530 (475), nerve ring 255-300 (285), secretory-excretory pore 325-405 (360) from anterior end. Spicules equal, similar, without alae 920-1100 (1030) long, about $\frac{1}{10}$ body length. 11 pairs caudal papillae: 3 pairs ventral and immediately pre-, ad- and post-cloacal respectively, 1 large pair lateral ad-cloacal, 2 pairs lateral pre-cloacal; 4 pairs papillae, pair phasids well posterior to cloaca, near tail tip (Figs 74, 75). Cloacal region with small cuticular bosses, ala-like expansions absent. Gubernaculum short, simple, sub-triangular in ventral view, 60 (n=1) long (Fig. 76). Tail 305-440 (375) long (Fig. 78).

Female: Length 18-35 (28) mm, width 560-765 (670). Cephalic bulb 325-425 (362) long by 274-425 (330) wide; cephalic hooks 1st row 150-176 (160), 2nd row 170-225 (190), 3rd row 115-145 (125) long. Oesophagus 1615-3740 (2272) long; cuticular dilation bearing 12-13 rows body hooks. Deirids 405-585 (495), nerve ring 260-390 (330), secretory-excretory pore (n=2) 405-470 from anterior end. Vulva not seen. Tail 565-970 (790). Eggs not measured.

Remarks

Linstowinema maplestoni sp. nov. resembles *L. warringtoni* in having up to 13 rows of body hooks, a relatively long oesophagus and five pairs of caudal papillae on the male. It differs from *L. warringtoni* in having 11-13 (male) and 12-13 (female) compared with 9-11 (male) and 11-13 (female) rows of body hooks. The oesophagus of *L. maplestoni*, extends beyond the cuticular dilation of the oesophageal region of the body whereas in *L. warringtoni* it terminates at the level of the 9th - 13th rows of body hooks. The body hooks of *L. maplestoni* are without undulating edges and those of *L. warringtoni* are with undulating edges. Male body spines extend along $\frac{1}{2}$ of the body dorsally and well above the lateral caudal papillae ventrally on *L. maplestoni* but on *L. warringtoni* they extend along $\frac{1}{3}$ of the body dorsally and almost to the lateral caudal papillae ventrally. All 6 pairs of pre-, post- and ad-cloacal papillae are the



same size on *L. warringtoni* but *L. maplestoni* has larger lateral ad-cloacal papillae. The spicules of *L. maplestoni* ($1/10$ body length) are relatively longer than those of *L. warringtoni* ($1/10$ body length). The arrangement of the papillae surrounding and anterior to the cloaca of *L. maplestoni* most closely resembles that for *L. inglesi* i.e., with the lateral ad-cloacal pair the largest and the ventral body spines not extending to the level of the caudal papillae. *Linstowinema maplestoni* differs from *L. inglesi* in having the oesophagus extend posterior to the body hooks without undulating edges rather than an oesophagus which terminates within the cuticular dilation at about the level of rows 8-9 of the body hooks with undulating edges. Male *L. inglesi* have only three pairs of papillae on the caudal tip but *L. maplestoni* have four. Male *L. maplestoni* on average have longer tails (305-440 (375)) than *L. inglesi* (150-350 (265)), the body spines of *L. maplestoni* extend along $1/3$ of the body dorsally compared with almost the whole body ($4/5$) on *L. inglesi*.

Linstowinema maplestoni can be distinguished from *L. latens*, which also has the oesophagus extending posterior to the body hooks, body hooks with undulating edges and four pairs of papillae on the caudal tip, in having 11-13 (male) and 12-13 (female) rows of hooks compared with 8-10 (male) and 9-12 (female) rows of body hooks in *L. latens*. Male *L. maplestoni* have body spines extending along $1/3$ of the body dorsally and well above the lateral caudal papillae ventrally compared with *L. latens*, which has body spines extending along $1/10$ of the body dorsally and level with the most anterior lateral caudal papillae ventrally. The lateral ad-cloacal pair of papillae is largest on *L. maplestoni* compared with all 3 pairs of lateral cloacal papillae being the same size on *L. latens*. Female *L. maplestoni* have on average shorter tails (565-970 (790)) than *L. latens* (790-1645 (1070)).

Linstowinema maplestoni can be differentiated from *L. cinctum* in having 11-13 (male), 12-13 (female) body hooks without undulating edges compared with 13-16 (male), 14-18 (female) body hooks with undulating edges; a long oesophagus terminating posterior to the rows of body hooks, not a short oesophagus terminating at the level of the 8-11 rows of hooks. *Linstowinema maplestoni* has four pairs of caudal papillae at the tail tip, while *L. cinctum* has three; the pair of lateral ad-cloacal

papillae is the largest on *L. maplestoni* but all six pairs of cloacal papillae are the same size on *L. cinctum*. *Linstowinema maplestoni* does not have an ala-like expansion surrounding the cloaca but *L. cinctum* does; the ventral body spines of *L. cinctum* extend almost to the level of the most anterior lateral pair of pre-cloacal papillae but in *L. maplestoni* they do not; the female tail of *L. maplestoni* (565-970 (790)) is shorter than that of *L. cinctum* (986-1122 (1050)).

The other species of *Linstowinema*, *L. peramelis* and *L. tasmaniense*, which have body hooks without undulating edges have three pairs of caudal papillae on the tail tip. These can be further differentiated from *L. maplestoni* by the number of rows of body hooks and the relative lengths of the oesophagus. *Linstowinema peramelis* has 10-12 rows of body hooks with the oesophagus terminating at the level of the 12th row; *L. tasmaniense* has 13-15 rows of body hooks with the oesophagus terminating at the level of the 8th - 10th row and *L. maplestoni* has 11-13 rows of body hooks with the oesophagus terminating posteriorly to the 13th row. *Linstowinema peramelis* has four pairs of lateral ad- and pre-cloacal papillae, compared with three pairs on *L. maplestoni* and relatively shorter spicules ($1/10$ of body length) compared with ($1/10$). *Linstowinema tasmaniense* has three large pairs of lateral cloacal papillae compared with the one large ad-cloacal pair of *L. maplestoni*.

Because of the small number of female specimens available, none was dissected, so although eggs were seen, it was difficult to determine which were mature and therefore suitable for measuring. As a result, no measurements were made.

Linstowinema maplestoni occurs in *P. naruna* and *L. macrourus* from Queensland and New South Wales although the examination of more hosts is required before the full extent of the geographic range of this species can be determined. In two *L. macrourus*, *L. maplestoni* occurred in mixed infections with *L. warringtoni*.

Etymology

The species is named after P.A. Mapleston, who together with W. Yorke, carried out pioneering work on the nematodes of Australian marsupials. *Echinonema maplestoni* was used on an updated museum label by Chabaud *et al.* (1980) for *Linstowinema* specimens from *L. macrourus* that were subsequently determined to be *L. warringtoni*.

Figs 67-78. *Linstowinema maplestoni* sp. nov. 67. Anterior end, optical section (lateral view). 68. Cephalic bulb (lateral view). 69. Cephalic end male, optical section at level of first row of hooks (ventral view). 70. Female tail (lateral view). 71. Male, posterior body spines (ventral view). 72. Body hook (lateral view). 73. Body hook (dorsal view). 74. Male tail tip (ventral view). 75. Male tail (ventral view). 76. Gubernaculum (ventral view). 77. Female tail tip (lateral view). 78. Male tail (lateral view). Scale bars = 500 μ m 67, 200 μ m 68, 70, 50 μ m 69, 75, 77, 25 μ m 71-73, 74, 76, 100 μ m 78.

*Type host**Perameles nasuta**Type locality*

Dinner Creek (17° 26'S, 146° 00'E), Queensland, Australia

Site in host

Small intestine

Type specimens

Holotype: male, QM30094; allotype: female, QM30095

Discussion

Linstowinema warringtoni appears to be the dominant species of *Linstowinema* in eastern Australian bandicoots, being found from northern Queensland through to South Australia, including Kangaroo Island. It occurs in all extant species of *Isodon* as well as one individual of *P. nasuta*, indicating a low prevalence in this latter host species. Although *L. latens* was found in northern Queensland populations of the northern brown bandicoot, together with *L. warringtoni*, it was the only species occurring in northern brown bandicoots from the Northern Territory and the north of Western Australia, while *L. inghisi* was the only species occurring in southern brown bandicoots in the south of Western Australia.

Only one species, *L. perameles*, occurring in five of 13 *P. bongainville* examined, has been found exclusively in *Perameles* spp. and three species *L. tasmanianse*, *L. latens* and *L. inghisi* exclusively in *Isodon* spp. *L. latens* occurs in *I. macrourus*; *L. tasmanianse* and *L. inghisi* occur in *I. obesulus*. Of the other three species, *L. maplestoni* has a north-eastern distribution occurring in *I. macrourus* and *P. nasuta*. *L. cinereum* a more south-eastern distribution occurring in *I. obesulus*, *P. nasuta* and *P. gunnii*.

Further collections of material from south-eastern Australia are needed before any hypothesis on the distribution of species of *Linstowinema* can be developed. It does appear that bandicoots (*I. obesulus*) on Kangaroo Island, but not Tasmania, may have been derived from stock in which all three species (*I. warringtoni*, *L. cinereum*, and *L. tasmanianse*) were prevalent. The continuing detrimental effects of European settlement have resulted in a patchy distribution of *I. obesulus* over a reduced range (Braithwaite 1995). This decline in the host population may have affected the distribution and prevalence of species of *Linstowinema* on the mainland. The current prevalence of the three species of *Linstowinema* in bandicoots on Kangaroo Island

may reflect past prevalences of these species in bandicoots on the mainland.

The ability to trap bandicoots varies with species, their age, species and locality (Gordon & Hulbert 1989). *Perameles nasuta* is apparently more difficult to trap than species of *Isodon* (Menkhurst & Seebeck 1995). This may be the reason for the small number of *Perameles* compared with *Isodon* collected in this study (see Table 1) and in the amount of material deposited in museum collections from each host genus. A further complicating factor is the possible difference in prevalence of infection with *Linstowinema* between the two. The records of the SAMA and QM indicate that 90 *P. nasuta* have been examined for helminth parasites and, of these, only eight were infected with *L. maplestoni*, six with *L. cinereum* and one with *L. warringtoni*. Similarly, of 51 *P. gunnii* examined, only four were infected with *L. cinereum* and one with *L. warringtoni*. It is unlikely that *Linstowinema* could have been overlooked during dissection as the worms are large and can be readily detected in the small intestine. These low prevalences of infection contrast with the prevalences found for species of *Isodon* dissected in this study. Of 72 bandicoots examined, 53 were infected with *Linstowinema* spp.

A working hypothesis would be that species of *Linstowinema* are dominant in the helminth communities of *Isodon* but not in those of *Perameles*. In some areas, species of bandicoot have overlapping geographic ranges, *L. macrourus* and *P. nasuta* in the north-east, *I. obesulus* and *P. nasuta* in the south-east and *I. obesulus* and *P. gunnii* in Tasmania. Their habitat preferences within each geographic region are different, and although they may not be in strict sympatry, opportunities for incidental infection and host switching would exist. Observations from this study suggest that species of *Linstowinema* may switch from *I. obesulus* to *P. gunnii* and *P. nasuta*; from *I. obesulus* to *P. bongainville* and perhaps from *P. nasuta* to *I. macrourus*. This might account for the occurrence of *Linstowinema* in *Perameles*.

Additional collections of material from *Perameles* spp. across Australia and especially *I. obesulus* from south eastern Australia are needed to test this hypothesis.

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**A NEW SPECIES OF FRESHWATER AMPHIPOD,
AUSTROCHILTONIA DALHOUSIENSIS SP. NOV.,
(CRUSTACEA: AMPHIPODA: HYALELLIDAE) FROM
DALHOUSIE SPRINGS, SOUTH AUSTRALIA**

*By W. ZEIDLER**

Summary

Zeidler, W. (1997) A new species of freshwater amphipod *Austrochiltonia dalhousiensis* sp. nov. (Crustacea: Amphipoda: Hyalellidae) from Dalhousie Springs, South Australia. Trans. R. Soc. S. Aust. 121(1), 29-42, 30 May, 1997.

A freshwater amphipod *Austrochiltonia dalhousiensis* sp. nov. is described and illustrated. It is endemic to a few artesian springs amongst the Dalhousie Springs complex in the north of South Australia. Morphologically it is very similar to other species of *Austrochiltonia* found in mound springs near Lake Eyre South but preliminary electrophoretic analysis of allozymes supports the recognition of a distinct species. It most closely resembles *A. australis* (Sayce, 1901) in that uropod 3 is two-articulate, but differs in a number of minor features, which collectively distinguish it from its congeners.

Key Words: *Austrochiltonia*, *dalhousiensis* sp. nov., new species, amphipod, artesian springs, Australia, taxonomy.

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Introduction

Amphipod species of the genus *Austrochiltonia* are among the most common crustaceans found in the permanent freshwaters of southern Australia ranging from New South Wales to Western Australia and including Tasmania. More recently *Austrochiltonia* has also been found in the inland waters of artesian springs in South Australia (Zeidler 1989) and at "Edghaston" north-east of Aramac, Queensland (personal collection, May 1988).

When I re-established the genus *Austrochiltonia* (Zeidler 1988) it was my intention to proceed with an Australian revision of the genus beginning with the description of species found in the mound springs near Lake Eyre South and at Dalhousie Springs in northern South Australia. Since then I have examined a large number of specimens from wide-ranging habitats in southern Australia and have found them all to be very similar morphologically and difficult to distinguish from the only previously-described species, *A. australis* (Sayce, 1901) and *A. subtennis* (Sayce, 1902). Williams (1962) revised the systematics of these two species based on type material and a range of specimens from New South Wales, Victoria, Tasmania and Rottnest Island, Western Australia and likewise found that, morphologically, specific differences are minimal. However, a preliminary analysis of allozymes of specimens from the South Australian mound springs using electrophoresis, indicates that *Austrochiltonia* is most likely a very speciose genus. Given its

potential enormity, the project was abandoned due to lack of resources.

The species found at Dalhousie Springs is most similar to *A. australis* Sayce, 1901 in that uropod 3 is two-articulate. It has a very restricted distribution, occurring at only three of about 80 active springs in the region (Zeidler 1989). Two of these springs are quite large, with large outflows of warm water (>40°C) but *Austrochiltonia* is found only in the distant overflow where the water is colder and close to ambient temperature. However, one isolated specimen was collected from the edge of the pool of the main spring, which has a water temperature of about 35°C. The other spring is a small, relatively cold spring on the southern edge of the spring complex. In each case the animals were only found in the shallow edges of swamps or channels amongst the base of the sedge *Cyperus laevigatus* L., 1771 and sometimes also the reed *Phragmites australis* (Cav., 1841).

The restricted and isolated distribution of this species of *Austrochiltonia* makes it vulnerable to habitat disturbance even though Dalhousie Springs is within Witjira National Park. The purpose of this paper is to establish the taxon so that park managers and visitors can appreciate its significance and potential vulnerability.

Materials and Methods

The Dalhousie Springs complex (Fig. 1) consists of about 80 active springs all of which were sampled in 1985 (Zeidler & Ponder 1989) but *Austrochiltonia* was found in only three springs (Fig. 2). The springs are coded following Zeidler & Ponder (1989, Fig. 2).

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5000

Animals were collected from amongst sedges and reeds with a small hand sieve or picked off plant debris with forceps. A total of 424 specimens (230 ♀♀, 174 ♂♂, 20 juveniles) was collected and examined.

Physicochemical data for the sites sampled are limited but some measurements were made near the main source of the spring. These data are given in

Table 1 and data on nearby springs are also available (Smith 1989).

The new species was compared with the descriptions of *Austrochiltonia* given by Williams (1962) and with specimens of *A. australis* from Dandenong Creek, Victoria (SAMA C3872) identified by Williams and used in the study by Smith & Williams (1983).

Material reported here is deposited in the South Australian Museum, Adelaide (SAMA) and the Australian Museum, Sydney (AM). All specimens are preserved in 75% ethanol or 2% formaldehyde/propylene-glycol solution. Of the types, only the holotype and allotype have been dissected (partially), with appendages removed from the left hand side of the animal unless otherwise indicated. Dissected appendages are preserved with the carcass or, in the case of the holotype, the mouthparts, uropods and telson are mounted in polyvinyl lactophenol on a microscope slide.

Specimen length is measured along a lateral parabolic line drawn from the anterior extremity of the head through the mid-line of the body to the posterior limit of the telson using a pair of dividers and scale.

The thoracic limbs are referred to as gnathopod 1 and 2 followed by pereopods 3-7. Size comparisons of gnathopods exclude the coxa and dactylus, and of the pereopods, the coxa, with articles being measured along the mid-line.

The following abbreviations are used in the text and figures. A1, A2 = first & second antenna; G1, G2 = first & second gnathopod; LL = lower lip; Md = mandible; Mx1, Mx2 = first & second maxilla; Mxp = maxilliped; O2-5 = oostegites from pereopods 2-5; P3-7 = pereopods 3-7; PH = first pleopoda; T = telson; U1-3 = uropods 1-3; UL = upper lip; r = used as suffix to indicate that appendage was taken from right hand side of the animal.



Fig. 1. Location of Dalhousie Springs, South Australia. From Zeidler 1991.

TABLE 1. Temperature measurements and physicochemical data (from Smith 1989) for springs from which amphipods were collected at time of collection (except for Cal - data from 1983 expedition)

Spring	Field Chemistry						
	Temp. Air °C	Temp. Water °C	Temp. °C	Cond. 25°C siemens	TDS mg l ⁻¹	pH	DO ppm
Cal - channel to main pool	-	-	4.3	1490	865	7.3	3.8
Cal - main pool	20	37	34	1780	1000	7.9	6.7
Cal - main discharge channel	25	36	33.5	2050	1150	7.7	4.7
Cd2 - SW edge of pool	15	32	32	1550	850	7.9	11.3
Cd2 - at or near swamp	15	11	18	1650	-	7.8	7.6
Gbl	13	16	20	7610	4850	7.1	4.8

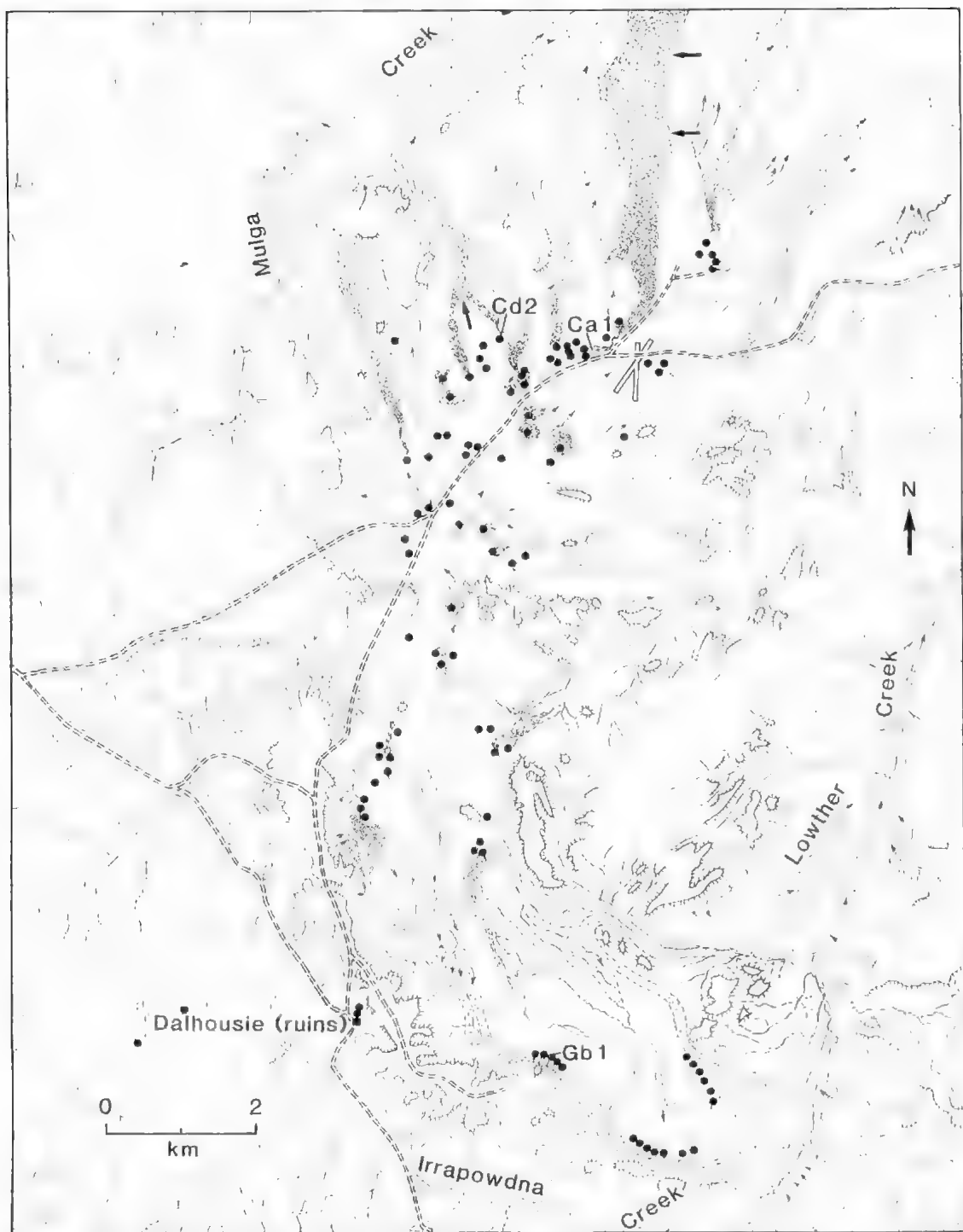


Fig. 2 Dalhousie Springs complex showing springs (coded) from which *Austrochiltonia dalhousiensis* sp. nov. was collected. Collection sites for Ca1 and Cd2 are arrowed. Other major springs are shown as dots. Swamps from springs and creek beds are stippled (light stippling indicates ephemeral stream beds and heavier stippling areas of 'permanent' water).

Systematics

Austrochiltonia dalhousiensis sp. nov.

(FIGS 3-9)

Austrochiltonia sp. Zeidler, 1989: 83-84, fig. 12.1B; 1991: 185

Holotype: ♂, Dalhousie Springs SA, from amongst reeds and sedges along eastern edge of swamp created by outflow from main spring (Ca1), 3.3 km north of edge of old airstrip, 26°23'07" S 135°30'26" E, 12.vi.1985. W. Zeidler & K.L. Gowlett-Holmes. SAMA C5651.

Allotype: Ovigerous ♀, SAMA C5652. Collected with holotype.

Paratypes: AMP48840, 10 ♀♀, 10 ♂♂, same data as holotype. SAMA C5653, 24 ♀♀ (one ovigerous), 17 ♂♂, same data as holotype. SAMA C5654, 37 ♀♀ (three ovigerous), 11 ♂♂, same data as holotype except 14.vi.1985. SAMA C5655, 23 ♀♀, 18 ♂♂, same data as holotype but 1.1 km further north, 26°22'26" S 135°30'26" E.

Other material examined: All from Dalhousie Springs area (Fig. 2). AM P48841, 1 ♀ (damaged), spring Ca1, 26°25'00" S 135°29'53" E, from edge of main pool, W. F. Ponder & D. Winn, 3.vi.1985. SAMA C5656, 21 ♀♀ (three ovigerous), 31 ♂♂, spring Cd2, from edges of swamp formed by outflow, approximately 0.9 km NW of source, 26°24'33" S 135°28'45" E, W. Zeidler & K. L. Gowlett-Holmes, 6.vi.1985. SAMA C5657, 14 ♀♀, 21 ♂♂, same data as previous lot except 14.vi.1985. AM P48842, 10 ♀♀ (one ovigerous), 6 ♂♂, spring Gb1, from edges of swamp, 26°31'12" S 135°29'26" E, W. F. Ponder & D. Winn, 5.vi.1985. SAMA C5658, 90 ♀♀ (three ovigerous), 61 ♂♂, 20 juveniles, same data as previous lot except collected W. Zeidler & K. L. Gowlett-Holmes.

Description of holotype male (Figs 3-6)

Length 3.8 mm. Head about as long as deep, length almost equivalent to first two pereonites. Antenna 1 about 3x length of head; peduncular article 1 length 1.5x width, articles 2 and 3 subequal in length about 0.75x length of article 1; flagellum slightly longer than 1.5x peduncle, of nine articles with one ventral aesthetasc at base of each of last four articles. Antenna 2 about 0.7x length of A1 with characteristic gland cone at base; peduncular article 1 slightly wider than long, article 2 width about 0.7x length, 2x as long as article 1 and 0.7x length of article 3; flagellum slightly longer than peduncle, of eight articles.

Upper lip slightly wider than long, apically rounded, bearing numerous short setae apically. Lower lip with vestigial inner lobes; outer lobes subovate with setose distal and inner margins.

Mandibles without palp; left with incisor of six

teeth, lacinia mobilis of five teeth, spine row of three feathered spines and triturative molar; right with incisor of five teeth, lacinia mobilis of three teeth, spine row of two feathered spines and triturative molar with one long feathered seta.

Maxilla 1 without palp, notched at palp's normal position; outer plate with nine comb-like spines apically; inner plate very narrow with two feathered spines apically.

Maxilla 2; outer plate about 1.5x length of inner plate, setal row restricted to apex; inner plate with one large seta medially about 0.4 from apex, setal row apically and medially, almost to large seta.

Maxilliped; inner plate large, sub-rectangular; reaching end of merus, maximum width about 3x length of outer margin, with three apical spine teeth, the inner one smaller, four plumose setae on inner margin and several apically; outer plate ovate, reaching midway along inner margin of carpus, about as wide as inner plate, apical margin with three setae, inner margin with several setae for distal half, palp large, 4-articulate; merus proximally narrow, sub-triangular, outer margin about 2x length of inner margin with two setae on inner distal angle; carpus slightly broader than long, slightly expanded distally, distal two-thirds of inner margin with row of setae, two setae on outer distal angle and also near inner distal angle; propodus slightly narrower and shorter than carpus, distal margin with several strong setae; curved dactylus with strong unguis.

Coxal gills sausage shaped, present from G2 to P6.

Gnathopod 1; coxa slightly longer than maximum width, proximal width about 0.7x distal width, anterior margin concave, posterior margin straight, distal margin evenly rounded with several evenly spaced setae; carpus triangular with large posterodistal lobe, with anterior margin almost 2x length of posterior margin, maximum width about 1.5x that of anterior margin, posterior margin with close-set row of nine stout, pectinate spines; propodus sub-rectangular, about 1.4x length of carpus, slightly wider distally, width 0.6x length, posterodistal corner with two stout spines on either side of dactylus, cluster of long setae on anterodistal corner, row of seven long setae medially, mixture of long and short setae near distal margin; dactylus slightly shorter than width of propodus fitting neatly against palm. Gnathopod 2 length 1.6x that of G1; coxal gill length 2x width, little shorter than coxa; coxa rectangular, slightly longer than wide, about 0.8x length of basis, distal margin evenly rounded with several evenly-spaced setae; merus with right-angled bend; carpus similar to G1 but without pectinate spines; propodus slightly shorter than basis, length anterior margin 1.5x maximum width, posteroproximal corner forming rounded lobe, palm oblique with numerous spines of varying lengths on

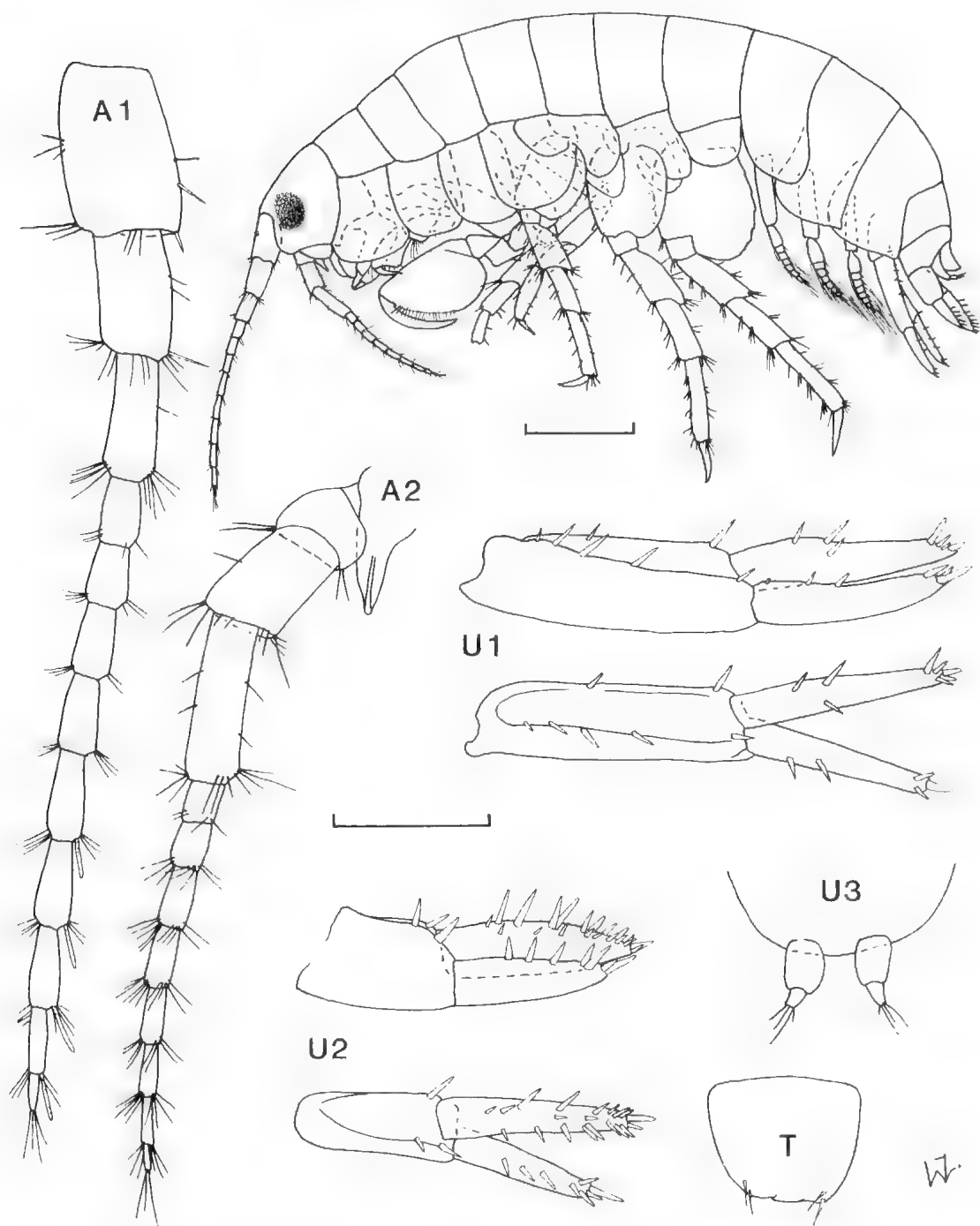


Fig. 3. *Austrochiltonia dalhousiensis* sp. nov., holotype ♂. Scale bars = 1.0mm (whole animal), 0.2 mm (A,U,T).

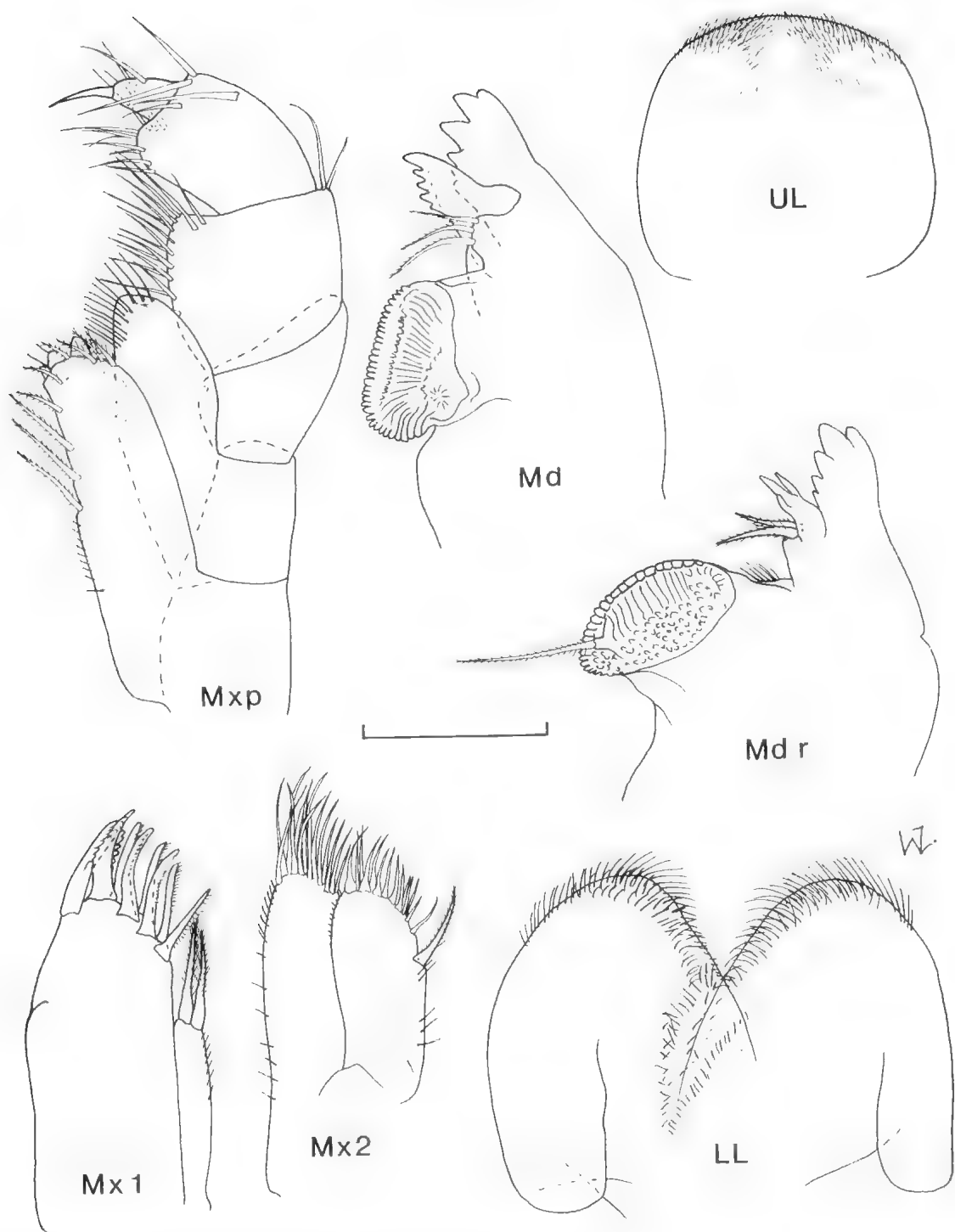


Fig. 4. *Austrochiltonia dalhousiensis* sp. nov., holotype ♂. Scale bar = 0.1 mm.

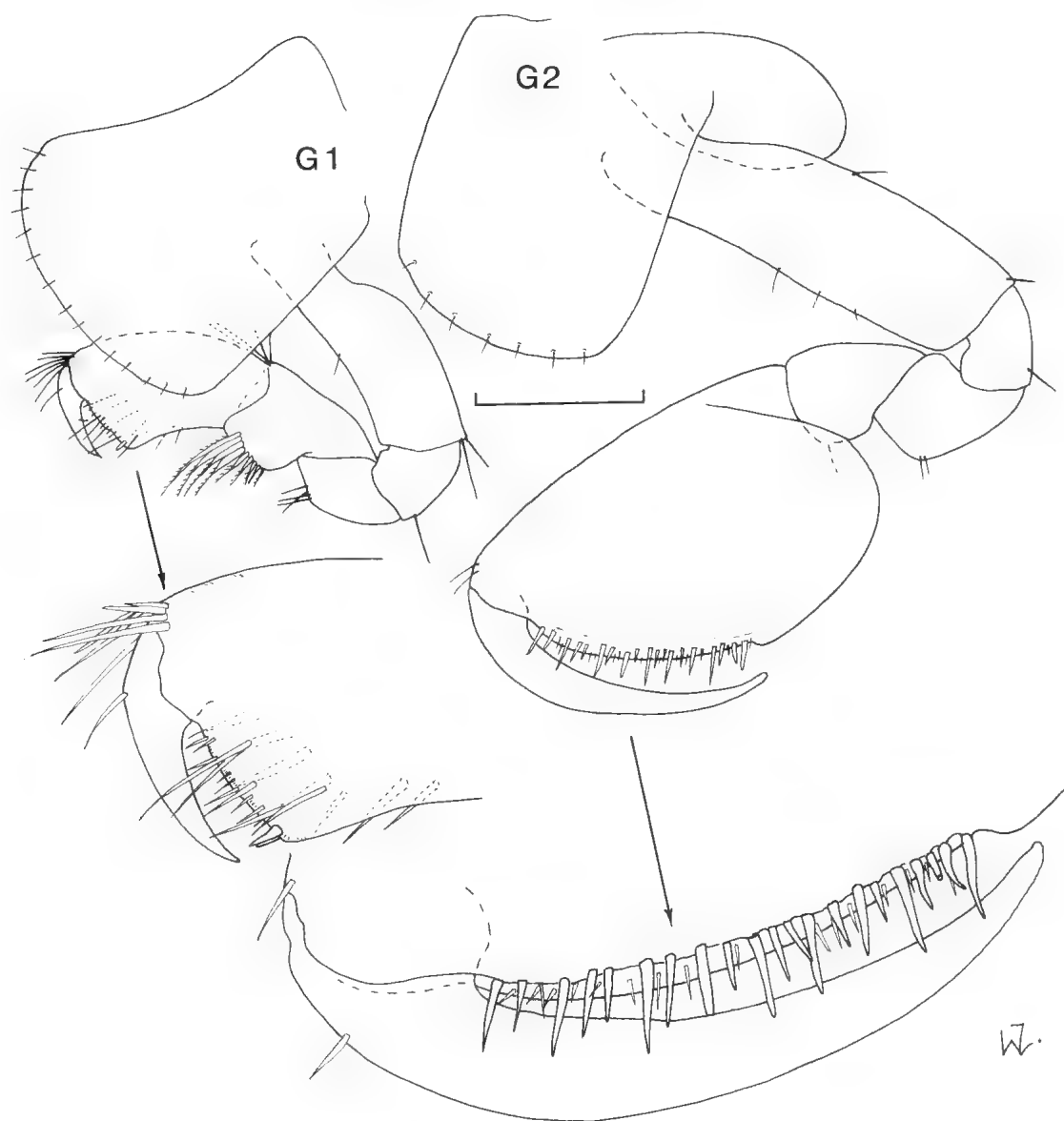


Fig. 5. *Austrochiltonia dalhousiensis* sp. nov., holotype ♂. Scale bar = 0.2 mm.

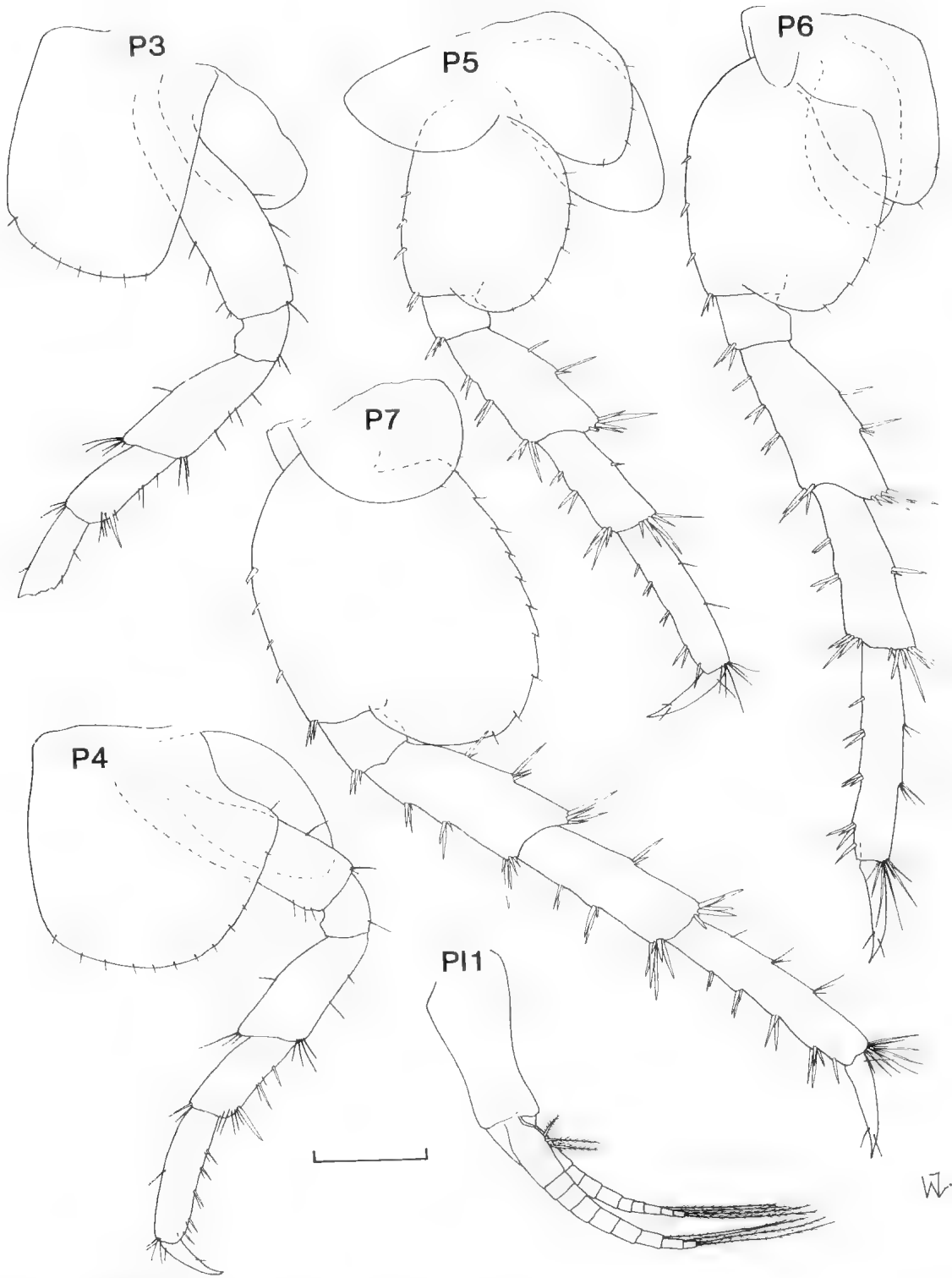


Fig. 6. *Austrochiltonia dalhousiensis* sp. nov., holotype ♂. Scale bar = 0.2 mm.

either side of cutting edge followed by shallow groove for tip of dactylus; dactylus claw-like, as long as anterior margin of propodus.

Pereopod 3 with part of propodus and dactylus missing on right; coxal gill length almost 2x width, about 0.75x length of coxa; coxa like that of G2 but slightly larger, slightly shorter than basis; merus 0.5x as long as basis, anterodistal corner produced; carpus 0.75x length of merus. Pereopod 4 similar to P3; slightly longer than G2; coxa with distinct posteroproximal excavation, maximum width slightly more than length, slightly longer than basis; propodus slightly longer than merus; dactylus stout, length slightly less than 0.5x of propodus. Pereopod 5 slightly longer than P4; coxal gill length about 2x width, slightly longer than basis; coxa width about 1.5x that of basis, anterior lobe slightly more than 0.5x length of basis, posterior lobe about 0.8x length of basis; basis slightly longer than wide with typical expanded posterior margin and posterodistal lobe reaching to about midway of ischium; merus with posterodistal corner produced, length about 0.7x that of basis; carpus slightly shorter than merus; propodus length 1.4x that of carpus; dactylus stout, 0.5x length of propodus. Pereopod 6 length 1.3x that of P5; coxal gill length about 2x width, about 0.75x length of basis; coxa almost as wide as basis, anterior lobe 0.3x length of basis, posterior lobe 0.8x length of basis; remaining articles like those of P5 but basis with straight posteroproximal shoulder and carpus slightly longer than merus. Pereopod 7 longest, slightly exceeding P6, like P6 but coxa semi-circular and lacking coxal gill, width 1.4x length, about 0.4x length of basis; posterodistal lobe of basis more expanded reaching to about midway of merus.

Pleopods all unmodified (not as in *Chiltonia*).

Uropod 1 about 1.5x length of U2; peduncle with spine on inner and outer distal corner, three large and one smaller spine on dorsal outer margin, one small spine on inner margin; outer ramus slightly shorter than inner, length 0.7x that of peduncle, with two median and three terminal spines; inner ramus with two small and three larger terminal spines and three medially. Uropod 2; peduncle with spine on inner and outer distal corner and additional one on dorsal margin; inner ramus 1.2x length of outer ramus and 1.3x that of peduncle, five large spines clustered terminally and three spaced evenly medially; inner ramus with 20 spines of varying sizes gradually closer together towards tip. Uropod 3 two-articulate, marginally more than 0.5x length of telson; ramus 0.5x length of peduncle with three long setae and one short seta terminally.

Telson entire, subrectangular, slightly wider than long, distal margin slightly concave with two small setae at each corner.

Description of allotype female (Figs 7-9)

Length 3.8 mm, ovigerous with 23 eggs in brood-pouch, same as male except for the following.

Antenna 2, flagellum of seven articles.

Gnathopod 1; coxa relatively narrower and longer than for male, width distally 0.8x length; posterior margin of carpus with close-set row of 10 pectinate spines; propodus relatively narrower than for male, slightly longer than carpus. Gnathopod 2 length 1.2x that of G1; coxal gill relatively smaller, less than 0.5x length of coxa; coxa with posterior margin produced to point medially, maximum width 0.8x length, as long as basis; remaining articles like those of G1 only relatively more slender. Pereopod 3 length about 1.3x that of G2; coxa similar in shape to that of G2. Pereopod 4 slightly shorter than P3; coxa without distinct proximal excavation, almost as wide as long. Pereopod 5 only marginally longer than P4; coxa width about 1.7x that of basis; merus, carpus and propodus relatively shorter than for male. Pereopod 6; basis with posterior margin rounded proximally; merus, carpus and propodus relatively shorter than for male. Pereopod 7 slightly shorter than P6; basis relatively narrower, and merus, carpus and propodus successively slightly shorter than for male.

Oostegites on coxae 2-5, all with curled margins and numerous small hooks, together forming tight marsupium. First heart-shaped, length 1.6x maximum width, about 0.7x length of G2; second trapezoid, length almost 0.5x that of P3, maximum width almost 0.5x length; third oval-shaped of similar size to second; fourth sub-rectangular with oblique distal margin, length anteriorly almost 0.5x that of P5, maximum width almost equal to length of posterior margin.

Uropod 1 length 1.6x that of U2; peduncle with five large and one small spine on outer margin, inner margin with two small spines proximally in addition to large spine on distal corner; outer ramus as long as inner, length 0.8x that of peduncle, with two large and two smaller spines terminally and two medially; inner ramus with three large and two smaller spines terminally and two medially. Uropod 2 peduncle with two large spines on outer margin; outer ramus slightly shorter than inner, length 1.3x that of peduncle, one large and two smaller spines terminally, three large spines medially; inner ramus with two terminal spines, cluster of four near tip and another two medially.

Telson with group of three small setae at each corner.

Etymology

Taken from the type locality in recognition of the restricted distribution of the species.

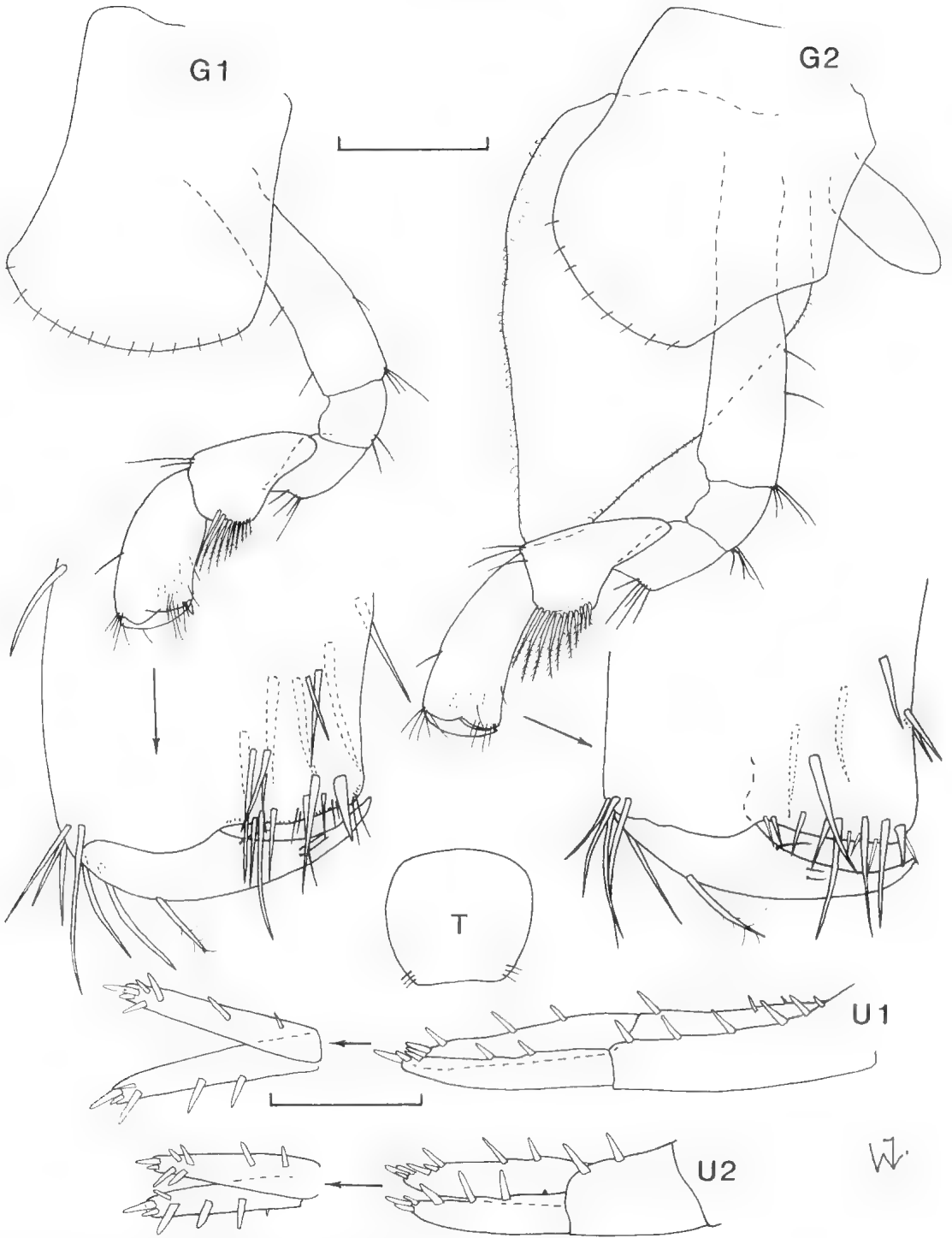


Fig. 7. *Austrochiltonia dalhousiensis* sp. nov., allotype ♀. Scale bars = 0.2 mm.

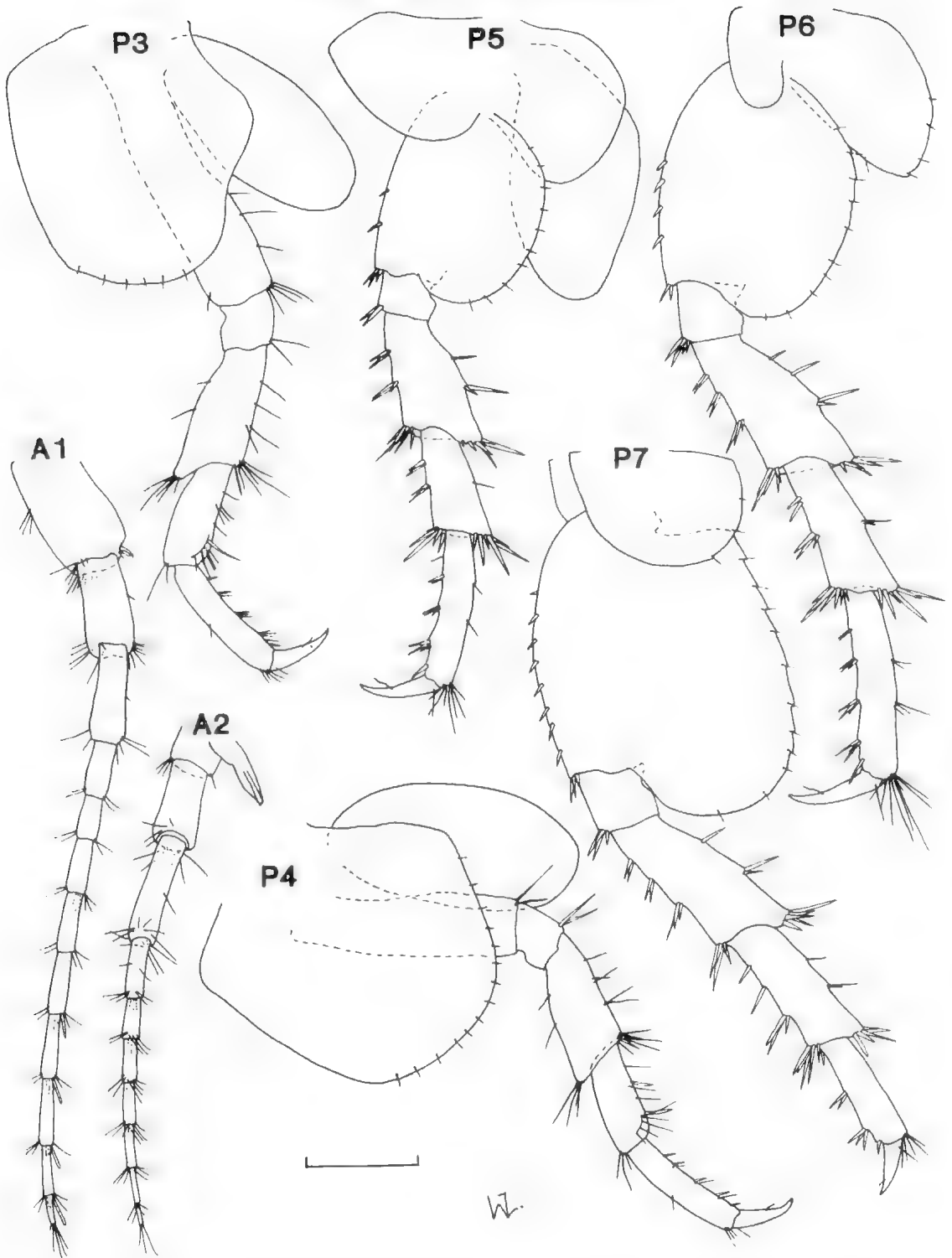


Fig. 8. *Austrochiltonia dalhousiensis* sp. nov., allotype ♀. Oostegites on P3-5 not illustrated. Scale bar = 0.2 mm

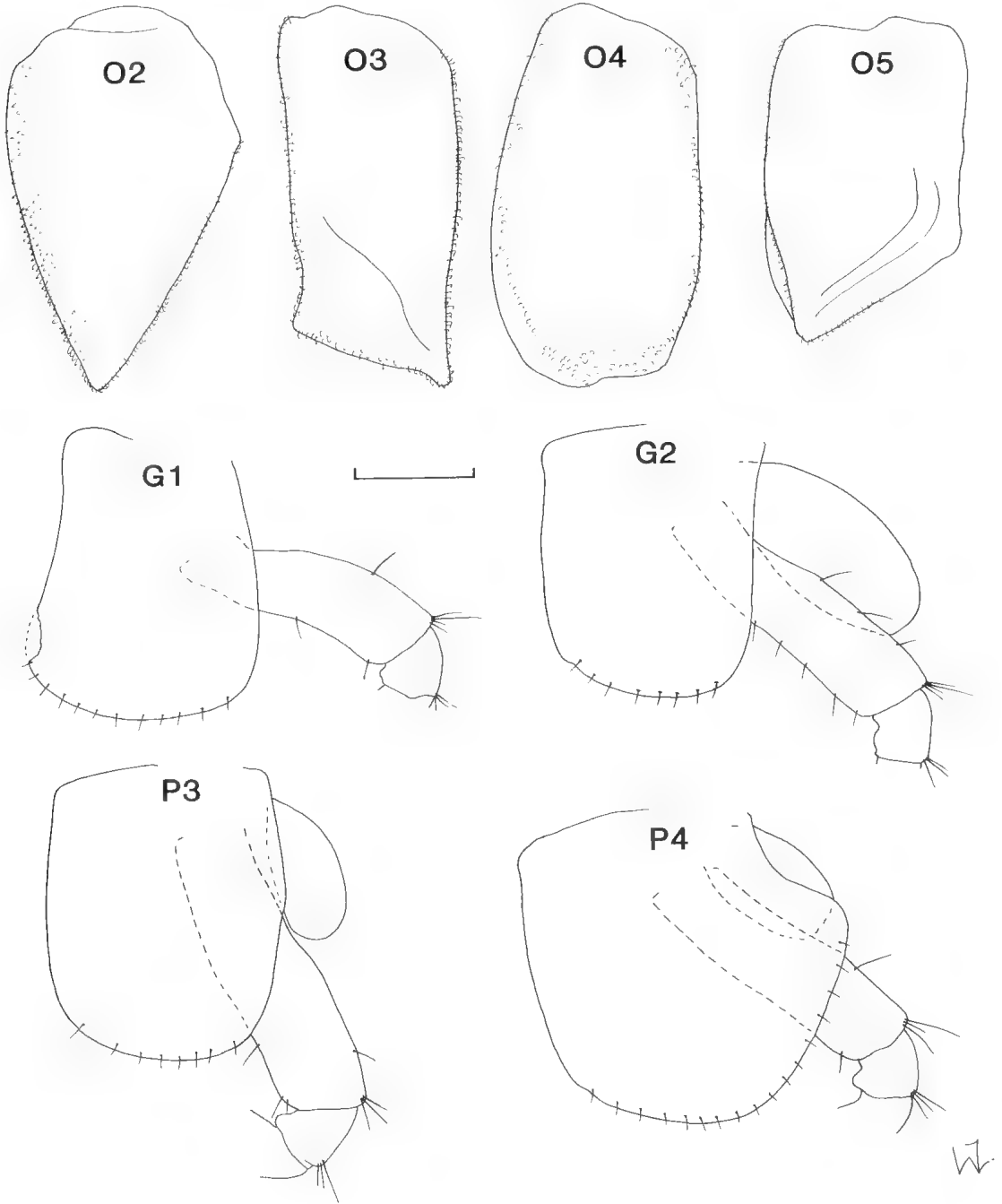


Fig. 9. *Austrochiltonia dalhousiensis* sp. nov. Oostegites from allotype ♀. G1-P4 from paratype ♀, 4.8 mm, from SAMA C5653. Scale bar = 0.2 mm.

Variation

Apart from minor variations due to size, paratype and other material examined is very similar to either the holotype or allotype. The maximum recorded size of males is 5.2 mm and that of females 6.5 mm but most specimens examined are around 4.0 mm long. Minor differences between specimens generally were noted as follows. The number of flagellar articles of A1 varies from eight to ten with one small specimen having seven; A2 has from six to nine flagellar articles but most specimens have only seven or eight. The number of aesthetascs on A1 is remarkably constant with only some larger specimens having an extra one (five). The number of pectinate setae on the carpus of G1 varies from seven to nine in males and eight to ten in females (similarly for G2 of females). In the allotype the coxae of G2-P4 are of an unusual shape, differing from males and non-ovigerous females (Fig. 9) in that the posterior margin is produced to a point medially and P4 is without a proximal excavation. In the holotype the basis of P6 has a relatively straight posteroproximal shoulder but in nearly all other specimens examined the posterior margin is evenly rounded. Pereopod 7 is usually longer than P6 but in the allotype it is slightly shorter, probably because of the relatively shorter propodus which is normally longer than the carpus. The spination of U1 & 2 varies slightly with larger specimens having one or two extra spines on the peduncle and ram. Uropod 3 is usually two-articulate and only one specimen (a female from C5653) had U3 with one article and then only on the right-hand side. Oostegites of females vary considerably in size but are expanded, as illustrated for the allotype, in ovigerous specimens.

The possibility that speciation may have occurred between springs without any obvious morphological changes was considered and specimens for allozyme electrophoretic analysis were collected from all three localities. A preliminary analysis of this material using methods outlined by Richardson *et al.* (1986) indicated fixed genetic differences of 10% or less (for 21 loci), thus supporting the morphological evidence of one species with little variation. Given these results, a more detailed analysis was considered unnecessary.

Discussion

The new species described here closely resembles *A. australis* in that U3 is two-articulate. However, a number of minor features collectively readily distinguish it from this species and its only other congener, *A. subtennis*. The main distinguishing features are as follow. Females reach a larger size than males and the species is genetically not as large as *A. australis* (males up to 10.0 mm, females up to 8.3

mm) or *A. subtennis* (males up to 10.0 mm, females up to 6.4 mm). Antenna 1 has fewer aesthetascs (5-7 in *A. australis*). Both antennae have fewer flagellar articles (A1 up to 17, A2 up to 11 in *A. australis*). The coxae of *A. dalhousiensis* sp. nov. are relatively wider and the excavation on coxa 4 is not as deep as in *A. australis* or *A. subtennis*. In both *A. australis* and *A. subtennis*, the lateral margin of the excavation of coxa 4 is at right-angles to the posterior margin whereas in *A. dalhousiensis* the angle of the coxal excavation is much greater than 90°. In ovigerous females of *A. dalhousiensis* the coxae of G2-P4 have the posterior margin produced to a point medially and coxa 4 is without a characteristic excavation. There are fewer pectinate spines on the carpus of G1 (males) and G1 & 2 (females) than in *A. australis* (usually >>10). For G1 (males) and G1 & 2 (females) the carpus is slightly shorter than the propodus whereas the reverse is true for *A. australis*. Other minor differences between the new and other species no doubt exist but were not evident in the present study.

Austrochiltonia dalhousiensis is also similar to *Phreanichiltonia unophthalma* Zeidler, 1991, a phreatic species which also has a limited distribution at Dalhousie Springs (Zeidler 1991), especially in that ovigerous females of *A. dalhousiensis* have coxa 4 without an excavation, a feature characteristic of *P. unophthalma*. Given the isolated habitat of Dalhousie Springs, one would suspect that these two species would have common ancestry. However, since electrophoretic analysis has shown that they differ at about 80% of the 21 loci examined, this does not appear to be the case.

The closest relatives geographically, apart from *P. unophthalma*, are species of *Austrochiltonia* found in the mound springs near Lake Eyre South. Although *A. dalhousiensis* is morphologically very similar to these species, electrophoretic analysis has shown that it differs from them at 73-80% of the 21 loci examined. Clearly a more detailed morphological and genetic study of the genus is required to determine relationships.

A single, damaged female of *A. dalhousiensis* was found in the pool of spring Ca1 (AM P48841). This record may be due to contaminated collecting equipment as the water temperature at that locality is 37°C and freshwater amphipods prefer cooler waters (Barnard & Barnard 1983). It therefore seems unlikely that *A. dalhousiensis* occurs naturally in the pool of Ca1 but its possible occurrence at this locality warrants further investigation.

The factors determining the distribution of this species are unknown. Its restricted distribution at Dalhousie Springs is puzzling as many apparently suitable habitats exist in which this species was not found. Although restricted in its distribution, the species is relatively abundant at all of the collection sites.

Like *P. anophthalma*, the presence of this species at Dalhousie Springs on the edge of the Simpson Desert suggests that it is a remnant of a once more widespread fauna during a time when central Australia was much wetter than it is today (Krieg 1989).

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I am most grateful to Dr W. F. Ponder (AM) for his assistance in organising the 1985 expedition to Dalhousie Springs. He is also thanked for his

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COMPOSITION OF THE STYLETS OF THE TARDIGRADE, MACROBIOTUS CF. PSEUDOHUFELANDI

BY ALAN F. BIRD* & STUART G. MCCLURE†

Summary

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The response of *M. cf. pseudohufelandi* to the environmental stimuli of anoxia, differences in pH and temperature change demonstrate that this tardigrade can reabsorb its stylets under stress and reform them when the stress is removed. The possible evolutionary links between tardigrades and molluscs that have darts composed of calcium carbonate are discussed.

Key Words: Tardigrade, stylets, *Macrobiotus* cf. *pseudohufelandi*, SEM, energy dispersive X-ray analysis, histochemistry, salivary glands.

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Introduction

Members of the Phylum Tardigrada (water bears) all feed using a pair of stylets whose composition is such that they dissolve and break down on the death of the tardigrade and in some commonly-used fixatives. Thus, they are frequently not included in the camera lucida drawings or photographs of the buccopharyngeal apparatus commonly used for taxonomic identification. The general composition, shape and purpose of the twin stylets seems to be similar throughout the phylum and so the chemical composition of stylets of one species probably holds for all. Because of their transient nature, dissolving on death or fixation, tardigrade stylets have not been analyzed. It has been suggested that they are calcareous in nature (Kaestner 1968; Kristensen 1976; Wenck 1914, Kristensen unpub. both cited by Nielsen 1996) and that they resemble nematode stylets in form and function (Riggall 1962 cited by Kinclün 1994). The stylets of *Macrobiotus* cf. *pseudohufelandi* are curved, sabre-shaped structures about 40 µm in length that exhibit marked birefringence under polarized light (Bird 1996).

In this paper we examine the dissolution of the stylets in various media under the polarizing microscope, their staining properties under bright field microscopy and their elemental composition using energy dispersive X-ray analysis in the scanning electron microscope. We also examine the reformation of the stylets after dissolution and discuss these structures in the light of tardigrade evolution.

Materials and Methods

Locality, soil type and extraction

The tardigrades were recovered from soil classified as a solonized brown earth from an experimental plot on a farm at Avon, South Australia (Bird 1996). After thorough mixing, 50 g aliquots of the soil were placed in a misting apparatus and processed as previously described (Bird 1996). The tardigrades so collected were picked out using a dental No. 3 nerve brush. Water which had passed through the soil was collected from the misting apparatus and filtered through a 0.2 µm membrane filter. The tardigrades were placed in a shallow layer of this water in a sterile Petri dish. Under these conditions, tardigrades remained viable for a week or more without feeding.

Stylet dissolution

The break-down of the stylets was observed, on slides with coverslips sealed with nail varnish, in solutions with pH ranging from 4-8 for different lengths of time (from the start of the experiment to several days) and at temperatures ranging from 15 - 30°C. Observations were made with polarized light and differential interference contrast (Nomarski) optics using a Vanox Olympus AIBT research microscope.

Stylet reformation

Specimens were mounted in distilled water in sealed slides with pieces of No. 1 glass coverslips acting as spacers to prevent crushing. These specimens were kept under observation, using Nomarski optics, until the stylets could no longer be observed (usually about 3 h). The coverslip was then gently

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removed under a dissecting microscope and the motionless tardigrades placed, together with some small nematodes to stimulate feeding activity, in shallow distilled water in a Petri dish. After about 12 h the tardigrades, which had resumed activity, were placed in sealed slides and re-examined under Nomarski optics.

Energy dispersive X-ray analysis of the stylets under the scanning electron microscope (SEM)

Because of the difficulties of obtaining intact stylets from tardigrades on sealed slides or after the use of acid fixatives such as FA 4:1, as used for the fixation of nematodes (Hooper 1986), a special technique was adopted for these studies as follows. The tardigrades were transferred to a small drop of water which was then swamped with an excess of 6% glutaraldehyde in Sørensen's buffer at pH 7.3. The tardigrades were then gently crushed under a coverslip to permit rapid entry of the fixative without causing undue damage to them. After 2 h in the fixative the tardigrades were removed, washed four times in 0.2 µm membrane-filtered distilled water and placed in a small drop of the membrane-filtered distilled water on the surface of a polished carbon stub. The tardigrades were manoeuvred close together and a second polished carbon stub was lowered on to the first so that the tardigrades were caught between the polished carbon surfaces. They were left in this position for 24 h to dry and then the uppermost stub was lifted directly upwards, thus pulling the tardigrades apart and exposing their inner organs, including the bucco-pharyngeal region. This technique was also used on fresh, unfixed material. The stubs were kept in a sealed dry container until examined and photographed in a Cambridge S 250 Mk 3 SEM operated at 20 kV using Ilford 120 roll film (FP4 Plus).

Energy dispersive X-ray (EDX) analysis was by means of a Link EDX system attached to the SEM. EDX analysis of characteristic lines with energies less than approximately 0.8 keV is not possible with this detector because of the absorption of the low energy X-rays by the detector's beryllium window. Consequently, the direct identification of elements with atomic numbers less than that of sodium is not possible.

Histochemistry of the salivary glands during stylet dissolution

The anthraquinone dye alizarin red S⁺, used as a stain for calcium, was made up as a 1% solution (50 mg 5 ml⁻¹) either in a buffer solution at pH 4.0 or in distilled water (pH 5.0). The tardigrades were placed in a drop of the alizarin red S solution and gently

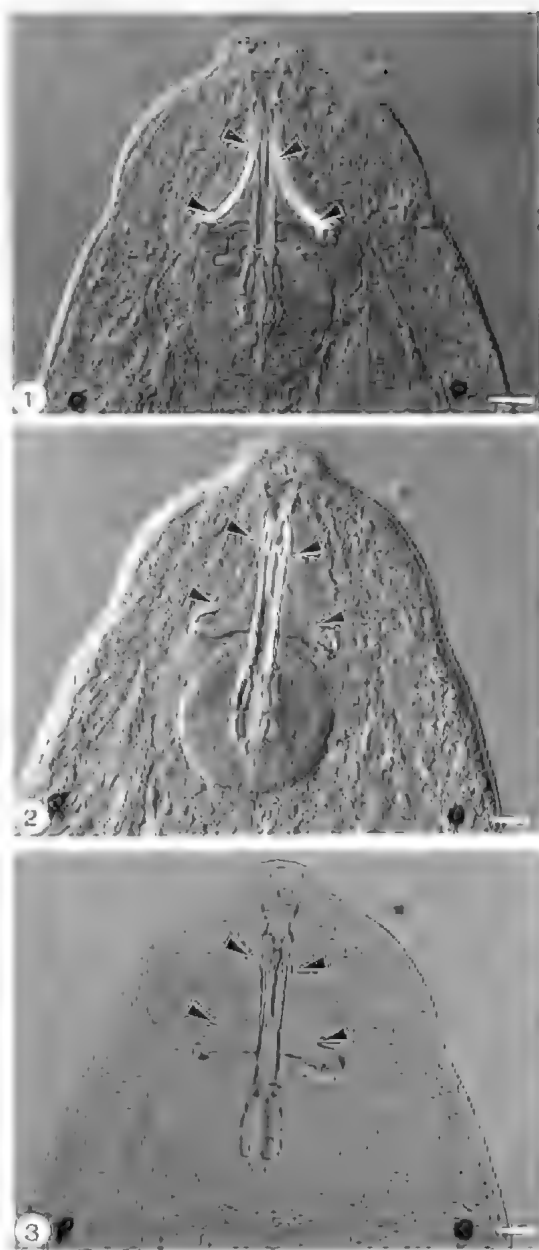


Fig. 1. Head of living specimen of *Macrobiotus cf. pseudohufelandi* immediately after being placed in distilled water on a sealed slide. Note the two eye spots in lower part of photograph and the two curved stylets (arrow heads). Nomarski optics. Scale bar = 10 µm.

Fig. 2. Same specimen as in Fig. 1 but photographed just after the stylets had dissolved 166 min later. Arrow heads indicate the original location of the stylets. Nomarski optics. Scale bar = 10 µm.

Fig. 3. The same as Fig. 2 but viewed under bright field optics. Arrow heads indicate the original location of the stylets. This photograph illustrates the bucco-pharyngeal structures used in the taxonomy of this genus. Scale bar = 10 µm.

squashed, without causing gross damage to them, by placing a glass coverslip over the drop and withdrawing the stain solution from under the coverslip with pieces of filter paper. The edges of the coverslip were then sealed with nail varnish and the specimens observed and photographed under bright field optics.

Results

Dissolution of the stylets

The time taken for dissolution of the stylets in distilled water, when a state of anoxia has been induced by sealing the tardigrades under a coverslip on a slide, is temperature dependent. Thus, at 30°C, total stylet dissolution occurred within three hours whereas at 15°C the stylets were only partially dissolved after this time.

The appearance of the head region of *M. cf. pseudohufelandi*, viewed under Nomarski optics, is shown prior to commencement of stylet dissolution at 25°C (Fig. 1) and after its completion three hours later (Fig. 2). The head region is also shown after three hours, photographed under normal bright field optics (Fig. 3).

The sequence of stages in the dissolution of the stylets is illustrated most clearly in a series of photomicrographs taken under the polarizing microscope (Fig. 4A-H). Stylet dissolution is gradual over the first two hours (Fig. 4A-D) but accelerates over the third hour (Fig. 4E-H) so that marked changes were detected at approximately 15-minute intervals from two hours onwards.

Stylet dissolution occurred more rapidly in acid solutions than in neutral or alkaline solutions. It took place within 50-90 min in 0.05M HCl and occurred immediately in 0.1M HCl and so is similar to CaCO_3 in this respect.

The birefringence exhibited by the muscles of the triadate pharynx of *M. cf. pseudohufelandi* did not disappear over a period of three hours (Fig. 4) and the brightness of these muscles, although not as marked as that of the stylets at the commencement of the experiment, remained constant throughout.

Reformation of the stylets

Tardigrades appear to have the capacity to reform their stylets under favourable conditions in what appears to be a reversal of the dissolution which occurs when they are placed in unfavourable situations. Specimens that had been induced to dissolve their stylets in sealed slides and had become motionless were observed to regain their muscular activity and reproduce stylets, over a 12 h period, when placed in shallow distilled water in an unsealed Petri dish, in the company of several small nematodes. This reformation did not always lead to precise realignment of the stylets and the efficiency of this

reformation and correct realignment may be dependent on the state of health of the tardigrade at the commencement of the experiment.

Energy dispersive X-ray analysis of the stylets

Examination under the SEM of the polished carbon surfaces holding the dried, squashed and disrupted tardigrades, clearly shows whole stylets or parts thereof (Fig. 5). By means of this technique, it is possible to obtain suitable EDX analyses of the elemental composition of the stylets. It can be seen from the EDX spectrum (Fig. 6) that the stylets are rich in calcium, with maximum X-ray intensity counts at energies matching the Ca α at 3.690 keV and the Ca β at 4.012 keV characteristic X-ray lines.

Histochemistry of the salivary glands during stylet dissolution

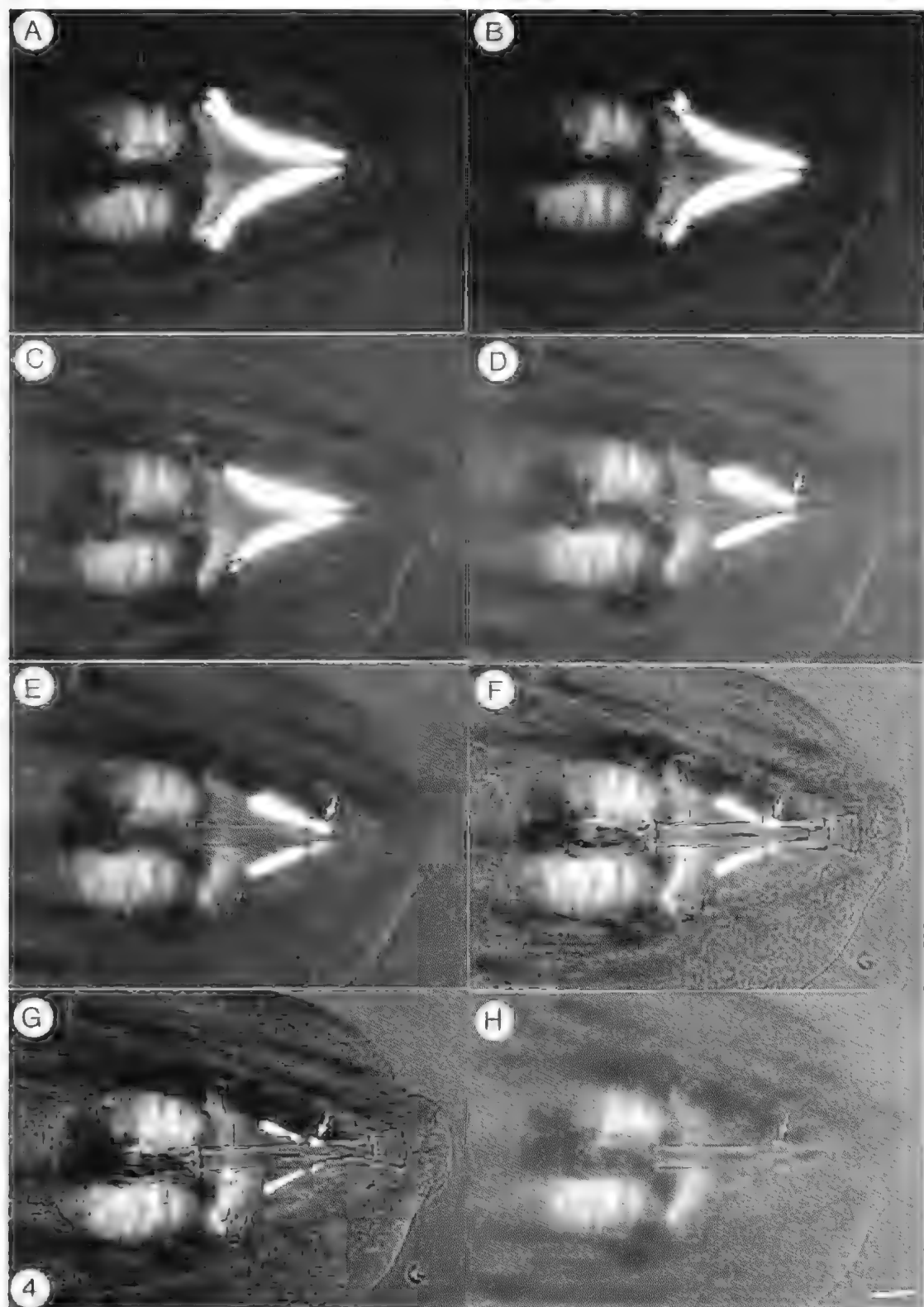
When the tardigrades were gently squashed in a 1% solution of alizarin red S at pH 5.0, the salivary glands surrounding the stylets gradually became a deep red (Figs 7, 8). This reaction was both marked and localized, provided that the body of the tardigrade had been crushed to allow rapid penetration of the stain. These glands, which are thought to be responsible for the secretion and dissolution of the stylets (Kinchin 1994), are apparently rich in calcium as indicated by their reaction to alizarin red S.

Discussion

Information on the nature of the tardigrade stylets is sparse and has received little or no attention in the two most recent general accounts of these organisms, notably a most informative book on their general biology by Kinchin (1994) and a collection of papers published in the Zoological Journal of the Linnean Society in 1996 and edited by Melones & Norman.

Tardigrade stylets were thought to have some similarity with nematode stylets by Riggall (1962) (cited by Kinchin 1994). However, it is clear that tardigrade stylets (Bird 1996) differ markedly from nematode stylets (Bird & Bird 1991) both in composition and structure. Thus, FA 4;1, a mixture of formaldehyde and acetic acid and a common fixative for nematodes, causes rapid dissolution of the tardigrade stylets because of its low pH and the high temperature used in the procedure. This fixative, however, does not cause dissolution of nematode stylets. Hoyer's medium, a mixture of gum arabic, chloral hydrate and glycerol (Kinchin 1994) does not dissolve tardigrade stylets and has the added advantage of functioning as a combined fixative and embedding medium. In many illustrations of the bucco-pharyngeal region of tardigrades, the stylets are not shown, presumably because they dissolved when fixed.

The small size of tardigrade stylets (40 μm) in



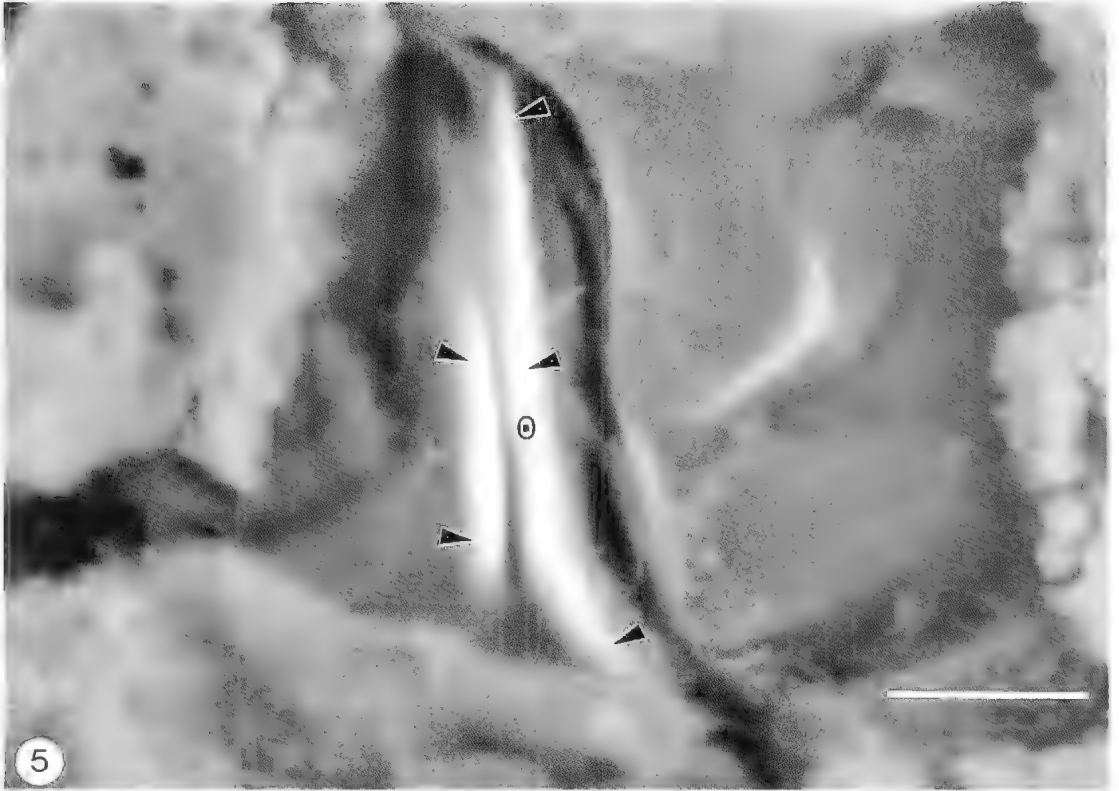


Fig. 5. Anterior region of dried and fractured *Macrobiotus cf. pseudohufelandi* (see Materials and Methods) viewed under the SEM showing parts of the two stylets (arrow heads). The site of EDX analysis is circled. Scale bar = 10 μ m.

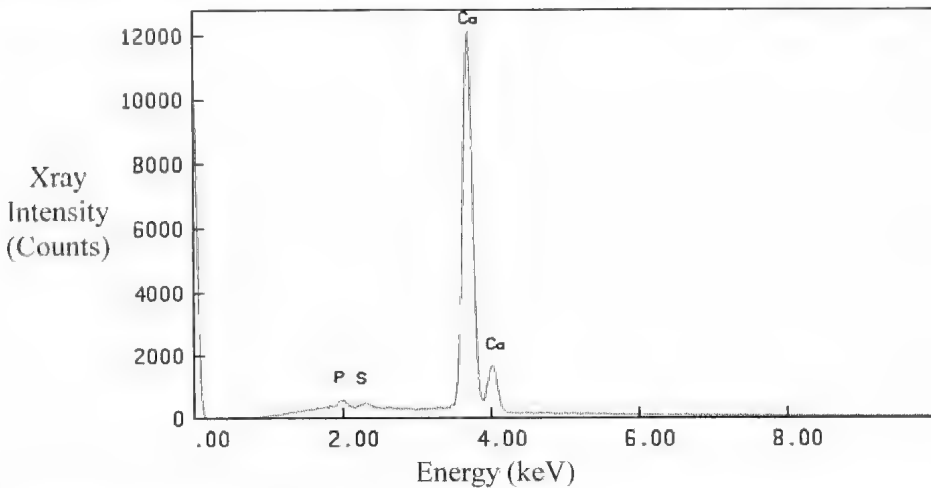


Fig. 6. EDX spectrum of the stylet shown in Fig. 5.

Fig. 4. Series of photomicrographs viewed under the polarizing microscope illustrating the stylets of a living specimen of *Macrobiotus cf. pseudohufelandi* exhibiting diminishing birefringence as they gradually dissolve in distilled water on a sealed slide as shown in Fig. 1 - Figs 2 & 3. A. At commencement. B. After 56 min. C. After 96 min. D. After 113 min. E. After 120 min. F. After 136 min. G. After 150 min. H. After 165 min. Arrows indicate parts of stylets. Note that the muscles in the pharynx do not lose their birefringence as the stylets dissolve. Scale bar = 10 μ m.

length in *Macrobionus cf. pseudohufelandi*) and their labile nature, have made it difficult to determine their composition. We have overcome this by adapting a technique used to separate the layers in a nematode's cuticle (Bird & Deutsch 1957) which takes into account the adhesive qualities of animal tissues to the surfaces on which they have been dried. In this instance, the two surfaces were polished carbon rods mounted on SEM stubs as described in Materials and Methods. In some instances, this technique led to the exposure of either the whole or large enough pieces of stylet to be recognizable (Fig. 5). These were then easily photographed and subjected to energy dispersive X-ray analysis measurements in the SEM. These measurements clearly show that the elemental composition of the stylets consists mainly of calcium (elements with atomic numbers less than that of sodium are not detectable). The rapid dissolution of the stylets in dilute acids and their marked birefringence (under polarized light, indicate that they are composed of calcium carbonate. Thus, the composition of tardigrade stylets differs from that of nematode stylets which are protein in nature.

Each tardigrade stylet lies in the lumen of a salivary gland (Kinchin 1994). Kristensen (1976) (cited by Nielsen 1996) has suggested that separate lobes of the salivary glands are responsible for the formation of the stylets and their supports in the tardigrade, *Ratillipes*. Whether or not this applies to *M. cf. pseudohufelandi* remains to be determined. We have not observed the formation or dissolution of the stylet supports in this tardigrade, indicating that their chemical composition is different from that of the stylets. We have no information on the origin and chemical composition of the stylet supports in *M. cf. pseudohufelandi*.

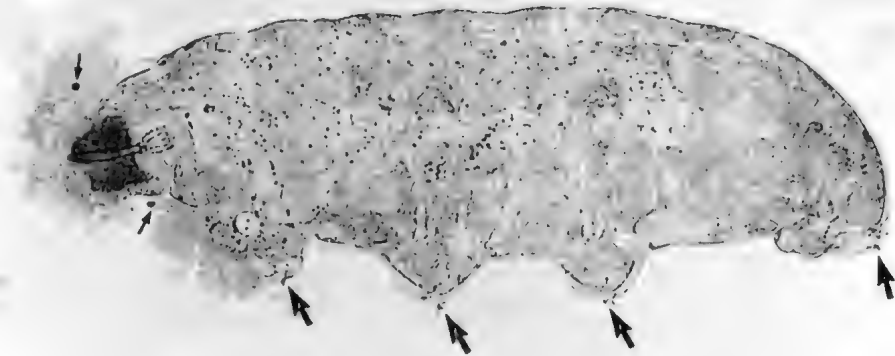
Our experiments indicate that the stylets of *M. cf. pseudohufelandi* are secreted and resubstituted by the salivary glands. We have shown that (Figs 7, 8), when the tardigrades are gently squashed in a dilute solution of the stain, alizarin red S at a pH of 5.0 and sealed, the cell surrounding each stylet stains as the stylets break down, indicating that calcium is liberated and diffuses throughout these two cells. Alizarin red S is recognized as a histochemical reagent for the detection of calcium (Conn 1977), changing in colour from yellow to red to purple over the pH range 3.7–5.2.

The gradual break down of the stylets in a slightly acidic and anoxic environment, as demonstrated in this paper, when photographed under polarized light (Fig. 4), closely resembles their step by step formation as depicted in drawings by Marens (1929) (cited and redrawn by Kinchin 1994) showing stages in their formation. Although stylets of calcium carbonate are unusual in the animal kingdom and appear to be both unique and common to all tardigrades, somewhat similar structures are found in other groups of animals. For instance, many of the terrestrial pulmonate gastropods shoot darts of calcium carbonate into each other prior to copulation. This behaviour is thought to act as a stimulant to the sexual act. The dart of *Helix aspersa* is about 8–10 mm in length (Tompa 1982), at least ten times the size of an entire tardigrade and some 200 times larger than the 40 µm stylet of *Macrobionus cf. pseudohufelandi*. The dart, which takes about five days to form, is secreted in a dart sac that is part of the reproductive system. The composition of these darts, when subjected to energy dispersive X-ray analysis, is identical to the tardigrade stylets with both Ca K α and Ca K β peaks (Hunt 1979). The evolutionary significance of these findings is obscure. However, they do lend some support to the phylogenetic position of the Tardigrada proposed, as a result of studies on the 18 S ribosomal gene sequence, by Moon & Kim (1996). These authors state "the tardigrade clade appears as an independent lineage from the nematode clade" and the calcareous nature of the tardigrade stylet as opposed to the proteinaceous nature of the nematode stylet, lends support to this hypothesis. Moon & Kim (1996) further suggest that the tardigrade clade is a sister group of the protostome euteleostome assemblage that emerged before the molluscs, annelids, arthropods and sipunculids evolved. This would suggest independent evolution of the calcareous structures in tardigrades and molluscs.

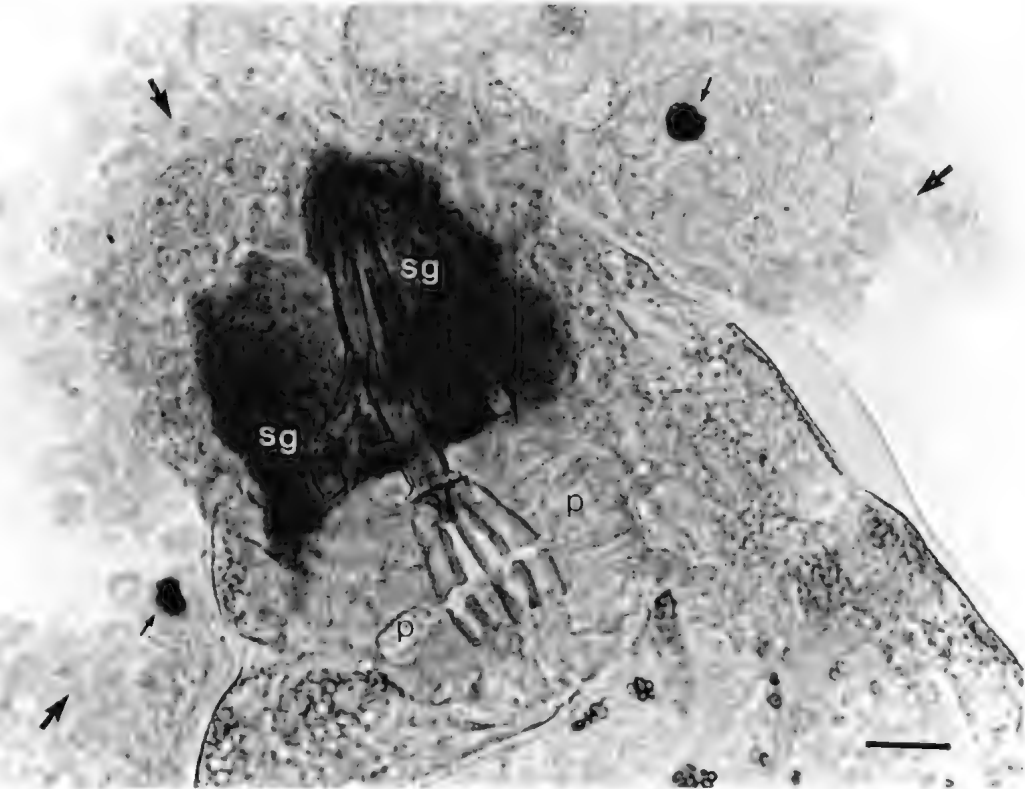
Some measure of the gaps in our knowledge of the origins and relationships of the Tardigrada is indicated by the fact that tardigrades are not mentioned in a book on the origins and relationships among lower invertebrates edited by Morris *et al.* (1985). However, some primitive Cambrian fossils share some characteristics with both Onychophora and Tardigrada, including poorly articulated limbs ending in claws (lobopodia), terminal mouths and the

Figs 7, 8. Whole specimen of *Macrobionus cf. pseudohufelandi* that has been crushed to permit the entry of alizarin red S at pH 5.0. The photograph was taken under bright field optics about 30 min after the commencement of staining. Showing eye spots (small arrows) and claws (large arrows). The area around the tardigrade contains material that has been exuded from the ruptured animal and the two salivary glands that lie just anterior to the muscular pharynx are heavily stained. Scale bar = 100 µm.

Fig. 8. Enlarged portion of Fig. 7 showing eye spots (small arrows), the stained salivary glands (Sg), the muscular pharynx (p) and material that has been exuded by rupturing to permit entry of the stain (large arrows). Scale bar = 10 µm.



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last pair of legs merging with the caudal end of the body (Kinchin 1994). For these reasons it is speculated by Kinchin (1994) that the Tardigrada and the Onychophora have originated from a lobopodian line that diverged from the arthropod line in the Cambrian period. However, Nielsen (1996) considers that Tardigrada are more closely related to Arthropoda than to Onychophora and suggests that all three phyla have originated from a group which he calls "Panarthropoda", and that the onychophorans diverged first. It is clear that the origins and lineage of the Tardigrada remain obscure and

that much remains to be discovered about them before they can be accurately traced and defined.

Acknowledgments

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STUDIES OF THE EGGS OF MACROBIOTUS CF. PSEUDOHUFELANDI (TARDIGRADA) FROM WHEAT FIELDS IN SOUTH AUSTRALIA

By ALAN F. BIRD & STUART G. MCCLURE†*

Summary

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Key Words: *Macrobiotus* cf. *pseudohufelandi*, microscopy, tardigrades, eggs, morphology, evolution, soil.

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Introduction

Tardigrades, also known as water bears or moss piglets (Kinchin 1994), belong to a discrete phylum of cosmopolitan distribution from diverse habitats including marine, fresh water and semi-terrestrial environments. The tardigrades responsible for the eggs described in this paper were identified as *Macrobotus* cf. *pseudohufelandi* Iharos 1966 by S. Choxon (Bird 1996) and are semi-terrestrial, having been isolated from sandy loam soil in a wheat field at Avon, South Australia.

The tardigrade egg shell is a useful taxonomic guide to species identification, particularly in genera such as *Macrobotus* where the shell is ornamented. *Macrobotus* cf. *pseudohufelandi*, which are only about 500 µm long by 150 µm wide when fully grown, lay comparatively large circular eggs which have highly ornamented reticulated shell surfaces with numerous "inverted goblet-shaped" projections (Bird 1996).

It has been shown by Bertolani & Rebecchi (1993) that differences in egg shell morphology in *Macrobotus hufelandi*, previously thought to be due to variability within this species, fall into seven distinct types that are related to different animal morphotypes. Using egg shell morphology, along with other characters, these workers have described a number of new species from the *M. hufelandi* group. Eggs that belong to this group have pitted or reticulated shells with protruding processes shaped like inverted goblets, chalices, thread spools or "cooling towers".

Bertolani *et al.* (1996) have stated that ornamented eggs are generally laid free in soil or water and smooth-shelled eggs are laid in the moulted cuticle (exuvium). These workers include the family Macrobiotidae, to which *M. cf. pseudohufelandi* belongs, in those families that lay free, ornamented eggs. Bertolani *et al.* (1996) have put forward an hypothesis in which they explain the evolution of tardigrade eggs.

In this paper we examine the structure of the egg shell of *M. cf. pseudohufelandi* and measure the processes protruding from the surface of the egg shell. We also discuss its egg-laying habits in relation to the hypothesis of Bertolani *et al.* (1996) and comment on feeding behaviour and population density.

Materials and Methods

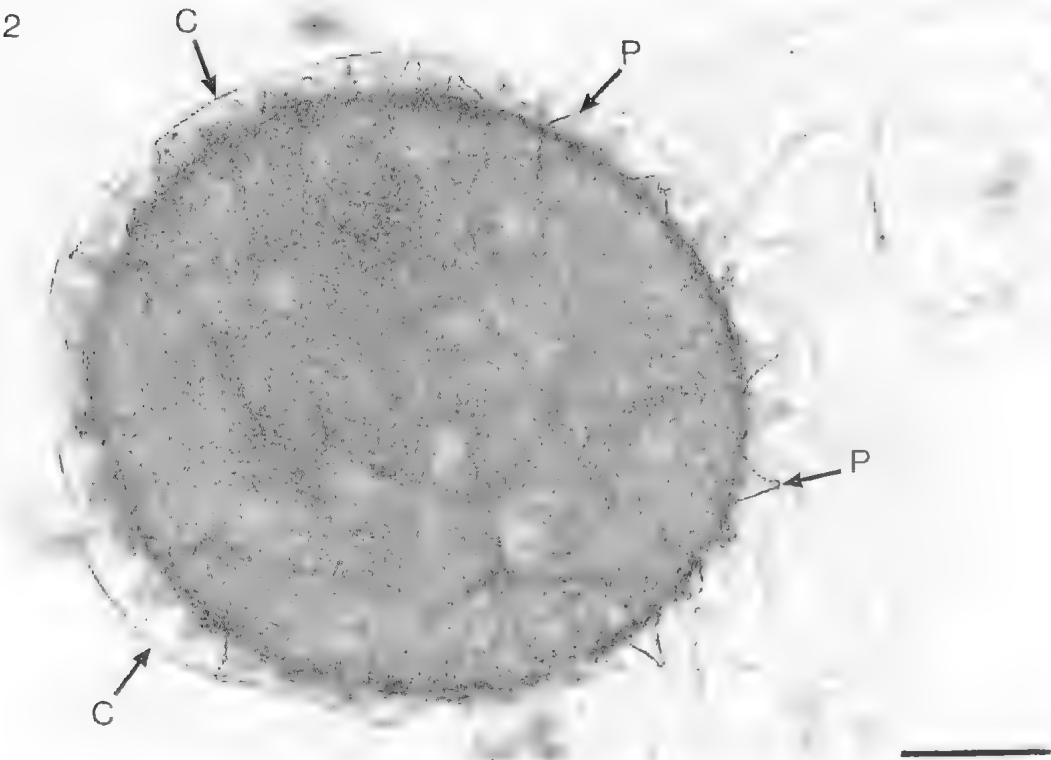
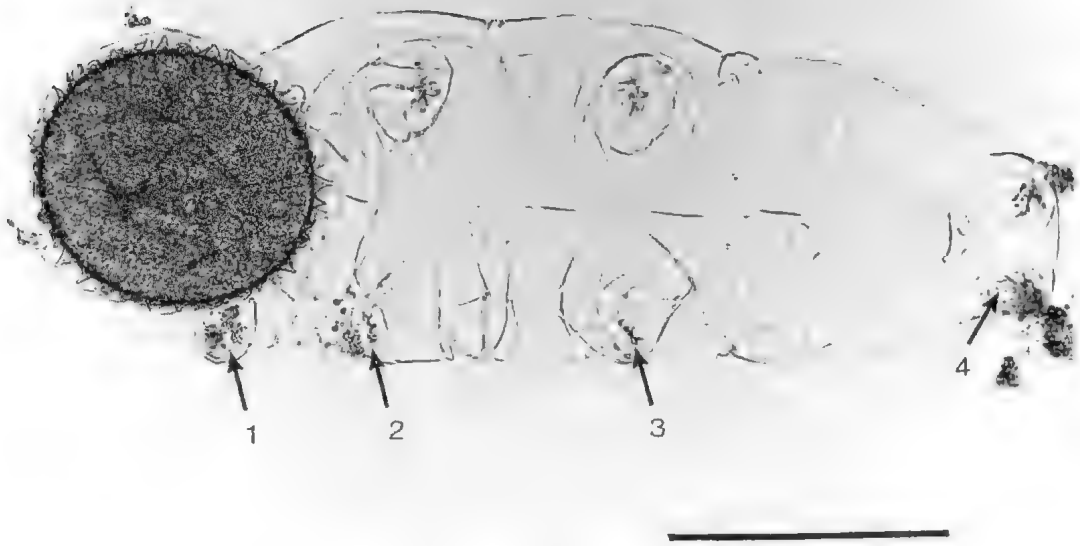
The tardigrades were collected on 18 July 1996 from sandy loam soil and from the same locality at Avon, South Australia (latitude 34° 14' S, longitude 138° 19' E), as those collected previously, using the sampling technique described by Bird (1996). The soil samples were collected in mid-winter so that the sites were wet and the tardigrades were feeding, reproducing and depositing eggs.

The tardigrades and other meiofauna, consisting predominantly of nematodes, were isolated from this soil over a period of three days using a misting apparatus (Yeates & Bird 1994). Tardigrades and nematodes were counted and tardigrade eggs were picked out using a dental No. 3 nerve broach and examined, alive, in distilled water under a coverslip, with the light microscope. Eggs to be examined under the scanning electron microscope (SEM) were fixed in

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6% glutaraldehyde in Sprensen's phosphate buffer at pH 7.2 and at 5° C and kept in this fixative for several days. They were then washed three times in distilled water and sonicated in an Eltra T420 sonicator at a frequency of 35 kHz for 10 sec or until shown by microscopic observation to be free of debris.

The eggs were freeze-dried by placing them between membrane filters which were frozen rapidly by placing them in a slurry of freon cooled by liquid nitrogen. These filters with the eggs were quickly transferred to a freeze drier and freeze-dried at -70° C. The dried eggs were picked up with double-sided tape which was attached to an SEM stub and coated with 30 nm of gold. This material was examined and photographed in a Cambridge S 250 Mk 3 SEM operated at 20 kV using FP4 Plus (Ford roll film).

Results

Numbers and feeding

At the time of collection the ratio of tardigrades to nematodes in 50 g of soil was 84:297. Feeding on nematodes was also observed during the course of this investigation and the nematodes held by the tardigrades usually did not move although once a nematode broke free and moved away. In one instance, a tardigrade was observed to be arching its back in the manner of a scorpion, during feeding activity.

Egg laying and eggs

Eggs that were about 90-100 µm in diameter in the living unfixed state (Figs. 1, 2) and about 60-70 µm in the fixed and dehydrated state (Fig. 3), were laid either within exuvia (cast cuticles) (Figs. 1, 2) or free (Fig. 3). Figures 2, 3, 4, 5 clearly show that these eggs have a morphology of the *M. hufelandi* group with reticulated shells and characteristically upturned-chalice-shaped protruding processes.

Although the pattern of the reticulations remains the same with the apertures on the reticulate surface of the egg shell being about 0.25 µm in diameter (Fig. 6), the shape of the protruding processes falls into two distinct groups. Type I is shorter than Type II, is narrow at the base and has a wide distal head (Fig. 4). Conversely, Type II is taller, wider at the base and has a narrower distal head than Type I (Fig. 5). For 10 processes of each type, the differences in the means are statistically significant with 95% confidence (Table 1).

When the processes were examined under the higher magnification of the SEM (Fig. 6), the dentate cog-shaped margins of the head were shown to consist of clusters of globules with a structure resembling madreporarian corals in appearance and were approximately 0.5 µm in diameter. The madreporarian globules and reticulated shell surfaces are similar in both the shell types described above.

Discussion

Bertolani *et al.* (1996) have proposed an hypothesis to explain the evolution of tardigrade eggs. According to these workers, the eggs of tardigrades have evolved as a result of two events, the first being the acquisition of ornamentation and the second the use of the shed exuvium as the site for egg laying, with the subsequent loss of ornamentation. Thus, the ornamented eggs of the Macrobiotidae are thought to be laid free. Our observations that the ornamented eggs of *M. cf. pseudohufelandi* can either be laid in exuvia (Figs. 1, 2) or free (Fig. 3) do not appear to be in accord with this hypothesis. The exuvia containing ornamented eggs were transparent and devoid of body contents and did not appear to be females that had died before completing egg laying. A possible explanation for the laying of the eggs in the exuvium by the *M. cf. pseudohufelandi* from the soil at Avon,

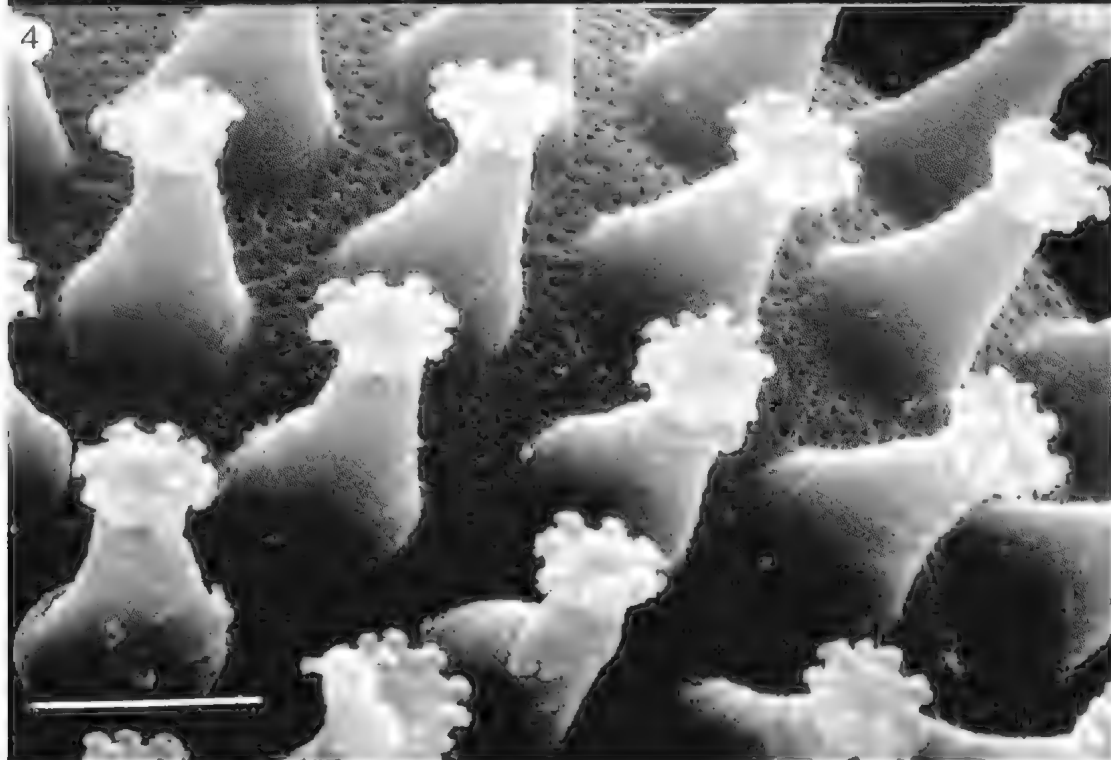
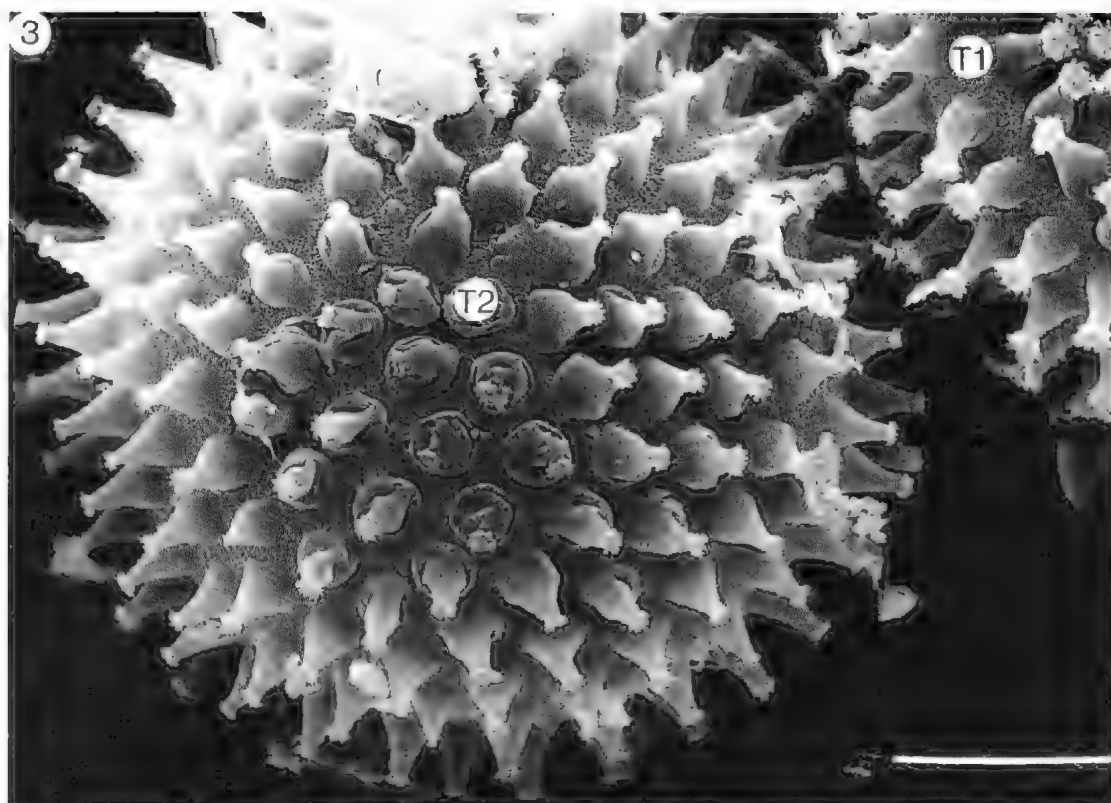
TABLE 1. Measurements of the two types of processes protruding from the egg shell surfaces of *Macrobiotus cf. pseudohufelandi*.

Type	No.	Height (µm)			Basal width (µm)			Distal Width (µm)		
		Mean	± SD	Range	Mean	± SD	Range	Mean	± SD	Range
I	10	5.9	0.5	5.4-6.5	4.3	0.2	3.9-4.8	3.3	0.2	3.0-3.7
II	10	6.4	0.4	5.7-7.4	5.3	0.2	4.9-5.6	2.1	0.1	2.1-2.4
t (0.95) > 2.26		2.47			11.18			16.97		

SD = Standard Deviation, t = Student's t-Test

Fig. 1. Egg of *Macrobiotus cf. pseudohufelandi* in cast cuticle (exuvium). Arrows indicate position of cast legs and claws. Bright field optics. Scale bar = 100 µm.

Fig. 2. Same specimen at higher magnification showing shell projections (P) covered by cast cuticle (C). Bright field optics. Scale bar = 20 µm.



is that this may be an adaptation to the hot, dry summers experienced there.

Our studies on the tardigrades and nematodes in soils from wheat fields at Avon in midwinter when the soils were wet and the populations of the meiofauna could be expected to be at their peak, show that tardigrades make up a substantial component, although they are not as numerous as nematodes. The ratio of 84 tardigrades to 297 nematodes per 50 g soil found in these experiments varies at other sites where the tardigrade numbers per 50 g soil may be less and nematode numbers greater (Bird 1996). However, it is clear that the tardigrade presence at Avon is widespread.

The tardigrades isolated from soil at Avon feed on nematodes and can survive hot dry summers in an anhydrobiotic state (Bird 1996). Feeding on nematodes was also observed during the course of this investigation and the nematodes held by the tardigrades did not usually appear to be moving, although they were coiled and therefore probably not dead, suggesting to us that they might have been paralyzed by some type of injected narcotic. Since there is no information on tardigrade diversity and geographical distribution in South Australia, further studies are warranted, particularly on their feeding habits, as they may have a role in the biocontrol of the parasitic nematodes which have been shown to occur in the wheat fields at Avon (Yeates & Bird 1994).

The fine structure of the egg shell in the genus *Macrobotus* is of great taxonomic importance. From our observations on the ultrastructure of the egg shells of the Avon tardigrades, it would seem that there may be two populations of *M. cf. pseudohufelandi*

in the Avon soil or there may be two different species, neither of which completely resembles those described so far for the *hufelandi* group (Bertolani & Rebecchi 1993; Biserov 1996). The reticulated surface of the shell and the structure of the globules on the heads of the projections are similar in the two forms of eggs described above but the diameter of the apertures on the reticulated surface of the egg shell is much less than that shown in the eggs of other members of the *hufelandi* group described by Bertolani & Rebecchi (1993), Kinchin (1994) and Biserov (1996). To our knowledge, the globules on the heads of the projections have not been described before and might prove, together with the reticulated surface, to be useful taxonomic criteria if the *hufelandi* group is further divided on the basis of egg ornamentation.

Clearly further studies are required on the taxonomy of these tardigrades and on their distribution in the semi-arid agricultural areas of South Australia and other similar regions of the Australian continent.

Acknowledgments

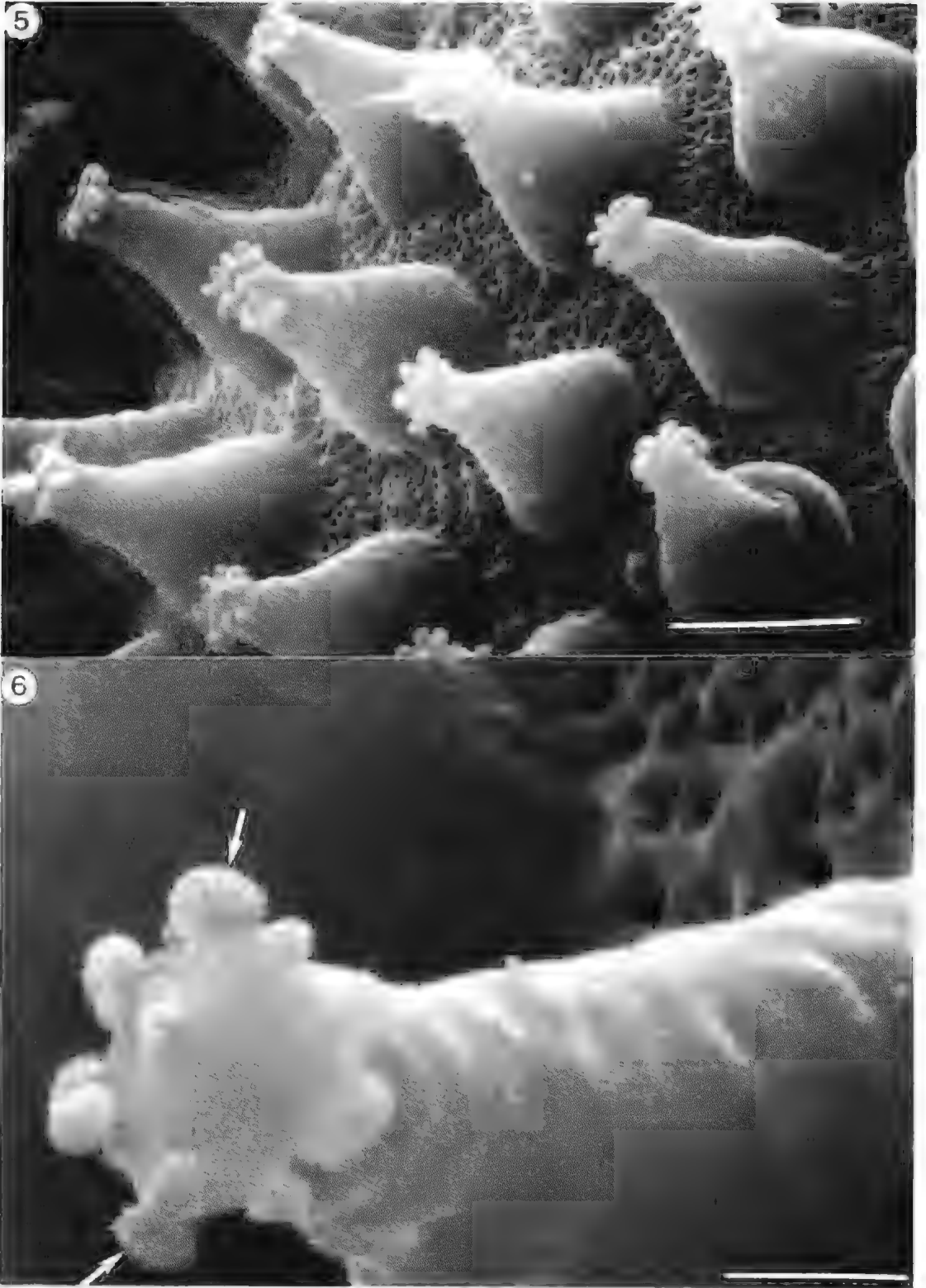
The senior author is grateful for a grant from the Australian Biological Resources Study which provided facilities that made this research possible and to CSIRO Land and Water Adelaide for accommodation and equipment. Dr W. R. Miller, Department of Biology Southwestern College Winfield Kansas USA and Dr W. L. Nicholas, Department of Botany and Zoology ANU Canberra ACT are thanked for constructive criticism of the manuscript.

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Fig. 3. Scanning electron micrograph of whole eggs of *Macrobotus cf. pseudohufelandi* showing the inverted goblet-shaped projections of Types I (T1) and II (T2). Scale bar = 20 µm.

Fig. 4. Scanning electron micrograph of part of the egg shell surface of a Type I egg showing projections with narrower bases and larger dentate cog-shaped heads than those of Type II. Note similarly reticulated surfaces of egg shells. Scale bar = 5 µm.



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- Fig. 5. Scanning electron micrograph of part of the egg shell surface of a Type II egg showing projections with wider bases and smaller cog-shaped heads than those of Type I. Note similarly reticulated egg shell surfaces. Scale bar = 5 μm .
- Fig. 6. Scanning electron micrograph of the head of one of the Type II projections at higher magnification showing the madreporarian globules (arrows). Note the size of the apertures on the reticulated surface of the egg shell on the top right hand side of the photomicrograph. Scale bar = 1 μm .
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**TWO NEW SPECIES OF ASPHONDYLIA
(DIPTERA: CECIDOMYIIDAE) FROM HALOSARCIA SPP.
(CHENOPODIACEAE) IN SOUTH AUSTRALIA**

*BY PETER KOLESIK**

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Two new gall midge species are described from South Australia. Asphondylia inflata sp. nov. was found at Port Adelaide in swollen branches of Halosarcia pergranulata subsp. pergranulata. Asphondylia ericiformis sp. nov. was found at Lyndhurst, at the southern edge of the Strzelecki Desert, forming spherical, spiky galls on branches of H. indica subsp. leiostachya. Descriptions of the larvae, pupae, males, females and galls are given for both species.

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Introduction

Halosarcia is a plant genus comprising 23 species commonly called samphires. The genus is endemic to Australia except for *H. indica* (Willd.) Wilson which also occurs in Malaysia and other countries bordering the Indian Ocean (Wilson 1986). Two species of *Halosarcia* were found to be infested by two undescribed gall midges (Diptera: Cecidomyiidae) collected in South Australia during 1996. These gall midges are described in the present paper. *Asphondylia inflata* sp. nov. causes swellings of branch segments on *H. pergranulata* (Black) Wilson subsp. *pergranulata* (Fig. 1) and *A. ericiformis* sp. nov. forms spherical, spiky galls on branch segments of *H. indica* subsp. *leiostachya* (Benth.) Wilson (Fig. 2).

Halosarcia pergranulata subsp. *pergranulata* is a shrub about 0.5 m high which grows in southern Australia (except Tasmania) associated with coastlines, estuaries, swamps and margins of inland lakes (Wilson 1984). The plant forms a substantial part of the vegetation cover of saltmarsh flats north-west of Adelaide. These saltmarsh flats are areas covered by small, hardy bushes that grow on the landward side of the mangrove swamps. Areas that are regularly inundated by tides are typically dominated by *Sclerostegia arbuscula* and *Sarcocornia quinqueflora*, while areas that are only occasionally flooded are dominated by *Maireana oppositifolia* and *Halosarcia* spp. In May 1996, a large number of galls caused by *A. inflata* sp. nov. was found on *H. pergranulata* subsp. *pergranulata* at Port Adelaide, about 400 m south of the Torrens Island bridge.

Halosarcia indica subsp. *leiostachya* is a small, decumbent to erect shrub widespread along the coast and around inland salt lakes of mainland Australia (Wilson 1984). It is a common plant in the Strzelecki

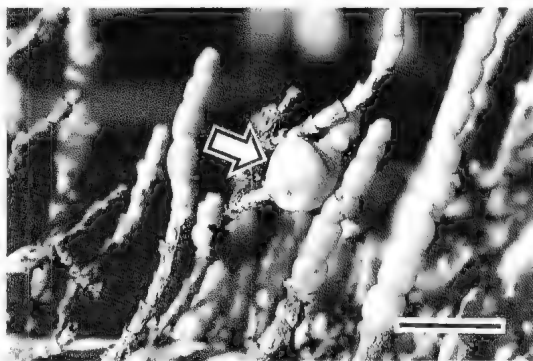


Fig. 1. Gall of *Asphondylia inflata* sp. nov. on *Halosarcia pergranulata* (Black) Wilson subsp. *pergranulata*. Scale bar = 10 mm.

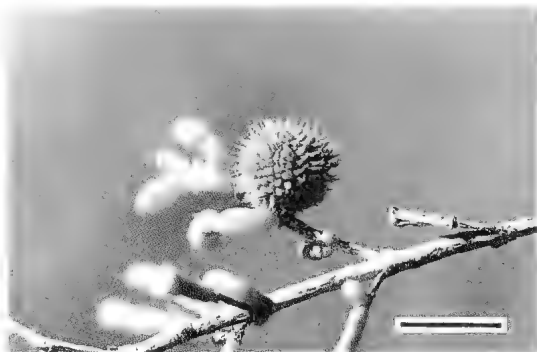
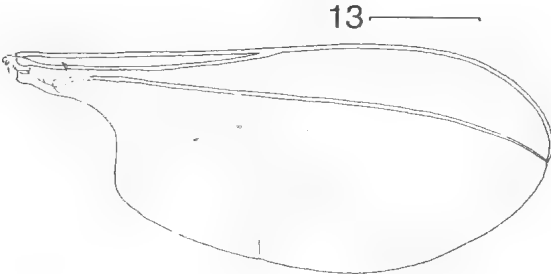
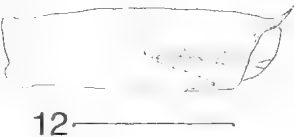
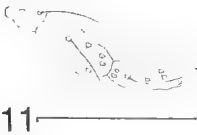
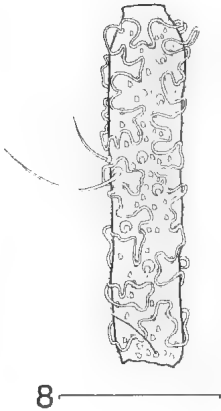
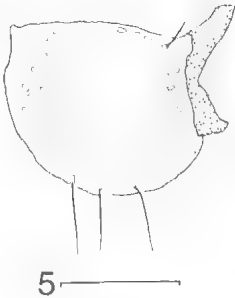
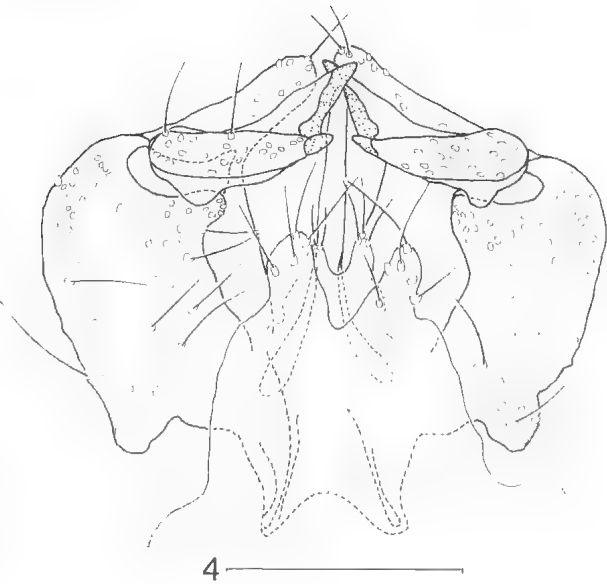
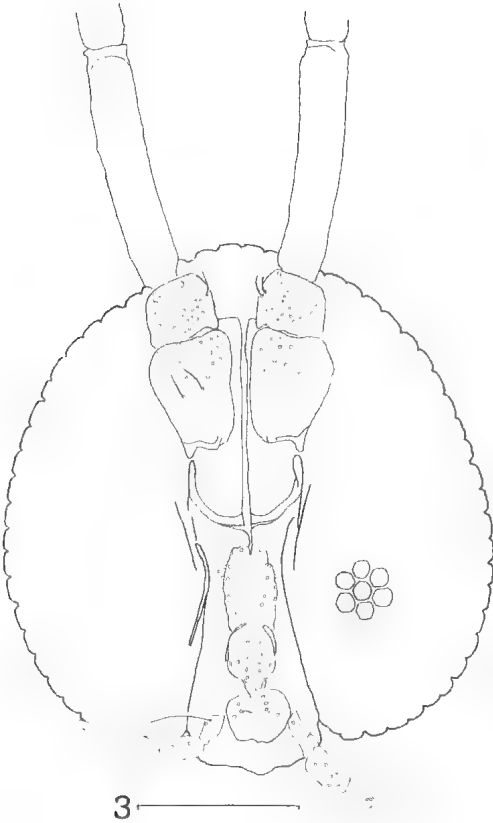


Fig. 2. Gall of *Asphondylia ericiformis* sp. nov. on *Halosarcia indica* subsp. *leiostachya* Wilson. Scale bar = 10 mm.

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Desert where it grows in a variety of habitats, including salt lake margins, open clay plains and gibber plains. It is one of the dominant plants around Lyndhurst, where, in February 1996, all examined shrubs exhibited a low to moderate infestation by the gall midge *A. erichformis* sp. nov.

Material and Methods

Galls were sampled from *Halosarcia indica* subsp. *leiotachya* at Lyndhurst (15.ii.1996) and *Halosarcia pergranulata* subsp. *pergranulata* at Port Adelaide (5.v.1996). The galls collected on both occasions were processed in one of two ways. A small number was cut open and the larvae preserved in 70% ethanol. A larger number of galls was kept in plastic bags and the larvae were reared to adults. Pupation took place within the galls. Plastic bags were examined daily and emerged adults preserved, together with their pupal skins, in 70% ethanol. Canada balsam mounts of type specimens for microscopic examination were prepared according to the technique outlined by Kolesik (1995a). All measurements refer to type series. 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 [ANIC].

Genus *Asphondylia* Loew, 1850

Loew, 1850: Dipterologische Beiträge, 1850: 21 and 37 (as subgenus of *Cecidomyia* Meigen, 1803)

Type species: *Cecidomyia sarothamni* Loew, 1850, l.c.: 38 (des. Karsch, 1877): Revision der Gallmücken: 15).

Asphondylia is a worldwide genus that currently comprises some 260 described species (Gagné 1994). It contains species that have a ventro-distal spine on the first tarsomere, the ovipositor with large basal lobes, female flagellomeres 9–12 progressively shortened, the gonocoxite with a ventro-apical lobe and a dorsally situated gonostylus that is about as wide as long and bears two basally merged teeth.

Asphondylia inflata sp. nov.

(Figs 1, 3–5, 7–9, 12–14, 16–18, 21, 24–27, 31, 34)

Holotype: ♂, Port Adelaide, South Australia (34°50' S, 138°30' E), emerged 6.v.1996. P. Kolesik, reared from branch gall on *H. pergranulata* (Black) Wilson subsp. *pergranulata*, gall collected 5.v.1996, 12/283 [SAMA].

Paratypes: 1♂, 3♀, 2 pupae, 1 pupal skin [SAMA], 1♂, 3♀, 1 pupa, 1 pupal skin [ANIC], all same data but emerged 5.v.–13.vi.1996; 1 larva [SAMA], collected with holotype.

Other material: 2♀, 13 pupal skins [SAMA], collected with holotype.

Male (Figs 3–5, 7–9, 12, 13)

Colour: sclerotized parts of body dark brown, non-sclerotized parts of abdomen orange.

Head: Antennae: scape broadest distally, length 1.5 × breadth at distal end, 1.6–1.8 × length pedicel, pedicel about as broad as long, first flagellomere 2.0–2.2 × length of scape, flagellomeres evenly cylindrical, circumfila dense, equally distributed along segments. Eye facets close together, hexagonoid, eye bridge 6–7 facets long. Frons with 12–18 setae per side. Labella reduced in size, fused, laterally with 3–6 setae, setulose. Maxillary palpus 3 segmented, length of third segment, as well as total length, variable.

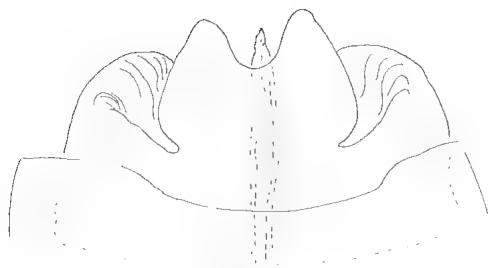
Thorax: Wing length 3.5 mm (range 3.4–3.5), width 1.4 mm (1.4–1.5). Sc cell pigmented proximally. Anepisternum and anepimeron covered with scales. Claws of all legs subequal in size, similar in shape, as long as empodia.

Abdomen: Genitalia: gonocoxites short, with long ventro-apical lobe; gonostylus with 2 unequal apical teeth, ventral about 2 × length of dorsal; aedeagus elongate and narrow.

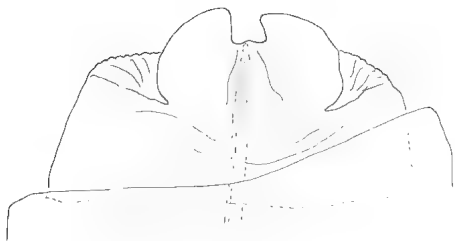
Female (Figs 14, 16–18, 21, 24)

Frons with 9–11 setae per side. Twelfth flagellomere sometimes fused with eleventh. Circumfila comprising two longitudinal bands connected by two short transverse bands. Wing length 3.4 mm (2.7–3.7), width 1.3 mm (1.1–1.4). Seventh abdominal sternite 2.2 × (2.0–2.3) length of sixth. Genitalia: ovipositor 2.2 × (1.9–2.4) length of seventh sternite, cerci glabrous. Other characters as in male.

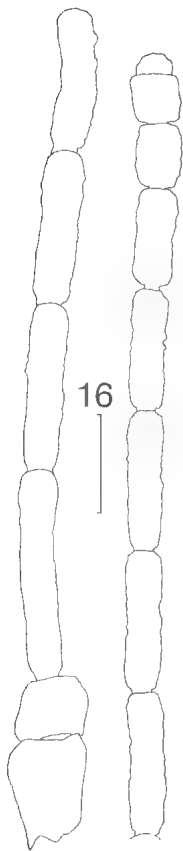
Figs 3–13. 3. Head of male *Asphondylia inflata* sp. nov. in frontal view. 4. Genitalia of male *Asphondylia inflata* sp. nov. in dorsal view. 5. Gonostylus of male *Asphondylia inflata* sp. nov. in posterior view. 6. Gonostylus of male *Asphondylia erichformis* sp. nov. in posterior view. 7. Last three flagellomeres of male *Asphondylia inflata* sp. nov. 8. Sixth flagellomere of male *Asphondylia inflata* sp. nov. 9. Male *Asphondylia inflata* sp. nov. Last tarsomere with claw and empodium. 10 & 11. Maxillary palpus of male *Asphondylia erichformis* sp. nov. 12. First tarsomere of male *Asphondylia inflata* sp. nov. 13. Wing of male *Asphondylia inflata* sp. nov. Scale bars = 100 µm 3, 4, 7–12; 50 µm 5, 6; 500 µm 13.



14



15



16



17



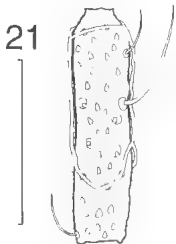
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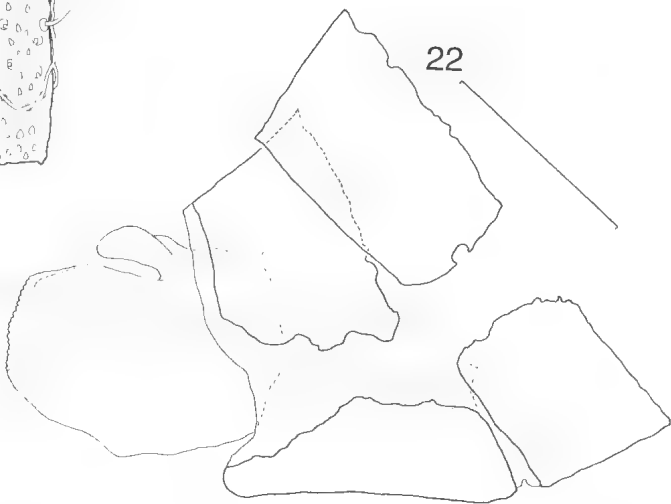
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21



22



23



24

Pupa (Figs 25-27, 31)

Colour: abdomen orange, remaining parts dark brown. Total length 3.0 mm (2.8 - 3.3). Antennal horns serrate medially, 185 µm (141 - 191) long. Upper and lower frontal horns simple. Two pairs of papillae on lower face, one of each pair with a seta. Prothoracic spiracle broad at base, narrow on distal half, curved beyond tracheal opening at mid-length. Abdominal segments 2 - 8 with two pairs dorsal papillae, two pairs pleural papillae, and one pair ventral papillae, all papillae setose. Abdominal dorsal spines simple, prominent pair on last segment curved laterally.

Last instar larva (Fig. 34)

Colour: orange. Integument covered with dense spiculae. Length 3.0 mm. Head capsule strongly pigmented, postero-lateral extensions shorter than length of head capsule. Spatula with two long, pointed anterior teeth, shaft narrowed near middle, widened again posteriorly, surrounded anteriorly and laterally by extensive pigmented, glabrous area. Papillar pattern generally as for *Asphondylia* (Möhn 1955) except only 2 lateral papillae on each side of spatula and no terminal papillae visible on the available specimen.

Etymology

The name "inflata" is a Latin adjective for inflated referring to the appearance of the galled branch.

Gall and biology

Branch segments of *Halosarcia pergranulata* subsp. *pergranulata* infested by this gall midge are 2 - 3 times larger than normal in volume, greyish-green and hard in contrast to the vivid, green colour and soft texture of uninfested branch segments (Fig. 1). Each gall has one to three chambers, with one larva in each chamber. The chamber wall is lined with hard, pile-green, 0.25 - 0.33 mm thick tissue.

Pupation takes place inside the gall. A circular brown area appears on the top of the gall before the pupa cuts an opening with its antennal horns. On 5 May, 1996, at Port Adelaide, the galls appeared very common in the host plant population covering several hundreds of m².

Asphondylia ericiformis sp. nov.

(FIGS 2, 6, 10, 11, 15, 19, 20, 22, 23, 28-30, 32, 33, 35)

Holotype: ♂, Lyndhurst, South Australia [30° 17' S, 138° 21' E], 20.ii.1996. P. Kolesik, reared from branch gall on *Halosarcia indica* subsp. *leuostachya* (Benth.) Wilson, gall collected 15.ii.1996, 121284 [SAMA].

Paratypes: 1 ♂, 2 ♀♀, 1 pupa, 1 pupal skin [SAMA], 1 ♂, 1 ♀, 1 pupa, 1 pupal skin [ANIC], all same data but emerged 25-27.ii.1996; 3 larvae [SAMA], 2 larvae [ANIC], collected with holotype.

Other material: 7 pupae, 4 pupal skins [SAMA], collected with holotype.

Male (Figs 6, 10, 11)

Frons with 6 - 8 setae per side. Wing length 3.4 mm (2.1 - 4.1), width 1.3 mm (0.9 - 1.6). Eye bridge 6 - 9 facets long. Ventral tooth on gonostylus as long as dorsal. Otherwise as in *A. inflata*.

Female (Figs 15, 19, 20, 22, 23)

Frons with 4 - 8 setae per side. Wing length 3.4 mm (2.3 - 3.9), width 1.2 mm (0.9 - 1.4). Seventh abdominal sternite 2.3 x (2.0 - 2.5) length of sixth. Ovipositor 1.9 x (1.8 - 2.0) length of seventh sternite, cerci glabrous, with line of teeth dorsally. Otherwise as in *A. inflata*.

Pupa (Figs 28-30, 32)

Total length 4.4 mm (4.1 - 4.7). Antennal horns 198 µm (154 - 214) long. Upper frontal horn simple; no other horn present. Dorsal spines of last abdominal segment about same length, straight.

Last instar larva (Figs 33, 35)

Total length 3.2 mm (2.4 - 4.8). Spatula with long, pointed anterior teeth, shaft short, broad, parallel-sided. Three lateral papillae on each side of thoracic segments, no terminal papillae visible on available specimens. Otherwise as in *A. inflata*.

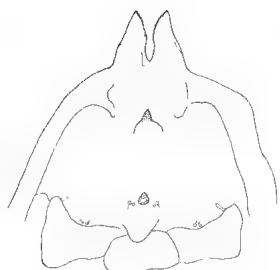
Etymology

The name "ericiformis" is a composed Latin adjective formed from "ericus" (hedgehog) and "formis", referring to the hedgehog-shaped gall.

Gall and biology

This species transforms branch segments of

Figs 14-24. 14, Female *Asphondylia inflata* sp. nov. Basal lobes of ovipositor in dorsal view. 15, Female *Asphondylia ericiformis* sp. nov. Basal lobes of ovipositor in dorsal view. 16, Antenna of female *Asphondylia inflata* sp. nov. 17 & 18, Maxillary palpus of female *Asphondylia inflata* sp. nov. 19 & 20, Maxillary palpus of female *Asphondylia ericiformis* sp. nov. 21, Sixth flagellomere of female *Asphondylia inflata* sp. nov. 22, Female *Asphondylia ericiformis* sp. nov. End of abdomen in lateral view. 23, Female *Asphondylia ericiformis* sp. nov. End of ovipositor in lateral view. 24, Female *Asphondylia inflata* sp. nov. End of ovipositor in lateral view. Scale bars = 100 µm 14-21, 23, 24; 500 µm 22.



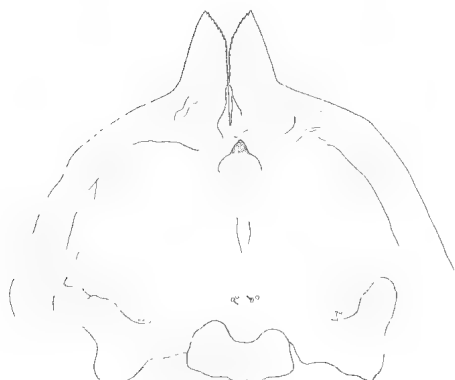
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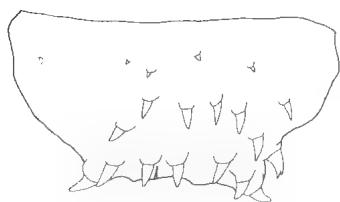
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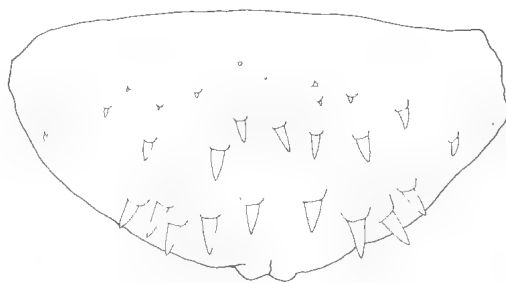
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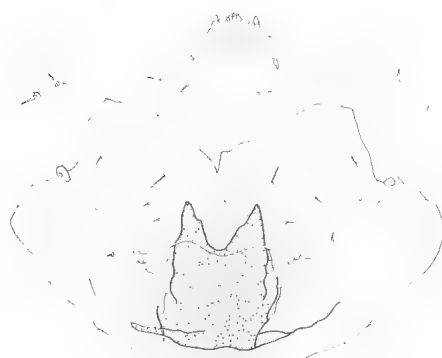
32—



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34—



35—

Halosarcia indica subsp. *leiostachya* into spherical, spiky, monothalamous galls, each occupied by one larva (Fig. 2). Outer diameter of gall 6–12 mm, inner diameter 2.0–2.5 mm. Chamber wall lined with hard, brown, 0.25–0.33 mm thick tissue.

Pupation takes place inside the gall. On 15 February, 1996, at Lyndhurst, 10 examined shrubs of the host plant bore a total of about 200 galls of the new gall midge species. The galls contained larvae or pupae.

Remarks

Four species of *Asphondylia* have been previously known to occur in Australia (Gagné 1989; Kolesik 1995b). *Asphondylia dodonaeae*, a South Australian species common in the Adelaide Hills, transforms terminal branch stems and primary leaf veins of *Dodonaea viscosa* (Sapindaceae) (Kolesik 1995b). Two species, *A. loewi* and *A. rubicunda*, were described in the previous century from adults caught in flight in Sydney, New South Wales, and their biology is unknown (Skuse 1888, 1890). The fourth, *A. hilli*, was described from females and pupae bred from an unknown plant in Darwin, Northern Territory (Edwards 1916). These last three species, which were described superficially and can not be compared on their descriptions, are not considered in the present paper, but I plan a review of Australian *Asphondylia* spp. at a later stage.

Morphological similarities between the two new species and the fact that their respective host plants belong to the same genus, suggest a close relationship. They form a distinctive group that excludes *A. dodonaeae*. *Asphondylia dodonaeae* differs from the two new species in the following respects. Adults have prominent labela and scapes as long as broad at the distal ends. The male has a short a ventro-apical lobe on the gonocoxite, small lobes adjacent to teeth on the gonostylus and the aedeagus much shorter than the gonocoxites. The seventh abdominal sternite in the female is three times longer than the sixth. The pupa has no frontal horns, the antennal horns are triangular and serrated laterally and the prothoracic spiracle is not considerably broader at the base. The area sur-

rounding the spatula in the larva is not pigmented.

Adults of the two new species differ from each other most prominently in the shape of the gonostylus and the end of the ovipositor. The gonostylus bears teeth of unequal length and the end of the ovipositor lacks external processes in *A. inflata*. In contrast, the gonostylus of *A. ericiformis* bears teeth of equal length and the end of the ovipositor is serrated. More differences are evident in the earlier developmental stages. The pupa of *A. inflata* has both upper and frontal horns present and a prominent pair of dorsal spines on the last segment is curved laterally; in *A. ericiformis* the pupa has the upper horn only and all dorsal spines on the last abdominal segment are equally strong and straight. The larvae differ in the shape of the spatula and the number of lateral papillae two per side in *A. inflata* but three per side in *A. ericiformis*. The two new species resemble each other in the shape of the antennal horns and prothoracic spiracles in pupae, the antennal segments in adults, the ventro-apical lobes on the gonocoxites in males and the relative lengths of the sixth and seventh abdominal sternites in females. The elongation of the ventro-apical lobe on the gonocoxite is unique to these two species and distinguishes them from the other *Asphondylia* spp.

Acknowledgments

I am grateful to P. G. Wilson, Western Australian Herbarium Como for the identification of *Halosarcia indica* subsp. *leiostachya*, R. J. Chinnock, South Australian Herbarium Adelaide for the identification of *Halosarcia pergranulata* subsp. *pergranulata*, T. B. Réardon who led a South Australian Museum collecting trip during which *Asphondylia ericiformis* sp. nov. was discovered, A. Stark, Halle Germany for providing copies of Karselt's and Loew's papers and J. D. Gray, Department of Horticulture, Viticulture and Oenology University of Adelaide and R. J. Gagné, Systematic Entomology Laboratory USDA Washington DC for their comments on an early draft of the manuscript.

Figs 25–35. 25. *Asphondylia inflata* sp. nov. Anterior part of pupa in ventral view. 26. *Asphondylia inflata* sp. nov. Anterior part of pupa in lateral view. 27. *Asphondylia inflata* sp. nov. Prothoracic spiracle of pupa. 28. *Asphondylia ericiformis* sp. nov. Anterior part of pupa in ventral view. 29. *Asphondylia ericiformis* sp. nov. Anterior part of pupa in lateral view. 30. *Asphondylia ericiformis* sp. nov. Prothoracic spiracle of pupa. 31. Pupa of *Asphondylia inflata* sp. nov. Last abdominal segment in dorsal view. 32. Pupa of *Asphondylia ericiformis* sp. nov. Last abdominal segment in dorsal view. 33. Larva of *Asphondylia ericiformis* sp. nov. Last two abdominal segments in dorsal view. 34. Anterior part of larva of *Asphondylia inflata* sp. nov. in ventral view. 35. Head and first thoracic segment of larva of *Asphondylia ericiformis* sp. nov. in ventral view. Scale bars = 100 µm.

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A LATE EARLY CAMBRIAN TRILOBITE FAUNULE FROM THE GNALTA GROUP, MT WRIGHT, NSW

*BY J. B. JAGO**, *LIN TIAN-RUI†*, *G. DAVIDSON‡*,
B. P. J. STEVENS§ & *C. BENTLEY**

Summary

Jago, J. B., Lin Tian-Rui, Davidson, G., Stevens, B. P. J. & Bentley, C. (1997) A Late Early Cambrian trilobite faunule from the Gnalta Group, Mt Wright, NSW. Trans. R. Soc. S. Aust. 121(2), 67-74, 30 May, 1997.

Trilobites from a new locality within a siltstone of the Cymbric Vale Formation, western New South Wales, are described here as *Redlichia* cf. *ziguiensis* Lin 1978 and *Hsuaspis cerastes* (Öpik 1975). The species described as *Strenax cerastes* Öpik and *Estaingia bilobata* Pocock from nearby localities are included in a single redefined species, *H. cerastes*. The genera *Pseudichangia* Chu & Zhou in Lu et al. (1974) and *Strenax* Öpik 1975 are placed in synonymy with *Hsuaspis*. The fauna described here is of late Early Cambrian (Late Botoman) age.

Key Words: Cambrian, Trilobita, Australia, New South Wales, *Hsuaspis*, Cymbric Vale Formation.

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by J. B. JAGO*, LIN TIAN-RUI[†], G. DAVIDSON[‡], B. P. J. STEVENS[§] & C. BENTLEY^{||}

Summary

JAGO, J. B., LIN TIAN-RUI, DAVIDSON, G., STEVENS, B. P. J. & BENTLEY, C. (1997). A Late Early Cambrian trilobite faunule from the Gnalta Group, Mt Wright, NSW. *Trans. R. Soc. S. Aust.* **121**(2) 67-74, 30 May, 1997. Trilobites from a new locality within a siltstone of the Cymbrie Vale Formation, western New South Wales, are described here as *Redlichia* cf. *ziguensis* Lin 1978 and *Huasaspis cerastes* (Öpik 1975). The species described as *Strenax cerastes* Öpik and *Ectastorgia bilobata* Pocock from nearby localities are included in a single redefined species, *H. cerastes*. The genera *Pseudochungia* Chu & Zhou in Lu *et al.* (1974) and *Strenax* Öpik 1975 are placed in synonymy with *Huasaspis*. The fauna described here is of late early Cambrian (Late Botomian) age.

KEY WORDS: Cambrian, Trilobita, Australia, New South Wales, *Huasaspis*, Cymbrie Vale Formation.

Introduction

Davidson¹ discovered a small area of fossiliferous siltstone of the Cymbrie Vale Formation in the Mt Wright area, western New South Wales (Fig. 1). Davidson identified the trilobites as *Strenax cerastes* Öpik and *Ectastorgia bilobata* Pocock of Öpik (1975b). More samples were collected recently and the results of the examination of the fossils are given below.

The Early to early Middle Cambrian Gnalta Group comprises three formations, from bottom to top: the Mount Wright Volcanics, the Cymbrie Vale Formation and the Coonigan Formation. The distribution of these formations as shown in Fig. 1 is after Warris² and Rose (1968).

The Gnalta Group crops out along a broad valley west of Cymbrie Vale homestead and is mostly confined by the Mt Wright Fault on the east and the Lawrence Fault on the west. A smaller area of Cymbrie Vale Formation crops out in the core of an anticline west of the Lawrence Fault. The structure of the Gnalta Group is very imperfectly known as a

result of geological complexity (faults and folds), poor outcrop in much of the area and a lack of bedding in the abundant volcanics of the Mt Wright Volcanics.

The siltstone to fine sandstone outcrop from which the fossils were collected (Fig. 1) is isolated from other outcrops by a cover of soil and cobbles representing a Cainozoic lag deposit. Hence there is no outcrop continuity with any identified Gnalta Group formation. The outcrop also contains no diagnostic rock type. The structure of the Gnalta Group is sufficiently complex to render it impossible to confidently place the outcrop in a formation. Davidson¹ placed this and nearby outcrops in the Cymbrie Vale Formation, while Kruse (1982) placed the nearby outcrops in the Coonigan Formation. As shown below, the species described by Öpik (1975b) from the Cymbrie Vale Formation as *Ectastorgia bilobata* and *Strenax cerastes* are found at the locality being considered here. No such fossils are known from either the Mt Wright Volcanics or the Coonigan Formation. Hence, the outcrop is probably Cymbrie Vale Formation.

Previous Work

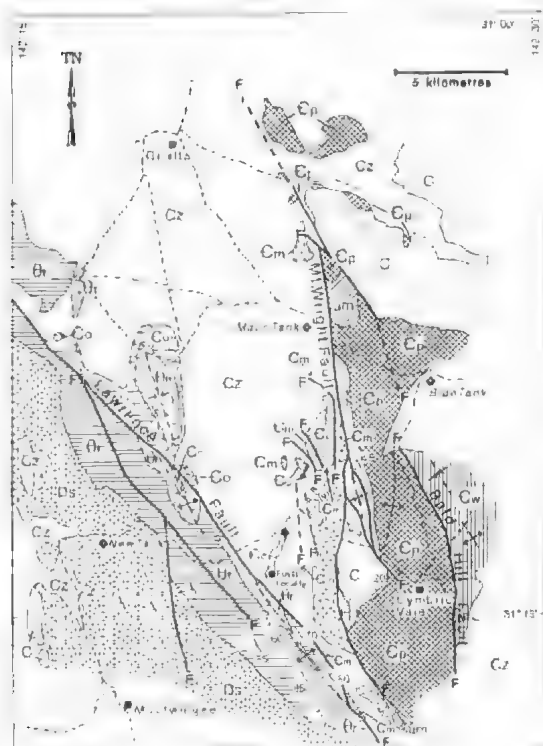
The term Gnalta Group was introduced by Warris² who assigned an Early to early Middle Cambrian age to the group. From limestone in the Mt Wright Volcanics, Warris identified algae and archaeocyathids, including *Thalamocyathus trachealis* Taylor. From the Cymbrie Vale Formation he identified *Ectastorgia bilobata*, *Calodiscus* sp. and *Paquetides* sp. and assigned a middle or late Early Cambrian age. He identified the trilobites *Redlichia idonea*, *Vystridura saint smithi*, *Pagena significans*, *Petronopsis normata*, *Orvetocephalus* sp. and

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[‡]Geology Department, University of Tasmania-GPO Box 252 Hobart Tas. 7001.

[§]Geological Survey of New South Wales, 32 Sulphide Street Broken Hill NSW 2880.

^{||}Davidson, G. (1981) A contribution to the geology of the Mt Wright area. BSc (Hons) thesis, Australian National University (unpub.).

WARRIS, B.J. (1967) The stratigraphy and palaeontology of northwestern New South Wales. PhD thesis, Sydney University (unpub.).



REFERENCE

- C1 Cambrian to Devonian, including tertiary dolomite, silicate, quartzite, etc.
- C2 Late Devonian to Carboniferous, including Harwood Formation and weathering sandstone.

- C3 Middle to Late Devonian Snake Cave Sandstone with thin, many conglomerate.

- C4 Early to Middle Devonian Nowena Formation sandstone, quartzite, etc.

- C5 Devonian to Carboniferous (including sandstone and conglomerate) etc.

- C6 Middle Devonian Gosses Formation limestone, shale.

- C7 Late Early Carboniferous Cymbria Vale Formation and equivalent, etc.

- C8 Early Cambrian Mt Wright Volcanics, etc.

- C9 Cambrian to Devonian, including Harwood Formation and weathering sandstone.

- C10 Late Paleozoic to Early Carboniferous, etc.

- C11 Ultramafic rocks, etc.

- C12 Fault

- C13 Trench

- C14 Fold

Dorypyge sp. from the Coonigan Formation, indicating an early Middle Cambrian age.

In terms of the Cymbria Vale Formation, Fletcher (1964) first recorded archaeocyatha from lenticular limestones near the base of the unit. Kruse (1982) noted four archaeocyath limestone-bearing lenses; he considered two to be of Aldabanian or Lenan age and two to be of Lenan age. The uppermost Cymbria Vale Formation contains well-bedded sandstones and carbonates with abundant fossils. Öpik (1975b) recorded the trilobites *Dinesus* aff. *granulosus*, *Ectostictus bilobatus*, *Sirenax cerastes*, *S. fletcheri*, *Serroniscus daedalus*, *Memsiculus memsicus*, *Dicranoceras fragum* and *Pagetia*, the monoplacophoran *Scenellu reticulata*, the inarticulate brachiopods *Botsfordia* cf. *caelata*, *Lingulella* and *Neobolus*?, corals and sponge spicules.

Age and Correlation

As shown below we consider that the species described by Öpik (1975b) as *Sirenax cerastes* and *Ectostictus bilobatus* from nearby localities should both be included within a single redefined species *Hsuaspis cerastes*. These localities Öpik considered to be equivalent to the Samashtyk'gol Horizon of the Altay-Sayan region which, as noted by Zhuravlev and Gravestock (1994), can be roughly correlated with the Botoman of Siberia. The archaeocyatha from the Cymbria Vale Formation which occur below the trilobites described by Öpik (1975b) were correlated with the informal archaeocyathid unit the *Syringocnema favius* beds by Zhuravlev and Gravestock (1994) which was considered to be equivalent to the middle to Late Botoman by these authors. These authors considered that the *Syringocnema favius* beds fall within the trilobite based *Parania janae* Zone of Jell (in Bengtson *et al.* 1990). Jell suggested that the *P. janae* Zone can be correlated with the Botoman and probably with the late Botoman (see also brief discussion by Jago 1996). As noted above, the exact stratigraphic position of the present fauna is a little unclear but it probably occurs high in the Cymbria Vale Formation and stratigraphically close to the faunas described by Öpik (1975b). The Coonigan Formation which overlies the Cymbria Vale Formation has a very early Middle Cambrian age (Öpik 1975a; Jell 1975; Shergold *et al.* 1985), thus providing an upper limit to the age of the fauna currently being described. Palmer and Rowell (1995) note that *Hsuaspis* is

Fig. 1. Geology of the Mt Wright area showing locality of fossils described herein. Geology from Warren, Rose (1968), Davidson, Kruse (1982), B. Stevens and A. Crawford (unpub. field data).

closely related to the Siberian genera *Bergemmiellus* and *Bergemiaspis* which characterise the Botoman of Siberia.

In China *Redlichia ziguensis* occurs in the late Early Cambrian *Pulacolemus* Zone of the Yangtze Gorge. This is approximately equivalent to part of the Toyonian of the Siberia Platform.

The above discussion suggests that the faunule described herein is of late Early Cambrian age and probably of Late Botoman age.

Systematic Descriptions

Terminology essentially follows Harrington *et al.* (1959). Specimen numbers refer to the palaeontological collection of the South Australian Museum (SAMP).

Family	Redlichidae Poulsen 1927
Subfamily	Redlichinae Poulsen 1927
Genus	<i>Redlichia</i> Cossman 1902
	<i>Redlichia</i> cf. <i>ziguensis</i> Lin 1978
	(Fig. 2A)

1978 *Redlichia ziguensis* Lin in Zhou & Lin 1978, p. 145, Pl. 20, Fig. 8.

Material

One incomplete cranidium, SAMP35344.

Description

Cranidium subrectangular, about 35 mm long. Glabella (including occipital ring) about 0.9 length of cranidium. Glabella tapers evenly forward to rounded glabellar anterior. Narrow shallow axial furrows. Three pairs of lateral glabellar furrows; 1p, moderately deep, directed slightly to posterior and meet at centre of glabella to form an evenly posteriorly arched furrow; 2p pair, shallow, directed slightly to posterior; 3p pair, represented by faint depressions on glabellar margins. Occipital furrow deepest laterally; shallow medially where it is arched slightly to anterior. Anterior border furrow of moderate depth; anterior border, very gently convex, and of uniform length (sag.). Very short (sag.) prelabellar field. Small anterior areas of fixigenae gently convex; long wide palpebral lobes extend from just to anterior of 3p furrows to level with occipital furrow. Narrow, distinct palpebral furrow shallows posteriorly. Palpebral areas of fixigenae very gently convex. Width of palpebral areas of fixigenae at their widest is about one-third that of glabella. Preocular sections of facial suture markedly divergent.

Discussion

A single incomplete internal mould of cranidium makes a definite specific identification difficult.

However, its size, outline, slender glabella, the position of the posterior of the palpebral lobes, the nature of the prelabellar area and the shape of the preocular section of the facial suture suggest *Redlichia ziguensis* Lin (in Zhou & Lin 1978, p. 145, Pl. 20, Fig. 8). However, it differs in having a more tapered glabella, a forward arching at the centre of the occipital ring, and a more sharply rounded glabellar anterior.

Superfamily	Ellipsocephaloidea Matthew 1887
Family	Ichangidae Zhu 1980
Genus	<i>Hsuaspis</i> Chang 1957

Hsuaspis Chang 1957, p. 45, Lu *et al.*, 1965, p. 85; Zhang *et al.*, 1980, p. 244; Jell in Bengtson *et al.*, 1990, p. 310; Palmer and Rowell, 1995, p. 16; Nediu, 1995, p. 36.

Estaingia Pocock 1964, p. 462; Öpik 1975b, p. 10. *Pseudichangia* Chu & Zhou in Lu *et al.*, 1974, p. 93; Zhu in Zhang *et al.*, 1980, p. 239.

Stenax Öpik 1975b, p. 13. *Zhuxiella* Zhang & Zhu in Zhang *et al.*, 1980, p. 247. Type species; *Lusatops yitensis* Chang, 1953, p. 128, Pl. 2, Figs 1-16.

Discussion

Jell (in Bengtson *et al.*, 1990) placed *Estaingia* Pocock 1964 and *Zhuxiella* Zhang & Zhu (in Zhang *et al.*, 1980) in synonymy with *Hsuaspis* Chang 1957, a move supported by Palmer & Rowell (1995), although the latter authors expressed some doubt as to the suprageneric position of *Hsuaspis*. In addition, Jell suggested that *Stenax* Öpik 1975 might be regarded as a junior synonym of *Pseudichangia* Chu & Zhou in Lu *et al.*, 1974 from southwestern China. The present authors support Jell in placing *Stenax* in synonymy with *Pseudichangia* but also consider that *Pseudichangia* is a junior synonym of *Hsuaspis*, thus also placing *Stenax* in synonymy with *Hsuaspis*.

The following species of *Pseudichangia* as figured in Zhang *et al.*, 1980, *P. damiaoensis* (Chang) (Pl. 76, Figs 13, 14; Pl. 77, 1-5), *P. rongqiensis* Zhu (Pl. 77, Figs 6-8), *P. zhuxiensis* Zhang & Zhu (Pl. 134, Fig. 2) and *Pseudichangia* (?) *invalida* Zhu, Pl. 77, Figs 9, 10, may all belong in a single species, i.e. *Hsuaspis damiaoensis* (Chang). *Zhuxiella hubiensis* Zhang & Zhu (see Zhang *et al.*, 1980, Pl. 134, Fig. 3) also appears to belong in *H. damiaoensis* as far as can be determined from the available figure although the glabella of *damiaoensis* extends further forwards than that of the type species of *Hsuaspis*, *H. sinensis*, and the anterior sections of the facial sutures of *sinensis* are more divergent than those of *damiaoensis*. We would regard these as specific rather than generic differences.

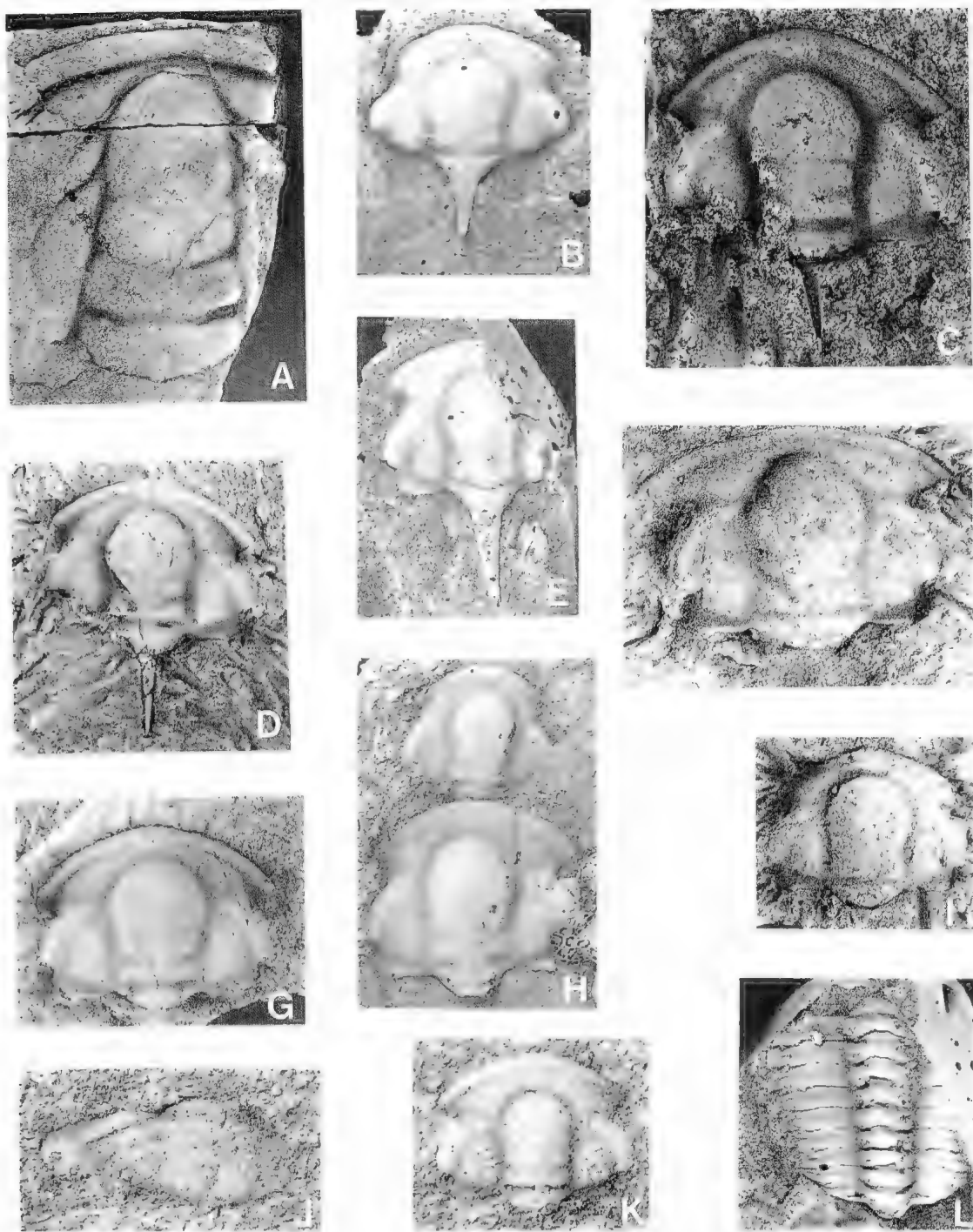


Fig. 2. A. *Redlichia* cf. *ziquiensis* Lin 1978, SAMP35344, cranidium, internal mould, $\times 1.5$. B-L *Hsuaspis cerastes* (Öpik 1975). B. SAMP35329, cranidium, external mould, $\times 2$. C. SAMP35340, cranidium, internal mould, $\times 5$. D. SAMP35335, cranidium, internal mould, $\times 2$. E. SAMP35331, cranidium, external mould, $\times 2$. F. SAMP35343, cranidium, internal mould, $\times 2$. G. SAMP35337, cranidium, internal mould, $\times 2$. H. Top. SAMP35327, cranidium, external mould, $\times 2$. Bottom. SAMP35328, cranidium, external mould, $\times 2$. I. SAMP35342, cranidium, internal mould, $\times 2$. J. SAMP35333, pygidium, external mould, $\times 6$. K. SAMP35332, cranidium, external mould, $\times 6$. L. SAMP35341, partial thorax, external mould, $\times 2$.

Jell (*in* Bengtson *et al.* 1990) queried the taxonomic position of *Estauingia bilobata* from western New South Wales as described by Öpik (1975b). In our view the specimens described by Öpik (1975b) do not belong in *Hsuaspis bilobata* (Pocock 1964) because the glabella of Öpik's specimens extends further to the anterior than does that of *H. bilobata* as described by Pocock (1964). In addition, in three of the four cranidia figured by Öpik, there is a marked forwards expansion of the glabella whereas in the type material of *H. bilobata* figured by Pocock (1964) the glabella is either tapering forwards or has a slight waist. In our view the specimens described and figured by Öpik (1975b, p. 11, Pl. 1, Figs 1-7) belong in the same species as those described by Öpik (1975b, p. 14, Pl. 2, Figs 1-6) as *Strenax cerastes*. Apart from the specimens figured herein, numerous other specimens are available and there is a complete gradation from specimens such as those figured here as Figs 2B, E which are quite similar to the cranidium illustrated by Öpik (1975b, Pl. 2, Fig. 1) as the holotype of *Strenax cerastes* gen. et sp. nov. to specimens such as those figured herein as Figs 2G, 3C which are indistinguishable from those figured as *Estauingia bilobata* by Öpik (1975b, Pl. 1).

Öpik (1975b, p. 16, Pl. 3, Figs 1, 2, text, Fig. 5) erected a subgenus of *Strenax*, i.e. *Strenax (Semaniscus)* based on four cranidia with the only illustrated cranidium having a length of only 3.8 mm. It is clearly an immature specimen which should not be the basis of a new taxon.

Jell (1990) erected *Hsuaspis occipitospina* which is characterised by a relatively long preglabellar field crossed by a preglabellar median ridge and the presence of a short slender occipital spine. It is possible that the specimens described by Palmer & Rowell (1995) from the Central Transantarctic Mountains as *Hsuaspis* cf. *H. bilobata* (Pocock) belong in *H. occipitospina*, because the Antarctic specimens have a glabella of similar length to *H. occipitospina* as well as a similar preglabellar median ridge. However, the Antarctic specimens have an occipital node rather than an occipital spine.

Hsuaspis cerastes (Öpik 1975)
(Fig. 2B-L, Fig. 3)

1975 *Strenax cerastes* Öpik 1975b, p. 14, Pl. 2, Figs 1-6, text, Fig. 4

1975 *Estauingia bilobata* Pocock, Öpik 1975b, p. 11, Pl. 1, Figs 1-7.

Material

Almost twenty cranidia, one partial free cheek (SAMP35334), an incomplete thorax (SAMP35341) and an incomplete pygidium (SAMP35333).

Diagnosis

Species of *Hsuaspis* with distinctly expanded anterior part of glabella; length of glabella (excluding occipital ring) about 0.75-0.8 that of cranium (excluding occipital ring); occipital ring bears a spine which in some specimens is a small node; in others it is long and slender.

Description

Gently convex cranium with width slightly greater than length (sag.). Deep wide axial furrows shallow anteriorly. Gently convex glabella of length (excluding occipital ring) about 0.75-0.8 that of cranium. Glabella increases in width to anterior with slight waist near 1p furrows; glabella widest at eye ridges, broadly rounded glabellar anterior. Four pairs lateral glabellar furrows: 1p furrows moderately deep and each extend about 1/3 of distance across glabella and directed slightly to posterior; 2p furrows shallow, extend about 1/3 distance across glabella, and directed very slightly to posterior; 3p furrows quite shallow and directed almost straight across glabella; 4p furrows occur as small indistinct pits. Occipital ring longest medially; it bears a spine the length of which varies considerably from specimen to specimen. In some specimens a small node present; in others there is a long slender spine which may have a length about 0.75 that of glabella (excluding occipital ring) in mature specimens (Fig. 2D) and somewhat longer in immature specimens (2B,F).

Occipital furrow shallow medially. Very short (sag.) gently convex preglabellar field. Anterior border gently convex with similar length (sag.) to preglabellar field. Poorly-developed plectrum present in some specimens (Fig. 2G). Shallow anterior border furrow. Gently convex palpebral areas of fixigenae have width about same as that of glabella. Prominent centro-posteriorly placed palpebral lobes have a length (exsag.) about 0.55 that of glabella. Posterior of palpebral lobes meet the broad posterolateral border furrows. Well-developed eye ridges slightly narrower than palpebral lobes. Shallow palpebral furrows. Narrow posterolateral borders. Preocular sections of facial suture diverge forwards at about 30° to the transverse. Short postocular sections of facial suture. Narrow posterolateral border.

The single partial librigenae has a wide border which extends into an incomplete genal spine. It has a reticulate ornamentation.

Thorax with at least nine segments. Convex axis has width about 0.3 that of segment. Centrally placed nodes on 4th and 5th segments of available thorax. Shallow pleural furrows; short broad pleural spines. The only available pygidium is poorly preserved. It is small and transversely elliptical. Axis has a width about 0.3 that of pygidium. Axis extends almost to

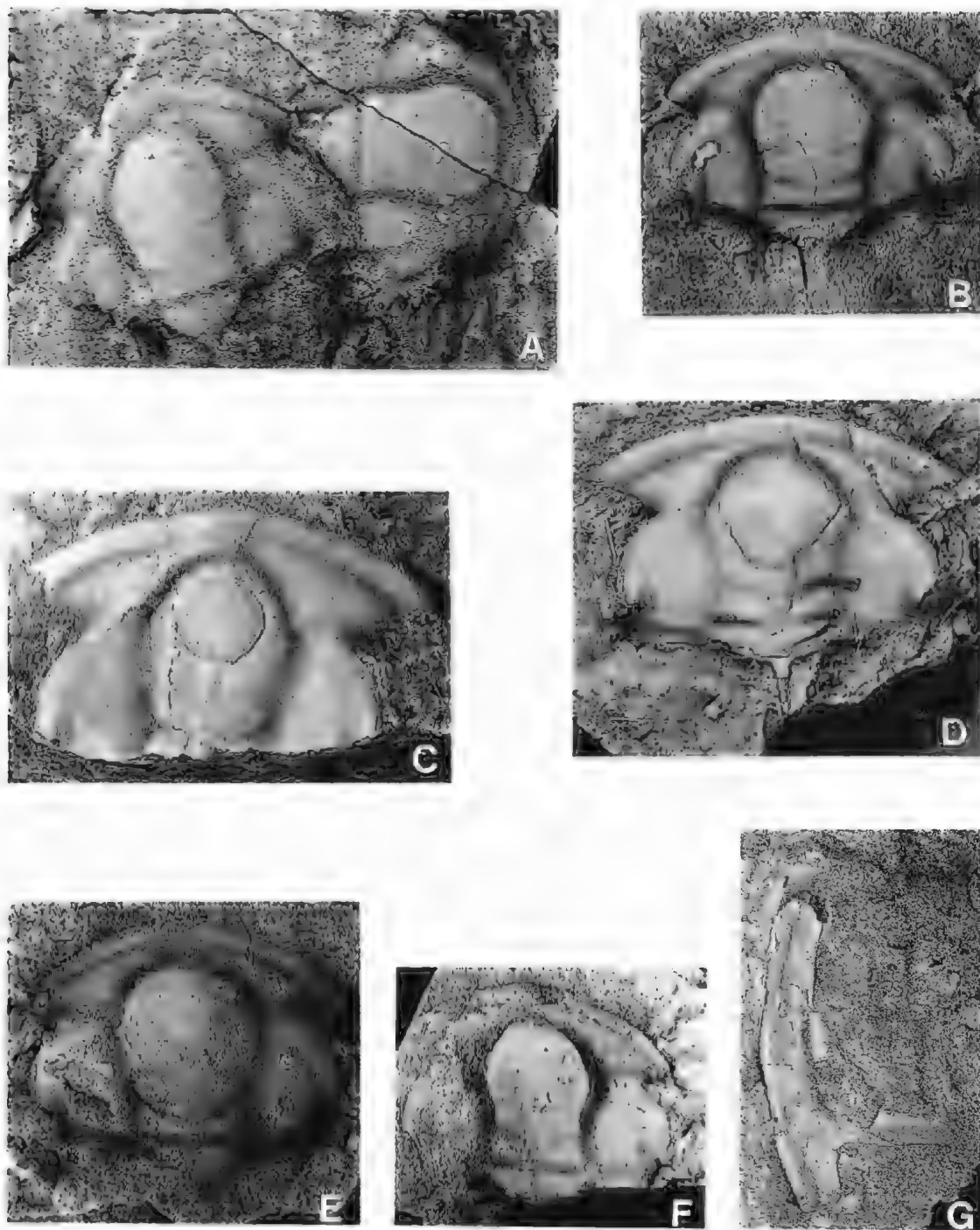


Fig. 3. *Hsianspis cerastes* (Öpik 1975). A. Left SAMP35325, cranium, internal mould, x3. Right, SAMP35326, cranium, internal mould, x3. B. SAMP35338, cranium, internal mould, x3. C. SAMP35330, cranium, internal mould, x2. D. SAMP35339, cranium, internal mould, x2. E. SAMP35323, cranium, internal mould, x3. F. SAMP35336, cranium, internal mould, x2. G. SAMP35334, librigena, external mould, x2.

posterior margin. Axis comprises two axial rings plus terminal axial piece. Two pleural furrows and one interpleural furrow present. Two border-spines can be seen in available specimen.

Morphogenesis

The smallest cranidium is that figured as 2K. In this specimen the length of the glabella (excluding occipital ring) is 0.7 that of cranidium. In larger specimens such as those figured in 3B,D the glabella has a length of 0.8-0.85 that of cranidium. The relative size of the occipital spine decreases - in smaller specimens (2B,f) the spine has a relatively thicker base than in more mature specimens (3B,D).

Discussion

The considerable variation in the shape of the glabella, the path of the facial suture, the shape and length of the occipital ring, and the length of the occipital spine, of the specimens described and figured here as *H. cerastes* raises the question as to the validity of placing all these specimens within a single species. However, as noted above, there appears to be a complete morphological variation present in the available specimens and hence we feel the erection of more than one species can not be justified. *Hsuaspis cerastes* as described herein differs from *H. damianensis* in having a relatively shorter glabella; the glabella of *H. damianensis* either reaches or almost reaches the anterior border furrow, whereas that of *H. cerastes* stops short of the border. However, it is worth noting that with respect to the length of the occipital spine, *H. damianensis*, as figured in Zhang *et al.* (1980, Pl. 76, Figs 13, 14; Pl. 77, Figs 1-5) shows considerable variation in length of occipital spine as does *H. cerastes*. The anterior of the glabella of *H. cerastes* is more expanded than is that of *H. damianensis*.

Hsuaspis occipitospina of Jell (1990) has a small well-developed occipital spine. The spine of *H. cerastes* arises from further back on the occipital ring than that of *H. occipitospina*; the spines on some specimens of *H. cerastes* are much longer than the biggest spines on *H. occipitospina*. In *H. cerastes* the ratio of the length of the glabella (excluding occipital ring) to the length of the cranidium (excluding occipital ring) is 0.75-0.80; in *H. occipitospina* it ranges from 0.65-0.70.

The glabella of *H. sinensis* extends further forwards than does that of *H. cerastes*. The anterior part of the glabella of *H. cerastes* is more expanded than *H. sinensis*. *H. sinensis* bears only a small median node rather than a prominent spine as in many specimens of *H. cerastes*.

The anterior part of the glabella of *H. cerastes* is more expanded than that of *H. bilobata*; the glabella of *H. cerastes* is relatively longer than that of *H. bilobata*. The glabella of *H. cf. H. bilobata* as described by Palmer & Rowell (1995) is shorter than that of *H. cerastes*.

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POORLY PRESERVED TRILOBITES AND BRACHIOPODS FROM THE KANMANTOO GROUP, FLEURIEU PENINSULA

BRIEF COMMUNICATION

Summary

The Kanmantoo Group (Fig. 1) is a thick (8-10 km) succession of predominantly clastic metasedimentary rocks which crop out in an arcuate belt from near Australia Plains in the northeastern Mt Lofty Ranges to the western end of Kangaroo Island. On Fleurieu Peninsula, the Kanmantoo Group rests unconformably on the Normanville Group¹, the uppermost formation of which, the Heatherdale Shale, contains a poorly preserved fauna of possible mid to late Botoman age². The highest well-dated fauna from the Normanville Group are archaeocyathids from the Fork Tree Limestone at Sellick Hill which indicate an age close to the Atdabanian-Botoman boundary³. These are at least 400 m below the top of the Heatherdale Shale. The top of the Kanmantoo Group is not exposed but lower parts of the group are intruded by the Rathjen Gneiss which has an age of 516 ± 4 Ma⁴, i.e. late Early Cambrian or early Middle Cambrian on recent Cambrian time scales^{5,6}. The stratigraphy of the Kanmantoo Group is described in detail by Daily & Milnes^{7,8}.

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The Kanmantoo Group (Fig. 1) is a thick (8-10 km) succession of predominantly clastic metasedimentary rocks which crop out in an arcuate belt from near Australia Plains in the northeastern Mt Lofty Ranges to the western end of Kangaroo Island. On Fleurieu Peninsula, the Kanmantoo Group rests unconformably on the Normanville Group¹, the uppermost formation of which, the Heatherdale Shale, contains a poorly preserved fauna of possible mid to late Botoman age². The highest well-dated fauna from the Normanville Group are archaeocyathids from the Fork Tree Limestone at Sellick Hill which indicate an age close to the Adabanian-Botoman boundary³. These are at least 400 m below the top of the Heatherdale Shale. The top of the Kanmantoo Group is not exposed but lower parts of the group are intruded by the Radtjen Gneiss which has an age of 516 ± 4 Ma⁴, i.e. late Early Cambrian or early Middle Cambrian on recent Cambrian time scales^{5,6}. The stratigraphy of the Kanmantoo Group is described in detail by Daily & Milnes⁷.

The Cambrian sequences as exposed on Fleurieu Peninsula, Kangaroo Island and Yorke Peninsula show considerable lateral and vertical lithological variation⁸. Currently, the limited biostratigraphic information makes it difficult to correlate accurately from one region to another and hence determine the timing and sequence of both stratigraphic and tectonic events.

One of the problems in this regard has been the lack of biostratigraphically useful body fossils in the Kanmantoo Group. The only such fossils reported to date are the inarticulate brachiopod *Lingulella* from about 10 m above the base of the basal unit of the Kanmantoo Group, the Carrickalinga Head Formation, at Carrickalinga Head⁹, and a possible hyolithid from near the top of the Carrickalinga Head Formation near Blowhole Creek¹⁰. Trace fossils have been reported from the Backstairs Passage Formation at Accommodation Hill near Truro¹¹.

This note reports the presence of further inarticulate brachiopods (Fig. 2D,E), from about 100 m above the base of the Carrickalinga Head Formation at Carrickalinga Head. They are small and poorly preserved, but appear to represent at least two species.

In a quarry near Parawa (Fig. 3), at 621,551 (Torrens Vale, 1:50,000 topographic map) on Callawonga Creek Road, the authors have found the first known trilobites from the Kanmantoo Group. The specimens come from a laminated metasiltstone, probably part of the Tunkalilla Formation but possibly upper Tapanappa Formation. To date we have found about 20 specimens, all of which are almost complete, thus indicating low energy depositional conditions. As

shown in Fig. 2A,B,C the specimens are poorly preserved, tectonically deformed and of no biostratigraphic use, although, within the limits of preservation, they seem to represent a single species. However, their presence indicates the possibility of the eventual discovery of biostratigraphically useful trilobites from the Kanmantoo Group.

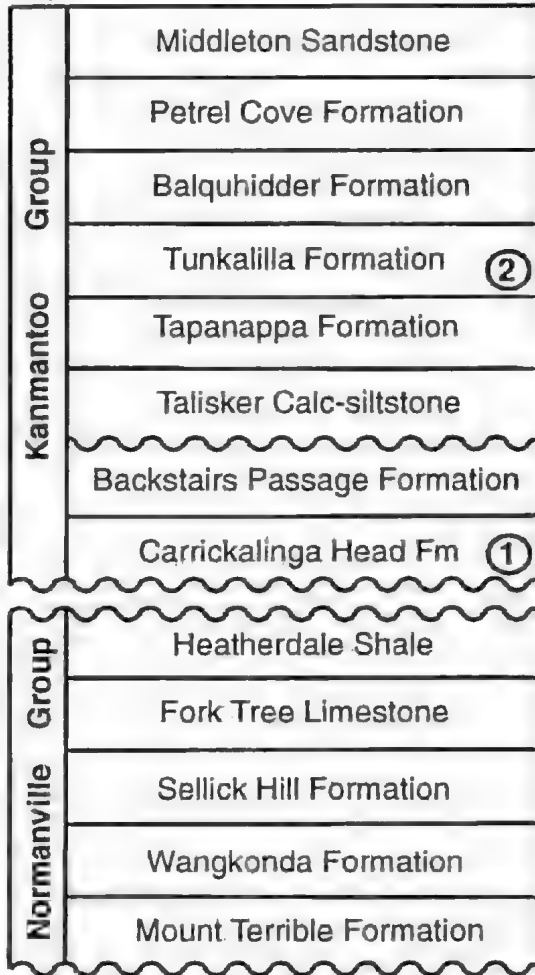


Fig. 1. Stratigraphic outline of Normanville and Kanmantoo Groups, Fleurieu Peninsula, showing the levels of the fossils figured herein.

Fig. 2. A-C. Trilobites from quarry near Parawa. A. Rubber cast of external mould, SAMP35345, $\times 3$. B. Internal mould, SAMP35346, $\times 4$. C. Rubber cast of external mould, SAMP35347, $\times 3$. D, E. Inarticulate brachiopods from Carrickalinga Head. D. Internal moulds, SAMP35348a and SAMP35348b, $\times 13$. E. Partially exfoliated specimen, SAMP35349, $\times 10$. Specimen numbers refer to the palaeontological collection of the South Australian Museum.

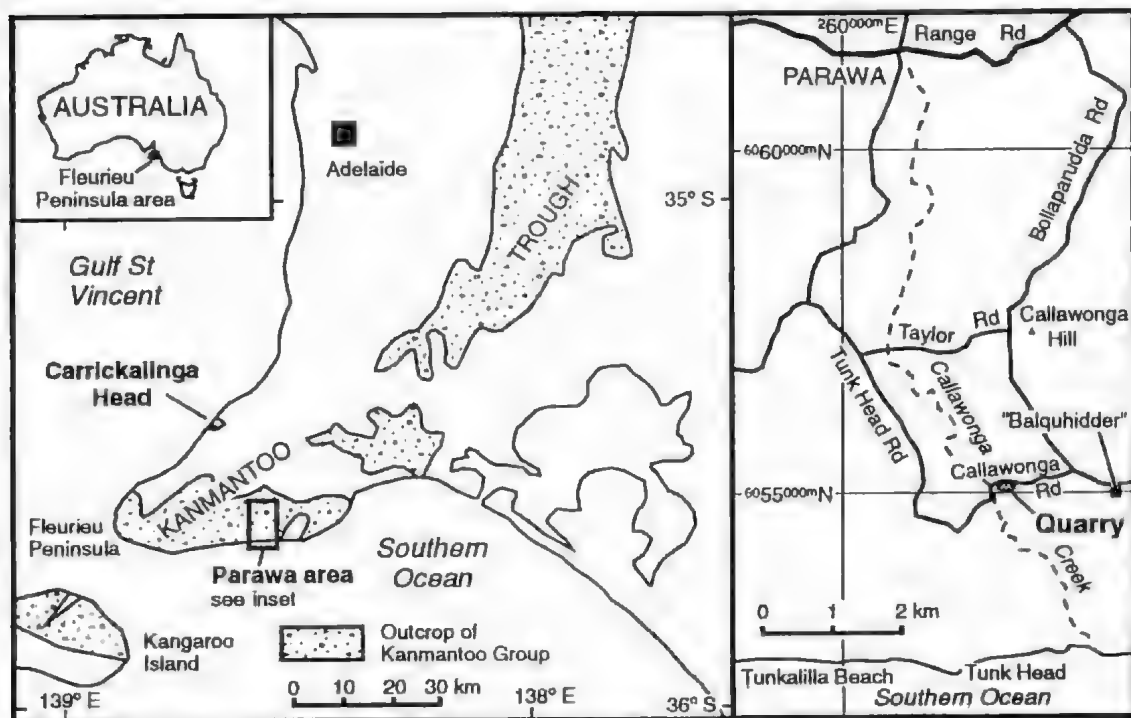
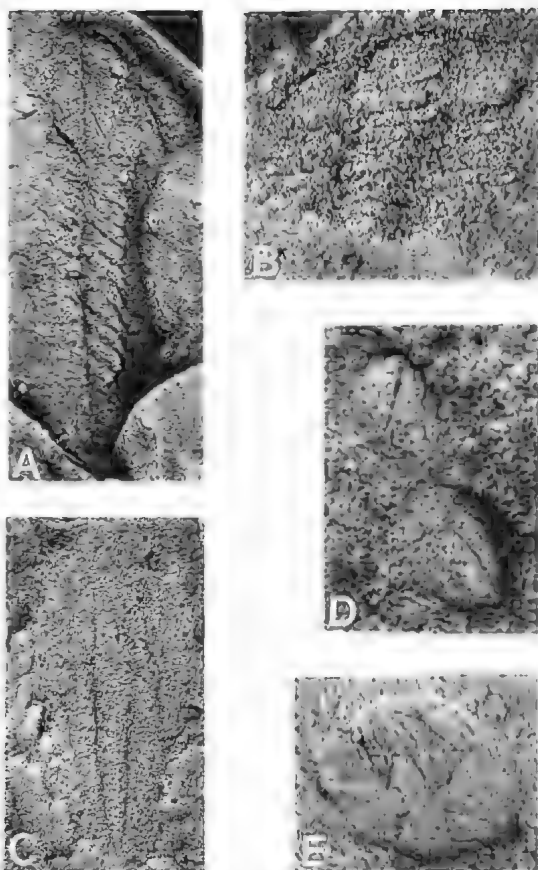


Fig. 3. Locality map.

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SIGHTINGS AND STRANDINGS OF THE PYGMY RIGHT WHALE *CAPEREA MARGINATA* NEAR PORT LINCOLN, SOUTH AUSTRALIA AND A REVIEW OF OTHER AUSTRALASIAN SIGHTINGS

BRIEF COMMUNICATION

Summary

The pygmy right whale *Caperea marginata* is a rarely sighted species known primarily from strandings. The latter occur frequently in South Australia, especially along the north coast of Kangaroo Island and near Port Lincoln^{1,2}. Migratory patterns are not known although it has been suggested that this species moves inshore in spring and summer^{3,4}. Sekiguchi et al.⁵ postulated that such a movement off South Africa may coincide with an increase in the abundance of copepods, one of the presumed main prey of *C. marginata*. Spring and summer are also the seasons when juveniles most frequently strand^{2,4}. There appears to be a broad mating, calving and weaning period between June and February². This paper describes two recent sightings of live animals off Lincoln National Park, about 10 km east-south-east of Port Lincoln, South Australia and summarises past sightings and strandings in that area. Other known sightings in the Australasian region are also reviewed.

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The pygmy right whale *Caperea marginata* is a rarely sighted species known primarily from strandings. The latter occur frequently in South Australia, especially along the north coast of Kangaroo Island and near Port Lincoln^{1,2}. Migratory patterns are not known although it has been suggested that this species moves inshore in spring and summer^{3,4}. Sekiguchi *et al.*⁵ postulated that such a movement off South Africa may coincide with an increase in the abundance of copepods, one of the presumed main prey of *C. marginata*. Spring and summer are also the seasons when juveniles most frequently strand^{2,4}. There appears to be a broad mating, calving and weaning period between June and February². This paper describes two recent sightings of live animals off Lincoln National Park, about 10 km east-south-east of Port Lincoln, South Australia and summarises past sightings and strandings in that area. Other known sightings in the Australasian region are also reviewed.

While sailing a 6-m yacht in Spalding Cove, off Lincoln National Park, two of the authors, J. D. and B. E., observed two pygmy right whales, an adult about 6 m long, accompanied by a calf about 2 m long. Paired blowholes (Fig. 1) confirmed that the adult was a baleen whale. Species identification was based on the curved jaw-line, medium-grey colour, a falcate dorsal fin placed well back on the body and the adult's broad back (Figs 1-3). The animals were seen between 1030 and 1130 h on 4 January and 1300 and 1400 h the following day. On both occasions they were deep in the cove at the fur south-western side, about 300 m from shore (Fig. 2). Water depth (as determined by a depth-

sounder) was about 5 m, water visibility 8 m, surface water temperature 20°C and the sea was calm. Spalding Cove is a shallow, sloping bay with a sandy bottom and extensive sea-grass beds.

Immediately prior to the sighting on 4 January, a large U-shaped swirl about 4-5 m diameter, followed by a curtain of bubbles, appeared 2 m from the boat. About 2-3 min later and 50 m away a large animal, the presumed adult female, surfaced and blew. This was followed by the blow of the calf near the adult. The calf swam slowly around the boat coming close to the bow and turning off, much as dolphins often do. It swam with an undulating motion, surfacing frequently for air (30-40 sec or as long as 2 min). At this stage the boat was under motor at a speed of 2-3 knots (3.5-5.5 kph) and the calf showed no sign of being disturbed by this. The calf alternated between swimming next to the boat and the nearby adult about 20-30 m away and sometimes swam above the adult, a common position for dependent calves of the southern right whale *Eubalaena australis* (C. Kemper

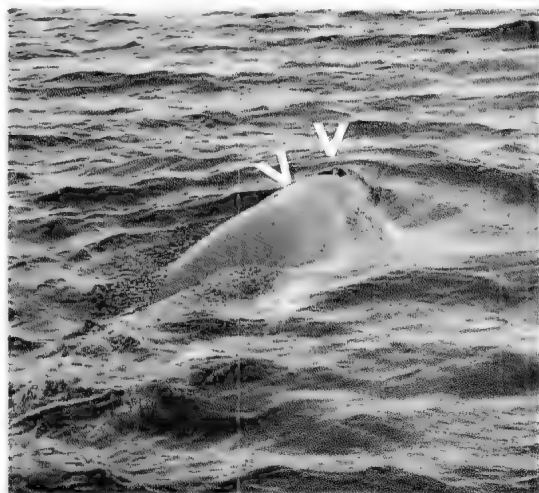


Fig. 1 - Adult *Caperea marginata* in Spalding Cove, South Australia, 4/5 January 1996. Arrows show the paired blowholes and indistinct white bar behind the head. Note also the broad back. Photo: J. Dutton.



Fig. 2 - Juvenile *Caperea marginata* in Spalding Cove, South Australia, 4/5 January 1996. The arrow marks the prominent, falcate dorsal fin set well back on the body. Photo: J. Dutton.

pers. obs.). The calf's grey back and sometimes its head showed as it surfaced and blew. Later examination of photos showed that the almost white ventral colour extended well up the side of the body and that a distinctive dark lateral patch interrupted this just behind the head (Fig. 3). A similar colour pattern has been observed on a South African juvenile *C. marginata* and a recently stranded neonate in New Zealand (van Helden pers. comm.).

The adult swam in large circles in the general vicinity of the boat, sometimes coming very close to it and at times turning on its side. It showed no sign of being disturbed by the presence of the boat. The adult surfaced to breathe much less often than the calf, about every 3 min or more. Later examination of photos showed that the adult was a medium-grey colour with a pale band or chevron just behind the head (Fig. 1). The belly was lighter than the back. Matsuoka⁶ also described and illustrated light chevrons on the backs of a large group of adult *C. marginata* observed at sea (Table 2).

The animals were in the same part of the cove during the afternoon of the next day when J. D. and B. E. returned to sail there. A net fisher operating in Spalding Cove during late January and much of February 1996 reported seeing a small whale there on several occasions. His description of the animal does not allow species identification but it may have been *C. marginata*, possibly one of the same animals observed in early January by J. D. and B. E.

The other recent South Australian sighting was made during the afternoon of 7 July 1996 by R. M., who observed, with the aid of binoculars, a small whale from the shore near Cape Donington lighthouse, Lincoln National Park (Fig. 4). It was about 50 m from shore and 60 m from the observer. The weather was sunny and the sea calm, with a light southerly to south-westerly breeze of 1–5 knots (2–9 kph). The animal was moving slowly towards deeper water, in a south-south-easterly direction. At times it swam just

below the surface with its mouth open. It was not possible to tell if the animal was feeding and no obvious signs of plankton swarms were visible to the observer. Several low, thin blows were seen. The animal's colour was dark grey on the back and light grey underneath. The features which suggested that this was a *C. marginata* were: 1) lighter patches between the mouth and the flippers, 2) whitish baleen plates which darkened towards the outer edges, and 3) a small, curved dorsal fin about $\frac{1}{3}$ of the way along the back. However, without observing the bowed jaw-line, the identification as *C. marginata* could not be considered confirmed since minke whales (*Balaenoptera acutorostrata*) share several of the above-mentioned features. Estimated body length of the animal R. M. observed was 3.5–4.0 m, suggesting that it was a post-weaning juvenile⁶.

Nine strandings of *C. marginata* have been recorded in the Port Lincoln area from before 1948 to 1993 (Table 1) and, as suggested in 1964 by Hale¹⁰, many more have probably occurred without being reported. All the reported strandings have been from Port Lincoln Proper and in, or at the entrance to, Spalding Cove (Fig. 4). Both are shallow, seagrass-covered, sandy/mudflat bays with large tidal movements. All strandings involved single animals, although in some cases there may have been a connection between certain events occurring within a short time of each other. For example, a 3.38 m juvenile was found recently dead on 2 February 1989 in Spalding Cove and on 1 March 1989 a decomposed adult (unknown sex) was found on Bickers Island at the entrance to the cove (stranding nos 6, 7, Fig. 4). On 6 April 1993 an adult female, with no evidence of lactation, washed up near on the south side of Port Lincoln Proper and six days later an extremely emaciated 3.15 m juvenile stranded alive in Spalding Cove (stranding nos 8, 9, Fig. 4). It is possible that both cases involved mother/calf pairs. Of the five adults that have stranded, three have been females and two of unknown sex.

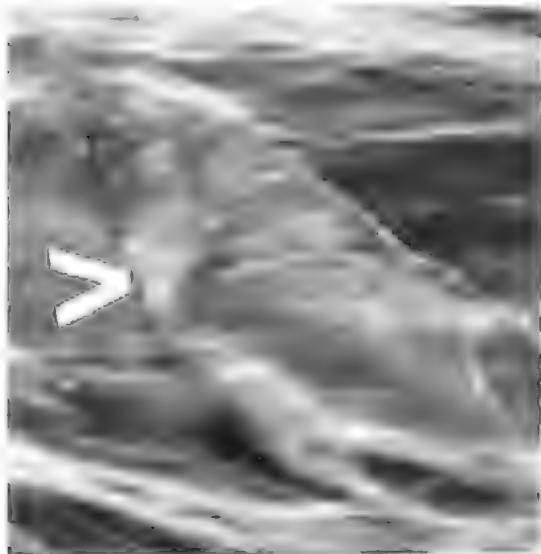


Fig. 3 Juvenile *Caperea marginata* in Spalding Cove, South Australia, 4/5 January 1996. The line drawing helps to distinguish the bowed jawline, which is slightly distorted by a wave. The arrow marks a lateral colour pattern of white just behind the head and a dark patch posterior to this. Photo: J. Dutton.



Fig. 4 - Map of Port Lincoln region showing positions of sightings (squares) and strandings (circles) of *Caperea marginata*. Numbers refer to strandings in Table 1 and sightings in Table 2.

These stranding results suggest that the region is frequently used by females and calves, although such information can be misleading if there is, as in this case, much human activity in the region and therefore possibility of discovering carcasses.

Reported sightings of *C. marginata*, summarised in Table 2, are not common in the Australasian region. To our knowledge, the Spalding Cove sighting of January 1996 is the first time a cow and calf have been sighted and photographed anywhere in the southern hemisphere. Not included in Table 2 are two unconfirmed records found in the Australian Nature Conservation Agency sightings database, one of three animals off Montague Island, NSW in June 1992 (record no. 876) and the other from near Bernier Island, WA in June 1993 (no. 1558). Since there was no supporting description of the animals to allow positive identification and *C. marginata* can be confused with the minke

whale, *B. acutorostrata*, the records have not been included here.

Many of the sightings listed in Table 2 and several from South Africa¹ were made inshore, suggesting that *C. marginata* inhabits coastal waters, at least for some part of its life or annual cycle. Unpublished stranding data show that dependent young and recently weaned juveniles (3.0–3.5 m) are more common along the central South Australian and western Victorian coast (Kemper unpub.). Four of the sightings listed in Table 2 involved dependent young or animals that, from their size, would appear to have been recently weaned. Three were from the Port Lincoln area and one was from Portland in western Victoria. Large, protected bays with shallow, sandy bottoms and extensive seagrass beds may be important calving and weaning areas for *C. marginata*. Some examples are Portland Bay, Nepean Bay and the Boston Bay region. Several strandings of *C. marginata* have been recorded in the Nepean Bay area¹.

The sighting made in Cockburn Sound in 1990 by B. and D. Parker (B. Parker pers. comm.) merits a special note because it records some notable behaviour as well as probable feeding by the 5-m animal they observed over a period of about one hour. The animal was swimming very fast, leaving a wake of water, and nodding its head noticeably. The whale came to investigate the 5-m boat, scraping itself the first time against the bottom of the hull. The second time it approached the boat very quickly, almost in a charge, lifted the boat out of the water and almost caused the occupants to be thrown out!

The authors wish to thank B. Parker and D. Coughran for supplying information on the sighting in Cockburn Sound and the Australian Nature Conservation Agency for searching their records for *Caperea* sightings. C. Kemper thanks all those who have provided information on pygmy right whale strandings and sightings records, especially South Australian National Parks and Wildlife officers and Department of Primary Industries South Australia (Fisheries) officers. J. Thurmer suggested and prepared the line drawing for Fig. 3.

TABLE 1. Records of *Caperea marginata* strandings in the Port Lincoln area. Stranding number (Fig. Ref.) cross-matched to Fig. 4, * estimated length based on skeletal measurements⁷. Museum no. M = specimen in South Australian Museum, S = no specimen in South Australian Museum.

Date	Location	Fig. Ref.	Sex	Length (m)	Museum No.	Comments
<1948	SW Port Lincoln Proper	1		2.73 ⁴	M5753	
26.12.1955	Tulka	2	M	3.05	M6110	seen alive before stranding
16.8.1960	Tulka	3	F	adult	S0009	decomposed, not collected
8.1984	Spalding Cove	4	-	6.03*	M14580	decomposed
18.5.1985	Port Lincoln Proper	5	J	6.20	M14465	washed up dead
2.2.1989	Spalding Cove	6	M	3.38	M15024	very fresh
1.3.1989	Bickers Island North	7	-	5.31*	M15374	very decomposed
6.4.1993	1 km SE Horse Rock	8	F	6.08	M17362	washed up dead
12.4.1993	3.2 km SE Stamford Hill	9	M	3.15	S0085	alive, very emaciated, returned to sea

TABLE 2. Sightings, including captures but not sightings immediately followed by strandings, of *Caperea marginata* in the Australasian region. Latitude and longitude given in degrees and minutes. Rel. is reliability of identification (1 = certain, 2 = probable, 3 = doubtful). A = adult, S = subadult, J = juvenile.

Date	Location	Lat. / Long.	Habitat	No.	Rel.	Size	Comments	Ref.
1.1874	north end Stewart I., NZ	46 50 S 168 00 E	-	-	1	S	captured amongst blackfish	8
9.1.1959	Bruny Island, Tas	43 17 S 147 18 E	bay, in 2-3m water	-	1	S	killed by fishers	9
7.1960	Port Lincoln, SA	-	protected bay	2	2	A, J	no description of animals	10
4.1980	~ 50 nm SE Cape Howe, NSW	38 20 S 150 20 E	open ocean, off shelf	5	1	-	observed from ship	11
4.1985	Soela Seamount, 120 nm SE Tas	43 50 S 150 22 E	open ocean, over sea mount	many	2/3	-	feeding, no description of animals	12
28.11.1986- 5.2.1987	Portland, Vic.	38 21 S 141 36 E	sandy, protected bay	1	1	S	shipping harbour possibly feeding	13
1.1989	Spalding Cove, SA	34 47 S 135 58 E	shallow, protected bay, seagrasses	2	2	A, J	Fig. 4 ref. no. 2	this study
19.10.1990	Cockburn Sound, WA	32 10 S 115 44 E	offshore	1	1	A	photos suggest feeding behaviour	B.Parker pers. comm
26.11.1992	420 nm S Cape Leeuwin WA	41 37 S 115 38 E	open sea	~80	1	A	three groups near each other	6
4.1.1996	Spalding Cove, SA	34 47 S 135 58 E	shallow, protected bay, seagrasses	2	1	A, J	stayed in area at least two days, Fig. ref. no. 3	this study
7.7.1996	Port Lincoln, SA	34 44 S 136 00 E	edge of Spencer Gulf	1	2	J	Fig. 4 ref. no. 4	this study

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THE AGE OF THE POORAKA FORMATION AND ITS IMPLICATIONS, WITH SOME PRELIMINARY RESULTS FROM LUMINESCENCE DATING

By R. P. BOURMAN*, P. MARTINAITIS†, J. R. PRESCOTT† & A. P. BELPERIO‡

Summary

Bourman, R. P., Martinaitis, P., Prescott, J. R., & Belperio, A. P. (1997) The age of the Pooraka Formation and its implications, with some preliminary results from luminescence dating. *Trans. R. Soc. S. Aust.* 121(3), 83-94, 28 November, 1997.

Stratigraphic relationships, supported by luminescence dating, suggest that the Pooraka Formation spans a far greater time interval than previously recognised on the basis of radiocarbon dating and stratigraphic analysis of discrete sedimentary sections. It extends back as far as the Last Interglacial. Re-evaluation of the radiocarbon ages that indicate an interstadial age (i.e. Oxygen Isotope Stage 3; 45 to 30 ka BP) for the sediments is required. Alternatively, a considerable time interval for deposition of the Pooraka Formation would necessitate that the unit be diachronous across the landscape. An age extending back to the Last Interglacial (Oxygen Isotope Substage 5c; c. 125 ka BP) would provide the appropriate palaeo-climates and palaeo-environments for fluvial sedimentation. The revised age has implications for landscape evolution, archaeological and palaeomagnetic prospecting as well as the antiquity of the *Diprotodon* in the Adelaide area.

Key Words: Pooraka Formation, Pleistocene stratigraphy, Last Interglacial, luminescence dating.

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Introduction

Large areas of the Adelaide Plains are underlain by the Pooraka Formation (Firman 1967, 1969; Callen *et al.*, 1995; Sheard & Bowman 1996), a reddish-brown coloured Pleistocene alluvial deposit with weakly developed calcareous pedogenic horizons that underlies river terraces and alluvial fans. This unit is also widespread beyond the Adelaide Plains, extending on to the Fleurieu Peninsula and into the mid-north of the state, where it flanks the Flinders and Gawler Ranges.

The red-coloured sediments that comprise the widespread Pooraka Formation have been ascribed different names by workers over time and in different areas. For example, they were originally referred to as the 'mammaliferous drift' by Tate (1879) because skeletal remains of the extinct, giant marsupial, *Diprotodon opatum*, were recovered from them in areas to the west of the city of Adelaide. Ward (1966) referred to the sediments as the Christies Bench Formation in the Noarlunga and Willunga sub-basins. Twidale (1968) named them the Klemzig Sand during his investigation of the terraces of the

River Torrens, and Bourman (1968, 1969¹) referred to them as the Adare Clay where they flank the Rivers Hindmarsh and Inman in the Victor Harbor area (Localities shown on Fig. 1). The red-coloured alluvium bears consistent stratigraphic relationships to a younger, grey-black alluvium [Waddeila Formation of Ward (1966), Walkerville Sand of Twidale (1968) and the Breckan Sand of Bourman (1968)], which forms lower terraces and floodplains set within valleys carved out of the red alluvium of the Pooraka Formation. Estuarine shells collected from within the Waddeila Formation in the lower reaches of the Onkaparinga River (Bourman 1972) returned a radiocarbon age of $4,580 \pm 160$ years B.P. (Bourman 1979). During this middle Holocene time the lower, near-coastal reaches of many streams were shallow, sheltered estuaries as revealed by the presence of fossiliferous marine deposits at depth up valley. This interpretation is supported by evidence from a locality several kilometres from the coast on the lower Onkaparinga River where an aboriginal kitchen midden containing estuarine shells dated at $5,820 \pm 90$ years B.P. (N.B. Tindale pers. comm. in Twidale *et al.* 1967) is sited on a well drained sand dune site at 20 m asl and adjacent to the former, more extensive estuary.

Ages ascribed to the Pooraka Formation and its equivalents

The Pooraka Formation has generally been ascribed to the Late Pleistocene, with most numerical ages, based on radiocarbon dating, falling within the range of 50,000-20,000 years (see review

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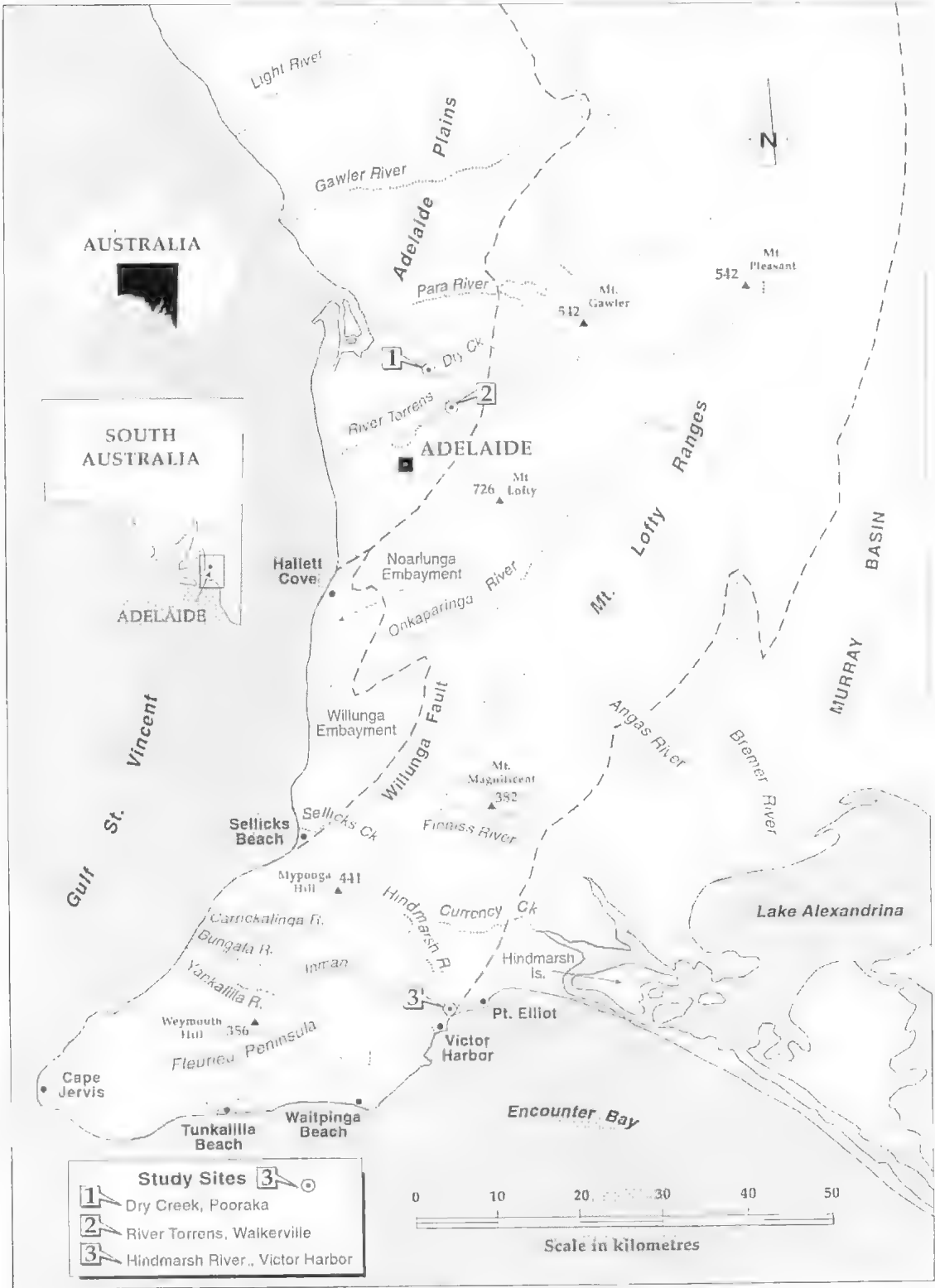


Fig. 1. Location map of sites.

in Callen *et al.* 1995). There has not been universal agreement on to which part of the Late Pleistocene the sediments should be allocated. Twidale (1968) assigned the Klemzig Sand to the Late Pleistocene and demonstrated that it must be older than 6,350 years BP. The distal end of the femur of a giant extinct marsupial, recovered from 3.6 m below the surface of a fillstrath terrace cut into the Adare Clay, in the Hindmarsh River, was dated at approximately 12,600 years BP (Gak - 2356) (Gill & Bourman 1972). Firman (1969) and Daily *et al.* (1976) also considered the Pooraka Formation to be of Late Pleistocene age, but younger than the *Anadara*-bearing Glanville Formation, which is now widely accepted to be of last interglacial age (c. 125,000 yr BP; Murray-Wallace *et al.* 1988; Murray-Wallace & Belperio 1991; Murray-Wallace 1995; Belperio *et al.* 1995). Confident separation between Late Pleistocene Pooraka Formation and earlier Pleistocene alluvial sediments is easily achieved in the coastal zone where they are separated by coastal facies. Inland, on the Adelaide Plains, the Pooraka Formation is readily distinguished from underlying Tertiary sands, the Keswick Clay and the Hindmarsh Clay. The Pooraka Formation is only weakly consolidated, carbonate impregnated and mottled in comparison with the underlying units (Sheard & Bowman 1996). Ward (1966) assigned the Christies Beach Formation to the Last Interglacial as he considered that the surface on it was graded to the last interglacial shoreline (his Epimonasterian high sea level) at approximately + 3 m above present sea level. However, at that time the Last Interglacial was thought to be considerably younger than the present 125,000 years BP.

From the Dry Creek alluvial fan, Williams (1969) described reddish-brown clay overlying older grey-green and red mottled clay, now known to be the Keswick Clay (Sheard & Bowman 1987a,b; M. Sheard pers. comm. 1997). Williams (1969) also noted a calcareous red-brown earth developed within the sediments containing nodules and cylindroids of pedogenic calcium carbonate. A radiocarbon age of $34,600 \pm 2700$ years BP on carbonised wood from sand 3 m below the land surface was obtained by Williams (1969). The carbonised wood was regarded as detrital in origin and thus was regarded as a reliable representation of the time of deposition. However, if the carbon were detrital, its age should predate the time of sedimentation, which would make the ^{14}C date somewhat older than the time of deposition. The date was taken to indicate a last glacial (Würm) age for the sediments. Further radiocarbon dates supporting a last glacial (Würm)

age were derived from a study of alluvial fans on the western side of the Flinders Ranges (Williams 1973). Carbonised detrital wood recovered from depths of 8-9 m and 15 m within the Pooraka Formation provided radiocarbon ages of 33,270 (+ 2130 - 1680 years) BP and > 37,000 years BP respectively.

Stratigraphic observations

Critical evidence concerning the age of the Pooraka Formation occurs at Victor Harbor. Here the relationships between the last interglacial shoreline and the Pooraka equivalent unit, the Adare Clay, suggest that the unit is much older than 50,000 years. Bourman (1968, 1969¹) established that red-coloured alluvium forms fill-top terraces along the Inman and Hindmarsh Rivers and grades to a shoreline at c. + 6 m above present sea level. The age of the shoreline is considered to be crucial with respect to the age of the terraces and the sediments which underlie them. Twelve species of shells have been identified from this shoreline deposit (Guppy 1943²) and it is significant that they contain the sub-fossil *Anadara trapezia*. Initially, Bourman (1968, 1969¹) followed Sprigg (1952) and assigned these shells to the Holocene. Subsequently, the shells were radiocarbon dated returning ages of $33,170 \pm 3,180$ - $2,270$ years BP (GaK-5561) and >30,320 years BP (GaK-6099).

Although the above dates are compatible with those of Williams (1969, 1973) they are questionable because the period around 30,000 years BP was a time of low sea level. Furthermore, it is now generally accepted that materials whose true ages are beyond the range of radiocarbon dating (> 40 ka for most laboratories) may yield younger apparent ages, due to the diagenic incorporation of low levels of radiocarbon from modern activity. Thus, materials with an infinite age by radiocarbon dating techniques may yield an apparent age of 37 ka due to the incorporation of 1% ^{14}C with a modern activity (Gupta & Polach 1985). Gill (1974) checked radiocarbon dates of this age against other dating techniques and concluded that radiocarbon dating may be reliable for young materials but older materials may return ages that are far too young. Similar conclusions were reported by Bowman & Harvey (1983) and Belperio *et al.* (1984).

Not only do *Anadara* shells occur at the + 6 m shoreline at the coast at Victor Harbor, but extremely large *Anadara* shells were recovered from a sewer trench c. 1.6 km upstream at a depth of 4 m below the surface, within the Pooraka Formation equivalent unit and at the same absolute elevation of 6 m as at the shoreline (Fig. 2). A drilling programme (CSIRO Soils Division) further revealed the intimate association of *Anadara* shells with the Pooraka Formation equivalent unit, demonstrating that here the *Anadara*, last interglacial deposits (Glanville

Guppy, D.J. (1943) Geological reconnaissance of part of the Hundreds of Encounter Bay and Goolwa. BSc (Hons) thesis, The University of Adelaide (unpub.).

Formation) and the Pooraka Formation are intercalated coastal and terrestrial equivalents. The *Anadara* shells have been dated both by Uranium-Thorium techniques (100,000–150,000 years BP) and by amino-acid racemisation studies (Kimber & Milnes 1984), which provided results consistent with

a last interglacial age.

Methods

The stratigraphic relationships between last interglacial molluscs and the Pooraka Formation

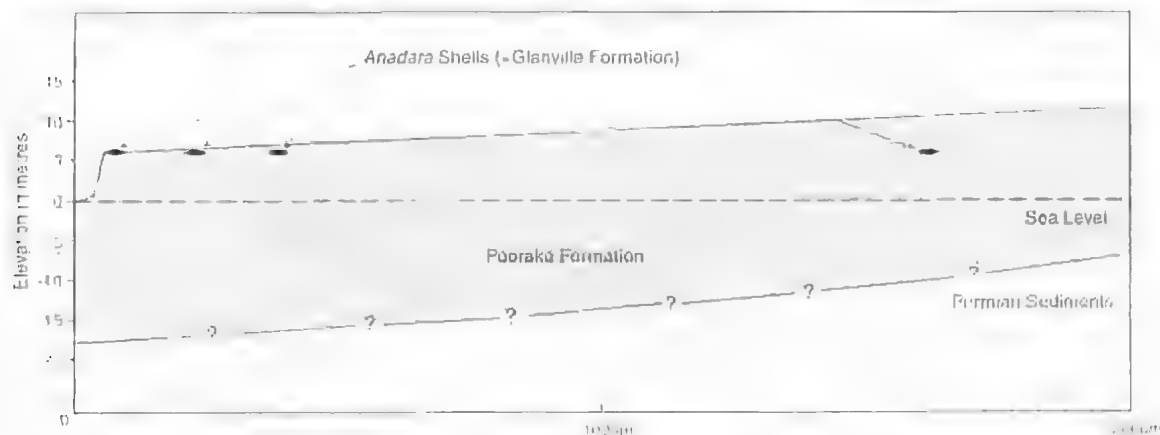


Fig. 2. Sketch section showing the interfingering relationships of the Glanville Formation and the Pooraka Formation in the lower Hindmarsh River at Victor Harbor.



Fig. 3. Photograph of 6 m high river bluff cut in Pooraka Formation sediments downstream of the Bridgeway Hotel on Dry Creek, Pooraka. Maximum section exposed c. 7 m. Red brown earth with associated calcium carbonate zones in upper part of section. At the base of the section the Pooraka Formation rests unconformably on an older Pleistocene unit that closely resembles the Taringa Formation of Ward (1966) but which Sheard & Bowman (1987a,b) consider is more likely to be the Keswick Clay.

equivalent, near the coast, at Victor Harbor provided strong indications that the Pooraka Formation might extend back to the time of the Last Interglacial. In order to test this hypothesis, and to determine whether the inland, terrestrial Pooraka Formation sediments were of an equivalent age, an attempt was made to obtain a numerical age for this formation using the technique of luminescence dating. A key site chosen for sample collection for luminescence dating was the Dry Creek (Pooraka) locality where Williams (1969) collected samples of detrital carbonised wood and carbonate for radiocarbon dating (Fig. 3). Unfortunately, the steep river bluff at this site has now been contoured and landscaped so that it was not possible to sample from exactly the same site as Williams (1969).

A second site on the River Torrens at Walkerville, where a thick Pooraka section had previously been exposed, was selected as a subsidiary luminescence dating sampling site. As both sites have suffered from human modification and landscaping of the former eroding river bluffs it was decided to collect samples for luminescence dating by drilling using an auger drill with an internal push cylinder. This method allowed sampling depths to be determined and the sample to be collected without exposure to light. Two holes were drilled at Pooraka and one at Walkerville. Samples were recovered at depths of 3.5 m, 4.5 m, 4.8 m and 7.5 m (for Pooraka) and 4.5 m, 5.5 m, 6.0 m, 7.5 m, 9.0 m and 9.3 m (for Walkerville). The drilling site at Pooraka was located 7.74 m above the base of Dry Creek and the second site was 11.68 m above the River Torrens level at Walkerville. The same holes were used for both sample collection and scintillometry for dose rate determination. A summary of data collected for the

Pooraka and Walkerville samples is shown in Table 1. Sample PK1S from a depth of 3.5 m is close to the level from which Williams (1969) collected detrital carbon for ^{14}C dating.

Luminescence dating methods

Three methods for luminescence dating (LD) of the sediments were used: selective bleach thermoluminescence (TL) of coarse-grain quartz (Prescott & Mojarrahi 1993) and green light stimulated-luminescence (GLSL) of both coarse grain quartz and of fine grain separates (Aitken 1994; Duller 1996). In the dating of sediments it is assumed that exposure to sunlight is the agency that resets the luminescence clock and that the sample has been exposed to sunlight for a sufficiently long time that the stored energy giving rise to the luminescence has been reduced to a low, near zero, level. This is a reasonable assumption in open sites exposed to strong sunlight, but this may not be true where there is the possibility that the material was deposited by, or under, water, as in the present sites, or in a generally colluvial environment. Both the TL selective bleach and GLSL methods seek to overcome this uncertainty by making use of an easily-bleached component which can be reset to zero by short exposure to sunlight. It is assumed that this component has, in fact, been reset. Details of the methodology are presented in the appendix.

Dating results

Pilot TL runs were carried out on coarse grain quartz from all samples except PK2S/4.8, WV1S/7.5 and WV1S/9.3. Such runs are designed to assess whether the sample is likely to be datable and, if so,

TABLE 1. Summary of collected data for Pooraka and Walkerville samples.

SAMPLE	PPM U	PPM Th	PPM U DNA	PPM Th DNA	PPM U Sct.	PPM Th Sct.	%K XRS	%K Sct	%H ₂ O
PK1S/3.5	1.5 ± 0.6	7.0 ± 2	1.48 ± 0.11	7.23 ± 0.5	1.74 ± 0.17	7.12 ± 0.29	1.08 ± 0.03	0.86 ± 0.02	6.8 ± 0.07
PK2S/4.5	1.1 ± 0.3	7.8 ± 1	1.26 ± 0.11	7.31 ± 0.4	1.75 ± 0.17	7.68 ± 0.29	0.89 ± 0.03	0.82 ± 0.02	3.7 ± 0.06
PK2S/4.8	1.1 ± 0.5	6.3 ± 1	1.10 ± 0.10	6.24 ± 0.4	1.34 ± 0.16	6.76 ± 0.28	0.89 ± 0.03	0.91 ± 0.03	4.4 ± 0.07
PK1S/7.5	1.2 ± 0.6	7.1 ± 2	1.22 ± 0.10	6.91 ± 0.4	1.74 ± 0.17	9.69 ± 0.32	1.20 ± 0.04	1.13 ± 0.03	12 ± 0.07
WV1S/4.5	1.8 ± 0.3	12 ± 1	1.81 ± 0.12	11.7 ± 0.5	1.89 ± 0.24	12.5 ± 0.44	1.85 ± 0.06	1.60 ± 0.04	8.8 ± 0.07
WV1S/5.5	1.6 ± 0.6	14 ± 2	1.93 ± 0.13	12.6 ± 0.6	2.33 ± 0.24	10.5 ± 0.42	1.81 ± 0.05	1.32 ± 0.04	7.5 ± 0.07
WV1S/6.0	1.9 ± 0.5	10 ± 1	1.86 ± 0.12	10.3 ± 0.6	2.47 ± 0.25	12.1 ± 0.48	1.59 ± 0.05	1.54 ± 0.04	8.3 ± 0.07
WV1S/7.5	1.7 ± 0.5	11 ± 2	1.66 ± 0.12	11.8 ± 0.6	2.66 ± 0.26	11.1 ± 0.47	1.71 ± 0.05	1.49 ± 0.04	15.7 ± 0.07
WV1S/9.0	1.8 ± 0.5	13 ± 1	1.77 ± 0.12	13.4 ± 0.6	2.95 ± 0.29	13.4 ± 0.50	2.19 ± 0.07	1.71 ± 0.04	18.0 ± 0.07
WV1S/9.3	1.2 ± 0.5	15 ± 2	1.88 ± 0.13	13.0 ± 0.6	2.95 ± 0.29	13.4 ± 0.50	1.98 ± 0.06	1.71 ± 0.04	16.4 ± 0.07

The first two columns are the results derived from Thick Source Alpha Counting. A DNA was done for uranium only: ppm Th (DNA) were obtained by combining the count-rate from thick source alpha counting and the uranium concentration from DNA. ppm U Sct, ppm Th Sct & %K Sct were derived from the on-site gamma ray scintillometry data.

to give a limited-accuracy estimate of the acquired luminescence and the sensitivity to radiation, and hence plan the schedule for a complete dating procedure. A pilot run consists of eight discs; half of these are bleached, after which two discs each of bleached and unbleached are given a radiation dose of 60 Gy. For all samples except PK1S/3.5, the shallowest of the Pooraka samples, the TL was clearly saturated and no further work on them was justified. Although PK1S/3.5 was approaching saturation, a full dating procedure was carried out for both TL and GLSL.

Such procedures give the Equivalent Dose, D_e , a measure in grays of the energy absorbed by the

sample from radiation in the environment since it was last reset to zero. The age of the sample is found by dividing the equivalent dose by the dose rate in gray per kiloyear ($Gy\ ka^{-1}$).

Equivalent doses, dose rates and ages

TL glow curves are shown in Figure 4a, shine-down curves in Figure 4b and corresponding dose curves are shown in Figures 5a, b respectively. None of the curves is sealed. It is evident that the dose curve of quartz (Fig. 5a) is close to saturation but that the growth curve for GLSL on fine grains (Fig. 5b) has a different shape and the curve continues to rise quasi-linearly for high doses. This is because the

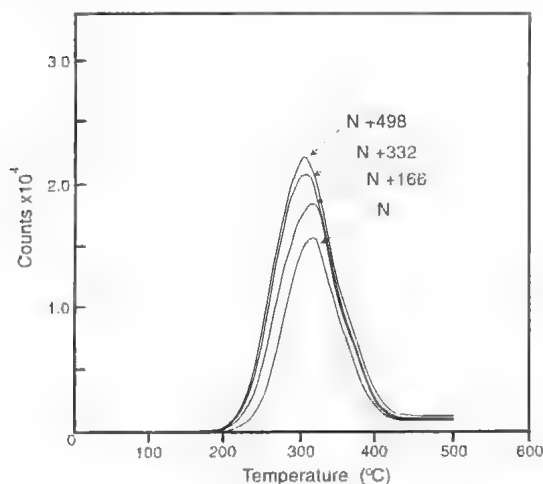


Fig. 4a. Glow curves for sample PK1S/3.5. The figures next to each curve indicate the dose in Gy.

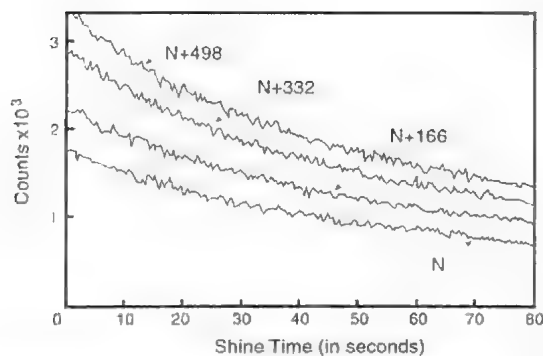


Fig. 4b. GLSL shine-down curves for sample PK1S/3.5. The figures next to each curve indicate the dose in Gy.

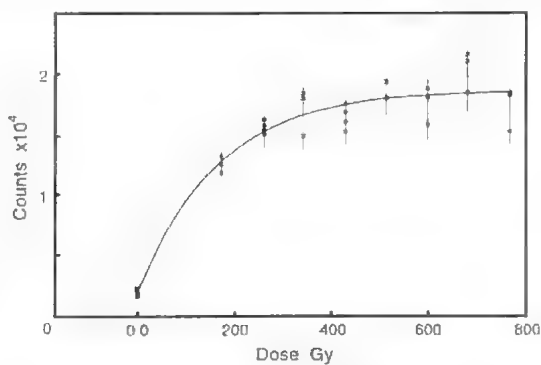


Fig. 5a. TL growth curve for sample PK1S/3.5 for the 10 interval at 305°C. For Figures 5a and b, the curves are fitted by the "Australian slide" method: the (natural + dose) points are shown by crosses; the (bleached + dose) points are shown by circles. There is an apparent sensitivity change for the TL bleached curve but the scaling factor does not differ significantly from unity.

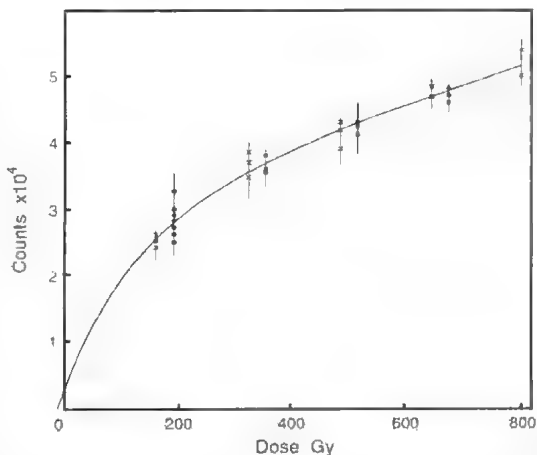


Fig. 5b. GLSL growth curve for sample PK1S/3.5 integrated over the first 100 s.

TABLE 2. Equivalent doses, dose rates and ages for sample PK1S/3.5

	COARSE GRAINED QUARTZ		FINE GRAINS	
	selective bleach TL	GLSL	GLSL	IRSL
D, Gy	249 \pm 58	208 \pm 44	294 \pm 15	> 250
dose rate	TSAC/DNA/XRS	SCINT	TSAC/DNA/XRS	SCINT
Gy ka ⁻¹	1.99 \pm 0.06	1.96 \pm 0.04	2.54 \pm 0.12	2.54 \pm 0.11
Weighted mean	1.97 \pm 0.03		2.54 \pm 0.08	
age ka	126 \pm 29	105 \pm 22	116 \pm 6	> 100

undifferentiated fine grains consist of a mixture of minerals in which quartz and feldspar are dominant. Thus although the quartz component saturates, the feldspar component does not. Equivalent dose values from all three methods appear in the first line of Table 2. It will be noted that the two methods of finding D_e give different values; this is characteristic of the methods.

Two distinct methods for finding the dose rates were used (described in the appendix), the aim being to get two independent values for each sample, to improve the statistical precision and as a check on the presence of radioactive disequilibrium (Prescott & Hutton 1995). The values obtained are included in Table 2. As with D_e, dose rates differ for coarse and fine grains. The values are in excellent mutual agreement and this shows that radioactive disequilibrium is absent.

The weighted mean dose rates are shown on line 3; line 4 shows the ages derived from the D_e using the age equation from the appendix. The weighted mean, 116 \pm 6 ka is dominated by the GLSL determination for fine grains.

Comment

Allowing for statistical fitting uncertainties, all three ages are in good agreement. Bearing in mind that they are based on different physical processes, all of which assume that the luminescence signal was set to zero in the past, it shows that this was very likely the case and that the age being determined is indeed the time of deposition. If it is not so, the apparent ages will be too large.

As already mentioned, the dose growth curve of Figure 5a, which is for quartz TL, shows that the luminescence is close to saturation. For this reason the estimate of relative uncertainty given by the analysis is large. This is also true for GLSL of quartz.

For GLSL of fine grains, on the other hand, the presence of the feldspar component allows D_e to be found with significantly better precision.

The best estimate of the time of deposition of sample PK1S/3.5 is the weighted mean age, 116 \pm 6 ka. In fact, this is dominated by the GLSL determination on fine grains. It is probably best to regard the quartz determinations by selective bleach and GLSL, as being supportive of the GLSL fine grain age. At the two standard deviation level the age exceeds 104 ka. Consistent with these numbers, the saturation of the luminescence of all the other samples shows that they are as old or older than this. Therefore, although only one sample has yielded a numerical age, there is enough evidence to establish a lower limit to the age of the formation and it is in support of the geomorphological and sedimentological evidence.

In addition to the three methods already described, infra-red stimulated luminescence (IRSL) of fine grains (Wintle 1994) was tried. IRSL uses only feldspars and is less susceptible to saturation, although it may be subject to long-term fading. Although the growth curve was similar in shape to the GLSL curve of Figure 5a, the statistical fitting procedures did not satisfy our criteria for an acceptable D_e, beyond showing that it was greater than 100 ka. Whether this is due to the sample or the methodology remains to be determined. However, the result is sufficiently encouraging to suggest that it may be possible to find ages from the lower levels at Pooraka and for Walkerville where quartz methods were unsuccessful.

Discussion

The location of the date derived from the upper section of the Pooraka Formation at a depth of 3.5 m below the surface is in complete accordance with the

numerical age obtained of 116 ± 6 ka, with the Last Interglacial ranging from approximately 132–118 ka (see Chen *et al.* 1991; Lambeck & Nakada 1992; Zhu *et al.* 1993; Stirling *et al.* 1995; Eisenhauer *et al.* 1996). The GLSL technique offers the possibility of obtaining a luminescence date for lower sections of the Pooraka Formation thereby facilitating the calculation of the rates of sedimentation during the Last Interglacial; it may be that sedimentation during warmer, wetter, last interglacial times was quite rapid and this technique offers the opportunity to test this idea.

These results suggest a far greater age range for the Pooraka Formation than has previously been recognised. In the past, the age of the Pooraka formation has been poorly constrained at about 20–30 ka BP, possibly because of the now-known limitations of radiocarbon dating. Furthermore, it should be noted that other methods such as TL, GLSL and IRSL were not available when many of the radiocarbon dates were carried out.

Many observations and cores indicate that, in places, the Pooraka Formation appears to be younger than the last interglacial Ghanville Formation, especially in subsiding areas. For example, Ludbrook (1976) in the Port Adelaide area described Pooraka Formation overlying calcareated Ghanville Formation, which in turn overlay Hindmarsh Clay. Belperio and Rice (1989) showed that of 62 cores from the Giffman area, 11 record the sequence of Holocene overlying calcareated Ghanville Formation without Pooraka Formation, and 5 record Holocene overlying Pooraka which overlies calcareated Ghanville Formation. The calcareated surfaces are interpreted as pedogenic features developed during subaerial exposure and would have formed prior to the deposition of the overlying sediments of the Pooraka Formation. In contrast, four of the cores record a sequence of Holocene/Pooraka/Ghanville Formation, without a well-developed calcareate on the Ghanville Formation, and one records intermixing of Pooraka and Ghanville. These last cores may indicate coeval Ghanville and Pooraka sedimentation or little time break between the two.

Extensive work by Sheard & Bowman (1996), which involved drilling cores to depths of 10 m at 170 sites over the Adelaide Plains, intersected Pooraka Formation in 80 cores. This work corroborates the findings of Belperio & Rice (1989) for the coastal zone. More landward sites indicated the sequences to be: Holocene/Pooraka/Keswick Clay/Hindmarsh Clay and Holocene/Pooraka/

Keswick Clay/Tertiary sands or Adelaidean rocks. At the 80 sites intersecting Pooraka Formation sediments, Sheard & Bowman (1996) rarely experienced difficulties in identifying Pooraka Formation from the overlying and underlying materials (M. Sheard pers. comm. 1997).

Recent drilling work by Woodhead *et al.* (1995) for Boulderstone Hornibrook in the Holdfast Shores (Glenelg/Patawalonga Redevelopment area) has demonstrated that deposits of Pooraka Formation 2–4 m thick occur well offshore from the present coast line. These deposits are detached from more landward deposits either by zones of non-deposition or by early Holocene erosion. Variable stratigraphic relationships are apparent in this locality. For example, the following relationships of Holocene/Pooraka/Ghanville/Hindmarsh Clay, Holocene/Ghanville/Hindmarsh Clay or Holocene/Eulham Sand/Pooraka/Ghanville/Hindmarsh Clay occur within an 800 m east-west section.

It may be that the Pooraka Formation was deposited over a considerable period of time. This view is also supported by the occurrence of palaeosols within Pooraka Formation equivalent sediments as exposed in Sellicks Creek and Cobblers Creek. The luminescence data indicate an age approximately coincident with the Last Interglacial (125 ka BP), but the results at any one place may be influenced by the terrestrial/marine interactions. For example, if there is not an active supply of alluvium to the coastline then marine deposition, exposure and calcareate formation will dominate, in places subsequently mantled by Pooraka or Holocene sediments. It may be that only where there is a sufficient supply of terrestrial sediments to the coastline, such as where streams debouch at the coastline in relatively constrained valleys (e.g. Hindmarsh River at Victor Harbor), that the interfingering characteristics of the two sediments can be demonstrated. It is also possible that Pooraka Formation sediments do not reach the position of the Ghanville Formation until after it has been calcareated. It should be noted that much of the Pooraka Formation has been deposited inland, well beyond the elevation and planimetric position of the last interglacial shoreline, so that in these situations there is no clear stratigraphic relationship between the two units.

Implications of the Pooraka Formation extending back to the Last Interglacial

If the interpretation that the Pooraka Formation extends back to the Last Interglacial is correct, a re-evaluation of the radiocarbon ages that indicate glacial or interstadial ages for the sediments is required. Alternatively, the conflicting results may suggest that there could be sediments, which

¹ Woodhead, E. R. L. & Rose Pty Ltd (1995) Appendix 3. Geotechnical investigations at Holdfast Shores in Boulderstone, Hornibrook, Glenelg Coastal Works and Ferry Wharf. Report to Urban Projects Authority of SA. (unpubl.)

although appearing similar, occupy a range of ages.

At a number of locations, the Pooraka Formation has been noted to overlie the Glanville Formation with a variably developed calcrete, suggesting surface exposure prior to burial by younger Pooraka Formation sediments. Elsewhere, such as in the lower Hindmarsh River, where there is an interplay of coeval coastal and terrestrial events, the stratigraphic relationships between the Pooraka and Glanville Formations may simply represent a facies change and not a geological succession. A considerable time interval may be required for the deposition of the Pooraka Formation so that its age could be diachronic, with deposition occurring during the rise in sea level up to and beyond that of the last interglacial level.

A last interglacial age provides appropriate palaeoclimatic and palaeo-sea level conditions for explaining the distribution of the Pooraka Formation. Close to the coast the unit relates to a shoreline higher than the modern one, while inland the wetter, interglacial conditions would have favoured aggradation of sediments as opposed to drier, glacial conditions that would have facilitated dissection. This timing would also ensure sufficient time both for the build up of extensive deposits of the Pooraka Formation over large areas including much of the city of Adelaide, and time during glaciials and interstadials for erosion of the Pooraka Formation to develop the extensive terrace system of the River Torrens (Twidale 1968).

A last interglacial age for the Pooraka Formation is of significance for archaeological prospecting. At the present time there is debate concerning the antiquity of humans on the Australian continent. Substantial changes in vegetation related to Aboriginal burning practices have been interpreted as resulting from human impact and used to infer the arrival of people in Australia as long ago as 140,000 years (Kershaw *et al.* 1993; Kershaw 1993, 1994, 1995). These claims have been questioned by various workers (e.g. Anderson 1994; Hope 1994; White 1994; Webb 1995). If the Pooraka Formation is of last interglacial age it may present a prospecting opportunity to test if Aboriginal colonisation had occurred in southern Australia prior to 125,000 years BP during the time of the penultimate glacial low sea level.

A minor palaeomagnetic event, the so-called "Blake Event", has been identified in the northern hemisphere in loess sequences (Hoghoj *et al.* 1995) at approximately 120 ka. Given that the general age of the Pooraka Formation is almost certainly of last interglacial age, and that the upper part of the formation has been ascribed a GISSL age of 116 ± 6 ka, there may be opportunities to identify the Blake event in the southern hemisphere.

A last interglacial age for the Pooraka Formation

has implications for the antiquity of the *Diprotodon* in the Adelaide area. Diprotodontid remains have been recorded well back into Tertiary strata in the North Flinders-Callabonna Plains areas (Callen & Tedford 1976; Pledge & Tedford 1990; M. J. Sheard pers. comm. 1997.) but not, so far, in the Adelaide area. Discoveries of *Diprotodon* remains have been made in the Pooraka Formation (Twidale 1968; N. Pledge pers. comm. 1996) of the Adelaide area and while the *Diprotodon* may have predated and survived well beyond the age of this sedimentary unit, it was almost certainly roaming the swampy, aggrading Adelaide Plains some 125,000 years ago.

The age has further implications for landscape evolution as there appears to have been a major erosional hiatus of some 120,000 years between the deposition of the Pooraka Formation and the grey-black Waldeila Formation, which is of mid-Holocene age. There were no sea levels higher than the present in the intervening period so that erosion would have dominated this interval of time. Alternatively, any sediments deposited during this time could have been removed in late stages of erosion.

Conclusions

The main conclusion from this work is that the Pooraka Formation must span a far greater time period than previously recognised, probably extending as far back as Last Interglacial time i.e. 125 ka. It appears that the tectonic and environmental setting, which influences the supply of terrestrial sediments to the coastline, is of extreme importance in interpreting the stratigraphic relationships between the Pooraka Formation and the Glanville Formation. Much more luminescence dating work is required to constrain or document the age ranges in different settings i.e. in the Victor Harbor setting where the two are intermixed, in contrast to the Port Adelaide setting where a major calcrete palaeosol separates them. We may expect luminescence dating techniques to document ages from last interglacial times, possibly through to 30–50 ka, if the quartz grains are sufficiently reset. This offers the possibility of providing a more reliable dating tool than radiocarbon techniques, which still struggle to provide meaningful dates past 40 ka.

The red-brown alluvial sediments, referred to as Pooraka Formation and equivalents, are considered to extend back to at least the Last Interglacial of c. 125,000 years BP. This is demonstrated by the stratigraphical relationships of the red-brown sediments to both younger and older sediments, the interdigitating of demonstrated last interglacial marine deposits with them, their grading to a +6 m higher shoreline containing last interglacial marine

fossils at Victor Harbor, and the fact that a higher sea level, together with associated warmer and wetter conditions would favour aggradation, whereas colder, drier glacial conditions associated with lower sea levels would have favoured erosion. All of these factors support a last interglacial age.

The luminescence data have demonstrated viability as an independent means of testing the hypothesis that the Pooraka Formation is of last interglacial age. Fluvial sediments present special problems for luminescence dating because the sediments being water-deposited, may not have been exposed to sunlight for sufficiently long to zero the quartz grains, resulting in inherited saturation levels within the grains. A further complication may be that in the Adelaide area, the sediments may have not been transported sufficient distances for the quartz grains to have been zeroed. Given these constraints, it is extremely gratifying that it was possible to achieve a reliable luminescence age for the Pooraka Formation at Dry Creek, offering the possibility of further advance in this area.

An aim of this project was to establish the effectiveness of luminescence as a dating technique

for Quaternary fluvial sediments in order to resolve differing interpretations of their ages and to facilitate correlation of river terraces in different valley systems. Clearly, there is a need for many further dates to be obtained from river terrace and alluvial fan deposits over wider-ranging areas to verify the conclusions of the present work. However, the implications of an age for the Pooraka Formation extending back to the Last Interglacial are so significant that our preliminary results are presented here and provide the basis for further study.

Acknowledgements

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Appendix: Methodology for luminescence dating

Quartz grains (90-120 µm) were extracted as described in Huntley *et al.* (1993). Briefly, pure quartz of the right size was obtained by pretreating with HCl, followed by NaOH to break up clay aggregates, sieving, etching with 40% HF for 40 minutes at 20° C, magnetic separation and floating on heavy liquid at specific gravity 2.67. For measurement, 5.0 ± 0.1 mg was deposited on stainless steel discs. Individual discs were post glow dose normalised with 6 Gy.

Fine grains (undifferentiated as to mineralogy) were separated after the HCl and NaOH extractions by settling from aqueous 0.01N NaOH, the 4-11 µm fraction being retained. This was then deposited on aluminium discs from acetone suspension, about 1 mg per disc. Individual discs were 0.5 s short-shine normalised.

As stated in the main text, both dating protocols make use of the easily bleached component of luminescence. In the case of TL this component is selected for by both temperature and wavelength of emission (Prescott & Mojarrabi 1993). For GLSL it is assumed that the stimulated emission comes from the easily-bleached component; optical filters also select for this component (Huntley *et al.* 1991). The output is expressed as intensity as a function of temperature for TL and as a function of shine-down time for GLSL.

For both protocols the emitted intensity is measured for "natural" samples and for samples which have received additional doses from a calibrated laboratory beta-source (N+B). About half of these samples are exposed to laboratory bleaching by sunlight filtered by a 475 nm long-wavelength-pass filter (Chris James 101); this bleach removes the rapidly bleaching component completely. Some bleached discs are also irradiated (YB+B) to provide the shape of the "missing" part of the dose curve at doses less than the natural dose. The data analysis follows the so-called "Australian slide" procedure (Readhead 1988; Prescott *et al.* 1993) and the data output is the equivalent dose D_e expressed in grays. Such curves are known as "dose curves".

Two methods of dose rate determination were used: *In situ* scintillometry (see e.g., Hutton & Prescott 1992) uses a sodium iodide scintillation crystal, 75 mm x 75 mm diameter in the auger hole from which the sample for dating

is taken. The instrument is calibrated for K, U and Th and, independently, for total gamma ray dose. Scintillometry gives a completely self-contained measure of dose rate.

Thick source alpha particle counting (TSAC) (Jensen & Prescott 1983; Huntley *et al.* 1986) gives a value for the contribution to the dose rate from U and Th together, and an estimate of the U and Th concentrations separately. In fact, the dose rate to the sample is effectively determined by the total alpha count and is almost independent of the relative amounts of U and Th. However, the measured ratio allows a (small) adjustment to be made to the dose rate. Combined with measurement of K, TSAC gives an independent measure of dose rate. X-ray fluorescence spectrometry is used to find K.

In addition, U was found using delayed neutron activation (DNA). If this differs significantly from the other methods of assay for uranium, it gives an indication of radioactive disequilibrium, which was not the case here. It is most conveniently combined with the data from alpha counting to give the U concentration and hence a more accurate value for Th. These are the values shown in Table 1.

Table 1 includes the elemental analyses for all samples. The dose rates calculated for PK1S/3.5 using the conversion factors of Nambi & Aitken (1986) are shown in Table 2. The water content measured at the time of sampling was used in the dose rate calculations. Cosmic ray dose rates have been added in (Prescott & Hutton 1994). All data are included in Table 1, even though a numerical age was found for only one sample.

The age calculation is conveniently expressed in terms of the so-called "Age Equation":

$$\text{Age (ka)} = \frac{\text{TL of sample}}{\text{TL per unit dose (TL/Gy)} \times \text{dose rate (Gy ka}^{-1}\text{)}}$$

In this equation, "TL of sample" (which measures the accumulated energy) and "TL per unit dose" (which defines the sensitivity of the material to radiation) are measured in the laboratory on quartz or fine grains extracted from the sample; and "dose rate" is determined from measurements in the field and/or laboratory.

NEW SPECIES OF *POTOROLEPIS* SPASSKII (CESTODA : HYMENOLEPIDIDAE) PARASITIC IN DASYURID MARSUPIALS FROM NEW GUINEA

by C. VAUCHER^{*} & I. BEVERIDGE[†]

Summary

VAUCHER, C. & BEVERIDGE, I. (1997) New species of *Potorolepis* Spasskii (Cestoda: Hymenolepididae) parasitic in dasyurid marsupials from New Guinea. *Trans. R. Soc. S. Aust.* 121(3), 95-102, 28 November, 1997.

Potorolepis aruensis sp. nov. is described from the small intestine of *Myoictis melas* from the Aru Islands of Irian Jaya. It is most closely related to *P. bradleyi* from which it differs in mean hook number (17 in *P. aruensis*, 13 in *P. bradleyi*), size of cirrus sac (0.27-0.42 mm in *P. aruensis*, 0.14-0.25 mm in *P. bradleyi*) and arrangement of testes. Cestodes tentatively allocated to *P. aruensis* were also found in *Antechinus naso*. *Potorolepis woolleyae* sp. nov., from the small intestine of *Murexia longicaudata* from Morobe Province, Papua-New Guinea, differs from all congeners in having longer rostellar hooks (163-182 µm). The generic diagnosis is re-assessed as well as the relationships between morphological sub-groups within the genus and the marsupial families they parasitise. A key to the species of hymenolepidid cestodes occurring in Australasian marsupials is given.

KEY WORDS: *Potorolepis*, cestodes, Hymenolepididae, marsupials, Dasyuridae, New Guinea.

Introduction

Cestodes of the family Hymenolepididae Ariola, 1899 are common parasites of birds, rodents and insectivores in most regions of the world (Czaplinski & Vaucher 1994). Vaucher *et al.* (1984) reviewed the species known from Australian marsupials, redescribing the three known species and erecting five new ones. All were allocated to the genus *Hymenolepis* Weinland, 1858 though it was noted that they formed a morphologically distinctive subgroup within this large genus. Subsequently, Jones & Anderson (1990) described a new species from a peramelid marsupial in New Guinea and transferred the other species occurring in marsupials to the closely-related genus *Vampirolepis* Spasskii, 1954. Spasskii (1994) erected a new genus, *Potorolepis*, to contain most of the species found in marsupials, although one, *H. cercarteti*, was transferred to the genus *Rodentolepis* Spasskii, 1954, with the implication that it was originally a parasite of rodents. Spasskii (1994) was apparently unaware of the species erected by Jones & Anderson (1990) and did not include it in his new genus. The hymenolepidid fauna of Australasian marsupials is relatively poorly known (Spratt *et al.* 1991) and its taxonomic and phylogenetic affinities are uncertain.

In this paper, we describe new species of *Potorolepis* parasitic in dasyurid marsupials in New Guinea and re-evaluate the definition of the genus proposed by Spasskii (1994) as well as the host-

parasite relationships between sub-groups within *Potorolepis* and families of marsupial hosts, a relationship first suggested by Vaucher *et al.* (1984).

Materials and Methods

Cestodes from *Myoictis melas* were collected when the host animals were autopsied after a short period in captivity at La Trobe University, Melbourne. The cestodes were relaxed in water and fixed in AFA (Pritchard & Kruse 1982). Cestodes from other hosts were collected in New Guinea. Following the death of the host, the entire gastrointestinal tract was fixed in 10% formalin and the cestodes were subsequently removed and stored in 70% ethanol.

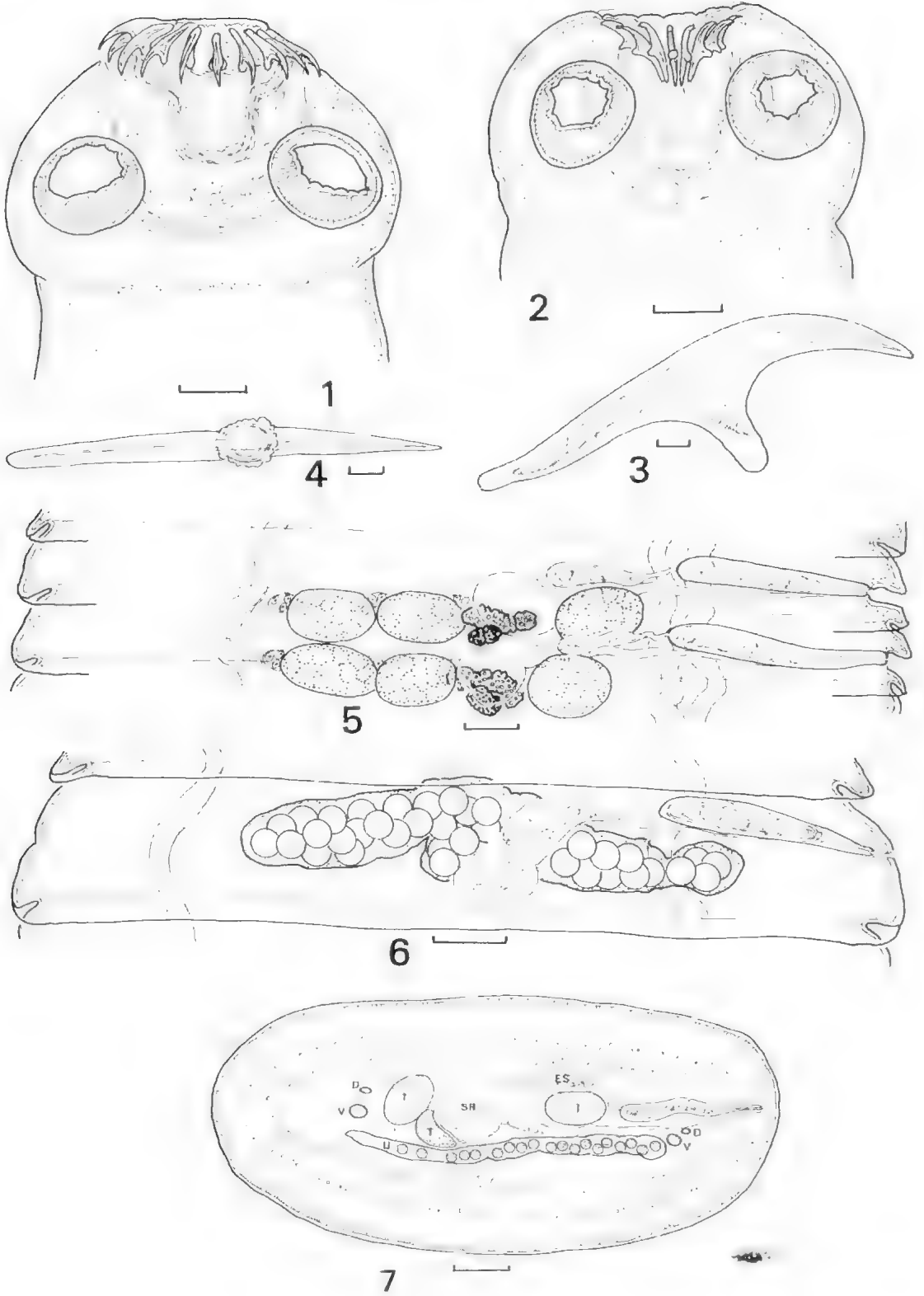
Cestodes were stained in Celestine blue, dehydrated in ethanol, cleared in methyl salicylate and mounted in Canada balsam. In contracted specimens, the tegument and dorsal and ventral musculature were removed with a fine scalpel after clearing (Jones 1990) to improve the visibility of the internal organs. Some scoleces of each species were mounted in Berlese's fluid. Serial sections were cut at a thickness of 9 µm in both longitudinal and transverse planes and stained with haematoxylin and eosin.

Measurements are given in millimetres as the range, followed by the mean and the number of measurements made in parentheses. Drawings were made using a drawing tube.

All specimens studied have been deposited in the South Australian Museum, Adelaide (SAMA) or the Muséum d'Histoire Naturelle, Geneva (MHNG).

Host nomenclature follows Flannery (1995) and

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Spratt *et al.* (1991). Tabulated morphological data were derived from Beveridge & Barker (1975), Vaucher *et al.* (1984) and Jones & Anderson (1990). Host distribution data were derived from Spratt *et al.* (1991).

Potorolepis aruensis sp. nov.

(FIGS 1-7)

Types: Holotype from small intestine of *Myoictis melas wallacei* Gray, 1858, Koboar Is., Aru group (6° 12'S 134° 32'E), Irian Jaya, 16.vi.1993, coll. P. A. Woolley, SAMA AHC 27877; paratypes, 23 whole mounts, 8 scoleces mounted in Berlese's fluid, serial sections, SAMA AHC 27878-27905; 2 whole mounts MHNG 23407 INVE; additional specimens: numerous specimens 2. xii. 1992, SAMA AHC 30586-30587; 3 specimens, 3. xii. 1992, SAMA AHC 30588; numerous specimens, 16.vi.1993, SAMA AHC 30589.

Material examined: From *Myoictis melas* (Müller, 1840): types. From *Antechinus nasutus* (Jentink, 1911): 5 specimens, Mt Kajindi (7° 21'S, 146° 41'E), Papua-New Guinea, SAMA AHC 27864-27876, 30584-30585.

Description

Based on types. Small cestodes up to 60 in length. Scolex globose, 0.52-0.65 (0.58, $n = 10$) in diameter. Suckers sub-circular in superficial views, unarmed; cup-shaped in section, with openings directed anteriorly, 0.13-0.16 (0.15, $n = 10$) \times 0.15-0.18 (0.17, $n = 10$). Rostellum muscular, 0.18-0.26 (0.21) \times 0.17-0.23 (0.21, $n = 10$); rostellar sac 0.26-0.38 (0.30, $n = 10$) \times 0.26-0.31 (0.28, $n = 10$). Hooks 16-18 (17, $n = 10$), arranged in single ring with broad, curved blades; slender handles prominent; blunt guards often with irregular surface; core of hook blade hollow. Hooks 0.128-0.147 (0.138, $n = 10$) long. Neck variable, 0.74-2.05 (1.26, $n = 10$) long. Segments craspedote; mature segments much wider than long, 0.06-0.17 (0.10, $n = 10$) long \times 0.93-1.63 (1.31, $n = 10$) wide; near gravid segments longer, but slightly narrower, 0.13-0.29 (0.22, $n = 10$) long, 0.81-1.22 (1.04, $n = 10$) wide. Genital pores unilateral. Three testes arranged linearly, one poral, two aporal; very little variation in testis distribution: single segment with 4 testes; single segment with 2 testes; single segment with 2 poral, 1 aporal testes. Testes oval, of similar size, 0.10-0.17 (0.15, $n = 10$)

long \times 0.08-0.11 (0.09, $n = 10$) wide. Vasa efferentia of antiporal testes run along dorsal margin of medulla to elongate, pyriform external seminal vesicle 0.06-0.16 (0.10, $n = 10$) long \times 0.04-0.09 (0.07, $n = 10$) wide, anterior and dorsal to poral testes; distal region of external seminal vesicle slender, sinuous, enters elongate cirrus sac 0.27-0.42 (0.35, $n = 10$) long \times 0.04-0.05 (0.05, $n = 10$) wide. Cirrus sac contains elongate internal seminal vesicle occupying two-thirds of volume of cirrus sac; no armature seen on cirrus. Genital ducts cross osmoregulatory canals dorsally.

Ovary median, with 3-4 indistinct lobules, 0.06-0.10 (0.08, $n = 10$) long, 0.10-0.19 (0.14, $n = 10$) wide; vitellarium reniform, posterior to ovary 0.03-0.06 (0.04, $n = 10$) long \times 0.05-0.07 (0.06, $n = 10$) wide. Vagina posterior and ventral to cirrus sac, dilating to form saciform seminal receptacle dorsal to ovary; seminal receptacle 0.14-0.24 (0.18, $n = 10$) long \times 0.08-0.16 (0.11, $n = 10$) wide. Uterus originales as transverse sac on ventral aspect of medulla, extends to osmoregulatory canals, developing small number of diverticula, never becoming reticulate. No segments found with fully-developed eggs in uteri. Ventral osmoregulatory canal 0.03-0.05 (0.04, $n = 10$) in diameter, dorsal canal narrower, 0.01-0.03 (0.02, $n = 10$) in diameter. Longitudinal strobilar musculature arranged in two concentric rings: outer ring composed of numerous small bundles with only 1-3 fibres per bundle; bundles of inner ring larger with 5-10 fibres per bundle.

Potorolepis woolleyae sp. nov.

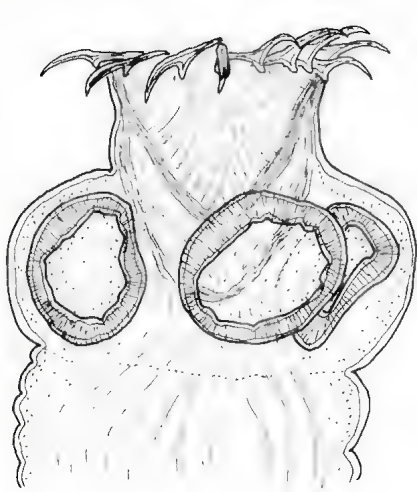
(FIGS 8-14)

Types: Holotype from small intestine of *Murexia longicaudata* (Shlegel, 1866), Mount Missim (7° 13'S, 146° 49'E), Morobe Province, Papua-New Guinea, coll. G. Gossek, 24.x.1984, SAMA AHC 27906; paratypes, 9 fragmented specimens, 1 scolex mounted in Berlese's fluid, serial sections, SAMA AHC 27907-27919, 30590; 2 specimens MHNG 23408 INVE.

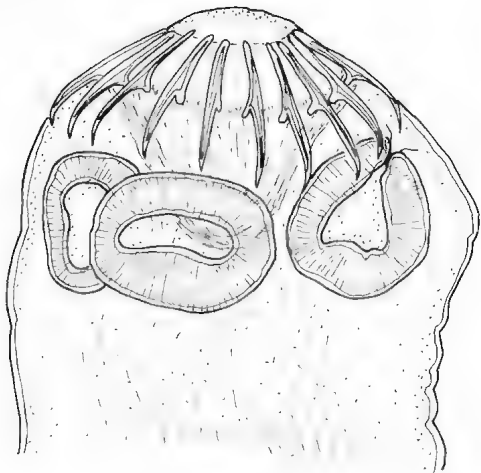
Description

Small cestodes, largest fragment 35 long. Scolex globose, 0.44-0.55 (0.50, $n = 9$) in diameter. Suckers sub-circular, unarmed, 0.13-0.21 (0.17, $n = 10$) long \times 0.10-0.19 (0.15, $n = 10$) wide. Rostellum muscular, 0.13-0.20 (0.17, $n = 9$) long \times 0.19-0.28 (0.23, $n = 9$)

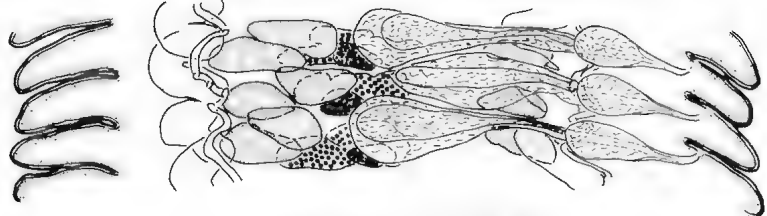
Figs 1-7. *Potorolepis aruensis* sp. nov. Types. 1. Scolex with rostellum everted. 2. Scolex with rostellum withdrawn. 3. Rostellar hook in profile. 4. Rostellar hook, view from posterior surface showing enlarged hook guard. 5. Mature segments. 6. Near-gravid segment. 7. Transverse histological section of mature segment: dorsal aspect towards top of page. Scale bars = 0.1 mm 1, 2, 5-7; 0.01 mm 3, 4. Legend: D, dorsal osmoregulatory canal; E.S., external seminal vesicle; SR, seminal receptacle; T, testis; U, uterus; V, ventral osmoregulatory canal.



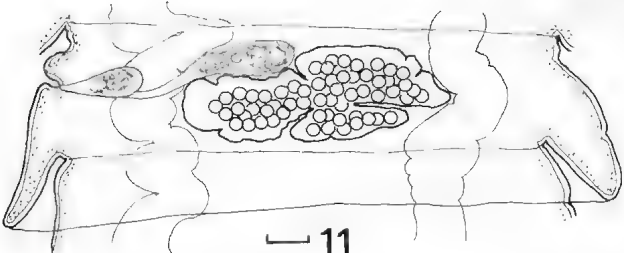
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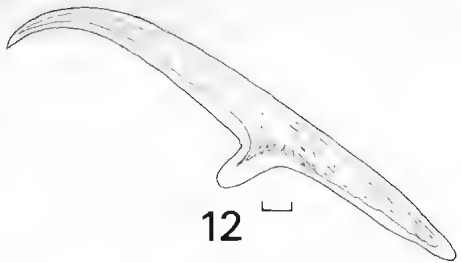
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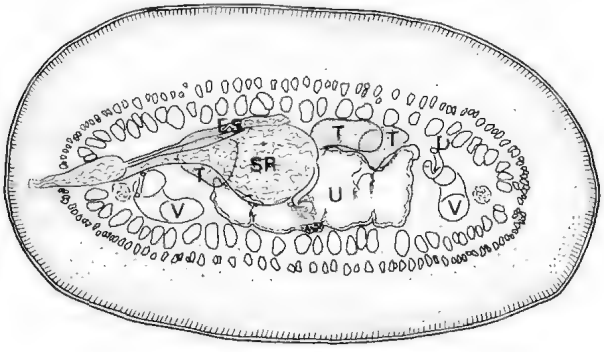
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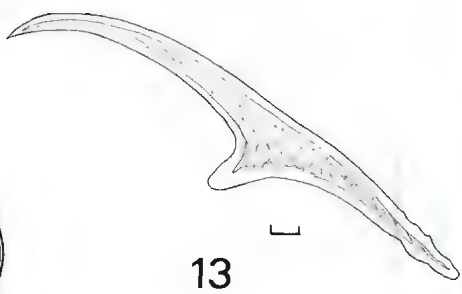
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13

wide; rostellar sac 0.26-0.29 (0.28, $n = 9$) long \times 0.20-0.29 (0.26, $n = 9$) wide. Hooks number 15-19 (17, $n = 6$), arranged in single ring; hooks with elongate, falcate blades, slender handles and blunt guards; core of hook blade hollow. Hooks 0.163-0.182 (0.172, $n = 10$) long. Neck variable, 0.90-1.41 (1.20, $n = 8$) long. Segments craspedote; mature segments much wider than long, 0.05-0.06 (0.06, $n = 5$) long \times 0.76-0.90 (0.85, $n = 5$) wide; gravid segments longer, of approximately the same width, 0.13-0.35 (0.20, $n = 5$) long, 0.57-1.22 (0.87, $n = 5$) wide. Genital pores unilateral. Three oval testes arranged in triangular array, with 1 poral and 2 aporal, of similar size, 0.08-0.13 (0.10, $n = 5$) long \times 0.04-0.05 (0.04, $n = 5$) wide. Vasa efferentia from aporal testes run along dorsal margin of medulla to elongate, pyriform, external seminal vesicle 0.13-0.18 (0.16, $n = 5$) long \times 0.023-0.049 (0.043, $n = 5$) wide, which extends along seminal receptacle. Cirrus sac pyriform, 0.14-0.17 (0.16, $n = 5$) long \times 0.036-0.042 (0.040, $n = 5$) wide; cirrus sac contains prominent internal seminal vesicle; cirrus unarmed. Genital ducts cross osmoregulatory canals dorsally. Ovary median, with indistinct lobules, c. 0.06 long \times 0.14 wide, on ventral surface of medulla; vitellarium reniform, posterior to ovary, 0.04-0.05 (0.05, $n = 5$) long \times 0.02-0.03 (0.03, $n = 5$) wide. Vagina posterior and ventral to cirrus sac, dilating to form sacciform seminal receptacle dorsal to ovary; seminal receptacle 0.10-0.13 (0.12, $n = 5$) long \times 0.05-0.07 (0.06, $n = 5$) wide. Uterus originates as transverse sac on ventral aspect of medulla, extends to osmoregulatory canals, developing few diverticula; never becoming reticulate. Eggs spherical, 0.032-0.045 (0.035, $n = 5$) in diameter. Ventral osmoregulatory canals 0.03-0.10 (0.05, $n = 5$) in diameter; dorsal osmoregulatory canals 0.01 in diameter. Longitudinal muscle arranged in two concentric rings; outer ring composed of numerous small bundles with few fibres; inner ring composed of larger bundles with 10-20 fibres per bundle.

Discussion

Spasskii (1994) created the genus *Potorolepis* for several species of cestode from Australian marsupials which had previously been allocated to *Hymenolepis* (see Vaucher *et al.* 1984) or to *Vampirolepis* by Spasskii (1954) and Jones & Anderson (1990). Species included in the new genus by Spasskii (1994) were *P. antechini* (Vaucher, Beveridge & Spratt, 1984), *P. aklei* (Beveridge &

Barker, 1975), *P. bettongiae* (Vaucher, Beveridge & Spratt, 1984), *P. bradleyi* (Beveridge & Barker, 1975), *P. isoodontis* (Vaucher, Beveridge & Spratt, 1984) and *P. peramelidarum* (Nybelin, 1917). To these should be added *P. peroryctis* (Jones & Anderson 1990) comb. nov. (syn. *Vampirolepis peroryctis* (Jones & Anderson, 1990)), the first species of the genus known from a New Guinean peramelid marsupial, *Peroryctes raffrayanus*. *Potorolepis peroryctis* is morphologically similar to *P. peramelidarum* and *P. isoodontis*, also from bandicoots, and clearly belongs within the genus *Potorolepis*. The species was presumably overlooked by Spasskii (1994) in erecting the new genus.

Spasskii (1994) characterised his new genus as having a rostellum armed with more than 10 hooks each longer than 50 μm , all with a well-developed, elongate blade, longer than the guard and with a tubular uterus which may develop diverticula.

The new species described above possess these key morphological characters and are therefore allocated to the genus *Potorolepis*. They are readily distinguishable from the known species based on hook number and size as well as from the disposition of the testes (Table 1). Based on hook number, the species of *Potorolepis* fall into two distinct groups, those with 10-23 hooks, all of which are parasitic in dasyurid marsupials, and those with 24-40 hooks which occur in peramelid and potoroid marsupials. The two new species, both from dasyurid marsupials, have hook numbers in the range 15-19 and therefore most closely resemble *P. aklei*, *P. antechini* and *P. bradleyi*. Both *P. aruensis* and *P. woolleyae* are distinguished from these species in having longer hooks. The lengths of hooks of *P. woolleyae* lie well outside the ranges of other species within this subgroup, though hook lengths of *P. aruensis* may overlap with those of *P. bradleyi*. *Potorolepis aruensis* can be distinguished by mean hook number (Table 1) but also by the cirrus sac which is shorter in *P. bradleyi* (0.190 \times 0.026 mm) than in *P. aruensis* (0.350 \times 0.050 mm). In *P. bradleyi*, the central testis lies dorsal to the ovary (Beveridge & Barker 1975) rather than aporal to it as in *P. aruensis*. For these reasons, the specimens described above from *Myoictis melas* are considered close to but distinct from *P. bradleyi* and warrant the erection of a new species. None of the specimens was fully gravid, the terminal segments instead having developing uteri which were only partly filled with eggs. This is surprising since the animals were transported to Melbourne following capture and maintained in the

Figs 8-14. *Potorolepis woolleyae* sp. nov. Types. 8. Scolex with rostellum everted. 9. Scolex with rostellum withdrawn. 10. Mature segments. 11. Gravid segment. 12-13. Rostellar hooks in profile. 14. Transverse histological section of mature segment; dorsal aspect towards top of page. Scale bars = 0.1mm 8-9, 11; 0.2mm 10; 0.01mm 12-13; 0.15mm 14. Legend: as for Figs 1-7.

laboratory until autopsy, providing adequate time for cestodes to mature.

The specimens from *Antechinus naso* are tentatively allocated to this species. They are poorly preserved and internal features are difficult to discern. Hook lengths are identical to specimens from *Myoictis*. The number of hooks, 18-22 (20) ($n = 5$), is larger than in specimens from *M. melas* but the range overlaps. They may represent a distinct but very similar species, although the current evidence is equivocal.

The cestodes from *Murexia longicaudata* were quite severely contracted, limiting the morphological details which were visible in whole mounts. Nevertheless, they represent a new species based on the features of the rostellar hooks alone. While they resemble *P. aruensis* in terms of mean hook number, the size of hooks immediately distinguishes the material from all congeners. In having the three testes arranged in a triangular fashion, *P. woolleyae* most closely resembles *P. aklei* and *P. antechini*.

Apart from adding to the hymenolepidid fauna known from marsupials in New Guinea, the new

species described support the erection of the genus *Potorolepis* by Spasskii (1994) in providing additional species which conform with the proposed diagnosis. Spasskii (1994) provisionally included in his diagnosis the character 'genital ducts crossing osmoregulatory canals dorsally'. This is unequivocally the case in *P. aklei*, *P. bradleyi*, *P. aruensis*, *P. woolleyae* and *P. peroryctis* and probably is similar in the remaining species of the genus. His generic definition (Spasskii 1994) also needs to be amended to allow for testes in either a linear or triangular array and for cirri which are either armed or unarmed. Apart from these minor modifications, the generic definition provided by Spasskii (1994) appears to be reliable.

The description of the new species also provides evidence in support of the suggestion first made by Vaucher *et al.* (1984) that each family of marsupials was parasitised by a distinctive morphological group of hymenolepidid cestodes. Spratt *et al.* (1991) reported *P. peramelidarum* from *Antechinus swainsonii* which would represent a potential exception. However, the identification was tentative

TABLE 1. Measurements and key morphological features of species of *Potorolepis* from marsupials.

Species	Host(s)	Hook Length	No. of Hooks	Testis Distribution
Species from dasyurid hosts				
<i>P. aklei</i>	<i>Antechinus</i> sp. (undescribed)* <i>A. flavipes</i> , <i>Pseudantechinus bilarnii</i> , <i>Smithopsis leucopus</i>	83-100 (91)	11-17 (13)	triangular
<i>P. bradleyi</i>	<i>Antechinus</i> sp. (undescribed)*	103-128 (114)	10-15 (13)	linear
<i>P. antechini</i>	<i>Antechinus swainsonii</i>	56-59 (58)	22-23	triangular
<i>P. aruensis</i>	<i>Myoictis melas</i>	128-147 (138)	16-18 (17)	linear
<i>P. woolleyae</i>	<i>Murexia longicaudata</i>	163-182 (172)	15-19 (17)	triangular
Species from peramelid hosts				
<i>P. peramelidarum</i>	<i>Perameles nasuta</i> <i>P. gunui</i> <i>Isodon obesulus</i>	93-101 (98)	35-38	linear
<i>P. isodontis</i>	<i>Isodon obesulus</i>	71-82 (79)	33-39	sub-triangular
<i>P. peroryctis</i>	<i>Peroryctes ruffinianus</i>	124-192	40	triangular
Species from potoroid hosts				
<i>P. potoroi</i>	<i>Potorous didactylus</i>	98-103 (102)	29-33	linear or triangular
<i>P. beptongiae</i>	<i>Beptongia gaimardi</i>	79-91 (86)	24-27	linear

* formerly identified as *Antechinus stuartii* (see Strahan 1995)

and based on incomplete specimens. This dubious record has therefore been eliminated from consideration until more material is collected and the host record confirmed. The species found in dasyurids, *P. aklei*, *P. antechini*, *P. urtensis*, *P. bradleyi* and *P. woolleyae*, belong to a group of species with a small number of rostellar hooks (10-23) compared with 33-40 hooks in *P. isodontis*, *P. peramelidarum* and *P. peroryctis* from peramelid hosts and 24-33 hooks in *P. potoroi* and *P. bettongiae* from potoroid hosts. The relative size of the ovary also separates the first two groups, the ratio of width of ovary to segment width being 9-15% in species from dasyurid hosts compared with 26-39% in those from peramelids. In the first group the uterus contains relatively few eggs, but it is clearly bilobed. More data are needed from hymenolepidids parasitising peramelids and potoroids to confirm the utility of this character. The observations of Jones & Anderson (1990) on a species from a New Guinean peramelid marsupial and the current descriptions of new species from dasyurid marsupials from New Guinea provide additional support for the hypothesis advanced by Vaucher *et al.* (1984). The data also suggest that the hymenolepidids of dasyurids from Australia are similar to those of New Guinea, as are the comparable cestodes of peramelid marsupials. Finally, we agree with Spasskii (1994) in allocating *Hymenolepis cercarteti* Vaucher, Beveridge & Spratt, 1984 to the genus *Rodentolepis*.

Key to the species of hymenolepidid cestodes occurring in Australasian marsupials based on rostellar hooks

1. Hooks small, shorter than 30 µm long, fratermoid in shape.....2
- Hooks larger, length greater than 50 µm long, not fratermoid in shape.....3

2. Hooks number 20-30, 14-18 µm long
 *Rodentolepis nana*
- Hooks 17-22, 17-22 µm long.....*Rodentolepis cercarteti*
3. Fewer than 22 hooks or, if 22 hooks present, hooks >100 µm long.....4
- More than 22 hooks or, if 22 hooks present, hooks <100 µm long.....7
4. Hooks shorter than or equal to 100 µm
 *Potorolepis aklei*
- Hooks longer than 100 µm.....5
5. Hooks 163-182 µm long.....*Potorolepis woolleyae*
- Hooks less than 150 µm in length.....6
6. Hooks 103-128 µm long, 10-15 in number
 *Potorolepis bradleyi*
- Hooks 128-147 µm long, 16-22 in number
 *Potorolepis urtensis*
7. Fewer than 28 hooks.....8
- More than 28 hooks.....9
8. Hooks 56-59 µm long, 22-23 in number
 *Potorolepis antechini*
- Hooks 79-91 µm long, 24-27 in number
 *Potorolepis bettongiae*
9. Hooks 124-192 µm long, 40 in number
 *Potorolepis peroryctis*
- Hooks less than 120 µm long, fewer than 40 in number
 10
10. Hooks shorter than 85 µm.....*Potorolepis isodontis*
- Hooks longer than 85 µm.....11
11. Hooks number 29-33.....*Potorolepis potoroi*
- Hooks number 35-38.....*Potorolepis peramelidarum*

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STRUCTURE OF THE ACOUSTIC SIGNALS OF *CRINIA GLAUERTI* (ANURA: MYOBATRACHIDAE) FROM SOUTH-WESTERN AUSTRALIA, AND COMPARISON WITH THOSE OF *C. SIGNIFERA* FROM SOUTH AUSTRALIA

by MURRAY J. LITTLEJOHN* & JOHN R. WRIGHT*

Summary

LITTLEJOHN, M. J. & WRIGHT, J. R. (1997) Structure of the acoustic signals of *Crinia glauerti* (Anura: Myobatrachidae) from south-western Australia, and comparison with those of *C. signifera* from South Australia. *Trans R. Soc. S. Aust.* 121(3), 103-117, 28 November, 1997.

Advertisement calls of 51 males of the Australian myobatrachid frog, *Crinia glauerti*, from five sites, and 45 males of the presumed cognate species *C. signifera* from four sites, were analysed and compared. Patterns of geographical variation in the advertisement calls of *C. glauerti* were explored and a cline was found in pulse rate. The structure and geographical variation in frequency of occurrence of another signal, the squelching call, of unknown function, in the acoustic repertoire of *C. glauerti*, were investigated. The findings are consistent with the earlier reports of more frequent occurrence of the squelching call in the south. Because of possible similarity in function, the squelching call of *C. glauerti* was compared with the encounter call of *C. signifera*.

KEY WORDS: *Crinia glauerti*, *Crinia signifera*, advertisement call, encounter call, acoustic analyses, pulse structure, spectral composition, geographical variation.

Introduction

The commonly produced call (= advertisement call, *sensu* Littlejohn 1977; Wells 1977) of the endemic south-western Australian species *Crinia glauerti* (Loveridge) was subjectively described by Main (1957) as: "A prolonged rattling call." Main (1957) also noted: "Adjacent to Perth the call of this species is constant and is predominantly a rattle, but occasionally a short squelching sound is made. On the south coast ... [away from related species], the squelching call is far more prominent" This observation of inter-populational variation in the calls of *C. glauerti* was considered by Brown & Wilson (1956) as a possible example of character displacement, with the squelching calls being more frequent in the populations that were allopatric to *C. insignifera* (Moore), a species which also has a squelch-like call (see Littlejohn 1959).

Although some values were cited by Brown & Wilson (1956) from A.R. Main (in litt., based on analyses by M.J. Littlejohn), the first published objective description, which included an oscillogram (= waveform) and an audiospectrogram, of the rattling call of *C. glauerti* was provided by Littlejohn (1959). This account was derived from the physical analysis of magnetic tape recordings of the calls of 12 males obtained at only one locality, South Perth (115°52' E, 31°59' S), near the northern limit of

geographic distribution (Littlejohn unpub.), so that there was no consideration of geographic variation in call structure within this species. Littlejohn (1959) also noted "occasional call variation in the form of a compressed series of pulses" which may be equated to the squelching call of Main (1957) and an oscillogram of one of these pulse trains was presented.

The disjunct allopatric south-eastern Australian taxon *C. signifera* (Girard) is presumed to be the cognate (sister) species of *C. glauerti*, with which it constitutes the *signifera* superspecies (Main 1957; Main *et al.* 1958). The advertisement call of this taxon is a short, rapidly repeated pulse train and the first published objective description, and an oscillogram, were provided by Littlejohn (1958). Littlejohn (1959, 1961) supported the proposed affinity of *C. glauerti* and *C. signifera*, on the basis of the much lower pulse rates of the advertisement calls, when compared with those in calls of the then recognized members of the related *insignifera* superspecies (Main 1957; Main *et al.* 1958). Quantitative descriptions of the calls of *C. signifera* were also provided by Littlejohn (1964, 1970), Littlejohn & Martin (1965), Hawe¹, Littlejohn *et al.* (1985) and Odendaal *et al.* (1986). Interpopulational variation in advertisement calls of *C. signifera* was considered by Littlejohn (1959, 1964), and by Odendaal *et al.* (1986). Straughan and Main (1966), through choice playback experiments in which tape-recorded advertisement calls of *C. signifera* and *C. parinsignifera* (Main) were offered as alternative stimuli, demonstrated that breeding females of *C. signifera* exhibited positive phonotaxis only to the conspecific calls. Encounter calls (*sensu* Wells 1977)

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¹ Hawe, S. M. (1970) Calling behaviour and Territoriality in Males of Two species of *Crinia* (Anura: Leptodactylidae). BSc (Hons) thesis, Department of Zoology, University of Melbourne (unpub.).

(= territorial calls, Littlejohn *et al.* 1985) of *C. signifera* were identified through field playback experiments by Hawel and Littlejohn *et al.* (1985). The squechling calls of *C. glauerti* may also have a territorial function but this has yet to be determined. In the absence of experimental documentation, the term "squechling call" (Main 1957) will be retained for the compressed series of pulses.

Tape-recorded samples of advertisement calls of 51 individuals were obtained at five localities across the geographic range of *C. glauerti* (Fig. 1, Table 1) to provide a measure of geographical variation. Mundaring Weir (Site 1) is the type locality for *C. glauerti* (Cogger *et al.* 1983). Squechling calls were

produced in the recorded sequences of 25 of these individuals. Sufficient squechling calls were obtained to provide a preliminary description of this type of signal for comparison with the conspecific advertisement call, and with the encounter calls of *C. signifera*, and to allow an estimation of geographical variation in the frequency of production relative to the advertisement call. Tape recordings of advertisement calls of 45 individuals from the closest populations of *C. signifera* were also obtained, namely from four localities in southern South Australia (Fig. 2, Table 1) at or near the western limits of the extensive geographic distribution of this species (see maps given by Brook 1983, 1984; Tyler

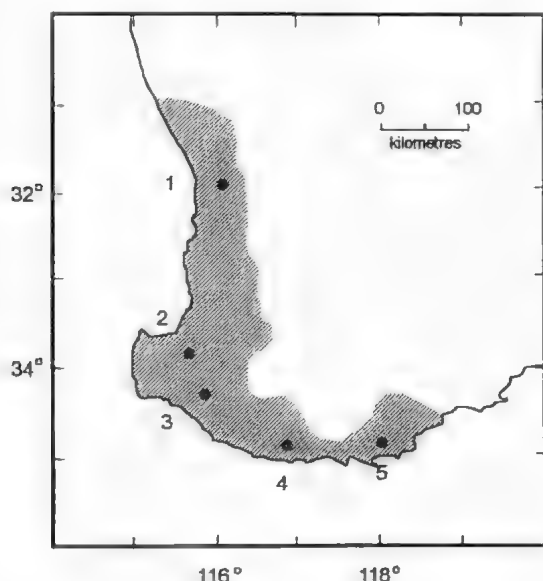


Fig. 1. Geographic distribution (based on Tyler *et al.* 1994) of *Crinia glauerti*, and locations of recording sites (see Table 1).

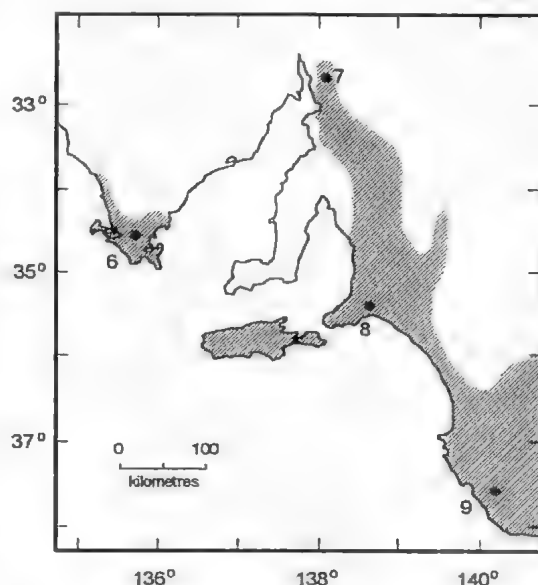


Fig. 2. Geographic distribution (based on Brook 1984) of *Crinia signifera* in South Australia and locations of recording sites (see Table 1).

TABLE 1. Details of recording localities.

All sites are in Western Australia for *Crinia glauerti* and in South Australia for *C. signifera*.

Species	Site	Dates of recording	Locality	Latitude (South)	Longitude (East)
<i>C. glauerti</i>	1	19, 23.vii.89	Helena River, at base of Mundaring Weir	31°57'	116°10'
	2	06.vii.86, 31.vii.89	21 km south-south-west of Busselton	33°51'	115°19'
	3	23.vii.86, 02.viii.86	Diamond Tree railway siding	34°22'	116°06'
	4	24, 25.vii.86	3 km east of Nornalup	34°59'	116°50'
	5	09, 10.viii.89	13 km east-north-east of Albany	34°59'	118°00'
<i>C. signifera</i>	6	18.viii.86; 15.viii.89	9.3 km south of Wamilla	34°36'	135°40'
	7	03, 04.vii.89	Yellowman Creek, 3.6 km south-east of Melrose	32°51'	138°13'
	8	28, 29.vii.90	9 km north-north-west of Victor Harbour	35°29'	138°36'
	9	26.vii.90	8.3 km north-north-east of Millicent	37°31'	140°23'

1985; Cogger 1992). The description of the encounter call (=territorial call) of *C. signifera* is based on accounts of Hawe¹ and Littlejohn *et al.* (1985, unpub.).

Materials and Methods

Recording of calls

Tape recordings were obtained at the breeding sites (Figs 1, 2, Table 1) with an open-reel recorder (Nagra IV-S) and a cardioid dynamic microphone (Beyer M 88). Males of both species call from a variety of sites: on the banks adjacent to water, while sitting in shallow water, or while floating and supported by emergent vegetation. The effective temperatures at the calling sites (surface water, wet-bulb air, depending on the calling position of the frog) were then measured with an electronic (thermistor) thermometer (Takara Digimulti Model D611, with sensor type SZL-64). The mean was used as the effective temperature when an individual was at the interface between air and water. Where possible, the recorded males of *C. glauerti* were collected, euthanased, preserved in Tyler's fixative (Tyler 1962), stored in 70% ethanol and lodged with the Western Australian Museum. If the specimen was preserved, the measurement of snout-urostyle length was later made with dial calipers (to 0.1 mm; rounded to 0.5 mm). Otherwise, a short plastic ruler (15 cm) was placed along the dorsal surface of the living specimen held in a thin, clear plastic bag, and the snout-urostyle length determined to the nearest 0.5 mm.

Acoustic analysis of recordings

For acoustic analysis, tape recordings were replayed on an open-reel tape recorder (Revox B 77 MkII or Sony TC-510-2). Advertisement calls were analysed by using a digital audio-spectrograph (Kay Elemetrics Model DSP-5500 Sona-Graph). Where there were high levels of low-frequency noise, a passive filter (Allison 2B, high pass, cut-off set at 512 Hz) was inserted between the output of the tape recorder and the input of the audio-spectrograph. Statistical procedures were carried out with SYSTAT, Version 5.03 (Systat Inc., Evanston).

Characteristics of equipment used in recording and analysis

Tape transport speeds (19 cm s^{-1}) of the recorders involved in recording and playback were periodically checked against a locally produced standard 1000 kHz calibration tape and a frequency counter (Heath Schlumberger SM-118A or Good Will GFC-8010G) (Revox, Sony), or against the 50 Hz AC mains frequency by a built-in stroboscope (Nagra); overall variations in tape speed through recording and

playback are estimated to be less than $\pm 0.5\%$. The frequency responses of all electronic components used in recording and analysis are presumed to be close to linear within the narrow range of frequencies of interest (c. 2.0–5.0 kHz), based on manufacturers' specifications. The relatively high sampling rates used in the digital analyses ($>44 \text{ kHz}$) preclude the production of artifacts from aliasing.

Structure and acoustic attributes of calls

The calls of the two species are of simple structure and each consists of a group of discrete damped oscillations (Figs 3–5). For convenience, and following previous usage, each of these oscillations is referred to as a "pulse," and the group (i.e. the pulse train) as a call (Figs 3, 4). The number of pulses in a call was determined by direct inspection of the displayed waveform. The depth of amplitude modulation of the last two pulses in a call was sometimes less than 100%; in such cases, separate pulses were recognized if the depth of modulation exceeded about 75%. The duration (to nearest ms) of a call was taken as the interval from the peak of the first pulse to the peak of the last pulse (= "peak-peak duration"). The pulses in the advertisement calls are produced in a quasi-periodic fashion, and the pulse rate (as p s^{-1}) was calculated over a complete call as $(n - 1 \text{ pulses}) \times 1000/\text{peak-peak duration in ms}$. Dominant frequencies were measured as the peaks in a power spectrum of the whole call. To describe the temporal and spectral properties of pulses in advertisement calls, a tape recording of one call of each of three individuals of each species (*C. glauerti*,

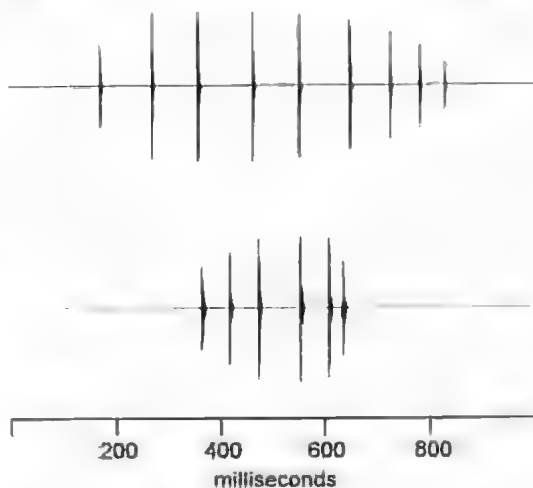


Fig. 3. Waveforms of advertisement calls. Upper, *Crinia glauerti*; Reference R439-7, Site 1; effective temperature, wet-bulb air = 11.8°C . Lower, *C. signifera*; Reference R408-2, Site 6; effective temperatures, wet-bulb air = 11.1°C , water = 12.5°C .

Site 1; *C. signifera*, Site 6) was replayed into a digital sound card (Sound Blaster SB16, Creative Labs Milpitas), installed in a desktop computer (IBM-PC compatible). The sampling rate was set at 44,100 Hz and the sample size at 16 bits. Files were prepared in the WAVE format with the Creative WaveStudio Version 2.0 software (Creative Technology Singapore), and further processed with this package and with Spectra Plus Professional, Version 3.0 (Pioneer Hill Software Poulsbo). The figures of the waveforms and spectra (Figs 3-5) were prepared by the same procedure. One pulse (the middle pulse or next after the midpoint of a call if an even number) of each call was used for analysis.

Conventional rise and decay times of pulses (from 10–90%, and 90–10%, respectively, of maximum amplitude) were not calculated because it would have been necessary to extrapolate between peaks of the carrier frequency (see below). Accordingly, the number of either positive or negative half cycles to reach maximum amplitude was counted and the time interval from background noise level to the peak

estimated. The pulse duration was measured as the interval from approximately 10% of the maximum amplitude (either positive or negative) at the start to the same level at the end of a pulse. Two dominant spectral peaks are present in most of the calls of both species (Fig. 4). There is a well-defined sinusoidal fundamental frequency within the wave train (Fig. 4) and this is referred to as the carrier frequency (CF), by analogy with amplitude modulation in electronics.

Rates of production of advertisement call were determined by playback of original recordings on a Sony TC-510-2 recorder. For *C. glauerti*, the durations of five consecutive cycles of calls and intervals were measured; for *C. signifera*, 10 cycles were measured. The following protocols were employed to arrive at the sequences of calls selected for measurement: *C. glauerti* - the first six clear calls in the recorded sequence; *C. signifera* - the last 16 calls in the sequence were digitised, then the last five discarded. The interval from the end of the first call to the end of the sixth (*C. glauerti*) or tenth (*C.*

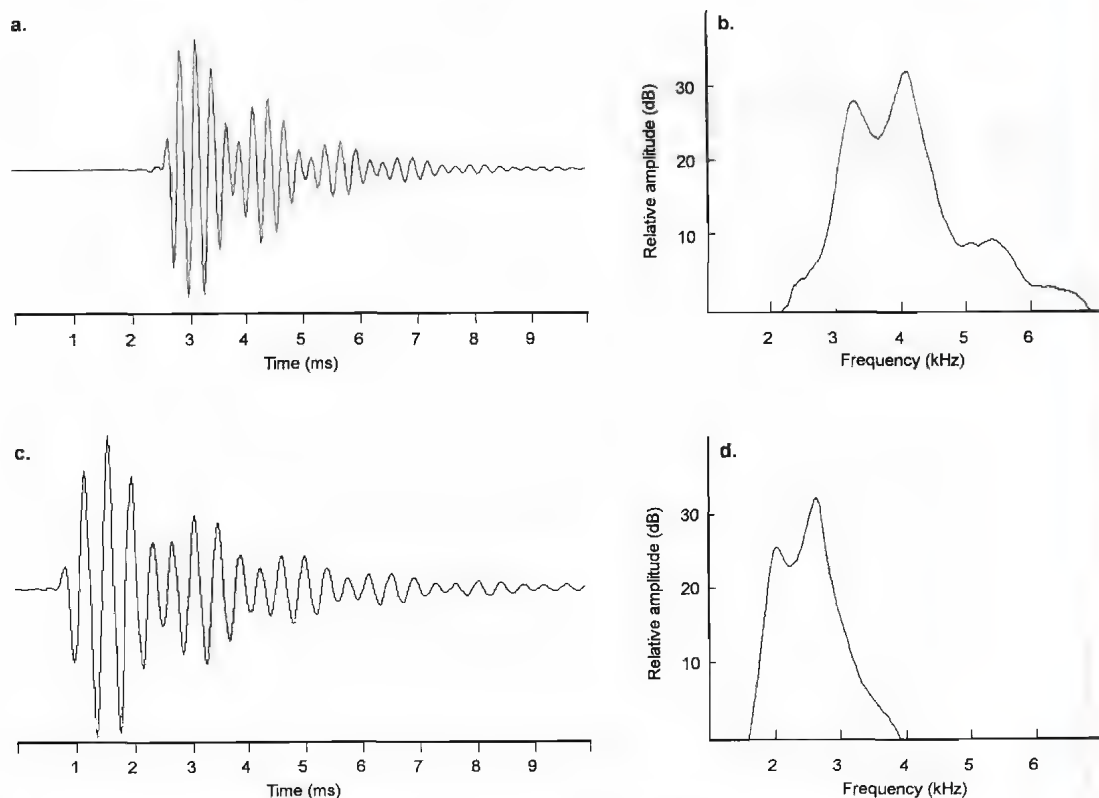


Fig. 4. Structure of pulses in advertisement calls. Upper panels. (a). Expanded waveform. (b). Frequency spectrum for *Crinia glauerti* (Reference: R439-9, Site 1; effective temperature = 12.2° C). Lower panels. (c). Expanded waveform. (d). Frequency spectrum for *C. signifera* (Reference: R408-5, Site 6; effective temperatures, wet bulb air = 10.9° C, water = 12.7° C).

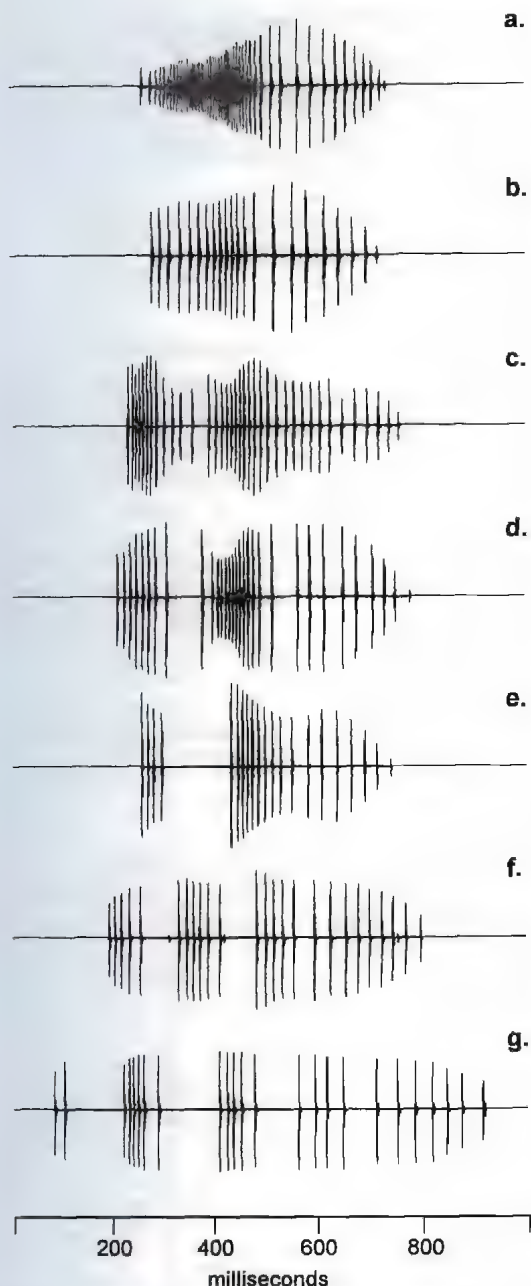


Fig. 5. Waveforms of squelching calls of *Crinia glauerti*. (a). R441-5, Site 5, effective temperature = 11.8° C. (b). R441-1, Site 5, effective temperature = 13.1° C. (c). R404-2, Site 2, effective temperature = 9.6° C. (d). R441-4, Site 5, effective temperature = 13.1° C. (e). R407-6, Site 3, effective temperature = 11.1° C. (f). R404-3, Site 3, effective temperature = 9.8° C. (g). R407-7, Site 3, effective temperature = 10.7° C.

a. *signifera*) call was then measured to the nearest millisecond.

Numbers of advertisement calls of individuals analysed

The number of advertisement calls of each individual to be analysed was determined as follows. Both species produce advertisement calls in long and regular sequences. In *C. glauerti*, production of the longer advertisement calls is slow - about 20% of the rate of *C. signifera* (see below). For *C. glauerti*, as the first step, four clear calls of each individual ($n = 10$) from Site 1 were chosen at random from the recorded sequence. If four clear calls could not be obtained, that individual was discarded from the analysis. For *C. signifera*, all individuals from Site 8 ($n = 10$) were used and data were obtained from three successive calls: the 12th, 13th and 14th (or the nearest clear call if there was an overlap) from the start of a natural sequence, or after recording had commenced. For each attribute of the call and for each species, an analysis of variance was carried out with comparison between individuals. The variance was partitioned and the proportion of the variation due to within-individual effects and that due to between-individual effects was calculated. For both species and all variables, variation between individuals was far greater than that within individuals. For *C. glauerti*, the within-individual variation accounted for 13-20% of the variation in the data. For *C. signifera*, the within-individual variation accounted for 24-25% of the variation. Based on these results of the analyses of variance, it was decided that for *C. glauerti*, the average of two calls per individual would provide a representative sample for that individual. As the calls of *C. signifera* were slightly more variable, it was decided to use the average of three calls for each individual. Mean values for individuals are used in the subsequent treatment of these data.

Effects of temperature

Linear regression analyses of the full data set for advertisement calls (Table 2) indicated that for *C. glauerti* there was a significant ($p < 0.05$) relationship between effective temperature and duration and between effective temperature and pulse rate. The linear regression analyses also indicated that there was a significant relationship between dominant frequency and effective temperature for advertisement calls of each species. Accordingly, values of the dependent variables were corrected to 11.0° C, the nearest integer to the pooled mean for effective temperature (*C. glauerti*, mean = 11.1° C; *C. signifera*, mean = 10.8° C); these values were used in subsequent calculations. Where the slope for the combined samples for each species was non-significant, the raw data were used in

TABLE 2. Influence of effective temperature on four attributes of the advertisement calls of *Crinia glauerti* ($n = 51$) and *C. signifera* ($n = 45$). Results of analyses by linear regression. See Table 4 for ranges of temperatures.

Attribute of call	Species	Slope	Significance of slope (p)	Coefficient of determination (r^2)
Duration	<i>C. glauerti</i>	-0.070	<0.001	0.291
	<i>C. signifera</i>	+0.013	0.240	0.032
Number of pulses	<i>C. glauerti</i>	-0.151	0.516	0.009
	<i>C. signifera</i>	+0.290	0.141	0.050
Pulse rate	<i>C. glauerti</i>	+1.448	<0.001	0.239
	<i>C. signifera</i>	+0.499	0.587	0.007
Upper dominant frequency	<i>C. glauerti</i>	-100.107	0.008	0.134
	<i>C. signifera</i>	156.566	<0.001	0.240

the subsequent analyses.

Occurrence of squelching calls of *C. glauerti*

The presence of squelching calls was determined subjectively, by replaying the tape-recorded sequences of each individual. In this analysis, three types of call were recognised: advertisement calls, squelching calls, and transitional calls - as it was not possible to assign some to either category. The squelching calls of *C. glauerti* also consist of pulse trains (Fig. 5). Because these calls are highly variable in temporal structure, and were produced only during the recorded sequences of about 50% of the individuals, they are only briefly described in a subjective way.

Results

Structure of pulses in advertisement calls

The pulses in calls of both species are similar, each with a sharp attack and a gradual (negative exponential) decay (Fig. 4). Estimated durations are 4 ms for *C. glauerti* and 4-7 ms for *C. signifera*. The maximum amplitude is reached within three positive or negative peaks of the carrier frequency, that is, in about 1 ms for both taxa. Examination of the expanded wave form of each pulse indicated the presence of a clear sinusoid (= fundamental/carrier) with a frequency that is close to the upper peak of the spectrum (Table 3). Accordingly, only the upper peak (= carrier frequency) was used in subsequent calculations. The frequency bandwidth at 10 dB

below the peak is about 1200 Hz for both species (Fig. 4). The envelope of the pulse is amplitude modulated to a depth of about 30-60% (based on the first cycle) with the envelope modulating frequency (EMF) within a range of 694 to 820 Hz for *C. glauerti*, and of 505 to 885 Hz for *C. signifera* (Fig. 4). These values are close to the difference between the upper and lower peak of the spectrum for each individual (Fig. 4, Table 3). It is suggested that the lower peak that is present in the spectrum of the advertisement calls of some individuals of each species (Fig. 4) is a sideband of the carrier frequency (i.e. the upper dominant frequency). The level of the lower peak is about 4-9 dB below that of the upper peak (Table 3).

Structure of the advertisement calls

Both species produce advertisement calls in long and regular sequences. For *C. glauerti* from Site 1, calls were produced at a mean rate of 26.5 calls min⁻¹ (range = 22.9 - 28.8; $n = 9$) at a mean effective temperature of 12.1° C (range = 11.4 - 12.8). For *C. signifera* from Site 8, the mean rate was 124.7 calls min⁻¹ (range = 81.1 - 187.1; $n = 11$) at a mean effective temperature of 11.4° C (range = 11.2 - 11.7). Values for three primary attributes (duration, number of pulses and carrier frequency) and the one derived attribute (pulse rate) for five samples of *C. glauerti* and four samples of *C. signifera*, corrected for the effect of temperature where appropriate, are

TABLE 3. Spectral characteristics of pulses in advertisement calls of *Crinia glauerti* and *C. signifera*. All values are in Hz. See text for explanation.

Species	Individual	Carrier frequency (CF)	Envelope modulation frequency (EMF)	Lower spectral peak (LSP)	Upper spectral peak (USP)	Difference between spectral peaks (DSP = USP - LSP)	Difference between CF and USP	Difference between EMF and DSP
<i>C. glauerti</i>	1	4065	820	3370	4048	678	17	142
	2	4167	694	3472	4134	662	33	32
	3	4049	820	3266	4048	782	1	38
<i>C. signifera</i>	1	2494	505	2050	2497	447	3	58
	2	2632	671	2068	2670	602	38	69
	3	3413	885	2454	3445	991	32	106

TABLE 4. Physical characteristics of advertisement calls of *Crinia glauerti* and *C. signifera*, corrected to an effective temperature of 11.0°C, where appropriate (see Table 2).

For each cell, the mean and standard deviation are given on the upper line, and range (in parentheses) on the lower line.

Species	Site	Sample size	Effective temperature (°C)	Call duration (ms)	Number of pulses	Pulse rate (p s ⁻¹)	Carrier frequency (Hz)
<i>C. glauerti</i>	1	10	12.17, 0.47 (11.4 - 12.8)	738, 87 (573 - 817)	9.70, 1.21 (7.5 - 11.5)	11.80, 1.94 (9.4 - 16.3)	4052, 229 (3584 - 4430)
	2	9	10.14, 0.64 (9.2 - 11.0)	724, 153 (552 - 982)	9.83, 1.50 (8.0 - 12.0)	12.66, 0.56 (12.0 - 13.6)	4279, 285 (3580 - 4540)
	3	13	10.27, 1.03 (7.7 - 11.5)	705, 115 (547 - 935)	11.50, 1.88 (9.0 - 15.5)	14.94, 1.80 (11.8 - 18.3)	4068, 215 (3770 - 4530)
	4	8	10.56, 0.57 (9.6 - 11.4)	526, 82 (438 - 655)	10.06, 1.84 (8.5 - 13.0)	16.91, 1.48 (14.2 - 18.6)	4031, 485 (3250 - 4570)
	5	11	12.27, 0.62 (11.0 - 13.1)	598, 85 (486 - 747)	11.23, 2.37 (8.0 - 16.0)	18.20, 2.90 (15.1 - 23.3)	4076, 292 (3640 - 4450)
	Combined sample	51	11.10, 1.18 (7.7 - 13.1)	664, 130 (438 - 982)	10.57, 1.92 (7.5 - 16.0)	14.93, 3.06 (9.4 - 23.3)	4098, 302 (3250 - 4570)
<i>C. signifera</i>	6	12	11.54, 0.54 (10.4 - 12.2)	272, 77 (150 - 437)	6.28, 1.54 (4.0 - 10.3)	19.68, 3.41 (15.5 - 28.8)	2790, 325 (2504 - 3568)
	7	13	10.64, 0.78 (9.2 - 11.2)	161, 70 (91 - 272)	5.31, 1.41 (4.0 - 9.0)	29.05, 7.56 (18.4 - 43.8)	2431, 241 (2092 - 2871)
	8	10	11.43, 0.18 (11.2 - 11.7)	182, 55 (101 - 237)	4.87, 0.69 (4.0 - 6.0)	22.50, 4.53 (17.5 - 29.7)	2569, 87 (2471 - 2710)
	9	10	9.25, 0.27 (8.9 - 9.8)	158, 20 (125 - 192)	4.37, 0.48 (4.0 - 5.0)	21.32, 1.91 (18.2 - 24.1)	2825, 169 (2549 - 3103)
	Combined sample	45	10.75, 1.02 (8.9 - 12.2)	195, 77 (91 - 437)	5.26, 1.34 (4.0 - 10.3)	23.38, 6.15 (15.5 - 43.8)	2645, 279 (2092 - 3568)

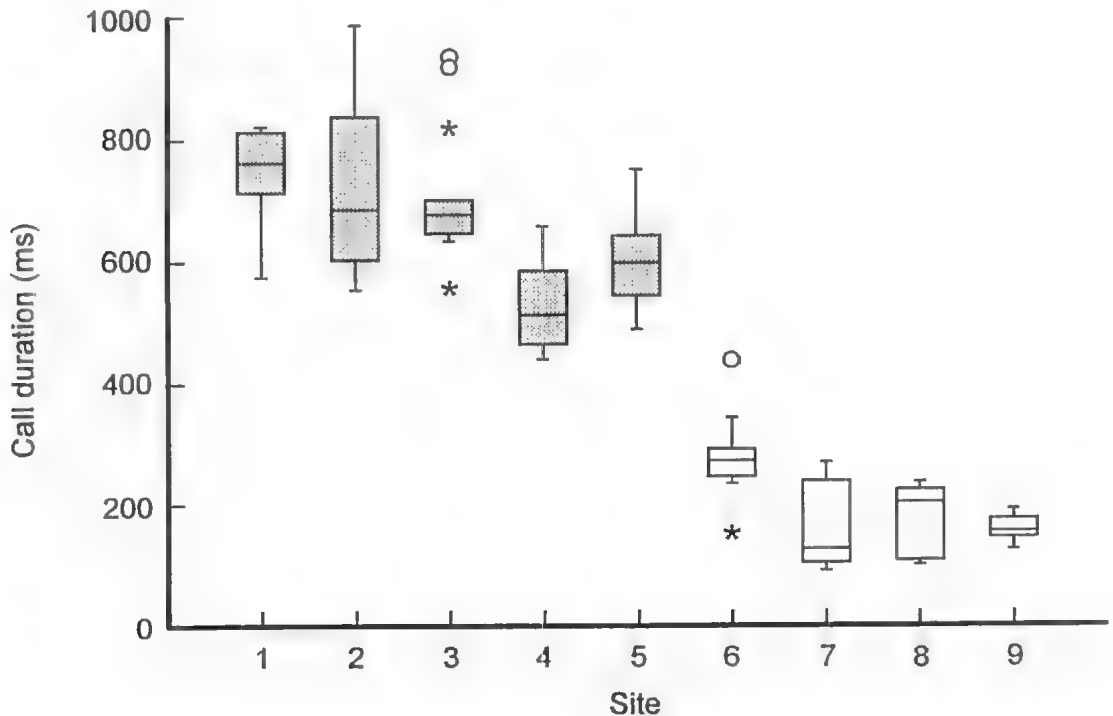


Fig. 6. Box plots for durations of advertisement calls at recording sites of *Crinia glauerti* (hatched boxes) and *C. signifera* (open boxes). Values are corrected to 11°C where slopes are significant. The box indicates the interquartile range and the included horizontal line is the median. The vertical lines outside the boxes (whiskers) connect to the last data points within $\pm 1.5 \times$ the interquartile range (the fences). The asterisks indicate outliers (values lying between ± 1.5 and $3.0 \times$ the interquartile range) and the open circles indicate extreme outliers (values beyond $3 \times$ the interquartile range).

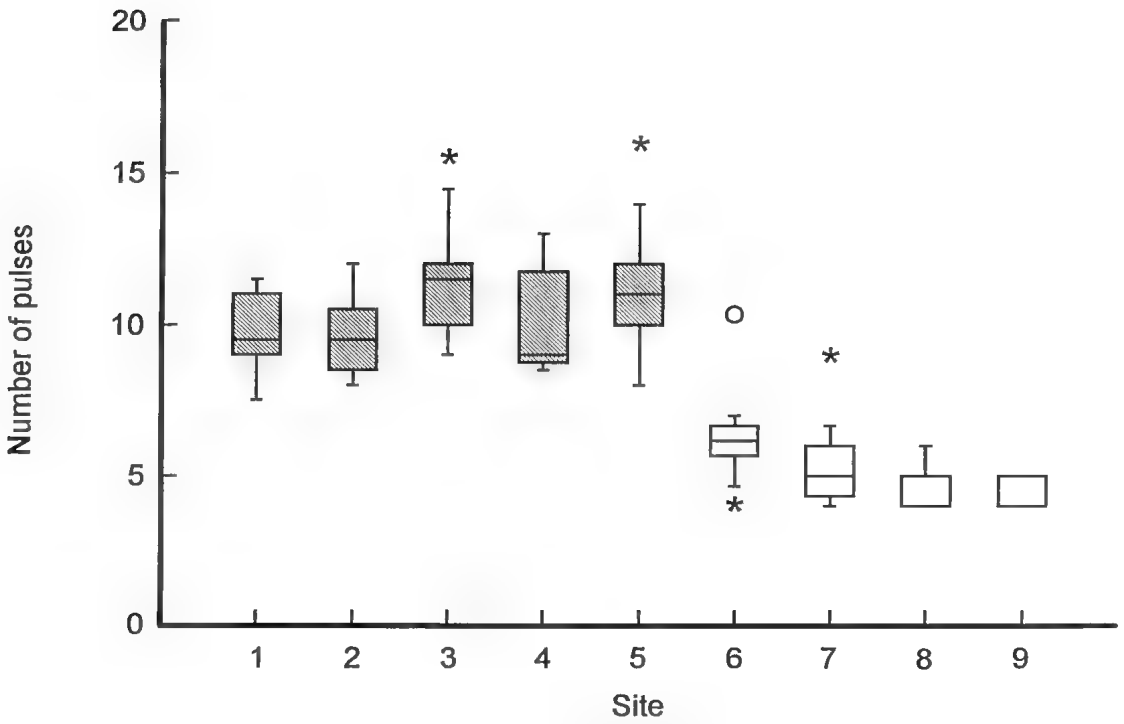


Fig. 7. Box plots for numbers of pulses in advertisement calls at recording sites of *Crinia glauerti* and *C. signifera*. See Fig. 6 for explanation.

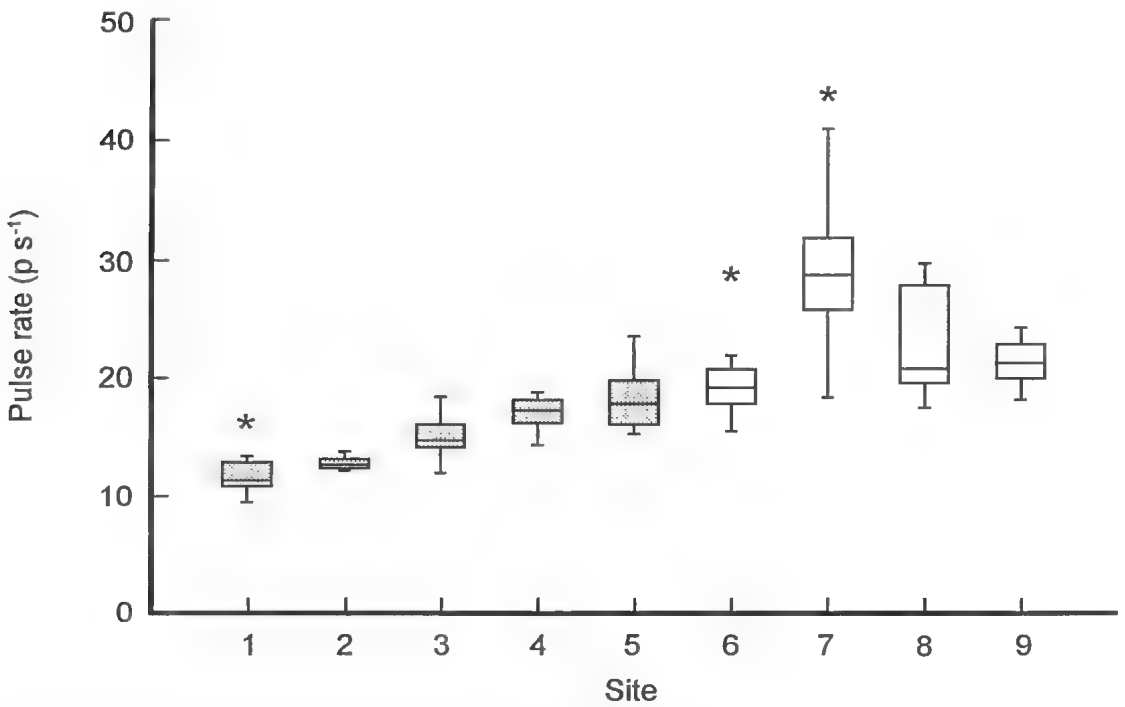


Fig. 8. Box plots for pulse rates of advertisement calls at recording sites of *Crinia glauerti* and *C. signifera*. Values are corrected to 11° C where slopes are significant. See Fig. 6 for explanation.

presented in Table 4. Values for combined samples of each species are also presented in Table 4. Box plots of these values at each site are presented in Figs 6-9.

Correlations of attributes of advertisement calls with body length

Calling males of *C. glauerti* are smaller than those of *C. signifera* (Table 5), with mean snout-urostyle lengths of 16.31 (range = 14.0–19.0; $n = 29$), and 21.31 (range = 18.0–25.0; $n = 16$) mm respectively (t -test; $p < 0.001$). There is no significant correlation of carrier frequency (corrected

to 11.0° C; Table 2) with snout-urostyle length when all collected specimens of *C. glauerti* are included ($r = -0.297$; $p = 0.118$; $n = 29$); but there is a significant negative correlation when only those specimens that were measured following preservation are considered ($r = -0.440$; $p = 0.032$; $n = 24$). For *C. signifera*, however, there is a highly significant negative correlation between carrier frequency and snout-urostyle length ($r = -0.796$; $p < 0.001$; $n = 16$, all specimens were alive when measured). A scattergram of the correlation of snout-urostyle length and carrier frequency is presented in Fig. 10.

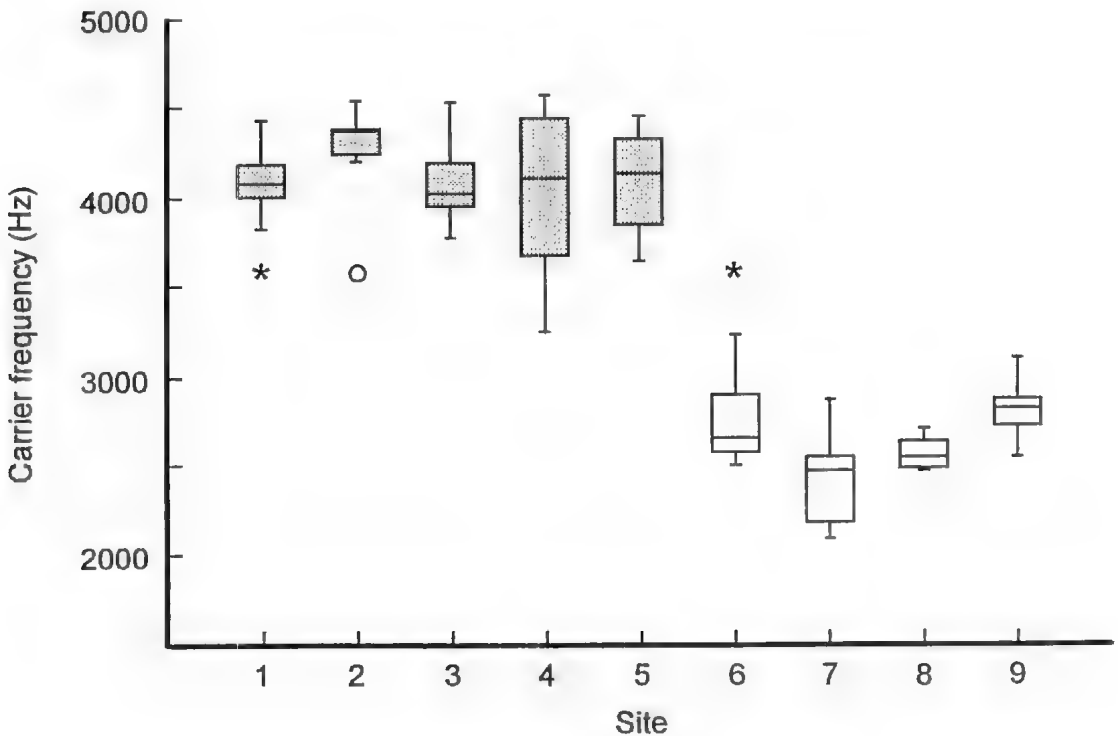


Fig. 9. Box plots for carrier frequencies of advertisement calls at recording sites of *Crinia glauerti* and *C. signifera*. Values are corrected to 11° C where slopes are significant. See Fig. 6 for explanation.

TABLE 5. Values (in mm) for snout-urostyle lengths of males of *Crinia glauerti* and *C. signifera* collected after their advertisement calls had been recorded.

Species	Site	Sample size	Mean	Range	Standard deviation	Condition of specimen
<i>C. glauerti</i>	1	8	17.2	16.5 - 19.0	0.80	preserved
	2	6	14.6	14.0 - 15.5	0.58	preserved
	3	7	16.2	15.5 - 17.0	0.49	preserved
	4	3	15.5	15.0 - 16.0	0.50	preserved
	5	5	17.6	17.0 - 18.0	0.55	live
	Total	29	16.31	14.0 - 19.0	1.25	
<i>C. signifera</i>	8	7	23.4	22.0 - 25.0	1.17	live
	9	9	19.7	18.0 - 21.0	1.41	live
	Total	16	21.31	18.0 - 25.0	2.31	

Geographical variation in advertisement calls of C. glauerti

Analysis of variance, with Site as the grouping factor, indicated that there are no significant differences for number of pulses ($p = 0.074$) and carrier frequency ($p = 0.411$). There are, however, significant differences for the means (adjusted to 11°C) of duration ($p < 0.001$) and pulse rate ($p < 0.001$). Across the distance of about 450 km covered by the five sites (Fig. 1), there is no consistent trend in duration (Fig. 6, Table 4), although a multiple comparison (Tukey test) indicated that the means for Sites 1-3 are significantly lower than those at Site 4, and Site 1 also differed from Site 5. There is a cline of increasing values for pulse rates (Fig. 8, Table 4). A Tukey test showed that the following means for pulse rate differ significantly: Site 1 from Sites 3, 4, and 5; Site 2 from Sites 4 and 5; and Site 3 from Site 5.

Geographical variation in advertisement calls of C. signifera

Sites 7, 8 and 9 are within the continuous distribution of *C. signifera* (see maps given by Brook 1983; Tyler 1985) and are spaced at about 300 km intervals. Site 6 is in the isolate on Eyre Peninsula and about 300 km from Sites 7 and 8 (Fig. 2).

Analyses of variance, with Site as the grouping factor, indicated that there were significant differences for all four attributes of the calls ($p \leq 0.003$). Multiple comparisons (Tukey test) revealed the following significant differences in means between sites: call duration - Site 6 from Sites 7-9; pulse number - Site 6 from Sites 8 and 9; dominant frequency (adjusted to 11°C) - Site 7 from Sites 6 and 9; pulse rate - Site 7 from Sites 6, 8 and 9.

Comparison of advertisement calls of C. glauerti and C. signifera

Results of analyses of variance, with Species as the grouping factor, indicated that the advertisement calls of the two species differed significantly ($p < 0.001$) in all four attributes. From a consideration of the combined samples for each species (Table 4), calls of *C. glauerti* are much longer, with means of durations differing by 3.4 times, and with no overlap in ranges of variation (Fig. 6). The mean value for number of pulses in advertisement calls of *C. glauerti* is twice that of *C. signifera* but there is an overlap of ranges between 7.5 and 10.3 (Fig. 7, Table 4). For pulse rates, although the mean for *C. glauerti* is only 64% of that for *C. signifera*, the ranges overlap extensively (Fig. 8, Table 4), particularly for the closest samples (Sites 5, 6). The mean for carrier

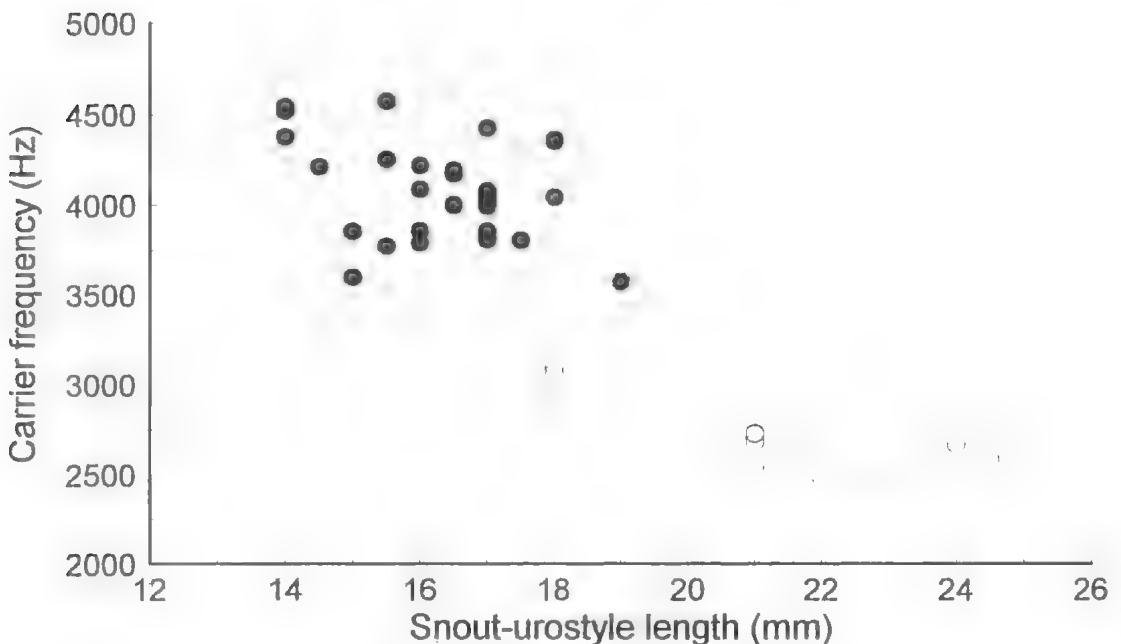


Fig. 10. Scattergram showing the correlation between carrier frequency and snout-urostyle length for males of *Crinia glauerti* and *C. signifera* that were collected after their calls had been recorded.

TABLE 6. Physical characteristics of seven squelching calls of *Crinia glauerti* from the same set of calls presented in Figure 5.

Individual (and tape reference)	Temperature (°C)	Duration (ms)	Number of pulses	Low pulse rate (p s ⁻¹)	High pulse rate (p s ⁻¹)	Overall pulse rate (p s ⁻¹)	Carrier frequency (Hz)
a. (R441-5)	11.8	475	50	43.2	205.9	103.2	3703
b. (R441-1)	13.1	438	22	31.1	79.0	48.0	3746
c. (R404-2)	9.6	524	37	46.7	125.0	68.7	4392
d. (R441-4)	13.1	569	31	36.3	137.2	52.7	4230
e. (R407-6)	11.1	478	21	37.4	92.3	41.8	4220
f. (R404-3)	9.8	603	25	40.2	61.7	39.8	4263
g. (R407-7)	10.7	832	24	29.7	105.3	27.6 ^a	4048
Means	11.31	559.9	30.0	37.80	115.20	54.55	4086
Ranges	9.6 - 13.1	438 - 832	21 - 50	29.7 - 46.7	61.7 - 205.9	27.6 - 103.2	3703 - 4392

^a Lower than low pulse rate because of the four long breaks in the train.

frequencies is higher in *C. glauerti*, by 1452 Hz, but with an overlap of ranges between 3229 and 3568 Hz (Fig. 9, Table 4).

Structure of the squelching call of *C. glauerti*

These calls are highly variable, as is indicated by the selection of waveforms presented in Fig. 5. The pulses are sometimes in groups within a call, and the pulse rate can vary greatly through a call (Fig. 5). Values for four attributes of the seven calls presented in Fig. 5 are given in Table 6. The pulses are of similar structure to those of the advertisement call and there are also two peaks in the frequency spectra, as in the advertisement call. For the seven calls presented in Fig. 5, the following data apply (see section on pulses of advertisement calls for methodology): duration - mean = 3.77 ms (range = 3.1 - 5.1); carrier frequency - mean = 3955 Hz (range = 3481 - 4427); upper frequency peak - mean = 3976 Hz (range = 3703 - 4414); envelope modulating frequency - mean = 877 Hz ($n = 5$; range = 735 - 1062); lower dominant frequency peak - mean = 3260 Hz ($n = 5$; range = 3100 - 3464). The difference between the means of peaks of upper and lower frequencies of 716 Hz is consistent with the explanation advanced for the pulses in the advertisement calls - of the lower sideband of an envelope modulating frequency. The pulses may be grouped within a call (Fig. 5) and the pulse rates can differ considerably between groups in one call (Table 6).

Geographical variation in frequency of occurrence of the squelching call of *C. glauerti*

Recorded sequences of calling by 25 of the 51 individuals included squelching calls. Because of confusion from the calling by two or more close individuals, only those of 21 could be reliably assessed, classified and counted (Table 7). A geographical trend is evident, with the frequency of production of squelching calls by individuals being higher in the southern and south-eastern samples

(Sites 4, 5, Table 8). No attempt was made to determine the extent of variation in the squelching calls of individuals, nor over time for a population.

Structure of the encounter calls of *C. signifera*

Littlejohn *et al.* (1985), by playback of advertisement calls of *C. parvisignifera* and *C. signifera* at peak sound pressure levels (0 dB re 20 μ Pa) above c. 98 and 104 dB respectively, evoked encounter calls (= territorial calls *sensu* Hawel; Littlejohn 1977) from eight males of *C. signifera* at Willowmavin in south central Victoria (37°16' S, 144°54' E). The encounter call (Fig. 11) is also a pulse train, with a regular pulse rate (Hawel;

TABLE 7. Numbers of advertisement calls, intermediate (transitional) calls and squelching calls, and proportions of the latter (of all calls of that individual), produced by 21 males of *Crinia glauerti*.

Note that because of overlap with neighbours, calls of 4 individuals could not be analysed.

Site	Individual	Number of advertisement calls	Number of intermediate calls	Number of squelching calls	Proportion of squelching calls
1	1	30	0	3	0.091
2	1a	12	2	7	0.33
2	2	9	1	11	0.52
3	2	18	4	4	0.15
3	3	27	1	8	0.31
3	6	20	1	5	0.19
3	7	21	4	11	0.31
4	6	13	0	7	0.35
4	8	14	2	4	0.20
4	2	10	4	4	0.22
5	1a	18	2	12	0.38
5	2a	10	5	4	0.21
5	3a	15	6	4	0.16
5	4a	24	0	1	0.04
5	5a	9	0	6	0.40
5	6	0	10	15	0.60
5	1b	11	5	6	0.27
5	2b	9	3	22	0.65
5	3b	15	1	8	0.33
5	4b	16	6	11	0.33
5	5b	10	5	13	0.46

TABLE 8. Numbers and proportions of males of *Crinia glauerti* producing squeelching calls at each site.

Site	Number of males assessed	Number of males producing squeelching calls	Proportion of males producing squeelching calls
1	10	2	0.200
2	11	3	0.273
3	12	5	0.417
4	8	4	0.500
5	11	11	1.000

Littlejohn 1977). A waveform of an encounter call from Site 5 is presented in Fig. 11. Values for means and ranges from the original data for advertisement calls and evoked encounter calls of the same five individuals discussed by Littlejohn *et al.* (1985) are presented in Table 9.

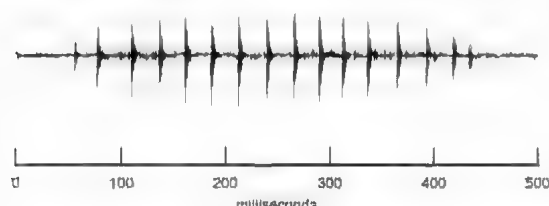


Fig. 11. Waveform of an encounter call of *C. signifera* (Reference: R408-9; Site 6; effective temperatures, wet-bulb air 11.3° C, water 12.5° C).

TABLE 9. Comparison of attributes of advertisement calls and encounter calls of *Crinia signifera* from Willowmavin Victoria (from data of Littlejohn *et al.* 1985).

Means and ranges (in parentheses) are given ($n = 5$). Data are not corrected for possible effects of temperature. Effective temperatures ranged from 10.7–13.2° C (mean = 12.04).

Attribute	Advertisement call	Encounter call
Duration (ms)	83 (56–108)	192 (179–210)
Pulses/note	4.2 (4–5)	17.8 (16–19)
Pulse rate (p s ⁻¹)	40.6 (30.8–53.7)	88.1 (74.2–100.1)
Upper dominant frequency (Hz)	3390 (3125–3642)	3217 (2825–3626)

Production of encounter calls by males of *C. signifera*

In a subjective evaluation during playback of the tape recordings of *C. signifera*, involving 53 individuals and some 3527 advertisement calls, three interactions, presumed to involve production of encounter calls, were noted. Otherwise, the recorded sequences of 47 individuals consisted only of advertisement calls.

Comparison of squeelching call of *C. glauerti* and territorial call of *C. signifera*

The variable-squeelching call of *C. glauerti* (Fig. 5, Table 6) is longer, contains more pulses, is of higher average pulse rate, and of higher dominant frequency than the territorial call of *C. signifera* (Fig. 11, Table 9). Even so, they are both pulse trains which are of similar carrier frequency but of longer duration, contain more pulses, and are of higher pulse rate than their respective advertisement calls (Fig. 3, Table 4).

Discussion

Structure of the advertisement calls of both species

The advertisement calls of both species are of similar structure, each consisting of a quasi-periodic pulse train. The pulses are short damped oscillations, each with a sharp attack and an exponential decay. There are more pulses in the calls of *C. glauerti*, and these are produced at a lower repetition rate. The frequency spectra are of similar shape, with most individuals having two peaks, the upper being attributed to the fundamental (= carrier frequency), while the lower is presumed to be produced as the side band of the envelope modulating frequency. The carrier frequency is higher in *C. glauerti*, and this may be correlated with the smaller size of males of this species – a usual characteristic of the calls of anurans (e.g. Robertson 1986). There is a trend of increasing pulse rate from north to south-east in the samples of *C. glauerti* and the durations are lower in the samples from Sites 4 and 5. Values for samples of the other two attributes display no obvious pattern.

Advertisement calls from Site 6 in the geographical isolate of *C. signifera* on lower Eyre Peninsula are longer and contain more pulses than those to the east in the main distribution of *C. signifera*. Thus the westernmost sample of *C. signifera* (from Site 6) is more similar to those of *C. glauerti* than are the others. The populations of *C. signifera* on Eyre Peninsula have probably been separated from the main distribution since the sea rose to its present level at the close of the last glacial period of the Pleistocene Epoch (from c. 12,000 to c. 6,000 years ago; see Littlejohn *et al.* 1993 for a summary and references) and this isolation may have contributed to the divergence.

Odendaal *et al.* (1986) recorded a sample of advertisement calls of *C. signifera* from the same location on Yellowman Creek (their Recording Site No. 5; our Site No. 7) and over a comparable range of effective (water) temperatures (10.8–12.2°C v. 9.2–11.2°C – this study). For all four attributes, however, their values are higher than those obtained in the present study. The use of other protocols and analytical techniques may account for some of the differences, but at this stage, no explanation can be offered.

Frequency of encounter calls in C. glauerti

More-recent observations by Littlejohn (unpub.) indicated that *C. glauerti* occurs in syntopy with *C. rubrinsignifera* (Littlejohn) near the eastern limit of its distribution (e.g. Site 5, Fig. 1). *Crinia rubrinsignifera* has an advertisement call that sounds like a “long low-pitched squech” (Littlejohn 1957, 1959). For two temporal attributes of the advertisement calls of 37 individuals of *C. rubrinsignifera*, corrected to an effective temperature of 10°C, the mean duration is 540 ms (range = 420–660), and the mean pulse rate is 174 (range = 129–210) (Littlejohn 1961). As these ranges overlap those of the squechling call of *C. glauerti* (Table 6), explanations other than reproductive character displacement must now be sought for the higher frequencies of occurrence of squechling calls in the south and south-east but none can be provided in present. Clearly, there is a need for further investigations, including playback experiments with advertisement calls and squechling calls as stimuli under controlled conditions. Such studies should be preceded by the documentation of frequency of occurrence of squechling calls in natural assemblages, and the context in which they are produced. The measurement of the sound pressure levels of calls of conspecific neighbours is also required so that the appropriate stimuli can be applied (Littlejohn *et al.* 1985). By varying the levels of stimulation, thresholds could then be determined and geographical patterns may be revealed.

Relationships of C. glauerti

From the presented data, it appears that the nearest populations of *C. glauerti* and *C. signifera* (Sites 5, 6) have the most similarly structured advertisement calls. The main difference between the calls of the two species is in carrier frequency which may be accounted for by the difference in sizes of the two taxa (Table 5, Fig. 10). The similarities in call structure are consistent with the postulated close relationship of the two taxa suggested by Main (1957), and subsequently supported by the multivariate numerical analyses of morphology and features of life history carried out by Blake (1973)

and Thompson (1981). Although consistent in showing a close association between them, molecular studies do not help in resolving the relationships of *C. glauerti* and *C. signifera*. The albumin immunological analysis of Daugherty and Maxson (1982) places *C. signifera* closest to *C. riparia* (15 ID units), followed by *C. glauerti* and *C. palmyrsignifera* (both 24 ID units) and *C. georgiana* (29 ID units). The cladistic analysis of allozymes carried out by Barendse (1984) offers several interpretations and appears inconclusive about the relationships: in one scenario *C. glauerti* and *C. signifera* are grouped with *C. georgiana*. Barendse (1984) did not include *C. riparia* in his study. Roberts & Watson (1993) have reviewed the recent literature on relationships within some groups of Australian frogs.

Three of the species of *Crinia* described since the work of Main (1957) – *C. bilingua* Martin, Tyler & Davies (Martin *et al.* 1980), *C. remota* Tyler & Parker (Tyler & Parker 1974) and *C. riparia* Littlejohn & Martin (Littlejohn & Martin 1965) – have clearly pulsatile advertisement calls. Tyler & Parker (1974) noted the similarity of the advertisement calls of *C. remota* and *C. glauerti*, but they did not provide information about the recording temperatures. As the recording of the call of *C. remota* was obtained at Morehead, Papua New Guinea in January, the ambient temperatures presumably were much higher than those applying to recordings analysed in the present study. Hence, a direct comparison cannot be made with the calls of *C. glauerti* obtained at temperatures of 13.1°C and lower. Blake (1973) noted that *Crinia riparia* lacks a tympanum and columella and placed the taxon into a different species group along with *C. tasmanensis* (Gunther). Because of the lack of a distinct tympanum in *C. remota* (Tyler & Parker 1974), it is suggested that there may not be a close relationship between this species and *C. glauerti*.

As the name indicates, the advertisement call of *C. bilingua* is strongly biphasic (Martin *et al.* 1980). In this species, males commence a calling sequence with short calls (<545 ms) of high pulse rate (>76 p s⁻¹), and then gradually change over to long calls (>580 ms) of low pulse rate (<54 p s⁻¹). Again, the high recording temperatures (wet-bulb air = 23.4–26.6°C) mean that it is not possible to make a proper comparison with the advertisement call of *C. glauerti*. Even so, the audiospectrogram of the short call appears to be similar to some of the variations in the squechling calls of *C. glauerti*. Martin *et al.* (1980) considered the functional significance of the two distinct calls of *C. bilingua* and raised the possibility that the short calls of higher pulse rate are mating calls, and that the long calls of lower pulse rate are territorial calls, the converse of the situation

for pulse rate in *C. signifera*. The long call of *C. bilingua* contains about twice as many pulses (>27) as in the advertisement call of *C. glauerti* (<16). If allowance is made for the difference in temperature (by using a Q_{10} of 2), the pulse rate of *C. bilingua* at 11°C would be about 20 p s $^{-1}$ and could overlap the pulse rates in the advertisement calls of *C. glauerti*. *Crinia bilingua* possesses a tympanum but possible close affinities with *C. glauerti* were not considered by Martin *et al.* (1980).

Acknowledgments

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of *C. signifera* from South Australia were obtained during the tenure of a research grant from the ARC, Number A 18831316 (1989). Some of the acoustic and statistical analyses, and preparation of parts of the manuscript, were carried out during the tenure of other grants from the ARC, Small grants Scheme (Grant Numbers SG 0935514, S 08917578) and the procedures that were developed have provided protocols for acoustic and statistical analytical techniques of wider application. Mrs P. G. Littlejohn assisted with recording at all of the sites in Western Australia and at two of the South Australian localities. Dr T. G. Littlejohn assisted with recording at the other two South Australian localities. Mr I. A. Smith, Western Australian Museum arranged for the curation of the preserved specimens and kindly made them available for subsequent examination and measurement during a subsequent visit. Dr M. J. Keough provided advice on statistical analyses and Dr H. C. Bennett-Clark provided an interpretation of the spectral and temporal structure of pulses in the advertisement calls.

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**THE BREEDING BIOLOGY AND
ADVERTISEMENT CALL OF LITORIA SPLENDIDA
TYLER, DAVIES & MARTIN**

By GRAEME F. WATSON & H. CARL GERHARDT†*

Summary

Watson, G. F. & Gerhardt, H. C. (1997) The breeding biology and advertisement call of *Litoria splendida* Tyler, Davies & Martin. Trans. R. Soc. S. Aust. 121(3), 119-124, 28 November, 1997.

Breeding biology and description of the advertisement call of *Litoria splendida* are presented. Analysis of a call of *L. caerulea* is also provided and shows that these similar, syntopic species have structurally similar calls and thus presumably show significant acoustic interactions in mixed choruses.

Key Words: *Litoria splendida*, *Litoria caerulea*, frogs, calls, breeding biology.

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Summary

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KEY WORDS: *Litoria splendida*, *Litoria caerulea*, frogs, calls, breeding biology.

Introduction

Litoria splendida Tyler, Davies & Martin, 1977, is one of the largest [adult body length 82–106 mm (Tyler 1992)] and most beautiful Australian frogs. The species is thought to be sparsely distributed throughout the widespread escarpment country of the Kimberley Division of northern Western Australia (Tyler 1992). *Litoria splendida* is notable for: hypertrophied parotoid and rostral glands (Tyler & Davies 1993), a characteristic it shares with senescent members of the closely related *Litoria caerulea*; an ability to utilize glandular secretions as a waterproof covering (Tyler & Davies 1993); and the production of pharmacologically active caerins in the skin secretions (Tyler & Davies 1993).

What little is known of the reproductive biology of *L. splendida* is based on reproduction by captive individuals (Tyler 1994). In an aquarium, a female laid 2000 eggs, depositing them in discrete clumps of up to 200 eggs, which Tyler (1992) has suggested may reflect an adaptation of females in the wild to lay batches of eggs in several temporary ponds to maximize the likelihood of at least some of the offspring surviving the larval stage. Maximum length of the tadpoles was 54 mm (Tyler 1992).

Litoria splendida is known to call, and presumably breed, after heavy rains in the early wet season (C. Done, Department of Conservation and Land Management Kununurra unpub. obs.). During the numerous field trips to the Kimberley Division undertaken by one of us (GFW) and colleagues from the University of Adelaide over the past 20 years, however, calls of the species have never been heard nor has breeding been observed. In fact, the species

is rarely encountered except when associated with artificial habitats, for example toilet blocks, where cool, moist sites are readily available (Tyler 1992).

During January, 1997, we visited the Kununurra area and encountered a breeding chorus of *L. splendida*. Here we describe the call of the species and provide brief notes on associated behaviour, and also a description of the call of syntopic *L. caerulea*, a phylogenetically closely related and ecologically similar species.

Methods

Recordings of calls of *L. splendida* were made using a Sony TCD-5PRO cassette recorder (tape speed 4.76 cm s⁻¹) and Beyer M-88 cardioid dynamic microphone. For comparative purposes, one call of a syntopic *L. caerulea* was obtained from a video sequence of the breeding chorus (Canon Digital camcorder, Hi 8 mm tape). Air wet-bulb temperatures (the effective temperature of frogs calling on land) were measured at the calling site of each individual using an electronic thermistor thermometer (Takara Digimulti Model D611). Recordings were analysed on a DSP 5500 digital Sona-Graph (Kay Elemetrics Corp.) using the in-built set-up #10 [sampling rate (samples sec⁻¹): 10240; frequency range: 4 kHz] with playback on a Nakamichi Dragon cassette recorder. Overall variations in tape speed (i.e. from recording to playback) are estimated at less than 0.5% and frequency responses of all audio-electronic components are close to linear within the relevant frequency range (based on manufacturers' specifications).

For each call, three primary attributes were determined: (i) duration, as the interval from the beginning of the first pulse to the end of the last pulse (ms); (ii) number of pulses per note (direct count), and (iii) dominant frequency (Hz), as the maximum

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value of the spectrum of power across the whole call. In addition, a derived characteristic, pulse repetition rate (pulses s^{-1}), was calculated as $1000/(n-1)$ pulses/duration in ms. Levels of resolution were less than 1 ms for temporal characteristics and less than 40 Hz for frequency.

Because there is no possibility of misidentifying these large and distinctive frogs and in the interests of their conservation, voucher specimens of recorded males were not taken. Video and 35-mm-photographic records of the calling males were obtained.

Results and Discussion

Breeding site and breeding behaviour

Breeding and calling were observed, following heavy afternoon rain, on the night of 18.i.1997 in an area of sandstone escarpment adjacent to a large, temporary pond near the main car park within the Hidden Valley National Park, Kununurra WA. The pond was formed within an ill-defined watercourse that ran along the base of the cliffs and was fed by run-off from a number of temporary waterfalls that flow down the cliff face after heavy rainfall. Occasional calls of males at other nearby sites were heard but chorus behaviour was confined to this one site. Four species of frogs, *Litoria splendida*, *L. caerulea*, *L. rubella* and *Limnodynastes ornatus*, were calling around the pond. Amplectant pairs of *L. splendida* and *L. caerulea* were observed in and around the pond. No pairs of the other two species were seen, although no exhaustive search was carried out. The foamy egg masses of *L. ornatus* were scattered over the pond as were large, floating, single-layered sheets of hyalid eggs, presumably those of *L. splendida* and *L. caerulea*, although we did not observe any pairs of either species depositing eggs. Nevertheless, contrary to the suggestion of Tyler (1992), on this occasion all *L. splendida* would, of necessity, have deposited their entire egg

complement in the one pond because no other aquatic habitats were available in the vicinity of the chorus.

Males of *L. splendida* called from exposed positions either on the near-vertical cliff face or on natural ledges upon the rocky surface. The two recorded males were calling approximately 1.5 and 2 m, respectively, above the pond. Several other individuals and amplectant pairs of *L. splendida* were observed in similar positions. Males of *L. caerulea* called from similar sites on the rock face as well as from elevated positions in surrounding trees and on the ground near the pond. *Litoria rubella* called from ground-level sites near the pond and *Limnodynastes ornatus* called whilst floating in the water.

Although we did not observe pair-formation or egg-laying, pairs of *L. splendida* can remain in the mating embrace for prolonged periods, at least up to 24 h. We observed several amplectant pairs sitting in the open, or in cliff-face crevices, throughout daylight hours before the night of chorus activity described above. Presumably these frogs had entered amplexus during the previous night.

Description of call

A wave-form display and spectrogram of the call of *L. splendida* are shown in Fig. 1. Table 1 lists the values of measured call attributes. The call is a long, pulsed and apparently well-tuned call that is regularly repeated (maximum call rate observed was 56 calls min^{-1}). The call is broad-band but has a tonal quality because its relatively high pulse rate (which exceeds the temporal resolution of the human auditory system and hence our ability to detect pulses at this rate) is perceived as a complex tone. The call is characterized by a very slow rise in amplitude with a rapid cut-off after maximum intensity is reached. The calls of both individuals displayed a number of frequency peaks in the power spectrum (Fig. 2, Table 1) with an inter-peak interval

TABLE 1. Summary of call attributes of *Litoria splendida* recorded in Hidden Valley National Park, Kununurra, Western Australia.

Values are based on analysis of five calls of two individuals. Frogs were calling on a sandstone cliff face between 1.5 and 2 m above a pond. Temperatures at the calling site were $A_{10} = 25.5^{\circ}C$ and $A_{18} = 25.1^{\circ}C$. Values for the first three attributes show the mean and range (in parentheses).

Individual	Call Duration (ms)	No. of Pulses	Pulse Repetition Rate (p s^{-1})	Dominant Frequency (Hz)	Other Notable Frequencies (Hz)
Call #1	666.4 (625-703)	82.8 (79-89)	122.8 (120.4-125.2)	1280	400, 520, 640, 780, 920, 1040, 1160, 1440, 1560, 1680
Call #2	710.6 (647-831)	82.2 (74-94)	141.5 (109.8-119.3)	1400	520, 640, 760, 880, 1000, 1260, 1520, 1640, 1760, 1880

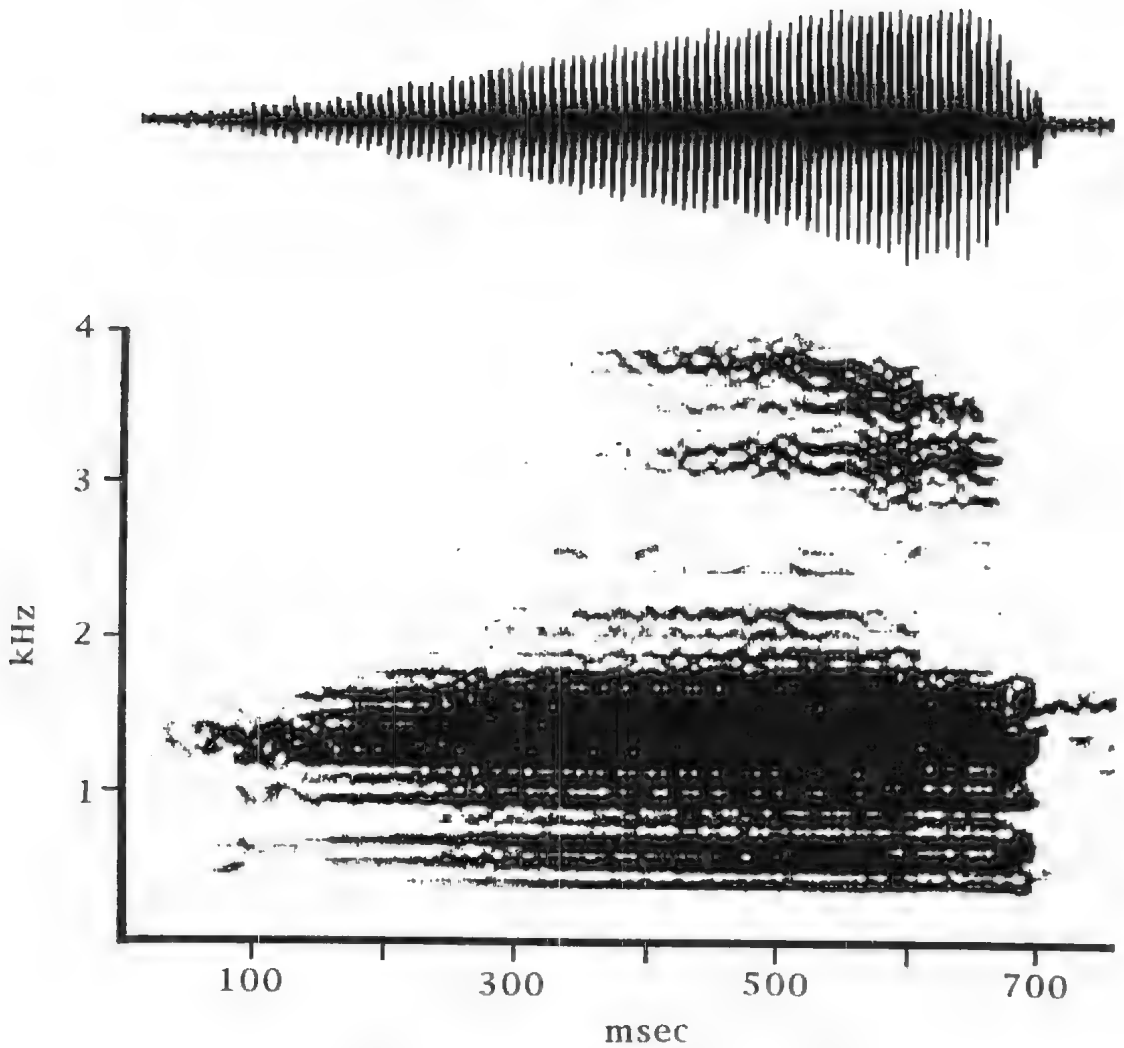


Fig. 1. Wave-form (upper) and audiospectrogram (lower) of the call of *Litoria splendida* recorded in Hidden Valley, Kununurra Western Australia. Wet-bulb air temperature at the calling site, 25.1° C. Note that the ordinate of the wave-form display is not labelled because it depicts a relative linear scale in volts. The apparent vertical discontinuity at around 600 ms on the audiospectrogram is an artifact of the printing process.

TABLE 2. Attributes of a representative call of *Litoria caerulea* recorded in Hidden Valley National Park, Kununurra Western Australia.

Temperatures at the calling site were $A_0 = 25.5^\circ \text{C}$ and $A_6 = 25.1^\circ \text{C}$.

Call Duration (ms)	No. of Pulses	Pulse Repetition Rate (p s ⁻¹)	Dominant Frequency (Hz)	Other Notable Frequencies (Hz)
210	32	147.6	1440	440, 580, 720, 1140, 1300, 1580

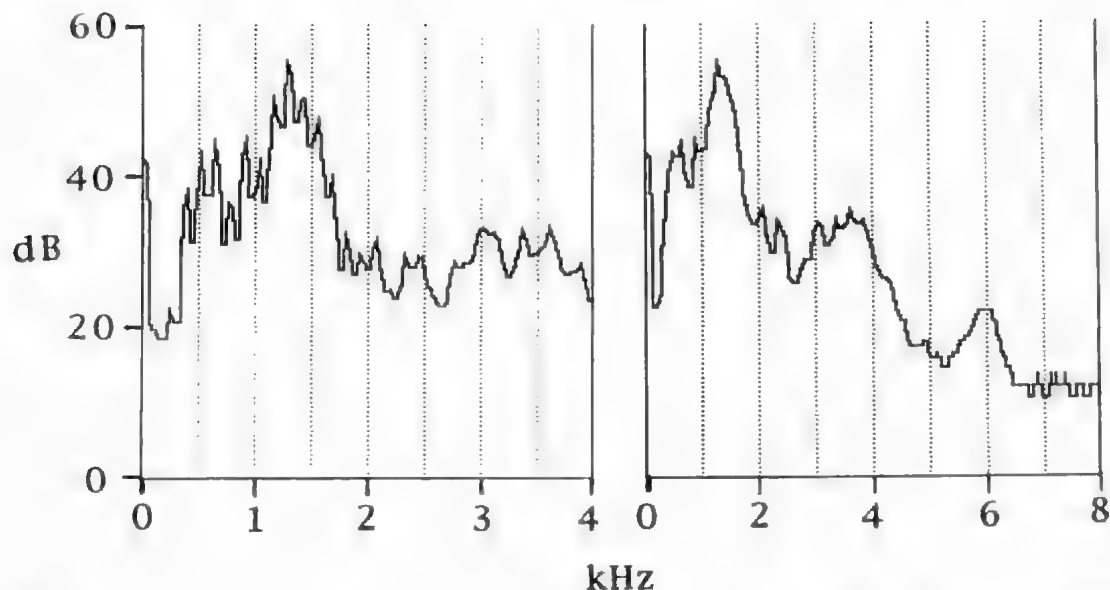


Fig. 2. Power spectra of the call of *Litoria splendida* across two ranges of frequency; 0–4 kHz, to show details of energy peaks and 0–8 kHz, to show that there is relatively little energy in the call above 4 kHz.

of approximately 120 Hz. Many of these frequency components result from amplitude modulation of a harmonic series generated by the vocal cords because the interval between components is nearly identical to the pulse repetition rate. Because of resonating and filtering characteristics of the sound-producing structures of the emitter, some of these frequency bands are emphasized, particularly those around 520 (the fundamental frequency of the call), 640, 900, 1280, 1420 and 1540 Hz (slight variations around modal values occur because frequency values are measured in 20 Hz steps on the digital sonograph). These spectral modifications make it difficult to determine confidently which components are part of the harmonic series and which are side bands arising from amplitude modulation. The frequency band with most energy (dominant frequency) differed between the two recorded males (1280 for male #1 and 1400 for male #2), with no within-individual variation (within the resolution of this analysis) found in the five calls of each male that were analysed. Although the call includes spectral energy peaks across a large frequency range (from around 500 to 4000 Hz), little energy is present above 4 kHz (Fig. 2).

Chorus structure

Although only three other species were calling in chorus with *L. splendida*, the chorus structure is of particular interest because the morphologically, behaviourally and ecologically similar species, *L.*

caerulea, was a conspicuous component (Fig. 3). Attributes of a representative call of syntopic *L. caerulea* are listed in Table 2 and a wave-form

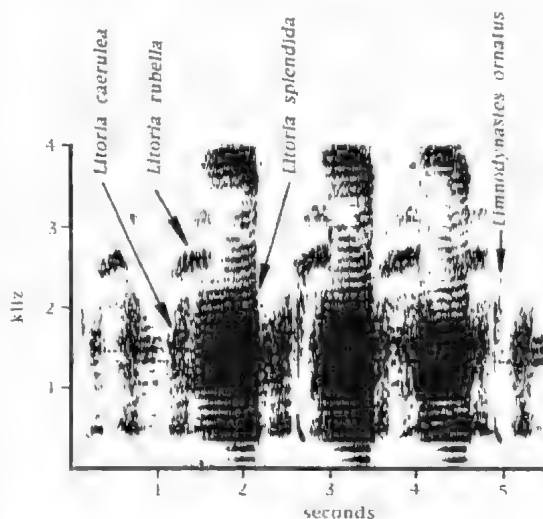


Fig. 3. Audiospectrogram of part of the chorus of four species recorded in Hidden Valley, Kununurra Western Australia. In this recording *Litoria splendida* has the loudest call, with background calls of *L. caerulea*, *L. rubella* and the very short call of *Limnodynastes ornatus*. Effective temperatures for calling males were: wet-bulb air temperature (*L. splendida*, *L. caerulea*; *L. rubella*), 25.1°C and water temperature (*L. ornatus*) 26.3°C.

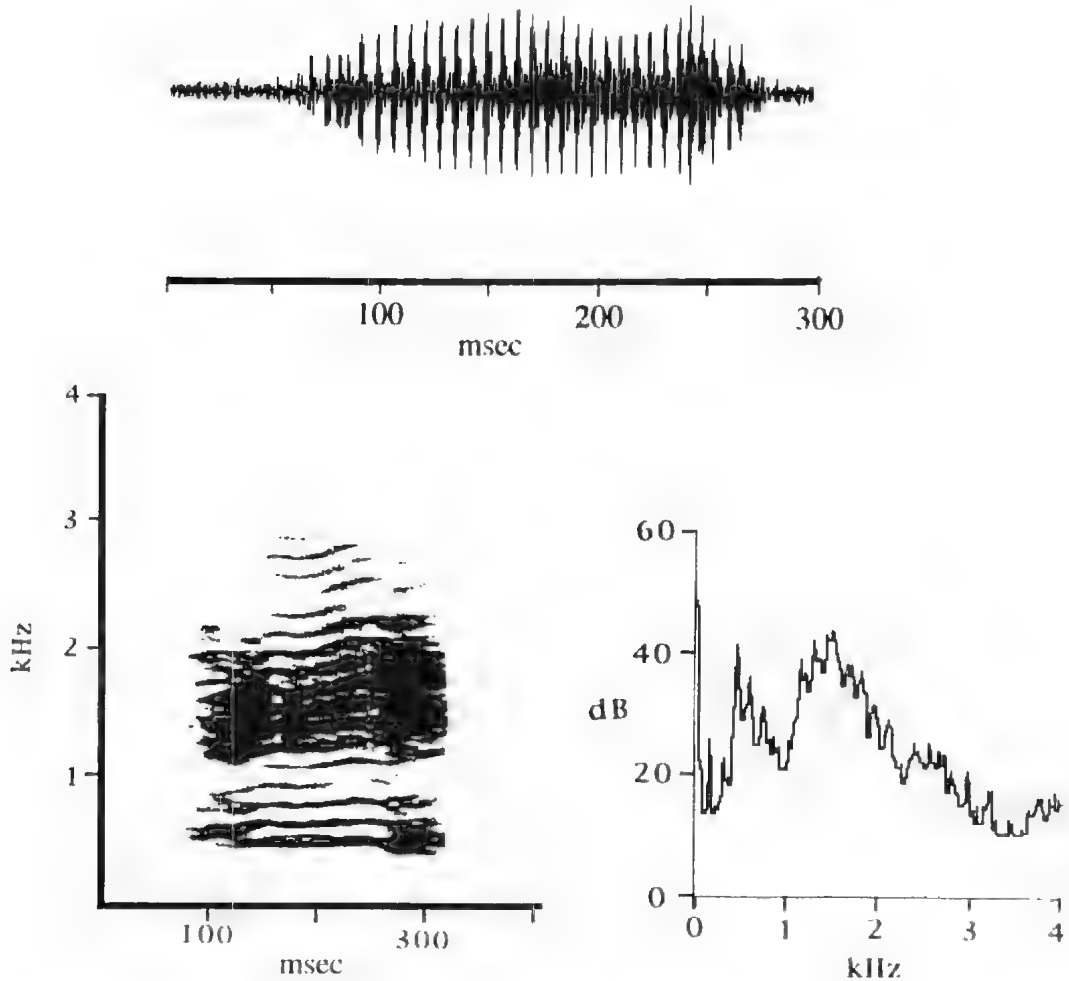


Fig. 4. Waveform, audiospectrogram and power spectrum of the call of *Litoria caerulea* recorded in Hidden Valley, Kununurra Western Australia. Wet-bulb air temperature at the calling site, 25.1° C. Note: (i) the different temporal scales on the wave-form and spectrographic displays; (ii) that the ordinate of the wave-form display is not labelled because it depicts a relative linear scale in volts.

display, spectrogram and power spectrum are shown in Fig. 4. The call has a similar dominant frequency and broad spread of peaks of energy as that of *L. splendida*, but it is considerably shorter, has fewer pulses, a much faster rise time and less abrupt cut-off, as well as a higher call repetition rate (130 calls min⁻¹). To the human ear, the call of *L. caerulea* has a harsher, less well-tuned quality. Nevertheless, because of the broad spectral overlap between these two large species and their use of similar calling positions there is the potential for significant acoustic interference between them.

Our observations of calling and breeding in *L.*

splendida do not support the previous speculation that this species breeds only in the early wet season. Although our observations were made in mid-January, the wet season of 1996-97 was well established, two cyclones/rain depressions having already passed over the Kununurra area in the preceding four weeks (pers. obs.). During our visit, heavy afternoon rains fell on most days and this stimulus appeared to trigger calling and breeding in *L. splendida*. Successful reproduction also requires a continuous aquatic habitat for larvae to complete their development and it is likely that *L. splendida* will successfully recruit new individuals to the

population only during wet seasons that have sufficient regular rainfalls to maintain temporary ponds. Although we have no information on the ultimate fate of larvae from the breeding episode reported here, it is likely that the pond in which breeding took place remained in existence for much of this season, which was marked by substantial and regular rainfall. This outcome contrasts with the calling and possible breeding reported by C. Done from a nearby site in Hidden Valley. When this site was visited by one of us (GFW) a short time afterwards, no free water was present and larval development would have been impossible. From this

experience of the unpredictable rainfall patterns of this area, even in the "wet" season, it is possible that successful reproduction in *L. splendida* is a relatively uncommon event.

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TRANSACTIONS OF THE

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SEA-LEVEL INDICATORS FROM A HOLOCENE, TIDE-DOMINATED COASTAL SUCCESSION, PORT PIRIE, SOUTH AUSTRALIA

BY *E. J. BARNETT**, *N. HARVEY**, *A. P. BELPERIO†* & *R. P. BOURMAN‡*

Summary

Barnett, E. J., Harvey, N., Belperio, A. P. & Bourman, R. P. (1997) Sea-Level indicators from a Holocene, tide-dominated coastal succession, Port Pirie, South Australia. *Trans. R. Soc. S. Aust.* 121(4), 125-135, 28 November, 1997.

Peritidal Holocene sediments at Port Pirie in the northern Spencer Gulf of South Australia contain several indicators of sea-level change over the last 7,000 years BP. The elevations of present subtidal, intertidal and supratidal environments and corresponding sediment facies were surveyed in order to establish critical boundaries relative to the tidal spectrum. The subtidal *Posidonia* facies occurs at or below mean low water spring (MLWS) tide; intertidal sandflat, mangrove and samphire facies occur over specific intervals between MLWS tide and mean high water spring (MHWS) tide. Each facies is clearly identifiable in the subsurface, with intertidal sandflat facies particularly characterised by in situ articulated bivalves *Anapella cycladae* and *Katelysia scalarina* or *K. peronii*. A combination of several palaeosea-level indicators from different tidal facies best defines local sea-level change over the millennial timescale.

Key Words: Holocene sea-level indicators, tidal zonation, prograding coastal sequence, facies boundaries.

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Summary

BARNETT, E. J., HARVEY, N., BELPERIO, A. P. & BOURMAN, R. P. (1997) Sea-Level indicators from a Holocene, tide dominated coastal succession, Port Pirie, South Australia *Trans. R. Soc. S. Aust.* **121**(4), 125-135, 28 November, 1997.

Peritidal Holocene sediments at Port Pirie in the northern Spencer Gulf of South Australia contain several indicators of sea-level change over the last 7,000 years BP. The elevations of present subtidal, intertidal and supratidal environments and corresponding sediment facies were surveyed in order to establish critical boundaries relative to the tidal spectrum. The subtidal *Posidonia* facies occurs at or below mean low water spring (MLWS) tide; intertidal sandflat, mangrove and samphire facies occur over specific intervals between MLWS tide and mean high water spring (MHWS) tide. Each facies is clearly identifiable in the subsurface with intertidal sandflat facies particularly characterised by *in situ* articulated bivalves *Anapelta cycladae* and *Katelysia scalarina* or *K. peronii*. A combination of several palaeosea-level indicators from different tidal facies best defines local sea-level change over the millennial timescale.

KEY WORDS: Holocene sea level indicators, tidal zonation, prograding coastal sequence, facies boundaries.

Introduction

Tide-dominated coastlines commonly generate prograding coastal sequences with excellent preservation of intertidal and shallow subtidal sedimentary facies (Belperio *et al.* 1988; de Boer *et al.* 1988; Fletcher *et al.* 1993). Such sequences can reveal high-resolution records of past sedimentation often containing a variety of palaeosea-level indicators (Ferwindt 1988). A thorough understanding of the relationships of present indicators and sea level, or inundation level, is required if correct interpretations of past relative sea levels are to be achieved. With critical appraisal of the present-day distribution of intertidal facies, flora and fauna, palaeosea level history from subsurface stratigraphy can be more confidently interpreted.

The northern Spencer Gulf, South Australia (Fig. 1), provides an excellent example of a wide, prograding coastal sequence in a mesotidal environment with an identifiable zonation of Holocene coastal depositional environments. A number of coastal studies has been conducted previously in this area (Firman 1965; Burne 1982; Burne & Colwell 1982; Belperio *et al.* 1984a,b, 1988; Gostin *et al.* 1984, 1988; Norrish *et al.* 1986).

In particular, Burne (1982) identified several important palaeosea-level indicators from beach ridges, the top of the subtidal *Posidonia* seagrass facies and base of the intertidal sandflat facies, and Belperio *et al.* (1984b) demonstrated the presence of a well-defined boundary between *Posidonia* seagrass and intertidal sandflat facies. Related stratigraphic studies in nearby Gulf St Vincent include those by Cunn & Gostin (1985), Belperio *et al.* (1986, 1988), and Belperio (1993, 1995). At Port Adelaide in Gulf St Vincent, Belperio (1993) confirmed that the boundary between the intertidal sandflat and mangrove facies was a reliable palaeosea-level indicator. From all these studies, it is apparent that there are local and regional differences in the reliability and distribution of various sea-level indicators. This paper provides a critical appraisal of the different palaeosea-level indicators in a mesotidal environment.

The wide prograding sedimentary sequence of the northern Spencer Gulf region, which forms the apex of a large relatively shallow inverse (or negative) estuary, is a direct response to the modern coastal environment. Warm temperatures and low rainfall in the region promote high rates of evaporation and salinities which are often higher than average for seawater, in excess of 40‰ and as much as 48‰ (Bye 1981; Nunes & Lennon 1986). Seawater temperatures for the northern gulf vary typically between 12° and 24°C (Nunes & Lennon 1986). The tides are mostly semi-diurnal, with spring and neap tidal ranges at Port Pirie of 3.5 m and 0.4 m, respectively. Due to the length of the gulf and relatively slow mean sea-level oscillations, wind stress can further increase the astronomical tide

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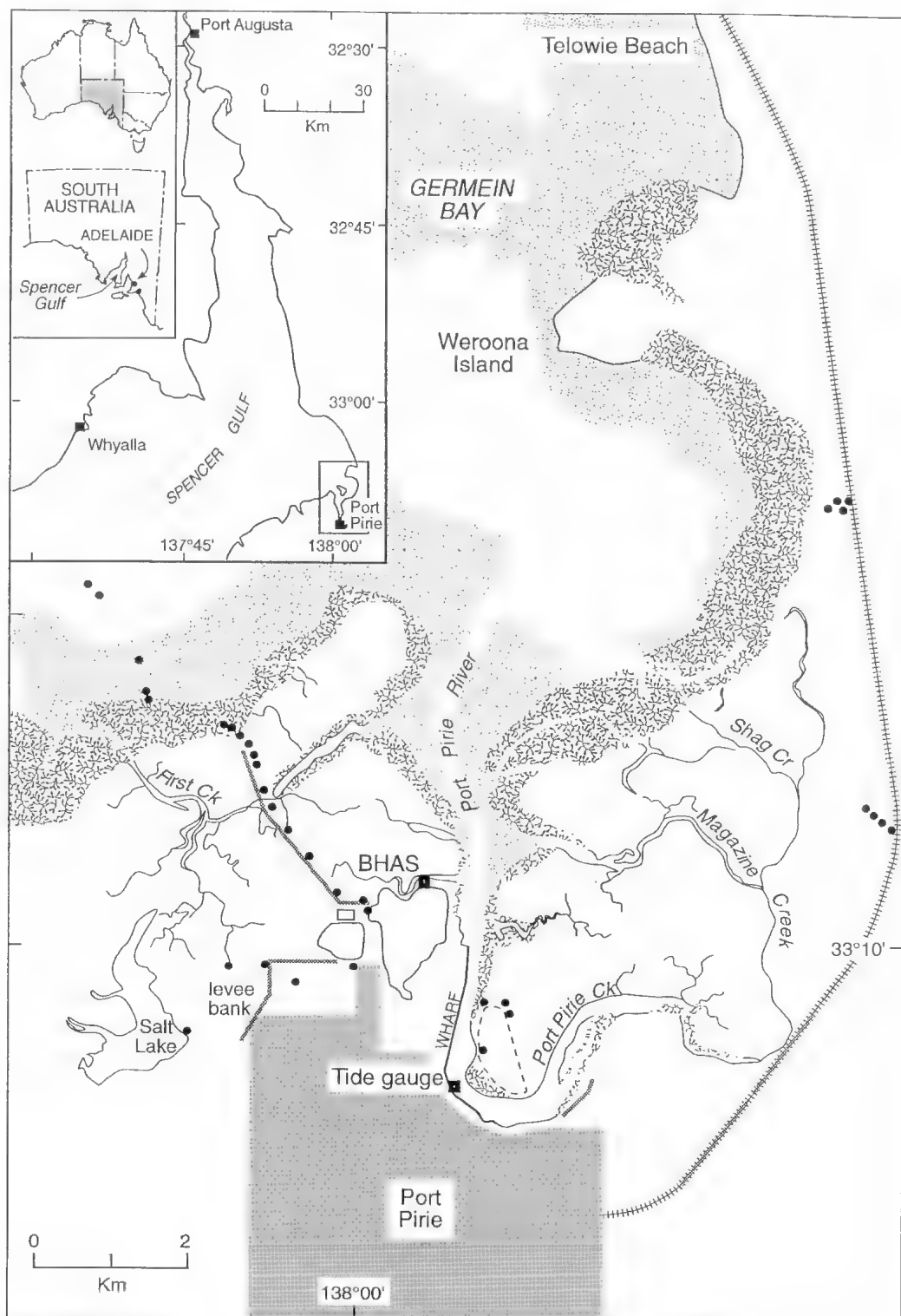


Fig. 1. Location diagram of the study area in the upper Spencer Gulf, South Australia, showing the Port Pirie coastal zone, sampling sites marked by infilled circles, the tide gauge and Broken Hill Associated Smelters (BHAS).

significantly. In Spencer Gulf and much of the southern coast of Australia (Nunes & Lennon 1986), there is a large spring-neap tidal modulation due to the nearly equal lunar and solar semidiurnal constituents causing a double tide once every fortnight when little tidal variation occurs. Schlüter *et al.* (1995) have postulated that this similar amplitude of the major semi-diurnal tidal constituents gives rise to particular shallow water tidal interactions in the upper gulf, which promote samphire and mangrove colonisation.

Given the prograding tidal sequence and the close proximity of a tide gauge with reliable long-term records at Port Pirie, this study was undertaken to determine the elevations of coastal sedimentary zones relative to modern sea level and to identify appropriate modern sediments as analogues of subsurface Holocene sedimentary facies. This approach provides an opportunity to identify the most reliable palaeosea-level indicators in a mesotidal environment; and to develop a methodology for subsequent studies of relative land/sea movements at sites where historic tidal data exist. The study is unique in that it highlights a number of sedimentary facies, surveyed relative to modern sea level, and identifies critical equivalent indicators in the geological record. It does not depend on one indicator in isolation, but uses a suite of subtidal to supratidal indicators to identify sea-level change.

Methods

It was necessary to survey the modern coastal environments in detail to establish elevation differences of the tidal zones relative to local tidal datum. This was done using both laser and automatic spirit levelling instruments. The first had an error of less than 1 cm over 200 m, and measurements were kept to within 400 m (i.e. ± 0.02 m). Using spirit levelling, the distance between each reading was less than 100 m, which generally kept vertical measurement errors to less than ± 0.01 m. Land-based sites within the sandflat, mangrove and samphire zones were surveyed to third-order Australian Height Datum (AHD) benchmarks. The surveying was conducted mostly in the Port Pirie coastal vicinity as well as further to the northeast within the Telowie Beach coastal region, in order to access all of the modern-day tidal settings (Fig. 1). The present-day levels of the seagrass and sandflat zones at Port Pirie were measured from water levels relative to the Port Pirie tide gauge. At Port Pirie, zero tidal datum (TD) is correlated with the lowest astronomical tide and related to AHD using a correction of 1.933 m (surveyed 17.03.1983; South Australia Ports Authority). Sea-level indicators

including seagrass, shell and mangrove remains within and at the top of each tidal zone were identified and recorded for later comparison with subsurface equivalents.

In order to establish and sample the subsurface stratigraphy, a total of thirty-five sites was selected within the broad coastal flats of Port Pirie (Fig. 1). A vibrocorer was used to obtain cores 75 mm in diameter and up to 4 m in depth. All of the vibrocores were corrected for sediment compaction by recording penetration depth versus core recovery length and applying a correction factor to the thickness of the sediments. Coring peripheral to and within mangrove woodlands was carried out using a peat auger. A back-hoe was used to excavate sediments in the supratidal region. Using this method, no correction for sampling compaction was necessary. Surface and subsurface elevations in land-based cores and excavations were surveyed to AHD. Marine-based cores were surveyed to TD and taken within a few kilometres of the tide gauge to reduce the effects of tidal lag and meteorological conditions. Samples were taken back to the laboratory, where the sediments were logged with particular attention being given to the elevations of facies boundaries and the presence of sea-level indicators.

Modern depositional tidal environments in the Port Pirie area

The coastal environment adjacent to Port Pirie (Fig. 2) is a tidally-dominated lowland. Subtidal, intertidal and supratidal zones were distinguished by the extent of marine influence or exposure and by their vegetation assemblages and sedimentary facies. Broad, shallow subtidal seagrass meadows pass laterally shoreward into intertidal sandflats, mangrove woodlands, samphire-algal marshes and supratidal evaporite flat environments. This association of peritidal environments and their vegetation zones has, to a large extent, controlled the successive development of the coastal plain around Port Pirie. A schematic summary of the tidal zones, associated vegetation and their relationships to elevation or inundation levels is given in Figure 3.

The subtidal zone

In the broad, shallow-marine environment northwest of Port Pirie township, seagrass meadows composed largely of *Posidonia australis* grow from around mean low water spring (MLWS) tide level (zero TD) to 10 m below TD (Figs 3, 4). *Posidonia australis* can only survive limited periods of emergence so that, at its upper growth limit, it is generally patchy and restricted to below 0.25 m TD. At depths below 4 m TD, *Posidonia sinuosa* dominates the seagrass assemblage, *Posidonia* leaf

sheaths and rhizomes are resistant to decomposition, and seagrass fibres become incorporated into and bind sediments. A highly distinctive sediment facies results, producing calcareous mud and sand bound by masses of pale cellulose fibre. High sediment production and the binding and baffling action of seagrass contribute to the rapid accumulation of sediments in this environment.

The intertidal zone

The region extending from MLWS tide to mean high water spring (MHWS) tide is defined as the intertidal zone (Fig. 3). This zone is characterised by periodic emergence and inundation during neap to spring high tides. At their most seaward boundary, broad sandflats have developed upon which some

seagrasses can grow above MLWS, *Posidonia australis* struggles to survive and is replaced by *Zostera muelleri*. Further shoreward, bare sandflats are dominant. These sandflats are host to numerous epibenthic organisms including the intertidal molluscs *Batillaria* sp., *Veneridae* sp., *Tellina* sp., *Clanculus* sp., *Anapella cycladae* and *Katelysia scalarina* or *K. peronii* and foraminifera that live on and beneath the sandflat surface. These organisms occasionally accumulate in shallow tidal channels.

Intertidal sandflats are replaced by mangrove woodlands above 1.32 m TD. Only one species of mangrove, *Avicennia marina* var. *resinifera*, has been recorded growing in South Australia (Butler *et al.* 1977; Gostin *et al.* 1984; Cann & Gostin 1985) (Fig. 5). Around Port Pirie, mangroves have formed dense



Fig. 2. Aerial photograph of the Port Pirie coastal zone. The subtidal and intertidal sandflats have been colonised by seagrasses (seagrass meadows). Further inshore, mangroves form dense woodlands along the coastal margin and grow along dendritic tidal channels. Samphire communities occur more landward in the intertidal to supratidal zone. In the supratidal zone, the vegetation cover is sparse in between broad expanses of saltpans. The photograph covers an area approximately 10 km x 10 km. The aerial photograph has been reproduced with the permission of the Department of Natural Resources, South Australia. Mapland, telephone (08) 8226 4946.

communities within clearly defined tidal limits. While the lower limit of mangroves is close to mean sea level (1.75 m TD at Port Pirie), their actual lower limit, 1.32 m TD at Port Pirie, can be significantly different. Their distribution is controlled fundamentally by their root system since the vertically protruding pneumatophores require both exposure to air and flushing of precipitated salts (Chapman 1975). A mangrove-algal association occurs at seaward levels of mangrove growth and along exposed tidal channels. Cyanobacterial mats also extend on to wide sandflats and into samphire areas in intertidal and supratidal zones. Numerous other organisms are associated with mangrove

woodlands, including the small mud crab, *Helice haswellianus*, which burrows into the substrate and promotes oxidation of the upper sediments. Gastropods, bivalves, polychaetes, decapods and other crustaceans, foraminifera and diatoms also occupy this zone.

Landward of the mangroves at elevations above 2.6 m TD, are broad, flat, gently undulating plains upon which samphire-algal communities grow (Fig. 6). *Sarcocornia quinqueflora*, *Sclerostegia arbuscula*, *Halosarcia halocnemoides* and *Suaeda australis* are the main samphire communities present in the Port Pirie environment, followed by minor occurrences of *Maireana oppositifolia* and

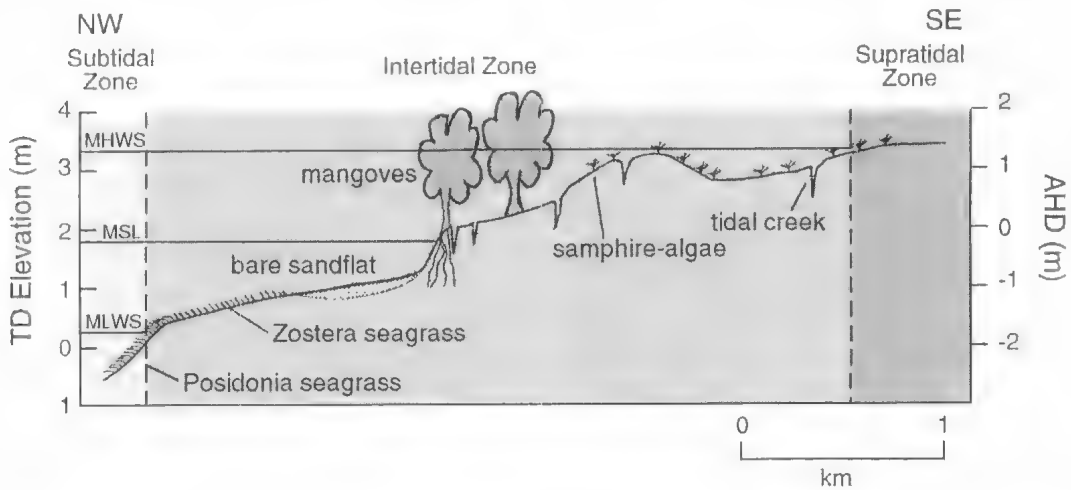


Fig. 3. Present tidal and vegetation zonation along core transect relative to the Port Pirie tidal datum (TD) and Australian Height Datum (AHD). MLWS - mean low water spring tide; MSL - mean sea level; MHWS - mean high water spring tide

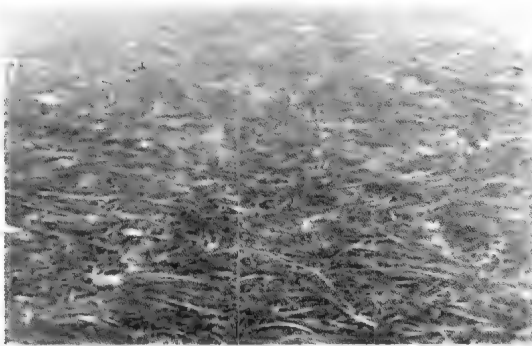


Fig. 4. Shallowly submerged seagrass meadow of *Posidonia australis* in the subtidal zone photographed during low tide. Width of field approximately 3 m.



Fig. 5. Landward intertidal mangrove margin with intertidal samphire communities. Only one species of mangrove, *Avicennia marina* var. *resinifera*, grows in this southern temperate latitude. Dieback of mature trees along the landward margin can be observed, which generally indicates marine regression. The dead mangrove in left centre of the photograph is approximately 1.2 m tall.

Halosarcia indica toward the supratidal margin.

The supratidal zone

Above MHWs tide elevation (3.2 m TD), the supratidal zone (Fig. 3) is flooded on only the few occasions when either high or king tides combine with storm surge activity, predominantly from the southwest, or during and shortly after extended periods of rainfall. Consequently, this zone is dominated by evaporative processes and their associated sediments. In some ponded areas, algal mats are well established and form cyanobacteria flats. Although this region consists mainly of bare, poorly draining saline and gypsiferous flats, some samphires and saltbushes survive (Fig. 7). Of these, *Halosarcia halconemoides*, *Atriplex paludosa*, *Halosarcia indica* and *Atriplex vesicaria* are most abundant. Within this zone, variations in elevation are created by aeolian deflation and formation of gypsiferous dunes between remnant tidal channels.

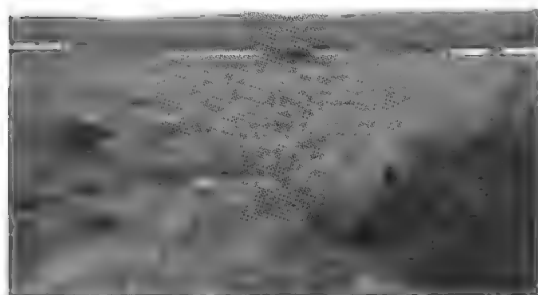


Fig. 6. Intertidal samphire zone including *Sarcocornia quinqueflora*, *Sclerostegia arbuscula*, *Halosarcia halconemoides* and *Suaeda australis*. The mangrove in the right foreground is approximately 2 m high and the samphire bushes are up to 30 cm in height.



Fig. 7. Supratidal samphire zone including occasional *Halosarcia halconemoides*, *Atriplex paludosa*, *Halosarcia indica* and *Atriplex vesicaria* and bare expanses of salt flat. The samphire species are up to 30 cm in height.

Lunettes have also formed on the leeward margins of sabkha flats or salt lakes.

The distribution of coastal environments around Port Pirie is shown in Figure 8. Six distinctive tidal zones transecting the coast have been identified. From seaward to landward, these are: i) subtidal seagrass meadows (not shown in figure), ii) low intertidal bare or *Zostera*-covered sandflats, iii) intertidal mangrove woodlands, iv) high intertidal samphire-algal marshes, v) supratidal evaporative flats, and vi) supratidal and extratidal clay and gypsiferous dunes and lunettes. Aerial photographic interpretation of the mangrove woodland reveals that only minor change in its distribution is apparent for the last 40 years or so (1957-1993). Mangroves have prograded seaward into intertidal seagrass/sandflat areas on the northwest peninsula of the Port Pirie River, between First and Second Creek and along the margins of the Port Pirie River itself. This is in contrast to rapid seaward mangrove colonisation that has occurred at Port Gawler (Cann & Gostin 1985) and landward colonisation in the Port Adelaide region (Burton 1982; Belperio 1993).

Evidence of depositional tidal sediments in the subsurface

Much of the sedimentary stratigraphy at Port Pirie represents aggradation and progradation of sediments in peritidal environments since the near stabilisation and slight fall in sea level from 7,000 years BP to present (Belperio 1995). Holocene sediments and Pleistocene alluvial sediments of the Pooraka Formation underlie most of the area, forming an undulating boundary with the overlying tidal sequence. In some places, the upper sections of the Pooraka Formation show evidence of being altered or gleyed by marine porewaters. The coastal sediments record an upward change in sediment facies that corresponds with the lateral change in the tidal zones.

The subtidal *Posidonia* facies is the most extensive Holocene tidal facies in the region. It consists of mostly grey, poorly sorted terrigenous and calcareous sandy mud, with numerous fibres of *Posidonia australis* and fragmentary molluscs (e.g. *Spisula* sp., *Phasianella* sp., *Cantharidus* sp., *Dorsinia* sp. and *Batillaria* sp.) and foraminifera. Its thickness varies from greater than 4 m in the present subtidal zone but thins inland underlying intertidal and supratidal sediments to between 0 and 2 m, depending on undulations in the surface of the underlying Pooraka Formation. The landward extent of this facies indicates that much of the present coastal environment was a shallow marine environment during the early to mid Holocene.

The intertidal sandflat facies is a grey to light grey,

poorly sorted, terrigenous and calcareous shelly muddy sand. It occurs extensively inland beneath much of the study area having developed in response to upward shoaling of the subtidal sedimentary environment. In most of the Port Pirie region, the intertidal sandflat facies is overlain by samphire facies. This is in contrast to the present-day tidal zonation where a transition from sandflat to mangrove woodland generally occurs.

The intertidal mangrove facies consists of brown or bluish grey, mostly noncalcareous sediments with fragments of roots, sheaths and fibres. It is largely restricted to the present-day distribution of mangrove woodlands, i.e. progradational development and preservation of strata have been limited and *Avicennia marina* var. *resinifera* woodlands appear to have developed in relatively recent times. Where it is undeveloped, modern mangrove roots penetrate into the underlying facies.

The sediment facies of the samphire flat forms a thin veneer over extensive areas of sandflat facies of the coastal plain. It consists of pale brown to light

grey, often mottled calcareous and terrigenous clay-rich muds with occasional small gastropods, bivalves and foraminifera. Small plant fibres and thin tubular roots are apparent in some regions but absent in others, depending on whether plant matter was originally present and/or preserved. Gypsum content is variable, due largely to elevation and evaporation history, with gypsarenite dune sediments preserved at the highest elevations of the supratidal zone. There is little distinction between intertidal and supratidal samphire sediment facies, and the two are considered to form a single unit. While particular samphire species can be identified growing in either the intertidal or supratidal zone, in the subsurface, samphire rootlets and remains cannot be identified to species level.

In addition to the sediment facies above, several microenvironments or subfacies occur in the region that have contemporary analogues. In particular, pockets of cyanobacterial facies are evident throughout the intertidal to supratidal zones. Wherever cyanobacterial mats are present in the

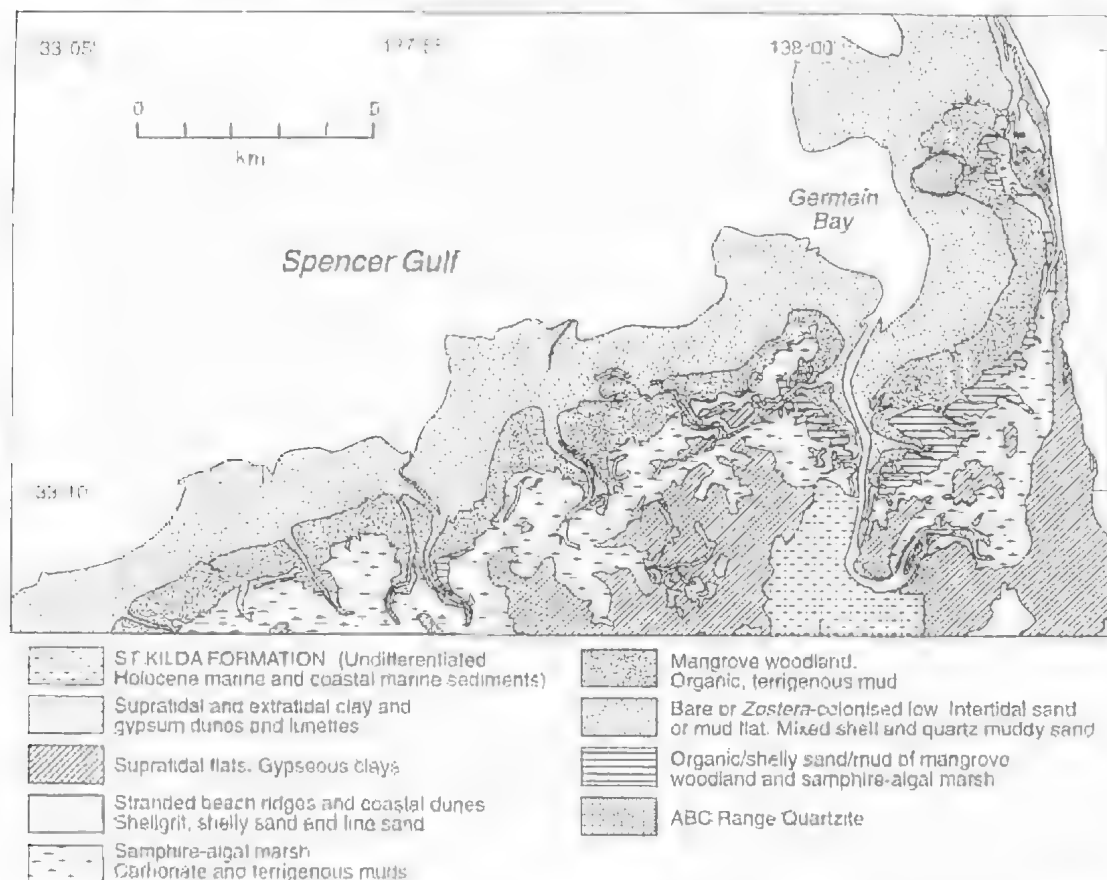


Fig. 8 Coastal geology map of the Port Pirie area compiled from the South Australian Geology Database: Mineral and Energy Resources South Australia.

intertidal or supratidal zone there are active sites of sediment aggradation. In the intertidal zone, storm ridge facies, or cheniers when developed over muddy sediments, have been formed during periods of combined high or king tides and storm events. Ridges are generally aligned parallel to the shoreline. Only one storm ridge is preserved in the western Port Pirie area, although several others occur to the east. The northerly orientation of the coastline generally protects the area from dominant southeasterly storm-ridge forming events.

Palaeosea-level indicators

The special significance of the northern Spencer Gulf is that the peritidal coastal succession contains a well-preserved record of palaeosea-level change. The sediments include various palaeosea-level indicators that have been used, with appropriate elevation data, to reconstruct palaeosea-levels. Although present-day tidal environments and equivalent sediment facies may range over significant vertical elevations, the contact between each sediment facies is generally more restricted. Subsurface facies contacts can provide relatively precise estimates of palaeosea-levels, given accurate

surveying of the vertical extent of present sedimentary facies and their contacts. Once the elevation range of a particular sedimentary contact is known, a height correction for that contact can be made relative to present sea level. This establishes the elevation at the time of deposition and indicates whether sea level has subsequently risen or fallen.

We have established that, in the Port Pirie area, the boundary between *Posidonia* facies and overlying shelly intertidal sandflat facies provides a palaeosea-level datum corresponding to an upper limit of 0.25 ± 0.25 m TD (Fig. 9). Consequently, the subsurface occurrence of distinctive, massed, fibrous *Posidonia* facies in land-based sediments at elevations higher than 0.25 ± 0.25 m TD implies that relative sea level was previously higher than at present.

In a similar fashion, the intertidal sandflat facies generally occurs between 0.25 and 2.2 m TD relative to present-day sea level. However, a more precise palaeosea-level estimate is provided by the sharp contact between intertidal sandflat facies and overlying mangrove facies that equates to 1.32 ± 0.2 m TD (Fig. 9). At Port Pirie, the mangrove facies mostly occurs directly beneath the present mangrove woodland, and confidence in using its contact with the top of the sandflat facies is greatest where

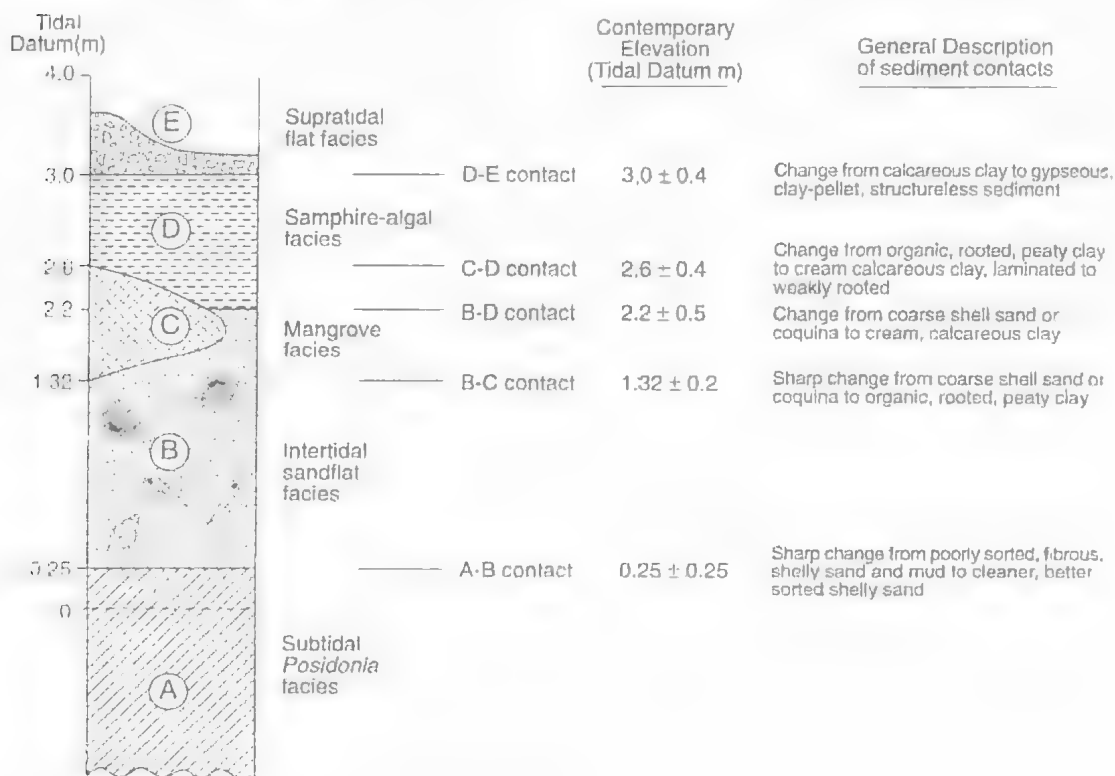


Fig. 9. Palaeosea-level criteria for the Port Pirie coastal region

massed articulated valves of *Anapella cycladina* and *Katelysia scalaris* or *K. peronii* are present, indicating *in situ* post-mortem preservation. Where the mangrove facies is absent, the contact between the sandflat and samphire facies is also sharp, although the present-day boundary between the intertidal sandflat and samphire zones is not well defined in the immediate vicinity of Port Pirie. The upper limit of the sandflat facies with samphire facies occurs around 2.2 ± 0.5 m TD (Fig. 9).

While the present Port Pirie tidal zones exhibit a transition from mangrove woodlands to samphire marshes at 2.6 ± 0.4 m TD, this is not commonly observed in the subsurface sediments due to the lack of progradational development of this stratigraphic horizon. Consequently, the level at which the samphire facies occurs in the subsurface provides only an approximate estimate of palaeosea-level relative to its present elevation range of 2.2 to 3.0 m TD. Although different samphire species are closely related to small elevation changes, these are not observed at the macro-level in the subsurface.

Discussion

Several factors must be addressed when interpreting the evidence for palaeosea-level change from prograding peritidal sequences. In particular, the relationship of each indicator to sea level at the time of its formation must be established. At Port Pirie, the subsurface presence of *in situ* fibrous remains of the seagrass *Posidonia australis* indicates that sea level was above this site at the time of deposition. The transition between *Posidonia* facies and overlying intertidal sandflat facies is a more powerful indicator of palaeosea-level, corresponding to 0.25 ± 0.25 m present-day TD. Similarly, mangroves grow within a fairly broad intertidal range, but their contact with the intertidal sandflat facies provides a datum of 1.32 ± 0.2 m. Mangroves have previously been cited as one of the more reliable fixed, *in situ* palaeosea-level indicators (Hopley & Thom 1983; Thom & Roy 1983). For northern Spencer Gulf, Burne (1982) reported a range in the elevation of seaward mangrove colonisation from 1.5 to 2.9 m TD (-0.4 to 1.0 m AHD) and as previously mentioned, we record a lower level of mangrove colonisation at 1.32 ± 0.2 m TD. Clearly, the level of seaward colonisation of mangroves depends primarily on local coastal dynamics or coastal orientation, and will occur at a variety of elevations relative to the tidal spectrum (Allen 1995). Therefore, it follows that the height of the contact between sandflat and mangrove facies will also vary. It is apparent from the differences in elevation that the use of mangroves as palaeosea-level indicators can only be applied locally, where

present-day elevations of mangrove seaward growth are well defined. Even in this case, the palaeoenvironment may have differed from the modern environment, producing different tidal ranges and mangrove distributions.

The boundary between sandflat and either mangrove or samphire facies has the potential to define palaeosea-level, particularly since its contact in the subsurface is sharp. However, the conundrum at Port Pirie is that while the present-day zonation from sandflat to mangrove woodland is extensive, this transition is not easily observed in the subsurface. Furthermore, while the present-day transition between sandflat and samphire zones is not well represented at Port Pirie, this contact in subsurface sediments is widespread. Near Port Pirie, the present elevation of the sandflat/samphire boundary is 2.2 ± 0.5 m TD. To the northeast at Telowie Beach, this boundary occurs at 2.5 ± 0.3 m TD, a slightly higher elevation than for Port Pirie possibly due to local geomorphic factors and sedimentary processes in the lee of Weeroona Island (Fig. 1). The elevation of the top of the sandflat varies depending on whether it is succeeded by mangroves or samphire. Thus, although the contact can be used as a determinant of sea-level change, there is a wide range in its elevation. This problem may be minimised by careful field surveying of the local region.

Beach ridges and the top of *Posidonia* seagrass deposits are relatively good indicators of palaeosea-levels. However, as with mangroves, beach ridge elevation data cannot be used on a regional basis since the elevations to which such ridges are constructed are highly dependent on local wave regimes. In regard to seagrass as a sea-level indicator, *Posidonia australis* presently grows to 0.25 m TD (-1.68 m AHD) at Port Pirie, but elsewhere in northern Spencer Gulf, an elevation of -0.1 m TD (-2 m AHD) has been observed (Burne 1982). These differences may be best explained by varying coastal orientation, wave regime and coastal circulation patterns. Although a shore-parallel zonation of sediments and vegetation is common throughout the northern gulf, each sediment and floral or faunal community, whether *Posidonia*-dominated seagrasses, *Anapella* or *Katelysia* sp. bivalves, mangroves or halophytes and saltbushes, has a broad regional range in elevation. Hence, it is imperative that local elevation controls and local conditions be used in assessing sea-level data rather than applying regional values.

Given that the elevation range of tidal facies and sea-level indicators can vary, greater accuracy in reconstruction of palaeosea-level is achieved if several different indicators are used. Each indicator, either relational or fixed, will provide evidence that either supports or challenges indicators from other

horizons. By using such an approach, some of the problems associated with tidal indicators, the elevations of which are influenced by local geomorphic and climatic variations, may be reduced. This study indicates that a combination of palaeosea-level indicators from the top of the *Posidonia* facies and the contact between sandflat and either mangrove or samphire facies is the most reliable method for establishing sea-level change in the Port Pirie area.

A further factor to consider in the reconstruction of palaeosea-levels is whether tectonic activity or subsidence, due to sediment compaction, has occurred subsequent to deposition. There is little evidence of local tectonism in the northern Spencer Gulf during the Holocene, but rather, the region has been uplifted in response to isostatic adjustment of the Earth's crust due to eustatic sea-level rise (Belperio 1995). The effects of sediment compaction in the region are less clear. While little compaction has most probably occurred in either the thin veneer of samphire facies or within the sandflat facies, it is feasible that the extensive, muddy, *Posidonia* facies has undergone some compaction. If this has occurred, it would affect elevation corrections relative to present sea level, acting to decrease the apparent height of former palaeosea-levels.

Conclusions

The tide-dominated coastal plain around Port Pirie has resulted from sediment aggradation, coastal progradation and relative sea-level regression associated with slight sea-level fall following stabilisation around 7,000 years BP. It consists predominantly of subtidal *Posidonia* and intertidal sandflat facies. These facies occur throughout the coastal stratigraphy and underlie present-day intertidal mangrove and supratidal samphire zones.

A tidal-vegetation-sediment relationship exists for each of the Holocene facies deposited within the coastal zone. In the upper subtidal zone, *Posidonia australis* dominates the seagrass community and binds the sediment. The intertidal zone is composed of bare or *Zostera*-covered sandflats that are replaced by *Avicennia marina* var. *resinifera* toward the shore. Further landward in the intertidal to supratidal samphire zone, *Halosarcia*, *Sarcocornia* and *Atriplex* communities have become established in between sabkha-like, bare supratidal flats. Associated cyanobacterial mats grow within

mangrove, samphire and supratidal environments.

For each sediment facies, biological palaeosea-level indicators are defined by their growth positions in relation to the tide. At Port Pirie, *Posidonia australis* represents the subtidal environment from just above mean low water spring (MLWS) tide (0.25 ± 0.25 m TD) to depths greater than 4 m TD. *In situ* articulated shells such as *Anapella cycladae* and *Katelysia scalarina* or *K. peronii* are representative of the intertidal sandflat environment from 0.25 ± 0.25 m to 1.32 ± 0.5 m TD, and mangrove facies represent deposition between 1.32 ± 0.2 and 2.6 ± 0.4 m TD.

Good precision in palaeosea-level interpretation can be obtained from peritidal sediments that reveal clear and consistent transitions and contacts from one facies to another. This study has established that the transition from *Posidonia* to sandflat facies and the sharp contact between sandflat and mangrove facies are the best palaeosea-level indicators in this environment. The contact between the sandflat and samphire facies can also be used to establish sea-level change, although only in areas where its present elevation can be established. Dangers are apparent in the broader, regional use of facies boundaries due to the often patchy and variable development of different facies along the coast.

The use of tidally-dominated sediment contacts as palaeosea-level indicators depends primarily on an accurate determination of their present-day elevation ranges relative to tidal datum. Our research has demonstrated that in order best to define palaeosea-level, fieldwork must be carried out at the local scale and take into account coastal processes that have been operating over the long or short-term in the region.

Acknowledgments

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**THE RESPONSE OF GALL-INDUCING SCALE INSECTS
(HEMIPTERA: ERIOCOCCIDAE: APIOMORPHA
RÜBSAAMEN) TO THE FIRE HISTORY OF MALLEE
EUCALYPTS IN
DANGGALI CONSERVATION PARK, SOUTH AUSTRALIA**

By P. J. GULLAN†, P. S. CRANSTON†* & L. G. COOK**

Summary

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Mallee communities, especially the plant components, are often considered to be fire-adapted but there is no information on how effectively any phytophagous insects re-establish their populations after a wildfire. We addressed this issue by studying the scale insect genus *Apiomorpha* Rübsaamen, in which species induce conspicuous, sexually dimorphic galls of species-specific morphology on *Eucalyptus* species. In early 1996 we surveyed the species richness and abundance of *Apiomorpha* galls in relation to fire history and species of host eucalypt in mallee vegetation at Danggali Conservation Park, South Australia. Half of the fourteen sites surveyed had been burnt by wildfire in late 1985, whereas the other seven sites had not been burnt for at least 45 years. Only the two commonest of nine *Apiomorpha* species showed little or no host-plant specificity. Long-unburnt sites did not differ in species richness nor in total abundance of *Apiomorpha* galls from sites burnt in 1985, although the two commonest *Apiomorpha* species differed in their responses to fire history.

Key Words: Fire history, mallee, galls, *Eucalyptus*, Coccoidea, *Apiomorpha*.

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KEY WORDS: fire history, mallee, galls, *Eucalyptus*, Coccoidea, *Apiomorpha*.

Introduction

Fire is a significant factor in Australian ecology and in much of the continent the flora is fire-adapted (Barlow 1981). Many plants, including most *Eucalyptus* L'Hér. species (Myrtaceae), possess fire-protected structures (epicormic buds or lignotubers) from which new growth sprouts, or have seeds that germinate after fires (Gill 1981a,b; Hodgkinson & Griffin 1982; Noble 1982). Such regeneration abilities are particularly characteristic of plants in mallee vegetation, that is, woodland communities dominated by multi-stemmed eucalypts, which are themselves also called mallee (Noble 1982). For many eucalypts, especially mallees, fire can facilitate seed germination (Wellington 1989) or eliminate phytophagous insects (Noble 1982) and parasitic mistletoes (Gill 1981a). Eucalypts dominate most of Australia's forested ecosystems and have complex relationships with native animals, including many insects (Greenlade & New 1991). Habitat management using fire, whether consistent with history (e.g. to recreate purported past Aboriginal land management practice) or for hazard reduction, has effects that are relatively well understood for

vegetation but the implications for many other important organisms, especially invertebrates, are largely unknown (Bradstock *et al.* 1995; Friend & Williams 1996). The few Australian studies of the effects of fire on invertebrates have concentrated on soil and litter-dwelling organisms (e.g. Campbell & Tanton 1981; Neumann & Folhurst 1991; York 1994) or have sampled a wider invertebrate assemblage using only pitfall traps (e.g. Friend & Williams 1996). Arboreal insects probably survive fires less well than epigeic and hypogeic species (Whelan 1995) and, provided sampling biases can be addressed, should be good candidates for studying the effects of fire on invertebrate populations. In the present study we examine the effects of fire history on endemic Australian scale insects (Hemiptera: Coccoidea) that live only in the canopy of eucalypts.

Scale insects of the genus *Apiomorpha* Rübsaamen (Eriococcidae) live within galls that they induce on their eucalypt hosts (Gullan 1984a,b). In *Apiomorpha*, each adult female resides in a large, often symmetrical and woody gall, usually on the stem but sometimes on leaves, buds or fruits of the host eucalypt (Gullan 1984a). These are easily recognised as coccoid galls because there is a small apical orifice through which the female can eliminate her waste honeydew and also mate with the male. Her offspring or first-instar nymphs, called crawlers, make their exit from the maternal gall through this same opening and then disperse to initiate new galls

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on suitable foliage. The galls of males are much smaller than those of the females, rarely more than one centimetre long, and are tubular with an apical orifice and sometimes an outwardly-directed flange at the apex. The shape of the gall of the female is peculiar to the *Apiomorpha* species that induces it, regardless of the identity of the host eucalypt. Most *Apiomorpha* species show some degree of specificity to a restricted range of *Eucalyptus* species (Gullan 1984a). *Apiomorpha* has 39 described species (Gullan 1984a; Gullan & Jones 1989), each of which forms characteristic, sexually-dimorphic galls. Generally, *Apiomorpha* can be identified to species level in the field, even by non-specialists with minimal training.

Scale insects are often claimed to have low vagility (for review, see Hanks & Denno 1993) because the wingless adult females usually spend their entire lives on a single host plant and oviposit there; adult males are short-lived and weak-flying, and all dispersal is due to the movement of the crawlers, which usually remain on their natal host if conditions are favourable (Greathead 1990; Nestel *et al.* 1995). In *Apiomorpha*, our field observations in sclerophyll woodlands have suggested that there is lower diversity and abundance of galls in areas subjected to frequent or severe burning. This reduction seems unrelated to the suitability of post-fire eucalypts for gall development, since the epicormic flush of foliage that follows a fire resembles the preferred plant material utilised by *Apiomorpha* in long-unburnt areas. It is more likely that after a fire kills the galls and their occupants, it takes time for recolonisation by crawlers to occur and if fires are frequent, or potential sources of colonists are distant, local populations may not re-establish. This hypothesis remains speculative in the absence of quantification of any differences in species diversity and abundance between burnt and long-unburnt areas. We investigated re-colonisation after fire by surveying the species richness and abundance of *Apiomorpha* in relation to both the fire history and the species of host eucalypt in mallee vegetation in South Australia.

This study was undertaken in mallee for several reasons. Firstly, mallee is a typically Australian vegetation that has been in serious decline for the past 150 years through land clearance and other forms of degradation (Land Conservation Council 1987; Cheal 1989; Harris 1990). Secondly, it has been hypothesised that mallee plant and animal communities are maintained by episodic fire (Noble 1982, 1989), but no research has been done to investigate how effectively any phytophagous insects re-establish their populations in mallee after fire. Thirdly, it is easier to count the galls on mallee

eucalypts than on the taller forest and woodland species.

Scale insects of *Apiomorpha* are good candidates for studying the effects of wildfire because, unlike more mobile insects (Whelan *et al.* 1980), they are not able to move from their host plants to avoid the flames and, although the thick wall of the galls has been suggested to be an adaptation for fire protection (Koteja 1986), the high intensity of mallee wildfires, usually kills the overstorey foliage (Bradstock 1990). In contrast to the well-known biases of pitfalling trapping and other methods of sampling soil or litter fauna (see Whelan 1995), our survey method for *Apiomorpha* potentially assesses the total number of galls on each tree. Further advantages of the use of *Apiomorpha* galls is that their abundance varies little with season of survey since the females of most species probably live for much longer than a year (L.C. Cook unpub.) and galls can remain on the trees for several years after the death of the occupant, thus providing a record of the presence of the species at a site. Lastly, in order to elucidate causal relationships between invertebrate abundance patterns and fire, selected invertebrate groups need to be examined at a finer level of taxonomic resolution than the order or family level that is used in most studies (Friend & Williams 1996). From this perspective, *Apiomorpha* is an ideal study genus because galls can be identified readily to species level, even in the field.

Methods

The work was carried out in Danggali Conservation Park which was established in 1976, became Australia's first Biosphere Reserve in 1977 and is now part of the Bookmark Biosphere Reserve. This quarter of a million hectare reserve is about 90 km north of Renmark in South Australia and lies in the northern half of the Murray basin, adjacent to the New South Wales border (Fig. 1). It includes both arid and mallee land systems and allows access to some spectacular old-growth mallee. Of particular significance to our study is the documented fire history of Danggali Conservation Park (from National Parks and Wildlife Service, South Australia). Fire has not been used as a management tool in the maintenance of its mallee for conservation; recorded wildfires either have been naturally-occurring, following lightning strikes, or the result of human accidents. Many areas have no evidence of burning for a considerable period, perhaps for over a century, or at least not since either 1917 or 1951 when extensive wildfires burnt much of the region. However, of special relevance to the present study is a major lightning-induced fire that burnt a large central area of the reserve in December

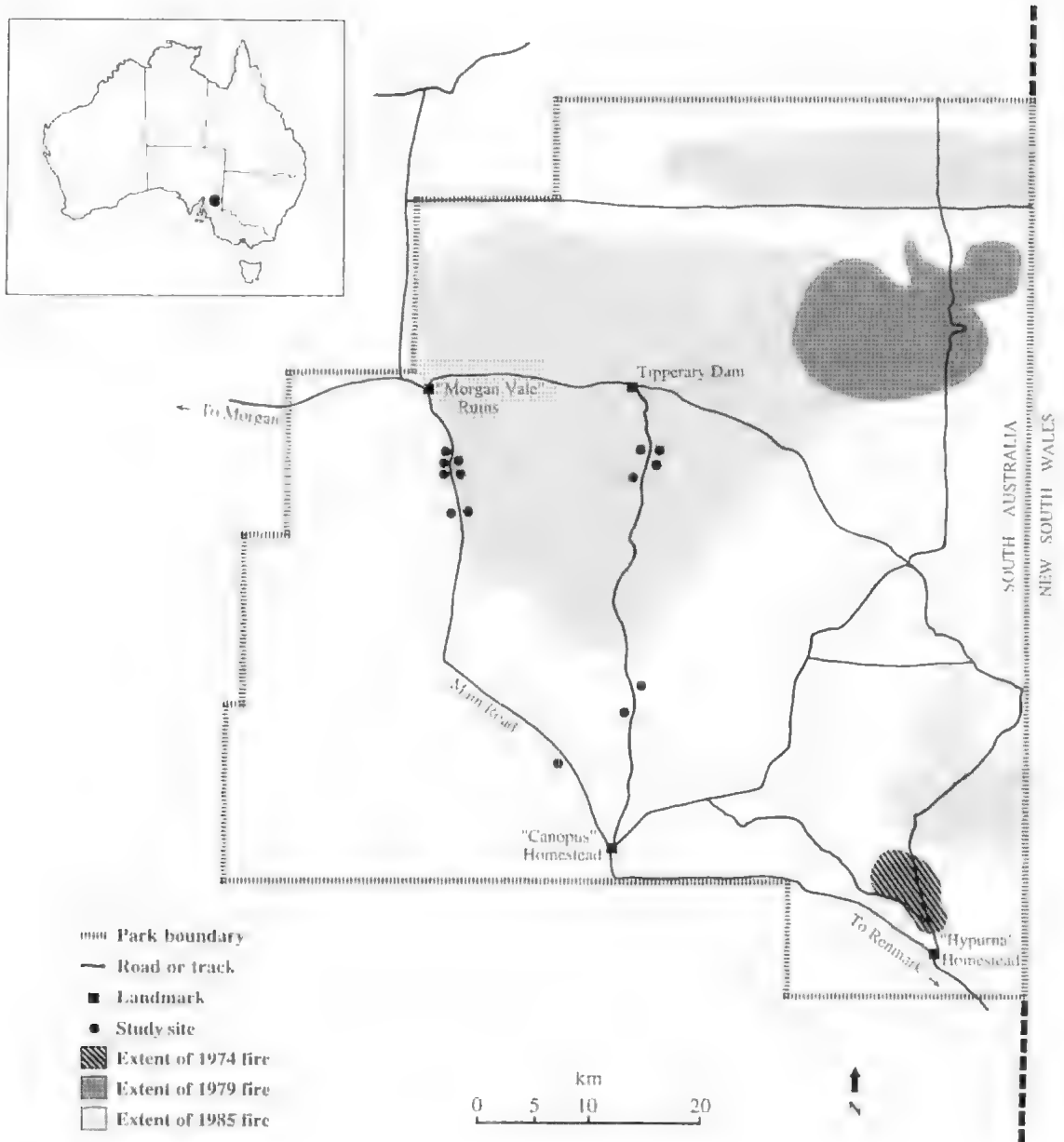


Fig. 1. Map of Dangali Conservation Park, South Australia, showing the extent of recent wildfires and the locations of the 14 study sites where galls of *Apiomorpha* were surveyed. Inset shows location of Dangali Conservation Park. (Figure based on map and aerial photographs from the National Parks and Wildlife Service, South Australia).

1985 (Fig. 1). Since then, the burnt eucalypts have regenerated from their mallee lignotubers, although the dead stags of past substantial limbs still protrude from the now-flourishing mallee regrowth.

We made comparisons between the *Apiomorpha* galls associated with eucalypts in the old-growth mallee ('long-unburnt' sites) and in the mallee that had regenerated after the 1985 fire ('burnt' sites). All fieldwork was conducted in April 1996. Fourteen sites were chosen (Fig. 1), seven in each treatment type (burnt versus long-unburnt), with the site coordinates as given in Table 1. All eucalypts at the burnt sites had been burnt completely in the 1985 fire and sites 6-9 were completely surrounded by post-fire regenerated mallee. We only used burnt sites in the central area of the reserve because we were certain that vegetation in this area had been completely destroyed in 1985, whereas the vegetation around Tipperary Dam and 'Morgan Vale' Ruins and in the two smaller areas also burnt in 1985 on the periphery of the reserve (Fig. 1) appeared to have been more patchily burnt. Five burnt and five long-unburnt sites had an understorey with porecupine grass, *Triodia irritans* R. Br. (Gramineae), sometimes as the dominant ground-layer plant. The other four sites either had reasonably bare ground or a mixture of shrub species.

The mallee eucalypt species at the study sites were *Eucalyptus incrassata* Sieber ex DC. (syn. *E. costata* F. Muell. & Behl ex F. Muell.), *E. dumosa* Cunn. ex Oxley, *E. gracilis* F. Muell., *E. oleosa* F. Muell. ex Miq. and *E. socialis* F. Muell. ex Miq. Identification was made using Costermans (1994), except that the name *E. incrassata* (syn. *E. costata*) is retained (M.L. Brooker pers. comm.). The proportions of each species varied according to locality but usually three of the five mallee eucalypts were present at all sites (Table 1). We chose sites in long-unburnt or post-fire regenerating patches to provide 10 multi-stemmed

mallee eucalypts, of between 3 and 6 m in height, per site. These 10 trees were chosen as representative of the proportions of each species in the local area. The height was imposed by the need to inspect the total foliage both from the ground and from a 3 m ladder placed in the centre of the tree.

For each tree we counted the number of galls containing live and dead *Apiomorpha* females. The surveyed galls varied in size from a few mm (young or aborted) to more than 4 cm long, and in shape from cylindrical and bud-like to urn-shaped or ovoid. Galls were recorded as containing dead females if they were old and brown or showed signs of attack by predators or parasitoids. Usually, the presence of a living cecid was confirmed by the presence of white powdery wax at the gall orifice. Only voucher material and galls of uncertain identity were collected, so the survey was relatively non-destructive. Voucher specimens of galls and slide-mounted insects of *Apiomorpha* have been deposited in the Australian National Insect Collection (ANIC), CSIRO, Canberra.

All data analyses pertain to galls containing live plus dead female insects, unless otherwise stated. The galls of dead insects were included in counts because any successful initiation of a gall was evidence that insect had reached the site and that the tree was a suitable host. Host specificity within *Apiomorpha* was examined by calculating the percentage of the surveyed trees of each eucalypt species that supported galls of females of each *Apiomorpha* species. The response of *Apiomorpha* species to fire was evaluated using one way analysis of variance (ANOVA) to compare burnt and long-unburnt sites in terms of the total numbers of galls of females (of all species summed), total numbers of galls of the seven least common species (i.e. galls of *A. malleacola* Gullan and *A. vicinipides* (Tepper) excluded), and total *Apiomorpha* species found at

TABLE 1. Site localities (from GPS readings) with fire history (long-unburnt (l-u) versus burnt in 1985 (b)) and the number of trees of each species sampled at each site. E. d. = *E. dumosa*, E. g. = *E. gracilis*, E. i. = *E. incrassata*, E. o. = *E. oleosa*, E. s. = *E. socialis*. Numbers at the foot of each species column refer to the total number of trees surveyed for that species.

Site	History	Latitude	Longitude	E. d.	E. g.	E. i.	E. o.	E. s.
1	l-u	33°17'12"	140°35'11"	3	0	3	0	4
2	l-u	33°17'11"	140°35'07"	3	1	0	4	2
3	b	33°17'16"	140°35'02"	0	2	0	6	2
4	b	33°17'00"	140°35'08"	3	3	0	4	0
5	l-u	33°19'20"	140°35'27"	6	0	0	0	4
6	b	33°16'03"	140°43'14"	3	1	1	1	4
7	b	33°16'04"	140°43'08"	6	0	0	0	4
8	b	33°16'34"	140°43'05"	5	1	0	0	3
9	b	33°16'50"	140°42'57"	1	5	0	0	4
10	l-u	33°24'36"	140°42'51"	0	5	0	0	5
11	l-u	33°25'02"	140°42'49"	3	4	0	0	3
12	l-u	33°27'19"	140°40'18"	3	2	3	0	2
13	l-u	33°17'04"	140°35'04"	4	4	0	2	0
14	b	33°19'20"	140°35'30"	6	2	0	0	2
				44	35	7	17	39

each site (14 units total). Analysis was carried out at the site level, not the tree level, because there were two or more different tree species per site and many trees had no or few galls. Two species, *A. malleacola* and *A. ovicoloides*, were common enough to examine their individual responses to fire at the site level using ANOVA but the data were transformed [$\ln(x+1)$] to correct for skewness. The responses of *A. malleacola* and *A. ovicoloides* to fire also were evaluated using individual trees as the units of analysis. In this case, binary presences and absences were analysed using Chi Square tests because galls were not abundant or widespread enough to satisfy underlying statistical assumptions at this level. All analyses were carried out using JMP[®] (SAS Institute Inc., © 1989-91).

Results

Apiomorpha species recorded

A total of nine species of *Apiomorpha* was recorded from the sites surveyed. These were: *A. calycina* (Tepper), *A. densispinosa* Gullan, *A. karschi* Riihsaamen, *A. malleacola*, *A. munita malleensis* Gullan, *A. ovicoloides*, *A. regularis* (Tepper), *A. strombylosa* (Tepper) and *A. urnalis* (Tepper). All of these species have been collected previously from mallee vegetation in southern Australia (Tepper 1893; Gullan 1984a).

Host-plant specificity of Apiomorpha

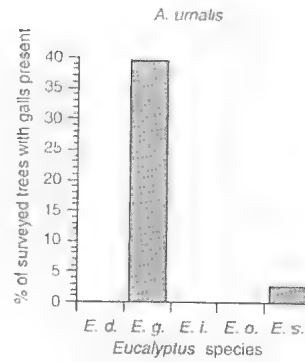
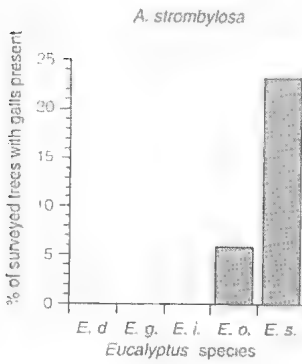
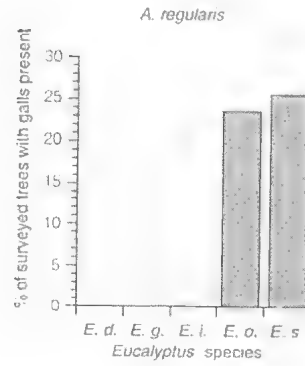
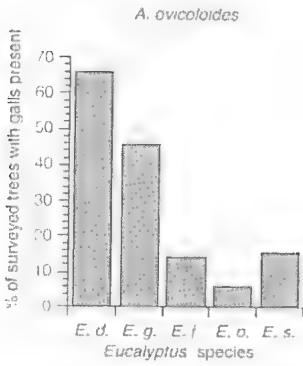
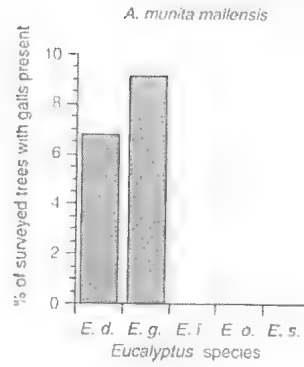
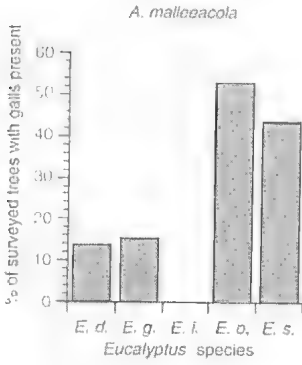
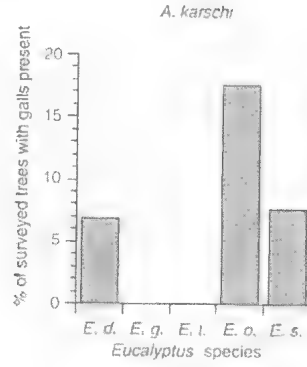
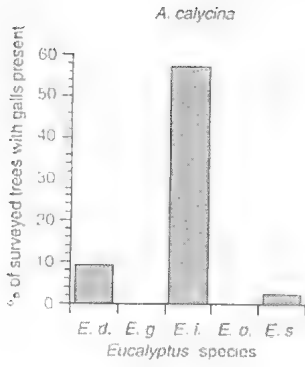
One species, *A. densispinosa*, was recorded from just three sites and solely on *E. dumosa* but only six galls were found and none of these contained a live coccoid. Six other of the nine species of *Apiomorpha* showed some degree of host-plant specificity (Fig. 2). Galls of *A. calycina* were found on four of the seven surveyed trees of *E. incrassata* as well as on two other eucalypt species. Galls of *A. karschi* also occurred on three eucalypt species, whereas *A. munita malleensis*, *A. regularis*, *A. strombylosa* and *A. urnalis* each were recorded from only two eucalypt species. However, 13 of the 14 trees that supported galls of *A. urnalis* belonged to *E. gracilis* and nine of the 10 trees with galls of *A. strombylosa* were *E. socialis*. Only one species, *A. ovicoloides*, was recorded on all five species of eucalypt; it was the commonest species, occurring on 52 of the 140 surveyed trees. The next most common species was *A. malleacola* which was found on four species of eucalypt and on 37 of the 140 surveyed trees.

Species richness and abundance of Apiomorpha in relation to fire history

All nine *Apiomorpha* species were found at both burnt and long-unburnt sites. Burnt and long-unburnt sites did not differ significantly in the number of *Apiomorpha* species recorded on survey trees ($F_{1,12}=3.57$, $p=0.08$) (Table 2). ANOVA of the total

TABLE 2. Means per site ± 1 SD, n with range in parentheses, and significance of differences due to fire history in diversity of *Apiomorpha* species, number of galls of all *Apiomorpha* species, number of galls of *A. malleacola*, number of galls of *A. ovicoloides* and number of galls of all species excluding *A. malleacola* and *A. ovicoloides*. (For *A. malleacola* and *A. ovicoloides*, means and ranges are from the raw data but F and p values are from transformed data, as indicated by [†]).

	Long-unburnt	Burnt	$F_{1,12}$ Value	p Value
n (sites)	7	7		
Mean number of <i>Apiomorpha</i> species per site	5.3 \pm 1.1	4.0 \pm 1.4	3.57	0.08
Mean number of <i>Apiomorpha</i> galls per site	37.4 \pm 9.3	24.3 \pm 14.8	3.96	0.07
Mean number of <i>A. malleacola</i> galls per site	6.9 (2-12)	7.6 (0-21)	0.40 [†]	0.54 [†]
Mean number of <i>A. ovicoloides</i> galls per site	13.3 (6-30)	3.4 (0-8)	11.37 [†]	0.01 [†]
Mean number of <i>Apiomorpha</i> galls per site with <i>A. malleacola</i> and <i>A. ovicoloides</i> excluded	16.6 \pm 8.4	12.7 \pm 14.1	0.39	0.54



numbers of galls of females (live and dead) recorded from each site indicated that the fire history of the sites did not affect gall abundances of *Apiomorpha* species ($F_{1,11}=3.96$, $p=0.07$) (Table 2). Burnt and long-unburnt sites did not differ in the percentage of live to dead *Apiomorpha*: 23% of galls at long-unburnt sites and 24% of galls at burnt sites were estimated to contain live cocooids. Except for *A. mallevacola* and *A. oviculaoides*, there were insufficient data for statistical analyses based on individual species, although for the third most abundant species, *A. unialis*, there were comparable populations at both burnt and long-unburnt sites.

For *A. mallevacola*, ANOVA of the transformed abundance [$\ln(x+1)$] at each site indicated that numbers of galls did not differ between burnt and long-unburnt sites ($F_{1,11}=0.40$, $p=0.54$) (Table 2). Chi Square analyses of presence-absence data for *A. mallevacola* on individual trees also indicated that fire history did not affect the likelihood of finding *A. mallevacola* galls ($\chi^2_{1,11}=0.04$, $p=0.84$), with galls being present on 27% of all trees sampled in long-unburnt sites and 26% of all trees sampled at burnt sites. If trees of *E. incrassata*, on which *A. mallevacola* was never found, were excluded, the results remained very similar ($\chi^2_{1,10}=0.214$, $p=0.64$; galls present on 30% of long-unburnt trees and 26% of burnt trees). Burnt and long-unburnt sites differed only slightly in the percentage of live to dead *A. mallevacola*: 33% of galls at long-unburnt sites and 39% of galls at burnt sites were estimated to contain live cocooids. Among the burnt sites surveyed, there was no evidence that galls of *A. mallevacola* were more abundant at sites close to (range 1-14 with mean of 6.7 galls per site), compared with distant from (range 0-21 with mean of 8.3 galls per site), long-unburnt areas.

In contrast, for *A. oviculaoides*, ANOVA of the transformed abundance [$\ln(x+1)$] at each site indicated that numbers of galls were significantly lower at burnt sites ($F_{1,11}=11.37$, $p=0.01$) (Table 2). Burnt and long-unburnt sites differed only slightly in the percentage of live to dead *A. oviculaoides*: 19% of galls at long-unburnt sites and 14% of galls at burnt sites were estimated to contain live cocooids. Chi Square analyses of presence-absence data for *A. oviculaoides* on individual trees also indicated that fire history affected the likelihood of finding *A. oviculaoides* galls ($\chi^2_{1,11}=9.04$, $p=0.003$), with galls being present on 49% of all trees sampled in long-unburnt sites, but on only 24% of burnt trees. Among the burnt sites surveyed, galls of *A. oviculaoides* were

slightly more scarce at sites 100-200 m from unburnt vegetation (range 0-3 with mean of 2.0 galls per site) than at sites several km distant from long-unburnt areas (range 1-8 with mean of 4.5 galls per site).

If both *A. mallevacola* and *A. oviculaoides* were excluded from the analysis of total numbers of galls, ANOVA of the gall abundance at each site indicated that numbers of galls of the other species combined did not differ between burnt and long-unburnt sites ($F_{1,11}=0.39$, $p=0.54$) (Table 2).

Mortality factors

The original occupants of many of the *Apiomorpha* galls that we recorded during our survey either had been killed by parasitoids, probably wasps, or removed by predators, probably cockatoos and parrots. Some galls had a single, large exit hole in the wall, providing evidence of the emergence of a dart-tailed wasp, *Cameronella* Dalla Torre (Pteromalidae) (Tillyard 1926; Bouček 1988; Naumann 1991), and other galls had many tiny emergence holes. Twelve galls had one side removed which is the typical appearance of a gall opened by a bird. Mortality of the latter kind was twice as common in the long-unburnt sites as in the burnt sites, but there were too few galls damaged in this way to determine whether the difference had statistical significance. Many other galls were brown and obviously dead but generally we could not determine the cause of death. A few other galls were deformed by inquiline, that is, other insects had occupied the gall tissue or the cavity but had not directly killed the *Apiomorpha* female. The identity of the inquilines was not determined because those still occupying the gall were either dipteran or hymenopteran larvae and no rearing to adults was attempted.

Discussion

In the event of fire, season of burn is believed to have the greatest influence on the plant composition of mallee communities, with frequent autumn fires causing substantial mortality of mallee eucalypts (Noble 1982, 1989). Continuous canopy growth of mallee eucalypts can occur after a summer wildfire and may be due to the absence of phytophagous insects (Noble 1982). Fire frequency (the interval between fires) is believed to have the most important long-term effect on mallee fauna because most animals adapt not to fire itself but to the floristic and structural features of the plant communities that result from different fire regimes (Land Conservation

Fig. 2. Host-plant specificity of *Apiomorpha* plotted as the percentage of the surveyed trees of each eucalypt species that supported galls of females of each *Apiomorpha* species. Eucalyptus species: E. d. = *E. dumosa*, E. g. = *E. gracilis*, E. i. = *E. incrassata*, E. o. = *E. oleosa*, E. v. = *E. viminalis*.

Council 1987). For invertebrates, which generally exhibit seasonal activity, inappropriate timing and particularly frequency of fire can have damaging consequences for populations (Land Conservation Council 1987; Friend & Williams 1996). For at least some *Triodia* mallee communities, it has been suggested that the natural fire frequency is unlikely to exceed more than one fire every 15–20 years because of the time required for fuel loads to accumulate (Noble 1989). At Danggali Conservation Park, many of the mallee sites that we studied had a *Triodia* understorey and it had been 10.5 years since wildfire had destroyed our burnt sites. Thus, if populations of *Apiomorpha* species in burnt sites could be shown to have recovered to pre-burn levels, the probable natural fire frequency of 15–20 years or more would be unlikely to have any long-term detrimental effects on populations of *Apiomorpha*.

The main findings of our survey were that the long-unburnt sites did not differ in species richness nor in total abundance of *Apiomorpha* galls from sites burnt 10.5 years ago, but that the medium-term effect of fire may vary for different *Apiomorpha* species. For the two species that were common enough to allow analysis of their abundance in relation to fire history, one (*A. malleecola*) was equally abundant in burnt and long-unburnt sites, whereas the other (*A. ovicoides*) was significantly less abundant at the burnt sites. Indeed, for *A. ovicoides*, re-establishment at burnt sites was low even where a source of potential colonists was just across a 10 m wide road. For this species with slow or limited post-fire re-establishment, the effect of another fire in the next five to 10 years might be virtual extinction, especially if no old-growth mallees, that may serve as fire refugia for such insects, survive the fire. The conservation of long-unburnt areas of mallee should be a management priority. Similarly, Friend & Williams (1996) have emphasised the importance of fire management to protect fire-sensitive species and habitats from too-frequent fires in mallee-heath shrublands of south-western Australia.

In contrast, *A. malleecola* and the third most common species, *A. urnalis*, had re-established populations equivalent to those recorded in long-unburnt sites at sites burnt 10.5 years previously (although the number of records for *A. urnalis* were insufficient for statistical analysis). In addition, there were no obvious fire effects on re-establishment of the other six *Apiomorpha* species but numbers of galls observed, at both burnt and long-unburnt sites for each species, generally were low compared with *A. malleecola*. Re-colonisation had occurred at burnt sites that were 10 km or more distant from the nearest stands of long-unburnt mallee. For vagile species, the post-fire flush of growth may be beneficial to gall establishment. This suggestion is

supported by the observation that in other environments, galls of *Apiomorpha* appear to be more abundant on young and regrowth eucalypts than on the foliage of older trees (LeBreton & Vaarwerk 1993; P. J. Gullan pers. obs.). Although this impression may be created by sampling bias (as it is easier to search low foliage of saplings and small trees than the canopy of more mature trees), old glasshouse rearing has shown that the first-instar nymphs will initiate galls only on the new foliage of actively-growing shoots. In another study (Yen 1989), the abundance of phytophagous insects, especially sap-sucking species, has been shown to be higher on coppice than mature mallee, perhaps because young leaves and shoots are more nutritious than old foliage and coppice trees have more young growth than mature mallees.

Some *Apiomorpha* species exhibit host-plant preferences for certain eucalypt species. Both *A. regularis* and *A. stramineola* occurred only on two eucalypt species, *E. socialis* and *E. oleosa*, which are closely-related species – both are in the series *Subulatae* of *Eucalyptus* (Chippendale 1988). Galls of *A. munita malleensis* were found only on *E. dumosa* and *E. gracilis*, which are in different series (Chippendale 1988). Two very closely-related *Apiomorpha* species, *A. calycina* and *A. urnalis* (Gullan 1984a; L.G. Cook unpub.), showed very different host preferences. Thirteen of the 14 surveyed trees with galls of *A. urnalis* were *E. gracilis*; whereas galls of *A. calycina* were most common on *E. incrassata* and never occurred on *E. gracilis*. Since the two most common *Apiomorpha* species, *A. malleecola* and *A. ovicoides*, also had the broadest host-plant ranges, differences in the occurrence and abundance of these two species in relation to the fire history of sites cannot be attributed to any variation in the composition of eucalypt species among sites. Instead, population differences among *Apiomorpha* species in relation to the fire history of sites may be best explained by differences in their propensity to disperse. The crawlers of some *Apiomorpha* species may disperse more readily to new trees than those of other species. There is ample evidence that first-instar scale insects of other groups are dispersed passively by the wind and, even though mortality is very high, may be carried for distances of a few m to several km, and more rarely a few hundred km, from the natal trees (reviewed by Pedgley 1982; Greathead 1990; Hanks & Denno 1993). Some scale insects crawlers have been reported to orientate downwind and stand on their hind legs with antennae and fore legs outstretched (Washburn & Washburn 1984; Washburn & Frankie 1985; Greathead 1990). Such behaviour probably ensures their dislodgement and dispersal by wind. The crawlers of a few species of

Apiomorpha have been observed displaying similar behaviour under glasshouse conditions (L. G. Cook unpub.). *Apiomorpha* species may differ in their propensity either to disperse actively from the host plant or remain on the natal tree. In contrast to the majority of *Apiomorpha* species, it is extremely difficult to establish infestations of *A. malleacola*, *A. calycina* and *A. unalis* by releasing crawlers on to potted eucalypts in a glasshouse (L. G. Cook unpub.); this suggests that at least some crawlers of the latter species may exhibit obligatory dispersal behaviour and, in the glasshouse, may suicide by actively departing from the only suitable host plant. Under natural conditions, however, natal trees probably would be surrounded by other suitable hosts, especially in mallee vegetation.

Dispersal ability may relate to morphological adaptations as well as behavioural ones. The flattened bodies and two or more long, filamentous caudal setae of scale insect crawlers are believed to enhance their dispersal potential (Wainhouse 1980; Pedgley 1982). Thus differences in body size and shape may partly account for differential dispersal among species. The crawlers of *Apiomorpha* have flattened, oval to subcircular bodies fringed with a continuous row of marginal setae (Gullan 1984a). In addition, the surface area of each marginal seta is extended by a thin sheet of waxy secretion (analogous in general appearance to the vane from the shaft of a feather). The first-instar nymphs of *A. ovicoides* are about the same length as, but narrower (195–225 µm at widest part) than those of *A. malleacola* (265–280 µm wide), although the marginal setae are approximately equal in length (34–44 µm) on both species (L. G. Cook unpub.). If

dispersal ability in *Apiomorpha* is correlated with the surface area of the body of the crawlers, the differences in abundances of *A. malleacola* and *A. ovicoides* in burnt and long-unburnt sites may be attributed at least in part to differences in the size and shape of their crawlers.

Selection for both active dispersal behaviour and body morphology that favours passive drift may occur in scale insect species that occupy unpredictable or temporary habitats, as has been suggested for armoured scale insects that feed on short-lived versus long-lived host plants (Greathead 1990). If this hypothesis is valid for *Apiomorpha*, then some species, such as *A. malleacola*, can be postulated to be better adapted to the vagaries of fire in the mallee environment.

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AN INTENSIVE MONITORING STUDY OF TWO WETLANDS OF THE RIVER MURRAY IN SOUTH AUSTRALIA; PHYSICO-CHEMICAL PARAMETERS AND CYANOBACTERIA CONCENTRATIONS

*By A. M. OLSEN**

Summary

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Quantitative data were collected on physico-chemical characteristics of surface water temperatures, pH, turbidity, conductivity, dissolved ammonia, dissolved reactive nitrate and total phosphate of Banrock and Loch Luna wetlands from 46 samplings in each wetland over a 20-month intensive monitoring study. Concentrations of the various physico-chemical parameters were within the ranges found in similar freshwater River Murray wetlands.

Key Words: Wetlands, River Murray, monitoring physico-chemical parameters, cyanobacteria, South Australia.

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Weather factors, such as strong winds, heavy rain runoff and lightning, produced perturbations in turbidity, conductivity, dissolved reactive nitrate and total phosphate levels in the two wetlands.

Nutrient concentrations in excess of 0.36 mg l⁻¹ total phosphate and 4.0 mg l⁻¹ dissolved reactive nitrate with rising water temperatures were related to rapid cell multiplication of the cyanobacteria *Anabaena* spp. Three *Anabaena* spp. were predominant in the two wetlands and reached their greatest numbers (23,700 cells ml⁻¹) in Loch Luna from late December 1994 to mid - January 1995.

KEY WORDS: Wetlands, River Murray, monitoring physico-chemical parameters, cyanobacteria, South Australia.

Introduction

In 1990 the Murray Darling Basin Commission through its Natural Resources Management Strategy (NRMS) funded a preliminary study of the water chemistry and aquatic invertebrates and land vertebrates of 10 wetlands of the River Murray floodplains in South Australia (Goonan *et al.* 1992). The survey was conducted during May - June 1990. Between May 1990 and February 1992, a second more detailed physico-chemical and biological survey of eight alkaline freshwater wetlands was carried out on the above - mentioned floodplains. Five of the eight wetlands were located between Clover Lake (Calpernum area) and the Berri Evaporation Basin and the remaining three were between Ramco Lagoon (Waikerie) and Lake Carlet (6 km upstream of Mannum) (Fig. 1). These results were reported by Suter *et al.* (1993).

Banrock Station Floodplain (Section 662, 681 and 682 - Hundred of Moorook) and associated wetland lie in about the middle of the 100 km (approx.) stretch of the river between the five upper and three lower wetlands studied by Suter *et al.* (1993).

Flow regulation of the River Murray at Lock 3 in 1925 helped create two permanent freshwater wetlands in the region, one located in the floodplain of Banrock Station (34° 08' S, 140° 20' E) and the other in the Loch Luna Wetland Complex (34° 12' S,

140° 22' E) opposite Banrock Station and about one km upstream of Lock 3 weir (ANCA 1996). Banrock Station wetland has a 90 to 130 ha area depending on water depth (20 cm - 1.1 m) and was created in the 1950s by damming the upper section of Banrock Creek. The wetland behind the dam wall is gravity

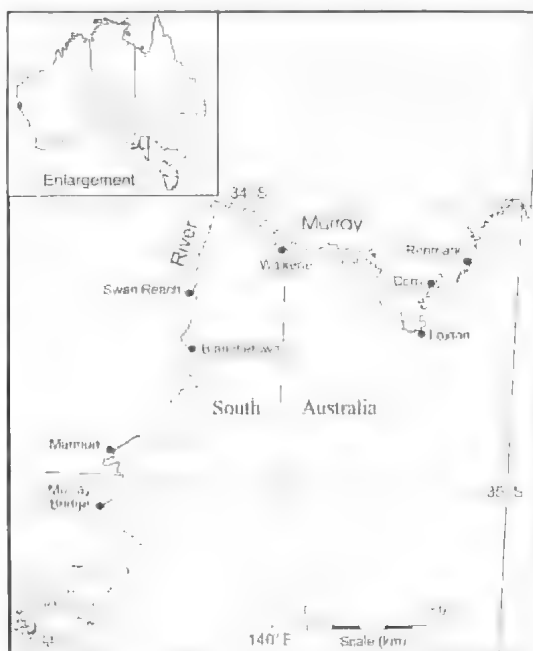


Fig. 1. Location map of wetlands studied - River Murray, SA.

fed by a channel from Lock 3 Pool. Water levels are maintained by controls at the inlet and outlet points and discharges flow into Lock 2 Pool. European carp control structures were erected at the inlet in 1994.

The study described below was undertaken to determine the cyclical changes in the physico-chemical characteristics of the waters of the two wetlands and their influence on the rise and decline of those cyanobacterial species likely to produce toxic outbreaks. In the summer of 1991-2 there had been visible blue green algal blooms in both wetlands.

Materials and Methods

Sampling

This monitoring study of the two wetlands of the River Murray began in November 1994 and ended in

June 1996. For 19 months water from only the River Murray catchment and upstream storages flowed through Lock 3 Pool. The Darling River did not flow because of the four-year drought in its drainage basin. Mixed River Murray - Darling River water flowed into Lock 3 Pool in June 1996 as a result of floods in the Darling River.

In each wetland, five sites were selected for water sampling for reasons of accessibility and representativeness and for sampling any increase in cyanobacterial concentrations irrespective of wind direction (Fig. 2). All water samples and temperature readings were taken in the morning and as near as possible to the same time at each visit. Wherever possible, Loch Luna was sampled first followed by Banrock wetland within 2 h. Collections of water samples were made weekly from October to December, fortnightly from January to March and monthly from

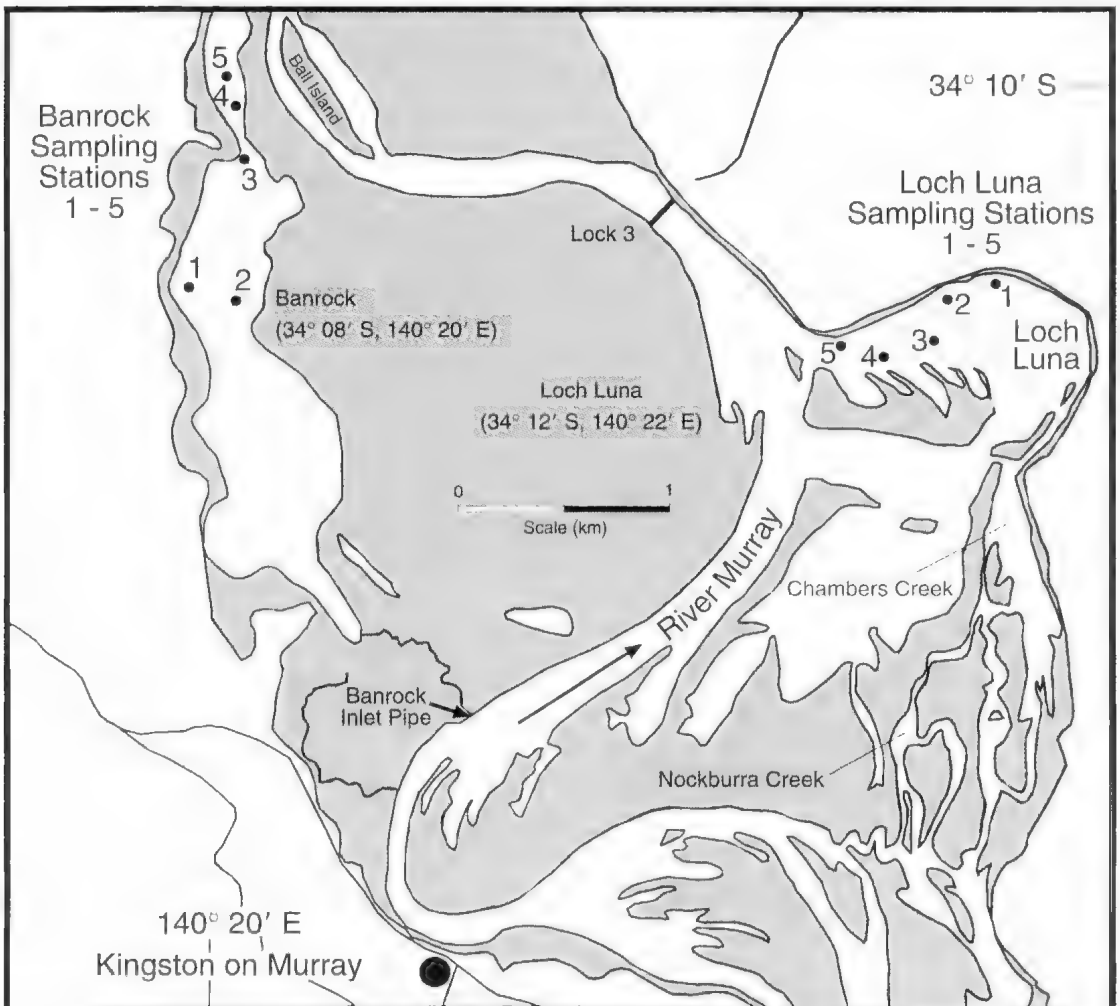


Fig. 2. Banrock and Loch Luna wetlands showing sampling sites. Note direction of flow.

TABLE 1. Numbers of cells of *Anabaena* spp. and concentrations of dissolved reactive nitrate and total phosphate - Loch Lomond 1994-96.

Date	Cells (mg l ⁻¹)	DRNitrate (mg l ⁻¹)	Total phosphate (mg l ⁻¹)
Nov 3, 1994	+	0	0.16
Nov 8	0	0	0.13
Nov 15	0	0	0.17
Nov 22	56	0.44	0.20
Nov 29	41	Tr.	0.25
Dec 6	434	0.44	0.13
Dec 13	1,230	0	0.27
Dec 20	5,590	0.44	0.47
Dec 27	23,700	2.20	0.16
Jan 3, 1995	10,600	Tr.	0.46
Jan 17	14,500	6.1	0.19
Jan 31	1,050	0.44	0.45
Feb 14	3,560	Tr.	0.07
Feb 28	97	3.52	0.10
Mar 14	437	0.88	0
Mar 28	172	2.20	0.23
Apr 18	425	2.20	0.36
May 16	909	0	0.25
June 13	100	1.32	0.17
July 18	11	0	0.17
Aug 16	8	3.52	0.19
Sept 5	0	0	0.30
Sept 19	2	Tr.	0.07
Oct 3	0	Tr.	0.53
Oct 10	8	0	0.47
Oct 17	6	0	0.43
Oct 24	12	0	0.95
Oct 31	11	0.44	0.04
Nov 7	24	0	0.20
Nov 14	6	4.4	0.21
Nov 21	450	0	0.17
Nov 28	1,183	0	0.23
Dec 5	1,220	7.48	0.30
Dec 12	1,150	Tr.	0.40
Dec 19	115	Tr.	0.67
Dec 26	1,270	2.2	0.20
Jan 9, 1996	997	6.6	0.20
Jan 23	3,190	4.4	0.17
Feb 6	2,530	0	0.08
Feb 20	368	Tr.	0.25
Mar 5	63	contaminated	contaminated
Mar 19	444	0	0.23
Apr 14	57	0	0.12
May 14	0	0	0.41
Jun 9	0	0	0.06

TABLE 2. Numbers of cells of *Anabaena* spp. and concentrations of dissolved reactive nitrate and total phosphate - Banrock 1994-1996.

Date	Cells (mg l ⁻¹)	DRNitrate (mg l ⁻¹)	Total phosphate (mg l ⁻¹)
Nov 3, 1994	14	0	0.20
Nov 8	0	0.44	0.17
Nov 15	+	0.44	0.27
Nov 22	0	0	0.30
Nov 29	1,460	Tr.	0.27
Dec 6	2,480	3.5	0.41
Dec 13	1,560	Tr.	0.60
Dec 20	303	Tr.	0.70
Dec 27	125	0	0.23
Jan 3, 1995	96	Tr.	0.15
Jan 17	245	4.0	0.33
Jan 31	146	2.2	0.21
Feb 14	373	0	0.12
Feb 28	311	7.9	0.06
Mar 14	883	0.88	Tr.
Mar 28	5	0	0.33
Apr 18	123	0	0.27
May 16	189	Tr.	0.33
June 13	wetland drained		
July 18	50	0	0.20
Aug 16	0	0	0.24
Sept 5	+	0	0.40
Sept 19	+	Tr.	0.25
Oct 3	0	0	0.28
Oct 10	0	0	0.39
Oct 17	14	0	0.35
Oct 24	0	0	0.23
Oct 31	11	4.4	0.27
Nov 7	24	Tr.	0.26
Nov 14	27	0	0.30
Nov 21	225	0	0.16
Nov 28	626	3.52	0.30
Dec 5	461	Tr.	0.30
Dec 12	455	0	0.36
Dec 19	135	Tr.	0.43
Dec 26	364	Tr.	0.18
Jan 9, 1996	2,300	4.4	0.21
Jan 23	1,040	1.32	0.18
Feb 6	2,170	0	0.02
Feb 20	240	0	0.41
Mar 5	71	0	0.60
Mar 19	328	0	0.40
Apr 14	28	0	0.12
May 14	0	0	0.33
Jun 9	0	0	0.24

April to September on the dates given in Tables 1 and 2.

At each site (Fig. 2) a one-litre surface water sample was taken and bulked in a five litre plastic bottle with samples taken from the other four sites. Aliquots of the bulked sample were transferred to air-free 500 ml polycarbonate plastic screwtop bottles for subsequent physico-chemical analyses at the Science Section, Glossop High School. The one-litre water samples for counting cyanobacteria were transferred to 1.25 l plastic screwtop bottles leaving a 250 ml headspace. The samples were kept chilled until delivery to the Australian Centre for Water Quality Research, Bolivar SA for enumeration of cyanobacteria cells (HMSO 1990). The special 1.25 l plastic bottles for the water samples were supplied from the Water Quality Laboratory.

A floating 'Der Grune Punk' No. 7428, blue alcohol column thermometer was used to record the surface water temperatures at each site. A mean surface water temperature was then calculated for each wetland. A plastic bodied minimum - maximum thermometer, (-30° - +50° C) with pressure adjustment for indicators on the mercury column was used to record minimum and maximum water temperatures between times of consecutive sampling visits. It was suspended 15 cm below the surface.

There was no 13 June 1995 collection in the Banrock wetland because this wetland was drained for maintenance work on the irrigation pumps used for highland vineyard irrigation. The Loch Luna 5 March 1996 sample was discarded because of suspected contamination.

Chemical analyses

Water samples were held at 4° C until required and in most instances were analysed within 48 h. Measurements of turbidity, dissolved ammonia, dissolved reactive nitrate and total phosphate were made using a HACH DREL/5 instrument and premixed reagents (Hach 1984). For dissolved ammonia each sample was filtered through a Double Rings 201 filter paper to remove suspended solids. A 25 ml aliquot was measured into a clean glass sample cell and 1 ml of Nessler reagent added (Hach 1992). The mixture was left for colour to develop. In this case the blank was distilled water (25 ml) with 1 ml of Nessler reagent included. Measurements were made at 425 nm and recorded as mg l^{-1} after applying a conversion factor of multiplication by 1.29 (Hach 1992).

For dissolved reactive nitrate (DRN) each sample was filtered through a Double Rings 201 paper to remove clay particles. A 25 ml aliquot was measured

into a clean glass sample cell and the contents of one foil sachet of premixed Nitrover 5 reagent added. This mixture was rapidly agitated for one minute then left for five minutes for colour to develop. Another filtered 25 ml sample was used as a blank. Measurements were made at 500 nm and recorded as mg l^{-1} after applying a conversion factor of multiplication by 4.4 (Hach 1992).

For total phosphate (TP) a digestive process was used to convert all forms of phosphate to the soluble orthophosphate form (Hach 1992). Fifty ml of the sample were measured into a clean 125 ml Erlenmeyer flask along with 4 ml 5.25 N H_2SO_4 and two foil sachets of $\text{K}_2\text{S}_2\text{O}_8$ (Hach 1992). The mixture was heated in a boiling water bath for 30 minutes, allowed to cool to room temperature and then 4 ml 5 N NaOH were added. The sample was split into two 25 ml portions in clean glass sample cells. One foil sachet of premixed Phosver 3 reagent was added to one container and the colour allowed to develop. The other was used as a blank for spectrometric analysis. Measurements were taken at 700 nm and recorded as mg l^{-1} after applying a conversion factor (division by 3). These DRN and TP results complement data collected for eight SA wetlands by Suter *et al.* (1993).

pH was measured using a Hanna HI 8424C pH meter. The probe was rinsed in distilled water between each test and left in the sample until the highest stable reading was reached.

For turbidity measurements, each sample was agitated vigorously and a 25 ml aliquot was added in a clean glass sample cell and placed in the DREL/5 spectrophotometer. Measurements were made at 450 nm and recorded as Nephelometric Turbidity (NTU) units. A blank of distilled water was used to zero the instrument.

Conductivity measurements were made using a EDT 141200 conductivity meter calibrated to 1413 Electrical Conductivity (EC) units between each use. The calibration solution was prepared by diluting 74.55 g of oven - dried KCl in 1000 ml distilled water. The probe was rinsed with distilled water prior to each use and the maximum reading taken each time it was used. Results were in EC units.

Results

Mean surface water temperatures

Throughout this study the mean surface water temperatures in the two wetlands showed almost identical trends. In general, water temperatures were higher in the more exposed shallow Banrock wetland than in the slightly more protected Loch Luna wetland. The highest surface water temperatures in Banrock, 28.5°, 28.6° and 28.4° C were recorded in the summer of 1994-5, corresponding temperatures

in Loch Luna were 27.4°, 28.5° and 25.3° C (Fig. 3). The lowest mean surface water temperatures were 10.3° C in Banrock and 10.2° C in Loch Luna on 18 July 1995.

In Banrock the greatest range in minimum and maximum water temperatures between consecutive visits was 20° C (15° - 35° C) between 3 and 17 January 1995 and the greatest range in Loch Luna was 14.5° C (14° - 28.5° C) between 22 and 29 November 1994. The monthly ranges in summer/autumn were often 15° C or greater, whereas in winter, they were 5° C or less. The least difference between minimum and maximum water temperatures between consecutive visits in Loch Luna was 0.5° C on 18 July 1995.

Lock 3 Pool surface water temperature 50 m upstream of the Banrock Station Intake in 1996 was slightly higher than the mean temperatures in Banrock and Loch Luna (Fig. 3).

pH

The pH values ranged up to 9.56 at Banrock (27 December 1994) and 9.04 at Loch Luna (3 January 1995) (Fig. 4). Lock 3 Pool water registered a maximum pH 8.62 on 14 November 1995 and a minimum pH 7.51 on 26 December 1995.

Turbidity

The shallower Banrock wetland mostly recorded higher turbidity values than those of Loch Luna (Fig. 5). Highest turbidity in Banrock was 200 NT units on 3 and 10 October 1995 and the lowest 30 NT units on 14 March and 28 November 1995 while in Loch Luna the highest turbidity was 170 NT units on 5 September 1995 and the lowest 10 NT units on 14 March 1995. Turbidity in Lock 3 Pool ranged 70 NT units on 14 May 1996 to 20 NT units on 26 December 1995. The mixed River Murray - Darling water had a turbidity value of 48 NT units on 9 June 1996.

Conductivity

The initial high conductivity of 1898 EC units in Banrock on 3 November 1994 decreased to 871 EC units in 6 weeks and more slowly thereafter to 500 EC units by 9 June (Fig. 6). In Loch Luna the initial conductivity of 1095 EC units on 3 November 1994 decreased to 687 EC units on 17 January 1995, rose slightly before falling to a minimum value of 327 EC units on 19 September 1995. Within a fortnight there were two sharp increases in concentrations (2720 EC units on 3 October 1995 and 1759 EC units on 31 October) before conductivity values decreased to 511 EC units on 9 June 1996.

The conductivity values of the River Murray water decreased slowly from 686 EC units on 31 October 1995 to 511 EC units on 14 May 1996. The mixed



Fig. 3. Comparison of mean surface water temperatures at Banrock and Loch Luna, November 1994-June 1996 and River Murray, October 1995-June 1996.

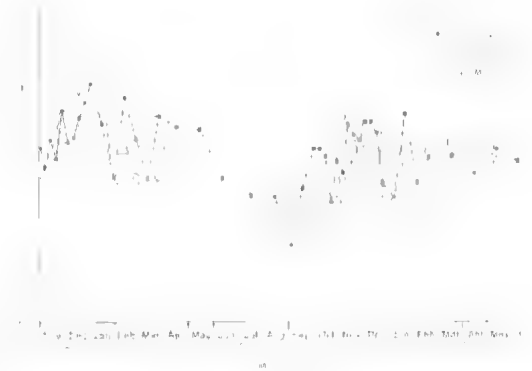


Fig. 4. pH, Banrock and Loch Luna, November 1994-June 1996 and River Murray, October 1995-June 1996.



Fig. 5. Turbidity, Banrock and Loch Luna, November 1994-June 1996 and River Murray, October 1995-June 1996.

River Murray - Darling water was 438 EC units on 9 June 1996.

Rainfall

Weather factors, such as heavy rain and strong winds, were found to influence some physical parameters in the two wetlands. The average annual rainfall at Barmera is 245 mm. The Barmera rainfall was considered to be representative of the area and its daily rainfall records for the 20-month period of the study showed that rainfall was irregular with intermittent occasional heavy falls of 27 mm on 4 January 1995, 29 mm on 1 May, 53 mm on 23 October 1995, 38.5 mm on 2 January 1996, 25 mm on 27-28 February and 20.1 mm on 3-4 June 1996.

Dissolved ammonia

The patterns of dissolved ammonia (Fig. 7) were similar in both wetlands. The range in Banrock was from 0.17 mg l⁻¹ on 28 November 1995 to 3.10 mg l⁻¹ on 7 October 1995 and in Loch Luna from 0.30 mg l⁻¹ on 3 January, 28 February and 31 October 1995 to 3.48 mg l⁻¹ on 21 November 1995.

Dissolved Reactive Nitrate (DRN)

In Banrock there were occasional high DRN concentrations, exceeding 4 mg l⁻¹, in the period November to March 1994-5 and again on 31 October 1995 and 9 January 1996. At most other times DRN was below detection. In Loch Luna there was high DRN on 17 January 1995 and between October and February 1995-6 there were four occasions when the concentrations exceeded 4.0 mg l⁻¹ (Fig. 8).

Total Phosphate (TP)

The highest TP concentrations recorded for Loch Luna were 0.95 mg l⁻¹ on 24 October 1995 and 0.67 mg l⁻¹ on 19 December 1995 (Fig. 9). At Banrock TP peaked at 0.7 mg l⁻¹ on 20 December 1994. On 13 December 1994 and on 5 March 1996 the next highest Banrock values were 0.6 mg l⁻¹. The mean TP for both wetlands was similar at about 0.3 mg l⁻¹.

Cyanobacteria

When water sampling started in Banrock on 3 November 1994 the total cyanobacterial count was 14 cells ml⁻¹ (Fig. 10). By 6 December 1994 cyanobacterial cells peaked in Banrock at 2480 cells ml⁻¹ and then declined steadily to 5 cells ml⁻¹ by 28 March. The second but smaller cyanobacterial cell multiplication in Banrock occurred a year later between 7 November 1995 and 9 January 1996. Cell numbers rose from 24 cells ml⁻¹ to a maximum of 2300 cells ml⁻¹ before declining to 71 cells ml⁻¹ on 5 March 1996 (Table 2). Three *Anabaena* species were predominant in the Banrock wetland.

In Loch Luna between 1994 and 1995 the same



Fig. 6. Conductivity, Banrock and Loch Luna, November 1994-June 1996 and River Murray, October 1995-June 1996.

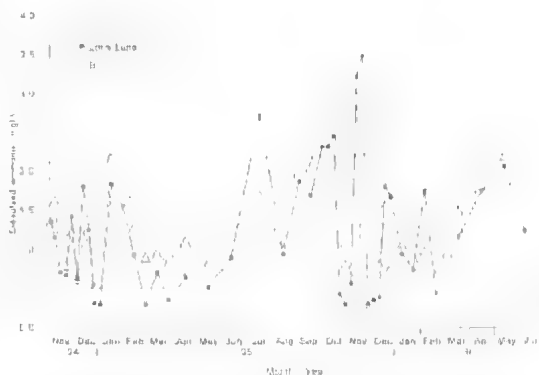


Fig. 7. Dissolved ammonia, Banrock and Loch Luna, November 1994-June 1996.

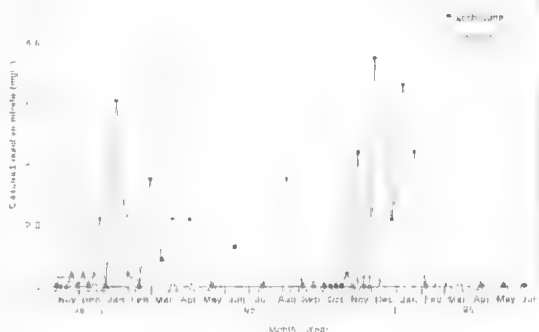


Fig. 8. Dissolved reactive nitrate, Banrock and Loch Luna, November 1994-June 1996.

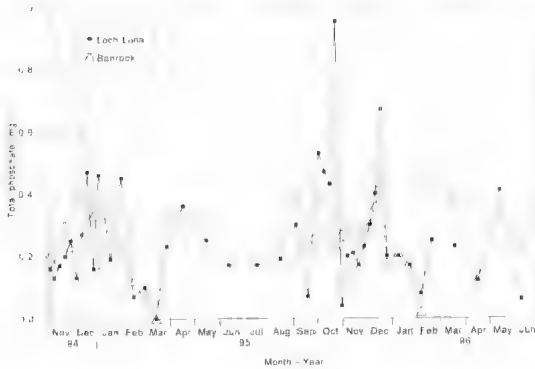


Fig. 9. Total phosphate, Banrock and Loch Luna, November 1994-June 1996.

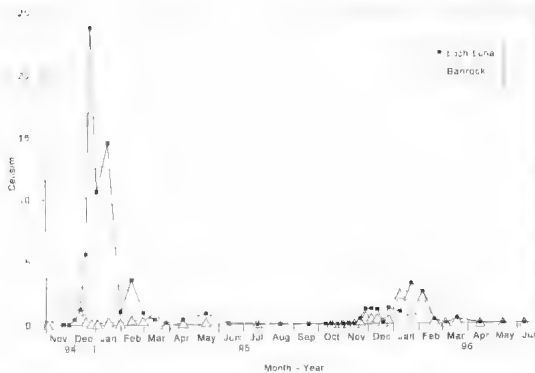


Fig. 10. Cyanobacteria (blue green algae), Banrock and Loch Luna, November 1994-June 1996.

three *Anabaena* species were predominant through the rise and subsequent decline of high cell multiplication (incipient blue green algal "bloom"). During November 1994 the number of cyanobacterial cells reached a low of 41 cells ml^{-1} but after 29 November their numbers increased rapidly to peak at 23,700 cells ml^{-1} on 27 December 1994 before declining to 97 cells ml^{-1} two months later (Fig. 10, Table 1). *Anabaena* coiled species was predominant until 3 January 1995 after which *Anabaena circinalis* displaced it until mid-February. The coiled species again became predominant until June 1995 when all three *Anabaena* species were present in low numbers until late November 1995 when multiplication of *Anabaena* coiled species began again. This species peaked at 2530 cells ml^{-1} in early February and a month later cell numbers fell to 63 cells ml^{-1} (Table 1). Cell numbers rose slightly to 444 cells ml^{-1} on 19 March 1996 but no cells were detected on 9 June 1996.

Other cyanobacterial species identified in the water samples, although occurring only in low numbers, were *Anabaenopsis elenkini* (6 December 1994 - 20 February 1995), *Aphanizomenon* sp. (22 November 1994 - 13 June 1995, 23 January - 19 March 1996), *Oscillatoria* sp. (3 November 1994 - 18 July 1995, 9 January - 19 March 1996). *Cylindrospermopsis raciborski*, *Planktothrix* spp., *Arthrospira* spp., *Microcystis aeruginosa* and *Pseudoanabaena* spp. were identified from time to time.

Discussion

Surface water temperatures, pH, turbidity and conductivity levels followed similar trends in both Banrock and Loch Luna wetlands and were comparable with the values recorded between 1990 - 1993 for the eight floodplain wetlands of the River Murray in South Australia by Suter *et al.* (1993).

River Murray turbidity values were highest (70 NT units) on 14 May 1996 and lowest (20 NT units) on 26 December 1995. Mixed waters of River Murray and Darling River (Lock 3 Pool) registered 48 NT units on 9 June 1996. In the 10-year period 1978-88 Lock 3 Pool water averaged 60 NT units (Mackay & Eastburn 1990).

The high conductivity value of 1898 EC units in Banrock on 3 November 1994 was caused by a blocked inlet pipe into Banrock; with the clearing of the blockage conductivity values in one week dropped to 1507 EC units. Turbidity in Banrock increased from 104 to 155 NT units between 5 and 8 November 1994 due to turbulence from the rush of water following clearing of the blockage. Seven weeks for conductivity values and five weeks for turbidity values were required to reach equivalence with Loch Luna values.

In Loch Luna conductivity levels rose from 327 to 2720 EC units on 3 October 1995 after spring rains and strong runoff. At Barmera, 13 mm of rain fell on 31 August, 9.6 mm on 5 September, 9.8 mm on 25 September, 10 mm on 3 October and 53 mm on 23 October 1995. Seiche effects in Lake Bonney and added runoffs caused the high conductivity water from Lake Bonney to flow through Chambers Creek into Loch Luna wetland. The outward movement of the high conductivity water (2970 EC units) from Lake Bonney was traced from data recorded on 6 October 1995 at position PO1517 in Nockburra Creek, a tributary of Chambers Creek. Six weeks elapsed before the high conductivity water from Lake Bonney had been diluted to 721 EC units (14 November 1995).

The range of DRN concentrations in Banrock was 0 - 7.9 mg l^{-1} and in Loch Luna 0 - 7.48 mg l^{-1} . The high registrations occurred mainly after heavy rains but there are also nitrate contributions from time to

time from water from the River Murray and from agricultural drains, town effluents and sewage discharges as well as localised autolytic breakdown of nitrogen-fixing blue-green algae (*Anabaena* spp.). There is an unknown DRN nutrient input from huge flocks of pelicans (> 1000 birds), swans, cormorants and ducks and lesser numbers of other water birds resident in Barrock and Loch Luna wetlands and on the banks of the River Murray. Nitrates are also produced by lightning (Smith 1996).

The highest TP level (0.95 mg l⁻¹) recorded in Loch Luna occurred on 24 October 1995 the day after 53 mm of rain fell at Bannera and 58 mm at Barrock Station (C. L. Rohlfach pers. comm. 1995). Such heavy rain and consequent runoff cause bottom disturbances in shallow wetlands which redistribute dissolved organic phosphorus compounds and inorganic phosphorus bound to suspended or disturbed bottom organic particulates in the water column. Briggs *et al.* (1985) have also drawn attention to the complexity of chemical relationships within wetlands and the effects of weather factors, such as winds and temperature, on water chemistry.

No blooms of cyanobacteria were observed in Barrock wetland. The multiplication of cyanobacterial cells in Barrock during December 1994 was halted by the increased water inflow following removal of the blockage in the inlet pipe. The cyanobacteria were flushed out preventing any further development of a cyanobacterial bloom in Barrock wetland that year.

In Loch Luna cyanobacterial cells reached a maximum of 23,700 cells ml⁻¹ on 27 December before declining to zero by 14 March 1995. After the collapse of the cyanobacterial population in Loch Luna in December 1994, a small but visible blue-green algal bloom developed downstream in February and March 1995 along the eastern bank of the River Murray adjacent to Lock 3 weir. It is likely that this bloom had its genesis in the November–December 1994 cell multiplication in Loch Luna upstream and on the same side of the River Murray. Small blue-green algal blooms had occurred in this same location in previous years (Lock 3 staff pers. comm. 1995).

Bowling (1994) reported the occurrence and possible causes of a severe *Anabaena circinalis* bloom in Lake Cargelligo NSW in late 1990–91 when cell numbers exceeded 100,000 cells ml⁻¹. The physico-chemical levels in the lake in 1990 had ranges close to the 1994–6 values in Loch Luna for water temperatures, pH, turbidity and conductivity but lower maximum concentrations of TP and DRN than were found for Loch Luna. Bowling (1994) expressed the view about the Lake Cargelligo bloom that "although several underlying causes of this

bloom are probable, the elevated nutrient concentrations, especially of total phosphorus, were major factors that contributed to it." He drew attention to the fact that most physico-chemical studies of cyanobacteria blooms were started after the blooms had occurred.

In this study of the physico-chemical properties of the two wetlands a search for bloom-forming toxic cyanobacteria species was started before any cell multiplication had commenced and a seasonal pattern is described. Cyanobacterial cells may remain dormant in cold waters and grow best at water temperatures exceeding 15 °C, with optimal growth rates at 25 °C or higher (Roberts & Zohary 1985). The effect of water temperatures on cyanobacterial cell numbers in Loch Luna is shown with data from Table 1 which show that blooms only occurred between November and February. Numbers of *Anabaena* spp. rose suddenly from zero on 15 November 1994 (20.1 °C) to 23,700 ml⁻¹ on 27 December 1994 (24.2 °C) and then began subsiding, even though the water temperatures were high, perhaps because of exhaustion of nutrients.

The rise and fall in cell numbers may also be related to the concentrations of the two nutrients, DRN and TP recorded during the growth and decline of the 1994–5 and 1995–6 blue-green algal outbreaks (Table 1). However, since the concentration of dissolved reactive phosphorus is not known, these relationships must be treated with caution.

There were four occasions (20 December 1994, 5 and 31 January 1995 and 18 April 1995) when TP concentrations in Loch Luna were at or above 0.36 mg l⁻¹ and DRN was present even in low concentrations (Tr. = 2.2 mg l⁻¹). After each of these events there was a rise in the numbers of cyanobacterial cells. In October 1995 (mean 16.9 °C) there were four TP concentrations between 0.43 and 0.95 mg l⁻¹ but DRN was low or absent and no cell multiplication developed.

A pattern related to nutrient availability and temperature can be seen in early 1996. After an increase to 3190 cells on 23 January 1996 the cell numbers began to decline possibly due to very low concentrations of DRN and fluctuating values of TP in the water column. The cyanobacteria population reached zero on 14 May 1996. The mean water temperature on that date was 13 °C which is near the minimum temperature range for growth of many free living cyanobacteria species.

From the data obtained in this study it is suggested that outbreaks of cyanobacterial blooms did not occur in the summers of 1994–5 and 1995–6 because there were inadequate concentrations of TP and DRN in the water column during the period of favourable growth for cyanobacteria. Data from this study indicate that TP concentration above 0.36 mg l⁻¹

and DRN concentration at or above 4.0 mg l^{-1} in the wetland may provide for continuous growth in the *Anabaena* species.

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**ASPHONDYLIA ANTHOCERCIDIS, A NEW SPECIES
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ON ANTHOCERCIS LITTOREA (SOLANACEAE)
IN WESTERN AUSTRALIA**

BY PETER KOLESIK, REBECCA WHITTEMORE† & HELEN M. STACE†*

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Key Words: Diptera, Cecidomyiidae, *Asphondylia anthocercidis*, *Anthocercis littorea*, Western Australia.

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The fruit galls on the Western Australian yellow tailflower, *Anthocercis littorea* Labill. (Solanaceae), reduce the reproductive potential of this plant, but their causative agent has, until now, been unknown. Our research has shown that a new gall midge species, *Asphondylia anthocercidis*, induces these galls. The larva, pupa, male and female of the new species are described and illustrated.

KEY WORDS: Diptera, Cecidomyiidae, *Asphondylia anthocercidis*, *Anthocercis littorea*, Western Australia

Introduction

The gall midge fauna of Western Australia is poorly known, with only two species having been described previously (Gagné 1989). One of them, *Ipomyia bornemisszai* Colless, is a species which presumably feeds on fungi growing in the soil and in leaf litter (Colless 1965). The biology of the second species, *Eocincticornia australasiae* Felt, is unknown (Felt 1915), although this species is likely to be a plant feeder considering that its congener, *E. malarskii* Kolesík, causes galls on *Eucalyptus fasciculosa* in South Australia (Kolesík 1995a).

The yellow tailflower, *Anthocercis littorea* Labill (Solanaceae), a shrub which grows to 3 m, is endemic to the south-west coast of Western Australia, primarily on calcareous sands in disturbed habitats such as recently burnt areas, roadsides, fire breaks and cleared lots (Purdie *et al.* 1982; Whitemore¹). The fruit galls on *A. littorea* have been known for some time (Purdie *et al.* 1982) but their causative agent has remained unknown. In July 1996, one of us (R. W.) collected fruit galls from *A. littorea* containing larvae and pupae, from which adults were reared. The gall-inducer proved to be a new species of gall midge which is described below. The development of the galls and their impact on the reproduction of *A. littorea* are described by Whitemore¹.

The genus *Asphondylia* in the context of this paper

is defined by Kolesík (1997) 'The new species is to be attributed to P. K.

Material and Methods

Stems of *Anthocercis littorea* bearing fruit galls were collected at Hillarys, about 20 km north-east of Perth, on 23.vii.1996. A small number of galls was dissected and the larvae and pupae preserved in 70% ethanol. Larvae and pupae retained within galls were reared to adults on stems which were kept in plastic vials. Larvae pupated within the galls. Emerged gall midges were preserved together with pupal skins in 70% ethanol. Canada balsam mounts of the type series for microscopic examination were prepared according to the technique outlined by Kolesík (1995a). All measurements refer to the type series. The type specimens and other material retained in 70% ethanol are deposited in the South Australian Museum, Adelaide (SAMA) and Australian National Insect Collection, Canberra (ANIC).

Asphondylia anthocercidis sp. nov. (FIGS 1-15)

Holotype: ♂, Hillarys, Western Australia [31°48' S, 115°45' E], emerged 28.vii.1996. R. Whitemore, reared from larva from fruit gall on *Anthocercis littorea* Labill., gall collected 23.vii.1996, 121335 [SAMA].

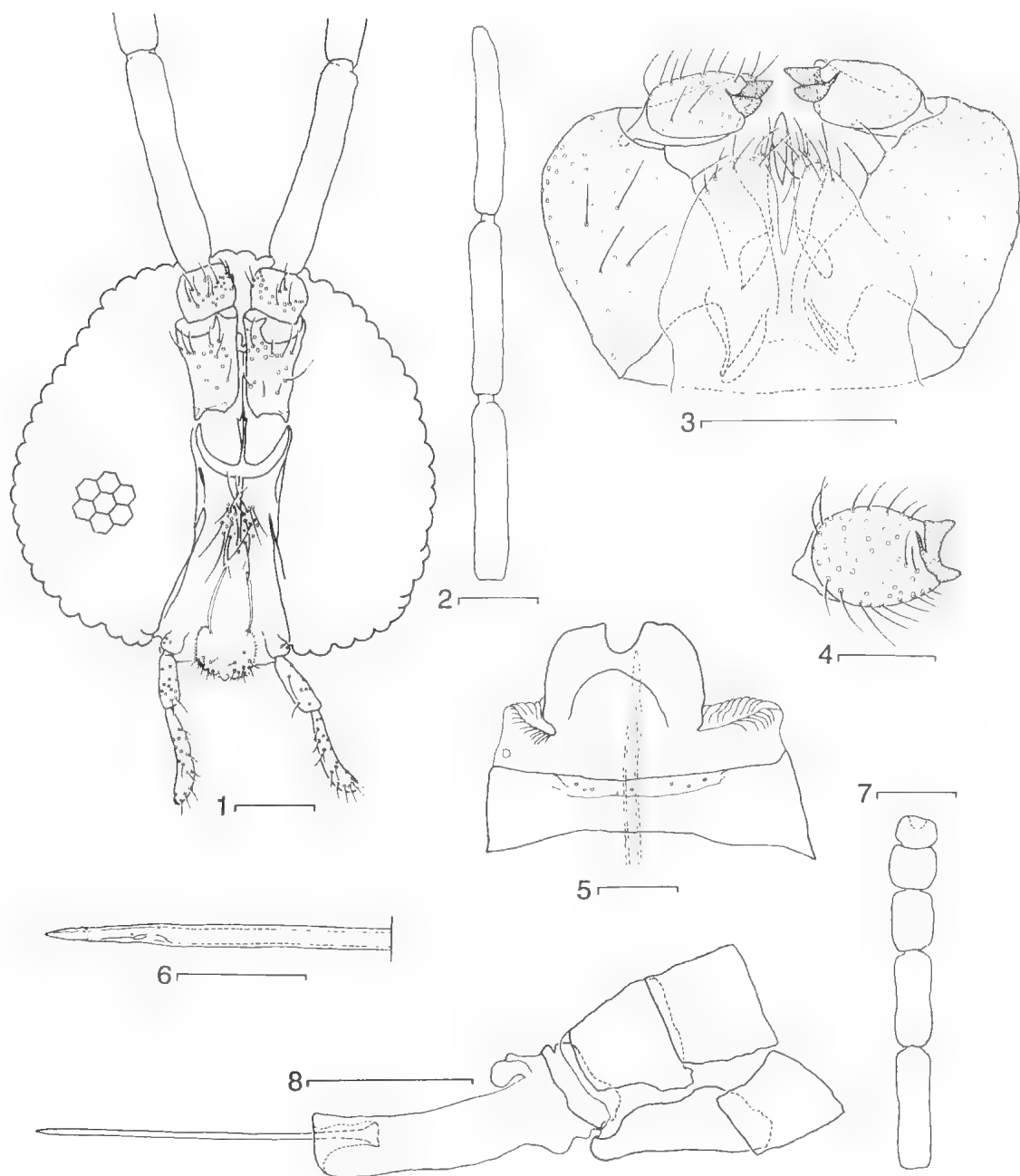
Paratypes: 2 ♂♂, 3 ♀♀, 5 pupal skins [SAMA], 3 ♂♂, 3 ♀♀, 4 pupal skins [ANIC], all same data but emerged 28-30.vii.1996; 2 larvae [SAMA], 2 larvae [ANIC], all collected with holotype.

Other material [all SAMA]: 2 ♂♂, 5 ♀♀, 2 pupal skins, 4 pupae, all same data as paratypes; 2 larvae, collected with holotype.

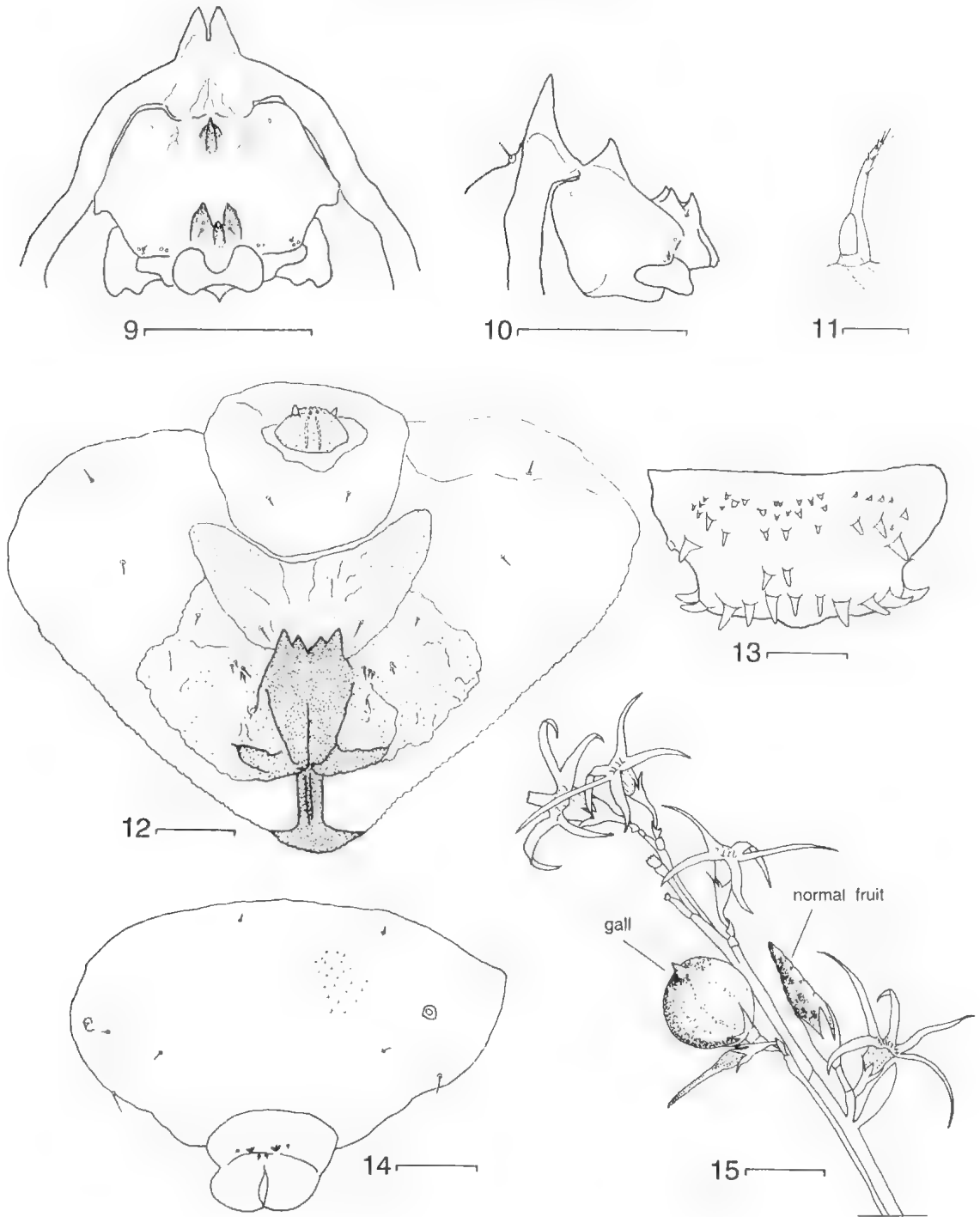
*Department of Horticulture, Viticulture and Oenology Faculty of Agricultural and Natural Resource Sciences, The University of Adelaide (PMB) Glen Osmond S. Aust. 5064

†Department of Botany, University of Western Australia, Nedlands, W. Aust. 6907

Whitemore¹ R. (1996) Aspects of the insect-induced fruit galls and reproductive biology of *Anthocercis littorea* (Solanaceae). BSc (Hons) thesis, University of Western Australia (unpubl.)



Figs 1-8. *Asphondylia anthocercidis* sp. nov.: 1-4 male; 5-8 female. 1. Head in frontal view. 2. Last three flagellomeres. 3. Genitalia in dorsal view. 4. Gonostylus in posterior view. 5. Basal lobes on ovipositor in dorsal view. 6. End of ovipositor in lateral view. 7. Last five flagellomeres. 8. End of abdomen in lateral view. Scale bars = 100 μ m 1-3, 5-7; 50 μ m 4; 500 μ m 8.



Figs 9 - 15. *Asphondylia anthocercidis* sp. nov.: 9 - 11, 13 pupa; 12, 14 larva; 15 infestation. 9. Anterior part in ventral view. 10. Anterior part in lateral view. 11. Prothoracic spiracle. 12. Head and first thoracic segment in ventral view. 13. Last abdominal segment in ventral view. 14. Last two abdominal segments in dorsal view. 15. Fruit gall on *Anthocercis litorea* Labill. [redrawn from Rippey & Rowland (1995)]. Scale bars = 500 μ m 9,10; 50 μ m 11; 100 μ m 12-14; 10 mm 15.

Description

Male (Figs 1-4)

Colour: sclerotized parts of body reddish-brown, non-sclerotized parts of abdomen grey.

Head. Antenna: scape broadest distally, 1.7-2.0 x breadth at distal end, 2.6-2.7 x length of pedicel; pedicel width 1.2-1.4 x length; first flagellomere 1.8-2.1 x length of scape, flagellomeres evenly cylindrical; circumfila dense, equally distributed along flagellomeres. Eye facets hexagonoid, eye bridge 8-9 facets wide. Frons with 10-17 setae per side. Labella prominent, laterally with 7-10 setae, setulose. Maxillary palpus 3-segmented, segments successively and progressively longer.

Thorax. Wing length 3.4 mm (range 3.1-3.7), width 1.3 mm (1.1-1.4). Sc cell pigmented proximally. Claws of all legs subequal in size and similar in shape, as long as empodia.

Abdomen. Genitalia: gonostylus with two large, apical teeth of same length; aedeagus elongate and narrow, reaching middle of gonostylus.

Female (Figs 5-8)

Frons with 9-20 setae per side, labella with 7-9 setae laterally. Circumfila comprising two longitudinal and two short transverse bands. Wing length 3.6 mm (3.3-3.9), width 1.4 mm (1.2-1.5). Seventh abdominal sternite 1.8 (1.6-2.2) x length of sixth. Genitalia: ovipositor 1.9 x (1.8-2.0) length of seventh sternite; basal lobes on ovipositor broad in dorsal view, divided in posterior third medially; fused cerci glabrous.

Pupa (Figs 9-11, 13)

Colour: brown. Total length 4.0 mm (3.6-4.5). Antennal horns not serrated, 242 µm (237-247) long. One upper and three lower frontal horns. Prothoracic horn slightly curved, basal part about 2 x width of terminal third, terminal third setose. Abdominal dorsal spines simple, straight, with 2-3 pairs on last segment curved laterally.

Mature larva (Figs 12, 14)

Colour: yellowish-white. Total length 3.4 mm (2.6-4.1). Head capsule strongly pigmented, posterolateral extensions not developed. Spatula with four anterior teeth, inner pair smaller than outer, shaft narrow, broadened both at mid-length and base, surrounded anteriorly and laterally by extensive pigmented area. Each side of spatula with triplet and pair of lateral papillae, all setose. Six terminal papillae present, one pair coriiform, 2 pairs with short setae, other papillae as for *Asphondylia* (Möhl 1955).

Gall and biology

This gall midge induces deformation of fruits of *Anthocercis littorea*. The unilocular ovaries are transformed into glabrous, spherical to ovate, nipped galls, 7-18 mm long and 7-13 mm wide (Fig. 15) and bright green to purple in colour. Inside the gall a chamber, about 3 mm long and 2 mm wide, is occupied by one larva. The chamber is always lined with fungal mycelia. Although the fungus was abundant in the many galls examined, no sexual stages were observed and the fungus remains unidentified. Viable seeds are rarely produced in galls although pollination is essential to retain the gall on the plant. The numbers of galls in *A. littorea* populations are often very high, with the galls outnumbering the normally-developed fruits by up to 38 times (Whitemore¹).

Pupation takes place within the gall. At the end of its development the pupa cuts an opening in the gall and lifts most of its body outside the gall. The pupal skin then splits open and the adult emerges. At Hillarys in 1996, the adults emerged throughout the entire host plant flowering period, i.e. from April to September.

Distribution

Asphondylia anthocercidis sp. nov. is sympatric with *A. littorea* across the entire geographic distribution of the host plant, which ranges from Kalbarri [27°50' S, 114°07' E] in the north to Israelite Bay [34°27' S, 119°23' E] in the south (Whitemore¹).

Etymology

The name is derived from the generic name of the host plant.

Remarks

Asphondylia is a worldwide genus with six species previously described from Australia. The life history of three of them is known: *A. dodonaeae* Kolesik induces galls on leaves of *Dodonaea viscosa* Jacq. subsp. *spatulata* (Smith) West. and *A. inflata* Kolesik and *A. ericiformis* Kolesik induce galls on branch segments of *Haloxa viridis* (Black) Wilson subsp. *pergranulata* and *H. indica* subsp. *leiosachya* (Benth.) Wilson, respectively (Kolesik 1995b, 1997). Life histories of two other species, *A. loewi* Skuse and *A. rubicunda* Skuse, are unknown (Skuse 1888, 1890). The remaining species, *A. hillii* Edwards, has been reported to induce galls on the stem of an unidentified plant (Edwards 1916). *Asphondylia hillii*, *A. loewi* and *A. rubicunda* are not considered in the present paper. The descriptions of these three species were superficial and therefore it is

not possible to compare them with each other or with *A. dodonaeae*, *A. inflata*, *A. ericiformis* or *A. anthocercidis*. A review of the Australian species of this genus is planned by P. K.

The new species differs from *Asphondylia dodonaeae* in the longer adult scapæ, the wider teeth on the gonostylus, the unserrated antennal horns and the presence of both upper and lower frontal horns in the pupa, the shafted spatula and the presence of a pigmented area around the larval spatula. The new species can be distinguished from both *A. inflata* and *A. ericiformis* by several characters. In *A. anthocercidis*, the aedeagus reaches the middle of gonostylus, pupae have three lower frontal horns, the prothoracic horn is setose at the distal third and is about twice as wide at the base as is the distal third. At least two of the dorsal spines on the last pupal segment are curved laterally and the spatula has four anterior teeth. In both *A. inflata* and *A. ericiformis*, the aedeagus extends beyond the middle of the gonostylus. The pupa of *A. inflata* has one lower

frontal horn and that of *A. ericiformis* has none. In both species, the prothoracic horns are asetose and about four times wider at the base than at the terminal third. In the pupa of *A. inflata*, only the prominent pair of abdominal dorsal spines on the last segment is curved laterally; in *A. ericiformis* all spines are straight. In both species the spatula has two anterior teeth.

Acknowledgments

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FIRST RECORD OF THE ORIENTAL LATRINE FLY, CHRYSONOMYIA MEGACEPHALA (FABRICIUS) (DIPTERA: CALLIPHORIDAE), FROM SOUTH AUSTRALIA

BRIEF COMMUNICATION

Summary

Blowflies are well known for their ecological, veterinary and forensic importance¹ but they are also significant medically as mechanical vectors of dangerous pathogens². The Oriental Latrine Fly, *Chrysomya megacephala* Fabricius, 1794³, is notorious in this regard. Adults of the synanthropic form of this species (see below) are attracted to foodstuffs, human and animal faeces and carrion⁴ and have been implicated in the transmission of viruses⁵, protozoans⁶, enteric bacteria⁷ and helminths⁸. The larvae are also known as facultative parasites in traumatic lesions in humans and other animals⁴.

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FIRST RECORD OF THE ORIENTAL LATRINE FLY, *CHRYSOMYA MEGACEPHALA* (FABRICIUS) (DIPTERA: CALLIPHORIDAE), FROM SOUTH AUSTRALIA

Blowflies are well known for their ecological, veterinary and forensic importance¹ but they are also significant medically as mechanical vectors of dangerous pathogens. The Oriental Latrine Fly, *Chrysomya megacephala* Fabricius, 1794² is notorious in this regard. Adults of the synanthropic form of this species (see below) are attracted to foodstuffs, human and animal faeces and carrion³ and have been implicated in the transmission of viruses⁴, protozoans⁵, enteric bacteria⁶ and helminths⁶. The larvae are also known as facultative parasites in traumatic lesions in humans and other animals⁷.

I report here the first record of *C. megacephala* in South Australia. It was caught in large numbers in a liver-baited trap on the North Terrace campus of the University of Adelaide in April, 1997. I had not previously encountered it at this site, despite periodic trapping of blowflies over the preceding seven years. Neither had I encountered it elsewhere in South Australia. There are no specimens of *C. megacephala* from this state in the entomological collection at the South Australian Museum and the closest record of it to South Australia is that of three females in Murrumbidgee, New South Wales (34°58' S, 149°02' E), approximately 950 km to the east of Adelaide (K. R. Norris, Division of Entomology CSIRO pers. comm. 1997).

Elsewhere in Australia, *C. megacephala* occurs across the far north of the continent, down the east coasts of Queensland and New South Wales and in south-west Western Australia. It has not been recorded from Victoria or Tasmania⁸.

Chrysomya megacephala is probably a recent introduction to South Australia, as it is actively expanding its range in other parts of the world. Since the 1970s it has invaded New Zealand⁹, several parts of Africa¹ and areas of South¹⁰, Central¹¹ and North America¹². It is also found in Japan and is widespread throughout the Oriental region and the Austro-Malayan and Polynesian subregions of the Australasian region¹.

Chrysomya megacephala occurs in two forms, which are morphologically and ecologically different. They have been defined by Kurahashi¹³ as the "normal" and "derived" forms. The normal form is restricted to tropical forests on South Pacific islands from the Bismarck Archipelago to Samoa. It is believed to be the plesiomorphic form of the species. The derived form is synanthropic and dispersive and is thought to have originated in Papua New Guinea in

the western boundary of the species' ancestral distribution¹⁴. The individuals collected from Adelaide are of this form.

The derived form can be distinguished from the normal form by the greatly-enlarged ommatidia in the upper two-thirds of the eye in males. The normal form has only slightly enlarged ommatidia in this region¹⁵. Since the two forms differ so markedly in their ecological preferences and in some aspects of their morphology, they may be sufficiently divergent genetically to warrant subspecific or even specific status. This might be revealed by biochemical analysis, as carried out recently for other closely-related blowflies of the genus *Calliphora*¹⁷, although a detailed morphological comparison would also be required before a conclusion about their status could be reached.

Both forms of *C. megacephala* can be distinguished from all other known Australian species of *Chrysomya* by the following morphological characters: hairs on prealar knob black; longer than height of knob; anterior thoracic spiracles blackish brown; legs black; subtibial setulae black; eyes in males with ommatidia in the upper two-thirds enlarged and sharply demarcated from the small ones in the lower third; frons in females wider in the middle^{13,14,16}. However, the species is similar physiologically to other species of *Chrysomya* in that it is thermophilic, and therefore, in South Australia, it will presumably be active only during the warmer months of the year, that is between October and April.

Because of its habits, *C. megacephala* deserves serious attention from a public health perspective and its distribution in Australia should therefore be monitored. Its larvae could also be encountered in forensic cases in the Adelaide region, but because their morphology bears superficial similarity to that of some other common carrion-breeding species of blowfly¹, they could be mistaken for them. Since the rate of development of *C. megacephala* at a given temperature differs significantly from these other species^{20,21}, misidentification of this important fly could lead to serious errors in estimates of the time since death of human corpses.

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THE STATUS OF CYCLOSTRONGYLUS MEDIOANNULATUS JOHNSTON & MAWSON, 1940

BRIEF COMMUNICATION

Summary

Cyclostrongylus medioannulatus Johnston & Mawson, 1940 was originally described by Johnston & Mawson¹ from three females found in the stomach of *Macropus thetis* (sic) now *Thylogale thetis* collected from the Burnett River district in Queensland. The authors commented that the worms differed from other species of *Cyclostrongylus* Johnston & Mawson, 1939 only in having a narrow supporting ring around the buccal cavity. Mawson² revised the genus and considered its relationships with related genera. She found the type species of *Cyclostrongylus* which had been erected in 1939³, to be identical with that of the type species of *Oesophagonastes* (Johnston & Mawson, 1942) and placed *Oesophagonastes* in synonymy with *Cyclostrongylus*.

BRIEF COMMUNICATION

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Of the other species previously assigned to *Cyclostrongylus*, *C. dissimilis* Johnston & Mawson, 1939 occurring in *W. bicolor* was referred to *Macropostrongylus* (Yamaguti, 1961) and *C. clelandi* Johnston & Mawson, 1939 occurring in *M. major* now *M. giganteus* to a new genus later described as *Alvostoma* Mawson, 1979³. Subsequently *C. gallardi* was redescribed as *Wallabinema gallardi*⁴.

In the case of *C. medioannulatus* Mawson² found that the specimen labelled as the type was a female *Rugopharynx australis* (Monning, 1926), obviously placed there in error. Since the original material could not be found she declared the species a *species inquirenda*.

Mawson² also revised the genus *Macropostrongylus* Yorke & Maplestone, 1926 and erected three new genera including *Papovastrongylus*. *Papovastrongylus* was characterised by an oesophagus with a cylindrical corpus, a narrow isthmus and ending in a bulb; and a buccal capsule which is thickest at midlength and has an anterior border

without projections. The species included the type species *P. wallabiae* (Johnston & Mawson, 1939), occurring in *M. rufogriseus* and *W. bicolor*, *P. pearsoni* occurring in *Petrogale lateralis*, *M. eugenii* and *M. rufogriseus* and *P. irma* occurring in *M. irma*. Beveridge⁵ then amended the generic diagnosis, extended the host range of *P. pearsoni* to include *M. fuliginosus* and described two new species, *P. macropodis* occurring in *M. giganteus*, *M. eugenii* and *M. robustus*, and *P. thylagale* occurring in *Thylagale stigmatica*, *T. brunii* and *Petrogale persephone*. Beveridge⁶ commented that *P. thylagale* occurred commonly in *T. stigmatica* in northern Queensland, and in *Petrogale persephone* from central Queensland but had not been found in *T. stigmatica* or *T. thetis* in southern Queensland. Spratt *et al.*⁷ listed *C. medioannulatus* as a species of *Papovastrongylus*.

Recently a slide (HC 2660) labelled *Cyclostrongylus medioannulatus* in P. M. Mawson's handwriting, was found in the South Australian Museum, Adelaide. The slide consists of pieces of two female worms mounted in resin and has attached to it another hand-written note by Mawson indicating that the specimens are two of the only three females ever collected. The characters of the oesophagus, buccal capsule, female tail and ovjector that can be distinguished in these two females are consistent with the characters of *Papovastrongylus*. Further, the buccal capsule has an annular thickening around the middle as is found in *P. thylagale*. The oesophagus (0.7) mm is shorter in *C. medioannulatus* than in *P. thylagale* (0.9–0.93) mm. The measurements of the posterior end of *C. medioannulatus* are not congruent with those of *P. thylagale*, vulva to tail tip 0.35 compared to 0.72–0.80, and tail 0.24 compared to 0.45–0.59 mm respectively. The vagina vera of *C. medioannulatus*, however, is the same length as that of *P. thylagale*. *Cyclostrongylus medioannulatus*, therefore, is clearly a species of *Papovastrongylus* and is most similar to *P. thylagale*. Additional material, including male specimens, is needed before an exact determination can be made. No other specimens of *Papovastrongylus*, however, have been found in *T. thetis* to date.

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