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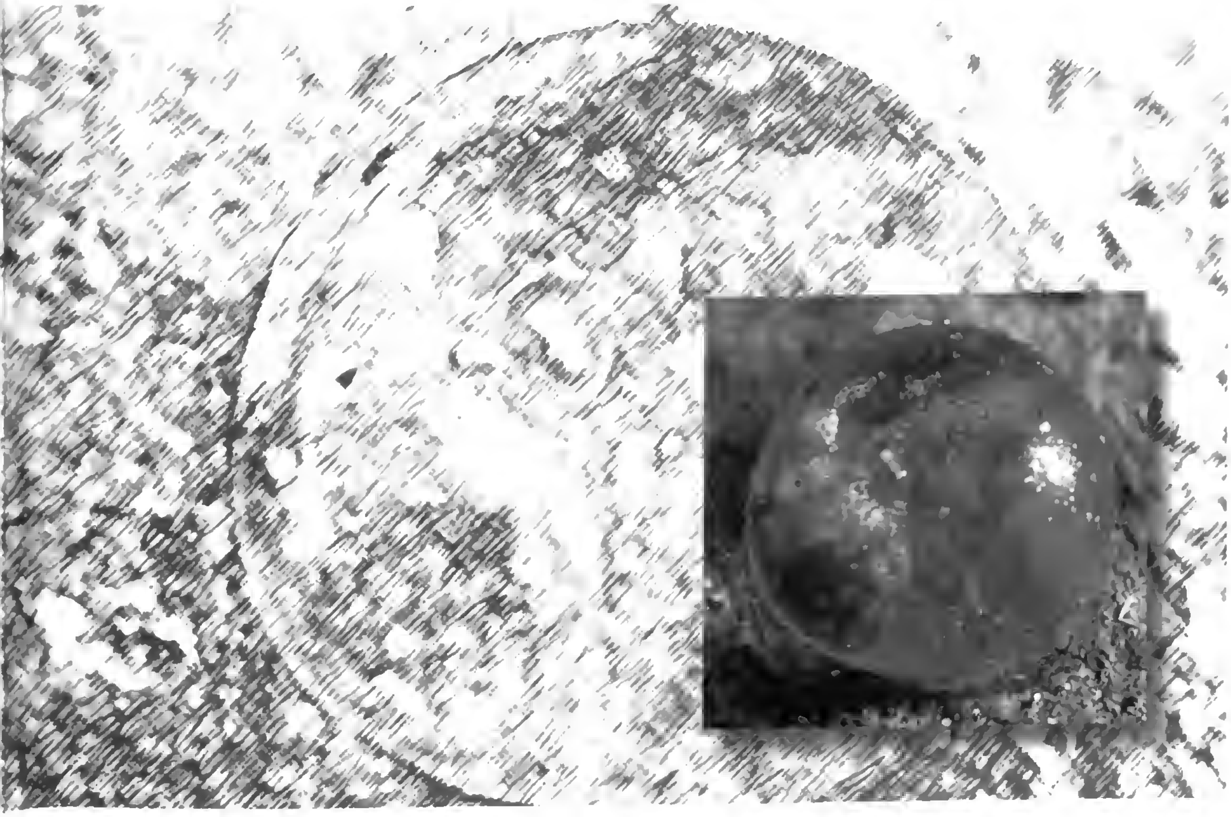

ISSN 1440–4788
brisbane | 15 march 2010

55(1)

Memoirs of the Queensland Museum | **Nature**

55(1)

PUBLISHED BY ORDER OF THE BOARD 15 MARCH 2010

PO Box 3300, South Brisbane 4101, Australia
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National Library of Australia card number
ISSN 0079-8835

COVER: Photograph of *Mixophyes coggeri* egg eight days after laying.

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A Queensland Government Project
Typeset at the Queensland Museum
Printed by Watson Ferguson & Co.,
655 Toohey Road, Salisbury Qld 4107

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Breeding behaviour of the Barred Frog *Mixophyes coggeri*

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Citation: Hoskin, C.J. 2010 03 15. Breeding behaviour of the Barred Frog *Mixophyes coggeri*. *Memoirs of the Queensland Museum — Nature* 55(1): 1-7. Brisbane. ISSN 0079-8835. Accepted: 26 March 2007.

ABSTRACT

A recent analysis of specimens assigned to the Northern Barred Frog *Mixophyes schevilli* Loveridge, 1933 of the Wet Tropics region of north-east Queensland revealed three genetically and morphologically distinct species (Mahony et al. 2006). *Mixophyes schevilli* was retained as a species distributed in the northern and central Wet Tropics, *M. coggeri* Mahony, Donnellan, Richards & McDonald, 2006 was described as a species distributed throughout the Wet Tropics, and *M. carbinensis* Mahony, Donnellan, Richards & McDonald, 2006 was described as a species restricted to the Carbine and Windsor Tablelands (Mahony et al. 2006). All three species are large, terrestrial, rainforest-restricted stream breeders. Importantly, the calls and breeding biology of the three species have not been described, and differences in habitat preferences and other ecological aspects have not been resolved. Here I present the advertisement (mating) call of *M. coggeri* and an observation of the breeding behaviour of this species. The call is a deep, reverberating 'worg' and the primary call parameters are presented. The breeding behaviour is described in detail and is characterised by the female flicking fertilised eggs up onto rocks and the bank overhanging a side-pool in the stream. The calls and breeding biology of the other two Wet Tropics *Mixophyes* species remain unresolved.

☐ *advertisement call, oviposition, Myobatrachidae, Australia, north-east Queensland, Wet Tropics.*

Until recently *Mixophyes schevilli* was the sole described *Mixophyes* species from the rainforest of the Wet Tropics region, between Townsville and Cooktown in north-east Queensland. A recent analyses, however, split *M. schevilli* into three genetically and morphologically distinct species in the Wet Tropics: two widely distributed species, *M. schevilli* and *M. coggeri*, and a species restricted to the Carbine and Windsor Tablelands, *M. carbinensis* (Mahony et al. 2006). Little information has been published on the breeding biology of *Mixophyes schevilli*, the call is generally described as a deep 'wark' (e.g. Barker et al. 1995; McDonald 2000) and oviposition has been reported as eggs 'laid on soil under banks above water' (McDonald 2000). The recent revision of *M. schevilli* makes it unclear which of the three species this information referes to, and descriptions of the breeding behaviour of each species are required. The breeding behaviour of the Wet Tropics species is of particular interest given the diversity in call structure and egg laying behaviour among the four *Mixophyes* species in south-east Australia (discussed below). Here I describe the call and a breeding observation of *M. coggeri* from the Kuranda region in the central Wet Tropics. *Mixophyes coggeri* occurs in lowland and upland rainforest through much of the Wet Tropics region, from Paluma (near Townsville) to Big Tableland (near Cooktown)

(Mahony et al. 2006). Across much of this distribution the species co-occurs with *M. schevilli*, while on the Carbine and Windsor Tableland it is sympatric with *M. carbinensis* (Mahony et al., 2006).

The calls, breeding observation and habitat notes presented herein come from the Kuranda region (16°45′-16°51′S, 145°33′-145°40′E, altitude 300-450m), west of Cairns. In this region I have observed *M. coggeri* across the full spectrum of rainforest types, from well-developed wet rainforest to thin riparian rainforest strips in otherwise open, sclerophyll-dominated forest. *Mixophyes coggeri* calls from the vicinity of pools on slow-moving streams that range in substrate from sandy and boggy through to rocky. Males and females are regularly observed foraging at night, generally along stream banks and at times some distance from streams. I have not observed *Mixophyes schevilli* at these sites, although it is known to occur in the Kuranda region (Mahony et al., 2006). All individuals herein were identified as *M. coggeri* based on the diagnostic morphological and pattern characters presented in Mahony et al. (2006): dorsal pattern consisting of a series of irregular blotches (e.g. Fig. 1), large size (male SVL > 80 mm) (Table 1), broad head shape (HW/SVL 0.45-0.47) (Table 1), and aspects of the patterning of the posterior surface of the thigh.

CALL CHARACTERISTICS

The calls of three male *M. coggeri* were recorded on Streets Ck (16°49′34″S 145°39′22″E) between 21:00 and 23:30 hrs on 1 March 2007. These were the only *M. coggeri* calling along a 350 m stream transect that night and no females were observed. Males 1 and 2 were calling on opposite sides of the stream where a deep stream pool flowed into riffles, and male 3 was calling 150 m upstream near a stream pool between cascades (Fig. 2A). The weather was overcast, warm, humid and still. All three males were calling from elevated earthy stream banks approximately 3 m from the water and were partly covered by leaf-litter but with the front half of the body exposed. Calls were recorded with a Marantz DAT recorder and a Sennheiser directional microphone, and air temperature was taken (Table 1). Following recording, each frog was placed in a clear plastic bag and identified and measured (Table 1), after which it was released at the exact point of capture and photographed. Male 3 was identified as that involved in the breeding observation the previous night (described below), based on a comparison of the dorsal pattern in photographs and the fact that male 3 was calling within 5 m of where the breeding pair had been found the previous night. The software Soundruler 0.9.6.0 was used to measure the following call parameters: call interval (time from the end of one call to the beginning of the next), call duration

TABLE 1. Call characteristics of *Mixophyes coggeri*. Table presents the average and range (in brackets) of each call parameter for three males, along with their snout to vent length (SVL), tibia length (TL), head width (HW), HW to SVL ratio (HW/SVL), and the air temperature (T°C). The last row is the average of all traits across the three males.

Individual	SVL (mm)	TL (mm)	HW (mm)	HW/ SVL	Call int. (sec.)	Call duration (sec.)	Pulses per call	Pulses per sec.	Dominant Freq. (Hz)	T°C
Male 1	87.2	52.6	39.6	0.45	31 (8-67)	0.218 (0.216-0.219)	13 (13-13)	59.7 (59.4-60.1)	536 (520-550)	23.5
Male 2	82.4	54.4	38.6	0.47	65 (29-78)	0.220 (0.200-0.237)	13 (12-14)	60.0 (59.2-60.4)	576 (560-580)	23.5
Male 3	85.8	51.9	40.1	0.47	31 (16-48)	0.259 (0.257-0.260)	15 (15-15)	58.0 (57.6-58.5)	574 (560-580)	23.0
Average	85.1	53.0	39.4	0.46	42	0.232	14	59.2	562	23.3

FIG. 1. *Mixophyes coggeri*, pair in amplexus.

(time from the beginning of the first pulse to the end of the last pulse), pulses per call, pulse rate (number of pulses divided by call duration), and dominant frequency (frequency at which the call is of greatest intensity). Five successive calls were analysed for each male to give the average and range for each call parameter for each male (Table 1).

The typical advertisement call of *M. coggeri* in the Kuranda region is a deep,

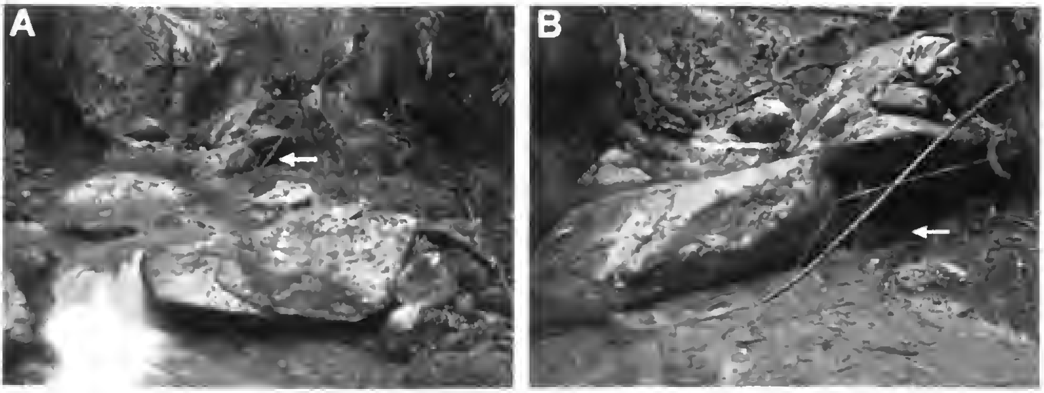

FIG. 2. Stream habitat on Streets Ck, with the oviposition site being the rock overhang marked by an arrow in photo A and in the close-up photo (B).

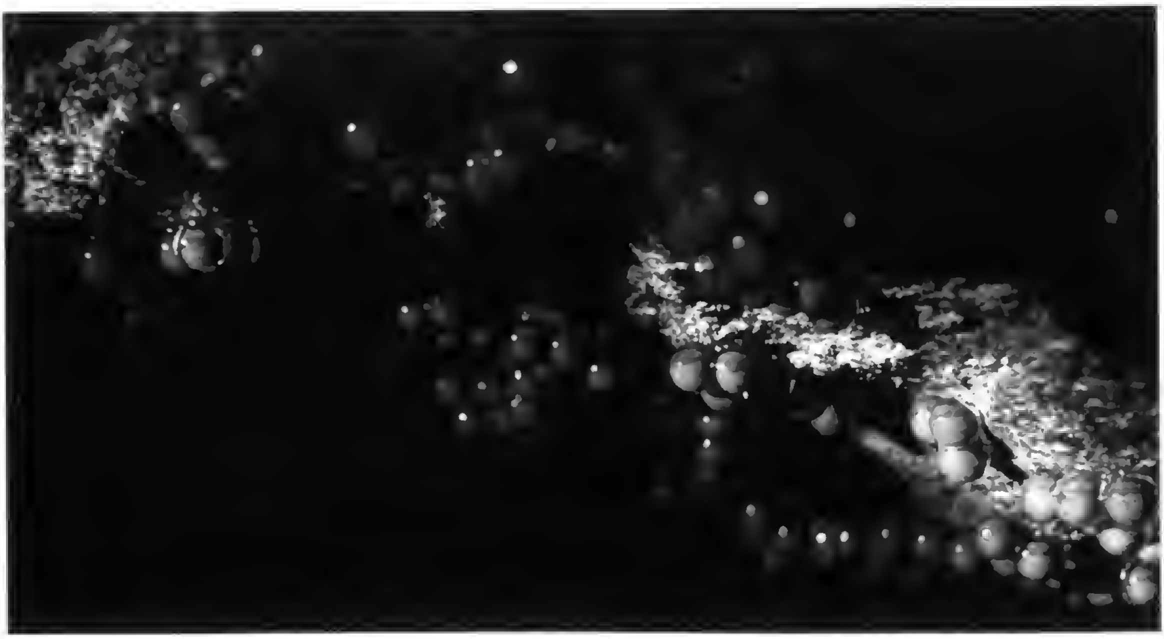

FIG. 3. *Mixophyes coggeri* eggs adhered to the under surface of the rock overhang 12 hours after laying.

reverberating 'worg' repeated infrequently. Call parameters of the three males recorded at Streets Ck are presented in Table 1. Of the approximately 50 calls recorded all were a single 'worg', except one which was a double 'worg worg'. More recordings are required to assess call variation in *M. coggeri* across the extent of its range.

I have heard a distinctly different, higher pitched and less reverberating 'wark' or 'wark wark' call at other sites in the northern and central Wet Tropics, similar to that presented for '*M. schevilli*' by Stewart (1998a). This is likely to be the mating call of *M. schevilli* but will remain unresolved until the call of this species is characterised and matched with genetic or morphology/pattern data. I have also recorded a similar 'wark' call from *Mixophyes* on the Windsor Tableland (where *M. schevilli* has not been recorded (Mahony et al. 2006)) from males that match the morphology of *M. carbinensis* but not *M. coggeri*. This suggests the call of *M. carbinensis* is similar to that of *M. schevilli* and differs from the deep, reverberating call of *M. coggeri*. However, once again this requires recordings matched with genetic or morphology/pattern data.

BREEDING OBSERVATION

An observation of *M. coggeri* breeding was made on Streets Ck on the night of 28 Febuary/1 March 2007. Weather conditions were overcast, warm (25°C), humid and still on the night. Heavy rain had fallen over the previous fortnight but little had fallen over the previous few days and the stream level had dropped back to a 'normal' level. A pair of *M. coggeri* were found in amplexus (Fig. 1) at 22:30 hrs, halfway up a steep earthy bank and about 1m from the edge of a shallow side-pool connected to the stream (top right of Fig. 2A). Amplexus at this stage was axillary, with the male clasping the female just behind the pectoral region. The pair remained amplexed for the remainder of the observations but movements described below were those of the female as she was carrying the male. Movement was characterised by short bursts of activity by the female separated by long periods where the pair remained perfectly still. At 23:45 hrs the female moved to the edge of the side pool (mid right of Fig. 2A) and the pair sat there until 00:30 hrs when the female worked her way through the middle of a rock pile in the creek, ending up in a shallow pool beneath a rock overhang (marked on Figs 2A & B). At 00:45 hrs the pair emerged from the overhang and sat on the edge of the main stream pool (mid right of Fig. 2B) until 01:30 hrs when the female moved around the side-pool back to the point where they first approached the stream (mid right of Fig. 2A). The pair nestled into muddy leaf-litter on the edge of the side-pool for 10 minutes before the female jumped into the side-pool, swam across it and then carried the male back through the rock pile to the small pool below the overhang (01:45 hrs). At this point no eggs had been laid in the overhang or in the side-pool. The position of the male had changed such that at this stage amplexus appeared inguinal (axillary earlier). The pair moved around in the small shallow pool below the overhang (marked in Figs 2A & B) and then at about 02:00 hrs started flicking eggs and water up onto the ceiling and walls of the rocky overhang. Sitting or floating in shallow water the female would pause, lean forward and flick a spray of eggs and water upwards with her back legs (presumably immediately after the eggs had emerged from her cloaca and been fertilised by the male). Then the amplexed pair would move around in the pool, pause, and flick again. The egg flicking behaviour was similar to that photographed in *M. fasciolatus* Günther, 1864 (Anstis 2002, p. 218). This behaviour was still continuing at 02:30 hrs when observations were ceased, and at this point eggs and dripping water were evident on the roof of the overhang and to a lesser degree on the adjacent sloping rock walls and earth banks.

FIG. 4. *Mixophyes coggeri* egg 8 days after laying. The tadpole is clearly discernable on the left hand side of the egg, with its head facing forwards and the tail curving away to the right. The tadpole hatched out during rainfall shortly after the photograph was taken.

Observations the next day (1 March 2007) revealed the pool beneath the overhang to be about 80 cm long, 40 cm wide and from 5-15 cm in depth. The rock above the pool made a roof about 20-30 cm above the water surface and the pool was almost completely surrounded by sloping rock and earth, with just two small 1 cm deep channels linking it to the stream (Fig. 2B). The rock pile was positioned between a slowly flowing pool (3 m wide, 50 cm deep) in the main stream channel and a linked side-pool (2 m wide, 20 cm deep) (Fig. 2A). Most eggs (approximately 300) were stuck to the rock roof of the overhang (Fig. 3) and were clumped (but generally in a single layer) directly above the water in a 60 cm by 30 cm strip, about 20 cm above the water surface. Others (approximately 150 eggs) were scattered on the sloping earth bank and sloping rocks around the pool, generally within 10 cm (but up to 30 cm) from the water, and a small number of eggs (about 40) were visible in the water. This gives a clutch size estimate of about 500 eggs. The eggs were pigmented (creamy brown) and with visible animal and vegetal poles (Fig. 3). The eggs stuck to the overhang hung with their darker, animal pole upwards. The egg diameter averaged about 3.8 mm (about 4.2 mm including the firm, clear egg capsule).

When I returned seven days later (8 March 2007) no live eggs were observed on the roof of the overhang but a small number of dry, shrivelled eggs (approximately 50) remained. I assume the remainder had hatched out and dropped into the pool. Approximately 50 eggs were still present on an earthy bank above the waters edge and these were now large and a well-developed larva was clearly visible in each (Fig. 4). The larva in the eggs resembled the few hatchlings that were visible in the pool below the overhang. It had rained very little since egg laying and the water level in the pool had dropped and it was now isolated from the stream. Heavy rain began falling as the observations were being completed and an egg on an earth bank about 5cm from the water was observed to rupture as it was wet by water dripping off rocks into the overhang. The hatchling wriggled vigorously until it entered the shallow pool. The hatchling was patterned with dark and golden markings and a dark bar across the base of the tail. Observations ceased due to heavy rain and it was assumed that other eggs would have hatched as water ran off rocks into the overhang, and that the pool below the overhang would have re-connected with the rising stream. Overall, the egg laying behaviour and development of the eggs is similar to that described for *M. fasciolatus* and *M. iteratus* Straughan, 1968 (Anstis 2002; Harry Hines, pers. comm.).

DISCUSSION

The mating call and breeding biology of the Wet Tropics *Mixophyes* species is of particular interest given the differences observed between the four south-east Australian species, which can be broken into two groups based on call structure and breeding behaviour/habitat: 1. *M. fasciolatus* and *M. iteratus* give a 'wark' or 'woh' style call and their breeding behaviour is characterised by the female (in amplexus) flicking fertilised eggs up onto rocks or banks overhanging stream pools, whereas, 2. *M. fleayi* Corben & Ingram, 1987 and *M. balbus* Straughan, 1968 give a stuttered 'ok-ok-ok-ok-ok' style call and lay their eggs in a circular depression (constructed by the female during amplexus) in gravel or leaf-litter in shallow stream riffles (Barker et al. 1995; Stewart 1998b; Lewis 2000; Meyer et al., 2001; Anstis, 2002). The call and breeding biology of *M. coggeri* conforms to group 1 (*M. fasciolatus* and *M. iteratus*). In particular, *M. coggeri* shows similarities to *M. iteratus* in being of very large body size and having a deep, reverberating call. Further research is required to assess call variation across the range of *M. coggeri* and to resolve the mating call and breeding biology of *M. schevilli* and *M. carbinensis*. This will determine whether the Wet Tropics *Mixophyes* display the variation in call structure and breeding behaviour seen in the south-east Australian species. Characterising differences in the advertisement call and habitat requirements between the three Wet Tropics species will also allow an assessment of the mechanisms of reproductive isolation between the sympatric species pairs.

ACKNOWLEDGEMENTS

I thank Greg Dawe and Eleanor Hoskin for assistance, and the reviewers for constructive comments. The research was conducted during a Tropical Landscapes Joint Venture Project between James Cook University (Miriam Goosem) and the Queensland Department of Main Roads, assessing the impact of highways on frogs.

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A Triassic conchostracan from near Murgon, SEQ.

Eastern Australian Early- to Mid-Triassic conchostracans have been described by Webb (1978) from the Sydney Basin and Tasch (1979) from the Bowen Basin. A major summary of Gondwanan occurrences, including Australia, was provided by Tasch (1987). I here report the first Mid to Late Triassic conchostracan from the Aranbanga Volcanics Group (Donchak et al. 1999), 14 km north of Murgon, southeast Queensland. The genus reported here is cosmopolitan in distribution (Tasch 1969) with many species known from the southern continents (Tasch 1987).

The Aranbanga Volcanics are a diverse suite of volcanics and volcanogenic sedimentary rocks occupying a wide band throughout the south Burnett region of south east Queensland. It contains a diverse flora and a fauna including insects and freshwater bivalves. The Aranbanga Volcanics have been ascribed a Mid to Late Triassic age based on the flora and a K-Ar date (Day et al. 1983).

Systematic Palaeontology

Order CONCHOSTRACA Sars, 1867

Suborder SPINICAUDATA Linder, 1945

Superfamily CYZICOIDEA Stebbing, 1910

Family EUESTHERIIDAE Defretin, 1965

Euestheria Depéret & Mazeran, 1912

Type Species. *Posidonia minuta* Von Zeiten, 1833 by subsequent designation of Raymond (1946), from the Upper Triassic of Great Britain.

Euestheria acampestria sp. nov. (Fig. 1)

Material. Holotype: QMF54807, right valve. Paratypes QMF54794-54806, QMF54808 (11 left, 3 right valves); all from QML1331, Aranbanga Volcanics Group mid- to late Triassic, near Murgon; 151° 53' 20" E, 26° 08' 10" S. Note that these specimens are selected from a slab bearing several hundred individuals.

Diagnosis. Valves medium sized (up to 8.8 mm long); hinge short; micro-ornament fine and papillate.

Etymology. Latin: *campestria* meaning flat plain, prefix '*a-*' meaning without; *acampestria* referring to an apparent lack of a flat elongate hingeline.

Description. Valves 6.1-8.8 mm long, elliptical with width approximately two-thirds of length; umbo small, subterminal, approximately one-sixth of the length of the valve in from point of maximum anterior bulge. Dorsal margin completely rounded, with hingleline very short (to the extent of appearing absent). Valve is fairly symmetrical about the midline transverse axis (perpendicular to dorsal margin). Maximum ventral bulge approximately at mid-length.

Growth bands comarginal, distinct, rugose, 10-16 per valve (in specimens under discussion, with larger valves having more bands), more pronounced toward ventral margin where they are closely spaced; elsewhere bands are more widely spaced. Growth bands nonexistent near umbo.

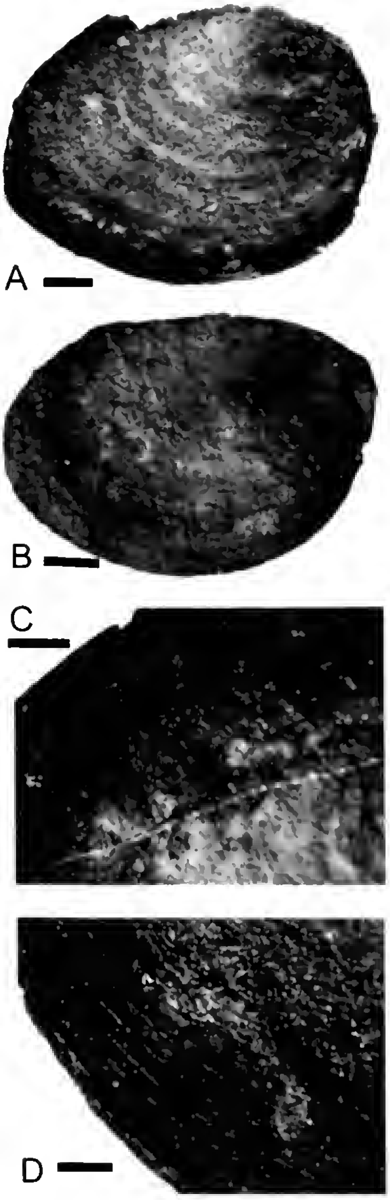

FIG. 1. *Euestheria acampestria* sp. nov.; A, Holotype QMF54807, right valve, lateral view, scale bar = 1 mm; B, Paratype QMF54805, right valve, lateral view, scale bar = 1 mm; C, Detail of ornament on paratype QMF54801, scale bar = 0.5 mm. D. Detail of ornament, paratype QMF54804, scale bar = 0.5 mm.

Micro-ornament uniformly spaced, small, round papillae, which are slightly smaller than the distance between growth lines; papillae more visible toward the margin.

Remarks. The material is assigned to *Euestheria* on the basis of prominent growth lines, the papillate ornament, resembling the 'polygons' in the type species and the relatively short hinge line. The material is similar to *Cyzicus (Euestheria) dualis* Tasch 1987 from the Lower Triassic Panchet Formation of India and *Cyzicus (Lioestheria) disgregaris* Tasch 1987 from the Jurassic Blizzard Heights and Storm Peak localities of Antarctica, with approximately symmetrical and elliptical valves and the small subterminal umbo lacking growth bands near it. It is distinguishable from C. *dualis* however by the lack of an elongate hingeline along the dorsal margin and from C. *disgregarious* by its fewer, more widely spaced growth bands, an umbo more anteriorly located and lack of barred ornament. The papillate micro-ornament is similar to *Cyzicus (Euestheria) castaneus* Tasch 1987 from the Jurassic at Blizzard Heights and Storm Peak in Antarctica, but in C. *castaneus* the microstructure is finer. C. *castaneus* also differs by having a more elongate hingeline. This is also the case for Endolimnadiopsis eichwaldi (Netshajev) (Shen, 1985) from the Upper Permian Kazan Formation of Russia. The species Endolimnadiopsis rusconii Gallego, 2004 from the Upper Triassic Cacheuta Formation of Argentina differs from E. acampestria in having an elongate posterior hingeline and finer, variably-sized papillate micro-ornament.

Acknoweldgements

Paul Tierney, Scott Hocknull and Mark Saul are thanked for supplying the specimens. Drs Alex Cook and Peter Jell are thanked for their input in the writing and editing of the manuscript.

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Peter J. Bishop, Queensland Museum, Geosciences, 122 Gerler Rd, Hendra Qld. 4011, Australia. 16th of January 2009.

A new subgenus and five new species of Australian Glow-worms (Diptera: Keroplatidae: *Arachnocampa*)

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Baker, C. H. 2010 03 15. A new subgenus and five new species of Australian glow-worms (Diptera: Keroplatidae: *Arachnocampa*). *Memoirs of the Queensland Museum — Nature* 55(1): 11-43. Brisbane. ISSN 0079-8835. Accepted: 25 February 2008.

ABSTRACT

A new subgenus, *Arachnocampa* (*Lucifera*) subgen. nov., is described to include the Tasmanian species, *Arachnocampa tasmaniensis* Ferguson and the Mount Buffalo glow-worm, *Arachnocampa buffaloensis* sp. nov. The new subgenus is separated from the subgenera *Arachnocampa* (*Arachnocampa*) and *Arachnocampa* (*Campara*) by differences in wing venation. The subgenus *Arachnocampa* now includes only the New Zealand species *A. luminosa* (Skuse) which differs from species of *Lucifera* and *Campara* by its unusual method of vertical pupal suspension. The Australian species *A. tasmaniensis*, *A. flava* Harrison and *A. richardsae* Harrison are redescribed. Five new species are described: *A. buffaloensis* sp. nov. (Victoria) within the subgenus *Lucifera*; and *A. tropica* sp. nov. (north Queensland), *A. gippslandensis* sp. nov. (eastern Victoria), *A. otwayensis* sp. nov. (western Victoria) and *A. girraweenensis* sp. nov. (southeast Queensland/northern New South Wales) within the subgenus *Campara*. ☐ *troglophile, rainforest, threatened species, glow-worm, Keroplatidae, Arachnocampa, Lucifera, Campara.*

The genus *Arachnocampa* (Edwards 1924) contains species with bioluminescent larvae that are commonly known as glow-worms. Historically *Arachnocampa* contained four described species, three of which are endemic to Australia: *A. flava* Harrison from southeast Queensland (Perkins 1935; Harrison 1966); *A. richardsae* Harrison from New South Wales (Harrison 1966) and *A. tasmaniensis* Ferguson from Tasmania (Ferguson 1925). The fourth species, *A. luminosa* (Skuse 1890), is endemic to New Zealand. *Arachnocampa* are recognised as commercially valuable organisms due to the importance of glow-worms to tourism (Baker 2002). However, little was known about the insects around which this industry is based (Baker 2004). In Australia, *Arachnocampa* have been documented from several locations well separated from the known distributions of the three described species (Table 1). Until this study, these populations had been tentatively assigned to either *A. flava* or *A. richardsae* (e.g. Crosby 1978). The most recent reviews of the *Arachnocampa* taxonomic literature are by Pugsley (1983), Meyer-Rochow (2007) and Baker (2009).

The first description of an Australian glow-worm was of *A. tasmaniensis* from the Ida Bay Caves, Tasmania (Ferguson 1925). The description was based on the adult form, with a brief mention of larval biology. Other large colonies of glow-worms known from Numinbah in the Nerang Valley, Queensland and from New South Wales (Perkins 1935) were subsequently described as *A. flava* and *A. richardsae* respectively, and both species were placed in a new subgenus, *Campara* Harrison, separated from the Tasmanian and New Zealand species based on wing venation (Harrison 1966). McKeown (1935) noted the presence

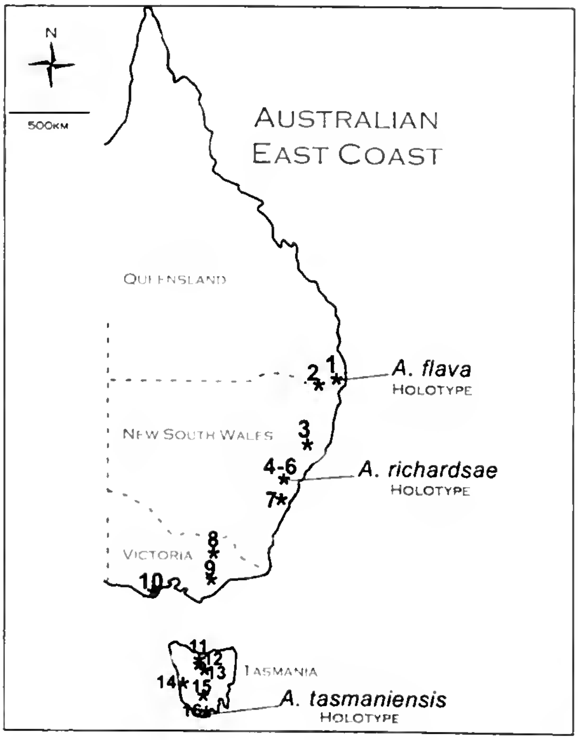

FIG. 1. Map of eastern Australia showing locations of published *Arachnocampa* sites based on literature surveys. Table 1 lists the names of each site. Three species of *Arachnocampa* have been described from these sites with many other sites documented but with no follow-up morphological identification until the present study.

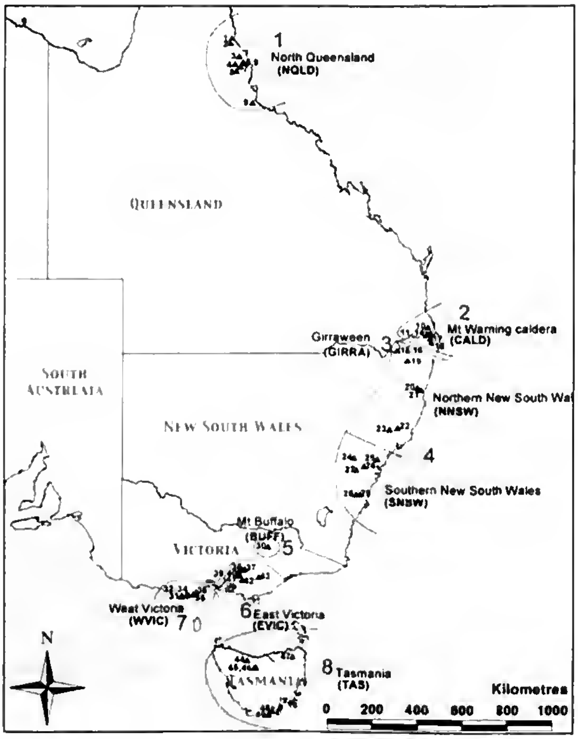

FIG. 2. Map of eastern Australia showing the collection localities of specimens used for morphological examination. Regional groups are encompassed within circled areas. Site names are found in Table 2.

of *Arachnocampa* in the Otway Forest, Victoria. Crosby (1978) later tentatively identified this population as *A. richardsae*. However, this colony of *Arachnocampa* represents a new species, and is described here. Traditionally glow-worms have been included within the Mycetophilidae but following a review of the higher taxonomy of the Mycetophiloidea, *Arachnocampa* and other bioluminescent genera were placed in the family Keroplatidae (Matile 1981).

Arachnocampa are highly susceptible to desiccation and therefore require high humidity or direct contact with water within their habitat for survival (Richards 1960; Baker & Merritt 2003; Baker 2004). All published *Arachnocampa* sites in Australia are in rainforest, wet sclerophyll forest or limestone or granite boulder caves (Fig. 1, Table 1). Many of these records simply noted the presence of larvae and provided no additional information. Furthermore, the taxonomy of Australian *Arachnocampa* species in relation to their apparently widespread but patchy distribution is poorly understood, with the last taxonomic study by Harrison (1966). *Arachnocampa* display limited mobility, a shortened adult dispersal stage, and are reliant on specific high humidity environments for survival (Richards 1960; Baker 2004). Their primary reliance on habitats of ancient

TABLE 1. Published records of known *Arachnocampa* spp. locations in Australia illustrated in FIG. 1. Holotype locations from published descriptions indicated as follows: *A. flava* holotype *, *A. richardsae* holotype **, *A. tasmaniensis* holotype ***.

Aust. State	Location of *Arachnocampa* spp. colony	Reference
QLD	1. Natural Bridge, Springbrook National Park *	Perkins 1935, Harrison 1966
	2. River Cave, Girraween National Park	Finlayson 1982
NSW	3. Gloucester Cave, Gloucester	Harrison 1966, Eberhard & Spate 1995
	4. Grose Valley, Blue Mountains	Currey 1966, Harrison 1966
	5. Hazelbrook, Blue Mountains	Harrison 1966
	6. Newnes railway tunnel **	Harrison 1966
	7. Bundanoon	McKeown 1935
VIC	8. Underground River Cave, Mt Buffalo National Park	Crosby 1978
	9. Walhalla mine shafts, Walhalla	Harrison 1966
	10. Madsen's Track, Melba Gully State Park	Department of Conservation 1994
TAS	11. Loongana (Old tourist cave)	Geode 1967
	12. Gunns Plains Caves (Guns Plains Tourist Cave)	McKeown 1935, Geode 1967
	13. Mole Creek Caves (Marakoopa, Wet, Lynds and Westmoreland caves)	Geode 1967, Ferguson 1925
	14. Kelley Basin (small unnamed cave)	Geode 1967
	15. Florentine Valley and Junee Area (Cashion Creek, Growling Swallet and Junee Caves)	Geode 1967
	16. Ida Bay Caves (Entrance and exit caves) ***	Geode 1967, Ferguson 1925

Gondwanan origin, means that many populations are likely to have been fragmented in refugial habitat pockets for millions of years through natural contractions and expansions, with little to no chance of present day dispersal across large geographic boundaries (Baker 2004; Baker et al. 2008).

Australian glow-worm populations are under increasing pressure due to their restricted habitat range, critical habitat requirements, and increasing tourism popularity in these regions (Baker 2002, 2004). Therefore there is an urgent need for careful management to ensure the long-term sustainability of these species in Australia. Correct management guidelines can only be procured through a better understanding of the species present and, as such, this study was long overdue.

The taxonomic descriptions appearing in this paper were intended to be published prior to a molecular phylogenetic study of Australian glow-worms (Baker et al. 2008). However, the molecular study was published before the present descriptive paper, and the scientific names of the new taxa described here were inadvertently used in that paper. Baker et al. (2008) did not

TABLE 2. Map locations for Figure 2 with site names and codes used in descriptions. GPS coordinates for each site are listed in the text. All sites are epigean unless specified as a cave or man-made tunnel.

Map location Figure 2	Site Name	Site Code used in text
1	Mossman Gorge	NQLD1
2	Mt Lewis	NQLD2
3	Lamb Range National Park	NQLD3
4	Mt Hypipamee National Park	NQLD4
5	Bartle Frere Cave, Wooroonooran National Park	NQLD5
6	Bartle Frere stream	NQLD6
7	Mungalli Falls	NQLD7
8	Charmilllan walking trail, Tully Gorge State Park	NQLD8
9	Birthday Creek Falls, Paluma National Park	NQLD9
10	Tamborine Mountain	TAM1
11	Natural Bridge, Springbrook National Park (large overhang)	CALD1
12	Springbrook Plateau	CALD2
13	Springbrook National Park	CALD3
14	Lamington National Park	CALD4
15	South Bald Rock Cave, Girraween National Park	GIRRA1
16	Ramsey Creek Cave, Girraween National Park	GIRRA2
17	Mt Warning National Park	CALD5
18	Protestors Falls, Nightcap National Park	CALD6
19	Washpool National Park	NNSW1
20	New England National Park	NNSW2
21	Dorrigo National Park	NNSW3
22	Barrington Tops National Park	NNSW4
23	Gloucester Cave	NNSW5
24	Newnes Railway tunnel (man-made tunnel)	SNSW1
25	Waterfall Springs Conservation Park	SNSW2
26	Upper Kurrajong	SNSW3
27	Grand Canyon walk, Blue Mountains National Park	SNSW4
28	Bundanoon	SNSW5
29	"The Grotto" Fitzroy Falls National Park (large overhang)	SNSW6
30	Underground River Cave, Mt Buffalo National Park	BUFF1
31	Melba Gully State Park	WVIC1
32	Beauchamp Falls, Otway National Park	WVIC2
33	Hopetoun Falls, Otway National Park	WVIC3
34	Beauty Spot Reserve	WVIC4
35	Grey River Picnic area, Angahook-Lorne State Forest	WVIC5
36	She-oak Picnic area, Angahook-Lorne State Forest	WVIC6
37	Upper Yarra Valley mine tunnel	EVIC1
38	O'Shannassy Weir (man-made tunnel)	EVIC2
39	Britannia Creek Cave, State Forest	EVIC3
40	Shining Star Gold Mine, Warburton (tunnel)	EVIC4
41	Shiprock Falls Cave, Kilnkurth State Forest	EVIC5
42	Labertouche Cave	EVIC6
43	Walhalla Mine tunnel	EVIC7
44	Gunns Plains Caves	TAS1
45	Marakoopa Cave	TAS2
46	Sassafras Cave	TAS3
47	Derby Mine tunnel	TAS4
48	Francis Gully, Ida Bay	TAS5
49	Entrance ('Mystery Creek') Cave, Ida Bay	TAS6

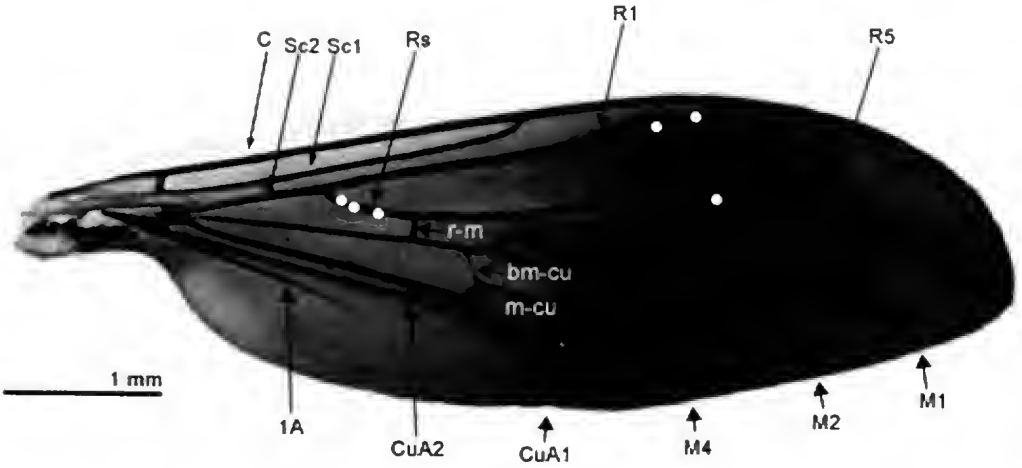

FIG. 3. Wing venation of *Arachnocampa* (dorsal view of right wing). Dots indicate the location of campaniform sensillae. C, costa; CuA1, anterior branch of cubitus; CuA2, posterior branch of cubitus; m-cu, posterior section of medial-cubital cross vein; M, media; r-m, radial-medial cross vein; R, radial vein; 1A, anal vein. Wing length measurements were taken from basal end to the wing apex.

fix holotypes for the new species, so the species names used there are not available (International Code of Zoological Nomenclature, 1999, Article 16.4). The subgenus name *Lucifera* as used by Baker et al. (2008) is also not available. It is a *nomen nudum* because the authors did not fix a type species (International Code of Zoological Nomenclature, 1999, Article 13.3). However, in order to preserve the link with the taxa referred to in the molecular paper (Baker et al. 2008), the same names are used here for the formal descriptions of the new subgenus and species.

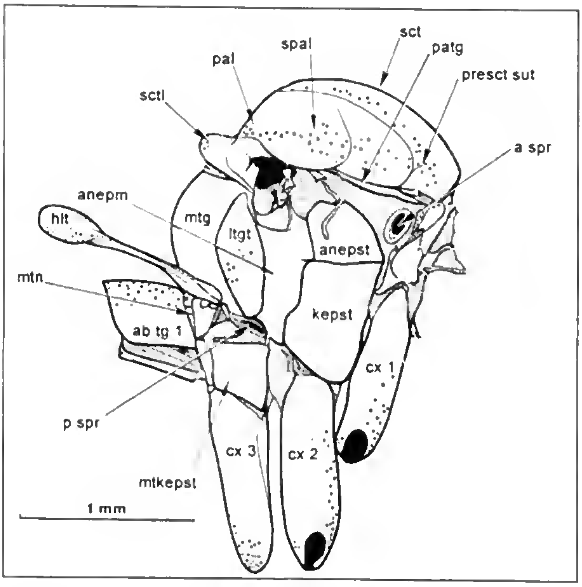

FIG. 4. Morphology and terminology of *Arachnocampa* thorax (revised from Matile 1990). ab tg 1, abdominal tergite 1; anepm, anepimeron; anepst, anepisternum; a spr, anterior spiracle; cx, coxa; hlt, haltere; keptst, katepisternum; ltgt, laterotergite; mtg, mediotergite; mtkepst, metakatepisternum; mtn, metanotum; pal, post alar region; patg, paratergite; p spr, posterior spiracle; presct sut, prescutal suture; sct, scutum; sctl, scutellum; spal, supra-alar region.

MATERIALS AND METHODS

Taxon Sampling, Rearing and Labelling. *Arachnocampa* larvae were collected from 49 sites including many new locations (Fig. 2, Table 2). A GPS (eTrex®) was used to record site coordinates, however, due to dense

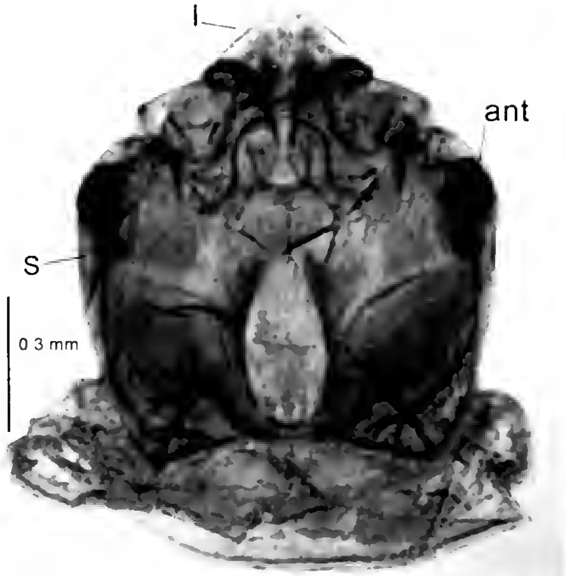

FIG. 5. Slide mounted *Arachnocampa flava* larval head capsule (dorsal view). ant, antennal stubb; l, labrum; s, stemmatal eye.

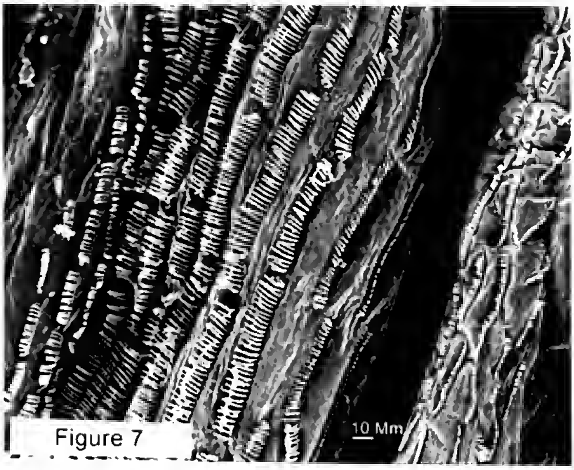

FIG. 7. SEM of setae on the distal end of *Arachnocampa flava* larva. These setae are used by larvae for movement.

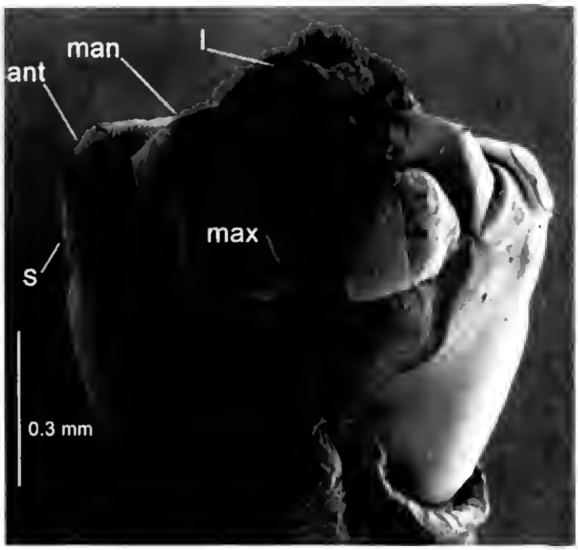

FIG. 6. Scanning electron micrograph (SEM) of *Arachnocampa flava* head capsule (ventral view). ant, antennal stubb; l, labrum; man, mandible; max, maxilla with maxillary teeth; s, stemmatal eye.

FIG. 8. 'Tiger stripe' colouration of the *Arachnocampa* abdomen (each segment is lighter basally and darker apically).

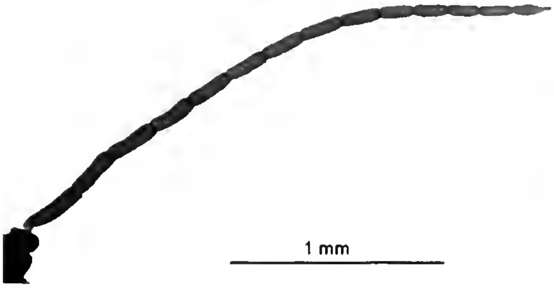

FIG. 9. Adult *Arachnocampa* antenna showing the progressive shortening of antennal segments from segments 1-13. Segment 14 is longer than 13, and is swollen, with a narrowed, apex.

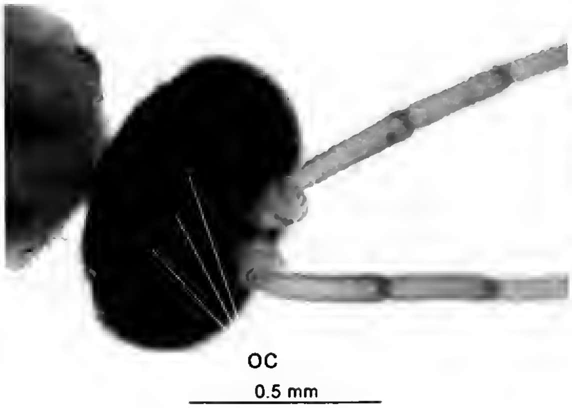

FIG. 10. Adult *Arachnocampa* head showing the placement of the ocelli on a raised ridge. The median ocellus faces anteriorly while the lateral ocelli are directed laterally.

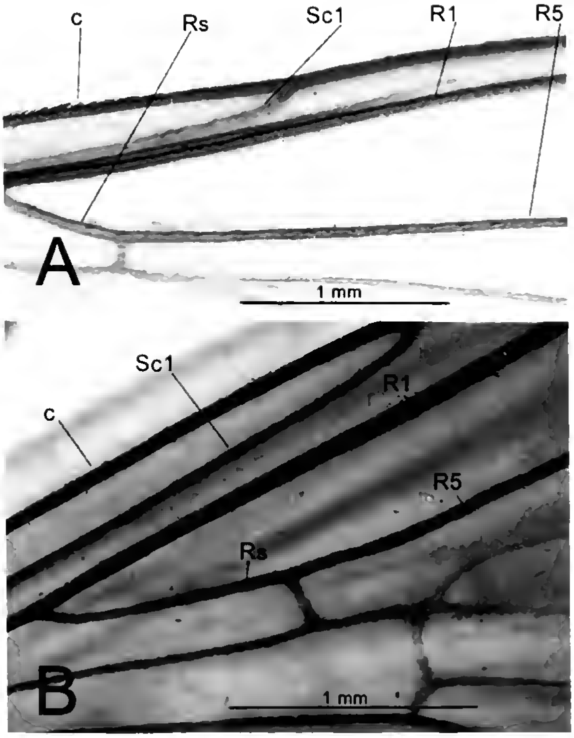

FIG. 11A-B. Wing vein setae placement in *Arachnocampa*. All species have setae on C (costal vein) and R_1 and R_5 (B), whilst *A. buffaloensis* also has setae on Sc_1 (A).

rainforest coverage the Geoscience Australia website was used to obtain GPS coordinates for some localities (http://www.ga.gov.au/map/names/). Specimens were sent live on ice to the University of Queensland where they were placed in individual containers for rearing to adulthood following methods outlined in Baker & Merritt (2003). Each examined specimen was labelled with the following data: state, locality, GPS coordinates, habitat, date and collectors. Holotype specimen are lodged in their corresponding state museums with paratypes distributed between the other state museums.

Terminology and Measurements. Morphological terminology follows McAlpine (1981) with minor modifications listed in the text. Terminology and measurements of wings and thoracic segments are illustrated in Figs 3-4. Measurements and terminology of the larval head capsule are indicated on Figs 5-6. Measurements listed in the text are taken primarily from the holotype, with paratype variation listed in parentheses or as ranges. In some instances, variation is listed from specific populations within a regional group, but mostly ranges are given separately for males and females from entire regional groups. Measurements were taken from at least six to ten specimens where possible. If the number of available specimens of a species was low, all specimens were measured. Counts of the number of maxillary teeth were taken from the 5th instar exuviae after the onset of pupation or adult emergence. Larvae moult their exoskeleton and push it to the posterior end of the pupal case (Baker & Merritt 2003). This method was used to avoid potential differences in the numbers of maxillary teeth among different instars.

Preparation and Examination of Slide-Mounted Material. Specimens stored in 70% ethanol were progressively dehydrated (increasing by 10% concentration at each change) to 100% ethanol, cleared in 10% KOH on a heating block for 15-30 minutes, and washed in distilled water before being slide-mounted in glycerin or glycerin gel. Characters were examined using a Zeiss™ Stemi SV6 binocular dissecting microscope or Zeiss™ Axioscop binocular compound microscope. Pictures were taken using a colour 3CCD digital camera mounted onto the microscope. Measurements and digital images were taken using Scion Image V. 1.62. Scale bars and annotations were added in Adobe Photoshop 5.5. Scanning electron micrographs (SEM) were taken by Anthony O'Toole and Frederic Beaulieu, School of Life Sciences, University of Queensland. Images were taken on a Phillips XL20 at the centre for Microscopy and Microanalysis, University of Queensland.

Type Material. Holotypes were chosen as the specimen that best represented the species based on morphological characters. Type specimens of previously described species proved to be brittle and shrivelled, and of limited use for morphological examination. Therefore fresh specimens obtained from the type localities were used to prepare redescriptions.

Permits For Specimen Collection. Specimens included in this study were collected under the following scientific permits: Queensland, permit number W4/002525/00/SAA, New South Wales permit number B2111, Tasmania permit number 00093, Victoria permit number 10000827. Abbreviations for field collectors listed in the material examined sections are as follows: AM, Andrew McDowell; CB, Claire Baker; AR, Andrew Ridley; DM, David Merritt; ASH, Andrew Shek; JF, Josh Fartch; AS, Amanda Smith; SB, Stuart Baird.

Type Deposition. Type specimens of described species were borrowed from the Australian National Insect Collection (ANIC), Canberra and The South Australian Museum (SAM), Adelaide. Types have been deposited as per permit requirements, with holotypes deposited in their respective state insect collections and paratypes deposited across various collections as follows: Australian Museum (AM), Sydney; Museum Victoria (MV), Melbourne; Queensland Museum, (QM), Brisbane; Tasmanian Museum and Art Gallery (TM), Hobart; University of Queensland Insect Collection (UQIC), Brisbane.

SYSTEMATICS

CHECKLIST OF THE GENUS *ARACHNOCAMPA*.

The following taxonomic checklist is modified from Matile (1981). A new subgenus, *Lucifera*, is proposed to include *A. tasmaniensis* and *A. buffaloensis*. Four new species are allocated to the subgenus *Campara*, with the type species, *A. luminosa* in subgenus *Arachnocampa*.

FAMILY KEROPLATIDAE

SUBFAMILY ARACHNOCAMPINAE

Genus *Arachnocampa* (Edwards, 1924)

Arachnocampa Edwards, 1924: 177. Type species: *Bolitophila luminosa* Skuse, 1890 by original designation.

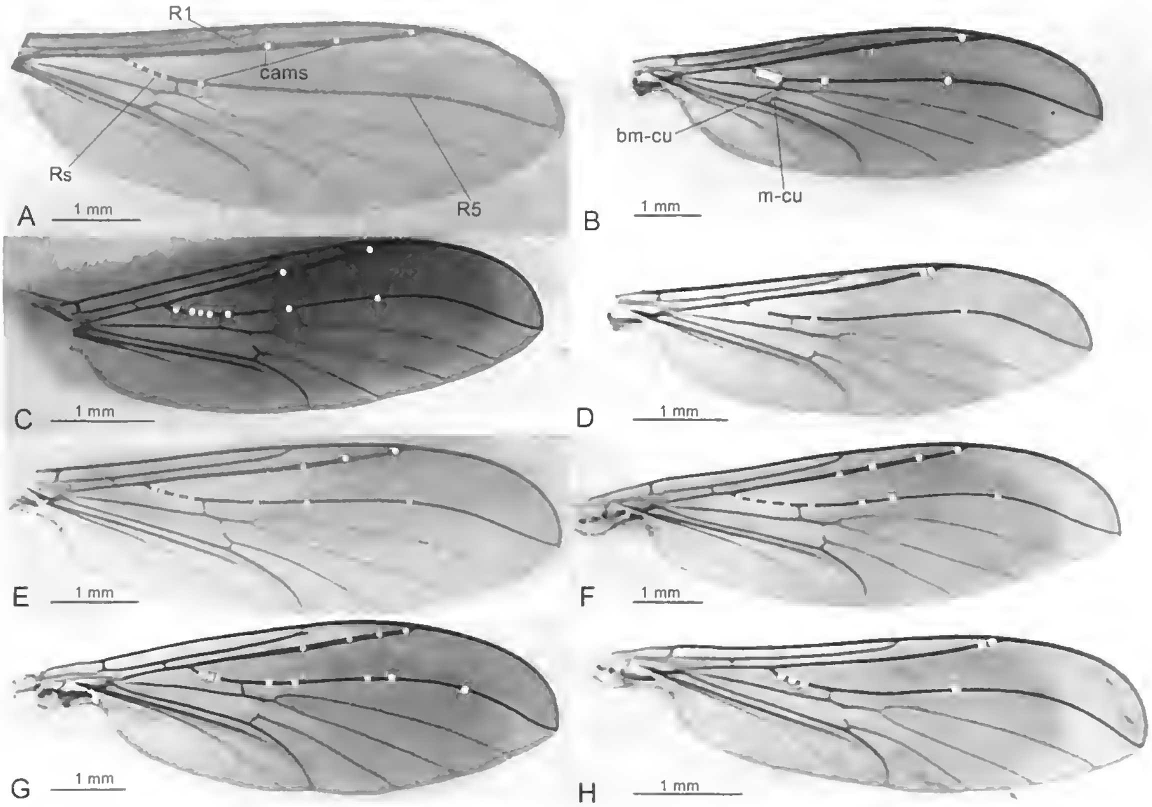

FIG. 12A-H. *Arachnocampa* spp. wings. A, *A. tasmaniensis*; B, *A. buffaloensis*; C, *A. tropica*; D, *A. flava*; E, *A. girraweenensis*; F, *A. richardsae*; G, *A. gippslandensis*; H, *A. otwayensis*. cams, campaniform sensillae.

Subgenus *Arachnocampa* Edwards

Arachnocampa Edwards, 1924: 177 (as genus). Type species: *Bolitophila luminosa* Skuse, 1890 by original designation.

Subgenus *Lucifera* subgen. nov.

tasmaniensis Ferguson, 1925: 487. Australia (TAS). Type species

buffaloensis sp. nov. Australia (VIC)

Subgenus *Campara* Harrison

Campara Harrison, 1966: 880. Type species: *Arachnocampa richardsae* Harrison 1966 by original designation.

flava Harrison, 1966: 880. Australia (Queensland)

richardsae Harrison, 1966: 881. Australia (New South Wales)

tropica sp. nov. Australia (Queensland)

girraweenensis sp. nov. Australia (Queensland/New South Wales)

otwayensis sp. nov. Australia (Victoria)

gippslandensis sp. nov. Australia (Victoria)

REDESCRIPTION OF *ARACHNOCAMPA* EDWARDS

DIAGNOSIS. Empodia and pulvilli absent. Radial sector originating far before middle of wing and far before tip of costa. R_4 absent. Larval head capsule as long as broad. Labrum hood-like. Larval mandibles longer than broad with prominent teeth. Larval antennae vestigial. Posterior abdominal segment of larva with papillae. Pupation taking place in larval web. Pupa not actively mobile, but upon disturbance

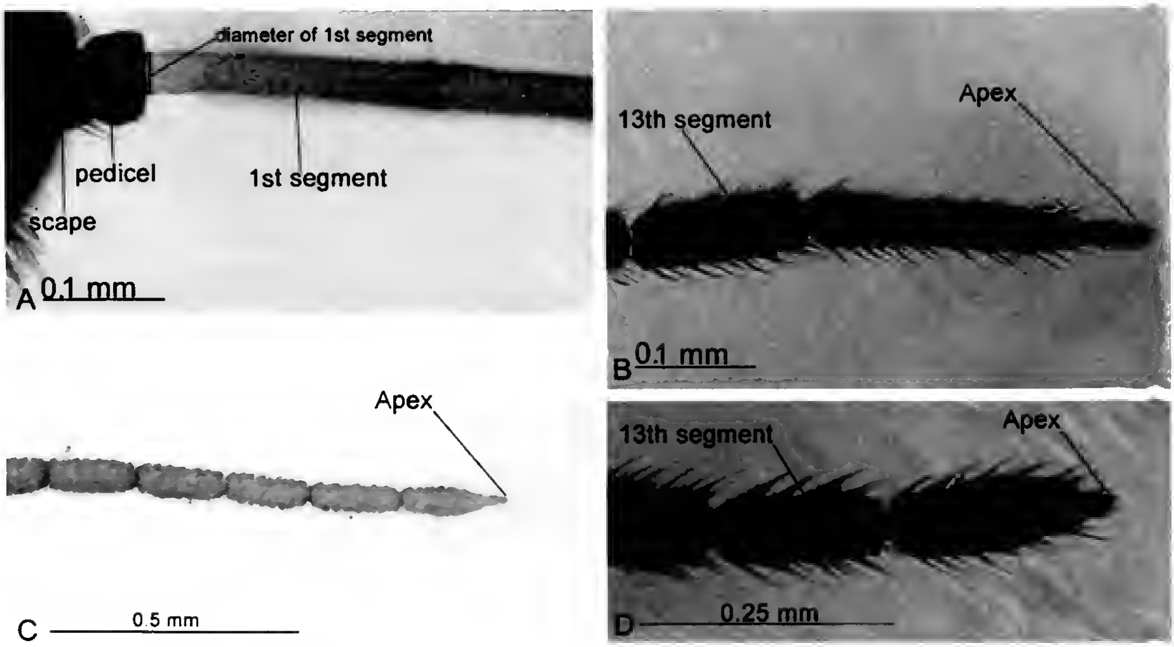

FIG. 13. Antennae of *Arachnocampa* spp. A, *A. tasmaniensis* antennal base indicating position at which diameter of 1st segment was measured; B, *A. tasmaniensis* male antennal apex. The apex of this species is elongate; C, *A. buffaloensis* female antennal apex; D, *A. richardsae* female antennal apex.

is capable of small movements within remains of larval snare.

Description. BIOLOGY: Larvae produce bioluminescence from posterior end. Larvae construct snares (webs) from silk and sticky mucous droplets in which they lie within a mucous tube. Snares consist of a number of silk 'fishing lines' with sticky mucous droplets for prey capture.

Morphology. Larval antenna vestigial and in the form of low hemispherical pale yellow protuberance (Figs 5-6). Larva with rows of fine setae at distal end (Fig. 7) and pair of large anal papillae. Larval mandibles with four apical teeth and one median tooth on inner surface (Fig. 6). Adult antennae with fourteen flagellar segments, longest segment at base, segments progressively shortening to 13th segment (Fig. 9); 14th segment longer than 13th, narrowing to a short, rounded apex. Front dark brown. Ocelli on prominent raised ridge facing anteriorly and laterally (Fig. 10); strong dark setae covering ridge. Face medium brown with thick cluster of setae over facial carina. Eyes covered with mat of fine, dark interommatidial hairs. Row of setae along lateral margins of scutum. Leg segments uniformly brown except lighter basal section of coxa. Hind legs darker. Legs covered in fine setae. Two apical tibial spurs on ventral side of mid and hind leg. One apical tibial spur on fore leg. Strong setae (quarter of length of ventral spurs) along tibiae and tarsi and clustered around dorsal apex of tibiae. Wing veins brown. Darker on costal (C), subcostal (Sc1) and radial veins (R). Strong dark setae on C, (setae on Sc1 in *A. buffaloensis* only, Fig. 11A) and R_1 and R_5 veins (Fig. 11B). Abdominal

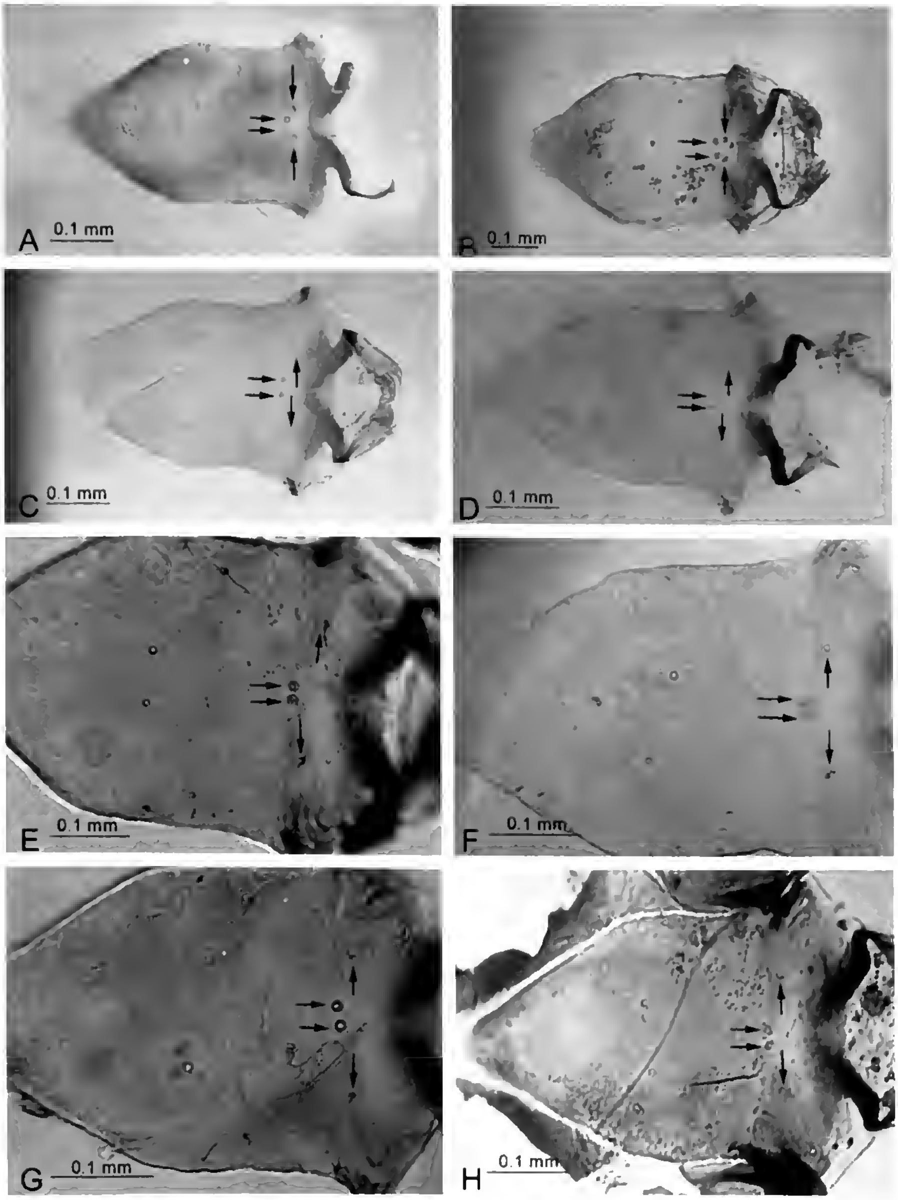

FIG. 14. *Arachnocampa* spp. larval sclerotised head plates indicating placement of campaniform sensillae (with arrows). This arrangement of the campaniform sensillae differentiates the subgenus *Campara* (C-H) from the subgenus *Arachnocampa* (A-B). A, *A. tasmaniensis*; B, *A. buffaloensis*; C, *A. tropica*; D, *A. flava*; E, *A. girraweenensis*; F, *A. richardsae*; G, *A. gippslandensis*; H, *A. otwayensis*.

segments 2-7 with tergites and sternites covered in black hairs. Abdominal segment 1 with tergite hairy, sternite with hairs on distal edge only. ♀ with more setae on basal abdominal segments than ♂. Eggs clearly visible through adult ♀ abdomen. All adult abdominal segments yellow to dark brown, darker at distal end of each segment, giving distinctive 'tiger stripe' colouration (Fig. 8).

KEY TO THE SUBGENERA OF *ARACHNOCAMPA* (MODIFIED FROM EDWARDS 1924)

1. Wing with m-cu cross vein basal to r-m cross vein; fore basitarsus equal to, or up to 1.3 times length of fore tibia; pupae suspended vertically; endemic to New Zealand . . *Arachnocampa (Arachnocampa)* Edwards
2. Wing with m-cu cross vein basal to r-m cross vein (Fig. 12A-B); fore basitarsus 1.55-2 times length of fore tibia; pupae suspended horizontally; endemic to Tasmania and Mt Buffalo, Victoria, Australia . . . . . *Arachnocampa (Lucifera)* subgen. nov.
3. Wing with m-cu cross vein distal to r-m cross vein (Fig. 12C-H); basal segment of fore tarsus 1.3-1.5 times length of fore tibia; pupae suspended horizontally; found in eastern Australia . . . . . *Arachnocampa (Campara)* Harrison

REDESCRIPTION OF SUBGENUS *ARACHNOCAMPA* BASED ON EDWARDS (1924)

Diagnosis. Adult wing with m-cu basal to r-m (Fig. 12A-B). bm-cu 0.72-1.6 times length of m-cu (Fig. 12A-B). bm-cu straight (Fig. 12A-B). Scape with full ring of setae around distal end. Larval head capsule with campaniform sensillae in block formation with setae (Fig. 14A-B). Larval malpighian tubules white (Fig. 15A-D). Pupae suspended vertically with one silk line connecting to thoracic region.

ARACHNOCAMPA (LUCIFERA) SUBGEN. NOV.

Arachnocampa (Lucifera) Baker et al., 2008 *nomen nudum*

Type species. *Arachnocampa tasmaniensis* Ferguson, 1925.

This study has supported Edward's (1924) division of *Arachnocampa* into two subgenera, *Arachnocampa* and *Campara*, based on the position of the m-cu vein. However, I have identified additional characters that further subdivide *Arachnocampa*. Consequently, I propose a new subgenus, *Lucifera*, for *A. tasmaniensis* Ferguson and *A. buffaloensis* sp. nov. *Lucifera* is distinguished from *Campara* by wing venation and sensillum pattern. The subgenus *Arachnocampa* is separated from *Lucifera* by the unique method of vertical pupal suspension of its now single constituent species, *Arachnocampa luminosa* (Skuse).

Diagnosis. Adult wing with m-cu basal to r-m (Fig. 12A-B). bm-cu 0.72-1.6 times length of m-cu (Fig. 12A-B). bm-cu straight (Fig. 12A-B). Scape with full ring of setae around distal end. Larval head capsule with campaniform sensillae in block formation with setae (Fig. 14A-B). Larval malpighian tubules white (Fig. 15A-D). Pupae suspended horizontally with one silk line connecting to thoracic region and another to the abdominal region.

Etymology. Lucifera, literally meaning 'light bringing', refers to the unique ability of *Arachnocampa* to produce light. It also has reference to the enzyme luciferase and substrate luciferin that produce the light in conjunction with adenosine 5'-triphosphate (ATP) and oxygen.

KEY TO SPECIES OF THE SUBGENUS *LUCIFERA*

1. Fore basitarsus 1.75-2 times length of fore tibia, endemic to Tasmania . . . . . *tasmaniensis* Ferguson
2. Fore basitarsus 1.55 times length of fore tibia, endemic to Mt Buffalo, Victoria . . . . *buffaloensis* sp. nov.

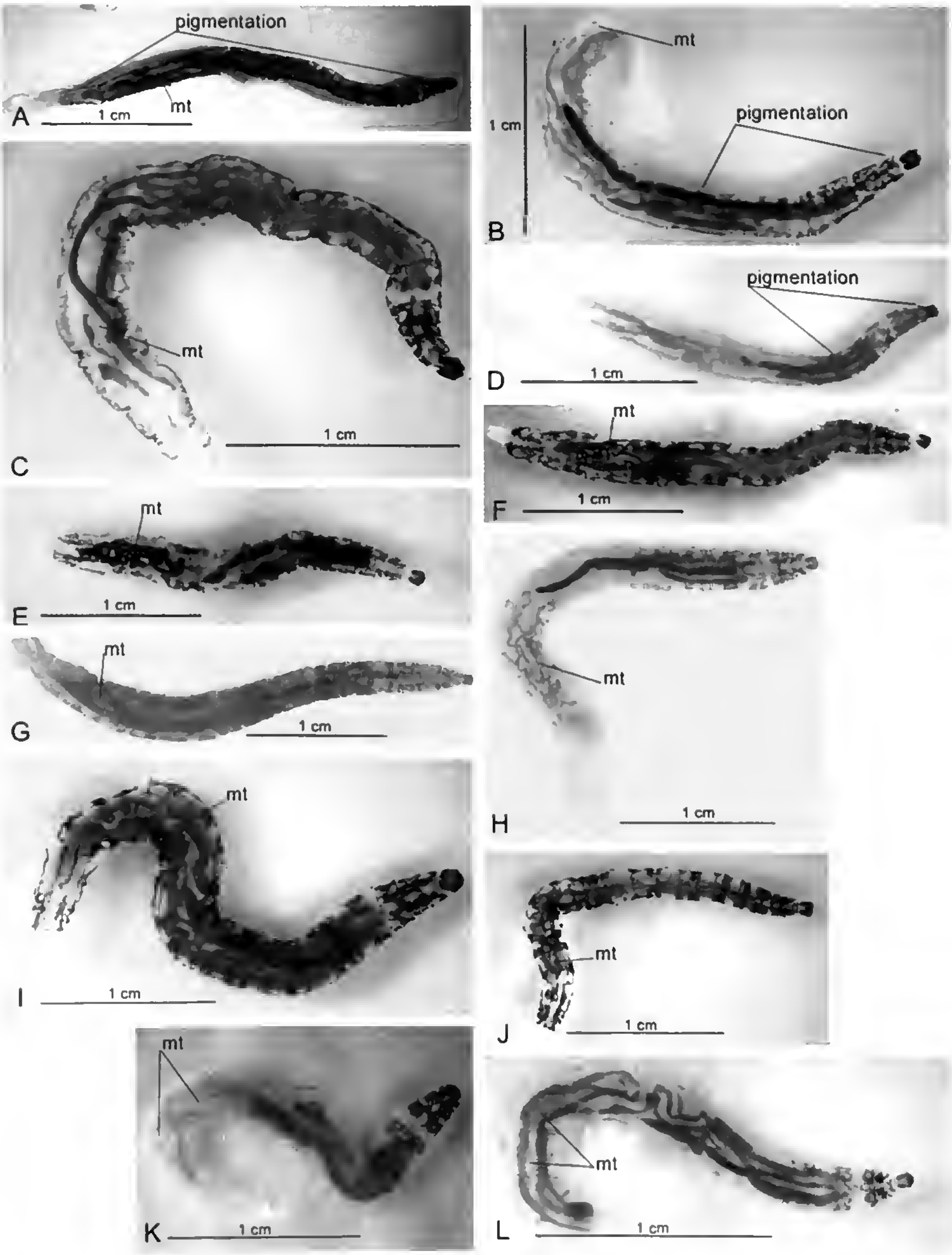

FIG. 15. *Arachnocampa* spp. larvae (live whole mounts). A, *A. tasmaniensis* (epigean); B, *A. tasmaniensis* (cave); C, *A. tasmaniensis* (cave); D, *A. buffaloensis*; E, *A. tropica*; F, *A. flava*; G, *A. girraweenensis* (cave2); H, *A. girraweenensis* (cave1); I, *A. richardsae* (cave); J, *A. richardsae* (epigean); K, *A. gippslandensis* (cave); L, *A. gippslandensis* (cave). mt, malphigian tubules.

REDESCRIPTION OF SUBGENUS *CAMPARA* BASED ON EDWARDS (1924)

Diagnosis. Adult wing with m-cu distal to r-m (Fig. 12C-H). bm-cu 1.4-4.5 times length of m-cu (Fig. 12C-H). bm-cu curved. Scape with half ring of setae on ventral side of distal end. Larval head capsule with campaniform sensillae in line with setae rather than block formation (Fig. 14C-H). Larval malpighian tubules white (Fig. 15G, K) to light brown (Fig. 15H, I, J, L) to black (Fig. 15E-F). Pupae suspended horizontally with one silk line connecting to thoracic region and another to abdominal region.

KEY TO SPECIES OF THE SUBGENUS *CAMPARA*

To accurately distinguish species in this subgenus, all life stages are needed. Genetic data and mating trials clearly indicate them to be distinct species. Large geographic boundaries between species and no evidence of sympatric speciation mean geographic information is often the easiest way to distinguish these species.

1. 5th instar larva with 10 maxillary teeth on one side and 11 on the other (Fig. 16B, D)...2

– 5th instar larva with 9 maxillary teeth on one side and 10 on the other (Fig. 16A, C)...3

2. Larval malpighian tubules black (Fig. 15E). Adult laterotergite with 2-30 setae (Fig. 17C); bm-cu 1.7-2.5 times length of m-cu (Fig. 12C). Found in wet tropical rainforests of north Queensland .... *tropica* sp. nov.

– Larval malpighian tubules white to light brown (Fig. 15G-H). Adult laterotergite with 0-5 setae (17E); bm-cu 1.8-4.5 times length of m-cu (Fig. 12E). Found in caves in Girraween National Park, south-east Queensland and rainforest in northern New South Wales (Washpool, Dorrigo and New England National Parks) .... *girraweenensis* sp. nov.

3. Larval malpighian tubules black (Fig. 15F). Adult laterotergite with 1-4 setae; bm-cu 1.9-2.7 times length of m-cu (Fig. 12D). Found in isolated rainforest gullies in Kroombit Tops National Park and rainforest of the Mt Warning Caldera including northern New South Wales .... *flava*

– Not with above combination of characters 4

4. Larval malpighian tubules pale to medium brown (Fig. 15I, J). Adult laterotergite with 0-21 setae; bm-cu 1.5-3 times length of m-cu (Fig. 12F). Found in rainforested regions of central to southern New South Wales (Blue Mountains, Bundanoon, Fiztroy Falls) .... *richardsae* Harrison

– Not with above combination of characters. Adult with never more than 3 small setae on laterotergite. Found in rainforest areas in southern Victoria 5

5. Adult body length 10-12.2 mm; wing length 6.5-8 mm; ♀ antennal length 3.2-3.3 mm; bm-cu 1.75-2.6 times length of m-cu (Fig. 12G). Found in Gippsland rainforest and isolated cave systems of Victoria .... *gippslandensis* sp. nov.

– Adult body length 6.5-8 mm, wing length 4.5-5.5 mm, ♀ antennal length 2-2.2mm; bm-cu 2.4-3.3 times length of m-cu (Fig. 12H). Found in rainforest west of Melbourne (including Otway National Park and Melba Gully and Angahook-Lorne State Parks) .... *otwayensis* sp. nov.

Arachnocampa (*Lucifera*) *tasmaniensis* Ferguson, 1925

Arachnocampa tasmaniensis Ferguson, 1925: 487; Harrison, 1966: 879 (redescription).

Material Examined. HOLOTYPE ♂ (in copula with paratype ♀), bearing the label: 'Ida Bay caves, Arthur M. Lea, December, 1909. In total darkness fully 1/4 mile from entrance', condition: poor. Card mounted, both holotype ♂ and paratype ♀ missing antennae, legs and wings glued to card (SAM).

Other Material. TASMANIA, 3♂♂, 5♀♀, Mole Creek Karst National Park, Marakoopa cave, 41°35′S, 146°17′E, 17.i.2001, CB/DM, collected as larvae, reared to adults in incubator by CB, TAS2#1,2,3,7,9,11,16; 2♀♀, Sassafras cave, 41°34′S, 146°21′E, 1.x.2001, CB/AS, collected as larvae, reared to adults in incubator by CB, TAS3#3-4; 3♂♂, Francistown, property of Arthur Clarke, rainforest gully along stream, 43°18.5′S, 146°59.4′E, 16.i.2001, CB, collected as larvae, reared to adults in incubator by CB, TAS5#1-2,5; 5♂♂, 7♀♀, Ida Bay caves, Mystery Creek cave (Entrance cave), 43°27.7′ S, 146°50.0′E, 16.i.2001, CB/DM, collected as larvae, reared to adults in incubator by CB, TAS6#1-2, 6-8, 12-14, 17-18, 22-23.

The following redescription and measurements are based primarily on ♂ TAS6#22, with other specimens measured for ranges and variation.

Diagnosis. Wing with m-cu located basal to r-m (Fig. 12A); bm-cu straight (not curved), angled backwards towards wing base and 0.72-1.6 times length of m-cu; bm-cu parallel to r-m (Fig. 12A). Laterotergite with 0-10 setae. Fore basitarsus 1.75-2 times length of fore tibia. Larvae with rows of 9 and 10 maxillary teeth plus lobe (Fig. 16A).

Redescription. *Adult.* ♂ holotype length 11.2 mm (range 10-13.5 mm (cave), 8-10.5 mm (epigean)). Wing length ♂ 6.5 mm (5.5-8 mm (cave ♂♂), 5-6mm (epigean ♂♂), 6-9 mm (cave ♀♀), 5 mm (epigean ♀♀)). Antennal length 5mm (♂♂), 3mm (♀♀). *Head:* Antennae brown, bases of first few flagellar segments lighter. Scape and pedicel brown. Flagellum with dense mat of brown hairs, except basal quarter of first segment. Diameter of scape 2.4 times diameter of basal flagellar segment (♂♂ 2.3-2.9x, ♀♀ 2.6-3x). First flagellar segment 1.2 times length of second flagellar segment (♂♂ 1.1-1.5x, ♀♀ 1.3-1.6x). Palpi yellow/brown; apical segment lengthened and slightly dilated (also darker); light covering of dark setae on palps. Proboscis yellow/brown (♀♀) to pale yellow (♂♂). *Thorax:* Cluster of long, dark setae on supra-alar region. Shorter, finer setae on post alar area. Laterotergite with 0/2 small setae (TAS2 1-10 setae, TAS5 1-4, TAS6 0-3); sometimes with unequal numbers of setae on each side. Scutum with medium to dark brown shading. Pleura entirely dark brown (encompassing laterotergite, anepimeron, anepisternum, katepsisternum) (Fig. 17A). *Legs:* Coxae white to pale yellow, darkening to dark brown at apices, more extensively so on hind coxa (Fig. 17A). Long dark hairs covering about one third of each coxa, predominantly at apices and on ventral surfaces. Mid basitarsus 1.1 times length of mid tibia; hind basitarsus 0.71 times length of hind tibia (♀♀ 0.77x). *Wings:* Entire wing shaded except for fainter patch basally. Campaniform sensilla located on ♂ wings as follows: 3 on R$_1$, 4 on Rs, and 1 on proximal end of R$_5$ (Fig. 12A). TAS2 ♂♂ (R1: Rs: R5) 2-3: 4-6: 1-3, ♀♀ 2-3: 4-6: 2-4, TAS5 ♂♂ 1-2: 2-4: 2-3, ♀♀ 2: 2: 2, TAS6 ♂♂ 1-4: 4-6: 1-2, ♀ 3/7: 5-6: 1-3). Halteres pale yellow/white basally, brown apically with fine hairs. *Abdomen*: External genitalia light brown. *Eggs*. Slightly ovoid. 0.55 x 0.5 mm, red/brown. *Larva*. Larval body colouration with sclerotised brown head capsule (TAS6-cave), body with faint brown/red pigmentation beginning at anterior end, extending down 75% of lateral edges of body (Fig. 15C) (range TAS2-cave: pigmentation green, extending down 60% of lateral edges (Fig.15B); TAS5-epigean: brown/black pigmentation extending entire length of lateral edges (Fig. 15A). Larve up to 4 cm long in fifth instar. Snares ~ 30 cm long in caves, <3 cm in epigean settings. *Pupa*. Suspended from distal tip of abdomen and anterior part of abdomen.

Distribution. *Arachnocampa tasmaniensis* colonies are relatively widespread throughout Tasmania (Goede 1967; Eberhard 1999, 2000). Larvae are primarily found in large numbers in limestone caves. Populations are also widespread in rainforest and along creek banks and walking trail cuttings (Baker 2004; Baker et al. 2008).

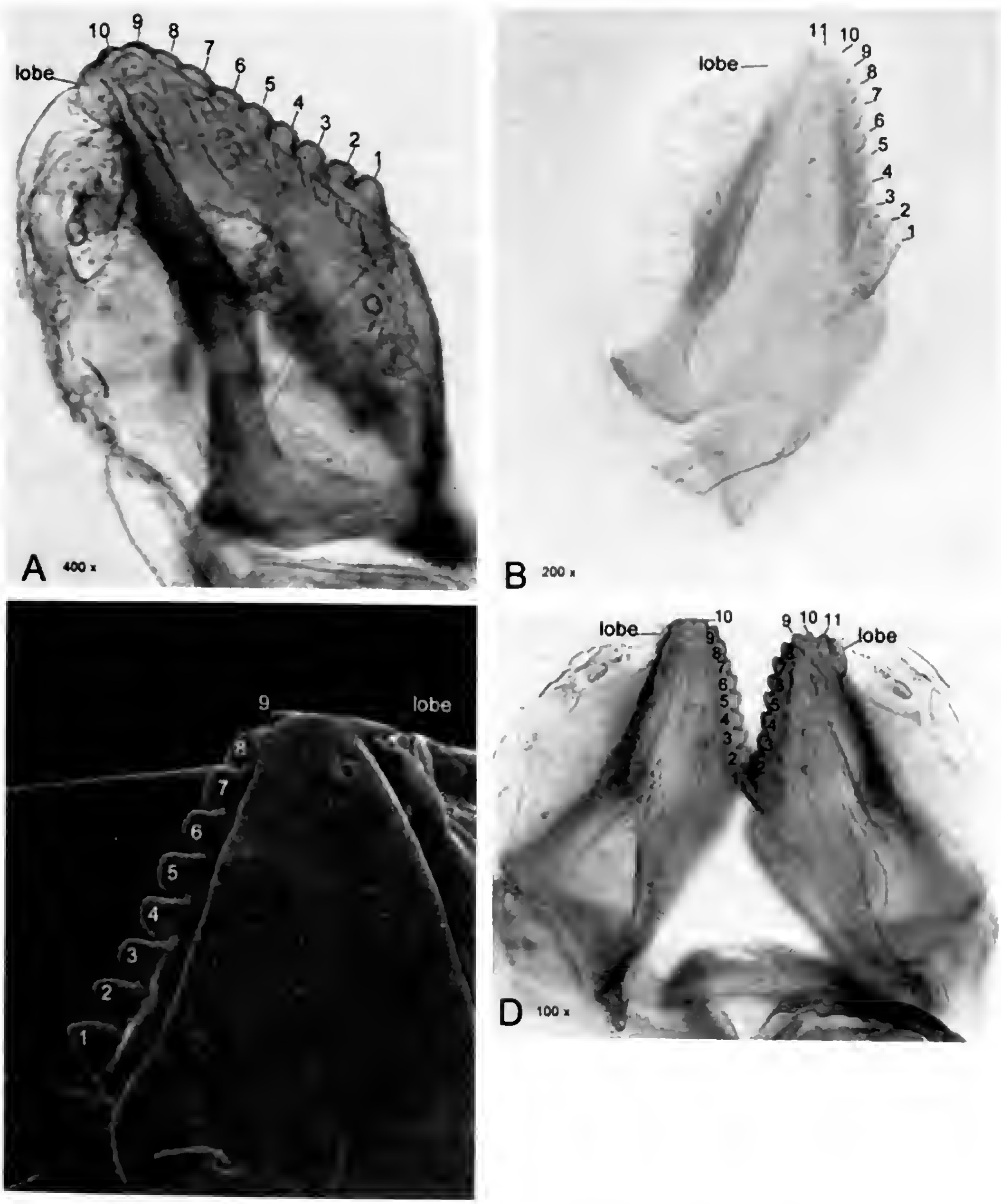

FIG. 16. *Arachnocampa* spp. maxillary teeth. A, *A. gippslandensis* (10 maxillary teeth plus lobe); B, *A. tropica* (10 and 11 maxillary teeth plus lobe); C, *A. flava* (9 and 10 teeth plus lobe (numbers 1-9! + lobe); D, *A. girraweenensis* (10 and 11 maxillary teeth). In most species the number of teeth on one maxilla is different to that on the other.

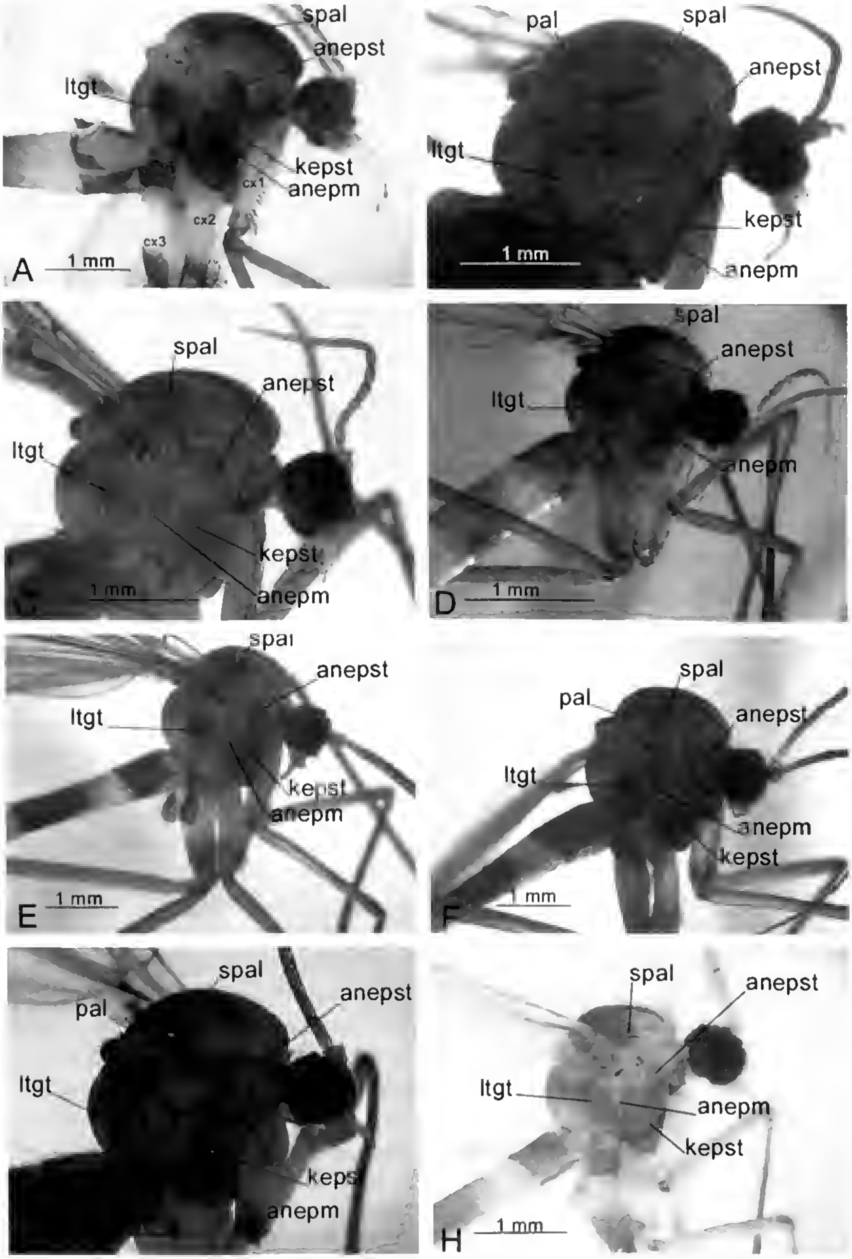

FIG. 17. *Arachnocampa* spp. thoracic segments. A, *A. tasmaniensis*; B, *A. buffaloensis*; C, *A. tropica*; D, *A. flava*; E, *A. girraweenensis*; F, *A. richardsae*; G, *A. gippslandensis*; H, *A. otwayensis*. anepm, anepimeron; anepst, anepisternum; kepst; ltgt, laterotergite; pal, post alar region; spal, supra-alar region.

Comments. Tasmanian populations from which adults were successfully reared for morphological examination were collected from four distinct areas and habitats. Three populations were sampled from limestone caves in both northern (TAS2, 3) and southern (TAS6) areas of the island, and one population was sampled from rainforest in the south (TAS5). Other populations identified during surveys did not produce adults for morphological examination (TAS4), or larvae were not collected from the site for identification (TAS1).

Obvious morphological variation was evident between cave and rainforest (epigean) populations (e.g. in larval colouration, adult body and wing lengths), suggesting that environmental differences experienced by cave and rainforest-dwelling populations have led to phenotypic changes within this species. The close proximity of caves to rainforest populations enables genetic exchange between these habitat types (Baker 2004, Baker et al. 2008). Some morphological variation is evident between northern and southern cave populations. For example, the number of setae on the laterotergite varies from 0-3 for southern cave populations, and 1-10 for northern cave populations. However, this may be due to differing degrees of rainforest population migration into caves or general plasticity within this taxon rather than evidence of speciation. Morphological characters used in this study support Ferguson's (1925) description of this species and its placement within the new subgenus *Lucifera*.

Arachnocampa (*Lucifera*) *buffaloensis* sp. nov.

Arachnocampa buffaloensis Baker et al. 2008 (unavailable name).

Material. HOLOTYPE ♀, Australia, Victoria, Mount Buffalo National Park, Underground River cave, glow-worm grotto, 36°43′S, 151°17′E, 13.iii.2000, CB, collected as adult, killed and stored in 70% ethanol, BUFF#2 (deposited in MV). PARATYPES. VICTORIA, 4 adult ♀♀, Mount Buffalo National Park, Underground River cave, glow-worm grotto, 36°43′S, 151°17′E, 13.i.2001, CB/JF, collected as larva, reared to adult in incubator by CB, BUFF#1,3,4,5. (paratypes deposited in MV and QM)

The following description and measurements are based primarily on the holotype, with other specimens measured for ranges and variation. No males were reared from larvae of this colony.

Diagnosis. Adult body length 10-12 mm. Wing length 6.5-7 mm. m-cu close to r-m (Fig. 12B); bm-cu running parallel to r-m and 1-1.6 times length of m-cu (Fig. 12B). Fore basitarsus 1.55 times length of fore tibia. Laterotergite bare (1 seta on some paratypes). Larvae with row of 10 maxillary teeth plus lobe (Fig. 16A). Larval body colouration: head capsule sclerotised brown, body red, green, blue and white in order from anterior to posterior end. Pigmentation limited to anterior end (Fig. 15D).

Description. *Adults* (♀♀). Body length 11 mm; wing length 7 mm; antennal length 2.8 mm.

Head. Antenna light brown, scape and pedicel light brown, flagellum with dense mat of brown hairs except basal sixth of first flagellar segment. Diameter of scape 2.5 times diameter of basal flagellar segment (range 2.3-2.5x). First flagellar segment 1.4 times length of second segment (1.3-1.45x). Front brown, ridge at dorsal corner of eye ending before centre of front. Longitudinal, deep sulcus above base of antennae. Palpi pale yellow. Apical segment lengthened and slightly dilated (also slightly darker). Proboscis pale yellow. *Thorax:* Large cluster of long, dark setae on supra-alar region, smaller much shorter hairs on post alar area (Fig. 17B). Thoracic dorsum with medium brown shading. Pleura darker brown, lighter in crevice between laterotergite and anepimeron (Fig. 17B). *Legs*: Coxae white to pale yellow. Faint traces of darkening at apices, more extensively so on hind coxa. Dark hairs covering about one third of each coxa. Mid basitarsus equal to length of mid tibia; hind basitarsus

0.81 times length of hind tibia. *Wing*: Shading covering entire wing. m-cu basal to r-m, but closely approximated; r-m sloped forwards towards apex of wing (Fig. 12B); bm-cu 1-1.6 times length of m-cu; m-cu sloping forwards towards apex of wing. Halteres pale yellow basally, brown apically. Campaniform sensillae located on R veins as follows: 1 on R_1, 6 on Rs, and 2 on R_5 (1-3: 6-7: 1-3) (Fig. 12B). *Abdomen*: External ♀ genitalia light brown. All abdominal segments dark brown (paratypes: light-medium brown; darker at distal end of each abdominal segment). *Eggs*. Not seen. *Larva*. Up to 4 cm in length. Larval snares up to 40 cm in length. *Pupa*. Suspended from apex of abdomen and anterior part of abdomen. Bracing thread from thorax to main anterior abdominal suspension thread. Head area black, thorax red/brown, abdomen pale yellow (other Mt Buffalo pupae suspended as for *A. flava*).

Etymology. The specific name refers to the type locality, a single cave in Mt Buffalo National Park, Victoria.

Distribution. At present this species is known only from the Underground River Cave (granite boulder infill cave, 300 m in length with constant water flow) in Mt Buffalo National Park, Victoria. Other caves on private land within the region have been reported to contain glow-worms. However, as yet entry to these other sites has not been granted to the author.

Comments. Data from molecular and morphological studies support *A. buffaloensis* as a sister species to the geographically isolated Tasmanian species *A. tasmaniensis* (Baker 2004; Baker et al. 2008). Theories explaining the current geographic isolation of these sister species are presented in Baker et al. (2008). The cave in which *A. buffaloensis* is found is sub-alpine, where snowfall and subsequent spring melt flooding are an annual event. The extreme seasonal variations and low humidity outside the cave habitat greatly decrease the chances of survival for colonies not within the safety of the cave environment. This species was nominated by the author and has since been listed as *threatened* under the Victorian Government's Flora and Fauna Guarantee Act 1988 on the basis of its extremely restricted habitat of one cave.

Arachnocampa (*Campara*) *tropica* sp. nov.

Arachnocampa tropica Baker et al. 2008 (unavailable name)
Arachnocampa tropicus Baker et al. 2008 (unavailable name)

Material. HOLOTYPE ♂, Australia, north Queensland, Mt Lewis Rd, Rainforest road cuttings near stream, 16°34.9′S, 145°17′E, 10.vii.2000, CB/AM, collected as larva, reared to adult in incubator by CB, NQLD2#2 (deposited in QM T152171). PARATYPES. QUEENSLAND, ♂, same data as holotype. NQLD2#6; 2♀♀, same data as holotype NQLD2#1, 5; 2♂♂, 5♀♀, Daintree National Park, Mossman Gorge section, council road off Mossman Gorge carpark, road cuttings, 16°25′S, 145°20′E, 14.vii.2000, CB/AM, collected as larvae, reared to adults in incubator by CB, NQLD1#1-6, 8; 1♀, Paluma National Park, Birthday Creek Falls, road cuttings near car park, 18°59′S, 146°10′E, 8.vii.2000, CB/AM, collected as larva, reared to adult in incubator by CB, NQLD9#1; 1♂, Wooroonoran National Park: Josephine Falls section, Bartle Frere trail, western approach, Bobbin Bobbin Falls, stream banks, 17°22′S, 145°47′E, 9.vii.2000, CB/AM, collected as larva, reared to adult in incubator by CB, NQLD6#1; 1♀, Wooroonoran National Park: Josephine Falls section, Bartle Frere trail, western approach, granite boulder cave off trail near summit, 17°22′S, 145°49′E, 9.vii.2000, CB/AM, collected as larva, reared to adult in incubator by CB, NQLD5#3; 5♂♂, 1♀, Mt Hypipamee National Park, Dinner Falls walking trail banks near stream, 17°26′S, 145°28′E, 9.vii.2000, CB/AM, collected as larva, reared to adult in incubator by CB, NQLD4#1-6; 1♀, Mt Hypipamee National Park, Dinner Falls walking trail banks near stream, 17°26′S, 145°28′E, 11.vi.2002, CB/AM, collected as larva, reared to adult in incubator by CB, NQLD4Ri#1; 2♂♂, 2♀♀, Tully Falls State Park, Charmillan walking trail banks near stream, 17°43′S, 145°31′E, 9.vii.2000, CB/AM, collected as larva, reared to adult in incubator by CB, NQLD8#1-4. (paratypes deposited in AM, MV, QM, TM and UQIC).

The following description and measurements are based primarily on the holotype, with other specimens measured for ranges and variation.

Diagnosis. Adult body length 7-8 mm (♂♂), 7-9 mm (♀♀). Wing length 5-6 mm (♂♂), 5.5-6.5 mm (♀♀). Antennal length 3-3.5 mm (♂♂), 2mm (♀♀). bm-cu curved backwards and 1.7-2.5 x length of m-cu. m-cu sloping forwards (Fig. 12C). Laterotergite with 2-12 (♂♂), 3-30 (♀♀) setae. Larvae with 10 and 11 maxillary teeth (Fig. 16B). Larval head capsule sclerotised brown, body with faint brown/red pigmentation beginning at anterior end, extending down entire length of lateral edges of body. Malpighian tubules black (Fig. 15E).

Description. *Adult.* ♂ holotype body length 8 mm; wing length 5 mm; antennal length 3.2 mm.

Head. Antennae yellow to brown, lighter at basal end of first flagellar segment; scape and pedicel yellow. Flagellum with dense mat of brown hairs, except basal quarter of first flagellar segment. Diameter of scape 2.25 times diameter of basal flagellar segment in holotype ♂ (♂♂ 2.25-2.7x, ♀♀ 2.6-3.4x). First flagellar segment 0.88 times length of second flagellar segment (♂♂ 0.88-1.4x, ♀♀ 0.93-1.2x). Front medium to dark brown. Dark setae on head. Face medium brown to dark brown with thick cluster of setae over facial carina. Palpi pale yellow; apical segment lengthened and slightly dilated; light covering of dark setae on palps. Proboscis pale yellow to brown. *Thorax*: Cluster of long, dark setae on supra-alar region and on post alar area (Fig. 17C). Laterotergite with 6 small setae (♂♂ 2-12, ♀♀ 2-30); sometimes with unequal numbers of setae on each side. All thoracic dorsum with medium brown shading. Pleura (encompassing laterotergite, anepisternum, anepimeron and katepisternum) slightly darker medium brown and more heavily shaded in centre of sclerites (Fig. 17C). *Legs:* Coxae pale yellow, darkening to medium/dark brown at apices, more extensively so on hind coxa. Long, dark hairs covering about one quarter of each coxa, predominantly at apices and ventral surfaces. Other segments of legs yellow/brown. Fore basitarsus 1.5 times length of fore tibia (1.2-1.5x); Mid basitarsus equal to length of mid tibia (♀♀ 0.83x); hind basitarsus 0.83 times length of hind tibia (♀♀ 0.66-0.83x). *Wings*: Shading covering entire wing except for a fainter patch at wing base. Halteres pale yellow basally, brown apically with fine hairs. Campaniform sensilla located on ♂♂ wings as follows: 2 on R_1, 4 on Rs, and 3 on R_5 (Fig. 12C) (♂♂ range 1-3: 3-6: 1-3, ♀♀ 1-3: 3-5: 1-4). *Abdomen*: External genitalia medium brown. *Eggs*. 0.48 x 0.43 mm, yellow/brown with slightly red tinge (virgin ♀♀ eggs). *Larva*. Intestines green. Larval snares <3 cm. *Pupa*. Suspended from apex of abdomen and anterior part of abdomen.

Etymology. The specific name tropica refers to the type locality's distribution within the world heritage-listed Wet Tropics region of north Queensland, Australia.

Distribution. This species has been recorded in rainforest and small granite boulder caves throughout the Wet Tropics rainforests of far north Queensland. It is likely that this species is more widespread in the rainforests of this region, however a detailed survey is yet to be conducted. Populations have been observed to expand rapidly during the northern wet season (November - March), only to drop back in numbers through the remainder of the year due to drier conditions (personal observations).

Comments. Morphological and molecular data distinguish *A. tropica* from all other species in the genus. A large geographic distance separates this northern clade from other Australian populations of *Arachnocampa*. Genetic data suggest two species may be present in far north Queensland following two phases of expansion into the tropics (Baker 2004, Baker et al. 2008). Verification of this distinction requires genetic analysis at the population level. Individual colonies of this species were usually low in numbers of individuals and density, with no spectacular displays noted. Larvae collected from the Wet Tropics were heavily parasitised by an undescribed species of ichneumonid wasp (Baker 2004; Chris Burwell, pers. comm.). This wasp has not been recorded from colonies further south but could represent a significant threat to the tourism industry associated with glow-worms in southeast Queensland if it dispersed or was translocated to the region.

Arachnocampa (*Campara*) *flava* Harrison, 1966

Arachnocampa flava Harrison 1966: 882.

Material Examined. HOLOTYPE ♂ (QM Reg. No. T6430) Queensland, Numinbah 21.iv.1935 F.A. Perkins (QM). OTHER MATERIAL. NEW SOUTH WALES, 3♂♂, 4♀♀, Mt Warning National Park, Korrumbyn picnic area, vertical creek banks, 28°24′S, 153°16′E, 27.iii.2000, CB/JF, collected as larvae, reared to adults in incubator by CB, CALD5#1-7; 2♀♀, Mt Warning National Park, Korrumbyn picnic area, vertical creek banks, 28°24′S, 153°16′E, 5.vii.2002, AR/CB, collected as larvae, reared to adults in incubator by CB, CALD5#Ri1-2; 4♂♂, 4♀♀, Nightcap National Park, Protesters Falls walk, vertical creek banks, 28°34′S, 153°17′E, 27.iii.2000, CB/JF, collected as larvae, reared to adults in incubator by CB, CALD6#1-8. QUEENSLAND: 6♂♂, 10♀♀, Springbrook-Mudgeeraba Road, Springbrook Gully, vertical creek banks, 28°12.5′S, 153°17.5′E, 23.v.2001, CB, collected as larvae, reared to adults in incubator by CB, CALD3#4, 12, 14-17, 21, 23, 31, 33, 34, 39, 41-43, Rix.

Diagnosis. Adult body length 6.5-8.5 mm (♂♂), 7-10 mm (♀♀); wing length 4.5-5 mm (♂♂), 4.6-6.5 mm (♀♀); antennal length 3.5-4 mm (♂♂), 2 mm (♀♀). bm-cu curved backwards and 1.9-2.7 times length of m-cu (Fig. 12D). Laterotergite with 0-7 setae. Larval colouration: head capsule sclerotised brown, body with dark brown/red pigmentation extending along entire lateral edges of body (Fig. 15F). Intestines green. Malpighian tubules black. Larval maxillae with rows of 9 and 10 teeth (Fig. 16C).

Description. *Adult.* ♂ holotype body length 8 mm; wing length 5mm; antennal length 4 mm.

Head. Antennae light to medium brown, light yellow at basal end of first few flagellar segments. Scape and pedicel pale yellow. Flagellum with dense mat of brown hairs, except basal fifth of first segment. Diameter of scape 2.7 times diameter of basal flagellar segment in holotype ♂ (♂♂ 2.6-3.1x) and 3-3.6 times length of second flagellar segment in ♀♀. Scape with very sparse setae around ventral apex. First flagellar segment 1.3 times length of second flagellar segment (♂♂ and ♀♀ 1.1-1.3x). Front medium to dark brown. Strong dark setae covering ridge. Face medium brown with thick cluster of setae over facial carina. Palpi pale yellow; apical segment lengthened and slightly dilated; light covering of dark setae on palps. Proboscis yellow/brown (♀♀) to pale yellow (♂♂). *Thorax*: Cluster of long, dark setae on supra-alar region. Shorter, finer setae on post alar area. Laterotergite with 2/1 small setae (0-7); sometimes with unequal numbers of setae on each side. Scutum with medium yellow/brown shading. Pleura (encompassing laterotergite, anepisternum, anepimeron and katepisternum) medium to dark brown, crevices between sclerites slightly lighter. *Legs:* Coxae white to pale yellow, darkening to dark brown at apices, more extensively so on hind coxa. Dark hairs covering about one quarter of each coxa, predominantly at apices and on ventral surfaces. Other segments of legs yellow to brown. Fore basitarsus 1.5 times length of fore tibia (♀♀ 1.1x); mid basitarsus 1.1 times length of mid tibia (♀♀ 0.77x); hind basitarsus 0.71 times length of hind tibia (♀♀ 0.77x). *Wings*: Shading covering entire wing with only a fainter basal patch. Halteres pale yellow basally, brown apically with fine hairs. Campaniform sensillae located on ♀♀ wings as follows: 2 on R_1, 2-4 on Rs, and 1-3 on R_5 (beyond r-m) (♀♀ 1-3: 2-5: 1-3). *Abdomen*: External genitalia yellow/brown. *Eggs*. 0.42 x 0.36 mm, orange/cream coloured when deposited; darkening over time to dark red/brown. *Larva*. 3-4 cm in length in 5th instar. Larval snares <5 cm. *Pupa*. Suspended from apex of abdomen and anterior part of abdomen. Abdomen orange.

Distribution. Populations are found in rainforest gullies and along rainforest stream banks throughout the Mt Warning caldera. Colonies reach their highest numbers in one congregation at a large overhang, Natural Bridge, Springbrook National Park. Other notable colonies are in the Sprinbrook Plateau, the Border Ranges, Main Range and Tamborine Mountain (David Newell, herpetologist, Southern Cross University, Conrad Hoskin, herpetologist, Australian National University, pers. comm.). These additional populations were not surveyed for this study.

Comments. Elevated numbers of *A. flava* within rainforest colonies occur during periods of warm, wet weather (Baker 2002). The distribution of *A. flava* now includes colonies from Mt Warning (CALD5) and Nightcap National Park (CALD6). Colonies at Tamborine Mountain (TAM1), O'Reilly's, Lamington National Park (CALD4), and Kroombit Tops (samples sent from Harry Hines, Queensland National Parks) are tentatively placed in this species based on molecular evidence from two mitochondrial genes (Baker et al. 2008). The author would like to conduct a morphological examination of adults from the Kroombit Tops population to ascertain their correct placement, as a large barrier of unsuitable habitat exists between these populations. However as yet, only preserved larvae have been obtained.

Arachnocampa (*Campara*) *girraweenensis* sp. nov.

Arachnocampa girraweenensis Baker et al. 2008 (unavailable name).

Material. HOLOTYPE ♂, Australia, Queensland, Girraween National Park, South Bald Rock cave, 28°54'S, 152°01'E, 24.iii.2001, ASH/CB/DM, collected as larva, reared to adult in incubator by CB, GIRRA2#12 (deposited in QM T152149). PARATYPES. QUEENSLAND, ♀, Girraween National Park, South Bald Rock cave, 28°54'S, 152°01'E, 6.vii.2002, AR/CB, collected as larva, reared to adult in incubator by CB, GIRRA2Ri#A; 2♂♂, 5♀♀, Girraween National Park, South Bald Rock cave, 28°54'S, 152°01'E, 24.iii.2001, ASH/CB/DM, collected as larvae, reared to adults in incubator by CB, GIRRA2#1, 4-6, 8 10-11; 2♂♂, 1♀, Girraween National Park, Ramsey Creek, Underground River cave, 28°51'38.9'S, 151°55'47.3E, 6.vii.2002, AR/CB, collected as larvae, reared to adults in incubator by CB, GIRRA1Ri#1-3; 1♂, 3♀♀, Girraween National Park, Ramsey Creek, Underground River cave, 28°51'38.9'S, 151°55'47.3E, 23.iii.2001, ASH/CB/DM, collected as larvae, reared to adults in incubator by CB, GIRRA1Ri#4,8,9,11. NEW SOUTH WALES, 1♀, Bellingen Shire, Cleaver's Bridge, 30°27'S, 152°54'E, 25.iii.2000, CB/JF, collected as larva, reared to adult in incubator by CB, NNSW2#1; 3♂♂, 1♀, Barrington Tops National Park, Gloucester Tops, Sharpe's Creek Walk, trail banks near creek, 32°03'S, 151°40'E, 24.iii.2000, CB/JF, collected as larva, reared to adult in incubator by CB, NNSW4#1, 3-5; 3♂♂, 2♀♀, Washpool National Park, Washpool walk, trail banks near stream, 29°16'S, 152°22'E, 26.iii.2000, CB/JF, collected as larvae, reared to adults in incubator by CB, NNSW1#1-5. (paratypes deposited in AM, MV, QM, TM and UQIC).

The following description and measurements are based primarily on the holotype, with ranges taken from other specimens.

Diagnosis. Adult body length 8.5-11 mm (cave ♂♂), 7-8.5 mm (epigean ♂♂), 8-11 mm (cave ♀♀), 7-9 mm (epigean ♀♀); wing length 5-6.2 mm (cave ♂♂), 6-7.2 mm (cave ♀♀), 5-6 mm (epigean ♂♂ and ♀♀); antennae 4-5 mm (cave ♂♂), 2-3 mm (cave ♀♀), 3-3.5 mm (epigean ♂♂), 2 mm (epigean ♀♀). Laterotergite with 0-5 setae. bm-cu curved and angled backwards, 2-4.5 times length of m-cu (cave) (1.8-3.2x epigean) (Fig. 12E). Larvae with 10 and 11 maxillary teeth (Fig. 16D). Larval head capsule sclerotised brown, body with brown/red pigmentation beginning at anterior end, extending down 30% of lateral edges of body (Fig. 15G, H). Malpighian tubules white to pale brown. Larval snares <5 cm.

Description. *Adult.* ♂ holotype (cave) body length 11 mm; wing length cave 6.2 mm; antennal length 5 mm. *Head*: Antennae medium brown, light yellow at bases of first few flagellar segments. Scape and pedicel pale yellow. Flagellum with dense mat of brown hairs, except basal sixth of first segment. Diameter of scape 2.6 (cave ♂♂ range 2.3-2.6, epigean ♂♂ 2.2-2.8) times diameter of basal flagellar segment, in ♂♂ and 2.4-3.3 times length of second flagellar segment in cave ♀♀ (epigean ♀♀ 3-3.7x). First flagellar segment 1.4 times length of second flagellar segment (range 1.1-1.4x). Front dark brown. Face medium to dark brown with thick cluster of setae over facial carina. Palpi yellow/brown; apical segment lengthened and slightly dilated (also darker); light covering of dark setae on palps. Proboscis yellow. *Thorax*: Cluster of long, dark setae on supra-alar region. Shorter, finer setae on post alar area. Laterotergite with 3/3 dark setae (range cave ♂♂ 3, epigean ♂♂ 0-3, cave ♀♀ 1-5, epigean ♀♀ 0-4); sometimes with unequal numbers of setae on each side. Row of small setae along lateral margins of scutum. Scutum with medium brown shading. Pleura light to medium brown (encompassing laterotergite, anepisternum, anepimeron and katepisternum); anepimeron lighter (Fig. 17E). *Legs:* Coxae pale yellow, darkening to light to medium brown at apices, more extensively so on hind coxa. Long dark hairs covering about one third of each coxa, predominantly at apices and ventral surfaces. Fore basitarsus 1.4 times length of fore tibia (♀♀ 1.4x); mid tarsus 1.1 times length of mid tibia (♀♀ 0.83x); hind basitarsus 0.71 times length of hind tibia (♀♀ 0.65x). *Wings*: Halteres pale yellow/white basally, yellow/brown apically with fine hairs. Campaniform sensillae located on ♂ wings as follows: 3 on R_1, 4 on Rs, and 3 on R_5 (Fig. 12E) (♂♂ cave range 2-4: 3-4: 2-3, ♂♂ epigean 2-3: 2-3: 1-3). *Abdomen*: External genitalia medium brown. *Eggs.* Slightly ovoid. 0.56 mm x 0.48 mm, yellow/brown (virgin ♀♀ eggs). Larval snares <4 cm. *Pupa.* Suspended from apex of abdomen and anterior part of abdomen. Abdomen yellow/brown with eggs clearly visible.

Etymology. The specific name refers to the type locality of Girraween National Park, Queensland, in which the two isolated cave populations are located.

Distribution. This species is restricted to two continuously wet granite boulder caves in Girraween National Park, Queensland, extending into nearby rainforest within and around Washpool National Park (NNSW1), New England National Park (NNSW2), Dorrigo National Park (NNSW3), Barrington Tops National Park (NNSW4) and one small cave in Gloucester, New South Wales.

Comments. Morphological differences are evident between the cave and rainforest (epigean) colonies described here (including body size, colour and the number of setae on the laterotergite). However, these differences are likely to result from the environmental conditions in the habitat in which they live rather than reflect species differences. Larval snares are short despite being in a cave environment. Molecular data support *A. girraweenensis* as the sister species to *A. flava*, and link the cave populations of *A. girraweenensis* in Queensland to those in nearby rainforest, now separated by unsuitable habitat (Baker et al. 2008).

Arachnocampa (*Campara*) *richardsae* Harrison, 1966

Arachnocampa richardsae Harrison, 1966: 881.

Material Examined. HOLOTYPE ♂ bearing the label: Australia, Newnes Railway Tunnel, New South Wales. Collected as pupa 15.x.1961, adult 20.x.1961, coll. A.M. Richards (ANIC).

Other Material. NEW SOUTH WALES, 3♂♂, 4♀♀, Wollemi National Park, Newnes Railway Tunnel, 33°11'S, 150°14'E, 14.vii.2000, CB/JF, collected as larva (1♂ and 1♀ collected as adults), reared to adult in incubator by CB, SNSW1#1-4, 6-8; 2♀♀, Wollemi National Park, Newnes Railway Tunnel, 33°11'S, 150°14'E, 28.vi.2002, CB/AR, collected as larvae, reared to adults in incubator by CB, SNSW1Ri#1, 4; 3♂♂, Blue Mountains National Park, Grand Canyon Walk, rainforest canyon near stream, 33° 39′S, 150°19′E, 23.iii.2000, CB/JF, collected as larvae, reared to adults in incubator by CB, SNSW4#1-3; 1♀, Blue Mountains National Park, Grand Canyon Walk, rainforest canyon near stream, 33°39′S, 150°19′E, 28.vi.2002, CB/AR, collected as larva, reared to adult in incubator by CB, SNSW4Ri#4; 2♂♂, 4♀♀, Morton National Park, Glow-worm Grotto, overhang over waterfall in rainforest, 34°39′S, 150°29′E, 23.iii.2000, CB/JF, collected as larvae, reared to adults in incubator by CB, SNSW6#1-6.

The following redescription and measurements are based primarily on a male, SNSW1#1, from Wollemi National Park, Newnes Railway Tunnel, with other specimens measured for ranges and variation.

Diagnosis. Body length 10-11 mm (♂♂ cave), 7-7.5 mm (♂♂ epigean), 9-11.5 mm (♀♀ cave), 9 mm (♀♀ epigean); wing length 6.5-7.5 mm (♂♂ cave), 5.2-6 mm (epigean ♂♂), 6-8.5 mm (♀♀ cave), 5-6 mm (♀♀ epigean); ♀♀ cave antennae 3 mm, epigean ♀♀ 2-2.2 mm. m-cu well distal to r-m. r-m cross vein straight. bm-cu curved and 1.5-3 times (SNSW1 1.8-2.8x, SNSW6 2.3x, SNSW4 1.5-3x) length of m-cu, sloping backwards, towards wing base (Fig. 12F). m-cu sloping forwards. Laterotergite with 0-21 setae. Larval malpighian tubules light to medium brown (Fig. 15I, J). Larval maxillary teeth 9 and 10 plus lobe (cf Fig. 16A, C). Larval colouration: head capsule sclerotised brown, body with green pigmentation extending along entire length of lateral edges of body. Some brown/red pigmentation at posterior end (Fig. 15I, J).

Redescription. *Adults.* ♂ holotype body length 11 mm; wing length 7.5 mm; antennal length 5 mm. *Head*: Antennae brown, lighter at bases of first few flagellar segments. Scape and pedicel yellow to light brown. Flagellum with dense mat of brown hairs, except basal sixth of first segment. Diameter of scape 2.4 times diameter of basal flagellar segment in ♂ (2.2-3.4x). First flagellar segment 1.04 times length of second flagellar segment (1.04-1.4x). Front dark brown. Dark setae behind ridge. Face medium to dark brown with cluster of setae over facial carina. Palpi yellow to light brown; apical segment lengthened and slightly dilated; light covering of dark setae on palps. Proboscis yellow/brown (♀♀) to pale yellow (♂♂). *Thorax*: Cluster of very long, dark setae on supra-alar region and post alar area (Fig. 17F). Laterotergite with 20/21 small setae on ♂ (♂♂ 6-21, 8-17 on ♀♀) (SNSW4 ♂♂ 1-7, SNSW4/SNSW6 ♀♀ 0-3); sometimes with unequal numbers of setae on each side. Scutum with medium brown shading. Pleura medium brown (encompassing laterotergite, anepisternum, anepimeron and katepisternum). *Legs*: Coxae pale yellow, darkening to medium brown at apices, slightly more extensively so on hind coxa. Very long dark hairs covering about one third of each coxa, predominantly at apices and ventral surfaces. Fore basitarsus 1.3 times length of fore tibia (♀♀ 1.2x); Mid basitarsus 1.1 times length of mid tibia; hind basitarsus 0.66 times length of hind tibia (♀♀ 0.65x). *Wings*: Shading covering entire wing, only with a fainter patch at base. Halteres pale yellow basally (♀♀), white (♂♂), brown apically with fine hairs. Campaniform sensillae located on ♂ wing as follows: 4 on R_1, 4 on Rs, and 4 on R_5 (Fig. 12F) (SNSW1 ♂♂ 3-4: 3-5: 4-6, SNSW1 ♀♀ 3-4: 4-5: 4/7, SNSW4 ♂♂ 2-3: 2-4: 3-5, SNSW6 ♀♀ 2:3:2, ♂♂ 2: 3-4: 2). *Abdomen*: External genitalia medium to dark brown. *Eggs*. 0.55 x 0.48 mm, cream brown - red/brown (virgin ♀♀ eggs). *Larva*. 5th instar 3-4 cm in length. Larval snares <5cm. *Pupa*. Suspended from apex of abdomen and anterior part of abdomen.

Distribution. This species is found in fragmented rainforest areas from Gosford (SNSW2), the Blue Mountains (SNSW1, 3, 4) to Bundanoon (SNSW5) and Fitzroy Falls (SNSW6), New South Wales.

Comments. Initially described by Harrison (1966), the largest known colony is found in the man-made Newnes railway tunnel. This is probably due to the water seepage within the tunnel, the abundance of prey items and protection from fire. Morphologically, cave and epigean populations exhibit differences in body size and colouration. Again these differences are likely to be due to morphological plasticity rather than reflect species differences. Harrison's use of colour for distinguishing *A. flava* from *A. richardsae* can be problematic given the large colour variation within these species. The darkened malpighian tubules in the larvae of *A. flava* is a more reliable character to separate the species.

Arachnocampa (*Campara*) *gippslandensis* sp. nov.

Arachnocampa gippslandensis Baker et al. 2008 (unavailable name).

Material Examined. HOLOTYPE ♂, Australia, Victoria, Yarra Valley, Old Warburton Road, Shining Star mine tunnel, 37°46'S, 145°38'E, 12.i.2001, CB, collected as larva, reared to adult in incubator by CB, EVIC4#3 (deposited in MV). PARATYPES: VICTORIA, 2♀♀, Yarra Valley, Old Warburton Road, Shining Star mine tunnel, 37°46'S, 145°38'E, 16.iii.2000, CB/JF, collected as larva, reared to adult in incubator by CB, EVIC4#1-2; 1♀, Yarra Valley, Old Warburton Road, Shining Star mine tunnel, 37°46'S, 145°38'E, 12.i.2001, CB, collected as larva, reared to adult in incubator by CB, EVIC4#4; 1♂, 1♀, Yarra State Forest, Britannia Creek Rd, Britannia Creek cave, 37°48'S, 145°40'E, 14.vi.2002, CB/AM, collected as larvae, reared to adults in incubator by CB, EVIC3#3-4; 1♀, Yarra Ranges National Park, Peninsula Road, Goldfields Walk, Upper Yarra goldmine tunnel, 37°39'S, 145°53'E, 14.vi.2002, CB/AM, collected as larvae, reared to adults in incubator by CB, EVIC1#2; 3♂♂, 1♀, Walhalla, Long Tunnel Extended, horizontal mine shaft, 37°57'S, 146°27'E, 14.vi.2002, CB/AM, collected as larvae, reared to adults in incubator by CB, EVIC7Ri #1-4. (paratypes deposited in AM, MV, QM, TM and UQIC).

The following description and measurements are based primarily on the holotype, with other specimens measured for ranges and variation.

Diagnosis. Adult body size 10-12 mm (♂♂), 11.5-12.2 mm (♀♀); wing length 6.5-7.5 mm (♂♂), 7-8 mm (♀♀); antennal length 4.5-5 mm (♂♂), 3.2-3.3 mm (♀♀). 0-1 setae on laterotergite. m-cu well distal to r-m. r-m at 90 degrees to R (EVIC3) or anteriorly sloped slightly backwards towards the base of wing (EVIC1, 4, 7) (Fig. 12G). bm-cu 1.75-2.6 times length of m-cu, curved, and angled backwards towards base of wing (EVIC1, 3, 7) (EVIC4 bm-cu 1.3-1.4 times length of m-cu, straight, angled forwards towards apex of wing). Larval maxillae with rows of 9 and 10 teeth (Fig. 16A). Larval colouration: Head capsule sclerotised brown, body with faint brown/red pigmentation beginning at anterior end, extending down 25% of lateral edges of body (Fig. 15K, L). Intestines brown to green. Malpighian tubules white to pale brown (Fig. 15K, L).

Description. *Adult.* ♂ holotype body length 11.5 mm; wing length 7 mm; antennal length 5 mm. *Head*: Antennae brown, lighter at bases of first few flagellar segments. Scape and pedicel light yellow to brown. Flagellum with dense mat of brown hairs, except basal fifth of first segment. Diameter of scape 2.8 times diameter of basal flagellar segment in ♂ (♂♂ 2-2.9x, ♀♀ 2.7-3.1x). First flagellar segment 1.5 times length of second flagellar segment (♂♂ 1.3-1.5x, ♀♀ 1.09-1.4x). Front dark brown. Face medium brown with thick cluster of setae over facial carina. Palpi yellow/brown; apical segment lengthened and slightly dilated (also darker); light covering of dark setae on palps. Proboscis yellow/brown. *Thorax*: Cluster of long, dark setae on supra-alar region (Fig. 17G). Shorter, finer setae on post alar area. Scutum medium brown shading. Pleura sclerotised dark brown (Fig. 17G) (encompassing laterotergite, anepisternum, anepimeron and katepisternum). *Legs:* Coxae yellow, darkening to medium brown at apices, more extensively so on hind coxa. Long dark hairs covering about one third of each coxa, predominantly at apices and on ventral surfaces. Other segments of legs brown. Fore basitarsus 1.4 times length of fore tibia (♂♂ and ♀♀); mid basitarsus 1.1 times length of mid tibia (♂♂ and ♀♀): hind basitarsus 0.71 times length of hind tibia (♀♀ 0.66x). *Wings*: Halteres pale yellow/white basally, brown apically with fine hairs. m-cu distal to r-m but position variable: EVIC1 with m-cu closer to r-m, EVIC3 and EVIC7 with m-cu closer to M vein split, EVIC4 with m-cu in middle. Campaniform sensillae located on ♂ holotype wing as follows: 4 on R1, 5 on Rs, and 5 on R5 (Fig. 12G) (♂♂ 3-4: 4-5: 3-5, ♀♀ 3-4: 3-5: 4-5). *Abdomen*: External genitalia light brown with black tips. *Eggs*. Slightly ovoid. 0.5 mm x 0.6 mm, brown (virgin ♀♀ eggs). *Larva*. Larval snares <3 cm. *Pupa*. Suspended from apex of abdomen and anterior part of abdomen. Threads turn golden after pupation (although may be an artefact of the environment).

Etymology. The specific name refers to the type locality of Gippsland, Victoria, Australia.

Distribution. *Arachnocampa gippslandensis* colonies are found in rainforest and man-made mine tunnels in the Gippsland region of Victoria.

Comments. There is strong morphological and molecular support for the separation of the eastern Victorian *Arachnocampa* populations as a distinct species (Baker et al. 2008). Specimens from this species were first noted in the literature by Harrison (1966) from samples collected at Walhalla by Elery Hamilton-Smith in 1965. At that time, this population was tentatively grouped with *A. richardsae*, but without morphological examination. Recent fires (February 2009) through this region may have greatly decreased the available habitat of this species and, as such, field surveys are recommended.

Arachnocampa (*Campara*) *otwayensis* sp. nov.

Arachnocampa otwayensis Baker et al., 2008 (unavailable name).

Material Examined. HOLOTYPE ♂, Australia, Victoria, Melba Gully State Park, Madsen Track, stream and trail banks, 38°41.8′S, 143°22.2′E, 10.vi.2002, CB/AM, collected as larva, reared to adult in incubator by CB, WVIC1Ri1 (deposited in MV). PARATYPES. VICTORIA, 1♂, Hopetoun Falls, stream banks, 38°40′S, 143°34′E, 9.iii.2000, CB/JF, collected as larva, reared to adult in incubator by CB, WVIC3#I; 1♂, 1♀, Angahook-Lorne State Park, Kennett River picnic area, stream banks, 38°40′S, 143°49′E, 9.iii.2000, CB/JF, collected as larvae, reared to adults in incubator by CB, WVIC5#2-3; 1♂, 1♀, Angahook-Lorne State Park, Sheoak picnic area, stream banks, 38°33′S, 143°56′E 12.iii.2000, CB/JF, collected as larvae, reared to adults in incubator by CB, WVIC6#1-2; 1♂, Angahook-Lorne State Park, Sheoak picnic area, stream banks, 38°33′S, 143°56′E, 10.vi.2002, CB/AM, collected as larvae, reared to adults in incubator by CB, WVIC6Ri#1; 2♂♂, 1♀, Beauchamp Falls, base of waterfall and surrounding stream banks, collected as larvae, reared to adults in incubator by CB, 38°39′S, 143°37′E, 12.iii.2000, CB/JF, WVIC2#1-3; 1♂, 1♀, Beauchamp Falls, base of waterfall and surrounding stream banks, 38°39′S, 143°37′E, 10.vi.2002, CB/AM, collected as larvae, reared to adults in incubator by CB, WVIC2Ri#1-2. (paratypes deposited in AM, MV, QM, TM and UQIC).

The following description and measurements are based primarily on holotype, with other specimens measured for ranges and variation.

Diagnosis. Adult body size 6.5-8.5 mm (♂♂), 8 mm (♀♀); wing length 4.5-5.5 mm ♂♂, 5-6 mm ♀♀. Antennae 4-5 mm ♂♂, 2-2.2 mm ♀♀. 0-5 setae on laterotergite. m-cu located halfway between r-m and fork of M (well beyond r-m) (Fig. 12H). r-m straight. bm-cu curved, 2.4-3.3 times length of m-cu, sloping slightly backwards, towards base of wing (Fig. 12H). Larvae with 9 and 10 maxillary teeth plus lobe (cf Fig. 16A, C).

Description. *Adult*. ♂ holotype body length 7 mm; wing length 5 mm; antennal length 4.5 mm. *Head*: Antennae brown, pale yellow at basal end of first few flagellar segments. Scape and pedicel yellow. Flagellum with dense mat of brown hairs, except basal seventh of first segment. Diameter of scape 2.6 times (2.6-3.2x) diameter of basal flagellar segment in ♂♂ (♀♀ 2.8-3.6x). First flagellar segment 1.3 times length of second flagellar segment (♂♂ 1.2-1.3x,

♀♀ 1.2-1.4x). Front medium to dark brown. Face medium brown with cluster of setae over facial carina. Palpi very pale yellow; apical segment lengthened and slightly dilated; light covering of dark setae on palps. Proboscis pale yellow. *Thorax*: Cluster of long, dark setae on supra-alar and post alar regions (Fig. 17H). Laterotergite with 0-3 small setae (0-5); sometimes with unequal numbers of setae on each side. Medium brown shading on scutum. Pleura dark brown (encompassing laterotergite, anepisternum, anepimeron and katepisternum). Entire thorax moderately shaded (light to medium brown). *Legs:* Coxae yellow to brown, darkening to dark brown at apices, more extensively so on hind coxa. Long dark hairs covering about one third of each coxa, predominantly at apices and on ventral surfaces. Other segments of legs brown. Fore basitarsus 1.3 times length of fore tibia (♀♀ 1.1x): Mid basitarsus 0.83 times length of mid tibia (♀♀ 0.74x): Hind basitarsus 0.62 times length of hind tibia (♀♀ 0.65x). *Wings*: Halteres pale yellow basally, brown apically with small hairs. Campaniform sensillae located on ♂♂ wings as follows: 2 on R1, 3 on Rs, and 1 on R5 (Fig. 12H) (♂♂ 1-2: 2-4: 1-3, total average = 7, range 6-8), (♀♀ 2–3: 4-5: range 1-3, total average = 9, range 8-10). *Abdomen*: External genitalia medium brown. *Eggs*. Slightly ovoid. 0.48 x 0.45 mm, cream/brown. *Larva*. Larval snares <3 cm. *Pupa*. Suspended from apex of abdomen and anterior part of abdomen.

Etymology. The specific name refers to Otway National Park, Victoria, which contains many colonies of this species.

Distribution. This species is restricted to rainforest gullies and stream banks in Otway National Park, Melba Gully State Park and Angahook-Lorne State Park and adjoining private land containing rainforest, southwest Victoria.

Comments. McKeown (1935) noted the presence of *Arachnocampa* in the Otway Forest, Victoria. This population of *Arachnocampa* species remained undescribed until the current study, although previously it had been tentatively identified as *A. richardsae* (Crosby 1978). Molecular data indicate *A. otwayensis* is the sister species to *A. gippslandensis* + *A. richardsae* (Baker et al. 2008). The colouration of fresh, live larvae of this species was not recorded before they were placed in ethanol or reared to the adults.

DISCUSSION

At the time of Harrison's (1966) revision of the Australian glow-worms, the genus *Arachnocampa* was included in the Mycetophilidae. Matile (1981) subsequently separated the monophyletic *Arachnocampa* from Mycetophilidae based on seven larval characters, many taken from Edwards (1924), placing them in the family Keroplatidae.

Morphologically, *Arachnocampa* is unusual in that populations of the same species exhibit morphological plasticity depending on their habitat type. Major morphological differences are evident between populations occurring in caves and in nearby epigean habitats (e.g. *A. richardsae*: SNSW1 vs SNSW2) thus making morphological comparisons between these groups detailed and lengthy. An example of this morphological variation is that cave populations display limited pigmentation, if any, along the lateral edges of the larval body (Figs 15B-D, G, H, K, L), whereas the larvae of nearby rainforest populations are generally heavily pigmented down the entire length of the lateral edges of the body (Figs 15A, E, F, J). The darker pigmentation may simply be the result of living in an epigean environment (due to contact with sunlight), and is possibly an adaptation to escape predation as the darker colouration makes them more difficult to see on dark earthy banks and vegetation. Cave-dwelling *Arachnocampa* larvae are lighter and creamier in colouration as they have no contact with pigment altering ultra-violet light (Meyer-Rochow pers. comm.), and pigmentation is presumably not a necessary adaptation for camouflage in a dark environment. Variation in larval pigmentation between geographically close populations has made morphological identification in the larval stage difficult. Larval descriptions include both cave and epigean colony colouration differences to illustrate this plasticity. The relatively recent availability of some of the man-made 'cave' environments (e.g. mine shafts in Victoria and the Newnes railway tunnel in New South Wales) and the obvious degree of morphological variation between these colonies and nearby epigean colonies strengthens the idea that such characters are plastic within the genus. Cave populations, such as those in Girraween National Park caves (*A. girraweenensis*) and Mt Buffalo cave (*A. buffaloensis*), that now appear entirely restricted to the cave environment may begin to exhibit other troglobitic attributes, as gene-flow from epigean colonies is extremely unlikely. *Arachnocampa buffaloensis* larvae show characteristics (e.g. larval colouration, arrangement of campaniform sensillae on the larval head plate and wings, wing venation) that clearly differentiate them from other mainland Australian *Arachnocampa*. Whether this is a result of their radically different habitat type, or simply chance phenetic mutation remains to be tested.

Other characters that may be important in separating populations are largely variable between cave and rainforest populations. One of these characters, larger body size (mirrored by larger wing and antennal lengths), is evident in all cave dwelling populations and has been suggested to result from a more suitable habitat (Pugsley 1980, 1984) and greater availability of prey (Richards 1960). In southern New South Wales, an artificial cave (a railway tunnel; built between 1906 and 1907 and abandoned in 1912) (NSW National Parks and Wildlife Service 1996) has provided a relatively new habitat for one *A. richardsae* colony (SNSW1). The larvae inhabiting this tunnel exhibit a much larger body size range than nearby rainforest populations (SNSW2-6), again indicating the limited usefulness of size as a character when dealing with organisms adapted to different habitats. A newly constructed limestone replica cave on Tamborine Mountain, Queensland, now contains thousands of *A. flava* originally bred from nearby rainforest gullies. This population now exhibits markedly larger body size after only four years of breeding within the cave system (personal observations).

A correlation has been made between latitude and body size in a number of insect groups (e.g. Muscidae: Alves & Belo 2002; Curculionidae: Chown & Klok 2003; Culicidae: Sota 1994). Epigean glow-worm colonies share very similar body length ranges from north Queensland to New South Wales and as do some in Victoria (see species descriptions for body ranges). However, an increase in body size is evident in cave females, and to a smaller degree, cave males (there are fewer data available for cave males) with increasing latitude, with the largest specimens recorded from caves in Tasmania. Epigean populations near to caves also show larger body sizes, potentially due to breeding with large-bodied cave glow-worms within the same species (e.g. *A. gippslandensis*). This increase in body size may be attributed to decreased temperatures in caves rather than a direct link with latitude. Decreased temperatures increase larval development times, thereby making food resources available for longer periods. This hypothesis has been tested in weevils and correlations were found between relatively aseasonally situated colonies and increased body size (Chown & Klok 2003). As larger caves have a relatively constant temperature due to thermal inertia (de Freitas & Schmekal 2003), this theory may also apply to the large limestone Tasmanian caves occupied by *A. tasmaniensis*. Further studies utilising morphometric analysis are recommended to identify possible factors driving the observed morphological variations.

All the newly described species share the same basic biological attributes in relation to snare building and maintenance (refer to Baker & Merritt 2003 for description of this behaviour). Differences occur in the length of the snare, but again, this is more likely an artefact of the environment in which they live. Cave environments inhabited by *Arachnocampa* are less exposed to wind turbulence and therefore snares can reach lengths of 20-40 cm without tangling. In contrast, epigean *Arachnocampa* are usually exposed to many weather related factors which combine to ensure snare lengths are short.

The cohabitation of this group in both cave and epigean environments presents an interesting model system for studying the transition of a troglophilic species to a troglobitic species. There have been many theories as to how this transformation occurs (see Holsinger 2000 for a review). For example, some authors believe that founder epigean individuals happen upon subterranean habitat and adapt to this environment. Other theories suggest species exhibit pre-existing characteristics that enable them to flourish in this new environment. If any, the second scenario appears more likely for *Arachnocampa*. For instance, their reliance on a constantly humid environment, their need for darkness to attract prey (with their bioluminescence) and their need for slow air movement for long snare building are examples of how a subterranean environment could provide a particularly suitable habitat. The species are equally adapted to rainforest or cave habitats. However, it is the cave habitat that often provides the prerequisites for colonies to reach very large numbers (i.e. the increase in overhang space for larval snare building).

Living in darkened environments, it is likely that species recognition is based on adult pheromone attraction and therefore future species identification for this genus may involve cuticular hydrocarbon analysis. Population level molecular analysis is recommended to ascertain historical gene flow between populations. In this area, microsatellite analysis may provide useful answers to further species identification in this genus.

ACKNOWLEDGEMENTS

This research is an outcome of a PhD project funded by the Sustainable Cooperative Research Centre, established by the Australian Government. Additional funding for the project came from Australian Geographic, Xenogen Coporation Pty Ltd, ABRS, JPT Tour Group (National Tour Company), Aries Tours Pty Ltd, Forest of Dreams and Queensland National Parks Service.

I would like to thank Greg Daniels, Jeff Skevington, Patrice Bouchard, Christine Lambkin and David Yeates for consultations regarding dipteran taxonomy; Susan Wright and Chris Burwell from the Queensland Museum for assistance with specimen deposition and Anthony O'Toole for providing the SEM photographs. Josh Fartch assisted with the figures. Mark Gahan, Kirsten Scott, Dan Pedersen, David Merritt and David Yeates provided helpful comments on the manuscript. Thanks must also go to those who assisted with surveys, collections or sent samples to me. These people include: David Chitty, Arthur Clarke, Neil Collinson, Michael Driessen, Lee Etherington, Bill Goebels, Harry Hines, Ian Houshold, Deb Hunter, Bevan Jenkins, Alison Marion, Lloyd Oldfield, Ian Roche, Andy Spate, Dave Smith and Gary Summers.

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Revision of *Flindersichthys denmeadi* Longman 1932, a marine teleost from the Lower Cretaceous of the Great Artesian Basin, Queensland

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Citation: Bartholomai, A. 2010 03 15. Revision of *Flindersichthys denmeadi* Longman 1932, a marine teleost from the Lower Cretaceous of the Great Artesian Basin, Queensland. *Memoirs of the Queensland Museum — Nature* 55(1): 43-68. Brisbane. ISSN 0079-8835. Accepted: 20 January 2009.

ABSTRACT

Prepared and naturally exposed specimens of the large, fossil teleost, *Flindersichthys denmeadi* Longman, 1932, in the collections of the Queensland Museum, form the basis of a revision of this relatively common, carnivorous, Lower Cretaceous (latest mid to late Albian) marine fish. Originally described from a single specimen, this larger sample has enabled the skeletal morphology of the taxon to be amplified and, where necessary, clarified. *Flindersichthys* has been referred to the Order Elopiformes within the Superorder Elopomorpha but is considered *incertae sedis* at familial level. Nearly all referred specimens have been derived from marine sediments of the Toolebuc and Allaru Formations in the northern part of the Eromanga Basin, part of the Great Artesian Basin but rare occurrences are recorded from the Normanton Formation in the Carpentaria Basin. The morphological description remains incomplete, especially in the post-cranial area, with the material studied being almost exclusively cranial or from the very anterior of the body. ☐ *Teleostei, Elopomorpha, Elopiformes, Flindersichthys denmeadi; Lower Cretaceous (latest mid to late Albian); Great Artesian, Eromanga and Carpentaria Basins; Toolebuc, Allaru and Normanton Formations; Euroka Arch.*

Lower Cretaceous (latest mid to late Albian) marine sediments of the Great Artesian Basin in central Queensland, Australia, have long been the source of a rich suite of fossil vertebrates and invertebrates. The earliest described vertebrate taxa were identified in Etheridge (1872) and the fauna is now known to include a range of marine fishes comprising both chondrichthyans and osteichthyan actinopterygians, together with numerous marine reptiles and even terrestrial vertebrates that were washed or carried out into the epeiric sea or which died and were preserved in littoral or deeper water situations. Among the actinopterygians already recorded, Bartholomai (1969) has revised the pachyrhizodontid teleost, *Pachyrhizodus marathonensis* (Etheridge Jnr. 1905) and later (Bartholomai 2004) he revised the aspidorhynchid, *Richmondichthys sweeti* (Etheridge Jnr. & Smith Woodward 1891). The ichthyodectiform, *Cooyoo australis* (Smith Woodward 1894) was revised by Lees & Bartholomai (1987), while a probable neoteleost, *Dugaldia emmelta,* was described by Lees (1990). Kear (2007) added the pachycormid, *Australopachycormus hurleyi* Kear from the Toolebuc Formation near Boulia in the north-west of the Eromanga Basin portion of the Great Artesian Basin.

The current study represents a continuation of work on this latest mid to late Albian fish fauna. It is almost exclusively based on a review of exposed and acetic acid prepared specimens in the collections of the Queensland Museum, mostly those added over the last few decades through field work by the author, his research assistant Ms Tempe Lees (retired), other staff of the institution, especially Mr Terry Tebble, Senior Preparator (retired) and through donations by members of the public,.

Almost all the fossil fish referable to *Flindersichthys denmeadi* have been derived from the marine Toolebuc Formation (with less from the Allaru Formation) in the northern Eromanga Basin, the largest part of the Artesian Basin. Indeed, no material referable to *Flindersichthys* has yet been discovered from the Eromanga Basin away from the inflow area across and below the basement Euroka Arch south of the current Gulf of Carpentaria and in the nearby Hughenden- Richmond area of north-central Queensland. Rare occurrences do occur further north of the Euroka Arch, within the Carpentaria Basin, from near Weipa, Cape York and at the Little Bynoe River crossing, in marine sediments interpreted as the Normanton Formation. Dating of the Toolebuc Formation as latest mid to late Albian is based on its correlation with the *Pseudoceratium ludbrookiae* dinoflagellate zone and the upper *Coptospora paradoxa- Phimopollenites pannosus zone* (Moore et al. 1986; McMinn & Burger 1986). A more refined age of early Late Albian for the Toolebuc has been suggested by Henderson (2004), based on ammonite and nannofossil biostratigraphy, with the Formation being no older than the upper *Prediscosphyraera columnata* zone and no younger than the *Mortoniceras inflatum* zone. However, the less precise age has been applied in the current work. The Toolebuc contributes only some 5-35 m of the total ca.2 km thickness of Lower Cretaceous marine sediment in the Eromanga Basin. The Allaru Formation deposited conformably on the Toolebuc is much thicker than the Toolebuc but is also considered to be of Late Albian age, again within the *P. pannosus* zone (Burger 1986). The Normanton Formation is generally regarded as having been deposited during the early Cretaceous.

Marine incursions into the Great Artesian Basin during the Lower Cretaceous were relatively short lived. Surface expression of the sedimentary deposits is extensive but poor because of extremely shallow dips and low topographic elevation. These physical characteristics have resulted in deep weathering and limited exposures through erosion of the predominant Toolebuc facies, viz. coquinite and organic-rich shale (Henderson 2004). Fortunately, many of the fossils found at the surface exist as the nucleus around which calcium carbonate was deposited within the sediments, creating hardened calcareous concretions. These appear to be related to the coquinite units and are often exposed on the surface by deflation or are concentrated in such gullies and streams as are rarely encountered. More complete teleost skeletons, not covered by concretionary structures, have been discovered in the coquinite units during recent excavations by the Kronosaurus Korner Museum, Richmond (Stumkat, *pers. comm.*).

The fossil fish remains in the current study are therefore predominately of cranial specimens preserved in concretions, occasionally including partial skeletons that are mostly of the anterior of the body. Scattered, disarticulated material is present and there are very rare instances where more complete skeletons have been encountered. Most species, including *F. denmeadi,* are represented by large to very large individuals. The occasional presence of more complete skeletons and identification of new taxa, regardless of the completeness of the material, encourages the continuation of further exploration, as does the presence of masses of disarticulated bones of very small individuals that are occasionally found in the coquinites at the surface. Small actinopterygians have also been encountered rarely in cores recovered from depth in the sequence (e.g. Parfrey, 1990).

The fossil fish fauna in general has come from the arc of sediments stretching from near Hughenden, in the northeast of the Eromanga Basin westwards through and above Richmond and Julia Creek and then down to beyond Boulia, in the northwest of the Eromanga Basin. The age attributed to the fauna suggests it has the potential to add to a better understanding of early teleost radiation in the oceanic and near-oceanic waters off the dispersing Gondwanaland tectonic plates. Unfortunately, Lower Cretaceous (Aptian) sediments from within the Great Artesian Basin have limited fossil fish records. Specimens from above and close to the Euroka Arch duringthe later Toolebuc-Allaru times must have had ready access to tidal, oceanic waters from the north, with the majority of fish finds continuing around the north and northwest of the Eromanga Basin, in keeping with a suggested anti-clockwise current flow within the epeiric sea. Glikson & Taylor (1986) concluded that the Euroka Arch intermittently restricted the area south of the Gulf of Carpentaria and that facies changes show that the eastern side of the entry strait across the Arch, from which a concentration of fossil fishes has been located, was shallow for a greater distance from land than usual. The entry was partially blocked by the N-S St. Elmo Structure towards the west. Depositional conditions in both Toolebuc and Allaru times are discussed in Wade (1993), as well as in Henderson (2004).

ABBREVIATIONS USED IN TEXT FIGURES

ace	anterior ceratohyal
ang	angular
ao	antorbital
apal	autopalatine
art	articular
asp	autosphenotic
bh	basihyal
boc	basioccipital
brr	branchiostegal ray
bsp	basisphenoid
cl	cleithrum
de	dermethmoid
den	dentary
df.	dilatator fossa
dhh	dorsal hypohyal
dpal.	dermopalatine
d.pl	dental plate
ecp	ectopterygoid
enp	endopterygoid
epo	epiotic
exo	exoccipital
fahm	hyomandibular facet
fica	foramen for internal carotid artery
fm	foramen magnum
foa	foramen for orbital artery
fr	frontal
fsp	foramen for occipital nerve
fuv.	fused vertebral centrum
hm.	hyomandibular
ic	intercalary
io	infraorbital (1-5)
iop.	interoperculum
l.e	lateral ethmoid
mes	mesethmoid
mpt	metapterygoid
m.s.c	mandibular sensory canal
mx.	maxilla
op	operculum
ors	orbitosphenoid
ot.s.c	otic sensory canal
pa	parietal
par.	parasphenoid
part.p	postarticular process
pce	posterior ceratohyal
pcl	postcleithrum
pec f	pectoral fin
pmx.	premaxilla
pop	preoperculum
pro	prootic

pro.ic	prootic-intercalar bridge
psp	pterosphenoid
ptf	post-temporal fossa
pto.	pterotic
ptfc	posterior opening of pars jugularis
ptt	post-temporal
qu	quadrate
rart	retroarticular
scl	supracleithrum
sc pl.	sclerotic plate
smx	supramaxilla (1-2)
so.	supraorbital
soc.	supraoccipital
soc sp	supraoccipital spine
sop	suboperculum
so.s.c.	supraorbital sensory canal
stt	supratemporal
sy.	symplectic
tpbh	basihyal tooth plate
vhh	ventral hypohyal
vo	vomer
I.	foramen for olfactory tract
II	foramen for optic tract
VIIhm.	foramen for hyomandibular trunk of facial
VIIot	foramen for otic branch of facial
IX.	foramen for glossopharangeal
X	foramen for vagus

SYSTEMATIC DESCRIPTIONS AND DISCUSSIONS

Division Teleostei

Superorder Elopomorpha

Order Elopiformes

Family *incertae sedis*

Discussion. Reference of fossil taxa within an acceptable Linnean classification is problematical in most instances for those that, in the fauna are shown to possess generalised elopomorph characters. Forey et al. (1996) indicate that the elopomorph fishes, including those referable to the Order Elopiformes, have a rich but patchy fossil record extending back to the Lower Cretaceous (Valanginian) and even to the Upper Jurassic (Kimmeridgian) where *Anaethalion* is concerned (see Forey 1973), considerably earlier than the marine Lower Cretaceous (Albian) sediments from which *Flindersichthys* has been recorded. However, these authors acknowledge the generalised features of many elopomorph fossils that result in their relegation as *incertae sedis* at various ranks and conclude that a number of older taxa traditionally referred to the Elopiformes should be regarded as Elopomorpha *incertae sedis*. Nonetheless, it has been considered reasonable to adopt a less conservative position in regard to the present taxon (see below).

It has been felt prudent to maintain an *incertae sedis* status for *Flindersichthys*, at the familial level, rather than to refer it to the Family Megalopidae, action taken by Taverne (1999) in regard to the somewhat similar elopiform, *Arratiaelops*, from the Lower Cretaceous Wealdon of England and Belgium.

Flindersichthys Longman, 1932

Flindersichthys Longman, 1932: 89; Taverne, 1999: 91-3.

Generic Diagnosis (emended). A very large elopiform with prognathous lower jaw, reaching in excess of 1.25 metres in total estimated body length. Neurocranial roof moderately broad, slightly depressed posteromedially. Maximum depth of neurocranium at occipital region. Orbit relatively small. Dermethmoid laterally with prominent, elongated, posteroventral processes and broad, medial, dorsal ridge, terminating in elevated opening above anterior of elongate, interfrontal fontenelle. Rostral absent. Outer margin of olfactory capsule defined anteriorly by dermethmoid process and posteriorly by lateral ethmoid below and by rarely preserved, relatively small supraorbital above. Antorbital present. Nasal plate-like. Parietal subovate but sometimes squarer anteriorly, longer than broad. Supraoccipital with strong posterior spine. Dilatator fossa elongate, anteriorly deep, shallow, partially roofed along its entire length by the pterotic, reduced posteriorly by prominent, curved ridge forming roof of hyomandibular facet. Strong, subparallel ridges occur longitudinally on the pterotic, parietal and the back of the frontal. Exoccipital excluded from margin of post-temporal fossa. Intercalar contributes significantly to the prootic-intercalar bridge. Autosphenotic spine extended posteroventrally into stout, lateral ridge. Descending lamina of frontal 'V' shaped, large, dished and deeply plicated longitudinally meeting anterodorsal margins of autosphenotic and pterosphenoid and posterodorsal margin of orbitosphenoid. Orbitosphenoid very large, extended dorsoventrally and anteriorly by ossified interorbital septum reaching to parasphenoid, with large, prominently walled foramen posteroventrally. Parasphenoid near planar, deepening into inverted 'Y' shape anteriorly, ventrolaterally supported to below orbit by posteriorly tapering vomerine processes. Vomer with small, multiserial, villiform teeth. Dermopalatine with larger teeth. Endopterygoid and metapterygoid very large. Maxilla extends posteriorly well beyond level of orbit. Sclerotic plates present. Circumorbital series incomplete above orbit. Jaws massive, with dentary shallower anteriorly and with relatively low coronoid process. Retroarticular not fused. A relatively extensive external part of the angular anteriorly meets the dentary and posteriorly joins with the retroarticular to produce prominent postarticular process. Mandibular sensory canal opens medially. Angular and articular contribute to articulatory cup internally, separated by prominent fissure. Gular elongate but narrow. Dentition on premaxilla, maxilla and dentary of very small, multiserial, villiform, conical teeth represented mainly by hollow, circular bases, set on expanded oral plates that often extend beyond the buccal margins. Occasional slightly larger, slightly recurved teeth occur internally. Hyomandibular with elongate process strengthened by strong, medial, angular ridge. Anterior ceratohyal very large, posteriorly deep, fenestrated towards dorsal margin. At least 14 pairs of branchiostegal rays present. Operculum and suboperculum large. Supratemporal extremely large. Ganoine present. Pectoral splint and at least 15 pectoral fin rays present. Vertebrae large, cylindrical, much shorter than high, laterally with numerous, fine, longitudinal striae.

Type and only species. *Flindersichthys denmeadi* Longman, 1932.

Flindersichthys denmeadi Longman, 1932
(Figs 1-8).

Flindersichthys denmeadi Longman, 1932: 69-97; Taverne, 1999: 91-3.

Specific diagnosis (emended). As for the genus.

Holotype. QMF2210, nearly complete skull, Flinders River, one mile east of Richmond, NCQ., from sediments now interpreted as Toolebuc Formation.

Material examined. QMF2388, partial posterior of skull and anterior of body, Hughenden district, NCQ. QMF5780, partial skull, crushed dorsoventrally, Stewart Creek, Hughenden, NCQ. QMF5798, partial skull, 'Boree Park' Station, west of Richmond, NCQ. QMF11042, posterior of neurocraium, Little Bynoe River crossing, NCQ. QMF12878, incomplete skull and body, 'Toronto Park' Station, 3 km. east of homestead in gully on ridge above creek, Toolebuc Fm., NCQ. QMF13735, QMF13736, QMF13769, QMF13797, QMF13800, QMF13804, QMF13809, QMF13811, QMF13848, QMF13888, partial skeletons, 'Dunraven' Station, nr. Hughenden, banks of unnamed branch of Stewart Creek, NCQ. QMF13720, nearly complete skull, 'Dunraven' Station, nr. Hughenden, unnamed tributary of Stewart Creek, NCQ. QMF13714, partial skull, 'Dunraven' Station, nr. Hughenden, Stewart Creek, west of Pelican Bore, NCQ. QMF13743, QMF13755, QMF13813, partial skeletons, 'Dunraven' Station, nr. Hughenden, Stewart Creek, downstream from Pelican Bore, NCQ. QMF13707, QMF13715, QMF52273, partial skull, 'Dunraven' Station, nr. Hughenden, cobble bed nr. Pelican Bore, NCQ. QMF13719, QMF13737, QMF13807, partial skeleton, 'Dunraven' Station, nr. Hughenden, Stewart Creek, upstream from junction with Soda Creek, NCQ. QMF13808, partial skeleton, 'Dunraven' Station, nr. Hughenden, Stewart Creek, upstream from Pelican Bore, NCQ. QMF15215, partial skull, 'Dunraven' Station, nr. Hughenden, NCQ. QMF13601, posterior of skull and anterior of body, 'Dunraven' Station, nr. Hughenden, at Pelican Bore, NCQ. QMF15986, partial skeleton, 'Alderley' Station, via. Hughenden, NCQ. QMF18916, skull and partial body, upper tributary of Myall Creek, 'York Downs' Station, nr. Weipa, Cape York, at 12° 40'S and 142° 22'E, mapped as undifferentiated Rolling Downs Group but most probably Normanton Fm. based on BMR Weipa 1 drill core, of Albian age, Carpentaria Basin (see Smart *et al.*, 1980). QMF52274, almost complete skull, 'Dunraven' Station, steep gully of Stewart Creek, at 20° 29.98′ S, 148° 55.5′ E, NCQ.

Formations and Age. Marine Toolebuc and Allaru Formations of Lower Cretaceous (latest mid to late Albian) age and Normanton Formation of Early Cretaceous age.

Description. A very large species with an estimated length exceeding 1.25metres and with an estimated body depth of more than 30 cm.

Neurocranium. The neurocranium is slightly less than three times as long as deep. Width of the neurocranium is often difficult to assess accurately because of distortion that is usual during preservation. However, it appears that maximum width across the occipital region, is only slightly more than across the area of the autosphenotic ridges. Maximum depth is in the occipital area. The orbit is relatively small and comprises about 17 % of the total length of the neurocranium.

The dermethmoid is a thin element forming the anterior end of the neurocranial roof. The bone is elongate, anteriorly narrow and broadest posteriorly and is constricted in dorsal view about one-third its length from the front. It is broadly 'V'-shaped anteriorly in dorsal view and anteriorly possesses a low, broad, median swelling becoming a well-defined ridge running longitudinally; this opens posteriorly through a large, slightly elevated and anteriorly directed pit at the anterior of an interfrontal fontenelle. A poorly developed groove parallels the lateral margin of the anterior point. No ethmoid commissure appears present. The front of the ethmoid area slopes posteroventrally and is sometimes separated by an unossified area from the mesethmoid below. The mesethmoid bears a maxillary facet on each side, behind the broadly pointed tip. It is possible that a further facet exists along each of the converging surfaces of the anterior point to accommodate the dorsal wing of the premaxilla. Ventral to the maxillary facet, the mesethmoid carries an articulating surface for contact with the autopalatine head. Internally, the ethmoid area appears largely cartilaginous posteriorly in some specimens. The anterior of the mesethmoid is narrowly dumbbell-shaped above the anterior of the vomer and appears to then expand posteriorly to broadly support the upper surface of that bone. A prominent, elongate, lateral process of the dermethmoid curves posteroventrally from near the middle of the dorsal margin, delimiting the anterior and anteroventral parts of the olfactory capsule. The lateral process is, in turn, sutured to the supraorbital and lateral ethmoid, towards the back and also below the lateral and posterior margins of the olfactory capsule. The dorsal surface of the dermethmoid in front of the anterodorsal margin of the olfactory capsule is shallowly indented to accommodate the front of the nasal.

The frontals make up the major part of the skull roof. Each frontal meets that of the other side along a medial, longitudinal suture that becomes interdigitated posteriorly. The lateral margin progressively widens above the lateral ethmoid. Anterior to this, the dorsal surface of the frontal is pointed to above the front of the olfactory capsule where it meets the back of the dermethmoid. It also provides the margin of the unossified, interfrontal fontenelle that variably separates the frontals anteriorly. Above the

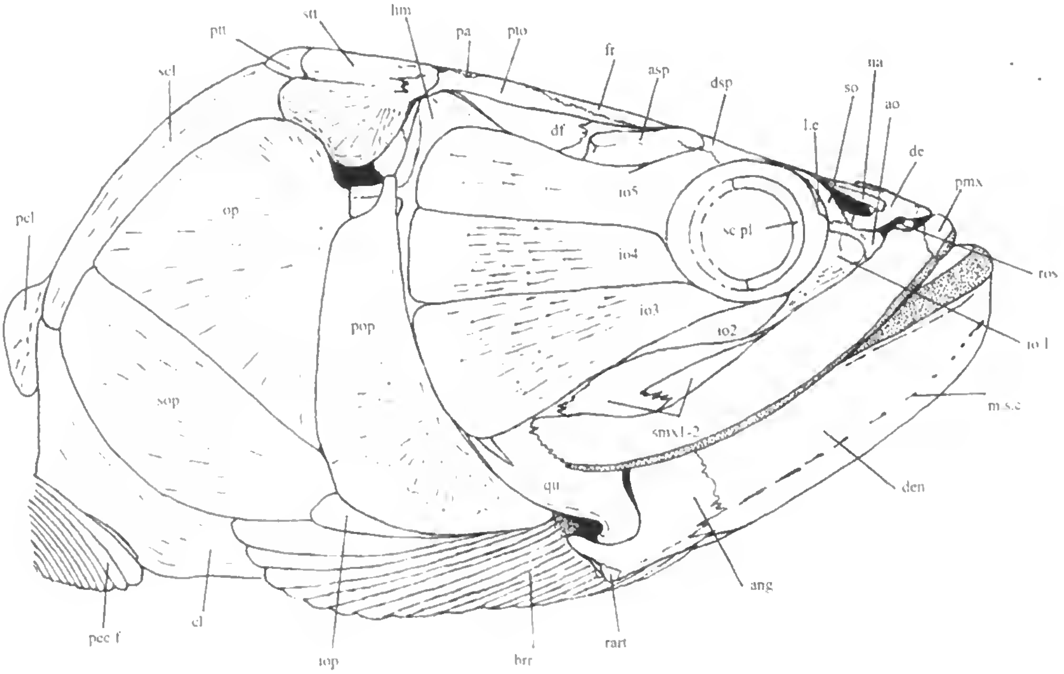

FIG. 1. *Flindersichthys denmeadi* Longman. Composite reconstruction of cranium in right lateral view; length ca. 31.8 cm.

orbit the lateral margin again expands before being gently concave for a relatively short distance, reflecting the presence of a relatively small eye. Greatest width of the frontal occurs above the autosphenotic. The frontal then narrows posteriorly to its junction with the parietal. The dorsal surface of the cranium along the medial suture is shallowly depressed in the posterior moiety but this is often accentuated by lateral or dorsoventral crushing during preservation. The supraorbital sensory canal is roofed and lies within a longitudinal ridge that extends from near the anterolateral margin behind the nasal, continuing back to the surface of the parietal. Strong subparallel, near longitudinal, subsidiary ridges emanate from above the middle of the autosphenotic and the main ridge onto the parietal while others pass posterolaterally onto the pterotic. Pores associated with the supraorbital sensory canal system occur irregularly towards the inner ends of some of the shallow grooves between the subsidiary ridges, especially posterolaterally and on the parietal. Ventrally, below the orbit, the frontal has a prominent, dished, 'V'-shaped descending lamina that is characterised by numerous, deep, longitudinal placations that often separate variable small to very small foramina. The lamina meets the dorsal part of the autosphenotic within the orbit, as well as the pterosphenoid and orbitosphenoid along its raised rims.

The nasal is rarely preserved and is only known from its anterior moiety. It is a thin, plate-like bone and carries the supraorbital sensory

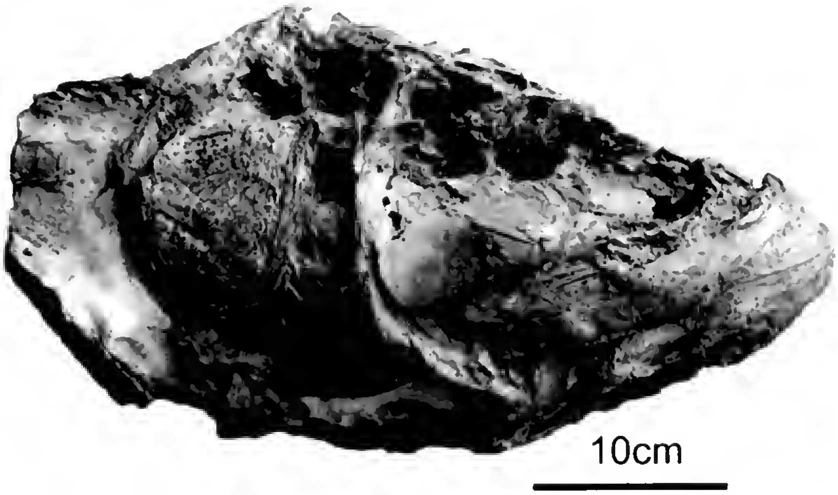

FIG. 2. *Flindersichtyys denmeadi* Longman. QMF13720, view of right side of incomplete skull (prepared by acetic acid treatment), unnamed tributary of Stewart Creek, 'Dunraven' Station, nr. Hughenden, NCQ., length 48 cm.

canal and would have covered much of the dorsomedial margin of the olfactory capsule.

No rostral element has been identified.

The parietal is a relatively small, irregularly ovate bone that is sometimes more squared anteriorly in some specimens. It is longer than broad and meets its counterpart along the midline except for a short distance posteriorly where the supraoccipital intrudes onto the dorsal surface for a short distance. The dorsal surface is ornamented by the extension of the main ridge of the supraorbital sensory canal and subsidiary ridges that are subparallel with the midline.

The posterolateral part of the skull roof is formed by the dorsal portion of the prominent pterotic. This forms the bulk of the roof of the post-temporal fossa. The posteromedial margin meets the dorsal part of the epiotic along a sinuous junction. The dilatator fossa is moderately elongate, anteriorly deep and shallow and is contributed to and partially roofed along its length by the lateral margin of the pterotic, which extends anteriorly to above the middle of the autosphenotic ridge. The dilatator fossa is limited posteriorly by a strong, obliquely anteroventrally curving ridge that excludes the fossa from the posterolateral corner of the neurocranium and forms the upper rim of the hyomandibular facet. The lower rim of the hyomandibular facet provides the roof of the relatively shallow sub-temporal fossa. Medially, the pterotic contributes to the lateral wall of the post-temporal fossa. Posteriorly, it contributes only relatively minimally to the dorsolateral margin of the post-temporal fossa external to its junction with the epiotic and above the dorsally extended intercalar. The dorsal surface of the pterotic is ornamented by continuations of the relatively strong, subparallel, subsidiary ridges, slightly angled away from the main supraorbital sensory canal ridge and pit lines from the supraorbital sensory canal are present posterolaterally.

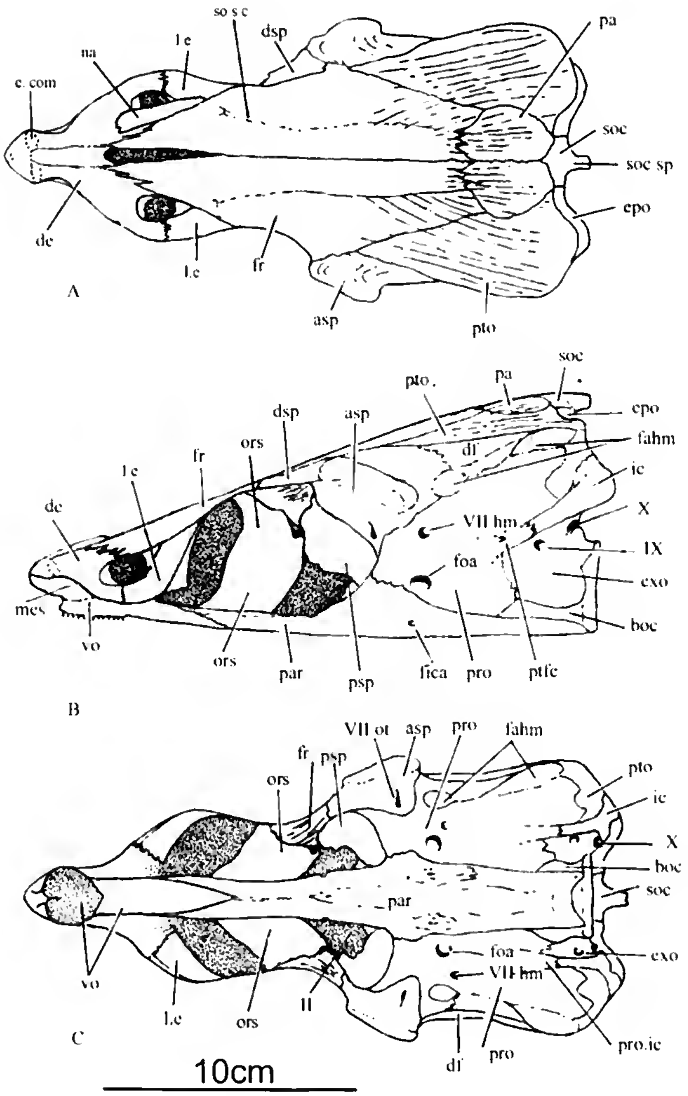

FIG. 3. *Flindersichthys denmeadi* Longman. Composite reconstructions of neurocranium. A, dorsal view; B, left lateral view; C, ventral view.

The epiotic is visible posteriorly and dorsally, the latter comprising a minor expansion along the posterodorsal margin of the neurocranial roof, together with a knob-like epiotic process development. The epiotic also forms almost all the medial margin of the opening of the post-temporal fossa and contributes to its medial wall but joins with the intercalar in excluding the exoccipital from the ventromesial margin of the post-temporal fossa. It is slightly dished across the posterior surface but not to the extent of forming a subepiotic fossa.

The supraoccipital is a relatively small bone which, posteriorly lies between the epiotics and posterodorsally extends onto the dorsal surface between the back of the parietals. It is shield-shaped in posterior view and possesses a stout, dorsomedial spine, directed posteriorly from the upper part of the posterior surface (2.7 cm long in the holotype). The bone is slightly dished across the posterior surface.

The exoccipital is excluded from contributing to the margin of the opening of the post-temporal fossa by the epiotic and intercalar. It meets its counterpart in a vertical junction above the foramen magnum but does not appear to meet below this foramen. It is dished inwards in posterior view but not developed into a definable subepiotic fossa. A small foramen is present for the occipital nerve, close to the foramen magnum. The exoccipital has a short junction with the intercalar posterolaterally and a much longer junction with the epiotic posterodorsally. The back of the lateral face of the exoccipital is not well preserved. However, a large foramen for the vagus nerve is present. Anteroventrally to this is a slightly smaller foramen for the glossopharangeal nerve. Ventrally, the exoccipital curves deeply over the dorsal surface of the basioccipital and then curves sharply anterodorsally towards and then below the anterior base of the intercalar-prootic bridge.

The intercalar forms a large cap over the posteroventral corner of the base of the opening of the post-temporal fossa. It is particularly well developed between its junctions with the exoccipital, epiotic and pterotic within the fossa. The posteroventral corner of the post-temporal fossa margin is extended backwards to form an angled knob on the intercalar to support the ventral limb of the post-temporal bone. Although the full extent of the anterior extension of the intercalar on the lateral face of the neurocranium has not been observed, a strong base for an anterior ridge is present as a significant contribution to the prootic-intercalar bridge standing clear of the neurocranial wall below the subtemporal fossa.

The basioccipital is broadly 'W'-shaped in posterior view with the central part contributing the posterior myodome. The posterior portion of the basioccipital extends dorsally to meet the exoccipital and is firmly united with a thin vertebral centrum that is often difficult to recognise as discrete in adult specimens. In younger individuals, the vertebra tapers dorsally in lateral view. Dorsally there is a short autogenous neural arch and spine but there are no pits developed to accommodate these on the dorsal surface of the attached vertebra. In lateral view, the basioccipital extends to the prootic along a near 45°, posterodorsally angled junction that reaches the anterior base of the exoccipital. The longitudinal junction with the exoccipital is broadly convex ventrally.

The prootic is imperfectly preserved anteriorly in all specimens and this may reflect poor ossification of this element. It is a relatively large bone. The lateral face is extended posteriorly into the anterior moiety of the prootic-intercalar bridge and contributes the bulk of the anterior of the relatively deep, subtemporal fossa. Foramina for the hyomandibular trunk of the facial nerve and for the orbital artery are well developed towards the anterior of the lateral face of the prootic and many small foramina are present immediately anterior to the base of the prootic-intercalar bridge. Above the base of the bridge, the junction of the prootic and exoccipital is penetrated by a foramen, believed to be for the jugular vein.

The autosphenotic is large and has an expanded anteroventral face that descends medially from a longitudinally elongated, 'ridge-like' autosphenotic spine, curving broadly then flattening below the frontal and then recurving to meet the posterolateral part of the pterosphenoid. The opening for the otic branch of the facial nerve is close to this contact. The autosphenotic also has an extensive junction anterodorsally with the back of the prominent, 'V'-shaped descending lamina of the frontal. The anterior of the hyomandibular facet is partially accommodated on the posterior of the bone.

The pterosphenoid anterodorsally has a significant, raised contact with the descending

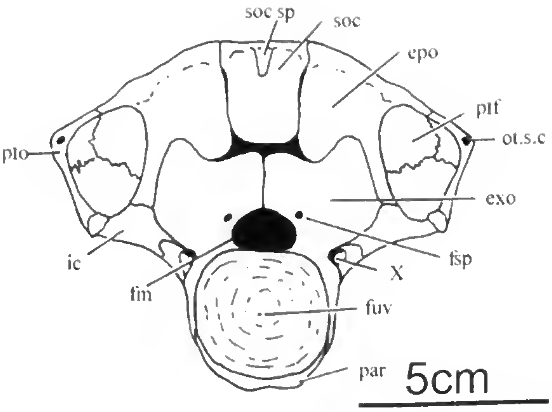

FIG. 4. *Flindersichthys denmeadi* Longman. Composite reconstruction of posterior of neurocranium.

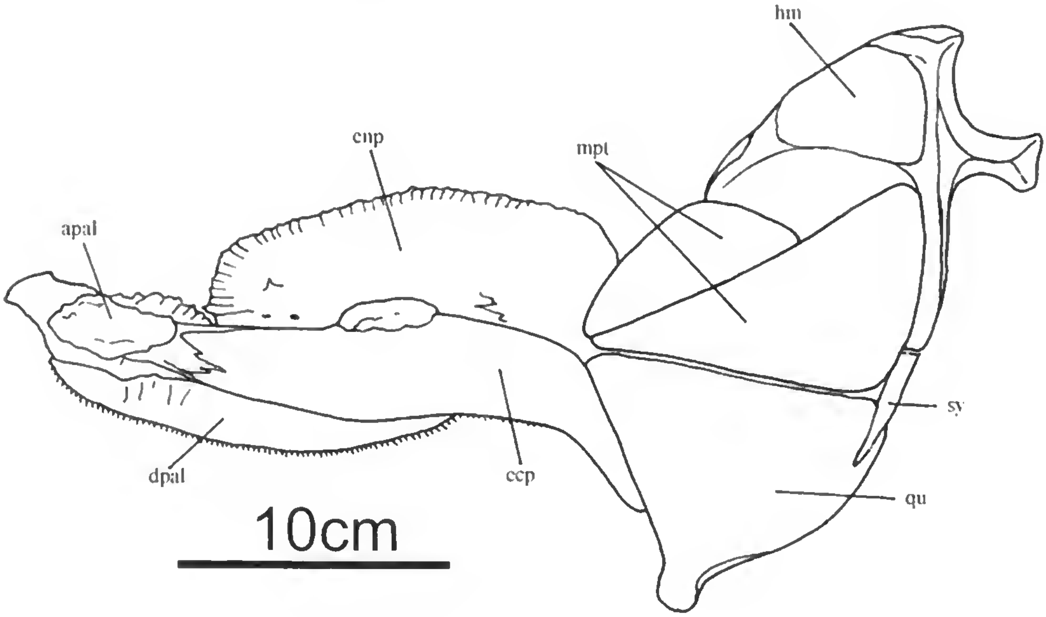

FIG. 5. *Flindersichthys denmeadi* Longman. Composite reconstruction of left hyopalatine bones in lateral view.

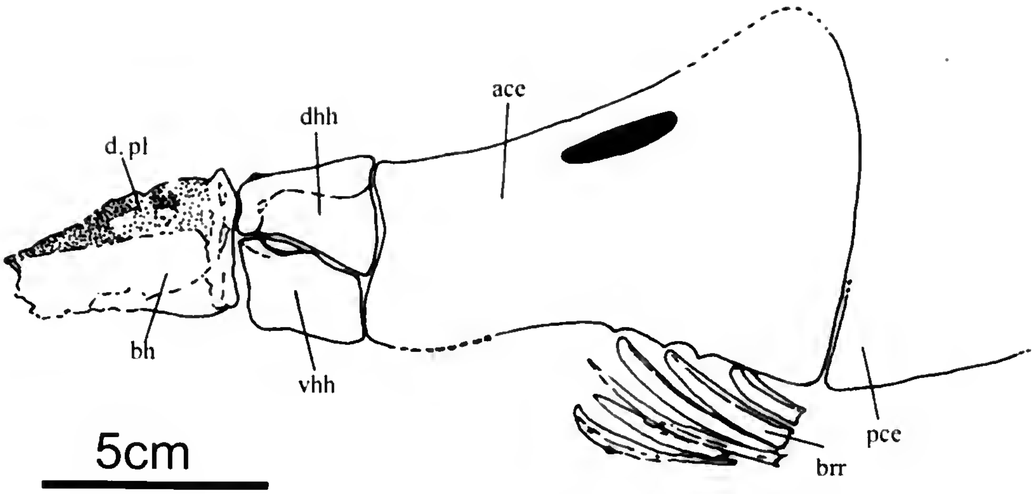

FIG. 6. *Flindersichthys denmeadi* Longman. Medial view of partial right hyoid bar and remains of anterior branchiostegal rays in QMF5798.

lamina of the frontal and a short contact with the orbitosphenoid, behind the raised wall of the large foramen at the back of that element. The bone also appears to provide a dorsal margin for the large opening for the optic tract.

The orbitosphenoid is a very large element, ventrally extending well anterior to the pterosphenoid. Posterodorsally, the bone unites with the anterior of the large, 'V'-shaped, descending lamina of the frontal along a raised rim. The dorsal part of the orbitosphenoid is laterally bulbous. An extensive, ossified, interorbital septum is present and its contact with the orbitosphenoid is sometimes deeply and coarsely interdigitated but the junction is often difficult to see. The contact is 'Y'-shaped in section and the anteroventrally angled septum meets the upper surface of the parasphenoid over an elongated contact. Posteriorly, the orbitosphenoid bears a large, foramen in front of the short junction with the pterosphenoid, surrounded by high walls around its base. The anterior margin of the orbitosphenoid is occasionally overlain by irregular flanges of bone from the lateral ethmoid.

The basisphenoid has not been identified in any specimen.

The lateral ethmoid is large and is curved anteroventrally to contact the posterior of the lateral dermethmoid process, below the anterior of the supraorbital. It also underlies the supraorbital below the back of the olfactory capsule, where it contacts the mesethmoid medially. It provides smooth anterior and dorsal upper surfaces for the front of the orbit and appears to meet its counterpart from the other side at the midline. It is sutured to the frontal posteriorly and is sometimes incompletely ossified where it meets and sometimes overlaps the anterior of the orbitosphenoid. The dorsal surface in some specimens appears to be exposed minimally between the back of the olfactory capsule, the possible lateral margin of the nasal and the supraorbital. Anteroventrally, it is terminated medial to this area by a large cartilaginous meniscus but does not otherwise meet the parasphenoid.

The parasphenoid is elongate and near planar, extending posteriorly from its contact with the vomer but is not well exposed in most specimens. It extends back to a position near the posterior rim of the basioccipital. Towards the junction with the vomer, the bone deepens dorsally assuming an inverted 'Y'-shape and is sandwiched laterally between the posterior arms of that bone. It is relatively narrow below the orbit, broadening posteriorly and forming the anterior floor of the posterior myodome. The central area is ventrally produced into a sharp, strongly developed median ridge, below the orbital area. This is reduced to a more rounded ridge anterior to the ascending wing, immediately anterior to an elevated medial foramen, presumably for the buccohypophysial canal. The bone then subdivides into two irregular and bulbous areas before reducing rapidly to reach the attached vertebra of the basioccipital. The notch between the posteriorly arms is penetrated by a large foramen leading into the myodome. The anterior of the base of each of the posterior arms is penetrated by a well defined foramen for the internal carotid artery. The posterior of the broad, ascending wing is slightly longer than the anterior and is produced dorsally. A small area of villiform teeth exists on the ventral surface of the parasphenoid below the back of the orbit in some individuals.

The vomer is incompletely exposed in all specimens. It is broadly attached to the base of the mesethmoid. It appears to have a broadened, heart-shaped dentigenous head covered with villiform teeth that are somewhat smaller than those on the dermopalatine. The middle of the toothed surface appears to have been longitudinally subdivided by an area of even smaller teeth. It extends and tapers posteriorly below the anterior of the parasphenoid and has elevated wings that sandwich the sides of the anterior of the parasphenoid.

Very large anterior sclerotic plates are present but posterior plates have been preserved only rarely.

Hyopalatine bones. The series is deeper than it is long in adult specimens, with the quadrate-mandibular articulation lying well behind the back of the orbit.

The hyomandibular is angled slightly posterior to the vertical. The head of the bone has anteriorly inclined, anterior and posterior articulating surfaces that fit into the relevant parts of the hyomandibular facet. Externally, the surface is marked by a strong ridge descending from below the posterior part of the head of the bone. Posterior to this ridge is a deep groove separating it from a short, thin posterodorsal margin above the opercular process. The opercular process is elongate and is strengthened by a sharply crested central ridge that merges with that from the posterior head of the bone. A sharp ridge curves anterodorsally from the main body of the bone, broadening to the anterior head of the bone. The anterior of the hyomandibular is expanded transversely and longitudinally into a cup-shaped surface. The area between the anterior ridge and the dorsal margin was thin, as was that ventral to the anterior ridge. The ventral limit of the main shaft of the bone appears to broadly abut the symplectic.

The symplectic is rarely seen but is elongate, curved and inclined anteriorly at approximately 45° to the vertical. It fits into a deep groove in the back of the quadrate and is partially overlain by the preoperculum over much of its length.

The quadrate is a very large, large fan-shaped bone. Posterodorsally, the back of the bone behind the deep notch for the symplectic, continues the scooped surface from the hyomandibular to accommodate the anterior base of the preoperculum. The external ridge formed by this, extends to just above the expanded condylar surface. Posterior to the condyle is a notch that probably limited the extent of the gape. The dorsal margin of the quadrate has a cartilage connection with the shallow groove along the ventral edge of the metapterygoid. Anterodorsally, the quadrate is laterally shelved to accommodate the uppermost supramaxilla.

The metapterygoid is a significant element. The thin posterior of the bone is broadly curved to fit into the cup-shaped anteroventral surface of the hyomandibular and preoperculum. It is flexed along a line approximately 30° to the horizontal that separates the bulk of the bone from a thin, anterodorsal wing that overlaps the back of the endopterygoid and part of the anteroventral margin of the hyomandibular. A partially separated, well-defined ridge is occasionally present along the flexure anteriorly.

The endopterygoid extends posteriorly to be overlapped laterally by part of the metapterygoid. The bone is thin and has a broadly convex dorsal margin. It is also shallowly curved medially along a longitudinal line. The bone is relatively deep, meeting the ectopterygoid along an elongated junction and apparently overlies part of the dermopalatine. Teeth appear to have been lacking on the endopterygoid.

The ectopterygoid is reasonably well-exposed in the holotype. It is shallow anteriorly, with a dorsolaterally developed process, presumably to support infraorbital bones. The posterior moiety of the bone is curved ventrally to meet the quadrate along the upper two-thirds of its anterior margin. The ventral margin of the ectopterygoid overlies the upper margin of the dermopalatine. The bone appears to be edentulous.

The autopalatine is ossified but appears to be edentate. It interdigitates deeply with the ectopterygoid. It is irregular dorsally and carries a large articulating surface for cartilaginous contact with the lateral ethmoid. Anteriorly, it has a strong, elongate process for additional articulations with the mesethmoid and maxilla.

The dermopalatine is plate-like and very elongate and carries multiserial, recurved teeth that were at least as well developed or even larger than the largest of the teeth on the jaws and are developed in continuity with those of the vomer. It extends anteriorly below the autopalatine to meet the back of the vomer.

Dermal upper jaw. The upper jaw extends from the tip of the snout, somewhat posterior to the anterior of the symphysis of the lower jaws, back to below the posterior of the orbit. The premaxilla is small, comprising slightly less than 14% of the total length of the upper jaw. The upper jaw is gently convex laterally over its posterior moiety, with the maxilla becoming more convex anteriorly towards the snout. Convexity increases even more around the anterior of the premaxilla. The oral border is gently sinuous in lateral view.

The premaxilla is relatively deep anteriorly, with its maximum depth equal to about 80% of its length. The bone tapers posteriorly, meets its counterpart medially and overlies the anterolateral base of the maxilla. The oral border is gently transversely curved into a plate-like structure that extends outwards beyond the line of the bulk of the external surface. The oral plate bears numerous, very small, multiserial, villiform teeth (ca. 400 per square centimeter). Nearly all have been lost n preserved specimens and are represented only by their shallow, round sockets.

The maxilla is elongate and relatively robust. Measurements for its length vary from 17.5 cm. to 25.2 cm. while maximum depth ranges from 3.1 cm to 4.0 cm. Anteriorly, the maxilla is ventrolaterally grooved to accommodate the overlying end of the premaxilla. It also extends and curves dorsomedially and is raised into a simple rounded head that would have abutted the anterolateral surface of the mesethmoid. Posterior to this articulating surface and internally, there is an emargination of the inner surface of the maxilla that together with a strong, elongate but low dorsal process for the cartilagenous attachment of the front of the palatine. The maxilla is deepest below the orbit (ca. 20% of its length) becoming slightly shallower posteriorly. However, its minimal depth occurs immediately posterior to the palatine attachment. The dorsal margin in lateral view is shallowly curved below the orbital area and is grooved dorsolaterally to accommodate the supramaxillae over the posterior moiety. The grooving does not reach the thin posterior margin, which is ornamented with a number of fine, near-longitudinal ridges. As with the premaxilla, the oral border is plate-like and is expanded laterally along its entire length as a slightly transversely convex platform that provides a base for numerous, small, multiserial, villiform teeth, largely represented by their sockets. These are circular and shallow and are present in similar numbers to those on the premaxilla. Teeth are rarely preserved but, where present, are small to very small, conical or slightly recurved and are enameled. Posteriorly, the tooth plate extends slightly beyond the lateral surface of the bone.

Two supramaxillae are present, partially overlying each other. The anterior supramaxilla is extended as a narrow spine to below the middle of the orbit. Its anterior limit is slightly overlain by a weakly developed and thin dorsal flange from the maxilla and extends only slightly more anteriorly than the overlying anterior spine of the posterior supramaxilla. The lateral face of the anterior supramaxilla bears an irregular, longitudinal, shallow groove that disappears ventrally. Posterodorsally, the bone is extended into a point set at about 60° to the horizontal that is ornamented dorsally for a short distance by an area of minor serrations. The posterior supramaxilla is a hook-shaped element whose anterior and anteroventral margins are slightly overlain by the anterior supramaxilla. The bone extends anteriorly in a narrow spine and is posterodorsally flanged and irregularly serrated at the margin to overlie the quadrate. The posteroventral expansion loosely overlies the upper margin of the maxilla and is also irregularly serrated at its margin. The dorsal part of the bone is thin and steps up abruptly to the much thicker ventral part. The longitudinal base of the step is slightly grooved and bears shallow pockets mesially.

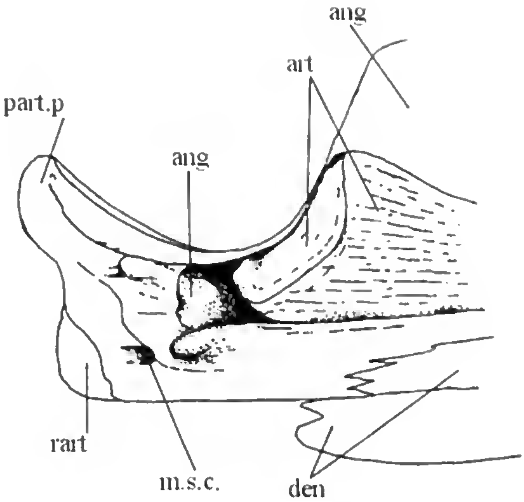

FIG. 7. *Flindersichthys denmeadi* Longman. Composite reconstruction of medial view of posterior of left mandible, mostly from QMF52273, approximately natural size.

Mandible. Regardless of the fact that the mandible protrudes in front of the premaxilla, giving the mouth an upwardly directed, prognathous gape, the total length of the lower jaw is only slightly longer than that of the upper jaw. The symphysis is relatively shallow and slopes posteriorly, giving the skull a rounded anterior outline in lateral view.

The dentary forms more than two-thirds of the mandible. The thin ventral margin is considerably inflected. The anterior of the dentary is markedly curved inwardly towards the symphysis. In lateral view, the oral margin is slightly concave and the dentary increases gradually in depth below this margin to a maximum depth anterior to a relatively weakly developed coronoid process. Teeth are borne on the surface of a transversely flattened to slightly convex oral plate. The teeth are rarely preserved but are represented by circular sockets of numerous, small, multiserial, villiform teeth. Where present, these are tiny, enamel-capped and often slightly recurved. The oral plate expands posteriorly and is generally extended beyond the lateral surface of the mandible. The plate is sometimes free of the extreme posterodorsal surface of the dentary, indicating presence of cartilage in young individuals. The longitudinal base of the lateral surface of the mandible is broadly rounded above the well defined groove that separates this surface from the expanded and inflected ventral flange. The ventral flange extends backwards over the entire length of the dentary and is deepest about one-third the distance back from the symphysis. At least nine large foramina for the mandibular sensory canal are present within the longitudinal groove in the dentary.

The posterior of the dentary laterally overlies a moderately large angular. Near the posteroventral corner of the mandible, this has a short, angled, sutured junction with the retroarticular. A well-defined groove is present immediately above the ventral margin of the angular, overlying the posterior of the mandibular canal. The angular is ornamented with relatively coarse ridges that are slightly inclined from the horizontal. Dorsally, it provides the lateral rim of the articulatory cup and extends around and higher than the posterior of the cup, being produced into a strong, extended, postarticular process. Internally, the angular and articular bones are distinct, with each contributing to the articulatory facet. The posterior, angular part of the facet is separated from the articular part by a transverse, presumably cartilage-filled fissure. The mandibular sensory canal opens medially above the retroarticular.

The retroarticular caps the posteroventral corner of the mandible. It extends anterolaterally to unite with the angular and posteriorly forms a truncated, near vertical back to the lower one-third of the postarticular process. Internally, it remains distinct and does not contribute to the articulatory facet. A small nugget of bone is present internally within the posterior surface of the mandible on some specimens and this is interpreted as an endosteal articular element. However, there does not appear to be any connection between this and the symplectic.

Circumorbital series. The circumorbital ring is poorly preserved or absent in all specimens. Dorsal components are rarely preserved and individual elements are often difficult to distinguish from underlying bones. Most, especially those in the cheek, were very thin and were generally distorted and fragmented during preservation where they were preserved.

The antorbital is present meeting the anterior base of the supraorbital. It barely reaches the anterior margin of the orbit below the lateral and posterior margins of the olfactory capsule. It is sigmoidal in shape and expands ventrally, while broadly meeting the anterior of the first infraorbital.

The supraorbital meets the antorbital towards the middle of the lateral margin of olfactory capsule and extends backwards, tapering above the anterodorsal margin of the orbit. It is a relatively small bone that also lies along the outer margin of the anteroventral process of the lateral ethmoid and the posterior and posterolateral margins of the olfactory capsule.

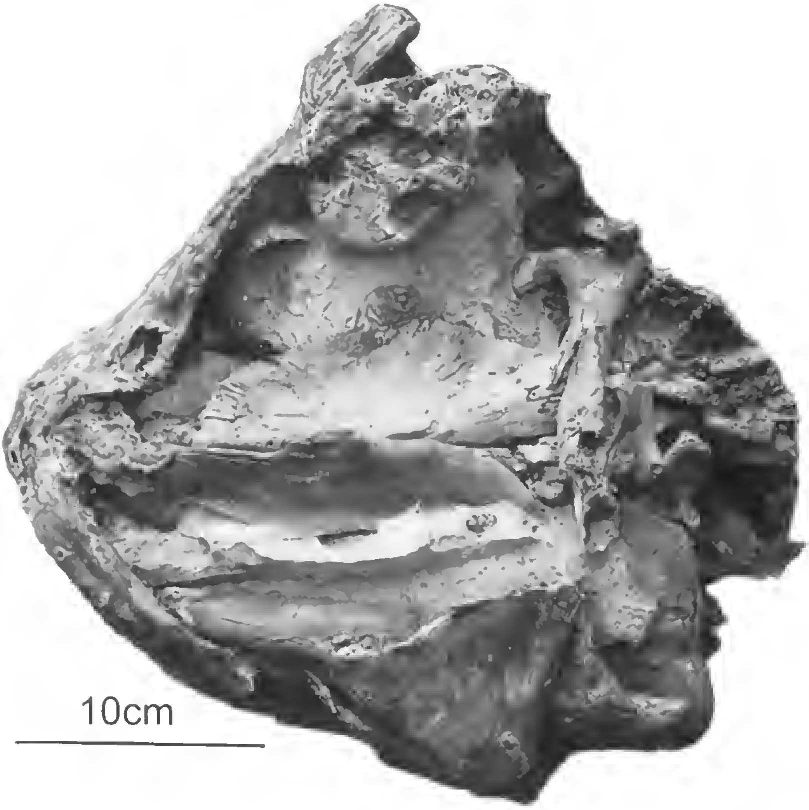

FIG. 8. *Flindersichthys denmeadi* Longman. QMF52273, view of left side of anterior of skull showing dermethmoid and olfactory capsule, anterior hyopalatine bones and remains of displaced gill arches, 'Dunraven' Station, nr. Hughenden, cobble bed nr. Pelican Bore, NCQ.

The anteroventral margin is ornamented with short digitations. Posteriorly, it does not reach the anterior of the dermosphenotic but terminates bluntly against the frontal, leaving the circumorbital ring incomplete.

The first infraorbital appears relatively well developed as an elongated sub-triangular element contributing the anterior and anteroventral margins of the orbit. It tapers posteriorly along its base and is ornamented by a number fine ridges that give the surface the appearance of a series of small, lozenge-shaped components. The second infraorbital is not well represented but appears sigmoidal in shape. It is a small bone, tapered anteriorly and posteriorly, contributing the middle of the ventral orbital margin above the anterior spines of the supramaxillae. The third infraorbital appears to have been the largest element, elongate and deep. It has a thickened anterodorsal margin that carries the infraorbital sensory canal. The fourth infraorbital is also large and provides the posterior part of the orbital margin. The fifth infraorbital is elongate and large. In lateral view it expands anterodorsally, in front of and below the autosphenotic ridge and provides the posterodorsal margin of the orbit. Foramina for the infraorbital sensory canal vary greatly in size. Those in the first infraorbital appear very small, while that in the third infraorbital is quite large with the opening supported by marginal ridges. Ornamentation of infraorbitals 3-5 is only present over part of their surfaces and comprises numerous, short ridges, subparallel to the upper and lower margins, attenuated anteriorly and thickened posteriorly. A thin covering of ganoine is present.

The dermosphenotic is a truncated wedge-shaped element and is inserted anterior to and around the front of the autosphenotic ridge and above the back of the orbit. It is penetrated by several large pores from the infraorbital sensory canal and has a rugose dorsal surface. Ventrally, it has numerous, very short, pointed projections. The anterior of the dermosphenotic is rough but did not meet the posterior of the supraorbital.

Hyoid arch, gill arches and gular plate. The ceratohyal is composed of both anterior and posterior parts, united by cartilage. The posterior ceratohyal has not been completely exposed in any of the prepared specimens and evidence for the presence of an interhyal is also lacking. The anterior ceratohyal is a very large bone, much deeper posteriorly than anteriorly. Posterior depth of the anterior ceratohyal varies from 6.5 cm to 9.6 cm. It is thickened at its anterior margin but is relatively thin posteriorly. It is strongly fenestrated close to its dorsal margin about half- way along its length.

The upper and lower hypohyals are separated from one another and from the front of the anterior ceratohyal by short gaps that would have been filled with cartilage in life. The upper hypohyal is much larger than the lower and its anterior curves medially. Its anterior margin appears thicker than its posterior margin. Several small knobs are present anterolaterally on its dorsal surface, presumably to lie against the basihyal. A foramen exists on the inner side of the upper hypohyal for the passage of the afferent hyoidean artery, although this foramen would normally be expected on the dorsal surface of the bone. The lateral surface of the upper hypohyal bears a significant foramen close to its posterior margin. A broken end of an oval-sectioned bone lies between the upper parts of the two upper hypohyals. This is probably an ossified part of the urohyal.

A plate covered with very fine rounded tooth sockets, similar to those on the mandibular and maxillary tooth plates, is present anterior to the upper hypohyals. This is interpreted as a basihyal toothplate and was possibly associated with underlying bone, interpreted as part of the basihyal. This has a posteroventral articulation to meet the processes of the hypohyals. The element appears to be about as long as the hypohyals.

Gill arches are generally incomplete and usually displaced. Those in QMF52273 are the best yet observed and are illustrated in Figure 8. It is likely that those exposed mostly represent anterior elements. They include parts of what are believed to be hypobranchials (possibly 1 and 2). Part of an anterior end of a ceratobranchial has a greatly deepened ventral flange immediately behind its articulatory end, separated from the medial body of the element by a sharply angular ridge that strengthens posteriorly up the face of the bone, broadening the dorsomedial surface. The most obvious component comprises a very large, robust epibranchial, probably epibranchial 1. Distally, this presents a large, oval socket, set at a right angle to the proximal head of the bone. It is 12 cm. long and 4.1cm. wide at its proximal end. The uncinate process is robust, short and only slightly separated by a shallow groove. A strong flange defines a deep medial groove, broadening the width of the body of the bone towards its centre. Remains of a further wide epibranchial (possibly epibranchial 2) with its uncinate process lost and lacking its distal moiety is preserved immediately posterior to the possible epibranchial 1. This has an angular anterolateral margin and is deeply 'spoon'-shaped along the medial shaft of the bone, at which point it is 2.2 cm. wide. A partial, stout, short infrapharangobranchial (possibly the first) is present above the possible epibranchial 1 and the back of the neurocranium. Numerous disassociated tooth plates bearing sockets for minute, multiserial, villiform teeth are widely distributed among the gill arch elements. No attempt has been made to reconstruct the gill arch because of the uncertainty relating to identification of the component elements.

There are at least 14 branchiostegal rays present on each side. The most anterior of these are subdivided towards their tips while the posterior rays are increasingly spathiform. At least the first five rays of the series are attached to the ventral margin of the anterior ceratohyal, which is scalloped to receive them.

The gular plate is elongate, extending posteriorly to below the articulatory cup. It is relatively narrow and bears broad, concentric, posteriorly convex ridges. Its posterior margin tapers and is marked by a central emargination.

Opercular series. The preoperculum is a large bone, with a relatively elongate, curved lower margin to below the middle of the quadrate and a more gently curved posterior margin from above the anteroventral limit of the operculum. It has a raised anterior rim. This provides a smoothly concave anterior face that is more deeply developed from about the middle of the metapterygoid to the mid-quadrate. The raised rim fits behind the raised posterior of the quadrate. The dorsal moiety of the anterior rim of the preoperculum fits and supplements the main ridge of the hyomandibular, ventral to the level of the opercular process. The preopercular ridge is ornamented by short, irregular ridges and grooves that parallel the anterior face of the bone in the upper two-thirds of the structure. The dorsal margin of the bone is extended into an elongated dorsal process lateral to the opercular process. The anterior moiety of the bone is thickened, especially ventrally and is often separated abruptly from the thin posterior of the element. At least nine foramina are present along the posterior base of this thickened anterior rim, associated with the preopercular sensory canal. The posterior of the rim is gently curved back onto the dorsolateral surface of the bone, becoming more angular ventrally. A series of minor, irregular, ridges radiate across the surface from the back of the rim, opposite the level of the dorsal limit of the quadrate.

The operculum is a large element, apparently rounded ventrally but with a prominent posteroventrally inclined demarcation above the ventral edge, set at about 40° to the horizontal. The bone articulates with the opercular process of the hyomandibular and this is achieved through a short but broad, anterolaterally and slightly dorsally directed process and facet. Below this process, the anterior margin is stepped medially to allow the back of the preoperculum to slightly overlie it. A slightly raised ridge closely parallels this step and is occasionally better developed. This appears to carry a sensory canal that opens through foramina. The surface of the operculum is ornamented by a radiating series of shallow grooves emanating from behind the articulating process and the surface is sometimes dimpled.

The suboperculum is also a large, elongate, deep element, extending slightly beyond the front of the operculum. It has a curved lower margin that is ornamented by fine ridges paralleling much broader and stronger, flattened ridges that radiate from a centre about one-third the distance from the anterior of the element. The upper one-half of the bone is occasionally somewhat rugose and is overlain to a reasonable degree by the ventral edge of the operculum.

The interoperculum appears to have been a small element.

Pectoral girdle and fin. The supratemporal is considered here, although it is not strictly a part of the pectoral girdle. It is an extremely large, thin element, extending from the back of the braincase to near the dorsal end of the supracleithrum, covering much of the post-temporal. It curves ventrolaterally to a rounded lower margin and has a bilobate posterior margin with the smaller upper lobe separated from the lower by a cleft. The supratemporal commissure is at least partially open, with several deep, longitudinal grooves running posteriorly from near the front of the upper moiety. Fine ridges paralleling the lower margins are supplemented by similar ridges radiating across the lower surface.

The post-temporal is a smaller, flat plate of bone that is slightly convex laterally. Its dorsal margin is slightly convex and posteriorly curls into a broad groove on the supracleithrum. The middle of its anteroventral margin is extended into a blunt, obtuse, triangular point separating two shallow indentations. Much of the bone underlies the supratemporal. The middle projection of the anteroventral margin has a large foramen ventrally associated with the lateral line. This opens from a roofed canal that itself opens into a groove along the margin, towards the supracleithrum. The ventral intercalary limb is acutely angled ventrally and is slightly curved ventrally but is slender, linking the bone to the back corner of the post-temporal fossa. A process to the epiotic process has not been observed. Additional foramina penetrate the lateral surface in the ventral moiety of the bone.

The supracleithrum is a very large bone that is dorsoventrally deep and slightly convex laterally, more so in the area of an extended posterodorsal process that underlies the post-temporal. In this area the bone is thin but the anterior of the bone is much thicker. The external surface anteroposteriorly is moderately convex and is extended along its front margin into a broad, convex plate that underlies the operculum and is separated by a significantly concave upper margin from the posterodorsal process. The lateral line canal is externally roofed, running obliquely across the upper part of the bone to a posteriorly directed foramen and groove at the back of the medial surface. The supracleithrum is ornamented by weak, dorsoventral ridges and a deep medial groove from near the middle of the upper part of the lateral surface.

The cleithrum is a large element that curves anteroventrally and that has a wavy external surface. A large, near vertical, roofed canal extends within a well-defined plication from a large foramen at the ventral margin. The dorsal margin of the cleithrum extends beneath the ventral part of the supracleithrum.

A moderately large, thin, postcleithrum is present behind the junction of the cleithrum and supracleithrum. This is ornamented with fine radiating ridges. Other post-cleithral elements have not been observed.

The coracoid is elongate and has a slightly concave ventral margin. It forms a sharp keel ventrally where it meets its counterpart from the other side. Between the coracoid and the cleithrum there is a large interosseous foramen. Posteriorly, the coracoid contacts the scapula laterally. Its contact with the mesocoracoid has not been observed.

The scapula spreads over the inner side of the cleithrum and encloses the scapular foramen. Support for the first of the fin rays is directly to the endochondral girdle but radial elements have not been preserved.

At least 15 pectoral fin rays are present but are only known proximally. A pectoral splint is present.

Vertebral column. No specimen in the available collections possesses a complete vertebral column. It is thus impossible to assess the number of vertebrae present. Vertebral centra are large, near cylindrical, with anterior centra circular in section and much shorter than they are deep. All are amphicoelous and pierced by the notochord. Laterally, all centra are marked by very fine longitudinal ridges, many of which subdivide or anastomose. Neural arches are autogenous and each centrum bears two deep pits dorsally to accommodate them. Anterior neural arches are expanded and bear strong, slender, straight neural spines that are separate from their counterparts and that are marked by a central groove. The centrum present as part of the neurocranium lacks dorsal pits and the first neural arch is not as expanded as those following. Parapophyses are present on all anterior vertebrae except that attached as part of the neurocranium. These are more ventral on the most anterior centra and are positioned progressively more dorsally along the abdominal part of the column.

Other skeletal elements. These are not present in the available sample.

DISCUSSION

Taverne (1999), in describing the genus, *Arratiaeiops* from the Early Cretaceous Wealden of Europe, has analysed characters that could be considered to determine the superordinal position of that taxon. Six were regarded as supportive of assigning the genus to the Elopomorpha, these being :

(1) oral dentition borne on dental plates;
(2) retroarticular fused to angular (a principal apomorphy of Elopomorpha, see Nelson, 1973);
(3) premaxillae articulate with the mesethmoid;
(4) parasphenoid has lost its basipterygoid process;
(5) hyomandibular has a long, narrow shaft; and
(6) pectoral fin has a pectoral splint.

Of these, *Flindersichthys* clearly possesses characters 1, 4, 5 and 6 and is believed to possess character 3. To these, Forey et al. (1996) additionally regarded the presence of rostral ossicles a putative character of elopomorphs but this character was not emphasised by Taverne (1999). No rostral ossicle has yet been observed in *Flindersichthys* .

Regarding fusion of the retroarticular and angular, Nelson (1973) suggested that the posterior of the primitive teleost mandible is comprised of three separate bones, the angular, the articular and the retroarticular. The Elopomorpha were regarded as derived because of fusion of the angular and retroarticular, with both elements contributing to the articularatory facet. *Flindersichthys* usually has the retroarticular separate from the angular, with the former not contributing to the jaw articulation. Only the British Museum (Natural History) specimen numbered P. 59694, illustrated by Taverne (1999) and undoubtedly referable to *F. denmeadi*, appears to have the retroarticular fused to the angular without an obvious suture, but the area of possible separation of the bones could have been obscured because of outward rotation of the oral margin of the mandible. Taverne (1999), however, states in his description that the retroarticular is fused to the angular. If this is so, then the character may be variable, reducing reliability of any suggestion that *Flindersichthys* is not an elopomorph. It is concluded that *Flindersichthys* should be included within the Superorder Elopomorpha and that early radiation within the Elopomorpha included taxa with a non-fused retroarticular.

Forey et al. (1996) concluded that the Elopomorpha contained three orders, the Elopiformes, the Albuliformes and the Notacanthiformes, with the Order Elopiformes embracing two families, the Elopidae and the Megalopidae. The Albuliformes were believed to include albulids, pterothrissids and possible stem-group Cretaceous albulids (*Osmeroides* and *Brannerion*). Again, Taverne (1999) has provided apomorphic character states for *Arratiaclops* that serve to support referral of that genus to the Elopiformes. *Flindersichthys* has generalised morphology suggesting it also is referable to the Order Elopiformes. Applying Taverne's listed character states for the elopiformes, *Flindersichthys* has a very prognathous mandible, with a deep dentary; its post-temporal fossa is large and deep; it has a large, rounded, olfactory capsule, surrounded anteriorly by a lateral dermethmoid process and posteriorly by the lateral ethmoid (at least in part); however, the mesethmoid appears to be incompletely ossified in some individuals; parasphenoid dentition is reduced; the supratemporal is very large; and the parietal is penetrated by the supraorbital sensory canal. Referral of *Flindersichthys* to the Order Elopiformes is herein proposed, but with less certainty than at the superordinal level. Although *Flindersichthys* appears to superficially resemble the megalopid elopids, it is difficult to reconcile a number of its character states with diagnoses at the familial level, as outlined by Forey (1973). For this reason, the genus is considered *incertae sedis* below the ordinal level.

Longman (1932) observed that the holotype of *Flindersichthys denmeadi*, QMF2210, had been subjected to 'considerable distortion' with the roof of the skull crushed down obliquely, displacing several of the elements. The marked, longitudinal depression in the posterior of the neurocranial roof of the holotype, regarded by him as one of the morphological characters of diagnostic importance, is re-interpreted as being emphasised by the same distortion. The sample now available shows that nearly all specimens referred to *F. denmeadi* have been distorted to some extent, reflecting the position of the body at the time of burial and preservation and the relative low strength of many of the neurocranial elements. In some, e.g. QMF13714 and QMF13719, lateral compression has resulted in the collapse of the neurocranial roof along the mid-line, giving the impression that the species in life was much narrower relative to its depth than it must have been. Other specimens (e.g. QMF12707, QMF13715 and QMF13888) were crushed dorsoventrally, artificially spreading the neurocranial elements, reducing the convexity of the skull roof and resulting in the impression of a more fusiform body shape than the animal had, in reality, during life. No specimen appears completely undistorted and the reconstruction of the skull in Figure 1 is based upon aspects of those individuals in which distortion is believed to have had minimal effect (e.g. the lateral view of the holotype, together with those of QMF13720 and QMF52274). QMF13720 is illustrated as prepared in Figure 2.

The additional material available has permitted a reassessment of the morphological characters considered by Longman (1932) to be of diagnostic significance in defining the taxon. A detailed composite reconstruction of the neurocranium in *Flindersichthys denmeadi*, based upon the holotype and referred material, is presented in Figures 3 and 4. Longman (1932) had suggested that the parietals were not separated posteriorly on the neurocranial roof. However, these elements are partially separated posteriorly by a short, anterior extension of the supraoccipital, similar to the situation observed by Forey (1973) in living *Elops hawaiensis* and *Tarpon atlanticus*. However, the parietals in *F. denmeadi* are usually relatively smaller bones. The 'oblique furrows' on the dorsal surface of the pterotic of the holotype, noted by Longman (1932), are present on all specimens studied but are variable in both strength and number from specimen to specimen and extend onto the frontal as well. The lateral spine of the autosphenotic, with its 'oblique trough' in its median surface (the anterior base of the dilatator fossa), also noted by Longman (1932), is present as a significant feature in all specimens where it is preserved but again, it is somewhat variable. Longman (1932) regarded the autosphenotic spine in *F. denmeadi* as a remarkable feature in the supraorbital region and considered it 'perhaps as distinctive as that in ... *Xiphactinus*'. Morphologically, the autosphenotic spines in these two genera are very different, with that in *Flindersichthys* being longitudinally and obliquely elongated in lateral extent and more appropriately described as an autosphenotic ridge, while that in *Xiphactinus* is distinctly peg-like (as depicted in Bardak, 1965).

Width of the neurocranial roof is quite variable, reflecting the extent and direction of the crushing that occurred during preservation, as well as the maturity of the individual at the time of death, together with intraspecific variation. Certainly, Longman's (1932) estimated width of at least 75 mm across the occipital area for the holotype, appears in error. The measure was at least 105 mm, in keeping with the autosphenotic width of 101 mm. Longman (1932) correctly noted that the autosphenotic width approximated that at the occipital margin.

The bone regarded by Longman (1932) as the suborbital plate is a part of the very expanded metapterygoid. A similar portion of a bone identified by Longman as a post-orbital plate is also part of the expanded metapterygoid, while the anterior of the bone considered by him to represent a preorbital part of the 'massive plate of bone' exposed in the cheek area is here shown to represent part of the endopterygoid. A composite reconstruction of the hyopalatine bones in *F. denmeadi* is provided in Figure 5.

The operculum in *F. denmeadi* is not sutured to the suboperculum as suggested by Longman (1932) but, as shown in Figures 1 and 2, their relationship includes ventral overlap (below an angled flexure on the operculum), with the overlap covering about 50% of the surface of the suboperculum.

Longman (1932) correctly suggested the presence of a gular plate. However, he mistook the flanged lower margins of the dentaries as part of a pair of gular plates. The single plate is narrow and elongate but is largely masked in the holotype. The holotype also exhibits parts of the anterior and posterior ceratohyals (the latter identified by Longman as an epihyal). Figure 6 is a composite reconstruction. Longman further suggested that there was a minimum of eight branchiostegal rays on each side, whereas the number is here shown to be at least 14. There is evidence on vertebral centra of the presence of a small, central perforation for a persistent notochord, a character that was considered absent by Longman (1932).

Circumorbital bones are very rarely preserved and, where present, are fragmented and distorted and difficult to separate from underlying elements. Apart from those positioned anteriorly and dorsally, they were generally very thin bones that were not strongly attached, although all were often lost before they were able to be preserved *in situ*. Those for QMF52274 are the best preserved but the reconstruction shown in Figure 1 is composite. The poor state of preservation of the base of the neurocranium, especially of the anterior of the prootic, is possibly attributable to thin bones as much as to crushing during fossilisation.

The massive expansion of the orbitosphenoid dorsoventrally and anteriorly by the ossification of the interorbital septum produces a development that parallels that of the ossified orbitosphenoid septum in some albuliformes (especially osmeroidids and albulids). This represents a significant morphological difference from described megalopids. However, *F. denmeadi* is not believed to be closely related to albuloids, differing in many characters including possession of covered sensory canals and large, sub-parallel post-temporal fossae; lack of a sub-epiotic fossa; presence of a larger intercalary and prootic-intercalar bridge;

and with the quadrate/mandibular articulation positioned well behind the orbit.

As noted above, the posterior of the lower jaw in *Flindersichthys* (Fig. 7) provides an interesting organisation of component elements. Nelson (1973) has reported on different patterns of bone fusion in this area of the lower jaws in a number of Late Mesozoic and Early Tertiary teleosts as a guide to clarifying relationships within the main groups. A prominent postarticular process of the angular bone is shown to be especially well developed in the Cretaceous forms. The articulatory facet in *F. denmeadi* is divided between two of the bones of the posterior of the mandible (unlike that in the pachyrhizodontids which Nelson records as being single and large, reflecting the fusion of the angular and articular, leaving the retroarticular separate). Nelson (1973) indicates that this arrangement in pachyrhizodontids is reflected in a medial opening of the mandibular sensory canal on the angular, more like that in the Ichthyodectiformes. An enclosed mandibular canal with the posterior opening positioned medially is a condition that Maisey & Blum (1991) conclude supports the view of Patterson & Rosen (1977) that this primitively characterises teleosts. In modern elopiform genera like *Elops* and *Megalops*, Nelson (1973) notes that the posterior part of the articulatory facet is partly separated from the articular portion by a transverse, cartilage-filled fissure and partly by the separation between the angular component and the articular bone. This is similar to the situation in *F. denmeadi* but the modern elopiforms mentioned lack the unfused retroarticular observed but possibly variable in *Flindersichthys*. It is possible that the presence of a usually separate retroarticular, medial opening of the mandibular sensory canal on the angular, separation of the angular and articular parts of the articulatory facet and the high postarticular process, as well as exclusion of the retroarticular from the articulatory facet, define presumably more primitive character states retained in some lineages within the early elopiform radiation, including that containing *Flindersichthys*.

Again as noted above, Taverne (1999) in redescribing the European Lower Cretaceous elopiform *Oligopleurus vectensis* Smith Woodward, 1890 and assigning it to the new genus, *Arratiaelops*, compared it with an incomplete skull of *F. denmeadi*, numbered P. 59694 from the collections of the British Museum (Natural History). The specimen as illustrated (Taverne, 1999, fig. 11) is somewhat distorted, with a number of elements redistributed. With access to a larger sample in the current study, it is probable that some of Taverne's morphological interpretations may not be correct. The question of a fused retroarticular and angular has been addressed above. The relatively low postarticular process, as illustrated, may also reflect outwards rotation of the oral surface of the mandible. The identity of the two fragments identified as infraorbitals 1 and 2 are difficult to determine from the drawing but differ greatly from infraorbitals 1 and 2 in the Queensland Museum specimens. The dermal upper jaw has been illustrated below the main part of the skull, while the suggested basibranchial is comparatively too elongate and is most likely part of the endopterygoid. The suggested fibrous membrane of the eye is probably from the ossified interorbital septum. The dermethmoid does not appear to present a medial ridge and a pit at the raised anterior margin to the interfrontal fontanelle. Sufficient morphological distinctions exist, especially in the circumorbital series, the hyopalatine series and the internal bones of the orbital area, having regard to Taverne's (1999) description and illustrations for *Arratiaelops*, to conclude that *Flindersichthys* is distinct.

The dentition and other morphological features in *F. denmeadi* are not dissimilar to those in a number of other Cretaceous teleosts, both elopoid and albuloid. For example, Maisey

& Blum (1991) have shown almost identical dentition in the large albuloid, *Paraelops* Silva Santos, 1971, from the Lower Cretaceous Santana Formation, Lagoa de Dentro, Chapado do Araripe, Pernambuco, Brazil, South America, described as numerous, small and conical teeth, attached to inflated bony pads extending laterally onto labial surfaces of maxilla, premaxilla and dentary. The lateral expansion onto the dentary appears to have been even greater than in *F. denmeadi*. The similarity between the dentition in such genera and the nature of their support is considered to represent synapomorphy.

The presence of small, isolated teleost vertebrae within the mouth in QMF13720 and the nature of the dentition, supports the conclusion that *F. denmeadi* was a predator of as yet unidentified smaller, shallow water marine fishes. Almost all specimens here referred have been collected from sediments deposited close to the suggested inflow /outflow point for the marine transgressions and subsequent regressions to and from the epeiric sea of the Great Artesian Basin and the Carpentaria Basin. This suggests that *F. denmeadi* was probably not able to exist comfortably at any great distance from the open oceans and, as such was probably not greatly different or was even conspecific with contemporaneous, extracontinental elopomorphs.

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A new Albian Teleost, *Euroka dunravenensis* gen. et sp. nov. and a new family, Eurokidae, from the Eromanga Basin of Queensland

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Citation: Bartholomai, A. 2010 02 15. A new Albian teleost, *Euroka dunravenensis* gen. et sp. nov. and a new family, Eurokidae, from the Eromanga Basin of Queensland. *Memoirs of the Queensland Museum – Nature* 55(1): 69-85. Brisbane. ISSN 0079-8835. Accepted: 16 January 2009.

ABSTRACT

The Lower Cretaceous (latest middle to late Albian) marine sediments of the Eromanga Basin portion of the Great Artesian Basin in Queensland, Australia continue to yield additional species of teleosts that expand knowledge of the early radiation of the Elopomorpha. The new genus and species, *Euroka dunravenensis*, is described from the Toolebuc Formation and a new family, the Eurokidae, has been created to accommodate this very specialised, large predator that has highly adapted morphological features especially those associated with the roof of its mouth. The parasphenoid and vomer are very broad to compensate for its solid, bar-like anterior hyopalatine elements. Vomerine and palatine teeth are extremely large. The lower jaw is also very strongly developed, with its lower margin recumbent and with a solid, broad, internal shelf present to further strengthen and accommodate the extent of the ventral penetration of the large teeth from the roof of the mouth. It appears that circumorbital bones may have been much reduced in number but heavy while the preoperculum was sigmoidally shaped and also robust. The neurocranium was very broadened and flattened. The taxon shows that early radiation of the elopomorphs was more complex than previously recognised. ❐ *Teleost, Albian, Eromanga Basin, Toolebuc Formation, Euroka dunravenensis, Elopomorpha, ?Albuloidei, Eurokidae.*

Among collections of teleost fishes made by the author and staff of the Queensland Museum from the Toolebuc and Allaru Formations of Lower Cretaceous (latest middle to late Albian) age in the northern part of the Eromanga Basin (a part of the Great Artesian Basin) are a number of early representatives of the Elopomorpha. These are being progressively prepared and are adding significant detail to the morphology of already identified species or are proving to represent taxa that are new to the described fauna.

Entry of oceanic waters into the epeiric sea that covered much of inland Queensland during the deposition of the Albian sediments was over the basement structure known as the Euroka Arch. This partially separated the Eromanga Basin from the more northerly Carpentaria Basin, both parts of the expansive Great Artesian Basin. The Toolebuc Formation is a thin body of sediment (much thinner than the Allaru Formation) that is especially rich in remains of marine fossils and, being widespread but poorly exposed, shows evidence for some variation in its vertebrate faunal composition from place to place. Most discoveries occur within residual calcilutite concretions located at the surface, as at localities above the Euroka Arch. However, there is increasing interest in rare exposures of the sedimentary rock itself and in quarries being worked by local authorities for road work. Discoveries of more complete specimens of several species of fish have been reported from the Kronosaurus Korner Museum, Richmond, working such quarries in its immediate vicinity in central northern Queensland.

The crushed and somewhat distorted neurocranium that is the holotype of *Euroka dunravenensis*, was prepared by acetic acid treatment from an isolated concretion, from close to the area underlain by the Euroka Arch and the referred posterior of a skull is from near Richmond. Unfortunately, no post-cranial remains have been found, other than those immediately behind the neurocranium of the holotype and it is to be hoped that future field work by the Queensland Museum or by local museums in the area will provide additional detail for this enigmatic fish.

The author wishes to acknowledge the preparation work undertaken on the holotype by his Assistant, Ms Tempe Lees and the critical review and input into the manuscript by Dr Alex Cook of the Queensland Museum.

ABBREVIATIONS USED IN TEXT FIGURES

ace	anterior ceratohyal
ang	angular
apal	autopalatine
asp	autosphenotic
bo	basioccipital
brr	branchiostegal ray
de	dermethmoid
den	dentary
df	dilitator fossa
dpal	dermopalatine
e.com	ethmoid commissure
ecp	ectopterygoid
enp	endopterygoid
epo	epiotic
exo	exoccipital
exo.ic	exoccipital-intercalar ridge
fahm	hyomandibular facet
fm	foramen magnum
fr	frontal
hm	hyomandibular
ic	intercalar
io	infraorbital
iop	interoperculum
l.e	lateral ethmoid
mes	mesethmoid
mpt	metapterygoid
m.s.c.	mandibular sensory canal
mx	maxilla
op	operculum
ors	orbitosphenoid
ot.s.c.	otic sensory canal
pa	parietal
par	parasphenoid
part.p	postarticular process
pop	preoperculum
pro	prootic
psp	pterosphenoid
ptf	post-temporal fossa
pto	pterotic
qu	quadrate
rart	retroarticular
smx	supramaxilla
soc	supraoccipital
soc sp	supraoccipital spine
sop	suboperculum
so. s.c.	supraorbital sensory canal
suf	subtemporal fossa
vhh	ventral hypohyal
vo	vomer
VII hm	foramen for hyomandibular trunk of facial
VII ot	foramen for otic branch of facial
IX	glossopharangeal foramen
X	foramen for vagus

SYSTEMATIC PALAEONTOLOGY

Order Elopiformes

Suborder ?Albuloidei

Family **EUROKIDAE** fam. nov.

Family Diagnosis. Elopiform fishes in which the skull is posteriorly very broad and very shallow. Subtemporal fossa is very weakly developed. Snout is moderately elongated and the mouth is terminal. Ethmoid commissure is incomplete. Supraorbital sensory canal does not extend onto parietal and its ridge is anteriorly shortened. Parietals are relatively small, diamond-shaped and separated posteriorly by supra-occipital. Occipital condyle is formed by basioccipital. Otic bullae insignificant. Ossified interorbital septum to the parasphenoid is elongated and very thickened posteriorly. Lateral ethmoid is relatively small but complex, with its posteromedial body firmly sutured ventrally to lateral margin of parasphenoid and posterolateral base abutting endopterygoid. Parasphenoid is edentulous and very broad. Vomer is solidly attached to the mesethmoid and locked in laterally by vertical, reciprocal, interlocking processes; it bears very large, near-conical teeth. Ectopterygoid, endopterygoid, dermopalatine and autopalatine are all very robust, united into solid bar; both palatine elements have very large, slightly incurved, conical teeth. Maxilla posteriorly carries relatively small, conical teeth, ankylosed to internal shelf and supported laterally by lateral flange. Two supramaxillae are present. Mandible is robust, strengthened by large internal shelf. Dentary deep anteriorly with ventral margin recumbent. Low coronoid process well anterior to articulatory facet. Mandibular teeth are larger than maxillary but are similarly attached; two, much larger, anterior, tusk-like teeth present. A small, robust, retroarticular is present. Gular is well developed and at least 20 branchiostegal rays exist on each side, with posterior rays very spathiform and elongated. Circumorbital series much reduced. The preoperculum is thickened anteriorly and sigmoidal in shape. Interoperculum and suboperculum are elongated and deep.

Euroka gen. nov.

Generic Diagnosis. As for the species until further taxa are defined.

Type Species. *Euroka dunravenensis* sp. nov.

Etymology. Named for the subsurface Euroka Arch above and to the south of which the holotype of the type species was collected.

Euroka dunravenensis sp. nov.
(Figs 1-8)

Holotype. QMF13766, almost complete skull, crushed dorsoventrally and posterolaterally with a degree of rolling giving it an exaggerated fusiform appearance, lacking the premaxilla, most of the maxilla and possibly some cheek bones and part of the posterior of the neurocranium, from bank of unnamed tributary of Stewart Creek, "Dunraven" Station, N of Hughenden, NCQ.

Referred Specimen. QMF12759, posterior of incomplete neurocranium, showing some dorsoventral crushing with slight anterior rotation of ventral elements and with some dorsal shedding of surface bone, from "Redcliffe" Station, ENE of Richmond, NCQ.

Formation. Toolebuc Formation of latest middle to late Albian (Lower Cretaceous) age.

Etymology. The species was named for "Dunraven" Station, N of Hughenden, NCQ, the property from which many fossil fish species have been collected.

Diagnosis. Large elopiform teleost with skull in holotype exceeding 30 cm in length and over 13 cm broad posteriorly. Neurocranial roof longitudinally flat, posteriorly broad and shallow (5.7 cm deep) and only slightly arched across occipital region, lacking strong ornamentation. Dilitator fossa shallow but very broadly roofed. Anterior of hyomandibular facet deeply pocketed and shared by both autosphenotic and prootic. Dermethmoid much broadened posteriorly

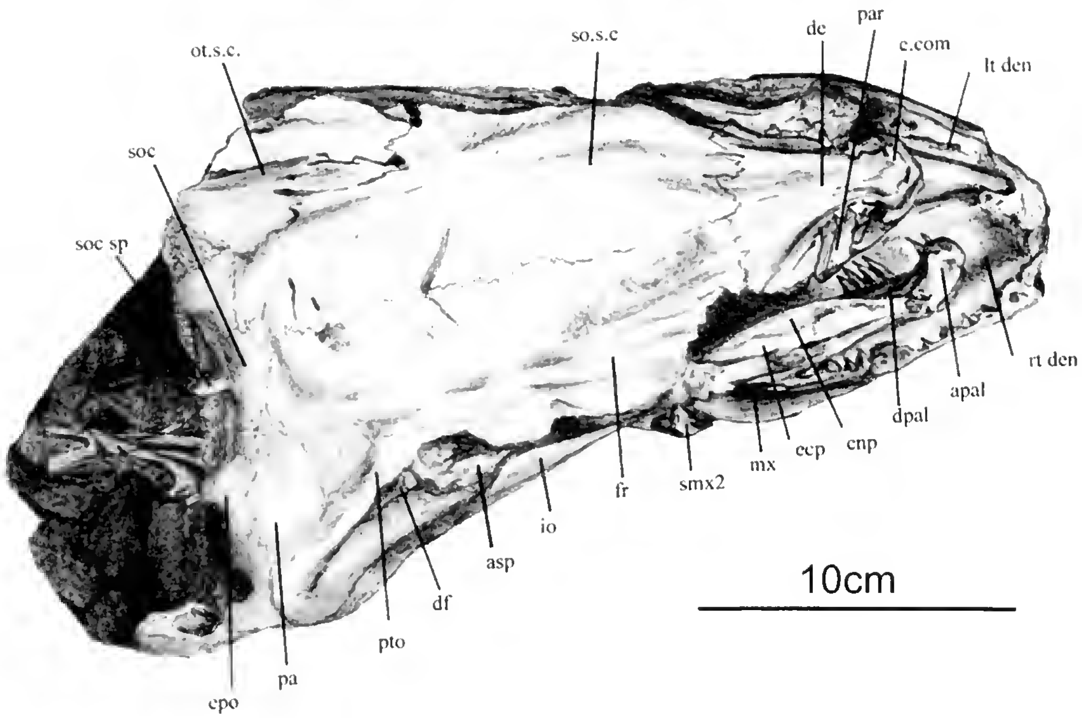

FIG. 1. *Euroka dunravenensis* gen. et sp. nov., Holotype, QMF13766, neurocranium in dorsal view.

and firmly sutured to the frontals; overlying medial body of mesethmoid and hooked over its anterodorsal surface. Mesethmoid complex, supporting robust vomer. Two large vomerine teeth present, slightly recurved and slightly longitudinally oval in section, with anterior exceeding 12 mm in length and posterior about 8 mm in length. Parasphenoid anteriorly very broad. Epiotic process weak. Supraoccipital spine relatively well developed. Angular, horizontal flexure present across exoccipitals, reducing sub-epiotic fossa. Subtemporal fossa almost non-existant, with bones on side of brain case almost horizontal. Post-temporal fossa angled anteromedially, with reduced external opening. Intercalar contributes minimally to exoccipital-intercalar ridge that terminates bluntly at exoccipital/prootic suture. Autosphenotic with weak spine and with ventral base broadly rounded; posterior face near vertical. Pterosphenoid lobate, relatively large. Orbitosphenoid with very thick interorbital septum. Infraorbitals reduced in number, with posteroventral infraorbital strong, elongated, lozenge-shaped. Quadrate / mandibular articulation below back of orbit. Two large autopalatine teeth present, with anterior 8 mm long and posterior 14 mm long, separated from from four, large, dermopalatine teeth by diastema. Anterior dermopalatine tooth 15 mm long and 7 mm in diameter. Palatine teeth round in section and slightly incurved at tips. Anterior ceratohyal elongate. Lower jaws very large, deep, basally recumbent, strengthened by broad internal shelf. Coronoid process low, well separated from jaw articulation. Teeth pointed, circular in section with tips slightly incurved and slightly larger than those on maxilla with latter up to 2.8 mm long. Mandibular teeth up to 9 mm long above rim of dentary (excluding two, larger, anterior, tusk-like teeth). Gular elongate, narrow anteriorly, broader and scalloped posteriorly between numerous longitudinal ridges.

Description. A large teleost probably exceeding a metre in total length. Neurocranium of holotype crushed dorsoventrally and posterolaterally. Sample lacks premaxilla, most of maxilla and, if ever present, most of the infraorbitals. The postcranial skeleton is largely unknown. The posterior neurocranial surface is shallowly concave transversely in dorsal view. The surface slopes anteriorly above and below a broadly angled, transverse flexure at the level of the foramen magnum at the junction of the exoccipitals with the epiotics and supraoccipital. The neurocranium is shallow in the occipital region but this still represents the deepest part of the skull. Occipital breadth in the holotype is ca. 13 cm but depth is not able to be measured. Occipital breadth in QMF12759 is 12.5 cm, while its occipital depth is 5.87 cm. Postorbital length in this specimen is 9.96 cm.

Neurocranium. The frontals and parietals make up the bulk of the longitudinally flat neurocranial roof. Transversely, the roof is only slightly convex in the occipital region. The frontals have strong, broad junctions with the dermethmoid. Each frontal carries a strong, curved, longitudinal ridge for the supraorbital sensory canal, positioned about one-half the distance from the medial frontal suture to the lateral border above the orbit. Posteriorly, the neurocranial roof is slightly depressed medially but this is probably accentuated by crushing. Above the orbit, the frontal is flattened across its sutured junction with its counterpart. The dorsal surface is only very slightly ornamented with variable ridges that originate from centres above the posterior of the orbit. Those more directly linking the centres of ossification are somewhat stronger. The anterolateral surface bears much broader, low, radiating folds from the same centres. The suture that unites each frontal and parietal is difficult to locate in the holotype but is more readily identifiable in QMF12759.

The dermethmoid in dorsal view is a large, spool-shaped, relatively simple element, much broader posteriorly than anteriorly, with a waisted section above the olfactory capsule. It is thin and anteriorly is bluntly pointed in dorsal view. Its posterior surface is slightly depressed medially, within low, anteriorly converging ridges that unite above the waisted area to form a slightly raised anteriorly surface. More sharply defined ridges are present immediately behind and above the olfactory capsule near the lateral margins of the bone, separated by shallow grooves from the inner ridges. These disappear posteriorly. The dermethmoid is bluntly pointed and overlies the body of the mesethmoid, wrapping around its anterodorsal border and contributing ventrolaterally to the upper border of a single premaxillary facet. This "hook" meets the vomer and is separated from the medial dorsal convexity of the dermethmoid by a shallow, well-defined groove that opens posteriorly on each side, separating the two longitudinal ridges on the bone. This groove is partially capped by remains of thin bone and appears to represent an incomplete, anteriorly curved, ethmoid commissure.

The mesethmoid is a complex element that appears to be fully ossified. Anteriorly, it continues ventrally from its junction with the dermethmoid, providing a shallow articulation dorsolaterally, the premaxillary facet. Ventrally, it meets and completes the anterior support for the vomer. Anterolaterally, it extends dorsally as an interlocking process, then extends posterodorsally, to underlie the back of the dermethmoid, meeting the upper surface of the vomer and anterior of the parasphenoid,. It contributes to the olfactory capsule posterventral to an interlocking, vertical arm of the vomer.

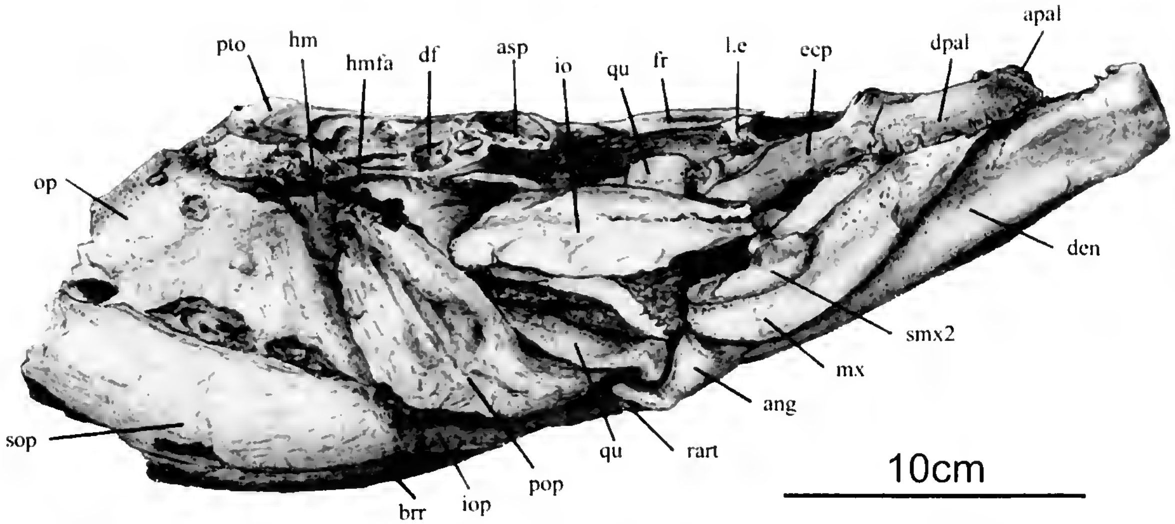

FIG. 2. *Euroka dunravenensis* gen. et sp. nov., Holotype, QMF13766, neurocranium in lateral view.

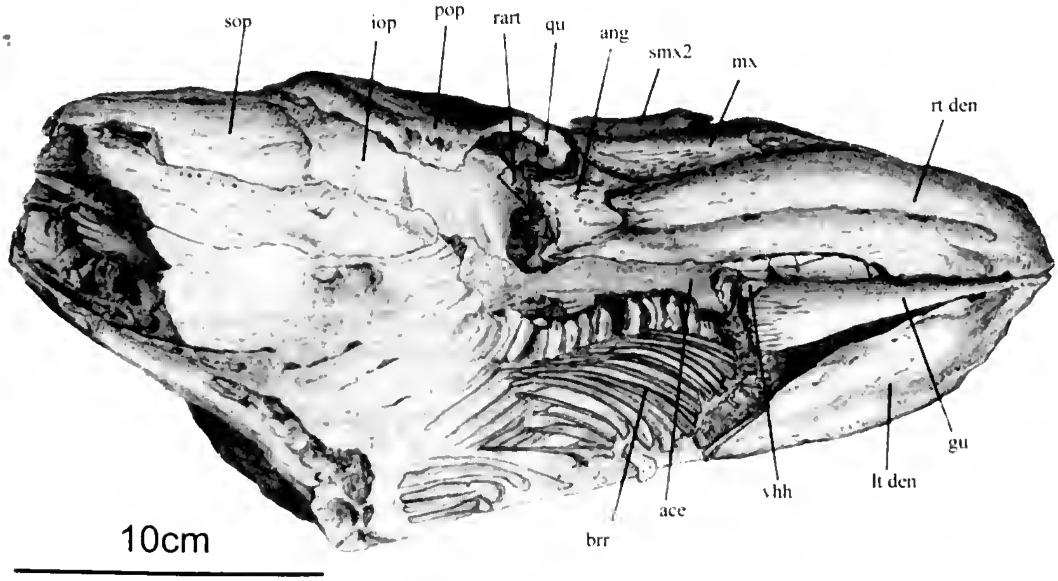

FIG. 3. *Euroka dunravenensis* gen. et sp. nov., Holotype, QMF13766, neurocranium in ventral view.

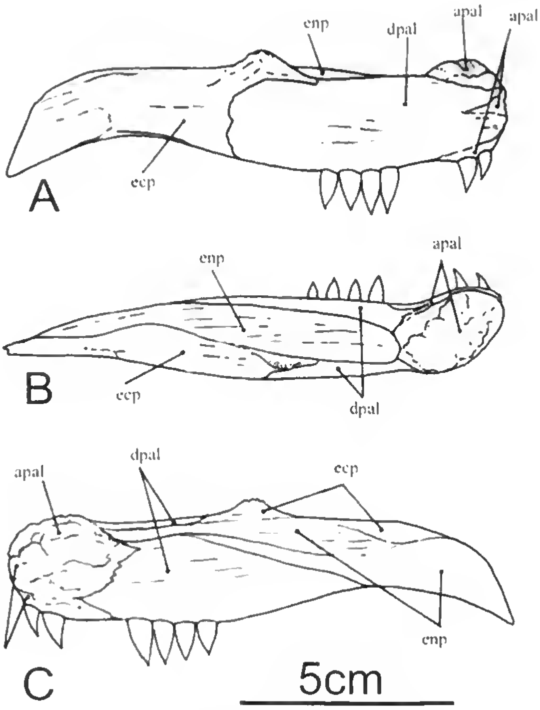

FIG. 4. *Euroka dunravenensis* gen. et sp. nov., Holotype, QMF13766, anterior hyopalatine bones. A, lateral view; B, dorsal view; C, medial view.

The parietal is a small bone, broader than it is long but its sutures with surrounding bones are difficult to define. It lies behind the posterolateral back of a depressed posterior of the neurocranial surface. A dorsal wedge of the supraoccipital separates the parietals. A continuation of the ridge on the frontal, above the supraorbital sensory canal, extends towards the parietal but does not appear to reach it. The parietal dorsal surface is relatively unornamented.

The pterotic makes up the bulk of the posterolateral part of the neurocranial roof and contributes the lateral and dorsolateral margins of the small, post-temporal fossa. Medially, the junction of the pterotic with the parietal is short. The cranium is widest at the posteroventral

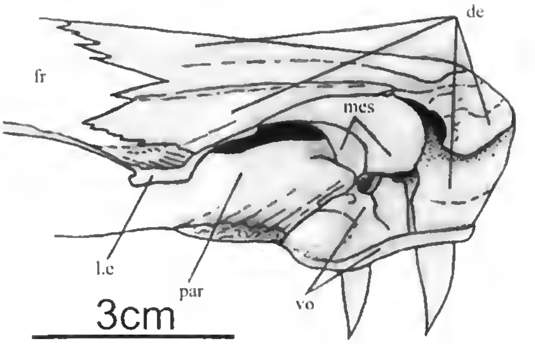

FIG. 5. *Euroka dunravenensis* gen. et sp. nov., Holotype, QMF13766, sketch of anterior of neurocranium, lateral view (premaxilla not preserved).

corner of the pterotics. The dilatator fossa is shallow and very broad and is almost fully roofed by the pterotic. The anterior of the dilatator fossa is provided by the autosphenotic. A large fenestra is present at the anterior of the dilatator fossa, penetrating medially. The pterotic also contributes the bulk of the roof of the hyomandibular facet that is separated from the base of the dilatator fossa by a strong, near-horizontal ridge. The otic sensory canal is not well defined but appears to have been covered. Dorsomedially the junction of the pterotic and parietal is short. The post-temporal fossa is well developed and angled anteromedially. Within the post-temporal fossa, the pterotic makes a broad, transverse contact with the intercalar but only just extends ventrally to form the extreme posteroventral margin of the fossa. Its longitudinal contact with the epiotic is in the base of the fossa. Posteroventrally, the pterotic is expanded and has long, sutured contacts with the intercalar and prootic.

The autosphenotic is subtriangular with a low, anterolateral shelf. Its body is tapered laterally and expanded at the tip into a reduced autosphenotic spine that does not extend beyond the margin of the neurocranial roof. The base of the spine is broadly convex anteroposteriorly and is ornamented with low ridges. Anteriorly, the face is penetrated by a foramen for the otic component of nerve VII. The posteromedial face is near vertical and forms the anterior of the dilatator fossa.

The supraoccipital is a relatively small element that is slightly transversely concave, positioned medially in the dished posterior neurocranial surface. It extends about one-half the distance from the midline to the inner margin of the post-temporal fossa. It is pocketed on each side of a moderate, posteriorly directed spine, with the pocket separated from the exoccipital by a dorsolateral ridge. The pocket extends across the back of the neurocranium onto the epiotic as a weak subepiotic fossa. The supraoccipital extends relatively broadly onto the dorsal surface of the neurocranium to separate the posterior of the parietals. It is strongly united with the epiotic laterally.

The epiotic extends laterally from its junction with the supraoccipital to near the middle of the dorsal rim of the post-temporal fossa beyond a muted epiotic process. It has greater expression on the dorsal surface than the supraoccipital. Its slightly pocketed posterior surface contributes to the poorly developed subepiotic fossa. It provides much of the dorsomedial margin and wall of the post-temporal fossa.

The exoccipital is relatively large but appears to be excluded from below the ventromedial margin of the post-temporal fossa by the epiotic and intercalar. It lies below the transverse flexure of the posterior neurocranial surface and provides the margins of the foramen magnum. It is penetrated by the foramen for the occipital nerve. It does not appear to form the floor of the foramen magnum. It curves anteroventrallyclose to the basioccipital and extends anteriorly to just behind the back of the parasphenoid. Laterally, it bears a low but major contribution to an exoccipital-intercalar ridge to the prootic. The foramen for the vagus nerve is small, beside the posterodorsal margin of the basioccipital and its junction with the exoccipital.

The intercalar is a relatively large element that caps the posteroventral, inner corner of the post-temporal fossa and extends across and dorsally to and slightly above the ventromedial part of the margin. It provides most of the posteroventral neurocranial surface, meeting the exoccipital along an elongated posterolaterally angled ridge, broadening anteromedially and contributing minimally to a low, exoccipital-intercalar ridge that terminates bluntly above the prootic-exoccipital suture. A foramen near this appears to be the opening for the pars jugularis. Laterally, the subtemporal fossa is almost non-existant.

The basioccipital forms the occipital condyle. Dorsally, it bears two deep pits for attachment of a neural arch and ventrally is deeply grooved towards the occipital condyle, at the back of the myodome, posterior to the prongs of the parasphenoid.

The prootic is large and complex. It is the largest element of the lateral neurocranial wall. Posterolaterally, it lies at only a slight angle from the horizontal and links laterally with the autosphenotic and pterotic, posteriorly with the intercalar, the exoccipital and the basioccipital, ventromedially with the exoccipital, the basioccipital and parasphenoid and anteriorly with the autosphenotic and pterosphenoid. Anterolaterally, it contributes the facet for the anterior of the hyomandibular. The shape of the hyomandibular facet indicates that the hyomandibular possessed a very broad head. A large foramen close to the ascending wing of the parasphenoid is for the hyomandibular trunk of the facial nerve. The foramen for the orbital artery is present anteromedially and close to this. The anterior face of the prootic forms much of the posterior margin of the orbit.

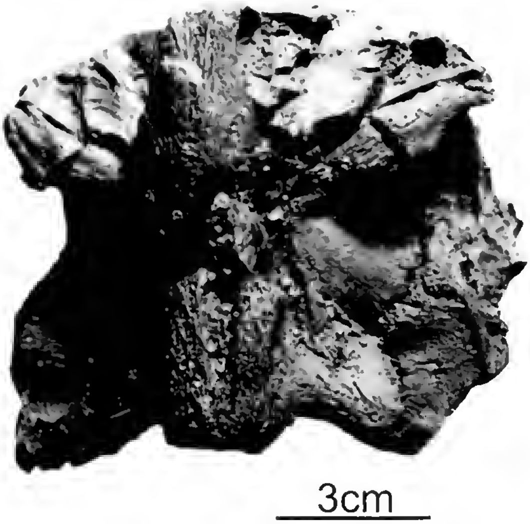

FIG. 6. *Euroka dunravenensis* gen. et sp. nov., QMF12759, ventral view of posterior of partial neurocranium.

Crushing has masked the foramina for the oculomotor nerve and the anterior opening of the pars jugularis.

The pterosphenoid is moderately large, near horizontal, being only slightly inclined anteriorly. Its anterolateral margin is rounded. Two small foramina are present towards the medial margin. The surface of the bone is plicated radially towards the lateral margin.

The basisphenoid is represented only by part of the upper arm of its broadly Y-shaped shape. This is angled posteriorly and separated from much of the medial margin of the petrosphenoid by an elongate, slit-like foramen for the optic nerve, but this has probably been narrowed by crushing.

The orbitosphenoid is represented only by its posterior margin. The dorsal attachment to the frontal is very solid and the bone has only minor penetration on each side, just above the level of the front of the pterosphenoid, possibly for passage of the olfactory tract. The orbitosphenoid is attached to the upper surface of the parasphenoid by an ossified interorbital septum that is massively solid, posteriorly almost as wide as the parasphenoid itself.

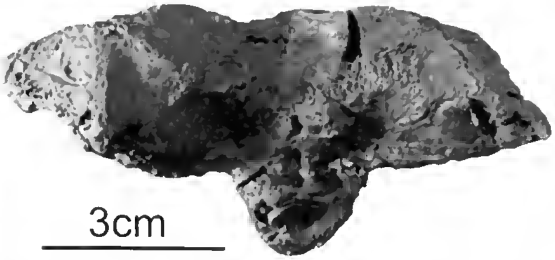

FIG. 7. *Euroka dunravenensis* gen. et sp. nov., QMF12759, posterior view back of partial neurocranium.

The parasphenoid is only partially known. It is very robust, short posteriorly, with the back produced into forked, short, thickened prongs. The ascending wings are almost non-existant and the foramina for the internal carotid arteries are present near their bases. Anterior to the ascending wings, the bone is transversely slightly convex with an edentulous but rugose surface. A medial foramen is present below the back of the orbitosphenoid, possibly for the efferent pseudobranchial artery. The lateral margin of the parasphenoid is greatly expanded, especially towards the front, greatly increasing its contribution to the roof of the mouth, compensating for the blockiness of the anterior hyopalatine elements. The extreme anterolateral margin is slightly deepened and appears to have contributed to the support for the anterior process of the dermopalatine.

The lateral ethmoid is a relatively complex element with its laterally visible body well posterior to the mesethmoid, firmly uniting the base of the frontal to the thin, upturned, lateral margin of the parasphenoid. This mesial, posteroventral projection together with the back of the body of the bone constitutes the posterior of the minor, anterior orbital margin. Anterodorsally, the body of the bone laterally provides the back of the olfactory capsule, while at the posteroventral external corner, a prominent but short process provides the articulatory surface for the cartilaginous connection with the dorsal process of the ectopterygoid. Separation of these two articulatory surfaces in the holotype shows that the backwards displacement of the dorsal neurocranial elements relative to the lower neurocranial elements, was of the order of 3.5 cm. Dorsally, the bone extends and underlies the concave, lateral margin of the frontal, progressively thinning to the anterolateral edge of the olfactory capsule. Anteromedially, it thins towards the anterior of the ossified interorbital septum and probably does not meet its counterpart from the other side. It projects anteriorly to the posterior of the mesethmoid, providing additional support for the upper, medial part of the parasphenoid.

The vomer is a very solid, unpaired bone broadly supported anterodorsally by the base of the mesethmoid below the hooked anterior of the dermethmoid. Posterodorsally, it thickens to meet the body of the mesethmoid and laterally meets the expanded anterior margin of the parasphenoid. It is produced into a vertical, interlocking process into the side of the mesethmoid, midway along the lateral margin. Ventrally, the vomer is broadly concave along its midline and anterolaterally bears a very large, pointed, 12 mm long tooth on each side in the holotype. The tooth is longitudinally ovate in section and its tip is recurved. A somewhat smaller but otherwise similar tooth is present on each side at the edge of the vomer and is separated from that at the front by a long diastema. This tooth is some 8 mm long and lies inside the front of the parasphenoid. Again, the left side counterpart of this tooth is not visible in the holotype. Posteroventrally, the vomer is pocketed to contribute, with the base of the front of the parasphenoid, to the facet for the anterior process of the dermopalatine.

Hyopalatine bones. Hyopalatine bones are, in part, incompletely preserved or are masked by overlying elements. The hyomandibular is covered by other elements but the hyomandibular facet is elongate and subparallel to the neurocranial roof, suggesting that the head of the hyopalatine was broad and the bone was somewhat less inclined anteriorly than the distortion noted in the holotype suggests.

The quadrate is expanded and widely fan-shaped. The articulation for the lower jaw is transversely broad and inclined anteriorly but this is again possibly somewhat accentuated by posterior movement of the neurocranium relative to the lower jaw. A deep groove that probably accommodated the symplectic, separates an expanded posterior margin. The extent of its contact with the metapterygoid is masked and the symplectic is similarly obscured. Contact with the descending arm of the ectopterygoid was limited.

The ectopterygoid is a deep, robust bone, with its lateral surface slightly convex dorsoventrally and with its dorsal surface expanding medially and separated by an abrupt drop to the endopterygoid. Towards the back, it carries a sharp ridge that crosses towards the posterior margin. It is firmly united anteriorly with the dermopalatine along a deeply sinuous junction. The posterior of the ectopterygoid is broadly attenuated and slightly flexed ventrally and this bears a shallow, facet to accommodate the anterodorsal edge of the quadrate. Anterolaterally, the ectopterygoid extends dorsally above the level of the dermopalatine as a strong articulatory lateral process to contact the lateral ethmoid.

The endopterygoid is somewhat shallower but longer bone than the ectopterygoid. It is strongly attached posterolaterally to the ectopterygoid and extends dorsally across as the slightly

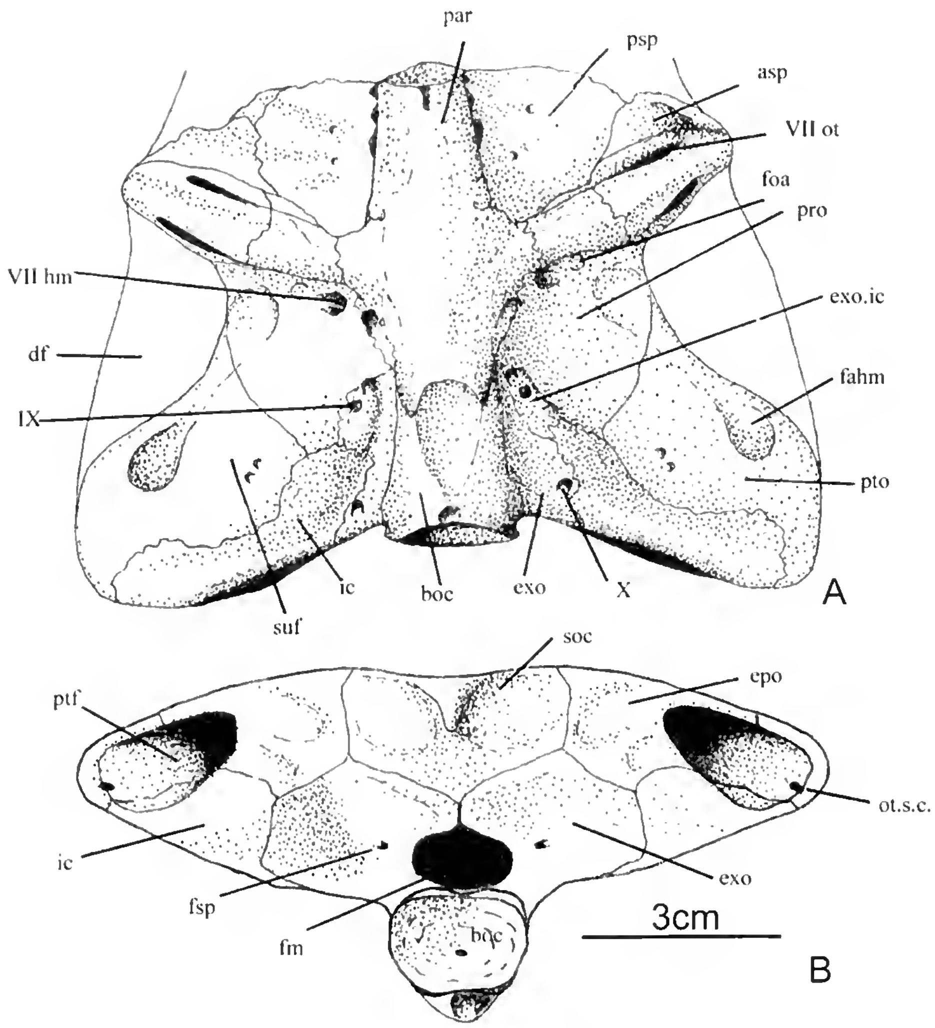

FIG. 8. *Euroka dunravenensis* gen. et sp. nov., reconstruction of QMF12759, posterior of partial neurocranium. A, ventral view; B, posterior view.

concave surface of the united elements to meet the autopalatine, behind the anterior process. This surface bears fine, irregular, longitudinal ridges. Its medial suture with the dermopalatine is angled posteroventrally. The bone meets the lateral arm of the dermopalatine along a dorsal rim that is deeper and sharper than that at the dorsolateral contact with the ectopterygoid, with the latter extending only to slightly below the level of the strong process on the ectopterygoid.

The autopalatine is a short but robust nugget of bone, forming the knob-like anterior process as well as the anteromedial and part of the anterior of the hyopalatine series. It is firmly united posteriorly with the anterior surfaces of the dermopalatine. The dorsal surface is sloped anterodorsally and somewhat dorsomedially as the anterior process and, while generally flattened transversely and gently curved longitudinally, it is marked by several small knobs and ridges at the outer edges.The ventral surface carries two large, pointed teeth that are near circular in section and that have their tips incurved and directed slightly backwards. The anterior tooth is smaller being 8 mm long, while the second tooth is 14 mm long.

The dermopalatine is a very large, deep, element that forms the majority of the anteromedial and anterolateral parts of the solid hyopalatine series. Laterally, it is deep and robust and extends posteriorly to its deeply digitated suture with the ectopterygoid. The lateral surface is gently dorsoventrally convex. Internally, the dermopalatine is attenuated from above its dentition along its junction with the endopterygoid. It bears at least four, extremely large, pointed and slightly incurved teeth along the anteroventral border, with the anterior one ca. 15mm long and 7 mm in diameter. These are closely placed in a single row but are separated by a short diastema from those on the autopalatine.

The metapterygoid is represented only by fragments of thin bone, largely masked by external bones of the skull.

Dermal upper jaw. The maxilla is known only from a posterior portion of the bone on the right side of the skull. It is relatively shallow and extends posteriorly to just in front of the articulation with the lower jaw. It has a narrow and thin upper flange that thickens markedly towards the tooth row, giving it a strongly convex profile across its ventral moiety. It is gently convex along its length but it appears to have been sinuous anteriorly. It is ornamented externally behind the tooth row with numerous, fine ridges and grooves and, more dorsally by numerous, very small tubercles. The back of the maxilla is convex, without a posterior notch. Internally, several small conical processes are directed medially. Maxillary dentition comprises a limited number of small, conical teeth in a single series, ankylosed to an internal shelf and supported laterally by a low flange. Teeth are up to 2.8 mm long.

A small but robust part of supramaxilla 2 is firmly attached to the posterodorsal corner of the maxilla, over the thin upper flange. The anterior of the bone is notched and then expands markedly in its anterodorsal moiety to a stout, rounded process that is directed posteromedially. This may have provided support for the back of the robust infraorbital positioned above. The head of the process bears a convex articulating surface. The anterior continuation of the flange of the maxilla and the notch in the anterior face of supramaxilla 2 supports the presence of a supramaxilla 1, lost during fossilisation in the holotype.

Mandible. The mandible is incomplete anteriorly but is only slightly reduced by this. It is elongate, very robust, deep and strongly developed with a shallow symphysis. The two sides of the lower jaw are only moderately divergent and the anterior is shallowly U-shaped across the symphysis. The base of the lower jaw is strongly inflected, especially in the area of a lower, well-developed flange.

The dentary comprises most of the mandible. The ventral margin is near horizontal in lateral view but the bone itself is anteriorly more expansive dorsoventrally than it is posteriorly. The oral margin curves gently ventrally, anterior to the low coronoid process, except where it descends more abruptly at the extreme anterior to the symphysis. It is tooth bearing over much of its length. The dentary teeth are moderately large, generally being much larger than those on the maxilla. Each is round in section, with slightly recurved tips. Remains of 12 teeth are present, each ankylosed at its base to an extensive, internal shelf of bone, slightly below a thin lateral flange of bone forming the oral border that supports the lateral bases of the teeth. A shallow groove exists internal to the bases of the teeth. Teeth in the back of the row increase gradually in size to the fourth last tooth, with smaller teeth then present to remains of the base of the third tooth from the front of the row preserved in the holotype. This tooth base and that in front of it suggest they were much larger than all other teeth in the dentary row and were tusk-like. In an undistorted specimen, they would have lain outside the large vomerine teeth. A very well developed, internal shelf is present medial to the bases of the teeth, curving abruptly to the lateral extent of the interior of the inflected basal flange of the bone. No coronoid teeth are present although the size of the inner shelf is similar to that where such teeth are present. The external surface of the dentary is externally marked by a deep, longitudinal groove that separates the upper, swollen body of the bone from the broad, thin flange running from the symphysis to below the articulation. The groove is penetrated by a number of prominent foramina for the mandibular sensory canal. The upper one-half of the main body of the dentary towards the rear of the tooth row is ornamented by very fine tubercles, becoming slightly larger posteriorly.

The angular is relatively small and deeply sutured to the dentary. It forms the outer part of the articulatory cup and posteriorly is elevated into a high, strong, prominent post-articular process. The interior of the posterior of the mandible is not exposed.

The retroarticular is present, represented by a small but robust knob of bone attached to the posterior end of the mandible, with contact with both the angular and the back of the basal, inflected flange of the dentary.

Circumorbital series. Only one infraorbital has been well preserved, positioned above the posterior of the supraorbital in the holotype. This is a robust, elongated, lozenge-shaped bone, with the anterior more attenuated. It is generally thicker than are most infraorbitals, ornamented externally with low, broad ridges and has the posterior moiety of its dorsal margin bevelled. Below the anterodorsal margin, the bone is thickened above an irregular, longitudinal groove and ventral flange. This is penetrated by small, posteroventrally directed canals and pores associated with the enclosed, infraorbital sensory canal. A prominent groove is present around the posteroventral edge before being directed posterodorsally across the lateral surface towards the anterior of the preoperculum.

Fragmentary remains of what appears to be other Infraorbitals and part of a possible dermosphenotic are present, displaced to above and behind this well preserved element.

Hyoid arch, gill arches and gular plate. The hyoid arch is only partly exposed. Only the posterior of a robust hypohyal element is exposed in the holotype. Articulating with this is much of the body of an extremely large ceratohyal. This is thickened anteriorly and becomes thinner and broader posteriorly, extending beyond the end of the mandible.

Branchiostegal rays are well exposed in the holotype, especially on the right side which has at least 20 rays present. The anterior 14 are relatively thin and distally pointed, with a thickened lateral surface, separated from a thinner surface by a longitudinal groove. The grooves diminish and almost disappear in the more posterior of these anterior rays; and these rays have a thickened posterior margin and a thin flange that broadens proximally. Within the series of branchiostegal rays, the more posterior 6 or possibly more become increasingly spathiform. Because of their thinning, they have been subjected to fretting of their edges, making it difficult to separate them. The last ray is extremely spathiform and has ornamentation of fine tubercles along its dorsal margin.

Gill arches are only represented by fragments that are not well enough preserved to warrant description.

The gular is present, lying between and dorsal to the lower flanges of the dentaries in the holotype. It is elongate, narrowly U-shaped ventrally towards the front, broadening and clearly scalloped posteriorly, with short, subparallel, longitudinal ridges extending into points and, with the intervening grooves, producing the scalloped margin.

Opercular series. The preoperculum is a solid, robust, sigmoidally-shaped bone with its sensory canal opening posteroventrally. It has a thickened anterior moiety that is slightly poteriorly curved at its dorsal tip and that is strongly curved anteriorly into a deep, ventral point that lies along the posterior of the quadrate. Its dorsal end lies close to the back of the pterotic but this may have resulted from displacement. The thickened anterior moiety is externally roughened and further ornamented by three broad grooves running subparallel to the posterior border. The posterior moiety of the bone is thinner, curves gently over the operculum and is more strongly curved posteroventrally to disappear near the anterior base of the element. Some shedding may have occurred at the posteroventral margin.

The operculum is known only from a small, poorly preserved portion of the bone, present over only one-half of the posterior body depth from above.

The interoperculum is an elongated bone underlying the posteroventral part of the preoperculum and extending to the back of the lower jaw. It is thickened along its anterodorsal margin and thins posteroventrally. Fine tubercles are present below the anterodorsal margin.

The suboperculum is very elongate and deep, bearing irregular and rare, shallow grooves curving obliquely from near its anterodorsal margin. Its depth may be exaggerated by loss of the ventral portion of the operculum that would have partially overlain it.

Vertebral column. Only a single anterior vertebral centrum has been preserved. This is a simple bone, lacking any laterally developed fossae. A notochordal pit is present. Remains of several neural arches are present, including one which was probably associated with the pits in the basioccipital, behind the foramen magnum.

DISCUSSION

The genus *Euroka* has superficial morphological character states that suggest it could have affinities with one of the existing families of the Suborder Albuloidei, either the Pterothrissidae Gill, 1893 or the Albulidae Bleeker, 1859, both of which have living as well as fossil representatives. Of these, closest similarities lie with the albulids, a family known from the Upper Cretaceous from Europe and North America (Forey 1973). A third family, the Osmeroididae, was established by Forey (1973) and was considered to possess few of the specialisations of the albulids or pterothrissids but was none the less regarded as a link between the Elopidae at the base of the elopiform radiation and the more specialised albuloids. It could be argued that, because of the limited number of specimens involved in the establishment of *E. dunravenensis*, it would be prudent to refer *Euroka* to the Albuloidei *incertae sedis*, rather than to erect a further family, the Eurokidae. However, the specialised morphological character states in the new taxon, especially those associated with the roof of the mouth, support formal differentiation at this time.

The Australian material is derived from the marine Toolebuc Formation within the Eromanga Basin part of the Great Artesian Basin, reliably dated as Lower Cretaceous (latest mid to late Albian) on the basis of dinoflagellate and spore-pollen zonation (Moore et al. 1986; McMinn &

Burger 1986). Later but less convincing dating of the Toolebuc by Henderson (2004) based on ammonite work suggested slight refinement of the dating but still retained a Late Albian age for the Formation. This indicates that early elopomorph radiation in the Australian region included local lineages closely contemporaneous with the earliest of the recorded osmeroidids from the northern hemisphere. The material presented specialised morphology differing significantly from the later occurring albulid taxa.

Marine transgressions into the Great Artesian Basin were short-lived with limited access to open oceanic waters across the basement structure of the Euroka Arch, south of the present Gulf of Carpentaria. This suggests that access to new, niche opportunities in the epeiric sea could have resulted in relatively rapid evolutionary responses from taxa entering the Basin, leading to endemic forms with specialised features, departing from trends developed within the extracontinental gene pool. On the other hand,

TABLE 1. Differences between *Euroka* and *Albula*.

No	Character	*Euroka*	*Albula*
i	Anterior cranial roof	Relatively shorter	Elongated
ii	Dermethmoid	Posteriorly broad	Posteriorly narrow
iii	Anterior ethmoid area	Complex/blocky	Complex/ attenuated
iv	Vomer	With very large teeth	Needle-like teeth
v	Parasphenoid	Very broad esp. anteriorly	Less broad anteriorly
vi	Parasphenoid teeth	Edentulous	Many rounded teeth
vii	Cranial depth	Posteriorly very shallow	Relatively less shallow
viii	Posterior cranial width	Very wide	Relatively narrower
ix	Post-temporal fossa	Relatively small	Relatively larger
x	Subepiotic fossa	Insignificant	Large
xi	Subtemporal fossa	Almost lacking	Very large
xii	Otic bullae	Insignificant	Very inflated
xiii	Interorbital septum	Very thick	Thin
xiv	Hyopalatine series	Anterior block-like	Anterior long, thin
xv	Palatine teeth	Extremely large	Small teeth if present
xvi	Maxillary teeth	Few posteriorly, small	Edentulous
xvii	Supramaxilla	Two	Single
xviii	Premaxilla articulation	To single facet	Double articulation
xix	Infraorbitals	Reduced, robust	Thinner, expansive
xx	Mandible	Solid, deep, elongated	Short, tapering
xxi	Dentary base	Inflected	Not inflected
xxii	Dentary teeth	Large, anterior fangs	Fine needle-like band
xxiii	Retroarticular	Present	Absent
xxiv	Postarticular process	Prominent	Absent
xxv	Coronoid process	Low	High
xxvi	Quadrate articulation	Below orbit back	Below front of orbit
xxvii	Gular	Relatively large	Small if present
xxviii	Preoperculum	Sigmoidal, thickened	Boomerang-shaped
xxix	Interoperculum	Elongate, deep	Small
xxx	Suboperculum	Elongate, deep	Large, hooked
xxxi	Branchiostegal rays	20	15

the localities from which *E. dunraveneusis* have come are both close to the inflow/outflow over the Euroka Arch, in possibly shallower waters to the east and southeast. For this reason, establishment of the Family Eurokidae draws attention to the possibly unique evolutionary responses within this less interactive, possibly early albuloid lineage. Certainly, pre-existing familial and even ordinal diagnoses such as those presented by Forey (1973), with classifications modified as in Forey et al. (1996), would need to be altered considerably and probably unnecessarily to accommodate *Euroka*.

E. dunraveneusis differs significantly when compared with albulids, based on the living *Albula vulpes* (Linnaeus 1758). These differences are summarised in Table 1. The Lower-Middle Eocene remains of *A. oweni* (Owen 1840) from Europe and North Africa, illustrated and discussed by Forey (1973) show even fewer similarities with specific character states in *E. dunraveneusis* than are present in *A. vulpes*.

The enlargement of the orbitosphenoid in *E. dunraveneusis* by addition of a massively ossified septum is similar to but more solidly developed than that in the Albulidae and in *Flindersichthys* Longman, 1932 and other taxa (in press) also from the Albian marine sediments of Queensland. However, strengthening of the orbitosphenoid area by ossification of an interorbital septum to contact with the parasphenoid, has been stated to occur sporadically in other groups by Forey (1973), who considers this character to lack strong phylogenetic value. Strengthening of the linkages between the parasphenoid and the roof of the neurocranium would increase support for the roof of the mouth. This would assist in overcoming the stresses associated with the bites employing the solid structure and massive teeth of the anterior hyopalatine bones. It is interesting to note the lack of teeth on the parasphenoid at the back of the roof of the mouth in this regard. This is at variance with the general situation in albuloids where parasphenoid tooth development is usually considerable.

It is unfortunate that the preserved remains of *E. dunraveneusis* lack almost all of the post-cranial skeleton. Certainly, the fusiform shape of the neurocranium, including the strongly inflected base of the lower jaw and the apparent loss of supraorbital and most of the infraorbital elements suggests the possibility of an eel-like body form. The increased solidity of many of the neurocranial bones would argue against rapid swimming and could be associated with a less mobile, more sedentary existence, with the animals being secretive, awaiting passing prey rather than actively hunting for food. Large, gripping teeth would be advantageous in ensuring that any prey captured from concealment would be unlikely to escape as they were dragged back into the possible area of concealment. The eels of the elopioform Order Anguilliformes are represented in the fossil record from the Upper Cretaceous (Middle Cenomanian) but the morphology displayed by *E.dunraveneusis* is generally more in keeping with interpretation of the taxon as being more albuliform. The relatively poor knowledge of the fossil history of the eels, noted by Forey et al. (1996), at this time precludes consideration of *Euroka* as a possible stem group genus associated with anguilliform evolutionary radiation within early elopomorph radiation.

Regardless, the presence of *E. dunraveneusis* in the Albian fossil fish fauna of the Great Artesian Basin indicates that early elopomorph evolution was none the less more complex than was believed previously.

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A Conchostracan from the Carboniferous Ducabrook Formation

The Lower Carboniferous Ducabrook Formation in the Drummond Basin, central Queensland contains a diverse fauna including fish and tetrapod remains (Thulborn et al, 1996, Warren & Turner, 2004). The formation was deposited in paralic and estuarine environments (Parker & Webb 2008). Although invertebrate remains are less common than those of vertebrates, molluscs, ostracodes and conchostracans are known. This note describes the conchostracans from near the Ducabrook Station, south of Bogantungan, approximately 350 km west of Rockhampton. Biostratigraphic control on the sequence was provided by Playford (1977, 1978, 1985) who indicated a late Viséan age for the Ducabrook Fomration.

Systematic Palaeontology
Order CONCHOSTRACA Sars, 1867
Suborder SPINICAUDATA Linder, 1945
Superfamily CYZICOIDEA Stebbing, 1910
Family LIOESTHERIIDAE Raymond, 1946
***Lioestheria* Depéret & Mazeran, 1912**
***Lioestheria* sp. (Fig. 1)**

Material. QMF54809, left valve; QMF54810, right valve; QMF54811, conjoined valves; all from QML1117, Ducabrook Formation, Carboniferous (Viséan) near Ducabrook Station, S. of Bogantungan, central Queensland.

Description. Valves 7-8 mm long, elliptical with width approximately two-thirds of length; umbo small, subterminal, approximately one-fifth of the length of the valve in from point of maximum anterior bulge. Hingeline long, occupying the middle two thirds of the dorsal margin; valve slightly asymmetrical about the midline transverse axis (perpendicular to dorsal margin), with a slightly narrower tapering to the point of maximum posterior bulge giving the valve an 'arrowhead' appearance. Maximum ventral bulge located approximately one-third of the length of the valve from the anterior. Growth bands comarginal, distinct, rugose and number 13-14 per valve (in specimens under discussion, with larger valves having more bands), more pronounced and closely spaced at anterior margin. Region near umbo with one or two growth bands. Micro-ornament not preserved.

Remarks. The material is similar to *Palaeolimnadia (Grandilimnadia) arcoensis* Tasch & Jones 1979 from the Lower Triassic Mount Goodwin Formation in the Bonaparte Basin, northwestern Australia (see Mory 1991). It can be distinguished by significantly fewer growth bands, and an extended hingeline, both features absent in *P. arcoensis*. *Palaeolimnadia (Grandilimnadia) profunda* Tasch & Jones 1979, also from the Mount Goodwin Formation lacks an extended hingeline, has growth lines near parallel to the dorsal margin for most of the valve length, unlike the Ducabrook specimens. The Ducabrook specimens are close to *Cyzicus (Lioestheria)* sp. undet. 1 Tasch 1979 from the Carboniferous Anderson Formation in the Canning Basin but are distinguished by being more asymmetrical about the midline transverse axis.

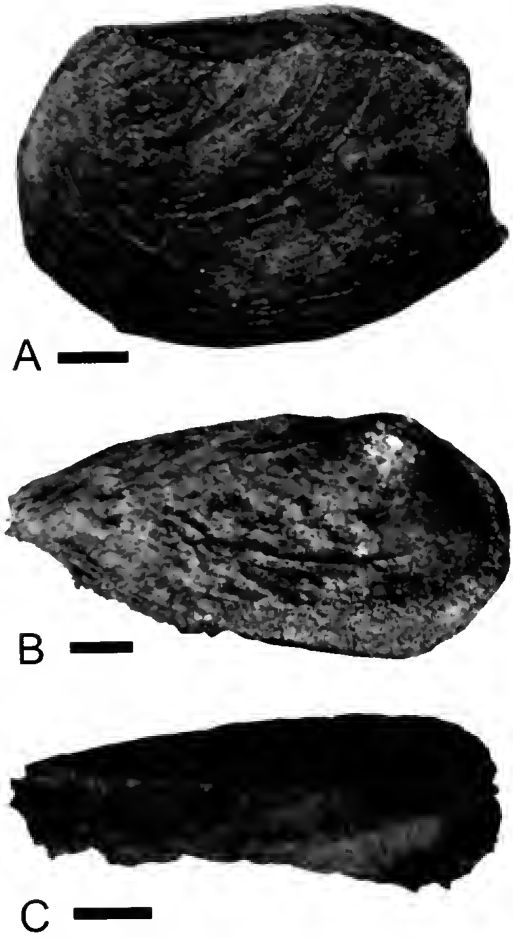

FIG. 1. *Cyzicus (Lioestheria)* sp., A. QMF54809, left valve, scale bar = 1 mm. B. QMF54810, right valve, scale bar = 1 mm. C. QMF54811, left and right valve, scale bar = 1 mm.

ACKNOWLEDGEMENTS

Anne Warren is thanked for providing the specimens. Drs Alex Cook and Peter Jell are thanked for their input in the writing and editing of the manuscript.

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Distribution of the estuary stingray (*Dasyatis fluviorum*) in Australia

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Citation: Pierce, S.J. & Bennett, M.B. 2010 02 15. Distribution of the estuary stingray (*Dasyatis fluviorum*) in Australia. *Memoirs of the Queensland Museum — Nature* 55(1): 89-97. Brisbane. ISSN 0079-8835. Accepted: 19 August 2009.

ABSTRACT

The extant distribution of *Dasyatis fluviorum* Ogilby, 1908 is confined to rivers, estuaries and near-shore marine waters along approximately 1700 km of the eastern Australian coastline from central New South Wales (34° 4´ S) northwards to central Queensland (20° 37´ S). Records of *D. fluviorum* from northern Australia, Papua New Guinea and eastern Indonesia appear to be misidentifications of *Dasyatis* sp. 1 (as described by White et al. 2006). An analysis of historical records shows no evidence of a contraction in distribution in south-eastern Australia as had previously been reported. However, the preferred habitats of *D. fluviorum* are heavily impacted by human activities throughout much of its range. ❒ *Biogeography, Chondrichthyes, Myliobatiformes, elasmobranch, distribution, conservation.*

Six of the seven freshwater and estuarine-specialist elasmobranch species in Australian waters (Last 2002) are listed as globally threatened on the 2007 IUCN Red List of Threatened Species (IUCN 2007). Little is known about the elasmobranch species inhabiting estuarine and mangrove ecosystems, though these habitats have suffered extensive modification and degradation from anthropogenic processes worldwide (Halpern et al. 2007; Lotze et al. 2006), and the sharks and rays that prefer to inhabit these environments may have suffered concomitant population declines (Compagno 2002; Last 2002). This situation is exemplified by the estuary stingray (*Dasyatis fluviorum*) Ogilby, 1908.

Dasyatis fluviorum is known from a number of rivers, estuaries and adjacent coastal waters on the highly-urbanised eastern coast of Australia (Last 2002). These areas are subject to a variety of anthropogenic pressures including urbanisation, habitat degradation, aquaculture and major fisheries, all of which are likely to impact on this species (Kyne et al. 2003; Pogonoski et al. 2002). The estuary stingray was listed as Vulnerable on the 2003 Red List of Threatened Species (Kyne et al. 2003) based on an apparent range contraction along the New South Wales (NSW) coast and anecdotal reports of population declines over the species' range (Last 2002; Last & Stevens 1994; Kyne et al. 2003; Pogonoski et al. 2002). The extant distribution of this poorly-known species has remained unclear (Last 2002; Pogonoski et al. 2002). Here we review all published literature, collate museum collection records and summarise unpublished sighting records to delineate the historical and extant distribution of the estuary stingray in Australasia.

MATERIALS AND METHODS

All available references and sighting records for *D. fluviorum* were located in the peer-

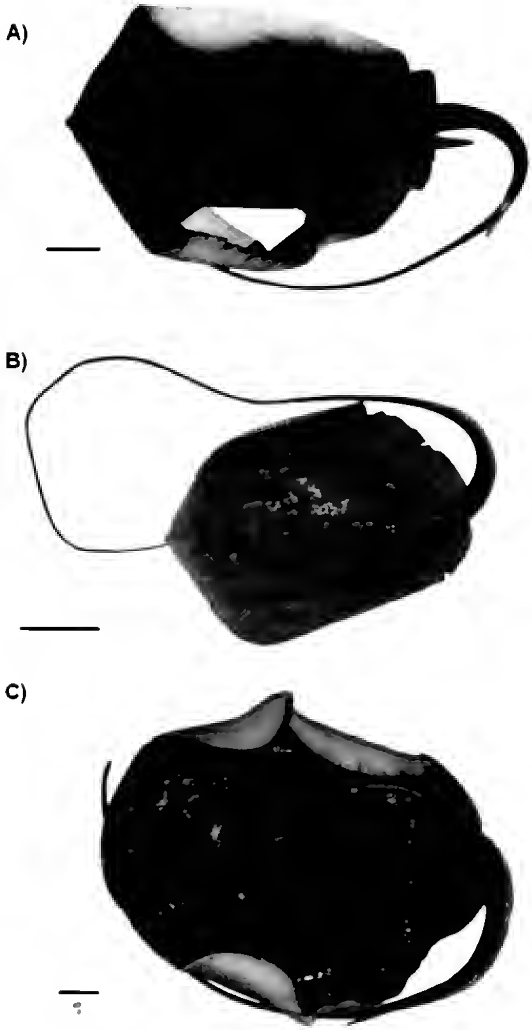

FIG. 1. Nominal *Dasyatis* sp. 1 (White et al., 2006) specimens from Indonesia and northern Australia. A, ANFC specimen H 5286-01 caught in the Kamora River estuary, Papua; B, NTM specimen S.14424-011 caught at Pocock's Beach in the Kakadu National Park; C, NTM S.15930-008 caught in the Keep River estuary, western Northern Territory. Scale bars represent 50 mm.

reviewed and grey literature through searches of published references, CrossSearch (ISI Web of Knowledge) databases and World Wide Web content using internet search engines. Details of museum and other major collection records were obtained through the Online Zoological Collections of Australian Museums (http://www.ozcam.gov.au) which included sightings and records from the Australian Museum (AM), the Australian National Fish Collection (ANFC) and the Museum and Art Gallery of the Northern Territory (NTM). Records from the Queensland Museum (QM) were obtained directly from that institution. Unpublished observations and sighting records were added from interviews with experienced observers. Although data collation focused on positive reports of *D. fluviorum* presence, other major surveys of potential or nominal *D. fluviorum* habitat that did not record the species from certain regions were also noted.

RESULTS

MELANESIA AND NORTHERN AUSTRALIA

Pre-2000 records of *D. fluviorum* from the coasts of eastern Indonesia (Fig. 1A) and Papua New Guinea (PNG) (Kailola 1975, 1987) and more recent observations from the Northern Territory in Australia are likely to have been misidentifications of an undescribed species currently known as the Merauke stingray, *Dasyatis* sp. 1 (White et al. 2006). This species is similarly-coloured to *D. fluviorum* and occupies a similar near-shore and estuarine habitat (White et al. 2006). Photographs of a specimen that was initially identified as *D. fluviorum* (H. Larson pers. comm. Fig. 1B) caught from Pocock's Beach, West Alligator Head, Kakadu National Park, show a long tail and well-developed row of medial thorns. These features are characteristic of *Dasyatis* sp. 1 (White et al. 2006), but are not present in similarly-sized *D. fluviorum* from Moreton Bay (S. Pierce unpub. data). Another, larger specimen from the Keep River estuary in the western Northern

Territory (H. Larson, pers. comm., Fig. 1C), has a similar morphology and these two specimens are provisionally assigned to *Dasyatis* sp. 1

A number of pre-1995 records from the Northern Territory have been shown to be misidentifications of the freshwater whipray *Himantura dalyensis* (Last & Manjaji-Matsumoto 2008) based on descriptions and photographs (Last 2002; Thorburn et al., 2003). Prior to this species being identified from the region, Stead (1963) stated that *D. fluviorum* had been recorded, under synonyms, at Port Darwin in 1878 and 1881 and from the Arafura Sea in 1880. Pollard (1974) caught a single specimen, listed as "*Dasyatis* sp. (*fluviorum*?)", from the East Alligator River and noted that further captures had been made from an adjacent freshwater lagoon. *Dasyatis fluviorum* were not recorded during freshwater elasmobranch surveys in 2002 (Thorburn et al., 2003) or among bycatch of the Northern Prawn Fishery (Stobutzki et al. 2002).

Records of *D. fluviorum* from Darnley Island in the Torres Strait proved to be misidentifications of *Neotrygon kuhlii* (Müller and Henle, 1841). *Dasyatis fluviorum* has not been recorded from fisheries catches in the Gulf of Carpentaria (Blaber et al. 1994; Stobutzki et al. 2002) or from fisheries-independent studies in northern Queensland (Blaber 1990; Blaber et al. 1995). Herbert et al. (1995) conducted a major freshwater fish survey of the Cape York Peninsula region and recorded stingrays from several rivers, listing species as either "*Dasyatis* sp." or "*Dasyatis* sp. (*fluviorum*?)". A photograph in a resulting publication (Herbert and Peeters, 1995) listed as *D. fluviorum* is actually *H. dalyensis*. A more recent survey of freshwater and estuarine elasmobranchs on the peninsula did not record *D. fluviorum*, though *H. dalyensis* was present in the region (Thorburn et al. 2003).

Material. Kamora River estuary, Papua, ANFC H 5286-01 (photograph); Pocock's Beach, West Alligator Head NTM S.14424-011 (photograph); NTM S.15930-008 (photograph); Darnley Island, Torres Strait, QM I 1519, I 1520 (both examined).

CENTRAL AND SOUTHERN QUEENSLAND

The confirmed distribution of *D. fluviorum* extends south from Repulse Bay in central Queensland (20° 37′ S; Fig. 2). There are records of the species from South Beach near Mackay, Warginburra Peninsula north of Yeppoon, Port Curtis near Gladstone (Connolly et al. 2006), Hervey Bay (A. Gutteridge, pers. comm.), Mary River (McPhee & Skilleter 2005), Noosa River (J. Johnson pers. comm.) and the Maroochy and Mooloolah rivers (Schlacher et al. 2005) on the Sunshine Coast. The species is common within Moreton Bay (Johnson, 1999; Pillans et al. 2007) and has been reported to occur in the Brisbane River "above tidal influence" (Ogilby 1908; Stead 1963). *Dasyatis fluviorum* has also been recorded from the Gold Coast Seaway (J. Johnson pers. comm.), Coombabah Creek (Ross 1999), Nerang River (Morton 1989) and Tallebudgera Creek (Morton 1992) on the Gold Coast in southern Queensland.

Material. Repulse Bay, ANFC H 4421-01 (site record); South Beach, Mackay, ANFC H 4595-01 (site record); Warginburra Peninsula, AM 134333008 (site record); Moreton Bay, QM I 26914, I 30175, I 627, ANFC H 5769-01 (site records); Brisbane River, QM I 1530, I 900, I 2101, I 11928, I 235, I 7720 (site records).

NEW SOUTH WALES

The majority of NSW records of *D. fluviorum* were from rivers and harbours. In northern NSW, *D. fluviorum* has been reported from Belongil Creek near Byron Bay (Parker 1999), from between 20 and 28 m depth off the coast east of Iluka, from the Clarence River (Kroon & Ansell 2006) where it has been recorded "at least as far inland as Grafton" (Stead 1963), and the Macleay (Gibbs et al. 1999; Macbeth et al. 2002), Manning (Gibbs et al. 1999), Wallamba (Gibbs et al., 1999), Hunter (Gibbs et al. 1999; Ruello 1976) and Hawkesbury Rivers (Gray 1990). There were records of *D. fluviorum* from Port Jackson between 1881 and 1914, and the species was caught from the Parramatta River and Sydney Harbour between 1975 and 1984 (P. Gibbs pers. comm.). Nine *D. fluviorum* were caught in Botany Bay fish surveys in 1978 and 1979 (SPCC 1981) and one was caught in April 2000 (Williams et al. 2004). *Dasyatis fluviorum* was listed on a checklist of fishes recorded from the Hacking River (34° 4´ S; Pease & Herbert 2002), and this was the southern-most record of the species.

Material. East of Iluka, ANFC H 4170-01 (site record); Clarence River, ANFC H 5964-01, H 5964-02 (site records); Hawkesbury River, AM I14625, I19951001 (site records); Port Jackson, AM B8395, I13456 (site records).

HABITAT PREFERENCES

Dasyatis fluviorum has been most commonly recorded from shallow coastal waters, particularly over mangrove-fringed sand/mud intertidal flats in sheltered bays and estuarine areas. The maximum depth record was from between 20 and 28 m depth offshore. The species may penetrate rivers to pure freshwater (Stead, 1963), though salinity preferences of 14 - 35 were noted in the Hunter River (Ruello, 1976). Mean monthly surface temperatures at the north of *D. fluviorum*'s distribution (Repulse Bay) range from an estimated 24°C in July to 29°C in January, while the temperature ranges from approximately 17°C in August to 23°C in February near the southern extent of distribution in Botany Bay (Department of Defence, 2007).

DISCUSSION

The results of this study indicate that *Dasyatis fluviorum* is an eastern Australian endemic, restricted to approximately 1700 km of the eastern coast from the Hacking River in NSW (34° 4´ S) in the south to Repulse Bay in Queensland (20° 37´ S) in the north. Considerable sampling effort in tropical north Queensland has failed to record the species (J. Johnson, pers. comm.). The centre of abundance for *D. fluviorum* appears likely to be the sheltered bays and estuaries of southern Queensland based on habitat preferences, distribution data and sighting records. Moreton Bay and Hervey Bay represent two likely population centres (Kyne et al. 2003).

The provisional identification of *Dasyatis* sp. 1 from the Northern Territory is the first record of this species from Australia. *Dasyatis* sp. 1 is not readily distinguishable from *D. fluviorum* (W. White pers. comm.) and is currently known solely from several juvenile specimens from Papua (White et al. 2006). The distinct taxonomic status of *Dasyatis* sp. 1 and the specific identity of Northern Territory *Dasyatis* cf. sp. 1 requires confirmation, as the results of the present study indicate that the extant distribution of *D. fluviorum* is substantially smaller (>50%) than was previously recognised (Last & Stevens 1994).

Recent (post-2000) observations of *D. fluviorum* from the central NSW coast, estuaries and rivers indicate that the southern extent of this species has not contracted northwards in recent decades. This hypothesised range contraction (Last & Stevens 1994; Pogonoski et al. 2002) was used as partial justification for listing *D. fluviorum* as Vulnerable on the IUCN Red List of Threatened Species (Kyne et al. 2003). The revised distribution for the species presented here does not alter the current listing of the species as Vulnerable. In fact, the relatively small range of *D. fluviorum* along the east coast may also add criteria B1ab as an additional risk factor, based on (1) an extent of occurrence of <20000 km^2, (2) possible population fragmentation because of specialised habitat preferences and (3) continued decline in habitat quality in many of the locations where the species is known to occur (IUCN 2001).

Records of *D. fluviorum* are predominantly from tidal rivers, estuaries, sheltered harbours, and only occasionally the adjacent coastline. The extent of this species' interchange between these habitats is unknown. Few data are available on the movement patterns of demersal rays. Short-term acoustic tracking studies on *D. lata* (Garman 1880) (Cartamil et al, 2003) and *Urobatis halleri* (Cooper 1863) (Vaudo and Lowe, 2006) have shown low rates of movement, while longer-term (months to years) tracking and tagging studies on *D. brevicaudata* (Hutton 1875) (Le Port et al. 2008), *Neotrygon kuhlii* (Pierce et al. 2009) and *U. halleri* (Vaudo & Lowe 2006) have found most individuals to be relatively site-resident. Studies of *D. sabina* (Lesueur 1824) in coastal lagoons found most individuals to be present year-round (Snelson et al. 1988), though two tagged specimens were recaptured 80 and 97 km from the point of tagging along the eastern coast of the United States (Schwartz & Dahlberg 1978). It is unknown how the relatively specialised habitat preferences of *D. fluviorum* affect its dispersal ability, although the single capture of a specimen in 20-28 m depth near the Clarence River mouth may imply that the species is capable of coastal movements. As habitat isolation can increase the overall extinction risk for a species (Reed 2004), determining the extent of interchange between what may be relatively isolated *D. fluviorum* populations is an important topic for future research.

The results of the current survey indicate that *D. fluviorum* faces several contemporary extrinsic threatening processes. Several publications list stingrays as bycatch of near-shore commercial fisheries along the northern and central NSW coasts. These records are ambiguous, recording species as "Dasyatididae/ Urolophidae (mixed spp.)" (Liggins et al. 1996; Liggins and Kennelly, 1996), "*Dasyatis* sp." (Gray 2002), "*Dasyatis* sp. (estuary stingray)" (Gray et al. 2003) or "*D. thetidis* (estuary stingray)" (Gray et al. 2001). However, these areas lie within the revised distribution of *D. fluviorum* and the species is likely to have been a component of these catches. Commercial prawn trawling (Gray et al. 1990; McPhee & Skilleter 2005; Ruello 1976) and estuarine gill net fisheries (Gray 2002), as well as recreational angling (Steffe et al. 2007; West & Gordon 1994) occurs in most known *D. fluviorum* habitats throughout its distribution.

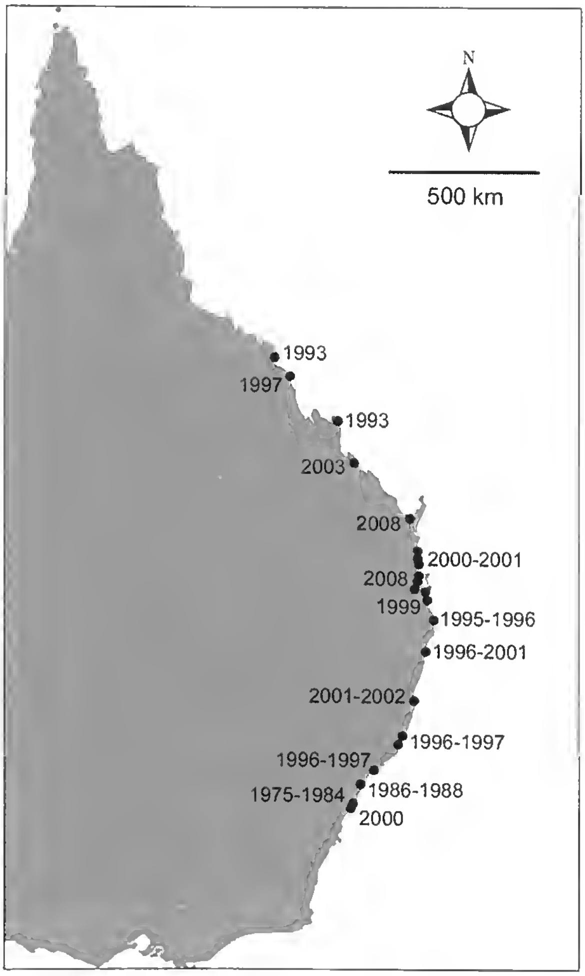

FIG. 2. Confirmed distribution of *Dasyatis fluviorum* on the east coast of Australia with the year last recorded from each site. Hyphenated years indicate the last sampling period during which *D. fluviorum* were recorded.

Habitat modification and degradation are also likely to affect *D. fluviorum*. Many large rivers have been modified through the construction of flood mitigation barriers, which can periodically lead to influxes of water with a low dissolved oxygen content and low pH (Gibbs et al. 1999; Kroon & Ansell 2006) causing fish kills (Macbeth et al. 2002). Occasional fish kills, from a variety of causes, have been noted in many known *D. fluviorum* habitats (Ruello 1976; Steffe et al. 2007). Many areas are also affected by pollutants (Ruello 1976; Williams et al. 2004), such as excess nitrogen loads (Schlacher et al. 2005) or organochlorines (Birch & Taylor 2000). Potential habitats have also been modified for residential developments such as canal estates (Morton 1992) or commercial industries such as ports (Connolly et al. 2006). Limited data on the use of modified habitats by elasmobranchs in southern Queensland (Morton 1989, 1992; Ross 1999) have not shown *D. fluviorum* to utilise residential canal estate habitats, although the species was present in adjacent unmodified areas. The majority of known *D. fluviorum* habitats, and particularly large rivers and harbour areas, are subject to multiple potential threatening processes (i.e. Birch & Taylor 2000; Johnson 1999; Ruello 1976).

Although anecdotal evidence suggests significant population decline overall (Kyne et al., 2003), *D. fluviorum* has been shown to persist in some highly-modified habitats for long time periods (> 100 years in some cases). It is difficult to ascertain the contemporary abundance of *D. fluviorum* in these habitats. Poor water quality or pollutants has been linked with endocrine dysfunction, health disturbances and decreased reproductive health in elasmobranch populations (Gelsleichter et al. 2005, 2006), which can potentially lead to reduced rates of population growth (Cortés & Parsons 1996). Habitat degradation has also been linked to increased mortality in juvenile sharks and a possible long-term decrease in carrying capacity (Jennings et al. 2008). While these factors have not been examined in *D. fluviorum*, it is possible that reductions in the quality and quantity of habitat have contributed to the species' population decline. Large stingrays are relatively difficult fish to sample because their size, benthic habit and general anatomy makes them difficult to enmesh in nets. Evaluation of their current status and abundance would be assisted by species-specific data collection during trawl surveys in deeper riverine waters and seine-netting in intertidal areas.

The revised distribution of *D. fluviorum* along the eastern coast overlaps with a large proportion of the most urbanised and modified coastal areas in Australia. The reduction, modification and degradation of inshore, and particularly estuarine habitats are likely to directly or indirectly impact upon *D. fluviorum* populations throughout much of this range. The species is also impacted by a variety of threats, such as commercial and recreational fisheries, that are known to directly reduce ray populations. This poorly-known species is worthy of increased attention from conservation managers.

ACKNOWLEDGEMENTS

Thanks to Helen Larson for information on NTM specimens and editorial comments. Phillip Gibbs provided extremely useful information on NSW records. Thanks also to Patricia Kailola, Jeffrey Johnson, Adrian Gutteridge, Stephen Taylor, Peter Kyne, William White, Colin Simpfendorfer and Charlie Huveneers for contributing additional records and comments. This research was supported by The University of Queensland, Project AWARE Asia-Pacific and the Tangalooma Marine Education and Research Foundation. Thanks also to one anonymous reviewer for helpful comments on this manuscript.

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Structure of a burrow of the fawn hopping-mouse *Notomys cervinus* (Rodentia: Muridae).

At approximately 0030 hrs on 4 May 2009, an adult hopping-mouse, subsequently identified as *Notomys cervinus*, was chased over a straight line distance of 100 m (although the actual path followed was zigzagged) until it disappeared into a vertical burrow (23° 46′ 08.9″S, 141° 01′13.6″E, GDA94) on a treeless, mostly grassless, claypan between Lake Constance and Hunters Gorge, Diamantina National Park, south-western Queensland. The 3 cm-diameter hole into which it retreated was flush with the claypan and not associated with any spoil from the burrow, however, another similar-sized hole 150 cm away had an obvious plume of granulated spoil (silt) flaring north-west from the hole but not surrounding the hole to form a conical depression.

Before beginning the excavation (under torch light) at the spoil-associated hole, a butterfly net was spread over the second hole 150 cm away. Dry silt was then shovelled from the inner side of the vertical exit shaft (i.e. the area between the two holes) until, at a depth of 43 cm, the burrow took a right-angle bend to lead horizontally in an arc toward the other exit. After 20 cm the burrow swung out to take on a semi-elliptical orientation. As successive biscuits of silt were shovelled off while following the 3 cm wide burrow, a hopping-mouse (adult female) fled the other exit and was trapped in, and immediately extracted from, the butterfly net. At approx. 90 cm along the burrow, four nestling mice were found in a chamber that expanded to 12 cm diameter. The young, whose eyes were unopened, were probably about 14 days old (see Watts 1983). They were found on a scant mattress of thin, chewed grass stems, the only vegetable matter to be found in the burrow complex. The chamber was palpably warm and humid.

Two burrows led from the nesting chamber, a 13 cm blind tunnel that was a perpendicular offshoot to the main burrow ellipse and another that constituted the natural extension of the main burrow. This led to the second vertical exit/entrance tunnel approximately 40 cm further on. The second vertical pipe (the one into which the chased mouse retreated from the clay pan) was 37 cm long and 3 cm in diameter. From the base of this pipe, the burrow continued on, but swung around to form the other arc of an ellipse that would eventually reconnected it with the entrance where the excavation began (Figs 1-3).

During excavation of the second half of the burrow ellipse, another hopping-mouse (adult male) erupted from a tunnel and began leaping around the open depression of the excavation. This individual was eventually hand-captured when it jumped up the inside of one of our shirts. Using a small portable plastic mouse cage furnished with a few calico collection bags and with the addition of the original nesting vegetation, the two adult mice were reintroduced to the four young, which on capture had been provided with a hot water bottle. Within minutes, the female was suckling the young.

Mid-way along the returning sweep of the burrow ellipse were two more blind tunnels: one, a short (14 cm) horizontal drive into the centre of the ellipse, and the other, a much longer (at 54 cm) upward-inclined, tangential spur, that began as a wide, smooth-walled gallery for approximately

FIG. 1. Plan view of burrow complex with flagging tape highlighting tunnels. Scale divisions in 1 cm and 10 cm intervals (photo: HJ).

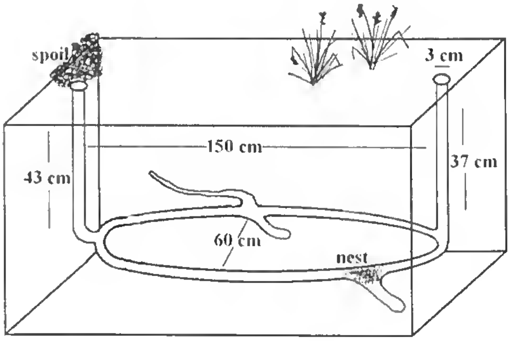

FIG. 2. Diagrammatic representation of burrow complex.

FIG. 3. Excavation (photo: JS).

18 cm, but then continued as a very narrow (2 cm) passageway. From this spur a live sub-adult male hopping-mouse was caught while trying to dig its way out.

Later, after releasing this subadult and driving away in our vehicle, another subadult was spotlit running from the opposite direction toward and eventually into the excavation pit from which it then quickly emerged and ran off. Within the 15 minutes it took us to drive approx. 2 km through claypan and gibber away from the excavation, we recorded by spotlighting an additional adult and a juvenile *N. cervinus* together, then a subadult, and finally two more juveniles*.

Some physical features of this burrow complex would appear to reduce the risk of snake predation. Firstly, it was positioned in stark 'lunar' habitat mostly devoid of vegetation or surface cracks, and so perhaps less likely to be visited by diurnal snakes due to the degree of exposure. Secondly, the horizontal elliptical nature of the tunnelling with the provision of pop holes at either 'end' of the loop could ensure escape from almost anywhere within the system. Thirdly, the nesting 'chamber' was not positioned at the end of a blind tunnel but in an expanded section of the main burrow. Even if nestlings were too young to escape, the reproducing adult(s) could. Blind galleries may be more important in providing points from which rapid-response exits can be dug when established exits are suddenly blocked. In this regard, the very narrow, upward rising tangential spur from which a subadult was collected toward the final sages of the excavation, probably represented the ongoing frantic execution of such a tunnel. Some features of the construction are more puzzling. For example, how, in the digging process 40 cm underground, do the mice connect the ends of the horizontal loop? How is burrow spoil (Fig. 4) moved up the vertical entrance/escape shaft? And why construct an all-horizontal system when stepping-up of burrow elements could provide early warning of incoming water or, escape from flooding?

Parts of Diamantina National Park were inundated by floodwaters between January and April 2009. This site was only 1.5 km from the main Diamantina River channel and at the same elevation (Fig. 6). Clearly, the superficial, contorting crust on the claypan on which the burrow excavation occurred indicated its relatively recent receipt of substantial rain and/or inundating floodwaters (Fig. 5). The ease of excavation (*ipso facto* burrow construction) through the homogeneous silt substrate may have resulted from relatively recent inundation, and the generational accumulation of burrow spoil may contribute to the establishment of the small raised hummocks that dot the claypans. In time these hummocks may deflect surface water from entrance tunnels, but their capacity to trap wind-blown seeds among grass tufts and scattered rubble, may be more significant.

While not labyrinthine in construction this one burrow complex builds on earlier reports that *N. cervinus* constructs 'very simple' burrows free of side galleries and devoid of radiating warrens (Finlayson 1939). It confirms that individuals live in small family groups (Finlayson 1939; Watts & Aslin 1981). We acknowledge however, that the burrow system we describe here may have been still

FIG. 4. Spoil plume from an adjacent *N. cervinus* burrow (photo JS).

FIG. 5. Northern view from excavation site across claypan (photo: HJ).

FIG. 6. Eastern view from excavation site toward Diamantina River channel (photo: HJ).

TABLE 1. Mammals trapped (T), hand-caught (H), or spotlit (S) in the vicinity of the excavation (all coordinates are GDA94) between 28 April and 4 May 2009 (975 trap-nights; 27 hrs spotlighting).

Dasyuroides byrnei	23°49'08.2"S, 141°11'18.9"E (T, adult M) 2/5/09
	23°45'48.2"S, 141°08'26.5"E (T, subadult F) 3/5/09
Planigale tenuirostris	23°34'35.9"S, 141°06'17.0"E (T) 1/5/09
Sminthopsis crassicaudata	23°33'37.0"S, 141°07'45.7"E (H) 30/4/09
	23°43'02.2"S, 141°10'56.5"E (T, juv) 4/5/09
Sminthopsis macroura	23°36'41.6"S, 141°03'15.2"E (T) 30/4/09
Notomys cervinus	23° 39' 44.2"S 141° 10' 38.6"E (H) (28/4/09)
	23° 41' 39.3"S 141° 04' 58.6"E (S) (29/4/09)
	23° 46' 35.4"S 141° 09' 08.5"E (H) (2/5/09)
	23° 45' 34.4"S 141° 08' 25.2"E (H) (2/5/09)
	23° 46' 08.9"S 141° 01' 13.6"E (H, 2 adult, 4 juv, 1 subadult) (S, 1 subadult) 4/5/09
	*23°45'50.0"S, 141°01'20.0"E (S, 1 adult, 1 juv) 4/5/09
	*23°45'31.6"S, 141°01'29.6"E (H, subadult) 4/5/09
	*23°45'10.0"S, 141°01'50.0"E (S, 2 juv) 4/5/09
Leggadina forresti	23°33'37.0"S, 141°07'45.7"E (H, juv) 30/4/09
	23°44'22.2"S, 141°10'30.6"E (H) 2/5/09

under construction, or may have been modified by reptiles or other mammals. Desert burrows are generally celebrated for ensuring cool humid conditions in hot climates but, inasmuch as this excavation occurred on a very cold night, it highlighted a burrow's capacity to also provide warm, humid conditions for adults and nestlings during periods of low ambient temperature.

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Distribution of the porcupine ray *Urogymnus asperrimus* (Bloch & Schneider, 1801) in Australian waters, with new records from Queensland

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Citation: Theiss, S.M., Kyne, P.M. & Chisholm, L.A. 2010 03 15. Distribution of the porcupine ray *Urogymnus asperrimus* (Bloch & Schneider, 1801) in Australian waters, with new records from Queensland. *Memoirs of the Queensland Museum – Nature* 55(1): 101-101. Brisbane. ISSN 0079-8835. Accepted: 20 May 2008.

ABSTRACT

Three specimens of the porcupine ray *Urogymnus asperrimus* (Bloch & Schneider, 1801) are reported from Heron Island on the Great Barrier Reef, Qld. These are the first records from the southern Great Barrier Reef and represent the southernmost records for this species on the east coast of Australia. An immature male with a disc width (DW) of 650 mm and two females measuring 620 mm DW and 545 mm DW were caught on the eastern side of the island using hand or seine nets. The two females were released alive after examination. Some morphometric data from two of the individuals are provided. The distribution, biology and ecology of this species are poorly-known, with only five catalogued Australian specimens held in Australian museums. The majority of these are not whole specimens and are in poor condition. There is further scattered information from photographs and live sightings. All known Australian records of *U. asperrimus* are summarised here. There are records of the species across tropical northern Australia, from Ningaloo Reef, WA (22°43'S) to Heron Island, Qld (23°26'S).

❒ *Myliobatoidei, Dasyatidae, Urogymnus, southern Great Barrier Reef, Heron Island.*

The porcupine ray *Urogymnus asperrimus* (Bloch & Schneider 1801) is a large dark brown to greyish batoid, identified by an oval-shaped disc covered in plate-like denticles and sharp thorns (Last & Stevens 1994). The tail lacks stinging spines and skin folds (Last & Stevens 1994), the latter separating the genus from the closely-related *Dasyatis* Rafinesque, 1810. *Urogymnus asperrimus* occurs in tropical waters throughout the Indo-West Pacific from east Africa to Fiji, and in the tropical Eastern Central Atlantic off west Africa (Last & Stevens 1994). It attains a maximum disc width (DW) of at least 1470 mm and is found inshore on sand and coral rubble substrate near reefs (Last & Stevens 1994; White et al. 2006). Very little is known about the biology of *U. asperrimus*, and detailed information on distribution and habitat is lacking.

Despite the wide distribution of *U. asperrimus*, it has not regularly been reported (Compagno 2000). Previous Australian records are limited to only a few specimens with little to no accompanying data, along with anecdotal sightings, photographs and live sightings from Western Australia (WA). The first Australian record of the species appears to be an individual caught in 1770 by the crew of the H.M. Bark *Endeavour* on James Cook's first voyage to the Pacific. This individual was taken off the mouth of the Endeavour River, with a description provided by botanist Daniel Solander, fitting that of *U. asperrimus* (description reprinted in Whitley 1939). There is only one previously catalogued specimen from the east coast of Australia (Queensland Museum, QM I.1112-4), which is registered as the holotype of the subspecies *U. asperrimus solanderi* Whitley, 1939. Whitley (1939) used Solander's description of the Endeavour River specimen, together with limited material (teeth, velum maxillare, buccal processes and skin) to 'give a new subspecific name to distinguish it from the Bombay type of the species', but did not provide an actual description of the subspecies, nor distinguishing features between it and the nominate form. *Urogymnus africanus* (Bloch & Schneider 1801) and *Raja africana* Bloch & Schneider 1801, are both synonyms of *U. asperrimus*, with the only other valid species in the genus being the pincushion ray *U. ukpam* (Smith 1863) of west African freshwater basins.

This paper reports on the location and habitat of three new *U. asperrimus* individuals collected from eastern Australia and summarises the known Australian records of the species.

MATERIALS AND METHODS

The first new specimen was examined at the Heron Island Research Station (HIRS), The University of Queensland, before being transported to and lodged at the Queensland Museum (QM), Brisbane, where it is preserved in ethanol. The second and third specimens were kept alive overnight in a large seawater tank at HIRS before being measured, photographed and released. Location, date, DW, disc length (DL), total length (TL), weight (for the live individuals only), sex and maturity, where possible, as well as some selected morphometrics for two individuals were recorded from the specimens following Last & Stevens (1994).

Information on Australian records of *U. asperrimus* in museum collections, as well as confirmed live sightings, were gathered in order to provide a summary on the distribution and biology of this species in Australian waters, and to compare this information with the newly recorded individuals presented here. The following abbreviations are used for institutions: AMS, Australian Museum, Sydney; NTM, Museums and Art Galleries of the Northern Territory, Darwin; QM, Queensland Museum, Brisbane; WAM, Western Australia Museum, Perth.

RESULTS

All three *U. asperrimus* specimens were collected from Heron Island (23°26'S, 151°54'E), part of the Capricorn Bunker Group of islands at the southern end of the Great Barrier Reef, 72 km off the coast of Gladstone, Qld.

The first specimen (QM I.31178, immature ♂, 650 mm DW, 665 mm DL, 1375 mm TL) was collected on 9 July 1998 at Shark Bay on the eastern end of Heron Island by seine net at dusk. Other measurements: 120 mm snout length, 290 mm head length, 250 mm trunk length and 835 mm tail length. The second specimen (♀, 620 mm DW, 650 mm DL, 1270 mm TL, 16.04 kg) was collected on 9 July 2006 from the shallows of Shark Bay after sunset by hand net. The third specimen (♀, 545 mm DW, 570 mm DL, 1130 mm TL, 11.70 kg) (Fig. 1A) was collected on 1 February 2008, also from Shark

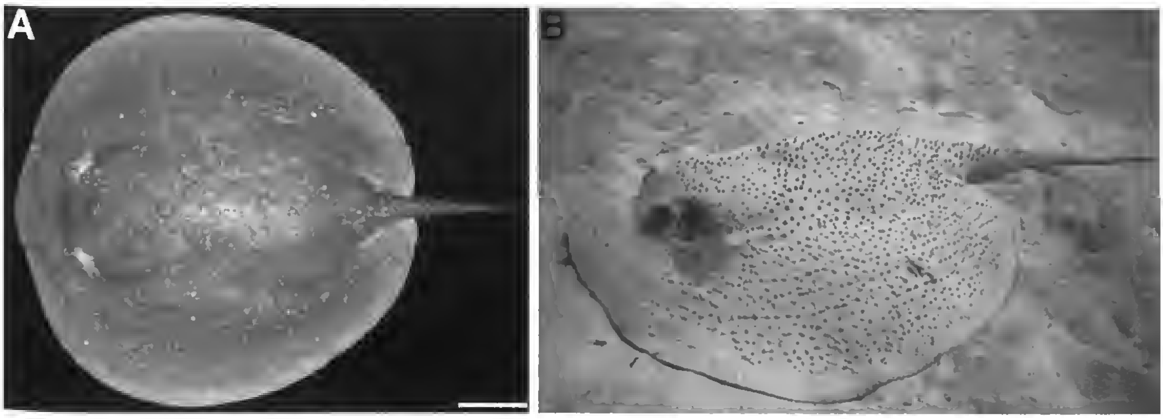

FIG. 1. Photographic records of the porcupine ray, *Urogymnus asperrimus*. A, Dorsal view of a 545 mm DW ♀ *U. asperrimus* collected from Heron Island, Qld and released alive. Scale bar = 10 cm; B, Underwater lateral view of *U. asperrimus* from Fitzroy Reef, Qld. (Photo: Brett Vercoe).

Bay, using a seine net on the incoming tide in the afternoon. Other measurements: 100 mm snout length, 230 mm head length, 235 mm trunk length and 665 mm tail length. This specimen was recaptured two days later with a hand net at high tide, approaching dusk, in nearly the same location within Shark Bay. Photographs of white spots found along the margin of the disc were used to identify the animal as the previously caught specimen. Maturity was not determined as the animals were released alive, but as females mature by 1000 mm DW (White et al., 2006) it is assumed that both specimens were immature. Minor abrasions were noted on the dorsal surface of the disc of the second specimen, but these were unrelated to the method of capture.

There are 25 known records of *U. asperrimus* from Australian waters (Table 1). Including the three new records reported here, there are nine records from Qld, 15 from WA and one from the Northern Territory (NT). A further two registered records held in Australian collections (AMS and QM) are from the Gilbert Islands, part of the Republic of Kiribati in the Western Central Pacific. As these records were not obtained from Australian waters, they are not included in the summary of records provided here. Of the 25 known records, 10 are live sightings recorded from visual surveys, six are from photographs (Fig. 1), three are dried skins (or parts of), one is small parts of an individual, two are whole specimens preserved in ethanol, one was used for research purposes, and one specimen could not be located. An additional historical account appears to represent the first Australian record from 1770. With the exception of the two ethanol preserved specimens, the catalogued material is generally in a poor state. Accompanying data is limited for many records. Some records have a detailed note of location and most records include a date of capture, but actual specimen data, including size, sex and maturity, are lacking in most instances (see Table 1).

DISCUSSION

Australian records of the porcupine ray are scattered across tropical northern Australia, with the southernmost point of occurrence on the west coast, Ningaloo Reef, WA (22°43′S) and on the east coast, Heron Island, Qld (23°26′S). The new specimens are the only confirmed records of the species from Heron Island and the southern Great Barrier Reef. They also

Museum	Registration number	Location caught	Latitude	Longitude	Date	Collector	Disc Width (mm)	Disc Length (mm)	Total Length (mm)	Sex and maturity	Remarks
-	Historical account	Endeavour River mouth, Qld	15°28′S	145°15′E	1770	Crew of H.M. Bark *Endeavour*	-	-	-	-	Taken on Cook's first voyage to the Pacific. Description provided by D. Solander (see Whitley, 1939).
AMS	AMS I.1721	Kingsmill Islands, WA	14°11′S	125°47′E	1888	J. Brazier	-	-	-	Female, immature	Dry skin, in Ethnological Collection
QM	QM I.1112-4	Darney Island, Qld	09°35′S	143°46′E	08/04/1913	J.R. Tosh	-	-	-	-	Buccal flaps in ethanol, dried jaws and tail; holotype of subspecies *Urogymnus asperrimus solanderi* Whitley, 1939
WAM	WAM P.4631-0001	WA	-	-	1959	G.F. Mees	-	-	-	-	No collection data. Specimen location unknown
WAM	Photograph	Dampier, WA	20°39′S	116°42′E	04/08/1978	J.B. Hutchins	-	-	-	Female	Caught in net, released alive
WAM	Photograph	Exmouth Gulf, WA	22°07′S	114°17′E	07/1991	J.B. Hutchins	-	-	-	-	Found dead on beach, not collected
-	Live sighting	Wellesley Islands, Gulf of Carpentaria, Qld	16°33′S	139°24′E	1998	H. Malcolm	-	-	-	-	Based on incidental sighting during underwater visual surveys of reef fish
QM	QM I.31178 (present manuscript)	Heron Island, Qld	23°26′S	151°54′E	09/07/1998	L.A. Chisholm	650	665	1375	Male, immature	Whole specimen in ethanol
-	Research specimen	Off Weipa, Gulf of Carpentaria, Qld	12°42′S	141°39′E	11/06/2003	L. Squire Jr.	460	490	1000	Female, immature	Healed umbilical scar
-	Photographs (present manuscript)	Heron Island, Qld	23°26′S	151°54′E	09/07/2006	S.M. Theiss	620	650	1270	Female, probably immature	Released alive. Mass 16.04 kg
-	Photograph	Fitzroy Reef, Qld	23°37′S	152°09′E	1/11/2007	B. Vercoe	-	-	-	-	Underwater photograph taken at 10 m depth
-	Photographs	Northern end of Flynn Reef, Qld	16°43′S	146°13′E	16/2/2007	B. Carter	-	-	-	-	Two underwater photographs taken at 5 m depth
-	Live sightings and photograph	Mangrove Bay & Point Cloates, Ningaloo Reef, WA	21°58′S 22°43′S	113°56′E 113°40′E	04/2007	J.D. Stevens	-	-	-	-	Nine confirmed sightings from two locations, with photograph
-	Photographs (present manuscript)	Heron Island, Qld	23°26′S	151°54′E	01/02/2008	S.M. Theiss	545	570	1130	Female, probably immature	Released alive. Recaptured in same location 2 days later. Mass 11.70 kg
NTM	Unregistered	Casuarina Beach, Darwin, NT	12°21′S	130°52′E	-	-	-	-	-	-	Beach-washed specimen, dried skin in poor condition
WAM	WAM P.29410-001	WA	-	-	-	-	617	642	1221	Female, probably immature	Whole specimen in ethanol, tail tip missing. No collection data.
WAM	WAM P.29573-001	Broome, WA	17°58′S	122°14′E	-	-	-	-	-	-	Dried piece of skin only

TABLE 1. Summary of all known Australian records of *Urogymnus asperrimus* (Bloch & Schneider, 1801). AMS, Australian Museum, Sydney; NTM, Museums and Art Galleries of the Northern Territory, Darwin; QM, Queensland Museum, Brisbane; WAM, Western Australia Museum, Perth.

represent the known southern distribution limit for the species on the east coast of Australia.

The eastern side of Heron Island is primarily a sandy bottom habitat of the reef lagoon with some coral rubble leading out to the inner reef. Large aggregations of batoids can be found in the lagoon, most commonly the pink whipray *Himantura fai* Jordan & Seale, 1906, the cowtail ray *Pastinachus atrus* (Macleay, 1883) and the giant shovelnose ray *Glaucostegus typus* (Bennett, 1830). All three *U. asperrimus* specimens, however, appeared to be solitary. Heron Island and the southern Great Barrier Reef are well surveyed regions and the low recorded abundance of the porcupine ray is probably an accurate indicator of the rarity of this species locally. Indeed, throughout its Australian range, this species is not regularly recorded and there is a lack of reliable records to confirm distribution, along with basic biological information. Although *U. asperrimus* is rarely encountered, it may be more widely distributed across northern Australia than current records indicate. In this area relatively turbid conditions markedly reduce the effectiveness of underwater visual survey techniques, compared to in clearer Great Barrier Reef and west coast waters. Overall, little biological information can be gathered from the existing Australian records.

Behavioural observations made from live sightings at Ningaloo Marine Park provide some insight into the ecology of this species (J.D. Stevens, pers. comm.). *Urogymnus asperrimus* appears to plough strongly through the substrate when feeding, which is different to the feeding strategies of other large rays, and there seems to be some suggestion that larger individuals are found at greater depths (J.D. Stevens, pers. comm.).

Urogymnus asperrimus is listed as Vulnerable on the *IUCN Red List of Threatened Species* due to the lack of regular records and an apparent decrease in abundance (Compagno, 2000). Although handling of *U. asperrimus* is difficult due to its rough dorsal surface, this species is commonly caught in South East Asia and used for its meat, cartilage and skin, which is of particularly high value (White et al., 2006). Basic biological information such as age, growth and reproduction are lacking, making an assessment of the species' resilience to fishing pressure difficult. Its rarity, inshore habitat and large size, however, may imply that it is unlikely to sustain prolonged targeted fishing.

ACKNOWLEDGEMENTS

Thanks go to Jeff Johnson for providing details on the specimen lodged at QM as well as other Australian records; Sue Morrison and Claire Bartron for information on lodged specimens at WAM; John Stevens for providing information gathered from visual surveys in Western Australia; Brett Vercoe for supplying a photograph of the Fitzroy Reef specimen; Janine Caira and Kirsten Jensen for details on the Weipa specimen; Nathan Hart, Shaun Collin, Blake Harahush, and Carla Atkinson for help with fieldwork; and the staff of the Heron Island Research Station, The University of Queensland.

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The Julia Creek dunnart and other prey of the barn owl in Mitchell grass downs of north-western Queensland

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Citation: Woolley, P.A. 2009 03 15. The Julia Creek dunnart and other prey of the barn owl in Mitchell grass downs of north-western Queensland. *Memoirs of the Queensland Museum — Nature* 55(1): 107-117. Brisbane. ISSN 0079-8835. Accepted: 18 February 2009.

ABSTRACT

Analysis of the contents of pellets produced by barn owls, *Tyto alba*, has provided information on the distribution of the Julia Creek dunnart, *Sminthopsis douglasi*, and five other species of small terrestrial mammals. The pellets were collected from 28 localities in Mitchell Grass downs country around the town of Julia Creek in north-western Queensland. Mammals formed the largest component of the diet of the owls, followed by birds. Reptiles, frogs and arthropods were also preyed upon. ☐ *Prey of Tyto alba, Sminthopsis douglasi, dasyurid marsupials, rodents, birds, Queensland, Mitchell grass downs.*

Barn owls, *Tyto alba*, feed mainly on small terrestrial mammals but they are known to take other vertebrates and insects (Taylor 1994). Studies on the diet of barn owls in Australia (see Morton 1975 which includes a summary of earlier studies; Morton et al. 1977; Morton & Martin 1979; Valente 1981; Smith & Cole 1989; Debus et al. 1999; Heywood & Pavey 2002) have shown that a variety of mammals, birds, reptiles, frogs and arthropods may be eaten, and that rodents such as *Rattus villosissimus* and *Mus musculus*, species that undergo large fluctuations in population size, often form the bulk of the diet. Barn owls usually swallow their prey whole and the undigested remains, including bones, hair, feathers, scales and hard parts of insects that are all generally readily identifiable, are regurgitated in compact pellets. Each pellet is thought to contain most of the remains from a single foraging expedition (Taylor 1994). Freshly ejected pellets are soft and covered with mucous which, as it dries, gives them a smooth, dark, glazed appearance. In dry conditions the glaze is lost after about 10 days but the pellets remain firm and darkly coloured for eight or more months (from Barn Owls On Site http://www.barnowltrust.org.uk/content_images/pdf [July 2008]). Barn owls roost in caves, old buildings, tree hollows and, occasionally, in trees, and pellets accumulate at the roost site.

Analysis of the contents of pellets provides not only information on the diet of the owl but also information on the composition of the fauna in the foraging area. This may lead to the detection of uncommon species, as happened in the case of a then little known species of dasyurid marsupial, the Julia Creek Dunnart, *Sminthopsis douglasi* (Woolley 1992). This species, at the time of its description by Archer (1979), was known from only four specimens in museum collections. These had been collected from three localities between the towns of Julia Creek and Richmond, Queensland. As a result of survey work commenced in mid-1990 (Woolley, 1992) the skeletal remains of Julia Creek dunnarts were found among a deposit of bones that were considered to have formed from the disintegration of owl pellets in a hollow tree. Trapping in an area close to where the bones

TABLE 1. The localities and collecting sites together with the dates on which owl pellets were collected, the number and condition (glazed - G, unglazed - U) of the pellets, and whether or not barn owls were present at the site. Localities (abbreviation in parentheses) ordered by date of earliest collection.

Locality and collecting sites	Date of collection	No. of pellets	Locality total	Barn owls
Eureka (EUR) - 20°50'S, 141°48'E abandoned homestead	30.4.1992	72 (G)		yes
	27.5.1992	43 (G)		yes
	29.6.1992	40 (G)		yes
	3.8.1992	33 (G)		yes
	5.10.1992	17 (G)		yes
	6.7.1994	33 (15U, 18G)		yes
	24.7.1994	15 (G)		yes
	2.9.1994	18 (G)	271	yes
Crendon (CRE) - 21°26'S, 142°07'E shearing shed	- 11.1993	31 (U)	31	no
Nelia (N) - 20°39'S, 142°13'E a) derelict house, b) racecourse buildings	19.6.1994 a	28 (G)		yes
	10.6.1995 b	50 (G)		yes
	26.7.1995 b	19 (G)		yes
	9.10.1995 b	9 (G)		no
	27.4.1996 b	36 (G)	142	no
Nelia West (NW) - 20°42'S, 142°04'E derelict shearer's quarters	19.6.1994	19 (U)		no
	21.3.1997	66 (U)	85	no
Osbert (O) - 20°30'S, 141°46'E outbuildings on unoccupied property	20.6.1994	215 (92U, 123G)		yes
	17.6.1995	54 (26U, 28G)	269	no
Lyrian (L) - 19°27'S, 141°12'E abandoned homestead, outbuildings, nearby tree hollow	21.6.1994	30 (G)		yes
	6.10.1995	56 (35U, 21G)	86	no
Auckland Downs (AD) - 20°15'S, 141°46'E derelict outbuilding	3.7.1994	22 (U)	22	no
Huddersfield (H) - 20°57'S, 141°53'E shearing shed, outbuildings	4.7.1994	76 (U)		no
	29.4.1995	33 (G)		yes
	6.6.1998	82 (G)		yes
	30.3.1999	12 (G)		yes
	3.6.1999	81 (G)		yes
	10.9.2000	6 (U)	290	no
Eulolo (EUL) - 21°14'S, 141°33'E outbuildings on unoccupied property	5.7.1994	264 (U)	264	no
Penola Downs (PD) - 21°31'S, 141°27'E derelict shearer's quarters	5.7.1994	115 (U)	115	no
Carrum (CAR) - 20°53'S, 141°43'E unoccupied house	6.7.1994	9 (G)	9	yes
Armidale (ARM) - 20°52'S, 141°41'E shearing shed	6.7.1994	18 (G)	18	yes
Waterloo Plains (WP) - 20°57'S, 141°43'E unoccupied house, shearing shed	7.7.1994	258 (191U, 67G)		yes
	.8.1994	4 (G)		yes
	.9.1994	6 (G)	268	yes
Kelloshiel (K) - 21°01'S, 141°42'E shearing shed	7.7.1994	5 (U)	5	no
Eastern Creek (EC) - 20°54'S, 141°47'E tree hollow at Waterloo Rd crossing	7.7.1994	20 (9U, 11G)	20	yes
Longford Plains (LP) - 20°46'S, 141°46'E abandoned homestead	8.7.1994	57 (G)	57	yes
Toorak (T) - 21°02'S, 141°48'E a) tree hollow in paddock no. 8, b) yards between paddocks 1 and 2, c) barn	8.7.1994 a	9 (G)		yes
	26.5.1998 b	43 (G)		yes
	24.5.1999 c	40 (G)		yes
	-.11.1999 c	11 (G)		yes
	20.8.2000 c	85 (G)		yes
	12.11.2001 c	22 (G)	210	yes
Eddington (ED) - 20°39'S, 141°33'E shearing shed	9.7.1994	16 (U)	16	no
Ardbrin (ARD) - 21°03'S, 142°17'E shearing shed, derelict shearer's quarters	15.6.1995	260 (99U, 161G)		yes
	16.8.1995	38 (G)		yes
	19.9.1995	19 (G)		no
	18.6.1996	28 (G)		no
	13.3.1997	16 (U)		no
	28.10.1999	15 (G)	376	no
Consentes (CON) - 20°16'S, 141°36'E derelict outbuilding	17.6.1995	98 (55U, 43G)	98	no
Broadlands (B) - 21°28'S, 141°17'E disused shearing shed	22.6.1995	32 (U)	32	no
Minamere (M) - 20°52'S, 142°18'E a) abandoned homestead, b) meat house at shearer's quarters	11.7.1995 a	23 (G)		yes
	15.8.1995 b	277 (170U, 107G)		yes
	19.9.1995 b	21 (G)		yes
	15.10.1995 b	40 (G)		yes
	27.11.1995 b	26 (G)		yes
	18.1.1996 b	33 (G)		no
	20.2.1996 b	2 (G)		no
	19.3.1996 b	19 (G)		no
	24.4.1996 b	6 (G)		no
	3.6.1998 b	9 (G)	456	no
Canobie (CAN) - 19°16'S, 140°58'E (hut at Hawkes Nest bore)	7.10.1995	72 (45U, 27G)	72	no
Shlmalier (S) - 20°10'S, 141°58'E disused shearing shed	17.4.1996	24 (U)	24	no
Quambetook (Q) - 21°12'S, 142°10'E shearing shed	17.10.1996	293 (159U, 134G)	293	yes
Proa (P) - 20°54'S, 142°09'E shearer's shower block	30.5.1998	46 (G)		yes
	28.5.1999	32 (G)		yes
	29.8.1999	15 (G)		yes
	1.11.1999	5 (G)	98	yes
Yorkshire Downs (YD) - 20°52'S, 141°58'E under trees	3.11.1999	6 (G)		yes
	31.5.2000	3 (G)	9	no
Rosevale (R) - 21°06'S, 142°00'E abandoned homestead	9.9.2000	113 (G)	113	yes

were found led to the collection of live Julia Creek dunnarts in 1992.

The present study of the prey of the Barn Owl in north-western Queensland was undertaken primarily to obtain information on the distribution of the Julia Creek Dunnart which, in turn, might lead to the finding of other trappable populations for study of the biology of the species, currently listed as Endangered (EPBC Act 1999).

METHODS

Collection of pellets. Searches for pellets of the Barn Owl were made between April 1992 and November 2001 in Mitchell Grass downs country around the town of Julia Creek in north-western Queensland, an area encompassing part of the presently known range of *S. douglasi* (Kutt 2003). Pellets were found in abandoned homesteads and outbuildings, in tree hollows and under trees in 28 localities (Table 1). At some localities pellets were collected from more than one site, and sometimes one or two barn owls were present at the site where the pellets were found. Most collecting localities were revisited, or checked by local residents, after the first collection was made. At some, no further accumulations of pellets were found and barn owls, if previously present, were no longer roosting at the site. The collecting sites at Eureka, Longford Plains and Armidale were demolished early in the collecting period. Pellets of the Southern Boobook, *Ninox novaeseelandiae*, which were also found at some sites but not collected, were easily distinguished from those of the Barn Owl by their generally smaller size and friable structure.

Intact pellets were picked up, classed as either unglazed or glazed, and packed singly for transport to the laboratory.

Preparation of pellets. Pellets were soaked individually in water, to which a few drops of detergent had been added, until soft (usually 30-60 minutes). The pellets were teased apart with forceps in a white enamel tray. By a process of differential flotation followed by sieving using a 1.2 mm mesh sieve the lighter hair, feathers and debris were separated from the heavier bones. Hair from some pellets, and distinctively patterned or coloured feathers, were saved. Once the water was relatively clear the bones and other hard parts were collected from the tray and placed in a petri dish to air dry. Before it was discarded the material in the sieve was felt for bones that may have been trapped in fur.

Identification of contents. Identification of the remains of vertebrate prey items was based primarily on characteristics of the skulls, teeth and lower jaws as seen in reference specimens. For rodents these included differences in the size of the skull, length of the molar tooth row and width of the molars. Notched incisors and a difference in the shape of the anterior edge of the zygomatic plate helped to distinguish *M. musculus* from *Leggadina forresti*. Among the dasyurids, the larger size (length of dentaries, width of third upper molar, canine teeth, pelvic girdle) was used to distinguish adult specimens of *S. douglasi* from adult *Sminthopsis macroura*. Dentaries of juvenile specimens of *Sminthopsis* that lacked teeth upon which identification could be made were assigned, if an adult was present in the same pellet, to the same species. The skeletal remains of *Planigale* were assumed to be those of *P. ingrami* based largely on the observation that this was the only species of *Planigale* either trapped or found in the study area (Woolley & Mifsud unpub. observations). Differences in the pelvic girdle (shape of obturator foramen and anterior edge of pubic bones) were found useful in distinguishing dasyurid marsupials from small rodents, and the rodents *M. musculus* and *L. forresti* from each other, and provided additional confirmation of identity. Experts (see acknowledgments) assisted with the identification of some taxa. The identity of one mammal was confirmed by examination of hair structure, and of some birds by distinctive feathers. The minimum number of individuals of a vertebrate prey item in a pellet was calculated

TABLE 2. The number of pellets obtained at each locality, and the number containing each taxon. For each taxon the number of pellets as a percentage of the total is shown in square parentheses, followed by the number of individuals (arthropods were not counted). Key to localities in Table 1.

Locality	No. of pellets	No. of pellets containing remains of each taxon, [% of total] , (no. of individuals)				
		Mammals	Birds	Reptiles	Frogs	Arthropods
EUR	271	227 [83.7] (295)	36 [13.2] (82)	14 [5.1] (15)	1 [0.3] (1)	13 [4.7]
CRE	31	10 [32.2] (10)	28 [90.3] (73)	5 [16.1] (8)	0	19 [61.2]
N	142	114 [80.2] (185)	25 [17.6] (36)	22 [15.4] (55)	23 [16.2[(82)	60 [42.2]
NW	85	64 [75.2] (85)	9 [10.5] (17)	7 [8.2] (7)	6 [7.0] (24)	22 [25.8]
O	269	149 [55.3] (215)	96 [35.6] (187)	46 [17.1] (176)	8 [2.9] (18)	50 [18.5]
L	86	84 [97.6] (131)	1 [1.1[(1)	1 [1.1] (1)	1 [1.1] (1)	3 [3.4]
AD	22	9 [40.9] (18)	0	9 [40.9](15)	8 [36.3] (35)	6 [27.2]
H	290	214 [73.7] (277)	77 [26.5] (132)	19 [6.5] (33)	7 [2.4] (13)	69 [23.7]
EUL	264	255 [96.5] (635)	29 [10.9] (39)	9 [3.4] (11)	3 [1.1[(6)	22 [8.3]
PD	115	111 [96.5[(271)	1 [0.8[(2)	1 [0.8] (2)	0	1 [0.8]
CAR	9	9 [100[(18)	1 [11.1] (2)	0	2 [22.2] (5)	2 [22.2]
ARM	18	16 [88.8] (33)	5 [27.7] (14)	1 [5.5] (1)	0	3 [16.6]
WP	268	170 [63.4] (295)	145 [54.1] (368)	9 [3.3[(11)	10 [3.7] (16)	101 [37.6]
K	5	3 [60.0] (8)	3 [60.0] (13)	0	1 [20.0] (1)	2 [40.0]
EC	20	16 [80.0] (20)	3 [15.0[(13)	0	0	1 [5.0]
LP	57	54 [94.7] (80)	2 [3.5] (2)	0	0	1 [1.7[
T	210	184 [87.6] (252)	60 [28.5] (108)	13 [6.1] (26)	10 [4.7[(14)	38 [18.0]
ED	16	9 [56.2] (10)	3 [18.7] (3)	11 [68.7] (48)	6 [37.5] (18)	12 [75.0]
ARD	376	329 [87.5] (664)	51 [13.5] (75)	65 [17.2] (159)	4 [1.0] (7)	89 [23.6]
CON	98	93 [94.8] (141)	1 [1.0] (1)	1 [1.0] (2)	2 [2.0] (22)	16 [16.3]
B	32	30 [93.7] (47)	1 [3.1] (1)	0	0	0
M	456	351 [76.9] (613)	137 [30.0] (310)	53 [11.6] (135)	10 [2.1] (21)	141 [30.9]
CAN	72	64 [88.8] (75)	1 [1.3] (1)	3 [4.1] (3)	9 [12.5] (30)	14 [19.4]
S	24	8 [33.3] (13)	1 [4.1[(1)	14 [58.3] (55)	18 [75.0] (58)	18 [75.0]
Q	293	161 [54.9] (232)	194 [66.2] (493)	41 [13.9] (140)	0	88 [30.0]
P	98	66 [67.3] (90)	31 [31.6[(37)	4 [4.0] (4)	1 [1.0] (1)	23 [23.4]
YD	9	9 [100] (9)	0	0	0	0
R	113	59 [52.2] (71)	42 [37.1] (42)	0	0	15 [13.2]
All localities	3749	2868 [75.5] (4793)	983 [26.2] (2053)	348 [9.3] (907)	130 [3.4] (373)	829 [22.1]

from the number of dentaries (mammals), lower mandibles (birds), lower jaws (reptiles) and ilia (frogs). The number determined in this way was often supported by counts of other elements e.g. for mammals the number of upper jaws and pelvic bones matched the number of dentaries, and for some birds the number of sacra / keels/ gizzards matched the number of lower mandibles. Mammals and birds were identified to species, reptiles to family and frogs to order.

Identification of the remains of invertebrate prey items, which included several orders of arthropods, was based on wing fragments, head capsules, mandibles and legs. The number of individuals of each invertebrate prey item in a pellet was generally not determined. The bulk of the material extracted from the pellets for identification has been lodged in the Queensland Museum.

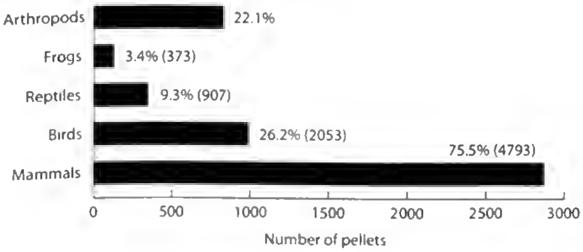


FIG. 1. Number of pellets containing the countable remains of prey items for each taxon. In the case of arthropods (mostly grasshoppers) the actual number of individuals was not determined. The number of pellets expressed as a percentage of all pellets examined (3,749) is shown at the end of each bar, together with the number of individuals in parentheses.

RESULTS

The contents of 3,749 pellets collected between April 1992 and November 2001 have been examined. They were obtained from 28 localities (Table 1), and the number of pellets per locality ranged from 5 to 456. At 16 localities, 15 of which were revisited, no more pellets were obtained after the initial collection. The pellets from 8 (CRE, AD, EUL, PD, K, ED, B and S) of these 16 localities were probably not of recent origin; they had lost their glaze and no barn owls were present at the sites at the time the pellets were collected. At some localities (e.g. WP, A, and M) where sequential collections were made the first, usually large, collection contained both unglazed and glazed pellets. However it was not known if the barn owls, present at the time the pellets were collected, had been roosting at the site continuously over a long period, or if the older (unglazed) pellets represented an earlier accumulation. The pellets varied greatly in size, ranging from balls about 2 cm in diameter to cylinders about 8 cm in length. The largest pellets were usually found to contain the remains of a single large prey item e.g. either a large rodent or bird.

The prey items identified included mammals, birds, reptiles, frogs and arthropods (mostly orthopterans). The contribution of each taxon to the diet (Table 2, Fig. 1) was based, in the case of vertebrate prey items, on the number of pellets that contained countable remains, i.e. remains upon which a count of the number of individuals eaten could be made and, for arthropods, the number of pellets in which they were found. Mammals were present in 75.5% of all pellets, birds in 26.2%, reptiles in 9.3%, frogs in 3.4% and arthropods in 22.1%. The contribution of each taxon to the diet varied between localities (Table 2). Mammals were represented in the pellet collection from every locality, and all taxa in the collections from 16 localities. Birds were not found in the pellets from two localities, reptiles from seven, frogs from nine and arthropods from two.

Mammals. The species identified included three rodents (*R. villosissimus*, *L. forresti* and the introduced house mouse *M. musculus*), three dasyurids (*Planigale ingrami*, *S. macroura* and *S. douglasi*), two bats (a single *Saccolaimus flaviventris* from Eulolo and one other, tentatively identified as *Mormopterus beccarii*, from Huddersfield) and one cat (*Felis catus*) from Toorak. Identification of the cat (a kitten) based on teeth was confirmed by examination of the structure of hairs from the same pellet. The last three species, of which only a single individual of each was found, are not further considered. No *Sminthopsis crassicaudata*, a species known to the author to occur to the east of the study area at Leslew Downs (20°59′S, 142°55′E) and to the south-west at McKinlay (21°16′S, 141°17′E), were found among the remains of mammals in the pellets.

Rattus villosissimus (mass up to 280 g) is the largest of the mammals frequently preyed upon and up to four individuals, but never more than two with adult dentition, were found in a single pellet. Many pellets contained recognisable hair and post-cranial bones of this species but not the countable remains (dentaries). Of the smaller rodents as many as six *L. forresti* (mass up to 20 g), or five *M. musculus* (mass up to 25 g),

TABLE 3. The number of mammals in the pellets from each locality, and the number of pellets containing the remains of each of the six species of mammals in each locality. The number of individuals of each species is shown in parentheses and this number, as a percentage of the mammals in the locality, in square parentheses. For all localities the number of pellets, as a percentage of the total number collected (3,749), and the number of each species as a percentage of the total number of mammals (4,793) is shown in bold figures. Key to localities in Table 1.

Locality (no. mammals)	No. of pellets containing remains of each species,]% of mammals], (no. of individuals)					
	R. villosissimus	*L. forresti*	*M. musculus*	*P ingrami*	*S. macroura*	*S. douglasi*
EUR (295)	201 [81.0] (239)	14 [7.1] (21)	0	20 [8.5] (25)	1 [0.3] (1)	5]3.1] (9)
CRE (10)	2]20.0] (2)	0	1]10.0] (1)	8]70.0] (7)	0	0
N (185)	63 [36.2] (67)	7]3.8] (7)	2 [1.1] (2)	52 [50.8] (94)	7 [4.3] (8)	7]3.8] (7)
NW (85)	56 [85.9] (73)	0	1]1.2] (1)	5]8.2] (7)	1 [1.2] (1)	3]3.5] (3)
O (215)	96 [51.6] (111)	17 [9.8] (21)	0	31 [25.1] (54)	13 [8.8] (19)	7]4.7] (10)
L (131)	83]91.6] (120)	0	0	9 [7.6] (10)	0	1]0.8] (1)
AD (18)	3 [16.7] (3)	0	0	8]77.8] (14)	1]5.5] (1)	0
H (277)	152]57.8] (160)	12 [4.7] (13)	0	38 [19 1] (53)	6]2.5] (7)	39]15.9] (44)
EUL (635)	47 [8.7] (55)	194 [52.0] (330)	26]6.8] (43)	43 [10.2] (65)	98 [22.2] (141)	1]0.1] (1)
PD (271)	38]15.5] (42)	85 [72.7] (197)	3 [1.1] (3)	7 [3.3] (9)	12 [7.0] (19)	1 [0.4] (1)
CAR (18)	4 [33.3] (6)	3 [16.7] (3)	0	1]11.1] (2)	4 [38.9] (7)	0
ARM (33)	10 [39.4] (13)	0	0	7 [45.5] (15)	0	4 [15.1] (5)
WP (295)	88 [35.3] (104)	1]0.3] (1)	3 [1.0] (3)	81 [60.7] (179)	3 [1.0] (3)	5 [1.7] (5)
K (8)	0	0	0	2 [87.5] (7)	0	1 [12.5] (1)
EC (20)	15]80.0] (16)	0	0	3]15.0] (3)	0	1]5.0] (1)
LP (80)	53 [90.0] (72)	1 [1.25] (1)	0	3]5.0] (4)	1 [1.25] (1)	2 [2.5] (2)
T (252)	125 [54.3] (137)	35 [18.6] (47)	6 [2.4] (6)	26 [15.1] (38)	8 [4.4[(11)	13 [5.2] (13)
ED (10)	0	3]30.0] (3)	0	5 [50.0] (5)	1 [10.0] (1)	1 [10.0] (1)
ARD (664)	237 [39.4] (262)	6 [0.9] (6)	0	140 [55 0] (365)	18]3.5] (23)	8]1.2] (8)
CON (141)	87 [72.3] (102)	2 [4.3] (6)	0	8]22.0] (31)	0	1]1.4] (2)
B (47)	22]49.0] (23)	13 [44.7] (21)	0	1 [2.1] (1)	2 [4.2] (2)	0
M (613)	205]40.8] (250)	31 [8.3] (51)	33 [10.9] (67)	115 [32.5] (199)	8]1.5] (9)	29 [6.0] (37)
CAN (75)	57 [77.4] (58)	1 [1.3] (1)	0	9 [20.0] (15)	1]1.3] (1)	0
S (13)	0	0	0	7]76.9] (10)	3]23.1] (3)	0
Q (232)	79]37.1] (86)	5]2.6] (6)	0	79]47.4] (110)	19 [8.2] (19)	10]4.7] (11)
P (90)	21]26.7] (24)	4]5.5] (5)	0	11 [16.7] (15)	7 [8.9] (8)	31 [42.2] (38)
YD (9)	8 [88.9] (8)	0	0	0	0	1 [11 1] (1)
R (71)	58]84.6] (60)	3 [7.0] (5)	0	1 [5.6] (4)	1]1.4] (1)	1 [1.4] (1)
All localities % pellets % mammals	1810 (2093) **48.3** **43.7**	437 (745) **11.6** **15.5**	75 (126) **2.0** **2.6**	720 (1341) **19.2** **28.0**	215 (286) **5.7** **6.0**	172 (202) **4.6** **4.2**

were found in a pellet. Up to 14 individuals of the smallest dasyurid preyed upon, *P. ingrami* (mass up to 5 g), but usually only one or two of the larger dasyurids, *S. macroura* (mass up to 25 g) and *S. douglasi* (mass up to 70 g), were found in a pellet. If larger numbers of either *S. macroura* or *S. douglasi* were found they were always individuals assessed as juveniles. It was not uncommon to find the remains of more than one species of mammal in a single pellet. *R. villosissimus* was found in 48.3% of all pellets, *L. forresti* in 11.6%, *M. musculus* in 2.0%, *P. ingrami* in 19.2%, *S. macroura* in 5.7% and *S. douglasi* in 4.6% (Table 3, Figure 2). The localities at which the remains of each of these species were found in the pellets can be seen in Figure 3.

Birds. Seventeen species were identified. Of the 2053 individuals found in the pellets 30 (1.4%) could not be identified. The species most commonly preyed upon was the Zebra Finch, *Taeniopygia guttata* (75.9% of the total number of birds), followed by the Budgerigar, *Melopsittacus undulatus* (7.8%); Black-faced Woodswallow, *Artamus cinereus* (4.2%); White-winged Triller, *Lalage sueurii* (2.5%); Red-capped Robin, *Petroica goodenovii* (2.3%); White-winged Fairy-wren, *Malurus leucopterus* (1.6%); Singing Bushlark, *Mirafra javanica* (1.6%) as well as, each at less than 1.0%, swallows, *Hirundo* sp.; Golden-headed Cisticola, *Cisticola exilis*; Little Button-quail, *Turnix velox*; Red-chested Button-quail, *T. pyrrhothorax*; Baillon's Crake, *Porzana pusilla*; Brown Songlark, *Cincloramphus cruralis*; Rufous Songlark, *C. mathewsi*; Spiny-cheeked Honeyeater, *Acanthagenys rufogularis*; pigeons, *Phaps* sp. and Australian Pratincole, *Stiltia isabella*. Up to seven zebra finches (mass 12-13 g) were found in a single pellet, but seldom more than two of any other species.

Reptiles. Representatives of three families, the Gekkonidae, Agamidae and Scincidae, were found in the pellets. Most of the jaw bones, upon which the count of individuals was made, were very delicate and some may have been overlooked in the preparation of the pellets. Thus the total number of individuals found (907) may be an underestimate of the extent to which reptiles are preyed upon. Some of the 907 specimens could not be identified, and some were not placed to family with certainty but the majority were considered to be geckoes (762 individuals), followed by agamids (85) and skinks (11). Frequently large numbers of geckoes (up to 18) were found in a single pellet. Geckoes were often seen in numbers at roosting sites in old buildings and so may have been very readily accessible to resident owls. Confirmation of identity for some of the agamids was provided by the presence of portions of tail, still covered with rough skin. One agamid was further identified as a juvenile *Pogona brevis* (G. J. Witten pers. comm.).

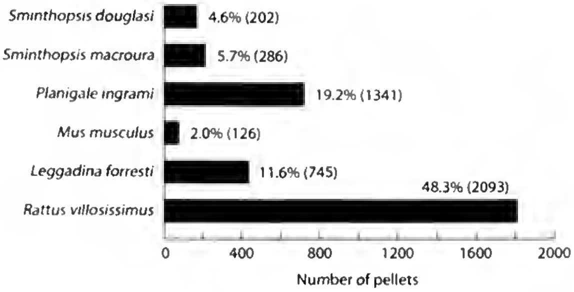


FIG. 2. Number of pellets containing each species of rodent (*R. villosissimus*, *L. forresti* and *M. musculus*) and dasyurid (*S. douglasi*, *S. macroura* and *P. ingrami*) preyed upon by the owls. The number of pellets, expressed as a percentage of all pellets examined (3,749), is shown at the end of each bar together with the number of individuals in parentheses.

Frogs. The remains of 373 frogs were found in the pellets. The ilium, upon which the estimate of numbers was based, ranged in length from 11 to 33 mm. Up to 20 individuals with short (13-14 mm) ilia were found in some pellets. Some indication of the size of the frogs preyed upon by the owls can be gained from measurements taken from the dry remains of an unidentified frog found in the study area. The body length of this specimen was about 75 mm, and the length of the ilium, 26.5 mm.

Arthropods. The remains of a few large spiders (*O. Araneae*) and one centipede (not further identified) were found in the pellets but the majority of the arthropods were insects, including beetles (*O. Coleoptera*), bugs (*O. Hemiptera*), mantids (*O. Mantodea*), and crickets and grasshoppers (*O. Orthoptera*). Grasshoppers were by far the most numerous of the arthropod prey items, and their eggs were frequently seen in the pellets. Some of the beetles and bugs were very small and they may have been ingested along with other prey such as frogs.

Other items. Seeds considered to have been ingested along with a prey item were found in many pellets, especially those containing bird remains. The large oval seeds of the paddy melon, *Cucumis melo*, were often found in pellets that contained the remains of *R. villosissimus*.

DISCUSSION

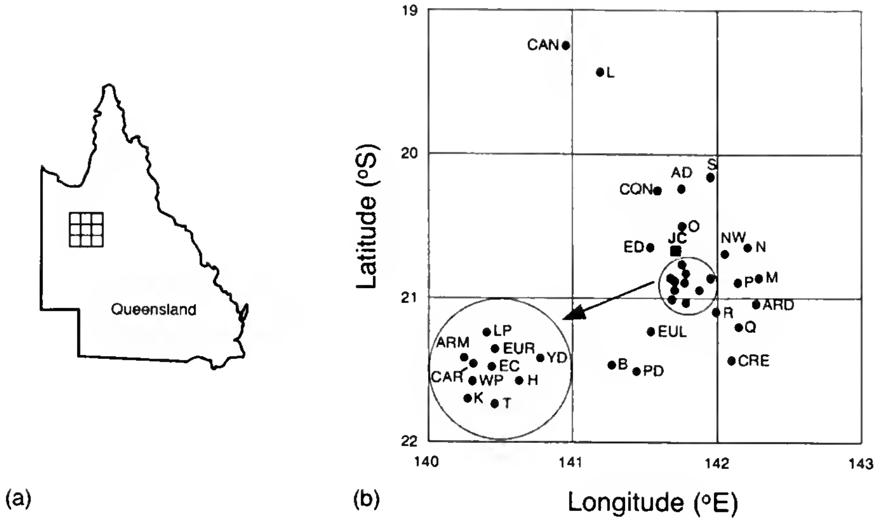
Consistent with the findings of studies on the diet of barn owls referred to above the prey of the owls in the study area in north-western Queensland included a variety of mammals, birds, reptiles, frogs and arthropods, with mammals forming the major component of the diet. The remains of individual mammals were found in three quarters of all pellets examined, and mammals were taken in greater numbers than individuals of other vertebrate taxa. All six species of small terrestrial mammals (3 rodents, 3 dasyurids) preyed upon were previously known to occur in the study area.

The most frequently taken species was *R. villosissimus* (43.7% of all mammals) and it was found in pellets from all but three localities. The area around Julia Creek is thought to be a 'refuge' area for *R. villosissimus* when it is not in plague proportions (Carstairs 1974). This species has been found to form a large component of the diet of the Barn Owl in some other studies e.g. Morton et al., 1977 (41.6%); Valente, 1981 (60.9%); Debus et al., 1999 (65%).

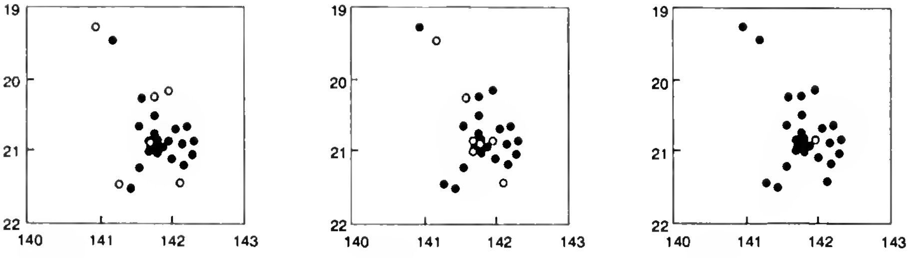
Smaller contributions to the diet were made by the other two species of rodents. In the case of *L. forresti* (15.5% of all mammals) the majority (527 of the 745 individuals) were found in pellets collected in July 1994 from just two of the nineteen localities in which it was detected. In one of the two, Eulolo, they constituted 52% of all mammals from that locality and at the other, Penola Downs, 73%. Although this species is seldom encountered in large numbers (Watts & Aslin 1981; Dickman et al. 2000) it seems that it was plentiful in these localities at the time the pellets accumulated. Morton & Martin (1979) also found it to form a large component of the diet of barn owls in 2 of their 11 study sites (59% at Coober Pedy and 20% at Warrina). The introduced house mouse, *M. musculus*, the least frequently preyed upon species (2.6% of all mammals) was found in pellets in only eight localities and the majority (110 of 126 individuals) were taken in just two; at Eulolo it constituted 6.8% of the mammals and at Minamere, 10.9%. When numbers of house mice were high at Fowler's Gap, N.S.W., they formed the bulk of the diet (up to 96.4%) of the owls (Morton & Martin 1979).

Planigale ingrami, the smallest of the three dasyurids, was the second most frequently preyed upon species (28% of all mammals) and it was found in pellets from all localities except one. *Sminthopsis macroura* (6% of all mammals) was preyed upon a little more frequently than *S. douglasi* (4.2%), and both species were found throughout the study area in a majority (21, 22 respectively) of the localities from which pellets were obtained. *Sminthopsis douglasi* has not previously been recorded as prey of the barn owl but *S. macroura*, which has a much larger distribution, has been found in owl pellets from other areas. Heywood & Pavey (2002) found it to be the major prey item (81.8% of identified items) in a sample of pellets from Connell's Lagoon on the Barkly Tableland at a time when numbers of *R. villosissimus*, a species known to occur in the same locality, were not found in the pellets. In the present study *S. macroura* never formed more than 38.9 % of the mammalian prey items at any one locality.

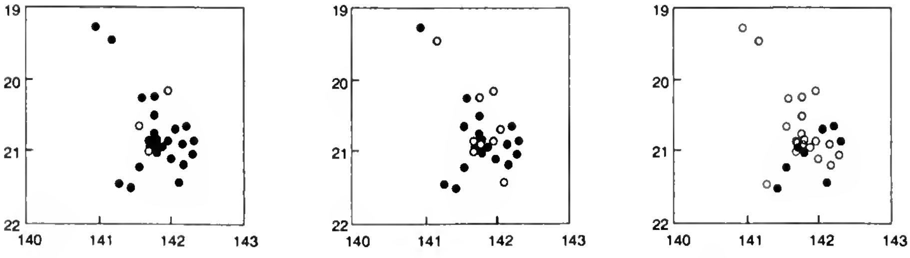
Among birds, the vertebrate taxon making the second largest contribution to the diet of the owls, the species most frequently preyed upon was the Zebra Finch, *T. guttata*. It is not known if this species was generally more abundant in the study area than others, or if some aspect of its behaviour makes it more susceptible to predation. It is known to nest in colonies throughout the year (Zann, 1996) and this may



(a) (b)



(c) *Sd* (d) *Sm* (e) *Pi*



(f) *Rv* (g) *Lf* (h) *Mm*

FIG. 3. Distribution of the species of dasyurids and rodents based on remains found in barn owl pellets collected in north-western Queensland. a) location of the study area; b) the collecting localities (see Table 1 for full names) around the town of Julia Creek (JC); c) *Sd* = *S. douglasi*; d) *Sm* = *S. macroura*; e) *Pi* = *P. ingrami*; f) *Rv* = *R. villosissimus*; g) *Lf* = *L. forresti* and f) *Mm* = *M. musculus*. A filled symbol indicates a record of a species; an open symbol, no record.

lead to several (up to seven) being taken at a time: barn owls have been observed to disturb communally roosting birds by beating their wings against the bushes in which the birds are roosting (Bunn et al. 1982).

No assessment of either seasonal or long term changes in the availability of prey species at the various localities within the study area can be made because the pellets were collected opportunistically over a period of 8-9 years, and in many cases the period over which the pellets had accumulated was not known. Differences between localities in the relative importance of the various prey taxa (see Tables 2 and 3) probably reflect what was readily available to the owls at the time they were present in the area. Frogs may form a larger component of the diet during wet periods, and insects such as grasshoppers when local infestations occur. The absence of a particular taxon from some localities may be due in part to the small number of pellets found at the locality.

From the information obtained on the distribution of the three species of rodents (*R. villosissimus*, *L. forresti* and *M. musculus*) and the three dasyurids (*S. douglasi*, *S. macroura* and *P. ingrami)* it seems likely that this suite of small mammals, with the possible exception of *M. musculus*, may be found throughout the study area. The absence of a species from the pellets from any one locality does not necessarily mean that the species does not occur there. *S. douglasi*, the species of particular interest, was not found in pellets collected from Crendon in 1993, but a live individual had been obtained from that locality in 1992. To date, live animals or carcasses of *S. douglasi* have been collected from 6 of the 28 localities, including Lyrian, Crendon, Nelia, Toorak, Proa and Yorkshire Downs (Woolley 1992; Woolley & Mifsud unpub. observations). Specimens have also been collected from other localities within the study area, including Euraba, Julia Creek, Edith Downs and Euroka (Woolley 1992), and one was found alive near Penola Downs (at 21°28'S, 141°10'E) in the wet season of 1997-98 (S. Malone pers. comm.). These localities all lie within the known range of the Julia Creek Dunnart (Kutt 2003).

ACKNOWLEDGMENT

My thanks are due to many people including all the property owners who allowed access to collecting sites; to B. Spreadborough, S. Malone, A. Alloway, S. O'Connor and especially G. Mifsud for assistance with the collection of owl pellets; to assistants, volunteers, students of Marsupial Biology at La Trobe University and the late Natalie Smith (who studied a subset of the collection for her Honours project in 1995) for help with the preparation of the pellets, and to G. Richards (bats), W. Boles (birds), P. Couper (reptiles), T. New and M. Cairns (arthropods), and B. Triggs (hair) for assistance with identification of material. As well as confirming the identity of a large number of the specimens of *L. forresti* A. Baynes provided valued assistance in the compilation of data and ideas for the presentation of the results. P. Green kindly assisted with the preparation of Figure 3. Financial assistance was received from La Trobe University and the Queensland Department of Environment and Heritage.

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A homonym of *Leptocleidus* Andrews, 1922 (Sarcopterygia, Plesiosauria, Leptocleidoidea, Leptocleididae) and a replacement name for *Leptocleidus* Mueller 1936 (Platyhelminthes, Monogenea).

Leptocleidus Andrews 1922 is an iconic plesiosaurian which is known from the Early Cretaceous of the United Kingdom, South Africa and Australia and is the root genus of the monophyletic family-level clade Leptocleididae (White 1940), as well as the superfamily-level clade Leptocleidoidea (Druckenmiller & Russell 2008) and the rank free higher clade Leptocleidia (Ketchum & Benson 2009). Andrews erected the genus on *L. superstes*, from the Wealden Clay of the United Kingdom.

Independently Mueller (1936) erected *Leptocleidus* upon the *L. megalonchus* for a taxon of platyhelminth flatworm. Shortly after its designation *Leptocleidus* Muller was synonymised with *Cleidodiscus* Muller 1934 by Mizelle & Hughes (1938) and later with *Urocleidus* Mueller 1936 by Price (1968). This nomenclatural arrangement was utilised until *Leptocleidus* Mueller was resurrected by Sullivan et al. (1978), who asserted its place as an independent genus.

Leptocleidus Mueller is invalid as the name is preoccupied and a new name must be chosen for the genus. We here designate *Muellerocleidus* gen. nov. as a replacement name for *Leptocleidus* Mueller 1936. The name honours Justus F. Mueller.

This new name eliminates the homonym and any confusion between the nomenclature of a Cretaceous plesiosaur and a modern platyhelminth.

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The Tribe Dufouriini (Diptera: Tachinidae: Dexiinae) recorded from Australia with the description of two new species

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Citation: Cantrell, B.K. & Burwell, C.J. 2010 03 15. The tribe Dufouriini (Diptera: Tachinidae: Dexiinae) recorded from Australia with the description of two new species. *Memoirs of the Queensland Museum – Nature* 55(1): 119-131. Brisbane. ISSN 0079-8835. Accepted: 8 August 2009.

ABSTRACT

Rondania albipilosa sp. nov. and *R. cinerea* sp. nov. are described and *Chetoptilia angustifrons* Mesnil is recorded from Australia, confirming the presence of the tribe Dufouriini in the Australasian Region. Other Australian species of *Rondania* are known, but remain undescribed because insufficient specimens are available to adequately resolve species limits. The distributions of *Chetoptilia* Rondani and *Rondania* Robineau-Desvoidy are extended to Australia. Two host records are noted, that of *Chetoptilia angustifrons* emerging from prepupae of a chrysomelid beetle and *Rondania cinerea* from an adult weevil. The presence of fully developed first instar larvae in the oviducts of specimens of *Rondania albipilosa* and *R. cinerea* indicate ovolarviparity, consistent with other Dexiinae. ☐ *Tachinidae, Dexiinae, Dufouriini, Chetoptilia, Rondania, new species, new record, Australia.*

The Tachinidae form a conspicuous element of the Australian dipteran fauna and are primarily parasitoids of other insects. The subfamily Dexiinae (= Proseninae of earlier authors) is a relatively distinct group of tachinids whose hosts are mainly Coleoptera (beetles). The Dufouriini are currently regarded as a tribe within the Dexiinae (see O'Hara & Wood 2004), but the included genera are poorly understood phylogenetically and have an unusual mix of specialised characters, indicating that the tribe is probably not monophyletic as presently constituted.

Cantrell (1988) and Cantrell & Crosskey (1989) noted the existence of specimens of Dufouriini (as Dufouriinae) from Australia in collections, but did not formally record the taxon from Australia because no species were described. Even today, the tribe is represented in Australian collections by relatively small numbers of specimens (often only of one sex) and the hosts remain unknown for many species.

This study was prompted by examination of a series of eleven adults of *Chetoptilia angustifrons* Mesnil from Queensland that were reared by CJB. Initially we thought that they represented a new species, but Dr D.M. Wood (CNC) recognised their similarity to *C. angustifrons* and loaned a male and female of the latter from the Philippines

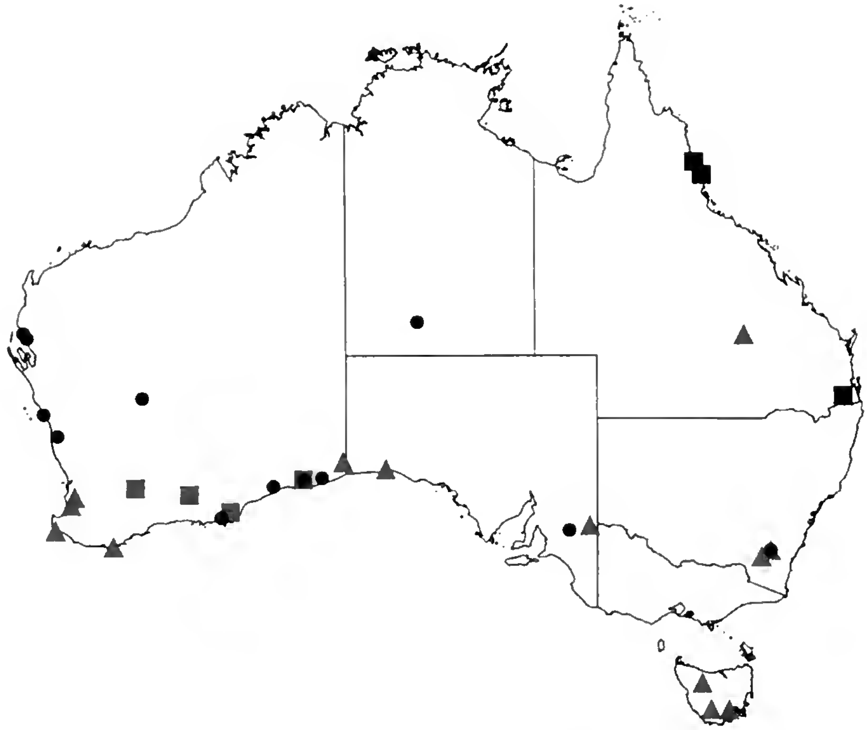

FIG. 1. Locality records for Australian Dufouriini. ■, *Chetoptilia angustifrons* Mesnil; ■, *Rondania albipilosa* sp. nov.; ●, *Rondania cinerea* sp. nov.; ▲, undescribed species of *Rondania*.

for comparison. It was immediately clear that all specimens were conspecific although the two older specimens from the Philippines were rather faded. This allowed the redescription of C. *angustifrons* based largely on Australian specimens.

The second part of this study was based on examination of *ca* 80 specimens of *Rondania* spp. from Australian insect collections (Fig. 1), enabling the description of two new species from southern Australia. However, other Australian species of *Rondania* remain undescribed because we were unable to resolve doubts about species limits from study of the small number of available specimens.

While our aim was to record the presence of the Dufouriini in Australia, we needed to consolidate our knowledge of the tribe by studying representatives of non-Australian genera and comparing them against the Australian taxa. This was achieved largely by referring to published literature, but we also examined specimens of a number of exotic taxa, including C. *angustifrons* from the Philippines, Neotropical *Comyops* van der Wulp and *Ebenia* Macquart and the European species *Dufouria chalybeata* (Meigen), *Eugymnopeza braueri* Townsend, *Rondania cucullata* Robineau-Desvoidy and *R. fasciata* (Macquart).

MATERIAL AND METHODS

Morphological terminology and abbreviations follow Crosskey (1973, 1976), except that ac not acr is used for the acrostichial setae and the

TABLE 1. Regional distribution of world genera of Dufouriini. Abbreviations: Neo, Neotropical; Nea, Nearctic; Palae, Palaearctic; Afro, Afrotropical; Aust, Australasian; Or, Oriental.

Genus	Neo	Nea	Palae	Afro	Aust	Or
Comyops	✓					
Ebenia	✓					
Euoestrophasia	✓					
Jamacaria	✓					
Oestrophasia	✓	✓				
Chetoptilia			✓	✓	✓	✓
Dufouria		✓	✓			
Eugymnopeza			✓			
Microsoma			✓			
Pandelleia			✓	✓		
Plesina			✓	✓		
Rondania		✓	✓		✓	
Mesnilana				✓		
Rhinophoroides				✓		

word seta or setae is omitted in combination with the relevant abbreviation e.g. pra means pre-alar seta.

Morphological abbreviations: ac, acrostichial setae; ad, anterodorsal; A.s., antennal segment; av, anteroventral; dc, dorsocentral setae; fr, frontal setae; ia, intra-alar setae; if, interfrontal area; iv, inner vertical setae; mmp, median marginal pair of setae on abdominal tergites; oc, ocellar setae; orb, orbital setae; ov, outer vertical setae; pd, posterodorsal; pf, parafacials; pfr, parafrontals; pra, pre-alar setae; post-, postsutural; pv, posteroventral; sa, supra-alar setae; stpl, sternopleural setae; T, abdominal tergite; v, ventral.

All measurements are in millimetres. Measurements of body length and V:HW (ratio of width of vertex at level of posterior ocelli to maximum width of head across eyes, both viewed dorsally) are expressed as means with ranges given in brackets; number of specimens measured is also shown.

Institutional abbreviations: ANIC, Australian National Insect Collection, Canberra; CNC, Canadian National Collection of Insects, Ottawa; QM, Queensland Museum, Brisbane; UQIC, University of Queensland Insect Collection, Brisbane; WAM, Western Australian Museum, Perth.

SYSTEMATICS

As stated above, an in-depth study of the Dufouriini was never our intention. However, our literature- and limited specimen-based review of the tribe allowed us to place the Australian species within *Chetoptilia* and *Rondania* with a degree of confidence.

The Dufouriini are known from all major zoogeographic regions except Oceania (Barraclough 2005; Cantrell & Crosskey 1989; Crosskey 1976, 1984; Guimarães 1977 (as Oestrophasiini); Herting 1984; O'Hara & Wood 2004) with the greatest generic diversity in the Palaearctic, Afrotropical and Neotropical regions (Table 1). The genera are diverse in appearance and the tribe is almost certainly not monophyletic as presently constituted. However, all genera for which the hosts are known parasitise Coleoptera, particularly Chrysomelidae and Curculionidae.

The composition of Dufouriini remains open to debate as several genera remain poorly studied. Based upon our brief overview, we include fourteen genera in the tribe, distributed as shown in Table 1. *Anthomyiopsis* Townsend, *Freraea* Robineau-Desvoidy and *Rossimyiops* Mesnil are no longer regarded as Dufouriines (Herting 1984; O'Hara and Wood 2004; Cerretti *et al.* 2009) and we exclude the problematic genus *Kambaitimyia* Mesnil. The doubtful position of the latter was discussed by Crosskey (1976) when he provisionally included it in the Oriental Dufouriini.

DIAGNOSIS OF AUSTRALIAN DUFOURIINI

The Australian Dexiinae comprise three tribes, Dexiini, Dufouriini and Rutiliini. As inferred above, it is difficult to succinctly characterise the Dufouriini to facilitate their easy recognition and the Australian fauna is no exception. Their muscoid facies and enlarged subscutellum clearly identify them as Tachinidae, but assigning specimens to a subfamily or tribe is often problematic, particularly if host data are lacking. Small size (length 3-5 mm), bare eyes and a long petiolate cell R5 will help to identify *Rondania* as belonging to the Dexiinae, as will the small size (4-5 mm), bare eyes (with enlarged upper facets in the male), metallic blue/green colour and cell R5 open or just closed at the wing margin in *Chetoptilia*. Knowledge that the flies were reared from beetle hosts would help confirm placement in the Dexiinae.

The Dufouriini may be distinguished from the Australian Dexiini and Rutiliini by characters including small size, bare parafacials, lack of a facial carina, bare propleuron, scutellum with 2-3 pairs of marginal setae and their generally non-bristly facies.

Diagnosis. Head: eye bare, strongly approximated or holoptic (with upper eye facets sometimes enlarged) in ♂ but widely separated in ♀ (facets of uniform size); ocellar triangle prominent in ♂ because of eye approximation; facial carina absent; antennal axis at or below level of eye middle; epistome not prominent, but sometimes extending anterior to profrons in profile; facial ridge bare; pf bare; antenna short, usually falling well short of epistome; arista micropubescent to plumose; oc present; orb present in ♀, absent in ♂; iv usually present in both sexes, but often weak and hairlike in ♂; ov variable, often absent or indistinguishable from postocular setulae; fr present in both sexes, usually in irregular rows; vibrissa present, but often not clearly distinguished from other setae on genal margin; palp present, well-developed; mouthparts (mentum plus labellum) normally developed, shorter than head height.

Thorax: prosternum and propleuron bare; chaetotaxy often irregular, with variation in both numbers and strength of setae, particularly dorsally; humeral callus usually with 2 setae; pra absent or weakly present, smaller than first post-ia; usually 2 post-ia; 2(3)+3 dc; 1(2)+2(3) ac; 2 stpl, anterior seta usually weaker; scutellum with 2 or 3 pairs of marginal setae, usually with strong apicals and basals, weaker laterals present or absent; wing with cell R_5 narrowly open, closed at the margin, or petiolate; leg setae often reduced.

Abdomen: T1+2 variable, from weakly excavate to excavate virtually to hind margin; chaetotaxy often irregular, with variation in both numbers and strength of setae; ovipositor a simple eversible tube, typically concealed in *Chetoptilia*, but usually at least partly protruding from preabdomen in *Rondania*.

KEY TO AUSTRALIAN GENERA AND SPECIES OF DUFOURIINI

Users of this key should be aware that there are several undescribed Australian species of *Rondania* (see discussion under *Rondania* below).

1. Arista plumose; cell R_5 narrowly open or just closed at wing margin; bend of M rounded and vein approaching wing margin at an acute angle (Fig. 2A); T1+2 excavate almost to hind margin; thorax, including legs, and abdomen dark, conspicuously shining black or green-black; thorax with thin dusting of silver pollinosity under some angles of light, particularly in ♀; ♂ eyes holoptic and upper eye facets conspicuously enlarged (Fig. 2B); ovipositor not usually visible externally.... *Chetoptilia angustifrons* Mesnil.

— Arista bare or pubescent; cell R_5 closed and distinctly petiolate; bend of M evenly rounded and vein approaching R_{4+5} at almost a right angle (Fig. 4A, B); T1+2 excavate at most in basal half; body colour grey-toned often with pale or yellow areas on head, legs or abdomen; ♂ eyes holoptic or dichoptic, with or without enlarged upper eye facets; ovipositor normally visible as a simple tubular structure extending beneath abdomen (*Rondania* spp.) 2

2. Abdomen grey (with darker rings around setal bases) in ♀, in ♂ similar medially and distally but lateral areas of T1+2 to T4 yellow or pale; [thoracic pleura dark-haired; scutellum with 3 pairs of marginal setae, weak laterals present; ♂ eyes narrowly separated by distance approximately equal to that between lateral ocelli; ♀ vertex broader (V:HW > 0.35)] ....*R. cinerea* sp. nov.

— Abdomen predominantly pale or yellow 3

3. Abdomen yellow, without pattern of dark spots or bands; thoracic pleura pale-haired; scutellum with 2 pairs of marginal setae, laterals absent; [♂ eyes holoptic; ♀ vertex relatively narrow (V:HW < 0.25)] ...... *R. albipilosa* sp. nov.

— Abdomen yellow, often shining, with pattern of dark markings, typically small median and lateral spots or transverse bands on T3 to T5, but sometimes limited to median spots; if dark abdominal markings absent, then either scutellum with 3 pairs of marginal setae or pleura dark-haired.....undescribed species of *Rondania*.

Chetoptilia Rondani

Chetoptilia Rondani, 1862: 166; Crosskey, 1976: 176; Herting, 1984: 159.

Chetoptilia is an Old World genus comprising six species: *C. puella* (Rondani) from Europe (type species); *C. plumicornis* Villeneuve from Africa; *C. cyanea* Mesnil and *C. metallica* Mesnil from Madagascar; *C. burmanica* (Baranov) from Asia; and *C. angustifrons* from Asia and Australia. *Chetoptilia* species are characterised by dark metallic colouration, a plumose or pubescent arista, a bare prosternum, three pairs of marginal scutellar setae, cell R_5 open or just closed at the wing margin and T1+2 excavate almost to the hind margin. The eyes are bare (sparsely short-haired at high magnification), holoptic or closely approximated in the male, with the upper facets enlarged.

Chetoptilia angustifrons Mesnil
(Figs 1, 2, 3A-B)

Chetoptilia angustifrons Mesnil, 1953: 164; Crosskey, 1976: 176.

Material. Philippines, 1♂, Luzon, Manila, xi.1914 (CNC); 1♀, Luzon, Limay, 21.iv.1913, G. Boettcher (? type, abdomen missing) (CNC). [Both specimens from the L. P. Mesnil collection labelled *Paraptilops angustifrons* Mesn.]. AUSTRALIA, QUEENSLAND, 4♂, 1♀, Ellis Beach, 16°44'S, 145°39'E, 28.iv.1998, C.J. Burwell and C.M. Rodriguez, ex prepupa of *Aspidimorpha deusta* on *Ipomaea pes-caprae* (Convolvulaceae); 3♂, 2♀, Bramston Beach, 17°21'S, 146°01'E, 3.v.1998, C.J. Burwell and C.M. Rodriguez, ex prepupa of *Aspidimorpha deusta* on *Ipomaea pes-caprae* (Convolvulaceae); 1♂, 16 km N of Boonah, 27°54'S 152°41'E, 14–15.xii.1996, C.J. Burwell, ex prepupa of *Cassida* sp. on *Polymeria calycina* (Convolvulaceae). All QM except as indicated.

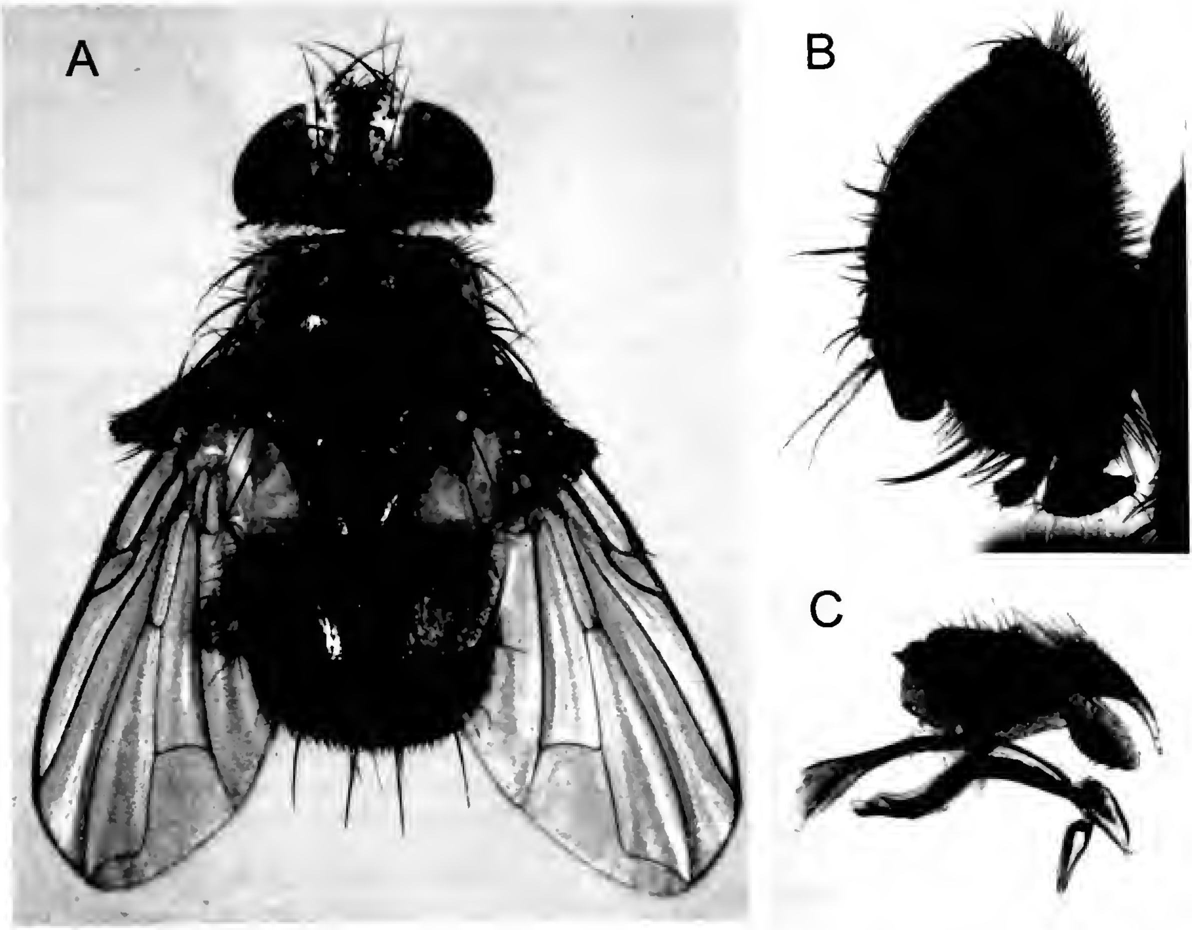

FIG. 2. *Chetoptilia angustifrons* Mesnil. A, ♀, dorsal view; B, ♂ head, lateral view; C, ♂ terminalia, lateral view.

Diagnosis: Small flies, shining green-black, but prescutum and scutum with fine dusting of silver pollinosity in female; tibiae and tarsi somewhat duller; antenna and palp dull yellow/orange; arista plumose; face dull silver pollinose; eyes bare (sparsely short-haired at high magnification); ♂ eyes holoptic, ♀ eyes widely separated; occiput pale-haired except for some dark setulae adjacent to postocular row; T1+2 to T5 lacking discal setae; ovipositor fully retracted in all available specimens.

Re-description. *Male*. Body length 4.62 (4.1 – 4.8) (n=9). Head: eyes holoptic, facets enlarged in slightly more than upper half, with clear line of demarcation between upper and lower facets (Fig. 2B); if area triangular, reddish-brown; pf, pfr and face faintly silver pollinose; ocellar triangle prominent; oc weak, hairlike, proclinate; 4-5 pairs of irregular fr between lunula and eye convergence; orb absent; iv convergent, often crossed at tips; ov not much stronger than postocular setulae; antenna yellow, inserted at or below level of middle of eye, short, not reaching epistome; arista yellow, plumose; epistome not prominent; vibrissa inserted at level of epistome, a few fine hairs above; facial ridge bare; pf bare; gena black-haired; mentum relatively short, not as long as palp, latter yellow with darker bases; occiput dark, pale-haired except for some dark setulae adjacent to postocular row.

Thorax shining black; small pra present, much weaker than first post-ia; 1+2 ia; 2(?3)+3 dc; 1(?2)+2 ac; propleuron and prosternum bare; 2 stpl, anterior seta weaker; humeral callus with 2 setae; scutellum with 3 pairs marginal setae (strong crossed apicals and slightly weaker basals and laterals); fore tibia with 1 pv; mid tibia without submedian v but with 1 submedian ad and 2 weaker pd; hind tibia with irregular ad and pd rows; wing with cell R_5 open or just closed at wing margin; m-cu weakly sinuate, shorter than length of M from insertion of m-cu to bend; 2nd costal sector haired ventrally; basal node of R_{4+5} with a few fine dark setulae on both wing surfaces; veins yellow; wing membrane clear, but upper and lower calypter opaque, smoky-coloured.

Abdomen shining black; T1+2 excavate almost to hind margin, without mmp; T3 with mmp; T4, 5 with marginal row of setae; T3-5 subequal in length dorsally. Terminalia as in Fig. 2C.

Female. (Fig. 2A) Body length 4.3 (4.2 – 4.4) (n=3); V:HW 0.25 (0.24 – 0.26) (n=4). Similar to male except as noted. Head: eyes broadly separated, all facets of uniform size, if area matt reddish-brown, pf, pfr and face faintly silver pollinose; gena and area between eye margin and postocular row of fine setulae lightly silver pollinose; 4–6 irregular fr; 2 pro-, 1 reclinate orb; oc strong, proclinate; iv strong, crossed; ov weaker, diverging; A.s.3 relatively longer, its tip almost reaching epistome. Thorax: prescutum and scutum with fine dusting of silver pollinosity; mid tibia with submedian v; upper and lower calypter translucent white. Abdomen: ovipositor not visible externally in specimens examined.

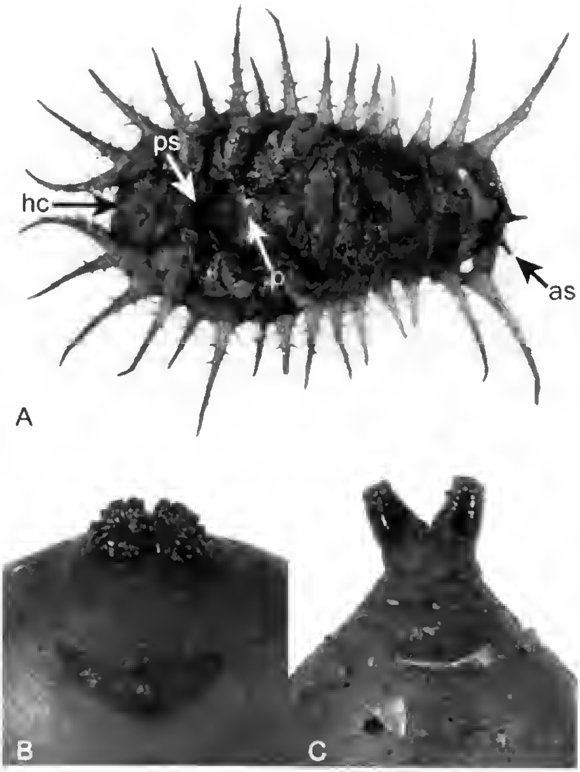

FIG. 3. Puparia. A, *Chetoptilia angustifrons* Mesnil, dorsal view showing puparium in remains of beetle host prepupa; B, C, ventral view of posterior part of puparium showing non-functional posterior larval spiracles: B, *Chetoptilia angustifrons* Mesnil C, *Rondania cinerea* sp. nov. as, anterior (larval) spiracles; hc, head capsule of beetle prepupa; p, puparium; ps, posterior (larval) spiracles.

Puparium. Oblong, brown, with black non-functional posterior larval spiracles raised above puparial cuticle (Fig. 3B), in end view larval spiracles semicircular, narrowly separated, each comprising about 12 elongate slits arranged in a crescent; non-functional anterior larval spiracles projecting anteriorly on diverging cuticular protuberances, each spiracle with a narrow black base and bearing about 10 terminal minute openings. Puparial respiratory horns absent.

The puparium lies within remains of host prepupa (Fig. 3A), with both the anterior and posterior ends of the puparium erupting through the ventral cuticle of the host prepupa. The posterior end projects from between the bases of the fore and mid legs of the host prepupa so that the posterior (larval) spiracles on the puparium are located just behind the head capsule of the beetle. The anterior end of the puparium projects between the 5th and 6th or the 6th and 7th abdominal segments of the host prepupa, and the anterior (larval) spiracles are clearly exposed.

Remarks. *Chetoptilia angustifrons* possesses all the generic characters noted above and was reared from a chrysomelid leaf beetle larva; this host association is also typical of the genus. Based on literature (Baranov 1938; Mesnil 1953, 1968; Tschnorsnig and Herting 1994; Villeneuve 1942) the plumose arista separates *C. angustifrons* from *C. cyanea* and *C. metallica* from Madagascar and *C. burmanica* from Myanmar, all of which have a pubescent arista. The holoptic eyes in the male and lack of discal setae on T5 distinguish *C. angustifrons* from the European *C. puella* and *C. plumicornis* from Africa.

As noted above, the north Queensland specimens of *C. angustifrons* were reared from *Aspidimorpha deusta*, a hispine chrysomelid beetle which occurs in northern Australia, New Guinea, Timor, Indonesia and Malaysia (Borowiec 1992; Boroweic & Świętojańska 2008), suggesting the fly may have a wider distribution than presently known. Like *C. angustifrons*, *A. deusta* has been recorded from the Philippines (Leyte Island; Medvedev 1995), although Medvedev suggested the beetle had been introduced. Consequently, the identity of the host of *C. angustifrons* in the Philippines requires confirmation.

Rondania Robineau-Desvoidy

Rondania Robineau-Desvoidy, 1850: 192; Herting, 1984: 160.

Rondania is primarily an Old World genus, comprising nine species including *R. albipilosa* sp. nov. and *R. cinerea* sp. nov. described below from Australia; *R. cucullata* Robineau-Desvoidy (type species), *R. dimidiata* (Meigen), *R. dispar* (Dufour), *R. fasciata* (Macquart) and *R. rubens* Herting from mainland Europe; plus *R. insularis* (Bigot) (Canary Islands). The sole New World representative is *R. dorsalis* (Coquillett) from North America. We examined specimens of *R. cucullata* and *R. fasciata* in addition to the Australian species. Several undescribed Australian species of *Rondania* are also known, but cannot be named at present because insufficient specimens are available to accurately resolve species limits.

Rondania is characterised by grey and yellow/orange colouration; a pubescent or bare arista; cell R_5 closed at the wing margin or petiolate and T1+2 excavate only basally.

All Australian specimens of *Rondania* examined were collected below the Tropic of Capricorn (23°26.5´S), mostly from mainland Australia but with a few records from Tasmania (Fig. 1). *Rondania cinerea* sp. nov. is a distinctive species with a grey pollinose abdomen, described from the type series collected in southern Western Australia, supplemented by specimens collected in Canberra and a few intervening localities. *Rondania albipilosa* sp. nov. is a smaller species with pale-haired thoracic pleura; it is known only from Western Australia, where the distributions of both species overlap to some extent in the Esperance to Madura region.

Confidently defining the species limits of the two *Rondania* species described below is complicated by a number of specimens which closely resemble those of the type series but differ in abdominal colour pattern, having more extensive dark markings. Consequently we have taken a conservative approach and excluded these specimens from the type

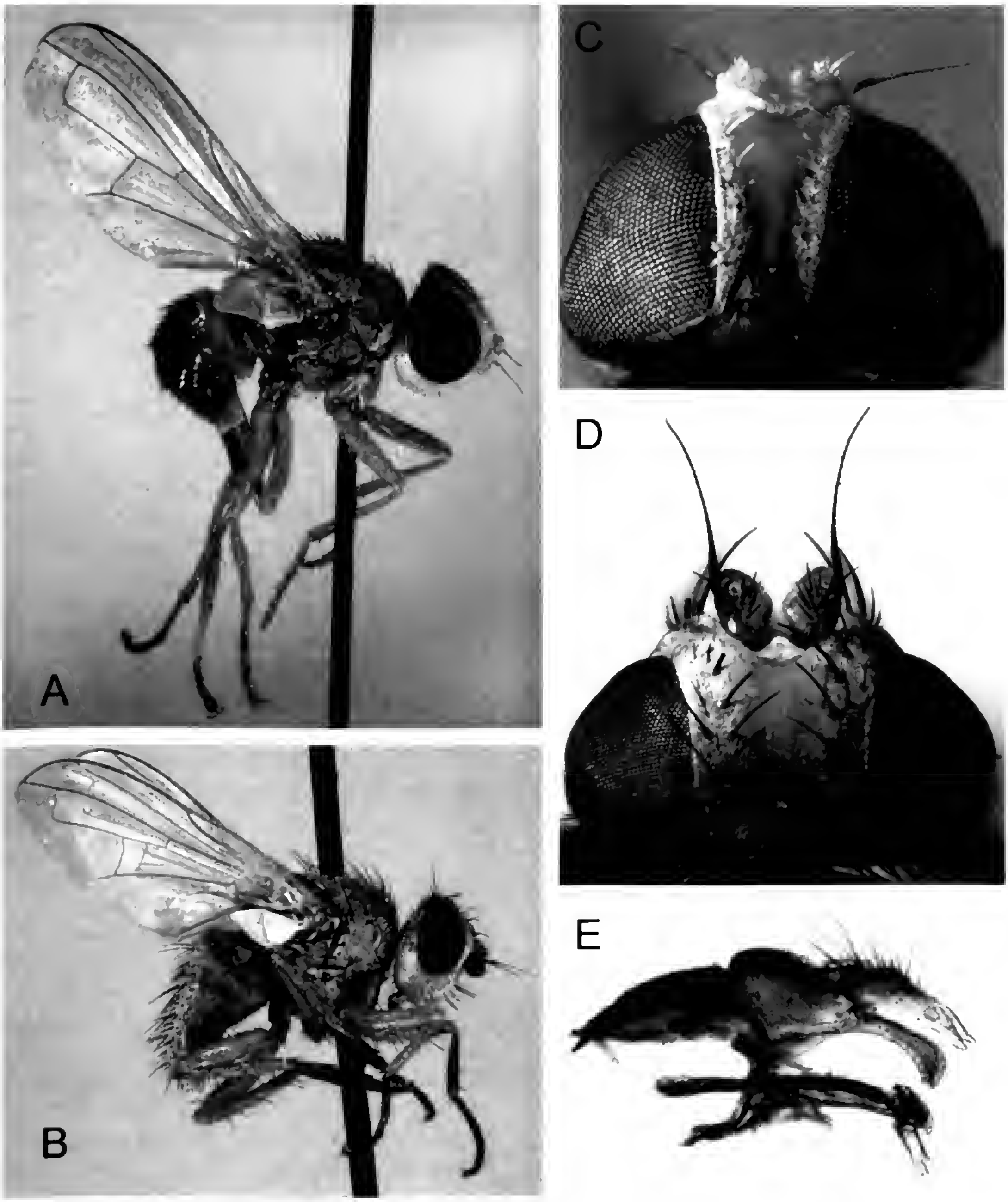

FIG. 4. *Rondania* spp. nov. A, C, *R. albipilosa* sp. nov.: A, ♂ lateral view; C, ♀ head, dorsal view; B, D, E, *R. cinerea* sp. nov.: B, ♂ lateral view; D, ♀ head, dorsal view; E, ♂ terminalia, lateral view.

series, but briefly discuss them in the remarks sections of the descriptions. Similar variations in abdominal colour pattern are also found in a number of the undescribed Australian species, as well as variation in the length of the petiole of cell R_5. Whether colour patterns and petiole length are highly variable intraspecifically, or these specimens are specifically distinct is uncertain and may only be resolved by the acquisition of additional material.

Roudania albipilosa sp. nov.
(Figs 1, 4A, C)

Etymology. Latin *albus*, white and *pilus*, hair; referring to the pale-haired pleura in this species.

Material. Holotype ♀: Western Australia, The Humps, 19 km N Hyden, 32°19´S, 118°57´E, 10.i.1986, G. and A. Daniels, mv lamp (QM). PARATYPES: WESTERN AUSTRALIA, 4♀, same data as holotype (UQIC); 1♀, 57 km S of Norseman, 32°38´S, 121°32´E, 31.xii.1985, G. and A. Daniels, mv lamp (UQIC); 1♂, 2♀, 8 miles (13 km) SW Mt Ragged, 33°27´S, 123°28´E, 22.iii.1968, I.F.B. Common and M.S. Upton (ANIC). OTHER MATERIAL: WESTERN AUSTRALIA, 1♀, Madura, 31°56´S, 126°58´E, 20.iii.1968, I.F.B Common & M.S. Upton (abdomen in glycerine) (ANIC).

Diagnosis. Small flies; head, legs and abdomen yellow, thorax grey pollinose on prescutum and scutum, but scutellum dark shining, without pollinosity; pleura grey pollinose, pale-haired; chaetotaxy difficult to discern on prescutum and scutum of ♀, except for posterior dc and ac; scutellum with 2 pairs of marginal setae; ♂ eyes holoptic, ♀ eyes narrowly separated.

Description. *Female.* (Fig. 4A, C) Body length 2.8 (2.4 - 3.0) (n=4); V:HW 0.215 (0.20 - 0.23) (n=9). Head: generally pale; if area relatively narrow, matt yellow; pfr and pf yellow with thin silver pollinosity; ocellar triangle dark; upper occiput dark except centrally; eye bare; oc proclinate; 2 proclinate orb; 5-6 pairs fr; small iv present, convergent but not crossed; ov not discernible from postocular setulae; antenna yellow-orange, arista somewhat darker; setae and hairs of head generally pale, including weak vibrissa, but upper fr, orb, oc and iv darker.

Thorax densely grey pollinose on prescutum and scutum, but scutellum dark shining, without pollinosity; pair of thin medial dark vittae on prescutum; chaetotaxy difficult to discern on prescutum and scutum except for posterior dc and ac; scutellum with 2 pairs of marginal setae (apicals and basals); stpl 0+1; dorsal setae and hairs dark, those on pleura pale; legs yellow, mostly pale-haired; fore femur with pd and pv setal rows; mid tibia without submedian v seta; hind femur with ad setal row; cell R_5 closed, petiole at least as long as length of M from bend to its junction with R_{4+5}; row of approximately 5 dark setulae on R_{4+5} between node and r-m crossvein; m-cu joining M much closer to r-m than bend.

Abdomen yellow-brown, without pollinosity, dark-haired, without discernible setae; basal half of T1+2 excavate; narrow dark bands on posterior margins of T4 and T5 in some specimens; pale tubular ovipositor exserted and recurved beneath body in many specimens, sometimes extending beyond head; T5 longer than T4.

Male. Body length 4.0 (n=1). Similar to ♀ except as noted. Head: eyes holoptic, facets enlarged in slightly more than upper halves; if area triangular due to eye convergence; ocellar triangle and vertex dark; ocellar triangle prominent, with weak proclinate oc; 7-8 pairs of weak fr between level of lunula and eye convergence; antenna yellow, but arista and dorsal edge of A.s.3 somewhat darker; A.s.1 and 2 with black setulae dorsally; poorly differentiated vibrissa and setae along margin of oral cavity black; epistome and profrons coincident in profile; gena with black hairs anteriorly, otherwise pale-haired; palp and mentum yellow.

Thorax finely silver pollinose dorsally on prescutum and scutum; 4 narrow dark vittae on prescutum and scutum; dorsal setae dark;

pleura grey pollinose, pale-haired; thoracic setae stronger than in ♀: humeral callus with 2 setae; pra absent; 1 sa; 1 weak post-ia near suture separating postalar calli; 2+4 dc, posterior strongest; 2+?3 ac; legs yellow with black hairing; hind tibia with sparse ad and pd setal rows.

Remarks. The following females in ANIC are similar to those of *R. albipilosa* but have more pronounced dark markings on the abdomen as indicated below. The taxonomic significance of these variant abdominal colour patterns is undetermined. MATERIAL. WESTERN AUSTRALIA, 1♀, 1 km NNW Eucla Pass, 31°05´S, 128°52´E, 10.iv.1983, E.S. Nielsen and E.D. Edwards - thin dark marginal bands on T1+2-5; 1♀, 7 km S by E of Albany, 35°05´S, 117°54´E, 18.iv.1983, E.S. Nielsen and E.D. Edwards – posterior portion on T3 and all T4 and T5 dark. SOUTH AUSTRALIA, 1♀, 14 km WNW Renmark, 34°07´S, 140°37´E, 7.xi–13.xii.1995, K. R. Pullen, flight intercept/ pitfall trap – small median and lateral dark spots on T3, T4 and scutellum lightly dusted with silver pollinosity.

The female of *R. albipilosa* has a distinctive facies, characterised by its relatively small size (<3.0mm), extensive pale coloration and reduced thoracic chaetotaxy. Although the male has more normally developed thoracic chaetotaxy, it otherwise generally resembles the female. This combination of characters sets it apart from *R. cucullata* which is larger, robustly setose and has extensive grey colouration. Other exotic species of *Rondania* also more closely resemble *R. cucullata* as discussed below under *R. cinerea* sp. nov.

Rondania cinerea sp. nov.
(Figs 1, 3C, 4B, D, E)

Etymology. Latin, *cinereus*, ash-coloured, grey; referring to the grey body colour.

Material. Holotype ♀: Western Australia, 19 miles (30 km) N by E of Mundrabilla HS, 31°51´S, 127°51´E, 16.x.1968, Britton, Upton, Balderson (ANIC). PARATYPES: WESTERN AUSTRALIA, 3♀, same data as holotype; 1♀, Mt Boyatup, 74 miles (118 km) E of Esperance, 33°44´S, 123°02´E, 23.iii.1968, I.F.B. Common and M.S. Upton; 1♀, 28 miles (45 km) W of Madura, 31°56´S, 126°58´E, 30.iv.1968, I.F.B. Common and M.S. Upton; 1♀, Drummond's Cove, Geraldton, 28°46´S, 114°16´E, 26.ix.1972, N. McFarland, at light; 2♀, 5 km ENE Caiguna, 32°15´S, 125°32´E, 11.iv.1983, E.S. Nielsen and E.D. Edwards; 3♀, 30 km SE by S Carnarvon, 25°07´S, 113°50´E, 29.iv.1971, Upton and Mitchell; all in ANIC; 5♂, 20 km N Eneabba, 29°49´S, 115°16´E, 21-23.ix.2002, G. and M. Wood, in WAM. OTHER MATERIAL: WESTERN AUSTRALIA, 6♀, 30 km SE by S Carnarvon, 25°07´S, 113°50´E, 29.iv.1971, Upton and Mitchell; 2♂, Sandstone, 27°59´S, 119°18´E, emerged 22.vii.1976 ex adult weevil *Acantholophus niveovittatus* collected 30.vi.1976, A.M. and M.J. Douglas. NORTHERN TERRITORY, 1♂, Tempe Downs, 24°23´S, 132°25´E, 11.ix.1963, P. Ranford. SOUTH AUSTRALIA, 1♀, Blanchetown, 34°21´S, 139°37´E, 26.xii.1966, Z. Liepa. AUSTRALIAN CAPITAL TERRITORY, 1♀, Canberra, 35°17´S, 149°13´E, 17.xi.1929, I.M. Mackerras; 11♂, Canberra, 12.xi.1936, W.J. Rafferty; 5♀, Canberra (Black Mtn), collected 7.ii.1957, 20.ii.1960, 12.xii.1960, 7.xi.1961 and 3.v.1967, I.F.B. Common, light trap. All in ANIC.

Diagnosis. Small flies; thorax and abdomen grey (latter pale laterally in ♂); head and legs yellowish in ♀, dark in ♂; pleura dark-haired; setae on prescutum and scutum of ♀ normally developed (not reduced as in *R. albipilosa*) and scutellum with 3 pairs of marginal setae; ♂ eyes narrowly separated, ♀ eyes broadly separated.

Description. *Female.* (Fig. 4B, D) Body length 3.6 (3.0 – 4.5) (n=21); V:HW 0.39 (0.37 – 0.40) (n=21). Head yellow; eyes bare, broadly separated, pfr not much narrowed dorsally; if area dull yellowish; pfr, pf and gena with yellow ground colour and silver pollinosity; vertex silver pollinose, upper part with dark ground colour and hairing, lower part yellow with pale hairing; A.s.1 and 2 yellow, A.s.3 darker, especially on outer surface; arista dark, bare; antenna short, falling short of epistome by a distance approximately equal to length of A.s.3; epistome slightly more pronounced than profrons in profile; palp yellow; mentum somewhat darker; oc prominent, proclinate; 4-5 pairs irregular fr; 2 pro-, 1 reclinate and laterally divergent orb; iv convergent but not crossed; ov smaller than iv, divergent; vibrissa relatively strong, row of weaker bristles below (along genal margin) and 1 above vibrissal insertions; gena dark-haired.

Thorax grey, with darker rings around setal bases, black-haired; humeral callus with 2 setae; pra absent; 1(?2)+2 ia; 2+3 dc; 2(3)+3 ac; scutellum with 3 pairs of marginal setae, strong crossed apicals, strong basals and weak laterals; legs yellow, tarsi somewhat darker; fore femur with pd and pv setal rows; mid tibia with 2 ad and 1 submedian v setae; hind femur with ad setal row; hind tibia with 2-3 ad, 1 av and 2 pd setae; wing veins yellow; cell R_5 closed, petiole at least as long as the length of M from the bend to its junction with R_{4+5}; node of R_{4+5} with 4-5 small black setulae; m-cu joining M closer to bend than r-m.

Abdomen grey, with darker rings around setal bases and shifting silver/bronze pollinosity; T1+2 excavate in basal half, with mmp; T3 and T4 with marginal row of setae; T5 with ill-defined rows of discal and marginal setae; pale tubular ovipositor partly protruding beyond tip of T5 in some specimens.

Male. Body length 3.7 (3.2 – 4.0) (n=15). Similar to ♀ except as noted: Head: ground colour mainly dark, with silver pollinosity; antenna pale yellow, although A.s.3 and arista darker; frons very constricted, narrowest part approximately as wide as distance between lateral ocelli; eye facets enlarged dorsally, with clear line of demarcation visible in well-preserved specimens; weak iv and ov, converging but not crossed; row of fine postocular setulae. Thorax: legs dark. Abdomen pale laterally on T1+2-4, pale area just extending to T5. Terminalia as in Fig. 4E.

Puparium. Oblong, brown, tapering posteriorly towards non-functional larval posterior spiracles, these set on diverging shining black cylindrical bases, narrowly separated medially (Fig. 3C); each spiracle comprises about 12 small slits, arranged in a crescent. Anterior larval spiracles missing from 2 available puparia. Puparial respiratory horns absent.

Remarks. The following males in WAM are similar to *R. cinerea*, but have yellow abdomens with median dark markings on T3-5 and a more rounded bend in M1. The terminalia of one male were briefly examined and showed differences in the shape of the cerci and surstyli compared with *R. cinerea*, suggesting they are a distinct species. MATERIAL. WESTERN AUSTRALIA, 2♂, 20 km N Eneabba, 21-23.ix.2002, G. and M. Wood.

Roudania cinerea has a facies most closely resembling *R. cucullata*, but may be distinguished by the petiolate cell R_5 (open or just closed at wing margin in *R. cucullata*). *Roudania dimidiata* (Meigen) and *R. dispar* (Dufour), however, have a petiolate cell R5, but the petiole is relatively short in both species, at most a third the length of M from the bend to its junction with $R_{4+5.}$ The petiole in *R. cinerea* is at least as long as the length of M from the bend to its junction with R_{4+5}. *Roudania fasciata* (Macquart) has a long petiole like *R. cinerea*, but is distinguished by its extensive yellow abdominal markings. [*R. cinerea* was not compared against literature descriptions of *R. insularis* (Bigot) (Canary Islands), *R. rubens* Herting (Spain), or *R. dorsalis* (North America).]

BIOLOGY

The Tachinidae exhibit several reproductive strategies, mainly oviparity or ovolarviparity where the egg develops *in utero* to a first-instar larva contained within the chorion. As soon as these are laid, the larvae break out and begin to search for a host. In some cases, females actually deposit their eggs on the host. The Dexiinae appear to be exclusively ovolarviparous (Cantrell 1988). In the course of this study, we noted the presence of fully developed first instar larvae in the oviducts of specimens of *Roudania albipilosa* and *R. cinerea*. Because of their small size, these larvae were not mounted for closer examination, but they confirm that the Australian Dufouriini are ovolarviparous like other Dexiinae.

Published records indicate that Dufouriini are parasitoids of beetles, primarily leaf beetles (Chrysomelidae) and weevils (Curculionidae) (see Baranov 1938; Cox 1994; Guimarães 1977, Kovaric & Reitz 2005, Parker *et al*. 1950; Tschorsnig & Herting 1994). Most records are of flies emerging from adult beetles. However, Cerretti & Mei (2001) recorded *Eugymnopeza braueri* Townsend parasitising adult *Blaps gibba* Laporte (Tenebrionidae) and give detailed descriptions of the life history of *E. braueri* in Italy. The two known host records for the Australian Dufouriini are discussed below.

Chetoptilia angustifrons is a solitary endoparasitoid of tortoise beetles (cassidoid Hispinae: Chrysomelidae) and has been reared from two species, *Aspidimorpha deusta* (Fabricius) and an undescribed species of *Cassida* L. Tortoise beetle larvae are external leaf feeders and most, including the above species, retain their cast larval exuviae upon a pair of supra-anal processes, forming a dorsal shield. The 5th and final instar has a dorsal shield comprising the exuviae of the four previous instars. In addition to the exuviae, many tortoise beetles, including both the known hosts of *C. angustifrons*, incorporate their own faecal material into the dorsal shield. Prior to pupation, 5th instar tortoise beetle larvae usually glue the ventral surfaces of their anterior abdominal segments to the substrate and undergo a prepupal stage of one to a few days.

Mature larvae of *C. angustifrons* pupariate within the dead remains of their host (Fig. 3A). The specimens of *C. angustifrons* from north Queensland emerged from prepupae of *A. deusta* attached to the leaves of its host plant *Ipomoea pes-caprae* (L.) (Convolvulaceae), a common trailing perennial growing above the strandline of sandy beaches. The male reared from the *Cassida* species in southeast Queensland also emerged from a prepupa, attached to leaf of the beetle's host plant, *Polymeria calycina* R. Br. (Convolvulaceae). The position of the fly puparium within the host prepupa was described above. The reverse orientation of the puparium facilitates the eclosion of the adult fly as the posterior abdominal segments of the beetle prepupa are slightly elevated above the substrate to enable the reflection of the dorsal shield over the dorsum of the prepupa.

No information is available on the ovipositional behaviour of *C. angustifrons*, nor on which life stage of the beetle host is initially attacked. However, it is interesting to note that the larvae of both known hosts incorporate faecal material into their dorsal shields in all instars. In contrast, the larvae of several species of Australian *Cassida* (often placed within the subgenus *Taiwania* Spaeth) have dorsal shields that are largely devoid of faecal material; only the first instars deposit a small blob of faeces on the supra-anal processes (Hawkeswood *et al*. 1997; CJB unpub. data). Two of these species, *Cassida diomma* Boisduval and *C. compuncta* (Boheman) are common in south-eastern Queensland, and despite CJB having reared a large number of field collected larvae, prepupae and pupae of both species, *C. angustifrons* has not been found attacking either (CJB unpub. data). Perhaps adult females of *C. angustifrons* use chemical odours emanating from the faeces incorporated into the dorsal shields as host finding cues.

Most extralimital species of *Chetoptilia* for which host records are known also attack tortoise beetles (cassidoid Hispinae). However, the life stage from which the adult fly emerges varies, with species recorded from larvae, pupae and adult beetles: *C. plumicornis* from an unidentified cassidoid larva in Uganda (Villeneuve 1942); *C. cyanea* from a pupa of *Aspidimorpha apicalis* (Klug) in Madagascar (Mesnil 1968) and *C. burmanica* from overwintering adults of *Craspedonta leayana* (Latrielle) in Myanmar (Garthwaite 1939). The only known exception to this pattern of cassidoid hosts is found in the type species of the genus, *C. puella*, a parasitoid of adult weevils (*Bytiscus betulae* L., Curculionidae) (Tschorsnig & Herting 1994).

Roudania cinerea attacks adults of the weevil *Acantholophus niveovittatus* (Curculionidae: Amycterinae). Two males in ANIC emerged from adult *A. niveovittatus* collected beneath *Spinifex* in Western Australia by Athol Douglas (see Zimmerman 1993: 214). However, no indication is given as to whether the specimens emerged from the same or separate adult weevils. The fly puparia are devoid of host remains and it is assumed that the mature fly larvae leave the host to pupariate in a similar manner to *R. cucullata* (see below). *Acantholophus* is a widespread and diverse genus known from all Australian states and territories and with more than 50 described species (Zimmerman 1993).

Extralimital species of *Roudania* for which host records are known, are also parasitoids of adult Curculionidae (Tschorsnig & Herting 1994). Female *Roudania* use their reflexed tubular ovipositor to lay eggs directly onto the adult host. *Roudania dimidiata* lays its eggs in the mouthparts of adults of *Brachyderes incanus* L. (De Fluiter & Blijdorp 1935). *Roudania cucullata* lays its eggs near the anal opening of adults of *Cleonus mendicus* Gyll., the mature larvae leaving the host to pupariate in soil (Menozzi 1939). *Eugymnopeza braueri* Townsend, a parasitoid of the ground beetle *Blaps gibba* Laporte (Coleoptera: Tenebrionidae), also lays its eggs in the mouthparts of adult beetles, but pupariates within the dead host beetle (Cerretti & Mei 2001).

ACKNOWLEDGEMENTS

We thank the following collaborators for helpful discussions on the taxonomy of Dufouriini, access to literature and loan of non-Australian specimens for study: Dr David Barraclough (School of Biological and Conservation Sciences, University of KwaZulu-Natal, Durban, South Africa), Dr Pierfilippo Cerretti (Centro Nazionale Biodiversita Forestale, Verona, Italy), Dr James O'Hara (CNC) and Dr Monty Wood (CNC). Geoff Thompson (QM) took the photographs of adult flies, Karin Koch (QM) prepared the distribution map and Susan Wright (QM) provided technical assistance. We also thank Greg Daniels (UQIC) and Dr David Yeates (ANIC) for loan of specimens and Dr Barbara Baehr (QM) for assistance with German translation.

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Dinosaur footprints from the lower Jurassic of Mount Morgan, Queensland

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Citation: Cook, A.G., Saini, N. & Hocknull, S.A. 2010 03 15. Dinosaur footprints from the Lower Jurassic of Mount Morgan, Queensland. *Memoirs of the Queensland Museum — Nature* 55(1): 135-146. Brisbane. ISSN 0079-8835. Accepted: 5 May 2009.

ABSTRACT

Over 190 partial and complete dinosaur prints which include six trackways are preserved in the ceilings of a disused clay mine near Mount Morgan central eastern Queensland, Australia. These represent the best record of Early Jurassic dinosaur footprints thus far discovered within Australia. *Anomoepus* dominates with other morphologies present including, *Grallator*, cf. *Eubrontes*, and *Skartopus* and several indeterminate prints. Only one possible manus print was observed. All preserved tracks are short walking tracks.
☐ *Lower Jurassic, dinosaur trackways, ornithopod, theropod, dinosaur footprints, Razorback Beds, Mount Morgan.*

Early Jurassic records of dinosaurs in Australia are scant with no Early Jurassic dinosaur skeletal material known, and only isolated occurrences of dinosaur prints known in Queensland (Bartholomai 1966; Bartholomai *in* Hill, Playford & Woods, 1966; Thulborn 1994). Dinosaur prints and trackways are known in Australia from the mid-Triassic onwards into the Late Cretaceous (Thulborn & Wade 1984; Thulborn 1998) and have proved essential in delimiting the diversity and evolutionary importance of otherwise unknown elements of the dinosaurian faunas of the continent. Dinosaur footprints have been recognised near Mount Morgan for over fifty years, but there has not been any documentation of their occurrence, composition and inferred palaeobiological information. Reconnaissance reports of this ichnofauna were made by Staines (1954), Bartholomai (1966) and Molnar (1991), but only isolated prints and no trackways were figured. This work concerns the dinosaur footprints prints exposed in the 'Fireclay Caverns' mine at Mount Morgan and the few trackways preserved in the ichnological assemblage.

Mount Morgan gold and copper deposit was exploited between 1882 and 1990. In support of mining operations, were a series of clay mines supplying raw material with which to make bricks for the smelting furnaces. These 'fireclay caverns' operated spasmodically between 1886 and 1925. Activity in the mine and subsequent chemical weathering exposed the lowermost surfaces of at least three layers of dinosaur footprints. A prime reason for the delay in investigating these occurrences of trackways was that they are exposed on the ceiling of the mine, 10-12 m above the mine floor. This rendered replication, photography or removal difficult. One small area of footprints was exposed in a suspended drive and was within 4-5 metres of the mine floor. It was these prints that Staines (1954) photographed.

STRATIGRAPHIC AND SEDIMENTOLOGICAL SETTING

Mount Morgan is located 38 km SW of the regional centre of Rockhampton, central eastern Queensland (Fig. 1). A ~65 m thick succession non-marine Jurassic sediments unconformably overlies Devonian basement (Fig. 2) and has been commonly called the Razorback Beds (Playford & Cornelius 1967, Day et al., 1983). Studies by Playford & Cornelius (1967) of these units indicate a lowermost Jurassic age and correlated the Razorback Beds with the Evergreen Formation of the Precipice Sandstone within the Great Artesian Basin to the west and south west.

Nearly 65 m of Jurassic sediments are exposed near the Mount Morgan Mine. Detailed logging of this section has been interpreted to represent three distinct facies groups; (1) Basal pebbly sandstone; (2) siltstone and (3) cross-bedded coarse sandstone.

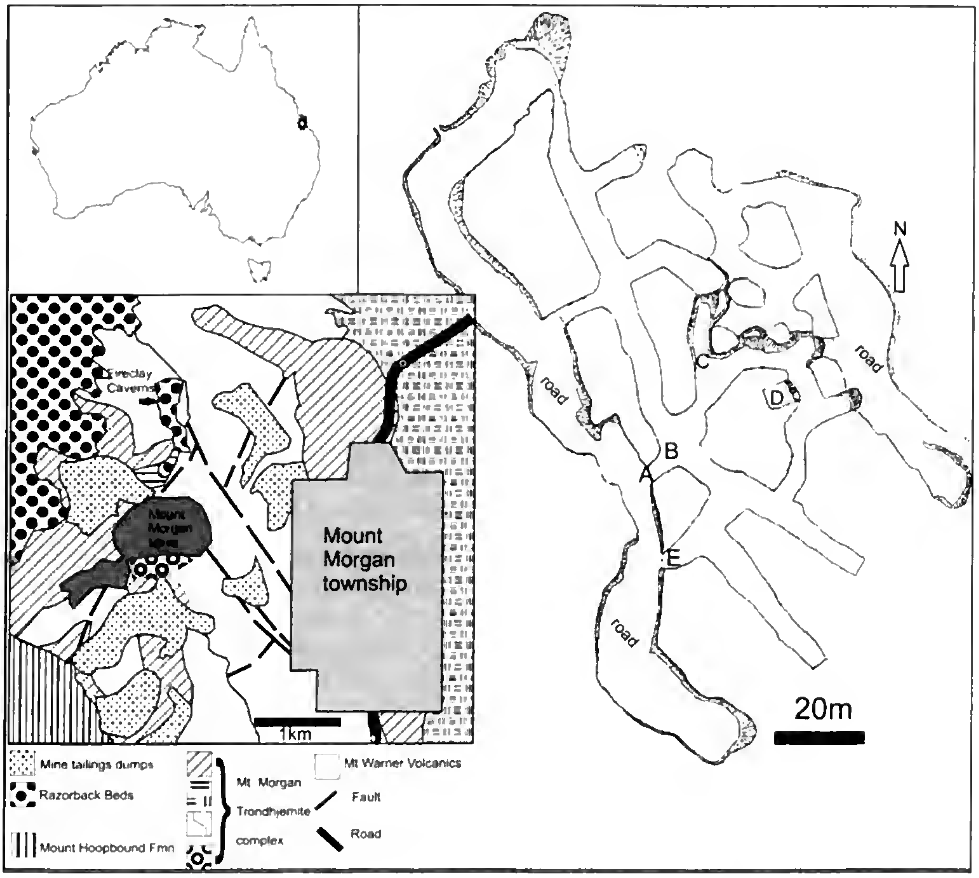

FIG. 1. Locality and general geology of Mt Morgan with map of Fireclay caverns after Staines (1954). Main footprint sites marked A-E.

Basal Pebbly sandstone facies. This facies lies unconformably atop Devonian porphyry and is approximately 20 m thick. Coarse massive quartz and sublithic sandstones, minor polymict conglomerates medium grained quartz sandstone units 0.6-2.2 m thick are intercalated with sporadic mudstone and siltstone units. Minor trough cross bedding and planar laminations are present in the coarser units. Scour bases and lithic breccia lenses are present in the lower parts of coarse units. Generally the facies fines upwards and is directly overlain by the thick siltstone facies described below. The sequence is interpreted as an alluvial fan deposit with sporadic channel and limited floodplain deposition.

Siltstone facies. Two metres of fine-medium siltstone is overlain by monotonous fine-grained laminated siltstone, over 16 m thick which dominates the middle of the sequence. Sedimentary structures include planar and parallel ripple cross laminations, isolated outsize quartz pebbles and subangular clay clasts. Significant pyrite crystals are distributed throughout which are considered secondary given the nature of the proximal orebody. Dinosaur prints are preserved in the uppermost one metre of this facies. The unit is interpreted as a lacustrine system which in uppermost parts shallows to form a regressive lacustrine system onto which footprints were impressed.

Cross bedded sandstone facies. In the study area this forms the uppermost 25 m of exposed section and is dominated by massive and planar and trough cross bedded coarse quartz and sublithic sandstones. Bedding sets are up to 2 m thick and have common basal pebble lags. The facies is interpreted as part of a small braided river system which built out over a restricted lacustrine environment.

PRESERVATION

Footprints are preserved as hyporelief and transmitted hyporelief prints throughout most of the clay caverns mine (Fig. 1). They are preserved in several layers of the uppermost 1 m of siltstone facies within the sequence. Their preservation mostly >10 m above the mine floor was a major impediment to earlier study. In addition the small area in which the prints are less than 5 m above the mine floor could not be cast as the prints were too fragile. This was exacerbated by pyrite growth throughout the siltstone producing large areas of friable and extremely fragile rock. Finally in

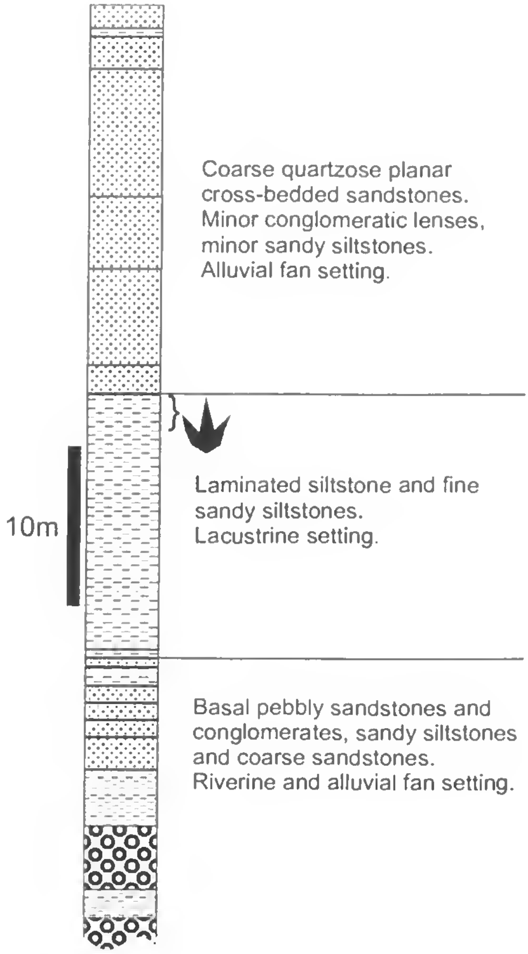

FIG. 2. Stratigraphic column for Razorback Beds in the vicinity of the Fireclay Caverns, Mount Morgan.

2007, using major scaffolding, a small section of footprints was moulded. The mould is lodged with the Queensland Museum (QMF54079).

METHODS

Initial work which formed part of reconnaissance studies (Cook et al., 2002) simply photographed the major footprint-bearing panels. These were then assembled as a photo mosaic for analysis. Two laser devices 10 cm apart were used to provide a scale for further work with photo mosaics. Individual images were either solarised or embossed in Adobe ™Photoshop 7.0. Rectified images were imported into ArcMAP™ 9.0 for further measurement. Because of the large distance between the floor of the caverns and the ceiling, approximately 10 m, all measurements are approximate.

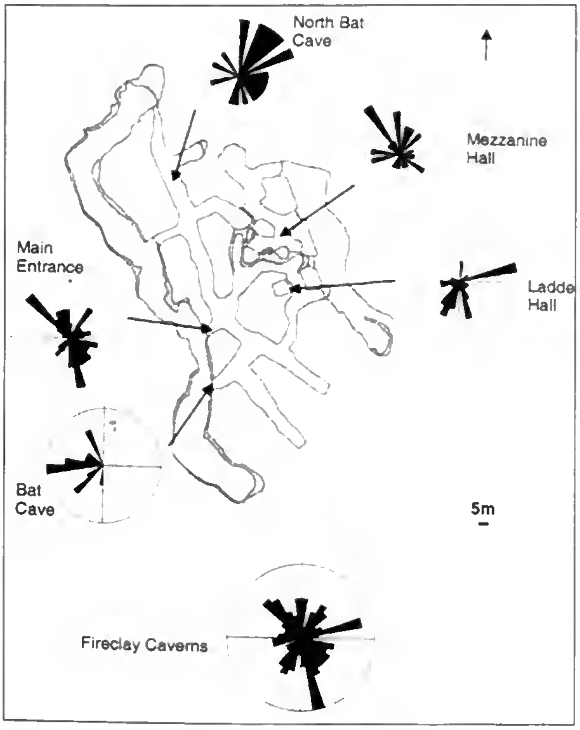

FIG. 3. Rose diagrams showing orientation of footprints within the Fireclay Caverns, with total distribution shown in lowermost rose.

Calculations of hip height follow Alexander (1976) and Thulborn (1990).

DISTRIBUTION

The prints are present in many parts of the mine ceiling. Areas with more concentrated prints sets were given informal names for convenience. Trackways are preserved in 'Bat Cave', 'Main Entrance', 'Mezzanine Hall', 'North Bat Cave' and 'Ladder hall' (Fig. 3).

No preferred overall orientation of prints was observed within the caverns (Fig. 3). Two areas with slight preference for trends of prints directed to the WSW and WNW for 'Bat Cave' and the 'Main Entrance' where there was an EW-NW bipolar orientation.

PRINTS

Only one possible manus print was observed in the caverns despite the observations of Bartholomai (1966) reported in Molnar (1991). Most prints were tridactyl pes prints. Largest prints were that of cf. *Eubrontes* had Foot Length (FL)=40 cm and the smallest, that of *Anomoepus* FL=5 cm. Seven print morphologies were identified, but only three can be confidently assigned to ichnotaxa. Many prints are eroded, with many of their features distorted by erosion. An equally large number of prints are transmitted prints or partial transmitted prints with digit 'breakthrough' from overlying layers. All prints are preserved in hyporelief.

Anomoepus (Fig. 4)

This is the dominant print present within the caverns represented by 69 full prints and 61 partial prints which can be confidently assigned. FL varies from 5 cm to 27 cm with most prints ranging in FL from 10-15 cm. Divaricance

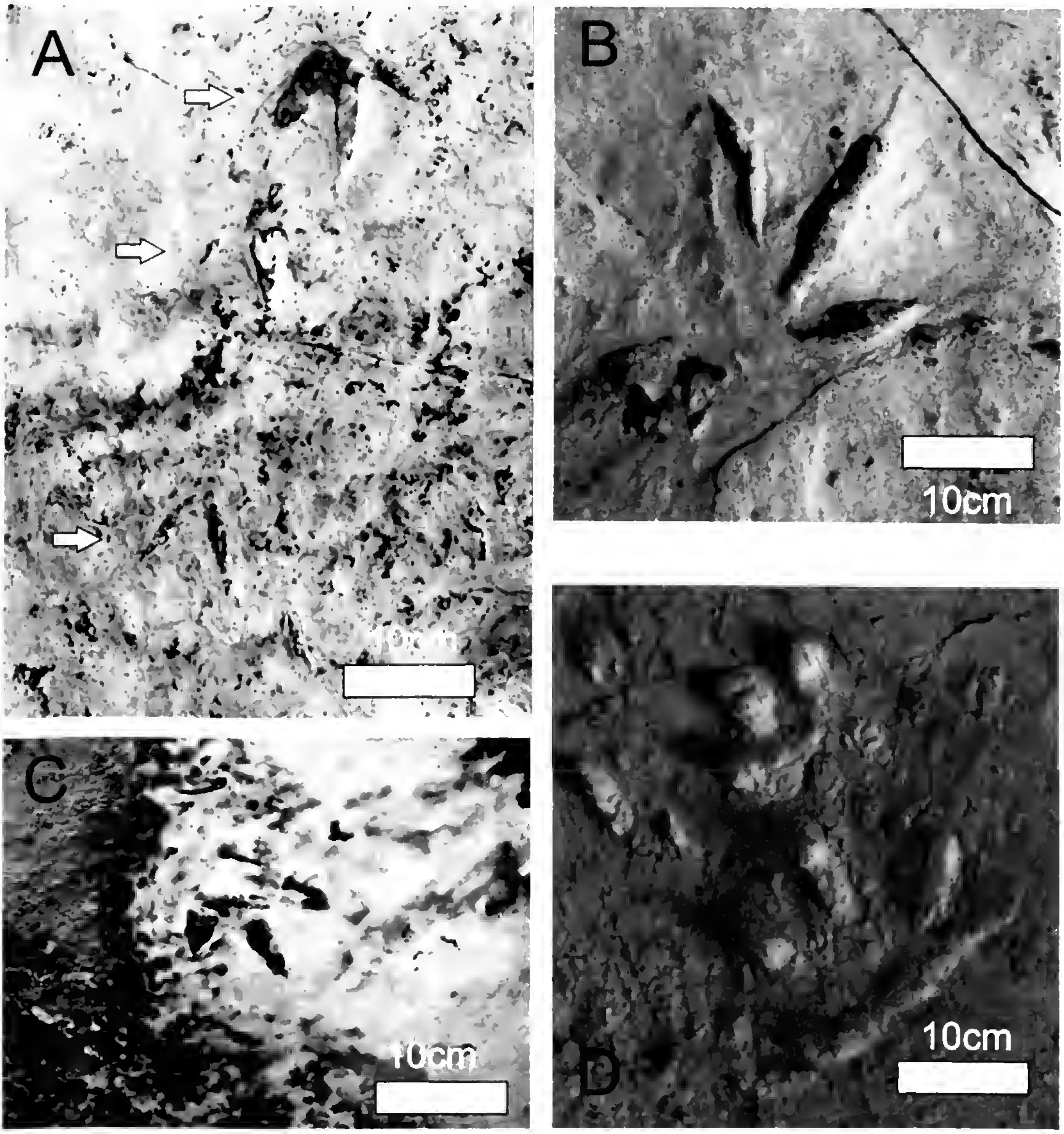

FIG. 4. A-C, *Anomoepus* from the Fireclay Caverns, Mount Morgan; D, Isolated partial pes and possible manus print, *Anomoepus*.

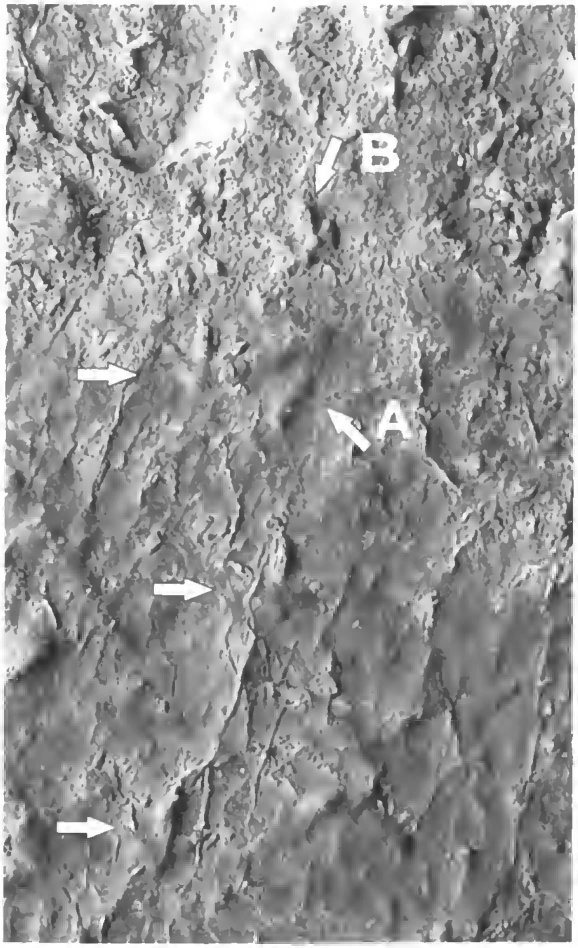

FIG. 5. A, Large transmitted theropod print; B, Stubby-toed ornithopod print. Note tracks are transmitted with breakthroughs on deeper distal digits, especially III.

is between 85-105°. Digits are relatively broad and a semiclaw is present in some specimens. Digits are long and tapered with digit (D) III longer and more tapered than DII or DIV. Slight medial swelling is present on DIII, however there is a pronounced swelling distally on DIV. Distal ends tapered more sharply on DIII, but are subrounded on the other two digits. Interdigital angle is greater on DII-III than DIII-IV.

One print is associated with an additional manus impression (Fig. 4D), consisting of three short stubby digits, approximately 7 cm long, with a divaricance of approximately 85°. These lie just anterior to a distinct partial *Anomoepus* pes print.

Four short trackways are attributable to *Anomoepus*. *Anomoepus* has been recorded in the Precipice Sandstone of Queensland by Thulborn (1994), but the specimens lodged in the Queensland Museum by Thulborn are generally smaller and have slightly narrower digits. *Moyenisauropus* has been used by many authors for prints similar in morphology to *Anomoepus*, but larger than 20 cm FL. A number of authors however assert that the forms are indistinguishable (Lockley & Meyer 2000; Olsen & Rainforth 2003; Olsen & Gatton 1984; Thulborn 1994). For the purposes of this work we regard them as size variants.

cf. ***Eubrontes*** (Fig. 6)

Fourteen individual prints and one trackway are assigned to this ichnotaxon. FL is between 16-40 cm. The prints assigned to cf. *Eubrontes* differ from *Grallator* in both size and that DIII is reduced in comparison to DII and DIV. In the Mount Morgan prints, the DII-IV divarification is between 50° and 70°. Claw marks are present in three of the 14 prints observed. These represent the largest of the prints at Mount Morgan.

Skartopus (Fig. 8C)

This is represented by a single small tridactyl print with FL of 5 cm, interdigital angles <40°. Digit III slightly longer than others. The single print is distinctive and unlike any other in the Fireclay Caverns. *Skartopus* is known from the medial Cretaceous of western Queensland (Thulborn & Wade 1984).

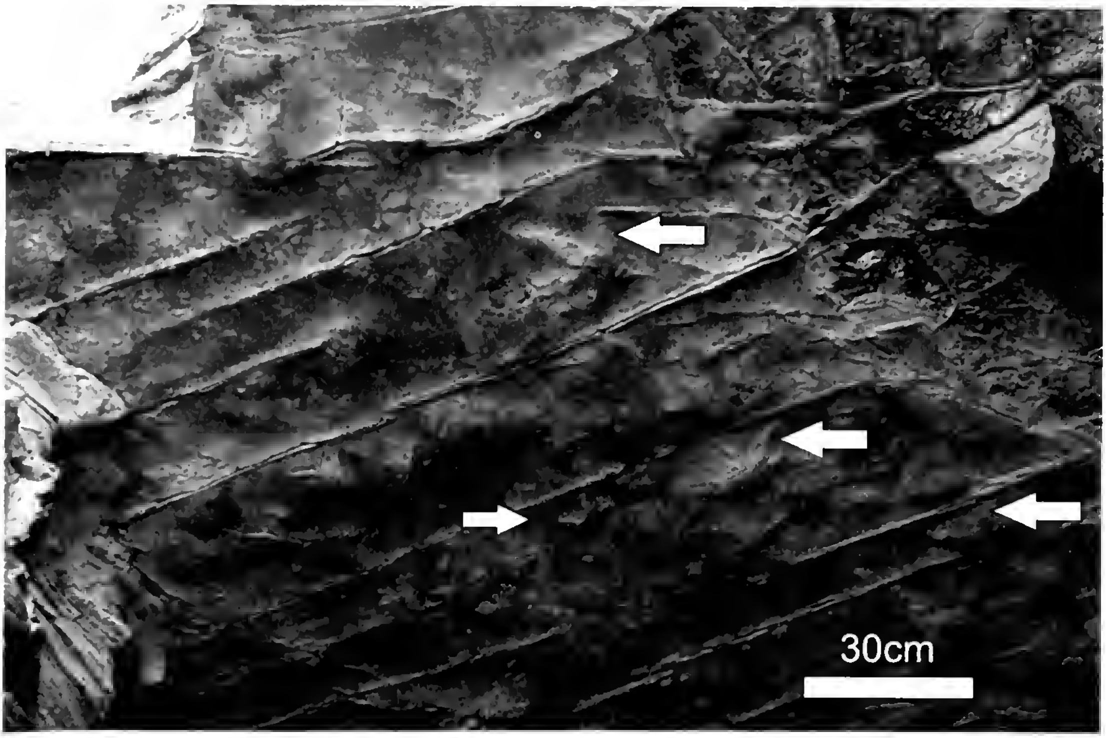

FIG. 6. cf. *Eubrontes* prints forming a short trackway near the entrance to Fireclay Caverns

Grallator (Fig. 5)

Tridactyl print, digit III is longer than DII and DIV, which are nearly equal in length. Divarification is between 85-95°. No hallux impression is present. Most prints are between 4-18 cm in FL but a single, much larger, print 28 cm long is present. This morphotype is represented by 16 complete and 8 partial prints. One short trackway is attributable to *Grallator*. The divarification is high in comparison to types of *Grallator* (Olsen, Smith & McDonald 1998) and other described footprints, but the general foot morphology is consistent. Lack of detail in the phalangial pad marks makes discrimination of individual phalangial swellings difficult.

The earliest record in Australia of grallatoroid tracks is that of Thulborn (1998) who described five prints from the mid-Triassic (Carnian) of Queensland. *Grallator* and its synonyms (Thulborn 1998) are common prints within Early Jurassic assemblages worldwide (Ellenberger 1974; Olsen & Galton 1984; Rainforth 2001).

INDETERMINATE PRINT 1 (Fig 7A-C)

Large tridactyl prints, up to 24 cm FL, with a divaricance of 70-100°. Digits are long and taper to a point. Rear of the print is crescent-shaped. DII-III angle is less than DIII-IV. DIII deep has a medial swelling. Two examples of this print have a probable hallux impression which extends approximately one quarter the distance behind the proximal part of the print. The sharp distal ends of the digit and the size suggest that these prints are attributable to a theropod.

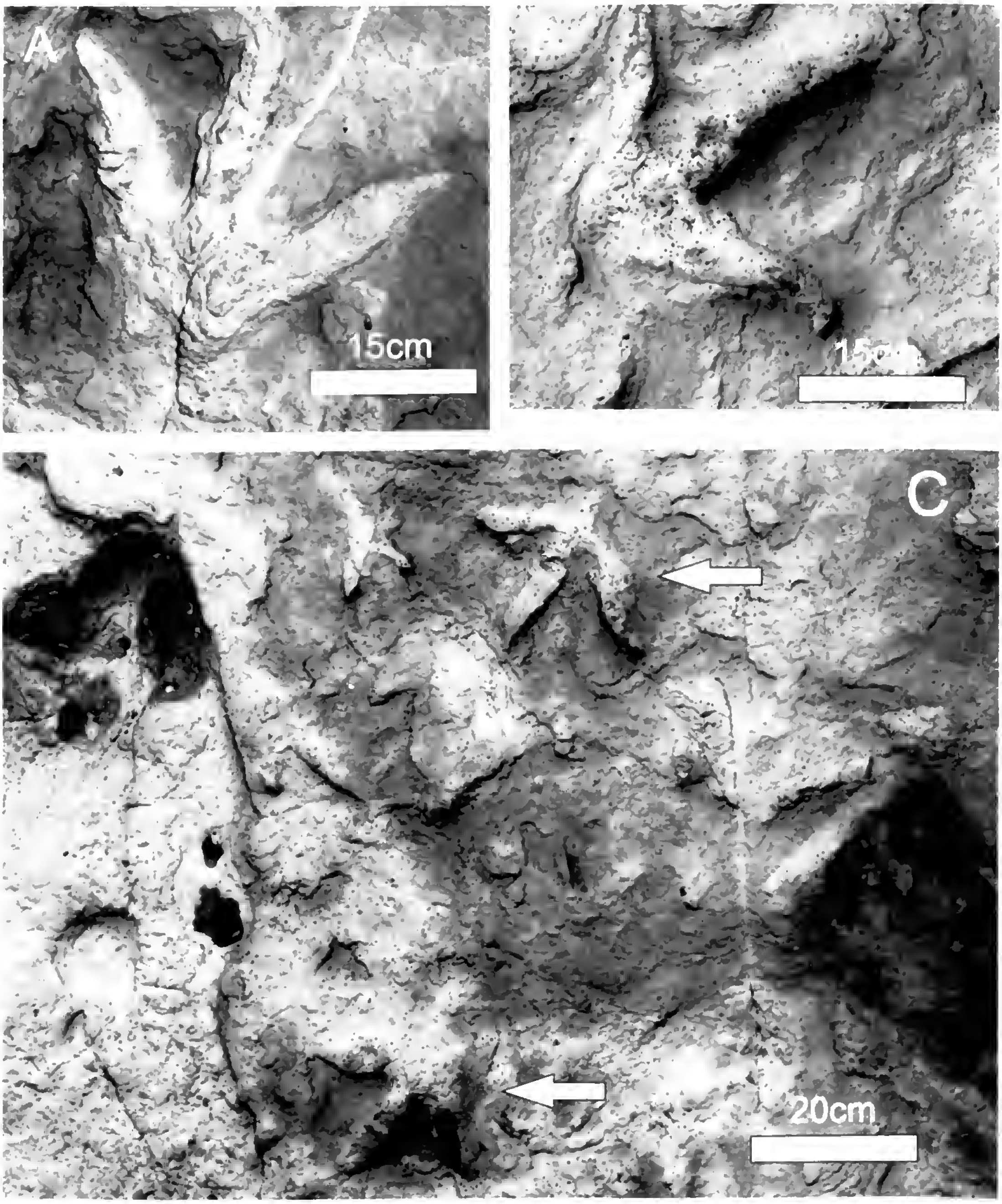

FIG. 7. Large indeterminate, weathered theropod prints.

INDETERMINATE PRINT 2 (FIG. 8A)

FL approximately 8 cm, consisting of three widely divaricant digits with an overall divaricance of 95°. Digits are short and blunt with rounded distal ends. DIII is slightly longer than DIV and has a slight swelling approaching the distal margin. DIV deep. DII shallower with less pronounced swelling at the distal end.

This print differs from Indeterminate print 3 by its wider divaricance and the connectedness of the digits. The blunt nature of the prints suggest an ornithopod origin.

INDETERMINATE PRINT 3 (Fig. 8B)

Foot length is approximately 12 cm. Print consists of three blunt digits with a divaricance of 50°. DIII longer and deeper than DII and DIV, with DIV longer than DII. Slight swelling at the proximal end of DIII. The three digits are almost unconnected on the print. The blunt toed nature of this print suggests an ornithopod origin

SIZES OF PRINTMAKERS

Thulborn (1990) suggested that the approximate relationship of FL to hip height and his formulae and conversion factors are followed here. *Anomoepus* prints suggest most animals with a hip height of 25-131 cm. One example suggested an animal with a hip height of 161 cm, but this single print is aberrant. Prints ascribed to cf. *Eubrontes* suggest animals in the range 70-180 cm at the hip and those assigned to *Grallator* indicate hip heights of between 20-120 cm.

ASSEMBLAGE

The variety of the prints within the assemblage is skewed by our decision to lump ichnotaxa. Nevertheless what is striking about this fauna is the high percentage of anomoepid prints in relation to theropod prints (Fig. 9). Prints attributable to ornithopods constitute just over two-thirds of the assemblage. This is in contrast to other Triassic-Jurassic assemblages worldwide which show greater percentages of

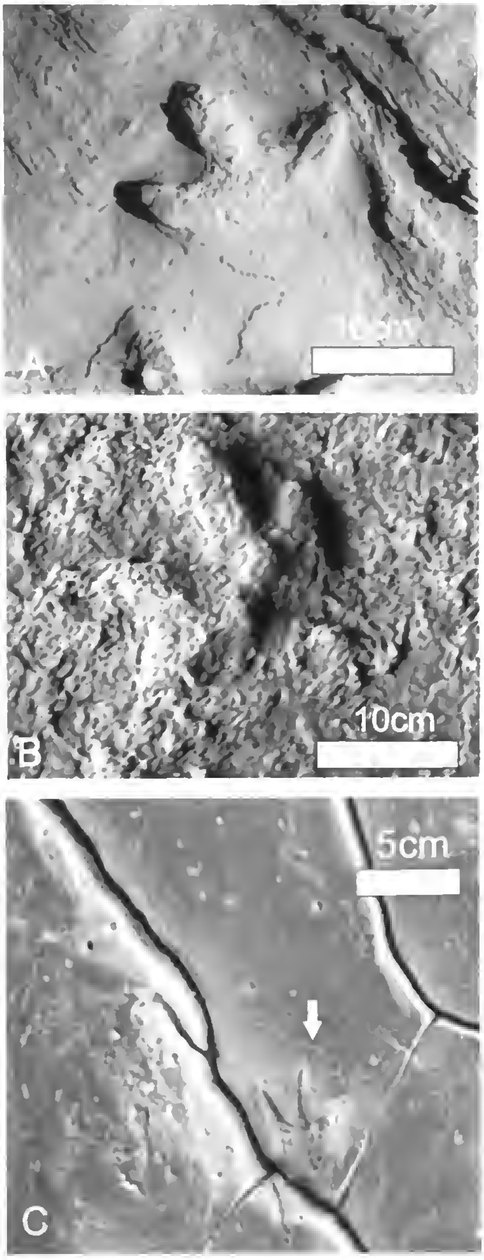

FIG. 8. A,B. small, blunt-toed probable ornithipod prints. A, digits show wide divaricance; B, Digit impressions only with moderate divaricance; C, Isolated *Skartopus* print.

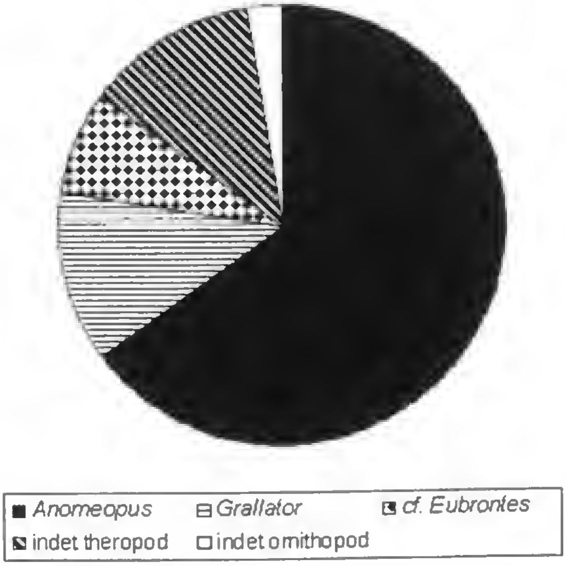

FIG. 9. Pie chart of proportions of prints found within the Fireclay Caverns. n=192. Single *Skartopus* print included in indeterminate theropod prints.

grallatoroid and other theropod prints (Lockley & Hunt, 1995; Lockley & Meyer, 2000, Gierlinski & Sawicki, 1998; Gierlinski & Niedzwiedzki, 2002; Niedzwiedzki & Pienkowski, 2004). A possibility is that the ecological setting for the site, essentially at lakes edge could account for the greater numbers of ornithopods, utilising the lake as a regular watering hole.

TRACKWAYS

Six trackways (Fig. 10) are present in the clay caverns, the longest of which is represented by 6 successive prints. Three are attributed to *Anomeopus* and of the remaining one to ?*Eubrontes* and two to *Grallator*. Pace lengths and other data are summarised in Table 1. Stride length to hip height ratios (Alexander 1976, Thulborn 1990) are all less than 1.3 indicating cursorial gaits for all the short trackways present. Data is too incomplete to make any other meaningful comment on speeds, however it is clear all the trackways represent walking tracks.

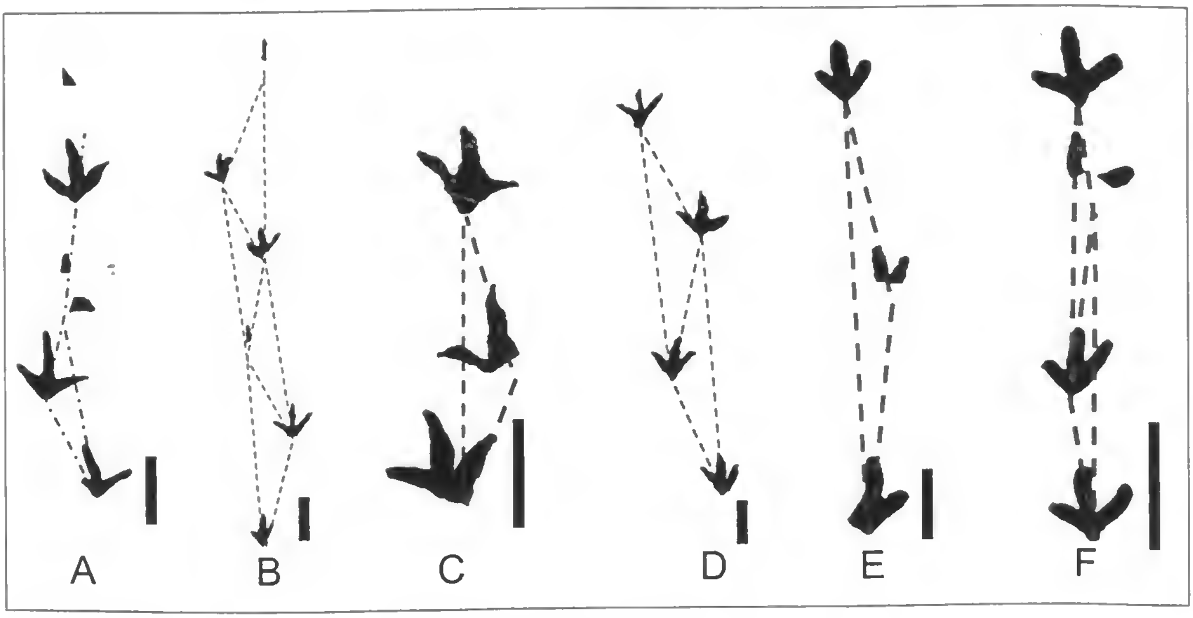

FIG. 10. Diagrams of the six short trackways within the Fireclay Caverns.

TABLE 1. Morphometric data for trackways within the Mt Morgan Fireclay Caverns.

Track and Print field number	Full/ partial print	Length (cm)	Width (cm)	Right/ left	Pace Length	Stride length	Pace angulation	Direction/ azimuth	taxon
LHT1									*Grallator*
LHFP26	F	8	7.1	L				198	
LHFP27	P	4.4+	4.5+	R	28.3		163	194	
LHFP28	P	9.9	5.7+	L	28.5	56.4		211	
LHT2									*Anomoepus*
LHFP33	F	9.5	10.4	L	19	43.4		171	
LHFP34	F	8.8	9.3	R	24.6		168	170	
LHFP35	P	5.6+	8.2	L	12.6	37.7	173	165	
LHFP36	F	10.4	11.4	R				165	
MET1									*Anomoepus*
MEFFP15	F	19.2	23	R	20.9	52		322	
MEFPP14	P	15.5+	14.3+	L	31.1			321	
MEFPP17	f	16.9	20.2	R				337	
MET2									*Grallator*
MEBFB30	F	17.5	15.7	R	42	102		191	
MEBFB19	F	18.5	18.4	L	60	98.5	145	182	
MEBFB18	F	18.7	21.7	R	37		138	209	
MEBFB11	F	16.4	19.6	L				213	
BCT1									?*Eubrontes*
BCFP5	F	21.9	22.6	L	26.9	63		262	
BCFP4	P	6.2+	7.3+	R	35.7	61	173	263	
BCFP3	F	20.6	20.7	L	24.8		180	276	
BCFP2	P	5.6+	4+	R				285	
EHT1									*Anomoepus*
EHFP4	F	16	11	L	56	101		227	
EHFP5	F	17	19	R	46	90.7	135	229	
EHFP6	P	9.0+	2.2+	L	47	87	143	227	
EHFP7	F	16	17	R	40	99	142	230	
EHFP8	F	14	14	L	59		127	226	
EHFP9	P	11.4+	1.9	R				228	

ACKNOWLEDGEMENTS

We thank the staff of the Rockhampton office of the Department of Mines and Energy (formerly Natural Resources and Water) for access to the site, and Tourism Queensland for invaluable funding assistance. The Australian Age of Dinosaurs is thanked for assistance in moulding the prints. Kristen Spring and Matthew Ng are thanked for field assistance. Alan Bartholomai and Matt White are thanked for helpful reviews of this manuscript

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Fossil fruit of the Macadamieae (Proteaceae) in the Tertiary of eastern Australia: *Eureka* gen. nov.

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Citation: Dettmann, M.E. & Clifford, H.T. 2010 03 15. Fossil fruit of the Macadamieae (Proteaceae) in the Tertiary of eastern Australia: *Eureka* gen. nov.. *Memoirs of the Queensland Museum — Nature* 55(1): 147-166. Brisbane. ISSN 0079-8835. Accepted: 13 October 2009.

ABSTRACT

Eureka gen. nov. is proposed to accommodate fossil fruits recovered from several mid-Tertiary (early Oligocene-Miocene) sites in eastern Australia. The type (*E. welcomensis* sp. nov.) and other described species (*E.*(*al. Conchotheca*) *turgida* (F. Muell.) comb. nov., *E. spechtii* sp. nov., *E. harslettiae* sp. nov.) have bilaterally symmetrical, ellipsoidal pericarps that are uniloculate, 1-seeded, and tardily dehiscent along the ventral suture and dorsal hinge line. The pericarp wall is radially structured and has a branched vasculature system capped by fibres embedded in a thick mesocarp; the radial fibres extend into the exocarp, and the endocarp is thin or lacking. The seed is orthotropous, attached apically and with a 2-layered seed coat that has an endotestal cuticle bearing impressions of transfer cells. *Eureka* is morphologically and anatomically consistent with fruits of extant members of *Bleasdalea* F. Muell., *Hicksbeachia* F. Muell., and *Gevuina* Molina of subtribe Gevuininae (tribe Macadamieae, family Proteaceae). Accordingly, the fossil fruit evidence implies that the Gevuininae had a former distribution range spanning some 20° of latitude in eastern Australia and taken together with fossil cuticle evidence a trans-Tasman distribution no longer mirrored in the present vegetation. *Eureka* also displays some resemblance to the tardily dehiscent fruits of extant *Panopsis* (subtribe Macadamiinae, tribe Macadamieae); however, morphological/anatomical details of extant members are imprecisely known. ❐ *Australia, Bleasdalea, Eureka, fossil fruit, Gevuina, Hicksbeachia, Macadamieae, Tertiary.*

Among recently recovered woody fossils from Tertiary sediments at several localities in Queensland are several different types of 1-seeded, tardily dehiscent, uniloculate fruits with vascularised pericarps similar to those of fruits borne by several extant genera included within tribe Macadamieae (Proteaceae) as recently redefined (Weston & Barker 2006; Mast et al. 2008). The Queensland fossil fruits are spheroidal to ellipsoidal, near-symmetrical about the vertical axis, and their thick pericarp has a distinctive radial structure reflecting a branched vasculature system embedded in a thick, woody mesocarp. Similarly structured pericarps characterise fruits borne by extant genera of tribe Macadamieae. The distinctive vasculature pattern with 'third-order radial vascular bundles' (Johnson & Briggs 1975, p.134; Douglas 1995, p.18) comprises prolific radial branching of the main vertical and lateral (tangentially-aligned) bundles in a woody ground mass of predominantly radially oriented fibre sheaths that surround the bundles as detailed for fruits of several extant members of the tribe (Filla 1926; Strohschen 1986a,b). The Queensland fossil fruits with their near vertical symmetry, near-smooth outer surface of pericarp, and one apically attached unwinged seed having a 2-layered, non-woody seed coat are more similar to fruits of several genera (*Gevuina* Molina, *Hicksbeachia* F. Muell., and *Bleasdalea* F. Muell.) of subtribe Gevuininae than to other members of tribe Macadamieae. Previously described fossil fruits that possess a thick pericarp with third order vasculature were assigned to *Conchotheca turgida* F. Muell., a taxon reported from mid-Tertiary deep lead sediments in Victoria (Mueller 1874a, Deane 1925) and Tasmania (Johnston 1880). Mueller (1874a) did not comment on the botanical affinity of *C. turgida*, but examination of his protocol material confirms these fossils, too, are morphologically consonant with fruits of subtribe Gevuininae, being similar to those of *Gevuina, Bleasdalea*, and *Hicksbeachia*. Evaluation of Mueller's protocol material and of the Queensland fossil fruits form the basis of the present study. Moreover, comparisons have been undertaken of the fossil material with fruits of extant *Gevuina, Hicksbeachia*, and *Bleasdalea*.

Extant *Gevuina* is monotypic and endemic to southern South America; *Bleasdalea* has two species, one each in New Guinea and eastern Australia, and *Hicksbeachia*, with two species, is endemic to eastern Australia (Fig 1A; Weston & Barker 2006). Fossil cuticles that are consistent with those of subtribe Gevuininae have been reported from Eocene sediments of Western Australia (Carpenter & Pole 1995) and from the Miocene of New Zealand (Pole 1998). Fossil wood similar to, but not identical with, *Gevuina* has been reported from the Oligocene of Patagonia (Pujana 2007).

The fossil pollen taxa, *Propylipollis reticuloscabratus* (Harris) Harris and Martin, and *P. tripartus* Harris, which occur in Campanian-Tertiary sediments of Australia, New Zealand and Antarctica, are morphologically similar to pollen of *Gevuina, Bleasdalea*, and *Hicksbeachia* (Martin 1982; Dettmann & Jarzen 1990, 1996, 1998). *P. reticuloscabratus* however, has been shown to be insufficiently discriminatory of the extant taxa in parsimony analyses (Sauquet et al. 2009); thus far, *P. tripartus* has not been tested in any comparable cladistic analysis.

MATERIAL

Fruits reported upon here include woody and charcoalified and permineralised specimens. The charcoalified specimens were recovered from subsurface sediments near Blackwater and Moranbah, central Queensland and Bundaberg, southeastern Queensland and the permineralised specimens are from an outcrop at Glencoe, central Queensland; all are held in the Queensland Museum (QMF). Also examined are woody and charcoalified fruits collected in the late 1800's and early 1900's from several goldfield sites in Victoria and New South Wales and housed in the Queensland Museum, the Australian Museum (AMF) and the Museum of Victoria (NMVP). The last-mentioned collection contains the type and other specimens of the protocol material of *Conchotheca turgida* F. Muell.,1874, which was originally housed in the Museum of the Geological Survey of Victoria (GSVF). Locality details of occurrences of *Eureka* gen. nov. are as follows (see also Fig. 1B).

Queensland. a) Picardy Station, near Moranbah (21°5′17.6′S 147°50′34.3′E) Rio Tinto Exploration Hole RDPD98MA21, sands, silts and lignites at 123-133 m; Early Oligocene (Dettmann & Clifford 2001).

b) Near Blackwater (24°1′1.3′S 148°48′50′E) South Blackwater Coal Pty Ltd Hole R8736, sands and lignites at 82m; Early-Late Oligocene (Dettmann & Clifford 2001).

c) Glencoe Station (23°36′S 148°06′E), near Capella, silcrete outcrop; Oligocene-?Early Miocene (Rozefelds 1990; Rozefelds & Christophel 1996; Dettmann & Clifford 2001).

d) N of Bundaberg (24° 46′49′S 152°18′17′E), Herberts on Welcome Creek Drain, subsurface sands and clays; Early Miocene (Dettmann & Clifford, 2003).

e) Near Clifton (27° 55′S 151° 55′E), Queensland Water Resources borehole, sands and lignites at 45-46 m; Tertiary (?Miocene).

New South Wales. Near Orange (33° 17′S 149° 06′E, Forest Reefs Mine, deep lead sediments; late Middle-early Late Miocene (Johnson 1989; Dettmann & Clifford 2001)

Victoria. a) Nintingabool (Crucible Co. Shaft), near Haddon (37° 18′S 146°32′E), SW of Ballarat, deep lead sediments; Oligocene-Miocene (Greenwood et al. 2000; Dettmann & Clifford 2001; Holdgate et al. 2006).

b) Foster (37° 10′S 146°14′E), deep lead sediments; Oligocene-Miocene (Rozefelds & Christophel 1996; Holdgate et al. 2008).

Tasmania. Brandy Creek, Beaconsfield (41° 12′S 148°49′E), deep lead sediments; Oligocene (Forsyth 1989)

METHODS

Fruits studied include carbonaceous specimens retaining well preserved morphological and anatomical characters of their woody tissues to severely vitrinised specimens retaining external and internal morphology but with few anatomical characters preserved. Some of the carbonaceous fruits are pyritised and, as a result of oxidation since collection, several have fragmented. Permineralised specimens are composed of amorphous and/or cryptocrystalline quartz that has preserved external and internal morphology of the fruits, but no anatomical detail of the original tissues is preserved.

Charcoalified specimens were photographed either after whitening with ammonium chloride to highlight surface features or without whitening to illustrate internal characters including those of the locules, seeds, and internal anatomy. Permineralised specimens were photographed without whitening. Thin sections of charcoalified specimens were cut using a slide microtome and mounted in glycerine jelly on glass slides for transmitted light microscope analysis. Fragments of several specimens were mounted on stubs and gold plated for scanning electron microscope analysis. Anatomical features of seed coats were examined in transmitted light after clearing in a weak solution of sodium hypochlorite, followed by thorough washing in distilled water.

Photographs were captured on either T Max film or digitally using an Olympus Cameida C-5050 camera. Images were processed using Photoshop 5LE.

SYSTEMATIC DESCRIPTION

FAMILY - PROTEACEAE JUSS.

SUBFAMILY - GREVILLEOIDEAE ENGL.

TRIBE - MACADAMIEAE C.VENKATA RAO

SUBTRIBE - GEVUININAE L.A.S. JOHNSON & B.G. BRIGGS

Genus -*Eureka* gen.nov.

Derivation of name. With reference to the association of 'Eureka' (Eureka Stockade, Eureka Flag, Eureka Deep Lead) with early gold mining activities in and around Ballarat, Victoria.

Generic diagnosis. Fruit unilocular, indehiscent to tardily dehiscent woody follicle; ellipsoidal or spheroidal, symmetrical about the vertical axis. Style base near-opposite stalk in the vertical plane; ventral suture and dorsal hinge line approximately equal in length; splitting along ventral suture and dorsal hinge into 2 near equal portions. Surface smooth or near-smooth. Pericarp largely composed of mesocarp, the outer thicker part with a branched vascular system composed of vertically aligned

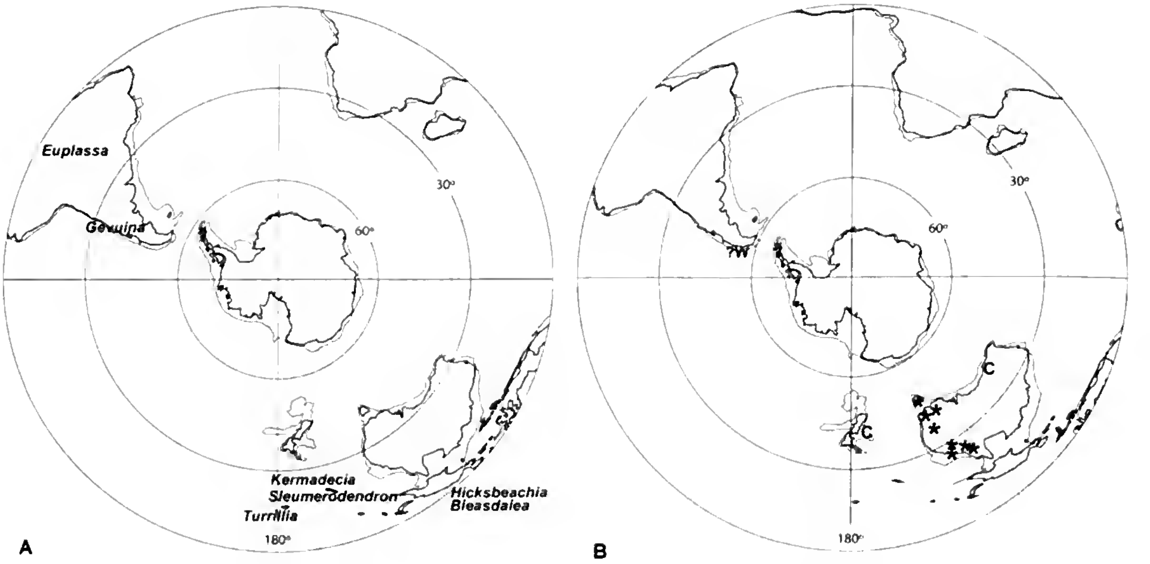


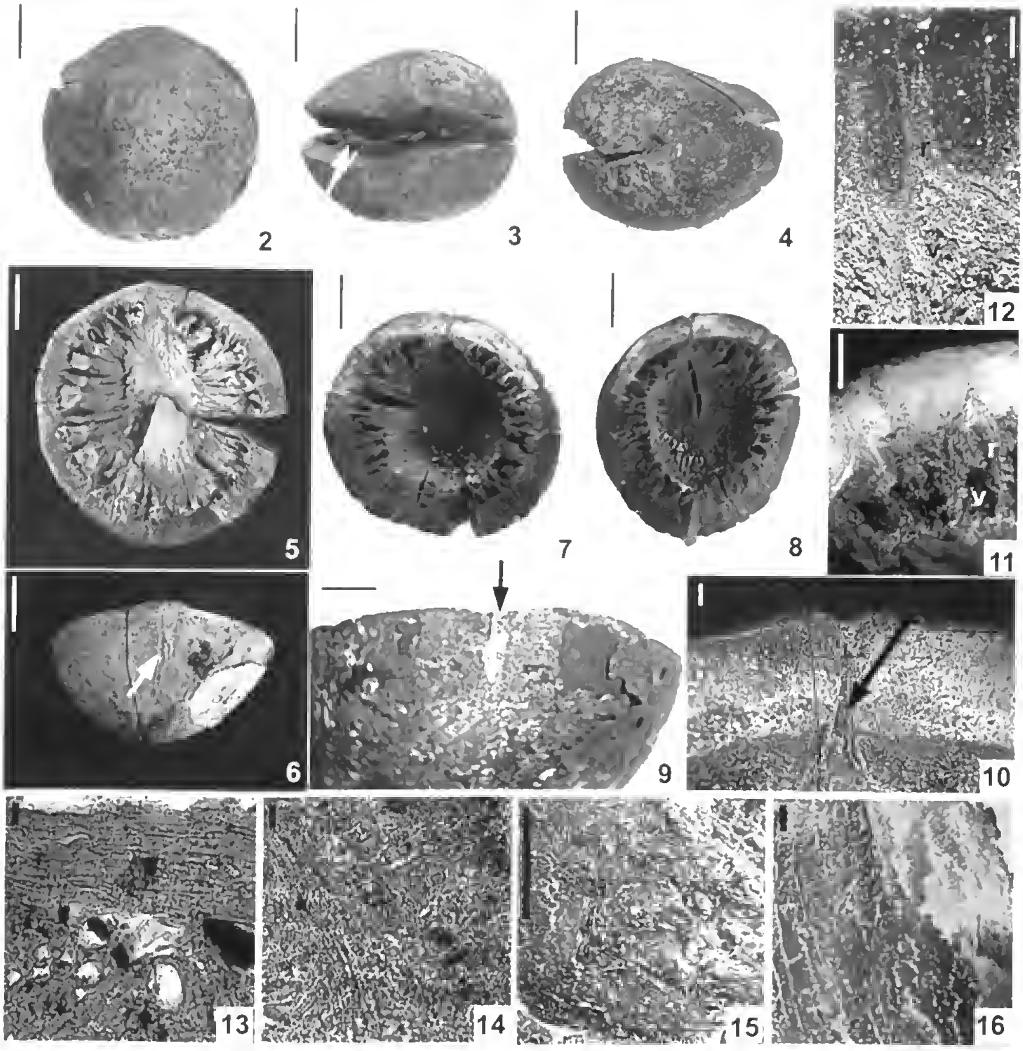
FIG. 1. Polar stereographic projections, based on Lawver & Gahagan (2003). A, Present Day showing distribution-range of extant members of Subtribe Gevuininae (excluding *Cardwellia*); B, Early Miocene (20 Mya) showing localities of fossil *Eureka* (*), fossil cuticles (C) of Subtribe Gevuininae, and fossil wood (W) questionably allied to Subtribe Gevuininae.

(tangential) primary bundles from which branch radially aligned secondary bundles that are surrounded by tangentially and radially aligned fibre bundles; fibres interspersed with parenchyma. Exocarp and endocarp thin. Seed solitary, unwinged, orthotropous, attached apically, filling, or almost so, locule. Seed coat 2-layered, the outer layer incompletely enveloping the inner; outer layer a cuticle with impressions of transfer cells; inner layer a cuticle with anticlinal walls of rectilinear cells.

Type species. *Eureka welcomensis* sp. nov.

Remarks and comparison. *Eureka* gen.nov. accommodates uniloculate fruits having a branched vascular system surrounded by fibre bundles in the mesocarp, and a single apically attached, orthotropous seed. In these respects *Eureka* differs from *Conchotheca* F. Muell., emend. Dettmann & Clifford 2005, which includes fruits having vertically aligned, unbranched vascular bundles in the mesocarp and laterally attached seeds. One taxon, *C. turgida*, allocated to *Conchotheca* by Mueller (1874a) is characterised by a pericarp with a branched vascular system and an apically attached, orthotropous seed; this species is transferred herein to *Eureka*.

Eureka is distinct from *Conchocaryon* F. Muell. 1879, which has asymmetric fruits and laterally attached winged seeds (Mueller 1879; Dettmann & Clifford 2005). Both *Plesiocapparis* F. Muell.1871 and *Celyphina* F. Muell. 1871 have indehiscent, unilocular, near-smooth fruits with branched vasculature in the mesocarp. They differ from *Eureka* in possessing large stone cell complexes (not radially oriented fibres) that cap and surround the vascular bundles in the fruit wall (Dettmann & Clifford, in prep.).



FIGS 2-16. *Eureka welcomensis* sp. nov.; **2-4**, Lateral, apical and basal views of holotype with seed (arrowed), QMF51143; scale bar = 5 mm; **5-6**, Pericarp, lateral view showing surface of locule and external lateral view showing V-shaped scar (arrowed) of style base, AMF11099; scale bar = 5 mm; **7, 8,** Pericarp, surfaces of locule, lateral view, QMF51144; scale bar =5mm; **9,** Detail of style scar (arrowed) on external surface of fruit, QMF51145; scale bar = 2.5 mm; **10,** Pericarp wall, transverse section at right angles to the dorso-ventral plane showing vasculature associated with style base (arrow), QMF51145; scale bar = 1 mm; **11, 12,** Pericarp wall, section in plane of dorsal hinge line and ventral suture showing vasculature comprising eroded vertical (v) bundles is cross section and radially aligned secondary bundles (r) surrounded by fibre complexes embedded in a ground mass of parenchyma, QMF51145; scale bar = 1 mm; **13, 14**, Pericarp wall, structure in transverse sections showing wall fibre bundle complexes surrounding vasculature, QMF51149; scale bar = 100 μm; **15, 16,** Pericarp wall in transverse section showing fibre bundles surrounding branched vasculature and detail of fibres, QMF51150; scale bar = 100 μm and 10 μm respectively.

Species - *Eureka welcomensis* sp. nov. (Figs 2-24)

Holotype. QMF51143 (Figs 2-4). Prolate ellipsoidal, unilocular, 2-valved fruit, partially dehisced into 2 subequal valves along ventral suture and dorsal hinge line; stalk scar indistinct, scar of style base oriented transverse to dorso-ventral plane extending 4-5 mm from apex towards base on mid face of each valve. Pericarp 4-5 mm thick in lateral regions, thinner (3 mm) at apex. Seed solitary, apically attached, orthotropous. Vertical axis 19mm; lateral axes 19 mm, 16 mm.

Other material. QMF51144-QMF51151 inclusive, AMF11099.

Type locality. Herberts on Welcome Creek Drain, N of Bundaberg, Queensland; Early Miocene.

Diagnosis. Fruit woody, prolate ellipsoidal, near symmetrical about the vertical axis; indehiscent or tardily dehiscent, unilocular, with 1 apically attached seed. Stalk attachment basal, inconspicuous; style base represented by a linear groove oriented transverse to the dorso-ventral plane and extending 4-5 mm from apex on lateral surface of each valve; groove underlain by vascular strands that extend into the pericarp and terminate near the seed cavity. Pericarp with near smooth outer surface, thickest (4-6 mm) in basal and mid regions of lateral surfaces, tapering to 3-4 mm at apex and along both ventral suture and dorsal hinge line; wall comprises thin exocarp overlying a thick vascularised mesocarp and a thin cuticle-like endocarp. Inner mesocarp predominantly of vertically aligned vasculature surrounded by fibre sheaths in a ground mass of parenchyma; at or near inner/outer interface of mesocarp the vascular bundles branch radially; outer mesocarp composed of the radially directed vascular branches and surrounding fibre sheaths. Preserved seed coat comprises exotesta of a thin, structureless cuticle, an endotestal cuticle bearing impressions of polygonal-shaped transfer cells (40-60 µm diameter) having internally directed fimbriae, and a tegmic cuticle with impressions of anticlinal walls of rectilinear cells (55-70 µm long, 20-25 µm wide).

Dimensions. Pericarp (8 specimens); vertical axis 12.5 (18.5) 23 mm, lateral axes 12.5 (16.8) 22 mm (in plane of dehiscence) x 10 (15.6) 20 mm (at right angles to dorso-ventral plane). Seed (4 specimens); vertical axis 12-16 mm, lateral axis 8-10 mm.

Derivation of name. With reference to the type locality and in allusion to 'The Welcome' gold nugget, recovered during 1858, from a Deep Lead at Bakery Hill near Ballarat, Victoria.

Remarks. The majority of specimens were collected in an undehisced state (Figs 2-4), but on drying after collection, the valves of several of them separated either partially or wholly from the apex and along the ventral suture thereby to reveal their seed coats attached to the pericarp wall (Fig. 17).

Distribution. Herberts on Welcome Creek Drain, N of Bundaberg; near Clifton, Darling Downs; Picardy Station near Moranbah Hole RDPD98MA21, 123-133 m, Qld; Forest Reef, near Orange, NSW.

Age range. Early Oligocene-early Late Miocene.

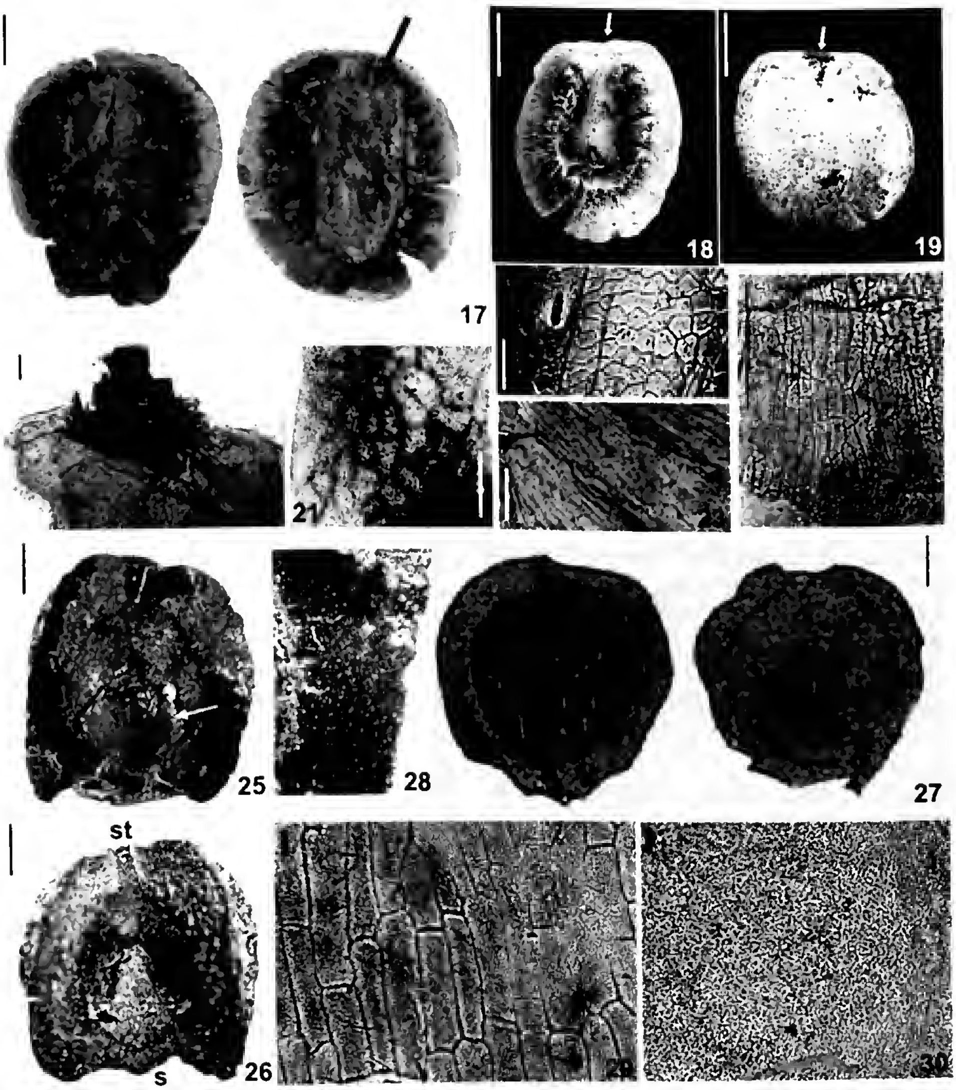
Species - *Eureka turgida* (F. Muell.) comb. nov. (Figs 25-30)

1874a *Conchotheca turgida* Mueller, p.42; Pl.X, 8, 12 (non figs 5-7, 9-11)

Lectotype. NMVP53987; Mueller, 1874a, Pl. X, fig. 8; Figs 25-30 herein. One valve of globose unilocular fruit, 12 mm long, 11 mm wide (dorsiventrally), stalk inserted into basal depression. Pericarp wall 2-3 mm thick; seed attached apically, with remnants of seed coat loosely adherent to pericarp in basal half of locule.

Type locality. Nintingbool, (Crucible Co.Shaft, ~23.2 m) near Haddon, SW of Ballarat, Victoria; basal sediments of a sequence beneath basalt: Oligocene-Miocene.

Diagnosis. Fruit woody, indehiscent or tardily dehiscent, spheroidal, unilocular, with 1 seed. Stalk 2-2.5 mm in diameter, inserted into basal depression 4-5 mm in diameter; style base



FIGS 17-30. *Eureka welcomensis* sp. nov. and *Eureka turgida* (F. Muell.) comb. nov.; **17-24,** *Eureka welcomensis* sp. nov.; **17,** Interior surfaces of opened fruit with preserved seed (arrowed), QMF51148; scale bar = 5 mm; **18, 19,** Internal and external surface, showing style base (arrowed), of one valve of opened fruit QMF51147; scale; bar = 5 mm; **20,** Cuticle of funicle and seed coat at base of seed, QMF51150; scale bar = 100 µm; **21, 22,** Inner layer of seed coat as viewed under light and scanning electron microscopes, cuticle showing impressions of polygonal-shaped transfer cells, QMF51150; scale bar = 100 µm; **23, 24,** Outer layer of seed coat as viewed under light and scanning electron microscopes, cuticle showing elongate cells, QMF51150; scale bar = 100 µm; **25-26,** *Eureka turgida* (F. Muell.) comb. nov., lectotype, interior surfaces of opened fruit showing traces to stalk (s) and stigma (st) and remnants of seed coat (arrow), NMVP53987; scale bar = 2.5 mm; **27,** Lectotype as illustrated by Mueller, NMVP53987; scale bar =2.5 mm; **28,** Detail of pericarp wall NMVP53987; scale bar = 1 mm; **29, 30,** Seed coat tissue, outer and inner layers respectively NMVP53987; scale bar = 10 µm.

represented by an ellipsoidal groove, the long axis 2-3 mm and oriented transverse to the dorso-ventral plane on lateral surface of valves; groove underlain by vascular strands that extend into the pericarp and terminate near the seed cavity. Pericarp with a near-smooth outer surface; wall 2.5-3 mm thick in mid regions of lateral surfaces, tapering to 1.5-2 mm at base of style; composed of thin exocarp overlying a thick vascularised mesocarp and a thin cuticle-like endocarp. Mesocarp a dense groundmass of fibre sheaths that surround the vasculature and are predominantly aligned in a radial direction. Preserved seed coat comprises exotesta of a thin, structureless cuticle, an endotestal cuticle bearing faint impressions of polygonal cells (40-50 µm in diameter) having occasional internally directed fimbriae, and a tegmic cuticle with impressions of anticlinal walls of rectilinear cells (80-120 µm long, 20-25 µm wide).

Dimensions. Pericarp (2 specimens); vertical axis 11, 12 mm, dorsiventral axis 10, 11 mm.

Comparison. *E. turgida* is smaller and the pericarp wall is thinner than that of *E. welcomensis*. Moreover, the latter species lacks a basal depression as occurs in *E. turgida*.

Distribution and age. Known only from the type locality: Oligocene-Miocene.

Species - *Eureka spechtii sp. nov.* (Figs 31-51)

1874a *Conchotheca turgida* Mueller, p.42; Pl.X, 5-7, 9-11 (non figs 8,12)

Holotype. (here designated) NMVP53958 (Mueller, 1874a, Pl. X , fig. 7), Figs 31-34 herein. Whole fruit, unilocular, ellipsoidal, vertical axis 13.5 mm, lateral axes each 10.5 mm. Stalk scar 3 mm.

Other material. NMVP52980, NMVP53096, NMVP53098, NMVP53960, QMF13208.

Type locality. Nintingbool, (Crucible Co.Shaft, ~23.2 m) near Haddon, SW of Ballarat, Victoria; basal sediments of a sequence beneath basalt: Oligocene-Miocene.

Diagnosis. Fruit woody, asymmetrically prolate ellipsoidal, near-smooth externally, unilocular, 1-seeded; indehiscent or tardily dehiscent, dehiscing from the apex along the sinuous, ridged ventral suture. Stalk scar indistinct or visible, 0.5-1.5 mm in diameter, inserted at base; style base indistinct, apical, underlain by vascular strands that extend into the pericarp and terminate near the seed cavity. Pericarp wall 2-2.5 mm thick in mid regions of lateral surfaces, thickening to 2.5-3.5 mm at base of style; composed of thin exocarp overlying a thick radially vascularised mesocarp and a thin cuticle-like endocarp. Mesocarp 1.8-2.2 mm in thickness in mid regions of lateral surfaces, composed of a dense groundmass of fibre sheaths that surround the vasculature and arranged predominantly in a radial direction. Preserved seed coat comprises exotesta of a thin, structureless cuticle, an endotestal cuticle bearing faint impressions of polygonal cells (40-50 µm in diameter) having occasional internally directed fimbriae, and a tegmic cuticle with impressions of anticlinal walls of rectilinear cells (80-120 µm long, 20-25 µm wide).

Dimensions. Pericarp (8 specimens); vertical axis 10 (11.8) 14 mm; lateral axes 8 (9.8) 11 mm (in plane of dehiscence) x 7.5 (8.4) 10.5 mm (at right angles to dorsal-ventral plane).

Derivation of name. Named in honour of Raymond Louis Specht, distinguished Australian ecologist.

Comparison. *E. spechtii* differs from *E. turgida* in shape (prolate ellipsoidal vs. spheroidal), wall thickness (thickest vs thinnest in apical regions) and the ventral suture line (sinuously ridged vs. straight).

Distribution. Nintingbool (Mueller, 1874a, 1874b); Foster (Deane, 1925), Victoria; Brandy Creek (Johnston 1880), Tasmania; Darling Downs (see Johnston 1880, p.27), Queensland.

Age range. Early Oligocene-early Late Miocene.

Species - *Eureka harslettiae* sp. nov.
(Figs 52-64)

Holotype (here designated).QMF51153, Figs 52-53. Whole fruit, unilocular, ellipsoidal, vertical axis 19 mm, lateral axes each 15.5 mm. Stigma scar 2.5 mm wide at apex , tapering along its length (7.5 mm) on both lateral surfaces.

Other material. QMF 51154-QMF 51157 inclusive.

Type locality. South Blackwater Coal Pty Ltd Hole R8736, 82 m, Queensland: Early-Late Oligocene.

Diagnosis. Fruit woody, indehiscent or tardily dehiscent, with a near-smooth surface; prolate ellipsoidal to subspheroidal with a prominent ridge (2-3 mm high) that encircles the stone in the longitudinal plane and situated along the ventral suture and dorsal hinge line; unilocular, 1-seeded. Stalk attachment basal, inconspicuous; style base represented by a V-shaped groove oriented perpendicular to the dorso-ventral plane and extending 7-9 mm from apex on lateral surface of each valve; groove widest (1.5-2.5 mm) at apex; underlain by vascular strands that extend into the pericarp and terminate near the seed cavity. Pericarp wall 4-6 mm thick, but thinning slightly around base of style; mostly composed of vascularised mesocarp external to a thin, cuticle-like layer (?endocarp). Mesocarp 3.8-5.8 mm in thickness, composed of a dense groundmass of fibre sheaths that surround the vascular mesh and are predominantly aligned in a radial direction. Seed coat comprises exotesta of a thin unstructured cuticle, and an endotestal cuticle bearing faint impressions of polygonal cells (40-50 μm in diameter) having sparsely distributed, internally directed fimbriae.

Derivation of name. Named in honour of Morwenna Jean Harslett, Queensland naturalist.

Dimensions. Pericarp (12 specimens); vertical axis 15 (16.7) 21 mm; lateral axes 13 (15.5) 21 mm (in plane of dehiscence) x 8 (11.8) 15 mm (at right angles to dorsal-ventral plane).

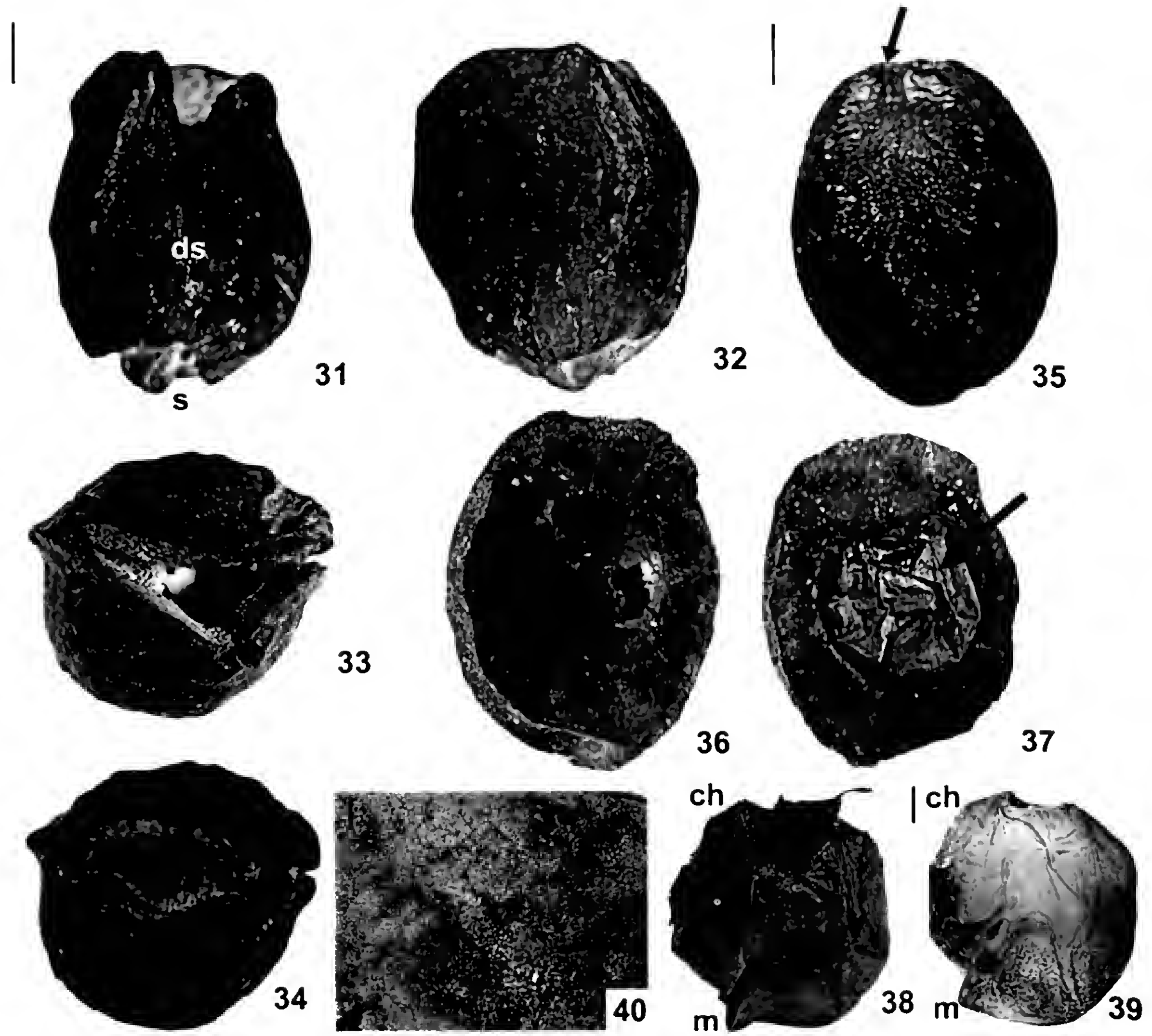
Remarks and Comparison. The holotype and all but one of the other specimens examined are charcoalified and their internal morphological and anatomical features are preserved. The sole permineralised example studied is known only from its external morphology. The species is similar in size to *E. welcomensis*, but is distinct in possessing a prominent ridge that encircles the fruit along the ventral suture and dorsal hinge line. Moreover, the V-shaped groove of the stigma scar is longer than that in *E. welcomensis*.

Distribution. South Blackwater Coal Pty Ltd Hole R8736, 82 m; Glencoe Station, near Capella, Queensland.

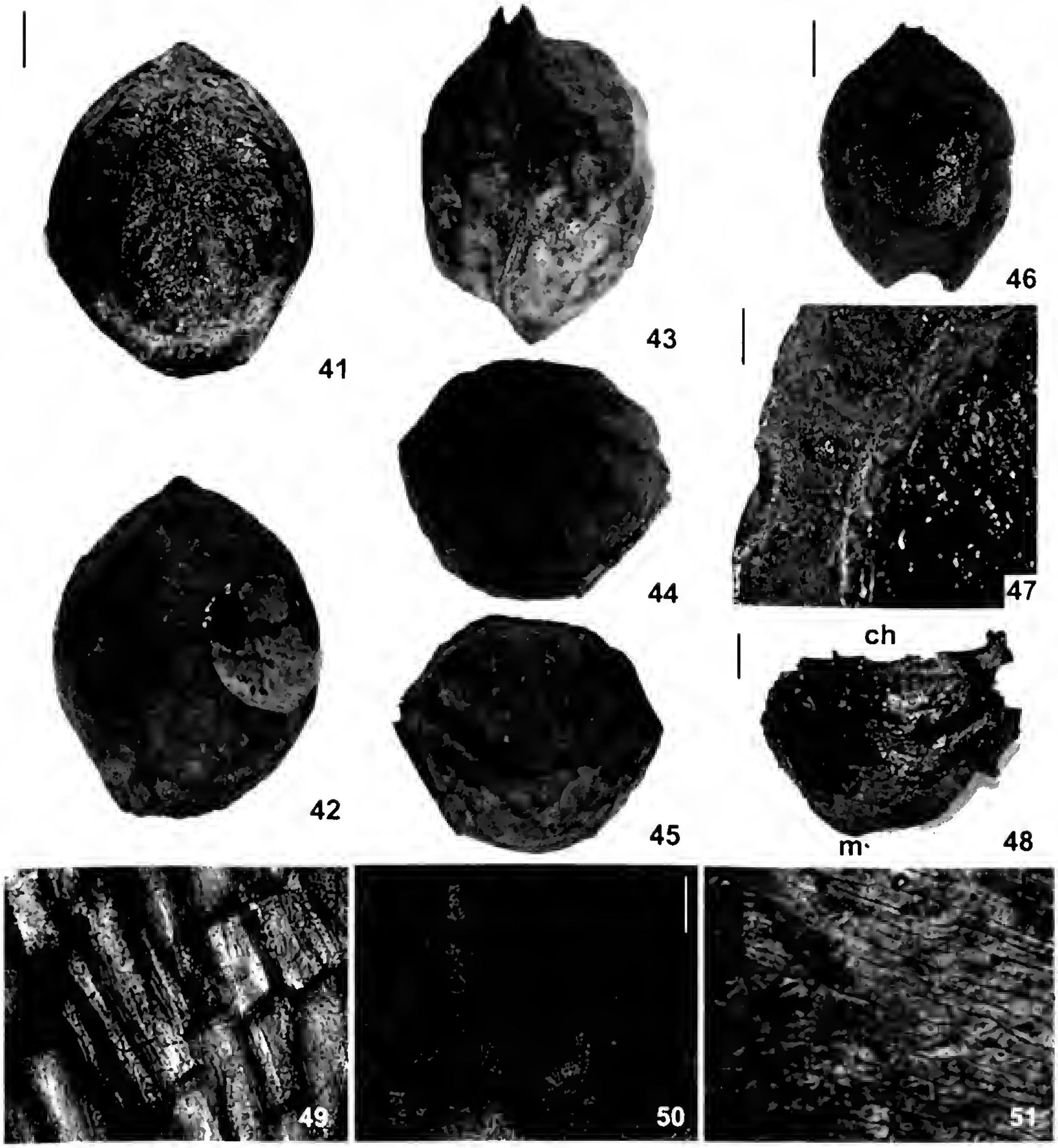
Age range. Early-Late Oligocene.

AFFINITIES OF *EUREKA*

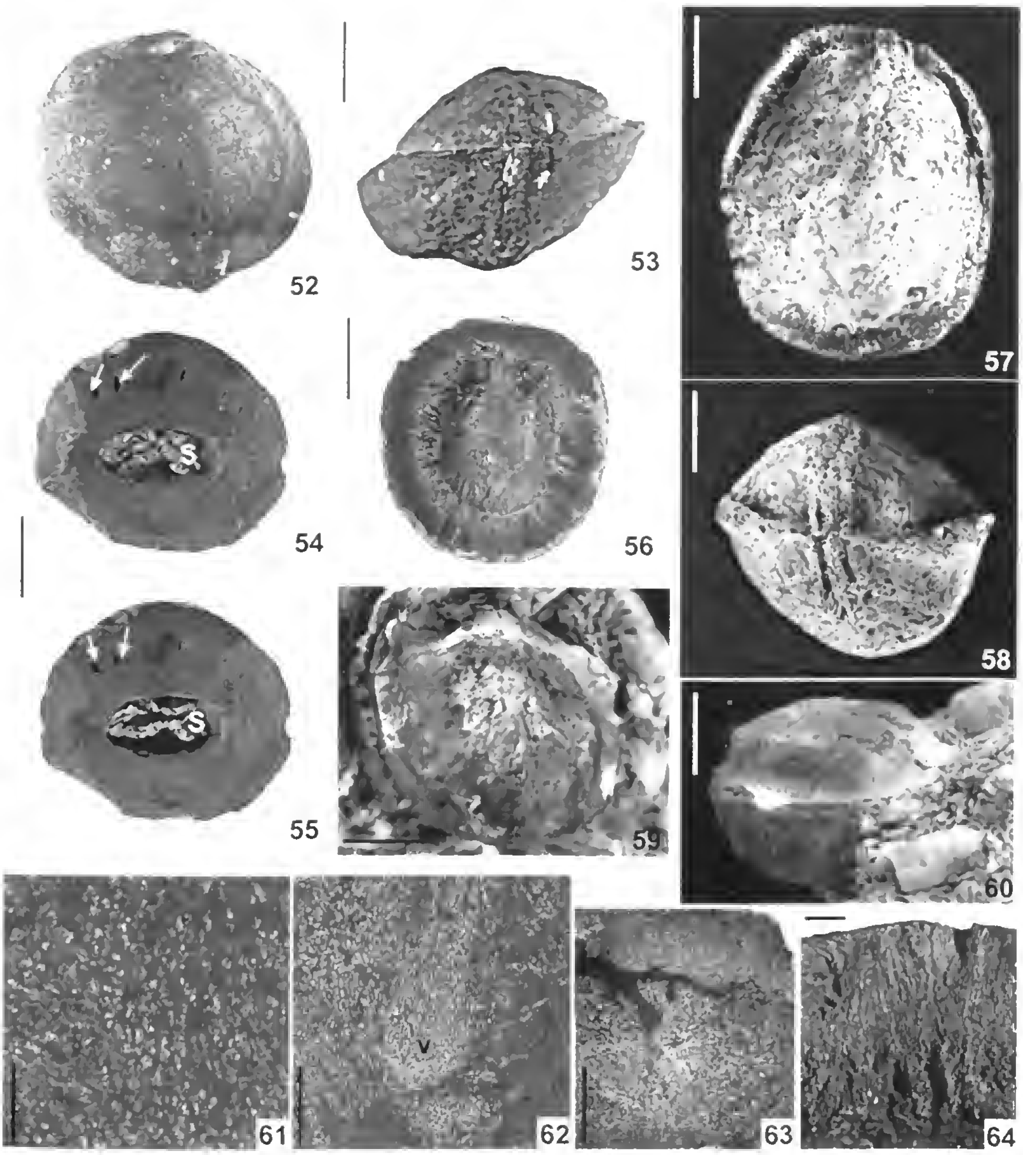
Pericarp vasculature of *Eureka* is consistent with that of fruits borne by several genera of the Proteaceae included within tribe Macadamieae, and in particular by members of subtribes Macadamiinae, Gevuininae, and Virotiinae (sensu Weston and Barker, 2006; Mast et al., 2008). The pericarps of genera included within these subtribes possess a complexly branched vascular system surrounded by sclerenchyma and/or fibre sheaths and/or stone cell complexes. The main vascular bundles are predominantly vertically aligned, occurring within the middle region of the mesocarp, and external to a narrow zone of parenchyma and/or sclereids of the innermost mesocarp. The vertical bundles branch radially, the radial branches extending into the outer region of the mesocarp where they are sheathed by sclerenchyma; the tissues between them are composed of fibres, stone cell complexes and/or thin-walled (and sometimes succulent) parenchyma. Thus, the middle region of the pericarp with its vertically aligned, sheathed vasculature is densely structured and may be woody and endocarp-like, whereas the outer region of the pericarp is predominantly radially structured (Figs 65-68,



FIGS 31-41. *Eureka spechtii* sp. nov. **31-34**, Holotype in lateral (31, 32), apical (33), and basal (34) views showing dorsal suture (ds) and stalk scar (s), NMVP53598; scale bar = 2.5 mm; **35-37**, External (35) and internal (36,37) views of pericarp showing style base (arrowed) and apically attached seed (arrow), NMVP53096; scale bar = 2.5 mm; **38-39**, Seed illustrated in Fig. 37 before (38) and after (39) treatment with sodium hypochlorite showing positions of chalaza (ch) and micropyle (m), NMVP53096; scale bar = 1 mm; **40**, Transfer cells of seed coat of holotype, NMVP53598; scale bar = 10 μm.



FIGS 41-51. *Eureka spechtii* sp. nov. **41-45.** Lateral (41-43), apical (44) and basal (45) views of pericarp, NMVP53960; scale bar = 2.5mm. **46-47.** Internal views of pericarp, NMVP53098; scale bars = 2.5 mm and 0.5mm respectively. **48.** Seed morphology showing chalaza (ch) and micropyle (m), NMVP53098; scale bar = 1 mm. **49.** Locule tissue, NMVP53598; scale bar = 40 µm. **50, 51.** Anatomy of seed coat showing transfer cells (50) and inner cuticle of elongate cells (51), NMVP53598; scale bars = 40µm.



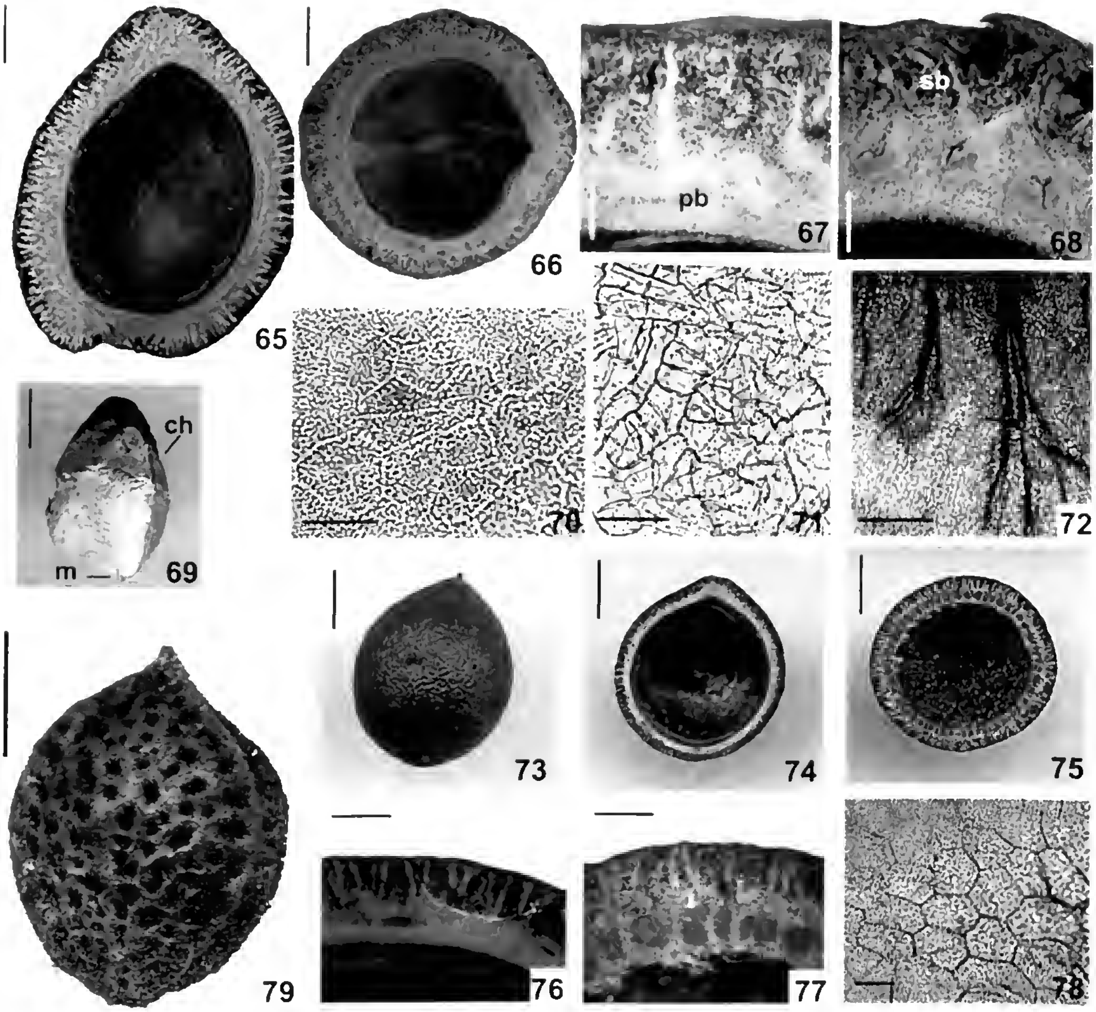
FIGS 52-64. *Eureka harslettiae* sp. nov.; **52, 53,** Holotype, lateral (52) and apical (53) views, QMF51153; scale bar = 5 mm; **54, 55,** Internal views of fruit cut transversely, showing seed (S) in locule and cavities (arrows) from which vascular bundles have been eroded from pericarp, QMF51154; scale bar = 5 mm; **56,** Internal view of pericarp cut longitudinally, QMF51155; scale bar = 5 mm; **57, 58,** Lateral and apical views, QMF51156; scale bar = 5 mm; **59, 60,** Lateral and apical views of permineralised specimen, QMF51157; scale bar = 5 mm; **61-63,** Longitudinal sections of pericarp showing vascular tissue (v) surrounded by fibre bundle complexes, QMF51155; scale bars = (100 µm, 0.5 mm, 1 mm respectively); **64,** Longitudinal section of pericarp showing radial orientation of fibre complexes surrounding partially eroded vascular bundles of the inner mesocarp region, QMF51155; scale bar = 1 mm.

TABLE 1. Fruit and seed wall characters of members of Subtribes Macadamiinae and Gevuininae (sensu Weston & Barker 2006), and fossil *Eureka*. Information sources, additional to present observations, on development and/or anatomy are from Filla (1926), Francis (1928), Hartung & Storey (1939), Hohman (1978), and Strohschen (1986a,b).

Subtribe/ fossil taxon	Fruit type/ dehiscence	Pericarp				Seed coat		
		Exocarp	Outer mesocarp	Middle mesocarp	Inner mesocarp	oe., outer integument	ie., outer integument	Seed sheath
Macadamiinae	follicle or drupaceous follicle; ?delayed dehiscence	epidermal cells with stomata and trichomes	leathery, radial vasc. and fibres	leathery vert. vasc.; outer surface smooth	parenchyma	woody or ?thin cuticle (*Panopsis*)	crystal layer, polygonal cells	thin, fragile 1-layered (derived from inner integument)
Gevuininae (excluding *Cardwellia*)	drupaceous/ follicle; delayed dehiscence	epidermal cells with stomata and trichomes	succulent-fibrous, radial vasc. and fibres	woody, vert. vasc.; outer surface smooth	parenchyma and sclereids adherent to testa	thin cuticle	crystal layer, polygonal cells	1-layered with elongate cells (derived from cuticle between outer and inner integuments)
Eureka	drupaceous/ follicle; delayed dehiscence	not known	?succulent, radial vasc. and fibres	woody, vert. vasc.; outer surface smooth	parenchyma and sclereids adherent to testa	thin cuticle	crystal layer, polygonal cells	1-layered with elongate cells

73-77, 80A-B). This pattern of vasculature was detailed for *Macadamia*, *Brabejum*, *Hicksbeachia*, and *Gevuina* by Filla (1926) and designated as fruit Type VI among the pericarps of Proteaceae known to him. Later, the vasculature pattern of pericarps was identified as a characteristic attribute (Johnson & Briggs 1973; Douglas 1995) of genera now included within subtribes Macadamiinae, Gevuininae, and Virotiinae (sensu Weston & Barker 2006).

Within these subtribes, fruits with a vascularised, radially structured pericarp and bearing 1-2, vertically attached, wingless seeds as occurs in *Eureka*, are borne by *Macadamia* F. Muell., *Panopsis* Salisb., *Brabejum* L. and *Lasjia* P.H. Weston & A.R. Mast (subtribe Macadamiinae); *Heliciopsis* Sleumer, *Athertonia* L.A.S. Johnson & B.G. Briggs, and *Virotia* L.A.S. Johnson & B.G. Briggs (subtribe Virotiinae); and *Sleumerodendron* Virot, *Euplassa* Salisb., *Gevuina* Molina, *Bleasdalea* F. Muell., *Hicksbeachia* F. Muell., *Kermadecia* Brongn. & Gris., and *Turrillia* A.C.Sm. (subtribe Gevuininae) (Sleumer 1955; Virot 1968; Johnson & Briggs 1975; Smith & Haas 1975; Smith 1985; Steyermark 2004; Weston & Barker 2006; Mast et al. 2008). The vascularised tissues of fruits of the extant genera are of mesocarp origin as confirmed from detailed developmental studies (Francis 1928; Hartung & Storey 1939; Strohschen 1986a, b) of fruits of *Macadamia ternifolia* F. Muell., *M. integrifolia* Maiden & Betche (Subtribe Macadamiinae), and *Hicksbeachia pinnatifolia* F. Muell. (Subtribe Gevuiinae). Furthermore, an endocarp *s.str.* (ie. a proliferation of woody tissue derived from the inner epidermis of the ovary wall) is not formed in mature fruit of the studied taxa. It seems likely that the woody or sometimes leathery 'endocarp' referred to by some authors (e.g. Sleumer 1955; Virot 1968; Smith & Haas 1975) in morphological descriptions of fruits of the extant taxa within subtribes Virotiinae, Gevuininae, and Macadamiinae instead represents tissues of the mesocarp.



FIGS 65-79. Fruits and seeds of *Hicksbeachia pinnatifolia* F. Muell. (65-72) and *Gevuina avellana* Molina (73-78), and fruit of *Athertonia diversifolia* (C.T. White) L.A.S. Johnson & B.G. Briggs (79); **65-68**, Pericarp *Hicksbeachia pinnatifolia*, longitudinal (65, 67) and transverse (66, 68) sections of pericarp showing vasculature comprising vertically aligned primary bundles (pb) of inner mesocarp and radially aligned secondary bundles (sb) extending into the exocarp; scale bars 65, 66 = 10 mm, 67 = 1 mm; **69**, Seed *H. pinnatifolia*, showing chalaza (ch) and micropyle (m); scale bar = 10 mm. 70-72. Tissues associated with seeds of *H. pinnatifolia*; **70**, Inner epidermis of testa showing polygonal cells with internally directed fimbriae (crystal layer); scale bar = 50 µm; **71**, Endocarp sclereids detached from pericarp and closely adherent to testa; scale bar = 100 µm; **72**, Chalazal tissue showing vasculature; scale bar = 0.5 mm; **73-77**, Pericarp of *Gevuina avellana*, lateral view (73), longitudinal (74, 76), and transverse (75, 77) sections; scale bar = 73-75 = 5 mm, 76, 77 = 1 mm; **78**,Seed tissue *G. avellana*, inner epidermis of testa showing polygonal cells with internally directed fimbriae (crystal cells); scale bar = 50 µm; **79**, *Athertonia diversifolia*, pericarp with exocarp removed, lateral view showing surface reticulation of mesocarp; scale bar = 5 mm.

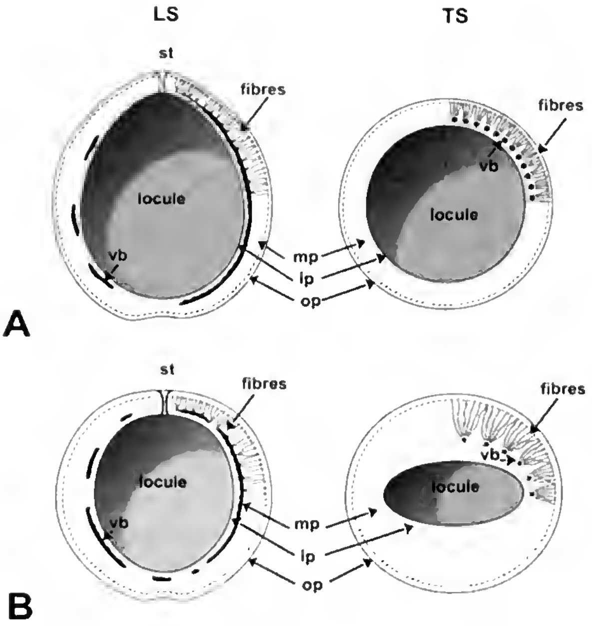


FIG. 80. Diagram illustrating pericarps of A, *Hicksbeachia pinnatifolia* and; B, *Eureka welcomensis* in longitudinal (LS) and transverse (TS) sections. ip, inner pericarp; mp, middle pericarp; op, outer pericarp; st, stigma scar; vb, vascular bundles.

Fruits of several genera within the Macadamiinae (*Macadamia, Nothorites,* and *Lasji*) are characterised as follicular (Willis 2007; Mast et al. 2008) as demonstrated from developmental studies of *Macadamia* (Francis 1928; Hartung & Storey 1939; Strohschen 1986a). The fruits dehisce along the entire or partial length of the ventral suture of the mature pericarp. Fruits of the other extant Macadamiinae (*Brabejum* and *Panopsis*) are characterised as indehiscent to tardily indehiscent (Willis 2007; Mast et al. 2008). However, by contrast to the woody pericarp of *Eureka*, the pericarp of *Brabejum* lacks significant lignified tissue (Filla 1926), whereas detailed anatomical and developmental studies have yet to be undertaken on fruits of *Panopsis* (Edwards & Prance 1993).

Developmental studies confirm that the indehiscent to tardily dehiscent pericarps of *Hicksbeachia pinnatifolia* are transitional between a follicle and a nut (Strohschen, 1986b). Fruits of this and other taxa included in subtribe Gevuininae (except *Cardwellia*) and those of subtribe Virotiinae are described as 'drupaceous', in possessing a woody, vascularised middle mesocarp and an outer, somewhat fleshy mesocarp with radially orientated vascular and fibre bundles (Weston & Barker 2006, p. 338; Mast et al. 2008). In fruits of the Virotiinae, the woody middle mesocarp possesses a reticulate or pitted outer surface (Sleumer 1955; Rozefelds 1990, 1992; Fig. 79) whereas, except for *Sleumerodendron austrocaledonicum*, the middle mesocarp of indehiscent fruits of the Gevuininae has a smooth surface (Figs. 73, 80A). The surface of the woody middle mesocarp of *S. austrocaledonicum* is sculpted into a series of irregular branched longitudinally-aligned, ribbon-like strips that are separated by transversely disposed fibres (Association Endémia 2001).

Thus the smooth-surfaced, vascularised, radially structured pericarps of *Eureka* are more similar in morphology to the indehiscent/tardily dehiscent fruits of *Panopsis* (Macadamiinae) and the Gevuininae than to those of the Virotiinae and Malagasiinae, each of which has a well defined synapomorphy. In the Virotiinae the inner mesocarp surface is pitted or reticulate, and in the Malagasiinae the outer mesocarp lacks prominent radiating vascular bundles (Weston & Barker 2006). Moreover, in Macadamiinae seeds possess a structureless, fragile seed sheath derived from the inner integument, whereas in studied seeds of the Gevuininae the seed sheath is a cuticle with elongate cells derived from a cuticle between the inner and outer integument (Table 1). Seeds of *Eureka* have an inner seed layer morphologically comparable to that of *Bleasdalea, Gevuina* and *Hicksbeachia* As the phylogeny of the character states displayed by *Eureka* has not been explored, it is uncertain whether they are synapomorphic of the Gevuininae; this matter is the subject of ongoing research.

Fruits of *Eureka* are prolate ellipsoidal, near symmetrical about the vertical axis, with the stalk and style in vertical alignment and the dorsal hinge line and ventral suture near equal in length. Extant Gevuininae having fruits possessing these features are *Gevuina, Hicksbeachia, Bleasdalea, Euplassa,* and *Turrillia*. Indehiscent or tardily dehiscent fruits of other genera comprising Subtribe Gevuininae differ in being asymmetric with respect to the vertical axis (*Sleumerodendron* - see Smith & Haas 1975) or in possessing an angled inner mesocarp (*Kermadecia* - see Smith & Haas 1975). *Eureka* possesses a single, wingless, orthotropous seed with a two layered seed coat, characters that are in accord with those detailed for *Gevuina* and *Hicksbeachia* (Hohmann 1978; Strohschen 1986b) and observed by us in these two genera and in *Bleasdalea* (Figs 70-72, 78). In each of the fossil species, the outer layer of the seed coat is closely adherent to the inner surface of the pericarp (Figs 65, 74) and envelops a cuticle bearing impressions of polygonal cells having internally directed fimbriae; these layers are interpreted to represent the outer and inner epidermis of the testa as has been precisely detailed for *Gevuina* and *Hicksbeachia* (Hohmann 1978; Strohschen 1986b). Strohschen's developmental studies confirm that in *Hicksbeachia pinnatifolia* F. Muell. tissues of the ovary wall and the outer layer (outer epidermis of outer integument) of the seed coat may be fused as is evident in *Gevuina avellana* Moliner (Hohmann 1978) and in *Eureka welcomensis*. Moreover, in both extant taxa (and in most grevilleoid genera) the inner epidermis of the testa is composed of polygonal-shaped, calcium oxalate-bearing, transfer cells with internally directed fimbriae (Hohman 1978; Strohschen 1986b). A further cuticle with impressions of elongate cells occurs beneath the testa and develops from the cuticles between the inner and outer integuments and the cuticle surrounding the nucellus (Strohschen 1986b); a morphologically comparable cuticle occurs beneath the testal cuticles in *Eureka welcomensis, E. turgida,* and *E. spechtii* (Figs 23, 24, 29, 51). Anatomical and morphological features of fruits of extant species of *Turrillia* and *Euplassa* (Gevuininae) and *Panopsis* (Macadamiinae) are unavailable and so detailed comparisons between these extant fruits and fossil *Eureka* are precluded.

In summation, fossil fruits included within *Eureka* have pericarps that possess a mosaic of morphological, anatomical, and organisational attributes consistent with pericarps of the Macadamiinae and Gevuinineae. However, seed coat structure of *Eureka* is more similar to that of the Gevuininae than the Macadamiinae (Table 1) and so the fossil taxon is provisionally placed in the Gevuininae.

IMPLICATIONS OF *EUREKA*

The fossils herein allocated to *Eureka* collectively imply a wide distribution of their parental plants in eastern Australia during Oligocene and Miocene times. Oldest occurrences are in sediments beneath basalts dated as 27-34 Mya (Oligocene) in central Queensland (Picardy, Blackwater) and youngest well-dated occurrences are also in sediments beneath basalts of 11.2-13 Mya (late Middle-early Late Miocene) at Forest Reefs Mine, New South Wales. Other localities from which *Eureka* has been reported are less precisely dated, but are within an Oligocene-Miocene age frame (34-5 Mya). If *Eureka* is a member of Gevuininae, this age range has implications for the history and past distribution of subtribe and for age calibrations relevant to divergence of those taxa of the subtribe having tardily dehiscent fruits with wingless seeds. Extant members of the subtribe that bear tardily dehiscent fruits with 1-2 wingless seeds are *Hicksbeachia* and *Bleasdalea* in northeastern Australia-New Guinea, *Kermadecia* and *Sleurmerodendron* in New Caledonia, *Turrillia* in Fiji and Vanuatu, and *Euplassa* and *Gevuina* in South America (Weston & Barker 2006). *Euplassa* with 20 species has the widest distribution range (mid-low latitudes of South America) whilst each of the other six genera has a narrow distribution range and few species (Fig. 1). Initially allocated to three separate subtribes within tribe Macadamieae (Johnson & Briggs 1975) molecular and morphological analyses (Hoot & Douglas 1998; Weston & Barker 2006) demonstrated the above-named genera together with *Cardwellia* (follicular fruit with winged seeds) form a monophyletic clade. The biogeography of the clade was investigated subsequently to test whether the present trans-southern Pacific distribution of the subtribe is better explained by vicariance or by transoceanic dispersal (Barker et al. 2007; Mast et al. 2008; Sauquet et al. 2009).

Age estimates based on Bayesian phylogenetic and molecular dating together with fossil calibration points returned an age of 51.4 (±10.5) Mya for divergence of subtribe Gevuininae (Barker et al. 2007, Fig.2, Node F), an age consistent with a vicariance model for its present distribution. By contrast, in their analyses of a more refined phylogeny of tribe Macadamieae (Mast et al. 2008) the minimum age for the most recent common ancestor (MRCA) of subtribe Gevuininae was set at 34 Mya based on the age of fossil cuticles assigned to the Gevuininae and reported from Middle Eocene sediments (Carpenter & Pole 1995). Even so, Mast et al. (2008) considered the analyses failed to discriminate between disjunction of the subtribe at 34 Mya or 13.6 Mya, and hence between a vicariance or dispersal model to account for the extant distribution of the genera in the Gevuininae. However, they propose an inferred age of 11.5 Mya for divergence between *Bleasdalea* (New Guinea and Australia) and its sister *Hicksbeachia* (Australia), and 8.1 Mya for disjunction between the sister taxa *Kermadecia* (New Caledonia) and *Turillia* (Fiji and Vanuatu). Accordingly, they argue that long distance dispersal accounts for the distribution of the latter sister taxa since the inferred age of disjunction postdates the tectonic events that account for the present day geography of this part of the southwest Pacific (Schellart et al. 2006). They propose that tardily dehiscent fruits with a spongy pericarp may be sufficiently buoyant for long distance water dispersal and suggest the Antarctic Circumpolar Current (ACC) may serve as a possible mechanism. This current is now believed to have been initiated in the Late Oligocene at 25-23 Mya (Lyle et al. 2009), and is confined to latitudes of approximately 40°S.

A further analysis based entirely on molecular data (Sauquet et al. 2009) yielded a cladogram whose topology for the subtribe differed from that presented by Mast et al. (2008), and different crown group age estimates for the constituent extant members of the clade. The age constraint of 70.7 Mya selected for the MRCA of crown Macadamiaeae (Sauquet et al. 2009; Fig. 1, Node I) is based on the Late Cretaceous occurrence of the fossil pollen taxon *Propylipollis crotonioides* Dettmann & Jarzen, which in parsimony analyses was considered suitable for calibration (Sauquet et al. 2009, Supporting Information, Fig. S2, Table S1). On this basis, the crown group age of Gevuininae was estimated as 37.4 Mya and 19.2 Mya for the crown group age of the clade sister to *Cardwellia* (comprising *Bleasdalea* and its sister taxa, all of which bear tardily dehiscent fruits). As discussed above the fruits of *Eureka* closely resemble those of *Bleasdalea*, *Gevuina* and *Hicksbeachia* and so the occurrence of *Eureka* in sediments as old as, or older than, 34 Mya (ie Early Oligocene) suggests that the crown group age of the sister clade to *Cardwellia*, proposed by Sauquet et al. (2009), may need to be reconsidered.

Based on occurrences of *Eureka* reported herein, the Oligocene-Miocene distribution of members of the subtribe having tardily dehiscent fruits spanned some 20° of latitude (~60°– 40°S palaeolatitude) in eastern Australia (Fig 1B). Other fossils reported from within this latitudinal band and accepted as those of the Gevuininae (Mast et al. 2008) are cuticles from the Middle

Eocene of southern Western Australia (Carpenter & Pole 1995) and the Early Miocene of New Zealand (Pole 1998). Thus, the fossil evidence demonstrates a former trans-Tasman distribution of the Gevuininae no longer mirrored in the present vegetation.

Questionably allied to the subtribe is fossil wood reported as similar to, but not identical with, that of *Gevuina* from the Oligocene of southern South America (Pujana, 2007). The pollen taxon, *Propylipollis reticuloscabratus* (Harris) Martin & Harris, which is widely distributed in Australian Campanian-Pleistocene sediments and known also from the Campanian-Eocene of the Antarctic Peninsula (Dettmann & Jarzen 1996), may not represent evidence of the subtribe in South America, as has been determined by Sauquet et al. (2009, Supporting Information). Though these authors undertook a cladistical analysis embracing pollen of all extant genera of Proteaceae and 25 fossil proteaceous-like pollen taxa, the results must be treated with caution because of the 22 pollen characters scored for pollen of extant species relatively few were available for most fossil taxa.

ACKNOWLEDGEMENTS

The authors thank E.Thompson, Museum of Victoria and R. Jones, Australian Museum for loan of fossil material from Victoria and New South Wales; to T. Spencer, South Blackwater Coal, G. Muggeridge, S. Mepes, and H. Rewald, CRA, and to P. Baker, Department of Natural Resources, Bundaberg for collection of fossil fruits. D. Lee, Department of Geology, University of Canterbury, New Zealand, P. Weston, Royal Botanic Gardens, Sydney, A. Specht, School of Environmental Science and Management, Southern Cross University, Lismore, G. Guymer, Queensland Herbarium, R. McKinnon, Brisbane Botanic Gardens, and W. Cooper, Atherton, Queensland are thanked for securing fruits of extant *Gevuina avellana*, *Bleasdalea bleasdalei*, *Hicksbeachia pinnatifolia* and *H. pilosa*. G. Guymer and P. Weston kindly arranged the loan of fruits of several species of *Virotia*. We are especially grateful to P. Weston and R. Hill for helpful reviewer's comments.

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A review of the Australian *Polyrhachis* ants of the subgenera *Myrmhopla* Forel and *Hirtomyrma* subgen. Nov. (Hymenoptera: Formicidae: Formicinae)

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Citation: Kohout, R.J. 2010 03 15: A review of the Australian *Polyrhachis* ants of the subgenera *Myrmhopla* Forel and *Hirtomyrma* subgen. nov. (Hymenoptera: Formicidae: Formicinae). *Memoirs of the Queensland Museum – Nature* 55(1): 167-204. Brisbane. ISSN 0079-8835. Accepted: 13 April 2009.

ABSTRACT

The Australian species of the *Polyrhachis* subgenus *Myrmhopla* are revised. A total of eight Australian species are recognised in four species-groups; four species in the sex*spinosa*-group, two species in the *bicolor*-group and single species in each of the *dives*- and *mucronata*-groups. A new subgenus *Hirtomyrma* is proposed to house ten species formerly included within the *P. viehmeyeri*-group of the subgenus *Myrmhopla*. *Polyrhachis dispar* sp. nov. is described and placed in the sex*spinosa*-group. *Polyrhachis bicolor nigripes* is raised to specific status and reported from Australia for the first time. The extralimital species *P. cyrtomyrmoides* Donisthorpe is considered synonymous with *P. mucronata* Fr. Smith. A neotype for *P. sexspinosa* (Latreillei) and lectotype for *P. reclinata* Emery are designated. All species are illustrated and their distribution and nesting habits are summarised. Keys to the subgenera of Australian *Polyrhachis* and to species of *Myrmhopla* and *Hirtomyrma* are included. ❑ *Polyrhachis, Myrmhopla, Hirtomyrma, bicolor-group, dives-group, mucronata-group,* sex*spinosa-group, Australia, distribution.*

Myrmhopla was established by Forel (1915) as a subgenus of *Polyrhachis* Fr. Smith, 1857, with *Formica armata* (Le Guillou, 1842) as the type species. Forel did not define his new subgenus but Emery (1925) later delimited *Myrmhopla* as follows (translation): "*Worker*. - Dorsum of thorax rounded, that is to say not marginate, except in some species (groups *cryptoceroides* and *viehmeyeri*); pronotal spines shorter than propodeal, sometimes absent; metanotal groove variable. Petiole variable amongst the groups and species; body of petiole in form of an elongate node, angled anterodorsally in profile or, to the contrary, forming a thick scale, higher than long, angular or rounded in front; generally bearing single pair of spines very variable in form, size and direction; rarely the spines are hook-like; in many species where they form a gaster embracing arc, there is between spines also a pair of teeth or small vertical spines. First gastral segment large. *Female*. - Very similar to the worker, with spines usually stronger and shorter."

When Emery published his diagnosis of *Myrmhopla*, the subgenus already included some 140 species and subspecific forms. In an attempt to partition the high degree of diversity within such a large subgenus, he subdivided *Myrmhopla* into six species-groups. Dorow (1995) divided the subgenus further, recognising 16 species-groups, the six proposed by Emery and ten that he established as new. Five of these groups are relevant to the Australian fauna; the *bicolor, dives, mucronata, sexspinosa* and *vielmeyeri*-groups.

However, as mentioned by previous authors (Bolton, 1975; Dorow, 1995), the large degree of morphological diversity within *Myrmhopla* presents problems with maintaining the subgenus as it was originally perceived. Virtually none of the characters originally used by Emery (1925) to define *Myrmhopla* consistently apply to the species currently placed within the subgenus and some characters vary within a single species-group. The concept of the subgenus has widely been criticised (Hung, 1967) and the formation of numerous species-groups within *Myrmhopla* has only partially alleviated the problem.

Considerable morphological differences between various species-groups are evident throughout the subgenus *Myrmhopla,* but nowhere as markedly as in relation to the *P. vielmeyeri*-group. For example, a marginate mesosoma is a particularly significant character separating species of the *vielmeyeri*-group from the rest of *Myrmhopla*, except perhaps some species of the extralimital *P. cryptoceroides*-group (e.g. *P. cryptoceroides* Emery) (Kohout, 2006a). In some respects, *vielmeyeri*-group species resemble members of the subgenus *Hedomyrma* Forel as they share a spinose and marginate mesosoma and a petiole featuring a more-or-less flat dorsum. However the characteristic vermiculate sculpturation, bristle-like pilosity and distinct reddish-brown colouration of species of the *vielmeyeri*-group clearly separate them from *Hedomyrma* species. The most remarkable feature of *vielmeyeri*-group species is their subterranean nesting habit combined with a sophisticated parasitic relationship with certain groups of ectatommine and poneroid ants (Maschwitz *et al.*, 2003). The morphological and behavioural distinctness of the *vielmeyeri*-group is further supported by a preliminary molecular phylogeny of *Polyrhachis* (S.K.A. Robson, *pers. comm.*) that places the *vielmeyeri*-group (i.e. *P. loweryi*) closest to species of the subgenus *Chariomyrma* Forel (*P. lata* Emery and *P. sokolova* Forel) and rather distant from representatives of other *Myrmhopla* species-groups. Considering these facts, I believe that the *vielmeyeri*-group should be removed from the subgenus *Myrmhopla* and a new subgenus *Hirtomyrma* is proposed below to incorporate its constituent species.

METHODS

Publication dates and the spelling of species epithets and authors' names follow Bolton *et al.* (2007). This study is principally based on the worker caste but notes are provided on associated queens. Associated males of only a few species are known and present in the ANIC and/or QM spirit collections. Their diagnosis is beyond the intended scope of this paper and has not been attempted.

The localities at which ants were collected by the Bishop Museum's collectors, were checked against that institution's list of New Guinean localities (BPBM, 1966, unpublished). In some cases the latitude and longitude co-ordinates, or altitude, are only roughly approximate. The use of the terms 'New Guinea' or 'Bismarck Archipelago' alone indicate the delimitation of these regions in a biogeographic sense regardless of current political boundaries.

Illustrations. Photographs of specimens were taken with an Olympus SZX12 Stereomicroscope and DP70 digital camera. Images were processed using Helicon Focus (Mac OSX version) and Photoshop CS2 (Adobe Inc., USA) software. The holotypes of *P. dispar* sp. nov., *P. bamaga* Kohout, *P. eremita* Kohout and *P. rustica* Kohout, the paratype of *P. loweryi* Kohout and type-compared specimens from Australian localities of other species are illustrated. The illustrations of *P. sexspinosa* (Latreille) are of the neotype designated below.

Standard measurements and indices. Measurements and indices follow those of Kohout (2006):

TL = Total length (the necessarily composite measurement of the outstretched length of the entire ant measured in profile); HL = Head length (the maximum measurable length of the head in perfect full face view, measured from the anterior-most point of the clypeal border or teeth, to the posterior-most point of the occipital margin); HW = Head width (width of the head in perfect full face view, measured immediately in front of the eyes); CI = Cephalic index (HW × 100/HL); SL = Scape length (excluding the condyle); SI = Scape index (SL × 100/HW); PW = Pronotal width (greatest width of the pronotal dorsum); MTL = Metathoracic tibial length (maximum measurable length of the tibia of the hind leg). All measurements were taken using a Zeiss SR stereomicroscope with an eyepiece graticule calibrated against a stage micrometer. All measurements are expressed in millimetres (mm).

Abbreviations. Names of the most frequently listed collectors are abbreviated as follows: ANA - Alan N. Andersen; CJB - C.J. Burwell; DJC - D.J. Cook; GBM - G.B. Monteith; RJK - R.J. Kohout; RWT - R.W. Taylor; SKR - S.K. Robson. Other abbreviations used in specimen data are: NP - National Park; Pen. - Peninsula; PNG - Papua New Guinea; R. - River; Ra. - Range; Rd - Road; rf. - rainforest; Stn - Station; w - worker/s.

Institutions and depositories. (with the names of cooperating curators) AMNH – American Museum of Natural History, New York, NY, USA (Dr J.M. Carpenter); AMSA – Australian Museum, Sydney, NSW, Australia (Drs D. Britton, D. Smith); ANIC - Australian National Insect Collection, CSIRO, Canberra, Australia (Dr S.O. Shattuck); BMNH - The Natural History Museum, London, UK (B. Bolton); BPBM – Bernice P. Bishop Museum, Honolulu, HI, USA (K.T. Arakaki); HNHM – Hungarian Natural History Museum, Budapest, Hungary (Dr J. Papp); IZAS – Institute of Zoology, Ukrainian Academy of Sciences, Kiev, Ukraine (Dr A.G. Radchenko); JCUT - James Cook University, Townsville, Queensland, Australia (Dr S.K.A. Robson); JWGU - Johan Wolfgang Goethe-Universität, Frankfurt am Main, Germany (Prof. Dr U. Maschwitz); MCZC - Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA (Dr S. Cover); MNHA – Museum of Nature and Human Activities, Hyogo Pref. University, Hyogo, Japan (Dr Y. Hashimoto); MNHN – Muséum National d'Histoire Naturelle, Paris, France (Dr J. Casevitz Weulersse); MSNG - Civic Museum of Natural History "G. Doria", Genova, Italy (Drs R. Poggi, V. Raineri); MVMA – Museum of Victoria, Melbourne, Vic., Australia (Dr K. Walker); NMNH – National Museum of Natural History, Washington, DC, USA (Dr T.R. Schultz); OXUM – Hope Entomological Collections, University Museum, Oxford, UK (Drs C. O'Toole, D.J. Mann); QM - Queensland Museum, Brisbane, Qld, Australia (Dr C.J. Burwell); TERC – Tropical Ecosysytems Research Centre, CSIRO Sustainable Ecosystems, Darwin, NT, Australia (Dr A.N. Andersen).

SYSTEMATICS

Genus ***Polyrhachis*** Fr. Smith, 1857

Polyrhachis Fr. Smith, 1857: 58. Type species: *Formica bihamata* Drury, 1773 by original designation.

KEY TO AUSTRALIAN SUBGENERA OF *POLYRHACHIS*
(based on worker caste)

1. Mesonotum armed with a pair of upwards and backwards curved spines; petiole distinctly higher than full height of mesosoma, terminating in a pair of hook-like spines (Fig. 1K) (arboreal) (Cape York Pen.) . . . . *Polyrhachis* (only *P. bellicosa* Fr. Smith)

— Mesonotum without spines; petiole lower than full height of mesosoma, dorsum armed with spines or teeth of various configurations or virtually unarmed . . . . 2.

2. Mesosoma completely laterally immarginate . . . . .3.

— Mesosoma at least partly laterally marginate .... 5.

3. Small species (HL 1.25-1.65); dorsum of mesosoma relatively short, strongly longitudinally and transversely convex; pronotal spines reduced to acute teeth or absent; body uniformly black, highly polished ....4.

— Small to large species (HL 1.40-3.60); dorsum of mesosoma elongate, only weakly to moderately convex; pronotal spines relatively long, acute; colour of body variable, mostly black, but also reddish-brown or bicoloured (Figs 1A-F, 4A-F) (arboreal or lignicolous) (tropical Qld and NT) ... *Myrmhopla* (part)

4. Sides of head with longitudinal carina separating gena from ventral parts of head; propodeal spines, if present, very short; petiole scale-like, armed with four spines or teeth of various lengths and configurations, (Fig. 1C) only rarely reduced to mere denticles (*P. brevinoda* Kohout) (arboreal) (NT, Qld and coastal NSW) ....*Cyrtomyrma*

— Sides of head without longitudinal carina; propodeal spines long; petiole columnar, armed with a pair of horizontal spines that conform to shape of first gastral segment and a pair of distinct intercalary teeth (Fig. 3E, F) (arboreal) (Cape York Pen. and north Qld) .... *Myrmhopla* (part) (only *P. mucronata* Fr. Smith)

5. Pronotal humeri simply rounded or, at most, bluntly angular (Figs 1A, D)......6.

— Pronotal humeri armed with spines or acute teeth (Figs 1E, G)............... 9.

6. Dorsum of petiole usually narrowly rounded, rarely with a distinct platform (*P. thusnelda* Forel), armed with a pair of more-or-less horizontal, backwards directed or diverging, acute spines; propodeal spines rarely hook-like (*P. ammonoeides* Roger); propodeal spines always present (Fig. 1D), mostly horizontal or weakly elevated (subterranean, rarely lignicolous or lithocolous) (Australia-wide, except south, south-west and Tasmania) ....*Hagiomyrma*

— Dorsum of petiole variable, with two, three or four upward directed spines or teeth of various lengths and configurations, or petiole virtually unarmed; propodeal spines present or reduced to mere teeth .... 7.

7. Small species (HL 1.15-1.65); petiole columnar with two or three spines; body light coloured, mostly yellowish- or reddish-brown (arboreal) (tropical north Qld and NT only)..........8.

— Small to large species (HL 1.10-2.80); petiole scale-like, usually with four teeth or short spines, but rarely also with one (*P. pseudothrinax* Hung) or two (e.g. *P. prometheus* Santschi) elongated spines or virtually unarmed with only shallow median emargination (Fig. 1A); body mostly black or rarely reddish-brown (*P. incerta* Kohout) (subterranean or lignicolous, nocturnal and crepuscular foragers) (Australia-wide, incl. Tasmania)........... *Campomyrma*

8. Petiole armed with three spines, middle spine distinctly longer than lateral spines; propodeal spines acute, distinctly elevated or virtually vertical (Fig. 1J) (arboreal) (NT and north Qld) .... *Myrmothrinax*

— Petiole armed with two short spines; propodeal spines reduced to short, upturned teeth (Fig. 1H) (arboreal) (north Qld) .... *Myrmatopa* (part) (only *P. lombokensis* Emery)

9. Pronotal humeri produced into broad-based short teeth with lateral margins distinctly expanded, virtually laminate; mesonotal and propodeal margins often elaborate, variously incised or with laterally dilated laminate lobes (e.g. *P. schoopae* Forel); body mostly broad and stocky (Fig. 1B) with short appendages, generally with abundant pilosity and pubescence often masking underlying sculpturation (subterranean or rarely lignicolous) (Australia-wide, except Tasmania) ....*Chariomyrma*

— Pronotal humeri produced into spines or acute teeth with lateral margins distinct, but not laminate; mesonotal and propodeal margins simple, never elaborate; body elongate with relatively long appendages and only rarely with abundant pilosity and/or pubescence (e.g. *P. (Hedomyrma) clotho* Forel) . . . . 10.

10. Pronotal humeri produced into long, horizontal, anteriorly directed spines; propodeal spines reduced to short, upturned teeth; petiole scale-like, armed with a pair of acute, upward directed spines and a tooth or blunt angle situated below their bases (Fig. 1G) (lignicolous or terrestrial) (Cape York Pen.) . . . . *Myrma*

– Pronotal humeri produced into horizontal or variously elevated, mostly anterolaterally directed spines or acute teeth; propodeal spines present or rarely reduced to acute teeth (*P. (Myrmatopa) alphea* Fr. Smith); petiole columnar with a pair of horizontal or elevated spines . . . . 11.

11. Small species (HL < 1.75); propodeal spines reduced to acute teeth; petiole armed with two, rather long, upward directed spines (arboreal) (Cape York Pen.) . . . *Myrmatopa* (part) (only *P. alphea* Fr. Smith)

– Larger species (HL > 1.75); propodeal spines always present; petiole with more-or-less flat dorsum, armed with a pair of horizontal or variously elevated spines . . . . 12.

12. Pronotal dorsum flat; humeri armed with acute, somewhat elevated, slender spines; propodeal spines acute, usually longer than pronotal pair, variously elevated; dorsum of petiole with rather vague, posteriorly sloping platform; dorsa of head, mesosoma and petiole with characteristic vermiculate sculpturation and short, bristle-like, brown hairs (Figs 1F, 6A-F, 7A-F) (subterranean) (Qld) . . . . *Hirtomyrma*

– Pronotal dorsum more-or-less longitudinally and transversely convex; humeri armed with mostly horizontal, dorsally flattened, laterally or anterolaterally directed acute spines or teeth (Fig. 1E); propodeal spines mostly horizontal, but also elevated; dorsum of petiole with rather conspicuous platform (except in *P. clio* Forel); body sculpturation never vermiculate, ranging from rugose to rather smooth; silvery or rich golden pilosity and pubescence in various densities over most body surfaces (lignicolous or rarely lithocolous) (tropical and coastal temperate Australia, except central and southern regions) . . . . *Hedomyrma*

Subgenus **Myrmhopla** Forel, 1915

Myrmhopla Forel, 1915: 107. Type species: *Formica armata* Le Guillou, 1842 by original designation.

KEY TO AUSTRALIAN SPECIES OF THE SUBGENUS *MYRMHOPLA*
(based on worker caste)

1. Larger species (HL >2.00); all body surfaces, including appendages, with relatively long, erect hairs; appressed or suberect pubescence present in various densities but usually not completely hiding underlying sculpturation; gastral pubescence organised in midline pattern (Fig. 5C, E) (*sexspinosa*-group) . . . . . 2.

– Smaller species (HL <2.00); body pilosity and pubescence highly variable between species-groups, from rather abundant to virtually lacking; gastral pubescence, if present, not forming midline pattern (Figs 2C, E, 3C, E) . . . . .5.

2. Smaller species (HL <2.70); head and anterior portion of mesosoma black with propodeum and petiole mostly reddish-brown; vertex of head coarsely rugose; pronotal dorsum rather smooth and polished or weakly and shallowly sculptured; short, sparse pubescence mostly greyish or white (Fig. 4B, E-F) *glabrinota* Clark.

– Larger species (HL >3.00); head and body mostly black; dorsum of head and pronotum reticulate-punctate or rugose beneath rather long, golden or silvery pubescence . . . . 3.

3. Head strongly tapered behind eyes; occipital margin narrow, forming lateral lobes that are more-or-less visible with head in full face

view (Fig. 5A, B); antennal scapes relatively long (SI >190) . . . . .4.

– Head not strongly tapered behind eyes; occipital margin broad, without distinct lateral lobes (Fig. 4A); antennal scapes relatively short (SI <160) . . . . *dispar* sp. nov.

4. Propodeal spines generally vertical to main axis of body or even inclined anteriorly; dorsum of head and mesosoma rather coarsely rugose (Fig. 5B, E-F) . . *sexspinosa* (Latreille)

– Propodeal spines oblique to main axis of body, directed posteriorly; dorsum of head and mesosoma shallowly and finely sculptured beneath dense pubescence (Fig. 5A, C-D) . . . . *reclinata* Emery

5. Body distinctly bicoloured; head and mesosoma black with gaster orange or light reddish-brown; appendages black, brown or orange (Fig. 2A-F) (*bicolor*-group) . . . .6.

– Body unicoloured, black, with appendages black or reddish-brown (Fig. 3A-F) . . . . 7.

6. Mandibles, apical antennal segments and gaster orange or light reddish-brown; antennal scapes and legs mostly black or very dark reddish-brown; mesosoma in lateral view with evenly convex outline (Fig. 2B, E-F) . . . . *nigripes* Emery

– Mandibles, antennae, legs and gaster orange or light reddish-brown; mesosoma in lateral view with mesonotum virtually flat (Fig. 2A, C-D) . . . . *bicolor* Fr. Smith

7. Pronotal spines relatively long and slender; body black, closely and uniformly reticulate-punctate, opaque (Fig. 3A, C-D) (*dives*-group) . . . . *dives* Fr. Smith

– Pronotal spines reduced to minute teeth; body jet-black with legs and apical antennal segments black to medium reddish-brown; sculpturation consisting very fine, superficial reticulation with scattered shallow pits (Fig. 3B, E-F) (*mucronata*-group) . . . . *mucronata* Fr. Smith

POLYRHACHIS BICOLOR SPECIES-GROUP

The *Polyrhachis bicolor* species-group was established by Dorow (1995) who subdivided the former *P. dives*-group (as delimited by Emery, 1925) and transferred many of its original constituents into three, earlier established groups (*P. armata*-, *sexspinosa*- and *viehmeyeri*-groups), or into five groups he newly proposed (*P. arachne*-, *bicolor*-, *cephalotes*-, *hector*- and *mucronata*-groups). As presently defined, the *bicolor*-group includes only four species. However, about 11 infraspecific forms are currently associated with the name-bearing species, *P. bicolor*. Many of these forms apparently represent valid species and, in addition, at least twice as many closely related new species are in collections awaiting description. This relatively small, but widespread and complicated group is in great need of revision but, with only two species relevant to the Australian fauna, this is beyond the scope of the present paper.

Diagnosis. (modified from Dorow, 1995) *Worker*: Mostly small to medium-sized ants (HL 1.15-1.85) with general characteristics of the genus. Mandibles smooth or very finely, longitudinally striate, rather polished with small piliferous pits towards bases. Anterior clypeal margin with shallow, central, medially emarginate flange, laterally flanked by teeth or acute angles. Head semicircular in side view, oval in frontal view; genae immarginate. Eyes moderately to strongly convex, clearly exceeding lateral cephalic outline in full face view. Mesosoma totally immarginate, armed with rather slender spines. Petiole nodi form with a pair of lateral spines usually embracing first gastral segment, without intercalary spines or teeth. Antennal scapes and tibiae slender and long, spider-like. Sculpturation of head, mesosoma and petiole mostly a fine punctation, usually obscured by rich pubescence, producing a matt appearance. Gaster shagreened or finely reticulate-punctate, opaque. All body surfaces with abundant, relatively long, erect hairs and silvery to golden, appressed or suberect pub-

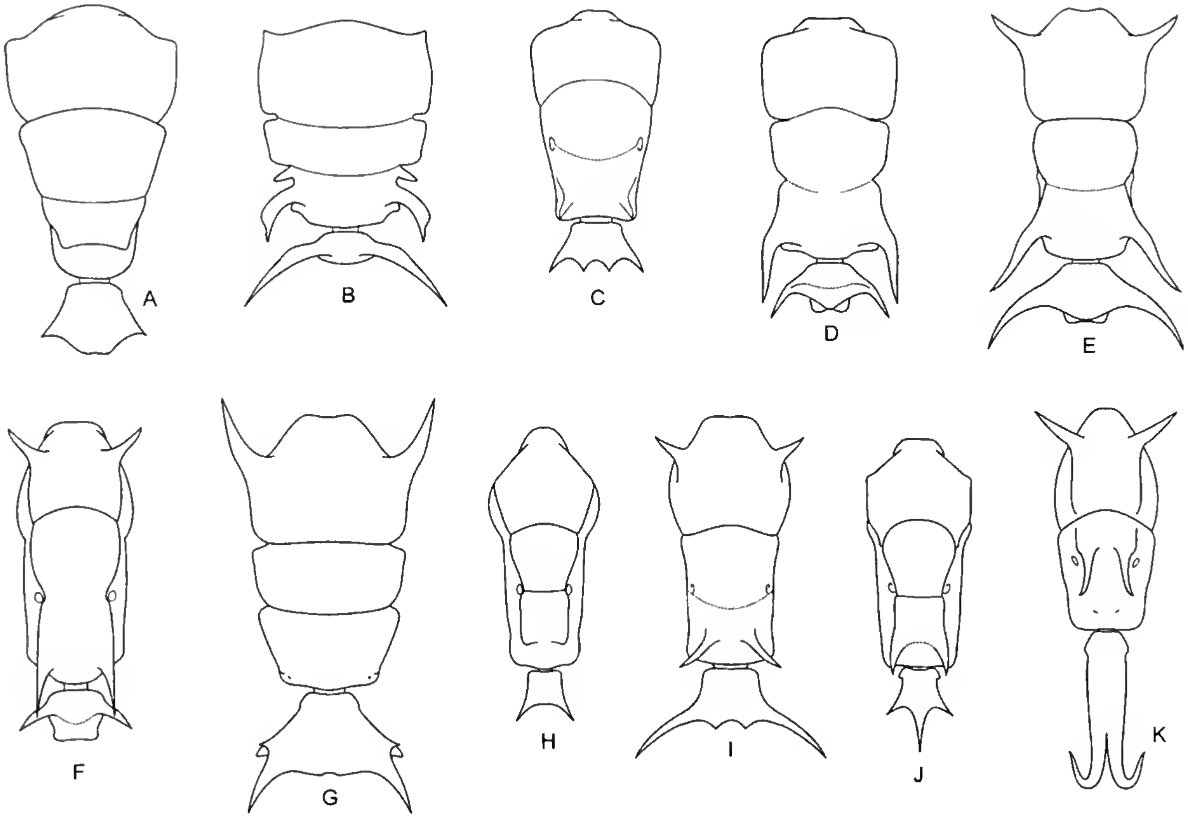

FIG. 1. Australian *Polyrhachis* subgenera, dorsal view of mesosoma and petiole in outline (pilosity omitted): A – *P. (Campomyrma) creusa* Emery; B – *P. (Chariomyrma) schoopae* Forel; C – *P. (Cyrtomyrma) australis* Mayr; D – *P. (Hagiomyrma) penelope* Forel; E – *P. (Hedomyrma) cupreata* Emery; F – *P. (Hirtomyrma) loweryi* Kohout; G – *P. (Myrma) foreli* Kohout; H – *P. (Myrmatopa) lombokensis* Emery; I – *P. (Myrmhopla) dives* Fr. Smith; J – *P. (Myrmothrinax) queenslandica* Emery; K – *P. (Polyrhachis) bellicosa* Fr. Smith (not to scale).

escence. Body bicoloured, mostly black with gaster and appendages light reddish-brown or amber-coloured (as in *P. bicolor*), or virtually unicoloured with body black and gaster, including appendages, black or very dark reddish-brown (as in *P. longipes* Fr. Smith, 1859).

Queen. Apart from sexual characters, very similar to worker. Armament of pronotum, propodeum and petiole distinctly reduced with spines shorter and stronger. Sculpturation, pilosity and colour virtually identical to worker.

Distribution and biology. *Polyrhachis bicolor*-group species are distributed throughout south-east Asia, including Myanmar, India, Thailand, Malaysia, Singapore, Vietnam and the Philippines, extending south to Indonesia, New Guinea and northern Australia. Members of the *bicolor*-group are arboreal nesters, building polydomous nests of silk and vegetation debris among the leaves of mostly rainforest trees and shrubs (Robson & Kohout, 2007).

Polyrhachis bicolor Fr. Smith, 1958
(Figs 2A, C-D, 9A, 10D)

Polyrhachis bicolor Fr. Smith, 1858: 65. Holotype queen. Type locality: BURMA (= MYANMAR), BMNH (examined).

Polyrhachis bicolor var. *concolor* Forel, 1910: 129. Syntype workers, queen, male. Type locality: PHILIPPINES, Luzon, Manila (C.S. Banks), BSMP, MHNG QM (examined). Synonymy by Kohout, 1998: 515.

Other material. INDIA, Bengal Baigachi, vi-viii.1943 (L.H. Weatherill) (w); S. Andamans, Port Blair, 4.xii.1906 (B. Osmaston) (w, ♀, ♂). S.E. THAILAND, Songkhla Prov., TonNga Chang Wildlife Sanctuary, 06°56′N, 100°14′E, 12.i.2002, lowland rf. (Surachai Tongierm) (w). SINGAPORE, Mandai, 01°27′N, 103°46′E, <5 m, 21.xi.1988 (P.S. Ward, #9581-4) (w). VIETNAM, Saigon, 8.ii.1925 (F. Silvestri) (w). PHILIPPINES, Los Baños (F.X. Williams) (w); Luzon, Manila, 20.iv.1918 (McGregor) (w); Camarines Sur, Panicuason Villiage, 18 km E of Naga City, 13°40′N, 123°19′E, 500-550m, 12.iii.2003 (D. General & G.D. Alpert) (w); Palawan, Honda Bay, ii.1988 (J.H. Martin) (w); Negros Or., Dumaguete, 1942 (J.W. Chapman) (w); Mindanao Or., Gingoog, Anakan Lbr. Co. (A. Reyes) (w). WEST MALAYSIA, Kulala Lumpur, i-ii.1989 (M. Edmunds) (w). EAST MALAYSIA, SABAH (as British Nth Borneo), W Coast Residency, Ranau, 500 m, 22-25.i.1959 (T.C. Maa) (w, ♀); Kinabalu Park, 19.v.1995 (Shanmuga Sundram) (w); Maliau Basin, Ginseng Camp, 04°44′N, 116°55′E, 700 m, 27.ii-11.iii.2005 (RJK & Effazilla Waty acc. 05.27) (w); ditto, Agathis Camp, 04°41′N, 116°54′E, c. 500 m, 16-19.iii.2005 (RJK & Lina Thomas acc. 05.70) (w). SARAWAK, Kuching (J. Hewitt) (w); Nanga Pelagus, nr Kapit, 180-585m, 7-14.viii.1958 (T.C. Maa) (w). BRUNEI, Brunei-Muara Distr., Tanjung Semesta, Brunei R., 5.vii.1994 (RJK et al. acc. 94.83) (w); Belait Distr., 1-2 km SE of Melilas Longhouse, 16.vii.1994 (RJK acc. 94.124) (w). INDONESIA, JAVA, Batavia (= Jakarta), iii.1921 (no further data) (w); Buitenzorg (= Bogor), 21.xii.1912 (V. Karavaiev #2382) (w); ditto, 4.ix.1909 (Bryant & Palmer) (w, ♀); SUMATRA, Pematang, Siantar, 1937 (W.M. Mann, NGS SI) (w, ♀). PAPUA NEW GUINEA, West Sepik Prov., Torricelli Mts, Lumi, 400-550 m, 03°28′S, 142°02′E, 4-13.viii.1984 (RJK acc. 84.283) (w), Central Prov., Thaira Boat Harbour, c. 15 km ESE of Port Moresby, 09°31′S, 147°17′E, 5.ix.1984, mangroves (RJK acc. 84.436) (w, ♀). AUSTRALIA, NORTHERN TERRITORY, Holmes Jungle, c. 15 km NE of Darwin, 12°25′S, 130°58′E, 16.xi.1993, monsoon rf. clearing (RJK acc.93.35) (w, ♀); Darwin, Nightcliff, 2.ix.1960 (J.L. Gressitt) (w); Berry Springs NP, 12°42′S, 130°59′E, 10.ii.1994 (RJK acc. 94.4) (w); ditto, 21.vii.1981 (BBL) (w).

Worker. Dimensions: TL c. 6.00-7.06; HL 1.43-1.68; HW 1.12-1.31; CI 77-79; SL 1.96-2.34; SI 172-182; PW 0.87-1.03; MTL 2.34-2.68 (10 measured)

Mandibles with 5 teeth, progressively reducing in length towards base. Anterior clypeal margin with shallow median flange, laterally flanked by acute angles. Clypeus with poorly defined, posteriorly weakly elevated, median carina; clypeus virtually straight in profile with rather shallow basal margin. Frontal carinae sinuate with well raised margins; frontal furrow indistinct. Sides of head in front of eyes converging anteriorly towards mandibular bases in virtually straight line; behind eyes sides rounding into convex occipital margin. Eyes strongly convex, in full face view clearly breaking lateral cephalic outline. Ocelli indistinct. Mesosoma laterally immarginate. Pronotal dorsum weakly convex in profile; humeri armed with slender, relatively long, acute, anterolaterally directed spines with tips slightly turned upwards. Promesonotal suture distinct; mesonotum straight in profile with metanotal groove marked by slight step in outline. Propodeal dorsum rather short with a pair of slender, obliquely elevated, subparallel, acute spines. Petiole nodiform with medially weakly elevated dorsum and pair of relatively long and slender, laterally and posteriorly curved, acute spines. Anterior face of first gastral tergite rounding in evenly convex line onto dorsum of segment.

Mandibles smooth and polished with shallow piliferous pits. Head, mesosoma and gaster closely reticulate-punctate with sculpture almost completely hidden by overlying pubescence. Spines weakly rugose at bases, smooth and polished towards tips. Gaster finelly shagreened.

Mandibular masticatory borders with curved, golden hairs. Anterior clypeal margin medially with several, medium length, anteriorly directed, golden setae. Head, including clypeus, mesosoma and gaster with numerous, mostly erect and variously curved, somewhat untidy, long silvery hairs, some longer than greatest diameter of eyes; hairs on gaster mostly posteriorly directed. Very distinct, relatively long, silvery pubescence almost completely hiding underlying sculpturation on head, mesosoma and petiole, except spines.

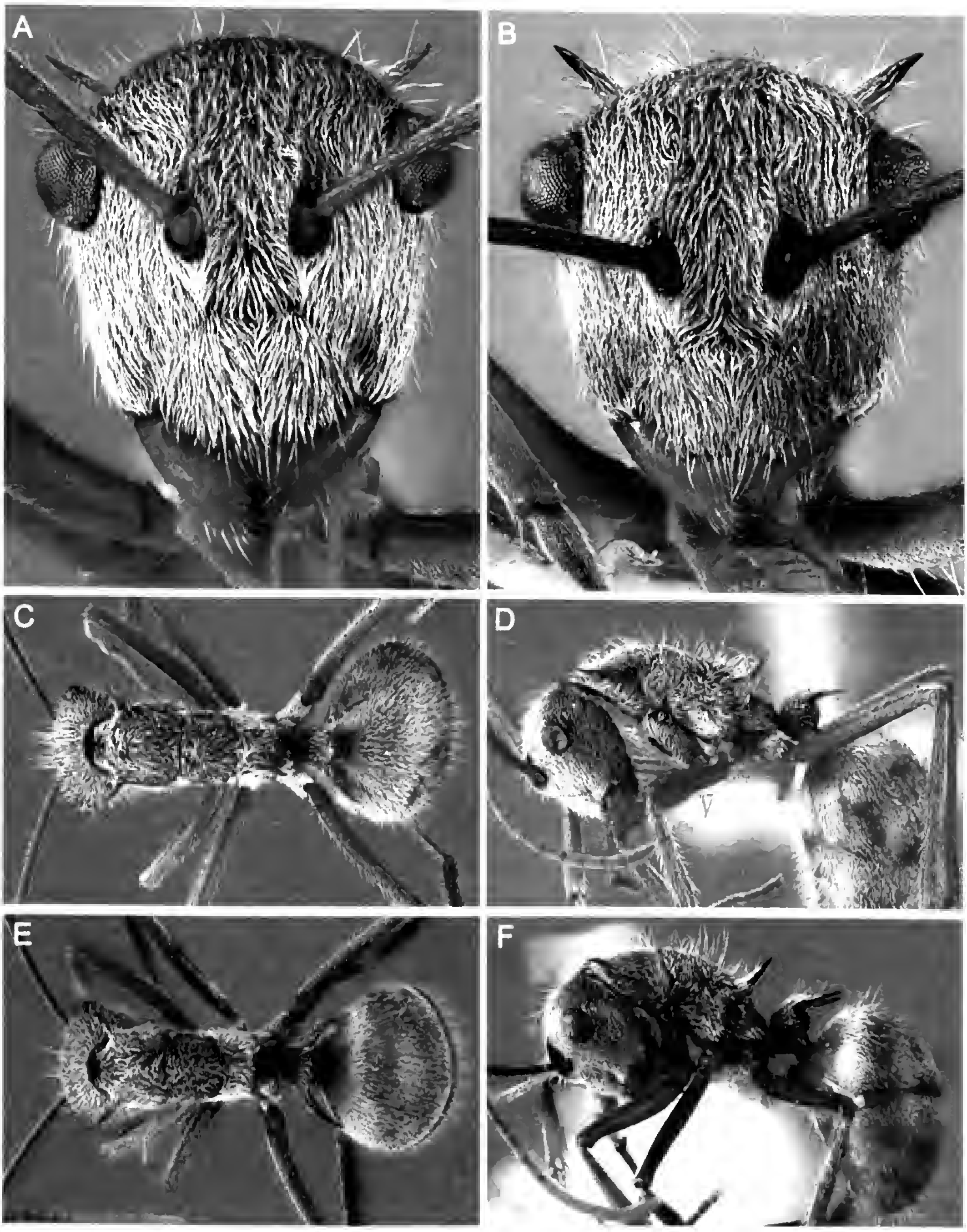

FIG. 2. *Polyrhachis (Myrmhopla)* species from Australia. Head in full face view (top); Dorsal view (left); Lateral view (right). A,C-D, *P. bicolor* Fr. Smith; B,E-F, *P. nigripes* Emery (not to scale).

Gastral pubescence more appressed and somewhat diluted, not obscuring fine sculpturation.

Head, mesosoma and petiole black; mandibles, median portion of anterior clypeal margin, antennae, legs, coxae, tips of spines, subpetiolar process and gaster, orange or light reddish-brown.

Queen. Dimensions: TL c. 8.97; HL 1.87; HW 1.40; CI 75; SL 2.62; SI 187; PW 1.78; MTL 3.06 (1 measured).

Very similar to worker and apart from sexual characters, including three ocelli, fully developed mesosoma and wings, differing as follows: Pronotal spines reduced to more-or-less triangular, acute teeth, barely longer than basal widths. Mesoscutum with anterior margin widely and evenly rounded in dorsal view; median line bifurcate anteriorly; parapsides rather flat anteriorly, raised posteriorly. Mesoscutellum weakly convex, slightly elevated above dorsal plane of mesosoma; metanotal groove distinct. Propodeal spines very short, obliquely elevated, somewhat dorsoventrally flattened, tips rounded. Petiolar spines similar to those in worker but stronger at base and distinctly shorter; dorsum of petiole with rather distinct, blunt intercalary tooth.

Males and immature stages (eggs, larvae and pupae) deposited in the QM spirit collection.

Remarks. *Polyrhachis bicolor* is a widespread species recorded from south-east Asia south to Indonesia, New Guinea and the Northern Territory in Australia. As noted by Kohout (2008: 295), across its distribution, *P. bicolor* forms a large number of overlapping populations that differ to some extent from the holotype. About eleven infraspecific forms are presently associated with *P. bicolor*, however, after examination of a large amount of material from across the entire range I consider the Australian population to represent the nominal form.

Polyrhachis bicolor is a relatively common species at suitable localities around Darwin, where it builds nests of silk and vegetation debris among the leaves of trees and shrubs notably along the margins of monsoon rainforests. In spite of being a rather common species in mangroves and lowland forests along the Gulf of Papua, it has not yet been recorded from Cape York Peninsula or elsewhere in north Queensland.

Polyrhachis nigripes Emery, 1897 **stat. nov.**
(Figs 2B, E-F, 9A)

Polyrhachis bicolor var. *nigripes* Emery, 1897: 592. Holotype worker. Type locality: NEW GUINEA: Paumomu River (= Angabanga R.) (L. Loria), MSNG. **Stat. nov.**

Other material. INDONESIA, IRIAN JAYA, Eramboe, 80 km ex Merauke, 1.ii.1960 (T.C. Maa) (w); Hollandia area, Cyclops Mts, W. Sentani, 2 00-1000m, 22-25.vi.1959 (T.C. Maa) (w). PAPUA NEW GUINEA, West Sepik Prov., Torricelli Mts, Lumi, x.1984 (D. Waisi) (w); Wum, Upper Jimmi Valley, 840m, 16.vii.1955 (J.L. Gressitt) (w); Morobe Prov., Huon Pen., lower Busu R., 27.iv-12.v.1955, lowland rf. (E.O. Wilson) (w - compared with holotype); Central Prov., Karema, Brown R., 8-11.iii.1955, lowland rf. (E.O. Wilson #601) (w); Bisianumu, E of Port Moresby, 500 m, 3.ix.1959 (T.C. Maa) (w); Catalina Estate, 48 km N of Port Moresby, 500 m, 3.iv.1959 (T.C. Maa) (w); Laloki, nr Port Moresby, 30.vii-2.ix.1959 (T.C. Maa) (w); Rouna, xi.1968 (N.L.H. Krauss) (w); Aroa Pltn, 16.v.1957 (J.H. Barrett) (w). AUSTRALIA, QUEENSLAND, Cape York Pen., Iron Ra. NP, Claudie R., 12°46'S, 143°16'E, <20m, 2.x.2000, monsoon rf. (RJK acc. 2000.136, 137) (w, ♀).

Worker. Dimensions: TL c. 5.74-6.25; HL 1.40-1.59; HW 1.15-1.31; CI 79-82; SL 1.87-2.06; SI 157-169; PW 0.87-1.03; MTL 2.18-2.46 (4 measured).

Mandibles with 5 teeth. Anterior clypeal margin with shallow, median flange, laterally flanked by rather acute teeth. Clypeus with poorly defined, posteriorly elevated median carina, weakly convex in profile with rather shallow basal margin. Frontal carinae sinuate with well raised margins; frontal furrow indistinct. Sides of head in front of eyes converging anteriorly towards mandibular bases in straight line; behind eyes sides rounding into convex occipital margin. Eyes strongly convex, relatively large, in full face view clearly breaking lateral occipital margin. Ocelli indistinct. Mesosoma laterally immarginate. Pronotal and mesonotal dorsa forming even, weakly convex line in profile;

pronotal humeri armed with fine, slender, relatively long, acute, anterolaterally directed spines, tips slightly turned downwards. Promesonotal suture distinct; metanotal groove feebly marked by rather flat, bowed line. Propodeal dorsum rather short with a pair of obliquely elevated, fine, slender, subparallel, acute spines. Petiole nodiform, dorsum medially weakly elevated, armed with a pair of relatively long, slender, laterally and posteriorly curved, acute spines. Anterior face of first gastral segment widely rounding onto dorsum of segment.

Mandibles rather smooth or very finely, longitudinally striate with shallow piliferous pits. Head, mesosoma and gaster closely reticulate punctate with sculpture almost completely hidden by overlying pubescence. Spines weakly rugose, tips rather smooth and polished. Gaster finely shagreened.

Mandibular masticatory borders with a few curved, golden hairs. Anterior clypeal margin medially with several, medium length, anteriorly directed, golden setae. Head, including clypeus, mesosoma and gaster with numerous, mostly erect and variously curved, somewhat untidy, long silvery hairs, some longer than greatest diameter of eyes; hairs on gaster somewhat shorter and mostly posteriorly directed. Very distinct, relatively long, silvery pubescence almost completely hiding underlying sculpturation on head, mesosoma and petiole, except apical portions of spines. Gastral pubescence more appressed and diluted, not obscuring fine sculpturation.

Head, including anterior clypeal margin, antennal scapes, mesosoma, including fore coxae, spines, and petiole, including subpetiolar process, black; legs, including mid and hind coxae and basal antennal segments dark to very dark reddish-brown or black; mandibles, apical antennal segments and gaster orange or light reddish-brown. Dorsum of first gastral tergite with darker, irregular, somewhat diffused, reddish-brown patch medially.

Queen. Dimensions. TL c. 8.52; HL 1.84; HW 1.50; CI 81; SL 2.34; SI 156; PW 1.75; MTL 3.81 (1 measured)

Essentially like worker and apart from sexual characters, including three ocelli and complete thoracic structure, differing as follows: pronotal spines distinctly reduced in length, about twice as long as their basal widths. Mesoscutum with anterior margin evenly rounded in dorsal view; median line bifurcate anteriorly and dorsally; parapsides weakly raised posteriorly. Mesoscutellum slightly elevated above dorsal plane of mesosoma; metanotal groove distinct. Propodeal spines short, obliquely elevated, their inner margins continued inwards but not meeting medially. Petiolar spines similar to those in worker but stronger and distinctly shorter; dorsum of petiole bluntly raised medially. Sculpturation, pilosity and colour virtually identical to worker.

Males unknown. Immature stages (eggs and larvae) deposited in the QM spirit collection.

Remarks. *Polyrhachis bicolor* and *P. nigripes* are certainly very closely related. The main differences separating them are their colour patterns which appear to be constant in all material examined. Another key difference is the profile of the mesosoma which features a virtually flat mesonotum in *P. bicolor* (Fig. 2D), while in *P. nigripes* the pronotal and mesonotal dorsa form a weak, but evenly convex line (Fig. 2F). In addition, *P. bicolor* has distinctly more slender spines, notably those on the propodeum, which, although they are closer together, are clearly separated at their bases and are parallel for their full length. In contrast the spines in *P. nigripes* are distinctly stronger, with the inner bases of the propodeal spines somewhat continuous across the propodeal dorsum, forming a medially incomplete 'U' shape in dorsal view. The propodeal spines are also slightly divergent and weakly curved along their length. New Guinean and Australian specimens of *P. nigripes* are very similar in appearance.

The distribution of *P. nigripes* in New Guinea appears to be concentrated mainly along the coast of the Gulf of Papua, with only a few doubtful records from Irian Jaya and the north of the island. In Australia, *P. nigripes* has been recorded only once from Iron Range National Park on Cape York Peninsula where a nest of silk and vegetation debris was collected on the ground in monsoon rainforest along the Claudie River. The twig and leaves upon which the nest was built were completely dry and had apparently fallen very recently from its original position higher on the tree. It contained a dealate queen, 19 workers and brood (many eggs and larvae).

POLYRHACHIS DIVES SPECIES-GROUP

The *Polyrhachis dives* species-group was originally delimited by Emery (1925) and has previously contained as many as 77 species and subspecies. Dorow (1995) redefined the group and transferred a number of species into the earlier established *P. armata-*, *sexspinosa-* and *viehmeyeri*-groups (all Emery, 1925), or into his newly proposed *P. arachne-*, *bicolor-*, *cephalotes-*, *hector-* and *mucronata*-groups. The *P. dives*-group, as presently defined, includes about 14 species and subspecies with only one Australian species, *P. dives*.

Diagnosis. (modified from Dorow, 1995) *Worker*. Mostly medium-sized ants (HL 1.40-2.00), some species exhibiting slight polymorphism. Mandibles rather densely longitudinally striate or rugose with numerous piliferous pits. Anterior clypeal margin with central, medially emarginate flange, laterally flanked by acute teeth. Head semicircular in side view, almost circular in frontal view. Genae immarginate or with a short carina running about half way from occipital margin towards mandibular bases (as in some extralimital species, e.g. *P. lacteipennis* Fr. Smith, 1858). Eyes rather flat or only moderately convex, in full face view not or only marginally exceeding lateral cephalic outline. Mesosoma totally immarginate. Pronotum armed with rather short or only moderately long spines (except in *P. dives belli* Forel, 1912, where pronotal spines are slender and relatively long); propodeal spines slender and elevated with their tips curved outwards. Petiole with lateral spines, that in most species conform to shape of gaster, and a pair of distinct intercalary teeth. Body rather distinctly, more-or-less regularly, reticulate-punctate (as in *P. dives*), moderately rugose (as in *P. lacteipennis*) or coarsely foveolate (as in *P. menelas* Forel, 1904). Gaster shagreened or closely punctate. Body with only a few, short, erect hairs; closely appressed, mostly silvery or pale golden pubescence rather sparse over head and body (as in *P. dives*) or virtually lacking (as in *P. lacteipennis*). Gaster with somewhat longer, silvery or golden pubescence, that is virtually lacking in several extralimital species. Body and appendages mostly black with gaster black or very dark reddish-brown.

Queen. Queen in several species (e.g. *P. dives*) distinctly larger than worker with usual characters identifying full sexuality, including three ocelli, complete thoracic structure and wings. Spines distinctly shorter with pronotal spines reduced to acute angles. Propodeal spines modified into blunt, horizontal, posteriorly directed and somewhat dorso-ventrally compressed stubs; petiolar spines very short, only weakly curved, almost straight. Body sculpturation, pilosity and colour identical to that in worker.

Distribution and biology. The *Polyrhachis dives* species-group is the most widespread species-group within *Myrmhopla*. It stretches from Guam Island in the Pacific, throughout east and south-east Asia (e.g. China, Japan, Taiwan, Philippines, Malaysia, Thailand, Myanmar, Nepal, India, Sri Lanka), the Middle East and Arabian Peninsula (e.g. Pakistan, Iran, Iraq, Israel, Saudi Arabia, Oman, Yemen) and reaches as far west as Morocco in northern Africa. From southern Asia it extends southwards to Indonesia, New Guinea and northern Australia. Members of this group are mostly arboreal, building nests upon the leaves and branches of trees and shrubs, preferably in open habitats, such as grassy woodlands, open forests and swamps (Fig 10C). However, some extralimital species (e.g. *P. lacteipennis* Fr. Smith) were observed to be lignicolous or subterranean nesters. The incorporation of silk and occasionally carton occurs in all arboreal nests. These nests can be either mono- or polydomous. Single and multiple queen colonies have been documented in *P. dives* (see Robson & Kohout, 2007).

Polyrhachis dives Fr. Smith, 1857
(Figs 1I, 3A, C-D, 8A, 10C,)

Polyrhachis dives Fr. Smith, 1857: 64. Holotype worker. Type locality: SINGAPORE (A.R. Wallace), BMNH (examined).

Polyrhachis (Myrmhopla) exulans Clark, 1941: 91, pl. 13, fig. 24. (w.) Type locality: AUSTRALIA, Northern Territory, Koolpinyah (C.L. Barrett). Synonymy by Kohout, 1988: 433.

(For full synonymic citations see Bolton, 1995: 347)

Other material. CHINA, Canton (C.W. Howard) (w); Mokanshan (N. Gist Gee) (w); Amoy (S. Ling) (w); Triet Giang Prov., xii.2001 (Bui Tuan Viet #3) (w). HONG KONG (J. Fellowes #1) (w) FORMOSA, Abato (Silvestri) (w); Kusukusu, 12.iv.1932 (L. Gressitt) (w); Rokki, 17.vi.1932 (L. Gressitt); T'ai Chung, 18.iv.1962 (A.C.F. Hung) (w). GUAM I., Andersen Air Force Base, iv.& xii.2003 (L. Hansen) (w, ♀, ♂). MYANMAR (as BURMA), (no further data) (w); Carin Chebà, 900-110m, v-xii.1888 (L. Fea); Bhamo, vii.1885 (Fea) (w). ASSAM, Cherrapoonji (Smythies) (w); Misamari, iv.1944 (A.C. Cole) (w). THAILAND, Chiang Mai Prov., Doi Ithanon NP, 16.viii.1992 (D.G. Furth) (w); Khao Yai N.P., 800-1000 m, 19.viii.1992 (D.G. Furth) (w); Payao, 12.ix.1951 (D. & E. Thurman); Petchburi, Kowyoi Nongchumphon Nonpoe, 28.vi.1952 (R.E. Elbel). VIETNAM, Thua Thien Hue Prov., Phong Dien Distr., iv.2001 (Bui Tuan Viet #7, 8) (w); Lang Son Prov., Cao Loc Distr., i.2001 (Bui Tuan Viet #4) (w). SINGAPORE, (no further data) (Bryant & Palmer) (w); ditto (no further data (Baker) (w). PHILIPPINES, Luzon, Manila, 19.ii.1918 (Mc Gregor) (w); Luzon, Luneta Hill, Baguio, 1450 m, 1.v.1981 (W.L. Brown) (w, ♂); Negros Or., Dumaguete, 1923 (J.W. Chapman) (w); ditto, Horns of Negros, 3600', 1942-43 (J.W. Chapman) (w); Negros, Victorias, 20.xii.1927 (W.D. Pierce) (w); Baguio, (J.W. Chapman) (w); Mindanao, Misamis, Gingoog, Anakan Lbr. Co. (A. Reyes) (w); Bukidnon, Musuan Maramag, 3.i.1985 (C.K. Starr & Pinto) (w). WEST MALAYSIA, Selangor, Kulala Lumpur (Army Scrub Typhus Unit); Selangor, UKM campus, 30.viii.1992, D.G. Furth) (w). EAST MALAYSIA, SARAWAK, Nanga Pelagus, nr Kapit, 180-585 m, 7-14.viii.1958 (T.C. Maa). SABAH, Tawau Distr., Kalabakan, 8-15.xi.1958 (T.C. Maa); Tawau, Quoin Hill, Cocoa Res. Stn, 4.xii.1962 (Y. Hirashima); 13km N of Marak Parak, 12.v.1985 (C.K. Starr) (w, ♀). BRUNEI, Belait Distr., 1-2 km SE of Melilas Longhouse, 16.vii.1994 (RJK accs 93.10, 94.127) (w, ♀); Bandar Seri Begawan, Gadong University grounds, 11.iv.1993 (RJK acc.93.2) (♀); Tutong Distr., Bukit Sulang nr Lamunin, 20-23.vii.1994 (RJK acc. 94.129) (w, ♀). INDONESIA, KALIMANTAN BARAT, 3 km N of Putussibau, 00°51'N, 112°55'E, 19-20.vi.1996 (C. Reid) (w, ♀); KALIMANTAN TENGAH, Banjarmasin, `Suaka Insan' Hospital, 6.vi.1983 (M. Bordsen). SUMATRA, Pematang, Siantar, 1937 (W.M. Mann, NGS SI Exp.); Brastagi, 1937 (Mann, NGS SI Exp.) (w); Medan, 21.x.1993 (Y.v. Nierop) (w); Langkat, ii.1925 (N. Dengas) (w). JAVA, Kebun Raja, Bogor Botan. Gdns, 06°35'S, 106°47'E, 290 m, 7-12.ix.1999 (S.K.A. Robson #816) (w); ditto, 3.i.1993 (Yayuk R. Suhardjono) (♀); Semarang, 13.x.1927 (L.G. Kalshoven) (w); Buitenzorg (= Bogor) (J. Barbour) (w). SULAWESI, Lore-Lindu NP, nr Dongi-Dongi shelter, 975-1020 m, 01°15'S, 120°20'E, 4-9.xii.1985 (Mal. traps) (C.v. Achterberg) (w); Latimodjong Mts (Clagg) (w); Malino, viii.1937 (C.T.& B.B. Brues) (w). SERAM, Piroe, 1937 (W.M. Mann, NGS SI Exp.) (w, ♀, ♂); ditto, above Haruru, nr Masohi, 50-150 m, 18.iii.1981 (W.L. Brown) (w, ♀, ♂). SULU, Mangole, 2 km W Mandafuhi Camp, c. 70 m, 7-24.iii.1995 (Mal. traps) (C.v. Achterberg & Y. Yasir) (w). FLORES, Nangagete, c. 60 km E Maumere, 19.vii.1972 (W.L. Brown) (w). BALI, 1937 (Springer) (w). AMBON, Amboina DEI, 1938 (F.I. Buitenbos) (w); ditto, 1937 (W.M. Mann, NGS SI Exp.) (w, ♀, ♂). IRIAN JAYA, Wamena, 1700 m, 10-25.ii.1960 (T.C. Maa) (w); Hollandia, 13.iii.1960 (T.C. Maa) (w); Waris, S of Hollandia, 450-500 m, 16-23.viii.1959 (T.C. Maa) (w). PAPUA NEW GUINEA, West Sepik Prov., Torricelli Mts, Lumi, 03°28'S, 142°02'E, 400-500 m, 4-13.viii.1984 (RJK acc. 84.249) (w); ditto, x.1984 (D. Waisi) (w, ♀); nr Aitape, 03°09'S, 142°21'E, 3.viii.1984 (RJK acc. 84.218) (w, ♀); nr Yapsiei, ii.1984 (S.van Dyck) (w); Subitana, Sogeri, 26.v.1957 (J.H. Barrett) (w); New Britain Prov., Linga Linga Pltn, W of Willaumez Pen., 9.iv.1956 (J.L. Gressitt) (w); ditto, Sio N Coast, 600 m, 24.vii.1956 (E.J. Ford Jn.) (w); Morobe Prov., Huon Pen., Mongi-Mape Watersheds, Sattelberg vic., 660 m, 4.iv.1955 (E.O. Wilson #722) (w); ditto, Mongi Watershed, Gemeheng, 1200-1300 m, 11-13.iv.1955 (E.O. Wilson #773) (w); Mt Missim (Stevens) (w); Wau, Mendi, 1600-1700 m, xi.1971 (N.L.H. Krauss) (w); Lae, 19.ix.1949 (N.L.H. Krauss) (w); Port

Moresby, 7.vi.1955 (E.O. Wilson #520) (w); 7km S of Maprik, 03.42'S, 143.03'E, 120 m, 11.ii.1989 (P.S. Ward #10175) (w); West New Britain Prov., Dami Res. Stn, 12 km SW of Hoskins, 27.viii.1984 (E.J. Brough) (w); New Ireland Prov., Lelet Plateau, 03°20'S, 151°56'E, 800-1000 m, 19-24.vii.1984 (RJK acc. 84.95, 99) (w). AUSTRALIA, NORTHERN TERRITORY, Koolpinyah, 1933 (C.L. Barrett) (w); Holmes Jungle, 15 km NE of Darwin, 12°25'S, 130°58'E, 16.xi.1993 (RJK acc. 93.33) (w). QUEENSLAND, Yarrabah, c. 11 km E of Cairns, 16°56'S, 145°52'E, 22-24.vii.1980 (RJK accs 80.113, 130, 141) (w, ., ;); South Mission Bch, 2 km NbyW, 17°55'S, 146°05'E, 13.vi.1980 (RJK accs 80.14, 15, 17, 18) (w, :) ; Tully, ii.1958 (Darlingtons) (w); 2 km NbyW of Sth Mission Beach, 17°55'S, 146°05'E, 13.vi.1980 (RJK acc. 80.14); Halifax, 8.vi.1919 (F.X. Williams) (w).

Worker. Dimensions. TL c. 5.39-7.71; HL 1.40-1.93; HW 1.18-1.65; CI 84-91; SL 1.56-1.96; SI 119-132; PW 0.87-1.15; MTL 1.87-2.56 (34 measured).

Mandibles with 5 teeth. Anterior clypeal margin with emarginate, shallow, median flange, laterally flanked by acute teeth. Clypeus virtually straight in profile, posteriorly rounding into weakly impressed basal margin. Frontal triangle distict. Frontal carinae sinuate with moderately raised margins. Sides of head in front of eyes weakly convex towards mandibular bases; behind eyes sides widely rounding into rather flat occipital margin. Eyes only moderately convex, in full face view not or only marginally exceeding lateral cephalic outline. Ocelli lacking, relative positions marked by shallow pits in cephalic structure. Mesosoma immarginate. Pronotum rather weakly convex in profile; humeri armed with straight, horizontal, anterolaterally directed, acute spines. Promesonotal suture distinct; mesonotum convex in profile. Metanotal groove poorly indicated; propodeal dorsum armed with slender, obliquely elevated, divergent spines, tips curved upwards and outwards. Petiole with dorsolaterally projecting acute spines that conform to shape of anterior gaster; dorsum medially with pair of distinct intercalary teeth. Anterior face of first gastral tergite higher than full height of petiole, widely rounding onto dorsum of segment.

Mandibles densely and closely longitudinally striate with piliferous pits. Head, mesosoma and petiole distinctly, more-or-less regularly, reticulate-punctate. Sides of mesosoma somewhat more deeply sculptured with numerous pits on meso- and metapleurae. Spines sculptured at bases, smooth and polished towards tips. Gaster finely shagreened.

Mandibles at masticatory borders with numerous, curved, golden hairs and short, appressed hairs towards bases. Anterior clypeal margin with several anteriorly projecting setae medially and a few shorter setae fringing margin laterally. Clypeus with a few, paired, medium length, erect hairs. Apical segments on dorsum and venter of gaster with a number of erect, relatively long, mostly posteriorly directed, golden hairs. Closely appressed, medium length, pale golden pubescence in various densities over most of head and body. Pubescence more silvery on sides of head, mesosoma and petiole. Gastral pubescence somewhat longer, rich golden and more abundant dorsally where it almost completely hides underlying sculpturation; pubescence paler and less dense on gastral venter.

Black, with only condylae and tip of apical antennal segments, light yellowish-brown; mandibular teeth dark reddish-brown.

Queen. Dimensions: TL c. 8.72-9.32; HL 2.03-2.18; HW 1.78-1.90; CI 85-91; SL 1.93-2.09; SI 108-112; PW 1.81-1.90; MTL 2.62-2.74 (14 measured).

Very similar to worker, apart from sexual characters, shorter spines and the following: anterior clypeal margin with median flange more deeply emarginate; clypeus with basal margin virtually flat in lateral view. Eyes more convex, always exceeding lateral cephalic outline. Pronotal spines reduced to minute teeth. Mesoscutum in lateral view relatively high, widely rounding onto flat dorsum with anterior margin evenly rounded in dorsal view; median line bifurcate anteriorly and posteriorly; parapsides flat. Mesoscutellum flat, not elevated above dorsal plane of mesosoma. Metanotal groove distinctly impressed. Propodeal spines very short, directed posteriorly, weakly elevated dorsally. Petiolar spines short, projecting laterally, very weakly curved. Sculpturation, pilosity, pubescence and colour identical to those in worker.

Males and immature stages (eggs, larvae and pupae) deposited in QM spirit collection.

Remarks. *Polyrhachis dives* is a very widespread species ranging from south-east Asia south to northern Australia, with recent reports of its occurrence as far east as Guam Island in the Pacific (L. Hansen *pers. comm.*). Throughout its distribution, *P. dives* is a morphologically very stable species with only a few, rather insignificant differences between individuals, even those from widely separated localities. However, south-east Asian specimens generally have a more deeply emarginate anterior clypeal margin and eyes that only rarely exceed the lateral cephalic outline. Most also have the tips of the propodeal spines more distinctly curved outwards and longer petiolar spines that are somewhat curved downwards from their midlength. In contrast, the anterior clypeal margin in Australian and New Guinean specimens is only shallowly emarginate and the eyes clearly exceed the lateral cephalic outline. The propodeal spines are only weakly curved outwards and the petiolar spines somewhat shorter and less curved.

In Australia *P. dives* is known from two isolated populations, one in the Northern Territory and the other in northern Queensland. It prefers mostly open savannah woodlands and swampy coastal plains, where it builds its silk and/or carton-based, relatively large, usually polydomous nests between the branches and leaves of small trees and shrubs (Fig. 10C).

POLYRHACHIS MUCRONATA SPECIES-GROUP

The *Polyrhachis mucronata* species-group of the subgenus *Myrmhopla* was delimited by Dorow (1995) who subdivided the earlier established *P. dives*-group (Emery, 1925). Dorow listed 36 species and subspecies within the group, however, the status of several subspecific forms still remains unresolved. Two new species were recently described from Sulawesi (Kohout, 2008) and one species is considered a junior synonym (see below). Only a single species of the group, *P. mucronata*, is relevant to the Australian fauna.

Diagnosis. (modified from Dorow, 1995) *Worker*: Small to medium-sized ants (HL 1.25-2.10) with general characteristics of the genus. Mandibles mostly longitudinally striate or finely rugose with numerous piliferous pits. Anterior clypeal margin with shallow, median flange (as in *P. mucronata*), or shallowly truncate (as in *P. retrorsa* Emery, 1900). Head usually semicircular in side view, oval in frontal view; genae immarginate. Eyes moderately to strongly convex, clearly exceeding lateral cephalic outline in full face view. Mesosoma totally immarginate, usually highly convex and relatively short (as in *P. mucronata*), but also somewhat elongated and distinctly less convex (as in *P. tristis* Mayr, 1867). Pronotum armed with acute teeth (as in *P. mucronata*), or rarely with long slender spines (as in *P. amana* Fr. Smith, 1861), or simply rounded (as in *P. moeschi* Forel, 1912). Propodeal spines relatively long and strong in most species, however, also short (as in *P. orpheus* Forel, 1911). Petiole columnar with a pair of lateral spines usually embracing first gastral segment; spines mostly slender, but also remarkably massive (as in *P. lucidula* Emery, 1893 and *P. ridleyi* Forel, 1912). Dorsum of petiole with a pair of more-or-less distinct intercalary teeth, except in some species (e.g. *P. amana* and *P. orpheus*). Sculpturation of head, mesosoma and petiole ranging from rather smooth and highly polished (as in *P. emmae* Santschi, 1920) to closely punctate (as in *P. oedacantha* Wheeler, 1919). Gaster usually more finely sculptured, shagreened and polished, only rarely closely punctate, opaque (as in *P. tristis*). Body pilosity and pubescence virtually lacking in most species, however, in

P. mitrata Menozzi, 1932 and *P. retrorsa* whole body covered with rather diluted, whitish pubescence. Body mostly black, rarely with purple metallic reflections (as in *P. oedacantha* and *P. phalerata* Menozzi, 1926). Gaster black or reddish-brown with appendages ranging from orange or light reddish-brown to black.

Queen. Queen very similar to worker with usual differences indicating caste, including three ocelli, complete thoracic structure and wings. Body armature, notably propodeal and petiolar spines distinctly shorter and stronger. Sculpturation, pilosity and colour essentially as in worker.

Distribution and biology. The *Polyrhachis mucronata* species-group is distributed throughout east and south-east Asia (China, Philippines, Laos, Malaysia, Thailand, Myanmar, India, Sri Lanka), extending south to Indonesia (Sumatra, Java, Sulawesi) and New Guinea (including Bismarck Archipelago), reaching the southern limit of its distribution in northern Queensland. The known members of this group are arboreal nesters, building nests of silk and vegetation debris upon the leaves of rainforest trees and shrubs, mostly in the lower arboreal zone (Fig. 10E).

Polyrhachis mucronata Fr. Smith, 1859
(Figs 3B, E-F, 9B, 10E)

Polyrhachis mucronatus Fr. Smith, 1859: 140. Holotype worker. Type locality: INDONESIA: Aru Is. (A.R. Wallace), OXUM (examined).

Polyrhachis (Myrmhopla) cyrtomyrmoides Donisthorpe, 1947: 195. Syntype worker, queen. Type locality: INDONESIA, IRIAN JAYA (as Dutch New Guinea), Maffin Bay, viii.1944 (E.S. Ross), CASC, BMNH (examined). **Syn. nov.**

Other material. INDONESIA, Aru I. (no further data) (w). IRIAN JAYA (as Dutch New Guinea), Maffin Bay, 17.vi.1944 (E.S. Ross) (w); Hollandia area, W. Sentani, Cyclop Mts, 150-1000 m, 16-19.vi.1959 (T.C. Maa) (w); Waris, S of Hollandia, 450-500 m, 16-23.viii.1959 (T.C. Maa) (w). PAPUA NEW GUINEA, West Sepik Prov., Torricelli Mts, Lumi, 400-550 m, 03°28′S, 142°02′E, 4-13.viii.1984 (RJK acc. 84.228, 249) (w); ditto, x.1984 (D. Waisi) (w); Morobe Prov., nr Wampit, c. 35km W of Lae, 06°45′S, 146°40′E, c. 50 m, 24& 27.viii.1984 (RJK acc. 84.365) (w); Naru, Gogol R., 20 km SW of Madang, 05°21′S, 145°41′E, 22.viii.1984 (RJK acc. 84.336) (w); Central Prov., Eilogo Rd., 4 km ESE of Sogeri, 09°25′S, 147°27′E, c. 500 m, 4.ix.1984 (RJK acc. 84.427) (w); Varirata NP, 550-760 m, 5-9.ii.1981 (W.L. Brown) (w). AUSTRALIA, QUEENSLAND, Cape York Pen., Iron Range, 12°43′S, 143°18′E, 26-31.vii.1981 (RJK accs 81.146, 147); ditto, 1-17.viii.1978 (S.van Dyck); Mt Hedley, 1-2 km N of Home Rule, 15°45′S, 145°17′E, 200-300vm, 11.vi.1996 (RJK & CJB acc. 96.44) (w); Cedar Bay NP, 15°48′S, 145°19′E, 16.vi.1997 (SKR #589) (w); Pilgrim Sands, c. 1 km NW of Cape Tribulation, 16°04′S, 145°28′E, 12-15.vi.1996 (RJK at al. acc. 96.47) (w); Cape Tribulation NP, 16°04′S, 145°27′E, 6.xii.1985 (RJK acc. 85.5) (w, ♀); Canopy Crane site, Cape Tribulation, 16°06′S, 145°27′E, 20-21.ii.2000 (RJK accs 2000.17, 21) (w, ♀); Oliver Ck, c. 8 km SW of Cape Tribulation, 16°08′S, 146°26′E, 14.vi.1998, lowland rf. (RJK acc. 98.53 (w); Mc Lean Ck, 19 km SbyW of Cape Tribulation, 16°15′S, 145°26′E, 15.vi.1996 (RJK acc. 96.54) (w); Bellenden Ker, Cableway Base Stn, 17°16′S, 145°54′E, 17-24.x.1981 (GBM & Earthwatch Exp.) (w); Russel R., Bellenden Ker Landing, 17°16′S, 145°56′E, 1-9.xi.1981 (GBM & Earthwatch Exp.) (w); Josephine Falls, 17°26′S, 145°51′E, 12.ii.1996 (GBM) (w); Garradunga, Seymour Ra., c. 7 km N of Innisfail, 17°28′S, 146°01′E, <100 m, 5-6.vi.1996 (RJK at al. 96.31) (w, ♀); Mission Bch, 17°45′S, 146°00′E, 10 m, 20.i.1996 (SKR #101) (w); Dunk I., 17°57′S, 146°09′E, viii.1927 (H. Hacker) (♀); Hinchinbrook I., Gayundah Ck, 18°21′S, 146°14′E, 100-500 m, 8-18.xi.1984 (GBM) (w).

Worker. Dimensions: (holotype cited first) TL c. 5.55, 5.34-6.50; HL 1.43, 1.40-1.65; HW 1.17, 1.12-1.31; CI 82, 76-82; SL 1.84, 1.65-2.12; SI 157, 146-164; PW 1.00, 0.94-1.15; MTL 1.93, 1.81-2.31 (31 measured).

Anterior clypeal margin medially with shallow flange, flanked laterally by acute angles. Clypeus with poorly defined median carina; clypeus in profile straight anteriorly, posteriorly rounding into moderately impressed basal margin. Frontal carinae sinuate with moderately raised margins. Sides of head in front of eyes weakly convex converging towards mandibular bases; behind eyes sides rounding into convex occipital margin. Eyes relatively large and convex, in full face view clearly exceeding lateral cephalic outline. Ocelli lacking. Mesosoma immarginate. Pronotal humeri armed with short, acute teeth. Promesonotal suture distinct; mesonotum virtually flat in profile. Mesopleural process a blunt lobe; metanotal groove indicated as a thin, bowed line. Propodeal dorsum very short, armed with rather strong, obliquely directed, diverging, acute spines; inner borders of spines continued medially for a short distance, but failing to meet, propodeal dorsum descending into relatively high, oblique declivity in uninterrupted line. Petiole columnar, dorsum armed with two strong lateral spines that conform to shape of anterior gaster and two short, acute intercalary teeth medially. Anterior face of first gastral tergite straight, widely rounding onto dorsum of segment.

Mandibles very finely, longitudinally striate with numerous piliferous pits. Head and dorsum of mesosoma and petiole finely reticulate-punctate with sculpturation distinctly coarser on sides of mesosoma; meso- and metapleurae weakly rugose and somewhat wrinkled. Gaster finely shagreened.

Mandibles at masticatory and outer borders with a few, curved, golden hairs. Anterior clypeal margin with several anteriorly directed setae medially and a pair of longer, suberect hairs arising from just behind margin. Tuft of medium length, erect hairs in front of subpetiolar process. Apical segments on dorsum and venter of gaster with a number of semierect, posteriorly directed, golden hairs. Very short, closely appressed pubescence arising from minute punctures and pits, distributed over most body surfaces, more distinct on gastral dorsum.

Body black, polished; mandibular bases, antennal scapes, fore coxae and tarsi black or very dark reddish-brown; mandibular masticatory borders, condylae, apical antennal segments and most of legs, except tarsi, light to medium reddish-brown.

Queen. Dimensions: TL c. 6.95-7.81; HL 1.65-1.75; HW 1.25-1.34; CI 75-77; SL 1.96-2.12; SI 153-160; PW 1.56-1.68; MTL 2.18-2.37 (10 measured).

Very similar to worker with usual differences indicating caste, including three ocelli, complete thoracic structure and wings. Median clypeal carina somewhat more distinct. Pronotal teeth dorsoventrally flattened; mesoscutum in lateral view with anterior margin widely rounding onto flat dorsum; median line bifurcate anteriorly; parapsides rather flat, weakly raised posteriorly; mesoscutellum convex, elevated above dorsal plane of mesosoma; metanotal groove strongly impressed. Propodeal spines shorter than in worker, almost straight; petiolar spines similar to those in worker but shorter. Sculpturation, pilosity, pubescence and colour virtually identical to worker.

Males and immature stages (eggs, larvae and pupae) deposited in QM spirit collection.

Remarks. Among the Australian species of *Myrmhopla*, *Polyrhachis mucronata* is very distinct, however, it superficially resembles some species of the subgenus *Cyrtomyrma* Forel. Despite their general similarity and identical nesting habits, *P. mucronata* can be easily distinguished from *Cyrtomyrma* species by the form of its petiole. The petiolar node in *P. mucronata* is columnar and armed with two, more-or-less horizontal, posteriorly directed spines that conform to the shape of the anterior gaster. The petiole also bears a pair of short, intercalary teeth. In contrast, in *Cyrtomyrma* species, the petiole is scale-like and armed with four teeth or spines of various configurations. Additionally, all Australian *Cyrtomyrma* species have a distinct posterolateral carina separating the gena from the ventral parts of the head. This carina is lacking in *P. mucronata*-group species. The two groups also differ in their immature stages with the pupae of *Myrmhopla* species being enclosed in cocoons, while in *Cyrtomyrma* species the pupae are naked (Kohout, 2006b).

Polyrhachis mucronata ranges from the islands of eastern Indonesia and New Guinea south to northern Queensland where it reaches the southern limit of its distribution. It is a relatively common species in the monsoon rainforests of Cape York Peninsula and the lowland rainforests of the Wet Tropics. Colonies of *P. mucronata* build nests the leaves of rainforest trees and shrubs, using mostly larval silk combined with leaf fragments and other vegetation debris (Fig. 10E).

When describing *Polyrhachis cyrtomyrmoides*, Donisthorpe (1947: 195) emphasised its close resemblance to ants of the subgenus *Cyrtomyrma* but failed to note its remarkable similarity to *P. mucronata*. I had the opportunity to examine the syntypes of *P. cyrtomyrmoides*, supplemented by additional specimens in the CASC collection (Maffin Bay, 17.vi.1944, E.S. Ross). Their comparison with the holotype of *P. mucronata* (OXUM) and abundant material of that species from New Guinea and Australia (ANIC, BMNH, BPBM, MCZC and QM) revealed that the two species were very similar. As noted earlier by Kohout (2000: 206), the Australian and New Guinean populations of *P. mucronata* differ somewhat from the holotype, with some specimens from Australia being remarkably close to those of *P. cyrtomyrmoides*, sharing the rather highly polished appearance which is typical of the latter species. However, the density of the generally fine reticulate-punctate sculpturation varies not only between different populations, but also to some extent between specimens of a single colony. The colour of the legs also varies, generally being a lighter red in Australian specimens and a darker, reddish-brown in most of New Guinean specimens. In addition, the eyes vary in the degree of their convexity with specimens from the Wet Tropics having the eyes simply convex, similar to those in *P. cyrtomyrmoides*, while the eyes in specimens from the mid and northern Cape York Peninsula are virtually protuberant. When considered individually, specimens of some populations appear quite distinct, however, when all the available material from the whole distribution range is compared, no consistent differences between *P. cyrtomyrmoides* and *P. mucronata* are evident. I therefore believe that the separate specific status of the former is not justified and consider them conspecific.

POLYRHACHIS SEXSPINOSA SPECIES-GROUP

The *Polyrhachis sexspinosa* species-group of the subgenus *Myrmhopla* Forel, 1915 was established by Emery (1925), who included 12 species and subspecies from New Guinea and south-east Asia. Bolton (1975) revised the world fauna of the group and recognised 12 valid species with all of the included infraspecific taxa considered synonyms. Three new species from the Philippines were later added, one subspecies (*P. sexspinosa reclinata* Emery, 1887) raised to specific status (Kohout, 1987) and one species (*P. barnardi* Clark, 1928) synonymised (Kohout & Taylor (1990), raising the number of valid species of the group to 15. Dorow (1995) recognised 17 species as constituents of the group, including *P. melpomene* Emery, 1897 and *P. olybria* Forel, 1912. However, these two species were later transferred to different subgenera (*P. melpomene* and its junior synonym *P. dolichocephala* Viehmeyer, 1914 to subgenus *Hedomyrma* and *P. olybria* to the nominal subgenus *Polyrhachis*), and two former subspecies (*P. arcuspinosa waigeuensis* Donisthorpe, 1943 and *P. sexspinosa esuriens* Emery, 1897) were raised to specific status by Kohout (1998). At present the *P. sexspinosa* species-group comprises 19 valid species, including one (*P. spinosa* Mayr, 1867) recently elevated to its original specific status (Kohout, 2008) and one described below as new (*P. dispar*). Four species of the group are relevant to the Australian fauna with two (*P. dispar* and *P. glabrinota* Clark, 1930) considered endemic. They appear to be derived from common ancestral stock, such as the New Guinea-based species *P. aureovestita* Donisthorpe, 1937 and *P. bubastes* Fr. Smith, 1863 (Bolton, 1975) and speciated after loosing connection with the maternal New Guinean populations following the sinking of the continental bridge between New Guinea and Australia. On the other hand, the more robust populations of the relatively common *P. sexspinosa* (Latreille, 1802) and *P. reclinata* Emery, 1887 maintained most of their original characteristics, with specimens from Cape York Peninsula indistinguishable from their New Guinean counterparts.

Diagnosis. *Worker*: Relatively large ants (HL >2.0), except for the rather small, extralimital *P. nofra* Bolton, 1975 (HL 1.52-1.53), with general characteristics of the genus. Mandibles smooth and polished apart from small piliferous pits towards bases. Anterior clypeal margin arcuate, often obtusely truncate medially or with shallow median emargination. Head contracted posteriorly, distinctly narrower behind than in front of eyes. Eyes with short, erect hairs; strongly convex or protuberant, clearly exceeding lateral cephalic outline in full face view. Occipital margin with more-or-less developed lateral angular prominences which are usually visible with the head in full face view (except in *P. dispar* and *P. glabrinota*). Mesosoma immarginate; pronotum strongly convex, humeri armed with rather strong, mostly forward curved spines. Promesonotal suture strongly impressed. Mesonotum flat or weakly convex in profile; mesopleural process present as a simple lobe (as in *P. dispar* and *P. sexspinosa*) or a dentiform structure, that can be acute or obtuse (as in *P. glabrinota* and *P. reclinata*); metanotal groove usually replaced by a minutely raised ridge. Propodeum armed with a pair of spines that are either vertical or inclined forwards (as in *P. sexspinosa*), or posteriorly reclined and often curved (as in *P. dispar, P. glabrinota* and *P. reclinata*). Petiole nodiform with a pair of lateral spines, without intercalary spines or teeth. Gaster, when contracted, broadly ovate. Sculpturation of head, mesosoma and petiole ranging from weak to rather heavy, gaster usually finely shagreened. All body surfaces, including appendages, with relatively long, erect hairs. Pubescence mostly appressed or suberect, somewhat radiating, present in various densities but usually not completely hiding underlying sculpturation. Pubescence on gastral dorsum organised in a characteristic midline pattern in virtually all species (except *P. nofra*) or almost completely absent (*P. exotica* Kohout, 1987). Body mostly black, or partly reddish-brown (as in *P. glabrinota*), with appendages usually lighter, reddish-brown.

Queen. Very similar to worker with usual characters of full sexuality, including three ocelli, complete thoracic structure and wings. Armament of pronotum, propodeum and petiole somewhat reduced with spines shorter, less curved and usually more stubby. Sculpturation, pilosity, pubescence and colour virtually as in worker.

Distribution and biology. *Polyrhachis sexspinosa*-group species are distributed throughout the Indo-Australian region, with only a few species known from the Oriental region and one from the Solomon Islands. In Australia, the group is limited to the northern part of Cape York Peninsula in Queensland, north of the 14°S parallel. Members of the *sexspinosa*-group are mostly arboreal nesters, building nests of silk and vegetation debris between the foliage of rainforest trees and shrubs. However, some species deviate from this behaviour and have their own characteristic methods of nesting. Colonies of *P. sexspinosa* invariably build pocket-like nests of silk, vegetation debris and bark fragments against the trunks of rainforest trees (Fig. 10A-B). In contrast, colonies of *P. dispar, P. glabrinota* and *P. reclinata* at Iron Range National Park were frequently found nesting within the hollow internodes of a bamboo, *Bambusa forbesii*. Only one colony of *P. reclinata* was located under the bark of a living tree, while most nests of *P. glabrinota* were constructed between leaves, usually in the lower arboreal zone, about 2-3 m above the ground.

Polyrhachis dispar sp. nov.

(Figs 4A, C-D, 8A)

Polyrhachis (Myrmhopla) barnardi Clark, 1928: 39, pl. 1, figs 37-38 (in part); Kohout & Taylor, 1990: 519.
Polyrhachis barnardi Clark; Bolton, 1975: 6 (in part).

Material. HOLOTYPE: QUEENSLAND, Cape York Pen., Iron Ra., 12°43'S, 143°18'E, 26-31.vii.1981, rf., ex nest in dry bamboo internode, R.J. Kohout acc. 81.202 (worker). PARATYPES: data (and nest) as

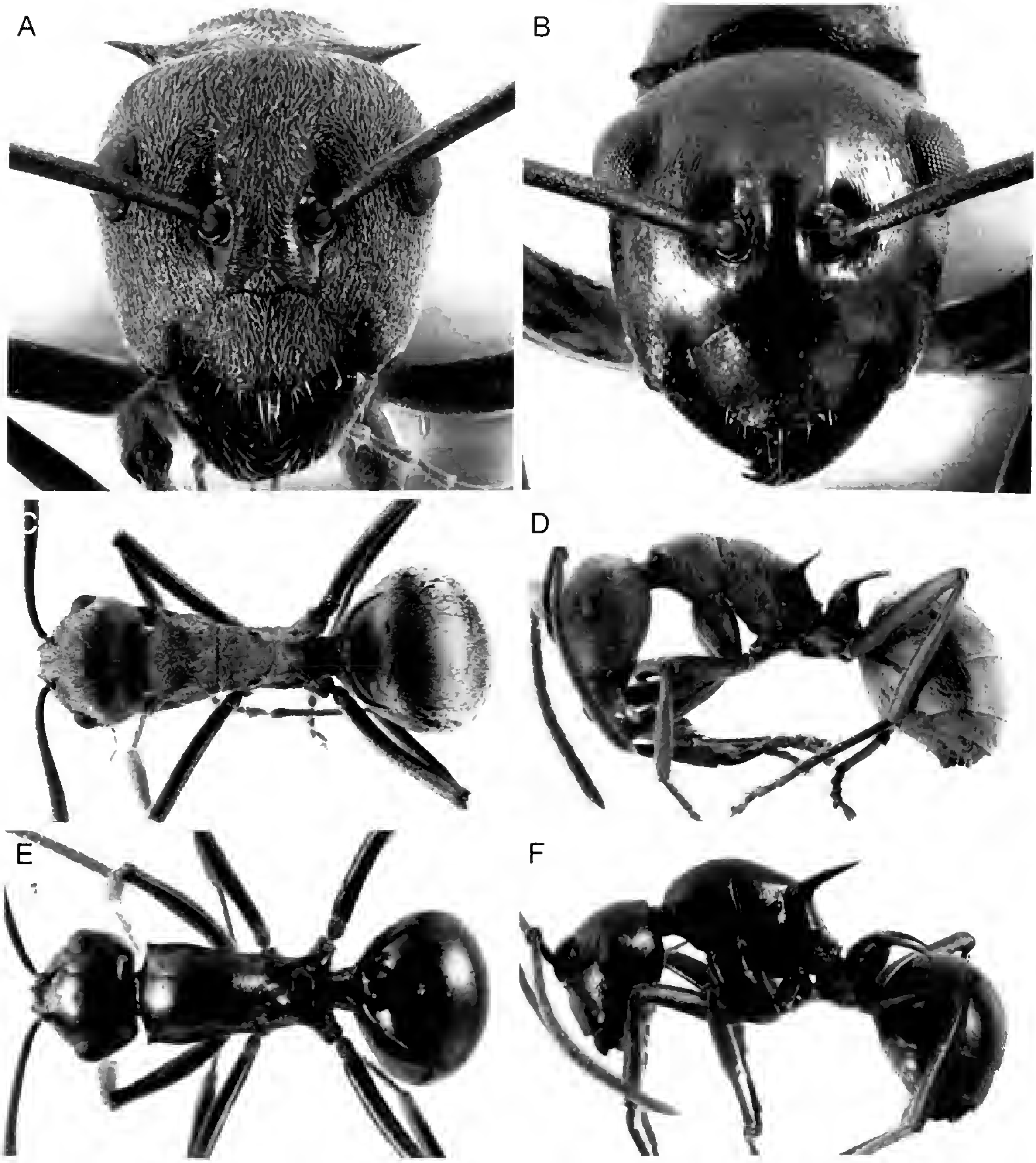

FIG. 3. *Polyrhachis (Myrmhopla)* species from Australia. Head in full face view (top); Dorsal view (left); Lateral view (right). A,C-D, *P. dives* Fr. Smith; B,E-F, *P. mucronata* Fr. Smith (not to scale).

for holotype (64 workers, alate queen); data as for holotype, except RJK accs 81.148, 195 (8 paratype workers); Cape York, W.B. Barnard (2 workers from original series of *P. barnardi* Clark in ANIC & MCZC). Type deposition: Holotype (QM T152321), most paratype workers and paratype queen (from holotype nest) in QM; 4 paratype workers (2 from holotype nest) each in ANIC, BMNH and MCZC; 2 paratype workers each in AMNH, AMSA, CASC, MHNG, MVMA, NMNH and NMHU.

Other material. QUEENSLAND, Cape York Pen., Lockerbie Scrub, 10°46'S, 142°29'E, 19-24.iii.1987, rf. (RJK acc. 87.61) (w, ♀); ditto, 25.i-12.ii.1984 (J.H. Sedláček) (♀); Iron Ra., 21.vi.1948 (D.P. Vernon) (w); ditto, viii.1949 (N.L.H. Krauss) (w).

Worker. Dimensions: (holotype cited first) TL c. 13.10, 11.39-14.10; HL 3.12, 2.87-3.40; HW 2.12, 2.02-2.44; CI 68, 68-74; SL 3.43, 3.17-3.72; SI 162, 152-165; PW 1.75, 1.51-1.96; MTL 4.33, 4.08-4.69 (25 measured).

Anterior clypeal margin arcuate, with shallow emargination medially; clypeus with distinct, blunt, median carina; clypeus virtually straight in profile, posteriorly rounding into moderately impressed basal margin. Frontal triangle distinct. Frontal carinae sinuate with acute, almost vertically raised margins; central area relatively narrow with distinct posterior carina. Sides of head in front of eyes weakly convex; behind eyes sides converging into relatively wide occipital margin. Eyes strongly convex, in full face view exceeding lateral cephalic outline. Median ocellus poorly developed, lateral ocelli lacking; positions indicated by distinctly raised cephalic sculpture. Pronotal dorsum weakly convex in profile; humeri armed with strong, acute, more-or-less horizontal, anterolaterally curved spines; promesonotal suture distinct. Mesonotum rather flat in profile; mesopleural process a blunt, simple lobe. Propodeal spines relatively long, obliquely elevated from their bases, curved posteriorly and moderately divergent. Dorsum of petiole with a pair of laterally and posteriorly directed, acute spines, with their tips turned slightly downwards.

Clypeus finely reticulate-punctate; sides of head in front of eyes smooth and polished; sculpturation on head increasing in density and intensity posteriorly, vertex and sides towards occipital margin coarsely sculptured. Dorsum and sides of mesosoma rugose; sculptural intensity decreasing posteriorly with propodeal dorsum and declivity relatively smooth. Gaster very finely shagreened.

Mostly whitish or pale yellow hairs present over all body and appendages, including antennal scapes and spines, with longest hairs on pronotal and mesonotal dorsa exceeding greatest diameter of eye in length. Rather diluted, mostly greyish, appressed or suberect pubescence variously developed, most dense and more appressed on clypeus, dorsal mesosoma and petiole, somewhat suberect and variously radiating on sides of mesosoma. Sides of head and vertex with distinctly less dense, suberect pubescence partly revealing underlying sculpturation. Gaster with relatively long, mostly golden appressed pubescence, ranging from somewhat diluted on venter to dense on dorsum, where it is arranged in a characteristic midline pattern.

Body generally black; mesosoma and petiole in some specimens very dark reddish-brown; masticatory borders of mandibles, apical antennal segments and legs, except tarsi, medium reddish-brown.

Queen. Dimensions: (paratype queen cited first) TL c. 14.08, 13.18-14.21; HL 3.17, 3.07-3.38; HW 2.17, 2.17-2.47; CI 68, 68-73; SL 3.43, 3.28-3.73; SI 158, 148-159; PW 2.37, 2.42-2.57; MTL 4.33, 4.23-4.74 (5 measured).

Very similar to worker with usual differences indicating full sexuality. Mesoscutum virtually as wide as long with lateral margins converging anteriorly into narrowly rounded margin; median line slightly raised; dorsum rather low and flat in lateral view with parapsides only weakly raised posteriorly. Mesoscutellum flat, not elevated above dorsal plane of mesosoma; metanotal groove distinct. Spines similar to those in worker, but shorter with propodeal pair distinctly less elevated. Sculpturation, pilosity, pubescence and colour virtually identical to worker.

Male unknown. Immature stages (larvae of various stages of development and pupae) in QM spirit collection.

Remarks. With its relatively broad occipital margin, *Polyrhachis dispar* is easily recognised within the *sexspinosa*-group. It is most similar to *P. reclinata* and, in addition to the lack of lateral occipital lobes, it can be distinguished by its less convex pronotal dorsum and distinctly rugose dorsum of the head and mesosoma. The pronotal dorsum in *P. reclinata* is distinctly higher and the sculpturation of the vertex, sides of head and pronotal dorsum consists of very fine reticulation beneath a rich pubescence that is much more diluted in *P. dispar*. Also, the mesopleural process in *P. dispar* is present as a blunt, simple lobe, while in *P. reclinata* the lobe is ventrally dentiform.

Kohout & Taylor (1990: 519) examined all the available specimens of the *P. barnardi* Clark, 1928 type series and concluded that it comprised two distinct species. The lectotype (originally furnished with a red tag inscribed 'Type') and two paralectotypes (all MVMA) were identified as *P. sexspinosa* (Latreille) and, consequently, *P. barnardi* has been considered a synonym of that species. Two remaining paralectotypes (that match Clark's original description and illustrations of *P. barnardi*) were deposited in other institutions (ANIC, MCZC) and are included in the type series of *P. dispar*.

Polyrhachis glabrinota Clark, 1930
(Figs 4B, E-F, 8B)

Polyrhachis (Myrmhopla) glabrinotum Clark, 1930: 13, fig. 1 nos 11, 11a. Syntype workers. Type locality: QUEENSLAND, Cape York (W.B. Barnard), ANIC, BMNH, MCZC, MVMA, (examined).

Polyrhachis glabrinota Clark; Bolton, 1975: 8.

Other material. QUEENSLAND, Cape York Pen., Lockerbie Scrub, 10°46'S, 142°29'E, 19-24.iii.1987, rf. (RJK acc. 87.38, 60, 61) (w, ♀); Bamaga, 10°53'S, 142°23'E, 18-24.iii.1987, rf. (RJK acc 87.11) (w); Jardine R., 11°08'S, 142°35'E, 14.x.1979 (M.S.& B.J. Moulds) (w); Hann Ck, W of Moreton Telegraph Stn, 28.vi.1988 (G. Kenning) (w); 14 km WSW of Captain Billy Landing, 11°41'S, 142°42'E, 9.ix.1993, rf. (S.O. Shattuck #3802-16) (w); Iron Ra., West Claudie R., 3-10.xii.1985, rf., 50 m (JBM & DJC) (w); Iron Ra., 12°43'S, 143°18'E, 1-17.viii.1978 (S.van Dyck) (w); ditto, 26-31.vii.1981 rf. (RJK accs 81.133, 134, 167, 180) (w, ♀); ditto, Gordon Ck x-ing, 6.x.2000 (RJK acc. 00.174) (w); 9 km ENE of Mt Tozer, Iron Ra. NP, 12°43'S, 143°17'E, 10.vii.1986 (D.C.F. Rentz) (w); 11 km ENE of Mt Tozer, 11-16.vii.1986 (T.Weir & A. Calder) (w).

Worker. Dimensions: (syntypes cited first) TL c. 10.18-11.00, 9.78-11.95; HL 2.50-2.64, 2.46-2.96; HW 1.62-1.69, 1.53-1.93; CI 63-66, 59-66; SL 3.12-3.32, 2.93-3.35; SI 190-197, 181-197; PW 1.44-1.48, 1.40-1.78; MTL 3.73-3.88, 3.58-4.18 (22 measured).

Anterior clypeal margin arcuate, entire. Clypeus with blunt median carina, straight or weakly convex in profile, posteriorly rounding into well impressed basal margin. Frontal triangle distinct. Frontal carinae sinuate with only moderately raised margins; central area with median longitudinal carina. Sides of head in front of eyes weakly convex; behind eyes sides distinctly tapering into relatively narrow occipital margin with lateral lobes weakly developed, not visible with head in full face view. Eyes protuberant, in full face view exceeding lateral cephalic outline. Ocelli lacking. Pronotal dorsum convex in profile; summit with more-or-less distinct, shallow, longitudinal depression; humeri armed with strong, acute, more-or-less horizontal, anterolaterally curved spines; promesonotal suture distinct. Mesonotum virtually flat in profile; mesopleural process a well-developed lobe. Propodeal spines relatively long, obliquely elevated from their bases, curved and moderately divergent. Dorsum of petiole with a pair of laterally and weakly posteriorly directed, acute spines, with their tips turned slightly downwards.

Clypeus and sides of head in front of eyes finely reticulate-punctate, rather smooth and polished; density and intensity of sculpturation increasing posteriorly with central area, vertex and sides of head towards occipital margin deeply and coarsely sculptured. Pronotal dorsum rather smooth and polished or with shallow weak rugosity. Mesonotum, sides of mesosoma and petiole rugose with propodeal dorsum relatively smooth. Gaster very finely shagreened.

Numerous, mostly white or pale yellow, relatively short hairs, not exceeding greatest diameter of eye in length, present over entire body and appendages, including antennal scapes and spines. Rather diluted, white or grey, appressed or suberect pubescence developed in various densities over all body surfaces, more dense and closely appressed on clypeus, sides of head and fore coxae; somewhat suberect and variously radiating pubescence on sides of mesosoma. Gaster with mostly white, appressed pubescence arranged in characteristic midline pattern.

Generally bicoloured; head black, mesosoma black or dark reddish-brown with propodeum and petiole distinctly lighter. Colour variable; black in most recently collected specimens but distinctly lighter reddish-brown in some syntypes. Mandibular masticatory borders, tips of apical antennal segments, and legs, including coxae, light to medium reddish-brown.

Queen. Dimensions: TL c. 11.34-13.10; HL 2.65-2.96; HW 1.62-1.81; CI 59-64; SL 3.17-3.53; SI 183-199; PW 1.90-2.21; MTL 3.93-4.33 (9 measured).

Apart from sexual characters, very similar to worker. Mesoscutum virtually as wide as long with lateral margins converging into narrowly rounded anterior margin; median line slightly raised; dorsum flat in profile with parapsides only weakly raised posteriorly. Mesoscutellum flat, marginally elevated above dorsal plane of mesosoma, posteriorly rounding into metanotal groove. Spines similar to worker but shorter with propodeal pair horizontal. Sculpturation, pilosity, pubescence and colour identical to worker.

Males and immature stages (eggs, larvae in various stages of development and pupae) in QM spirit collection.

Remarks. With its smaller size, rather smooth and polished pronotal dorsum and short, sparse pubescence, *P. glabrinota* is easily distinguished from all other Australian members of the group. However, it closely resembles *P. bubastes* Fr. Smith, 1863 from New Guinea, with both species similar in size, general body form and shape of the petiole. They differ in the intensity of the pronotal sculpturation that, in *P. glabrinota*, is only weakly sculptured, rather smooth and polished, while it is very coarsely sculptured in *P. bubastes*. The body in *P. glabrinota* is also generally bicoloured with the parts of mesosoma and petiole more-or-less reddish-brown, while the body in *P. bubastes* is mostly uniformly black.

Recent examination of a considerable amount of *sexspinosa*-group material from eastern Indonesia and New Guinea has revealed a number of specimens closely comparable to *P. glabrinota*. Like that species, they have smooth pronotal dorsums and are bicoloured, but more distinctly than most of the recently collected Australian specimens. The reddish-brown colour of the specimens from Australia is somewhat darker and more-or-less restricted to the propodeum, petiole and appendages, while the specimens from the Aru Islands and New Guinean mainland are distinctly bicoloured with the head black and all of the mesosoma, petiole and appendages light to medium reddish-brown. These specimens also bear a rather prominent, median, longitudinal depression on the pronotal dorsum, which is only shallowly indicated in some of the Australian specimens. Specimens from Wammar, Aru Is (V. Karavaiev #2595, IZAS) were misidentified as *P. rugifrons* Fr. Smith (Karavaiev, 1927: 25), while a series from Wanuma, Madang District (N.L.H. Kraus, BPBM) were furnished with an identification tag of unknown origin inscribed 'cf. *bubastes* new'. In addition, two nest series of closely comparable specimens, complete with

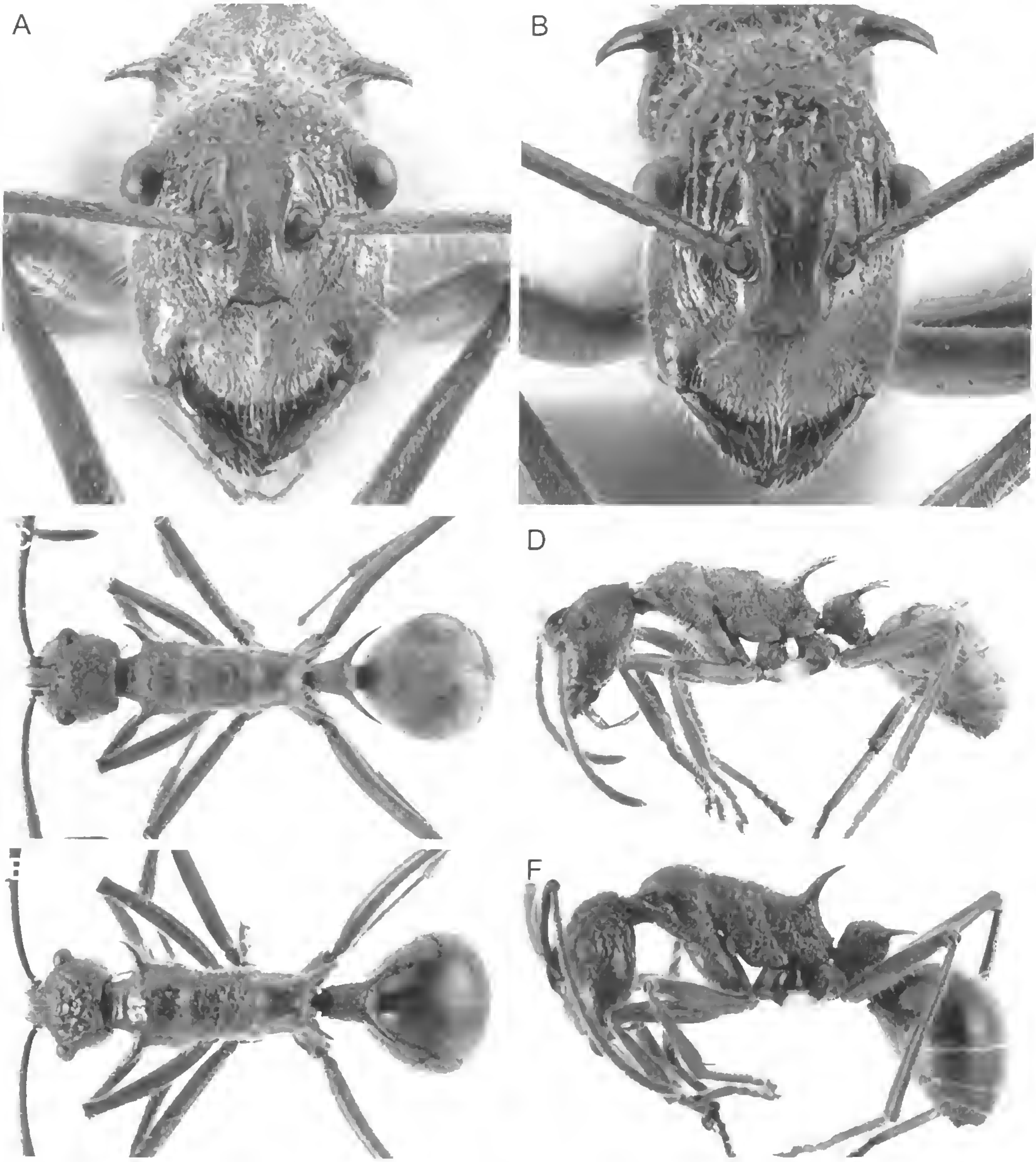

FIG. 4. *Polyrhachis (Myrmhopla)* species from Australia. Head in full face view (top); Dorsal view (left); Lateral view (right). A,C-D, *P. dispar* sp. nov.; B,E-F, *P. glabrinota* Clark (not to scale).

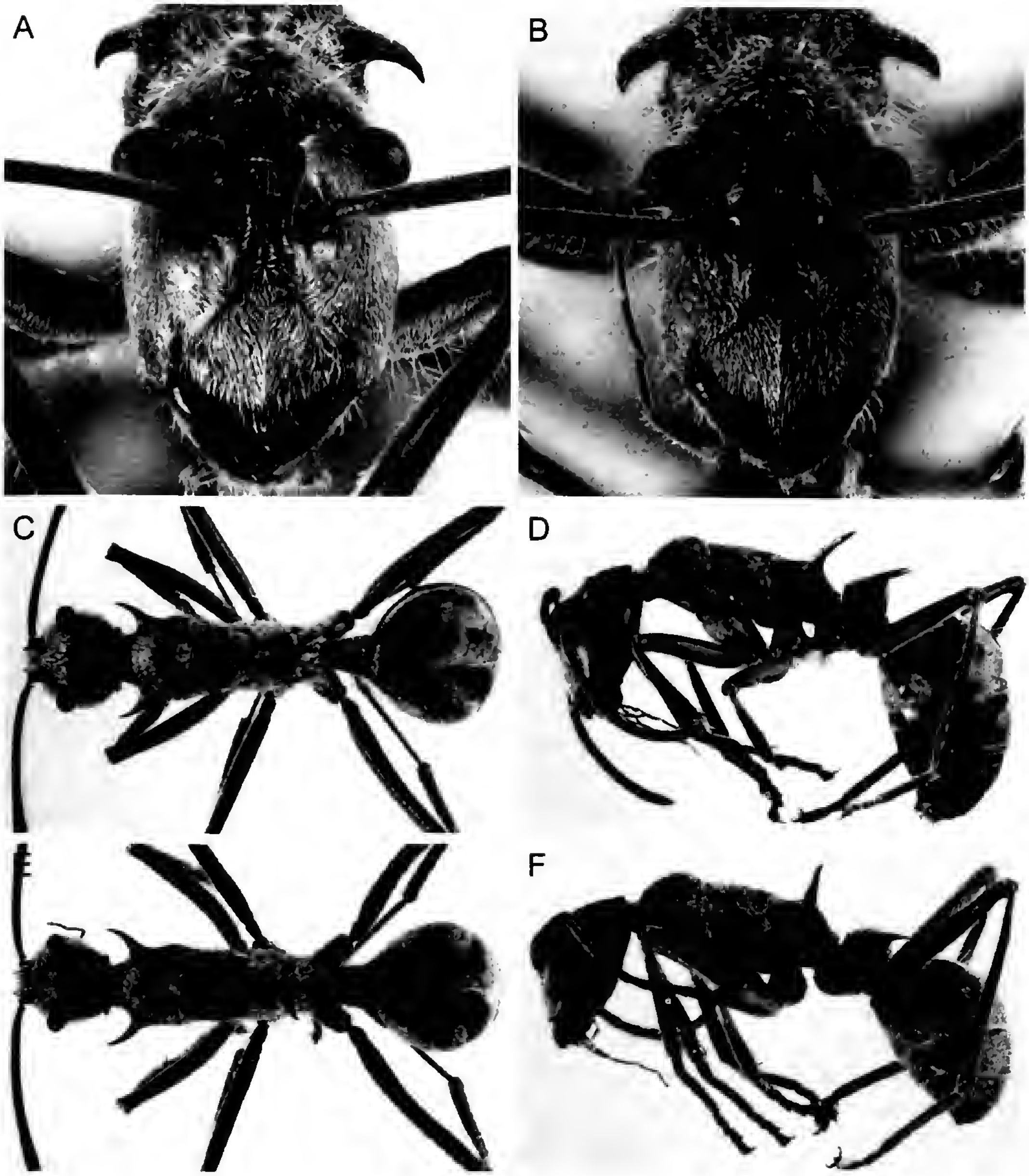

FIG. 5. *Polyrhachis (Myrmhopla)* species from Australia. Head in full face view (top); Dorsal view (left); Lateral view (right). A,C-D, *P. reclinata* Emery; B,E-F, *P. sexspinosa* (Latreille) (not to scale).

sexuals, were more recently collected at Lumi, Torricelli Mts (RJK accs 84.271, 283). Specimens of all these populations vary in several characters, including the direction and length of the propodeal spines and the relative height of the petiole, but overall the specimens are very similar. However, when directly compared with *P. glabrinota*, these specimens appear rather distinct and in spite of some similarity I am hesitant to consider them conspecific. Like Bolton (1975), I consider *P. glabrinota* to be an Australian endemic and believe that the Indonesian and New Guinean material belong to a closely allied, but separate biological species.

Polyrhachis glabrinota is a predominantly arboreal species that builds nests between leaves in the lower arboreal zone. However, several colonies were located nesting in bamboo internodes. In contrast, the nests of the closely allied, possibly polydomous, New Guinean species noted above, were collected from the crown of a recently felled rainforest tree.

Polyrhachis reclinata Emery, 1887
(Figs 5A, C-D, 8C)

Polyrhachis sexspinosa var. *reclinata* Emery, 1887: 236. Lectotype worker (by present designation) and paralectotype workers. Type locality: NEW GUINEA, Fly River, xii.75 (L.M. D'Albertis), MSNG (examined). *Polyrhachis sexspinosa* (Latreille, 1802); Bolton, 1975: 12 (in part).

Polyrhachis reclinata Emery; Kohout & Taylor, 1990: 518. Raised to species.

LECTOTYPE SELECTION

I have examined five syntypes of the original series of *P. sexspinosa reclinata*, three of which were lodged in Emery's collection and two in the separately housed main collection of the MSNG. The specimens bear the following labels: 'Nuova Guinea, Fly River, xii.75, L.M. D'Albertis', '*P. sexspinosa* Latr. var. *reclinata* Em.' and 'Collezione Emery'. Besides the syntypes, I had the opportunity to examine additional specimens identified as *P. sexspinosa reclinata* and lodged in various other collections, however, in spite of some being furnished with a tag inscribed 'Cotype', their locality labels appeared to be of doubtful origin and not identical to those on the syntypes.

To establish the nomenclatural stability of the species and to prevent any future selection of a lectotype from outside of Emery's original series, I have designated, in accordance with Article 74.7.3 of the *International Code of Zoological Nomenclature* (Fourth Edition), a syntype worker specimen as the lectotype of *Polyrhachis reclinata* Emery. The specimen is lodged in the Emery collection (MSNG) and, in addition to the labels listed above, it bears a red original tag inscribed 'Typus'. The remaining specimens of the original series consequently become paralectotypes and are labelled accordingly.

Other material. PAPUA NEW GUINEA, Morobe Prov., Huon Pen., lower Busu R., 8-10.v.1955, lowland rf. (E.O. Wilson #923, 984, 1003) (w, ♀). Western Prov., Oriomo Govt. Stn, 26-28.x.1960 (J.L. Gressitt) (w); Daru I. (no further data) (w); Central Prov., Eigolo Rd., 4 km ESE of Sogeri, 09°25'S, 147°27'E, 4.ix.1984, c. 500 m, rf. (RJK accs 84.427, 423, 424) (w, ♀). AUSTRALIA, QUEENSLAND, Cape York Pen., Lockerbie Scrub, 10°46'S, 142°29'E, 19-23.iii.1987, rf. (RJK accs 87.21, 30, 31, 32, 33, 34, 39, 48, 64, 69, 71, 72) (w, ♀); ditto, i.1958 (Darlingtons) (w); Bamaga, 10°53'S, 142°23'E, 18-23.iii.1987, rf. (RJK acc. 87.9) (w); Bamaga-Lockerbie, 25.i-12.ii.1984 (J.H. Sedláček) (w); Iron Ra., 12°43'S, 143°18'E, 1-17.viii.1978 (S. Van Dyck) (w); ditto, 1-3.vii.1976 (P. Filewood) (w); ditto, 26-31.vii.1981, rf. (RJK accs 81.145, 148, 163, 168, 185, 195, 196, 201, 209, 210, 212) (w, ♀); ditto, i.1958 (Darlingtons) (w); ditto, West Claudie R., 3-10.xii.1985, rf. (GBM & DJC) (w); ditto, Lockhard R. Ranger Stn., 12°45'S, 143°17'E, 26.viii.2004, rf edge (G.D. Alpert) (w); 11 km ENE of Mt Tozer, 12°43'S, 143°18'E (T. Weir & A. Calder) (w).

Worker. Dimensions. (lectotype cited first): TL c. 14.01,11.44-14.31; HL 3.48, 2.92-3.48; HW 2.37,1.89-2.37; CI 68, 62-68; SL 4.13, 3.53-4.13; SI 174, 174-195; PW 1.86, 1.56-1.86; MTL 5.09, 4.28-5.11 (23 measured).

Anterior clypeal margin arcuate, narrowly and shallowly emarginate medially; clypeus with blunt median carina, clypeus weakly convex in profile, posteriorly curving into shallow basal margin. Frontal carinae sinuate with acute, highly raised margins; central area with median longitudinal carina. Sides of head in front of eyes convex; behind eyes sides strongly tapering into narrow occipital margin with rather weakly developed occipital lobes. Eyes strongly convex, in full face view clearly exceeding lateral cephalic outline. Median ocellus usually present, lateral ocelli lacking; positions indicated by distinctly raised cephalic sculpture. Pronotal dorsum weakly convex in profile with anterior slope almost flat; humeri armed with acute, more-or-less horizontal, anterolaterally directed spines; promesonotal suture distinct. Mesopleural process a simple dentiform lobe. Mesonotal dorsum flat or weakly convex in profile. Propodeal spines long, divergent, obliquely elevated from their bases and more-or-less curved posteriorly. Dorsum of petiole with a pair of slender, widely diverging, acute spines.

Clypeus and sides of head finely reticulate-punctate, distinctly smooth; intensity of sculpturation increasing posteriorly with a few shallow rugae on vertex and towards occipital margin. Mesosoma rugose dorsally and laterally, except for relatively smooth propodeal dorsum. Gaster very finely shagreened.

Mostly yellow or pale golden hairs, of variable length and density over entire body and appendages, including antennal scapes. Relatively long, suberect, mostly golden or brassy pubescence variously developed, most dense and more appressed on dorsum of head and mesosoma where it almost completely hides underlying sculpturation. Gastral pubescence ranging from somewhat diluted on venter to dense on dorsum, where it is arranged in a characteristic midline pattern.

Body generally black; propodeum and petiole often lighter, reddish-brown; masticatory borders of mandibles, antennae and legs, including coxae, medium reddish-brown with fore coxae and tarsi distinctly darker.

Queen. Dimensions: TL c. 13.55-14.46; HL 3.12-3.28; HW 1.96-2.07; CI 61-64; SL 3.83-3.88; SI 185-195; PW 2.02-2.12; MTL 4.64-4.79 (4 measured).

Differing from worker in usual characters identifying full sexuality, including three ocelli, complete thoracic structure and wings. Mesoscutum marginally wider than long with narrowly rounded anterior margin in dorsal view; median line raised; dorsum flat in lateral view with parapsides only weakly raised posteriorly. Mesoscutellum flat, not elevated above dorsal plane of mesosoma; metanotal groove distinct. Spines similar to those in worker but shorter, propodeal pair distinctly less elevated. Sculpturation, pilosity and colour virtually identical to worker.

Males and immature stages (eggs, larvae in various stages of development and pupae) in QM spirit collection.

Remarks. *Polyrhachis reclinata* is a rather common species closely resembling *P. sexspinosa*. However, they are easily separated by the following characters. The head in *P. sexspinosa* is strongly tapered behind the eyes and the occipital margin forms prominent, well-developed lateral lobes that are clearly visible in full face view. In addition, the vertex and sides of the head behind the eyes are rather coarsely rugose and covered with more-or-less diluted, mostly white or silvery pubescence. The propodeal spines in *P. sexspinosa* are virtually vertical to the main axis of the body, or are even inclined forwards when viewed laterally. In contrast, the head behind the eyes in *P. reclinata* is generally shorter and distinctly less strongly tapered with the lateral occipital lobes relatively weakly developed and less prominent in full face view. The sculpturation on the clypeus and sides of the head is rather smooth, with a few shallow rugae on the vertex, and is usually masked by rather dense, golden or brassy, appressed pubescence. The propodeal spines are oblique to the main axis of the body and usually curved posteriorly in side view.

The type locality of *P. reclinata* is the Fly River delta, which is only about 150 km from Cape York Peninsula on the opposite side of Torres

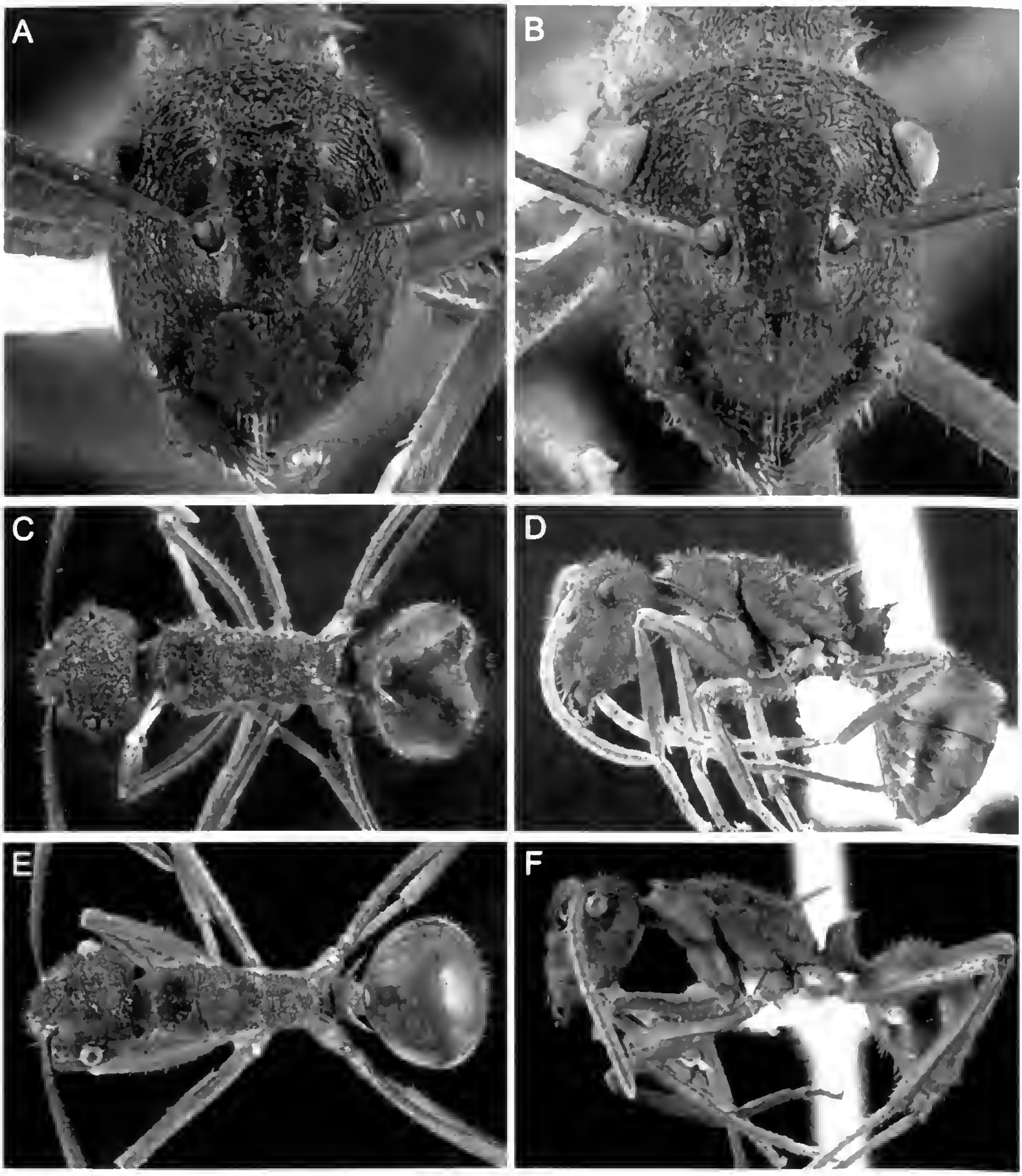

FIG. 6. *Polyrhachis (Hirtomyrma)* species from Australia. Head in full face view (top); Dorsal view (left); Lateral view (right). A,C-D, *P. bamaga* Kohout; B,E-F, *P. eremita* Kohout (not to scale).

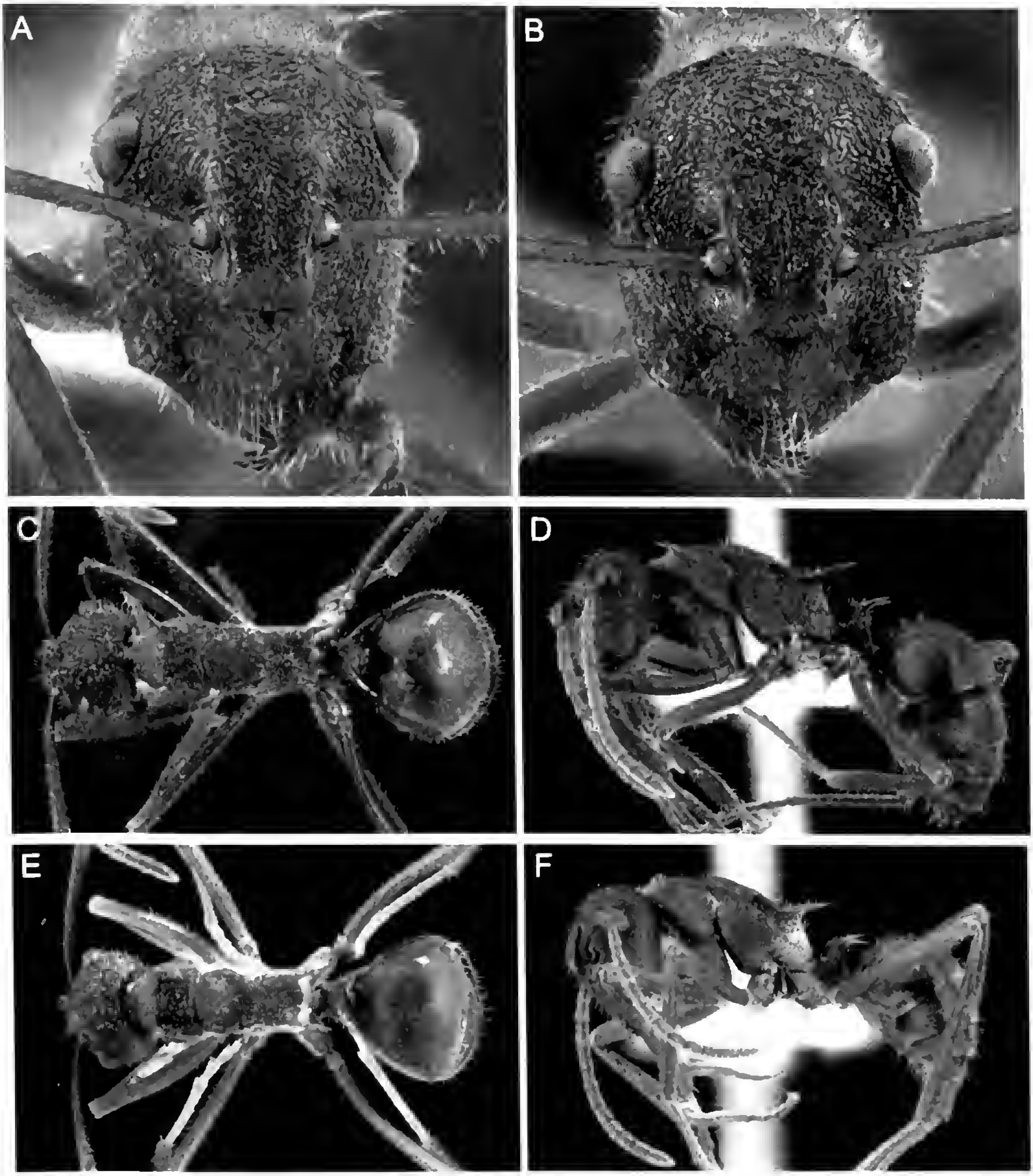

FIG. 7. *Polyrhachis (Hirtomyrma)* species from Australia. Head in full face view (top); Dorsal view (left); Lateral view (right). A,C-D, *P. loweryi* Kohout; B,E-F, *P. rustica* Kohout (not to scale).

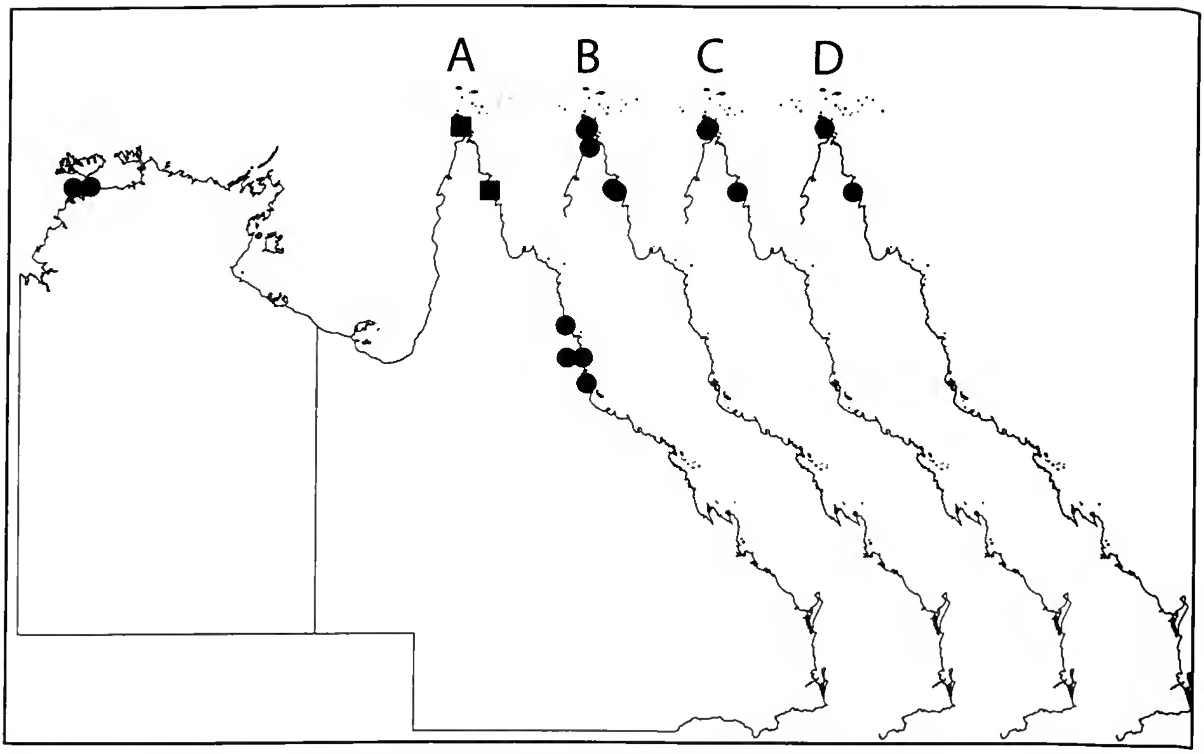

FIG. 8. Distributions of Australian *Polyrhachis* (*Myrmhopla*) species (extralimital distributions not indicated). A, ● *P. dives*, ■ *P. dispar*; B, *P. glabrinota*; C, *P. reclinata*; D, *P. sexspinosa*.

Strait. Specimens from either side of Torres Strait are closely comparable, differing only in the shape and direction of spines. The pronotal spines of the specimens from the Fly River are more slender, longer and less strongly curved forwards compared to Australian specimens. The propodeal spines are almost straight while they are shorter and more strongly curved posteriorly in Australian specimens. The mesopleural process is a simple, ventrally dentiform lobe in both New Guinean and Australian specimens.

Polyrhachis reclinata is known from lowland rainforest along the Gulf of Papua, including the Fly River delta (type locality), the lower Busu River, the Port Moresby area and Daru Island. In Australia *P. reclinata* has been collected from Lockerbie Scrub south to Iron Range. Most colonies collected at the latter locality were nesting within the hollow internodes of *Bambusa forbesii* growing as several relatively large stands within monsoon rainforest. Only a single colony of this species was located nesting under the bark of a living tree.

Polyrhachis sexspinosa (Latreille, 1802)
(Figs 5B, E-F, 8D, 10A-B,)

Formica sexspinosa Latreille, 1802: 126, pl. 4, fig. 21. Neotype worker (by present designation). Type locality: PAPUA NEW GUINEA, West Sepik Prov., Pes Mission, 12 km SW of Aitape, 03°11'S, 142°15'E, <50 m, rf., 3.viii.1984 (RJK acc. 84.207), ANIC (examined).

Polyrhachis barnardi Clark 1928; 39, pl. 1, figs 37-38 (in part). Synonymy, and lectotype designated by Kohout & Taylor 1990: 519 (see under remarks section of *P. dispar* above).

Polyrhachis sexspinosa (Latreille). Fr. Smith,1858: 59; Bolton, 1975: 12.

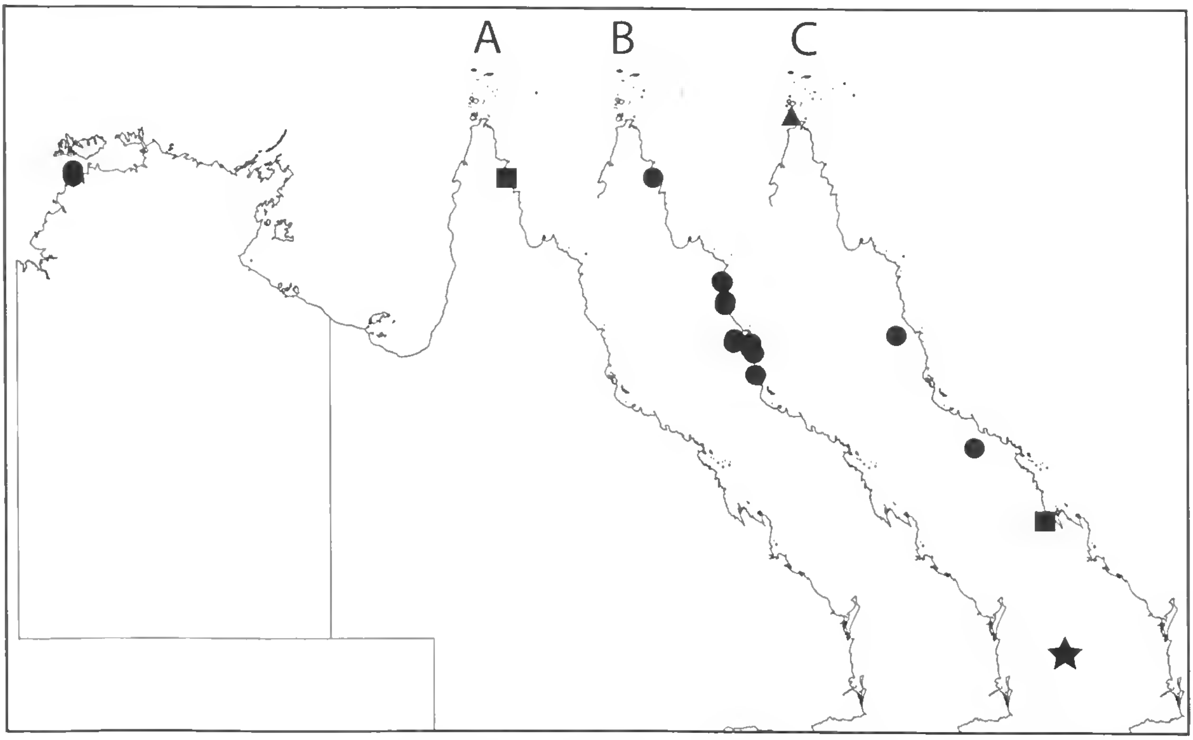

FIG. 9. Distributions of Australian *Polyrhachis* (*Myrmhopla*) and *Polyrhachis* (*Hirtomyrma*) species (extralimital distributions not indicated). A, ● *P. bicolor*, ■ *P. nigripes*; B, *P. mucronata*; C, ▲, *P. bamaga*, ●, *P. rustica*; ■, *P. eremita*; star, *P. loweryi*.

NEOTYPE DESIGNATION

The holotype queen of this species should be lodged in the MNHN, but an extensive search by the author failed locate it there or in any collections examined and it is considered lost. To establish the nomenclatural stability of the species, I have designated, in accordance with Article 75.3.5. of the *International Code of Zoological Nomenclature* (Fourth Edition), a worker specimen as the neotype of *Polyrhachis sexspinosa* (Latreille). The specimen was selected from a colony of 50+ workers, a dealate queen and several males collected from a pocket nest on the trunk of a rainforest tree. The neotype has been deposited in ANIC.

Other material. INDONESIA, Aru Is, Wokam, 1908 (Merton) (w); ditto, Kobror, 1925 (Karavaiev #2534) (w). PAPUA NEW GUINEA, West Sepik Prov., Pes Mission, c.12 km WSW of Aitape, 03°11′S, 142°15′E, <50 m, 31.vii-3.viii.1984 (RJK accs 84.148, 171, 207) (w, ♀, ♂); Northern Prov., Owen Stanley Ra., Mamba Pltn, c. 7 km WNW of Kokoda, 08°51′S, 147°41′E, 500 m, 31.viii-1.ix.1984 (RJK accs 84.398, 399, 403) (w, ♀). AUSTRALIA, QUEENSLAND, Cape York, xi.1927 (W.B. Barnard); Cape York Pen., Lockerbie Scrub, 10°46′S, 142°29′E, 19-23.iii.1987 (RJK accs 87.40, 41, 42, 43, 48, 57, 70) (w, ♀); Iron Ra., 12°43′S, 143°18′E, 26-31.vii.1981 (RJK accs 81.162, 172, 173) (w, ♀); ditto, 1-3.vii.1976 (P. Filewood) (w); ditto, West Claudie R., 3-10.xii.1985 (GBM & DJC) (w).

Worker. Dimensions. TL c. 12.60-14.76; HL 3.12-3.58; HW 1.84-2.17; CI 57-62; SL 3.78-4.48; SI 195-216; PW 1.81-2.03; MTL 4.79-5.74 (27 measured).

Anterior clypeal margin arcuate, often with very shallow median emargination. Clypeus with median carina, virtually straight in profile, posteriorly curving into moderately impressed basal margin. Frontal carinae sinuate with acute, highly raised margins. Sides of head in front of eyes almost straight, weakly diverging towards mandibular bases; behind eyes sides strongly tapered into narrow occipital margin with strongly developed occipital lobes. Eyes strongly convex, in full face view clearly exceeding lateral cephalic outline. Ocelli lacking, positions indicated by distinctly raised cephalic sculpture. Pronotal dorsum convex in profile, distinctly higher than mesonotum; humeri armed with strong, acute, more-or-less horizontal, anterolaterally directed spines; promesonotal suture distinct. Mesopleural process a distinct, dentiform lobe. Mesonotum and propodeum weakly convex in profile. Propodeal spines relatively long, virtually straight, in lateral view usually vertical to main axis of body or inclined forwards, tips sometimes curved posteriorly or inwards. Dorsum of petiole with a pair of lateral, dorsoposteriorly directed, acute spines.

Mandibles with numerous piliferous pits. Clypeus and sides of head finely reticulate-punctate with intensity and density of sculpturation distinctly increasing posteriorly, vertex and occiput rather coarsely sculptured. Mesosomal dorsum rugose with intensity decreasing posteriorly with propodeal dorsum finely reticulate-punctate. Gaster very finely shagreened.

Mostly silvery or grey, erect or variously curved hairs of variable lengths and densities over the entire body and appendages, including antennal scapes. Longest hairs on mesosomal dorsum, clearly longer than greatest diameter of eye. Head and mesosoma with somewhat untidy, relatively long, mostly silvery, suberect pubescence that never completely hides underlying sculpturation; most dense and more appressed on dorsum of head and mesosoma, somewhat radiating on sides. Gastral pubescence ranging from diluted on venter to dense on dorsum, where it is arranged in characteristic midline pattern.

Body black; mandibles, except bases, apical antennal segments and legs, including coxae, mostly light to medium reddish-brown.

Queen. Dimensions: TL c. 13.46-16.28; HL 3.17-3.78; HW 1.86-2.37; CI 57-63; SL 3.73-4.59; SI 189-211; PW 2.02-2.82; MTL 4.74-5.64 (11 measured).

Queen very similar to worker; apart from usual characters identifying full sexuality, including three ocelli, complete thoracic structure and wings differing mainly in configuration of spines; pronotal spines shorter, projecting more anteriorly, tips directed forwards; propodeal spines distinctly shorter, oblique to main axis of body, weakly curved posteriorly; petiolar spines straight, distinctly shorter than in worker; sculpturation, pilosity and colour pattern identical to worker.

Males and immature stages (eggs, larvae in various stages of development and pupae) in QM spirit collection.

Remarks. *Polyrhachis sexspinosa* was originally described from a queen collected in the 'East Indies', however like Bolton (1975), I have been unable to locate the type in any of the collections examined and consider it lost. I therefore support the earlier decision of Kohout & Taylor (1990: 518-520) who recognised the specimens of a nest series from Papua New Guinea (see above) as the voucher specimens of *P. sexspinosa* by designating one of these workers as the neotype for this name (ANIC, QM).

Polyrhachis sexspinosa resembles *P. reclinata*, with their main distinguishing characters given in remarks section under the latter species. *Polyrhachis sexspinosa* is a relatively common and widespread species reported from most of the New Guinean mainland and islands of eastern Indonesia, including several doubtful records from the southern Philippines (Kohout, 1989). In Australia it ranges from Lockerbie Scrub south to Rocky River, northeast of Coen. *Polyrhachis sexspinosa* is somewhat singular within the *sexspinosa*-group in that it builds pocket-like nests of silk, vegetation debris and bark fragments against the trunks of rainforest trees (Figs 10A-B).

Subgenus *Hirtomyrma* subgen. nov.

Myrmhopla Forel, 1915: 107 as subgenus of *Polyrhachis* Fr. Smith (in part).

Myrmhopla Forel; Emery, 1925 (in part – as *P. viehmeyeri*-group).

Myrmhopla Forel; Kohout, 1990 (in part – as *P. viehmeyeri*-group).

Myrmhopla Forel; Dorow, 1995 (in part – as *P. viehmeyeri*-group).

Type species. *Polyrhachis hirta* Viehmeyer, 1914.

The subgenus *Hirtomyrma* as conceived here effectively replaces the *Polyrhachis viehmeyeri*-group that was originally established by Emery (1925), within the subgenus *Myrmhopla* Forel, for two, rather unusual species from New Guinea (*P. hirta* Viehmeyer, 1913 and *P. viehmeyeri* Emery, 1921). A third species (*P. davydovi* Karavaiev) from the Aru Is, Indonesia, was described by Karavaiev in 1927. The former group was reviewed by Kohout (1990) who described four new species from northern Australia (*P. bamaga* Kohout, *P. eremita* Kohout, *P. loweryi* Kohout and *P. rustica* Kohout) and two extralimital species (*P. greenslade*i Kohout from the Solomons and *P. stigmatifera* Kohout from Seram I., Indonesia). An additional species from South East Asia (*P. lama* Kohout) was described by Kohout in 1994, thus raising the number of known species of the group to ten.

Diagnosis. *Worker*. Medium sized-ants (HL 1.75-2.20) with general characteristics of the genus. Mandibles with 4 or 5 teeth, very finely longitudinally striate. Anterior clypeal margin truncate medially; posterior margin usually deeply impressed. Frontal carinae rather flat, widely separated. Eyes with numerous, short, erect hairs, strongly convex, almost hemispherical, clearly exceeding lateral cephalic outline in full face view. Median ocellus distinct (as in *P. eremita* and *P. loweryi*), vestigial (as in *P. rustica*) or lacking (as in *P. bamaga*). Pronotal and propodeal dorsa laterally marginate, virtually flat; mesonotal dorsum transversely convex with less distinct, rather blunt, lateral margins. Pronotum armed with somewhat dorsally flattened, acute spines (except in extralimital *P. lama*); their length, direction and degree of elevation usually highly variable, even asymmetrical, within a single species (as in *P. rustica*). Propodeal spines acute, usually longer than pronotal pair, variously elevated. Dorsum of petiole with poorly defined, more-or-less posteriorly sloping platform, bearing a pair of widely separated, diverging spines, without intercalary spines or teeth. Head, mesosoma and petiole with characteristic vermiculate-rugose sculpturation and bristle-like hairs, distinctly shorter than maximum eye diameter. Gaster shagreened, or with base of first tergite finely micro-reticulate and more-or-less shiny (as in most Australian species). Body mostly light to dark reddish-brown, with mandibles, clypeus, frontal carinae, spines and posterior margins of gastral tergites usually narrowly bordered very dark brown.

Queen. Differing from worker in usual characters identifying full sexuality, including three ocelli, complete thoracic structure and wings. Spines shorter and more stubby than in worker. Sculpturation, pilosity and colour essentially as in worker.

Distribution and biology. The main distribution of the subgenus *Hirtomyrma* ranges from the Moluccas, New Guinea and Bismarck Archipelago to the Solomons and extends south to northern Australia. However, the range of one species (*P. lama* Kohout, 1994) extends from Java and Hong Kong to the Tibetan Plateau in the Himalayas. All known species of this group are apparently social parasites of other ants, notably Ectatomminae and Ponerinae. The association of *P. loweryi* with the genus *Rhytidoponera* Mayr and the extralimital *P. lama*, with the genus *Diacamma* Mayr, were studied by Prof. U. Maschwitz (formerly of Johan Wolfgang Goethe-Universität in Frankfurt am Main, Germany) and his team (Maschwitz *et al.* 2000, 2003).

KEY TO AUSTRALIAN SPECIES OF THE SUBGENUS *HIRTOMYRMA*
(based on worker caste)

1. Base of first gastral tergite finely shagreened, rather polished (Fig. 6E); mandibles with 4 teeth. . . . . 2.
– Base of first gastral tergite closely, transversely striate, opaque (Fig. 6C); mandibles with 5 teeth, but with basal tooth often vestigal . . . . *bamaga* Kohout

2. Larger species (HL >1.85); median ocellus well developed, distinct . . . . 3.
– Smaller species (HL <1.80); median ocellus rather small, indistinct . . . . *rustica* Kohout

3. Body bicoloured, medium reddish-brown with most of head, pronotal collar and anteromedian patch on mesosomal dorsum light yellowish-brown; antennal scapes shorter (SI <144) . . . . *eremita* Kohout
– Body more-or-less unicoloured, dark reddish-brown, with only mandibles, spines and subpetiolar process lighter; antennal scapes longer (SI >146) . . . . *loweryi* Kohout

Polyrhachis bamaga Kohout, 1990
(Figs 6A, C-D, 9C)

Polyrhachis bamaga Kohout, 1990: 500, fig. 4. Holotype and paratype workers. Type locality: QUEENSLAND, Cape York Pen., Bamaga (R.J. Kohout), QM (examined).

Remarks. In spite of revisiting the type locality of *P. bamaga* specifically to collect more specimens (see Maschwitz *et al*., 2003), the types remain the only specimens of this species known. They were originally collected along the edge of a lowland riverine rainforest, foraging over low vegetation in association with *Polyrhachis paxilla* Fr. Smith, 1863 (see Kohout, 1990: 501).

Polyrhachis eremita Kohout, 1990
(Figs 6B, E-F, 9C)

Polyrhachis eremita Kohout, 1990: 502. Holotype and paratype workers. Type locality: QUEENSLAND, 4-10 km N of Marlborough (R.J. Kohout), QM (examined).

Remarks. A thorough search conducted at the type locality and in brigalow forest north of Marlborough (see Maschwitz *et al*., 2003), produced no nests of the large *Rhytidoponera* species with which *P. eremita* was thought to be associated. I also visited the area in 2006 and found no *Rhytidoponera* nests, as well as a general decline in the number of other ant species previously found there in 1981. This could be due to considerable degradation of the habitat, including substantial deforestation.

Polyrhachis loweryi Kohout, 1990
(Figs 1F, 7A, C-D, 9C)

Polyrhachis loweryi Kohout, 1990: 505. Holotype and paratype workers. Type locality: QUEENSLAND, Miles (B.B. Lowery), ANIC (examined).

Other material. QUEENSLAND, c. 5.5 km NNW of Miles, 26°36′S, 150°10′E, 6-8.iii.2000, dry (U. Maschwitz *et al.*) (w, ♀, ♂ - associated with *Rhytidoponera* sp.).

Queen. (not previously described) Dimensions: TL c. 9.27; HL 2.00; HW 1.56; CI 78; SL 2.34; SI 150; PW 1.81; MTL 3.22 (1 measured).

Closely resembling worker and apart from sexual characters, including three ocelli, complete thoracic structure and wings, differing as follows: pronotal spines distinctly reduced to more-or-less triangular, acute teeth. Mesoscutum with anterior margin evenly rounded in dorsal view; in profile anterior face distinctly swollen, widely rounding onto flat dorsum; median line bifurcate dorsally; parapsides flat anteriorly, weakly raised posteriorly. Mesoscutellum in lateral view elevated above dorsal plane of mesosoma, relatively flat, rounding posteriorly into distinct metanotal groove. Propodeal spines short, obliquely elevated; petiolar spines similar to those in worker but distinctly shorter, their inner margins continued medially and posteriorly, forming rather blunt, V-shaped posterior margin of petiolar dorsum. Sculturation, pilosity and colour virtually identical to worker.

Males and immature stages (eggs, larvae and pupae) originally deposited in the Forschungsinstitute Senckenberg, Frankfurt am

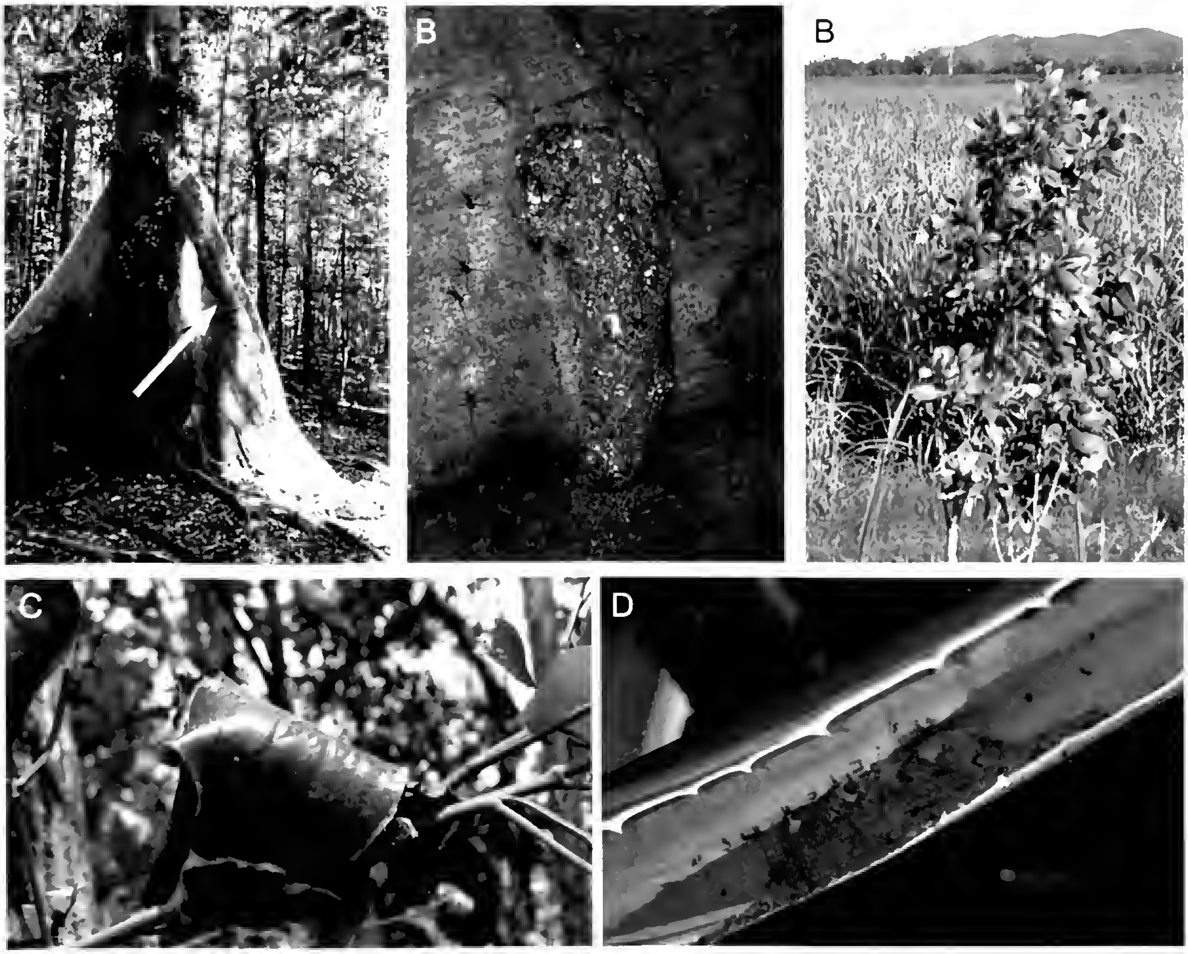

FIG. 10. Nests of Australian *Polyrhachis (Myrmhopla)* species. A-B. Pocket nest of *Polyrhachis sexspinosa* (Latreille) attached to a buttress of a cauliflorai rainforest tree at Lockerbie Scrub, Cape York Peninsula (Photo R.J. Kohout); C. Polydomous nest of *Polyrhachis dives* Fr. Smith on small sapling in north Queensland (Photo S.K.A. Robson); D. Nest of *Polyrhachis bicolor* Fr. Smith in curled leaf (Photo A. N. Andersen); E. Nest of *Polyrhachis mucronata* Fr. Smith (Photo J. Wright).

Main, Germany (see Maschwitz *et al.*, 2003) were accidently destroyed (Dorow, *pers. comm.*).

Remarks. A successful visit to the vicinity of Miles (see above) yielded numerous nests of *Rhytidoponera* spp. (*aciculata*- and *convexa*-groups). Following examination of ten nests of the *aciculata*-group sp. and five nests of the *convexa*-group sp., six colonies of *P. loweryi* were located within the nests of the former. However, on a subsequent visit to the same locality, several worker specimens of *P. loweryi* were also located within a nest of a *Rhytidoponera* species belonging to the *convexa*-group.

Polyrhachis rustica Kohout, 1990
(Figs 7B, E-F, 9C)

Polyrhachis rustica Kohout, 1990: 505. Holotype and paratype workers, queen. Type locality: QUEENSLAND, 4km N of Collinsville (B.B. Lowery), ANIC (examined).

Other material. QUEENSLAND, Chewko Rd. nr Mareeba, 3.viii.1975 (B.B. Lowery) (w - associated with *Rhytidoponera ?aurata* Roger).

Remarks. Both the original localities at Collinsville and Mareeba were visited in February, 2000 by Maschwitz *et al.* (2003) in search of *P. rustica*. However, in spite of locating and examining numerous nests of two unidentified *Rhytidoponera* species, no associated *Polyrhachis* specimens were found.

ACKNOWLEDGEMENTS

I am very grateful to the Australian Biological Resources Study for a research grant supporting my work on the systematics of Australian *Polyrhachis* ants. This work was also supported by three Ernst Mayr Grants that allowed me to travel and study specimens in the Museum of Comparative Zoology, Harvard University and several other museums and institutions in the USA and UK. I am also indebted to the Smithsonian Institution for a Short-Term Visitor Grant to study the *Polyrhachis* ants in the collection of the National Museum of Natural History, Washington. My sincere thanks go to Drs Steve Shattuck (ANIC), Stefan Cover (MCZC) and Barry Bolton (BMNH) for unlimited access to the collections in their care. I thank Prof. U. Maschwitz (formerly of JWGU) for the opportunity to join the expedition to northern and central Queensland, financed by the Deutsche Forschungsgemeinschaft. My thanks are due to Dr Yoshiaki Hashimoto (MNHA) for his patience and care in the preparation of the digital images used for illustrations, to Geoff Thompson (QM) for producing the distribution maps and to Ms Natalie Barnett (ANIC) for computer-based enhancement of the line drawings. I also thank Dr Gary Alpert and Mary Corrigan (both Harvard University) for their hospitality during my visits to the MCZC. To Dr Premek Hamr (Upper Canada College, Toronto, Canada) I owe my thanks for assistance with the translation of the French diagnosis of *Myrmhopla*. I thank the curators and staff of the museums and institutions listed earlier for their help and kindness during my visits and for providing loans of types and other specimens. My sincere thanks go to my colleagues, Drs Chris Burwell, Geoff Monteith, Ms Susan Wright (all QM), for their valuable support during the course of this study. I would also like to extend my gratitude to the Environmental Protection Agency and the Department of Natural Resources for issuing the permits to allow collecting in Queensland's National Parks and State Forests. My thanks are also due to Parks Australia, Department of Environment and Heritage and to the Parks and Wildlife Commission of the Northern Territory for permits to collect in Kakadu and other National Parks in the Northern Territory. Finally a special thankyou to Chris Burwell (QM) for reading and commenting on a draft of the manuscript.

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Rabaulichthys squirei, a new species of Sailfin Anthias (Serranidae: Anthiinae) from the Coral Sea

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Citation: Randall, J.E. & F. Walsh 2010 03 15 *Rabaulichthys squirei*, a new species of Sailfin Anthias (Serranidae: Anthiinae) from the Coral Sea. *Memoirs of the Queensland Museum – Nature* 55(1): 205-211. Brisbane. ISSN 0079-8835. Accepted: 23 September 2009.

ABSTRACT

Rabaulichthys squirei is described as a new species of the serranid subfamily Anthiinae from 12 specimens collected at Flinders Reef and Flora Reef in the Coral Sea from 6 to 54 m. A huge population was also observed at Holmes Reef in 55 m. The species is distinct from three others of the genus by the combination of a high count of 23 or 24 lower-limb gill rakers, relatively long snout, a very high spinous portion of the dorsal fin of the male, and subtle differences in colouration. It forms small elusive aggregations that feed on zooplankton, mainly over open substrata of coral rubble. ❒ *Coral Sea, Serranidae, Anthiinae, Rabaulichthys, new species.*

The Sailfin Anthias, *Rabaulichthys altipinnis*, was described as a new genus and species of serranid fish of the subfamily Anthiinae by Allen (1984) from specimens collected near Rabaul, New Britain. Six specimens, 34.8–45.5 mm SL, were collected from small aggregations about a meter above a sloping coral-rubble bottom in 30–40 m. This species typically forms aggregations of about three to eight individuals. The new genus was characterised by a slender body, the dorsal fin of 10 weak flexible spines, and 15 or 16 rays, the spinous part greatly elevated in the male, 19–21 pectoral rays, over 50 lateral-line scales, no teeth on the vomer and palatines, and fleshy papillae on the edge of the posterior half of the orbit.

A second species of the genus, *R. stigmaticus*, was described by Randall & Pyle (1989) from four specimens collected in 35 m over a rubble bottom at Ari Atoll, Maldive Islands. Its occurrence in Sri Lanka was confirmed by a photograph of an adult male sent by Rohan Pethiyagoda.

A third species, *Rabaulichthys suzukii*, was described by Masuda & Randall (2001) from three specimens taken in 5–15 m at Izu Peninsula, Shizuoka Prefecture, Japan.

As mentioned by Randall & Pyle (1989) and Masuda & Randall (2001), the Bishop Museum in Honolulu has 40 specimens of a small species of *Rabaulichthys* that were collected by dredging in 1972 by the US National Marine Fisheries Service at Condor Reef in the Caroline Islands from a depth range of 37–46 m. This species is distinct in its very slender body and having a filament on the tip of each caudal-fin lobe. Because of the poor condition of the specimens and no information on life color, this species has not been described.

Two specimens of a fifth species of the genus were collected in October, 2007 by aquarium fish collector Tim Bennett from 54 m at Flinders Reef in the Coral Sea, 220 km east of Townsville, Queensland. One fish is a male with the expected very high spinous portion of the dorsal fin, and the other a female with a dorsal fin of near-uniform height. The male has a lateral-line scale count of 57 on one side and 59 on the other, whereas the female has counts of 51 and 52 lateral-line scales. This is more variation than expected for a single species of anthiine fish, so we waited for additional material. Ten months later, 10 specimens were collected by Cadel Squire at Flora Reef in 6–9 m. Their lateral-line scale counts of both sides filled the gap between 52 and 57, with seven counts of 54 scales and five of 55 scales.

We present here the description of the new species of *Rabaulichthys* from the Coral Sea, the first of the genus for Australian waters.

METHODS AND MATERIALS

Lengths of specimens are given as standard length (SL), measured from the front of the upper lip to the base of the caudal fin (posterior end of the hypural plate); head length (HL) is measured from the same anterior point to the posterior end of the opercular flap; body depth is taken vertically from the base of first dorsal spine; body width is the maximum width just posterior to the gill opening; orbit diameter is the greatest fleshy diameter, and interorbital width the least fleshy width; upper-jaw length is taken from the front of the upper lip to the mid-posterior end of the maxilla; caudal-peduncle depth is the least depth, and caudal-peduncle length the horizontal distance between verticals at the rear base of the anal fin and the caudal-fin base; lengths of fin spines and rays of the dorsal and anal fins are measured to their extreme base; caudal-fin length is the horizontal distance from the base of the fin to a vertical at the tip of the longest ray; caudal concavity is the horizontal distance between verticals at the tips of the longest and shortest rays; pectoral-fin length is the length of the longest ray; pelvic-fin length is measured from the origin of the pelvic spine to the tip of the longest soft ray. Pectoral-fin ray and lateral-line scale counts were made on both sides. Gill-raker counts were made on the first gill arch of the right side and include rudiments; the raker at the angle is contained in the count of the lower-limb.

In the description of the new species, data in parentheses refer to paratypes. Measurements in Table 1 and the diagnosis are given as percent of the standard length, those in the description as proportions of the standard length or head length, rounded to the nearest .05.

Specimens for this study have been deposited in the fish collections of the Bernice P. Bishop Museum, Honolulu (BPBM); the Queensland Museum, Brisbane (QM), the National Museum of Natural History, Washington, D.C. (USNM); and the Western Australian Museum, Perth (WAM).

KEY TO THE SPECIES OF *RABAULICHTHYS*

1. Snout short, 5.5–6.4% SL; lower-limb gill rakers 21–22; length of longest dorsal spine of mature male 25.3–26.2% SL; body depth 26.6–29.7% SL (New Britain) .... *altipinnis*

– Snout not short, 6.8–7.4% SL; lower-limb gill rakers 23–24; length of longest dorsal spine of mature male 28.7–39.0% SL; body depth 23.8–27.7% SL 2

2. A narrow, elliptical, black band parallel to back near middle of soft portion of dorsal fin; a large, pale-edged, nearly square, dark reddish blotch on body below soft portion of dorsal fin (Maldive Islands and Sri Lanka; only males available) ....*stigmaticus*

– No black band in soft portion of dorsal fin; no large, nearly square, pale-edged, dark reddish bar on body below soft portion of dorsal fin 3

3. Body depth 23.8–25.3% SL; caudal-fin length

of males 31.8–35.8% SL (Coral Sea) ....*squirei*, sp. nov.

- Body depth 26.0–27.7% SL; caudal-fin length of males 25.5–31.2% SL (only males available, Shizuoka Prefecture, Japan)..........*suzukii*

Rabaulichthys squirei Randall & Walsh sp. nov. (Figs. 1A-D)

Etymology. We are pleased to name this species for Cadel Squire who collected most of the type specimens.

Material. HOLOTYPE: QM I.38237, 62.2 mm SL, Coral Sea, Flinders Reef, north end, 17°24'1"S, 148°25'3"E, 54 m, barrier net, T. Bennett, 1/10/2007. PARATYPES. QM I.38441, 53.0 mm, same data as holotype; QM I.38420, 4: 36.2–47.6 mm SL, Coral Sea, Flora Reef, 16°45'S, 147°46'E, 6–9 m, 8/2008; BPBM 40978, 2: 35.0–46.6 mm; USNM 395918, 2: 37.2–43.1 mm; and WAM P.33113-001, 2: 37.8-42.5 mm, all with same data as QM I.38420.

Diagnosis. Dorsal rays X,16; anal rays III,7; pectoral rays 19--21 (rarely 21); lateral-line scales 51–59; gill rakers 9 + 23–24; body depth 23.8–25.3% SL; head length 28.5–30.6% HL; snout length 6.8–7.4% SL; longest dorsal spine of mature males 28.7–31.3% SL; caudal fin of mature males 31.8–

TABLE 1. Proportional measurements of type specimens of *Rabaulichthys squirei* as percentages of the standard length

	Holotype	Paratypes					
	QM 1.38237	QM 1.38441	QM 1.38420	QM 1.38420	WAM P.33113	QM 1.38420	QM 1.38420
Standard length (mm)	62.2	53.0	47.6	47.2	42.5	39.5	36.2
Sex	male	female	male	male	male	female	female
Body depth	24.2	23.8	25.2	25.0	24.0	24.5	25.3
Body width	14.1	14.7	13.2	13.7	14.8	14.6	13.8
Head length	28.7	28.5	29.2	30.3	30.6	30.4	30.5
Snout length	7.4	7.1	7.0	6.8	7.0	6.8	7.3
Orbit diameter	7.6	7.9	8.5	8.7	9.0	9.0	9.6
Interorbital width	8.8	8.6	8.9	9.2	9.5	9.5	9.7
Upper-jaw length	12.3	12.2	13.0	13.4	13.5	12.8	13.5
Caudal-peduncle depth	10.7	10.7	11.5	11.6	11.8	11.0	10.9
Caudal-peduncle length	24.2	24.5	25.2	25.0	25.0	25.1	24.0
Predorsal length	25.8	26.3	25.2	26.0	26.7	26.6	27.8
Preanal length	57.8	59.8	59.5	59.7	57.4	59.9	58.7
Prepelvic length	29.0	27.9	28.5	28.7	27.8	27.7	27.6
Dorsal-fin base	60.5	60.2	60.5	60.3	60.5	60.8	58.7
First dorsal spine	9.0	7.5	9.2	9.2	8.7	7.7	7.9
Second dorsal spine	15.2	9.7	16.3	15.0	14.9	10.1	10.1
Longest dorsal spine	30.4	13.2	31.0	31.3	27.4	13.7	13.0
Longest dorsal ray	19.3	12.2	18.8	19.1	19.1	12.9	13.1
Anal-fin base	17.7	17.3	16.8	16.5	17.8	16.8	17.7
First anal spine	4.7	4.5	4.4	4.6	4.7	5.1	5.2
Third anal spine	9.5	8.2	9.3	9.5	9.6	8.8	9.1
Longest anal ray	14.4	13.0	12.6	13.7	14.4	15.2	13.3
Caudal-fin length	31.8	27.0	34.7	35.2	35.8	27.7	28.3
Caudal concavity	21.4	13.7	17.6	22.5	24.0	12.8	13.9
Pectoral-fin length	25.7	25.2	25.2	25.4	25.9	26.2	25.7
Pelvic-spine length	12.9	13.3	12.7	12.1	13.5	13.4	13.8
Pelvic-fin length	22.9	20.8	23.0	23.4	23.5	20.8	22.1

35.8% SL; no black band in soft portion of dorsal fin; a series of indistinct dark bars of unequal width in middle third of standard length, none with pale margins; colour in life light red, the scale centres pale, the dark bars reddish brown; an oblique, pale-edged, brownish orange band from snout through eye and across cheek; pelvic fins black with red rays; remaining fins pink to yellowish. Largest specimen, 62.2 mm SL.

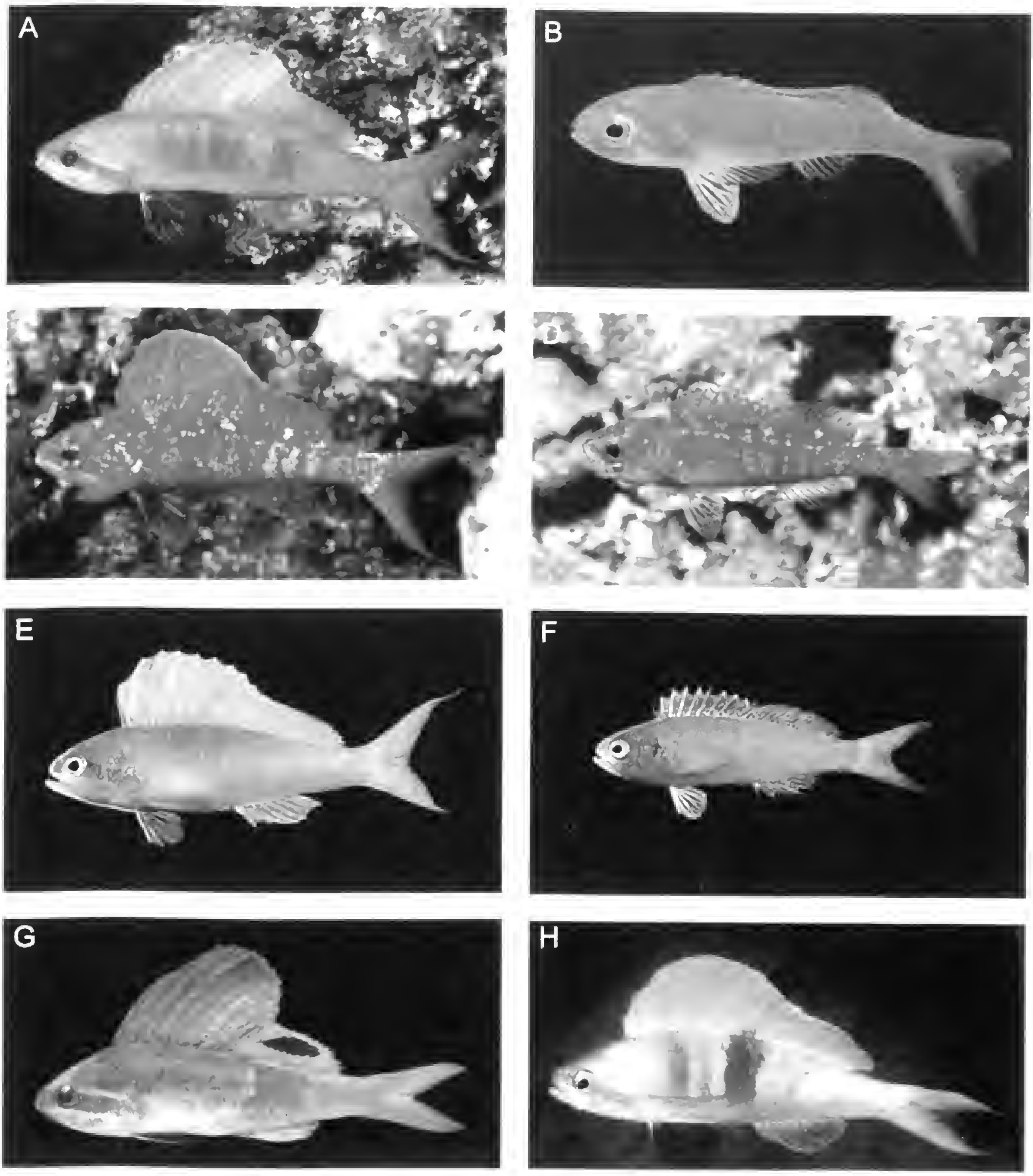
Description. Dorsal-fin rays X,16, the first 3 (3–6) soft rays unbranched, the last branched to base; anal-fin rays III,7, all soft rays branched; pectoral-fin rays 19 (19–21, only one of 11 paratypes with 21), the rays branched except upper two and lowermost; pelvic rays I,5, all soft rays branched; principal caudal-fin rays 15, the middle 13 branched, upper and lower procurrent caudal-fin rays 12, the posterior three segmented; lateral-line scales 57 (51–59); scales above lateral line to middle of spinous portion of dorsal fin 3.5; scales below lateral line to origin of anal fin 15; lowest count of circumpeduncular scales 28; gill rakers 9 + 24 (9 + 23–24, five of 11 with 24); pseudobranchial filaments of holotype 15; vertebrae 10 + 16; supraneural (predorsal) bones 2, projecting toward first neural spine; first two dorsal spines close together, associated with first dorsal pterygiophore, in space between first two neural spines; pterygiophores of third and fourth dorsal spines in space between second and third neural spines; remaining pterygiophores one on one for each vertebra.

Body elongate, the depth 4.15 (3.95–4.2) in SL; body compressed, the width a little more than one-half body depth, 1.95 (1.95–2.0) in HL; snout length 3.9 (4.0–4.5) in HL; eye diameter 3.8 (3.2–3.6) in HL; posterior half of orbit with 14 small fleshy papillae; interorbital space convex, the least fleshy width 3.25 (3.25–3.4) in HL; caudal-peduncle depth 2.7 (2.6–2.85) in HL; caudal-peduncle length 1.2 (1.15-1.25) in HL.

Mouth moderately large, the maxilla reaching slightly posterior to middle of eye, the upper-jaw length 2.35 (2.25–2.4) in HL mouth terminal and moderately oblique, forming an angle of about 40° to horizontal axis of body; posterior end of maxilla truncate, the upper corner rounded; front of upper jaw with a pair of stout, blunt, forward-projecting, conical teeth (double on one side of holotype), about one-fourth pupil diameter in length, separated by an indented symphyseal gap of one-half pupil diameter; side of upper jaw with a row of 16 small, slender, conical teeth, progressively shorter posteriorly, the tips not reaching edge of upper lip; lower jaw with a pair of stout, very blunt, canine teeth that project laterally as much as anteriorly, and fit medially to upper canine teeth when jaws closed; side of lower jaw with a row of 16 teeth, more slender than upper teeth; anterior teeth of lower jaw retrorse and progressively larger to eighth, which is recurved; remaining teeth more slender, near-vertical, and unevenly spaced; no teeth on vomer or palatines; tongue thin and leaf-like with sharply pointed tip, the upper surface with small papillae. Gill rakers long and slender, the longest at angle three-fourths orbit diameter.

Anterior nostril a short fleshy tubule, the rim higher posteriorly, about three-fourths pupil diameter before centre of eye; posterior nostril ovate, without a rim, about 1.5 anterior nostril diameters dorsoposterior to anterior nostril.

FIG. 1. A, *Rabaulichthys squirei*, holotype, QM I.38237, male, 62.2 mm SL, Flinders Reef, Coral Sea (F. Walsh). B, paratype, immature female, 35.0 mm SL, Flora Reef, Coral Sea (F. Walsh). C, paratype, WAM P.33113, male, 42.5 mm SL, Flora Reef, stress colour pattern (F. Walsh); D, paratype, QM I.38420, female, 36.2 mm SL, Flora Reef, stress colour pattern (F. Walsh); E, *R. altipinnis*, holotype, WAM P.28179, male, 45.5 mm SL, New Britain (G.R. Allen); F, *R. altipinnis*, paratype, WAM P.28280, female, 38.6 mm SL, New Britain (G.R. Allen). G, *R. stigmaticus*, male, Sri Lanka (R. Pethiyagoda); H, *R. suzukii*, male, Suruga Bay, Japan (A. Mishiku).


A
B
E
F
G
H

Opercle with three small flat spines, the middle one largest and most posterior; opercular membrane extending a spine's length beyond tip of middle spine; posterior edge of preopercle of holotype with 45 serrae, progressively larger, in general, ventrally, with only five small serrae continuing on ventral edge (largest paratype with 34 serrae posteriorly on preopercle, and smallest paratype with 29).

Scales coarsely ctenoid, less so ventrally, and cycloid on abdomen before anus; head fully scaled, including maxilla, except a narrow zone around orbit that is broader anteriorly to include nostrils; scales dorsally on snout progressively smaller and more embedded anteriorly, the extreme front naked; no scales on dorsal and anal fins; scales on caudal fin extending nearly to posterior margin; scales present on about basal one-third to two-fifths of pectoral fins; pelvic fins with a pointed, midventral, scaly process that extends two-thirds length of pelvic spine.

Lateral-line ascending in a straight line to 3.5 scale rows below base of fifth dorsal spine, then following contour of back to base of caudal fin. Pores of cephalic lateral-line system small. Those apparent are: dorsally at front of snout, above posterior nostril, one on each side in interorbital, and as a series of very small pores around orbit, ending in pore below anterior nostril; 11 pores in preopercular-mandibular series.

Origin of dorsal fin slightly anterior to upper end of gill opening, the predorsal length 3.9 (3.6–3.85) in SL. Dorsal-fin spines very slender and flexible; first spine 3.2 (3.2–3.95) in HL; second spine 1.9 (1.8–2.05) in HL in males, (2.95–3.0) in females; fifth spine longest, longer than HL in males, 3.3 (3.2–3.5) in SL, and (7.3–7.7) in females; first soft ray longest, 1.5 (1.55–1.6) in HL in males, (2.15–2.3) in females. First anal-fin spine 6.1 (5.9–6.6) in HL; second spine notably thicker than third spine, but slightly shorter; third spine 3.0 (3.1–3.5) in HL; second soft ray longest, 2.0 (2.0–2.3) in HL. Caudal fin lunate, its length in males 3.15 (2.8–2.9) in SL, in females (3.5-3.7) in SL; caudal concavity in males 1.35 (1.25–1.65) in HL, in females (1.15–1.2) in HL. Pectoral fins pointed, the middle rays longest, 1.1 (1.15–1.2) in HL. Pelvic spine 2.2 (2.15–2.5) in HL; third soft ray longest, 1.15 (1.25–1.3) in HL in males, (1.35–1.45) in females.

Colour of holotype in alcohol pale yellowish with four dusky bars on side of body, about one-fourth of their length above lateral line; first dark bar a double bar, the third bar about twice as broad as others and darker anteriorly; occipital region dusky; pelvic fins with pale grey rays and blackish membranes; remaining fins with pale lavender-grey rays and translucent pale yellowish membranes.

Colour of holotype in life as in Fig. 1A. The colour of paratypes is shown in Fig. 1B–D. The darker red and more strongly barred pattern of the male and female of Figs. C and D are stress colouration.

Remarks. The genus *Rabaulichthys* is currently represented by four described species from widely separated localities of the Indo-Pacific region: Maldive Islands and Sri Lanka, New Britain, Japan, and with the description of *R. squirei*, reefs of the Coral Sea off Queensland.

All four species share the same fin-ray counts, and any difference in the number of lateral-line scales will be modal at best. Among the meristic characters, only the lower-limb gill-raker count provides a slight separation of the type species, *R. altipinnis*, from the remaining three species. The salient morphological difference is in the more slender body of *R. squirei*, 23.8–25.3% SL, compared to 25.5–29.7% SL for the others. Although there is a sharing of salient features of colour pattern, red to pink overall, with an oblique, pale-edged, brownish orange band from the eye across the cheek, and predominantly black pelvic fins in the male, some colour differences are evident from a comparison of the images of Fig. 1.

The species of *Rabaulichthys* form small aggregations that feed on zooplankton above the substratum. They are generally found over open stretches of coral rubble, and therefore avoid the many predators of coral reefs. Because of their small size, they readily take shelter in the rubble. The paucity of specimens of this genus can be partly explained by this habitat, which is not often visited by scubadivers, whether sport divers or aquarium fish collectors.

Our first two specimens of *R. squirei*, the 62.2-mm male holotype and the 53.0-mm female paratype, were collected from Flinders Reef in 54 m. Our next 10 specimens, which include males that measured 35.0–47.6 mm SL, were collected in 6–9 m at Flora Reef. In view of the difference in size of the specimens, the different depth of the two collections, and the different localities, we wondered if the fish might represent two different species. The collectors assured us they are the same, explaining that the species is generally larger in deeper water. We could find no differences in colour or morphology in specimens from the two localities.

In addition to Flinders Reef and Flora Reef, this species has been seen at Holmes Reef (16°43′S, 147°55′E) in about 55 m, where thousands occur over a very large expanse of nearly flat rubble bottom. They swim together in small groups, often as only two or three individuals, and feed from 1–3 m above the substratum. In shallower water, this species sometimes mixes with aggregations of other anthiine fishes, especially *Pseudanthias dispar* (Herre), and is easily overlooked.

Mature males of all the species of *Rabaulichthys* have the spinous portion of the dorsal fin greatly elevated, and as expected, display it fully erect during courtship. The first species of the genus was named *R. altipinnis* for this feature. Ironically, it has the lowest spinous dorsal fin of the four known species. Mature males also have longer and more lunate caudal fins and longer pelvic fins than females (see Table 1).

Immature males and females of *Rabaulichthys squirei* are morphologically indistinguishable, but black pigment develops in the pelvic fins of the males before the dorsal spines become longer.

ACKNOWLEDGMENTS

We thank foremost Cadel and Lyle Squire and Tim Bennett for their special effort to collect this elusive species for us. We are also very grateful to Gerald R. Allen, Rohan Pethiyagoda, and Akihiko Mishiku (via Hiroshi Senou) for providing photographs of species of *Rabaulichthys*. The photograph of the male of *R. suzukii* is filed as KPM-NR 34642 in the image Database of Fishes of the Kanagawa Prefectural Museum of Natural History. Thanks are also due Loreen R. O'Hara of the Bishop Museum for x-rays, and Helen A. Randall for review of the manuscript.

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A putative hybrid of the Murray Crayfish, *Euastacus armatus* (Crustacea: Decapoda: Parastacidae)

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Citation: Street, D., Edney, G., Rowe, D. & Lawler, S.H. 2010 03 15. A putative hybrid of the Murray Crayfish, *Euastacus armatus*, (Crustacea: Decapoda: Parastacidae). *Memoirs of the Queensland Museum – Nature* 55(1): 213-224. Brisbane. ISSN 0079-8835. Accepted: June 2009

ABSTRACT

An unusual population of freshwater crayfish of the genus *Euastacus* found in the East Buffalo River, Victoria, is morphologically distinguishable from other populations, and in particular has a marbled or camouflage pattern on the carapace. The cheliped dactylar spine counts and the number of zygocardiac teeth anterior to the ventral ear of the zygocardiac ossicle (TAP) are somewhat reduced but these values overlap with the range of the most similar species (*E. armatus*). Genetic sequences from the CO1 and 16S mitochondrial DNA regions were also undertaken, and the results indicated that these animals may represent an aberrant population of *E. armatus* (the Murray Crayfish) or perhaps a hybrid between *E. armatus* and *E. woiwuru*, two species that are found downstream and upstream, respectively, of the population investigated. The conservation status of the population remains unclear. ❒ *Decapoda, Parastacidae, mitochondrial DNA, Buffalo River, conservation, Murray Cray, hybrid.*

Australian freshwater crayfish are an ancient and diverse group that are increasingly in need of conservation (Horwitz 1990a; Merrick 1997; O'Brien 2007). Spiny freshwater crayfishes of the genus *Euastacus* are found on the east coast of Australia, from the Great Dividing Range in Victoria to isolated mountains in northern Queensland (Clark 1941; Morgan 1986, 1988, 1997). New species have recently been described from north-eastern New South Wales (Coughran 2002, 2005). Most species in the genus are considered short-range endemics (Harvey 2002), and looking at a map of their distributions (eg. Shull et al. 2005) makes it easy to see why; *Euastacus* species are usually limited to a single catchment or mountain top. They are most commonly found in cold, clear mountain streams and rivers, and their preferred habitat may be at risk due to climate change.

The Murray Cray, *Euastacus armatus* (von Martens 1866), has the widest distribution in the genus, being found in both the Murray and Murrumbidgee Rivers and their tributaries (McCarthy 2005; Gilligan et al. 2007). The species is considered to be remarkably invariant morphologically, even across its broad range (Morgan 1986).

Euastacus woiwuru (Morgan 1986) is a small species which occurs on both sides of the Great Dividing Range in Victoria. This species is found in the Dandenong ranges near Melbourne, as well as in central and northern Victoria. Its most closely related species is *Euastacus kershawi* (Smith 1912),

FIG. 1. A, the marbled *Euastacus* and B, *E. armatus*, both found at Schultz Track on the East Buffalo River.

the Gippsland spiny crayfish (Shull *et al.* 2005). Both *E. armatus* and *E. woiwuru* are found in the Buffalo River in northeast Victoria.

In 2002 we visited Dandongadale, on the Buffalo River near the junction of the Rose River, in order to recollect *Euastacus woiwuru* that had first been collected at that locality by P..Horwitz in 1982 (Morgan 1986). When we searched the area this time we could only find *E. armatus*. We continued to search upstream and found an unusual population of crayfish at Schultz Track in 2002 with a marbled carapace (Fig. 1). Further searches of the Buffalo River were interrupted by the bushfires of 2003, which closed some roads for 18 months. When we were able to return to the site, it had been altered by bulldozers and the water was affected by heavy erosion and ash from the fire. We were unable to find any crayfish at that time. In 2006 the fires came again, with heavy fire-fighting taking place near Schultz Track. When the roads opened again in 2007, we were finally able to collect a number of crayfish at Schultz Track and upstream of the site. We were also thus able to determine that the marbled population of *Euastacus* at the Schultz Track site actually occurred at the boundary between *E. armatus* and *E. woiwuru* populations.

The marbled *Euastacus* at Schultz Track have a distinctive colour pattern on the carapace (Fig. 1), and a few other characters that differ from the other spiny crayfish species in the river. We originally misidentified these crayfish as *Euastacus crassus* (Riek 1969) and included the DNA in a large phylogeny of *Euastacus* (specimen number KC2654 in Shull et al. 2005), however, its position on the phylogeny showed clearly that it was not *E. crassus* (Shull et al. 2005). The specimen was then sent to Dr John Short of the Queensland Museum, who said he believed it to be a new species (pers. com.). As such it was listed as an undescribed species in a recent review of the conservation status of Victorian freshwater crayfish (O'Brien 2007).

For measures to be invoked toward the management of crayfish populations, species have to be recognised as threatened and in need of protection (Merrick 1997). The conservation status of the unknown crayfish at Schultz Track could not be clarified until its taxonomic status was resolved. Further collections were interrupted by road closures due to wild fires in 2003 and 2006. We were finally able to collect more individuals in 2007, and discovered that the site where we found the unusual population occurred on the species boundary between *E. armatus* and *E. woiwuru*. In this study we compare the unusual crayfish with other local *Euastacus* species using both morphological and genetic characters.

METHODS

Description of the study site. The Buffalo River flows north from the Barry Mountains and joins the Ovens River near Myrtleford, Victoria.

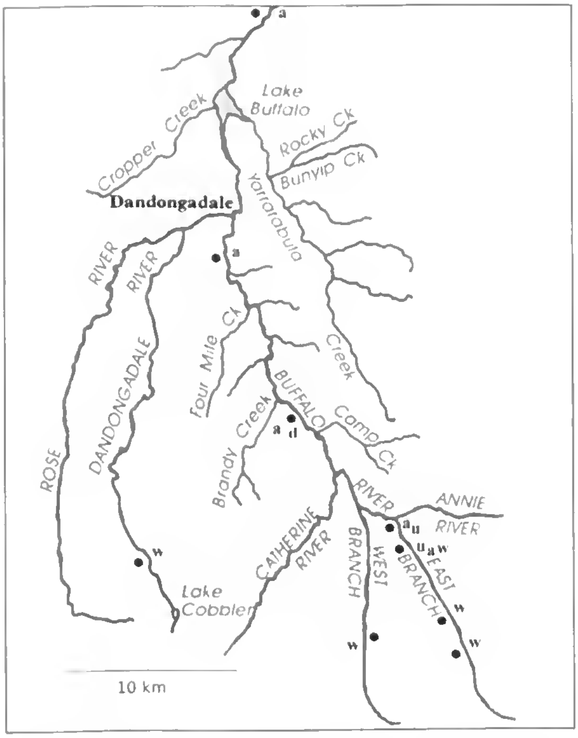

FIG. 2. A map of the Buffalo River showing the locations of Lake Buffalo and Dandongadale. The letters a, u and w indicate sites where *E. armatus*, the unknown (or marbled *Euastacus*) and *E woiwuru* have been collected, respectively. The letter d indicates *Cherax destructor.*

South of Lake Buffalo (a man-made reservoir), the Buffalo River is adjacent to pine plantations and cattle stations as well as State Forest and the Alpine National Park. Schultz Track, where we found the marbled *Euastacus*, is in the East Branch of the upper Buffalo River, about a kilometre above where the East and West Buffalo join (Fig. 2).

Collection of specimens. Specimens were collected using drop nets, bait nets, dip nets and by hand. Concerns for the conservation of this population meant that only two individuals could be retained from each site, so some animals were released after a portion of a leg was removed for DNA analysis. Because they can grow their legs back, this allowed us to get genetic samples without killing the animals. It did, however, limit the number of specimens available for taxonomic work. Some specimens were collected and released live without removing any legs. They were used to record the distribution of crayfish in the river (Fig. 2) but are not part of the material examined.

Material collected but not retained. *Cherax destructor:* Buffalo River, Manna Gum Campsite, VIC, (36°50′S, 146°39′E), 5 Mar. 2002, G. Edney, ♀.

Euastacus armatus. Buffalo River, 1.5 km upstream of Schultz Track, VIC (37°00′S, 146°49′E), 1 May 2007, G. Edney, 2 , ♀.

Taxonomic and morphometric examinations. A total of 45 crayfish were examined for 38 characteristics and 15 measurements that were turned into ratios following to Morgan (1986, 1987 1997). Twenty eight of these were *E. armatus*, seven were *E. woiwuru*, three were *E. crassus*, one was *E. reiki* and six were marbled *Euastacus* from the East Buffalo River. A Categorical Principal Component Analysis (CATPCA) was performed using SPSS version 15 to determine which characters best distinguished species.

Material examined for morphological characters. Currently in the research collection in the Department of Environmental Management and Ecology, but will be deposited in the Museum of Victoria after current ongoing research is completed.

Euastacus armatus. Tallangatta Creek, VIC, (36°17′S, 147°33′E), 20 Apr. 1995, S. Lawler, 5 ♂, ♀; Koetong Creek, VIC, (36°06′S, 147°27′E), 15 May 1995, G. Closs, ♂, 3 ♀♀; Hinces Creek, Burrowa Pines N.P., NSW, (36°05′S, 147°46′E), 26 April 1995, G. Closs & M. Shirley, 5 ♂, 4 ♀; Murray River, Barnawartha VIC, (36°02′S, 146°45′E), 11 July 1995, J. Sloan, ♀; King River, Oxley, VIC, (36°27′S, 146°22′E), 24 June 1995, M. Versteegen, ♂; Tumbarumba Creek, Tumbarumba, NSW, (35°51′S, 148°02′E), 9 July 1995, M. Versteegen, 2 ♂, ♀; Nug Nug, Buffalo River, VIC, (36°40′S, 146°41′E), 6 Dec. 1996, P. Suter, ♀; Ovens River, VIC, (36°02′S, 146°11′E), Sep. 1999, B. Holloway, ♀; Manna Gum Campsite, Buffalo River, VIC, (36°50′S, 146°39′E), 5 Mar. 2002, G. Edney, ♂; Schultz Track, East Buffalo River, VIC, (36°59′S, 146°48′E), 10 Mar. 2002, G. Edney, ♂.

Euastacus woiwuru. Rollason's Falls, Mt. Buffalo NP, VIC, (36°42'S, 146°47'E), 15 Feb. 2000, M. Chapman, ♂; Dobson's Creek, Fern Tree Gully, VIC, (37°52'S, 145°19'E), 23 Mar. 2002, K. Sewell, ♂; West Buffalo River, VIC, (37°02'S, 146°46'E), 23 Nov. 2006, G. Edney, 2 ♂; East Buffalo River, 1.5 km upstream of Schultz Track, VIC, (37°00'S, 146°49'E), 30 Apr. 2007, G. Edney, ♂; East Buffalo River, 4.5 km upstream of Schultz Track, VIC, (37°01'S, 146°49'E), 15 Jul. 2007, G. Edney, ♂; Dandongadale River, near Lake Cobbler, VIC, (37°01'S, 146°37'E), 30 Aug. 2007, G. Edney, ♀.

Euastacus rieki. Tumbarumba Creek, Tumbarumba, NSW, (35°51'S, 148°02'E), 9 July 1995, M. Versteegen, ♂;

Euastacus crassus. Basalt Hill, Falls Creek, VIC, 17 Jan. 2006, D. Heinze, ♂; Native Dog Flat, Buchan River, VIC, (36°90'S, 148°09'E), 26 Feb. 2000, G. Edney, ♂; Tributary of Big River, Dartmouth Dam, VIC, (36°39'S, 147°18'E), 26 Jan. 2007, G. Edney, ♀.

Marbled *Euastacus*. Schultz Track, East Buffalo River, VIC, (36°59'S, 146°48'E), 10 Mar. 2002, G. Edney, QMW 26596, KC2654, ♂; Schultz Track, East Buffalo River, VIC, (36°59'S, 146°48'E), 10 Mar. 2002, G. Edney, ♀; Schultz Track, East Buffalo River, VIC, (36°59'S, 146°48'E), 10 Jul. 2002, G. Edney, ♀; Schultz Track, East Buffalo River, VIC, (36°59'S, 146°48'E), 21 Apr. 2007, G. Edney & S. Lawler, ♀; Schultz Track, East Buffalo River, VIC, (36°59'S, 146°48'E), 22 Apr. 2007, G. Edney & S. Lawler, 2 ♀.

Genetic analysis. The mitochondrial genes COI and 16S were used because they have been used extensively to clarify taxonomy and examine evolutionary processes in freshwater crayfish (Crandall et al. 1995, 1999; Versteegen & Lawler, 1997; Lawler & Crandall 1998; Hughes & Hillyer 2003; Austin et al. 2003; Munasinghe et al. 2003; Shull et al. 2005; Gouws et al. 2006; Ponniah & Hughes 2004, 2006). These gene regions have been used to find cryptic species in other freshwater macroinvertebrates (Chenoweth & Hughes 2003; Baker et al. 2004).

DNA was extracted from tissue (usually gill or a bit of a leg) using guanidium iso-thiocyanate (GIT) buffer and a phenol-chloroform extraction as in Crandall et al. (1995). The DNA was resuspended in 100µl, two microlitres of which was used as the template for a polymerase chain reaction (PCR).

Two different PCR products were amplified from the mitochondrial genome: 720 base pairs of the cytochrome c oxidase subunit I (COI) and 503 base pairs of the 16S rRNA. COI was amplified using the LCO1490 and HCO2198 primers from Folmer et al. 1994. The 16S rRNA fragment was amplified using the 16sL and 1472 primers from Shull et al. 2005. A BioRad PTC-0200 DNA Engine Peltier Thermal Cycler was used to amplify the DNA, with details of the reaction mixtures and temperature profiles available from Street 2007. PCR products were sent to Macrogen Inc. (Seoul, Korea) for single extension DNA sequencing.

Material used for Mitochondrial DNA Amplification. *Euastacus armatus*. Arm1= Manna Gum Campsite, Buffalo River, VIC, (36°50'S, 146°39'E), 5 Mar. 2002, G. Edney, ♂; Arm2 = Ovens River, VIC, (36°02'S, 146°11'E), Sep. 1999, B. Holloway, ♀; Arm3 = Brad Betts Memorial, Yackandandah Creek, VIC, (36°20'S, 146°48'E), 29 Jun. 2007, G. Edney; Arm4 = Buffalo River, VIC, 10 Mar. 2002, G. Edney, QMW26582, KC2653.

Euastacus woiwuru. Woi1 = ♂; East Buffalo River, 1.5 km upstream of Schultz Track, VIC, (37°00'S, 146°49'E), 30 Apr. 2007, G. Edney, ♂; Woi2 = West Buffalo River, VIC, (37°02'S, 146°46'E), 23 Nov. 2006, G. Edney, ♂; Woi3 = East Buffalo River, 4.5 km upstream of Schultz Track, VIC, (37°01'S, 146°49'E), 15 Jul. 2007, G. Edney, ♂; Woi4 = Dobson's Creek, Fern Tree Gully, VIC, (37°52'S, 145°19'E), 23 Mar. 2002, K. Sewell, ♂; Dandongadale River, near Lake Cobbler, VIC, (37°01'S, 146°37'E), 30 Aug. 2007, G. Edney, ♀; Woi5 = West Buffalo River, VIC, (37°02'S, 146°46'E), 23 Nov. 2006, G. Edney, ♂.

Euastacus crassus. Cra1 = Native Dog Flat, Buchan River, VIC, (36°90'S, 148°09'E), 26 Feb. 2000, G. Edney, ♂; Cra2 = Native Dog Flat, Buchan River, VIC, (36°90'S, 148°09'E), 19 Mar. 2002, G. Edney, KC2649, ♂; Cra3 = Native Dog Flat, Buchan River, VIC, (36°90'S, 148°09'E), 20 Mar. 2002, G. Edney, KC2720. *Euastacus yarraensis*. Yar 1 = Love Creek, VIC, (38°48'S, 143°58'E), 1 Jan. 2004, K. Sewell & G. Edney, KC2831; Yar 2 = Cockatoo, VIC (37°94'S, 145°49'E) 21 Mar. 2002, KC2651.

Marbled *Euastacus*. Unk1 = Schultz Track, East Buffalo River, VIC, 10 Jul. 2002, G. Edney, ♀; Unk2 = Schultz Track, East Buffalo River, VIC, 10 Mar.

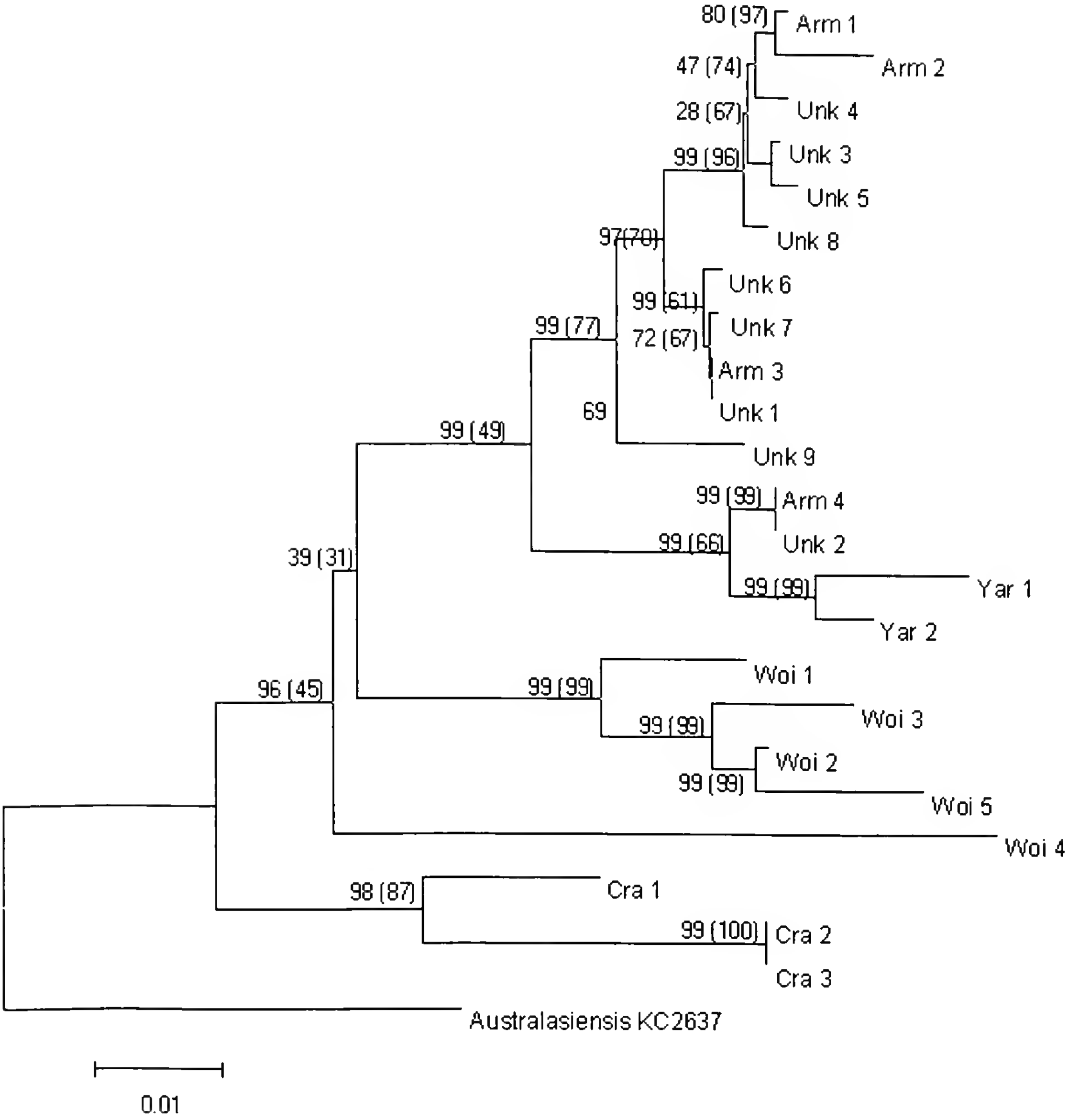

FIG. 3. Neighbour-joining consensus tree using 16S and COI mitochondrial DNA sequences. Interior branch test probabilities are shown on nodes with bootstrap values shown in parentheses, both using 100,000 replications. Arm = *E. armatus*, Unk = Marbled *Euastacus*, Woi = *E. woiwuru*, Yar = *E. yarraensis*, Cra = *E. crassus* and the outgroup is *Euastacus australasiensis*. For information on collection sites see methods section.

TABLE 1. Some morphological characters of the *Euastacus* of the Buffalo River, Victoria. The characters for *E. armatus* and *E. woiwuru* agree with Morgan (1986), who examined many more individuals.

	Marbled *Euastacus*	*E. armatus*	*E. woiwuru*
Number examined	6	28	7
TAP	4 – 5	5 – 7	7 – 9
Urocardiac Ridge	8	9 – 10	9 – 11
Marginal mesal dactylar spines	0 – 1	0 – 3	0 – 1
Dorsal mesal dactylar spines	0 – 5	0 – 3	2 – 5
Mesal carpal spines	2	2	3
Male cuticle partition	no	no	yes
Telsonic spines	yes	yes	no

2002, G. Edney, QMW 26596, KC2654, ♂; Unk3 = Schultz Track, East Buffalo River, VIC, 22 Apr. 2007, G. Edney & S. Lawler, ♀; Unk4 = East Buffalo River, 1.5 km upstream of Schultz Track, VIC, (37°00′S, 146°49′E), 30 Apr. 2007, G. Edney & D. Street (leg only); Unk5 = East Buffalo River, 1.5 km upstream of Schultz Track, VIC, 1 May 2007, G. Edney & D. Street (leg only); Unk6 = East Buffalo River, Schultz Track, VIC, 22 Apr. 2007, G. Edney & S. Lawler; Unk7 = East Buffalo River, Schultz Track, VIC, 22 Apr. 2007, G. Edney & D. Street (leg only); Unk8 = Schultz Track, East Buffalo River, VIC, (36°59′S, 146°48′E), 21 Apr. 2007, G. Edney & S. Lawler, ♀; Unk9 = Schultz Track, East Buffalo River, VIC, 3 July 2007, G. Edney & D. Street, (leg only).

Phylogeny construction. DNA sequences were aligned using Cluster W in the computer program MEGA Version 4.0 (Kumar et al., 2004; Tamura et al., 2007). Only specimens that were successfully sequenced for both mitochondrial gene regions were used for phylogeny construction. *Euastacus australasiensis* (KC2637) was used as an outgroup, and other sequences were included for comparison, including the marbled *Euastacus* KC2654, *E. armatus* KC2653, *E. crassus* KC2720 and *E. yarraensis* KC281 and KC 2651 (Shull et al. 2005).

A consensus tree for the two gene regions was constructed using the neighbour joining method in MEGA. Two different probabilities, the bootstrap and interior branch test, were measured for each node on the phylogeny (Fig. 3).

RESULTS

Distribution. We found a total of 10 crayfish in the Buffalo River that, while clearly belonging to the genus *Euastacus*, did not resemble any known species. Three of these 'marbled' *Euastacus* were collected in 2002 and seven in 2007. Four of the animals caught in 2007 were released on site after removing a portion of a leg for genetic analysis. All of these animals were found in a stretch of river only a few kilometres long in the East Buffalo River (Fig. 2).

Euastacus armatus are widely distributed in the Buffalo River below the lake, and in the Ovens River into which the Buffalo River empties. They were also found near Dandongadale (the locality), at Schultz Track, and 1.5 km upstream of Schultz Track, where they occurred in sympatry with *E. woiwuru*.

Euastacus woiwuru were found on top of Mount Buffalo, where they had not been previously recorded, but were not found near Dandongadale where they had been recorded in 1982 (Morgan 1986). They were also found at Schultz Track and 1.5 km, 4.5 km, and 6.8 km upstream from Schultz Track in the East Buffalo River. They were also found in the West Buffalo River and in the upper Dandongadale River, so their distribution is in the headwaters of the catchment (See Fig. 2). Both *E. armatus* and *E. woiwuru* are found in sympatry with the marbled *Euastacus* 1.5 km upstream of Schultz Track.

The common yabby, *Cherax destructor*, was found in the Buffalo River, 6 km south of Dandongadale (Fig. 2), and *Engaeus* burrows are common throughout the catchment. We have not dug up any burrows or actively sampled the burrowing crayfish, but the species is probably *Engaeus cymus* (Clark 1936) (Horwitz 1990b).

During the taxonomic examinations of old collections, we found another case of *Euastacus armatus* in sympatry with another species of *Euastacus*. A collection from a single site (Tumbarumba Creek, NSW in 1995) was found to contain both *E. armatus* and *Euastacus reiki* (Morgan 1997). These species both have white claws and similar spination, highlighting the degree to which different species can appear similar in this genus. One of the characters used to distinguish *E. reiki* from *E. armatus* is the TAP count.

Morphological examinations. A total of 45 *Euastacus* specimens were scored for 38 characteristics and 15 measurements that were turned into ratios according to Morgan (1986, 1987, 1997). Our ratios fell well within the range of Morgan's data for all the species examined, and hierarchical cluster analyses in SPSS grouped the animals into species clusters (Street 2007). The CATPCA test in SPSS produced a list of morphological characters that were most useful in differentiating these species of *Euastacus*. A shorter list emphasising the morphological differences in the Schultz Track population is shown in Table 1.

The characters used to distinguish the three *Euastacus* species were the male cuticle partition, telsonic spines, mesal carpal spines and the TAP (Morgan, 1986, 1997). The number of teeth anterior to the posterior margin of the zygocardiac ossicle ear, or TAP, is a morphological character that was described by Francois (1962), is considered to be a useful character for crayfish taxonomy (Growns & Richardson 1990) and has been used in the description of *Euastacus* species (Morgan 1986; 1988; 1997). The TAP of *E. armatus* is between 5 and 7, while the range of TAP in *E. woiwuru* is between 7 and 9 (Morgan 1986).

The Schultz Track population, or the marbled *Euastacus*, had TAPs at or below the range of *E. armatus*, with at least half of them having five teeth in one ear and four in the other. These assymetrical individuals were given a TAP score of 4.5, while somel individuals had four teeth in both ears, which is outside of the published range of *E. armatus* (Table 1).

All of the six marbled specimens examined for morphology were small, with occipital carapace lengths (OCLs) less than 44 (28, 28, 28, 29, 37 43). The larger ones had white on the tips of their claws. It is possible that they develop white claws as they grow larger. *E. armatus* also change from green or brown claws to white as they grow, but the size where this change occurs seems to vary between populations (pers. obs., SL).

Genetic analysis and phylogeny. Phylogenies constructed for the two mitochondrial DNA regions (16S and COI) produced the same topology. The consensus tree is shown in Fig. 3. The phylogeny shows all the marbled *Euastacus* in the same clade with *E. armatus*. According to the mitochondrial DNA phylogeny, the unusual *Euastacus* is not a separate species from *E. armatus*, however, DNA analysis using nuclear genes (Ji et al. 2003) may yet show that this population is different.

DISCUSSION

An unusual population of crayfish of the genus *Euastacus* was found in a very short stretch of river. This population is designated the marbled *Euastacus* in this paper, and its taxonomic status remains unclear. The location of this population between two different species (Fig. 2) suggests that it could be a hybrid.

Genetic sequences mitochondrial DNA genes 16S and COI were used to test the hypothesis of a hybrid zone. These genes were chosen because they have been used for many studies of speciation and population structure of Australian freshwater decapods (Crandall et al., 1995; Hughes and Hillyer, 2003; Chenoweth & Hughes, 2003; Shull et al., 2005; Schultz et al., 2007).

The use of the mitochondrial gene cytochrome oxidase (COI) to identify species is also known as barcoding (Mitchell 2008). Although it has been used to identify cryptic species in Crustacea (Witt et al. 2006) and in insect groups (Rubinoff & Sperling 2004; Hebert et al. 2004; Smith et al. 2006), there are also instances in which COI has been unable to distinguish between species (Meier et al. 2006; Hickerson et al. 2006; Whitworth et al. 2007). Nevertheless, some authors claim it is effective for measuring hybridisation events, defining hybrid zones and discovering cryptic species (Rubinoff & Holland 2005).

Failures to resolve species boundaries using mitochondrial genes are more likely when the species have recently diverged, or in cases of inter-specific hybridisation (Shaw 2002). Nelson et al. (2007) were able to identify nine species of blowflies using DNA barcoding, but misidentified the one hybrid specimen using this techinique.

Our data clearly separated known species of the genus *Euastacus*, with *E. armatus* and *E. woiwuru* forming well defined monophyletic groups (Fig. 3). The marbled *Euastacus* fell within the *E. armatus* clade using consensus sequences of the mitochondrial genes COI and 16S. This pattern is suggestive rather than conclusive, however, because mitochondrial DNA is inherited directly from the mother without undergoing recombination. If the mothers of the hybrids consistently belong to the species *E. armatus*, this pattern would still occur. Behavioural constraints could result in a bias during inter-specific matings, particularly if the animals involved have a consistent size difference. For example, we know that small males can mate with larger females, and the species *E. armatus* usually grow larger than *E. woiwuru* (Morgan 1986).

Some authors say that *E. armatus* is not found in sympatry with other members of its genus (Gilligan et al. 2007). This perception may be due to the lack of sampling in areas of potential overlap, because we have found *E. armatus* and *E. woiwuru* at the same site in the Buffalo River, and we also identified at least one site in New South Wales where *E. armatus* is found in sympatry with *E. rieki*. We did not recognise the sympatry at the time of collection (in 1995) because *E. rieki* had not yet been described (Morgan 1997). *Euastacus reiki* and *E. armatus* are so similar morphologically that we have to dissect the gastric mill to tell them apart, which makes them very hard to distinguish in the field.

Almost 30 years ago, *Euastacus woiwuru* were found near Dandongadale, but only Murray Crays (*E. armatus*) are found there now. *Euastacus woiwuru* are now found about 20 kms south of Dandongadale in the East and West branches of the Buffalo River. The apparent movement of the Murray Cray upstream could be explained by the alteration of habitats by human disturbance or by the warming of the river due to climate change or many years of drought. Either way, the change in distribution may indicate that the species boundary between *E. armatus* and *E. woiwuru* has been moving for decades. The fact that an unusual morphological variant is found at this boundary is highly suggestive of a hybrid zone. However, if they are hybrids, they do not appear to form a self sustaining breeding population, because both parent species are present at the localities where the marbled form is found.

Marbled *Euastacus* are morphologically distinct in their colouration and the fact that some of their TAPs (the number of teeth anterior to the posterior margin of the zygocardiac ossicle ear) are below the published range of *E. armatus* and *E. woiwuru*. Interestingly, Morgan states that the TAPs of *E. woiwuru* are generally lower in Murray River tributaries like the Buffalo River, and that a specimen collected at Dandongadale was unusual (Morgan 1986, p. 49). Perhaps this location, which is at the edge of the distribution of both species, contains some unique morphological variants.

The marbled *Euastacus* were all very small, with OCLs (occipital carapace length) below 44 mm. However, since the larger of the marbled *Euastacus* had white tips on their claws, it is possible that the marbled crays are a unique juvenile variant, and that these animals grow into adult Murray Crays with white claws and a uniformly coloured carapace. Normally, juvenile Murray Crays do not have the white claws that are a distinctive feature of the adults, but neither do they have a marbled pattern. The substrate at this site did not obviously differ from other stretches of the river where *E. armatus* juveniles do not show this marbled pattern, but it is possible that there is a yet to be identified environmental factor affecting their colour. Because our permit did not allow us to retain and raise these animals, we were unable to confirm the adult colouration of the marbled specimens.

Many threatening processes are controllable, but for measures to be invoked toward the management of crayfish populations, species have to be recognised as threatened and in need of protection (Merrick 1997). The sedentary nature of crayfish and limited gene flow between catchments (Fetzner & Crandall 2001; Gouin et al. 2006) makes them susceptible to over-fishing and habitat alteration (Merrick 1997; O'Brien 2007). The first step toward listing a population is to determine if it is different enough to be considered a conservation unit (Fraser & Bernatchez 2001).

Unique fauna are often found in unregulated headwater streams (Baker et al. 2004), and this study provides an example of an unusual population of spiny crayfish. The conservation status of this population needs to be clarified. The location is subject to several threatening processes. Cows are allowed to roam freely in and out of the river, and fires and fire control measures combined to significantly disturb the site in 2003 and 2006. Given the fire history of the area, we can expect reduced water flows in the catchment for decades.

Speciation is a slow process in this genus (Ponniah & Hughes 2006). If we have found an unusual population of *E. armatus*, it could still be different enough to be deserving of conservation. On the other hand, finding this crayfish at the boundary of two *Euastacus* species means that the possibility of hybridisation must be taken seriously, particularly since introgression is a possibility (Ballard & Whitlock 2004; Funk & Omland 2003; Shaw 2002).

We are planning to sequence nuclear genes using ITS primers (Ji et al. 2003) and will continue to make field observations. Investigation of freshwater crayfish species boundaries in the Buffalo River may enlighten us about the ecology and evolution of Australian spiny freshwater crayfish.

ACKNOWLEDGEMENTS

This research was supported by a series of permits from Victorian Fisheries (RP906, RP562, RP751), New South Wales Fisheries (FSP/CW/135), Victorian Department of Sustainability and Environment (10002702 and 10004059) and by animal ethics permits from La Trobe University (AEC Invert/03-4(W) and AEC07/21(W)).

We would like to thank Christine Street, Susan Street, Robbie Schaeffer, Kim Sewell, Ryan

Sewell, David Blair, Phil Suter, Ben Holloway, Mick Chapman, Gerry Closs, Michael Shirley, Mardi Versteegen, Dean Heinze and Dale McNeil for help with field work and collections. We would also like to thank Warren Paul for assistance with statistical analyses, Leo McGuire for the use of his cabin, and Peter Davies for comments on an earlier version of this manuscript.

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New records of the Japanese devilray *Mobula japanica* (Müller & Henle 1841) for Australian waters

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Citation: Townsend, K.A. & Kyne, P.M. 2010 03 15. New records of the Japanese devilray *Mobula japanica* (Müller & Henle 1841) for Australian waters. *Memoirs of the Queensland Museum — Nature* 55(1): 225-230. Brisbane. ISSN 0079-8835. Accepted: 2 February 2009.

ABSTRACT

New Australian records of the Japanese devilray *Mobula japanica* (Müller & Henle 1841) are documented from photographs taken at Ribbon Reefs, Fraser Island, off Noosa and off Southport, Qld, and from a specimen beach-washed on North Stradbroke Island, Qld. This specimen, measuring 2224 mm disc width, was located on 02/09/2007 and is the first sexually mature male recorded in Australian waters. Morphometrics for this specimen are generally consistent with previously published accounts. Where differences exist, these are marginal. Within Australian waters, *M. japanica* has thus far only been recorded from the east coast, within the latitudinal range 14°57′–32°59′S. The recent increase in records suggests the species is more common in Australian waters than previously thought. ❒ *Myliobatoidei, Mobulidae, North Stradbroke Island.*

The Japanese devilray *Mobula japanica* (Müller & Henle 1841) (Rajiformes: Myliobatoidei: Mobulidae) is thought to be circumglobal in warm temperate and tropical waters of the Atlantic, Pacific and Indian Oceans (Last & Stevens 1994). However, its detailed distribution, along with its biology is poorly-known, and it was previously thought to be rare, or at least rarely documented in Australian waters (Kyne et al. 2005).

The family Mobulidae is comprised of two genera: *Manta* Bancroft, 1829 and *Mobula* Rafinesque, 1810, separated by the position of the mouth; at end of snout tip in *Manta*, and ventral on the head and posterior of the snout tip in *Mobula*. There are nine recognised valid species of *Mobula* worldwide (Notarbartolo-di-Sciara 1987). Distinguishing characters of *Mobula japanica* include: elliptical spiracles situated dorsal to the level of the pectoral fins, white tip to dorsal fin, very long tail (when unbroken) and the presence of a caudal spine (Notarbartolo-di-Sciara 1987; Last & Stevens 1994). This latter character is shared only with *Mobula mobular* (Bonnaterre 1788), which is possibly endemic to the Mediterranean, although the systematics concerning the relationship between *M. japanica* and *M. mobular* remain unresolved (Notarbartolo-di-Sciara 1987).

Four species of mobulids have been confirmed for Australian waters. *Manta birostris* (Donndorff 1798) and *Mobula eregoodootenkee* Garman 1913 are reasonably common in tropical waters, while *Mobula thurstoni* (Lloyd 1908) is known from a single record off Mackay, Qld, and *Mobula japanica* from two previous specimens from the east coast (Last & Stevens 1994; Kyne et al. 2005).

Mobula japanica is a medium to large devilray, attaining a disc width (DW) of at least 3100 mm (Paulin et al. 1982).

The first recorded Australian specimen of *M. japanica* was a 1880 mm DW individual collected by net fisherman, inshore Lake Macquarie, NSW (32°59'S, 151°35'E) on 04/04/1968 (AMSIB.8021). The sex is unknown, as only the head was lodged in the AMS collection, however, from accompanying original photographs it appears to be female (Kyne et al. 2005). The second specimen was a 1088 mm DW immature male found beach-washed on Eurong Beach, Fraser Island, Qld (25°31'S, 153°08'E) on 17/08/2000 (QMI.33855) (Kyne et al. 2005). This paper presents information on a number of new records for Australian waters, in particular a beach-washed specimen from North Stradbroke Island, Qld.

METHODS

All records were identified using Notarbartolo-di-Sciara (1987) and Last & Stevens (1994). The North Stradbroke Island specimen was reportedly alive when first located by a member of the public. Upon collection it was dead but very fresh. Morphometrics and photographs were taken of the fresh specimen on arrival at the Moreton Bay Research Station, Dunwich. Thirty-four morphometrics were recorded, including 29 following the methodology of Notarbartolo-di-Sciara (1987), and additional measurements of the claspers and caudal spine. Morphometrics were compared to previously published results from the E Pacific (Notarbartolo-di-Sciara 1987) and the Fraser Island specimen (Kyne et al. 2005). The following abbreviations are used for institutions: AMS, Australian Museum, Sydney; QM, Queensland Museum, Brisbane.

Following fresh examination, the specimen was transported to the QM. Space restrictions precluded fixation and storage of the whole animal, however, a fibreglass cast of the fresh whole specimen was made for public display at the QM. The head (including cephalic fins) and region posterior from the dorsal fin (including dorsal fin, pelvic fins, claspers, tail and caudal spine) were dissected from the whole specimen and lodged in the QM Ichthyological Collection. Some sections of gill arches were also preserved, as well as liver and muscle tissue samples in alcohol for possible future DNA analysis.

Photographs were obtained of individuals from a number of locations along the eat coast of Qld: Fraser Island (beach-washed specimen; individual not retained), off Southport (live sightings), Ribbon Reefs (live sighting) and off Noosa (fisheries bycatch; specimens not retained).

RESULTS AND DISCUSSION

A 2224 mm DW mature male *M. japanica* (QMI.38137) (Fig. 1A-D) was beach-washed on Flinders Beach, North Stradbroke Island, Qld, Australia (27°24'59"S, 153°29'12"E) on 02/09/2007. Table 1 presents morphometrics for the specimen. For comparison, those from the second Australian specimen (Fraser Island, Qld; QMI.33855; Kyne et al. 2005) and the range of values for the 29 measurements given in Notarbartolo-di-Sciara (1987) for specimens from the E Pacific are also included.

The measured size of the specimen (2224 mm DW) is within the reported maximum for the species, which is at least 3100 mm DW (Paulin et al. 1982; Last & Stevens 1994). White et al. (2006) estimated size at maturity for male *M. japanica* from eastern Indonesian waters (DW_{50} with confidence intervals) as 2016 mm (1984–2050 mm) DW. The North Stradbroke specimen represents the only known mature male of the Australian records.

Over one third of the 29 morphometric measurements were outside of the range reported by Notarbartolo-di-Sciara (1987) for specimens from the E Pacific (Table 1). Nine of the 11 of these were above the previously published range, while

TABLE 1. Proportional dimensions as thousandths of disc width for *Mobula japanica* from North Stradbroke (QMI.38137) and Fraser Islands (QMI.33855; Kyne et al. 2005), Qld, Australia, and those given by Notarbartolo-di-Sciara (1987). * denotes proportional measurements which fall outside the previously reported range.

	QMI.38137	QMI.33855	Notarbartolo-di-Sciara (1987) Range
Location	North Sradbroke Is., Qld	Fraser Is., Qld	Eastern Pacific
1. Disc width (mm)	2224	1088	1316–2259
2. Disc length	544*	445	448–531
3. Anterior projection	354	310	321–379
4. Rostrum to pelvic fin	560	453	457–561
5. Predorsal length	461*	373	373–441
6. Dorsal fin base	42	42	39–55
7. Dorsal fin height	45	34	35–47
8. Precloacal distance	441*	388	367–430
9. Tail length	517*	1245	641–1075
10. 1st gill opening length	56	50	47–57
11. 2nd gill opening length	60	51	51–62
12. 3rd gill opening length	61	53	49–61
13. 4th gill opening length	58	48	44–58
14. 5th gill opening length	44	36	34–44
15. 1st interbranchial distance	122*	90	108–119
16. 5th interbranchial distance	56	41	46–69
17. Rostrum to 1st gill openings	122*	105	103–121
18. Rostrum to 5th gill openings	225*	190	193–221
19. Pelvic fin length	123	86	108–131
20. Cephalic fin length	128*	107	117–127
21. Cephalic fin width	34*	49	52–68
22. Eyeball diameter	21	23	21–26
23. Cranial width	188*	161	148–169
24. Preoral length	58*	38	38–43
25. Head length	153	138	132–163
26. Mouth width	124	103	110–126
27. Internarial distance	108	98	99–110
28. Upper toothband length	90	80	83–94
29. Lower toothband length	90	77	81–96
Clasper length inner	110	38	-
Clasper length outer	41	13	-
Clasper width	22	6	-
Dorsal spine length	36	48	-
Ventral spine length	10	17	-

two were below (tail length and cephalic fin width). The tail was damaged, explaining the lower range for that value. Kyne et al. (2005) noted the unreliability of this as a diagnostic feature due to its susceptibility to damage. The following measurements associated with the head were all above the previously published range: cranial width, preoral length and cephalic fin length, as were disc length and the predorsal length (Table 1). However, with the exception of tail length, all differences were marginal (0.1 to 2.0% of DW), and may be related to either measuring technique (although the present study followed Notarbartolo-di-Sciara (1987) very closely), or a limited number of replicates from the original study (n=19; Notarbartolo-di-Sciara, 1987). Alternatively, some differences may reflect regional or population-level variability. Genetic analysis may be able to shed some light on the latter possibility.

Table 2 summaries the 13 known records of *M. japanica* for Australia. In addition to the North Stradbroke Island specimen detailed above, a number of photographs of *M. japanica* were obtained from Qld waters. Ian Banks filmed an individual at 6 m depth off Main Beach, Gold Coast (27°58'S, 153°25'E) on 13/02/2006 and later filmed two individuals nearby (27°56'S, 153°25'E) on 11/05/2008 (still photographs were provided from the video footage). On 03/10/2007, Julie Meles photographed a beach-washed individual 1 km north of McLaughlan Rocks on Fraser Island (25°19'S, 153°13'E). The sex of the specimen was not noted, but it was estimated to measure 3100 mm DW (information provided by Jeff Johnson, QM and Ivan Thrash, QNPWS). Chris Witty photographed an individual on a reef between Ribbon Reef #9 and #10 on the Great Barrier Reef (14°57'S, 145°40'E) at ~10-15 m depth on 01/01/2008 (a total of four devilrays were sighted, but only one individual could be identified as *M. japanica*) (information provided by Qamar Schuyler, Undersea Explorer). A professional fisher caught five specimens from 670 to 1060 mm DW by gill net at 7-12 m depth on ~20/05/2008 just north of the Noosa River mouth (26°23'S, 153°05'E). All were released and sex was not recorded (information provided by Jeff Johnson, QM and S. McCulloch, QDPI & F).

TABLE 2. Summary of Australian records of *Mobula japanica*.

Record & specimen no. (if applicable)	Date of record	Location	Co-ordinates	Collection method	Reference/source
1. AMSIB.8021	04 Apr 1968	Lake Macquarie, NSW	32°59'S, 151°35'E	Estuarine net bycatch	Kyne et al. (2005)
2. QMI.33855	17 Aug 2000	Fraser Island, QLD	25°31'S, 153°08'E	Beach-washed	Kyne et al. (2005)
3.	13 Feb 2006	Off Main Beach, Gold Coast, QLD	27°58'S, 153°25'E	Live sighting (photographs)	I. Banks
4. QMI.38137	02 Sep 2007	North Stradbroke Island, QLD	27°25'S, 153°29'E	Beach-washed	Present study
5.	03 Oct 2007	Fraser Island, QLD	25°19'S, 153°13'E	Beach-washed (photographs)	J. Meles & I. Thrash
6.	01 Jan 2008	Ribbon Reefs, Great Barrier Reef, QLD	14°57'S, 145°40'E	Live sighting (photographs)	C. Witty & Q. Schuyler (Undersea Explorer)
7-8.	11 May 2008	Gold Coast Seaway, QLD	27°56'S, 153°25'E	Live sighting (photographs)	I. Banks
9-13.	~20 May 2008	Off Noosa, Sunshine Coast, QLD	26°23'S, 153°05'E	Gillnet bycatch (photographs)	S. McCulloch (QDPI&F)

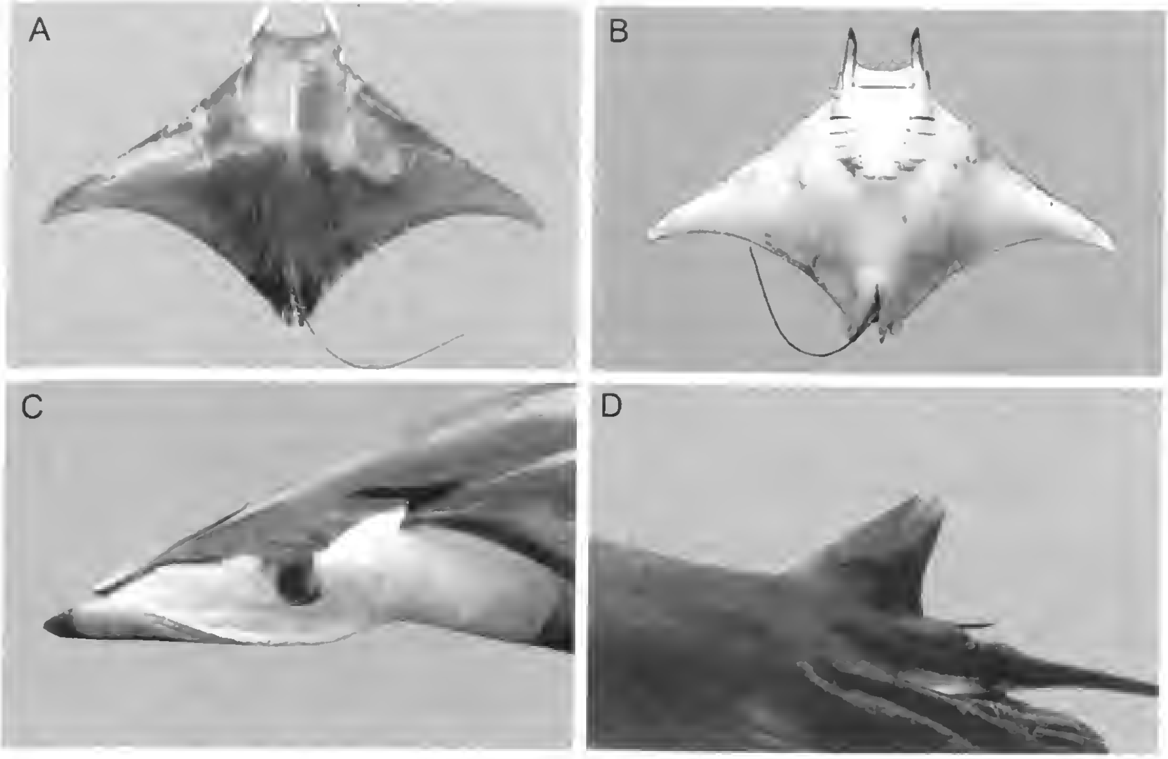

FIG. 1. *Mobula japonica*, QMI.38137, 2224 mm DW. A, Whole animal, dorsal view. B, Whole animal, ventral view. C, Head, lateral view. D, Dorsal fin, caudal spine and tail base, lateral view. (Photos: P. Fugelli).

Mobula japanica is the only devilray species found within the Indo-Pacific which possesses a caudal spine. However, Notarbartolo-di-Sciara (1987) noted that the caudal spine can occasionally be missing in the species (2.5% of specimens examined). Furthermore, for *M. japanica* specimens from New Zealand waters, Paulin et al. (1982) noted that in many of the individuals examined, the caudal spine was very small or broken. As such, when identifying specimens in the field, the absence of a caudal spine does not necessarily discount *M. japanica*. Diagnostic characters specified in Notarbartolo-di-Sciara (1987) and Last & Stevens (1994) should be used in combination to ensure the correct identification of Indo-Pacific mobulids.

Very little is known about the stock structure of *M. japanica*, despite its wide distribution. Although thought to be circumtropical, the presently known distribution is disjunct. The connectivity of regional populations or stocks, for example, where the species occurs in the E Pacific and the W Pacific, is unknown. Even locally within Australia and SE Asia it is unknown whether there is one interbreeding stock, or several distinct populations. The latter would have implications for mobulid fisheries where they occur regionally in Indonesia and the Philippines, with the risk of stock depletion greatly increased.

In Australia, *M. japanica* has only been recorded along the east coast, with present records within the latitudinal range 14°57′–32°59′S. The closest records appear to be from New Zealand where the species is relatively common in waters off the North Island during the summer months to at least 38°22′S (Paulin et al. 1982; Duffy & Abbott 2003). Since the Japanese devilray is commonly caught in Indonesian waters (White et al. 2006), it is expected that it will be recorded more widely from northern and western Australian waters in the future. The number of recent beach-washed records, together with live sightings and fisheries bycatch, suggests a more common occurrence off eastern Australia than previously thought.

ACKNOWLEDGMENTS

We thank Jack Jackson and the Straddie Wildcare group for notification of the North Stradbroke Island specimen, Fabrice Jaine for assistance with specimen examination and Petter Fugelli for photography of that specimen, Jeff Johnson (Ichthyology, QM) for curatorial assistance and providing information on additional records, Ian Banks, Julie Meles, Ivan Thrash (QNPWS), Chris Witty and Qamar Schuyler (Undersea Explorer), and S. McCulloch (QDPI&F) for access to photographs and information on additional records.

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A technique for examination of diagnostic characters of penicillate millipedes

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Citation: Short, M. & Huynh, C. 2010 03 15. A technique for examination of diagnostic characteristics of penicillate millipedes. *Memoirs of the Queensland Museum — Nature* 55(1): 231-234. Brisbane. ISSN 0079-8835. Accepted: 5 August 2009.

ABSTRACT

We describe a simple method for examination of penicillate millipedes. The internal tissues are dissolved and the stain Fast Green used to give excellent contrast for dissection and to provide clear visualisation of characters necessary for identification of both freshly collected and museum specimens. ☐ *Histology, Fast Green stain, Diplopoda, Penicillata, Polyxenida.*

Millipedes in the subclass Penicillata, order Polyxenida have been overlooked in the study of terrestrial invertebrate fauna in Australia. Penicillates are commonly known as bristly, dwarf or pincushion millipedes. They differ from other millipedes in that adults are less than 5 mm in length, the cuticle is unmineralised and the animals are covered in bristles or trichomes (Hopkin & Read 1992). Due to their small size and soft structure, penicillates need to be specially prepared for high-power microscopic examination in order to clearly view their diagnostic characters. Diagnostic features used include insertion patterns of the cephalic, tergal and caudal trichomes; number and nature of antennal and leg sensilla; details of the mouthparts (labrum and gnathochilarium); and number of ocelli (Nguyen Duy-Jacquemin 2006; Short & Huynh 2006). No information is available on histological techniques used to examine penicillates other than preparation of whole mounts. This paper describes the technique we have developed to make permanent mounts using the stain Fast Green, a stain more commonly used in botanical microscopy (Ruzin 1999) and illustrates a selection of the characters used in identification of genera and species. The method has been modified from that described by Upton (1991) for mounting small arthropods for microscopic examination.

MATERIALS AND METHOD

Due to their small size penicillate millipedes are most commonly collected from bark and litter samples using Tullgren funnel extractions and stored in 70-80% ethanol. Selected specimens at least 2 mm in size are then prepared for microscopic examination as described below:

1. Removal and mounting of trichomes: This allows the clearest view of the pattern of trichome insertion points. Place a specimen in a drop of 100% isopropanol on a glass slide and remove trichomes with fine forceps and a microprobe. Gently disperse to separate them and after the isopropanol has evaporated cover the trichomes with a drop of DPX mounting medium and cover-slip.
2. Maceration and clearing: Body contents are digested while retaining details of the exoskeleton including sensory hairs and colxal gland openings. Place previously preserved

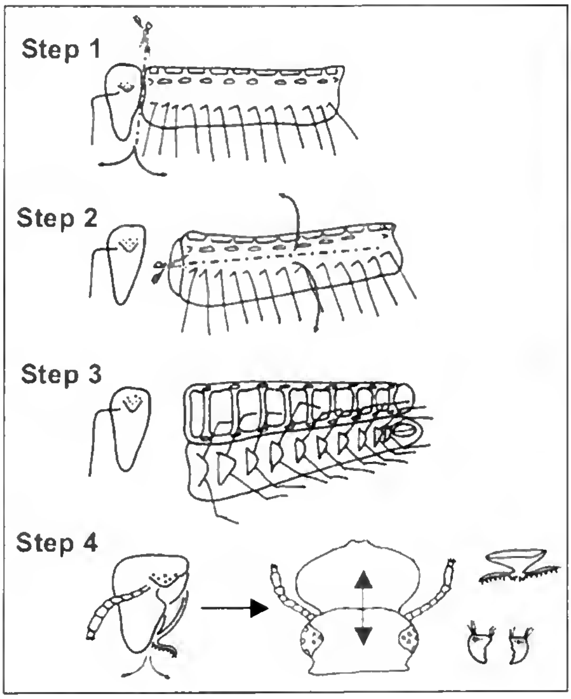

FIG. 1. Technique for opening up exoskeleton of penicillate millipedes in order to remove contents and prepare exoskeleton for staining.

specimens in an Eppendorf tube with 15% potassium hydroxide and heat gently in a water-bath for 2 minutes at 80°C followed by rinsing in distilled water. Damaged specimens or those preserved for many decades need just 1 minute in potassium hydroxide, while fresh specimens require a longer period of up to 12 hours immersion.

3. Dehydration and staining: Rinse the cleared specimen in water and then place into 20% acetic acid for 2 minutes to neutralise, followed by dehydration through a series of ethanol solutions from 70%, 80%, 90% to 100% (2 minutes per solution), followed by 2 minutes in 1% Fast Green in 100% ethanol. Return the specimen to 100% ethanol to remove excess stain.

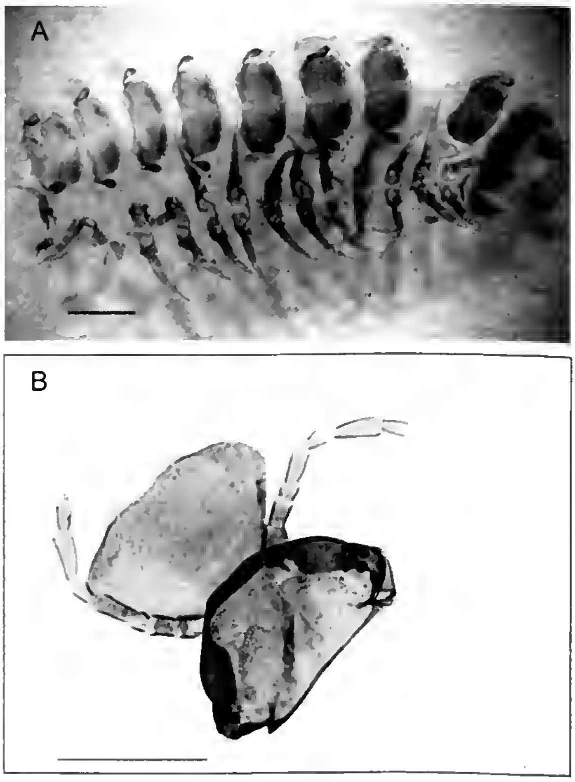

FIG. 2. Exoskeleton of body (A) and head (B) after slide preparation showing both dorsal and ventral features. Scale bars = 500µm.

4. Cleaning and dissection: The cleared and stained millipede is opened up using microprobes and micro-scissors in a series of steps as illustrated in Fig. 1, followed by removal of body contents. The Head is detached from the body. Removal of contents and opening out of the body and head are required to facilitate viewing of morphological characters of the exoskeleton.
5. Re-staining and mounting: Return the head and body to 1% Fast Green solution in 100% ethanol for 2 minutes followed by 100% isopropanol for 1 minute and finally into xylene for at least 1 minute. Specimens can be left in xylene until ready to mount. Mount

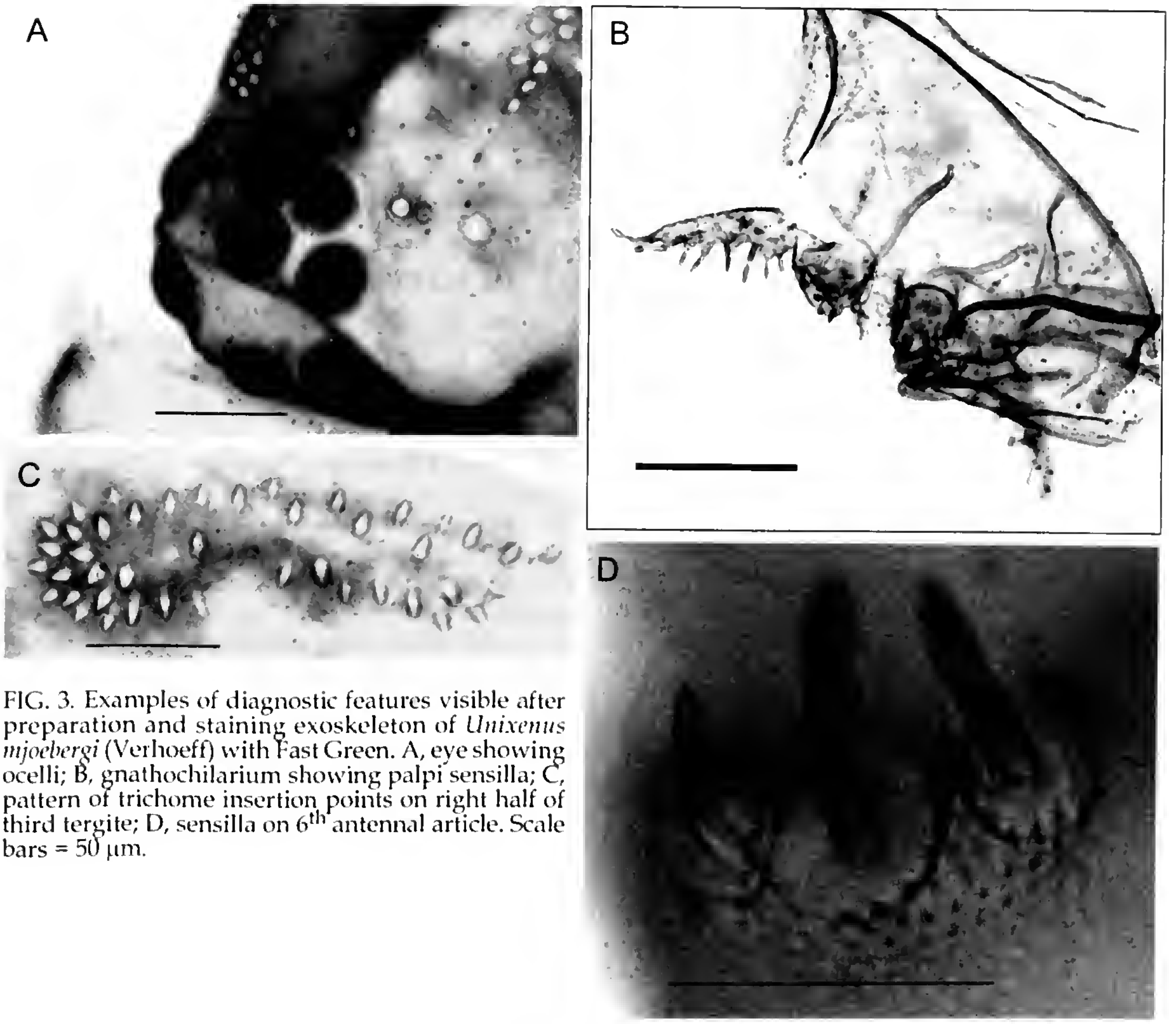

FIG. 3. Examples of diagnostic features visible after preparation and staining exoskeleton of *Unixenus mjoebergi* (Verhoeff) with Fast Green. A, eye showing ocelli; B, gnathochilarium showing palpi sensilla; C, pattern of trichome insertion points on right half of third tergite; D, sensilla on 6th antennal article. Scale bars = 50 µm.

the head and body separately in a drop of xylene on a glass slide followed by a drop of mounting medium DPX. DPX is preferred as it dries faster than Canada Balsam or Euparal. When mounting the head, tease apart the antennae and mouthparts with microprobes so that all relevant diagnostic features are clearly visible. When mounting the body, arrange the split body so that both dorsal and ventral surfaces are in the same plane for ease of viewing.

Images were taken using a Nikon Coolpix 4500 digital camera with an Olympus Vanox compound microscope.

RESULTS AND DISCUSSION

The body and head after preparation and staining are illustrated in Fig. 2. Having a permanent preparation of both dorsal and ventral features in the one field of view, enables efficient examination and documentation of diagnostic features. Fig. 3 illustrates a selection of these features. The method provides clearer views of features in comparison with a whole mount in which the gut contents often obscure important features such as the pattern of tergal trichome insertions. A further advantage is that staining prior to dissection enables the specimen to be more easily visualised for dissection after maceration renders penicillates transparent and hard to manipulate. As well only one specimen is required to view all features. This is an important factor when only a small number of specimens is available. A final advantage of the technique is reduction of the depth of field of the preparation with the body opened out and the contents removed.

We have used the method successfully with specimens from the penicillate families Synxenidae, Polyxenidae and Lophoproctidae including museum specimens lacking any colouration after decades in preservative.

ACKNOWLEDGEMENTS

Comments from R. Mesibov and an anonymous reviewer improved an earlier version of this paper.

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