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Front cover: What could be more symbolic for the International Year of Biodiversity than a gaudy pink shrimp? This new species, *Lebbeus rubrodentatus*, comes from 360–390 metres deep in the Timor Sea (see Bruce pages 75–77). Painting by David Percival, reproduced courtesy of A. J. Bruce.



RECORDS OF THE MUSEUMS AND ART GALLERIES
OF THE NORTHERN TERRITORY

Volume 26, December 2010
CONTENTS

SHORT, P.S. – New species of <i>Cleome</i> L. (Cleomaceae) from the Northern Territory, Australia.....	1
ALVAREZ, B. and HOOPER, J.N.A – Taxonomic revision of the order Halichondrida (Porifera: Demospongiae) of northern Australia. Family Dictyonellidae.....	13
WATSON, C. – Revision of the pantropical genus <i>Treptopale</i> (Annelida: Phyllodocida: Chrysopetalidae): redescription of <i>Treptopale rudolphi</i> Perkins, 1985 and description of two new species including comparison of <i>Treptopale</i> populations in northern Australia.....	37
GLASBY, C.J. and HOCKNULL, S.A. – New records and a new species of <i>Hermundura</i> Müller, 1858, the senior synonym of <i>Loandalia</i> Monro, 1936 (Annelida: Phyllodocida: Pilargidae) from northern Australia and New Guinea	57
BRUCE, A.J. – <i>Typtonoides nieli</i> gen. nov., sp. nov., a new pontonine shrimp (Crustacea: Decapoda: Palaemonidae) from the Chesterfield Islands	69
BRUCE, A.J. – <i>Lebbeus rubrodentatus</i> sp. nov. (Crustacea: Caridea: Hippolytidae) from the Australian North West Shelf.....	75
SALGADO-KENT, C. and McGUINNESS, K. – Spatial and temporal variation in relative numbers of grapsid erabs (Decapoda: Grapsidae) in northern Australian mangrove forests	79
BROWN, G.R. – <i>Curvothynnus</i> gen. nov. erected for two unusual species of thynnine wasps (Hymenoptera: Thynnidae: Thynninae: Rhagigasterini)	89
BROWN, G.R. – Two new orchid-pollinating wasps (Hymenoptera: Thynnidae) from Australia.....	97
BAEHR, M. – A new species of the genus <i>Microlestodes</i> Baehr from Arnhem Land, Northern Territory, Australia (Insecta: Coleoptera: Carabidae: Lebiini).....	103
BERRA, T.M. – Clarification of field characters for three freshwater sharks and a photographic atlas of <i>Glyphis glyphis</i> and <i>G. garricki</i> from the Adelaide River, Northern Territory, Australia	109
TYLER, M.J. – A new fossil species of frog of the Australian limnodynastid genus <i>Limnodynastes</i> Fitzinger from the Oligocene Kangaroo Well Local Fauna of the Northern Territory and tabulation of ilial features of all extant and extinct species.....	115
Short communication	
COWIE, I.D. – Notes on the identity, distribution and conservation status of the threatened plant species <i>Utricularia singeriana</i> F. Muell. (Lentibulariaceae).....	119
Guide to authors.....	122

New species of *Cleome* L. (Cleomaceae) from the Northern Territory, Australia

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ABSTRACT

Four new species of herbaceous flowering plants, *Cleome bundeica*, *C. insolata*, *C. limmenensis* and *C. lophosperma*, all endemic to the Northern Territory, are described. A modified description of *C. microaustratica* H. Iltis, within which *C. limmenensis* was previously included, is provided, as is a key to all formally named species of *Cleome* occurring in the Northern Territory.

KEYWORDS: Cleomaceae, *Cleome*, new species, *C. bundeica*, *C. insolata*, *C. limmenensis*, *C. lophosperma*.

INTRODUCTION

Cleome L. is predominantly a pantropical genus of herbaceous flowering plants and, depending on the circumscription, has between 250 and 280 species (Sánchez-Acebo 2005; Iñda *et al.* 2008; Mabberley 2008), with 14 species, five of which are naturalised, currently recognised from Australia (Craven *et al.* 2010; Australian Plant Census; excluding phrase names). For many years the genus was placed in the family Capparaceae (e.g. Cronquist 1981; Kers 2003), but phylogenetic studies have suggested its placement in either an expanded Brassicaceae (e.g. Judd *et al.* 1999) or in its own family Cleomaceae (e.g. Hall *et al.* 2002; Mabberley 2008). The latter treatment is now widely adopted and followed here.

The most recent treatment of *Cleome* in Australia by Hewson (1982) does not satisfactorily account for the many entities which occur in the Northern Territory, and indeed, elsewhere in Australia. Since her work, the introduced species *C. aculeata* L., *C. gynandra* L. and *C. rutidosperma* DC. have been found in the Northern Territory. Furthermore, following field work in the Top End of the Northern Territory for the *Flora of Darwin* project, it became evident about ten years ago that a number of undescribed taxa exist and that the status and circumscription of several taxa recognised by Hewson needed further examination. However, only two new taxa have been described for Australia since Hewson's account, these being *C. nncifera* subsp. *microphylla* Keighery, which occurs in both Western Australia and the Northern Territory (Keighery 2002), and *C. arenitensis* Craven *et al.* from Western Australia (Craven *et al.* 2010). The name *C. limnophylla* (O.Schwarz) Pax & K. Hoffm. has also been reinstated for a species once treated as a variety of *C. tetrandra* DC. (Short 2006).

In this paper four new species are described from the Northern Territory but further work is required to assess the rank and final circumscription of many other taxa, both in the Northern Territory and elsewhere in northern Australia. In several cases better specimens are required before formal naming and description. For example, because of a lack of data regarding petal orientation and staminal characteristics, the author has decided against formally describing a species possibly restricted to the vicinity of Flying Fox Creek in Kakadu National Park. The single specimen by which it is known is housed at the Northern Territory Herbarium (DNA) under the phrase name '*Cleome* sp. Flying Fox Creek (D.J. Dixon 1089 & I.D. Cowie) P.S. Short'. With just five stamens and a seed with a single claiosome, it keys to the *C. tetrandra* group in the key given below. The most distinctive feature of this species is its perennial habit, other Northern Territory specimens referred to this group being annuals.

The above example is one of many specimens held at DNA lacking essential or desirable information required for the identification and description of taxa. Mature seeds are frequently absent from specimens, a critical absence as positive identification may depend on being able to observe features such as testa ornamentation and the number and morphology of claiosomes. Thus, collectors should always endeavour to gather mature seeds. Similarly, to assist in increasing our knowledge of *Cleome* in northern Australia, notes concerning features such as petal orientation, the number and placement of stamens, and the colour of floral organs should be recorded in the field and included on specimen labels. As with seed characteristics, the aforementioned floral organs exhibit many taxonomically useful features which are lost, or difficult to ascertain, in pressed material.

Herbarium abbreviations follow Holmgren *et al.* (1990).

TAXONOMY

Cleome bundeica P. S. Short, sp. nov.

(Figs 1, 2A–D)

A ceteris gregis *C.* tetrandrae cum petalis erectis in proprietatibus sequentibus differt: foliolis ovatis vel obovatis vel oblanceolatis, 5–24 mm longis, 2–10 mm latis, marginibus integris, apice emarginato; petalis interdum spatulatis, basibus unguiformibus, 11–14.5 mm longis, 2–4.3 mm latis, staminibus 6 binatim, par longissimum filamentis 10–14 mm longis, par medianum leviter brevius, par brevissimum filamentis 5–9 mm longis; fructus cylindricus 15–40 mm longus, 2–4 mm diametro, striatus longitudinaliter, pilis glandulis dispersis pedunculis; semina suborbicularia 1.4–1.5 mm, cristis latitudinalibus distinctis, annulis concentricis inconspicuis, elaiosomate singulare grandio.

TYPE. Australia, Northern Territory, Mt Bunday. In low-lying, inundated loamy soil at base of boulders. P.S. Short 5153 (HOLOTYPE: DNA D172228; ISOTYPES: K, MEL).

Additional specimens examined. NORTHERN TERRITORY: Mary River NP, near Mary River Billabong, 24 February 2004, I.D. Cowie 9984 (DNA); Mt Bunday, 14 December 1990, C.R. Dunlop 8762 (DNA); Plum Tree Creek crossing, Kakadu Stage 3, 25 February 1989, K. Menkhurst 258 (DNA); Plum Tree Creek crossing,

Kakadu Stage 3, 25 February 1989, K. Menkhurst 269 (DNA); Mt Bunday region, sandy soil in open woodland near Arnhem Hwy, 3 January 2002, P.S. Short 5134 (CANB, DNA, MEL).

Description. Annual herb with ascending to erect branches to approx. 30 cm long, with scattered but prominent indumentum of stalked, rigid glandular hairs.

Leaves mostly 3-foliolate, upper ones simple; petioles 2.5–70 mm long, or uppermost leaves subsessile. Leaflets subsessile or petiolule distinct but only to approx. 0.5 mm long; ovate or obovate to oblanceolate, 5–24 mm long, 2–10 mm wide, margins entire, apex emarginate.

Inflorescence terminal raceme of up to approx. 8 flowers, each lower flower usually subtended by small, unifoliate leaf. Sepals linear, lanceolate or oblanceolate, 3.5–5.5 mm long, 0.3–0.9 mm wide, mostly pale green, with scattered stalked glandular hairs. Petals somewhat spatulate, claw-like at base, 11–14.5 mm long, 2–4.3 mm wide, all 4 held somewhat erect, mostly shades of yellow throughout but middle 2 petals with 1 or 2 (lowest may not be well-defined or absent) dark orange or reddish bands at apex of claw and often darker yellow to orange-red below. Stamens 6, filaments free, in 3 pairs, longest pair 10–14 mm long and red-brown, middle pair slightly shorter and red-brown, inner pair 5–9 mm long and yellowish; anthers curved, grey. Gynophore absent. Ovary glabrous or almost so; style red-purple.

Capsules on pedicels 10–18 mm long, cylindrical, 15–40 mm long, 2–4 mm diameter, held at about 90° or less to peduncle, longitudinally striate, with stalked glandular hairs along prominent, slightly raised nerves; beak 8–13 mm long. Seeds 5–20, suborbicular, 1.4–1.5 mm across longest axis, orange-brown but maturing to dark brown or black, cross-ribs distinct, concentric rings faint; elaiosome single, mostly only extending into approx. half or less of the cleft and although prominent never appearing to completely surround funicle.

Distribution and habitat. *Cleome bundeica* is endemic to the Top End of the Northern Territory and to date is only known from the vicinity of Mt Bunday, Mary River Billabong and near Plum Tree Creek crossing (Kakadu National Park). It is locally common in eucalypt woodland on sandy soil and sometimes associated with *Pandanus spiralis*.

Flowering and fruiting. Recorded for December and January.

Remarks. The flowers appear to be bisexual but strongly protandrous, with those observed at the Mt Bunday population having shed their pollen while the ovary and style are, together, only 2–4 mm long.

A further distinctive, undescribed taxon as represented by Short 5154, and collected from a disturbed site across the road from the type locality of *C. bundeica*, is similar to this species. Although the petals tend to be longer, the flowers also have three pairs of stamens, and the seeds are morphologically identical, or nearly so, to those in



Fig. 1. Holotype specimen of *Cleome bundeica* sp. nov. (P.S. Short 5153, DNA D172228).

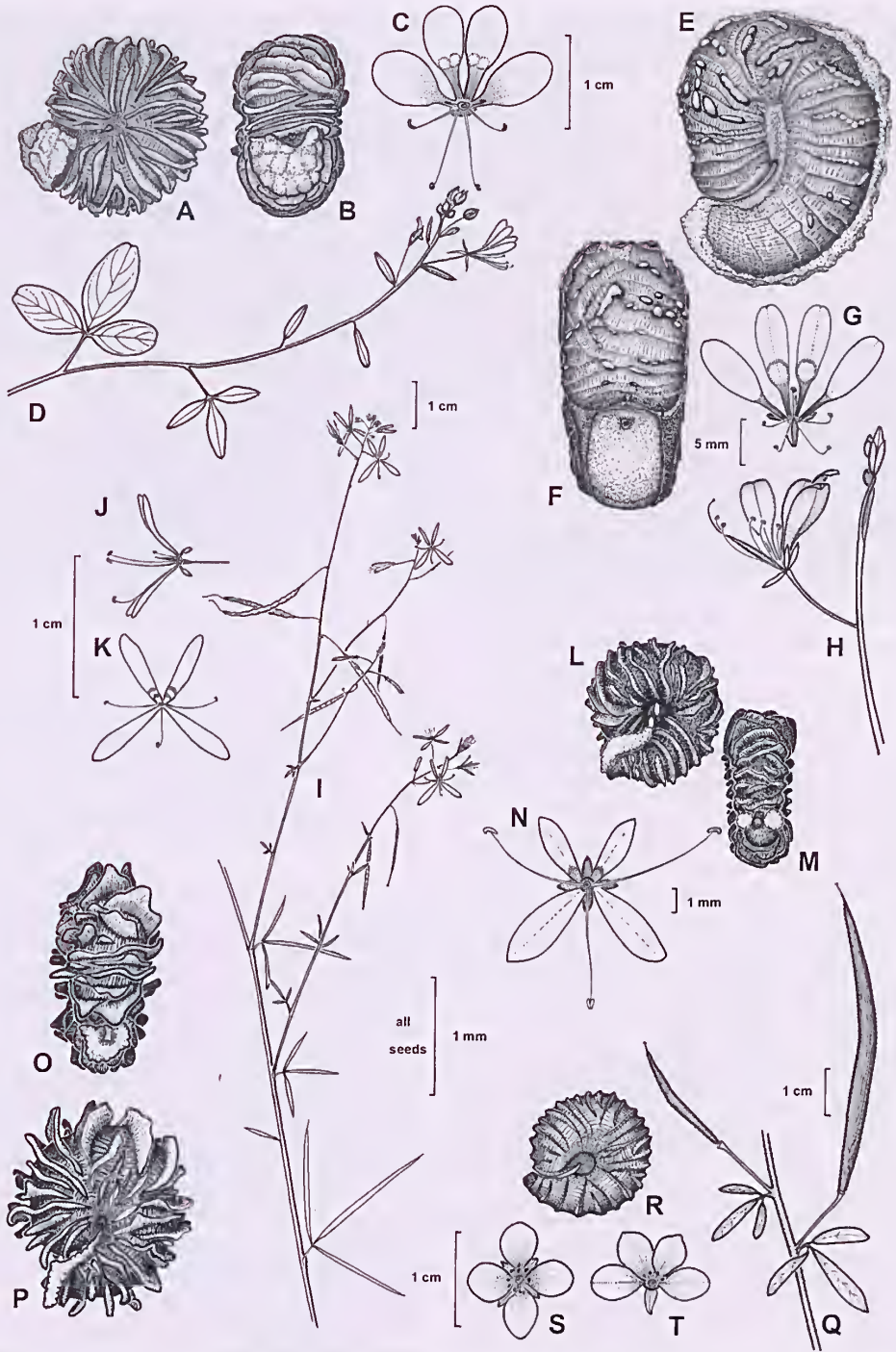


Fig. 2. A–D. *Cleome bundeica* sp. nov.: A, B, seed showing faint concentric rings, prominent cross-ribs and single elaiosome; C, flower with 3 pairs of stamens; D, flowering branchlet, with emarginate leaflets on lowest leaf (A–D, P.S. Short 5153, type). E–H. *Cleome insolata* sp. nov.: E, F, seed showing faint concentric rings, shallow cross-ribs, wart-like protuberances, and extensive elaiosome; G, flower with 5 stamens; H, flower, side view (E–H, P.S. Short 5172, type). I–K. *Cleome tetrandra* DC. s. lat. I, flowering branchlet; J, K, flower with 4 stamens, uppermost very short (I–K, P.S. Short 5149). L–N. *Cleome linophylla* sp. nov.: L, M, seed with 2 elaiosomes; N, flower with 3 stamens (L–N, P.S. Short 5138). O, P, *Cleome lophosperma* sp. nov.: views of seed showing crest- or shield-like cross ribs and single elaiosome (O, P, P.S. Short 5155, type). Q–T. *Cleome viscosa* auct., probably s. str.: Q, branchlet with leaves and fruit; R, seed, note absence of elaiosome; S, T, flowers showing arrangement of petals (Q–T, P.S. Short 5135).

C. bundeica. However, the leaflets are apically acute, not emarginate, are frequently somewhat linear, linear-oblongate or linear-lanceolate and less than 3.5 mm wide, and the capsules are glabrous.

Conservation status. There are a few specimens, suggesting that that species is moderately localised, and the size of each of the known populations has not been assessed. Following the IUCN criteria (Standards and Petitions Working Group 2006) for the conservation category of a species, *C. bundeica* is probably best classified as Data Deficient.

Etymology. The specific epithet reflects the fact that the species occurs in the Mt Bundeia region; the Latinised regional name being Bundeia (the adjectival form being *bundeicus*).

***Cleome insolata* P. S. Short, sp. nov.**

(Figs 2E–H, 3, 4A, B)

A ceteris gregis *C. tetrandrae* cum petalis erectis in proprietatibus sequentibus differt: foliola sessilia, linearia, foliolo mediano plerumque multo longius quam foliolis lateralibus, (1.5) 6–17 mm longa, 0.25–0.5 mm lata, glabra; petala interdum spatulata parte tertius basale unguiforme, 10.5–12.5 mm longa, 2.3–3.8 mm lata; stamina 5 interdum inaequalia, 5–10 mm longa; fructus subcylindricus inter semina constrictus, 11–30 mm longus, circa 2 mm latus, striatus longitudinaliter inconspicuus glabrus; semina axe longiore 2.3–2.5 mm, axe breviora 1.7–1.9 mm brunnea vel nigra, cristis latitudinalibus distinctis sed saepe incompletis, annulis concentricis inconspicuis et interdum absentibus, protuberationibus verruciformibus saepe praesentibus; elaiosome singulare, secus paginam externam extenso.

TYPE. Australia, Northern Territory, Woodside Reserve near Solar Village, Humpty Doo, 12°36'49"S, 131°05'38"E. Inundated low sedgeland over laterite gravel with silty loam soil. 31 March 2004. P.S. Short 5172 (HOLOTYPE: DNA D172198; ISOTYPES: AD, K, MEL).

Additional specimens examined. NORTHERN TERRITORY: behind Solar Village, Humpty Doo, 18 April 2002, P.S. Short 5139 (DNA).

Description. Annual herb with ascending to weakly erect branches to approx. 40 cm long, with mostly sparse indumentum of shortly stalked, rigid glandular hairs.

Leaves mostly 3-foliolate, few upper ones unifoliolate; petioles (1.5) 5–8 mm long or uppermost leaves subsessile. Leaflets sessile, linear, with middle leaflet usually manifestly (to twice the length) longer than laterals, (1.5) 6–17 mm long, 0.25–0.5 mm wide, glabrous, margins entire, apex somewhat rounded except for minute mucro.

Inflorescence terminal raceme, of (1) 2–5 flowers. Sepals lanceolate or oblanceolate, 1.8–3.2 mm long, 0.4–1 mm wide, pale green, glabrous or with few stalked glandular hairs. Petals somewhat spatulate, about basal one-third claw-like, 10.5–12.5 mm long, 2.3–3.8 mm wide, all 4 erect, mainly dark yellow but the middle 2 petals with

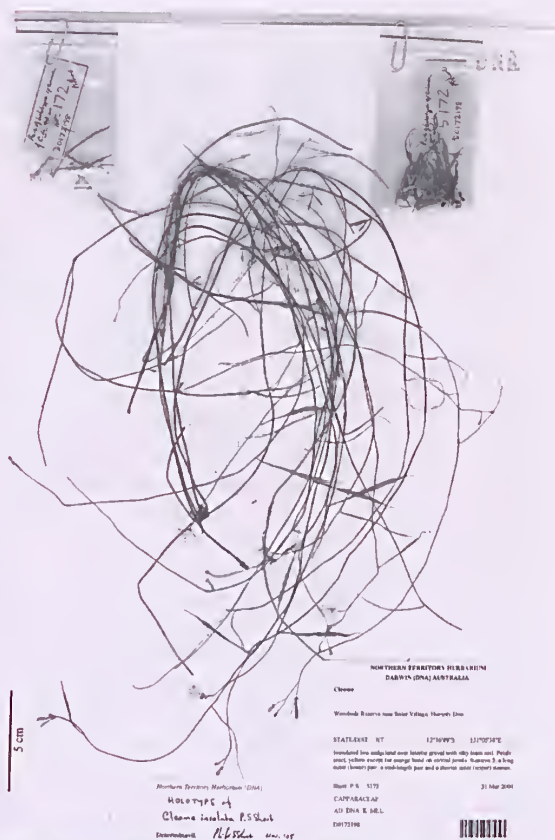


Fig. 3. Holotype specimen of *Cleome insolata* sp. nov. (P.S. Short 5172, DNA D172198).

orange band immediately above claw. Stamens 5, in 2 pairs plus 1 upper stamen; filaments free, unequal, 5–10 mm long, yellow-green with some reddish tint below anthers; anthers 0.8–1 mm long. Gynophore to approx. 1.5 mm long at anthesis, subsequently elongating. Ovary glabrous; style mostly pale whitish but upper part purplish.

Capsules on pedicels 6–9 mm long, gynophores 3.5–6.5 mm long, subcylindrical and usually constricted between individual seeds, 11–30 mm long, approx. 2 mm wide, held at about 90° or less to peduncle, faintly longitudinally striate, glabrous; beak 2–5 mm long. Seeds 1–6, comma-shaped, longest axis 2.3–2.5 mm, shortest axis 1.7–1.9 mm, brown to black, cross-ribs generally distinct but often incomplete, concentric rings very faint and sometimes not apparent, wart-like protuberances often common on surface and frequently following cross-ribs; elaiosome single, extending from hilum as narrow band along outer surface for approx. one-third to total length of seed, filling or mostly filling cleft.

Distribution and habitat. *Cleome insolata* is endemic to the Northern Territory. It is known from one population behind the Solar Village near Humpty Doo where most plants grow in inundated sedgeland on silty loam with an overlay of laterite gravel but also on an adjoining,

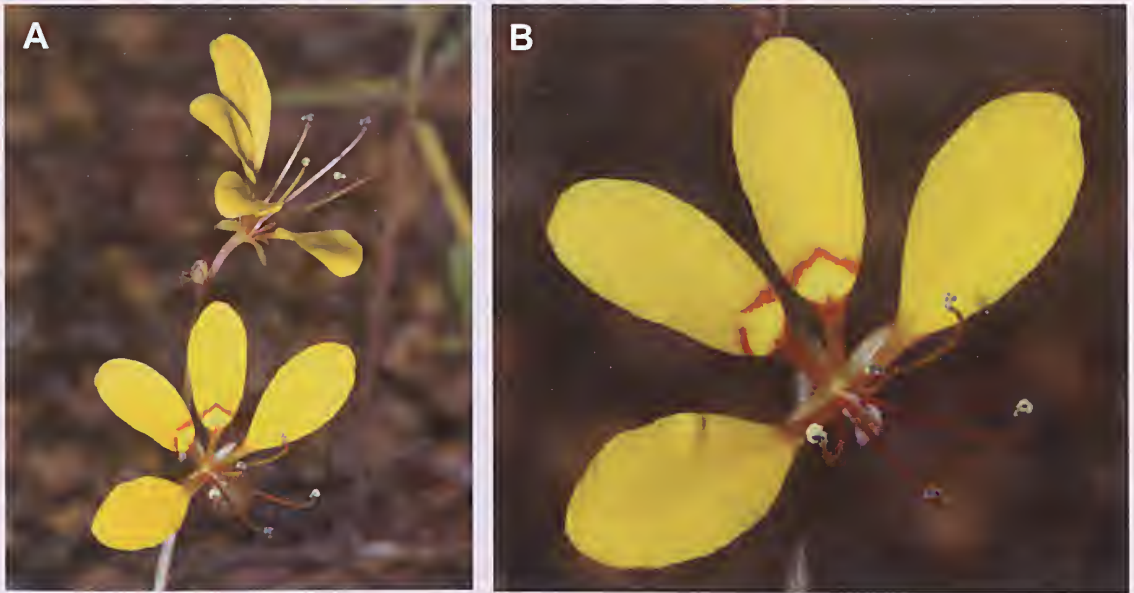


Fig. 4. Photographs of *Cleome insolata* sp. nov. at the type locality: **A**, inflorescence showing petal colour and arrangement of sepals, petals and stamens (note that an anther is missing from a stamen in the upper flower); **B**, single flower showing arrangement and colour of floral parts (note that the style is poorly developed, the flowers apparently strongly protandrous). Photographs: Ben Stuckey.

disturbed roadside verge. The population is on the edge of the Elizabeth River catchment, but the extent to which it occurs in the catchment has not been ascertained.

Flowering and fruiting. Recorded from March to April.

Remarks. The wart-like protuberances on the surface of the seed (Fig. 2E,F) have not been observed in any other Australian species of *Cleome*.

Conservation status. On each occasion when the type locality was visited in 2002, 2004 and 2010 probably several hundred plants were present in an area of approx. 4000 m² but the extent of this population has not been determined. There is an element of data deficiency associated with this species but as most of the population is on private land it is, arguably, assessed as Vulnerable (criterion D2) under IUCN (Standards and Petitions Working Group 2006).

Etymology. The specific epithet, meaning 'exposed to the sun', alludes to both the exposed sedgeland habitat and the locality of the only known population, the Solar Village near Humpty Doo, Northern Territory.

***Cleome limmenensis* P. S. Short, sp. nov.**

(Figs 5, 6D)

A.C. microaustralasiaea plantis foliis rigidioribus viscidis, foliolis obtusis ad apicem vel emarginatis, nunquam acutis, mucro apicale, semine elaiosomate utrinque funiculi, nunquam elaiosomate singulare.

TYPE. Australia, Northern Territory, McArthur River area. Sandstone plateau near Glyde River, 15°50'17"S, 135°21'24"E, 31 January 1976, L.A. Craven 3569 (HOLOTYPE: DNA A54996; ISOTYPE: CANB, n.v.)

Synonymy.

Cleome microaustralica auct. non H.H. Iltis; Hewson (1982, p.p., as to the inclusion of Craven 3569).

Additional specimens examined. NORTHERN TERRITORY: Glyde River, near intersection between east and west branches, 21 February 2003, K.G. Brennan 5809 (DNA); Glyde River, west branch, 23 February 2003, K.G. Brennan 5836 (DNA); Limmen National Park, approx. 35 km WNW of Ranger Station, 19 April 2008, I.D. Cowie 11956 (B, DNA, LD, MEL, MO); Broadmere Station, 5 November 2006, S. Legge 12 (DNA); Limmen Gate, 29 May 1996, C. Michell 149 (DNA).

Description. Subshrub to approx. 50 cm or more tall, beset with near-sessile (sometimes possibly sessile) to short-stalked glandular hairs approx. 0.6–0.55 (1.5) mm long, apical gland prominent and somewhat spheroidal, hairs common and often dense on stems, leaves, pedicels, calyx and gynoecium, and resulting in parts of plant being manifestly viscid.

Leaves almost sessile to distinctly petiolate; petiole to approx. 14 mm long; mostly 3-foliolate but 2- and 4- or 5-foliolate leaves may also be present; uppermost flower-subtending leaves may be unifoliate, generally smaller than lower cauline leaves. Leaflets obovate to (mostly) oblanceolate, 5–20 mm long, 1.5–6.7 mm wide, entire, variable in length within leaf, in 3-foliolate leaves central leaflet about same length as, or longer than, 2 lateral leaflets; gradually tapering to base, petiolule absent or somewhat poorly defined, to approx. 0.4 mm long; apex obtuse to distinctly emarginated with small, bluntish mucro.

Inflorescence leafy, terminal raceme of approx. 4–6 flowers, each flower being in axil of leaf; pedicels 6–13 mm

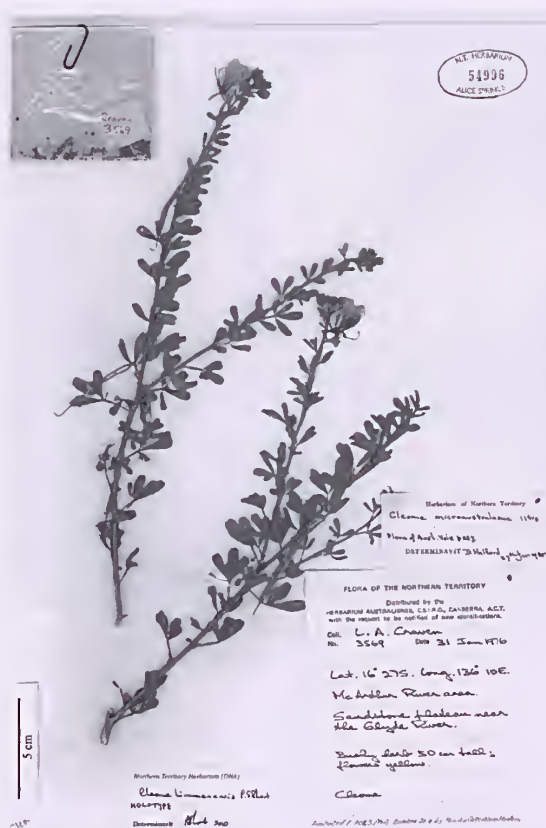


Fig. 5. Holotype specimen of *Cleome limmenensis* sp. nov. (L.A. Craven 3569, DNA A54996).

long at flowering and fruiting. Sepals narrowly elliptic to lanceolate or somewhat obovate, apically acute, 5.6–5.9 mm long, thinly herbaceous and often with prominent venation, outer surface glabrous and margins with glandular hairs, inner surface glabrous. Petals oblanceolate, 13.5–22 mm long, 4.4–7.5 mm wide, all 4 assumed to be somewhat erect and not in an x-shaped arrangement, usually gradually tapering towards base and not obviously claw-like in about lower third, seemingly all yellow throughout but on drying often pale yellow, white-yellow or purplish and venation visible. Stamens 9–14; filaments free, 6.2–15 mm long, arrangement not visible in dried specimens, in dried specimens at least basal part and sometimes much of filament purple-brown; anthers 1.8–2 mm long, initially straight but becoming curved. Gynophore absent or almost so. Ovary with numerous stalked glandular hairs; style approx. 6–9 mm long at anthesis, glabrous.

Capsules on pedicels 6–12 mm long and gynophores approx. 1 mm long, subcylindrical, approx. 25–45 mm long, approx. 1.5–3.5 mm diameter, straight to curved, densely glandular-hairy, sometimes appearing to be held erect but probably mostly held below 90° to peduncle; beak approx. 7–14 mm long. Seeds approx. 60, in large capsules, somewhat comma-shaped or suborbicular in outline,

1.5–1.7 mm across longer axis, 1.2–1.45 mm across shorter axis, brown to dark brown-black or black, concentric rings very faint but with many prominent, complete or broken, cross-ribs; claiosomes 2, yellowish or whitish, one on either side of funicle and filling cleft.

Distribution and habitat. *Cleome limmenensis* is only known from the Limmen Gate region, including the vicinity of the Glyde River, in the Northern Territory.

All specimens have been collected in sandstone country and it is often, if not always, associated with *Triodia*, e.g. it has been gathered from amongst cracks in the sandstone escarpment where it was growing with *Eucalyptus aspera*, *Acacia mimula* and *Triodia microstachya* (Miehell 149).

Flowering and fruiting. November to May.

Remarks. The species *C. microaustratica* was described by Iltis (1982, *Flora of Australia* 8: 390), the only specimen cited by him being the type specimen. In the same volume of the *Flora*, the treatment of the genus as a whole is ascribed to Hewson (1982) and when citing specimens she also referred Craven 3569, a specimen collected from a sandstone plateau near the Glyde River, to *C. microaustratica*. That gathering is the one here nominated as the type specimen of the new species, *C. limmenensis*.

Collectors have not recorded whether the petals are all erect or arranged in an x-shape and the author has not observed this species in the field. However, the arrangement of the petals on dried specimens, plus an apparent close-relationship with *C. microaustratica*, leaves me in no doubt that they are erect.

There is no mention on labels as to fresh petals being anything other than yellow, while dried petals may be yellow or fade to white or pale purple. In some species, including variants within *C. microaustratica*, there are distinct orange or reddish markings on the claw of each of the two middle petals (or upper petals in the case of species with petals held in a cross). Such colours, although often lost on drying, are not visible on any specimens here referred to *C. limmenensis*.

The holotype specimen has one flower with just five stamens and it is here assumed that some have been lost; the other flower on the specimen has 14 stamens while those in other specimens have no fewer than nine.

Morphologically this species is most similar to *C. microaustratica*. It differs by having more rigid and viscid foliage with apically obtuse to emarginated leaflets, never obtuse to acute apices; by having stalked glandular hairs on the stems which are commonly less than 0.6 mm long, not commonly 1 mm or more long; by having approx. 9–14 stamens per flower, not approx. 14–22; and by the seed having two elaiosomes, not one. The species' distributions are also markedly disjunct. *Cleome microaustratica* was described from Bickerton Island and is also found on Groote Eylandt and sandstone regions in and near Kakadu and Nitmiluk national parks. All such collections are to the north and north-west of *C. limmenensis*.

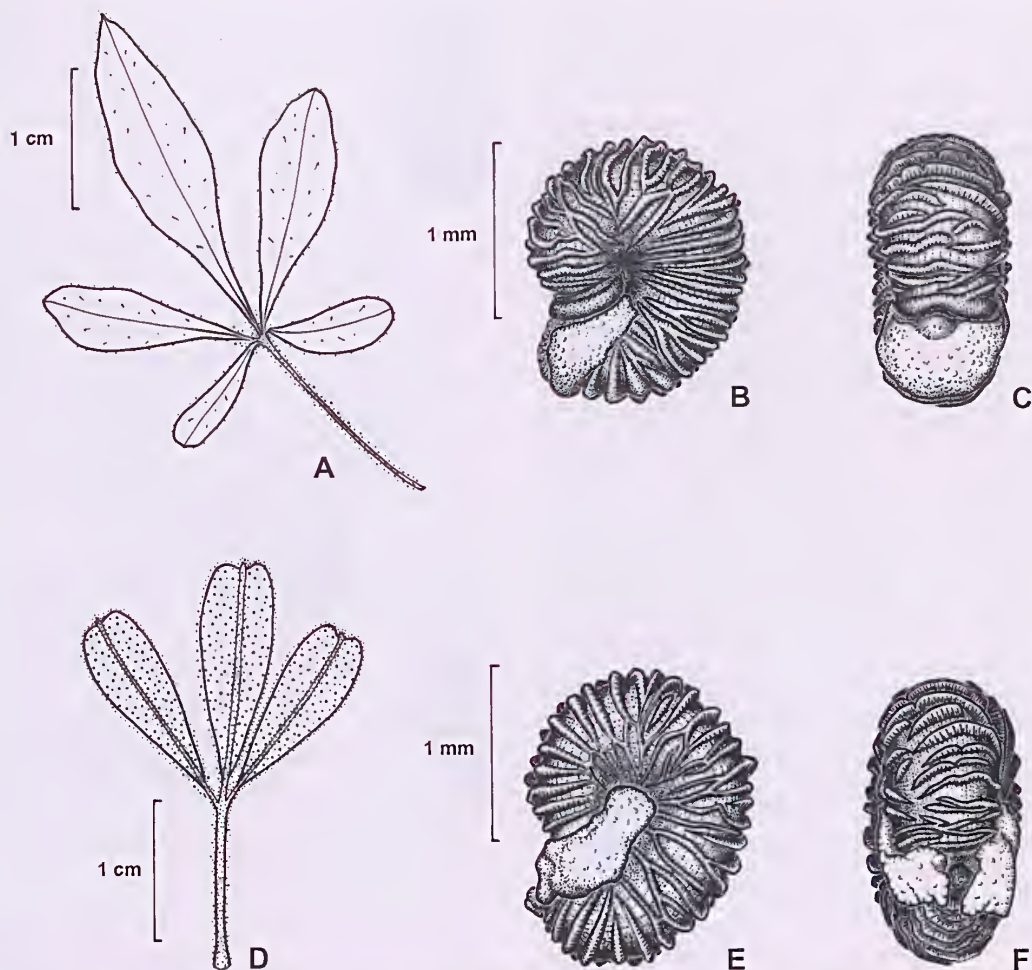


Fig. 6. A–C. *Cleome microaustralis* Hlts: A, leaf (upper surface) showing the obtuse to acute apices and stalked glandular hairs commonly found in the species; B,C, seed showing prominent cross-ribs and single claiosome only extending part way into cleft (A–C, J. Russell-Smith 1041). D–F, *Cleome limmenensis* sp. nov.: D, leaf (lower surface) showing emarginate apex and glandular hairs; E,F, seed showing prominent cross-ribs and two claiosomes, one on either side of the funicle and filling the cleft (D, L.A. Craven 3569, type; E,F, C. Michell 149).

Conservation status. *Cleome limmenensis* is only known from a few localities spread over an area less than 200 km long but in relatively remote and rarely accessed sandstone country. As such, it is highly unlikely to be threatened by human activities. However, lack of data on its biology, number and extent of individual populations suggests that under the IUCN criteria (Standards and Petitions Working Group 2006) for the conservation category of a species, *C. limmenensis* should be classified as Data Deficient.

***Cleome lophosperma* P. S. Short sp. nov.**

(Figs 20,P, 7)

A ceteris gregis *C. tetrandrae* petalis quattuor in cruce dispositis, semine cristis grandissimis latitudinaliter ordinatis, claiosomate singulare differt. Haec species

plerumque glabra est, plerumque foliis trifolium, staminibus (3) 4 (5) in quoque flore.

TYPE. Australia. Northern Territory, approx. 1 km E of Girraween Road (sealed) along dirt road following power lines, 12°31'30"S, 131°06'54"E. Low, open woodland with *Grevillea pteridifolia*; deep sand. 6 March 2003, P.S. Short 5155 (HOLOTYPE: DNA D172220; ISOTYPES: AD, BRI, MEL).

Additional specimens examined. NORTHERN TERRITORY: Arnhem Hwy, 8 km E of Adelaide River, 7 January 2003, R.K. Harwood 1230 (DNA); Koolpinyah sand pit, Howard River, 17 January 1979, M.O. Rankin 1695 (BRI n.v., CANB n.v., DNA, K n.v.); approx. 1 km E of Girraween Road (sealed section) along dirt road near T-junction with road heading north, 21 December, 2001, P.S. Short 5130 (AD, DNA); approx. 8 km SE of Adelaide River along Arnhem Hwy, 11 December 2002, P.S. Short

5143 (AD, CANB, DNA, MEL); 12.5 km W of Corroboree Park along Arnhem Highway, 19 February 2003, P.S. Short 5144 (DNA, MEL); Howard River area, Whitewood Road, 29 December 2009, B. Stuekey 478 (DNA).

Description. Annual herb with ascending to erect branches to approx. 40 cm long, mostly glabrous but with occasional stalked, rigid, multiseptate whitish or purplish glandular hairs to approx. 0.4 mm long on branches and leaves.

Leaves. Basal and mid-cauline leaves mostly 3- or rarely 5-foliolate, upper and sometimes some basal leaves unifoliate; petioles approx. 1–40 mm long and at least upper leaves sessile or nearly so. Leaflets subsessile, linear-oblaneeolate or linear-elliptic, with middle leaflet much longer than laterals, all leaflets (2) 4–35 mm long, 0.3–2 (4) mm wide, glabrous or with few scattered hairs as on stem and branches, margins entire and slightly inrolled, apically tapering to small, bluntish mucro.

Inflorescence terminal, leafless raceme of 5–14 flowers; pedicels at flowering approx. 6–7 mm long. Sepals ovate or triangular to narrowly triangular, 1.1–2 mm long, 0.3–0.5 mm wide, pale green or whitish and usually at least slightly purplish, glabrous. Petals oblanceolate and gradually tapering to base, 5.4–7.2 mm long, 1.2–1.9 mm wide, arranged in an x with 2 petals held erect and 2 pointing down; upper petals mainly yellow, each with orange to slightly reddish band towards base and tending to be darker yellow beneath band; lower petals entirely yellow. Stamens (3) 4 (5); filaments free, 3.5–5.8 mm long, unequal and with one shorter than the others, yellow-green; anthers curved, 0.5–1 mm long, purplish but tending to brown on drying. Gynophore absent. Ovary glabrous.

Capsules on pedicels 5.5–12 mm long, subcylindrical, 14–34 mm long, approx. 1.5 mm wide, mostly greenish to pale brown-purple and sometimes with one or both lines of dehiscence distinctly purple, glabrous, usually constricted around individual seeds, held at about 90° or less to peduncle, faintly longitudinally striate; beak 2–4 mm long. Seeds (2) 5–22, comma-shaped or suborbicular in outline, 1.6–2.3 mm long across longest axis, 1.3–1.8 mm across shortest axis, pale brown, grey or blackish, cross-ribs very prominent, being crest-like, concentric rings somewhat indistinct to distinct; elaiosome single, whitish, and extending into approx. half or all of cleft on both sides of seed, tending to be most prominent immediately to the sides of funicle, not surrounding funicle but forming along its outer side.

Distribution and habitat. *Cleome lophosperma* is endemic to the Top End of the Northern Territory, where it occurs in the general vicinity of Koolpinyah and further east towards the Adelaide River crossing of the Arnhem Highway. It has been recorded from low-lying, seasonally inundated low open woodland dominated by *Grevillea pteridifolia*, *Melaleuca nervosa* and *Pandanus spiralis*, with *Dapsilanthus* sometimes common in the herb understorey; always growing in sand or very sandy loam.



Fig. 7. Holotype specimen of *Cleome lophosperma* sp. nov. (P.S. Short 5155, DNA D172220).

Flowering and fruiting. December to March.

Remarks. Included within the circumscription of this species are two collections (Harwood 1230, Short 5143) which have immature seeds and an undeveloped elaiosome, but which appear to be developing prominent cross ribs. Examination of immature and mature seeds from single plants in other collections indicates that the elaiosome is late-developing in the species. Therefore, I have no doubt that the aforementioned specimens belong to *C. lophosperma*.

Cleome tetrandra s. str., as its name suggests, has four stamens, a feature it shares with *C. lophosperma* and a number of other undescribed entities which I refer to the *C. tetrandra* group. The question must be asked as to whether *C. tetrandra* and *C. lophosperma* are distinct.

Candolle (1824) indicated that he described *C. tetrandra* from a specimen in the Joseph Banks' herbarium in BM. At the Natural History Museum, London website it is recorded that in 1985 the taxonomist, H.H. Iltis, identified a specimen gathered by Banks and Solander and numbered BM 629036 as the holotype specimen of the name *C. tetrandra*. I have not viewed this specimen. Candolle's (1824) description is brief and of little value. It lacks any description of the seed, but if accurate then material of *C. lophosperma* must

be excluded from *C. tetrandra* s. str. by virtue of plants being described as glabrous (they are mostly glabrous in *C. lophosperma*) and having 3-foliolate leaves in which the leaflets are 2–3 lines long (i.e. about 4.2–6.3 mm long). In *C. lophosperma* they are 4–35 mm long. Candolle (1824) also stated that the capsules are sessile, which they are not in *C. lophosperma*, but it may be that he was referring to the lack of a gynophore, not the lack of a pedicel.

There is a specimen held in the Candolle Prodrum Herbarium (G-DC) (seen on IDC microfiche 800/121) with an annotation indicating that it was sent from the Banks' herbarium by Robert Brown in 1819. If it is an isotype specimen then the two plants which comprise it are not in agreement with the description as, although the photograph lacks a scale, the leaflets appear to be in accord with *C. lophosperma* in size and shape and, although plants are fewer-branched and have apparently ascending branches, are not unduly dissimilar in general appearance to specimens of *C. lophosperma*.

As *C. lophosperma* is quite localised, has a distinctive combination of characters and seeds with uniquely crest-like cross ribs (Fig. 2O,P) not seen in other Northern Territory material, and because the type of *C. tetrandra* was collected from a coastal or near-coastal location in Queensland, I do not doubt that it is a distinct species.

Conservation status. Unless it is in full bloom, this species can be difficult to detect amongst other herbs and thus its range may be wider than currently known. Lack of a species-specific survey in areas of potential habitat – of which there is much – and the inconspicuous nature of the flowers suggest that in regard to the IUCN criteria (Standards and Petitions Working Group 2006) for the conservation category of a species, *C. lophosperma* is best classified as Data Deficient.

Etymology. The epithet *lophosperma* is a Greek compound word derived from *lopho-* (crest-) and *-sperma* (seed) and it refers to the distinctive, crest-like cross-ribs of the seed.

***C. microaustralica* H. H. Iltis, 1982**

(Fig. 6A–C)

TYPE. Australia, Northern Territory, South Bay, Bickerton Is., Gulf of Carpentaria. 14 June 1948, R.L. Specht 552 (HOLOTYPE: K, n.v.; ISOTYPES: AD, CANB n.v., GH n.v., PERTH n.v., US n.v., WIS n.v.).

Synonymy.

Cleome viscosa auct. non L.: Benth., *Flora australiensis* 1: 91 (1863), p.p.

Illustrations. Brennan, *Wildflowers of Kakadu* 22 (1986), as *C. viscosa*; Brock, *Top End Native Plants* 122 (1988 and subsequent reprints, incl. as *Native Plants of Northern Australia*), as *C. viscosa*.

Specimens examined. NORTHERN TERRITORY: approx. 16 km S of Oenpelli, 15 February 1973, L.G. Adams & C.R. Dunlop 2980 (DNA); near (NW of) Katherine, 26 April 1947, S.T. Blakc 17496 (DNA); Kakadu

National Park, Little Nourlangie Rock, 1 March 2004, K.G. Brennan 6121 (DNA); Kakadu National Park, Graveside Gorge, 19 March 2004, K.G. Brennan 6210 (DNA); upper Jim Jim Creek, 15 March 2009, K.G. Brennan 7904 (DNA); Mt Callanan, 11 April 1977, G. Brown (DNA D11397); Katherine Gorge, 16 January 1967, N. Byrnes 68 (DNA); Katherine Gorge, 5 May 1968, N. Byrnes 677 (DNA); Waterfall Creek, South Alligator River, 5 January 1972, N. Byrnes 2447 (DNA); Kakadu Hwy, Moline Creek, 19 March 1987, M.J. Clark 832 (DNA); 4 km NNE of Koongarra, near Buffalo Springs, Mt Brockman, 22 May 1980, L.A. Craven 5769 (DNA); Mt McMinns Stn, E of turnoff to Roper Bar, 20 March 2002, D.J. Dixon 1007 (DNA); Little Nourlangie Rock, 17 March 1978, C.R. Dunlop 4709 (DNA); approx. 70 km NE of Pine Creek, El Sharana Road, 5 March 1985, C.R. Dunlop 6767 (DNA); Kakadu National Park, 22 April 1990, C.R. Dunlop 8578 (DNA); 17 km SE of Twin Falls, 20 March 1988, R. Fensham 696 (DNA); Jim Jim Falls, 3 December 1989, P.I. Forster 6124 (DNA); Nourlangie Rock, 4 July 1973, N.M. Henry 877 (DNA); Mt Brockman outlier, 15 km SE of Jabiru, 20 April 1989, R.W. Johnson 4654 (DNA); approx. 7.5 miles SE of Mt Gilruth, 28 February 1973, M. Lazarides 7925 (DNA); Bickerton Is., South Bay, 7 May 1993, G.J. Leach 3717 (DNA); Nitmiluk National Park, 8 February 2001, C.R. Michell 3370 (DNA); 25 km from Jabiru towards Oenpelli, 20 May 1988, A.A. Munir 5775 (DNA); Katherine Gorge, 27 April 1972, J. Must 976 (DNA); UDP Falls, 13 January 1973, J.L. McKean B869 (DNA); Plum Tree Creek crossing, Kakadu National Park, 1 February 1989, K. Menkhurst 235 (DNA); near Cannon Hill, Kakadu National Park, 14 March 1983, J. Russell-Smith 523 (DNA); Kakadu National Park, 29 January 1984, J. Russell-Smith 1041 (DNA); upper East Alligator River region, 25 April 1988, J. Russell-Smith 5350 (DNA); Kakadu National Park, Nawalandja, 16 April 1992, J. Russell-Smith 8642 (DNA); Kakadu National Park, 10 km ESE from the junction of Katherine River and Gimbat Creek, 18 Apr. 1990, A.V. Slee & L.A. Craven 2542 (DNA); Bardalumba, Groote Eylandt, 31 May 1977, J. Waddy 693 (DNA); gorge between Twin Falls & Jim Jim Falls, 24 March 1984, G. Wightman 1300 (DNA).

Description. Herb or subshrub to approx. 1 m tall, beset with stalked glandular hairs and somewhat viscid, hairs variable in length, approx. 0.2–1.5 (2.3) mm long.

Leaves mostly 3–5 (6)-foliolate, upper ones unifoliate; petioles mostly 10–50 (75) mm long, upper unifoliate leaves often sessile or almost so and approx. 10 mm long and 1 mm wide. Leaflets sessile or shortly petiolulate, elliptic to narrowly elliptic, lanceolate to narrowly lanceolate or linear-lanceolate, or oblanceolate to narrowly oblanceolate, 10–50 (57) mm long, (1) 3–9 (13) mm wide, entire, apex commonly acute but sometimes obtuse and even slightly emarginate with obtuse to acute leaves often on the one plant, glandular hairy and sometimes slightly viscid.

Inflorescence terminal raceme of 4–10 or more flowers, each flower subtended by 1 leaf, leaves reducing in size and becoming single foliate and bract-like towards apex; pedicels to approx. 12 mm long, with stalked glandular hairs. Sepals narrowly elliptic, lanceolate, narrowly oblanceolate or somewhat linear, 10–15 mm long, 1–2.3 mm wide; apex acute to acuminate, green or reddish and often manifestly so in about lower half or more, glandular hairy. Petals somewhat spatulate, 15–23 mm long, 4.7–8.5 mm wide, all 4 erect, with 1 claw approx. one-third length of petal, mostly yellow throughout and pale yellow or whitish on drying but at least basal part of claw may be red-orange, occasionally 1 or 2 red-orange bands may be present in middle 2 petals (see below). Stamens 12–22, unequal; filaments free, 10–23 mm long, longest in flower approx. 5–8 mm longer than shortest, commonly reddish or purple; anthers 1.8–2 mm long, becoming curved. Gynophore obscure at anthesis. Ovary glandular-hairy.

Capsules on pedicels 8–17 mm long and with gynophores to approx. 2 mm long, subcylindrical, 20–110 mm long, approx. 2–3 mm diameter, commonly held well above 90° to peduncle, straight to distinctly curved, densely glandular-hairy with hairs often all short but sometimes highly variable in length, approx. 0.2–0.65 mm long; beak 7–14 mm long. Seeds approx. 80 or more, in large capsules, somewhat comma-shaped or suborbicular, 1.1–1.5 mm across longest axis, 0.95–1.2 mm across shortest axis, brown, dark red-brown, or dark purple-brown, concentric rings absent or faint but with prominent cross-ribs; elaiosome single, prominent and thick and mostly restricted to around funicle and extending less than halfway into cleft.

Distribution and habitat. *Cleome microaustraliana* was described from Bickerton Island and is also found on Groote Eylandt and sandstone regions in and near Kakadu and Nitmiluk national parks. All such collections are to the north and north-west of *C. limmenensis*, to which it appears most closely related.

It is a species of sandstone outcrops commonly dominated by eucalypt–spinifex woodland.

Flowering and fruiting. Recorded from January to July.

Remarks. As defined here, the species is quite variable and specimen records indicate a disjunction of 250 km or more between populations from Groote Eylandt and Bickerton Island (the type locality) and other collections from central Arnhem Land. There is considerable variation in leaf shape and petiole length but I suspect that, at least in part, this reflects variation in habitat and whether plants have resprouted after fire. Hair length varies considerably within a plant but is particularly variable in Brennan 6121, where the shortest hairs on the stems are only about 0.15 mm long and the longest nearly 2.5 mm. Furthermore, as noted in the description above, all four petals are usually yellow throughout except for a darkening of the claw. However,

the illustration in Brennan (1986: 22) shows two red-orange bands on each of the inner petals, there being a band just above the claw and, above that, a narrower, irregular, semicircular band. In Brennan 7904 the two inner petals have just a single, narrow, irregular orange-red band above the claw.

Conservation status. *Cleome microaustraliana* is widespread in the central and eastern parts of Arnhem Land, including Kakadu and Nitmiluk national parks, and following the IUCN criteria (Standards and Petitions Working Group 2006) for the conservation category of a species should be classified as one of Least Concern.

KEY TO SPECIES OF *CLEOME* FOUND IN THE NORTHERN TERRITORY

This key is to species whose names are accepted under the rules of the International Code of Botanical Nomenclature (McNeil *et al.* 2006). Thus, it excludes the distinctive perennial entity from Flying Fox Creek referred to above. It also excludes one of several taxa which will key to the *C. viscosa* group, this being a large-flowered, coastal entity to which the name *Polanisia viscosa* var. *grandiflora* Benth. (Bentham 1963) may or may not apply. The combination does not exist in *Cleome viscosa* while the combination *C. grandiflora* (Benth.) F. Muell. (1886) is illegitimate, being a later homonym. The circumscription of the latter taxon is somewhat unclear but similar specimens are found along much of the northern Australian coastline, including many near-coastal islands off the Top End, where it commonly frequents sand dunes. It is curated in the Northern Territory Herbarium under the phrase-name '*Cleome* sp. large coastal (Barritt 1797)'.

A specimen which does not key out as a recognised species should key to either the *C. viscosa* species group or the *C. tetrandra* species group. Specimens referred to the *C. viscosa* species group have seeds which lack an elaiosome. Usually, if not always, they have more than ten stamens per flower – none of which are held in distinct pairs – and petals appearing to be held in a circle (albeit a cross-shaped arrangement) or half-circle (Fig. 1S,T). Specimens attributed to the loosely-defined *C. tetrandra* group, which includes *C. bundeica*, *C. insolata*, *C. linophylla* and *C. lophosperma*, should have seeds with one or two elaiosomes, fewer than ten stamens – with two or more usually held in distinct pairs – and all four petals either held erect (as in Fig. 1C,G) or arranged in a cross, with two pointing up and two down (as in Fig. 1K,N).

Species marked with an asterisk are naturalised weeds. Illustrations of taxa additional to those described in this paper are included in Fig. 1 to show some of the morphological variation referred to in the key.

- 1a. Leaves in basal rosette *C. oxalidea*
 1b. Leaves cauline..... 2
- 2a. Stipules spinescent..... 3
 2b. Stipules absent or not spinescent 4
- 3a. Petals less than 10 mm long; leaves 3-foliolate.....
 **C. aculeata*
 3b. Petals more than 10 mm long; leaves 5–8-foliolate .
 **C. sesquiorygalis*
- 4a. Stems and leaves with sessile or near-sessile glandular
 hairs, when visible their stalks are stout and rarely
 as long or very slightly longer than the length of
 the globular heads (Tanami region; leaflets obovate,
 2.5–9 mm long; petals erect; stamens 6 in 3 pairs) .
 *C. uncifera*
 4b. Stems and leaves glabrous or with a sparse to dense
 cover of distinctly-stalked glandular hairs, if sessile
 or near-sessile glandular hairs present then so too are
 long-stalked glandular hairs in which the stalk is at
 least twice the length of its globular or subglobular
 head 5
- 5a. Stamens connate in at least their lower half 6
 5b. Stamens free or almost so 7
- 6a. Petals 50–100 mm long *C. cleomoides*
 6b. Petals 5–20 mm long..... **C. gynandra*
- 7a. Petals mostly or only coloured pink or mauve
 **C. rutidosperma*
 7b. Petals mostly or only coloured yellow or white 8
- 8a. Seeds lacking elaiosomes; flowers probably always
 with the four petals erect and forming a semi-eirele
 or near-complete eirele around the ovary (Fig. 1S,T)
 *C. viscosa* group
 8b. Seeds with 1 or 2 elaiosomes; flowers with the petals
 erect (Fig. 1C,D,G,H) or two petals erect and two
 pointing down (Fig. 1J,K,N)..... 9
- 9a. Flowers with all petals erect (Fig. 1C,D,G,H).....
 10
 9b. Flowers with two petals erect and two pointing down
 (cross-shaped arrangement) (Fig. 1J,K,N).....
 (*C. tetrandra* group) 14
- 10a. Stamens (9) 12 to approx. 20 11
 10b. Stamens 5 or 6 (7) (*C. tetrandra* group) 12
- 11a. Seed with 2 elaiosomes, one on either side of the
 funicle; leaflets with obtuse or emarginate apices, at
 least the upper leaves often very viscid (Fig. 2D–F)
 *C. limnenensis*
 11b. Seed with a single elaiosome extending around the
 funicle; leaflets with obtuse to acute apices, the upper
 leaves usually not manifestly viscid (Fig. 2A–C)
 *C. microaustralica*
- 12a. Seeds with wart-like protuberances on their surface
 and a single elaiosome extending around the outer
 surface (Fig. 1E–H)..... *C. insolata*
 12b. Seeds lacking wart-like protuberances, elaiosome(s)
 not as above..... 13
- 13a. Plants with leaflets ovate or obovate, 5–24 mm long,
 2–10 mm wide, emarginate; stamens 6 in 3 pairs;
 elaiosome single (Fig. 1A–D)..... *C. bundeica*
 13b. Plants lacking the above combination of characters.
 *C. tetrandra* group
- 14a. Leaves entire (1-foliolate) and linear; elaiosomes 2
 (Fig. 1L–N) *C. linophylla*
 14b. Leaves 3- or 5-foliolate, at least near the base of the
 plant, entire leaves may also be present; elaiosomes
 probably only 1, perhaps 2 in some entities 15
- 15a. Seeds with very prominent, erect-like cross ridges
 (Fig. 1O,P) *C. loposperma*
 15b. Seeds with low cross-ridges..... *C. tetrandra* group

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Taxonomic revision of the order Halichondrida (Porifera: Demospongiae) of northern Australia. Family Dictyonellidae

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ABSTRACT

Eight species in five genera of the family Dictyonellidae, including one new species (*Dictyonella chlorophyllacea* sp. nov.), are recorded for northern Australia as part of a revision of the order Halichondrida in this region. The genera *Dictyonella*, *Phakettia* and *Scopalina* represent new records for the region. *Dictyonella sensu stricto* and *Phakettia* have not been recorded in Australian waters previously. All the species reported here are common throughout northern Australia and are more widely distributed in the Indo-Pacific Ocean. Descriptions and discussion of those species are presented here. Lectotypes for *Acanthella carteri* Dendy, 1889 and *A. aurantiaca* Keller, 1889 are designated.

INTRODUCTION

The family Dictyonellidae was revised by Van Soest *et al.* (2002). It is a relatively new family erected within the order Halichondrida to receive a group of genera included in the polyphyletic former order Axinellida (Van Soest *et al.* 1990; Van Soest 1991). It currently includes 10 genera and approximately 86 species segregated amongst the genera as follows: *Acanthella* (30 species); *Dictyonella* (12 species); *Liosina* (3 species); *Lipastrothethya* (4 species); *Phakettia* (5 species); *Rhaphoxya* (8 species); *Scopalina* (12 species); *Stylissa* (14 species); *Svenzea* (5 species); *Tethyspira* (1 species) (Van Soest *et al.* 2008). The species of this family are characterised by the lack of an ectosomal skeleton, a fleshy or 'cartilaginous' appearance and a dendritic-halichondroid choanosomal skeleton composed mainly of styles, but complemented with oxas and/or strongyles in several species.

Some dictyonellid genera such as *Acanthella* and *Stylissa* include polyphyletic assemblages of species, which compromises the integrity of the family as a monophyletic taxon. Based on the definitions given in *Systema Porifera* (Hooper & Van Soest 2002), species of *Acanthella*, formerly a genus of the Axinellidae, have been consistently mistaken for the axinellid genus *Phakellia* (e.g. *Phakellia dendyi* Bergquist) and vice-versa (e.g. *Phakellia cavernosa* (Dendy)). Equally, species of *Stylissa* have been mistaken for *Anletta* (e.g. *Auletta constricta* Pulitzer & Finali), *Axinella* (e.g. *Axinella carteri* (Dendy), *A. massa* Carter), *Phakellia* (e.g. *Phakellia conulosa* Dendy), *Acanthella* (e.g. *Acanthella inflexa* Pulitzer and Finali), and with the halichondrid genus *Hymeniacidon* (e.g. *Hymeniacidon conulosa*). The taxonomic confusion among these genera is one of the reasons for the long-lasting debate regarding

the monophyly of Halichondrida and its families, including Dictyonellidae (see Alvarez *et al.* 2000; Erpenbeck *et al.* 2005b; Erpenbeck & Van Soest 2005; Erpenbeck *et al.* 2006). Phylogenetic studies based on molecular data also showed the family as non-monophyletic (e.g. Alvarez *et al.* 2000; Erpenbeck *et al.* 2005a, 2005b, 2006). Regional taxonomic revisions have an important role for the understanding and definition of these groups of genera which are characterised by very few and apparently simplistic characters, and which include species with a high degree of morphological variability, and such revisions are expected to produce additional knowledge to clarify the classification of Halichondrida.

The present paper represents the second contribution of the revision of the order Halichondrida in the northern Australian region, and it includes only the family Dictyonellidae. Alvarez & Hooper (2009) have already provided a detailed and extended introduction to the order and the family Axinellidae. Revision of the two remaining families represented in the region, Halichondriidae and Heteroxyidae, will follow in subsequent papers.

MATERIALS AND METHODS

This revision is restricted to material of Dictyonellidae from the tropical northern Australian waters of the Northern Territory and Queensland coast, from the Admiralty Gulf in the west to Torres Strait in the east, approximately between 125° E and 142° E (Alvarez & Hooper 2009: Fig. 1). It does not extend into the species-rich areas of the Great Barrier Reef or the Northwest Shelf of the northeastern and northwestern Australian coasts, respectively. These regions are the subjects of future studies on their poriferan faunas.

Complete locality and collection data for non-type voucher material deposited at the Queensland Museum and the Museum and Art Gallery of the Northern Territory are listed in the Appendix. The distribution of species is given according to the marine provinces defined by Spalding *et al.* (2007). Measurements of spicules are based on 25 spicules (unless indicated in square brackets) and denoted as range (and mean \pm 1 S.E.) of spicule length and width. All other methods are as presented in Alvarez & Hooper (2009).

ABBREVIATIONS

Abbreviations used in the present paper are: AIMS, Australian Institute of Marine Sciences; BMNH, Natural History Museum, London (formerly British Museum (Natural History)); CRRF, Coral Reef Research Foundation, Palau; GBR, Great Barrier Reef, Queensland, Australia; MAGNT/NTM, Museum and Art Gallery of the Northern Territory (formerly Northern Territory Museum), Darwin; NT, Northern Territory, Australia; MNHN, Muséum national de Histoire Naturelle, Paris, France; MSNG, Museo Civico di Storia Naturale 'Giacomo Doria', Genoa, Italy; SMF, Senckenberg Research Institute and Natural History Museum, Frankfurt; QLD, Queensland, Australia; QM, Queensland Museum, Brisbane; WA, Western Australia, Australia; ZMA, Zoologisch Museum, University of Amsterdam; ZMB, Museum für Naturkunde und der Universität Humboldt zu Berlin, Berlin, Germany.

Numbers with Q666C, 0CDN, 0M9H prefixes are the cross-reference sample numbers collected for the United States National Cancer Institute, under the 'Collection of Shallow-water Organisms' program, by the Australian Institute of Marine Sciences, CRRF and MAGNT (subcontracted through CRRF) respectively.

TAXONOMY

Family Dictyonellidae Van Soest, Diaz & Pomponi, 1990

Genus *Acanthella* Schmidt, 1862

Gender feminine. Type species, by monotypy, *Acanthella acuta* Schmidt, 1862. Recent, Adriatic Sea.

Acanthella cavernosa Dendy, 1922

(Figs 1, 2A,B; Table 1)

Acanthella cavernosa Dendy, 1922: 120; Van Soest 1989; Hooper *et al.* 1992 [in part]; Alvarez *et al.* 2000: 195. Not Burton 1934: 565 and Hooper & Lévi 1993: 1414, fig. 13B–D [= *Acanthella klethra* Pulitzer-Finali, 1982: 93]. Not Alvarez *et al.* 2007 [= *Acanthella pulcherrima* Ridley & Dendy, 1886].

Acanthella pulcherrima.—Capon & Macleod 1988.

Acanthella ? *stipitata*.—Ridley & Dendy 1887: 178.

Material examined. TYPE MATERIAL.—*Acanthella cavernosa*: HOLOTYPE, BMNH 1921.11.7.100, Amirante,

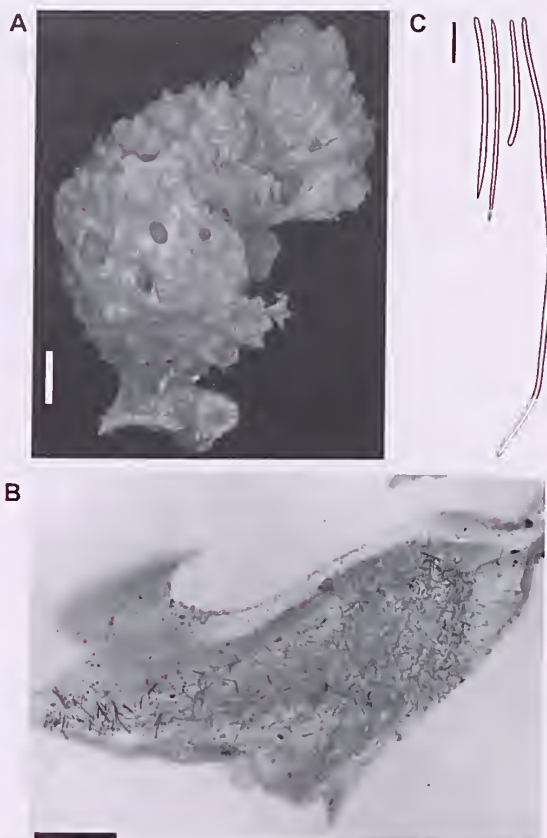


Fig. 1. *Acanthella cavernosa*: A, Holotype, BMNH 1921.11.7.100. B, light micrograph of skeleton (BMNH 1921.11.7.100). Scale bars: A, 2 cm; B, 500 μ m, C, 100 μ m.

60 m depth, 17 October 1905, coll. HMS Sealark (Fig. 1A). ADDITIONAL SPECIMENS.—Burton's record, BMNH 1930.8.13.142, off North Anchorage, 18 m depth, 17 October 1928, coll. Great Barrier Expedition, Agassiz trawl. Ridley & Dendy's record, BMNH 1887.5.2.73, off Cape York, Torres Strait, 8 September 1874, coll. HMS Challenger. *Acanthella klethra* Pulitzer-Finali, 1982: Holotype MSNG CE 46927, Wistari Reef (Capricorn Group), 7 m depth, 24 April 1979; paratype MSNG CE 46928, Heron Island, reef slope, "Blue Pools" area, 15 m depth, 23 August 1980; paratype MSNG CE 46929, Heron Island, north reef slope, "Blue Pools" area, 15 m depth, 3 October 1979. *Acanthella xutha* (De Laubenfels, 1954), holotype, USNM 23097, Caroline Islands, Truck Islands, Kuop atoll, 2 m depth, 17 August 1949, coll. M.W. De Laubenfels. Indian Ocean: ZMA Por. 10989, -5.6833, 53.5833, Seychelles, Ile Desroches, Atoll, W. rim, 10 m depth, 30 December 1992, coll. R.W.M. van Soest. Papua New Guinea: G312925, Z.3572. Darwin Harbour: G303338, Z.2092, Z.2633, Z.5168 (0M9H2086-K), Z.5856, Z.5871. Wessel Is; Z.5172 (0M9H2702-F). Malaysia: Z.5861–Z.5862, Z.5866–Z.5868. Gulf of Carpentaria, G303512.

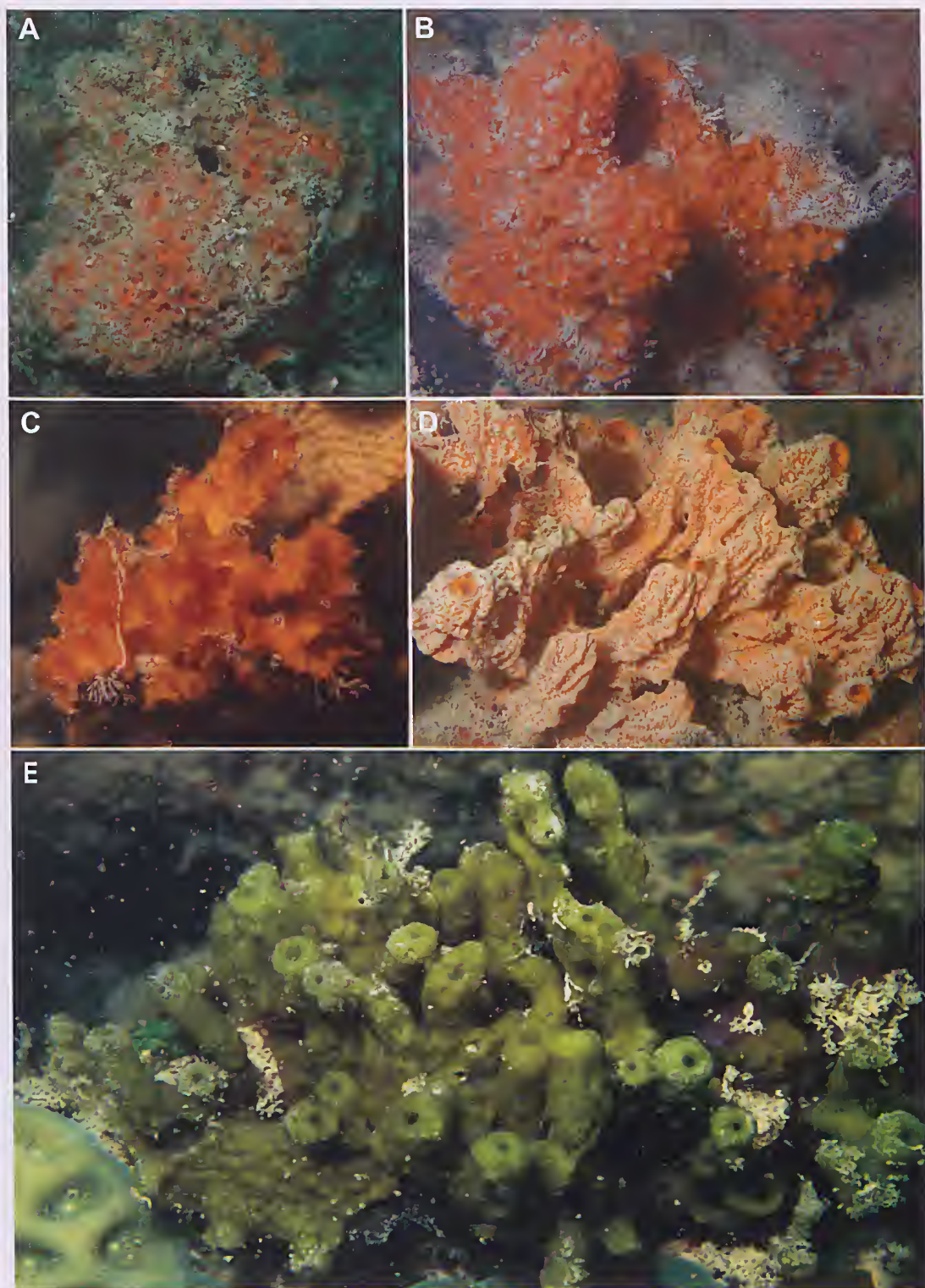


Fig. 2. *Acanthella cavernosa*: A, specimen at Rimbija I., Wessel Is; B, specimen *in situ* in Darwin Harbour. *Acanthella pulcherrima*: C, Z.5870 *in situ* in Darwin Harbour; D, specimen *in situ* in Raragala I., Wessel Is. *Dietyonella chlorophyllacca* sp. nov.: E, specimen *in situ* in Darwin Harbour. Photographs: A,B,E – M. Browne; C – B. Alvarez; D – P. Colin.

Description. Shape. (Figs 1A, 2A,B) Variable with 3 basic morphotypes: massive to semi-spherical; bushy with flat-spikey branches arising from multiple bases or from short peduncle, with crowded and complex branching, or in honeycombed reticulation; lobate-tubular with thick lobes joined at base. Transitional forms between these morphotypes in any combination are common.

Colour. Generally orange, but beige specimens also found (e.g. G303512); beige in alcohol

Oscula. Terminal at lobes or branches, with membranous rims slightly elevated, less than 10 mm in diameter; or flushed and irregularly distributed. Minute ostia aggregated in surface grooves.

Surface. Clathrate, rubbery, cartilaginous membranous skin with blunt or spikey short conules, irregularly or evenly distributed, fused laterally forming ridges; sometimes with shallow grooves of irregular shape.

Skeleton (Fig. 1B). Cavernous, with dendritic and ascending axes of interwoven spicules echinated by single spicules or short tracts.

Spicules (Fig. 1C, Table 1). Strongyles thick and thin (mostly broken), 430–1824 (or longer) \times 2–15 μ m. Styles straight, slightly bent or curved, 262–1402 \times 3–21 μ m. Styles in same size category with rounded ends, slightly sinuous, or bent near base, less frequent. Anisoxeas transitional to styles, less frequent, 310–798.44 \times 5–15 μ m.

Remarks. The holotype of *Acanthella cavernosa* was re-examined (Fig. 1A). The specimen is globular to elongated, 8 cm high by 5 cm maximum width, attached to a narrow and short base, soft and compressible. Its surface is marked by thick choanosomal fibres projecting in short and blunt conules, up to 2 mm long, organised in longitudinal rows in some areas. An organic, slightly transparent membrane stretches over the conules and

fibres. The oscules are irregularly distributed, conspicuous, up to 5 mm in diameter, flush and opening at the surface membrane. The external morphological features of the species are however much more variable as shown in the material examined. Several morphotypes can be identified among the specimens we have studied, but as in other species of Halichondrida, particularly those of Axinellidae (e.g. *Axinella arnensis*; Alvarez & Hooper 2009), they cannot be easily separated, but placed into a gradient of variation with intermediate forms that share a combination of characteristics. Skeletal features and spicule composition and dimensions in *Acanthella cavernosa* seem to be more homogeneous among the material we studied and these allow its differentiation from other very similar species such as *Acanthella pulcherrima* (see below).

The specimen from the GBR recorded by Burton (1934) was also re-examined and compared to additional material from the GBR and Palau. All of these specimens are similar in external morphology to *Acanthella cavernosa* but they differ from this species in skeletal architecture. They are characterised by the presence of fragile (always broken in microscopic slide preparations) and thin strongyles interwoven in the main skeletal axes (appearing as hair-lines in the sections) and lightly bounded by ill-defined spongin fibres, and styles with oxocote modifications. We conclude that these specimens are conspecific with *Acanthella klettra* Pulitzer-Finali, 1982 from the GBR, a species included as a synonym of *Acanthella cavernosa* Dendy, 1922 by Hooper & Wiedenmayer (1994), but considered here as valid. *Acanthella klettra* is also very similar to a central Pacific species, *Axinella xutha* De Laubenfels, 1954, but examination of the type material indicates that the species is better allocated to *Acanthella*, and is likely to be conspecific with Pulitzer-Finali's species (which would make De

Table 1. Comparison of spicule dimensions among specimens of *Acanthella cavernosa*. Measurements in micrometres.

Specimen	Locality	Strongyles	Styles	Anisoxeas
BMNH 1921.11.7.100	Amirante, Indian Ocean	779.6–1824.8 (1046.7 \pm 194) \times 4.7–11.4 (7.5 \pm 1.7)	306–509.8 (416.3 \pm 60) \times 7–21.4 (15.3 \pm 4.5)	
BMNH 1887.5.2.73	Torres Strait	undetermined broken \times 2.9–6.7 (4.8 \pm 1)	270.7–745.1 (431 \pm 108) \times 4.8–13.6 (8.8 \pm 1.7)	
ZMA Por. 10989	Seychelles Is	520–1400 (901 \pm 285.6) [10] \times 8–15 (11.2 \pm 2.1) [10]	303–740 (427.2 \pm 87.9)	310–670 (436.3 \pm 85.5) [16] \times 5–15 (9.1 \pm 2.1) [16]
G312925	Papua New Guinea	466.04–1430.35 (977.12 \pm 222.58) \times 3.05–11.11 (8.04 \pm 1.99)	312.11–1402.77 (510.56 \pm 279.19) \times 3.78–12.68 (7.85 \pm 2.15)	355.43–798.44 (500.47 \pm 202.72) [4] \times 6.8–9.93 (8.28 \pm 1.29) [4]
Z.5861	Malaysia	571.94–996.2 (780.42 \pm 105.42) \times 4.74–11.14 (6.94 \pm 1.64)	277.57–645.4 (446.96 \pm 86.35) \times 5.97–12.06 (9.05 \pm 1.43)	
Z.5856	Darwin Harbour	636.7–1200.21 (851.4 \pm 139.91) \times 2.34–8.92 (4.8 \pm 1.76)	262.54–682.41 (446.48 \pm 107.51) \times 5.39–12.79 (8.31 \pm 1.94)	
Z.5172	Wessel I	s430.03–1115.64 (804.07 \pm 164.79) \times 3.7–14.05 (8.22 \pm 2.12)	279.86–1031.29 (465.99 \pm 147.72) \times 3.05–13.19 (8.67 \pm 2.72)	

Laubenfels' name the senior synonym). At this stage we prefer to keep the species separate, until more material from the central West Pacific can be examined and compared to the type material.

The identity of the specimen identified as *Acanthella* ?*stipitata* by Ridley & Dendy (1887) [not *A. stipitata* Carter, 1881] remains enigmatic. Both the external form and the skeleton resemble also *Acanthella klethra*. The strongyles in this specimen are thin and mostly broken, thus their average length is unable to be determined. The skeleton is slightly halichondroid with poor definition of the ascending axes of the strongyles. Ridley & Dendy were uncertain in the generic allocation of this specimen and compared it with *Acanthella stipitata* (Carter) pointing out the similarities in the spicule composition, but they also commented on the similarity in external form with *Clathria (Thalysias) vulpina* and indicated affinities with the genus *Echinoclathria*.

Distribution. The species is widely distributed, with validated records in several marine provinces: Western Indian Ocean (Scyehelles), Sahul Shelf (Bonaparte Coast, Arnhem Coast to Gulf of Carpentaria), Western Coral Triangle (North Borneo and Indonesian ecoregions),

Eastern Coral Triangle (Southeast Papua New Guinea) and Northeastern Australian shelf (Coral Sea).

It is common in shallow waters between 5–20 m depth, but recorded also from deeper waters (down to 60 m, from where the holotype was collected).

Acanthella pulcherrima Ridley & Dendy, 1886

(Figs 2C,D, 3; Table 2)

Acanthella pulcherrima Ridley & Dendy, 1886: 479; Ridley & Dendy 1887: 177; Alvarez *et al.* 2000: 195. Not Lévi 1998: 103. Not Capon & Macleod 1988 [= *Acanthella cavernosa* Hooper & Wiedenmayer, 1994]. Not *Acanthella pulcherrima* var. *calyx* Dendy, 1922: 120.

Acanthella sp.– Ridley 1884: 463.

Phakellia pulcherrima – Hooper & Lévi 1993: 1415 [in part]; Hooper & Wiedenmayer 1994:78.

Acanthella cavernosa – Hooper *et al.* 1992 [in part]; Alvarez *et al.* 2007.

Material examined. TYPE MATERIAL – *Acanthella pulcherrima*: HOLOTYPE – BMNH 1887.5.2.23, Prince of Wales Chanel, Torres Strait, northern Queensland, 14.5 m depth, 8 September 1874, coll. HMS Alcrt (Fig. 3A);

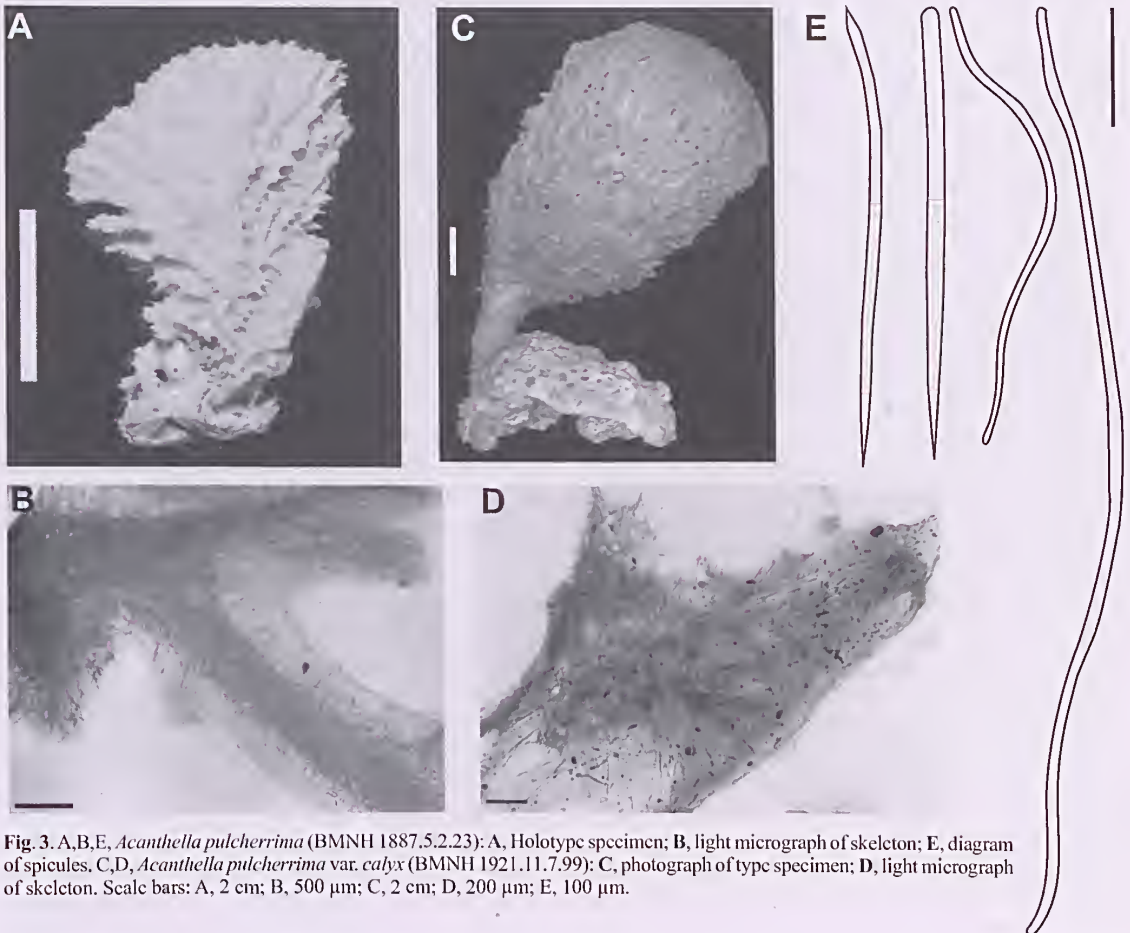


Fig. 3. A,B,E, *Acanthella pulcherrima* (BMNH 1887.5.2.23): A, Holotype specimen; B, light micrograph of skeleton; E, diagram of spicules. C,D, *Acanthella pulcherrima* var. *calyx* (BMNH 1921.11.7.99): C, photograph of type specimen; D, light micrograph of skeleton. Scale bars: A, 2 cm; B, 500 µm; C, 2 cm; D, 200 µm; E, 100 µm.

Acanthella pulcherrima var. *calyx*, BMNH 1921.11.07.099 (Fig. 3C), Cargados Carajos, Indian Ocean, 55 m depth, 28 March 1905, coll. Sealark expedition. OTHER MATERIAL – Hooper & Lévi's (1993) record: G300019, Stn. 102, mid-channel, Canal Woodin, SW. lagoon, 22:23:01' S, 166:48:01'E, New Caledonia, 33 m depth, 28 April 1976, coll. P. Laboute, ORSTOM Noumea. Ashmore Reef, Hibernia Reef and Cartier Reef. WA: G301053, G301091, G301155, Z.2751; Bynoe Harbour: Z.4461 (0M9H2365-N), Z.4487, Z.4489; Z.5169 (0M9H2397-W). Darwin Harbour: G300174, G303386, G303391, Z.429, Z.961 (brown in alcohol), Z.1968, Z.2021, Z.2155, Z.2192, Z.2251, Z.2379, Z.2706, Z.2720, Z.5857, Z.5858, Z.5865, Z.5870; Cobourg Peninsula: Z.2533; English Company Is: Z.3954, Z.3960; Wessel Is: Z.3924, Z.5170 (0M9H2649-V), Z.5171 (0M9H2679-F); eastern Arnhem Land: Z.4493; Gulf of Carpentaria: G303489.

Description. Shape (Fig. 2C,D). Erect, semi-spherical or nearly globular, stalked on short or long peduncle, with foliose, bushy, lamellate, pointed or flat branches; complex and crowded branching sometimes in honeycombed reticulation, or forming lobes. Specimens 120 cm in diameter and up to 150 cm high.

Colour. Beige, pale yellow, or orange.

Oscula. Large and apical in lobate specimens, or on margins of branches, variable in size, up to 7 mm diameter, flush with membranous rims slightly elevated.

Surface. Pointed conules irregularly distributed on margins of branches or lobes; cartilaginous, with membranous skin stretching over conules and branches; marked and pierced unevenly by choanosomal spicules and tracts.

Skeleton (Fig. 3B, D). Cavernous, with thick (5–7 mm), ascending columns of interwoven megascleres, dividing irregularly or dendritically, echinated by either plumose tracts, tightly close, diverging towards surface and ending in conules or, by single spicules that occasionally project through surface. Sheets of light spongin, free of spicules, joining main ascending axes in some areas of choanosome.

Spicules (Fig. 3E, Table 2). Sinuous strongyles highly variable in size and thickness, 299–1901 x 2.2–17.9 μm ; smaller and thicker strongyles less frequent. Styles straight or slightly bent, few with rounded ends, 252.5–768 x 4.7–19.3 μm . Anisoxeas, with hastate, stepped, blunt or pointed tips, often bent at one end; sometimes slightly crooked or sinuous. Relative proportions between anisoxeas and styles is variable among individuals, but in general anisoxeas dominant.

Remarks. *Acanthella pulcherrima* was described by Ridley & Dendy (1886), based on a single specimen from Torres Strait collected during the 'Alert' expedition (Ridley 1884). The type specimen is a small fan, 35 mm high by 29 mm wide, on a peduncle, with its surface marked with longitudinal ridges, up to 3 mm high, that are regularly distributed across the fan. The examination of the northern Australian collections indicates that the external

morphology of this species is much more variable and complex than that exhibited by the holotype (see above). The skeleton and spicule composition of the material we examined corresponds closely to the holotype. Most specimens we examined, including the holotype, have anisoxeas, styles and sinuous strongyles, the latter located in the axis of the thick ascending columns that form the skeleton. The proportion of anisoxeas in relation to styles, is variable among individuals, as seen in species of the genus *Axinella* (Alvarez & Hooper 2009), but anisoxeas in general predominate and styles are less frequent or even absent, as seen in the specimens from Ashmore Reef and Cartier Island, NW Australia. *Acanthella pulcherrima* can easily be confused with *A. cavernosa*, as reflected by the numerous misidentifications reported here. Indeed the two species do share many characteristics. They are similar in shape, but *A. pulcherrima* is generally a stipitate, fan-shaped sponge with a tendency to become bushy and compact. The opposite is seen in *A. cavernosa* which is typically globular-massive shaped and some specimens develop into more erect fan-like forms. The skeletal architecture of both species is nearly identical, but in general the skeleton seems to be more regular in *A. pulcherrima* compared to a less organised skeleton in *A. cavernosa*, and the axes that form the skeleton are slightly thinner. The spicule composition is also similar between the two species, but in general the dominance of anisoxeas relative to styles allows the distinction of *A. pulcherrima* from *A. cavernosa*; the spicule dimensions are quite comparable, and the average length of strongyles is generally longer in *A. cavernosa*.

Acanthella pulcherrima was recorded from New Caledonia by Hooper & Lévi (1993) [as *Phakellia*] and by Lévi (1998). Both the external morphology and skeleton of the specimens from New Caledonia are very similar to the holotype; however, and as noted by those authors, it lacks the characteristic anisoxeas present in the holotype from Torres Strait and in the specimens examined here. The populations from New Caledonia were found to be conspecific with material recorded from Taiwan (De Voogd & Alvarez, unpublished data), and probably belong into a new species of *Acanthella* which will be described elsewhere.

The material described by Dendy (1922) from the Indian Ocean (Carjados) as *Acanthella pulcherrima* var. *calyx* [BMNH 1921.11.7.99, examined here Fig. 3C] does not agree with the northern Australian populations of this species either and is considered to be a different species. This specimen has a fleshy consistency, and it is folded into a perfect cup, approximately 7 cm high and 6 cm in diameter, on a narrow and long peduncle. The surface on both sides of the cup is fleshy with conules about 2 mm long, organised in nearly parallel and longitudinal rows. The skeleton is lax, halichondroid, bounded by a moderate amount of slightly darker collagen, occupying the whole thickness of the cup, without clear axes of wavy strongyles, echinated by styles and anisoxeas, as in the holotype of *A. pulcherrima* from Torres Strait. Styles (363.8–632.3 μm

Table 2. Comparison of spicule dimensions among specimens of *Acanthella pulcherrima*. Measurements in micrometres.

Specimen	Locality	Strongyles	Styles	Anisoxeas
BMNH1887.52.23 (Holotype)	Torres Strait	476.2–1901.4 (936.6±286.1) x 3.1–17.9 (7.2±3.2)	256.4–420 (331.2±46.1) x 6.7–11.6 (8.7±1.3)	269.1–344.2 (309.3±23) x 4.4–12.1 (8.3±1.9)
Z.2751	Ashmore Reef	213.6–944.7 (591.7±253.8) x 1.5–8.6 (4.6±2.5)	355.6–904.4 (601.7±173.8) [21] x 4.7–12.2 (7.4±1.8) [21]	247.3–420 (313±38.8) x 4.1–10.4 (6.9±2.1)
Z.4461	Bynoe Harbour	298.9–597.6 (434.8±82.5) x 2.2–7.1 (4±1.3)	288.6–701 (413±108.6) x 5.2–14.6 (10.3±2.3)	298.1–426.4 (363.7±40.5) x 8.9–14.1 (10.8±1.5)
Z.5870	Darwin Harbour	388.5–1199.8 (794.2±188.4) x 4–17.3 (9.2±2.7)	252.5–706.9 (484.7±94.5) x 9.7–19.3 (13.6±2.7)	337.9–488.4 (412.9±46.3) x 8.2–15.6 (11.6±2)
Z.2533	Cobourg Peninsula	580–1055.4 (781±199.4) [4] x 4.4–9.9 (7.9±2.5) [4]	288.4–716.5 (404.5±102.4) [20] x 7.6–16.8 (11.5±2.2) [20]	268.8–493.7 (368.1±52.9) x 7.3–15.7 (11.8±2.3)
Z.3954	English Company Is	592.2–1028.2 (895.5±144) [8] x 3.7–7 (5.4±1.2) [8]	374.1–768 (499.5±116.9) [19] x 4.7–11.2 (7.5±1.6) [19]	258.5–604.3 (364.5±94.2) x 5.4–10 (7.1±1.1)
Z.3924	Wessel Is	616.3–954.3 (763.3±96.3) [10] x 4.3–8.2 (6.2±1.3) [10]	374.3–723.2 (519.6±75.1) x 7–14.4 (10.6±1.8)	243.8–485.9 (346.4±56.9) x 4–11.3 (7.8±1.7)

(518.2±62) x 5–19.4 µm (11.2±3.2) are dominant through the skeleton and project slightly towards the surface or in sparse disorganised groups (Fig. 3D). Less frequent strongyles are found intermixed in the skeleton. Only a few strongyles up to 131.6 µm long by 5.2–8.4 µm thick were found in the slide prepared from the holotype and a few anisoxeas, measuring 448.6–492.8 µm x 10.5–10.6 µm, were also present. The specimen could be mistaken for a species of *Stylissa*, but strongyles are not included in the diagnoses of that genus (see below).

Distribution. The species is common in northern Australia with validated records from the Northwest Australian Shelf and the Sahul Shelf where it is found in shallow waters from 10–50 m depth and associated with muddy and sandy bottoms. Its distribution might also extend to the Northeast Australian shelf (Coral Sea) according to unverified records at the QM. It is also known from other localities in Indonesia (Alvarez & De Voogd, unpublished data).

Discussion on the genus *Acanthella*. The genus *Acanthella* includes 32 valid species according to the *World Porifera Database* (Van Soest *et al.* 2008). Only two of these (*A. cavernosa* and *A. pulcherrima*) are represented in northern Australia. Other species of *Acanthella* reported from Australia (Hooper & Wiedenmayer 1994) are: *Acanthella? costata* Kieschniek, 1900, a dubious species first recorded from Indonesia; *Acanthella inflexa* Pulitzer-Finali, 1982, which does not agree with the concept of the genus and is better allocated to *Stylissa* (see below); *A. klethra* Pulitzer-Finali, 1982, from the GBR, a species very similar to *A. cavernosa*, but considered here as valid after re-examination of the holotype and recent material from the GBR and Palau; and *A. tenuispicnata* Dendy, 1897 recorded from Port Phillip Heads, Victoria. Other Australian species currently accepted under *Phakellia*, mainly from southern Australia, such as *P. cardms* (Lamarek, 1814), *P. dendyi* Bergquist, 1970 and *P. stipitata* Carter, 1881, also

belong to *Acanthella*. None of the later species were found in the study area.

The plasticity of the external morphology and the similarity of skeletal architecture and composition and dimensions of the spicules in species of *Acanthella* have confused authors for decades and as a consequence species have been misidentified regularly as *Axinella* and *Phakellia*. Species of *Acanthella* fall in a gradient of variation with fuzzy limits as in other axinellid genera. The distribution of the species generally overlaps, as in the case of the northern Australian species, making the separation of species even more difficult. It is also possible that some species might be a complex of cryptic species or part of an hybridisation series.

Phylogenetic relationships derived from molecular studies (Alvarez *et al.* 2000; Erpenbeck *et al.* 2005b, 2006) show strong support (i.e. with strong bootstrap values) for some species of *Acanthella*, including the type species of the genus *A. acuta* Smith, 1862, to be closely related to species of *Cymbastela*, a characteristic genus of the Axinellidae, with cup-shaped morphology and a regular plumo-reticulated skeleton and with only oxeas. The skeleton of *Cymbastela* differs greatly from *Acanthella*, which is dendritic with the spicules densely packed in thick axes or columns and echinated either with individual spicules or short plumose tracts of spicules. The consistency of the species included in the two genera is also very different. *Acanthella* is characteristically cartilaginous and *Cymbastela* is soft and velvety. The phylogenetic relationships derived from molecular studies remain at this stage intriguing but unexplained.

Molecular genetic studies (e.g. microsatellite analyses or DNA sequences of appropriate genes) of local populations of *Acanthella* taxa are therefore essential for the delimitation of species within the genus and testing of the species hypotheses presented here. In the meantime, allocation to *Acanthella* using traditional morphological characters will remain imprecise.

Genus *Dictyonella* Schmidt, 1868

Gender feminine. Type species, by subsequent designation of De Laubenfels (1936), *Dictyonella cactus* Schmidt, 1868. Recent, Adriatic Sea.

***Dictyonella chlorophyllacea* sp. nov.**

(Figs 2E, 4; Table 3)

Material examined. HOLOTYPE – Z.5018 (0M9H2121), Weed Reef, entrance to West Arm, Darwin Harbour, 12°29.338'S, 130°48.019'E, 4–10 m depth, 2 August 2002, coll. B. Alvarez & party. PARATYPE – Z.5177 (0M9H2564-F), Nightcliff bommies, off Nightcliff jetty, Darwin Harbour, 12°22.751'S, 130°50.116'E, 5–8 m depth, 8 August 2003, coll. B. Alvarez & party. ADDITIONAL (NON-TYPE) SPECIMENS – Bynoc Harbour, Fish Reef, G303449, Darwin Harbour: QM G300220 (NTM Z.3177), NTM Z.3199, Z.5175 (0M9H2262-Z), Z.5176 (0M9H2264-C), Z.5896.

Description. Shape (Fig. 2E). Thickly lamellate (up to 20 cm) or thickly encrusting (up to 10 cm thick), with small tubular projections up to 40 mm long and approximately 5–10 mm diameter. Growing in patches approximately 25 cm in maximum diameter, following substrate.

Colour. Deep green-purple on shaded side

Oseula. Terminal on the small tubular projections.

Surface. Nodulose, with small rounded tubercles; hispid, with choanosomal spicules projecting slightly through a membranous ectosome; slightly felty texture; marked by shallow grooves irregularly shaped but sometimes running longitudinally along the tubes or branches.

Skeleton (Fig. 4A,B). Halichondroid to plumoreticulated, with longitudinal wavy multispicular tracts, generally ascending and anastomosing towards surface, irregularly connected by single spicules, or short multispicular tracts oriented in any direction. Main skeletal tracts end at surface in brushes of few spicules that project through the membranous ectosome. Skeleton at subectosomal region might become dense and quite halichondroid. Spongin is scarce.

Spicules (Fig. 4C, Table 3). Styles, often slightly sinuous or bent at base or with rounded ends, 200–438 x 5–16 µm. Twisted or sinuous oxoas, some transitional to styles, located generally at subectosomal region, less frequent and in same size category of main styles. Thin forms of styles, 2–4 µm thick, are very common in some specimens.

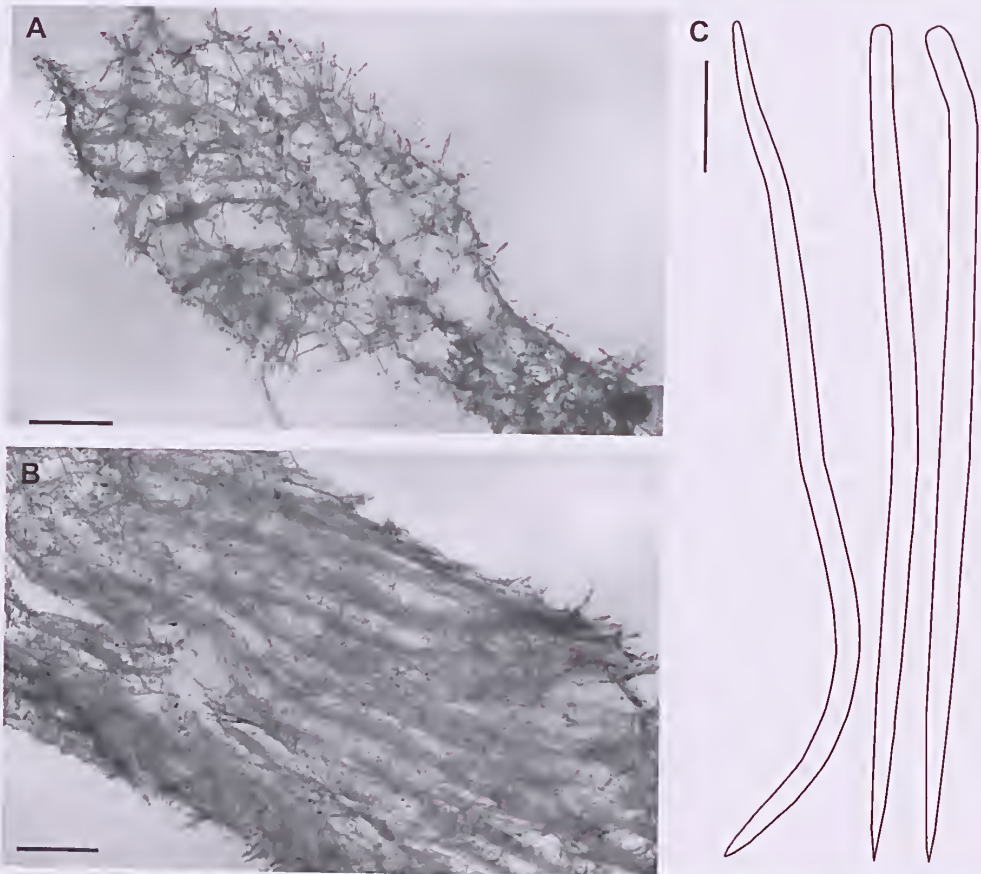


Fig. 4. *Dictyonella chlorophyllacea* sp. nov.: A, Holotype, Z.5018, light micrograph of skeleton; B, Paratype, Z.5177, light micrograph of skeleton; C, diagram of spicules. Scale bars: A,B, 500 µm; C, 50 µm.

Table 3. Comparison of spicule dimensions among specimens of *Dictyonella chlorophyllacea*. Measurements in micrometres.

Specimen	Locality	Styles
G303449	Bynoe Harbour	335.4–438.5 (374.1±30.2) x 9.2–15.8 (12.3±1.7)
Z.5018	Darwin Harbour	272.2–426.6 (379.6±38.1) x 4.8–14.8 (9.7±2.7)
Z.5177	Darwin Harbour	200.8–412.3 (344±43.7) x 4.8–12.7 (9.2±1.8)

Distribution. The species is not common in northern Australia with only isolated populations at Bynoe Harbour and Darwin Harbour. It is found between 3–12 m depth. Also known from East Kalimantan, Indonesia (Alvarez & De Voogd unpublished).

Etymology. The species is named after its ability to accumulate chlorophyll.

Remarks. *Dictyonella chlorophyllacea* is characteristically covered by a green veneer, with resident cyanobacterial symbionts testing positive for chlorophyll (Hooper unpublished).

The species is assigned to *Dictyonella* with some reservation. Most features agree with that genus, especially the external morphology and surface characteristics; however, the majority of *Dictyonella* species have longer styles than the present one. The closest species to *D. chlorophyllacea* is *D. conglomerata* (Dendy, 1922) from the Indian Ocean, but the skeleton of that species is disorganised compared to the one of *D. chlorophyllacea* which is almost plumoreticulated thus resembling skeletons observed in Axinellidae.

Other species described in *Dictyonella* from the central Indo-Pacific are *D. australiensis* Pulitzer-Finali, 1982 (type material MSNG CE 46934–46935, examined here) which is better allocated to *Scopalina*, and *D. dasiphylla* De Laubenfels, 1954 (holotype USNM 23102, examined here) which is a member of the Raspailiidae and should be synonymised with *Thrinacophora agariciformis* Ridley & Dendy, 1886.

Genus *Phakettia* De Laubenfels, 1936

Gender feminine. Type species, by original designation of De Laubenfels (1936), *Phakettia cactoides* Burton, 1928. Recent, Indian Ocean.

***Phakettia euctimena* (Hentschel, 1912) new comb.**

(Figs 5A,B, 6; Table 4)

Acanthella euctimena Hentschel, 1912: 414

Material examined. HOLOTYPE – SMF 1012, Aru Is, SW Von Lola, 8–10 m depth, 1 April 1908, coll. H. Merton. ADDITIONAL SPECIMENS – Papua New Guinea: QM G312921, G312938. Ashmore Reef: G300180 (NTM Z.2792), Z.2774, Z.2793. Parry Shoals: Z.3126 (G300580). Darwin Harbour: Z.2047, Z.5173 (0M9H2089-N), Z.5174 (0M9H2279-T). Gulf of Carpentaria: G303495, G311853 (Q66C4687-L, G300758). Wessel Is: Z.3914, Z.5167 (0M9H2660-J)

Description. Shape (Fig. 5A,B). Fan-shaped, bushy, or with single or multiple erect digits, branches or tubes, projecting from common broad base with sides partially fused. Projections slightly flattened, bulbous, or pointed. Specimens reach up to 140 mm high and 130 mm diameter.

Colour. Orange or beige

Consistency and texture. Compressible to spongy; rough sandpaper-like texture.

Oscula. Located at ends of branches or projections.

Surface. Membranous ectosome, micro-hispid, shaggy, micro-conulose to conulose, tuberculate, convoluted with fused ridges.

Skeleton (Fig. 6A). Ectosomal skeleton not specialised; covered by dermal skin. Choanosomal skeleton compressed at base; generally halichondroid, formed by multiple multispicular vaguely plumose tracts, fanning out towards surface and with ends of spicules projecting through ectosome; connected irregularly by numerous spicules with disorganised arrangement. High spicule density and low spongin.

Spicules (Fig. 6B, Table 4). Thick styles in wide size range, 322–1402 µm in length; but thin forms also common. Subtylostyles with bases slightly twisted also common, especially in the smaller size categories.

Remarks. This species was initially allocated to *Acanthella* by Hentschel (1912). Although aspects of the surface and consistency agree with that genus, the general architecture of the skeleton and the spicule composition correspond to *Phakettia* (see remarks of the genus below).

Distribution. The type species was previously known only from the Aru Is, Indonesia (Sahul Shelf province, Arafura Sea), but the present work extends this distribution to include two additional ecoregions of the Sahul Shelf (i.e. Bonaparte Coast and Arnhem Coast to Gulf of Carpentaria), as well as the Northwest Australian shelf (Exmouth to Broome) and the Eastern Coral Triangle (Southeast Papua New Guinea) provinces. The species is found between 4 and 50 m depth.

Table 4. Comparison of spicule dimensions among specimens of *Phakettia euctimena*. Measurements in micrometres.

Specimen	Locality	Styles
SMF 1912 (Holotype)	Aru Islands	321.6–1061.3 (602±143.1) x 10.6–28.5 (21.7±4.8)
G312938	Papua New Guinea	483.1–947.7 (748.4±110.9) x 11.3–21.7 (15.5±2.4)
G300180	Ashmore Reef	431.3–790.1 (521.1±70.3) x 10–21.2 (15.9±2.9)
Z.5173	Darwin Harbour	416.9–1402.3 (817.2±292.9) x 8.1–31 (19.6±6.1)
Z.5167	Wessel Is	419.6–1156.5 (730.7±199.4) x 5.8–24.1 (13.9±5.4)

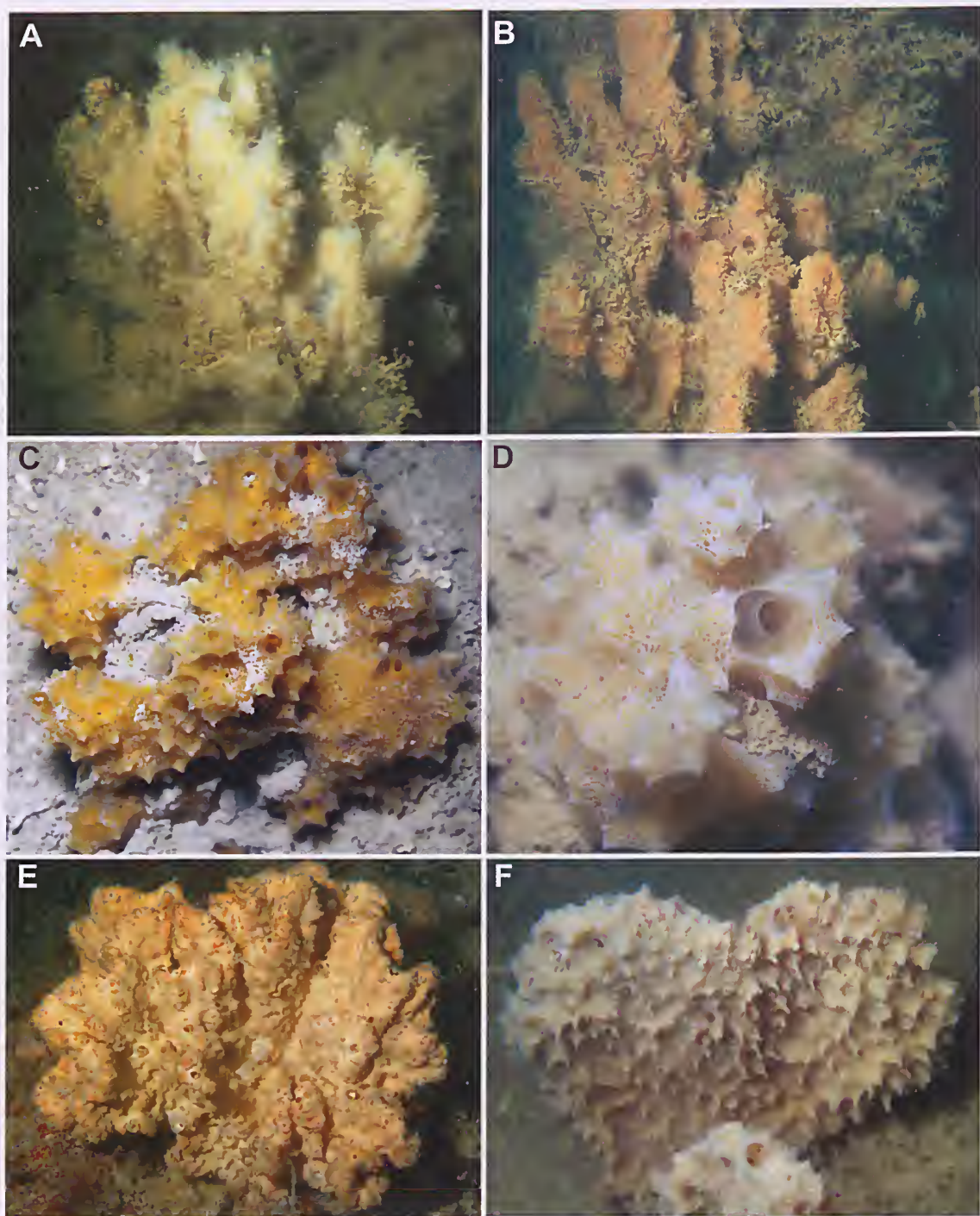


Fig. 5. A,B, *Phakettia euctimena*: specimens *in situ* from Darwin Harbour, cream and orange colour forms. C,D, *Scopalina hapalia*: C, specimen *in situ* from Bynoe Harbour; D, specimen *in situ* from Bynoe Harbour, detail of surface; E, *Stylissa carteri*, specimen *in situ* from Wessel Is; F, *Stylissa flabelliformis*, specimen *in situ* from Darwin Harbour. Photographs: A,B,D – B. Alvarez; C – H. Nguyen; E,F – P. Colin.

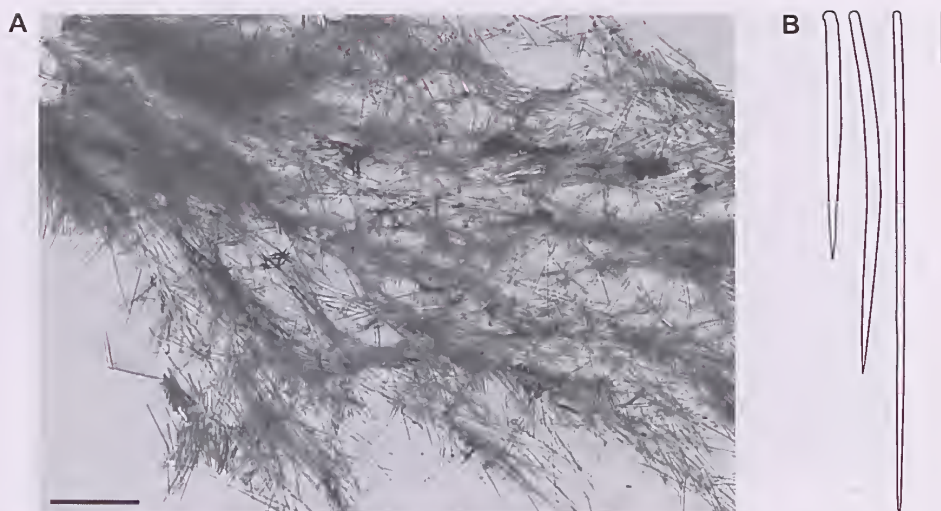


Fig. 6. *Phakettia euctimena*: A, Z.5173, light micrograph of skeleton; B, diagram of spicules. Scale bars: A, 500 μ m; B, 100 μ m.

Phakettia virgultosa (Carter, 1887) new comb.

(Fig. 7; Table 5)

Axinella virgultosa Carter, 1887: 68, pl. 5, fig. 11.

Material examined. HOLOTYPE – BMNH 1887.4.26.3 (fragment of the type) and 1889.6.9.3, King Is, Mergui Archipelago, coll. J. Anderson. ADDITIONAL SPECIMENS – Darwin Harbour: Z.421, Z.5694. Gulf of Carpentaria: G303494.

Description. Shape (Fig. 7A). Generally small specimens, with thin 'fringe-like sherds' projecting from broad base.

Colour. Orange or cream-brown.

Consistency and texture. Soft and delicate.

Oscula. Not visible.

Surface. Hispid, with spicules projecting through erect projections. Transparent membrane covering surface at base.

Skeleton (Fig. 7B). Thick dendritic axes, multispicular, running longitudinally along erect filamentous processes; regularly plumo-echinated by spicules, single or in thin brushes (3–5). Skeleton at base halichondroid.

Spicules (Fig. 7C; Table 5). Thick styles, commonly slightly sinuous or crooked, occasionally with rounded ends; some much smaller with enlarged and recurved bases, located at base of specimen, others some with rounded ends. Styles with recurved bases (some nearly rhabdostyles) common (particularly in specimen G303494), generally less than 500 μ m long, but cannot be distinguished as a separate size class. A transitional series from recurved bases to straight styles is found in large size range (173.4–1214.5 x 5–24 μ m).

Remarks. Two fragments of what appears to be the holotype of this species were examined at the BMNH. Its characteristics coincide with both Carter's (1887) description and figure and with the rest of the material examined and allocated to this species. Carter (1887) assigned the species to *Axinella*, but it agrees with the

current definition of *Phakettia* and therefore is referred here to that genus.

Distribution. The species was initially recorded from the Mergui Archipelago (Andaman Sea province), and it is now recorded from northern Australia (Sahul Shelf province, including Bonaparte Coast and Arnhem Coast to the Gulf of Carpentaria). It is found from the intertidal zone to a depth of 52 m.

Remarks on *Phakettia*. De Laubenfels (1936) erected *Phakettia* for species generally included in *Phakellia* but with styles as the only type of megasclere. The definition of the genus was revised by Van Soest *et al.* (2002) based on the redescription of the type species (*Phakettia cactoides*) and reserved for species with a central region of long styles in a confused and dense mass from which they radiate outwards. The two species described above fit the expanded definition of *Phakettia* well and are therefore included in this genus.

De Laubenfels (1936) suggested further species should be included in *Phakettia*. Most of these are now accepted either in their original genera or in different combinations (see Van Soest *et al.* 2008). Of the species suggested by De Laubenfels for *Phakettia*, only *Phakellia fusca* Thiele, 1899 and *Phakellia ridleyi* Dendy, 1887 could possibly

Table 5. Comparison of spicule dimensions among specimens of *Phakettia virgultosa*. Measurements in micrometres.

Specimen	Locality	Styles
BMNH 1889.6.9.3 (Holotype)	Indian Ocean	301.8–829.4 (696.6 \pm 150.2) x 8.3–22.8 (15 \pm 3.6)
Z.421	Darwin Harbour, Lee Point	497.9–1011.4 (800.2 \pm 126.6) x 5–21.5 (13.4 \pm 4.5)
Z5694	Darwin Harbour, Channel 1.	487–717.3 (636.6 \pm 57.1) x 11.3–19 (15.5 \pm 1.9)
G303494	Gulf of Carpentaria	173.4–1214.5 (593.3 \pm 255.6) x 6.1–24.2 (17.2 \pm 4.4)

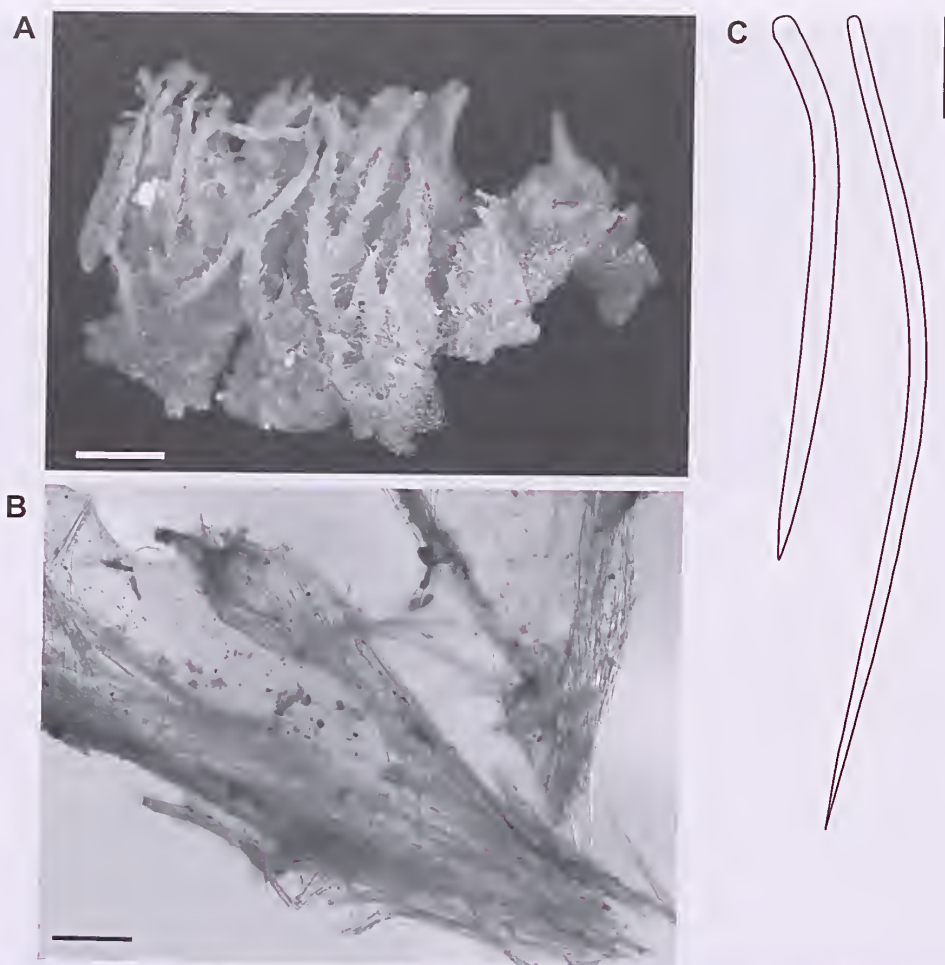


Fig. 7. *Phakettia virgultosa*: A, Holotype, BMNH 1889.6.9.3; B, Z.5694, light micrograph of the skeleton; C, diagram of spicules. Scale bars: A, 2 cm; B, 500 μ m; C, 100 μ m.

be accepted as members of this genus. We have not been able to re-examine the type specimens of these species so those assignments are subject to confirmation and might support a synonymy between *Phakellia fusca* and *Phakettia euctimena*.

After examination of the type material it is concluded that *Homaxinella domantayi* Lévi, 1961 from the Philippine Is [MNH LBIM DCL698] and *H. phrix* De Laubenfels, 1954 from the Caroline Is [USNM 23080] both belong to *Phakettia*. Both are very similar to *P. euctimena*, but it is necessary to examine more specimens from the populations from the Philippine Is and the Caroline Is to be able to confirm their conspecificity. The skeleton of *P. domantayi* is much denser, highly spiculate and more disorganised. The styles are characteristically robust and less variable in length 455.1–855.7 μ m (645 \pm 81.9) \times 14.6–36.4 μ m (25.8 \pm 5.3) than in *P. euctimena*. *Phakettia phrix* (De Laubenfels, 1954) shares with *P. euctimena* the habit, the characteristic compressible and resilient consistency, and the large range

of sizes of the styles (i.e. 218.5–1357.3 μ m (814.8 \pm 405.3) \times 2.3–13 μ m (7.8 \pm 3.2)), but is relatively thinner, more fragile and slightly curved.

Genus *Scopalina*

Gender feminine. Type species, by monotypy, *Scopalina lophyropoda* (Schmidt, 1862). Recent, Mediterranean Sea.

Scopalina hapalia (Hooper, Cook, Hobbs & Kennedy, 1997) **comb. nov.**

(Figs 5C,D, 8; Table 6)

Hymeniacidon hapalia Hooper, Cook, Hobbs & Kennedy, 1997: 58.

Material examined. HOLOTYPE – NTM Z.184, Dudley Point Reef, East Point, 12°25.01' S, 130°48.01' E, intertidal, 13 September 1981, coll. J.N.A. Hooper & party. PARATYPES – QM G303414, N of South Shell I, Darwin Harbour, 12°29.1334' S, 130°52.16' E, 14 m depth, 25 September 1993, coll. J.N.A. Hooper & L.J. Hobbs. ADDITIONAL SPECIMENS – Papua New Guinea: QM G304789 (0CDN1966V). Bynoe



Fig. 8. *Scopalina hapalia*: A, Z.184, light micrograph of skeleton; B, diagram of skeleton; C, diagram of spicules. Scale bars: A, 500 μ m; C, 100 μ m.

Harbour; NTM Z.5178 (0M9H2436-P). Darwin Harbour: QM G303280, G315920, NTM Z.272, Z.286, Z.2146, Z.2560, Z.5165 (0M9H2237-X), Z.5882.

Description. Shape (Fig. 5C,D). Thickly to thinly encrusting, up to 5–10 mm thick, following contours of substrate and covering areas up to 40 cm in maximum diameter; sometimes with erect and branching projections.

Colour. Orange alive.

Oscula. Flush between conules, with transparent, membranous and elevated rims.

Surface. Transparent ectosome, marked with tangential and neat reticulation of thin spongin [?] fibres (only observable underwater and when specimens are fully expanded) (Fig. 5D), with long spiky conules, or small branching projections.

Consistency and texture: Soft and fleshy, slimy, falling apart and releasing mucus when collected.

Skeleton (Fig. 8A). Basal plate of spongin, very granular, with ill-defined spongin fibres cored by single styles, or paucispicular or multispicular tracts. Skeleton (when examined via light microscope) obscured by granular pigments.

Spicules (Fig. 8B, Table 6). Styles, slightly curved with rough or uneven ends, or stepped, occasionally with rounded ends, 375–662 by 5–17 μ m. Thinner forms (less than 5 μ m thick) and in similar length are common, but do not seem to constitute separate class.

Remarks. The species was originally described in the genus *Hymeniacidou* with some reservation and under

the assumption that an ectosomal skeleton was absent. It was thought to be related to other poecilosclerids (e.g. *Batzella corticata* or *Strongylacidon intermedius*) based on the presence of smaller strongylote styles. However, a re-examination of the type material indicates that the strongylote styles are derived from the thin category of styles and do not constitute a relevant character for the generic allocation of the species.

The species is better allocated to *Scopalina*, a genus not previously reported from Australian waters. *Scopalina hapalia* shares with other species of the genus the soft consistency, the presence of spongin fibres rising up from a basal plate, the ending in conules, and the granular aspect of the choanosome which is probably due to the presence of pigmented granular cells. This is also characteristic of other species of *Scopalina* (Blanquer & Uriz 2008) and other members of Dictyonellidae (i.e. *Svenzea* (Alvarez *et al.* 2002), *Liosina* and *Stylissa flabelliformis*, see below).

Scopalina hapalia is similar to *S. australiensis* Pulitzer-Finali, 1982 (type material MSNG CE 46934 and CE 46935, examined here), but it differs slightly in its spicule composition and the size of the styles. In *S. australiensis* oxeate modifications of styles are common and styles are on average thinner. The choanosome of *S. hapalia* is heavily granular, to the point that is hard to distinguish the structure of the choanosomal skeleton. It needs to be determined whether the amount of granular pigment present in the choanosome of *S. hapalia* is related to the general habitat conditions (silty and turbid) of the northern Australian populations. It is a characteristic found in other species of Dictyonellidae and also across genera (i.e. *Liosina* and *Svenzea*), and therefore might not be of enough significance to separate taxa at the species level.

Populations of *Scopalina* allegedly belonging to one single species (i.e. *Scopalina lophyropoda* Schmit, 1862) from the Mediterranean and the eastern Atlantic were shown to be part of a complex of genetically distinct cryptic species (Blanquer & Uriz 2008) that could be separated only using a combination of morphological characters. It is likely that populations from northern Australia here assigned to *S. hapalia*, might be genetically distinct from those of the northeastern region and currently allocated to *S. australiensis*. Detailed study of these populations might reveal further characteristics of their morphology that could be used for unequivocal separation of species.

Distribution. Very common in the area of Darwin Harbour and Bynoe Harbour (Sahul Shelf province, Bonaparte Coast ecoregion), from the intertidal zone to 14 m. It is also found in the Eastern Coral Triangle (Southeast Papua New Guinea).

Genus *Stylissa*

Gender feminine. Type species, by original designation of Hallmann (1914), *Stylotella flabelliformis* Hentschel, 1912. Recent, Aru Is, Indonesia.

Table 6. Comparison of spicule dimensions among specimens of *Scopalina hapalia*. Measurements in micrometres.

Specimen	Locality	Thick styles	Thin styles
Z.184 (Holotype)	Darwin Harbour	375.1–550.6 (503.4±36.7) x 6.7–11.2 (9±1.2)	320.6–439.6 (376±31.8) x 2.4–4.8 (3.6±0.7)
G303414 (Paratype)	Darwin Harbour	455.6–662.7 (532.7±50.6) x 5.4–16.9 (8.8±2.5)	351.5–619.2 (444±63.3) x 2.7–5.8 (4±0.9)
G304789	Papua New Guinea	419.7–583.4 (521.4±35.4) x 6.3–12 (8.7±1.5)	304.7–463.3 (374.8±49.9) x 2.1–5.8 (3.8±0.9)
Z.5178	Bynoe Harbour	450.7–626.8 (551.5±51.5) x 6.3–15.6 (9.6±2.2)	182–572.5 (427.1±95.1) x 1.5–7.3 (3.4±1.4)

Stylissa carteri (Dendy, 1889)

(Figs 5E, 9; Table 7)

Acanthella carteri Dendy, 1889: 93; Dendy 1905: 193; Dendy 1922: 119; Lévi 1961: 16.*Acanthella aurantiaca* Keller, 1889: 396. – Topsent 1906: 6; row 1911; 356; Van Soest 1989: 228.*Axinella carteri* – Burton 1959: 258; Thomas 1973: 41; Thomas 1981: 29; Hooper & Lévi 1993: 1410; Hooper & Wiedenmayer 1994: 72; Lévi 1998: 102; Alvarez *et al.* 2000.*Stylissa carteri* – Van Soest *et al.* 2002: 783.*Stylissa flabelliformis* – Hooper & Lévi 1993: 1422 [in part]; Erpenbeek *et al.* 2005b: 95.*Teichaxinella labyrinthica* – Hooper *et al.* 1992: 265.

Material examined. LECTOTYPE – BMNH 1889.1.21.53 (here designated), dry, Tuticorin Pearl Banks, Gulf of Manaar, coll. E. Thurston, 1889 (Fig. 9A). Lectotype chosen from three specimens collected by E. Thurston from the Gulf of Manaar, and bearing a hand-written red label: “No. 65, Brit. Mus. Reg. 89.1.21.53. Loc: Gulf of Manaar. Coll. Thurston (2).” PARALECTOTYPES – BMNH 1889.1.21.11, wet, Tuticorin Pearl Banks, Gulf of Manaar, coll. E. Thurston, 1889; BMNH 1890.6.28.4, dry, P. Amban[?], Gulf of Manaar, shallow water, coll. E. Thurston. ADDITIONAL SPECIMENS – *Acanthella aurantiaca* Keller, 1889: ZMB 0182, lectotype

(here designated), dry, Red Sea, coll. Hemprick & Ehrenberg, 1889; ZMB 2921, paralectotype, wet, Suakin, Red Sea, 5 August 1889. Lectotype chosen from two syntypes bearing the original hand-written label: “*Acanthella aurantiaca*, Rothes Meers” and matching Keller’s illustration. Indonesia, Barang Lompo: ZMA Por.17668, 17690. Laeepede Is, Western Australia: NTM Z.2321, Z.2351. Ashmore Reef and Cartier I.: QM G300183, G301051, G301081, G301082, G301094, G301138, G301152, Z.629, Z.2797, Z.2798. Melville I.: Z.37, Z.607, Z.616. Parry Shoals: G310143, Z.3063, Z.3081. Bynoe Harbour: Z.5180 (0M9H2521-1). Darwin Harbour: G303366, Z.2710, Z.5179 (0M9H2291-1). Gunn Point: Z.1447; Cobourg Peninsula: Z.28. Wessel Is: G300750, G311872, Z.3926, Z.5183 (0M9H2604-W).

Description. Shape (Fig. 5E). External growth form very variable, with habits including thickly flabellate, digitate, branching, bushy, buttressed, tuft-like, thickly encrusting to bulbous; erect, stipitate, attached to substrate directly or by stalk of variable height and diameter, 20–90 mm long, up to 40 mm diameter; with massive, lobate, irregularly planar or globular projections, up to 350 mm wide or, branches projecting in one or several planes, consisting of relatively thick, flattened planar or buttressed lamellae, 4–11 mm

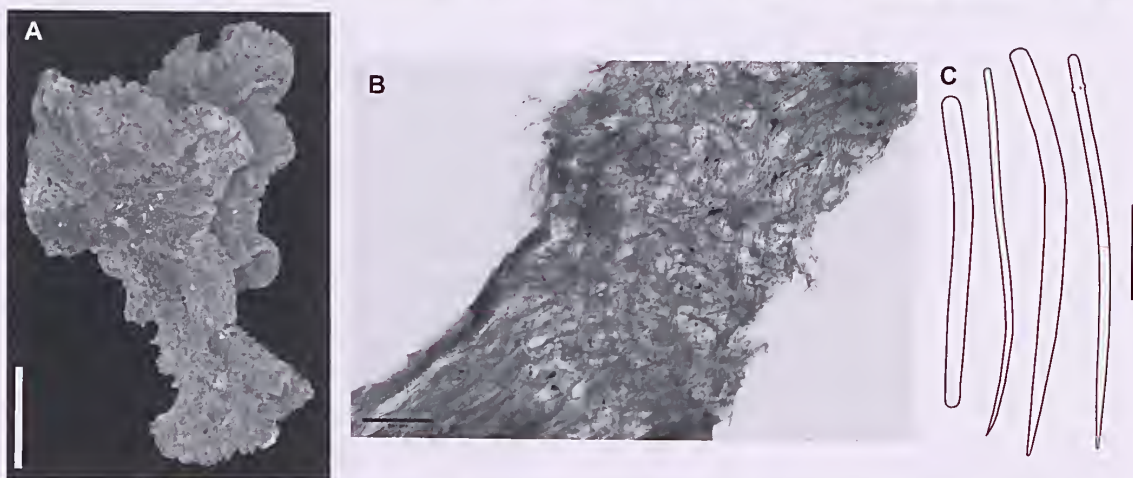


Fig. 9. *Stylissa carteri*: A, Lectotype, BMNH 1889.1.21.53; B, light micrograph of skeleton; C, diagram of spicules. Scale bars: A, 2 cm; B, 500 μ m; C, 100 μ m.

thick, with irregular margins. Growing from 10–400 mm high.

Colour. Bright, light, pale orange-brown alive (Munsell 2.5YR 7/8), pale orange-brown in ethanol. Surface slightly darker than interior of sponge.

Oscula. Flushed with elevated membranous rims, irregularly distributed.

Surface. Fleshy, conulose, irregularly striated, sculptured, rough; with irregular sharp conules, 3–5 mm high, solitary or joined to form meandering surface ridges. Mottled dusty appearance very characteristic, but not always obvious.

Consistency and texture. Rubbery, compressible, easily torn.

Skeleton (Fig. 9B). Axial skeleton condensed into several multispicular bundles, 100–250 µm wide, running more or less longitudinally through lamellae, fully cored by long slender styles, bound together by very light spongin fibres, and interconnected at irregular angles by vaguely plumose, ascending, paucispicular extra-axial tracts of styles or individual spicules. Fibre reticulation relatively close meshed, with lacunae forming elongate oval chambers, up to 300 x 70 µm. Collagen in mesohyl relatively light compared with ectosomal region.

Spicules (Fig. 9C, Table 7). Single category of style present, though variable in thickness, 272–651 x 4–28 µm, occasionally strongylote; styles relatively long, slender or robust, usually slightly curved symmetrically or towards basal end, sharply pointed, fusiform, with evenly rounded

base or slightly constricted. Relative proportions of thinner and thicker styles also vary within and between populations.

Remarks. This species has been moved between *Acanthella* and *Axinella* mainly because it shares a number of characteristics with both genera. The shape and consistency of some individuals are nearly identical to those of species like *Acanthella cavernosa* or *A. pulcherrima* (see above), making it difficult to separate them based on those features alone. *Stylissa carteri* differs from species of *Acanthella* in the organisation of the skeleton and in both spicule composition and dimensions. The strongyles, some of which are sinuous, observed in some specimens led some authors to allocate the species to *Acanthella*. After examination of a large number of specimens it is concluded that those strongyles are derived from styles and they do not constitute a separate type of spicule as in the case of species of *Acanthella* where the strongyles are clearly distinguished from the styles and oxcas, and are mainly located in the core of the choanosomal tracts (or axes).

Stylissa carteri closely resembles *S. flabelliformis*, especially individuals from Indonesian populations. The two species share a number of external characteristics, such as shape, surface and colour, but both the skeleton and the spicule composition are distinctive (see below for further discussion).

Conversely, *Stylissa carteri* resembles *S. massa* (Carter, 1887) in skeletal architecture, composition and spicule dimensions, but differs clearly in habit and surface characteristics. The two species can be sympatric (although not in the present study area). Molecular studies indicate that these species are closely related to species of the genus *Axinella* (see below for further discussion on this topic).

Distribution. *Stylissa carteri* is a very common species through the Indo-Pacific and its distribution extends well beyond the present study area. Based on reported and verified records the species is present throughout a number of provinces including Red Sea and Gulf of Aden, western Indian Ocean, central Indian Ocean islands, Northwest Australian Shelf, Sahul Shelf, Northeast Australian Shelf, and tropical Southern Pacific Ocean. It is found between 5 and 25 m deep within the study region, but deeper in other provinces (e.g. up to 76 m in the Northwest Australian Shelf province).

Genetic studies of populations might reveal that *Stylissa carteri* constitutes a complex of cryptic species which would explain the wide distribution observed in this species.

Lectotypes for *Acanthella carteri* and its junior synonym *A. aurantiaca* are designated here to provide reference to the species described by Dendy (1889) and Keller (1889) respectively.

Stylissa flabelliformis (Hentschel, 1912)

(Figs 5F, 10; Table 8)

Stylotella flabelliformis Hentschel, 1912:355; Hallmann 1914: 355; Hooper & Lévi 1993[in part]; Van Soest *et al.*

Table 7. Comparison of spicule dimensions among specimens of *Stylissa carteri*. Measurements in micrometres.

Specimen	Locality	Styles
1889.01.21.053 (Lectotype)	Indian Ocean, Gulf of Mannar	324.5–453.6 (395.9±33.8) x 6–16.9 (12±3.2)
1889.1.21.11 (Paralectotype)	Indian Ocean, Gulf of Manaar	272.5–510.4 (394.9±58.9) x 11.9–22 (15.9±2.5)
1890.6.28.4 (Paralectotype)	Indian Ocean, Gulf of Mannar	355.7–466.9 (395.4±27) x 4–18.3 (11.2±3)
ZMB0182 (Lectotype of <i>Acanthella aurantiaca</i>)	Red Sea	355.4–651.1 (494.6±56.2) x 10.5–18.6 (14.1±2.3)
ZMB2921 (Paralectotype of <i>Acanthella aurantiaca</i>)	Red Sea	332.7–493.9 (423.9±33.7) x 6.3–14.8 (10.3±2.3)
G301051	Cartier I.	428.5–574.4 (507.8±36.5) x 11.6–28.5 (20.8±4.3)
Z.5180	Bynoc Harbour	288.6–442.2 (392.8±37.2) x 7.7–21.5 (15.6±3.3)
Z.5179	Darwin Harbour	325–479.3 (403.1±40.8) x 8–22.5 (16.1±4.2)
Z.5183	Wessel Is	355.9–603.3 (480.3±65.2) x 6.7–17.6 (11.5±3)

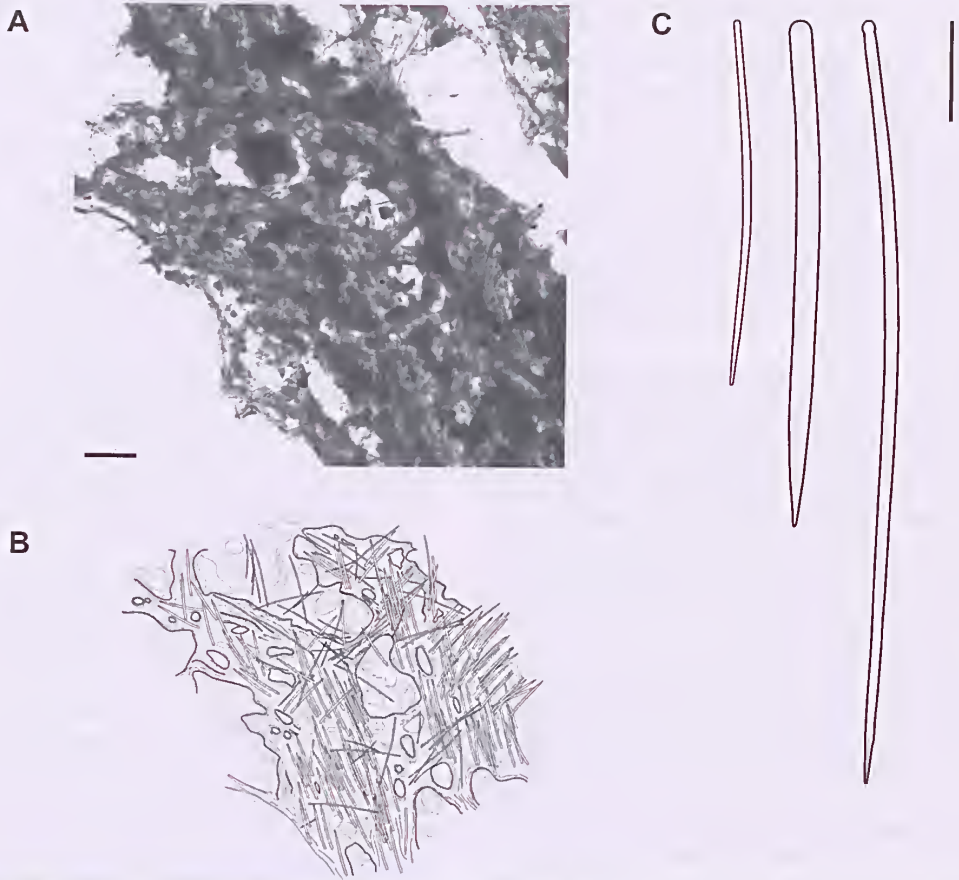


Fig. 10. *Stylissa flabelliformis*: A, SMF 1587, light microphotograph of skeleton; B, diagram of skeleton; C, diagram of spicules. Scale bars: A, 500 μ m; C, 100 μ m.

2002: 783. Not Erpenbeek *et al.* 2005b [= *Stylissa carteri* (Dendy, 1889)].

Ulosa sp. – Alvarez *et al.* 2000.

Material examined. LECTOTYPE designated by Hooper & Lévi (1993) – SMF 1587 Aru Is, SW von Lola, Station 9, Indonesia, 8 m depth, coll. H. Merton, 1 April 1908, dredge. PARALECTOTYPES – Aru Is, Indonesia, coll. H. Merton, dredge, Aru and Kei Is expedition, 1 October 1907, 31 August 1908; SMF 1527, Station 8, 6–10 m depth, 31 March 1908; SMF 1534, Station 8, 8–10 m depth, 1 April 1908; SMF 1538, Station 12, 15 m depth, 8 April 1908; SMF 1689; SMF 1690. ADDITIONAL SPECIMENS – Adele Is, Western Australia: NTM Z.713, Z.718. Bynoe Harbour: Z.5166 (0M9H2435-O), Z.5182 (0M9H2394-T), Z.5886. Darwin Harbour: QM G300143, G303402; NTM Z.87, Z.187, Z.188, Z.189, Z.433, Z.817, Z.862, Z.2654, Z.4456 (0M9H2007-X), Z.5184 (0M9H2101-Z), Z.5885. Cobourg Peninsula: QM G316834. Gulf of Carpentaria: QM G303506, G304937, G304941.

Description. Shape (Fig. 5F). Thin fans up to 5 mm thick, uni-planar to multi-planar, on narrow base or

short peduncles; or in form of irregularly shaped digits. Specimens up to 300 mm high.

Colour. Pale red, orange, yellow, beige-brown.

Oscula. Flush on surface with bubble-like transparent membranes; less than 5 mm in diameter.

Consistency and texture. Soft, floppy, fleshy.

Surface. Soft, membranous highly conulose, marked with thick choanosomal axes. Soft conules, up to 6 mm long, evenly or irregularly distributed. Dermal membrane transparent, delicate and collapsible out of water, stretched over conules and supported by choanosomal fibres.

Skeleton (Fig. 10A). Plumose traets ascending to surface, forming irregular reticulation, enveloped by sheaths or slightly to well-developed spongin fibres. In larger specimens, dendritic choanosomal axes up to 5 mm diameter, oriented longitudinally through fan and becoming thinner close to fan margin, irregularly interconnected, or anastomosing forming, an ill-defined reticulation. Most specimens with characteristic grainy pigment (when observed via light microscope) obscuring arrangement of skeleton.

Table 8. Comparison of spicule dimensions among specimens of *Stylissa flabelliformis*. Measurements in micrometres.

Specimen	Locality	Styles	Anisoxeas-oxeas
SMF 1587	Aru Is	401.3–550 (470±47.1) x 6.7–25 (16.6±4.5)	290–540 (436.7±130.5) [3] x 8–25 (15.3±8.7) [3]
SMF 1689	Aru Is	354.5–480.7 (413.7±38.5) x 3.7–14.8 (8.7±3.1)	255.7–442.5 (330.5±60.3) [20] x 6.7–15.7 (9.5±2.1) [20]
SMF 1690	Aru Is	345.4–643.3 (463.8±74.1) x 8.4–22.5 (13.8±2.8)	
Z.718	Adele I., WA	397–530.4 (467.5±41.9) x 4.5–20 (12.6±3.2)	390.7–568.7 (511.2±63.3) [7] x 11.7–22 (17.8±3.5) [7]
Z.5182	Bynoe Harbour	411.6–562.3 (479±44) x 11.1–29 (18.1±4)	387.1–548.9 (495.2±44.8) [15] x 15.7–27.6 (20.9±3) [15]
Z.4456	Darwin Harbour	341.6–518 (437.6±48.6) x 10.8–25.7 (18.7±3.1)	457.2–596.2 (511.4±59.5) [4] x 16.3–19.3 (17.6±1.3) [4]

Spicules (Table 8, Fig. 10B). Styles of variable thickness, some with rounded ends, 341–643 x 3–29 µm. Anisoxeas and oxeas less frequent, with tips stepped or rounded, slightly bent at one-third of total length, 255–596 x 6–27 µm thick; thin forms are common in some specimens.

Remarks. As mentioned above, this species is similar to *Stylissa carteri*. Both share a number of characteristics including those of shape, surface and colour. In the field they can be distinguished by consistency, texture and surface characteristics – firm, rubbery and compressible with a discontinuous dust-like dermal membrane in *S. carteri* versus a soft, thin and floppy with a thin transparent membrane in *S. flabelliformis*. The two species can be further distinguished by their skeletal arrangement – robust with thick multispicular bundles forming a close mesh reticulation in *S. carteri* versus a grainy choanosome with thick dendritic fibres/tracts ascending irregularly to the surface and forming an ill-defined reticulation in *S. flabelliformis*.

The surface characteristics of *Stylissa flabelliformis* are remarkably similar to those of species of *Scopalina*, both having long and soft conules and a transparent and collapsible dermal membrane. They also share the grainy appearance of the skeleton (a feature also observed in species of the dictyonellid genus *Svenzea*) and some aspects of the skeletal organisation such as the dendritic fibres ascending to the surface. Furthermore, *Stylissa flabelliformis* was shown to be more closely related to species of *Scopalina* than to *Stylissa carteri* in an analysis based on sequence data from the 28S rDNA (see Alvarez *et al.* 2000). Species of *Scopalina*, however, are encrusting to thickly-encrusting, a feature not observed in *Stylissa flabelliformis*. The close relationship between *Stylissa flabelliformis* (which is the type species of the genus) and species of *Scopalina* is interesting and should be further explored as it might have implications for the classification of the Dictyonellidae (see below under remarks on the genus *Stylissa*).

Distribution. This species is distributed mainly through the Sahul Shelf province and occurs between 3–15 m. It

is also recorded from Adele I, Western Australia, in the adjacent Northwest Australian Shelf province, and found at 59 m depth. It has also been observed in Papua New Guinea (Alvarez unpublished).

Remarks on the genus *Stylissa*. *Stylissa* was erected by Hallmann (1914) to receive *Stylotella flabelliformis* Hentschel, 1912, which did not agree with the genus *Stylotella* (currently a junior synonym of *Hyueniacidon*, see Van Soest *et al.* 2002). The genus was later related to *Homaxinella* (Suberitidae) by De Laubenfels (1936) based on the presence of styles and to *Dragnaxia* (Axinellidae) by Hooper & Lévi (1993). Following the revision of Van Soest *et al.* (2002), the genus is now considered an established member of the family Dictyonellidae with at least seven species (Van Soest *et al.* 2008). Of those, only *S. flabelliformis* and *S. carteri* are represented in the present study area. The similarities of these species to other members of the genus are discussed above.

Four additional species from the Indo-Pacific realm are referred to *Stylissa* in this paper after examination of the type material – *Homaxinella acanthelloides* Lévi, 1961 (MNHN LBIM DCL697, Zamboanga, Philippines), *Anletta constricta* Pulitzer-Finali, 1982 (MSNG CE 46930, GBR), *Ptilocaulis flexibilis* Lévi, 1961 (MNHN LBIM DCL416, Nha Trang, Vietnam), and *Phakellia inflexa* Pulitzer-Finali, 1982 (MSNG CE 46931, GBR). Some of these species might be closely related to *S. carteri* (i.e. *S. constricta*, *S. flexibilis*) or to *S. massa* (i.e. *S. acanthelloides* and *S. inflexa*). Proper study of the local populations of those species is necessary to confirm these affinities. As seen above, morphological characters of the species within the genus *Stylissa* are highly overlapping and subject to a high degree of variability. *Phakellia crassistylifera* Dendy, 1905 from the Gulf of Manaar (type specimen not examined) might also belong in *Stylissa* as suggested in Alvarez & Hooper (2009).

The wide distribution of some species of *Stylissa* (i.e. *S. carteri* and *S. massa*) suggests that they might constitute species complexes that could only be detected

using molecular methods. Phylogeographic studies will be extremely useful to determine the real limits of these allegedly widespread species.

As mentioned above, there are remarkable similarities between the type species of *Stylissa* (i.e. *S. flabelliformis*) and species of *Scopalina*. They share the surface features and the grainy appearance of the choanosome (also seen in the dictyonellid genera *Svenzea* and *Liosina*). This relationship is supported by molecular evidence from Alvarez *et al.* (2000) which showed the Caribbean species *Scopalina rutzleri* (Wiedenmayer, 1977) was closely related to *S. flabelliformis* (misidentified as *Ulosa sp.* in that publication) based on partial sequences of the 28S rDNA. *Stylissa flabelliformis* was also found to be closely related to *Axinella* and *Agelas* by Erpenbeek *et al.* (2005). The specimen used in that analysis was re-examined here and it is *S. carteri*.

Based on molecular evidence from different data sets and gene regions (Lafay *et al.* 1992; Chombard *et al.* 1997; Alvarez *et al.* 2000; Borehiellini *et al.* 2004; Erpenbeek *et al.* 2005b, 2006; Holmes *et al.* 2007), *Stylissa carteri* and *S. massa* have been consistently related to species of the genus *Axinella* including *A. arnensis* (Hentschel, 1912), *A. corrugata* (George & Wilson, 1919), *A. damicornis* (Esper, 1794) and *A. verrucosa* (Esper, 1794). This polyphyletic cluster of species is shown as also related to members of the order Agelasida in these studies. It is also important to note that this group of species shares similar classes of chemical compounds (Van Soest & Brackman 1999 and references within), providing additional evidence to support their relationship. These close relationships between species presently in different orders and without any obvious morphological similarities remain unexplained at this stage. Indeed, they challenge the value of the currently accepted characters (both morphological and molecular) for the study of halichondrid sponge phylogenetics.

The evidence presented above indicates that the genus *Stylissa* is not monophyletic, which explains some of the discrepancies of the phylogenetic relationships within the Halichondrida. However, there is currently not enough information from other species of *Stylissa* to test the monophyly of this genus and its position within the classification. Studies using both molecular and morphological characters will be undertaken in the future to explore this hypothesis.

DISCUSSION

This revision indicates that the family Dictyonellidae is represented in the region under study by a total of eight species belonging to the genera *Acanthella*, *Dictyonella*, *Phakettia*, *Scopalina* and *Stylissa*. Three of these genera (i.e. *Dictyonella*, *Phakettia* and *Scopalina*) and the species they contain were not previously recorded for Australian waters.

Other genera of the Dictyonellidae, such as *Liosina*, *Rhaphoxya*, *Lipastrotethya*, *Tethyspira* and *Svenzea* are not

present in the study region. However, species of *Liosina* (e.g. *L. paradoxa* Thiele, 1899) and *Svenzea* (e.g. *S. devoogdae* Alvarez, Van Soest & Rutzler, 2002) are common in regions adjacent to the study area, such as Indonesia and the GBR.

All the species of Dictyonellidae reported here are not restricted to the region under study and are common throughout northern Australia, including the Northwest Australian Shelf, Sahul Shelf, Northeast Australian shelf (Coral Sea), and other localities in Indonesia. Species of *Acanthella* and *Stylissa* in particular are widely distributed with validated records in several marine provinces of the Indo-Pacific, including the Western Indian Ocean. Characterisation of the populations of these species along their distributional ranges using morphological, morphometric and molecular characters are essential to decide whether they include complexes of cryptic species. As in other species of Axinellidae (e.g. *Axinella arnensis*), species of these dictyonellid genera are characteristically variable with intermediate forms along a large morphological continuum that can be detected only by examination of the taxonomic characters across a large number of specimens.

This revision has established that besides the affinities between *Stylissa*, *Axinella*, and members of Agelasida there are also morphological similarities and limited molecular evidence (Alvarez *et al.* 2000) to relate the type species of *Stylissa* (i.e. *Stylissa flabelliformis*) to species of the genus *Scopalina*. This suggests that the genus *Stylissa* is non-monophyletic and its current allocation within sponge classification is debatable. All this evidence however is currently circumstantial and needs to be confirmed in future studies using an appropriate set of taxa selected specifically to explore such puzzling relationships and answer the question of monophyly of the genus *Stylissa* and of the family Dictyonellidae itself.

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APPENDIX

Collection and locality data for material examined in the collections of QM and NTM

QM material

G300143	Lee Point Reef, Lee Point, Darwin, NT, 12°19.0001'S, 130°53'E, intertidal, 26 Oct 1984, coll. Hooper, JNA
G300174	Dudley Point Reef, East Point, Darwin, NT, 12°25.0001'S, 130°48.01'E, 10.5 m, 3 Apr 1986, coll. Hooper, JNA
G300180	Passage West 1., outer reef, Ashmore Reef, WA, 12°14'S, 122°56'E, 15.5 m, 27 Jul 1986, coll. Hooper, JNA
G300183	Ashmore Reef, outside entrance to west islet passage, outer reef edge, WA, 12°15'S, 122°55.01'E, 16.5 m, 28 Jul 1986, coll. Hooper, JNA
G300220	Dudley Point Reef, East Point, Darwin, NT, 12°30'S, 130°48.01'E, .5 m, 10 Sep 1987, coll. Hooper, JNA
G300750	Gugari Rip 100 m NE, E Guluwuru I, Wessel Is, NT, 11°34.0001'S, 136°22.12'E, 8 m, 13 Nov 1990, coll. NCI, Australian Institute of Marine Science
G301051	Cartier I, windward reef slope, W side of reef, WA, 12°32.0334'S, 123°31.16'E, 12 m, 4 May 1992, coll. Hooper, JNA
G301053	Cartier I, windward reef slope, W side of reef, WA, 12°32.0334'S, 123°31.16'E, 12 m, 4 May 1992, coll. Hooper, JNA
G301081	Cartier I, outer reef slope, N side reef, WA, 12°31.0667'S, 123°33.05'E, 14 m, 6 May 1992, coll. Hooper, JNA
G301082	Cartier I, outer reef slope, N side reef, WA, 12°31.0667'S, 123°33.05'E, 14 m, 6 May 1992, coll. Hooper, JNA
G301091	Cartier I, outer reef slope, N side reef, WA, 12°31.0667'S, 123°33.05'E, 22 m, 7 May 1992, coll. Hooper, JNA
G301094	Cartier I, outer reef slope, N side reef, WA, 12°31.0667'S, 123°33.05'E, 22 m, 7 May 1992, coll. Hooper, JNA
G301138	Hibernia Reef, entrance to lagoon, NE side reef, WA, 11°57.1334'S, 123°22.06'E, 23 m, 10 May 1992, coll. Hooper, JNA
G301152	Hibernia Reef, lagoon patch reef, E side lagoon, WA, 11°58.05'S, 123°22.06'E, 30 m, 11 May 1992, coll. Hooper, JNA
G301155	Hibernia Reef, outer reef slope, N side of reef, WA, 11°58.0167'S, 123°21.04'E, 27 m, 12 May 1992, coll. Hooper, JNA
G303280	South Shell I., reef N of boatramp, East Arm, Darwin Harbour, NT, 12°29.1334'S, 130°53.09'E, 0 m, 19 Sep 1993, coll. Hooper, JNA and Hobbs, L.J.
G303338	East Point Bonmics, Darwin Harbour, NT, 12°24.0834'S, 130°48.14'E, 10 m, 23 Sep 1993, coll. Hooper, JNA and Hobbs, L.J.
G303366	Stevens Rock, Weed Reef, Darwin Harbour, NT, 12°29.1667'S, 130°47.19'E, 19 m, 24 Sep 1993, coll. Hooper, JNA and Hobbs, L.J.
G303386	Stevens Rock, Weed Reef, Darwin Harbour, NT, 12°29.1667'S, 130°47.19'E, 19 m, 24 Sep 1993, coll. Hooper, JNA and Hobbs, L.J.
G303391	Stevens Rock, Weed Reef, Darwin Harbour, NT, 12°29.1667'S, 130°47.19'E, 19 m, 24 Sep 1993, coll. Hooper, JNA and Hobbs, L.J.
G303402	South Shell I., rock on N side of island, Darwin Harbour, NT, 12°29.1334'S, 130°52.16'E, 14 m, 25 Sep 1993, coll. Hooper, JNA and Hobbs, L.J.
G303449	Fish Reef, west side, Bynoc Harbour, NT, 12°26.0167'S, 130°26.09'E, 11 m, 26 Sep 1993, coll. Hooper, JNA and Hobbs, L.J.
G303489	Duyfken Point, W Gulf of Carpentaria, QLD, 12°30.0167'S, 141°2.04'E, 50 m, 4 Nov 1993, coll. Cook, SD. and Kennedy, J. on CSIRO RV Southern Surveyor
G303494	Duyfken Point, W Gulf of Carpentaria, QLD, 12°31.0167'S, 141°2.07'E, 51 m, 5 Nov 1993, coll. Cook, SD. and Kennedy, J. on CSIRO RV Southern Surveyor
G303495	Duyfken Point, W Gulf of Carpentaria, QLD, 12°31.0167'S, 141°2.07'E, 51 m, 5 Nov 1993, coll. Cook, SD. and Kennedy, J. on CSIRO RV Southern Surveyor
G303506	Duyfken Point, W, Weipa, QLD, 12°27.0167'S, 141°3.12'E, 53 m, 6 Nov 1993, coll. Cook, SD. and Kennedy, J. on CSIRO RV Southern Surveyor
G303512	Duyfken Point, W, Weipa, QLD, 12°27.0167'S, 141°3.12'E, 53 m, 6 Nov 1993, coll. Cook, SD. and Kennedy, J. on CSIRO RV Southern Surveyor
G304789	N coast, N Jais Aben, off Rewo Village small I., Papua New Guinea, 8°8.0667'S, 145°48.04'E, 2 m, 11 Nov 1993, coll. NCI, Coral Reef Research Foundation
G304937	Duyfken Point, W Gulf of Carpentaria, QLD, 12°25.15'S, 141°4.09'E, 48 m, 3 Mar 1995, coll. Cook, SD. on CSIRO RV Southern Surveyor
G304941	Duyfken Point, W, Weipa, QLD, 12°27.0167'S, 141°3.12'E, 50 m, 3 Mar 1995, coll. Cook, SD. on CSIRO RV Southern Surveyor
G310143	Pary Shoals 35 nm W Bathurst I., NT, 11°6.9001'S, 129°25.51'E, 20 m, 13 Aug 1987, coll. Thom, B. and Locker, R
G311853	Small island 0.5 nm NW of Mainland, N Cape Wilberforce, Melville Bay, Govc. NT, 11°31.5667'S, 136°19.98'E, 20 m, 11 Nov 1990, coll. NT Fisheries
G311872	100 m NE Gugari Rip, East side Guluwuru Is., Wessel Is, NT, 11°20.4'S, 136°13.63'E, 8 m, 13 Nov 1990, coll. Hooper, JNA
G312921	12 mile sandbank, Kupiano, SE Papuan Lagoon, Papua New Guinea, 10°11.0501'S, 148°10.14'E, 20 m, 15 Dec 1996, coll. Hooper, JNA
G312925	12 mile sandbank, Kupiano, SE Papuan Lagoon, Papua New Guinea, 10°11.0501'S, 148°10.14'E, 20 m, 15 Dec 1996, coll. Hooper, JNA
G312938	12 mile sandbank, Kupiano, SE Papuan Lagoon, Papua New Guinea, 10°11.0501'S, 148°10.14'E, 20 m, 15 Dec 1996, coll. Hooper, JNA
G315920	Lagoon entrance, Osprey Reef, Coral Sea, QLD, 13°53.137'S, 146°33.54'E, 20.5 m, 13 Dec 1999, coll. Kennedy, JA and Edson, DW
G316834	Torres Strait, QLD, 9°18.6'S, 142°55.2'E, 11 m, 23 Jan 2004, coll. QDPI RV Gwendoline May

APPENDIX

Collection and locality data for material examined in the collections of QM and NTM
NTM material

Z.37	Trepang Bay, Cobourg Peninsula, NT, 11°7'S, 131°58.01'E, 15 Oct 1981, coll. Hooper, JNA
Z.87	Coral Bay, Port Essington, Cobourg Peninsula, NT, 11°11.5001'S, 132°2'E, 18 Oct 1981, coll. Hooper, JNA and Alderslade, PN
Z.187	Dudley Point Reef, East Point, Darwin, NT, 12°25.0001'S, 130°48.01'E, 0-0.5 m, 13 Sep 1981, coll. Hooper, JNA and party
Z.188	Dudley Point Reef, East Point, Darwin, NT, 12°25.0001'S, 130°48.01'E, 0-0.5 m, 13 Sep 1981, coll. Hooper, JNA and party
Z.189	Dudley Point Reef, East Point, Darwin, NT, 12°25.0001'S, 130°48.01'E, 0-0.5 m, 13 Sep 1981, coll. Hooper, JNA and party
Z.272	Dudley Point Reef, East Point, Darwin, NT, 12°25.0001'S, 130°48.01'E, 0.3 m, 17 Sep 1981, coll. Hooper, JNA
Z.286	Dudley Point Reef, East Point, Darwin, NT, 12°25.0001'S, 130°48.01'E, 1 m, 18 Sep 1981, coll. Hooper, JNA and Murray, P
Z.421	Lee Point, Darwin, NT, 12°19.0167'S, 130°53'E, 13 Dec 1981, coll. Hooper, JNA
Z.429	Lee Point, Darwin, NT, 12°19.0167'S, 130°53'E, 13 Dec 1981, coll. Hooper, JNA
Z.433	Lee Point, Darwin, NT, 12°19.0167'S, 130°53'E, 13 Dec 1981, coll. Hooper, JNA
Z.607	Cootamundra Shoals, North of Melville I., NT, 10°49.0667'S, 129°12.09'E, 36 m, 6 May 1982, coll. Thom, B and Lockyer, R
Z.616	Cootamundra Shoals, North of Melville I., NT, 10°50.2167'S, 129°13.17'E, 22 m, 10 May 1982, coll. Lockyer, R
Z.629	Unnamed shoal N Melville I, NT, 11°33'S, 130°3.01'E, 18 m, 25 May 1982, coll. Lockyer, R., Cootamundra Shoals Survey
Z.713	N Adele I., Collier Bay, NW Shelf, WA, 15°58.0167'S, 122°39.07'E, 59 m, 21 Apr 1982, coll. CSIRO R.V.SPRIGHTLY
Z.718	N Adele I., Collier Bay, NW Shelf, WA, 15°58.0167'S, 122°39.07'E, 59 m, 21 Apr 1982, coll. CSIRO R.V.SPRIGHTLY
Z.817	Channel I., Middle Arm, Darwin, NT, 12°32.0167'S, 130°51.02'E, 11 m, 16 Jul 1982, coll. SCOTT CHIDGEY (CALDWELL CONNELL ASS)
Z.862	Channel I., Middle Arm, Darwin, NT, 12°32.0667'S, 130°52.04'E, 13 m, 20 Aug 1982, coll. Alderslade, PN
Z.961	East Point Reef, East Point, Darwin, NT, 12°24.05'S, 130°48.01'E, 12 m, 13 Sep 1982, coll. Hooper, JNA
Z.1447	Blue Hole, Gunn Point, NT, 12°9.0001'S, 131°0'E, 25 m, 19 Aug 1983, coll. Alderslade, PN
Z.1968	West side of Weed Reef, Darwin, NT, 12°29.2001'S, 130°47.1'E, 11 May 1984, coll. Hooper, JNA and party
Z.2021	West side of Weed Reef, Darwin, NT, 12°29.2001'S, 130°47.1'E, 11 May 1984, coll. Hooper, JNA and party
Z.2047	Dudley Point Reef, East Point, Darwin, NT, 12°25.0001'S, 130°48.01'E, 10 May 1984, coll. Hooper, JNA
Z.2092	northern tip of Weed Reef, outer reef slope, Darwin Harbour, NT, 12°29.2001'S, 130°37.61'E, 23 Aug 1984, coll. Hooper, JNA
Z.2146	Dudley Point Reef, East Point, Darwin, NT, 12°25.0001'S, 130°48.01'E, 27 Sep 1984, coll. Hooper, JNA
Z.2155	northern tip of Weed Reef, outer reef slope, Darwin Harbour, NT, 12°29.2001'S, 130°37.61'E, 5 Oct 1984, coll. Hooper, JNA
Z.2192	northern tip of Weed Reef, outer reef slope, Darwin Harbour, NT, 12°29.2001'S, 130°37.61'E, 16 Nov 1984, coll. Hooper, JNA
Z.2251	Dudley Point Reef, East Point, Darwin, NT, 12°24.5'S, 130°48.01'E, 10 12 Apr 1985, coll. Hood, C and party
Z.2321	NW Lacepede Is, NW Shelf, WA, 16°31.0001'S, 121°28.01'E, 38-40 m, 17 Apr 1985, coll. Russell, BC
Z.2351	NW Lacepede Is, NW Shelf, WA, 16°34'S, 121°27.01'E, 40-46 m, 17 Apr 1985, coll. Russell, BC
Z.2379	Dudley Point Reef, East Point, Darwin, NT, 12°24.5'S, 130°48.01'E, 8 m, 29 Jul 1985, coll. Hooper, JNA
Z.2533	Orontes Reef, mouth of Port Essington, Cobourg Peninsula, NT, 11°3.6001'S, 132°5.41'E, 17 Sep 1985, coll. Hooper, JNA
Z.2560	Dudley Point Reef, East Point, Darwin, NT, 12°24.5'S, 130°48.01'E, 12 Dec 1985, coll. Mussig, AM and Hood, C
Z.2633	Dudley Point Reef, East Point, Darwin, NT, 12°24.5'S, 130°48.01'E, 3 Apr 1986, coll. Hooper, JNA and party
Z.2654	Dudley Point Reef, East Point, Darwin, NT, 12°24.5'S, 130°48.01'E, 3 Apr 1986, coll. Hooper, JNA and party
Z.2706	Dudley Point Reef, East Point, Darwin, NT, 12°24.5'S, 130°48.01'E, 3 Apr 1986, coll. Hooper, JNA and party
Z.2710	Dudley Point Reef, East Point, Darwin, NT, 12°24.5'S, 130°48.01'E, 3 Apr 1986, coll. Hooper, JNA and party
Z.2720	Dudley Point Reef, East Point, Darwin, NT, 12°24.5'S, 130°48.01'E, 3 Apr 1986, coll. Hooper, JNA and party
Z.2751	Lagoon, NE west islet, Ashmore Reef, WA, 12°14.4'S, 122°58.89'E, 14 m, 22 Jul 1986, coll. Johnson, C
Z.2774	Channel into lagoon, NW entrance, Ashmore Reef, WA, 12°13.4'S, 122°59'E, 26 Jul 1986, coll. Vail, L
Z.2793	Ashmore Reef, near entrance W islet passage, outer reef edge, WA, 12°14.3'S, 122°56'E, 15.5 m, 27 Jul 1986, coll. Mussig, AM
Z.2797	Ashmore Reef, near entrance W islet passage, outer reef edge, WA, 12°14.3'S, 122°56'E, 15.5 m, 27 Jul 1986, coll. Mussig, AM
Z.2798	Ashmore Reef, near entrance W islet passage, outer reef edge, WA, 12°14.3'S, 122°56'E, 15.5 m, 27 Jul 1986, coll. Mussig, AM
Z.3063	Parry Shoals, Arafura Sea, NT, 11°11.7167'S, 129°43.25'E, 16 m, 12 Aug 1987, coll. Mussig, AM and NCI team

APPENDIX

Collection and locality data for material examined in the collections of QM and NTM

NTM material

Z.3081	Parry Shoals, Arafura Sea, NT, 11°11.4'S, 129°43.01'E, 18 m, 13 Aug 1987, coll. Mussig, AM and NCI team
Z.3126	Parry Shoals, Arafura Sea, NT, 11°12'S, 129°43.01'E, 16 m, 12 Aug 1987, coll. Mussig, A.M. and NCI (AIMS)
Z.3199	East Point Reef, East Point, Darwin, NT, 12°29.5'S, 130°48.01'E, 10 m, 17 Sep 1987, coll. Smit, N
Z.3572	Horseshoe Reef, Outer Barrier Reef, Papua New Guinea, 9°40.0001'S, 147°30'E, 18-24 m, 21 Jun 1988, coll. Cook, SD on CSIRO RV Southern Surveyor
Z.3914	NE tip Wigram I., English Company Is, Gove Peninsula, NT, 11°44.3834'S, 136°37.79'E, 20 m, 12 Nov 1990, coll. Hooper, JNA
Z.3924	Cumberland Strait, northern bay, Wessel Is, Gove Peninsula, NT, 11°27.5'S, 136°28.8'E, 20 m, 14 Nov 1990, coll. Hooper, JNA
Z.3926	Cumberland Strait, northern bay, Wessel Is, Gove Peninsula, NT, 11°27.5'S, 136°28.8'E, 20 m, 14 Nov 1990, coll. Hooper, JNA
Z.3954	N side Pugh Shoal, reef slope, NE Truant I., English Company Is., Gove Peninsula, NT, 11°36.5667'S, 136°53.39'E, 20 m, 18 Nov 1990, coll. Hooper, JNA
Z.3960	N side Pugh Shoal, reef slope, NE Truant I., English Company Is., Gove Peninsula, NT, 11°36.5667'S, 136°53.39'E, 18 m, 18 Nov 1990, coll. Hooper, JNA
Z.4456	Iron Ore Wharf, 100 m E Fort Hill Wharf, Darwin Harbour, NT, 12°28.34'S, 130°50.58'E, 5-15 m, 17 Aug 2002, coll. Alvarez, B and party
Z.4461	Dawson Rock, 3 km SSE Rankin Point, Bynoe Harbour, NT, 12°42.207'S, 130°35.459'E, 3-7 m, 25 May 2003, coll. Alvarez, B and party
Z.4487	Dawson Rock, 3 km SSE Rankin Point, Bynoe Harbour, NT, 12°42.207'S, 130°35.459'E, 5 m, 1 Jun 2005, coll. Alvarez, B
Z.4489	Dawson Rock, 3 km SSE Rankin Point, Bynoe Harbour, NT, 12°42.207'S, 130°35.459'E, 5 m, 1 Jun 2005, coll. Alvarez, B
Z.4493	Bawaka I. near Port Bradshaw, Eastern Arnhem Land, NT, 12°35.206S, 136°46.327E, 12-14 m, coll. Wolf, C
Z.5165	Wiekham Point, 2.5 km SW of East Arm Wharf, East Arm, Darwin Harbour, NT, 12°30.12'S, 130°52.39'E, 4-7 m, 15 Sep 2002, coll. Alvarez, B and party
Z.5166	Spencer Point, Indian I., Bynoe Harbour, NT, 12°35.465'S, 130°31.257'E, 6-12 m, 10 Jun 2003, coll. Nguyen, H
Z.5167	Raragala I., bay on SW coast, Wessel Is, eastern Arnhem Land, NT, 11°38.600'S, 136°17.839'E, 17-20 m, 30 Mar 2004, coll. Alvarez, B
Z.5168	Plater Roek, 1 km E Tale Head, off Cox Peninsula, Darwin Harbour, NT, 12°28.61'S, 130°47.24'E, 5-16 m, 21 May 2002, coll. Alvarez, B and party
Z.5169	Dawson Rock, 3 km SSE Rankin Point, Bynoe Harbour, NT, 12°42.207'S, 130°35.459'E, 5-10 m, 26 May 2003, coll. Alvarez, B and party
Z.5170	Raragala I., bay on SW coast, Wessel Is, eastern Arnhem Land, NT, 11°38.600'S, 136°17.839'E, 17-20 m, 30 Mar 2004, coll. Alvarez, B
Z.5171	Thumb Point, Trafalgar Bay, Marchinbar I., Wessel Is, eastern Arnhem Land, NT, 11°06.690'S, 136°41.262'E, 9-12 m, 31 Mar 2004, coll. Alvarez, B
Z.5172	Rimbija I., 2.8 km W of Cape Wessel, Wessel Is, eastern Arnhem Land, NT, 11°00.208'S, 136°43.836'E, 17-20 m, 1 Apr 2004, coll. Alvarez, B
Z.5173	Plater Roek, 1 km E Tale Head, off Cox Peninsula, Darwin Harbour, NT, 12°28.61'S, 130°47.24'E, 6-14 m, 22 May 2002, coll. Alvarez, B and party
Z.5174	South Shell I., East Arm, Darwin Harbour, NT, 12°29.869'S, 130°53.141'E, 4-11 m, 18 Aug 2002, coll. Alvarez, B and party
Z.5175	Plater Roek, 1 km E Tale Head, off Cox Peninsula, Darwin Harbour, NT, 12°28.61'S, 130°47.24'E, 3-12 m, 5 Jun 2002, coll. Alvarez, B and party
Z.5176	Channel Island, 100-400 m N bridge, Middle Arm, Darwin Harbour, NT, Australia, Australia, 12°33.09'S, 130°52.43'E, 4-8 m, 7 Jun 2002, coll. Alvarez, B and party
Z.5178	Spencer Point, Indian I., Bynoe Harbour, NT, 12°35.465'S, 130°31.257'E, 6-12 m, 10 Jun 2003, coll. Alvarez, B and party
Z.5179	Angler Reef, approx. 3.5 km NW of Lee Pt, Beagle Gulf, NT, 12°18.78'S, 130°54.03'E, 10-12 m, 1 Sep 2002, coll. Alvarez, B and party
Z.5180	Raft Point, Bynoe Harbour, NT, 12°37.682'S, 130°32.175'E, 5-8 m, 26 Jun 2003, coll. Alvarez, B
Z.5182	Dawson Rock, 3 km SSE Rankin Point, Bynoe Harbour, NT, 12°42.207'S, 130°35.459'E, 5-10 m, 26 May 2003, coll. Alvarez, B and party
Z.5183	Wigram I., The English Company Is, eastern Arnhem Land, NT, 11°45.822'S, 136°31.900'E, 13-16 m, 29 Mar 2004, coll. Colin, P
Z.5184	off Dudley Point, Fannie Bay, Darwin Harbour, NT, 12°24.96'S, 130°48.83'E, 4-7 m, 4 Jun 2002, coll. Alvarez, B and party
Z.5694	Channel I., Middle Arm, Darwin, NT, 12°32.0667'S, 130°52.04'E, 13 m depth, 20 August 1982, coll. Alderslade, PN
Z.5856	'Bottle Washer' artificial reef, approx. 5 km NW Lee Pt, Beagle Gulf, NT, 12°18.14'S, 130°51.75'E, 8-13 m, 2 Sep 2002, coll. Alvarez, B and party
Z.5857	Channel Island, 100-400 m N bridge, Middle Arm, Darwin Harbour, NT, Australia, Australia, 12°33.09'S, 130°52.43'E, intertidal not exposed m, 6 May 2002, coll. Alvarez, B and party

APPENDIX

Collection and locality data for material examined in the collections of QM and NTM
NTM material

Z.5858	Dawson Rock, 3 km SSE Rankin Point, Bynoe Harbour, NT, 12°42.207'S, 130°35.459'E, 6 m, 27 Apr 2007, coll. Alvarez, B
Z.5861	N Edgell, off Kota Kinabalu, Malaysia, 6°00.629'N, 115°59.382'E, 10-28 m, 23 Oct 2005, coll. Alvarez, B
Z.5862	N Gaya I., off Kota Kinabalu, Malaysia, 6°02.068'N, 116°00.385'E, 10-18 m, 23 Oct 2005, coll. Alvarez, B
Z.5865	Plater Rock, 1 km E Talc Head, off Cox Peninsula, Darwin Harbour, NT, 12°28.61'S, 130°47.24'E, 5-16 m, 21 May 2002, coll. Alvarez, B and party
Z.5866	S Edgell, Kota Kinabalu, Malaysia, 6°00.259' N., 115°59.169'E, 10-20 m, 25 Oct 2005, coll. Alvarez, B
Z.5867	S Edgell, Kota Kinabalu, Malaysia, 6°00.259' N., 115°59.169'E, 10-20 m, 25 Oct 2005, coll. Alvarez, B
Z.5868	S Gaya I., Kota Kinabalu, Malaysia, 6°00.403' N., 116°01.572'E, 10-12 m, 25 Oct 2005, coll. Colin, P
Z.5870	Stevens Rock, Weed Reef, Darwin Harbour, NT, 12°29.1667'S, 130°47.19'E, 10 m, 8 May 2006, coll. Alvarez, B
Z.5871	Stevens Rock, Weed Reef, Darwin Harbour, NT, 12°29.2001'S, 130°47.1'E, 5-19 m, 8 May 2002, coll. Alvarez, B and party
Z.5882	'Bottle Washer' artificial reef, approx. 5 km NW Lee Pt, Beagle Gulf, NT, 12°18.14'S, 130°51.75'E, 8-13 m, 2 Sep 2002, coll. Alvarez, B and party
Z.5885	Channel Island, 100-400 m N bridge, Middle Arm, Darwin Harbour, NT, Australia, Australia, 12°33.09'S, 130°52.43'E, 4-8 m, 6 May 2002, coll. Alvarez, B and party
Z.5886	Dawson Rock, 3 km SSE Rankin Point, Bynoe Harbour, NT, 12°42.207'S, 130°35.459'E, 3-12 m, 1 Jun 2005, coll. Alvarez, B
Z.5896	off Dudley Point, Fannie Bay, Darwin Harbour, NT, 12°24.96'S, 130°48.83'E, 4-7 m, 4 Jun 2002, coll. Alvarez, B and party

Revision of the pantropical genus *Treptopale* (Annelida: Phyllodocida: Chrysopetalidae): redescription of *Treptopale rudolphi* Perkins, 1985 and description of two new species including comparison of *Treptopale* populations in northern Australia

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ABSTRACT

The monotypic genus *Treptopale*, originally described from the Atlantic Ocean, is now extended – with the description of two new species with a broad and almost sympatric distribution – throughout the Indo-Pacific Ocean. The type species, *Treptopale rudolphi* Perkins, 1985, is redescribed from additional material from the type locality in the Florida Keys, western Atlantic Ocean, and from material examined from the Cape Verde Islands and Cape Town, South Africa. The morphology of the notochaetal lateral paleae group separates the Atlantic *Treptopale rudolphi* from a cryptic *Treptopale* species complex that extends from the Seychelles, western Indian Ocean, throughout the western Indo-Pacific to Hawai'i, eastern Pacific Ocean. Morphological analysis of tropical northern Australian populations of the two new *Treptopale* species, which are typically found among *Halimeda* algae on coral reefs, revealed two species separated primarily on the shape and insertion point of a transitional lateral palea and a marked difference in the degree of raised ribs of the main paleae: *Treptopale homalos* sp. nov. is predominantly found along the eastern Queensland coast from Heron Island north to New Guinea; *T. paramolos* sp. nov. is predominantly found along the Northern Territory coast. The two species occur sympatrically in a number of localities across tropical northern Australia and both are present on offshore and mainland reefs of northern Western Australia. Reproductive and larval states and chaetal patterns within and between species are presented. The two patterns of morphology and diversity present in these taxa, observed also across the Indo-Pacific, are plausibly related to ancient colonisation histories.

KEYWORDS: Annelida, Polychaeta, Chrysopetalidae, *Treptopale*, cryptic new species, coral reefs, taxonomy, systematics, larval morphology, biogeography.

INTRODUCTION

The Chrysopetalidae is one of the most common families of polychaete worms associated with habitat complexity in tropical embayments and fringing mainland and offshore coral reefs of the Indo-Pacific and Western Atlantic (Peyrot-Clausade 1974 [Tulear reefs, Madagascar]; Hutchings & Murray 1982 [Great Barrier Reef (GBR), north-eastern Australia]; Bailey-Broek 1995 [Western Pacific]; Peyrot-Clausade 1976 [Tiahura reefs, Moorea]; Perkins 1985 [Gulf of Mexico, Florida, Caribbean]). In common with many coral reef dwelling polychaetes, chrysopetalids find refuge in algal cover overlying a hard substratum (Bailey-Broek 1980).

Throughout the Indo-Pacific, adults of the chrysopetalid genus *Treptopale* are commonly collected from dead coral rubble often associated with calcareous algae of the genus *Halimeda*. *Treptopale* are small, highly fragmentable chrysopetalids with elongate bodies and translucent to pale golden fans composed of symmetrical paleae held in tight fans over the dorsum. *Treptopale* species have separate sexes

and adults are also recorded from the plankton (Watson Russell 2000a).

Treptopale was first listed as part of the Australian chrysopetalid fauna by Watson Russell (2000a). The *Treptopale* species complex was subsequently collected from habitats ranging from algae and rubble in clear deep water from the edge of the continental shelf of the outer Great Barrier Reef, Queensland and Scott Reef, Western Australia, to shallow muddy mainland reefs with high turbidity in Darwin, Northern Territory, to fringing reefs of Ningaloo, Western Australia.

Analysis of the *Treptopale* species complex from tropical northern Australia revealed two morphotypes, based primarily on shape and insertion point of a single transitional lateral palea (labelled subunit 1 palea) and a related marked difference in the degree of ornamentation of the raised ribs on the main paleae. The 'robust' morphotype (designated in 'type 1') was predominantly found along the eastern Queensland coast from Heron Island north to New Guinea, and the more 'fragile' morphotype (designated 'type 2') predominated along the Northern Territory coast. Type 1

and type 2 morphotypes were present either sympatrically or separately from offshore and mainland reefs of northern Western Australia.

Similar 'robust' and 'fragile' morphotypes were also found throughout the Indo-Pacific Ocean from similar coral reef habitats. In this paper, on the basis of morphological observations, these morphotypes are interpreted as separate species and are described herein as new species.

MATERIALS AND METHODS

Additional *Treptopale* material from five northern Australian localities was collected for molecular work (Fig. 10). These specimens are marked with an asterisk after the museum registration number in the Material examined sections below. Tissue samples are being analysed using the markers, cytochrome c oxidase subunit 1 (CO1) of mitochondrial DNA (mtDNA) and histone 3. These results will be presented in a separate paper (Wei & Watson in prep.).

Setal terminology follows that of Watson Russell (1986) with designations of notochaetal palcae types based on position: i.e. lateral group inserts below the acicula; main group inserts above the acicula; and median group inserts at the mid-dorsal line. The category 'subunit 1 palca' used in this paper refers to one or two small palcae that insert between the lateral and main groups. Description of species is based on the holotype with numerical data derived from additional material in brackets.

Abbreviations. Within Material examined sections, additional information is included: E, entire specimen; NE, specimen not entire; L, length; W, width. Note that many collections are composed of 'fragments' only.

The material examined for this study is housed in the following institutions: Muséum National d'Histoire Naturelle, Paris (MNHN); Zoological Museum Berlin (ZMB); National Museum of Natural History, Washington (USNM); Australian Museum, Sydney (AM); Museum Victoria, Melbourne (NMV); Museum and Art Gallery of the Northern Territory [formerly Northern Territory Museum], Darwin (NTM); Queensland Museum, Brisbane (QM); Phuket Marine Laboratory, Thailand (PML); Berenice P. Bishop Museum, Honolulu, Hawai'i (BPBM). Other acronyms used in the paper are Australian Institute of Marine Science (AIMS), Charles Darwin University (CDU) and Great Barrier Reef (GBR).

SYSTEMATICS

Family Chrysopetalidae Ehlers, 1864

Treptopale Perkins, 1985

Treptopale Perkins, 1985. Gender masculine. Type-species, by monotypy, *Treptopale rudolphi* Perkins, 1985. Recent, Florida, USA.

Diagnosis. Body elongate, tapering at anterior end; body segments very fragmentable. First segment achactigerous with 2 pairs of tentacular cirri. Second segment biramous with notochaetae, pair of dorsal cirri; neuropodium with neurochaetae, ventral cirri absent. Mid-body notopodia with lateral, main and median palcae types. Main palcae symmetrical, robustly to minimally ornamented with raised ribs. Lateral palcae blunt-tipped, almost rod-like, with marginal serration absent to minimal, low number of ribs or pointed with distinct margin serration and higher number of ribs. Subunit 1 palca small, pointed or larger, robust with equal margins or fragile with unequal inner margin. Mid-body neurochaetae faleigerous. Pygidium quadrate with two anal cirri.

Description. Maximum segment number 120; segments broadly rectangular in section. Body colour in live animals pale yellow to white, often with bright yellow or orange internal notopodial and neuropodial pigment spots; opaque white patch very common interramally (under compound microscope light looks black in gametogenic individuals). Greenish black algal material may be present in gut; oil droplets common in parapodia. Translucent to pale golden palcae in transverse row on notopodium with leading edges visible distally; median palcae interlock at mid-line forming slight convex median ridge.

Prostomium small, rounded, often compressed between anterior 3 segments. Eyes 2 pairs, violet to red; anterior pair larger and often fused in part to posterior pair. Single, large, distally swollen median antenna and 2 slightly longer lateral antennae, basally swollen and distally cirriform, insert on anteroventral margin of prostomium. Palps 2, ovoid, insert on ventral edge of prostomium. Proboscis eversible with 2 slender stylets with slightly darker distal tips; mouth flap small, usually triangular when relaxed; when contracted, a swollen glandular ridge. Dark pigment spots may be present on mouth fold and surrounding area. Glandular nuchal fold present; visible in varying degrees, capable of covering posterior half of prostomium.

First segment reduced, achactigerous, supporting 2 pairs of dorsal and ventral tentacular cirri; ventral pair originate adjacent to palps. Second segment biramous, with notopodial fasciole with 3–5, short, almost symmetrical palcae; neuropodium with fasciole of spinigerous neurochaetae; dorsal cirrus present, ventral cirrus absent. Third segment, fused in part with segment 2, directed anterolaterally. All subsequent setigers directed laterally.

Mid-body notopodium with 2–3 (6) slender, subacicular lateral palcae including blunt-tipped, almost rod-like laterals with 1–2 ribs and marginal serration absent to minimal (Atlantic species) or pointed with 3–6 (8) ribs and marginal serration mostly developed (Indo-Pacific species). Symmetrical subunit 1 palcae number 1–2 with serrate margins. Within posterior 10 segments, subunit 1 palca often replaced by much shorter, slim palca with low number of ribs. Small, short, notosetal spines may be present in lateral-anterior position of main palcae group.

Mid-body notopodium with symmetrical (to sub-symmetrical) main palcae, numbering 10–16 (20), with very shallow to short apical points; possess 14–21(23) ribs with variable raised rib pattern, highly sculptured with 2–3 major and nearly every other rib highly ornamented or with 2–3 major and some other ribs either highly or finely serrate or no major ribs and very little to no ornamentation. Main palcae with broad to more rounded distal ends, both margins either robustly or finely serrated. Most-medial main palca more rounded distally, more slender, with fewer number of ribs.

Mid-body notopodium with 3–4 (5) median palcae arising from similar insertion point, comprising 2 taller, broader more laterally positioned palcae and 2 shorter more medial palcae. Possess 9–15(17) internal ribs with 1–3 major and sometimes additional raised and finely to coarsely serrated ribs (that extend part or full length of palcae) to minimal ornamentation. Median palcae range from usual broad and asymmetric to slender, just sub-symmetrical shape. Apices of all palcae types may be covered in minute hoods. Dorsal cirrostyle subulate, strongly to weakly pseudoarticulated, inserting at lateral posterior edge of notopodium. Interramal region ciliate.

First chaetigerous neuropodium with all spinigerous neurosetae; setigers 2–5 with 1–2 spinigers and long-bladed falcigers. Mid-body broad, pointed neuropodium with single long acicula below which insert fascicle of heterogomph neurochaetae; superior group of 1–3 serrate, long-bladed falcigers, mid-group with about 20 falcigers with medium length serrate blades, inferior group with about 6–8 falcigers with shorter slender blades with fine dentition; narrowest blades found in posterior setigers. All neurochaetal shaft cores subdivided internally with longitudinal and horizontal striae. Ventral cirrus short and broad to more filiform, weakly pseudoarticulated, inserting below neurosetal fascicle. Pygidium quadrate, with 2 filiform anal cirri on posterolateral edge. Anus ventral.

Remarks. The majority of chrysopetalid palcate genera (e.g. *Treptopale*, *Arichlidon*, *Bhawania* and *Paleaquor*) comprise cryptic species that are morphologically difficult to separate (pers. obs.). Complexes of cryptic species of these genera have, on close inspection, subtle morphological differences, often based on the presence and shape of a single paleal notochaeta. It is these single palea that insert 'between' the main palcae groups that turn out to be a key species character e.g. subunit 1 palca in *Treptopale* and medial-most main palca in *Arichlidon* (Watson Russell 1986, 1998, 2000b).

Day (1962: 635) incorrectly synonymised *Paleanotus* with *Chrysopetalum*. Both genera are clearly distinguished not only by the very characteristic notochaetal types but by differences of the anterior end. Perkins (1985: 865) recognised these two genera as distinct and further created two new genera, *Treptopale* and *Hyalopale*, closely related to *Paleanotus* as they share the same anterior end configuration as well as similarities of chaetal types.

Species of *Treptopale* are distinguished by predominantly symmetrical main palcae, whereas *Paleanotus* possesses asymmetrical main palcae, as does the very small and rarely occurring *Hyalopale*, which possesses a number of paleanotine neotenous characters. Perkins (1985) did not observe the *Treptopale* pygidium, but its quadrate shape with two small anal cirri (Fig. 8B) is the same as that of *Paleanotus* and *Hyalopale* (pers. obs.).

Perkins (1985) stated that *Treptopale* differs from *Paleanotus* in two characteristics – the position of the mouth opening related to possible differences in the structure of the proboscis, and the overall number of body segments. According to the author's present research there are no structural proboscis differences between these two genera. The position of prostomium and its appendages plus that of the mouth fold changes according to the degree of contraction of the anterior end within the anterior segments. When the anterior end is contracted tightly, the prostomial appendages are hardly visible dorsally and better viewed in ventral position (Fig. 6B), but when more relaxed they are more visible in antero-dorsal view (Fig. 4A). When contracted, the mouth fold appears as a triangular structure immediately below the palps near chaetiger 1 and 2 boundary (Fig. 6B). When the mouth is more open, it can appear as a horizontal or longitudinal gash at a level between chaetiger 2 and 3, with the revealed lips covered in dark glandular spots, which may also be seen on the surrounding ventrum (Fig. 6C). Perkins (1985) recorded entire specimens of *Treptopale* reaching 60 segments and *Paleanotus* to 40 segments. Material recorded in this paper and observed by the author increases the former to 120 segments and the latter to 60 segments.

Treptopale does not possess a discreet rounded caruncle, as in *Chrysopetalum*, but a glandular nuchal fold. This fold is also present in *Paleanotus* and in most other chrysopetalid genera. Perkins (1985) described *Treptopale* as having no caruncle, but in both Atlantic and Indo-Pacific specimens where the prostomium is not fully contracted, a glandular nuchal fold is clearly evident (Fig. 6A). However, *Treptopale* does have greater narrowing of the anterior segments compared to other genera and, while a glandular nuchal area is always visible, a discrete nuchal membranous fold is sometimes not visible.

The insertion points of the notochaetal paleae types and the numbers of lateral, main and median palcae, including their rib numbers, are similar between *Treptopale* and *Paleanotus*, as also are the shapes of the dorsal and ventral cirri, with the dorsal cirri often sharing the same characteristic downward 'hang' (Figs. 1A,C).

Treptopale differs from *Paleanotus* in the possession of symmetrical palcae and uniquely shaped subunit 1 palea(e); the longer body has an anterior end comparatively narrower and body segments more fragmentable. The three *Treptopale* species described in this paper are all more similar to each other in comparison to a much larger suite of clearly morphologically differentiated species of *Paleanotus*. A

paper on *Paleanotus* is currently in preparation by the author, including DNA sequences, the results of which will help to clarify relationships between these two genera.

At first glance, it can be easy to confuse *Treptopale* (especially *T. homalos* sp. nov) and species of the genus *Arichlidon* in their possession of ornate symmetrical main palcae. However, *Treptopale* lacks the dense granules of the main palcae seen in *Arichlidon*. Both genera have different body shapes, that of *Arichlidon* being much broader throughout its length and its palcae often being flecked with a brown scale. The small lateral fascicle in *Treptopale* is distinct and separate with slender, short palcae in comparison to the broad lateral fascicle of *Arichlidon* which forms a smooth intergrading fascicle with the main group (Watson Russell 1998).

Treptopale and the rarely occurring *Bhawania riveti* (species complex), can co-occur in the same coral rubble habitat, and both have similarly shaped lateral, symmetrical main and median palcae. However, *Treptopale* is associated with *Halimeda* and rubble, and *Bhawania riveti* lives deeper, inside cavities in coral blocks. The body form and colour of both are very different: *Treptopale* has a pale body with silvery to pale golden palcae fans and up to 120 segments, whereas *B. riveti* has a brown body with dark golden palcae fans, ventral dark brown interramal spots and is overall more slender, with up to 300 segments.

Habitat and Distribution. Members of the genus *Treptopale* are found in the tropical regions of the major continents (pantropical) on mainland and offshore coral reefs between 24°N and 33°S. *Treptopale* species inhabit coral rubble associated with *Halimeda* and coralline algae or rubble in sand from LWS to 35 m.

Key to species of the genus *Treptopale*

1. Mid-body notopodial subacicular lateral palcae include 2 (3) slender, blunt tipped, almost rod-like, palcae with 1–2 ribs; margin serration absent to minimal
..... *Treptopale rudolphi* (Atlantic, Fig. 1A)
- Mid-body notopodial subacicular lateral palcae with 2–4 (6) slender, pointed palcae with 3–6 (8) ribs; marginal serration mostly well developed.....
..... 2 (Indo-Pacific, Fig. 3A)
2. Mid-body notopodia with robust subunit 1 palca (palca between lateral and main groups) inserting supra-acicularly, with symmetrical margins, 6–12 ribs including 1–4 raised ribs; main palcae with robustly ornamented raised ribs.....
..... *Treptopale homalos* sp. nov. (Fig. 3B)
- Mid-body notopodia with less robust subunit 1 palca inserting either overlying or sub-acicularly, pointed with inner margin asymmetrical, 6–11 ribs (including 1–2 finely raised ribs); main palcae with minimal to finely ornamented raised ribs.....
..... *Treptopale paromolos* sp. nov. (Fig. 7)

Treptopale rudolphi Perkins, 1985

Figs 1 A–D, 2

Treptopale rudolphi Perkins, 1985: 905–907; Núñez 1998: 21–27.

HOLOTYPE (not examined) – USNM 97370, 1E, 60 segments, L: 5.5 mm, W: 0.5 mm, Western Atlantic, United States, Florida, Ragged Keys, 25°32'N, 80°10'W, 2–3 m, hard substrate (data from Perkins 1985).

Material examined. WESTERN ATLANTIC OCEAN: USNM 1148243, anterior end, 3 sets fragments, W: 0.72 mm, United States, Florida, Mud Key, 24°42'N, 81°45'W, coll. Cr. 17, R.V. *Hernan Cortez*, April 1965; MNHN PNT 25, fragments, W: 1.4 mm. EASTERN ATLANTIC OCEAN: Cape Verde Islands, Stn. 52, rocky bottom, 20 m, coll. R.V. *Calypso*; ZMB 5763, anterior end, mid-body fragments, 40 NE, W: 1.2 mm, South Africa, Cape Town, Simonstown, coll. Deutsche Südpolar Expedition, July 1903; SAM 21453, fragments, W: 1.4 mm, South Africa, Seal Island.

Description (based on composite of fragmented material). Body elongate, pale yellow; palcae pale golden to almost transparent, in uniform rows down dorsum. Prostomium with 2 pairs of red eyes, short median antenna, 2 filiform lateral antennae, 2 rounded palps; nuchal fold very small, obscured. Segments 1 and 2 with 3 pairs of dorsal and ventral cirri (Perkins 1985: figs 26 A,B).

Mid-body notopodium with 2–3, slender, blunt-tipped, almost rod-like lateral palcae with 1–2 ribs; no marginal serration on lower edge, very slight serration on upper margin (Fig. 1 A–D). Subunit 1 palcae, numbering 1–2, with serrate margins, 3–5 ribs, pointed distally, no raised ribs (Fig. 1 D). Few small anterior spines present, observed only in Florida individual. Symmetrical main palcae 10–13 with 17–21 (23) ribs and 2–4 lightly ornamented ribs. Three asymmetrical median palcae present with 11–12 ribs (Florida and Cape Verde Islands) and 14–15 (16) (Simonstown and Seal Island); 0–3 very lightly beaded ribs (Fig. 1C).

Mid-body neuropodium with 2–3 superior long-bladed falcigers, 3–4 shorter long-bladed falcigers, 8–10 medium-bladed falcigers and 4–6 short-bladed inferior falcigers. Total about 20 (Cape Verde specimen). Pygidium quadrate, with 2 slender anal cirri.

Remarks. Perkins' (1985: 907) original description stated that the lateral palcae of *Treptopale rudolphi* have serrate margins and "about 5 ribs". He did not figure any lateral palcae but did figure "anterior group palca" (Perkins 1985: fig. 27D) which correspond to the subunit 1 palca of this study. It appears that Perkins collapsed the description of the lateral palcae with that of the subunit 1 palca(e). *Treptopale rudolphi* examined from Mud Key, Florida (near the type locality of Ragged Keys) and from three other eastern Atlantic localities, all possess the same morphology of the subacicular lateral palcae fascicle, i.e. blunt-tipped laterals with 1–3 ribs and little or no marginal serration.

The Mud Key specimen has one to two subunit 1 palcae, inserting above the dorsal acicula which are short, possess 4–5 ribs, arc pointed distally, and have serrate margins

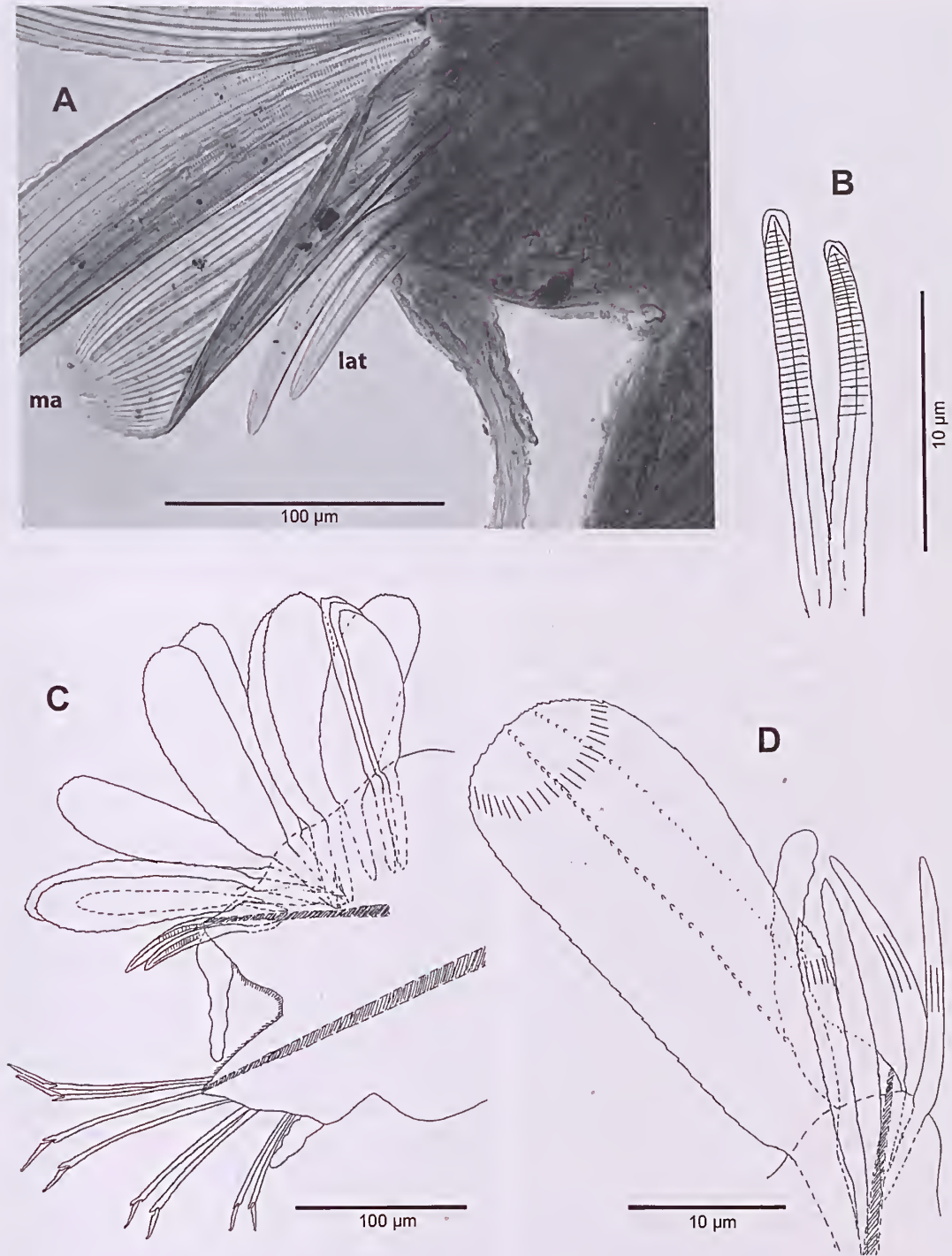


Fig. 1. *Treptopale rudolphi* sp. nov.: A,C, ZMB 5763, South Africa, slide preparation, mid-body parapodium, la = lateral paleac, ma = main paleac; B, MNHN PNT 25, Cape Verde Islands, detail of lateral paleae mid-body parapodium; C, mid-body parapodium with notochaetae lateral, main and median paleae groups [Note: not all neurochaetae drawn]; D, USNM 1148243, Mud Key, Florida, mid body parapodium, detail of lateral and subunit 1 paleae. Scale lines: A –100 µm; B –0.01mm; C –0.1mm; D –0.01 mm.

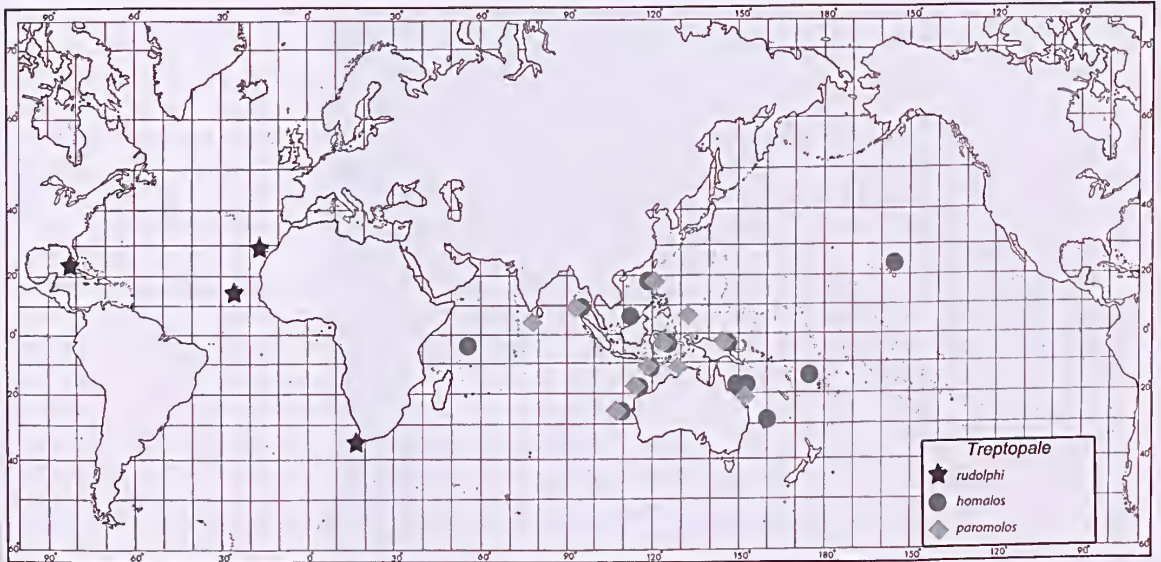


Fig. 2. World map showing distribution of species of the genus *Treptopale*.

(Fig. 1D). The larger Simonstown individual has one subunit 1 palea with 10–11 ribs (Fig. 1C). This latter specimen also possesses lightly ribbed main and median paleae very similar to those seen in the specimens from Florida. The other South African Seal Island specimen has slightly heavier ribbed main paleae. Unfortunately it was not possible to examine the lateral paleae morphology or a small unusual neuropodial structure described for a *Treptopale rudolphi* specimen from the Canary Islands (Núñez 1998: fig. 2G, specimen lost, Núñez, pers. comm.).

Detailed morphological examination comparing the very similar Atlantic and Indo-Pacific *Treptopale* material revealed small but consistent differences in the shape and number of the lateral paleae fasciole. The lateral paleae morphology is the most important character separating the Atlantic *Treptopale* species (Fig. 1A–D) from the Indo-Pacific species (compare Figs. 3A, 4E,F, 8A, and see Key). Atlantic specimens also have main and median paleae with none or few very shallow raised ribs (see Perkins 1985: fig. 27; SEM Núñez 1998: fig. 3C; this paper Fig. 1A,D). This degree of ornamentation is closer to that seen in the Indo-Pacific *Treptopale paromolos* sp. nov. and distinct from the highly ornamented Indo-Pacific *Treptopale homalos* sp. nov.

The question of whether *Treptopale rudolphi* is truly an ampho-Atlantic species needs to be tested at the molecular level with a larger sample size. Trans-Atlantic dispersal of meiofaunal polychaetes of the same species has been recorded by Westheide *et al.* (2003) based on evidence from molecular data.

Habitat and Distribution. *Treptopale rudolphi* is found between 24°N (Florida) and 33°S (Cape Town, South Africa), western and eastern Atlantic Ocean. The species

is associated with hard rocky bottoms (Perkins 1985) and sponges (Núñez 1998), from 2–20 m.

Treptopale homalos sp. nov.

Figs 2, 3A,B, 4A–F, 10

Material examined. HOLOTYPE – QM G232165, 51 segments, entire, L: 7 mm, W: 0.8 mm, Australia, Queensland, GBR, Lizard Island, SW Palfrey Island, Stn. CGLI024, 14°41'S, 145°6'E, coral rubble, 4 m, coll. M. Ekins, April 2008. PARATYPE – NTM W.23074*, 1, Lizard Island, Mermaid Cove, 14°38'S, 145°27'W, Stn. CG LI006, Halimeda & rubble, 2 m, coll. C. Watson, April 2008.

Additional (non-type) material examined. QUEENSLAND: GBR, NTM W. 23221, 2 (1 adult, 40NE, 1 post larvae, 10E), off Townsville, inner shelf, Philips Reef, 18°59'S, 146°36'E, coral rubble, coll. M. Riddle, October 1985; NTM W. 23076*, 1, Lizard Island, bommie near entrance to lagoon, 14°41'S, 145°27'W, 15 m, coll. C. Glasby, April 2008; NTM W.23077*, 1, North Direction Island, Stn. CGLI019, 14°44'S, 145°30'W, 5 m, coll. M. Ekins, April 2008; NTM W.22891*, 1E, male, 118 segments, L: 21.2 mm, W: 1.5 mm, Outer Barrier Reef, Hicks Reef, Stn. CWLI020, 14°38'S, 145°7'E, coral rubble, 2–18 m, coll. C. Watson & K. Mills, February 2009; NTM W.22892*, 1NE, 60 segments, L: 9.6 mm, W: 1.0 mm, ovigerous female, Hicks Reef, Stn. CWLI047, 14°26'S, 145°26'E, 10 m, coll. M. Blazewicz & N. Bruce, February 2009; NTM W.22891*, 1E, 120 segments, L: 21.2 mm, W: 1.5 mm, Day Reef, Stn. CWLI048, 14°30'S, 145°0'E, 30 m, coll. J. Caley & K. Mills, February 2009; NTM W.22889*, 1, Yonge Reef, Stn. CWLI015, 14°36'S, 145°37'W, 2 m, coll. C. Watson, February 2009; NTM W.23055, 1E, Snake Pit, Stn. CWLI054A, 14°40'S, 145°34'W, *Halimeda* compacted banks, 30 m, coll. J. Caley & S. Smith, February 2009; NTM W.22890*, 1, MacGillivray Reef, Stn. CWLI058, 14°39'S,

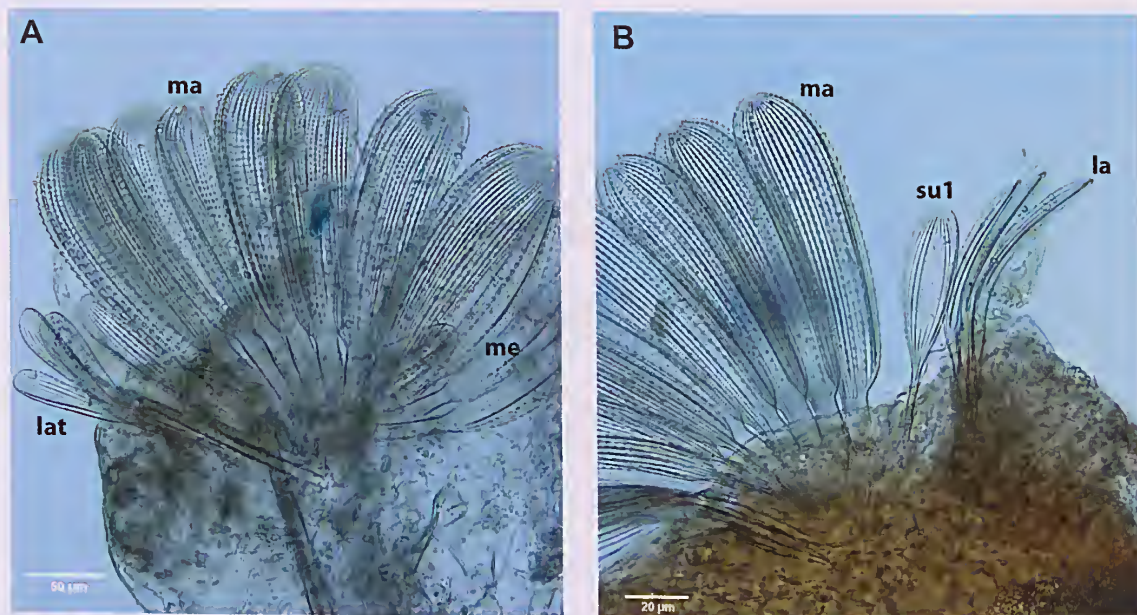


Fig. 3. *Treptopale homalos* sp. nov.: NTM W.22891, Lizard Island, Great Barrier Reef. A, slide preparation, mid-body notopodium in part, lat = lateral palcae group, ma = main palcae group, me = median palcae group; B, slide preparation, mid-body notopodium in part, su1 = subunit 1 palcae.

145°29'W, 30 m, coll. K. Mills & S. Smith, February 2009; NTM W.23058, 1, Linnet Reef, Stn. CWLI027, 14°46'S, 145°20'W, 4 m, coll. M. Blazewicz, February 2009; NTM W.23071*, 1, Heron Island, Capricorn Group, South East Lamont Reef, Stn. HI09-059, 23°35'S, 152°3'E, coarse coral rubble, 15 m, coll. N. Bruce, November 2009; NTM W.23072*, 1, North Wistari Reef, Stn. HI09-002, 23°27'S, 152°52'E, coarse coral rubble, 12 m, coll. M. Capa & P. Hutchings, November 2009; NTM W.23073*, 1, Sykes Reef, Stn. HI09-046, 23°25'S, 152°2'E, coarse coral rubble, 10 m, November 2009; NTM W.23070*, 1, Sykes Reef, Stn. HI09-046, 23°26'S, 152°2'E, coarse coral rubble, 10 m, November 2009; NTM W.23079, 1, Lamont Reef, Stn. HI09-031, 23°36'S, 152°3'E, coarse coral rubble, 30 m, coll. S. Smith & A. Anderson, November 2009; NTM W.23080, 1, Twin Peaks, Stn. HI09-012, 23°28'S, 152°57'E, 2 m, coarse coral rubble, coll. M. Capa, November 2009. NEW SOUTH WALES: AM W.23356, 1NE, anterior end, W: 0.5 mm, Elizabeth Reef, 29°55'S, 159°01'E, Stn. 43, LWS, from algac, coll. P. Hutchings, December 1987; AM W.23362, 1E, 32 segments, L: 2.6 mm, Elizabeth Reef, Stn.36, coll. P. Hutchings, December 1987. NORTHERN TERRITORY: NTM W. 22944*, 1NE, 49 segments, W: 1.5 mm, Darwin, Channel Island, 12°33'S, 130°52'E, *Halimeda*, brown & red algae, rubble, LWS, coll. C. Watson, September 2007. WESTERNAUSTRALIA: NTM W. 4158, 1E plus fragments, Ashmore Reef, 12°S, 123°E, coralline algae & coral rubble, 15 m, coll. B.C. Russell, February 1984; NTM W.7288, 1NE, 74 segments, male, Cartier Reef, Stn. RH6, outer reef slope, 14 m, coll. J.R. Hanley, May 1992; NTM W.2273, 11NE, W: 1.52 mm,

Broome, Cable Beach, 17°58'S, 122°11'E, under rocks, LWS, coll. J.R. Hanley, September 1984; AM W.36172, 1NE, Dampier Archipelago, north east Delambre Island, coll. P. Hutchings, August 2000; NTM W.5107, 1, ovigerous female, 85NE, W: 1.7 mm, Exmouth, S.S. *Mildura* wreck, 21°86'S, 114°07'E, inside rubble, LWS, coll. J.R. Hanley, February 1988; NTM W.23082*, fragments, Ningaloo, 22°5'S, 113°61'E, Stn. NR09-004, coarse coral rubble, 17 m, coll. P. Hutchings *et al.*, May 2009. WESTERN PACIFIC OCEAN, NEW GUINEA: NTM W.21788, fragments, W: 1.3 mm, Wongat Island, 5°8'N, 145°49'E, Stn. RH91/88, coral reef and sand, 10 m, coll. J.R. Hanley, October 1991; NTM W.21782, 1, Malamal Island, 5°9'N, 147°5'E, Stn. RH91/104, scagrass, sand & coral, 1 m, coll. J.R. Hanley, October 1991; NTM W.21786, 1, Padoz Reef, patch reef inside lagoon, 5°9'S, 145°48'E, Stn. RH 91/83, 21 m, coll. J.R. Hanley, October 1991; NTM W.21783, 1, Tripod Reef, Madang, 5°10'S, 145°50'E, Stn. RH 91/108, 8 m, coll. J.R. Hanley, 26 October 1991; AMERICAN SAMOA: AM W.36675, 1, Vatia Bay, 14°14'S, 170°4'E, Stn. 9, 28 m, coll. Reath & Bonito, October 2000. INDONESIA: NTM W.21790, fragments, Flores, Maumerc, coral rubble & sand, 24–27 m, coll. B.C. Russell, Nov 1991; AM W.36676, 1, Togian Island, Hut Reef, 0°3'S, 121°41'S, outer reef slope, coralline algae, 35 m, coll. P. Hutchings, September 1999. MALAYSIA, SOUTH CHINA SEA: NTM W.13139, 50NE, Sabah, Kota Kinabalu, Sapi island, 5°58'N, 116°05'E, coral rubble & algac, 1.5 m, coll. C. Watson, August 1995. PHILIPPINE ISLANDS: NTM W.23363, fragments, Luzon, Cape Bolinao, 16°25'N, 119°50'E, coral rubble, sponge, red algae, 12–25 m, coll.

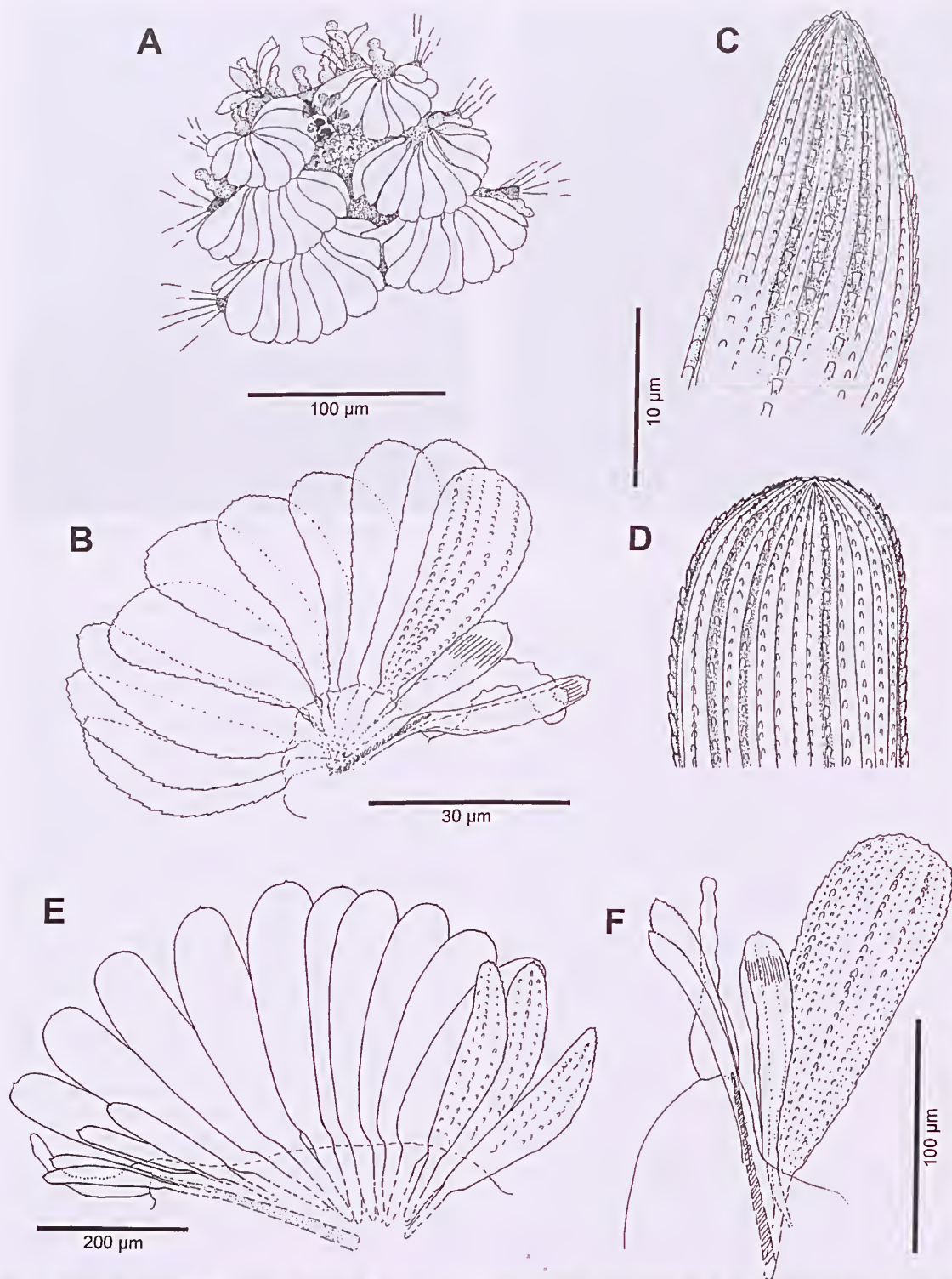


Fig. 4. *Treptopale homalos* sp. nov. A,B, Holotype, QM G232165, Lizard Island, Great Barrier Reef: A, anterior end, dorsal view; B, notopodium, setiger 3; C,D, AM W.196779, Lizard Island, Great Barrier Reef, planktonic specimen, C, median palca detail, D, main palca detail; E, MNHN A845, Seychelles, mid-body notopodium; F, NTM W. 23225, Hawaii, mid-body notopodium in part. Scale lines: A – 0.1 mm; B – 0.1 mm; C – 0.01 mm; D – 0.01 mm; E – 0.2 mm; F – 0.1 mm.

B.C. Russell, October 1995. EASTERN PACIFIC OCEAN, HAWAII: NTM.W.23225, anterior and posterior ends and fragments, Oahu Island, 21°30'N, 158°00'W, Kaneohe Bay, coral reef, shallow, coll. J. Broek; NTM.W.23224, anterior & posterior ends, Kaneohe Bay, coral reef, deep, coll. J. Broek. INDIAN OCEAN: THAILAND: NTM.W.23359, fragments, Surin Island, 10°N, 98°E, amongst oyster shells, coll. A. Nateewathana & J. Hylleberg, February 1981. SEYCHELLES: MNHN A845, fragments, 4°35'S, 55°40'E, Tanikely, coll. Cherbonnier, April 1960. PLANKTON, ADULT MATERIAL: AM.W.196779, 2 midbody fragments, W: 0.72 mm, Osprey Island, Stn.16.7.2, 20.36 hr, 3 m, coll. J. Leis, July 1979; AM.W.196780, 1E, 44 segments, L: 4.2 mm, W: 0.7 mm, Lizard Island lagoon, Stn.24.7.2, 19.55 hr, 3 m, coll. J. Leis, July 1979. POST-LARVAL MATERIAL: NTM.W.17860, 10E, L: 0.64 mm, W: 0.28 mm, Queensland, Dip Reef, 18°25'S, 147°27'E, coll. M. Riddle, October 1985; NTM.W.18249, 13E, length 0.6 mm, width 0.32 mm, Lodestone Reef, mid-shelf, 18°42'S, 147°06'E, coll. M. Riddle, October 1985; NTM.W.18250, 12E, Philips Reef, inner shelf, 18°59'S, 146°36'E, coll. M. Riddle, October 1985.

Description. Body elongate, white to pale yellow (pale greenish in some live specimens); deep to pale gold paleae in uniform rows covering dorsum. Quadrate-shaped prostomium partly contracted ventrally, with scattered dark maroon-red eye pigment; median antenna short, bulbous distally; 2 filiform lateral antennae with bulbous bases; 2 rounded palps; nuchal fold small, clearly visible glandular area posterior to prostomium (Fig. 4A). Segment 1 uniramous, achaetigerous with 2 pairs of tentacular cirri. Segment 2 (setiger 1) biramous; notopodium with up to 4 short paleae with 4–6 ribs and dorsal cirrus; neuropodium with fascicle of spinigerous setae, ventral cirri absent.

Setiger 2 with lateral and main paleae, no median paleae present. Setiger 3 with 1–2 lateral paleae with 5–6 ribs; subunit 1 palea with serrate margins, 9 ribs including 2 raised, inserting above dorsal aciculum and at base of lateral main paleae; 7 main with 16 ribs heavily ornamented; 3 broad median paleae (Fig. 4B). Mid-body lateral paleae number 2–3 (4,5), with 5–8 (9) ribs; subunit 1 numbering 1–2, with 8–12 (13) ribs and 1–4 slightly ornamented ribs (Fig. 3A,B).

Main paleae with heavily ornamented raised ribs present from setiger 2. Mid-body symmetrical main paleae number 10–13 (15) with 15–18 (20) ribs, with up to 18 ribs raised and ornate. Medial-most main paleae slightly more slender and rounded distally; lateral-most main paleae usually robust (Figs. 3A,B, 4D). Asymmetrical 3–4 robust median paleae with 11–13 (14) ribs with 3–4 major raised ribs and 3–6 minor raised ribs (Fig. 4C, E,F).

Anterior neuropodium with spinigers and long-bladed falcigers; mid-body neuropodium with 2 superior long-bladed falcigers, about 15–20 medium length bladed falcigers, about 6–8 short-bladed falcigers; total about 30

in large specimens. Pygidium quadrate with 2 slender anal cirri.

Remarks. In addition to the two major characters given in the key, *Treptopale homalos* consistently exhibits a number of other characters differentiating it from *T. paromolos*: darker golden paleae; body with a squarer cross section; paleal fans sitting more erect, almost like a 'shelf'; and main and median paleae types with larger serrations on margins (Figs. 3A,B, 4C,D,F). In comparison, *Treptopale paromolos* possesses: silvery to very pale golden paleae; body with a rectangular cross section; paleae fans sitting flatter on dorsum; and main and median paleae types with finer serrations on margins (Figs 7, 8A,E).

Observations on intraspecific variation within *T. homalos* included an atypical long, slender ovigerous female with large eggs from Lizard Island (NTM.W.22892). It exhibited all paleal types with fewer ribs than usual; lateral 3–4, main 10–14, and median more slender, symmetrical with 7–10 ribs and serration not as heavy. A specimen from Heron Island had similar paleal types. Both possessed typical *T. homalos* subunit 1 paleae and, as only two specimens with these lower rib counts were found, they are considered to belong to this species. Specimens of *T. homalos* from the plankton at Lizard Island exhibited a typical morphology (Fig. 4C,D) with no chaetal specialisations.

Entire specimens of 51 segments (Lizard Island) and 71 segments (Heron Island) were dissected to observe changes down the body. Shorter and squarer, heavily ornamented main paleae are evident in anterior setigers, from setiger 2 (Fig. 3B). The mid-body main paleae are similarly ornamented with slightly less ornamentation in the main paleae of posterior 5–10 setigers. Robust subunit 1 paleae are present from around anterior setiger 5 to posterior setiger 10 whereafter a slim, short subunit 1 palea is observed in a similar position in the notochaetal fascicle. Lateral paleae are fairly consistent in number throughout the body (i.e. 2–3), but number 4–5 in posterior third of body with larger numbers occurring on some segments very infrequently. Lateral paleae in some Heron Island individuals also had margins with finer to less serration than seen usually.

The author observed that the rarely occurring much larger, broader specimens such as that from the Seychelles had main paleae that were longer, more slender, and more rounded distally (Fig. 3E) compared to those seen in smaller specimens from Hawai'i (Fig. 4F).

The three tiny larval individuals from reefs off Townsville have white bodies dorsally covered with transparent paleae fans, are filled with yolk, possess laeunae with oil in the neuropodia and are similar in shape to the 10 segmented specimen of *Treptopale paromolos* from the Ashmore Reef. Their mid- to posterior-body main paleae have 15 ribs with the majority raised; the lateral main paleae are more slender with 9–10 ribs and 3 raised. There are three broad asymmetrical median with 13 ribs. The degree of ornamentation of main paleae down the body indicates these individuals belong to *T. homalos*. The Philips Reef

benthic post-larva was also in the same collection as adult *T. homalos*. However, there is no sign of the typical *T. homalos* adult subunit 1 palea. The subunit 1 palea present is long, broad and oddly-shaped, a bit like *T. paromolos* but different enough to be questionable.

Habitat and Distribution. *Treptopale homalos* lives among coral rubble often associated with *Halimeda* algae, corallines, seagrass and encrusting sponges in depths from LWS to 35 m. It is known from the western Indian Ocean, Seychelles, commonly recorded in the western Pacific and extends across to Hawai'i in the eastern Pacific. Within Southeast Asia it presently occurs from New Guinea to the Philippines, and within tropical northern Australia from the east coast Elizabeth Reef to Ningaloo Reef on the west coast.

Etymology. The species name *homalos* is a noun in apposition from the Greek meaning 'even' or 'equal' and refers to the equal-sized margins of the robust subunit 1 palea.

Treptopale paromolos sp. nov.

Figs. 2, 5, 6A–D, 7, 8A–E, 9A–C, 10

Bhawania sp. B Hartmann-Sehröder, 1979: 79, figs 11–13.

Material examined. HOLOTYPE – NTM W.23048, 44E segments, L: 7.60 mm, W: 1.2 mm, ovigerous female with large eggs, Australia, Northern Territory, Darwin, Lee Point, 12°18'S, 130°53'E, *Halimeda* mats, coral rubble, 1 m, coll. J. Just, September 1984. PARATYPES – NTM W.25295, include 1E, 51 segments, L: 7.40 mm, W: 1.1 mm, ovigerous female and 1NE 25 segments, male, location and collection details same as holotype.

Additional (non-type) material examined. NORTHERN TERRITORY: NTM W.23061, 2E, Darwin, Lee Point, *Halimeda* mats on reef, 1 m, coll. C. Watson, September 1984; NTM W.22945*, 2E, Channel Island, 12°33'S, 130°52'E, *Halimeda*, sand and coral rubble, LWS, coll. C. Watson, August 2007; NTM W.23069*, 1NE, 49 segments, W: 1.5 mm, Channel Island, *Halimeda* washings, LWS, coll. C. Glasby, December 2009; NTM W.4062, fragments, 1E, 60 segments, L: 5.5 mm, W: 0.7 mm, Channel Island, *Halimeda*, LWS, coll. C. Watson, December 1986; NTM W.3020, 1E, 53 segments, Channel Island, *Halimeda* and rubble, LWS, coll. P. Alderslade, October 1985; NTM W.23049, 1E, 88 segments, L: 7 mm, W: 1.7 mm, Nightcliff, algal washings from isolated rocky pools in sandflats exposed on 0.4 m tide, coll. C. Watson, 21 September 2009; NTM W. 13126, 1E, Middle Arm, Darwin Harbour, Stn. 98A, fine sand, 18 m, July, 1993, coll. Marine Ecology Unit; NTM W.02968, fragments, East Point, Fannie Bay, LWS, *Halimeda*, *Caulerpa* washings, coll. C. Watson, October 1985. QUEENSLAND: GBR, AM W.36208, 1, W: 0.6 mm, Lizard Island, between bommies inside entrance to lagoon, corer in sediment, 18 m, coll. C. Watson & A. Jones, October 1978; NTM W.23075*, fragments, Outer GBR, Day Reef, Stn. CGLI016, 14°28'S, 145°32'E, *Halimeda*



Fig. 5. *Treptopale paromolos* sp. nov., NTM W.23049, Darwin, Northern Territory, anterior end of live individual from algal washings in isolated rocky pools on sand flats exposed at 0.4 m tide. Photograph: Chris Glasby.

rubble, 12 m, coll. M. Ekins, April 2008; NTM W.23403*, 1NE, Day Reef, lip of lagoon behind reef crest, CWLI074, 5–10 m, dead *Acropora*, sand and seagrass, coll. L. Avery, September 2010; NTM W.23402*, fragment, Day Reef, CWLI074, reef dropoff, 18 m, coll. S. Smith, September 2010; NTM W.23360, Low Isles, 1 small posterior end, south side drop off, *Halimeda*, algal mat, coral rubble, 6–8 m, coll. C. Watson, December 1987. WESTERN AUSTRALIA: NTM W.2911, fragment, Seott Reef, intertidal reef flat, coral rubble with coralline, green & brown algae, coll. B.C. Russell, August 1984; NTM W.22943*, 1NE, South Seott Reef, middle of western reef, Stn.CWSR-7, 14°08'S, 121°44'E, *Halimeda*, sand, rubble, LWS, coll. C. Watson, October 2008; NTM W.22941*, 1NE, South Seott Reef, southwest corner, Stn.CWSR-6, 14°12'S, 121°47'E, *Halimeda*, sand, rubble, LWS, coll. C. Watson, October 2008; NTM W. 22942*, 1NE, South Seott Reef, southwest corner, Stn.CWSR-6, *Halimeda*, sand, rubble, LWS, coll. C. Watson, October 2008; NTM W.4158, fragments, Ashmore Reef, coralline algae and coral rubble, 15 m,

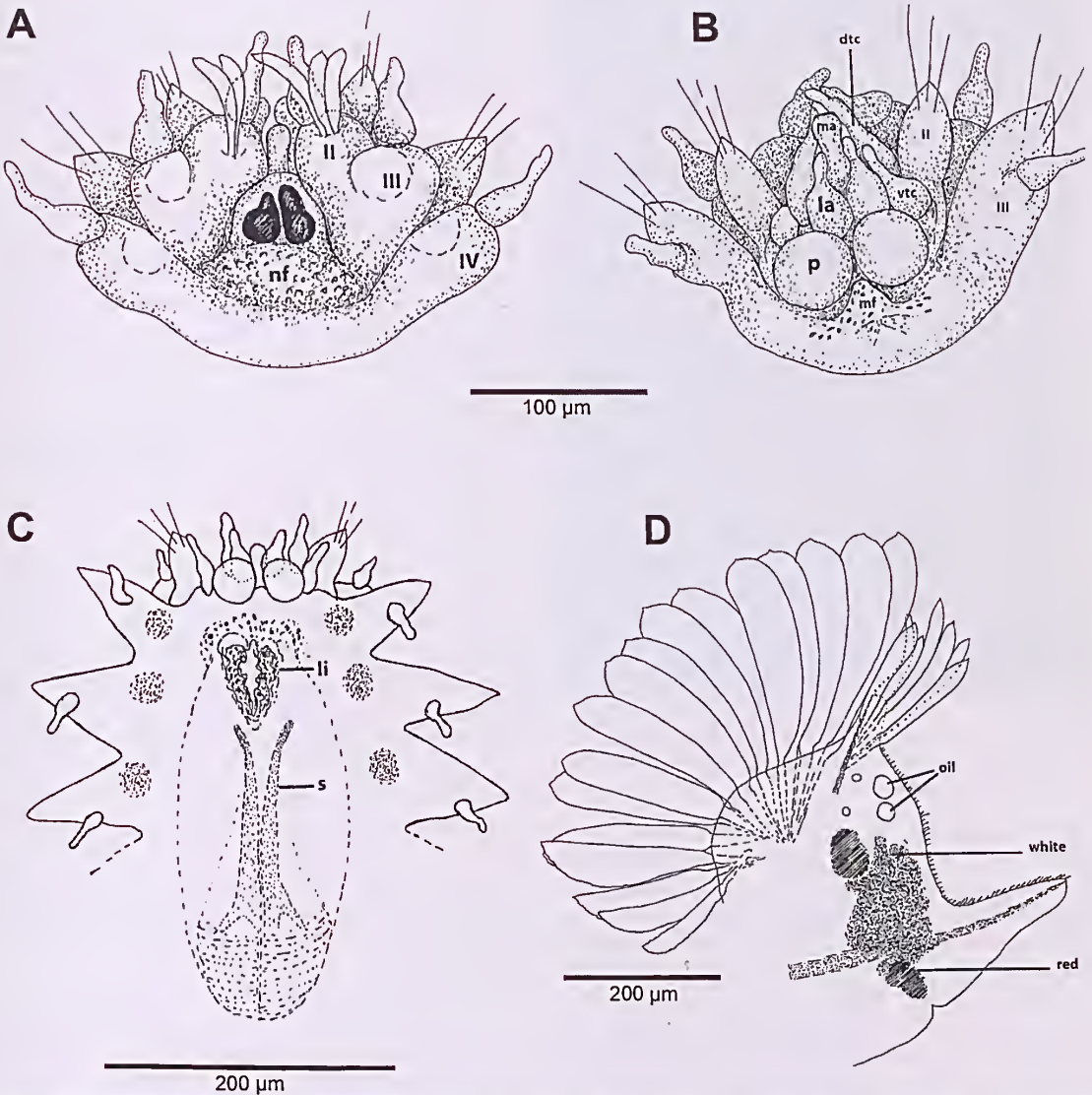


Fig. 6. *Treptopale paromolos* sp. nov., NTM W.02529, Paratype, Darwin, Northern Territory: **A**, anterior end, dorsal view, nf = nuchal fold, II, III, IV segments 2–4; **B**, ventral view, ma = median antenna, la = lateral antenna, p = palps, dtc = dorsal tentacular cirrus segment 1, vtc = ventral tentacular cirrus segment 1; II = segment 11 (setiger 1), III = segment 3, mf = mouth fold; **C**, NTM W.23049, anterior end, ventral view, li = lips of mouth opening, s = stylets; **D**, NTM W.23049, mid-body parapodium of live individual, oil = oil globules, white = white interramal pigment mass, red = red pigment patches. Scale lines: A – 0.1 mm; B – 0.1 mm; C – 0.2 mm; D – 0.2 mm.

coll. B.C. Russell, February 1984; NTM W.9310, 1NE, ovigerous female, fragments, Ashmore Reef, lagoon patch reef, *Halimeda*, coral rubble, encrusting sponge, 5 m, coll. B.C. Russell, April 1987; AM W.33630, 1, Kimberley coast, Albert Island, Stn. 43, 14°5'S, 124°9'E, rock platform, July 1988, coll. P. Hutchings; AM W.3363, fragments, Kimberley coast, Lucas Island, Stn. 43, 15°2'S, 124°5'E, 30 m, coll. P. Hutchings, July 1988; NTM W.2963, 54 NE, Bedout Island, intertidal reef platform, coral rubble, coll. B.C. Russell, June 1985; AM W.33632, 2NE, Dampier Archipelago, Rosemary Island, Hungerford Bay, 20°49'S, 116°57'E, crevice fauna, 6

m, coll. P. Hutchings, April 1987; AM W.33633, 1, ovigerous female, W: 0.8 mm, 1NE, Exmouth, Bundegi Reef, Stn. 391, 21°8'S, 114°2'E, 1–2 m, rocky rubble with coralline algae, green epiphyte, coll. H. Stoddart, January 1984; NTM W. 22992*, 1 NE, Ningaloo, 21°5'S, 113°00'E, Stn. NIN13B, Ningaloo Reef near Tantabiddi, reef slope, coll. N. Bruce, June 2008; NTM W.23367*, 1, ovigerous female, Ningaloo, Stn. CWNR10-011, 12 m, ARMS artificial settling plates, May 2010. WESTERN PACIFIC OCEAN. NEW GUINEA: NTM W.21784, 1, 40NE, Madang, Reef inside Ras Passage, 5°10'S, 145°50'E, Stn. RH91/94B, coral

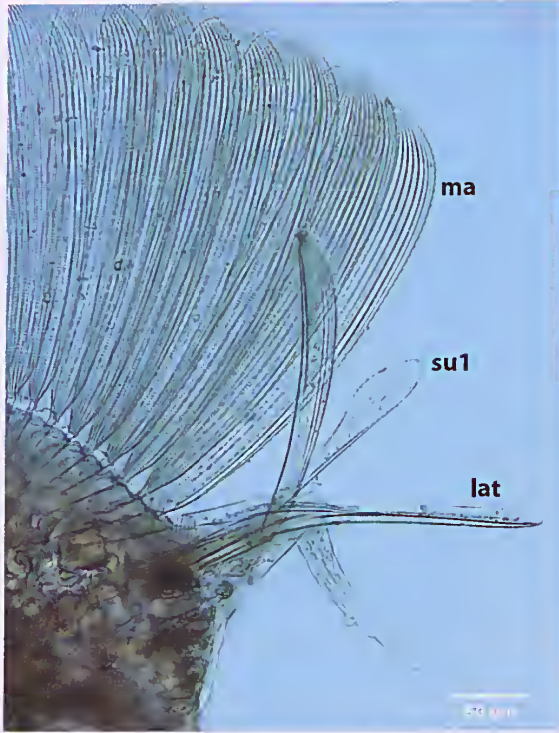


Fig. 7. *Treptopale paromolos* sp. nov., NTM W.21784, Madang Reef inside Ras Passage, Papua New Guinea, slide preparation mid-body notopodium in part, lat = lateral paleae, su1 = subunit 1 palea, ma = main paleae group.

reef, 14 m, coll. J.R. Hanley, October 1994. INDONESIA: NTM W.21789, fragments, Flores, Maumere, Halimeda, red algae, 3–6 m, coll. B.C. Russell, November 1991. PHILIPPINE ISLANDS: NTM W.13168, fragments, Luzon, Cape Bolinao, 16°25'N, 119°50'E, coral rubble, sponge, red algae, 12–25 m, coll. B.C. Russell, October 1995. PALAU ISLANDS: USNM 1076942, fragments, Iwayama Bay, 7°19'N, 134°29'E, eel grass, algae, sand and coral flat, coll. F.W. Bayer, July 1955. INDIAN OCEAN. THAILAND: NTM W.232261, 59E, Similan Island, 9°N, 98°E, dead *Acropora*, coll. A. Natchewathana & J. Hylleberg, January 1981. SRI LANKA: NTM W.23361, fragments, Galle, 6°04'N, 80°09'E, reef flat beneath lighthouse, *Halimeda*, coral rubble, fine sand, 0.5 m, coll. B.C. Russell, October 1991. POST-LARVAL/JUVENILE MATERIAL: NTM W.23062, 10E, length 2.04 mm, width 0.84 mm, Western Australia, Ashmore Reef, 12°44'S, 122°59'E, sand coral rubble, patches *Porites* microatolls & seagrass, fine leaved *Halimeda* in clumps, 1 m, coll. H. Larson, August 1986; HZM P. 16717, 1 NE (original description 14E), L: 0.8 mm, W: 0.4 mm, Port Hedland, coarse sand flats at estuary mouth of Pretty Pool, coll. Hartmann-Schröder, September 1975.

Description. Body pale yellow-white, with silvery to very pale golden paleae covering dorsum (Fig. 5). Long, quadrate-shaped prostomium with 2 pairs fused dark maroon-red eyes, median antenna short, distally bulbous,

2 filiform lateral antennae with bulbous bases, 2 rounded palps. Prostomium contracted between 2 anterior segments, covered posteriorly by small nuchal fold (Fig. 6A,B). Mouth fold triangular, small, with scattered brown pigment spots immediately below palps near segment 3 boundary; pharynx with 2 slender stylets, pale yellow with brown distal tips (Fig. 6C).

Segment 1 uniramous, achaetigerous with 2 pairs of tentacular cirri. Segment 2 (setiger 1) biramous; notopodia with 3–4 short, slender paleae with 7 ribs and dorsal cirrus; neuropodia with fascicle of spinigerous chaetae, ventral cirri absent (Fig. 6A,B). Segment 3 (setiger 2) notopodium with 1 lateral palea, 1 subunit one palea, 12 main paleae; latter short, symmetrical, distally broad with 8–10 ribs and raised ribs. Median paleae absent, first present about segments 4 to 5.

Mid-body notopodium with 2–4 (6) slender, subacicular lateral paleae with 5–8 (9) ribs with fine serration on both margins. Shorter, more fragile, subunit 1 paleae overlying dorsal acicula with pinched, asymmetric inner margin (Figs 7, 8E). Symmetrical main paleae number 10–15 (18,20) with 17–21 (23) ribs with none to 3–4 lightly ornamented raised ribs (Figs 7, 8E). Lateral and medial main paleae slightly more rounded distally and mid main slightly broader. Asymmetrical 3–4 (5) median paleae present with 10–13 (15) ribs with hardly visible 1–3 lightly beaded ribs or slightly more robust with 3–5 ribs raised (Figs 6D, 8A).

Anterior-most neuropodia with spinigers and long bladed falcigers. By segment 5, neuropodial superior spinigers drop out and replaced by 2 superior long bladed falcigers. Mid-body neuropodium with 3 superior long bladed falcigers, 3–4 less long bladed falcigers, 10–15 medium bladed falcigers and 4–8 inferior short bladed falcigers (Fig. 8D). Pygidium quadrate with 2 slender anal cirri (Fig. 8B).

Intraspecific variation. An entire specimen of *T. paromolos* from Darwin with 41 segments was dissected to observe its chaeta types, especially lateral and subunit 1 paleae, down the body. Shorter and squarer, more heavily ornamented main paleae are evident in anterior setigers, as seen in *T. homalos* (Fig. 3B), becoming much less ornamented after setiger 5 and decreasing in ornamentation almost entirely down the body. The anterior five setigers showed a typical mixture of juvenile transition and adult paleae with fully adult paleae types at setiger 6.

Subunit 1 paleae are present from setiger 6 throughout the body to setiger 40 and an occasional notopodium has two subunit 1 paleae. The laterals increase in number from setigers 10 to 15, with the mid-body setigers 20 to 26 exhibiting even larger numbers. As noted for *T. homalos*, a few random notopodia had larger numbers of lateral paleae (e.g. setiger 12 possessed one notopodium with 6 laterals plus a few spines; the corresponding notopodium had 3 laterals). Small anterior spines, of the type seen in the *T. rudolphi* specimen from Florida, are very infrequent,

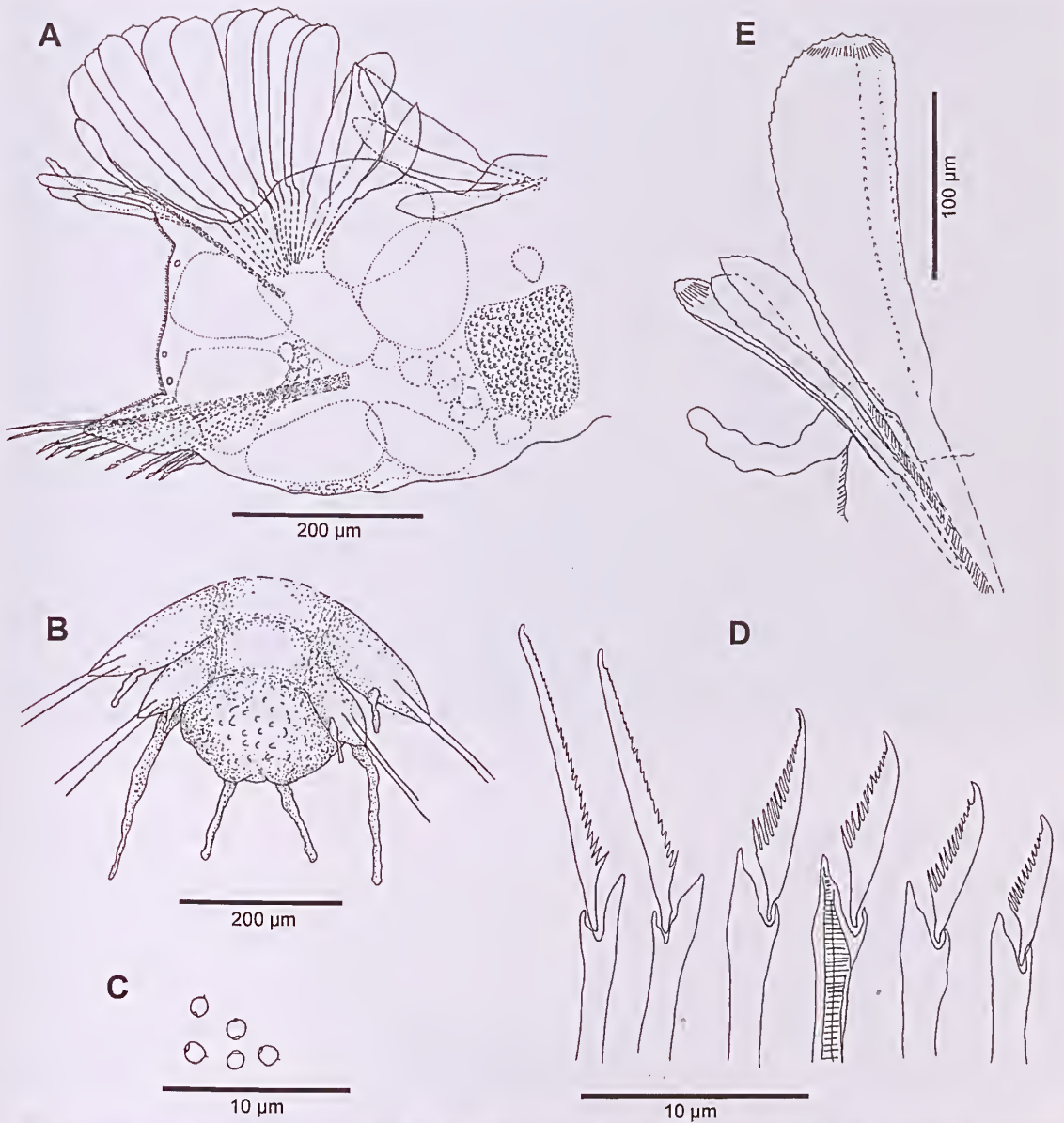


Fig. 8. *Treptopale paromolos* sp. nov. A, Holotype, NTM W.23048, Lee Point, Darwin, Northern Territory, female with large eggs, mid-body parapodium; B, Paratype, NTM W.2529, pygidium; C, Paratype, NTM W.2529, Lee Point, Darwin, Northern Territory, sperm; D, Paratype, NTM W.2529, Lee Point, Darwin, Northern Territory, neurochaetal types from mid-body neuropodium – superior long faleiger, mid-superior long faleiger, middle faleigers, inferior short faleiger; E, NTM W.23361, Sri Lanka, mid-body notopodium in part figuring lateral, subunit 1 and lateral-most main palcae. Scale lines: A – 0.2 mm; B – 0.2 mm; C – 0.01 mm; D – 0.01 mm; E – 0.1 mm.

and are no doubt larval remnants (see spine in juvenile, Fig. 9C). Within the last 10 chaetigers the laterals become fewer with fewer ribs.

Largest numbers of main palcae occur mid-body at the greatest width of the body. In the dissected individual the main palcae overall are fragile and mid-body setigers showed 1–2 medial-most main palcae comparatively more slender and more distally pointed with fine, dense ribs (Fig. 8A). Median palcae anterior to about setiger 10 have

three typical broad juvenile palcae, with the mid-body possessing four adult median palcae and an occasional notopodium with five adult median palcae. Within the posterior 10 setigers, median numbers become less and the two medial-most median are small and slender. All main and median palcae have a typical fine 'broken line' raised ribs. It is interesting to note this *T. paromolos* specimen had two anterior notopodia exhibiting the larger *T. homalos* type subunit 1 palcae. This has also been observed very

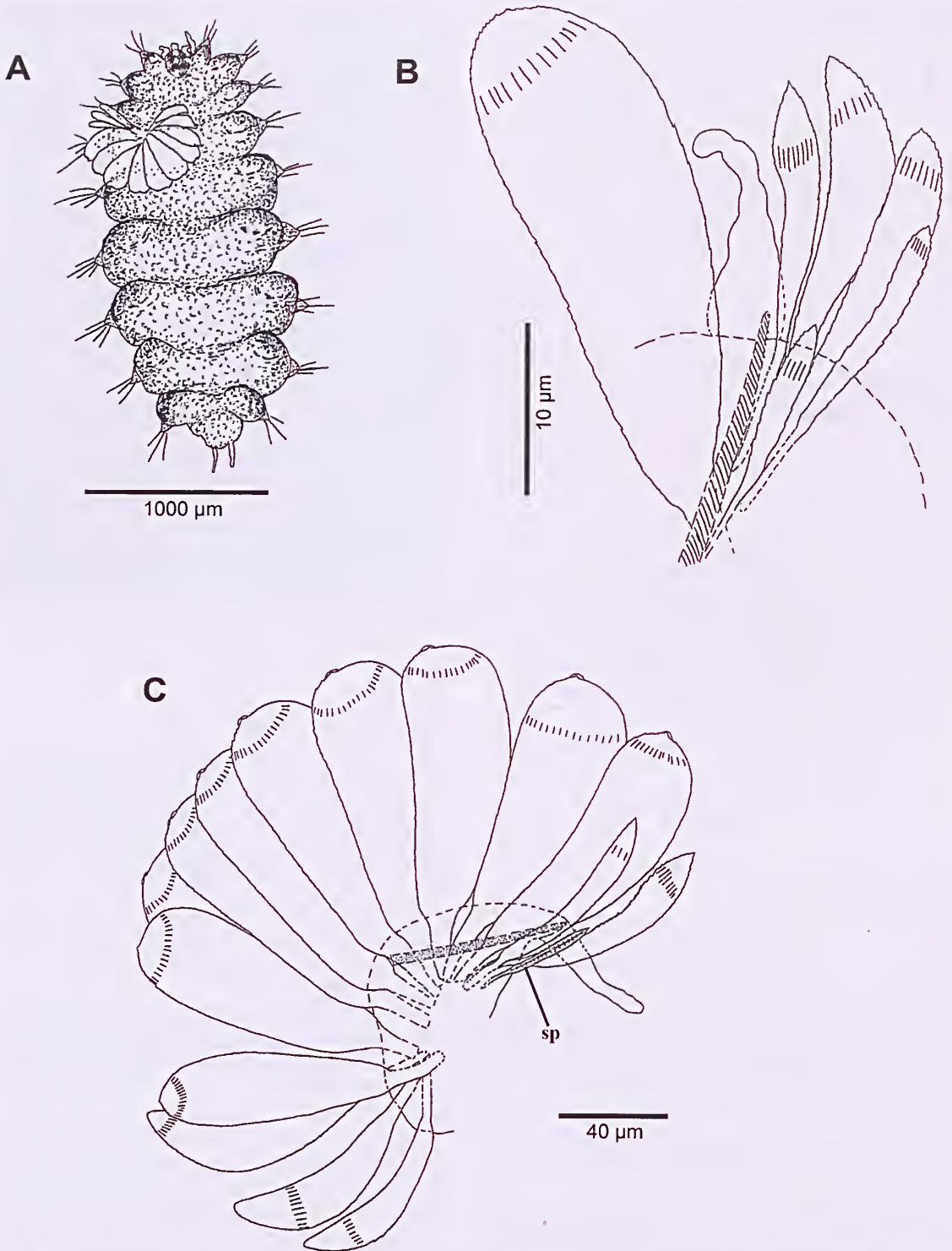


Fig 9. *Treptopale paromolos* sp. nov., A,B, NTM W.23062, Ashmore Reef, Western Australia: A, 10E post larva; B, detail of notopodium of setiger 6; C, HZM P.16717, Port Hedland, Western Australia, notopodium of setiger 11(14 E). Scale lines: A – 1.00 mm; B – 0.01 mm; C – 0.04 mm.

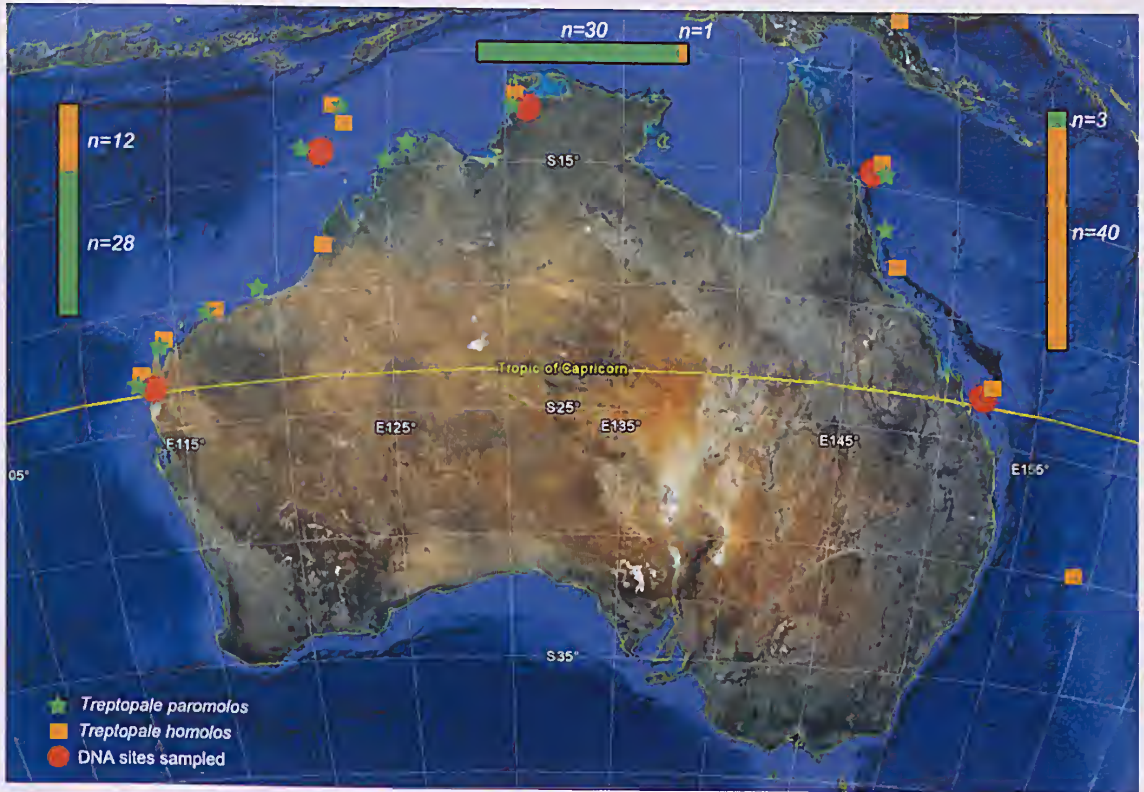


Fig. 10. Map of Australia showing distribution of *Treptopale paromolos* and *T. homalos*. Bars indicate the number of individuals of each species collected within the different regions, defined as: Eastern coast = Elizabeth Reef to Lizard Island; Northern coast = Darwin region; Western coast = Kimberley region to Ningaloo.

infrequently in one or two setigers in anterior ends of other *T. paromolos* specimens.

Intraspecific differences observed included a number of larger specimens from Western Australia (Bedout Island, Ningaloo) that possessed the highest numbers of main paleae and numbers of ribs (see numbers in brackets in species description).

Description of post-larvae (Fig. 9A,B). Yellowish body with brownish pigment patches on anterior edges of notopodia, transparent paleae fans cover dorsum. Anterior 5 setigers tapered; body segments broadest and deepest at setigers 6 and 7, narrowing thereafter with clear segmental lines. Body puffed up with pale yolk granules; oil globules present in neuropodia (Fig. 9A). Prostomium with 2 large pairs of red eyes, bulbous median antenna, pair of lateral antennae and ventral ovate palps. Segment 1 with pair of dorsal and ventral tentacular cirri and segment 2 (setiger 1) with dorsal cirri, no ventral cirri. In dorsal view, 2 tiny stylets visible below glandular nuchal fold which is posterior to prostomium, extending to segmental line of setiger 3.

Setiger 1 with 5 typically short, 'lateral-type' paleae with 3–5 ribs. Setiger 2 with more transitional paleae types, inserting in eirele formation, with 1–2 broad lateral and slender main paleae with 8–11 ribs and 6–8 raised ribs.

Asymmetric median paleae rounded distally with 8 ribs all raised.

Increasing adult paleal types from setiger 3, inserting in horizontal ridge with 3 lateral and 6 main paleae with 12–13 ribs and about 5 raised ribs; median paleae broadly asymmetric with 8–10 ribs, about 3–4 raised. Setiger 6 exhibits classic adult types: 4 lateral paleae with 4–7 ribs and adult subunit 1 palea with 8 ribs, plus main with 13 ribs and very lightly ribbed (Fig. 9B). Posterior setiger 9 has 3 slender lateral with 3–6 ribs plus 1 subunit 1, palea with 7 ribs; 1 main with 16 ribs and very lightly 4–5 raised ribs; 2 small slender median with 3 and 6 ribs.

Setiger 1 has spinigerous neurochaetae and setiger 2 has long-bladed falcigers. Adult type falcigerous neurochaetae present from setiger 3 and adult inferior falcigers with broad short blades present from setigers 5–6. Neurochaetae of setigers 8–9 all slender.

Description of juvenile. Nuchal area glandular but no discreet nuchal fold seen. Setiger 1 with 3 short 'lateral' type paleae with 3–6 ribs; setiger 2 with similar laterals plus main paleae with 13 ribs; typical juvenile broad median with 7–8 ribs. Mid-body has 7–9 main with 14–16 ribs. Setiger 11 possesses 1 small lateral spine with 2 ribs and serrated margins and 1 lateral plus typical adult subunit 1 palea with 7–8 ribs; 2 broad type median with 9–10 ribs

(Fig. 9C). Neurochaetae mid-body with typical superior long-bladed faleigers and inferior short-bladed faleigers. Mid-superior group, medium length bladed faleigers with particularly long basal serrations (Hartmann-Schröder 1979: 160, fig. 13).

Remarks. In addition to the distinctive asymmetric subunit 1 palea and much less raised rib and paleal marginal serrations, *Treptopale paromolos* possesses paler paleae, the body has a rectangular cross section, and the paleal fans sit flatter on the dorsum.

Paleal types of setigers 1 and 2, paleal insertion pattern, transitional notochaetal types plus main paleae with greater number of raised ribs within the anterior five setigers, seen in post-larval material, are retained in adults of both *Treptopale* species. The retention of more ornamented paleae plus the rare occurrence of *T. homalos* subunit 1 type palea, within the anterior five most conservative setigers of *T. paromolos*, illustrates its close relationship with *T. homalos*.

Habitat and Distribution. *Treptopale paromolos* is often found amongst coral rubble on muddier sands of intertidal reef flats, from sand and seagrass flats and coral rubble associated with *Halimeda* algae, corallines and encrusting sponges from LWS to 30 m. It is presently known from Sri Lanka and from localities along the rim of the western Indian Ocean, from Thailand to the coast of tropical Western Australia. In the western Pacific Ocean, *T. paromolos* is present from the Palau Islands to New Guinea and the tropical coasts of northern and eastern Australia.

Both *Treptopale* species occur sympatrically in collections from the Philippines and they also co-occur in the same areas of Indonesia and Thailand. At present it is not known whether the absence of *Treptopale paromolos* from the wider western Indian Ocean and eastern Pacific range of *T. homalos* is due to lack of specific habitat collecting.

Etymology. The species name *paromolos* is a noun in apposition from the Greek meaning 'nearly equal' and refers to the pinched, asymmetric inner margin of the subunit 1 palea.

REPRODUCTION AND DEVELOPMENT IN *TREPTOPALE*

Treptopale has separate sexes which are illustrated in this paper. Individuals possess typical glandular swollen rod-like internal structures posterior to the dorsal cirrus, as in all mature paleate chrysopetalid species (Perkins 1985, Watson Russell 2000a). Within the parapodia of mature males of both *Treptopale homalos* and *T. paromolos* are large cream-coloured sacs that contain very small ovoid to rounded sperm, some observed with minute tails (Fig. 8C). The sperm is not to be confused with similar-sized elongate white pigment granules (which appears as a dark greyish mass under a compound microscope) present between the rami in gametogenic male and female individuals (Fig. 6D).

Thousands of these granules can be seen spilling out of the planktonic specimens of *T. homalos* that also carry sperm. The function of these white granules is unknown.

Samples overall had small numbers of females with mature eggs. *Treptopale paromolos* females from populations in Ningaloo and Darwin possessed mature eggs (both with a size range of 130–200 µm), with latter individuals having about eight per mid-body parapodium (Fig. 8A). These large eggs, with the nucleus just visible, as well as smaller eggs (40 µm) that occur in the same parapodia have a very granular surface. The small eggs appear to be made up of many smaller ones, referred to as an egg 'packet' with no nucleus visible (as compared with *Arichlidon*, Watson Russell 1998). Three *T. paromolos* females were observed to have large eggs in clusters on the ventrum. It was difficult to ascertain whether these clusters had been extruded by the female when it was collected or they were an attached brood. Slide preparations show enhanced glandular structure along the ventral parapodial edge, posterior to the ventral cirrus. Ultrastructural studies are needed to ascertain whether the eggs are brooded.

Mature females of *Treptopale paromolos* from populations from Ashmore Reef and Madang possessed notopodia and neuropodia stacked full of small eggs (size range of 20–30 µm) with a granular surface and numbering 200 plus per mid-body parapodium (Fig. 7). Mature females of *T. homalos* predominantly had 'packet' type eggs measuring 40–60 µm. One individual from Exmouth had eggs (80–120 µm) with clear nuclei numbering about 40 per parapodium. Only one *T. homalos* specimen, from Lizard Island, with the identifiable subunit 1 palea and ornamented main (referred to as an atypical in the species discussion), had large eggs (120–150 µm) in a cluster on the ventrum.

Assuming that small numbers of large eggs in clusters indicates lecithotrophy and very numerous smaller eggs indicates planktotrophy, the above data shows that either different reproductive modes are employed within *Treptopale paromolos* and *T. homalos* or that more than one species is actually present within these presently defined morphological units.

Benthic post-larval individuals of 10 segments display main paleae similar to an adult and their gut is filled with yolk. Oil globules evident in the larvae (Fig. 9A) are also retained within the parapodia of adults (Figs 6D, 8A). Oil globules may be small or large and seep out in yellow globules from lacunae in broken segments. Live individuals may also possess within their parapodia bright yellow and orange, as well as white, pigment patches (Fig. 6D). The former is referred to as an "internal cavity containing clear substance, perhaps oil" and the latter as "glands containing opaque granules" by Perkins (1985: 907) for *T. rudolphi*. Oil globules are also present in parapodia of adult *Paleanotus* but appear absent in other chrysopetalid genera (pers. obs.).

Males of *Treptopale homalos*, found in mid-water, possess no accessory chaetae as documented for species of *Arichlidon* reported from the plankton (Watson Russell 1998,

2000a). The retention of oil globules in adult *Treptopale* may enable individuals to rise up and maintain stability within the water column. *Treptopale* species also have large, broad segments in the mid-body that break apart like pieces of a jigsaw puzzle, observed also in *Thraumastos* living at abyssal depths at hot vents and the only other chrysopetalid genus exhibiting extreme fragmentability (Watson 2001). Body fragmentation is allied with a benthic and mid-water behaviour that includes jettisoning of segments under stress.

Treptopale homalos adults have been reported from mid-water (Watson Russell 2000a, this paper) but no *Treptopale* early larval stages have been found in the plankton. Species that show wide distributions are either old species that have time to take advantage of emerging stepping stones during low sea level stands, or species that have long larval stages (Hoeksema, 2007). There is no evidence as yet that *Treptopale* possess free-living larvae capable of long distance dispersal.

OCCURRENCE AND HABITAT OF *TREPTOPALE* IN NORTHERN AUSTRALIA

At present there appears no latitudinal species pattern between inshore and offshore reefs or longitudinal north-south differences based on morphology. *Treptopale homalos* appears to be the predominant *Treptopale* species on the eastern Australian coast. Material has been examined from over 40 collecting sites from Queensland offshore islands and reefs and mainland fringing reefs from the southern and northern Great Barrier Reef and from four different sites around Madang, Papua New Guinea, comprising over 60 individuals (Fig. 10). *Treptopale homalos* has been collected from two sites at Elizabeth Reef atop submerged volcanic sea mounts, lying at the southern boundary of the Coral Sea at 29°S. Single specimens of *Treptopale paromolos* have been collected from three sites on the north-east Australian coast and one site from Madang in rubble and silty sand habitats. *Treptopale paromolos* and *T. homalos* occur sympatrically at one site, Day Reef, on the Outer Barrier, GBR.

The largest populations of *Treptopale paromolos* are inferred to occur in northern Australia, predominantly from silty reefs in Darwin Harbour, Northern Territory with over 40 individuals counted. Only one individual of *T. homalos* has been found in the same Darwin collection as *T. paromolos* in a habitat of *Halimeda*, coral rubble, brown and red algae on a silty reef at LWS (Fig. 10).

Both species of *Treptopale* are present on the offshore and mainland reefs off northern Western Australia with no particularly clear pattern, although *T. paromolos* is slightly more common. *Treptopale homalos* represents 12 specimens from six sites and *T. paromolos* 28 specimens from nine sites. Both species occur sympatrically at three of these localities (Fig. 10). *Treptopale paromolos* and *T. homalos* co-occurred in a very large sample of coral rubble with

coralline algae, sponge, soft coral and tunicate growth from Ashmore Reef, Timor Sea. The former species appeared in three subsequent trips to Ashmore Reef, including sand and seagrass habitats, whereas *T. homalos* turned up from Cartier Island just to the south of Ashmore Reef. Further south, the massive coral banks of Scott Reef on the edge of the continental shelf have had six sites visited over a period of 26 years and all visits resulted in only *T. paromolos* being collected. *Treptopale homalos* and *T. paromolos* are both found from the Western Australian mainland and nearshore island reefal sites from the northern Kimberley coast to Ningaloo at 21°S (Fig. 10). Both species are present in coarse coral rubble, with the latter also found with coralline algae on intertidal reef platforms and from coarse sand flats at the mouth of estuaries.

At present there is some evidence that reproductive isolation is maintained by habitat partitioning for these two species (see above) which co-occur within a reefal environment and inhabit a similar depth range. *Treptopale paromolos* has been reported from finer sediments from the deeper lagoonal sediments of Lizard Island, predominance among the silty rubbles of Darwin and offshore north western Australian shallow reefs of sand and seagrass habitats. *Treptopale homalos* is most common amongst coral rubbles of the less sedimentary, deeper, clearer water reefs of the GBR.

DISCUSSION

The biogeographic distribution of a species is intrinsically linked to its developmental mode, habitat preference, and geological and climatic history. The presence of *Treptopale rudolphi*, *T. homalos* and *T. paromolos*, three morphologically very closely related species, within a pantropical belt including sympatric distribution of the two latter two across the Indo-Pacific Ocean, is indicative of a geologically old species complex. Although it appears adults have the ability to rise up in the plankton, the absence of a planktonic larval stage suggests even more strongly that these present species represent lineages derived from an ancestor that evolved within a shallow water Tethyan fauna present before the Cenozoic. This uniform pantropical fauna was disrupted by a series of plate tectonic events in the early Mioocene (approx. 20 million years ago, with the collisions of Africa/Arabia with Europe and Australia/New Guinea with Indonesia) and the Middle Mioocene (rise of the Central American Isthmus). The isolation of continents, reorganisation of oceanic circulation systems and imposition of a steep latitudinal gradient led to effective barriers for migration and subsequent speciation within two main tropical foci – the Indo-West Pacific and the Atlantic-Caribbean-East Pacific (Crame & Rosen 2002).

Much more recently, over the past 130,000 years, sea levels associated with glacial cycles have profoundly modified the Australian shallow water reefal systems. Levels

dropped to 120 m below present sea level around 18,000 years ago, with the result of isolating Australia's north-eastern coast from the west due to the closure of Torres Strait (Choat & Russell 2008). The loss of the emergent coral reefs on the Australian continental shelves and also the fringing reefs throughout the western Pacific island chains meant that coral communities had to move downwards with descending sea levels along relatively steep continental or volcanic island margins to survive (Potts 1984). Water exchange between the Pacific and Indian Oceans became obstructed due to narrower and shallower sea passages and the amount of freshwater runoff and suspended sedimentation increased. These conditions and the emergence of physical barriers led to isolated, disconnected populations which may have caused subsequent speciation (Hoeksema 2007).

During the Pleistocene, reef corals remained in fringing reefs in eastern Indonesia along the edge of the Sunda Shelf, in northwestern Australia along the Sahul Shelf and in eastern Australia along the outer barrier at the edge of the continental shelf. Rapid sea-level rise in the Holocene, 18 to 6 thousand years ago, led to inundation of continental shelves and re-establishment of coral communities by organisms with planktonic larvae and adult movement (Hoeksema 2007). Potentially the organisms colonising these available areas would constitute both relict species that were able to survive in reefal open refuges during glaciation as well as new species that had evolved as a result of disruption to the range of an ancestral species. The present distribution of *Treptopale homalos* and *T. paromolos* across northern Australia begs a number of questions. A first scenario postulated is that of the two morphological forms, *Treptopale homalos* and *T. paromolos*, evolved from a common ancestor that had a widespread western Pacific and Australasian distribution long before the Pleistocene. The change in physical conditions and emergence of barriers (e.g. closure of Torres Strait during the last glacial maximum) would have separated existing northern Australian populations of *Treptopale homalos* and *T. paromolos*. Speciation may have then taken place without phenotypic differentiation. The sympatry of the two species evident today is a reflection of *in situ* lineages that recolonised substrates after deglaciation on the east and west Australian coasts and with probable secondary colonization subsequently.

Another scenario postulates that *Treptopale paromolos* evolved during the glacial period in response to the greater sedimentary conditions of shallow seas of the Arafura and Sahul Shelf by, for example, selection of minimal paleae ornamentation. The conditions of freshwater runoff and suspended sedimentation, present in the Pleistocene, are still apparent today in areas of the Sahul Shelf, Java and Arafura Seas (Hoeksema 2007). The presence of *T. paromolos* currently along the northern and northwestern Australian silty coasts could reflect *in situ* lineages that may also include secondary colonisers.

Ongoing phylogenetic analyses of *Treptopale* (Watson in prep.) and DNA studies (Wei & Watson in prep.) will no doubt prove useful in sorting out these scenarios.

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New records and a new species of *Hermundura* Müller, 1858, the senior synonym of *Loandalia* Monro, 1936 (Annelida: Phyllodocida: Pilargidae) from northern Australia and New Guinea

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ABSTRACT

The Principle of Priority (ICZN 1999) is applied in resurrecting the generic name *Hermundura* Müller, 1858 for pilargid polychaetes (Annelida) formerly referred to as *Loandalia* Monro, 1936 and *Parandalia* Emerson & Fauchald, 1971. All available specimens of *Hermundura* from northern Australia and New Guinea are described based on material held in the collections of Australia's natural history museums. Our study recognises two species, *H. gladstonensis* (Marks & Hocknull, 2006) comb. nov. and a new species, *H. philipi* sp. nov., from near Mornington Island in the southern Gulf of Carpentaria. The former species is redescribed, and new information on intraspecific variability is provided, including the presence of hardened, cuticular structures and a muscle band (sphincter) of the anterior alimentary canal. Analysis of these structures has led to a re-evaluation of the so-called 'jaws' of the closely related monotypic genus *Talehsapia* Fauvel, 1932, and the conclusion that they are homologous with the pharyngeal sphincter of *Hermundura*. *Talehsapia* therefore is also synonymised with *Hermundura*. The genus *Hermundura* now contains 17 species including the type species, *Hermundura tricuspis* Müller, 1858, *H. philipi* sp. nov., and fifteen others, which are all new name combinations, viz. *Hermundura annandalei* (Fauvel, 1932), *H. aberrans* (Monro, 1936), *H. fauveli* (Berkeley & Berkeley, 1941), *H. americana* (Hartman, 1947), *H. gracilis* (Hartmann-Schröder, 1959), *H. indica* (Thomas, 1963), *H. ocularis* (Emerson & Fauchald, 1971), *H. maculata* (Intes & Le Locuff, 1975), *H. bennei* (Solís-Weiss, 1983), *H. riojai* (Salazar-Vallejo, 1986), *H. vivianneae* (Salazar-Vallejo & Reyes Barragán, 1986), *H. evelinae* (León-González, 1991), *H. salazarvallejoi* (León-González, 1991), *H. fredrayorum* (Marks & Hocknull, 2006) and *H. gladstonensis* (Marks & Hocknull, 2006). The genus *Hermundura* appears to be restricted to the tropics and subtropics, both in Australia and globally.

KEYWORDS: Polychaeta, Pilargidae, systematics, taxonomy, redescription, synonymy, new combination.

INTRODUCTION

The concept and validity of *Loandalia* Monro, 1936, a genus of pilargid polychaetes, has been in flux since it was originally described by Monro (1936) based on *L. aberrans* from a specimen from the continental shelf off Angola, southwest Africa. Monro was unable to assign it unequivocally to a family, although he favoured the Hesionidac. Later, *Loandalia* was assigned to the Pilargidac by Hartman (1947), and it was treated as an established member of that family in the revision by Pettibone (1966). Pettibone regarded the monotypic *Hermundura* Müller, 1858 as a questionable synonym of *Loandalia*. Later, Salazar-Vallejo (1990) redescribed the type species of *Hermundura*, *H. tricuspis* (as *Parandalia tricuspis*), designated a neotype, and established unequivocally that it represented a senior synonym of *Parandalia*. When Salazar-Vallejo (1998) synonymised *Parandalia* with *Loandalia*, *Hermundura* became the senior synonym of both *Parandalia* and *Loandalia*, but because Salazar-Vallejo

(1990) recommended the continuing use of the junior synonym name (*Parandalia*), the name *Hermundura* was ignored. However, under current ICZN (1999) rules, in which strict publication criteria need to be applied in order to suppress a senior synonym, we consider it appropriate to abide by the Principle of Priority and resurrect the senior synonym name for this taxon.

Emerson & Fauchald (1971) re-examined the type species of *Loandalia*, *L. aberrans*, and concluded that, as its name implies, it has several unique features that set it apart from other synclmines, most importantly the absence of notopodial spines (and notoacicula) and the presence of branchiae. They restricted the concept of the genus to include only the type species and moved the other species in the genus to *Parandalia*. Salazar-Vallejo (1998) demonstrated that the so-called branchiae were in fact enlarged nephridial papillae and, in his opinion, the presence of nephridial papillae could not be used as a feature to separate *Loandalia* from *Parandalia*. Further, because of contradictory information over whether notopodial spines

are present in the type – observed by Monro, but not by Emerson & Fauchald (1971) – this feature could not be used to diagnose the genus. We follow Salazar-Vallejo's (1998) interpretation of the type species, and his conclusion that *Parandalia* is a junior synonym of *Loandalia*. This action also addresses the concern of Licher & Westheide (1994) that monophyly of *Parandalia* was questionable.

The monotypic genus *Talehsapia* Fauvel, 1932 was also regarded as a junior synonym of *Loandalia*, albeit questionably (Pettibone 1966). The taxonomic history of *Talehsapia* and its single species *T. annandalei* Fauvel, 1932 is summarised by Salazar-Vallejo *et al.* (2001), who also redescribed specimens from the type locality. They concluded that the genus should be maintained and it can be recognised by its completely fused palps and the presence of denticulate bands, which originally were interpreted as jaws. However, we demonstrate herein using a large range of differently preserved specimens of *H. gladstonensis*, that these two features should not be used to distinguish *T. annandalei* from other *Hermundura*. Thus *Talehsapia* also becomes a junior synonym of *Hermundura*.

Four species of *Hermundura* are currently known from the Indo-west Pacific, *H. annandalei* comb. nov. (Thailand), *H. indica* (Thomas, 1963) comb. nov. (India), and two species from Australia, *H. fredrayorum* (Marks & Hocknull, 2006) comb. nov., from the type locality Moreton Bay near Brisbane, and *H. gladstonensis* (Marks & Hocknull, 2006) comb. nov. from the type locality Gladstone, NE Queensland (Table 1). In this paper we describe all available *Hermundura* specimens from northern Australia and New Guinea based on material held in the collections of Australia's natural history museums.

MATERIALS AND METHODS

All specimens were fixed in 10% formaldehyde-seawater and preserved in 70% ethanol. Observations were made using a Nikon SMZ 1500 stereomicroscope and a Nikon Eclipse 80i compound microscope with Nomarsky optics; photographs were made on both microscopes using a Qimaging Micropublisher 5.0 RTV digital camera; stacked images were combined with Helicon Focus software (version 4.77) and line drawings were compiled from digital images using a Wacom Intuos 4 drawing pad with Adobe Illustrator CS2.

Generic and species level descriptions were constructed using the DELTA system, Descriptive Language for Taxonomy, a standardised format for coding taxonomic descriptions (Dallwitz 1980; Dallwitz & Paine 1986; <http://www.biodiversity.uno.edu.delta>). Features included in the generic description were not repeated at the species level and vice versa. The key was constructed manually. The distribution maps were made using PanMap software (Dipenbrock *et al.* 2000).

Abbreviations. The following abbreviations are used in this paper: AM – Australian Museum, Sydney; LACM

(formerly AHF) – Los Angeles County Museum of Natural History, Los Angeles; LIPI – Pusat Penelitian Oseanografi, Lembaga Ilmu Pengetahuan, Jakarta; MEU – Marine Ecology Unit, formerly belonging to NTM; NTM – Museum and Art Gallery, Northern Territory (formerly Northern Territory Museum), Darwin; QM – Queensland Museum, Brisbane.

MORPHOLOGY OF *HERMUNDURA*

Body. *Hermundura* species have a more or less uniformly cylindrical body except for the anterior 5–10 segments which are inflated, and the posterior body may be slightly flattened. The body surface has a smooth to acrocolated texture, not shining or papillated like other pilargids. Pigmented subdermal glands may be present on the lateral body and the pygidium (as a pair of spots) (Fig. 1).

Head. The prostomium is reduced and indistinct, rectangular or ovate in shape, and together with the reduced palps the head appears bluntly triangular in shape. The palps are biarticulated (comprising a palpophore and a palpostyle) and separated from each other (though they may appear to be medially fused when the head is contracted). At least two species, *H. tricuspis* Müller, 1858 and *H. annandalei* comb. nov., are reported in the literature to have fused palps but this needs to be confirmed based on fresh specimens. Palpostyles maybe button-like or rod-like in shape and occur singly or in a pair within each palpophore (see Marks & Hocknull 2006). A palpal papilla is absent. Nuchal organs are not apparent. The antennae are absent. The cyscs, if present, are subdermal, lying on the brain. The brain is often visible dorsally through the body wall as an elongate, tripartite structure projecting posteriorly from the prostomium and extending through the first few anterior chaetigers; the mid-brain often has paired subdermal eyespots. The first annulus (referred to in recent literature as both the peristomium or segment 1) lacks parapodia or tentacular cirri, and it may be set off from the prostomium or fused with it.

Parapodia. The parapodia in *Hermundura* are 'sub-biramous', with the anterior one or two chaetigers lacking notospines, and dorsal cirri are absent in all species except *H. aberrans* comb. nov. The chaetal lobe is rectangular, rounded distally and does not project far from the body wall. The ventral cirri are subdistal and start on chaetigers 3–8, thereafter they are present on all chaetigers. The start of the ventral cirri is a useful character to separate species. Nephridial papillae may be present on the posteroventral margin of the neuropodia of posterior chaetigers (only in *H. aberrans* comb. nov. and *H. maculata* comb. nov.).

Chaetae. The notochoetae include straight notospines (rarely absent, *H. aberrans* comb. nov.), which start on chaetigers 2–10, and a few accompanying capillaries. The first few notospines may be overlooked because they have not fully emerged from the parapodium, but they can be seen on slide-mounted specimens under a compound microscope. The first occurrence of notospines appears not to be body-

size dependent as in other pilargids (e.g. *Siganbra*), and is therefore a good species-level character. The neurochaetae are distinctive, hirsute capillaries that have a whorl of hairs along a variable portion of the chaeta. The notoaciculacae are absent, although some earlier authors have interpreted the single notospine as an emergent notoacicula (e.g. Hartman (1947)); a single neuroacicula is present, and the tip may be tapered or knobbed.

Pygidium. The pygidium is spoon-like with a dorsal concavity, and ovate to rounded. It bears 2, 3 or 5 anal cirri.

Alimentary canal. The anterior-most part of the alimentary canal consists of a short, non-muscular buccal tube which extends from the mouth posteriorly to a muscular pharynx. The buccal tube, which is exposed when the pharynx is partially everted, may carry one or a few hardened denticles which appear to be derived from the cuticle (Fig. 2A), however these features of the buccal tube appear not to be consistent within a species and therefore are given no taxonomic importance herein. Occasionally the denticles appear to be located within the pharynx itself (Figs 2C, 3D), nevertheless they resemble the denticles of the buccal tube rather than the ‘denticulated bands’ described by Salazar-Vallejo *et al.* (2001). When the proboscis is fully everted, a ring of up to 10 papillae can be seen at the junction between the buccal tube and the muscular pharynx.

On the anterior margin of the muscular pharynx a narrow light-refractive band of soft tissue encircles the opening. It appears to be homologous with the ‘denticulated bands’ that Salazar-Vallejo *et al.* (2001) found in *Talehsapia*. The intestinal caeca are absent.

SYSTEMATICS

Pilargidae Saint-Joseph, 1899

Synelminae Sallazar-Vallejo, 1986

Hermundura Müller, 1858

Hermundura Müller, 1858: 216. Gender feminine. Type species, by monotypy, *Hermundura tricuspis*. Recent, Santa Catarina Island, Brazil.

Talehsapia Fauvel, 1932: 251–252. Gender feminine. Type species, by monotypy, *Talehsapia annandalei*. Recent, Songkhla Lagoon, Thailand. New synonymy.

Loandalia Monro, 1936: 193. Gender feminine. Type species, by original designation, *Loandalia aberrans*. Recent, St Paul de Loanda, Angola.

Parandalia Emerson & Fauchald, 1971: 19. Gender feminine. Type-species, by original designation, *Parandalia ocularis*. Recent, Santa Barbara Channel, California, USA.

Table 1: Currently accepted *Hermundura* species worldwide, arranged chronologically, together with the original name and author, type locality and depth, and nomenclatural/taxonomic comments.

Original combination	Authority	Type locality, depth	Nomenclatural/taxonomic comments
<i>Hermundura tricuspis</i>	Müller, 1858	São Antonio de Lisboa, Santa Catarina Island, Brazil; intertidal	Neotype designated by Salazar-Vallejo (1990)
<i>Talehsapia amandalei</i>	Fauvel, 1932	Songkhla Lagoon, Thailand; no depth stated	Redescribed by Salazar-Vallejo <i>et al.</i> (2001)
<i>Loandalia aberrans</i>	Monro, 1936	Off St Paul de Loanda, Angola, 64–65 m	
<i>Loandalia fauveli</i>	Berkeley & Berkeley, 1941	Newport Bay, California, USA; intertidal	
<i>Loandalia americana</i>	Hartman, 1947	Biloxi, Mississippi, USA; intertidal	Synonym of <i>H. fauveli</i> according to Pettibone (1966).
<i>Loandalia gracilis</i>	Hartmann-Schröder, 1959	La Herradura, El Salvador; intertidal	Synonym of <i>H. fauveli</i> according to Pettibone (1966)
<i>Loandalia indica</i>	Thomas, 1963	Arabian Sea, off west coast of India; 15–18 m	
<i>Parandalia ocularis</i>	Emerson & Fauchald, 1971	Santa Barbara Channel, off southern California; 42–46 m	
<i>Loandalia maculata</i>	Intes & Le Loeuff, 1975	Off Ivory Coast, west Africa; 15–100 m	
<i>Parandalia bennei</i>	Solis-Weiss, 1983	Mazatlan Bay, Pacific coast of Mexico; 3.5–25 m	
<i>Loandalia riojai</i>	Salazar-Vallejo, 1986	Bahia de Manzanillo, Colima, Mexico; 30–80 m	
<i>Parandalia vivianneae</i>	Salazar-Vallejo & Reyes-Barragán, 1986	Laguna La Mancha, Veracruz, Gulf of Mexico; shallow water	
<i>Parandalia evelinae</i>	León-González, 1991	Baha California Sur, Mexico, west coast; 106 m	
<i>Loandalia salazarvallejoi</i>	León-González, 1991	Baha California Sur, Mexico, west coast; 80 m	
<i>Loandalia fredrayorum</i>	Marks & Hocknull, 2006	Moreton Bay, Queensland, Australia; 3–11 m	
<i>Loandalia gladstonensis</i>	Marks & Hocknull, 2006	Gladstone Harbour, Queensland, Australia; intertidal to 5 m	
<i>Hermundura philipi</i> sp. nov.	Glasby & Hocknull, 2010	North of Mornington Island, Gulf of Carpentaria, Australia; 35–45 m	

Diagnosis. Body long, slender, subcylindrical, inflated anteriorly; surface smooth to areolated. Prostomium and palps reduced; combined structure bluntly triangular. Palps biarticulated, separated from each other; palpostyles single or double; palpal papilla absent. Antennae absent. Prostomial eyes absent. Brain longer than wide, divided into fore-, mid- and hind-brain; forebrain bifurcate, divided anteriorly into 2 lobes, hind brain with 2 lobes; ocular spots present on mid- and hind-brain. First annulus lacks parapodia or tentacular cirri. Parapodia with notopodia reduced, notoaciculae absent and dorsal cirri usually absent. Ventral cirri present, subdistal. Notochaetae including emergent straight notospines and few capillaries. Neurochaetae hirsute capillaries. Neuroaciculae present. Pygidium spoon-shaped plaque (dorsal concavity), bearing 2, 3 or 5 anal cirri. Ring of distal papillae between buccal tube and pharynx; cuticular denticles of various shapes may be present on buccal tube or anterior pharynx, pharynx with a sphincter on anterior margin. Intestinal caecae absent. Nephridial papillae present or absent.

Remarks. In 1990 Salazar-Vallejo redescribed the only species of *Hermundura*, *H. tricuspis* (as *Parandalia tricuspis*) and designated a neotype. Later (1998) he synonymised *Parandalia* with *Loandalia*. Therefore, *Hermundura* became the oldest available name for the taxon. Salazar-Vallejo (1990) stated that the name *Hermundura* "has not been used formally for a long time" and should it be adopted... "confusion would result". However, under the present ICZN Code (1999) the younger name *Loandalia* can only be used by successfully arguing the ease for 'prevailing usage' (ICZN 1999: Article 23.9.1.2). However, *Loandalia* is a rarely reported taxon and it would be difficult to satisfy the publication criteria set out under Article 23.9.1.2, especially because other names such as *Parandalia* and *Talehsapia* have also been used for members of the taxon in the last 50 years. The issue would almost certainly need to be referred to the Commission for a ruling. Therefore, the simplest and most effective option is to apply the Principle of Priority strictly and use the oldest available generic name, which is *Hermundura*, for the taxon.

We have expanded the diagnosis of *Hermundura* slightly to include the newly synonymised *Talehsapia* Fauvel, 1932. *Talehsapia* was differentiated from other synelmine pilargids by its completely fused palps and the presence of pharyngeal denticulate bands (Salazar-Vallejo *et al.* 2001). However, examination of a large number of specimens of *Hermundura* during this present study have shown that members of this genus also have palps that are very short and retractile, and that in the retracted state the palps often appear to be fused (Fig. 3A,B) as in *Talehsapia*. Further, although not mentioned by Salazar-Vallejo *et al.* (2001), the palps of *Talehsapia* appear to be bi-articulated with minute bifid palpostyles (see his fig. 1c), which is a condition only known in some species of *Hermundura*. Finally, *Hermundura* species also have

pharyngeal structures resembling denticulate bands. As Salazar-Vallejo *et al.* (2001) correctly pointed out, the bands are not true jaws as described by Fauvel (1932) because they are not a solid structure nor do they have cusps or any other features normally associated with jaws. He observed that the denticulate bands are symmetrical but discontinuous laterally, and 'rugose' or 'granular' due to the presence of 'many tiny denticles'. Bands of the same form (Fig. 2D,E) and texture (Fig. 2F) were also observed in our material of *Hermundura*, although the degree of granularity was generally less in our material. We believe that the granularity represents the minute protruberances (e.g. papillae) in the overlying tissue, because the graininess in our specimens extends beyond the limits of the bands (Fig. 2F). The bands appear to represent a sphincter because of their position at the anterior opening of the pharynx.

Hermundura gladstoneensis (Marks & Hocknull, 2006)
comb. nov.

(Figs 1, 2A–F, 3A–N, 5A)

Loandalia gladstoneensis Marks & Hocknull, 2006, 65–66, fig. 3a–d; Hocknull & Glasby 2009: 544 (in part).

Material examined. HOLOTYPE – QM G222948, Gladstone Harbour, 23°51.0'S, 151°37.0'E, coll. S.A. Marks, 26 July 2002. Additional material: AUSTRALIA: **Western Australia:** Port George, Kimberley coast, NTM W.23378, 15°23'S, 124°42'E, coll. J. Jelbart. **Northern Territory:** Darwin Harbour, approx. 12°30'S, 130°47'E, 1–21 m, coll. MEU, July 1993/March 1994, NTM W.10296, NTM W.10297, NTM W.10305, NTM W.10310, NTM W.10298, NTM W.10299, NTM W.10302, NTM W.10307, NTM W.10304, NTM W.10308, NTM W.10300, NTM W.10306, NTM W.10301, NTM W.10309, NTM W.10303, NTM W.13853, NTM W.13844, NTM W.13849, NTM W.13848, NTM W.13868, NTM W.13867, NTM W.13862, NTM W.13864, NTM W.13874, NTM W.13846, NTM W.13845, NTM W.13847, NTM W.13851, NTM W.13843, NTM W.13850, NTM W.13859, NTM W.13860, NTM W.13878, NTM W.13863, NTM W.13870, NTM W.13854, NTM W.13861, NTM W.13856, NTM W.13852, NTM W.13857, NTM W.13876, NTM W.13858, NTM W.13871, NTM W.13879, NTM W.13865, NTM W.13877, NTM W.13869, NTM W.13872, NTM W.13855, NTM W.13866, NTM W.13873, NTM W.13875; opposite Port, Wickham Point, NTM W.23368, 12°31.107'S, 130°52.485'E, coll. K. Metcalfe, Dry Season 2005; Bleesers Creek, NTM W.23369, 12°27.5713'S, 130°54.7586'E, coll. M. Neave, 16 April 2007; Hudson Creek, NTM W.22284 (includes DNA sample), 12°28.93'S, 130°55.6'E, coll. M. Neave, 1 May 2007; Charles Darwin National Park, NTM W.22277 (includes DNA sample), 12°27.43'S, 130°52.01'E, coll. M. Neave, 20 April 2007, NTM W.22304, 12°27.43'S, 130°52.01'E, coll. M. Neave, 20 August 2007, NTM W.22318, 12°27.43'S, 130°52.01'E, coll. M. Neave, 2 August 2007; Kitchener Bay, NTM W.21120, 12°28.09'S,



Fig. 1. *Hermundura gladstonensis*, entire animal approx. 12 mm long, lateral view, head facing downwards. Non-type specimen NTM W.23395. Photograph: C. Glasby.

130°50.478'E, 3.3 m, coll. C. Clark, 23 April 2007, NTM W.19239, 12°28.11'S, 130°50.83'E, 1 m, URS consultants, 22 September 2004. Melville Bay, Gove, approx. 12°12'S, 136°42'E, 5–18 m, coll. J.R. Hanley, July 1991/March 1992, NTM W.16824, NTM W.16825, NTM W.16828, NTM W.16830, NTM W.16831, NTM W.16832, NTM W.16833, NTM W.16834, NTM W.16836, NTM W.16842, NTM W.16846, NTM W.16848, NTM W.16849, NTM W.16850, NTM W.16852, NTM W.16853, NTM W.16855, NTM W.16856, NTM W.8229, NTM W.16826; NTM W.16840, NTM W.16841, NTM W.16843, NTM W.16851, NTM W.16844, NTM W.16837, NTM W.16835, NTM W.16838, NTM W.16839, NTM W.16845, NTM W.16847, NTM W.16854, NTM W.16823, NTM W.16827, NTM W.16829; Mangrove Creek, 12°12'S, 136 43'E, coll. NT Fisheries Department, 22 August 1971 NTM W.592; Bing Bong, McArthur River, 15 37'S, 136 23'E, coll. MEU, September

1992–March 1993, NTM W.7800. Queensland: Burnett River Estuary, NTM W19341, 24 46'S, 152 25'E, coll. P. Crosser, November 1987; AM W.13200, Gladstone, Auckland Creek, St. 4, coll. P. Saenger, August 1976; AM W13568, Gladstone, Calliope River, St. 2, coll. P. Saenger, May 1976. INDONESIA: Papua, Timika, approx. 5°S, 137°E, NTM W.23370, coll. LIPI, 9 August 2003, NTM W.23371, coll. LIPI, 28 June 2004, NTM W.23372, coll. LIPI, June 2004, NTM W.23373, coll. LIPI, 28 June 2004, NTM W.23374, coll. LIPI, 28 June 2004, NTM W.23375, coll. LIPI, 9 November 2009, NTM W.23376, coll. LIPI, 24 June 2004, NTM W.23377, coll. LIPI, 24 October 2002, NTM W.23379, NTM W.23380, NTM W.23381, coll. LIPI, 1 August 2002, NTM W.23382, coll. LIPI 28 June 2004, NTM W.23383, coll. LIPI, 28 June 2004, NTM W.23384, coll. LIPI, 28 June 2004, NTM W.23385, coll. LIPI 28 July 2004, NTM W.23386, coll. 28 June 2004, NTM W.23387, coll. LIPI 1 July 2004, NTM W.023388, coll. 1 July 2004, NTM W.23389, coll. LIPI, coll. LIPI, 1 July 2004, NTM W.23390, coll. LIPI, 29 July 2004, NTM W.23391, coll. LIPI, 1 July 2004, NTM W.23392, coll. LIPI 28 June 2004, NTM W.23393, coll. LIPI, NTM W.23394, coll. LIPI, August 2004, NTM W.23395, coll. LIPI 19 November 2009; Digul, approx. 7°S, 138°E, NTM W.23396, coll. LIPI, October 2002, NTM W.23397, coll. LIPI, 22 October 2002, NTM W.23398, coll. LIPI, 21 October 2002, NTM W.23399, coll. LIPI, 22 October 2002, NTM W.23400, coll. LIPI, 17 October 2002, NTM W.23401, coll. LIPI, October 2002.

Diagnosis. Palps with bifid, divergent palpostyles; buccal tube with 2–5 peg-like structures, honey-coloured to clear, or lacking any apparent structures; dorsal cirri absent; ventral cirri present from chaetiger 5; notopodial spines present from chaetiger 2, initially small and embedded, large and emergent from chaetiger 7–12; 5–9 neuropodial chaetae; neuroaciculae more or less tapered, but may have coloured distal knobs in mid-anterior body; pygidium bearing 3 anal cirri, middle one centrally positioned on plaque.

Description. Material examined ranges in size from 3.7–60 mm long, 0.4–1.5 mm wide (maximum width excluding parapodia), bearing 30–130 chaetigers. Brown pigment patches on lateral body and paired circular-shaped patches on pygidium (fading over time in alcohol). Body surface arcolated; anterior body region (chaetigers 4–5) inflated. Brain with 2 pairs of pigment spots – one pair on mid-brain, other pair on posterior lobes; reddish-brown to black. Palps biarticulated, separate from each other; palpostyles rod-like, bifid. Palpophores not fused. Buccal tube with 4–5 peg- or jaw-shaped denticles, or absent; honey-coloured to clear. Pharynx with distal ring of 10 papillae (rarely 8); all papillae more or less same size.

Notopodial lobes low (absent on first 4–6 chaetigers). Notochaetae comprising spines and capillaries; spines present from chaetiger 2, but not fully emergent until

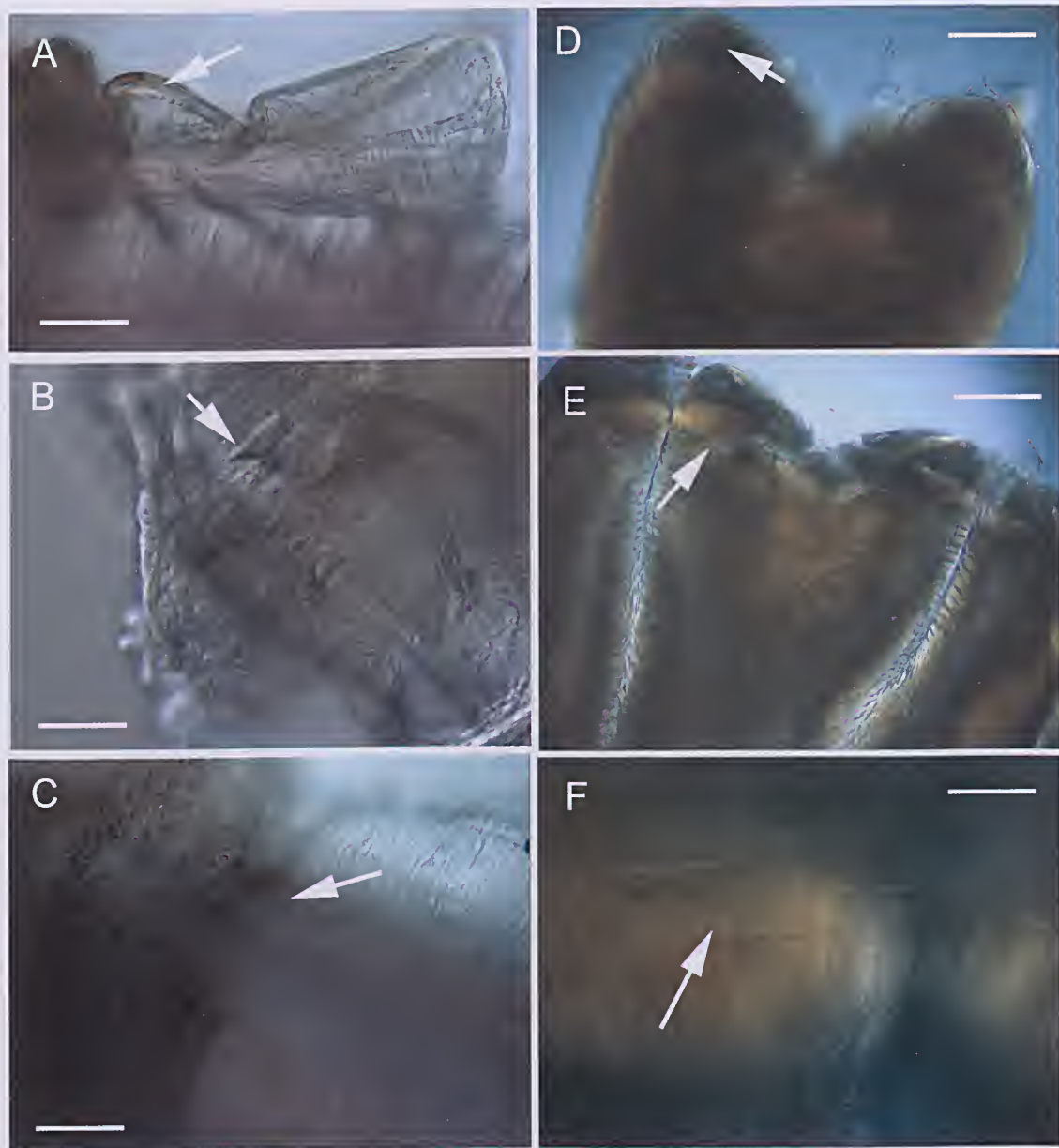


Fig. 2. *Hermundura gladstonensis*, structures associated with anterior alimentary canal including buccal tube (A–C) and pharynx (D–F): A, jaw-like denticle (NTM W.23395); B, conical denticle (NTM W.23392); C, sickle-shaped denticle (NTM W.23386); D, undissected pharynx, anterior end, showing laterally well-developed musculature resembling jaws (NTM W.22304); E, dissected pharynx, anterior end, showing transverse sphincter and longitudinal muscle sutures (NTM W.22318); F, dissected pharynx showing close up of sphincter (NTM W.22318). Scale bars: A–E, 0.1 mm; F, 20 μ m

chaetigers 7–8, some with reddish-brown colouring distally (may also fade in alcohol); spines well developed until last chaetiger. Notopodial capillary chaetae present from chaetiger 2. Notoaciaculae absent. Neuropodial lobe digitiform, very low on first 1–3 chaetigers, gradually increasing in size to maximum length in mid body. Ventral cirri present from chaetiger 5. Neurochaetae capillary-like, with numerous transverse rows of slender teeth over short

portion of chaeta, 5–9 per fascicle. Neuroaciaculae present, distally knobbed or tapered (knob-tipped types sometimes present on chaetigers 8–22). Paired lateral anal cirri present, papilliform. Mid-anal cirri present, papilliform, centrally positioned on plate. Anal opening dorsal.

Remarks. The large amount of material available for study, covering a wide geographic range, has allowed us to document the intraspecific variability of this common

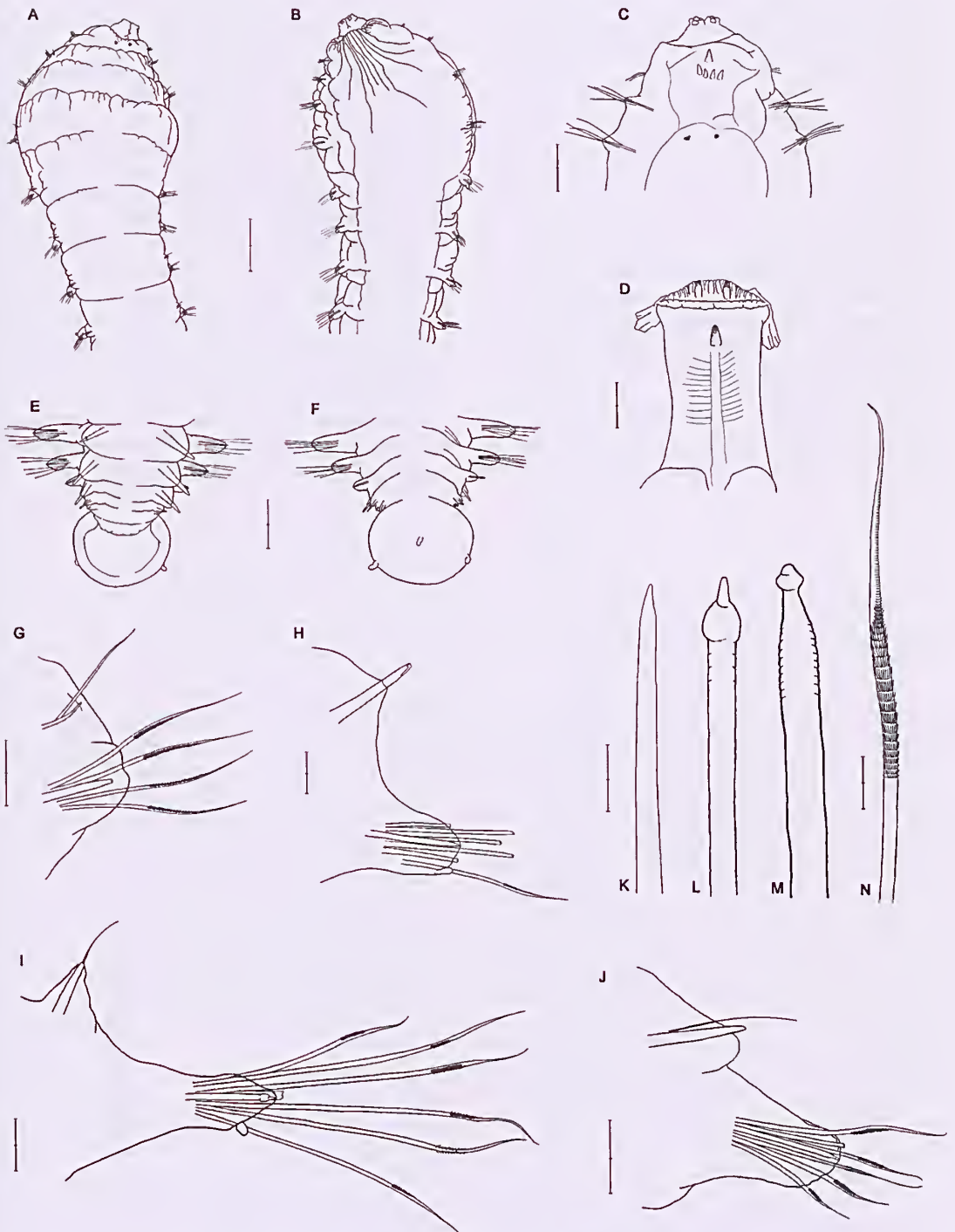


Fig. 3. *Hermundura gladstonensis*, A, anterior end, dorsal view (NTM W.22318); B, anterior end, ventral view (NTM W.22318); C, anterior end, dorsal view, specimen partially cleared with glycerol to show buccal denticles (NTM W.23373); D, pharynx dissected from body showing denticles (NTM W.23386); E, pygidium dorsal view (NTM W.22318); F, pygidium ventral view (NTM W.22318); G, parapodium of chaetiger 2 (NTM W.22318); H, parapodium of chaetiger 60 (NTM W.22318); I, parapodium of chaetiger 17 (NTM W.23373); J, parapodium of chaetiger 13 (NTM W.23373); K, L, M, neuroacicula, anterior chaetiger (NTM W.22318); N, hirsute neurochaeta, anterior chaetiger (NTM W.22318). Scale bars: A, B: 0.5 mm; C–F, 0.2 mm; G–J, 0.1 mm; K–M, 40 μ m; N, 25 μ m.

species, which until now was only known from the type description and the brief account of the forms from the Gulf of Carpentaria by Hocknull & Glasby (2009) (which is actually a composite of two species – *H. gladstonensis* and *H. philipi* sp. nov.). Two of the most interesting variable features are the presence of cuticularised denticles on the buccal tube and the pigmented knobbed-tipped neuroaaciculae. The cuticularised denticles may be elongate and resemble serrated jaws (Fig. 2A), or be conical to sickle-shaped (Figs 2B,C; 3C,D); the denticles numbered from 1 to 4 and were sometimes arranged 2 ventrally and 2 dorsally. Their occurrence within the taxon appears likely to be size-related (i.e. more common in larger worms) rather than geographic- or sex-related. Hardened structures of the buccal tube have not been reported previously for the family, although similar structures of the pharynx were thought to exist (see Remarks for genus).

Similarly, variability in the presence or absence of knob-tipped neuroaaciculae could not be easily explained. They were observed only in parapodia of the first 20 or

so chaetigers; the neuroaaciculae of some individuals were always tapered (Fig. 3K), whilst those of others showed various degrees of knobiness (Fig. 3 L, M). In addition, the presence of knobbed-tipped neuroaaciculae appeared to correspond with a reddish pigment spot at the tip of the same neuropodium – whether the tip itself was red or it was the tissue of the distal neuropodium could not be established. Knob-like protruberances have also been reported by Salazar-Vallejo (1990) on the distal region of the notopodial spines of the type species (*H. tricuspis*) raising the possibility that they represent aberrations common to members of the genus.

Habitat. *Hermundura gladstonensis* occurs from the lower intertidal zone to about 20 m in soft sediments (for the northern Australia material). It is not present in the higher intertidal zone under the mangrove canopy in Darwin Harbour (CJG pers. obs.).

Distribution. Sahul shelf including northern Australia and eastern Indonesia; also coastal north-eastern Australia, excluding the Great Barrier Reef (Fig. 5A).

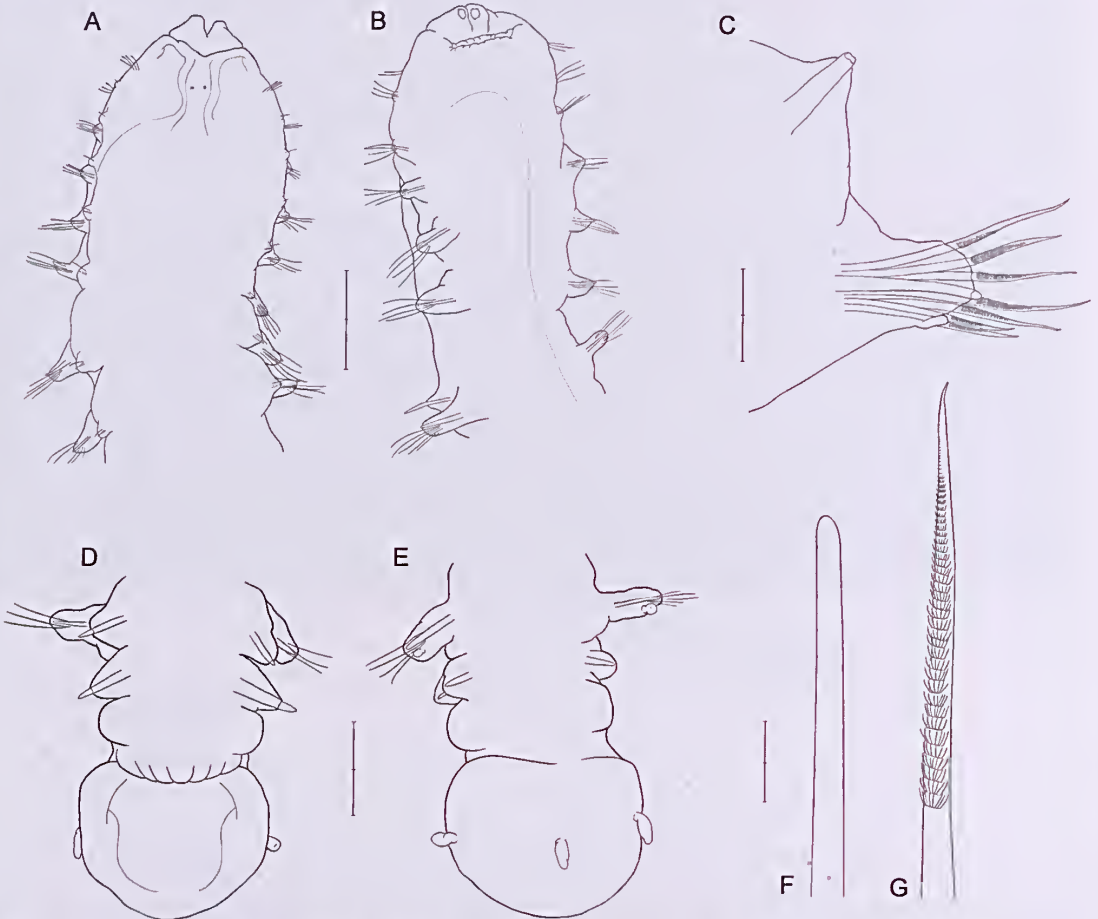


Fig. 4. *Hermundura philipi* sp. nov. Holotype, A, anterior end, dorsal view; B, anterior end, ventral view; C, parapodia from chaetiger 16; D, pygidium dorsal view; E, pygidium ventral view; F, Neuroaacicula, anterior chaetiger; G, hirsute neurochaeta, anterior chaetiger. Scale bars: A, B, 0.2 mm; C, 0.05 mm; D–E, 0.1 mm; F–G, 15 μ m.

Hermundura philipi sp. nov.

(Fig. 4A–G, 5B)

Loandalia gladstonensis Marks & Hocknull, 2006, 65–66, fig. 3a–d; Hocknull & Glasby 2009: 544 (in part).

Material examined. HOLOTYPE – QM G230618, Queensland, Gulf of Carpentaria, north of Mornington Island, coll. CSIRO R.V. *Southern Surveyor*, 15°59.4486'S, 139°53.346'E, 37.8 m, 2 March 2005. PARATYPES – collection details as for holotype, 1(QM G230616), 15°48.4818'S 139°47.4612'E, 42.6 m, coll. 1 March 2005; 3(QM G230619), 16°0.5412'S, 139°45.5016'E, 39.8 m, coll. 3 March 2005; 1(QM G230620), 16°1.3464'S, 139°36.0294'E, 39.8 m, coll. 3 March 2005; 1(QM G230624), 15°48.5046'S, 139°45.5112'E, 43.6 m, coll. 4 March 2005; 1(NTM W.21979), 15°56.5596'S, 139°41.109'E, coll. 2 March 2005; 1(NTM W.21980), 15°55.4136'S, 139°53.7162'E, coll. 2 March 2005; 1(NTM W.21981), 16°0.5676'S, 139°37.4982'E, coll. 3 March 2005.

Non-type material. QUEENSLAND: Gulf of Carpentaria, north of Mornington Island, coll. CSIRO R.V. *Southern Surveyor*, QM G230611, 15°58.3164'S, 139°39.3606'E, 41.4 m, coll. 4 March 2005; QM G230612, 16°9.5718'S, 139°44.4606'E, 35.4 m, coll. 28 February 2005; QM G230613, 15°55.4622'S 139°28.497'E, 43 m, coll. 27 February 2005; QM G230614, 15°58.488'S, 139°40.4964'E, 41.4 m, coll. 27 February 2005; QM G230615, 15°59.5026'S, 139°41.4948'E, 40.6 m, coll. 1 March 2005; QM G230617, 15°58.9056'S, 139°44.0076'E, 39.8 m, coll. 2 March 2005; QM G230621, 16°0.5676'S, 139°37.4982'E, 41.6 m, coll. 3 March 2005; QM G230622, 16°7.9314'S, 139°46.479'E, 37.8 m, coll. 4 March 2005; QM G230623, 15°58.3164'S, 139°39.3606'E, 41.4 m, coll. 4 March 2005; QM G230625, 15°59.6574'S, 139°39.2496'E, 41 m, coll. 4 March 2005; QM G230626, 16°9.4224'S, 139°39.5118'E, 34.6 m, coll. 4 March 2005; QM G230627, 15°59.4978'S, 139°42.498'E, 39.8 m, coll. 4 March 2005; QM G230628, 16°0.6588'S, 139°35.2044'E, 41.8 m, coll. 5 March 2005; QM G230629, 15°58.5228'S, 139°44.4756'E, 40.4 m, coll. 5 March 2005; QM G230630, 15°57.4908'S, 139°36.5082'E, 41.8 m, coll. 5 March 2005; QMG 230631, 16°1.3656'S, 139°46.4376'E, 39.4 m, coll. 5 March 2005; QM G230632, 16°1.6434'S, 139°39.7044'E, 41.4 m, coll. 6 March 2005.

Diagnosis. Body with constriction after anterior inflated segment (between chaetigers 6–7); palps with simple, button-like palpostyle; pharynx and buccal tube unarmed; dorsal cirri absent; ventral cirri present from chaetiger 7; notopodial spines present from chaetiger 5, initially small and embedded, large and emergent from chaetiger 7; 5 or 6 neuropodial chaetae, with large proportion of chaetae hirsute; neuroaediculae of mid-body tapered; pygidium bearing 3 anal cirri, middle one located centrally on plaque.

Description. Holotype 6.0 mm long, 0.45 mm wide (max. width including parapodia) for 35 chaetigers. Paratypes range in size from 2.2–10.0 mm long, 0.40–0.50 mm wide, with 21–55 chaetigers. Brown pigment

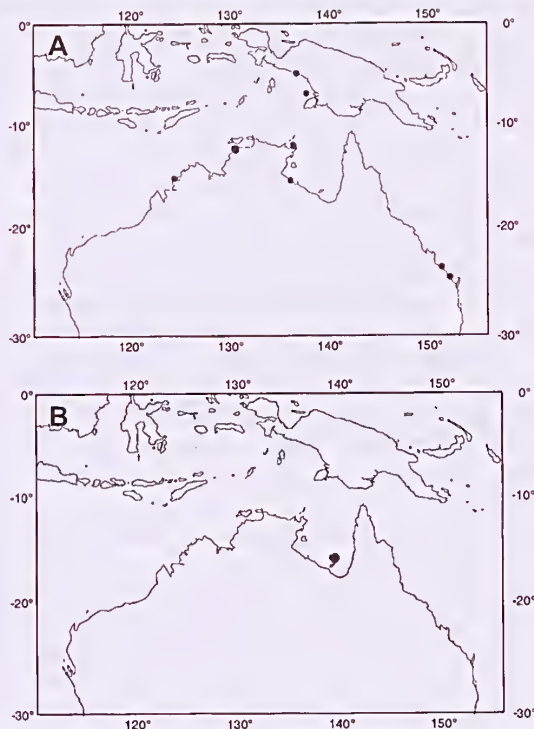


Fig. 5. A, Distribution of *Hermundura gladstonensis*; B, distribution of *H. philipi* sp. nov.

patches on lateral body and paired circular-shaped patches on pygidium. Body surface arcolated anteriorly, smooth posteriorly; anterior body region (chaetigers 1–6) inflated, with slight constriction between chaetigers 6–7 (Fig. 4A,B). Brain with 3 pairs pigment spots; 2 pairs on mid-brain and 1 pair on hind-brain. Palps biarticulated, separate from each other; palpostyles button-like; simple. Buccal tube with tooth-like structures not observed.

Notopodial lobes low (absent on first 6 chaetigers). Notochaetae comprising spines and capillaries; spines present from chaetigers 5–6 very small and not emergent initially; from chaetiger 7 onward, large fully developed emergent spine to last chaetiger (Fig. 3C). Notopodial capillary chaetae present from chaetiger 2, 0–3 per fascicle. Notoaediculae absent. Neuropodial lobe digitiform. Ventral cirri present from chaetiger 7. Neurochaetae capillary-like, with numerous transverse rows of slender teeth covering large portion of chaeta, 5–6 per fascicle (Fig. 4G). Neuroaediculae present, tapering to a slightly expanded tip (Fig. 4F). Pygidium plate-like (Fig. 4D). Paired lateral anal cirri present, papilliform; mid-ventral anal cirri present, positioned centrally on plate (Fig. 4E). Anal opening dorsal.

Intraspecific variation. The largest non-type specimen was 16 mm long, 0.75 mm wide for 59 chaetigers (incomplete). Specimen QM G230627 was encased in a hyaline tube, similar to those of species of *Phyllochaetopterus* and *Spiochaetopterus* (Chaetopteridae).

It is therefore possible that *H. philipi* is commensal with a chaetopterid, especially because other *Hermundura* species have also been found associated with *Phyllochaetopterus* tubes (Berkeley & Berkeley 1941; Thomas, 1963), and other pilargids are known to be commensal with chaetopterids, for example, *Pilargis berkeleyae* is known to be associated with *Chaetopterus* tubes (Britaev 1993).

Etymology. The new species is named in honour of Philip Marks, the junior author's father.

Remarks. The brief account of *Hermundura gladstonensis* by Hocknull & Glasby (2009) is a composite of two species, *H. gladstonensis* and *H. philipi* sp. nov.

The new species appears to be closest in morphology to *H. fredrayorum* and *H. indica* (Thomas, 1963), which also have ventral cirri starting on chaetiger 7. *Hermundura fredrayorum* differs in being a much larger species (181 mm long, 2.55 mm wide with chaetae), with its notopodial spines starting on chaetiger 9, in having a greater number of both notopodial capillaries (2–4) and neuropodial chaetae (20–24), and in lacking a mid-ventral anal cirrus. *Hermundura indica* differs in having the first few chaetigers biramous, notopodial spines present from chaetiger 7, and having 5 anal cirri. The new species may be distinguished from all other species in the Indo-west Pacific region using the key below.

Habitat. *Hermundura philipi* occurs in about 35–45 m in soft sediments.

Distribution. This species is presently known only from the southern Gulf of Carpentaria (Fig. 5B).

DISCUSSION

The expanded definition of *Hermundura* containing both *Talehsapia* and *Parandalia* now gives the genus a total of 17 species worldwide (Table 1). Three species of *Hermundura* occur in the northern Australian region. Although *H. gladstonensis* and *H. philipi* potentially overlap in distribution in the southern Gulf of Carpentaria, it appears that they are disjunct based on habitat preference. *Hermundura gladstonensis* is restricted to coastal areas down to 20 m, whereas *H. philipi* occurs in waters from 35–45 deep. This pattern of habitat partitioning agrees with the general pattern identified for the northern Australia Pilargidae (Hocknull & Glasby 2009), viz. an inshore component (e.g. *H. gladstonensis*, *H. fredrayorum*), a shallow shelf component (*H. philipi*), and a deep shelf component (includes other pilargids, but no species of *Hermundura* in this category).

Interestingly, *Hermundura fredrayorum* was not reported in this study. It appears to have a limited distribution in the subtropical east coast of Australia. The three species may be distinguished from each other and from remaining Indo-west Pacific *Hermundura* species using the following key.

Key to *Hermundura* species of Australia and the Indo-west Pacific

1. Ventral cirri present from chaetiger 4; palpostyles bifid *H. annandalei*
- Ventral cirri present from chaetiger 5; palpostyle bifid, divergent *H. gladstonensis*
- Ventral cirri present from chaetiger 7; palpostyles simple 2
2. Notopodial spines present from chaetiger 5, initially small and embedded, large and emergent from chaetiger 7; pygidial plate with 3 anal cirri *H. philipi* sp. nov.
- Notopodial spines present from chaetiger 7; pygidial plate with 5 anal cirri *H. indica*
- Notopodial spines present from chaetiger 9, initially small and embedded, large and emergent from midbody; pygidial plate with 2 anal cirri *H. fredrayorum*

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Typtonoides nieli gen. nov., sp. nov., a new pontoniine shrimp (Crustacea: Decapoda: Palaemonidae) from the Chesterfield Islands

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ABSTRACT

A small pontoniine shrimp, *Typtonoides nieli*, from the Chesterfield Islands, New Caledonia, is described and illustrated. Its systematic position is obscure as only a single second pereopod is preserved. It is possibly related to the sponge-associated genus *Typton* Costa as the scaphocerite is similarly strongly reduced, but its host remains unknown.

KEYWORDS: *Typtonoides nieli* gen. nov., sp. nov., Crustacea, Decapoda, Pontoniinae, Chesterfield Islands, Coral Sea.

INTRODUCTION

The pontoniine shrimp fauna of the reefs of the Chesterfield Islands, New Caledonia, has received little attention. So far only four species have been reported, all from less than 100 m: *Isopontonia platycheles* Bruce, 1982 and *Periclimanaens stylirostris* Bruce, 1969 from 15 m and 21 m are the only ones from less than 50 m, with *Thaunastocaris streptopus* Kemp, 1922 from 68–70 m and *Odontonia simplicipes* (Bruce, 1996) from 71 m (see Bruce 1996). *Isopontonia platycheles* and *Odontonia simplicipes* are still known only from the holotype specimens.

The discovery of a single specimen of a pontoniine shrimp that can not be referred to any of the presently known pontoniine genera is therefore of interest. An illustrated description is now provided. The specimen is deposited in the collections of the Museum and Art Gallery of the Northern Territory, Darwin.

Abbreviations used: CL, postorbital carapace length; NTM, Museum and Art Gallery of the Northern Territory, Darwin (formerly Northern Territory Museum).

SYSTEMATICS

Palaemonidae Rafinesque, 1815

Pontoniinae Kingsley, 1879

Typtonoides gen. nov.

Typtonoides Bruce. Gender masculine. Type species, by present designation and monotypy, *Typtonoides nieli*. Recent, Chesterfield Islands, Pacific Ocean.

Diagnosis. Rostrum elongate, dentition 9/1, carapace compressed, with orbit obsolescent, paraorbital spine present, antennal, hepatic and supraorbital spines absent, inferior orbital angle obsolete; scaphocerite strongly

reduced, much shorter than carapace; mandible without palp, incisor process uni-dentate; maxillipeds not filtratory baskets, third maxilliped with normal slender exopod; thoracic sternites narrow, unarmed; first pereopod fingers spatulate; major second pereopod chela with fingers simple, cutting edges sharp, dentate; ambulatory dactyls simply biunguiculate; telson with 2 pairs of dorsal spines, 3 pairs of posterior spines.

Etymology. Derived from the pontoniine generic name *Typton*, first used by Costa (1844) and *-oides* (Greek), resembling, with reference to the scaphocerite.

Systematic position. Almost all pontoniine genera are characterised by the possession of a well-developed scaphocerite. The scaphocerite is greatly reduced in the genera *Typton* Costa, 1844, *Typtonychus* Bruce, 1996 and *Paratypton* Balss, 1914. *Paratypton* is readily distinguishable by the absence of an exopod on the third maxilliped and many other features suggesting that the genus is not at all closely related to the other genera. *Typtonychus* is distinguished from *Typton* and *Typtonoides* primarily by the presence of maxillipedal filtratory baskets, not present in the other genera. *Typtonoides* also differs from *Typton* in the following features: (1) Well-developed long rostrum with numerous dorsal teeth (vs short rostrum, with few or no dorsal teeth); (2) Second pereopod fingers with sharp, non-shearing dentate cutting edges. *Typton* is characterised by the presence of shearing cutting edges on the minor second pereopod but the state of this appendage is unknown in *Typtonoides*.

Remarks. As only a single second pereopod has been preserved, a full diagnosis for the genus cannot be provided as it is not certain if this is the major or the minor pereopod, or if the second pereopods are subequal and similar or unequal or dissimilar. The single second pereopod resembles neither the major nor the minor second pereopods

found in *Typton* species. However, on account of its large size the single second pereiopod is assumed to be the major chela. The fingers of the major second pereiopod in *Typton* are robust with the cutting edges lacking teeth, while the fingers of the minor second pereiopod close with a shearing action and are also unarmed.

Typtonoides nieli sp. nov.
(Figs 1-6)

Material examined. HOLOTYPE - ♂, dissected, RV *Lady Basten*, 19°53'S, 158°19'E, Long Island, Chesterfield Islands, New Caledonia, 15 m, rubble from seaward reef edge, 5 May 1979, coll. N.L. Bruce, AJB #2999, NTM Cr.16899.

Diagnosis. With the characters of the genus.

Description. Male (Fig. 1). A small-sized, slender species of typical pontoniine form.

Rostrum (Fig. 2A,B) about 0.68 of CL, slender, compressed, depressed, reaching to end of antennular peduncle, dorsal carina feebly developed, with 9 well-

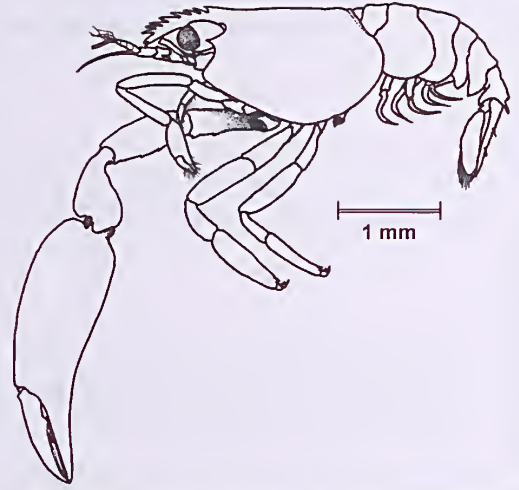


Fig. 1. *Typtonoides nieli* gen. nov., sp. nov., holotype, male (NTM Cr.16899), Long Island, Chesterfield Islands, 15 m.

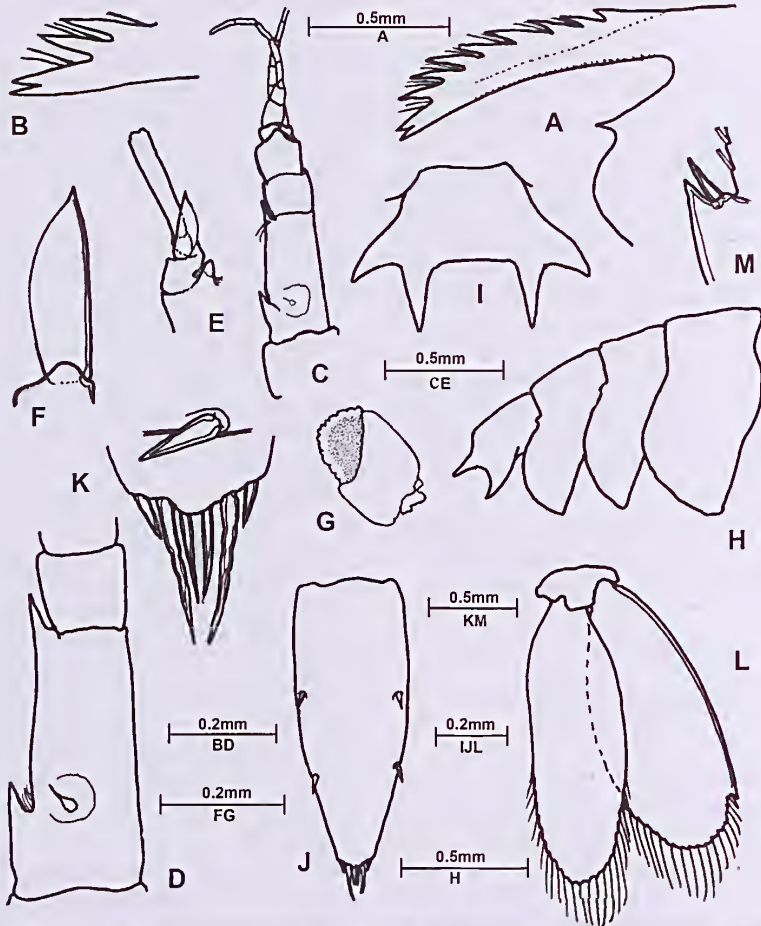


Fig. 2. *Typtonoides nieli* gen. nov., sp. nov., holotype, male (NTM Cr.16899): A, anterior carapace and rostrum; B, rostrum, tip; C, antennule; D, same, proximal peduncular segment; E, antenna; F, same, scaphocerite; G, eye, dorsal; H, abdomen, third to sixth segments, lateral; I, same, sixth segment, dorsal; J, telson; K, same, posterior spines, inset: distolateral spine; L, uropod; M, same distolateral exopod.

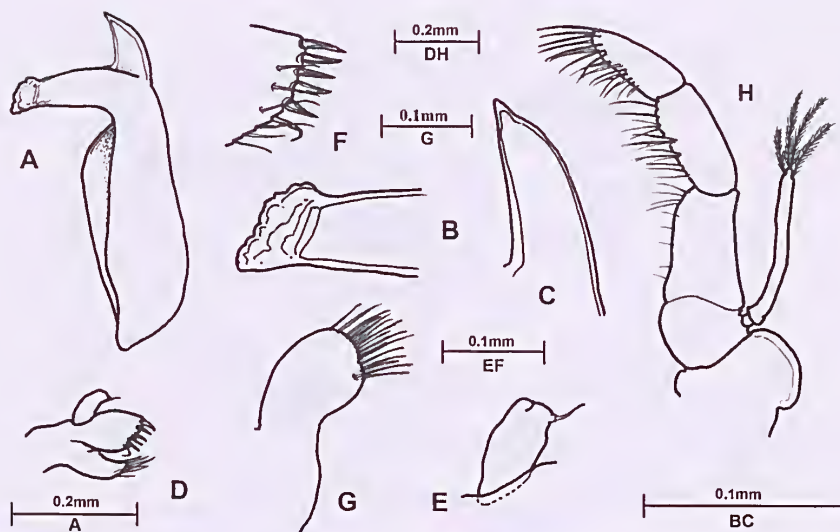


Fig. 3. *Typtonoides nieli* gen. nov., sp. nov., holotype, male (NTM Cr.16899): A, mandible; B, molar process; C, incisor process; D, maxillula; E, same, palp; F, same, distal upper lacinia; G, maxilla, basal endite; H, third maxilliped.

developed slender acute teeth, all pre-orbital, preterminal tooth smaller, presenting as a bifid tip, teeth separated by long slender simple median setae, ventral margin concave, unarmed, non-setose.

Carapace (Fig. 2A) smooth, glabrous, with acute marginal paraorbital spine, without supraorbital spines or tubercles, postorbital, antennal or hepatic spines, without orbital carinae, inferior orbital angle completely obsolete, pterygostomial angle slightly produced, obtusely rounded.

Abdominal segments (Fig. 2H) smooth, glabrous, first without median anterior dorsal lobe, third tergite not posteriorly produced, sixth segment (Fig. 2I) about 0.27 of CL, subequal to fifth segment length, 2.0 times longer than deep, posterolateral angle acute, strongly produced, posteroventral angle larger, acute, first to third pleura rounded, fourth and fifth ventrally produced, subacute.

Telson (Fig. 2J) 0.35 of CL, about 2.7 times as long as anterior width, lateral margins feebly convex, convergent, dorsal spines (Fig. 2K) subequal, about 0.07 of telson length, anterior pair submarginal, at 0.4, posterior pair marginal at 0.66 of telson length, posterior margin about 0.33 of anterior width, broadly rounded, without median point, lateral posterior spines (Fig. 2K) distinctly smaller than dorsal spines, intermediate spines well developed, robust, about 0.12 of telson length, submedian spines 0.6 of intermediate spine length, non-ectulose.

Antennule (Fig. 2C) with proximal segment (Fig. 2D) of peduncle 2.4 times as long as central width, medial margin straight, non-setose, without ventromedial tooth, lateral margin almost straight, feebly convergent, not laterally produced proximally, distolateral angle with long slender tooth, without anterior medial lobe, stylocerite reduced, acute, reaching to 0.4 of segment length, statoyst obsolescent, without statolith; intermediate and distal segments subcylindrical, intermediate segment subequal

to distal segment length, combined length 0.66 of proximal segment length; upper flagellum biramous, upper ramus with 2 proximal segments fused, with 1 small free segment, 5 groups of aesthetases, longer ramus slender, with 5 segments, lower flagellum incomplete.

Antenna (Fig. 2E) with basicerite laterally unarmed, earpocerite slender, subcylindrical, 5.0 times longer than width, extending far beyond scaphocerite, to about distal end of intermediate segment of antennular peduncle; scaphocerite (Fig. 2F) reaching to about half earpocerite length, about 3.2 times longer than central width, lateral margin straight, acutely pointed distally, lamella obsolete, margin convex, non-setose, flagella missing.

Eye (Fig. 2G) with globular cornea, oblique, about 0.2 of CL, poorly pigmented, without accessory pigment spot, eyestalk about as wide as long.

Ophthalmic somite without median process or pigment spot; epistome unarmed.

Mandible (Fig. 3A) with corpus robust, without palp; incisor process (Fig. 3C) reduced, tapering to single acute distal tooth; molar process (Fig. 3B) well developed, subcylindrical, distally truncate, obscurely tuberculate, without obvious setae.

Maxillula (Fig. 3D) with palp (Fig. 3E) stout, very feebly bilobed, ventral lobe with short sinuous ventral spinule; upper lacinia (Fig. 3F) broad, transversely truncate distally, with single row of 5 simple articulated marginal spines, with 3 slender submarginal spiniform setae; lower lacinia bluntly rounded distally, with numerous slender simple spiniform setae.

Maxilla, first and second maxillipeds damaged in dissection. Maxilla with basal endite (Fig. 3G) broadly simple with about 16 slender simple marginal setae distally. First maxilliped with basal and coxal endites fully fused, medial margin straight, basal portion with sparse long feebly

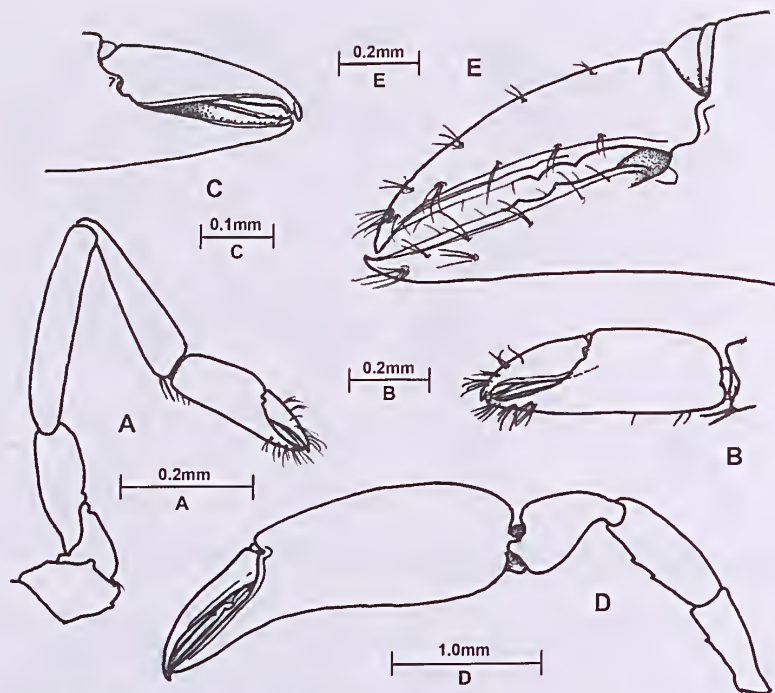


Fig. 4. *Typtonoides nieli* gen. nov., sp. nov., holotype, male (NTM Cr.16899): A, first pereiopod; B, same, chela; C, same, fingers; D, second pereiopod; E, same, fingers.

setulose setae, coxal region with sparse slender simple marginal setae; epipod large, cordiform, bilobed. Second maxilliped endopod of normal form, dactylar segment with numerous long stout finely denticulate spines along medial margin.

Third maxilliped (Fig. 3H) short, robust, reaching to end of intermediate segment of antennular peduncle, ischiomerus and basis distinct, ischiomerus short, 1.7 times longer than central width, tapering slightly distally, medial margin sparsely setose, lateral margin glabrous; carpal segment subequal to meral length, 2.2 times longer than central width, with numerous simple setae along medial margin, lateral margin glabrous, with several groups of slender simple setae medially; terminal segment slightly shorter than carpus, 2.6 times longer than proximal width, tip blunt; with numerous slender simple spiniform setae medially and distally; basipodite well developed, about 0.6 of ischiomerus length, exopod with slender flagellum, slightly exceeding ischiomerus, with four plumose terminal setae; coxa medially convex, with well-developed low rounded lateral plate, without arthrobranch.

Thoracic sternites narrow; fourth without slender median process, posterior sternites unarmed.

First pereiopod (Fig. 4A) normal, chela (Fig. 4B) about 0.45 of CL, palm compressed, 1.6 times longer than deep centrally, with very sparse cleaning setae proximo-ventrally, fingers (Fig. 4C) broadened, narrowly spatulate, tapering distally with small tridentate tips, central tooth largest, dactyl about 3.0 times longer than proximal depth, medial

and lateral cutting edges feebly laminar distally, entire, fixed finger similar; carpus 1.1 times chela length, 4.2 times longer than distal width, tapering proximally, with few slender cleaning setae distoventrally; merus 1.4 times chela length, 1.2 times carpus length, 6.4 times longer than central width; ischium, 0.8 of chela length, 2.7 times longer than distal width, tapering proximally; basis about 5.0 of chela length; coxa robust, without distoventral process.

Major second pereiopod (left) (Fig. 4D) well developed, with large chela, 2.25 times CL, palm oval in section, moderately compressed, about 2.2 times longer than maximal depth, at about 0.33 pf length, smooth, tapering slightly distally, glabrous, fingers (Fig. 4E) about 0.38 of palm length, not in-curved, dactyl robust, compressed, about 3.5 times as long as proximal depth with convex dorsal margin, tip feebly bluntly hooked, cutting edge with 2 small low teeth at about 0.45 of length, distal cutting edge, sharp, entire, fixed finger about 2.4 times longer than proximal depth, with blunt feebly hooked tip, cutting edge with 2 low teeth on central portion, distal cutting edge sharp, entire; carpus about 0.5 of palm length, 1.8 times longer than distal width, distally expanded, tapering strongly proximally, slightly excavate distally, unarmed; merus about 0.5 of palm length, 2.4 times as long as central width, slightly swollen centrally, ventral margin with 2 small acute denticles; ischium about 0.4 of palm length, 2.6 times longer than distal width, tapering strongly proximally, ventral margin with 1 small acute denticle; basis and coxa stout, without special features.

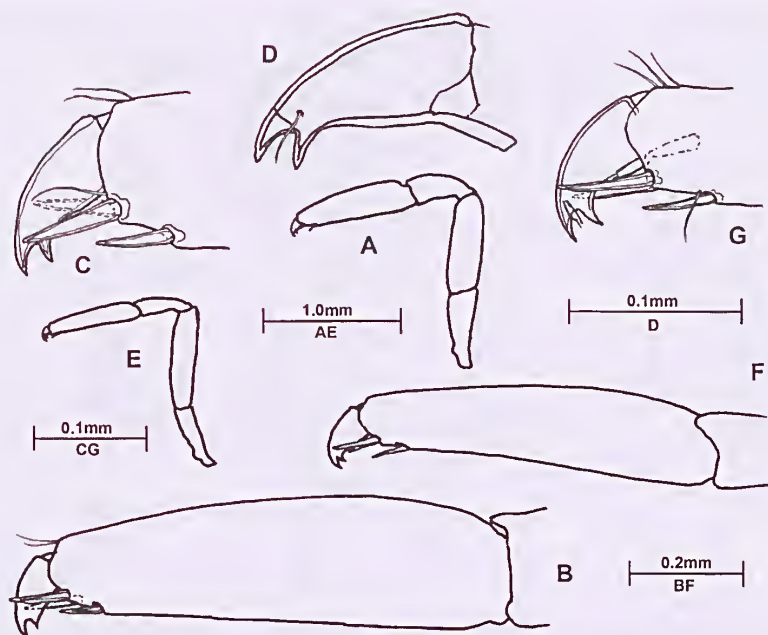


Fig. 5. *Typtonoides nieli* gen. nov., sp. nov., holotype, male (NTM Cr.16899): A, third pereiopod; B, same, propod and dactyl; C, same, distal propod and dactyl; D, same, dactyl; E, fourth pereiopod; F, same, propod and dactyl; G, same, distal propod and dactyl.

Minor second pereiopod (left) missing.

Third pereiopod (Fig. 5A) exceeding the distal end of antennular peduncle by propod and dactyl; propod about 0.67 of CL; dactyl (Fig. 5D) compressed, biunguiculate, about 0.16 of propod length, unguis short, 0.21 of corpus length, clearly demarcated, 2.0 times longer than basal width, slender, simple, very acute, corpus twice as long as deep, dorsal margin feebly convex, ventral margin with stout, strongly curved terminally acute distal accessory tooth, slightly smaller than unguis, ventral margin feebly convex, unarmed, without ventral or basal armament, with long simple distal sensory setae medially and laterally; propod (Fig. 5B) 3.5 times longer than deep, sparsely setose, tapering distally, distal width about half of proximal, with 2 robust distoventral spines (Fig. 5C), lateral spine about 4.8 times longer than basal width, 0.8 of distal propod width, medial spine about 0.8 of lateral spine length, 1 preterminal distal ventral spine, slightly smaller than distal medial spine; carpus about 0.55 of propod length, 3.0 times longer than central width, unarmed; merus about 0.9 of propod length, 3.2 times longer than central width, unarmed; ischium 0.66 of propod length, 3.0 times longer than distal width, unarmed; basis and coxa robust, without special features.

Fourth pereiopod (Fig. 5E) similar to third, propod (Fig. 5F) shorter, slender, about 0.85 of third propod length, 4.6 times longer than width, tapering distally, spines (Fig. 5G) similar to third propod but more slender; proximal segments also similar but more slender.

Fifth pereiopods missing.

First pleopod (Fig. 6A) with basipodite (Fig. 6C) 2.4 times as long as broad; exopod subequal to basipodite

length, 5.5 times longer than broad; endopod (Fig. 6B) 0.4 of exopod length, 3.0 times longer than wide, tapering distally, without medial accessory lobe, with 5 marginal spiniform setae.

Second pleopod (Fig. 6D) basipodite 2.1 times longer than broad, slightly longer than first basipodite length; exopod subequal to basipodite length; endopod (Fig. 6E) 0.95 of exopod length, appendices at 0.3 of medial margin length, appendix masculina with corpus greatly reduced, obsolescent, with single long slender simple terminal spine, well exceeding tip of endopod, about 0.66 of endopod length; appendix interna about half length of terminal spine of appendix masculina, with few distal cincinnuli.

Uropod (Fig. 2L) with protopodite posterolaterally rounded; rami broad; exopod 2.3 times longer than broad, lateral margin convex, non-setose, with small distolateral tooth, slightly longer spine medially (Fig. 2M), diacresis obsolete; endopod about subequal to exopod length, 3.0 times longer than broad.

Measurements (mm). Post-orbital carapace length, 1.25; carapace and rostrum, 2.1; total body length (approx.), 4.7; second pereiopod chela, 5.4.

Colouration. No data.

Etymology. Named after the collector, Dr Niel L. Bruce, a close relative of the author.

Systematic position. As discussed in the generic diagnosis.

Host. Unknown.

Remarks. If the second pereiopods of this species are asymmetrical, on account of its relative size, the only second pereiopod preserved can be safely assumed to be the major

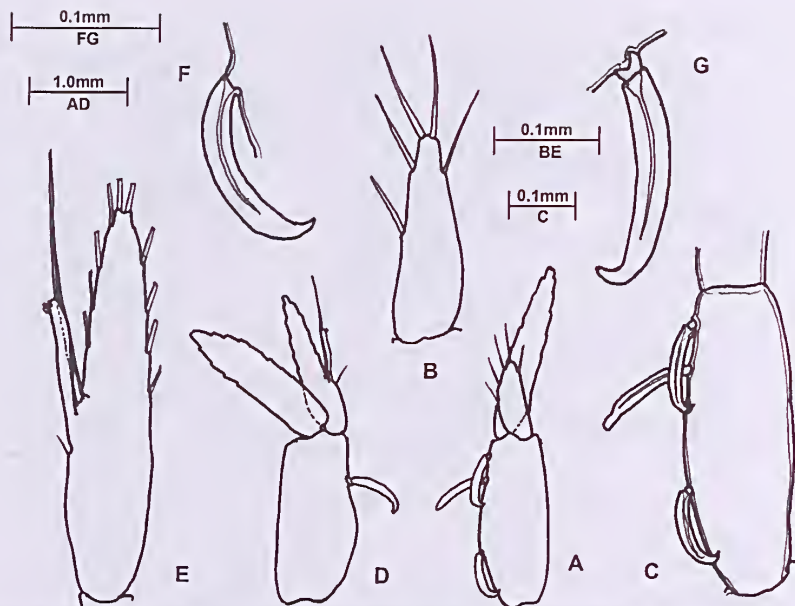


Fig. 6. *Typtonoides nieli* gen. nov., sp. nov., holotype, male (NTM Cr.16899): A, first pleopod; B, same, endopod; C, same, basipodite with attachments; D, second pleopod; E, same, endopod and appendices; F, G, attachments to basipodite.

second pereiopod. Regardless of whether the single second pereiopod is a major or minor appendage (if they are not subequal and similar) it does not resemble either the major or the minor second pereiopods in *Typton*, *Typtonychus* or *Periclimenaeus*. It resembles particularly closely the second pereiopod of *Onycozoides stenolepis* (Holthuis, 1952). The holotype of this species is immediately distinguishable by its greatly reduced, toothless rostrum and a large scaphocerite with a very well-developed lamella and very large distolateral tooth. The holotype shows a second pereiopod without acute ventral denticles on the merus and ischium. The specimen reported from Sigatoka, Fijian Islands, is noted to have the ventral margins of the merus and ischium feebly tuberculate (Bruce 1972: 76, fig. 6A,B), thereby increasing the resemblance. This Fijian specimen was collected together with a *Periclimenaeus*, probably from a sponge host. It seems most likely that *Typtonoides nieli* is also a sponge associate.

The first and second pleopods have attached to both medial and lateral margins of the basipodites several curved cylindrical objects (Fig. 6F,G). These have thick walls and a narrow lumen, with a hooked distal extremity, with no evidence of internal structures. The more posterior pleopods have not been examined. The identity of these presumed parasites is uncertain. The possibility of empty rhizocephalan kentrogon was considered, but this is thought unlikely (Jens Hoeg pers. comm.).

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Lebbeus rubrodentatus sp. nov. (Crustacea: Caridea: Hippolytidae) from the Australian North West Shelf

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ABSTRACT

A new species of the hippolytid genus *Lebbeus* White, 1847, *L. rubrodentatus* sp. nov., is described and illustrated. Its colour pattern in life is diagnostic. The single specimen was sorted from a benthic trawl sample obtained in 360–396 m in the Timor Sea. A key to the five carinate species of the large genus *Lebbeus* is provided.

KEYWORDS: *Lebbeus rubrodentatus*, new species, Decapoda, Hippolytidae, Timor Sea.

INTRODUCTION

A recent paper by McCallum & Poore (2010) reported on the carinate species of *Lebbeus* White, 1847 (i.e., those species possessing a high, bilaterally compressed dorsal keel on the carapace) with particular reference to the Australian species. Two new species, *L. clarehannah* McCallum & Poore, 2010 and *L. cristagalli* McCallum & Poore, 2010, were described and illustrated in detail. In the remarks on *L. cristagalli* it was noted that one specimen was significantly different from the 10 type specimens, none of which had the carinal dentition resembling the present specimen. These authors noted that the specimen might belong to another new species. It was suggested that the reduced size of the two distal teeth might be due to damage in life. The colouration was also significantly different. Re-examination of the carinal teeth by the present author shows no suggestion of traumatic origin, with the teeth forming a graduated, though exaggerated, series when compared to the other species of this group. McCallum & Poore (2010) also clearly demonstrate that the striking colour patterns of the other species of this group are species-specific, as shown by their excellent colour illustrations. There is no reason to doubt that the distinctive colour pattern found in the present specimen is not also species-specific. Thus the specimen can safely be regarded as a distinct species and is now here provided with a name.

The unique holotype is held in the collections of the Museum and Art Gallery of the Northern Territory, Darwin. Abbreviations used: CL, postorbital carapace length; NTM, Museum and Art Gallery of the Northern Territory Museum (formerly Northern Territory Museum), Darwin; QM, Queensland Museum, Brisbane.

SYSTEMATICS

Family Hippolytidae Bate, 1888

Genus *Lebbeus* White, 1847

Gender masculine. Type species, by monotypy, *Lebbeus orthorhynchus* (Leach mss) White, 1847 (= *Alpheus polaris* Sabine, 1824). Recent, Circum-Arctic. The genus name *Lebbeus* White, 1847 has been conserved under the Plenary Powers of the International Commission on Zoological Nomenclature and placed on the Official List of Generic Names in Zoology (ICZN 1963: Opinion 671).

Synonyms of *Lebbeus* are *Hetairus* Bate, 1888 and *Birulaecaris* Dons, 1915 (Holthuis 1993).

Lebbeus rubrodentatus sp. nov.

Figs 1, 2

Lebbeus cristagalli McCallum & Poore, 2010: 134 (in part), fig. 4E.

Material examined. HOLOTYPE – NTM CR.6897, ovig. ♀, CL 15.2 mm, Timor Sea, 9°35'S, 129°28'E, 360–396 m, trawl, coll. B. Wallner on F.V. *Territory Pearl*, 18 January 1988.

Description.

Carapace with very well developed triangular dorsal carina bearing 5 acute teeth, posterior first tooth small, narrowly acute, second and third teeth similar, much enlarged, broadly acute, second slightly larger than third, fourth and fifth anterior teeth very small, acute; terminal segment of third maxilliped with about 25 spines; epipods present on first three pereopods, 4 pairs of dorsal telson spines; other morphological characters as in *L. cristagalli*.

Colouration (Fig. 1). Body and appendages generally pale pink, most intense over postorbital region and dorsal carapace, paler over branchiostegal region; dorsal carapace



Fig. 1. *Lebbeus rubrodentatus* sp. nov., ovigerous female holotype, Timor Sea, 360–396 m, NTM CR.6897, *pinxit* D. Percival.



Fig. 2. *Lebbeus rubrodentatus* sp. nov., ovigerous female holotype, Timor Sea, 360–396 m, NTM CR.6897, carapace and rostrum.

and lower half of carina with numerous red spots, largest in postorbital area and decreasing in size peripherally, largest spots with pale centre; carinal teeth all distally deep red, with similar red patches on distal scaphocerite and carpoцерite; antennal flagella whitish. Ova dark grey.

Etymology. From *rubrum* (Latin), red, and *dentatus* (Latin), toothed, a reference to the distal red of the dorsal carapace teeth.

Remarks. Five carinate species of *Lebbeus* are now known, all from moderately deep water, with *L. yaldwini* occurring from 190 m to 470 m, with the other species at intermediate depth. *Lebbeus compressus* occurs in Japanese waters, all other species are known only from Australian waters. McCallum & Poore (2010) noted that these species form a discrete species group on the basis of the elevated carina on the carapace and presence of epipods on the first and second pereopods only. The new species also has an epipod on the third pereopod. The carina is a very characteristic feature that suggests that these species should be generically separate from the other *Lebbeus* species. The carapace of *L. rubrodentatus* (Fig. 2) has a small supraorbital spine above an obsolescent orbit, with the inferior orbital

angle strongly produced, the antennal spine is slender and acute, reaching to the level of the tip of the inferior orbital angle, and the lower anterior margin of the carapace is convex above a small pterygostomial tooth. The terminal segment of the third maxillipeds bears about 25 cornified spines extending over almost the whole segment length. The third ambulatory dactyl has a slightly larger distoventral spine and four slender ventral spines, the fifth is similar with three ventral spines.

Revised key to the carinate species of *Lebbeus*

1. Dorsal carina of carapace low, convex, with 9–11 slender teeth 2
 - Dorsal carina of carapace elevated, triangular, with 4–8 broadly acute teeth 3
2. Carinal teeth broader, 10 teeth (carapace pale yellow and green, with rows of scarlet spots; abdominal somites 1–3 with rows of scarlet spots)
 - *L. clarehanuah* MacCallum & Poore
 - Carinal teeth slender, 9–11 teeth (carapace pale yellow and green, with rows of scarlet spots; abdominal somites 1–3 with rows of scarlet spots)
 - *L. yaldwyni* Kensley, Tranter & Griffin
3. Second and third carinal teeth very large, fourth and fifth very small (dorsolateral carapace and lower half of carapace crest with pink spots, some ocellate, abdominal somites 1–3 without markings)
 - *L. rubrodentatus* sp. nov.
 - Carinal teeth (except first) large, forming a regularly diminishing series distally 4
4. Terminal segment of third maxilliped with 8–10 corneous spines; with 4–7 carinal teeth, rostrum very acute (dorsal carapace with dense small red spots, dorsal carina white, feebly red spotted, branchiostegite and abdomen and proximal segments of appendages scarlet) *L. coupressus* (Yokoya)
 - Terminal segment of third maxilliped with more than 19 corneous spines; with 6–8 carinal teeth, rostrum distally sub-truncate (carapace colour pattern of 6–10 oblique scarlet stripes, or with stripes broken into many small scarlet spots)
 - *L. cristagalli* MacCallum & Poore

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Spatial and temporal variation in relative numbers of grapsid crabs (Decapoda: Grapsidae) in northern Australian mangrove forests

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ABSTRACT

Crabs belonging to the family Grapsidae are possibly one of the most important components of the fauna of mangrove forests globally, in part because of their influence in nutrient cycling by feeding on litterfall. This study investigated spatial and temporal patterns in relative numbers of 11 grapsid species in northern Australian mangrove forests. The results indicated that *Perisesarma* spp., *Neosarmatium meinerti* and an undescribed species of *Episesarma* were most abundant, followed by *Chistocoeloma merguensis*, *Ilyograpsus pahudicola*, *Sesarnoides borneensis*, *Metopograpsus frontalis* and *Sarmatium* spp. Mangrove assemblage was the most important spatial factor affecting the distribution and abundance of these species. *Perisesarma* sp. was most abundant in mid- and low-intertidal assemblages, whereas *N. meinerti* and *Episesarma* sp. were largely limited to high intertidal assemblages. In many cases, crab species occurrence and abundance were specific to certain assemblages, areas, aspects, and times during the two-year study period, which probably reflects the specificity of species to particular environmental conditions.

KEYWORDS: crab abundance and distribution, environmental conditions, habitat, mangroves, Grapsidae, *Perisesarma*, *Episesarma*, *Neosarmatium*.

INTRODUCTION

Grapsid crabs are one of the most abundant and important faunal components of intertidal mangrove forests globally (Golley *et al.* 1962; Jones 1984; Smith III *et al.* 1991; Lee 1998), particularly in the Indo-west Pacific. Recent studies of their activities in mangrove forests indicate that by attacking mangrove seeds and seedlings they may affect forest structure (Smith III 1987; McGuinness 1997) by feeding on litterfall (Fig. 1), and by burrowing they influence nutrient cycling and alter the sediment geochemistry (Robertson 1986; Smith III *et al.* 1991; Kristensen 2008; Nerot *et al.* 2009). There is also evidence of competition between grapsid crabs and other invertebrate species in the forest (Fratini *et al.* 2001).

Although there have been some studies of grapsid diversity (Davie 1982; Abele 1992), studies of distribution and abundance in mangrove forests, at both local and geographic scales, are limited. Investigations of temporal patterns are even rarer. Spatial patterns in abundance have only been studied in Australia, Africa and Hong Kong (Micheli *et al.* 1991; Smith III *et al.* 1991; Frusher *et al.* 1994; Lee & Kwok 2002; Metcalfe 2007). In Australia, these studies have found that species of crabs that occur in mangrove forests change across the continent, and so do their numbers (Smith III *et al.* 1991). On a local scale, the abundance and distribution of different species appear to

change across intertidal zones, and also, along tidal creeks (Frusher *et al.* 1994).

The variation in species diversity, distribution, and abundance may result from differences in habitat within and among mangrove forests and the evolution of species to fit a particular niche. For instance, it is known that grapsid crabs have a wide range of feeding habits, varying from detritivory, to herbivory (feeding on leaves and propagules), and to carnivory (Nishihira 1984; Lee 1998). This difference in feeding behaviour among species makes it possible for crabs to live in a diversity of habitats.

There is no published information on spatial and temporal patterns in the population structure of grapsid crabs in mangrove forests. Characteristics of the population structure, such as size and gender distribution, and the presence of gravid females may also be affected by environmental conditions occurring in different locations (Lee & Kwok 2002), and would certainly influence crab energy requirements. Changes in energy requirements may result in alterations in food preferred by crabs and the quantity of food consumed, thus influencing the role that crabs play within the ecosystem.

Studies on activity and social behaviour are more numerous (e.g., Seiple 1981; Willason 1981; Seiple & Salmon 1982; Micheli *et al.* 1991; Smith III *et al.* 1991; Frusher *et al.* 1994; Kneib *et al.* 1999). Grapsid crabs may alter their behaviour according to the environmental

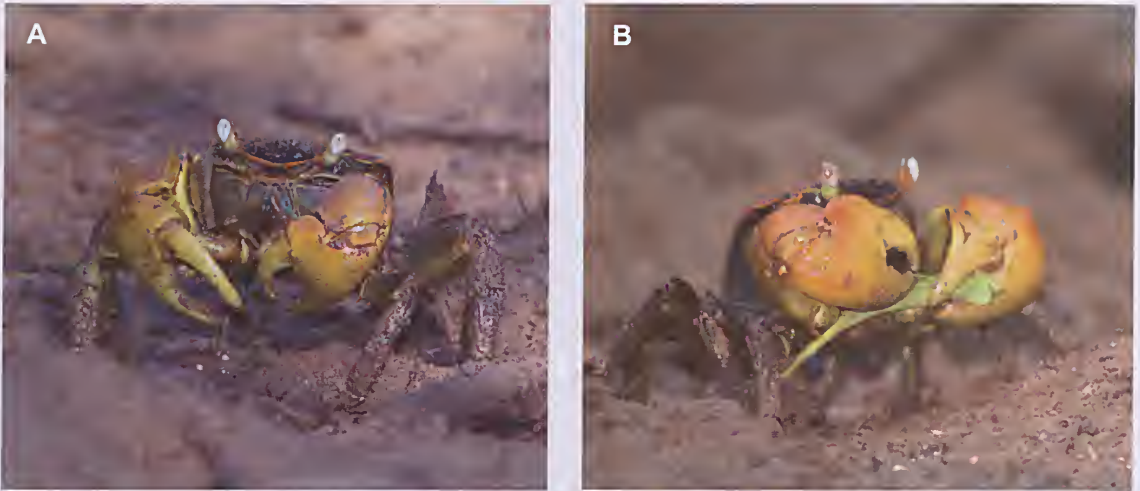


Fig. 1. *Neosarmatium meinerti* is one of the most abundant grapsid crabs high in the intertidal zone in mangrove forests in Darwin Harbour. A, An adult foraging at low tide. B, An adult feeding on a fallen mangrove leaf. Photographs: Keith McGuinness.

conditions in the mangrove forests that they inhabit. These alterations, for instance, may be in the time spent feeding or burrowing. This is relevant to studies of abundance, as changes in crab activity can influence estimates of relative abundance. Several studies report high crab activity during spring tides (Seiple 1981; Micheli *et al.* 1991, Smith III *et al.* 1991; Frusher *et al.* 1994), so trapping has been done during this period of the tidal cycle. These studies were however, done on the east and south-east coast of Australia, and it is not known if the pattern exists in more tropical regions.

Underwood (2000) wrote: "There is no possible doubt that observations of patterns or lack of patterns are the fundamental starting-blocks for ecological study. Until patterns have been described, there is no basis for invoking explanatory models about processes". The aims of this present study were to test for, and describe, spatial and temporal patterns in the abundance of the most common grapsid crabs in Darwin Harbour, and briefly to investigate their relationship to environmental conditions. This is an important first step in investigating the ecology of these animals. The specific objectives of this study were: (1) to test for spring-neap patterns in relative abundance; (2) to determine the best phase for the subsequent long-term, large-scale studies; and (3) to test for spatial (within plots, among assemblages, between aspects, and between areas) and temporal patterns in the relative abundance, and population structure, of the dominant grapsid crabs.

MATERIALS AND METHODS

Darwin Harbour is located in tropical northern Australia, between latitudes 12°20' and 12°45' S and longitudes 130°45' and 131°05' E (Fig. 2). It supports mangrove forests occupying about 20 000 ha and containing 36 of the world's 70 true species of mangrove (Polidoro *et al.* 2010). The mangrove communities of the Harbour have

been identified as a significant resource, comprising about 5% of the total area of mangroves in the Northern Territory and approximately 0.1% of remaining world mangrove areas (Broeklehurst & Edmeades 1996).

Broeklehurst & Edmeades (1996) identified 10 mangrove associations, or assemblages, in the Harbour forests and the three most common were studied: (a) tidal creek (dominated by *Rhizophora stylosa* Griffith and *Avicennia marina* (Forsskål) Vichr.); (b) tidal flat (dominated by *Ceriops australis* Ballment, Smith & Stoddart; that was mentioned in Broeklehurst & Edmeades (1996) by the older name of *Ceriops tagal* Robinson); and (c) hinterland (dominated by *Ceriops australis*). A fourth assemblage (d) mixed-species woodland (dominated by *Ceriops australis* with *Lumnitzera racemosa* Willd. and *Excoecaria ovalis* Endlicher co-dominant or locally dominant) was also

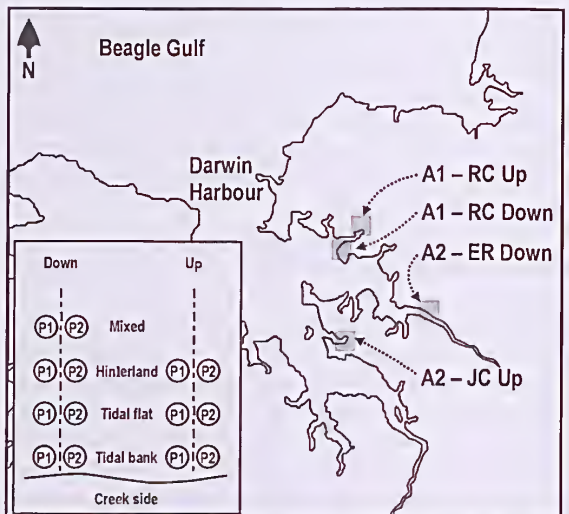


Fig. 2. Location of study sites along Reichardt Creek (Area 1), Elizabeth River and Jones Creek (Area 2) within Darwin Harbour.

included as it was an important component in the areas studied.

Study sites. Three creeks within Darwin Harbour were selected for the study: Reichardt Creek, Elizabeth River and Jones Creek (Fig. 2). Reichardt Creek is on the northern side of the Harbour, referred to here as Area 1. Elizabeth River and Jones Creek are to the south, a location referred to here as Area 2. Within each of these areas, an upstream location and a downstream location, referred to here as 'aspects', were selected along the creeks. In Area 1, these locations were both on Reichardt Creek. In Area 2 these were upstream on Elizabeth River and downstream on Jones Creek.

Downstream aspects included four assemblages: tidal creek, tidal flat, hinterland and mixed-species woodland. Upstream aspects, due to the natural distribution of assemblages, included only the tidal creek, tidal flat, and hinterland. The word 'site' used in this paper refers to a combination of an assemblage, aspect, and area. Sampling was conducted within two replicate circular plots, 20 m in diameter, at each site.

Crab sampling. Pitfall traps were used to estimate relative abundance of grapsid crabs for three reasons: (a) they were most effective among an array of methods tested for sampling multiple species in the same location over time (Salgado Kent & McGuinness 2006); (b) they sampled all species with little disturbance to the habitat (c) they allowed information on population characteristics to be collected. Salgado Kent & McGuinness (2006) found that observational and photographic methods were useful only for sampling consistently surface-active species (i.e., species that were surface-active infrequently were not accurately represented), while excavation was too destructive for accurate repeated measures of abundance in the same location over time. While the use of pitfall traps has been suggested potentially to result in size-biased sampling (towards larger crabs; Salgado Kent & McGuinness 2006), the usefulness of measuring this parameter is not diminished since insight into spatial patterns can be obtained from comparisons of relative size (Salgado Kent & McGuinness 2006).

Two replicate traps were placed at random locations – chosen by identifying a reference tree in the centre of each plot then moving a random direction and distance (as in Smith III *et al.* 1991) – within each plot at each sampling time. As some species were observed travelling one or two metres from their burrows while foraging, traps were placed at least 3 m apart.

Traps were set during low tides and checked daily for two days (Salgado Kent & McGuinness 2006). Grapsids caught were identified, sexed, and had their carapace width measured to the nearest 0.01 mm, at the widest point including the spines (Davie 1992). Any ovigerous female was noted. Before release, the crabs were marked on their carapace with a blue permanent marker pen (known to last at least three days) to avoid duplicate counts. Some crabs drowned in traps when they drained slowly during heavy

rain or extreme spring high tides, so this mortality were noted as well. The effects of mortality on estimates from trap captures are discussed below.

Crabs were identified to the lowest taxonomic level which could be easily distinguished in the field. As a consequence, *Perisesarma darwinensis* Campbell and *Perisesarma semperi* Bürger were grouped together as *Perisesarma* sp. *Sarmatium unindentatus* Davie, *Sarmatium hegerli* Davie and *Sarmatium germaini* Milne Edwards were recorded as *Sarmatium* sp. The species of *Episesarma* was easily identified but, as it has been neither described nor named at present, is referred to simply as *Episesarma* sp. *Neosarmatium meinerti* de Man (Fig. 1), *Clistocoeloma merguensis* de Man, *Ilyograpsus paludicola* Rathbun, *Sesarmoides borneensis* Tweedie and *Metopograpsus frontalis* White could all be readily distinguished morphologically. All these genera are common to the Indo-west Pacific and/or Africa and only two species appear to be endemic; *Perisesarma darwinensis* and *Episesarma* sp. Because grouping species according to their congeners was required for some species (to reduce errors from misidentification in the field), meaningful information for these species is drawn from the species grouping level, rather than the species level.

Spatial and temporal patterns in relative abundance. Crabs were sampled on spring tides on 12 occasions from January 1999 to December 2000. During each year, crabs were sampled once in the early wet season (January), once in the late wet season (March), once in the wet to dry transition (May), once in the early dry season (July), once in the late dry season (September), and once in the dry to wet transition (November).

To explore spatial and temporal patterns in abundance, PERMANOVA analyses (which have no assumptions of normality such as does ANOVA) were conducted. Analyses were limited to species with very large numbers (*Perisesarma* sp.). Included in the analysis were the following factors: sample time (six levels, fixed), year (two levels, fixed), area (two levels, random), aspect (two levels, fixed), and assemblage (three levels, fixed). The mixed-species woodland assemblage was not included since there were virtually no *Perisesarma* sp. in this assemblage, and inclusion would have only potentially introduced zero inflation into the analysis. Data were log transformed for analysis since this resulted in more equal variances (a recommendation for PERMANOVA).

ANOVAS were done on carapace width, proportion of females, and proportion of ovigerous females, for species with sufficient captures (since assumptions for ANOVA were met). The number of factors, included in the latter analyses was dependent upon the number of crabs captured, but included one or more of the following: sample time (six levels, fixed), assemblage (two levels, fixed) and area (two levels, random). Assemblage for *Perisesarma* only included the tidal flat and tidal creek.

Variation in numbers during spring and neap tides. A preliminary test for spring-neap changes in activity was conducted by sampling at these two stages in the tidal cycle (Spring: 4–7 June 2000; Neap: 10–13 June 2000). Due to time constraints, only one spring-neap cycle could be sampled and only on the upstream aspect of Reichardt Creek (so there was no replication of tide). Here two plots in each of the three assemblages present (the hinterland, the tidal flat and the tidal creek) were sampled. Data for *Perisesarma* sp., the only abundant species, were analysed with a three-factor ANOVA (all assumptions were met). Factors included tide (two levels, fixed), assemblage (three levels, fixed) and plot (two levels, random and nested in assemblage).

Spatial and temporal variation in *N. meinerti* burrow counts. While pitfall traps certainly capture *N. meinerti*, Salgado Kent & McGuinness (2006) found that they may not provide reliable estimates of abundance. Hence, the abundance of this species was also estimated by burrow counts, a method that is practical because their large, hooded burrows are easily identifiable (Micheli *et al.* 1991) and because burrows do not last more than about three weeks (hence overestimates from abandoned burrows are not likely to be large; Micheli *et al.* 1991; Emmerson & McGwynne 1992). Emmerson (2001) however, found in some cases multiple crabs inhabiting one burrow, which could lead to underestimates. No attempts were made here to differentiating active burrows, abandoned burrows, or co-inhabited burrows because this would have required destruction of the burrows. Burrows were counted, on the day that pitfall traps were first buried, in two randomly placed 1 × 1 m quadrats in each plot. Burrow counts were, however, not started until part-way through the main sampling program (September 1999), so did not span two full years.

RESULTS

Variation in numbers during spring and neap tides. Forty-one crabs were captured during this study: 24 *Perisesarma* sp., 5 *N. meinerti*, 5 *Episesarma* sp., 5 *S. borneensis*, and 2 *Ilyograpsus paludicola*. More individuals of all species were caught during the spring tide (17 *Perisesarma* during the spring tide and 7 during the neap; all 5 *N. meinerti* and 5 *Episesarma* during the spring tide; 4 *S. borneensis* during the spring tide and 1 during the neap, and both *I. paludicola* during the spring tide). Only *Perisesarma* were sufficiently abundant for analysis. For this species, there was a significant interaction between tide and assemblage ($F_{2,6} = 22.17$, $P < 0.05$), due to the number of crabs decreasing during the neap tide in the tidal flat (spring = $3.00 \pm \text{SE}$ per trap; neap = $0.25 \pm \text{SE}$) but remaining stable in the other two assemblages (tidal creek spring = 0.00; neap = 0.25; hinterland spring = 1.25; neap = 1.25).

Spatial and temporal variation in relative grapsid numbers. *Perisesarma* was the most abundant (554

individuals) of the 11 species of grapsids captured during the two-year study. Numbers of crabs for the other seven species sampled were: 67 *N. meinerti* (and 201 burrows), 39 *Episesarma*, 27 *C. merguensis*, 25 *I. paludicola*, 18 *S. borneensis*, 14 *M. frontalis* and 8 *Sarmatium*. Proportions of crabs surviving in traps were: *C. merguensis*, 100% (based on 12 traps with crabs); *I. paludicola*, 89% (22 traps); *S. borneensis*, 80% (15 traps); *Episesarma*, 75% (28 traps); *N. meinerti*, 63% (53 traps); *Perisesarma*, 62% (263 traps); *M. frontalis*, 50% (12 traps); and *Sarmatium*, 29% (7 traps).

There were complex spatial and temporal patterns in the abundance of *Perisesarma*. Overall, *Perisesarma* was almost entirely absent in the mixed-species assemblage ($n=2$), so this assemblage was excluded from the analysis. In the analysis, many interactions among factors were significant, with the main effects of year and assemblage, and interactions among area, assemblage and aspect being associated with particularly large mean squares (Table 1). Interactions between year and assemblage were significant, although to a lesser extent. Regardless of area or aspect, *Perisesarma* were always uncommon in the hinterland (Fig. 3). The crabs were more abundant in the other two assemblages – tidal creek and tidal flat – but the relationship between these differed among areas and aspects. In area 1, the crabs were more abundant in the tidal creek downstream and the tidal flat upstream, whereas in area 2 they were more abundant in the tidal flat downstream with little difference upstream. Overall abundance decreased from 1999 to 2000 in the tidal creek and tidal flat, but not in the hinterland (Table 1, Fig. 4).

Because of the fewer numbers associated with *Neosarmatium meinerti*, no statistical analyses were conducted because of the clear pattern in distribution. *Neosarmatium meinerti* crabs were more abundant in the higher shore assemblages – hinterland (mean = 0.22 per trap \pm 0.05 SE) and mixed-species woodland (0.23 \pm 0.05) – than in the lower shore assemblages where they were virtually absent – tidal creek (0.01 \pm 0.01) and tidal flat (0.02 \pm 0.01). Greater numbers of *N. meinerti* were caught during the second year of the study but other consistent temporal trends were not evident (Fig. 5).

Table 1. PERMANOVA of spatial and temporal patterns in relative numbers of *Perisesarma* crabs in Darwin Harbour in 1999 and 2000. Analyses were done using both areas, both aspects (upstream and downstream) and three assemblages (hinterland, tidal flat, and tidal creek). Only interactions which were significant in at least one analysis, or had one of the five largest mean squares, are listed.

Source	df	Mean Squares
Year (Yr)	1	0.87**
Time (Ti)	5	0.09
Area (Ar)	1	0.01
Aspect (Asp)	1	0.01
Assemblage (Abg)	2	1.94***
Yr×Abg	2	0.33*
Ar×Asp×Abg	2	0.93***

With respect to the six less common species, four species – *Clistocoeloma merguensis*, *I. paludicola*, *M. frontalis* and *Sarmatium* – showed broadly similar patterns to *Perisesarma*, being most abundant in the tidal creek and tidal flat (Figs 6, 7). *Clistocoeloma merguensis* and *I. paludicola* were caught in similar numbers in both

aspects but *M. frontalis* was more common upstream and *S. borneensis* was rarely captured downstream (Fig. 7). *Episesarma*, like *N. meinerti*, was most abundant in the higher shore assemblages, hinterland and mixed-species woodland (Fig. 6), and was rarely captured in the tidal creek or tidal flat. *Episesarma* was, however, also rarely

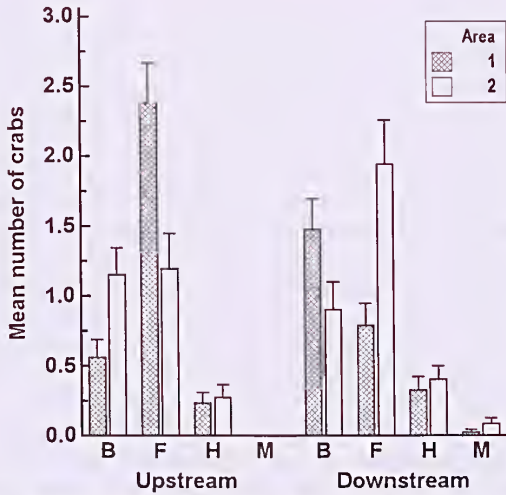


Fig. 3. Mean number of *Perisesarma* (per trap) in the two areas, two aspects and four assemblages in Darwin Harbour (mean + SE). Assemblages include tidal creek (B), tidal flat (F), hinterland (H), and mixed-species woodland (M).

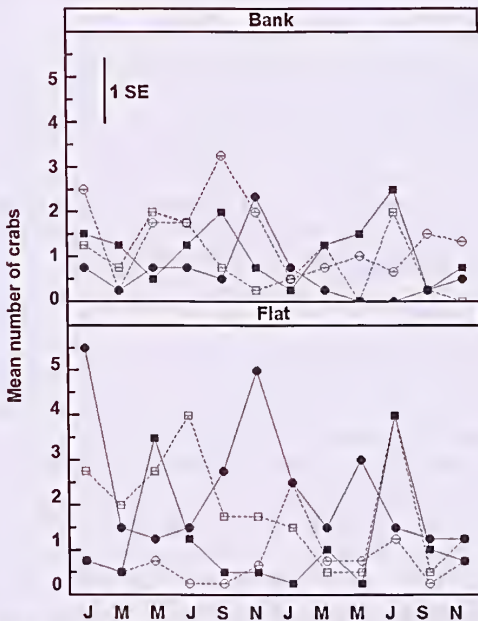


Fig. 4. Mean number of *Perisesarma* (per trap) over the two years of the study for the assemblages in which the species was common. Open symbols are for the upstream aspect; hatched for the downstream. Circles are area 1; squares are area 2. For clarity, error bars are not plotted but the line shows the average standard error.

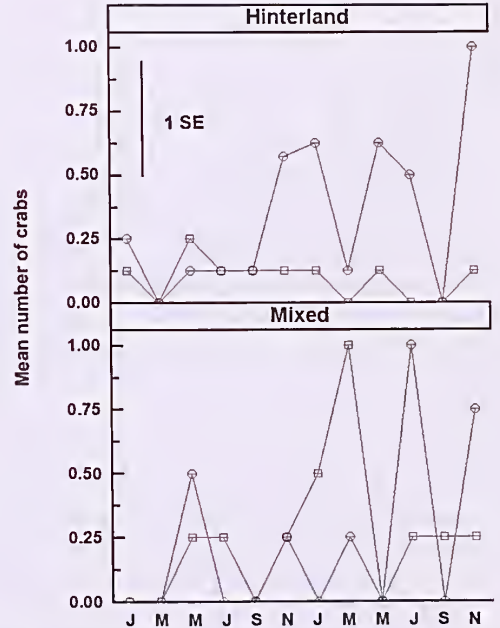


Fig. 5. Mean number of *Neosarmatium meinerti* (per trap) over the two years of the study for the assemblages in which the species was common. Circles are area 1; squares are area 2. For clarity, error bars are not plotted but the vertical line shows the average standard error.

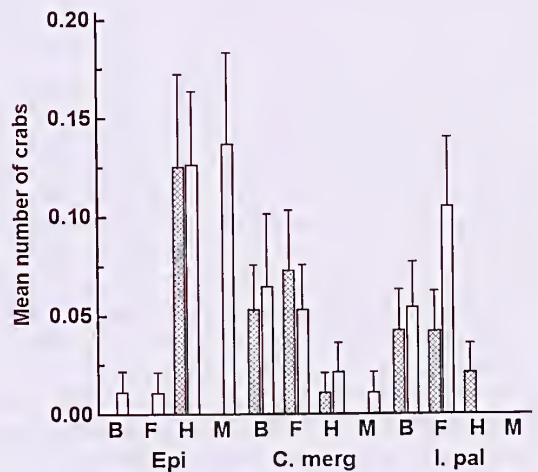


Fig. 6. Mean numbers of three species of crabs (per trap) in two aspects and four assemblages in Darwin Harbour (mean + SE). Assemblages include tidal creek (B), tidal flat (F), hinterland (H), and mixed-species woodland (M). Aspects were downstream (open bars) and upstream (hatched bars). Species were: Epi = *Episesarma*; C. merg = *C. merguensis*; I. pal = *I. paludicola*.

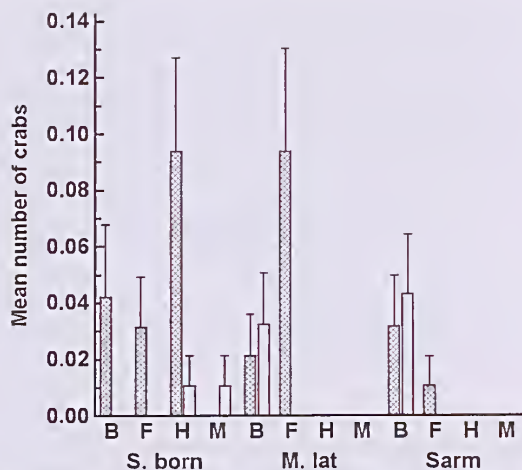


Fig. 7. Mean numbers of three species of crabs (per trap) in two aspects and four assemblages in Darwin Harbour (mean + SE). Assemblages include tidal creek (B), tidal flat (F), hinterland (H), and mixed-species woodland (M). Aspects were downstream (open bars) and upstream (hatched bars). Species were: S. born = *S. borneensis*; M. lat = *M. frontalis*; Sarm = *Sarmatium*.

caught in the hinterland of Area 2 (Salgado Kent 2004). In terms of temporal patterns, *I. paludicola* variability was greater during both March and May, and for *N. meinerti* only in May (Salgado Kent 2004). For *Perisesarma* there was greater variability during March, May, and July than at other times, but this was only true for 1999 (Salgado Kent 2004). *Metopograpsus frontalis* had high variability between plots during March and December of 2000, and only during December in 1999 (Salgado Kent 2004).

Numbers of *N. meinerti* burrows. About 3.7 times as many burrows were counted as crabs were caught (201 burrows versus 54 crabs, for the period September 1999 onwards, when both variables were recorded). Mean, per plot, burrow counts and *N. meinerti* numbers were significantly, but weakly, correlated ($r = 0.41$, $n = 224$, $P < 0.001$; the comparison was done on a 'per plot' basis because crab traps and burrow quadrats were in different, randomly selected, locations in each plot). As for trap captures, the number of burrows was greater in the hinterland than in other assemblages, and particularly in the downstream of Area 1 (mean = 1.33 per quadrat \pm 0.22 SE), the hinterland in the upstream aspect of Area 2 (1.17), than in other combinations of these factors (other means \leq 0.71).

Population structure: size, sex ratio, and proportion of ovigerous females. The largest crabs, on average, were *N. meinerti*, followed, in order from the largest to the smallest, by *S. borneensis*, *Perisesarma*, *Sarmatium*, *Episesarma*, *C. merguensis* and *I. paludicola* (Table 2). Overall, there were many more male crabs captured than females and ovigerous females were only observed for *Perisesarma* and *C. merguensis*.

Differences in size of *Perisesarma* were observed between areas ($F_{1,106} = 3.86$, $P < 0.05$), with area 1 having larger

Table 2. Means and standard errors for carapace width, proportion female and proportion of ovigerous females of crabs caught. For each species and variable, n is the number of traps (not crabs) for which data were available (i.e. which contained crabs).

Species	Carapace width (cm)			Proportion female			Proportion ovigerous		
	n	Mean	SE	n	Mean	SE	n	Mean	SE
<i>C. merguensis</i>	23	1.07	0.06	22	0.36	0.10	10	0.10	0.10
<i>Episesarma</i>	26	1.12	0.06	25	0.13	0.07	4	0.00	0.00
<i>I. paludicola</i>	20	0.49	0.07	5	0.00	0.18	5	0.00	0.00
<i>N. meinerti</i>	52	2.24	0.09	51	0.28	0.06	17	0.00	0.00
<i>S. borneensis</i>	15	1.30	0.10	14	0.39	0.13	5	0.00	0.00
<i>Sarmatium</i>	7	1.18	0.12	6	0.17	0.17	1	0.00	–
<i>Perisesarma</i>	263	1.24	0.02	252	0.33	0.02	123	0.25	0.04

erabs than area 2 (means = 1.33 and 1.26, respectively). The proportion of *Perisesarma* females did not vary among sample times, assemblages, years or areas (all $P > 0.05$), however the proportion of ovigerous females increased during the wet season months ($F_{5,85} = 2.66$, $P < 0.05$; means were Jan: 0.43; Mar: 0.39; May 0.13; Jul: 0.09; Sep: 0.43; Nov: 0.39). Also there were more ovigerous females in the tidal creek than in the tidal flat assemblage ($F_{1,85} = 4.41$, $P < 0.05$; means = 0.38 and 0.16).

There was no significant variation in *N. meinerti* carapace width among sample times or between years, but the proportion of females did vary between years with more females caught in 1999 than in 2000 ($F_{1,39} = 6.51$, $P < 0.05$; means = 0.47 and 0.18).

DISCUSSION

Effects of crab mortality on estimates from trap captures. Mortality of crabs during sampling can be a concern in studies that involve temporal sampling since crab densities would be reduced artificially by traps each time the crabs are sampled. Even though the percentage of crabs surviving in pitfall traps was 62% for the most abundant species sampled (*Perisesarma*), the mean mortality was not more than one crab in each circular 20 m diameter plot. This mortality rate was insignificant since the mean true abundance of *Perisesarma* crabs across assemblages in Darwin Harbour was 1.35 crabs per m^2 (Salgado Kent & McGuinness 2006). For *Sarmatium*, the species of grapsid with the highest mortality and lower abundance, there was an average mortality of 71% of crabs caught in pitfall traps. Densities estimated in Salgado Kent and McGuinness (2006) during that period were one *Sarmatium* per 3 m^2 . Captures of *Sarmatium* in traps were rare enough so that less than one in about every 100 crabs in a plot would be removed from the population by mortality. This number is also insignificant and indicates that trap related mortality did not interfere with results.

Variation in grapsid numbers during spring and neap tides. Crabs were more active during spring tides than during neap tides. Although results from this experiment were

restricted by the limited spatial and temporal replication included in the experiment, the results suggest that crabs in Darwin Harbour have similar patterns of activity to those found elsewhere (Mieheli *et al.* 1991; Frusher *et al.* 1994; Nobbs 1999). Mieheli *et al.* (1991) found much of the greatest activity of *N. meinerti* during spring tides was due to increased time digging (presumably digging is easier when soil is moist) and suggested that this may be required when a high water level causes burrows to collapse.

The absence of a spring-neap pattern in the activity of grapsids in the tidal creek assemblage may reflect the regular pattern of tidal inundation, which results in consistently high soil saturation in this habitat. This is consistent with the observations of Mieheli *et al.* (1991) of a reduced spring-neap difference in activity of the land crab, *Cardisoma carnifex* Herbst, during a period of high soil and air moisture (caused by a full moon spring tide and nocturnal rain showers). Similar observations have been made in other studies on land crabs (Goshima *et al.* 1978).

Comparison of *N. meinerti* number and *N. meinerti* burrow counts. The relative abundance of *N. meinerti* estimated by burrow counts in the majority of cases was almost four times the estimate of numbers of *N. meinerti* captured in pitfall traps. The relationship between pitfall trap captures and burrow counts was significant but the R^2 was small. Of the two methods, burrow counts most likely provided a better estimate as *N. meinerti* appear to spend little time on the surface.

Population structure. The apparent difference in size of *Perisesarma* between areas is difficult to explain as there were no obvious patterns in soil condition or litter fall rates (unpublished data) to account for it. Lee & Kwok (2002) suggested that difference in size of crabs between mangroves forests in Hong Kong was due to variations in the dominant mangrove species. In this study, however, the areas had similar mangrove composition, so other environmental differences (as also suggested by Lee & Kwok 2002) may play a role.

For most species of crabs in this study, more males were caught than females. This is consistent with a study by Lee & Kwok (2002) on *Perisesarma bidens* de Haan and *Parasesarma affinis*, but contrasts with findings on *Aratus pisonii* Milne Edwards populations in New World mangroves (Conde & Diaz 1989). The dominance of males could simply reflect a trap bias. Traps tend to capture larger crabs more often than smaller crabs, and males are slightly larger than females in most species in this study. Furthermore, larger males (with larger chelae) may be less susceptible to predation and therefore be more active on the surface than females.

The increased number of ovigerous *Perisesarma* females captured during the wet season is potentially of some significance and could be associated with the strong wet and dry seasons in northern Australia (Rabalais & Cameron 1982). The tidal creek also had a noticeably greater proportion of ovigerous female *Perisesarma* crabs than the

tidal flat assemblage, possibly because it has conditions which are more suitable for the production of eggs and dispersal of larvae (see Thurman II 1985) for use of tides by *Uca* for dispersal). In particular, the nearby tidal creek may be used for dispersal, as has been found for crabs in other estuarine systems (Christy & Morgan 1997), where larvae are conspicuous to predators and dispersal is important to avoid predation.

Spatial and temporal variation in relative grapsid numbers. During the two year study on relative abundance of grapsids in the assemblages studied in Darwin Harbour, *Perisesarma* was the most abundant crab species, followed in order of abundance by *N. meinerti*, *Episesarma* sp., *C. merguensis*, *I. paludicola*, *S. borneensis*, *M. frontalis* and *Sarmatium* spp. Underestimates of *Episesarma* may have been possible because these crabs, like *N. meinerti*, may have limited activity (Sivasothi 2000) since they live in relatively dry assemblages in Darwin Harbour.

In general, mangrove forest assemblage was the most important factor influencing the distribution and relative abundance of grapsid crab species within the Harbour. This observation is consistent with other studies conducted elsewhere (Mieheli *et al.* 1991; Frusher *et al.* 1994). Of the grapsids that were most abundant in this study, *Perisesarma* dominated the lower intertidal assemblages, while *N. meinerti* dominated high intertidal mangroves. These patterns are also similar to those from other sites elsewhere (Mieheli *et al.* 1991; Emmerson & McGwynne 1992).

The observed distribution of grapsid crabs among assemblages is probably related to soil conditions such as soil moisture and salinity. Frusher *et al.* (1994), examined the relationship of grapsid numbers to environmental conditions (pore-water salinity, Eh, pH, and percent silt, clay and organic matter) in the Murray River mangrove forests. The two most numerous crabs in that study, *Sesarma messa* Campbell and *Sesarma brevipes* de Man, were most common in forests with sandy sediments. *Sesarma messa* was also in greater numbers in forests with sediment containing a high organic matter content while the abundance of *S. brevipes* appeared to increase with increasing sediment acidity. Frusher *et al.* (1994) indicated, however, that these environmental variables did not appear to explain the limited distributional patterns observed in *Perisesarma semperi* or *Sesarma brevicristatum* Campbell. *Perisesarma semperi* was present in much lower numbers than were *S. messa*, *S. brevipes*, and *S. brevicristatum*, and only occurred in the low intertidal habitats of the river mouth.

Both *Perisesarma semperi* and *P. darwinensis* appear to be fairly widespread in Darwin Harbour, at least one species of this genus occurring in all assemblages, areas, and aspects. It seems possible, therefore, that the three more abundant species in the study by Frusher *et al.* (1994) (i.e., *S. messa*, *S. brevipes*, and *S. brevicristatum*) may outcompete *P. semperi* for the more desirable habitats in that region. It is also possible, however, that *P. darwinensis* (only occurring in northern Australia) has, in part, filled the ecological niche

occupied by other sesamids that occur on the Murray River. Smith (1998) suggested that, although *P. semperi* and *P. darwiniensis* appear to overlap in distribution in Darwin Harbour, the former may prefer lower intertidal zones, and the latter higher zones. Competition between these species may explain some of the patterns in distribution that are not explained by environmental conditions.

Of the species that were less abundant in the assemblages sampled during this study, *Sesarmoides borneensis* showed consistent patterns of greater numbers upstream than downstream. Frusher *et al.* (1994) observed a similar difference in abundance upstream and downstream of the Murray River, but for different species of crabs. In that study, *Sesarma brevipes* dominated the upstream sites, whereas *Perisesarma semperi* was restricted to the river mouth. The distribution of *S. brevipes* in the Frusher *et al.* (1994) study appeared to be related to soil acidity.

Metopograpsus frontalis had the most specific distribution, in that it occurred almost entirely in the tidal flat and tidal assemblage of the upstream of area 2. This species was also commonly observed in the shoreline forest, an assemblage not included in this study that is lower in elevation than the tidal creek. The shoreline forest is dominated by the mangroves *Rhizophora stylosa* and *Sonneratia alba* Smith, and is commonly inundated by tides. The tidal flat and tidal creek assemblages upstream of area 2 appeared to be inundated by tides more often than the same assemblages at other sites, so factors such as tidal flow or elevation gradient may be important for *M. frontalis*, and merit further study.

Finally, *Episesarma* sp. was the only species to show a distinct increase in numbers during the wet season months. Metcalfe (2007) observed a similar increase in grapsid abundance during the wet season in the hinterland margin in Darwin Harbour. It is difficult to know whether this is a result of an actual change in population size, or whether surface activity of crabs simply increased due to wetter conditions from wet season rains (Frusher *et al.* 1994; Nobbs 1999; Lee & Kwok 2002).

Overall, there were strong general patterns in distribution among assemblages for the majority of the species of crabs in this study, however the large number of interactions among factors indicates that crab species occurrence and abundance were often specific to certain plots, assemblages, areas, aspects, and times during the study. These interactions indicated that while clear patterns existed, crab distribution and abundance were often patchy and fluid through space and time. In conclusion, this study has confirmed the importance of habitat heterogeneity on demarcating broad distributional ranges of grapsids observed in studies elsewhere. The work has also highlighted the likely role of environmental variability and change on the fluid nature of abundance, distribution, and population structure of grapsid crabs in mangrove forests.

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Curvothynnus gen. nov. erected for two unusual species of thynnine wasps (Hymenoptera: Thynnidae: Thynninae: Rhagigasterini)

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ABSTRACT

The genus *Curvothynnus* is erected for two unusual species previously placed in *Rhagigaster* Guérin – *R. laevigatus* Smith and *R. neptunus* Turner. In this genus the pronotum of the male is distinctive in that the anterior surface is concave with the dorsal margin sublaminated and directed forward. Both species are redescribed, the female of the latter being described for the first time. A key to species is given as is a key to Australian genera in the tribe Rhagigasterini.

KEYWORDS: Northern Australia, Thynnidae, Thynninae, Rhagigasterini, *Curvothynnus*, *Rhagigaster*.

INTRODUCTION

The genus *Rhagigaster* was erected by Guérin in 1838 for a previously undescribed species of thynnine wasp, *Rhagigaster unicolor*. The description was based on a single male which had a distinctively elongate, parallel-sided metasoma with the segments strongly depressed anteriorly and posteriorly such that the metasoma appeared filiform in profile, and the apical spine of the hypopygium was strongly upturned apically.

Since then approximately 60 additional species have been described, mostly by Turner (1907), and a further 64 are yet to be described, all with these characteristics in the male. Turner (1907) also divided the genus on the basis of the presence/absence of a transverse frontal carina below the ocelli in the male. However, this carina is often present but weakly developed and therefore difficult to interpret. As a consequence, Turner (1910) subsequently reversed this decision without considering a more elaborate grouping of species.

It is now apparent that an examination of the male genitalia is essential to detect cryptic genera and species (Brown 2008). Such an examination of all available specimens of *Rhagigaster sensu* Turner, 1910 confirms the existence of six groups that warrant generic status. These differences are also supported particularly by the microsculpture in both sexes and the shape of the last tergite of the male. These are given in more detail in the key to genera below.

This paper follows on from a revision of *Umbothynnus* Brown (2008) which was erected for *Rhagigaster alexius* (Guérin) and seven new species, and is the second in a series of generic revisions. Although, no new species of *Curvothynnus* gen. nov. are known, the two species are reviewed within a new generic context. Apart from these two

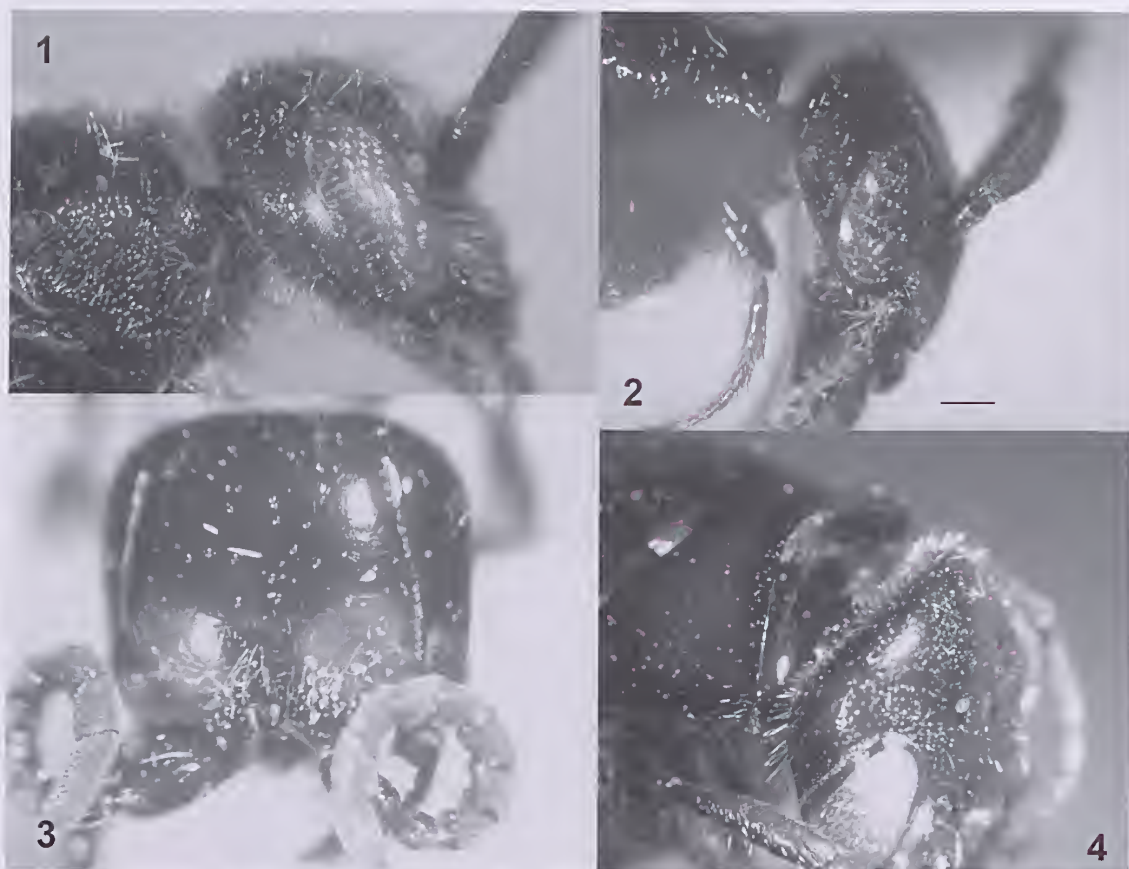
revisions, the tribe *Rhagigasterini* has not been reviewed since Turner (1910).

The biology of the genus is unknown. Like other members of the Thynninae, species of *Curvothynnus* are presumed to be idiobiont parasitoids of soil-dwelling scarab beetle larvae (that is, the adult female prevents further development of the host larva by paralysing or killing it). However, this assumption is based on less than 20 records for the more than 1000 Australian species in the entire subfamily Thynninae (Brown 2005). It is also presumed that the adults preferentially feed on the nectar of myrtaecous plants, although this is deduced from collecting records rather than testing food preferences in the field.

Terminology follows Snodgrass (1941), Nauman (1991) and Brown (1997a,b). Relative terms relating to microsculpture are interpreted as follows: sparsely punctate = punctures greater than two puncture-diameters apart; punctate = punctures at most two puncture-diameters apart, but never confluent; closely punctate = punctures almost confluent; rugosely punctate = punctures partially confluent; finely punctate = punctures small and shallow; coarsely punctate = punctures large and deep; obscurely punctate = punctures small, sparse, shallow and only visible at certain angles.

Abbreviations. Morphological characters: T1–7, metasomal tergites 1–7; S1–8, metasomal sternites 1–8.

Institutional abbreviations: AM, Australian Museum, Sydney; ANIC, Australian National Insect Collection, CSIRO, Canberra; BMNH, The Natural History Museum, London; CUO, Carleton University, Ottawa, Canada; MV, Museum Victoria, Melbourne; NSW, Primary Industry, New South Wales, Orange; NTM, Museum and Art Gallery of the Northern Territory (formerly Northern Territory Museum), Darwin; OUM, Oxford University Museum, Oxford; QDPI, Primary Industries (Queensland



Figs 1–4. *Rhagigaster lyelli* and *Curvothynnus laevigatus*, detail of heads: 1, *R. lyelli*, male; 2, *C. laevigatus*, male; 3, *R. lyelli*, female; 4, *C. laevigatus*, male head and pronotum. Scale lines: 1 = 0.4 mm; 2,4 = 0.5 mm; 3 = 0.25 mm.

Department of Employment, Economic Development and Innovation), Indooroopilly, Brisbane; QM, Queensland Museum, Brisbane; UQIC, University of Queensland Insect Collection, St Lucia, Brisbane; WADA, Western Australian Department of Agriculture, South Perth.

SYSTEMATICS

Rhagigasterini Ashmead, 1903 (*sensu* Turner 1910)

This tribe was erected by Ashmead (1903) in a key to genera. However, it lacked description, was ambiguous, and associated unrelated genera. The tribe was redefined and formally described by Turner (1910) to include only three genera from Australia (*Rhagigaster*, *Dimorphothynnus* Turner, *Eirone* Westwood) and *Aehurns* Klug from South America.

Turner (1907) divided *Rhagigaster* when he erected *Rhytidogaster*. He later (Turner 1910) synonymised the two genera, but the genus was revived by Brown (2008) and given the replacement name *Rhytidothynnus*.

Based on the structure of the male genitalia and other characters, *Rhagigaster* Turner, 1910 comprises six species groups that warrant generic status. The majority of species belong to *Rhagigaster* or *Rhytidothynnus* and, apart from

Curvothynnus, there are two other genera yet to be described. These genera are distinguished in the following key.

This is the second paper in a series revising these genera and follows that of *Umbothynnus* Brown (2008).

Key to the Australian genera of Rhagigasterini

[Note: only one species of *Umbothynnus* is known from the female, and no attempt has been made here to separate this genus in that sex from *Rhytidothynnus*]

- 1 Male (winged) 2
- Female (wingless) 9
- 2(1) S8 rounded, not spinose, often fringed apically with short stout setae; T7 punctate, convex, not heavily sclerotised, not carinate *Eirone* Westwood
- S8 not rounded, apically spinose; T7 variable, not simply convex, truncate or rounded apically and usually variously carinate 3
- 3(2) T7 broadly truncate apically, truncation may be marginally carinate but without other marginal carinae, rarely slightly rounded, disc flat, punctate to longitudinally multicarinate; elypeus with irregular, inverted V-shaped carina; cuspis granulate
..... *Dimorphothynnus* Turner

- T7 variable, convex at least basally with apical margin and carinae more complex, never broadly truncate apically; elypeus not rugose-carinate; cuspis not granulate 4
- 4(3) Pronotum with anterior margin of disc vertically raised, often carinate and always preceded by preapical transverse groove; anterior surface of pronotum flat and vertical; head and thorax usually closely punctate to rugosely-punctate; head as in Fig. 1, vertex usually short, gena clearly visible throughout; mesoseutellum weakly curved, not strongly raised relative to, or produced over metanotum in profile
.....[*Rhagigaster sensu* Turner] 5
- Pronotum with anterior margin of disc sublamellate and produced anteriorly such that anterior vertical surface is concave, preapical transverse groove on disc indistinct (Fig. 4); head and thorax sparsely punctate; head in profile as in Fig. 2, vertex long (behind eyes) long, gena mostly hidden ventrally; mesoseutellum strongly raised relative to the metanotum and slightly produced over latter (in profile)*Curvothynnus* gen. nov.
- 5(4) Tergites closely and finely scitiferously punctate posterior to gradulus, setae usually forming transverse white bands; antennal prominence with strongly developed V-shaped earina; T7 with lateral carinae which are usually strongly convergent posteriorly and ending before apical margin; basiparameres strongly produced posterodorsallygenus 'Z'
- Tergites not closely and finely scitiferously punctate posterior to gradulus, setae not forming transverse white bands; antennal prominence variable; T7 rarely with strongly convergent lateral carinae; basiparameres not strongly produced posterodorsally 6
- 6(5) T7 produced, rounded and more or less flat apically; S8 unispinose; anterior margin of pronotum strongly produced laterally; dorsal margin of parameres strongly curved apically genus 'R'
- T7 variable, if rounded apically, then either strongly convex, or S8 trispinose; anterior margin of pronotum not produced laterally; dorsal margin of parameres usually not strongly curved apically 7
- 7(6) T7 apically raised, usually as either convex process delineated by oblique sulci or as pentagonal area (sometimes obscure), without alae or lateral carinae (although posterior margin may be carinate e.g. *R. marginatus* Turner); S8 uni- or trispinose; anterior margin of pronotum usually carinate (Fig. 1); frons at least weakly transversely carinate; dorsal margin of parameres produced or lobed
.....*Rhagigaster* Guérin *sensu stricto*
- T7 narrowly truncate or rounded apically, not raised, with or without alae; S8 unispinose; anterior margin of pronotum rarely carinate; frons usually not transversely carinate; dorsal margin of parameres not produced 8
- 8(7) Head widened such that face wider than high*Umbothynnus* Brown
- Head not widened, face not wider than high
.....*Rhytidothynnus* Brown
- 9(1) Mesothoracic coxae separated by lamellate bilobed mesosternal process 10
- Mesosternal process absent *Eirone* Westwood
- 10(9) T2 transversely multicarinate; T6 longitudinally rugose or multicarinate
.....*Dimorphothynnus* Turner
- T2 not transversely multicarinate; T6 usually not longitudinally rugose or multicarinate
.....[*Rhagigaster sensu* Turner] 11
- 11(10) Vertex with pair of punctate depressions, rarely represented by suborbicular areas of deep punctures (with interstices not depressed) but then T6 notched and frons with yellow maculae 12
- Vertex without punctate depressions; if frons with yellow maculae then T6 not notched 13
- 12(11) Frons deeply punctate, without underlying reticulation; postgena not shortened
.....*Curvothynnus* Brown gen. nov.
- Frons with or without deep punctures, finely reticulate; postgenae shortgenus 'Z'
- 13(11) Head and body deeply longitudinally rugose-punctate or longitudinally multicarinate; eyes large, strongly convex; frons with yellow maculae, or frons and vertex orange; metasoma coneolourous...genus 'R'
- Head and body not deeply rugose-punctate, not multicarinate; eyes usually not large, not strongly convex; frons with or without maculae; metasoma coneolourous, or apical two segments ferruginous. 14
- 14(13) Longitudinal sulcus (Fig. 3) from inner orbit of eye to near posterior margin of head (absent in *R. cinerellus* Turner, *R. consanguinens* (Turner) and *R. reflexus* Smith then body is smooth and densely setose and dorsal surface of propodeum is quadrate and may be specialised ant parasitoids); frontal maculae usually present*Rhagigaster* Guérin
- Head without such sulci; propodeum not quadrate, longer than wide; frontal maculae absent
.....*Rhytidothynnus* Brown



Fig. 5. Distribution of species of *Curvothynnus*: \blacktriangle = *C. neptunus*, \bullet = *C. laevigatus*.

***Curvothynnus* gen. nov.**

(Figs 2, 4–23)

Gender masculine. Type species here designated *Rhagigaster laevigatus* Smith, 1897. Recent, Champion Bay, North West Coast, Western Australia.

Included species. *C. laevigatus* (Smith, 1879). comb. nov.; *C. neptunus* (Turner, 1907). comb. nov.

Diagnosis. Male. Medium to large thynnine wasps, body length 12–29 mm, head and body sparsely and shallowly punctate, wings black with blue reflections; head with vertex and gena as in Fig. 2; disc of pronotum without transverse preapical groove and anterior margin curved forward that it is directed forward forming a vertically concavity (Fig. 4); and mesoseutellum (Fig. 7) strongly raised above, and slightly projecting over, the metanotum (in profile).

Female. Medium to large, body length 11–21 mm. Vertex with a pair of punctate depressions (Figs 7–8, 17–18); frons not reticulate.

Description. Male. Head in profile as in Fig. 2, vertex lengthened (behind eyes), gena mostly hidden ventrally; elypeus raised basally, flattened apically, with weakly developed inverted V-shaped earina, apical margin truncate to weakly emarginated (Fig. 9); antennae short, not reaching propodeum, segments less than 2x longer than wide, apical segments arcuate; antennal prominence broadly U-shaped, raised, not carinate; transverse frontal carina absent; pronotum weakly laterally produced, anterior margin carinate, procurved and directed anteriorly such that anterior surface is concave (Fig. 4); mesoseutellum angulate in profile near metanotum (Fig. 7); mesosternum with transverse anteroventral earina that is less well developed laterally and strongly emarginated medially; propodeum angulate in profile (Fig. 7) with dorsal and posterior surfaces



Figs 6–9. *Curvothynnus laevigatus*, male: 6, apex of abdomen, lateral; 7, mesoseutellum projecting above propodeum, lateral (a = mesoseutellum, b = propodeum, c = T1); 8, habitus; 9, front of head. Scale lines: 6,7,9 = 1 mm; 8 = 2 mm.



Figs 10, 11. *Curvothynnus laevigatus*, female: 10, habitus; 11, head and pronotum. Scale lines: 10 = 1 cm; 11 = 0.5 mm.

delineated; 2m-cu received distal in 1r-m on M by distance less than half length of 1r-m; metasoma elongate fusiform; T1 angulate in profile, wider than long; S1 wider than long, medially raised; T7 convex, apex at least weakly produced, rounded and raised; S8 concave dorsally, with strongly developed upwardly eurved apical spine (Fig. 6), basal angles spinose or angulate; paramere-basiparamere suture distinct; parameres without internal brush of setae; parapenal lobes and digitus absent (Figs 14–17).

Colour. Head and body black; wings black with violet reflections.

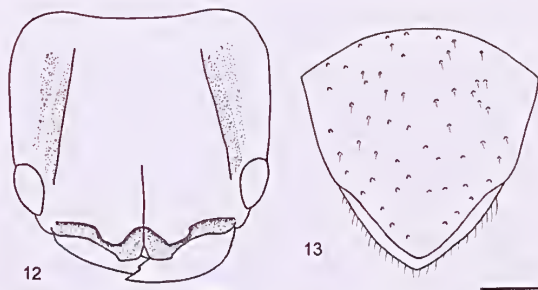
Female. Clypeus raised medially, with inverted Y-shaped carina, apical margin emarginate; mandibles bidentate; maxillary palps 6-segmented; labial palps 4-segmented; frons not reticulate; head with punctate depressions posterior to eyes (Figs 11–12, 21–22); head subrectangular; pronotum weakly convex, not tuberculate, not sulcate; dorsal surface of propodeum almost as long as, or longer than, wide; T1 anteriorly truncate, anterior angles not subtuberculate; T5 and S5 not tuberculate; T6 sub-triangular (Fig. 13) or subparallel (Fig. 23), punctate to closely punctate.

Colour. Head and body dark brown to black.

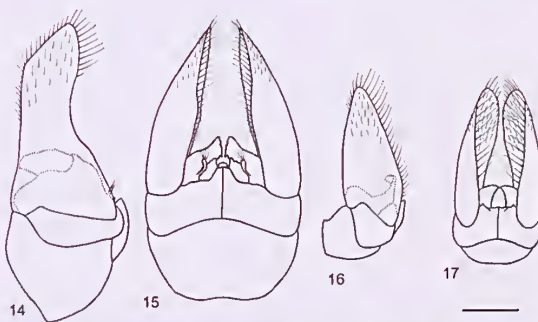
Distribution. Northern and north-eastern Australia, not inland (Fig. 5).

Remarks. The orientation of the eye relative to the posteroventral margin of the head and the shape of the pronotum and mesoseutulum in the male are unique and diagnostic within the tribe. Other characters that distinguish this genus from *Rhagigaster* include the frons being without transverse carina such that the head is evenly curved in profile from the vertex to the clypeus; the clypeus is triangularly flattened and polished rather than convex, carinate and punctate; mesosternum with transverse anteroventral carina that is less well developed laterally and strongly emarginated medially rather than not carinate or emarginate; S1 wider than long rather than vice versa and S8 without a precapical spine on the dorsal margin (viewed in profile). [The latter is a lateral expansion of the sternite that closes the genital cavity ventrally.]

Females are distinguished by the presence of a pair of broad setiferously punctate depressions that run longitudinally from the frons to the vertex. These paired depressions are unique to this genus and undescribed genus “Z”. *Curvothynnus* is also close to *Rhagigaster*; but the



Figs 12–13. *Curvothynnus laevigatus*, female: 12, head; 13, T6 (and posterior margin of S7). Scale lines = 0.5 mm.



Figs 14–17. *Curvothynnus* spp., male genitalia: 14, *C. laevigatus*, lateral; 15, *C. laevigatus*, dorsal; 16, *C. neptunus*, lateral; 17, *C. neptunus*, dorsal. Scale line = 0.5 mm.

latter has a longitudinal setiferously punctate line from the inner margin of the eye near the top posteriorly to almost the posterior margin of the head.

Etymology. The generic name is derived from the Latin *curvus* and is a reference to the anterior margin of the pronotum of the male which is bent forward.

Key to species of *Curvothynnus*

Male

- 1 S8 without lateral spines; T7 apically rounded; paracuspis present (Figs 14–15); body length greater than 20 mm *C. laevigatus* (Smith)
- S8 with lateral spines; T7 apically truncate; paracuspis absent (Figs 16–17); body length less than 20 mm ..
..... *C. neptunus* (Turner)

Female

- 1 Depressions on vertex broad and long (Figs 11–12); head and thorax rugose-punctate; body length greater than 15 mm *C. laevigatus* (Smith)
- Depression on vertex short, narrow and lunulate; head and thorax punctate (Figs 21–22); body length less than 15 mm *C. neptunus* (Turner)

Curvothynnus laevigatus (Smith) comb. nov.

(Figs 2, 4, 5–15)

Rhagigaster laevigatus Smith, 1879: 176. Turner 1907: 226; Kimsey & Brown 1993: 321 (lectotype designation).*Thynnus levigatus* Dalla Torre, 1897: 110.**Material examined.** LECTOTYPE: BMNH, ♂, Champion Bay, North West Coast, Western Australia. PARALECTOTYPE: BMNH, 1♀, same data as lectotype.**Additional (non-type) material examined.** WESTERN AUSTRALIA: WADA, 1♂, Kimberley Research Station near Kununurra, 4 March 1961, K.T. Richards; WADA, 1♀, Kimberley Research Station near Kununurra, 15 April 1962, K.T. Richards; UQIC, 1♂, 1♀, Black Rock, 12 miles north of Kununurra, on *Eucalyptus ?pruinosa*, 6 March 1973, E.M. Exley. NORTHERN TERRITORY: ANIC, 1♂, 11°1'S, 136°45'E, Rimbija Island, Wessel Islands, 17 Feb. 1977, R.A. Barrett; MV, 2♂, 1♀, Borroloola, 26 January–2 February 1912, G.F. Hill. QUEENSLAND: QM, 1♂, 1♀, Weipa, 3–5 February 1976, G.B. Monteith; MV, 1♂, Banks Island, Torres Strait, 1 June 1969, A. Neboiss; NSW, 1♂, Cape York, Fauvel; NSW, 1♂, Cape York, 1907; ANIC, 2♂, 1♀, Cape York, 1909, H. Elgner; ANIC, 2♂, Cape York, 1906, H. Elgner; MV, 1♂, Westwood, 31 December 1923, A.N. Burns; AM, 1♂, Westwood, 20 November 1978, R. Eastwood; ANIC, 3♂, 1♀, De Saily Range 63 miles north of Mareeba, 25 January 1973, J.G. Brooks; UQIC, 1♂, 1♀, Dimbulah, February 1961, I.C. Cunningham; QDPI, 1♂, 1♀, Dimbulah, February 1965; QDPI, QM 3♂, Townsville, 14–17 January 1900, F.P. Dodd; ANIC, 1♂, Townsville, January 1901, F.P. Dodd; AM, 1♂, Mackay, 1947, A. Marriage; ANIC, 1♂, Rockhampton, May 1911, H. Brown; ANIC, 1♂, Mount Walsh National Park, Biggenden, 9 January 1973, H. Frauca; QDPI, 1♂, Yinyarandi, 2 January 1936.**Redescription of male.** Body (Fig. 8) length 21–29 mm; fore wing 13–20 mm; hind wing 11–14. Head (Fig. 9) rounded, not emarginate posteriorly, produced and subparallel behind eyes; mandibles bidentate, not tuberculate; clypeus truncate, weakly convex, with obscure inverted V-shaped carina, branches broad, clypeus punctate laterally, sparsely punctate medially; antennal prominence broadly U-shaped, not carinate, projecting to antennal insertion; frons not transversely carinate, sparsely punctate, medially sulcate on lower half; vertex and gena sparsely punctate. Pronotum as wide as head, sparsely punctate, anterior margin strongly emarginate, strongly raised and produced anteriorly, carinate, not projecting laterally; mesoscutum, tegulae and mesoscutellum sparsely and shallowly punctate; mesoscutellum strongly convex, weakly medially carinate, triangular; metanotum sparsely punctate, below level of mesoscutellum; propodeum (Fig. 7) obliquely truncate posteriorly, not transversely carinate, sparsely punctate anteriorly, finely transversely punctate posteriorly; fore coxae punctate; mesopleura finely punctate. Metasoma elongate fusiiform; T1–6 impunctate with at most single line of subapical punctures; S1–7 punctate; gradulus straight and

shallow, impunctate in T2, scrobiculate on T3–6 and S3–4, punctate and obscure on S5–6, absent on S7. T1 truncate anteriorly, not tuberculate; S1 weakly and broadly raised, anterior V-shaped carina weakly produced ventrally; S2 anteromedially subtuberculate; T7 rounded posteriorly; S8 with strongly angulate basal angles; genitalia as in Figs 14–15, cuspis weakly hooked; paracuspis of medium length.

Colour. Black; wings black with violet reflections.

Redescription of female. Body (Fig. 10) length 17–21 mm. Head (Figs 11–12) subrectangular, posterior angles rounded; clypeus narrowly emarginate with inverted Y-shaped carina; frons longitudinally rugose-punctate, medially sulcate; depression behind eye broad, inner margin straight, outer margin indistinct, densely setose; vertex rugose-punctate, not medially depressed; gena rugose-punctate; eyes large, elliptical; mandibles weakly bidentate. Pronotum flat, weakly depressed near posterior angles, anterior angles not produced, rugose-punctate; mesoscutellum weakly convex, weakly narrowed posteriorly; propodeum weakly convex, not laterally depressed, truncate posteriorly, not densely setose, rugose-punctate dorsally, impunctate laterally with closely punctate dorsal margin, closely and finely punctate posteriorly. Metasoma with T1–5 and S1–5 punctate; T1 truncate, anterior angles rounded; T5 and S5 not produced; T6 (Fig. 13) subtriangular, not spinose, longitudinally rugose-punctate.

Colour. Dark ferruginous to black.

Distribution. Coast, coastal ranges and adjacent islands of northern and north-eastern Australia from Wyndham, Western Australia, to Biggenden, Queensland (Fig. 5). Most records are south of about 16°S with the exception of Weipa on the Queensland coast of the Gulf of Carpentaria. The record for Geraldton, Western Australia, is much further south (and west) from all others and needs to be confirmed.**Remarks.** Turner (1907) considered this species rare. While it is not common, there are now over 30 specimens in collections.*Curvothynnus laevigatus* is the largest known species in the Rhagigasterini.*Curvothynnus neptunus* (Turner) comb. nov.

(Figs 5, 9, 20–27)

Rhagigaster neptunus Turner, 1907: 227.**Type Material.** HOLOTYPE: OUM, ♂, Port Essington, Northern Territory.**Additional (non-type) material examined.** NORTHERN TERRITORY: NTM, 1♂, Adelaide River, 13°14'S, 131°06'E, January 1996, G. Dally; NTM, 1♂, Adelaide River, 13°14'S, 131°06'E, 20 December 1995, G.R. Brown & G. Dally; ANIC, NTM, 8♂, 6♀, Brocks Creek, Burnside, 18–22 Apr. 1929, T.G. Campbell; QDPI, QM, 2♂, Darwin, G.F. Hill; NTM, 1♂, Virginia nr Darwin, 12°33'S 131°02'E, 29 October 1996 S.M. Gregg; NTM 93–117, 1♂, Kapalga Research Station, Kakadu National Park, eucalypt woodland malaise trap, 11–25 December 1993, S. & J. Peck; NTM, 2♂, East Alligator Ranger Station,



Figs 18–19. *C. neptunus*, male: 18, habitus; 19, Front of head. Scale line: 18 = 1 cm; 19 = 0.3 mm.



Figs 20–21. *Curvothynnus neptunus*, female: 20, habitus; 21, head. Scale line: 20 = 0.8 mm; 23 = 0.5 mm.

Kakadu National Park, 12°26'S, 132°57'E, 11 March 2006, A. Young; NTM, 1♂, East Alligator Ranger Station, Kakadu National Park, 12°26'S, 132°57'E, 8 March 2006, A. Young. QUEENSLAND: QM, 4♂, 1♀, Cairns district, F.P. Dodd.

Redescription of male. Body (Fig. 18) length 12–16 mm; fore wing 9–12 mm; hind wing 7–10 mm. Head (Fig. 19) rounded, not emarginate posteriorly, produced and subparallel behind eyes; mandibles bidentate, not tuberculate; elypeus weakly emarginate, raised with flat triangular area depressed near apex bounded by obscure inverted V-shaped carina, elypeus closely and finely punctate laterally, sparsely punctate medially; antennal prominence broadly U-shaped, not carinate, produced to antennal insertions; frons not transversely carinate, sparsely punctate with narrow closely punctate band on inner orbit of eye, sagittally sulcate to near mid ocellus, not depressed; vertex and gena sparsely punctate. Pronotum as wide as head, sparsely punctate, anterior margin strongly emarginate, strongly raised and produced anteriorly, carinate, weakly projecting laterally; mesoseutum sparsely punctate; tegulae sparsely punctate; mesoseutellum impunctate, flat, narrowly triangular; metanotum impunctate medially,

closely punctate laterally, below level of mesoscutellum; propodeum obliquely truncate, weakly transversely carinate above truncation, sparsely punctate anteriorly, finely transversely rugose-punctate posteriorly; fore coxae sparsely punctate; mesopleura punctate. Metasoma elongate fusiform; T1–5 sparsely punctate, impunctate posteriorly, T6 punctate; S1–7 closely punctate; gradulus weakly curved and weakly serobieulate on T1–6, weakly curved, oblique and discontinuous medially on S3–7; T1 obliquely truncate anteriorly, not tuberculate; S1 medially raised and carinate, anterior V-shaped carina strongly produced and blade-like ventrally; S2 anteromedially subtuberculate; T7 truncate and weakly raised posteriorly; S8 with spinose basal angles; genitalia as in Figs 16–17, cuspis short and incurved; paracuspis absent.

Colour. Black; wings black with violet reflections.

Description of female. Body (Fig. 20) length 11 mm. Head (Figs 21–22) subrectangular, posterior angles rounded; elypeus emarginate, with an inverted Y-shaped carina; frons closely punctate, medially sulcate; depression behind eye narrow, curved, inner and outer margins sharply defined, densely setose; vertex sparsely punctate, not medially depressed; gena closely and deeply punctate; eyes elliptical; mandibles bidentate. Pronotum weakly convex, weakly depressed near posterior angles, anterior angles not produced, punctate; mesoscutellum weakly convex, weakly narrowed posteriorly, punctate; propodeum weakly convex, not laterally depressed, emarginate posteriorly, not densely setose, closely punctate dorsally, closely and finely punctate laterally and posteriorly. Metasoma with T1–5 and S1–5 closely punctate; T1 truncate, anterior angles rounded; T5 and S5 not produced; T6 (Fig. 23) subparallel, not spinose, longitudinally rugose-punctate.

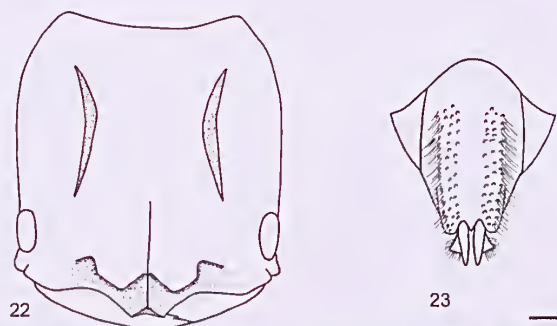
Colour. Head (except mandibles) and body dark brown; mandibles and legs brownish orange.

Distribution. Coastal northern Australia from Darwin, Northern Territory, to Cairns, Queensland (Fig. 5). Most records are north of 14°S with the Queensland specimen from the Cairns district being three degrees further south.

Remarks. The female has not previously been described.

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Figs 22–23. *Curvothynnus neptunus*, female: 22, head; 23, T6 (and posterolateral margins of S6). Scale line = 0.5 mm.

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Two new orchid-pollinating wasps (Hymenoptera: Thynnidae) from Australia

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ABSTRACT

Two new species of Australian flower wasps (Thynnidae) are described, each being known only from the male. They are *Arthrothynnus latipinus* sp. nov. from the sandstone escarpment of western Arnhem Land in the Northern Territory, the pollinator of the Robust Elbow Orchid (*Arthrochilus latipes*), and *Lestricothynnus hastata* sp. nov. from south-western Victoria, the pollinator of the threatened Mellbolm's Spider Orchid (*Arachnorchis hastata*).

KEYWORDS: Australia, Northern Territory, Victoria, Hymenoptera, Thynninae, *Arthrothynnus*, *Lestricothynnus*, Orchidaceae, *Caladenia*, orchid pollinators.

INTRODUCTION

Relatively little is known about insect-veetored pollination of Australian native plants, yet an understanding of pollinator biology, as well as plant pollination strategy, is essential for the management of rare and endangered plants. Arguably one of the most interesting strategies for plants is that of sexual deception. Orchids of the subfamily Diuridaceae, including such genera as *Chiloglottis*, *Caladenia*, *Arthrochilus* and *Drakaea*, have flowers that produce chemicals mimicking the sex pheromones of female thynnine wasps (Schiestl *et al.* 2003; Schiestl 2004). These chemicals lure and deceive males into attempting to mate with the flower. This behaviour achieves pollen transfer and ultimately pollination (Bower 1992; Brown 1997b).

Of particular interest with this strategy is that the wasp-orchid relationship is species-specific, such that a single species of wasp pollinates a single species of orchid. This relationship has been tested experimentally using picked and translocated flowers as bait for wasps (Bower & Brown 1997). Flowers that consistently attract the same species of wasp are conspecific, while those that attract a different species are not. This baiting method has become a standard technique for recognising cryptic species of orchid (Bower & Brown 2009).

The two species of wasps described here belong to unrelated genera – *Arthrothynnus*, which was erected and reviewed by Brown (1997b) and contains many pollinators of *Arthrochilus* orchids, and *Lestricothynnus*, a genus not previously recognised as including specific orchid pollinators. These wasps are the pollinators of the Robust Elbow Orchid, *Arthrochilus latipes* D.L. Jones and Mellbolm's Spider Orchid, *Arachnorchis hastata* (Nicholls) Rupp. respectively. The latter is listed as a threatened species and was thought

to be extinct until the discovery of six plants in 1996 (DSE 2006).

Terminology follows Snodgrass (1941), Brown (1997a, b) and Naumann (1991). Relative terms relating to microsculpture are interpreted as follows: sparsely punctate = punctures greater than two puncture-diameters apart; punctate = punctures at most two puncture-diameters apart, but never confluent; closely punctate = punctures almost confluent; rugosely punctate = punctures partially confluent; finely punctate = punctures small and shallow; coarsely punctate = punctures large and deep; obscurely punctate = punctures small, sparse, shallow and only visible at certain angles.

Abbreviations. Morphological characters: T1–7, metasomal tergites 1–7; S1–8, metasomal sternites 1–8. Specimen repositories: ANIC, Australian National Insect Collection, CSIRO, Canberra; BMNH, Natural History Museum, London; MV, Museum Victoria, Melbourne; NTM, Museum and Art Gallery of the Northern Territory (formerly Northern Territory Museum), Darwin.

SYSTEMATICS

Arthrothynnus Brown, 1997

Gender masculine. Type species, by original designation, *Arthrothynnus huntiaanus* Brown, 1997. Recent, Mt Canobolas, New South Wales, Australia.

A diagnosis for the genus was given by Brown (1997b), and the species described here is the seventh species to be placed in *Arthrothynnus*.

This genus was erected for six undescribed species from south-eastern Australia including some that pollinate terrestrial orchids of the genus *Arthrochilus* (Brown 1997b). Currently there are 10 species of *Arthrochilus* with one



Figs 1–3, *Arthrothynnus latipinus* sp. nov., male: 1, head; 2, habitus; 3, S8, ventral; 4, Blooms of orchid *Arthrochilus latipes*. Scale lines: 1 = 0.5 mm; 2 = 10 mm; 3 = 0.1 mm; 4 = 5 mm. All photographs: author except Fig 4, which is courtesy Ian Morris.

extending into New Guinea plus a further five species placed in the closely related genera *Phoringopsis* or *Thynniorchis* (Jones *et al.* 2002). All are likely to be pollinated by species of *Arthrothynnus* that are as yet uncollected or unrecognised.

There are two species of orchid in the Northern Territory that are, or are likely to be, pollinated by a species of thynnine wasp. Firstly, *Arthrochilus latipes* D.L. Jones is an orchid that occurs in *Allosyncarpia* forest at the base of the sandstone escarpment and flowers in the late dry season/early wet season and its pollinator is described here. Secondly, *Phoringopsis byrnesii* (Blaxell) D.L. Jones & M.A. Clem. is an orchid that occurs on the top of the sandstone escarpments and flowers in the middle of the wet season. The latter is inaccessible during the flowering season without a helicopter, and the pollinator is yet to be collected. There are further species of orchids in northern Queensland for which the pollinators are also as yet unknown.

Arthrothynnus latipinus sp. nov.

(Figs 1–4)

Material examined. HOLOTYPE – NTM 1.5918, ♂, Northern Territory, near Oenpelli *Allosyncarpia* forest track, attracted to *Arthrochilus latipes* flowers, 12°23'S, 133°01'E, 30 November 1996, G.R. Brown & J. Purdie.

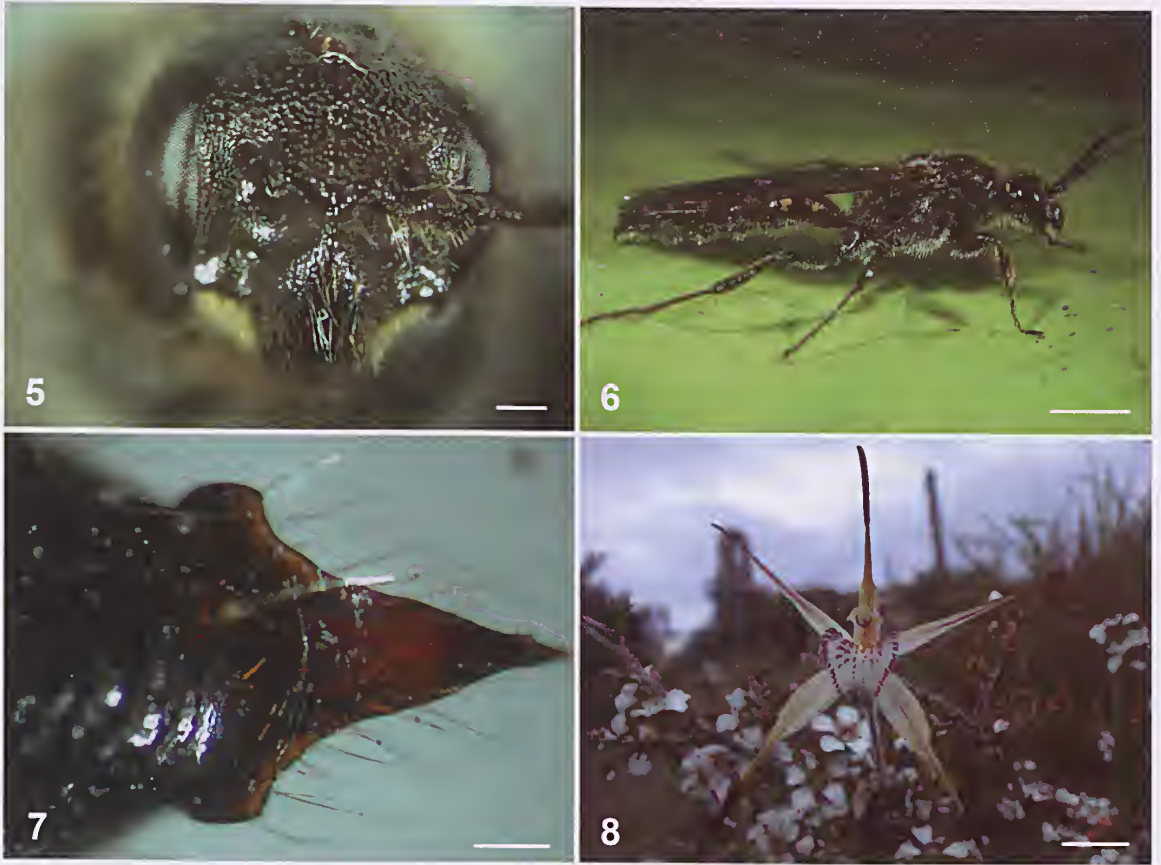
PARATYPES – ANIC, BMNH, NTM, QM, 7♂, same data as holotype; NTM, 3♂, 12°22'S, 133°03'E, near Oenpelli reservoir, 27 November 1996, G.R. Brown & J. Purdie; NTM, 1♂, Kakadu National Park, Anbangbang Billabong, 12°52'S, 132°48'E, 25 February 1996, G.R. Brown.

Description of male. Body (Fig. 2) length 6–8 mm; fore wing 5–6 mm; hind wing 4–5 mm.

Clypeus weakly raised medially, finely rugosely punctate, apical margin narrowly truncate (Fig. 1); frons rugosely punctate; antennal prominence transversally carinate (discontinuous medially); vertex and gena finely rugosely punctate.

Pronotum slightly swollen laterally, deeply and closely punctate, anterior end raised and subcarinate; mesoscutum and mesoseutellum deeply and closely punctate; metanotum closely punctate; propodeum rugosely punctate and transversely striate, dorsal surface impunctate; mesopleuron rugosely punctate; fore coxae closely and finely punctate, small, conical with shallow depression apically on ventral surface.

Metasoma elongate fusiform, T3–4 widest, T1 as wide as long; tergites sparsely punctate, polished; epipygium deeply and closely punctate, apical margin with transverse sinusoidal carina and narrow membranous plate laterally;



Figs 5–7, *Lestricothynnus hastata* sp. nov., male: 5, head; 6, live specimen; 7, apex of metasoma, dorsal; 8, Bloom of orchid *Arthrochilus hastata* (in front of *Leptospermum continentale* flowers). Scale lines: 5 = 5 mm; 6 = 4 mm; 7 = 0.1 mm; 8 = 20 mm. All photographs: author.

sternites closely punctate, closer on S1, anterior groove on S2–5 scrobiculate; S1 medially raised; hypopygium (S8) subparallel, lateral spines long, acute and divergent, apical spine long and narrow (Fig. 3).

Genitalia with parameres (in profile) subparallel and curved downward, margins gently converging distally and narrowly subtruncate apically; basiparameres (dorsally collectively) long with margins parallel basally, and convergent and subtriangular apically and subtruncate apically; cuspis short, subtriangular, apex slightly inturned with small preapical tooth on outer margin, digitus larger and arising from the outer surface ventrally.

Colour. Black; mandibles (except tip) with small transverse yellow mark above antennal insertion; anterior margin of pronotum (discontinuous medially) and disc of metanotum completely yellow. Wings hyaline to weakly infuscate, veins dark brown to black. Setae white.

Distribution. Known only from the Oenpelli area and adjacent regions of Kakadu National Park, Northern Territory, Australia.

Remarks. This species is tentatively placed in *Arthrothynnus* because of the structure of the antennal prominence, clypeus, metasoma, and hypopygium as these

preclude it from all other available genera. The subtruncate rather than deeply emarginate apex of the basiparameres (combined) distinguishes this species from all the other *Arthrothynnus* species and also suggests that this species may warrant a separate new genus. However, I am reluctant to create a new genus without seeing other species from northern Australia.

Arthrothynnus latipimus keys to *A. huntianus* Brown in the key given by Brown (1997b), but *A. huntianus* has orange legs and the metasoma is longer than the mesosoma. In comparison as stated above, the legs of *A. latipimus* are black and the metasoma is shorter than the mesosoma.

Arthrothynnus latipimus is presumed to be the pollinator of the orchid of *Arthrochilus latipes* (Fig. 4) based on its strong attraction to flowers of this orchid that were picked from the *Allosyncarpia* forest near Oenpelli and moved about 100 m away. Although no pollen transfer was observed, this strong attraction is typical of thynnine orchid pollinators (pers. obs.).

The only other known pollinators of *Arthrochilus* orchids are *Arthrothynnus huntianus*, which pollinates *Thynniorchis* (= *Arthrochilus*) *huntianus* (F.Muell.) D.L. Jones & M.A. Clem. in Victoria and New South Wales, and

Arthrothynnus rufiabdominalis Brown, which pollinates *Arthrochilus irritabilis* F. Muell. in Queensland.

Etymology. This species name is derived from a combination of the epithet of the orchid which this wasp pollinates and the Latin suffix *-imus* meaning pertaining to. It is intended as a noun in apposition.

***Lestricothynnus* Turner, 1910**

Gender masculine. Type species, by original designation, *Thynnus mubilipennis* Smith, 1879. Recent, Queensland, Australia.

A diagnosis for *Lestricothynnus* was given by Brown (2009). Currently there are 16 described species in the genus including three not currently placed in this genus (Brown pers. obs.) in addition to the species described here.

Males of the genus *Lestricothynnus* are mostly large in comparison to other thynnine wasps and they are extensively covered in yellow markings. They have not been reported previously as orchid pollinators, although *L. modestus* is probably the pollinator of *Arachnorchis corynephora* A.S. George with two undescribed species probably pollinating *Arachnorchis clavula* D.L. Jones and *Arachnorchis septuosa* D.L. Jones, respectively (Brown pers. obs.).

Arachnorchis is a large and diverse genus of ground orchids with 132 species and 18 subspecies described and many more undescribed (Jones 2006). These taxa are divided into 10 species groups with most of them being pollinated by thynnine wasps (Jones 2006). However, it should be noted that the validity of this genus is not universally accepted, and species are often referred to *Caladenia* R. Br. where they were placed previously (e.g. Phillips *et al.* 2009). A more detailed discussion of *Caladenia sensu lato* is also given in Phillips *et al.* (2009).

To date, 11 genera of thynnine wasps have been recorded as being attracted to *Arachnorchis* flowers (i.e. *Aeolothynnus*, *Campylothynnus*, *Chilothynnus*, *Lophocheilus*, *Macrothynnus*, *Neozeleboria*, *Phymatothynnus*, *Tachynomyia*, *Thynnoides*, *Zaspilothynnus* and *Zeleboria*) (Brown & Bower pers. obs.).

***Lestricothynnus hastata* sp. nov.**

(Figs 5–8)

Material examined. HOLOTYPE – NTM (I.5819), ♂, Victoria, east-west track (*Goodenia* site), Point Danger, near Portland, 19 October 2009, K. Vlcek & G.R. Brown. PARATYPES – Victoria: MV, NTM (not registered), 4♂ – same location as holotype but: 29 October 2009, K. Vlcek and G.R. Brown (MV 1♂); 7 November 2009, K. Vlcek (MV 1♂); 8 November 2009, K. Vlcek (NTM not registered, 2♂).

Description of male. Body (Fig. 6) length 16 mm; fore wing 11 mm; hind wing 8 mm.

Clypeus closely and finely punctate, disc punctate with punctures deeper; antennal prominence broadly rounded, flat, not distinctly carinate, weakly sagittally sulcate to near mid-ocellus and ending short by 1 ocellus diameter; frons

rugosely punctate, punctures larger dorsally (Fig. 5); vertex and gena finely and rugosely punctate with punctures coarser at level of ocelli; occipital carina almost continuous dorsally.

Pronotum closely and finely punctate with anterior margin sharply raised, but not carinate, not laterally produced, narrower than posterior margin and head; mesoscutum, tegulae, mesoscutellum and metanotum closely and finely punctate; mesoscutellum (in profile) mostly flat, convex anteriorly, propodeum closely to rugosely punctate and transversely multistriate, sagittally grooved anteriorly, obliquely and slightly rounded in profile, dorsal surface not delineated, lateral surfaces weakly separated and longitudinally multistriate dorsally; scrobal groove short almost horizontal, not quite reaching posterior margin; fore coxae punctate, shallowly concave over most of surface with apical angle produced, triangular and directed perpendicularly; mesopleura longitudinally multistriate.

Metasoma elongate, slightly flattened, constricted between segments; tergites punctate to closely punctate, closer on T1–2, not as close on disc of most tergites, deeper on posterior segments; T1 as wide as long, spiracles raised; sternites rugosely punctate; T7 apically subtruncate with 3 strong U-shaped carinae, membranously produced beyond carinae; S1 longitudinally convex with short sagittal groove apically, slightly longer than wide; S2–5 tuberculate, in profile tubercles progressively larger from S2 to S5 with those on S4–5 subequal in size, tubercles visible ventrally as posterolateral carinae that converge and are more strongly raised posteriorly with carinae forming the ridge of the tubercle; hypopygium (S8) with basal angles produced and truncate without spines, abruptly rounded distally then narrowly triangular to delicate upturned apical spine, transversely multicarinate dorsally (Fig. 7).

Genitalia with parameres narrow with margins parallel and slightly curved over most of length; aedeagus very narrow; digiti large, setose on outer surface, subtruncate distally, conspicuous in profile; cuspides narrow, almost lamellate, vertical, parallel, and elongate subtriangular.

Colour. Black; mandibles (except tip) pale yellow, yellow on inner and outer orbits between base of mandibles and level of antennal insertions and briefly extending onto margin of clypeus laterally; transverse yellow line laterally on vertex behind eye; elongate yellow spot on mesoscutellum; small yellow spot on metanotum; and small lateral yellow spot on T1–4 (larger on T2). Wings hyaline, veins brown. Setae mostly white but darker on frons, vertex, pronotum and mesoscutum.

Distribution. Coastal south-western Victoria in heath near Portland.

Etymology. This species takes its name directly from that of the orchid it pollinates, *Arachnorchis hastata* (Nicholls) Rupp (Fig. 8). It is intended as a noun in apposition.

Remarks. The yellow spots on the tergites are unusually variable and may be reduced or absent, but they are always small when present. This is unusual in the genus

Lestricothynnus, in which all species except *L. vigilans* are extensively marked with yellow or orange.

Also unusual within the subfamily is the pallor of the mandibles, the sternal tubercles and the narrow parameres. These characters are rare and occur in a few unrelated species, although the latter is typical of the genus *Catocheilus*. Narrow parameres also occur in at least one undescribed species of *Thynnoides* as well as *L. vigilans*. The sternal tubercles are unique within the genus.

Within the genus, *Lestricothynnus hastata* could only be confused with *L. vigilans* (Smith), but is readily distinguished by the presence of tubercles on the sternites. These two species are distinct, and are part of a complex of species present in south-eastern Australia that needs to be resolved with molecular studies.

DISCUSSION

Neither of the two Northern Territory orchid species pollinated, or potentially pollinated, by thynnine wasps is presently listed as threatened (<http://www.nt.gov.au/nreta/wildlife/animals/threatened/specieslist.html#plants>). However, *Phoringopsis byrnesii* is restricted to sandstone escarpments and it only flowers during the wet season. As such, it (and its thynnine pollinator, which is presently unknown) is inaccessible and its conservation status is unclear (i.e. Data Deficient). Previously it has been considered threatened (Briggs & Leigh 1995).

However, orchids in southern Australia are under higher pressure from land clearing and other human interference. In addition, more species are listed as threatened (Jones 2006) and a larger proportion are known to be pollinated by thynnine wasps (Brown & Bower pers. obs.). Despite the status of these orchids, management programs tend to concentrate on the propagation of more plants rather than on the factors that affect the abundance of the pollinator, even when the wasps are rare or unknown (Brown & Vlcek 2009). Mellblom's Spider Orchid is currently one of Australia's rarest orchids. It was plentiful in the 1950s but suffered a rapid decline in numbers with only six plants existing in 1996 (DEWHA 2009). Propagation and management had increased this number to 180 flowering plants plus 600 seedlings a decade later (DSE 2006). However, the discovery of the pollinator is a major breakthrough for the long term management of this orchid.

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A new species of the genus *Microlestodes* Baehr from Arnhem Land, Northern Territory, Australia (Insecta: Coleoptera: Carabidae: Lebiini)

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ABSTRACT

A new species of the beetle genus *Microlestodes* Baehr is described from Arnhem Land in the Northern Territory, Australia: *M. arnhemensis* sp. nov. This new species is closely related to the widespread *M. macleayi* (Csiki), and to *M. rufoniger* Baehr and *M. inoculatus* Baehr, both latter species from northern tropical Australia, but can be distinguished by the different colour pattern, wider pronotum with wider base, and the differently shaped aedeagus. It is included in the key to the species of the genus *Microlestodes* (vide Baehr 1987: 29). For comparison of body shape, photographs of the three related species are included.

KEYWORDS: Coleoptera, Carabidae, Lebiini, *Microlestodes arnhemensis*, taxonomy, Arnhem Land, Northern Territory.

INTRODUCTION

With about 40,000 described species and subspecies worldwide, the Carabidae is one of the largest families of beetles. The family belongs to the suborder Adephaga which also includes a few families of aquatic and semiaquatic beetles and which is mainly characterised by the rather plesiomorphic structure of their leg insertions and by their primitive campodeiform larvae which still possess well articulated legs. In Australia, about 2750 species and subspecies of Carabidae are presently recorded (Baehr unpubl. checklist), but the number of actual existing species certainly is much greater.

Lebiini (or Lebiinae, according to the opinion of different authors) is a highly evolved tribe (or subfamily) of carabid beetles, mainly characterised by their abbreviated elytra, and in many species, denticulate tarsal claws. Lebiini is a very large tribe of remarkably differently shaped and coloured species which possess very different habits. The tribe is divided into several subtribes, the status and limits of some of which are still subject of discussion. The tribe is distributed worldwide, but certainly is much more common and diverse in the tropics than in temperate regions. This may be partly due to the large number of tree-dwelling species that occur in tropical and subtropical forests. In Australia, the number of lebiine species that occur in and under the bark of a great variety of tree species is particularly numerous.

From Australia, so far 33 genera of Lebiini are recorded but additional ones are already known to exist or are being described (Baehr unpubl.). The number of presently recorded species and subspecies is 338, but this number does not equal the number of actually existing species by a

long way. In particular, modern revisions of several of the large genera of arboricolous lebiine species would raise this number considerably.

The single specimen of the new species was detected in a small batch of carabid specimens collected near the northern coast of Arnhem Land. This description is regarded as a further supplement to my revision of the genus *Microlestodes* (Baehr 1987).

Although description of species based on a single specimen has to be done with some caution because of the risk of describing an aberrant specimen as new, I believe that the differences in body shape, colour pattern, and shape and structure of the male aedeagus, between the mentioned specimen and the three most similar species are substantial. Moreover, the specimen was compared with ample material of all three species, including paratypes.

METHODS

Description and measurements follow the style used in my revision of the genus *Microlestodes* (Baehr 1987) and the supplementary descriptions (Baehr 1990, 2009). Body length has been measured from the apex of the labrum to the apex of the elytra; the length of pronotum was measured along the midline.

For dissection of the male genitalia the holotype was relaxed overnight in a jar with a moist atmosphere, then the genitalia were removed and subsequently cleaned for a short while in hot KOH. The photographs of the whole animal were obtained with a digital camera using ProgRes Capture Basic and AutoMontage, and subsequently processed using Corel Photo Paint 11.

The holotype of the new species is deposited in the Museum and Art Gallery of the Northern Territory (formerly Northern Territory Museum), Darwin (NTM).

TAXONOMY

Genus *Microlestodes* Baehr

Microlestodes Baehr, 1987. Gender masculine. Type species, by original designation, *Microlestes macleayi* Csiki, 1932 (= *Dromius humeralis* Macleay, 1871). Recent, Australia.

This genus of rather small lebiine beetles was erected by Baehr (1987) for four Australian and one New Guinean species that were formerly included in the almost worldwide genus *Microlestes* Schmidt-Göbel, 1846. *Microlestodes* differs from *Microlestes* mainly by the presence of three impilose basal antennomeres instead of two, and by the structure of the paraglossae which are free and do not encircle the glossa, as in *Microlestes*. Both these character states are regarded plesiomorphic in *Microlestodes* as compared with those of *Microlestes*.

Baehr (1987, 1990, 2009) described several additional species from Australia, and also the subgenus *Cyclolestodes* for *M. ovatus* Baehr, 1987. Species of *Microlestodes* occur almost everywhere in Australia (including Tasmania), but most species apparently possess rather restricted ranges, whereas one species [*M. macleayi* (Csiki, 1932)] is very widely distributed. At present 13 species are recorded from Australia and one from Papua New Guinea. So far three species are known from the far north of the Northern Territory, namely *M. macleayi* (Csiki, 1932), *M. rufoniger* Baehr, 1987, and *M. inoculatus* Baehr, 1987, but no species has been recorded from Arnhem Land, except Kakadu National Park.

The species of *Microlestodes* are ground-living beetles that are apparently predominantly active at night, because they are commonly attracted to lights. During the daytime, individuals probably hide on the ground under stones, in leaf litter, and in cracks in the soil. Some species are found more commonly near water, others in rather dry savannah and woodland areas, and others even on the floor of tropical to temperate rain forest and in rather dense sclerophyll forest. Apart from the short-winged *M. ovatus* Baehr, 1987, of montane south-eastern Australia, all species are fully winged and in open tropical and subtropical savannah and woodland areas they are sometimes attracted to light in large numbers.

Microlestodes arnhemensis sp. nov.

(Figs 1, 2)

Material examined. HOLOTYPE – NTM I.5920, ♂, Northern Territory, Arnhem Land, Djinkar Ridge, south of Maningrida, 12°12.567'S, 134°17.0'E, B. Baehr, 23 September 2009.

Etymology. The name refers to the recorded range of this species, which is Arnhem Land in the north of the Northern Territory.

Diagnosis. Distinguished from the most similar species *M. macleayi* (Csiki, 1932) by the wider pronotum which is less cordiform and which bears a relatively wider base, and by the more distinctly bisinuate lower surface of the aedeagus, its slightly knobbed apex, and the lack of sclerotised teeth in the orificium. From *M. rufoniger* Baehr, it is distinguished by the generally lighter colour, the less distinct colour pattern of the elytra, and likewise by the shape of the aedeagus; and from *M. inoculatus* Baehr, by the wider pronotum, longer elytra, presence of the common subapical pale spot on the elytra, and less knobbed apex of the aedeagus.

Description. Measurements. Length: 3.1 mm; width: 1.25 mm. Ratios: Width/length of pronotum: 1.39; widest diameter/width of base of pronotum: 1.16; length/width of elytra: 1.49.

Colour (Fig. 2). Head piceous, pronotum brown, basal angles of pronotum inconspicuously paler. Elytra brown to piceous, with yellow base and large, common, median, subapical yellow spot that reaches apex; dark colour near suture prolonged laterally; but colour pattern poorly defined and little contrasting. Margins of labrum, mandibles, palpi, and antenna yellow to pale reddish. Legs dirty yellow. Lower surface of head laterally brownish, in middle reddish, rest of lower surface, including epipleurae, dirty yellow.

Head (Fig. 2). Slightly narrower than pronotum. Eys large, moderately protruded laterally, orbits short, oblique and slightly convex. Clypeal suture distinct, labrum transverse, rectangular, 6-setose, mandibles rather short. Mentum edentate. Palpi normal-shaped. Antenna short, pilose from 4th antennomere, surpassing base of pronotum by about 3 antennomeres, 6th and 7th antennomeres approx. 1.4–1.5 x as long as wide. Surface smooth, without any wrinkles, with very fine, very little impressed, about isodiametric microreticulation and with extremely fine, scattered punctures which are visible only under very high magnification, glossy and slightly sericeous.

Pronotum (Fig. 2). Wide, much wider than long, little narrowed towards basal angles, rather depressed, widest slightly behind anterior fourth. Apex wide, concave, apical angles protruded but rounded. Lateral margins evenly but gently convex, very slightly sinuate in front of obtuse basal angles. Base in middle far protruded posteriad, laterally obliquely convex. Apex in middle not margined, lateral margin narrow, marginal channel narrow and very shallow,

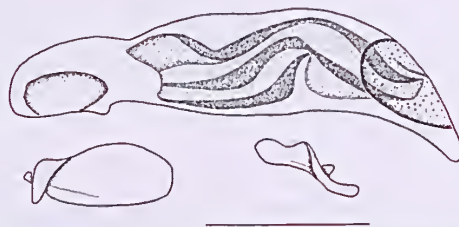


Fig. 1. *Microlestodes arnhemensis* sp. nov. Male aedeagus in lateral view and parameres. Scale bar: 0.25 mm.



Figs 2-5. *Microlestodes* species, habitus (body length in brackets): 2, *Microlestodes arnhemensis* sp. nov. (3.1 mm); 3, *M. macleayi* (Csiki) (3.8 mm); 4, *M. rufoniger* Baehr (3.8 mm); 5, *M. inoculatus* Baehr (3.5 mm).

base inconspicuously margined. Median line shallowly impressed, narrow, neither attaining apex nor base. Anterior and posterior transverse sulci barely indicated, basal grooves shallow. Anterior marginal seta situated at widest diameter, posterior seta at basal angle. Surface with only traces of extremely fine, highly superficial, isodiametric microreticulation and with very difficult to distinguish scattered punctures, moderately glossy and sericeous.

Elytra (Fig. 1). Comparatively elongate, laterally slightly convex, widest slightly behind middle, surface depressed. Humeri widely rounded, apex very gently concave, lateral apical angles rounded, sutural angle shortly rounded. Striae barely impressed, inconspicuous, very finely punctate, intervals absolutely depressed. Third interval with 2 setiferous punctures located slightly in front of middle and at apical third. Punctures very inconspicuous and setae extremely short. Series of marginal setae consisting of 5 basal and 8 apical setae; setae, if still present, elongate. Surface with barely recognisable, finest traces of transverse lines and with very fine, sparse punctures which are perceptible only at very high magnification, surface markedly sericeous.

Lower surface. Metepisternum fairly elongate, slightly less than twice as long as wide at anterior margin. Whole surface with extremely fine and superficial microreticulation, glossy, and with extremely short, erect pilosity, perceptible only at very high magnification. Terminal sternum in male slightly excised medially, bisetose.

Legs. Of average size. Fifth tarsomeres with few setae on lower surface. Tarsal claws with 3 fairly elongate teeth. Three basal tarsomeres of male protarsus slightly widened and biserially squamose.

Male genitalia (Fig. 1). Genital ring narrow, narrowed to apex, slightly asymmetric. Aedeagus rather compact, lower surface evidently bisinuate, apex moderately elongate (in genus), slightly bent down and slightly knob-shaped. Orificium rather short, situated on left upper surface. Internal sac with large, elongate, coiled, finely denticulate plate, but without any sclerotised teeth or spines. Left paramere fairly large, triangular-elongate, right paramere small.

Female genitalia. Unknown.

Variation. Unknown.

Collecting circumstances. The holotype was running in leaf litter on the ground together with specimens of two new species of the genus *Scopodes* Erichson, 1842 (Carabidae, Pentagoniini) (for information about the *Scopodes* see Baehr 2010).

Distribution. Northern margin of Arnhem Land. Known only from the type locality.

Relationships. According to the colour pattern and the shape of the aedeagus *Microlestodes arnhemensis* is most closely related to the widespread *M. macleayi* (Csiki), and to *M. rufoniger* Baehr and *M. inoculatus* Baehr, both occurring only in tropical northern Australia.

Key to the genus *Microlestodes* (emended)

For identification of the new species, couplet 10 in the key to the genus *Microlestodes* (Baehr 1987: 29) is easily reached, but then it must be changed as follows. Figure captions from the mentioned key are inserted as B87 fig.:

10. Elytra without common, median, preapical spot (Fig. 5); aedeagus with short, but definitely knob-like apex (B87 fig. 32) *M. inoculatus* Baehr
- Elytra with common, median, preapical spot (Figs 2–4); aedeagus either with nearly straight lower surface and without knob-like apex (B87 figs 30, 31), or aedeagus with lower surface remarkably bisinuate and with moderately short, slightly knob-like apex (Fig. 2)..... 11
11. Head, pronotum, and elytra deep black, elytra in apical two thirds black, borders of dark areas well delimited (Fig. 4; B87 fig. 21); aedeagus on lower surface almost straight, with short, obtuse, but not knob-like apex (B87 fig. 31) *M. rufoniger* Baehr
- Head black or brown, pronotum reddish to light brown, elytra in apical two thirds brown to piceous, borders of dark areas poorly delimited (Figs 2, 3; B87 figs 15, 16); aedeagus either on lower surface markedly bisinuate, with moderately short, slightly knob-like apex (Fig. 5), or orificium of aedeagus with two small sclerotized teeth (B87 fig. 30)..... 11a
- 11a. Pronotum wider, ratio width/length 1.39, with wider base, ratio widest diameter/base 1.16 (Fig. 2; aedeagus on lower surface markedly bisinuate, without sclerotized teeth in the orificium (Fig. 2) *M. arnhemensis* sp. nov.
- Pronotum narrower, ratio width/length <1.30, with narrower base, ratio widest diameter/base >1.19 (Fig. 3); aedeagus on lower surface barely bisinuate, with two sclerotized teeth in the orificium (B87 fig. 30)..... 12
12. = as in Baehr (1987).

REMARKS

According to the general colour pattern and shape of the aedeagus *Microlestodes arnhemensis* is most closely related to the very widespread *M. macleayi* and the northern Australian *M. rufoniger* and *M. inoculatus*. Although the general colouration and the colour pattern of the elytra is quite similar to those of *M. macleayi*, *M. arnhemensis* differs from that species by the wider pronotum and the lack of sclerotised teeth in the orificium of the aedeagus. From both *M. rufoniger* and *M. inoculatus*, it differs by its colour pattern, whereas the differences in shape and structure of the

aedeagus are less obvious. From all three species it further differs by its very small body size which is equalled only by extremely small specimens of the other mentioned species.

These three species and *M. arnhemensis*, together with a few additional, southern species, belong to a group within the genus *Microlestodes*, the species of which are mainly found in more or less open woodland and even in semiarid areas. All the species of this group bear more or less distinctly bicoloured elytra which usually have the basal third pale and the apical two-thirds darker, with or without a common, median, subapical, pale spot. The dorsal surface, or at least the elytra, of all these species is markedly sericeous which may be adaptative to life in rather open, sunny places.

Although the carabid fauna of Kakadu National Park and of the lowlands and floodplains west of this park are reasonably well known due to some sampling efforts during the previous 30–40 years, the fauna of Arnhem Land itself is almost completely unknown. The present paper therefore also should encourage scientists and likewise the land owners to explore this large and in parts rugged area that promises to be home of a peculiar and probably also quite endemic fauna.

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Clarification of field characters for three freshwater sharks and a photographic atlas of *Glyphis glyphis* and *G. garricki* from the Adelaide River, Northern Territory, Australia

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ABSTRACT

Eighty-two *Glyphis glyphis*, one *G. garricki* and two *Carcharhinus leucas* were caught at six localities in the Adelaide River on 66 gill-netting trips from mid-May to mid-December during 2001, 2003–05 and 2009. Photographs are presented that differentiate these euryhaline sharks. The small second dorsal fin of *C. leucas* clearly separates it from *Glyphis* species. The waterline (i.e. junction of dark dorsal and pale ventral colouration) on *G. glyphis* extends just under the eye whereas it extends well below the lower margin of the eye in *G. garricki*. Photographs showing shark bite marks on other species are presented. Because of the presence of *G. glyphis* under 610 mm TL with umbilical scars, it is postulated that Marrakai Creek is a nursery area and an important juvenile habitat of this species especially from September–December.

KEYWORDS: Adelaide River, Bull Shark, Northern River Shark, Spartooth Shark, *Carcharhinus leucas*, *Glyphis garricki*, *Glyphis glyphis*.

INTRODUCTION

Thirty-one of the 54 known species of whaler sharks (family Carcharhinidae) are found in Australia and three of these can occur far up rivers well into fresh water (Last & Stevens 2009). Prior to the commencement of Nurseryfish (*Kurtus gulliveri*) life history studies in 2001 (Berra 2003; Berra *et al.* 2007 and papers cited therein), the Spartooth Shark (*Glyphis* sp. A) and the Northern River Shark (*Glyphis* sp. C) (Last & Stevens 1994) were undocumented from the Adelaide River. *Glyphis* sp. A was subsequently determined to be conspecific with *Glyphis glyphis* (Müller & Henle, 1839) and *Glyphis* sp. C was described as a new species, *G. garricki* (Compagno, White & Last, 2008). DNA barcoding, based on mitochondrial cytochrome oxidase I gene (cox 1) sequences supported the taxonomic placement and separation of the two species of *Glyphis* (Wynen *et al.* 2009).

The cosmopolitan Bull Shark, *Carcharhinus leucas* (Müller & Henle, 1839) (Fig. 1A), is known from many of Australia's northern rivers including the Ord, Daly, Adelaide, and East Alligator (Berra 2007; Last & Stevens 2009). *Carcharhinus amboinensis* (Müller & Henle, 1839) is morphologically very similar to the Bull Shark, but much less likely to be found upstream in fresh water (Last & Stevens 2009). The extent of Spartooth Shark, *G. glyphis* (Fig. 1B), distribution is unknown, but it has been taken from

the Alligator Rivers of the Northern Territory in addition to the Adelaide River, as well as from the Bizant and Wenlock Rivers of Queensland and the Fly River in southern New Guinea (Peverell *et al.* 2006; Compagno *et al.* 2008; Pillans *et al.* 2009). The Northern River Shark, *Glyphis garricki* (Fig. 1C), has an uncertain distribution in parts of southern New Guinea and northern Australia including the entrance to Cambridge Gulf, King Sound, Ord River and Doctors Creek in Western Australia, and the Adelaide, East, and South Alligator Rivers in the Northern Territory (Thorburn & Morgan 2004; Compagno *et al.* 2008; Pillans *et al.* 2009).

Compagno *et al.* (2008) recognised five species of *Glyphis*: *G. gangeticus*, *G. glyphis*, *G. siamensis*, *G. garricki*, and an undescribed species from Borneo (*Glyphis* sp. B). The latter has recently been described as *G. fowlerae* (Compagno *et al.* 2010). Compagno *et al.* (2008) provided a comprehensive review of *G. glyphis*, described *G. garricki* and listed many internal and external taxonomic characteristics that distinguish the species. However, a few published characters used to distinguish *G. glyphis* from *G. garricki* are problematical to apply in the field in some cases (Compagno *et al.* 2005, 2008; Last & Stevens 2009; Wynen *et al.* 2009). The purposes of this paper are to clearly state and illustrate how to distinguish the shark species likely to be found in fresh water in the Adelaide River using only field characters on living specimens and to present a record of photographs of *Glyphis*.



Fig. 1. Sharks from freshwater reaches of Northern Territory rivers: A, *Carcharhinus leucas* (Bull Shark), Beatrice Creek, Adelaide River, 27 July 2001, released; B, *Glyphis glyphis* (Spartooth Shark), Adelaide River, 7.2 km downstream from boat ramp, 17 October 2003, released; C, *Glyphis garricki* (Northern River Shark), Marrakai Creek, Adelaide River, 26 October 2009, released; D, *Glyphis glyphis*, Marrakai Creek, Adelaide River, 26 October 2009, released. Note umbilical sear and black tips of ventral surface of pectoral fins; E, *Glyphis glyphis*, Marrakai Creek, Adelaide River, 26 October 2009, released. Note elongate, smooth lower jaw teeth, pointed snout and position of waterline at eye; F, Top, *Glyphis glyphis* (S. 15095-001) West Alligator River, 1 June, 1999. Bottom, *Glyphis garricki* (S. 15098-001), Smith's Landing, East Alligator River, 10 June, 1999. Note dark pigment on the ventral surface of the pectoral fins of both species and the position of the waterline on the ventral aspect of the head; G, *Glyphis garricki*, Marrakai Creek, Adelaide River, 26 October 2009, 930 mm TL, released. Note the waterline (grey pigment) well below the lower eye margin. Compare to E; H, *Glyphis garricki* (S. 15302-001) Cooper Creek, East Alligator River, 25 February 2001; (S. 16158-002) Adelaide River, 27 February 2004. Note waterline well below the lower eye margin in preserved specimens. All photographs: author.

METHODS

Four and five inch mesh (101–127 mm) monofilament gill nets were set, usually on rising neap tides, on 66 occasions at localities in the Adelaide River (Fig. 2) and its tributaries in various months of the dry season during 2001 (27 trips May–November), 2003 (17 trips October–November), 2004 (9 trips July–August), 2005 (9 trips November–December), and 2009 (4 trips September–October). Since Nurseryfish were the object of the study, sharks were generally counted, sometimes photographed, and immediately released alive without sexing or precise measurement. Marrakai Creek (12°40.86'S, 131°20.1'E) was the most commonly sampled locality since it consistently yielded Nurseryfish. Sharks were netted as by-catch. Three male and two female *G. glyphis* were deposited in the Museum and Art Gallery of the Northern Territory, Darwin (NTM). Their registration numbers are S.15304-001, S.15305-001, S.15351-001, S.16262-001 and S.16255-001. Four additional specimens of *G. glyphis* (S.15095-001, S.15299-001, S.15301-001, S.15303-001) and four specimens of *G. garricki* (S.15098-001, S.15302-001, S.16158-001, -002) at the NTM were also examined and photographed.

RESULTS

Eighty-two *Glyphis glyphis*, one *G. garricki* (930 mm TL) and two *Carcharhinus leucas* were netted at six localities (Fig. 2). The total length (TL) of *G. glyphis* specimens that were measured ranged from 540 to 1010 mm. Three live specimens of *G. glyphis* were taken to the aquarium at the Territory Wildlife Park. They survived the month-long quarantine period in approx. 7 ppt brackish water, but died when transferred to completely fresh water. The vast majority of the netted *G. glyphis* were smaller than 1 m TL. The largest specimen was estimated at less than 2 m TL. Other estimated specimens include one approx. 1300 mm TL, and five were approx. 1 m TL. Umbilical sears were present on the smallest specimens 540–610 mm TL (Fig. 1D). During the 2009 Nurseryfish collections, six *G. glyphis* (4F: 2M) 760–1010 mm TL were tagged as part of the “Estimating fishing-related mortality and designing sustainable management protoeols for shark fisheries in Northern Australia” by Northern Territory Fisheries (Department of Resources). To date, 12 *Glyphis* have been tagged, and no recaptures have been recorded as of July 2010 (Grant Johnson pers. comm.).

Interestingly, the two *G. glyphis* taken from the lower reaches of the Adelaide River at E and F Creeks (Fig. 2) were caught on 18 May 2001. In spite of 15 subsequent netting trips from 29 May through 30 August, no *Glyphis* were taken upstream in Marrakai Creek until 11 September 2001. A total of four *G. glyphis* were taken in September, 22 in October, 35 in November and 19 in December of all years. The single *G. garricki* was caught on 26 October

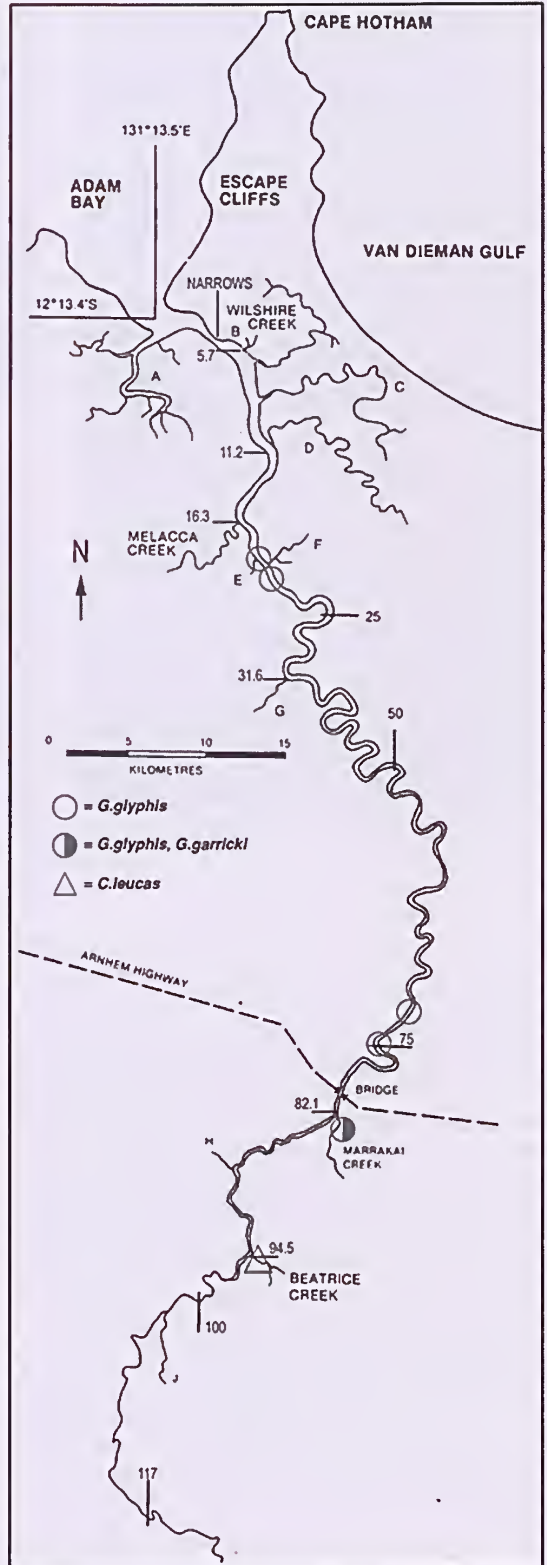


Fig 2. Map of Adelaide River showing location of collections.

2010 and the two Bull Sharks were caught at Beatrice Creek (Fig. 2) on 27 July 2001.

Glyphis can be distinguished from the Bull Shark by the large size of the second dorsal fin of *Glyphis* relative to the first dorsal fin (Last & Stevens 2009) (Fig. 1A–C). The height of the second dorsal fin of *Glyphis* is at least half the height of the first dorsal fin, whereas in the Bull Shark, the second dorsal fin is only one-third as high as the first dorsal fin. *Glyphis* caught in the Adelaide River are relatively sleek and silvery-grey with a bright white ventral surface, whereas Bull Sharks tend to be more robust-bodied and brownish grey (Figs 1A–C). The *Glyphis* snout is slightly pointed (Fig. 1E), as opposed to the bluntly rounded snout of Bull Sharks, and the eye of *Glyphis* is smaller than the eye of a similar sized Bull Shark (Peverell *et al.* 2006). The lower jaw teeth of *Glyphis* are smooth and narrow, hence the vernacular name “spartooth” (Fig. 1E), whereas Bull Sharks have serrated, triangular, stout lower jaw teeth (Last & Stevens 2009).

The most useful field character for separating *G. glyphis* from *G. garricki* is the relationship between the waterline (i.e. the junction of dark and light or dorsal and ventral colour delineation) and the eye (Compagno *et al.* 2008). In *G. glyphis* the waterline is at the lower margin of the eye (Fig. 1B,E) and is not visible in a ventral view of the head (Fig. 1F). In *G. garricki* the waterline extends well below the lower margin of the eye by at least an eye diameter (Fig. 1G), and is visible in a ventral view of the head (Fig. 1F). This character is visible in life and persists in preserved specimens (Fig. 1H). However, the colour paintings in Compagno *et al.*'s (2005) field guide show the waterline of *G. garricki* (*G. sp. C*) and *G. glyphis* (*G. sp. A*) as identical. Drawings in more recent publications have corrected this inaccuracy (Compagno *et al.* 2008).

Compagno *et al.* (2008) and Last & Stevens (2009), stated that *G. glyphis* has a black blotch at the ventral tip of the pectoral fin and that *G. garricki* lacks this blotch. Wynen *et al.* (2009: Table 2) erroneously reversed this characteristic. The living and preserved specimens of *G. glyphis* I have observed from the Adelaide River definitely have a black blotch at the distal end of the ventral aspect of the pectoral fin (Fig. 1D). However, the one living and four preserved specimens of *G. garricki* examined also have dusky pigment on the apex of the ventral pectoral fin (Fig. 1F, bottom). It is not quite as dark as on *G. glyphis* (Fig. 1, top), but this distinction may be too subtle to be applied in the field.

Shark predation is a fact of life faced by fishes in the freshwater reaches of the Adelaide River. Figure 3 shows damage probably inflicted by *Glyphis* on several species. It is not possible to determine if the bites occurred while the specimens were trapped in the gill net, or if the fish

became trapped after being bitten. However, the former seems most likely.

SIMPLIFIED KEY TO THE SHARK SPECIES IN FRESH WATER IN THE ADELAIDE RIVER

- 1a. Second dorsal fin approx. one-third height of first dorsal fin; lower jaw teeth triangular and serrated ...
.....*Carcharhinus leucas* (Bull Shark)
- 1b. Second dorsal fin approx. one-half height of first dorsal fin; lower jaw teeth elongate and smooth 2
- 2a. Waterline extends just below ventral edge of eye; waterline pigment not visible in ventral view
.....*Glyphis glyphis* (Spartooth Shark)
- 2b. Waterline extends at least one eye diameter below ventral edge of eye; waterline pigment visible in ventral view.....
.....*Glyphis garricki* (Northern River Shark)

DISCUSSION

Although little is known of the biology of *Glyphis glyphis*, it is relatively common in the Adelaide River and easily distinguished from the Bull Shark. It occurs sympatrically with its less common congener *G. garricki*, from which it can be distinguished by the location of the waterline relative to the eye. On 26 October 2009, 3.25 hours of netting produced 11 *G. glyphis* and one *G. garricki*. Although the author cannot rule out the possibility that a specimen might have been captured more than once, this seems to approximate the perception of their relative occurrence. The numerical tagging program begun by Northern Territory Fisheries (Department of Resources) will hopefully lead to a greater understanding of the movements and life history of both species of *Glyphis*, subjects addressed by Pillans *et al.* (2009).

Since many of the small *G. glyphis* bore umbilical scars and were under 610 mm TL it is likely that Marrakai Creek is a nursery ground as well as an important juvenile habitat for this species. The months of September to December appear to be the time of their greatest abundance in Marrakai Creek, however, field work in the wet season (January–April) is nearly impossible there. Thorburn & Rowland (2008) demonstrated that the rivers of northern Australia act as nurseries for juvenile Bull Sharks, *C. leucas*. Although the specimens caught in the Adelaide River were only small due to the gill net mesh size, on 8 December 2005 nine *Glyphis* were netted in 2.5 hours and one was estimated at 2 m. When the net was lifted, only the head was visible and it quickly tore through the net and submerged.



Fig. 3. Shark bites: A, *Kurtus gulliveri* (Nurseryfish), Marrakai Creek, Adelaide River, 24 November 2005; B, *Pristis microdon* (Freshwater Sawfish) Marrakai Creek, 15 June 2001, released. Note crescent-shaped bite above left pectoral fin; C, *Latcs calcarifer* (Barramundi), Marrakai Creek, 29 September, 2009. All photographs: author.

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Thanks to D. Wedd, Q. Allsop, K. Buckley and G. Johnson for help in the field. When I returned from a Nurseryfish field trip to the Museum and Art Gallery of the Northern Territory with my first *Glyphis* in 2001, B. Russell and H. Larson alerted me to the possibility of 'unknown' sharks in the Adelaide River. Little did I know that I would eventually catch over 80 *Glyphis*. G. Dally facilitated examination of specimens in the fish collection of the Museum and Art Gallery of the Northern Territory. The Territory Wildlife Park generously made its boat available for field trips, and Northern Territory Fisheries (Department of Resources) provided the gill nets and permits. B. Gray assembled Figures 1 and 3 and added the distribution points to Figure 2, which was composed by B. Glasby. G. Johnson and R. Heuter provided helpful comments on the manuscript. I am especially grateful for the generous comments of two anonymous reviewers and the editor for significantly improving this manuscript. This paper was begun while the author was a Fulbright Senior Specialist in residence at Charles Darwin University.

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A new fossil species of frog of the Australian limnodynastid genus *Limnodynastes* Fitzinger from the Oligocene Kangaroo Well Local Fauna of the Northern Territory and tabulation of ilial features of all extant and extinct species

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ABSTRACT

A new species of the limnodynastid genus *Limnodynastes* Fitzinger is described from the Oligocene Kangaroo Well Local Fauna on the Deep Well pastoral station in the Northern Territory. The material comprises the proximal portions of a left and right ilium and is named *L. waterhousae*. The new species appears to be most similar to *L. antecessor* Tyler, 1990 from Oligo-Miocene sites at Riversleigh, Queensland. The major characteristics of the ilium of all 30 extant and extinct Australian frog genera are summarised.

KEYWORDS: Anura, Limnodynastidae, *Limnodynastes waterhousae*, ilium, Oligocene, Kangaroo Well Local Fauna, Northern Territory.

INTRODUCTION

The Late Oligocene Kangaroo Well Local Fauna was named by Stirton *et al.* (1968). It comprises a diverse faunal assemblage located on the Deep Well pastoral station, at the extreme north western extremity of the Lake Eyre Basin in the Northern Territory, and is approximately 40 km south of Alice Springs.

Megirian *et al.* (2004) provided an overview of the fauna, named the limestone surrounding the fossils the Ulta Limestone, and interpreted the climatic events during deposition. Amongst the diverse faunal elements, they reported that four species of frogs had been located there. One of these species was identified as the myobatrachid (now limnodynastid) *Limnodynastes* species. The other species are *Australobatrachus ilius* Tyler, 1976, *Australobatrachus* sp. and *Litoria* sp. Here the *Limnodynastes* species is described and compared with congeners. To aid ilial identification the principal features of all extant and extinct genera are tabulated. Terminology of ilial features follows that of Tyler (1976). The specimens are deposited in the Museum and Art Gallery of the Northern Territory (NTM).

SYSTEMATICS

Order Anura Rafinesque, 1815

Family Limnodynastidae Lynch, 1971

Genus *Limnodynastes* Fitzinger, 1843

Generic Definition: When the ilial characteristics were first defined by Tyler (1976), the genus included *L. ornatus* (Gray, 1842) and the closely related *L. spenceri* (Parker,

1940). These two species differed from all of the congeners examined in possessing a distinct dorsal crest and in having a moderately formed dorsal acetabular expansion, compared with a high and acutely pointed spike in congeners. Frost *et al.* (2006) removed these two species from *Limnodynastes* and resurrected *Opisthodon* Steindachner, 1867 for them. However, *Platyplectrum* Günther, 1863 takes priority, as noted by Tyler & Doughty (2009). As a consequence of the separation of *ornatus* and *spenceri*, the ilial definition of *Limnodynastes* must be modified:

The ilial shaft is slightly curved and bears a medial groove. The acetabulum is of variable size and bisected by the ventral margin of the ilial shaft. The ventral acetabular expansion is small and narrow. The dorsal acetabular expansion rises into a high and acutely pointed spike. The dorsal prominence is conspicuous and broad and rounded. The dorsal protuberance is level with or anterior to the anterior rim of the acetabulum.

Features of the ilia of all extant and extinct genera found in Australia are listed in Table 1.

Limnodynastes waterhousae sp. nov.

(Fig. 1)

Type material. HOLOTYPE (Fig. 1A) – NTM P.2692-14, proximal portion of a left ilium from Kangaroo Well, Deep Well pastoral station, Northern Territory, Australia (24°13.417'S, 134°12.717'E), 7 August 2002, D. Megirian. PARATYPE (Fig. 1B) – NTM P2780-11, fragment of the proximal portion of a right ilium, same data as holotype.

Description (based on holotype). The dorsal acetabular expansion is large, tapering and inclined at approximately 45° to ilial shaft (Fig. 1A). A distinct depression approximately

Table 1. Features of ilia of Australian frog genera. Data derived from Tyler (1976 and pers. obs.) except for *Etmabatrachus* and *Spicospina* which are derived from Hocknull (2005) and Roberts *et al.* (1997), respectively.

Genus	Iliac Shaft Crest	Iliac Shaft Rim	Dorsal Protuberance	Dorsal Prominence / Anterior Rim of Acetabulum
<i>Adelotus</i>	absent	present	prominent	anterior
<i>Arenophryne</i>	absent	absent	absent	level
<i>Assa</i>	absent	absent	inconspicuous	level
<i>Anstrabotrachus</i>	absent	absent	inconspicuous	anterior
<i>Austrochaperina</i>	absent	absent	inconspicuous	posterior
<i>Cophixalus</i>	absent	absent	inconspicuous	anterior
<i>Crinia</i>	absent	present or absent	moderate or inconspicuous	anterior
<i>Cyclorana</i>	absent	present or absent	inconspicuous	anterior
<i>Etmabatrachus</i>	absent	absent	inconspicuous	posterior
<i>Geocrinia</i>	absent	absent	absent	level
<i>Heleioporus</i>	absent	absent	prominent	anterior
<i>Hylophorbus</i>	absent	absent	prominent	posterior
<i>Lechriodus</i>	present	absent	moderate	posterior
<i>Limnodynastes</i>	absent	absent	prominent	anterior or level
<i>Litoria</i>	absent	present or absent	moderate	usually anterior
<i>Metaerinia</i>	absent	absent	absent	level
<i>Mixophyes</i>	present	absent	inconspicuous	anterior
<i>Myobatrachus</i>	absent	absent	absent	posterior
<i>Neobatrachus</i>	absent	absent	prominent	anterior
<i>Notaden</i>	absent	absent	prominent	posterior
<i>Nyctimystes</i>	absent	absent	moderate	level
<i>Paracrinia</i>	absent	absent	prominent	anterior
<i>Phyllorhina</i>	absent	present	prominent or inconspicuous	anterior
<i>Platyplectrum</i>	absent	present	inconspicuous	posterior
<i>Pseudophryne</i>	absent	absent	moderate	level
<i>Rana</i>	present	absent	inconspicuous	posterior
<i>Rheobatrachus</i>	absent	absent	prominent	posterior
<i>Spicospina</i>	absent	absent	inconspicuous	anterior
<i>Taudactylus</i>	absent	absent	prominent	anterior
<i>Uperoleia</i>	absent	absent	prominent	anterior

0.7 mm in length is located on the superior margin of the shaft directly above the anterior portion of the acetabulum. A conspicuous foramen is located anterior to this depression. The acetabular fossa is very large and shallow and lacks a detectable rim. The preacetabular expansion is very narrow and poorly developed and the dorsal protuberance is laterally disposed and very small. The distance from the tip of the dorsal acetabular expansion to the inferior termination of the iliac shaft is 4.6 mm. The length along the mid-section of the shaft is 3.02 mm.

Structurally the paratype differs in that it is partially less complete and slightly smaller than the holotype. The majority of the dorsal acetabular expansion is missing as is the preacetabular zone. However, the ventral acetabular expansion is more extensive than in the holotype, with a depth equivalent to two-thirds of the acetabular fossa. The maximum dimension of the paratype is 4.2 mm.

Comparison with other species. Although almost all of the iliac shaft is missing in both specimens, the proximal portion of the ilium displays sufficient features to permit adequate comparison with other Oligocene taxa. The most

similar is *Limnodynastes antecessor* Tyler, 1990, which is abundant at numerous sites of Oligo-Miocene age at Riversleigh in northwest Queensland, approximately 400 km northeast of Kangaroo Well. *Limnodynastes waterhousae* is distinguished by its more acute dorsal acetabular expansion, less prominent dorsal prominence, less developed acetabular rim and narrower preacetabular zone.

There is a slight resemblance between *L. waterhousae* and the extant *L. peronii* (Duméril & Bibron, 1841), which is also known from the Mid-Pleistocene of New South Wales (Tyler *et al.* 1998) and from the late Cenozoic of central Queensland (Hocknull 2005). The latter species differs in having a shorter dorsal acetabular expansion, and its inclination to the tibial shaft is more obtuse.

Limnodynastes archeri Tyler, 1982 was described from the Oligocene Etadunna Formation of South Australia, but it resembles *P. ornatum* very closely and it is now evident that it should be referred to *Platyplectrum*.

Etymology. Named for Lyn Waterhouse of the Microscopy Unit at the University of Adelaide, to whom the author is indebted for the SEM figures of the frog ilium

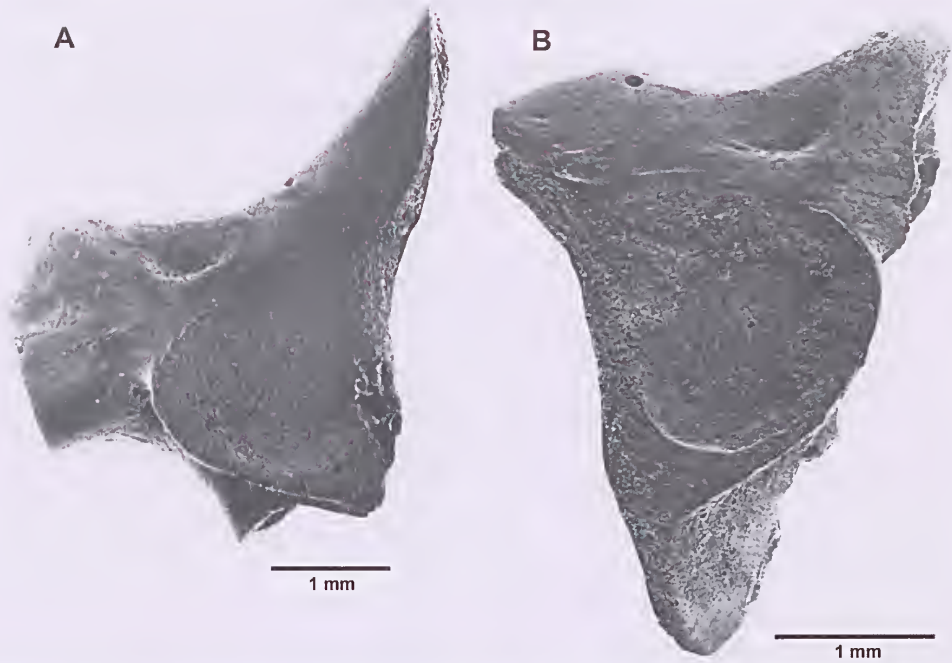


Fig. 1. SEM photographs of type material of *Limnodynastes waterhousae* sp. nov.: A, holotype (NTM P.2692-14), proximal portion of left ilium; B, paratype (NTM P.2780-11), proximal portion of right ilium.

in this paper and numerous other figures that have been published elsewhere.

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I am deeply indebted to the late Dirk Megirian who initiated my interest in the frog fossil fauna of the Northern Territory. His friendship and support have been vital to my involvement and he was in total agreement that the new species should be named after Lyn Waterhouse. I am indebted to Régis Martin and Richard Willan for their valuable contribution in improving the quality of the figure.

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Short Communication

Notes on the identity, distribution and conservation status of the threatened plant species *Utricularia singeriana* F. Muell. (Lentibulariaceae)

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Collection and examination of considerable *Utricularia* material from the Northern Territory over the last 15 years has provided a better understanding of morphological variation and allowed further interpretation of diagnostic characters in *Utricularia singeriana* F. Muell., among others. It is here regarded as a Northern Territory endemic species restricted to the Darwin-Katherine area while the specimens from Western Australia (WA) formerly attributed to *U. singeriana* are considered to be a distinct, probably undescribed, taxon requiring further collecting and research.

Taylor's (1989) revision of the genus *Utricularia* revealed that the Northern Territory (NT), especially the sandy, poorly drained lowlands found in parts of the western Top End, is a world centre of diversity for the genus with some 36 species in total. Since that time, an additional small-flowered species has been described and the distribution of a number of NT species has been extended to the Kimberley region and *visa versa* (Lowrie *et al.* 2008). At the time of Taylor's work *Utricularia holtzei* F. Muell., *U. singeriana* F. Muell., *U. triflora* P. Taylor and a number of other NT species were known from very few collections. Among these, *U. singeriana* was described by Taylor as occurring near Darwin, (the type specimen – N. Holtze 1026 and Bleeser 212) and in the Kununura – Wyndham area of WA (Glover 81 & 82). While Taylor visited the NT and studied a number of species in the field, *U. singeriana* appears not to have been among these. Although the Darwin subpopulation has not been relocated since Bleeser's (1926) collection, several more populations have been discovered in the Edith – Fergusson River area, north of Katherine over the past ten years (Kerrigan & Cowie 2007). Recently (May 2010), an additional subpopulation was discovered near the Finnis River (K. Brennan pers. comm.). The species has been collected in flower from mid-March to late May and is known to occur along the seasonally waterlogged margins of drainage flats amongst a relatively sparse grass layer. Examination of the type specimen, plants in the field and considerable extra dried and spirit material has provided a better understanding of morphological variation and allowed further interpretation of diagnostic characters. Collections examined were: Brennan 6535, 8632; Cowie 12540; Egan

5141; Gibbons 41 & Cowie; Holtze 1026; Kerrigan 434; and Michell 2699.

The additional collections reveal that in *U. singeriana* the leaves are oblanceolate to spatulate and apically obtuse while the upper calyx lobe is widely ovate or obovate and the lower lobe is depressed-ovate and 2.5–4 mm wide. The spur of the corolla is patent to ascending, almost appressed to, or diverging at less than 30° from, the lower lip, 6–8 mm long, and at least in fresh flowers more than half the length of the lower lip and often slightly exceeding it. At the base, it is tetragonous in cross section, 3.5–4 mm wide and tapers relatively abruptly to a narrow, retuse, dorso-ventrally flattened apex (Figs 1, 2). The lower lip is 6–11 mm long with the pattern of veins radiating from the palate forming two longer central areoles with a group of three, sometimes four, shorter areoles either side of these. Outside of these shorter areoles lie three longer areoles. The upper lip is 9–12 mm long and the veins form four long, prominent areoles extending from the base for two-thirds of its length. In some collections these areoles are paler and clearly raised from the surface (Cowie 12540; Kerrigan 434). Moreover, the fresh corolla is a rich purple in the field and very dark in colour in dried specimens, even in the type which was collected in 1890. In the field, the corolla lips are held almost parallel to the ground.

Examination of Glover 81 reveals a number of characters that distinguish it from *U. singeriana*. It has very narrowly elliptic, acute leaves, the corolla spur is only 2 mm wide at its base and it diverges widely from the lower lip while the dried corolla is pale in colour (Fig. 3). In addition, the lower calyx lobe is ovate, the spur is 4–4.5 mm long, less than half the length of the lower lip which is 12–12.5 mm long, while the upper lip is only 5–6.4 mm long and lacks distinctive long, prominent areoles. Glover 82 is illustrated in Taylor (*loc. cit.*) and this illustration reveals that it also has a widely divergent corolla spur which is less than 2 mm deep at the base and that the patterns of the veins radiating from the palate form a single longer central areole with a group of four shorter areoles either side. Also the illustration of the upper lip is approx. 4.5 mm long and does not show distinctive long areoles. In addition, the two Glover collection localities are geographically disjunct by some



Fig. 1. Flower of *Utricularia singeriana*. A. Showing the relatively long upper lip with prominent areoles in the venation. The retuse apex of the spur can be seen just protruding from beneath the lower lip. B. Lateral view of flower showing the sub-planar orientation of the corolla lobes and the pale, tapering spur almost adpressed beneath the lower lip. The lower lip is 17 mm wide and the spur approx. 8 mm long. (I. D. Cowie 12540).

380 km from the nearest NT localities. While the taxon represented by these two collections needs further collection and research to determine its identity, it is clearly distinct from *U. singeriana*.

Utricularia singeriana is currently listed as Vulnerable under the *Territory Parks and Wildlife Conservation Act (NT)*, due to its small population size and restricted distribution. It is not listed under the *Commonwealth Environment Protection and Biodiversity Conservation Act*, as the taxon has previously been regarded as occurring in both Western Australia and the Northern Territory (Kerrigan & Cowie 2007). As these authors note, the type population from near Darwin probably no longer exists and was apparently quite localised. Nicholas Holtze noted on his collection (No. 1026) that it was “So far only known [from] one small sandy flat (near Palmerston) of a few hundred square yards, where this species is to be found,



Fig. 2. A backlit flower from the holotype of *Utricularia singeriana* showing the typical relatively long, broad-based corolla spur against the lower lip. The lower lip is 19 mm wide. (N. Holtze 1026).



Fig. 3. *Utricularia* sp. from near Kununurra, WA. Note the short, relatively narrow spur which diverges widely from the lower lip, and the relatively short upper lip. Scale divisions = 0.5 mm. (Glover 81).

but there it grows very plentifully.” Three known extant subpopulations are restricted to the upper Fergusson River area between Pine Creek and Katherine with two in Nitmiluk National Park. The fourth extant subpopulation is on Wagait Aboriginal land and appears localised, extending in a narrow zone along the edge of a drainage flat for a distance of some 50 m. Despite an intensive survey of *Utricularia* species in the Darwin rural area, and parts of Litchfield and Kakadu National Parks extending over several wet seasons, no additional subpopulations were located (Kerrigan & Cowie 2007). However, comparatively little survey work specifically targeted at *Utricularia* species has been conducted within the southern and western part of the range of *U. singeriana*.

Thus, it is appropriate that the Northern Territory conservation code of Vulnerable should now be applied at the National level. While in the past, species-specific survey has been hampered by lack of knowledge of habitat requirements, this has become less of an issue with additional collecting. It is likely that further surveys in the late wet to early dry season using appropriate methodology would reveal other subpopulations, at least in the Fergusson and Finnis River areas.

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GUIDE TO AUTHORS

A comprehensive style guide is available from the Editor (e-mail: richard.willan@nt.gov.au), on the internet (<http://www.nt.gov.au/nreta/museums/magn/publications/index.html>) or at the postal address for the Editor provided on the inside front cover. Manuscripts not in *The Beagle* style will be returned to authors for revision.

Manuscripts should be submitted electronically as e-mail attachments in MS Word format. Manuscripts should be in English, double or 1.5 line spaced throughout, and have a margin of at least 3 cm on the left-hand side.

Where appropriate, articles should conform to the sequence: Title, Author's name and address, Abstract, Keywords, Introduction, Materials and Methods, Results/Findings, Discussion, Conclusions, Acknowledgments, References, Appendices.

The Title should be concise and informative.

The Abstract should not exceed 150 words, and should state concisely the scope of the work and give the principal findings.

Keywords to facilitate information retrieval, of up to 15 in number, should be chosen to outline the main subjects covered.

The Introduction, including a review of literature, should not exceed what is necessary to indicate the reason and significance of the work, and to provide the essential background. Abbreviations used may be explained at the end of the Introduction, or placed separately in a Materials and Methods section.

The International System of units should be used.

Numbers from one to nine should be spelt out and numerals used for numbers over nine. For associated groups, numbers should be expressed consistently, e.g. 5 to 10, not five to 10.

Systematic papers must conform to the International Codes of Zoological or Botanical Nomenclature, as appropriate, and should follow the recommendations of the respective Commissions.

Synonymies should be given in the short form (taxon author, date: page) and the full reference cited in the References section at the end of the paper. Subsequent citations of taxa given in synonymies should be separated from the original and from each other by an em dash (—) as in the following examples:

Acanthella pulcherrima.—Capon & Macleod 1988.

Bougainvillia balei Stechow, 1924: 58.—Stechow 1925: 199, fig. B; Watson 1996: 78.

(Note that a comma is only used between the original author and date of the taxon.)

In the general text, citation of taxonomic authorities (name only, no date) should be given when a taxonomic name is first mentioned; such citations should not be listed in the References.

List Material Examined in the sequence: country or principal geographic region, number of specimens (followed, in brackets, by data pertaining to these specimen(s) if necessary, such as sex, size, number of segments, condition), institutional acronym and registration number, detailed locality (in descending order), co-ordinates (in degrees and decimal minutes), depth / habitat, collector, date (with months written in full). Note that all data are separated by commas within a single entry.

An example for a terrestrial or freshwater lot would be – NORTHERN TERRITORY: 1 (male, 12 mm), NTM P.530, approx. 6 km S Oenpelli, 12°50.222'S, 130°50.222'E, in low-lying inundated loamy soil at base of boulders, coll. C.R. Dunlop, 26 September 1947. An example for a marine lot would be – NORTHERN TERRITORY: 1 (male, 12 mm), NTM P.530, Darwin Harbour, Lee Point, 12°50.222'S, 130°50.222'E, 5 m, in coarse sand pocket on coral reef, coll. C.R. Dunlop on R.V. *Calypso*, 26 September 1947.

Lengthy lists of Material Examined can be shortened to number(s) of specimens and institutional acronym and registration number as follows – NORTHERN TERRITORY: 1 (male, 12 mm), AM C.530; 1 (male, 12 mm), NTM P.5303; 5 (males), etc.

TABLES

Tables should be numbered with Arabic numerals and accompanied by a caption. Horizontal rules are inserted only above and below column headings and at the foot of the table. Footnotes to tables should be kept to a minimum and be reserved for specific items in columns. All other explanatory material should be incorporated in the caption.

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Crowley, L.M. 1949. *Working class conditions in Australia, 1788–1851*. Unpublished PhD thesis. University of Melbourne.

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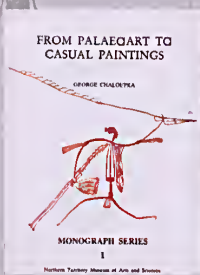
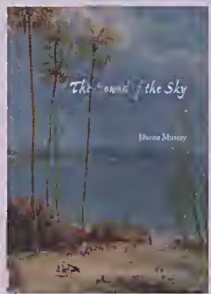
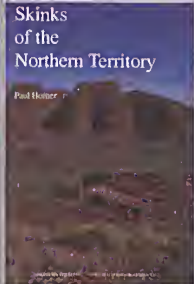
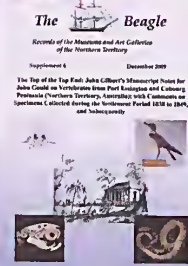
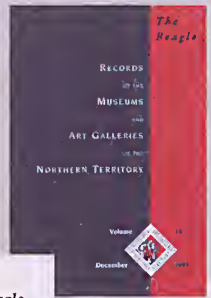
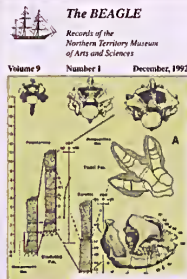
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Records of the Museums and Art Galleries of the Northern Territory

Volume 26, December 2010

CONTENTS

SHORT, P.S. – New species of <i>Cleome</i> L. (Cleomaceae) from the Northern Territory, Australia	1
ALVAREZ, B. and HOOPER, J.N.A – Taxonomic revision of the order Halichondrida (Porifera: Demospongiae) of northern Australia. Family Dictyonellidae	13
WATSON, C. – Revision of the pantropical genus <i>Treptopale</i> (Annelida: Phyllodocida: Chrysopetalidae): redescription of <i>Treptopale rudolphi</i> Perkins, 1985 and description of two new species including comparison of <i>Treptopale</i> populations in northern Australia	37
GLASBY, C.J. and HOCKNULL, S.A. – New records and a new species of <i>Hermundura</i> Müller, 1858, the senior synonym of <i>Loandalia</i> Monro, 1936 (Annelida: Phyllodocida: Pilargidae) from northern Australia and New Guinea	57
BRUCE, A.J. – <i>Typtonoides nieli</i> gen. nov., sp. nov., a new pontonine shrimp (Crustacea: Decapoda: Palaemonidae) from the Chesterfield Islands	69
BRUCE, A.J. – <i>Lebbeus rubrodentatus</i> sp. nov. (Crustacea: Caridea: Hippolytidae) from the Australian North West Shelf	75
SALGADO-KENT, C. and MCGUINNESS, K. – Spatial and temporal variation in relative numbers of grapsid crabs (Decapoda: Grapsidae) in northern Australian mangrove forests	79
BROWN, G.R. – <i>Curvothynnus</i> gen. nov. erected for two unusual species of thynnine wasps (Hymenoptera: Thynnidae: Thynninae: Rhagigasterini)	89
BROWN, G.R. – Two new orchid-pollinating wasps (Hymenoptera: Thynnidae) from Australia	97
BAEHR, M. – A new species of the genus <i>Microlestodes</i> Baehr from Arnhem Land, Northern Territory, Australia (Insecta: Coleoptera: Carabidae: Lebiini)	103
BERRA, T.M. – Clarification of field characters for three freshwater sharks and a photographic atlas of <i>Glyphis glyphis</i> and <i>G. garricki</i> from the Adelaide River, Northern Territory, Australia	109
TYLER, M.J. – A new fossil species of frog of the Australian limnodynastid genus <i>Limnodynastes</i> Fitzinger from the Oligocene Kangaroo Well Local Fauna of the Northern Territory and tabulation of ilial features of all extant and extinct species	115
Short communication	
COWIE, I.D. – Notes on the identity, distribution and conservation status of the threatened plant species <i>Utricularia singeriana</i> F. Muell. (Lentibulariaceae)	119
Guide to authors	122