The *Records of the Western Australian Museum* publishes the results of research into all branches of natural sciences, and social and cultural history, primarily based on the collections of the Western Australian Museum and on research carried out by its staff members.

Collections and research at the Western Australian Museum are centred on Earth and Planetary Sciences, Zoology, Anthropology, Archaeology and History. In particular the following areas are covered: systematics, ecology, biogeography and evolution of living and fossil organisms; mineralogy; meteoritics; anthropology and archaeology; history; maritime history and maritime archaeology; and conservation.

Western Australian Museum
Francis Street, Perth, Western Australia 6000
Tel. (08) 9427 7000
Fax. (08) 9427 2882
E-mail ann.ousey@museum.wa.gov.au

Minister for Culture and the Arts  The Hon. Sheila McHale MLA
Chair of Trustees  Dr Ken Michael AM
                BE (Hons), DIC, PhD, FTS, Hon FIE Aust, FCIT, FAIM
Executive Director  Dr Gary J. Morgan B.Sc. (Hons), Ph.D.
Editor  Dr Fred E. Wells B.Sc., M.Sc., Ph.D.

The *Records of the Western Australian Museum* is published approximately three times per year. A series of Supplements is also produced. The *Records* are available for sale and exchange. The current price being $11 plus postage per part. Each volume comprises four parts. Subscriptions can be taken out for whole volumes at a rate of $33 plus postage. Supplements can be purchased from the W.A. Museum Bookshop. Prices on request. Prices include GST.

Printed and published by the Western Australian Museum
© Western Australian Museum, June 2002
ISSN 0312 3162

Western Australian Triplectidinae (Trichoptera: Leptoceridae): descriptions of the female of *Triplectides niveipennis* and larvae belonging to four genera

Rosalind M. St Clair
Environment Protection Authority, Freshwater Sciences, GPO Box 4395QQ, Melbourne 3001, Victoria, Australia
email: Ros.StClair@epa.vic.gov.au

Abstract — Larvae of *Condocerus aptus*, *Notoperata tenax*, *Symphitoneuria wheeleri*, *Triplectides niveipennis*, and *Triplectides enthesis* are described for the first time. The female of *Triplectides niveipennis* is also described for the first time. Variation in larvae and adults of *Triplectides niveipennis* is discussed, together with unusual characters in the larvae requiring redefinition of the genus. Minor changes to the generic descriptions of *Condocerus*, *Notoperata* and *Symphitoneuria* are also made.

INTRODUCTION

Leptoceridae is a major family of Trichoptera in Western Australia, being both diverse and common. The adult leptocerid fauna of Western Australia is moderately well known, due largely to the efforts of Arthur Neboiss (1982). The Monitoring River Health Program has resulted in large numbers of specimens of larvae available for study to augment distribution data based on adults. These data indicate three leptocerid faunas in Western Australia; one in the cooler wetter south west, one in the large rivers of the north, and one in the dry areas with little permanent fresh water. The southern fauna is largely endemic while the northern fauna is generally spread right across the north to Queensland and the arid area fauna is found throughout arid Australia.

Quite a deal of work remains to associate larvae with adults. Some Western Australian larvae were assigned to species by St Clair (2000) but not described. Most of these species are described here. Many other species were designated voucher numbers by St Clair (2000) as they could not be associated with adults and these species require the most study in Western Australia.

Larvae of *Condocerus aptus*, *Notoperata tenax*, *Symphitoneuria wheeleri*, *Triplectides niveipennis*, and *Triplectides enthesis* are described for the first time. The female of *Triplectides niveipennis* is also described for the first time. All of these species appear to be restricted to the southwestern part of the state, none reported from north of Perth. Exceptions are one record of *T. enthesis* from the far north and the extension of the range of *S. wheeleri* into South Australia.

Larvae and adults of *Triplectides niveipennis* are found to be variable but not enough adult or reared specimens are available to resolve problems at this time. The larvae are unusual and require redefinition of the genus.

Most specimens examined were collected during the Land and Water Resources Research Development Corporation funded Monitoring River Health Program and material is to be lodged in the Western Australian Museum. Site data for this material start with MUR for sites sampled by Murdoch University, CALM for Department of Conservation and Land Management, ECU for Edith Cowan University and UWA for the University of Western Australia. Numbers beginning with AV refer to specimens lodged in the Museum of Victoria. Numbers beginning with WAM refer to Western Australian Museum registration numbers. Some larvae examined were collected by Pierre Horwitz at Edith Cowan University as part of a program looking at peat areas. All other specimens are in the Western Australian Museum unless otherwise specified. All specimens listed under Material examined are larvae unless the male or female symbols are used to designate adults.

**Condocerus** Neboiss

This Australian genus is represented by two species only, very similar in appearance as larvae, with one from each side of the continent. The larvae of both species feed by attaching their case to something solid at the surface of the water in fast flow and lying with their long back legs outstretched to collect live or dead animals drifting past. This method of feeding is unique to this genus, although last instar larvae of *Triplectides similis* feed on similar food.
As a result of associating Condocerus aptus, the larval generic description given by St Clair (1994) requires modification. The labrum is described as not having secondary setae but they are present in the species described here. This character is shared in Australia with Triplexa and Oecetis (St Clair, 1994) and with Notoperata tenax (see below).

Condocerus aptus Neboiss
Larva
Figures 1-5, 32

Diagnosis
The front of the frontoclypeus and the labrum have secondary setae (Figures 1 and 2).

Description
Head (Figures 1, 2 and 3)
Width measured across, and including, the eyes about 0.7 mm. Brown, paler laterally with lightly contrasting brown spots and contrasting yellow spot centrally towards anterior margin of frontoclypeus, sometimes with small paired paler spots anterior and/or posterior to this yellow spot; frontoclypeus widest on anterior margin; secondary setae present at front margin of the head and on labrum; ventral apotome narrow medially.

Thorax (Figures 1 and 4)
Pronotum mostly uniform brown; mesonotum with few slightly contrasting spots; metanot al sclerites brown; metasternum with row of setae and additional setae anterior to this row, most setae with small but prominent sclerite at base; legs uniform in colour, long spine-like setae present ventrally on fore- femora, tibiae and tarsi, mid femur, tibiae and tarsi and hind trochanters, femora, tibiae and tarsi (Figure 5).

Abdomen
Setae on first abdominal segment each with small but prominent sclerite at base; two pairs of short gills on segments 4 to 6 (rarely 3 to 6) only and additional gills at the tip of the abdomen; dorsal sclerite on abdominal segment 9 small and very pale, pigment spots obvious only occasionally; anal claws each with three small dorsal teeth.

Body Length
About 12 mm.

Case
Made of small pieces of plant matter, often green, arranged to form tapering tube. Usually with additional long sections of detritus on sides and back appearing to act as stabilisers to help hold animal on the water surface and in current. Tube usually about 1.5 times length of larva but case often longer due to long “stabilisers.” Identical to that of C. paludosus.

Early instar larvae
Pronotum with six or seven sclerites or hind legs with long spine-like setae and without pale setae on most segments allow identification of many earlier instar larvae.

Remarks
This species is extremely similar to C. paludosus from eastern Australia, differing only in the presence of secondary setae on the labrum and front of the frontoclypeus and slight differences in colour of the head.

Material examined
Western Australia: AV-0472 Foster Brook, North Dandalup, 32°29'S 116°03'E Coll. S. Bunn 19 September 1981, 4; Foster Brook, North Dandalup, 32°29'S 116°03'E, in drift, Coll. S. Bunn 31 Jul. 1981, 3; ECU27, Blackwood River at Spearwood, 34°05'07"S 115°18'47"E, 10 October 1994, Channel, 2; ECU21, Ellis Creek, 33°55'59"S 115°52'53"E, 23 September 1994, 1; MUR08, Dirk Brook, 32°26'39"S 116°01'34"E, 7 September 1994, Macrophyles, 4, Channel, 1; MUR12, Little Dandelup River, 32°35'31"S 116°01'34"E, 7 September 1994, Macrophyles, 2, Channel, 2; MUR13, Big Brook, 32°52'51"S 116°06'16"E, 8 September 1994, Channel, 8; MUR17, Stones Brook, 33°21'43"S 115°57'01"E, 15 September 1994 Riffle, 1; MUR18, Ernest River, 33°11'33"S 116°01'49"E, 15 September 1994 Channel, 15; MUR23, Harvey River at Hoffmans Mill, 33°04'41"S 116°06'56"E, 9 September 1994, Macrophyles, 35, Channel, 4; MUR24, Harvey River Tributary, 33°01'10"S 116°05'37"E, 9 Sep 1994, Channel, 2; UWA01, Beedleup Brook at Steep Road, 34°24'47"S 115°52'29"E, 15 October 1994 Channel, 2, Macrophyles, 4; UWA04, Fly Brook at Alamein Track, 34°27'59"S 115°50'09"E, 16 October 1994, Macrophyles, 16; UWA08, Treen Brook, track off Eastern Break Road, 34°26'59"S 115°57'25"E, 15 October 1994, Organics, 1; UWA10, Un-named stream on Lewis Road, 34°35'32"S 115°54'46"E, Macrophyles, 45; UWA13, East Brook at Raspy Road, 34°27'55"S 116°02'00"E, 13 October 1994, Macrophyles, 3; UWA17, Un-named tributary at Marron Rd, 34°48'01"S 116°21'27"E, 12 October 1994 Macrophyles, 1; UWA18, Shannon River at Nelson Road, 34°42'24"S 116°21'27"E, 11 October 1994, Macrophyles, 5; UWA20, Forth River at Chesapeake Road, 34°51'52"S 116°25'29"E, 12 October 1994, 24; UWA22, Tributary of Weld River, 34°41'23"S 116°31'15"E, 9 October 1994, Macrophyles, 13; UWA25, Deep River at Bevan Road, 34°35'36"S 116°33'06"E, 9 October 1994, Macrophyles, 1;
Figures 1–5  Condocerus aptus larva, specimen vial AV-0472: 1, head and thorax dorsal; 2, labrum dorsal; 3, head ventral; 4, metasternum; 5, right hind leg posterior. All scale bars 0.1 mm.
Habitat and Distribution

Western Australia, confined to areas with permanent flow in the Southwest (Figure 32).

Notoperata Neboiss

This is a genus of five described species, all from Australia. I recognise larvae from a further two species (St Clair, 2000). At least three species occur in Western Australia. The description here of the larva of Notoperata tenax is the first of the larva of a species from Western Australia, the other species in this state not having been associated with the adult. A key separating the larvae of the species was provided by St Clair (2000).

The larval generic description given by St Clair (1994) requires modification in that the labrum of the species described here has nine pairs of setae dorsally along the mid section of the labrum. In Australia, as noted above, secondary setae are also present on labra of larvae of Condocerus, Triplexa and Deccis although many more additional setae are present on the labra of these three genera than on this species of Notoperata.

Notoperata tenax Neboiss

Larva

Figures 6–9, 33

Diagnosis

The labrum has a transverse medial line of nine pairs of setae (Figure 6), there are comparatively long extensions on anterior pronotal corners (Figure 6) and about 8 metasternal setae are present (Figure 8).

Description

Head (Figures 6 and 7)

Width measured across, and including, the eyes 7.2 mm. Dark brown with paler spots; fronsoclypeus long, widest on anterior margin; ventral apomote tapering.

Thorax (Figures 6 and 8)

Pronotum dark brown with paler spots, anterior margin scalloped, anterolateral corner much extended and cut away laterally; mesonotum dark brown with paler spots; metanotum pale with dark patches, lateral sclerites about 1/3–1/2 length of segment; metasternum with about eight scattered setae and no sclerites; legs with darker bands, with some moderately long spine-like setae ventrally and long setae (Figure 9).

Abdomen

Gills single filaments on segments 2 to 4 dorsally, 2 to 3 or 5 laterally and 2 to 5 or 6 ventrally; tergite 9 very pale and comparatively large; anal claw with two dorsal teeth.

Body Length

About 9 mm.

Case

Tubular, made of detritus.

Remarks

This species shares with the two species already described as larvae (St Clair, 1994) the anterolateral pronotal extensions and cutaway anterolateral pronotal margin. It differs markedly in the presence of a line of nine pairs of long setae on the labrum, which is unique in the Australian Leptoceridae but very similar to several genera of Calamoceratidae which have eight pairs of setae.

Material examined

Western Australia: Lake Smith, Donnelly Catchment, 34°25'48"S 115°43'36"E, FBA, January 1995, P. Horwitz, 1, WAM 27555; ECU5, Hamersley River at Tallawarra, 33°43'43"S 121°14'48"E, 2 January 1995, Macrophytes, 2; ECU32, Margaret River at Canebrake Road, 33°52'35"S 115°17'23"E, 17 January 1995, Macrophytes, 1; MUR08, Dirk Brook, 32°26'39"S 116°01'34"E, 7 September 1994, Macrophytes, 2, Channel, 4; UWA01, Beedelup Brook at Steep Road, 34°24'47"S 115°52'29"E, 28 January 1995, Cowan, 1, WAM 27555; ECU5, Shannon River at Curtin 4 Road, 34°34'12"S 116°25'49"E, 18 January 1995, Macrophytes, 1; UWA08, Treen Brook, track off Eastern Break Road, 34°26'59"S 115°57'25"E, 15 October 1994, Channel, 2.

Habitat and Distribution

Rivers and lakes in southwestern Western Australia (Figure 32). Possibly cool waters only. The far eastern site, ECU5, seems anomalous but I have not had the opportunity to check it.

Symphitomeuria Ulmer

The genus Symphitomeuria is known from three Australian species, S. exigua described from
Figures 6–9 *Notoperata tenax* larva WAM 27555: 6, head and thorax dorsal, showing pronotal anterolateral corner detail; 7, head ventral; 8, metasternum and mesosternal sclerites; 9, right hind leg posterior. All scale bars 0.1 mm.
Queensland, S. opposita described from Victoria and recently found in the Mt Kosciuszko region of NSW, and S. wheeleri described from Western Australia and recently found to occur in South Australia as well. The larva of S. opposita was described by St Clair (1994). The larva of S. wheeleri is described here. A photograph of the larvae of a third species was figured by St Clair (2000) as Symphitonuria sp. AV 1. This may be the larva of S. exigua. If so, this species occurs from North Queensland to mid New South Wales.

The larval generic description given by St Clair (1994) requires minor modification as this species does not have a long extension on the pronotal anterolateral corner.

**Symphitonuria wheeleri** Banks

**Larva**

Figures 10-12, 32

**Diagnosis**

The pronotal anterior margin is only lightly scalloped, the pronotal anterolateral corner only slightly elongate and angled or scooped out laterally and the mesonotum is much paler than pronotum (Figure 10).

**Description**

*Head* (Figures 10 and 11)

Width measured across, and including, the eyes 0.73 mm. Brown with pale spots; antennae about 1/3 length of the frontoclypeus on its anterior margin; ventral apex tapers slightly.

*Thorax* (Figures 10 and 11)

Pronotum brown with paler spots; mesonotum paler with dark spots; metanotal sclerites pale with dark spots, sometimes with a small sclerite at base of each long posterior seta; metanotum with numerous setae, without metasternal sclerite; legs sometimes with darker bands, claws dark brown and contrasting with rest of leg segments, and hind legs with moderately long spine-like setae and most setae dorsal (Figure 12).

*Abdomen*

Gills single filaments on segments 1 to 8 or 2 to 8, 2 to 5 or 7 laterally; lateral line moderately short and pale or dark; tergite 9 very pale, not visible; brown spots on lateral sclerites, rest very pale; anal claws each with one dorsal tooth.

*Body Length*

14 mm.

*Case*

Tubular, made of coarse sand grains or detritus.

**Early instar larvae**

Recognised by case (if sand grains used), small metanotal sclerites, divided hind tibiae and only pale basal sclerites on the metasternum.

**Remarks**

**Distribution** can be used to identify the three Australian species, however, both *S. opposita* and *S. wheeleri* occur in South Australia, although probably in different areas. *Symphitonuria wheeleri* is readily identified by the relatively unmodified front margin and anterolateral corners of the pronotum and by the colour contrast between the pro- and mesonotum.

**Material examined**


**Habitat and Distribution**

This species is found in lakes and rivers in southern Western Australia (Figure 32) and South Australia. This species is usually found in saline waters and its distribution may be increasing with increasing salinity.

**Triplectides Kolenati**

*Triplectides* is one of the larger genera in Australia, both in number of species and the size of the larvae. It also occurs in South America and Asia. Only three species are known from south-western Western Australia, although *Triplectides niveipennis* is either polymorphic or two closely related species. Two, *T. niveipennis* and *T. enthesis*, are endemic to the Southwest while the third, *T. australis*, is one of very few caddis species found throughout the continent. *Triplectides niveipennis* was associated with the adult recently and is described here. The larva of *T. enthesis* is yet to be associated but the larva designated to *Triplectides* sp. AV 1 (see St Clair, 2000) is found in appropriate habitats and is almost certainly the larva of *T. enthesis*. It is described here.
Figures 10–12  *Symphitoneuria wheeleri* larva, specimen vial AV-0468: 10, head and thorax dorsal, showing pronotal anterolateral corner detail; 11, head and thorax ventral; 12, right hind leg posterior. All scale bars 0.1 mm.
as the larva of *T. enthesis*. The larva of *T. australis* was described and figured by St Clair (1994) and figured in part by St Clair (2000).

The generic description given by St Clair (1994) requires amendment following the association of *Triplectides niveipennis*. The antennae of all larval *Triplectides* are short, one eighth to one quarter the length of the frontoclypeus at its front margin. This character was the only one that completely defines the genus but now the larva of *T. niveipennis* is known to have long antennae. The larva of *T. niveipennis* are also unique in the genus in their tendency for each lateral metanotal sclerite to divide into 2 sclerites and in having a long two-pronged extension on the pronotal margin on each side near the anterolateral corners. The full implications of these unusual characters are discussed below.

**Key to final instar *Triplectides* larvae of southwestern Western Australia**

1. Three large yellow spots on frontoclypeus, one in posterior tip and one on each side of constriction; metasternum with about 4 small sclerites, usually associated with pairs of setae; final instar larva with only slight scalloping on front margin of pronotum; ventral apotome fairly broad posteriorly (St Clair 1994, 2000) .......................... *Triplectides australis*

   - No large spots on frontoclypeus (Figures 19, 25); metasternum without sclerites or with extremely small sclerites at base of single setae (Figures 23, 27); two-pronged extension on front margin of pronotum on each side, near the anterolateral corner, which may be long to very short (Figures 20, 25); ventral apotome tapering but not to point (Figures 22, 26) .......................... *Triplectides niveipennis*

   - No large spots on frontoclypeus (Figure 29); metasternum with large but pale central sclerite (Figure 30); final instar larva with only light scalloping on front margin (Figure 29); ventral apotome strongly tapering to point (Figure 30) .......................... *Triplectides enthesis*

***Triplectides niveipennis* Mosely**

Figures 13–28, 34

*Triplectides niveipennis* is either a polymorphic species or a species complex but too few adult or reared specimens are available at present to resolve this issue. The species is unique in the Australian Leptoceridae fauna in that it has two distinct larval colour morphs. These two morphs are separated and designated different Australian Voucher species numbers for the larvae, *Triplectides* sp. AV 20 and *Triplectides* sp. AV 21 (see St Clair, 2000).
Figures 13–18 Triplectides niveipennis adult female WAM 27557: 13, right fore wing dorsal; 14, right hind wing dorsal; 15, last abdominal segment ventral; 16, last abdominal segment lateral. Adult female WAM 27556: 17, last abdominal segments ventral, showing long transparent process; 18, last abdominal segments lateral, showing long transparent process. Scale bars for figures 13 and 14 1.0 mm, all other scale bars 0.1 mm.
and confirms this species' uniqueness within the genus.

The larva of *T. niveipennis* has a sclerite posteriorly on the metanotum, although often divided into two sclerites. This sclerite is only found in *Triplectides* and helps separate it from larvae of its related genera. Unfortunately it is only found in about half the species. The case used by *T. niveipennis* is always a piece of stick or stem hollowed out by the larva. This case type is only found in *Triplectides* and is used by most, if not all, of the species in the genus but not all individuals of many species. The presence of the posterior metanotal sclerite and the case type clearly place this species in *Triplectides*.

Several larvae of *T. enthesion* have the lateral metanotal sclerite divided into two. This also occurs frequently in larvae of the three species of *Lectrides* but has not been seen in other genera or other species of *Triplectides*.

The long antennae, the frequent division of the lateral sclerites on the metanotum and two pronged processes on the front margin of the pronotum combine to give the larvae of this species a unique place within the genus and do not align it within any species group. The arrangement of metasternal sclerites and setae is also unusual but there is more variation within the species groups in this character. The larva shows no particular similarity with the larva of *Triplectides enthesion*.

**Adult**

**Description**

Female: Adult females similar to males in having dark segments distally on fore- and mid legs and palps. Forewings (Figure 13) with sectoral crossvein almost straight; posterior vein forming discoidal cell almost straight, S4 longer than in male forewing. Hind wings (Figure 14) pale but not white; not as enlarged and lacking additional veins present in hind wing of described male (Morse and Neboiss 1982). (The two males reared to the winged stage also lack these additional veins in the hind wing, although the wing is still very broadened).

Genitalia: (Figures 15 to 18) dorsal setose lobes short; each without sensilla bearing process, although very small pale process is present on the margin of the setose lobe (giving a bilobed appearance) but without sensilla; lamellae moderately long, each with distinct longitudinal ridge dividing it into two sections almost as long as each other and with surfaces at right angles to each other (thus appearing broad in both lateral and dorsal views), with short setae but apparently without striae. Spermathecal sclerite with long rounded anterior extension. Spermathecal sclerite most similar to that of *T. elongatus* but with some similarities also to *T. australis* and *T. enthesion*. One female has a long membranous projection extending from segment IX dorsally (Figures 17 and 18), but such process was much shorter in one other specimen and completely absent in the remaining specimen.

**Larva**

**Diagnosis**

The antennae are long, at least 1/4 the width of the frontoclypeus on the anterior margin (rare specimens with shorter antennae) (Figure 19); the pronotal anterior margin is lightly scalloped and with two long or short two-pronged extensions and the anterolateral margin is rounded (Figure 20); the metanotum has five sclerites but long lateral and/or posterior sclerites may be divided into two, giving as many as eight sclerites (Figure 21). Some or all of these sclerites may be very pale.

**Description**

*Triplectides* sp. AV 20

**Head** (Figures 19 and 22)

Width measured across, and including, the eyes 0.93 mm. Orange with triangular dark patch on top of the head extending almost to back of head, ventrally pale with numerous very pale spots in bands.

**Thorax**

Pronotum orange anteriorly and posteriorly, brown transverse band medially, with medial prong of two-pronged process longer than lateral (Figure 20); prosternal sclerite comparatively large (Figure 23); hind legs very long and slender (Figure 24); mid and hind legs each with coxa orange, rest of leg dark brown; foreleg orange. (This species was originally designated Leptoceridae Genus B sp. AV 3.)

*Triplectides* sp. AV 21

**Head** (Figures 25 and 26)

Width measured across, and including, the eyes 0.88 – 1.01 mm (2 specimens). Dark red-brown with paler spots.

**Thorax** (Figures 25 and 27)

Pronotum dark red-brown with paler spots; mesonotum brown; metanotum pale brown; hind legs pale brown, uniform in colour (Figure 28). (This species was originally designated Leptoceridae Genus B spp. AV 1 and 2.)

**Description applying to both larval types**

**Head** (Figures 19, 22, 25 and 26)

All setae on head comparatively pale;
Figures 19–24  *Triplectides niveipennis* sp. AV 20 larva, WAM 27558: 19, head dorsal; 20, pronotum, dorsal, showing some variation in anterolateral corner detail; 21, meso- and metanota dorsal; 22, head, ventral; 23, pro-, meso-, and metasternal sclerites; 24, right hind leg posterior. All scale bars 0.1 mm.
Figures 25–28 *Triplectides niveipennis* sp. AV 21 larva, WAM 27559: 25, head and thorax dorsal; 26, head ventral; 27, pro-, meso-, and metasternal sclerites; 28, right hind leg posterior. All scale bars 0.1 mm.
frontoclypeus wider on anterior margin; ventral apotome tapering posteriorly.

**Thorax** (Figures 20, 21, 23, 25 and 27)
Four to seven metasternal setae each often with small, pale, obvious sclerite at base.

**Abdomen**
Gills long, on segments 1 to 5 or 6 dorsally, 2 to 3 or 6 laterally and 2 to 6 or 7 ventrally; lateral line moderately long and pale or dark; tergite 9 very pale, scarcely visible; anal claws each with one dorsal tooth.

**Body Length**
About 13 mm.

**Case**
Hollowed stick or macrophyte stem.

**Early instar larvae**
The extension of the pronotum appears to grow rapidly with later instars so that early instars lack it and third or fourth instar have just a rounded area on the pronotum where the extension will form. These larvae also have a more strongly tapering ventral apotome. Early instar larvae are likely to be confused with early instar larvae of *T. enthisos* as both have the pronotum much darker than the mesonotum.

**Remarks**
The long antennae, the occasional division of lateral and posterior metanotal sclerites, and the two-pronged extension on the pronotum are very distinctive of this species and unusual within *Triplectides*. The case, always a stem or stick hollowed by the larva, is typical of *Triplectides*.

**Material examined**
*Triplectides niveipennis* (sp. AV 20): Western Australia: Swamp 25 km NW of Walpole, 100m NW of Beardmore Rd., 34°49'S 116°32'E, Coll. R. St Clair, 28/10/1997, preserved 3/11/1997, 1; ECU33, Margaret River at Challis on Mownen, 33°55'46"S 115°15'51"E, September 1994, Macrophytes, 3 (1, WAM 27558); AV-0507, Margaret River on Great North Rd., 1–2 September 1985, M.S. Harvey and T.J. Doeg, 2.

Reared specimens: AV-5697, Swamp 25 km NW of Walpole, 100m NW of Beardmore Rd., 34°49'S 116°32'E, Coll. R. St Clair, 28/10/1997, 1 δ, locality data lost, Coll. R. St Clair, October 1997, 1 δ.

*Triplectides niveipennis* (sp. AV 21): Swamp 25 km NW of Walpole, 34°49'S 116°32'E, Coll. R. St Clair, 28/10/1997, preserved 3/11/1997, 3; AV-5649, Swamp near Finlay Brook, 20 km S of Jarrahdale, 30 August 1985, M.S. Harvey and T.J. Doeg, 2; AV-0504, Margaret River on Great North Rd, 1–2 September 1985, M.S. Harvey and T.J. Doeg, 3; AV-0500, 2 km E of Grimwade, 31 August – 1 September 1985, M.S. Harvey and T.J. Doeg, 3; AV-0501, St John’s Brook 2 km E of Cundinup, 1 Sep, 1985, M.S. Harvey and T.J. Doeg, 5; AV-0506, Barrabup Rd NW of Nannup, temporary pool, 1 September 1985, M.S. Harvey and T.J. Doeg, 1; 3 AV-0503, Hamilton River 11 km WNW of Collie, 31 August 1985, M.S. Harvey and T.J. Doeg; AV-0540, Dillon Brook North Dandalup, Coll. S. Bunn, 31 August 1981, 10 early instars, AV-0509, 22 early instars, station 10 drift sample, 1810–2010 hrs, AV-0547, 30 July 1981, 26 early instars; ECU43, Headwater reach of Ludlow River, 33°43'47"S 115°27'07"E, September 1994, Macrophytes, 7 (1, WAM 27559); ECU33, Margaret R at Challis on Mownen, 33°55'46"S 115°15'51"E, 28 September 1994, Macrophytes, 2; ECU34, Margaret River at River Road, 36°56'35"S 115°06'59"E, September 1994, Macrophytes, 2; ECU29, Scott River at Milyeannup Road, 34°17'54"S 115°23'54"E, 14 September 1995, Channel; 3; MUR02, Death Adder Creek, 32°08'10"S 116°10'36"E, 5 September 1994, Macrophytes, 6, Macrophytes, 28 (fourth instar? With very slight projections) Channel; 3; MUR04, Wungong Brook, 32°18'47"S 116°11'05"E, 5 September 1994, Macrophytes, 2; MUR06, Serpentine River, 32°30'31"S 116°17'25"E, 6 September 1994, Organics, 1; MUR10, Yarragill Brook, 32°49'56"S 116°12'10"E, 8 September 1994, Rifle, 1, Channel, 2; MUR20, Glen-Mervyn Tributary, 33°30'29"S 116°06'17"E, 13 September 1994, Organics, 8; MUR21, Ferguson River Tributary, 33°27'03"S 115°56'24"E, 13 September 1994, Channel, 1, Organics, 8 (few with long processes); MUR23, Harvey River at Hoffmans Mill, 33°04'41"S 116°06'56"E, 9 September 1994, 3, Channel, 1; MUR30, Dale River, 32°20'40"S 116°28'51"E, September 1994, Macrophytes, 1; UWA09, Dudjug Creek on Whim Landing Road, 34°07'55"S 116°14'40"E, 14 October 1994, Macrophytes, 5; Channel, 4; UWA14, Quinنينup Brook at Sutton Road, 34°27'27"S 116°15'20"E, 13 October 1994, Macrophytes, 3; UWA15, Shannon River Curtin 4 Road, 34°34'12"S 116°25'49"E, 10 October 1994, Macrophytes, 1; UWA22, Tributary of Weld River, 34°41'23"S 116°31'15"E, 9 October 1994, Macrophytes, 1; UWA24, Deep River at Weld Road, 34°42'05"S 116°37'02"E, 9 October 1994, Organics, 1; UWA25, Deep River at Bevan Road, 34°35'36"S 116°33'06"E, 9 October 1994, Macrophytes, 3; UWA29, Walpole River off Plain Road, 34°57'40"S 116°42'17"E, 8 October 1994, Macrophytes, 5; UWA30, Nile Creek at Break Road, 34°50'41"S 117°02'37"E, 29 September 1994, Macrophytes, 2 (one in *Notoperata* style case); UWA32, Styx River, 0.5km up from Styx Road, 34°52'57"S 117°08'21"E, 27 September 1994, Macrophytes, 1; UWA34, Denmark River at Granite...
Figures 29–31  *Triplectides enthesis* larva, WAM 27560: 29, head and thorax dorsal; 30, head and thorax ventral; 31, right hind leg posterior. All scale bars 0.1 mm.
Western Australian Triplectidinae

Road, 34°49'47"S 117°15'02"E, 28 September 1994, Macrophytes, 2; UWA40, Gaalgegup Creek at Walshpool Road Bridge, 34°35'28"S 117°55'42"E, 23 September 1994, Macrophytes, 8.

Reared specimens: Swamp 25 km NW of Walpole, 100 m NW of Beardmore Rd., 34°49'S 116°32'E Coll. R. St Clair 28 October 1997, 2 ♀ (one lodged in the Museum of Victoria, AV-5696), 1 ♂ WAM 27556; Dammed Creek 11 km WNW of Collie, 33°19'S 116°02'E, Coll R. St Clair, 30 October 1997 1 ♀, 1 ♂ (lodged in the Museum of Victoria, AV-5695) and 1 ♀ WAM 27557.

Habitat and Distribution
Permanent still and flowing waters in southwest Western Australia (Figure 34). This species inhabits forest streams or streams in more open habitat. It seems to tolerate warmer waters than Triplectides enthesis and still waters.

*Triplectides enthesis* Neboiss
Larva
Figures 29–31, 33

Diagnosis
The ventral apotome tapers strongly (Figure 30); the pronotal anterior margin is only slightly scalloped (Figure 29); the pronotal anterolateral corners are only slightly elongate and angled or scooped laterally (Figure 29); the mesonotum is much paler than the pronotum (Figure 29); the metasternum has a very pale, moderately large, central sclerite (Figure 30).

Description

**Head** (Figures 29 and 30)
Width measured across, and including, the eyes 0.82 mm. Red-brown with pale spots; antennae about one eighth length of frontoclypeus on anterior margin; ventral apotome tapering to point.

**Thorax** (Figures 29 and 30)
Pronotum red-brown with pale elongate spots; mesonotum much paler than pronotum; metanotal sclerites very pale; about 10 metasternal setae; legs fairly uniform in colour (Figure 31).

**Abdomen**
Gills single filaments dorsally on segments 2 to 6, ventrally on segments 3 to 6, segment 3 only laterally; tergite 9 extremely pale, not visible, with 6 long setae; each anal claw with three dorsal teeth.

**Body Length**
About 8 mm.

**Case**
Whole stick.

**Early instar larvae**
These are likely to be confused with early instar larvae of *T. niveipennis* as both have the pronotum much darker than the mesonotum. The pronotal processes of *T. niveipennis* are very short or even absent in fourth instar and the larvae are then indistinguishable from *T. enthesis* early instars.

---

Figure 32  Map showing distribution of specimens of *Condocerus aptus* and *Symphitoneuria wheeleri* examined for this study, not including the specimen of *S. wheeleri* from South Australia.
Figure 33  Map showing distribution of specimens of *Notoperata tenax* and *Triplectides enthesis* examined for this study, not including the specimen of *T. enthesis* from the North.

Figure 34  Map showing distribution of specimens of *Triplectides niveipennis* sp AV 20 and *Triplectides niveipennis* sp AV 21 examined for this study.

unless the sclerite on the metasternum is apparent.

Remarks
Larvae of this species are very similar to those of *T. proximus* from eastern Australia and, apart from the metasternal sclerite, both fit the above diagnosis.

Material examined
Western Australia: AV-0541, Carey Brook 20 km W of Pemberton, 26 November 1978, Coll A. Neboiss, 1; AV-0542, Waterfall Gully, Jarrahdale, 18 May 1981 Coll. S. Bunn 1; AV-0543, Seldom Seen Brook, Coll. S. Bunn, 6 October 1982, Station 7, 1, AV-0544, 14 June 1982, 5 early instar, AV-0545, 1 April 1982, 1; AV-0546, Little Dandalup Creek,
Habitat and Distribution

This species is restricted to cool, permanently flowing streams in forested areas (Figure 33). The record from Millstream in northwest Western Australia is very odd, but as it is from a spring-fed channel, this may be from a relict population in cool water.

ACKNOWLEDGEMENTS

The association of Notoperata tenax was made by Dr. Stuart Bunn. A large amount of material was collected in WA as part of the Monitoring River Health Program and the funding for the Taxonomy Project within this Program enabled examination of this material, both funded by LWRDCC. Drs. Stuart Halse, Jenny Davis, Pierre Horwitz, and Don Edward are thanked for access to this material.

Specimens for rearing and association of Triplectides niveipennis were collected under permit number SF002275 from CALM. Collections in National Parks were acquired with permit number NE001750 and exported to Victoria for rearing and examination under permit number EA002989. Fiona Wells is thanked for providing the distribution maps. The reviewers, Drs. John Morse and Alice Wells, are thanked for very helpful comments.

REFERENCES


Manuscript received 18 December 2000; accepted 24 October 2001.
Western Australian Onychophora (Peripatopsidae): a new genus, Kumbadjena, for a southern species-complex

Amanda Reid
6 Sturt Place, Bulli, New South Wales, 2516, Australia. Email: mandy.reid@optusnet.com.au

Abstract — Two species of Onychophora (Peripatopsidae) were previously known to occur in the south-western corner of Western Australia: Occiperipatoides occidentalis (Fletcher, 1895) and Occiperipatoides gilesii (Spencer, 1909). These two taxa occupy geographically disjunct regions. Using morphological characters, Occiperipatoides 'occidentalis' is shown to comprise a species-complex; three species are described here, two of which are new. A new genus, Kumbadjena, is erected for O. 'occidentalis' to reflect the significant morphological and molecular differences between members of this complex and O. gilesii. The Kumbadjena gen. nov. group occupies a region of relatively high rainfall in the southernmost portion of the state, its distribution reflecting that of karri Eucalyptus diversicolor (Mueller). The monotypic Occiperipatoides gilesii is found in the area surrounding Perth on the Swan Coastal Plain and along the scarp and western parts of the Darling Range plateau. The distribution of these two taxa is discussed in relation to past geographical events.

INTRODUCTION

The present study was prompted by the discovery of considerable variation among specimens previously assigned to Occiperipatoides occidentalis (Fletcher, 1985) (Reid, 1996). In addition, the number of pronounced morphological differences distinguishing O. occidentalis and O. gilesii (Spencer, 1909) and the documentation of 81% fixed gene difference between representatives of these two taxa (Briscoe and Tait, 1995), suggested that generic separation was justified (Reid, 1996). An impediment to addressing both of these issues was the lack of sufficient numbers of well-preserved specimens from a number of populations of O. occidentalis and the absence of O. occidentalis type material for comparison: the type specimens are believed lost.

In addition to collections made in recent times by members of the Western Australian Museum, the collection of new material undertaken by the author in 1995 and 2000 has enabled some of these difficulties to be overcome, but has also introduced some new ones.

However, detailed comparison of these new, and previously collected museum specimens strongly supports the separation of the Western Australian onychophoran fauna into two genera. A new genus, Kumbadjena gen. nov. is erected here for species belonging to what could be described as the ‘occidentalis’ species-complex and a neotype for K. occidentalis is designated. Within this complex, two new species, K. kuta sp. nov., and K. shannonomensis sp. nov. are described.

Aside from these new species designations, I have been unable to find reliable morphological characters to distinguish what I believe will ultimately prove to be a complex of species belonging to Kumbadjena gen. nov. This is typical for Australian Onychophora, particularly among populations that are geographically widespread. Morphological crypsis among populations occupying narrow distributional ranges is the norm, so the future discovery of new Kumbadjena gen. nov. species should not be surprising. However, until additional suites of characters are examined, such as allozymes, gene sequences, and/or karyology, it is not possible to determine the number of species present within this complex. Given the biological importance and significant conservation status of Onychophora, a detailed study based on additional characters should be a high priority for future research.

Evolutionary relationships

The results of a phylogenetic analysis undertaken by Reid (1996), which included 62 peripatopids, showed Occiperipatoides occupying a basal position in the cladogram with respect to many of the remaining Australian peripatopsids (most of the latter formed part of a large, mostly unresolved clade). The Occiperipatoides clade was supported by six unambiguous apomorphies, only one of which was unique: the presence of crural glands extending the length of the body from anterior (the first pair of oncopods) to posterior. This result contrasts radically with that presented in Gleeson et al. (1998).
of an analysis based on comparison of sequences from the mitochondrial cytochrome oxidase subunit I gene. In this analysis, Occiperipatoides (represented by O. gilesii from Jandakot 32°07'S; 115°50'E) occupies a more terminal position with respect to the other Australian taxa included in the study, though the resolution of the clade containing O. gilesii was poor. However, both analyses (Reid, 1996; Gleeson et al., 1998) show Euperipatoides Ruberg, from eastern Australia, and Occiperipatoides to be sister taxa. There are some problems with both the morphological and molecular analyses of the peripatopsids that have been undertaken to date. Unfortunately it is still necessary to conclude that we know very little at present about the evolutionary relationships between the onychophorans from Western Australia and those from the rest of Australia and elsewhere.

**MATERIALS AND METHODS**

**Specimen collection and preservation**

This study is based on the examination of preserved specimens, most of which were hand collected from within and under decomposing logs and leaf litter. Specimens collected by the author were preserved, partially following the method of Reid (1996). Animals were anaesthetised by exposure to ethyl acetate vapour for 10 min; dipped in 70% ethanol to render the cuticle less hydrophobic; fixed in 4% formalin for 2–3 days; then stored in 70% ethanol. Animals preserved in this way are destended, enabling characters to be examined more easily than is possible in contracted specimens. Formalin fixation allows internal structures (particularly the male reproductive tract) to be dissected and examined without tissue breakage.

**Tissue preparation for scanning electron microscopy**

Tissue dissected from fixed and preserved specimens was dehydrated in a graded ethanol series. Following three washes in 100% ethanol, tissue pieces were impregnated in hexamethyldisilazane (HMDS) by taking them though a graded ethanol/HMDS series to 100% HMDS, air dried and gold coated. Each step in the dehydration series lasted five minutes. Specimens were examined in a Phillips 505 scanning electron microscope operated at 20.1 kv.

For males and females of all populations collected by the author, the following tissue samples were prepared for scanning electron microscopy (SEM) as above: dorsal integument; nephridiopores; crural papillae from oncopods 1, 3, 7 and 12; anterior accessory gland papillae and the area surrounding the posterior accessory gland foramen.

**Terminology**

Terminology for all characters follows Reid (1996). Head width is used as an indicator of size as this measure is less prone to variation due to the degree of distension of the body than are other size indicators such as total length. Except in the case of K. occidentalis, where measurements and counts are given, these refer only to type specimens. Measurement values are expressed as minimum–mean–maximum.

**Abbreviations**

EDI eye diameter index (eye diameter expressed as a proportion of head width)

HWE width of head measured dorsally between the midpoint of each eye

AM Australian Museum, Sydney, Australia

ANIC Australian National Insect Collection, Canberra, Australia

BMNH The Natural History Museum, London, United Kingdom

MNHN Muséum National d’Histoire Naturelle, Paris, France

QM Queensland Museum, Brisbane, Australia

WAM Western Australian Museum, Perth, Australia

ZMH Zoologisches Institut und Zoologisches Museum, Universität Hamburg, Hamburg, Germany

**Species boundaries**

In this study, species are defined on the basis of discrete morphological gaps that indicate the occurrence of species boundaries. The resulting inferences about species boundaries are working hypotheses, subject to further testing with genetic markers, behavioural observations, or additional morphological characters.

Not all morphological discontinuities, however, indicate species boundaries: they may be artifacts of insufficient sampling (many populations of Onychophora are indeed represented by only a few specimens) or reflect intraspecific polymorphism. Because of this, a conservative approach has been taken towards species determination. For the majority of populations of Kumbadjena gen. nov. observed variation may simply be the result of geographical variation. The nature of sampling over the range of the genus means that it is not possible to determine whether there is sympathy among phenotypes. If sympathy can be identified in future studies, populations can more confidently be assigned to distinct species. Careful genetic and ecological studies are needed to demonstrate whether the observed variation represents different species, intraspecific polymorphism, or an intermediate situation involving assortative mating and only partial reproductive isolation. Until these studies are undertaken, I prefer not to attempt to
assign all *Kumbadjena* gen. nov. populations collected to date to one of the three species described below.

**SYSTEMATICS**

The Western Australian Onychophora could clearly be assigned to two genera on the basis of nine clear apomorphies distinguishing these taxa (Table 1). These two genera are described below as *Occiperipatoides* Rubberg, and *Kumbadjena* gen. nov.

Within the *Kumbadjena* gen. nov. complex, the determination of species boundaries based only on morphological characters has proved problematic. Reid (1996) reported that populations representing this complex (formerly the *O. occidentalis* complex) could be assigned to five putative species. However, the collection of more material has largely served to blur these boundaries rather than clarify them. Intra-population variation has swamped the supposed inter-species variation observed earlier. The main difficulty lies in the interpretation of colour patterns. While some patterns seem to be specific for particular populations, in all populations examined specimens were found that lacked any body pattern at all. Also, considerable variation can be found in colour patterns within a population, making diagnoses based on this trait difficult.

Some differences were found, however, in some populations in the structure of the crural papillae on the first pair of oncopods in males. Three variants of this structure were observed and as a result, three species within the complex can be recognised. As differences in this structure can only be seen in males using scanning electron microscopy, only those populations in which it was possible to study this trait in detail are recognised as belonging to one of the three species: *K. occidentalis*, *K. kaata* sp. nov. and *K. shannomensis* sp. nov. To assist with future studies, additional specimens belonging to this genus that cannot be reliably assigned to one of these three species are listed in the Appendix.

The type species of each genus is redescribed. Only those traits that differ from those described in the type species are included in new species descriptions.

**Kumbadjena** gen. nov.

Table 1

Dorsal primary papillae with ribbed scales in both sexes, microcristae not fused (Figure 14a)

first pair of oncopods not greatly enlarged, similar in size to remaining oncopods

crural papillae oncopods 1 protrude between third (proximal-most) spino-s pad and adjacent plica

crural papillae oncopods 2-14 very broad basally, conical distally, not elongate

crural papillar foramen oncopod 1 not obviously demarcated (Figures 3c, 6a, 10c, 12c, 13)

anterior accessory glands long, extend anteriorly approximately to oncopods 11

posterior accessory gland foramen joined, inverted Y-shaped (Figure 3h)

posterior accessory glands long and narrow, uniform width (Figure 4)

<table>
<thead>
<tr>
<th>Table 1 Distinguishing features of <em>Kumbadjena</em> gen. nov. and <em>Occiperipatoides</em> Rubberg.</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Kumbadjena</strong> gen. nov.</td>
</tr>
<tr>
<td>15 oncopod pairs</td>
</tr>
<tr>
<td>dorsal primary papillae scales ribbed proximally, partially ribbed distally (microcristae fused at tips of scales) in both sexes (Figures 3a,b; 6c,d; 10a,b; 12a,b)</td>
</tr>
<tr>
<td>first pair of oncopods greatly enlarged in males (Figure 1); slightly enlarged in females</td>
</tr>
<tr>
<td>crural papillae oncopods 1 protrude between third (proximal-most) spino-s pad and adjacent plica</td>
</tr>
<tr>
<td>crural papillae oncopods 2-14 very broad basally, conical distally, not elongate</td>
</tr>
<tr>
<td>crural papillar foramen oncopod 1 not obviously demarcated (Figures 3c, 6a, 10c, 12c, 13)</td>
</tr>
<tr>
<td>anterior accessory glands long, extend anteriorly approximately to oncopods 11</td>
</tr>
<tr>
<td>posterior accessory gland foramen joined, inverted Y-shaped (Figure 3h)</td>
</tr>
<tr>
<td>posterior accessory glands long and narrow, uniform width (Figure 4)</td>
</tr>
</tbody>
</table>
first pair of oncopod feet enlarged in males, slightly enlarged in females. Crural papillae oncopods 1 protrude between third (proximal-most) spinous pad and adjacent plica; foramen not obviously demarcated from rest of papillae. Crural papillae oncopods 2-14 very broad basally, conical, not elongate distally; papillar scales and scale microcristae fused, or partially fused, smooth; foramen a transverse slit opening on inner side of smooth region. Posterior accessory gland foramen joined, inverted Y-shaped. Posterior accessory glands long and narrow, uniform width. Crural glands extending length of body from first pair of oncopods. Ovoviparous, ova follicular.

Remarks
A new genus is proposed here for representatives of the O. 'occidentalis' species-complex because all of its members share a number unique characters that are not present in O. gilesii, the type species of the genus Occiperipatoides Ruhberg, 1985. The differences between these two genera are shown in Table 1. In addition, O. gilesii from Mundaring (31°51'S; 116°10'E) and a representative of the C. 'occidentalis' species-complex from Ferguson R. (33°23'S; 115°45'E) were shown to differ at 81% of 21 allozyme loci by Briscoe and Tait (1995). This level of difference is similar to that observed between distinct onychophoran genera that were included in the same study.

The sister-group relationship between these two taxa was well supported in the phylogenetic analysis of Reid (1996), and given the distributions of these two species, both occurring in the southwestern corner of Western Australia, is not surprising.

The enlarged feet on the first pair of oncopods of males of this genus (Figure 1) can be seen in males of all sizes examined, including juveniles and unborn specimens (presumably males but not possible to sex by other means) present in the uteri.

Etymology
The generic name is composed of words borrowed from the Nyungar dialect, a language spoken by the Aboriginal inhabitants of southwestern Western Australia (Dench, 1999). Kumba, means 'big', and djena, 'foot'. The name refers to the enlarged first oncopod feet in members of this genus. Gender feminine.

**Kumbadjena occidentalis** (Fletcher), comb. nov.  
Figures 2–4, 8

**Peripatus leuckarti** var. occidentalis Fletcher, 1895: 185–186.


**Material examined**

**Neotype**  
♂ Western Australia, Bridgetown Jarrah Park, 20.3 km west of intersection of South Western Hwy and Brockman Hwy, 34°01'S; 116°00'E, 250 m, 3 Apr 2000, coll. A. Reid and R. Roberts (WAM T42554).

**Other material examined**  
Western Australia: 13♂, 13♀, 1 juv., data as for neotype (WAM T42555); 1♂, 2♀, 1 juv., Karri Gully, 25.4 km west of intersection of South Western Hwy and Brockman Hwy, 34°01'S; 115°58'E, 300 m, 2 Apr 2000, coll. A. Reid and R. Roberts (WAM T42556).

**Diagnosis**  
Dorsomedially body indistinctly patterned, or not patterned. Crural papillae on oncopod 1 broad basally, abruptly tapered, cylindrical distally; crural papillae on oncopods 2–14 broad basally, abruptly tapered, conical, blunt distally. Crural papillae on oncopod 1 with finely ribbed scales basally, distally scales with distinct ribs; oncopods 2–14 crural papillae with finely ribbed scales basally, smooth distally (only very slightly crenulated), papillar scales and microcristae fused.

---

*Figure 1*  
*Kumbadjena shannonensis* sp. nov.: a, ventral foot oncopod 1; b, ventral foot oncopod 2, drawn to the same scale, male 0.99 mm HWE (WAM 91/1132). Scale bar 0.05 mm. (Figure reproduced from Reid, 1996: 821.)
Description

Measurements

HWE males 0.90–1.02–1.07 mm (n=15, neotype 1.07 mm HWE); females 1.05–1.16–1.25 mm (n=14).

Colour pattern

Body pigmented. Pigment not soluble in alcohol. Dorsomedially body indistinctly patterned, or not patterned; ground-colour tan, orange, or greyish-blue; primary papillae light-coloured basally, dark tipped. Mid-dorsal dark stripe absent; every fourth plica with 1–2 dark-coloured papillae on each side of mid-dorsal line (Figure 2a) (not clearly visible in dark ground colour specimens (Figure 2b)); rest of dorsal integument with regular mottling, scattered light-based papillae (Figure 2b), or, tan and orange specimens with dark longitudinal bands dorsilaterally (Figure 2a). Few specimens with indistinct regular pattern of series of dark crosses (arms of crosses extend toward oncopods) over indistinct lighter-coloured diamonds (Figure 2c). Laterally with longitudinal light-coloured band dorsal to oncopods, or with light-coloured patches between oncopods. Some specimens with dark longitudinal bands immediately above and between oncopods. Oncopods colour similar to, or slightly paler than body; with light-coloured patches at junction with feet. Papillae around anal opening pigmented as for rest of body. Ventral pigment very pale; dark patches between ventral organs and base of oncopods. Spinous pads pale yellow or greyish-blue. Integument between genital and anal openings pigmented as for rest of ventrum, or darker than rest of ventrum.

Antennal rings banded: tan or with tan mottle dorsally and ventrally, or not banded, ground-colour; when present, dorsal banding on every fourth ring distal to and including ring five, or in tan and brown specimens, proximal half to two-thirds of antennae tan, sometimes with some greyish-blue pigment on each antennal ring; distal half to two-thirds of antennae greyish-blue.

Newborn animals and posterior-most embryos in uteri pigmented.

Figure 2  *Kumbadjena occidentalis* (Fletcher), dorsal integument: a, male 1.00 mm HWE (WAM T42555); b, female 1.20 mm HWE (WAM T42555); c, male 1.0 mm HWE (WAM T42555). Scale bars 1.0 mm.
Figure 3  *Kumbadjena occidentalis* (Fletcher) (SEM’s): a, primary papilla, male 1.05 mm HWE (WAM T42555); b, primary papilla, female 1.25 mm HWE (WAM T42555); c, crural papilla oncopod 1, male, 1.00 mm HWE (WAM T42555), arrow indicates foramen; d, crural papilla oncopod 3, male, 1.00 mm HWE (WAM T42555); e, crural papilla oncopod 7, male 1.0 mm HWE (WAM T42555), arrow indicates foramen; f, crural papilla oncopod 12, male 1.00 mm HWE (WAM T42555), arrow indicates foramen (partly obscured by crural gland exudate); g, anterior accessory gland papilla, male 0.90 mm HWE (WAM T42555); h, posterior accessory gland foramen, male 1.07 mm HWE (WAM T42555). Scale bars a–g, 100 μm, h, 200 μm.
Antennae

Approximately 30 antennal rings in adults and juveniles; wide and narrower antennal rings alternate; two rows of bristles on rings (counting from distal to proximal) 3, 4, 6, 8, 12, or 3, 6, 9. Distal 7–10 antennal rings with sensory bulbs. Proximal antennal rings expanded ventrally to form sensory pads; sensory pads with up to 2–3 rows of sensilla.

Eyes

EDI males 0.05–0.10–0.12; females 0.10–0.11–0.12.

Head (males)

Males with no modification of head papillae (i.e. papillae on head do not differ from remaining dorsal papillae). Eversible head structure absent.

Head (females)

Females with no modification of head papillae.

Jaws

Inner jaw with 5–6 denticles; diastema absent; outer jaw without accessory tooth. Tongue with longitudinal row of 5–6 teeth. Buccal folds in single unbroken row.

Integument

Dorsum with 12 complete plicae between oncopods; wide and narrower plical folds alternate. Males with 11–13–15, females with 13–15–18 papillae counted from mid-dorsal line to junction of oncopod 10. Dorsal body papillae approximately uniform size; alternate plicae with slightly larger primary papillae; primary papilla with short, narrow bristle between pair of larger primary papillae with longer, more robust bristles and smaller secondary papillae between primary papillae; dorsal primary papillae cylindrical; conical apical piece absent; papillar scales ribbed proximally (microcristae well defined), partially ribbed distally (microcristae fused at tips of scales) in both sexes (Figure 3a,b); lateral primary papillae slightly enlarged or elongate, with more prominent pair between oncopods in line with junction of oncopods and body; papillae around anal opening slightly larger than those on rest of body; remaining integument with small scales.

Oncopods

Fifteen pairs in both sexes. First pair of oncopod feet enlarged in males, slightly enlarged in females. Last pair of oncopods well developed in both sexes, orientation as for remaining oncopods. Basal foot papillae absent. Distal foot papillae one anterior, one median, one posterior; both sexes with 1–2 bristles on anterior distal foot papillae oncopod one, 1–2 bristles on posterior distal foot papillae and one bristle on median foot papillae. Distal foot papillae on remaining feet each with single sensory bristle. With three complete spinous pads; fourth broken spinous pad present. Spinous pads well-developed on all oncopods. Nephridiopores at centre of third spinous pad on fourth and fifth oncopod pairs; nephridiopore foramen U-shaped.

Figure 4  

*Kumbadjena occidentalis* (Fletcher). Male reproductive tract and associated glands: male 1.05 mm HWE (WAM T42555); aag, anterior accessory gland; cg, crural gland; pa, posterior accessory gland; sv, seminal vesicle; t, testis; ve, vas deferens; vd, vas efferens. (Only the posterior parts of the crural glands are shown. They extend anteriorly to oncopod 1.) Scale bar 2 mm.
Male reproductive tract

Male genital pad low, semicircular; gonopore cruciform (with arms equidistant), arms extending close to rim of genital pad. Vasa efferentia with thin, flexible walls; proximal vasa efferentia separate, do not lie parallel, or lie parallel for part of their length before fusing to form vas deferens; broad; vas deferens continues directly (without looping posteriorly) from paired vasa efferentia to gonopore (Figure 4), not thick walled, opaque, not shiny. Spermatophore pouch present.

Male glands and gland papillae

Crural papillae, one per oncopod, present on ventral side of oncopods 1–14; protrude between third (proximal-most) spinous pad and adjacent plica (oncopod 1), or between plicae 4–5 (counting from third spinous pad) on oncopods 2–14. Papillae shape differs among oncopods: papillae broad, semicircular proximally, cylindrical distally, divided into distinct basal and distal regions (oncopod 1), or broad based, semicircular proximally, abruptly tapered, conical, blunt distally (oncopods 2–14); with finely ribbed scales basally, distally scales with distinct ribs (oncopod 1) (Figure 3c), or with finely ribbed scales basally, smooth distally (very slightly crenulated), papillar scales and microcristae fused oncopods 2–14 (Figure 3d–f); crural papillae oncopods 1 open close to, but slightly proximal to distal tip of papilla via a short slit (Figure 3c); crural papillae oncopods 2–14 open via a long transverse slit on inner side of papilla at base of smooth region (Figure 3e,f). Crural glands extend into lateral haemocoel from oncopod 1, or do not extend into lateral haemocoel, confined to oncopods (oncopods 2–14); glands extending from oncopods 1 straight, extend length of body posteriorly to oncopod 11 (Figure 4). Coxal organs absent. Anterior accessory gland papillae on genital segment at base of last pair of oncopods; do not protrude significantly, with ill-defined margins; without smooth distal region; foramen a longitudinal slit (Figure 3g). Anterior accessory glands present; long; lying freely within perivisceral haemocoel; extending anteriorly approximately to oncopods 11 (Figure 4). Posterior accessory glands present; foramen approximately midway between genital and anal openings; gland foramen joined, forming inverted Y shape (Figure 3h); glands long narrow, approximately uniform width (taper slightly distally), folded (Figure 4).

Female reproductive tract

Females without ovipositor; ovoviviparous; gonopore not borne on raised pad; foramen shape cruciform, (with arms equidistant). Ovarian tubes separate, suspended along entire length to pericardial floor; with thin walls; oviducts unite close to ovary; ova follicular. Spermathecae present; open into oviducts via single duct. Additional pouches present. Embryos in individual uteri at successive stages of development along length of uteri.

Female glands and gland papillae

Crural papillae absent (see Remarks). Uterine glands absent.

Remarks

Fletcher’s (1895) description of P. occidentalis was based on some specimens that were sent to him in Sydney by A. M. Lea. Lea was the Government Entomologist of Western Australia from 1895–1898, and was later based at the South Australian Museum. The locality name in the description was given only as ‘Bridgetown’, no type specimens were designated, and the depository for the specimens was not indicated. Despite considerable searching and correspondence to a number of institutions (including the South Australian Museum), the types have not been traced. For this reason, a neotype is designated here to define the nominal taxon. Because the original description is not very detailed and there are no illustrations, the designation of a neotype is necessary to enable comparisons to be made between K. occidentalis and other taxa.

According to the International Code of Zoological Nomenclature (1999) a neotype must come from, ‘as nearly as practicable from the original type locality’ (Article 75.3.6: 85). Despite extensive searching over a number of days on two fieldtrips (one in May 1995, and the other in April 2000), no onychophorans were found in the immediate vicinity of Bridgetown.

A number of possibilities could explain why we were unable to find specimens in Bridgetown:

1. The area surrounding Bridgetown itself was very dry and largely cleared, in marked contrast to the forest in the Bridgetown Jarrah Park from which specimens were easily found. It is possible that Bridgetown may have experienced a higher rainfall (and therefore more suitable onychophoran habitat) over a century ago when the specimens were collected. This possibility is likely as it is well known that extensive land clearing, as has occurred in the vicinity of Bridgetown over the last hundred years, can radically alter localised rainfall patterns. Indeed, it appears that there has been a significant decrease in annual precipitation at Bridgetown over the period for which records are available (1888–1999) (Figure 5). Whether this has any bearing on onychophoran distribution, or if other correlates have greater significance, is unknown.

2. The collector may have used the locality name ‘Bridgetown’ for the specimens he collected because it was the nearest named place to
where the specimens were found, rather than the exact locality. If this is the case, the type specimens may not have been found in the immediate vicinity of the town.

3. Onychophorans do occur at Bridgetown but they have not yet been found.

Despite this latter possibility I have decided, in order to stabilise the taxonomy and nomenclature pertaining to this species, to designate a neotype from our available material. The neotype was selected from the nearest possible place to Bridgetown: the Bridgetown Jarrah Park, approximately 12.5 kilometres west of the town (20.3 kilometres by road).

The *K. occidentalis* specimens from Bridgetown Jarrah Park described above agree with the original description in all but one of the few characters that were used to diagnose the species. Fletcher (1895: 185) notes, ‘the males have white papillae on most of the legs, but not on those of the first pair’. If he is referring to the crural papillae in this statement (which seems likely, as they are most obviously white on each oncopod), the specimens described here differ in having crural papillae on the first pair of oncopods. All the male Western Australian Onychophora I have examined to date have crural papillae on the first pair of oncopods. It may be that Fletcher overlooked these papillae because their position on the first pair of oncopods differs from

---

**Figure 5** Annual rainfall measured at Bridgetown, WA, 33°57'28"S; 116°08'12"E for the period 1888-1999. Regression of annual rainfall against time (plotted as yearly averages). Regression equation \( Y = -0.937X + 2656.1; P = 0.0105 \ (P<0.05), r^2 = 0.017 \). proportion of total variation accounted for by regression. Data obtained from the Severe Weather Section Regional Office of the Bureau of Meteorology, Perth.
those on the remaining oncopods. Because the crural papillae on the first oncopod pair are positioned distally and abut the third spinous pad, they are not as obvious as those on the other oncopods, particularly if they are retracted.

Dakin (1920) noted the presence of crural glands in female *Occiperipatoides*. He stated that they occur only occasionally and, ‘when found there is no regularity as to the legs containing them’ (Dakin, 1920: 379). In his paper, Dakin referred to a single species, *Peripatoides occidentalis*, and calls the northern form (here referred to as *Occiperipatoides gilesii*) *Peripatoides occidentalis* var. *gilesii*. For this reason it is difficult to determine from his detailed anatomical study to which species he refers in describing the presence of crural glands in females. No attempt was made in this study to section the oncopods of females to look for crural papillae, and no crural glands were observed in any of the specimens examined. However, because of Dakin’s (1920) remarks, the possibility that crural glands do occur in females of either Western Australian genus cannot be excluded.

The description of this species given in Reid (1996) was based on the only specimens available to the author at that time from as close as possible to the type locality, but some distance away (the Shannon River area, approximately 34°46’S; 116°22’E). Examination of more material in the present study, and more importantly, specimens from close to the type locality has shown that the Shannon River specimens belong to a new species described here as *K. shannonensis* sp. nov.

Specimens from the Leeuwin Naturaliste National Park and Big Brooke State Forest (see Appendix) are very similar to *K. occidentalis*, particularly in the lack of fusion of the distal scale microcristaee on the crural papillae of oncopods 1 (Figure 6a,b), which is diagnostic for *K. occidentalis*. They differ from *K. occidentalis* in that some (but not all) specimens are distinctively patterned (Figure 7a–d). In addition, the general body papillar scale microcristae show a greater degree of fusion on the distal papillar scales in specimens from the Leeuwin Naturaliste NP than those of *K. occidentalis* (Figure 6c,d, compare with Figure 3a,b). For these reasons the specimens from

![Figure 7](image-url)
these two localities are not assigned to *K. occidentalis*.

**Habitat**

In and under rotting logs. Hand collected specimens were usually lying flat and straight when first exposed.

**Distribution**

Western Australia: Bridgetown Jarrah Park, 34°00'S; 116°00'E to Karri Gully 34°01'S; 115°58'E (Figure 8).

*Kumbadjena kaata* sp. nov.

Figures 8–10

**Material examined**

**Holotype**

δ Western Australia, Porongurup NP, Scenic Drive, 3.1 km W of intersection of Scenic Drive and Bolganup Rd., 34°39'S; 117°51'E, 320 m, 11 Apr 2000, coll. A. Reid and R. Roberts (WAM T42557).

**Paratypes**

18δ, 4♀, 4 juv., data as for holotype (WAM T42558).

**Other material examined**

Western Australia: 6δ, 5♀, Porongurups Ra., 4 Mar 1994, coll. Monteith and Janetzi (QM S29906); 1δ, Porongurup NP, 6 Mar 1979 (AM KS14993); 1δ, Porongurup NP, (AM KS14528); 1δ, 1♀, 1 juv., Porongurup NP, 34°41'S; 117°52'E, 7 Oct 1981, coll. I. D. Naumann and J. C. Cardale (ANIC); 1♀, Porongurup NP, S.end of Millinup Pass, 34°42'S; 117°54'E, 30 Mar 1993, coll. M. S. Harvey and J. M. Waldock (WAM 95/499); 2♀, data as for previous (WAM 95/491-3); 1δ, 3♀, 31 Mar 1993, coll. M. S. Harvey and J. M. Waldock (WAM 95/494-7); 1♀, Porongurups Ra., 1.85 miles (3 km) along scenic drive to Woodlands Rd from Bolganup Dam, 15 Feb 1974, A. Solem (FMNH).

**Diagnosis**

One to three rows of 1–3 dark papillae on each side of dorsal midline, remaining dorsal integument with regular mottling. Crural papillae oncypods 2–
14 abruptly tapered, broad basally, conical distally. Crural papillae with finely ribbed scales basally, smooth distally; papillary scales and microcristae fused completely at base of smooth region, only partially fused at distal tips giving knobbly appearance (most obvious on crural papilla on oncopod 1).

Description

Measurements
HWE males 1.00–1.09–1.20 mm (n=14, holotype 0.12 mm HWE); females 1.00–1.13–1.25 mm (n=11).

Colour pattern
Ground colour tan, grey, buff brown, or greyish-blue; primary papillae unicolorous, or light-coloured basally, dark tipped. Most specimens with 1–3 rows of 1–3 dark brown or black papillae (median pair darkest) on each side of dorsal midline forming distinct patches dorsal to and between each oncopod pair (those between each oncopod pair most pronounced) (Figure 9a), sometimes forming dark median stripe (Figure 9b); rest of dorsum with regular mottling (Figure 9c) (particularly in tan specimens), light-coloured median band bordered by darker pigment (Figure 9a), or not patterned (usually dark specimens) (Figure 9d). Some specimens with longitudinal light-coloured band laterally, dorsal to oncopods (one male with prominent broad tan band), or some specimens with light-coloured patches dorsal to oncopods. Papillae around anal opening pigmented as for rest of body. Tan specimens with dark grey patches beside ventral organs. Spinous pads tan or grey.

Antennal rings not banded, ground-colour (greyish blue specimens), or banded, tan or with tan mottle dorsally for half antennal length (tan and brown specimens); dorsal banding on alternate rings distal to, and including ring five, or (in tan and brown specimens), proximal half to two-thirds of antennae tan, sometimes with greyish-blue pigment on each antennal ring, distal half to two-thirds of antennae greyish-blue (ventral banding present only in tan specimens, usually concentrated on basal antennal rings).

Figure 9  *Kumbadjena kaata* sp. nov., dorsal integument: a, male paratype 1.10 mm HWE (WAM T42558); b, male paratype 1.20 mm HWE (WAM T42558); c, female paratype 1.05 mm HWE (WAM T42558); d, male paratype 1.10 mm HWE (WAM T42558). Scale bars 1.0 mm.
Newborn animals pigmented.

**Antennae**

Two rows of bristles on rings (counting from distal to proximal) 3, 4, 6, 8. Distal 8–9 antennal rings with sensory bulbs. Sensory pads with up to three rows of sensilla.

**Eyes**

EDI males 0.10–0.11–0.12; females 0.09–0.11–0.12.

**Integument**

Males with 10–13–16, females with 12–14–20 papillae counted from mid-dorsal line to junction of oncopod 10. Papillar scales ribbed proximally, partially ribbed distally (microcristae fused at tips of scales) in both sexes (Figure 10a,b).

**Oncpods**

Males with 1–3 bristles on anterior distal foot papillae oncopod one; 1–2 bristles on posterior...
distal foot papillae and 1–2 bristles on median foot papillae. Distal foot papillae on remaining oncopods each with single sensory bristle.

**Male reproductive tract**
Proximal vasa efferentia lying close together, parallel for part of their length before fusing to form vas deferens; broad; vas deferens continues anteriorly from paired vasa efferentia for short distance before looping posteriorly toward gonopore, or loops posteriorly immediately following junction of paired vasa efferentia toward gonopore.

**Male glands and gland papillae**
Crural papillae protrude between third (proximal-most) spinous pad and adjacent plicae (oncopod 1), or between plicae 3–4 (counting from third spinous pad) on oncopods 2–14. Papillae shape differs among oncopods: papillae semicircular proximally, cylindrical, taper distally (oncopod 1) (Figure 10c), or broad based, semicircular proximally, abruptly tapered, conical distally on oncopods 2–14 (Figure 10d–f); with finely ribbed scales basally, smooth distally, papillar scales and microcristae fused completely at base of smooth region, only partially fused at distal tips giving knobby appearance (most obvious on crural papilla on oncopod 1) (Figure 10c–f); crural papillae open via short transverse slit at base of smooth region (oncopod 1), or via a long transverse slit on basal half of smooth region (onycopods 2–14); foramen openings on inner side of papillae. Crural glands oncopods 1 extending length of body posteriorly to oncopods 12–13. Anterior accessory glands extending anteriorly approximately to oncopods 10–11.

**Remarks**
One male with tan ground colour has regular mottling consisting of a broad tan band dorsally, flanked by dark grey bands laterally and a narrow grey band along midline. One specimen (QM S29906) has distinctive tan bands dorsal to the oncopods.

Females collected in March, April and October contained embryos in the oviducts and many juveniles were found when specimens were collected in April 2000.

*Kumbadjena kaata* differs from other members of the genus in two characters: the dorsal body patterning, and the shape of the distal tip of the crural papillae on the first pair of oncopods in males. Specimens are easy to find in the Porongurup National Park and there is a good deal of suitable timber on the ground for onychophorans to inhabit. They would seem to be common in the Porongurups Range.

**Habitat**
Specimens were found in rotting logs and leaf litter. Hand collected specimens were usually lying flat and straight when first exposed, or with the anterior half of body curved, and head partially tucked in loop of body.

**Distribution**
Western Australia, Porongurup NP, approximately 34°39’S; 117°51’E–34°41’S; 117°52’E (Figure 8).

**Etymology**
The specific name is derived from the word ‘kaat’, meaning ‘hill’ or ‘mountain’ in the Nyungar dialect, a language spoken by the Aboriginal people of the south-west of Western Australia (Dench, 1999). It refers to the range of hills in which this species is found.

*Kumbadjena shannonensis* sp. nov.
Figures 1; 8; 11a,b; 12

**Material examined**

**Holotype**
♂ Western Australia, Shannon NP, Giant Karri Grove, Deeside Coast Rd, 5 km S of intersection of Middleton Rd and Deeside Coast Rd, 34°38’S; 116°20’E, 150 m, 8 Apr 2000, coll. A. Reid and R. Roberts (WAM T42559).

**Paratypes**
12♂, 10♀, 6 juv. data as for holotype (WAM T42560).

**Other material examined**

**Diagnosis**
Usually with dark brown papilla on each side of midline dorsal to each oncopod pair surrounded by squarish light-coloured patch. Some specimens distinctly patterned. Crural papillae with finely ribbed scales basally, crenulated distally, papillar scales and microcristae partially fused, smooth.
Figure 11  Dorsal integument: a, Kumbadjena shannonensis sp. nov., female paratype 1.12 mm HWE (WAM T42560); b, K. shannonensis sp. nov., male paratype 0.92 mm HWE (WAM T42560); c, Mt Chudalup, male 0.95 mm HWE (WAM T42567); d, Walpole Nornalup NP, female 1.20 mm HWE (WAM T42568); e, William Bay NP, female 0.87 mm HWE (WAM T42573); f, West Cape Howe NP, female 1.20 mm HWE (WAM T42574). Scale bars 1.0 mm.

Description

Measurements

HWE males 0.92-1.00-1.12 mm (n=13, holotype 1.00 mm HWE); females 0.97-1.07-1.12 mm.

Colour pattern

Ground colour tan, buff brown, olive green, grey, or greyish-blue; primary papillae light-coloured basally, dark tipped. Dark brown papilla usually present on each side of dorsal midline dorsal to
each oncopod pair (18 of 24 specimens) surrounded by squarish light coloured patch (Figure 11a) (light coloured patch indistinct or absent in dark ground colour specimens); remaining integument with evenly scattered tan or tan-based papillae, or additional light ground-coloured patches dorsolaterally between median light coloured patches (Figure 11b); light coloured patches bordered by dark pigment (except in dark ground colour specimens). Laterally with longitudinal light coloured band dorsal to oncopods. Papillae around anal opening pigmented as for rest of body, or tan. Spinous pads pale yellow or greyish-blue.

Antennae

Two rows of bristles on rings (counting from distal to proximal) 3, 4, 6, 8 (not always on all 4 rings). Distal eight antennal rings with sensory bulbs. Sensory pads with up to 2-3 rows of sensilla.

Figure 12  *Kumbadjena shannonensis* sp. nov. (SEM’s): a, primary papilla, male paratype, 1.00 mm HWE (WAM T42560); b, primary papilla, female paratype, 1.12 mm HWE (WAM T42560); c, crural papilla oncopod 1, male paratype, 1.12 mm HWE (WAM T42560), arrow indicates foramen; d, crural papilla oncopod 3, male paratype, 1.00 mm HWE (WAM T42560), arrow indicates foramen; e, crural papilla oncopod 7, male, paratype, 1.00 mm HWE (WAM T42560); f, crural papilla oncopod 12, male paratype, 1.00 mm HWE (WAM T42560). Scale bars 100 μm.
Eyes
EDI males 0.07–0.10–0.12; females 0.07–0.10–0.12.

Integument
Males with 10–13–15 papillae counted from mid-dorsal line to junction of oncopod 10, females with 12–15–20 papillae counted from mid-dorsal line to junction of oncopod 10. Papillar scales ribbed proximally, smooth distally (microcristae fused) in both sexes (Figure 12a,b).

Oncopods
Males with two bristles on anterior distal foot papillae oncopod one; 1–3 bristles on posterior distal foot papillae and 2–3 bristles on median foot papillae oncopod one. Distal foot papillae each with single sensory bristle on remaining oncopods.

Male reproductive tract
Proximal vasa efferentia lying close together, parallel for part of their length before fusing to form vas deferens, or separate, do not lie parallel for part of their length before fusing to form vas deferens; not markedly broad; vas deferens continues directly (without looping posteriorly) from paired vasa efferentia to gonopore.

Male glands and gland papillae
Crural papillae greatly reduced on oncopods 14. Papillae shape differs among oncopods: papillae semicircular proximally; cylindrical, taper distally (oncopod 1) (Figure 12c), or broad based, semicircular proximally, abruptly tapered, conical, blunt distally on oncopods 2–14 (Figure 12d–f); with finely ribbed scales basally, crenulated distally, papillar scales and microcristae partially fused, smooth. Crural papillae open via a short transverse slit at base of smooth region (oncopod 1) (Figure 12c), or via a long transverse slit on basal half of smooth region (oncopods 2–14); foramen openings on inner side of papillae (Figure 12d–f). Anterior accessory glands extending anteriorly approximately to oncopods 9–11.

Remarks
The second pair of feet in males are enlarged, but not to the extent of the first pair of feet. Some juveniles have enlarged feet on the first pair of oncopods. It is likely they are males; they were too small to dissect to confirm this. Some of the preserved males collected in April 2000 had extruded material extending in a thick thread from the anterior accessory glands. Some of the females collected at this time contained well-developed

Figure 13 Crural papilla on oncopod 1 in males (SEM's): a, Mt Chudalup, 1.00 mm HWE (WAM T42567); b, Walpole Normalup NP, 1.15 mm HWE (WAM T42568); c, West Cape Howe NP, 1.00 mm HWE (WAM T42574). Scale bars a, 200 μm; b, c, 100 μm.
embryos in uteri and large numbers of juveniles were found at the site.

Specimens from the following localities have crural papillae on the first pair of oncopods that are similar to those in this species (smooth distally, with microcristae partially fused) (Figure 13): Mt Chudalup (WAM T42567), Walpole Normalup National Park (WAM T42568), William Bay National Park (WAM T42573) and West Cape Howe National Park (WAM T42574). When patterned, these populations show some similarities to and some differences from patterned *K. shannonsensis* (for example the squarish light-coloured patch) (compare Figure 11a,b with 11c–f). Until other (possibly molecular) characters are examined, specimens from these localities are not assigned to *K. shannonsensis*, however, the similarities suggest they may be closely related to this species.

**Habitat**

Leaf litter and under bark, under moss on logs, in logs. Hand collected specimens were usually lying flat and straight when first exposed.

**Distribution**

Western Australia, Shannon National Park from Fish Creek Rd, 34°23.75'S; 116°26.2'E to Dog Pool on Shannon River, 34°46'S; 116°22'E (Figure 8).

**Etymology**

The specific name is derived from the type locality of this species, Shannon National Park.

**Occiperipatoides Ruberg**

Table 1


**Type species**

*Peripatoides gilesii* Spencer, 1909, by original designation.

**Diagnosis**

Dorsal primary papillae with ribbed scales in both sexes (microcristae not fused). Sixteen oncopod pairs; first pair of oncopod feet not enlarged. Crural papillae on oncopod 1 protrude between plicae 2–3 (counting from the third spinous pad). Crural papillae on oncopods 2–15 moderately broad basally, cylindrical, elongate distally, blunt; papilar scales and scale microcristae fused, or partially fused, smooth. Crural papillae open distally (oncopods 1–3), smooth rim surrounding foramen lip-shaped; crural papillae foramen a transverse slit opening on inner side of smooth region (oncopods 6–15). Crural glands extending length of body from first pair of oncopods posteriorly to oncopods 10 or 11. Posterior accessory gland foramen separated; posterior accessory glands broad and saccate. Ooviviparous, ova follicular.

**Occiperipatoides gilesii** (Spencer)

**Figures 14–16**


**Material examined**

**Syntypes**

**Western Australia:** *Peripatoides gilesii* 4? (dehydrated, sex unknown), Armadale, 32°09’S; 116°00’E, 26 Mar 1907, coll. H. M. Giles (MV); *Peripatoides woodwardi* δ Lion Mill (near Perth) [Mt Helena 31°13’54”S; 115°54’00”E], 1905, coll. W. Michaelson (Paris Boc7 and ON 29); ?, data as for previous specimen, 20 Aug 1905, coll. Hambg SW Aust. exp. (BMNH).

**Other material examined**

Figure 14 Occiperipatoides gilesii (Spencer) (SEM’s): a, primary papilla; b, crural papilla oncopod 1; c, crural papilla oncopod 3; d, crural papilla oncopod 7, arrow indicates foramen; e, crural papilla oncopod 13. a-e, male 1.20 mm HWE, Pickering Brook, Kattororia Heritage Trail, 32°02'S; 116°06'E (unregistered specimen). Scale bars 100 μm.

Sep 1974, coll. G. H. Lowe (WAM 76/13); 1♀, Hay Creek, Mundaring Weir, 31°58'S; 116°10'E, 19 Jul 1914, coll. W. B. Alexander (WAM 14/985); 1♂, Kalamunda, 31°58'S; 116°03'E, Jun 1962, coll. R. P. McMillan (WAM 97/2566); 1♂, Lesmurdie, 32°01'S; 116°03'E, Jul 1963, coll. R. P. Mc Millan (WAM 91/1115); 1♀, data as for previous specimen (WAM 91/1116); 2♂, Darlington Ranges, Pickering Brook, Kattororia Heritage Trail, 32°02'S; 116°06'E, coll. P. T. Bailey (WAM); 4♂ 3♀, Jandakot 32°07'S; 115°50'E, 7 Mar 1991, coll. S. Doyle (AM KS40071); 1♂, Roleystone, 32° 07'S; 116 °04'E, 29 Aug 1978, coll. D. Burtenshaw (WAM 91/1119); 1♀, Mt Dale, W side of, 32°07'S; 116°18'E, 29 Sep 1997, coll. S. Slack-Smith and J. M. Waldock (WAM 99/246); 1♀, 3 km NE of Jarrahdale, 32°09'S; 116°05'E, 9 Nov 1995, coll. O. G. Nichols (WAM 97/2565); 1♀, Gleneagle, 32°15'S; 116°10'E, 22 Sep 1971, coll. J. A. Springett (WAM 76/7); 1♀, Jarrahdale, Alcoa mine site, 32°19'S; 113°59'E, 1997, coll. K. E. Brennan (WAM T40857); 1♀, Gleneagle, ~32°19'S; 116°11'E, 22 Oct 1971, coll. J. A. Springett (WAM 76/7); 1♀, near Gleneagle, 10 km ENE of Jarrahdale, 32°19'S; 116°11'E, 14 Aug 1992, coll. O. Nicholls (WAM 95/484); 3♀, Serpentine, 32°22'S; 115°58'E, 28 Aug 1928, coll. L. Glauert (WAM...
13713–5); 1♂, 1♀, Serpentine R., ~32°23'S, 116°00'E (WAM 91/1120–1); 1♀, Serpentine Falls, 27 July 1969, coll. S. Slack-Smith (WAM 76/6); 1♀, Karmet Brook, 32°24.4'S; 116°01.6'E, 29 July 1998, coll. S. L. Judd (WAM T40858); 2♂, Mt Cooke, 32°25'S; 116°18'E, 30 June 1991, coll. J. M. Waldock (WAM 91/1117–8); 1♀, locality as for previous specimen, 20 June 1992, coll. D. Black (AM KS40072); 2♀ locality as for previous specimen, 31 July 1991, coll. M. S. Harvey and J. M. Waldock (WAM 95/487–488); 2♀, Escarpment between Whittakers Mill and North Dandalup, 32°33'S; 116°00'E, 15 June 1969, coll. S. Slack-Smith (WAM 76/2–3); 1♀, Whittaker Forest Block, Scarp Rd, 32°33.6'S; 116°00.3'E, 29 July 1998, coll. S. L. Judd (WAM T40865); 2♀, 31 km NE Dwellingup (North East Rd), 32°43'S; 116°04'E, 21 June 1992, coll. D. Black (AM KS40117); 1♀, Dwellingup, Young Block, 32°43'S; 116°02'E, Apr 1980, coll. I. Abbott (WAM 91/1112); 1♂, 3 km NE of Jarrahdale, 34°54'S; 117°55'E, 9 Nov 1995, coll. O. G. Nicholls (WAM 97/2565); 1♀, Jarrahdale, 34°54'S; 117°55'E (WAM 91/1113); 1♂, 13.8 km NNE of Jarrahdale, adjacent to McAllister Rd, 1.2 km from Albany Hwy, 6 Jul 1994, coll. F. Nichols (WAM 95/485); 1♀, John Forrest NP, Sep 1976, coll. G. H. Lowe (WAM 91/1114).

Diagnosis
As for genus.

Description

Measurements
HWE males 1.08–1.29–1.40 mm; females 1.26–1.41–1.53 mm.

Colour pattern
Body pigmented. Pigment not soluble in alcohol. Body patterned; ground-colour tan or greyish-blue; primary papillae light-coloured basally, dark tipped (some papillae tan-based with dark brown or grey apices). Mid-dorsal dark stripe absent; every fourth plica with transverse row of dark grey papillae, rows of four (two each side of mid-dorsal line) alternate with two (one each side of mid-dorsal line); remaining integument with regular tan and dark mottle, or very dark grey specimens with scattered tan, or tan-based papillae. Predominantly tan specimens with grey mottle, every 4th plica with two dark grey plicae (one each side of midline) and longitudinal greyish bands dorsal to oncopods. Some specimens with head anterior to eyes and base of antennae tan (WAM T40856, WAM 99/250, WAM 99/249 (all from caves in the Yanchep National Park) and WAM 95/488 from Mt Cooke). Laterally with longitudinal light-coloured band dorsal to oncopods, or without pattern, colour as for rest of body. Oncopods often with light-coloured patches close to body (pale yellow), or primarily greyish blue; without light-coloured patches at junction with feet. Papillae around anal opening pigmented as for rest of body. Ventral pigment mainly absent; with few scattered greyish-blue papillae. Spinous pads pale yellow or greyish-blue. Integument between genital and anal openings pigmented as for rest of ventrum, or darker than rest of ventrum.

Antennae
Approximately 30 antennal rings in adults and juveniles; wide and narrower antennal rings alternate; two rows of bristles on rings (counting from distal to proximal) 3, 6, 8 or 3, 4, 6, 8. Distal 8–9 antennal rings with sensory bulbs. Proximal antennal rings expanded ventrally to form sensory pads; sensory pads with up to two rows of sensilla.

Eyes
EDI males 0.06–0.08–0.08; females 0.06–0.07–0.08.

Head (males)
Males with no modification of head papillae (i.e. papillae on head do not differ from remaining dorsal papillae). Eversible head structure absent.

Head (females)
Females with no modification of head papillae.

Jaws
Inner jaw with five denticles; diastema absent; outer jaw without accessory tooth. Tongue with longitudinal row of five teeth. Buccal folds in single unbroken row.

Integument
Dorsum with 12 complete plicae between oncopods; wide and narrower plical folds alternate. Males with 14–17–20, females with 15–19–22 papillae counted from mid-dorsal line to junction of oncopod 10. Dorsal body papillae approximately uniform size; alternate plicae with slightly larger primary papillae; primary papilla with short, narrow bristle between pair of larger primary papillae with longer, more robust bristles and smaller secondary papillae between primary papillae; remaining integument with small scales; dorsal primary papillae cylindrical; conical apical piece absent; papillar scales ribbed in both sexes (microcristae well defined) (Figure 14a); lateral primary papillae slightly enlarged or elongate, with more prominent pair between oncopods in line with junction of oncopods and body; papillae around
anal opening slightly larger than those on rest of body. Ventral organs whitish.

**Oncopods**

16 pairs in both sexes. First pair of oncopod feet not enlarged in males, similar in size to remaining feet. Last pair of oncopods well developed in both sexes, orientation as for remaining oncopods. Basal foot papillae absent; distal foot papillae: one anterior, one median, one posterior, each with single sensory bristle. With three complete spinous pads (third spinous pad narrow, often broken), fourth broken spinous pad present. Nephridiopores at centre of third spinous pad on third and fourth oncopod pair; foramen broad, U-shaped.

**Male reproductive tract**

Male genital pad low, semicircular; gonopore cruciform (with arms equidistant), arms extending close to rim of genital pad. Vasa efferentia with thin, flexible walls; proximal vasa efferentia separate, do not lie parallel for part of their length or not separate, lie parallel for part of their length before fusing to form vas deferens; broad (Figure 15); vas deferens loops posteriorly at junction of paired vasa efferentia toward gonopore, not thick walled, opaque, not shiny. Spermatophore pouch absent.

**Male glands and gland papillae**

Crural papillae, one per oncopod, present on ventral side of oncopods 1–15; protrude between plicae 2–3 (counting from third spinous pad) (oncopod 1), and protrude between plicae 5–6 on oncopods 2–15. Papillae differ in shape and nature of opening: oncopods 1–3 papillae broad basally, taper abruptly, cylindrical, blunt distally with finely ribbed scales basally, distally scales with distinct ribs; smooth region surrounding distal foramen wide, lip-shaped, positioned distally (Figure 14b,c); foramen oncopods 4–5 displaced dorsolaterally; oncopods 6–15 crural papillae cylindrical, tapered gradually, narrow, elongate distally, blunt with finely ribbed scales, or scales smooth, microcristae fused on distal scales; smooth region surrounding mediolateral slit-like foramen (Figure 14d,e) not strongly demarked from rest of papilla; scales fused, smooth or slightly crenulated to distal tip of papilla. Crural glands extend into lateral haemocoel from oncopod 1, or do not extend into lateral haemocoel, confined to oncopods (oncopods 2–15); glands extending from oncopod 1 straight, extend length of body posteriorly to oncopods 10 or 11. Coxal organs absent. Anterior accessory gland papillae do not protrude significantly, with ill-defined margins, without smooth distal region; foramen a longitudinal slit; anterior accessory glands present; moderate length; lying freely within perivisceral haemocoel, extending anteriorly to oncopods 14 or 15; glands opaque, silvery, shiny. Posterior accessory glands present; foramen approximately midway between genital and anal openings; gland foramen separate; glands broad and saccate; blunt distally, sometimes, truncate distal knob (Figure 15).

**Female reproductive tract**

Females without ovipositor; ovoviviparous;
led to the placement of these taxa (the latter comprising a species-complex) in two separate genera. Their differences are listed under the diagnoses for each genus and in Table 1.

None of the females examined contained well-developed embryos in the oviducts, though most contained yolky eggs, some of which were quite large. This could be because the females examined were collected predominantly between June–November. Van Der Lande (1978) observed well-developed embryos in females killed and dissected in January, with juveniles born in March–April.

**Habitat**

Leaf litter and under logs and stones. The specimen from an unnamed cave in the Carabooda area was collected ‘off moonmilk on rock in the dark zone’ (WAM 99/250 specimen label).

**Distribution**

Western Australia: from Yanchep NP, 31°31'S; 115°41'E to Jarrahdale, 34°54'S; 117°55'E (Figure 16).

**DISCUSSION**

**Biogeography**

The Western Australia onychophorans inhabit a relatively small region in the south-west corner of the state. *Occipерipatoides gilesii* is found within the area of the Perth Basin: a long, narrow trough of sediments extending from north of the Murchison River (27°30'S; 115°00'E) to the south coast. *Kumbadjena* spp. are distributed further south, with a west–east range approximately from the Leeuwin Naturaliste National Park (34°06'S; 115°03'E) to Two People's Bay (34°57'S; 118°11'E), with northern outliers occurring south-east of Bunbury and in the Stirling Ranges (Figure 8).

Both genera (like much of the south-western flora and fauna) are endemic to Western Australia, undoubtedly due to the marine, edaphic, or climatic barriers to migration which have occurred since the Eocene. As noted by Hopper (1979: 415), who examined speciation in the flora of south-west Australia, ‘these barriers have effectively isolated most components of the flora from related groups in eastern Australia, and have been responsible primarily for the maintenance of high specific endemism in the region’.

The general landscape and vegetation where *Occipерipatoides* occurs is very different to that where *Kumbadjena* are found. The region of the Perth Basin has a lower rainfall than areas further south. The primary vegetation types are eucalypt- and banksia-dominated woodlands on the leached sands of the Swan Coastal Plain, with jarrah and marri forests on the eastern margins of the range of *O. gilesii*.

---

Female glands and gland papillae

Crural papillae absent (see Remarks, *Kumbadjena occidentalis*). Uterine glands absent.

**Remarks**

Ruhberg (1985) erected the genus *Occipерipatoides* to distinguish the Western Australian species, *O. gilesii* and *O. occidentalis*, from the eastern Australian *Euperipatoides* and *Peripatoides* from New Zealand.

Reexamination of *O. gilesii* and *O. occidentalis* has
In contrast (with the exception of a few outliers), most representatives of the K. 'occidentalis' group are found in forest dominated by karri (Eucalyptus diversicolor F. Mueller) occurring on lateritic soils (Figure 8). Karri forest requires a relatively high rainfall and is primarily limited to the 1100 mm isohyet, though other factors, such as soil type, influence the limits of its distribution. The range and frequency of karri has decreased with aridity over the last 5000 years (Churchill, 1968): this appears also to be true for Onychophora, with populations not only found within the main karri forest belt, but within outlying pockets of karri forest (for example in the western Leeuwin Naturaliste National Park and the Porongurups Range).

Because of the commercial importance of karri, its distribution and biology have been well studied, and it is interesting to compare such studies with what is known so far about the Onychophora inhabiting these forests. Coates and Sokolowski (1989) examined genetic diversity in karri and found relatively low levels of genetic divergence over the main part of the distributional range (the central block extending from near Nannup, 33°59'S; 115°45'E, in the north and southeast to Denmark, 34°58'S; 117°21'E). Clear genetic differentiation was found in populations occurring on coastal limestone to the west (corresponding to the Leeuwin-Naturaliste National Park in the present study), from the Porongurups Range at the far east of the range, and a site at Rocky Gully (east of the main forest block). Interestingly, outlying coastal populations at William Bay and Mt Manypeaks showed insignificant genetic divergence from the main forest. This led Coates and Sokolowski (1989) to postulate that populations on the southern coastal sands appear to have been remained connected with the main forest until relatively recently, while the three clearly differentiated populations listed above probably became isolated at the beginning of the dry period about 5000 B.P.

Of the three clearly differentiated karri populations, I have identified in this paper a morphologically distinct species of Onychophora, K. kaata, from the Porongurups Range. No obvious morphological differences could be found between the specimens from the Leeuwin Naturaliste National Park and populations further east. In April 2000 I visited Rocky Gully, but found remnants of karri only on private land and time constraints did not permit a thorough search in the general vicinity.

Species occurring in the main (central) karri forest block, including the outlying coastal populations, are very similar morphologically, though two species of onychophoran, K. occidentalis and K. shannonensis are recognised.

If we infer from the assumption that morphological and genetic divergence generally increases between species through time, we can assume that the morphologically distinct taxa, Occiperipatoides and Kumbadjjena can be regarded as evolutionary relicts, while the species and suspected cryptic species within Kumbadjjena are more recently evolved. Perhaps the two genera, Kumbadjjena and Occiperipatoides, evolved from a once continuous population that became divided as a result of changes in sea level during the Quaternary when phases of marine transgression and regression opened and closed coastal migration routes and led to the formation of the Swan Coastal Plain. Combined with the results of increased aridity, Occiperipatoides now appears to be physiologically better adapted to less humid microhabitats than Kumbadjjena.

It is possible that K. kaata from the Porongurups evolved during the Eocene period when a major period of marine transgression occurred. At this time, the sea extended inland to the east of Denmark, creating islands of the Stirling and Porongurups Ranges as well as coastal promontories such as those at West Cape Howe National Park, Torndirrup National Park, and Two People's Bay Wildlife Reserve (McWhae et al., 1958). However, since the other Kumbadjjena species can only be regarded as close morphological relatives, the Eocene period seems too remote to account for the evolution of this species. As Coates and Sokolowski (1989) conclude for the genetically distinct karri population in the Porongurups, it is more likely that K. kaata evolved following isolation during a more recent dry period.

That Kumbadjjena populations are so similar morphologically over a comparatively wide distributional range (relative to onychophoran distribution in eastern Australia), can probably be explained by similar reasons to the lack of genetic diversity in karri over the same area. The large, mostly continuous karri belt in the south has probably persisted as a result of climatic stability (with high rainfall) and the preservation and continued formation of lateritic soils throughout the mid-late Tertiary and Quaternary. Such a stable population structure favours slow evolution and speciation (Hopper, 1979).

Implications for conservation
The tall forested regions of south-western Western Australia contain a unique assemblage of animals and plants with special conservation significance (Christensen, 1992). These areas of relatively high rainfall have provided a refuge for elements of the old Gondwanan fauna, such as the Onychophora during long epochs of climate change (Hopper et al., 1996). The strong link between Kumbadjjena and karri distributions in the south provide a strong impetus for the conservation of the
karri communities upon which these (and other) animals depend.

While only three species of *Kumbadjena* have been described, it is suspected that the group comprises a cryptic species complex. This needs to be examined using additional characters, perhaps molecular, and/or karyology. It is important that such studies are published, that they include decisions regarding species boundaries and formal descriptions, and include the lodgement of reference specimens in museum collections. Recognition of taxa represented only by locality names is a virtually useless exercise as it does not permit any future comparative studies to test species hypotheses. It is also possible that more than one species may occur at a given locality. These are not trivial matters: unless species are formally named, and can be referred to as such, they have little conservation status. Formally named species have higher conservation status on state and federal lists of threatened species in Australia than unnamed taxa. These points are worth mentioning as it is a problem that occurs recurrently in molecular studies.

Given the strong links that have been discovered between karri and onychophoran distributions, it would be valuable to see whether Onychophora can be found within outlying karri populations that have not been explored to date (for example, near the south coast adjacent to Mt Manypeaks; Yallingup; Black Point, east of Albany and Rocky Gully, north-west of Denmark; the Donnybrook Sunklands and the Perup Nature Reserve). Hopper *et al.* (1996: 36–37) also refer to the interpretation of topography to assist the recognition of potential collecting sites: ‘minor changes in altitude and relief provided by remnants of the older land surface, or granite outcrops’ and ‘seasonally wet places on the old land surface or tops of breakways’ are localities likely to contain Gondwanan elements. Onychophorans occupying such remnant pockets may require particular protection. Obviously this would be true if new species are discovered that occur only in isolated pockets. Protection may also be needed for already known species found in outlying isolated populations: these would be important reservoirs of genetic diversity for the species in question. The importance and vulnerability of habitats supporting Gondwanan relicts is discussed by Hopper *et al.* 1996.

It seems that in contrast to *Kumbadjena*, *Occiperipatoides* is represented by a single relatively widespread species. However, this should also be tested using molecular characters, because its extensive distribution is quite unusual for an Australian onychophoran. If all populations are referable to a single species, its status is relatively secure, but should be monitored given its proximity to Perth and potential vulnerability due to the encroachment of urban areas and resultant destruction of suitable habitat.

ACKNOWLEDGEMENTS

I am very grateful to Bert Roberts for accompanying me on fieldwork conducted in April 2000, and to Joan Clark from the Zoology Department at Melbourne University for help with scanning electron microscopy. I also wish to thank the following people for specimen loans: Dr M. Harvey (WAM), Dr B. Halliday (ANIC), Mr P. Hillyard (BMNH), Dr M. Gray (AM), Dr J.-P. Mauries (MNHN), Dr R. Raven (QM) and Dr H. Rubberg (ZMH). Thanks also to the referees for their helpful comments. This work was supported by the Australian Biological Resources Study (Environment Australia).

REFERENCES


*Manuscript received 18 June 2001; accepted 6 November 2001.*
Appendix

*Kumbadjena*, gen. nov. collection sites

Representatives of this genus have been collected at the following sites. Further work, including the examination of an additional suite of characters (perhaps molecular and/or karyology) will be necessary before specimens from these localities can reliably be assigned to species. Specimen lots are listed geographically from west to east. Figure 8 shows the distribution of members of this genus. Alt. = altitude.

<table>
<thead>
<tr>
<th>No and sex</th>
<th>Locality</th>
<th>Latitude</th>
<th>Longitude</th>
<th>Alt.</th>
<th>Date</th>
<th>Collector(s)</th>
<th>Depository</th>
<th>Habitat</th>
</tr>
</thead>
<tbody>
<tr>
<td>2♂, 2♀</td>
<td>Leeuwin Naturaliste NP, Boranup Karri Forest Scenic Drive, 13.9 km north of intersection of Caves Rd and Forest Grove Rd</td>
<td>34°06'S</td>
<td>115°03'E</td>
<td>80 m</td>
<td>5 Apr 2000</td>
<td>A. Reid &amp; R. Roberts</td>
<td>WAM T42561</td>
<td>in logs</td>
</tr>
<tr>
<td>5♂, 7♀</td>
<td>&quot;</td>
<td>&quot;</td>
<td>&quot;</td>
<td></td>
<td>4 Apr 2000</td>
<td>&quot;</td>
<td>WAM T42562</td>
<td>&quot;</td>
</tr>
<tr>
<td>1♀</td>
<td>Nindup, W of Witchcliffe</td>
<td>34°03'S</td>
<td>115°03'E</td>
<td></td>
<td>6 Feb 1993</td>
<td>J. M. Waldock</td>
<td>WAM 95/489</td>
<td>&quot;</td>
</tr>
<tr>
<td>1 juv.</td>
<td>Witchcliffe are, cave WL112 (Labour Cave), 3 m from bottom of entrance hole</td>
<td>&quot;</td>
<td>&quot;</td>
<td></td>
<td>9 Apr 1994</td>
<td>R. Foulds</td>
<td>WAM 95/512</td>
<td>&quot;</td>
</tr>
<tr>
<td>1♂, 3 juv.</td>
<td>near Devils Lair Cave</td>
<td>34°08'S</td>
<td>115°08'E</td>
<td>100 m</td>
<td>14 May 1995</td>
<td>A. Reid</td>
<td>WAM T42563</td>
<td>under log</td>
</tr>
<tr>
<td>1♀</td>
<td>Augusta, E side of estuary (from well on property of N. Ellis)</td>
<td>-34°20'S</td>
<td>115°09'E</td>
<td></td>
<td>12 Oct 1980</td>
<td>S. Slack-Smith &amp; M. Ellis</td>
<td>WAM 89/384</td>
<td>&quot;</td>
</tr>
<tr>
<td>1♀</td>
<td>2 km SW of Margaret River</td>
<td>33°57'S</td>
<td>115°24'E</td>
<td></td>
<td>4 Jan 1992</td>
<td>J. M. Waldock</td>
<td>WAM 95/486</td>
<td>&quot;</td>
</tr>
<tr>
<td>1♀</td>
<td>Karri Valley Resort</td>
<td>34°26'S</td>
<td>115°51'E</td>
<td></td>
<td>21 Oct 1997</td>
<td>J. M. Waldock</td>
<td>WAM T40859</td>
<td>karri litter</td>
</tr>
<tr>
<td>1♂, 2♀</td>
<td>Pemberton, forest opposite Youth Hostel</td>
<td>-34°24'S</td>
<td>115°58'E</td>
<td></td>
<td>20 May 1995</td>
<td>A. Reid</td>
<td>WAM T42564</td>
<td>in log</td>
</tr>
<tr>
<td>1 juv.</td>
<td>Treen SF</td>
<td>34°24'S</td>
<td>115°58'E</td>
<td></td>
<td>17 May 1995</td>
<td>A. Reid</td>
<td>WAM T42565</td>
<td>in log</td>
</tr>
<tr>
<td>1♀</td>
<td>Pemberton Youth Hostel</td>
<td>34°24'S</td>
<td>115°58'E</td>
<td></td>
<td>2 May 1992</td>
<td>M. S. Harvey &amp; J. M. Waldock</td>
<td>WAM 91/1133</td>
<td>&quot;</td>
</tr>
<tr>
<td>1♀</td>
<td>Pemberton, East Brook</td>
<td>-34°24'S</td>
<td>115°58'E</td>
<td></td>
<td>22 Aug 1956</td>
<td>B. Y. Main</td>
<td>WAM 89/1125</td>
<td>Casuarina bark</td>
</tr>
<tr>
<td>2♀</td>
<td>Pemberton HL 62, Big Brook 12</td>
<td>-34°24'S</td>
<td>116°00'E</td>
<td></td>
<td>15 Nov 1971</td>
<td>J. A. Springett</td>
<td>WAM 76/8-9</td>
<td>&quot;</td>
</tr>
<tr>
<td>9♂, 8♀, 2 juv.</td>
<td>Big Brooke SF, near Pemberton</td>
<td>34°24'S</td>
<td>116°00'E</td>
<td>150 m</td>
<td>6 Apr 2000</td>
<td>A. Reid &amp; R. Roberts</td>
<td>WAM T42566</td>
<td>in logs</td>
</tr>
<tr>
<td>1♂, 1♀</td>
<td>Bombakup SF, creek line</td>
<td>34°36.5'S</td>
<td>116°01.9'E</td>
<td></td>
<td>28 Jan 1999</td>
<td>S. L. Judd</td>
<td>WAM T40855</td>
<td>dense litter at base of karri</td>
</tr>
<tr>
<td>1♀</td>
<td>Bombakup SF, creek line</td>
<td>34°36.5'S</td>
<td>116°01.9'E</td>
<td></td>
<td>28 Jan 1999</td>
<td>S. L. Judd</td>
<td>WAM T40854</td>
<td>&quot;</td>
</tr>
<tr>
<td>1♀</td>
<td>Preston Conservation Park</td>
<td>33°36.2'S</td>
<td>116°03.8'E</td>
<td></td>
<td>24 Nov 1998</td>
<td>S. L. Judd</td>
<td>WAM T40862</td>
<td>hand collected in old growth jarrah</td>
</tr>
<tr>
<td>7♂, 3♀, 1 juv.</td>
<td>Mt Chudalup, 15.7 km S of Northcliffe</td>
<td>34°46'S</td>
<td>116°05'E</td>
<td>100 m</td>
<td>7 Apr 2000</td>
<td>A. Reid &amp; R. Roberts</td>
<td>WAM T42567</td>
<td>in logs</td>
</tr>
<tr>
<td>1♀</td>
<td>Mt Chudalup</td>
<td>34°46'S</td>
<td>116°05'E</td>
<td></td>
<td>3 Sep 1990</td>
<td>G. Wardell &amp; Johnston</td>
<td>WAM 90/1723</td>
<td>&quot;</td>
</tr>
<tr>
<td>1♀</td>
<td>Walpole Normanup NP</td>
<td>34°54'S</td>
<td>116°29'E</td>
<td></td>
<td>9 Apr 2000</td>
<td>A. Reid &amp; R. Roberts</td>
<td>WAM T42568</td>
<td>in log</td>
</tr>
<tr>
<td>Sex, Age</td>
<td>Location Description</td>
<td>Latitude</td>
<td>Longitude</td>
<td>Distance</td>
<td>Collected</td>
<td>By</td>
<td>Museum Code</td>
<td>Notes</td>
</tr>
<tr>
<td>----------</td>
<td>---------------------</td>
<td>----------</td>
<td>-----------</td>
<td>----------</td>
<td>-----------</td>
<td>-----</td>
<td>-------------</td>
<td>-------</td>
</tr>
<tr>
<td>1δ, 1 Η, 1 juv.</td>
<td>Walpole Normalup NP, Conspicuous Beach Rd, 2.9 km S of South Coast Hwy</td>
<td>34°54'S</td>
<td>116°29'E</td>
<td>70 m</td>
<td>9 Apr 2000</td>
<td>A. Reid &amp; R. Roberts</td>
<td>WAM T42569</td>
<td>in logs</td>
</tr>
<tr>
<td>1δ, 2♀</td>
<td>Walpole Normalup NP, Broke Inlet, beside Broke Inlet Rd, 7 km from intersection with South Western Hwy</td>
<td>34°39.6'S</td>
<td>116°42.2'E</td>
<td>10 Apr 2000</td>
<td>A. Reid &amp; R. Roberts</td>
<td>WAM T42570</td>
<td>in logs</td>
<td></td>
</tr>
<tr>
<td>1δ</td>
<td>Long Thompson Forest Block</td>
<td>34°39'S</td>
<td>116°49'E</td>
<td>100 m</td>
<td>11 Jan 1999</td>
<td>S. L. Judd</td>
<td>WAM T40860</td>
<td>in log</td>
</tr>
<tr>
<td>1δ</td>
<td>Mt Frankland NP</td>
<td>34°48.2'S</td>
<td>116°53.0'E</td>
<td>10 Jan 1999</td>
<td>A. Reid &amp; R. Roberts</td>
<td>WAM T40861</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1♂, 1♀</td>
<td>Rate Forest Block</td>
<td>34°50'S</td>
<td>117°00.4'E</td>
<td>9 Jan 1999</td>
<td>S. L. Judd</td>
<td>WAM T40863</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1♀</td>
<td>23 km east of Denmark, Tennessee South Rd</td>
<td>-34°57'S</td>
<td>117°21'E</td>
<td>8 Dec 1974</td>
<td>P. Smith</td>
<td>WAM 89/383</td>
<td>in shade at base of tree under log</td>
<td></td>
</tr>
<tr>
<td>1♀</td>
<td>William Bay NP, beside Byleveld's Lake</td>
<td>35°00'S</td>
<td>117°13'E</td>
<td>40 m</td>
<td>22 May 1995</td>
<td>A. Reid</td>
<td>WAM T42572</td>
<td>in and under logs</td>
</tr>
<tr>
<td>3♂, 6♀, 2 juv.</td>
<td>West Cape Howe NP, 1.6 km S of intersection of Coombes Rd and Shelley Beach Rd, 0.4 km inside NP entrance</td>
<td>35°05'S</td>
<td>117°38'E</td>
<td>150 m</td>
<td>13-14 Apr 2000</td>
<td>A. Reid &amp; R. Roberts</td>
<td>WAM T42574</td>
<td>in log</td>
</tr>
<tr>
<td>1♀</td>
<td>West Cape Howe NP, S of Torbay Hill nr Sth Rd</td>
<td>-35°05'S</td>
<td>117°38'E</td>
<td>27 Mar 1993</td>
<td>M. S. Harvey &amp; J. M. Waldock</td>
<td>WAM 95/511</td>
<td>karri litter</td>
<td></td>
</tr>
<tr>
<td>1♀</td>
<td>Torbay Head, Lot 40 adjacent to West Cape Howe NP</td>
<td>-35°05'S</td>
<td>117°38'E</td>
<td>B. Y. Main</td>
<td>WAM 91/1126</td>
<td>karri litter</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1♂, 1 juv.</td>
<td>gully outside N edge of Torndirrup NP on Limeburners Rd</td>
<td>35°05'S</td>
<td>117°54'E</td>
<td>26 Mar 1993</td>
<td>M. S. Harvey &amp; J. M. Waldock</td>
<td>WAM 95/498</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1♂, 2♀</td>
<td>&quot;</td>
<td>&quot;</td>
<td>&quot;</td>
<td>&quot;</td>
<td>M. S. Harvey, J. M. Waldock &amp; B. Y. Main</td>
<td>WAM 95/508-10</td>
<td>litter</td>
<td></td>
</tr>
<tr>
<td>1♀</td>
<td>Stirling Range NP, Wedge Hill</td>
<td>34°23’17&quot;S</td>
<td>118°10'18&quot;E</td>
<td>27 May-17 Dec 1996</td>
<td>M. S. Harvey, J. M. Waldock &amp; B. Y. Main</td>
<td>WAM 99/245</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1♀</td>
<td>Two People's Bay</td>
<td>-34°57'S</td>
<td>118°11'E</td>
<td>22 May 1970</td>
<td>J. A. Springett</td>
<td>WAM 76/4-5</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
The asterostomatid echinoid *Antillaster* from the Paradash Group (Middle Eocene) of the Nakhichevan Region of Azerbaijan

Kenneth J. McNamara¹ and Oktay H. Melikov²

¹ Department of Earth and Planetary Sciences, Western Australian Museum, Francis Street, Perth, Western Australia 6000, Australia
² Azerbaijan State Oil Academy, 370102 Azadlik pr. 20, Baku, Azerbaijan

Abstract – The asterostomatid echinoid *Antillaster* has previously been recorded only from the Caribbean region and northeastern South America. Here we report the first occurrence of this genus from outside the Americas, in the Lesser Caucasus, where it has been found in Middle Eocene sediments of the Paradash Group in the Nakhichevan region of Azerbaijan. The material is described as *Antillaster bagmanovi* sp. nov. It is the earliest known occurrence of the genus. Its presence in the Paratethys, in a region far removed from previous known occurrences, has significant palaeobiogeographic implications. Its disappearance from the Lesser Caucasus, but persistence in the Caribbean, may be linked to the contraction of the Tethys during the Cenozoic.

INTRODUCTION

Eocene sediments in the Nakhichevan region of Azerbaijan have long attracted the attention of many investigators, due to their good exposure and extensive foraminiferal and molluscan fauna. The dating of the predominantly clay-sand facies as being Eocene is based on this rich foraminiferal and molluscan fauna (Azizbekov 1961; Bagmanov 1966, 1980; Paffengoltz 1979). The presence of an Eocene echinoid fauna in the Nakhichevan region remained unknown until 1958 when, in addition to the foraminifers and molluscs from sections in Juga, Daralik, Ilanlak and Bilav, M.A. Bagmanov collected a rich fauna of echinoids from the Paradash Group. Unfortunately, this fauna remained unstudied for many years. However, in 1984 Bagmanov kindly passed his echinoid collection over to one of us (O.H.M). During 1985-87 Melikov, to supplement this collection, collected additional material from Bagmanov’s sections. These collections from the Paradash Group have yielded a rich echinoid fauna, comprising 25 species (Melikov in prep.). Current work by Melikov suggests that these species can be assigned to 14 genera in 11 families, and 5 orders. It is interesting that this species richness is in strong contrast to a fauna of equivalent age occurring in sediments in the neighbouring territory of Armenia, a mere 40-50 km away. Here only six species are known.

One of the more surprising echinoid finds from these sediments was large specimens of *Antillaster*. The asterostomatid echinoid *Antillaster* has previously been described only from the Caribbean region and northern South America, specifically from Eocene to Miocene sediments in Venezuela, Cuba, Jamaica, Bonaire, Antigua, Puerto Rico and Mexico (Kier 1984). Here we report the first record of this genus from outside the Caribbean region, in Middle Eocene sediments of the Lesser Caucasus region in Azerbaijan. This provides the earliest record of asterostomatid echinoids in the Paratethys region.

GEOLOGICAL SETTING AND BIOSTRATIGRAPHY

Middle Eocene sediments are are widespread in the southwestern part of the Nakhichevan region of Azerbaijan, extending to the Arax River, which marks the border with Iran. These sediments are separated by a pronounced unconformity from underlying Triassic sediments. This boundary is marked by a thick basal conglomerate. The Middle Eocene sediments are divided into three groups, which extend through six foraminiferal zones (Figure 1).

Daralik Group

Lower subgroup

Along the south-west limb of the Nakhichevan synclinal basin, particularly at Daralik (on the right bank of the Alinjachai River), this basal unit of the Middle Eocene sequence encompasses the Nummulites laevigatus zone and is represented mainly by conglomerates containing a series of isolated packets and lenses of limestones, clay-shale and sandstones. It is characterised by its reddish-
brown colouring. The thickness of the subgroup varies between 5–10 m to 120–150 m. This subgroup contains abundant Nummulites of Middle Eocene age, notably N. laevigatus (Brug.), N. laevigatus var. lantensis Lerisch (B) and the echinoids Porosoma lamberti Checcia-Rispoli, Triplacida veronensis Bittner, Echinolampas daralagesensis Poretzkaja, E. blaviensis Cotteau, Echinanthus cf. issyaviensis (Klein) and Cyclaster subquadratus (Desor). The presence of N. laevigatus indicates a Lower Lutetian age, foraminiferal zone P10.

Upper subgroup
This encompasses the Morozovella aragonensis zone. Up the section this predominantly conglomerate subgroup is intermixed with layers of shelly-sandstone, argillites and rarely limestones, containing abundant Nummulites. Within this subgroup in the Julfa region, occurs lenses of gypsumised shale and aleurolites, 150 m thick. These sharply decrease in thickness along both limbs of the Bilav fold. The most common foraminifers in the zone are Nummulites laevigatus (Brug.) and N. uranensis Heim. Other foraminifers include Acarina bulbrooki Bolli and Globigerina postiloculinoides Chalilov. Acarina bulbrooki occurs in the Lower Lutetian, P9 and P10. N. uranensis occurs in P10. Echinoids occurring in this upper subgroup are Schizaster (Schizaster) rindensis Poretzkaja, S.(S.) sp. nov., Maretia hoffmanni Goldfuss and M. sp. nov.

Bilav Group
This is represented by tuffaceous conglomerate, tuff, tuffite of andesite-dacite composition and lenses of sandy shale. The total thickness of this group is 875 m. Bagmanov (1966) identified Nummulites laevigatus (Brug) within this group. Highly developed olistoliths of very different-sizes is a characteristic feature of this group.

Paradash Group
Palaeontologically this group is divided into four biostratigraphical zones from the lowest Globigerinatheka subconglobata zone up through the Acarina rotundomarginata zone, the Truncorotaloides rohri zone to the Globigerina corpulenta zone. The lower three are included within the Middle Eocene, the Globigerina corpulenta zone being Upper Eocene.

Figure 1  Biostratigraphic chart showing the foraminiferal zonation, stratigraphic groups and range of Antillaster bagmanovi in the Nakhichevan region of Azerbaijan Republic.
Globigerinatheka subconglobata zone

This overlies the tuffaceous conglomerate of the Bilava Group and is represented in its lower part by repeated beds of argillites, sandstones and clay/shales, having a total thickness of 126 m. These rocks are overlain by 70 m of repeated beds of dark red clay/shale, argillites and subordinate interbedded sandstones. Over these lie a 100 m thick sequence of greyish clay. This lowest subgroup is capped by a sequence of repeated sandstone and clay/shale 55 m thick, with a 4 m thick conglomerate at its base. The beds of this subgroup extend along the southern limb of Ilzandag Mountain.


*Acarinina* rotundomarginata zone

This is represented by repeated beds of clay, sandstone and argillites having a total thickness of 391 m. Foraminifers present include *Subbotina frontosa* Subbotina (P11–P14), *Acarinina vievensis* Morozoova, *Morozovella lehnerii* Cushman (P12–P13), *Hantkenina alabamensis* Cushman (P12), *Nummulites acutus* (Sowerby) and *N. striatus* (Brug.). The species of echinoids recovered from this zone are: *Antillaster* sp. nov., *Gualtieria* (*Gualtieria*) *damesi* Koch, *Triplacidia veronensis* Bittner, *Schizaster* (*Schizaster*) sp. nov., *Schizaster* (*Paraster*) *rimosus* L. Agassiz, *Conoclypus conoides* Leske, and *C. leymerei* Cotteau. The planktic foraminifers indicate a foraminiferal zone of P12, which is Upper Lutetian to early Lower Bartonian.

Truncorotaloides rohri zone

This consists of red-brownish (43 m) and greyish (25 m) clay with interbeds of sandstones containing nummulites. This zone is characterised by the presence of numerous *Truncorotaloides rohri* Brönnimann and Bermudez (P11–P14), *Globigerina incretacea* Chaliov, *G. praebuloides* Blay., *Nummulites brongniarti* D’Archic and Haime (P12–P14), *N. perforatus* (Mont.) (P12–P14), *N. striatus* (Breys.). Echinoids occurring in this zone are *Conoclypus conoides* Leske and *Antillaster* sp. nov. The foraminifers indicate a possible Upper Bartonian age.

Globigerina corpulenta zone

Sediments within this zone consist of repeated beds of nummulitic sandstones, clays and conglomerates, 50 m thick. Foraminifers present include *Nummulites striatus* (Brug.), *N. brongniarti* D’Archic and Haime, *N. paradashensis* Mamedov, *N. fabiani* Prever, *N. rectus* Currey. *N. brongniarti* is Bartonian, and *N. fabiani* uppermost Bartonian to Lower Priabonian.

The Paradash Group would therefore seem to range from near the Lower-Middle Lutetian boundary to the Upper Bartonian or earliest Priabonian. The sequence at Daralik probably occupies the entire Middle Eocene, possibly extending into the lowest part of the Upper Eocene.

**SYSTEMATIC PALAEONTOLOGY**

Order Spatangoidea Claus, 1876

Family Asterostomatidae Pictet, 1857

Genus *Antillaster* Lambert, 1909

Type species
*Asterostoma cubensis* Cotteau, 1871; by original designation of Lambert, 1909, p. 103.

**Diagnosis**

Test large, low to high; apical system ethmolytic with 3 or 4 genital pores; petals long, wide, open, flush with test, or very slightly depressed; anterior ambulacrum with small pores, in slight groove or flush with test; some plates occluded at ends of petals; peristome large; periproct large, inframarginal; tubercles small, no fascioles; palastron mesamphisternum with large labrum, narrow sternal plates, large episternal plates; in some species first plate in interambulacrum 1 followed by single plate (after Kier 1984:131).

**Remarks**
Species of *Antillaster* are particularly characterised by their very large test size, typically reaching in excess of 100 mm test length, but sometimes to over 150 mm. *Antillaster* lacks any evidence of fascioles, hence its assignment to the Asterostomatidae. *Antillaster* bears a superficial resemblance to the brissid *Pharaonaster*, which is known from the Eocene of North Africa (Roman and Stroug 1994). However, *Antillaster* can be distinguished by its much larger test size and absence of fascioles; peripetalal and subanal fascioles are present in *Pharaonaster*. Another superficially similar form is *Hypsopatagus*, which is known from the Eocene to Oligocene of parts of Europe, Asia and North America. However, unlike *Antillaster* it has a peripetalal fasciole; is smaller; and has closed, rather than open, petals. On account of its large size,
absence of fascioles, distally open petals that are almost flush with the surface of the test, the form described herein from Azerbaijan is considered to be a species of *Antillaster*.

*Antillaster bagmanovi* sp. nov.

Figures 2–7

Diagnosis
Species of *Antillaster* with very slightly sunken petals; anteriorly divergent petals with very narrow interporiferous zone; peristome sunken; ambulacrum III deeply sunken orally.

Material
Holotype WAM 99.428, from Daralik, Nakhichevan region of Azerbaijan Republic; paratypes WAM 99.429 and 99.432 from the same horizon and locality; other specimens WAM 99.427, 99.430, 99.431 and 99.433 from the same horizon and locality. All specimens collected by O. H. Melikov from the *Acarinina rotundamarginata* zone, Paradash Group (Middle Eocene – Upper Lutetian to early Lower Bartonian).

Etymology
Named in honour of palaeontologist M. A. Bagmanov.

Description
Test very large, reaching up to 154 mm TL; cupola-shaped, with apex anterior of centre; height about 50%TL; test longer than wide, ranging between 90–94%TL. Aboral surface declines more steeply anteriorly; ambitus broadly rounded. Shallow anterior notch present. Apical system anteriorly eccentric, 41–46%TL from anterior ambitus; ethmolytic, with four genital pores, madreporite extending posteriorly the same distance again as the distance between the anterior and posterior pairs of genital pores.

Ambulacrum III very slightly depressed aborally; pore pairs very small. Anterior petals slightly flexuous, curving anteriorly distally; very slightly

Figure 2  *Antillaster bagmanovi* sp. nov. WAM 99.428; holotype, aboral view; from Paradash Group (Middle Eocene), Daralik, Nakhichevan region of Azerbaijan Republic; x1.
sunken; width 8-9%TL; diverging anteriorly at about 140°; long, 43-48%TL, extending to the ambitus; distally open; with up to 46 pore pairs in each row; inner pores circular, outer pores slightly elongate, not conjugate; interporiferous zone narrow, being less than width of pore pairs in smallest specimen (TL 89.5 mm) to slightly greater in largest specimen. Posterior petals also very slightly sunken; straight; slightly longer than anterior, being 46-52%TL; with up to 51 pore pairs in each row; nature of pore pairs and width of interporiferous zone same as in anterior petals; slightly wider than anterior petals, being 8-10%TL. Terminal ambulacrum plates of petals sometimes occluded.

Aboral tubercles relatively sparsely distributed; range in diameter from 0.8 to 1.6 mm in largest specimen. Set in a dense field of miliary tubercles. Fascioles absent.

Oral surface with moderately convex interambulacral areas and sunken ambulacra. These are very weakly sunken ambitally, increasing in depth to relatively deeply sunken peristome. Ambulacrum III deeply sunken throughout. Peristome width 11%TL; moderately crescentic; posterior of peristome situated 30–35%TL from anterior ambitus. Labrum strongly arcuate anteriorly. Plastron length 24–34%TL, being relatively longer in smaller specimens; width 17–21%TL; gently convex. Episternal plates about half the length of sternal plates, but episternal and preanal plates combined are longer than sternal plates. Periproct inframarginal, transversely oval, width 12–13%TL. Adoral tuberculation slightly more dense than on aboral surface; primary tubercles of more even diameter; up to 1.5 mm; slightly smaller on plastron than on lateral interambulacra; set in field of dense miliary tubercles.

Ontogenetic variation

While the partially weathered and usually somewhat crushed nature of the specimens precludes any detailed ontogenetic assessment of the species, some differences are apparent between the smallest specimen (WAM 99.429, test length 89 mm), compared with the other, larger, individuals (125 to 154 mm). The plastron in the smaller individual is distinctly narrower, with a length to width ratio of 1:1.77, compared with 1:1.27 – 1:1.40 (n=5) in the larger ones. Furthermore, the petals are slightly more sunken in larger individuals, as is the anterior ambulacrum on the oral surface. The interporiferous zone increases slightly in relative width during ontogeny, being slightly narrower than the width of the pore pairs in the smallest specimen, becoming wider than pore pair width in the largest specimens.

Remarks

Kier (1984) considered that there were two species groups of Antillaster present in the Caribbean region. One he characterised by its possession of a
large, very high, steep-sided test, with a flat ventral surface and very wide petals. Species within this group range in age from the Oligocene to Miocene. Kier characterised the second group (which comprises species ranging in age from Eocene to Miocene) by the possession of relatively lower, more elongate test, more rounded ventral surface and narrower petals. In its possession of narrow petals and relatively lower test with more rounded ventral surface, *A. bagmanovi* resembles the second, probably more primitive, group.

*Antillaster bagmanovi* can be readily distinguished from all other described species of *Antillaster* by virtue of its slightly sunken petals that have a very narrow interporiferous zone, and orally possessing a relatively deeply sunken ambulacrum III. The only other known Eocene species of *Antillaster* are *A. arnoldi* Clark in Arnold and Clark, 1927 from the Eocene of Jamaica and *A. albeari* Kier, 1984 from the Middle to Late Eocene of Cuba. The apical system is less anteriorly situated in *A. bagmanovi* than in these two species. Moreover, it has sunken petals that are more anteriorly divergent and narrower interporiferous zone. Although sharing slightly sunken petals, *A. bagmanovi* can be distinguished from *A. albeari* by possessing more anteriorly divergent petals, very much narrower anterior and posterior petals and interporiferous zone, more vaulted test and deeper anterior ambulacrum on the oral surface.

Like *A. elegans* Jackson, 1922 from the Miocene of Puerto Rico, *A. bagmanovi* has an apical system in a similar relative position, a little anterior of central, and slightly anteriorly divergent petals. However, the Azerbaijan species has slightly sunken petals, narrower interporiferous zone, deeper anterior
Asterostomatid echinoid *Antillaster* from Azerbaijan

Figure 5  *Antillaster bagmanovi* sp. nov. WAM 99.432; paratype, A, partial adoral plating, B, lateral profile; from Paradash Group (Middle Eocene), Daralik, Nakhichevan region of Azerbaijan Republic; x0.9.
ambulacrum orally and narrower labrum. Another species to possess a narrow interporiferous zone is *A. fernandezi* (Sanchez Roig, 1952) from the Oligocene-Miocene of Cuba (Kier 1984). However, *A. bagmanovi* has narrower petals that are anteriorly more divergent, a less vaulted test and four, not three, gonopores.

*Antillaster bagmanovi* can also be distinguished from *A. vaughani* (Jackson, 1922) from the Oligocene-Miocene of Antigua, Mexico and Cuba (Kier 1984) by its narrower interporiferous zone, sunken petals, deeper anterior ambulacrum orally, narrower peristome and narrower plastron. *A. sanchezi* Lambert in Lambert and Thiéry, 1924 from the Early – Middle Miocene of Cuba (Kier 1984) has, like *A. bagmanovi*, a very narrow interporiferous zone and slightly sunken petals, but the Azerbaijan species has a more central apical system, more anteriorly divergent petals that are not so parallel-sided, and a deeper anterior ambulacrum orally.

**BIOGEOGRAPHIC IMPLICATIONS**

The highly disjunct Eocene populations of *Antillaster*, with nine Eocene to Miocene species in the Caribbean and one Middle Eocene record in the Lesser Caucasus, suggests an originally widespread distribution as far east as the Eastern Paratethys that contracted rapidly to the west in the Oligocene. Whether *Antillaster* originated in the west or the eastern parts of the orginal range is hard to establish. Evidence from other echinoids indicates that up until the Early Oligocene there was a relatively free exchange of taxa across the Atlantic Ocean, mainly in a westerly direction. For example, * Clypeaster* appeared earlier in the Tethyan region than in the Caribbean (Ali 1983). Likewise *Echinolampas* first appeared in the Mediterranean region during the Late Paleocene, but did not appear in the Caribbean region until the Middle Eocene (Roman 1977). Similarly *Rhyncholampas* first appeared in the Caribbean at this time, although it is found in the Early Eocene in France (Roman 1977). Comparable east to west migrations are shown by *Eupatagus* (Roman 1970) and *Maretia* (Roman 1977). Perhaps of more interest than the likelihood of *Antillaster* forming part of this east to west migration of faunal elements in the Middle Eocene, is the fact that it disappeared from the eastern part of its range so soon after. This may be a function of its mode of life. Kier (1984) suggests that, like living asterostomatids, *Antillaster* probably lived on the top of the substrate, lacking features associated with a burrowing mode of life, and in relatively deep water, perhaps up to 800 m deep, like living members of the family. Its disappearance from the Lesser Caucasus may have been associated with a shallowing of the sea as Tethys contracted through the Cenozoic and a separation of the deep basins of the Eastern Paratethys from deeper basins to the west.
ACKNOWLEDGEMENTS

We thank Dr Kevin Kelly, Director of Azerbaijan Relief International, for his assistance; Vasif Melikov for helping with computer services; Dr Andrew Smith for his constructive comments on the manuscript; Dr Stefan Rivets for assistance with foraminiferal biostratigraphy; Kris Brimmell for photography and Danielle West for help with the line drawings.

REFERENCES


Manuscript received 31 October 2000; accepted 30 November 2001.
The axial postcranial structure of *Griphognathus whitei* from the Upper Devonian Gogo Formation of Western Australia: comparisons with other Devonian Dipnoans

K.S.W. Campbell and R.E. Barwick
Geology Department, Australian National University, Canberra, 0200, Australia.
e-mail ken.campbell@anu.edu.au and richard.barwick@anu.edu.au

Abstract – The skeleton of the pectoral and pelvic girdles, the foremost axial region, and the scales of *Griphognathus whitei*, and the pectoral and pelvic girdles and scales of *Chirodipterus australis*, have been described previously. The posterior parts of the postcranial skeleton of these fishes have been commented on in passing, but new material permits a description of the centra, the neural and haemal arches and the incomplete medial fins of *G. whitei*. The limb skeletons have not been preserved in our material. The new material of *G. whitei* adds considerably to the information available on the axial skeleton and the medial fins of Devonian dipnoans. Of these dipnoans, only *Dipterus* has the axial skeleton without the centra well preserved, though fragments of the centra of some of the other genera are poorly preserved. The new specimens of *G. whitei* have well preserved centra along the full length of the body of the animal. The neural and haemal arches give the best information available on Devonian species. The medial fins are sufficiently well preserved to compare with those of *Fleurantia* and *Scaumenacia* from the Upper Devonian of Canada, and the Australian *Barwickia* and *Houdipterus* from the Givetian of Victoria. Gross differences occur between all the above genera in the structure of the medial fins. The function of the fins and the centra are discussed, and an attempt is made to show how the whole structure of the movement of *G. whitei* is related to the bottom dwelling environment in which the animals lived.

INTRODUCTION

From the Gogo Formation in the Canning Basin of Western Australia, the lungfishes *Griphognathus whitei* and *Chirodipterus australis* have parts of the postcranial skeleton preserved, and fragments of *Holodipterus* are available but we do not have sufficient material at present to be worth describing. Of these *Griphognathus* is the best preserved, and work on the anterior vertebral column has already been published (Campbell and Barwick 1988, 1999). Pridmore and Barwick (1993) also figured parts of the vertebral column and the median fins, but did not comment on the details. The structure of the pectoral girdle and the pelvic girdle have been described (Young et al. 1989; Campbell and Barwick 1999). No examples of the pectoral or pelvic fins have been observed.

We now have a more or less complete body of *Griphognathus whitei* which lacks its caudal fin. Nineteen other specimens have been prepared, some of which show details of the posterior end of the skeleton, others show the detail of a number of axial segments, others show the centra and the ribs, and still others show the support structures of the medial fins and their lepidotrichs. Scale coverings of the fins are also partly known. In addition we have specimens of *Griphognathus* in which several ribs are preserved. The attachment of the ribs to the centra are well preserved and the shapes of the ribs and their attachment surfaces are clear. These features are not known from any other Devonian dipnoans.

In none of the previous works is there any discussion of the articulations of the elements, presumably because they were not preserved. The Gogo material permits an examination of the articulations and hence a better understanding of the function of the fins and the body during locomotion.

TERMINOLOGY

We will not discuss the details of relationships between sarcopterygians, and so there will be no need to become involved with a discussion of terminology as it might apply to other groups as well as dipnoans. So that our work will fit in with what is being done in other Palaeozoic dipnoans, we will use the terminology used by Ahlberg and Trewin (1995) in describing the axial skeleton of
Dipterus valenciennesi. In so doing we will provide a basis for the direct comparison with the most recently described species which occurs in rocks older than our material. More recently, Cloutier (1996) has described the postcranial exoskeleton of the Late Devonian Scaumenacia and Fleuranitia from Canada, and these species show structures not known in Dipterus valenciennesi. Where appropriate we have used Cloutier’s terminology.

PREVIOUS WORK ON THE POSTCRANIAL STRUCTURE OF DEVONIAN DIPNOANS

Ahlberg and Trewin (1995) in a discussion of the postcranial skeleton of Dipterus valenciennesi, mentioned the lack of information on the postcranial skeleton of Devonian dipnoans. The reason for this is clear; so few specimens have been found showing the structures in position, and only a few genera have ossified centra. Specimens found in shale provide most of the data available. Their vertebrae were cartilagenous or were crushed, and the fin supports are hidden beneath the strong covering of scales. Isolated vertebral centra have been used to describe their internal structure (Schultze 1970), but there are too few of these to make a consistent statement about Devonian dipnoans. The discovery of postcranial skeletons from Gogo, sometimes in association with much of the body, offers the opportunity to develop this information in this “potentially important field” (Ahlberg and Trewin 1995: 159).

Schultze (1970) described the axial centra of Grphognathus sculpta and G. multidentis from Germany, and Jarvikia and ?Soderberghia from Greenland. The main purpose of his paper was to examine the vertebral structures, attempting to understand the similarities and differences between dipnoans and other sarcopterygians. He came to the conclusion that their structures “show that it is more convincing to place the dipnoans with the teleostomes and near the coelacanths, rather than place them with the elasmobranchiomorphs....”. On the other hand he concluded that the evidence indicated a “much stronger comparison with the vertebrase of other teleostomes or tetrapsods”. The axial skeleton of Rhinodipterus ulrichi, Dipterus cf valenciennesi, and Grphognathus sculpta, have been described from various localities in Europe by Schultze (1975), but they added little evidence because of the poverty of the material available.

The most complete work on the European Devonian genera is that of Ahlberg and Trewin (1995). This dealt with Dipterus valenciennesi. It discussed the evidence from a number of specimens from Scotland, and described parts of the axial skeleton, the haemal and neural arches, and the medial fins. Much of the material was poorly preserved, and few of the fine details were available for description. For example, no information on the internal structure of the centra, and no structures of the haemal or neural arches were available, the organisation of the ribs was not displayed, and the support structures for the median fins were only partly exposed.

More recently, Cloutier (1996) has provided a list of the work previously done on the Canadian genera Scaumenacia and Fleuranitia. Jarvik (1959, 1980) has also commented on these genera, following up the work done by Graham-Smith and Westoll (1937). Cloutier’s work is more complete, and for the first time the postcranial skeleton of Scaumenacia has been described in detail. This work provides the best account of the Canadian genera.

Long (1993) described the postcranial ribs in a number of Devonian dipnoan genera, especially Barwickia and Howiodipterus from the Givetian deposits at Mt Howitt in Victoria. He also has further details of these genera in a manuscript, which we have been given permission to examine. These specimens are preserved in shale, and were studied by latex moulds. They are very useful in that they give a better understanding of Australian material than we had previously. They will be dealt with in a later part of this paper.

MATERIALS AND METHODS

All the specimens examined have been in the collections of the Australian National University Geology Department (ANU), the Western Australian Museum (WAM), and the Australian Museum, Sydney (AMF). Apart from one specimen collected from South of Lloyd’s Hill, all others were collected from Paddy’s Valley, Gogo Station, Canning Basin, Western Australia.

ANU 35641; 35645; 49114-49116; 49120; 491207; 49282-49284; 49900.
WAM 87.8.24; 86.9.25; 86.9.645; 86.9.650; 86.9.651. AMF 72402

All specimens have been prepared by solution of the matrix in acetic acid, impregnating the exposed bone with a dilute plastic, and continuing with the solution until the bone we wished to examine has been exposed.

GROSS STRUCTURE OF GRPHOGNATHUS WHITEI

The Structure of the Centra

As has been illustrated on several occasions (Miles 1977, figures 11, 12, 30; Campbell and Barwick 1999, figures 2, 3), the posterior of the skull has centra fused to it and these occupy all the space dorsal to the posterior part of the parasphenoid.
None of these elements have cranial ribs attached.

The free centra from *Griphognathus whitei* are well preserved. They include large anterior centra, the fulcral centra, and posterior centra from the caudal region of adults, and some juveniles with centra from a variety of positions along the axial column. It has been possible to section some of them, providing the largest sample of Devonian dipnoan centra yet available. They are apparently single structures, and are not made of units subsequently fused. In this they are quite unlike the centra of other sarcopterygians.

Many segments of ANU 49116 (Figure 1A,B) are known, and in particular those of the proximal part of the caudal region are well preserved. These illustrate the reduction of the length of the centra at a clear cut point along the length of the vertebral column. Three centra at the anterior end of the caudal region average 6.3 mm long, whereas the next three average 4.5 mm long. The break in size occurs rapidly. Four more posterior centra are each only 3 mm long.

We have isolated centra from almost throughout the whole column. In adults they are solid blocks of
tissue in the axis of which is a small perforation which runs the length of the block. In juveniles, and in the small centra in the caudal region mentioned above, the cavity is proportionately larger. On ANU 49116, the cavity is 1.4 mm in diameter in a centrum 6.5 mm in maximum diameter, whereas the more anterior centra on other larger specimens have cavities 0.7 mm wide in bones 13 mm maximum diameter.

The caudal region of ANU 49116 shows considerable variation in the length of the centra. As shown in Figure 1, the lengths of a series of centra (in mm) from posterior to anterior is 6.9, 6.5, 7.0, 6.0, 4.8, gap, 3.9, 4.6, gap, 3.0, 4.2. Despite this
Postcranial structure of *Griphognathus whitei*

variation, there is a general reduction in the lengths of the centra, towards the posterior, as well as a relative increase in the size of the central perforations. No centra from the tip of the caudal region are available. Although the fourth last centrum preserved has a strong haemal arch preserved, the subsequent ones do not have arches. They must have been lost during preservation.

A second specimen with a long run of centra is ANU 49114, but it is not so well preserved (Figure 2A,B). The more posterior centra were lost by erosion before the specimen was collected. WAM 86.9.651 includes vertebra from the posterior end of a young specimen, and some of these have haemal arches attached (Figure 3 P,Q). The advantage of these specimens is that they show isolated features which are lost when the centra are still joined together. This specimen also shows variation of the length of the centra, and this is not correlated with their diameter.

Other centra will be dealt with as we deal with other aspects of the skeleton.

**The First Three Centra**

The first centrum has no evidence of a rib. It is known from only one individual (ANU 35645), but the surface of the centrum shows no sign of a surface for the attachment of a rib. The second and third centra show a small break in the surface on each side of the specimen, and this has been interpreted as indicating the attachment of ribs (Campbell and Barwick 1988, figures 34-36). The nature of this attachment shows up as a small scar low down on the side of the centrum, and they may indicate where the ribs themselves, or less possibly the sites of a parapophysis, were loosely attached. Assuming that the scar represents the original attachment point, the ribs would have pointed posteroventrally. These ribs are well preserved and are figured below (Figures 4 D-F; 5).

The first centrum has a convex anterior face. Each subsequent centrum is amphicoelous, but has a small median cavity to transmit the notochord. No articular facets break the continuity of the anterior and posterior margins of the centra. The first three centra lie close together, and their lateral margins are deeply excavated. On the external surface, the axis of the centrum is covered with a shiny layer of tissue, and its edges are prominent (Campbell and Barwick 1988, figures 34B, 36A). These edges mark the boundary of intercentral capsules which contain the fluid of the joints. The space between them is occupied by laminar tissue which forms the articular surfaces of the centra. The shiny tissue carries the ventral nerve root ventrally as was shown by Campbell and Barwick (1988, figure 36). It contains large numbers of pores, some isolated and others joined by grooves. The surfaces on the centra are placed together and would limit lateral movement (Campbell and Barwick 1988, figures 34-36). Such movement would not have been expected, judging from the the arrangement of the neural arches which cross the boundaries of the centra and have loose attachments to adjacent neural arches.

**The Pleural Centra**

The number of rib bearing units remains unknown, but it must have been at least twenty. The best preserved material comes from WAM 86.9 625 (Figures 12 A,B) and WAM 86.9.650 (Figures 10 A,C,E), which provided most of the centra which were sectioned. The posterior centra are more elongate than the first three described above, and though most of their lateral walls are covered with a perichondral layer of bone, the anterior and posterior edges of this perichondral bone do not stand out to form a sharp edge (Figures 7 E; 10 B-D) against what must have been a connective intercentral capsule. The margins of the centra where they contact one another, consists of finer grained porous bone making a narrow band, and this can be seen on ground surfaces and in thin sections to be the more recently added layers of tissue (Figure 12 A-C). These must have been deposited in sequence against the soft tissue occupying the space between the centra.

On the ventrolateral sides of each centrum is a well developed parapophysis (Figures 7 C; 10 A–C, 11), which is the ossified version of the basiventral cartilage found in extant dipnoans. This is fused to the centrum (Figure 14 A), but the junction between this and the centrum can be distinguished by a suture which is not continuous. The degree of fusion varies from specimen to specimen, and in some individuals the parapophysis falls free from the centrum. Usually the junction is best seen on the posterior and the ventral faces, because the anterior face has a covering of periosteal material.

Each parapophysis is flat or slightly concave at its base. The ventral surface has lightly impressed radial markings which have the appearance of muscle attachments (Figure 7 C). In dorsal view, the anterior end of the parapophysis is turned backwards at 25° to the median line. The front face of the process is also flattened and meets the base in a slightly rounded angle. The posterior face is naturally much shorter than the others, and is distinctly concave.

The terminus of the parapophysis is almost triangular, but its dorsal edge has a slightly rounded extremity as is best shown on WAM 86.9.650 (Figures 9;10). This attachment surface lies almost vertically, but the details are hard to find in an uneroded condition. Some complete ones are oriented at an angle of about 70° to the axial line, indicating that the ribs must have had a strong posterior orientation. Vascular bone occupies much
of the paraphysis, and can be seen to be made of unbroken bubbles of bone. Its terminus fits precisely with the end of a rib.

Between the two paraphyses on a centrum, the basal surface of the centra are distinctly concave longitudinally and laterally (Figure 7 C). The surface apparently was covered by a thin layer of periosteal bone, some of which has been removed during preservation and preparation, to expose the coarse vesicular tissue of the centra. This cavity would have housed the upper part of the haemal system.

The Centra Posterior to the Body Cavity

These are known from several specimens (Figures 10 A–C; 11). The neural arches are not well preserved and usually fall free. The haemal arches are discussed below. ANU 49116 shows centra well along the caudal fin and these have long haemal arches. It is not known if these arches continue to the extremity of the caudal region. All the centra are small, circular in cross section, have a disproportionately large foramen for the notochord, and are relatively shorter in comparison with their width in the more posterior positions.

One small specimen, ANU 35641, is available and has several centra preserved. Some of these are only 4 mm in diameter, but show that the concavities in both fore and aft faces are deep, and the opening in the middle of the centrum is relatively large (Figure 12 D).

Specimens of the posterior centra of the small specimen ANU 49262 are illustrated in Figures 12 D,E; 13A,B. Of course, rib paraphysis are not present on these specimens and they have neither neural nor haemal arches. It is assumed that they therefore come from a posterior position in the animal. The canal for the notochord is large with respect to the diameter of the centrum, and the amphicoelous faces are deep. Details of the internal structure are shown, and these are very similar to those of the more anterior centra. Photographs of the centra are shown in Figures 12 D,E; 15 A,B, and these indicate that the concentric layering of the inner structure is more regular than those of the pleural centra. Nevertheless the concentric layers are connected by struts, and a large number of perforations occur in the laminae. Thin sections show that the central part of the centrum is composed of poorly defined tissue, probably ossified cartilage.

Histology of the Centra

Sections of pleural centra of adult specimens have been cut longitudinally and obliquely along the central notochordal axis, and vertically especially through the paraphysis. Most of these sections have been cut from WAM 86.6.650 (Figures 13 C,E–G; 14 A–C) and another from ANU 49284 (13 A,B; 15 A,B). The centra from posterior to the anal fin from a Paddys Valley, Gogo specimen, now ANU 49262, was sectioned to show the formation of an individual which has a large notochordal opening. The specimens were partly etched with acetic acid before sectioning, so that the orientation of the sections could be determined. The result of this is that it is possible to examine the tissue still embedded in matrix as well as embedded in the plastic impregnating solution. The only work on Devonian dipnoans with which we can make comparisons is that of Schultze (1970) where he wrote on *Griphognathus sculpta* Schultze, *Jarvikia artic* Lehman, and *Soederberghia*. Of these, the work on *G. sculpta* is the more complete. The structure of the small posterior centra are described first because they show the early stages of development of the centra.

Small Posterior Centra

In vertical section, the small posterior centra of ANU 49262, show the space around the notochordal opening occupied by poorly organised tissue which contains a large number of spaces filled with a black substance. We interpret these as infilled cartilagenous cell spaces. In places the tissue contains oval shaped openings, and these show up best in crossed polars (Figure 15 A,B). This is reminiscent of the section of *G. sculpta* figured by Schultze (1970, Plate 39, figure 1a). At large magnifications (Figure 13 D) the tissue shows weak concentric lineations, and along these the black cartilagenous cell spaces are aligned. This axial zone passes laterally into the concentric

---

**Figure 3** Centra and haemal spines from a specimen WAM 86.9.651, in which most of the units have become separated. All specimens show the notochordal canal, the large opening for the caudal artery, and the two smaller openings for the caudal veins. The position for each unit can be identified by reference to Figure 1 and Figure 10 D, A–C. Lateral, posterior and anterior views of an element from the anterior end of the caudal fin. D–F. Same three views of a more caudal element. G, H. Lateral and anterior views of an even more caudal element. I, J. Lateral and posterior views of a unit from dorsal to the main anal fin support. K, L. Lateral and posterior views of a posterior caudal unit. M, N. Lateral and posterior of a unit dorsal to the main anal fin support. This specimen has been partly broken. O. Two units from anterior to the anal fin. A large foramen (arrowed) carries a branch of the caudal artery. P, Q. Two views of three caudal units showing distortion. The haemal arches are almost complete, but the middle one is joined to the posterior one on one side and has a caudal radial attached to it. R. Two units from even further forward of the anal fin, the anterior unit having two openings that enter the caudal artery canal. This specimen has been partly broken. Scales = 1 mm.
Postcranial structure of *Griphognathus whitei*

lamellae which form the bulk of the centra. Between the lamellae the spaces which are now open would have been filled with cartilage in the living animal. Each lamella has a core of calcified cartilage with large black cell spaces, and this is surrounded by a thin layer of laminated tissue which lines the open spaces through the centrum.

The outermost layer of the centrum is not well developed. It consists of very finely laminated tissue, which in places has a botryoidal surface. It is comparable with the thicker material described below for the pleural centra.

In longitudinal sections the axis is composed of the same tissue described above. This continues around the articulating faces and the lateral parts of the centra (Figure 13 A,B). Branches of this material extend into the laminae that make up the bulk of the centrum, and it is clear that at this stage of the development of the centra there is continuity between the tissue forming the amphicoelous surfaces and the laminae of the main body. Growth lines indicate that the new material is added concentrically to the whole centrum.

**Pleural Centra**

The pleural centra have also been cut vertically and horizontally. They are bounded by a shiny layer of tissue which we have referred to as perichondral. The reason for this is that it encompasses the lateral parts of the centrum which would have been made of cartilage originally. Thin sections show that in places it lies on bone but elsewhere it is on calcified cartilage. This layer contains many perforations for nutrient canals. In thin sections the layer is made of fine-grained closely spaced layers which is organised into spherical or domed patterns, and in places the surface is botryoidal (Figure 13 C,D). It contains no osteocyte spaces. During growth this layer must have been resorbed and a new layer redeposited subsequently.

The horizontal section of a large specimen shows that the bones consist of two types. I. The main part of the centrum is made of elongate bony layers running parallel with the lateral margins. These layers contain abundant osteocyte spaces. Polished surfaces (Figure 12 A–C) show that the elongate bony layers are partly in sheets and partly in tubes of bone. These tubes are circular in places but in others they are elongate, and ovate in cross section. Variation in size is great, and layers are often interconnected. This is easily seen in oblique views of a polished surface, and in cross section (Figure 14

\[ \text{Figure 5} \] The three most anterior vertebrae of ANU 35645 in posterior view, drawn to show the sharp-edged perichondral layer surrounding the centra. The rib orientation is taken from the shapes of the attachment surfaces of the ribs. No rib was attached to the first centrum.

\[ \text{Figure 4} \] A, B. Lateral and dorsal views of the main support of the second dorsal fin from WAM 86.9.651. The dorsal view is enlarged to show the left-right bifacial terminus. Part of this specimen has been broken. C. Anterior view of a proximal supraneural with the terminus that fitted into the concave surface on the neural spine. Same specimen. D, E. The ribs from the second centrum photographed in different orientations, from ANU 35645. F. Rib from the third centrum of same specimen, viewed from both sides. The lower of the two figures shows the attachment surface. G. An isolated half of a neural arch with the crest broken. H, I. Another half of a neural spine, H being slightly rotated to show the split of the dorsal nerve into two units. J, K. Similar views of another arch. Specimens G–K from ANU 49900. L. Reassembled supraneural spines from WAM 86.9.625. The original specimen is photographed on Figure 21 A,B. A broken neural arch is shown on the bottom right with its crest well preserved. M. Slightly tilted crests of same to show the groove along the crest with nodes along their margins. N, O. A supraneural spine from ANU 49900, photographed from both sides. P, Q adjacent spines from the same specimen. Note the fine grooves on both sides of each specimen, but particularly on N and O. Scales A–K = 1 mm; L, M = 10 mm; N–Q = 1 mm.
Figure 6  The neural arches consist of left and right units which readily fall apart on ANU 49900. A, B. These two figures are drawn from a slightly posterior view of two left arches to show the passage of the dorsal neural nerve which splits into two branches. Compare with Figs 4 H, J. The surface dorsal to the furrow for the ligament is smooth, but the most dorsal part is where the two sides of the arch join beneath the surface for the proximal neural spine.

A,B). The thin sections show the discontinuity of the bony layers as the cut surface runs into and out of the discontinuous tubes and sheets. 2. The concave surfaces facing the adjacent centra are composed of cancellar bone forming a strengthening band. This layer runs into the corners of the centrum and usually forms an edge which projects lateral to the marginal perichondral layer. Medially it forms part of the wall of the axial canal (Figure 12 A). This material was deposited from the soft tissue occupying the space around the notochord, which must have contained cells capable of depositing bony tissue.

Vertical sections (Figure 14 A–C), show concentric layers of the bones in Type 1 above, and many new details are revealed. The elongate bony layers are two sided and in places are thin banded. Within a single bony layer where the the two sides separate (Figure 14 B), a dark layer of material is present. This seems to be made of opaque material within which it is sometimes possible to identify single units. From some of these it is possible to recognise thin dark fibrils which extend into the surrounding bone. In other places the lamellae in the bone can be seen to grade into the dark tissue. From this we conclude that the dark material is partly calcified cartilage which grades laterally into the junction between the two layers of bone. Sections through the tubular part of the tissue show a dark core which also represents the calcified cartilage around which the bone was deposited.

Long thin canals of perichondral bone run deeply into the centrum (Figures 13 F,G; 14 A) and other oblique canals are common. These are the inward extension of the nutrient canals noted in the lateral walls of the centrum.

In addition, the above sections of *G. whitei* have passed through the parapophysis on the ventrolateral edges of the centra. As indicated in the section on the gross structure, the boundary between the parapophysis and the centrum is best shown on the ventral and posterior margins. The dorsal edge is well joined to the centrum. The thin sections are oblique to the parapophysis and pass anteriorly to the junction with the ribs. The whole surface cut is surrounded by a continuous bone layer which is thickest on the dorsal side. Close to the junction with the centrum the dorsal layer thickens and is composed of parallel fibres at right angles to its surface and with numerous osteocyte spaces. The contact with the centrum remains secure and rarely in specimens does it open up. The
Figure 7  A, B. Medial and lateral views of an isolated rib showing the detailed sculpture on their surfaces and the nodes along the lateral faces. WAM 86.9.650. C. Ventral view of two centra showing the posterolaterally directed parapophyses, and their sharp junction with the centrum (arrowed). The deep medial cavity is dorsal to the haemal canal. ANU 49115. D. Lateral view of the anterior dorsal fin support. Note the dorso-ventral shape of the attachment to the neural arch (arrowed). WAM 86.9.645. E, F. The original specimen from which Figure D was obtained. Note the elongate neural arch which is broken through, the elongate proximal supraneural spines which have flat termini for the distal supraneural spines. Scales = 10 mm.
ventral edge is thin bone and fades away in places.

Internally the parapophysis contains widely spaced bony layers. In places these are joined to the bones making up the concentric layers of the centrum, and no sharp boundary is visible. These bony layers are thin and discontinuous (Figure 14 A), indicating that they were in process of resorption and redevelopment during growth. This was apparently necessary because the junction between the ribs and the parapophyses is so open that movement along this junction must have been possible. The passage of an occasional bony layer across the junction would still allow small movement to take place especially if it was not anchored at either end.

Summary

From these two sets of data we conclude that the early growth stages were rapidly ossified forming a strip of hard tissue around which the perichondral layer was deposited. Following this the perichondral layer was resorbed, and expansion took place by the formation of lamellae to increase the diameter. The margins of the centrum were formed of the ossified cartilagenous layer. Next the space for the notochord was relatively reduced, and the ossification of the cartilage forming the lamellae took place by the addition of layers of clear bone on their surfaces. This process continued until most of the laminae had been ossified. The thick interfacial surfaces were added to independently in the adult stages, and the continuity between these layers of this tissue and that of the body lamellae was lost. In addition, the lamellae were formed laterally at the margin of the centrum and the ossified cartilage was replaced by the lamellae. At the core of the centrum, ossified cartilage was converted to endochondral bone.

Ribs

As indicated above, no cranial ribs have been found in this species.

In this discussion we mention the most anterior ribs on the free centra. On the second centrum which is only 13 mm in diameter, the ribs are only 16 mm long (Figure 4 D,E). They have a modified triangular cross section over most of their length, and are thickest medially. The sharp edges of the ribs have some nodes similar to those of the major ribs. The third centrum has ribs 28 mm long (Figures 4 F; 5), but these are not so uniform as the first ribs in shape, although they are largely triangular in cross section.

The pleural ribs are well preserved. The details of their positions along the column are not known at present, but ANU 49116 shows that the centra up to ten in front of the second dorsal fin do not have a parapophysis for rib attachment. Another badly distorted specimen (ANU 49282) has 16 rib-bearing
Figure 10  A. Lateral view of three pleural ribs showing the parapophyses for the ribs, the narrow perichondral layer, and the canal for the ventral nerve (arrowed). Anterior edge of the first centrum (right) eroded. WAM 86.9.650. B. Centra from ANU 49900, showing the unworn surface with finely punctate perichondral surface, the narrow bands of bone forming the junction with the adjacent centra, and the canal for the ventral nerve (arrowed). Anterior to the left. C. ANU 49900. Centra with the ribs present but slightly displaced. D. Part of the vertebral column of ANU 49207 dorsal to the anal fin. White arrows show the haemal arches short and posteriorly directed. Black arrow shows the first of the haemal arches with a longer spine, coming from the position posterior to the fin support. E. WAM 86.9.650. The attachment ends of three ribs showing the shapes and the conchoidal attachment surfaces of their cores.
centra passing back to centra with a strong haemal arch.

The pleural ribs are directed postero-ventrolaterally at an angle of about 70° to the axial line. The axes of the proximal parts of the ribs are almost straight, but lateral to that they are gently bent. Restored to their approximate position on the end of the paraphysis, the ribs project posterolaterally and then curve posteroventrally (Figure 10 C). The body shape must have been narrow in the region of the body cavity.

In cross section the ribs are sub-triangular proximally, and are slightly grooved on their surfaces (Figs 7 A, B; 8 A, B; 10 A, E) producing a pattern that meets the ends of the paraphysis. The deepest groove is on the posterior side of the rib. Lateral to the dorsal edge, the surface of the rib has a short flattened surface which dies out against the strong dorsal ridge. The lateral ridge is very variable in shape, in some it is rounded and in others it is low but sharp, with elongate ridges along its crest. The ventral edge is sharp and often carries flat elongated nodes. As the lateral ridge dies out distally, the lateral face of the rib becomes domed and then flat. The median face is also flat so that in adults the distal cross section of the ribs is ovate. In adults the proximal parts of the lateral and internal surfaces of the ribs are covered with fine linear markings. These probably represent the attachment surfaces to the myosepta which shows how the flexure of the body cavity was accommodated.

The attachment of the ribs to the paraphysis was made of cartilage, and the evidence is that it was a mobile junction. Thus, although the centra were relatively rigid with a limited amount of movement possible from the point of view of body flexure, the ribs would have been capable of movement independently of the centra. This would account for the surface structure on the ribs described above. It would also account for the nodes on the ribs which possibly indicate points where the muscles of the myotomes acted from rib to rib.

The smaller specimens in the collection generally show the same structures as the adults, but they tend to be more rounded in cross section distally, and they have few markings on their surfaces.

We do not have any specimens with ribs in natural position, but the orientation of the articulation and the distal flattening of the ribs, indicates that the ribs ran posterolaterally and angled across as many as 10 segments as defined by the centra. The cross section of the body cavity is also known from the whole specimen AMF 72402, and this supports the proposition that the ribs have the shape described above.

Haemal Arches

Arches Anterior to the Attachment of the Anal Fin

On ANU 49114 (Figure 16 H) the anal fin is approximately in position. This shows three haemal spines in front of the anal fin attachment. They are curved posteroventrally, and the one anterior to the fin is bent around the anterior end of the anal fin support (Figure 2 A). The two anterior to it are shorter and are more acute at their tips. All three arches have small incomplete ends to which
proximal haemal spines must have been attached. The most posterior one is preserved and is 4 mm long. The anterior faces of the haemal arches have a shallow groove into which the spine anterior to it would fit. The main fin support is attached to the axial column by a short straight haemal arch.

ANU 49120 has five centra anterior to the anal fin attachment (Figure 16H). Only the most posterior one has the full haemal arch present, and the others are broken. No proximal haemal spines are preserved, and the one anterior to the anal arch has a complete terminus showing that no spine was present.

ANU 49116 (Figure 1) does not show the attachment of the anal fin to the haemal arch which supported it, but it does have an approximate position for the second dorsal fin which lies opposite the attachment of the anal fin in other specimens. This is an important point because it allows us to estimate the position of the posterior end of the body cavity. At least eight of the centra in front of the attachment have some haemal arches present, although they are all broken.

WAM 86.9.651 has isolated vertebrae from the posterior half of a specimen, and judging from the
fact that some of them have short haemal spines turned sharply backwards and have a small space for the attachment surface for a tiny proximal haemal spine such as occurs in ANU 49114, we consider that they are from the area anterior to the anal fin. Two of these have vertebrae still in association. One has a large ventral opening through the haemal spine and enters posteriorly into the large central cavity in the arch (Figures 3 O), the other has lateral openings (Figure 3 I). Some of these openings were at first thought to be gaps in the wall resulting from preparation, but further investigation shows that they are genuine openings. Still other arches have small openings irregularly scattered over their surfaces, and entering the haemal canal (Figure 3 R). These seem to be openings for the circulation of the blood into the posterior part of the body. Similar openings are present on one of the arches on ANU 49116.

Arches Posterior to the Anal Fin Attachment

ANU 49114 has six depressed arches posterior to the anal fin. The sixth is somewhat longer than the others. This pattern allows for the anal fin to be pushed up close to the body. The seventh is broken by a crack in the rock, but it was much longer than the sixth, and it may have had a subhaemal spine, but this is not determinable because of the crack. The terminus of the seventh is well rounded and shows no sign of a further attachment. The eighth is also badly broken, but it has lepidotrichs attached to its terminus, and has more subsequent haemal arches which are short and followed by radials with lepidotrichs. Presumably the eighth is the first of the caudal series. Figures 19 A, B have been reconstructed with a similar break.

On ANU 49120, four arches posterior to the attachment of the anal fin are depressed and bent backwards ventral to the haemal opening (Figure 16 H). The fifth arch is also bent, but it has a short subhaemal spine. The sixth is also short and bent, but it is incomplete.

WAM 86.9.651 has several posterior vertebrae preserved, and some of them are isolated. All were etched from a single block of rock, and presumably came from a single specimen. Some of the haemal arches are short and have no sign of subhaemal spines, so they are probably from vertebrae 4 and 5 described above from ANU 49114. Some of these haemal arches have openings through the wall, and these do not have a regular arrangement. Some are small and others are almost as large as the canal itself. They open directly into the central canal. ANU 49116 has one haemal arch in this position (Figure 1B, marked with an arrow) and it has a large ventral opening in its wall. Other specimens show larger centra, and must come from the area anterior to the anal fin attachment, and have occasional large openings. Others are more elongate, have strong surfaces for the attachment of spines and represent the first of the caudal radials.

The internal structures of the haemal arches are best preserved on the isolated units from WAM 86.9.651. They are illustrated on Figure 3. A large central space occupies the central part of the arch. Its walls are thin, and they make a circuit around the central space, except for the surface against the centra. This canal would have carried the caudal artery. Lateral to the central space, and against the centrum on each side is a small tube which opens fore and aft, and was connected between vertebral units. They open laterally between the haemal arches, and presumably connected with the myotomes. These lateral canals would have carried caudal veins. Other veins would have been located laterally in the body. The structure of the centra is almost identical with that of Protopterus annectans Owen, as figured by Schultze (1970, plate 40, figure 1a,b).

Arches in the Caudal Region

These are best preserved on ANU 49116, but broken fragments also occur on ANU 49114 (Figures 1, 2). Isolated elements also occur on WAM 86.9.651 (Figure 3). The arches on ANU 49116 do not show clearly where the first of the caudal arches occurs. We have placed it at the first element which has a terminus to which a caudal radial may have been attached. The lepidotrichs are not preserved in this region, and so they cannot be used to support our interpretation. The arches decrease in length after the first two. The more anterior arches 3 to 8 have concave distal termini, indicating that the radials attached to them were able to move.
Figure 14  A. An incomplete vertical section produced by printing the section itself on photographic paper. The light coloured material is hard tissue, and the dark is open space. The bony tissue contains small spaces containing dark material. Note the notochordal canal surrounded by irregular ossified cartilage, and then by elongate layers of bone. The parapophysis contains an open meshwork of bone which does not make continuous layers. The outer layer on the parapophysis is thicker on the dorsal side and makes a strong junction with the centrum. B. Enlarged thin section of the same specimen with the light spaces being gaps. Layers of light tissue is bone surrounding dark ossified cartilage. C. Axial section around a central notochordal canal. Limestone still occupies the matrix throughout. Note the narrow space occupied by ossified cartilage passing laterally into more or less concentric bony layers. All sections from WAM 86.9.650. Scales A,C= 1 mm and B= 0.1 mm.
laterally. The first two arches are more slender than those following, and their termini are rounded rather than concave. All the preserved arches have grooves down the posterior faces and weaker ones on the anterior faces, again allowing lateral movement to take place.

Judging from the shapes displayed on ANU 49116, we have determined that some of the units obtained from WAM 86.9.651 came from the caudal region. These are illustrated on Figure 3 D–F, G, H, all of which have a divided space at the end of the haemal arch. Figure 3 A–C, K, L and P, Q, were from the front of the caudal region, each with a long arch and an undivided tip.

**Neural Arches**

*Arches on the Anterior Centra*

The first few arches are well preserved on ANU 35645. They have been described by Campbell and Barwick (1988), commented upon by Campbell and Barwick (1999), and they have been illustrated in both of these papers. The most significant points are:

1. the arch has an attachment to centra in front and behind;
2. each is attached to the neural arch in front;
3. short sharp supraneural processes are directed laterally;
4. the dorsal and ventral nerves can be clearly traced;
5. the first neural arch is depressed and shows no sign of a dorsal surface like those on subsequent arches.

These structures suggest that the anterior part of the vertebral column was rather inflexible, and the dorsal and ventral nerves passed through well defined gaps in the bone.

*Arches on the More Posterior Centra*

In more posterior vertebrae, most neural arches are broken off from the centra, but each was connected with two centra (Figures 7 F; 9; 10 A, B; 11). These connections were made of globular bony surfaces, without any evidence of fusion. Thus they would impede lateral movement at each junction, although this limitation would have been restricted. None of these more posterior neural arches shows an epineural spine such as those on the anterior arches.

The surfaces of the centra were partly destroyed by acid, and it is difficult to detect the details of the attachment surfaces of the neural arches. Occasionally, as on ANU 49115 and ANU 49900 (Figures 10 A, B) which come from dorsal to the body cavity, the ventral nerve root is preserved between ridges of periosteal bone as in the anterior vertebrae (Campbell and Barwick 1988, figures 34 B, C; 36 A). The surfaces adjacent to this groove, labelled p ana and a ana in the 1988 diagram, are not well preserved, but can be outlined on ANU 49900, ANU 49115, and less well on WAM 86.9.650 (Figures 10; 11). The posterior attachment of the neural arch is triangular in shape, and the anterior one is more ovate and is tucked in beneath the uplifted margins of the ventral nerve canal. The small individual ANU 35641, has more caudal

![Figure 15](image-url)

Figure 15  A. Vertical section through ANU 49262 showing the large space occupied by ossified cartilage around the notochordal canal. Central part of slide still contains limestone. Outer elements with elongate bony layers. Thin section printed directly onto photographic print paper. B. Electronic enlargement of Figure A showing more detail of the hard tissue, and the transition from ossified cartilage (small black arrows), to the bony layers (large black arrows). Scales = 1mm.
Figure 16  A, B. The second dorsal fin photographed from both sides of WAM 86.9.645. C. The tip of the main support structure showing the dorsoventral bifacial attachment and the muscle scars for the movement of the support. The lower of the two views shows the terminus in anterodorsal view showing the broken left-right bifacial face indicating left-right movement also. D, E. The two sides of the anal fin of WAM 86.9.645. Note especially the sharp ridge separating the area where muscle attachment occurs, cf. Figure 1 F,G. Much enlarged isolated main anal support structure of WAM 86.9.651. Figure F is a slightly oblique view showing the broad flat surface on the posteroventral edge. The row of small dots is from the impregnating solution. G. Opposite side of same enlarged to show the muscle attachment for the muscles which move the radials. H. View of ANU 49120. Second dorsal fin well preserved. The neural arches and the proximal supraneural spines, and the neural arches anterior to and posterior to the anal fin, all preserved. Main support for the anal fin partly preserved and pushed posteriorly from its attachment. Main support for the second dorsal fin also pushed posteriorly. (For reconstruction see Figure 17 C). Scales A, B and D–H = 10 mm. C = 1 mm.
Postcranial structure of *Griphognathus whitei*

vertebrae, and an occasional specimen also shows the groove for the ventral nerve cord, and the areas adjacent to it are also small.

Traces of the dorsal nerve canals are visible on some broken arches, and they are not well enough preserved to be described. On the other hand, ANU 49900 has broken so that four of the neural arches have split down the midline exposing the nerve canals and the dorsal ligament canal. Three of these are well preserved, but the others have lost much of the periosteal lining on its inner face (Figures 4 G–K; 6 A, B). A pair of openings exit the dorsal edge on each side of the arch, and these join to make a single groove directed to the anteroventral corner, where it would join the dorsal nerve canal. These were for the two dorsal nerve canals which were described as entities in the first neural arches (Campbell and Barwick 1988, figures 34–36). A strong dorsal ligament canal occupies the surface dorsal to the two nerve canals, and dorsal to that the two sides of the arch are loosely joined together. The distal edge of the arch has two faces bent medially to which the supraneural bone was attached.

These same specimens show the attachment points of the two sides of the neural arches, and indicate why the two sides fall apart on etching. The surfaces of attachment to the centra are rounded bony surfaces indicating a loose cartilagenous connection. Between the two exits of the dorsal neural canals is an ovate surface with similar rounded bony surfaces, indication a connection between the two sides. Dorsal to the these canals, is a transverse strip which also contains similar bony plates, and these connect the two sides. Dorsal to the dorsal ligament canal there is an open space which may have contained an expansion of the dorsal ligament. Finally, the dorsal crest contains a junction which is strongest along the anterior edge where it is made of periosteal bone, but is also present between the two surfaces for the attachment of the supraneural bone, where it is made of small rounded bony surfaces. Although many points of attachment are present they are so weak that during preparation even slight pressure causes them to separate.

The dorsal surface of the centra shows only slight furrows where the neural cord passed along the surface. This is much smaller a groove than the one for the haemal canal.

**Supraneurals**

Specimen WAM 86.9.625 has some of the more anterior neural arches preserved. The most anterior part of the specimen available, Part B, has been photographed during preparation (Figure 21 A,B), and after the arches have been separated by etching (Figure 4 L,M). Judging from the position of the preserved ribs and the shape of the neural arches, the anterior centrum preserved is probably just posterior to the three that were figured by Campbell and Barwick (1988, figures 34–36). The neural arches are thin-walled and are inclined to the axis. The most anterior supraneural element preserved is a large bone, flattened laterally, and with a groove along its crest. Posterior to this are three large distal supraneurals, each also having a similar groove along its crest. By aligning the groove along the crests of these distal supraneurals with that of the enlarged anterior distal supraneural, the relative positions of the elements can be determined. The large unit extends ventrally much further than the other three. Its ventral end it is slightly broken but it has the appearance of being attached to a smaller structure. The most anterior neural arch preserved in ANU 35645 has a small crest dorsal to the dorsal ligament canal, and an unformed surface for the attachment of the large element described above. The subsequent distal supraneurals also have slight grooves on their front margins which allow the elements to be aligned. The first two units have incomplete ventral ends at present, but they are well enough preserved on the original photographs. The supraneurals ventral to them have elongate dorsal edges which will match them. The third supraneural is complete, is much shorter than the others, and shows a rounded surface which would have provided an attachment for the supraneural below.

The longitudinal spacing of the supraneural elements cannot be determined from the specimen itself because they were not in position when etching occurred. However we note that on ANU 35645, the second and third neural arches have dorsal surfaces to which supraneural elements were attached (Campbell and Barwick 1988, figures 34–36), and it is quite clear that there were no gaps between the supraneurals. What is not clear is the possibility that the the large supraneurals may have been separated by smaller units. The specimen as preserved at present shows that lateral compression has taken place and that some of the neural arches have been pushed posteriorly. A solution to the problem of spacing depends on the discovery of a less distorted specimen.

As indicated above, the crests of the distal supraneurals are grooved. Along the edges of the grooves are slight eminences with sharp margins, and the surface of the distal supraneurals are slightly ridged beneath them. The whole surface gives the appearance of muscle attachment. This should be compared with specimen ANU 49900 described below. This is a most significant feature, suggesting that the crest of the distal supraneurals was attached to the connective tissue beneath the scales. Posterior to the four distal supraneurals just described, the neural elements are too poorly preserved to be described in detail, but it is clear
that proximal supraneurals and short distal supraneurals, are present.

ANU 49900 is a partly disaggregated specimen with ribs attached to some of the centra. Apart from the ribs, two features of interest have been observed. Two isolated distal supraneurals like the large individuals described above in WAM 89.9.625, with a depression along their crests (Figure 4 N–Q), show the flanks well preserved and on these there are ridges which run parallel with the depression in the crest. These have the appearance of muscle attachment surfaces. The attachment end is planar.

The specimen ANU 49120 (Figure 16 H) shows the neural arches beneath the second dorsal fin, and the neural arches and supraneurals anterior to the fin which are more complete than those in other individuals. The arches ventral to the fin are depressed, inclined, pointed at their crests, and fit closely beneath the fin supports. The arches anterior to the fin are higher, concave on their crests, and support long thin proximal supraneurals. The one anterior to the main support is bent to fit into the curvature of the support, and has a sharp tip with no evidence of a distal radial. The second proximal supraneural is also pointed, but it curves slightly posteriorly at its tip. The third to fifth proximal neurals are of approximately the same length, and have tips which carried the distal supraneurals.

Four broken arches from anterior to the second dorsal fin are preserved on ANU 49114 (Figure 2 A). The neural arches are relatively short structures, approximately 1.5 times as long as the centra, and inclined at ca. 20° to the axial column. They are surmounted by proximal supraneurals which are twice as long as the neural arches. They are oriented at the same angle as the neural arches, but some are curved slightly dorsally. The distal ends of the proximal supraneurals have an attachment surfaces for distal supraneural spine, but none of these spines is preserved on this specimen. These indicate that the dorsal surface of the body must have been high in this region leading up to the high second dorsal fin. It also implies that first dorsal fin must have been well forward of the second fin.

The specimen ANU 49116 (Figure 1) has the region in front of the second dorsal fin preserved, but the centra are all out of their proper orientation, neural arches have all been destroyed, and only the broken up supraneurals are present. These also show that the first dorsal fin must have been placed well forward. The proximal supraneurals have a double attachment to the neural arch indicating that they could move laterally on the dorsal surface of the neural arches, and the distal supraneurals have rounded distal tips.

WAM 86.9.645 (Figure 7 E,F) has a support for the anterior dorsal fin and a number of supraneurals posterior to it. The neural arches are long, and the proximal supraneurals are long and thin. They have a lateral bifacial junction with the neural arches as would be expected, and their distal tips are not complete indicating that distal supraneurals were present, but none of them are preserved in this specimen.

Medial Fins

The Anal Fin Structure

These are well known from four specimens. ANU 49114 is a large specimen with its centra anterior to the anal fins being approximately 130% greater in diameter than those in ANU 49116. The attachment of the anal fin is situated well forward of the anterior edge of the caudal fin. ANU 49114 shows that there were seven axial centra between the attachment of the anal fin and the first caudal fin segment. The other two specimens WAM 86.9.645 and 86.9.651, are incomplete but they show distinctive features, and will be discussed separately.

On ANU 49116 and 49114 (Figures 1; 2; 19 B) the main anal fin support is large, and flattened laterally but with distinct grooves running back to the surfaces which support the radials. The dorsal surface is concave in lateral view and gently convex in cross section. The ventral edge is convex in lateral view, and gently convex in cross section except at the posterior end, which has a broad flattened surface. However, the presence of lateral extensions on the grooved ventral surface suggests that muscles or ligaments were present and that these could have been vital for the movement of the lepidotrichs described above.

The main anal fin supports are strong structures which have a thick periosteal ossification over an open meshwork of struts. On ANU 49116, the attachment of the bone to the axial skeleton shows a bifacial vesicular surface, the ventral edge being turned backwards. On this same specimen, another plate, much smaller than the one just described, occupies its posterodorsal corner (Figures 1 A; 18 C). Its edge lies in line with the dorsal edge of the main anal plate. We refer to this plate as the secondary anal fin support. In this specimen the dorsal plate is isolated. In ANU 49114 the dorsal plate is fused to the main anal support plate, although the boundary between the two is clearly visible (Figure 2 A,B). The surface of this dorsal plate carries radial ridges to the points of attachment of the radials, identical to those on the main anal fin support plate. The attachments for the radials form a stepped edge along the anal support plates. Three radials are attached to the main anal support plate, and three to the secondary plate. The proximal radials are strong plates with longitudinal ridges forming the corners of the plates. They expand slightly towards their posterior ends. It is not clear from these specimens if the proximal
Figure 17  A, B. The two sides of the anal fin of WAM 86.9.645 drawn to show the support structures, the radials, and the lepidotrichs and their attachments. C. Reconstruction of ANU 49120 with the radials, neural arches and some of the haemal arches in position.
radials are followed by one or two rows of distal radials. The most distal radials are deeply encompassed by the proximal lepidotrichs. The ventral edge of the main anal fin support has a flattened surface with slight lateral flanges that are extended into slight ridges. These ridges are parallel with the ridges on the main anal support plate. The most likely explanation of the structure is that it provided attachment for the muscles which activated the ventral lepidotrichs (see below).

Towards the anterior end of the main anal support plate on ANU 49116 lies a stellate array of ridges (Figures 1 A,B; 18 C). These are similar to the ridges near the radial attachment. They are also present on the proximal radials. They probably mark the insertion points for muscles attached to the anal fin support and extending to the lepidotrichs. The stellate array has grooves running forward, and these probably mark the muscle fibres from the anal support to the axial skeleton, permitting the movement of the fin base. The proximal lepidotrichs are strong, long, slightly flattened proximally. Their outer faces have shallow grooves which probably mark the muscle attachment sites. ANU 49114 shows the inner face of part of the fin and these are well rounded. The radials are covered with lepidotrichs. This arrangement must have given the fin rays a great deal of support, and such an arrangement must be taken into account when considering the muscle attachment.

WAM 86.9.645 (Figures 16 D,E; 17 A,B) is comparable in size to ANU 49116. It has the main support plate and a second posterodorsal plate of the same kind. On both specimens each radial support plate carries three articulations for radials. The main support plate has the upper two attachments fused together, while the lower one is separate. The small secondary plate has three attachments, the most dorsal one of which is much smaller than the others. The preserved radials are short in comparison with the proximal radials on ANU 49116, and one is a double structure with two plates joined together. It fits neatly against the double structure on the main support plate. The distal radials are long and extend back into the lepidotrichs as much as 1.3 cm. Only the proximal lepidotrichs are preserved. In cross section and they vary in shape from ovate to flattened.

WAM 86.9.651 is the smallest specimen from which we have extensive postcranial material (Figure 16 F,G). The main support structure of the anal fin is 65% of that in ANU 49116, and 48% of ANU 49114. The main support structure of the anal fin is all that is preserved of the structure, but the secondary support plate is attached to the main plate, and no sign of a bounding suture is present. The secondary plate is distinguished only because it extends more posteriorly. The main plate carries three radial attachments, but the smaller plate carries two rather than three radial attachments. Posteroventrally the main plate has the same distinguishing feature of a flared surface with slight lateral projections which is well shown on Figure 16 F. The lateral flanges do not extend uniformly along the whole length of the plate, but have a rounded extension on each side. On these there are small projections which have the appearance of ligament attachments. The position of the main support and the orientation of the projections suggest that the ligamenta would have been attached to the soft tissues, and would have been for stability rather than movement of the main support structure. The dorsal edge is like that of ANU 49116. The anterior attachment on the main plate is dorsoventrally bifacial, and very similar to that of ANU 49116. The dorsal face is the larger, and the ventral face is turned backwards at ca. 80°, indicating that the support would have a dorso-ventral movement.

Second Dorsal Fin Structure

Parts of this fin are preserved on ANU 49114, 49116, 49120, WAM 86.9.645 and 86.9.651. The fin supports are not complete on any specimen, but it is apparent that there is considerable variation in the arrangement of the secondary support structures.

We describe ANU 49116 first, as it is the most complete. The fin has a main support and five ancillary supports posterior to it (Figures 1; 18 B). The main support is large, anterodorsally placed in the overall fin structure. The following five are much smaller and are arcuate in shape, each one fitting against the element in front. Each of these five elements has a finished blade-like ventral edge, without any sign of attachment.

The main support plate has a gently concave base which was continued by the bases of the subsequent arcuate plates. These bases are all rounded. The dorsal edge is more strongly concave and turns dorsally where it is broken off. The dorsal anterior end is lost, but presumably it was as is shown by the other specimens. The posterodorsal edge is very slightly concave in lateral view, and its surface is slightly flattened. The posteroventral edge is more concave and the ventral part of its edge is flattened where it is adjacent to the next plate. The posterior face has surfaces for the attachment of three radials. The posterior two thirds of the plate carry ridges which begin from an irregular ridge, and terminate against the radial attachment posteriorly. These are directly comparable with the ridges described for the anal fin above.

The first three arcuate secondary support plates are similar in shape. They can be oriented precisely in place because their edges are clear and because the ridges they carry can be aligned. The fourth plate is shorter, differently shaped because of the
Postcranial structure of *Griphognathus whitei*

Figure 18  A. Reconstruction of WAM 86.9.645 showing the second dorsal fin and its relation to the inferred neural arches and haemal arches. Note especially the secondary support structures. B. The second dorsal fin from ANU 49116, showing the reconstructed organisation of the secondary support structures. C. The anal fin of ANU 49116, with its proximal and distal radials and some lepidotrichs. D. Anal fin of ANU 49114 with the proximal and distal radials restored to position.

increased inclination and its fitting into the third plate, and the fifth plate is even shorter and its shape is even more modified as it joins the fourth plate. Each of these plates has a single oblique ridge on its surface, and each has a radial attached at its end, except for the fifth one which has two radials, one of which is smaller than the others. This makes nine radials articulated to the support surfaces. As can be seen from Figures 1 and 18 B, the first radials are steeply inclined.
Perhaps the most important part of these plates is that their ventral edges is blade-like and they show no sign of being attached to any other structure. They are internal to the fin. As ANU 49120 (Figures 16 H; 17 C) shows they are placed immediately above the the neural arches. They cannot be compared with the plates in such genera as Flustrantia and Scutumenactia in which the supports for the posterior of the fin rays are supraneruals. In fact, the structure in Grifinhognathus is similar to the Dipterus type with more supporting elements within the fin.

The proximal radials are long and narrow, being slightly dumbell-shaped in lateral view, and quadrate in cross section. They must have fitted closely together. The distal radials are not well preserved, but they are shorter and similar to the primary radials in other respects. The specimen does not have further radials aligned in any location, but some radials are attached in the lepidotrichs, and these must be third radials. They are similar in shape to the distal radials.

The lepidotrichs are not preserved in sequence. They are thinner than those on the anal fin, and are more rounded in cross section. There is a possibility that they may have occurred in clusters around each of the radials, but this is not clear.

On WAM 86.9.645, only the main fin support, three of the secondary fin supports, and a couple of broken radials are preserved. Nevertheless this is a most important specimen because almost the whole edge of the main support of the second dorsal fin is preserved (Figures 16 A,B; 18 A). The attachment surface is not quite complete, but it has left and right surfaces indicating that lateral movement was endorsed, as well as some dorsoventral movement (Figure 16 C). The anterior edge is strongly convex and it is sharply up-turned dorsally. The anterodorsal edge is truncated and where it joins the dorsal edge it has a small lateral projection on each side. This is comparable with the projections described on the main anal support structure described above. The dorsal edge also expands to these projections. All these edges are rounded and complete, and show no evidence of any other plate attached. The posteroventral edge is slightly worn, but it has attachment surfaces for three proximal radials. These attachment surfaces are not completely isolated from one another because of wear. The posteroventral edge is almost straight and is attached to the next support structure.

On WAM 86.9.645, the first secondary support structure is large, slightly curved, and its anterior edge is close up against the posterior edge of the main support. It carries two oblique ridges along its length, and it supports two radials. The second support is long at its base and tapers dorsally where it supports one proximal radial. The third is also long at its base, but it expands dorsally to support three proximal radials, the posterior one of which has been partly broken off. This makes the number of radials to be nine. The posterior end of the third support was almost horizontal and there is no evidence that a fourth support lay behind it. With the secondary supports cleaned and their ventral edges aligned (Figure 18 A) it is obvious that the radial attachments are strongly stepped backwards from dorsal to ventral.

ANU 49120 is a small specimen in which the second dorsal fin is attached to the same centrum as the anal fin (Figures 16 H; 17 C). In addition, the fin is not pushed down onto the axis, and a row of inclined neural arches lies between the fin and the axis. The main support has the standard structure of the species. Its attachment surface is small in comparison with the other specimens, and it has a laterally bifacial surface but no evidence of a dorsosventral bifacial surface. Posterodorsally it has attachment surfaces for four proximal radials, and each surface is marked off by low ridges on the lateral surface. The first of the secondary support structures is bulbous in outline, and constricts dorsally to allow the fourth proximal radial on the main support to fit into the pattern. It supports one radial. The secondary support has two oblique ridges, and it supports two proximal radials. The third support is much smaller, and fits neatly into the back of the previous support and carries two proximal radials. A neural arch lies close up against the ventral edge of the third support, thus indicating that no further supports were present. The number of proximal radials in the fin is nine. The ventral proximal radials have been stripped off, but the more dorsal radials are present. They are almost square in cross section. No lepidotrichs are preserved.

The main support structure on ANU 49114 is attached to two branches of the neural arches from successive centra (Figures 2; 19 A,B). The neural arches where the fin is attached are not uniform in this animal, and the more anterior arch is narrow and may have been broken away from the proximal part against the centrum. The neural arch behind the posterior attachment lies up against the main support plate. Part of one side of the main fin support is eroded away, but this support is nevertheless of considerable value, because the outline of the plate is still preserved. The main support is very similar to that described above for WAM 86.9.645. Judging from the size of the nearby proximal radials and the size of the attachment surface, the main support carried only two proximal radials. The first secondary support structure is arcuate, larger than the first support in any other specimen, and carries the articulation for two proximal radials. The second support structure is longer at the base than the first, and tapers to carry two proximal radials. The third is too incomplete to
be worthy of description, but it appears to have supported two proximal radials. No lepidotrichs are preserved.

Only a fragment of the main support plate of WAM 86.9.651 is preserved, but it shows all the features of this plate as preserved on WAM 86.9.645. The attachment surface is better preserved than on any other specimen, and it has two faces set left and right, approximately normal to each other. This is supported by WAM 86.9.645 and ANU 49120. Two secondary support structures are also present, though the sites of their attachment are not
preserved. Each support has attachments for two proximal radials. The four proximal radials preserved are all thick walled, have rims around the attachment surfaces, and have flattened faces where they contacted adjacent radials.

First Dorsal Fin Structure

Only one example of the main support of the first dorsal fin is well preserved (WAM 86.9.645 C, Figure 7 D–F). On the same block are eleven centra, a number of broken neural arches, and fragments of haemal arches. The main fin support is isolated, and the neural arch to which it was attached is absent. This is not preserved on any of our other specimens. The presence of ten centra, with neural arches and neural spines attached posterior to the main support, indicates that there must have been a large distance between the first and second dorsal fins.

The support is robust, and lies in an unusual position (Figure 7 D). The surrounding structures are largely in correct orientation and we see no reason to consider that the support has been inverted. Note that the attachment end is protruded as in the second dorsal and anal fins, and there is little doubt that the orientation we have adopted is correct in this sense. The alternative is that this end was for the attachment to a radial, similar to that figured by Ahlberg and Trewin (1995, figure 9 b) for Dipterus. We do not accept that possibility because the other end of the specimen does not have a surface that could be used for attachment, even though it has a small opening at its tip. This opening was at first thought to be a break in the wall, but the detail shows that it is real with a small indentation at one end. Possibly a small bone was attached at that point.

The attachment surface of the support is well preserved. It is dorsoventrally bifacial, indicating that it was capable of dorsoventral movements. Having fixed the dorsoventral orientation, it now remains to determine the anterior and posterior faces. Ahlberg and Trewin (1995, figures 5; 9) figure the lateral projection as dorsal in position, and this is supported by Long (pers comm.) who figures a specimen of Barwickia with the support in position. In the absence of other information, we follow this view. The ventral edge of the support unit is slightly concave, the anterodorsal edge is more strongly concave, is well rounded in cross section, and shows no sign of muscle or ligament attachment. This leaves the posterior edge as the only place for the attachment of the fin rays. This is unusual because this surface has no evidence of sharply bounded surfaces to which radials would have been attached like those on the other fins. Nor is there any evidence of radial ridges on the flanks of the support structures such as those on the other fin supports. As indicated above, the posterodorsal edge of the posterior face was apparently open but it has no indication of surfaces to which radials could be attached. On the other hand it has slight radial ridges around the opening, suggesting muscle attachment. This may indicate that lepidotrichs were attached directly to the main fin support. Ahlberg and Trewin (1995, figure 9 b) show a similar arrangement in Dipterus, and the whole structure they described as “a single unjointed radial and an oblong basal plate.” The lepidotrichs are shown in their figures 5 b and 9 b as having been derived from the anterior dorsal fin support and from the radial. In both Barwickia and Howidipterus, Long has observed proximal radials derived directly from the main fin support, and dividing into multiple lepidotrichs distally (Long pers comm.).

In G. whitei the posterodorsal part of the support is slightly expanded and has a posteriorly directed surface which has a median ridge dividing it ventrally. The significance of this surface is not understood.

Caudal Fin Structure

This fin is partly preserved on ANU 49114 and 49116, and an external mould with some fin skeleton and caudal scales still attached, is found on ANU 49285. The first radial of the caudal fin lies about nine centra posterior to the attachment of the anal fin. The specimen ANU 49114 is broken in this region. The final haemal arch before the caudal fin, is very long and it supports a short radial with a rounded end. The first caudal radial is longer, and extends down into the caudal lepidotrichs.

On ANU 49116 the haemal arches are also short and they have concave termini to which the caudal radials were attached, thus showing that the radials had lateral movement on the haemal arches. As would therefore be expected, the radials have proximal termini with a raised rim around the
Postcranial structure of *Griphognathus whitei*

Figure 21  A, B. The two sides of WAM 86.9.625 before final etching. The structures shown in Figure 4 L,M, were etched from this individual. C. Specimen as found in the field. ANU 49285. Note details on the surface of the scales, the fine structure of the lepidotrichs, and the anterior edge of the caudal fin. Scales = 5 mm.
terminus, and are slightly concave indicating that the ligament attachment to the haemal arches was strong and presumably very flexible. The radials are 2 cm long on the anterior part of the fin, but six radials back they shorten to about 1cm. All the radials are deeply embedded in the lepidotrichs, most of which are rounded in cross section, but others are flattened or have a quadrate section.

It is not known how many verteabrae are involved with the caudal fin as no tail is complete. However, there must have been at least 15 or 16 ossified centra present on ANU 49116, and judging from the shape of the caudal section, there could have been at least another 10 beyond these. Some of these may have been unossified.

A single specimen with the caudal fin attached to a few scales (ANU 49285, Figure 21 C) is identified as a specimen of *Griphognathus* because of its scale surface. It has long proximal lepidotrichs and ventrally it has an estimated 35 distal lepidotrichs. The first distal lepidotrichs were thick and with furrows along their inner surfaces. On the ventral part of the fin, they number up to twenty elements in each row. Some of the most distal lepidotrichs are also preserved. They are of comparable length to the more proximal ones, but they are only 0.3 mm in diameter. They also have a groove down their median faces. It is not possible to count their number, but on the ventral part of the fin it must have been about fifteen in a single row. The tips of the rays probably result from the splitting of the elements, and this can be observed on a limited scale. No lepidotrichs have cosmine on the surface.

The centra and haemal arches of the caudal region of WAM 86.9.651 have been described above.

**FUNCTIONAL SIGNIFICANCE OF MEDIAL FINS AND BODY**

In interpreting the postcranial structure of *Griphognathus*, it is necessary to examine first the head and the opercular region. The genus has a large head with all its bones ossified, its mandible tucked into its snout at full closure, and the whole profile indicating that it was a bottom feeder (Campbell and Barwick 1999, figures 2; 3). The opercular is large and has a tight fit against the pectoral lobe. The body scales are elongate, well ossified and strongly overlapping. As shown by Pridmore and Barwick (1993) the overlapping of scales is such that the lateral parts of the body are protected by 4-5 scale thicknesses. The ossification of the head in association with the heavy scolation and the shape and organisation of the scales, support the view that the animal was a bottom feeder.

The Flexibility of the Body

A number of factors enable us to comment on the flexibility of the body – the body shape, the shape of the head, the scale pattern, the design of the vertebral centra, the pleural ribs, and the pattern of the neural arches. We deal with these matters as follows.

(a) Pridmore and Barwick (1993) discussed the fineness ratios of the species and compared them with the values derived by Weihs and Webb (1983). The values for *G. whitei* are in excess of what is needed for cruising, sprinting or accelerating. The head is flattened and had the form of a bottom dwelling animal. The body tapers towards the posterior end, but the anal and second dorsal fins are close to the caudal fin.

(b) The scale pattern was explored by Pridmore and Barwick (1993), and we do not wish to alter their conclusions. On the flanks of the animal each scale was overlapped by six other cranial scales, and overlaps six more caudal scales. This would have restricted the lateral movement of the body. More caudally each scale 'appears to overlap only three scales, and to be overlapped by three others'. In other words the caudal region would have been less restricted.

(c) The centra as described above are amphicoelicous throughout almost the whole body length. The edges of the centra show evidence of strong intervertebral soft tissues which would have controlled the stiffness of the body.

(d) The presence of neural arches which are attached to two centra would also have contributed to this stiffness. The edges of the centra are more or less in close contact (see Figure 12), though in life they would have been more separated. This suggests a restriction on the amount of lateral and vertical movement.

(e) The nature of the ribs supports the interpretation that the anterior part of the body was relatively inflexible. The ribs were large, closely spaced, postero-ventro-laterally directed, heavily ossified, and with their faces closely spaced. Markings on the rib surfaces indicate that they were well bound into the myosepta, and the presence of nodes along their distal and ventral edges suggests that longitudinal muscles were firmly attached. The orientation of the ribs shows that contraction of these muscles would not have caused much flexure of the body.

(f) The supraneurals and distal supraneurals are of value in determining mode of movement. On the anterior three segments the distal supraneurals are flat, and the crests of the distal supraneurals have ridges for the attachment of muscles. No doubt these distal supraneurals were situated close to the surface of the fish, and they lay in the myoseptum. Although they are prominent features, specimen AMF 72402 shows that the surface was only gently raised above the posterior surface of the head. The muscles attached to the distal supraneurals must
have been attached to the connective tissue beneath the scale pockets or to the myotomes surrounding the supraneural arches. These would make the first few elements very stable as was suggested above by the structure of the centra. This stability is not matched by any other dipnoan, and the only sarcopterygian (Hitchcock, 1995) with large supraneurals is *Eusthenopteron*, which differs in many details. Their function in *G. whitei* has to be interpreted from first principles. Their stability would provide strength at the back of the head for the thrust generated posteriorly by the movement of the posterior fins, and this allowed the head to stir up the bottom sediment.

(g) The neurals and supraneurals extend for some distance along the body, and these would have been in a position to resist torsion when the animal moved.

Flexibility of the body was limited; the greatest flexibility was at the posterior, where the scales were thinner and the body narrower.

From their investigation of the postcraniar material available to them, Pridmore and Barwick (1993) suggested that sub-carangiform or carangiform swimming was the norm for *Griphognathus*. With this view we are in agreement for the reasons given above. Other workers have analysed the movement of the Devonian lungfishes (Belles-Isles, 1992), and have concentrated on the position of the fins. In our view fin position is only one of the features, and it must be considered in the light of the other characters listed above. Taking all this into account, we now consider the medial fin structure.

Role of the Medial Fins in Propulsion

The caudal fin is long, and it was slightly upswept. The centra are well developed for a considerable distance back into the caudal region, and the haemal arches are well ossified. The caudal radials are long, well ossified and extend well into the lepidotrichs. The proximal lepidotrichs are thick, and some are ovate in section indicating a strong imbricate array. ANU 49285 shows that the proximal lepidotrichs become rapidly shorter dorsally, and the scales continue along the part of the caudal fin preserved. There is no evidence of scales preserved over the ventral proximal lepidotrichs, but the presence of large scales anterior to the lepidotrichs suggests that they were present. The capacity to move the fins increased towards the distal region of the fin. In comparison with *Dipterus*, this species has an elongate mobile part of the caudal fin.

The articulatory termini of the most anterior haemal arches where the caudal radials were attached, are markedly concave laterally, indicating the presence of a large mobile attachment to the radials, and considerable lateral movement of the radials. The attachment surface of the radials is swollen, and the surface is surrounded by a thickening. This pattern also indicates a strong junction with the haemal arches. More posteriorly, the ends of the haemal arches are flattened and join with the flattened ends of the radials. This design supports the argument that the tail was strong, that movement of the ventral part of the fin took place by lateral movement at the haemal junction, but slighter movement took place more dorsally. Strength was added to the movement by the elongate radials which extended so far into the long proximal lepidotrichs, and strong muscles which leave grooves on both the haemal arches and the radials. Movement of the caudal region must have been interrelated with the action of the distal lepidotrichs.

We have been unsuccessful in finding other sarcopterygians with which to make comparisons of the anal fin. Coelacanths, as represented by *Latimeria*, have a support system which has almost no features in common with *Griphognathus*, and its axis has a single row of ossifications arranged in a unique way. *Eusthenopteron* has some features in common with three radials, but it has only a small main support, only one set of radials and short proximal lepidotrichs. It was a pointed fin situated well in front of the caudal arch.

Judging from the shape of the haemal arches which are bent back at a low angle to the axial column in this region, the anal fin in *Griphognathus* lay close up under the body. The fin supports are variable in shape and number, sometimes having only one unit and more commonly two. The attachment edge of the main support is dorsoventrally bifacial, with the lower face being set approximately normal to the upper. Obviously this allowed the support to move dorsoventrally with respect to the animal body. To activate this system, muscles must have run from the support unit to the haemal arches. Such muscle scars are present on the anterior part of the main support. Scars are also present running posteriorly to the surfaces where the radials were attached. These must have been powerful muscles judging from the deep grooves they leave in the surface of the support unit. This dorsoventral movement raises an interesting point, because the articulation gives no indication that the lateral movement of the supports was part of the design. This is understandable because the main fin support is large and lies between five pairs of myotomes which must have provided lateral restraint. In addition, the radials are heavily ossified, each joined by a flat surface to the main support along a staggered line of junction which did not provide a unified hinge for movement, and joined to the main support by strong muscles which ran along their lengths. The proximal radials were quadrate in cross section, and
had a strong face-to-face junction with similarly shaped ends on the main support, indicating a minimum amount of movement along this junction. These are followed distally by a line of distal radials with quadrate cross sections, and with strong face-to-face junction with the proximal radials. These distal radials extended from 1.0 to 1.5 cm into the proximal lepidotrichs, which are thick structures and are closely bound together. All this means that most of the anal fin was a relatively rigid structure, and the main movement of the fin was caused by movement of the distal lepidotrichs, of which we have little evidence. Such a view is supported by the presence of a flattened surface at the posterodorsal end of the main support, and the presence of lateral expansions on these flanges being for the attachment of ligaments. These would have been attached to the myotomes, and would have stabilised the ventral end of the main support.

What would be the function of such a large anal fin? Firstly, since it had some dorsoventral movement, and when it was ventrally directed it would lift the caudal region, an important point for a bottom dwelling animal. This point is supported by the shape of the head. Secondly it would have acted with the caudal fin to produce a lepidotrichial sweep also causing the tail to rise and forcing down the head, but we have no indication of the presence of distal lepidotrichs in our specimens. If they were present they could also have acted with those of the second dorsal fin conceivably to provide some ballistic propulsion, but this is a suggestion which awaits the discovery of the distal lepidotrichs. Consequently we see the anal fin as providing little in the way of propulsive force for forward movement, but providing an uplift for the posterior of the animal and providing propulsion to push the head downwards during feeding from the sediment.

The second dorsal fin is another complex structure, as it is in most Devonian dipnoans. It has a main and several ancillary support units, the main one being several times as large as the others. The attachment surface of the main support unit is laterally bifacial, with its two facets so arranged that lateral movement was possible with respect to the neural arches to which it was attached. The auxiliary supports, the ventral edges of which have no signs of attachment to the underlying neural arches, and hence they were able to move laterally independently of the main support. This is supported by the fact that they all fit together along closely placed margins, and they must have been able to move one against the other. The whole support structure of the fin is massive, and its proximal part must have been largely enclosed within myotomes. Distally it carries eight to nine proximal radials, and these are followed by a set of distal radials. The support units have elongate ridges and grooves which continue onto the radials, indicating that the muscles joining them were strong. Each distal radial has up to ten lepidotrichs attached to it.

The attachment of the proximal radials to the support structures does not form a straight line, but consists of a series of offsets, the more ventral ones being more posteriorly placed. Hence it does not make a linear hinge, and the radials may have been able to move independently of one another.

A most interesting point is the small anterodorsal scar on the main support which has a small lateral process on each side. Note that this is placed at the anterior end of the support rather than at the posterior as in the anal support, and that it is much smaller. Assuming that small connections with the myotomes were attached to these points, these would not have had a stabilising effect on the support, but would have given the structure an axis along with the main support, around which lateral movement would have taken place.

The first dorsal fin is poorly understood. The attachment scar is bifacial dorsoventrally, again indicating dorsal and ventral movement rather than lateral. Assuming that we have interpreted the fragments we have correctly, this fin would have had short lepidotrichs and presumably they would have an undulatory movement. They would have been so small that they would not have been able to propel the animal, and presumably they would have been to provide stability, a feature mentioned by Alexander (1970).

Summary of Locomotion

We conclude that the body shape does not indicate fast movement, but that it had the capacity to lift the tail and push the head down into the substrate. The strength of the caudal region shows that it acted as a gross propellant by movement of the whole region in an undulose fashion. The caudal fin would have been oar-like with the junction between the haemal arches and the radials flexible, proximal lepidotrichs embedded in robust scales, and the distal fins being small with respect to the whole animal.

This would be supported by the anal fin which was rather a rigid structure and with a capacity to sit ventrally on the substrate. Its long lepidotrichs indicate that movement would have been possible mainly through the distal lepidotrichs, and their position close up under the caudal fin, shows that it would act with the caudal fin to lift the tail. The posterior position of the second dorsal fin, its position close to the body of the fish, and the number of secondary support structures, indicates that it would have acted to propel the fish forwards if fully active and would have counterbalanced the strong action of the caudal and anal fins where necessary.
COMPARISON WITH OTHER DEVONIAN DIPNOANS

Centra

The specimens of Jarvikia and Soederberghia worked on by Schultz (1970), are not complete, and we have not been able to make useful comparisons with them. The structure of the centra in G. sculpta and G. minutidens provide the only information against which the centra of G. whitei can be directly compared. These also have been described by Schultz (1970). The specimens he described and figured on Pls 39 and 40, have centra about 5 mm and 7 mm across, and in our terms it is about the same size as our smaller individuals. Our comparative comments have to be restricted to these juvenile stages of growth.

The central core around the notochordal canal is made of the same material in the two species, and the marginal tissue as shown in Schultz (pl. 39, fig. 1b) is also comparable. Comparisons with the lamellae are difficult to make, as we have not seen the Liesegang Rings in our species. The large open spaces in the lamellar region are also missing, and G. sculpta does not have long narrow pores in the lamellae.

One important point is that the centra and the ribs of Griphognathus whitei are strongly ossified, as also are the neural and haemal arches. Scamennacina and Fleurantia both have ossified neural and posterior haemal arches, but their centra are not ossified. In both these genera the ribs extend back to the anterior end of the second dorsal fins, but in Griphognathus there are at least 12 centra anterior to the second dorsal fin before the most posterior ribs appear.

Fin Structure

The postcranial skeleton of Dipterus valenciennesi from the Middle Devonian, and Rhinodipterus ulrichi, Scamennacina curta, and Fleurantia denticulata and Griphognathus sculpta and G. minutidens from the Late Devonian, have been described, and provide a good basis for an understanding of the Devonian postcranial skeletons. Of these, the material of Rhinodipterus ulrichi is the least organised and shows fewer elements of the skeleton than the others. In addition the genera Barwickia Long and Howidipterus Long from the Givetian of Victoria have given us more information on Late Devonian changes, but the detailed description is still in preparation. Data on these genera have been made available to us by Dr John Long of the Western Australian Museum.

First we make a comparison with G. sculpta which comes from the Frasnian at Bergish-Gladbach, Germany. The median and anal fins are known from distal skeletal units outside the scales, and so no comparison with the fin support structures can be made. The ossified centra are present in the posterior part of the skeleton, but they contain no ossified haemal or neural arches. The lepidotrichs are very similar to those on G. whitei.

G. whitei is closer to Dipterus in many respects than it is to any other Devonian dipnoan, especially in the supporting plates that underlie the first and second dorsal fins and the anal fin. Scamennacina and Fleurantia have a simple anal fin support. Fleurantia has a small support for the first dorsal fin, but this also is a simple structure different from that in G. whitei. Both these latter fish also have a second dorsal fin composed of numerous radials each given off from supraneural arches. These features are an advance on the more primitive Dipterus stage in which the second dorsal fin is short, and is not closely associated with the caudal fins, which is a feature of Carboniferous and later genera.

G. whitei has a main support plate and a variable number of smaller plates carrying proximal and distal radials. This does not mean that it is a morphological intermediate between the Dipterus level and the Fleurantia level for the following reasons.

It has been commonly accepted that the support structures for the median fins arose from the junction of a number of parallel radials (Jarvik 1980). Ahlberg and Trewin (1995: 171) comment that in the typical sarcopterygian "posterior dorsal or anal fins support, comprising a basal plate and a number of parallel radials, is derived from a row of independent radials without a basal plate". Comparatively they indicate that a row of independent radials "seems to be the primitive gnathostome condition", and that the basal plate was formed from "fused basal segments of originally separate radials". This statement which adheres to the view of metamerically sequential units each giving rise to the radials, does not take into consideration the possibility that at the origin of the sarcopterygians there may have been a sudden major change in the genetic control of fin supports. After all, we see no record of any forms earlier or later stratigraphically, which show evidence of grouping of radials to make larger fin supports. Miles (in Moy-Thomas and Miles 1971: 111) commented that "the first appearance of the crossopterygians in the Lower Devonian is in a disconcertingly fully developed condition, and in structure they are quite distinct from actinopterygians". In the thirty years since then we see no reason to change this statement, except that the sarcopterygian genus Psarolepis may have come from the Late Silurian.

In our view the fossil evidence supports the concept that the preserved sarcopterygian primitive condition consisted of a support unit, probably without secondary support structures. Even in genera with short second dorsal fins such as
Dipterus and G. whitei there is evidence that two or three distal fin radials may derive from a single proximal fin radial, and this phenomenon can be seen in the anal and the caudal fins of Chirodipterus as shown in our collections from Gogo. The fin structure of these forms indicates that the single fin support gives rise to multiple divisions to produce the complex structure of the fins.

As has been well known for many years (Dollo 1895, Westoll 1949) the shape of the medial anal and dorsal fins together with caudal fins, have produced a diphyceracal organisation (Long 1993, figure 7; Ahlberg and Trewin 1995, figure 11). It is difficult to produce this long series of forms from a primitive such as Dipterus, within which the fin radials were supported from a single support plate attached to a single neural arch. Most of this change took place in the Devonian, and the only evidence of change in the fin supports is towards the reduction of the main supports and the introduction of new ancillary supports. This is well illustrated by the genera Barwickia Long and Howidipterus Long, in which a main support lies at the anterior end of the second dorsal fin, and an extended posterior part of the fin made up of several radials each attached to a single neural arch.

In G. whitei up to five secondary supports are found behind the main fin support in the second dorsal fin, the number varying from individual to individual. The ventral edge of these secondary supports is a sharp-edged linear strip without any signs of an attachment edge. These supports are totally confined to the fin, and they lie at an angle to the neural arches beneath them. In other words they have an entirely different origin from the radials found in the graded sequence of genera such as Scamennacia and Fleuranitia. In G. whitei the second dorsal fin does not approach the caudal region to make contact with an epichordal lobe. It seems most likely that both second dorsal and anal fins in G. whitei were developed to produce structures permitting head down feeding, whereas the development of the elongate fins which join with the epichordal fin were used for free swimming.

Neural Arches and Dorsal Elements

Few Devonian dipnoans preserve skeletons of the neural regions. A summary of the data was given by Schultze (1975), and some specimens were figured by Lehman (1959). More recently described species (Long, in prep) in which the axial region is preserved, do not show any unusual features. Once again, the best comparison is with D. valenciennesi. Ahlberg and Trewin (1995, figure 9b) published a reconstruction from a badly dismembered specimen, but the supraneurals are long and thin and highly inclined. They have no similarity to those of G. whitei. As we have indicated in the section on function, the peculiar arrangement in G. whitei is a specialisation related to its mode of feeding.

Cranial Ribs

Cranial ribs occur in living lungfishes where they are associated with air breathing. They are attached to the back of the cranium rather than to the vertebral column, they are wide paddle-shaped structures, and they hang down posterior to the cranium. The presence of cranial ribs does not prove the presence of air breathing, because so many other factors are involved in producing the passage of air. Long (1993) discovered the presence of these ribs in two genera from the fresh water beds in the Givetian at Mt Howitt, in Victoria, and they are associated with other features of air breathing animals. We have attempted to find such structures in G. whitei, though air breathing would not be expected in a bottom dwelling marine animal of this kind. To date we can find no evidence of where they would have attached to the cranium, and though we have ribs attached to the first few vertebrae, we can find no evidence of cranial ribs in our etches and this correlates with the inflexibility of the neck which was described above.

ACKNOWLEDGEMENTS

Thin sections have been prepared by John Vickers of the Geology Department, A.N.U. Specimens of Griphogathus were collected on two trips by us to the Gogo locality, by Gavin Young of the Australian Geological Survey Organisation (now of the Geology Department, A.N.U.), and by John Long of the Western Australian Museum. John Long also provided us with a preprint of his paper on Barwickia and Howidipterus. Our field work and laboratory work was done with the assistance of an A.R.C. grant. Work in the A.N.U. was done with the permission and support of the Head of the Geology Department.

REFERENCES


Postcranial structure of Griphognathus whitei


*Manuscript received 28 May 2001; accepted 22 November 2001.*
Bees of the *Euhesma crabronica* species-group
(Hymenoptera: Colletidae: Euryglossinae)

Elizabeth M. Exley
Department of Zoology & Entomology, The University of Queensland, St. Lucia, Queensland 4072, Australia

Abstract – Seven endemic Australian species of *Euhesma* bees are described as new: *E. evansi*, *E. lucida*, *E. sulcata*, *E. thala*, *E. undeneya*, *E. wouine* and *E. yeatesi*. Line drawings and a key to females enable separation of species. Known distributions are mapped.

INTRODUCTION

The primitive bee family Colletidae is better represented in Australia than in any other continent. Of its three subfamilies, the Euryglossinae is entirely endemic with large numbers of species still being discovered and described. Recent collections from Western Australia contain many new species particularly in the genus *Euhesma* Michener. This taxon was proposed by Michener in 1965 as a subgenus of *Euryglossa* Smith for all the species that did not fit easily elsewhere. It was subsequently (Michener, 2000) raised to genus level and remains so numerous and varied its study is being tackled in manageably sized natural species-groups.

*Euhesma crabronica* (Cockerell) was described from Brisbane in 1914. It is now clear at least one other species in Queensland and several in Western Australia share characteristics. A “like-species” group based on morphology is considered here as the *Euhesma crabronica* species-group.

Those associations recorded show females on flowers of the plant family Myrtaceae which remains typical for Euryglossinae although recent collections from other plant families, particularly in Western Australia, are revealing many new species. One natural grouping of species based on association with *Eremophila* flowers was recently published (Exley, 1998).

Among the many populations of previously unknown species of euryglossines are large (>6 mm) robust bees in which the head and mesosoma are coarsely and strongly punctate, the propodeum in profile is almost completely vertical, the inner hind tibial spur is pectinate and the wing venation is striking with the anterior side of the second submarginal cell of the forewing much shorter than the posterior side, and the second transverse cubital vein strongly curved or sinuate.

Three species with these characters were described in three genera: *Euryglossa crabronica* Cockerell 1914, *Euryglossinmorpha abnormis* Rayment 1935 and *Dasyhesma robusta* Michener 1965. Michener (1965) placed the first two in separate subgenera of *Euryglossa*: *E. (Euhesma) crabronica* and *E. (Dermatothesma) abnormis*. Subsequently, Michener (2000) considered *abnormis* and *robusta* to be species in one genus *Dasyhesma* Michener, 1965.

At least 32 new species share the characteristics given above. The females of seven of them are striking, black bees about 10 mm long with yellow markings laterally on the metasomal terga. They are similar to *E. crabronica* and with it are considered here a species-group of *Euhesma*. This generic placement may change when more groups in *Euhesma* are revealed and better understood.

Bees of the other new species that show the characters above are smaller and differently coloured and many are currently considered *Dasyhesma* spp.

METHODS

In descriptions of species, “relative head measurements” express concisely the size relation between measurements on one head. As most specimens are females, the key presented is for females.

New species names except *evansi* and *yeatesi* are to be treated as nouns in apposition to *Euhesma*.

Abbreviations used are: ANIC, Australian National Insect Collection, Canberra; BMNH, The Natural History Museum, London; KU, Snow Entomological Collection, University of Kansas, Lawrence; LACM, Los Angeles County Museum of Natural History, Los Angeles; MCZ, Museum of Comparative Zoology, Harvard; MV, Museum of Victoria, Melbourne; QM, Queensland Museum, Brisbane; UQIC, University of Queensland Insect Collection, Brisbane; WAM, Western Australian Museum, Perth.
Euhesma crabronica species-group

Description
Length of female about 10 mm, head wider than long with antennae at about middle of face; head and mesosoma coarsely and strongly punctate; propodeum in profile almost completely vertical; forewing (Figure 1) with macrotrichia plentiful, pterostigma much shorter than costal margin of marginal cell, prestigma nearly as long as pterostigma from its base to base of Rs, second submarginal cell with anterior side much shorter than posterior side, junction of posterior side with second recurrent vein about two-thirds along its length base to apex, second transverse cubital vein curved or sinuate; dorsal surface of fore basitarsus of females flat, shining, almost hairless, with outer lateral margin with a row of forwardly bent setae (Figure 2); inner hind tibial spur pectinate, basitibial plate of females completely bounded by carinae. In those males seen, length is about 7 mm, there are long hairs on the volsellae of the genitalia (Figure 8), the seventh gastric sternum has four somewhat odd lobes (Figures 5, 9) and the eighth gastric sternum has a distinctively expanded head on a narrow shaft and a strong keel forward from the spiculum (Figures 6, 10).

Despite intraspecific variability in colour markings, the use of colour characters in the key is justified. As now understood, the crabronica species-group contains at least eight species.

Key to females of the Euhesma crabronica species-group
1. Head wholly black ........................................ E. yeatesi sp. nov.
   Head black with yellow markings ..................... 2
2(1). Mesoscutellum yellow ................................ E. thala sp. nov.
   Mesoscutellum black .................................... 3
3(2). Clypeus yellow and black with yellow marking somewhat anchor-shaped as in Figure 3 ........................................ E. ewansi sp. nov.
   Clypeus almost entirely yellow .......................... 4
4(3). Distal two-thirds of forewing infuscate; metasomal terga polished between large obvious punctures ........................................ E. lucida sp. nov.
   Distal two-thirds of forewing not infuscate; metasomal terga minutely roughened, dull, punctures not obvious ..................... 5
5(4). Metasomal foveae linear, furrowed, 9 or 10 times as long as wide .......... E. sulcata sp. nov.
   Metasomal foveae flat, curved, 2-5 times as long as wide ........................................ 6
6(5). Mandibles black; forewing with anterior half of marginal cell and wing beyond lightly infuscate ..................... E. undeneya sp. nov.

Mandibles yellow on at least outer surface; no infuscation on forewing .................................... 7
7(6). Supraclypeal area yellow on lower half; Western Australia .......... E. wowine sp. nov.
   Supraclypeal area black; eastern Australia ......... ........................................ E. crabronica

Euhesma crabronica (Cockerell)
Figures 4, 5, 6
Euryglossa crabronica Cockerell, 1914, pp. 142, 143.
Euryglossa (Euhesma) crabronica Cockerell: Michener, 1965, p. 91.

Material Examined
Holotype
Australia: Queensland: 2, Brisbane, 17 October 1913, H. Hacker (QM).

Other Material Examined
Australia: Queensland: 19, same data as holotype; others taken in Brisbane by Hacker on the following dates: 19, 3 October 1912; 19, 7 October 1913; 19, 13 October 1914; 19, 6°, 10 October 1916; 19, 24 October 1916; 19, 15 October 1917; 19, 22 October 1917; 29, 7 November 1917; 29, 8 October 1918 (all in QM); 19, Brisbane, October 1923, G.E. Hardy; 19, Brisbane, 20 September 1941, I. Common; 19, Caloundra, Deane (UQIC); 19, Beerwah, 26 October 1958, C.D. Michener (KU); 19, Beerwah, 28 October 1965, J.C. Cardale, on Tribania (UQIC); 29, Mt Emlyn, 20 October 1949, J.McQ (MV); 11°, 29, 6 km N Leyburn, 27°58'S 15°38'E, 28 October 1985, G. Daniels; 19; 19, Burrem Heads, 25°11'S 152°36'E, 6 September 1987, G. and A. Daniels; 19, Isis district nr. Childers, September 1973, H. Frauca (all in UQIC). New South Wales: 29, 79, Pilliga Scrub, 9 km N Coonabarabran, 5 December 1976, E.M. Exley and T. Low, on Leptospermum flavescens (UQIC).

Description
Female
Length about 10.0 mm; wing length about 6.5 mm. Relative head measurements: width 3.4; length 2.9; lower interocular distance 2.0; upper interocular distance 2.0; interantennal distance 0.5; antennal distance 0.5; interocular distance 0.5; ocellocular distance 0.4. Anterior margin of clypeus broadly truncate, upper margin of clypeus concave; facial foveae curved towards lateral ocelli, less than 1/2 length of eye; genal area narrower than eye seen from side; antennae short, above middle of
Bees of the *Euhesma* crabronica species-group

face; all flagellar segments except last about as wide as long; basitibial plate about 1/3 length of hind tibia; tarsal claws with large sub-median tooth, dorsum of head and thorax with strong punctures, interspaces shining; foveae of second tergum of metasoma about 4 times as long as wide.

Head black with clypeus and mandibles yellow; mesosoma black with pronotal tubercles yellow; legs black with fore tibiae anteriorly and base of mid tibiae yellow; dorsal surface of metasoma black with antero-lateral corners of segments 2–5 yellow; venter black.

Forewing with veins and pterostigma black, membrane slightly dusky; macrotrichia strong and plentiful over whole wing; second recurrent vein joining second submarginal cell as in Figure 1. Second submarginal cell considerably narrowed towards costa; second transverse cubital vein gently curved.

Pubescence: Sparse, long white hairs on frons, vertex, genae, mesosoma, legs, metasomal sterna, long brown hairs on metasomal tergum 5.

**Male**

Length about 7.5 mm; wing length about 4.5 mm. Relative head measurements: width 2.8; length 2.3; lower interocellar distance 1.5; upper interocellar distance 1.7; interantennal distance 0.5; antennocular distance 0.3; interocellar distance 0.6; ocellocular distance 0.3. Anterior margin of clypeus broadly truncate; upper margin of clypeus concave; facial foveae about 1/3 length of eye; genal area narrower than eye seen from the side; antennae long, slightly above middle of face, pedicel longer than first flagellar segment, all flagellar segments except first two longer than wide; basitibial plate with carinae and terminal tubercle, about 1/3 length of hind tibia; tarsal claws bifid; frons above antennae with close punctures, dorsum of mesoscutum with close punctures, interspaces shining; foveae of second tergum of gaster about 4 times as long as wide.

Head black with clypeus, paraocular areas to level of antennal sclerites, mandibles (except tip which is red), pale yellow; antennal scape ventrally pale yellow; mesosoma black with pronotal tubercles with yellow spot; legs yellow with all coxae and mid and hind tibiae dorsally, dark brown; dorsal surface of metasoma black with antero-lateral corners of segments 2–6 yellow; venter yellow.

Forewing: As in female.

Pubescence: Long white hairs on clypeus, scapes, frons between antennae, genae, mesosoma and bases of legs; sparse on metasoma.

Terminalia: Figures 5, 6.

*Euhesma evansi* sp. nov.

Figures 3, 4

**Material Examined**

**Holotype**

Australia: Western Australia: ♂, Nilemah Sta, 50 mi S Denham, 8–9 October 1969, H. Evans, R.W. Matthews (MCZ).

**Paratypes**

Australia: Western Australia: 6♀, 1♂, same data as holotype (MCZ, LACM, UQIC).

**Other Material Examined**

Australia: Western Australia: 5♀, 9 km NNE of

---

**Figures 1–3** 1, Portion of forewing of *Euhesma evansi*; 2, Basitarsus of foreleg of *Euhesma wuciae*, female, distal end at left. Scale line = 1 mm; 3, Yellow and black “anchor” pattern on clypeus of *Euhesma evansi* female. Yellow of “handle” continues to supraclypeal area in most specimens. Scale line = 0.5 mm.
Eurardy HS on NW Coastal Highway 27.30S 114.43E, 25–28 October 1996, T.F. Houston on flowers of *Calytrix formosa* (Myrtaceae); 4♀, some data on flowers of *Baeckea* sp., 1♀, 15.5 km N of Eurardy HS on NW Coastal Highway, 27.26S 114.40E, 25 October 1996, T.F. Houston, on flowers of *Calytrix formosa*; 2♀, 54 km 27°E of N from Kalbarri on VP Fence, 27°16′02″S 114°25′15″E, 19 November 1998, T.F. Houston on flowers of *Baeckea affin pentagonantha*; 3♀, 54 km, 27°E of N from Kalbarri on VP Fence, 27°16′02″S 14°25′15″E, 24 November 1998 on flowers of *Melaleuca*; 1♀, same data on 19 November on *Baeckea blackallii*; 1♀, 10 km WNW of Eurardy HS 27°32′18″S 114°34′54″E, 21–24 October 1998, T.F. Houston and O. Mueller, on *Baeckea blackallii*; 2♀, same data on *Phymatocarpus porphyrocephalus*; 5♀, Pinjarrega Lake Nature Res. 23 km SW Coorow, 30°01′40″S 115°49′25″E, 17 November 1997, T.F. Houston, on flowers of *Leptospermum*; 1♀, same data except on flowers of *Pileanthus peduncularis peduncularis*; 1♀, same data except on mauve flowers of *Melaleuca*; 2♀, Watheroo National Park (NW corner), 30°11S, 115°44E, 15–16 November 1997, T.F. Houston, on flowers of *Eremaea violacea* (all in WAM).

**Description**

Similar to *E. crabronica* with the following differences:

**Female**

Length 10–11 mm; wing length about 7.0 mm. Relative head measurements: width 3.5; length 2.8; lower interocular distance 1.7; upper interocular distance 2.1; interantennal distance 0.4; antennocular distance 0.5; interocellar distance 0.6; ocellocular distance 0.5; foveae of second metasomal tergum about 3 times as long as wide.
Bees of the Euhesma crabronica species-group

Head and mesosoma with large punctures separated by shining surface; area between punctures greatest on mid scutum, almost no space between punctures on metanotum; anterior metasomal terga dull, minutely roughened with most punctures laterally, sterna with distinct punctures separated by shining surface; propodeal triangle minutely roughened, shining.

Head dark brown/black with the following pale yellow: labrum, mandibles, clypeus anteriorly and posteriorly medianly (Figure 3), anterior corners of paraocular areas, patch on supraclipeal area; thorax and propodeum dark brown; legs dark brown with fore tibiae anteriorly and base of mid tibiae yellow; dorsal surface of metasoma dark brown/black with antero-lateral corners of segments 2–5 yellow; venter dark brown.

Forewing: Prestigma almost as long as distance from base of pterostigma to vein r.

Body covered with long white hair with long dark hair on metasomal terga 5 and 6.

Male

Length about 7.0 mm; wing length about 4.0 mm. Relative head measurements: width 2.6; length 2.0; lower interocular distance 1.1; upper interocular distance 1.5; interantennal distance 0.9; antennocular distance 0.3, interocellar distance 1.0; ocellocular distance 0.4.

Head black with the following pale yellow; clypeus, supraclipeal area, paraocular areas below level of antennae, labrum, mandibles, antennal scapes ventrally, pedicels, small patch on genae behind mandibles; thorax black with pronotal tubercles and tegulae yellow; legs predominantly clear yellow; dorsal surface of gaster black with antero-lateral corners of segments 2–6 yellow; venter yellow.

Long white hair on head, thorax and trochanters and femora of forelegs.

Remarks

Specimens included in this species vary (size, colour markings, integument details) and initially were separated into three species corresponding to the three areas marked on the map (Figure 4). The type specimens are from the northern-most population and include the only male recognised. The females are brown rather than black no doubt related to their age. The middle populations are most variable – the diagnostic colouring of the clypeus is not always so distinctly marked, the basal half of T1 is amber in most and the normally black areas of the metasoma are orange-red in some. [See also E. sulcata].

Etymology

The specific name, a noun in the genitive case, honours my friend Howard E. Evans whom I first met on his field trip to Australia in 1969–70 when he collected this species.

Euhesma lucida sp. nov.

Material Examined

Holotype

Australia: Western Australia: ♂, 15.5 km N of Eurardy HS on NW Coastal Highway, 27.26S 114.40E, 25 October 1996, T.F. Houston, on flowers of Calytrix formosa (WAM).

Paratypes

Australia: Western Australia: ♂, same data as holotype (WAM); ♂, 9 km NNE of Eurardy HS, 27.30S, 114.43E, 25–28 October 1996, T.F. Houston, on flowers of Calytrix nigrastrigosa (WAM).

Other Material Examined


Description

Female

Length about 11.0 mm; wing length about 7.0 mm. Relative head measurements: width 3.8; length 3.3 clypeal length 1.2; lower interocular distance 2.1; upper interocular distance 2.1; clypeo-antennal distance 0.4; interantennal distance 0.4; antennocular distance 0.7; interocellar distance 0.5; ocellocular distance 0.5; metasomal foveae shallow, about 4 times as long as greatest width.

Head, mesosoma and metasoma with large punctures separated by shining surface, punctures closer together on scutum, scutellum and metanotum so that surface appears less shining; labrum and propodeal triangle very minutely roughened, almost glabrous.

Head black, with clypeus, basal half of supraclipeal area, small patch on paraocular areas pale yellow; labrum black; mesosoma black with pronotal lobes and patch anteriorly on tubercles yellow. Wings with basal 1/3 clear, distal 2/3 dark brown.

Remarks

The females from Dragon Rocks Nature Res. and
10 km WNW of Eurardy HS do not have a yellow patch on the tegulae.

This species is immediately recognised by the wing colour and the polished metasoma.

Etymology

The specific name is from the Latin and refers to the polished nature of the metasoma between the very numerous punctures.

*Eu hesma sulcata* sp. nov.

**Figure 4**

**Material Examined**

**Holotype**

Australia: Western Australia: 9°, 9 km NNE of Eurardy HS on NW Coastal Highway, 27.30S 114.43E, 25–28 October 1996, T.F. Houston, on flowers of *Calytrix strigosa* (WAM).

**Paratypes**

Australia: Western Australia: 5♀, same data as holotype (WAM); 1♀, same data as holotype on *Calytrix formosa* (WAM).

**Other Material Examined**

Australia: Western Australia: 1♀, Pinjarrega Lake Nature Res, 23 km SW Coorow, 30°01'40"S, 115°49'25"E, 17 November 1997, T.F. Houston, on yellow flowers of *Calytrix* (WAM).

**Description**

**Female**

Length about 10.0 mm; wing length about 6.0 mm. Relative head measurements: width 3.5; length 3.3; clypeal length 1.0; lower interocular distance 1.8; upper interocular distance 1.9; clypeo-antennal distance 0.4; interantennal distance 0.3; antennocular distance 0.5; interocellar distance 0.5; ocellocular distance 0.4; metasomal foveae clearly grooved, 9 or 10 times as long as wide. Head and mesosoma with large punctures separated by shining surface, metasomal terga minutely roughened, dull.

Head black with clypeus, basal half of supracycpeal area, patch on paracocular areas and mandibles yellow; labrum black; mesosoma black with pronotal lobes partly yellow; metasoma orange-red.

**Remarks**

In some, the typical yellow maculations are only partially visible laterally and in all but two specimens some part of the metasomal terga is black. The specimen from Pinjarrega Lake Nature Res. has the typical metasoma of this species-group (black marked with yellow).

The specimens available to me raise the question—Do these bees alter colour with age? I have seen the chrysolomid beetle *Aesternia australica* Baly completely red orange on emergence and 24 hours later with beautiful blue-green elytra. I suspect these bees might emerge with metasoma red-orange that gradually changes to black.

**Etymology**

The specific name is from the Latin and refers to the groove-like metasomal foveae.

*Eu hesma thala* sp. nov.

**Figure 4**

**Material Examined**

**Holotype**

Australia: Western Australia: 9°, 16 km WSW Yannarrie River Xing NW Coastal Hwy, 22°53'53"S 114°47'50"E, 30 September 1997, T.F. Houston and P. Mathiasen, on flowers of *Pileanthus limacis* (WAM).

**Paratype**

Australia: Western Australia: 1♀, same data as holotype (WAM).

**Description**

**Female**

Length about 10.0 mm; wing length about 6.0 mm. Relative head measurements: width 3.4; length 2.8; clypeal length 1.0; lower interocular distance 2.0; upper interocular distance 2.0; clypeal-antennal distance 0.3; interantennal distance 0.5; antennocular distance 0.6; interocellar distance 0.6; ocellocular distance 0.4. Foveae on 2nd segment of metasoma about as wide as scape, 5 times as long as wide.

Head and mesosoma with shining surface separating large punctures; metanotum most closely punctate; metasoma with anterior terga dull, minutely roughened, punctures laterally; sterna with large punctures on shining surface; propodeal triangle minutely roughened, shining.

Head black with face below level of antennae (except labrum), basal half of mandibles and antennal scapes ventrally, yellow; mesosoma black with the following yellow: pronotal lobes, patch on pronotum, patch on tegulae, scutellum, patch on metanotum. Metasoma black with basal half of $T_2$–$T_3$ yellow and small patch of yellow on each side of $T_1$.

**Remarks**

This species has more yellow colour (scutellum and basal half of metasomal terga) than any other.
Bees of the *Euhesma crabronica* species-group

**Etymology**

The name "thala" is a Western Australian aboriginal word for bee.

*Euhesma undeneya* sp. nov.

Figure 4

**Material Examined**

**Holotype**

Australia: Western Australia: ♀, Eneabba, 15 October 1985, R.F. McMillan on *Verticordia* (WAM)

**Paratypes**

Australia: Western Australia: ♀, same data (WAM, UQIC).

**Other Material Examined**

Australia: Western Australia: ♀, Mingenew, 15–22 October 1915, R.E. Turner (BMNH).

**Description**

Similar to *E. crabronica* with the following differences:

**Female**

Length about 10.0 mm; wing length about 6.0 mm. Relative head measurements: width 3.5; length 2.8; clypeal length 1.1; lower interocular distance 1.9; upper interocular distance 2.2; clypeo-antennal distance 0.3; interantennal distance 0.5; antennocular distance 0.6; interocellar distance 0.5; ocellocular distance 0.5.

Figures 5–10  Male terminalia: 5, 6, seventh and eighth gastral sterna of *E. crabronica*; 7–10, *E. wowine*: 7, 8, genitalia (dorsal 7, ventral 8); 9, 10, seventh and eighth gastral sterna. Scale line = 0.5 mm.
Metasomal foveae about three times as long as wide; anterior surface of T, polished, few hairs; metasomal terga lightly punctured, dull; sterna with distinct punctures separated by shining surface; propodeal triangle minutely roughened, shining.

Head black with clypeus and small spot on supraclypeal area yellow; mandibles predominantly black with tips red; mesosoma black; legs black with fore tibiae anteriorly and basal spot on mid tibiae yellow; dorsal surface of metasoma black with yellow maculations on gastral terga 2–5; venter black.

Forewing with anterior half of marginal cell lightly infuscate.

Etymology

In his description of E. crabronica, the only member of this group previously known, Cockerell referred to its likeness at first sight to a wasp. The name "undeneya" is an aboriginal word for wasp.

Euhesma wowine sp. nov.

Figures 2, 4, 7–19

Material Examined

Holotype

Australia: Western Australia: ♀, 3.5–5.5 km S of Yellowdine (31°18’S 119°39’E), 27 October 1978, T.F Houston, on flowers of Melaleuca scabra (WAM)

Paratypes

Australia: Western Australia: ♀, same data as holotype (ANIC, QM, UQIC); ♂, same data on flowers of Baeckea ? leptospermoides (WAM); ♂, same data except flying around Acacia foliage (WAM).

Other Material Examined


Description

Similar to E. crabronica with the following differences.

Female

Length about 10.0 mm; wing length about 7.0 mm. Relative head measurements: width 3.8; length 3.0; clypeal length 1.1; lower interocular distance 2.2; upper interocular distance 2.3; clypeo-antennal distance 0.3; interantennal distance 0.5; antennocular distance 0.6; interocellar distance 0.7; ocellocular distance 0.5.

Head and mesosoma with large punctures separated by shining surface, no large interspace area on mid scutum, anterior metasomal terga dull, minutely roughened, sterna with distinct punctures separated by shining surface; propodeal triangle minutely roughened, dullish.

Head black, with clypeus, basal half of supraclypeal area, small patch of paraclypeal area anteriorly in some, outer surface of mandibles yellow; mesosoma black with pronotal tubercle partially yellow in some; legs dark brown with fore tibiae anteriorly, apices of middle femora and bases of middle tibiae, yellow; dorsal surface of metasoma black with antero-lateral corners of segments 2–5 yellow; venter dark brown with margins of segments yellowish (entirely yellow in specimens from Weowanie Rock and Bodallin).

Male

Length about 6.0 mm; wing length about 4.5 mm. Relative head measurements: width 2.8; length 2.1; lower interocular distance 1.5; upper interocular distance 1.7; interantennal distance 0.5; antennocular distance 0.4; interocellar distance 0.6; ocellocular distance 0.4.

Head black with everything below antennae pale yellow; patch on genae behind mandibles pale yellow; antennal scapes and pedicels pale yellow ventrally; mesosoma black with pronotal tubercles, tegulae and ventral surface between legs I and II, yellow; legs yellow; dorsal surface of metasoma black with yellow markings laterally on segments 2–6; venter yellow.

Long white hair on head, thorax and trochanters and femora of forelegs.

Terminalia. Figures 7–10

Remarks

The females of E. wowine and E. crabronica are very similar. The head is wider in E. wowine but this is not useful as a key character. The lower half of the supraclypeal area is consistently yellow in E. wowine, in some E. crabronica specimens a small splotch of yellow is present there. Males are distinct — the ventral thorax between coxae I and II is yellow in E. wowine, black in E. crabronica.

Etymology

The name "wowine" is a Western Australian aboriginal word meaning "similar" and refers to the similarity of the females of this species to E. crabronica.
Bees of the *Euhesma crabronica* species-group

*Euhesma yeatesi* sp. nov.

Figure 4

Material Examined

Holotype

Australia: Queensland: 9, Mt Moffatt National Park, the Chimneys, 14 December 1987, D.K. Yeates (QM).

Paratypes

Australia: Queensland: 2?, same data (UQIC); 3? Tantitha, Bundaberg, 18 October 1973, H. Frauca (ANIC).

Description

Similar to *E. crabronica* with the following differences:

Female

Length about 10.0 mm; wing length about 7.0 mm. Relative head measurements: width 3.4; length 2.9; lower interocular distance 2.0; upper interocular distance 2.0; interantennal distance 0.5; antennocular distance 0.5; interantennal distance 0.5; interocellar distance 0.6; ocellocular distance 0.5; dorsum of head with interspaces shining, much more strongly punctate than thorax where interspaces are minutely roughened and dullish. Head black, mandibles black with tips red; mesosoma black with pronotal tubercles yellow; legs black with fore tibiae anteriorly and fore tarsi yellowish; dorsal surface of metasoma black with antero-lateral corners of segments 2–5 yellow, posterior half of segment 5 wholly yellow; venter black.

Remarks

It is surprising to find a second species in relatively close proximity to *E. crabronica* in southern Queensland. Unfortunately only females are known. They differ from all others in the species-group in that the clypeus is black and the posterior half of metasomal tergum 5 is yellow.

Etymology

This specific name, a noun in the genitive case, honours David Yeates, a colleague of many years who collected the specimens that alerted me to the species.

REFERENCES


Manuscript received 11 April 2000; accepted 21 December 2001.
Description of a new genus and species of miniature monacanthid fish from the Seychelles and Marshall Islands

J. B. Hutchins
Department of Aquatic Zoology, Western Australian Museum,
Francis Street, Perth, Western Australia 6000, Australia

Abstract – A new genus and species of monacanthid fish, Enigmamacanthus filamentosus, is described from three specimens, one from the Seychelles in the Indian Ocean and two from the Marshall Islands in the Pacific. It is characterised by the structure and positioning of its epineural ribs (distal extremities branched or expanded, ribs commencing on the third abdominal vertebra). The new taxon has no apparent close relatives, but appears most similar to Paramonacanthus, particularly in body shape. However, it lacks the distinctively elevated soft dorsal and anal fins in the male of Paramonacanthus, as well as having no sexual dimorphism of the osteological structures supporting these fins. Like members of the monacanthid genera Rudarius and Acreichthys, the new taxon matures at sizes smaller than 30 mm SL, and may be categorised as another miniature representative of the family.

INTRODUCTION

Monacanthids have often been described on the basis of small to minute specimens. Most of these have turned out to represent the juvenile form of species that grow considerably larger (e.g. Monacanthus nitens Hollard, 1854, holotype 41 mm in standard length (SL) = Pervagor janthinosoma Bleeker, 1854, maximum size 113 mm SL; Monacanthus peroni Hollard, 1854, holotype 45 mm SL = Pseudomonacanthus peroni, maximum size 350 mm SL; and Brachaluteres taylori Woods, 1966, holotype 14 mm SL = B. taylori, maximum size 50 mm SL). Tyler (1970) was the first to describe a truly minute monacanthid, Rudarius minutus, which is sexually mature at only 17 mm SL. Hutchins (1977) subsequently presented a description of an even smaller species, Rudarius excelsius, which reaches sexual maturity at 15 mm SL. In their redescription of Acreichthys radiatus (Popta, 1900), Tyler and Lange (1982) reported mature specimens as small as 20 mm SL. The purpose of the present paper is to describe as new another miniature monacanthid which achieves maturity at sizes less than 30 mm SL. Although new, descriptions of this species have appeared before, but taxonomic confusion has masked its true identity.

Fraser-Brunner (1940), in his revision of the monacanthid genus Stephanolepis, provided the first description of this species under the name Stephanolepis freycineti. He believed that his small specimen from the Seychelles (BMNH 1908.3.23.294, 36 mm SL, originally reported in a list by Regan [1908] as Monacanthus setifer Bennett) represented a species first described from Mauritius by Quoy and Gaimard (1824) as Balistes freycineti. Unfortunately, a subsequent examination by the present author of the type of Balistes freycineti (MNHN A.4100, 178 mm SL) showed that it is a member of the Australian genus Meuschenia with a distribution restricted to southern Australia (Hutchins, 1977). As reported by Whitley (1943), the collections of Quoy and Gaimard—which included material from both Mauritius and Australia—were on board the “L’Uranie” when it was shipwrecked in the Falkland Islands in 1820. These were saved and eventually conducted to France, but not before some of the material was apparently mixed up. Whitley (1943), for example, reported on the atherinid Atherina jacksoniana; this was described by Quoy and Gaimard (1824) from a specimen supposedly collected in Sydney Harbour but in fact was from South America. Also the description of Balistes hippocrepis Quoy and Gaimard, 1824 was based on an Australian specimen and not an example from Mauritius as stated. Therefore, the fish from the Seychelles that was presented as Stephanolepis freycineti by Fraser-Brunner cannot be the species described by Quoy and Gaimard.

Some twenty-five years later, Woods (1966) provided a detailed description of a pair of monacanthids from the Marshall Islands in the Pacific under the earlier name of Paramonacanthus oblongus (Schlegel, 1850). Woods believed his small (27–35 mm SL) specimens represented immature individuals of that species.

As part of an investigation on the systematics of the family by the present author (Hutchins, 1988),
the three specimens of Fraser-Brunner and Woods were re-examined. They were all found to represent an undescribed genus and species, and were placed in the phylogenetic suprageneric category referred to as Group A (this contains all monacanths that possess a movably articulated pelvic fin rudiment, see Hutchins, 1997). A description of the new taxon is presented below, and includes a discussion of its apparent relationships with other members of the family.

Methods of counting and measuring follow those of Hutchins (1977, 1986), whereas terminology follows Hutchins (1997). The term "epineural rib" may be better stated as "epineural bone" (A.C. Gill, pers. comm.), but this is not followed here. Abbreviations for institutions are recorded in the acknowledgements.

SYSTEMATICS

Family Monacanthidae Nardo

Genus Enigmacanthus gen. nov.

Type species
Enigmacanthus filamentosus sp. nov. (see below).

Diagnosis
Distinguished from all other Group A genera (i.e., those possessing a pelvic fin rudiment movably articulated with the pelvis) of Hutchins (1988) by the structure and positioning of its epineural ribs. These ribs possess branched or expanded distal extremities, and commence on the third abdominal vertebra (all other Group A genera have epineural ribs with unexpanded extremities that, with the exception of Colurodontis and two species of Paramonacanthus, commence on the second abdominal vertebra). Other distinctive characters are given in the species diagnosis presented below.

Relationships
Hutchins (1988) was able to find only one derived character to separate this genus (referred to by Hutchins as "Genus b") from other genera in his Group A category. This entailed the branched or expanded distal extremities of the epineural ribs, a feature shared with one Group B genus (Aliterus) and several Group C genera (Rudarius, Brachaluteres, and Paraluteres) (see Hutchins, 1997 for a list of genera belonging to Groups A, B, and C). All other monacanths have unexpanded extremities. He surmised that this derived condition evolved independently in the three lineages involved. Another derived state concerning the positioning of the epineural ribs (commencing on the third abdominal vertebra versus the second abdominal vertebra) is also shared with Colurodontis and two species of Paramonacanthus, all from Group A; however this apparent synapomorphy is not supported by other shared derived characters (see remarks section in species account below).

Enigmacanthus is most similar to Paramonacanthus in body shape, but lacks the anteriorly elevated soft dorsal and anal fins that characterise the latter genus (Hutchins, 1997). Its scoliation is quite different from Stephanolepis (scale spinules are not supported by a broad-based pedicle, and there are no mandibular sensory scales in the lateral line sensory system, features that distinguish Stephanolepis from all other monacanths), but it shares some characters with Pervagor (scale spinules more robust, positioned along a transverse ridge, and one species of Pervagor possesses 1–2 elongate filamentous rays in the soft dorsal fin); however the characteristic deep caudal peduncle, robust first dorsal spine and robust pelvic fin rudiment (see Hutchins, 1986) of the latter genus are not present in Enigmacanthus. The monotypic Colurodontis also possesses a deep caudal peduncle (male condition only), and has two uniquely derived characters (very slender pelvis, and internal tusks in the lower jaw) that are not present in Enigmacanthus. The lack of clear-cut synapomorphies makes it difficult to decide whether any of these taxa are closely related to this new genus.

Etymology
Enigmacanthus is formed from "enigma" (meaning puzzling) and "acanthus" (the stem of numerous monacanthid genera). It refers to the unresolved relationships between this genus and other monacanthid taxa. The gender is masculine.

Enigmacanthus filamentosus sp. nov.
Figures 1, 2 and 3; Table 1

Monacanthus setifer (non Bennett, 1830): Regan, 1908: 252

Stephanolepis freycineti (non Quoy and Gaimard, 1824): Fraser-Brunner, 1940: 523, figure

Paramonacanthus oblongus (non Schlegel, 1850):
Woods 1966: 90, plate 133b.

“Genus b” Hutchins, 1994: 568

Holotype
USNM 140642, 35 mm SL, male, Marshall Islands (Pacific Ocean), Rongelap Atoll, lagoon 3 km W of Bush Island, dredge at 36 m, 21 June 1946 (S-46-232).

Paratypes
USNM 361255, 27 mm SL, female (cleared and stained), collected with holotype; BMNH
A new miniature monacanthid fish

Figure 1 Enigmacanthus filamentosus, holotype, USNM 140642, 35 mm SL, male, Marshall Islands (colour pattern markings based on the photograph of Woods, 1966).

1908.3.23:294, 36 mm SL, male, Seychelles, Gardiner Collection, 67 m, no other data.

Diagnosis
A monacanthid with the following combination of characters: maximum known size small (36 mm SL); soft dorsal rays 27–28; anal rays 26; pectoral rays 11/11; dorsal profile of snout straight in male (Figure 1), slightly concave in female, without prominent hump just before nostrils; soft dorsal and anal fins not elevated anteriorly, outer margins convex; soft dorsal fin of male with second ray elongate and filamentous (damaged in both male specimens); caudal fin moderately long (about equal to head length), posterior margin convex; pelvis capable of moving vertically through an arc of about 40 degrees, producing a moderately large ventral flap; lobe on rear of pelvis small, directed dorsoposteriorly; pelvic fin rudiment relatively short and small, posterior segment movably articulated with pelvis; midbody scales each with up to six minute spines located on a transverse ridge, those on caudal peduncle of male slightly longer, recurved, forming a poorly defined patch of bristles.

Description
Measurements of the holotype and paratypes are presented in Table 1. The following counts and proportions in parentheses represent the ranges for the paratypes when they differ from those of the holotype.

Soft dorsal rays 28 (27–28); anal rays 26; pectoral rays 11/11; vertebrae 7+12=19 (from radiographs and cleared and stained material); vertebral column of male paratype deflected ventrally, presumably the result of a deformity; branchiostegals 1+4=5.

Body compressed and rather elongate, noticeably deeper in female, width 2.5 (1.8–2.2) in head length.

Table 1 Fin ray counts and morphometrics of Enigmacanthus filamentosus

<table>
<thead>
<tr>
<th>Measurement</th>
<th>Holotype USNM 140642</th>
<th>Paratype USNM 361255</th>
<th>Paratype BMNH 1908.3.23:294</th>
</tr>
</thead>
<tbody>
<tr>
<td>Standard length</td>
<td>35</td>
<td>27</td>
<td>36</td>
</tr>
<tr>
<td>Head length</td>
<td>12</td>
<td>9.8</td>
<td>12</td>
</tr>
<tr>
<td>Body depth</td>
<td>14</td>
<td>13</td>
<td>12</td>
</tr>
<tr>
<td>Body width</td>
<td>4.7</td>
<td>4.5</td>
<td>6.6</td>
</tr>
<tr>
<td>Snout length</td>
<td>7.9</td>
<td>6.8</td>
<td>8.3</td>
</tr>
<tr>
<td>Eye diameter</td>
<td>3.9</td>
<td>3.2</td>
<td>3.7</td>
</tr>
<tr>
<td>Interorbital width</td>
<td>3.3</td>
<td>3.1</td>
<td>4.0</td>
</tr>
<tr>
<td>Gill slit length</td>
<td>1.7</td>
<td>#</td>
<td>1.8</td>
</tr>
<tr>
<td>Snout to dorsal spine</td>
<td>12</td>
<td>#</td>
<td>12</td>
</tr>
<tr>
<td>Lower jaw to PFR</td>
<td>22</td>
<td>#</td>
<td>25</td>
</tr>
<tr>
<td>Dorsal spine length</td>
<td>7.8</td>
<td>7.2</td>
<td>7.2*</td>
</tr>
<tr>
<td>Interdorsal space</td>
<td>8.5</td>
<td>7.2</td>
<td>10</td>
</tr>
<tr>
<td>Longest dorsal ray</td>
<td>4.1</td>
<td>#</td>
<td>3.6*</td>
</tr>
<tr>
<td>Longest anal ray</td>
<td>3.6</td>
<td>#</td>
<td>4.1*</td>
</tr>
<tr>
<td>Longest pectoral ray</td>
<td>3.1</td>
<td>#</td>
<td>3.8*</td>
</tr>
<tr>
<td>Length of caudal fin</td>
<td>12</td>
<td>#</td>
<td>12*</td>
</tr>
<tr>
<td>Length of dorsal fin base</td>
<td>12</td>
<td>9.2</td>
<td>12</td>
</tr>
<tr>
<td>Length of anal fin base</td>
<td>10</td>
<td>7.9</td>
<td>11</td>
</tr>
<tr>
<td>Length of caudal peduncle</td>
<td>3.3</td>
<td>1.8</td>
<td>3.2</td>
</tr>
<tr>
<td>Depth of caudal peduncle</td>
<td>4.1</td>
<td>2.7</td>
<td>4.6</td>
</tr>
<tr>
<td>Length of PFR</td>
<td>1.6</td>
<td>1.4</td>
<td>1.7</td>
</tr>
<tr>
<td>Soft dorsal fin ray count</td>
<td>28</td>
<td>27</td>
<td>28</td>
</tr>
<tr>
<td>Anal fin ray count</td>
<td>26</td>
<td>26</td>
<td>26</td>
</tr>
<tr>
<td>Pectoral fin ray count</td>
<td>11,11</td>
<td>11,11</td>
<td>11,11</td>
</tr>
<tr>
<td>Sex</td>
<td>Male</td>
<td>Female</td>
<td>Male</td>
</tr>
</tbody>
</table>

# Measurement not taken due to damage
* Measurement affected by distortion/damage
and depth 2.5 (2.1–3.0) in SL; head rather long, length 2.9 (2.8–3.0) in SL; dorsal profile of snout when viewed laterally straight to slightly concave, more concave in female, length 4.4 (4.0–4.3) in SL; eye diameter 3.1 (3.1–3.2) in head length, 0.8 (1.0–1.1) in interorbital width; gill opening a short slit, length 7.1 (6.7) in head length, positioned in advance of pectoral fin base, centred below posterior quarter of eye; pelvic flap relatively moderate in size, posterior margin of flap broadly joined to pelvic fin rudiment.

Mouth small, terminal, lips not obviously fleshy; dentition consisting of three outer and two inner teeth on each side of upper jaw (exposed portion of both inner teeth small but obvious); three teeth on each side of lower jaw, posterior tooth very small; anterior pair of teeth in both jaws with pointed extremities.

First dorsal spine originating over posterior third of eye to slightly in advance of rear border; spine moderately long, length 1.5 (1.4) in head length, somewhat circular in cross-section, tapering to acute tip; smallest specimen available (female paratype, 27 mm SL) with four rows of barbs on dorsal spine, two adjacent rows of double-branched barbs on anterior face, downward directed branch prominent in middle of spine, but upward-directed branch strongest on proximal and distal portions (Figure 2), and two rows of larger, downward-directed barbs on posterior face, projecting mostly posterolaterally; in largest specimen (male paratype, 36 mm SL) anterior series of barbs worn but still visible, posterior series with some barbs double branched, downward-directed one strongest; posterior barbs support relatively long, branched tentacles, some anterior barbs with small, simple tentacles; second dorsal spine small, hidden in skin at rear base of first spine; shallow groove in interdorsal space for receiving first dorsal spine when folded rearwards; soft dorsal and anal fins not elevated anteriorly; profile of outer margin of fins convex in both sexes, although second ray of dorsal fin of male prominently elongate and filamentous (damaged in holotype and paratype); longest non-filamentous dorsal ray 2.9 in head length, slightly longer than longest anal ray; length of soft dorsal base 2.9 (2.9–3.0) in SL, slightly longer than anal base, length 3.5 (3.3–3.4) in SL; bases of fin membranes not perforated; origin of soft dorsal well in advance of anal fin origin; interdorsal space slightly greater than length of first dorsal spine in adult (equal in female paratype), profile between fins flat to slightly elevated in male, slightly more elevated in female; base of pectoral fin below a point ranging from slightly behind rear border of eye to slightly in advance of rear border; caudal fin moderately long, length in male equal to head length, with convex posterior margin; caudal peduncle slightly tapered, length 3.6 (3.8–5.4) in head length, 1.2 (1.4–1.5) in caudal peduncle depth; pelvic fin rudiment (Figure 3) relatively small in size, length 2.4 (2.2–2.3) in eye diameter, consisting of five encasing scales with small barbs and spinules, an anterior pair (segment 1), a middle pair (segment 2), and a single posterior scale (segment 3); scales of segment 2 separated from each other.

Figure 2  Diagram of portion of the skull and vertebral column of Enigmacanthus filamentosus, paratype, USNM 361255, 27 mm SL, female, showing structure of first dorsal spine and predorsal neural spines (anterior end faces left; horizontal line represents 5 mm).
along ventral midline of rudiment by a prominent gap as in the monacanthid genus *Lalmohania* (see Hutchins 1994, figure 3); segment 3 movably articulated with both segment 2 and rear end of pelvis; pelvic fin rudiment broadly joined to posterior margin of ventral flap (Figure 1).

Midbody scales of cleared and stained female paratype small, imbricate, elliptical in shape, each with three spinules, middle one somewhat stronger, distal extremities curving posteriorly, supported by a transverse, somewhat V-shaped ridge, acute portion directed anteriorly; scales slightly larger on caudal peduncle; male holotype with up to six spinules arranged transversely along a ridge on each midbody scale, some spinules directed anteriorly; spinules on caudal peduncle slightly longer, distal extremities curving anteriorly, forming a poorly defined patch of short bristles (some scales on posterior half of peduncle with only a single bristle); scales on forehead and breast enlarged, circular and more robust, with numerous short robust spinules; skin velvety to slightly coarse; relatively large, multibranched cutaneous tentacles on body.

Colour of holotype in alcohol: ground colour pale brown, fins and ventral flap more translucent to hyaline; ventral profile from lower jaw to just anterior to pelvic fin rudiment mostly brownish, forming three darker cross-bars (Figure 1); ventral flap pale, with prominent dusky posterior margin; posterior portion of caudal peduncle brownish; median portion of caudal fin with indications of 1-2 curved dusky cross bars. The male paratype from the Seychelles has 3 broad longitudinal stripes on the side of the body, in addition to the markings described for the holotype (also see following colour description).

Colour in life is unknown, but the following description (shortened and modified) from Woods (1966) of preserved male and female specimens—the present holotype and one paratype—from the Marshall Islands presents some clues (Figure 1): ground colour light brown, throat and breast crossed by 2-3 indistinct bars; base of soft dorsal and anal fins each with 2 large brown blotches; series of white dots running obliquely from eye, beneath pectoral fin to belly; 4-5 incomplete horizontal rows of small white spots on sides; ventral flap with dark brown or black posterior margin; dorsal spine with 3 dark brown cross bars, membrane dusky; soft dorsal and anal fins colourless; caudal fin pale, dusky at base, with series of transverse spots and bars on middle of fin giving appearance of a blackish cross bar. The preserved male specimen from the Seychelles (second paratype) was described and figured by Fraser-Brunner (1940: figure 1) as having 3 broad longitudinal stripes on the side of the body, a blackish area along the ventral surface from mouth to pelvic fin rudiment, a dusky posterior margin to the ventral flap, and a caudal fin with a broad median band and 4 submarginal bands, membranes with longitudinal series of carmine spots.

**Etymology**

This species is named *filamentosus* in reference to the filamentous second ray in the male's soft dorsal fin.
Distribution

*Enigmacanthus filamentosus* is known only from the Marshall Islands in the Pacific and the Seychelles in the Indian Ocean.

Remarks

*Enigmacanthus filamentosus* is a very small species that apparently inhabits sandy bottoms in depths between 36 and 67 m. It is probably widely distributed across insular areas of the Indo-West Pacific but has remained largely undetected because of its size and depths of habitation. Its strong scale spinules on the dorsal and ventral surfaces of the head, like those found on coral reef dwellers such as members of *Pervagor*, *Amanses*, and *Oxymonacanthus*, suggest that it inhabits coral areas. However, as it was dredged from soft substrates, perhaps it favours scattered coral clumps on the sandy bottoms of deep lagoons.

*Enigmacanthus* is one of four monacanthid genera that possess an elongate filamentous ray in the soft dorsal fin (*Stephanolepis*, *Paramonacanthus*, and *Pervagor* are the other three). It is most similar in general appearance to *Paramonacanthus*, particularly two species from the Western Indian Ocean, *P. frenatus* and *P. nematophorus*. It differs from these two in the following ways: 1) lacks elevated soft dorsal and anal fin rays anteriorly in the male, 2) the osteology of the underlying pterygiophores supporting the elongated rays is different (the male does not develop enlarged interpterygiophore spaces, see Hutchins, 1997), 3) it lacks the characteristic dark streak on the anal fin of the male, 4) it only has one foramen in the basal pterygiophore of the spinous dorsal fin instead of two, 5) the pelvis is more elevate with a much smaller dorsal flange, and 6) scale spinules are more robust in *Enigmacanthus*. In addition, this species does not appear to form schools, unlike all species of *Paramonacanthus*.

Additional material examined

*Meuschenia freycineti*, MNHN A.4100, 178 mm SL, holotype of *Balistes freycineti*, *Ile Maurice* (should be Australia, see above), Quoy and Gaimard; *Meuschenia hippocrepis*, MNHN B.2015, 250 mm SL, holotype of *Balistes hippocrepis*, *Ile Maurice* (should be Australia, see above), Quoy and Gaimard.

ACKNOWLEDGEMENTS

I wish to thank A.C. Wheeler and A.C. Gill of the Natural History Museum, London (BMNH) and M.-L. Bauchot of the Muséum National d’Histoire Naturelle, Paris (MNHN) for the loan of specimens and providing information. My wife, Anne, capably prepared the translations of several foreign papers. Finally, I would like to acknowledge the assistance provided by S.M. Morrison of the Western Australian Museum, Perth (WAM) during the period of this study.

REFERENCES


A new miniature monacanthid fish


Manuscript received 3 July 2000; accepted 30 December 2001.
Guide to Authors

Subject Matter:
Reviews, observations and results of research into all branches of natural science and human studies will be considered for publication. However, emphasis is placed on studies pertaining to Western Australia. Longer papers will be considered for publication as a Supplement to the Records of the Western Australian Museum. Short communications should not normally exceed three typed pages and this category of paper is intended to accommodate observations, results or new records of significance, that otherwise might not get into the literature, or for which there is a particular urgency for publication. All material must be original and not have been published elsewhere.

Presentation:
Authors are advised to follow the layout and style in the most recent issue of the Records of the Western Australian Museum including headings, tables, illustrations and references.

The title should be concise, informative and contain key words necessary for retrieval by modern searching techniques. An abridged title (not exceeding 50 letter spaces) should be included for use as a running head.

An abstract must be given in full length papers but not short communications, summarizing the scope of the work and principal findings. It should normally not exceed 2% of the paper and should be suitable for reprinting in reference periodicals.

The International System of units should be used.
Numbers should be spelled out from one to nine in descriptive text; figures used for 10 or more. For associated groups, figures should be used consistently, e.g. 5 to 10, not five to 10.

Spelling should follow the Concise Oxford Dictionary.
Systematic papers must conform with the International Codes of Botanical and Zoological Nomenclature and, as far as possible, with their recommendations.
Synonymsies should be given in the short form (taxon, author, date, page) and the full reference cited at the end of the paper. All citations, including those associated with scientific names, must be included in the references.

Manuscripts:
The original and two copies of manuscripts and figures should be submitted to the Editors, c/-Publications Department, Western Australian Museum, Francis Street, Perth, Western Australia 6000. They must be in double-spaced typescript on A4 sheets. All margins should be at least 30 mm wide. Tables plus heading and legends to illustrations should be typed on separate pages. The desired position for insertion of tables and illustrations in the text should be indicated in pencil. Tables should be numbered consecutively, have headings which make them understandable without reference to the text, and be referred to in the text.

High quality illustrations are required to size (16.8 cm x 25.2 cm) or no larger than 32 cm x 40 cm with sans serif lettering suitable for reduction to size. Photographs must be good quality black and white prints, not exceeding 16.8 cm x 25.2 cm. Scale must be indicated on illustrations. All maps, line drawings, photographs and graphs, should be numbered in sequence and referred to as Figure/s in the text and captions. Each must have a brief, fully explanatory caption. On acceptance a computer disk containing all corrections should be sent with amended manuscript. The disk should be marked with program (e.g. Word, WordPerfect, etc).

In papers dealing with historical subjects references may be cited as footnotes. In all other papers references must be cited in the text by author and date and all must be listed alphabetically at the end of the paper. The names of journals are to be given in full.

Processing:
Papers and short communications are reviewed by at least two referees and acceptance or rejection is then decided by the editors.
The senior author is sent one set of page proofs which must be returned promptly.
The senior author will receive fifty free offprints of the paper. Additional offprints can be ordered at page proof stage.
CONTENTS

R.M. St Clair
Western Australian Tripletidinae (Trichoptera: Leptoceridae): descriptions of the female of Tripletides niveipennis and larvae belonging to four genera  111

A. Reid
Western Australian Onychophora (Peripatopsidae): a new genus, Kumbadjena, for a southern species-complex  129

K.J. McNamara and O.H. Melikov
The asterostomatid echinoid Antillaster from the Paradash Group (Middle Eocene) of the Nakhichevan Region of Azerbaijan  157

K.S.W. Campbell and R.E. Barwick
The axial postcranial structure of Griphognathus whitei from the Upper Devonian Gogo Formation of Western Australia: comparisons with other Devonian dipnoans  167

E.M. Exley
Bees of the Euhesma crabronica species-group (Hymenoptera: Colletidae: Euryglossinae)  203

J.B. Hutchins
Description of a new genus and species of miniature monacanthid fish from the Seychelles and Marshall Islands  213