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*By R. K. SCHUMACHER**, *A. D. AUSTIN†* & *R. B. FLOYD‡*

Summary

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Key Words: Autumn gum moth, *Mnesampela privata*, Geometridae, *Glyptapanteles*, *Cotesia*, *Casinaria*, *Heteropelma*, *Isdromas*, *Mesochorus*, *Elasmus*, *Megadicylas*, Braconidae, Ichneumonidae, Elasmidae, Pteromalidae.

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Parasitoids were reared from cocoons present in larval shelters of *Mnesampela privata* (Guenée) collected at Altona and Shepparton, Victoria and Canberra (Lyneham Ridge), ACT. The most common primary parasitoid was a gregarious braconid wasp, described here as *Cotesia geometricae* Austin sp. nov. This species attacked host larvae of all locations and emerged from the fourth or fifth instar, pupating gregariously. A second braconid, described here as *Glyptapanteles mnesampela* Austin sp. nov., was found at Lyneham Ridge. This parasitoid was superficially similar to *C. geometricae*, attacked early-instar host larvae and also emerged from the fourth or fifth instar to pupate gregariously. One other solitary primary parasitoid, *Casinarina micra* Jerman & Gauld (Ichneumonidae), emerged from fourth or fifth instar larvae and pupated externally. At least five species of hyperparasitoids emerged from the cocoons of *C. geometricae* collected in Victoria: two species of *Isdromus* (Ichneumonidae), *Mesochorus* sp. (Ichneumonidae), *Elasmus* sp. (Elasmidae) and *Megadicylus* sp. (Pteromalidae), with one of the *Isdromus* species being most common. The larval-pupal parasitoid *Heteropelma scaposum* (Morley) (Ichneumonidae) emerged from 10% of pupae reared from larvae collected in the ACT over the same period as adults of *M. privata*. Sex and viability significantly influenced the weight of pupae of *M. privata* but pupae parasitised by *H. scaposum* could not be separated using weight. Notes and an illustrated key are provided to facilitate the easy identification of the parasitoids.

KEY WORDS: Autumn gum moth, *Mnesampela privata*, Geometridae, *Glyptapanteles*, *Cotesia*, *Casinarina*, *Heteropelma*, *Isdromus*, *Mesochorus*, *Elasmus*, *Megadicylus*, Braconidae, Ichneumonidae, Elasmidae, Pteromalidae.

Introduction

The autumn gum moth, *Mnesampela privata* (Guenée) (Geometridae) is endemic to Australia and occurs throughout the south-eastern and south-western parts of the continent as well as Tasmania (McQuillan 1985; Abbott 1993). Larvae feed on a wide range of eucalypt species (McQuillan 1985) but prefer the juvenile foliage of trees in the blue gum group (Elliott & Bashford 1978), which includes the important plantation species *Eucalyptus nitens* (Deane & Maiden) Maiden and *E. globulus* Labill. (Abbott 1993; Bashford 1993; Neumann 1993; Phillips 1993). *Mnesampela privata* can occur in high numbers in young, even-aged stands of planted eucalypts and cause severe defoliation (Elliott &

Bashford 1978; Roberts & Sawtell 1981; Elliott *et al.* 1990; Abbott 1993; Neumann 1993; Phillips 1993; Farrow *et al.* 1994). Outbreaks can be economically costly as severe defoliation can reduce the growth of trees (Floyd & Farrow 1994) and may eventually kill them if defoliation occurs over several successive years (Came *et al.* 1974).

Currently, management of outbreaks of *M. privata* consists of broad-scale spraying with non-specific chemical insecticides (de Little 1981; Elliott *et al.* 1990; Neumann 1993; Phillips 1993; Neumann & Collett 1997). These chemicals have undesirable effects on the environment, may exacerbate outbreaks of *M. privata* and other defoliators by eliminating natural enemies and may induce insecticide resistance (Huffaker 1980; Risch 1987; Neumann 1992). Alternative pest management techniques such as biological control, target-specific chemicals and silvicultural methods have the potential to minimise environmental damage and contribute to sustainable management practices (Huffaker 1980; Ohmart 1990; Floyd & Farrow 1994). However, successful implementation of any pest management programme requires a thorough knowledge of the ecology of the pest and its natural enemies (Ohmart 1990). Despite the importance of

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©C. LITTLE, D. W. (1981) A study of the autumn gum moth, *Mnesampela privata* Guenée (Lepidoptera: Geometridae) in *Eucalyptus nitens* in north-west Tasmania. Associated Forest Holdings, Internal Report, Hobart (unpubl.).

M. privata as a pest there have been few studies of its biology (e.g. Elliott & Bashford 1978; de Linde 1981; Lukacs 1999) and information concerning its parasitoids is fragmentary.

The aim of this study was to identify parasitoids and hyperparasitoids associated with the larvae of *M. privata* in the ACT and Victoria, conduct an investigation of parasitoid host age preference and examine the influence of sex, viability and parasitism on the pupal weight of *M. privata*. A key to the parasitoid species reared in this study is given and two new braconid species, *Cotesia geometricae* Austin sp. nov. and *Glyptapanteles mnesampela* Austin sp. nov. are described.

Materials and Methods

Study sites

The study was undertaken at two sites in Victoria in September 1992 and one in the ACT during late autumn and winter 1993 and 1994. The sites in Victoria comprised a plantation of *E. globulus globulus* at Altona (37° 50' S, 144° 48' E), and a farm planting at Shepparton (36° 20' S, 145° 13' E) comprising *E. g. globulus*, *E. g. pseudoglobulus* and *E. g. bicostatus*. Both locations had heavy infestations of *M. privata* (up to 100% defoliation by larvae). The ACT site was at Lynham Ridge, Canberra (35° 14' S, 149° 6' E), comprising mixed eucalypt species which were only lightly infested by *M. privata* (approximately 10% defoliation by larvae).

Rearing parasitoids

Parasitoids were reared from late-instar larvae of *M. privata*, the former having pupated in the leaf-bag in which host larvae shelter during the day (Elliott & Bashford 1978; McQuillan 1985). Leaf-bags containing late-instar host larvae and parasitoid cocoons were collected from 44 *E. g. globulus* at Altona, and approximately 10 trees (comprising *E. g. globulus*, *E. g. pseudoglobulus* and *E. g. bicostatus*) at Shepparton. One leaf-bag containing late-instar larvae and parasitoid cocoons was collected from *E. g. bicostatus* at Lynham Ridge in late August 1994.

Each parasitoid cocoon (or group of cocoons that were spun together in the instances of multiple parasitism) was trimmed from the leaf-bag, placed in a ventilated vial (2 cm diam. x 8 cm high) and incubated at 20 ± 2°C. Approximately 130 such samples resulted from material collected from Altona, 13 from Shepparton and one from Lynham Ridge. Vials were checked weekly until parasitoids began to emerge and then every 1–3 days for two

weeks. A final check was made after 18 days. Adult parasitoids were removed as they emerged and placed in 70% ethanol.

Host age preference

To investigate the host age preference of larval parasitoids, a range of available instars was collected from *E. g. bicostatus* at Lynham Ridge on eight occasions in 1993. Collections were made 2–3 weeks apart, over the period that larvae were present (early May to late August). On each occasion 2–12 trees were inspected and groups of 1–19 (median of 5.5) larvae collected from each tree. Larvae were reared in ventilated plastic containers (120 mm diam. x 95 mm high), provided with a small branch of juvenile *E. g. bicostatus*, the stem of which was placed through a hole in the base of the container and into water below. Foliage was changed twice weekly. Larvae were reared at 25 ± 2°C under natural light conditions. When larvae or pupae of parasitoids were observed with a dead or dying *M. privata* larva, the date, number of parasitoids present and the instar of the host larva were recorded. Larvae that died for reasons other than parasitisation were not included in the analysis. Head capsule size was used to estimate the larval instar of *M. privata* (Elliott & Bashford 1978). Parasitoid larvae or pupae were removed to individual ventilated vials (2 cm diam. x 8 cm high) and incubated at 22 ± 2°C until the adults emerged. Adults were stored in 70% ethanol.

Pupal weight

Mnesampela privata larvae collected from Lynham Ridge that pupated successfully were weighed within three days of pupation. Each pupa was incubated in a ventilated vial (20 mm diam. x 80 mm high) at a temperature of 4.0 ± 0.5°C and 70% relative humidity until late October. In November, pupae were placed outside in natural light and temperature regimes and relative humidity was maintained at 70%. Pupae were inspected monthly from mid-January for the emergence of parasitoids or adult *M. privata*. Parasitoids emerging from host pupae were stored in 70% ethanol. The sex of adult *M. privata* was determined using the morphology of the frenulum (after Elliott & Bashford 1978) and that of non-viable pupae by the position of the genital scar (Lawrence *et al.* 1991). One-way ANOVA was performed to test if the outcome of pupae of *M. privata* (i.e. the emergence of either a male or female adult *M. privata*, an adult parasitoid or the death of the pupae) influenced weight at pupation (Sokal & Rohlf 1981), with significantly different groups separated by Scheffé's test of multiple contrasts (Zar 1984). A chi-square goodness-of-fit test was used to compare the sex ratios of pupae and adults with an expected ratio of 1:1 (Sokal & Rohlf 1981).

† LUKACS, Z. (1999) Phenology of the autumn gum moth *Mnesampela privata* (Cresson). PhD thesis, University of Tasmania (unpubl.).

Pearson's chi-square was performed to determine if successful pupation to adult was independent of the sex of the pupa (Sokal & Rohlf 1981).

Results

Parasitoid complex

Cocoons formed by two species of primary parasitoids were present in the leaf-bags collected at Altona and Shepparton (Table 1). The most common cocoon, made by *Cotesia geometricae* (Braconidae), was white, about 4 mm in length and found in groups spun together with silk. The other type of cocoon, formed by *Casinaria micra* Jermin & Gauld (Ichneumonidae), was mottled orange-brown, about 6 mm in length and solitary. Five species of hyperparasitoids emerged from the cocoons of *C. geometricae* (Table 1), the most numerous being a species of *Isdromas* (Ichneumonidae) (hereafter referred to as *Isdromas* species A). A second species of *Isdromas* (*Isdromas* species B), *Megadicylus* sp. (Pteromalidae), *Mesochorus* sp. (Ichneumonidae) and *Elasmus* sp. (Elasmidae) also emerged from the cocoons of *C. geometricae*. *Cotesia geometricae* also emerged from cocoons present in the leaf-bag collected at Lyneham Ridge in 1994. However, *C. geometricae* was not reared from larvae collected at Lyneham Ridge in 1993. Instead, another braconid, *Glyptapanteles mnesampela*, pupated in groups of one or two white cocoons external to the late-instar host (Table 2). *Casinaria micra* was also reared from a larva collected at Lyneham Ridge in 1993 and the larval-pupal parasitoid, *Heteropelma scaposum* (Morley) (Ichneumonidae) emerged from the pupae of *M. privata* reared over the summer of 1993-94.

Relative frequency of parasitoids reared from parasitoid cocoons present in leaf-bags

Of the 130 samples collected from Altona, 69 resulted in the emergence of *C. geometricae* and/or its hyperparasitoids (536 individuals) and 10 with *C. micra* (Table 1), while 51 did not yield any parasitoids. The 13 samples from Shepparton resulted in four without emergence, four with *C. geometricae* and/or its hyperparasitoids (17 individuals) and five with *C. micra*. The single sample collected in 1994 at Lyneham Ridge yielded 14 individuals of *C. geometricae*. The cocoons in each group of *C. geometricae* were not counted or examined closely for prior emergence, so it was not possible to determine the average number of cocoons per group based on the number that emerged, or to calculate accurately the relative frequency of successful emergence, non-viability and hyperparasitisation. Bearing this in mind, about one-third of the groups of *C. geometricae* cocoons resulted in the exclusive emergence of *C. geometricae*, one-third resulted in an initial emergence of *C. geometricae* followed by the emergence of *Isdromas* sp. A from the remainder of the cocoons (N.B. six of these groups also yielded *Isdromas* sp. B, *Megadicylus* sp. and *Mesochorus* sp. after an initial emergence of *C. geometricae*), and one-third exclusively yielded hyperparasitoids, *Isdromas* sp. A, *Isdromas* sp. B, *Megadicylus* sp. and *Mesochorus* sp. emerged from cocoons collected at Altona, and *Isdromas* sp. A and *Elasmus* sp. from Shepparton (Table 1). Thus, at the two sites in Victoria, *C. geometricae* was the most frequent primary parasitoid of larvae but about half of its cocoons were hyperparasitised, primarily by *Isdromas* sp. A.

TABLE 1. Parasitoid species emerging from cocoons associated with the larvae of *Mnesampela privata* collected in Altona and Shepparton, Victoria in 1992. *Total number of cocoons per group was not counted.

Cocoon type	Biology	Species emerged	Altona		Shepparton	
			No. individuals	% of total No. individuals	No. individuals	% of total No. individuals
White, gregarious	Primary parasitoid	<i>Cotesia geometricae</i>	252	47.0	4	23.6
	Hyperparasitoid	<i>Isdromas</i> sp. A	246	45.9	10	58.9
		<i>Mesochorus</i> sp.	18	3.4	0	-
		<i>Isdromas</i> sp. B	11	2.1	0	-
		<i>Megadicylus</i> sp.	9	1.7	0	-
		<i>Elasmus</i> sp.	0	-	3	17.7
		Total No. individuals	536	-	17	-
	*Median No. of emergences/group	6	-	4	-	
Orange, solitary	Primary parasitoid	<i>Casinaria micra</i>	10	-	5	-

TABLE 2. Parasitisation of larvae of *Mnesampela privata* collected at Lyneham Ridge (Canberra, ACT) in 1993. *In 1994 *Cotesia geometricae* was reared from parasitoid cocoons present in a *M. privata* leaf-bag.

<i>M. privata</i> collection		Parasitoid emergence			
Date	Instar	Date	Host instar	No. emerged	Parasitoid species
2/05/93	2	22/06/93	4	1	<i>Glyptapanuleles mnesampela</i>
2/05/93	2	22/06/93	4	2	<i>G. mnesampela</i>
16/05/93	3	22/06/93	4	1	<i>G. mnesampela</i>
2/07/93	4	11/07/93	5	1	<i>Casinarvia micra</i>

Casinarvia micra occurred less frequently and did not appear to have any hyperparasitoids. Estimates of the relative frequency of larval parasitoids at Lyneham Ridge in 1994 could not be made as only a single sample was collected and a comprehensive survey was not undertaken.

Relative frequency of parasitoids reared from collected larvae of *M. privata*

The 426 larvae of *M. privata* collected at Lyneham Ridge in 1993 yielded only four individuals of *G. mnesampela* and one of *C. micra* and neither species was hyperparasitised (Table 2). The collection of *M. privata* larvae prevented hyperparasitism of parasitoid cocoons and probably limited hyperparasitism via the larval host. However, none of the larvae collected in their fourth or fifth instar (28%) contained secondary parasitoids, suggesting that the frequency of hyperparasitoids was very low at this site. Fifty-six percent of pupae resulting from collected larvae died before mid January 1994, 34% pupated successfully

to adult *M. privata* and 10% resulted in the emergence of *H. scaposum*. Thus, the larval-pupal parasitoid *H. scaposum* was the most successful parasitoid attacking larvae at Lyneham Ridge in 1993.

Host age preference

Three larvae collected in their second or third instar yielded *G. mnesampela* in the fourth instar (Table 2). This result shows that *G. mnesampela* can parasitise second instar hosts. The possibility that first instar hosts can be parasitised was not confirmed and insufficient parasitoids were reared to determine if later host instars are also vulnerable. The host age preference of *C. micra* is unclear as only one host larva, collected in its fourth instar, was parasitised. *Heteropelma scaposum* were observed attempting to parasitise both early- and late-instar larvae of *M. privata* in the field. However, percent parasitism by *H. scaposum* did not increase significantly with host age suggesting that parasitisation of later instars was not as successful (Table 3).

TABLE 3. Percent emergence of the larval-pupal parasitoid, *Heteropelma scaposum*, in relation to the instar at which its host, *Mnesampela privata*, was collected Lyneham Ridge (Canberra, ACT.)

Instar of <i>M. privata</i> at collection	No. pupae	% emergence		
		<i>H. scaposum</i>	<i>M. privata</i>	No emergence
2	57	11	32	58
3	73	10	38	52
4	50	10	32	58
5	29	10	34	55

TABLE 4. Effect of the outcome of pupae on the weight of pupae of *Mnesampela privata* three days after pupation. * $p < 0.05$; Scheffé's test of multiple contrasts.

Outcome	Mean weight \pm SE (mg)	F
Adult male <i>M. privata</i> v. adult female <i>M. privata</i>	149 \pm 3.7 v. 127 \pm 3.2	17.68*
Male pupae that died v. female pupae that died	130 \pm 3.1 v. 109 \pm 2.6	26.63*
Adult <i>M. privata</i> v. pupae that died	140 \pm 2.8 v. 119 \pm 2.2	31.89*
Adult <i>M. privata</i> v. adult <i>H. scaposum</i>	140 \pm 2.8 v. 142 \pm 5.8	0.46
Adult <i>H. scaposum</i> v. pupae that died	142 \pm 5.8 v. 119 \pm 2.2	17.44*

Pupal weight

The outcome of pupae (categorised by the emergence of either a male or female adult *M. privata*, an adult *H. scaposum* or the death of the pupae) significantly influenced the weight of pupae at pupation ($F = 22.9$; $df = 4, 200$; $p < 0.001$). Pupae that died were significantly lighter than both pupae that successfully produced adult *M. privata* and

parasitised pupae resulting in adult *H. scaposum* (Table 4). Pupae resulting in adult female *M. privata* were significantly heavier than those resulting in males. However, the weights of pupae resulting in adult *H. scaposum* were not significantly different from those of pupae resulting in adults of *M. privata* (Table 4). The sex ratios of pupae of *M. privata* (not including pupae that resulted in *H. scaposum*) and *M. privata* that emerged as adults were 1:1.04 ($n = 188$) and 1:1.33 ($n = 72$) (male : female) respectively. Neither ratio was significantly different from 1:1 ($\chi^2 = 0.085$ and 1.389 respectively, $df = 1$, $p > 0.05$). Successful pupation was independent of the sex of the pupa ($\chi^2 = 1.61$; $df = 1$; $p > 0.05$).

Biology of parasitoids

Family Braconidae

Cotesia geometricae Austin sp. nov.

&

Glyptapanteles mnesampela Austin sp. nov.

(FIGS 5, 9, 10)

All known species of the microgasterine genera *Cotesia* and *Glyptapanteles* are endoparasitoids of macrolepidopterans (Austin & Dangerfield 1992) although there is no previous record of either genus parasitising larvae of *M. privata*. The species reared during this study are unknown and described below as two new species. *Cotesia* and *Glyptapanteles* can be easily recognised from other parasitoids associated with this host by the absence of venation in the distal part of the fore wing, the absence of vein 2mcu (Fig. 5), their small size and dark colour. Superficially, they are similar to each other and could be easily misidentified as a single species. However, the shape and sculpturing of the first and second metasomal tergites can be used to readily separate them (Figs 9, 10) (see descriptions below for further detail).

Glyptapanteles mnesampela can parasitise second instar larvae of *M. privata* although it is not known if first or later instars are also vulnerable. Final-instar larvae of *G. mnesampela* and *C. geometricae* emerge from the penultimate or final instar of *M. privata*, aggregate and pupate near the pupae. This life history is consistent with other members of *Glyptapanteles* and *Cotesia* except that not all species in these two genera are gregarious; some are known to be solitary (Austin & Dangerfield 1992). Adult *C. geometricae* emerged 13–24 days after the collection of their cocoons at the field site in Altona, Victoria (Fig. 1).

Family Ichneumonidae

Casnarina micra Jerman & Gauld

(FIGS 3, 12)

All known species of *Casnarina* are solitary endoparasitoids of lepidopteran larvae. This study

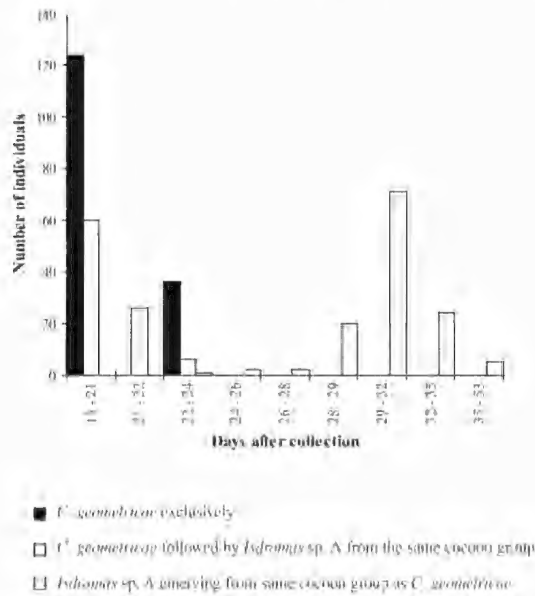


Fig. 1. Temporal pattern of emergence of the gregarious, primary parasitoid *Cotesia geometricae* sp. nov. and its hyperparasitoid *Ischnomyia* sp. A. from groups of cocoons associated with the larvae of *Mnesampela privata* (Guenée) collected at Altona, Victoria.

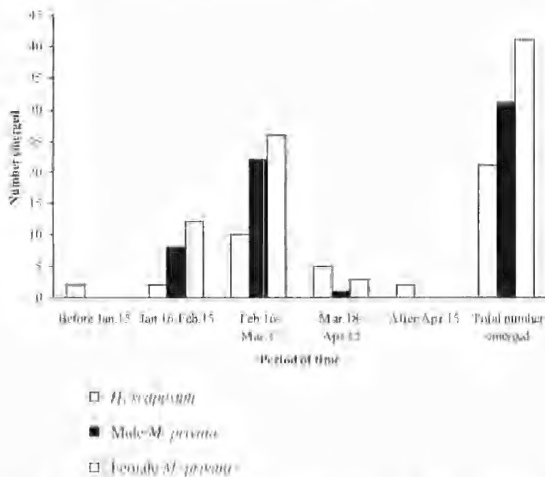


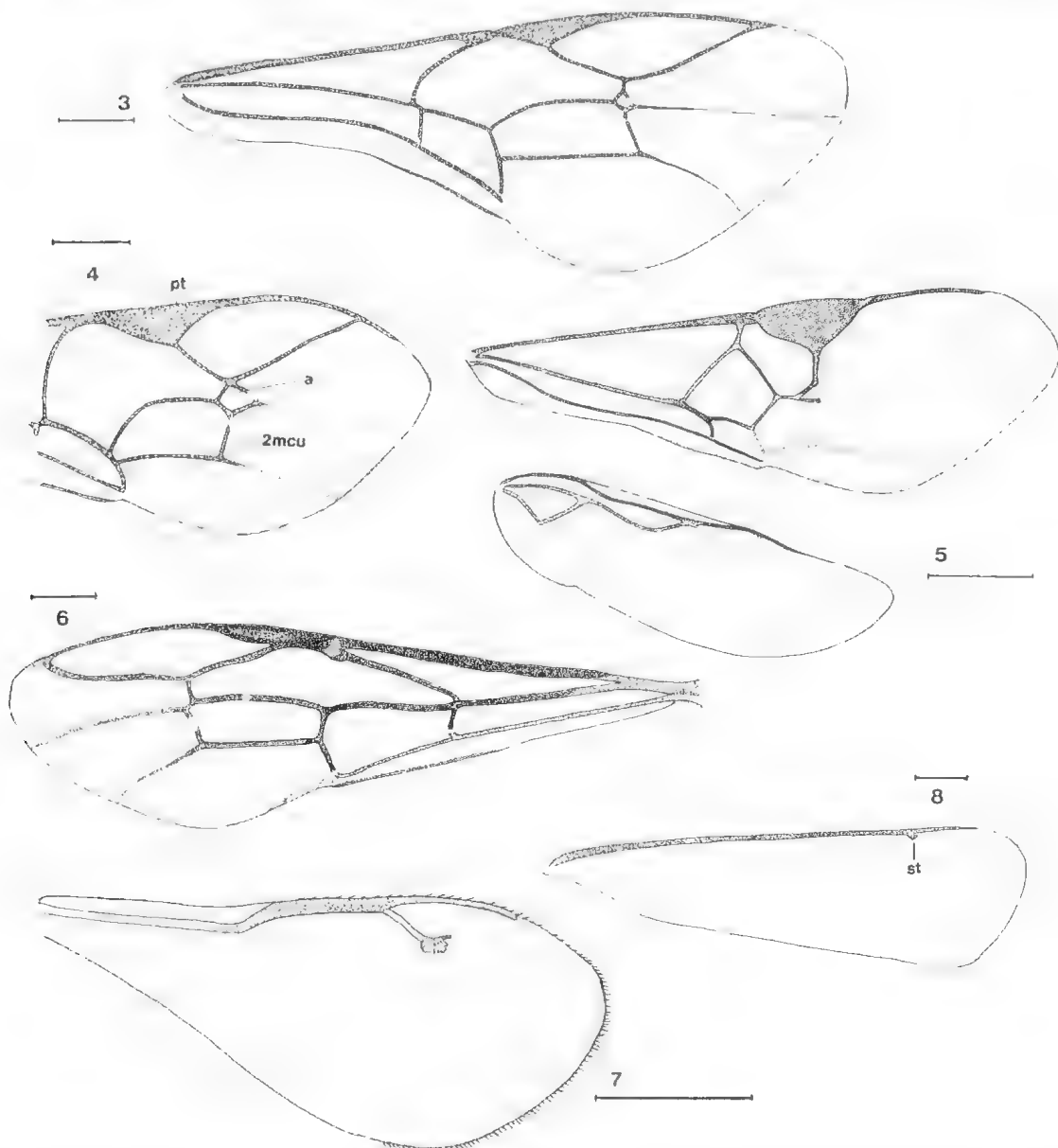
Fig. 2. Temporal pattern of emergence of adult *Mnesampela privata* (Guenée) and the larval-pupal parasitoid *Heteropelma scaposum* (Morley).

provides the first record of *C. micra* reared from *M. privata*. Specimens of a *Casinaria* were reared from *M. privata* larvae collected by Elliott and Bashford (1978) but were not identified to species. In this study, *C. micra* killed late-instar larvae. This result differs from that of Jerman and Gauld (1988) who observed *C. micra* killing *Muesampela* (species not specified) in an early instar. However, Allen (1990) found adults of *C. micra* emerging from mid- to late-instar larvae of *Uraba lugens* Walker (Noctuidae).

The specimens reared from cocoons in Victoria were all solitary emergences which occurred 15-27 days after collection.

Heteropelma scaposum (Morley)
(FIGS 6, 14)

This species is a common solitary larval-pupal parasitoid with numerous host associations including *Pararguda australasia* (F.) (formerly *Digglesia*



Figs 3-8. Wings. Fig. 3. *Casinaria micra* Jerman & Gauld. Fig. 4. *Mesochorus* sp. Fig. 5. *Glyptapanteles muesampela* sp. nov. Fig. 6. *Heteropelma scaposum* (Morley). Fig. 7. *Megadictylas* sp. Fig. 8. *Elasmus* sp. Scale bars = 0.5 mm 3-5, 7; 1.0 mm 6; 200 μm 8. Abbreviations: a = arcolet; pt = pterostigma; st = stigmal vein.



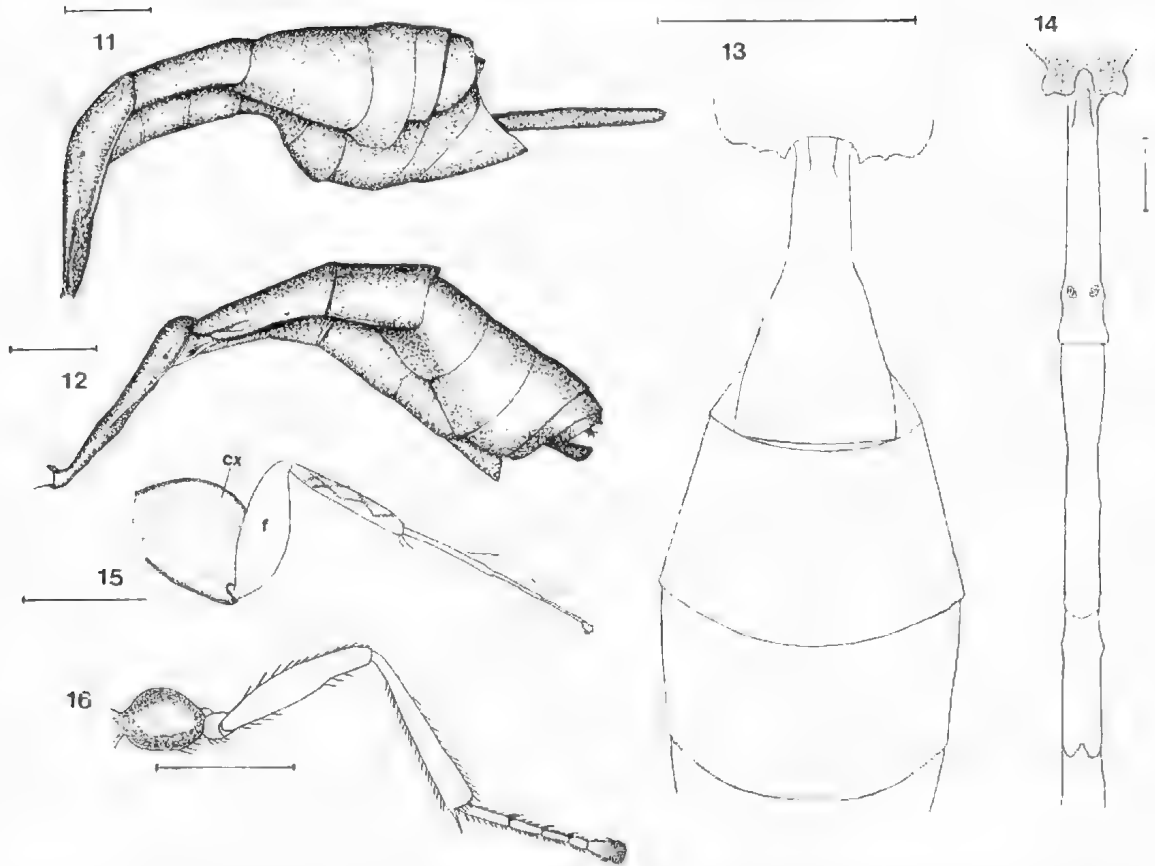
Figs 9, 10. Propodeum and metasomal tergites 1-3. Fig. 9. *Cotesia geometricae* sp. nov. Fig. 10. *Glyptapanteles mnesampela* sp. nov. Scale bars = 100 μ m.

australasia) (Lasiocampidae) and the agricultural pests *Helicoverpa armigera* (Hübner) and *Spodoptera litura* F. (Noctuidae) (Gauld 1984). In these associations *H. scaposum* parasitises its host in an early instar (Gauld 1984). It has previously been identified as a larval-pupal parasitoid of *M. privata* in Tasmania and Victoria (de Little 1981¹; Lukacs 1999²). In this study, *H. scaposum* appeared to be most successful in parasitising early-instar larvae (Table 3). This is consistent with early instars of *M. privata* not forming protective leaf bags and thus being more vulnerable to parasitoid attack and with the fact that larger late-stage larvae exhibit more effective defensive responses (rearing and regurgitating drops of *Eucalyptus*-scented fluid) (Elliott & Bashford 1978; Schumacher, pers. obs.). In addition, Lukacs (1999²) observed oviposition in

first instar larvae of *M. privata* but none in later instars. Larvae of *H. scaposum* do not develop beyond the first instar until the host pupates (Gauld 1984). The average weight of pupae that yielded *H. scaposum* was not significantly different from that of the mean weight of viable pupae (Table 4), indicating that parasitism by *H. scaposum* does not influence the behaviour or growth of larval hosts. The temporal patterns of emergence of male and female *M. privata* and *H. scaposum* were similar (Fig. 2) with most emerging between mid-February and mid-March.

Isdromus spp.
(FIG. 13)

Isdromus species are commonly reared as hyperparasitoids from small ichneumonid or



Figs 11, 12. Lateral metasoma. Fig. 11. *Mesochorus* sp. Fig. 12. *Cosinaria micra* Jerman & Gauld. Figs 13, 14. Dorsal metasoma (sculpturing not shown). Fig 13. *Isdromus* sp. A. Fig. 14. *Heteropelma scaposum* (Morley). Figs 15, 16. Hind leg. Fig. 15. *Elasmus* sp. Fig. 16. *Megadictylus* sp. Scale bars – 1.5 mm 11, 12; 0.5 mm 13, 15, 16; 1.0 mm 14. Abbreviations: cx = coxa, f = femur.

braconid cocoons, particularly from microgasterine braconids, although they are also recorded as primary parasitoids of a range of lepidopteran hosts (Gauld 1984). There are about 30 species known from Australia, all except three are undescribed including the two species reared during the present study. There is no doubt that they are hyperparasitoids in the cocoons of *C. geometricae* (Table 1), given that no other cocoons were present and the larval cadavers of *M. privata* were not left in the rearing vials. The peak of the subsequent emergence of *Isdromus* sp. A occurred 11-16 days after *C. geometricae* emergence (Fig. 1).

Mesochorus sp.
(FIGS 4, 11)

Mesochorus spp. are hyperparasitic on the endophagous larvae of Braconidae and Tachinidae (Gauld 1984). Within lepidopteran hosts, mesochorines will often attack gregarious endo-

parasitoids, especially microgasterine braconids (Gauld 1984; Allen 1990). In this study *Mesochorus* sp. was reared from cocoons of *C. geometricae*. Species of *Mesochorus* also parasitise *Cotesia urabae* Austin & Allen (Braconidae) and *C. micra* via *U. lugens* (Austin & Allen 1989; Allen 1990), as well as the tachinid parasitoids of *Paropsis atomaria* Olivier (Coleoptera: Chrysomelidae) (de Little 1982) and *Perga* spp. (Hymenoptera: Pergidae) (Carme 1969).

Family Elasmidae
Elasmus sp.
(FIGS 8, 15)

Members of this genus are obligate hyperparasitoids of Lepidoptera. One species, *E. australiensis* Girault, has been reared from *C. micra* and two microgasterine braconids via *U. lugens*. In this study only three specimens of *Elasmus* sp. were reared from *C. geometricae* via *M. privata* and they

may be similarly parasitic on *C. miera* although this association was not confirmed.

Family Pteromalidae
Megadictylus sp.
(FIGS 7, 16)

Megadictylus spp. are primary parasitoids of lepidopteran larvae and pupae in cocoons, or are hyperparasitoids on them. They have previously been associated with several lepidopteran families, as well as microgastrine braconid cocoons (Bauček 1988). This is the first record of a species being reared from *M. privata*. It is most likely a hyperparasitoid of *C. geometricae* as no other cocoon types were noticed and the cadavers of *M. privata* larvae were not left in the rearing vials. Only one species has been recorded from Australia, *M. dubius* (Girault) but the association with *M. privata* has not been confirmed as this species.

Other parasitoids associated with
Mnesampela privata
(Ichneumonidae and Tachinidae)

Apart from the species discussed above a number of other parasitoids has been previously reared from *M. privata* but these were not recorded in the present study. They include the ichneumonids *Eriborus* sp., *Megaceria pagana* (Morley), *Prislicerox* sp., *Campoplex* sp. and ?*Anacris* sp., and an unidentified tachinid fly (Elliott & Bashford 1978; de Little 1981; Gauld 1984; Lukaec 1999?) (Table 5). Of these species, all have been reared from *M. privata* in Tasmania with the exception of *M. pagana* which is known only from Victoria (Gauld 1984). However, Gauld (1984) recorded an unknown species of *Megaceria* from *M. privata* in Tasmania and it is very likely to be this species. Based on the biology of other species belonging to these ichneumonid genera, all of them are probably solitary primary endoparasitoids (Gauld 1984). We have not been able to examine material of these species and so have not included them in the key, although their distribution and biological characteristics are compared with the species recorded in the present study in Table 5.

Key to the parasitoids of *Mnesampela privata* at
the three study sites

1. Fore wing with relatively complete venation (Figs 3-6); small to large species, > 2.5 mm in length 2
2. Fore wing with pigmented venation reduced to anterior margin (Figs 7, 8); minute to small species, < 2.5 mm in length 8
3. Fore wing with venation distal to pterostigma wanting (Fig. 5); vein 2m-cu absent (Braconidae) 3
3. Fore wing with distal veins present and well-pigmented; vein 2m-cu present (Figs 3, 4, 6) (Ichneumonidae) 4
4. Propodeum and metasomal tergites 1 and 2 virtually smooth; tergite 1 narrowing apically; tergite 2 with subtriangular median field (Fig. 10) *Glyptopanteles mnesampela* sp. nov.
5. Propodeum and metasomal tergites 1 and 2 with obvious dense punctation; tergite 1 moderately broad, parallel-sided; tergite 2 broad and rectangular (Fig. 9) *Cotesia geometricae* sp. nov.
4. Fore wing with an areolet (Figs 3, 4) 5
5. Fore wing without an areolet (Fig. 6) 6
5. Scutum and propodeum densely punctate or rugulose; ovipositor very short, not protruding past posterior metasomal tergites (Fig. 12) (body 7-8 mm in length, dark brown to black, legs reddish; ♂ genitalia without pair of long rods) *Casinaria miera* Jerman & Gauld
6. Scutum and propodeum generally unsculptured (except for propodeal carinae and micropunctures associated with pilosity); ovipositor about 1/3 to 1/2 length of metasoma (Fig. 11) (body 3-4 mm in length, yellow brown with darker markings; ♂ genitalia with pair of long rods protruding posteriorly) *Mesochorus* sp.
6. Metasomal tergite 1 narrow and very elongate (Fig. 14); fore wing with radial cell elongate (Fig. 6) (♀ body length about 20 mm, ♂ 10-12 mm; head and mesosoma black, legs and metasoma yellow to orange-brown) *Heteropelma scaposum* (Morley)
7. Metasomal tergite 1 broadening apically (Fig. 13); fore wing with radial cell short and broad (body length 2.3-3.2 mm not including ♀ ovipositor; head and mesosoma black, metasoma either dark or yellow with dark markings) (*Isdromus* spp.) 7
7. Scutum smooth; fore wing stigma of ♀ clear in posterior half, white anteriorly; ♂ evenly translucent; legs yellow; metasoma either dark and sometimes with lighter transverse bands at sutures or yellow with darker markings *Isdromus* sp. A
8. Scutum with dense punctate sculpturing; fore wing stigma of ♀ and ♂ evenly dark; fore and mid legs light brown, hind legs dark brown; metasoma dark brown to black *Isdromus* sp. B
8. Hind coxa developed as large flat disc; hind tibia with distinct criss-cross pattern of setae (Fig. 15); fore wing with stigmal vein very short (Fig. 8); body dark, tegula and legs

TABLE 5. *Comparison of larval and larval-pupal parasitoids associated with Mnesampela privata at different latitudes in Australia. Sources of data: Elliott & Bashford 1978, de Little 1981, Gauld 1984, Lukacs 1999; this study. la = low altitude (< 500 m asl), ha = high altitude (> 500 m asl). *Species not identified.*

Host stage attacked / emerged	Family	Parasitoid species								
		S Tas. ^a (la)	NW Tas. ^b (ha)	Tas. ^c	Central & NW Tas. ^d (ha)	Vic. ^e	S Tas. (la) & Vic. ^h	S Vic. ^e	ACT ^f	
Primary parasitoid of early instar / L4-5	Braconidae	-	-	-	-	-	-	-	<i>Cotesia geometricae</i>	<i>Cotesia geometricae</i> <i>Glyptapanteles mnesampela</i> <i>Casiniaria micra</i>
	Ichneumonidae	-	-	-	-	-	-	-	-	-
Primary parasitoid of L ₂ larva / L ₂ larva	Ichneumonidae	<i>Casiniaria</i> sp.	-	-	-	-	-	-	-	-
	Ichneumonidae	<i>Eriborus</i> sp. <i>Campoplex</i> sp.	-	<i>Eriborus</i> sp.	-	-	-	-	-	-
Primary parasitoid of L ₂ larva / pupa	Ichneumonidae	-	<i>Heteropelma scaposum</i> Unidentified Cryptinae	<i>Megaceria</i> sp. <i>Pristiceros</i> sp.	<i>Heteropelma scaposum</i> ? <i>Anacis</i> sp. * 1 sp.	<i>Megaceria pagula</i>	<i>Heteropelma scaposum</i> ? <i>Anacis</i> sp.	pupae not reared	<i>Heteropelma scaposum</i>	
	Tachinidae	* 1 sp.	* 1 sp.	-	-	-	-	pupae not reared	-	
Hyperparasitoid of ichneumonid or braconid parasitoids, stage unknown / parasitoid pupa	Ichneumonidae	-	-	-	-	-	-	-	2 spp. of <i>Isdromus</i>	
	Ichneumonidae	-	-	-	-	-	-	-	<i>Mesochorus</i> sp.	
Hyperparasitoid via lepidopteran host, stage unknown / parasitoid pupa	Elasmidae	-	-	-	-	-	-	-	<i>Elasmus</i> sp.	
	Pteromalidae	-	-	-	-	-	-	-	<i>Megadictylus</i> sp.	

2.7 mm, ♂ 1.3-1.9 mm) (Elasmidae).....
*Elasmus* sp.
 Hind coxa normal size; hind tibia without
 criss-cross pattern of setae (Fig. 16); fore wing
 stigmal vein elongate (Fig. 7); body vivid
 iridescent green or blue-green (♀ body length
 3.2 mm, ♂ 2.3 mm) (Pteromalidae).....
*Megadicylus* sp.

Description of new species

Cotesia geometricae Austin sp. nov.
 (FIG. 9)

Holotype: ♀, Victoria, Altona, Dow Chemical Plant,
 10.ix.1992, ex *Mnesampela privata* (ANIC).

Paratypes: 25 ♀♀, 10 ♂♂, same data as holotype
 but 10.ix.1992 and 8.vii.1994 (ANIC, WARI); 10
 ♀♀, 2 ♂♂, Lyneham Ridge, Canberra, ACT (ANIC,
 WARI).

Female

Length: 2.9 mm.

Colour: Head black; face, vertex and occiput with
 dull lustre; antennae and mesosoma black; coxae
 black, legs yellow-brown, apex of hind femur and
 tibia sometimes with darker patch, tarsi black;
 metasoma black except for laterotergites of segments
 1-3 which are yellow-brown; wings hyaline, stigma
 uniformly dark as are fore wing veins C+Sc+R, 1-
 R1, r and 3-Rs, these veins being darker than the rest.

Head: Face, temples and lateral frons with fine,
 dense punctation associated with pilosity; medial
 frons and vertex between ocelli smooth and hairless;
 eyes densely covered with hairs, face slightly
 narrower than half width of head (3.1:6.5), inner
 margins of eyes adjacent to face evenly curved and
 slightly converging ventrally; ocelli large, forming
 slightly obtuse triangle, lateral ocelli separated by
 distance from lateral ocellus to eye margin; antennae
 moderately long, about as long as body.

Mesosoma: Scutum with fine, dense punctation
 associated with dense pilosity, posterior half with
 smooth medial longitudinal line; notauli only very
 faintly indicated by shallow depressions; dorsal
 scutellum smooth except for a few scattered
 punctures along lateral margins; lateral band of
 scutellum very broad and smooth; metanotum not
 fitting against posterior scutellum so that phragma
 of scutellum exposed laterally; propodeum coarsely
 rugulose-punctate, with slight mid longitudinal
 depression and a few short striae radiating from
 ventral margin; lateral pronotum with deep dividing
 grooves which are very slightly punctate; meso-
 pleuron with fine punctation associated with pilosity
 in anterior half and ventrally below precoxal groove,

the rest smooth and shining; precoxal groove finely
 punctate; hind coxa finely punctate in anterior $\frac{2}{3}$ and
 associated with dense pilosity.

Wings: Fore wing stigma broad, 2.3 x as long as
 broad; hind wing broad, vannal lobe convex with
 long marginal fringe of hairs throughout.

Metasoma: T1 slightly longer than wide (3.3:2.9),
 virtually parallel-sided, smooth in anterior half,
 rugulose-punctate in posterior part but much finer
 compared with propodeum; T2 subrectangular, 2.3 x
 as wide as long, lateral margins curving inwards in
 anterior part, surface rugulose-punctate but slightly
 less coarse than on anterior part of T1, longitudinal
 mid-line slightly raised and smoother than lateral
 areas, posterior and lateral margins with single line
 of more distinct punctures; length of T2-T3 1.6:2.0;
 length of T2-T4 equal; T2-T6 smooth and shining,
 with long scattered hairs along posterior margin;
 hypopygium with a few scattered long hairs,
 posterior margin straight to very slightly concave;
 ovipositor sheaths very short and straight, with a few
 long apical hairs.

Male

As for female.

Host

Reared from *Mnesampela privata* (Geometridae).

Comments

The sculpturing on the propodeum and T1-T3, the
 shape of these sclerites, the form of the hypopygium
 and ovipositor, clearly place this species in the genus
Cotesia Cameron. *Cotesia* has previously been
 referred to as the *glomeratus* species-group of
Apanteles s.l. (see Mason 1981; Austin &
 Dangerfield 1992) and it is the largest genus of
 Microgastrinae, comprising hundreds of species
 world-wide. In Australia the genus is both common
 and diverse but other than several species introduced
 from Europe and North America as biological
 control agents for certain lepidopteran pests (see
 Austin & Dangerfield 1992), the Australian fauna
 remains virtually unstudied. One other species, *C.*
urabae Austin & Allen, is also associated with a
 eucalypt-feeding host viz. *Uraba lugens*. *Cotesia*
geometricae differs from this species in that it is
 gregarious, the first metasomal tergite is parallel-
 sided (not broadened posteriorly), the first and
 second tergites are more finely sculptured, the
 median field of the second tergite has rounded
 anterior corners (not angled anteriorly) and the third
 tergite is smooth throughout (not sculptured
 anteriorly). This species is named after the family of
 its host.

Glyptapanteles mnesampela Austin sp. nov.
(FIGS 5, 10)

Holotype. ♀, Australian Capital Territory, Lynham Ridge, 30.iii.1993, ex *Mnesampela privata* 22.vi.1993 (ANIC).

Paratypes. 1 ♀, 3 ♂♂, same data as holotype (ANIC, WARI).

Female

Length: 2.5 mm.

Colour: Head, antennae and mesosoma black but propleuron yellow-brown; fore and mid legs yellow-brown, including coxae, tarsi darker; hind femur and tibia yellow-brown, coxae black, tarsi darker than tibia, distal tibia black; dorsal metasoma yellow-brown in anterior half, black posteriorly, ventral metasoma yellow-brown in anterior two-thirds, black posteriorly; wings hyaline, venation moderately dark, stigma uniformly dark.

Head: Face, temples and lateral frons smooth except for scattered micropunctures associated with hairs; medial frons, vertex between ocelli and occiput smooth and hairless; eyes densely covered with hairs, face slightly narrower than half width of head (2.6:5.8), inner margins of eyes adjacent to face evenly curved; ocelli forming broad obtuse triangle, lateral ocelli separated by more than distance from lateral ocellus to eye margin; antennae long, much longer than body.

Mesosoma: Scutum finely and discretely punctate medially, becoming more densely punctate-reticulate towards lateral margin, densely covered with hairs; notauli only very faintly indicated by shallow depressions; dorsal scutellum smooth with a few small scattered punctures; lateral band of scutellum very broad; metanotum fitting closely against posterior scutellum, phragma of scutellum only exposed in lateral corners; propodeum smooth with a few small radiating striae postero-medially; anterior half of propodeum with a few hairs and associated micropunctures; mesopleuron smooth, covered with hairs in anterior one-third and ventrally below precoxal groove; precoxal groove unsculptured; hind coxa finely punctate, covered with hairs.

Wings: Fore wing with stigma broad, about 2.5 × as long as broad; base of 2-M pigmented; hind wing broad, vannal lobe convex with long marginal fringe of hairs throughout.

Metasoma: T1 mostly smooth with a few faint striae, lateral margins evenly narrowing, with a few scattered long hairs; median field of T2 delimited laterally and posteriorly by distinct sulci, almost an equilateral triangle in shape, length of T2-T3 1.3:1.6; T2-T6 smooth and shining, T2 without hairs, T3-T6

with long scattered hairs; hypopygium with a few scattered long hairs; ovipositor sheaths very short and straight, with a few long apical hairs.

Male

As for female except as follows: Antennae longer and more robust; head and scutum with denser white hairs; scutum with denser punctation; metasoma all black; hind legs with femur darker or infuscate.

Host

Reared from *Mnesampela privata* (Geometridae), the autumn gum moth.

Comments

Glyptapanteles is a large cosmopolitan genus of several hundred species, which comprises mostly the *viripennis* and *octonatus* species-groups (sensu Nixon 1965), as well as a number of smaller groups, all of which are extra-limital except for the monospecific *demeter* group from New Zealand (Nixon 1965; Mason 1981). In Australia and Tasmania there are an estimated 100 plus species of *Glyptapanteles*, only one of which is described, *G. deliata* Austin & Dangerfield. The genus is most diverse in the tropical parts of the continent, and appears to be disproportionately represented in the microgastrine fauna of the south eastern Pacific, from where a number of aberrant species have been described, e.g. *G. demeter* (Wilkinson) from New Zealand, which is strongly dorso-ventrally flattened and *G. ufimatuana* (Fullaway) from Samoa, which has a complete medial propodeal carina, vasiform T1 and stub of vein 3-Rs present in the fore wing (Austin & Dangerfield 1992).

Glyptapanteles mnesampela can be distinguished from *G. deliata* and most other undescribed Australian species by its colour, shape of metasomal tergites 1 and 2, and sculpturing of the scutum and propodeum. Although the degree of host specificity of *Glyptapanteles* spp. is poorly known, it is also likely that host associations provide a useful initial guide to the identity of many microgastrine parasitoids and this is probably the case for this species. *Glyptapanteles mnesampela* is named after the host genus.

Discussion

This study has expanded the known parasitoid complex of larvae of *M. privata* in south-eastern Australia to include the primary parasitoids *Casimaria miera* and two new braconid species, *G. mnesampela* and *C. geometricae* and five species of hyperparasitoid, in addition to several previously recorded species (Elliott & Bashford 1978; de Little 1981; Gauld 1984; Lukacs 1999) (Table 5). The

parasitoid complex of a host species is often stable between geographical locations when the host feeds on the same (or taxonomically related) plant species (Askew & Shaw 1986; Mills 1993). However, the parasitoids reared from *M. privata* do not appear to follow this generalisation in that the species reared at the two mainland sites (Victoria and the ACT) differed both from each other and from those previously reported from Tasmania and Victoria (Table 5). In particular, *G. muesampela* has only been found in the ACT but no hyperparasitoids were recorded from this site and are also apparently absent in Tasmania. Two species of larval parasitoid recorded in Tasmania (Elliott & Bashford 1978; Gauld 1984) have not been recorded from the mainland and several larval-pupal parasitoids recorded in Tasmania and Victoria (Elliott & Bashford 1978; de Little 1981; Gauld 1984; Lukacs 1999) were not found in this study. In addition, two different species of primary parasitoid were collected in consecutive years at Lyneham Ridge although it is possible that both species were present during both years but were not found due to the low level of parasitism at the site. In part, differences between parasitoid complexes may reflect collecting bias and an initial naive separation of different parasitoid species in the 1992 Victorian collection (i.e. pupae were not reared and *G. muesampela* may have been confused with *C. geometrianae*). However, the relative abundance of a host can significantly influence the composition and number of parasitoid species it can support (Mills 1990; Mills & Kenis 1991). The greater species richness of the parasitoid complex found at Altona and to a lesser extent Shepparton, therefore, may also be due to the higher relative host abundance at these locations. The paucity of parasitoids in the de Little (1981) study (Table 5), which was also undertaken during a severe outbreak, may be because only parasitoids seen ovipositing into larvae were identified. Differences in host phenology may also contribute to differences in the make-up of parasitoid complexes (Askew & Shaw 1986). Although most populations of *M. privata* have a dominant autumn-winter population (McQuillan 1985) and an almost insignificant summer population (Lukacs 1999), the latter study found that populations at higher altitudes in Tasmania (> 300m ash) can also have a large summer-—autumn population and are potentially bivoltine. With this in mind it should be noted that the survey by de Little (1981) was made during a summer outbreak at a high altitude location in NW Tasmania whereas Elliott & Bashford (1978) and this study examined lower altitude populations present over autumn and winter (N.B. Lukacs (1999) did not differentiate between summer and autumn populations of host larvae or specifically record the altitude of the

collecting sites). Further investigation of the influence of temporal and geographical variation of host abundance on the composition of the parasitoid complex utilising larvae of *M. privata* will be required to clarify these discrepancies.

This study found that *M. privata* had an equal sex ratio at both pupation and emergence. However, although the present results did not show a significant departure from a 1:1 sex ratio, the trend towards a greater proportion of female adults resembles that found by Elliott & Bashford (1978) who obtained 64% female adults from reared larvae. The significantly lower weight of pupae that died suggests that larvae must achieve some critical weight to survive the pupal period. The degree of overlap of weights between viable male and female pupae of *M. privata* indicates that prediction of sex based on weight is not feasible.

The primary parasitoids of *M. privata* larvae recorded in this and other studies (Elliott & Bashford 1978; de Little 1981; Gauld 1984; Lukacs 1999) kill their host in late instars or as pupae. These parasitoids may reduce defoliation to some extent as larvae are most destructive in their fourth and fifth instars (Elliott & Bashford 1978). However, in addition to their effect during the current season, larval parasitoids may reduce the number of *M. privata* that emerge in the next generation. The potential role of these parasitoids in biological control, therefore, is likely to be one of regulation and prevention of outbreaks rather than as a method of control when an outbreak is occurring.

Although the causes of outbreaks of *M. privata* are unclear it appears that large monocultures of genetically similar species are especially vulnerable (Neumann & Collett 1997). The ineffectiveness of parasitism in such situations (Elliott & Bashford 1978; de Little 1981; Neumann & Collett 1997) may be due to low numbers of natural enemies limited by the lack of alternative food sources, coupled with rapid population growth of the insect herbivore in an area of dense and abundant resources (Root 1973; Altieri & Letourneau 1984; Altieri *et al.* 1993). In addition, the use of non-specific insecticides will curtail the numerical response of larval parasitoids and thus prevent their contribution to stabilising host populations.

Research into the sustainable management of pest insects is seen as an important step to improve the currently poor economic returns from eucalypt forests (Stone 1993). Current research in Australia has included the evaluation of strains of *Bacillus thuringiensis* Berliner (Harcourt *et al.* 1996; Neumann & Collett 1997), the use of naturally resistant species and provenances of *Eucalyptus* (Farrow *et al.* 1994) and interactions between the scoliid egg parasitoid, *Ichneumon* sp., and its host

M. privata (Schumacher 1997; Lukacs 1999). The effect of augmenting or encouraging natural populations of larval and egg parasitoids of *M. privata* through practices such as the use of selective insecticides and the provision of alternative food sources for adult parasitoids has not been investigated, although the benefits of such practices have been shown in eucalypt plantations in South America (Bragança *et al.* 1998) as well as other pest-parasitoid systems (Idris & Graius 1995; Orr & Pleasants 1996). The accurate identification of the natural enemies of *M. privata* and an understanding of their ecology will be essential to the success of such research in Australia.

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FOSSIL LIZARDS FROM THE EARLY PLIOCENE BLUFF DOWNS LOCAL FAUNA

BY BRIAN S. MACKNESS & MARK N. HUTCHINSON†*

Summary

Mackness, B. S. & Hutchinson, M. N. (2000) Fossil lizards from the Early Pliocene Bluff Downs Local Fauna. *Trans. R. Soc. S. Aust.* 124(1), 17-30, 31 May, 2000.

The lizard fauna of the Early Pliocene Bluff Downs Local Fauna consists of members of the families Scincidae, Gekkonidae, Agamidae and Varanidae. At least three living scincid taxa, *Egernia hosmeri*, *Tiliqua scincoides* and a member of the *Eulamprus quoyii* complex, have been identified from dentary, maxillary and skull roof elements.

Key Words: Pliocene, Bluff Downs Local Fauna, lizards, *Egernia*, *Tiliqua*, *Eulamprus*, *Heteronotia*, ?*Megalania*, varanids.

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The lizard fauna of the Early Pliocene Bluff Downs Local Fauna consists of members of the families Scincidae, Gekkonidae, Agamidae and Varanidae. At least three living scincid taxa, *Egernia hosmeri*, *Tiliqua winemans* and a member of the *Eulamprus quoyii* complex, have been identified from dentary, maxillary and skull roof elements. The gekkonids are represented by a nearly complete dentary, which is tentatively referred to the living genus *Heteromotis*. Agamids are represented by unidentified dentary remains. A giant varanid, *Megalania* sp., was the only extinct lizard found; other smaller varanid remains were also recovered. The gekkonid is the first published Pliocene record of the family from Australia. The fauna, consisting largely of taxa with close phyleric links to the modern lizard fauna of eastern Australia, is a further example of the evolutionary conservatism of Australian herpetological assemblages since the Miocene.

KEY WORDS: Pliocene, Bluff Downs Local Fauna, lizards, *Egernia*, *Tiliqua*, *Eulamprus*, *Heteromotis*, *Megalania*, varanids.

Introduction

Squamates are poorly represented in the Australian fossil record (Molnar 1982, 1984a,b, 1985, 1991). The few records older than the K-T boundary (Bartholomai 1979) are suspect, as the groups to which they were assigned (Paliguaniidae and Profaetertiformes) are now thought to be non-squamate or, at best, of uncertain affinities. Molnar (1985) reported that vertebrae of a small lepidosaur (possibly a sphenodontid) had been found in the Cretaceous Toolebuc Formation of Queensland. Some fragmentary remains of 'lizards' including a rib (Flannery & Rich 1981), a humerus (Molnar 1980) and an incomplete maxillary (or dentary) (Molnar 1985) have yet to be fully described. A supposed lizard jaw from the early Cretaceous Dinosaur Cove has proven to be a fish (Molnar & Czechura 1990).

The earliest Australian Tertiary lizard mentioned in the literature (based on a submitted manuscript cited in Rich *et al.* 1991) is from the Eocene Tingamarra Local Fauna (Molnar 1991). Now published, this paper (Godthelp *et al.* 1992) reports no lizards. Unpublished data do exist to indicate the presence of squamates at the site (MNH, pers. obs.) but the remains are at present, too few and fragmentary to reach conclusions regarding their relationships to the

living fauna. The first confirmed record of lacertilians with modern day counterparts comes from the Oligo-Miocene deposits of central Australia (Stirton *et al.* 1967 (this record is actually of a snake vertebra) (see Estes 1984) (Estes 1984; Pledge 1984). The Miocene limestone deposits of the Riversleigh area of north-western Queensland are known to contain fossils of agamids, varanids, gekkonids and scincids (Archer *et al.* 1989, 1991; Covacevich *et al.* 1990; Hutchinson 1992; Shea & Hutchinson 1992).

Pliocene records of lizards include *Varanus* sp. indent. and *Tiliqua* sp. from the Currumbulka Local Fauna (Pledge 1992), *Tiliqua* sp. from Wellington Caves (Hand *et al.* 1988), *Megalania* sp. from the Chinchilla Local Fauna (Hecht 1975) and a lizard from the Bow Local Fauna (Skillebeck 1980). Archer (1976) reported an agamid and *Varanus* sp. from the Early Pliocene Bluff Downs Local Fauna. A number of non-squamatan taxa has been previously reported from this fauna (Archer 1976, 1982; Bartholomai 1978; Archer & Dawson 1982; Rich & van Tets 1982; Boles & Mackness 1994; Mackness 1995 a,b; Willis & Mackness 1996; Thomson & Mackness 1999; Wroe & Mackness 1999). The present paper describes the lizards identified to date and discusses the implications for palaeoecology of the site and the pattern of lizard evolution in Australia.

Materials and Methods

Fossil remains of reptiles were obtained through quarrying or through wet-sieving of sediments.

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TABLE 1. Measurement (mm) of dorsal ?*Megalania vertebrae* against *Varanus giganteus* vertebrae. Measurements as defined in Methods. Range (mean \pm standard deviation). Data for *V. giganteus* are taken from Smith (1976)

Specimen	No	Pr-Po	BW /Pr-Po	CW/Pr-Po	Pr-Pr/Pr-Po
<i>V. giganteus</i>	20	24.5-27.1 (25.7 \pm .14)	0.54-0.64 (0.58 \pm .005)	0.55-0.63 (0.59 \pm .006)	0.88-1.01(0.92 \pm .007)
Fossil	7	31.7-45.8 (36.4 \pm 5.3)	0.48-0.57 (0.53 \pm .04)	0.56-0.72 (0.63 \pm .06)	1.07-1.21(1.14 \pm .06)

TABLE 2. Measurements (mm) of individual ?*Megalania vertebrae*. Measurements as defined in Methods. (Mean \pm standard deviation).

Specimen	Pr-Po	Pr-Pr	Po-Po	BW	CW	Type
F9135	31.7	38.2	34.5	15.9	19.9	Dorsal
F23234	40.0	46.5	42.5	22.0	25.9	Dorsal
F23235	33.7	-	-	-	-	Dorsal
F23236	32.1	-	32.0	16.8	-	Dorsal
F23237	32.7	35.8	-	15.7	19.9	Dorsal
F23681	38.9	41.8	-	22.3	24.8	Dorsal
F23686	45.8	53.5	-	25.7	32.9	Dorsal
F23684	38.3	-	29.0	-	14.3	Cervical
(Mean/S.D)	(36.4 \pm 5.31)	(43.2 \pm 7.05)	(36.3 \pm 5.48)	(19.7 \pm 4.2)	(24.1 \pm 5.5)	

Specimens were examined using a Wild M3Z stereo-microscope with eyepiece micrometer and drawing tube. X-ray microanalysis was carried out using a JEOL JSM 35 scanning electron microscope and energy dispersive X-ray detector. Terminology for bones follows Romer (1956).

Measurements

Measurements made using vernier calipers accurate to 0.05 mm are summarised below and largely follow Smith (1976). Statistical analysis of these measurements is provided in Tables 1 & 2.

VERTEBRAL LENGTH (PR-PO) - measured as the greatest distance from the anterior edge of the prezygapophysis to the posterior edge of the postzygapophysis.

PREZYGAPOPHYSIAL WIDTH (PR-PR) - measured as the greatest distance between the edges of the prezygapophyses.

POSTZYGAPOPHYSIAL WIDTH (PO-PO) - measured as the greatest distance between the edges of the postzygapophyses.

CENTRUM MINIMUM WIDTH (BW) - measured as the smallest distance across the centrum.

CONDYLAR WIDTH (CW) - measured as the greatest distance between the condyle.

Abbreviations for specimen numbers: QM F, Queensland Museum fossil numbers; SAMA, South Australian Museum, Adelaide; AR, University of New South Wales Research Collection. Site localities are listed in Archer & Wade (1976) and Mackness (unpub.).

Systematics

Family Gekkonidae Gray, 1825

Subfamily Gekkoninae Underwood, 1954

cf. *Heteronotia* sp. (Gray, 1845)
(FIG. 1A)

Material examined: A single nearly complete left dentary (QM F23655) from EVS Site.

Characters

Gekkonid dentition is characterised as isodont with a large number of cylindrical, pointed teeth confined to the marginal bones (Edmund 1969). Sumida & Murphy (1987) have amended this by reporting that gekkonoids typically have bicuspid tooth crowns, the cusps being separated by an apical groove. Allocation of this specimen to *Heteronotia* is justified below.

Description

The specimen is an almost complete left dentary, complete anterior to the level of the posterior end of the tooth row and retaining most of the angular process. There are 36 teeth or tooth loci. The jaw is relatively slender and curves mesially at about the level of the 18th tooth. Meckel's groove is completely obliterated by dentary overgrowth. The internal septum is not exposed by the splenial notch, which extends anteriorly to the level of the 29th tooth.

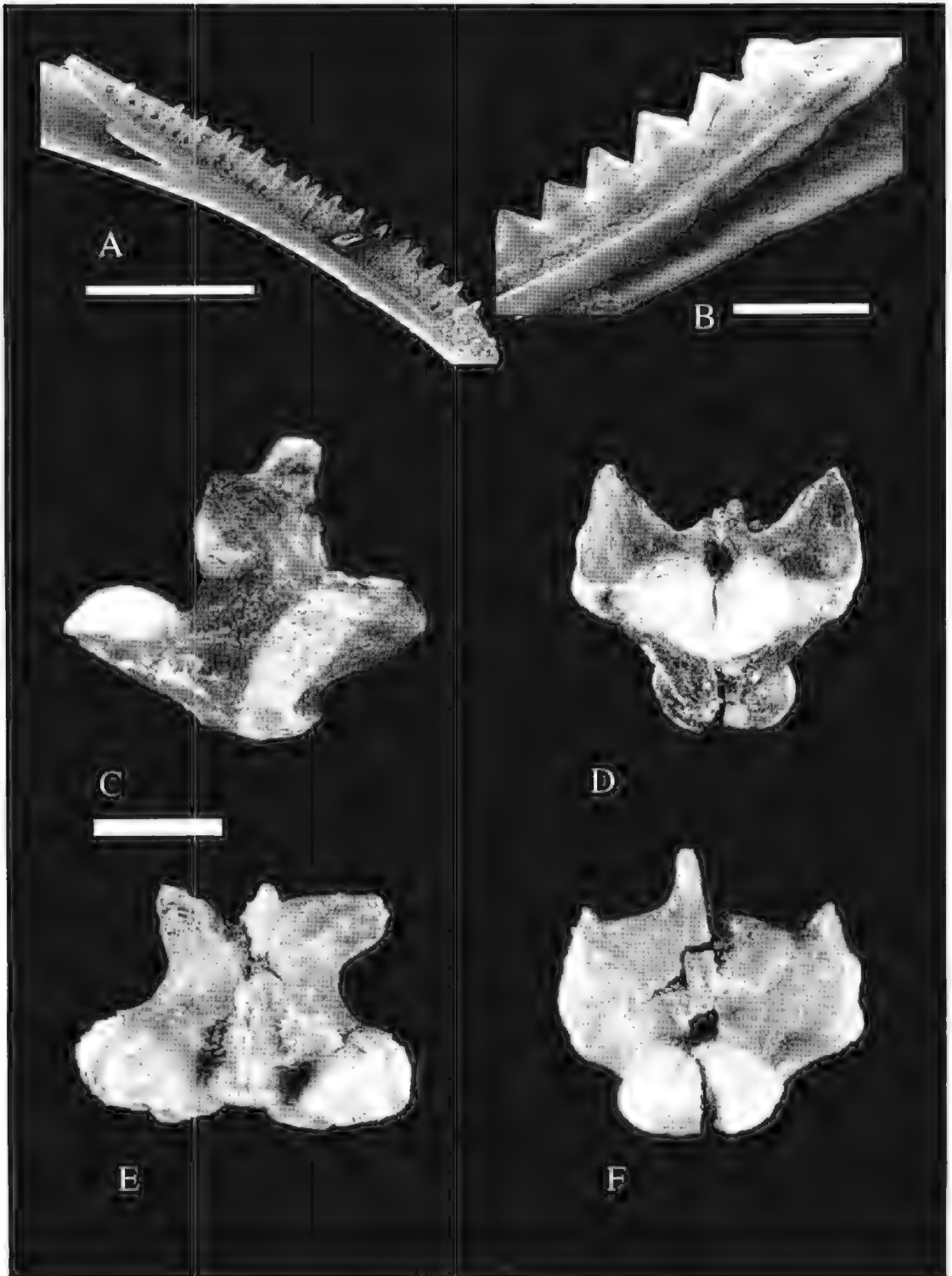


Fig. 1 (A). cf. *Heteronotia* sp. QM F23655 left dentary, lingual. Scale bar = 2 mm. (B). Agamid indent. QM F7812 dentary, lingual. Scale bar = 1 mm. (C-F). ?*Megalania* sp. QM F23686, dorsal vertebra. (C). Lateral, (D). Anterior, (E). Dorsal, (F). Posterior. Scale bar = 20 mm.

The teeth are delicate, sharply pointed and weakly bicuspid, with a lingual cusp set off by a groove and lying lower than the apical cusp. There is little variation in tooth size apart from a slight diminution posteriorly. The dental sulcus is well demarcated by a lingual parapet. Labially, the jaw bears four widely-spaced mental foramina, the most posterior level with the 25th tooth.

Dimensions

Jaw depth (at the level of the posterior most tooth), 2.6 mm; length of tooth row, 12 mm; height of 14th tooth, 0.4 mm.

Remarks

The dentaries of gekkonids are conservative, making identification difficult. Pygopods have highly variable and specialised jaws (Hutchinson 1997), none of which strongly resembles the specimen described. Most of the larger carphodaetylines have distinctive, tapering multi-toothed (> 40) dentaries quite unlike this specimen. However most diplodaetylines and the Australian gekkonines have less specialised jaws which are superficially similar to each other. Of the genera examined (all Australian gekkonoids except *Pseudothecadactylus* (= *Rhacodactylus*)), the most similar to QM F23655 is *Heteronotia*. At present, this attribution is based only on the combination of jaw proportions, tooth number and size; objective criteria for most gekkonid jaws have still to be developed.

Heteronotia binoi (Gray, 1845) is a wide ranging complex of at least two bisexual species and numerous all-female parthenogenetic clones. Members of the complex are found throughout mainland Australia (Moritz 1983; Moritz *et al.* 1989) in a variety of habitats ranging from deserts to closed forests. *Heteronotia binoi* is nocturnal and feeds on arthropods (Bustard 1968, 1970). The relationships of the two other species, *H. spelea* (Kluge, 1963) and *H. planiceps* Storr, 1989 to the known chromosome races and to each other are yet to be clarified. Pending the clarification of species boundaries, we can make no firmer allocation of the fossil specimens than as a possible *Heteronotia* species.

Fossil gekkonids have also been recorded from the Quaternary of Queensland (Archer 1978)

Family Agamidae Gray, 1827

Unidentified Material (FIG. 1B)

Material examined. Two fragmentary right dentaries, the symphyseal region of the jaw (QM

F23656) EVS site, the other (QM F7812), a partial dentary bearing the mid-to-rear section of the tooth row from Main Site.

Characters

Agamid reptiles are distinguished by having a dentition combining one to three anterior pleurodont teeth followed by acrodon teeth. Other agamid features are summarised by Estes (1983).

Description

Both specimens are from relatively moderate-sized individuals. The partial right dentary (QM F7812) bears seven acrodon teeth. The last implanted tooth is followed by an empty locus. The dentary is broken anteriorly at what is estimated to have been about the mid-point of the tooth row.

The second specimen, (QM F23656), is the symphyseal region of a right dentary. It bears two pleurodont tooth loci (one tooth present, one absent), followed by five partly damaged acrodon teeth. Three closely-spaced mental foramina are preserved on the labial surface of the specimen, the third being situated below the first acrodon tooth.

Dimensions

Jaw length (QM F7812), 7.8 mm; (QM F23656), 5.9 mm.

Remarks

Archer (1976) suggested that the small right dentary (QM F7812) was similar to some species of *Amphibolurus*. Since that time, the generic classification of Australian agamids has been considerably revised (e.g. Storr 1982) and further review of the phylogeny of the Australian dragons is likely (Greer 1989). Covacevich *et al.* (1990) identified several problems in identifying agamid remains and we follow their caution in not identifying these dentary fragments past family level.

Dragon lizards are divided into three lineages within Australia: the amphibolurids (*sensu* Hutchinson & Donnellan 1993), *Hypsilurus* and *Physignathus*. The amphibolurids inhabit nearly all environments except wet forests (Hutchinson & Donnellan 1993). *Physignathus* occurs along streams in a variety of habitats while *Hypsilurus* is restricted to closed canopy forests (Witten 1993).

Fossil agamids have been recorded from the Quaternary of Queensland (Bennett 1876; Archer 1978; Archer & Brayslaw 1978), New South Wales (Ryder 1974; Dodson *et al.* 1993; Balme 1995) and South Australia (Hale & Tindale 1930; Hope *et al.* 1977; Smith 1976, 1982; Smith 1982; Pledge 1990).

Family Varanidae Gray, 1827

?Megalania sp.
(FIGS 1C-E, 2A-C)

Material examined: Two isolated cervical vertebrae (QM F23684) JHY Site, (QM F23233) Main Site, seven isolated dorsal vertebrae (QM F9135, QM F23234, QM F23235, QM F23236, QM F23237) Main Site; (QM F232686, QM F232687) DML Site and condyle fragments (QM F23688).

Characters

Megalania is characterised, in part, by having massive thoracic and lumbar vertebrae with weakly developed zygosphenes (absent in typical *Varanus*) as well as small depressed neural canals. The adult teeth of *Megalania* are large and slightly recurved distally. The anterior cutting edge is rounded and serrated distally. The posterior cutting edge is thin, blade-like and serrated along its entire length (Hecht 1975).

Description

The two isolated fossil cervical vertebrae are similar in overall morphology to those from an extant *Varanus varius* (White, 1790) (AR7641) but are some 22% larger. Both fossil vertebrae lack neural spines but bear hypapophyses with the grooved, knob-like extremities characteristic of large-sized varanids. The cotyle is more robust and less flattened than that of the extant species and the condyle is less ovate. Both these features may be allometric in nature, however. The dorsal vertebrae are much more massive than those of any extant varanid. Tables 1 & 2 summarise the measurements of the *?Megalania* vertebrae. The animal represented was clearly larger than modern varanid counterparts such as the perentie *Varanus giganteus* with the largest dorsal vertebra being almost 70% larger than those measurements supplied for a perentie by Smith (1976).

Remarks

The assignment of the larger varanid vertebrae to *Megalania* is made on the basis of convention. *Varanus* and *Megalania* are the two genera recognised from Australia, but the two are separated primarily on size. Estes (1983) doubts whether the two ought to be generically distinct. *Megalania prisca* Owen, 1860 is the only species currently recognised and is significantly larger than all extinct and extant varanids. Large varanid vertebrae are also known from the Chinchilla Local Fauna (Hecht 1975) and these along with those from Bluff Downs are currently being studied by one of the authors

(B.M.). Hecht (1975) in his study of *M. prisca* noted that there seemed to be fewer caudal and cervical vertebrae associated with remains of *Megalania* compared with the expectation based on *Varanus*. This suggested to him that *Megalania* may have had a proportionally shorter neck and tail than extant varanids. No caudals have been recovered from the large varanid from Bluff Downs.

Varanus sp.
(FIG. 2D-I)

Material examined: Isolated dorsal vertebrae (QM F7774, QM F23238, QM F23659) Main Site; (QM F23683) EVS Site; isolated caudal vertebrae (QM F7777, QM F9131) Main Site; (QM F23681, QM F23682) EVS Site; and isolated teeth (QM F23685).

Characters

Varanids are recognised by having vertebrae characterised by oblique condyle-cotyler articulations, particularly in the thoracic and lumbar region with the vertebral centra constricted anterior to the condyles. The bases of the teeth are expanded and sculptured with fine vertical fluting (Fejervary 1935; McDowell & Bogert 1954; Romer 1956; Hoffstetter & Gase 1969; Hecht 1975).

Description

The dorsal vertebrae show characteristic varanid morphology and with a range of centra lengths (Table 3) which indicate a medium-sized goanna such as *Varanus gouldii* (Gray, 1838).

TABLE 3. Measurements (mm) of centra of fossil varanids and *Varanus varius* (AR7641)

	Dorsal		Cervical
QM F7774	14.2	QM F9131	22.6
QM F23683	13.8	QM F23681	18.2
QM F23659	10.8	QM F23682	15.7
QM F23238	10.5	QM F7777	10.9
AR7641(a)	15.3		
AR7641(b)	15.3		
AR7641(c)	15.4		
AR7641(d)	15.4		
AR7641(e)	15.6		
AR7641(f)	15.7		

Remarks

Given that there appears to be a narrow range of measurement within the dorsal section of the vertebral column of individual goannas and that there are two distinct size classes of fossil dorsal vertebrae, it is reasonable to assume that either two

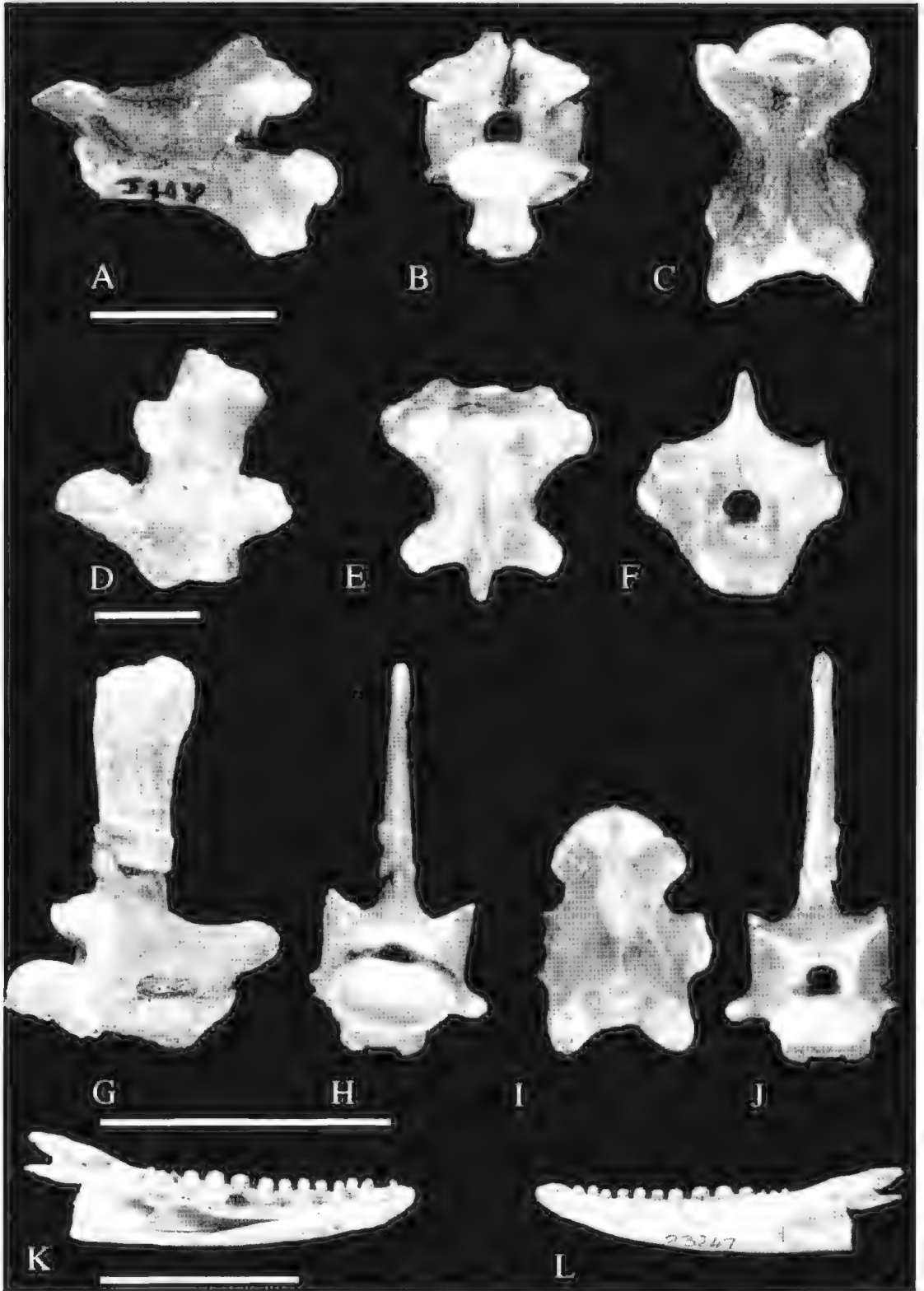


Fig. 2 (A-C). ?*Megalania* sp. QM F23686 cervical vertebra. (A). Lateral. (B). Posterior, (C). Dorsal. Scale bar = 40 mm. (D-F). *Varanus* sp. QM F7774 dorsal vertebra. (D). Lateral. (E). Dorsal. (F). Posterior. Scale bar = 10 mm. (G-J). *Varanus* sp. QM F9131 caudal vertebra. (G). Lateral. (H). Anterior. (I). Dorsal. (J). Posterior. Scale bar = 50 mm. (K-L). *Tiliqua scincoides* QM F23247 left dentary. (K). Lingual. (L). Labial. Scale bar = 20 mm.

sympatric species or two size morphs are represented in the fauna. The caudal vertebrae show a much wider range of measurements which is typical of this section of the vertebral column. Once again however, two size classes can be inferred indicating that either two sympatric species or two size morphs are present. Only one of the caudal vertebrae (QM F9131) has a complete neural spine.

Mertens (1942) suggested a relationship between body length and tail length which Hecht (1975) further extrapolated, suggesting that the long tails of some varanids may be a reason for the disparate appearance of caudal vertebrae over those from other regions of the body in the fossil record. An equal number of dorsal and caudal varanid vertebrae has been recovered from Bluff Downs. Wilkinson (1995) has recently listed a number of vertebral features for different *Varanus* species. Although potentially useful, these characters have been selected from single isolated specimens and therefore cannot take into account interspecific and intraspecific variation in varanid vertebral characters. It is not possible to identify the fossil vertebrae beyond *Varanus* sp., partly due to the current lack of information and because the vertebrae recovered were not articulated and were possibly from several individuals. The vertebrae also came from two different sites, even though those sites are from comparable depositional sequences (Mackness unpub.). The size of the animal cannot be extrapolated from the vertebrae given the problems identified above as well as those identified by Hecht (1975).

Varanids are found over a wide range of habitats including aquatic, terrestrial and arboreal and from tropical forests to arid deserts (Cogger & Heatwole 1981). They range over a wide area and eat most food items including invertebrates, vertebrates and carrion (King & Green 1979, 1993 a,b; Losos & Greene 1988; James *et al.* 1992).

Fossil varanids are known from the Quaternary of Queensland (Archer 1978; Walters 1980; Hope 1981; Horton 1981; Wilkinson 1995), New South Wales (Tedford 1967; Aplin quoted in Hope 1981), South Australia (Hale & Tindale 1930; Mulvaney *et al.* 1964; Smith 1976, 1982; Smith 1982; Hope *et al.* 1977; Williams 1980; Pledge 1990) and Western Australia (Archer 1977).

Family Scincidae Gray, 1825

Subfamily Lygosominae Mittleman, 1952

Tiliqua Gray, 1825

Tiliqua scincoides (White, 1790)

(FIG. 2 K-L)

Material examined: Almost complete left dentary (QM F23247) EVS Site.

Characters

The closed Meckelian groove and the presence and form of several large hemispherical-conical cheek teeth uniquely characterise this as belonging to the genus *Tiliqua* (Shea & Hutchinson 1992).

Description

The specimen is left dentary minus angular process, a vertical broken edge runs just posteriorly to the level of the internal facet for the dentary process of the coronoid bone, but the complete, posteriorly projecting coronoid process of the dentary is still present. Sixteen teeth or alveoli are present, cheek teeth increasing in size posteriorly with the largest being the 11th, 12th and 13th, after which last three are abruptly smaller. A buttress supporting the mandibular symphysis rises abruptly below the dentary as a low keel at about the level of the 6th tooth, visible as a fold running posteriorly along the ventral face of the dentary to about the level of the anterior alveolar foramen. The anterior end of this foramen, that is, the apex of the splenial notch, is at the level of the 10th tooth.

The crowns of the enlarged cheek teeth are markedly wider than the tooth bases, with almost horizontal flattened peripheral occlusal surfaces rising to a central point. Striae radiate over the occlusal surface from this central point.

Measurements

Tooth row length 22 mm; jaw depth at level of last tooth 9.5 mm

Remarks

The *Tiliqua* dentary was found lying on top of the ground at EVS Site, in an area undisturbed by quarrying. Fossils are often exposed at the Bluff Downs site through rain and other disturbances. The colour of this particular dentary was different from others recovered from the site, raising doubt about its provenance. X-ray microanalyses of mineral content (Figs 1-4) were undertaken on the *Tiliqua* jaw from EVS Site, an extant *Tiliqua*, as well as on fossil bone fragments of a turtle and a python, both from EVS Site.

The results of these microanalyses showed that silica was a prominent constituent of the fossil bones, whereas in the extant *Tiliqua*, little silica was present. Since the calcium phosphate of the bone is often changed by the addition or substitution of other minerals, such as silica, during fossilisation, these results indicate that the *Tiliqua* jaw from EVS Site was fossilised and probably contemporaneous with the other reptiles sampled.

The Bluff Downs specimen is not distinguishable from the living *T. scincoides* and at least one other Pliocene *Tiliqua*, reported by Pledge (1992) from

Curramulka, can also be allocated to this species. Examination of these specimens (partial dentary maxilla and frontal) by MNH shows them to be indistinguishable from those of the living species. However, another much larger specimen referable to *Tiliqua*, recently discovered from the Pliocene Chinchilla Local Fauna (Hutchinson & Mackness unpub.), is markedly different from any living or extinct species of the genus.

Tiliqua scincoides and its sister species *T. gigas* (Schneider, 1801) (Shea 1990) are the most tropical and forest-adapted members of this genus. *Tiliqua scincoides* is an adaptable species, found in a wide variety of habitat types and its presence does not have strong palaeoecological implications.

Egernia Gray, 1838

Egernia hosmeri Kinghorn, 1955

(FIG. 3A)

Material examined: A partial right maxillary fragment (QM F23654) EVS Site.

Characters

The maxillary is identified as a spiny-tailed skink (*E. cunninghami* (Gray, 1832) group (*sensu* Horton 1972)) on the basis of its tooth morphology, having compressed crowns with occlusal blades oriented such that the teeth in the jaws form a serrated cutting edge.

Description

The specimen is the posterior, suborbital portion of the right maxillary tooth row. The V-shaped notch for the jugal is almost complete as is the dorsal edge (orbital rim). Posterior nine teeth or tooth loci are preserved. The crowns of more intact teeth are labiolingually compressed, with angular occlusal cutting edges. Crowns are also somewhat flared in lingual view, producing an overall 'ace-of-spades' shape. This tooth shape is limited to members of the *Egernia cunninghami* species group (Horton 1972) which comprises *E. cunninghami*, *E. depressa* (Günther, 1875), *E. hosmeri* and *E. stokesii* (Gray, 1845).

The four living members of this species-group differ in the details of their dentition. *Egernia cunninghami* and *E. depressa* have squared-off, somewhat chisel-shaped crowns. *Egernia stokesii* and *E. hosmeri* show the greatest similarity to each other and to QM F23654, all three having teeth with linguo-labially flattened crowns which rise to a medial point. SAMAs specimens of *E. stokesii* differ slightly from those of *E. hosmeri* in being rather more flared in lingual view, this expansion being true even of the most posterior teeth. In *E. hosmeri* and QM F23654 the last few teeth are narrower and more acutely pointed than those of *E.*

stokesii. The fossil is not distinguishable from *E. hosmeri* and is therefore allocated to that species.

Measurements

Length of specimen, 6.9 mm; depth at level of jugal suture, 2.1 mm; height of largest tooth, 1.7 mm

Remarks

Spiny-tailed skinks are all crevice dwellers, typically in rock outcrops but sometimes also in logs and stumps. The better studied species (*E. cunninghami* and *E. stokesii*) are almost entirely herbivorous in the wild (Brown 1991).

Eulamprus Fitzinger, 1843

Eulamprus quoyii complex

(FIG. 3C-F)

Material examined: A right dentary (QM F9137) Main Site. A frontal (QM F23657) Main Site and several other fragments (QM F23658). AB Site are possibly also referable to this taxon.

Characters

Eulamprus comprises the larger, more generalised members of the *Sphenomorphus* Group (Greer 1979) in Australia. Its definition is currently based mainly on scalation and reproductive characters, but initial work (Hutchinson 1992) shows that by using tooth crown morphology as well as jaw robustness at least two morphological groups are recognisable osteologically, the more gracile water skinks, *E. quoyii* (Dumeril & Bibron, 1839) and its relatives, and the more robust tropical forest species such as *E. murrayi* (Boulenger, 1887).

Description

The dentary is nearly complete, with a tooth row bearing 24 teeth or tooth loci. The dental sulcus is demarcated lingually by a pronounced parapet which diminishes and disappears at about the level of the 22nd tooth. Meckel's groove is widely open along the ventrolingual face of the dentary. The internal septum of the dentary is poorly developed and does not show much posterior extension. Seven mental foramina are present, the last at about the level of the 19th tooth. The teeth crowns are not flared or thickened. The lingual face of each tooth crown is vertical, with an inward-projecting buttress offset to the rear. The junction of the lingual face of the tooth crown with the occlusal surface is demarcated by a groove which separates two closely apposed low ridged edges.

Measurements

Length of tooth row, 12 mm; depth of dentary at level of the 20th tooth, 2.6 mm.

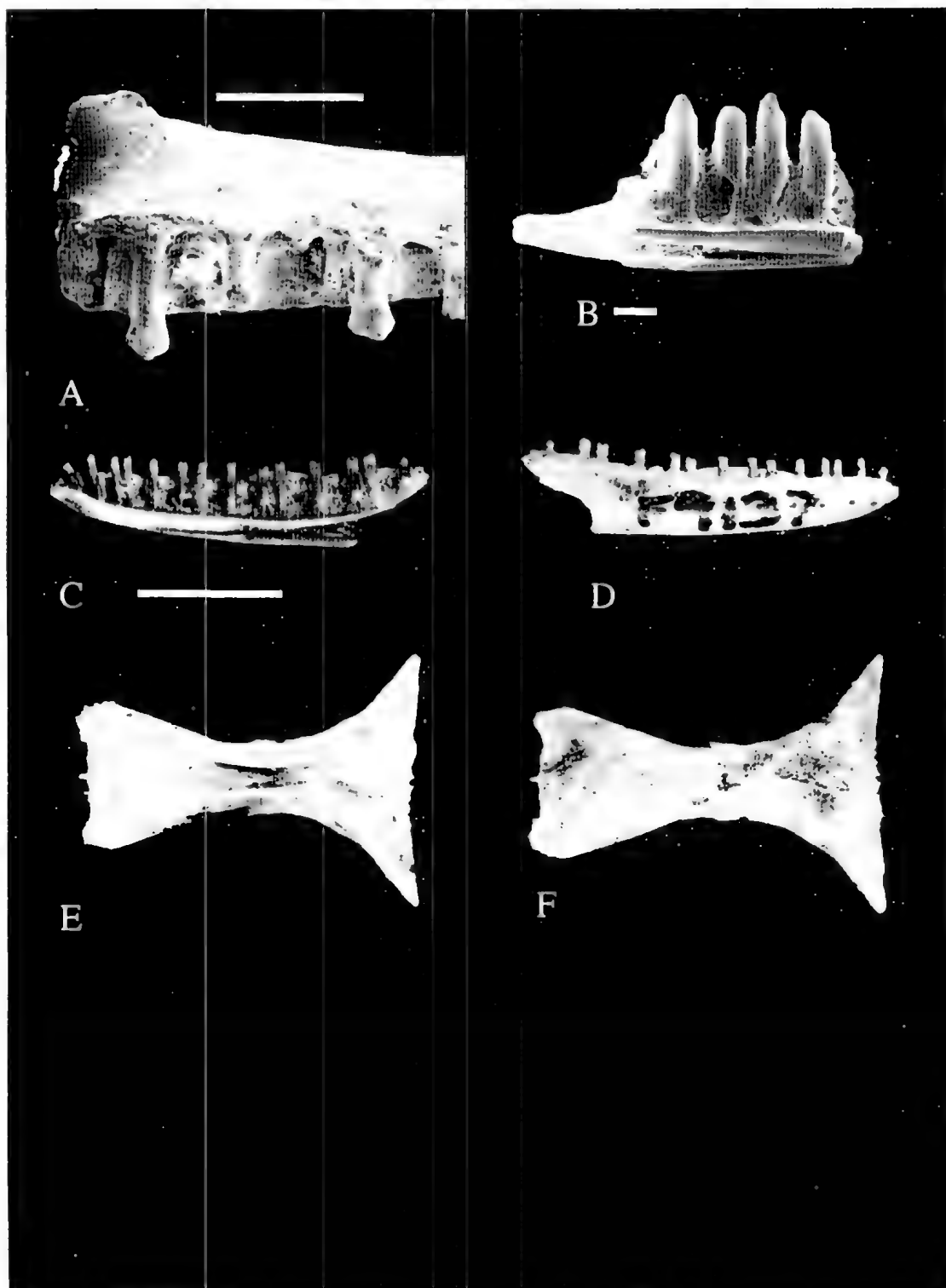


Fig. 3. (A). *Egernia hosmeri* QM F23654 right maxillary fragment. Scale bar = 2 mm. (B). Scincidia indent. QM F23659. Scale bar = 1 mm. (C-D). *Eulamprus quoyii* complex QM F9137 right dentary. (C). Lingual. (D). Labial. Scale bar = 20 mm. (E-F). *E. quoyii* complex. QM F23657 frontal. (E). Ventral. (F). Dorsal. Scale bar = 20 mm.

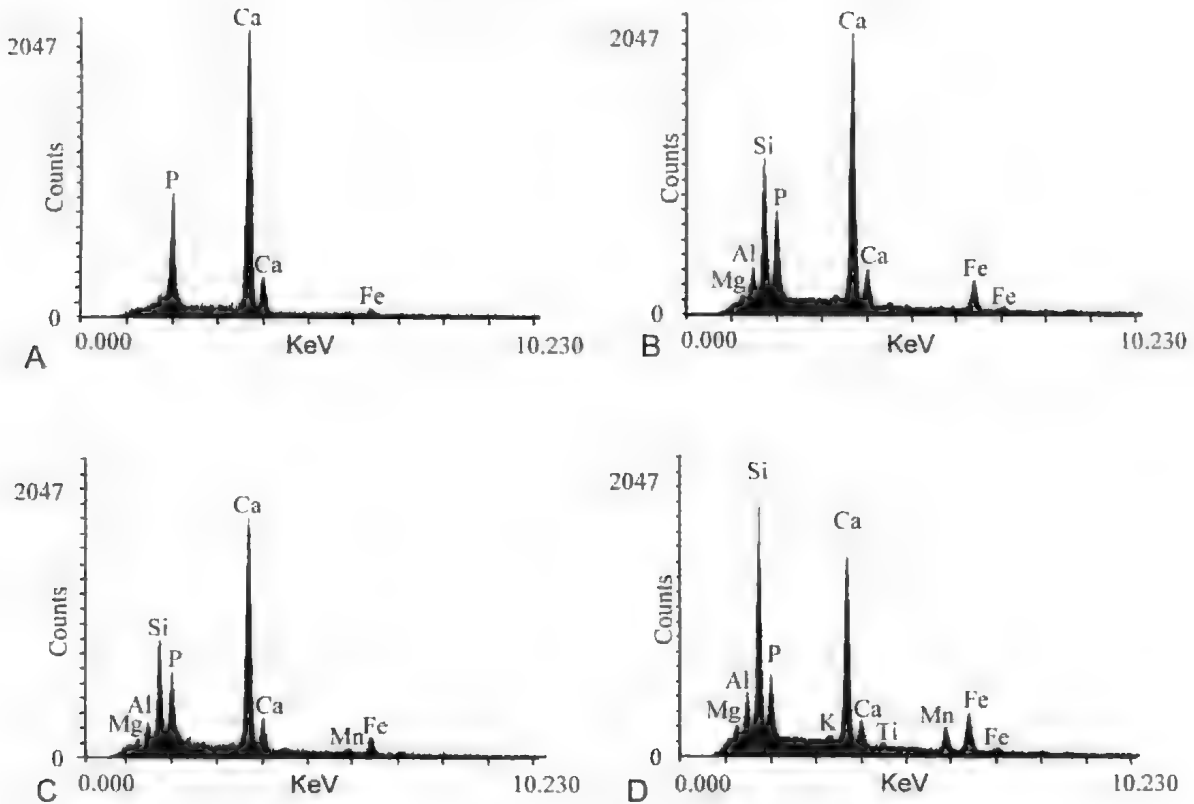


Fig. 4. X-ray microanalysis of bone. (A). Recent *Tiliqua scincoides* dentary. (B). Fossil *T. scincoides* dentary. (C). Fossil turtle shell. (D). Fossil python vertebra.

Remarks

This specimen is very similar to living water skinks and is clearly distinct from the more robust rainforest *Eulamprus* spp. such as *E. murrayi* in that it lacks their deep jaws and somewhat large, durophagous cheek teeth. However, the fossil appears to differ from *E. quoyii*, the living species in the area today. Specimens of *E. quoyii* of comparable jaw size have a longer, narrower dentary bearing up to 30 teeth. Thus, if this specimen were *E. quoyii*, it would have to be regarded as having an anomalously low tooth count. The proportions and the number of teeth accord better with *E. tympanum* (Linnberg & Andersson, 1913) and *E. heatwolei* (Wells & Wellington, 1984), both restricted today to south-eastern Australia.

Water skinks are largely confined to permanent water with this habit enabling them to inhabit a wide range of habitats. They are diurnal and carnivorous, feeding on invertebrate and small vertebrate prey (Daniels 1987; Brown 1991).

Scincidae indent. (FIG. 3B)

Material examined: Three fragments (QM F23658) EVS Site; one small fragment (QM F23659) AB Site and an isolated vertebra (QM F23660) Main Site.

Remarks

Four fragments of lizard dentary and a vertebra are not sufficient to be assigned. The three pieces from the larger skink compare well with members of *Eulamprus* and are tentatively assigned cf. *Eulamprus*. The other remaining fragment represents another type of skink but not enough remains for any generic assignment. The vertebra is identified as a scincid on the basis of characters outlined by Smith (1976).

Fossil skinks are known from the Quaternary of Queensland (Trezise 1970; Bartholomai 1977; Archer & Brayshaw 1978; Molnar 1978). New South Wales (Kreffit 1867, 1870, 1871; Lampert 1971;

Thorne 1971; Marshall 1973; Ryder 1974; Dodson *et al.* 1993; Balme 1995). Tasmania (Bowdler 1974), South Australia (Stirling 1889; Hale & Tindale 1930; Tindale 1933; Mulvaney 1960; Mulvaney *et al.* 1964; Smith, 1976, 1982; Hope *et al.* 1977; Smith, 1982; Pledge 1990, 1992;) and Western Australia (Cook 1960, 1963; Balme *et al.* 1978).

Discussion

The paucity of information about lizards in the Pliocene makes the Bluff Downs material particularly noteworthy. The fauna, in so far as it can be identified, is composed of species or species groups that occur in the modern Charters Towers area, the only obvious exception being the extinct *Megalania*. In this respect, the lizard fauna of the Bluff Downs Local Fauna is similar to the older Riversleigh deposits (Hutchinson unpub.) in that it represents an early establishment of modern forms in the area, contrasting with the contemporaneous mammal fauna which includes many extinct taxa.

Slow rates of faunal turnover, when compared with mammals, seem to be the rule in Tertiary and Quaternary squamates. This has been addressed most recently by the detailed study of the Rancho La Brea snakes by Li Duke (1991). His explanation of low rates of extinction, evolution and faunal turnover in reptiles (compared with mammals and birds) centres on two concomitants of reptile ectothermy: - low energy requirements and small size enabling survival

of reptile populations in refugia too small for the rapidly metabolising and generally larger endotherms (witness the recent situation in Australia regarding mammal versus reptile extinctions). Thus, during periods of environmental change, many endotherm populations and species can be driven to extinction by habitat reduction, while the syntopic reptiles and amphibians merely suffer range contraction or fragmentation. Restoration of former climatic regimes permits re-establishment by the former reptile populations but may require evolutionary change or migration before a new mammal fauna emerges.

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NEW GALL MIDGES (DIPTERA: CECIDOMYIIDAE) INFESTING NATIVE AND INTRODUCED SOLANUM SPP. (SOLANACEAE) IN AUSTRALIA

By PETER KOLESIK*, RACHEL E. C. MCFADYEN† & ANTHONY J. WAPSHERE‡

Summary

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Three new *Asphondylia* species are described from five *Solanum* species in New South Wales and Queensland, Australia. *Asphondylia sturtiana* Kolesik sp. nov. induces a stem swelling on *Solanum sturtianum* F. Muell., an Australian native plant with fruits toxic to sheep and cattle, *Asphondylia paucidentata* Kolesik sp. nov. causes fruit galls on the native *Solanum aviculare* G. Forster and *Solanum linearifolium* Geras. Ex Symon, and *Asphondylia obscura* Kolesik sp. nov. causes fruit galls on *Solanum chenopodioides* Lam. and *Solanum physalifolium* Rusby var. *nitidibaccatum* (Bitter) Edmonds, native South American plants that have become weeds in Australia. The newly described gall midges limit reproduction of their host plants.

Key Words: Diptera, Cecidomyiidae, *Asphondylia*, *Solanum aviculare*, *Solanum chenopodioides*, *Solanum linearifolium*, *Solanum physalifolium* var. *nitidibaccatum*, *Solanum sturtianum*, Australia.

NEW GALL MIDGES (DIPTERA: CECIDOMYIIDAE) INFESTING NATIVE AND INTRODUCED *SOLANUM* SPP. (SOLANACEAE) IN AUSTRALIA

by PIĀTER KOLESĪK¹, RACHEL E. C. MCFADYEN¹ & ANTHONY J. WAPSHERE²

Summary

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Three new *Asphondylia* species are described from five *Solanum* species in New South Wales and Queensland, Australia. *Asphondylia sturtiana* Kolesik sp. nov. induces a stem swelling on *Solanum sturtianum* F. Muell., an Australian native plant with fruits toxic to sheep and cattle. *Asphondylia paucidentata* Kolesik sp. nov. causes fruit galls on the native *Solanum aviculare* G. Forster and *Solanum linearifolium* Geras. ex Symon, and *Asphondylia obscura* Kolesik sp. nov. causes fruit galls on *Solanum chenopodioides* Lam. and *Solanum physalifolium* Rusby var. *nitidibaccatum* (Bitter) Edmonds, native South American plants that have become weeds in Australia. The newly described gall midges limit reproduction of their host plants.

KEY WORDS: Diptera, Cecidomyiidae, *Asphondylia*, *Solanum aviculare*, *Solanum chenopodioides*, *Solanum linearifolium*, *Solanum physalifolium* var. *nitidibaccatum*, *Solanum sturtianum*, Australia.

Introduction

Solanum elaeagnifolium Cav., silverleaf nightshade, indigenous to central and south-western North America and temperate South America, is a weed of cultivation and disturbed land in New South Wales, Victoria and South Australia (Parsons & Culbertson 1992). It is a major weed in South Africa where it has been a target of biological control since the 1970s (Olekers & Zimmermann 1995). Biological control has been considered in Australia but no agents have been introduced (Wapshere 1988). Consequently, there is a continuing interest in insects attacking *S. elaeagnifolium* and other similar *Solanum* species, whether native or introduced. The cecidomyiid species described here were collected in the course of investigations into insects as biological control agents of *Solanum* spp. in Australia.

Solanum sturtianum F. Muell. (thargomindah nightshade), is a shrub occurring in central-western Western Australia, southern Northern Territory, South Australia, south-western Queensland and north-western New South Wales (Purdie *et al.* 1982). In Queensland, it is more commonly found in the south-west but also occurs in the north (Henderson 1997) after winter rain (P. Jeffreys, Queensland

Department of Natural Resources, Charters Towers, pers. comm. 1998). The ripe fruit is reported to be toxic to stressed sheep and cattle (Cunningham *et al.* 1981).

Solanum aviculare G. Forst. and *S. linearifolium* Geras. ex Symon are related species known by the common names of kangaroo apple and mountain kangaroo apple, respectively. Both species occur mainly in New South Wales and Victoria with *S. aviculare* occurring additionally in eastern Queensland, South and Western Australia, Papua New Guinea, New Zealand, Lord Howe Island, Norfolk Island and New Caledonia (Purdie *et al.* 1982). The ripe berries of *S. aviculare* were consumed by Australian Aborigines and the plant has been cultivated as a source of steroidal alkaloids (Purdie *et al.* 1982; Symon 1994; Kittipongpatana *et al.* 1998).

Solanum chenopodioides Lam., known as whitetip nightshade, and *S. physalifolium* Rusby var. *nitidibaccatum* (Bitter) Edmonds are native to South America but are now established in localised populations in the eastern states of Australia with *S. physalifolium* var. *nitidibaccatum* a sporadic weed of agriculture (Purdie *et al.* 1982). In Australia *S. physalifolium* var. *nitidibaccatum* has been mistakenly referred to *S. sarrachoides* Scmidt, ex Macf. (also a South American native) for many years. *Solanum sarrachoides* is now known to occur in Australia only on Montague Island (Lepschi 1996).

The new gall midges belong to the genus *Asphondylia*. Together with *A. anthocercidis* Kolesik from fruit galls on *Anthocercis* spp. (Kolesik *et al.* 1997; Lepschi *et al.* 1999), the new species form a

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natural group of Australian species associated with Solanaceae.

Materials and Methods

The new gall midges were reared on four occasions. In June 1985, adults (males only) of *A. obscura* were reared (by AJW) from fruit galls on *S. chenopodioides* and *S. physaliifolium* var. *mitilhuacamm* collected at Mt Tomah, New South Wales. Adults and pupae of *A. paucidemota* were reared (by AJW) from fruit galls on *S. linearifolium* collected at Boyd Tower, New South Wales, in November 1985 and on *S. aviculata* collected in Bunya Mountains, Queensland, in January 1986. Larvae, pupae and adults of *A. sturtiana* were reared (by RECM) from stem swellings on *S. sturtianum* collected near Charters Towers, Queensland, in September 1998. The taxonomy in this paper is the responsibility of PK. Canada balsam mounts of the specimens for microscopic examination were prepared according to the technique outlined by Kolesik (1995). The type series are deposited in the Australian National Insect Collection, Canberra (ANIC).

Genus *Asphondylia* Loew, 1850

Loew, 1850: *Dipterologische Beiträge*, 1850: 21 and 47 (as subgenus of *Cecidomyia* Meigen, 1803)

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

Asphondylia is one of the largest genera of Cecidomyiidae occurring worldwide with about 260 species known (Gagné 1994). It contains species that have a ventrodistal spur on the first tarsomere, the ovipositor with large basal lobes, the last four female flagellomeres progressively shortened, the gonocoxite bearing a ventroapical lobe and a dorsally situated gonostylus that is about as wide as long with two basally merged teeth.

Asphondylia sturtiana Kolesik sp. nov. (FIGS 1-13)

Holotype: ♂, Gregory Highway, 52 km south of Charters Towers, Queensland (20° 25' S, 146° 12' E), reared from stem swelling on *Solanum sturtianum* F. Muehl., gall collected ix.1998, R. E. C. McFadyen, 6176 (ANIC).

Paratypes: ♂, 6 ♀♀, 3 pupal skins, 2 larvae (with pupal skins inside), same data.

Male (Figs 1-5)

Colour: antennae brown, eyes dark-brown, palpi grey, thorax dark-brown, abdomen with non-sclerotised parts red and sclerotised parts dark brown, legs grey with dark-brown setae, genitalia dark-brown.

Head: Antenna: scape cylindrical, only slightly widened distally, length 1.7 x breadth at distal end, 1.7 - 2.0 x length pedicel; pedicel slightly wider than long; first flagellomere 1.9 - 2.1 x length scape. Flagellomeres evenly cylindrical, circumfila dense, equally distributed along segments. Eye facets close together, spheroid, eye bridge 8 - 11 facets long. Frons with 16 - 20 setae per side. Labella crescent-shaped, laterally with 7 - 10 setae, setulose. Maxillary palpus 3 segmented, segments successively and progressively longer.

Thorax: Wing length 3.0 mm (range 2.9 - 3.0, n = 2), width 1.2 mm (1.1 - 1.2), R₁ interrupted proximally to areculus, with strongly sclerotised protrusion anterior to areculus. Ventrodistal spur on first tarsomere bent at midlength at right angle. Claws of all legs similar in size and shape, as long as empodia.

Abdomen: Genitalia: ventroapical lobes on gonocoxites short; teeth on gonostylus equal in size, large, symmetrical in posterior view; aedeagus tapered distally; cerci large, hemispherical, setose, setulose; hypoproct with several setae in distal half, setulose.

Female (Figs 6-9)

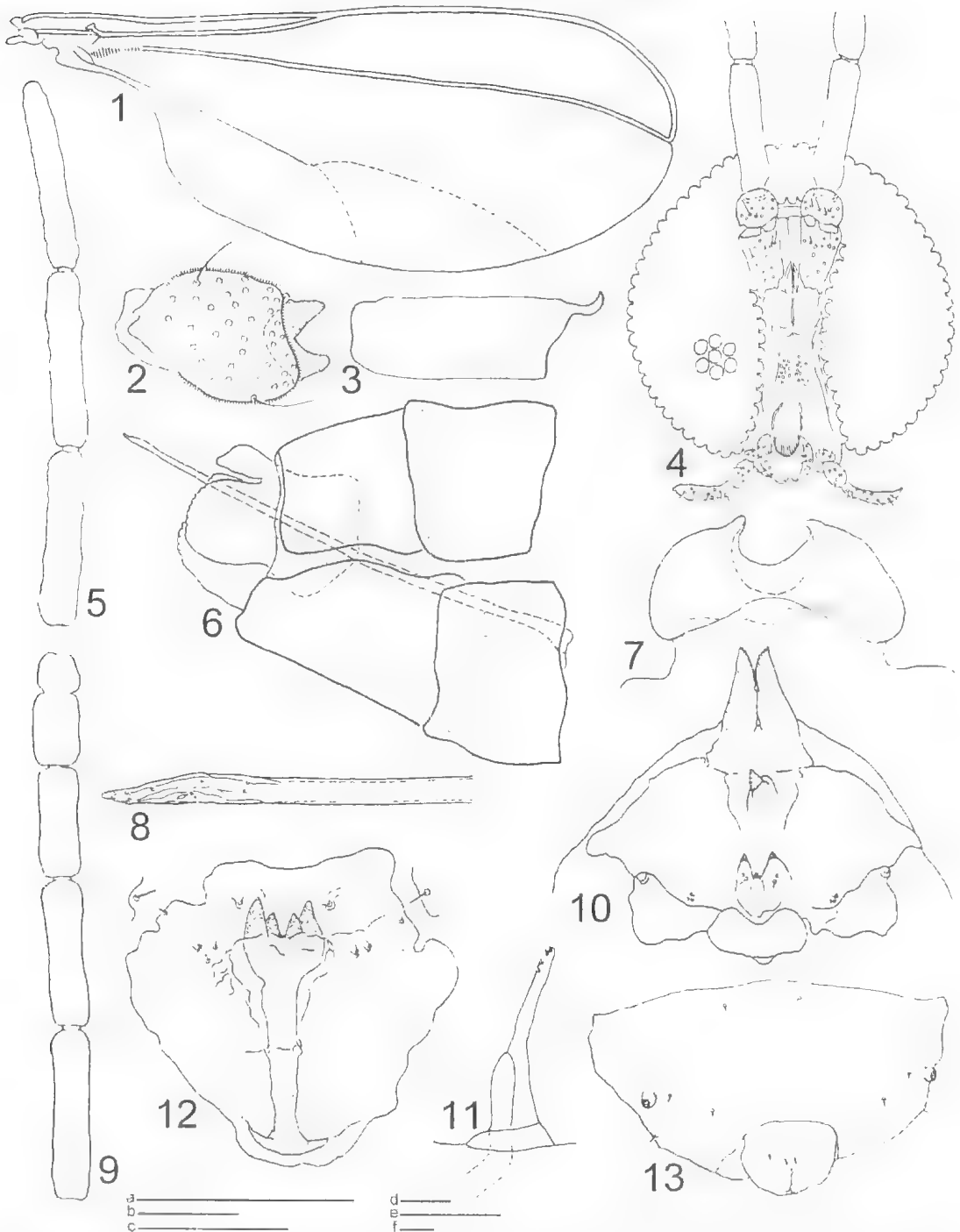
Colour as in male. Frons with 19 - 20 setae per side. Circumfila sparser than in male. Wing length 3.4 mm (3.3 - 3.6, n = 6), width 1.4 mm (1.3 - 1.4). Seventh abdominal sternite 1.8 x (1.6 - 2.0) length sixth. Genitalia: ovipositor 1.9 x (1.8 - 2.0) length seventh sternite; basal lobes with small, distal processes in dorsoventral view, densely covered with long setulae. Other characters as in male.

Pupa (Figs 10, 11)

Colour: antennal horns, frontal horns, abdominal spines dark-brown, rest of body light-brown. Length 3.0 mm (2.8 - 3.3, n = 3). Antennal horns serrated along entire inner edge, 278 µm (266 - 289) long, with small free space between them basally. One upper and three lower frontal horns. Prothoracic spiracle slightly curved at midlength, basal third about 3 x width terminal third, terminal third setose, trachea reaching midlength. Abdominal dorsal spines simple, straight, 2 - 3 pairs on last segment curved laterally.

Larva (Figs 12, 13)

Colour: orange-red. Length 2.2 mm (2.1 - 2.3, n = 3). Head capsule with no posterolateral extensions.



Figs 1-13. *Asphondylia sturtiana* sp. nov. 1-5 male, 6-9 female, 10, 11 pupa, 12, 13 larva. Fig. 1. Wing. Fig. 2. Gonostylus in posterior view. Fig. 3. First tarsomere of middle leg. Fig. 4. Head in frontal view. Fig. 5. Last three flagellomeres. Fig. 6. End of abdomen in lateral view. Fig. 7. Basal lobes on ovipositor in dorsal view (setae omitted). Fig. 8. End of ovipositor in lateral view. Fig. 9. Last five flagellomeres. Fig. 10. Anterior part in ventral view. Fig. 11. Prothoracic spiracle. Fig. 12. Sternal spatula with adjacent papillae. Fig. 13. Last two abdominal segments in dorsal view. Scale bars: a = 1 mm (Fig. 1); b = 50 μ m (Figs 2, 11); c = 100 μ m (Figs 3, 8); d = 100 μ m (Fig. 4); e = 100 μ m (Figs 5-7, 9, 12, 13); f = 100 μ m (Fig. 10).

Spatula with four anterior teeth, inner pair smaller than outer, shaft long and narrow, broadened both at midlength and base, surrounded anteriorly and laterally by extensive pigmented area. Each side of spatula with two pairs of lateral papillae, all setose. On the only specimen with undamaged terminal part, three setose terminal papillae.

Gall and biology

This gall midge induces a stem swelling on *Solanum sturtianum*, 5–20 mm long and 6–8 mm wide, not different in colour from normal stems. Inside the swelling are several chambers, each occupied by one larva. Pupation takes place within the gall.

Etymology

The name is derived from the specific name of the host plant.

Asphondylia paucidentata Kolesik sp. nov. (FIGS 14–23)

Holotype: ♂, Bunya Mtns, Queensland (26° 53' S, 151° 37' E), reared from fruit galls on *Solanum aviculare* G. Forster; gall collected 24.i.1986, A. J. Wapshere, 6177 (ANIC).

Paratypes: 2 ♂♂, ♀, same data; 3 ♂♂, 4 pupal skins, Boyd Tower, New South Wales (34° 02' S, 150° 03' E), reared from fruit galls on *Solanum linearifolium* Geras. ex Symon, gall collected 29.xi.1985, A. J. Wapshere.

Male (Figs 14–19)

Wing length 3.3 mm (range 3.2–3.4, $n=6$), width 1.3 mm (1.2–1.3). Genitalia in dorsoventral view: gonostylus 1.4 x ($n=2$) longer (teeth included in measurement) than wide, distal edge slightly concave to straight, teeth on gonostylus asymmetric. Spur on first tarsomere bent gradually at 45–60°. Other characters as in *A. sturtiana*.

Female (Figs 20, 21)

Wing length 3.7 mm ($n=1$), width 1.4 mm. Basal lobes on ovipositor with no apparent distal processes in dorsoventral view. Otherwise as in *A. sturtiana*.

Pupa (Figs 22, 23)

Length 4.2 mm (3.5–4.7, $n=4$). Antennal horns 373 µm (360–385) long, with 3–4 teeth at the midlength of inner edge, otherwise smooth, closely attached to each other along entire length. Prothoracic spiracle strongly curved at midlength, basal third about 4 x width terminal third. Otherwise as in *A. sturtiana*.

Larva unknown.

Gall and biology

This gall midge causes a deformation of fruits on *Solanum aviculare* and *S. linearifolium*, similar to that caused by *Asphondylia anthocercidis* Kolesik on *Anthocercis littorea* Labill. (Solanaceae) (Kolesik *et al.* 1997) and *A. antsantha* Endl. (Lepesché *et al.* 1999), and *Asphondylia obscura* sp. nov. on *S. physalifolium* var. *nitidibaccatum* and *S. chenopodioides*. Pupation takes place within the gall.

Etymology

The name *paucidentata* is a compound Latin adjective from *paucus* and *dentis*, meaning "few" and "tooth", referring to the small number of teeth on the pupal antennal horns.

Asphondylia obscura Kolesik sp. nov. (FIGS 24–29)

Holotype: ♂, Mt Tomah, New South Wales (33° 33' S, 150° 25' E), reared from fruit galls on *Solanum physalifolium* Rusby var. *nitidibaccatum*, gall collected 4.vi.1985, A. J. Wapshere, 6178 (ANIC).

Paratypes: 3 ♂♂, same data; 5 ♂♂, same data but from fruit galls on *Solanum chenopodioides* Lam.

Male (Figs 24–29)

Wing length 3.5 mm (range 3.1–3.8, $n=9$), width 1.4 mm (1.2–1.5). Genitalia in dorsoventral view: gonostylus 1.7–1.8 x ($n=3$) longer than wide, distal edge strongly concave. Other characters as in *A. paucidentata*.

Female, pupa, larva unknown.

Gall and biology

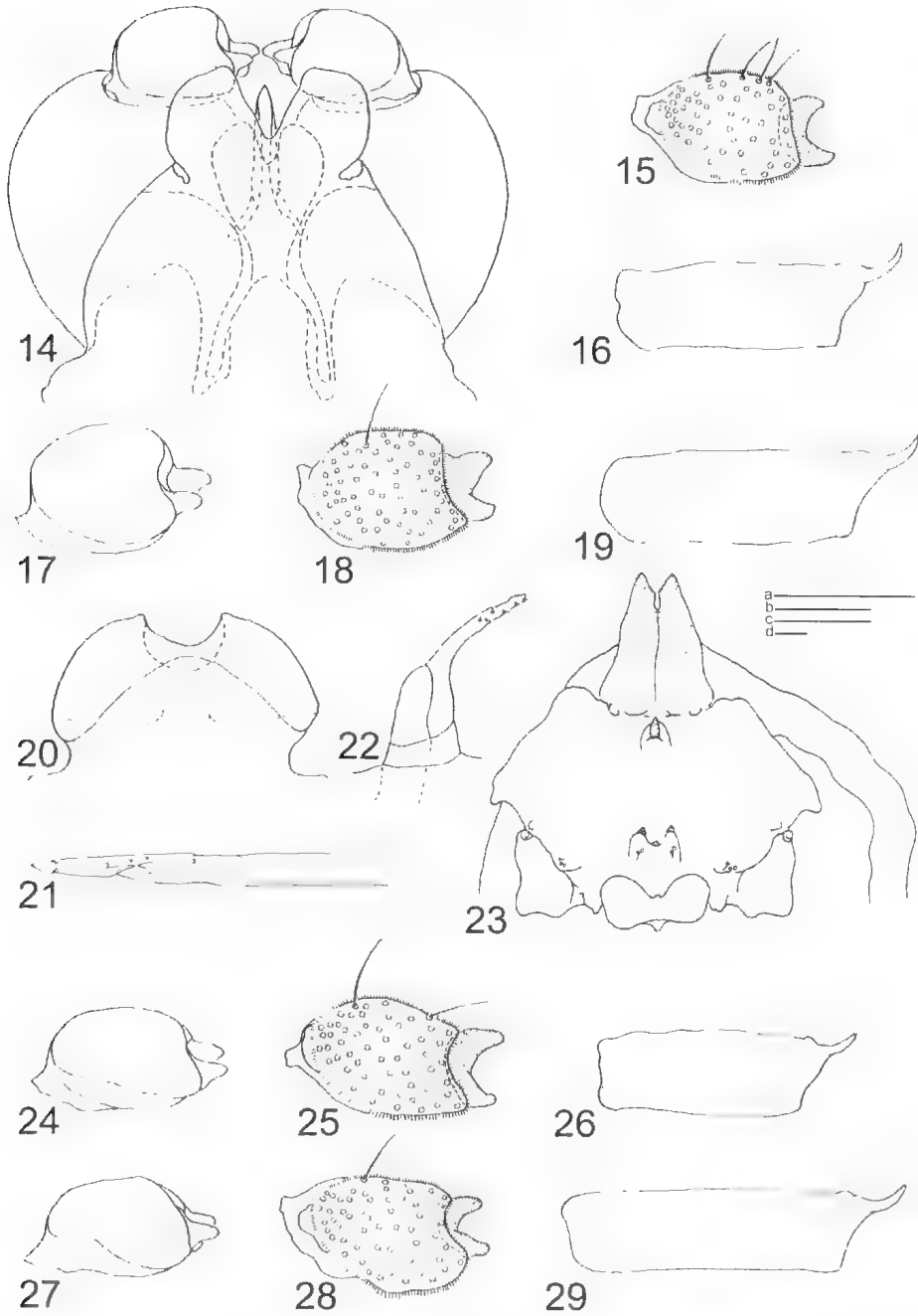
The gall midge causes a fruit gall on *Solanum physalifolium* var. *nitidibaccatum* and *S. chenopodioides*, similar to galls of *A. paucidentata* and *A. anthocercidis*. Pupation takes place within the gall.

Etymology

The name means "obscure" in Latin, referring to the fact that the gall midge was found on non-native plants and therefore its primary host and original geographical distribution are ambiguous.

Remarks

The three new species are morphologically close to each other and to *Asphondylia anthocercidis*, a species that causes fruit galls on *Anthocercis littorea* Labill. (Kolesik *et al.* 1997) and *Anthocercis antsantha* Endl. in Western Australia (Solanaceae) (Lepesché *et al.* 1999). Together, these four species form a natural group associated with plants of the



Figs 14-23. *Asphondylia paucidentata* sp. nov. 14-19 male, 20, 21 female, 22, 23 pupa. Fig. 14. Genitalia in dorsal view. Fig. 15. Gonostylus in posterior view. Fig. 16. First tarsomere of middle leg. Fig. 17. Gonostylus in dorsal view. Fig. 18. Gonostylus in posterior view. Fig. 19. First tarsomere of middle leg. Fig. 20. Basal lobes on ovipositor in dorsal view (setae omitted). Fig. 21. End of ovipositor in lateral view. Fig. 22. Prothoracic spiracle. Fig. 23. Anterior part in ventral view. Specimens in 17 & 18 reared from *Solanum linearifolium*, remaining from *Solanum aviculare*

Figs 24-29. Male of *Asphondylia obscura* sp. nov. Fig. 24. Gonostylus in dorsal view. Fig. 25. Gonostylus in posterior view. Fig. 26. First tarsomere of middle leg. Fig. 27. Gonostylus in dorsal view. Fig. 28. Gonostylus in posterior view. Fig. 29. First tarsomere of middle leg. Specimens in 24-26 reared from *Solanum sarrahoïdes*, 27-29 from *Solanum chenopodioides*. Scale bars: a = 100 µm (Figs 14, 16, 19, 21, 26, 29); b = 50 µm (Figs 15, 17, 18, 22-25, 27, 28); c = 100 µm (Fig. 20); d = 100 µm (Fig. 23).

family Solanaceae that is morphologically distinguishable from other known Australian *Asphondylia* spp. by the long, cylindrical antennal scape, three lower frontal pupal horns, a setose pupal prothoracic spiracle and long-shafted larval spatula with four anterior teeth. *Asphondylia anthocercidis* differs from the three new species in the gonostylus being narrow in dorsoventral view, in having a narrow and shallow posterior incision on the basal lobes on the ovipositor when viewed dorsoventrally and the smooth antennal horns on the pupa. *Asphondylia sturtiana* can be distinguished from *A. paucidentata* by the ventroapical spur on the first tarsomere being bent at a right angle, basal lobes on the ovipositor ending in small processes, pupal antennal horns being serrate along the entire inner edge and only a slightly-bent prothoracic spiracle in the pupa as opposed to the ventroapical spur being bent at 45–60°, basal lobes on the ovipositor with no obvious processes, pupal antennal horns with a small number of teeth in the middle of the inner edge and a strongly-bent prothoracic spiracle in the pupa, respectively. *Asphondylia paucidentata* differs from *A. obscura* sp. nov. in the ratio between the length and the width of the gonostylus in the dorsoventral view being 1.4 as opposed to 1.7–1.8 for *A. obscura*

Solanum chenopodioides and *S. physalifolium* var. *nudibaccatum*, the host plants of *A. obscura*, are not native to Australia. Although no *Asphondylia* has been known to be associated with these plants in their native South America (Gagné 1994), it is currently not possible to determine the primary host and the area of distribution of this gall midge due to the limited knowledge of gall midge fauna associated with Solanaceae in Australia and South America.

The new species restrict reproduction and growth of their respective plant hosts by turning the fruit into a seedless gall and deforming the stem. Further investigation is needed, though, to clarify the role of fruit-galling *A. paucidentata* and *A. obscura* in the pollination of their hosts, a phenomenon assumed in *A. anthocercidis* (Kolesik *et al.* 1997).

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HELMINTH PARASITES OF THE PURPLE-NECKED ROCK WALLABY, *PETROGALE LATERALIS PURPUREICOLLIS*, FROM QUEENSLAND

BY C. BRADLEY*, I. BEVERIDGE*, N. B. CHILTON* * P. M. JOHNSON†

Summary

Bradley, C., Beveridge, I., Chilton, N. B. & Johnson, P. M. (2000) Helminth parasites of the purple-necked rock wallaby, *Petrogale lateralis purpureicollis*, from Queensland. *Trans. R. Soc. S. Aust.* 124(1), 37-40, 31 May, 2000.

Examination of 12 *Petrogale lateralis purpureicollis* from north-western Queensland for helminths yielded one species of cestode and 12 species of nematodes, five of which represent new host records. The diversity of the helminth community present was comparable with that found in other species of rock wallabies. The helminth community was divisible into three distinct groups, species known only from the various subspecies of *P. lateralis*, species found only in rock wallabies and species found commonly in the sympatric macropodid *Macropus robustus*, presumably acquired by host switching in shared habit.

Key Words: Nematoda, Cestoda, *Petrogale lateralis purpureicollis*, Macropodidae, new records.

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Introduction

The helminth parasite faunas of many species of wallabies and kangaroos are still relatively poorly known (Spratt *et al.* 1991; Beveridge & Spratt 1996). Among rock-wallabies of the genus *Petrogale* Gray, 1837, only the parasites of species occurring along the eastern coast of Queensland, members of the *P. penicillata* (Gray, 1825) complex (the brush-tailed rock wallabies) (i.e. *P. assimilis* Ramsay, 1877, *P. godmani* Thomas, 1923, *P. herberti* Thomas, 1926, *P. inornata* Gould, 1842, *P. mareeba* Eldridge & Close, 1992, *P. penicillata*, *P. sharmani* Eldridge & Close, 1992) and *P. persephone* Maynes, 1982 (the Proserpine rock wallaby) have been studied in any detail (Beveridge *et al.* 1989; Begg *et al.* 1995). By contrast, records of parasites from black-footed rock wallabies, members of the *P. lateralis* Gould, 1842 complex, the short-eared rock wallaby, *P. brachyotis* (Gould, 1841) and the yellow-footed rock wallaby, *P. xanthopus* Gray, 1855, are based on incidental collections from a very small number of hosts. No helminth parasites have been reported from the monjon, *P. burbidgei* Kitchener & Sanson, 1978, the Cape York rock wallaby, *P. coenensis* Eldridge & Close, 1992 or Rothschild's rock wallaby, *P. rothschildsi* Thomas, 1904 (Spratt *et al.* 1991).

The parasites of the purple-necked rock wallaby, *P. lateralis purpureicollis* Le Souef, 1924, from north-western Queensland are poorly known, with current records based on the examination of a small number

of specimens from Dajarra, Queensland (Beveridge *et al.* 1989). The parasites of this subspecies of rock wallaby are of particular interest, since they appear to differ significantly from those found in members of the *P. penicillata* complex from coastal Queensland (Beveridge *et al.* 1989). The different subspecies of *P. lateralis* occur in disjunct populations across the entire western half of the Australian continent (Briscoe *et al.* 1982; Strahan 1995) with *P. l. purpureicollis* being the most eastern subspecies of the complex. *Petrogale lateralis purpureicollis* is separated from the most western populations of *P. assimilis*, a member of the *P. penicillata* complex, by approximately 500 km and might therefore be expected to act as an indicator of the extent of differences between parasite faunas of the *P. penicillata* and *P. lateralis* complexes.

It is not possible to conduct extensive samplings of rock wallaby populations which are uncommon or which occur in a restricted geographic range simply to investigate their helminth parasites. Therefore, animals which have died from other causes often provide valuable information about the prevalence and intensity of infection with internal parasites. This paper presents data on parasites of *P. l. purpureicollis* obtained from animals killed by motor vehicles in north-western Queensland and investigates the similarities of its parasite fauna with that found in members of the *P. penicillata* complex.

Materials and Methods

Rock wallabies were collected as fresh road kills in the Mt Isa (20° 44' S, 139° 29' E) and Cloncurry (20° 42' S, 140° 30' E) regions of north-western

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Queensland and were stored at -20°C prior to examination. Subsequently, carcasses were thawed, the sex and approximate age of each specimen was noted and body measurements were recorded. At autopsy, body cavities were examined for filaroid nematodes, the bile ducts for cestodes and the oesophagus for strongyloid nematodes. The entire content of the stomachs was preserved in 10% formaldehyde. The small and large intestines were opened and also examined for helminths. Any cestodes observed were washed in water and preserved in AFA (Pritchard & Kruse 1982) while the remaining intestinal content was preserved in 10% formaldehyde. Cestodes were stained with Celestine blue, dehydrated in ethanol, cleared in methyl salicylate and mounted in Canada balsam.

The stomach content was washed with tap water to remove the formaldehyde and the number of nematodes counted in a 5 or 10% subsample. All nematodes in the subsample were cleared in lactophenol and identified to determine the total numbers of each species present. The content of the small and large intestines was examined microscopically for helminths; if oxyuroid nematodes were present in the colon, their numbers were determined by a dilution method. All specimens collected have been deposited in the South Australian Museum, Adelaide (SAMA).

The prevalence and intensity of infection of each species of helminth was calculated (Margolis *et al.* 1982). The diversity of the community was assessed using the reciprocal of Simpson's Index (Greig-Smith 1964) and the prevalence classes of helminth species were used to separate "core", "secondary" and "satellite" species (Hanski 1982; Bush & Holmes 1986).

Results

Of the 12 *P. l. purpureicollis* examined, nine were males and three were females. Although no parasites were found in the body cavities, bile ducts or oesophagus, one species of cestode, *Triplasma mirabilis* Boas, 1902 was found in the small intestine, 10 species of nematodes were found in the stomach, all belonging to the subfamily Cloacinae Stossich, 1899 and consisting of one species of *Ryngopharynx* Moennig, 1927 and nine species of *Cloacina* Linstow, 1898, while two species of nematode, the strongyloid *Macropostrongyloides baylisi* (Wood, 1931) and the oxyuroid, *Macropoxyuris* sp., were found in the large intestine (Table 1).

The percentages of helminth species in each 10% prevalence class were approximately tri-modal in distribution (Fig. 1); those helminths in the 0-10% prevalence class were classified as "satellite"

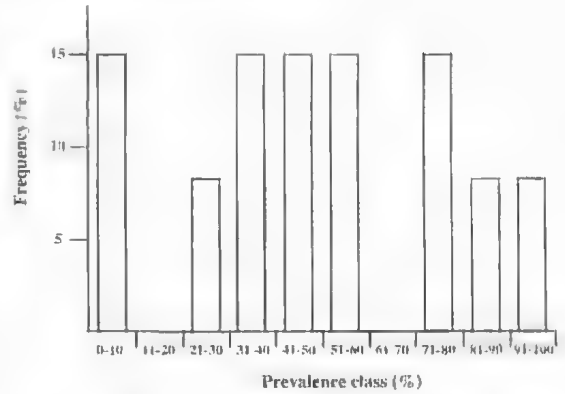


Fig. 1. Frequency distribution of occurrence of helminth species in different prevalence classes.

species, those in the 21-60% class as "secondary" species and those in the 71-100% class as "core" species, following Bush & Holmes (1986). The classification of each species on the basis of prevalence is shown in Table 1. The diversity of the helminth community assessed by the reciprocal of Simpson's Index was 9.85.

Discussion

The collections of parasites from *P. l. purpureicollis* reported here significantly increase the number of parasite species known from this host. Beveridge *et al.* (1989) found seven species of helminths in the animals they examined (the cestode *Triplasma fimbriata* Beveridge, 1976 and the nematodes *Cloacina ornabellae* Johnston & Mawson, 1938, *C. hydriformis* Johnston & Mawson, 1938, *C. pearsoni* Mawson, 1971, *C. vaenis* Beveridge, 1998 (= *C.* sp. 1 of Beveridge *et al.* 1989), *Pharyngostromyloides lambdi* Mawson, 1965, *Ryngopharynx alpha* (Johnston & Mawson, 1938) (syn. *R. australis* in part)). Subsequently, Spratt *et al.* (1991) reported an unidentified species of *Papillostrongylus* Johnston & Mawson, 1939 and Beveridge (1998) reported *C. petrogale* Johnston & Mawson, 1938, *C. parva* Johnston & Mawson, 1938 and *C. frequens* Johnston & Mawson, 1938 from this host. The current study adds the cestode *Triplasma mirabilis* Boas, 1902 and the nematodes *C. macropodis* Johnston & Mawson, 1938, *C. langetablata* Johnston & Mawson, 1938, *C. celidne* Beveridge, 1998 and *Macropostrongyloides baylisi* (Wood, 1931) to the parasites known from *P. l. purpureicollis*. The species of *Macropoxyuris* found in the colon of one rock wallaby also represents a new record but is not considered further because of the unresolved status of a number of undescribed species within the genus (Beveridge *et al.* 1992, 1998).

TABLE 1. *Helminth parasites of Petrogale lateralis purpureicollis from north-western Queensland.*

Species	Prevalence (%)	Intensity Range (mean)	Group ^a
STOMACH (Nematoda)			
<i>Rugopharynx alpha</i> (Johnston & Mawson, 1938)	75	60-10710 (1400)	C
<i>Cloacina caenis</i> Beveridge, 1998	100	590-13230 (3210)	C
<i>Cloacina echidna</i> Beveridge, 1998	58	32-630 (206)	2
<i>Cloacina ernabella</i> Johnston & Mawson, 1938	83	50-1358 (428)	C
<i>Cloacina frequens</i> Johnston & Mawson, 1938	33	20-65 (40)	2
<i>Cloacina longelabiata</i> Johnston & Mawson, 1938	42	40-97 (60)	2
<i>Cloacina macropodis</i> Johnston & Mawson, 1938	50	32-1060 (263)	2
<i>Cloacina parva</i> Johnston & Mawson, 1938	58	60-206 (100)	2
<i>Cloacina pearsoni</i> Mawson, 1971	75	36-630 (304)	C
<i>Cloacina petrogale</i> Johnston & Mawson, 1938	33	20-413 (138)	2
SMALL INTESTINE (Cestoda)			
<i>Triplotaenia mirabilis</i> Boas, 1902	25	-	2
LARGE INTESTINE (Nematoda)			
<i>Macropostrongyloides baylisi</i> (Wood, 1931)	9	1	S
<i>Macropoxyuris</i> sp.	9	725	S

classification based on prevalence : C= core species, 2= secondary species, S= satellite species

The diversity of the helminth community in *P. l. purpureicollis* (reciprocal of Simpson's Index = 9.85) is comparable with that found in other rock wallabies such as *P. assimilis* (10.87), *P. godmani* (13.89), *P. herberti* (10.64), *P. inornata* (11.24) and *P. persephone* (14.30) (Beveridge *et al.* 1989; Begg *et al.* 1995), as well as those of the small wallabies such as the northern naitail wallaby, *Onychogalea unguifera* (Gould, 1841) (10.9), and the spectacled hare wallaby, *Lagorchestes conspicillatus* Gould, 1842 (11.8) (Beveridge *et al.* 1992). It is lower than values found in the red-legged pademelon, *Thylogale stigmatica* (21.9) (see Beveridge *et al.* 1992), the swamp wallaby, *Wallabia bicolor* (17.5) and various species of *Macropus* found in north and central Queensland (14.4-26.6) (see Beveridge *et al.* 1998). The helminth community of *P. l. purpureicollis* is thus moderately diverse in comparison with most macropodids and its diversity is comparable with that found in other small wallabies and rock wallabies.

The examination of prevalence classes suggested

that the helminth community present in *P. l. purpureicollis* was broadly divisible into three groups, "satellite", "secondary" and "core" species, utilising the terminology of Bush & Holmes (1986). Beveridge *et al.* (1989) used the same terminology for helminths of rock wallabies of the *penicillata* complex, although the prevalence limits of the three classes differed. Of the satellite species present in *P. l. purpureicollis*, *M. baylisi* is a common parasite of the wallaroo, *Macropus robustus* Gould, 1841 (see Beveridge *et al.* 1993) which is abundant in the area in which the rock wallabies were collected. The secondary species encountered included the cestode, *Triplotaenia mirabilis*, known only from the MacDonnell Ranges race of *P. lateralis* and *P. l. purpureicollis*, and the nematodes *C. petrogale*, known only from the rock wallabies *P. lateralis* and *P. brachyotis*, and *C. echidna*, *C. frequens*, *C. longelabiata*, *C. macropodis* and *C. parva*, which are primarily parasites of *M. robustus* (Beveridge 1998; Beveridge *et al.* 1998). The core species included *R. alpha* and *C. ernabella*, which are restricted to the

CAUSES OF RARITY IN ABUTILON OXYCARPUM AND HIBISCUS BRACHYSIPHONIUS (MALVACEAE) ON THE RIVER MURRAY FLOODPLAIN, SOUTH-EASTERN AUSTRALIA

BRIEF COMMUNICATION

Summary

A central problem in deciding conservation priorities for plant species in arid and semi-arid areas is that some species appear briefly following particular environmental triggers and then disappear for years until the trigger recurs. Such transient species¹ are often listed as rare but are not necessarily threatened as long as the natural cycle continues without interference. So far, work on such species in semi-arid Australia has been concentrated on post-fire pioneers^{1,2}. However, many transient species are triggered by infrequent rainfall events³. Because their ecology and conservation are poorly understood, here we use long-term data from 1983 till 1999 to explore the issues involved, including causes of rarity and the amount of rainfall needed to trigger germination and growth.

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Abutilon oxycarpum (F. Muell.) F. Muell. ex Benth. var. *malvaefolium* Benth. (Malvaceae) (Fig. 1) is a herb which may reach 8 cm and which behaves as an annual in Victoria. Data are also presented for *Hibiscus brachysiphonius* F. Muell. (Malvaceae), a subshrub to 15 cm high which resprouts from a perennial rootstock. Both species have their main growth period following rain in the warmer months of the year, in our area principally from November until April. Both taxa occur in all mainland states and at least as far north as 20° S.

Abutilon oxycarpum and *H. brachysiphonius* were unknown in Victoria until 1983 when they were recorded in close proximity at Bottle Bend near Red Cliffs, Vic. (Browne 1986; Fig. 2). This was in the first week of March following 32 mm of rain. For both taxa, the Victorian stands are widely disjunct from those elsewhere in Australia and represent their southern limit. Neither taxon is threatened in Australia and frequencies greater than 50% have been recorded for them in some central Queensland communities. However, in Victoria, *A. oxycarpum* is rated vulnerable and *H. brachysiphonius* endangered. They will be referred to as *Abutilon* and *Hibiscus* throughout this paper.

The known Victorian range of *Abutilon* and *Hibiscus* is in an area less than three km across on grey cracking clays of the River Murray floodplain within 0.6 km of the river near Bottle Bend (Fig. 2). *Abutilon* and *Hibiscus* occur together at sites 1 and 2 and *Abutilon* occurs at sites 3 and 4. Site 4 is a depression dominated by scattered shrubs of *Muehlenbeckia florulenta* Meisn. (Tangled Lignum); all other sites contain *Eucalyptus largiflorens* F. Muell. (Black Box) woodland with a sparse understorey of occasional chenopods and *Zygophyllum* spp.

The climate is semi-arid, with a mean annual rainfall of 290 mm at Red Cliffs, the wettest months being from May to October. The rainfall is highly variable, especially in summer when rain usually occurs as heavy downpours during thunderstorms. Summers are hot and winters mild, with frosts occurring.

Site 2 was inspected in January 1991 (12 plants) and site 3 in January 1984 (4 plants). No further inspections were made due to track closures. Other sites were inspected at

least annually in summer-autumn between 1983 and 1995 and again between 1997 and 1999 (Table 1). Areas of the same habitat in nearby Kings Billabong Wildlife Reserve, Lambert Island and elsewhere were searched intensively for the two taxa without success. Voucher specimens are lodged at MEL.

The plant data recorded in Table 1 refer to *Abutilon* plants less than one year old and to resprouts from perennial rootstocks of *Hibiscus*. Rainfall data are from Red Cliffs, less than 10 km away.

The first stands of both taxa seen (at site 1) were in an area where trees had been felled and soil disturbed by

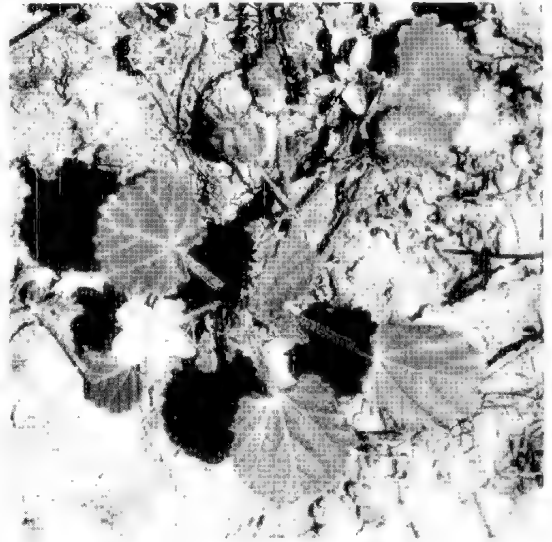


Fig. 1. *Abutilon oxycarpum* 5 cm across at Bottle Bend Reserve, showing flower and fruit.

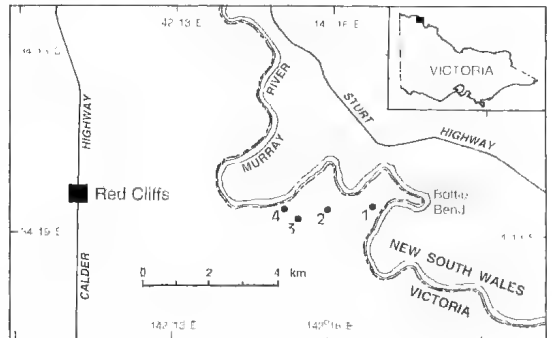


Fig. 2. Location of Bottle Bend Reserve, showing the only four sites where *Abutilon oxycarpum* has been seen in Victoria. Sites 1 and 2 also carry stands of *Hibiscus brachysiphonius*.

TABLE 1. Monthly rainfall totals (mm), significant rainfall episodes and numbers of *Abutilon* and *Hibiscus* at site numbers 1 and 4, Bottle Bend Reserve for November to April 1982-1999.

Year	Rainfall (mm)						Major rainfall episodes	Plant numbers			Notes on Site 4
	Nov	Dec	Jan	Feb	Mar	Apr		<i>Abutilon</i> Site 1	<i>Abutilon</i> Site 4	<i>Hibiscus</i> Site 1	
1982-83	4	1	0	1	48	10	32 mm, 2-7 Mar	50	30	8	
1983-84	23	20	49	4	14	21	28 mm, 1-3 Jan	100	47	13	
1984-85	8	0	7	0	3	6	None	0	0	0	
1985-86	38	35	0	11	0	6	26 mm, 6 Nov; 24 mm, 9 Dec	0	3	5	
1986-87	20	43	11	15	14	9	21 mm, 8 Dec	0	0	0	
1987-88	4	31	22	2	12	38	No falls above 10 mm until Apr (23 mm)	0	0	0	
1988-89	59	27	12	2	74	66	37 mm, 14 Mar	present	present	10	
1989-90	34	25	11	9	8	35	26 mm, 4-6 Nov; 26 mm, 21-23 Apr	0	0	0	
1990-91	4	9	88	0	0	23	32 mm, 7 Jan; 39 mm, 24 Jan	present	0	200+	Flood, then dense <i>Eleocharis</i>
1991-92	31	3	1	9	6	12	26 mm, 26 Nov	0	0	0	Dense <i>Eleocharis</i>
1992-93	56	94	77	10	11	0	Falls of more than 30 mm in Nov, Dec & Jan	0*	0	present	Flood, then dense <i>Eleocharis</i>
1993-94	23	62	5	95	0	3	29 mm, 22 Dec; 49 mm, 11 Feb; 27 mm, 14 Feb	0*	0	present	Dense <i>Eleocharis</i>
1994-95	15	11	54	20	0	18	19 mm, 6 Jan; 10 mm, 16 Jan; 16 mm, 30 Jan	0	0	present	Dense <i>Eleocharis</i>
1995-96							No data				
1996-97							No data				
1997-98	31	9	37	26	0	47	No falls above 17 mm	0	0	present	
1998-99	19	3	17	38	17	5	29 mm, 12 Feb	present	present	present	

* The *Abutilon* part of Site 1 flooded briefly in November 1992, resulting in a dense *Chloris* stand in 1993-94.

tractor to lay a telephone cable, suggesting pioneer-type behaviour as in some other Malvaceae¹. However, all subsequent stands found have been in intact vegetation lacking soil disturbance.

When observations started, the area was lightly grazed by Western Grey Kangaroos and cattle; these animals readily eat both *Abutilon* and *Hibiscus* and marked grazing effects were observed.

The falls of rain tabulated usually resulted from single warm-season storms, but sometimes significant rains over two or three consecutive days are given (Table 1). Over the 15 years studied, *Abutilon* appeared in 5 years at any one site and *Hibiscus* in 10 years (Table 1). At least one episode of rain of more than about 26 mm between November and March seems to be needed for plants of both species to appear in the study area. In seasons like 1994-95 and 1997-98, a series of smaller falls than this scattered through a month is enough for *Hibiscus* but not *Abutilon* to grow (Table 1). Single falls of 26 mm (e.g. 1991-92) or less usually do not produce either species (Table 1).

Following germination in *Abutilon*, development is rapid. After the significant rainfall of 2-7 March 1983,

Abutilon had flowers and fruit in 5 weeks and mature seed in 7.5 weeks despite little extra rain. Plants only 4 cm high can produce seed. Most *Hibiscus* plants were partly grazed off, but flower buds were produced by 2 weeks.

Of the original eight re-sprouting *Hibiscus* plants seen in 1983, all were still alive in 1989 and four were still alive in 1999, giving a minimum lifespan of 16 years. In the study area, cattle grazing was discontinued in 1988 and following 32 mm of rain on 7 January 1991, a further 200 resprouting *Hibiscus* plants were found in an area adjoining the original stand and which had been searched previously for this species. We believe that this occurred through a combination of the rainfall and the absence of cattle grazing, with the grazed-off plants being undetectable in the presence of cattle. This more recent, larger population continues to appear, given appropriate rainfall. Since 1988, it is clear that some kangaroo grazing of both taxa occurs, especially of *Abutilon* at site 4.

In the second half of 1990 the lowest site, site 4, was flooded by high river levels. It was still flooded and dominated by a dense stand of the sedge *Eleocharis acuta* R. Br. in November 1990. This almost certainly caused the

absence of *Abutilon* in 1990-91 despite suitable rainfall (Table 1).

November 1992 had the highest river levels since 1981, flooding site 4 again and the *Abutilon* and part of the *Hibiscus* stand at site 1. Hence dense *Eleocharis* continued to dominate site 4 until at least 1994-95, accounting for the absence of *Abutilon* in the three years 1992-95, despite suitable rain. No small plants occur within the dense stem and rhizome systems of *Eleocharis*, presumably because they are outcompeted.

At the site 1 *Abutilon* stand, higher than site 4, the flood drained away quickly. A dense stand of the grass *Chloris truncata* resulted, accounting for the absence of *Abutilon* following good rains in the two years 1993-95 (Table 1). By the time of the 1997-99 records of *Abutilon* and *Hibiscus* (Table 1), *Chloris* and *Eleocharis* had disappeared from the sites.

We conclude that the major abiotic determinants of *Abutilon* mature plant occurrence in the area are warm season rainfall and flooding, the former necessary for recruitment and the latter temporarily excluding *Abutilon* by promoting dense stands of competing species. Assuming that an episode of rain of more than 26 mm between November and March is needed for germination, in seven of the 15 years site 1 experienced rainfall suitable for *Abutilon* occurrence, but for two of these *Abutilon* was excluded by post-flooding competition (or for three of them in the case of the lower-lying site 4). *Hibiscus* growth was stimulated under drier conditions than was *Abutilon* germination, possibly because of its perennial rootstock.

In some desert species, falls of rain as low as 10 mm can produce germination¹¹. While 26 mm was the minimum rainfall recorded here which produced seedling emergence of *Abutilon*, the actual quantity of rain needed will be greatly influenced by the high clay content of the study area, which has an unfavourable influence on water supply in this climate due to the inverse texture effect¹².

Plant species of arid and semi-arid areas are often grouped into 'summer flora', 'winter flora' or those that can germinate and establish in both seasons¹³. The species studied here are clear examples of summer flora. In our study area, *Sida trinopoda* (Malvaceae) behaves very much like *Hibiscus*. In north-western Victoria, probably all

species of *Abutilon* and *Sida* are of the summer-growing type¹⁴. The taxa of *Abutilon* and *Hibiscus* studied here can occur in areas with less than 200 mm mean annual rainfall, much lower than the study area¹⁵. Further work is needed to explain why they do not extend further south; lower incidence of summer rain, lower temperature regimes (including frost effects) or both may be involved. A further important factor in *Abutilon* and *Hibiscus* occurrence is grazing, with cattle removal having beneficial effects at least on the *Hibiscus* population.

Abutilon is a transient species which can be absent from a site for at least six years before re-appearing. This behaviour almost certainly relies on hard-coated seeds forming a persistent soil seed bank as it does in *Abutilon theophrasti*¹⁶. Parsons & Browne¹⁷ give examples of longer intervals before re-appearance.

Many transient species regenerate profusely during favourable circumstances. Their absence over years during dry seasons does not mean that they are threatened as long as seeds are produced often enough to ensure that germination occurs during favourable seasons. Many such species are not listed as either rare or threatened¹⁸. Nevertheless, more recent work points out that if the habitat is not continuously fit for occupation because of transient climatic conditions, this can increase extinction risk and so this factor is built into the new rules for classifying such risk¹⁹.

While *Abutilon oxycarpum* is not threatened Australia-wide, there is concern about the Victorian stands, especially because they are widely disjunct from the species' core area and are at its southern limit. The most serious threat is grazing; while parts of site 1 and all of site 4 were fenced against stock in 1984, the fences are not kangaroo-proof and kangaroo grazing prevented seed set by most *Abutilon* plants in 1999 and some previous years. The fact that the maximum number of *Abutilon* plants recorded was well below 250 mature individuals in any one season means that the species qualifies as endangered in Victoria using the basic IUCN Red List rules for risk assessment²⁰. The most important management recommendation following from our work is provision of kangaroo proof fencing.

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RECORDS OF MOSQUITOES (DIPTERA: CULICIDAE) FROM THE COOPER BASIN IN NORTH-EASTERN SOUTH AUSTRALIA

BRIEF COMMUNICATION

Summary

The mosquitoes (Diptera: Culicidae) of arid and central Australia are not well documented. Although Lee and Woodhill¹, O’Gower² and Marks^{3,4} have provided limited distribution records for some species, most data for mosquitoes in this region stem from the investigations of Kay⁵ and Kay et al⁶ in Charleville, south-western Queensland. Given the abundance of industry and agriculture in the region and the presence of mosquito-borne viral illness^{7,8,9} a greater understanding of the vectors in this region is required. There is also a suggestion that mosquito-borne encephalitis viruses periodically invade south-eastern Australia from more northerly foci^{7,10}. No published information exists for mosquitoes in north-eastern South Australia (SA).

BRIEF COMMUNICATION

RECORDS OF MOSQUITOES (DIPTERA: CULICIDAE) FROM THE COOPER BASIN IN NORTH-EASTERN SOUTH AUSTRALIA

The mosquitoes (Diptera: Culicidae) of arid and central Australia are not well documented. Although Lee and Woodhill, O'Gower and Marks¹ have provided limited distribution records for some species, most data for mosquitoes in this region stem from the investigations of Kay and Kay *et al.*² in Charleville, south-western Queensland. Given the abundance of industry and agriculture in the region and the presence of mosquito-borne viral illnesses³ 'a greater understanding of the vectors in this region is required. There is also a suggestion that mosquito-borne encephalitis viruses periodically invade south-eastern Australia from more northerly foci'. No published information exists for mosquitoes in north-eastern South Australia (SA).

From December 1998 to December 1999, we conducted a study of mosquitoes at four sites in north-eastern SA, in the locality of the Moomba and Tirrawarra oil and gas fields. A history of seasonally high mosquito numbers in this area⁴ and heavy rainfall in September 1998 were catalysts for this study, the aim of which was to determine the species of mosquitoes in the area.

The sites were located within the Cooper landscape region of Barlow⁵, commonly referred to as 'channel country' which featured grasslands, shrublands, alluvial plains and dunes and watercourses, in a subtropical-dry climate (Type III of Walter & Lieth⁶).

Mosquitoes were sampled at Moomba camp (28°06' S, 140°11' E), at Gidgealpa waterhole, an ephemeral freshwater body in open *Eucalyptus* and *Acacia* woodland 30 km to the north (27°47' S, 140°10' E) and at two sites on a floodplain near Embarka swamp, approximately 50 km north of Moomba camp and 50 km south of the Coongie Lakes system. The swamp, on the Cooper Creek, is in the middle of a floodplain supporting lignum shrubland (*Muehlenbeckia florulenta* Meissner), nardoo (*Maritima drummondii* A. Braun.), and sparse *Acacia* woodland. Embarka swamp Site 1 was at the northern end of the shrubland/floodplain, approximately seven km north of the Tirrawarra oil and gas camp (27°37' S, 140°09' E). Embarka swamp Site 2 was approximately one km north of the camp.

Mosquitoes were sampled using dry-ice baited miniature light traps⁷. These traps predominantly capture host-seeking adult female mosquitoes. A single trap was set at least one hour before sunset and retrieved at least one hour after sunrise at each site on three (sometimes four) occasions from December 1998 to April 1999. Two further traps were set at Gidgealpa waterhole and Embarka swamp Site 1 on 11/11/99. Four traps were set at Moomba camp on 27/12/99 in response to heavy rainfalls there during December (97.8 mm from 16/12/99 to 27/12/99). Mosquitoes were identified using the keys of Lee *et al.*⁸ and Russell⁹.

Eleven species were captured in dry-ice baited traps (Table 1). From December 1998 to April 1999, Gidgealpa waterhole and Moomba camp were characterised by very low catch numbers. In contrast, large numbers were captured at Embarka swamp with *Culex annulirostris* Skuse most abundant. *Anopheles annulipes* s.l. Walker and *Anopheles unctus* Edwards were captured in large numbers periodically at the Embarka swamp sites. The two traps set on 11/11/99 yielded only a single, male *Aedes (Macleana)* Marks species 126 at Gidgealpa waterhole. No mosquitoes were caught at Embarka swamp Site 1 on this day.

Traps set at Moomba camp on 27/12/99 captured large numbers of *Aedes edwardsensis* Mackerras, with smaller numbers of *Aedes sapientis* Marks, *Aedes (Ochlerotatus)* Marks species 85 and *Cx. annulirostris*. Rainfall at Moomba in mid-December 1999 was probably responsible for the large numbers of *Aedes* mosquitoes, which have desiccation-resistant eggs that hatch upon inundation. This trait makes some *Aedes* species well adapted to environments where rainfall is episodic.

Mosquitoes biting humans were captured from bare legs from the knees down and on feet using a mouth operated aspirator and stored in polystyrene drinking cups covered with nylon netting. All mosquitoes were caught by the authors (75 kg and 90 kg respectively) sitting opposite each other, using a single aspirator, combining the catch from both pairs of legs. This method was used despite the risk of mosquitoes in the area carrying arboviruses, of which both authors were aware. During the day, this was done whenever biting mosquitoes were evident. Nocturnal collections were made on three occasions for ten minutes every hour from sunset until sunrise at Embarka swamp Site 2 and Moomba camp (Table 2). Several other biting catches commenced at sunset and continued for two to three hours.

Mosquitoes were caught from humans at Embarka swamp Site 2 on 9/12/98, 12/1/99, 26/1/99, 16/2/99, 18/3/99 & 11/11/99. *Culex annulirostris* was the predominant biting species at this site. All night biting collections of this species (Table 2) peaked five to six hours after sunset (i.e. 0130 to 0230 h). Of those species not sufficiently abundant to present all night catch data, *Aedes edwardsensis* was caught biting during the day and throughout the night, whereas *An. unctus* and *An. annulipes* were only caught during the night. *Aedes bancroftianus* Edwards was caught biting at sunset at this site.

At Moomba camp, *Cx. annulirostris* and *An. annulipes* were caught at sunset on 8/12/98. On 27/12/99, *Aedes edwardsensis* was caught biting humans throughout daylight hours and was the predominant biting species when an all night catch was performed (Table 2). *Culex annulirostris*, *Aedes sapientis* Marks s., *Aedes theobaldi* (Taylor) and *An. annulipes* were caught in smaller numbers throughout the night at this site.

TABLE 1. Mosquitoes captured by dry-ice baited miniature light traps from December 1998 to April 1999 and December 1999.

Species	December 1998-April 1999 ^a				Dec. 1999 ^c
	Moomba Camp causeway	Gidgealpa waterhole	Embarka Swamp Site 1	Embarka Swamp Site 2	Moomba Camp
<i>Aedes alternans</i> (Westwood)	0	1	0	0	6
<i>Ae. eidsvoldensis</i> Mackerras	0	1	6	18	1215
<i>Ae. sapiens</i> Marks	0	0	0	0	102
<i>Ae. theobaldi</i> (Taylor)	0	0	0	0	8
<i>Ae. (Och.)</i> Marks sp. 85	0	0	0	0	40
<i>Ae. (Mac.)</i> Marks sp. 126	0	1	0	0	0
<i>Anopheles annulipes</i> s.l. Walker	0	2	104	289	23
<i>An. amictus</i> Edwards	0	0	24	238	0
<i>Culex annulirostris</i> Skuse	6	1	314	1789	37
<i>Cx. australicus</i> Dobrotworsky & Drummond	1	0	20	5	0
<i>Cx. quinquefasciatus</i> Say	24	0	0	0	0
total	31	6	468	2339	1431
no. sampling nights	3	3	4	3	1 ^b

^a 1998/99 sampling dates: Moomba causeway - 8/12, 12/1, 18/3; Gidgealpa waterhole - 9/12, 12/1, 18/3; Embarka swamp Site 1 - 8/12, 12/1, 18/3, 1/4; Embarka swamp Site 2 - 8/12, 26/1, 18/3

^b Moomba camp was sampled using four traps on 27/12/99.

TABLE 2. *Culex annulirostris* and *Aedes eidsvoldensis* mosquitoes biting humans for a 10 minute period each hour from sunset (SS) to sunrise (SR) at Embarka swamp Site 2 and Moomba camp.

Time of sampling	Embarka swamp Site 2		Moomba camp
	26/1/99 ^a	16/2/99 ^b	27/12/99 ^c
	<i>Culex annulirostris</i>		<i>Aedes eidsvoldensis</i>
SS - 1	0	0	3
SS	19	4	22
SS + 1	19	20	9
SS + 2	22	32	4
SS + 3	8	34	7
SS + 4	32	41	2
SS + 5	33	58	3
SS + 6	38	63	0
SS + 7	16	41	1
SS + 8	18	50	8
SR	15	27	3
total	220	370	62

^a SS: 2100h, SR: 0600h; ^b SS: 2040h, SR: 0540h; ^c SS: 2030h, SR: 0530h

All water bodies encountered during this study were examined for the presence of mosquito larvae using a standard dipping technique. Any larvae collected were identified in the laboratory using the key proposed by Russell.

Larval collections returned large numbers of *Cx. annulirostris* and *Culex australicus* Dobroworsky & Drummond at locations less than 200 m from Finbarka Swamp Site 2 on 26/1/99, 16/2/99, 18/3/99 and 1/1/99. These locations featured an abundance of shallow (less than 0.5m deep), clear, fresh water. Most larvae were collected from the fringes of waterways, particularly where the bank had been disturbed by livestock, leaving isolated water filled hoofprints. These often contained thousands of larvae of both *Culex* species. Despite this, adult *Cx. australicus* were only collected in small numbers in baited light traps (Table 1). This species is apparently more attracted to unbaited light traps.

On 27/12/99, numerous ephemeral ground pools within a 1 km radius of Moomba camp were found to contain *Cx. annulirostris* and *An. annulipes* larvae. These waters were created by rainfall during the preceding ten days.

This study has added four species to the list of mosquitoes recorded from SA¹². *Ae. sapiens* and *Aedes (Dichromatus)* Marks species 85 have been recorded from several sites throughout the arid zone in north west NSW,

south-west and central Qld¹³ and from Alice Springs NT. *Aedes (Macleaya)* Marks species 126 has been found 520 km to the east at Cunnamulla, Qld, 750km to the north-west at Alice Springs, NT¹⁴ and near Balgo, WA¹⁵. This is also the first record of *An. annulipes* from SA, previously recorded from Charlotte Waters NT (550 km west-north-west), Cunnamulla Qld¹⁶ and Charleyville Qld¹⁷, indicating a wide range throughout arid Australia. Previously, *Aedesvoldensis* has only been recorded in SA from Inmaninka, 60 km east-south east of Tirrawarra camp¹⁸. Twelve mosquito species have thus far been identified from this part of SA.

This study has extended our knowledge of mosquito incidence in the Cooper Basin of SA. High numbers of *Cx. annulirostris*, a vector of Ross River virus, Murray Valley encephalitis and Japanese encephalitis¹⁹, are of particular interest. Together with an abundance of feral pigs and native birds (reservoirs for mosquito-borne encephalitides), high biting rates by *Cx. annulirostris* may render the north-east of SA vulnerable to mosquito borne viral disease.

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**RANGE EXTENSION AND NEW HOST RECORDS OF THE
ECTOPARASITE PSEUDOSTEGIAS SETOENSIS SHIINO 1933
(CRUSTACEA: ISOPODA: BOPYRIDAE)**

BRIEF COMMUNICATION

Summary

The bopyrid ectoparasite, *Pseudostegias setoensis* Shiino, 1933 is here reported as occurring on *Clibanarius taeniatus* (H. Milne Edwards, 1848) and *Clibanarius virescens* (Krauss, 1843) collected from South Cooe Bay (23° 08.5' S. 150° 45.7' E) on the east coast of Central Queensland, Australia. This represents the most southern and eastern locality reported thus far for this parasite. *Clibanarius taeniatus* and *C. virescens* are new host records for this parasite.

BRIEF COMMUNICATION

RANGE EXTENSION AND NEW HOST RECORDS OF THE ECTOPARASITE *PSEUDOSTEGIAS SETOENSIS* SHIHO, 1933 (CRUSTACEA: ISOPODA: BOPYRIDAE)

The bopyrid ectoparasite *Pseudostegias setoensis* Shiho, 1933 is here reported as occurring on *Chibanarius taeniatus* (H. Milne Edwards, 1848) and *Chibanarius virescens* (Krauss, 1843) collected from South Coode Bay (23° 08.5' S, 150° 45.7' E) on the east coast of Central Queensland, Australia. This represents the most southern and eastern locality reported thus far for this parasite. *Chibanarius taeniatus* and *C. virescens* are new host records for this parasite.

Pseudostegias setoensis has been recorded as being parasitic on hermit crabs of the genus *Chibanarius*, only. Previously, *P. setoensis* has been reported from Seto, Japan where the parasite was reported on *C. bimaculatus* (de Haan, 1849), Taiwan where it parasitised *C. striolatus* Dana, 1852, Hong Kong, on *C. bimaculatus* and *C. ransoni* Forest, 1953 and Phuket, Thailand, infesting *C. padavensis* de Man, 1888.

Two species of *Chibanarius* are common in rocky intertidal areas of Central Queensland, where tide-pool temperatures may exceed 38°C during summer months. Shallow tide-pools at the collection sites of both *C. taeniatus* and *C. virescens* are mostly of coral rubble or sand substrate, lined with

micro- and macroalgae and surrounded by unstable rocks. *Pseudostegias setoensis* was found to parasitise both *C. taeniatus* and *C. virescens* collected from South Coode Bay.

The first specimen (Queensland Museum QM W23487) was collected on 15 January, 1998 from the abdomen of *C. taeniatus* and was later identified by J. Markham as an adult female and male *P. setoensis* pair. The small, worm-like male was observed on the ventral, abdominal surface of the larger female in what Shiho describes as a "marsupial-like cavity produced by lamellated-endopodites of pleopods", while the female was clinging with its dorsal side closest to the dorsal aspect of the hermit crab's abdomen (Fig. 1).

Collections of male/female *P. setoensis* pairs from *C. virescens* were also made on, 14 October, 1998 (QM W25093), 5 November, 1998 (QM W25095), 18 November, 1998 (QM W25096), 8 October, 1999 (gravid females) (QM W25100 and QM W25101), 22 November, 1999 (gravid female) (Central Queensland University Museum CQUM 221199 and personal collection), 14 December, 1999 (QM W25103 and Smithsonian USMN 290248) and 31 January, 2000 (gravid female) (QM W25104). On 2 November, 1998 a solitary male *P. setoensis* (QM W25094) was collected slightly posterior to the carapace of the branchial region on a *C. virescens* specimen. Collections of *P. setoensis* pairs from *C. taeniatus* were also made on 11 March, 1999 (QM W25097), 15 March, 1999 (QM W25098), 18 August, 1999 (QM W25099 and personal collection), 1 November, 1999 (QM W25102) and 27 January, 2000 (Australian Museum P58345). A single *P. setoensis* male/female pair, collected 15 September, 1998, was used for SFM work. The incidence rate of *P. setoensis* in a sample of 387 hermit crabs collected between 16 September, 1999 and 25 October, 1999 was 1.6%. On deshelled hermit crabs the opaque, cream-coloured parasite was easily seen, covering up to one half the total length of the abdominal segment of the crab and measuring as much as 9 mm in length. Parasitised hermit crabs did not display obviously different behaviour from non-parasitised ones, nor did they show visible signs of abdominal puncture nor physical deterioration before or after the parasites were removed.

With the exception of the report from the north-eastern Indian Ocean (Phuket), the previous and current records of *P. setoensis* indicate a Western Pacific distribution from Japan to east Australia for this species.

Sincerest thanks are extended to J. Markham of the Arch Cape Marine Laboratory, Arch Cape Oregon USA for his identification of the parasite.

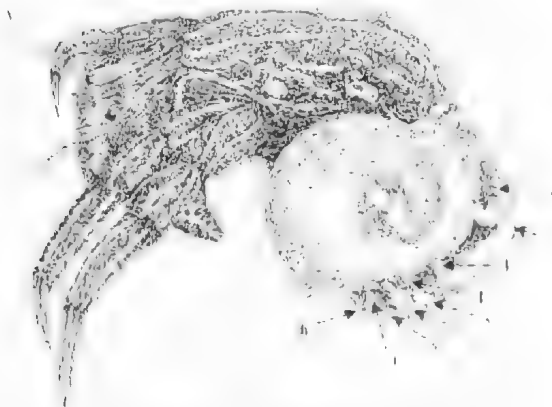


Fig. 1. View of the bopyrid parasite *Pseudostegias setoensis* (a) showing shape and size on the dorsal abdominal aspect of the hermit crab *Chibanarius taeniatus*. Note head region (a), thoracic legs (b), thoracic segment (c) and ventral surface (d) of parasite. The male is characteristically found beneath the lamellated endopodites (e) of the pleopods. Pleopods are not distinct in this view. (Scale bar = 1 mm)

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OBITUARY

ALAN FRANCIS BIRD, B.Sc (Hons), MSc, PhD, DSc

11.ii.1928 – 13.xii.1999

Summary

Alan Bird died suddenly from a heart attack on December 13, 1999, leaving a large void for his family, friends and scientific colleagues. Alan is perhaps most widely known as an internationally renowned nematologist but he also was naturalist in its most traditional sense. An obituary emphasizing this first facet of Alan's professional career has recently been published (*J. Nematol.* 32, 1-3, 2000); here I will focus a little more on Alan as a naturalist, for it was in this guise that he is known most widely to his friends in Australia.



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Alan Bird died suddenly from a heart attack on December 13, 1999, leaving a large void for his family, friends and scientific colleagues. Alan is perhaps most widely known as an internationally renowned nematologist but he also was naturalist in its most traditional sense. An obituary emphasizing this first facet of Alan's professional career has recently been published (*J. Nematol.* **32**, 1-3, 2000); here I will focus a little more on Alan as a naturalist, for it was in this guise that he is known most widely to his friends in Australia.

Alan Bird was born on 11 February, 1928 at Seremban in what were then the Federated Malay States. In 1937 he travelled to Northern Ireland and was enrolled as a boarder in Gloucester House, Enniskillen which was the Prep. School for Portora Royal School, which he subsequently attended. During this time, Alan developed a passion for Rugby Union football that stayed with him for his entire life, and indeed, one of the last conversations we had was over the phone, just after Australia won the Rugby World cup (it was about 3 am in Australia at the time!)

Alan travelled to Perth in 1946, and enrolled as an agricultural science student at the University of Western Australia where he seems to have spent much of his time playing rugby, both for the University (and was awarded a much coveted "blue") and also for the State team. His rugby career in WA included a match against the New Zealand All Blacks, I suspect a rather frightening experience for a little scrum half. Alan switched disciplines and earned a BSc (Hons) in Zoology in 1952, with a research project on blow flies that necessitated him maintaining a small flock of sheep which grazed, tethered to trees on the UWA Grounds. That same year he moved to Adelaide and began to work on animal-parasitic nematodes for an MSc, which was granted by the University of Adelaide in 1955. He continued to play rugby, for the University and for the State of South Australia but had now developed the skills to balance sport with academic achievement; his thesis on "The cuticle and exsheathing mechanism of third stage infective strongyle larvae" resulted in four publications, one in *Nature*, one in *Science* and two in *Experimental Parasitology*.

Newly married to Jean, Alan went to Scotland in 1954 to work on a PhD which was awarded by the

University of Edinburgh in 1956. During those two years, Alan also taught full time as an Assistant Lecturer in helminthology and nematode physiology at the University of Edinburgh. His ability to produce a PhD thesis (on "The nematode cuticle") and publish four additional papers in what must be close to record time can be attributed to two factors (apart from Alan's inherent ability). First, the intellectual environment in the Zoology Department at Edinburgh in the mid-1950s was of the highest calibre, and Alan's supervisor, Peter Mitchell FRS, subsequently won a Nobel prize. Second were the pressures inflicted by the poverty-level salary then paid to Assistant Lecturers. It was as a PhD student in Edinburgh that Alan began to use the (then new) electron microscope and microscopy remained an essential, although not exclusive tool for his entire career.

Alan and Jean returned to Australia in 1957, and Alan began to work for CSIRO Division of Horticultural Research, first at Merbein but from 1958, in Adelaide. In 1984 he moved across the car-park from the Division of Horticulture to the Division of Soils. During this second Australian period Alan published an additional 114 papers. By any measure, this is an impressive scientific achievement. Even more striking is that fact that on 100 of his papers, he was the first or sole author. Significantly, his co-authors often were sabbatical visitors drawn to Alan's lab: Drs S. D. Van Gundy (USA, 1965-66); M. A. McClure (USA, 1974-75); V. H. Dropkin (USA, 1976-77); B. S. Stynes (WA, 1977-78); D. L. Riddle (USA, 1983); C. Preston (Wales, 1986); K. A. Wright (Canada, 1986); B. M. Zuckerman (USA, 1988); G. W. Yeates (New Zealand, 1993). This list which spans some 30 years, indicates for just how long Alan was at the forefront of Nematology, and is all the more striking for the diversity of sub-disciplines it encompasses (including nematode ecology, nematode-microbe interactions, classical plant-Nematology, ultra-structure and behaviour). Alan's international collaborations extended further through his own sabbatical travels, with stints at the University of Leeds (UK), Saga University (Kyushu, Japan) as a Visiting Professor, and as a Regents' Lecturer (the first for a nematologist) at the University of California-Riverside.

Alan's move from Horticulture to Soils marked a

change in emphasis away from plant-Nematology and he became increasingly interested in biocontrol of parasitic nematodes using other nematodes, fungi and bacteria. He was particularly interested in the surface coat of nematodes and the means and effects of adhesion of pathogens to it. He also became interested in nematodes in the soil and those in rivers and freshwater lakes, an interest which he retained until his death.

Alan formally retired as a Chief Research Scientist in 1993, although he remained an Honorary Post Retirement Fellow but, in fact, his retirement was in name only. His study at home had been converted to a small laboratory (complete with microscopes), a darkroom was built in a corner of the cellar and the cars were obliged to share space with growth chambers. Soon after his retirement he was awarded a grant to study nematodes in lakes and rivers in southern Australia and this work resulted in several papers. During his examination of nematodes in soil from wheat fields he isolated a tardigrade, which led to a slight digression from nematodes and resulted in three papers. After his retirement, Alan published ten papers and one chapter and had two chapters in press. At the time of his death, Alan had received a grant to identify nematodes collected from every freshwater body in South Australia and was the PI (with Mike Hodda, CSIRO Entomology) on another award to compile a practical pictorial key of nematodes.

Throughout his career Alan received various awards, including being made a Fellow of the

Society of Nematologists (1983), and being appointed an Honorary Member of the Helminthological Society of Washington in 1997. In 1991, he was awarded the Vereo Medal of the Royal Society of South Australia, and shortly before his untimely death Alan was made an Honorary Fellow of the same society (October 1999). Alan was named a Fellow of the Australian Society for Parasitology in 1993. However, the honor that gave Alan the most satisfaction and the one that, perhaps, best reflects the merit of his collective research career, occurred in 1975 when he was awarded the degree of DSc from the University of Edinburgh.

In his CV, Alan listed microscopy and history as his hobbies (although he probably also should have included wine-tasting). Although he certainly pursued the former, he didn't actually get involved in the latter, apart from being an avid reader of history. Joining the SA Historical Society was something that he often talked about but research always managed to take a front seat. Shortly before he died, Alan and I completed a chapter on plant nematodes for a general Nematology text. It struck me as we were writing that it would be possible to produce a fairly comprehensive article citing only papers by Alan Bird. Writing together was a surprisingly enjoyable experience and one that, most sadly, I won't have the opportunity to do again. Alan is survived by his wife Jean and two children. Mary and me; we three have much to be proud of in Alan.

DAVID MCK. BIRD

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OBITUARY

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13.iv.1915 – 16.xii.1999

Summary

Patricia M. Thomas was born in Melbourne on 13 April 1915, the elder daughter of Sir Douglas and Lady Mawson. Her father was Professor of Geology at the University of Adelaide. Her secondary education was undertaken at Woodlands Church of England Girls Grammar School, Adelaide, where she completed her Leaving Certificate in 1932 in English, French, Geography, Geology, Mathematics and Biology and matriculated in 1933. She graduated from the University of Adelaide with the degree Bachelor of Science in 1936 and completed a Masters degree in Zoology, under the supervision of Professor T. H. Johnston, in 1938. The subject of her research was "Studies in Australian Nematoda". She subsequently held various teaching and research positions at the University of Adelaide until 1946.



PATRICIA MARIETJE THOMAS
BSc. MSc. AO

OBITUARY

PATRICIA MARIETJE THOMAS, BSc, MSc, AO

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Patricia M. Thomas was born in Melbourne on 13 April 1915, the elder daughter of Sir Douglas and Lady Mawson. Her father was Professor of Geology at the University of Adelaide. Her secondary education was undertaken at Woodlands Church of England Girls Grammar School, Adelaide, where she completed her Leaving Certificate in 1932 in English, French, Geography, Geology, Mathematics and Biology and matriculated in 1933. She graduated from the University of Adelaide with the degree Bachelor of Science in 1936 and completed a Masters degree in Zoology, under the supervision of Professor T. H. Johnston, in 1938. The subject of her research was "Studies in Australian Nematoda". She subsequently held various teaching and research positions at the University of Adelaide until 1946. In 1947, she married Hor M. Thomas, then a lecturer in marine biology at the University and from 1950 to 1980 occupied a variety of part-time positions within the Department of Zoology, including Junior Research Fellow, Research Assistant and Technical Officer, which she competently combined with the obligations of raising a family of three sons while also engaging in research, primarily on parasitic nematodes. In 1954 she undertook a period of study overseas, visiting the laboratory of Dr Schuurmans Stekhoven, an eminent student of free-living nematodes, at Deventer in Holland and published with him a series of papers on free-living nematodes as well as on mermitiids. She also visited the Institute of Parasitology at McGill University, Montreal, Canada, where she worked under the aegis of the director, Prof. T. W. M. Cameron, as a Nutfield fellow, a position funded by the Royal Society.

Pat's subsequent scientific career was spent in the Zoology Department of the University of Adelaide until her retirement in December 1980. Following her retirement from the University, Pat moved to the position of Honorary Curator of Helminths at the South Australian Museum, a position which she held until ill-health forced her to relinquish it in 1995 at the age of 80.

When Pat began at the museum the collection of parasitic helminths held there was limited and consisted primarily of types deposited by T. H. Johnston and his students. In collaboration with Madeline Angel and Stan Edmunds, Pat enlarged the helminth parasite collection of the museum to the point where it became pre-eminent in Australia, with

the largest number of accessions and the largest number of primary types. The parasite collection is supported by an extensive collection of reprints and other related literature available nowhere else in Australia as well as by host-parasite catalogues and literature summaries for each parasite genus. These also are available in no other Australian institution nor are they available, and probably never will be, electronically. During the 1970s, Pat sought, with the support of the Australian Society for Parasitology, to have the collection housed in the SA Museum named the Australian Helminthological Collection and for it to form the basis of a national collection. Her endeavours were successful to a large degree and resulted in funding from the Australian Biological Resources Study to catalogue fully the parasite collection records as well as funding from the Australian Society for Parasitology for computers and the development of an electronic database. Finally, in 1994, the museum appointed its first full time curator of helminths, although this position is currently vacant. The contribution of Pat Thomas and her colleagues to the discipline of parasitology in Australia has therefore been quite unique.

Pat's contributions to Science were both significant and varied. A large component of her formal employment at the University involved running large practical classes for first year students of zoology who probably viewed her, with considerable fear, as something of a disciplinarian. Those who progressed in their studies of zoology undoubtedly got to know her a little more intimately and discovered a caring person, with an enquiring mind, who was not only interested in their zoological studies but also in the progress of their personal development. They also gained an appreciation of the depth of her commitment to scientific research.

The manifestations of her commitment to the advancement of science were diverse. She acted as editor, following the death of Prof. T. Harvey Johnston, for many of the series of scientific reports (on Zoology and Botany) resulting from her father's expeditions to Antarctica. These were published as the British, Australian and New Zealand Antarctic Research Expedition reports and covered botanical and zoological explorations in Antarctica between 1929 and 1931. The first of these was published in 1937; the most recent issue of the series (Porifera) was published in 1976, Volume 3, on the mammals,

is expected to be published in the near future and is likely to be the last of the series.

Pat Thomas's most significant scientific legacy undoubtedly lies in her publications, the majority of which were published under her maiden name (P. M. Mawson). Numbering in excess of 100, her papers made a significant contribution to the study of parasitic nematodes in Australia, an impact which was highly respected both within Australia and overseas. The papers published from her Masters thesis during 1938, 1939 and 1940 probably represent the most significant single contribution to our knowledge of the nematode parasites of marsupials made to date. They indicated that an enormously diverse fauna of nematode parasites was present in Australian marsupials and thereby laid the foundations for subsequent studies, which are still in progress. Later papers covered the nematode parasites of frogs, fishes, lizards, snakes, eutherians and marsupials and, particularly, birds. Numerous papers on this latter topic culminated in 1986 in the publication (in conjunction with Madeline Angel and Stan Edmonds) of a definitive checklist of the helminths of Australian birds, a monograph which remains an essential resource for Australian parasitologists. The parasitic nematode fauna of Australian vertebrates is unique and extraordinarily diverse and Pat's papers represented the first real attempt to document it comprehensively. While the enterprise of documentation continues, and will undoubtedly continue for some considerable time, her collected papers represent probably the most significant advance made in this area in date. An outstanding feature of her work was that she studied and published on virtually all of the known orders of parasitic nematodes. Furthermore, she crossed the gulf which divides many nematologists i.e. the

division between parasitic and free-living forms. Few nematologists have published significant series of papers in both areas of research but Pat was one of this group. Today, in an era of intense specialisation, such a broad and comprehensive approach is almost incomprehensible and, therefore, probably has not achieved the recognition which it deserves.

Pat's achievements have been recognized in a number of ways. She was awarded the Verco Medal of the Royal Society of South Australia in 1974 for her scientific publications and became the first (and until 1999 the only) woman to be made a Fellow of the Australian Society for Parasitology. In 1994, Pat was awarded an Order of Australia for her contributions to science in Australia. Apart from her activities as a parasitologist, Pat was also a member of the Handbooks Committee (Handbook of the Flora and Fauna of South Australia) for more than twenty years and a very active member of the National Parks Commission. She was also a Council Member of the Royal Society of South Australia from 1977-1992 being Membership Secretary from 1982-1992.

Her passing will be noted with regret not only by colleagues in Australia but also overseas, particularly in France, Britain, Poland, the United States and Canada, countries in which she established long standing scientific collaborations and friendships. Her contributions to parasitology were highly regarded, but she will also be remembered for her extremely generous hospitality, her culinary skills, her forthright manner, her sense of humour and, in particular, for her generosity in sharing scientific material.

Pat was predeceased by her husband Hor and is survived by her sons Gareth, Alan and Emily.

IAN BEVERIDGE

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TRANSACTIONS OF THE

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PLEISTOCENE FOSSIL VERTEBRATE SITES OF THE SOUTH-EAST REGION OF SOUTH AUSTRALIA

BY E. H. REED & S. J. BOURNE†

Summary

Reed, E. H. & Bourne, S. J. (2000) Pleistocene fossil vertebrate sites of the South East region of South Australia. *Trans. R. Soc. S. Aust.* 124(2), 61-90, 30 November, 2000. This paper provides a summary of the Pleistocene vertebrate fossil sites of the South East region of South Australia and builds upon an earlier paper by Williams (1980). It also provides the first detailed review of all known Pleistocene faunal sites of the Naracoorte Caves World Heritage Area. Each known site in the region is listed with details of the site and faunal assemblage, fossil collections made from it and references to previous literature. The representation of the major vertebrate groups in the Pleistocene sites of the South East and the level of scientific attention they have received are discussed.

Key Words: Vertebrate palaeontology, caves, South East, Naracoorte, South Australia, Pleistocene, Quaternary, vertebrate fossils.

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This paper provides a summary of the Pleistocene vertebrate fossil sites of the South East region of South Australia and builds upon an earlier paper by Williams (1980). It also provides the first detailed review of all known Pleistocene faunal sites of the Naracoorte Caves World Heritage Area. Each known site in the region is listed with details of the site and faunal assemblage, fossil collections made from it and references to previous literature. The representation of the major vertebrate groups in the Pleistocene sites of the South East and the level of scientific attention they have received are discussed.

KEY WORDS: Vertebrate palaeontology, caves, South East, Naracoorte, South Australia, Pleistocene, Quaternary, vertebrate fossils

Introduction

The South East region of South Australia (Fig. 1) is predominantly a karst terrain characterised by features such as dolines, caves and cenotes (sinkholes). The Oligocene to Miocene Gambier and Naracoorte limestones of the South East contain numerous caves, with more than 170 having been recorded for the Upper South East and more than 400 in the Lower South East (Lewis 1979¹; Matthews 1985; K. Mott pers. comm. 1999). Many of these caves contain skeletal material of Pleistocene vertebrates. These sites have received much scientific attention and will be the main focus of this paper. Williams (1980) published the first catalogue of Pleistocene vertebrate fossil sites of South Australia, but listed only a small number of sites for the South East. Palaeontological research in the region has been steadily increasing since 1980, particularly on sites in the Naracoorte Caves World

Heritage Area and surrounds. Thus, with further research, ongoing cave exploration and, most recently, vineyard development new cave sites have been discovered highlighting the need to review the fossil sites of the region in depth. The current paper builds on Williams' (1980) study and includes sites that were only under preliminary investigation at that time, sites omitted by that author and those discovered and investigated more recently by the present authors and the palaeontological research team at Flinders University. This study originated as part of the PhD studies of one of us (E.H.R.).

The majority of the sites discussed in this paper are in caves. Various modes of bone accumulation have been suggested, including natural traps and predator accumulations (Smith 1971, 1972; Pledge 1980a, 1990; Wells *et al.* 1984; Baird 1985; Newton 1988²; Barrie 1997; Brown 1998³; Brown & Wells 2000; Moriarty *et al.* 2000). Many of the sites display multiple and overlapping accumulation modes. Less common in the region are surface sites and others such as the accidental finds where drilling of holes or construction works have led to discoveries (Wells & Pledge 1983). Several of the fossil deposits in the region have been extensively researched, such as those of Henschke's Fossil Cave (5U91, 5U97), Green Waterhole Cave (5L81) and the Victoria Fossil Cave (5U1) in which research has been continuous for almost 30 years (Smith 1971, 1972, 1976; Van Tets & Smith 1974; Wells 1975; Wells *et al.* 1984; Moriarty *et al.* 2000). Other caves such as Wombat Cave (5U58) have received little more than preliminary investigation, while others have only been surveyed and fossils identified *in situ*, e.g. Rabbit Cave (5U66). Some of these cave sites no

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¹ LEWIS, I. D. (1979) 'South Australian Cave Reference Handbook, Occasional Paper No. 5' (Cave Exploration Group of South Australia, Adelaide).

² NEWTON, C. A. (1988) *A taphonomic and palaeoecological analysis of the Green Waterhole (5L81), a submerged late Pleistocene bone deposit in the lower southeast of South Australia* BSc (Hons) Thesis, The Flinders University of South Australia (unpub.)

³ BROWN, S. P. (1998) *A geological and palaeontological examination of the Pleistocene Cathedral Cave fossil accumulation, Naracoorte, South Australia* BSc (Hons) Thesis, The Flinders University of South Australia (unpub.)

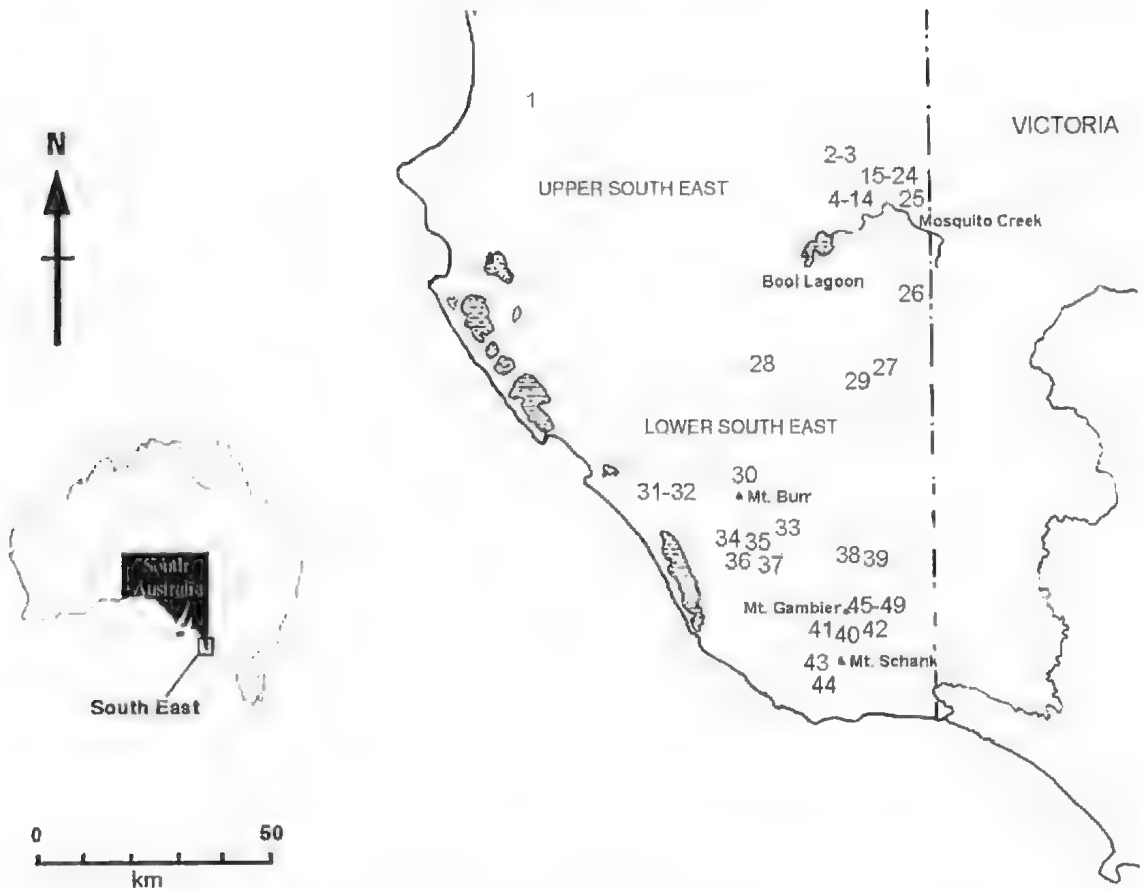


Fig. 1. Map of the South East of South Australia, with sites marked by a Number corresponding to those mentioned in the text. Divisions of Upper and Lower South East sub-regions are indicated.

longer exist, due to land development and others are yet to be fully explored. This paper is up-to date as of 31 July 2000 but research in the region is continuing, particularly in the Naracoorte Caves World Heritage Area.

This paper is not intended for use as a biogeographical database but simply provides faunal lists for each of the sites, along with some background information. Due to differing chronological sequences, it should not be assumed they are contemporaneous. The main aim of the paper is to report on new sites in the region, to highlight their significance and to provide more up to date faunal lists, particularly for sites within the Naracoorte Caves World Heritage Area.

The Naracoorte Caves World Heritage Area

The presence of bone material in the caves of Naracoorte was recognised soon after the discovery of Blanche Cave in 1845 (Wells & Pledge 1983). The

first significant work on vertebrate fossils from the region was carried out by Woods in 1857 and 1858, and recorded in his book "Geological Observations in South Australia" (Woods 1862). Later, vertebrate fossils were reported from Specimen Cave by Stirling (Stirling 1908, 1912; Wells & Pledge 1983). Very little palaeontological research was subsequently undertaken in the region until the 1960s, when material from Haystack Cave and Henschke's Fossil Cave was investigated (Merrilees 1965; Pledge 1980c; Barrie 1997). The discovery in 1969 of the Fossil Chamber in Victoria Fossil Cave (then known as Victoria Cave) and subsequent fossil discoveries in other caves of the Naracoorte Caves Conservation Park, led to an upsurge in research activity in the region and a growing awareness among the scientific community of its importance.

The significance of the Pleistocene fossil deposits of the Naracoorte Caves Conservation Park was recognised internationally in 1994 when the Park was inscribed on to the World Heritage List. The

Naracoorte Caves deposits, together with Riversleigh in Queensland, form the Australian Fossil Mammal Sites. The Pleistocene faunal record at the Naracoorte Caves is extensive, the caves having acted as pitfall traps and owl roosts, collecting examples of the fauna of this small geographic region over at least the last 400,000 years (Ayliffe *et al.* 1998; Brown 1998; Brown & Wells 2000; Moriarty *et al.* 2000). Within the World Heritage Area, 11 of the 26 caves have yielded vertebrate bone material. When combined with recent climatic and geochronological work, the potential of the bone material for resolving palaeoecological and other contentious issues, such as the timing of the megafaunal extinctions, is considerable (Ayliffe *et al.* 1998; Moriarty *et al.* 2000).

Materials and Methods

The list of sites and faunas provided in this paper has been compiled from the collections and records of the South Australian Museum and the Flinders University vertebrate palaeontology laboratory, current research, published literature, personal communication with researchers studying sites in the region and field research by the authors. The locations of the fossil sites discussed in this paper are shown in Fig. 1. Their numbers correspond to site numbers given in the lists of sites and faunas provided and in Table 3. The format is similar to that of Williams (1980) but additional information, including site details and current research is provided for each site. Cave numbers (i.e. Cave Exploration Group of South Australia CEGSA registration numbers) follow those of Lewis (1979¹), Matthews (1985) and current CEGSA records. For these numbers "5" indicates the state of South Australia and "U" or "L" upper or lower South East sub-region. The division into Upper and Lower sub-regions used in this paper (Fig. 1) conforms with the CEGSA divisions for cave locations. Within these sub-regions sites have been grouped according to district, determined by the authors as encompassing an approximately 25 km radius of the major townships of the South East. The Naracoorte Caves World Heritage Area is presented separately from the Naracoorte district. Site names follow Williams (1980), CEGSA records and the published literature. The storage location of fossil collections from each site is also included, as are the sources for the information presented. Sites under investigation by the authors are identified.

Systematics

Checklists of faunas represented in the Pleistocene deposits described in this study are presented in Tables 1 & 2. Table 3 shows the distribution of species between the sites presented in the main text. Phylogenetic order for marsupials follows Aplin & Archer (1987). Robinson *et al.* (2000) are followed for placental mammals, reptiles, amphibians and birds. Names, taxonomic authorities and distributional data were taken primarily from Robinson *et al.* (2000), with some additional information taken from Strahan (1995) for mammals, Cogger (2000) for reptiles and amphibians and Pizzey & Knight (1997) for birds. Names and authorities for fossil species follow Archer *et al.* (1984) for mammals, Baird (1985), Van Tets & Smith (1974) and Stirling & Zietz (1896) for birds, and Smith (1976) for the fossil reptile *Womambi naracoortensis*. References for authorities for names published subsequently are included in the References section of this paper. Distributional and survival status changes are indicated for each species in the list of sites and the faunal checklists (Tables 1 & 2), with *† referring to species which became extinct during the Pleistocene, *‡ referring to historically extinct species, and * indicating those species which are locally extinct, or currently not found in the South East region.

Faunal names used in the faunal lists conform with current usage. Nomenclatural changes that affect species included in this paper are summarised in Table 4. This table lists the current name (as used in this paper), the previous name as it appeared in earlier publications for Pleistocene sites of the South East and the relevant references. Changes in identification of fossil specimens are noted in the faunal lists with appropriate references given.

Williams (1982²) provided revised diagnoses for the genus *Diprotodon*. He listed *†*Diprotodon australis* and *†*D. optatum* as separate species. The identification provided for site 32 conforms with Williams' diagnoses (R. Wells pers. comm. 2000). Smith (1972) identified **Antechinus stuartii* from site 4a. Subsequent work has changed the concept of the modern species of **A. stuartii* and populations formerly included in **A. stuartii* actually comprise two sibling species, **A. stuartii* and **A. agilis* (Dickman *et al.* 1988; Dickman 1998). On the basis of modern ranges (Strahan 1995), any identification of **A. stuartii* from Pleistocene fossil deposits of the South East is likely to be the newly recognised **A. agilis* rather than the true **A. stuartii*.

Results

The following list of sites and faunas provides a

¹ WILLIAMS, D. L. G. (1982) The late Pleistocene of the Flinders and Mt Lofty Ranges. PhD Thesis, The Flinders University of South Australia (unpubl.)

TABLE 1. Checklist of amphibian, reptile and bird species identified or tentatively identified from Pleistocene fossil sites of the South East of South Australia.

CLASS AND ORDER	FAMILY AND SUB-FAMILY	GENUS AND SPECIES
AMPHIBIA		
ANURA	Hylidae (Tree frogs)	<i>Litoria ewingi</i> (Duméril & Bibron, 1841)
	Myobatrachidae (Southern Frogs)	<i>Crinia signifera</i> (Girard, 1853) <i>Geocrinia luevis</i> (Günther, 1864) <i>Limodynastes dumerilii</i> Peters, 1863 <i>Limodynastes tasmaniensis</i> Günther, 1858
REPTILIA		
TESTUDINES	Chelidae (Side-necked Tortoises)	<i>Chelodina longicollis</i> (Shaw, 1794) * <i>Emydura macquarii</i> (Gray, 1830)
SQUAMATA	Agamidae (Dragon lizards)	<i>Pogona barbata</i> (Cuvier, 1829)
	Scincidae (Skinks)	<i>Egernia whitii</i> (Lacépède, 1804) <i>Eulamprus tympanum</i> (Lonnberg & Andersson, 1913) <i>Lerista bougainvillii</i> (Gray, 1839) <i>Tiliqua nigrohutea</i> (Quoy & Gaimard, 1824) <i>Tiliqua rugosa</i> (Gray, 1825)
	Varanidae (Goannas)	* <i>Varanus gouldii</i> (Gray, 1838) * <i>Varanus varius</i> (White, ex Shaw, 1790)
	Madtsoiidae (Madtsoiid snakes)	*† <i>Womambi naracoortensis</i> Smith, 1976
	Elapidae (Elapid snakes)	<i>Notechis scutatus</i> (Peters, 1861) * <i>Pseudechis porphyriacus</i> (Shaw, 1794) <i>Pseudonaja nuchalis</i> Günther, 1858
AVES		
STRUTHIONIFORMES	Casuariidae (Cassowaries & Emus)	<i>Dromaius novaehollandiae</i> (Latham, 1790)
	Dromornithidae (Dromornithids)	*† <i>Genyornis newtoni</i> Stirling & Zietz, 1896
GALLIFORMES	Megapodiidae (Megapodes)	<i>Leipoa ocellata</i> Gould, 1840
	Phasianidae (Pheasants, quails & allies)	*† <i>Progora naracoortensis</i> Van Tets, 1974 <i>Coturnix pectoralis</i> Gould, 1837 <i>Coturnix ypsilophora</i> Bosc, 1792
ANSERIFORMES	Anatidae (Geese, swans & ducks)	Gen. et sp. indet.
PELICANIFORMES	Phalacrocoracidae (Cormorants)	<i>Phalacrocorax melanoleucos</i> (Vieillot, 1817)
FALCONIFORMES	Accipitridae (Osprey, hawks, eagles & allies)	<i>Accipiter</i> Brisson, 1760 sp. indet. <i>Aquila audax</i> (Latham, 1802)
	Falconidae (Falcons)	<i>Falco berigora</i> Vigors & Horsfield, 1827
GRUIFORMES	Rallidae (Rails, crakes & allies)	* <i>Gallinula mortierii</i> (Du Bus, 1840) <i>Gallinula tenebrosa</i> Gould, 1846 <i>Gallirallus philippensis</i> (Linnaeus, 1766)
TURNICIFORMES	Turnicidae (Button-quails)	<i>Turnix varia</i> (Latham, 1802)
CHARADRIIFORMES	Pedionomidae (Plains-wanderer)	* <i>Pedionomus torquatus</i> Gould, 1840
	Scolopacidae (Sandpipers & allies)	
	Gallinagoninae	<i>Gallinago hardwickii</i> (Gray, 1831)
	Tringinae	<i>Tringa glareola</i> Linnacus, 1758
	Calidrinae	<i>Calidris ruficollis</i> (Pallas, 1776)
	Burhinidae (Stone curlews)	<i>Burhinus grallarius</i> (Latham, 1802)
	Charadriidae (Plovers & dotterels)	* <i>Charadrius australis</i> (Gould, 1841)
COLUMBIFORMES	Columbidae (Pigeons & doves)	<i>Phaps chalcoptera</i> (Latham, 1790)

PSITTACIFORMES	Cacatuidae (Cockatoos & cockatiel)	<i>Cacatua tenuirostris</i> (Kuhl, 1820) <i>Callocephalon fimbriatum</i> (Grant, 1803) <i>Calyptrorhynchus banksii</i> (Latham, 1790) * <i>Calyptrorhynchus lathamii</i> (Temminck, 1807)
	Psittacidae (Parrots)	* <i>Pezopodus walliens</i> (Kerr, 1792) <i>Platycercus</i> Vigors, 1825 sp. indet. *† <i>Centropus colossus</i> Baird, 1985
CUCULIFORMES	Cuculidae (Cuckoos)	<i>Ninox novaeseelandiae</i> (Gmelin, 1788)
	Strigidae (Typical owls)	<i>Iyo alba</i> (Scopoli, 1769)
STRIGIFORMES	Tytonidae (Barn Owls)	<i>Iyo novaehollandiae</i> (Stephens, 1826) <i>Ducelo novaeguineae</i> (Hermann, 1783)
CORACIIFORMES	Alcedinidae (Kingfishers, bee-eaters & rollers)	
PASSERIFORMES	Acanthizidae (Bristlebirds, thornbills, scrubwrens & allies)	<i>Dasyornis broadbenti</i> (McCoy, 1867)
	Meliphagidae (Honeyeaters & Australian chats)	<i>Munorina melanoleuca</i> (Latham, 1802)
	Orthonychidae (Chowchillas, quail-thrushes & allies)	*† <i>Orthonyx hypsilophus</i> Baird, 1985
	Dieruridae (Monarchs, drongos, magpie-larks & allies)	<i>Grallina cyanoleuca</i> (Latham, 1802)
	Artamidae (Woodswallows, butcherbirds & allies)	<i>Gymnathina tibicen</i> (Latham, 1801)
	Corvidae (Crows)	<i>Corvus</i> Linnaeus, 1758 sp. indet.
	Hirundinidae (Swallows & martins)	<i>Hirundo neovenena</i> Gould, 1842
	Estrildidae (Grass-finches)	Gen. et sp. indet.

Incomplete identifications are included only if they represent the only entry representing the family or genus concerned. *† indicates species extinct during the Pleistocene, ** indicates historically extinct taxon, * indicates taxon no longer occurs in the region.

catalogue of all known Pleistocene fossil vertebrate sites and faunas of the South East.

Sites and Faunas of the Upper South East region

Kingston district

1. BLACKFORD DRAIN

LOCATION: 21 km NE of Kingston.

SITE DESCRIPTION: Fossils were uncovered in the north side of the creek-bed during bridge construction in 1954 in a bed of "waterworn stones" at a depth of approximately 3.5 - 4.5 m (Williams 1980). A letter from R. V. Flint accompanying the specimens described the lowest level as "a hard stone which looked like a flow of black mud, thickly impregnated with small white shells" (Williams 1980).

COLLECTION: South Australian Museum palaeontology collection (vertebrate fossils).

FAUNA:

MAMMALS

Diprotodontidae: *†*Diprotodon* sp. indet.,

*†*Zygomaturus trilobus*; Macropodidae: *Macropus giganteus*, *M. rufogriseus*, *†*Procoptodon* sp. indet., *†*Simosthenurus occidentalis*.

REFERENCES: Williams (1980); N. Pledge (pers. comm. 2000); South Australian Museum palaeontology collection records.

Naracoorte Township

2. HENSCHKE'S FOSSIL CAVE 5U91, 5U97 (also known as Henschke's Quarry Cave)

LOCATION: Outskirts of Naracoorte township at Henschke's Quarry.

SITE DESCRIPTION: The cave was exposed by quarrying and found to contain a rich and diverse fossil assemblage. It was excavated by workers from the South Australian Museum from 1969 to 1981 to salvage material from the cave, which was part of the active quarry (Pledge 1990). Subsequent excavation was carried out by J. Barrie from 1981 to 1997, investigating an extensive section radiating from the location of the earlier excavations (Barrie 1997). As quarrying has continued the cave has been completely destroyed.

TABLE 2. Checklist of mammal species identified or tentatively identified from Pleistocene fossil sites of the South East of South Australia.

CLASS AND ORDER	FAMILY AND SUB-FAMILY	GENUS AND SPECIES
MAMMALIA		
MONOTREMATA	Tachyglossidae (Echidnas or spiny anteaters)	*† <i>Megalibgwilia ramsayi</i> (Owen, 1884) <i>Tachyglossus aculeatus</i> (Shaw, 1792)
MARSUPIALIA		
DASYUROMORPHIA	Thylacinidae (Thylacines) Dasyuridae (Carnivorous marsupials)	** <i>Thylacinus cynocephalus</i> (Harris, 1808) <i>Antechinus flavipes</i> (Waterhouse, 1837) <i>Antechinus minimus</i> (Geoffroy, 1803) * <i>Antechinus stuartii</i> Macleay, 1842 * <i>Antechinus swainsonii</i> (Waterhouse, 1840) * <i>Dasyurus geoffroyi</i> Gould, 1841 * <i>Dasyurus maculatus</i> (Kerr, 1792) * <i>Dasyurus viverrinus</i> (Shaw, 1800) * <i>Ningauia yvonnae</i> Kitchener, Stoddart & Henry, 1983 * <i>Phascogale calura</i> Gould, 1844 * <i>Phascogale tapoatafa</i> (Meyer, 1793) * <i>Sarcophilus harrisii</i> (Boitard, 1841) †‡ <i>Sarcophilus lanianus</i> (Owen, 1838) <i>Sminthopsis crassicaudata</i> (Gould, 1844) * <i>Sminthopsis leucopus</i> (Gray, 1842) <i>Sminthopsis murina</i> (Waterhouse, 1837) <i>Isodon obesulus</i> (Shaw, 1797) * <i>Perameles bougainville</i> Quoy & Gaimard, 1824 * <i>Perameles gunnii</i> Gray, 1838
PERAMELEMORPHIA	Peramelidae (Bandicoots & bilbies)	<i>Phascolarctos cinereus</i> (Goldfuss, 1817) *† <i>Phascolarctos stirtoni</i> Bartholomai, 1968
DIPROTODONTIA	Phascolaretidae (Koalas)	
	Diprotodontidae (Large extinct marsupial quadrupeds)	
	Zygomaturinae	**† <i>Zygomaturus trilobus</i> Macleay, 1858
	Diprotodontinae	**† <i>Diprotodon australis</i> (Owen, 1844) *† <i>Diprotodon optatum</i> Owen, 1838
	Palorchestidae (Large extinct tapir-like marsupials)	*† <i>Palorchestes azael</i> Owen, 1874 *† <i>Palorchestes parvus</i> De Vis, 1895
	Vombatidae (Wombats)	** <i>Lasiorhinus krefftii</i> (Owen, 1872) * <i>Lasiorhinus latifrons</i> (Owen, 1845) <i>Vombatus ursinus</i> (Shaw, 1800) *† <i>Warendja wakefieldi</i> Hope & Wilkinson, 1982 *† <i>Thylacoleo carnifex</i> Owen, 1858
	Thylacoleonidae (Marsupial 'lions')	
	Phalangeridae (Brush-tail possums & cuscuses)	<i>Trichosurus vulpecula</i> (Kerr, 1792)
	Hypsiprymnodontidae (Sectorial-toothed rat-kangaroos)	*† <i>Propleopus oscillans</i> (De Vis, 1888)
	Potoroidae (Potoroos, bettongs & rat-kangaroos)	* <i>Aepyprymnus rufescens</i> (Gray, 1837) * <i>Bettongia gaimardi</i> (Desmarest, 1822) * <i>Bettongia lesueur</i> (Quoy & Gaimard, 1824) * <i>Bettongia penicillata</i> Gray, 1837 * <i>Potorous platyops</i> (Gould, 1844) * <i>Potorous tridactylus</i> (Kerr, 1792)
	Macropodidae (Wallabies, kangaroos & tree-kangaroos)	
	Sthenurinae (extinct browsing kangaroos)	**† <i>Procoptodon goliath</i> (Owen, 1846) *† <i>Procoptodon rapha</i> Owen, 1874 † <i>Simosthenurus baileyi</i> (Prideaux & Wells, 1998) *† <i>Simosthenurus browni</i> (Merrilees, 1968)

		*† <i>Simosthenurus gilli</i> (Merrillees, 1965)
		*† <i>Simosthenurus maddocki</i> (Wells & Murray, 1979)
		*† <i>Simosthenurus newtonae</i> Prideaux, 2000
		*† <i>Simosthenurus occidentalis</i> (Glauert, 1910)
		*† <i>Simosthenurus pales</i> (De Vis, 1895)
		*† <i>Sthenurus andersoni</i> Marcus, 1962
	Macropodinae	*† <i>Congruus congruus</i> McNamara, 1994
		** <i>Lagorchestes leporides</i> (Gould, 1841)
		* <i>Lagostrophus fasciatus</i> (Péron & Lesueur, 1807)
		* <i>Macropus eugenii</i> (Desmarest, 1817)
		<i>Macropus fuliginosus</i> (Desmarest, 1817)
		<i>Macropus giganteus</i> Shaw, 1790
		** <i>Macropus greyi</i> Waterhouse, 1845
		<i>Macropus rufogriseus</i> (Desmarest, 1817)
		*† <i>Macropus titan</i> Owen, 1838
		** <i>Onychogalea lunata</i> (Gould, 1841)
		*† <i>Protemnodon anak</i> Owen, 1874
		*† <i>Protemnodon brehms</i> (Owen, 1874)
		*† <i>Protemnodon roechus</i> Owen, 1874
		* <i>Thylogale billardieri</i> (Desmarest, 1822)
		<i>Wallabia bicolor</i> (Desmarest, 1804)
	Burramyidae (Pygmy-possums)	<i>Cercartetus concinnus</i> (Gould, 1845)
		<i>Cercartetus lepidus</i> (Thomas, 1888)
		<i>Cercartetus nanus</i> (Desmarest, 1818)
	Pseudocheiridae (Ringtail Possums & Greater Glider)	* <i>Petaurides volans</i> (Kerr, 1792)
	Petauridae (Striped Possum, Leadbeater's Possum & wrist-winged gliders)	<i>Pseudocheirus peregrinus</i> (Boddaert, 1795)
	Acrobatidae (Feathertail Glider)	<i>Petaurus breviceps</i> Waterhouse, 1839
		<i>Acrobates pygmaeus</i> (Shaw, 1794)
PLACENTALIA		
CHIROPTERA	Vespertilionidae (Ordinary bats)	<i>Miniopterus schreibersii</i> (Kuhl, 1817)
		<i>Nyctophilus geoffroyi</i> Leach, 1821
CARNIVORA	Canidae (Dogs, foxes & allies)	<i>Canis lupus familiaris</i> Linnaeus, 1758
		<i>Vulpes vulpes</i> Linnaeus, 1758
	Felidae (Cats)	<i>Felis catus</i> Linnaeus, 1758
	Otariidae (Eared seals)	<i>Arctocephalus</i> Geoffroy & Cuvier, 1826 sp. indet.
ARTIODACTYLA	Suidae (Pig)	<i>Sus scrofa</i> Linnaeus, 1758
	Bovidae (Horned ruminants)	<i>Ovis aries</i> Linnaeus, 1758
RODENTIA	Muridae (Rats and mice)	** <i>Conilurus albipes</i> (Lichtenstein, 1829)
		<i>Hydromys chrysogaster</i> Geoffroy, 1804
		* <i>Mastacomys fuscus</i> Thomas, 1882
		<i>Notomys mitchellii</i> (Ogilby, 1838)
		<i>Pseudomys apodemoides</i> Finlayson, 1932
		* <i>Pseudomys australis</i> Gray, 1832
		* <i>Pseudomys fumeus</i> Brazenor, 1934
		* <i>Pseudomys gouldii</i> (Waterhouse, 1839)
		<i>Pseudomys shortridgei</i> (Thomas, 1907)
		<i>Rattus fuscipes</i> (Waterhouse, 1839)
		<i>Rattus lutreolus</i> (Gray, 1841)
		* <i>Rattus tunneyi</i> (Thomas, 1904)
		<i>Oryzotolagus cuniculus</i> (Linnaeus, 1758)

Incomplete identifications are included only if they represent the only entry representing the family or genus concerned. *† indicates species extinct during the Pleistocene, ** indicates historically extinct taxon, * indicates taxon no longer occurs in the region.

TABLE 4. Summary of nomenclatural changes related to species included in this paper.

THIS PAPER	PREVIOUS NAME	REFERENCES FOR THE SOUTH EAST IN WHICH THE PREVIOUS NAME APPEARED
Myobatrachidae	Leptodactylidae	Tyler (1977, 1991); Williams (1980); Wells & Pledge (1983); Brown & Wells (2000); Moriarty <i>et al.</i> (2000).
<i>Crinia signifera</i>	<i>Ramidella signifera</i>	Tyler (1977); Williams (1980); Wells & Pledge (1983); Wells <i>et al.</i> (1984); Pledge (1990); Moriarty <i>et al.</i> (2000).
<i>Pogona barbata</i>	<i>Amphibolurus barbatus</i>	Smith (1976); Williams (1980); Wells & Pledge (1983); Wells <i>et al.</i> (1984); Pledge (1990); Moriarty <i>et al.</i> (2000).
<i>Eulamprus tympanum</i>	<i>Sphenomorphus tympanum</i>	Smith (1976); Williams (1980); Wells & Pledge (1983); Wells <i>et al.</i> (1984); Moriarty <i>et al.</i> (2000).
<i>Tiliqua rugosa</i>	<i>Trachydosaurus rugosus</i>	Smith (1976); Williams (1980); Wells & Pledge (1983); Wells <i>et al.</i> (1984); Cogger (2000).
<i>Coturnix ypsidophora</i>	<i>Coturnix australis</i>	Van Tets & Smith (1974); Williams (1980); Wells & Pledge (1983); Wells <i>et al.</i> (1984); Baird (1991); Baird <i>et al.</i> (1991).
<i>Gallirallus philippensis</i>	<i>Rallus philippensis</i>	Van Tets & Smith (1974); Williams (1980); Wells & Pledge (1983); Wells <i>et al.</i> (1984); Newton (1988 ²); Baird (1991); Baird <i>et al.</i> (1991).
<i>Burhinus grallarius</i>	<i>Burhinus magnirostris</i>	Newton (1988 ²); Baird (1991).
<i>Charadrius australis</i>	<i>Peltohyas australis</i>	Van Tets & Smith (1974); Williams (1980); Wells & Pledge (1983); Wells <i>et al.</i> (1984); Baird (1991); Baird <i>et al.</i> (1991).
<i>Calyptrorhynchus banksii</i>	<i>Calyptrorhynchus magnificus</i>	Baird (1985); Newton (1988 ²); Baird (1991); Baird <i>et al.</i> (1991).
Dicruridae	Grallinidae	Van Tets & Smith (1974); Williams (1980); Wells & Pledge (1983); Wells <i>et al.</i> (1984); Baird (1991); Moriarty <i>et al.</i> (2000).
Artamidae	Craetidae	Van Tets & Smith (1974); Williams (1980); Wells & Pledge (1983); Wells <i>et al.</i> (1984); Baird (1991); Moriarty <i>et al.</i> (2000).
<i>Megalibgwilia ramsayi</i>	<i>Zaglossus ramsayi</i>	Murray (1978); Pledge (1980c); Williams (1980); Wells & Pledge (1983); Wells <i>et al.</i> (1984); Pledge (1990); Griffiths <i>et al.</i> (1991).
<i>Thylacinus cynocephalus</i>	<i>Thylacinus major</i>	Williams (1980).
<i>Vombatus</i>	<i>Phascalomys</i>	Tindale (1933); Williams (1980).
<i>Potorous tridactylus</i>	<i>Potorous apicalis</i>	Smith (1971); Williams (1980); Wells & Pledge (1983); Wells <i>et al.</i> (1984).
<i>Pseudomys apodemoides</i>	<i>Pseudomys albocinctus</i>	Wells & Pledge (1983); Wells <i>et al.</i> (1984).

COLLECTION: South Australian Museum palaeontology collection (vertebrate fossils).

FAUNA:

AMPHIBIANS

Hylidae: *Litoria wingi*; Myobatrachidae: *Crimma sepioides*, *Geocrinia laevis*, *Limnodynastes tasmanianus*.

REPTILES

Chelidae: *Chelodina longicollis*, cf. **Emydura macquarii*; Agamidae: *Pogona* sp. indet.; Scincidae: *Tiliqua nigrolutea*, *T. rugosa*; Varanidae: *Varanus* sp., cf. **V. gouldii*; *Varanus* sp., cf. **V. varius*; Madsonidae: **Wonambi naracoortensis*; Elapidae: *Pseudonaja* sp. indet.

BIRDS

Casuaritidae: *Dromaius novaehollandiae*; Megapodidae: **Progora naracoortensis*; Phasianidae: *Coturnix* sp. indet.; Anatidae: undescribed taxon; Rallidae: **Gallinula mortierii*; Turnicidae: *Turux varia*; Psittaciformes, family indet.; Passeriformes, family indet.; Corvidae: *Corvus* sp. indet.; Hirundinidae: *Hirunda neoxena*.

MAMMALS

Tachyglossidae: *††Megalibgwahia ramsayi*, *Tachyglossus aculeatus*; Thylacimidae: **Thylacinus cynocephalus*; Dasyuridae: *Antechinus* sp., cf. *A. minimus*, **Dasyurus viverrinus*, **Phaseogale* sp. indet., **†Sarcophilus lantarius*, **Smithopsis leucopus*; Peramelidae: *Isodon obesulus*, *Perameles* sp., cf. **P. bougainville*, *Perameles* sp., cf. **P. gunnii*; Phaseolaretidae: *Phaseolaretos* sp., cf. *P. cinereus*; Diprotodontidae: *††Diprotodon optatum*, **Zygomaturus trilobus*; Palorchestidae: **Palorchestes azael*; Vombatidae: *Lusiorhinus* sp., cf. **L. krefftii*, *Vombatus ursinus*; Thylacoleonidae: **†Thylacoleo carnifex*; Phalangeridae: *Trichosurus vulpecula*; Hypsiprymnodontidae: *††Propleopus oscillans*; Potoroidae: **Aepyprymnus rufescens*, *Bettongia* sp., cf. **B. gaimardi*, **Bettongia lesueur*, *Bettongia* sp., cf. **B. penicillata*, *Potorous* sp., cf. **†P. platyops*, **P. tridactylus*; Macropodidae: ***Lagorchestes leporides*, **Lagostrophus fasciatus*, *Macropus* sp., cf. *M. ergamensis*, **M. ervsi*, *M. rufogriseus*, **M. jilka*, ***Onychogalea lunata*, **†Procoptodon rapha*, **†Protemnodon roechus*, **†Simosthenurus browni*, *†S. gilli*, **†S. maddocki*, **†S. newtonae*, **†S. occidentalis*, *††S. pales*, ***Sthenurus andersoni* (= *††Sthenurus athlstandersoni* of Pledge 1990, see Pledgeaux 1999*), *Wallabia bicolor*; Burramyidae: *Cercartetus nanus*; Pseudocheiridae: *Pseudocheirus peregrinus*; Petalidae: *Petalurus brevirops*; Vespertilionidae: *Nyctophilus* sp., cf. *N. geoffroyi*,

Muridae: **Conturus* sp. indet., *Hydromys chrysogaster*, **Masiacomys fuscus*, *Pseudomys* sp. indet., *Rattus* sp. indet.

REFERENCES: Van Tets (1974); Tyler (1977, 1991); Pledge (1977, 1980c, 1990, 1991); Murray (1978); Williams (1980); Barrie (1990, 1997); Baird (1991b); Baird *et al.* (1991); Griffiths *et al.* (1991); McNamara (1997); Pledgeaux (1999, 2000); Scanlon & Lee (2000); South Australian Museum palaeontology collection records.

3. JAMES' QUARRY CAVE 5U29

LOCATION: Naracoorte township.

SITE DESCRIPTION: This small cave was uncovered by quarrying in 1956, discovered by A. James, proprietor of the quarry. It contained a partial skeleton of *Thylacoleo carnifex* (Daily, 1960). The cave has since been destroyed by quarrying.

COLLECTION: South Australian Museum palaeontology collection (vertebrate fossils).

FAUNA:

MAMMALS

Peramelidae: *Perameles bougainville*; Vombatidae: *Vombatus ursinus*; Thylacoleonidae: **Thylacoleo carnifex*; Potoroidae: **Bettongia gaimardi*, *B. lesueur*; Macropodidae: *Macropus ergamensis*, *M. rufogriseus*, **Onychogalea lunata*, **Simosthenurus gilli*.

REFERENCES: Daily (1960); Pledge (1977); Williams (1980); South Australian Museum palaeontology collection records.

Naracoorte Caves World Heritage Area

The Naracoorte Caves World Heritage Area has a total area of approximately 305 hectares and is centred 11 km southeast of the Naracoorte township. There are 26 caves on the reserve, many of which contain deposits of Pleistocene and/or Holocene vertebrates, with a particularly rich record of marsupials. The Naracoorte Caves were inscribed on to the World Heritage List in December 1994 as an Australian Fossil Mammal Site (serial nomination with Riversleigh, Queensland) for their exceptional natural and scientific value.

4. VICTORIA FOSSIL CAVE 5U1

LOCATION: Naracoorte Caves World Heritage Area.

DESCRIPTION: Large cave of approximately 4 km of mapped passages and chambers. The cave contains five known fossil deposits, with the largest and most studied being that in the Main Fossil Chamber, which was discovered in 1969 by members of CEGSA. Other chambers containing fossils have been found since then. All are currently under investigation by Flinders University palaeontologists and the faunas identified to date are listed below. Uranium-series dating of speleothems associated

† Prof. A. G. J. (1999) Systematics and evolution of the extinct kangaroo subfamily, Sthenurinae. PhD Thesis, The Flinders University of South Australia (unpubl.).

with these fossil deposits has placed their age range from Middle to Late Pleistocene (Ayliffe *et al.* 1998; Moriarty *et al.* 2000).

COLLECTION: Flinders University vertebrate palaeontology collection; South Australian Museum palaeontology collection (vertebrate fossils).

4a. MAIN FOSSIL CHAMBER

SITE DESCRIPTION: This chamber has an extensive bone deposit within a large sediment cone and fan. The deposit has a complex depositional history with multiple modes of accumulation and concentration evident, chiefly pitfall trap predator accumulation (avian and mammalian) and hydraulic transport. Uranium-series dating of flowstone on the surface of the deposit has provided a minimum age of about 213 ka (Ayliffe *et al.* 1998; Moriarty *et al.* 2000).

COLLECTION: Flinders University vertebrate palaeontology collection; South Australian Museum palaeontology collection (vertebrate fossils).

FAUNA:

AMPHIBIANS

Hylidae: *Lioria ewingi*; Myobatrachidae: *Crinia signifera*, *Geocrinia* sp. cf. *G. laevis*; *Limnodynastes* sp. cf. *L. dumerili*, *Limnodynastes tasmaniensis*.

REPTILES

Chelidae: *Emydura macquarii*; Agamidae: *Pagana* sp. cf. *P. barbata*; Scincidae: *Egernia whiti*, cf. *Eulamprus tympanum*, *Icrista boagvillii*, *Tiliqua nigrolutea*, *T. rugosa*; Varanidae: *Varanus* sp. cf. *V. gouldii*, *Varanus* sp. cf. *V. varius*; Madtsoiidae: *Womambi naracoortensis*; Elapidae: *Notechis* sp. cf. *N. scutatus*, *Pseudochis* sp. cf. *P. porphyriaeus*, *Pseudonaja* sp. cf. *P. nuchalis*.

BIRDS

Casuaridae: *Dromaius novae-hollandiae*; Megapodiidae: *Leipod ocellata*, *Progero naracoortensis*; Phasianidae: *Columus pectoralis*, *C. ypsilon*; Rallidae: *Gallirallus philippensis*; Turnicidae: *Turnix varia*, *Turnix* sp. indet.; Pedionomidae: *Pedionomus torquatus*; Scolopacidae: *Calidris ruficollis*, *Gallinago hardwickii*, *Tringa glareola*; Charadriidae: *Charadrius australis*; Psittacidae: *Pezoporus wallicus*; Tytonidae: *Tyto novae-hollandiae*; Diuridae: *Grallina cyanoleuca*; Artamidae: *Gymnorhina tibicen*; Corvidae: *Corvus* sp. indet.

Rallus gellifruis listed by Moriarty *et al.* (2000) appears to be misspelling (W. Boles, pers. comm. 2000).

MAMMALS

Tachyglossidae: *Megalibgwaha ramsayi*, *Tachyglossus aculeatus*; Thylacinae: *Thylacinus cynocephalus*; Dasyuridae: *Antechinus flavipes*, *A. stuartii*, *A. swainsoni*, *Dasyurus maculatus*, *D. viverrinus*, *Ningaui* sp. cf. *N. yvonneae*, *Phascogale calura*, *P. tapoutafa*, *Sarcophilus* sp.

cf. *S. lanianus*, *Sminthopsis crassicaudata*, *S. murina*; Peramelidae: *Isaodon obesulus*, *Perameles boagvillii*, *P. gunnii*; Phascolaridae: *Phascolarctos cinereus*; Diprotodontidae: *Diprotodon* sp. indet., *Zygomaturus trilobus*; Palorchestidae: *Palorchestes azueli*; Vombatidae: *Lasiorchinus krefftii*, *L. latifrons*, *Vombatus ursinus*; Thylacoleonidae: *Thylacoleo carnifex*; Phalangeridae: *Trichosurus vulpecula*; Hipsiprymnodontidae: cf. *Propithecus oscillans*; Potoroidae: cf. *Aepyprymnus rufescens*, *Bemungia gainardi*, *Bemungia* sp. cf. *B. lesueur*, *B. penicillata*, *Potorous platyops*, *P. tridactylus*; Macropodidae: *Lagorchestes leopoldes* (= *Lagorchestes* sp. cf. *L. conspicillatus* of Wells *et al.* 1984 and Moriarty *et al.* 2000, see McNamara 1997), *Macropus eugenii*, *M. fuliginosus*, *M. giganteus*, *M. greyi*, *M. fuliginosus*, *M. titan*, *Procoptodon goliath* (= *Procoptodon rapah* of Wells *et al.* 1984, see Prideaux 1999), *Protemnodon roechus*, *Sminthomurus baileyi*, *S. browni*, *S. gilli*, *S. muddocki*, *S. newtoni*, *S. occidentalis*, *S. palex*, *Sthenurus andersoni* (= *Sthenurus atlas* of Wells *et al.* 1984, see Prideaux 1999), *Wallabia bicolor*; Burramyidae: *Cyrcarctus lepidus*, *C. nanus*; Pseudocheiridae: *Pseudocheirus peregrinus*; Petauridae: *Petaurus breviceps*; Acrobatidae: cf. *Acrobates pygmaeus*; Vespertilionidae: *Miniopterus* sp. indet.; Muridae: *Coniurus albipes*, *Hydromys chrysogaster*, *Musacommys fuscus*, *Notomys* sp. cf. *N. mitchelli*, *Pseudomys* sp. cf. *P. australis*, *Pseudomys* sp. cf. *P. fumeus*, *Pseudomys* sp. cf. *P. gouldii*, *P. shottidgei*, *Rattus fuscipes*, *R. tunneyi*.

Moriarty *et al.* 2000 listed two additional marsupials, *Dasyurus cristicauda* and *Perameles nasuta*. However, no specimens can be located to support these identifications, which appear unlikely. They have therefore been omitted from this list.

4b. GRANT HALL (also known as White Chamber)

SITE DESCRIPTION: Excavations have yielded bone material from the sediment floor of the chamber, at the base of a large talus cone. The bone deposits are associated with several levels of speleothems, uranium-series dating of which indicates that the deposits accumulated between about 206 ka and 76 ka (Ayliffe *et al.* 1998; Moriarty *et al.* 2000). The site is currently under investigation by Rebecca Gresham from Flinders University.

COLLECTION: Flinders University vertebrate palaeontology collection.

FAUNA:

REPTILES

Agamidae: gen. et. sp. indet.; Varanidae: *Varanus* sp. indet.; Madtsoiidae: *Womambi naracoortensis*; Elapidae: gen. et. sp. indet.

BIRDS

Order indet.

MAMMALS

Fachyglossidae: *Fachyglossus aculeatus*; Thylacnidae: ^{††}*Thylacinus cynocephalus*; Phascolarctidae: *Phascolarctos cinereus*; Diprotodontidae: [†]*Zygomaturus trilobus*; Vombatidae: *Vombatus ursinus*; Thylacoleonidae: ^{††}*Thylacoleon carnifex*; Potoroidae: [†]*Bettongia pennicillata*; Macropodidae: *Macropus giganteus*, *M. rufogriseus*, *Macropus* sp. indet., ^{††}*Simosthenurus browni*, ^{††}*S. gilli*, ^{††}*S. newtonae*, *Wallabia bicolor*; Burramyidae: *Cercartetus lepidus*, *C. nanus*; Muridae: [†]*Musacomys fuscus*, *Pseudomys apodemoides*, [†]*P. australis*, *Pseudomys* sp. cf. ^{††}*P. goldii*, *P. shortridgei*, *Pseudomys* sp. indet., *Rattus fuscipes*, [†]*R. numeyi*.

4c. SPRING CHAMBER (also known as Starburst Chamber)

SITE DESCRIPTION: Bone material has been excavated from the sediment floor of this large chamber. Although only preliminary work has been done on the site, uranium-series dating of associated speleothems suggests that deposition began before 327 ka and upper layers of the deposit accumulated between 280 ka and 210 ka (Moriarty *et al.* 2000). The site is currently under investigation by palaeontologists from Flinders University.

COLLECTION: Flinders University vertebrate palaeontology collection.

FAUNA:

MAMMALS

Dasyuridae: *Dasyurus* sp. cf. [†]*D. viverrinus*; Phascolarctidae: *Phascolarctos cinereus*, *Phascolarctos* sp. cf. ^{††}*P. stiboni*; Vombatidae: gen. et sp. indet.; Macropodidae: *Macropus giganteus*, *M. rufogriseus*, *Macropus* sp. indet., ^{††}*Simosthenurus gilli*, ^{††}*S. occidentalis*, ^{††}*S. palex*; Muridae: *Hydromys chrysogaster*, [†]*Rattus numeyi*.

4d. UPPER AND LOWER OSSUARIES

SITE DESCRIPTION: These two chambers in the distal part of the cave contain immensely rich bone deposits. Discovered in the early 1970s by B. Wright and R. Galbreath (CEGSA), they remain largely untouched as a reference site. To date, surface material only has been examined, mostly *in situ*. No excavation has been done in these chambers. A few specimens were removed from the access tunnel for identification when the chambers were discovered. Additional material has been identified *in situ* by the authors.

COLLECTION: Flinders University vertebrate palaeontology collection.

FAUNA:

BIRDS

Casuariidae: cf. *Dromaius novaehollandiae*.

MAMMALS

Fachyglossidae: ^{††}*Megalibgwilia ramsayi*; Thylacnidae: ^{††}*Thylacinus cynocephalus*; Dasyuridae: *Sarcophilus* sp. cf. ^{††}*S. lanianus*; Diprotodontidae: [†]*Zygomaturus trilobus*; Thylacoleonidae: ^{††}*Thylacoleon carnifex*; Macropodidae: *Macropus* sp. cf. *M. giganteus*, *M. rufogriseus*, ^{††}*Simosthenurus browni*, ^{††}*S. gilli*, ^{††}*S. madlocki*, ^{††}*S. occidentalis*, [†]*Sthenurus andersoni*.

4e. BUTCH AND LAKE CHAMBER

SITE DESCRIPTION: A small chamber adjacent to the Main Fossil Chamber discovered in the early 1970s by A. Lake and B. Alvarez (CEGSA). Bone material was discovered and collected. Additional material was collected in 1997/1998 and identified by one of the authors (E. H. R.) and colleagues from Flinders University. All bone material within the chamber is found within the rock pile on the chamber floor, without any sedimentary context, thus providing some interesting preservational features (Moriarty *et al.* 2000).

COLLECTION: Flinders University vertebrate palaeontology collection.

FAUNA:

REPTILES

Varanidae: *Varanus* sp. indet.

MAMMALS

Thylacnidae: ^{††}*Thylacinus cynocephalus*; Phascolarctidae: *Phascolarctos cinereus*; Thylacoleonidae: ^{††}*Thylacoleon carnifex*; Macropodidae: *Macropus* sp. cf. *M. fuliginosus*, *Macropus* sp. cf. *M. rufogriseus*, *Simosthenurus* sp. cf. ^{††}*S. gilli*.

REFERENCES: Smith (1971, 1972, 1976); Van Tets & Smith (1974); Pledge (1977, 1980b, c, 1991); Tyler (1977, 1991); Wells (1978); Wells & Murray (1979); Williams (1980); Dawson (1982); Wells & Pledge (1983); Wells *et al.* (1984); Baird (1991a, b); Baird *et al.* (1991); Griffiths *et al.* (1991); McNamara (1997); Ayliffe *et al.* 1998; Prideaux & Wells (1998); Prideaux (1999, 2000); Turner (1999); Moriarty *et al.* (2000); M. Hutchinson (pers. comm. 1999, 2000); A. Baynes (pers. comm. 2000); R. Gresham (pers. comm. 2000); C. Williams (pers. comm. 2000); Flinders University vertebrate palaeontology collection database; South Australian Museum palaeontology collection records.

5. BAT CAVE 5U2

LOCATION: Naracoorte Caves World Heritage Area.

SITE DESCRIPTION: Bone material was collected

Fig. 1. (1999) Investigation of the genus *Macropus* (Marsupialia: Macropodidae) from the Victoria Fossil Cave deposit, Naracoorte, BSc (Hons) Thesis, The Flinders University of South Australia (unpubl.).

from sediment beneath a ledge in the entrance chamber by Walsh in 1959. The deposit is estimated to be of Late Pleistocene age by faunal association, although it is likely that more recent material has been included with the collection.

COLLECTION: South Australian Museum palaeontology collection (vertebrate fossils).

FAUNA:

MAMMALS

Dasyuridae: [†]*Dasyurus maculatus*, [†]*Dasyurus* sp. indet., [†]*Phascogale tapoutafa*, *Sarcophilus* sp. cf. [†]*S. harrisi*; Phalangeridae: *Trichosurus vulpecula*; Potoroidea: [†]*Bettongia gaimardi*; Macropodidae: ^{††}*Smotherurus browni*, ^{††}*S. gilli*; Petauridae: *Petaurus breviceps*; Muridae: ^{††}*Conilurus albipes*, [†]*Mastacomys fuscax*, *Rattus* sp. indet.

REFERENCES: South Australian Museum palaeontology collection records.

6. ALEXANDRA CAVE 5U3

LOCATION: Naracorte Caves World Heritage Area.

SITE DESCRIPTION: Bone material was recovered from sediment when the second tourist entrance of the cave was dug out in 1978. Other fossil material was discovered during cave exploration excavations of small sediment filled tunnels in the current tourist section of the cave. Only preliminary investigation of this site has so far been attempted.

COLLECTION: Flinders University vertebrate palaeontology collection; South Australian Museum palaeontology collection (vertebrate fossils).

FAUNA:

MAMMALS

Dasyuridae: [†]*Dasyurus maculatus*, [†]*D. viverrinus*, *Sarcophilus* sp. cf. [†]*S. harrisi*; Phascolartidae: *Phascolarctos cinereus*; Vombatidae: *Vombatus ursinus*; Thylacoleonidae: ^{††}*Thylacoleo carnifex*; Phalangeridae: *Trichosurus vulpecula*; Potoroidea: [†]*Bettongia* sp. indet.; Macropodidae: *Macropus* sp. cf. *M. giganteus*, *Macropus* sp. cf. *M. rufogriseus*, *Macropus* sp. indet., ^{††}*Procyptodon gobah*, ^{††}*Simotherurus browni*, ^{††}*S. gilli*, ^{††}*S. occidentalis*, *Wallabia bicolor*.

REFERENCES: Pledge (1977); Williams (1980). Flinders University vertebrate palaeontology collection database; South Australian Museum palaeontology collection records.

7. BLANCHE CAVE 5U4, 5U5, 5U6

LOCATION: Naracorte Caves World Heritage Area.

SITE DESCRIPTION: Fossil material from this cave was described last century by Woods (1862), with additional material having been collected since then, mostly in the 1970s (notably the *Genyornis* specimen). A small number of bones has been collected from the third chamber of the cave by cave explorers.

COLLECTION: Flinders University vertebrate palaeontology collection; South Australian Museum palaeontology collection (vertebrate fossils).

FAUNA:

BIRDS

Casuariidae: *Dromaius novaehollandiae*; Dromornithidae: ^{††}*Genyornis newtoni*.

MAMMALS

Dasyuridae: [†]*Dasyurus* sp. indet., [†]*Sarcophilus* sp. indet.; Peramelidae: [†]*Perameles bompainville*; Phascolartidae: *Phascolarctos cinereus*; Thylacoleonidae: ^{††}*Thylacoleo carnifex*; Phalangeridae: *Trichosurus vulpecula*; Potoroidea: [†]*Bettongia gaimardi*; Macropodidae: ^{††}*Lagorchestes leporides*, *Macropus* sp. cf. *M. giganteus*, *M. rufogriseus*, ^{††}*Onychogalea lunata*, ^{††}*Protemnodon brehus*, ^{††}*Smotherurus gilli*; Pseudocheiridae: *Pseudocheirus peregrinus*.

REFERENCES: Woods (1862, 1866); Rich (1979); Wells & Pledge (1983); Baird (1991b); Baird *et al.* (1991); McNamara (1997); Flinders University vertebrate palaeontology collection database; South Australian Museum palaeontology collection records.

8. WET CAVE - Stick Entrance 5U10, Tomato Entrance 5U11 (also known as Tomato-Stick Cave)

LOCATION: Naracorte Caves World Heritage Area.

SITE DESCRIPTION: Excavation was carried out in 1997/1998 in the distal fan sediments of a large sediment cone in the current tourist cave by Flinders University researchers. Abundant bone material was recovered, particularly small animals, with some megafaunal species at the lower levels of the sequence. The site is currently under investigation by M. McDowell (Flinders University). Preliminary results suggest a Late Pleistocene to Holocene age for the deposit. Other material has been collected from the cave in the past and lodged with the South Australian Museum.

COLLECTION: Flinders University vertebrate palaeontology collection; South Australian Museum palaeontology collection (vertebrate fossils).

FAUNA:

AMPHIBIANS

Family indet.

REPTILES

Agamidae: gen. et sp. indet.; Scincidae: *Egernia whitii*, *Tiliqua nigrolutea*, *T. rugosa*; Varanidae: *Varanus* sp. cf. *V. varius*; Madtsoiidae: ^{††}*Womamb naracortensis*; Llapidae: *Notechis scutatus*, [†]*Pseudochis porphyriacus*, *Pseudomaja nicholisi*.

BIRDS

Psittacidae: gen. et sp. indet.; Tytonidae: *Tyto alba*; Artamidae: gen. et sp. indet.; Estrildidae: gen. et sp. indet.

MAMMALS

Thylaciniidae: ^{**}*Thylacinus cynocephalus*; Dasyuridae: *Antechinus flavipes*, ^{*}*Dasyurus geoffroi*, [†]*D. viverrinus*, ^{*}*Ningaui yunnanae*, ^{*}*Phascogale tapoatafa*, ^{*}*Sarcophilus harrisi*, *Smynthopsis crassicaudata*, *S. murina*; Peramelidae: [†]*Perameles gunnii*; Phascolarctidae: *Phascolarctos cinereus*; Diprotodontidae: ^{**}*Zygomaturus trilobus*; Thylacoleonidae: ^{**†}*Thylacoleon carnifex*; Phalangeridae: *Trichosurus vulpecula*; Potoroidae: [†]*Bettongia lesueur*, ^{**†}*Potorous platyops*; Macropodidae: *Macropus giganteus*, *M. rufogriseus*, *Macropus* sp. indet., ^{††}*Protemnodon brehms*, ^{**†}*Protemnodon* sp. indet., ^{**†}*Simosthenurus browni*, ^{**†}*S. gilli*, ^{**†}*S. newtonae*, ^{**†}*S. occidentalis*; Burramyidae: *Cercartetus concinnus*, *C. lepidus*, *C. nanus*; Pseudocheiridae: *Pseudocheirus peregrinus*; Petauridae: *Petaurus breviceps*; Vespertilionidae: *Miniopterus schreibersii*; Muridae: ^{**}*Conilurus albus*, ^{*}*Macuromys fuscus*, *Notomys mitchellii*, *Pseudomys apodemoides*, ^{*}*P. australis*, ^{*}*P. jenkinsi*, *Pseudomys* sp. cf. ^{**†}*P. gouldii*, *P. shorridgei*, *Rattus fuscipes*, *R. luridulus*, ^{**}*K. tumeyi*

REFERENCES: Williams (1980); M. McDowell (pers. comm. 1999, 2000); Flinders University vertebrate palaeontology collection database; South Australian Museum palaeontology collection records.

9. CATHEDRAL CAVE 5U12, 5U13

LOCATION: Naracoorte Caves World Heritage Area. SITE DESCRIPTION: A large chamber in the distal part of the cave has a sediment cone deposit containing a large amount of bone material, some in association with dated flowstone. Uranium/thorium dating of these speleothems suggests that the material accumulated between approximately 279 ka and 159 ka (Brown 1998[†]; Brown & Wells 2000). Brown (Brown 1998[†]; Brown & Wells 2000) concluded that the primary accumulation mode was pitfall via a now-blocked solution tube. Other material including *Thylacoleon carnifex*, was collected from other small passages in the cave by CUEGSA members in March 1959 and reported by Daily (1960).

COLLECTION: Flinders University vertebrate palaeontology collection; South Australian Museum palaeontology collection (vertebrate fossils).

FAUNA:

AMPHIBIANS

Myobatrachidae: *Limodynastes* sp. indet.

REPTILES

Scincidae: *Tiliqua rugosa*

BIRDS

Family indet.

MAMMALS

Thylaciniidae: *Thylacinus cynocephalus*; Dasyuridae: *Antechinus flavipes*, *Antechinus* sp. indet., *Dasyurus maculatus*, ^{*}*D. viverrinus*

^{*}*Phascogale vulturna*, *Smynthopsis murina*; Peramelidae: *Isodon obesulus*, [†]*Perameles bougainville*, ^{*}*P. gunnii*; Diprotodontidae: ^{**†}*Zygomaturus trilobus*; Vombatidae: gen. et sp. indet., [†]*Lastorhinus latrans*; Thylacoleonidae: [†]*Thylacoleon carnifex*; Potoroidae: ^{*}*Bettongia pennicillata*, ^{*}*Bettongia* sp. indet., ^{**†}*Potorous platyops*, ^{**†}*P. tridactylus*; Macropodidae: *Macropus giganteus*, *M. rufogriseus*, *Macropus* sp. indet., ^{**†}*Procoptodon gollah*, ^{**†}*Simosthenurus browni*, ^{**†}*S. gilli*, ^{**†}*S. occidentalis*, *Wallabia bicolor*; Burramyidae: *Cercartetus nanus*; Muridae: ^{*}*Mastacomys fuscus*, *Notomys mitchellii*, ^{**†}*Pseudomys australis*, *P. shorridgei*, *Pseudomys* sp. indet.

REFERENCES: Daily (1960); Pledge (1977); Williams (1980); Ayliffe *et al.* (1998); Brown (1998[†], pers. comm. 2000); Brown & Wells (2000); Moriarty *et al.* (2000); Flinders University vertebrate palaeontology collection database; South Australian Museum palaeontology collection records.

10. ROBERTSON CAVE 5U17, 5U18, 5U19

LOCATION: Naracoorte Caves World Heritage Area. SITE DESCRIPTION: The inner chamber of the cave contains a rich bone deposit, particularly of small mammal remains. Megafaunal species have been found at the lower levels of the sequence suggesting a Pleistocene age. The site is currently under investigation by M. McDowell (Flinders University). COLLECTION: Flinders University vertebrate palaeontology collection.

FAUNA:

AMPHIBIANS

Family indet.

REPTILES

Agamidae: gen. et sp. indet., Scincidae: *Ligernia whitii*, *Tiliqua nigrolutea*, *T. rugosa*; Varanidae: *Varanus* sp. cf. ^{*}*V. varius*; Elapidae: *Notychus scutatus*, ^{*}*Pseudechis porphyriaeus*, *Pseudonaja nuchalis*.

BIRDS

Family indet.

Psittacidae: gen. et sp. indet.; Tytonidae: *Tyto alba*; Artamidae: gen. et sp. indet.; Estrifidae: gen. et sp. indet.

MAMMALS

Dasyuridae: *Antechinus flavipes*, ^{*}*Dasyurus geoffroi*, ^{*}*D. viverrinus*, ^{*}*Ningaui yunnanae*, ^{*}*Phascogale tapoatafa*, *Smynthopsis crassicaudata*, *S. murina*; Peramelidae: *Isodon obesulus*, ^{*}*Perameles gunnii*; Phascolarctidae: *Phascolarctos cinereus*; Vombatidae: *Vombatus ursinus*; Phalangeridae: *Trichosurus vulpecula*; Potoroidae: [†]*Bettongia lesueur*, ^{**†}*Potorous platyops*; Macropodidae: *Macropus giganteus*, *M. rufogriseus*, ^{**†}*Protemnodon* sp. indet., ^{*}*Simosthenurus occidentalis*; Burramyidae: *Cercartetus lepidus*, *C.*

natus; Pseudocheeridae: †*Petauroides volans*, *Pseudocheirus peregrinus*; Petauridae: *Petaurus breviceps*; Vespertilionidae: *Miniopterus schreibersii*; Muridae: ***Conilurus albipes*, *Hydromys chrysogaster*, *Mastacomys fuscus*, *Notomys utiellii*, *Pseudomys apodemoides*, **P. australis*, **P. fumeus*, *Pseudomys* sp. cf. ***P. gouldii*, *P. shortridgei*, *Rattus fuscipes*, *R. lutreolus*, **R. luncevi*

REFERENCES: M. McDowell (pers. comm. 1999, 2000): Flinders University vertebrate palaeontology collection database.

11. FOX CAVE 5U22

LOCATION: Naracoorte Caves World Heritage Area.
SITE DESCRIPTION: Fossil material has been recovered from this large cave, with excavations being conducted by researchers from the South Australian Museum and Flinders University. The deposit consists of numerous bones contained in the sediment floor of the cave and large sediment cone.
COLLECTION: Flinders University vertebrate palaeontology collection; South Australian Museum palaeontology collection (vertebrate fossils).

FAUNA:

BIRDS

Megapodiidae: †*Progrura naracoortensis*; Alcedinidae: *Dacelo* sp. cf. *D. novaeguineae*.

MAMMALS

Tachyglossidae: †*Megalibgwilia ramsayi*, *Tachyglossus aculeatus*; Thylacimidae: ***Thylacinus cynocephalus*; Dasyuridae: **Dasyurus maculatus*, **D. viverrinus*, *Sarcophilus* sp. cf. †*S. lanianus*; Peramelidae: *Woodon obesatus*, **Perameles gunnii*; Diprotodontidae: †*Zygomaturus trilobus*; Vombatidae: *Vombatus ursinus*; Thylacoleonidae: †*Thylacoleon carnifex*; Phalangeridae: *Trichosurus vulpecula*; Potoroidae: †*Bertongia gainardi*, **Potorous tridactylus*; Macropodidae: *Macropus* sp. cf. *M. giganteus*, ***M. greyi*, *M. rufogriseus*, *Macropus* sp. cf. †*M. titan*, †*Procoptodon volah*, †*Simosthenurus browni*, †*S. gilli*, †*S. occidentalis*, *Wallabia bicolor*; Pseudocheeridae: *Pseudocheirus peregrinus*; Muridae: †*Mastacomys fuscus*, *Rattus* sp. cf. *R. lutreolus*.

REFERENCES: Pledge (1977, 1980c); Murray (1978); Baird (1991b); Baird *et al.* (1991); Flinders University vertebrate palaeontology collection database; South Australian Museum palaeontology collection records.

12. UN-NAMED CAVE 5U49

LOCATION: Naracoorte Caves World Heritage Area.
SITE DESCRIPTION: A small cave with a solution pipe entrance and very little cave development. Bone material is contained within a sediment cone beneath a blocked former solution pipe entrance. No

excavations have been conducted in this cave but identifications were made from a small amount of material collected by the authors from areas that had been previously disturbed.

COLLECTION: Flinders University vertebrate palaeontology collection.

FAUNA:

REPTILES

Varanidae: *Varanus* sp. indet.

BIRDS

Megapodiidae: †*Progrura naracoortensis*.

MAMMALS

Thylacimidae: †*Thylacinus cynocephalus*; Vombatidae: *Vombatus ursinus*; Macropodidae: *Macropus* sp. indet., †*Simosthenurus gilli*.

REFERENCES: None.

13. WOMBAT CAVE 5U58

LOCATION: Naracoorte Caves World Heritage Area.

SITE DESCRIPTION: The second chamber of the cave was discovered in the early 1970s, with a small collection of bone material being lodged with the South Australian Museum. Additional material has been identified *in situ* on a rubble slope adjacent to a large area of speleothem development, much of which has formed over what was probably a cone beneath a solution pipe. The site is currently under investigation by one of the authors (E.H.R.).

COLLECTION: Flinders University vertebrate palaeontology collection; South Australian Museum palaeontology collection (vertebrate fossils).

FAUNA:

BIRDS

Megapodiidae: †*Progrura naracoortensis*.

MAMMALS

Dasyuridae: **Dasyurus viverrinus*; Peramelidae: **Perameles gunnii*; Vombatidae: *Vombatus ursinus*; Phalangeridae: *Trichosurus vulpecula*; Macropodidae: *Macropus* sp. cf. *M. giganteus*, *M. rufogriseus*, †*Protemnodon* sp. indet., †*Simosthenurus browni*, †*S. gilli*, **Sthenurus andersoni*.

REFERENCES: Baird (1991b); Baird *et al.* (1991); Flinders University vertebrate palaeontology collection database; South Australian Museum palaeontology collection records.

14. SAND FUNNEL CAVE 5U72

LOCATION: Naracoorte Caves World Heritage Area.
SITE DESCRIPTION: Bone material was collected from surface sediment in the 1970s, context unknown.

COLLECTION: Flinders University vertebrate palaeontology collection.

FAUNA:

MAMMALS

Macropodidae: †*Macropus eugenii*, †*Simosthenurus maddocki*.

REFERENCES: Flinders University vertebrate palaeontology collection database

Other Naracoorte [district] cave sites

15. BROWN SNAKE CAVE 5U14

LOCATION: Naracoorte Forest, Forestry SA.

SITE DESCRIPTION: Bone material collected by CEGSA members, context unknown.

COLLECTION: South Australian Museum palaeontology collection (vertebrate fossils).

FAUNA:

MAMMALS

Macropodidae: *†*Simosthenurus gilli*.

REFERENCES: Williams (1980); South Australian Museum palaeontology collection records.

16. HAYSTACK CAVE 5U23

LOCATION: Private land

SITE DESCRIPTION: Bone material was excavated by W. Rouse and M. R. Wallis and N. Pledge and R. Callen, from within the cave during the 1960s, with abundant bone material discovered in the slope and fan of a large sediment cone.

COLLECTION: South Australian Museum palaeontology collection (vertebrate fossils). Some identifications of material *in situ* were made by the authors.

FAUNA:

REPTILES

Scincidae: *Tiliqua nigrolutea*; Madtsoiidae: *†*Wombombi naracoortensis*.

MAMMALS

Tachyglossidae: *Tachyglossus aculeatus*;

Thylaciniidae: ***Thylacinus cynocephalus*;

Dasyuridae: *Antechinus* sp. indet., **Dasyurus viverrinus*,

*†*Sarcophilus lanianus*; Peramelidae: *Isodon obesus*,

**Perameles gunni*; Phascolarctidae:

Phascolarctos sp. indet.; Diprotodontidae: *†*Zygomaturus trilobus*;

Vombatidae: *Vombatus ursinus*;

Thylacoleonidae: ***Thylacoleon carnifex*;

Potoroidae: **Aepyrymnus rufescens*, **Bettongia gurnardi*,

*†*Potorous platyops*, †*P. tridactylus*;

Macropodidae: *Macropus giganteus*,

M. rufogriseus, *Procoptodon*

sp. cf. †*P. galah*, *†*Simosthenurus browni*, †*S. gilli*,

*†*S. maddocki*, ***S. newtonae*, *†*S. occidentalis*,

Wallabia bicolor; Burramyidae: *Creartetus nanus*;

Pseudocheiridae: *Pseudocheirus peregrinus*;

Muridae: **Mastacomys fuscus*, *Rattus lutreolus*.

REFERENCES: Merrilees (1965); Pledge (1977, pers. comm. 2000); Williams (1980); South Australian Museum palaeontology collection records.

17. UN-NAMED CAVE 5U28

LOCATION: North of Naracoorte township.

SITE DESCRIPTION: Small cave 60 m from VDC Cave (5U26). Bone material was collected during

cave exploration, context unknown.

COLLECTION: South Australian Museum palaeontology collection (vertebrate fossils).

FAUNA:

MAMMALS

Macropodidae: *Macropus* sp. indet., *†*Simosthenurus browni*.

REFERENCES: South Australian Museum palaeontology collection records.

18. SPECIMEN CAVE 5U35 – (also known as Zietz Cave)

LOCATION: Private land.

SITE DESCRIPTION: A solution pipe leads down to a large chamber with bone deposits in sediment associated with flowstone layers. Stirling reported material of extinct marsupials, including *Thylacoleon carnifex*, from the cave in 1908 (Stirling 1908; Wells & Pledge 1983). Another report by Stirling in 1912 mentioned *T. carnifex* material from the Naracoorte Caves which had been presented to the South Australian Museum by W. Redden, the caretaker of the Caves. The name of the site from which this material was collected did not appear in the report. However, it is most likely to be Specimen Cave.

COLLECTION: Flinders University vertebrate palaeontology collection; South Australian Museum palaeontology collection (vertebrate fossils).

FAUNA:

REPTILES

Scincidae: *Tiliqua rugosa*

MAMMALS

Thylaciniidae: ***Thylacinus cynocephalus*;

Dasyuridae: **Dasyurus* sp. indet., *Sarcophilus* sp. cf.

*†*S. lanianus*, *Smintropsis* sp. indet.; Peramelidae:

**Perameles* sp. indet.; Vombatidae: *Vombatus*

ursinus; Thylacoleonidae: *†*Thylacoleon carnifex*;

Potoroidae: **Bettongia penicillata*, ***Putorous*

platyops; Macropodidae: *Macropus giganteus*,

M. rufogriseus, *Macropus* sp. cf. *†*M. titan*,

Macropus sp. indet., *Protemnodon* sp. cf. *†*P. muuk*,

*†*P. roechus*, *†*Simosthenurus baileyi*, *†*S. browni*,

*†*S. gilli*, *†*S. maddocki*, *†*S. occidentalis*,

*†*Thylacule* sp. indet.

REFERENCES: Stirling (1908, 1912); Pledge (1977);

Williams (1980); Wells & Pledge (1983); Flinders

University palaeontology collection database; South

Australian Museum palaeontology collection

records.

19. RABBIT CAVE 5U66

LOCATION: Private land.

SITE DESCRIPTION: This small cave has bones evident *in situ* on the surface of the sediment floor of a small distal chamber. No excavation has been conducted in the cave. However, identifications of material *in situ* were made by the authors.

COLLECTION: None made

FAUNA:

MAMMALS

Macropodidae: *Macropus* sp. cf. *M. fuliginosus*, *Simosthenurus* sp. cf. †*S. browni*, *Simosthenurus* sp. cf. †*S. gilli*.

REFERENCES: None.

20. POSSUM CAVE 5U81

LOCATION: Private land.

SITE DESCRIPTION: Plentiful bone material apparent within a large sediment cone and on the sediment surface, particularly the distal fan and beneath rock ledges. Thus far, only preliminary investigations have been made, with a very small amount of material collected for identification. The site is under further investigation by the authors.

COLLECTION: Flinders University vertebrate palaeontology collection.

FAUNA:

MAMMALS

Macropodidae: *Macropus* sp. cf. *M. fuliginosus*, †*Protemnodon brevis*, †*Simosthenurus browni*.

REFERENCES: Prideaux (1999³); Flinders University vertebrate palaeontology collection database.

21. CABLE CAVE 5U125

LOCATION: Private land

SITE DESCRIPTION: The cave was discovered by workers laying cables in 1981, hence the name. A small solution pipe entrance leads to a steep talus cone, the distal portions of which contain abundant bone material within the sediment. Some preliminary collection and identifications have been made in disturbed areas.

COLLECTION: Flinders University vertebrate palaeontology collection.

FAUNA:

MAMMALS

Thylacimidae: †*Thylacinus cynocephalus*, Peramelidae: *Isodon obesulus*, †*Perameles* sp. indet., Vombatidae: *Vombatus ursinus*; Thylacoleonidae: †*Thylacoleo carnifex*; Potoroidae: †*Bettongia lesueur*, †*Bettongia* sp. indet.; Macropodidae: *Macropus* sp. cf. *M. giganteus*, †*M. titan*, *Macropus* sp. indet., †*Simosthenurus* sp. indet.

REFERENCES: Flinders University vertebrate palaeontology collection database.

22. SOS CAVE 5U132

LOCATION: Private land

SITE DESCRIPTION: The entrance to this cave opened up naturally in 1983. Some bone material has been

collected by members of CEGSA and taken to the South Australian Museum for identification. This material included an almost complete skeleton of *Thylacinus cynocephalus* and the holotype of the extinct wallaby *Congruus congruus*.

COLLECTION: South Australian Museum palaeontology collection (vertebrate fossils).

FAUNA:

MAMMALS

Thylacimidae: †*Thylacinus cynocephalus*, Macropodidae: †*Congruus congruus*, †*Simosthenurus newtonae*.

REFERENCES: McNameara (1994); Sefton (1998⁷); Prideaux (1999³, 2000); South Australian Museum palaeontology collection records.

23. BUCKRIDGE CAVE 5U169

LOCATION: Private land.

SITE DESCRIPTION: Small cave uncovered during vineyard preparation in early 1999 and subsequently filled in within 72 hours of its discovery. The authors and colleagues were contacted by members of CEGSA to investigate the site which was found to contain significant fossil material. A salvage excavation was undertaken during the night to prevent the complete loss of the material and information. All obvious bone material and most sediment were removed from an approximately 4 m² area to a depth of approximately 50 cm. No other material was visible. Preliminary taphonomic analysis suggests that this small cave may have acted as a den for carnivores, notably Tasmanian Devils and *Thylacoleo carnifex*. Bone material from the site is currently under investigation by the authors.

COLLECTION: Currently held by the authors.

FAUNA:

REPTILES

Elapidae: *Notechis scutatus*.

BIRDS

Casuaridae: *Dromaius novaehollandiae*; Megapodiidae: cf. †*Proguara naracoortensis*.

MAMMALS

Tachyglossidae: †*Megalibgwilia ramsayi*; Thylacimidae: †*Thylacinus cynocephalus*; Dasyuridae: †*Dasyurus maculatus*, †*D. viverrinus*, *Sarcophilus* sp. cf. †*S. latitarsis*; Peramelidae: *Isodon obesulus*, *Perameles* sp. cf. †*P. gunnii*; Palorchestidae: †*Palorchestes uzbeki*; Vombatidae: †*Lasiorchinus* sp. indet.; Thylacoleonidae: †*Thylacoleo carnifex*; Potoroidae: †*Bettongia gainardi*, †*B. lesueur*, †*B. penicillata*; Macropodidae: *Macropus* sp. cf. *M. fuliginosus*, *Macropus* sp. cf. *M. giganteus*, †*M. greyi*, *M. rufogriseus*, †*M. titan*, *Macropus* sp. indet., *Protemnodon* sp. cf. †*P. anak*, †*Simosthenurus* sp. indet., †*Sthenurus andersoni*, †*Thylagale billardieri*, *Wallabia bicolor*; Muridae:

⁷SEFTON, M. (1998) SOS Cave (5U132) Cave Exploration Group of South Australia News, 43, 18-53

Notomys mitchellii, **Pseudomys australis*, ***P. gonldii*, *P. shortridgei*, *Pseudomys* sp. indet.
REFERENCES: None

24. CRAWFORD'S CORNUCOPIA CAVE 5U171

LOCATION: Private land.

SITE DESCRIPTION: Small cave recently uncovered during vineyard preparation in mid-1999; subsequently opened up by machinery. A small sediment cone contains very fragile bone material with a lower, cemented layer with numerous cranial and post-cranial elements, some in articulated and associated states. Investigation of the site by the authors has begun.

COLLECTION: Currently held by the authors.

FAUNA:

REPTILES

Chelidae: gen. et sp. indet., Elapidae: gen. et sp. indet.

BIRDS

Casuariidae: *Dromaius novaehollandiae*;
Megapodiidae: *Progunia* sp. cf. *†*P. naracoortensis*.

MAMMALS

Thylacinae: †*Thylacinus cynocephalus*; Dasyuridae: *Sarcophilus* sp. cf. *†*S. lanianus*; Peramelidae: *Isodon obesulus*, **Perameles* sp. indet.; Phaseolaretidae: *Phascolarctos cinereus*; Vombatidae: *Vombatus ursinus*; Thylacoleonidae: *†*Thylacoleo carnifex*; Potoroidae: **Bettongia levaueri*; Macropodidae: *Macropus* sp. cf. *M. giganteus*, *M. rufogriseus*, †*Protemnodon brachius*, *†*Simosthenurus baileyi*, *†*S. browni*, *†*S. gilii*, *†*S. maddocki*, *†*S. occidentalis*, *Wallabia bicolor*.

Muridae: gen. et sp. indet.

REFERENCES: G. Pridoux (pers. comm. 1999)

25. CHIESE AND PUTTY CAVE 5U76

LOCATION: Private land.

SITE DESCRIPTION: Material collected from the cave in 1967 by G. Langcluddeke, and lodged with the South Australian Museum; context unknown.

COLLECTION: South Australian Museum palaeontology collection (vertebrate fossils).

FAUNA:

MAMMALS

Macropodidae: *Macropus* sp. indet.; †*Simosthenurus* sp. indet.

REFERENCES: South Australian Museum palaeontology collection records.

26. COMAUM FOREST CAVE 5U118 (also known as Comaum Quarry Cave)

LOCATION: Comaum Forest, Forestry SA.

SITE DESCRIPTION: Bone material excavated from the cave by the South Australian Museum in the early 1980s.

COLLECTION: South Australian Museum

palaeontology collection (vertebrate fossils)

FAUNA:

REPTILES

Chelidae: gen. et sp. indet.; Scincidae: *Dilqua rugosa*.

BIRDS

Family indet.

MAMMALS

Tachyglossidae: *†*Megalibgwilia ramsayi*, *Tachyglossus aculeatus*; Thylacinae: ***Thylacinus cynocephalus*; Dasyuridae: *Antechinus* sp. indet., **Dasyurus maculatus*, **D. viverrinus*, *†*Sarcophilus lanianus*; Peramelidae: **Perameles gunii*; Phaseolaretidae: *Phascolarctos cinereus*; Vombatidae: *Vombatus ursinus*, †*Wacudja wakfieldi*; Thylacoleonidae: *†*Thylacoleo carnifex*; Potoroidae: **Bettongia gaimardi*, **Potorous tridactylus*; Macropodidae: *Macropus giganteus*, ***M. greyi*, *M. rufogriseus*, *†*Protemnodon* sp. indet., *†*Simosthenurus browni*, *†*S. gilii*, *†*S. maddocki*, *†*S. newtoni*, *†*S. occidentalis*, *†*S. pater*, *†*Simosthenurus andersoni*, **Thylagale billardieri*, *Wallabia bicolor*; Burramyidae: *Cercartetus nanus*; Pseudocheiridae: *Pseudocheirus peregrinus*; Muridae: gen. et sp. indet.

REFERENCES: Flannery & Pledge (1987); South Australian Museum palaeontology collection records.

Sites and Faunas of the Lower South East region

Penola district

27. PENOLA

LOCATION: 22 km NNW of Penola.

SITE DESCRIPTION: Bones were discovered during the sinking of a well on the edge of a swamp in the mid-nineteenth century.

COLLECTION: Whereabouts of material unknown.

FAUNA:

BIRDS

Dromornithidae: *†*Gentornis* sp. indet.

REFERENCES: Woods (1866); Stirling & Zietz (1896, 1900); Rich (1979); Williams (1980); Wells & Pledge (1983); Baird *et al.* (1991).

28. MONBULLA CAVE 5LS

LOCATION: Monbulla area, west of Penola.

SITE DESCRIPTION: Bone material was collected in 1978 and 1992 by cavers, from a low passage in the entrance chamber of the cave on the surface of the cave floor. The presence of *Simosthenurus browni* material from the cave indicates some Pleistocene material.

COLLECTION: South Australian Museum palaeontology collection (vertebrate fossils)

FAUNA:

REPTILES:

Scincidae: *Tilqua rugosa*.

MAMMALS

Vombatidae: *Vombatus ursinus*; Macropodidae:

*†*Simosthenurus browni*; Felidae: *Felis catus*;

Bovidae: *Ovis aries*; Muridae: ***Comilurus albipes*.

REFERENCES: South Australian Museum palaeontology collection records.

29. UN-NAMED CAVE 5L122

LOCATION: Near Penola.

SITE DESCRIPTION: Bone material was collected by F. W. Aslin, and presented to the South Australian Museum in October 1970.

COLLECTION: South Australian Museum palaeontology collection (vertebrate fossils).

FAUNA:

MAMMALS

Macropodidae: *Simosthenurus* sp. cf. *†*S. gilli*.

REFERENCES: J. McNamara (pers. comm. 1999); South Australian Museum palaeontology collection records.

Millicent district

30. Mt Burr Cave 5L69, 5L70

LOCATION: Mt Burr Forest, Forestry SA.

SITE DESCRIPTION: Bone material collected by cavers during exploration; context unknown.

COLLECTION: South Australian Museum palaeontology collection (vertebrate fossils).

FAUNA:

MAMMALS

Macropodidae: ***Simosthenurus gilli*, *†*S. occidentalis*.

REFERENCES: Williams (1980); South Australian Museum palaeontology collection records.

31. UN-NAMED SITE NEAR MILLICENT

LOCATION: Unknown.

SITE DESCRIPTION: Fossils found in a peat matrix at a depth of approximately 2 m, suggesting an ancient swamp accumulation. The find was reported in Waterhouse (1882).

COLLECTION: Whereabouts of material unknown.

FAUNA:

MAMMALS

Diprotodontidae: ***Diprotodon* sp. indet., ***Zygomaturus trilobus*.

REFERENCES: Waterhouse (1882); Williams (1980).

32. UN-NAMED SITE

LOCATION: Private land, Millicent area.

SITE DESCRIPTION: Following excavation of a new dam in March 2000 the landowner collected bones from a pile of sediment discarded during bulldozing.

The landowner brought the bone material to the attention of the authors who identified some of the elements as belonging to megafaunal species and others to macropodids, sheep and pigs. In order to determine the stratigraphic position of the megafaunal elements, and the extent of the deposit, the authors partially drained the dam, which had been filled, and searched for more bone material. Bones of diprotodontids, shenurine kangaroos and other macropodids were collected from a thick, black organic mud matrix at a depth of approximately 1.5 m below the land surface. No introduced species were found at this level, therefore their presence in the material collected by the landowner from the discarded sediment suggests mixing of material during excavation and dumping of sediment. The site represents a swamp accumulation and is currently under further investigation by R. Wells, the authors, and colleagues from Flinders University.

COLLECTION: Flinders University vertebrate palaeontology collection.

FAUNA:

MAMMALS

Tachyglossidae: *Tachyglossus aculeatus*; Dipro-

odontidae: ***Diprotodon australis*, ***Zygomaturus*

trilobus; Macropodidae: ***Macropus greyi*.

Macropus sp. indet., *Shenurus* sp. cf. *†*S.*

andersoni; Suidae: *Sus scrofa*; Bovidae: *Ovis aries*.

REFERENCES: R. Wells (pers. comm. 2000).

Mount Gambier district

33. GLENCOE

LOCATION: 22 km NW of Mt Gambier.

SITE DESCRIPTION: The preservation of the fossils (i.e. white bone with red sediment adhering) is suggestive of a cave deposit, possibly Glencoe West Cave (5L77) or Glencoe East Cave (5L108). Further information is unavailable.

COLLECTION: South Australian Museum palaeontology collection (vertebrate fossils).

FAUNA:

MAMMALS

Diprotodontidae: gen. et sp. indet.; Macropodidae:

Macropus sp. indet., *†*Simosthenurus gilli*, *†*S.*

occidentalis.

REFERENCES: Tindale (1933); Williams (1980); South Australian Museum palaeontology collection records.

34. TANTANOOKA CAVE 5L12

LOCATION: Near Tantanooka.

SITE DESCRIPTION: Bone material has been collected from a sediment-floored tunnel and in breccia in the current tourist cave. Beach sediments and sea-shells partially filled the cave (N. Pielke pers. comm. 2000).

COLLECTION: South Australian Museum palaeontology collection (vertebrate fossils).

FAUNA:

MAMMALS

Dasyuridae: **Dasyurus* sp. indet., **Sarcophilus* sp. indet.; Peramelidae: *Isaodon* sp. indet.; Diprotodontidae: *†*Zygomaturus trilobus*; Vombatidae: *Vombatus ursinus*; Phalangeridae: *Trichosurus vulpecula*; Macropodidae: *†*Protemnodon roechus*, *†*Simosthenurus gilli*, *†*S. occidentalis*; Otaridae: *Antiocephalus* sp. indet.; Muridae: *Hydromys* sp. indet., *Rattus* sp. indet.

REFERENCES: Tindale (1933); Williams (1980); South Australian Museum palaeontology collection records.

35. TINDALE'S CAVE "E" 5L18

LOCATION: Tantanoola.

SITE DESCRIPTION: Bone material was collected by cavers and presented to the South Australian Museum.

COLLECTION: South Australian Museum palaeontology collection (vertebrate fossils).

FAUNA:

MAMMALS

Macropodidae: *†*Simosthenurus gilli*.

REFERENCES: Tindale (1933); J. McNamara (pers. comm. 1999); South Australian Museum palaeontology collection records.

36. MORGANS CAVE 5L34

LOCATION: Tantanoola.

SITE DESCRIPTION: Material was collected in 1958 by B. Daily; context unknown.

COLLECTION: South Australian Museum palaeontology collection (vertebrate fossils).

FAUNA:

MAMMALS

Macropodidae: *Macropus rufogriseus*, *†*Simosthenurus gilli*.

REFERENCES: South Australian Museum palaeontology collection records.

37. GREEN WATERHOLE CAVE 5L81 (also known as Fossil Cave)

LOCATION: 22 km NW of Mt Gambier.

SITE DESCRIPTION: A water-filled cave, with fossils discovered by divers on the surface of a rockpile, at a depth of 15 m. Collections were made by divers during the mid to late 1960s and 1970s and taken to the South Australian Museum and Australian Museum. Extensive collecting trips were organised by R. T. Wells in 1979. It has been suggested that the probable accumulation mode was drowning of animals that fell into the cave, trying to use it as a drinking water source (Pledge 1980a; Newton 1988').

COLLECTION: Australian Museum palaeontology collection; Flinders University vertebrate palaeontology collection; South Australian Museum palaeontology collection (vertebrate fossils).

FAUNA:

BIRDS

Phasianidae: *Coturnix* sp. indet.; Accipitridae: Undescribed taxon; Falconidae: *Falco* sp. cf. *F. berigora*; Rallidae: **Gallinula mortierii*; *Gallinula* sp. cf. *G. tenebrosa*; Turnicidae: *Turnix varia*; Burhinidae: *Burhinus* sp. cf. *B. grallarius*; Columbidae: *Phaps chalcoptera*, *Phaps* sp. indet.; Cuckoo: *Cacatua tenuirostris*, *Callocephalon imbricatum*, **Calyptorhynchus banksii*, *C. latroni*, *Calyptorhynchus* sp. indet.; Psittacidae: *Platycercus* sp. indet.; Cuculidae: *†*Centropus colossus*; Strigidae: *Ninox novaeseelandiae*; Alcedinidae: *Dacelo novaeguineae*; Acanthizidae: *Dasyornis broadbenti*; Meliphagidae: *Manorina melanoccephala*; Orthonychidae: *†*Orthonyx hypsilophus*; Corvidae: *Corvus* sp. indet.; Hirundinidae: gen. et sp. indet.

MAMMALS

Thylacinae: *†*Thylacinus cynocephalus*; Dasyuridae: **Dasyurus maculatus*, **Sarcophilus* sp. indet.; Peramelidae: *Isaodon obesulus*; Phascogaleidae: *Phascogalea cinerea*; Vombatidae: *Vombatus ursinus*; Thylacoleonidae: *†*Thylacoleon carnifex*; Phalangeridae: *Trichosurus vulpecula*; Hypsiprymodontidae: *†*Propleopus uschilans*; Potoroidae: **Bettongia penicillata*; *Potorous* sp. cf. **P. tridactylus*; Macropodidae: *Macropus* sp. cf. *M. giganteus*, *†*M. greyi*, *M. rufogriseus*, *†*M. thom.*, *Macropus* sp. indet., *Protemnodon* sp. cf. *†*P. anak*, *†*Protemnodon* sp. indet., *†*Simosthenurus gilli*, *†*S. maddocki*, *S. newtonae*, *†*S. occidentalis*; *Wallabia bicolor*; Chiroptera: family indet.; Suidae: *Sus scrofa*; Bovidae: *Ovis aries*; Muridae: gen. et sp. indet.

Newton (1988') listed *Macropus rufus* for the deposit. However, no specimen can be located by the authors to support this identification, which appears unlikely. This species has therefore been omitted from the list. Newton (1988') also listed *†*Sthenurus stirlingi*, which was later found to be a misidentification (G. Prideaux pers. comm. 2000).

REFERENCES: Wells & Murray (1979); Pledge (1980a); Williams (1980); Baird (1985); Newton (1988'); Baird (1991a, b); Baird *et al.* (1991); Prideaux (1999', 2000); Flinders University palaeontology collection database; South Australian Museum palaeontology collection records.

38. WANDILO FOREST CAVE 5L365

LOCATION: Mount Gambier Forest, Forestry SA.

SITE DESCRIPTION: This small cave was discovered in 1997 by members of CEGSA. Numerous bones

were obvious on the surface of the floor sediment, and within the sediment cone. A small number of bones was collected by CEGSA and taken to the South Australian Museum for identification. The authors and M. C. McDowell visited the site with CEGSA in August 1998, when further identifications of some fossil material were made *in situ*.

Collection: South Australian Museum palaeontology collection (vertebrate fossils).

FAUNA:

MAMMALS

Phascolaretidae: *Phascolaretos cinereus*; Diprotodontidae: cf. ^{††}*Zygomaturus trilobus*; Vombatidae: *Vombatus ursinus*; Thylacoleonidae: ^{††}*Thylacoleon carnifex*; Potoroidae: [†]*Potorous tridactylus*; Macropodidae: *Macropus giganteus*, *M. rufogriseus*, ^{††}*Procoptodon* sp. indet., ^{††}*Simosthenurus browni*.
REFERENCES: Reed (1998); South Australian Museum palaeontology collection records.

39. WANDILO CAVE 5L74

LOCATION: Mount Gambier Forest, Forestry SA.

SITE DESCRIPTION: Bone material was collected by cavers during exploration in 1992 and taken to the South Australian Museum.

COLLECTION: South Australian Museum palaeontology collection (vertebrate fossils).

FAUNA:

MAMMALS

Vombatidae: *Vombatus ursinus*; Phalangeridae: *Trichosurus vulpecula*; Macropodidae: *Macropus* sp. cf. *M. giganteus*, *Macropus* sp. cf. *M. rufogriseus*, ^{††}*Simosthenurus maddocki*, ^{††}*S. occidentalis*.
South Australian Museum palaeontology collection records.

40. MOORAK

LOCATION: 5 km south of Mount Gambier.

SITE DESCRIPTION: Probable cave deposit, context unknown.

COLLECTION: South Australian Museum palaeontology collection (vertebrate fossils).

FAUNA:

MAMMALS

Thylacoleonidae: ^{††}*Thylacoleon carnifex*. Macropodidae: *Macropus giganteus*, *Macropus* sp. indet., ^{††}*Simosthenurus pales*.
REFERENCES: Pledge (1977); Williams (1980); South Australian Museum palaeontology collection records.

41. KILSBY'S HOLE 5L46

LOCATION: 5 km south west of Mount Gambier.

SITE DESCRIPTION: Bone material was found in the fill from a small solution tube exposed by excavation in 1988, of a ramp to the water level in the sinkhole.
COLLECTION: South Australian Museum palaeontology collection (vertebrate fossils).

FAUNA:

MAMMALS

Tachyglossidae: *Megalibgwilia* sp. cf. ^{††}*M. ramsayi*; Thylacnidae: ^{††}*Thylacinus cynocephalus*; Dasyuridae: [†]*Dasyurus maculatus*, [†]*Sarcophilus* sp. indet.; Peramelidae: *Isodon obesulus*, [†]*Perameles bougainville*, [†]*P. gunni*; Phascolaretidae: *Phascolaretos cinereus*; Diprotodontidae: ^{††}*Zygomaturus trilobus*; Vombatidae: *Vombatus ursinus*; Thylacoleonidae: ^{††}*Thylacoleon carnifex*; Phalangeridae: *Trichosurus vulpecula*; Potoroidae: [†]*Bettongia lesueur*, [†]*Potorous tridactylus*; Macropodidae: ^{††}*Lagorchestes leporides*, *Macropus* sp. indet., ^{††}*Protemnodon* sp. indet., ^{††}*Simosthenurus gilli*, ^{††}*S. newtonae*, ^{††}*S. occidentalis*, ^{††}*S. pales*, ^{††}*S. sthenurus andersoni*; Burramyidae: *Cercartetus* sp. cf. *C. nanus*; Pseudocheiridae: *Pseudocheirus peregrinus*; Chiroptera: family indet.; Canidae: *Canis lupus familiaris*; Bovidae: *Ovis aries*; Muridae: ^{††}*Conurus albipes*, [†]*Mastacomys fuscus*, *Rattus* sp. indet.; Leporidae: *Oryctolagus cuniculus*.
REFERENCES: McNamara (1997); South Australian Museum palaeontology collection records.

42. SIMPSON'S HOLE 5L42 (also known as Ten-eighly Sinkhole)

LOCATION: Near Mount Gambier.

SITE DESCRIPTION: Bones discovered by divers in the flooded section of the cave.

COLLECTION: Flinders University vertebrate palaeontology collection.

FAUNA:

MAMMALS

Diprotodontidae: ^{††}*Diprotodon* sp. indet.; Macropodidae: *Macropus* sp. indet., ^{††}*Protemnodon roechus*.
REFERENCES: Flinders University palaeontology collection database.

43. GOULDENS HOLE 5L8 (also known as Gouldens Hole Cave)

LOCATION: Several kilometres west of Mt Schank.

SITE DESCRIPTION: A small tunnel on SSE side of the cenote (Gouldens Hole), was uncovered by a farmer digging an access ramp to the water. The tunnel floor was covered with silt containing fossil material and bones of modern vertebrates. The site was excavated by researchers from the South Australian Museum in 1982. Pledge (1991) suggests that the bones were probably derived from a filled entrance further up-slope in the tunnel, and reached the lower extremity of the tunnel by water-

[†] REED, E. H. (1998) A "pressing" engagement with some sortously good fossils at 5L362, Wandilo Cave Exploration Group of South Australia News, 43, 103-104.

winnowing. He describes it as a "reworked, mixed assemblage" (Pledge 1991).

COLLECTION: South Australian Museum palaeontology collection (vertebrate fossils).

FAUNA:

REPTILES

Family indet.

BIRDS

Phalacrocoracidae: *Phalacrocorax melanoleucus*; Accipitridae: *Aquila audax*.

MAMMALS

Tachyglossidae: *Megalibgwila* sp. cf. *†*M. ramsayi*; *Tachyglossus aculeatus*; Thylacimidae: **†*Thylacinus cynocephalus*; Dasyuridae: **Dasyurus maculatus*; †*Dasyurus* sp. indet., *†*Sarcophilus* sp. indet.; Peramelidae: *Isodon* sp. cf. *I. obesulus*, *Perameles* sp. cf. *†*P. gunii*; Phascolarctidae: *Phascolarctos cinereus*; Palorchestidae: *Palorchestes* sp. cf. *†*P. parvus*; Vombatidae: *Vombatus ursinus*; Thylacoleonidae: *†*Thylacoleo carnifex*; Phalangeridae: *Trichosurus vulpecula*; Potoroidae: *†*Bettongia gaimardi*, *†*Potorous tridactylus*; Macropodidae: *Macropus giganteus*, *M. rufogriseus*, *†*M. titan*, *Macropus* sp. indet., *†*Protemnodon brehms*, *†*P. roechus*, *†*Simosthenurus gilli*, *†*S. maddocki*, *†*S. newtonae*, *†*S. occidentalis*, *†*Sthenurus andersoni*, *Wallabia bicolor*; Pseudocheiridae: *Pseudocheirus peregrinus*; Canidae: *Canis lupus familiaris*, *Valpes vulpes*; Felidae: *Felis catus*; Bovidae: *Ovis arvensis*; Muridae: *†*Mastacomys fuscus*, gen. et sp. indet.
REFERENCES: Pledge (1991); Baird (1991b); Baird *et al.* (1991); South Australian Museum palaeontology collection records.

44. TANKSTAND CAVE 5L65

LOCATION: 3 km west of Mt Schank.

SITE DESCRIPTION: Bone material was collected from the drowned part of cave, situation unknown.

COLLECTION: South Australian Museum palaeontology collection (vertebrate fossils).

FAUNA:

MAMMALS

Macropodidae: *†*Simosthenurus gilli*.

REFERENCES: Williams (1980); South Australian Museum palaeontology collection records.

Mount Gambier Township

45. UN-NAMED CAVE

LOCATION: Derrington Street, Mount Gambier (town).

SITE DESCRIPTION: Cave exposed by earthworks for a sewer trench in 1963.

COLLECTION: South Australian Museum palaeontology collection (vertebrate fossils).

FAUNA:

MAMMALS

Peramelidae: *Perameles* sp. indet.; Phascolarctidae:

Phascolarctos sp. indet.; Diprotodontidae: *†*Zygomaturus trilobus* (= *Nototherium* of Williams 1980); Thylacoleonidae: **†*Thylacoleo carnifex*; Potoroidae: *†*Bettongia* sp. indet.; Macropodidae: *†*Simosthenurus browni*, *†*S. gilli*, *†*S. maddocki*, *†*Sthenurus andersoni*; Pseudocheiridae: *Pseudocheirus peregrinus*.

REFERENCES: Pledge (1977); Williams (1980); South Australian Museum palaeontology collection records.

46. UN-NAMED CAVE

LOCATION: Mount Gambier (town); other details unknown.

SITE DESCRIPTION: Unknown.

COLLECTION: Natural History Museum (London).

FAUNA:

BIRDS

Dromornithidae: *†*Genyornis* sp. indet.

REFERENCES: Stirling and Zietz (1896, 1900); Rich (1979); Williams (1980); Baird *et al.* (1991).

47. UN-NAMED CAVE

LOCATION: Grey Street, Mount Gambier (town).

SITE DESCRIPTION: Cave exposed by excavation.

COLLECTION: South Australian Museum palaeontology collection (vertebrate fossils).

FAUNA:

MAMMALS

Macropodidae: *†*Simosthenurus browni*, *†*S. gilli*.
REFERENCES: Williams (1980); South Australian Museum palaeontology collection records.

48. ENGELBRECHT CAVE 5L19

LOCATION: Jubilee Highway, Mount Gambier (town).

SITE DESCRIPTION: Bones have been recovered by divers in the flooded section of the current tourist cave. The bone material was identified by palaeontologists from Flinders University.

COLLECTION: Engelbrecht Cave management.

FAUNA:

MAMMALS

Vombatidae: *Vombatus ursinus*; Macropodidae: *Macropus* sp. cf. *M. giganteus*, *Protemnodon* sp. cf. *†*P. brehms*.

REFERENCES: None.

49. THE BLUE LAKE

LOCATION: Mount Gambier.

SITE DESCRIPTION: Bone material has been found in a solution cavity during excavation of an access tunnel at a depth of between 41 m and 42 m from the lower pump station entrance.

COLLECTION: South Australian Museum palaeontology collection (vertebrate fossils).

FAUNA:

MAMMALS

Macropodidae: †*Sinosthenurus* sp. indet.

REFERENCES: South Australian Museum palaeontology collection records.

Discussion

As the data presented above clearly demonstrate, the South East of South Australia holds a significant record of Pleistocene sites and vertebrate fossil faunas. The numerous cave systems and other sites in the region have accumulated vertebrate remains over an extended period of time and with increased palaeontological research in the region more sites are being discovered. Recent improvements in geochronological techniques have enabled researchers to concentrate on developing chronologies for several of the sites in the region, particularly those within the Naracoorte Caves World Heritage Area (Ayliffe & Veeh 1988; Ayliffe *et al.* 1998; Morjariy *et al.* 2000). Current taphonomic research being carried out on various deposits within the World Heritage Area and its surrounds is allowing us to piece together the accumulation history of many of these deposits and to determine their representativeness and suitability for use in palaeoecological reconstructions. Only with a thorough knowledge of the faunas, taphonomy, geology and chronologies of these sites can valid palaeoecological analyses be made.

The distributions of taxa between the sites are summarised in Table 3. The data reveal some interesting patterns in the faunas represented and the level of scientific attention that they have received. There has been very little research done on the amphibian fossils from the region since Tyler (1977, 1991) worked on material from cave sites at Naracoorte. There is now more material available and a review of this group could reveal more species. As all of the species listed by Tyler (1977, 1991) are still living in the region today, the frog assemblages could be very useful in palaeoecological reconstructions. The fossil reptile faunas have also received little attention since the 1970s, with the exception of the work of Barrie (1991), Williams (1999) and Scamlon & Lee (2000). The varanids, agamids and elapids all require further research.

The fossil bird faunas of the region have received some attention (Van Tets 1974; Van Tets & Smith 1974; Rich 1979; Baird 1985, 1991a, b; Baird *et al.* 1991; M. McDowell pers. comm. 2000) but further investigation of material recovered in recent years, particularly from the Naracoorte Caves World

Heritage Area, is required as it may reveal more species. Baird (1985, 1991a) did extensive work on avian taphonomy and described different modes of accumulation for bird remains. A comparison between sites, particularly the Main Fossil Chamber in the Victoria Fossil Cave (site 4) and Green Waterhole Cave (site 37) which have the largest fossil bird assemblages from the region, reveals quite different species compositions, probably related to different accumulation modes. Further research on the bird faunas may reveal some other interesting taphonomic biases.

Some research has been carried out on the fossil small mammal faunas of the region (Smith 1971, 1972; M. McDowell pers. comm. 1999, 2000; A. Baynes pers. comm. 2000). Recent work in Wei Cave (site 8) and Robertson Cave (site 10) (M. McDowell pers. comm. 2000) reveals assemblages composed primarily of small mammals (see Table 3), perhaps derived mainly from owl pellets rather than a pitfall trap, which has been suggested as the main mode of accumulation in many other cave sites.

Re-investigation of some of the fossil small mammal material may be required to confirm some identifications. One example is the fossil *Antechinus* material. Four species of *Antechinus* have been identified in Pleistocene faunas from the South East (Table 3); of these species, *A. flavipes* and *A. minimus* are still living in the region (Strahan 1995; Robinson *et al.* 2000). Two species, †*A. stuartii* (see Systematics section) and †*A. swainsonii*, are not found in the South East today (Strahan 1995, Robinson *et al.* 2000), and are only listed for one Pleistocene site (site 4a) in the region, as is *A. minimus* (site 2). These four species may have been part of a more diverse fauna during the Pleistocene or alternatively, one or more of these may represent misidentification. The fossil *Antechinus* material from the South East needs further work to resolve such issues. Another group that has been very little studied is the fossil bats. There are currently around 11 species living in the region (Robinson *et al.* 2000), of which at least five are known to inhabit caves, yet only two species (*Myotis schreibersi* and *Nyctophilus geoffroyi*) have so far been identified from fossil deposits (see Table 3). As owls are still active predators of bats in the region and have been accumulators of small mammal remains in the past, a more intensive study of the plentiful fossil small mammal material (particularly from the Naracoorte Caves World Heritage Area) should reveal more bat species.

The fossil large mammals (>5 kg live weight) have received more attention than other groups in the region (Daily 1960; Merrilees 1965; Pledge 1977, 1980a, c, 1990, 1991; Murray 1978; Wells & Murray 1979; Wells *et al.* 1984; Flannery & Pledge 1987,

WELLS, M. C. (1999) Fossil faunal identification methods. A case study of birds. *Lepidoptera* species, BSc (Hons) Thesis, The University of Adelaide, computer.

Griffiths *et al.* 1991; McNamara 1994; Brown 1998; Pridéaux & Wells 1998; Pridéaux 1999^a, 2000; Turner 1999^b). The sites of the South East contain a rich record of the extinct megafauna, particularly the sthenurine kangaroos (Merrilees 1965; Wells & Murray 1979; Pledge 1980a; Pridéaux & Wells 1998; Pridéaux 1999^a, 2000). The macropodids are the dominant group with 26 species represented; of these 16 became extinct during the Pleistocene, three totally extinct following European settlement and three locally extinct (Table 3). Currently there are only four species found in the region (Robinson *et al.* 2000). The large diprotodontids are sparsely represented in the deposits with **Zygomaturus trilobus* the most commonly found (recorded in 15 sites). Palorchestids are particularly rare. These may represent real abundances in the ancient faunas or taphonomic biases related to the modes of accumulation. Of the large mammalian carnivores, **Thylacoleo carnifex* is well represented in the region (recorded in 23 sites), **Thylacinus cynocephalus* moderately well represented (19 sites) and the devils (*Sarcophilus* spp.) represented in 17 sites (Table 3).

Material representing species for which there is only a single record from the region may require careful re-investigation to ensure that the identifications are correct (see the note regarding **Dorcereus criniticauda* and **Perameles nasuta* for site 4a). However, single specimens of **Congruus congruus* (McNamara 1994) and **Warendia wakefulhi* (Flannery & Pledge 1987), indicate such records can be reliable. McNamara (1997) has also highlighted the need for re-investigation of some material with his work on the small macropodids of South Australia. Closer examination of the wealth of fossil material from the South East has the potential for resolving other issues such as the taxonomic status of the devils (**Sarcophilus harrisi* and **S. lanianus*), and the question of whether these represent distinct species or sub-species, or the extant species represents a dwarfed form of the larger **S. lanianus* (Marshall & Corruccini 1978; Dawson 1982; Werdelin 1987). Both have been recorded from sites in the South East. Similarly, the distinction between the koalas *Phascolarctus chlorurus* and **P. stirtoni* has been the topic of discussion (Archer & Hand 1987), and both species are listed for Pleistocene sites of the South East.

Collection biases can be reduced by employing thorough excavation methods and reducing the number of specimens simply collected from sites without regard to provenance. Examination of the data summarised in Table 3 reveals a great number of sites with practically no record of amphibian, reptile, bird or small mammal species, and this may be related to collection biases where mainly large bone

material has been collected. Exceptions to this are sites where recovery of small specimens is difficult (e.g. Green Waterhole Cave and swamp sites).

An interesting feature of the South East is the variation in the 'types' of sites (e.g. caves, sinkholes and swamps) within the region. All of the Pleistocene sites in the Naracoorte area, and much of the Upper South East, are cave sites. Swamp sites are found in the Penola and Millicent areas. The Mount Gambier area has cave sites, but also has sinkholes which are unique to this area and are not found in the Upper South East. Obviously the type and morphological features of a site have a direct influence on the species represented in the deposit and this highlights the importance of taphonomic research.

Within the South East region there has been a bias towards sites of the Upper South East, particularly the sites around Naracoorte. This is probably due to the much higher level of research and exploration conducted in this area. Thus, further investigation of the Lower South East region is an important next step to understanding the vertebrate palaeontology of the region as a whole.

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A MIDDLE PLEISTOCENE VERTEBRATE FOSSIL ASSEMBLAGE FROM CATHEDRAL CAVE, NARACOORTE, SOUTH AUSTRALIA

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Located in the Naracoorte Caves Conservation Park, Cathedral Cave represents one of the more fossil-rich vertebrate sites within the region. An analysis of the geology and palaeontology of the fossil assemblage, coupled with U-series dating, has enabled a reconstruction of both the accumulation modes and the proximal environment between about 280,000 and 160,000 years ago, during the Middle Pleistocene. A pitfall trap is suggested as the primary mechanism for collecting animals whose remains became incorporated in the deposit. The fauna indicates an environment dominated by large herbivores inhabiting a grassy open forest or woodland with little suggestion of aridity.

Key Words: Naracoorte, Cathedral Cave, fossil assemblage, U-series dating, taphonomy, Middle Pleistocene, pitfall trap.

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Introduction

The Oligo-Miocene limestone (Naracoorte Member of the Gambier Limestone) underlying much of the Naracoorte region contains an extensive system of caves well known for their fossil content. The best studied are the richly fossiliferous deposits in Victoria Fossil Cave (e.g. Smith 1971, 1972, 1976; Van Tets & Smith 1974; Wells 1975; Tyler 1977; Wells *et al.* 1984). However, little is known about the fossil content of other caves in the region. Ongoing geochronological and palaeontological research (Ayliffe & Veeh 1988; Ayliffe *et al.* 1998; Moriarty *et al.* 2000) has encompassed many 'new' fossiliferous cave sites. The Fossil Chamber in Cathedral Cave is one such site (Fig. 1). The present study presents a detailed geological, taphonomic and faunal analysis of the Cathedral Cave fossil deposit.

Materials and Methods

Geology: stratigraphy and sedimentology

A survey datum was established on a limestone block in close proximity to the sediment cone in the fossil Chamber (Fig. 2). The sediment fill was systematically probed with a 1 m long 10 mm diameter rod to locate subsurface limestone blocks. A 75 mm diameter soil auger was then used to sample the sediment to a depth of 2 m avoiding the buried blocks. Auger holes were spaced at 5 m

intervals across the sediment fill. Each bore hole was sampled at 10 cm increments and a subsurface stratigraphy constructed. All depths to datum were measured. A sample of sediment from each 10 cm interval was placed into a clear snap-lock plastic bag and labelled with the auger hole location and depth. Samples were returned to The Flinders University of South Australia and scored for sediment colour (Munsell colour charts), clay content, calcium carbonate content, grain size and sorting (following the procedures of Day 1965), and grain morphology (McCullough sand gauge).

Palaeontology

Access to the Fossil Chamber was via a dug crawlway approximately 120 m in length (Fig. 1). Excavation of fossiliferous sediments was carried out over a three-month period to April 1998. Two pits were excavated within the Fossil Chamber (Fig. 2). The first (Pit A) measured 2.8 m x 1.5 m x 0.76 m and the second (Pit B) measured 2.6 m x 2.1 m x 1.04 m.

Sediment was carefully excavated along the bedding planes using trowels, dental picks and brushes. Exposed fossils were left *in situ* while the following data were collected; the depth below, distance to, and direction from datum; the dip and bearing of the specimens. A sighting compass, tape measure and a line level were used to accomplish this. Specimens were then removed from the sediments and transported to the laboratory where they were cleaned and stabilised with a polyvinyl butyrate (Mowital[®], Hoechst). Due to the difficulty of removing sediment from the cave it was dry screened on site using 5 mm mesh sieves.

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Taphonomic analysis

Each specimen was identified where possible to species or genus and element type. It was then examined for breakage pattern, presence of predator marks, abrasions, weathering and any other noticeable surface modifications (root etching, burning, colour alteration). Breakage patterns were

classified as irregular perpendicular, crenulated, spiral and compression following Lyman (1994) and Marshall (1989). Characterisation of weathering stages follows Behrensmeyer (1978).

Following Andrews (1990), all large mammal skeletal elements were counted (N_i) and their relative abundance (R_i) calculated. The relative

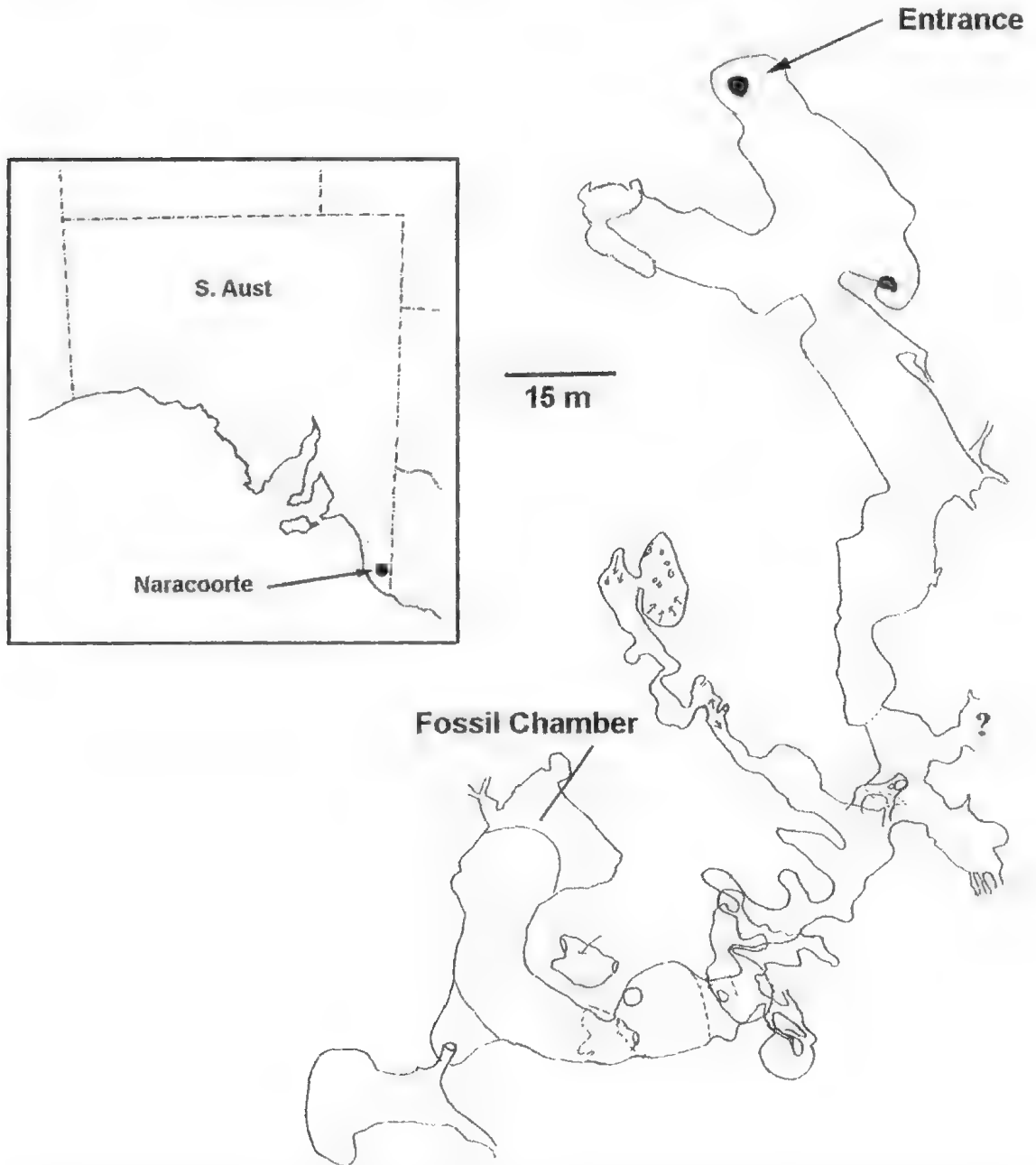


Fig. 1. Map of Cathedral Cave, Naracoorte, showing the position of the study site. Modified from Cave Exploration Group of South Australia surveyed map of Cathedral Cave.

abundance counts were based on the relationship between the N_i , the expected numbers of each element (E_i) within a complete skeleton, and the minimum number of individuals (MNI). This is summarised as:

$$Ri \% = \frac{N_i}{(MNI)(E_i)} \times 100$$

The MNI was produced by summing the most abundant skeletal element referable to the taxon in question and dividing this by the number represented in a complete skeleton. These results were then totalled to give an overall large mammal MNI. Species MNI were based primarily on the number of craniodental specimens, as these contain the species-specific characters, while MNI values for genera were based on elements, usually post-cranial, which could not be identified to species level. E_i was calculated by multiplying the MNI by the number of each element type present in a complete skeleton. The Red Kangaroo, *Macropus rufus* (Desmarest, 1922) was used as the comparator skeleton for E_i calculations. To enhance accuracy, caudal vertebrae were excluded from these calculations, as there is considerable variation in the number of tail vertebrae between species.

Results

Cave sediments

Sediments accumulated as a simple cone beneath a

solitary roof entrance now choked with sediment, limestone blocks and calcite formation. Within the cone, four sedimentary units were easily identified (designated 1, 2, 3 and 4) on the basis of colour. All units consist of quartz sands with variable quantities of admixed clay (Table 1). Carbonaceous material is abundant in Units 1 and 2, sparse in Unit 3 and absent from Unit 4. Vertebrate fossils were recovered from all units with the exception of Unit 4. Units 1, 2 and 4 are continuous throughout the Fossil Chamber. Unit 3 is restricted to the distal regions of the sediment cone. All sediments have similar characteristics of grain size (Fig. 3) and shape, and clay content. Sediment colour was unique for each unit.

Geochronology

Three U-series dates on calcite deposits interlayered with the fossiliferous sediments in Cathedral Cave were reported by Ayliffe *et al.* (1998). These ages along with an additional date (CCFC FS-4) obtained during this study are presented in Table 2. A small quantity of bone was found deposited within the flowstone structure (CCFC FS-2) dated at 159.2 ± 2.2 ka. A flowstone (CCFC FS-3) dated at 279.2 ± 7.2 ka lies below Unit 3 while overlying Unit 4. The stratigraphic relationship between the sedimentary units and the dated flowstones is shown in Fig. 2.

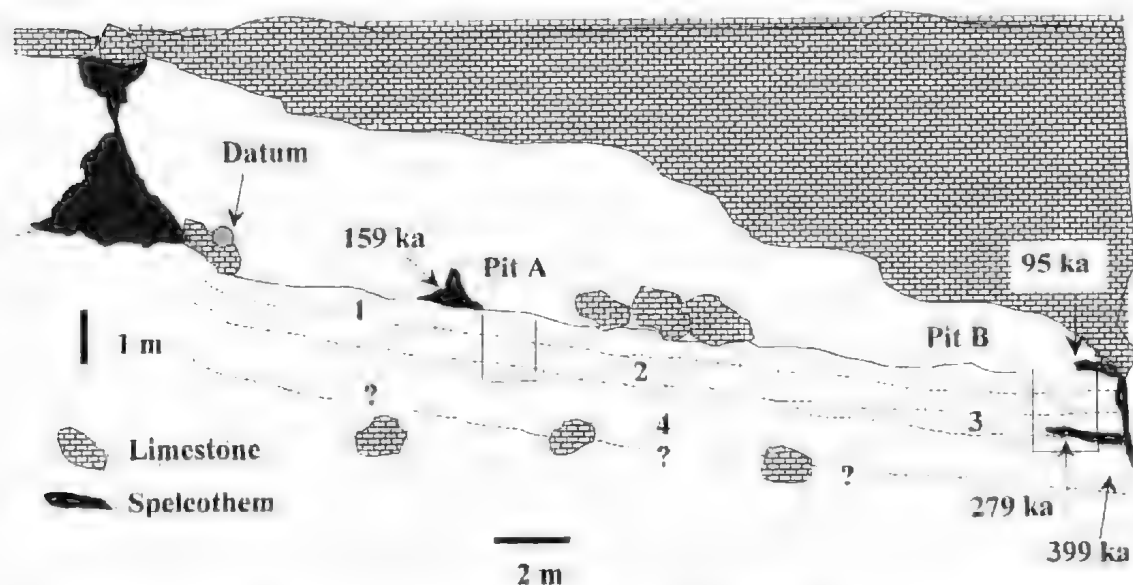


Fig. 2 Section of the Cathedral Cave Fossil Chamber showing the stratigraphy, dated speleothems, the position of the excavation pits and the location of the datum. Vertebrate fossils were recovered from sedimentary Units 1, 2 and 3.

Palaeontology

ASSOCIATION AND ARTICULATION

During excavation it was evident that some bones were either in association or articulation.

All of the associated specimens were from either extinct (*Procoptodon*, *Sthenurus*) or extant (*Macropus*) species of kangaroos. Based on MNJ calculations, parts of five (3 *Sthenurus* spp., 1 *Procoptodon* sp. and 1 *Macropus* sp.) individuals were found in association representing 2.8% of the total number of specimens recovered.

Figure 4 shows an articulated specimen *in situ*. Articulated material represented 1.6% of the total number of specimens recovered. Articulated

specimens include both extinct (*Sthenurus gilli* Merrilees, 1965, one individual) and extant (*Macropus* sp., one individual) kangaroos and an extant bandicoot (*Isodon* sp., one individual). The discovery of the articulated partial skeleton of *S. gilli* is the first ever recovered and will be described elsewhere. The articulated bandicoot skeleton was encased within a mass of calcite. The arrangement of its bones was not consistent with an owl pellet.

BREAKAGE PATTERNS

Figure 5 shows the distribution of breakage patterns for the total fossil assemblage.

TABLE 1. Characteristics of sedimentary units within the Cathedral Cave Fossil Chamber.

Unit No.	Clay %	CaCO ₃ %	Sand %	Sediment colour Munsell	Sand colour Munsell	Grain shape
1	8.7	5	86.3	Yellowish red 5YR5/8	Reddish yellow 5YR6/8	SR-SA
2	6.5	7.1	86.4	Dark red 2.5YR4/8	Yellowish red 5YR5/8	SR-SA
3	8.2	3	88.8	Reddish yellow 5YR6/8	Very pale brown 10YR8/2	SR-SA
4	8.9	2.3	88.8	Very pale brown 10YR8/4	Very pale brown 10YR8/3	SR-SA

Sand colour refers to the colour of dry sediment after removal of the clays.

Grain shape: SA = sub-angular; SR = sub-rounded.

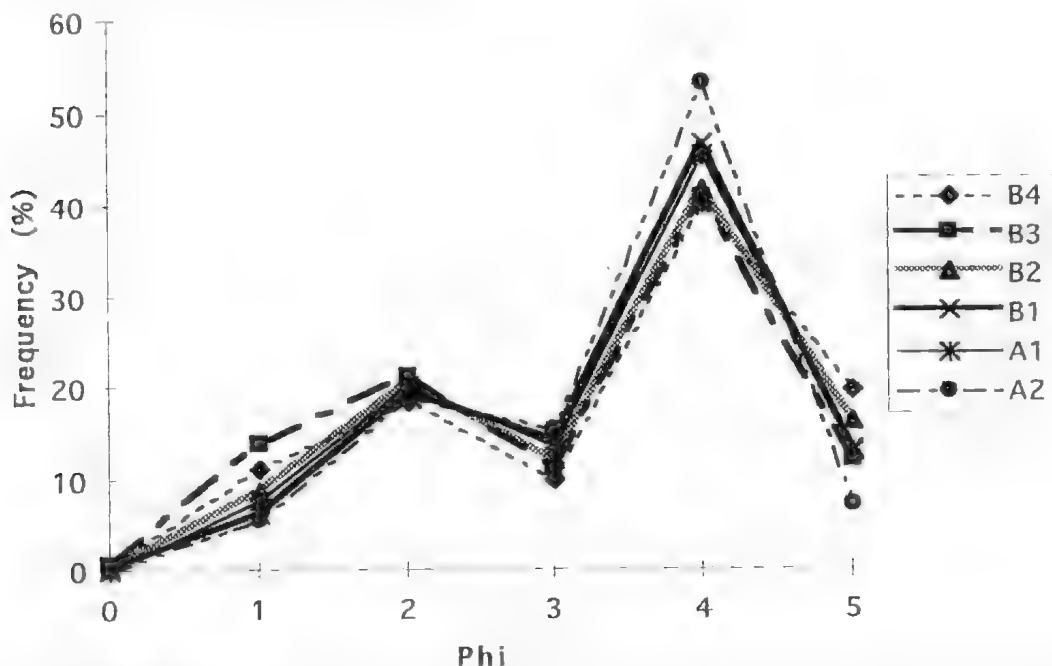


Fig. 3. Grain size distribution of all sediment units from the Cathedral Cave Fossil Chamber. Alphabetical prefixes refer to excavation pit and the sediment unit number follows

TABLE 2. Summary of *U/Th* dates on calcite deposits in Cathedral Cave Fossil Chamber.

Code number	Date (ka)	Comments
CC FC FS-4	95.2 ± 1.3	Overlies Units 1, 2 and 3, Pit B.
CC FC FS-2	159.2 ± 2.2	Overlying all sedimentary units; provides minimum age of fauna; sediment influx ceases
CC FC FS-3	279.2 ± 7.2	Underlies fossil bearing sediments; gives maximum age for Units 1, 2 and 3
CC FC St-1	399 ± 19	Provides absolute maximum age of fauna

Dates and sample code numbers from Ayliffe *et al.* (1998) and Ayliffe (pers. comm. 1998). Code number abbreviations: CC, Cathedral Cave; FC, Fossil Chamber; FS, flowstone; St, stalactite.

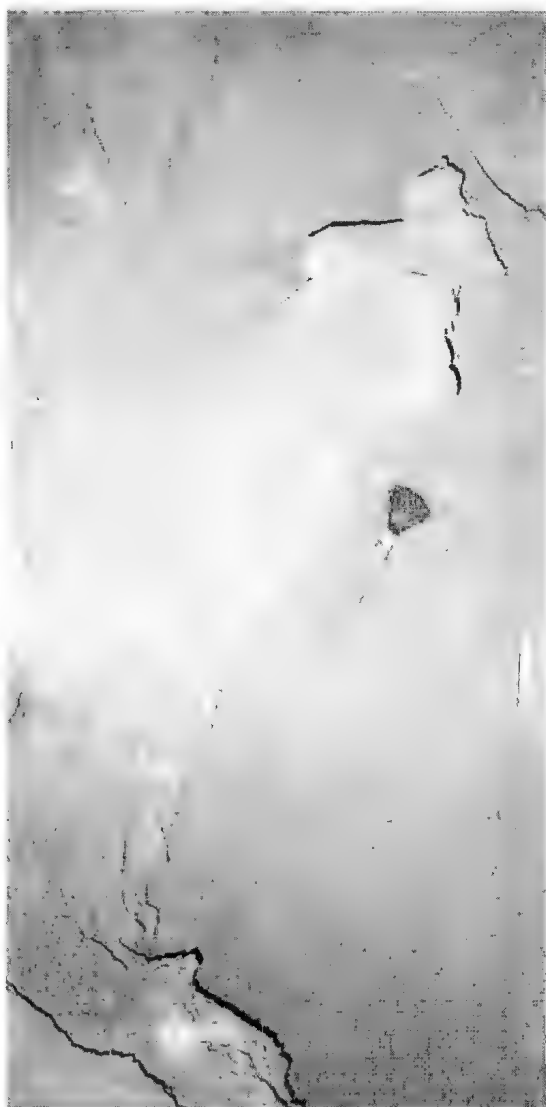


Fig. 4. An example of one of the articulated specimens *in situ* in the Cathedral Cave fossil deposit. This large macropodine vertebral column (cervical to sacral vertebrae) including some pelvic elements, was retrieved intact. Scale bar = 10 cm.

Approximately half of all specimens collected (48%) were entire (i.e. no breakage); another 25% showed evidence of clean recent breakage during excavation and/or removal. The remainder showed breakage patterns of more ancient origin that included irregular perpendicular (22.5%), crenulated (2.3%), spiral fracture (1.4%) and compression (0.8%). The majority of compression fractured specimens were concentrated in the lower Unit 3.

PREDATION AND SCAVENGING

Bone damage caused by predation or scavenging (including surface markings such as puncture wounds and crenulated gnaw damage) was evident on 2.5% of specimens. Predation or scavenging damage was restricted to bones of kangaroos of the genus *Macropus* with an estimated body mass of less than 60 kg. None of the very large extinct marsupial species (e.g. *Zygomaturus*, *Procoptodon*) exhibited predator damage.

SURFACE FEATURES

Few specimens from the Cathedral Cave fossil assemblage showed evidence of burning. Burning is commonly recognised by the carbonisation of the bone collagen, discolouring the bone to black (charring) or producing a chalky white texture from prolonged exposure to high temperatures (calcination) (Brain 1981).

A few long bone fragments had a uniform deep brown surface discoloration that in places penetrated into the cancellous core. Specimens from swamp sites such as Rocky River on Kangaroo Island show similar discoloration.

No evidence of root etchings or abrasions was found on any specimen from the fossil sample. Some 'pseudo-abrasion' patterns were observed (i.e. abraded cancellous bone), but these were interpreted as preparation damage.

Few specimens showed evidence of sub-aerial weathering. Figure 6 shows the frequency distribution of bone weathering with the vast majority of specimens categorised as weathering stage 0.

SKELETAL ELEMENT ABUNDANCES

The skeletal element abundances for large mammals from each fossiliferous sedimentary unit in each pit are presented in Table 3. On average, the relative abundances (mean Ri%) of skeletal elements representing large mammals are between 4.3% and 6.3%. The highest relative abundance values are for mandibles (mean of 19.6%), femora (11.1%) and tibiae (12.4%). The lowest mean relative abundance

values obtained are for phalanges (0.7%), carpals (0.6%) and metacarpals (0.2%). Although the absolute numbers of vertebrae and ribs are the highest for most units, their relative abundances are close to the mean.

SPECIES MNI

Tables 4 and 5 show the MNI values for each species identified from the Cathedral Cave fossil

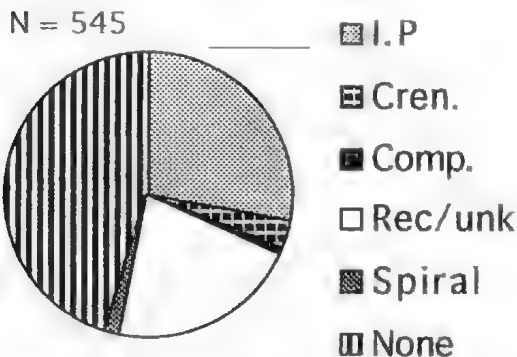


Fig. 5. Distribution of the various breakage patterns observed on the entire Cathedral Cave fossil sample (N = 545). Abbreviations: I. P., irregular perpendicular; Cren., crenulated; Comp., compression; Rec./unk., recent (post depositional) or unknown damage.

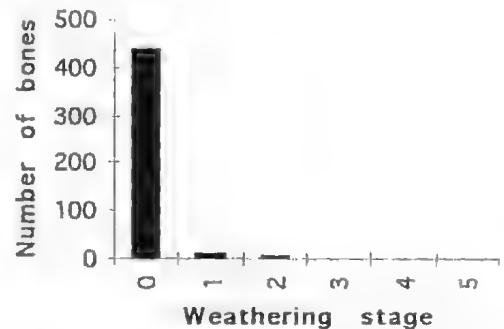


Fig. 6. Frequency distribution of specimens displaying characteristics of the various weathering stages (following Behrensmeier 1978) from the Cathedral Cave fossil assemblage.

TABLE 3. Large mammal skeletal element abundance (No.) and relative abundance (Ri%) from both excavation pits and all fossiliferous sedimentary units in the Cathedral Cave Fossil Chamber, Naracoorte.

Element	B 3		B 2		A 2		B 1		A 1		Mean Ri%
	No.	Ri%	No.	Ri%	No.	Ri%	No.	Ri%	No.	Ri%	
Skulls	4	12.1	3	7.5	1	7.7	1	11.1	0	0.0	7.7
Maxillae	4	6.1	11	13.8	1	3.8	1	5.6	0	0.0	5.9
Mandibles	13	19.7	22	27.5	4	15.3	3	16.7	3	18.8	19.6
Individual teeth	9	0.8	6	0.4	13	2.9	0	0.0	5	1.8	1.2
Vertebrae	46	5.2	61	5.6	19	5.4	13	5.3	18	8.3	6.0
Ribs	24	2.8	21	2.0	10	3.0	3	1.3	12	5.8	3.0
Scapulae	4	6.1	1	1.3	0	0.0	1	5.5	1	6.3	3.8
Humeri	3	4.5	4	5.0	1	3.8	1	5.5	1	6.3	5.0
Radius	3	4.5	3	3.8	2	7.7	0	0.0	3	18.8	7.0
Ulnae	1	1.5	4	5.0	1	3.8	2	11.1	1	6.3	5.5
Carpals	0	0.0	0	0.0	1	0.5	0	0.0	3	2.7	0.6
Metacarpals	0	0.0	0	0.0	1	0.8	0	0.0	0	0.0	0.2
Pelvic elements	13	4.9	9	3.8	3	2.9	3	4.2	1	1.6	3.5
Femora	16	24.2	9	11.3	2	7.7	0	0.0	2	12.5	11.1
Tibiae	11	16.7	6	7.5	1	3.8	5	27.8	1	6.3	12.4
Fibulae	2	3.0	1	1.3	1	3.8	2	11.1	1	6.3	5.1
Tarsals	10	2.2	7	1.3	5	2.7	0	0.0	3	2.7	1.8
Metatarsals	13	4.9	16	5.0	5	4.8	0	0.0	1	1.6	3.3
Phalanges	12	0.7	12	0.6	8	1.1	2	0.4	4	0.9	0.7
Totals	188		196		79		37		60		
Mean Ri%		6.3		5.4		4.3		5.6		5.6	

assemblage. A total of 103 large mammal and 107 small vertebrate individuals is represented by the fossil collection. The most common species was the Eastern Grey Kangaroo, *Macropus giganteus* (Shaw, 1789). In total, kangaroos of the sub-family Macropodinae are the most frequently represented species (49.5%), followed by those of the extinct Sthenurinae (37.9%). The most prevalent small mammal species were rodents.

SPECIES ABUNDANCES

Figure 7 shows the proportions of each large mammal species within the entire fossil sample based on MNI values. Herbivores are represented by 97.1% of all large mammal fossils. Approximately half (51.5%) of herbivores in the deposit are extant kangaroo species of the genera *Macropus* and *Wallabia*. *Macropus* spp. dominate the grazing niche, while the extinct sthenurine kangaroos (37.4%) along with *Wallabia bicolor* (Desmarest, 1804) make up the majority of browsing herbivores. Large carnivores make up only 3% of the total fauna.

BODY MASS DISTRIBUTION

Figure 8 displays the body mass distribution for large mammals (>5 kg). Body mass estimates were obtained from Calaby (1995), Jones (1995), Lee & Ward (1989), Merchant (1995), Murray (1984, 1991), Poole (1995), Rounsevell & Mooney (1995), Wells (1995) and Wroe *et al.* (1999) using maximum male weights. The large mammal distribution shows a high frequency of individuals weighing between 5 and 20 kg and between 40 and 60 kg. Very few very large individuals (>100 kg) are represented in the fossil deposit.

MAMMAL HABITATS

Table 6 shows the preferred or inferred habitats of all the mammal species represented in the Cathedral Cave fossil assemblage. The majority of species inhabited an open forest or woodland environment. Some species are known to occupy a wide range of present day habitats and, consequently, are less informative. *Zygomaturus trilobus* (Macleay, 1858) has been suggested by Murray (1984) to have

TABLE 4. Minimum number of individuals (MNI) for large mammals from all fossiliferous sedimentary units, Cathedral Cave, Naracoorte.

Pit Unit	A	A	B	B	B
	1	2	1	2	3
<i>Thylacinus cynocephalus</i>				1	
Total Thylacinidae MNI				1	
<i>Lasiorchinus latifrons</i>		1			1
Vombatidae Indet.			1		1
Total Vombatidae MNI		1	1		2
<i>Macropus giganteus</i>	2	3	4	10	1
<i>Macropus rufogriseus</i>		1		2	5
<i>Macropus</i> sp. Indet.	1	3	1	10	6
<i>Wallabia bicolor</i>					2
Total Macropodinae MNI	3	7	5	22	14
<i>Sthenurus gilli</i>	1	1		5	5
<i>Sthenurus browni</i>	1	1		2	1
<i>Sthenurus occidentalis</i>				2	1
<i>Sthenurus</i> sp. Indet.	2	2	2	5	6
<i>Procoptodon goliath</i>				1	1
Total Sthenurinae MNI	4	4	2	15	14
<i>Zygomaturus trilobus</i>	1	1	1	1	1
Total Zygomaturinae MNI	1	1	1	1	1
<i>Phylacoleo carnifex</i>				1	1
Total Phylacoleonidae MNI				1	1
Total No. extinct species	4	4	2	8	8
Total No. extant species	2	4	3	3	5
Total No. species	6	8	5	11	13
Total MNI extinct species	5	5	3	18	17
Total MNI extant species	3	8	6	22	16
Total MNI	8	13	9	40	33

N.B. *Sarcophilus harrisi* is present in the assemblage but was recovered during a previous excavation and the stratigraphic origin is unknown.

inhabited wetlands, such as swamps or billabongs and its diet may have included vegetation growing along the banks of water holes.

Discussion

Geology

Cathedral Cave lies within the Naracoorte East Dune which contains a series of potential sediment sources for cave fills, including Pleistocene beach-dune, estuarine-

lagoonal and lacustrine facies, and Pliocene marine and fluvio-lacustrine facies (Cook *et al.* 1977; Grimes 1994). These sandy facies, individually or in a combination, are a likely source for the Cathedral Cave sediments, although soil formation, leaching and/or mixing makes it difficult to establish firmly sediment provenance.

The sedimentary units within the Fossil Chamber appear to be continuous between excavation pits with the exception of Unit 3. No distinction between sedimentary

TABLE 5. Minimum number of individuals (MNI) for small mammals, reptiles, amphibians and birds from all fossiliferous sedimentary units, Cathedral Cave, Naracoorte. Indeterminate family or class individuals were not included in total extinct/extant species calculations.

Pit	A	A	B	B	B
Unit	1	2	1	2	3
<i>Sminthopsis murina</i>		1			
<i>Antechinus flavipes</i>			1		
<i>Antechinus</i> sp. Indet.		1		1	
<i>Phascogale calura</i>		1	1	1	
<i>Dasyurus viverrinus</i>	1	1			
<i>Dasyurus maculatus</i>			1		
Total Dasyuridae MNI	1	4	3	2	
<i>Perameles bougainville</i>	3		1		
<i>Perameles gunnii</i>	2	2		1	
<i>Perameles</i> sp. Indet.	6	1	1	3	
Peramelidae Indet.	3	5		1	1
Total Peramelidae MNI	15	8	2	4	1
<i>Cercartetus nanus</i>		1			
Total Phalangeridae MNI		1			
<i>Bettongia penicillata</i>	1	1		1	
<i>Potorous platyops</i>	2			2	1
<i>Potorous tridactylus</i>					1
<i>Bettongia</i> sp. Indet.		1		1	
Total Potoroidae MNI	3	2		4	2
<i>Mastacomys fuscus</i>	8	3	4	5	1
<i>Pseudomys australis</i>	5	1		8	
<i>Pseudomys shortridgi</i>	1				
<i>Notomys mitchelli</i>		1		2	
<i>Pseudomys</i> sp.	2				
Total Muridae MNI	16	5	4	14	1
Aves Indet.	3	1	3		1
Total Aves MNI	3	1	3		1
<i>Liliqua rugosa</i>	2	1		1	
Total Reptilia MNI	2	1		1	
<i>Limnodynastes</i> sp. Indet.	2	1			
Total Leptodactylidae MNI	2	1			
Total No. extinct species	1	0	0	1	1
Total No. extant species	21	14	6	10	2
Total No. species	22	14	6	11	3
Total MNI extinct species	2	0	2	1	
Total MNI extant species	36	17	9	23	3
Total MNI	42	23	12	25	5

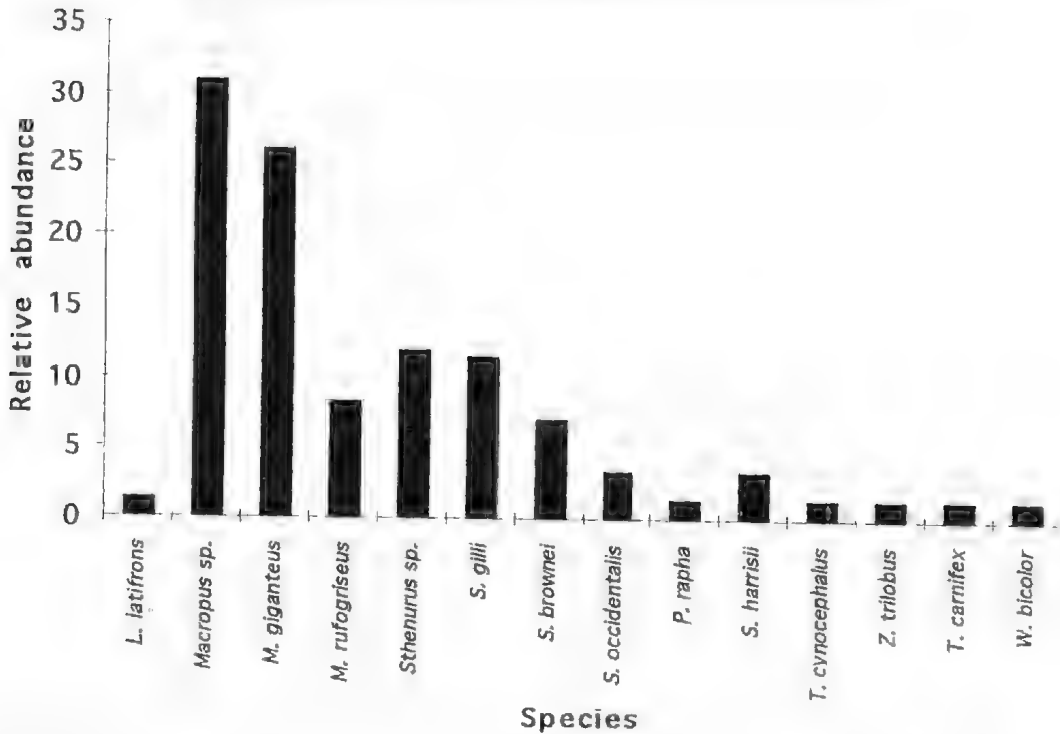


Fig. 7. Frequency of the number of individuals of the various large mammal species expressed as percentages of the total number of individuals from the Cathedral Cave fossil assemblage.

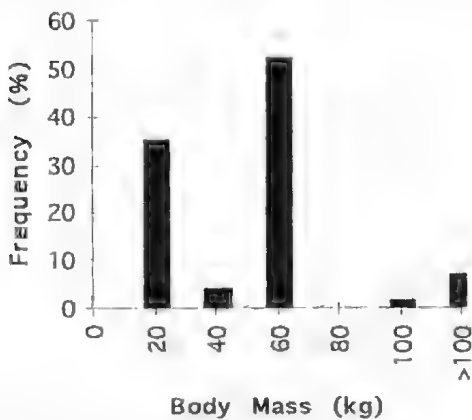


Fig. 8. Distribution of all large mammal species based on MNI values plotted by weight classes from the Cathedral Cave fossil assemblage.

units could be made based upon the grain size distribution or grain shape. Calcium carbonate and clay content varied between the sedimentary units with little similarity with the sediments of the region (Brown 1998). The variation in calcium carbonate content of the cave sediments may have occurred following incorporation of cave limestone via fretting from the Fossil

Chamber roof (Wells *et al.* 1984). Pleistocene beach dune facies are prevalent in the region but are not interpreted as the source for the Cathedral Cave sediments due to their very high amount of calcium carbonate content. Moriarty *et al.* (2000) suggested that the cave fills at Naracoorte were sourced from surface soils during periods with a wet climate regime with abundant vegetation (i.e. interglacials, stadials and interstadials). However, Units 3 and 4 contain little or no carbonaceous material suggesting that surface soil development may not be significant during the deposition of these units and they may have originated during more arid periods where rainfall and vegetation cover were low.

The speleothem dates provide a time frame and suggest environmental conditions under which sediment accumulated within the Fossil Chamber. The buried flowstone (CC FC FS-3) gives a maximum age (279.2 ± 7.2 ka) for sediment and fauna accumulation in Units 1, 2 and 3 and a minimum age for the underlying Unit 4 sediments.

A U-series date from near the lower end of the buried stalactite (399 ± 19 ka) provides a maximum age for Unit 4, as burial of this speleothem had to occur following its formation.

The speleothem developed on the upper surface of the sediment cone, dated at 159.2 ± 2.2 ka, provides a minimum date for cessation of sediment deposition

TABLE 6. Preferred or inferred habitats of mammal species recovered from the Cathedral Cave fossil assemblage, *Nauyasorte*.

Species	F	S	H	O.F.	W	R
<i>Antechinus flavipes</i>			X	X	X	X
<i>Sminthopsis murina</i>			X	X	X	X
<i>Dasyurus viverrinus</i>		X	X	X		
<i>Dasyurus maculatus</i>			X	X	X	
<i>Sarcophilus harrisi</i>			X	X	X	
<i>Thylacinus cynocephalus</i>		X		X	X	
<i>Phascogale calura</i>				X		
<i>Isodon obesulus</i>			X	X	X	
<i>Perameles bougainville</i>			X	X	X	
<i>Perameles gunnii</i>		X	X	X		
<i>Betongia penicillata</i>		X	X	X	X	
<i>Potorous platyops</i>				X	X	
<i>Potorous tridactylus</i>			X	X	X	
<i>Lasiornis latifrons</i>		X				
<i>Macropus giganteus</i>		X		X	X	
<i>Macropus rufogriseus</i>			X	X	X	
<i>Wallabia bicolor</i>		X	X	X	X	
<i>Sthenurus gilli</i>				X		
<i>Sthenurus browni</i>				X		
<i>Sthenurus occidentalis</i>				X		
<i>Procyptodon goliath</i>		X		X		
<i>Cercartetus nanus</i>				X	X	X
<i>Zygomaturus trilobus</i>				X	X	
<i>Thylacoleo carnifex</i>				X	X	
<i>Mastomys fuscus</i>			X	X	X	X
<i>Pseudomys australis</i>	X	X				
<i>Pseudomys shortridgei</i>			X			
<i>Natomys mitchelli</i>				X		

Data obtained from Archer (1981), Bradley (1995), Christensen (1995), Edgar & Belcher (1995), Fox (1989, 1995), Friend & Burbidge (1995), Godsell (1995), Happold (1995), Heinsolin (1966), Jarman and Phillips (1989), Johnston (1995), Murray (1984), Seebach *et al.* (1989), Tate (1947), Turner & Ward (1995), Walton (1988), Watts & Aslin (1981) and Wells (1995). F = Forbs. S = Savannah. H = Heath. O.F. = Open forest, W = Woodland and R = Rainforest.

in the chamber, which probably occurred following blockage of the solution tube entry point. In other words, the entire Cathedral Cave fauna from Units 1, 2 and 3 dates between 279.2 ± 7.2 and 159.2 ± 2.2 ka corresponding with oxygen isotope stages 6, 7 and 8 (Shackleton & Opdyke 1973; Martinson *et al.* 1987).

Laphonomys

ACCUMULATION MODE(S)

The fossil evidence supports accumulation of animals via a pitfall trap. The low number of mammalian carnivores and the scarcity of carnivore tooth markings and gnaw damage (characterised by crenulated breakage patterns), suggest that the fossils were not accumulated by mammalian carnivores and the chamber was not used as a den or a lair (cf. Lundelius 1966; Sutcliffe 1970; Brain 1980; Haynes 1980; Scott & Klein 1981; Cruz-Urbe & Klein 1994; Skinner *et al.* 1998). Furthermore, the absence

of root etching and the small number of burnt or sub-aerial weathered bones argue against a surface accumulation where animal remains would be easily accessible to carnivores. The few specimens displaying characteristics of carnivore activity were most likely hydraulically transported into the cave from locations proximal to the entrance or resulted from an entrapped carnivore within the chamber.

Although water transport of animal remains into the Fossil Chamber may account for some post-mortem damage, the aforementioned evidence suggests that bone accumulation did not occur by this means. All evidence is consistent with a pitfall trap.

The deep brown discoloration of some bones seems to contrast with the paler colours typical of the deposit. The deep brown specimens are comparable to bones found in swamp deposits at Rocky River on Kangaroo Island (Wells *et al.* 1999) where the colour

has been attributed to tannin uptake or staining. Perhaps this type of surface colouring present on some Cathedral Cave specimens indicates local ponding within the cave system, at a time when outside conditions of high vegetation cover increased the quantity of tannins into the downward percolating ground water.

The data obtained for the small vertebrate fauna (Table 5) suggest at least two modes of accumulation. The low total number of individuals and the small number of arboreal species are not inconsistent with a pitfall trap. Arboreal species would be more able to climb out of the cave had they fallen or climbed in. However, the higher number of rodent individuals recovered from Pit A, Unit 1 and Pit B, Unit 2 suggests that an avian predator may have roosted within the cave or solution tube or in an overhanging tree. One might infer from the relatively small number of individuals compared with other extensive owl deposits at Naracoorte (McDowell 2000²) that this only occurred for a short time.

ARTICULATED SPECIMENS

The presence of articulated fossil specimens suggests that some animals entered the cave intact. These were presumably live animals, trapped by the pitfall mechanism: which either died from the fall into the cave and decomposed on the cone or survived the fall and were subsequently able to move about within the chamber. As the majority of articulated material was recovered from the distal fan regions within the Fossil Chamber, the latter scenario seems the more likely. Observations by one of the authors (RTW) of contemporary accumulations suggest that following entrapment, starving animals became thigmotaxic and tended to seek out the security of walls and crevices and died there. This evidence further supports the hypothesis that a pitfall mechanism was the primary mode of accumulation for large mammals and indicates that the burial of some bones occurred rapidly before disarticulation could occur.

The lack of articulated material representing very large mammals (>100 kg) (i.e. *Procoptodon* sp. and *Zygomaturus* sp.) suggests that either their remains were transported into the cave or the diameter of the solution tube acted as a 'body mass sieve', preventing the passage of larger, intact animals. As already discussed above, the absence of weathering, abrasions from hydraulic transport and any extensive

bone surface discoloration suggests that the bones did not accumulate outside the cave. The size of individuals of these species may have prevented their falling directly into the chamber below. The individuals would be trapped and then die within the solution tube, with their remains gradually incorporated into the fossil deposit as the carcasses decomposed. The low MNI values for these large herbivore species suggest one or all three possibilities; that few became trapped, that they could readily extricate themselves, that their numbers were low in the immediate vicinity of the pitfall.

SKELETAL ELEMENT ABUNDANCES

The skeletal element abundances for each unit and excavation pit indicate that the relative number of skeletal elements recovered (Ri%) is low. Accepting the hypothesis of a pitfall mechanism capturing live animals at random, the majority of bone in the deposit would result from decomposition of whole or near whole animals within the Fossil Chamber. In this case, an individual's entire skeleton should be represented within the total fossil deposit and so would give high Ri% values were the entire deposit to be sampled. The low observed relative abundances are thus interpreted as an artefact of sampling. These values also indicate dispersal of elements following accumulation under transport regimes such as sediment mass movement, water flow and/or bioturbation.

Palaeontology

COMPARISON WITH VICTORIA FOSSIL CAVE

Victoria Fossil Cave, located about 700 m from Cathedral Cave, contains several fossil sites that have yielded an array of Middle Pleistocene faunas, though only the main Fossil Chamber has been thoroughly researched (Wells *et al.* 1984; Moriarty *et al.* 2000). The Fossil Chamber assemblage is by far the largest and richest in all the caves at Naracoorte (Wells *et al.* 1984). Fossil-rich sediments appear to have been deposited prior to 213 ka and span many thousands of years (Ayliffe *et al.* 1998; Moriarty *et al.* 2000). A pitfall trap is suggested to be the primary mechanism responsible for the accumulation of animals (Wells *et al.* 1984). A majority of the more common megafaunal species also occurs within Cathedral Cave (e.g. *Sthenurus gilli*, *S. browni* Merriëes, 1967; *S. occidentalis* Glauert, 1910 and *Zygomaturus tribovis*). The major faunal differences between the two assemblages lie in the presence of the rarer species in Victoria Fossil Cave (e.g. *Palorchestes azeel* Owen, 1873; *S. mulersani* Marens, 1962; *S. maddocki* Wells & Murray, 1979; *S. pates* DeVis, 1895; *Sthenurus* sp. nov.; *S. bathyi* Prideaux & Wells, 1998 and *Protemnodon roechus*

²Atkinson, A. C. (2000) The small mammals and a dipodomys of Eocene Cave, West Horn of Naracoorte Caves Conservation Park, South Australia. Abstract of poster presented at the Geological Society of Australia Regional Analysis of Australian Quaternary Studies and the International Biogeography Conference, 2000, 29-31 October 2000, Canberra.

Owen, 1874) and are likely to reflect differences in sample size.

Preliminary faunal samples have been obtained from dated deposits in Spring Chamber and Grant Hall within Victoria Fossil Cave (Moriarty *et al.* 2000). Many species detected in the Cathedral Cave fossil assemblage were not recovered from Spring Chamber. This may be an artefact of the small sample size from Spring Chamber. U-series dates obtained indicate that the Spring Chamber fauna is older than that of Cathedral Cave (Ayliffe *et al.* 1998; Moriarty *et al.* 2000), although some overlap occurs during the period 282–211 ka corresponding to the upper portion of the Cathedral Cave date range (270–159 ka).

Grant Hall sediments appear to have a higher fossil content than those of Spring Chamber and the fauna is more like that of Cathedral Cave. The megafauna represented closely resembles the Cathedral Cave fossil assemblage. Moriarty *et al.* (2000) suggested an age between 160 and 80 ka for sediment accumulation in Grant Hall. However, they argue that this may not be the true age of the sediment influx and fauna due to the potential for reworking of previously deposited sediments.

PROXIMAL COMMUNITY AND PALAEOENVIRONMENTAL RECONSTRUCTION

An understanding of the taphonomic biases within the fossil assemblage gives more confidence to any palaeoenvironmental reconstruction, but, as the fauna accumulated during a period of approximately 170 ka, time-averaging may compromise this interpretation.

It can be concluded that the large mammal component of the proximal community consisted primarily of herbivores. Of these, grazing types (*Macropus* spp.) were the most abundant. The browsing herbivore fauna consisted of the extinct sthenurine kangaroos, *Wallabia bicolor* and *Zygomaturus trilobus*. Vegetation allowing this mix of herbivores to coexist within the same region would include shrubs, trees and grasses. An open forest or woodland with a grassy understorey is the most likely environment. However, grazing kangaroos could also forage in more open areas within a forest, on the forest edge or adjacent grasslands. Murray (1984) suggested that the morphology of the *Zygomaturus* nasals may be an adaptation for browsing on reeds within shallow water, suggesting the possible presence of wetlands or swamps.

The presence of *Lasiorhinus latifrons* (Owen, 1845) in the deposit appears inconsistent with this environmental reconstruction. Today, this species inhabits semi-arid to arid savannah regions (Wells 1995). However, in the Mid-Pleistocene, this species

may have inhabited the outer edge of open forest or woodland, as even in historic times its range extended into higher rainfall areas (Wood-Jones 1924).

Most of the small animal fauna is indicative of an open forest/woodland environment. A smaller number occurs today in savannah and heath vegetation suggesting it may have occurred in close proximity to Cathedral Cave during the Middle Pleistocene.

Medium-sized mammals such as bandicoots (*Perameles* and *Isododon*) need sufficient ground cover for refuge and the presence of low-lying scrub is suggested. *Antechinus flavipes* (Waterhouse, 1838), *Phascogale calura* (Gould, 1844) and *Cercartetus nanus* (Desmarest, 1818) are arboreal species. This further supports the presence of abundant trees consistent with an open forest/woodland. The only arid species recovered from the fossil deposit was the Plains Rat, *Pseudomys australis* (Gray, 1832) which Walton (1988) suggests prefer today rocky arid regions.

The fauna suggests a vegetation structure similar to that of the region prior to European land clearing. Croft *et al.* (1999) indicate that the vegetation community of the Naracoorte region was dominated by open eucalypt forest/woodlands with intermittent tussock grasslands and sedge/land prior to European settlement. The diversity in vegetation for the region during the Middle Pleistocene as indicated by the Cathedral Cave fossil fauna suggests that on a local scale the vegetation may have been ecotonal.

PALAEOCLIMATE

During the period bracketing the Cathedral Cave fossil assemblage (between 159 and 270 ka) a glacial maximum occurred at 170 ka along with an interglacial (oxygen isotope stage 7e) and warm interstadial periods centred on 240, 220 and 195 ka (Ayliffe *et al.* 1998; Winograd *et al.* 1997). Martinson *et al.* (1987) reported three radiolarium high temperature peaks for the Southern Ocean (RCH-120) during the time of faunal accumulation at 240, 220 and 195 ka with a maximum temperature of about 0.5 °C higher than present and lowest temperatures averaging 3 °C below present. The high temperature peaks correlate with the interglacial or warm interstadial events of this period. Ayliffe *et al.* (1998) suggest speleothem deposition followed these phases corresponding to stadials and cool interstadials. Little lime accumulated during periods of speleothem formation suggesting that the majority of animal remains were accumulated during the warmer interglacials and interstadials. Accepting this hypothesis enables the dates for the span during which the faunal remains were accumulating to be refined to the period 240 ka to 195 ka.

Ayliffe *et al.* (1998) indicated that the regional hydrological balance at present is an analogue for interglacial conditions, and taking this into account it is concluded that the majority of animal remains accumulated during periods of local climate similar to that of the present time.

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**SPECIES OF RAILLIETINA FUHRMANN, 1920
(CESTODA: DAVAINIIDAE) FROM THE EMU,
DROMAIUS NOVAEHOLLANDIAE**

*By MICHAEL G. O'CALLAGHAN**, *MARGARET DAVIES** & *ROSS H. ANDREWS**

Summary

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Four new species of Raillietina Fuhrmann, 1920 (Cestoda: Davainiidae) are described from the intestine of the emu, Dromaius novaehollandiae. Raillietina australis (Krabbe, 1869) Fuhrmann 1924 is redescribed from specimens collected in Australia. The new species differ from R. australis and from each other, in the size and number of rostellar hooks and in the dimensions of the cirrus sac.

Key Words: Cestoda, emu, Raillietina, new species, Dromaius novaehollandiae.

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Four new species of *Raillietina* Fuhrmann, 1920 (Cestoda: Davainiidae) are described from the intestine of the emu, *Dromaius novaehollandiae*. *Raillietina australis* (Krabbe, 1869) Fuhrmann 1924 is redescribed from specimens collected in Australia. The new species differ from *R. australis* and from each other, in the size and number of postellar hooks and in the dimensions of the cirrus sac.

KEY WORDS: Cestoda, emu, *Raillietina*, new species, *Dromaius novaehollandiae*.

Introduction

The emu, *Dromaius novaehollandiae* (Latham, 1790), is one of only two ratites (Struthioniformes: Dromalidae) inhabiting Australia. Restricted to mainland Australia, emus are now farmed for meat, oil, leather and eggs. In 1995 there were 650 licensed emu farms in Australia with a population of 71,000 emus producing 78,000 chicks annually (Mannion *et al.* 1995). Recently Clarke *et al.* (1996), Tully & Shane (1996) and Shane (1998) reviewed the infectious and parasitic diseases of farmed emus although they did not include any information on cestode parasites.

Cestodes were first recorded in emus in 1869 when Krabbe published a description of *Taenia australis* (Davainiidae) recovered from the intestine of a captive emu which had died in the Copenhagen (Kjærboelling's) Zoological Garden in 1867. The emu had arrived from Australia 1.5 years earlier as a fully-grown bird (Krabbe 1869).

Later, Fuhrmann (1909) described another davainiid species, *Cotugnia collini*, from an emu in the Museum for Natural Sciences in Berlin. The exact locality for this specimen is not known because the geographic distribution of the host is reported as eastern Australia. No subsequent records of cestodes in the emu exist and the identity of the cestodes infecting these birds in Australia is unknown. Both of the described parasites of emus are recognised as valid species (Schmidt 1986) although Krabbe's (1869) description of what is now *Raillietina*

australis lacks a number of morphometric and descriptive characters.

Our study of farmed and wild emus has resulted in the recognition of five species of cestode. All are assigned to *Raillietina* Fuhrmann, 1920 (*sensu* Jones & Bray 1994) on the basis of the possession of two rows of numerous hammer-shaped hooks, uni-lateral genital pores, a small cirrus sac, which does not reach or just crosses the osmoregulatory canals and egg capsules containing several eggs. One species is identified as *Raillietina australis* whilst the other four are undescribed. Here we redescribe *R. australis* from the holotype and new material and describe the new species.

Materials and Methods

Cestodes were collected from farmed and wild emus in South Australia. Additional material was obtained from the Australian Helminthological Collection of the South Australian Museum (AHC). Cestodes were relaxed in tap water, fixed in 10% buffered formalin and stored in 70% ethanol. Whole mounts were stained with Heidenhain's haematoxylin, Celestine blue or Semichon's acetocarmine, dehydrated in a graded series of ethanol, cleared in clove oil and mounted in Canada balsam. Sections were mounted in DeFaire's medium. Measurements are given in the text, in mm, as the range followed, in parentheses, by the mean and the number of observations. Descriptions and measurements of cestodes are based on the examination of up to 50 specimens of each species. Drawings were made with the aid of a camera lucida attached to an Olympus BH microscope. Type specimens have been deposited in the Australian Helminth Collection (AHC) South Australian

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Museum, Adelaide (SAMA) and the British Museum (Natural History), London (BMNH).

Railhetina australis (Krabbe, 1869) Fuhrmann, 1924 (FIGS 1-7)

Taenia australis Krabbe, 1869. K. Danske Vidensk Selsk. Skr. Naturv. Og Math. Afd. 8, 249-363, Figs 296-298.

Davameia australis (Krabbe, 1869) Blanchard, 1891

Ransomia australis (Krabbe, 1869) Fuhrmann, 1920

Kolanja australis (Krabbe, 1869) Lopez-Neyra, 1931

Holotype: In Zoologisk Museum, Copenhagen, Denmark

Paratypes: Kadma, South Australia (SA) (33° 58' S, 137° 48' E). Coll. M. O'Callaghan, 11.vii.1995, SAMA AHC 31376, BMNH 2000.5.17.1-10.

Other material examined: Werrbee, Victoria (Vic.), Coll. K. E. Harrigan, April 1988, SAMA AHC 18391; Shelley River, Queensland, 29.ix.1907, SAMA AHC 227; Kinchega, New South Wales (NSW), Coll. I. Beveridge, 31.iii.1974, SAMA AHC 10006; Yunta, SA, Coll. G. E. Ford, 1.ix.1981, SAMA AHC 11181; North West, Western Australia, Coll. T. H. Johnston, SAMA AHC S20431.

Description

Cestodes of moderate size, up to 50 in unrelaxed specimens and up to 110 in relaxed specimens. Maximum width 1.2, Strobila containing approximately 1150 proglottides. Scolex 0.416-0.568 (0.498, $n=20$) in diameter with eversible rostellum (Figs 1, 2), rarely everted in fixed specimens. Rostellum 0.200-0.288 (0.249, $n=10$) in diameter armed with 280-362 (326) hammer-shaped hooks arranged in two rows. Larger rostellar hooks 0.021-0.030 (0.025, $n=250$) in length, smaller rostellar hooks 0.016-0.023 (0.020, $n=250$) (Fig. 3). Base of rostellum armed with 16-20 rows small, rose-thorn-shaped accessory spines 0.002-0.004 in length. Suckers 0.136-0.168 (0.149, $n=30$) in diameter armed with eight diagonally-arranged rows of hooks 0.005-0.011 in length (Fig. 4).

Proglottides craspedote. Mature proglottides wider than long, 0.160-0.184 (0.171) \times 0.800-0.848 (0.822, $n=10$) (Fig. 5). Genital pores single, unilateral, 0.016 in diameter; genital ducts passing between longitudinal osmoregulatory canals. Dorsal osmoregulatory canal 0.048 in maximum diameter, lying internal to smaller ventral osmoregulatory canal, 0.020 in diameter. Transverse osmoregulatory

canals connecting left and right ventral canals at posterior margin of each proglottis.

Genital atrium small, situated in anterior half of lateral proglottis margin and surrounded by an accumulation of cells. Cirrus sac elongate 0.152-0.164 (0.158) \times 0.016-0.024 (0.020, $n=10$) (Fig. 6) extending to but not beyond dorsal osmoregulatory canal. Distal region of cirrus of greater internal diameter than mid region, armature not seen; proximal region forming small, spherical, internal seminal vesicle, 0.016 in diameter. Cirrus sac in holotype specimen 0.149 \times 0.023, also with internal seminal vesicle 0.016 in diameter. Coiled vas deferens passing towards centre of proglottis where it becomes convoluted, occasionally overlying seminal receptacle before passing posteriorly towards ovary. Testes in poral and aporal fields, number 4-7 (5) poral and 11-13 (11, $n=10$) aporal, bounded by lateral osmoregulatory canal. Testes 0.044-0.052 (0.048, $n=10$) in diameter.

Vagina opening to genital atrium posterior to cirrus sac (Fig. 7). Distal region slightly enlarged 0.024-0.032 (0.029) \times 0.010-0.016 (0.015, $n=10$). Mid region, narrow, coiled 0.005 in diameter, leading to seminal receptacle medially posterior to vas deferens, 0.084-0.128 (0.122) \times 0.024-0.032 (0.026, $n=10$) and lying anterior and dorsal to poral lobe of ovary. Ovary distinctly bilobed, situated in mid line of proglottis. Poral lobe 0.040-0.072 (0.049) \times 0.040-0.060 (0.048, $n=10$), aporal lobe 0.044-0.072 (0.060) \times 0.032-0.072 (0.043, $n=10$) with 3-5 lobules in each lobe. Vitellarium irregularly lobulate, post ovarian, slightly aporal, occasionally dorsal to aporal lobe of ovary, 0.060-0.080 (0.068) \times 0.036-0.048 (0.042, $n=10$). Uterine duct passing anteriorly to developing merus. Gravid proglottides extending transversely 0.720 \times 0.350 with large osmoregulatory canal up to 0.120 in diameter. Egg capsules irregularly ovoid 0.108-0.132 \times 0.08-0.104. Egg capsules 76-110 (88, $n=10$) per gravid proglottis containing 10-14 (11, $n=40$) eggs. Terminal proglottides extending transversely, as wide as long 0.580-0.800 \times 0.600-0.880. Oncosphere 0.012 in diameter, oncospherical hooks 0.005-0.007 long.

Host

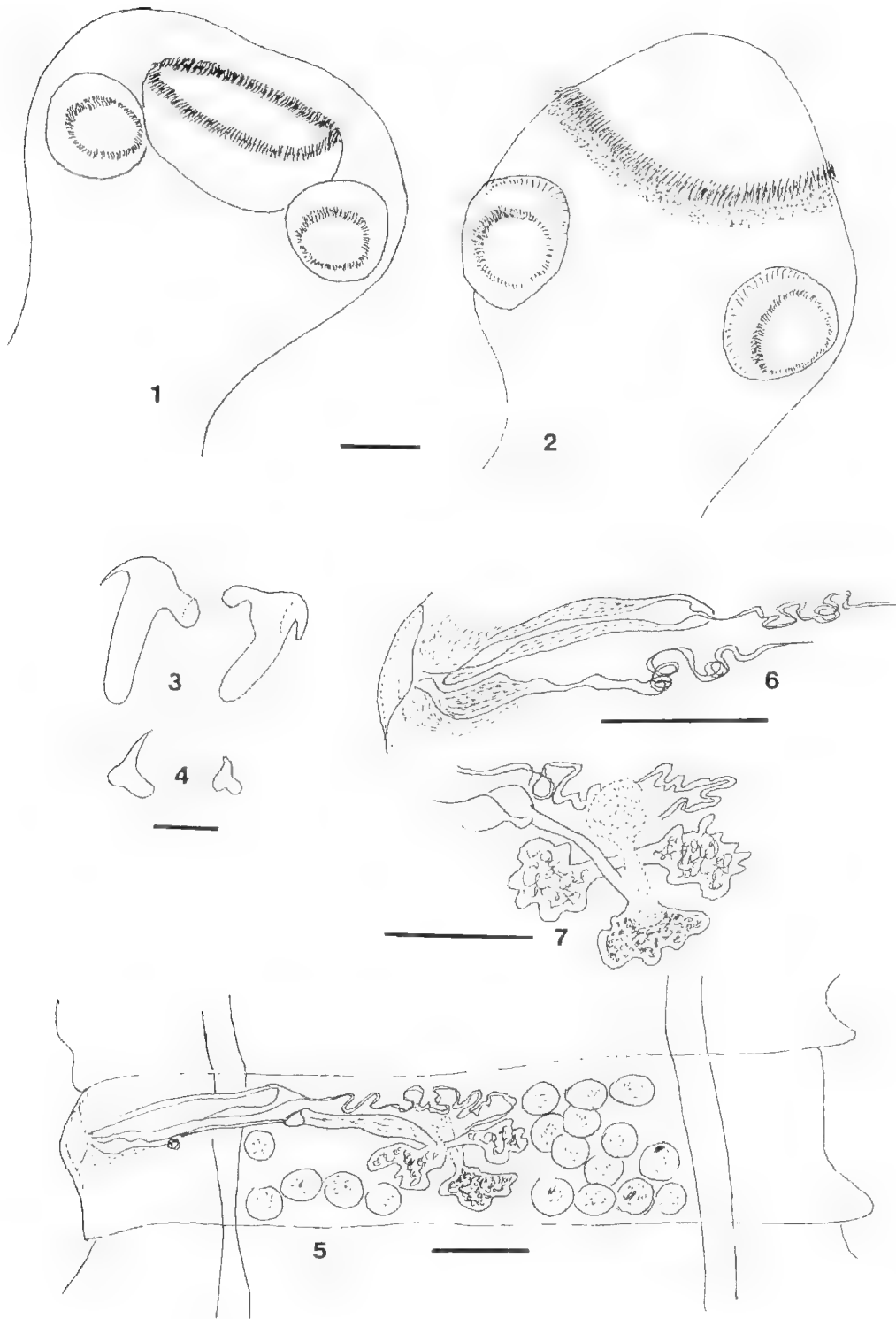
Dromaius novaehollandiae (Latham, 1790) (Struthioniformes, Dromadidae).

Location in host

Small intestine.

Remarks

Krabbe (1869) omitted the dimensions of the scolex, rostellum and suckers in his description of *R. australis* and the strobila was inadequately



Figs 1-7. *Raillietina australis* Krabbe. 1. Scolex with retracted rostellum. 2. Scolex with fully everted rostellum. 3. Rostellar hooks 4. Sucker hooks. 5. Single mature proglottis. 6. Cirrus and distal vagina. 7. Female genitalia. Scale bars = 0.1 mm, 1, 2, 5-7; 0.01 mm, 3, 4.

described. The material described above, based on the examination of 50 cestodes, indicates that Krabbe's (1869) measurements of the rostellar hooks (12-14 mm) are consistent with hook width but not hook length although this cannot be confirmed because of the absence of a scolex in the type material examined. The fragments of type material obtained, however, do not differ from specimens examined in this study and have thus enabled the redescription of *R. australis*:

Railletina heveridgei sp. nov.
(Figs 8-14)

Holotype: Keith, SA (36° 06' S, 140° 19' E), Coll. M. O'Callaghan, 30.iii.1999, SAMA AHC S28300.

Paratypes: Lock, SA (33° 34' S, 135° 45' E), Coll. M. O'Callaghan, 9.iii.1996, SAMA AHC S28301, 31377, BMNH 2000.5.17.11-30.

Other material examined: Yunta, SA, Coll. G. E. Ford, 1.ix.1981, SAMA AHC 11181, S21347; Werribee, Vic., Coll. I. Beveridge, 23.vi.1995, SAMA AHC 26698; Mundulla, SA, Coll. Dinning, February 1933, SAMA AHC 1187; Bairnsdale, Vic., Coll. I. Beveridge, 5.xii.1994, SAMA AHC S27717, S27718; Condobolin, NSW, Coll. Ryan, 27.i.1971, SAMA AHC 9179; Vic., Coll. D. Turner, 1994, SAMA AHC S26205; NSW, Coll. T. H. Johnston/T. L. Bameroft, 1914, SAMA AHC S20430, S 20433; La Trobe, Vic., Coll. I. Beveridge, 24.vi.1972, SAMA AHC S20837; Bairnsdale, Vic., Coll. I. Beveridge, Scolex only, 5.vii.1994, SAMA AHC S27717, S27718; Vic., 1994, SAMA AHC S26205.

Description

Large cestode, up to 160 long in unstretched specimens and up to 600 in relaxed specimens; gravid strobila containing approximately 750 segments. Strobila with max. width 3.8 in relaxed specimens. Scolex 0.480-0.736 (0.609, n=25) wide at suckers (Fig. 8). Retracted rostellum 0.192-0.258 (0.234, n=10) diam. with 304-412 (370, n=10) hammer-shaped hooks in two rows. Larger rostellar hooks 0.016-0.021 (0.019, n=250) long; smaller rostellar hooks 0.014-0.019 (0.016, n=250) long (Fig. 9). Very small accessory rostellar spines approximately 0.001-0.002 in length only visible under high magnification. Suckers circular 0.136-0.168 (0.150, n=10) in diameter armed with 12-18 rows hooklets 0.004-0.011 long (Fig. 10) Neck variable, up to 0.250 in length. Calcareous corpuscles present in posterior half of scolex.

Proglottides craspedote. Mature proglottides wider than long, 1.554-1.932 (1.730) x 0.273-0.399 (0.326, n=20) (Fig. 11). Genital pores single, unilateral.

Large, ventral, longitudinal osmoregulatory canal 0.108 max. diam. joined by transverse canal connecting left and right lateral canals in posterior margin of each proglottis. Dorsal canals not seen. Genital anlage appear in approximately segment 150. Male and female genitalia mature in proglottides 200 and 300 respectively; first eggs appear in 480.

Genital atrium small, situated in anterior half of lateral proglottis margin. Cirrus sac 0.256-0.328 (0.298, n=10) x 0.080 extending to ventral osmoregulatory canal (Fig. 12). Distal region of cirrus lined with spines, of greater internal diameter than sinuous mid region; proximal region forms spherical internal seminal vesicle 0.060-0.092 (0.079) x 0.052-0.060 (0.056, n=10), not detectable in proglottides of every cestode examined. Vas deferens greatly coiled, extending anteriorly across midline of each proglottis then returning posteriorly towards ovary. Testes distributed in poral and aporal fields within area defined by ventral osmoregulatory canals, number 5-9 (7, n=30) poral and 12-18 (15, n=30) aporal. Testes sub-circular, 0.080-0.100 (0.088) x 0.080-0.088 (0.083, n=10) not overlying ovary or vitellarium.

Vagina opening to genital atrium posterior to cirrus sac. Distal region with thickened muscular wall 0.088-0.120 (0.106, n=10). Mid region of vagina narrow, coiled, leading medially, posterior to vas deferens to seminal receptacle varying in length from 0.088-0.240 (0.100, n=20) in length, lying anterior to testes and poral lobe of ovary. Sperm duct passing posteriorly from seminal receptacle. Ovary bilobed, 0.084-0.132 (0.110) x 0.080-0.088 (0.082, n=10) with 4-6 lobules in each lobe (Fig. 13). Vitellarium ovoid, 0.112-0.136 (0.120) x 0.080-0.100 (0.087, n=10) situated posterior to ovary; uterine duct passing anteriorly to developing uterus. Gravid proglottides wider than long, 2.5-2.7 x 0.4-0.5. Terminal proglottides longer than wide, 1.0 x 0.9 (Fig. 14). Gravid proglottides containing 30-40 (35, n=10) egg capsules, 0.168-0.200 (0.184) x 0.144-0.196 (0.161, n=10) each containing 10-12 eggs, 0.040 in diameter. Oncosphere 0.014-0.016 (0.016) x 0.011-0.016 (0.013, n=10). Oncospheral hooks 0.004-0.006 (0.005, n=10).

Host

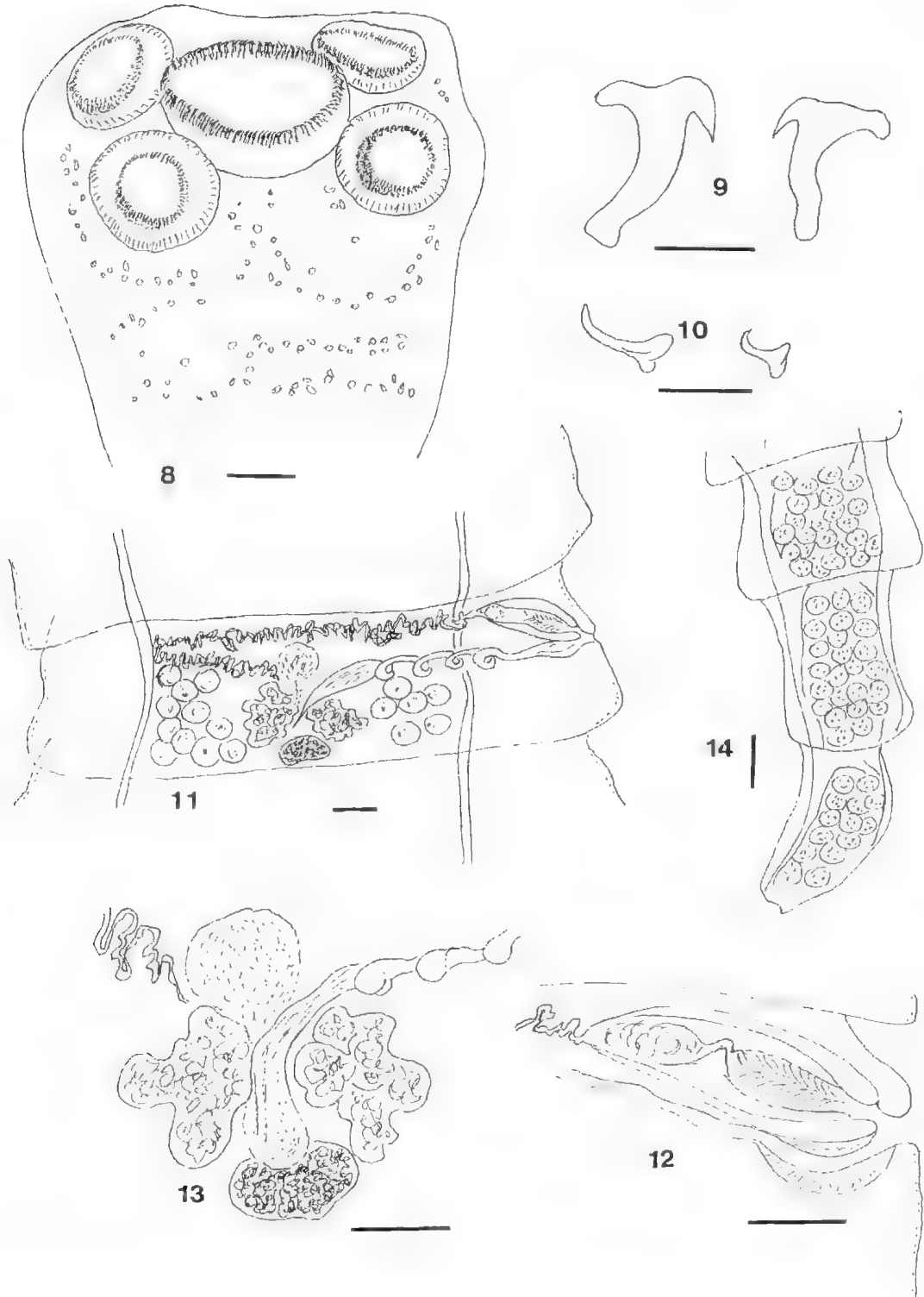
Dromaius novaehollandiae (Latham, 1790) (Struthioniformes: Dromadidae)

Location in host

Small intestine.

Etymology

This species named for Dr I. Beveridge in recognition of his outstanding contribution to our



Figs 8-14. *Raillietina beveridgei* sp. nov. 8. Scolex. 9. Rostellar hooks. 10. Sucker hooks. 11. Single mature proglottis. 12. Cirrus and distal vagina. 13. Female genitalia. 14. Terminal gravid proglottides. Scale bars = 0.1 mm, 8, 11-14; 0.01 mm, 9, 10.

knowledge of the parasites of the Australian endemic fauna and his guidance to the senior author.

Railletina chiltoni sp. nov.
(FIGS 15-22)

Holotype: Keith, SA (36° 06'S, 140° 19'E), SAMA AHC 528302.

Paratypes: Kersbrook, SA (34° 47'S, 138° 51'E), Coll. I. Beveridge, 1.iv.1989, SAMA AHC 31378, BMNH 2000.5.17.31-40.

Description

Cestodes up to 90 in relaxed specimens, maximum width 1.4. Strobila contain approximately 360 proglottides. Scolex 0.545-0.832 (0.643, $n=20$) in diameter with eversible rostellum, 0.336-0.480 (0.383, $n=10$) in diameter, retracted in majority of specimens (Figs 15, 16). Rostellum armed with 302-378 (335, $n=10$) hammer-shaped hooks in two rows. Larger rostellar hooks 0.026-0.039 (0.032, $n=250$) in length; smaller rostellar hooks, 0.022-0.034 (0.027, $n=250$) in length (Fig. 17). Base of rostellum armed with rose-thorn-shaped accessory spines, 0.003 in length, visible under high magnification only and in specimens with fully everted rostellum. Suckers 0.136-0.200 (0.171, $n=30$) in diameter, armed with 8-14 rows of hooks 0.005-0.013 long (Fig. 18). Neck variable in length, 0.4-0.8 in relaxed specimens.

Proglottides craspedote. Mature proglottides 0.890-1.400 x 0.072-0.1400 (Fig. 19). Genital pores single, unilateral; genital ducts passing between osmoregulatory canals. Dorsal osmoregulatory canal extremely narrow, diam. 0.002, lying internal to ventral osmoregulatory canal, 0.012 max. diam. Transverse osmoregulatory canals connecting right and left ventral canals at posterior margin of each proglottis. Dorsal commissures not seen. Genital anlage appearing in proglottis 40 approximately; first mature proglottis 160; first gravid proglottis 280.

Genital atrium small, situated in anterior half of lateral proglottis margin. Cirrus sac 0.104-0.112 (0.108) x 0.036-0.040 (0.038, $n=10$), not reaching longitudinal osmoregulatory canals (Fig. 20). Cirrus un-armed, distal region of greater internal diameter than mid region; leading uncoiled to internal seminal vesicle 0.015 (0.012-0.016) x 0.012 (0.012-0.014). Vas deferens greatly coiled, passing towards centre of proglottis. Testes distributed in two lateral groups, 3-5 (4, $n=20$) poral and 7-11 (9, $n=20$) aporal. Testes 0.056-0.068 (0.062, $n=20$) in diameter; not overlying female genital organs.

Vagina opening to genital atrium posterior to cirrus sac; distal region surrounded by cells, 0.032-0.036 (0.035) x 0.012-0.020 (0.015, $n=10$). Mid region coiled, often dilated with sperm, leading medially

posterior to vas deferens, greatly dilated and saecular anterior to poral lobe of ovary (Fig. 21). Ovary bilobed, situated in proglottis midline, enlarging in consecutive mature proglottides, maximum size 0.220 x 0.080 in posterior mature proglottides. Vitellarium similarly enlarging, maximum dimensions 0.184 x 0.080, situated posterior and distal to aporal lobe of ovary. Sperm duct passing posteriorly between lobes of ovary, uterine duct passing anteriorly to developing uterus. Gravid proglottides 1.200-1.700 x 0.200-0.440 (Fig. 22) containing 32-50 (38, $n=10$) spherical egg capsules, 0.136-0.184 x 0.136-0.192, with 14-17 (15, $n=10$) eggs per capsule. Oncosphere circular, 0.016-0.020 in diameter, oncospherical hooks 0.006-0.008.

Host

Dromaius novaehollandiae (Latham, 1790) (Struthioniformes: Dromaiidae).

Location in host

Small intestine.

Etymology

This species is named for Dr N. Chilton of the University of Melbourne for his contribution to parasitology in Australia.

Railletina dromaius sp. nov.
(FIGS 23-30)

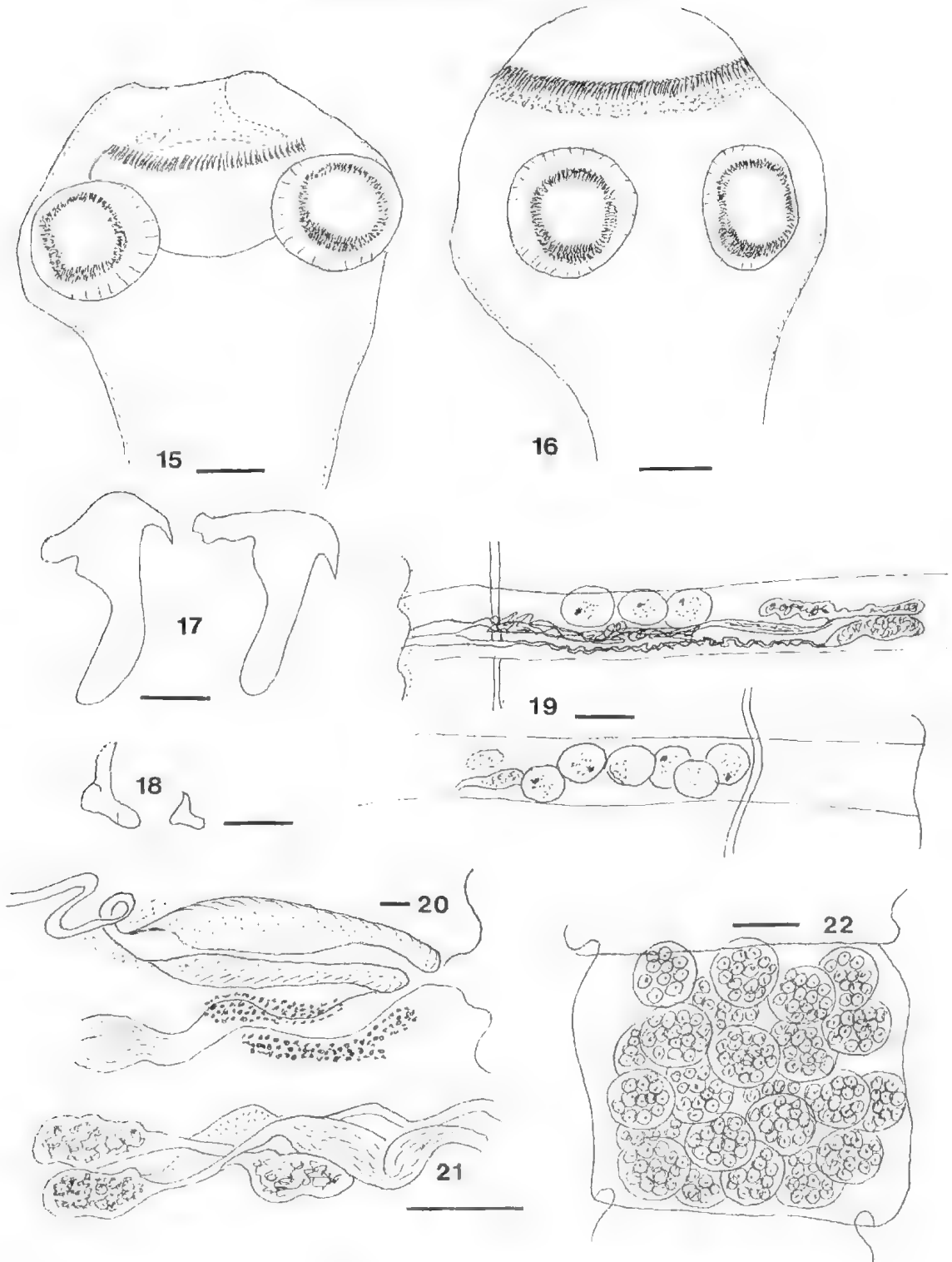
Holotype: Keith, SA, SAMA AHC 528303.

Paratypes: Kingston, SA (34° 14'S, 140° 21'E), Coll. M. O'Callaghan, 10.viii.1998, SAMA AHC 528304, 528305, 31379, BMNH 2000.5.17.41-60.

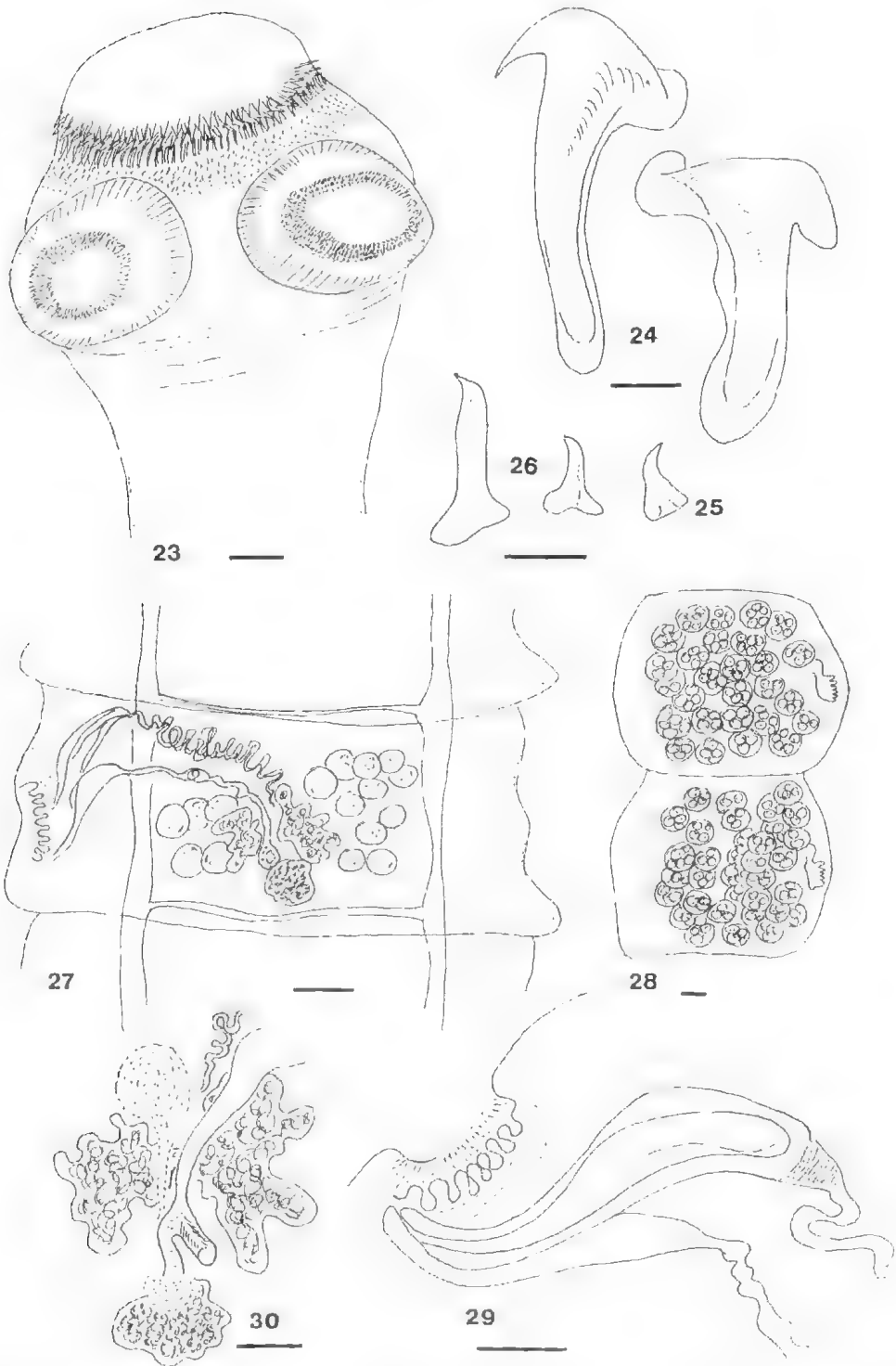
Other material examined: Wagga, NSW, 7.xii.1994, SAMA AHC 27716; Kinchega, NSW, Coll. I. Beveridge, 31.iii.1974, SAMA AHC 10005; Menindee, NSW, Coll. I. Beveridge, 10.viii.1977, SAMA AHC 11008; Pine Plains, Vic., Coll. I. Beveridge, 14.v.1971, SAMA AHC 10511; Condrobin, NSW, 27.i.1971, SAMA AHC 9179; Wagga, NSW, Coll. I. Beveridge, 7.vii.1994, Scolex only, SAMA AHC 27716.

Description

Cestode up to 45 long in unrelaxed specimens and up to 200 in relaxed specimens. Gravid strobila contain 940 proglottides. In relaxed specimens, strobila with a maximum width of 2.12. Scolex 0.480-0.752 mm (0.594, $n=20$) wide at suckers. Rostellum everted, 0.336-0.448 (0.397, $n=20$) in diameter (Fig. 23), with 124-156 (142, $n=10$) hammer-shaped hooks in two rows. Larger, inner rostellar hooks 0.050-0.063 (0.056, $n=110$) long,



Figs 15-22. *Raillietina chiltoni* sp. nov. 15. Scolex with retracted rostellum. 16. Scolex with everted rostellum. 17. Rostellar hooks. 18. Sucker hooks. 19. Single mature proglottis. 20. Cirrus and distal vagina. 21. Female genitalia. 22. Gravid proglottis. Scale bars = 0.1 mm. 15, 16, 19, 21, 22; 0.01 mm. 17, 18, 20.



Figs 23-30. *Ruillettina thomasi* sp. nov. 23. Scolex. 24. Rostellar hooks. 25. Accessory rostellar spine. 26. Sucker hooks. 27. Single mature proglottis. 28. Gravid proglottides. 29. Cirrus and distal vagina. 30. Female genitalia. Scale bars = 0.1 mm, 23, 27, 28: 0.05 mm, 24-26: 0.05 mm. 29, 30.

smaller outer hooks 0.043-0.054 (0.048, n=110) (Fig. 24). Base of rostellum armed with 15-19 (17, n=25) diagonal rows of rose-thorn shaped accessory spines 0.008-0.0100 (0.009, n=20) long (Fig. 25). Suckers sub-circular 0.192-0.280 (0.234, n=20) x 0.168-0.260 (0.231, n=20) armed with 8-12 rows of hooklets varying in length from 0.008-0.020 (Fig. 26). Neck 0.160-0.400 long. Calcareous corpuscles present in the neck and less frequently in posterior half of scolex.

Proglottides craspedote. Mature proglottides wider than long, 0.722-1.050 (0.893, n=10) long x 0.205-0.370 (0.301, n=10) wide (Fig. 27). Gravid proglottides 0.920-0.980 x 0.740-0.790, 8-10 terminal, urn-shaped proglottides 0.500-0.730 (0.556) x 0.430-0.600 (0.472, n=10) (Fig. 28). Genital pores unilateral, opening into a muscular, plicate genital atrium 0.114-0.135 (0.123, n=10) wide x 0.041-0.082 (0.052, n=10) (Fig. 29), extending from the mid-point into posterior half of lateral proglottis margin. Lateral dorsal osmoregulatory canals 0.024-0.032 in diameter joined by transverse commissures in posterior region of proglottides. Ventral osmoregulatory canals not seen. Elongate cirrus sac, 0.246-0.271 (0.257) x 0.041-0.053 (0.044, n=10), extending anteriorly and towards but not reaching lateral osmoregulatory canal. Distal region of cirrus narrow, remainder wide, un-coiled. Vag. deferens coiled, voluminous, extending transversely in anterior margin of proglottides. Testes 10-18, in poral and aporal groups, 2-6 (4, n=15) poral and 8-12 (10, n=15) aporal, 0.041-0.057 (0.048, n=15) x 0.040-0.050 (0.040, n=15), lying within lateral osmoregulatory canals.

Vagina opening to genital atrium posterior to male genital pore. Distal region of vagina enlarged, 0.040-0.050 (0.048, n=5) x 0.020-0.024 (0.022, n=5). Mid region sinuous, leading anteriorly and medially, occasionally overlying testes, into a large seminal receptacle, 0.088-0.120 x 0.028-0.040, lying anterior to poral lobe of ovary; sperm duct passes posteriorly, lined with bristles. Ovary bipartite, each lobe of approximately equal size 0.090-0.130 (0.106, n=10) x 0.041-0.061 (0.050, n=10) (Fig. 30). Vitellarium medial, post ovarian, sub-circular 0.074-0.090 (0.082) x 0.066-0.094 (0.08, n=10). Uterine duct passing anteriorly to developing uterus. Egg capsules 0.156 (0.136-0.190) x 0.124 (0.099-0.140), spheroidal, 12-18 (15, n=20) in each proglottis; containing 15-22 (17, n=10) eggs, 0.045-0.051 (0.049) x 0.036-0.041 (0.038, n=5). Oncosphere oval 0.017-0.018 (0.018, n=5) x 0.014-0.016 (0.015, n=5), embryonic hooks 0.005-0.007 long.

Host

Dromaius novae-hollandiae (Latham, 1790) (Struthioniformes: Dromaiidae)

Location in host

Small intestine.

Etymology

This species is named after the host, *Dromaius novae-hollandiae*.

Raillietina mitchelli sp. nov. (FIGS 31-38)

Holotype: Keith, SA (36°06'S, 140°19'E), SAMA AHC S28306.

Paratypes: Keith, SA, SAMA AHC S28307, 31380, BMNH 2000.5.17.61-65.

Other Material examined: Yunta, SA, Coll. G. E. Ford, Lix. 1981, SAMA AHC 11181

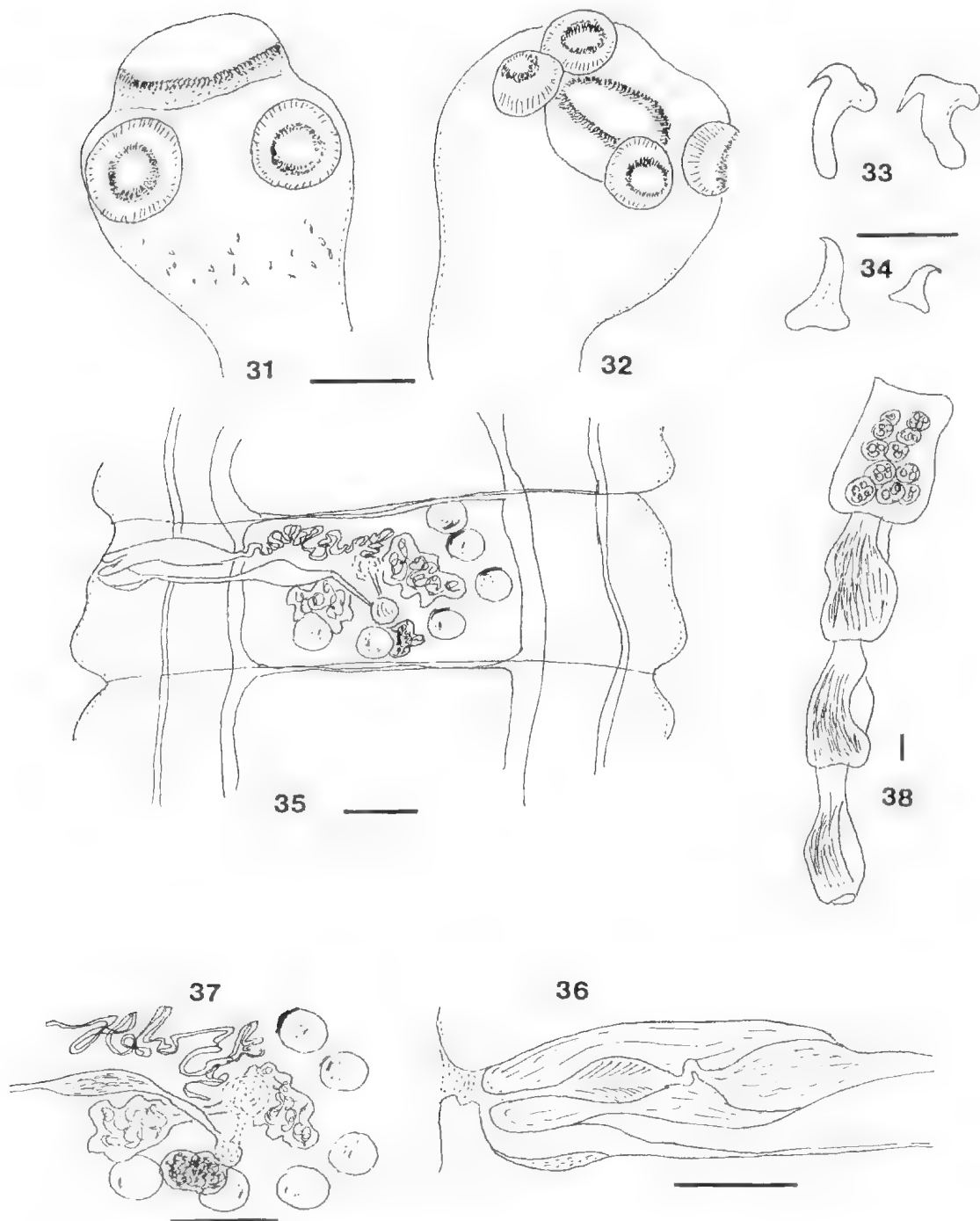
Description

Cestodes up to 120 long in relaxed specimens. Strobila containing approximately 1120 proglottides. Scolex small, 0.224-0.340 (0.298, n=45) in diameter (Figs 31, 32), usually with eversible rostellum 0.108-0.154 (0.138, n=40) in diameter. Rostellum armed with 296-380 (316, n=20) hammer-shaped hooks in two rows. Larger, inner rostellar hooks 0.009-0.012 (0.011, n=70) long; outer, smaller rostellar hooks 0.008-0.010 (0.009, n=70) long (Fig. 33). Surface of everted rostellum, anterior to rostellar hooks, covered by minute accessory spines, 0.010-0.020 long, visible under high magnification only. Suckers 0.055-0.088 (0.072, n=40) in diameter, armed with 4-6 rows of hooks 0.004-0.010 long (Fig. 34). Neck absent.

Proglottides craspedote. Mature proglottides wider than long, 0.600-0.900 (0.822) x 0.180-0.220 (0.204, n=10) (Fig. 35). Genital pores, single, unilateral. Genital ducts passing between osmoregulatory canals, larger ventral osmoregulatory canal, 0.020 in max. diam., lying internal to dorsal canal, 0.012 in max. diam. Ventral canal joined by transverse osmoregulatory canal in posterior margin of proglottides. Transverse dorsal canal not seen.

Genital outlage first appearing in proglottides 400-520. Male and female genitalia mature in proglottides 640-750. First gravid proglottides 1000 with 100-120 gravid proglottides terminating with 10-20 compact proglottides becoming progressively longer than wide.

Genital atrium small, situated in anterior half of lateral proglottis margin. Cirrus sac 0.152-0.176 (0.161) x 0.052-0.044 (0.038, n=10) (Fig. 36) not reaching ventral osmoregulatory canal. Distal region of cirrus lined with spines, of greater internal diameter than sinuous mid region; proximal region forms spherical internal seminal vesicle 0.028-0.052



Figs 31-38. *Raillietina mitchelli* sp. nov. 31. Scolex with everted rostellum. 32. Scolex with retracted rostellum. 33. Rostellar hooks. 34. Sucker hooks. 35. Single mature proglottis. 36. Cirrus and distal vagina. 37. Female genitalia. 38. Terminal gravid proglottides. Scale bars = 0.1 mm, 31, 32, 35, 37, 38; 0.01 mm, 36; 33, 34; 0.05 mm.

(0.040) x 0.020-0.032 (0.026, n=10). Vas deferens slightly coiled at midline of proglottis. Testes 0.048-0.060 (0.053, n=10) in diameter, dorsal to and overlying female genital glands. Testes 5-6 (5, n=20) per proglottis, one frequently overlying vitellarium with additional testes. 1 poral and 3-4 aporal.

Vagina opening to genital atrium posterior to cirrus sac. Distal region, dilated, 0.082 x 0.024-0.032, mid region, narrow, straight, leads medially posterior to vas deferens, terminating in fusiform seminal receptacle 0.124-0.152 (0.143) x 0.024-0.036 (0.028, n=10). Ovary bilobed (Fig. 37). Poral lobe 0.064-0.096 x 0.104-0.112, consisting of 1-3 transversely elongate lobules. Aporal lobe, 0.112-0.160 x 0.128-0.160 consisting of 3-4 lobules. Vitellarium irregularly ovoid, 0.056-0.076 (0.070) x 0.040-0.056 (0.049, n=10). Mehlis gland spherical, anterior to vitellarium 0.024-0.032 (0.028, n=10) in diameter. Uterine duct passing anterior to vitellarium, terminating dorsal to ovary. Uterus absent. Gravid proglottides wider than long 0.084-1.120 (0.964) x 0.272-0.360 (0.316, n=10) containing 9-15 egg capsules 0.140-0.170 (0.150) x 0.100-0.150 (0.130, n=10) each with 12-18 (15, n=10) eggs 0.041-0.049 (0.045) x 0.035-0.045 (0.040, n=10). Terminal segments shrivelled (Fig. 38). Oncosphere 0.015-0.018 (0.017) x 0.014-0.017 (0.016, n=10); oncospherical hooks 0.004-0.006 long.

Host

Dromaius novaehollandiae (Latham, 1790) (Struthioniformes: Dromaiidae).

Location in host

Small intestine.

Etymology

This species is named for Sir Mark Mitchell in acknowledgment of support of this project through the Sir Mark Mitchell Foundation.

Comparison with other species

Of the species of *Raillietina* with hosts in the Struthioniformes, *R. dromaius* sp. nov. resembles *R. casuarii* found in the New Guinean cassowary, *Casuarinus picticollis* in the size of the rostellar hooks (Kotlán 1923). However, *R. dromaius* is smaller than *R. casuarii*, has fewer rostellar hooks (142 v. 250), fewer and smaller testes and there are fewer eggs per capsule. *Paroniella appendiculata* Fuhrmann, 1909 described from an unknown host in New Guinea is similar in size to *R. dromaius* with 130 rostellar hooks 0.036-0.043 in length. However, *P. appendiculata* has only one egg per capsule (diagnostic for the genus *Paroniella*), a smaller cirrus sac and more testes than *R. dromaius*.

Raillietina chiltoni sp. nov. resembles *R. infrequens* (Kotlán, 1923) in the size of the strobila, scolex and rostellar hooks, the number of rostellar

TABLE 1. Key features of *Raillietina* species in emus

	<i>R. australis</i>	<i>R. beverleyae</i>	<i>R. chiltoni</i>	<i>R. dromaius</i>	<i>R. mitchelli</i>
	Mean	Mean	Mean	Mean	Mean
	Range	Range	Range	Range	Range
Size of Large Rostellar hooks	0.025	0.019	0.032	0.056	0.011
Size of small Rostellar hooks	0.020	0.016	0.027	0.048	0.009
Dimension of Cirrus sac					
Length	0.158	0.298	0.108	0.257	0.161
Width	0.020	0.080	0.038	0.044	0.038
Number of Rostellar hooks	280-362	304-412	302-378	124-156	296-380
Dimension of Scolex	0.416-0.568	0.480-0.736	0.545-0.832	0.480-0.752	0.224-0.340

hooks and testes. However, *R. chiltoni* differs from *R. infrequens* in the size of the cirrus sac (0.108 x 0.038) compared with (0.180-0.200 x 0.060) in *R. infrequens*. In addition, the cirrus of *R. chiltoni* has no armature and the internal seminal vesicle is smaller (0.015 x 0.012 v. 0.054 long). *Railletina chiltoni* has a larger rostellum (0.383) than *R. infrequens* (0.250) and has testes in distinctly aporal and poral groups that are never in the midline.

In the struthioniformes, *Cotugnia collini* can be distinguished from *Railletina* species by the presence of two sets of bilateral genital organs.

The species of *Railletina* described here can be distinguished from all congeners in the Struthioniformes by the size and number of the rostellar hooks, size of the scolex and size of the cirrus sac (Table 1).

Acknowledgments

We wish to thank I. Beveridge for his advice and comments in the early stages of this study which was supported by a grant from the Sir Mark Mitchell Foundation.

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**A NEW BLOOD-FLUKE, CARDICOLA FORSTERI, (DIGENEA:
SANGUINICOLIDAE) OF SOUTHERN BLUE-FIN TUNA
(THUNNUS MACCOYII) IN AQUACULTURE**

By THOMAS H. CRIBB*, MARTIN DAINTITH† & BARRY MUNDAY‡

Summary

Cribb, T. H., Daintith, M. & Munday, B. (2000). A new blood-fluke, *Cardicola forsteri* (Digenea: Sanguinicolidae) of southern blue-fin tuna (*Thunnus maccoyii*) in aquaculture. *Trans. R. Soc. S. Aust.* 124(2), 117-120, 30 November, 2000.

Cardicola forsteri sp. nov. (Digenea: Sanguinicolidae) is described from the heart of captive southern blue-fin tuna, *Thunnus maccoyii* (Scombridae), from South Australia. The new species is distinguished from other species of *Cardicola* by its very extensive testis, the length of its oesophagus, the length of its gut caeca and the form of its ovary. *Cardicola smithi* appears to be associated with heart and gill lesions¹.

A NEW BLOOD-FLUKE, *CARDICOLA FORSTERI*, (DIGENEA: SANGUINICOLIDAE) OF SOUTHERN BLUE-FIN TUNA (*THUNNUS MACCOYII*) IN AQUACULTURE

by THOMAS H. CRIBB¹, MARTIN DAINITTH¹ & BARRY MUNDAY²

Summary

CRIBB, T. H., DAINITTH, M. & MUNDAY, B. (2000) A new blood-fluke, *Cardicola forsteri*, (Digenea: Sanguinicolidae) of southern blue-fin tuna (*Thunnus maccoyii*) in aquaculture. *Trans. R. Soc. S. Aust.* 124 (2), 117-120, 30 November, 2000.

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Introduction

The southern blue-fin tuna (*Thunnus maccoyii*) has been used for aquaculture in southern Australia since 1992. The industry is based on the capture of juvenile fish and their subsequent fattening over a period of 6-9 months. The tuna have been subject to remarkably few diseases so far. Here we report a new parasite, a sanguinicolid blood-fluke; the associated pathogenesis will be described elsewhere.

Materials and Methods

Trematodes were collected from the hearts of freshly-killed fish hosts and fixed by pipetting them into near boiling phosphate buffered saline followed by immediate preservation in 10% neutral buffered formalin. Whole-mounts were stained with Mayer's haematoxylin, cleared with methyl salicylate and mounted in Canada balsam. Specimens for sectioning were embedded in paraffin wax, stained with haematoxylin and eosin and mounted in DEPEX. The following abbreviations are used: AHIC, The Australian Helminthological Collection at the South Australian Museum, Adelaide; QM, Queensland Museum, Brisbane.

Systematics

Family Sanguinicolidae von Graff, 1907
Cardicola Short, 1953

Cardicola forsteri sp. nov. (FIG. 1)

Type host: Scombridae - *Thunnus maccoyii* (Castlenau, 1872).

Type locality: Off Rabbit Island, South Australia, 34° 36' S, 135° 59' E

Other localities: Louth Island, South Australia, 34° 35' S, 135° 57' E.

Site: heart.

Material examined: 15 adults including 3 sets of histological sections from Rabbit Is., 11 from Louth Is.

Deposition of specimens: Holotype and 9 paratypes (including 3 sets of sections) AHIC 28331-28340; 5 paratypes QM G 218017-21.

Description

(Measurements in µm of 10 gravid adults (means in parenthesis))

Body lanceolate, highly compressed dorso-ventrally, almost flat ventrally and convex dorsally, 2512-3688 (3228) x 608-928 (759). Tegumental spines restricted to distinct ventro-lateral rows (Fig. 1 a, c, d). Nerve commissure dorsal to oesophagus and just posterior to anterior end of body; main nerve bundles highly prominent in anterior half of body and discernible almost to posterior end of body.

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² COOPER, S. L. (1999) Histopathological changes in, and immune response of, southern blue-fin tuna (*Thunnus maccoyii*) infected with *Cardicola* sp. (Digenea: Sanguinicolidae). Honours thesis, University of Tasmania (unpubl.).

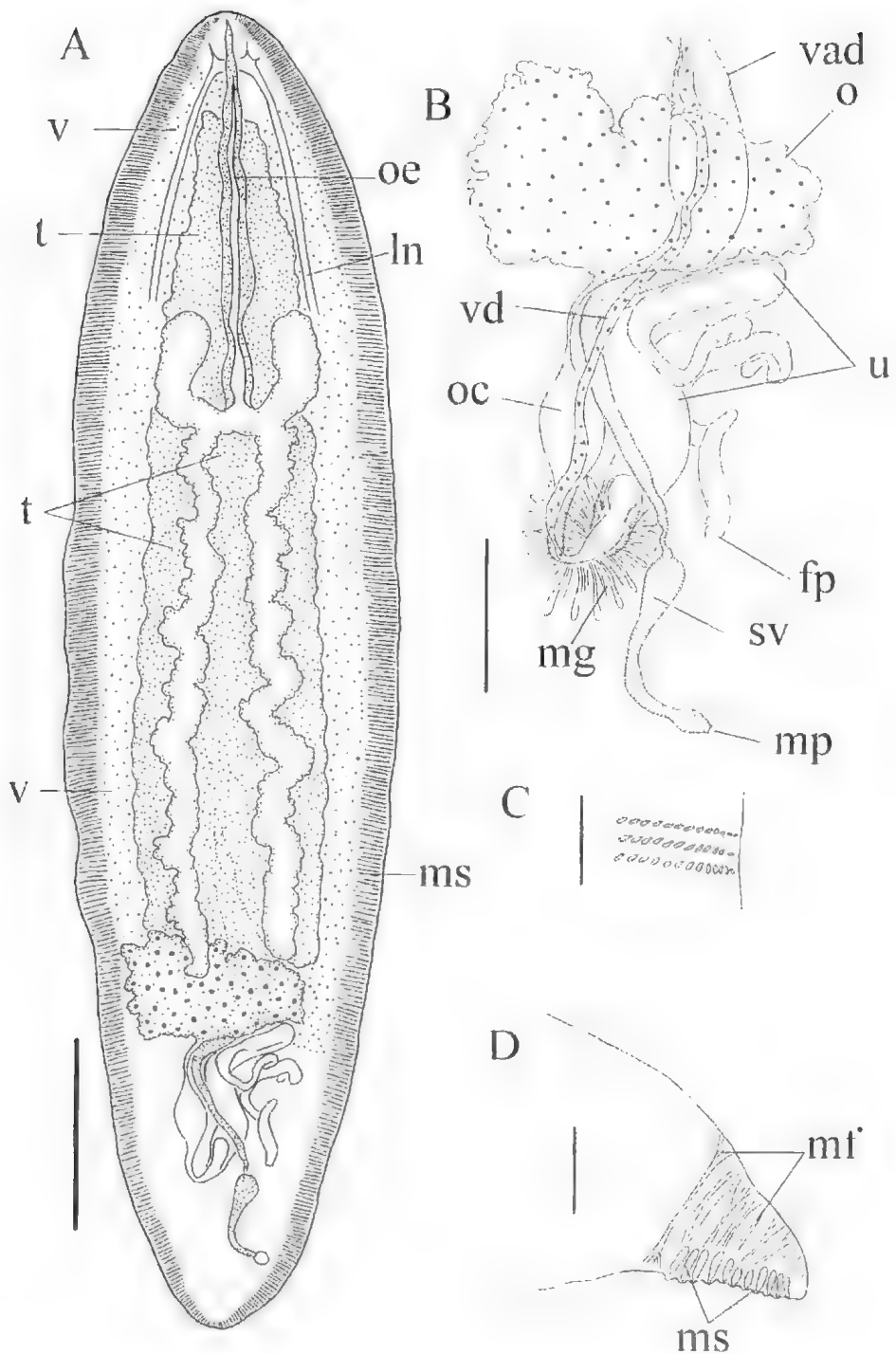


Fig. 1. *Cardicola forsteri* sp. nov. A. Adult, ventral view. B. Terminal genitalia, ventral view. C. Marginal spines, ventral view. D. Marginal spines and lateral muscles in transverse section. Scale bars = 500 μ m A; 200 μ m B; 50 μ m C, D. Abbreviations: fp - female pore, ln - lateral nerve, mf - muscle fibres, mg - Mehlis' gland, mp - male pore, ms - marginal spines, o - ovary, oe - oviductal chamber, oe - oesophagus, sv - seminal vesicle, t - testis, u - uterus, v - vitellinum, vad - vas deferens, vd - vitelline duct.

Mouth inconspicuous, opening ventro-subterminally. Oesophagus highly muscular; straight, 816-1136 (1014) long, 29.1-33.4 (31.5)% body length. Caeca H-shaped, sinuous; extending anteriorly to 672-928 (833) from anterior end of body; posterior caeca usually of distinctly uneven length, extending to 560-912 (777) from posterior end of body. Testis usually indistinct and difficult to discern, intra- and extra-caecal, extending from ovary posteriorly to just behind nervous commissure anteriorly; penetrated by dorso-ventrally orientated muscle fibres throughout. Vas deferens broad, prominent, originating midventrally to testis, running sinuously posteriorly, dorsal to ovary and ventral to uterus before entering seminal vesicle. Cirrus-sac absent. Seminal vesicle elongate, evenly curved, 116-238 (174) x 26-64 (45). Male genital pore sinistro-dorsal, close to lateral margin of body. Ovary irregularly lobed, penetrated by dorso-ventrally orientated muscle fibres throughout, 138-321 (237) x 263-462 (376). Oviduct originating posteriorly and passing posteriorly immediately to expand into oviducal chamber of variable size containing either oocytes (and perhaps zygotes) or sperm; if filled with sperm, chamber may become relatively enormous - up to 757 x 146. Duct emerging from oviducal chamber joined by vitelline duct then turning antero-medially and forming a type surrounded by prominent Melnik's gland cells. Vitelline follicles are diffuse and throughout body from level of anterior margin of ovary (sometimes lateral to ovary as well), dorsal and ventral to testis, and as far anteriorly as nervous commissure. Vitelline duct passes ventral to testis and ovary. Uterus filled with eggs, winding sinuously to ovary and then posteriorly to female genital pore, directly anterior to and well separated from male pore. Eggs very thin-walled and compressed against each other, 19-27 (23) x 11-16 (14). Excretory system not observed.

Etymology

The species is named for Mr Ron Forster, South Australian tuna farmer, in recognition of his contribution to the development of the enlightened management of captive tuna.

Discussion

The new species shows close affinity with the genus *Cardicola* Short, 1953 and is here identified as a new species in that genus. *Cardicola* is distinguishable from other genera of marine Sanguinicolidae by the combination of an H-shaped gut, a single largely inter-caecal testis, lack of a cirrus-sac, post-ovarian uterus and separate submarginal genital pores (Herbert *et al.* 1994). The present species agrees with all these characters except

that the testis is both inter- and extra-caecal, although one other species of *Cardicola*, *C. mugilis* Yamaguti, 1970, also has a partly extra-caecal testis. Only species of *Deontocylis* Linton, 1910 and *Pearsonellum* Overstreet & Koie, 1989 also have extra-caecal testes. Species of *Deontocylis* Linton, 1910 have a testis comprising "longitudinally elongated wings" (Yamaguti 1970) which extend lateral to the caeca in a form entirely different from that seen in the present species. The distribution of the vitellarium in the sole species of *Pearsonellum*, *P. corventum* Overstreet & Koie, 1989, is comparable to that of the present species, being both anterior to the caecal bifurcation and lateral to the posterior caeca, but that genus is distinct from the present species in possessing a cirrus-sac (Overstreet & Koie 1989).

Cardicola was erected (Short 1953) for *C. larvae* Short, 1953 from two species of *Cynoscion* (Sciaenidae). Subsequently, nine further species have been described or combined with this genus (Smith, 1997a,b) namely *C. ahi* Yamaguti, 1970, *C. cardicola* (Manter, 1947) Short, 1953, *C. chaetodontis* Yamaguti, 1970, *C. carinulacis* Manter, 1954, *C. grandis* Lebedev & Mamaev, 1968 (not mentioned by Smith, 1997a,b), *C. mugilis* Yamaguti, 1970, *C. whittemi* Manter, 1954, *C. congnema* Lebedev & Mamaev, 1968 and *C. brasiliensis* Knoff & Amato, 1992. Two of the species, *C. ahi* and *C. congnema* have been reported from tuna (family Scombridae, subfamily Thunninae).

The present species is immediately distinguished from all these species by the more extensive distribution of the testis which is both anterior to the caecal bifurcation and well lateral to the posteriorly directed caeca. In this study, however, we found the distribution of the testis exceedingly difficult to interpret and, although we find it convincing as a species-level character, we conclude that it is not an ideal character for recognition of species in this genus. Fortunately, several other characters also serve to distinguish this species. The length of the oesophagus, occupying 29-33% of the body length serves to distinguish it from *C. ahi* in which it is very short (approx. 18%) and species in which it is very long *C. cardicola* (41%) and *C. larvae* (50%). The relatively very short posterior caeca of *C. congnema* and the short divergent anteriorly directed caeca of *C. brasiliensis*, *C. chaetodontis*, *C. mugilis* and *C. whittemi* are distinct from the relatively long posterior caeca and the parallel anteriorly directed caeca of the present species. The present species generally resembles *C. carinulacis* but has a relatively larger and irregularly lobed rather than smooth ovary and has relatively shorter anteriorly directed gut caeca. Finally, *C. grandis* from a mutton (*Makaira* sp.) is a much larger worm (4.7-7.0 mm long compared with 2.5-3.7 mm for the present species). Its general

organisation is similar to that of the present species except that the testis is described as a single mass immediately behind the caecal bifurcation.

Overstreet & K  ie (1989), Herbert *et al.* (1994) and other authors have frequently referred to the presence of numerous dorso-ventrally orientated "ducts" or "structures" in sanguinicolids. These often pass through the gonads. Such structures are abundant in *Cardicola forsteri* and are here interpreted, as suggested in Herbert *et al.* (1994), as

muscle fibres. This interpretation appears reasonable in terms of the appearance of these refringent structures and in terms of function in trematodes where the requirement for flattening against the walls of blood vessels is clearly of great importance.

Acknowledgments

We thank D. Scott and T. Wright for assistance with the preparation of the specimens.

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**A NEW GALL MIDGE SPECIES (DIPTERA: CECIDOMYIIDAE)
INFESTING FRUIT OF PUNTY BUSH, SENNA ARTEMISIOIDES
(CAESALPINIACEAE) IN AUSTRALIA**

By PETER KOLESIK & SAUL A. CUNNINGHAM†*

Summary

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Key Words: Gall midge, Cecidomyiidae, *Contarinia sennicola*, *Senna artemisioides*, punty bush, Australia.

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KEY WORDS: Gall midge, Cecidomyiidae, *Contarinia sennicola*, *Senna artemisioides*, punty bush, Australia.

Introduction

A new species of gall midge, *Contarinia sennicola* Kolesik, is described from fruits of the punty bush, *Senna artemisioides* (DC.) Randell in south-eastern Australia. The new gall midge species was found independently by SAC during a study of the effect of habitat fragmentation on reproduction by plants in central New South Wales during 1997 and 1998 and by PK in 1998 during a South Australian Museum ecological survey in the Scotia Sanctuary, New South Wales. The host plant, *Senna artemisioides* (DC.) Randell (Caesalpinaceae), commonly known as the punty bush, is an endemic species widespread through the inland of mainland Australia (Harden 1990). It is a variable species, with 10 subspecies and nothosubspecies recognised (Harden 1990), including what was earlier considered to be *Cassia eremophila*. *Senna artemisioides* is invasive in grazed land in Western New South Wales (Cunningham *et al.* 1981) and commonly occurs in disturbed areas such as roadsides.

Materials and Methods

Branches of *Senna artemisioides* bearing fruits infested with larvae of the new species were collected in the Scotia Sanctuary, New South Wales

in November 1998. Branches were brought to the laboratory and the fruits processed in one of two ways. A small number was dissected and the larvae preserved in 70% ethanol. A larger number was cut open and the larvae transferred with entomological forceps into rearing pots containing wet sand into which they dug themselves. Pupation took place in the sand. Emerged adults together with pupal skins were preserved in 70% ethanol. Canada balsam mounts of type specimens were prepared according to the technique outlined by Kolesik (1995a). The types are deposited in the South Australian Museum, Adelaide (SAMA) and the Australian National Insect Collection, Canberra (ANIC). Dried samples of infested plants are deposited in the State Herbarium of South Australia, Adelaide (AD). Measurements refer to the holotype and paratypes.

To determine the distribution of *Contarinia sennicola* 20 fruits were collected from two plants at each of 11 sites (i.e. 440 fruits) in December 1997 and 1998. Sites ranged from a large reserve (i.e. Nombinnie Nature Reserve >140,000 ha) to narrow roadside strips of vegetation in central New South Wales (Table 1). All fruits were opened and inspected for the presence of *Contarinia sennicola* larvae. Because it is possible to overlook larvae if they are present in small numbers or when they are young and thus very small, the frequency of occurrence recorded here is likely to be a conservative estimate.

Genus *Contarinia* Rondani, 1860

Contarinia Rondani, 1860: 289

Type species: Tipula loti De Geer, 1776 by original designation

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TABLE 1. *Infestation of Senna artemisioides* fruits by larvae of *Contarinia sennicola*.

Year	Site	Latitude	Longitude	% fruits with larvae (plant 1, 2)
1998	Stackpoole SF	33° 50.6'	145° 50.6'	95, 82
1998	Roadside near Stackpoole SF	33° 48.1'	145° 51.2'	55, 35
1997	Roadside near Denny SF	34° 01.3'	145° 51.2'	45, 45
1998	Pulletop NR	33° 58.1'	146° 04.9'	45, 80
1997	Roadside near Pulletop NR	33° 56.2'	146° 07.3'	10, 50
1997	Nombinnie NR	33° 02.0'	146° 06.6'	65, 65
1997	Conaparra SF	33° 51.1'	146° 23.4'	75, 45
1997	Roadside near Conaparra SF	33° 51.8'	146° 23.8'	55, 20
1997	Roadside near Taleeban	33° 53.3'	146° 28.0'	20, 25
1997	Gubbatta NR	33° 38.3'	146° 33.0'	35, 44
1997	Roadside near Gubbatta NR	33° 38.3'	146° 31.5'	35, 30

SF = State Forest, NR = Nature Reserve

Contarinia is a large, worldwide genus used as a catch-all category for the tribe Cecidomyiini. It includes species with long, tapered ovipositors, bifilar male flagellomeres and terminal larval papillae consisting of two pairs of setose and one of aetose, stublike papillae. So far 12 species of this genus have been found that are native to Australia, with 11 of them forming a natural group feeding on inflorescences and seed-heads of grasses (Harris 1979). The new gall midge together with *Contarinia bursariae* from fruits of *Bursaria spinosa* (Pitosporeaceae) (Kolesik 1995h), are the only non-grass feeding species of this genus known from Australia.

Contarinia sennicola Kolesik sp. nov.
(FIGS 1-9)

Holotype: ♂, Scotia Sanctuary, New South Wales, Australia (30°11' S, 141°11' E), 11.xii.1998, P. Kolesik, reared from fruits of *Senna artemisioides* (DC.) Randell, larvae collected 21.xi.1998, (SAMA, I21480)

Paratypes: 2 ♂♂, 3 ♀♀, 3 pupal skins (SAMA, I21481-I21488), 2 ♂♂, 2 ♀♀, 2 pupal skins (ANIC), same data but emerged 13.xii.1998 - 17.i.1999; 3 larvae, (SAMA, I21489-I21491), 2 larvae (ANIC), collected with holotype.

Other material: galls, collected with holotype, AD107823, AD107824 (AD).

Male (Figs 1-4)

Colour: Head yellow with eyes dark brown, antennae brown, thorax brown, abdomen with sclerotised parts grey and non-sclerotised parts yellow.

Head: Postvertical peak present. Antenna: scape and pedicel as broad as long; flagellomeres 12 in number, first and second fused; circumilar loops

reaching midlength of next node. Palpus four-segmented. Eye facets rounded, close together, eye bridge 8 - 10 facets long. Labella large, triangular in frontal view, pointed apically, each with 7 - 9 lateral setae. Frons with 4 - 6 setae per side.

Thorax: Wing length 1.2 mm (1.0 - 1.3, $n = 5$), width 0.5 mm (0.4 - 0.5); vein C broken at juncture with R_5 , R_5 barely visible, in form of pigmented area. M_{1+2} not visible; C, R_4 , Cu pigmented. Claws simple, curved at midlength, empodium as long as claws.

Abdomen: Sclerites with a pair of anterior trichoid sensilla and setae more or less evenly distributed. **Genitalia:** gonocoxites cylindrical, setose, setulose; gonostylus about same width entire length, sparsely, evenly setose, with small setulose area at base, distally with strong tooth; cerci rectangular, slightly broadened distally, separated by shallow, wide incision, setose distally, setulose; hypoproct fleshy, bilobed, lobes round, each with few setae apically, setulose; aedeagus tapered distally, shorter than cerci.

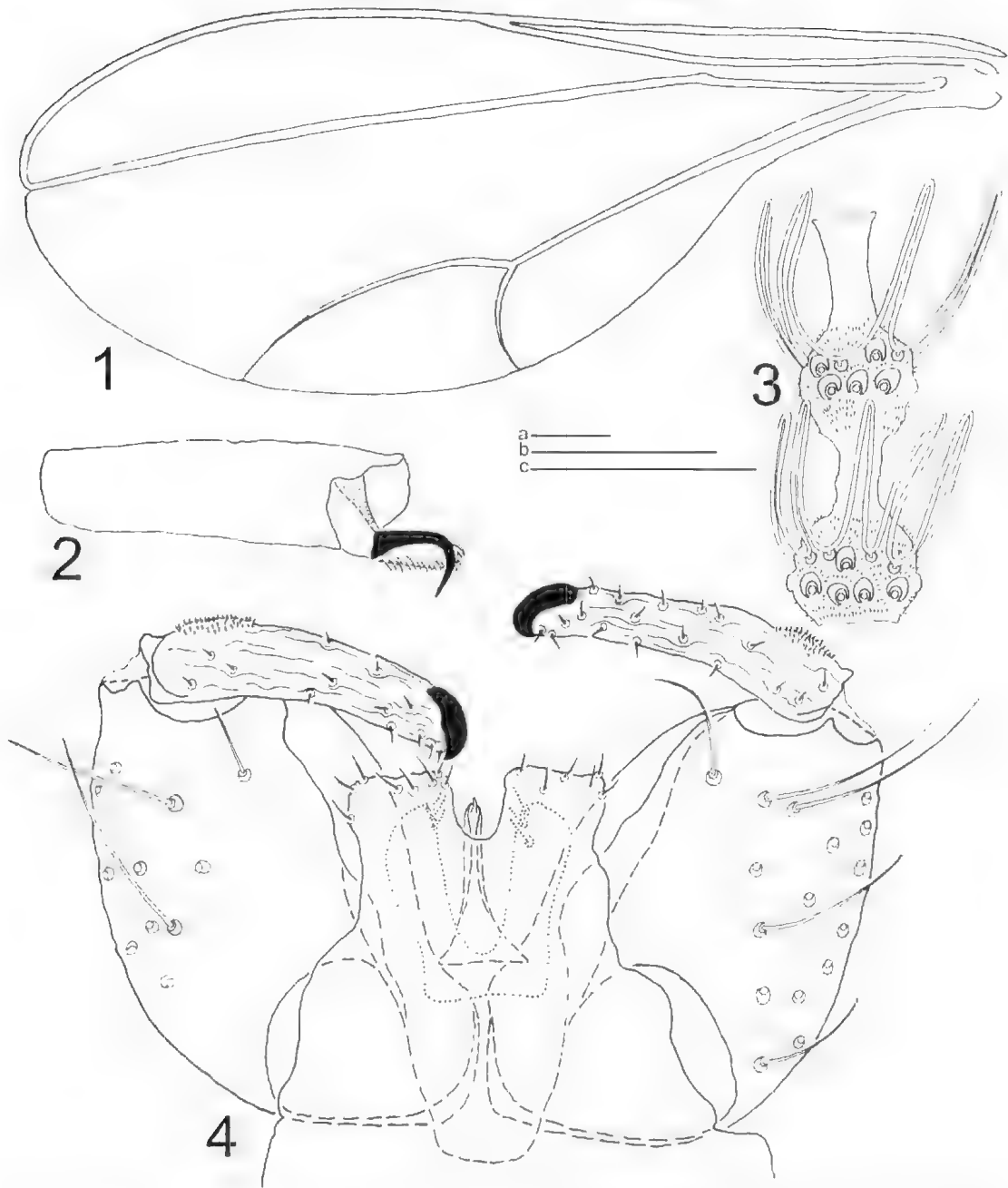
Female (Figs 7, 8)

Head: Flagellomeres with necks about $1/3$ length nodes. Circumfila appressed, consisting of two transverse rings connected by two longitudinal bands.

Thorax: Wing length 1.5 mm (1.4 - 1.6, $n = 5$), width 0.6 mm (0.5 - 0.6). Colour and other characters as in male.

Pupa (Fig. 9)

Colour: antennal horns, prothoracic spiracles, dorsal spines light brown, remaining parts unpigmented. Length 1.8 mm (1.5 - 2.2, $n = 5$) Antennal horns small, angular, sclerotised. Cephalic papillae with long, robust setae. Two pairs of lower facial papillae, one of each setose and one aetose, A

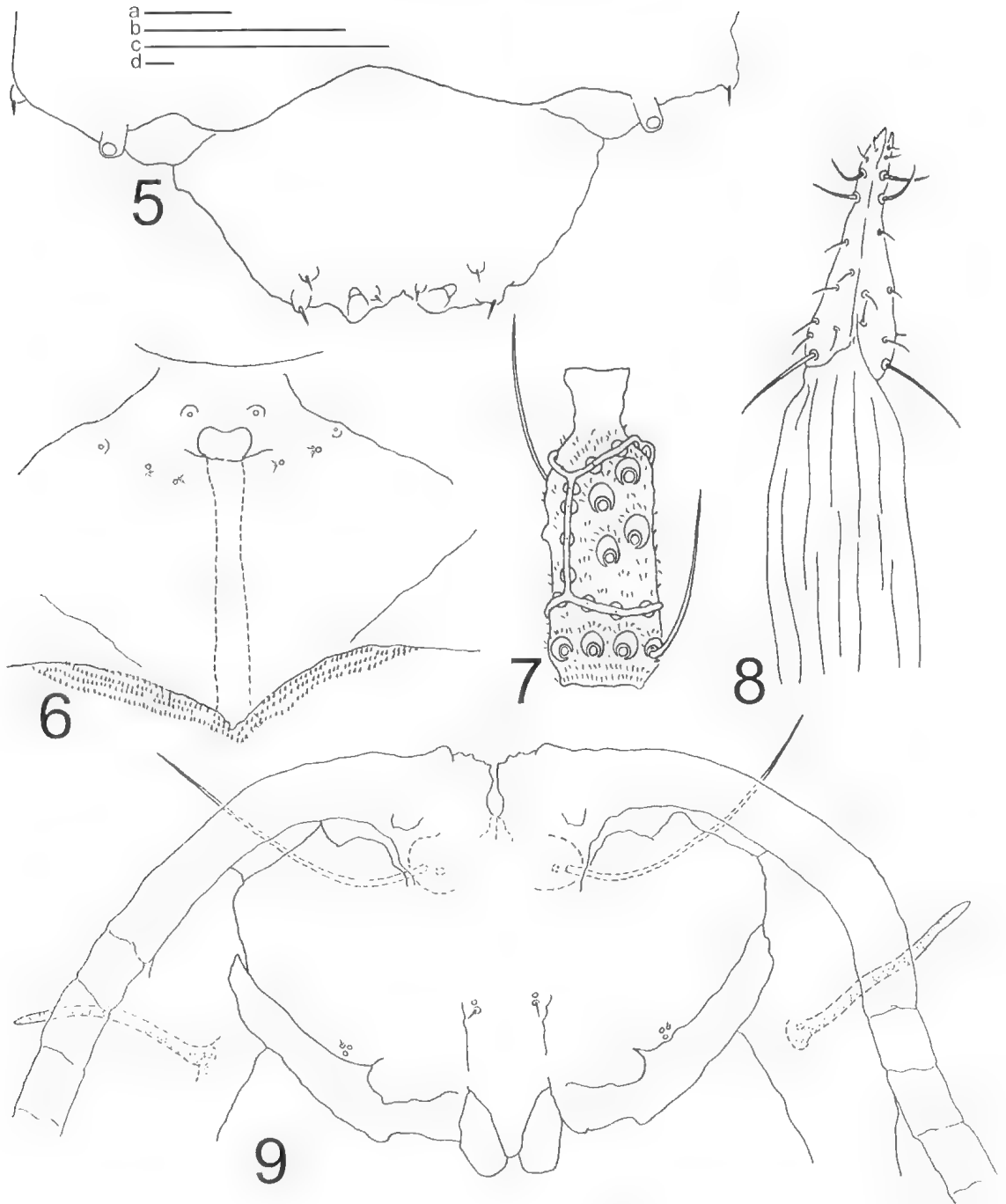


Figs 1-4. Male of *Contarinia semnicola*. 1. Wing. 2. Last tarsomere with claw and empodium. 3. Sixth flagellomere. 4. Genitalia in dorsal view. Scale bars = 50 μ m (Fig. 1 = a, Figs 2, 4 = b, Fig. 3 = c).

pair of triplets of lateral facial papillae, one of each triplet with minute seta, two acetose. Prothoracic spiracle long, narrow, trachea ending at its apex. Integument of abdominal segments covered with spiculae, slightly larger and denser dorsally. Second to eighth abdominal segments with sclerotised, simple dorsal spines.

Last instar larva (Figs 5, 6)

Colour: yellow. Length 2.2 mm (2.0 - 2.4, n = 5). Integument smooth except several ventral transverse rows of spiculae on anterior half of abdominal and second and third thoracic segments. Head with postero-lateral apodemes as long as head length. Spatula with long shaft, narrow apical enlargement



Figs 5-9. *Contarinia sennicola*. 5, 6 larva, 7, 8, female, 9 pupa. 5. Terminal segment in dorsal view. 6. Sternal spatula with adjacent papillae. 7. Sixth flagellomere. 8. End of ovipositor with cerci. 9. Anterior part in ventral view. Scale bars = 50 μ m (Figs 5, 6 = a, Fig. 7 = b, Fig. 8 = c, Fig. 9 = d).

with small, rounded lobes divided by shallow incision. Basal papillae typical for supertribe (Gagné 1989), terminal papillae: one pair stublike, three pairs with thick setae. Anus ventral.

Etymology

The specific name is a combination of "*Senna*", the generic name of the host plant and "*cola*", Latin for dweller/inhabitant.

Fruit damage, biology and geographical distribution

Larvae of the new species live inside fruit capsules of *Senna artemisioides* without causing any apparent deformation of the capsule but reducing the number of seeds that develop. In transmitted light, 5–50 larvae can be recognised feeding inside the capsule. Late instar larvae create single or multiple openings in the capsules and leave the fruits by jumping up several centimetres. Pupation takes place within the soil. The biology and infestation symptoms of the new species are very similar to those of its Australian congener *Contarinia bursariae*, a species that infests fruit capsules of *Bursaria spinosa* Cav. (Pittosporaceae) (Kolesik 1995b). The incidence of *Contarinia sennicola* larvae in fruits examined was very high. All of the 22 plants sampled, in sites separated by as much as 106 km, had larvae in one or more fruits (Table 1).

Remarks

Contarinia sennicola differs morphologically from the other known Australian, non-grass feeding, congener, *C. bursariae* in several characters. In *C. sennicola*, the male cerci are broadened distally, the female cerci have one long proximal sensory seta each and the larval spatula has rounded apical lobes and a narrow, equally wide shaft. In *C. bursariae*, the male cerci are not broadened distally; the female cerci have two short proximal setae each and the larval spatula has angular apical lobes and a distally widened shaft.

The frequency of aborted and damaged seeds in fruits of *S. artemisioides* occupied by *C. sennicola* larvae suggests that the larvae might be responsible for reducing seed production in this leguminous plant. In some plant species, especially in legumes, predispersal seed predation by insects is an important factor in low seed production (Auld 1983, 1986; Cunningham 1997, 2000b). Cunningham (2000a) found high levels of predispersal insect seed predation in *S. artemisioides* during a study of plant reproduction in habitat fragments in the areas considered in the present paper. *Contarinia sennicola* was found at sites with relatively few fruiting shrubs as well as at those with abundant fruit production. Larvae were found in fruits with few seeds as well as in those with many undamaged seeds. The pervasive presence of *Contarinia sennicola*, in spite of this heterogeneous fruiting pattern, might indicate that it causes widespread seed loss, but is not a key determinant of variation in seed production by *S. artemisioides*. *Contarinia sennicola* may nevertheless play a role as one of the factors in the population dynamics of the plant.

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INTESTINAL HELMINTHS OF FIVE SPECIES OF SCINCID LIZARDS (SAURIA: SCINCIDAE) FROM WESTERN AUSTRALIA

BY *STEPHEN R. GOLDBERG** & *CHARLES R. BURSEY†*

Summary

Goldberg, S. R. & Bursey, C. R. (2000) Intestinal helminths of five species of scincid lizards (Sauria: Scincidae) from Western Australia. *Trans. R. Soc. S. Aust.* (2000). 124(2), 127-133, 30 November, 2000.

Intestines of five species of scincid lizards, *Ctenotus brooksi*, *C. pantherinus*, *Egernia depressa*, *E. inornata* and *E. striata* from Western Australia were examined for helminths. One species of Cestoda, *Oochoristica australiensis* and eight species of Nematoda, *Kreisiella chrysocampa*, *Maxvachonia chabaudi*, *Parapharyngodon kartana*, *Pharyngodon kartana*, *P. tiliquae*, *Wanaristrongylus ctenoti*, *W. papangawurpae* and *Abbreviata* sp. (larvae) were found. Fifteen new host records were reported.

Key Words: Cestoda, Nematoda, scincid lizards, Australia.

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KEY WORDS: Cestoda, Nematoda, scincid lizards, Australia.

Introduction

Scincidae is the dominant lizard family in Australia. It contains some 313 species (Cogger 2000) which constitute approximately 57% of all lizard species in Australia (Greer 1989). Helminth records exist for 49 species (Mawson 1972; Goldberg and Bursley 1995; Goldberg *et al.* 1999; Pichelin *et al.* 1999). The purpose of this paper is to report additional helminth records for *Ctenotus brooksi* (Loveridge, 1933), *C. pantherinus* (Peters, 1866), *Egernia inornata* Rosen, 1905, *E. striata* Sternfeld, 1919 and the first helminth records for *E. depressa* (Günther, 1875). Patterns of helminth infections in Australian skinks are examined and 19 new host records are added to the checklist of Pichelin *et al.* (1999).

Ctenotus brooksi inhabits sandy deserts of south-eastern Western Australia and adjacent desert areas of South Australia, the Northern Territory and parts of Queensland and New South Wales. *Ctenotus pantherinus* is widely distributed in south-western Western Australia, northern South Australia, the Northern Territory and western Queensland. *Egernia depressa* occurs in central-western coastal regions of Western Australia. *Egernia inornata* is widely distributed through the southern half of Western Australia from South Australia to western Queensland, in western New South Wales and north-western Victoria. *Egernia striata* is widely distributed through the interior of Western Australia to south-western Northern Territory and north-western South Australia (Cogger 2000).

Materials and Methods

Ninety three preserved lizards were borrowed from the herpetology collection of the Natural History Museum of Los Angeles County (LACM) and examined for intestinal helminths. These specimens had been collected between October 1966 and October 1968 for use in an ecological study (Pianka 1972) and were subsequently fixed in formalin and preserved in alcohol. Because the ecological study included stomach analysis, only small and large intestines remained with the carcasses. Stomachs had been deposited in the Western Australian Museum, Perth, Western Australia and carcasses in LACM. Numbers of individuals, mean snout-vent length (SVL), museum accession numbers and collection sites (longitudes, latitudes) for each species are given in the Appendix.

The small and large intestines, body cavity and liver of each lizard were examined for helminths using a dissecting microscope. Each helminth was placed on a glass slide in a drop of undiluted glycerol for study under a compound microscope. Nematodes were identified from these preparations; the cestode was stained with hematoxylin and mounted in balsam for identification.

Results

Gravid individuals of one species of Cestoda, *Ochhoristica australiensis* Spasskii, 1951 and seven species of Nematoda, *Kreisiella chrysocampa* Jones, 1985, *Maxyachonia chabaudi* Mawson, 1972, *Parapharyngodon kartana* (Johnston & Mawson, 1941), *Pharyngodon kartana* (Johnston & Mawson, 1941), *P. tiliquae* Baylis, 1930, *Wammatstrongylus ctenoti* Jones, 1987, *W. papangawurpae* Jones, 1987,

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were found. Cysts containing larvae of *Abbreviata* sp. were also found. Prevalence, mean intensity \pm SD, range, location of helminth infections by host species and 15 new host records are presented in Table 1. Because physalopterid nematodes normally inhabit the stomach (Anderson 1992), the values in Table 1 may under-report *Kreisiella chrysoecampa*. Cysts containing larvae of *Abbreviata* occasionally

occur on stomach walls (Jones 1995) and may also be under-reported in Table 1.

Discussion

Infections of Australian scincid lizards by nematodes are summarized in Table 2. Infections by trematodes, cestodes and acanthocephalans are

TABLE 1. Prevalence (%), mean intensity ($\bar{x} \pm$ SD), range (r) and location for helminths from five species of Australian scincid lizards.

Host Helminth Location	<i>Crenotus brooksi</i>		<i>Crenotus pantherinus</i>		<i>Egernia depressa</i>		<i>Egernia inornata</i>		<i>Egernia striata</i>			
	%	$\bar{x} \pm$ SD	%	$\bar{x} \pm$ SD	%	$\bar{x} \pm$ SD	%	$\bar{x} \pm$ SD	%	$\bar{x} \pm$ SD		
Cestoda												
Anoplocephalidae												
<i>Oochoristica australiensis</i>	-	-	-	-	*13	1.0	-	-	-	-		
Small intestine												
Nematoda												
Physalopteridae												
<i>Abbreviata</i> sp. (larvae)	*4	1.0	-	*60	36 \pm 42.7	1-121	-	-	-	-		
cysts in visceral pentoneum												
<i>Kreisiella chrysoecampa</i>	16	1.3 \pm 0.5	1-2	10	1.5 \pm 0.7	1-2	-	-	37	4.3 \pm 4.7	1-13	
Small intestine, large intestine												
Cosmoceridae												
<i>Maxvachonia chabaudi</i>	*8	1.0	-	*15	1.7 \pm 1.2	1-3	-	-	*11	5.5 \pm 6.4	1-10	
Small intestine, large intestine												
Pharyngodonidae												
<i>Parapharyngodon kartana</i>	-	-	-	*35	11.3 \pm 19.1	1-52	-	-	*14	2.3 \pm 2.3	1-5	
Small intestine, large intestine												
<i>Pharyngodon kartana</i>	-	-	-	*15	7.7 \pm 10.7	1-20	-	-	-	-	-	
Large intestine												
<i>Pharyngodon tilliquae</i>	-	-	-	-	-	-	*88	94.0 \pm 55.1	12-177	*42	41.1 \pm 23.7	12-76
Large intestine												
Amphibiophiliidae												
<i>Wanaristrongylus crenoti</i>	*4	4.0	-	20	1.8 \pm 1.0	1-3	-	-	*81	14.8 \pm 14.0	2-46	
Large intestine												
<i>Wanaristrongylus papangawarpae</i>	-	-	-	-	-	-	-	-	16	5.3 \pm 6.7	1-13	
Large intestine												

*: New host record

listed in Pichelin *et al.* (1999). Additional records for scincid lizards are given in Goldberg & Bursey (1995) and Goldberg *et al.* (1999). Including the data from this paper, helminth records now exist for 50 species of Australian skinks; 16% (50/313) of the Australian scincid fauna. Mean number of helminth species per skink species was 2.8 ± 2.1 SD, range 1–12 helminth species. *Tiliqua scincoides* had the greatest helminth diversity (12 species); 18 different skink species are reported to harbour a single helminth species.

Of the Trematoda that infect Australian lizards, *Paradistomum crucifer* (Nicoll, 1914) has been reported from the scincids, *Hemiergis peronii*, *Lerista bougainvillii*, *Tiliqua scincoides* and *Trachydosaurus rugosus*, as well as a pygopodid, a gekkonid, and a varanid, *Mesocoelium microon* Nicoll 1914 from *Tiliqua scincoides*, *Microphallus* sp. from *Trachydosaurus rugosus*, an unidentified trematode from *Lerista bougainvillii*, and unidentified dioecoelids from an agamid (Pichelin *et al.* 1999). *Mesocoelium microon* has also been reported from amphibians collected in Queensland (Nicoll 1914). Species of *Microphallus* are parasites of freshwater fishes, although experimental infections have been established in amphibians, reptiles and mammals (Yamaguti 1958).

Five species of Cestoda have been reported from Australian scincid lizards, namely, *Cylindrotaenia allisonae* (Schmidt 1980) from *Hemiergis peronii* and *Lerista bougainvillii*, *C. hickmani* (Jones 1985) from *Lampropholis delicata* (De Vis, 1888), *L. guichenoti* (Duméril and Bibron, 1839), *Nannoscincus macrasi* (Lucas and Frost, 1894), *Saproscincus challengeri*, and *S. mustelinus* (O'Shaughnessy, 1874), *Ochhoristica australiensis* Spasskii, 1951 from *Trachydosaurus rugosus*, *O. trachysauri* (MacCallum, 1921) from *T. rugosus* and *O. vacuolata* Hickman, 1954 from *Egernia whitei* (Pichelin *et al.* 1999). M. Jones (1987) reported *Cylindrotaenia allisonae* to occur also in a gekkonid. MacCallum (1921) described *Taenia trachysauri* from specimens discovered in the intestine of a specimen of *Trachydosaurus rugosus* that had died in the New York Zoological Garden. Baer (1927) moved *T. trachysauri* to *Ochhoristica*. Johnston (1932) reported *O. trachysauri* in *T. rugosus*. Spasskii (1951) believed that substantial differences existed between the specimens described by MacCallum (1921) and Johnston (1932) and established *Ochhoristica australiensis* for Johnston's specimens. A major difference between *O. australiensis* and *O. trachysauri* is the arrangement of the testes; *O. australiensis* has one cluster, *O. trachysauri* has two. The specimen from *Egernia depressa* exhibited one cluster of testes. Unidentified species of *Ochhoristica* have been reported from

Hemiergis peronii and *Lerista bougainvillii* (Angel & Mawson 1968).

Cystacanths of Acanthocephala have been reported from Australian scincid lizards. *Sphaerorchinothynchus roundocaputatus* Johnston and Deland, 1929 from *Eulamptus quoyii* (Duméril & Bibron, 1839), *Hemiergis decresiensis* (Cuvier, 1829) and *Lampropholis guichenoti*, collected in New South Wales, and unidentified cystacanths from *Hemiergis peronii* collected in South Australia (Pichelin *et al.* 1999).

The pentastome *Ralhetella scincoides* Ali, Riley & Self 1984 was described from *Tiliqua scincoides* collected in South Australia (Ali *et al.* 1984) and has been reported from a gekkonid (Bursey & Goldberg 1999). Pentastomids were not listed in Pichelin *et al.* (1999).

Nematodes reported from Australian scincid lizards are listed in Table 2. Not included in Table 2 are reports of unidentified species of *Skryabinelazia* from *Ctenopus schomburgkii* collected in South Australia (Goldberg & Bursey 1995), reports of *Parapharyngodon kartana* and *Skryabinodon leristae* from a species of *Lerista* (= *Rhodona*) from South Australia (Mawson 1971) and reports of pharyngodonid or physalopterid larvae (Jones 1992, 1995; Goldberg *et al.* 1999; this paper). An unidentified species of *Skryabinelazia* was also reported from a gekkonid lizard from South Australia (Angel & Mawson 1968; Mawson 1971). Males of this species of *Skryabinelazia* have yet to be found; thus no species of *Skryabinelazia* has been reported from Australian hosts.

Unidentified specimens of Pharyngodonidae were reported from *Cryptoblepharus plagiocephalus* by Jones (1995) which could belong to any one of the nine oxyurid species listed in Table 2. More difficult to assess are reports (Jones 1992, 1995; Goldberg *et al.* 1999) of encysted larvae identified as *Abbreviata* sp., *Physaloptera* sp. or physalopterid larvae. Seventeen species of *Abbreviata* and two species of *Skryabinoptera* occur in Australian reptiles (Baker 1987); adults of species of *Physaloptera* are not known as parasites of Australian reptiles but seven species are known from Australian mammals, five from marsupials and two from native rodents (Norman & Beveridge 1999). Physalopterid larvae are widely distributed in Australia and have been reported from the scincid lizards, *Cryptoblepharus plagiocephalus*, *Ctenopus calurus*, *C. dux*, *C. grandis*, *C. helwae*, *C. pantherinus*, *C. quattuordecimlineatus*, *C. schomburgkii*, *Egernia mornata*, *E. striata*, *Eulamptus quoyii* and *Lerista guichenoti* (Wescher 1881) as well as from agamid, gekkonid and varanid lizards and several species of snakes (Jones 1995). Studies on diet have shown that varanid

lizards and the feral cat, *Felis catus* L., 1758, feed on skinks (Jones & Coman 1981; Shine 1986; James *et al.* 1992). Because these larvae are encysted and in relatively high prevalences, the skinks may serve as paratenic hosts.

Of the nematode species harboured by Australian scincid lizards (Table 2), *Hedriuris longispicula*, *Johupearsonia egeriina*, *Pharyngodon asterostoma*, *P. australis*, *P. hindlei*, *P. illiquae*, *Pneumonema illiquae*, *Spinicauda australiensis*, *Theladros trichysauri* and *Veyerzia tuberculata* are known only from skinks. *Abbreviata antarctica* is known from scincids, agamids, varanids and snakes. *Kreisiella chrysoampa*, *K. lesneuri*, *Parapharyngodon fitzroyi* are known from scincids and agamids. *Mutuvuhtonia brygool* is known from scincids, agamids and a varanid. *M. chabaudi* is known from scincids, a gekkonid, a varanid and a snake. *Parapharyngodon kartana* occurs in scincids, agamids and gekkonids.

Pharyngodon kartana and *Wanuristrongylus pipungawurpae* occur in scincids and gekkonids. *Physalopteroides filicauda* is known from scincids, agamids, gekkonids and varanids. *Pseudoricetularia disparilis* occurs in scincids, amphibians and mammals. *Skrjabinoptera goldmanae* is known from scincids, agamids, a gekkonid and varanids and *Wanuristrongylus etenoti* is known from scincids, an agamid, a gekkonid and a varanid (Owen & Moorhouse 1980; Pichelin *et al.* 1999).

Helminthological studies on additional species are needed before the helminth diversity of Australian skinks is known.

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Appendix

Scincid lizards borrowed from Natural History Museum of Los Angeles County (LACM) with longitude and latitude of collection sites and helminths deposited in the U.S. National Parasite Collection (USNPC).

Ctenotus brooksi (N = 25, Mean SVL = 42 mm \pm 3 SD, range = 37-48 mm) collected 1967 Western Australia (WA), LACM (55525, 26° 32' S, 125° 58' E), (55529-55531, 55533-55534, 26° 06' S, 127° 11' E), (55539, 23° 49' S, 128° 51' E), (55558, 55560-55561, 55563-55564, 55566, 55570, 55573-55574, 55578, 55584, 28° 08' S, 123° 55' E), (55585, 28° 09' S, 123° 56' E); Northern Territory, LACM (55541, 23° 13' S, 129° 54' E) (55544, 55548, 55550-55551, 55553, 23° 13' S, 129° 54' E). USNPC 89250 *Abbreviata* sp. (3rd stage larva); USNPC 89247 *Kreisiella chrysocampa*; USNPC 89248 *Marybachonia chabaudi*; USNPC 89249 *Wanaristromylyus crenati*; *Ctenotus pantherinus* (N = 20, Mean SVL = 42 mm \pm 3 SD, range = 37-48 mm) collected 1967, WA, LACM (55986-55988, 28° 27' S, 119° 05' E), (55991, 56000-56001, 56004, 28° 30' S, 125° 50' E), (56032, 56035, 28° 08' S, 123° 55' E), (56038, 56040-56043, 28° 28' S, 122° 50' E), (56046, 26° 14' S, 121° 13' E), (56053-56054, 56058-56059, 56061, 26° 17' S, 121° 00' E). USNPC 89256 *Abbreviata* sp. (3rd stage larva); USNPC 89251 *Kreisiella chrysocampa*;

USNPC 89252 *Marybachonia chabaudi*; USNPC 89255 *Parapharyngodon kattana*; USNPC 89254 *Pharyngodon kattana*; USNPC 89255 *Wanaristromylyus crenati*; *Egeria depressa* (N = 8, Mean SVL = 91 mm \pm 7 SD, range 81-101 mm) collected 1968, WA, LACM (56403, 56404, 28° 27' S, 119° 05' E), (56409-56413, 56418, 27° 05' S, 119° 37' E). USNPC 89257 *Oochoristia australiensis*; USNPC 89258 *Pharyngodon tiliquae*; *Egeria inornata* (N = 19, Mean SVL = 73 mm \pm 4 SD, range 66-80 mm) collected 1966-1968, WA, LACM (56434, 56436, 56438, 56440, 56442-56443, 28° 27' S, 119° 05' E), (56447, 56450-56452, 28° 08' S, 123° 55' E), (56455, 56463-56464, 56466, 56472, 56474, 56477-56479, 28° 30' S, 125° 50' E). USNPC 89259 *Kreisiella chrysocampa*; USNPC 89260 *Marybachonia chabaudi*; USNPC 89261 *Pharyngodon tiliquae*; USNPC 89262 *Wanaristromylyus papangawipae*; *Egeria striata* (N = 21, Mean SVL = 95 mm \pm 8 SD, range 78-103 mm) collected 1967, WA, LACM (56513-56517, 56521-56525, 56530-56531, 56533, 56535-56537, 56539, 28° 28' S, 122° 50' E), (56541, 56545, 28° 28' S, 122° 51' E), (56546, 56548, 28° 28' S, 122° 50' E). USNPC 89263 *Parapharyngodon kattana*; USNPC 89264 *Pharyngodon tiliquae*; USNPC 89265 *Wanaristromylyus crenati*.

RE-EVALUATION OF THE DISTRIBUTION OF GEOCRINIA LAEVIS (ANURA: LEPTODACTYLIDAE) IN SOUTH AUSTRALIA

BY STEVEN J. WALKER† & PETER M. GOONAN**

Summary

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A survey of the known range of the Smooth Frog, *Geocrinia laevis* (Günther, 1864) in South Australia was undertaken to determine the current distribution and abundance of this species. A total of 58 locations was visited throughout the South East and *G. laevis* was collected or heard calling at 13 sites within or near the Reedy Creek / Dismal Swamp drainage system. Despite very few reports of this species in recent years it is locally abundant and under no obvious threat of decline.

Key Words: *Geocrinia laevis*, distribution, frogs, South Australia, frog census, status, conservation.

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Introduction

There have been few comprehensive studies to document the distribution of the frogs of South Australia. Brook (1984) produced an atlas of the known distribution of the frog fauna of SA by condensing published and unpublished data from various sources. Other published studies have generally been focused on unusual range extensions and first records in the State (Tyler 1971; Bird & Tyler 1990; Johnston 1990). Overviews and species lists for the State are given in Tyler (1977, 1978, 1994, 1997).

Since 1994 the South Australian Environment Protection Agency has conducted an annual frog census in September (November in the first year, September thereafter) involving the public making tape recordings of the frogs calling from waterways throughout South Australia. This work has highlighted the distribution and a measure of the seasonal abundance of frogs, mostly from the more southern parts of SA (Goonan *et al.* 1997, 1998; Walker *et al.* 1999). Some species are poorly represented or have not been recorded through the method being applied by the census, including *Geocrinia laevis* (Günther, 1864) which had not been recorded (Goonan *et al.* 1997, 1998; Walker *et al.* 1999). *Geocrinia laevis* is mainly an autumn-winter breeder, calling only infrequently during the period in which the frog census has been carried out.

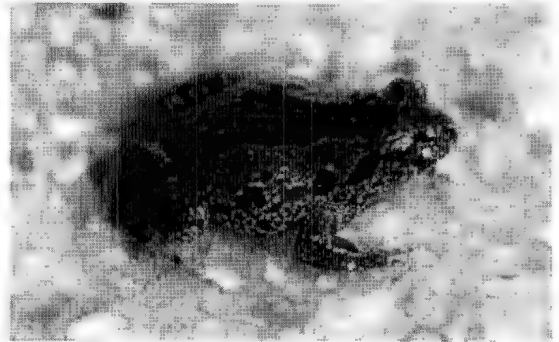


Fig. 1. *Geocrinia laevis* from Canunda Conservation Park (SVL = 33 mm).

Geocrinia laevis is a medium sized frog (22 – 35 mm snout vent length) with short limbs and smooth skin (Fig. 1) that may be easily confused with *Crinia signifera* Girard, 1853 or members of the genus *Pseudophryne* Fitzinger, 1843 (Barker *et al.* 1995). Distinguishing characteristics include pale pink patches underneath the legs, in the groin and sometimes in the axillae (Woodruff & Tyler 1968; Tyler 1978; Barker *et al.* 1995).

Like *Pseudophryne*, *G. laevis* does not breed in water. Males call from the ground in moist leaf litter and amongst grass. The advertisement call is a long slowly pulsed rattling or creaking sound, the first note often being the longest - "cre-e-e-e-e-e-ek cre-e-e-e-ek cre-e-ek cre-e-ek" (Woodruff & Tyler 1968; Barker *et al.* 1995). *Geocrinia laevis* lays large, unpigmented eggs in loose, elongated masses attached to moist terrestrial vegetation. Major development occurs inside the egg capsule and following flooding tadpoles hatch in the water, with complete

development taking about six months (Tyler 1994; Barker *et al.* 1995). The habitat of *G. laevis* is reported as being leaf litter in dry *Eucalyptus* or pine forests subject to temporary flooding (Tyler 1978; Barker *et al.* 1995).

Geocrinia laevis was first reported in South Australia from a specimen (South Australian Museum, Adelaide (SAMA) R8118) collected near Mt Burr in 1966 (Woodruff & Tyler 1968). Before this it had been found in Tasmania, King Island, the Grampians and in South West Victoria from Dartmoor to Pt Campbell (Woodruff & Tyler 1968; Beck 1975). Beck (1975) surveyed the South East of South Australia between 1968 and 1974 and found

that *G. laevis* was confined to the Reedy Creek and Dismal Swamp drainage system in the lower South East. Since then, there have been no major reports of this species.

With the major and continual modifications to the drainage system in the South East of South Australia it seemed pertinent to determine the current status of *G. laevis* in the region. As *G. laevis* may inhabit areas which are vulnerable to agricultural development and because there is no detailed knowledge of its current distribution it is possible that any future development may impact significantly upon populations of this species. The purpose of this study was to determine the current

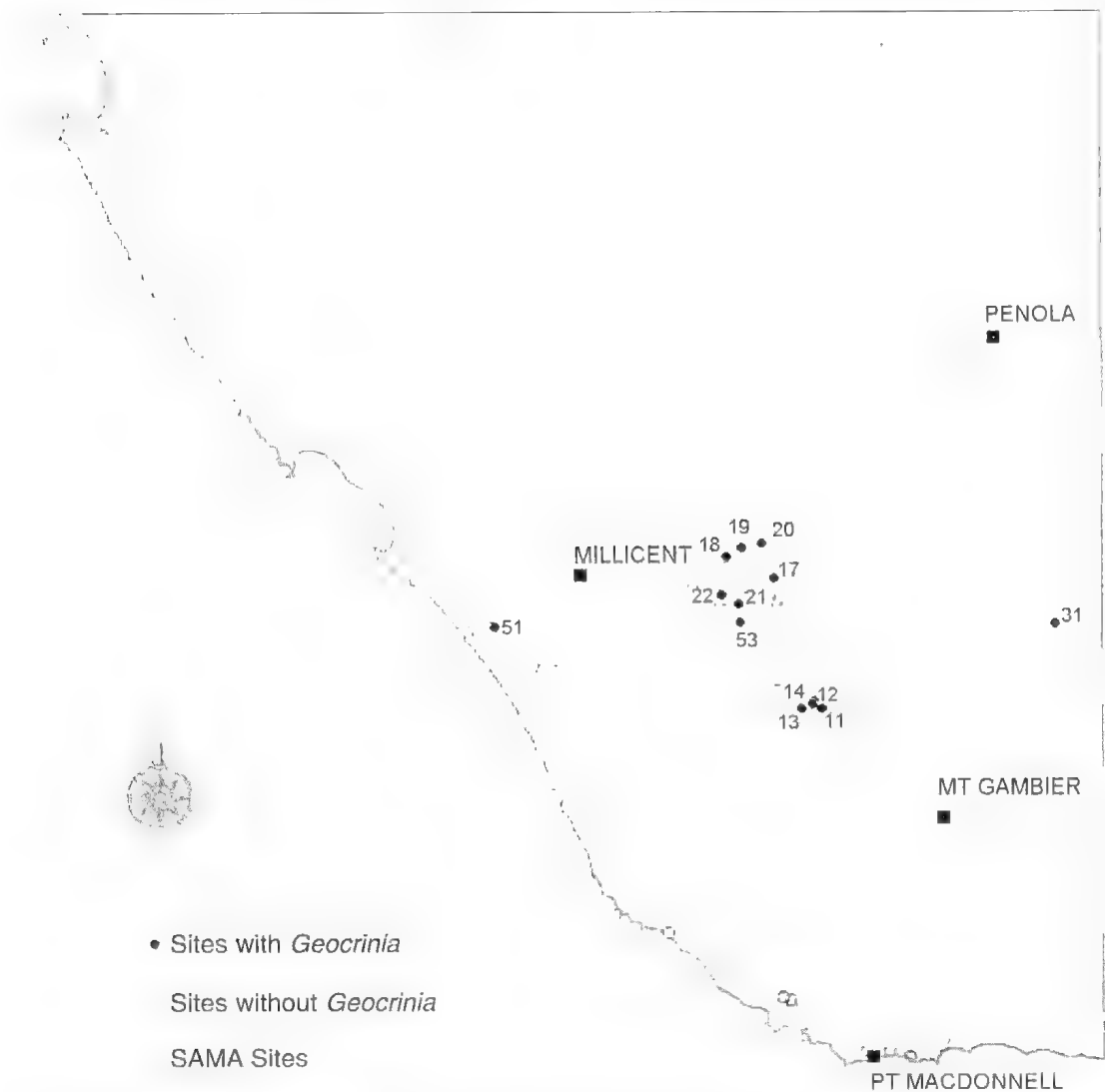


Fig. 2. Surveyed distribution of *Geocrinia laevis* in the South East of South Australia. Sites from SA Museum records are included for reference.

distribution and status of *G. laevis* in South Australia.

Materials and Methods

Existing data sources (published and unpublished) including SAMA records and NP&WS regional surveys (see Foulkes 1998) were examined. Locations were subsequently superimposed on floristic vegetation maps of the South East in order to predict possible suitable habitat for *G. laevis*. B. Grigg from Forestry SA also provided maps of forestry land and suggested areas where frogs might occur.

Surveys were undertaken during March, June and August 1999. A total of 58 locations was visited (Fig. 2), including 10 sites based on SAMA records and two sites from the NP&WS survey. The recorded coordinates for some of the SAMA sites appeared to be imprecise or inaccurate because the sites did not have suitable habitat for *G. laevis*; in these cases, sites with suitable habitats which were nearby the recorded coordinates, were sampled instead. Each site with *G. laevis* present was visited only once, with the exception of some sites visited in March which were revisited in June and SAMA sites which did not have *G. laevis* calling in June; these sites were sampled again in August. Sites visited on multiple occasions did not have *G. laevis* calling during subsequent visits.

Calling *G. laevis* males were sought by ear or by use of a directional microphone attached to a Sony DAF recorder. Where possible any calling males were located, usually by triangulation, and captured. The call of *Crinia signifera* is quite variable and can sometimes sound very similar to the call of *G. laevis* or *Pseudophryne* sp. Therefore, any calls which

could not be identified immediately were recorded for later examination.

In addition, searches were carried out at each site. This involved looking under logs, leaf litter, stones, and amongst vegetation, for a minimum of one hour, during the day or early evening. Any frogs found were collected and placed in large cotton or plastic bags for later examination. A number of frogs was collected when they were seen on wet roads at night, but no *G. laevis* were found at these times. Frogs were released on site at the conclusion of collecting and identification.

Numerous plant samples were also collected for later identification to determine the common composition of flora associated with the sites at which *G. laevis* were found.

Results

Geocrinia laevis was present at 12 sites within the Reedy Creek / Dismal Swamp drainage area, and also from a site in the Canunda National Park (Table 1). It was not found in the Pt MacDonnell area where it has been listed in SAMA records. A total of six *G. laevis* was collected (two from "The Marshes" wetland, two from Mt Burr, one from "Honan's Scrub" and one from Canunda National Park). The presence of calling males permitted a positive identification of the species at these and other locations (Table 1). Analysis of the recordings of unidentified calls using a computer based spectrograph (Specht 1998) identified only one other site (site 17) where *G. laevis* occurred. All other recordings were confirmed as being *C. signifera*.

Since the Beck survey a small number of *G. laevis* has been collected in South Australia, some reported

TABLE 1. Summary of sites where *Geocrinia laevis* were detected.

Site	Site Name	Species Present	Northing	Eastings
11	Honan's Scrub 1	GL, CS, LD, LE	5825111	467855
12	(Boggy Field) 20 km S of Kalangadoo	GL, LE	5825930	467020
13	Honan's Scrub 2	GL, CS, LE	5825057	465885
14	Honan's Scrub 3	GL, LE	5825661	466967
17	Brookshy's Lane (nr Lake Leake)	GL, CS, LE	5838999	462902
18	Mt Burr Forest 1	GL, CS, LE	5841169	457848
19	Mt Burr Forest 2 (nr Quarry)	GL	5842091	459437
20	Roadside (nr Mt Burr)	GL, LE	5842629	461534
21	The Marshes 1	GL, LE	5836207	459157
22	The Marshes 2	GL, CS, LE	5837195	457385
31	Roadside 2 (Mingbool)	GL, CS	5834231	492158
51	Canunda CP 2	GL	5833737	433832
53	The Marshes 3	GL	5834345	459415

Northings and Eastings as on Australian Map Grid, Zone 54.

(GL = *Geocrinia laevis*, CS = *Crinia signifera*, LD = *Limnodynastes dumerili*, LE = *Litoria owinqi*).

to the SAMA (M. Hutchinson pers. comm. 1999) and others to the SA Frog and Tadpole Study Group (E. Baskett pers. comm. 1999). Included in the SAMA records are two sites to the west of Pt MacDonnell near the coast. One location (SAMA record listed as "Blanche Bay") was a coastal shrubland / sedge/land in sand dunes which seemed to be an unlikely habitat for *G. laevis*. The closest location, just inland from the sand dunes, which may have been suitable habitat for frogs did have *Limnodynastes peroni* (Duméril and Bibron, 1841) and *C. signifera*, but there was no indication of any *G. laevis*. A number of sites sampled around the other southern location ("Section 346 Hundred of Kongorong") also yielded no sign of *G. laevis*. There was nothing obvious to suggest that there had been any significant land use changes in the area since the frogs in the SAMA were collected there in 1983. The predominant land use appeared to be grazing of livestock with most of the land cleared of natural vegetation.

Discussion

Geocrinia laevis was found at 13 sites in the South East of South Australia during this study. Apart from the site in Canunda National Park all of the sites were within the Reedy Creek / Dismal Swamp drainage area. This corresponds to the distribution recorded by Beck (1975) with the addition of the Mingbool site further to the east.

Beck (1975) speculated that the site at Canunda was probably the result of "eggs or larvae washed down one of the man-made drains which cross the area between the Millicent Hills and the coast". It seems more likely however that the population at Canunda National Park is a relict of a previous distribution that covered much of the South East north of Mt Gambier. Prior to the drainage scheme in the South East, which first began around 1867, much of the Upper South East of South Australia experienced periods of severe flooding and inundation (South East Drainage Board 1980), with many localities having permanent or near permanent waters. The water movement in the Millicent area tended to be directed North West towards Kingston SE, or South West towards Lake Bonney (i.e. in the direction of what is now Canunda National Park).

Geocrinia laevis were found in depressed clearings subject to inundation at the edges of native forests or pine plantations (Fig. 3), although one site was a boggy farm paddock (site 12). This site was located only a few hundred metres from a nearby forested area. *Geocrinia laevis* was also found at sites 17, 20 and 31 in clearings near forested areas alongside main roads.

The clearings usually comprised reeds, grasses and



Fig. 3. Clearing in Mt Burr Forest: typical habitat of *Geocrinia laevis* in the South East of South Australia.

sedges, with the occasional shrub and herbaceous plant. The major plants collected from the sites were the nobby clubbrush (*Isalepis nodosa* (Roth.), 1810), sea rush (*Juncus kraussii* Hochst., 1845), and variable sword-sedge (*Lepidosperma laterale* R. Br., 1810). Other plants commonly seen included the buttercup (*Ranunculus* sp. Linn.), spiny mudgrass (*Pseudonaphis spinescens* (R. Br.) Vickery, 1952) and other assorted grasses. A number of fallen branches and other timber from logging also provided habitat under which frogs could shelter.

The dead and dying reeds, sedges and grasses formed a dense mat which retained moisture and provided a network of refuges in which *G. laevis* and other frogs could hide. As a result, it was almost impossible to catch the frogs, even when triangulation suggested they were only a few centimetres from the collectors. An intensive search through the undergrowth and under fallen timber produced little more success. It is quite possible that non-calling individuals may have been present, but not detected, at some sites.

The locations where *G. laevis* can now be found are all areas which previously had permanent swamps and wetlands, including the Canunda site, and would have formed a continuous or nearly continuous expanse of water during the wet months (South Eastern Drainage Board 1980). Even though man-made drains were created to increase surface flow to the Lake Bonney area, to drain land for agricultural development and to allow expanded settlement in the region, this area always had a high rainfall and natural drainage features that probably enabled populations to colonise the Canunda location prior to drainage activities.

Although *G. laevis* has a restricted distribution, the majority of locations identified had more than 50 males calling. The species is still found in the area where it was reported in 1974 and consequently does

not appear to be under any obvious threat of decline in the region. Both "The Marshes" wetland area and "Honan's Scrub" are large native Forest Reserves with the same status as Conservation Parks, and therefore are not likely to be planted or disturbed (B. Grigg pers. comm. 1999). The sites within Mt Burr Forest are located in unused areas that are unsuitable for planting due to flooding (B. Grigg pers. comm. 1999). It is possible that these sites may be planted at the next rotation, in approximately 25 years, but only if flooding could be excluded.

Following the survey recorded above the EPA ran a census of the frogs calling from South Australian waterways in September 1999. *Geourinia laevis* was recorded from "Honan's Scrub" and "Crouches" within the Dismal Swamp / Reedy Creek area; "Crouches" was not included in the present study. Fewer than ten calling *G. laevis* were recorded from these locations (Walker *et al.* unpub.).

Acknowledgments

We are greatly indebted to M. Bradbury and particularly B. Smith (University of Adelaide) for their considerable enthusiasm and assistance in the field trips. M. Hutchinson provided the SAMA records and S. Carruthers (Planting SA) produced the floristic vegetation maps. B. Grigg (Forestry SA) was especially helpful in allowing access to Forestry land and sharing information about the region. D. Rogers (University of Adelaide) kindly gave us the use of his DAT recorder and helped with the analysis of calls on computer. D. Gooding (EPA) helped in the preparation of the distribution map. This project was funded by a grant from the Wildlife Conservation Fund and both support and facilities were provided by the Environment Protection Agency.

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**REDEFINITION OF THE AUSTRALIAN FROG
LIMNODYNASTES DEPRESSUS TYLER (MYOBATRACHIDAE:
LIMNODYNASTINAE)**

By MARGARET DAVIES & THOMAS C. BURTON†*

Summary

Davies, M. & Burton, T. C. (2000) Redefinition of the Australian frog *Limnodynastes depressus* Tyler (Myobatrachidae: Limnodynastinae) *Trans. R. Soc. S. Aust.* 124(2), 141-150, 30 November, 2000.

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Key Words: *Limnodynastes depressus*, Anura, frog, osteology, morphology, musculature.

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Introduction

Limnodynastes depressus Tyler, 1976 was described from a single specimen collected in 1972 by a Western Australian Museum survey party from near the Argyle Homestead in the Kimberley Division of Western Australia prior to its inundation by the Ord River. No further specimens were found until 1998, when I. Morris recorded frogs in the Keep River National Park that have been identified on the basis of call and developmental biology as conspecific with *Limnodynastes depressus* (Tyler & Davies 2000; Morris & Tyler unpub; Watson, Tyler & Morris unpub.).

We have examined some of the Keep River specimens as well as material collected earlier but not positively identified as *L. depressus*, and have identified morphological features that can be used to separate the species from similar congeners such as *L. tasmaniensis* Günther and *L. fletcheri* Boulenger. We have also examined further material from the Northern Territory to clarify the identity of records of *L. tasmaniensis* from WA and the NT. Here we redescribe the species incorporating osteological and myological data unavailable for the original description.

Materials and Methods

Specimens examined are housed in the Queens-

land Museum (QM), the Western Australian Museum (WAM), the South Australian Museum (SAMA), the Museums and Art Galleries of the Northern Territory (NTM) and the University of Adelaide Osteological Collection (UAZ). The muscles of the throat, jaw, pectoral girdle, hand, leg and foot were dissected with the aid of a Wild M9 dissecting microscope. Osteological preparations were made after the method of Dingerkus & Uhler (1977). Measurements (in mm) were taken using dial calipers reading to 0.05 mm and follow Tyler (1968). Illustrations were made using a Wild M9 dissecting microscope with attached camera lucida.

Material examined

QM J55565–71, Keep River, NT, SAMA R23862–4, Newry Station, NT, WAM R 58833 Kununurra, WA, NTM R13110, R13112, R13122, R13125, R13127, Keep River NP, R18608, R18623, R24881, R24912, R24913, Bradshaw Station, NT, R24332, Auvergne Station, NT, R24467, Fish River, off Daly River, NT, UAZ B623, Newry Station, NT, UAZ B2645, B2647 Cockatoo Lagoon, Keep River NP, UAZ B2649–50, offspring of mating of adults from Cockatoo Lagoon, Keep River NP.

Results

Limnodynastes depressus Tyler, 1976
(FIGS 1–12)

Limnodynastes depressus Tyler, M. J. (1976) Rec. West Aust. Mus., 4, p.45.

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Division of Biological Sciences, La Trobe University, Bendigo,
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Holotype

WAM R 43896, adult male.

Definition

A moderate-sized species (males 30 - 44 mm S-V, females 34 - 37 mm S-V) characterised by an elongate thumb comprising one phalanx, prominent upper eyelid jutting outward as a shelf, outer metatarsal tubercle absent, moderately long vomerine teeth, breeding females with well-developed finger flanges, frontoparietal fontanelle widely exposed, maxillary process of nasals absent, preorbital process of pars facialis of maxilla absent, narrow unexpanded alae of parasphenoid, origin of m. depressor mandibulae from the dorsal fascia and the tympanic ring but with no fibres originating from the otic ramus, exposure of the anterior margin of the m. coracoradialis, pennate insertion of mm. lumbricalis indicis brevis and flexor teres indicis on the palmar surface of the metacarpal

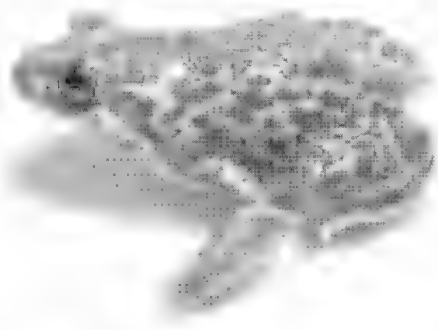


Fig. 1. Male *Limnodynastes depressus* in life (tapping 43 mm S-V). From Newry Station, NT.

Morphology

The external morphology of this species shows little variability and conforms with the type description (Fig. 1). The palmar tubercle at the base of the first digit was extremely large in the material examined, not indicated in the illustration of the type (Tyler 1976). Breeding females have flanges on the first two fingers.

Measurements, in mm, are as follows (means followed by ranges in parentheses): S-V - males 29.6 - 44.1; females 34.5 - 36.6; TL/S-V 0.42 (0.39-0.47); HL/HW 1.17 (1.01 - 1.25); HL/S-V 0.36 (0.32 - 0.38) E-N/IN 0.86 (0.73 - 1.00).

Osteology (Description from UAZ B2645)

Skull moderately ossified. Sphenethmoid poorly ossified, not in bony contact with nasals (Fig. 2A), extending anteriorly between vomerine teeth and posteriorly about $\frac{1}{3}$ length of orbit in ventral view. Prootic and exoccipital incompletely fused. Crista parotica short and stocky, widely separated laterally with poorly expanded otic ramus of squamosal. Frontoparietal fontanelle widely exposed. Frontoparietal poorly ossified, anterior extremities $\frac{1}{4}$ length of orbit. Orbital edges of frontoparietal straight, then angled slightly posterolaterally. Anterior margins of frontoparietal fontanelle formed by sphenethmoid about $\frac{1}{3}$ anteriorly along length of orbit. Posterior margin undefined because of lack of medial ossification of exoccipitals. Nasals well ossified, perforated centrally, crescentic anteriorly. Maxillary process absent. Nasals not in contact with pars facialis of maxilla. Palatines moderately slender medially, underlying dentigerous processes of vomers; widely expanded posterolaterally, not reaching palatal shelf of maxilla posterolaterally (Fig. 2B).

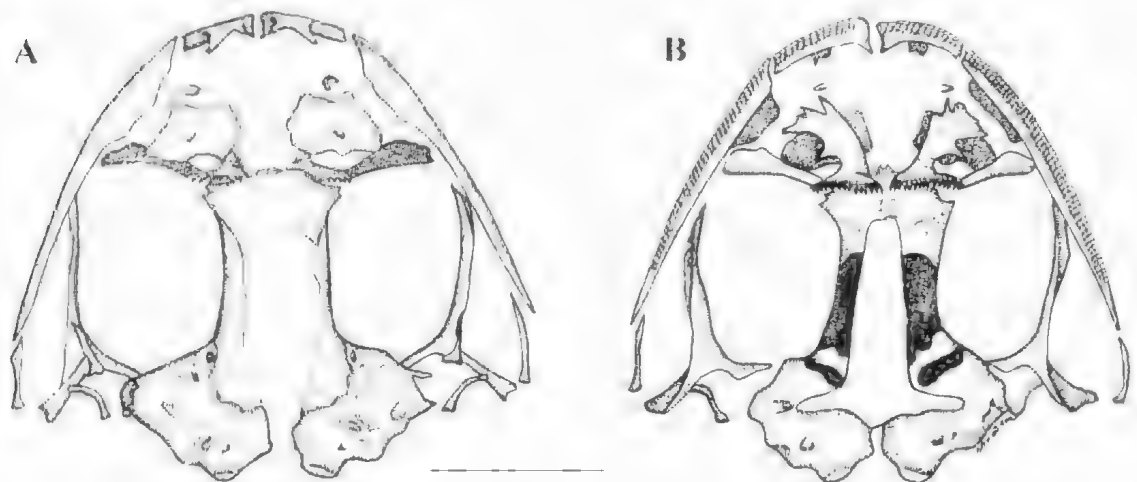


Fig. 2. Female *Limnodynastes depressus* (UAZ B2645). A. Dorsal and B. Ventral views of the skull. Scale bar = 5.0 mm.

Parasphenoid moderately robust, extending about $\frac{1}{2}$ length of orbit. Alae slender, not expanded laterally. Pterygoid robust. Anterior ramus long, in bony contact with palatal shelf of maxilla. Pterygoid process absent. Medial ramus moderately long, subacuminate, not overlying alae of parasphenoid. Posterior ramus slender. Junction of the three rami, extremely robust.

Quadratojugal slender and entire. Squamosal moderately robust with moderately long, slender zygomatic ramus and short slightly expanded otic ramus.

Maxilla and premaxilla dentate. Pars facialis of maxilla moderately deep; preorbital process absent. Alary processes of premaxillae broad, slightly bifurcated and directed posterodorsally. Palatine processes short, not in medial contact. Pterygoid process of palatal shelf absent. Vomers reduced anteriorly and medially with moderately long dentigerous processes. Columella bony and sigmoid in shape.

Pectoral girdle arciferal and robust. Slender cartilaginous omosternum with stalked, knobbed anterior extension. Xiphisternum broad, not bifid. Sternum cartilaginous. Clavicles slender, strongly curved and widely separated medially. Coracoids robust, widely separated medially. Bicapitate scapula robust. Suprascapula about $\frac{1}{2}$ ossified. Moderately well-developed anteroproximal crest on humerus.

Carpus of five elements. Single sesamoids at junction of metacarpals and proximal phalanges of digits 2-4, and at junctions of adjacent phalanges in digits 3 and 4. Medial flange on metacarpal I absent. Phalangeal formula 1, 2, 3, 3. First metacarpal elongate (Fig. 3C).

Seven procoelous, non-imbriate presacral vertebrae. Vertebrae I and II fused. Relative widths of transverse processes III>IV>SD>II>V>VI>VII>VIII. Sacral diapophyses poorly expanded (Fig. 3B). Ilii extending to about the centre of the sacral diapophyses. Urostyle crest approximately $\frac{1}{2}$ length of urostyle.

Iliac crest absent. Dorsal prominence prominent, nonfiliform. Dorsal protuberance posterolateral (Fig. 3A).

Three tarsal elements. Prehallux narrow (Fig. 4A).

Hyoid plate wider than long; posterior processes moderately slender. Anterior processes expanded. Anteromedial processes of anterior hyate well developed, broad. Posterior cornua ossified (Fig. 4B).

Variation

Material examined

QM J55568 (♂), QM J55571 (♀), B623 (♂), B2649 (subadult), B2650 (subadult), B2643 (♂), NTM R24912 (♂).

The alae of the parasphenoid are more elongate in both NTM R24912 and UAZ B623; UAZ B623 also has extremely broad palatines with extensive anterior expansions about half way along their length. A single narrower extension on the left palatine is present in NTM R24912. The hyoid on UAZ B623 is extensively calcified (Fig. 5). The frontoparietals are more extensively ossified posterolaterally in UAZ B2649 and the palatines are more extensively expanded laterally in QM J55568.

Myology

The m. depressor mandibulae arises from the dorsal fascia and the tympanic ring but no fibres originate from the otic ramus. The anterior margin of the m. coracoradialis is exposed rather than being completely hidden by the m. supracoracoideus and m. episternohumeralis (Fig. 9). The mm. lumbicalis indicis brevis and flexor teres indicis insert pennately on the palmar surface of the metacarpal (Fig. 10B).

Comparison with other species

Limnodynastes depressus is morphologically similar to *L. tasmaniensis* and *L. fletcheri*. It differs from both of these species in the loss of a phalanx on the first finger, although it shares the externally elongated thumb of *L. fletcheri* (Fig. 6). From *L. fletcheri*, *L. depressus* is further distinguished by a more widely exposed frontoparietal fontanelle, absence of a maxillary process on the nasals and by its narrow unexpanded alae of the parasphenoid (Fig. 7). From *L. tasmaniensis*, *L. depressus* is further distinguished by its narrow unexpanded alae of the parasphenoid, by its more extensive ossification of the prootic and by its shallower pars facialis of the maxilla (Fig. 8).

Myologically, *L. depressus* resembles closely *L. fletcheri* and *L. tasmaniensis* in the musculature of the throat, leg and foot. Consistent differences occur in the musculature of the jaw, pectoral girdle and first finger.

In *L. fletcheri* and *L. tasmaniensis*, the m. depressor mandibulae originates from three sites: the dorsal fascia, the otic ramus of the squamosal and the posterior margin of the tympanic ring; in *L. depressus* the insertion on the otic ramus is lacking.

The pectoral musculature is similar in all three species, except that the m. coracoradialis is completely hidden by the m. supracoracoideus and m. episternohumeralis in *L. fletcheri* and *L. tasmaniensis*, whereas in *L. depressus*, the anterior margin of the m. coracoradialis is exposed (Fig. 9).

In most frogs, including *L. fletcheri* and *L. tasmaniensis*, the mm. lumbicalis indicis brevis and flexor teres indicis insert on the basal phalanx of digit II of the hand (Fig. 10A); in *L. depressus*,

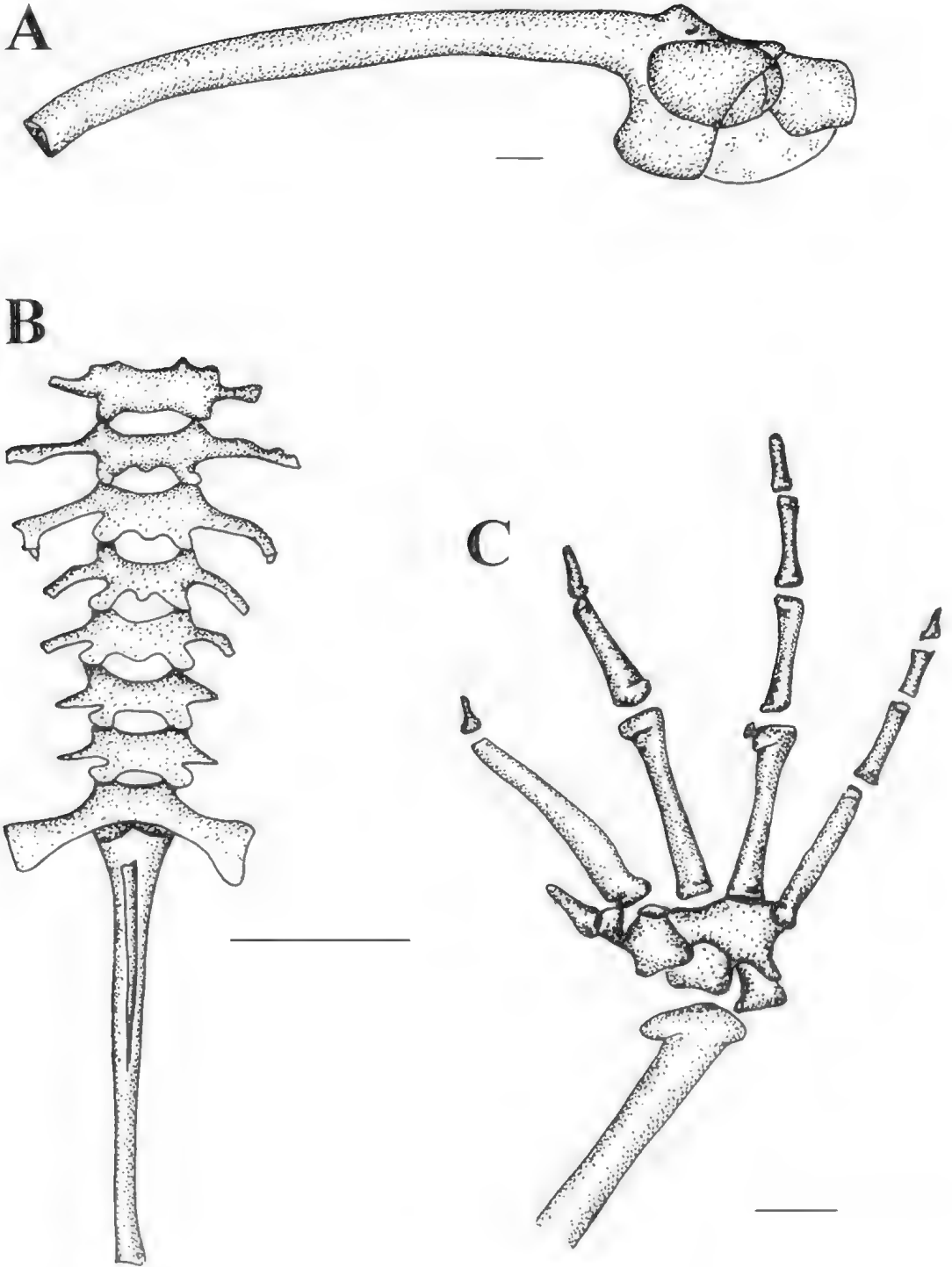


Fig. 3. Female *Limnodynastes depressus* (UAZ B2645). A. Lateral view of the pelvis. B. Dorsal view of the vertebral column. C. Dorsal view of right hand. Scale bars = 1.0 mm A, C; 5.0 mm B.

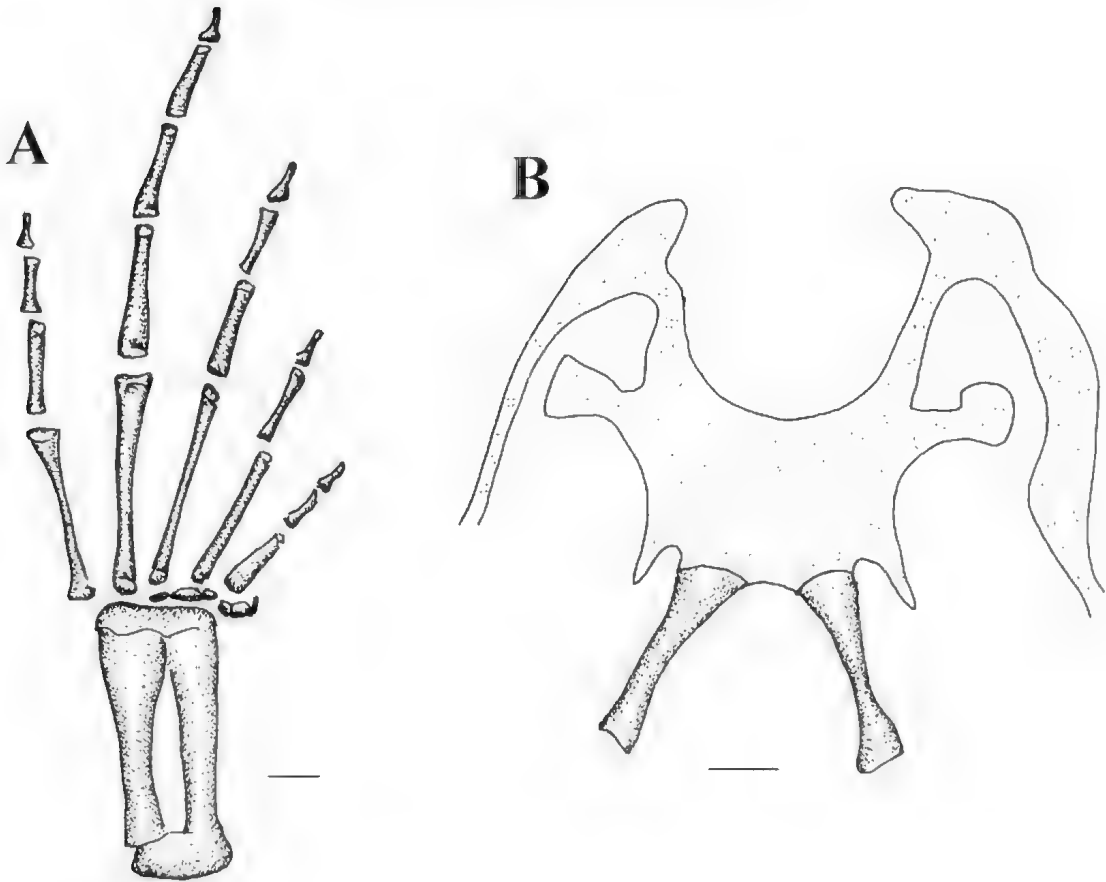


Fig. 4. Female *Limnodynastes depressus* (UAZ B2645). A. Dorsal view of the left foot. B. Ventral view of the hyoid. Scale bars = 1.0 mm.

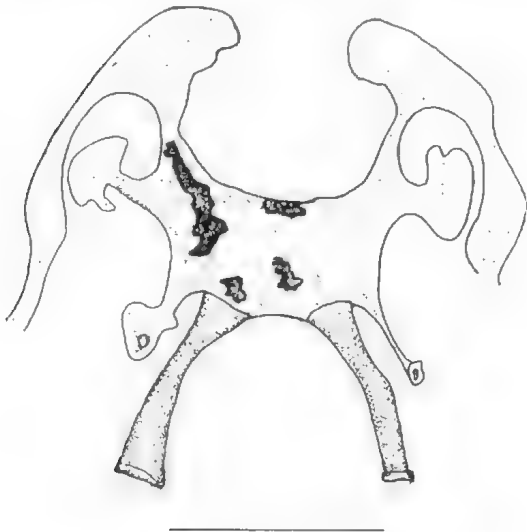


Fig. 5. Male *Limnodynastes depressus* (UAZ B623). Ventral view of the hyoid. Heavy stippling indicates calcification. Scale bar = 5.0 mm.

insertion is pennately on the palmar surface of the metacarpal (Fig. 10B)

The larvae of *L. depressus* are similar to those of *L. fletcheri* in general morphology (Davies 1992; Tyler & Davies 2000), although those of *L. depressus* are often much longer. However, they differ greatly from those of *L. tasmaniensis* in their pigmentation and the structure of the oral disc. Features of the chondrocranium also separate the species (Tyler & Davies 2000).

Other material

Prior to the collection of the material from Keep River NP, a species identified as *Limnodynastes tasmaniensis* was collected at Kununnurra and was considered to be an introduction (Martin & Tyler 1978). Further material collected at Newry Station, NT near the Keep River, was also attributed to *L. tasmaniensis* (Watson *et al.* 1995). This latter material exhibited abnormalities of the fingers and toes (Figs 11, 12) and the elongate thumb was considered to be another abnormality. A high level of

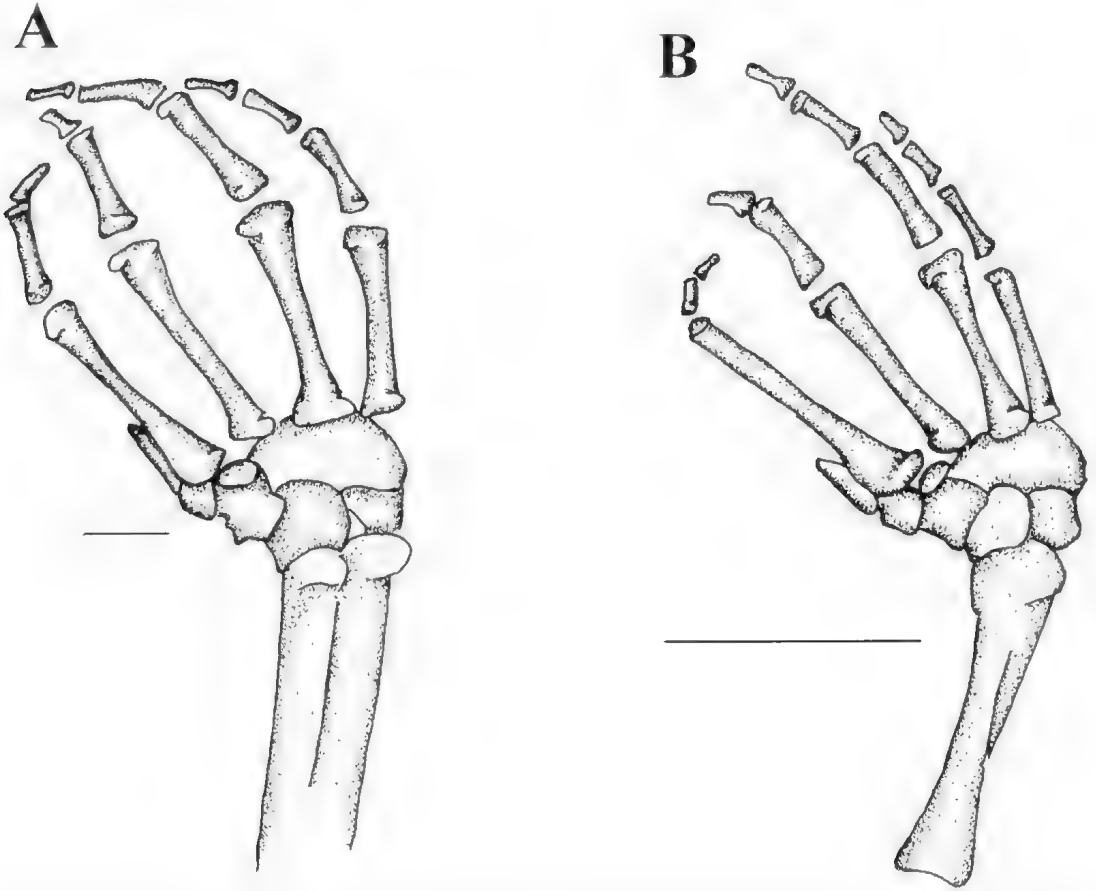


Fig. 6. Female *Limnodynastes tasmaniensis* (UAZ A1461). A. Dorsal view of right hand. Female *L. fletcheri* (UAZ A1733). B. Dorsal view of right hand. Scale bars = 1.0 mm A; 5.0 mm B.

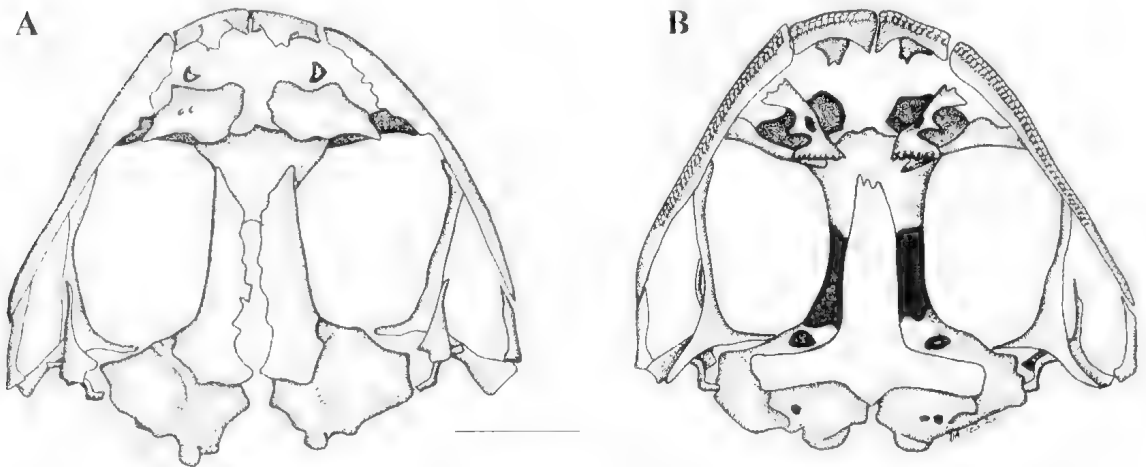


Fig. 7. Female *Limnodynastes fletcheri* (UAZ A1733). A. Dorsal and B. Ventral views of the skull. Scale bar = 5.0 mm.

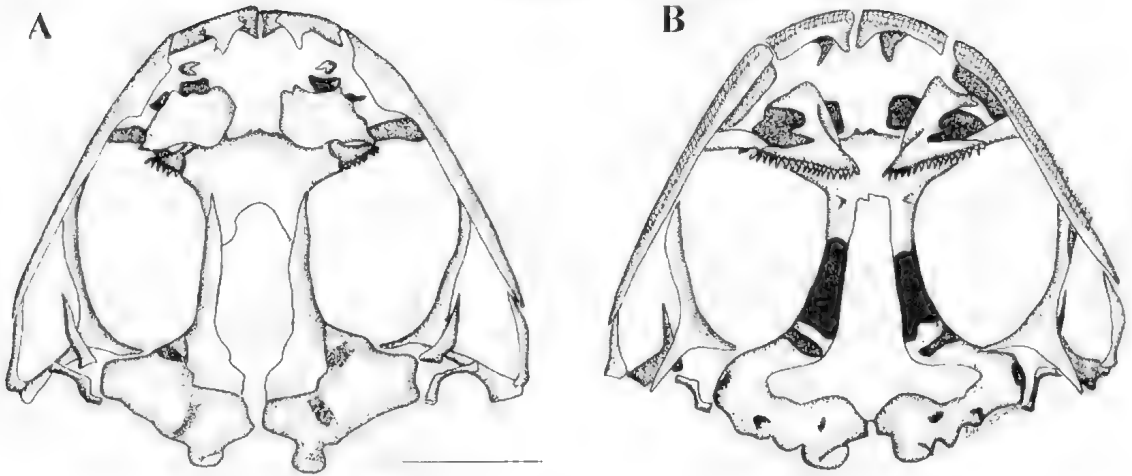


Fig. 8. Female *Limnodynastes tasmaniensis* (UAZ.A1461). A, Dorsal and B, Ventral views of the skull. Scale bar = 5.0 mm.

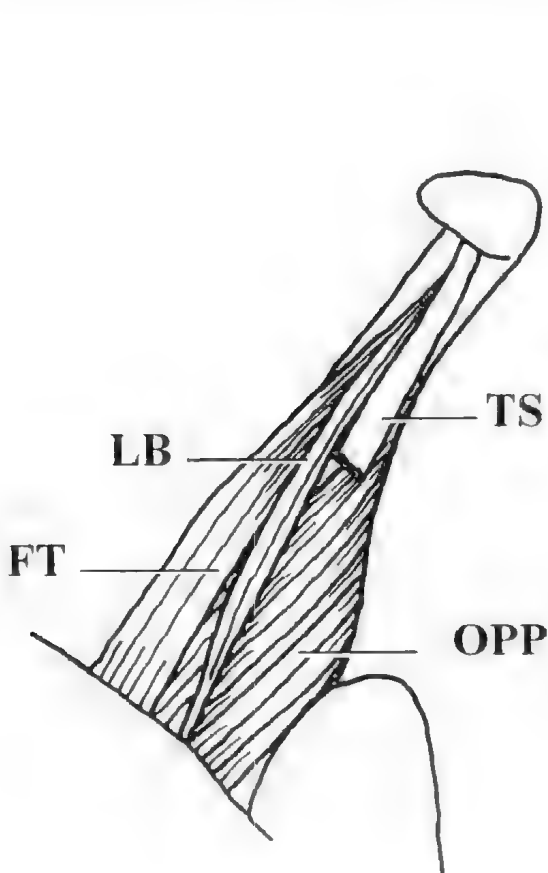


Fig. 9. Index (first) digit of right hand of *Limnodynastes depressus* palmar surface with tendosuperficialis severed and removed. FT = m flexor tenes; LB = m lumbriacalis brevis; OPP = m opponensindictis; TS = severed tendon of tendosuperficialis

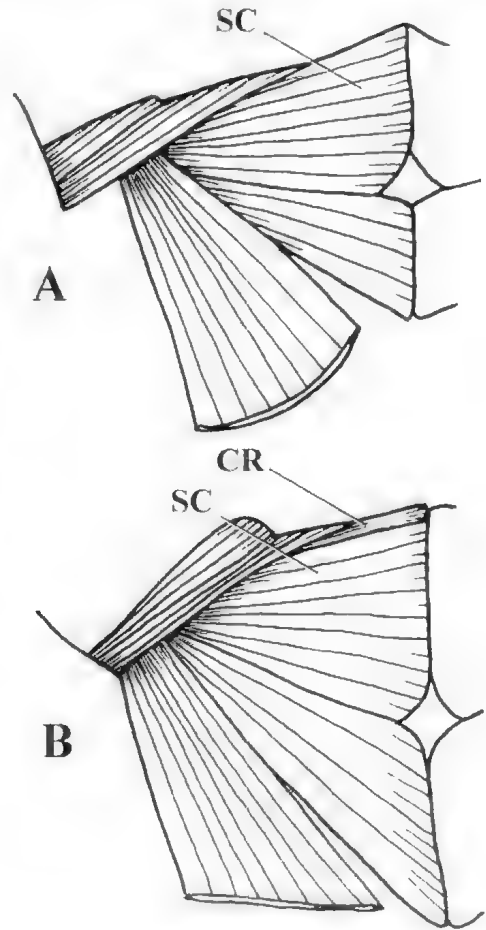


Fig. 10. Ventral view of right side of pectoral girdles of A *Limnodynastes tasmaniensis* and B. *L. depressus*. CR m coracoidealis; SC = m supracoracoideus.

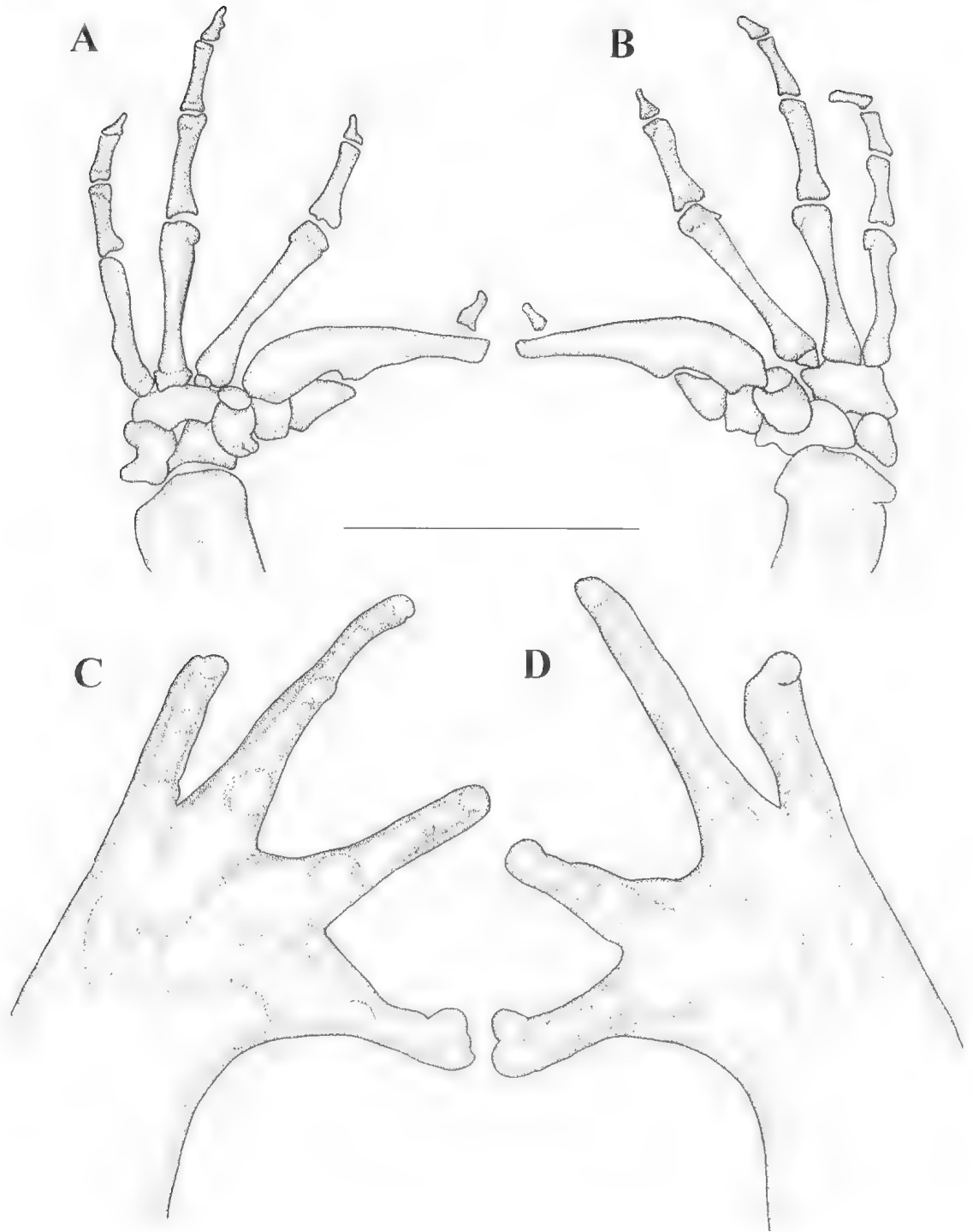


Fig. 11. Male *Limnodynastes depressus* (UAZ B623). Dorsal views of bones of A. left and B. right, hands. Ventral views of C. left and D. right hands. Scale bar = 5.0 mm.

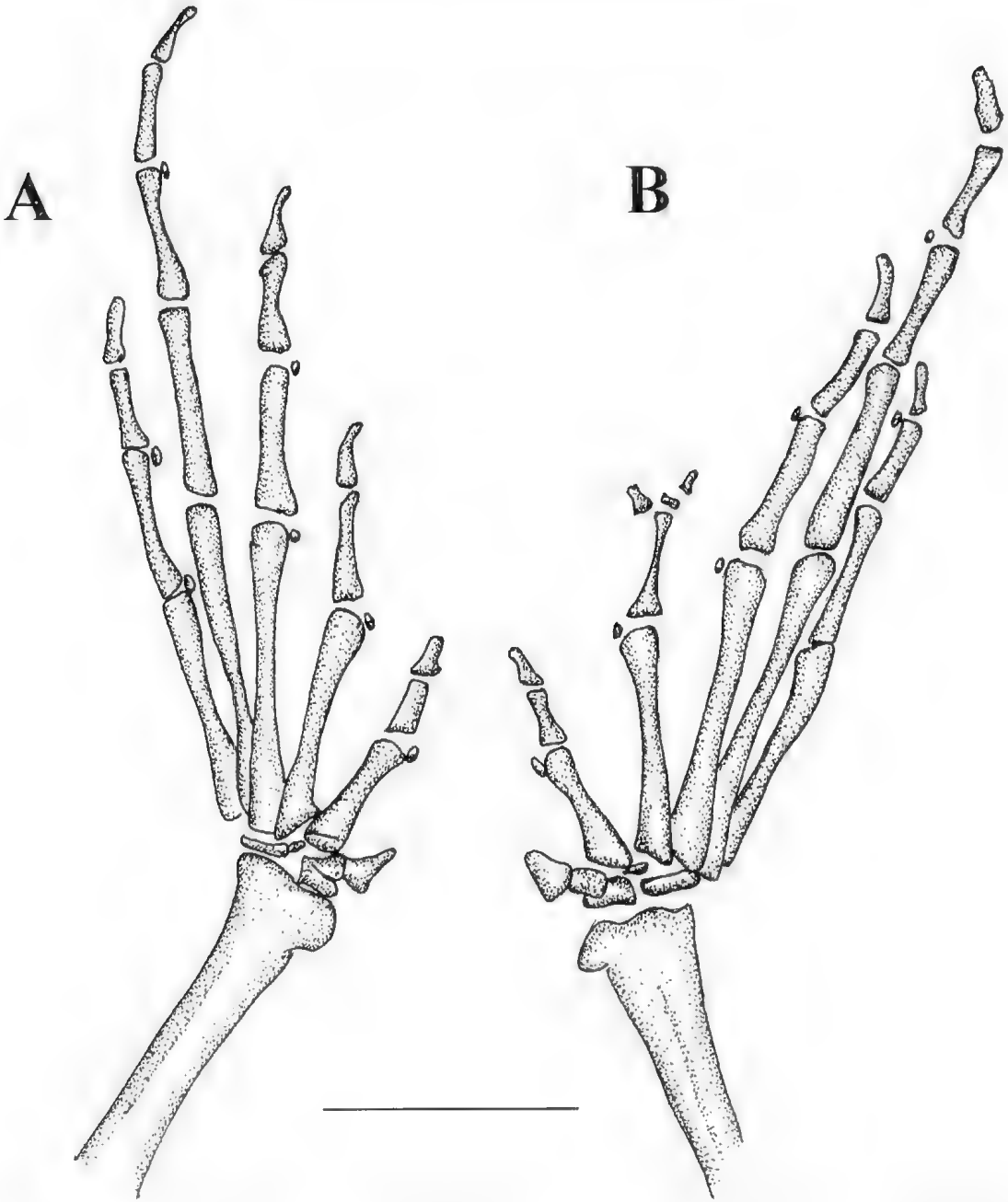


Fig. 12. Male *Limnodynastes depressus* (UAZ B623). Dorsal views of bones of A. left and B. right feet. Scale bar = 5.0 mm.

abnormality was detected in other frogs collected at this site (Watson *et al.* 1995). Parker (1940) recorded disarticulation in the terminal phalanges of *L. peronii* (Duméril & Bibron) (which usually shows a similar reduction in the phalanges of the thumb as in *L. depressus*), similar to that recorded in the Newry Station specimens. Parker's material, however, had two terminal phalanges. He commented that the bone may penetrate the skin. This was not apparent in the *L. depressus* specimens. *Limnodynastes peronii* differs substantially in morphology from *L. depressus*.

One of us, TCB, has dissected the material from Kununnurra and has identified the elongate thumb with associated musculature found in the Keep River

material. Together with the abnormal material from Newry Station, we attribute all of this material to *Limnodynastes depressus*. We have further examined material collected from other localities in the Northern Territory and attribute all these specimens to *L. depressus*.

Acknowledgments

We thank P. Horner (NT Museums and Art Gallery), P. Couper, (Qld Museum) and K. Aplin, (WA Museum) for the opportunity to examine material in their care and S. Walker for assistance with the figures.

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**NEW RECORDS OF THE CESTODE GENUS
PSEUDOTOBOTHRIUM (TRYPANORHYNCHA:
OTOBOTHRIIDAE) FROM AUSTRALIAN FISHES**

*BY I. BEVERIDGE**, *R. A. CAMPBELL†* & *M. K. JONES‡*

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Key Words: Cestodes, fishes, new host records, *Pseudotobothrium*, *Otobothrium dipsacum*, *Otobothrium arii*, Otobothriidae.

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KEY WORDS: Cestodes, fishes, new host records, *Pseudotobothrium*, *Otobothrium dipsacum*, *Otobothrium arii*, Otobothriidae.

Introduction

Cestodes (tapeworms) of the order Trypanorhyncha Diesing, 1863 occurring in Australian fishes are still relatively poorly known since large numbers of potential host species as well as geographic regions around the continent remain to be examined. Amongst the most poorly investigated families of this cestode order is the Otobothriidae Dollfus, 1942, currently represented in this region only by *Otobothrium mugilis* Hiscock, 1954 (Hiscock 1954) and *Pocillancistrum caryophyllum* (Diesing, 1850) (Beveridge & Campbell 1996).

In the present paper, the occurrence of the genus *Pseudotobothrium* Dollfus, 1942, based on its only known species, *P. dipsacum* (Linton, 1897), is reported for the first time in fishes from northern Australia. *Otobothrium arii* Bilqees & Sharkat, 1976 is also reported from teleost fishes from Queensland and is placed within the genus *Pseudotobothrium*. Because the definition of the genus and descriptions of both species included in this report are incomplete (Beveridge *et al.* 1999), redescriptions based on Australian specimens as well as other specimens available for examination in museum collections are

provided. In addition, the taxonomic relationships of *Pseudotobothrium* within the family Otobothriidae are reassessed.

Materials and Methods

Cestodes collected by the authors were placed in tap water to induce evagination of the tentacles and were then fixed with 10% formaldehyde or 70% ethanol. Specimens were subsequently stained with Celestine blue, dehydrated in an ethanol series, cleared in methyl salicylate and mounted in Canada balsam. Tentacles were detached from strobilae using a scalpel and were then mounted in glycerine jelly for examination of the tentacular armature. Drawings were made using a BH-2 Olympus microscope with Nomarski interference optics, fitted with a drawing tube. Measurements are presented in micrometres unless otherwise stated as the range followed by the mean and number of specimens measured in parentheses.

Specimens in the collections of the South Australian Museum, Adelaide (SAMA), the Queensland Museum, Brisbane (QM), the British Museum (Natural History), London (BMNH), the Muséum national d'Histoire naturelle, Paris (MNHN) and the United States National Parasite Collection, Washington (USNPC) were examined.

A complete synonymy for *P. dipsacum* was provided by Dollfus (1942). Consequently, the references cited here are those in which novel host or geographic records are listed including those cited by

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Bates (1990). Records such as those of Linton (1913), Pintner (1934), Joyeux & Baer (1936) and Southwell (1913, 1930) which merely repeat previously published accounts have been excluded.

Host nomenclature follows Paxton *et al.* (1989), Robins *et al.* (1991) and Allen (1997).

Pseudotobothrium Dollfus, 1942

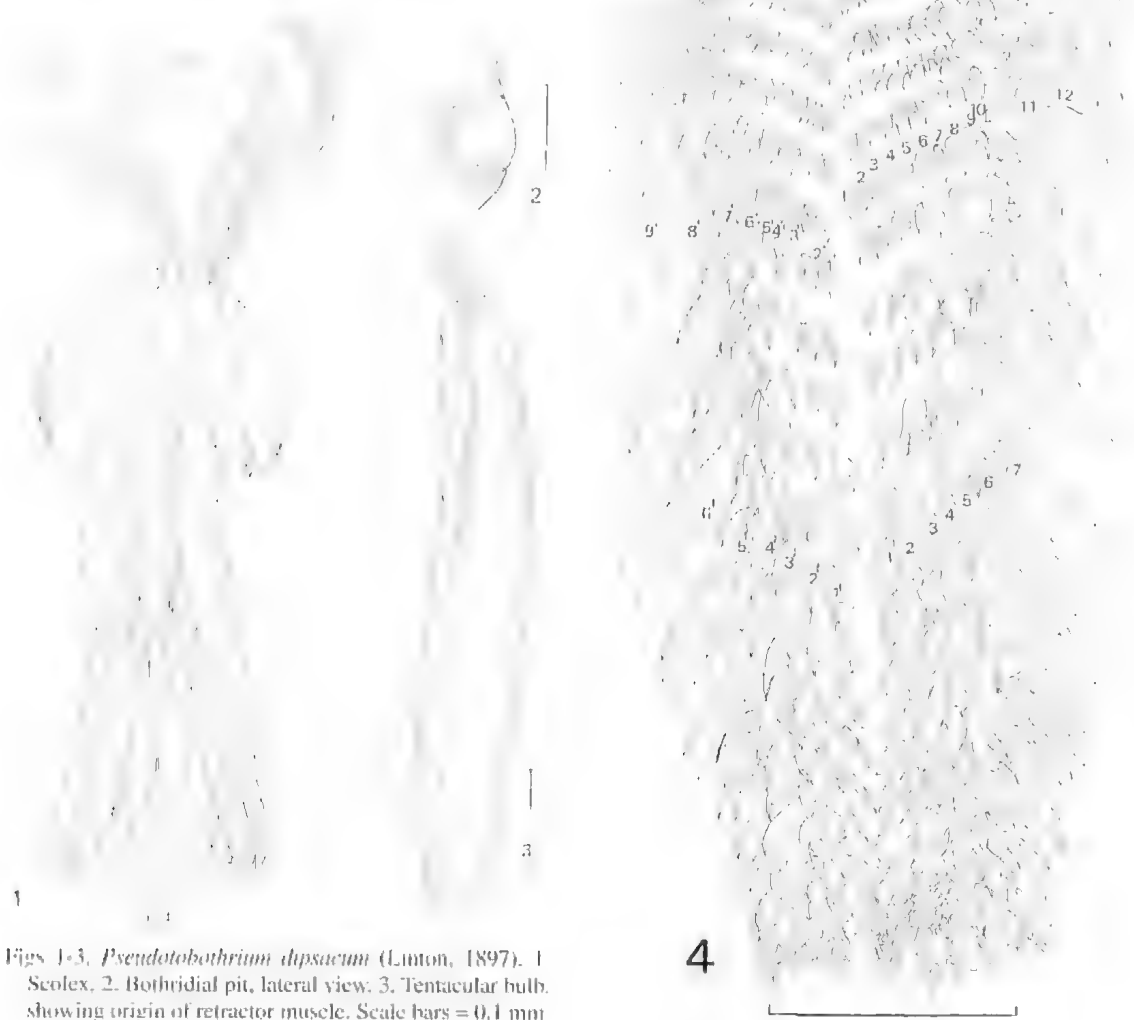
Type species: *P. dipsacum* (Linton, 1897)

Pseudotobothrium dipsacum (Linton, 1897)

(FIGS 1-9)

Otobothrium dipsacum Linton, 1897, pp. 806-807, pl. 64, figs 1-5 (*Pomatomus saltatrix* (Linnaeus, 1766), Atlantic, North America, Massachusetts); Linton, 1901, pp. 412, 451 (*Pomatomus saltatrix*); Linton, 1905, pp. 329, 331, 375 (*Centropriestis striata* (Linnaeus, 1758), Atlantic, North America,

North Carolina); Southwell, 1912, pp. 270, 278, figs 19-21 (identified as *O. insigne*) (*Epinephelus undulosus* (Quoy & Gaimard, 1824) (= *Serranus undulosus*), *Parastromateus niger* (Bloch, 1795) (= *Stomateus niger*), *Diagramma crassispinum* Rüppell, 1838, *Balistes* spp., Sri Lanka (illustrations are not of *O. dipsacum*); Linton, 1924, p. 2, 53



Figs 1-3, *Pseudotobothrium dipsacum* (Linton, 1897). 1 Scolex, 2. Bothridial pit, lateral view. 3. Tentacular bulb, showing origin of retractor muscle. Scale bars = 0.1 mm

(*Aluterns schoepfi* (Walbaum, 1792) (= *Ceratacanthus schoepfi*), *Xiphias gladius* (Linnaeus, 1758), Atlantic, North America,

Massachusetts; *Trachinotus falcatus* (Linnaeus, 1758) (= *Mycteroperea falcata*), Atlantic, North America, Florida); Southwell, 1924, p. 489



Figs 4-6 *Pseudotobothrium dipsacum* (Linton, 1897), basal and metabasal tentacular armature. 4. Antribothridial surface of tentacle showing origins of ascending hook rows with slight space between files 1 and 1' in metabasal region. 5. External surface of tentacle showing ascending rows of hooks from left to right and band of hooklets on bothridial (right) side of tentacle. 6. Bothridial surface of tentacle showing band of hooklets in centre with prominent space on either side of the band. Scale bars = 0.01 mm.

(*Epinephelus undulosus*, *Diagramma crassispinum*, Sri Lanka); Southwell, 1929, pp. 291-292, 311, fig. 47 (*Epinephelus undulosus*, *Diagramma crassispinum*, *Sufflamen fraenatus* (Latreille, 1804) (= *Balistes mitis*), *Lutjanus dodecacanthus* (Bleeker, 1853); *Lethrinus ornatus* Valenciennes, 1830, Sri Lanka, p. 311, *Abalistes stellatus* (Lacépède, 1798) (= *Balistes stellatus*), *Lethrinus ornatus*, *Parastromateus niger*); Yamaguti, 1952, pp. 69-70, fig. 105 (*Chelidomichthys kumu* (Cuvier, 1829), Japan); Palm *et al.*, 1994, pp. 153, 156, 159, fig. 4 (*Cynoglossus senegalensis* (Kaup, 1858), *Petrocephalus hane* (Lacépède, 1803), Gulf of Guinea).

Otobothrium (*Pseudotobothrium*) *dipsacum*: Dollfus, 1942, pp. 253-255, fig. 157 (*Polynemus quadrifilis* Cuvier & Valenciennes, 1829) East

Atlantic, Africa (Congo)(identification uncertain); Cruz-Reyes, 1973, 25-29, figs 1-5 (*Balistes polylepis* Steindachner, 1876, Pacific Ocean, Mexico).

Pseudotobothrium dipsacum: Ward, 1954, p. 255, fig. 8 (*Sphyraena barracuda* (Walbaum, 1792), Miami, USA); Palm, 1995, pp. 102-103, 154-162 (*Haemulon plumieri* (Lacépède, 1801), Brazil); Palm *et al.*, 1997b, pp. 71, 72, 75 (*Pseudupeneus maculatus* (Bloch, 1793), *Haemulon plumieri*, Atlantic, Brazil), 1997b, p. 84, figs 1c, 1d.

Types: Holotype (larval) from *Pomatomus saltatrix* (Linnaeus, 1766) (USNPC 4794).

Material examined:

From Australia:

from *Abalistes stellatus* (Lacépède, 1798): 5

7

8

9

Figs 7-9. Profiles of hooks from the tentacular armature of *Pseudotobothrium dipsacum* (Linton, 1897). 7. Metabasal region, from left, first hook in row, hook in middle of row, hook near end of row, terminal hook of row, outer hooklet from band, inner hooklet from band. 8. Hooks of rows 10-15 from the base, from left, first hook of row 10, first hook of row 15, hook in middle of row 15, hook at end of row 15, outer hooklet of band, inner hooklet of band. 9. Hooks from base of tentacle, from left, lobed hook on antitobothridial surface, outer hook of band, inner hook of band. Scale bar = 0.01 mm.

specimens, Heron Island, Qld (QM G217928-32);

from *Cephalopholis cyanostigma* (Kuhl & van Hasselt, 1828): 1 specimen, Heron Island, Qld (QM G214959);

from *Epinephelus stillus* (Valenciennes, 1828): 7 specimens, Cape Cleveland, Qld (SAMA 31342);

from *Istiophorus platypterus* (Shaw & Nodder, 1792): 4 specimens, Cape Bowling Green, Qld (QM G212165, 212799);

from *Makaira indica* (Cuvier, 1832): 2 specimens, Cape Bowling Green, Qld (QM G212166, 212800);

from *Makaira mazara* (Jordan & Snyder, 1901): 2 specimens, Cape Moreton, Qld (QM G212785, 212798);

from *Naso flamingii* (Valenciennes, 1835): 1 specimen, Heron Island, Qld (QM G212960);

from *Pseudocaranx dentex* (Bloch & Schneider, 1801): 2 specimens, Heron Island, Qld (QM G214961, 217936);

from *Plectropomus leopardus* (Lacépède, 1802): 2 specimens, Heron Island, Qld (QM G214962);

from *Plectropomus maculatus* (Bloch, 1790): 1 specimen, Heron Island, Qld (QM G206964);

from *Rhinecanthus rectangularis* (Bloch & Schneider, 1801): 3 specimens, Heron Island, Qld (QM G217933-5);

from *Gymnosardus utticolor* (Rüppel, 1836): 2 specimens, Clerke Reef, WA (SAMA 31343).

From Indian Ocean:

from *Lutjanus gibbus* (Forsskål, 1775): 1 specimen, Hulule, Maldives (QM GL 10508).

From East Africa:

from *Cephalopholis sonnerati* (Valenciennes, 1828): 1 specimen, Zanzibar (BMNH 1961.6.26.120-5);

from *Epinephelus malabaricus* (Bloch & Schneider, 1801): 5 specimens, Zanzibar (BMNH 1961.6.26.120-5);

from *Epinephelus tauvina* Forsskål, 1775: 3 specimens, Zanzibar (BMNH 1961.6.26.120-5);

from *Epinephelus chlorostigma* (Valenciennes, 1828): 4 specimens, Persian Gulf (BMNH 1992.7.13.1-5);

From Sri Lanka (Ceylon):

from *Sufflamen fraenatus* (Lacépède, 1804) (= *Balistes minis*): 1 specimen (BMNH 1997.11.15.33-7);

from *Abalistes stellatus* (Lacépède, 1798): 6 specimens (BMNH 1977.11.15.33-7);

from *Lethrinus ornatus* Valenciennes, 1830: 2 specimens (BMNH 1977.11.15.31-2);

from *Lethrinus* sp.: 1 specimen (BMNH 1977.11.15.58-62);

from *Epinephelus undulosus* (Quoy & Gaimard, 1824) (= *Serranus undulosus*): 5 specimens (USNPC 49816).

From South America:

from *Haemulon plumieri* (Lacépède, 1801): 1

specimen, Brazil (in personal collection of H. Palui).

From North America:

from *Pomatomus saltatrix* (Linnaeus, 1766): type;

from *Myxteropora phena* Jordan & Swain, 1884: 8 specimens, New York Aquarium (USNPC 35777);

from *Haemulon parra* (Desmarest, 1823) (= *Neomaculis parra*): 2 specimens, New York Aquarium (USNPC 35780, 35781);

from *Canthidermis sufflamen* (Mitchell, 1815): 2 specimens (USNPC 35782);

from *Canthidermis maculatus* (Bloch, 1786): 1 specimen, New York Aquarium (USNPC 35852);

from *Ocyrus cheysirius* (Bloch, 1791): 1 specimen, New York Aquarium (USNPC 35783);

from *Harpe rufa* Linnaeus, 1758: 1 specimen, New York Aquarium (USNPC 35850);

from *Scorpaena plumieri* Bloch, 1789: 1 specimen (USNPC-35851);

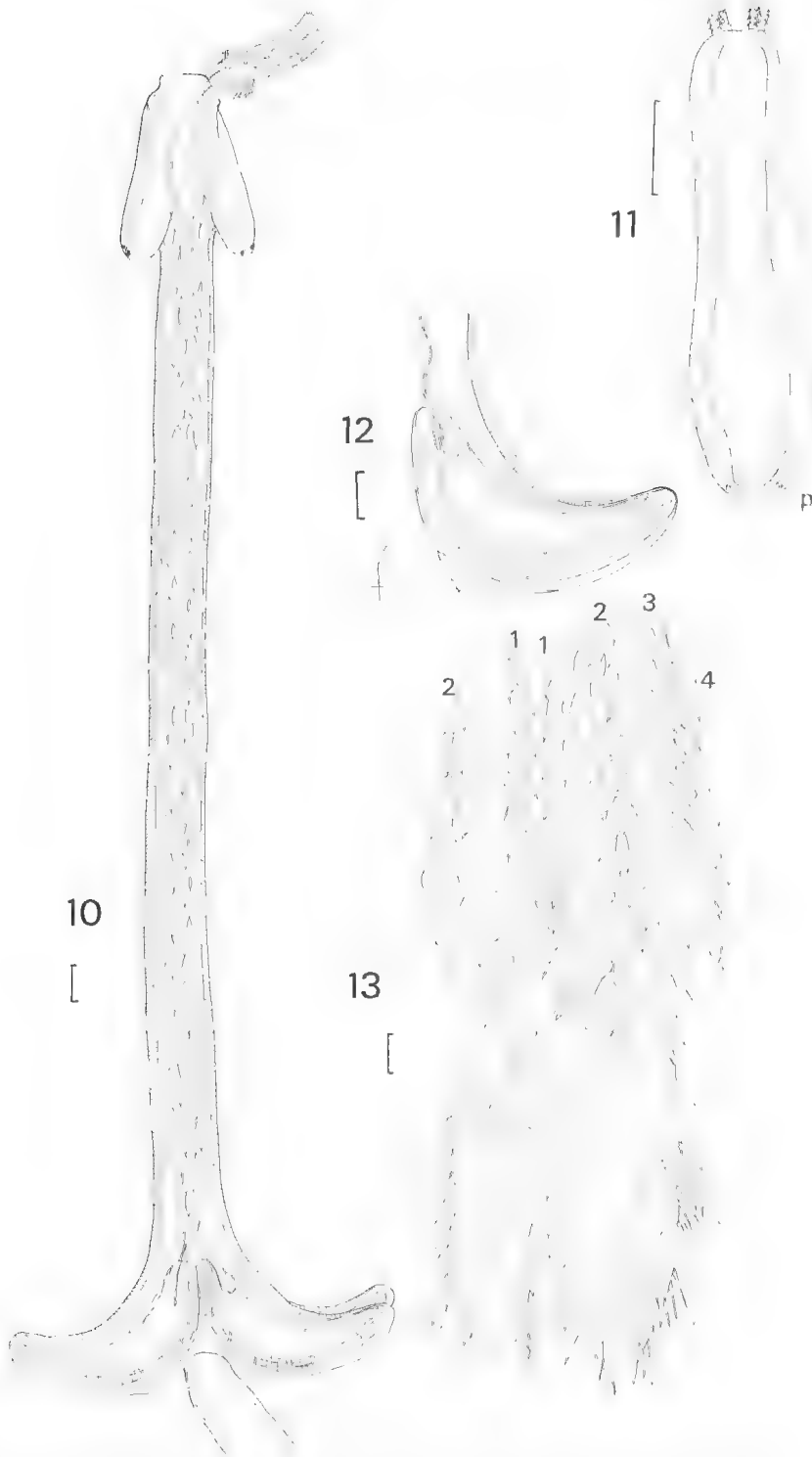
from *Diacope analis* Cuvier & Valenciennes, 1830 (= *Neomaculis analis*): 1 specimen, New York Aquarium (USNPC 35853);

from *Lawmolaimus maximus* (Waulbaum, 1792): 1 specimen, New York Aquarium (USNPC 36028).

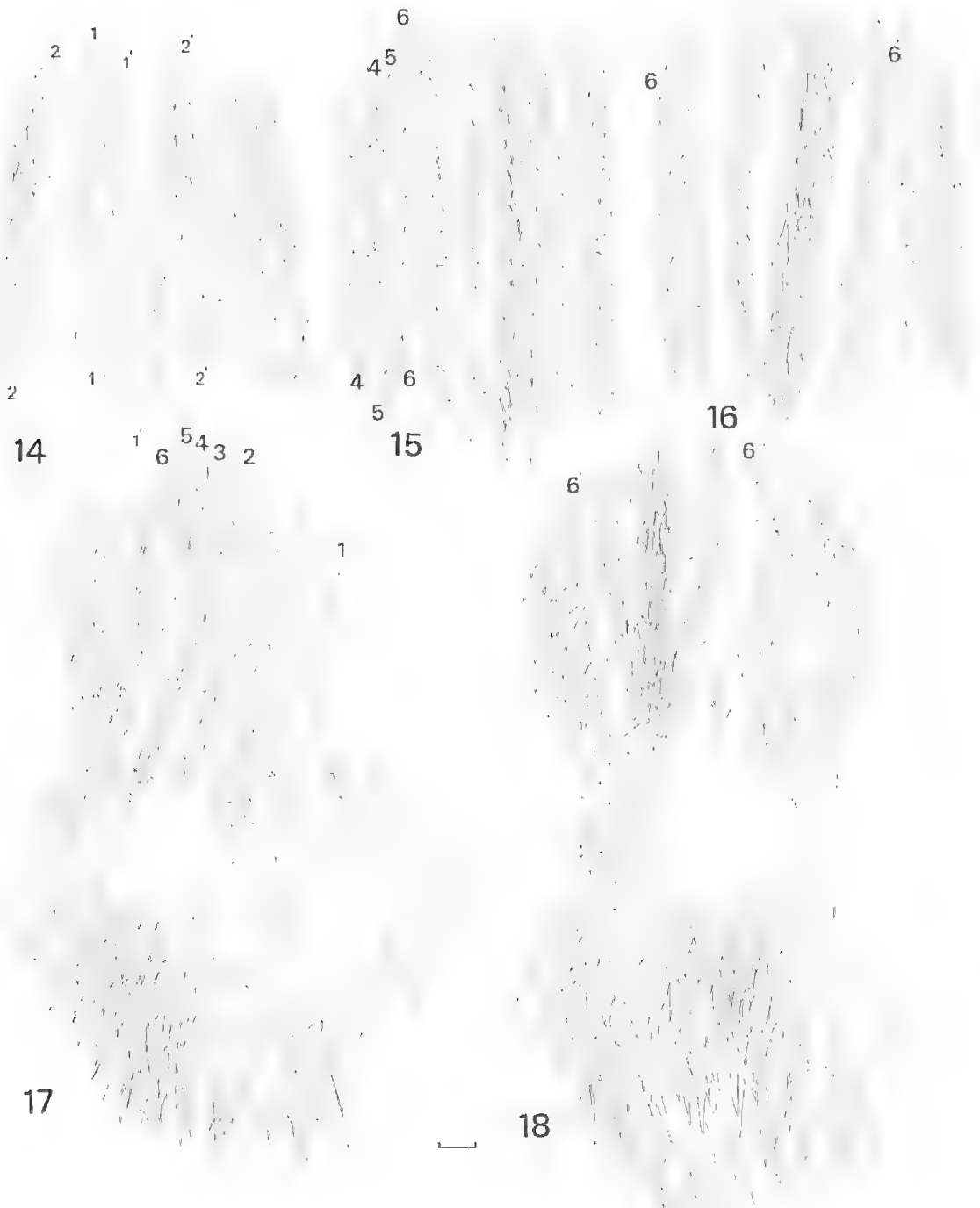
Description

Measurements from Australian specimens. Scolex 3.3-5.0 (4.2, n=10) mm long; maximum width at posterior extremity 0.83-1.42 (1.12, n=10) mm; pars bothridialis 1.05-1.40 (1.28, n=10) mm, 2 bothridia with thick margins, posterior margin of each bothridium with 2 prominent fusettes; pars vaginalis variable in length, depending upon state of contraction of specimen, 1.88-3.40 (2.58, n=10) mm, prominent longitudinal muscles between tentacular sheaths; bulbs elongate, 1.19-1.70 (1.42, n=10) mm long, 0.20-0.30 (0.25, n=10) mm wide, length:width ratio 4.10-7.35 (5.92, n=10), posterior extremities of bulbs directed laterally, terminating at postero-lateral margin of velum; prebulbar organ absent; retractor muscle originating from anterior half of internal wall of bulb; no gland cells present within bulbs; scolex ratio (pb:pvag:pbulb = 1:1.23:1.10); scolex eraspedote, length of velum 0.26-0.50 (0.39, n=10) mm long, pygidium 0.40-0.65 (0.54, n=10) mm long.

Tentacles of relatively uniform diameter for most of length, without basal swelling, slightly narrower at base, 80-150 (120, n=10) in diameter at base, 100-160 (140, n=10) in diameter in metabasal region; 1450-2200 (1940, n=10) long when fully extended, tapering at tip, with approx. 125 rows of hooks. Arrangements heteroacanthous, heteromorphous; hooks hollow; no distinct basal armature. Hooks arranged in ascending half rows; rows beginning on antiothridial surface, terminating on bothridial surface; slight space between hook files 1 and 1' on antiothridial surface, most prominent between rows 6 and 20; number of hooks changes along tentacle: 10 rows from base, 10



Figs 10-13. *Pseudotobothrium arii* (Bilquees & Shaukat, 1976) comb. nov. 10. Scolex showing lateral extension of posterior region of pars bulbosa. 11. Bothridium showing bothridial pits (p) at posterior extremity of bothridium. 12. Tentacular bulb, showing origin of retractor muscle. 13. Basal and metabasal armature, bothridial surface, showing interlocking files of hooks at base and origins of ascending hook rows of metabasal region. Scale bars = 10-12, 0.1 mm; 13, 0.01 mm.



Figs 14-18. *Pseudotobothrium arii* (Bilquees & Shaukat, 1976) comb. nov. Tentacular armature. 14. Metabasal region, bothridial surface, showing origins of hook rows. 15. Metabasal region, external surface, showing ascending rows of hooks on left and band of hooklets on right. 16. Metabasal region, antibothridial surface, showing central band of hooklets with flanking file of hooklets on each side. 17. Basal region, external surface, bothridial aspect with interlocking large hooks on right hand side, bill-hooks on antibothridial surface on left hand side. 18. Basal region, oblique view of antibothridial surface showing bill-hooks on antibothridial surface of base and origin of band of hooklets in metabasal region Scale bar = 0.01 mm.

hooks per principal row; 20 rows from base, 15 hooks per row; 25 rows from base, 40 hooks per row; increase in number of hooks occurs at origins of rows on antibothridial surface; number of hooks per row diminishes towards tip of tentacle; 110 rows from base, 30 hooks per row, 120 rows from base, 20 hooks per row. Hooks change slightly in shape along tentacle. At base, hooks on antibothridial surface uncinatc, blade tips bulbous, bases broad, hooks 20-33 (28, n=10) long, base 12-20 (18, n=10); on bothridial surface of tentacle hook tips sharp, bases elongate; from rows 5 to 10, hooks 1(1') small, uncinatc, 21-33 (26, n=10) long, base 21-25 (23, n=10), blade becoming much longer than base along row, largest hooks of rows elongate, falcate to triangular, 50-62 (56, n=10) long, base 13-20 (17, n=10); from rows 10-15, hooks 1(1') diminish in size, remain uncinatc; hooks 7(7'), 8(8') elongate, falcate to spiniform; from row 20 distally, hooks 1(1') to 20 (20') small, uncinatc, with narrow base and sharply rebated hook tip, 13-19 (15, n=10) long, base 6-9 (7, n=10), closely packed; hooks on internal and external surfaces elongate, spiniform, longest hooks of each row 52-67 (60, n=10) long, base 14-20 (18, n=10); final file of hooks of each principal row 35-50 (44, n=10) long, base 8-17 (13, n=10). On bothridial surface, distal to row 5, space present between final hook of principal row and central band of 10 files of smaller hooklets. At base of tentacle, all hooklets of band uncinatc, with elongate base; in metabasal region, hooklets of outer files with short bases, 32-36 (35, n=10) long, base 8-11 (10, n=10); hooklets of inner files retain elongate bases, 26-44 (35, n=10) long, base 12-22 (16, n=10). Band of hooklets with 1 row of hooklets for each principal hook row; arrangement of band of hooklets not perfectly regular. Adult unknown.

Pseudotobothrium arn

(Bilquees & Shaikat, 1976) comb. nov.
(FIGS 10-18)

Oobothrium arn Bilquees & Shaikat, 1976, pp. 119-124, fig. 1 (*Arms serratus* Day, 1877, Karachi).

Types: School of Parasitology, Department of Zoology, University of Karachi (not examined).

Material examined:

From *Arms serratus* Day, 1877: Pakistan: 1 specimen, Karachi, ident. by Dr F. M. Bilquees, BMSH 1989.5.18.14.

From *Arms groefii* Kuer & Steindachner, 1866: Australia: 3 specimens, Brisbane, Queensland, coll. M. K. Jones, 8.ix.1997 (SAMA 28271), 23.x.1997 (SAMA 28266).

Description

Measurements from Australian specimens. Scolex

3.1, 3.5, 4.1 mm long, maximum width in pars vaginalis 0.15, 0.16, 0.22 mm, at posterior extremity 0.94, 1.10, 1.23 mm; pars bothridialis 0.45, 0.49, 0.55 mm, 2 bothridia with distinct margins, posterior margin of each bothridium with 2 small but prominent fossettes; pars vaginalis variable in length, depending upon state of contraction of specimen, 2.74, 3.11, 3.50 mm; bulbs elongate, 0.50-0.70 (0.57, n=5) mm long, 0.15-0.22 (0.18, n=5) mm wide, length:width ratio 2.73-3.68 (3.26, n=5), bulbs directed almost laterally, terminating at posterolateral margin of velum; prebulbar organ absent, retractor muscle originating in anterior extremity of internal wall of bulb; no gland cells present within bulbs; scolex craspedote, length of velum 0.15 mm; scolex ratio (pb:pvag:pbulb) = 1:6.24:1.14.

Tentacles with distinct basal swelling, 50, 60 in diameter at base, 40, 40 in diameter in metabasal region. Armature heteroacanthous, heteromorphous; hooks hollow; distinct basal armature. Basal armature with hooks 1(1') on bothridial surface greatly enlarged, bases close together such that blades interdigitate, 40-70 (57, n=10) long, base 20-30 (26, n=5). Hooks on posterior part of internal and external surfaces of basal swelling arranged in c. 10 rows; hooks spiniform with narrow bases, 19-27 (22, n=10) long, base 4-8 (6, n=10); anterior part of basal swelling on both internal and external surfaces devoid of hooks. External surface of basal swelling with row of bill-shaped hooks, 25-32 (28, n=10) long, base 5-8 (6, n=10). Metabasalar armature; hooks arranged in ascending half-rows; rows begin on bothridial surface, terminate on antibothridial surface; 6 hooks per principal row; very slight space between hook files 1 and 1' on bothridial surface, diminishing in width posteriorly and disappearing at level of base. Hooks 11(1') large, uncinatc, 28-32 (30, n=5) long, base 18-26 (21, n=5). Hooks 2(2') uncinatc, smaller, 19-30 (25, n=10) long, base 14-20 (17, n=10); hooks 3(3') erect, uncinatc with sharply recurved tips and narrow bases, 17-32 (22, n=10) long, base 5-8 (7, n=10); hooks 4(4') to 6(6') spiniform with very narrow bases and recurved tips, 20-31 (25, n=10) long, base 4-10 (6, n=10). On antibothridial surface, space present between final hook of principal row (6(6')) and central band of hooklets. Outer file of hooklets spiniform, 17-30 (23, n=10) long, base 4-6 (5, n=10), separated from central band of 4 files of spiniform hooklets 18-30 (23, n=10) long, base 4-6 (5, n=10); single row of hooklets per principal row. Adult unknown.

Discussion

Pseudotobothrium dipsacum has been described by several authors. Linton (1897) gave a brief description of the species but did not describe the

armature in detail, apart from noting the closely spaced rows of hooks and the increase in number of hooks per row along the tentacle. The redescription provided by Cruz-Reyes (1973) was more detailed but the description of the armature was limited to one surface of the tentacle, that on which the hook rows commence.

Palm *et al.* (1994) provided scanning electron micrographs of the armature, while Palm (1995) provided a brief summary of the morphological features of *P. dipsacum* and a re-interpretation of its armature. He (1995, 1997a) proposed that the armature was of the typical heteroacanthous type with the hook rows beginning on the internal surface and terminating on the external surface of the tentacle, without extra rows of hooks on the latter surface. The armature had previously been considered to be of the atypical heteroacanthous type in which additional hooks are usually present on the external surface of the tentacle (Dollfus 1942). On the basis of this re-interpretation, Palm (1995) created a new family, Pseudotobothriidae, for the species, although he cited it subsequently as "Pseudotobothriidae Ward, 1954" (Palm 1997b, p. 75). The current re-description of the species provides morphological evidence which contradicts Palm's (1995, 1997a) hypotheses. Firstly, the hook rows in *P. dipsacum* begin on the antibothridial surface of the tentacle and end on the bothridial surface, a feature which has not been recorded previously in this species. In most trypanorhynch, the principal rows begin on the internal surface and terminate on the external surface (Dollfus 1942; Campbell & Beveridge 1994). Exceptions to this pattern are the genera *Natorella* Euzet & Radujkovic, 1989 and *Prochristianella* Dollfus, 1946, with rows beginning on the bothridial surface of the tentacle (Campbell & Beveridge 1994; Beveridge & Jones 2000). Palm *et al.* (1994) and Palm (1995, figs 155, 157) mistakenly identified the antibothridial surface as the external surface and the bothridial surface as the internal surface in descriptions of the armature. Palm subsequently (1997b, figs 1e,d) identified the bothridial surface as the external surface.

The second significant feature, noted here for the first time in this species, is the space between the principal rows of hooks and those occupying the centre of the bothridial surface of the tentacle. This space is clearly visible in various views of the tentacle but may be obscured when detached tentacles are manipulated in glycerine (Fig. 5), compressing some hooks against the surface of the tentacle. In addition to the spaces observed, there are significant differences in shape between the hooks at the ends of the principal rows and those in the centre of the bothridial surface of the tentacle (Figs 7, 8). For these reasons, the interpretation advanced here is

that the principal rows terminate as they approach the bothridial surface and that the hooklets on the bothridial surface form a "band", with each row in the band corresponding to a principal hook row. This interpretation conforms with the limited observations of Linton (1897) and Dollfus (1942) that there are no "extra" rows of hooks on the bothridial surface. The distinct "band" is a characteristic of the poecilacanthous trypanorhynch in the system of Dollfus (1942) or the otobothriids in the system of Campbell & Beveridge (1994) and is a feature of the related otobothriid genus *Poecilacanthum* Dollfus, 1929, in which there are three rows of hooklets for each principal row (Beveridge & Campbell 1996).

Consequently, *P. dipsacum* is an otobothriid trypanorhynch on the basis of its armature and is allied with *Poecilacanthum* in the family Otobothriidae. An additional family, Pseudotobothriidae, is not required and we therefore place Palm's (1995) family as a synonym of Otobothriidae.

There are, nonetheless, several unique features in the armature of *P. dipsacum*. The dramatic increase in numbers of hooks per principal row along the tentacle has been reported from no other trypanorhynch cestode. The number of hooks in the principal row is usually constant or diminishes distally along the length of the tentacle. In addition, it is unusual for the final or penultimate hook of the principal row to be the longest. Usually, the largest hook is at the commencement of or in the middle of the principal row. Thus there are adequate reasons for maintaining *P. dipsacum* as an independent species. Comparison of Australian specimens with material in museum collections suggests that *P. dipsacum* is a cosmopolitan species which is morphologically uniform throughout its geographic range. The material examined from Australia and other regions considerably expands the host range of the species.

Dollfus (1942) sub-divided the genus *Otobothrium* into two subgenera and erected the sub-genus *Pseudotobothrium* (with type species *O. dipsacum*) primarily on the basis of armature. The sub-genus *Otobothrium* was characterised as having extra hooks or hook rows on the external surface of the tentacle, while in *Pseudotobothrium*, the numbers of hook rows were the same on both surfaces of the tentacle. Dollfus (1942) also noted that in *Pseudotobothrium* the bulbs were elongate, while in *Otobothrium* they were generally short. Yamaguti (1959) also subdivided *Otobothrium* into sub-genera, basing the division primarily on the lengths of the bulbs and designating *O. linstowi* as the type species of the sub-genus *Pseudotobothrium*, apparently overlooking the taxonomic decision of Dollfus (1942). Schmidt (1986) did not accept Yamaguti's

(1959) subdijivisa, while Campbell & Beveridge (1994) accepted the sub-genera but, following Yamaguti (1959), erroneously cited *O. linstowi* as the type species of the sub-genus *Pseudotobothrium*. Schmitt (1986) did not recognise the two sub-genera.

Cruz-Reyes (1973) redescribed *O. dipsacum* and considered *Otobothrium insigne* Linton, 1905 as its synonym for reasons which were not explained. Consequently, the host list for *P. dipsacum* given by Palm (1995), which follows Cruz-Reyes (1973), is a composite. As *O. insigne* is here regarded as a valid species based on the redescription by Hildreth & Lumsden (1985), the valid records of *O. dipsacum* are therefore those listed in the synonymy. Dollfus (1942) reported six possible specimens of *O. dipsacum*, plerocerei collected from *Polynemus quadrifilis* and *Brachydeuteres auritus* (Valenciennes, 1831) (= *Otoporeta aurita*) from Pointe Padron, Congo (=Zaire). The illustrations of the specimens (Dollfus 1942, fig. 157) suggest that they belong to an undescribed species related to *O. insigne*, based on specimens from the same geographical region in Dollfus' collection (MNHN). There are no specimens of *P. dipsacum* in the Dollfus collection in MNHN and therefore Dollfus' (1942) records have not been included in the current list of hosts of *P. dipsacum*.

Bilquees & Shaukat (1976) described *O. arii* based on plerocerei from the musculature of a catfish, *Arius serratus*, from Pakistan. They distinguished it from congeners primarily on the basis of number of files of hooks and the laterally divergent bulbs. They did not, however, give a detailed description of its armature. The three Australian specimens examined, also from a catfish, *Arius graeffii*, are identical to *O. arii* based on comparisons with a specimen in BMNH from the type host and locality, identified by Dr Bilquees. Both the scolex shape and the armature are highly distinctive. The pars vaginalis is extremely long and slender and the bulbs extend laterally, as in *O. penetrans* Linton, 1907, *O. pephrikos* Dollfus, 1969 and *O. kurisi* Shields, 1985. Palm (1995) considered *O. kurisi* to be a synonym of *O. penetrans*. *Otobothrium penetrans* has a basal swelling and distinctive basal armature as does *O. arii*. However, while the metabasal armature of *O. penetrans* consists of principal rows of seven hooks with two intercalary hooks between each row (Palm 1995; Palm *et al.* 1993), there are six hooks in the principal row in *O. arii* followed by a file of hooks (7/7) separated from the previous file by a distinct space (Fig. 16). In the centre of the antibothridial surface of the tentacle is a band of hooklets, four files wide. The metabasal armature of *O. arii* differs therefore from every species of *Otobothrium* in which this feature has been adequately described (*O.*

penetrans, *O. pephrikos*, *O. insigne*, *O. vuitatou* Subhadrpradha, 1955) but resembles that of the genera *Pseudotobothrium* and *Poecilancistrum*, both of which have bands of hooklets on the external surface of the tentacle (Palm 1995; Beveridge & Campbell 1996). *Otobothrium arii* differs from *P. dipsacum* in possessing a distinctive basal swelling and armature, as well as lacking an increase in the number of hooks per principal row along the tentacle and having the rows of hooks beginning on the bothridial surface of the tentacle rather than the antibothridial surface as in *P. dipsacum*. It differs from *Poecilancistrum* in having only one row of hooklets per principal row compared with three in *Poecilancistrum* (Beveridge & Campbell 1996).

Otobothrium arii also resembles *Poecilancistrum oweni*, described by Palm (1995) from an unidentified catfish from Papua New Guinea. The scolex of *P. oweni* appears to differ in having an extremely thick tegument, being much broader in the pars vaginalis (0.75 mm in *P. oweni*, 0.17 mm in *O. arii*) and having longer bulbs (1.1 mm in *P. oweni*, 0.57 mm in *O. arii*). The basal armature of the two species is remarkably similar. They differ however, in that while *P. oweni* has a chainette composed of triangular hooks on the external surface of its tentacle, *O. arii* has a band of hooklets.

While it may be possible to advance arguments for the erection of a new genus to accommodate *O. arii*, the existence of two monotypic genera within the Otobothriidae, *Pseudotobothrium* and *Poecilancistrum*, as well as uncertainties concerning relationships with the monotypic genus *Poecilocanthum*, leads us to adopt a conservative approach in allocating *O. arii* to the genus *Pseudotobothrium*. The definition of the genus must now include species with and without a basal armature and with the hook rows originating on either the bothridial or antibothridial surfaces of the tentacle. The key feature which distinguishes *Pseudotobothrium* from *Otobothrium* remains the character identified by Dollfus (1942), namely that the number of rows of hooks on the external surface of the tentacle is the same as on the internal surface in *Pseudotobothrium* whereas there are more rows on the external surface in *Otobothrium*. *Pseudotobothrium* and *Poecilancistrum* both differ from *Otobothrium* in possessing a band of hooklets on the tentacle rather than a single row of hooks interpolated between the intercalary rows. *Pseudotobothrium* differs from *Poecilancistrum* in possessing one row of band hooks per principal row compared with three rows of band hooks in *Poecilancistrum*. All three genera differ from *Poecilocanthum* which possesses a chainette in the metabasal region. Details of the strobila as well as the addition of new species to these genera may facilitate the clarification of their relationships which

remain obscure at the present time.

The genus *Pseudotobothrium*, as described here, includes two distinctive species of cestodes, intermediate between *Otobothrium* and *Poeciluncistrub*. It may ultimately need to be dismembered, but indicates a hitherto unsuspected degree of diversity within the Otobothriidae, suggesting that additional novel species await discovery. A revised generic diagnosis is given below.

Pseudotobothrium Dollfus, 1942

Definition

Otobothriidae Dollfus, 1942. Scolex craspedote. Two bothridia with pair of fosselles on posterior margin. Pars vaginalis elongate. Bulbs elongate; retractor muscle originating from anterior part of bulb; prebulbar organ absent. Pars postbulbosa absent. Armature heteroacanthous, heteromorphous; hooks hollow. Distinctive basal armature present or absent. Hook rows begin on bothridial or

antibothridial surfaces of tentacles, terminate on opposite surface of tentacle; space present between principal rows and band of hooklets on bothridial or antibothridial surface of tentacle; band regularly arranged, with same number of rows as principal rows.

Type species: *P. dipsacum* (Linton, 1897).

Other species: *P. arii* (Bilguez & Shaukat, 1976) comb. nov.

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SEDIMENT IN A FRESHWATER ROCK-HOLE IN THE
NORTHERN TERRITORY**

BY WARWICK L. NICHOLAS & M. HODDA†*

Summary

Nicholas, W. L. & Hodda, M. (2000) *Dorylaimus baylyi* sp nov. (Dorylaimidae, Dorylaimida) a nematode collected from sediment in a freshwater rock-hole in the Northern Territory. *Trans. R. Soc. S. Aust.* 124(2), 163-168, 30 November, 2000.

A new species of *Dorylaimus* is described from the sediment of a freshwater rock-hole in the Northern Territory, Australia. It is distinguished from other species by a combination of characters: the cuticle has about 30 longitudinal ridges in the mid region of the body, the odontostyle varies from 43 to 46 μm in length with an aperture covering 43 to 46% of its length and is about ten times as long as it is in diameter, the male tail is short and rounded and the female tail is conoid, terminating in a short flagellum, the spicules are 55-61 μm long, and there are 22-25 supplements in a contiguous row.

Key Words: *Dorylaimus*, freshwater, nematode, rock-hole, taxonomy.

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A new species of *Dorylaimus* is described from the sediment of a freshwater rock-hole in the Northern Territory, Australia. It is distinguished from other species by a combination of characters: the cuticle has about 30 longitudinal ridges in the mid region of the body, the odontostyle varies from 43 to 46 µm in length with an aperture covering 43 to 46% of its length and is about ten times as long as it is in diameter, the male tail is short and rounded and the female tail is conoid, terminating in a short flagellum, the spicules are 55-61 µm long, and there are 22-25 supplements in a contiguous row.

KEY WORDS. *Dorylaimus*, freshwater, nematode, rock-hole, taxonomy.

Introduction

Nematodes of the genus *Dorylaimus* Dujardin 1845 are among the most commonly occurring freshwater nematodes and are obvious because of their large size. The genus has been little studied in Australia. Late last century Cobb described *D. latus* Cobb 1891 from grass and *D. spiralis* Cobb 1893 from carrots near Sydney and *D. minimus* Cobb 1893, *D. subsimilis* Cobb 1893, *D. pusillus* Cobb 1893 and *D. perfectus* Cobb 1893 from sugar cane in northern NSW. At the time, the concept of the genus was much broader than it is now, *Dorylaimus* being the only genus in what is now regarded as the superfamily Dorylaimoidea. Cobb's descriptions are insufficient to place these taxa even to genus. All were described from females, only the first and last named were illustrated and no type specimens were designated.

The USDA Nematode Collection contains three species labelled *Dorylaimus monohystera*, *Dorylaimus miser* and *Dorylaimus perfectus* collected from soil under wheat at Nhill, Victoria and donated by Thorne in September 1963. *Dorylaimus monohystera* was later transferred to the genus *Eumemnus* and *D. miser* to *Eudorylaimus* (Thorne 1974) and the specimens of *D. perfectus* appear to be more correctly placed in the genus *Mesodorylaimus*.

Bishop (1974) observed that nematodes of the

genus *Dorylaimus* were common in temporary freshwater pools near Sydney but published no descriptions and kept no voucher specimens. Hodda *et al.* (in press) collected aquatic nematodes extensively throughout southeastern Australia and confirmed that in that environment members of the genus are often present.

This paper presents a description of a new *Dorylaimus* collected by I. Bayly from a rock-hole (gamma) at Warumbi Hill in The Northern Territory in 1991. Subsequent sampling of the type locality by Dr Bayly yielded further dorylaims but no additional specimens of the new species.

Type and Voucher specimens are deposited in the National Nematode Collection (ANIC) at the CSIRO Division of Entomology, Canberra ACT.

Materials and Methods

Specimens collected with a 0.15 mm mesh net were fixed in 70% alcohol. For processing they were washed in water and transferred to 5% aqueous glycerol. The water was slowly evaporated and the specimens were transferred to anhydrous glycerol in which they were mounted for microscopy with cover slips supported by glass beads of the appropriate size. Measurements were made from camera lucida drawings. All measurements were along the curved median line.

One specimen was washed in water and post-fixed in aqueous OsO₄, washed again in water and freeze dried. The specimen was mounted on a metal stub, coated with gold/palladium and examined and photographed in the scanning electron microscope.

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Dorylaimus baylyi sp. nov.
(FIGS 1-14)

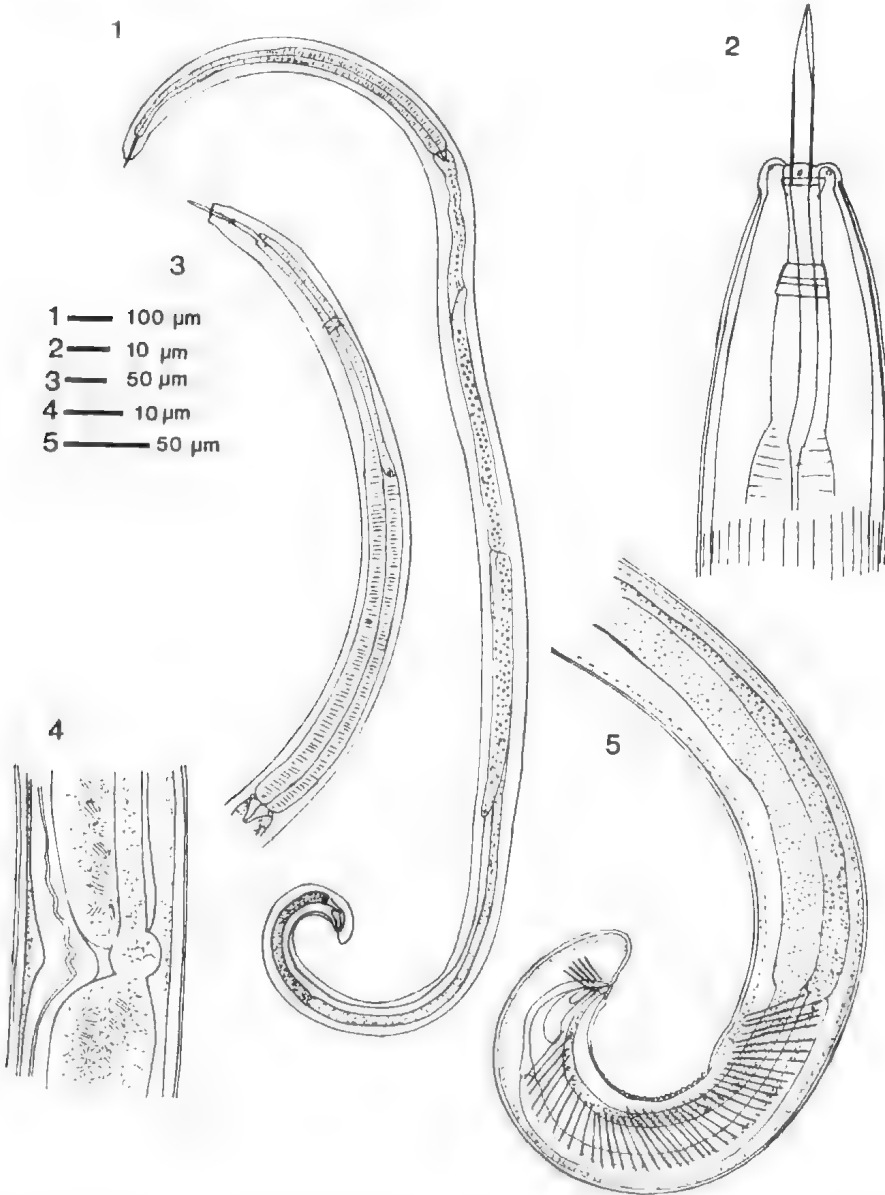
Holotype: ♂, ANIC 81-340, I. Bayly, Warumbi Hill, near Papunya, NT, 5.v.98.

Paratypes: 6 ♂♂, ANIC 81-341 to 346, 6 ♀♀, ANIC 81-347 to 351, I. Bayly, Warumbi Hill, near Papunya, NT, 5.v.98.

Measurements: Table 1.

Description of Holotype male (Figs 1-5)

Body large, slender, cylindrical. Tapered cervical region, six rounded slightly offset lips. Tail short, rounded. Cuticle very finely annulated in cervical region (below resolution of the light microscope, but visible with SEM), with 28-32 longitudinal ridges at mid body. Amphidial fovea stirrup-shaped, aperture a longitudinal slit just behind lips. Odontostyle straight, strongly built, 10 x diameter or 2.3 x width of lips, aperture 45% of length, guide



Figs 1-5. *Dorylaimus baylyi* sp. nov. male. 1. Entire holotype. 2. Head with odontostyle fully protruded. 3. Pharyngeal region. 4. Junction of two testes with vas deferens. 5. Posterior of body and copulatory organs.

ring double. Odontophore slightly curved, slightly longer than odontostyle. Pharynx cylindrical, muscular throughout its length, narrow at odontophore junction, expanded half way along its length, nerve ring 25% of pharynx length from head end, with dorsal pharyngeal gland adjacent to expansion. Cardia triangular, with length greater than diameter, enclosed by anterior intestine. Gland cells between pharynx and intestine present. Intestine slightly sinuous to level of anterior testis, compressed by gonads, a relatively wide straight tube from level of posterior testis to prerectum. Prerectum short, straight, tubular, set off from intestine by sphincter muscle, terminating in narrow, cuticle-lined rectum. Diorchic, testes not reflexed, mature spermatozoa filiform, in clusters, vas deferens a straight tube, on left side of intestine near anterior end and ventral to intestine at posterior end, ejaculatory duct not distinct from vas deferens. Prominent oblique copulatory muscles from anterior to posterior of prerectum. Spicules

identical, dorylaimoid, ventrally arcuate, with capitulum and lateral guiding pieces (cruria) Supplements, adanal pair, then gap, then row of 22 contiguous supplements.

Paratype males

Similar to holotype, but numbers in row of supplements differ from 22-25. Number of longitudinal cuticle ridges very difficult to count but probably in range 28-32.

Paratype females (Figs 6-14)

Females resemble males in most characters, apart from reproductive system and tail, which is conoid ending in short flagellum. Females didelphic and amphidelphic with reflexed ovaries. Scanning electron micrographs of one additional female (Figs 11-14) show that ridges present in the mid body region cease on tail and cervical region. Very fine annulations, below resolution of light microscope, evident in cervical region and vulva is small oval pore.

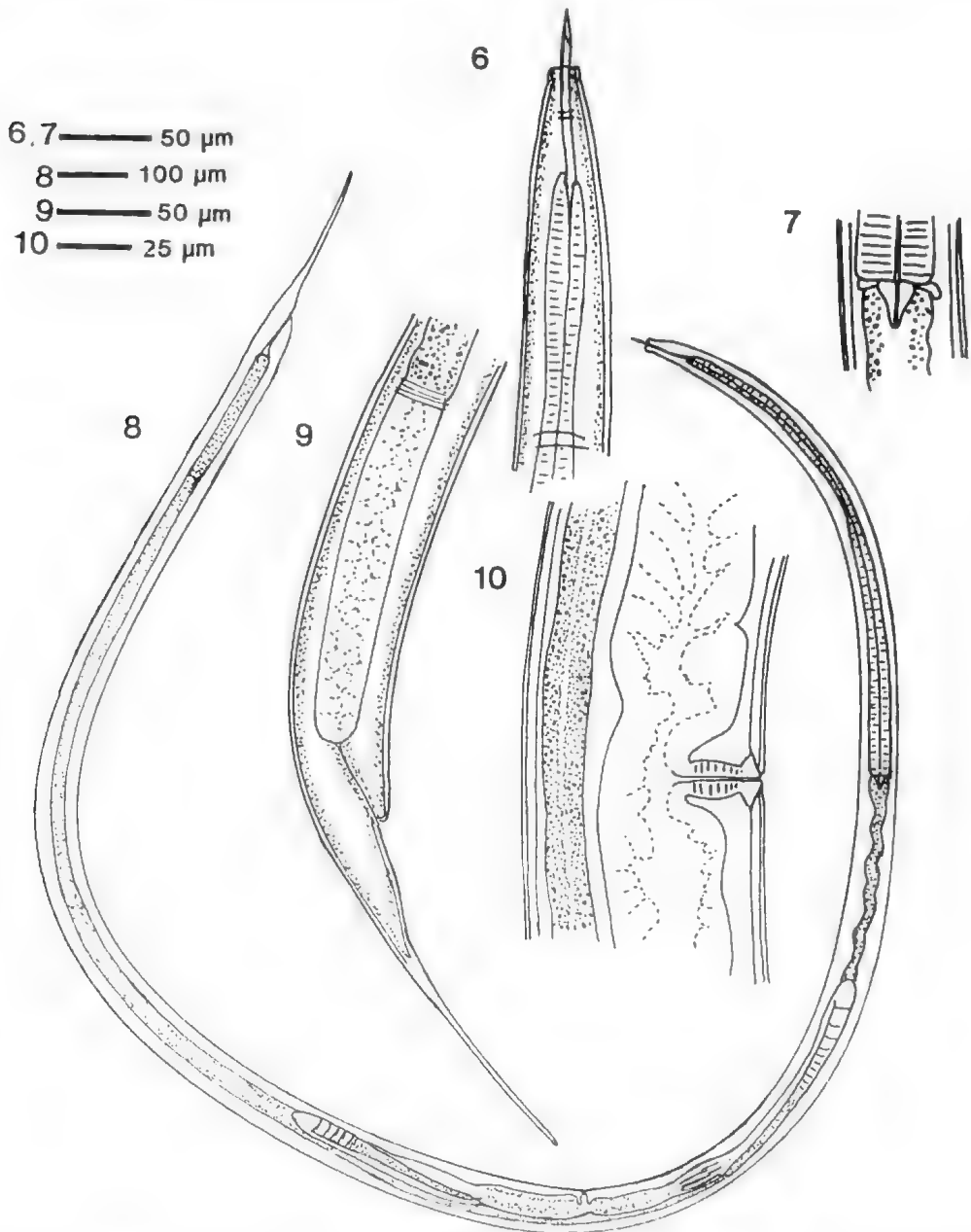
TABLE 1. Measurements (μm) of *Dorylaimus baylyi* sp. nov.

Type	Male Holotype			Male/Para n=6			Female/Para n=6		
		Mean	Range	Mean	Range	SD	Mean	Range	SD
Length	3748	3872	3345-4313	382	4044	3425-4352	366		
Max. width	70	71.5	62-82	7.4	76	66-83	8.4		
Width at lips	19	18	16-21	1.9	19	18-19	0.5		
Odontostyle length	44	45	43-46	1.2	45	43-46	1.2		
Odontostyle aperture	19	19	17-22	2.0	19	17-22	2.1		
Odontophore length	57	61	55-65	3.7	60	39-66	10.3		
Head to amphid opening	5	6.1	3.9-10	2.3	7	3.9-9.5	2.4		
Head to guide ring	26	26	23-28	1.8	29	25-35	4.9		
Head to nerve ring	190	191	175-204	11.6	197	180-216	17		
Head to pharyngeal expansion	423	395	343-450	41	396	342-423	28		
Head to end of pharynx	846	819	768-866	36	877	846-887	17		
Width at cardia	70	55	61-71	4.4	71	64-81	6.3		
Head to tip of anterior gonad	1188	1302	1128-1531	159	1315	1128-1572	194		
Head to vulva	-	-	-	-	1871	1612-2257	303		
Head to vas deferens	1814	1721	1625-1828	77	-	-	-		
Head to tip of posterior gonad	2476	2326	1828-2982	399	2284	1781-2518	379		
Prerectum length	221	199	130-250	49	240	200-350	46		
Rectum length	79	72	60-81	82	64	50-86	13		
Head to anus	3708	3829	3307-4347	377	3807	3253-4142	340		
Tail length	40	43	38-58	5.9	237	190-295	46		
Width at anus	45	45	41-49	3.2	36	30-42	5.1		
Spicule length	57	56	55-61	2.4	-	-	-		
Number of supplements in row	22	24	22-28	2.4	-	-	-		
Anus to supplement row	79	83	79-117	16	-	-	-		
Length of supplement row	71	97	71-156	33	-	-	-		
De Man's a	.54	.55	.46-.66	7.6	.51	.48-.67	.7		
De Man's b	1.1	5.0	4.4-5.1	0.3	4.6	3.9-5.0	0.4		
De Man's c'	.94	.91	.77-.99	7.9	.17	.15-.20	.3		
DeMan's e	0.9	1.1	0.8-1.3	0.2	6.6	6.0-7.0	7.0		
De Man's V%	-	-	-	-	40	41-54	5.4		

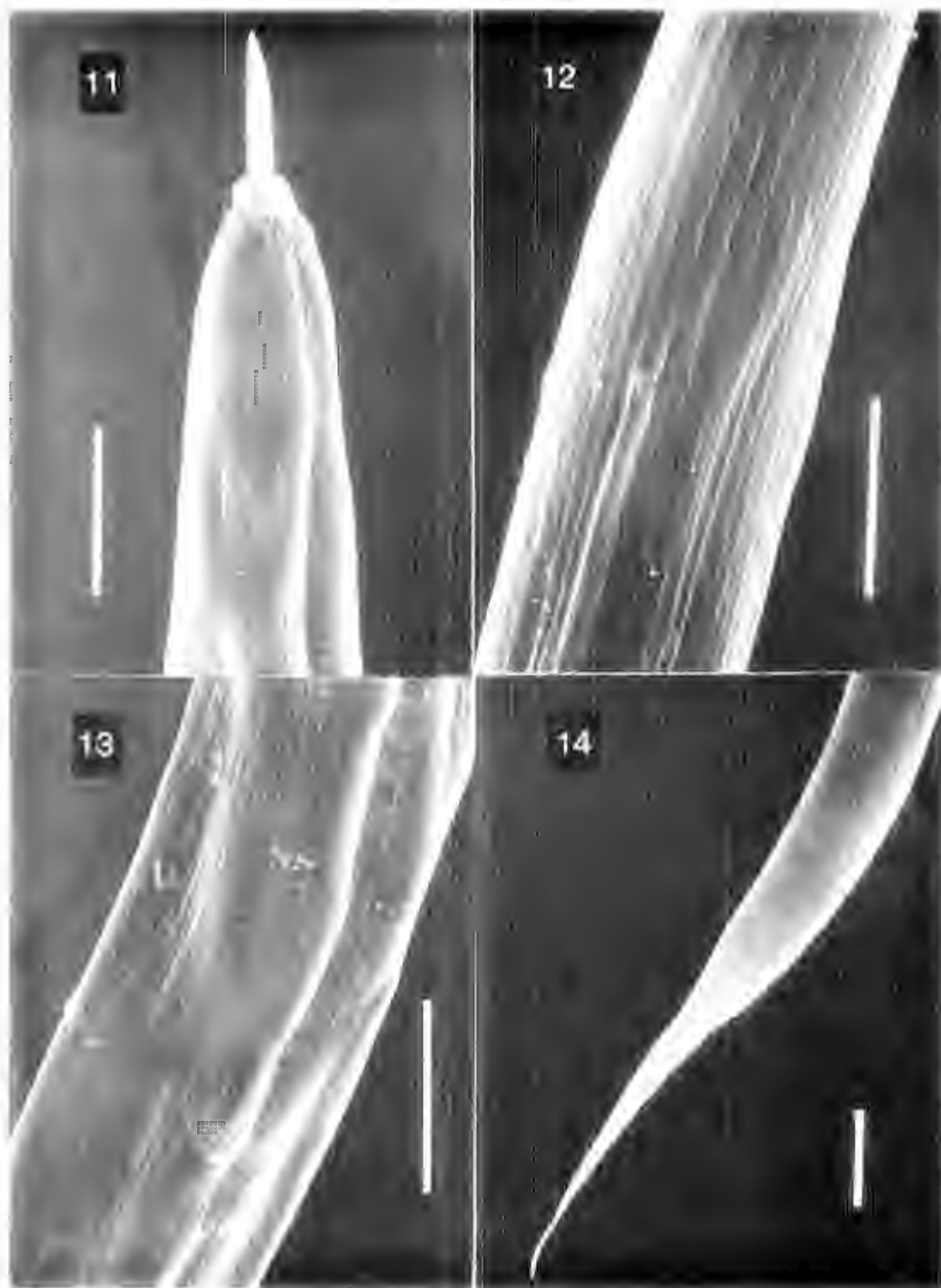
Differential diagnosis

Dorylaimus baylyi sp. nov. differs from all other species of the genus in spicule length, number of longitudinal ridges in cuticle, length of tail in adult females and lack of papillae near vulva. *Dorylaimus baylyi* sp. nov. differs from the closest species (*D. siddiqii* Ahmad & Jairajpuri 1982) in having a longer odontostyle (44-46 μm cf. 35-36 μm in *D. siddiqii*),

a shorter tail in adults of both sexes (De Man's $c = 15-21$ cf. 14 in *D. siddiqii* for adult females and 77-99 cf. 53-64 in *D. siddiqii* in adult males) and having fewer ventromedian supplements (22-25 cf. 31-34). *Dorylaimus baylyi* sp. nov. is also similar to *D. deaconi* Botha & Heyns (1991). Both have very fine annulations in the cervical region anterior to the full development of the longitudinal ridges but *D. baylyi*



Figs 6-10, *Dorylaimus baylyi* sp. nov. female paratype. 6. Head and cervical region. 7. Cardia. 8. Entire female. 9. Tail. 10. Vulval region.



Figs 11–14. Scanning electron micrographs of female *Dorylaimus baylyi* sp. nov. 11. Head and cervical region. 12. Mid region of body showing cuticular ridges. 13. Vulva. 14. Tail. Scale bars = 50 μ m.

sp. nov. has fewer longitudinal ridges (28-32 cf. 33 in *D. deaconii*), a longer odontophore (56-66 μm cf. 43-53 μm), much shorter spicules (55-61 μm cf. 71-86 μm), fewer supplements (22-25 cf. 35-42) and the vulva pore-like rather than a longitudinal slit. *Dorylaimus baylyi* sp. nov. differs from the very widespread *D. stagnalis* in the ratio of length to diameter of the odontostyle (10 cf. 6.7-7.3 in *D. stagnalis*), the odontostyle being shorter (43-46 μm cf. 47-51 μm), the odontostyle aperture being relatively longer (0.37-0.43 of the total length cf. 0.33), having fewer supplements (22-25 cf. 30-40), having much shorter spicules (55-61 μm cf. 100-110 μm) and in having filiform spermatozoa (ovoid in *D. stagnalis*) (Abebe & Coomans 1992; Mulvey & Anderson 1979).

Type locality and habitat

Freshwater rock-hole (gamma).

Distribution

Known only from Warumbi Hill, 3 km from

Papunya in The Northern Territory (23°15' S, 131°54' E). Collected by I. Bayly 5.v.98.

Etymology

In gratitude to Dr Ian Bayly for the specimens, we named the new species after him.

Remarks

Baermann extraction of mud samples from a later collection at the same rock-pool produced *Mesodorylaimus rotundolabiatum* Basson & Heyns (1974) and *Heterocephalobus* sp. (Cephalobidae). These specimens are also deposited in the ANIC Nematode collection. *M. rotundolabiatum* as ANIC 81-352.

Acknowledgments

We thank the Electron Microscope Unit of The Australian National University for the use of the Scanning Electron Microscope.

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**DEVELOPMENTAL BIOLOGY AND LARVAL MORPHOLOGY
OF THE FROG LIMNODYNASTES DEPRESSUS TYLER
(MYOBATRACHIDAE: LIMNODYNASTINAE)**

By MICHAEL J. TYLER & MARGARET DAVIES**

Summary

Tyler, M. J. & Davies, M. (2000) Developmental biology and larval morphology of the frog *Limnodynastes depressus* Tyler (Myobatrachidae: Limnodynastinae). *Trans. R. Soc. S. Aust.* 124(2), 169-175, 30 November, 2000.

The larval morphology, early developmental biology and chondrocranium of *Limnodynastes depressus* are described and compared with the morphologically similar *L. tasmaniensis* and *L. fletcheri*. Advanced tadpoles reach a total length of 80 mm or more and the mouth disc has three upper (one divided) and three lower (one divided) rows of labial teeth. Larvae resemble those of *Limnodynastes fletcheri* but are generally larger. Spawn is laid as a foamy mass in water-filled depressions in the ground. The chondrocranium differs from that of *L. tasmaniensis* and *L. fletcheri* in the attachment of the processus ascendens of the arcus subocularis with the prootic.

Key Words: *Limnodynastes depressus*, developmental biology, tadpoles, spawn, chondrocranium, frog, Myobatrachidae.

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Introduction

Limnodynastes comprises three recognisable lineages (Tyler *et al.* 1979; Mahony & Robinson 1986; Roberts & Maxson 1986), one of which is a group of so-called marsh frogs that includes *L. depressus* Tyler, 1976. This species has previously been known only from the holotype but recent field and laboratory observations (Davies & Burton 2000; Morris & Tyler unpub.; Watson, Tyler & Morris unpub.) will contribute substantially to knowledge of this frog.

Spawn clumps and early developmental stages have been observed in the field and captive specimens have bred in the laboratory. Here we describe the developmental biology of the species and include morphological data on the chondrocranium of the larval stages.

Materials and Methods

Initial observations of egg deposition sites and breeding behaviour were made at Cockatoo Lagoon in the Keep River National Park, Northern Territory (15° 59' S, 129° 03' E) from 10-12 February 1998. Early developmental stages were collected and preserved in Tyler's (1962) preservative. A captive pair of *Limnodynastes depressus* collected at Keep River spawned in the University of Adelaide Zoology Department Aquarium Room overnight

3/4.in.1998 and larvae were reared to metamorphosis. The room was maintained at 30°C ±1°. Larvae were reared in shallow glass aquaria (25 x 25 x 8 cm) in aerated, dechlorinated tap water and were provided with a diet of boiled, organically grown, lettuce leaves supplemented by SERA goldfish flakes. Representative larval stages were preserved in Tyler's fluid. Stages follow Gosner (1960). Chondrocranial preparations were made after the method of Dingerkus & Uhler (1977). Drawings were made with the aid of a camera lucida attached to a Wild M9 dissecting microscope. Measurements were made with dial calipers reading to 0.05 mm and with an eyepiece micrometer. Chondrocranial descriptions follow Haas & Richards (1999). Temperature measurements in the field were taken with a Digitron D2060 digital temperature probe within the spawn clump toward the base and in the water or mud beside the clump.

Results

Field observations

HABITAT

Cockatoo Lagoon is an elongate billabong whose southern limit is within 3 km of the Victoria Highway connecting Kununurra, WA with Katherine in the NT. The billabong is approximately 150 m wide for its entire length and extends for approximately 1 km in a northeasterly direction. The most detailed map readily available is Keep, sheet 4766 (1:100000) of the National Topographic Map Series.

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Fig. 1. Spawn clump of *Limnodynastes depressus* in a depression adjacent to Cockatoo Lagoon, Keep River NP, NT.

At the time of the visit in 1998, there had been little rain and the billabong was reduced to a series of isolated pools. The observations reported here were undertaken in the area adjacent to the Keep River National Park Office and Interpretation Centre and the extreme southern portion of Cockatoo Lagoon, extending for 400 m south of the Centre.

SPAWN

Seventeen clumps of spawn were located at two areas within the study site, on the periphery of a shallow pool in depressions created by Brahmin cattle (Fig. 1) and amongst dense patches of the perennial grass *Pseudoraphis spinescens* (R. Br.) Vic. Details of representative clumps and site temperatures are provided in Tables 1 and 2. Tyler (1994) reports spawn of *Litoria rubella* (Gray) in water temperature of 42° C and tadpoles of various species in water temperatures ranging from 35–45° C in other areas in northern Australia.

Newly-hatched larvae were at stage 23/24. Of 25 larvae examined, filamentous gills were present only on the left hand side in all but one which had gills still present on both sides. Adhesive glands were lightly pigmented. The mouth was perforated and the beak was keratinised. At two days post-hatching, larvae were at stage 24 and stage 25. At stage 25, labial tooth rows remained unkeratinised.

Laboratory observations

A spawn clump was laid overnight between 3.iii.1998 and 4.iii.1998. The egg mass was a foamy

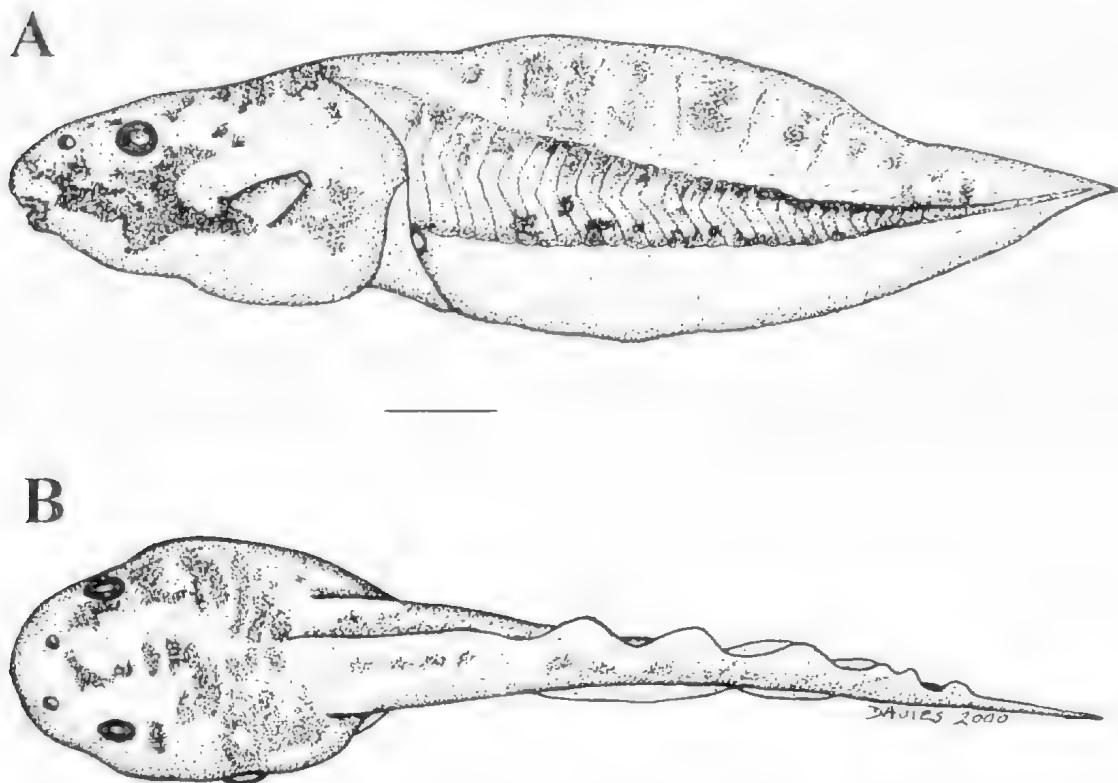


Fig. 2. A. Lateral and B. dorsal views of *Limnodynastes depressus* tadpoles Stage 26. Scale bar = 5 mm.

TABLE 1. Dimensions (mm) of spawn clumps of *Limnodynastes depressus* and deposition cavities at Cockatoo Lagoon, Keep River National Park.

Reference	Spawn clump	Deposition cavity	Cavity water depth
A	50 x 45	160 x 100	45
B	75 x 50	180 x 120	35
C	60 x 60	105 x 80	20
D	90 x 80		100

TABLE 2. Temperatures ($^{\circ}\text{C}$) in spawn clumps of *Limnodynastes depressus* and the surrounding water or mud at Cockatoo Lagoon, Keep River National Park.

Ident.	Date	Time	Temp. in clump	Temp. of adjacent water	Temp. of adjacent mud
1	10.ii.1998	1200	37.7	34.9	
1	11.ii.1998	1050	31.1		30.5
1	11.ii.1998	1355	39.6		33.2
1	11.ii.1998	1600	36.3		35.9
1	11.ii.1998	1928	28.8		31.5
2	10.ii.1998	1210	39.5	35.0	
2	10.ii.1998	1905	30.5	31.6	
3	10.ii.1998	1300	39.8	37.9	
3	10.ii.1998	1900	29.4	30.5	
3	11.ii.1998	1100	27.7	28.2	
4	10.ii.1998	1215	37.5	36.3	
4	10.ii.1998	1930	26.0	30.4	
4	11.ii.1998	1115	28.9	28.8	
5	10.ii.1998	1220	36.1	35.6	
5	10.ii.1998	1940	28.6	30.7	
5	11.ii.1998	1130	31.8		30.2
5	11.ii.1998	1400	37.0		34.3
5	11.ii.1998	1615	36.6		35.3
5	11.ii.1998	1940	29.6		31.7
6	10.ii.1998	1955	28.7		32.1
6	11.ii.1998	1140	32.6		31.1
6	11.ii.1998	1350	41.4		34.3
6	11.ii.1998	1555	39.3		37.0
6	11.ii.1998	1925	27.7		30.7
7	10.ii.1998	2005	29.7		31.6
7	11.ii.1998	1045	31.7	30.3	30.4
7	11.ii.1998	1355	38.2	37.7	35.5
7	11.ii.1998	1600	35.4	36.2	36.5
7	11.ii.1998	1930	27.1		30.9
8		2010	28.8	31.3	
8		0725	28.2		28.4
8		1100	31.1	31.4	30.3
8		1400	37.4	38.9	34.4
8		1605	36.5		36.4
8	11.ii.1998	1935	27.1		31.4
9	10.ii.1998	2015			31.6
9	11.ii.1998	0730			29.3
9	11.ii.1998	1100			30.3
9	11.ii.1998	1610			33.8
9	11.ii.1998	1935			30.4

clump which did not collapse until well after hatching. An egg count could not be obtained as some of the larvae had hatched quickly and not all could be rescued from the holding tank. The first larva reached stage 42 on 20.vi.1998 and metamorphosis was completed at stage 46 by 22.vi.1998, 110 days after spawning.

Pigmentation of larvae was sparse in early stage 30, but by stage 32, larvae were well pigmented.

A larva at stage 26 is shown in Fig. 2. The body is ovoid and widest behind the eyes. The snout is evenly rounded in dorsal view and slightly truncated laterally. The nares are more dorsal than lateral, not elevated and opening anterolaterally. The spiracle is sinistral, relatively short and visible from above. It is attached to the body wall along its medial edge with the diameter of its orifice being slightly less than the diameter of the tube. Tapering of the spiracle is minimal. The anal tube is median and opens along the ventral edge of the ventral tail fin. The tail fins are well arched, the dorsal fin commencing in the posterior $\frac{1}{10}$ of the body. The dorsal fin is deepest about $\frac{1}{3}$ along its length and the ventral fin about $\frac{2}{3}$ along its length. At its terminus, the tail is pointed but not sharply acuminate. The tail musculature is moderately thick and tapers to a point posteriorly. Blotchy chocolate pigmentation on a cream background is located on the tail musculature with little melanism on the fins. The body is covered with blotches of pigment over a poorly pigmented background. Neuromast cells of the lateral lines are well differentiated (Fig. 3).

The mouth is anterior. The oral disc is surrounded laterally and posteriorly with a double row of papillae that are pigmented at their bases and in the centre. Papillae are absent anteromedially. There are three upper and three lower rows of labial teeth. The first upper and second lower rows are divided (Fig. 4).

Measurements of larvae are provided in Table 3. Body length at metamorphosis ranged from 25.0–31.9 mm in four individuals.

Chondrocranium

The chondrocranium of a stage 36 larva is illustrated in Fig. 5. The cartilago labialis superior is composed of a pars alaris (lateral wing) and a pars corporis (frontal bar). The pars alaris is synchondrotically connected proximally with the pars corporis. The articulation of the upper jaw with the cornua trabeculae is mainly by the pars alaris. Viewed ventrally, the partes of the cartilago labialis superior form a simple arch. The cornua trabeculae are the anterior extensions of the trabeculae cranii of the cranial floor. These moderately-broad diverging bars have a lateral process near their proximal base to which the ligamentum quadratoethmoidale is attached.

The cartilago meckelii is sigmoid and transversely oriented. The medial part of its anterior face articulates with the cartilago labialis inferior. The cartilago labiales inferiores form a U-shaped arch in ventral view. They are connected medially by a non-chondrified symphysis.

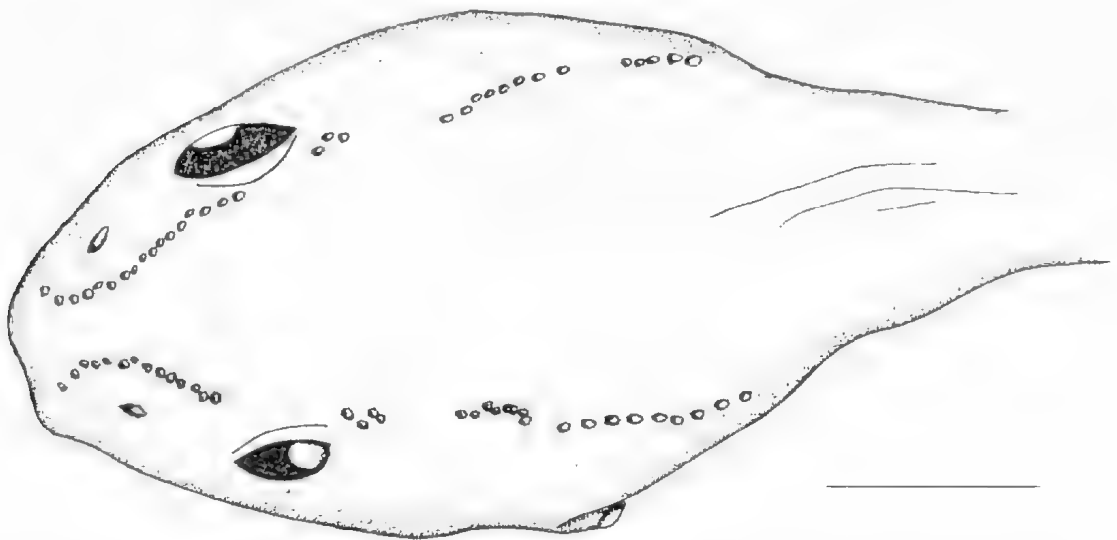


Fig. 3. Dorsal view of Stage 34 tadpole of *Limnodynamis depressus* showing neuromast cells. Scale bar = 5 mm.

TABLE 3. Measurements of tadpoles of *Limnodynastes depressus* expressed in mm as mean and range.

Stage	Body length	Total length	No.
26	10.6 8.6-12.4	31.07 25.7-35.9	3
27	12.03 10.9-14.1	37.03 32.7-43.4	4
28	12.95 10.4-17.0	38.13 32.1-51.1	4
29	11.8 11.2-12.4	34.5 30.2-38.8	2
30	12.9 10.2-15.6	39.5 31.7-38.8	2
31	11.8	38.1	1
32	12.25 11.2-15.3	39.8 35.9-43.7	2
34	13.25 10.4-15.0	43.18 34.6-50.7	4
35	18.9 16.8-21.0	57.3 50.0-64.6	2
36	16.05 12.0-20.7	51.12 36.6-61.4	6
37	17.39 13.3-21.8	55.15 38.8-66.5	8
38	19.35 18.9-19.8	63.3 62.0-64.6	2
39	21.0	64.6	1
40	22.87 22.5-23.1	74.9 72.5-79.2	3
41	21.6	81.0	1
42	25.0		

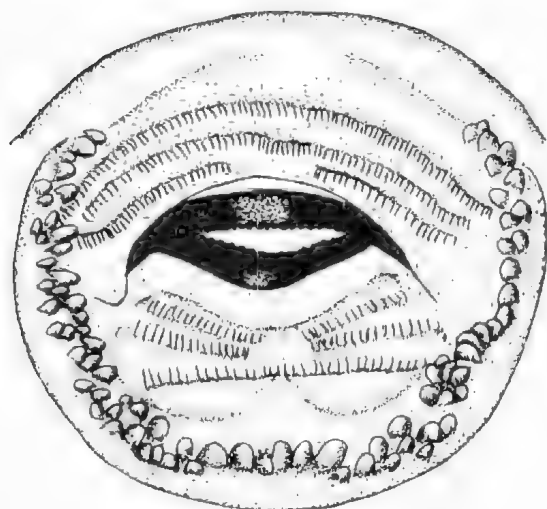


Fig. 1. Oral disc of Stage 26 tadpole of *Limnodynastes depressus*. Scale bar = 1 mm.



Fig. 5. Dorsal view of the chondrocranium of *Limnodynastes depressus* (Stage 36). Scale bar = 5 mm.

The roof of the braincase is incomplete and is formed by the tectum synoticum and the taenia ethmoidale. The callilago orbitalis is high. The basis cranii is perforated by the paired foramina carotica and oculomotoria.

The processus muscularis quadrati rises from the lateral margin of the palatoquadrate and terminates with a bluntly rounded apex. The processus ethmoidalis is shorter than wide and the processus pseudopterygoideus is elongate and prominent. The arcus subocularis is attached anteriorly to the neurocranium by the commissura quadrato cranialis anterior. The larval processus basalis between the palatoquadrate and the otic capsule is prominent. The processus ascendens of the arcus subocularis is not overlain by the otic capsule. The maximum width of the neurocranium and palatoquadrate is at the level of the processus ascendens.

Comparison with other species

Limnodynastes depressus is morphologically most similar to *L. tasmaniensis* Günther and *L. fletcheri* Boulenger (Davies & Burton 2000). Hence here we confine comparisons of the larval and chondrocranial morphology of *L. depressus* to those two species. Larvae of *L. depressus* are very similar to those of *L. fletcheri* (Davies 1992) although advanced tadpoles of *L. depressus* reach a total length of 80 mm or more whilst those of *L. fletcheri* are recorded as reaching 69 mm total length at stage 40 (Davies 1992). The



Fig. 6. Dorsal views of the chondrocrania of A. *Limnodynastes tasmaniensis* Stage 32, B. *L. fletcheri* stage 34. Scale bars = 5 mm

oral disc; external morphology and pigmentation are identical. Larvae of *L. tasmaniensis* usually are very heavily pigmented (virtually black), although some larvae in western New South Wales approach the pigmentation of *L. fletcheri* and *L. depressus* (M. Austin pers. comm. 2000). The oral disc of *L. tasmaniensis* has more tooth rows than do those of *L. depressus* and *L. fletcheri* (five upper and three lower) (Martin 1965; Martin & Littlejohn 1982).

The major difference in the chondrocrania lies in the relationship of the processus ascendens of the arcus subocularis with the otic capsule (Fig. 6). In both *L. fletcheri* and *L. tasmaniensis*, the otic capsule overlies the processus ascendens. In addition, the

larval processus basalis is very poorly developed in both these species.

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**FIRST RECORD OF THE SOUTHERN RIGHT WHALE DOLPHIN,
LISSODELPHIS PERONII (LACÉPÈDE, 1804) (ODONOCETI :
DELPHINIDAE), FROM WATERS OFF SOUTH AUSTRALIA**

BRIEF COMMUNICATION

Summary

The southern right whale dolphin *Lissodelphis peronii* is a small pelagic dolphin that is rarely observed close to land. What little is known about its biology has been gathered from stranded specimens¹. The species occurs only in Southern Hemisphere waters where it appears to be largely restricted to the region bounded by the Antarctic Front in the south and the Subtropical Front in the north². It is unusual amongst dolphins occurring in the Australasian region in that it lacks a dorsal fin³. *Lissodelphis peronii* appears actively to avoid ships and this and its unobtrusive behaviour when not alarmed may result in the species being under-recorded.

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The southern right whale dolphin *Lissodelphis peronii* is a small pelagic dolphin that is rarely observed close to land. What little is known about its biology has been gathered from stranded specimens¹. The species occurs only in Southern Hemisphere waters where it appears to be largely restricted to the region bounded by the Antarctic Front in the south and the Subtropical Front in the north². It is unusual amongst dolphins occurring in the Australasian region in that it lacks a dorsal fin³. *Lissodelphis peronii* appears actively to avoid ships and this and its unobtrusive behaviour when not alarmed may result in the species being under-recorded.

Whilst conducting surveys of seabirds from the bridge of the CSIRO research vessel 'Franklin' during a voyage that included five days cruising in Australian territorial waters off South Australia, groups of whales and dolphins were sighted on several occasions. On 11 August 1998, when the ship was 92 nautical miles south of Cape Gantheaume, Kangaroo Island, South Australia (37° 32' 10" S, 137° 27' 40" E) and proceeding in a north-easterly direction a herd of small dolphins was observed surfacing 200 m from the ship. On the basis of an absence of any dorsal fin and the striking combination of white ventral surfaces and a largely black dorsum the dolphins were identified as *L. peronii*.

At the time of the sighting (11.05 - 11.07 a. m. Aust. CST) viewing conditions were good. With a southerly wind of less than five knots, the sea surface was glassy smooth, with only a slight swell (~2 m). Air temperature was 14.0 °C, barometric pressure was 1020.3 hp and steady and the conditions were cloudy but bright. Water temperature at the sea surface was 12.87 °C and salinity 34.98 ppm. The dolphins were observed 44 nautical miles south of the continental shelf in deep (4904 m) pelagic waters, just

south of the Subtropical Front. Slightly warmer water (13.5-14.5 °C) was encountered later in the same day only several nautical miles to the north of this sighting. At first my attention was drawn to an area of small splashes on the surface of an otherwise calm sea. By the use of 10 X 50 binoculars small dark backed dolphins were identified as the cause of this disturbance. The dolphins were travelling slowly (2-5 knots) away from the vessel. When rising to blow they broke the surface gently, exposing only the very top of their dorsal surfaces but the complete absence of a dorsal fin was immediately obvious. The dolphins were travelling as a compact group all heading in the same direction and it was difficult to assess their number. This behaviour continued for approximately 30 sec before the dolphins abruptly changed direction placing them on a course heading across the bow of the ship. At the same time they began porpoising clear of the surface. After travelling less than 50 m the herd abruptly changed direction again returning to their initial course heading away from the vessel. The dolphins were now more easily counted and I estimated the herd comprised 20 individuals. No young were seen. They continued to move away from the ship on a fairly direct course and when last seen, approximately two min later, were still travelling at a sustained speed and porpoising clear of the water.

As each animal leapt clear of the water, good views of it were obtained. The following composite description was made from field notes taken at the time of the sighting. The dolphins were small and slender and were about two metres in length. When porpoising their bodies appeared disproportionately elongated, although this feature was presumably enhanced by the absence of dorsal fins. Each individual had a striking but simple pied pattern that

TABLE 1. Sightings and strandings of *Lissodelphis peronii* in the Australian region.

Date	Location	Position	Comments	Source
11 Jan. 1802	Off southern Tasmania	c. 44° S, 141° E	type specimen	Peron (1802) in 1
7 Jan. 1824	Off SE Australia	c. 45° S	harpooned	6
Pre 1884	Tasmania	?	specimen	7
Aug. 1968	c. 100 miles SW of Australia	?	sighting of six individuals	4
Oct. 1978	Cloudy Bay, Bruny Island, Tas.	43° 25' S, 147° 15' E	Stranding (Tas. Mus. specimen # A1301)	1
Aug. 1970	mid Great Aust. Bight (WA or SA)	?	sighting of 50 individuals	4
13 Sept. 1985	Off South-west Cape, Tas.	41° 41' S, 145° 40' E	sighting of 25 individuals	D. W. Fades pers. comm. 1999
14 Feb. 1986	South of WA	46° 03' S, 126° 52' E	sighting of c. 500 individuals	8
Sept. 1986	Bendalong, NSW	35° 15' S, 150° 32' E	apparent stranding (see text)	5
29 Sept. 1995	Chinamans Bay, Maria Island, Tas.	42° 40' S, 148° 03' E	stranding	R. M. Warneke pers. comm. 1999
11 Aug. 1998	92 miles off Cape Gantheaume, Kangaroo Island SA	37° 32' S, 137° 27' E	sighting of 20 individuals	this study

appeared consistent across the herd. White ventral surfaces extended dorsally to the rostrum and face. The upper surface of the flippers, and the remaining dorsal surfaces were black. The border where black and white met was sharply defined, and curved from the middle of melon down the sides of the head to a point at, or just above, the flipper; it then curved upwards slightly before continuing along the flanks and tail stock as a fairly straight line.

To the best of my knowledge this sighting is the first documented occurrence of *L. peronii* in waters off South Australia and the 11th for waters around Australia (Table 1). Previous records have included 4 strandings and/or specimens and 6 sightings, with most being from waters south of Tasmania. There are no records from Victoria and just one or two from waters off Western Australia. However, one of these sightings may have occurred in waters off South Australia as the record was simply noted as 'in the middle of the Great Australian Bight'⁴. The most northerly record of *L. peronii* in Australian waters is of a stranded animal at Bendalong in NSW (35° S)⁵. However, this record should be treated as unconfirmed as enquiries by the author failed to locate any specimen, photographs, notes or first hand knowledge of this individual.

The complete absence of strandings along the southern coast of mainland Australia and the scarcity of records elsewhere in Australian waters may be attributable to the species' preference for pelagic waters⁶. The small size of *L.*

peronii further reduces the likelihood of dead animals being washed ashore as scavengers are likely to consume such small carcasses before they are able to drift to the coast from pelagic waters. Although the species has been known to ride on the bow wave of vessels on occasions, this behaviour is apparently uncommon⁷. An apparent avoidance of vessels, as noted in the observation documented here, has been reported by other observers⁸. This avoidance behaviour, combined with the species' small size, and inconspicuous nature when not alarmed, may result in individuals or small herds being overlooked. Indeed the individuals observed off South Australia are unlikely to have been sighted had sea surface conditions been more typical and white caps of any size been present. Combined with the knowledge that competent field observers have, until quite recently, had few opportunities to systematically or routinely visit deep pelagic waters of the cool temperate zone of the Australian region the status of *L. peronii* in the region remains unclear.

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