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Front cover: Helicteres serpens, a new species of creeping plant, is endemic to the northern part of the Northern Territory (see Cowie, pages 48-49). Drawing by Monika Osterkamp.
CONTENTS

BROCKWELL, S., BOURKE, P., CLARKE, A., CRASSWELLER, C., FAULKNER, P., MEEHAN, B., O’CONNOR, S., SIM, R. and WESLEY, D. – Holocene settlement of the northern coastal plains, Northern Territory, Australia ................................................................. 1

JACKES, B.R. – The vine *Embelia tiwiensis* (Angiospermae: Myrsinaceae), a new species from the Northern Territory, Australia ................................................................. 23

COWIE, I.D. – New taxa and notes on *Helicteres* L. (Malvaceae: Helicteroideae) from the Northern Territory, Australia ................................................................. 27

ALVAREZ, B. and HOOPER, J.N.A. – Taxonomic revision of the order Halichondrida (Porifera: Demospongiae) of northern Australia. Family Halichondriidae ................................................................. 55

BRABY, M.F. – New larval food plant associations for some butterflies and diurnal moths (Lepidoptera) from the Northern Territory and eastern Kimberley, Australia ................................................................. 85

BROWN, G.R. – *Dimorphothynmis* (Hymenoptera: Thynnidae: Rhagigasterini) newly recorded from the Northern Territory, Australia ................................................................. 107

BRUCE, A.J. – *Periclimenaeus pullitzerafiniali* sp. nov., a new pontoniine shrimp (Crustacea: Decapoda: Palamonidae) from East Africa ................................................................. 113

DAVIE, P.J.F. – A new species and new records of *Oncinopus* (Crustacea: Brachyura: Inachidae) from northern Australia ................................................................. 123

REID, A. – *Empyrura pardalota* sp. nov. (Cephalopoda: Sepiolidae), a new dumpling squid from northern Australia ................................................................. 135

NIELSEN, J.G. and SCHWARZHANS, W. – A new genus and species of Bythitidae (Teleostei: Ophidiiformes) from northwestern Australia ................................................................. 143

SCHWARZHANS, W. and NIELSEN, J.G. – Revision of the genus *Microbrotula* (Teleostei: Bythitidae), with description of two new species and a related new genus ................................................................. 147

SCHWARZHANS, W. and MOLLER, P.R. – New Dinematichthyini (Teleostei: Bythitidae) from the Indo-west Pacific, with the description of a new genus and five new species ................................................................. 161


TAKITA, T., LARSON, H.K. and ISHIMATSU, A. – The natural history of mudskippers in northern Australia, with field identification characters ................................................................. 189
Holocene settlement of the northern coastal plains, Northern Territory, Australia

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ABSTRACT

The northern Australian coastal plains are relatively recent landforms that have undergone dynamic evolution over the last 10,000 years. Over 300 radiocarbon dates have enabled archaeologists and geomorphologists to provide a more detailed interpretation of human settlement and resource use. This paper provides a synthesis of the archaeological evidence and integrates it within the palaeo-environmental frameworks. It characterises the timing, pattern and nature of human-environment interaction in this newly formed landscape over the last 10,000 years.

KEYWORDS: Northern Australia, coastal plains, landforms, anthropology, archaeology, radiocarbon dates, human settlement, resource use.

INTRODUCTION

Following the post-Pleistocene marine transgression, broad plains formed along coastal northern Australia and continued to develop throughout the Holocene through processes of sedimentation and coastal progradation. They contain large tidal flats and salt pans interspersed with cheniers and are drained by substantial rivers with extensive floodplains and estuaries (Lees & Clements 1987: 312).

There has been considerable archaeological and geomorphological work undertaken on the Northern Territory coastal plains, although mostly independent of each other. The notable exceptions are joint studies on the South Alligator River (Hope et al. 1985; Woodroffe et al. 1988), the Blyth River by John Chappell and Rhys Jones (unpublished data), and the Sir Edward Pellew Group (Prebble et al. 2005). The geomorphological evidence demonstrates that the coastal plains of northern Australia are relatively recent formations that have undergone dynamic evolution from the mid to late Holocene. Studies have been carried out on the Victoria and Daly Rivers in the west, Darwin Harbour, the Adelaide, Mary and South Alligator Rivers, Magela Creek, Blyth River, and Groote Eylandt and the Edward Pellew islands in the east (Fig. 1). The evolutionary sequence of the coastal plains was similar right across the Northern Territory, the differences being caused by topography and timing.

How did humans respond to these newly created landscapes? This question has been addressed by an extensive body of research over the past 40 years focused on the archaeology of the Northern Territory coastal plains. The early research effort was concentrated mainly in the Alligator Rivers region of what is today Kakadu National Park (Kamminga & Allen 1973; Schrire 1982; Jones 1985; Allen & Barton 1989), but the last 15 years has seen many other regions investigated. As a result of this research, many more radiocarbon dates have become available, providing an emerging pattern of Holocene settlement across the coastal plains of the Top End as a whole. This paper presents a synthesis of these new data to provide an overview of the chronology of occupation and the changing nature of the archaeological record, which includes several different site types – rockshelters, shell mounds, shell middens, earth mounds, artefact concentrations and contact sites.
In addition, information about palaeoclimates and the geomorphological evolution of the northern coastal plains is summarised to provide the environmental framework for the archaeological data. Visibility plays a major role in site location. Archaeological sites are difficult to observe in some coastal environments such as lateritic plains and swampy areas. During the marine transgression, former shorelines and associated archaeological evidence were submerged (Woodroffe et al. 1988). As well, the extensive nature of mangrove cover during the Big Swamp phase may have almost completely removed evidence of occupation, most of which for this period is found in rockshelters. Open sites proliferated after sea level stabilisation approx. 6000 years ago, which is almost certainly a function of improved visibility.

**PALAEOCLIMATE**

It is widely acknowledged that there has been an increase in climatic variability in the Australasian region in the last few thousand years, in particular from approximately 1000 BP to the present (Kershaw 1983; Wasson 1986; Gagan et al. 1994; Kershaw 1995; Shulmeister 1999; Gagan & Chappell 2000; Prebble et al. 2005; Wasson & Bayliss 2010; Williams et al. 2010). Many of the longer-term trends in climate change that have occurred during the period spanning the mid Holocene to the present day are related to the El Niño/Southern Oscillation (ENSO) cycle, which has strongly influenced climatic patterns in Australia (McGlone et al. 1992; Shulmeister & Lees 1992; Jones et al. 1999; Shulmeister 1999; Gagan et al. 2004; Turney & Hobbs 2006), and at present represents the principal source of inter-annual climatic variability within the Indo-Pacific region (Glantz 1991; Diaz & Markgraf 1992; Allan et al. 1996; Rowland 1999) (Fig. 2).

The pattern of climatic shifts portrayed in recent reviews of the climate history of the South Pacific region indicates a change from low seasonality in the early Holocene to increased seasonality in the late Holocene (Markgraf et al. 1992; Shulmeister 1999). There also appears to be a general trend toward increased aridity in the mid to late Holocene, as supported by data extracted from coral, foraminifera, and varve, lake and sea bottom sediments from sites in Australia and the circum-Pacific region (McPhail & Hope 1985; Brookfield & Allan 1989; Singh & Luly 1991; McGlone et al. 1992; Hope & Golson 1995; Kershaw 1995; Nott et al. 1999; Rodbell et al. 1999; McCarthy & Head 2001; Kim et al. 2002; Koutavas et al. 2002). Evidence from pollen records on Groote Eylandt are also indicative of this environmental change from continuously increasing rainfall (effective precipitation) during the early Holocene, to a period of reduced rainfall and increased climatic variability after 4000 BP (Shulmeister & Lees 1995). In the Groote Eylandt archipelago, effective precipitation declined sharply soon after 3700 BP, with evidence across Australia indicating that climate became more variable after this time (Shulmeister & Lees 1995). Geomorphic data from cheniers and coastal dunefields (Lees & Clements 1987; Lees et al. 1990; Lees 1992; Lees et al. 1992) indicate that some of the observed changes in these systems were synchronous across northern Australia, and may represent coherent, broad-scale climatic signals (Shulmeister 1999; Prebble et al. 2005) (Fig. 2).
Holocene settlement of northern Australian coastal plains

The dated archaeological sites are located roughly in five regions - (1) the West Coast represented by the Reynolds River (Guse & Majar 2000; Guse 2005); (2) the Darwin Region, including Darwin Harbour, Hope Inlet (Hiscock 1997; Bourke 2000; Hiscock & Hughes 2001; Crassweller 2002; Bourke 2004, 2005a, 2005b; Bourke & Crassweller 2006; Crassweller 2006); the Adelaide River (Smith 1995; Crassweller 1996; Brockwell 2001, 2006a, 2009) and Mary River (Baker 1981; Guse 1992); (3) western Arnhem Land, including the Alligator Rivers and Magela Creek (Schrire 1982; Mechan et al. 1985; Woodroffe et al. 1988; Allen & Barton 1989; Roberts et al. 1990; Mowat 1995; Roberts et al. 1998), Bald Rock and Malarrak in the Wellington Ranges (May et al. 2010) and the Cobourg Peninsula (Mitchell 1994a, 1994b, 1996); (4) central Arnhem Land represented by the Blyth River and Milingimbi (McCarthy & Setzler 1966; Mulvaney 1975; Mechn 1982, 1988, 1991; Roberts 1991, 1994; Brockwell et al. 2005); and (5) eastern Arnhem Land along the east coast of the Gulf of Carpentaria, including Cape Arnhem (Bourke 2001); Port Bradshaw (Schrire 1972), Blue Mud Bay (Faulkner & Clarke 2004; Faulkner 2006, 2008, 2009; Faulkner & Clarke 2009), Groote Eylandt (Clarke 1994; 2000a, 2000b; Clarke & Frederick 2006; 2008, 2011) and the Edward Pellew islands (Sim 2002; Prebble et al. 2005; Sim 2005; Sim & Wallis 2008) (Fig. 1).

The landscape covered by the study areas is diverse and includes: dissected sandstone and lateritic plateaux bordering the coastal plains; large rivers and creeks; immense floodplains containing vast freshwater wetlands; and saline mudflats further towards the coast. Mangrove forests fringe coastal cheniers and tidal mudflats, headlands protrude onto coastal salt flats, mixed woodland dominates on slopes and plains. There are large stretches of open mixed woodland, broad sandy beaches and extensive dune fields, pockets of monsoon rainforest, and grassland, broad sandy beaches, shallow bays and off-shore islands, some substantial in size that can sustain permanent human populations.

ARCHAEOLOGY AND CHRONOLOGY

This complex landscape is reflected in the archaeology, which consists of numerous occupied rockshelters dating back to the Pleistocene (Kamminga & Allen 1973; Schrire 1982; Jones & Johnson, 1985a, 1985b; Allen & Barton 1989, Roberts et al. 1990, 1998), thousands of panels of magnificent rock art in the escarpment and outliers on

Dates have been calibrated in order to ensure a robust comparison of the conventional radiocarbon ages from different regions and the different site types. Over 300 radiocarbon dates are now available. Details of calibration methods and a tabulated list of dated sites can be found in Brockwell et al. (2009). Evidence from rockshelters suggests that Aboriginal people began to occupy and use the resources of the coastal plains at the time of their formation over 10,000 years ago, but the majority of sites are 4000 years or younger. Fig. 3 illustrates chronology by location. On the basis of the environmental evidence, the archaeology can be divided into five temporal periods:

**10,000–6000 BP.** Evidence of occupation on the coastal plains has been dated from the early to mid Holocene period, encompassing the time of rising sea levels and the ‘Big Swamp Phase’. Effective precipitation and temperature were gradually increasing during this phase. During the post-Pleistocene transgressive phase, the down-cut river valleys of northern Australia were drowned. The various river systems responded differently to this event. Some, like Darwin Harbour, became deep-water embayments. Others, through processes of sedimentation, formed vast mangrove swamps. This has been described as the ‘Big Swamp Phase’ and dates from about 7000 BP to approx. 4000 BP (Woodroffe et al. 1985, 1986; Chappell 1988; Woodroffe 1988; Woodroffe & Mulrennan 1993) (Fig. 4).
Allen (1996: 198, 201; Allen & Barton 1989: 104) made the point that the mangrove forests of the Big Swamp Phase would have presented a formidable barrier to movement and settlement. Access to the river channels and the coastal plains may have been impossibly difficult. The distribution of sites during the Big Swamp Phase in western Arnhem Land reflects this situation and is consistent with Allen and Barton’s prediction that “Seasonal movement and sites would have been restricted to the plateau valleys, the plateau margins, and the lowland corridors between the tidal floodplains” (Allen & Barton 1989: 104).

This period is represented by cultural sequences mainly from rockshelters and two middens. In the west, Djagorda 2 shelter on the Reynolds River contained a low density of stone artefacts (Guse 2005: 113). At the edge of floodplains in sub-coastal western Arnhem Land, the lower levels of Nawamoyn and Ngarradj Warde Djobkeng shelters in the Alligator Rivers region were dominated by estuarine shellfish soon after the establishment of the vast mangroves of the Big Swamp Phase approx. 7000 BP (Kamminga & Allen 1973: 45–47; Schrire 1982: 85–97, 118–30; Allen & Barton 1989: 89). At Nawamoyn and Malakunanja II fragments of mammals (open woodland), fish (unidentified) and reptiles (woodland) occurred throughout the midden levels, as did stone artefacts and bone tools (mostly spatulate points at Nawamoyn). There were human burials in Nawamoyn and Malakunanja II. Malarrak and Bald Rock in the Wellington Ranges were first occupied in the Pleistocene and appear to have been occupied throughout the Holocene (May et al. 2010). Although not dated, the base of the deposit at Borngolo Shelter in eastern Arnhem Land contains marine fauna, which Schrire (1972: 662) surmises is consistent with occupation after sea level stabilisation 6000–7000 years ago. Also in eastern Arnhem Land, the lower levels of Mushroom Rock (VB17) and Wobuya Shelter (WS) on Vanderlin Island in the Edward Pellew islands contain stone artefacts and the remains of shellfish from mangroves and open mudflats (Sim & Wallis 2008: 102) (Fig. 5). During this period, the Edward Pellew islands were still attached to the mainland. Following the post-glacial marine transgression, the islands appear to have been abandoned approx. 6700 years BP and not reoccupied until 4200 years ago (Sim & Wallis 2008: 102).

In western Arnhem Land, one date was taken from a midden (Kapalga P) buried on the lower South Alligator River floodplains, which is dominated by the mangrove shellfish *Telescopium telescopium*. The substrate contains mangrove wood from the Big Swamp Phase (Woodroffe et al. 1988: 97). Muyu-ajirrapa midden on the Blyth River in central Arnhem Land was also dated to this period. However, there may be a problem with this charcoal date, as its shell pair was much younger. The midden is dominated by *Dosinia sp.*, an open beach species that proliferates in sandy mudflats.

Although direct correlation of art styles, climatic phases and Aboriginal settlement is problematic, it has been argued that the pattern of settlement and economic organisation described above is reflected in the rock art, and can suggest
The period 6000–4000 BP encompassed sea level stabilisation and the decline of the ‘Big Swamp Phase’. Following the cessation of sea-level rise approx. 6000 BP, sedimentation and coastal progradation resulted in vertical accretion of the floodplains, and caused the development of extensive coastal plains. Effective precipitation and temperature continued to increase until approximately 5000 BP. With the decline of tidal influence, mangroves retreated seawards and towards the banks of the rivers and had mainly disappeared from the floodplains by 4000 years BP (Woodroffe et al. 1988: 98; Woodroffe & Mulrennan 1993) (Fig. 4).

There are dates from rockshelters, shell mounds and earth mounds during this period. On the Reynolds River, three Tabletop Range rockshelters, Djagorda 2 and Walker Creek 6, were excavated. Although only Majar was dated to this period, dates and rates of deposition from these sites imply an increasing site usage in the region after 4500 BP. There was also a large increase of stone artefacts deposited at Majar approximately 4000 years ago (Gusc 2005: 97).

In western Arnhem Land, there is a marked decrease in the mangrove-associated shellfish *Polymesoda erosa* and *Telescopium telescopium* and an increase in *Cerithidea* sp. [probably *C. anticipata*] between the lower and upper midden levels at Malangangerr and Nawamoynt (Schrire 1982: 88–89, 120–22, 233–34; Hiscock 1999: 94–95), linking these sites to the decline of the Big Swamp Phase. *Telescopium telescopium* prefers a *Rhzophora* mangrove habitat, which dominated in the Big Swamp Phase. Similarly, *Polymesoda erosa* is likely to be more abundant in *Rhzopora* forests where it is found along small streams. *Cerithidea* sp. can be gathered in large numbers from the trunks of *Avicennia* and *Bruguiera* mangrove trees, which survive in drier conditions, and replaced *Rhzophora* at the end of the Big Swamp Phase in archaeological sites in western Arnhem Land (Hiscock 1999: 95–96). Malangangerr and Nawamoynt contain many bone tools, with an increase in bipoints in the upper midden levels (Schrire 1982: 85–97). Based on ethnographic evidence, which associates bone uni and bipoints with multi-pronged spears used for fishing in western Arnhem Land, Schrire (1982: 63, 95, 249) speculates that this pattern indicated a shift from exploitation of mangrove/mudflat shellfish to a greater reliance on fishing towards the end of this period.

Malakunja II contains a similar range of fauna to Malangangerr. It also contains burials (Kamminga & Allen 1973: 45–46). Allen & Barton (1989: 90) argue that the dating of the top spit of Malakunja II to the latter part of this period indicates that this site was mostly abandoned coexistent with the retreat of the mangroves. Unifacial and bifacial stone points first appeared in the sands below the midden at Ngarrad in 4862 – 3837 cal. BP (Allen & Barton 1989: 93). As Allen and Barton said of the rockshelters in western Arnhem Land, "The fact that every date that can be reliably associated with the mangrove/mudflat shell middens at these sites falls between 3000 and 7000 years BP suggests a high degree of correlation between the archaeo logical record and the geomorphological evidence for the local occurrence of mangroves" (1989: 90).
Holocene settlement of northern Australian coastal plains

Fig. 6. Dynamic figure. Photograph: Daryl Wesley.

Birds) (Schrire 1972: 662, 665). There is no evidence for occupation during this period at Vanderlin Island in the Edward Pellew islands, which appears to have been abandoned just before it was truncated from the mainland by rising sea levels (Sim & Wallis 2008: 102).

Anadara-dominated shell mounds begin to appear during this period in the west at Werat 1 on chenier ridges of the coastal plains of Reynolds River (Gusc 2005: 114), and on Field Island 1 and 2 in western Arnhem Land (Hiscock & Mowat 1993; Mowat 1995: 154–55). This pattern reflects exploitation of beach species from open sandy mud flats, the preferred habitat of Anadara granosa. On the West Alligator River some undated shell mounds were dominated by Anadara granosa, and others by open beach species such as Marcia hiantina and Circe sp., which suggests that the occupants were exploiting open mud and sandy beaches extant in the mid-Holocene (Mowat 1995: 154–55). Variability in species composition between these mounds is linked to the formation of mounds at different times and reflects changing environmental conditions along the coast in the mid to late Holocene (Mowat 1995: 154, 163). Mowat (1995: 163) concludes that the coastal areas were not abandoned as conditions changed, but rather the inhabitants adapted their foraging strategies accordingly. Hiscock (1999: 96) observes that the existence of shell mounds from different regions indicates widespread foraging along the coast at this time.

The base of earth mound HD1 on the now sub-coastal portion of the Adelaide River floodplains contains estuarine shell associated with the Big Swamp Phase (Brockwell 2006a); and while data about shell species were not collected, Woodroffe et al. (1988: 97) record grindstones, hammerstones and manuports from the surface mound Kapalga H2 on the black soil plains of the lower South Alligator River in western Arnhem Land, which elsewhere has been classified as an earth mound (Brockwell 2006b).

At Point Stuart on the mouth of the Mary River, Baker (1981: 79) infers a date of 4500 years BP for a midden located on a chenier ridge on the basis of geomorphological investigations. In the lower levels Telescopium telescopium and Crassostrea sp. dominate the midden. These estuarine species inhabit stands of Rhizophora mangroves, which were extant on the floodplains during the Big Swamp Phase.

Rock art during this period, such as ‘Simple Figures with boomerangs’ and ‘Yam Style Figures’ (Chaloupka 1985), shows increasing diversity and regionalisation (Taçon 1993: 114; Taçon & Chippindale 1994: 217). Early X-ray art also appears. It shows simple internal features and is dated to a minimum age of 4000 years BP, based on radiocarbon dating of beeswax from a rockshelter in western Arnhem Land (Nelson et al. 1995; Waterman & Jones 2002). A greater diversity of animal species is depicted, including those from the estuarine floodplains of the Big Swamp, such as barramundi (Lates calcarifer), eel (Arias sp.) and estuarine crocodile (Crocodylus porosus) (Chaloupka 1985: 277; Lewis 1988: 50–55; Chaloupka 1993: 162; Taçon 1993; Taçon & Chippindale 1994: 217; Chippindale & Taçon 1998: 107). There are changes in
material culture too. Boomerangs, associated with hunting large animals on open plains, disappear and new weapons make their appearance, including spear-throwers, spears with hafted spear points and three-pronged spears associated with fishing (Chaloupka 1985: 277; Lewis 1988: 55, 96; Chaloupka 1993: 146; Taçon & Chippindale 1994: 224; Chippindale & Taçon 1998; Brockwell & Akerman 2007).

It is suggested that large battle scenes depicted in the art of this period may reflect more tightly organised societies in conflict over access to resource bases (Taçon & Chippindale 1994: 224–225). Lewis (1988: 90) suggested that conflict might have been created by the drowning of coastal land by rising seas and forced migration inland onto other territorial land, although there is no direct evidence for this. It is also suggested by some authors that the Yam Figures might be associated with rising seas (Chaloupka 1985; Lewis 1988; Chaloupka 1993: 138–145; Taçon & Chippindale 1994; Taçon et al. 1996). Chaloupka (1985: 276) argued that yams need over 120 cm of rainfall to thrive and may have been an important staple replacing grass seeds in the preceding drier period. He also comments that the break from both previous and subsequent styles was such that it implies major ideological and cultural shifts (1993: 143). Likewise, Taçon et al. (1996) argue that the appearance of the Rainbow Serpent motif, a hugely important feature of current mythology, was associated with increased rainfall and sea-level rise in the mid-Holocene. Taçon & Brockwell (1995: 25) point out that land lost to rising water was probably observable in a lifetime. Taçon et al. (1996: 117) argue that “ultimately, the most unusual aspects of change – snakes slithering away from drowning landscapes, rainbows overhead and strange ‘new’ creatures such as pipefish washed ashore – were combined into a powerful metaphor and symbol of change itself.” Lewis (1988: 91) suggests that the Rainbow Snake, which became a common image in many different accessible locations at or near campsites in this period, acted as a unifying symbol in times of change. Drawing an association between the mid-Holocene establishment of the monsoon pattern of rain and rock art, Chaloupka (1985: 277) speculates that the Lightning Man (Namarrgon) may have appeared in the art at this time.

**4000–2000 BP.** Sites dated to 4000–2000 BP encompass a Transition Phase between estuarine conditions and the beginnings of the Freshwater Phase on the floodplains of the north. Higher effective precipitation continued into this period until approximately 3700 BP, followed by increasing patterns of aridity. The rivers underwent a so-called ‘Sinuous Phase’, which describes their meandering nature across the coastal plains. The following ‘Cuspatate Phase’ of river development refers to the formation of wide reaches and pointed bends, which occurred after 2500 years ago. Continued sedimentation and the slowing of coastal progradation during this phase led to a cut-off of the tidal influence. Palaeochannels were created and the floodplains contained a mosaic of estuarine, freshwater and mudflat areas (Woodroffe et al. 1986; Chappell 1988; Woodroffe 1988; Woodroffe & Mulrennan 1993) (Fig. 4).

Increasing numbers of shell mounds, earth mounds and middens fall within this time period. Initial observations suggest established settlement patterns developed in the Reynolds River area after 4000 BP. Another indicator is perhaps the uniformity of the artefact assemblages across the different environmental zones after 4000 BP (Gusc 2005: 112). In western Arnhem Land, Allen & Barton (1989: 90–91) concluded that all four rockshelter sites, Malakunanja II, Malangangerr, Nawamoyn and Ngarradj Warde Jobkeng, were mostly abandoned by the end of the Transition Phase and only sporadically occupied afterwards. However, Hiscock (1999: 96) argued that the timing for this model of abandonment may be too rigid and that at the rockshelter of Paribari accumulation of midden deposit continued for sometime afterwards. The existence of an intermediate saline mudflat phase in the development of the floodplain is consistent with and confirmed by the compositional changes in the middens in the nearby archaeological sites. At Malangangerr, Nawamoyn and Paribari, there is a shift over time from exploitation of the bivalve species *Polymesoda erosa* in the lower midden levels to the mud whelk *Cerithidea* sp. in the upper levels (Schrire 1982: 233). This event is dated to about 3000 years BP at Paribari (Schrire 1982: 51). The abandonment of Malangangerr, Nawamoyn, Ngarradj Warde Jobkeng and Malakunanja II at the same time suggests local shifts in settlement and subsistence according to the increasingly mosaic environment on the floodplains during the Transition Phase (Hiscock 1999: 96).

According to Allen and Barton (1989: 93–94), the earliest secure date for the appearance of stone unipoints and bipoines in western Arnhem Land plains rockshelters is 4000 BP and they were not widespread in the region until after 3500 BP, although Jones & Johnson (1985a: 206) argue for an older date for their first appearance. The fact that these tools appear for the first time only in the upper levels of Nawamoyn and Malangangerr suggests the abandonment theory approx. 3000 BP. Stone unipoints and bipoines appear only in the lower levels of Paribari.

Surface mound (Kapaiga N) on the lower South Alligator River coastal plains located above freshwater black soil (floodplain clay) contain *Nerita balteata*, which lives mangrove trunks, and *Cerithidea* sp., found in the substrates of stands of the drier *Avicennia* and *Bruguiera*, suggesting exploitation of mangroves in the Transition Phase (Woodroffe et al. 1988: 96–97).

There is an increase in numbers of open sites toward the end of this period around 2000 BP. Earth mounds HD1 and MP2 on the Adelaide River floodplains contain increasing quantities of stone artefacts, fish bone and bone points that have been associated with multi-pronged spears for fishing (Brockwell 2005, 2009; Brockwell & Akerman 2007) (Fig. 7). Nearby is Scotch Creek I, an open site located next to a deep and permanent freshwater billabong.
in open woodland two to three kilometres southeast of the main floodplains of the Adelaide River. In 1980, Smith (1981; Smith & Brockwell 1994) excavated a test pit and located cultural remains in a layer of black soil between 60 to 70 cm in depth above a clay substrate. A horizon of stone points located 10 to 15 cm above the clay substrate is dated to approx. 3000 BP and therefore to the Transition Phase (Smith & Brockwell 1994: 91; Smith 1995). On the basis of ethnographic association of stone points with light weight dueling spears, Smith (1995) speculates that the point horizon might represent a period of conflict associated with the changing and unpredictable nature of the resource base on the floodplains during this period. It is argued that the age of the site is no older than 4000 years as there are no mangrove shellfish present (Smith & Brockwell 1994: 93). The site has been occupied repeatedly since then (Crassweller 1996: 1). There are stone artefacts and faunal remains throughout the excavation (Smith & Brockwell 1994: 91). The animal taxa present include macropods, bird, freshwater turtles and fish (the only identified species being *Arius* sp.). The faunal analysis indicates that macropods (open woodland) are always a relatively more important taxon than at the main Adelaide River floodplain sites. Crassweller (1996: 78) concludes that the site was used as a base camp to exploit the billabong and open woodland and that manufacture and repair of stone artefacts took place there.

Hiscock (1999: 97) suggests that settlement may have shifted away from the escarpment and floodplains to the coast in this period, which was rapidly prograding and probably productive during the Transition Phase. This is supported by the increasing number of coastal sites. Sites dating from this period include Werat 14 in the west, which is located on a chenier ridge of the coastal plains of Reynolds River. It is dominated by the open beach species *Anadara granosa* (Gusc 2005), as is MAl in the Darwin region (Bourke 2000; 2005b). The shell mound Mari-Maramay 1 on Croker Island is dominated by *Gafiarium tumidum*, another open beach species (Mitchell 1994a: 281). Macassar Well shell mound at Milingimbi (McCarthy & Setzler 1960; Mulvaney 1975) and the shell mounds at Blue Mud Bay (BMB/29, BMB/82) are also dominated by *Anadara granosa* (Faulkner & Clarke 2004; Faulkner 2006: 189; Hiscock & Faulkner 2006; Faulkner 2008, 2009) (Fig. 9). In central Arnhem Land on the Blyth River, Maganbal midden dates to early in this period and is dominated by *Anadara granosa*. In eastern Arnhem Land, Gaynada midden on Cape Arnhem is dominated by *Marcia hiantina*, another open beach species (Bourke 2001). At Blue Mud Bay, BMB/018 is the oldest dated midden in the study area and is dominated by *Pinctada* sp. (pearl oyster) found in shallow water and *Melo* sp. (baler shell) found on sandflats or mudflats (Faulkner 2006: 112; 2008). BMB/033 and BMB/067 are dominated by species from shallow water and sandy mudflats (Faulkner 2006: 169). On Groote Eylandt, the base of Mahndinga midden is dominated by marine shells (Clarke 1994).

Sub-coastally, several shell middens are recorded on the lower South Alligator River, western Arnhem Land. Kapalga D is located on a salt mudflat surface and dominated by mangrove shellfish species *Terebralia palustris* and *Telescopium telescopium*. Palaeochannel middens (concentrated shell) Kapalga F and K are located on freshwater black soil (floodplain clay) and on the bank of a palaeochannel, respectively. Shell from Kapalga F was not collected but Kapalga K contains the mangrove species *Polymesoda erosa* and *Cerithidea* sp. (Woodroffe et al. 1988: 97). The mixed composition of the soil substrates and shell species and the concentrated location of sites suggest varying and mobile foraging strategies in response to the mosaic and dynamic nature of the floodplains during the Transition Phase.

On the other hand, the pattern of occupation in rockshelters on Vanderlin Island in the Edward Pellew islands follows a somewhat different trajectory. While (Wobuya Shelter) was reoccupied or occupied for the first
time during this period (Worungulumba, Babangi, Walala III, Victoria Bay III, Scissibar Creek, Boimnmanda), this was followed by a low intensity or abandonment phase of these sites between 2500 and 1700 years BP (Sim & Wallis 2008).

More complex and diverse rock art forms emerge towards the end of this period, including stick figures, abstract designs, beeswax figures and detailed X-ray art (Lewis 1988: 95; Taçon 1993: 114; Chippindale & Taçon 1998: 107). The X-ray art depicts a mixture of estuarine and freshwater species, especially fishes (Taçon 1987) (Fig. 8). It is argued that multi-pronged spears portrayed in the art are associated almost exclusively with fishing as a major economic activity on the floodplains during the Transition Phase (Brockwell & Akerman 2007). Some rock art complexes in western Arnhem Land contain scenes of large numbers of human figures and spears in a mêlée that suggests fighting, perhaps over changing resource availability, during this Transition Phase. Most of this change occurs in the latter half of this period and accelerates throughout the next period, after 2000 BP (Lewis 1988: 309; Taçon 1993: 114).

2000-500 BP. This period encompasses the early Freshwater Phase, when freshwater from the annual monsoons ponded behind cheniers and in palaeochannels. By 2000 BP this process had created the vast freshwater floodplains and wetlands that are a major feature of the northern coastal plains today (Chappell 1988; Woodroffe et al.1988) (Fig. 4). With a continuing decline in effective precipitation, climatic variability increased in the region from approx. 1000 BP. There are dates from increasing numbers of sites including rockshelters (all but one located on the east coast), shell mounds, earth mounds and especially shell middens. The midden dates are predominantly from 1000 to 500 BP.

Allen and Barton (1989: 90–91) argue that the rockshelters of Malangangerr and Ngarradj Warde Jobkeng were reoccupied in this period after a period of abandonment of at least 2000 years. Although not dated, the upper levels of Paribari are dominated by freshwater fauna and flora that link the site firmly to the Freshwater Phase (Schrire 1982: 51–55, 58). Silica-polished adze flakes associated with experimental harvesting of *Eleocharis dulcis* (Akerman 1986), a reed that grows in freshwater swamps, are found in the upper levels of Paribari (Schrire 1982: 72). Polished flakes are also found in the upper levels at Nawamoyen (Schrire 1982: 137). There is a hint that Malakununja II continued to be occupied sporadically or was reoccupied in the Freshwater Phase, as freshwater mussel shell appears in the upper few spits (Kamminga & Allen 1973:45). Recent work on rockshelters in the Wellington Range in western Arnhem Land by Wesley and colleagues also indicates increased use of this environment after 1500 BP (May et al. 2010; Taçon et al. 2010). The resources of the wetlands and billabongs, coupled with a stable coastline, no doubt made these rockshelters desirable habitation sites, particularly during the wet season.

The inhabitants of Borngolo shelter in eastern Arnhem Land continued to exploit a similar range of marine, rocky shore, mudflats and open woodland species, as they did in the lower level of the site (see above). Schrire (1972: 666) notes that fish bones increase in the upper level, while mammal bones decrease, which she concludes represents a change in subsistence patterns with increasing sedentism.
Holocene settlement of northern Australian coastal plains

over time. Shell fish hooks also appear in the upper level only, about 1000 years ago. Schrire believes that this technology was a result of contact with South-east Asia. However, there is currently no conclusive archaeological evidence for contact between Aboriginal people with South-east Asia for this period. In the Edward Pellew islands, shell middens in rockshelters (Boinmarnda, Mushroom Roek, Komandarri-naboya, Turtle Shelter) accumulated steadily indicating more intensive occupation of Vanderlin Island during this period (Sim & Wallis 2008).

A large number of dates for shell mounds fall within this period. In the Darwin region, 21 shell mounds, dominated by the open mudflat species *Anadara granosa*, were located (Hiscock 1997; Bourke 2000; Hiscock & Hughes 2001; Bourke 2004, 2005b; Crassweller 2002, Bourke & Crassweller 2006; Crassweller 2006) (Fig. 10). Excavated shell mounds contain varying frequencies of stone artefacts and other faunal remains in addition to shell, mostly fish and crab with minor quantities of land animals and bird. Turtle shell mounds contain varying frequencies of stone artefacts and pottery (Mitchell 1994a: 321); one post-contact midden (Port Bremer 19) contains *Atactodea striata* and pottery (Mitchell 1994a: 224–225). In central Arnhem Land, this period is represented by Aningarra, Jilan-gajerra, Larrakun-ajirripa West and Muyu-ajirrapa on the Blyth River (Meehan 1982: 165–168), and Rulku and Balma 83 middens at Milingimbi (Roberts 1994: 178–179). Dates from eastern Arnhem Land, include Gaynada at Cape Arnhem (Bourke 2001), Blue Mud Bay – BMB3/17, 61, 67, 84 (Faulkner & Clarke 2004; Faulkner 2006, 2008, 2009), Groote Eylandt – Aburrkumanja, Dirrangumurunja and Malmudanga (Clarke 1994); and East Neck Saddle (ENII) on the Edward Pellew islands (Sim 2005; Sim & Wallis 2008).

Roek art in this period was prolific and significant (Taqon 1993: 113). Fully developed X-ray art, also called ‘Freshwater’, ‘Later’ or ‘Decorative X-ray’, coincides with the arrival of freshwater conditions on the floodplains. It features specific and precise representation of inner organs and is the dominant form in western Arnhem Land and exhibits much more regional variation at this time (Chaloupka 1985; Taqon 1987; Lewis 1988: 59–102; Chaloupka 1993: 114; Taqon 1993) (Fig. 16). Throughout this period, this art becomes increasingly elaborate and decorated and the internal features became more abstract (Chaloupka 1985: 277; Taqon 1987; Lewis 1988: 99; Taqon 1993). It depicts freshwater fauna and flora, such as magpie goose (*Anseranus semipalmata*) and lotus lilies (*Nelumbo nucifera*); and new technology, such as large stone blades ‘leiliras’, ‘goose’ spears and spear throwers (Chaloupka 1985: 277–278; Lewis 1988: 59, 101–102). It should be noted that ‘goose’ spears were not used for spearing geese – but rather were lightweight spears used with a ‘goose’ spearthrower – so-called because the wax hook made it look like a goose head (Lewis 1988: 384; Allen 2011: 78). These spears appear to have been used for dueling. Guse & Woolfe (2006) further demonstrate that the occupation of the coastal plains in western Arnhem Land is reflected by rock art that expanded from gorges and shelters in the escarpment to the outliers with the progression of floodplain evolution. Analysis of the spatial and temporal distribution of these sites indicates a late Holocene reorganisation of land use strategies, social economies and group interactions for the plateau and plains. Guse & Woolfe (2006) conclude that late Holocene changes in the rock art sequence reflect a growing confidence to occupy openly accessible sites in terms of social ecological stability and security, related to ecological abundance and diversity following sea level
stabilisation. The art of this period displays great diversity and regionalisation (Tacon 1993).

**Post 500 BP.** This period encompasses the later Freshwater Phase and the Contact Period. The Contact Period can be separated roughly into two overlapping phases, the South-east Asian period from at least the 1660s (probably older) through to the early 1900s, and the European contact period beginning in the early 1800s (Macknight 1976; Mitchell 1994a: 56; Clarke 2000; Clarke & Frederick 2008; May et al. 2010; Tacon et al. 2010; Wesley 2011). The latter part of this period was dominated by environmental changes brought about by European contact, with impacts from feral animal and exotic weed species adversely affecting productivity, especially of the floodplains (Petty et al. 2007; Bradshaw 2008; Walden & Gardener 2008). Dates come from rockshelters, fewer shell mounds and earth mounds, and an increasing number of shell middens.

Macassans, Bugis and others from South Sulawesi and nearby islands established a trade in trepang (bêche de mer), which they obtained and processed on annual visits to northern Australia and sold onto the Chinese who regarded it as a tonic and aphrodisiac. The Southeast Asians supplied the Aborigines with trade goods such as metal, tobacco, beads and cloth in return for access to their lands and other benefits (Macknight 1976; Mitchell 1994: 181). The exact beginnings of this trade are uncertain and debatable (see Discussion below).

Two rockshelters from western Arnhem Land, Malakanunja II and Malangangerr, date to this period. Allen & Barton (1989: 90–91) interpret this as reoccupation following a long period of abandonment of 2500 years. In eastern Arnhem Land at Borngolo shelter, plant remains in the uppermost levels indicate that the inhabitants continued exploiting the sea shore, monsoon forests, and open woodland, with a range of implements including stone points, scrapers, hammers (Schrire 1972: 662–663). Schrire (1972) concludes that the deposit at Borngolo represents pre and post-contact Aboriginal subsistence behaviour. She interprets more intensive occupation in the upper levels as being the desire of the Aborigines to be in close contact with the Macassans for trade benefits. On Groote Eylandt, five rockshelters (Angwurkburna, Dadirringka, Lerrumungumanja, Marngkala Cave, Mungwujirra) belong to this period.

There are only four shell mounds recorded. One mound from the lower South Alligator River floodplains (Kapalga B) includes open beach species (Woodroffe et al. 1988: 97). The others are in central Arnhem Land on the Blyth River (Ngalijibama, Yuluk-adjirrapa), both dominated by open beach species, *Macra* sp. and *Dosinia* sp., and Blue Mud Bay in eastern Arnhem land (BMB 116) dominated by another open beach species (*Anadara antiquata*) (Faulkner & Clarke 2004; Faulkner 2006, 2008, 2009).

There are dates from seven earth mounds in this period. In the west, Djingurr 1 is located on the Reynolds River. In the Darwin region on the Adelaide River, a modern date was obtained from NP20, which also contains contact material (Brockwell 2005: 11). On the Mary River, Site 38 is also dated as modern. In western Arnhem Land, the deposit at Kina adjacent to the freshwater wetlands on the South Alligator River floodplains is dominated by the freshwater mussel *Veleusio angasi* and polished flakes, similar to those found in the upper levels of Paribari (Meehan et al. 1985: 150). Kina is associated with a large open
artefact concentration, one of many lining the floodplain margins of the South Alligator River (Meehan et al. 1985; Brockwell 1996). These sites contain hundreds of thousands of artefacts, including polished flakes and trinogral or 'cilifla' blades, which are also commonly found in upper levels of rockshelter sites dated to the last 1000 years in outliers of the Arnhem Land escarpment (Jones & Johnson 1985b: 208). Hiscock (1999: 99-100) speculates that there may have been a shift inland from the coast to the freshwater wetlands following the cessation of shell mound building approx. 500 years BP. Supporting this theory is intensified occupation at the Adelaide River earth mounds dating to less than 600 years BP (Brockwell 2009).

Most of the middens recorded belong to this period. In the Darwin region, two shell concentrations, MASb and WIN10, are dominated by mangrove species *Telescopium telescopium* (Bourke 2005a) suggesting that the Darwin mudflats were being recolonised by mangroves at this time. In western Arnhem Land, on the floodplains of the lower South Alligator River, seven middens (Kapalga A, B, E, L, M1, M2), contain a mixture of mainly mangrove species (Woodroffe et al. 1988: 97). On Cobourg Peninsula, Site V1 at Vashon Head is dominated by *Atactodea striata* and *Marcia hiantina*, both sand and mudflat bivalve species. On the basis of site content, Mitchell defines 17 sites as belonging to pre-Macassan contact (pre 1720 AD) and 12 post-contact midden sites. He concludes that the post-contact midden sites were substantially larger than the pre-contact sites and contain a wider variety of exotic artefacts and remains of large marine fauna (1994a: 377–398).

In central Arnhem Land, there are three middens from the Blyth River (Aningarra, Guna-jengga, Jilan-gajerra) (Meehan 1982: 165–168; Brockwell et al. 2009) (Fig. 17). In eastern Arnhem Land, there are four middens at Blue Mud Bay. BMB 16 and 84 are dominated by open beach species, while BMB 15 contains mangrove shellfish and BMB 22 contains rocky coast species (Faulkner & Clarke 2004; Faulkner 2006, 2008). On Groote Eylandt, the 11 middens from this period are dominated by marine shell (Clarke 1994). On the Edward Pellew islands, five surface shell scatters (Investigator Bay, Vanderlin Creek 2, Wabuya Creek, Walala Dunes, Kedge Point) date from this period and through to the Contact Period (Sim & Wallis 2008) (Fig. 18). Sim & Wallis (2008: 103) report that there is no direct evidence of Macassan contact in the Edward Pellew islands archaeology, despite the well-known historical presence of trepanning in the region, as well as the linguistic and rock art record and use of dug out canoes that show contact. Nor is there evidence of intensified occupation of archaeological sites associated with Macassan presence and trade goods, as is argued for the Groote Eylandt, Borngolo Shelter and the Cobourg Peninsula (cf Schrire 1972; Mitchell 1995, 1996; Clarke 2000). However, Sim & Wallis (2008: 103) suggest that the marked decline in the manufacture and use of stone artefacts post 500 years BP may be evidence of replacement with metal tools brought by Macassans.

Aboriginal rock art traditions continue through this phase of occupation. The Contact Period is recorded through images of South-east Asian perahus and items of material culture, and European ships, guns and introduced animals such as horses and buffaloes (Chaloupka 1985: 278; Chaloupka 1996; Chippendale & Tacon 1998; Clarke & Frederick 2006; May et al. 2010; Tacon et al. 2010; Clarke
Holocene settlement of northern Australian coastal plains

2 Sigma summed probability age ranges by site type

Shelter Sites \((n = 76)\)

- 0
- 2000
- 4000
- 6000
- 8000
- 10000

Earth Mounds \((n = 31)\)

- 0
- 2000
- 4000
- 6000
- 8000
- 10000

Shell Middens \((n = 71)\)

- 0
- 2000
- 4000
- 6000
- 8000
- 10000

Shell Mounds \((n = 126)\)

- 0
- 2000
- 4000
- 6000
- 8000
- 10000

Fig. 19. C14 graphs by site type.

We argue that regional variation in chronology and site distribution is due largely to local topography, and the timing and nature of landscape formation. The evidence for earlier Holocene occupation of these landscapes comes from rockshelters that only occur in some areas where the escarpment is adjacent to the coastal plains. There does appear to be some preservational bias in the record, and it is obvious that it plays a role in site distribution. For example, rockshelters are effective information traps preserving older chronostratigraphic sequences. Early Holocene open sites are rare as unless they are rapidly buried they do not preserve organics. Buried open sites are rarely located and sampled. There is also a geographic bias in our current site sample. Across the broader region, the east coast is the best dated with 134 dates, and the western region, represented by the Reynolds River, the least well-dated with only eight dates. This discrepancy has the potential to skew the data, particularly when combined with a research focus on open sites in a number of regions, making interpretation of settlement patterns through time difficult.

That said, however, and given the preliminary nature of the analysis, several interesting patterns begin to emerge. We can see variability in the timing and nature of occupation relative to the geomorphic and climatic parameters outlined. This is particularly evident when considering the differential occurrence of open sites. The pattern of settlement on the coastal plains of the Northern Territory prior to Southeast Asian contact, more or less tracks the evolution of the landscape and changing opportunities in terms of the creation of new resource zones. With rising seas, evidence of occupation 10,000 years ago was confined mainly to rockshelters on the margins of the coastal plains. Groote Eylandt and the Edward Pellew islands were cut off from the mainland by rising seas approx. 7000 years ago. Shortly after the spread of the mangroves in the Big Swamp Phase, people began foraging along the edges of the vast swamps of the northern floodplains from 7000 BP and the rockshelters adjacent were occupied more intensively. With increasing sedimentation the mangroves declined and after 4000 BP people began to move out onto the floodplains and the rapidly prograding coastline, witnessed by the increasing number of open sites in this period. People also began to bordering open woodland. Apart from a few older examples from the Reynolds and Adelaide rivers and Kakadu, the majority of earth mounds are less than 2000 years old.

Shell middens occur along the coast and adjacent to palaeochannels on the floodplains of major rivers across the Top End. They are mostly less than 2000 years old, with the majority being less than 1000 years old (Fig. 19). The older exceptions are in western Arnhem Land, where middens are found buried on the South Alligator River floodplains, and one site in central Arnhem Land, on the Blyth River.
travel offshore, rehabituting the Edward Pellew islands approx. 4000 years ago. Between 4000 and 2000 BP, there was a diversity of fresh and estuarine environments being exploited on the floodplains, reflected in the faunal assemblages from rockshelters and open sites. Following the Big Swamp Phase, the combination of sea-level recession, continued sedimentation in former shallow embayments built out intertidal mudflats suitable for shellfish biomass. This saw the proliferation of shell mounds in a number of regions across the Territory between approx. 3000 to 500 BP. Figure 2 shows the chronology of shell mounds relative to the environmental data. From 2000 BP, freshwater conditions were established on the sub-coastal plains and earth mounds and artefact concentrations proliferated along the floodplain margins. Between 800 and 500 years BP, environmental change in shoreline characteristics and climatic variability associated with ENSO activity led to a decline of sandy/mudflat shell beds and shell mounding behaviour all but ceased in the Northern Territory (Bourke et al. 2007). Subsequently, mangrove-lined beaches and coastal wetlands were established, economies diversified and middens became more common with molluscs harvested from varied habitats after 500 years BP. There is some suggestion that there may have been some relocation from the coast to the seasonally abundant sub-coastal freshwater wetlands during this period (Hiscock 1999).

There are debates about the socio-cultural implications of the archaeological record. Some authors (e.g. Bourke 2005b), quoting the ethnographic literature, have associated mound-building behaviour between approx. 3000 to 500 BP with ceremonial activities and territorial demarcation. Contrary to this, Hiscock and Faulkner argue that there is no historical analogue for shell mounding and the social and economic systems that produced them no longer exist. They hypothesise that the diverse mythology recorded ethnographically that surrounds shell mounds is a recent construction to explain the existence of alien landscape features within modern foraging and social practices (Hiscock & Faulkner 2006: 218).

In the sites under discussion, stone unipoints and bipoints appear to be concentrated in a narrow horizon dating from 4000 BP and are rare in the upper levels less than 2000 years old. Stone points are frequently recorded in surface artefact concentrations from the northern coastal plains and although undated may be from this period. The appearance of stone points is part of a widespread technological change across the Top End in the mid Holocene. It is widely agreed to be dated from at least 5000 until 1500 years BP (Allen & Barton 1989: 94-95; Hiscock 1999: 98; Clarkson 2006b: 165–166; Smith & Brockwell 1994: 101). Hiscock (1999: 98) argues that points appear as early as 7000 BP coinciding with the Big Swamp Phase and that mid Holocene changes in stone technology were driven by changes in resource availability created by the evolution of the coastal plains. He goes on to say that unipoints and bipoints are part of a continuum of manufacture, and represent a risk strategy in times of uncertainty (Hiscock 1994a, 1994b, 1999: 98). Clarkson (2006a: 105, 2006b: 165–166) agrees with this analysis and argues that regional technological change was a response to environmental variability created by the onset of ENSO (El Niño Southern Oscillation) from 3000–2000 years ago. Smith & Brockwell (1994: 102) argue that concentrated manufacture of stone unipoints and bipoints at Scotch Creek between 3800 and 2100 cal. BP coincides with the Transition Phase, a period of environmental stress when increasing aridity and the changing nature of the floodplains made resources unpredictable. Smith (1995) associates stone points with spear tips and suggests that tensions over access to resources and inter-group conflict led either directly to warfare or threatening displays at ceremonies. Certainly depictions of inter-group fighting in western Arnhem Land rock art became more common in this period (Taçon & Chippindale 1994). However, a phytolith study conducted to investigate environmental change was unable to firmly establish the connection between changes in climate and changes in archaeology (Clarkson & Wallis 2003). It might be noted that there are no ethnographic examples of spears hafted with small unifacial or bifacial points known from the northern coastal areas, though they do occur in the Kimberley region.

It is suggested that South-east Asian contact may have occurred from perhaps as long ago as 800 years BP (Clarke 2000b: 325–328; Clarke & Frederick 2011:151). Macknight (1976, 1986) and Mitchell (1994: 56) argue that it more likely dates from the 1720s when there is documentary evidence for the Macassan trade in trepang with the Chinese. However, recent dating has shown that the image of a Macassan perahu on the walls of a rockshelter in western Arnhem Land has a minimum age of 1664 and may be as old as 1517 AD (Taçon et al. 2010). Whatever the timing, these visits had a profound impact on Aboriginal social and economic organisation on the northern coastal plains (Clarke 2000b). In eastern Arnhem Land, Schrire (1972) posits that the people of Port Bradshaw replaced traditional stone and bone tools with metal artefacts and became increasingly sedentary as a result of contact with Macassans. Mitchell (1994a, 1994b, 1996) argues persuasively that the economy and settlement patterns of Cobourg Peninsula in western Arnhem Land were completely reorganised and local populations were able to rely much more on exploitation of large marine animals as a result of the adoption of the dugout canoe and access to metal to manufacture harpoons. Metal axes also allowed Aborigines to exploit the hard dupes of Pandanus, which contain an energy-rich kernel (Mechan et al. 1979). These new technologies allowed groups to extend their hunting range and access previously under-utilised resources (Faulkner 2006: 6). It is argued that contact with Macassans stimulated ceremonial exchange cycles and trade networks, involving a variety of objects including stone, shell, metal, spears, cloth, baskets, nets etc, that extended from eastern Arnhem Land into western and southern Arnhem Land and beyond (Allen 1996a, 1997;
Merndt 1951; Davidson 1935; Evans & Jones 1997; Jones & White 1988; Mitchell 1994b, 1996; Paton 1994; Thomson 1949). This network included trade in large stone blades manufactured at Ngilipiti quarry in north-eastern Arnhem Land (Jones & White 1988). Production of similar artefacts, manufactured in the quarries of western Arnhem Land (Jones & Johnson 1985a: 188) and found in the rockshelters and open sites restricted to the last 1000 years, may also have been stimulated by this Arnhem Land wide phenomenon.

From 180 years ago, Europeans and later Chinese began penetrating the coastal plains of the Northern Territory. The earliest incursions were British settlements on Bathurst and Melville Islands and on Cobourg Peninsula (Allen 1980; Keen 1980; Mitchell 2005). Apart from the devastating impact of introduced diseases which greatly reduced the Aboriginal population, one effect of these early settlements was the spread of feral buffaloes throughout the coastal plains, especially between Darwin and western Arnhem Land, where they wreaked havoc on the freshwater wetlands. Apart from the damage to wetlands resources, Mechan (1991: 203–205) points out that as Aboriginal people feared buffaloes, this also had the effect of altering their hunting and foraging patterns on the coastal plains in general. In 1858, South Australia annexed the Northern Territory and there was a brief settlement at Cape Hotham near the mouth of the Adelaide River, which subsequently moved to Port Darwin. These initial settlements were followed by pastoralists, buffalo shooters, miners, timber getters, pearlers, fishermen and missionaries. European and Chinese presence had profound effects on Aboriginal social and economic systems and settlement patterns, some of which are reflected in the archaeological record. For example, on Groote Eylandt, as people became more settled on the missions they became more reliant on European food supplies. When they did forage, they targeted easily accessible and favourite bush foods (Clarke 2011). Consequently, midden sites examined on Groote Eylandt relating to this period consist of a limited number of taxa, all of which were available in the immediate environment.

As a result of this process, these sites are seen to conform to the criteria outlined by Meehan (1988) for ‘dinner-time’ or temporary camps (Clarke 1994: 458). People are presumed to have operated a dual subsistence system – one that had a commodity-based component involving the consumption of European resources, and a hunter-gatherer lifestyle that integrated traditional practice with elements of the new (Clarke 1994: 462). As indicated previously, however, many of these traditional practices arose during the period of contact with Macassans (Faulkner 2006: 8). A similar situation existed on the Adelaide River, where earth mounds from the Contact Period were dominated by estuarine shellfish, as the resources of the freshwater wetlands were impacted negatively by the incursions of feral animals and exotic weeds (Brockwell 2005: 15-16).

CONCLUSION

The above synthesis is a preliminary attempt to integrate the archaeological evidence within an environmental framework. With only a few exceptions, environmental and archaeological research on the coastal plains of the Northern Territory was not undertaken in tandem. This means that research questions often had different foci and the data sets do not necessarily intersect. We hope that future research is more inter-disciplinary in nature. In this way multiple lines of evidence can be used to reconstruct both the natural and cultural landscape and aid in interpretation of the interactions between the two.

Although extensive geomorphological work has been done, there has been little palaeo-climatic research in this region of northern Australia. We envisage that future research programs would explicitly address questions of climatic variability and its impact on human settlement and mobility. Such research would be dedicated to investigating regional and local patterns through isotope analysis and coral proxies. This research could also be integrated with palaeoecological investigations through analysis of pollen, diatoms and phytoliths from both existing archaeological soil samples and coring programs into the many suitable swamps of the Northern Territory. Due to the comparative paucity of work to date in the western region of the Northern Territory, we see this area as a priority area for future research.

The archaeological record demonstrates that the last 10,000 years have witnessed recurrent economic and social reorganisation for the occupants of the coastal plains of the Northern Territory. We argue that the evidence clearly suggests this is a result of variable climatic and environmental conditions and landscape evolution combined with contact with peoples from South-east Asia [and later Europeans] within at least the last 400 years. This may seem to be an overly deterministic point of view, but is not unlike the conclusions from other archaeological studies in the coastal areas of northern Australia. They have implied that major environmental changes, rather than strictly social changes, preceded growth in human populations, and that the growing productivity of newly created landscapes combined with higher population levels, were causal factors in cultural change, variations in mobility, and increasing land and sea use during the Holocene (cf. Beaton 1985; Jones 1985b: 291–293; Mechan et al. 1985:153; Sullivan 1996: 7). In explaining the variability of coastal occupation in the north over the Holocene, a number of researchers have focused on environmental explanations such as changes in local ecological habitats (e.g. Hiscock 1999; Hiscock & Mowat 1993; Mowat 1995; O’Connor 1999), as well as pointing to the links between the appearance of mounds and evidence for increasing aridity and the northward movement of the northern monsoon on the coast (O’Connor & Sullivan 1994; O’Connor 1999). This particular type of ecological perspective does not view human culture as
being determined by the environment, nor does it assume perfect adaptation of humans to their environment. Rather, it suggests that the archaeological manifestation of a defined set of human behaviours, such as the structure of economic activity, may best be viewed in terms of the formation of a particular environment (Allen 1996b; Cribb 1996:150; Faulkner 2006: 18).

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Holocene settlement of northern Australian coastal plains


Holocene settlement of northern Australian coastal plains


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The vine *Embelia tiwiensis* (Angiospermae: Myrsinaceae), a new species from the Northern Territory, Australia

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ABSTRACT

The vine *Embelia tiwiensis* is a new species occurring on Bathurst and Melville islands, Northern Territory. It is described from sterile specimens based on distinctive leaf characters as no flowering or fruiting material was available. A key to species of *Embelia* from the Northern Territory and Timor is provided for comparison.


INTRODUCTION

*Embelia* Burm. f. is a genus of about 130 species (Stähl & Anderberg 2004) occurring in the Old World tropics. It is one of six genera in the family Myrsinaceae occurring in Australia. Recently the Angiosperm Phylogeny Group included the Myrsinaceae in the family Primulaceae where it is treated as a subfamily (Stevens 2011). However, in this paper the Myrsinaceae is still regarded as a separate family. The genus *Embelia* can be distinguished by habit, being vines or scramblers, and by the flowers, which have five free petals. Vegetatively *Embelia* is distinguished from some species of *Maesa* (now in the family Maesaceae), which also have a scrambling habit, by the secretory glands in the leaves. In *Embelia* the glands are chiefly globular or shortly lineate, but in *Maesa* they form long thin cells. Reynolds (1991) recognised four species of *Embelia* in Australia, of which one, *E. curvinervia* S.T. Reynolds, occurs in both Queensland and the Northern Territory. Ten species are known from New Guinea and the Solomon Islands (Sleumer 1987) and there are at least three species on the Lcsser Sunda Islands. Here I describe a new species from the Tiwi Islands, *Embelia tiwiensis* Jackcs. This species is known from four collections, one from Melville Island and three from Bathurst Island. Although the material is sterile it can be readily distinguished from other species of *Embelia* based on leaf features, in particular possession of globular pellucid glands in the leaves. These differences are outlined in the key to species occurring in the Northern Territory and nearby areas.

TAXONOMY

*Embelia tiwiensis* sp. nov.
(Figs 1, 2D,E)


*Embelia tiwiensis* ab aliis speciebus Embeliae quibus in Australia, Nova Guinea and Insulis Minoribus Sundae habitant, laminis chartaceis cum glandibus numerosis globularibus secretoris pellucidis in lucem transmissis et pilis ferrugineis in pagina infera differt.

Material examined. Type – Australia, Northern Territory, Bathurst Island, Ngaru Swamp, 11°43′19″S, 130°20′57″E, 13 June 2011, J.A. Risler 645 & D.J. Dixon (HOLOTYPE: DNAD146206, 2 sheets; ISOTYPES: BRI, CNS).


Description. Vine, semi-prostrate, rarely exceeding 60 cm tall, adventitious roots common, lenticels inconspicuous. Young twigs covered with reddish-brown glandular papillae and/or short hairs. Leaves alternate; petioles 7–21 mm long, papillate; lamina elliptical to broadly elliptical to obovate, (3.5–) 6.5–17.5 cm long, (1.6–) 3.5–7.8 cm wide, chartaceous, discolored; base
cuneate, symmetrical to somewhat asymmetrical; apex acuminate; margin entire or coarsely and irregularly toothed in upper half of lamina; glands globular in transmitted light, pellucid, appearing dark in surface view; hairs spherical, red-brown and scale-like, present on both surfaces, more common on lower surface; midrib slightly depressed on upper surface, prominent below; lateral nerves 8–12 on either side of midrib, looping near the margin. Flowers and fruits not seen.

**Distribution and habitat.** *Embelia tiwiensis* is only known from Bathurst and Melville Islands in the Tiwi Island group. It has been found in seasonal spring-fed swamps and riparian jungles. Here the common dominants are *Calophyllum soulattri*, *Hanguana malayana*, *Hydriastele wendlandiana*, *Syzygium angophoroides* and *S. nervosum*.

**Etymology.** The specific epithet reflects the occurrence of the species on the Tiwi group of islands including Bathurst and Melville islands. It is adjectival.

**Note.** Contrary to the labels accompanying the sheets comprising the holotype specimen, an isotype stated to be in JCT is housed in CNS.

The specimen label attached to sheet 2 of the holotype specimen was generated in 2011 from the latest Northern Territory Herbarium electronic database. This has resulted in some discrepancies between that label and the one accompanying sheet 1. Importantly, there is a correction in citation of the collection number, from Risler & Dixon 645 to Risler 645 & Dixon. There is also a minor difference, due to computer programming, of the cited latitude of the collection; both sheets are part of the one gathering.

Herbarium abbreviations follow Thiers (2011).

**Key to species of *Embelia* from the Northern Territory and Timor**

1. Glands in lamina pellucid to pale orange when viewed in transmitted light
   - Glands in lamina chiefly dark red to black when viewed in transmitted light

2. Glands pale orange, both globular and lineate, lamina glabrous
   - Glands pellucid, globular only, lamina with rusty papillae/hairs on lower surface particularly on the veins

3. Inflorescence paniculate, much-branched, longer than leaves, 5-merous
   - Inflorescence a cluster of racemes, shorter than leaves, 4-merous

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Fig. 1. Holotype specimen of *Embelia tiwiensis* sp. nov. (J.A. Risler 645 & D.J. Dixon, DNA D146206 – 2 sheets. For a note on label discrepancies, see text.)
Embelia tiwiensis (Angiospermae: Myrsinaceae) sp. nov. from the Northern Territory

Fig. 2. Embelia curvinervia and E. tiwiensis, from Jackes et al. (in press) Myrsinaceae, Flora of the Darwin Region Vol. 1. A–C, Embelia curvinervia S.T. Reynolds: A, leaf (lower surface) and inflorescence; B, male flower from above; C, fruit (A, B, C, R. Dunlop 5025; C, D.C. Franklin D154622); D, Embelia tiwiensis sp. nov., leaf shapes, both showing lower surface (J.A. Risler 645 & D.J. Dixon, holotype). All illustrations were based on herbarium specimens.

4 Leaves chartaceous, subtending bracts about 1 mm long. E. frangulifolia (Wetar Island)
- Leaves firm, subtending bracts 2–3 mm long. ................. E. curvinervia (NT and QLD)

N.B. Embelia frangulifolia Mez has not been recorded from Timor but it does occur on nearby Wetar Island. It may be distinguished from E. curvinervia by the chartaceous versus firm leaves and by subtending bracts about 1 mm long versus bracts 2–3 mm long and the latter is generally a much more robust vine.

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New taxa and notes on *Helicteres* L. (Malvaceae: Heliceroideae) from the Northern Territory, Australia

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ABSTRACT

Six new species and a new subspecies of *Helicteres* from the wet-dry tropics of the Northern Territory, Australia are described and illustrated (*H. darwinensis*, *H. kombolgiana*, *H. macrothrix*, *H. serpens*, *H. sphaerotheca*, *H. tenuipila* and *H. cana* subsp. *latifolia*). *Methorium integrifolium* is reinstated as a species and a new combination is made in *Helicteres* (*H. integrifolia*) to accommodate it, while *Helicteres dentata* is reduced to subspecific level under *H. integrifolia*. Two varieties of *H. dentata* are raised to specific level (*H. procumbens* and *H. flagellaris*). A key to the 13 species known from the Northern Territory is provided and variation in some widespread taxa is discussed.


INTRODUCTION

The family Malvaceae *s. lat.* is cosmopolitan, especially tropical, in distribution with nine subfamilies, 113 genera and c. 5000 species (Mabberley 2008). It is widespread in tropical and temperate Australia. While the genus *Helicteres* L. has traditionally been included in the family Sterculiaceae (e.g. Cronquist 1981), more recent phylogenetic studies support its inclusion in a broadened Malvaceae (APG 1998; APG II 2003; Mabberley 2008). Subfamily Heliceroideae is one of the smallest subfamilies in Australia and is represented only by *Helicteres* which contains perhaps 60 species. *Helicteres* has a major centre of diversity in central and South America where some 38 species are recorded with an apparently lesser one in the Asian-Australian tropics (Christobal 2001).

The only Australian treatment for the genus is that of Bentham (1863) who recognised five taxa, all of which occur in the Northern Territory (N.T.). Additional Australian species have been described since that time by Fitzgerald (1918) and Mueller (1865). Wheeler (1992) provided the only modern Australian flora treatment, for the Kimberley Region of W.A. Recent flora treatments are also available for Thailand with seven species (Phengklai 2001) and for China with ten species (Tang *et al.* 2007). Four species were recognised for Java by Baeker & Van den Brink (1963) and seven for British India by Masters (1874). Many of the east Asian and Malesian taxa appear to be relatively widespread with a few extending to Australia (Phengklai 2001; Tang *et al.* 2007).

In Australia, the incompleteness of available treatments and variability of leaf and indumentum characters especially has resulted in the misapplication of names. It has become evident over the past 25 years that a number of undescribed taxa occur in the northern N.T., Qld and W.A. A number of new taxa are described here in particular for inclusion in the *Flora of the Darwin Region*. As the type specimens of at least four taxa treated by Bentham (1863) are from the N.T., the clarification of the taxonomy of the N.T. species is of some value in progressing knowledge of the genus in Australia as a whole.

Christobal (2001) recognised seven sections within the genus, with only two of these (section *Helicteres* and section *Orthocarpaea*), occurring in Asia and Australia, the others being restricted to South and central America. As circumscribed by her, section *Helicteres* is monospecific including only *H. isora* L. while all other Asian-Australian species belonged to section *Orthocarpaea*. Section *Helicteres* was distinguished by the geniculate, pseudozygomorphic flowers with the upper petals distinct from the lower; the curved androgynophore which significantly exceeds the calyx; the petals with scattered minute glandular hairs or glabrous, red or orange or white, rarely white-green; stamens 10, usually connate at the base; one of the lower petals longer than the calyx; 2 (–5) flowered axillary cymes with extraloral nectararies present; the androecium and gynoecium set at an angle on the androgynophore; the capsule spiral and the seeds without fins (Christobal *loc. id.*). She distinguished section *Orthocarpaea* as having 10 or fewer stamens; the androgynophore shorter than the calyx or just longer and always straight; the androecium...
and gynoecium set at an angle on the androgynophore; the petals violet, the lower ones clearly differentiated from the upper and with a tuft of long glandular hairs; the capsule not spiral; the seeds without ribs; the axes of inflorescence with nectaries; and the flowers in simple cymes.

Herbarium abbreviations follow Thiers (2010). Only duplicates examined in the course of preparation of this treatment have been cited, except for unseen type specimens indicated by the abbreviation u.v. (i.e. non visus – not seen).

MORPHOLOGY OF SPECIES IN THE NORTHERN TERRITORY

Habit. All species are shrubs or subshrubs with either erect or trailing stems. Two primary resprouting forms are evident. Firstly, there are those with annual above-ground parts which resprout from a perennial rootstock either at or near to ground level. This group contains usually multi-stemmed perennial subshrubs either with erect or prostrate stems and includes H. darwinensis, H. integrifolia, H. macrothrix and H. sphaerotheca. In at least some members of the group which have been grown in cultivation (H. integrifolia subsp. dentata and H. integrifolia subsp. integrifolia), the annual dying-back of above-ground parts and the low multi-stemmed, resprouting habit occur even in the absence of fire.

The second life form comprises taller, more erect, open, usually few-stemmed shrubs with lower stem regeneration as in for example H. angustifolia L., H. isora and H. kombolgiana. The open, much branched, few-stemmed habit of H. kombolgiana is maintained in cultivation. In some cases H. isora may be multi-stemmed after resprouting from fire but is typically taller and develops an open shrubby habit when fire protected, Helicteres cana and H. hirsuta Lour. are somewhat intermediate being few-stemmed but lower in stature, the former at least resprouting at ground level after annual fire.

Indumentum. Most vegetative parts and the calyx have sessile or stipitate stellate hairs with short or long multiangulate aims. The size of these hairs is often diagnostic of a species. The new growth often also has scattered, red, minute, digitiform, glandular hairs. A few species have long hairs on the upper surface of the leaf (H. angustifolia, H. procumbens) and sometimes H. sphaerotheca), while most other species have only stellate hairs. Long or short, soft bristles (these bearing stipitate or sessile stellate hairs) are sometimes present on the calyx (H. kombolgiana) and are often present on the fruit (e.g. H. hirsuta, H. integrifolia, H. macrothrix, H. tenellula). These bristles appear broadly comparable with those of Trinquetta fruit (Halford 1997).

Density of stellate hairs was classified into five classes: very dense, with the underlying surface obscured or nearly so; dense, with the branches touching to overlapping; moderately dense, with the hairs touching to 1 diameter apart; sparse, with the hairs 1–5 diameters apart; scattered, with the hairs more than 5 diameters apart.

Leaves. Leaves are simple, almost sessile to petiolate, the lamina usually has serrate margins or is sometimes entire, and in the case of H. isora (Fig. 1) also with short acute lobes lateral to the apex. Most commonly leaves are lanceolate to broadly ovate, less often linear (H. cana subsp. cana, H. sphaerotheca) or suborbicular (H. cana subsp. latifolia). In H. darwinensis the leaves appear at least partly accrescent, continuing to expand through the wet season until growth is apparently halted by the onset of dry conditions. Consequently leaves of specimens collected late in the wet season may be up to 180 mm long and thus many times larger than those present at flowering. The lower leaf surface in all species has a sparse to dense indumentum of stellate hairs, while the upper surface may be glabrous, or have stellate hairs, simple hairs or a mixture of hair types.

Stipules are usually subulate with an indumentum of stellate hairs.

Inflorescence. Cristobal (2001) recognised three distinct inflorescence variants, concluding that the partial inflorescence in Helicteres had undergone a progressive reduction from a symmetric or asymmetric double cincinnus to a simple multi-flowered cincinnus (e.g. H. hirsuta) and lastly to a 2-flowered or 1-flowered cincinnus. In turn these types of partial inflorescences may be arranged in a diversity of synflorescences. In the monospecific section Helicteres (H. isora) the cincinni are 2-flowered, rarely 3-flowered, while in section Orthocarpaea cincinni are basically 2-flowered or multi-flowered as in H. hirsuta and the south east Asian H. viscida. The basic inflorescence unit of a 1-, 2- or 3-flowered cincinnus is most common and in most taxa these are arranged in cymose inflorescences which may be contracted (e.g. H. macrothrix) to lax (H. serpens, H. flagellaris). In H. hirsuta the inflorescence is indeterminate, appears racemose, and can have up to 19 flowers with one flower, bract and extraafloral nectary per node. Cristobal (2001) interpreted this as a multiflowered cincinnus formed by reduction from a symmetric double cincinnus. There are no species with a symmetric or asymmetric double cincinnus.

Extra-floral nectaries. Sessile extrafloral nectaries are widespread in the genus and are present at the base of the pedicels on the internal face of the axis of the inflorescence in most species, including those considered here (Cristobal loc. id.). However, in H. hirsuta the gland is lateral to the base of the pedicel and on alternate sides of the rachis on successive flower nodes. These extra-floral nectaries are present in most taxa, with the notable exception of H. procumbens, and may be green, yellow-green or yellow when fresh but often drying dark to dark red. In all species, glands are sessile to slightly raised, orbicular to oblong or irregular depending on placement, smooth, glossy, glabrous and often depressed and darker in the centre. They appear to be frequented by a number of species of ants, including Green Tree Ants (Oecophylla smaragdina) and meat ants (Iridomyrmex).
Flowers. All species have flowers of the ‘geniculate’ type, in this case with the androecium and gynoecium set obliquely on the androgynophore rather than with the androgynophore or calyx set at an angle to the pedicel (Cristobal 2001). In these species the calyx is bilabiate and with the flower appearing somewhat zygomorphic (pseudozygomorphic of Cristobal 2001). Local species vary considerably from strongly bilabiate in *H. isora* and less so in *H. cana* and *H. hirsuta*, or weakly bilabiate, to virtually actinomorphic in species such as *H. darwinensis* and *H. procumbens* (Figs 2, 6, 9–11, 13, 15, 18, 20).

In *H. isora*, flowers last two days and are functionally male on the first day of opening and functionally female on the second (Winkler 1906, cited in Cristobal 2001). My observations confirm that there is a change in petal colour from pale blue to orange over the two days, and the limb of the petals is strongly reflexed and held against the calyx on the first day becoming perpendicular to it on the second (Fig. 1A.). The anthers are reported to be ripe on the first day and the stigma receptive on the second while nectar is produced by the calyx on the first and by the stigma on the second day. In other N.T. species, no change of flower colour is evident and longevity has not been investigated.

Calyx. *Helicteres* has a 5-lobed, weakly or strongly 2-lipped calyx, with the tube longer than the lobes (Fig. 7L). The calyx is green, subcylindrical, narrowly obconical, ellipsoidal or ovoid to campanulate. The lower three calyx teeth are usually distinct from the upper pair although otherwise similar in appearance. All species have a basal nectary gland but in most species except *H. isora* this incompletely covers the base of the calyx tube. In these species the gland is usually on the “upper” side adjacent to the adaxial petals or sometimes lateral to the adaxial and abaxial petals and extends from 0.3 to 0.5 mm from the base, or in *H. hirsuta* 1 mm from the base. In *H. isora* the nectary extends upwards to c. 3 mm from the base and completely eneicles the androecium and gynoecium. The margin of the gland may be irregular or entire. The calyx usually abseises from its base and persists loosely on the androgynophore through into the fruiting stage.

Corolla. The corolla of *Helicteres* is composed of five petals. Characters found to be useful to distinguish taxa included the degree of differentiation between the upper and lower petals, especially in the morphology of the claw and the relative length of the calyx and corolla (Christobal loc. id.). The upper (adaxial) pair and lower (abaxial) three petals may be weakly to strongly dimorphic but are always clawed with a cuneate limb and one or two appendages at the base of the limb (rarely absent). These structures have been variously referred to as auricles, auriculate appendages, (lateral) teeth, or crosse crests (Bentham 1863; Masters 1874; Fitzgerald 1918; Wheeler 1992; Cristobal 2001; Phengklai 2001). The appendages on the lower claws are less robust and less well developed than those on the upper petals. The two upper petals tend to be imperfect mirror images of each other, as is also the case for the two outer, lower petals (Figs 3D, E, J, K, 7C, E). The upper petals especially differ slightly in the placement of appendages. When dissected out and laid flat, the upper pair often curve towards each other, while the outer lower petals curve away from each other (Fig. 7C, E). The central lower petal is usually close to straight and symmetric.

In *H. isora* the limb is strongly geniculate or reflexed, while in *H. cana* and *H. hirsuta* the petals are bent at 90 degrees. In other taxa the petals are araeate so that the limb curves out to about 90 degrees with the claw. The limb of petals is usually mauve to mauve-pink or pink, rarely maroon (*H. hirsuta*). In *H. isora* the petals are very pale blue on the first day changing to pale...
orange in the evening and becoming darker orange on the second day. The upper petals in a number of species (H. cana, H. darwinensis, H. integri folia, H. kombol gia, H. macrothrix, H. procumbens, H. tem ripta) are white at the base of the limb, corresponding to the glabrous area discussed below. The lower petals are usually uniformly coloured to the base of the limb, although in H. darwinensis frequently longitudinally striate or striped at the base of the limb and in some others darker. Helicteres hirsuta has a paler area at the base of the limbs of the lower petals.

Most species have sparse, patent to appressed, sepalate, apparently glandular hairs c. 0.1 mm long over the limb and similar but slightly longer hairs on parts of the claw. In three species (H. cana, H. hirsuta and H. isora), the base of the limb in all petals is smooth or with scattered minute, erect, glandular hairs and lacks an area of matted hairs on the inner surface. However, in other species the lower three (abaxial) petals have a distinct area of matted, simple, septate hairs to 1 mm long at the base of the inner surface of the limb while the upper (adaxial) petals have a smooth, glabrous, thickened and raised area at the base of the limb (Fig. 7). Helicteres isora has dark coloured, capitate, sessile glands of varying size scattered over the claw and base of limb of the upper petals and at the base of the limb on lower petals.

In the lower (abaxial) three petals the appendages are ‘lateral’ (on the margin and in a plane with the surface of the petal) whereas in the upper petals one appendage is ‘sublateral’ (at the margin but near to perpendicular to the surface of the petal) and the other ‘medial’ (located towards the centre between the margins and near to perpendicular to the surface of the petal). These lateral appendages help to hold the claws in a pseudo-floral tube while the sublateral and medial appendages serve to position the androgynophore and hold it away from the adaxial petals, leaving a clear path for the central ones sub-rhomboidal to sub-cylindrical with adjoining ends obliquely truncate, or if the capsule has a paler area at the base of the limbs of the lower petals.

Androgynophore. In N.T. species of section Orthocarpae, the apex of the androgynophore is just exerted from the calyx and floral ‘tube’ although in H. cana it is more strongly exerted. In H. isora (section Helicteres) the androgynophore is curved and greatly exceeds the reflexed corolla lobes. The androecium and gynoecium are mounted obliquely on the androgynophore and orientated adaxially in all species (Fig. 1A). In most species of section Orthocarpae, the androecium and gynoecium rest on or just past the area of matted hairs on the lower petals. In H. darwinensis and H. macrothrix they may be virtually obscured by these hairs.

Androecium. All species have an inner whorl of 5 minute staminodes and an outer whorl of 10 equal stamens, free or fused at the base. The staminodes are shorter than the staminal filaments and narrowly oblanccolate to spatulate, but acute. Stamens are shorter on the adaxial side of the flower. In most species, anthers are dithecal and transverse but usually inclined slightly inwards at anthesis. In H. hirsuta the anthers are introrse at anthesis. Nine pollen types have been recognised for the genus (Pire & Cristóbal 2001).

Gynoecium. The ovary is hairy and the styles are always conenate, straight and may be twisted or not, even in species with non-twisted carpels. In H. isora the style and stigma are bent at 90 degrees to the axis of the stamens. In other species the style is parallel or slightly oblique to the stamens.

Within the Thai species of section Orthocarpae, Phengklai (2001) recognised three taxa as having flattened slightly 5-lobed stigmas (H. angustis folia, H. elongata and H. hirsuta), the others having a simple stigma either narrowed to a point or with 5 pin-like teeth. These stigma types can also be recognised in N.T. taxa; they are distinctly flattened in H. hirsuta and straight with 5 cohering pin¬like lobes in H. cana, H. darwinensis, H. integri folia and H. isora. In H. cana, H. integri folia subsp. dentata and H. procumbens at least, the stigmas may diverge slightly at the apex. However, in contrast to Phengklai’s findings, Australian and Malesian material of H. angustis folia sens. lat. that I have seen appears to have a style consisting of 5 pin-like lobes, slightly expanded towards the apex.

Capsule. The fruit is a capsule and in Helicteres is composed of five unilocular carpels and may be ovoid to ellipsoid or subbyellindrical. With the exception of H. isora (Fig. 1B), all species have straight valves and even in this species valves, although normally twisted spirally, may sometimes be partly straight, incompletely twisted or even with the twist reversing (e.g. Booth 23; Cowie 12406; Scarlett 16). The carpels dehisce along the inner suture, becoming partly separated with age. The indumentum varies considerably in density and hair size and the presence or absence of soft bristles. In descriptions, capsule dimensions include the layer of bristles or other indumentum. In some taxa (e.g. H. angustis folia, H. cana) the styles may at times be acerecent and the apex of the beak becomes apiculate as it develops.

Seeds. The seeds are arranged in a single row in each carpel, together forming an elongated mass, flattened or angled laterally along the inner angle of the carpel and cut obliquely to transversely between the seeds. Thus the basal and terminal seeds are conoidal or sub-conical and the central ones sub-ellipsoid to sub-ellindrical with the adjoining ends obliquely truncate, or if the capsule has one seed it may be ellipsoidal and flattened. The size and number of seeds varies from numerous and about 2 mm long in H. isora, to few and more than 3.5 mm long in a number of species.
RELATIONSHIPS OF NORTHERN TERRITORY SPECIES

While *H. isora* is clearly distinct at the sectional level, within species of *Helicteres* section *Orthocarpaea* four loosely-defined groups can be recognised.

*Helicteres cana* group (*H. cana*): Plants erect, the indumentum is fine, leaves are virtually entire, with both surfaces densely hairy, the corolla is distinctly 2-lipped, the lower (abaxial) petals lack an area of matted hairs, petals are more strongly bent, relatively long, and the androgynophore is clearly exerted.

*Helicteres hirsuta* group (*H. hirsuta*): Similar to *H. cana* except the indumentum is coarser, leaves are toothed, discolorous, the inflorescence is racemose and indeterminate, the androgynophore is scarcely exerted and the anthers intorse at dehiscence.

*Helicteres darwinensis* group (*H. darwinensis, H. macrothrix, H. sphaerotheca, H. ftagellaris, H. integrifolia, H. kombolgiana, H. procumbens, H. cana* except the indumentum is finer, leaves are more strongly toothed, the inflorescence is racemose and indeterminate, the androgynophore is scarcely exerted and the anthers intorse at dehiscence.

*Helicteres integrifolia* group (*H. angustifolia, H. integrifolia, H. kambolgiana, H. procumbens, H. sphaerotheca, H. tenuipila, with *H. flagellaris* perhaps transitional to the previous group): Plants are erect or prostrate, the indumentum often fine to coarse, leaves usually irregular, relatively large, abaxial petals with matted hairs, androgynophore as long as calyx.

*Helicteres tenuipila* group (*H. hirsuta* group [*H. darwinensis, H. integrifolia*, *H. integrifolia* group [*H. darwinensis, H. angustifolia*]): Similar to *H. integrifolia* except the indumentum is finer, leaves are more strongly toothed, the inflorescence is racemose and indeterminate, the androgynophore is scarcely exerted and the anthers intorse at dehiscence.

CONSERVATION STATUS OF NORTHERN TERRITORY SPECIES

The conservation status of all species has recently been reassessed against IUCN criteria following IUCN guidelines as part of a five-yearly review of the conservation status of the N.T. flora (IUCN 2001, 2003; IUCN Standards and Petitions Subcommittee 2010). Most species have been assessed as IUCN Least Concern.

*Helicteres cana* is regarded as Near Threatened partly because of its restricted distribution. Among the factors contributing to the Endangered status of *Helicteres macrothrix* are past and projected loss of populations due to land clearing for horticulture, subdivision, railway or road maintenance and quarrying. Both species are threatened to varying degrees by invasion of habitat by the perennial weed Gamba Grass (*Andropogon gayanus*). The resulting changes in fire regimes, soil hydrology, nitrogen availability and light are serious developing threats (Cowie, Kerrigan & Stuckey in press; J. Westaway & I. Cowie unpubl.).

TAXONOMY

*Helicteres cana* (Schott & Endl.) Bentham, 1863

(Figs 2, 3A, B, 4)

*Methiorium canum* Schott & Endl., Meltemata Botanica 29, t. 5 (1832).

_Type Citation:* “Habitat in Novae Hollandiae tropicae septentrionalis sinu Carpentaria” [Australia, N.T., 1803], F. Bauer s.n. (HOLOTYPE: ?BP, n.v.).

_Description.* Open shrub to 2 m tall, stems 1–several, sparingly branched, often grey or grey-green. Stems and both leaf surfaces hoary, densely and shortly stellate-puberulous with hairs 0.1–0.5(0.7) mm diam.; calyx and capsule densely and shortly stellate-pubescent with stellate hairs and straight or flexuose bristles to 3 mm long. Stipules caducous, linear, 2.2–12 mm long. Petiole 3–13 mm long. Leaf lamina lanceolate to ovate, less often linear, narrowly oblong, suborbicular or very broadly obovate, 27–150 mm long, 7–88 mm wide, 1–11 times longer than wide, concolorous to weakly discolorous, often folded longitudinally, base broadly attenuate or rounded to cordate, 3–5-nerved, closely reticulate and raised on under surface, margins entire, rarely toothed in upper half, apex acute to obtuse or rounded, sometimes apiculate or shortly acuminate. Inflorescence axillary, eynome, contracted, 2–many-flowered, dichasia 2-flowered; extra-floral nectaries present; bracts linear, 1–5 mm long; pedicels 1–3 mm long. Calyx tubular to elliptoidal, 6–11 mm long, basal nectary incomplete, margin minutely irregular, lobes triangular, 1–3 mm long. Corolla 2-lipped. Petals mauve, slightly dimorphic, 10–20 mm long, 3.5–5 mm wide, long-clawed, euneate-spathulate, with scattered short simple spreading or patent hairs, apex truncate to obcordate; lower 3 petals narrower than upper pair, on the inner surface with (0) 1 or 2 lateral auricles at base of limb, pad of woolly matted hairs absent; upper pair petals on the inner (adaxial) surface with one lateral and one medial or sublateral auricle at base of limb, with a glabrous glossy, slightly callused area just above auricles. Androgynophore 7.5–14 mm long, straight, medially with scattered, short simple hairs, longer than calyx; stamens 10, scarcely connate at base, 1–1.5 mm long; anthers transverse; staminodes 5, lanceolate to narrowly obovate, 0.5–0.7 mm long. Style 1–1.2 mm long, straight; stigma of 5 pin-like lobes, tereate, diverging.
slightly at apex. Capsule ellipsoid to oblong, 7–32 mm long, 7–11 mm diam., apex shortly beaked or not; carpels straight, 2–7-seeded. Seeds variable in shape, sub-rhomboidal to conoidal, laterally compressed, 2–3 mm long, 1.5–2 mm wide, finely rugose, dark brown. Flowers and fruits: most

Distribution and ecology. The species is endemic to Australia (N.T., Qld). It occurs in the northern N.T. and on nearby islands of the Gulf of Carpentaria, Qld, and grows in open Eucalyptus-dominated vegetation, usually on well drained sandy or stony soils.

Notes. The species is characterised by the hoary, concolorous or weakly discolorous leaves, fine indumentum, the lack of a woolly or smooth, glossy callus on the lower (abaxial) petals and the androgynophore which is distinctly longer than the calyx. It differs from H. angustifolia especially in that leaf laminae are concolorous or weakly discolorous and the upper surface of the lamina is densely and shortly stellate-tomentose and hoary; the petals lack a woolly or smooth, shiny callus; the calyx, corolla and androgynophore are all longer than for H. angustifolia.

Schott & Endlicher (1832) provide a detailed illustration of H. cana, leaving no doubt as to the application of the name and cited a Bauer specimen from the northern Gulf of Carpentaria as the type specimen. However, it is not immediately clear if this specimen is part of the same gathering as a Brown collection at BM labelled in Brown's hand “Orthocarpus incana, North Coast” (duplicate MEL222172) and apparently collected from Sierss Island (island a), Gulf of Carpentaria on 17 Nov 1802 (Stearn 1960). The specimen attributed to Bauer could represent either a separate gathering or part of the Brown collection retained by Bauer for illustrative purposes. The taxon is common in eastern Arnhem Land and Bauer would probably have had opportunity to gather material from a number of places from Groote Eylandt north to Arnhem Bay. This area fits better with the 'northern Gulf of Carpentaria' locality given by Schott & Endlicher (1832) than does Sierss Island which is in the southern Gulf of Carpentaria. For these reasons I treat the Brown and Bauer collections as distinct gatherings. An additional sheet, MEL (222171), labelled "Helicteres aff. H. cana, North Coast" and collected by Brown is in fact H. integrifolia subsp. dentata.

As recognised here, H. cana is variable in the size, shape and degree of folding of leaves, the degree of serration of the margin, the distance the main lateral veins extend up the leaf lamina, and in the length of the fruit and indumentum. Using these characters two geographically distinct entities can usually be distinguished. However, specimens displaying intermediate attributes do exist in the Pine Creek to Nitmiluk N.P. area and this fact, coupled with an absence of critical features on regenerating plants (e.g. Cowie 6668), has led me to recognise them as subspecies, subsp. cana and subsp. latifolia.

Leaves mostly strongly channelled (or folded longitudinally when dry), lamina linear to ovate or elliptic, 2–11 times longer than wide, major lateral veins mostly extending less than 50% of lamina length, margin usually entire in upper half; capsule 7–20 mm long...........................................subsp. cana

Leaves not strongly channelled or folded longitudinally, lamina ovate or elliptic to suborbicular or very broadly obovate, 1–3.1 times longer than wide, major lateral veins mostly extending more than 50% of lamina length from base, margin usually at least partly serrate in upper half; capsule 14–32 mm long ..................subsp. latifolia

Helicteres cana (Schott & Endl.) Beuth. subsp. cana

Others specimens examined. NORTHERN TERRITORY: McArthur River Station, CSIRO paddocks, 14 June 1985, M. Andrew 1009 (DNA); Cape Arnhem, 7 March 1995, M. Barritt 1741 (DNA, MEL); Nhulunbuy, Whitewood Rd, 3 February 1997, R. Booth 1399 (DNA); Nhulunbuy, Gaynagaru Walk, 5 February 1997, R. Booth 2137 (DNA); Kakadu N.P., near Coronation Hill gate, Gimbah, 6 March 1991, K. Brennan 1146 (DNA); Kakadu N.P., Gimbah, 6 April 1990, K. Brennan 218 (DNA); 15 km WSW of Cape Arnhem, site B9, 14 February 1994, K. Brennan 2439 (DNA); Kakadu Stage 3 Fauna Survey, site 14, 19 April 1990, K. Brennan 3 & T. Orr (DNA); English Company Islands, Inglis Is., 7 September 1996, K. Brennan 3321 (DNA); M15, MacArthur River mine lease, 7 April 2003, K. Brennan 5889 & K. Metcalfe (DNA); Kakadu N.P., lookout hill near Coronation Hill, 8 August 1990, K. Brennan 694 (DNA); Gove, Latram River, 20 May 2008, K. Brennan 7688 (DNA); Carpentaria, 1802, R. Brown s.n. (MEL, NSW); 3 miles [4.8 km] S of Larrimah, 5 February 1969, N.B. Byrnes 1354 (DNA, NT); Borroloola, McArthur River road, 7 April 1970, N.B. Byrnes 1854 (DNA, NT); 16 km SW of Goyder River crossing, 16 June 1972, N.B. Byrnes 2638 (CANB, DNA, K, L, NSW, NT); Arnhem Land, Mamingrida-Oenpelli road, 19 July 1987, M.J. Clark 1171 (DNA); Arnhem Land, 3 km NE of Bulman, 16 September 1987, M.J. Clark 1191 (DNA); NE Arnhem Land, 29 September 1987, M.J. Clark 1521 (DNA, MEL); Nhulunbuy, 200 m S of ovals, 1 March 1985, P. Clemisson 18 (DNA); Gove Peninsula, August 1974, J.F. Cooper s.n. (NSW); Arafura Swamp, old homestead, 19 May 1990, I.D. Cowie 1233 (DNA); west of Old Arafura, 22 May 1990, I.D. Cowie 1311 (DNA, MEL); S of Ramingining, 22 May 1990, I.D. Cowie 1312 (BRI, DNA, MEL, PERTH); McMinns Bluff, near Pine Creek, 25 January 1991, I.D. Cowie 1472 & C.R. Dunlop (BRI, CANB, DNA, MEL); Groote Eylandt, 5 km N of Angurugu, 10 September 1991, I.D. Cowie 1997 & P.S. Brocklehurst (BRI, DNA); Groote Eylandt, 1.3 km NNE of Angurugu, 11 April 1992, I.D. Cowie 2567 (BRI, DNA, MEL); Arnhem Bay, Raymangirr, 22 May 1992, I.D. Cowie 2788 (DNA); Nh...
Fig. 3. A, B. *Helicteres cana* subsp. *cana*. A, leaf shape variation (Clark 1521, Blackshall 68); B, flowering branchlet (Clark 1521). C. *Helicteres cana* subsp. *latifolia*: fruiting branchlet (Cowie 976 & Estbergs). D–G. *Helicteres kombolgiana*. D, central lower petal; E, upper petals (D–E, Cowie 12530); F, flowering branchlet; G, fruit. (F–G, Egan 4528). H–K. *Helicteres tenuipila*. H, flowering branchlet (Cowie 3269); I, fruit (Cowie 5347 & Taylor); J, upper petals; K, central lower petal (J–K, Cowie 10361 & Egan, type). Scale bars: A = 3 cm, B = 2 cm, C, F, G, H, I = 1 cm, D, E, J, K = 5 mm.
of Oenpelli, Mt Borradaile road, 23 June 1992, I.D. Cowie 3022 & R. Booth (BRI, DNA, MEL); Biakertoon Is., near airport, 29 April 1993, I.D. Cowie 3903 & C.R. Dunlop (BRI, CANB, DNA, MEL); Blue Mud Bay, Woodah Is., 1 May 1993, I.D. Cowie 4011 & C.R. Dunlop (DNA); Rorruwuy Outstation, Arnhem Bay, 31 August 1995, I.D. Cowie 6068 (DNA); Flinders Peninsula, E side opposite S end of Probable Is., 28 April 1996, I.D. Cowie 6695 & P. Bakarre (BRI, DNA); Inglis Is., north side, 30 April 1996, I.D. Cowie 6828 (DNA); eastern Arnhem Land, near Murrangga, 16 June 1999, I.D. Cowie 8348 (DNA); central Arnhem Land, near Emu Springs, 18 September 1999, I.D. Cowie 8405 (DNA, MEL); Groote Eylandt, c. 18 km NE of Angurugu, 7 March 2005, I.D. Cowie 10530 & K. Brennan (BRI, DNA, L, MEL); c. 14 km SE of Nhulunbuy, on road to airport, 25 November 2007, I.D. Cowie 11800 (DNA); cultivated at Lucy Ct, Driver (provenance Nhulunbuy area), 7 June 2010, I.D. Cowie 12542 (DNA, SING); McArthur...


**Description.** Calyx and capsule densely and shortly stellate-puberulous or densely pilose with stellate hairs and straight or flexuose bristles. Stipules caducous, linear, 2.5–12 mm long. Petiole 3–13 mm long. Leaf lamina lanceolate to ovate, less often linear, narrowly oblong, 37–150 mm long, 7–40 mm wide, 2–11 times longer than wide; more or less discoloured, main lateral veins at base extending 32–50% of leaf length, margin usually entire, rarely toothed in the upper half, apex acute to obtuse. Calyx 6–10 mm long. Petals 10–14 mm long. Androgynophore rarely 5.8 km c. 5.8 km.

**Distribution and ecology.** Widespread in the eastern part of the Top End, extending from Kakadu N.P. and Gove Peninsula around the Gulf hinterland into the Qld Gulf country.

**Helicteres cana** subsp. *latifolia* Cowie, subsp. nov. (Figs 3C, 4, 5)

*A Helicteres cana* Schott & Endl. subsp. *cana* lamina folii non valde caniculata vel longistorsum pliaca, latiore et ovata vel elliptica ad suborbiculare vel latissime ovata, 1–1.3-plo longiore quam latiore, venis magnis basis pro parte maxima ultra 50% laminae extensis, marginis plus...
minusve serrato dimidio supero ad capsula longioribus (14–32 mm longa) differens.

**Type:** Australia, N.T., Gregory N.P.; near entrance, off Victoria Hwy, 10 February 1992, I.D. Cowie 2209 & P.S. Brocklehurst (HOLOTYPE: DNA; ISOTYPES: AD, BRI, CANB, K, MEL, NSW, PERTH).

**Other specimens examined.** NORTHERN TERRITORY. Jarrome Yards, 10 May 1994, M. Barritt 1208 (DNA); Kapalga, SW of mining hut, 21 December 1991, K.G. Brennan 1718 (DNA); Kakadu Hwy, 0.3 km N of turnoff to Goodparla, 22 December 1991, K.G. Brennan 1720 (DNA); Edith Falls, 13 June 1985, J. Brock 87 (DNA); 18 miles [29 km] E Pine Creek, 28 January 1969, N.B. Byrnes 1345 (DNA); Kapalga, 13 December 1988, I.D. Cowie 718 (DNA); near Mining hut, Kapalga, 15 February 1990, I.D. Cowie 976 & J.A. Estbergs (DNA); Big Nellie Ck, 7 December 1990, I.D. Cowie 1449 & C.R. Dunlop (DNA); near Raft Point, c. 22 km from Mandorah turnoff, 1 February 1991, I.D. Cowie 1490 & C.R. Dunlop (DNA); Nitmiluk N.P., near Edith Falls, 23 November 2001, I.D. Cowie 9511 & G.M. Holland (DNA); Kapalga, road to mining hut, 16 August 1991, J. Cusack s.n. (DNA); Edith Falls, 13 April 1995, J. Egan 4724 (DNA); 18 miles [29 km] NE of Pine Creek township, 11 March 1965, M. Lazarides 161 (DNA); Edith River arca, 4 February 1999, C.R. Michell 2370 & J.A. Rister (DNA); Nitmiluk N.P., 1 March 2001, C.R. Michell 3297 & S. Boyce, (DNA); Edith Falls area, 7 May 2002, C.R. Michell 3615 (DNA); Frances Creek mine, 23 May 2000, D. Napier 57 (DNA); Nitmiluk N.P., site 472, 6 April 2001, J.A. Risler 1302 & M. Waetke (DNA); 5 km E of Winwyurr Ck crossing, 4 February 1984, J. Russell-Smith 1106 (DNA); Victoria River, Gregory N.P., 25 February 1986, G.M. Wightman 2733 (DNA).

**Description.** Calyx and capsule hoary, densely and shortly stellat-puberulous with hairs 0.1–0.4 mm diam. Stipules caducous, linear, 2.2–5 mm long. Petiole 3–10 mm long. Leaf lamina ovate to suborbicular, very broadly ovate or very broadly obovate, rarely lanceolate, 42–105 mm long, 17–88 mm wide, 1–3.1 times longer than wide, discolorous, main lateral veins at base extending 46–87% of the length of the lamina, the lamina often irregularly dentate, serrate or sinuate in the upper half, apex acute or acuminate to rounded. Calyx 7–11 mm long; lobes 1–3 mm long. Petals 11–20 mm long. Androgynophore 12–14 mm long. Capsule 14–32 mm long. Flowers: (Aug.) Nov-Feb. Fruits: (Aug.) Nov–Feb.

**Distribution and ecology.** This subspecies is endemic to the western Top End of the N.T., from the lowlands of Kakadu N.P. and the western margins of Nitmiluk N.P. to Bynoe Harbour and south to Gregory N.P. It grows in woodland dominated by species such as Eucalyptus tectifica, E. minitata, E. patellaris and E. phoenicea, often with perennial grasses on coarse sandy to clay loam soils on granite, sandstone, basalt and laterite and in various topographic situations.

**Notes.** Collections from near Pine Creek and the western side of Nitmiluk N.P. have narrower leaves and are closer to subs. *cana* than those from elsewhere.

**Etymology.** From the Latin *latus*, broad and *-folius*, leaved, referring to the broad leaves of this subspecies.

**Helicteres danvinensis** Cowie, sp. nov. (Figs 4, 6, 7F-I, 8)

Ab *Helicteres integrifolia* habitu prostrato, indumento grosso, pilis stipitatis stellatis, stipulis persistentibus, longioribus, 7–20 mm longis, inflorsectis 30–50 mm longis, bracteis, calyce, petalis et androgynophoro omnibus longioribus discrepans.

**Type:** Australia, N.T., Channel Island Rd, SW of Palmerston, 20 November 2008, I.D. Cowie 12221 (HOLOTYPE: DNA; ISOTYPES: AD, B, BRI, CANB, K, L, MEL, MO, NSW, NY, PERTH).

**Illustrations.** Brock, *Top End Native Plants* 217 (1988 and subsequent reprints, incl. as *Native Plants of Northern Australia*), as *Helicteres* sp. (lower illustration).

**Other specimens examined.** NORTHERN TERRITORY. E of Fogg Bay, 13 August 1946, S. Blake 16793 (DNA); Mandorah, track off main Darwin road, 21 December 2008, C.R. Michell 3297 & S. Boyce (DNA); Edith Falls area, 7 May 2002, C.R. Michell 3615 (DNA); Frances Creek mine, 23 May 2000, D. Napier 57 (DNA); Nitmiluk N.P., site 472, 6 April 2001, J.A. Risler 1302 & M. Waetke (DNA); 5 km E of Winwyurr Ck crossing, 4 February 1984, J. Russell-Smith 1106 (DNA); Victoria River, Gregory N.P., 25 February 1986, G.M. Wightman 2733 (DNA).
Helicteres (Malvaceae) from the Northern Territory

1994, R. Booth 234 & P.F. Munnis (DNA); Edith Falls, 10 November 1986, D. Bowman 299 (DNA); Munmulary, 3 May 1986, D. Bowman 367 (DNA); Kakadu N.P., below Mt Brockman massif, 1 April 1990, K.G. Brennan 217 (DNA); Kakadu N.P., Ranger Lease, 10 December 1990, K.G. Brennan 796 (DNA); Ranger Lease, 5 December 1991, K.G. Brennan 1645 (DNA); Mungella, 3 September 1866, J. Brock 136 (DNA); Darwin River region, Labersheda, 1 October 1983, J. Brock 149 (DNA); Darwin River Dam area, Labersheda, 28 September 1986, J. Brock 154, 135 (DNA); Berrimah, Quarantine road, 10 March 1969, N.B. Byrnes 1402 (DNA); East Arm Rd, near easucsway, 16 October 1986, M.J. Clark 705 (DNA); near Marlow Lagoon, Palmerston, 14 March 1990, I.D. Cowie 975 (DNA); near Marlow Lagoon, Palmerston, 12 June 1990, I.D. Cowie 1315 (DNA); E of Pioncer Ck. Mandorah Road, 9 June 1990, I.D. Cowie 3116 (DNA); Old Jim Jim road, 16.4 km from Arnhem Hwy, 8 February 1991, I.D. Cowie 1370 & R. Booth (DNA); Litchfield N.P., 23 November 1990, I.D. Cowie 1425 & C.R. Dunlop (DNA); Jabiru, below lake wall, 30 December 1991, I.D. Cowie 2142 (DNA); c. 2 km N Koongarra Saddle, beside road, 1 January 1992, I.D. Cowie 2143 (BRI, DNA); N end Koongarra Airstrip, 1 January 1992, I.D. Cowie 2145 (DNA); N of Brogeden Pt, 10 October 1992, I.D. Cowie 3185 (DNA); Arnhem Hwy, Oenpelli turnoff, 15 October 1992, I.D. Cowie 3249 (DNA); near Numbubaw Rock, 13 May 1997, I.D. Cowie 7354 (DNA); Stuart Hwy, c. 35 km N of Katherine, 23 November 2001, I.D. Cowie 9518 & G.M. Holland (BRI, DNA); Daly River road, just S of Survey Ck, 3 December 2002, I.D. Cowie 9658 & C.P. Mangion (DNA); 10 km S of junction Arnhem Hwy-Pine Creek road, 18 May 1980, L. Craven 5376 (CANB, DNA); 35 km SSW Coindra, Pine Creek road, 19 May 1980, L. Craven 5398 (CANB, DNA); Margin of Jabiru airstrip, 22 March 1984, L. Craven 8238 & G.M. Wightman (DNA); 23 km S of Darwin along Stuart Hwy, 24 May 1987, L. Craven 8589 & J.P. Grace (CANB, DNA); 1 km W of Mt Bundey Ck, Arnhem Hwy, 14 December 1990, C.R. Dunlop 8774 & I.D. Cowie (DNA); Litchfield N.P., along main rd, 24 April 1993, J. Egan 2178 (DNA); Litchfield N.P., 17 December 1993, J. Egan 2911 (DNA); Mount Todd mine site, 17 March 1995, J. Egan 4441 (DNA); road to Umbrwarin Gorge, 5 April 1995, J. Egan 4643 (DNA); Kangaroo Flats-Wangi Falls road, 23 December 2004, J. Egan 5459 (DNA); Edith Falls road, 10.5 km from Stuart Hwy, 3 December 1990, M. Evans 3474 (DNA); Melville Is., 13 April 1986, R. Feussham 86 (DNA); Melville Is., 3 September 1986, R. Feussham 271 (DNA); Mandorah Road, 62 km past Berry Springs, 21 November 1989, P. Forster 6053 (DNA); Takamprimili Ck, Pickertaranooro, Melville Is., 24 November 1989, P. Forster 6085 (DNA); Mt Brockman, 25 October 1974, B. Fox 701 (DNA); c. 12 km N of Daly River Police Stn, 22 May 1983, P. Fryxell 4247 (CANB, DNA); Port Darwin, 26 July 1913, G.F. Hill 97 (MEL); Port Darwin, 1883, G. M. Holtze s.n. (MEL); Port Darwin, 1883, M. Holtze 545 (MEL); Port Darwin, 1888, M. Holtze s.n. (MEL); Port Darwin, s.d., M. Holtze s.n. (NSW); Port Darwin, 5 March 1905, M. Holtze 1134 (MEL); Port Darwin, 5 March 1905, M. Holtze 1235 (MEL); c. 5 km from Dundee Beach turnoff, N along Cox Peninsula Road, 12 October 2001, A.M. Hope 21 & D. Dixon (DNA, SING); Palmerston, near junction of Lambrick Avenue/Stuart Hwy, 23 November 2001, A.M. Hope 32 (DNA); Munmulary Stn, 15 April 1973, P. Latz 3902 (DNA); Melville Is., on Macleay Crk road, 20 January 1992, G.J. Leach 2942 & I.D. Cowie (DNA); Finniss River road to Litchfield N.P., 21 September 1992, G.J. Leach 3259 (DNA); Emerald Springs, 22 September 1992, G.J. Leach 3264 (DNA); Jindarie Station, Stray Ck catchment, Daly Basin, 13 November 2003, D.L. Lewis 395 (DNA); Cox Peninsula, 13 April 1988, K.M. Manning 368 (DNA); Koongarra area, s.d., O.H. Marshall s.n. (CANB); 5 miles [8 km] NW of Humpty Doo, 8 November 1971, J.L. McKean 25 (DNA); Darwin Harbour, Wickham Point, 14 January 1997, K. Metcalfe s.n. (DNA); Edith River Area, 12 April 1999, C.R. Michell 2340 & J.A. Rischer (DNA); Nitmiluk N.P., 28 March 2002, C.R. Michell 3616 (DNA); 12 miles [19 km] W.S.W. of Mudginberri H/st, 20 November 1970, J. Must 582 (DNA); Acacia Gap turn-off, 39.6 miles [63.4 km] S of Darwin, 15 June 1964, D.J. Nelson 1195 (DNA); Batchelor area, 17 December 1974, M.O. Parker 614 (DNA); Horns Ck, 8 November 1978, M. Raukin 1554 (DNA); Berrimah Riding School, 9 December 1982, M. Rankin 2680 (DNA); 11 km from Stuart Hwy along Umbrwarra Gorge road, 12 January 1999, J.A. Rischer 77 & R.A. Kerrigan (DNA); Charles Darwin N.P., 5 March 1998, P.S. Short 4666 & C.R. Dunlop (DNA); Elizabeth River crossing, Channel Is. road, 20 March 1989, N.M. Smith 1424 (DNA); near Robin Falls, Mt Bundy station, 3 November 1985, B.W. Strong 783 (DNA); Holmes Jungle, 12 km NE Darwin, 18 April 1980, I.R.H. Telford 7432 & J. Wrigley (CANB); 4 km ESE Jabiru, 18 April 1980, I.R.H. Telford 7547 & J. Wrigley (CANB); Fannie Bay, 1886, J.E. Tenison-Woods 595 (DNA); Charles Darwin N.P., 15 April 1992, G.J. Leach 2942 & I.D. Cowie (DNA); Darwin Harbour, Wickham Point, 14 January 1997, K. Metcalfe s.n. (DNA); Edith River Area, 12 April 1999, C.R. Michell 2340 & J.A. Rischer (DNA); Nitmiluk N.P., 28 March 2002, C.R. Michell 3616 (DNA); 12 miles [19 km] W.S.W. of Mudginberri H/st, 20 November 1970, J. Must 582 (DNA); Acacia Gap turn-off, 39.6 miles [63.4 km] S of Darwin, 15 June 1964, D.J. Nelson 1195 (DNA); Batchelor area, 17 December 1974, M.O. Parker 614 (DNA); Horns Ck, 8 November 1978, M. Raukin 1554 (DNA); Berrimah Riding School, 9 December 1982, M. Rankin 2680 (DNA); 11 km from Stuart Hwy along Umbrwarra Gorge road, 12 January 1999, J.A. Rischer 77 & R.A. Kerrigan (DNA); Charles Darwin N.P., 5 March 1998, P.S. Short 4666 & C.R. Dunlop (DNA); Elizabeth River crossing, Channel Is. road, 20 March 1989, N.M. Smith 1424 (DNA); near Robin Falls, Mt Bundy station, 3 November 1985, B.W. Strong 783 (DNA); Holmes Jungle, 12 km NE Darwin, 18 April 1980, I.R.H. Telford 7432 & J. Wrigley (CANB); 4 km ESE Jabiru, 18 April 1980, I.R.H. Telford 7547 & J. Wrigley (CANB); Fannie Bay, 1886, J.E. Tenison-Woods s.n. & M. Holtze (MEL); about halfway between Stuart Hwy & Berry Springs, 25 September 1980, J.T. Waterhouse 9834 (NSW);
Fig. 7. A-E. Helicteres macrothrix. A, flowering branchlet; B, bristle from fruit (A-B, Dunlop 9805); C, upper petals; D, androgynophore; E, lower petals (C-E, Cowie 9656 & Kerrigan). F-I. Helicteres darwinensis. F, flowering branchlet and mature leaf (Dunlop 8774 & Cowie, Rankin 2680); G, fruit (Cowie 1315); H, upper petals; I, central lower petal (H-I, Cowie 12221, type). J-N. Helicteres serpens. J, flowering branchlet (Evans 3483); K, fruit; (Leach 4379) L, calyx; M, central lower petal; N, upper petals (L-N, Cowie 2139). O-S. Helicteres sphaerotheca. O, flowering branchlet; P, leaf; Q, upper petals; R, central lower petal (O-R, Cowie 2146, type); S, fruit (Dunlop 6120). Scale bars: A, J = 2 cm, F, G, H, I, K, L, O, P, S = 1 cm, C, D, E, M, N, Q, R = 5 mm, B = 2 mm
**Helicteres** (Malvaceae) from the Northern Territory

**Fig. 8.** Holotype of *Helicteres darwinensis.*

0.5 km W Geringbark scarp, SE corner of Jabiluka outlier, 5 December 1980, J.T. Waterhouse 10938 (DNA, NSW); Mary River Camp, s.t., M. White 30 (CANB); Berrimah, 7 October 1983, G.M. Wightman 688 (DNA); Lowther Rd, 21 November 1984, G.M. Wightman 1768 (DNA).

**Description.** Multi-stemmed perennial subshrub with prostrate annual above-ground stems to 0.5 m long and a woody perennial root stock. Most vegetative parts and calyx densely stellate-hirsute with sessile and stipitate (0.3 mm long) hairs. Hair sparse to dense on upper surface of leaf lamina, the new growth with scattered digitiform glandular hairs. Petiole 5-10 mm long. Leaf lamina usually ground-hugging, accrescent, lanceolate to ovate or orbicular, 12-16 mm long, claw auriculate, limb cuneate, callused near base, claw and limb with scattered to sparse, simple, sepalate hairs c. 0.15 mm long; lower 3 petals c. 9.5 mm wide, with 0-2 small appendages on claw, callus with matted simple sepalate hairs c. 1 mm long; upper pair, c. 5.5 mm wide, with 2 prominent appendages on claw, callus smooth, obscure. Androgynophore 5-7 mm long, straight, sparsely hairy, distinctly shorter than calyx; stamens 10, shortly connate at base, 0.7-1.2 mm long; anthers transverse; staminodes 5, spathulate-acute, c. 0.8 mm long. Style straight, c. 1 mm long; stigma of 5 pin-like lobes, terecete. Capsule adpressed to ground, depressed globose to obloid, 5-9 mm long, 6-7 mm diam., sparsely stellate-pilose, brown, styles caducous; carpels straight, 1-3-seeded. Seeds sub-ellipsoid, c. 2.5 mm long, 2 mm wide, irregularly rugose, dark brown. Flowers: Aug.-Jan. Fruits: Dec.-June.

**Distribution and ecology.** The species is endemic to the northern N.T. and very common in the north-western Top End, north of Pine Creek and west of the Goomadeer River, including the Tiwi Islands. It grows in Eucalyptus forest and woodland on lateritic soils.

**Notes.** *Helicteres darwinensis* differs from *II. integrifolia* by the prostrate habit, coarse indumentum with stipitate stellate hairs, longer, persistent stipules which are 7-20 mm long, inflorescence 30-50 mm long, and with the bracts, calyx, petals, and androgynophore all longer. While the new shoots are often erect at emergence, they quickly become prostrate.

This species has been referred to as *Helicteres* A78389 Darwin and *Helicteres* sp. Darwin (S.T. Blake 16793) on herbarium specimen labels and unpublished checklists from DNA.

**Etymology.** A reference to the City of Darwin, Northern Territory, around which the species is a common component of the *Eucalyptus* woodland.

**Helicteres flagellaris** (Benth.) Cowie, comb. et stat. nov. (Figs 4, 9).

*Helicteres dentata* var. flagellaris Benth., *Flora australiensis* 1: 233 (1863); *H. semiglabra* var. flagellaris (Benth.) F.M. Bailey, *The Queensland Flora* 1: 142 (1899).

**Type:** Australia, N.T., Port Essington, Apr. 1840, J. Armstrong 533 (Holotype: K, n.v., photo DNA).

**Other specimens examined.** NORTHERN TERRITORY. Aranu Swamp, 8 June 1996, R. Booth 1893 (DNA); along track to Black Jungle Spring, 1 January 1992, K. Brennan 1675 (DNA); Kakadu N.P., Arnhem Hwy, 1 km W of Flying Fox Ck, 13 January 1991, K. Brennan 841 (DNA); 1.7 km S of Danger Point, Cobourg Peninsula, 6 May 1987, M.J. Clark 1052 (DNA); 25.1 km E of Kerr Pt, Weipa, 21 April 1991, J. Clarkson 9013 & V.J. Neldner (BRI, DNA, K, L MBA, PERTH); N of Bertie Ck, 25 February 1992, J. Clarkson 9202 & V.J. Neldner (BRI, DNA, MBA); Kapalga, 15 December 1976, R. Collins 175 (BRI), CANB, DNA); Kakadu N.P., Kapalga, near Red Lily turn-off, 13
Description. A subshrub with prostrate annual aboveground stems to 0.5 m long and a woody perennial tap root. Most parts with a sparse to very dense indumentum of sessile, stellate hairs 0.2–0.4 mm diam. Stipules persistent, subulate, 4–5.5 mm long. Petiole 1.5–5 mm long. Leaf lamina discolorous to strongly discolorous, ovate to suborbicular, 1.8–6.5 cm long, 1.1–5.1 cm wide, 1–1.5 times longer than wide, upper surface usually glabrous or with simple hairs, lower surface often hoary, base cordate, rarely rounded, 5–7-nerved, margin irregularly dentate or serrate throughout, apex rounded to acute, often shortly apiculate. Inflorescence an interrupted axillary eyme, 30–140 mm long, with 1–6 flowers; bracts subulate, rarely leafy, 3–4 mm long; extrafloral nectaries present, dark red; pedicels 0–4 mm long. Calyx 4.5–9 mm long, tube 4–5 mm long, lobes 1.5–5.5 mm long. Corolla scarcely 2-lipped. Petals mauve, slightly dimorphic, slightly bilabiate, 10–16 mm long, long clawed; limb broadly cuneate to depressed ovate, callused near base, both surfaces with a sparse indumentum of erect to appressed short septate hairs c. 0.1 mm long; lower 3 petals with 2 small appendages on margins of claw; callus woolly hairy; upper 2 with 2 prominent appendages on claw, callus smooth, shiny, glabrous. Androgyneophore 4.5–6 mm long; androecium oblique; stamens in diam. Growing on sites with finer textured soils and those with coarse, stipitate stellate hairs (0.5) 1.0–1.5 mm in diam. Growing on sites with finer textured soils and those with finer, sessile stellate hairs 0.1–0.3 (0.6) mm diam. and in sandy soils. Within the large hair group some specimens have calyx lobes longer than the tube (Short 4807 & Dunlop; Cowie 8397 & Harwood), and in Cowie 8767 the lobes are also almost glabrous (rather than densely hairy).
Helicteres (Malvaceae) from the Northern Territory

on the abaxial surface. Several specimens from the Mary River area (Cowie 5171, 10346; Napier 63) have lanceolate or oblong lanceolate or very broadly elliptic floral bracts, with long stipitate stellate hairs along their margins.

Further examination of material from Queensland is required. A number of specimens e.g. L.J. Brass 19587, J. Clarkson 10028 & V.I. Neldner appear to be closely related and may be referable to this taxon.

The species differs from H. integrifversica by the prostrate habit, persistent stipules 4–5.5 mm long, leaves typically ovate to suborbicular, the upper leaf surface glabrous or with simple hairs, the eymes 30–140 mm long, petals 10–16 mm long and the longer androgynophore. Helicteres flagellaris has also been referred to as "Helicteres D47082 prostrata" on herbarium specimen labels and unpublished checklists lists from DNA.

Helicteres integrifolia (F.Muell.) Cowie, comb. nov. (Fig. 4).

Methorium integrifolium F.Muell., Transactions of the Philosophical Institute of Victoria 3: 40 (1859).

Type citation: "On rocky declivities of the sandstone tableland of the Upper Victoria River". Type details: Australia, N. T., upper Victoria River, January 1856, F. Mueller s.n. (Holo type: MEL (MEL222173); Isotype: K, n.v., photo DNA).

Helicteres cana anet non. (Schott & Endl.) Bentham, Flora australiensis 1: 232 (1863).

Description. Erect to spreading, multi-stemmed subshrub to 0.5 m, with annual above-ground parts and a woody perennial root stock. Most vegetative parts and calyx with moderately dense to very dense sessile stellate hairs 0.1 to 0.6 (-1.2) mm diam., hairs sessile or sometimes shortly stipitate; new growth with scattered red minute glandular hairs. Stipules caducous, subulate, 1.5–6 mm long. Leaf lamina ovate to elliptic to suborbicular, less often lanceolate, oblonslanceolate, or oblanceolate to obovate, 18–115 mm long, 8–50 (–75) mm wide, 1.1–3.2 times longer than wide, scarcely to strongly discolorous, under surface usually hoary or grey-green when young becoming less so with age, upper surface with sparse to dense stellate hairs, green to grey, base cordate to rounded or cuneate, symmetric to sometimes asymmetric, 3-nerved for 1/3 to 3/4 of length, margins entire near base, usually becoming serrate near apex, apex acute to rounded. Inflorescence axillary, cymose, to 35 mm long, with few-many dichasia, dichasia 2- or 3-flowered; extra-floral nectaries present; bracts 1–4 mm long, subulate; pedicels 0–6 mm long. Calyx tubular to narrowly obconical-campanulate, 3–6 mm long; basal nectary short, incomplete, margin truncate; lobes triangular, 0.5–2 mm long. Corolla weakly 2-lipped or not. Petals mauve-pink, slightly dimorphic, 5–10 mm long, long clawed, limb cuneate, with sparse, minute, erect, glandular hairs, slightly callused near base, apex truncate to obliquely truncate, irregular; lower 3 slightly longer than upper pair, claw with 1–2 small appendages, callus woolly hairy; upper pair with 2 prominent appendages on claw, callus smooth shiny glabrous, claw with sparse longer simple sepalate hairs. Androgynophore 2.5–4.5 mm long, straight, with scattered minute hairs on adaxial side, shorter than or equal to calyx; staminodes 5, oblanceolate to spatulate-acute, c. 0.7–1 mm long. Style 1–1.2 mm long; stigma of 5 pin-like lobes, terete, caducous. Capsule ovoid to ellipsoid or globular, 8–19 mm long, 6–14 mm diam., with a mid-dense covering of sessile stellate hairs, stellate-hairy bristles absent or present and then sub-dense or dense, floccose, 1.5–4 mm long; carpels straight, 1–4-seeded. Seeds variously shaped, ellipsoid to conoid or sub-rhomboidal, often laterally compressed, 1.8–3.8 mm long, 1.7–2.5 mm wide, irregularly rugose, dark brown. Flowers: Sept.–Feb. Fruits: Feb.–June.

Notes. Bentham (1863) reduced Methorium integrifolium F.Muell. to synonymy under H. cana. While the leaves of the type of M. integrifolium have almost entire margins and a similar greyish colour and indumentum to H. cana, I believe that the species currently known as M. integrifolium must be reinstated and transferred, as above, to the genus Helicteres. The type specimen of M. integrifolium has a calyx 4–5 mm long, the petals are c. 7 mm long, the lower petals have a patch of long, mattèd, glandular hairs and the androgynophore is 3.5–4 mm long. In contrast, H. cana has a calyx 7–11 mm long, the petals 11–20 mm long, the lower ones lack a patch of long mattèd hairs and the androgynophore is 7.5–14 mm long. These character differences are maintained in populations of H. cana which are sympatric with M. integrifolium.

Further investigation shows that H. integrifolia and H. dentata form part of a complex varying in leaf width, discolorousness, density of indumentum on the leaf surfaces, length of bristles on the fruit and degree of serration of the leaf margin. Variation appears to be partly related to edaphic factors and partly clinal.

I here recognise two subspecies within H. integrifolia, i.e. subsp. integrifolia and subsp. dentata. However, there are some specimens which do not comfortably fit within either subspecies and for the time being are simply referred by me to H. integrifolia. Thus, a series of collections from southeast Arnhem Land and adjacent Limmen N.P. (Cowie 12368, 12382, Lewis 1008, 1018, Mannig 425, Wilson 1285) have relatively small concolorous but bifacial leaves, a coarse open indumentum of hairs 0.5–1.2 mm diam., are almost devoid of short glandular hairs on the new growth and have densely long-bristled fruit. Flowers have not been seen. These may prove to represent a distinct taxon allied to H. integrifolia, H. sphaerocistea and H. tenuipila and the variation exhibited by them is not included in the description above. Similarly, the specimens Brennan 1994, 270 and Cowie 8565 may represent an additional undescribed taxon. They are distinctive in having entire or few-toothed, lanceolate, concolorous leaves, a short, close indumentum and fruit with bristles to 0.5 mm long, although the flower
size is consistent with \textit{H. integrifolia}, \textit{H. angustifolia}, \textit{H. sphaerotheca} and \textit{H. tenuipila}. These characters and the small flowers are also consistent with specimens of the southeast Asian \textit{H. lanceolata} (Tang et al. 2007). A number of collections from the Douglas Springs area, which lack flowers, are also tentatively referred to this species pending further collections from that area.

Both subspecies maintain their low, multi-stemmed growth habit in cultivation, regenerating each wet season from a perennial, woody rootstock, even when protected from fire.

1 Leaf lamina slightly discolorous, upper surface densely hairy; capsule densely covered with floccose, stellate-hairy bristles 1-4 mm long .........................

Leaf lamina strongly discolorous especially when young, upper surface with sparse to scattered hairs; capsule lacking stellate-hairy bristles or bristles scattered, rarely to 2 mm long ...........subsp. \textit{dentata}

\begin{itemize}
  \item \textit{Helicteres integrifolia} (F.Muell.) Cowie subsp. \textit{integrifolia}
  \item \textit{Helicteres integrifolia} subsp. \textit{dentata} (F.Muell. ex Benth) Cowie, comb. et stat. nov.
\end{itemize}


\textbf{Description.} Leaf lamina often grey-green, slightly discolorous, the upper surface densely hairy. Capsule 11-14 mm diam., densely covered with floccose, stellate-hairy bristles 1-4 mm long. Flowers: Nov. Fruits: Feb.–June.

\textbf{Distribution and ecology.} This subspecies is endemic to the northern N.T. and grows in \textit{Eucalyptus} woodland on sandy soils.

\textbf{Notes.} Specimens of subsp. \textit{integrifolia} with almost concolorous leaves can look superficially similar to \textit{H. cana} subsp. \textit{latifolia}, but subsp. \textit{integrifolia} has a shorter androecynophore, calyx and corolla and the lacks long, matted, glandular hairs on the lower petals.

This subspecies has been referred to as \textit{"Helicteres D29330 multicaulis"} and \textit{"Helicteres sp. many stems (G.M. Wightman 3410)"} on herbarium specimen labels and unpublished checklists lists from DNA.

\textbf{Helicteres integrifolia subsp. dentata} (F.Muell. ex Benth) Cowie, comb. et stat. nov. (Figs 4, 10)


\textbf{Other specimens examined.} NORTHERN TERRITORY. King River, W of Katherine, 15 November 1995, \textit{M. Barratt} 2042 (BRI, DNA, MEL); Daly River Rd, adjacent to Adelaide River crossing, 16 February 1996, \textit{R. Booth} 1464 & \textit{I.D. Cowie} (BRI, DNA, MEL, K); Kapalga, rocky hills just north of Barramundi Gorge turn-off on Kakadu Hwy, 15 May 1991, \textit{K. Brennan} 1374 (DNA); Kakadu Hwy, 1.6 km N of Barramundi Ck, 22 November 1991, \textit{K. Brennan} 1620 (DNA): 1.5 km SE Fisher airstrip, 12 December 1991, \textit{K. Brennan} 1679 (DNA); Kapalga; E slope of hill, 21 December 1991, \textit{K. Brennan} 1716 (DNA); Kakadu N.P., on track to Barramundi Gorge, e.200 from Kakadu Hwy turn-off, 13 January 1992, \textit{K. Brennan} 1777 (DNA); English Company Islands, island just SW of Bosanquet Is., 6 September 1996, \textit{K. Brennan} 3311 (DNA); Cobourg Peninsula, 9 April 2006, \textit{K. Brennan} 7116 (DNA); Kakadu N.P., Old Darwin road, 6 November 2008, \textit{K. Brennan} 7876 (DNA); Melville Bay, 16 February 1803, R. Brown s.n. (BM, CANB); North Coast, R. Brown (DBN, MEL, NSW); Melville Is., Penelli road, 24 June 1874, \textit{M.J. Clark} 1236 (BRI, DNA, MEL); Gove Peninsula, Arnhem Land, \textit{J.F. Cooper} (DNA, K); Gove Peninsula, Arnhem Land, \textit{J.F. Cooper} s.n. (NSW); I km past Adelaide River, Daly River Rd, 42
Helicteres (Malvaceae) from the Northern Territory

Helicteres on (G.M. Wightman 3410) et calyce setis pilos stellatos ferens, foliis et ramulis pilos caulibus paucis, partibus supra terram perennibus, ramulis modernem township of Timber Creek (Gregory & Gregory 12 km west of the on the upper Victoria River estuary c. date indicates that it was probably collected a little further of the same gathering. Despite the Upper Victoria River of the original material used to describe he does H. dentata, collection has been annotated with a 'B' to indicate it was ascribes the epithet to Mueller. "Me thorium dentation herbarium specimen labels and unpublished checklists lists from DNA. Distribution and ecology. The subspecies is endemic to the northern N.T., from Melville Island to Victoria River and east to Gove Peninsula. It grows in Eucalyptus woodland on sandy, clayey or lateritic soils. It flowers profusely on woodland Eucalyptus east to Gove Peninsula. It grows in the northern N.T., from Melville Island to Victoria River and becoming less so with age, upper surface with sparse to scattered hairs. Capsule 6–12 mm diam., with a moderately dense covering of sessile stellate hairs, stellate-hairy bristles usually absent or scattered, rarely to 2 mm long. Flowers: Sept.–Feb. Fruits: Feb.–June. Notes. This subspecies has also been referred to as Helicteres D20342 Gove (G.M. Wightman 3410) on herbarium specimen labels and unpublished checklists lists from DNA. The holotype bears Mueller’s field label with the name “Methorium dentatum m. sp.” and Bentham (1863) clearly ascribes the epithet to Mueller. There is an additional collection of Mueller’s at MEL labelled “Sea Range [Yambarran Range], Oct [18]55” (MEL222177). While the corner of the label of this collection has been annotated with a ‘B’ to indicate it was apparently seen by Bentham and presumably formed part of the original material used to describe H. dentata, he does not cite it specifically. Specimens on both the K and MEL sheets are at a similar stage of growth and it is plausible that they are in fact part of the same gathering. Despite the Upper Victoria River locality on the label of the K sheet, the October collection date indicates that it was probably collected a little further inland than the vicinity of the depot established by Gregory on the upper Victoria River estuary c. 12 km west of the modern township of Timber Creek (Gregory & Gregory 1884). This locality is only 30 km or so from Yambarran Range, the location on the MEL sheet. Because of this uncertainty, the Sea Range specimen at MEL is included here as a possible isotype.

Helicteres kombolgiana Cowie, sp. nov.
(Figs 3D–G, 4, 11, 12)
Helicteres integrifoliae affinis, sed habitu creuco, caulisibus paucis, partibus supra terram perennibus, ramulis et calyce setis pilos stellatos ferens, foliis et ramulis pilos duarium classium amplitudinem ferens, folii parvioribus acutis, carpellis rostris longis, inflorescentis brevibus, floraibus paucis distinguunt.


Other specimens examined. NORTHERN TERRITORY. Mt Brockman Range, 13 km S of Jabiru, 23 February 1973, L.G. Adams 3089 (CANB, DNA); Nourlangie Rock car park, 16 May 1995, R. Booth 960 (DNA); Kakadu N.P., below Brockman massif, 1 April 1990, K.G. Brennan 216 (DNA); Nourlangie Rock near main galleries, 28 December 1991, K.G. Brennan 1741 (DNA); Kakadu fire plot 132, Leichhardt Spring, 23 March 1999, K.G. Brennan 3809 (DNA); Upper Deaf Adder Creek, Kakadu fire plot 63, 21 March 2009, K.G. Brennan 7930 (DNA); Upper Liverpool River, on road between Kulunguyi and Mirbirk, 22 April 2009, K.G. Brennan 8011 (DNA); Kakadu N.P., Birdie Creek, 18 April 1990, I.D. Cowie 1091 & G.J. Leach (DNA); Koongarra Saddle, 1 January 1992, I.D. Cowie 2144 (DNA); Arnhem Land, Magela Creek upper catchment, 11 April 1995, I.D. Cowie 5604 & K.G. Brennan (DNA); Kakadu N.P., near East Alligator River, W of Rock Holes, 20 April 1999, I.D. Cowie 8299 (DNA); c. 24 km E Myra Falls, Western Arnhem Land, 17 March 2000, I.D. Cowie 8578 (DNA); Western Arnhem Land, Magela Falls Gorge, 23 August 2004, I.D. Cowie 10271 & Crase, B. (DNA); cultivated at Palmerston from seed collected at Magela Falls, 6 June 2006, I.D. Cowie 10644 (DNA); Palmerston, Widdup Creek, cultivated, 5 January 2010, I.D. Cowie 12530 (CANB, DNA, SING); Little Nourlangie Rock, 19 March 1979, C.R. Dunlop 4767 (DNA); Little Nourlangie Rock, 12 May 1978, C.R. Dunlop 4830 (DNA); Jim Jim Falls, 26 March 1982, C.R. Dunlop 6227 (BRI, DNA); Mount Brockman, Kakadu N.P., 27 March 1995, J. Egan 4328 (DNA); Kakadu N.P., 10 km NNE of Jabiru, 28 April 1995, J. Egan 4835 & Knox, S.F. (DNA); Kakadu N.P., Baroalla Springs, 25 May 1983, P. Fryxell 4727 (CANB, DNA); Kakadu N.P., Mt Brockman, 22 May 1980, M. Lazarides 8908 (AD, CANB, DNA, MEL); Kakadu Nat. Park, 14 km E of Slipsbeek, 18 April 1990, G.J. Leach 2755 & I.D. Cowie (BRI, DNA, MEL); 2 km W of Nabarlek Airstrip, 24 April 1979, M. Rautenk 2170 (DNA); Koongarra Jump-up, 12 June 1978, B. Rice 2925 (CANB, DNA); 5 km from Oenpelli, 21 July 1983, J. Russell-Smith 777 (DNA); Goomad carcass, escarpment country, 28 October 1987, J. Russell-Smith 3830 & D. Lucas (DNA); Upper East Alligator River, Arnhem Land, 19 April 1988, J. Russell-Smith 5243 & D. Lucas (DNA); Kakadu, 16 June 1988, J. Russell-Smith 5681 (DNA); Mt Brockman outlier, Kakadu N.P., 20 April 1989, J. Russell-Smith 8039 (DNA); 12 km E of Mudginberri Homestead, Kakadu N.P., 1988, J. Russell-Smith 8461 & J. Brock (DNA); Upper Magela Creek valley, Arnhem Land, 3 May 1991, J. Russell-Smith 8467 & J. Brock (DNA); Kakadu N.P., Koongarra Arca, 16 April 1992. J. Russell-Smith 8590 (BRI, DNA); Manbulloo Stn, Limestone Creek area, 27 November 1996, N.M. Smith 3924 (DNA); Darwin, W.B. Spencer s.n. (NSW); Kintore Caves Reserve, 5 March 1996, S. Taylor 362 & D.J. Liddell (DNA); Gregory N.P., 6 km NE of Bullita Outstation, 8 February 1986, B.G. Thooren 1124 (DNA); Gregory N.P., 15 km E of Victoria River Inn, 27 February 1986, B.G. Thooren 1238 (DNA); Victoria River, Gregory N.P., 25 February 1986, G.M. Wightman 2771 (DNA); Cape Frewett, Bathurst Is., 8 April 1987, G.M. Wightman 3586 & N.M. Smith (DNA); Cuto River mouth area, Djurlipunguy, NE Arnhem Land, 16 February 1988, G.M. Wightman 4214 (DNA, MEL).
Helicteres (Malvaceae) from the Northern Territory

1992, J. Russell-Smith 8638 & D. Lucas (DNA); Magela Ck catchment, Kakadu N.P., plots 7B2, 6B1, 13 April 1995, J. Russell-Smith 10348 & D. Lucas (DNA, SING); Deaf Adder Ck, Gorge, 22 April 1980, I.R.H. Telford 7997 & J. Wrigley (CANB); 6.5 km SSW Mt Brockman, 23 April 1980, I.R.H. Telford 8040 & J. Wrigley (CANB); 0.5 km NE Koongarra Saddle, 16 August 1980, I.R.H. Telford 8421 & J. Wrigley (CANB).

Description. Open, perennial shrub to 3 m tall, stems few, much branched. Branchlets, young growth, stipules and leaf surfaces covered with a mid-dense to very dense, white indumentum (hyaline on leaf upper surface) of sessile stellate hairs of 0.1–0.3 mm diam., grading into an overlying layer of stipitate stellate hairs 0.5–1.2 mm diam. Calyx also with scattered bristles to 0.7 mm long, bearing stellate hairs. Stipules caducous, subulate, 2.5–5 mm long. Petiole 3–10 (19) mm long. Leaf lamina antrorse, lanceolate to ovate or elliptic, 25–70 (105) mm long, 10–35(60) mm wide, 1.6–3 times longer than wide, slightly to strongly discolorous, hoary or grey-green below when young, base cordate to rounded, symmetric to slightly asymmetric, 3–5-nerved, margins serrate, apex acute to sometimes obtuse. Inflorescence axillary, to 10 mm long, few-flowered (often a single dichasium), extra-floral nectaries present; dichasia 1–2-flowered; bracts 2.5–5 mm long, subulate; pedicels 0–1 mm long. Calyx tubular to obovoid-urceolate, 4–6.5 mm long, basal nectary incomplete, truncate; lobes triangular or narrowly triangular, 1–4 mm long. Corolla weakly 2-lipped. Petals mauve, the upper pair paler than lower 3, slightly dimorphic, 5.5–9 mm long, long clawed, limb euneate, with scattered minute erect hairs, with a callus near base, apex truncate to rounded; lower 3 slightly longer than upper pair, claw with 2 small appendages, calmas woolly hairy; upper pair broader, with 2 prominent appendages on claw (one adaxial, one lateral), callus glabrous, smooth. Androgynophore 3–5 mm long, straight, shorter than calyx; stamens 10, shortly connate at base, c. 0.7 mm long; anthers transverse; staminodes 5, spathulate-acute. Style straight, 1–1.5 mm long; stigma of 5 pin-like lobes, terete. Capsule ovoid to subglobular, 10–22 mm long, c. 12 mm diam., densely covered with floccose bristles to 4 mm long, bristles bearing stellate hairs 0.6–0.8 mm diam., styles persisting and forming a beaked apex; carpels straight, 2–5-seeded. Seeds variously shaped, ellipsoid to oboconoidal or subrhomboidal, often laterally compressed, c. 3 mm long, c. 2.5 mm wide, irregularly rugose, dark brown. Flowers: Jan.–May. Fruits: Jan.–July.

Distribution and ecology. Endemic to the northern N.T., in Kakadu N.P. and adjacent areas of western Arnhem Land, almost to Maningrida. Grows in Allosyncarpia forest or Eucalyptus woodland, on sandy soils on scree slopes or closely associated with other outcropping sandstone.

Notes. This species is allied to Helicteres integrifolia but distinguished by the erect habit, few-stemmed perennial above-ground parts, branchlets and calyx with bristles bearing stellate hairs, hairs of two size classes on the leaves and branchlets; the smaller and acute leaves; long, beaked apices of the carpels and short, few-flowered inflorescences. The open, much branched, few-stemmed growth habit of this taxon is maintained in cultivation.

The type collection was grown from seed gathered from I.D. Cowie 10644, collected at Magela Gorge Falls, N.T.

Fig. 11. Helicteres kombolgiana. Flower and leaf (I. D. Cowie 10644).

Fig. 12. Holotype of Helicteres kombolgiana.
Helicteres macrothrix Cowie, sp. nov.
(Figs 4, 7A–E, 13, 14)

Ab Helicteres integrifolia et specierum cognatis inflorescentis congestis, indumento densissimo, pilis grandioribus, diametro 1.5–4.5 mm, androgynophoro breviori, capsulis dense hirsutis diagnoescendo. Affinis Helicteres darwinensis Cowie, sed ea habitu erecto, multienae, inflorescentis congestis, indumento densissimo, pilis grandioribus distincta.


Other specimens examined. NORTHERN TERRITORY. 54 miles [86 km] S of Darwin, Stuart Hwy, 10 January 1969, N.B. Byrnes 1280 (DNA); near Glenluckie Ck, Stuart Hwy, 25 January 1991, I.D. Cowie 1481 & C.R. Dunlop (DNA); near Glenluckie Ck, Stuart Hwy, 15 March 1991, I.D. Cowie 1565 & P.E. Muirns (DNA); Marrakai Road, W of turnoff to Lake Bennett, 29 November 2002, I.D. Cowie 9654 (DNA); near Lake Bennett, E side, 29 November 2002, I.D. Cowie 9656 & R.A. Kerrigan (DNA); Lake Bennett, c. 70 km S of Darwin, 26 January 1994, C.R. Dunlop 9805 (BRI, DNA); 8.4 km W of Annaburroo, 12 September 1992, J. Egan 402 (DNA); 8 km W of Annaburroo, 12 September 1992, J. Egan 403 (DNA); 8 km W of Annaburroo, 1 October 1993, J. Egan 902 (DNA); Annaburroo, 8 km E of dam, 10 January 1993, J. Egan 903 (DNA); Arnhem Hwy, near Annaburroo, 27 March 1995, J. Egan 4472 (DNA); Mt Bundey area, 8 km W of Annaburroo, near Glenluckie Ck, Arnhem Hwy, 14 November 2001, A.M. Hope 23 & I.D. Cowie (DNA, SING); Mt Bundey area, 8 km W of Annaburroo, near Arnhem Hwy, 14 November 2001, A.M. Hope 24 & I.D. Cowie (DNA); Mt Bundey area, 6.5 km W of Bark Hut/Annaburroo, 14 November 2001, A.M. Hope 27 & I.D. Cowie (DNA).

Description. Erect, multi-stemmed subshrub to 0.6 m, with annual above-ground parts and a woody perennial rootstock. Vegetative parts, calyx and bracts usually with a dense to very dense indument of multiangulate stellate hairs. Leaf lamina ovate, occasionally elliptic or broadly ovate, 50–170 mm long, 40–110 mm wide, 1.3–1.7 times longer than wide, discolorous, base shallowly cordate or rounded, margins senate to dentate, apex acute to obtuse. Inflorescence axillary, congested, cymose, to 40 (70) mm long, with up to 12 flowers, dichasia 2-flowered; extra-floral nectaries present; bracts linear, 8–13 mm long; pedicels 0–1 mm long. Calyx ellipsoid or ovoid, 6–11 mm long, basal nectary incomplete, margin entire; lobes 2–6 mm long, triangular. Corolla not or scarcely 2-lipped. Petals mauve-pink, weakly dimorphic, 9–14 mm long, glabrous on exterior (abaxial) surfaces, limb cuneate to obcordate, callused near base; lower 3 petals with 1 or 2 small appendages on margin of claw, callus woolly hairy; upper pair with 2 prominent appendages on claw, callus smooth, shiny, glabrous. Androgynophore 3–4 mm long, straight; stamens 10, shortly connate at base, c. 1 mm long; anthers transverse; staminodes 5, spathulate-acute, c. 0.7 mm long. Style c. 1.5 mm long; stigma of 5 pin-like lobes, terete. Capsule ellipsoid, 13–17 mm long, indumentum very dense, of long-stalked stellate hairs or bristles to 6 mm long each bearing 2–5 stellate hairs, apex attenuate; carpels 3–5-seeded. Seeds rhomboidal, truncate, 3–3.5 mm long, c. 2 mm wide, finely rugose, brown. Flowers: Nov.–Mar. Fruits: Jan.–Mar.

Distribution and ecology. The species is endemic to the northern N.T. and known from three subpopulations between Batchelor and Mt Bundey. It grows in Eucalyptus tectifica or E. miniata woodland on clayey soils derived from siltstone or sandy soil derived from granite.

Notes. This species may be distinguished from H. integrifolia and related species by the erect multi-stemmed habit, congested inflorescences, very dense indument of long stellate hairs and comparatively small flowers. It is allied to H. darwinensis, but distinct from it by the erect multi-stemmed habit, more compact inflorescences, and the indumentum of long stellate hairs, denser and coarser on most parts.

The isotype specimens were unfortunately dispersed before examination for preparation of this description and are without determinavit slips indicating their type status.

This species has been referred to as Helicteres D2164 Glenluckie Ck and Helicteres sp. Glenluckie Ck (N.B. Byrnes 1280) on herbarium specimen labels, unpublished checklists lists, other literature (e.g. Kerrigan & Cowie 2007) and listings under the N.T. Government Territory Parks and Wildlife Conservation Act and Commonwealth Parks and Wildlife Conservation Act and Commonwealth
**Helicteres (Malvaceae) from the Northern Territory**

**Fig. 14.** Holotype of *Helicteres macrothrix*.

**Government Environment Protection and Biodiversity Conservation Act.**

**Etymology.** From the Greek *macro* – large and *thrix*, a hair, a reference to the unusually large hairs present in this species.

*Helicteres procumbens* (F. Muell ex Benth.) Cowie, *comb. et stat. nov.*

(Figs 4, 15).


**Type citation:** Macadam Range. **Type details:** Australia, N. T., M‘Adam Range (K), between Macadam Range and Providence Hill (MEL), Oct. 1855, F. Mueller (Holotype: K, n.v., photo DNA; IsoType: MEL (MEL222174)).

**Other specimens examined.** WESTERN AUSTRALIA. 58 miles [93 km] N of Kununurra, 2 June 1969, F.C.J. Lulfitz & N. Mackenzie (PERTH); Vicinity of Kimberley Research Station, D.H. Mackenzie 69/102-19 (CANB). NORTHERN TERRITORY. Litchfield Station, 2 miles [3.2 km] SW of homestead, 3 May 1968, N.B. Byrnes 665 (DNA, NT); headwaters of Lahnagang Ck, 16 May 1994, I.D. Cowie 5075 & N. Walsh (CANB, DNA, MEL); Daly River road, c. 0.5 km N of Silver Mine Ck, 3 December 2002, I.D. Cowie 9660 & C.P. Mangion (B, BRI, CANB, DNA, MEL, MO, NSW); Daly River road, c. 10.7 km N of Daly River Police Stn, 3 December 2002, I.D. Cowie 9662 & C.P. Mangion (B, BRI, CANB, DNA, MEL, MO, NSW); Daly River road, c. 7.27 km N of Daly River Police Stn, 3 December 2002, I.D. Cowie 9663 & C.P. Mangion (BRI, DNA, SING); Daly River road, 12.7 km N of Daly River Police Stn, 17 December 2004, I.D. Cowie 10343 (B, DNA, L, MEL, MO); c. 12 km N of Daly River Police Stn, 22 May 1983, P. Fryxell 4246 (CANB, DNA); Peppimenarti, Moyle River, 31 October 2000, A.A. Mitchell 6406 (CANB); Karruwa Ck, Daly River Reserve, 16 October 1988, J. Russell-Smith 6295 (DNA); Litchfield N.P., 27 April 1995, S. Taylor 280 (DNA); Daly River Mission area, 26 February 1992, G.M. Wightman 5642 (DNA); Daly River Mission area, 24 March 1993, G.M. Wightman 6026 (DNA).

**Description.** Multi-stemmed subshrub, with prostrate annual above-ground stems to 0.5 m long and a woody perennial root stock. Upper leaf surface with sparse long simple or stellate hairs, leaf undersurface and branchlets with sparse sessile stellate hairs, moderately dense on calyx, stipitate stellate hairs usually absent. Calyx with bristles present towards apex. Stipules caducous or persistent, subulate, 2-6 mm long. Petiole 1.5-5 mm long. Leaf lamina patent, ovate to oblong-ovate or broadly ovate, rarely elliptic, 2.5-8.5 cm long, 1.7-4.8 cm wide, 1.4-2.2 times longer than wide, slightly discolorous, base cordate to rounded, asymmetric, 3-nerved, margins entire to serrulate, apex acute to rounded. Inflorescence axillary, eymose, to 40 mm long, few-many flowered, glands absent; bracts 1-4 mm long, sessile; pedicels 1-6 mm long. Calyx tubular, 3.5-5.5 mm long; lobes triangular, 1.5-2 mm long. Corolla not 2-lipped. Petals mauve-pink, slightly dimorphic, 6-9.5 mm long, long clawed, limb cuneate, with scattered minute erect hairs, with a callus near base, apex truncate to obliquely truncate, irregular; lower 3 slightly longer than upper pair, claw with 2 small appendages, callus woolly hairy; upper pair with 1 or 2 prominent appendages on claw, callus glabrous, smooth. Androgynophore 4-4.5 mm long, straight; stamens 10, c. 0.5 mm long; staminodes 5. Style c. 1 mm long; stigma of 5 pin-like lobes, terete. Capsule ellipsoid, 6-14 mm long, 6-8 mm diam., with a moderately dense covering of sessile stellate hairs, and stellate-hairy bristles to 1 mm long; carpels straight, 2-3-seeded, styles caducous. Seeds not seen. Flowering: Oct.–Dec. Fruiting: Mar.–May.

**Distribution and ecology.** In the northern N.T. and adjacent W.A., from near Kununurra to Litchfield N.P. In D.R., known from near Daly River settlement and along the Daly River road to the western side of Litchfield N.P. Grows in *Eucalyptus* woodland on sandy soils.

**Notes.** The MEL sheet bears three labels, the middle clearly in Bentham’s hand writing reading “Both I believe forms of *H.* (Methorium) *dentata* of which we have many”
and the K sheet with Bentham’s determination “H. dentata var. procumbens” written on the sheet, indicating both were seen by him. While the type details apparently vary slightly between the K and MEL sheets, one is regarded here as a good match and it appears that they form part of the same gathering. The holotype bears Mueller’s label with the name “Methorrhion procumbens n. sp.”. Although Bentham (1863) does not ascribe the epithet to Mueller, he has clearly used Mueller’s name and the authorship can thus be cited as “Helicteres procumbens F.Muell. ex Benth.”.

Helicteres procumbens differs from H. integrifolia by the prostrate habit, lack of inflorescence glands, leaves with a sparse indumentum below (not hoary or grey-green) and presence of long simple or sessile stellate hairs on the upper surface. It is also similar to H. flagellaris, but H. procumbens has a short inflorescence which lacks glands, shorter petals, a shorter androgynophore and caducous stipules.

Helicteres serpens Cowie, sp. nov.
(Figs 4, 7J–N, 16)

Helicteres darwinensis similis, sed stipulis deciduis, petiolis saepe longioribus, inflorescentiis apertis, paniculatis, 30–140 mm longis, bracteis 4–7 mm longis, petalis 8–12 mm longis, androgynophoro breviore, capsula setis ad 2.5 mm longis dense tecta distans.


Helicteres (Malvaceae) from the Northern Territory

HOLOTYPE

Fig. 16. Holotype of Helicteres serpens.


Description. Multi-stemmed subshrub, with prostrate annual above-ground stems to 0.7 m long and a woody perennial root stock. Most vegetative parts and calyx hirsute with sessile or stipitate stellate hairs, sparse to dense sessile stellate hairs on upper surface of leaf lamina. Stipules deciduous, subulate, 4-10 mm long. Petiole 3-40 mm long. Leaf lamina sometimes ground-hugging, lanceolate to ovate, 40-140 mm long, 23-90 mm wide, discoloured when young, hairs of the upper surface 0.4-1.2 mm diam., on the lower surface 0.4-1.7 mm diam., base cordate, asymmetric, 5-nerved, margins irregularly serrate, apex acute to rarely rounded. Inflorescence axillary, open, paniculate, 30-140 mm long, 6-21-flowered, dichasia 1-2-flowered; extra-floral nectaries present; bracts 4-7 mm long, filiform; pedicels 0-3.5 mm long. Calyx funnel-shaped or ellipsoid-cylindrical, 5-9 mm long, hairs 0.3-1.1 mm diam., basal nectary incomplete; lobes narrowly triangular, 2-4 mm long. Petals mauve-pink, dimorphic, 8-12 mm long, clawed to long clawed, limb cuneate, minutely hairy, callused near base; lower 3 petals slightly longer, with 0-2 small appendages on claw; callus woolly hairy; upper pair with 2 prominent appendages on claw, callus smooth. Androgynophore 3.5-5.5 mm long, straight, distinctly shorter than calyx; stamens 10, shortly connate at base, c. 1.5 mm long; anthers transverse; staminodes 5, lanceolate or elliptic, 0.5-0.7 mm long. Style c. 1.3 mm long; stigma of 5 pin-like lobes, terete. Capsule ovoid to ellipsoid, 8-20 mm long, 11-14 mm diam., densely covered with stellate-hairy bristles to 5 mm long, hoary, hairs 0.8-1.2 mm diam., styles eaduceous; carpels straight, 3-5-seeded. Seeds sub-rhomboidal, c. 2.7 mm long, 2 mm wide, irregularly rugose, dark brown. Flowers: Dec.-Apr. Fruits: Feb.-June.

Distribution and ecology. The species is endemic to the northern N.T., where it is common from Kakadu N.P. to near Mataranka and east to near Maningrida. It grows in Eucalyptus woodland mostly on deep sandy soils.

Notes. Similar to H. darwinensis but separated by the deciduous stipules, petioles often longer than in H. darwinensis (to 40 mm), the open, paniculate inflorescences 30-140 mm long, the bracts 4-7 mm long, the petals 8-12 mm long, the androgynophore shorter, and the capsule densely covered with bristles to 2.5 mm long.

As with H. darwinensis, this species flowers early in the wet season on the shoots of the new growth arising from the woody rootstock. The new growth is very densely hairy and at first acquaintance strikingly different from the sparser indumentum of the mature leaves present later in the wet season. The species shows clinal variation in density of the indumentum with it becoming sparser along a gradient from south of Katherine to Kakadu and Arnhem Land. Specimens from southern Kakadu also have smaller hairs than those from elsewhere.

This species has been referred to as Helicteres D4247 elongate and Helicteres sp. elongate (J. Must 887) on herbarium specimen labels and unpublished checklists from DNA.

Etymology. From the Latin serpens - creeping, a reference to the prostrate habit.

Helicteres sphaerotheca Cowie, sp. nov. (Figs 4, 70-S, 17)

Ab Helicteres integrifolia et specibus cognatis stipulis persistentibus, lamina folii angusti lanceolata ad anguste oblanceolate, 2-7 mm lata, 5-8.5-plo longiore quam latiore, concolora, pagina supera pilis sparsis simplicibus, capsula globosa, setis densis, usque ad 2 mm longis vestita discrepans.


Others specimens examined. NORTHERN TERRITORY. Arnhem Hwy, 300 m E West Branch of WAlligator River, 3 December 1990, K.G. Brennan 1642 (DNA); Arnhem Hwy, 300 m E of West Branch of W Alligator R, 11
Description. Erect, multi-stemmed subshrub to 0.6 m, with annual above-ground parts and woody perennial root stock. Most vegetative parts and calyx with sparse sessile stellate hairs, sparse simple hairs on upper surface of leaf lamina. Stipules persistent, setose, 1–2 mm long. Petiole 0.5–1 mm long. Leaf lamina patent to recurved, narrowly lanceolate to narrowly oblanceolate, 15–35 mm long, 2–7 mm wide, 5–8.5 times as longer than wide, concolorous, base rounded, symmetric, 3-nerved, margins entire, or irregularly serrate near apex, apex acute to rounded. Inflorescence axillary or terminal on short lateral shoots, cymose, 10–15 mm long, few-flowered, diehasis 3-flowered; extra-floral nectaries present; bracts c. 1 mm long, setose; pedicels 1–4.5 mm long. Calyx tubular to funnel-shaped, 3.5–4.5 mm long, basal nectary short, incomplete, truncate; lobes triangular, c. 0.5 mm long. Petals mauve-pink, scarcely dimorphic, 7–9.5 mm long, long clawed, limb cuneate, minutely hairy, callosed near base, apex obliquely truncate; lower 3 petals slightly longer than upper pair, claw with 1–2 small lateral appendages, callus woolly hairy; upper pair with 2 prominent appendages on claw, callus glabrous, smooth. Androgynophore 4.5–5 mm long, straight, equal in length to calyx; stamens 10, shortly connate at base, c. 0.8 mm long; anthers transverse; staminodes 5, spathulate-acute, c. 0.7 mm long. Style c. 1.3 mm long; stigma of 5 pin-like lobes, terec. Capsule globular, 8–11 mm diam., densely covered with stellate-hairy bristles to 2 mm long, hoary, styles caducous; carpels straight, 1–3-seeded. Seeds sub-rhomboidal, c. 2.5 mm long, 2 mm wide, irregularly rugose, dark brown. Flowers: Dec.–Jan. Fruits: Mar.

Distribution and ecology. The species is endemic to the northern N.T., between the Mary River and the South Alligator River. It grows in Eucalyptus miniata woodland on sand.

Notes. Differing from Helicteres integrifolia and related species by the persistent stipules; the lamina narrowly lanceolate to narrowly oblanceolate, 2–7 mm wide, 5–8.5 times as longer than wide, concolorous, upper surface with sparse simple hairs and the globular capsule with bristles to 2 mm long.

This species has been referred to as “Helicteres D21039 linifolia” and “Helicteres sp. linear leaves (L. Craven 7854)” on herbarium specimen labels and unpublished checklists lists from DNA.

Etymology: from the Greek, sphaera - a ball or globe and thece - a case or container, in reference to the globular capsule.

Helicteres tenuipila Cowie, sp. nov. (Figs 3H–K, 4, 18, 19)

Ab H. integrifolia et speciebus cognatis indumento sparsiore et grossiore, foliis oblanceolatis grandis, pilis stellatis sparsioribus in paginis ambabus, parum discoloribus; calyce pilis stipitatis stellatis frequentibus secedus.

Type: Australia, N.T., Litchfield N.P., opposite turnoff to Green Ant Creek, I.D. Cowie 10361 & J.L. Egan (Holotype: DNA (3 sheets); Isotypes: AD, B, BRI, CANB, K, L, MEL, MO, NSW, PERTH).

Helicteres (Malvaceae) from the Northern Territory

Fig. 18. Helicteres tenuipila. Flowers and leaves. Inset. Flower (I. D. Cowie 10361).


Description. Erect, multi-stemmed subshrub to 0.5 m, with annual above-ground parts and a woody perennial root stock. Most vegetative parts with sparse to moderately dense sessile stellate hairs, denser on calyx, stipitate stellate hairs occasional on stems, common on calyx. Stipules caducous, setose, 5–7 mm long. Petiole 4–7 mm long. Leaf lamina elliptic to oblanceolate or obovate, rarely ovate or lanceolate, 45–95 mm long, 15–40 mm wide, 2.4–3.3 times longer than wide, slightly discolorous, hairs of the upper surface 0.6–1.5 mm diam, on the lower surface 0.4–1.5 mm diam., base cuneate to rounded, symmetric or asymmetric, 3-nerved, margins entire near base, becoming serrate near apex, apex acute to rounded. Inflorescence axillary, umbellate, c.15 mm long, few flowered, extra-floral nectaries present; bracts c. 4 mm long, linear; pedicels c. 1 mm long; dichasia 2-flowered. Calyx cupular to urceolate, ellipsoid or tubular, c. 6 mm long, basal nectary incomplete, margin oblique; lobes triangular, c. 1 mm long. Corolla weakly 2-lipped. Petals mauve-pink, the upper pair paler than lower, slightly dimorphic, 7–9 mm long, long clawed, limb cuneate, minutely hairy, callused near base, apex truncate to obliquely truncate; lower 3 slightly longer than upper pair, claw with 0–2 small appendages, callus woolly hairy; upper pair with 2 prominent appendages on claw, callus glabrous, smooth. Androgynophore c. 3.5 mm long, straight, shorter than calyx; staminodes 5, spathulate-acute, c. 0.7 mm long. Style 0.8–1.5 mm long; stigma of 5 pin-like lobes, terete, sometimes slightly divergent. Capsule globular to ellipsoid, 12–20 mm long, 10–13 mm diam., densely covered with stellate-hairy bristles to 5 mm long, styles caducous or persistent; carpels straight, 1–3-seeded. Seeds variously shaped, conoidal to depressed cylindric or fusiform, often laterally compressed, 1.5–3.5 mm long, c. 2.5 mm wide, irregularly rugose, dark brown. Flowers: Nov.–Dec. Fruits: Jan.–May.
**Distribution and ecology.** The species is endemic to Litchfield N.P. in the northern N.T., where it is found on the surface and side slopes of the Mt Tolmer Plateau. It grows in *Eucalyptus miniata / E. tetrodonta* open forest on sandy soils.

**Notes.** It is separated from *H. integrifolia* and allied species by the sparser and coarser indumentum, larger leaves which are oblanceolate, more coarsely and irregularly serrate with sparser stellate hairs on both surfaces, only slightly discolorous, and with stipitate stellate hairs common on the calyx.

Several collections from the Wingate Mountains - Fish River Conservation Reserve are tentatively placed here (Cowie 12604, 12606; Walsh 3671). They differ in having narrower, linear leaves 50–100 mm long, 5–11 mm wide, 6.5–19 times longer than wide and a coarser indumentum of stellate hairs 0.7–2 mm diam. with the branches touching to distinctly overlapping, but the underlying surface is highly visible. No flowers have been seen, although the length of both the remains of the persistent calyx and the androgynophore are consistent with *H. tenuipilia*.

This species has been referred to as "Helicteres D27003 Litchfield" and "Helicteres sp. Litchfield (D.M.J.S. Bowman 185)" on herbarium specimen labels and unpublished checklists from DNA.

**Etymology.** From the Latin *tenuis*, thin or fine and *pihus*, a hair, referring to the sparse indumentum of the leaves of this species.

**Notes on other species**

*Helicteres angustifolia* L. (not illustrated). The name *Helicteres angustifolia* L. is applied here in a broad sense and may include a number of both described and undescribed taxa (Masters 1874; Baeker & van den Brink 1963; Cristobal 2001; Phengklai 2001; Tang et al. 2007). Overseas and most Australian material share the following common features of a short, close indumentum on the stems and lower surface of leaves; stipules caducous, 3.5–6 mm long, leaves strongly discolorous, lanceolate to narrowly elliptic (sometimes oblong, ovate or oblanceolate), 2–6.3 times longer than wide, usually glabrous on the upper surface and hoary below, margins entire, inflorescences short, axillary, 2–11-flowered; cincinni 2-flowered, extrafloral nectaries present; calyx 4–8 mm long, weakly 2-lipped, sub-cylindrical; petals 5–11 mm long, weakly dimorphic, mauve or purplish, the lower three with a woolly hairy callus at base of limb; the upper pair with a smooth glabrous area at base of limb, androgynophore 3–7.5 mm long, style apparently with 5 pin-like lobes; capsules ovate to oblong, 7–23 mm long, densely stellate-pilose with bristles absent or up to 4 mm long; and carpels straight, 2–7-seeded. Stellate hairs of the stem and calyx are 0.2–0.8 mm diam. The growth habit is an erect open shrub.

In Australia and overseas, there is variation in indumentum colour, the size and apex of the leaf, the indumentum of the upper leaf surface and in size, apex and indumentum of the fruit. A number of entities can be recognised. Some entities have leaves with the upper surface densely hairy with stellate, or stellate and simple hairs, or may be united by a similar capsule apex and indumentum, but are otherwise not readily distinguished by other characters. Much, but not all, of the variation in individual characters seen in Australian material falls within the range observed in overseas material. Some Australian entities have a localised geographic distribution while others are geographically more scattered, morphologically more variable and scarcely distinguishable from some Malesian material. The name *Corchorus allenii F.Muell.*, described by Mueller (1892) from a specimen collected in the Prince Regent River area by Bradshaw and Allen, represents a species of *Helicteres* and is likely to apply to one of the above entities. Further examination of these entities is needed and especially in relation to Malesian material from the Java to New Guinea area where relatively few specimens have been seen.

*Helicteres hirsuta* L. (Fig. 20). Australian (i.e. N.T.) material of *Helicteres hirsuta* may be worthy of formal recognition as a distinct taxon at some level but further examination of material from India and Lesser Sunda Islands is required. Compared to material from China, Vietnam, Laos, Thailand, Peninsular Malaysia, Borneo, Sumatra, Philippines and Java (largely at SING), N.T. material mostly has a hyaline to stramineous indumentum rather than a hyaline to stramineous or apparently ferruginous one, the leaves are often less densely hairy below, the calyx and corolla are mostly shorter, the androgynophore is almost always shorter (5–12 mm long as opposed to 12–19 mm long) and leaf shape and petiole length are not as variable (although included within the range of variation). However, the apparently darker indumentum may well be an artefact of storage conditions as considerable darkening of specimens within a few years of collection has been observed by the author where specimens are subject to un-airconditioned storage under tropical conditions. Most of the Malesian material seen was collected pre-1940. Also, specimens of...
similar age from China, Vietnam and Philippines at both AD and LUND had only white to stramineous indumentum. Some Philippine material (e.g. Borrowmeo s.n. Aug 1915 (SING), Acedibo 33463 (SING); Merrill 506, 547 (SING); Ramos 1437 (SING), s.n. Nov. 1909 (LD)) has an indumentum density on leaves and stems close to N.T. specimens, with a shorter calyx down to 10 mm long (7–11 mm long in Australian material) and petals down to 15 mm long (11–18 mm long in Australian material). Also, Chow 78282 (at AD) from China has leaf size and indumentum very similar to Australian material, but with a longer calyx and corolla. No material from the islands east of Java has been seen and it is not clear if the taxon occurs in the Lesser Sunda Islands. Further study of any material from these areas is needed to determine if Australian material is morphologically distinct.

KEY TO SPECIES OF HELICTERES IN THE NORTHERN TERRITORY

1 Leaves linear, less than 8 mm wide (Fig 7P–S).............................................H. sphaerotheca

1: Leaves lanceolate, ovate, elliptic, orbicular or obovate, more than 8 mm wide ..................................2

2 Androgyneophore 8 mm or longer; all petals lacking an area of matted hairs at base of limb .........3

2: Androgyneophore 7 mm or shorter; lower 3 (abaxial) petals with a distinct area of matted hairs at base of limb ..........................................................5

3 Leaf margins entire, rarely toothed in upper half (Figs 2, 3A–C) ..............................................H. cana

3: Leaf margins toothed throughout ..........................................................4

4 Calyx more than 15 mm long; carpels twisted spirally; inflorescence cymose (Fig. 1)......................H. isora

4: Calyx less than 15 mm long; carpels straight; inflorescence racemose (Fig. 20)......................H. hirsuta

5 Upper surface of leaves glabrous or nearly so or simple hairs present, with or without stellate hairs .......... 6

5: Upper surface of leaves stellate hairy, sometimes sparsely so, simple hairs absent .................................. 8

6 Leaf margins entire; erect shrub; leaves white below ..................................................H. angustifolia sens. lat.

6: Leaf margins serrate; plant prostrate; stems long and trailing in mature plants ..................................7

7 Petals 10–16 mm long; inflorescence 30–140 mm long; extra-floral nectaries present (Fig. 9) ...H. flagellaris

7: Petals 6–9.5 mm long; inflorescence to 40 mm long; extra-floral nectaries absent (Fig. 15) ........................................H. procumbens

8 Plants prostrate, stems long and trailing in mature plants ..........................................................9

8: Plants ascending to erect when well developed ... 10

9 Inflorescence elongate, interrupted; usually more than 30 mm long (Fig. 7J–N)..............................H. serpens

9: Inflorescence contracted, often congested; usually less than 30 mm long (Figs 6, 7F–I).............H. darwinensis

10 Leaf indumentum coarse, hairs mostly more than 1.3 mm diam.; petals 11 mm or more long; stipules more than 6 mm long (Figs 7A–E, 13)..............................H. macrothrix

10: Leaf indumentum fine to medium, hairs mostly less than 1.3 mm diam.; petals mostly 10 mm or less long; stipules 6 mm or less long (rarely longer in H. tenuipila) ..............................................11

11 Leaves with sparse hairs on both surfaces, the lower surface green (Figs 3I–K, 18) ..............H. tenuipila

11: Leaf with the lower or both surfaces densely hairy and obscured, the lower surface often white or grey-green below ..........................................................12

12 Leaf hairs of two size classes; calyx with bristles and stellate hairs; few-stemmed perennial shrubs to 2 m tall (Figs 3D–G, 11) ..............H. kombolgiana

12: Leaf hairs of one size class; calyx with stellate hairs only; multi-stemmed subshrubs to 0.5 m tall resprouting each year from a woody rootstock (Fig. 10) ..............H. integrifolia

ACKNOWLEDGEMENTS

Greg Leach generously obtained photos of many east Asian and Australian type specimens and literature from K, L, and BM during his time as Australian Botanical Liaison Officer at K. Gordon Guymer and Philip Short reviewed the paper and their constructive comments resulted in considerable improvements. Richard Willan saw it through the editorial process. David Halford kindly drew the name Corchus allenii F.Muell. to my attention. Raelee Kerrigan, Chris Mangion and Andrea Hope accompanied me on field trips specifically to collect and assess the conservation status of Helicteres. The curators of AD, CANB, MEL, NSW and PERTH provided loans of specimens. At BRI and SING, the Curator and Keeper, respectively, provided access to collections, allowed use of facilities and made me welcome. Russell Barrett provided input on W.A. entities and records. Emma Short checked the Latin diagnoses. Clyde Dunlop provided guidance in the early stages of the project and passed on much knowledge both on various field trips and in the herbarium. The help of all these people is greatly appreciated.
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Taxonomic revision of the order Halichondrida (Porifera: Demospongeae) of northern Australia. Family Halichondriidae

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ABSTRACT

Fifteen species in six genera of the family Halichondriidae, including two new species, Halichondria (Halichondria) carotenoica sp. nov. and Halichondria (Halichondria) microbiana sp. nov., are recorded for northern Australia as part of a revision of the order Halichondrida (Porifera: Demospongeae) in this region. Descriptions and discussion of these species are presented here. Eight new combinations within the family Halichondriidae are here established, i.e. Amorphinopsis fenestrata (Ridley, 1884, as Leucophloeus), Amorphinopsis maculosa (Pulitzer-Finali, 1996, as Topsenella), Axiosyssa bergquistae (Hooper et al., 1997, as Halichondria), Axiosyssa mertoni (Hentschel, 1912, as Ciocalypta), Axiosyssa gracilis (Hentschel, 1912, as Ciocalypta nitida gracilis), Axiosyssa terpis (De Laubenfels, 1954, as Phycopsis), Ciocalypta vanesesti (Hooper et al., 1997, as Halichondria) and Topsenella ridleyi (Hooper et al., 1997 as Halichondria) and one species is relocated into the family Dictyonellidae, i.e. Stylissa vernonensis (Hooper et al., 1997, as Hymeniacidon). A lectotype is designated for Ciocalypta stalagmites Hentschel, 1912.

Keywords: sponge, Porifera, Halichondrida, Halichondriidae, northern Australia, new species, taxonomy.

INTRODUCTION

The family Halichondriidae was revised by Erpenbeck & Van Soest (2002). Its definition is based entirely on a few skeletal characters, i.e. presence of an ectosome with specialised skeleton, a disorganised choanosomal skeleton, dimensions of osteas and styles, absence of microscleres. Other morphological characters (e.g. general shape of megascleres, presence or size categories among the megascleres, spicule density and its relation to consistency, orientation of spicules at the ectosomal level) are used in combination with the diagnostic characters to separate species and genera within this family. All these characteristics are very simplistic, and often displayed as a gradient of variation which makes separation of species very subjective as reflected by the large number of synonyms (see Van Soest et al. 2008).

The family includes 14 genera and at least 296 valid species (Van Soest et al. 2008); however, the status and generic allocation of many of the species listed on this database on the Internet needs to be revised and validated against the current concept of the genera.

The Australian Faunal Directory (Hooper 2005) currently lists a total of 42 species of Halichondriidae. Twenty species were reported and described for the Beagle Gulf (northern Australia) by Hooper et al. (1997). No other revision of species of Halichondriidae in Australia or adjacent areas is presently available.

The present paper represents the third part of a revision of the order Halichondrida in the northern Australian region and includes the family Halichondriidae. Alvarez & Hooper (2009, 2010) provided details and presented an introduction to the revision of the order and the families Axinellidae and Dityonellidae.

MATERIALS AND METHODS

This revision includes material of the family Halichondriidae recorded for the tropical northern Australian waters of the Northern Territory and Queensland coast (from Admiralty Gulf in the west to Torres Strait in the east, approx. between the 125°E and 142°E).

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 available in Appendix 1.

The distribution of species is given according to the marine provinces defined by Spalding et al. (2007). Spicule measurements are in micrometres and are based on 25 spicules (unless indicated in square brackets) and denoted as range (and mean ± 1 S.E.) of spicule length and width. All other methods as discussed in Alvarez & Hooper (2009, 2010).
ABBREVIATIONS

Abbreviations used in the manuscript are: AIMS, Australian Institute of Marine Sciences, Townsville; BMNH, Natural History Museum, London (formerly British Museum (Natural History)); CRFF, Coral Reef Research Foundation, Palau; GBR, Great Barrier Reef; MAGNT, Museum and Art Gallery Northern Territory (formerly Northern Territory Museum); MNHN, Musee National d’Histoire Naturelle, Paris, France; MSNG, Museo Civico di Storia Naturale ‘Giacomo Doria’, Genoa, Italy; NHMB – Naturhistorisches Museum, Basel, Switzerland; SMF, Senckenberg Research Museum and Art Gallery Northern Territory; QLD, Queensland, Australia; QM, Queensland Museum, Brisbane; WA, Western Australia; ZMA, Zoologisch Museum, University of Amsterdam, ZMB, Museum für Naturkunde and der Universitét Humboldt zu Berlin, Berlin, Germany.

Numbers prefixed with Q666C, OCDN, OM9H are the cross-reference sample number collected for the United States National Cancer Institute, under the ‘Collection of shallow-water organisms’ programme, by the Australian Institute of Marine Sciences, CRFF and MAGNT (subcontracted through CRFF) respectively.

TAXONOMY

Family Halichondriidae Gray, 1867

Genus Amorphinopsis Carter, 1887

Gender feminine. Type species, by monotypy, Amorphinopsis excavans Carter, 1887. Recent, Indian Ocean.

Amorphinopsis excavans Carter, 1887

(Figs 1A, 2)


Description

Shape (Fig. 1A). Thinly to thickly encrusting (up to 50 mm thick), massive to lobate, or developing short projections and small lumps, generally growing in patches and following substrate, semi-buried in substrate.

Surface. Hispid, bumpy.

Skeleton. Ectosomal skeleton (Fig. 2A) thin, detachable tangential layer, composed by a disorganised criss-cross reticulation of paucispicular-multispicular tracts of oxeas, up to 100 μm thick, with small styles tangentially to paratangentially oriented, sometimes in disorganised tufts. Choanosomal skeleton (Fig. 2B) halichondroid, with large oxeas oriented in all directions, sometimes grouped in directionless multispicular tracts; slightly cavernous at subectosomal area with short multispicular tracts supporting the ectosomal skeleton.

Spicules (Fig 2C). Oxeas, hastate, in a large range of sizes, 213.4–94.5 μm (598±221) x 5.9–25.1 μm (16.3±5.5). Smaller ectosomal styles 140.8–264.9 μm (193.8±41.3) x 4.1–7.5 μm (5.5±0.9).

Remarks. The material examined here agrees with the description of the syntype by Erpenbeck & Van Soest (2002: 790).

The specimen described under Amorphinopsis sacciformis by Hooper et al. (1997) is better allocated to *A. excavans*. It does not agree with the syntype of *Ciocalypta sacciformis* Thiele which, as mentioned below (see under remarks of *A. carpentariensis*), should be interpreted as *Halichondria*. The material described by Hooper et al. (1997) is a thin crust covering a bivalve shell with skeleton similar to the rest of the material assigned here to *A. excavans*.

Species considered synonyms of *Amorphinopsis excavans* by Hooper & Wiedenmayer 1994, following Burton (1959), were excluded by Hooper et al. (1997) and Erpenbeck & Van Soest (2002).

Distribution. The species was recorded originally from the Mergui Archipelago (Andaman province). Records from Singapore and northern Australia extend the distribution of the species to the Sunda and Sahul Shelf provinces. The northern Australian and Singaporean populations seem to be common at the intertidal region associated with piers and wharfs. The species is found also subtidally between 9 and 16 m.

Amorphinopsis fenestrata (Ridley, 1884) comb. nov.

(Figs 1B, 3)

Leucophloeus fenestratus Ridley, 1884: 464; Dendy 1922: 124; Burton 1928: 127.

Leucophloeus fenestratus unnamed variety. – Ridley 1884: 464.

Siberites oculatus Kieschnick, 1896: 534.

Hymeniacidon fenestratus. – Lindgren 1897: 483.

Ciocalypta confissa. – Thiele 1900: 75.

Ciocalypta oculata maxima Hentschel, 1912: 428.


Ciocalypta confissa Hooper et al., 1997: 23.


Ciocalypta oscillans Hooper et al., 1997: 20.

Fig. 2. Amorphinopsis excavans (NTM Z.5213): A, light microphotograph of tangential section of ecosomal skeleton, showing oxeas organised in bundles and small styles, paratangentially oriented in disorganised brushes; B, light microphotograph of section perpendicular to surface, showing choanosomal skeleton; C, diagram of spicules. Scale bars: A,C, 100 μm; B, 500 μm.


Description.
Shape (Fig. 1B). Massive to subspherical, with tapering, hollow, rudimentary, subconical or volcano-shaped fistules, up to 18 mm long and 30 mm diameter; basal portion buried beneath sediment and fistules protruding through substrate.
Halichondriidae from northern Australia

Fig. 3. *Amorphinopsis fenestrata*: A, light microphotograph of tangential section of ectosomal skeleton (NTM Z.5206), showing spicule tracts criss-crossing and forming a reticulation of polygonal meshes; B, light microphotograph of section perpendicular to surface (NTM Z.5215) showing choanosomal skeleton; C, diagram of spicules. Scale bars: A-B, 500 μm; C, 100 μm.

Colour. Yellow, brown or pale mauve, alive.

Oscula. Large, up to 10 mm in diameter or, grouped on a terminal sieve-plate, on apex of fistules.

Texture and consistency. Compressible, harsh, easily torn.

Surface. Irregular, rugose, translucid, hispid, marked in some specimens with longitudinal channels.

Skeleton. Ectosomal skeleton (Fig. 3A) detachable, supported by subectosomal multispicular tracts. Formed by multispicular tracts of larger choanosomal styles, up to 3 spicules abreast, lying tangential to surface, directionless or criss-crossing, forming a nearly regular reticulation of polygonal meshes; and, irregular bundles of smaller ectosomal styles arranged mostly paratangential to surface as plumose brushes or tufts. Choanosomal skeleton disorganised, halichondroid criss-cross of both unispicular and multispicular tracts, containing 5–20 spicules abreast, with larger choanosomal styles mainly confined to central region; becoming more wide-meshed, paratangentially oriented and cavernous at subectosomal region. In fistules choanosomal tracts more compressed in central region (Fig. 3B), cavernous towards periphery. Single spicules, including smaller styles scattered through choanosome.

Spicules (Fig. 3C, Table 1). Choanosomal styles and styloids (thicker in apical third and with basal ends narrower than the centre), slender, straight or slightly curved at centre, fusiform, in a great size range (163–895 x 3.3–17.4 μm). Smaller styles can be transitional to subtylostyles. Relative proportions of styles, styloids and subtylostyles vary among populations.

Remarks. The species was originally described by Ridley (1884) under *Leucophloeus*, a junior synonym of *Ciocalypta* (Van Soest et al. 1990; Erpenbeck & Van Soest 2002) and related to species of *Ciocalypta* by Hooper et al. (1997) based on the characteristics of the ectosomal skeleton, and the presence of styles. As described above, the growth form of *Amorphinopsis fenestrata* is characterised by the presence of fistule-like projections of several shapes...
with a system of exhalant channels. They project from a semi-buried massive base and protrude through the substrate/sand. The skeletal architecture in these fistulose projections, although similar, is considered here not to be homologous to the one observed in \textit{Ciocalypta} species, oriented longitudinally and radiating towards the surface. Based on these arguments, we suggest that the species is better allocated to the genus \textit{Amorphinopsis}.

It needs to be noted however, that the skeleton of the present species is composed totally by styles with a great size range and lacks of ‘true’ oxeas, a diagnostic characteristic of this genus. In the majority of specimens examined, including the type of styles but differ in external form and in having larger and thicker styles. Study of local populations and examination of the type material is required to establish whether the two species are conspecific.

### Distribution

\textit{Amorphinopsis fenestrata} is common throughout the Northern Territory coast (Sahul Province), from Parry Shoals (NW of Darwin Harbour) to the Gulf of Carpentaria. The records of Lindgren (1897, 1898) from Northern territory, of Burton (1928) from the Malay Archipelago need to be verified.

### Amorphinopsis subacerata

\textit{Amorphinopsis subacerata} (Ridley & Dendy, 1886) from the Philippine Islands is very similar to \textit{A. fenestrata} and as stated by those authors they share many characteristics including the type of styles but differ in external form and in having larger and thicker styles. Study of local populations and examination of the type material is required to establish whether the two species are conspecific.

### Material examined


**Description**

- **Shape.** Thickly encrusting, following substrate with convoluted ridges and short projections.
- **Colour.** Light grey or yellow alive; yellow inside beige in ethanol.
- **Oscula.** Inconspicuous, of different diameter, flushed and irregularly distributed or aggregated in top of the short projections (Fig. 1C).
- **Surface.** Smooth, lumpy, with dural skin of reticulated appearance.
- **Consistency and texture.** Firm but crumbly.

### Table 1. Comparison of spicule dimensions among specimens of \textit{Amorphinopsis fenestrata}.

<table>
<thead>
<tr>
<th>Specimen</th>
<th>Locality</th>
<th>Styles</th>
</tr>
</thead>
<tbody>
<tr>
<td>BMNH 1882.2.23.255</td>
<td>Darwin Harbour</td>
<td>193.6-611.8μm (390.4±136.4)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>x 5.3-12.7μm (8.6±2)</td>
</tr>
<tr>
<td>BMNH 1882.2.23.195</td>
<td>Arafura Sea</td>
<td>252.9-895.3μm (617.7±217.3)</td>
</tr>
<tr>
<td>(Ridley’s unnamed variety</td>
<td></td>
<td>x 5.9-15.4μm (9.6±2.6)</td>
</tr>
<tr>
<td>SMF 680</td>
<td>Termate, Indonesia</td>
<td>210.2-761.6μm (431.1±160)</td>
</tr>
<tr>
<td>(Syntype of \textit{Suberites oculatus})</td>
<td></td>
<td>x 4.7-17.4μm (8.1±2.8)</td>
</tr>
<tr>
<td>SMF 971</td>
<td>Aru Is, Indonesia</td>
<td>306.4-892.8μm (563.3±176)</td>
</tr>
<tr>
<td>(Syntype of \textit{Ciocalypta oculata maxima})</td>
<td></td>
<td>x 3.3-11.6μm (6.6±1.8)</td>
</tr>
<tr>
<td>NTM Z.3106</td>
<td>Parry Shoals</td>
<td>217.8-649μm (448.9±149.7)</td>
</tr>
<tr>
<td>(Holotype of \textit{Ciocalypta confossa})</td>
<td></td>
<td>x 6.4-12.6μm (9.2±1.9)</td>
</tr>
<tr>
<td>QM G303560</td>
<td>Bynoe Harbour</td>
<td>175.1-690.4μm (502.7±155.8)</td>
</tr>
<tr>
<td>(Holotype of \textit{Ciocalypta ochitan})</td>
<td></td>
<td>x 5.2-13.3μm (8.7±2.2)</td>
</tr>
<tr>
<td>NTM Z.5215</td>
<td>Darwin Harbour</td>
<td>178.5-891.1μm (427.1±199.8)</td>
</tr>
<tr>
<td>QM G314247</td>
<td>Gulf of Carpentaria</td>
<td>218.8-599.3μm (412.2±20.3)</td>
</tr>
</tbody>
</table>

Note: (Figs 1C, 4)
Halichondriidae from northern Australia

Fig. 4. *Amorphinopsis maculosa* (QM G313577): A, light microphotograph of tangential section of ectosomal skeleton showing brushes of small styles with ends projecting through surface; B, light microphotograph of section perpendicular to surface showing choanosomal skeleton; C, diagram of spicules. Scale bars: A, 100 μm; B, 500 μm; C, 100 μm.

Skeleton. Ectosomal skeleton (Fig. 4A) consisting of tangential to paratangential crust, approx. 200–300 μm thick, supported by choanosomal tracts of spicules and with disorganised brushes of small styles with ends projecting through surface, forming a discontinuous palisade spaced roughly at regular distances. Choanosomal skeleton (Fig. 4B) halichondroid, forming oval to round lacunae, 300–1000 μm in diameter, becoming compact towards surface, with very little collagen and abundant spicule content. Spicule tracts long and multiprespicular, running either towards surface or parallel to surface at the subectosomal area.

Spicules (Fig. 4C, Table 2). Oxeas and much less frequent styles in a large size variation, 207–994 x 5–38 μm; small ectosomal styles (and transitional to oxeas), 139–274 x 3–8 μm.

Remarks. The holotype of *Topsentia maculosa* Pulitzer-Finali was examined and is comparable in external morphology and skeletal characteristics to material collected in the Gulf of Carpentaria and Shoal Bay. The species is redescribed using this material and assigned to the genus *Amorphinopsis*.

Table 2. Comparison of spicule dimensions among specimens of *Amorphinopsis maculosa*.

<table>
<thead>
<tr>
<th>Specimen</th>
<th>Locality</th>
<th>Oxeas</th>
<th>Styles</th>
</tr>
</thead>
<tbody>
<tr>
<td>MSNG 48701 (Holotype of <em>Topsentia maculosa</em>)</td>
<td>Papua New Guinea</td>
<td>240.2–994.6 μm (633.7±255.1) x 7.4–37.6 μm (21.7±9.9)</td>
<td>138.5–259.2 μm (211±35.5) [16] x 3–9.7 μm (6.6±1.8) [16]</td>
</tr>
<tr>
<td>QM G313577</td>
<td>Gulf of Carpentaria</td>
<td>369.1–863.6 μm (675.8±124.6) x 7.9–20.3 μm (15.2±3.2)</td>
<td>143.7–273.8 μm (187.7±35.2) x 3.2–7 μm (4.8±1)</td>
</tr>
<tr>
<td>QM G314255</td>
<td>Gulf of Carpentaria</td>
<td>207.9–819.5 μm (560.1±166.3) x 4.5–22.1 μm (12.6±4)</td>
<td>147.5–240.4 μm (174.2±20.9) x 3–7.8 μm (5.6±1)</td>
</tr>
</tbody>
</table>
Amorphinopsis maculosa is very similar in habit and skeletal organisation to A. fenestrata (Ridley, 1884) but that species has only styles as megascleres and lacks the oxeas of variable sizes present in this species (see above). Fistulous projections, as observed in A. fenestrata, are not present in the examined material of A. maculosa.

The specimen assigned to Axinyssa alysinoides (Dendy) by Hooper et al. (1997) was re-examined and has characteristics (i.e. habit, ectosomal skeleton, oxeas and smaller styloids) that agree with Amorphinopsis maculosa.

Amorphinopsis maculosa was also compared to other species of Amorphinopsis recorded for northern Australia and adjacent biogeographical regions – Amorphinopsis excavans (Dendy, 1889) from the Indian Ocean, A. foetida (Dendy, 1889) from the Gulf of Manasar, A. maza (De Laubenfels, 1954), A. oculata (Kieschnick, 1896), and A. saccoformis from Indonesia. Amorphinopsis excavans has similar habit, skeletal structure and spicule composition, but differs in the organisation of the ectosomal skeleton; in A. excavans it consists of a tangential layer of thick intercrossing tracts of large oxeas, and loose oxeas of all sizes with small styles filling up the spaces (Erpenbeck & Van Soest 2002). The material of A. excavans from northern Australia described above also has a clearly tangential and detachable ectosomal skeleton of large oxeas grouped in bundles and small styles tangentially to paratangentially oriented, sometimes in disorganised tufts. Other characteristics that differentiate A. maculosa from A. excavans are the predominance of small styles in the ectosome (instead oxeas and styles as reported in most populations of A. excavans) and the lacunar appearance of the choanosomal skeleton.

Amorphinopsis foetida (type specimen BMNH 1889.1.21.55, examined) is also a massive and slightly lobose species but with a skeletal architecture and spicule geometry different to A. maculosa. The ectosomal skeleton of A. foetida is formed by a halichondroid dermal erust, tangential-paratangential oriented, 500–900 μm thick, with a mixture of oxeas and small styles projecting through the surface, and with vague tracts and small rounded meshes approx. 100–300 μm. The choanosomal skeleton is halichondroid, cavernous, with large rounded lacunae, 500–700 μm approx., and ill-formed multispicular tracts spaced and running towards the surface where they merge with the ectosomal skeleton. The skeleton is formed entirely by oxeas in a great size range 195–706 μm. The skeleton of SMF 1818 includes styles in low frequency 463–525 μm (491.2±17.4) x 6–16 μm. As admitted by Thiele, the styles might be modifications of oxeas.

Distribution. Papua New Guinea (Eastern Coral Triangle Province), Gulf of Carpentaria and outer region of Shoal Bay (Sahul Shelf province) between 6–28 m depth. It is also found in Torres Strait (Northeastern Australian Province) (Alvarez & Hooper unpublished data).

Remarks on Amorphinopsis. Amorphinopsis includes approx. 13 valid species (Van Soest et al. 2008) distributed mainly throughout the Indian Ocean but with species also recorded from the Atlantic and Mediterranean oceans.

The genus is represented in northern Australia (Sahul Shelf Province) by three species – Amorphinopsis excavans, A. fenestrata comb. nov., and A. maculosa comb. nov.

Amorphinopsis foetida was recorded by Hooper et al. (1997) from the Beagle Gulf but it is concluded here that the specimen is better allocated to A. fenestrata.

The species originally described as Lencoploheus fenestratus Ridley, 1884 is common in the study area. Its habitat and skeletal characteristics have been interpreted as typical from the genus Ciocalyptia but as discussed above, these similarities are considered not homologous and we propose to include the species in Amorphinopsis. The choanosomal skeleton of A. fenestrata is formed entirely by styloids and lacks 'true' oxeas as seen in other species of Amorphinopsis and other genera of Halichondriidae. We propose to expand the definition of Amorphinopsis slightly to include species with speicules differentiated into oxeas and/or styles.

Genus Axinyssa Lendenfeld, 1897
Gender feminine. Type species, by original designation, Axinyssa topsenti Lendenfeld, 1897: 116. Recent, western Indian Ocean.

Axinyssa bergquistae (Hooper et al., 1997) comb. nov.
(Figs 1D, 5)
Halichondria bergquistae Hooper et al., 1997: 45.

**Description**

Shape (Fig 1D). Massive-lobate, bulbous-digitate; with erect columns or irregular coalescent plates. Individuals approx. 70–100 mm high, 45–200 mm thick.

Colour. Purple-mauve, grey-brown; some individuals with lighter tinges.

Oscula. Variable in size (3–7mm diameter), conspicuous, discrete, with raised white and opaque membranous lips (Fig. 1D), irregularly distributed.

Surface. Smooth to microconulose at base with shallow and meandering channels covered by a translucent membrane; becoming distinctively conulose at erect columns or digits. Conules up to 2 mm long organised in longitudinal rows along erect columns and digits, with brushes of larger choanosomal spicules protruding through surface.

Texture and consistency. Hispid due to projection of spicules through surface, firm and incompressible.

Skeleton (Fig. 5A,B). Ectosome without specialised skeleton, with lightly coloured collagenous skin. Choanosomal skeleton halichondroid, with high spicule density in deeper regions; becoming more organised at subectosomal region, with multispecific spicule tracts, 50–200 μm running longitudinally and ascending towards surface, becoming more radial and plumose near periphery; ending in disorganised brushes that project through ectosome.

Spicules (Table 3, Fig. 5C). Mixture of oxeas of variable thickness and length (354–948 x 4–27.8 μm), slightly bent...
and sometimes slightly sinuous. Styloid modifications common.

Remarks. The species was initially described under *Halichondria*. Examination of additional material considered conspecific with the specimen described by Hooper *et al.* (1997) allowed us to conclude that the species is better allocated in *Axinyssa*. The plumose conules observed in some areas of the surface of *A. bergquistae* resembles *Axinyssa mertoni* (described below), but that species has a more lax skeleton with less spicular density and more collagen. It differs also in general shape, colour and the oscula morphology.

*Axinyssa bergquistae* is comparable to *A. valida* (Thiele, 1899: 12) [holotype NHMB 13, examined] in external morphology, skeletal organisation and size of spicules [(290.3–859.3 μm (599±210.8) x 9.7–34.8 μm (20.6±8.3))] and could possibly be conspecific. But both the skeleton and the size of spicules of most *Axinyssa* species are very similar and the separation of species is difficult and subjective (see below under remarks on the genus). The examination of more material from Indonesia (Alvarez & De Voogd in progress) will help to determine whether the northern Australian populations belong to the same species.

**Distribution.** Darwin Harbour and Bynoe Harbour (Sahul Shelf Province). Probably present also in the Northeast Australian Shelf Province (Alvarez & Hooper unpublished data).

### Table 3. Comparison of spicule dimensions among specimens of *Axinyssa bergquistae*.  

<table>
<thead>
<tr>
<th>Specimen</th>
<th>Locality</th>
<th>Oxeas</th>
</tr>
</thead>
<tbody>
<tr>
<td>QM G303351</td>
<td>Darwin Harbour</td>
<td>407.3–793.8 μm (619.7±82.8) x 10.3–27.8 μm (15.5±4.3)</td>
</tr>
<tr>
<td>(Holotype of <em>Halichondria bergquistae</em>)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>NTM Z.5224</td>
<td>Bynoe Harbour</td>
<td>366.3–948.1 μm (749.2±135.7) x 4.5–33.2 μm (21.3±7)</td>
</tr>
<tr>
<td>QM G313572</td>
<td>Gulf of Carpentaria</td>
<td>353.6–747.3 μm (618.3±77.5) x 4–20.9 μm (14.7±4.2)</td>
</tr>
</tbody>
</table>

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*Axinyssa mertoni* (Hentschel, 1912) com. nov.  
(Figs 1E, 6)

*Ciocalypta mertoni* Hentschel, 1912: 424; Burton 1934: 564.


*Pseudaxinyssa pity's* De Laubentels, 1954: 178; Bergquist 1965: 175 [?].


**Material examined.** Type material – *Ciocalypta mertoni*, holotype, SMF 1608, Aru Is, North of Penambulai; station 10, 8 m depth, 2 April 1908, coll. Merton exp. 1908. *Pseudaxinyssa pity's*, holotype, USNM 23103, Caroline Islands, Palau Is, Koror L., Iwayama Bay, 2 m depth, 1 September 1949, coll. De Laubenfels, M.W. Additional specimens – Darwin Harbour: NTM Z.5221 (0M9H2189-V).

**Description**  
Shape (Fig. 1E, 6A). Massive with conspicuous fistules up to 50 mm long, 1–2 mm thick, projecting from semi-buried basal portion up to 100 mm diameter.

Colour. Grey alive.

Oscula. On top of fistules, flushed, less than 5 mm diameter.

Surface. Regularly conulose with transulcent membrane stretching over conules; marked with choanosomal axes.

Skeleton (Fig. 6B). Ectosomal skeleton absent. Choanosomal skeleton plumose to halichondroid with multispiracular axes of spicules running longitudinally, nearly parallel and close to each other, anastomosing and diverging towards surface and becoming dendritic, bounded with collagen and ending in disorganised plumose brushes that project through surface. Spongin fibres ill-defined and short, direction-less, embedding spicule tracts.

Spicules (Fig. 6C, Table 4). Oxeas, hastate, slightly bent, straight or crooked, 476–1470.2 μm x 11.2–29.7 μm. Style and strongly modifications also present.

Remarks. *Ciocalypta mertoni* is conspecific with *Pseudaxinyssa pity's* and is better allocated to the genus

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**Fig. 6.** *Axinyssa mertoni*: A, preserved specimen (NTM Z.5221); B, light microphotograph of perpendicular section through surface showing choanosomal skeleton with longitudinal tracts projecting through surface (Holotype, SMF 1608); C, diagram of spicules. Scale bars: A, B, 500 μm; C, 100 μm.
Axinyssa. The type material of both species were examined here, and they are identical in all their characteristics. *Ciocalypta mertoni* was considered a junior synonym of *Halichondria tyleri* by Hooper & Wiedenmayer (1994) (following Burton 1959), but this synonym was later rejected by Hooper *et al.* (1997) who considered it a valid species of *Halichondria*, but admitted that the lack of an ectosomal skeleton was atypical of that genus. The species agrees well with the concept of *Axinyssa*, as it lacks an ectosomal skeleton and has a halichondroid to vaguely plumose choanosomal skeleton bounded by relatively high amounts of collagen and formed by oxeas of variable size and common styles and strongyles. The growth form of this species however, is not reported for other species of *Axinyssa*, thus a slight expansion in the diagnosis of the genus is necessary to accommodate species with fistulose projections.

A single specimen found in Darwin Harbour is assigned to this species. It differs from the type material examined only on spicule dimensions. The oxeas of the Darwin specimen are in average longer and thicker, but this might correspond to intraspecific variation within the species.

**Distribution.** *Axinyssa mertoni* is rare within the study area with only one specimen recorded here. The distribution of the species is extended to the Sahul Shelf and the Tropical Northwestern Pacific provinces. The record of Bergquist (1965) from Palau needs to be verified as there are several sympatric species of *Axinyssa* occurring in the area (Lori Bell Colin pers. comm.).

**Remarks on Axinyssa.** *Axinyssa* is represented in the area of the Indo-Pacific by several species: *A. aculeata* Wilson, 1925 (Philippines); *A. aphynoides* (Dendy, 1922) (Seychelles); *A. oinops* (De Laubenfels, 1954) (central West Pacific); *A. topsenti* Lendenfeld, 1897 (Tanzania); *A. variabilis* Lindgren, 1897 (Malaysia); and *A. valida* (Thiele, 1899) (Indonesia). The new combinations established in this revision extend the list by two additional species — *A. mertoni* (Sahul Shelf and Tropical Northwest Pacific provinces) and *A. bergquistae* (Sahul Shelf and probably Northeast Australian Shelf). Two additional species from the central Indo-Pacific region are also referred to *Axinyssa* after examination of type material — *Ciocalypta rutula gracilis* Hentschel, 1912 (SMF 1566, Aru Is., examined) and *Phycopsis terpis* De Laubenfels, 1954 (Caroline Is, Central Pacific, USNM 23061, examined).

We were not able to revise all the type material of the Indo-Pacific species of *Axinyssa* thoroughly, therefore it remains inconclusive whether *A. mertoni* and *A. bergquistae* might be conspecific with other species recorded from the region. As mentioned above, the skeletal organisation and the size of spicules among *Axinyssa* species is very similar and separation of species is subjective. The external morphological characteristics seem to be more discrete, but study of individual populations is necessary to determine the actual range of variability present within these species.

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**Table 4. Comparison of spicule dimensions among specimens of Axinyssa mertoni.**

<table>
<thead>
<tr>
<th>Specimen</th>
<th>Locality</th>
<th>Oxeas</th>
</tr>
</thead>
<tbody>
<tr>
<td>SMF 1608</td>
<td>Aru Island, Indonesia</td>
<td>515.6-779.6μm (691.4±61)</td>
</tr>
<tr>
<td>USNM 23103</td>
<td>Caroline Is, Central West Pacific</td>
<td>514.3-871μm (788.2±74.9)</td>
</tr>
<tr>
<td>NTM Z.5221</td>
<td>Darwin Harbour, NT</td>
<td>476-1470,2μm (979.5±285.9)</td>
</tr>
</tbody>
</table>

Study of different populations of *Axinyssa* through Indonesia (Alvarez & De Voogd unpublished data) is currently in progress and will help to re-define the limits of *Axinyssa* species.

The diagnosis of *Axinyssa* is here expanded to include species like *Axinyssa mertoni* with fistulose projections. We note however, that the skeletal organisation of the fistules observed in *A. mertoni* is considered not to be homologous with the organisation observed in species of *Ciocalypta*. The fistulose projections of *Ciocalypta* spp. are transparent with the skeleton formed by a central axis of spicules and extra-axial tracts diverging towards the surface. The fistulose projections of *A. mertoni* are opaque, tough-cartilaginous, arising from a massive base, and without a central axis of spicules which is diagnostic for *Ciocalypta*.

*Axinyssa mertoni* shares with the Indian Ocean *Ciocalypta digitata* (Dendy, 1905) the lack of an ectosomal skeleton, and the presence of fistulose projections; however, the fistules of *C. digitata* are transparent with a spicular axis from which thick bundles of spicules diverge towards the surface ending in conules (Erpenbeck & Van Soest, 2002). In our view the expansion of the definition of *Axinyssa* to include species with fistular projections such as *A. mertoni* does not affect the current position of *C. digitata* or the definition of the *Ciocalypta*.

The current position of the genus *Axinyssa* within the family Halichondriidae is debatable as molecular data (Erpenbeck *et al.* 2005) indicate that some species currently allocated to this genus are related to other dicytendellid genera such as *Acathemma* and *Dictyonella*. From a morphological point of view, the lack of an ectosomal skeleton, the presence of abundant collagen in the skeleton and the common occurrence of styles, strongyles and transitional forms, also points to possible relationships with members of Dictyonellidae. These relationships should be further explored to confirm the placement of this genus within the family Halichondriidae. However, taxonomic verification of the species of *Axinyssa* used in the molecular analyses should also be taken in consideration, particularly given the paucity of morphometric characters in this group and our still rudimentary understanding of character homology.

**Genus Ciocalypta Bowerbank, 1862.**

Gender feminine. Type species, by monotypy, *Ciocalypta pectinillus* Bowerbank, 1862. Recent, eastern Atlantic Ocean.
**Ciocalypta heterostyla** Hentschel, 1912
(Figs 1F, 7)


**Material examined.** HOLOTYPE – SMF 1569, Aru Is, N Penanbuli, 8 m depth, 2 April 1908, coll. H. Merton.
ADDITIONAL SPECIMENS – Darwin Harbour, NTM Z.5902.

**Description**
Shape (Fig. 1F). Fistulose, with semi-buried and massive base. Fistules pointed, projecting perpendicularly from base, 20–30 mm long, less than 10 mm diameter wide, slightly translucent especially at tips.

Colour. Light yellow.

Oscula. Apical on fistules.

Surface. Smooth, microconulose.

Ectosomal skeleton (Fig. 7A). Thin layer formed by tangentially oriented pauci- to multispicular tracts of spicules, crossing over and forming a reticulation of triangular meshes; supported by choanosomal tracts.

Choanosomal skeleton. Differentiated at fistules, with central column formed by thick multispicular tracts oriented longitudinally and expanding into thick brush at tip of fistule (Fig. 7B). Secondary tracts, 20–100 μm thick, slightly plumose, diverging nearly perpendicularly from central column toward surface, regularly spaced and connected irregularly by unispicular-paucispicular tracts of spicules; becoming thicker and ending in fan-like brushes at the subectosomal area, generally with smaller spicules oriented with their ends towards surface. Skeleton at base

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*Fig. 7. Ciocalypta heterostyla* (Holotype SMF 1569): A, light microphotograph of tangential section of ectosomal skeleton, showing tracts of spicules, forming a reticulation of triangular meshes; B, light microphotograph showing choanosomal skeleton at a fistule; C, diagram of spicules. Scale bars: A-B, 500 μm; C, 100 μm.
Halichondriidae from northern Australia

Halichondroid, with directionless multispecific tracts and single spicules in confused reticulation.

Spicules (Fig. 7C, Table 5). Mixture of styles in a large range of sizes, straight to slightly curved, some sinuous, some with rounded ends, 184–809 x 4–19 μm.

Remarks. Ciocalypta heterostyla was originally described from the Aru Is (Indonesia) and it has not been re-described or recorded until this present study. The material from Darwin Harbour agrees closely with the type. Only the spicule dimensions are on average slightly larger in the specimen from Darwin. The species is not very conspicuous due to its cryptic habit. It is apparently rare in the study area with only one specimen collected so far.

Hooper & Wiedenmayer (1994) followed Burton (1959) and considered this species a synonym of Ciocalypta tyleri Bowerbank. The two species are certainly similar in external morphology and skeletal organisation, however the skeleton of C. heterostyla is formed exclusively by styles instead of oxeas, and the skeleton within the fistules is much more organised with a regular reticulation. Because of these characters we considered that C. heterostyla is not only a valid species but also it can be easily differentiated from its South African relative.

Distribution. Known only from the type locality (Aru Is, Indonesia) and from Darwin Harbour (Sahul Shelf province). It is found between 8–12 m depth.

Table 5. Comparison of spicule dimensions between specimens of Ciocalypta heterostyla.

<table>
<thead>
<tr>
<th>Specimen</th>
<th>Locality</th>
<th>Styles</th>
</tr>
</thead>
<tbody>
<tr>
<td>SMF 1567</td>
<td>Aru Is, Indonesia</td>
<td>199.9–584.1 μm (387.3±137)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>x 3.5–14.8 μm (8.3±3.2)</td>
</tr>
<tr>
<td>NTM 5902</td>
<td>Darwin Harbour</td>
<td>184–809.2 μm (466.5±229.1)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>x 3.9–18.6 μm (9.4±5.5)</td>
</tr>
</tbody>
</table>

Ciocalypta stalagmites Hentschel, 1912

(Figs 1G–H, 8)


Description

Shape (Figs 1G–H, 8A). Flat cushion-shaped or massive base, buried or semi-buried, strongly attached to substrate, up to 35 mm thick, 4–100 mm diameter, with fistules projecting perpendicularly above surface. Fistules

Fig. 8. Ciocalypta stalagmites (Lectotype, SMF 1567): A, Preserved lectotype; B, light microphotograph showing choanosomal skeleton at fistule; C, light microphotograph showing choanosomal skeleton at base; D, diagram of spicules. Scale bars: A, 2 cm; B-C, 500 μm; D, 100 μm.
sharply pointed, globular or flattened, mammiform, tubular, rounded, 5–125 mm long, laterally fused sometimes or branching at tips.


Oscula. Generally at apex of fistules or tubes but also observed irregularly distributed along fistules, with membranous rims.

Consistency and Texture. Compressible-spongy, easily torn.

Surface. At fistules, smooth to slightly conulose, marked with longitudinal rows of minute conules. Choanosomal tracts of spicules, visible through the ectosome of translucent specimens. At base smooth, opaque, rough, spiculous.

Skeleton. Ectosomal skeleton, tangential layer of variable thickness (5–300 µm) easily peeled in some specimens, formed by a dense mass of smaller oxeas and supported by choanosomal skeleton. Choanosomal skeleton (Fig. 8C) at base, halichondroid, densely spiculous, with mixture of large and smaller oxeas and no distinct tracts of spicules. In fistules (Fig. 8B), becoming distinctive and organised, with central column of large spicules oriented longitudinally and smaller spicules criss-crossing. Multispicular tracts generally formed by medium-size spicules radiating from central column towards surface, connected by shorter tracts and single spicules, forming a regular reticulation. Large subectosomal spaces (up to 5 mm diameter) in some areas.

Spicules (Fig. 8D, Table 6). Two size classes of oxeas: I, smaller, thinner, fusiform, straight or slightly flexuous (147–321 x 4–10 µm); II, large, thick and slightly curved, fusiform, occasionally crooked-sinuous (378–886 x11–40 µm), and styles in equivalent size categories are common.

Remarks. The growth form of Ciocalypta stalagmites is remarkably variable. Fortunately this variation is also well represented in the type material. The external colouration is also variable and is possibly related to the presence of different cyanobacterial associations. The skeletal organisation, composition and size of spicules, however, are consistent and very similar among specimens with different habits and colouration. A very consistent characteristic throughout all the populations we examined is that the oxeas are differentiated in size categories not only by their length but also by their thickness. Proper statistic and morphometric analyses could be employed to demonstrate whether this is diagnostic to separate C. stalagmites from other Ciocalypta species.

Ciocalypta stalagmites is very similar to C. tyleri Bowerbank, 1873 from South Africa, and it was interpreted as such by Hooper et al. (1997) but allocated to the genus Halichondria (following Van Soest et al. 1990; Van Soest 1991). Both species are now referred to Ciocalypta under the revised concept of Halichondriidae (Erpenbeck & Van Soest 2002). The two species are similar in external morphology and skeletal organisation, however, the skeleton of C. stalagmites seems to be less organised. Despite similarities between these two species, it is unlikely that the Indonesian and northern Australian populations are conspecific with their South African relatives, thus we propose to reserve C. stalagmites for those populations inhabiting the Sahul Province and adjacent areas. Future independent evidence might demonstrate whether C. tyleri and C. stalagmites belong to a complex of cryptic species that cannot be easily separated using traditional morphological characters, or are instead conspecific and genuinely a widely distributed species.

Ciocalypta stalagmites is also very similar to C. vansoesti (Hooper et al., 1997), comb. nov. The two species have similar growth form and skeletal characteristics, but they can be differentiated from each other by some distinctive characteristics (see below).

Distribution. Ciocalypta stalagmites is very common throughout the northern Australian localities of the Sahul Shelf province and its distribution extends to adjacent provinces including the Northeast Australian Shelf, Papua New Guinea (Alvarez & Hooper unpublished), and Indonesia (Alvarez & De Voogd unpublished). It is found from the intertidal zone to 40 m.

Table 6. Comparison of spicule dimensions between specimens of Ciocalypta stalagmites.

<table>
<thead>
<tr>
<th>Specimen</th>
<th>Locality</th>
<th>Oxea type I</th>
<th>Oxea type II</th>
</tr>
</thead>
<tbody>
<tr>
<td>SMF 1567 (Lectotype)</td>
<td>Aru Is, Indonesia</td>
<td>167.8–240.2 µm (200.8±17.4)</td>
<td>377.7–837 µm (626.2±102.8)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>x 4.4–10 µm (7.9±1.3)</td>
<td>x 12.3–37.1 µm (18.7±4.7)</td>
</tr>
<tr>
<td>NTM Z.5212</td>
<td>Bynoe Harbour</td>
<td>165.3–320.6 µm (238.2±34)</td>
<td>411.4–659.5 µm (524.9±56.8)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>x 5.5–10.3 µm (7.6±1.2)</td>
<td>x 11.1–26.3 µm (18.9±4.1)</td>
</tr>
<tr>
<td>NTM Z.5210</td>
<td>Darwin Harbour</td>
<td>188.3–258.7 µm (214±19.1)</td>
<td>440.1–662.8 µm (601.8±53.9)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>x 5.6–9.2 µm (7.4±0.9)</td>
<td>x 11.3–38.5 µm (21.9±7.7)</td>
</tr>
<tr>
<td>NTM Z.5218</td>
<td>Wessel Is</td>
<td>147.2–202.7 µm (169.1±12.8)</td>
<td>437.7–886.5 µm (588.1±135.1)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>x 5.3–9.4 µm (6.7±0.9)</td>
<td>x 8.7–39.5 µm (21.7±7.9)</td>
</tr>
</tbody>
</table>
now referred to *Ciocalypta* under the revised concept of Halichondriidae (Erpenbeck & Van Soest 2002).

As mentioned by Hooper *et al.* (1997) and above, *Ciocalypta vansoesti* is closely related to *C. stalagmites*, both with similar growth form, skeletal organisation and type of spicules. Both species have fistules projecting from a buried-semiburied mass, but in the case of *C. vansoesti* the fistules are transluscent-white with the surface regularly conulose and subectosomal tracts and central column visible beneath (Figs 11, 9A). However, the skeleton in the fistules, when compared to *C. stalagmites*, is denser and slightly disorganised; the central column is not as condensed and the extra axial reticulation is vague (Fig. 9B, Hooper *et al.* 1997, figs. 22a, 23a). The dimensions of the oxeas are similar and overlap with those of *C. stalagmites*, but in *C. vansoesti* there is not a clear difference in size categories, with the two classes of spicules overlapping both in length and in width (Table 7).

*Ciocalypta vansoesti* is also similar in some of the field characteristics to *Axinyssa mertoni*, indicating once again that fistule-like growth forms are common among halichondrids and so are not useful to differentiate species unless they are used in combination with other skeletal characters.

**Distribution.** *Ciocalypta vansoesti* is common in Darwin Harbour and Bynoe Harbour. It is also recorded from Cobourg Peninsula and the Gulf of Carpentaria. It is found intertidally and subtidally to 40 m depth.

**Remarks on *Ciocalypta*.** Burton (1959) considered many species of halichondriid genera with a fistulose habit conspecific with *Ciocalypta penicillus* (type species of *Ciocalypta*). These synonyms were not properly substantiated and some of them have been rejected by Hooper *et al.* (1997) and the present revision, i.e. *Ciocalypta heterostyla*, *C. stalagmites*, *C. tyleri*, *C. oculata maxima* (referred here to *Amorphinopsis fenestrata*), and *C. mertoni* (referred here to *Axinyssa mertoni*).

Additional species of *Ciocalypta* recorded from the Sahul Shelf Province and adjacent areas besides the three revised here (i.e. *C. heterostyla*, *C. stalagmites* and *C. vansoesti*) are *C. rutila gracilis* Hentschel, 1912 (see below), *C. digitata* (Dendy, 1905, as *Collocalypta*), *C. melichlora* Sollas, 1902, *C. rutila* Sollas, 1902, and *C. simplex* Thiele, 1900: 76.

One of the syntypes of *Ciocalypta rutila gracilis* Hentschel, 1912 (SMF 1566, examined) belongs in *Axinyssa*. Both the external morphology (based on Hentschel’s description) and the arrangement of skeleton agree with the concept of that genus. The skeleton of the material examined is formed by two classes of oxeas: straight 480.8–706.4 μm (601.6±76.7)x 9–24 μm (17±3.1) and vermicular, crooked sinuous, relatively thinner, and often bent up to a 90 degree angle, 193–600.7 μm (406.7±110.6) x 5.3–16 μm (10.6±3) [18]; less often styles are also present. Specimens recorded for Northeast Australian Shelf and Indonesia correspond with the type examined (Alvarez & Hooper unpublished data; Alvarez & De Voogd unpublished data) and will be redescribed under the name of *Axinyssa gracilis* in forthcoming publications.

Ciocalypta digitata (Dendy, 1905) resembles *Ciocalypta stalagmites* and *C. vansoesti* in habit but differs in skeletal

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**Table 7.** Comparison of spicule dimensions between specimens of *Ciocalypta vansoesti*.

<table>
<thead>
<tr>
<th>Specimen</th>
<th>Locality</th>
<th>Oxea type I</th>
<th>Oxea type II</th>
</tr>
</thead>
<tbody>
<tr>
<td>NTM Z.2648</td>
<td>Darwin Harbour, East Point</td>
<td>185.3–459.7 μm (320±60.9)</td>
<td>x 6.4–9.5 μm (8±0.9)</td>
</tr>
<tr>
<td>QM G303450</td>
<td>Bynoe Harbour</td>
<td>194.1–361.7 μm (275.3±45.6)</td>
<td>x 2.1–9.8 μm (6.8±1.8)</td>
</tr>
<tr>
<td>QM G303524</td>
<td>Gulf of Carpentaria</td>
<td>237.5–429.2 μm (314.9±56.5)</td>
<td>x 6.4–11.9 μm (8.4±1.3)</td>
</tr>
</tbody>
</table>
organisation and composition and size of spicules. This species lacks an ectosomal skeleton, but the fistular processes have spicular axis and extra-axial tracts as in other species of Ciocalypta.

**Genus Halichondria Fleming, 1828**

Gender feminine. Type species, by subsequent designation (of Bowerbank 1862), *Spongia panicea* Pallas, 1766. Recent, East England.

**Subgenus Halichondria (Halichondria) Fleming, 1828**

*Halichondria (Halichondria) carotenoidea* sp. nov. (Figs 10A,B, 11)


*Axinella* sp. 244. – Hooper et al. 1992.


**Description**

Shape (Figs 10 A,B). Fan shaped, digito-palmate, multiplanar, arborescent, erect, stalked, bifurcated at base, with complex branching; branches or digits flattened generally with pointed tips but round tips also common; specimens reaching up to 350 mm high, 300 mm wide.

Colour. Orange. Blue-grey, or beige in alcohol.

Consistency and texture. Soft, easily torn, rubbery.

Oscula. Regularly distributed along lateral side of branches (Fig 10B) less than 5 mm in diameter, generally in rows, with membranous rims slightly elevated. Some specimens with subectosomal thin canals ending in oscula.

Surface. Smooth, wrinkled, evenly covered with microconules when exposed to air. Marked with subectosomal drainage canals in some specimens.

Skeleton (Fig 11 A, B). Ectosomal skeleton formed by 100–200 μm thick continuous layer, supported by choanosomal skeleton and packed mainly with smaller category of oxeas, in short, ill-defined and cross-crossing bundles, oriented tangentially-paratangentially, protruding occasionally through surface in disorganised manner (Fig. 11A). Choanosomal skeleton, halichondroid to plumose, formed by ill-defined bundles of larger spicules, cross-crossing in all directions in the inner region of choanosome. Skeleton becomes more organised at subectosomal region, with a vague reticulation of ascending tracts connected by short bundles and single spicules. Near surface, spicule tracts become more defined and even slightly plumose, supporting ectosomal skeleton and occasionally protruding through surface (Fig. 11B).

Skeleton of some specimens is obscured by granular pigments and cyanobacteria when examined under light microscope.

Spicules (Fig. 11C, Table 8). Mixture of oxeas not separable into size categories 112–389 x 2–12 μm, hastate, pointed, straight or occasionally slightly bent in middle.

**Remarks.** *Halichondria carotenoidea* is diagnosed by a unique combination of features (i.e. growth form, organisation of the skeleton, and the size and composition of spicules) not found in other species of *Halichondria* revised here or reported for adjacent areas (see Table 9).

The skeleton and spicule composition of all the material examined is almost identical to *Halichondria (H.) microbiana* sp. nov. (see below). Both species are sympatric and include a high density of cyanobacteria in the choanosome. The two species clearly differ in shape, which is branching to arborescent in *(H.)* carotenoidea and massive to cushion shape in *(H.)* microbiana. Both species can be further distinguished by the size of the oxeas, which are separated into class categories in *(H.)* microbiana but not in *(H.)* carotenoidea.

The material described by Hooper et al. (1997) as *Halichondria stalagnites* (Hentschel) is a composite of *(H.)* carotenoidea and *Halichondria stalagnites* (Hentschel) as described by Hentschel (1912). Additional material, an in situ
Halichondriidae from northern Australia

Table 9. *Halichondria* (Halichondria) species from the Central Indo-Pacific (after Van Soest et al. 2008), with remarks on current taxonomic allocation, type material and description.

<table>
<thead>
<tr>
<th>Species</th>
<th>Remarks</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Halichondria</em> (Halichondria) armata Lindgren, 1897</td>
<td>Unrecognisable from the description; no type material available.</td>
</tr>
<tr>
<td><em>Halichondria</em> (Halichondria) bergquistae Hooper, Cook, Hobbs &amp; Kennedy, 1997</td>
<td>Referred here to <em>Axinyssa</em> (see Remarks of <em>Axinyssa</em> this revision).</td>
</tr>
<tr>
<td><em>Halichondria</em> (Halichondria) cartilaginea (Esper, 1794)</td>
<td>Valid, common species through Indo-Pacific. Always associated to symbiotic green algae (<em>Lim</em> et al. 2008).</td>
</tr>
<tr>
<td><em>Halichondria</em> (Halichondria) darwinensis Hooper, Cook, Hobbs &amp; Kennedy, 1997</td>
<td>Valid (see under genus <em>Halichondria</em>, this revision).</td>
</tr>
<tr>
<td><em>Halichondria</em> (Halichondria) fragilis Kieschnick, 1896</td>
<td>Unrecognisable from the description; no type material available.</td>
</tr>
<tr>
<td><em>Halichondria</em> (Halichondria) incrustans Kieschnick, 1896</td>
<td>Unrecognisable from the description; no type material available.</td>
</tr>
<tr>
<td><em>Halichondria</em> (Halichondria) pelliculata Ridley &amp; Dendy, 1886</td>
<td>Valid, recognisable from the description. Type material not examined. Distinctive shape and surface characteristics, not comparable to the new species recorded here.</td>
</tr>
<tr>
<td><em>Halichondria</em> (Halichondria) ridleyi Hooper, Cook, Hobbs &amp; Kennedy, 1997</td>
<td>Referred in this revision to <em>Topsentia</em> (see Remarks of <em>Topsentia</em> this revision).</td>
</tr>
<tr>
<td><em>Halichondria</em> (Halichondria) stalagnitica (Hentschel, 1912)</td>
<td>Valid. Type material examined (MSNG 48700). Detachable ectosome differentiated into a thick layer, with spicules oriented paratangentially, disorganised. Choanosome halichondroid with some ill-defined, multispirular, ascending to surface and supporting ectosome. Oxeas several sizes, 256.4-706.7μm (539.3±137) x 5.2-19μm (13±3.7); few styles.</td>
</tr>
<tr>
<td><em>Halichondria</em> (Halichondria) syringea Pulitzer-Finali, 1996</td>
<td>Referred here to <em>Ciocalypta</em> (see remarks of <em>Ciocalypta</em> this revision).</td>
</tr>
<tr>
<td><em>Halichondria</em> (Halichondria) vansoesti Hooper, Cook, Hobbs &amp; Kennedy, 1997</td>
<td>Refered here to <em>Ciocalypta</em> (see under genus <em>Ciocalypta</em>, this revision).</td>
</tr>
</tbody>
</table>

Table 10. Comparison of spicule dimensions among specimens of *Halichondria* (Halichondria) darwinensis.

<table>
<thead>
<tr>
<th>Specimen</th>
<th>Locality</th>
<th>Oxeas</th>
</tr>
</thead>
<tbody>
<tr>
<td>NTM Z.3205 (Holotype)</td>
<td>Darwin, Point</td>
<td>272.3–659.6μm (467.2±112) x 3.7–13.2μm (8.5±2.5)</td>
</tr>
<tr>
<td>QM G303252 (Paratype)</td>
<td>Darwin, East Arm</td>
<td>307–627.5μm (538.8±90.6) x 4.3–16μm (10.2±3.2)</td>
</tr>
<tr>
<td>NTM Z.5211</td>
<td>Darwin, Reef</td>
<td>386.2–663.7μm (524±68) x 7–14.9μm (11.8±1.9)</td>
</tr>
</tbody>
</table>

photograph (Fig 10C), and spicule measurements (Table 10) are provided here to complement the original description. *Halichondria darwinensis* is very inconspicuous and represented so far by only three individuals (including the holotype and the paratype). Its encrusting habit with small and insubstantial digits makes it inconspicuous and hard to find. The re-examination of the available material and additional measurements of spicules, indicate that the differences in the thickness of the spicules reported by Hooper et al. (1997) as a distinctive character for the species, no longer appear to be significant (see Table 10). Both the length and the thickness of the oxeas are variable, but not divisible into size classes.

The species seems to have affinities with the genus *Axinyssa*. The skeleton is poorly developed, with very little spongian and relatively less spicule density when compared to other *Halichondria* species; the ectosomal skeleton is quite undifferentiated and the spicules are similar in shape and dimensions to other *Axinyssa* species. Therefore, the assignment of this species to the genus *Halichondria* is inconclusive.

**Distribution.** *Halichondria darwinensis* is presently known only from Darwin Harbour. It occurs intertidally and subtidally to 10 m.

*Halichondria (Halichondria) phakellioides* Dendy & Frederick, 1924 (Figs 10 D, E, 12) *Halichondria phakellioides* Dendy & Frederick, 1924: 498; Burton 1934: 600; Hooper et al. 1997.


**Remarks.** *Halichondria phakellioides* was described by Hooper et al. (1997). Additional material, illustrations (Figs 10D, E, 12), and spicule measurements (Table 11) are provided here to complement the original description.
Halichondriidae from northern Australia

Fig. 11. Halichondria (Halichondria) carotenoida sp. nov. (NTM Z.5909): A, light microphotograph of tangential section of cetosomal skeleton showing ill-defined and criss-crossing bundles of spicules; B, light microphotograph of perpendicular section through surface showing organisation of ehoanosomal skeleton and part of cetosomal skeleton layer (left upper corner of section); C, diagram of spicules. Scale bars: A, 100 μm; B, 500 μm; C, 50 μm.

Distribution. Halichondria phakellioides is widely distributed through the Northwest Australian Shelf and Sahul Shelf provinces. It is found from the intertidal to 20 m depth.

Halichondria (Halichondria) microbiana sp. nov. (Figs 10F, 13)


Description

Shape (Fig.10F). Cushion-shaped with globular, subspherical or massive base, sometimes semi-buried

Table 11. Comparison of spicule dimensions among specimens of Halichondria (Halichondria) phakellioides.

<table>
<thead>
<tr>
<th>Specimen</th>
<th>Locality</th>
<th>Oxea type I</th>
<th>Oxea type II</th>
</tr>
</thead>
<tbody>
<tr>
<td>NTM Z.5223</td>
<td>Bynoe Harbour</td>
<td>170.1–308.4 μm (232±30.7) x 4.1–10.3 μm (8±1.5)</td>
<td>363.2–524.6 μm (440.6±40.8) x 11.5–24.4 μm (17.9±3.7)</td>
</tr>
<tr>
<td>NTM Z.5219</td>
<td>Darwin Harbour</td>
<td>154.2–293.2 μm (228±34.5) x 5–10.3 μm (7.3±1.4)</td>
<td>356.7–499.6 μm (425.5±38.7) x 10.5–20.2 μm (16.3±3)</td>
</tr>
<tr>
<td>NTM Z.5228</td>
<td>Wessel Is</td>
<td>162.1–313.9 μm (242.4±48.6) x 3.7–7.5 μm (5.6±0.9)</td>
<td>326.5–519.3 μm (440.5±45.5) x 10.6–21.1 μm (15.6±3)</td>
</tr>
</tbody>
</table>
Halichondria (Halichondria) phakellioides (NTM Z.5228): A, light microphotograph of tangential section showing organisation of ectosomal skeleton; B, light microphotograph of perpendicular section through surface, showing organisation of choanosomal skeleton.

Scale bars: A-B, 500 μm.

in substrate, and small tapering erect projections (from 10 mm long and less than 5 mm diameter) at apex. Erect projections vary in shape, i.e. fistulose-like, convoluted, bifurcating and lobate; generally small 30–70 mm diameter, 10–20 mm thick.


Consistency and texture. Soft, easily torn, rubbery.

Oscula. Apical and conspicuous on small digits, with membranous rims.

Surface. Semitransparent at apex of digits in some specimens.

Skeleton (Fig. 13A,B). Ectosomal skeleton, halichondroid, formed by a thin (less than 50 μm), wavy, loose membranous layer, with oxeas tangentially oriented and supported by choanosomal tracts (Fig. 13A). Choanosomal skeleton, halichondroid, formed by ill-defined bundles of larger spicules, criss-crossing and without any particular orientation connected by short bundles and single spicules. In subectosomal region, skeleton becoming cavernous with large lacunae, 100–600 μm diameter (Fig. 13B) and vague reticulation of pauci-multispicular, ill-defined tracts, diverging towards surface or condensed and running nearly parallel to it, supporting ectosomal skeleton. High densities of filamentous cyanobacteria present in both ectosome and choanosome, especially near surface. Spongin or collagen scarce.

Spicules (Fig. 13C; Table 12). Oxeas, hastate, straight, possibly in two size categories, larger and thicker (249–587 x 3.3–7.1 μm) and smaller and thinner (88–217 x 3–7 μm). Style modifications slightly common within larger category.

Remarks. We compared Halichondria inicrobiana with the valid species recorded for the Central West Pacific (Table 7) and those reported in this revision. It is diagnosed by a unique combination of features (i.e. growth form, organisation of the skeleton, size and composition of spicules and presence of cyanobacteria in the ectosome and the choanosome) not found in those species.

All the specimens examined here have a high density of filamentous cyanobacteria in the choanosome, generally concentrated at the subectosomal region, a character shared with H. (H.) carotenoides. As mentioned above, this new species is also very similar in skeletal characteristics to H. (H.) carotenoides sp. nov., but it differs in habit and size of spicules, which are larger and separated in size categories in H. (H.) microbiana.

Hooper et al. (1997) interpreted this species as Halichondria stalagmites. However, a thorough re-examination of the type material of that species indicates that it is not conspecific with H. (H.) microbiana (see description of C. stalagmites above).

Distribution. Halichondria microbiana is relatively common at Darwin and Bynoe Harbours, and it was also observed at Wessel Is (Raragala I.) and recorded from the Northeastern Australian Shelf (Alvarez and Hooper, unpublished data). It occurs between 6–12 m depth.

Etymology. Named after the symbiotic microorganisms hosted by the species. The specific name is intended as a noun in apposition.

Remarks on Halichondria (Halichondria). The subgenus Halichondria is large with approx. 95 valid species (Van Soest et al. 2008). Table 7 lists species distributed within the Central Indo-Pacific Realm (following Spalding et al. 2007) which includes the study area and adjacent areas. Some of those species, in particular the

<table>
<thead>
<tr>
<th>Specimen</th>
<th>Locality</th>
<th>Oxea type I</th>
<th>Oxea type II</th>
</tr>
</thead>
<tbody>
<tr>
<td>NTM Z.5907</td>
<td>Darwin Harbour, NT</td>
<td>87.9–203μm (126.5±24.8) x 3.3–7.1μm (5±0.9)</td>
<td>249.2–587μm (482.9±75.1) x 6.3–14.2μm (8.9±1.8)</td>
</tr>
<tr>
<td>NTM Z.5908</td>
<td>Bynoe Harbour, NT</td>
<td>91.3–217μm (137.8±32) x 2.9–7.2μm (5.1±1)</td>
<td>282.5–572.1μm (446.6±93.5) x 5.2–13.2μm (8.8±2)</td>
</tr>
</tbody>
</table>
ones described by Kiesehnick (1896) and Lindgren (1897), are unrecognisable and their type material has never been relocated. Other species reported for the area have been allocated to other genera as result of this revision, thus *Halichondria* (Halichondria) is represented within this realm by nine species including the two new species described above.

The subgenus *Eumastia* Schmidt, 1870 is not represented in the study area at all and it is reserved for *Halichondria*-like species from high latitudes (Erpenbeck & Van Soest 2002).

**Genus Hymeniacidon Bowerbank, 1858**


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**Hymeniacidon gracilis (Henschel, 1912)**

(Fig. 14)


**Material examined.** As listed by Hooper et al. (1997).

**Remarks.** The species was well described by Hooper et al. (1997) and elevated to full species rank in the genus *Hymeniacidon*. We provide a new illustration of the type material (Fig. 14) and additional spicule measurements (Table 13) to complement the description given by Hooper et al. (1997).

Only three specimens are recorded for the study area; no new material was located in recent collections.

**Distribution.** As recorded by Hooper et al. (1997).

**Remarks on the genus Hymeniacidon.** *Hymeniacidon gracilis* is the only valid species of the genus from the study area. Other species of *Hymeniacidon* recorded for the
Sahul Shelf Province and adjacent areas are *H. vernonensis* Hooper et al., 1997 and *H. flaccida* Pulitzer-Finali, 1996. The material described under *H. vernonensis* by Hooper et al. (1997) was revised and it does not agree with the current concept of the genus. The species is formally transferred here to the dictyonellid genus *Stylissa*. As admitted by Hooper et al. (1997), it is very similar to *Stylissa jlabelliforniis* but *S. vernonensis* includes distinctive styles, curved at the centre, sinuous or rhabdose and frequent anisocaps with one telescoped point. It should be noted however, that these spicule modifications are common among species of *Stylissa* and therefore they are not reliable for the delimitation of species. Both species are similar in growth form, surface characteristics and skeletal organisation. The choanosomal skeleton of *S. vernonensis* however, is nearly halichondroid with only vague tracts of spicules and with a much higher spicule density and no spongion fibres (whereas in *S. flabelliformis* is vaguely plumo-reticulated and with well developed spongion fibres).

The type specimen of *Hymeniaddon flaccida* (MSNG 48703) from Laing Is., Papua New Guinea, was re-examined and it does not correspond to the genus *Hymeniaddon*. The species belongs also to the dictyonellid genus *Stylissa* and is likely to be conspecific with *Stylissa massa* (Carter, 1887). The specimen examined however, includes distinctive subtylostyles transitional to strongyles with tylote modifications. As is the case with *S. vernonensis*, these style modifications are common among the genus. Population genetics and additional morphometric analyses might reveal whether these style modifications of *Stylissa* are reliable characters for the separation of species.

### Table 13. Comparison of spicule dimensions between specimens of *Hymeniaddon gracilis*.

<table>
<thead>
<tr>
<th>Specimen</th>
<th>Locality</th>
<th>Styles</th>
</tr>
</thead>
<tbody>
<tr>
<td>SMF 970</td>
<td>Indonesia</td>
<td>220.5–261.1μm (238.4±9.6) x 3.3–8.9μm (6.1±1.5) [25]</td>
</tr>
<tr>
<td>NTM Z.883</td>
<td>Darwin Harbour</td>
<td>243.1–279.1μm (265.6±11.1) x 3–7.4μm (5.1±1.1)</td>
</tr>
</tbody>
</table>

---

**Fig. 14.** *Hymeniaddon gracilis* (Synype SMF 970). A. light microphotograph of perpendicular section through surface, showing organisation of choanosomal skeleton; B, diagram of spicules. Scale bars: A, 500 μm; B, 50 μm.

**Genus Topsentia**

Gender feminine. Type species, by original designation, *Anisoxyla glabra* Topsent, 1898. Recent, Azores Is.

**Topsentia dura** (Lindgren, 1897)

(Figs 10G, 15)


**Remarks.** Hooper et al. (1997) assigned material from the Beagle Gulf to this species under the genus *Topsentia*. Additional specimens from recent collections agree also with this material and are assigned to this species. Further illustrations (Figs 10G, 15) and spicule measurements (Table 14) are provided here to complement that description. The description agrees with the current concept of *Topsentia*, however it remains inconclusive whether the material from the Beagle Gulf is conspecific with Lindgren’s species from Indonesia as the type was not examined. Examination of additional specimens from Indonesia (Alvarez & De Voogd unpublished data) and a re-description of the type might provide additional evidence to confirm if these populations belong in the same species.

**Distribution.** Indonesia [?], Darwin Harbour and Wessel Is. *Topsentia dura* occurs the intertidal zone to 25 m depth.

**Remarks on Topsentia.** Hooper et al. (1997) described material under the Red Sea species *Topsentia halichondrioides* (Dendy, 1905) that seems very similar
Halichondriidae from northern Australia

Fig. 15. *Topsentia dura* (NTM Z.5209): A, light microphotograph of perpendicular section through surface, showing organisation of choanosomal skeleton and palisade of erect oxcas at surface; B, diagram of spicules. *Topsentia halichondrioides* (QM G303442); C, light microphotograph of perpendicular section through surface, showing organisation of choanosomal skeleton and oxcas oriented perpendicularly at surface level; D, diagram of spicules. *Topsentia ridleyi* (QM G303309, Holotype); E, light microphotograph of perpendicular section through surface, showing organisation of choanosomal skeleton; F, diagram of spicules. Scale bars: A,C,E, 500 µm; B,D,F, 100 µm.

Topsentia halichondrioides*, and sunken and small in *T. dura*). *Halichondria ridleyi* Hooper et al., 1997 is referred here to the genus *Topsentia* (comb. nov.) and it is also very similar to *T. dura* (Fig. 15E,F). It differs from *T. dura* in having some surface fistules and processes.
Table 14. Comparison of spicule dimensions among specimens assigned to Central Pacific species of Topsenlia.

<table>
<thead>
<tr>
<th>Species</th>
<th>Specimen</th>
<th>Locality</th>
<th>Oxea type I</th>
<th>Oxea type II</th>
</tr>
</thead>
<tbody>
<tr>
<td>Topsenlia ridleyi</td>
<td>QM G303309</td>
<td>Darwin Harbour</td>
<td>142.3-273.5µm (207.7±39.4)</td>
<td>335.6-576.7µm (443.9±52.7)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>x 3.3-7.6µm (5.4±1.2)</td>
<td>x 6.7-16.6µm (12±2.6)</td>
</tr>
<tr>
<td>Topsenlia ridleyi</td>
<td>NTM Z.3262</td>
<td>Cobourg Peninsula</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Topsentia halichondrioides</td>
<td>G303442</td>
<td>Bynoe Harbour</td>
<td>160.6-331.2µm (257.4±50.3)</td>
<td>421.6-716.5µm (555.3±62.7)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>x 4.2-12.3µm (8.2±2.3)</td>
<td>x 14-24.4µm (19.3±2.6)</td>
</tr>
<tr>
<td>Topsentia halichondrioides</td>
<td>NTM Z.5233</td>
<td>East Point</td>
<td>111.4-165.9µm (142.2±13.8)</td>
<td>348.6-568.1µm (448.9±57.8)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>x 5.9-8.9µm (7.2±0.9)</td>
<td>x 13-30µm (18.9±4.4)</td>
</tr>
<tr>
<td>Topsenlia dura</td>
<td>NTM Z.5234</td>
<td>Wessel Is</td>
<td>142.4-333.5µm (220.1±47.2)</td>
<td>373.9-565.5µm (477.9±79.2)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>x 3.7-10.3µm (7.3±1.7)</td>
<td>x 10-23.9µm (15±3.2)</td>
</tr>
<tr>
<td>Topsenlia dura</td>
<td>NTM Z.5209</td>
<td>Darwin Harbour</td>
<td>151.2-399.7µm (248.3±61.9)</td>
<td>352.5-525.1µm (441.4±46.2)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>x 3-11.7µm (7.6±2.3)</td>
<td>x 9.9-18.5µm (13.7±2.4)</td>
</tr>
<tr>
<td>Topsenlia dura</td>
<td>NTM Z.3178</td>
<td>Darwin Harbour</td>
<td>189.4-357.5µm (269.9±41.9)</td>
<td>341.2-611.2µm (482.6±69.2)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>x 4-9.7µm (7.1±1.4)</td>
<td>x 8.3-22.7µm (15.6±3.4)</td>
</tr>
<tr>
<td>Topsenlia dura</td>
<td>NTM Z.1442</td>
<td>Gunn Point</td>
<td>189.6-387.1µm (254.5±52.5)</td>
<td>492.7-1078.1µm (734.4±125)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>x 5.5-12.5µm (7.8±2)</td>
<td>x 11.1-39.4µm (21.7±5.5)</td>
</tr>
</tbody>
</table>

An additional species of Topsenlia recorded from Aru Is, Indonesia, is T. indica Hentschel, 1912 (syntype SMF 995 and 997, examined).

The differentiation of these species using traditional morphological characters is extremely subjective. Molecular and morphometric studies of local populations might contribute to a better understanding of the concept of this species.

Other species of Topsenlia recorded for the Sahul Province and adjacent areas that are better placed elsewhere include Topsenlia maculosa Pulitzer-Finali, 1996 from Papua New Guinea (it belongs in Amyrophophis, see above) and Topsenlia plurisclera Pulitzer-Finali, 1996 (holotype, MSNG 48702, examined) is a species of Petrosia.

DISCUSSION

This revision of species of Halichondriidae from northern Australia recognises a total of 15 species belonging to the genera Amyrophophis, Axinysa, Ciocalypta, Halichondria (Halichondria), Hymeniacidon, and Topsenlia. Other genera of the family (i.e. Epipolasis, Laminospingos, Vosmaeria, Ciocalypta, and Spongosphorites) are not represented in the Sahul Shelf Province. Epipolasis and Spongosphorites are however represented in the Northeast Australian Shelf (Alvarez and Hooper, unpublished data).

Of the species reported in this revision, Axinysa bergquistae, Ciocalypta vansoestii and the two new species Halichondria (Halichondria) carotenoidae and H (H.) microbiana are so far known only from northern Australian waters. The rest of the species have extralimital distributions through the Central Indo-Pacific realm. Axinysa mertoni (Hentschel, 1912) in its new generic combination is recorded from northern Australia and it represents a new record for the study area.

As in other members of the order Halichondrida, particularly in Axinellidae and Dictyonellidae, species within and across all genera of Halichondriidae are extremely di fficult to delimit. This problem is demonstrated by the large number of misidentifications in previous studies due to the lack of adequate generic definitions and also to the poor understanding of the importance, or indeed relevance, of some of the alleged pivotal characters that currently differentiate both species-groups and genera within the Halichondriidae. The additional information obtained from the collection of new material plus the revised generic definitions of the family (Erpenbeck & Van Soest 2002) allowed us to clarify the concept of halichondrid species of northern Australia and to allocate them to more appropriate genera.

Nevertheless, differentiating species within Halichondriidae continues to be ambiguous based solely on the present limited suite of accepted morphological characters, with a number of them shared among species and even genera. For example, Ciocalypta heterostyla, Ciocalypta vansoestii, and Axinysa mertoni are species with filose-like growth form, nearly indistinguishable in the field (Fig 1). However, they all are easily diagnosed based on skeletal characteristics. This suggests that the growth form of these species in particular, might be an adaptation to the habitat where they occur (i.e. soft and muddy sediments). Amyrophophis foetida and A. maculosa are also very similar in habit and in their skeletal characteristics but they can be distinguished by the predominance of oxes and styles.

Separation of species based on the dominance of styles or oxes however might be debatable, as this could possibly be related to intraspecific variation as seen in some species of Axinellidae (Alvarez et al. 1998; Alvarez & Hooper 2009).

Spicule morphometrics (i.e. size variation of spicules) within Halichondriidae seems to be a useful tool for the
differentiation of species. *Ciocalypta stalagnites*, for example, is distinguished from the other species by the distinctive and nearly constant size of two categories of oxeas. Similarly, *Halichondria (H.) microbiana* can be distinguished from *H. (H.) carotenoida* by the size of the larger category of oxeas. On the other hand, all the *Axinella* species we have studied have always a mixture of oxeas in a large size range, thus spicule sizes is not a useful character for the distinction of species within this genus.

These examples indicate that the characters currently used to separate genera and species within the family are extremely homoplastic and suggest that genera and species within Halichondridae might be non-monophyletic. The study of local populations using both morphological and genetic methods will help to clarify whether these taxa are monophyletic.

This study represents the final contribution to the present taxonomic revision of the order Halichondrida of northern Australia, restricted to the marine province identified as the Sahul Shelf in the classification of Spalding et al. (2007). The result of this and previous studies (Alvarez & Hooper 2009, 2010) indicates that the group is represented in the study area mainly by the families Axinellidae (Alvarez & Hooper 2009), Dictyonellidae (Alvarez & Hooper 2010) and Halichondridae (this revision).

One additional family, the Heteroxyidae (formerly Desmoxoideae see Van Soest & Hooper 2005), is represented in the area by two very common species: *Myrmekioderma granulatum* (Esper, 1830), which is documented and illustrated by Hooper et al. (1997); and *Higginsia mixta* (Hentschel, 1912). The type of *H. mixta* (SMF 968) was examined and it agrees with material deposited at the collections of QM and NTM and recorded for the study area. The ectosomal skeleton of the specimens studied have a relatively thick tangential crust formed by a dense mass of spined microxeas and interrupted by disorganised brushes of thin raphidiform oxeas and extra long styles-strongyles (mostly broken in the preparations) projecting through surface. The similarities of this type of skeletal organisation with raspailiid genera such as *Ceratopsis* are remarkable and worth further investigation. Phylogenetic affinities based on molecular data (Erpenbeck et al. 2005) indicated that members of Heteroxyidae (i.e. *Didiscus* and *Myrmekioderma*) are closely related to the axinellid genera *Rientochnia* and *Ptilocaulis*. The position of these genera within Axinellidae (Halichondrida) and its relationships based on molecular data with other raspailiid genera such as *Axechna* has already been discussed (Alvarez 2009 and references within). Sequencing data of additional genera currently allocated to Heteroxyidae, and in particular of the species represented in the Sahul Shelf province will help to clarify these relationships and classification.

The family Hubaridae is the only family of Halichondrida not represented in the area of study.

ACKNOWLEDGEMENTS

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REFERENCES


### APPENDIX I

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

#### QM material

| G301034 | SW Vrilya Point, SW, Gulf of Carpentaria, QLD, 11°29.0167'S, 142°55.09'E, 18 m, 1 Dec 1991, coll. Cook, SD. on CSIRO RV Southern Surveyor |
| G303252 | 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 & Hobbs, L.J. |
| G30287 | 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 & Hobbs, L.J. |
| G30309 | Dudley Point Reef, East Point, Darwin, NT, 12°25.05'S, 130°49.01'E, 0 m, 20 Sep 1993, coll. Hooper, JNA & Hobbs, L.J. |
| G30442 | Fish Reef, west side, Bynoe Harbour, NT, 12°26.0167'S, 130°26.09'E, 11 m, 26 Sep 1993, coll. Hooper, JNA & Hobbs, L.J. |
| G30450 | Fish Reef, west side, Bynoe Harbour, NT, 12°26.0167'S, 130°26.09'E, 11 m, 26 Sep 1993, coll. Hooper, JNA & Hobbs, L.J. |
| G30524 | Duyfken Point, W Gulf of Carpentaria, QLD, 12°41.0501'S, 141°3.01'E, 42 m, 11 Nov 1993, coll. Cook, SD. & Kennedy, J. on CSIRO RV Southern Surveyor |
| G30558 | Cape Hotham, NW of cape, NT, 12°10.05'S, 131°13.16'E, 34 m, 9 Oct 1993. |
| G30560 | Bynoe Harbour, 2 nmls E Fish Reef, NT, 12°24.1334'S, 130°28.16'E, 17 m, 6 Oct 1993, coll. CCNT Ocean Rescue 2000 Program |
| G30561 | Shoal Bay, outer region of bay, NT, 12°6.15'S, 130°49.16'E, 18 m, 12 Oct 1993, coll. CCNT Ocean Rescue 2000 Program |
| G30595 | Vernon Is, W of Knight Reef, NT, 12°10.0334'S, 131°3.16'E, 22 m, 11 Oct 1993. |
| G30658 | Vernon Is, N marsh Shoal, NT, 12°07.0001'S, 130°56.1'E, 16 m, 11 Oct 1993, coll. CCNT stn. 138. Dredge |
| G30677 | Shoal Bay, middle of bay, NT, 12°13.0167'S, 130°56'E, 17 m, 12 Oct 1993, coll. CCNT Ocean Rescue 2000 Program |
| G310137 | Parry Shoals 35nm W Bathurst I., NT, 11°7.0321'S, 129°25.9'E, 16 m, 12 Aug 1987, coll. mussig, AM and NCI team |
| G310170 | Darwin Harbour, NT, 12°15.1834'S, 130°29.11'E, 9 m depth, 17 Aug 1987, coll. mussig, AM and NCI team |
| G31543 | N Bathurst I., Timor Sea, NT, 11°13.98'S, 130°34.21'E, 41.2 m, 5 Oct 1997, coll. Cook, SD. on RV Southern Surveyor |
| G31572 | SW Groote Eylandt, NT, 14°25.0801'S, 135°58.51'E, 20.3 m, 13 Oct 1997, coll. Cook, SD. on RV Southern Surveyor |
| G31577 | SW Groote Eylandt, NT, 14°20.22'S, 136°34.98'E, 19.6 m, 14 Oct 1997, coll. Cook, SD. on RV Southern Surveyor |
| G314246 | N Groote Eylandt, Gulf of Carpentaria, NT, 13°32.2801'S, 136°18.13'E, 20 m, 27 Sep 1998, coll. Leys, SP. on RV Southern Surveyor |
| G314247 | N Groote Eylandt, Gulf of Carpentaria, NT, 13°32.2801'S, 136°18.13'E, 21.7 m, 27 Sep 1998, coll. Leys, SP. on RV Southern Surveyor |
| G314255 | W of Groote Eylandt, Gulf of Carpentaria, NT, 14°8.8'S, 136°8'E, 13 m, 6 Oct 1998, coll. Leys, SP. on RV Southern Surveyor |
| G314267 | SW of Groote Eylandt, Gulf of Carpentaria, QLD, 14°20.8'S, 136°2.2'E, 22.1 m, 6 Oct 1998, coll. Leys, SP. on RV Southern Surveyor |
| G315207 | SW of Groote Eylandt, Gulf of Carpentaria, NT, 14°22.5'S, 136°9.12'E, 22.2 m, 13 Oct 1998, coll. Wassenberg T |
| G320819 | Gulf of Carpentaria, QLD, 15°20.037'S, 140°19.84'E, 28 m, 24 may 2003, coll. Bartlett C, Cook S on RV Southern Surveyor 2380403 CSIRO "Effects of Trawling" |
| G320904 | Gulf of Carpentaria, QLD, 15°20.037'S, 140°19.84'E, 28 m, 11 mar 2003, coll. Bartlett C, Cook S on RV Southern Surveyor 2380403 CSIRO "Effects of Trawling" |
### Collection and locality data of material examined in the collections of QM and NTM

| Z.194 | 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.241 | Indian Is, Bynoe Harbour, NT, 12°35.5'S, 130°33.01'E, 3 m, 18 Nov 1981, coll. Byers, P. F. V. Skeleton |
| Z.592 | Table Head, Port Essington, Cobourg Peninsula, NT, 11°13.5'S., 132°10.51'E., 3 m depth, 4 May 1982, coll. Hooper, JNA |
| Z.919 | Dudley Point Reef, East Point, Darwin, NT, 12°25.0001'S, 130°48.01'E, 10 m, 31 Aug 1982, coll. Hooper, JNA |
| Z.934 | East Point Reef, East Point, Darwin, NT, 12°24.05'S, 130°48.01'E, 12 m, 13 Sep 1982, coll. Hooper, JNA |
| Z.941 | East Point Reef, East Point, Darwin, NT, 12°24.05'S, 130°48.01'E, 12 m, 13 Sep 1982, coll. Hooper, JNA and party |
| Z.945 | East Point Reef, East Point, Darwin, NT, 12°24.05'S, 130°48.01'E, 12 m, 13 Sep 1982, coll. Hooper, JNA and party |
| Z.986 | Dudley Point Reef, East Point, Darwin, NT, 12°24.5'S, 130°48.01'E, m, 26 Oct 1982, coll. Hooper, JNA |
| Z.987 | Dudley Point Reef, East Point, Darwin, NT, 12°24.5'S, 130°48.01'E, m, 26 Oct 1982, coll. Hooper, JNA and party |
| Z.997 | Dudley Point Reef, East Point, Darwin, NT, 12°25.0001'S, 130°48.01'E., m, 22 Dec 1982, coll. Hooper, JNA |
| Z.1358 | Coral Bay, Port Essington, Cobourg Peninsula, NT, 11°11.3'S., 132°23.71'E., 5-6 m, 16 May 1983, coll. Hooper, JNA and party |
| Z.1391 | Coral Bay, Port Essington, Cobourg Peninsula, NT, 11°11.3'S., 132°23.71'E., 6 m, 17 May 1983, coll. Hooper, JNA |
| Z.1395 | Coral Bay, Port Essington, Cobourg Peninsula, NT, 11°10.4'S, 132°28.8'E, 2 m, 19 May 1983, coll. Hooper, JNA |
| Z.1442 | Blue Hole, Gunn Point, NT, 12°9.0001'S, 131°0'E, 25 m, 19 Aug 1983, coll. Alderslade, PN |
| Z.1979 | West side of Weed Reef, Darwin, NT, 12°29.0001'S, 130°47.17'E, m, 11 May 1984, coll. Hooper, JNA and party |
| Z.1991 | West side of Weed Reef, Darwin, NT, 12°29.0001'S, 130°47.17'E, m, 11 May 1984, coll. Hooper, JNA and party |
| Z.2018 | West side of Weed Reef, Darwin, NT, 12°29.0001'S, 130°47.17'E, m, 11 May 1984, coll. Hooper, JNA and party |
| Z.2026 | West side of Weed Reef, Darwin, NT, 12°29.0001'S, 130°47.17'E, 11 May 1984, coll. Hooper, JNA and party |
| Z.2086 | Dudley Point Reef, East Point, Darwin, NT, 12°24.5'S, 130°48.01'E, m, 20 Jul 1984, coll. Hooper, JNA |
| Z.2215 | Vestey's Beach, Bullocky Point, Darwin, NT, 12°26.2'S, 130°49.89'E, 21 Jan 1985, coll. Hooper, JNA |
| Z.2245 | Dudley Point Reef, East Point, Darwin, NT, 12°24.5'S, 130°48.01'E, 10 m, 12 Apr 1985, coll. Hood, C and party |
| Z.2648 | Dudley Point Reef, East Point, Darwin, NT, 12°24.5'S, 130°48.01'E, m, 3 Apr 1986, coll. Hooper, JNA and party |
| Z.2651 | Dudley Point Reef, East Point, Darwin, NT, 12°24.5'S, 130°48.01'E, 3 Apr 1986, coll. Hooper, JNA and party |
| Z.2697 | Dudley Point Reef, East Point, Darwin, NT, 12°24.5'S, 130°48.01'E, 3 Apr 1986, coll. Hooper, JNA and party |
| Z.3106 | Parry Shoals, Arafura Sea, NT, 11°12.5167'S, 129°42.07'E, 20 m, 15 Aug 1987, coll. Mussig, AM and NCI team |
| Z.3133 | Parry Shoals, Arafura Sea, NT, 11°11.4'S., 129°43.01'E., 18 m depth, 13 Aug 1987, coll. Mussig, AM and NCI team |
| Z.3147 | Parry Shoals, Arafura Sea, NT, 11°12.5167'S, 129°42.07'E, 16 m, 15 Aug 1987, coll. Mussig, AM and NCI team |
| Z.3178 | East Point Reef, East Point, Darwin, NT, 12°29.5'S, 130°48.01'E, 0.5 m, 10 Sep 1987, coll. Smith, N |
| Z.3195 | Dudley Point Reef, East Point, Darwin, NT, 12°24.5'S, 130°48.01'E, 9 m, 16 Sep 1987, coll. Smith, N |
| Z.3205 | Dudley Point Reef, East Point, Darwin, NT, 12°24.5'S, 130°48.01'E, 25 Sep 1987, coll. Smith, N |
| Z.3262 | Table Head, Port Essington, Cobourg Peninsula, NT, 11°13.5'S., 132°10.51'E., 11 Sep 1986, coll. Hooper, JNA & Johnson, C |
| Z.3920 | Cumberland Strait, NE bay, Wessel Is, Gove Peninsula, NT, 11°26.8'S, 136°30.2'E, 13 m, 14 Nov 1990, coll. Hooper, JNA |
| Z.4085 | Near Boat Ramp, East Arm Port, Darwin, NT, Australia, 12°29.8'S, 130°53.5'E, intertidal, 20 September 2001, coll. B. Glasby & party, by hand |
| Z.4093 | Near Boat Ramp, East Arm Port, Darwin, NT, 12°29.8'S, 130°53.5'E, intertidal, 20 September 2001, coll. B. Glasby & party, by hand |
| Z.4100 | Near Boat Ramp, East Arm Port, Darwin, NT, 12°29.8'S, 130°53.5'E, intertidal, 18 October 2001, coll. B. Glasby & party, by hand |
| Z.4122 | Near Boat Ramp, East Arm Port, Darwin, NT, 12°29.8'S, 130°53.5'E, intertidal, 18 October 2001, coll. B. Glasby & party, by hand |
| Z.4123 | Near Boat Ramp, East Arm Port, Darwin, NT, 12°29.8'S, 130°53.5'E, intertidal, 19 October 2001, coll. B. Glasby & party, by hand |
| Z.4125 | Near Boat Ramp, East Arm Port, Darwin, NT, 12°29.8'S, 130°53.5'E, intertidal, 19 October 2001, coll. B. Glasby & party, by hand |
| Z.4451 | Stevens Rock, 1.25 km SE Tale Head, off Cox Peninsula, Darwin Harbour, NT, 12°29.103'S, 130°47.111'E, 8-14 m, 7 May 2002, coll. Alvarez, B and party |
Halichondriidae from northern Australia

Z.5206 South Shell I., East Arm, Darwin Harbour, NT, 12°29.869'S, 130°53.141'E, 10–12 m, 21 Aug 2002, coll. Alvarez, B and party

Z.5207 Dawson Rock, 3 km SSE Rankin Point, Bynoe Harbour, NT, 12°42.238'S, 130°35.557'E, 5–10 m, 23 May 2003, coll. Alvarez, B and party

Z.5208 Dawson Rock, 3 km SSE Rankin Point, Bynoe Harbour, NT, 12°42.207'S, 130°35.459'E, 7–12 m, 24 Jul 2003, coll. Alvarez, B and party

Z.5209 Nightcliff bommies, off Nightcliff Jetty, Darwin Harbour, NT, 12°22.751'S, 130°50.116'E, 5–8 m, 8 Aug 2003, coll. Alvarez, B and party

Z.5210 Stevens Rock, 1.25 km SE Tale Head, off Cox Peninsula, Darwin Harbour, NT, 12°29.188'S, 130°47.110'E, 12–14 m, 22 Aug 2003, coll. Alvarez, B

Z.5211 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.5212 Raragala E, 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.5213 South Shell I., East Arm, Darwin Harbour, NT, 12°29.869'S, 130°53.141'E, 7–11 m, 19 Aug 2002, coll. Alvarez, B and party

Z.5214 West Arm, 2.5 km N of Stokes Point, Darwin Harbour, NT, 12°31.300'S, 130°48.500'E, 4–5 m, 3 Aug 2002, coll. Alvarez, B and party

Z.5215 Wickham Point, 2.5 km SW of East Arm Wharf, East Arm, Darwin Harbour, NT, 12°30.12'S, 130°53.229'E, 4–7 m, 15 Sep 2002, coll. Alvarez, B and party

Z.5216 Stevens Rock, 1.25 km SE Tale Head, off Cox Peninsula, Darwin Harbour, NT, 12°29.188'S, 130°47.110'E, 8–14 m, 22 Aug 2003, coll. Alvarez, B


Z.5218 Channel Rock, 4 km NE West Pt on Cox Peninsula, Darwin Harbour, NT, 12°24.94'S, 130°47.04'E, 12–18 m, 16 Sep 2002, coll. Alvarez, B and party

Z.5219 Approx. 3 km NE Charles Point, Cox Peninsula, NT, 12°22.782'S, 130°38.371'E, 9–12 m, 23 Aug 2003, coll. Browne, M

Z.5220 Channel Island, 100–400 m N of bridge, Middle Arm, Darwin Harbour, NT, 12°26.555'S, 130°46.055'E, 9–12 m, 5 Sep 2003, coll. Alvarez, B and party

Z.5221 South Shell I., East Arm, Darwin Harbour, NT, 12°29.869'S, 130°53.141'E, 7–14 m, 20 Aug 2002, coll. Alvarez, B and party

Z.5222 East Arm Wharf, East Arm, Darwin Harbour, NT, 12°29.19'S, 130°53.35'E, 0.6 m, 1 Mar 2002, coll. Alvarez, B and party

Z.5223 Dawson Rock, 3 km SSE Rankin Point, Bynoe Harbour, NT, 12°42.238'S, 130°35.557'E, 5–10 m, 23 May 2003, coll. Alvarez, B and party

Z.5224 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.5225 Spencer Point, Indian l., Bynoe Harbour, NT, 12°35.351'S, 130°31.454'E, 6–8 m, 11 Jun 2003, coll. Alvarez, B and party

Z.5226 Moira Reef, Bynoe Harbour, NT, 12°30.799'S, 130°30.527'E, 8–9 m, 25 Jun 2003, coll. Browne, M

Z.5227 Wickham Point, 2.5 km SW of East Arm Wharf, East Arm, Darwin Harbour, NT, 12°30.12'S, 130°53.229'E, 4–7 m, 15 Sep 2002, coll. Alvarez, B and party

Z.5228 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 and party

Z.5229 Channel Rock, 4 km NE West Pt on Cox Peninsula, Darwin Harbour, NT, 12°24.94'S, 130°47.04'E, 12–18 m, 16 Sep 2002, coll. Alvarez, B and party

Z.5230 Approx. 3 km NE Charles Point, Cox Peninsula, NT, 12°22.782'S, 130°38.371'E, 9–12 m, 23 Aug 2003, coll. Browne, M

Z.5231 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.5232 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 and party

Z.5233 Lee Point, Darwin, NT, 12°20.538'S, 130°52.184'E, 9–12 m, 7 Aug 2003, coll. Nguyen, H


Z.5237 Channel Rock, 4 km NE West Pt on Cox Peninsula, Darwin Harbour, NT, 12°24.94'S, 130°47.04'E, 12–14 m, 3 Sep 2002, coll. Alvarez, B and party

Z.5238 Channel Island, 100–400 m N of bridge, Middle Arm, Darwin Harbour, NT, 12°33.099'S, 130°52.433'E, intertidal 0.02 m, 7 Nov 2006, coll. Alvarez, B

Z.5239 Channel Island, 100–400 m N of bridge, Middle Arm, Darwin Harbour, NT, 12°33.099'S, 130°52.433'E, intertidal 0.02 m, 7 Nov 2006, coll. Alvarez, B

Z.5240 Lee Point, Darwin, NT, 12°20.538'S, 130°52.184'E, 9–12 m, 7 Aug 2003, coll. Nguyen, H

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<th>Date</th>
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<td>20 m</td>
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<td>Larrakeyah sewerage outfall, Darwin Harbour, NT, Australia, 12°28.04'S, 130°49.77'E, 19.5 m depth, 22 April 2009</td>
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<td>10–16 m</td>
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<td>12°25.01'S, 130°48.88'E</td>
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<td>Channel Rock, 4 km NE West Pt on Cox Peninsula, Darwin Harbour, NT, 12°24.94'S, 130°47.04'E, 13–16 m, 5 Sep 2003</td>
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New larval food plant associations for some butterflies and diurnal moths (Lepidoptera) from the Northern Territory and eastern Kimberley, Australia

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ABSTRACT
This paper documents 122 insect-plant associations for 10 families of butterflies/diurnal moths (Castniidae, Sessidae, Immidae, Geometridae, Hesperiidae, Papilionidae, Pieridae, Nymphalidae, Lycaenidae and Noctuidae (Agaristinae)) from the Northern Territory and eastern Kimberley, of which 76 associations are newly recorded for Australia and 46 are newly recorded for the Northern Territory and/or Western Australia. Of particular note are the first recordings of the families Lecythidaceae for Antltene (Lycaenidae), Santalaceae for Theclinesthes (Lycaenidae), Vitaceae and Rubiaceae for Periopta (Agaristinae), and Vitaceae for Radinocera (Agaristinae). For Cephrenes augiades and Borbo impar (Hesperiidae), the native larval food plants and natural breeding habitats in the Northern Territory are documented for the first time. For Candalides delospila, C. erinus and C. geminus (Lycaenidae), errors in previously reported larval food plants are corrected, and for two of these species (C. delospila, C. erinus) facultative ant associations are recorded for larvae for the first time. New attendant ant associations are also recorded for several lycaenids, notably Ogyris zosine and Theclinesthes miskini, in which the larvae have obligate relationships with ants.

KEYWORDS: butterfly, day-flying moth, insect-plant associations, larval food plant, Lepidoptera.

INTRODUCTION
The following catalogue of larval food plants for butterflies and day-flying moths is based on field observations and rearing of the early stages from the central arid zone and the ‘Top End’ of the Northern Territory (NT) and the eastern Kimberley of Western Australia (WA) by the author during the five year period, October 2005 to December 2010. The eastern Kimberley region extends from Pinkerton Range-Spirit Hills, NT, to north-western WA. The Lepidoptera covered here include the Castniidae, Sessidae, Immidae, Geometridae, Hesperiidae, Papilionidae, Pieridae, Nymphalidae, Lycaenidae and Noctuidae (Agaristinae). The new records are in addition to those reported in the review by Meyer (1996) for part of the region, and contribute to the growing body of knowledge of insect-plant associations for the Australian Lepidoptera as a whole (see Common 1990; Braby 2000 for review).

The catalogue is presented in annotated form for each association: the (scientific and common) name of the lepidopteran appears first as a subheading in bold, followed by the larval food plant and voucher number, and then the relevant field observations. The field observations summarise details of locality, date, early stages and, in some cases, rearing data and other biological notes (e.g. attendant ants for Lycaenidae) where these are poorly documented. The new Lepidoptera-larval food plant associations are arranged into two groups; firstly, those that comprise new records for Australia as a whole, and secondly, those that are new for the NT and/or WA. In many cases, samples of the early stages of Lepidoptera were preserved, photographed and/or reared to adulthood in captivity to confirm species level identification, and vouchers of these specimens are lodged in the Museum and Art Gallery of the Northern Territory, Darwin (NTM) or the Australian National Insect Collection, Canberra (ANIC). In some cases, however, the early stages were not reared, and identifications of eggs, larvae or pupae were determined on the author’s field experience and knowledge of the relevant species.

Nomenclature for butterflies follows Braby (2010), while that for moths follows Nielsen et al. (1996). The ants were identified by Alan Anderson. Voucher specimens of the ants have been lodged in the CSIRO Tropical Ecosystem Research Collection, Darwin. Botanical nomenclature follows a recent updated checklist of vascular plants published by the Northern Territory Herbarium (Short et al. 2011). Voucher numbers refer to plant specimens lodged in the Northern Territory Herbarium, Palmerston (DNA). Introduced, naturalised and ornamental plants are designated by an asterisk (*). For consistency, geocoordinates are given.
in, or have been converted to, decimal degrees, followed by datum (e.g. AGD66, WGS84 or GDA94). The level of precision of coordinates is not given, though in general the spatial area of sites sampled varied from 10–500 m radius, though was usually about 50–100 m.

NEW LEPIDOPTERA LARVAL FOOD PLANT ASSOCIATIONS FOR AUSTRALIA

The following catalogue of species comprises plants that, to the author’s knowledge, have not previously been documented as larval food plants for Australian Lepidoptera.

CASTNIIDAE


Caiman Creek, Cobourg Peninsula, NT (11.22504°S, 132.2036°E; WGS84), 4 February 2007, M.F. Braby & V. Kessner. Several females were observed at 1215–1245 hr ovipositing on _Chrysopogon latifolius_ growing in savannah woodland that was regenerating after fire; numerous eggs were laid in soil at the base of thick stems/rhizomes of _C. latifolius_.

Victoria Hwy, Pinkerton Range, NT (15.98698°S, 129.51213°E; WGS84), 1 February 2008, M.F. Braby & V. Kessner. Two empty pupal exuviae were collected protruding from soil at the base of separate tussocks of _C. latifolius_ growing in savannah woodland on flat low-lying terrain adjacent to a sandstone outcrop; four pairs of adults were also collected mating around midday as they sat in copula on these and other nearby tussocks of _C. latifolius_. Two of the females had almost certainly emerged from the pupal exuviae.

_Synemon_ sp. ‘Roper River’. No common name. _Chrysopogon fallax_ S.T.Blake (Poaceae). (voucher M.F. Braby 51, DNA).

Nathan River Ranger Station, Limmen National Park, NT (15.57681°S, 130.82500°E; WGS84), 14 May 2009, M.F. Braby & N. Collier. Four pupal exuviae were collected protruding from soil close to clumps of _Chrysopogon fallax_ growing in grassy open woodland on flat terrain in a valley between sandstone ridges/outcrops; one freshly emerged female was also collected at rest drying its wings within a clump of _C. fallax_. The habitat had been extensively burnt three days earlier.

SESIIDAE


Lee Point, Casuarina Coastal Reserve, NT (12.33166°S, 130.89444°E; WGS84), 28 March 2009, M.F. Braby & A. Kallies. Numerous larvac and pupae were collected from within the main stem of several vines of _Anmpelocissus acetosa_, which grew in eucalypt open forest, and reared to adult in captivity.

East Point, Darwin, NT (12.41140°S, 130.82500°E; WGS84), 31 January 2010, M.F. Braby. One pupal exuvia was collected protruding from the stem of _A. acetosa_ growing about 1.5 m distant from where a freshly emerged male was perched, at 1055 hr, on a large leaf of a vine growing along the edge of coastal semi-deciduous monsoon vine-thicket.

_Anmpelocissus frutescens_ Jackes. (Vitaceae). (not vouchered).

Mt Burrell, Tipperary Station, Daly River district, NT (13.49623°S, 131.03572°E; WGS84), 4 February 2007, M.F. Braby & L.J. Aitchison. Numerous larvae were collected from within the stem of a single shrub of _Anmpelocissus frutescens_ which had not yet shed its leaves and which was growing at the base of a hill; several larvae were reared to adult in captivity. Most of the other short-lived aerial stems of this perennial vine were already senescent following onset of the dry season, suggesting that _A. frutescens_ may not be a widely used food plant.

IMIIDAE

_Birthana cleis_ (R. Felder & Rogenhofer, 1875). No common name.

_Dendrophthoe odontocalyx_ (F.Muell. ex Benth.) Tiegh. (Loranthaceae). (voucher M.F. Braby 29, DNA).

Gurrumuru outstation, Gove Peninsula, NT (12.59302°S, 136.23194°E; WGS84), 21 June 2007, M.F. Braby. A cohort of 15 early instar larvae was recorded on a leaf of _Dendrophthoe odontocalyx_, a mistletoe parasitising the host tree _Grevillea pteridifolia_ growing in savannah woodland; three larvae were reared to adult in captivity. The remains of an old cohort of _Deltas argenthona_ were evident on the same mistletoe clump (see below).

HESPERIIDAE


Yellow Water, Jim Jim Creek, Kakadu National Park, NT (12.89689°S, 132.51749°E; WGS84), 20 April 2008, M.F. Braby, K. Nishida & L.J. Aitchison. Numerous larval shelters and adults were recorded on _Hymenachne acutignuma_ growing in standing water of floodplain wetland. The site was revisited on 8 June 2008 and one mid-instar larva was collected from _H. acutignuma_.

_Taractrocera ina_ Waterhouse, 1932. No-brand Grass-dart.


Mt Burrell, Tipperary Station, Daly River district, NT (13.49623°S, 131.03572°E; WGS84), 6 May 2006, M.F. Braby & D.A. Young. One late instar larva was collected
from within its shelter on Cymbopogon procerus growing in low woodland at the summit of a rocky hill; the larva was subsequently reared to adult in captivity. The site was revisited on 6 March 2010 and two larvae were collected from C. procerus; one developed directly and was reared to adult in captivity within a few weeks, the other remained dormant as a final instar and did not feed for six months until it was removed by hand from its shelter.

Sorghum sp. (Poaceae). (not vouchered).

Mt Burrell, Tipperary Station, Daly River district, NT (13.49623°S, 131.03572°E; WGS84), 6 March 2010, M.F. Braby & S. Keates. Two larvae were collected from within their shelters on Sorghum sp., an annual grass growing in savannah woodland on the lower slope; one larva developed directly and was reared to adult in captivity within a few weeks, the other remained dormant as a final instar and did not feed for many months.


Stuart Hwy, 10 km NW of Katherine, NT (14.40684°S, 132.19710°E; WGS84), 26 January 2009, M.F. Braby & V. Kessner. Six larvae were collected from within loose shelters on new growth of Sorghum macrosporum growing in degraded mixed vine-thicket-woodland on limestone; four larvae were reared to adult in captivity. Sorghum macrosporum is a localised annual grass endemic to the Katherine district (Lazarides et al. 1991).


Ischaemum australis R.Br. (Poaceae). (voucher M.F. Braby 60, DNA).

El Questro Gorge, El Questro Wilderness Park, WA (16.02135°S, 128.02356°E; WGS84), 14 July 2009, M.F. Braby. A female was observed at 1050 hr depositing a single egg on a broad fresh blade of Ischaemum australis, which grew as a dense understory grass along the edge of a creek. Adults were locally common at the site where I. australis grew in sunlit areas.

Telicota colou argea (Plötz, 1883). Pale-orange Darter.

*Paspalum scrobiculatum* L. (Poaceae). (voucher M.F. Braby 77, DNA).

Fogg Dam Conservation Reserve, NT (12.55769°S, 131.29701°E; WGS84), 29 May 2010, M.F. Braby, S. Keates & D. Bisa. One mid-instar larva was collected from within its shelter on Paspalum scrobiculatum growing in paperbark swampland and reared to the pupal stage.


Carpentaria acuminata (H.Wendl. & Drude) S.T.Blake (Areaceae). (not vouchered).

Greenant Creek, Litchfield National Park, NT (13.20015°S, 130.69971°E; WGS84), 6 November 2010, M.F. Braby. A pupa was collected from within its shelter on Carpentaria acuminata growing in riparian wet monsoon forest, and a male emerged the following morning; males were commonly recorded between 1500 hr and 1600 hr as they perched on foliage of understory trees 7–8 m above the ground in sunlit patches along the edge of the habitat where they appeared to establish mating territories.

Wangi Falls, Litchfield National Park, NT (13.16305°S, 130.68166°E; WGS84), 7 November 2010, M.F. Braby & L.J. Aitchison. One late instar larva was collected from within its shelter on C. acuminata growing abundantly in wet monsoon forest; the larva was reared to adult in captivity. A female of this hesperiid was previously recorded at this location on 17 April 2006, but the larval food plant was not determined.

Robin Falls, creek upstream of falls, NT (13.34877°S, 131.12622°E; WGS84), 29–30 April 2011, M.F. Braby & J.J. Armstrong. Three larvae were collected from within shelters on C. acuminata growing in riparian evergreen monsoon forest below a sandstone escarpment, one of which was reared to adult in captivity. Males were commonly recorded during mid-afternoon (1530–1600 hr) establishing territories in the mid-canopy along the western edge of the breeding habitat that received direct sunlight.

Cepheorus trichopepla (Lower, 1908). Yellow Palm-dart.

Livistona humilis R.Br. (Areaceae). (not vouchered).

Mt Burrell, Tipperary Station, Daly River district, NT (13.49623°S, 131.03572°E; WGS84), 21 February 2009, M.F. Braby & D.A. Young. A female was observed ovipositing on Livistona humilis growing in low woodland at the summit of a rocky hill. The site was revisited on 21 November 2009 and a late instar larva close to the prepupal stage was recorded within its shelter on L. humilis growing on the slope of a hill. On 6 March 2010 another larva in early instar was recorded on L. humilis growing at the summit of the hill.

Livistona mariae F.Muell. (Areaceae). (not vouchered).

Palm Valley, Finke Gorge National Park, NT (24.03333°S, 132.69528°E; WGS84), 13 October 2005, M.F. Braby & L.J. Aitchison. Several early instar larvae were recorded from within their shelters on small individuals of Livistona mariae growing along Palm Creek; one female was reared to adult in captivity.


El Questro Gorge, El Questro Wilderness Park, WA (16.02135°S, 128.02356°E; WGS84), 14 July 2009, M.F. Braby & L.J. Aitchison. Several larvae were collected from within their shelters on Livistona nasnophila growing in riparian monsoon forest and reared to adult in captivity.

Pentecost River, 4 km NW of El Questro Wilderness Park, WA (15.97504°S, 127.94561°E; WGS84), 2 April 2010, M.F. Braby & L.J. Aitchison. One final instar larva was recorded within its shelter on L. nasnophila growing in riparian woodland.

Livistona victoriae Rodd. (Areaceae). (not vouchered).
Echidna Chasm, Purnululu National Park, WA (17.32272°S, 128.41183°E; WGS84), 2 July 2009, M.F. Braby & L.J. Aitchison. One empty egg shell, two larvae and numerous empty shelters were recorded on *Livistona victoriae* growing in depauperate monsoon forest along a gorge.

Mini Palm Gorge, Purnululu National Park, WA (17.33083°S, 128.40916°E; WGS84), 2 July 2009, M.F. Braby & L.J. Aitchison. Two early instar larvae and one empty pupal shell were collected from within their shelters on *L. victoriae* growing in mixed monsoon forest-riparian woodland; one larva was reared to adult in captivity.

**PAPILIONIDAE**


*Polyalthia longifolia* (Sonn.) Thwaites. (Annonaceae). (not vouchered).

Casuarina, Darwin, NT (12.366°S, 130.867°E; AGD66), 29 September 2010, M.F. Braby. Four larvae comprising one early instar and three late instars were recorded on new leaf growth of young ornamental trees of *Polyalthia longifolia*, which grew adjacent to Casuarina Shopping Centre. The site was revisited on 3 October 2010 and a further three mid-instar larvae were collected and reared to adult in captivity.

**PIERIDAE**

*Encrea hecabe* (Linnaeus, 1758). Large Grass-Yellow.

*Senna alata* (L.) Roxb. (Fabaceae). (not vouchered).

Dhamiyaka outstation, 17.5 km SSE of Gapuwiyak, Gove Peninsula, NT (12.65666°S, 130.85833°E; WGS84), 16 June 2006, M.F. Braby & I. Morris. A female was observed ovipositing on *S. alata* growing near the edge of monsoon vine-forest; eggs were laid singly on the upperside of the leaves.

*Senna obtusifolia* (L.) H.S.Irwin & Barneby. (Fabaceae). (voucher M.F. Braby 35, DNA).

Berrimah (CSIRO complex), Darwin, NT (12.41333°S, 130.92194°E; WGS84), 2 April 2008, M.F. Braby. Two females were observed at 1215 hr ovipositing on a low shrub (< 1 m high) of *S. obtusifolia* growing on sandy-loam at the base of an escarpment. The larvae were feeding together with those of *Belenois java* (see below). The site was revisited on 24 January 2010 and one final instar larva was recorded on *C. umbonata*.

**NYMPHALIDAE**


*Dendrophthoe odontocalyx* (F.Muell. ex Benth.) Tiegh. (Loranthaceae). (voucher M.F. Braby 29, DNA).

Gurrumuru outstation, Gove Peninsula, NT (12.59302°S, 136.23194°E; WGS84), 21 June 2007, M.F. Braby. One remnant pupal exuvia was found attached to a leaf of *D. odontocalyx*, a mistletoe parasitising the host tree *Grevillea pteridifolia*, growing in savannah woodland; several east larval skins and larval damage to leaves were also evident. No other mistletoe species grew on the host tree or on adjacent eucalypt trees. A cohort of *Bithurana cleis* was also present on the same mistletoe clump (see above).

*Danais petilia* (Stoll, 1790). Lesser Wanderer.

*Cynarchum pedunculatum* R.Br. (Apocynaceae). (voucher M.F. Braby 84, DNA).

Nanguluwur Art site, Nourlangie Rock, Kakadu National Park, NT (12.8425°S, 132.8156°E; WGS84), 13 November 2010, M.F. Braby & J. Westaway. A female was observed at 1008 hr for several minutes searching and inspecting a vine of *Cynarchum pedunculatum*, which grew of *Elophina* that occurs in the NT, was not recorded at this site on either occasions, and its geographic range may not extend this far south in the Top End.

*Appias panini ega* (Boisduval, 1836). Yellow Albatross.

*Capparis sepiaria* L. (Capparaceae). (voucher M.F. Braby 15, DNA).

Black Point, Cobourg Peninsula, NT (11.15515°S, 132.14391°E; WGS84), 3 February 2007, M.F. Braby. A female was observed ovipositing on *Capparis sepiaria* growing in coastal monsoon vine-thicket; several eggs were laid singly on new shoots.

*Cepora perimale* (Donovan, 1805). Caper Gull.

*Capparis umbonata* Lindl. (Capparaceae). (vouchers M.F. Braby 4, 64, DNA).

Education campground, Litchfield National Park, NT (13.11361°S, 130.79805°E; WGS84), 17 April 2006, M.F. Braby & L.J. Aitchison. A female was observed ovipositing on *C. umbonata* growing in savannah woodland on a gentle rocky slope; five mid-instar larvae were also recorded on the larval food plant.

1 km ENE of Nanguluwur, Nourlangie Rock, Kakadu National Park, NT (12.84375°S, 132.8558°E; WGS84), 20 December 2009, M.F. Braby. Four late instar larvae were recorded feeding on an almost leafless, spiny shrub of *C. umbonata*, which grew on sandy-loam at the base of an escarpment. The larval feeding together with those of *Belenois java* (see below). The site was revisited on 24 January 2010 and one final instar larva was recorded on *C. umbonata*. 

**Brevioptera**

*Yellow Grass-Yellow*...
amongst footslope sandstone boulders; a single egg was eventually laid on the underside of a leaf of the food plant. 

Euploea sylvester pelor Doubleday, 1847. Two-brand Crow.

Parsonsia alboflavescens (Dennst.) Mabb. (Apocynaceae). (not vouchered).

Rocky Bay, 5 km SSE of Yirrkala, Gove Peninsula, NT (12.29583°S, 136.90305°E; WGS84), 3 July 2006, M.F. Braby. A female was observed at 1215 hr depositing a single egg on a vine of Parsonsia alboflavescens growing in mixed tall paperbark swampland with rainforest elements in the understory; the larva was reared to mid-instar.


5.5 km NE of Adelaide River, NT (13.21222°S, 131.14750°E; AGD66), 4 June 2006, M.F. Braby & V. Kessner. A female was observed depositing a single egg on a vine of Marsdenia geminata growing in regenerating riparian forest along the bank of the Adelaide River.

Parsonsia alboflavescens (Dennst.) Mabb. (Apocynaceae). (not vouchered).

Rocky Bay, 5 km SSE of Yirrkala, Gove Peninsula, NT (12.29583°S, 136.90305°E; WGS84), 30 August 2007, M.F. Braby, P. Wise & B. Marika. Five eggs and two early instar larvae were collected from Parsonsia alboflavescens growing in mixed tall paperbark swampland with rainforest elements in the understory; the early stages were reared to the pupal or adult stage in captivity.

Melanitis leda bankia (Fabricius, 1775). Evening Brown.

*Cynodon dactyliflorus* Roth ex Roem. & Schult. (Poaceae). (voucher M.F. Braby 49, DNA).

Nathan River Ranger Station, Limmen National Park, NT (15.57681°S, 135.42783°E; WGS84), 11 July 2009, M.F. Braby & L.J. Aitchison. One late instar larva was recorded feeding on a blade of Ischaemum australis growing in a dry seasonal gully.

*Hypochrysops apelles* (Fabricius, 1775). Copper Jewel.


Buffalo Creek, Leanyer swamp, NT (12.35353°S, 130.90407°E; WGS84), 27 April 2008, M.F. Braby. Four larvae were collected from foliage of Ceriops australis growing in mangroves some distance from the landward edge and reared to adult in captivity; larvae were attended by black ants, Crematogaster sp. (species group C).


Gardenia megasperma F.Muell. (Rubiaceae). (not vouchered).

Litchfield National Park, NT (13.12555°S, 130.80305°E; WGS84), 15 April 2006, M.F. Braby & L.J. Aitchison. Two larvae were collected feeding on large, broad leaves of shrubs of Gardenia megasperma growing on a rocky sandstone plateau; the larvae were attended by numerous coconut ants, Pappius sp. (*nudus* species group), and were reared to adult in captivity.


Gunlom, Kakadu National Park, NT (13.43555°S, 132.41565°E; WGS84), 28 August 2008, M.F. Braby & L.J. Aitchison. Two recent empty pupal exuviae and one parasitised pupa were recorded within curled leaves of a sapling (approx. 1.5 m high) of Corymbia bella growing in open flood plain of South Alligator River; a pair of freshly emerged adults was also observed at 1700 hr mating on the same plant; nests of the attendant green-tree ant, Oecophylla smaragdina, were present. Adults of Arhopala micale were not detected on C. bella, or elsewhere at the site.

Terminalia ferdinandiana Excell. (Combretaceae). (not vouchered).

Nanguluwur Art site, Nourlangie Rock, Kakadu National Park, NT (12.84262°S, 132.81895°E; WGS84), 7 December 2009, M.F. Braby & J.J. Armstrong. Several larvae were recorded on a shrub (1.5 m high) of Terminalia ferdinandiana growing in savannah woodland; larvae were attended by green-tree ants, Oecophylla smaragdina, and were noticed to have caused considerable damage to the foliage; adults alighted frequently on the foliage of T. ferdinandiana.

Arhopala micale Blanchard, [1848]. Shining Oak-blue.

Brachychiton diversifolius R.Br. (Malvaceae). (not vouchered).

Berrimah (CSIRO complex), Darwin, NT (12.41333°S, 130.92194°E; WGS84), 10 January 2007, M.F. Braby. Three eggs were collected from mature leaves of Brachychiton diversifolius growing in savannah woodland; one egg hatched and was reared to final instar on new fresh foliage of B. diversifolius.

Sterculia quadrifida R.Br. (Malvaceae). (voucher M.F. Braby 90, DNA).

Bullocky Point, Darwin, NT (12.43777°S, 130.83377°E; WGS84), 18 December 2010, M.F. Braby & J. Westaway. Five late instar larvae were recorded feeding on soft new leaf growth of medium sized trees of Sterculia quadrifida, which grew in monsoon vine-thicket on a low lateritic cliff above the beach; larvae were attended by Oecophylla smaragdina ants. The site was revisited on 20 December 2010 and four additional larvae, one pupa and a freshly emerged adult were recorded on S. quadrifida; the pupa was located inside a silken shelter comprising a rolled mature leaf and attended by numerous ants.


Diplotia grandibractea (F.Muell. & Tate) Tiegh. (Loranthaceae). (voucher M.F. Braby 78, DNA).

Near Lake Mary Ann, 5 km NNW of Tennent Creek, NT (19.60678°S, 131.25052°E; WGS84), 12 April 2009, M.F. Braby et al. Two hatched eggs were recorded on new leaves of Diplotia grandibractea; feeding damage from first instar larvae was also evident, but no larvae were detected.

Hypolycaena phorbas phorbas (Fabricius, 1793). Black-spotted Flash.

Decaisnina signata (F.Muell. ex Benth.) Tiegh. (Loranthaceae). (not vouchered).

Black Point, Cobourg Peninsula, NT (14.06946°S, 131.25052°E; WGS84), 12 April 2009, M.F. Braby & L.J. Aitchison. Several females were observed at 1415–1430 hr ovipositing on flower buds of Barringtonia acutangula growing in riparian monsoon forest on a steep sandy bank; one final instar larva was also collected feeding on soft new leaves of B. acutangula and reared to adult in captivity; the pupal duration was six days.

Caudalides margarita gilberti Waterhouse, 1903. Trident Pencil-blue.

Decaisnina triflora (Span.) Tiegh. (Loranthaceae). (voucher M.F. Braby 12, DNA).

Nawurlandja (Little Nourlangie Rock), Kakadu National Park, NT (12.85701°S, 132.79053°E; WGS84), 19 April 2008, M.F. Braby & K. Nishida. Two hatched eggs were recorded on new leaves of Decaisnina triflora; feeding damage from first instar larvae was also evident, but no larvae were detected.


Cassytha filiformis L. (Laureaceae). (voucher M.F. Braby 27, 082, DNA).

Ovipositing females, eggs and larvae were frequently recorded (and subsequently reared to adult in captivity) on Cassytha filiformis growing in heathland or woodland on sandstone from many locations in western Arnhem Land, including Gubara Track, Nourlangie Rock and Gunlom of Kakadu National Park, and Katherine Gorge of Nitmiluk National Park, NT, during January, May, July, August, November and December 2007–2009.

Cassytha capillaris Meisn. (Laureaceae). (not vouchered).

Nourlangie Rock, Kakadu National Park, NT (12.85463°S, 132.81677°E; WGS84), 4 May 2008, M.F. Braby & L.J. Aitchison. Females were observed at 1410–1412 hr ovipositing on Cassytha capillaris parasitising Triodia sp. growing in heathy woodland on sandstone; eggs were laid singly on flowers or new soft tendrils; two
mid-instar larvae were also collected on *C. capillaris* and reared to adult in captivity.

*Caudalides heathi heathi* (Cox, 1873). Rayed Blue

*Prostanthera striatiflora* F.Muell. (Lamiaceae). (voucher M.F. Braby 8, DNA).

Larapinta Drive, approx. 95 km W of Hermannsburg, NT (23.88722°S, 131.90805°E; WGS84), 12 October 2005, M.F. Braby & L.J. Aitchison. Nine larvae of various instars were collected from *Prostanthera striatiflora* and reared to adult in captivity; eggs were also recorded singly on leaves, flowers and developing fruits; the pupal duration varied from six months to three years.

*Nesolycaena uranella* (Tindale, 1922). Spotted Opal

*Boronia laxa* Duretto. (Rutaceae). (vouchers M.F. Braby 25, 026, DNA).

Nourlangie Rock, Kakadu National Park, NT (12.85930°S, 132.82558°E; WGS84), 30 September 2006, M.F. Braby. Females were observed ovipositing on foliage of *Boronia laxa*, but she did not lay any eggs.

1 km ENE of Nanguluwur, Nourlangie Rock, Kakadu National Park, NT (12.84375°S, 132.82558°E; WGS84), 27 January 2007, M.F. Braby & L.J. Aitchison. A female was observed at 1140 hr ovipositing on a herb of *Boronia laxa*, which grew in heathy woodland on sandstone; eggs were laid singly on the underside of broad new leaves of separate plants; a second female was observed at 1315 hr depositing a single egg on the underside of a leaf of *B. laxa*. The site was revisited on 4 May 2008 and a female was observed at 1350 hr ovipositing on petals of *B. laxa*.

The site was revisited on 10 June 2006 and a female was observed at 1125 hr depositing a single egg on the underside of leaves of *M. nesophilus*, which grew in coastal vine-thicket; additional eggs and early instar larvae were also recorded on the underside of leaves of *M. nesophilus*

The site was revisited on 8 October 2006 and an egg and first instar larva were collected from *M. nesophilus* and reared to adult in captivity.

*Dodonaea hispidula* Endl. (Sapindaceae). (vouchers M.F. Braby 37, 054, DNA).

Mt Cahill, Kakadu National Park, NT (12.86488°S, 132.70468°E; WGS84), 3 May 2008, M.F. Braby & L.J. Aitchison. Numerous eggs were recorded on the underside of leaves of *Dodonaea hispidula* growing in eucalypt woodland with a heath understorey on a rocky quartzite-sandstone slope; a female was also observed displaying oviposition behaviour (i.e. trailing and probing her abdomen on *M. nesophilus*), but she did not lay any eggs.

Mt Burrell, Tipperary Station, Daly River district, NT (13.49623°S, 130.03570°E; WGS84), 14 March 2009, M.F. Braby. Three larvae were collected from the underside of leaves of *D. hispidula* growing in low woodland at the summit of a rocky hill; the larvae were subsequently reared to adult in captivity. The site was revisited on 17 April 2010 and a female was observed at 1125 hr depositing a single egg on the underside of a new leaf of *D. hispidula*; one mid-instar larva was also recorded on the underside of a leaf of *D. hispidula*.

Amalia Gorge, El Questro Wilderness Park, WA (15.98124°S, 128.03708°E; WGS84), 2 April 2010, M.F. Braby & L.J. Aitchison. Empty egg shells and one late instar larva were recorded on foliage of *D. hispidula* growing near the entrance of the sandstone gorge.

*Theclistes sulphius* (Miskin, 1890). Samphire Blue.


12.5 km SW of Palmerston, NT (12.56246°S, 130.90619°E; WGS84), 25 April 2007, M.F. Braby. Several egg shells and larval feeding damage were recorded on *Tecticornia halocnemoides* growing in saltmarsh. The site was revisited on 10 June 2006 and a female was observed at 1325 hr depositing a single egg on *T. halocnemoides*; several additional eggs were also recorded on *T. halocnemoides*.


*Acacia difficilis* Maiden. (Fabaceae). (voucher M.F. Braby 5, DNA).

Litchfield National Park, NT (13.12555°S, 130.80305°; WGS84), 15 April 2006, M.F. Braby & L.J. Aitchison. Six prepupae and pupae were collected from foliage of *Acacia difficilis* growing on a rocky sandstone plateau; the early stages were attended by meat ants, *Iridomyrmex rubrurus*, and were subsequently reared to adult in captivity.

1 km ENE of Nanguluwur, Nourlangie Rock, Kakadu National Park, NT (12.84375°S, 132.82558°E; WGS84), 24 January 2010, M.F. Braby & L.J. Aitchison. All early stages were attended by meat ants, *Iridomyrmex rubrurus*, and were subsequently reared to adult in captivity.

*Acacia difficilis* Maiden. (Fabaceae). (vouchers M.F. Braby 2, DNA).

East Point, Darwin, NT (12.41140°S, 130.82500°E; WGS84), 30 September 2006, M.F. Braby. Females were observed ovipositing on fresh leaves of *Mallotus nesophilus* growing along the edge of coastal semi-deciduous monsoon vine-thicket; additional eggs and early instar larvae were also recorded on the underside of leaves of *M. nesophilus*. The site was revisited on 10 June 2006 and a female was observed at 1125 hr depositing a single egg on petals of *B. laxa*. The site was revisited on 17 April 2010 and a female was observed at 1125 hr depositing a single egg on *B. laxa*. The site was revisited on 10 June 2006 and a female was observed at 1125 hr depositing a single egg on a flower of *B. laxa*. The site was revisited on 4 May 2008 and a female was observed at 1350 hr ovipositing on petals of *B. laxa*.

1 km ENE of Nanguluwur, Nourlangie Rock, Kakadu National Park, NT (12.84375°S, 132.82558°E; WGS84), 24 January 2010, M.F. Braby & L.J. Aitchison. All early stages were recorded in abundance on *A. difficilis* growing in a sandstone gully; larvae and pupae were attended by small brown ants, *Iridomyrmex pallidus*, and were subsequently reared to adult in captivity.
Acacia platyarpa F.Muell. (Fabaceae). (not vouchered). Gurandaling, Keep River National Park, NT (15.87478°S, 129.05144°E; WGS84), 2 February 2008, M.F. Braby & V. Kessner. Numerous eggs, three larvae and one pupa were recorded on several shrubs of *Acacia platyarpa*; larvae were attended by swarms of meat ants, *Iridomyrmex* sp. (not vouchered).

Corymbia bella K.D. Hill & L.A.S. Johnson. (Myrtaceae). (not vouchered). Flora River Nature Park, NT (14.75744°S, 131.59694°E; WGS84), 31 January 2008, M.F. Braby & V. Kessner. Several larvae were recorded on a sapling of *Corymbia bella* growing in open vine-thicket on limestone; larvae were attended by numerous sugar ants, *Iridomyrmex* sp.

Corymbia ferruginea (Schaumer) K.D. Hill & L.A.S. Johnson. (Myrtaceae). (not vouchered). Cabbage Gum, Charles Darwin University, Katherine, NT (14.39932°S, 132.14186°E; WGS84), 25 January 2009, M.F. Braby & V. Kessner. All stages were recorded on a sapling (approx. 1 m high) of *Corymbia ferruginea* growing in monsoon vine-thicket on limestone karst; larvae were observed at 1450 hr ovipositing on a tall shrub (approx. 3 m high) of *C. ferruginea*. (voucher M.F. Braby 4, DNA).

Santalum lanceolatum R.Br. (Santalaceae). (voucher M.F. Braby 36, DNA). Jasper Gorge, approx. 58 km SW of Victoria River Roadhouse, NT (16.03119°S, 130.80275°E; WGS84), 21 March 2008, M.F. Braby & V. Kessner. A female was observed at 1450 hr ovipositing on a tall shrub (approx. 3 m high) of *Santalum lanceolatum*, which grew in woodland along a dry rocky sandstone seasonal gully; numerous eggs were also present on new leaf growth; one pupa was found at the base of the stem where it was well protected beneath debris; a pupal exuvia was also recorded on the underside of a leaf of *S. lanceolatum*.


Escarpment Walk, Gregory (Juturre) National Park, NT (15.61325°S, 131.11597°E; WGS84), 16 March 2008, M.F. Braby & V. Kessner. Females were observed ovipositing on *Sesbania simpliciuscula* growing in savannah woodland at the base of an escarpment; numerous eggs were also recorded on flower buds of *S. simpliciuscula*.


Duncan Road, Hicks Creek crossing, NT (16.19774°S, 129.05383°E; WGS84), 19 March 2008, M.F. Braby & V. Kessner. A female was observed ovipositing on *Sesbania simpliciuscula*, which grew in abundance along a roadside. Duncan Road, Rosewood Station, NT (16.46031°S, 129.03348°E; WGS84), 19 March 2008, M.F. Braby & V. Kessner. Several females were observed ovipositing on *S. simpliciuscula*, which grew in abundance along a roadside.

Zizeeria karsandra (Moore, 1865). Spotted Grass-blue. Tribolopus bicolor F.Muell. (Zygophyllaceae). (voucher M.F. Braby 75, DNA). Interseuction of Buchanan Hwy and Victoria Hwy, 2 km SE of Timber Creek, NT (15.74320°S, 130.64830°E; WGS84), 1 April 2010, M.F. Braby & L.J. Aitchison. Several eggs were recorded on the underside of leaves of *Tribolopus bicolor* growing in a disturbed roadside verge in savannah woodland; numerous adults were observed flying in close proximity or settling on *T. bicolour*.


Magnetic Termite Mounds, Litchfield National Park, NT (13.10500°S, 130.84250°E; WGS84), 15 March 2006, M.F. Braby & D.A. Young. A female was observed during mid-afternoon ovipositing on a twining creeper of *Vigna vexillata*, which grew in savannah woodland; numerous additional eggs were also present on tendrils of *V. vexillata*.

NOCTUIDAE: AGARISTINAE

Agarista agricola biforis Butler, 1884 (Fig. 1). Painted Day-moth. Lekea rubra Blume ex Spreng. (Vitaceae). (voucher M.F. Braby 83, DNA).

Mt Bundy, Mary River National Park, NT (12.85990°S, 131.60281°E; WGS84), 30 October 2010, M.F. Braby. A female was observed at 1415 hr ovipositing on *Lekea rubra* growing along the edge or ecotone of deciduous monsoon vine-thicket during overcast conditions with light rain; a second female was subsequently observed at 1600 hr actively searching *L. rubra* on which to lay eggs during bright sunny conditions; eggs were bright green and laid on stems and dry leaf bracts, and hatched five days later; four early instar larvae were also collected from the foliage of three separate shrubs and reared to adult in captivity on *L. rubra*, as well as on *L. indica* (Burm.f.) Merr. The site was revisited on 14 November 2010 and a further four early instar larvae were collected from *L. rubra* growing in the ecotone or in savannah woodland adjacent to deciduous monsoon vine-thicket; one larva was reared to adult in captivity.

Conocrus belri (Angas, 1847) (Fig. 2). Mistletoe Day-moth. Amyema maidenii (Blakely) Barlow. (Loranthaceae). (not vouchered).

Alice Springs Desert Park, Alice Springs, NT (23.700°S, 133.833°E; WGS84), 13 February 2010, M.F. Braby & L.J. Aitchison. Three larvae were collected from clumps of the mistletoe *Amyema maidenii* that were parasitising *Acacia aneura* and reared to adult in captivity; a final instar larva was also collected crawling rapidly along the ground.
beneath the mulga host tree in search of a pupation site. Several adults were present at the breeding site.

_Aunya saugninea_ (F.Muell.) Danser. (Loranthaceae). (not vouchered).

Limbutnya Station, Victoria River District, NT (17.52339°S, 130.05701°E; WGS84), 25 July 2010, M.F. Braby. A cohort of nine late instar larvae was recorded feeding openly, but not gregariously, on a single clump of the mistletoe _Aunya saugninea_ that was parasitising the host tree _Corynia_ sp. growing in eucalypt open woodland with a ground layer of _Triodia_ sp. on red sandy soil; six larvae were collected, two of which were reared to adult in captivity.

_Cruria tropica_ (T.P. Lucas, 1891) (Fig. 3)


Howard Springs Nature Reserve, NT (12.45240°S, 131.05347°E; WGS84), 16 and 24 February 2008, 8 and 24 March 2008, M.F. Braby. Several females were observed during mid-afternoon (1430–1530 hr) during the wet season ovipositing on _Typhonium flagelliforme_, a seasonal geophytic herb, which grew in paperbark-pandanus swamp woodland; leaves of other plants) in savannah woodland. This food plant was only recently described, and is listed as _Hibbertia brevipedunculata_ or on nearby objects (i.e. _H. brownii_). Several of which were reared to adult in captivity.

_Idaliina aethrius_ (Turner, 1908). No common name. (Fig. 4)

_Hibbertia cistifolia_ R.Br. ex DC. (Dilleniaceae). (voucher M.F. Braby 23, DNA).

Caiman Creek, Cobourg Peninsula, NT (11.22504°S, 132.20236°E; WGS84), 22 February 2007, M.F. Braby & D.A. Lane. One late instar larva was recorded on the foliage of _Hibbertia cistifolia_ growing in savannah woodland.

_Hibbertia brevipedunculata_ Toelken. (Dilleniaceae). (voucher M.F. Braby 21, DNA).

3 km N of Berry Springs, NT (12.67554°S, 131.00994°E; WGS84), 14 January 2007, M.F. Braby. Two females were observed at 1440 hr and 1535 hr ovipositing on the foliage of _Hibbertia brevipedunculata_ or on nearby objects (i.e. ground, leaves of other plants) in savannah woodland. The site was revisited on 2 November 2008 and 11 larvae in various instars were recorded on the larval food plant, several of which were reared to adult in captivity. This food plant was only recently described, and is listed as _Hibbertia_ sp. Mt Finnis in Kerrigan & Albrecht (2007) and was vouchered in DNA under that name.

_Idaliina leonora_ (Doubleday, 1846). No common name. (Fig. 5)

_Hibbertia brownii_ Benth. (Dilleniaceae). (voucher M.F. Braby 24, DNA).

Caiman Creek, Cobourg Peninsula, NT (11.22364°S, 132.21402°E; WGS84), 21 February 2007, M.F. Braby & D.A. Lane. Females were observed at 1520 hr and 1745 hr ovipositing on _Hibbertia brownii_ growing in savannah woodland; eggs were laid singly on flower buds or dead twigs; one mid-instar larva was collected from the underside of a leaf and reared to the pupal stage. The site was revisited on 15 March 2007 and females were observed at 1543 hr, 1550 hr and 1655 hr ovipositing on _H. brownii_; empty egg shells were also located on _H. brownii_; all eggs were laid singly, mostly on flower buds or sometimes on leaf bracts of developing flower spikelets and on new leaf shoots at the apex of a branch of _H. brownii_.

_Hibbertia caudiculae_ Benth. (Dilleniaceae). (voucher M.F. Braby 67, DNA).

1 kmENE of Nanguluwur, Nourlangie Rock, Kakadu National Park, NT (12.84375°S, 132.82558°E; WGS84), 20 December 2009, M.F. Braby. Two larvae were collected from _Hibbertia caudiculae_ growing in sandy-loam at the base of an escarpment; one larva was reared to adult in captivity.

0.4 km NE of Nanguluwur, Nourlangie Rock, Kakadu National Park, NT (12.84535°S, 132.82072°E; WGS84), 24 January 2010, M.F. Braby & L.J. Aitchison. Two early instar larvae and one late instar larva were collected from separate shrubs of _H. caudiculae_ growing in open woodland on a sandstone plateau; one larva was reared to adult in captivity.

0.6 km W of Gubara Track, Nourlangie Rock, Kakadu National Park, NT (12.83721°S, 132.84970°E; WGS84), 27 November 2010, M.F. Braby. One final instar larva was collected from _H. caudiculae_ and reared to adult in captivity.

_Periopta ardescens_ (Butler, 1884). No common name. (Fig. 6)

_Ampelocissus frutescens_ Jackes. (Vitaceae). (vouchers M.F. Braby 57, 058, DNA).

Bullita Rd, 11 km SSE of Timber Creek, NT (15.75712°S, 130.51135°E; WGS84), 10 December 2008, M.F. Braby & V. Kessner. Numerous larvae were recorded feeding on new regenerating leaves of _Ampelocissus frutescens_ growing in savannah woodland; several larvae were reared to adult in captivity; most larvae developed directly and emerged a few weeks later, but others emerged one or two years later. The larvae occurred together with those of _Radinocera vagata_ (see below).

Mt Burrell, Tipperary Station, Daly River district, NT (13.49623°S, 131.03572°E; WGS84), 12 December 2008, M.F. Braby. One late instar larva was collected from _A. frutescens_ growing in woodland at the base of a hill and reared to adult in captivity.

_Ampelocissus acetosa_ (F.Muell.) Planch. (Vitaceae). (not vouchered).

Buffalo Creek, Lee Point, NT (12.33639°S, 130.90389°E; WGS84), 28 November 2009, M.F. Braby. Seven larvae in various instars were collected from _Ampelocissus acetosa_ growing in savannah woodland regenerating after dry season burns and pre-monsoon storms; a few larvae were reared to adult in captivity. The larvae occurred together with those of _Radinocera vagata_ (see below).
Nanguluwur Art site, Kakadu National Park, NT (12.84262°S, 132.81895°E; WGS84), 7 and 19 December 2009, M.F. Braby & J.J. Armstrong. Females were observed at 1730 hr and 1845–1850 hr (just before sunset) ovipositing on *A. acetosa* growing in woodland near the base of an escarpment; numerous larvae in various instars were also recorded on *A. acetosa*.

*Periopta diversa* (Walker, 1865). No common name. (Fig. 7)

*Spermococe phalloides* Harwood. (Rubiaceae). (not vouchered).

Leanyer Recreation Park, Darwin, NT (12.39055°S, 130.91167°E; WGS84), 21 December 2005, 5, 20 and 21 January 2006, M.F. Braby. Numerous larvae were recorded on *Spermococe phalloides* growing in disturbed grassland, several of which were reared to adult in captivity. *Oldenlandia* sp. (Rubiaceae). (vouchers M.F. Braby 10, 11, DNA).

Leanyer Recreation Park, Darwin, NT (12.39055°S, 130.91167°E; WGS84), 4, 20 and 21 January 2006, M.F. Braby. Numerous females were observed at 1710–1855 hr (within a few hours of dusk) ovipositing on *Oldenlandia* sp., as well as on other small herbs, including grass blades, growing in disturbed grassland; eggs were laid singly; several larvae were also collected from *Oldenlandia* sp. and reared to adult in captivity.

Holmes Jungle National Park, NT (12.400°S, 130.916°E; AGD66), 6 February 2010, M.F. Braby. Several females were observed at 1720–1740 hr ovipositing on *Oldenlandia* sp. growing in a disturbed area along a track; eggs were laid singly and directly onto leaves of *Oldenlandia* sp.; two larvae were also recorded on *Oldenlandia* sp.

*Radinocera vagata* (Walker, 1865). No common name. (Fig. 8)

*Amplelocissus acetosa* (F.Muell.) Planch. (Vitaceae). (voucher M.F. Braby 17, DNA).

Caiman Creek, Cobourg Peninsula, NT (11.22504°S, 132.20236°E; WGS84), 7 and 22 February 2007, M.F. Braby & V. Kessner. Three larvae were collected from vines of *Amplelocissus acetosa* growing in savannah woodland; two larvae were reared to adult in captivity.

Lee Point, Casuarina Coastal Reserve, NT (12.33166°S, 130.89444°E; WGS84), 16 February 2008, M.F. Braby. Two late instar larvae were recorded on a vine of *A. acetosa* growing around *Corymbia bella* in parkland adjacent to coastal semi-deciduous monsoon vine-thicket.

Buffalo Creek, Lee Point, NT (12.33639°S, 130.90389°E; WGS84), 28 November 2009, M.F. Braby. Ten larvae in various instars were collected from *A. acetosa* growing in savannah woodland that was regenerating after a dry season burn and pre-monsoon storms; all larvae were feeding singly, with a maximum of two per vine; several larvae were reared to adult in captivity. The early stages occurred together with those of *Periopta ardenscens* (see above).

*Amplelocissus frutescens* Jackes. (Vitaceae). (voucher M.F. Braby 58, DNA).

Bullita Rd, 11 km SSE of Timber Creek, NT (15.75712°S, 130.51135°E; WGS84), 10 December 2008, M.F. Braby & V. Kessner. Six larvae were collected feeding openly on *Amplelocissus frutescens* growing in savannah woodland; most larvae were on separate plants and several were reared to adult in captivity. The larvae occurred together with those of *Periopta ardenscens* (see above).

9 km SE of Timber Creek, NT (15.57325°S, 130.51804°E; WGS84), 10 December 2008, M.F. Braby & V. Kessner. Several larvae were recorded on *A. frutescens* growing in savannah woodland.

*Cayratia maritima* Jackes. (Vitaceae). (voucher M.F. Braby 14, DNA).

2 km ENE of Black Point, Cobourg Peninsula, NT (11.15015°S, 132.16125°E; WGS84), 13 March 2007, M.F. Braby. One late instar larva was collected from *Cayratia maritima* growing in paperbark woodland adjacent to a swamp and reared to adult in captivity; the pupal duration was approx. seven months.

Buffalo Creek, Lee Point, NT (12.34497°S, 130.90578°E; WGS84), 8 March 2008, M.F. Braby. Two late instar larvae were recorded on a vine of *C. maritima*, which grew around the trunk of a dead *Acacia* sp. along the edge of a paperbark swamp. The site was revisited on 7 November 2010 and two early instar larvae were collected from new leaf growth of *C. maritima* growing on the trunk of a *Melaleuca* sp. tree and reared to adult in captivity.

*Cayratia trifolia* (L.) Domin. (Vitaceae). (voucher M.F. Braby 89, DNA).

Mt Bundy, Mary River National Park, NT (12.85990°S, 131.60281°E; WGS84), 30 October 2010, M.F. Braby. Four early instar larvae were collected from new growth of *Cayratia trifolia* growing on the trunk of a eucalypt in savannah woodland and reared to adult in captivity.

**NEW LEPIDOPTERA LARVAL FOOD PLANT ASSOCIATIONS FOR THE NORTHERN TERRITORY AND/OR NORTHERN WESTERN AUSTRALIA**

The following catalogue of species comprises plants that have previously been recorded as larval food plants from eastern Australia (e.g. Common 1990; Braby 2000) but, to the author’s knowledge, have not been previously documented for the NT and/or the Kimberley region of western NT and north-western WA.

**GEOMETRIDAE**

*Dysphania unmanua* (Cramer, 1779). Six O’clock Moth.

*Carallia brachiata* (Lour.) Merr. (Rhizophoraceae). (not vouchered).
Ovipositing females and/or the early stages were frequently recorded on *Carallia brachiata* growing in riparian monsoon forest and semi-deciduous monsoon vine-thicket from many locations, including Darwin, Litchfield National Park, Beatrice Hill, Kakadu National Park and Gove Peninsula. Females were observed ovipositing during the late afternoon (1540–1745 h); eggs were laid on the underside of mature leaves and stems of *C. brachiata*; larvae fed solitarily on young soft foliage and pupated within a shelter made from two or more mature foliage of *C. brachiata*.

**HESPERIIDAE**

*Chaetocneme deniita* (Hewitson, 1867). Ornate Dusk-flat.

*Planchonia careya* (F.Muell.) Kunth. (Lecythidaceae). (not vouched).

Black Point, Cobourg Peninsula, NT (11.15515°S, 132.14391°E; WGS84), 19 February 2007, M.F. Braby & D.A. Lane. One first instar larva was collected from a small regenerating sapling of *Planchonia careya* growing in disturbed savannah woodland and reared to adult by DAL.

Berrimah (CSIRO complex), Darwin, NT (12.41333°S, 130.92194°E; WGS84), 11 March 2008, M.F. Braby. A freshly emerged male and a pupal shelter were collected from a small tree of *Planchonia careya* growing in degraded savannah woodland; the adult perched upside-down on the underside of a leaf at midday.

**Taraotcera sp. (ina Waterhouse, 1932, or anisomorpha Lower, 1911). Grass-dart.**


Standley Chasm, West MacDonnell Ranges, NT (23.72150°S, 133.46982°E; WGS84), 4 March 2007, M.F. Braby & C.M. Palmer. Numerous larvae were recorded within their tubular shelters on *Eulalia aurea* growing in water or damp areas in riparian eucalypt open forest. Adults of both species were present in the habitat and either may have been using this native grass.

**Taraotcera sp. (ina or anisomorpha). Grass-dart.**

*Cenchrus ciliaris* (Kuntze) L. (Poaceae). (not vouched).

Standley Chasm, West MacDonnell Ranges, NT (23.72150°S, 133.46982°E; WGS84), 2 March 2007, M.F. Braby & C.M. Palmer. Several eggs and larvae were recorded on *Cenchrus ciliaris* growing in riparian eucalypt open forest. Adults of both species were present in the habitat and either may have been using this invasive, introduced, perennial tussock grass.

**Taraotcera sp. (ina or anisomorpha). Grass-dart.**


Standley Chasm, West MacDonnell Ranges, NT (23.72150°S, 133.46982°E; WGS84), 4 March 2007, M.F. Braby & C.M. Palmer. Numerous larvae were recorded within their tubular shelters on the broad-leaved tufted perennial grass *Paspalum conjugation*, which grew in water or damp areas in riparian eucalypt open forest. Adults of both species were present in the habitat and either may have been using this introduced grass.

**PAPILIONIDAE**


Mt Bundy, Mary River National Park, NT (12.85990°S, 131.60281°E; WGS84), 28 November 2010, M.F. Braby. Two females were observed at 1250 h for several minutes ovipositing on shrubs of *Miliusa traceyi* growing along the edge of semi-deciduous monsoon vine-thicket; numerous eggs were laid on the underside of leaves, including new growth as well as older mature leaves; two early instar larvae were also noted feeding on the new soft leaves of *M. traceyi*.

**Papilio aegens aegens** (Donovan, 1805). Orchard Swallowtail.

*Citrus* sp. (Rutaceae). (not vouched).

Nhulunbuy, Gove Peninsula, NT (12.17805°S, 136.78361°E; WGS84), 6 September 2007, M.F. Braby & P. Wise. Two larvae were collected on *Citrus* sp. growing in a residential garden and reared to adult in captivity; the larvae pupated on 13 September 2007 and emerged as adults 11 days later. The site was revisited on 24 June 2008 and a further three larvae were collected from *Citrus* sp. and reared to adult in captivity; the larvae pupated the following month and emerged 13 days later.

**Papilio fuscus canopus** Westwood, 1842. Fuscous Swallowtail.

*Citrus* sp. (Rutaceae). (not vouched).

eggs and several first instar larvae were collected from new leaf growth of *Citrus* sp. growing in an orchard adjacent to monsoon vine-thicket; 15 larvae were collected and reared in captivity, with adults emerging up to 10 months later.

Wanguri, Darwin, NT (12.57308°S, 130.88657°E; WGS84), 29 June 2008, M.F. Braby. One pupal exuvia was recorded on a stem of *Citrus* sp. growing in a nature strip adjacent to a residential garden.

*Papilio demoleus sthenicus* W.S. Macleay, 1826. Chequered Swallowtail.

*Calicen cinereum* (Lindl.) J.W. Grimes. (Fabaceae). (not vouchered).

Victoria River eroding, approx. 2 km S of Victoria Hwy, NT (15.63072°S, 131.13261°E; WGS84), 4 April 2010, M.F. Braby & L.J. Aitchison. Several females were observed ovipositing on seedlings of *Calicen cinereum* growing in open dry floodplain near the Victoria River.

**PIERIDAE**

*Catopsilia pomona* (Fabricius, 1775). Yellow Migrant.

*Catopsilia pomona* (Fabricius, 1775). Yellow Migrant.


Town Lagoon, Nhulunbuy, Gove Peninsula, NT (12.17805°S, 136.78361°E; WGS84), 27 January 2008, M.F. Braby & L.J. Aitchison. A female was observed at 1140 hr ovipositing on leaves of a trailing creeper of *Galactia tenuiflora*, which grew along the edge of paperback swamp adjacent to monsoon vine-thicket; numerous additional eggs were also present on leaves of *G. tenuiflora*.

Coolibah Station, Victoria River District, NT (15.58340°S, 130.97647°E; WGS84), 18 March 2008, M.F. Braby & V. Kessner. Females were observed at 1000 hr, 1109 hr and 1110 hr ovipositing on a creeper of *G. tenuiflora*, which grew over rock scree on a sheltered slope in monsoon vine-thicket; all the eggs were laid singly on new soft leaf growth; additional eggs were also present on leaves of the larval food plant.

Mt Burrell, Tipperary Station, Daly River district, NT (13.49623°S, 131.03572°E; WGS84), 21 February 2009, M.F. Braby & D.A. Young. A female was observed at 1100 hr ovipositing on a leaf of a twiner of *G. tenuiflora*, which grew in eucalypt woodland on a rocky slope of a hill; additional eggs were also present on new leaves; several early instar larvae were also collected on the new leaf growth and reared to adult in captivity; the larvae pupated the following month and emerged as adults five or six days later.

*Eurema hecabe* (Linnaeus, 1758). Large Grass-Yellow.

*Sesbania cannabina* (Retz.) Poir. (Fabaceae). (vouchers M.F. Braby 72, DNA).

Rapid Creek, Darwin, NT (12.38083°S, 130.86462°E; WGS84), 20 March 2010, M.F. Braby. One late instar larva was recorded on *Sesbania cannabina*, which grew in profusion in a disturbed area along the edge of mangroves; numerous females were also observed alighting on the larval food plant but they did not appear to oviposit. The early stages occurred together with those of *Theclinesthes miskini* (see below).


Eggs and larvae were frequently recorded (and subsequently reared to adult in captivity) on new soft leaf growth of *Brenya curta* growing in monsoon vine-forest or riparian monsoon forest from many locations, including Darwin, Mary River Park and Fogg Dam Conservation Reserve, usually from November to June (i.e. wet season-early dry season).

*Belenois java tentorula* (Fabricius, 1775). Caper White.

*Capparis umbonata* Lindl. (Capparaceae). (voucher M.F. Braby 64, DNA).

Leanyer, Darwin, NT (12.37500°S, 130.89667°E; WGS84), 14 December 2005, M.F. Braby. Several larvae and numerous pupae (approx. 200) were recorded on a small...
tree of *Capparis umbonata* growing in parkland, and a series was reared to adult in captivity. The site was revisited on 17 October 2007 and more than 100 late instar larvae and approx. 20 pupae were recorded on the same tree. The tree was subsequently destroyed by Tropical Cyclone Helen on 5 January 2008.

1 km ENE of Nanguluwur, Nourlangie Rock, Kakadu National Park, NT (12.84375°S, 132.82558°E; WGS84), 20 December 2009, M.F. Braby. Two late instar larvae were recorded on an almost leafless, spiny shrub of *C. umbonata*, which grew on sandy-loam at the base of an escarpment. The larvae were feeding together with those of *Cepora perinata* (see above).

**NYMPHALIDAE**


*Tylophora flexuosa* R.Br. (Apocynaceae). (voucher M.F. Braby 63, DNA). Emma Gorge Resort, El Questro Wilderness Park, WA (15.90753°S, 128.12909°E; WGS84), 17 July 2009, M.F. Braby & L.J. Aitchison. A female was observed at 1130 hr ovipositing on *Tylophora flexuosa* growing on sandstone rock scree in open woodland above Emma Creek; numerous additional eggs and two larvae were also present on the larval food plant.

*Euploea coreina* (W.S. Macleay, 1826). Common Crow. *Marsdenia viridiflora* R.Br. (Apocynaceae). (voucher M.F. Braby 68, DNA). 1 km ENE of Nanguluwur, Nourlangie Rock, Kakadu National Park, NT (12.84375°S, 132.82558°E; WGS84), 20 December 2009, M.F. Braby. A female was observed at 1020 hr depositing a single egg on the underside of a leaf of a vine of *Marsdenia viridiflora*, which grew in woodland at the base of an escarpment; two early instar larvae were also recorded feeding on new soft leaves of *M. viridiflora*. *Secamone elliptica* R.Br. (Apocynaceae). (voucher M.F. Braby 74, DNA). Bulloektey Point, Darwin, NT (12.43777°S, 130.83377°E; WGS84), 23 February 2010, M.F. Braby. One mid-instar larva was recorded feeding on a vine of *Secamone elliptica*, which grew around *Buchnera linearis* in degraded monsoon vine-thicket.

Fogg Dam Conservation Reserve, NT (12.55769°S, 131.29701°E; WGS84), 29 May 2010, M.F. Braby, S. Keates & D. Bisa. A female was observed at 1145 hr ovipositing on *H. angustifolia*, as well as on adjacent objects, including a dead twig of an *Acacia* sp. sapling and dead dry leaves of grass, in mixed paperbark swampland adjacent to monsoon vine-forest.

**Hypolinias bouchia urina** (Fabricius, 1775). Varied Eggfly.


Bullocky Point, Darwin, NT (12.43777°S, 130.83377°E; WGS84), 23 March 2010, M.F. Braby. Two females were observed at 1245–1255 hr ovipositing on *Syndrella nodiflora*, a herb growing in shade beneath a large African Mahogany tree; all eggs were laid singly on the underside of leaves. The site was revisited on 24 March 2010 by M.F. Braby & S. Keates and a female was observed at 1240–1250 hr ovipositing on introduced *Tridax procumbens* (Asteraceae), as well as a species of grass on which a cluster of five eggs were laid on the underside of a blade. Since both plants were growing amongst numerous herbs of *S. nodiflora*, the suitability of these species as larval food plants requires confirmation. On 7 April 2010 one late instar larva was collected from under the ground underneath *S. nodiflora* and reared to adult in captivity on this food plant.

**Melanitis leda bankia** (Fabricius, 1775). Evening Brown.

*Imperata cylindrica* (L.) Reausch. (Poaceae). (not vouched).

Nathan River Ranger Station, Limmen National Park, NT (15.57681°S, 135.42783°E; WGS84), 12 May 2009, M.F. Braby & N. Collier. Numerous larvae and several pupae (mostly diseased) were recorded on *Imperata cylindrica*, as well as on introduced *Cynodon radiatus* (Poaceae) (see above), growing along the bank of a river.


Cockatoo Lagoon, Keep River National Park, NT (15.96505°S, 129.04099°E; WGS84), 1 February 2008, M.F. Braby. One pupa was collected from under the bark of a eucalypt host tree supporting several clumps of the mistletoe *Amyema bifurcata* growing in the canopy; a male was also netted perched in the canopy of the host tree.

Victoria Hwy, approx. 35 km E of Kununurra, WA (15.96229°S, 128.96069°E; WGS84), 6 July 2009, M.F. Braby. One pupa was collected (and reared to adult in captivity) from under loose bark at the base of the host tree *Corymbia grandifolia* (R.Br. ex Benth.) K.D.Hill & L.A.S. Johnson, which supported numerous clumps of *A. bifurcata*, growing in savannah woodland on a sandplain.

The pupa was found together with a cohort of *O. zosinea* larvae, which were attended by sugar ants, *Camponotus sp.* (hamilior species group).


Larapinta Drive, NNE of Kings Canyon, NT (23.99472°S, 131.48583°E; WGS84), 12 October 2005, M.F. Braby & L.J. Atchison. One mid-instar larva was collected (and reared to adult in captivity) from a mallee eucalypt host tree supporting clumps of the mistletoe *Amyema bifurcata*. The larva was found together with a cohort of *O. anathyris meridionalis* larvae.

**Amyema miquelii** (Lam. ex Miq.) Tiegh. (Loranthaceae). (not vouched).

6 km S of Hermannsburg, NT (23.99111°S, 132.77555°E; WGS84), 14 October 2005, M.F. Braby & L.J. Atchison. One late instar larva and one prepupa were collected (and reared to adult in captivity) from loose bark at the base of the host tree *Eucalyptus camaldulensis* Dehn., which supported clumps of the mistletoe *Amyema miquelii*, growing along the Finke River; the larva was attended by three ants, *Crematogaster sp.* (longiceps species group).

Trephina Gorge National Park, East Macdonnell Ranges, NT (23.52805°S, 134.38000°E; WGS84), 30 April 2006, M.F. Braby. Ten larvae in various instars were collected (and reared to adult in captivity) from a mallee eucalypt supporting clumps of the *A. miquelii*; a few larvae were attended by ants, *Crematogaster sp.* (longiceps species group); larvae were polymorphic in colour, varying from green, through pale green-brown and pale brown, to dark brown.

Luritja Road, 30 km N of Lasseter Hwy, NT (24.93221°S, 132.27826°E; WGS84), 16 August 2010, M.F. Braby. One mid-instar larva was collected from under loose bark of a mallee eucalypt host tree supporting numerous clumps of *A. miquelii*; the larva was not attended by ants. Several adult males were collected during the afternoon as they settled on dead branches in the canopy of the breeding trees where they appeared to be defending encounter sites to detect receptive females.


Trephina Gorge National Park, East Macdonnell Ranges, NT (23.52805°S, 134.38000°E; WGS84), 30 April 2006, M.F. Braby. One final instar larva was collected (and reared to adult in captivity) from a mallee eucalypt host tree supporting the mistletoe *Amyema miquelii* growing adjacent to a breeding colony of *O. oroetes* (see above).
**Ogyris zosine** (Hewitson, [1853]). Northern Purple Azure.

*Amyema bifurcata* (Benth.) Tiegh. (Loranthaceae), (not vouchered).

Mary River Billabong, Mary River National Park, NT (12.89245°S, 131.63890°E; WGS84), 19 July 2008, M.F. Braby & S. Keates. A female was observed at 1500–1515 hr ovipositing on the host tree *Corymbia bella* supporting a small clump of the mistletoe *Amyema bifurcata* growing in the canopy (approx. 8 m from ground level) in savannah woodland; eggs were laid on patches of rough bark of the trunk below the mistletoe clump. The site was revisited the following week and six recently hatched egg shells were collected; no attendant ants were present on the host tree.

*Ebony Creek*, Limmen National Park, NT (16.35714°S, 135.69812°E; WGS84), 11 May 2009, M.F. Braby & N. Collier. A cohort of nine larvae in various instars and one pupa were collected (and reared to adult in captivity) from soil at the base of the trunk of the host tree *Corymbia grandifolia* supporting two clumps of *A. bifurcata* in savannah woodland; the early stages were attended by numerous sugar ants, *Camponotus* sp. (*humilior* species group).

*Amyema sanguinea* (F.Muell.) Danser. (Loranthaceae). (not vouchered).

Limbunya Station, Victoria River District, NT (17.30592°S, 129.77728°E; WGS84), 24 July 2010, M.F. Braby, V. Kessner & T. Parkin. A cohort comprising 13 early to mid-instar larvae and one final instar larva was collected (and reared to adult in captivity) from under a small rock at the base of a *Corymbia* sp. host tree, which supported a single clump of the mistletoe *Amyema sanguinea* growing near the canopy (approx. 7 m from ground level) in woodland on a steep mixed limestone outcrop; the larvae were attended by numerous pale brown sugar ants *Camponotus* sp. (*humilior* species group). Of eight females reared to adult in captivity, four had the basal areas on the upperside of the wings bright purple, while the remaining four were bright blue.

Limbunya Station, Victoria River District, NT (17.55211°S, 130.07086°E; WGS84), 25 July 2010, M.F. Braby. One pupa was collected from the base of a small *Corymbia* sp. host tree, which supported three clumps of *A. sanguinea*, growing in eucalypt open woodland with a ground layer of *Triodia* sp.; the pupa was attended by five sugar ants, *Camponotus* sp. (*crozieri* species group), a darker brown species compared with *Camptonotus* sp. (*humilior* species group).

Buntine Hwy, 31 km SW of Top Springs, NT (16.75994°S, 131.61429°E; WGS84), 28 July 2010, M.F. Braby. A cohort of 10 larvae was found at the base of a eucalypt host tree supporting a large clump of *A. sanguinea* growing 1.5 m above ground level; most larvae were parasitised by braconid wasps and only two pre-pupae, which were attended by several sugar ants, *Camptonotus* sp. (*novachollandiae* species group), were not parasitised and reared to adult in captivity.


Bullocky Point, Darwin, NT (12.43777°S, 130.83377°E; WGS84), 18 December 2010, M.F. Braby & J. Westaway. Five larvae in various instars were recorded feeding on soft new leaf growth of *Cupaniopsis anarcardioides*; larvae were attended by *Ocophylla snaaraguida* ants.

*Candalides erinus erinus* (Fabricius, 1775). Small Dusky-blue.

*Cassythya capillaris* Meisn. (Lauraceae). (voucher M.F. Braby 34, DNA).

Jinumum Gorge, Keep River National Park, NT (15.83376°S, 129.11018°E; WGS84), 2 and 4 February 2008, M.F. Braby & V. Kessner. A female was observed at 1005 hr depositing a single egg on a flower bud of *Cassythya capillaris* parasitising grass growing in savannah woodland on sandy loam on a gentle slope adjacent to a gorge; three larvae were also collected from new growth of the larval food plant and reared to adult in captivity; one of these larvae was attended by a small black ant, *Iridomyrmex* sp. (*mattirolsi* species group), and everted its eversible organs in presence of the ant. The site was revisited on 20 March 2008 and a female was observed at 1048 hr ovipositing two eggs on flower buds of the food plant; two larvae and one pupa, neither of which were attended by ants, were also collected from *C. capillaris* and reared to adult in captivity. Overall, the larvae were polymorphic in colour, varying from green, through pale green-brown and pale brown, to dark brown. The early stages were found together with those of *Candalides delospila* (see below).

Joe Creek, Gregory (Jutpurra) National Park, NT (15.59754°S, 131.07042°E; WGS84), 16 March 2008, M.F. Braby. One mid-instar larva, which was not attended by ants, was recorded on *C. capillaris*.

Seenie Lookout, Timber Creek, NT (15.64580°S, 130.45827°E; WGS84), 18 March 2008, M.F. Braby. A female was observed at 1455 hr depositing a single egg on a young tendril of *C. capillaris* parasitising *Triodia* sp. (Poaceae) growing in eucalypt woodland on sandstone; one late instar larva, which was not attended by ants, was also collected feeding openly on *C. capillaris* and it was reared to adult in captivity.

Amalia Gorge, El Questro Wilderness Park, WA (15.98124°S, 128.03708°E; WGS84), 2 April 2010, M.F. Braby & L.J. Aitchison. One final instar larva, which was not attended by ants, was collected from *C. capillaris* parasitising *Triodia* sp. growing on a lower slope of the gorge with a north facing aspect and it was reared to adult in captivity.
Candalides delospila (Waterhouse, 1903). Spotted Dusky-blue.

Cassyttha capillaris Meisn. (Lauraceae). (vouchers M.F. Braby 28, 034, DNA).

The early stages were frequently recorded (and subsequently reared to adult in captivity) on Cassyttha capillaris parasitising Triodia spp. and other grasses growing in open woodland on rocky sandstone plateaux or on sandy loam from many sites in Gregory (Jutpurra) and Keep River National Parks, NT, during visits in February, March and July 2007 and 2008. Eggs were collected from, and females were observed ovipositing on, new growth of C. capillaris; all eggs were laid singly; larvae were found at rest or feeding openly on C. capillaris during the day (i.e. they were not concealed amongst clumps of the host grass); most larvae were not attended by ants, but one was attended by a single black ant, Iridomyrmex sp. (gracilis species group); pupae were collected from stems of the host plant Triodia sp. around which the larval food plant grew. The larvae were polymorphic in colour, varying from green, through pale green-brown and pale brown, to dark brown. At Keep River, the early stages were found together with those of Candalides erinus (see above). At all other sites where Candalides delospila was recorded (e.g. Limbunya Station, Riveren Station, Timber Creek, Jasper Gorge, near Elliott, NT; Picaninny Creek Purnululu National Park, WA) adults flew in close proximity of C. capillaris.

Prosotas dubiosa dubiosa (Semper, [1879]). Purple Line-blue.

Acacia auriculiformis A.Cunn. ex Benth. (Fabaceae). (not vouchered).

East Point, Darwin, NT (12.41140°S, 130.82500°E; WGS84), 1 April 2006, M.F. Braby. A female was observed at 1500 hr ovipositing on flower buds of Acacia auriculiformis growing in coastal semi-deciduous monsoon vine-thicket.

Theclinesthes miskini miskini (T.P. Lucas, 1889). Wattle Blue.

Acacia holosericea A.Cunn. ex G.Don. (Fabaceae). (not vouchered).

The early stages were frequently recorded on Acacia holosericea growing in a variety of woodland habitats from many locations, including Channel Island, Beatrice Hill, near Black Point Cobourg Peninsula, Muirella Park Kakadu National Park, NT, and the Pentecost River El Questro Wilderness Park, WA. The early stages were usually attended by meat ants, Iridomyrmex reuburns, or sometimes small black ants, Iridomyrmex sp. (mattiroloi species group), or medium-sized black ants, Iridomyrmex sp. (aucep species group). Atalaya varifolia F.Muell. ex Benth. (Sapindaceae). (voucher M.F. Braby 30, DNA).

Victoria Hwy, Pinkerton Range, NT (15.98698°S, 129.51213°E; WGS84), 1 February 2008, M.F. Braby & V. Kessner. A female was observed ovipositing on a sapling of Atalaya varifolia (approx. 1.5 m high) growing in savannah woodland on a sandstone outcrop; about 40 additional eggs were also present on new soft terminal growth of A. varifolia; numerous meat ants, Iridomyrmex sp., were present on the food plant.

Bullitla Rd, 11 km SSE of Timber Creek, NT (15.75712°S, 130.51135°E; WGS84), 10 December 2008, M.F. Braby & V. Kessner. Numerous larvae and pupae were recorded on A. varifolia growing in savannah woodland; the early stages were attended by small black ants, Iridomyrmex sp. (minor species group). Sesbania cannabina (Retz.) Poir. (Fabaceae). (voucher M.F. Braby 72, DNA).

Rapid Creek, Darwin, NT (12.38083°S, 130.86462°E; WGS84), 20 March 2010, M.F. Braby. Numerous females were observed ovipositing on new leaf growth of Sesbania cannabina growing in a disturbed area along the edge of mangroves adjacent to Rapid Creek. The early stages were found together with those of Eurema hecabe (see above).

Jamides phaseli (Mathew, 1889). Purple Cerulean. Canavalia rosea (Sw.) DC. (Fabaceae). (not vouchered).

Bullocky Point, Darwin, NT (12.38777°S, 130.82777°E; WGS84), 28 May 2009, M.F. Braby. A female was observed at 1340 hr ovipositing on flower buds of Canavalia rosea, which grew amongst Ipomea pes-caprae (Convolvulaceae) in coastal sand dunes adjacent to mangroves; three larvae were also recorded feeding inside flower buds and flowers of C. rosea.

Zizeeria karsandra (Moore, 1865). Spotted Grass-blue.

Tribulus cistoides L. (Zygophyllaceae). (voucher M.F. Braby 20, DNA).

Gunn Point, NT (12.22833°S, 131.03000°E; WGS84), 10 December 2006, M.F. Braby. All stages were recorded on the underside of leaflets of Tribulus cistoides growing in coastal open beach shrubland above high tide mark; the larvae were not attended by ants; two pupae were reared to adult in captivity.

5.1 km ENE of Black Point, Cobourg Peninsula, NT (11.14695°S, 132.19014°E; WGS84), 23 April 2008, M.F. Braby & K. Nishida. A female was observed at 1230 hr ovipositing on the underside of leaflets of T. cistoides growing in beach sand along the edge of coastal semi-deciduous monsoon vine-thicket; several larvae were also recorded on the underside of foliage of T. cistoides.

Bullocky Point, Darwin, NT (12.43777°S, 130.83377°E; WGS84), 25 May 2010, M.F. Braby. Eggs and one early instar larva were recorded on the underside of leaflets of T. cistoides growing in profusion on beach sand. The site was revisited on 11 June 2010 and a female was observed at 1230 hr ovipositing on T. cistoides. On 1 September 2010, a mid-instar larva was collected from the underside of leaves of T. cistoides and reared to adult in captivity.


Mt Burrell, Tipperary Station, Daly River district, NT (13.4962°S, 131.0357°E; WGS84), 16 August 2008, M.F. Braby. Females were observed at 1230 hr ovipositing on *V. vexillata* growing on a beach cliff; numerous additional eggs were collected from leaves, new soft stems and flower buds; two early instar larvae were also collected from *M. atropurpureum*, feeding on flowers or developing pods, and were reared to adult in captivity.

*Barngoenius adolphi* (Regan, 1911), *Pseudocoris vigilans* (Regan, 1911), *Helopeltis turbinata* (Vill., 1833), *Heteronyx cinerea* (Scopoli, 1787), *H. pulchella* (Scopoli, 1787), *H. canescens* (Scopoli, 1787), *T. anisomorpha* (Fab., 1787), *T. trichopepla* (Herrich-Schäffer, 1869), appear to be erroneous (Braby 2008a; M.F. Braby unpublished data).

In total, 122 insect-plant associations are documented, of which 76 are new for Australia and 46 are new for the NT and/or WA. Of particular note are the first recordings of two plant families for two lycaenid species: the Lecythidaceae is recorded for the genus *Anthele*, and the Santalaceae is recorded for the genus *Theclinesthes*. New ant associations are also recorded for the larva and/or pupae of several lycaenids, notably of *Ogyris zosine* and *Theclinesthes miskini*. In addition, new larval food plant associations are reported for six species of agaristines (*Cepheus trichopepla* (Herrich-Schäffer, 1869), *Cepheus mesoptis* (Linnaeus, 1758), *T. ancilla* (Herrich-Schäffer, 1869), *T. augias* (Linné, 1758)).

**DISCUSSION**

In the NT, *Barngoenius adolphi* has been recorded only from a limited number of locations at and near Darwin, but the native larval food plant and natural breeding habitat have up until now remained unknown. All previous food plant associations (Meyer 1997b) comprise naturalised grasses from Africa that grow commonly in suburban areas of Darwin. The occurrence of *B. adolphi* in the floodplains of the South Alligator River suggests that the hesperiid is a specialist of lowland floodplains and was possibly formerly restricted to that habitat, but following European settlement has colonised non-natural areas through its ability to utilise introduced grasses.

The native larval food plants of *Taractrocera ina* have also not previously been recorded; all known food plants comprise introduced or naturalised grasses (Braby 2000). The introduced *Paspalum conjugatum* has been previously recorded as a larval food plant for the species from central Qld (De Baar 1979), but not from the NT. Atkins (1975) observed a female *Taractrocera* sp. lay an egg on Buffel Grass *Cenchrus ciliaris* in the Gogango Ranges, Queensland, and considered the species to be *T. anisomorpha* based on the presence of males in the immediate vicinity. Atkins (1991) subsequently recorded the native *Eulalia aurea* as the main food plant for this hesperiid in the Alice Springs area.

*Telicota colon* is the only grass-feeding member of the genus represented in the Kimberley and Top End, the other species, *T. angius* (Linnaeus, 1763), specialises on *Flagellaria indica* (*Flagellariaceae*) (Meyer 1996). The two other species of *Telicota* reported from the Northern Territory, *T. mesoptis* (Herrich-Schäffer, 1869), appear to be erroneous (Braby 2008a; M.F. Braby unpublished data).

The native larval food plant and natural breeding habitat *Cepheus angiades* ssp. ‘Top End’, which is endemic to the NT, has not previously been recorded, and there are few records outside Darwin. The natural habitat of this species comprises riparian evergreen monsoon vine-forest, but the species often breeds on cultivated palms in suburban areas of Darwin, an artificial habitat which it has no doubt invaded in recent decades following the extensive cultivation of palms in gardens and parklands since Tropical Cyclone Tracy. Dunn (1996) listed *Carpentaria acuminata* (1891) as a food plant for *Cepheus angiades*, but this was based on the presence of early stages of the eastern form utilising cultivars in the Mount Coot-tha Botanic Gardens, Brisbane.

Brady (1996) listed *Livistona mariae* as a food plant for *Cepheus trichopepla* based on observations of a single larva in the Mount Coot-tha Botanic Gardens, Brisbane;
however, the natural utilisation of this palm, which is restricted to the West McDonnell Ranges, has not been confirmed until now. Dunn (2009) also observed two mature larvae of this hesperid in shelters on a species of Livistona at Cahills Crossing, and this record almost certainly refers to L. benthamii.

Papilio aegaeus has become established on the mainland in north-eastern Arnhem Land only in the last decade since about 2000 (L. Wilson pers. comm.). Previously, P. aegaeus was restricted to Groote Eylandt and Marchinbar Island in the Wessel Islands where it breeds on Microclemum minutum (G.Forst.) Wight & Arn. (Rutaceae) (Fenner 1991). The usual larval food plants for Papilio fuscus in the Top End are M. minutum and Glycosmis trifoliata (Blume) Spreng. (Rutaceae) (Hall 1976; Meyer 1996). Cultivated Citrus sp. has previously been recorded for this species from the eastern Kimberley at Kununurra, WA (Common & Waterhouse 1981).

Meyer (1996) listed Senna leptoclada as a larval food plant of Catopsilia scylla in the Kununurra district of the eastern Kimberley, WA, but it has not previously been recorded as a food plant from the NT. Moss (2008) recently reviewed and updated the larval food plants for Eurema alitha in Queensland and noted that Galactia teniflora and G. muelleri are the preferred legumes compared with Glycine tabacina, the previously known food plant. The larval food plant in the Top End, however, has not previously been reported.

In the NT, Elodina padhsa appears to be parapatric with E. walkeri Butler, 1898, which occurs predominantly in the higher rainfall areas of the monsoon tropics where it specialises on Capparis sepitaria, whereas E. padhsa occurs mainly in the arid zone. The two species have a narrow range of overlap in the drier semi-arid inland areas of the monsoon tropics, but it is not known if they share the same larval food plants in this region. Available data suggests they may exploit different species of Capparis.

The usual food plant of Appias paulina in the Top End is Drypetes deplanchei (Brongn. & Griseb.) Merr. (Putranjivaceae) (Meyer 1996; Braby et al. 2010). The butterfly is known to utilise Capparis spp. in eastern Australia (Braby 2000) and elsewhere within its geographical range. The extent to which A. paulina uses Capparis in the NT is not known, but is possibly infrequent.

The usual larval food plant of Enploea alcatine in north-eastern Arnhem Land is Parasoula alboflavescens (Braby 2009), but it appears that occasionally larvae of E. coriina and E. sylvester also feed on this vine. The usual larval food plant of E. sylvester is Marsdenia geminata (Meyer 1997a), which is widespread across the Top End, but the extent to which E. coriina uses this vine is not known.

Grund and Hunt (2001) recorded the introduced weed Passiflora foetida as a larval food plant for Acraea andromacha in the northern Kimberley, WA, where females were observed to lay large batches of eggs on it in the Kalumburu area, but it has not previously been reported as a food plant from the Top End.

Hypochrysops apelles in the Top End is restricted to mangrove communities where the usual larval food plant near Darwin is Lumnitzera racemosa Willd. (Combretaceae) (Meyer 1996; Eastwood et al. 2008), which typically grows along the landward edge of the habitat. Despite the presence of many other species of mangroves, which are utilised as food plants elsewhere in the geographical range of H. apelles in eastern Queensland, these plants do not seem to be utilised in the Northern Territory. However, at Buffalo Creek in the early dry season when the species is particularly abundant, larvae of H. apelles were found to be associated mainly with L. racemosa and less frequently with Ceriops australis, whereas later in the dry season (May–September) larvae were found only on L. racemosa. These observations suggest that species of mangroves other than L. racemosa are exploited but only during periods of high population densities.

Reared adults of Ogyris oroetes from the eastern Kimberley and other material collected elsewhere in the Top End are similar to specimens from northern Queensland in that the males have narrow black margins and the upperside ground colour iridescent pale lilac, and are better placed with the nominate subspecies than with the 'arid form' proposed by Braby (2000). However, reared adults and material collected from central Australia are similar to specimens from southern Australia in that the males have a broad black apex of the fore wing. In many respects they resemble O. oroetes apiculata (Quick, 1972) described from Western Australia, except that the upperside ground colour is iridescent dark lilac or purple, rather than blue as in the type specimen. However, the holotype appears to be aberrant or not representative of populations elsewhere in southern Australia in which the males are typically dark lilac. Specimens from central Australia are therefore provisionally placed with O. oroetes apiculata rather than with the 'arid form' proposed by Braby (2000).

The usual food plant for Ogyris anamryllis in the central arid zone appears to be Amyema maidenii, which often parasitises Acacia aneura F.Muell. ex Benth. (see also Grund 2005), but several other species have now been recorded, viz: Amyema miquelii, Amyema bifurcata and Diplatia grandibractea. In addition, Amyema sanguinea has been recorded as a larval food plant in the Seherin Mural Crescent, WA (M.F. Braby & J.J. Armstrong unpublished data). The extent to which these four other mistletoes are utilised in central Australia is not well understood.

In the Northern Territory, the purple morph of female Ogyris zosine has only rarely been recorded, the blue phenotype being the predominate morph. Le Souëf (1971) listed the species from Elliott, and examination of his material (reared to adult in October 1969) in the ANIC revealed that two of the three female specimens collected are bright purple above. Elliott is located at similar latitude to the sites further west at Limbunya Station, both locations being situated in semi-arid areas at
the southern boundary of the monsoon tropics biome. More recently, Weir et al. (2011) recorded the purple morph from a population in suburban coastal Darwin in which five females (18%) from a sample of 28 pupae reared during the wet season (December) were of the purple phenotype. Weir et al. (2011) suggested that female polymorphism in this species may be influenced by environmental factors, such as humidity (with high humidity promoting the purple morph); however, the purple morphs from Limbunya were reared to adult during the late dry season (August to September) when conditions were comparatively cool and dry. These observations suggest that phenotypic variation in O. zosine may be under genetic control but the allele for the femal purple morph occurs in low frequency.

The usual food plant of Hypolycaena phorbas in the Top End is Clerodendrum floribundum R.Br. (Lamiaceae), but larvae have also been recorded on Stenolax australis R.Br. (Smilacaceae) (Meyer 1996). Elsewhere, the butterfly is associated with a wide range of plant families (Braby 2000), but rarely has it been recorded from mistletoes (Valentine & Johnson 1988).

The only larval food plant previously recorded for Candalides margarita in northern Australia is Decaisnina signata (Loranthaceae) (Samson & Wilson 1995; Braby 2008b); however, given that the geographical distribution of the butterfly is wider than that of this mistletoe, other food plants are expected to be utilised. Therefore, the new record for D. triflora as a host plant is not unexpected.

In an earlier publication (Braby 1995), I listed Cassytha pubescens R.Br. as the larval food plant for Candalides geminus in sandstone habitats on the Burra Range, Qld, but this record is incorrect and refers to Cassytha filiformis. In that same publication (Braby 1995) I listed Cassytha filiformis as the larval food plant for Candalides delospila from the Burra Range, Qld; however, this record is also in error and refers to C. capillaris. In another publication (Braby 1997), I listed Cassytha pubescens as a larval food plant for Candalides erinus based on records from several localities in northern Queensland; however, these records also refer to Cassytha filiformis. All of these determinations of Cassytha species were made prior to the monograph of Weber (2007), which explains the misidentifications. The usual food plant of Candalides erinus in the Northern Territory is Cassytha filiformis (M.F. Braby, unpublished data), but in the drier semi-arid areas of the Top End the butterfly was occasionally found breeding on Cassytha capillaris, which grows as a finer, less vigorous hemiparasitic vine on Triodia spp. and other grasses on sandstone or sandy soils. Cassytha delospila is endemic to the monsoon tropics (Braby 2008a) where it appears to be ecologically specialised on Cassytha capillaris, which likewise is restricted to northern Australia. Grund & Hunt (2001) recorded Cassytha capillaris as a larval food plant for both Candalides erinus and Candalides delospila in the Tanami Desert at the Northern Territory-Western Australian border.

Facultative ant associations are here recorded for the larvae of Candalides erinus and C. delospila, two species not previously known to associate with ants, and these records add to the growing list of ant-butterfly associations among the Australian Lycaenidae (Eastwood & Fraser 1999; Eastwood et al. 2008).

The usual food plants of Nesolycaena urumelia in the Top End are Boronia lanceolata F.Muell. in western Arnhem Land and areas closer to Darwin (Edwards 1980; Meyer 1996) and B. lanuginosa Endl. in subcoastal heathy woodland on sand in Gove Peninsula and Eleho Island (Braby 2000; M.F. Braby, unpublished data), but in the drier rocky areas of western Arnhem Land, the butterfly was found breeding on both B. laxa and B. lanceolata.

Meyer & Wilson (1995) listed Tecticornia indica (Wild) K.A.Sheph. & Paul G.Wilson as one of two larval food plants for Thelycinistes stilpnesis in the Top End based on observations near Darwin. Although this saltbush grew together with Tecticornia halocnemoides at the site near Palmerston, neither eggs nor larvae were present on Tecticornia indica.

The Mistletoe Day-moth Conocerus behri has not previously been recorded from the Northern Territory, although there is a small series of adults in the Museum and Art Gallery of the Northern Territory from Alice Springs collected by I. Arehillibald. This species is widespread and abundant in the temperate areas of south-eastern Australia, but it appears to be rare and seasonal in the Top End.

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REFERENCES


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**Dimorphothynnus** (Hymenoptera: Thynnidae: Rhagigasterini) newly recorded from the Northern Territory, Australia

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**ABSTRACT**

The predominantly southern Australian genus *Dimorphothynnus* Turner is newly recorded from the Northern Territory, and two new species, *D. fulvicms* and *D. nigricrus*, are described. Both species are relatively small in size, and only known from male individuals. A key to males of 15 species of *Dimorphothynnus* is given; that is, all but two of the known species. A key to females of eight species of *Dimorphothynnus* is given under the assumption of species fidelity of mates. Two new combinations are made—*Rhagigaster haemorrhoidalis* Guérin is transferred to *Rhytidothynnus*, and *R. obtusus* Smith is transferred to *Dimorphothynnus*.

**KEYWORDS:** Northern Australia, Thynnidae, Rhagigasterinini, *Dimorphothynnus*.

**INTRODUCTION**

The genus *Enteles* was erected by Westwood (1844). However, this name was preoccupied by the weevil genus *Enteles* Schoenherr (1833), and so in 1910 Turner proposed the replacement name *Dimorphothynnus*. This genus has never been revised and the most recent key to species is over a century old (Turner 1907).

Males are very similar to those of *Rhagigaster* Guérin, and the related genera *Rhytidothynnus* Brown and *Umbothynnus* Brown. The males of these genera are distinguished by a long, cylindrical metasoma with strong constrictions between the metasomal segments. However, those of *Dimorphothynnus* have the clypeus with an inverted V-shaped carina which is not sharply defined (Fig. 1), the propodeum has a transverse carina separating the dorsal and posterior surfaces, the epipygium is flat with the apical margin straight or almost so (Fig. 2), and the genitalia have the cuspsides long with the outer surface denticulate apically. Females however, are unique within the tribe in that metasomal tergite 2 is transversely multicarinlate. The latter character is more typical of the tribe Thynnini, where it occurs in most genera (Turner 1910).

As in all Thynninae the sexes of *Dimorphothynnus* are completely dimorphic; males are typical winged wasps, while females are wingless and strongly modified for burrowing in soil. This makes the association of sexes on morphological grounds impossible. Matching the sexes is further complicated by the prevalence of miscoupling (Brown 1993, 2001) in the subfamily. Mis coupling occurs when two different species couple, and thus there is no guarantee that pairs collected in copula are actually the same species. This makes it difficult to compare species if the types are of different gender, as discussed for the genus by Given (1959).

Nothing is known of the biology of *Dimorphothynnus*. As with most species of Australian Thynninae, they are presumed to be parasites of scarab larvae (Burrell 1935; Given 1953; Ridsdill Smith 1970), but this is based on fewer than 20 records. Adults have a preference for feeding on the nectar of myrtaceous flowers but they are attracted to other flowers as well as insect exudates. This biological information was summarised by Brown (2005).

There are now 15 described species of *Dimorphothynnus* including the two new species described here. Most are restricted to coastal regions of southern Australia except *D. barnardi* (Turner) and *D. integer* (Fabricius) from tropical Queensland as well as the two Northern Territory species described here.

![Fig. 1. Dimorphothynnus nigricrus, male: head. Scale line = 0.1 mm.](image-url)
Fig. 2. Dimorphothynnus fulvicnts, male: epipygium. Scale line = 0.05 mm.

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: Tl-7, metasomal tergites 1-7; Sl-8, metasomal stemites 1-8. Specimen repositories: ANIC, Australian National Insect Collection, CSIRO, Canberra; MNG, Museo Civicodi Storia Naturale di Genova, Genoa, Italy; NTM, Museum and Art Gallery of the Northern Territory (formerly Northern Territory Museum), Darwin; OUM, Oxford University Museum, Oxford, United Kingdom.

SYSTEMATICS

Dimorphothynnus Turner, 1910

Enteles Westwood, 1844. Gender masculine. Type species, by original designation, Enteles bicolor Westwood, 1844. Recent, King George’s Sound, Western Australia. Preoccupied by Enteles Schoenherr, 1833 (Insecta: Coleoptera).


As explained above, Dimorphothynnus is a replacement name for the preoccupied Enteles Westwood (1844). Dalla Torre (1897: 100) used Enteles as a subgenus of Thynnus and Ashmead (1899: 50, 52, 1903: 103) inadvertently misspelt Enteles as Entelus.

I have examined the holotype of Enteles bicolor Westwood, 1844, which is deposited in the OUM.

Dimorphothynnus fulvicnts sp. nov.

(Figs 2, 3, 5, 7)


Description of male. Body (Figs 2, 3) length 12 mm; fore wing 8 mm; hind wing 6 mm.

Clypeus with obscure inverted V-shaped carina which is flattened and not sharply defined, rugosely punctate between branches of carina, finely rugosely punctate laterally; frons with short, flat, with V-shaped carina above antennal insertion, transversely carinate below mid-ocellus, rugosely punctate; vertex and gena rugosely punctate.

Pronotum rugosely punctate; dorsum transversely rugose, anterior margin sharply carinate; mesoscutum coarsely transversely rugosely punctate; mesoscutellum coarsely rugosely punctate; metanotum rugosely punctate; propodeum closely punctate becoming transversely rugosely punctate on posterior surface, dorsal and posterior surfaces delineated by carina; mesopleuron coarsely rugosely punctate dorsally becoming finely punctate ventrally; fore coxae small, conical, closely punctate.

Metasoma with anterior groove on T2–5 and S2–5 scrobiculate; tergites closely and finely punctate, punctures sparser posterolaterally and coarser on T7; epipygium (Fig. 2) rounded apically with narrow semi-membranous apical margin; sternites closely punctate, less so on disc of S2–6; S1 weakly medially raised; hypopygium subparallel basally becoming sinusoidal distally without prominent lateral lobes or spines thence produced into long recurved apical spine.

Genitalia (Fig. 7): parameres (in profile) long and narrow, ventral margin evenly conavelly curved over most of length, dorsal margin subparallel over basal 2/3 then abruptly converging (and slightly concave) with ventral margin over most of length, apex narrowly rounded and slightly

Fig. 3. Dimorphothynnus fulvicnts, male: habitus. Scale line = 1 mm.
upturned; aedeagus (Figs 5,7) short, subtriangular medially
with highly modified valves sheathing the remainder of the
aedeagus basally; cuspsides large, subtriangular (viewed
dorsally), outer margin serrated with small basally directed
teeth, inner margin straight with flat vertical inner surface;
digitii small, inconspicuous and knob-like with erect cluster
of setae.

**Colour.** Black; tegulae and legs (except fore coxae)
orange; setae white, and forming posterior or ventral
bands on most metasomal segments especially laterally
and ventrally; wings hyaline, veins black becoming orange
basally.

**Distribution.** Only known from above the northern
bank of Adelaide River in the township of Adelaide River,
Northern Territory.

**Remarks.** This species, one of the smallest in the
genus, can be distinguished from all the other species of
*Dimorphothynnus* by the combination of orange legs,
hyaline wings and a black metasoma. The setal banding
on the metasoma suggests a relationship with *D. integer*
from northern Queensland, but *D. integer* has a distinctive
mesoscutellum which is almost impunctate and higher
posteriorly with a distinct flat posterior surface that is
delineated dorsally by a transverse carina. The new species
differs from *D. obtusus* by the presence of setal bands on
the metasoma. The shape of the sheathing valve at the base
of the aedeagus (Fig. 5) also distinguishes this species from
*D. nigricrus* (Fig. 6).

**Etymology.** This species name is derived from Latin
and is a reference to leg colour. It is intended as a noun in
apposition.

### *Dimorphothynnus nigricrus* sp. nov.

(Figs 1, 4, 6, 8)

**Material examined.** Holotype – NTM 1.6203, σ
campsite near Oenpelli reservoir, Northern Territory,
12°23’S, 133°06’E, uv light, 27 November 1996, G.R.
Brown & J. Purdie.

**Description of male.** Body (Fig. 4) length 14 mm; fore
wing 10 mm; hind wing 7 mm.

![Fig. 4. Dimorphothynnus nigricrus, male: habitus. Scale line = 1 mm.](image)

Figs 5, 6. *Dimorphothynnus* species, aedeagi (and apex of
basiparameres), dorsal view: 5, *Dimorphothynnus fulvicrus*;
6, *Dimorphothynnus nigricrus*. Scale line = 0.1 mm.

Figs 7, 8. *Dimorphothynnus* species, male genitalia, dorsal view:
7, *Dimorphothynnus fulvicrus*; 8, *Dimorphothynnus nigricrus*. Scale
line = 0.1 mm.

**Clypeus** (Fig. 1) with obscure inverted V-shaped
carina which is flattened and not sharply defined, rugosely
punctate between branches of carina, finely rugosely
punctate laterally; frons with short, flat, V-shaped carina
above antennal insertions, transversely carinate below
mid ocellus, rugosely punctate; vertex and gena closely to
rugosely punctate.

**Pronotum** rugosely punctate, dorsum transversely rugose,
anterior margin sharply carinate; mesoscutum coarsely
transversely rugosely punctate; mesoscutellum coarsely and
closely punctate; metanotum rugosely punctate; propodeum
closely punctate, dorsal and posterior surfaces delineated
by obscure carina; mesopleuron coarsely rugosely punctate
dorsally becoming finely and closely punctate ventrally; fore
coxae small, conical, closely punctate.

**Metasoma** with anterior groove on T2–5 and S2–5
scrobiculate; tergites closely punctate, punctures sparser
posterolaterally on T2–5 and coarser on T7; epipygium
rounded apically without narrow semi-membranous apical
margin; sternites closely and deeply punctate; S1 weakly
medially raised; hypopygium subparallel basally becoming
sinuous distally without prominent lateral lobes or spines
thence produced into long recurved apical spine.
Genitalia (Fig. 8) with parameres (in profile) long and narrow, margins almost straight, ventral margin slightly sinuosoidal, dorsal margin converging with ventral over most of length, apex narrowly rounded; aedeagus (Figs 6, 8) short, subtrigonal medially with highly modified valves sheathing remainder of the aedeagus basally; cuspides large, subtriangular (viewed dorsally) with ventral lobe arising from lateral margin, outer margin (viewed dorsally) serrated with small basally directed teeth, inner margin straight with flat vertical inner surface; digiti apparently absent.

Colour. Black; setae white, and forming posterior or ventral bands on most metasomal segments especially laterally and ventrally; wings hyaline, veins black.

Distribution. Dimorphothynnus nigricrus is only known from the vicinity of Oenpelli, Northern Territory, from a creek flat downstream from Oenpelli reservoir.

Remarks. This species is similar to D. fulvicrus in that both are smaller than most other species in the genus and have the tergites uniformly and closely punctate, but D. fulvicrus has orange legs rather than black legs. It is also distinguished from D. integer and D. obtusus as discussed for D. fulvicrus above.

Etymology. This species name is derived from Latin and is a reference to leg colour. It is intended as a noun in apposition.

KEYS TO THE SPECIES OF DIMORPHOTHYNNUS

The majority of type specimens within Dimorphothynnus (as well as the subfamily) are male. However, two species, D. bicolor and D. fimbriatus (Smith), were described from the female only. Unfortunately both of these are a part of a complex of species that also includes D. apicalis (Smith), a species misidentified as D. haemorrhoidalis (Guérin), D. haemorrhoidalis (Guérin) comb. nov. and as discussed above. D. fimbriatus (Smith), were described from D. bicolor (as well as the subfamily) are male. However, two species, D. fimbriatus (Smith) comb. nov. and D. obtusus (Smith) comb. nov. are considered to be a species of Dimorphothynnus by Turner (1907), and is therefore not included in the key.

Male (winged)

1 Wings fulvous; legs black [only known from the types from Geraldton, WA] ............ D. destructor (Smith)
   - Wings hyaline, fuscous or black (although veins may be orange); legs black or orange .................. 2

2(1) Clypeus with sharply defined inverted Y-shaped carina, branches enclosing polished triangular area [Qld] ................................................. D. barnardi (Turner)
   - Clypeus with inverted V-shaped carina, carina not sharply defined, not enclosing a large or polished triangular area .................................................. 3

3(2) Metasoma black (if lightly testaceous as in D. testaceipes, then wings black) .......................... 4
   - Metasoma at least partially ferruginous .................. 10

4(3) Wings hyaline to weakly infuscate .............. 5
   - Wings black ........................................ 8

5(4) Mesoscutellum almost impunctate, vertically truncate posteriorly with carina sharply delineating dorsal and posterior surfaces [Qld] ....... D. integer (Fabricius)
   - Mesoscutellum punctate to rugosely punctate, without distinct posterior surface clearly delineated from dorsal surfaces ............................................. 6

6(5) Tergites closely and uniformly punctate, posterior margin of tergites (weakly so medially in D. fulvicrus and D. nigricrus) and sternites and ventral margins of pleuries with dense fringe of white setae .............. 7
   - Tergites punctate to closely punctate, punctures variable in size and spacing, tergites, sternites and pleuries not fringed with white setae [NSW, Vic, SA] .................. D. obtusus (Smith) comb. nov.

7(8) Legs orange [NT] ....................... D. fulvicrus sp. nov.
   - Legs brown to black [NT] ...... D. nigricrus sp. nov.
Thynnine wasps of the genus *Dimorphothynnus*

8(4) Epipygium punctuate, with punctures longitudinally aligned; legs dark; mesoscutellum truncate posteriorly; mesopleura deeply and rugosely punctate [Qld, NSW, Vic, SA] ........................................... *D. trunciscutus* Turner
- Epipygium longitudinally multicarinate or irregularly longitudinally multistriate; legs orange; mesoscutellum narrowly rounded posteriorly; mesopleura punctate ................................................... 9

9(8) Metasoma lightly testaceous [NSW, Vic, SA] ........................................... *D. testaceipes* (Turner)
- Metasoma black [WA] ........................................... *D. bicolor* (Westwood)

10(3) Metasoma entirely ferruginous [Qld, NSW] ........................................... *D. dimidiatus* (Smith)
- Metasoma with only apical 2 segments ferruginous ........................................... 11

11(10) Wings dark; pronotum transversely carinate [Qld] ........................................... *D. conjugatus* (Turner)
- Wings hyaline; pronotum punctate to rugose ........................................... 12

12(11) Mesopleurac red [WA], ........................................... *D. simillimus* (Smith)
- Mesopleurae black ........................................... 13

13(12) Fore coxae with deep, large, longitudinal, smooth and polished cavity on the inner ventral surface that is delineated by a sharp carina [WA] ........................................... *D. bicolor* (Westwood)
- Fore coxae if depressed or partially concave, not deeply so and not margined by a carina ........................................... 14

14(13) Prosternum (and adjacent areas of fore coxae) concave, concavity polished and sparsely punctate [WA] ........................................... *D. fimбриatus* (Smith)
- Prosternum not concave, punctuation more uniform [WA] ........................................... *D. apicalis* (Smith)

**Female (wingless)**

1 Pygidium notched ........................................... *D. apicalis* (Smith)
- Pygidium notched ........................................... 2

2(1) Dorsum of T1 finely transversely carinate, not punctate; head medially depressed ........................................... *D. integer* (Fabricius)
- T1 not transversely carinate; head not medially depressed ........................................... 3

3(2) Posterior angles of head weakly excavate ........................................... *D. bicolor* (Westwood)
- Posterior angles of head not excavate ........................................... 4

4(3) Apex of metasoma ferruginous ........................................... *D. dimidiatus* (Smith)
- Metasoma concolorous ........................................... 5

5(4) Head and body dark brown or black ........................................... 6
- Head and metasoma black, mesosoma ferruginous ........................................... 7

6(5) T3 with transverse carinae mostly restricted to anterior half of sclerite ........................................... *D. obtusus* (Smith) comb. nov.
- T3 with transverse carinae more evenly distributed on sclerite ........................................... *D. morio* (Westwood)

7(5) T1 transversely carinate (in addition to apical margin and weak preapical carina); apex of metasoma with a long brush of setae lateral to pygidium ........................................... *D. simillimus* (Smith)
- T1 not transversely carinate (other than apical margin and weak preapical carina); apex of metasoma without long brush of setae ........................................... *D. siamillius* (Smith)

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**REFERENCES**


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Periclimenaeus pulitzerfinali sp. nov. (Crustacea: Decapoda: Palaemonidae), a new pontoniine shrimp from East Africa

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ABSTRACT

A small pontoniine shrimp, Periclimenaeus pulitzerfinali, from Shelly Beach, Mombasa, Kenya, is described as new and illustrated. An appendix presents a complete list of Periclimenaeus species recorded from East Africa (Kenya, Zanzibar, Tanganyika).

Keywords: Periclimenaeus pulitzerfinali sp. nov., Crustacea, Decapoda, Pontoniinae, Mombasa, Kenya, sponge associate.

INTRODUCTION

The genus Periclimenaeus Borradaile, 1915 is the second most speciose genus of the subfamily Pontoniinae with at present 70 described species – 55 from the Indo-west Pacific region, 4 from the eastern Pacific and 11 from the Atlantic region. The various species are associated with sponge or ascidian hosts, although the hosts of a number of species have not yet been reported or identified. The present report describes and illustrates a further new species from an East African sponge host, increasing the number of Indo-west Pacific species known to 56. The single specimen is deposited in the collection of the Museum and Art Gallery of the Northern Territory, Darwin.

The names Tanganyika and Zanzibar are used in their geographical sense only, as the two entities are now politically united as Tanzania.

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

SYSTEMATICS

Family Palaemonidae Rafinesque, 1815
Subfamily Pontoniinae Kingsley, 1879
Genus Periclimenaeus Borradaile, 1915


Periclimenaeus pulitzerfinali sp. nov. (Figs 1–5)

Material examined. Holotype – NTM Cr. 17287 (previously Ajb # 2098), ovigerous ♀, CL 5.2 mm, reef front off Shelly Beach, Mombasa, Kenya, SCUBA, 16 m, coll. J. Wood, 23 January 1974.

Diagnosis. Rostral dentition 7/0, without supraorbital spines or tubercles, first abdominal segment tergite with small narrow anterior median lobe, scaphocerite tooth not exceeding lamella, first pereiopod slender, fingers stout, semi-spatulate, half palm length, major second pereiopod with feeble molar process, palm and merus ventrally spinulate, minor second pereiopod dactyl elongate, extending well beyond fixed finger, cutting edge convex, entire, tip strongly bifid, fixed finger short, cutting edge grooved, edges entire, third pereiopod dactyl robust, biunguiculate, ventral corpus minutely denticulate, telson with dorsal spines well developed, at 0.15 and 0.53 of telson length, exopod of uropod with distolateral tooth and spine only.

Description. Female holotype, a small-sized pontoniine shrimp of subcylindrical, slightly compressed body form, complete with both second pereiopods.

Rostrum (Fig. 1A) slender, slightly depressed, about 0.33 of CL, reaching to about distal margin of proximal segment of antennular peduncle, with 7 slender acute teeth extending over whole of rostral length, fifth tooth longest, with numerous long setae interspersed, tip acute, ventral margin feebly convex, unarmed, non-setose.

Carapace (Fig. 1B,C) slightly compressed, glabrous, without epigastric, supraorbital or hepatic spines, with feeble postorbital ‘shoulders’, antennal spine well developed,
submarginal, inferior orbital angle small rounded, curved medially, anterolateral margin of brachioistegite feebly produced, rounded.

Abdomen glabrous, first segment tergite with small anterior median lobe (Fig. 1H), sixth segment (Fig. 1L) length about 1.5 times length of fifth, depressed, about 1.2 times longer than anterior width, posterolateral angle small, rounded, with small acute tooth, postero-ventral angle large, broadly acute; first to fourth pleura enlarged, rounded, fifth postero-ventrally subrectangular (Fig. 1I), margin feebly setose.

Telson (Fig. 1K) about 1.8 times sixth segment length, 0.5 of CL, 2.0 times longer than anterior width, lateral margins feebly convex, posteriorly convergent, dorsal telson spines about 0.10 of telson length, at 0.15 and 0.53 of telson length, anterior pair slightly longer than posterior. Posterolateral margin (Fig. 1L) broadly convex without median point, 0.25 of anterior telson length, lateral posterior spines thin, about 0.08 of telson length, 2.5 times lateral spine length, submedian spines slightly longer and more slender than intermediate spines, densely setulose.

Ophthalmic somite (Fig. 1F) anteriorly with median vertical carina.

Eye (Fig. 1G) with large globular cornea, diameter about 0.1 of CL, well-pigmented, without obvious accessory
pigment spot, stalk short, about as broad as long, 0.8 of corneal diameter, length about 0.8 of corneal diameter.

Antennule (Fig. 1D) of normal form, damaged on right, proximal peduncular segment about twice as long as central width, distally tapering, anterolateral margin with well-developed acute tooth on left, abnormal, rounded on right, lateral margin expanded proximally, rounded, medial margin straight, thickened, sparsely setose, with well-developed ventromedial tooth at about half length, stylocerite large, broadly phylliform, distally acute, sparsely setose laterally, stoteocyst normal with granular statolith; intermediate segment short, about 0.16 of proximal segment length, longer than wide, distal segment similar, upper flagellum biramous, right abnormal, 2 proximal segments fused, short ramus with single segment, about 4 groups of long aesthetascs, left with 7 segments fused, shorter ramus with 2 segments, with 5 groups of aesthetascs, longer ramus slender, with 10 segments, lower flagellum similar, slender with 19+ segments.

Antenna (Fig. 1E) of normal form, basicerite short, with acute tooth laterally, carpoecerite subcylindrical, about 3.0 times longer than width, reaching to about 0.75 of seaphoecerite length, few short setae medially; seaphoecerite 2.5 times longer than wide, greatest width distally at about 0.5 of length, anterior margin bluntly angular, lateral margin straight, with well-developed distal tooth at about 0.85 of seaphoecerite length, reaching level of distal margin of lamella.

Thoracic sternites with third and fourth broad, unarmed, posterior sternites narrow and unarmed.

Mouthparts of normal *Periclimenaeus* morphology.

Mandible (Fig. 2A) with corpus stout, without palp; incisor process (Fig. 5A) slender, tapering, transversely truncate distally, with 4 slender subequal acute teeth, medial margin entire; molar process (Fig. 5BC) robust, subcylindrical, obliquely truncate distally, with 4 stout marginal teeth, with 2 small brushes of short simple setae.

Maxillula (Fig. 2B) with feebly bilobed palp (Fig. 5D), upper lobe short, glabrous, lower lobe stouter, with small simple spinule; upper lacinia moderately broad, dorsal margin strongly convex, distal margin (Fig. 5E) with 10 short robust spines, feebly denticulate on ventral surface (Fig. 5F), lateral surface with several oblique rows of slender spiniform setae; lower lacinia short, subcylindrical, distally rounded, with numerous long terminal setae.

Maxilla (Fig. 2C) with simple tapering palp, proximal lateral margin with several short plumose setae, distally rounded, shorter than basal endite, basal endite bilobed, dorsal lobe expanded with dense simple setae, distolateral margin with several transverse rows of simple setae, ventral lobe smaller and shorter than dorsal lobe, with numerous simple setae distally; coxal endite obsolescent,
medial margin slightly produced, convex, non-setose; scaphognathite well developed, narrow, about 3.4 times longer than central width, anterior lobe narrow, rounded, medial margin slightly excavate, posterior lobe well developed, one third of scaphocerite length.

First maxilliped (Fig. 2D) with elongate flattened subcylindrical tapering palp, about 5.0 times longer than central width, reaching anterior margin of basal endite, with single preterminal plumose seta medially; basal endite fused with coxal endite, combined medial margin straight, distal margin produced, rounded, margins with numerous long spiniform setae; exopod with normal flagellum with 4 plumose terminal setae, some short plumose setae long spiniform setae; endopod, dactylar segment narrow, about 3.0 times longer than central width, basal region slightly expanded, medially serrulate spines, propodal segment normal, distomedial to carpus, merus and ischiobasis without special features; coxa medially produced; exopod normally developed with 4 plumose terminal setae; epipod lost in dissection.

Second maxilliped (Fig. 2E) with normally developed endopod, dactylar segment narrow, about 3.0 times longer than central depth, medial margin straight, with numerous serrulate spines, propodal segment normal, distomedial margin not produced, with several robust spines and shorter spiniform setae, carpus, merus and ischiobasis without special features; coxa medially produced; exopod normally developed with 4 plumose terminal setae; epipod lost in dissection, small.

Third maxilliped (Fig. 2F) with endopod reaching to about middle of carapocerite, ischiomerus fully fused to basis, point of junction on medial margin indicated by small marginal swelling, combined segment about 4.6 times longer than central width, basal region slightly expanded, medially rounded, without marginal setae, with submarginal row of 17 short plumose setae (Fig. 5H), distolateral angle (Fig. 5G) with 2 short simple submarginal spines, ischiomerial portion with numerous long slender spiniform marginal setae; penultimate segment about 0.32 of antepenultimate segment length, 3.0 times longer than wide, with numerous long simple setae medially; terminal segment about 0.75 of penultimate segment length, tapering distally, without strong terminal spine, with several transverse rows of spiniform setae medially; exopod normally developed with 4 plumose terminal setae, several short plumose marginal setae distolaterally, coxa not medially produced, with low rounded lateral plate, without arthrobranch.

First pereiopods (Fig. 3A) moderately slender, exceeding carapocerite by distal fifth of merus, chela (Fig. 3B,C) with palm subcylindrical, moderately compressed, 2.5 times longer than deep, dorsal and ventral margins feebly tuberculate, fingers (Fig. 3D) 0.43 of palm length, robust, subspatulate, with groups of short stiff setae, dactylus 2.2 times longer than basal width, dorsal margin convex, tip hooked, with stout medial tooth flanked by 2 smaller teeth, cutting edges robust, entire; carpus 1.6 of chela length, 5.5 times longer than distal width, tapering proximally, dorsal and ventral margins feebly tuberculate; merus subequal to carpus length, 5.9 times longer than maximal width, tapering slightly distally; ischiuim about 0.62 of merus length; basis without special featured, and coxa with small setose distoventral process.

Second pereiopods grossly unequal, dissimilar. Major second pereiopod (Fig. 4A) with massive chela, about 1.33 times CL, chela (Fig. 4B) with palm minutely tuberculate (Fig. 5I), oval in section, twice as long as deep, tapering slightly distally, dactylus (Fig. 4C,D) with tip missing, about 0.42 of palm length, strongly compressed, 2.5 times longer than depth, proximal cutting edge with low elongated molar process, with posterior end projecting, distal cutting edge concave, entire; fixed finger about 1.1 times longer than proximal depth, robust, with shallow fossa proximally, distally grooved, medial margin with acute tooth proximally, lateral margin with rounded setose process, tip feebly hooked, distinctly bidentate, preterminal tooth rounded, terminal tooth acute; carpus about 0.33 of palm length, 1.3 times longer than wide, tapering strongly proximally, distally slightly excavate, unarmed; merus (Fig. 4E) 0.37 of palm length, 1.6 times longer than broad, slightly expanded centrally, ventral margin tuberculate (Fig. 5J); ischiuim (Fig. 4E) subequal to meral length, distally broadened, about 2.8 times longer than distal width, ventral margin strongly tuberculate (Fig. 5K); basis and coxa robust, without special features.

Minor second pereiopod (Fig. 4F) with chela about 0.6 of CL, 0.53 of major chela length, palm oval in section, dorsally convex, smooth, ventrally straight, finely tuberculate, 2.2 times longer than deep, tapering slightly distally, projecting slightly posteriorly, sparsely setose distoventrally; dactylus (Fig. 4G,H) extending well beyond tip of fixed finger (Fig. 4G), 2.12 times longer than deep, strongly compressed, dorsal margin strongly convex, cutting edge convex, sharp, entire, tip robust, feebly hooked, distally bidentate; fixed finger short, stout, about as long as deep proximally, with small acute tip separated by small notch from cutting edge, cutting edge grooved, edges concave, entire; carpus short, stout, about 0.25 of palm length, distally expanded, tapering proximally, unarmed; merus about 0.33 of palm length, 1.5 times longer than deep, with ventral margin with numerous acute tubercles; ischiuim about 0.38 of palm length, twice as long as wide, tapering proximally, ventral margin with numerous submucate tubercles; basis and coxa robust, without special features.

Ambulatory pereiopods robust; third pereiopod (Fig. 3E-G) reaching to end of scaphocerite, with dactyl (Fig. 3H) 0.29 of propod length, unguis distinctly demarcated, 2.5 times longer than basal width, curved, unarmed ventrally, corpus compressed, about 1.6 times longer than basal width, tapering strongly distally, dorsal margin moderately convex, ventral margin with acute distal slightly preterminal antcroverted accessory tooth, ventral margin feebly convex, with 4 minute denticles, with basal process; propod about 0.25 of CL, 3.6 times longer than propod length, tapering slightly distally, distoventral angle armed with 2 stout spines, slightly unequal, longer spine subequal to dorsal corpus length, ventral margin with 4 spaced spines, lengths decreasing slightly proximally; carpus about 0.7 of propod length, 2.5 times longer than
Periclimenaeus pulitzerfinali sp. nov., from Kenya

Fig. 3. *Periclimenaeus pulitzerfinali* sp. nov., holotype female, Mombasa, Kenya, NTM Cr. 17287: A, first pereiopod; B, same, chela; C, same, oblique; D, same, fingers; E, third pereiopod; F, same, propod and dactyl; G, same, distal propod and dactyl; H, same, dactyl; I, same, merus.

Central depth, tapering proximally, unarmed; merus (Fig. 3I) 1.1 times propod length, 3.1 times longer than central depth, ventral margin with numerous subacute tubercles (Fig. 5L); ischium 0.9 of propod length, 0.8 of meral length, ventral margin with numerous subacute tubercles, basis and coxa robust, without special features.

Fourth pereiopod similar to third, subequal in length, more slender, about 4.4 times third propod length, 4.5 times longer than proximal width, tapering slightly distally, with similar spination, spines slightly smaller.

Fifth pereiopod similar, propod 1.2 times third propod length, 6.0 times longer than proximal width, with single distoventral spine only, several distal transverse rows of cleaning setae; fourth and fifth dactyls similar to third, but no ventral denticles discernible.

Uropod (Fig. 1M) with protopodite posterolaterally acute; exopod about 0.8 of telson length, 2.0 times longer than broad, lateral margin slightly convex, with numerous submarginal ventral setae, with small acute tooth distally, with adjacent straight spine, about 2.0 times longer than tooth, diaeresis distinct; endopod subequal to exopod, 2.6 times longer than broad.

Measurements (mm). Female holotype, postorbital carapace length, 5.2; carapace and rostrum, 6.8; total body

117
Fig. 4. *Periclimenaeus pulitzerfinali* sp. nov., holotype female, Mombasa, Kenya, NTM Cr 17287: A, major second pereiopod; B, same, chela; C, same, fingers, medial; D, same, lateral; E, same, merus and ischium; F, minor second pereiopod; G, same, fingers; H, same, dactylus.

length (approx.), 17.0; major second pereiopod chela, 6.7; minor second pereiopod chela, 5.7.

**Colouration.** Uniform bright yellow.

**Host.** *Spirastrella* sp., undescribed species [Porifera: Spirastrellidae], det. G. Pulitzer-Finali, 7 January 1975.

**Etymology.** Named in honour of Gustavo Pulitzer-Finali (Trieste, October 1915 – Rapallo, 21 November 2006), in recognition of his studies on the systematics of the Porifera, of which he described 260 species (pers. comm. J.N.A. Hooper), and his assistance in the identification of sponge shrimp hosts from East African waters.

**Systematic position.** *Periclimenaeus pulitzerfinali* is a typical member of its genus without major morphological differences from other species of the genus, while still being readily distinguishable from all the other species.

Of the 54 Indo-west Pacific species of *Periclimenaeus*, only six have the carapace without supraorbital tubercles, the first pereiopod with fingers of the chela simple, cutting edges entire, the minor second pereiopod dactyl with a simple cutting edge, the third ambulatory pereiopod dactyl biunguiculate with the unguis unarmed, the ventral corpus denticulate and lacking a basal process, and the exopod of the uropod with a dis talateral tooth and a mobile spine only. Of these six species that fully meet this character list, all can be distinguished from *P. pulitzerfinali* as follows:

*Periclimenaeus garthi* Bruce, 1976 scaphocerite with distolateral tooth small, falling far short of distal lamella margin; first pereiopod fingers as long as palm, tips simple; third pereiopod dactyl with stout recurved access tooth.

*Periclimenaeus hebedactylus* Bruce, 1970 second pereiopod fingers distally truncate, lateral posterior telson spines preterminal.

*Periclimenaeus lobiferus* Bruce, 1978 with large antero-median dorsal lobe on first abdominal tergite, dactyl of first pereiopod with conspicuous dorsal tuft of long setae.

*Periclimenaeus nielbrucei* Bruce, 2006 rostral denticulation 11/0, with distal teeth divergent, corpus of third ambulatory dactyl with robust denticules.
Periclimenaeus pulitzerfinali sp. nov., from Kenya

Fig. 5. *Periclimenaeus pulitzerfinali* sp. nov., holotype female, Mombasa, Kenya, NTM Cr. 17287. Mouthpart details: A, incisor process; B, molar process, dorsal; C, same, ventral; D, maxillula, palp; E, same, distal upper lacinia; F, same, marginal spine; G, third maxilliped, distolateral ischiomerus; H, same, proximomedial ischiomerus. Ventral pereiopodal tuberculations; I, major second pereiopod, palm; J, same, merus; K, same, ischium; L, third pereiopod, merus.

*Periclimenaeus solitus* Bruce & Coombes, 1995 rostral dentition 3/0; scaphocerite with distolateral tooth small, exceeding lamella margin, first pereiopod fingers more that half palm length, palm and carpus non-tuberculate, minor second pereiopod fixed finger simple, third pereiopod merus ventrally non-tuberculate.

*Periclimenaeus usitatus* Bruce, 1969 with ventral rostral tooth, dentition 5/1, major second pereiopod with fixed finger grooved, edges of grooves covered with minute acute tubercles, corpus of third ambulatory dactyl with corpus without ventral denticulations.

*Periclimenaeus pulitzerfinali* most closely resembles *P. solitus* Bruce & Coombes, 1995 from the Cobourg Peninsula, Northern Territory, Australia, and known only from the holotype specimen. It differs in having a rostral dentition of 7/0 (versus 3/0), the scaphocerite with a strong distolateral tooth reaching to the distal margin of the lamella (versus a small tooth, slightly exceeding the lamella), the first pereiopod with the palm and propod minutely tuberculate (versus non-tuberculate), the major second pereiopod with the fixed finger bidentate (versus simple), third pereiopod propod ventrally minutely tuberculate (versus non-tuberculate), distoventral spines simple (versus minutely dentate), dactyl with unguis about 0.5 of corpus length (versus 0.8), corpus with 4 acute ventral denticles, (versus 3 more robust small teeth), distolateral tooth more acute, slender, 0.28 of unguis length (versus more robust, 0.15 of unguis length), dorsal telson spines shorter, 0.1 of telson length (versus 0.18).

Remarks. Of the 54 presently known Indo-west Pacific species of *Periclimenaeus*, 32 are known only from the type material. Of these, 23 are known only from the holotype specimen only. *Periclimenaeus* species generally are found in small sponges or ascidians as heterosexual pairs. The males, being smaller than the females, seem to be frequently overlooked. Five species are known from heterosexual pairs only, and more numerous specimens may occur in larger hosts. *Periclimenaeus echinimanus* Đuriš, et al., 2011 is unusual in that the type material consists of 16 specimens, from six sponge hosts. Where numerous specimens of a species are available they show a high degree of morphological consistency in small details. Consequently an unidentified specimen can be readily distinguished on the basis of its morphology. Indeed, the author has a 'cheat-sheet' atlas of the third pereiopod dactyls of the Indo-west Pacific species of *Periclimenaeus* which generally
A. J. Bruce

allows, with occasional exceptions, the almost immediate identification of a specimen so that only confirmation by comparison with the original or more modern description is required.

The number of *Periclimenaeus* species known from the waters of Kenya, Zanzibar and Tanganyika is now 19 and a list is appended below, with their original references and other major descriptive reports. This region includes the type localities for six species and five species are not known from elsewhere in the Indo-West Pacific region.

**LIST OF CENTRAL EAST AFRICAN PERICLIMENAEUS SPECIES (KENYA, ZANZIBAR, TANGANYIKA)**

*Periclimenaeus arborescens* (Calman, 1939)
*Periclimenes (Periclimenaeus) arborescens* Calman, 1939: 210–211, fig. 4.

*Periclimenaeus arborescens.* — Holthuis 1952: 13, 130.
Kenya: Mombasa (Bruce 1976b); North Kenya Banks, 82 m, Wasin Island, Wasin Channel; Mombasa, Old Port (Bruce 1976c). Zanzibar: Prison Island; Bawi Island; Chawamba Reef (Bruce 1976c). Tanganyika: Kunduchi (Bruce 1976c). Also known from Oman to Fijian Islands.

*Periclimenaeus dimitauris* Bruce, 1970
*Periclimenaeus dimitauris* Bruce, 1970: 310–312; 2005: 395, 397, fig. 5.

Kenya: Mombasa, Ras Iwatine (Bruce 1976b). Also known from type locality, Heron Island, Great Barrier Reef, Australia.

*Periclimenaeus bidens* Bruce, 1970
Kenya: Mombasa, Shelly Beach (Bruce 1976b). Zanzibar: Bawi Island, type locality (Bruce 1970); Zanzibar Harbour; Mkokotoni Harbour (Bruce 1976c). Also known from Papua New Guinea, New Caledonia and Australia.

*Periclimenaeus diabolus* Bruce, 1970
Zanzibar: Mangapwani, in *Plakinastrella ceylonica* (Dendy, 1905) (Bruce 1976c). Also known from Israel, Jibuti, Madagascar, Vietnam and Queensland.

*Periclimenaeus favatus* Bruce, 2006
*Periclimenaeus favatus* Bruce, 2006a: 33–43, figs 1–6. Zanzibar: Fungu Fawatu, Unguja, type locality (Bruce 2006a). Known from type locality only.

*Periclimenaeus hebedactylus* Bruce, 1970
*Periclimenaeus hebedactylus* Bruce, 1970: 308–310. Zanzibar: Makunduchi, 91.5 m, type locality (Bruce, 1970). Known from type locality only.

*Periclimenaeus hecate* (Nobili, 1904)
*Coralliocaris hecate* Nobili, 1904: 232; 1906: 58, pl. 3, fig. 2.


*Periclimenaeus leptodactylus* Fujino & Miyake, 1968
Zanzibar: Grave Island, Chumbe Island, Shangani (Bruce 1976c). Kenya: Wasin Channel (Bruce 1976c). Otherwise known only from the type locality in Amami Islands, Japan.

*Periclimenaeus minutus* Holthuis, 1952
*Periclimenaeus minutus* Holthuis, 1952: 134–137, figs. 57–59; Bruce 2010a: 9, fig. 6F–L.
Zanzibar: Mbweni; Fuwatu Reef (Bruce 1976c). Type locality, Banda Island, Indonesia. Also reported from Somalia, Philippines and Western Australia.

*Periclimenaeus aff. minutus* Holthuis, 1952
*Periclimenaeus minutus.* — Bruce 2010a: 9 (not *P. minutus* Holthuis, 1952).
Kenya: Shimoni, Ras Iwatine, Banburi, Jadini, Mombasa Island (Bruce 1976c). Type locality, Auau Channel, Hawaiian Islands, 51–79 m (Rathbun 1906). Also reported from Mariana Islands.

*Periclimenaeus rhodope* (Nobili, 1904)
*Coralliocaris (Onycocaris) rhodope* Nobili, 1904; 1906: 61, pl. 2, fig. 8.

*Periclimenaeus rhodope.* — Holthuis 1952: 125–129, figs 54, 55, 55bis; Bruce 1974: 1558–1562, figs 1–2, 3A,B, 7A,B.
Zanzibar: Chwaka, Makunduchi, Chumbe Island (Bruce 1976c). Tanganyika: Kunduchi (Bruce 1976c). Kenya: Shiminoni, Ras Iwatine, Banburi, Jadini, Mombasa Island (Bruce 1976c). Also known from Somalia, Seychelle Islands, and Queensland, possibly from China (South China Sea).

*Periclimenaeus robustus* Borradaile, 1915
Kenya: Mombasa, Ras Iwatine, 119-141m (Bruce 1976c). Also known from type locality, Seychelle Islands.

*Periclimenaeus trispinosus* Bruce, 1969
Zanzibar: Mkokotoni, type locality (Bruce 1969). Known from type locality only.
Periclimenaeus tuamotae Bruce, 1969
Kenya: Mombasa Island, Fort Jesus; Wasin Island (Bruce 1976b). Tanganyika: Kunduchi (?) (Bruce 1969). Type locality: Mururoa Atoll, Tuamotu Islands. Also reported Zanzibar: Off Unguja: 7°46′48″S. 39°42′36″E, 20 m, type locality (Bruce 1969). Known from type locality only. Otherwise reported only from Queensland, Australia.

Periclimenaeus uropodialis Barnard, 1958
Periclimenaeus uropodialis Barnard, 1958: 18–20, fig. 6. Kenyaa: Mombasa, Old Port; Wasin Channel (Bruce 1976c), Zanzibar: Mkokotoni (Bruce 1976b). Tanganyika: Mafia Island (Bruce 1976c). Type locality: Delagoa Bay, Mozambique. Also reported from Queensland, Australia.

Periclimenaeus usitatus Bruce, 1969

Periclimenaeus zanzibaricus Bruce, 1969

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A new species and new records of *Oncinopus* (Crustacea: Brachyura: Inachidae) from northern Australia

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**ABSTRACT**

A new species of the Indo-west Pacific majoid spider crab genus *Oncinopus* is described from Darwin Harbour (Northern Territory), as well as the North West Shelf (Western Australia) and the Gulf of Carpentaria (Queensland). It can be distinguished from other species by differences in the morphology of the male first gonopod, rostral shape, the setation of the dactyl of the first pereiopod, and the length of the last two pairs of pereiopods. *Oncinopus angustifrons* Takeda & Miyake, 1969 is recorded from the North West Shelf, and is the first record of this species from Australia. *Oncinopus aranea* (De Haan, 1839) is recorded from northwestern Australia for the first time. Five species of *Oncinopus* are now recognised, with four of these now known from Australia. A key to distinguish them is provided.

Keywords: Inachidae, northern Australia, North West Shelf, Darwin, taxonomy, new species, new records.

**INTRODUCTION**

Species in the majoid genera *Oncinopus* and *Achaeus* (family Inachidae) are distinctive in having the dactyli and propodi of their fourth and fifth pereiopods subchelate, very much like the 'carrying crabs' of the families Dorippidae and Dromiidae. Unlike those crabs however, inachids do not use these structures for carrying objects over their back, but for clinging tightly to the substrate in areas with strong currents, with their carapaces, chelipeds and other legs extended in the current to gather food (Ng et al. 2008). In particular, the first two pairs of ambulatory legs of these genera have remarkably long comb-like spines used to trap food particles.

*Oncinopus* has been considered to contain four species: *O. aranea* (De Haan, 1839); *O. neptunus* Adams & White, 1848; *O. angustifrons* Takeda & Miyake, 1969; and *O. postillonensis* Griffin & Tranter, 1986. Ng et al. (2008) also listed, in error, *O. subpellucidus* Simpson, 1857 as a valid species, with *O. angulatus* Haswell, 1880 as a junior synonym. However, both species were described from Port Jackson, New South Wales, and both were treated as junior synonyms of *O. neptunus* by Griffin & Tranter (1986), who found only *O. neptunus* to be present in Port Jackson. Griffin & Tranter (1986: 38) also indicated that they had seen a female specimen from the Mortensen Pacific Expedition to Mindoro, Puerto Galera, the Philippines, which they believed to be a new fifth species, but refrained from describing it because they lacked a male.

The male first gonopod of *Oncinopus* species is very unusual amongst majoids in being strongly twisted about three times. This was critically described by Takeda & Miyake (1969), who first recognised the importance of this structure in species discrimination.

The present study was stimulated by the discovery of the new *Oncinopus* species during identifications of beam-trawl catches, following an environmental impact survey of Middle Arm, Darwin Harbour, Northern Territory, for the development of the new city of Weddell. Further investigation revealed that this new species was also present in other unidentified material from northern Australia in the collections of the Queensland Museum. Also amongst this latter material were two other *Oncinopus* species representing new distributional records, and these are also reported here.

*Oncinopus aranea* and *O. neptunus* are widespread Indo-west Pacific species, and well known from Australian waters (Griffin & Tranter 1986; Davie 2002; Poore 2004). However the other two species, *O. postillonensis* and *O. angustifrons*, appear to have a more limited range, so far being only known from southern Japan, the East China Sea, the Philippines and Indonesia (see Griffin & Tranter 1986; Marumura & Takeda 2009). Thus, it was of interest to discover *O. angustifrons* amongst the present material from north-western Australia. Poore et al. (2008) have already tentatively identified *O. cf. angustifrons* from somewhat further south in Western Australian waters, and thus, given the present material, it is more likely that their identification was correct, although their material was not re-examined as part of this study.

Institutional abbreviations: NTM, Museum and Art Gallery of the Northern Territory (formerly Northern Territory Museum), Darwin; QM, Queensland Museum, Brisbane.
Fig. 1. Oncinopus kathae sp. nov., dorsal views. A, holotype female (NTM-Cr17096); B, paratype male (NTM-Cr17097).
Abbreviations: cb, carapace breadth; G1, male first gonopod; P2–P5, pereiopods 2–5. Measurements are of carapace breadth at the widest point followed by carapace length.

SYSTEMATICS

Family Inachidae Macleay, 1838

Oncinopus De Haan, 1839

Gender masculine. Type species, by monotypy, Inachus (Oncinopus) aranea De Haan, 1839. Recent. Japan (no specific locality given).

Inachus (Oncinopus) De Haan, 1839: 87.


Diagnosis. Carapace rounded triangular, depressed, without spine; rostrum obtusely bilobate. Eyes non-rectangular. Basal antennal article very slender, free distally, not reaching anterior margin of eyestalk. Weakly developed interantennular septum, no interantennular spine. Last pair of pereiopods in subdorsal position, last two pairs subchelate. Abdomen distinctly 7-segmented in both sexes. Male first gonopod twisted about 3 times.

Oncinopus kathae new species

(Figs 1–3, 4A, B, 5E)

Material examined. Holotype – NTM Cr.17096, female (7.1 × 9.8 mm, 8.8 mm postrostral), West Arm, Darwin Harbour, Stn 35, 12°34.997'S, 130°53.668'E, beam trawl, 8.9 m, coll. N. Smit & party, 28 Mar 2011. Paratypes – NTM Cr.17097, male (6.6 × 9.9 mm, 8.8 mm postrostral), West Arm, Darwin Harbour, Stn 37, 12°35.518'S, 130°53.618'E, beam trawl, 12.6 m, coll. N. Smit & party, 28 March 2011. QM W29099, male (6.0 × 8.8 mm, 8.0 mm postrostral), North West Shelf, Western Australia, CSIRO Stn 02B09BT, 19°04.4’S, 118°50.5’E, beam trawl, 83 m, coll. T. Ward & party, 27 April 1983. QM W23654, male (5.9 × 7.9 mm), North West Shelf, Western Australia, CSIRO Stn 02B05BT, 19°04.3’S, 118°50.5’E, beam trawl, 83 m, coll. T. Ward & party, 27 April 1983. QM W23657, male (5.9 × 7.1 mm), North West Shelf, Western Australia, CSIRO Stn 02B05BT, 19°28.5’S, 118°55.5’E, beam trawl, 40 m, coll. T. Ward & party, 26 April 1983. ADDITIONAL (NON-TYPE) MATERIAL – QM W23656, ovig. female (6.1 × 7.6 mm), North West Shelf, Western Australia, CSIRO Stn 03B03BT, 19°55.5’S, 117°55.5’E, beam trawl, 43 m, coll. T. Ward & party, 26 June 1983. QM-W17314, male (5.8 × 8.0 mm), female (6.3 × 7.4 mm), Gulf of Carpentaria, 12°00.5’S, 141°11.9’E, dredged, R.V. Southern Surveyor, CSIRO/QM party, 37 m, 3 December 1990.

Description. Carapace sub-triangular, more widely flanged posteriorly adjacent leg bases; carapace width approx. 0.75 (male) to 0.8 (female) postrostral carapace length. Surface smooth, but obscured by epibenthic fouling when alive; regions somewhat defined, with long swollen postrostral gastric elevation with slightly elevated mesogastric tubercle; rounded cardine elevation armed with a pair of indistinct blunt lateral tubercles; intestinal region smooth. Rostrum of 2, narrow, triangular, flattened, blunt spines; outer lateral margins subparallel, separated by a broad V-shaped hiatus; length approx. 0.1 times postrostral carapace length; inner margins with long curled stout setae; outer margins with shorter straight setae. Supraorbital cave not obviously broadened, but distinctly elevated, eyestalks clearly visible dorsally for most of their length; eyestalk short and stout, cornea enlarged. Hepatic margin produced laterally as broad rounded triangle, often quite pronounced. Branchial region with longitudinal rows of curled hairs on dorsal margin. Basal antennal article slender, smooth, distally free; second segment subequal or slightly shorter than basal segment, similarly slender; third segment about half length second; antennal flagellum long. Frontal margin deflected below rostrum as a broad rounded lobe, not visible in dorsal view; interantennular septum obsolete. Antennules slender; palps folding transversely.

Third maxillipeds smooth; ischium with a low, longitudinal ridge below articulation with merus, inner margin produced as a long broad rounded lobe extending about two-thirds length of merus; menis longer than wide, anterolateral angle not produced, inner lateral margin with raised ridges. Pereiopods region narrow, smooth; margin weakly indicated, smooth. Sternum generally smooth; sternites 3–4 deeply laterally excavated, with high narrow medial longitudinal ridge.

Male cheliped stout, relatively short, smooth; ischium and menis with longitudinal row of long bristle-like setae ventrally on outer face and a row of shorter hooked setae dorsally; carpus elongate, inner margin broadly rounded, with row of long bristle-like setae, outer face with shorter hooked setae; chela with short hooked setae dorsally and ventrally; palm approx. 2.3 times as long as high; fingers approx. 0.4 times as long as palm, weakly incurved; a narrow, smooth gape between fingers in proximal two thirds, finely dentate distally.

First ambulatory leg (measured from attachment to tip of daeyl) about 2.5 times (approx. 2.6) postrostral carapace length (female holotype), smooth, propodus and dactylus dorsoventrally flattened, length of propodus about 4.4 times width. P2 and P3 similar; anterior and posterior margins of carpus, propodus and dactylus with fringing rows of long strong setae; a row of short curled setae also present dorsally on merus, carpus and propodus; dactylus with a thick brush of long, softer setae on inner margin. P4 and P5 similar, subchelate, sexually dimorphic being obviously shorter in female; P5 shortest, angled dorsally, length (measured from attachment to base of daeyl) approx. 1.7 times postrostral carapace length in male, and 1.3 times in female; merus of P5 6.5 times

Oncinopus (Inachidae) from northern Australia
longer then wide in male versus 5.1 times in female; merus, carpus and propodus with sparse, long, plumose setae; carpi with cluster of plumose setae disto-ventrally; propodus arched, bearing thick setae on inner margin; dactyl strongly recurved, armed with row of 6–8 small teeth ventrally along its length.

Male abdomen broad, 7 free segments, third somite with lateral margin strongly produced, convex; somites 4–6 longitudinally ridged, with a medial tubercle anteriorly; sixth somite about two thirds as wide as third segment, width about 3.5 times length; telson broadly rounded, approx. 2.8 times wider than long. Female abdomen with fused somites;
Oncinopus (Inachidae) from northern Australia

a large medial tubercle on each of somites 3–5; a low medial ridge on sixth somite and telson. Female gonopore with simple ventral opening, not elevated; holotype with 9 large eggs.

Male first gonopod twisted, aperture terminal and abdominal; first major twisted section very wide and stout, second twist much narrower; distal portion beyond last twist tubular, extended about 0.3 times total length of G1, slightly recurved apically, tip truncate, not developed into prominent snout.

Remarks. Oncinopus kathae sp. nov. can be distinguished from other species of Oncinopus using the key provided. As pointed out by Takeda & Miyake (1969), gonopod morphology appears to be very good for species discrimination (see Fig. 5). By this feature, O. kathae is probably closest to O. neptunus but differs from that species in having a long, untwisted, tubular distal portion (Fig. 5E), and noticeably shorter pereiopods 3 and 4 (cf. Fig. 1B and 5A). The next most similar species is O. angustifrons, but again, the G1 of O. kathae differs by its simple tubular tip, and enlarged first twisted section which is much broader than the second twist (cf. Fig. 5B and 5E). Also the rostral lobes of O. angustifrons are more widely divergent, and the outer lateral margins are also divergent in that species (Fig. 4D, E), versus subparallel in O. kathae (Fig. 4A, B). Oncinopus postillonensis differs from all others by the long.

Fig. 3. Oncinopus kathae sp. nov., A, B, D: paratype male (NTM-Cr17097); C: holotype female (NTM-Cr17096); A, dorsal view of male pereiopods 4 and 5; B, third maxilliped; C, detail of female second pereiopod showing carpus, propodus and dactylus; D, ventral view of propodus and dactylus of male pereiopods 4 and 5.
Fig. 4. A, B, Oncinopus kathae sp. nov., paratype male (NTM-Crl 7097), dorsal and ventral views of frontal region. C–F, Oncinopus angustifrons Takeda & Miyake, 1969: C, male (4.3 mm cl) (QM-W23655); D, carapace of holotype; E, ventral view of frontal region of allotype female; F, second pereiopod of holotype. (Figures D–F, after Takeda and Miyake, 1969: fig. 4).
Oncinopus (Inachidae) from northern Australia

dorsoventrally flattened rostral lobes (Fig. 6D, E) and by the broad interorbital region which conceals most of the eyestalk (Fig. 6E). Finally, *O. aranea* also differs in G1 morphology by its shorter distal section ending in a "duck's head", and by having the second twist of the G1 at least as large and prominent as the first (Fig. 5C).

Poore et al. (2008) reported a single specimen of *Oncinopus aranea* from off the Western Australian coast (27°08'S) from 414 m depth. The carapace shows a marked resemblance to *O. kathae* sp. nov. however, as it appears to be a female and missing most limbs, it can not be unambiguously attributed to the present new species, at least not without direct examination.

The presence of a thick brush of long, softer setae on the outer margin of the dactyli of P2 and P3 (Figs 1A, 3C), has not been noted or illustrated for other species (cf. Fig. 6) and appears to be a unique character for *O. angustifrons* or *O. aranea* studied here.

*Oncinopus kathae* sp. nov. also appears to have fewer, and relatively larger, eggs than the ovigerous female of *O. angustifrons*, and it would be interesting to compare this character with other species.

**Habitat.** Although field notes were made on the type of bottom for most of the West Arm stations sampled during the Weddell Survey, they were not recorded specifically for stations 35 or 37. However, it is likely to have been a mixture of low rocky clumps on a muddy sand substrate. Nearby sites were noted as being gravely mud with some shell grit, or gravelly sandy mud. The North West Shelf sites were located in deeper, much cleaner, offshore areas, and there were small amounts of clean coral sand associated with some of the specimens. The depth range for *Oncinopus kathae* sp. nov. is 8 to 83 m.

**Etymology.** Named for my beautiful wife Kathleen – because the promise of a new species is long overdue, and not because of any morphological similarities!

*Oncinopus angustifrons* Takeda & Miyake, 1969 (Figs 4C–F, 5B)


**Material examined.** QM W23655, 2 males (3.1, 4.3 mm eb) 3 females (4.0, 5.1, 5.4 mm eb), North West Shelf, Western Australia, CSIRO Stn 02B06BT, 19°04.4'S, 118°47.3'E, beam trawl, 82 m, coll. T. Ward & party, 26 April 1983. QM W29100 (ex W23654), male (4.8 mm eb), North West Shelf, Western Australia, CSIRO Stn 02B08BT, 19°04.3'S, 118°45.5'E, beam trawl, 83 m, coll. T. Ward & party, 27 April 1983. QM W29101 (ex W23657), ovig. female (4.8 mm), North West Shelf, Western Australia, CSIRO Stn 02B09BT, 19°28.5'S, 118°55.3'E, beam trawl, 40 m, coll. T. Ward & party, 26 April 1983.

**Diagnosis.** Carapace strongly tapered anteriorly from broad hepatic region to constriction behind rostral lobes; gastric region circular, convex, median posterior part faintly demarcated from greater remaining part; cardiac region isolated, distinctly bifid at summit; rostral lobes weak, triangular, not dorso-ventrally flattened, separated by broad hiatus; lobes divergent; interorbital region only concealing basal part of unretracted eyestalk. Chelipeds slender, merus fringed with row of long, stout, setae along both borders; palm not swollen, slightly shorter than fingers. Male G1 strongly widened subapically; female gonopore weakly elevated, opening more posteriorly than medially. (After Sakai et al. 2004).

**Remarks.** The Australian material agrees very well with the detailed description of Takeda & Miyake (1969), and in particular the male G1 is a perfect match with their figure (see Fig. 5B). Interestingly, at some sites on the North West Shelf, it was collected sympatrically, in the same beam trawls, with specimens of the new species, *O. kathae*. Poore et al. (2008) tentatively identified *O. cf. angustifrons* from somewhat further south in Western Australian waters and although that material has not been studied as part of the present report, the present specimens add weight to their identification being correct.

**Distribution.** Japan – Ogasawara-shoto (Takeda & Miyake 1969, Takeda 1973); East China Sea (Takeda & Miyake 1969); Philippines – San Bernadino Strait (Griffin & Tranter 1986), Sulu Archipelago – off Jolo (Griffin & Tranter 1986); Indonesia – Kepulauan Kai and Aru (Griffin & Tranter 1986). Now extended to the North West Shelf, Western Australia. The bathymetric range for *Oncinopus angustifrons* is from 36 to 200 m.

*Oncinopus aranea* De Haan, 1839

(Figs 5C, 6B, C)

*Inachus (Oncinopus) aranea* De Haan, 1839; 100, pl. 29, fig. 2, pl. 11; Yamaguchi 1993: 585.

*Oncinopus aranea.* – Adams & White 1848: 3; Miers 1886: 20; Ortmann 1893: 37; Alecock 1895: 183; Rathbun 1902: 133; 1906: 879; 1911: 247; Yokoya 1933: 137; Sakai 1936: 80, pl. 18, fig. 3; 1938: 206, fig. 3, pl. 21, fig. 3; 1976: 155, pl. 48, fig. 1; Takeda & Miyake 1969: fig. 5e–f, Takeda 1979: 153; Griffin & Tranter 1986: 35; Yamaguchi & Baba 1993: 331, fig. 109; Muraoka 1998: 22; Davie 2002: 295; Poore 2004: 364, fig. 107b; Sakai et al. 2004: 256, 6 figs; Poore et al. 2008: 59, unnumbered fig.

*Oncinopus aranea.* – Sakai 1935: 65; 1965: 66, pl. 27, fig. 1; Serène & Vadon 1981: 123; Ng, Guinot & Davie 2008: 112.

**Nomenclatural note.** The specific epithet *aranea* is a Latin noun meaning a spider. De Haan (1839) introduced it intentionally as a noun in aposition and his spelling has been followed by the majority of authors. Sakai (1935) and
Fig. 6. A, *Oncinopus neptunus* Adams & White, 1848 (original figure from Adams & White, 1848: pl. 2, fig. 1); B, C, *O. aranea* (De Haan, 1839) (B, from De Haan, 1839, pl. 29 fig. 2; C, lectotype male, following Yamaguchi & Baba, 1993: fig. 109); D–H, *O. postillonensis* Griffin & Tranter, 1986 (After Griffin & Tranter 1986): D, carapace, dorsal view; E, frontal region, ventral view; F, second left pereiopod, dorsal view; G, fourth left pereiopod; H, fifth left pereiopod.
Oncinopus (Inachidae) from northern Australia

Fig. 5. Sternal and abdominal views of male first gonopods from known \textit{Oncinopus} species. A, \textit{O. neptunus} Adams & White, 1848 (from Port Jackson, NSW; holotype G1 is figured by Takeda and Miyake, 1969: fig. 3); B, \textit{O. angustifrons} Takeda & Miyake, 1969 (holotype); C, \textit{O. aranea} (De Haan, 1839)(from Amakusa Is., Japan); D, \textit{O. postillonensis} abdominal view (holotype); E, \textit{O. kahae} sp. nov. (paratype male NTM-Cr17097). A–C after Takeda & Miyake (1969); D after Griffin & Tranter (1986).

Material examined. QM W23658, male (2.9 mm eb), North West Shelf, Western Australia, CSIRO Stn 01B16BT, 19°59.3’S, 117°03.5’E, beam trawl, 52 m, coll. T. Ward & party, 22 February 1983. QM W23660, male (3.1 mm cb), North West Shelf, Western Australia, CSIRO Stn 01B17BT, 20°00.2’S, 117°00.5’E, beam trawl, 53 m, coll. T. Ward & party, 22 February 1983.

Diagnosis (after Sakai et al. 2004). Carapace moderately tapered from hepatic region to constriction behind rostral lobes; gastric region circular; convex, median posterior part faintly demarcated from remaining greater part; cardiac region isolated, distinctly bifid at summit; rostral lobes weak, triangular - not dorso-ventrally flattened, lobes divergent, interorbital region only concealing basal part of unretracted eyestalk. Chelipeds slender, menis fringed with row of long, stout setae along both borders; palm not swollen, slightly shorter than fingers. Male G1 strongly widened distally, with subapical beak-like lateral lobe; female gonopore distinctly elevated, opening medially.

Remarks. The two specimens (both male) available to me from northwestern Australia agree with previous descriptions, and with the figure of the male G1 given by Takeda & Miyake (1969). Yamaguchi & Baba (1993) designated a lectotype and provided photographs of the male lectotype and female paralectotype.

Distribution. Seychelles and Cargados Carajos (Rathbun 1911); Laccadives (Alcock 1895); Maldives – (Alcock 1895), Nallandu (Rathbun 1902); Sri Lanka (Alcock 1895); Andamans (Alcock 1895); Malay Peninsula (Alcock 1895); Japan – (De Haan 1839), Kagoshima (Ortmann 1893), west of Suno-saki (Yokoya 1933), Shimoda (Sakai 1935), Tateyama Bay, Misaki, Shimoda, Nanki Shirahama, Ibusuki, and Nagasaki (Sakai 1938), Sagami Bay (Sakai 1965), Tokyo Bay, Sagami Bay, Shimoda, Kii Nagashima, and Kii Minabe (Sakai 1976), Shiono-misaki (Takeda 1979), Tosa Bay (Muraoka 1998); Philippines – north of Lubang Island (Serène & Vadon 1981); Sulu Archipelago – off North Ubian and off Jolo (Griffin & Tranter 1986); Indonesia – Moluccas Passage (Miers 1886), Lesser Sunda Islands, Selat Sunda, Selat Bali, Flores Sea, Seram, and Kepulauan Kai (Griffin & Tranter 1986); Arafura Sea (Miers 1886); Hawaiian Islands – Kauai and Modu Manu (Rathbun 1906). Bathymetric range: 3–400 m; Australia – southern Australian coast (Miers 1886; Poore 2004), Moreton Bay and Saumarez Reef, Queensland (Griffin & Tranter 1986a); range now extended to northwestern Australia.

KEY TO SPECIES OF \textit{ONCINOPUS}

1. Rostral lobes broad, dorsoventrally flattened, separated by a narrow hiatus, inner margins of lobes parallel, outer margins curved, converging distally; interorbital region broad, concealing most of unretracted eyestalk...........
   \textit{O. postillonensis} Griffin & Tranter

2. Male G1 tubular or only slightly widened before apex; female gonopore a simple ventral opening, not elevated..................3
   \textit{O. postillonensis} Griffin & Tranter

3. Male G1 strongly widened before apex, or with a lateral lobe; female gonopore at least weakly elevated.....4

\textit{Oncinopus} (Inachidae) from northern Australia
3. Male G1 with apex moderately flanged, last twist extending almost to tip; pereiopods 4 and 5 very long, merus of male P5 approx. 12 times longer than wide.

- Male G1 with apex simple, truncate, distal portion tubular beyond last twist, extended about 0.3 times total length of G1; pereiopods 4 and 5 relatively shorter, merus of male P5 approx. 6.1 times longer than wide. O. kalhae sp. nov.

4. Male G1 strongly widened subapically; female gonopore on a weak elevation, opening more posteriorly than medially.

- Male G1 with a beak-like lateral lobe subapically; female gonopore distinctly elevated and opening medially. O. anustisflOURS Takeda & Miyake

- Male G1 with apex simple, truncate, distal portion tubular beyond last twist, extended about 0.3 times total length of G1; pereiopods 4 and 5 relatively shorter, merus of male P5 approx. 6.1 times longer than wide. O. aranea (De Haan)

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Oncinopus (Inachidae) from northern Australia


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Euprymna pardalota sp. nov. (Cephalopoda: Sepiolidae), a new dumpling squid from northern Australia

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ABSTRACT

Examination of specimens of Euprymna Steenstrup, 1887 from northern Australia led to the discovery of a new species. It is described here as Euprymna pardalota sp. nov. It is distinguished from all but one other nominal species of Euprymna (E. phenax Voss, 1962) in having two rows of suckers on the arms, rather than four rows. It differs from E. phenax in a number of traits, including: the possession of large spots over most of the body, the shape of the funnel organ, the modification of the hectocotylus, and spermatophore length and structure. In addition, the discovery among the Australian Museum collection of a specimen of E. phenax, previously known only from the single male holotype, supports the validity of this taxon, which was previously described as unresolved.

KEYWORDS: Cephalopoda, Sepiolidae, sepiolid, Euprymna, Euprymna phenax, Euprymna pardalota, dumpling squid.

INTRODUCTION

The most recent review of the genus Euprymna Steenstrup, 1887 is that of Norman & Lu (1997). In that work, 12 nominal species were recognised, with five species considered valid: E. berryi Sasaki, 1929; E. hoytei Adam, 1986; E. morsei (Verrill, 1881); E. scolopes Berry, 1913; E. tasmanica (Pfeffer, 1884) and an undescribed species, E. sp. 1. Two species, E. schneehageni (Pfeffer, 1884) and E. pusilla (Pfeffer, 1884), were considered to be nomen dubia, and the status of E. albatrossae Voss, 1962; E. bursa (Pfeffer, 1884), E. phenax Voss, 1962 and E. stenodactyla (Grant, 1833) was deemed to be unresolved. In the same year, an additional species, E. hylebergi Natsukawatana, 1997, from the Andaman Sea, Thailand, was described. More recently, another species, Euprymna megaspadicea Kubodera & Okutani, 2002 has been recognised from Japan.

In Norman & Lu’s (1997) paper, only one species, E. tasmanica, was reported to occur in Australia. It is found in shallow waters around southern Australia from Moreton Bay, Queensland, through to Bass Strait, Victoria. However, two unresolved taxa, one from northern Australia and one from south-western Australia, were mentioned by Norman & Lu (1997). The morphology of the northern unresolved taxon (treated as E. stenodactyla in Lu & Phillips (1985)) is described as very similar to that of E. tasmanica, although DNA analyses has demonstrated that it is distinct (M. Nishiguchi unpublished data). The second unresolved taxon, also very similar to E. tasmanica, is described by Norman & Lu (1997) as represented by insufficient material to fully resolve. (For this reason, the distribution of E. tasmanica in Reid & Jereb (2005) is described as extending north to Shark Bay in Western Australia.) All the abovementioned Australian species have four transverse rows of suckers on the arms.

A visit to the Museum and Art Gallery of the Northern Territory in 2008 led to the discovery of a distinct species of Euprymna collected in northern Australian waters. More specimens were subsequently found among the collections of the Western Australian Museum and the Australian Museum. Unlike nearly all other nominal Euprymna species, this one has two transverse rows of suckers on the normal (non-hectocotylised arms). The only described species with two rows of suckers is E. phenax from the Philippines. Comparison of the Australian material with the E. phenax holotype (previously the only known specimen) indicated that the northern Australian form belongs to a new species and can be distinguished from E. phenax by a number of traits. This new species is described as E. pardalota.

MATERIALS AND METHODS

Terminology, measurements, indices, and abbreviations for anatomical structures follow Roper & Voss (1983), with a few minor differences (Table 1). In the current paper, ASC refers to the total number of suckers on each designated arm (this abbreviation refers to the number of suckers on the basal half of each arm in Roper & Voss (1983), with ASCT
used for the total number of arm suckers). All measurements are in millimetres (mm). Measurements and counts for individual mature specimens are presented in Table 2; the range of values for each character is expressed as a percentage of mantle length. As only two mature female specimens were available for study, the measurements differ slightly from those tabulated in Voss (1963). Other abbreviations: AM, Australian Museum; MV, Museum Victoria; NTM, Northern Territory Art Gallery and Museum; WAM, Western Australian Museum.

For scanning electron microscopy, arm and club suckers (and in one case a whole arm) were removed from the middle of designated arms and the tentacular club, mounted, then air dried and examined in a Zeiss Evo LS15 SEM using a Robinson Backscatter detector.

As only two mature female specimens were available for examination, the female reproductive tract was not removed for examination. Similarly, the digestive tract was not removed to avoid excessive damage to type material. Some difficulty was experienced dissecting out the male reproductive tract intact and pinning it out for examination and illustration, despite attempting to do so with valuable type material. Should more, particularly fresh material, become available, it would be useful to examine and fully describe these internal structures. It was not possible to do so for this work.

### TAXONOMY

**Euprymna Steenstrup, 1887.**

Gender feminine. Type species, by original designation, *Litoctethis morsei* Verrill, 1881. Recent. Western Pacific and eastern Indian Oceans.

**Diagnosis.** Broad ligament between head and mantle; commissure greater than one-third of head width. Transverse suckers in 2 or more rows on normal (non-hectocotylised) arms. Stalked suckers in 6 or more transverse rows on tentacular clubs. Left arm 1 hectocotylised in mature males; distally with 2-4 rows of small suckers on elongate, columnar pedicels; suckers with narrow openings and chitinous rims; basal part of hectocotylised arm with normal suckers and 1-2 papillae in ventral sucker row, sometimes bearing tiny sucker(s). Enlarged arm suckers usually present in male (not markedly so in *E. phenax* and *E. pardalota* sp. nov.). Paired light organs in mantle cavity, ventral and closely adherent to ink sac. Gladius absent.

**Euprymna pardalota** sp. nov. (Figs 1-9; Tables 1, 2)

**Material examined.** Holotype—NTM P.15796, 1 cf (8.6 mm ML, mature), Western Australia, Timor Sea, Cartier Reef, rotenone station on slope, 12°32'S, 123°33'E, 13 m, coll. H.K. Larson and M. Selway, 15 March 1990. Paratypes—NTM P.2496, 1 (7.8 mm ML, mature), Western Australia, Timor Sea, Cartier Reef, southern reef flat, rotenone station, 12°32.8'S, 123°32.3'E, 0.2-0.6 m, coll. R.C. Willan, 5 May 1992; NTM P.2497, 9 (9.0 mm ML, mature), Western Australia, Timor Sea, Cartier Reef,
A new species of dumpling squid from northern Australia

SW corner, spur and groove region on coral reef at low tide, 12°32.8'S, 123°32.4'E, 10–20 m, coll. B.C. Russell, 8 May 1992; WAM S.34548, 1σ (8.5 mm ML, mature), Western Australia, Kimberley, southwest end of Long Reef, 13°48'S, 125°47'E, 12 m, coll. F.E. Wells and C.W. Bryce, 17 August 1991; AM C.303908, 1σ (9.5 mm ML, mature), Queensland, Great Barrier Reef, E of Lizard Island, Yonge Reef, 1 m N of platform, coral and sand, back reef, 14°35.00'S, 145°37.00'E, 1–15 m, coll. D.F. Hoese, 1 December 1978.

Non-type material — NTM P.17968, 1 juvenile (2.8 mm ML, immature), Australia, Western Australia, Timor Sea, boat anchorage off West Island, Ashmore Reef, attracted to light at night, 12°14'S, 122°56'E, 0.5 m, coll. H.K. Larson, 15 September 1987; NTM P.15788, 2 juveniles (3.2 mm, 3.5 mm ML, immature), Western Australia, Timor Sea, Ashmore Reef, surface, attracted to light, 12°25'S, 122°57'E, 0.5 m, coll. H.K. Larson, 13 September 1987; NTM P.2494, 1 juvenile (5.2 mm ML, immature), Western Australia, Timor Sea, western end of Cartier Reef, in surge channel on coal reef, 12°32.2'S, 123°31.80'E, 10–14 m, coll. B.C. Russell, 4 May 1992; NTM P.2495, 19 (4.3 mm ML, immature), Western Australia, Timor Sea, SW corner of Cartier Reef, 12°32.6'S, 123°32.2'E, 8–15 m, coll. B.C. Russell, 9 May 1992; AM C.453180, 1σ (7.0 mm ML, immature), Queensland, Great Barrier Reef, Limet Reef, W side, 14°47.00'S, 145°20.00'E, 3–15 m, coll. Australian Museum, 22 November 1975; AM C.456838, 1σ (7.3 mm ML, immature), Queensland, Great Barrier Reef, Capricorn Group, One Tree Island, fine sandy sediment, 23°30.00'S, 152°28.00'E, 4 m, coll. G. Anderson, 7 February 1975.

Other material examined. *Euprymna phenax* Voss 1962: Holotype — USNM 575328, 1σ (11.0 mm, mature), Philippines, Panay Island, Naso Point [not Nogas Point as stated in Voss, 1962], 11°10'N 122°30'E, dip net, coll. *FV Albatross*, 3 February 1908; AM C.453179, 1σ (8.1 mm ML, immature), Philippines, Luzon Island, Lingayen Gulf, coral, rotenone, 16°26.00'N 119°55.00'E, 2–15 m, coll. D.F. Hoese and party, 16 April 1980.

Diagnosis. Small species, up to 9.5 mm mantle length. Funnel organ dorsal element spade-shaped. Left dorsal arm hectocotylised in male: basally, 2 pairs of normal suckers; third sucker pedicel in ventral row modified into distally directed, enlarged, fleshy papilla, without terminal sucker; following 2–3 rows suckers normal; distal end of arm bears 9–15 pairs of suckers on enlarged columnar sucker pedicels. Spermatophores with discrete cement body, SLL 46.5–75.8. Preserved specimens cream with large, deep purple irregularly-shaped pigment spots on dorsal and ventral head and mantle. Fins with 1–3 large spots close to junction with mantle. Aboral surface of arms with mediolateral row of large dark purplish blotches and smaller spots between base of each sucker and extending on to sucker pedicels. Aboral surface of club with row of large blotches close to keel and smaller blotches or bars and spots toward club margin.

Description. Counts and indices for individual specimens are given in Table 2. Only mature specimens were measured.

Species small: ML mature male 8.5–9.0–9.5 (SD, 0.5), female 7.8–8.4–9.0 (SD, 0.8). Mantle short, broad, dome-shaped, rounded posteriorly; MWI male 84.2–90.0–101.2 (SD, 7.8), female 70.0–79.9–89.7 (SD, 14). Dorsoventral margin on head, ventral mantle margin straight or distinct wide 'm' shape. Fins rather small, rounded; fin length approx. 50% ML, Fila male 23.5–30.1–39.5 (SD, 6.8), female 34.6–35.1–35.6 (SD, 0.7); fin width about 20% ML, FW male 36.8–40.2–47.1 (SD, 4.7), female 38.5–38.7–38.9 (SD, 0.3), attached dorso-laterally towards posterior half of mantle; posterior margins curved; anterior margins with well-developed lobes, lateral lobes crescentric. Anterior edges of fins do not project to level of anterior mantle margin (Figs 1A, B).
Reid

Fig. 2. *Euprymna pardalota* sp. nov., male paratype, NTM P.15796, 8.6 mm ML: A, funnel, scale bar 2 mm; B, funnel organ, scale bar 0.5 mm.

Funnel long, conical, base broad, tapered, projecting anteriorly beyond junction of ventral arms 4 (Figs 1B, 2A); FuLl male 55.3–62.4–69.8 (SD, 6.0), female 66.7–66.7–66.7 (SD, 0); free for most of its length, FFul male 32.7–38.5–41.2 (SD, 3.0), female 35.6–37.0–38.5 (SD, 2.1). Funnel valve small, flaplike, rounded anteriorly. Funnel organ dorsal element broad, spade-shaped, rounded anteriorly broadening posteriorly with small projection medially (Fig. 2B) and indistinct median ridge; ventral elements ovoid with acute anterior tips. Funnel locking cartilage long, narrow, parallel-sided with shallow groove of uniform depth (Fig. 2A). Mantle cartilage compliments funnel member: short straight ridge.

Fig. 3. *E. pardalota* sp. nov. male paratype, AM C.456837, 9.4 mm ML: A, SEM, arm 3, right side, scale bar 2 mm; B, SEM, enlargement of sucker rim, scale bar 10 μm; C, hectocotylus, ventral side view, scale bar 1 mm.

spherical throughout (Fig. 3A). Chitinous rim of arm suckers without teeth on inner margin. Infundibulum with 3–4 rows of stalked processes, with broader, ovoid, outermost rims; processes contain tufts of finger-like papillae (Fig. 2B), peripheral sucker rim processes rectangular, radially arranged, without finger-like papillae. Suckers on arms 2 and 3 larger than those on arms 1 and 4 in both sexes; suckers largest medially, basal few and extreme distal few rows of suckers abruptly smaller. Male arms suckers larger than female arm suckers (Table 2) (but not greatly enlarged). Sucker counts range from 20–32 on each arm, mean sucker counts on arms 1–4 in male 23, 27, 25 and 22 respectively; mean sucker counts on arms 1–4 in female 27, 30, 30 and 24 respectively. All arms connected by relatively shallow webs, protective membranes absent.

Left dorsal arm of male hectocotylised: basally, 2 pairs of normal suckers (not enlarged or modified); third sucker pedicel in ventral row modified into distally directed, enlarged, fleshy papilla, without terminal sucker; following 2–3 rows suckers normal; distal end of arm bears 9–15 pairs of suckers on enlarged columnar sucker pedicels (Fig. 3C); proximal-most sucker pedicels in modified
A new species of dumpling squid from northern Australia

Fig. 4. *Euprymna pardalota* sp. nov. male paratype, AM C.303908, 9.5 mm ML: A, club, scale bar 2 mm; B, SEM, scale bar 400 µm; C, enlargement of club suckers, scale bar 35 µm; D, enlargement of individual club sucker, scale bar 10 µm.

Portion broadest and separate; distal-most columnar sucker pedicels closely packed. Hectocotylised arm slightly longer than corresponding unmodified right dorsal arm.

Tentacles long, slender, stalks naked, semicircular in section; oral surface convex. Club relatively short, between 0.25x to 0.3x mantle length; CILI male 22.3–27.5–34.9 (SD, 5.3), female 25.6–28.4–31.1 (SD, 3.9), crescent shaped, tapers to pointed end distally (Fig. 4A, B). Sucker-bearing face of club convex. Suckers approx. 0.1 mm diameter in centre of club; arranged in 6–9 oblique rows. Swimming keel on aboral side of carpus broad, extends posteriorly beyond carpus. Keel forms groove on oral side (Fig. 4A, B). Club sucker dentition (Fig. 4C, D): inner ring without teeth; infundibulum with 3 rows of processes; inner 2 rows sub-rectangular bearing rows of comb-like papillae. At periphery, processes narrower and more elongate, without papillae.

Well-developed paired light organs present overlying and joined to ink sac (Fig. 5). Individual lobes rectangular medially, with large, rounded, shoulder-like bulbi anteriorly, slightly enlarged, rounded, posteriorly and angled outer margin.

Gills with 22–23 lamellae per demibranch (*n* = 5). Buccal membrane with six lappets and fringed inner margin; suckers absent.

Radula with 7 transverse rows of teeth (Fig. 6A). Rhachidian teeth simple, without cusps, triangular, slightly concave laterally and ventrally. First lateral teeth similar in size and shape to rhachidian teeth with pointed cusps displaced laterally and directed towards midline of radula. Second and third laterals with elongate bases, longer than the first, curved. Third laterals with serylte-like teeth, longer than second laterals.

Upper beak (Fig. 6B) with long, pointed rostrum, hood curved, high above crest posteriorly; jaw angle only slightly acute (angle almost 90°); lateral wall edge with slight indentation. Lower beak (Fig. 6C, D) with blunt pointed protruding rostrum, rostral edge obtuse with distinct inner angle; hood pointed posteriorly (Fig. 6D); hood notch absent, wings almost straight, widely spread. Distinct dark pigmentation restricted to rostrum and hood of upper and lower beaks.

Gladius absent.
Male reproductive tract similar in structure to congeners (Fig. 7). Accessory spermatophoric gland large, well developed. Spermatophores (17 in spermatophore storage sac of specimen AM C.456837) approx. 0.5x to 0.75x mantle length; SpLI 46.5-61.3-75.8 (SD, 14.6, n = 3). Sperm reservoir contains coiled sperm cord. Cement body unipartite; aboral end cup-shaped, connects to sperm reservoir via a narrow duct; oral end broadens toward junction with ejaculatory apparatus (Fig. 8A). Oral end of ejaculatory apparatus with 3-4 simple coils.

Female reproductive tract: Ovary large, occupies large proportion of posterior end of mantle cavity; displaces other organs when mature. Opens via single thick-walled oviduct at anterior end on left side. Nidamental glands paired, broad, located ventral to ovary toward anterior end. Inverted cream coloured U-shaped accessory nidamental glands located toward distal end of nidamental glands. Eggs spherical, 0.4 mm diameter (n = 1); EgDI 5.1 (n = 1).

Colour in alcohol cream with large deep purple irregularly shaped spots, sometimes with darker centres, on dorsal and ventral head and mantle; spots larger on dorsal surface of mantle and head than those on ventral surface (Fig. 1A–B). Shiny bluish iridophores on head around eyes. Fins with 1–3 large spots (usually one large and 1–2 smaller) close to junction with mantle, otherwise chromatophores absent from fins dorsally and ventrally. Aboral surface of arms with medio-longitudinal row of large dark-purplish blotches and smaller spots between base of each sucker and extending on to sucker pedicels. These latter, smaller chromatophores are predominant on ventral side of arms 2–4, with fewer on arms 1. Spots sometimes present between dorsal arm suckers, if present, usually on distal portion of arms. Arms appear barred. Aboral surface of club with row of large blotches close to keel and smaller blotches or bars and spots toward club margin (Fig. 8C). Distinct patterning also visible on juveniles.

Habitat. Coral reef.

Type locality. Western Australia, Timor Sea, Cartier Reef, 12°32'S, 123°33'E, 13 m.

Distribution. Australia: Western Australia, from 12°14'S, 122°56'E to Queensland, 23° 30.00'S, 152° 28.00'E, depth range 0.2 m to 20.0 m (Fig. 9). While the scale of the distribution map would suggest that this species occurs in the open ocean, all specimens collected are, in fact, associated with reefs.

Etymology. The species name, pardalota, is derived from the Greek, pardalotus, meaning ‘spotted like a leopard’ and refers to the large and prominent spots that are distinctive in this species. It is adjectival.

DISCUSSION

The discovery of a new Euprymna in Australian waters is an exciting one. Unlike E. tasmanica, this northern Australian taxon clearly differs in having two rather than four transverse rows of arm suckers. The only other nominal species with two rows of arm suckers is E. phenax from the Philippine islands. Comparison of the E. phenax holotype with the northern Australian Euprymna, together with a single additional non-type E. phenax specimen (also from the Philippines), indicates that the taxon from Australia is distinct.

A number of morphological characters distinguish the specimens from these two localities. Euprymna phenax has smaller, and many fewer chromatophores than E. pardalota (Fig. 1). The fins of the E. phenax (Fig. 1C, D) are smaller and are positioned more anteriorly on the body than those observed in the Australian specimens. The dorsal member of the funnel organ is spade-shaped in E. pardalota and inverted V-shape in E. phenax. Differences are also apparent in the hectocotylus. While both species have the third sucker pedicel from the base of the arm enlarged into
A new species of dumpling squid from northern Australia

a fleshy papilla, *E. pardalota* has only 2–3 pairs of normal arm suckers distal to this papilla (proximal to the series of columnar suckers), while *E. phenax* has approx. seven pairs of normal suckers distal to the fleshy papilla, followed by about 10 pairs of columnar suckers (versus 9–15 in *E. pardalota*). The fleshy papilla bears a sucker in the *E. phenax* holotype (but not in specimen AM C.453179), but none of the male *E. pardalota* examined had a sucker on this papilla. In addition, based on Voss's measurements, and measurement of the arm suckers of C.453179, the arm suckers are smaller in *E. phenax* males than in *E. pardalota* (Table 2). Variation in the size and arrangement of arm suckers has been used to diagnose other *Euprymna* species (Norman & Lu, 1997). Many of the suckers are absent in the holotype, a fact noted by Voss (1963: 46) who stated, “one cannot overlook the possibility that one or more may be enlarged in a complete specimen”. However, the more recently collected non-type *E. phenax* specimen (albeit not fully mature) has intact suckers that are slightly enlarged

Table 2. *Euprymna pardalota* sp. nov. Measurements (mm), counts and indices of mature specimens of both sexes. Measurements for the *E. phenax* holotype are included for comparison (some of Voss’ 1963 data were used, for example sucker diameters, as most suckers have now fallen off the holotype).

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Within it, and the relationship of this group to *E. phenax* have not yet been described, the available evidence clearly supports the recognition of the Australian taxon as a species new to science. In the future, if more specimens have strongly projecting lobes, indicating this is a variable trait, perhaps affected by preservation or degree of contraction.

While *E. phenax* is only known from the single male type specimen and one other non-type male, and female *E. phenax* have not yet been described, the available evidence clearly supports the recognition of the Australian taxon as a species new to science. In the future, if more *E. phenax* from close to the type locality are collected and the species can be fully described, this hypothesis can be properly tested. Ideally, a comparison of both morphological and molecular traits over the distributional range of both taxa would be invaluable.

In addition, the discovery among Australian museum collections of a second specimen from the Philippine islands that clearly matches the character traits of the *E. phenax* holotype (until now the only known specimen of that taxon) supports the validity of this species that was previously described as “unresolved” (Norman & Lu 1997).

The generic diagnosis has been modified from that given in Norman & Lu (1997) to accommodate this new species and *E. phenax*. [Steenstrup’s (1887) original description of the genus is a single line only in Latin and refers only to the broad ligament joining the mantle and head and the extraordinary formation of the tentacle.] The arm suckers are now diagnosed as having two or more transverse rows of suckers (rather than four or more); the tentacular clubs have six or more transverse rows of suckers (rather than 16), and most (but not all species) have enlarged suckers in mature males. The light organs are described here as paired rather than a single ‘saddle-shaped light organ’. While the term ‘saddle shaped’ has persisted in the literature, the light organs are not joined anteriorly ventral to the rectum. A more detailed diagnosis awaits a full generic revision. A comprehensive phylogenetic analysis, including morphological and molecular traits, is needed to check the monophyly of *Euprymna*, the position of *E. pardalota* and *E. phenax* within it, and the relationship of this group to other sepiolids.

**ACKNOWLEDGEMENTS**

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I would also like to thank the Australian Biological Resources Study (ABRS) for providing funding via a Non-Salaried Researcher Grant that enabled me to undertake this study and visit the WAM in July 2009.

**REFERENCES**


Voss, G.L. 1962. Six new species and two new subspecies of Cephalopods from the Philippine Islands. *Proceedings of the Biological Society of Washington* 75: 169–176. [A number of authors have given the date 1963 for the publication of *E. phenax* by Voss. This is incorrect. A short description was given in Voss (1962) followed by a more comprehensive description with illustrations in Voss (1963).]


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A new genus and species of Bythitidae (Teleostei: Ophidiiformes) from northwestern Australia

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ABSTRACT

A new genus and species of bathyal bythitid fish (Teleostei: Ophidiiformes) is described based on a single specimen caught at a depth of 392 m in the Timor Sea off the coast of northwestern Australia. *Timorichthys disjunctus* gen. nov., sp. nov. differs from all other bythitid genera by the position of the anus midway between the tip of the snout and origin of the anal fin. The joined vertical fins and the type of intromittent organ furthermore place the new genus in the subfamily Bythitinae.

**KEYWORDS:** Bythitidae, *Timorichthys disjunctus* gen. nov., sp. nov., viviparous brotula, taxonomy, northwestern Australia.

INTRODUCTION

The intensive bottom trawling off northwestern Australia by the Research Vessel *Southern Surveyor* in 2007 revealed a number of new and rare ophidiiform fishes (Nielsen 2010, 2011). The present paper deals with one 39 mm SL adult male trawled at a depth of 392 m. At first it did not seem similar to any family known from the area. However, the ratio of the number of dorsal and anal pterygiophores to the number of adjacent vertebrae being more than one, the joined vertical fins, the single pelvic fin ray and the presence of a copulatory organ being an integrated part of the fleshy genital hood with the penis present as a small soft papilla without pseudoclaspers place the specimen in the subfamily Bythitinae of the viviparous family Bythitidae, order Ophidiiformes (Nielsen et al. 1999).

The specimen is distinctly different from any of the 15 genera presently referred to the Bythitinae first and foremost by the position of the anus midway between the tip of the snout and origin of the anal fin. The joined vertical fins and the type of intromittent organ furthermore place the new genus in the subfamily Bythitinae.

**MATERIAL AND METHODS**

The specimen is curated in Museum Victoria (NMV), according to the standards for museum collections Fricke & Eschmeyer (2011). Ichthyological terminology, measurements and counts follow Nielsen et al. (1999); the terminology of the head pores and otoliths follows Schwarzhans et al. (2005).

SYSTEMATICS

**Timorichthys** gen. nov.

Type species, here designated, *Timorichthys disjunctus* sp. nov. Gender masculine.


**Remarks.** The combination of the position of the anus, the hidden opercular spine, the head pores, and the form of the body is so unique that *Timorichthys* does not resemble any other bythitid genus.

**Etymology.** The generic name refers to the Timor Sea, from which the holotype originated.
Timorichthys disjunctus sp. nov.

(Figs 1–3)

Material examined. Holotype – NMV A29734-002, 39 mm SL, male, eastern Indian Ocean, Timor Sea, off northwestern Australia, approx. 78 km south of Cartier Island, Kulumburu L29 transect, 13°13′29″S, 123°23′44″E to 13°13′20″S, 123°23′17″E, R.V. Southern Surveyor, Sherman skd, 392 m, 5 July 2007.

Diagnosis. See generic diagnosis above.

Description (Figs 1–3).

Meristic characters. Rays in dorsal fin 74, caudal fin 11-12, anal fin 46, pectoral fin 11 or 12, pelvic fin 1. Vertebrae 16+36= 52. Pseudobranchial filaments 2. Anterior gill arch with 6 long rakers. Origin of dorsal fin above vertebra no. 9, origin of anal fin below vertebra no. 24 and dorsal fin ray no. 28. Anus placed below dorsal fin ray no. 3.

Morphometric characters (in % SL). Head 18.5, depth at origin of anal fin 9.7, depth at origin of dorsal fin 11.0, upper jaw 7.7, depth of posterior maxilla 2.3, orbit 1.3, eye ball 0.6, interorbital 3.8, snout 3.6, postorbital 13.5, preanal
New genus and species of bathyal Bythitidae

52, anus to origin of anal fin 26.5, predorsal 24.5, base of pelvic fins to origin of anal fin 37.0.

Head and body naked. Body non-tapering and compressed (Fig. 1). No lateral line. Head high with blunt snout. Vertical fins joined. Dorsal fin origin above anterior half of pectoral fin. Anal fin origin near midpoint of fish. Pectoral fin below midline of fish with peduncle almost as broad as long. Pelvic fins below opercle, almost reaching anus. Anus midway between snout and origin of anal fin (Fig. 2 A). Mouth oblique with upper jaw ending well behind eye. Posterior end of maxilla vertically expanded. Snout twice as long as eye diameter. Anterior nostril close to upper lip ending in a tube; posterior nostril a mere hole close to eye (Fig. 2 B). Opercular spine weak and covered by skin. No spine on preopercle. Anterior gill arch with 2 small knobs on upper branch, 1 long raker in angle and lower branch with 5 long rakers followed by 8 small knobs. All knobs and long rakers with small, densely placed spines. Long rakers almost twice as long as gill filaments; 2 pseudobranchial filaments.

Axial skeleton (from radiographs). Number of precaudal vertebrae 16. Anterior neural spine one-third length of second spine. All neural and haemal spines with pointed tips. Neural spines 2–10 decreasing in length and no. 11–16 slightly increasing in length. Preeaudal vertebrae 3–8 with depressed tips, no. 4–16 with enlarged basal parts and no. 7–16 with rather short neural spine. Parapophyses developed on vertebrae 7–16. Pleural ribs observed on vertebrae 3–7. Epipleural ribs not observed, but they may be too thin to show up on radiographs.

Dentition. Palatines with very few and small teeth in 1 row. Vomer boomerang formed with few, small teeth in 1 row. Premaxilla with 2 or 3 rows of small teeth near symphysis, decreasing to one row posteriorad. Dentary with 3 or 4 rows of small teeth near symphysis, decreasing to 1 row posteriorad.

Head pores (Fig. 2 B–D). Three anterior infraorbital pores forming dense pattern close to upper lip in front of eye; infraorbital pores large, about size of posterior nostril. One anterior mandibular pore at tip of lower jaw corresponding to first anterior mandibular pore in terminology of Schwarzhans et al. (2005); anterior mandibular pore large, with papilla at anterior rim. One moderately large posterior mandibular pore behind termination of maxilla corresponding to third posterior mandibular pore in terminology of Schwarzhans et al. (2005).

Otolith (Fig. 3 A–C). Small, elongate, with length to height ratio of 2.0 and height to thickness ratio of 1.8. Anterior and posterior tips nearly symmetrical, pointed, slightly shifted dorsally. Dorsal and ventral rims gently curved without prominent angles. Inner face nearly flat with central, small, oval, undivided sulcus with single shallow colliculum. Otolith length to colliculum length = 3.5; colliculum length to height = 2.2. Dorsal depression and ventral furrow feble. Outer face distinctly convex, smooth.

Male copulatory organ (Fig. 2 E–F). Large, broad hood with free, small genital papilla inserted in proximal, ventral position.

Colour. Head and body brown with numerous, tiny, black spots most dense on snout, check and jaws. Eye bluish with greenish lens.

Biology. Viviparous species, living near to, or on, the bottom on the deep northwestern Australian Plateau.

Distribution. Only known from the holotype trawled at 392 m off northwestern Australia.

Etymology. From disjunctus (Latin) = separated, distant, referring to the position of the anus midway between the tip of the snout and the origin of the anal fin. The name is adjectival.
ACKNOWLEDGEMENTS

We are grateful to Martin Gomon and Dianne Bray (NMV) who let us borrow this interesting fish. Ronald Fricke (SMNS) is thanked for his careful review of the manuscript.

REFERENCES


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Revision of the genus *Microbrotula* (Teleostei: Bythitidae), with description of two new species and a related new genus

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ABSTRACT

Following recent systematic revisions of Anderson (2005, 2007), seven species of the viviparous genus *Microbrotula* (Teleostei: Bythitidae) have been described, all from the Indo-west Pacific Ocean. Six of these species are here recognised as valid: *M. bentleyi*, *M. greenfieldi*, *M. punicia*, *M. queenslandica*, *M. randalli* and *M. rubra*. *Microbrotula polyactis* is regarded as a junior synonym of *M. bentleyi*. Two additional new species, *M. andersoni* and *M. hamata*, obtained from Christmas Island (eastern Indian Ocean) and New Caledonia, respectively, are described herein. The main specific characters distinguishing the new species are the number of precaudal vertebrae, numbers of pectoral, caudal and dorsal fin rays, number and distribution of head pores, number and distribution of sensory papillae on the head and lateral line, presence or absence of a (mostly hidden) curved spine at the lower angle of the preopercle, and otolith morphology. The limits of the genus *Microbrotula* are redefined and the genus is compared with other shallow water bythitine genera. *Calamopteryx* is regarded as the genus that is most closely related to *Microbrotula*. As a result of the redefinition of *Microbrotula*, one of its previously assigned species, *M. randalli*, is placed in a new genus, *Ematops*, characterised by the head pore pattern, unique presence of scales partly covering the eye, number of precaudal vertebrae, number of pectoral and caudal fin rays and the otolith proportion.

Keywords: Bythitidae, viviparous brotulas, Indo-west Pacific, coral reef fishes, new genus, new species, *Microbrotula*, *Ematops*.

INTRODUCTION

Fishes of the family Bythitidae are widely distributed in the world's oceans, ranging in habitats from intertidal pools, reefs and salt-water coves, across the continental shelf, to bathyal depths. They are generally near-bottom fishes, benthopelagic in the deeper seas and often secretive on the continental rise and in reefal or rocky habitats. The secretive mode of life of many of the species of the subfamily Bythitinae results in relatively few of them being caught. Investigations over the last decade as well as ongoing research indicate that bythitins may not be as rare as previously thought in near-shore and continental slope environments. In fact, certain groups seem to be adapted to this specific mode of life. In shallow water, genera of cryptic tropical reef and occasional subtropical rocky shore dwellers include *Acarobythites* Machida, 2000, *Anacanthobythites* Anderson, 2008, *Calamopteryx* Böhlke & Cohen, 1966, *Grammornus* Gill, 1896, *Microbrotula* Gosline, 1953 and *Stygobrotula* Böhlke, 1957. Some members of the genera *Grammornus* and *Lucifuga* Poey, 1858 have also invaded salt water coves, and occasionally even freshwater coves, and evolved endemics therein.

*Microbrotula* Gosline, 1953 is a genus of Bythitinae characterised by the male copulatory organ being an integrated part of the fleshy genital hood with the penis present as a small soft papilla without pseudoclaspers, and the caudal fins being broadly joined to the dorsal and anal fins (in all but a few species of *Lucifuga* and *Grammornus*). Fishes of the genus *Microbrotula* inhabit hollows and crevices in tropical reefs of the Indo-west Pacific. Since the description of the genus (Gosline 1953), six species are now recognised. One of these, *M. randalli* Cohen & Wourms, 1976, is significantly different from the other five and from the two new species herein described, and is therefore placed in a new genus, *Ematops*.

MATERIAL AND METHODS

A total of 39 specimens of *Microbrotula* and *Ematops* gen. nov. were examined for this study, including the type material of all the previously described species.

Institutional abbreviations follow Fricke & Eschmeyer (2011).

Comparative material of the three species of the genus *Calamopteryx* and one of two species of *Anacanthobythites* was also examined.


Calamopteryx robinsorum Cohen, 1973: holotype, USNM 26748, Caribbean Panama; 2 paratypes, ZMUC P77573-574, Caribbean Mexico; 1 non-type, USNM 359299, off Caribbean Columbia.

Anacanthobythites tasmaniensis Anderson, 2008: 1 paratype, CSIRO H 6280-02, off Port Davey, Tasmania.

Morphometric characters are given as a percentage of standard length (SL) and head length (HL). In the descriptions, holotype values are given first, followed by paratype values in parentheses. The size of the eye is measured as the horizontal diameter of the pigmented eyeball. Counts were made from radiographs, except for the pectoral fin rays, gill rakers, teeth and scale rows. Abbreviations used for counts are: D/V = anterior dorsal fin ray above vertebra number; D/A = anterior anal fin ray below dorsal fin ray number; V/A = anterior anal fin ray below vertebra number.

Otoliths were removed through the gill cavity by making a small incision in the otic capsule above the gills on the right side. Otolith measurements include length, height and thickness of the otolith and length of the colliculum, a structure filling the sulcus on the inner face (for otolith terminology see Schwarzhans et al. 2005). Measuring of the colliculum was selected over measuring the sulcus, the usual measurement in otoliths, because in the otoliths of many bythitins, including Microbrotula and Ematops, the colliculum has a sharper outline than the sulcus, resulting in more repeatable values.

Head drawings and pore counts follow the standards established for the description of Dinematichthyinae in Moller et al. (2004) and Schwarzhans et al. (2005). In Ematops, an additional set of pores is present on the operculum that require specific description (see p. 156).

Scale length was taken on scales from under the pectoral fin.

The distribution map (Fig. 10) was created using Microsoft Encarta 2001 digital world atlas.

Family Bythitidae Gill, 1861

Subfamily Bythitinae Gill, 1861

KEY TO SHALLOW WATER GENERA OF BYTHITINAE

The following key includes genera, of which some species inhabit deeper water.

1a. Maxilla narrow posteriorly, not expanded .............. 2
1b. Maxilla vertically expanded posteriorly .................. 3

2a. Body and head naked; head pointed; precaudal vertebrae 12 or 13........................................... Acarobythites
2b. Body and part of head with scales; head blunt; precaudal vertebrae 14 ..................................... Stygnobrotula

3a. Head scales partly extending over eye; precaudal vertebrae 13 or 15; caudal vertebrae 38–42; caudal fin rays 3 or 4; pectoral fin rays 9–11; supraorbital pores 6 or 7 (including one median interorbital) .............................................. Ematops gen. nov.
3b. No scales extending over eye; precaudal vertebrae 10–13; caudal vertebrae 33–38; caudal fin rays 6–10; pectoral fin rays 11–29; supraorbital pores 0 or 1 ......... 4

4a. Pectoral fin rays 19–29; branchiostegal rays 8; lateral line with 2 or more series of papillae; no preopercular spine ............................................................. Grammonus
4b. Pectoral fin rays 11–19; branchiostegal rays 6 or 7; lateral line with single series of papillae; preopercle with exposed or covered forward-curved spine (absent in Microbrotula punicea and rubra) ............. 5

5a. Pectoral fins supported by elongate radials .............. 6
5b. Pectoral fin radials not elongate .............................. Calamopteryx

Table 1. Comparison of morphological characters between Microbrotula, Ematops gen. nov., Calamopteryx and Anacanthobythites.

<table>
<thead>
<tr>
<th>Character</th>
<th>Microbrotula</th>
<th>Ematops</th>
<th>Calamopteryx</th>
<th>Anacanthobythites</th>
</tr>
</thead>
<tbody>
<tr>
<td>Precaudal vertebrae</td>
<td>11–13</td>
<td>13–15</td>
<td>11–12</td>
<td>11–12</td>
</tr>
<tr>
<td>Caudal fin rays</td>
<td>6–9</td>
<td>3–5</td>
<td>10</td>
<td>10</td>
</tr>
<tr>
<td>Supraorbital pores</td>
<td>none</td>
<td>6–7</td>
<td>1</td>
<td>none</td>
</tr>
<tr>
<td>Lower preopercular pores</td>
<td>mostly 1–2</td>
<td>1–2</td>
<td>none</td>
<td>none</td>
</tr>
<tr>
<td>Spine at lower preopercle angle</td>
<td>mostly present, hidden</td>
<td>absent</td>
<td>free</td>
<td>free or hidden</td>
</tr>
<tr>
<td>Developed rakers on 1st gill arch</td>
<td>2–4</td>
<td>2–4</td>
<td>2</td>
<td>none</td>
</tr>
<tr>
<td>Palatine teeth</td>
<td>present / absent</td>
<td>present</td>
<td>present</td>
<td>none</td>
</tr>
<tr>
<td>Pectoral radials</td>
<td>short</td>
<td>short</td>
<td>elongated</td>
<td>short</td>
</tr>
<tr>
<td>Head squamation</td>
<td>patchy; cheek, opercle, oeciput</td>
<td>entire head, partly over eye</td>
<td>patchy; cheek, opercle, oeciput</td>
<td>patchy; cheek, oeciput</td>
</tr>
<tr>
<td>Otolith length : otolith height</td>
<td>1.9–2.4</td>
<td>2.4–2.7</td>
<td>2.4–2.9</td>
<td>2.7</td>
</tr>
<tr>
<td>Interorbital width in % SL</td>
<td>3.9–7.0</td>
<td>1.1–1.7</td>
<td>3.9–6.4</td>
<td>5.4–5.7</td>
</tr>
</tbody>
</table>

148
Revision of Microbrotula (Teleostei: Bythitidae)

Fig. 1. Species of Microbrotula: A, Microbrotula andersoni sp. nov. Holotype, WAM P.25084-004, female, 52 mm SL; B, Microbrotula hamata sp. nov. Holotype, NMNZ P.29559, female, 33.5 mm SL; C, Microbrotula aff. bentleyi Anderson, 2005, NSMT 71423, female, 34.5 mm SL.

6a. No palatine teeth; no preopercular pore; no developed rakers on first gill arch. Aracanthobythites

6b. Palatine teeth present or absent; preopercular pores 1 or 2; 2–4 developed rakers on first gill arch. Microbrotula

Microbrotula Gosline, 1953
(Tables 1–3)

Gender feminine. Type species, by original designation, Microbrotula rubra Gosline, 1953. Type locality: Kaneohe Bay, Oahu Island, Hawaii.

As redefined in this paper, Microbrotula comprises seven species – M. andersoni sp. nov. (Fig. 1A), M. bentleyi Anderson, 2005, M. greenfieldi Anderson, 2007, M. hamata sp. nov. (Fig. 1B), M. punicea Anderson, 2007, M. queenslandica Anderson, 2005 and M. rubra Gosline, 1953. Microbrotula polyactis Anderson, 2005 is considered a junior synonym of M. bentleyi (see discussion of M. bentleyi). A previously recognised Microbrotula species, M. niger Gosline, 1953, is now valid as Grammonus watiki (Cohen, 1964) (see Nielsen et al. 1999).

Table 2. Morphological comparison of the species of *Microbrotula* and *Ematops*. * includes one tentatively assigned specimen (outside values in brackets). ** Holotype included in range from original description.

<table>
<thead>
<tr>
<th></th>
<th><em>Ematops</em></th>
<th><em>Microbrotula</em></th>
<th><em>beattleyi</em></th>
<th><em>greenfieldii</em></th>
<th><em>hanaita</em></th>
<th><em>mnniciea</em></th>
<th><em>queenslandica</em></th>
<th><em>rubra</em>*</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of specimens studied</td>
<td>8</td>
<td>1</td>
<td>17</td>
<td>2</td>
<td>2</td>
<td>7</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Pectoral fin rays</td>
<td>9–11</td>
<td>3–4</td>
<td>8</td>
<td>7–8</td>
<td>8</td>
<td>7</td>
<td>8</td>
<td>7</td>
</tr>
<tr>
<td>Total vertebrae</td>
<td>51–57</td>
<td>46</td>
<td>19</td>
<td>70</td>
<td>59</td>
<td>8</td>
<td>14</td>
<td>13</td>
</tr>
<tr>
<td>Anal fin rays</td>
<td>63–75</td>
<td>70</td>
<td>70</td>
<td>62–70</td>
<td>58–61</td>
<td>6</td>
<td>14</td>
<td>14</td>
</tr>
<tr>
<td>Dorsal fin rays</td>
<td>78–87</td>
<td>14–19</td>
<td>14–15</td>
<td>6</td>
<td>7</td>
<td>8–10</td>
<td>21</td>
<td>21</td>
</tr>
<tr>
<td>Palatine teeth</td>
<td>strong, 1+0</td>
<td>absent</td>
<td>present</td>
<td>present</td>
<td>present</td>
<td>absent</td>
<td>present, with two points</td>
<td>absent</td>
</tr>
<tr>
<td>Mandibular pores</td>
<td>3+3</td>
<td>3+3</td>
<td>3+3</td>
<td>3+3</td>
<td>3+3</td>
<td>3+3</td>
<td>3+3</td>
<td>3+3</td>
</tr>
<tr>
<td>Preopercular pores</td>
<td>1–2+0</td>
<td>3+1</td>
<td>3+0</td>
<td>3+3</td>
<td>3+3</td>
<td>3+3</td>
<td>3+3</td>
<td>3+3</td>
</tr>
<tr>
<td>Infraorbital pores</td>
<td>3+1</td>
<td>3+0</td>
<td>3+3</td>
<td>3+3</td>
<td>3+3</td>
<td>3+3</td>
<td>3+3</td>
<td>3+3</td>
</tr>
<tr>
<td>Head papillae</td>
<td>anterior half</td>
<td>between eyes and low, jaw few</td>
<td>anterior half to entire head</td>
<td>lower jaw</td>
<td>anterior half</td>
<td>between eyes</td>
<td>entire head</td>
<td>entire head</td>
</tr>
<tr>
<td>Lateral line papillae</td>
<td>anterior 1/4</td>
<td>patches</td>
<td>patches</td>
<td>patches</td>
<td>patches</td>
<td>patches</td>
<td>yes, no detail unknown</td>
<td></td>
</tr>
<tr>
<td>Otolith length : otolith height</td>
<td>2.4–2.7</td>
<td>2.1</td>
<td>1.9–2.1 (2.2)</td>
<td>2.0</td>
<td>2.2</td>
<td>2.4</td>
<td>2.3</td>
<td>unknown</td>
</tr>
<tr>
<td>Otolith length : colliculum length</td>
<td>2.8–3.3</td>
<td>2.8</td>
<td>2.5–2.7</td>
<td>2.4</td>
<td>3.5</td>
<td>3.1–3.5</td>
<td>2.4</td>
<td>unknown</td>
</tr>
<tr>
<td>Interorbital width in % SL</td>
<td>1.1–1.7</td>
<td>3.9</td>
<td>4.5–7.0</td>
<td>5.7–6.4</td>
<td>4.3–4.5</td>
<td>4.1–4.3</td>
<td>4.2–4.5</td>
<td>6.1–7.0</td>
</tr>
</tbody>
</table>

*M. rubra*), 3 anterior infraorbital, no posterior infraorbital (except 3 in *M. rubra*).

**Comparison and discussion.** *Microbrotula* resembles *Calanopteryx*, *Anacanthobythites* and *Ematops* gen. nov. (Table 1). Of these genera, *Calanopteryx* was hitherto thought to be well defined by the forward-curved spine at the lower angle of the preopercle, but the observation of a similar spine in *Lucifina inopinata* Cohen & McCosker, 1998, and also in the genus *Anacanthobythites* and many species of *Microbrotula* invalidates it as a diagnostic character of *Calanopteryx*. Thus, *Microbrotula* is presently distinguished from *Calanopteryx* merely by the short pectoral peduncle (versus elongate) and the presence of 1–2 lower preopercular pores (versus none). *Microbrotula* differs from *Anacanthobythites* by the presence of 1–2 lower preopercular pores (versus none), palatine teeth present (versus absent) and 2–4 developed gill rakers on first branched arch (versus none). Species of *Anacanthobythites* generally grow larger than species of *Microbrotula* (50–106 mm SL versus mostly less than 60 mm SL). For a comparison with *Ematops* gen. nov. see p. 159. Apparently all four genera are closely related. *Calanopteryx* represents the New World counterpart of the Indo-west Pacific tropical genus *Microbrotula*, and *Anacanthobythites*, its southern temperate relative.

**KEY TO SPECIES OF MICROBROTULA**

1a. Pectoral fin rays 11; preopercular spine with 2 points ........................................... *M. queenslandica*

1b. Pectoral fin rays 13–19; preopercular spine with single point or absent .................................... 2
Revision of Microbrotula (Teleostei: Bythitidae)

Fig. 2. *Microbrotula andersoni* sp. nov. Holotype, WAM P.26084-004, female, 52 mm SL.: A, lateral view of head; B, dorsal view of head; C, median view of right otolith; D, ventral view of right otolith.

2a. Pectoral fin rays 12–14; caudal fin rays 6; preopercular spine present or absent

2b. Pectoral fin rays 15–19; caudal fin rays 7–9; preopercular spine present

3a. Dorsal fin rays 62–70; no cephalic lateralis pores; preopercular spine present; otolith length 2.4 times length of colliculum

3b. Dorsal fin rays 80–92; cephalic lateralis pores present; preopercular spine absent; otolith length 3.1–3.5 times length of colliculum (not known for *M. rubra*).

4a. Upper preopercular pore absent; posterior infraorbital pores absent; posterior 5 or 6 precaudal vertebrae without ribs; D/A 18–21; papillae on head only between eye

4b. Upper preopercular pore 1; posterior infraorbital pores 3; posterior 1–2 precaudal vertebrae without ribs; D/A 9, papillae on entire head

5a. Dorsal fin rays 76; scale patches on cheek, opercle and occiput connected; otolith length 3.5 times length of colliculum

5b. Dorsal fin rays 61–70; scale patches on cheek, opercle and occiput separated; otolith length 2.5–2.8 times length of colliculum

6a. Pectoral fin rays 15–17; anal fin rays 50–57; papillae on anterior fourth to half of lateral line; otolith not expanded anteriorly

6b. Pectoral fin rays 19; anal fin rays 59; few papillae on lateral line; otolith anteriorly expanded

*Microbrotula andersoni* sp. nov.

(Tables 2, 3, Figs 1 A, 2A–D, 10)


Diagnosis. Vertebrae 11+35=46; dorsal-fin rays 70, anal-fin rays 59, pectoral-fin rays 19, caudal-fin rays 8. D/V 8; D/A 14; V/A 13. Head with separated scale patches on cheeks, opercle and occiput. Papillae on anterior part of head only. Hidden, forward-curved spine at lower angle of preopercle. Posterior mandibular pores 3, lower preopercular pores 2. Palatine teeth absent. Otolith shape anteriorly expanded, otolith length to otolith height 2.1, otolith length to colliculum length 2.8.

Description (Figs 1A, 2A,B). The principally meristic and morphometric characters of *Microbrotula andersoni* are shown in Table 3. Head large with pointed snout. Head with separate scale patches on cheek (containing 3 vertical rows of scales), opercle and occiput, reaching anteriorly to posterior margin of eye (Fig. 2A,B). Horizontal diameter of scales on body about 3% SL. Maxillary ending far beyond eye, dorsal margin of maxillary covered by dermal lobe of upper lip, posterior end vertically expanded and angular. Small anterior nostril just above upper lip. Posterior nostril very small, about 0.1 size of eye. Opercular spine thin, needle-like, covered by skin. Forward-curved spine at lower
Table 3. Meristic and morphometric characters of 2 new species of Microbrotula spp. and of Ematops randalli. HT = holotype; PT = paratype; numbers in parentheses represent means

* The low numbers are most probably caused by broken rays

<table>
<thead>
<tr>
<th>Characters</th>
<th>Andersoni</th>
<th>Hamata</th>
<th>Ematops randalli</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Meristic characters</strong></td>
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<td></td>
<td></td>
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<tr>
<td>Standard length in mm (SL)</td>
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<td>33.5</td>
<td>23</td>
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<tr>
<td>Dorsal fin rays</td>
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<td>Caudal fin rays</td>
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<td>Anal fin rays</td>
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<td>62</td>
<td>60</td>
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<td>15</td>
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<td>Pelvic fin rays</td>
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<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Precaudal vertebrae</td>
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<td>12</td>
<td>11</td>
</tr>
<tr>
<td>Total vertebrae</td>
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<td>48</td>
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<tr>
<td>Dorsal fin origin above vertebra number</td>
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<td>8</td>
</tr>
<tr>
<td>Anal fin origin below dorsal ray number</td>
<td>14</td>
<td>14</td>
<td>15</td>
</tr>
<tr>
<td>Anal fin origin below vertebra number</td>
<td>13</td>
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<td>14</td>
</tr>
<tr>
<td>Long rakers on anterior gill arch</td>
<td>3</td>
<td>3</td>
<td>3</td>
</tr>
</tbody>
</table>

| **Morphometric characters in % of SL** | | | |
| Head length | 29.0 | 28.5 | 29.5 | 27.0 (28.5) 31.0 |
| Depth at origin of dorsal fin | 17.5 | 18.0 | 15.0 | 16.0 (17.9) 19.0 |
| Depth at origin of anal fin | 17.0 | 16.0 | 13.0 | 14.0 (16.0) 19.0 |
| Snout length | 5.7 | 6.3 | 5.7 | 4.2 (4.5) 5.0 |
| Max. head height | 16.0 | 15.0 | 14.5 | 13.5 (14.7) 15.5 |
| Max. head width | 15.0 | 14.0 | 12.5 | 9.0 (10.9) 13.5 |
| Upper jaw length | 14.5 | 14.0 | 15.0 | 12.5 (13.2) 15.0 |
| Diameter of eye ball | 4.1 | 3.3 | 3.5 | 2.9 (3.4) 3.8 |
| Interorbital width | 3.9 | 4.5 | 4.3 | 1.1 (1.5) 1.7 |
| Maxillary height | 5.5 | 5.1 | 4.3 | 4.5 (5.0) 5.3 |
| Postorbital length | 19.5 | 19.0 | 18.5 | 17.0 (19.3) 21.0 |
| Preopercle width | 26.0 | 25.0 | 24.5 | 20.5 (21.3) 22.5 |
| Preanal length | 47.0 | 52 | 47.0 | 48.5 (50.8) 52.0 |
| Predorsal length | 39.5 | 36.0 | 32.5 | 39.0 (41.9) 44.5 |
| Base of pelvic fin to anal fin origin | 23.0 | 25.0 | 21.5 | 28.0 (30.0) 31.0 |
| Length of pectoral fin | 15.5 | 17.5 | 14.3 | 13.0 (15.5) 19.5* |
| Length of pelvic fin | 11.5+ | 19.0 | 22.6 | 10.5 (13.2) 18.0* |

Angle of preopercle covered by skin. Anterior gill arch with 3 elongate rakers.

**Head sensory pores** (Fig. 2A,B). No supraorbital pores. Anterior infraorbital pores 3, no posterior infraorbital pores. Mandibular pores 6 (3 anterior and 3 posterior). 2 lower preopercular pores, no upper preopercular pore.

**Dentition.** Premaxillary with several rows of granular teeth and a few fangs near symphysis. Teeth on vomer separated into 2 circular patches with fewer than 10 pointed teeth in each. Dentary with several rows of small granular teeth; inner row with somewhat larger pointed teeth. Palatine teeth absent.

**Otolith** (Fig. 2C,D). Elongate, otolith length to height 2:1. Anterior tip broadly rounded, expanded; posterior tip narrower. Dorsal and ventral rims regularly curved, smooth, highest anterior to the middle. Otolith length to sulus height 2:8. Sulus positioned slightly anteriorly, undivided, with single oval colliculum, not inclined against otolith axis. Ventral furrow feeble, close to ventral rim of otolith.

**Axial skeleton.** Neural spine of vertebrae 4–5 inclined and 6–8 depressed, with broad base. Parapophyses present on vertebrae 7 to 11. Pleural ribs on vertebrae 2 to 10. First anal fin pterygiophore not elongate.

**Colour.** Light brown to beige in alcohol.

**Comparison.** Microbrotula andersoni, together with M. bentleyi and M. punicea, are the only species of the genus growing to sizes greater than 45 mm SL. Microbrotula andersoni belongs to a group of species having 15 or more pectoral fin rays and 7–9 caudal fin rays, which also includes M. bentleyi and M. hamata sp. nov. Microbrotula andersoni is readily distinguished from these species by its large size and 19 pectoral fin rays (versus 15–17). It is closest to M. bentleyi, from which it is further distinguished by having few papillae on the head and a total lack of papillae on the lateral line as well as a different shape of its otolith.

**Distribution** (Fig. 10). Only known from the holotype, collected from Christmas Island in the eastern Indian Ocean.
**Etymology.** Named in honour of M. Eric Anderson for his contribution to knowledge of the genus Microbrotula.

**Microbrotula bentleyi Anderson, 2005**

(Table 2, Figs. 1C, 3A–I, 10)


**Material examined:** (17 specimens, 21.5–60 mm SL) – *Paratypes* of *M. bentleyi* (5 specimens): BPBM 37875, Egypt, Red Sea, Gulf of Aqaba, Ras Abu Galum, 170–180 feet, coll. J. Randall, O. Gon and R. Kurutz, 2 August 1976; USNM 227220 (male, 36 mm SL, female 40.5 mm SL), Red Sea, Gulf of Aqaba, bay at El Hamira, 9–12 m, coll. V. Springer and party, 8 September 1969; USNM 227226 (male, 33.5 mm SL, female, 29 mm SL), Red Sea, Gulf of Aqaba, bay at El Hamira, 0–16 m, coll. V. Springer and party, 19 July 1969. – *Paratypes* of *M. polyacis* (8 specimens): USNM 227221 (male, 39 mm SL), Philippines, Negros Island, off Bais, 9°36.9′N, 123°10.1′E, 0–37 m, coll. V. Springer and party, 17 June 1978; USNM 227224 (male, 32.5 mm SL, female, 26.5 mm SL), Philippines, Cebu Island, Caceras Reef, 24–31 m, coll. Libbey and party, 18 May 1979; USNM 227227 (4 males 21.5–33.5 mm SL and 1 female, 25.5 mm SL). Indonesia, Ambon Island, 3°47′S, 128°01′E, 10.6–13.7 m, coll. J. Randall and Gordon, 28 September 1974. – *Non-type material* (3 specimens): BPBM 18222 (male, 45 mm SL), Red Sea, Gulf of Aqaba, 1 km north of Coral Island, pro-noxfish, 15 m, coll. J. Randall and O. Gon, 22 September 1974; BPBM 38625 (male, 60 mm SL), Red Sea, Gulf of Aqaba, Eilat, rotenone, 15 m, coll. J. Randall and Gordon, 28 September 1974; BPBM 38626 (female, 49 mm SL), Red Sea, Gulf of Aqaba, Eilat, rotenone, coll. J. Randall and Gordon, 28 September 1974.

**Tentatively assigned specimens:** (1 specimen) NSMT 71423 (female, 34.5 mm SL), Indonesia, Ambon Island, Lilbooi, Ambon Bay, 3°45′S, 128°1′E, 300 m, coll. K. Matsuura and K. Shibukawa, 5 December 1998.


**Discussion.** *Microbrotula bentleyi* was based on the holotype taken off South Africa and five paratypes from the Gulf of Aqaba. *Microbrotula polyacis* was described from the holotype from off Cape York, northern Queensland, Australia, and nine paratypes from Indonesia and the Philippines. Anderson (2005) lists three characters as the diagnostic differences between the two species: the caudal fin ray count (6 in *M. bentleyi* versus 7–8 in *M. polyacis*), the pectoral fin ray count (14 in *M. bentleyi* versus 16–17 in *M. polyacis*), and the scale size (lateral scale rows 54–55 in *M. bentleyi* versus 47–50 in *M. polyacis*). All the paratypes of *M. bentleyi* and eight paratypes of *M. polyacis* were studied during the course of this review. The holotype of *M. bentleyi* was studied again by O. Gon and M.E. Anderson at SAICAB. All investigated specimens as well as four non-type specimens exhibited 7 or 8 caudal fin rays except for some specimens, which did not warrant reliable caudal fin ray counts due to poor preservation of the caudal fin, and 16 or 17 pectoral fin rays. Only two specimens had 15 pectoral fin rays, one paratype of *M. bentleyi* (BPBM 37875), which is considered to be within the variability of the species and one tentatively assigned specimen (NSMT 71423). Differences in the scale sizes could not be verified.

In conclusion, none of the characters used for separating *M. bentleyi* and *M. polyacis* are validated. Consequently, we consider the two species are conspecific and select *M. bentleyi* as the senior synonym. We conclude that a relatively large degree of intraspecific variability occurs in *M. bentleyi*. These differences concern the abundance of papillae on the head and lateral line (Fig. 3A–E) and otolith proportions (length: height = 1.9 to 2.2) (Fig. 3F–I).

One specimen is tentatively placed in *M. bentleyi* – NSMT 71423 from off Ambon Island, Indonesia (Fig. 1C). Several of its meristic values are at the lower limit of, or just outside, the variation observed in *M. bentleyi* (Table 2): vertebrae 11+33=44, dorsal fin rays 61, anal fin rays 50, pectoral fin rays 14, D/A 12, V/A 15. The otolith is the most slender found in the species with a length to height ratio of 2.2 (Fig. 31). Most strikingly though, the well-preserved specimen shows a short snout and abundant and well developed papillae all over its head and along the anterior half of the lateral line (Figs. 1C, 3D–E). This specimen may possibly represent yet another species, but we have refrained from establishing a separate species in light of the large spread of variation observed in *M. bentleyi* and the lack of further supporting material.

**Distribution** (Fig. 10). *Microbrotula bentleyi* is the most widely distributed species of the genus, ranging from South Africa to the Red Sea in the western Indian Ocean and from the Philippines to Cape York Peninsula in northern Australia. The large gap in the distribution is probably a collecting artefact rather than indicative of a true distribution.

**Microbrotula greenfieldi Anderson, 2007**

(Table 2, Figs 4A–D, 10)

**Material examined:** (1 specimen, male, 30.5 mm SL). **Paratype** – CAS 223980, Fiji, Vanua Levu, Paceoe Reef, 16°50′S, 178°13′E, 10.6–13.7 m, coll. D. Greenfield and party, 4 April 2002. The holotype, CAS 222542, from the same location, was studied by the senior author prior to the description by Anderson.

**Diagnosis.** Vertebræ 11–12+34–35=45–47, dorsal-fin rays 62–70, anal-fin rays 58–61, pectoral-fin rays 14, caudal-fin rays 6, D/V 7–8; D/A 14–15; V/A 14. Small forward-curved spine at lower angle of preopercle. Head with separated scale patches on cheeks, operculum and occiput. Papillae on lower jaw only. No posterior mandibular pores, no lower preopercular pores. Palatine teeth minute, in single row. Otolith length to otolith height, 2.0, otolith...
Fig. 3. Microbrontula bentleyi Anderson, 2005: A, Paratype of *M. bentleyi*, USNM 227220, female, 40.5 mm SL, lateral view of head; B, Paratype of *M. polyactis* Anderson, 2005, USNM 227224, male, 32.5 mm SL, dorsal view of head; C, Paratype of *M. bentleyi*, BPBM 37875, male, 37.5 mm SL, lateral view of head; D-E, tentatively assigned specimen, NSMT 71423, 34.5 mm SL, D, lateral view of head, E, dorsal view of head; F, Paratype of *M. polyactis* Anderson, 2005, USNM 227227, male, 33.5 mm SL, median view of right otolith; G-H, Paratype of *M. bentleyi*, BPBM 37875, male, 37.5 mm SL, G, median view of right otolith, H, ventral view of right otolith; I, tentatively assigned specimen, NSMT 71423, 34.5 mm SL, median view of right otolith.
Fig. 4, Microbrotula greenfieldi Anderson, 2007. Holotype, CAS 222542, male, 34 mm SL.: A, lateral view of head; B, dorsal view of head; C, median view of right otolith; D, ventral view of right otolith.

length to colliculum length, 2.4. Male copulatory organ with 3 small papillae at base of genital hood.

Remarks. Additional previously unreported characters of M. greenfieldi are related to the otoliths (Fig. 4C,D). A detailed figure of the head is also provided (Fig. 4A,B).

Distribution (Fig. 10). It is endemic to Fiji.

Microbrotula Itamata sp. nov. (Tables 2, 3, Figs IB, 5A-D, 10)

Material examined. (2 specimens, 22.5–33.5 mm SL). Holotype (33.5 mm SL, female) – NMNZ 29559, New Caledonia, 8 nautical miles WSW of Noumea, Seche Croissant Reef, 22°19.0’S, 166°21.0’E, 8–10 m, coll. C. Roberts and C. Paulin, 29 October 1992. Paratype (22.5 mm SL) – MNHN 2011-0815, same data as holotype.

Diagnosis. Vertebrae 11–12+36–37=48, dorsal-fin rays 76, anal-fin rays 60–62, pectoral-fin rays 15 or 16, caudal-fin rays 8–9. D/V 8; D/A 14–15; V/A 14. Head with continuous scale patches from cheek and opercle to occiput, except for narrow gap between cheek and opercle. Few papillae on anterior half of head. Forward-curved spine at lower angle of preopercle, hidden by thin skin. Posterior mandibular pores 3, lower preopercular pores 1. Palatine teeth very small. Otolith elongate, length to height, 2.2; otolith length to colliculum length, 3.5.

Description (Figs IB, 5A,B). The principal meristic and morphometric characters of Microbrotula hamata are in Table 3. Head slender with pointed snout. Head with interconnected scale patches on cheek, opercle and operculum, except for narrow gap between cheek and opercle (Fig 5A,B). Horizontal diameter of scales on body about 2% SL. Maxillary ending far beyond eye, dorsal margin of maxillary covered by dermal lobe of upper lip, posterior end angular and vertically expanded. Small anterior nostril just above upper lip. Posterior nostril very small, about 0.1 diameter of eye. Opercular spine thin, needle-like, covered by skin. Well-developed forward-curved spine at lower angle of preopercle covered by thin skin. Anterior Gill arch with 3 elongate rakers.

Head sensory pores (Fig. 5A,B). No supraorbital pores. Anterior infraorbital pores 3, no posterior infraorbital pores. Mandibular pores 6 (3 anterior and 3 posterior). 1 lower preopercular pore, no upper preopercular pore.

Dentition (holotype). Premaxillary with several rows of granular teeth and a few fangs near symphysis. Teeth on vomer separated in 2 circular patches each with about 10 teeth of which 1–4 are developed as fangs. Dentary with a few rows of granular teeth and inner row with many fangs. Palatine with very small teeth.

Otolith (Fig. 5C,D). Elongate, length to height, 2.2. Anterior tip pointed, narrowed.; anterior tip dorsally expanded. Ventrals fins regularly curved, smooth, deepest at middle; dorsal fin shallow, smooth, without prominent angles. Otolith length to sulcus length, 3.5. Sulcus positioned slightly towards anterior end, undivided, with single, oval colliculum, slightly inclined against otolith axis. Ventral furrow very feeble; dorsal depression indistinct.

Axial skeleton. Neural spine of vertebrae 4 or 5 inclined and 6–8 depressed, with broad bases. Parapophyses present from vertebrae 7 or 8 to 11 or 12. Pleural ribs on vertebrae 2–10. First anal fin pterygiophore not elongate.

Colour. Preserved specimens dark grey to brown.

Comparison. Microbrotula hamata, together with M. andersoni and M. bentleyi, belong to a group of species having 15 or more pectoral fin rays and 7–9 caudal fin rays. However, M. hamata differs in having a higher number of
dorsal fin rays (76 versus 61–70), continuous squamation on the head, and an extraordinary small sulcus of the otolith expressed in the high ratio of otolith length to colliculum length (3.5 versus 2.5–2.8). It is further distinguished by the presence of only 1 lower preopercular pore (versus 2, occasionally 1 in *M. bentleyi*). It further differs from *M. andersoni* in having a lower number of pectoral fin rays (15 or 16 versus 19).

**Distribution** (Fig. 10). It is endemic to New Caledonia.

**Etymology.** From *hamatus* (Latin) = hook, referring to the forward-curved spine at the lower angle of the preopercle. The name is intended as a noun in apposition.

**Microbrotula punicea** Anderson, 2007

(Table 2, Figs 6A–D, 10)

**Material examined:** (7 specimens, 38.5–57.5 mm SL).

**Holotype** – NMNZ P.41062 (male, 43 mm SL), Kermadec Islands, Raoul Island, 29°16.3'S, 177°57'W, rotenone, 8.5-11.5 m, coll. A. Stewart, 6 November 2004. **Paratypes** – NMNZ P.41036 (1 male, 38.5 mm SL, 2 females, 52–57.5 mm SL), Kermadec Islands, Raoul Island, Meyer Islet, 29°14.7'S, 177°53.1'W, 8.5–11.5 m, coll. A. Stewart and party, 7 November 2004; NMNZ P.41086 (female, 52 mm SL), Kermadec Islands, Raoul Island, 29°17.25'S, 178°11.2'W, rotenone, 14–16 m, coll. A. Stewart and party, 10 November 2004. **Non-type material** – NMNZ P.43555 (2 specimens, 42+– 45 mm SL), Kermadec Islands, Raoul...
Revision of Microbrotula (Teleostei: Bythitidae)


**Diagnosis.** Vertebrae 11–13+38–41=49–53, dorsal-fin rays 77–82, anal-fin rays 64–71, pectoral-fin rays 14, caudal-fin rays 6. D/V 8–10; D/A 18–21; V/A 15–16. Head with connected scale patches on cheek, opercle and operculum. Papillae on head only between eyes; lateral-line papillae along anterior quarter. No spine at lower angle of preopercle. Posterior mandibular pores 3, lower preopercular pores 1. Palatine with strong, recurved teeth, in single row. Otolith elongate, length to height, 2.4; otolith length to colliculum length, 3.1–3.5.

**Remarks.** Additional previously unreported characters of *M. pimicea* are related to the otoliths (Fig. 6C,D). A detailed figure of the head is also provided (Fig. 6A,B).

**Distribution** (Fig. 10). Endemic to the Kermadec Islands.

**Microbrotula queenslandica** Anderson, 2005

(Table 2, Figs 7A–C, 10)

**Material examined:** (1 specimen, 31 mm SL). Paratype - AMS 1.20206-041, Australia, Great Barrier Reef, One Tree Island, 23°30′S, 152°05′E, 22–30 m, coll. F. Talbot and party, 3 December 1969.

**Diagnosis** (Holotype included in range from original description). Vertebrae 12+36=48, dorsal-fin rays 78–80, anal-fin rays 62 or 63, pectoral-fin rays 11, caudal-fin rays 6. D/V 11; D/A 9; V/A 15–17. Head with scales on cheek, opercle and operculum. Papillae numerous, on entire head; lateral-line papillae along entire length of body. No spine at lower angle of preopercle. Posterior mandibular pores 3, posterior infraorbital pores 3, lower preopercular pores 1, upper preopercular pore 1. Palatine teeth strong, in single row.

**Remarks.** The otoliths were not preserved in the paratype of *M. rubra* we studied. A detailed figure of the head is provided (Fig. 8A,B).

**Distribution** (Fig. 10). Endemic to Hawaii.

**Ematops** gen. nov.

(Tables 1–3, Figs 9A–F, 10)


**Microbrotula rubra** Gosline, 1953

(Table 2, Figs 8A,B, 10)

**Material examined:** (1 specimen, male, 35.5 mm SL). Paratype - ZMUC P 77471, Kaneohe Bay, Oahu, Hawaii, rotenone, 1 m, Gosline, 2 October 1948.

**Diagnosis** (Holotype included in range from original description). Vertebrae 11+35=46, dorsal-fin rays 81–92, anal-fin rays 72–80, pectoral-fin rays 12–14, caudal-fin rays 6. D/V 11; D/A 9; V/A 13. Head with scales on cheek, opercle and operculum. Papillae numerous, on entire head; lateral-line papillae along entire length of body. No spine at lower angle of preopercle. Posterior mandibular pores 3, posterior infraorbital pores 3, lower preopercular pores 1, upper preopercular pore 1. Palatine teeth strong, in single row.

**Remarks.** The otoliths were not preserved in the paratype of *M. rubra* we studied. A detailed figure of the head is provided (Fig. 8A,B).

**Distribution** (Fig. 10). Endemic to Hawaii.

Fig. 7. *Microbrotula queenslandica* Anderson, 2005, Paratype, AMS 1.20206-041, male, 31 mm SL: A, lateral view of head (head scales rubbed off); B, median view of right otolith; C, ventral view of right otolith.
**Diagnosis.** Dwarf bythitine species, reaching 40 mm SL. Head continuously covered by scales on cheek, opercle and occiput, extending over eye from behind and above, covering almost half of eye. Head pores: 3 anterior mandibular, 3 posterior mandibular, 6-7 supraorbital positioned as follows from anterior to posterior: 1 on snout in cavity above nostril, 1 in front of eye, 1 median interorbital, 3 or 4 above and behind eye, the last situated above lower preopercular pores, 2 lower preopercular, no upper preopercular, 3 anterior infraorbital, 0 or 1 posterior infraorbital situated below eye close to last anterior infraorbital pore. Head length 27.0–31.0% SL. Dorsal fin rays 78–87. Anal fin rays 63–75. Vertebrae 13–15 + 38–42 = 51–57. Caudal fin rays 3 or 4. Dorsal fin origin above vertebrae 9–11. Anal fin origin below vertebrae 15–19. Pectoral fin rays 9–11. Pectoral peduncle not elongate. Branchiostegal rays 7. Interorbital width 1.1–1.7% SL. Anterior nostril tubular, situated just above upper lip. Rear
Revision of Microbrotula (Teleostei: Bythitidae)

Fig. 10. Sample sites for specimens examined of species of the genera Microbrotula and Ematops. One symbol may represent several samples.

Comparison and discussion. Ematops is readily recognised and distinguished from all other bythitine genera by the unique development of the head squamation, which extends partially over the eye. The pore pattern on the occiput is also highly diagnostic and very similar to the presumably unrelated, bathyal genus Pseudomts Garman, 1899. Ematops randalli was previously placed in Microbrotula, from which it is further distinguished by its higher number of vertebrae (13-15 + 38-42 = 51-57 versus 11-13 + 33-38 = 44-51), lower number of pectoral-fin rays (9-11 versus (11) 13-19) and lower number of caudal-fin rays (3 or 4 versus 6-8). We postulate that these are autapomorphic characters, supporting a derived status of Ematops, which separates it from the genera Microbrotula, Calamopteryx and Anacanthobythites.

Contained species. Ematops is monospecific, with the widespread E. randalli (Cohen & Wourms, 1976) occurring on reefs in the Indo-west Pacific Ocean, from Christmas Island in the eastern Indian Ocean to Vanuatu. Etymology. From ichthy-emata (Greek) = fish-scale and ops (Greek) = face, eye; referring to the unique partial covering of the eye by head scales, which is not known in any other living ophidiform fish.

Ematops randalli (Cohen & Wourms, 1976) (Tables 2, 3, Figs 9A–F, 10)

Material examined: (8 specimens, 25.5–39.5 mm SL): 2 paratypes – USNM 214112 (female, 37 mm SL), American Samoa, Tutuila Island, Fagafite Bay, 30–38 m, coll. J. Randall and party, 8 May 1974; USNM 214703 (male, 38 mm SL), Vanuatu, Efate (Vate) Island, February 1974. Non-type material: USNM 227223 (male, 29 mm SL), Philippines, Apo Island, 9°04'38"N, 123°16'44"E, 0–40 m, coll. V. Springer and party, 7 June 1978; USNM 227225 (female, 39.5 mm SL), Papua New Guinea, Hermit Island, 1°33'S, 144°59'E, 0–15 m, coll. V. Springer and party, 30 October 1978; USNM 363745 (female, 38 mm SL), Vanuatu, Rowa Islands, 13°38'32"S, 167°30'18"E, 23–29 m, coll. J. Williams and party, 20 May 1997; WAM P.26097-011 (female, 31.5 mm SL), Christmas Island (Indian Ocean), White Beach, 10°29'S 105°40'E, 30–40 m, coll. G. Allen and R. Steene, 26 May 1978; WAM P.31140-003 (male, 25.5 mm SL), Papua New Guinea, New Britain, Kimbe Bay, 5°13'S 150°23'E, rotenone, 10–11 m, coll. G. Allen, 8 April 1996; WAM P.31141-015 (male, 29.5 mm SL), Papua New Guinea, New Britain, Kimbe Bay, 5°18'S 150°08'E, rotenone, 5–6 m, coll. G. Allen, 13 April 1996.

Diagnosis. See diagnosis of genus.

Distribution (Fig. 12). Christmas Island in the eastern Indian Ocean to the Philippines, Papua New Guinea, Vanuatu and Samoa in the western and central Pacific.

DISTRIBUTION OF SPECIES

Figure 10 shows known records of Microbrotula and Ematops. Members of these genera are most speciose and abundant on reefs of the tropical western Pacific, chiefly the coasts of the Philippines, Indonesia, New Guinea and northern Australia. Endemism has apparently developed in areas of prolonged geographic isolation such as Hawaii, the Kermadec Islands, Fiji, New Caledonia, Christmas Island, and the southern Great Barrier Reef. In contrast, there appears to be only two geographically widespread...
species, namely *Ematopsis randalli* which ranges from from Christmas Island to the Philippines, New Guinea, Pohnpei, Vanuatu and Samoa, and *Microbrotula bentleyi* which ranges from off northeastern South Africa and the Red Sea and from the northeastern tip of Australia to Indonesia and the Philippines. The apparently disjunct distribution seen in *M. bentleyi* is a recurrent pattern in modern Indo-west Pacific coral reef fishes and is probably a collecting artefact rather than indicative of the true distribution.

The distribution of *Microbrotula* and its endemic species is similar to the distribution of species in Dinematichthyini (Schwarzans et al. 2005; Schwarzans & Moller 2007; Moller & Schwarzans 2008). However, unlike in the Dinematichthyini, *Microbrotula* is not (yet) recorded from northern New Zealand, Western Australia, Taiwan, Japan or Polynesia. On the other hand, *Microbrotula* does occur off Hawaii and the Kermadec Islands, where Dinematichthyini have not been recorded.

**ACKNOWLEDGEMENTS**

We wish to thank the following people for providing material and/or information: Gerald Allen (WAM), Eric Anderson (SAIAB), Alastair Graham (CSIRO), Mark McGrouther (AMS), Amanda Hay (AMS), Peter Last (USNM), Sue Morrison (WAM), Peter Moller (ZMUC), Sandra Raredon (USNM), Clive Roberts (NMNZ), David Smith (USNM), Andrew Stewart (NMNZ), Gento Shinohara (NSMT), Martin Gomon and Barry Russell are thanked for carefully reviewing the manuscript.

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New Dinematichthyini (Teleostei: Bythitidae) from the Indo-west Pacific, with the description of a new genus and five new species

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ABSTRACT

After completion of the revision of the dinematichthyine fishes (Ophidiiformes: Bythitidae: Brosmophycinae) of the Indo-west Pacific based on more than 6500 specimens in 2008, extensive additional material was reviewed from the collections of the Western Australian Museum and the South African Institute of Aquatic Biodiversity. This material has not only led to a better definition of the species Brosmolus longicaudus but also to a recognition of the following new taxa: Didymothallus nudigena sp. nov. from northwestern Australia, Paradiancistrus christmasensis sp. nov. from Christmas Island (Indian Ocean), Nielsenichthys pullus gen. nov., sp. nov. from Nusa Penida, Indonesia, Majungaichthys agalegae sp. nov. from northern Madagascar and Agalega Islands and Mascarenichthys remotus sp. nov. from Rodrigues Island. The status of Alionematichthys sp. 2 in Moller and Schwarzhans (2008) is resolved and placed into A. crassiceps Moller and Schwarzhans, 2008, thereby extending the distribution of the species to northwestern Australia.

Keywords: Viviparous brotulas, Indo-west Pacific, Australia, Indonesia, Madagascar, Rodrigues Island, coral reef fishes, Dinematichthyini, new genus, new species.

INTRODUCTION

The review of the dinematichthyine fishes of the Indo-west Pacific was published in four parts between 2005 and 2008 (Schwarzhans et al. 2005; Moller & Schwarzhans 2006, 2008; Schwarzhans & Moller 2007). Since then, two additional major collections have been made available for review. These were the ichthyological collection of the Western Australian Museum (WAM) at Perth, Western Australia, which was visited by both authors during the occasion of the Indo-Pacific Fish Congress in Perth in 2009, and from the South African Institute of Aquatic Biodiversity (SAIAB) at Grahamstown.

The WAM material provided extensive material from the Western Australian shelf with a number of specimens that allow redifinition of the rare and hitherto poorly defined Brosmolus longicaudus, placement of Alionematichthys sp. 2 of Moller and Schwarzhans (2008) to Alionematichthys crassiceps and the description of Didymothallus nudigena sp. nov., which was previously only known from a few female or juvenile male specimens tentatively placed in Didymothallus mizolepis. Material obtained from Christmas Island in the Indian Ocean has revealed the fourth species of the genus Paradiancistrus - P. christmasensis sp. nov. Finally, recently collected fish from the shores of Sumbawa Island, Indonesia, has yielded another new genus and species - Nielsenichthys pullus gen. nov., sp. nov. This discovery proves that the Indonesian Archipelago still represents one of the areas where dinematichthyine knowledge remains poorly known and new data have to be expected from there. A male specimen from northwestern Madagascar proved to represent the same species previously recorded only from female specimens from the nearby Agalega Islands, which was tentatively placed in Majungaichthys simplex by Schwarzhans and Moller (2007), and is now described as Majungaichthys agalegae sp. nov.

The material made available for review by SAIAB was primarily collected along the eastern African shores, Madagascar and the islands of the western Indian Ocean. It has added important information about the areal distribution of Mascarenichthys heemstraui and yielded a new species of the same genus - Mascarenichthys remotus sp. nov. – endemic to the remote Rodrigues Islands.

MATERIAL AND METHODS

Nearly 6500 specimens of Indo-west Pacific Dinematichthyini have been reviewed for the revision published in four parts between the years 2005 and 2008. The additional material studied at WAM and from SAIAB comprised about 1000 additional specimens. However, only the material of SAIAB and specific loans from WAM are
described in the following and were counted. Any other
identified but not counted specimens from WAM are not
described here.

The material described herein belongs to the following
institutions: AMS (Australian Museum, Sydney); BPBM
(Bishop Museum, Honolulu, Hawaii); SAIAB (South
African Institute for Aquatic Biodiversity, formerly RUSI
(JLB Smith Institute of Ichthyology, Grahamstown); WAM
(Western Australian Museum, Perth); ZMUC (Natural
History Museum of Denmark, Zoological Museum,
University of Copenhagen, Copenhagen). Abbreviations
follow the standards for museum collections given by Fricke
& Eschmeyer (2011).

Comparative material of Indo-west Pacific
Dinematichthyini was described by Schwarzhans et al.
(2005), Moller & Schwarzhans (2006 and 2008) and
Schwarzhans & Moller (2007). Comparative material of
American Dinematichthyini was described by Moller et al.
(2004a) and Moller et al. (2005). Comparative material of
Brosmophycinae and Bythitinae was described by Moller
et al. (2004b).

The methods used in analysing dinematichthyine fishes
follow Moller et al. (2004a) and Schwarzhans et al. (2005).
Abbreviations used in meristic counts are: D/V = anterior
dorsal fin ray above vertebra number; D/A = anterior anal
fin ray below dorsal fin ray number; V/A = anterior anal
fin ray below vertebrae number; D-A = number of dorsal
fin rays minus number of anal fin rays; V in D = number of
dorsal fin rays per ray-bearing vertebra.

The ecology of most of the species is poorly known.
From available station data we have gathered some
information about habitat and depth range, but we have very
little data about behaviour, live coloration or feeding. Few
females were examined for reproductive data, e.g., number
and size of embryos.

The distribution maps were created using Microsoft
Encarta 2001 digital world atlas. Standards of fish
classification, original descriptions and type catalogues
follow Eschmeyer & Fricke (2011).

**TAXONOMY**

**Family Bythitidae Gill, 1861**

**Subfamily Brosnophycinae Gill, 1862**

**Tribe Dinematichthyini Cohen & Nielsen, 1978**

**Diagnosis.** Male copulatory organ with penis and 1 or 2
(rarely 3) pairs of pseudoclaspers in cavity of ventral body
wall covered by fleshy hood. First anal fin pterygiophore
slightly to strongly elongate. Head pore system generally not
reduced, 6 mandibular, 2–4 preopercular, 5–7 infraorbital

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**Fig. 1. Alionematichthys crassiceps** Moller & Schwarzhans, 2008, WAM P.25113-005, male, 75 mm SL: A, lateral view of head; B, ventral
view of head; C, view of left pseudoclasper from inside; D, median view of right otolith; E, ventral view of right otolith.
Alionematichthys Moller & Schwarzhans, 2008
Gender masculine. Type species, by original designation, Dinematichthys rinkensis Aoyagi, 1954. Recent, Ishigaki Island, Ryukyu Islands, Japan.

Alionematichthys crassiceps Moller & Schwarzhans, 2008
(Figs 1, 2)
Alionematichthys crassiceps Moller & Schwarzhans, 2008: 95.
Alionematichthys sp. 2 Moller & Schwarzhans, 2008: 127.

Material examined. 57 specimens: 54 specimens in Moller & Schwarzhans, 2008; 3 additional specimens - WAM P.25113-005, 1 male, 75 mm SL, 1 female, 73 mm SL, 20°28'S, 116°32'E, Kendrew Island, Western Australia, 6 November 1974; WAM P.30908-002, 1 female, 90 mm SL, 16°26'S, 123°21'E, Mermaid Island, Western Australia, 18 November 1994.

Remarks. The three new specimens from Western Australia fall entirely within the meristic variations observed in this species, which has been widely reported from Micronesia in the northern Pacific (Palau, Chuuk) to Vanuatu, Fiji and Tonga in the southern Pacific. This is also true for the pseudoclasper morphology of the single large male included in the additional material, the massive head without cirri on the snout, the narrow scale patch on the cheek and the presence of a small scale patch above the opercular spine and finally the otolith morphology characterised by the poor distinction of ostium and cauda and the small size of the cauda.

A single previous record from the northwestern Australian coast based on a large female specimen was reported in Moller & Schwarzhans (2008) as Alionematichthys sp. 2, then thought to represent an undescribed species. Among the characteristics mentioned, the transformation of the upper preopercular pore to a wart stands out as the only one significantly different from A. crassiceps. The new specimens from the same location now show that mostly the preopercular pore is still evident and only in minor instances has it been transformed to a wart, usually on one side of the head only. Therefore, Alionematichthys sp. 2 can now be confidently synonymised with A. crassiceps, thereby significantly extending the geographic distribution of the species to the west.

Brosmolus Machida, 1993
Gender masculine. Type species, by monotypy, Brosmolus longicaudus Machida, 1993. Recent. Type locality: 11°50'S, 130°05'E, Beagle Gulf, Northern Territory, Australia.

Brosmolus longicaudus Machida, 1993
(Figs. 3, 4)


Remarks. The holotype (and only specimen at the time) described by Machida represents a male with not fully developed pseudoclaspers (see Schwarzhans & Moller 2007: fig. 9 C, D). Two additional specimens studied by Schwarzhans & Moller were small females. The additional specimens studied for this paper have yielded one large female of 97 mm SL and a male with fully developed pseudoclaspers. These new specimens now allow adequate description and comparison.

Male copulatory organ (Fig. 3 A,B): A single pair of (outer) pseudoclaspers about half the size of the penis. The pseudoclaspers are broad and flap like and contain two...
short supporters behind each other. The pseudoclasper flap is slightly incised between the supporters in one pseudoclasper.

Further additional information includes a well preserved otolith (Fig. 3 C,D) and an extension of certain meristic ranges: dorsal fin rays 118–132, anal fin rays 90–98, caudal vertebrae 41–44, D/A 35–42.

The monotypic genus *Brosmolus* was regarded as being closely related to *Beaglichthys* Machida, 1993 by Schwarzhans and Moller (2007) and potentially considered synonymous with it, but synonomy was deferred “until the nature and distinction of the two established genera can be analyzed from a broader base of specimens”. The additional male with the small single pseudoclasper containing two supporters now clearly distinguishes *Brosmolus* from *Beaglichthys*, which has a copulatory organ with a large outer pseudoclasper with a single supporter and a smaller, complex inner pseudoclasper which is attached to the outer pseudoclasper to different extents in the three species of the genus. In fact, male copulatory organs with a single (outer) pseudoclasper and two supporters behind each other are rare in the dinematichthyines, the only other genera possessing this character are *Didymothallus* Schwarzhans and Moller, 2007 from the Indo-west Pacific and *Gunterichthys* Dawson, 1966 from tropical America. It is therefore now concluded that *Brosmolus* is most closely related to *Didymothallus*, differing in the small pseudoclasper (half the length of the penis versus as long as, or longer than, the penis), the high precaudal and total vertebrae count (14 or 15 and 56–59 versus 12 or 13 and 40–45) and the high dorsal and anal fin ray counts (118–132 and 90–98 versus 69–97 and 52–73).

*Didymothallus* Schwarzhans & Moller, 2007

Gender masculine. Type species, by original designation, *Didymothallus criniceps* Schwarzhans & Moller, 2007. Recent. Type locality One Tree Island, Great Barrier Reef, Queensland, Australia.

*Didymothallus nudigena* sp. nov.

(Figs 5–7; Table 1)

*Didymothallus mizolepis* (Günther, 1867). – Schwarzhans & Moller 2007: 56 (pars: Fig. 17 C, H, K, non Fig. 17 A, B, D–J = *Didymothallus mizolepis*).

**Material examined.** (38 specimens, 17–66 mm SL). **Holotype** – WAM P.27671-032, male, 47 mm SL, 16°51’S, 122°05’E, Lacepede Islands, Western Australia, Rock pool at western tip, coll. G.R. Allen & F. Wells, 29 February 1982. **Paratypes** – AMS 1.17060-035, 1 male, 33 mm
New Dinematichthyini (Teleostei: Bythitidae) from the Indo-west Pacific

Fig. 6. Didymothallus nudigena sp. nov.: A, lateral view of head, holotype; B, ventral view of head, holotype; C, lateral view of head, WAM P.22431-050, female, 45 mm SL; D, inclined lateral view of male copulatory organ, holotype; E, ventral view of male copulatory organ, holotype; F, view of left pseudoclasper from inside, holotype; G, view of left pseudoclasper from inside, WAM P.22431-050, 49 mm SL; H, view of left pseudoclasper from inside, WAM P.22431-050, 43 mm SL; I, median view of right otolith, holotype; J, ventral view of right otolith, holotype.

SL, 1 female, 44 mm SL, 22°15'S, 114°15'E, Exmouth Gulf, Western Australia; BPBM 17405, 1 female, 45 mm SL, 20°S, 116°E, Kendrew Island, Dampier Archipelago, Western Australia; WAM P.22431-050, 8 males and 10 females, 17-49 mm SL, 20°S, 116°E, Dampier Archipelago, Western Australia, 5 November 1971; WAM P.25111-033, 1 female, 51 mm SL, 20°S, 116°E, Dampier Archipelago, Western Australia; WAM P.27368-014, female, 35 mm SL, 17°58'S, 122°14'E, Broome, Western Australia, July 1981; WAM P.27967-038, 1 male, 37 mm SL, 24°29'S, 113°25'E, off Beagle Hill, Western Australia; WAM P.27980-065, 1 male, 42 mm SL, 20°26'S, 115°35'E, Montebello Islands, Western Australia; WAM P.28417-021, 1 male, 47 mm SL, 2 females, 27-49 mm SL, 17°21'S, 122°09'E, Coulomb Point, Western Australia, 1 September 1981; WAM P.31013-010, 6 specimens, 22°06'S, 114°31'E, Exmouth Gulf,
Western Australia; WAM P.31015-031, 1 female, 51 mm SL, 22°07'S, 114°29'E, Exmouth Gulf, Western Australia; WAM P.31392-002, female, 30 mm SL, 16°S, 122°E, Beagle Bay, Western Australia, 28 August 1997; WAM P.31506-001, 1 male, 51 mm SL, 1 female, 66 mm SL, 20°28'S, 116°52'E, Dolphin Island, Western Australia.

Diagnosis. Vertebræ 12+28–31=40–43, dorsal fin rays 78–90 (95), anal fin rays 57–69, V in D 1.9–2.3. Head with few small, non-inbricate scales on upper cheeks only. Single (outer) pseudoclasper wing-shaped with two slender supports, anterior supporter shorter than posterior one with small distal appendix on inner face, posterior supporter curved, hockey-stick shaped. Otolith with undivided short sulus, its centre anterior to centre of otolith, sulcus not inclined, otolith length to otolith height 2.25–2.35, otolith length to sulus length 1.9–2.1.

Description (Figs. 5, 6). The principal meristic and morphometric characters of Didymothallus nudigena are shown in Table 1. Body slender, mature at about 30 mm SL. Head and body slender. Head with scale patch only on upper cheek consisting of few, small, non-inbricate scales covered by thin skin and thus difficult to observe (Fig. 6A, C). Horizontal diameter of scales on body about 1.1% SL, in 17–23 horizontal rows. Maxillary ending far behind eyes, dorsal margin of maxillary covered by upper lip dermal lobe, posterior end slightly expanded, with small knob. Anterior nostril positioned low, 1/4–1/5 the distance from upper lip to anterior margin of eye. Posterior nostril small, about 1/4 the size of eye. Opercular spine with free tip, pointed. Anterior gill arch with 10–15 rakers, thereof 2–4 elongate. Pseudobranchial filaments 1.

Head sensory pores (Fig. 6A–C). Supraorbital pores 3. Infrarostral pores 6 (3 anterior and 3 posterior); three posterior pores about 1/2 the size of three anterior pores. Mandibular pores 6 (3 anterior and 3 posterior); first anterior mandibular pore without cirrus. Preopercular pores: 3 lower, first and second with joined opening; third non-tubular; tubular upper preopercular pore.

Dentition (of holotype). Preamaxilla with 3 outer rows of granular teeth and one inner row of larger teeth anteriorly. Anteriormost teeth in inner row up to 1/2 diameter of pupil. Vomer horseshoe-shaped, with 1 row of about 5 large teeth up to 1/2 diameter of pupil. Palatine with 1 row of about 7 large teeth up to 1/2 diameter of pupil. Dentary with 4 outer rows of granular teeth and 1 inner row of larger teeth anteriorly, up to about 1/2 diameter of pupil.

Otolith (Fig. 6I–J). Elongate in shape, length to height 2.25–2.35 (48–66 mm SL) and moderately thin (otolith height to otolith thickness about 2.0). Anterior tip slightly pointed, posterior rim expanded. Dorsal rim with rounded pre- and angular postdorsal angles, section in between long and straight, small concavity towards anterior and posterior tips; ventral rim gently curved, deepest anterior

Table 1. Meristic and morphometric characters of Didymothallus nudigena n. sp.

<table>
<thead>
<tr>
<th>Character</th>
<th>Holotype WAM P.27671-032</th>
<th>Holotype WAM P.27671-032 + 22 paratypes</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td>Standard length in mm</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Meristic characters</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dorsal fin rays</td>
<td>87</td>
<td>86.0 (78–95)</td>
<td>23</td>
</tr>
<tr>
<td>Caudal finrays</td>
<td>14</td>
<td>14.4 (14–16)</td>
<td>15</td>
</tr>
<tr>
<td>Anal fin rays</td>
<td>64</td>
<td>63.7 (57–69)</td>
<td>23</td>
</tr>
<tr>
<td>Pectoral fin rays</td>
<td>20</td>
<td>20.4 (18–22)</td>
<td>14</td>
</tr>
<tr>
<td>Caudal vertebrae</td>
<td>12</td>
<td>12.0 (11–12)</td>
<td>23</td>
</tr>
<tr>
<td>Caudal vertebrae</td>
<td>30</td>
<td>29.3 (28–31)</td>
<td>23</td>
</tr>
<tr>
<td>Total vertebrae</td>
<td>42</td>
<td>41.3 (40–43)</td>
<td>23</td>
</tr>
<tr>
<td>Rakers on anterior gill arch</td>
<td>6+3-1+1</td>
<td>11.9 (10–15)</td>
<td>22</td>
</tr>
<tr>
<td>Pseudobranchial filaments</td>
<td>1</td>
<td>1.0 (0–1)</td>
<td>22</td>
</tr>
<tr>
<td>D/V</td>
<td>5</td>
<td>5.5 (5–6)</td>
<td>23</td>
</tr>
<tr>
<td>D/A</td>
<td>28</td>
<td>27.5 (22–31)</td>
<td>23</td>
</tr>
<tr>
<td>V/A</td>
<td>14</td>
<td>14.2 (14–15)</td>
<td>23</td>
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<tr>
<td>Morphometric characters in % of SL</td>
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<tr>
<td>Head length</td>
<td>25.1</td>
<td>24.9 (23.9–25.8)</td>
<td>13</td>
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<tr>
<td>Head width</td>
<td>11.7</td>
<td>11.4 (10.0–12.3)</td>
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<tr>
<td>Head height</td>
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<td>Snout length</td>
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<td>5.5 (5.1–5.8)</td>
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<td>Upper jaw length</td>
<td>11.7</td>
<td>12.4 (11.4–14.1)</td>
<td>13</td>
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<td>Diameter of pigmented eye</td>
<td>2.2</td>
<td>2.5 (2.1–3.1)</td>
<td>12</td>
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<tr>
<td>Diameter of pupil</td>
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<td>Interorbital width</td>
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<td>Posterior maxilla height</td>
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<td>Postorbital length</td>
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<td>17.7 (16.8–18.4)</td>
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<td>Preanal length</td>
<td>47.9</td>
<td>48.8 (45.0–52.0)</td>
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<td>Predorsal length</td>
<td>29.6</td>
<td>30.3 (28.3–33.7)</td>
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<td>Body depth at origin of anal fin</td>
<td>14.6</td>
<td>14.9 (12.9–16.5)</td>
<td>15</td>
</tr>
<tr>
<td>Pectoral fin length</td>
<td>14.4</td>
<td>14.1 (12.8–17.7)</td>
<td>12</td>
</tr>
<tr>
<td>Pectoral fin base height</td>
<td>5.2</td>
<td>5.7 (4.9–6.4)</td>
<td>13</td>
</tr>
<tr>
<td>Ventral fin length</td>
<td>20.0</td>
<td>20.1 (15.8–25.0)</td>
<td>20</td>
</tr>
<tr>
<td>Base ventral fin – anal fin origin</td>
<td>29.8</td>
<td>30.9 (27.8–34.3)</td>
<td>13</td>
</tr>
</tbody>
</table>
New Dinematichthyini (Teleostei: Bythitidae) from the Indo-west Pacific

of the middle. Inner face moderately convex, outer face flat to slightly concave, both smooth. Otolith length to sulcus length 1.9–2.1. Sulcus positioned slightly towards anterior, with fused colliculi, not inclined towards otolith axis. Ventral furrow distinct, close to ventral rim of otolith, curved upwards anteriorly and posteriorly.


Male copulatory organ (Fig. 6 D–H). Single pair of large (outer) pseudoclaspers, wing-shaped, tips bend backward, with two long supporters, anterior being considerably shorter than posterior, with small distal appendix on inner face, posterior supporter curved, hockey-stick shaped. Penis curved, slightly longer than pseudoclaspers, pointed, with broad base.

Colour. Live colour known from two specimens (WAM P.31015-031 and WAM P.27967-038, see Schwarzhans & Moller, 2007, Fig. 16 A as D. mizolepis), which both show a uniform dusky red to reddish violet body colour, lighter ventrally and darker dorsally. The vertical fins bear the same colour, but are lighter and translucent. Preserved colour is variable brown to greyish-brown, often rather dark.

Comparison and Discussion. Specimens of Didymothallus nudigena were incorporated in D. mizolepis in Schwarzhans & Moller (2007) due to the lack of adequate mature male specimens. It was noted, however, that it appeared that “the more western specimens (Exmouth Gulf) tend to show lower meristic numbers, lesser cheek squamation and bent supporters in the pseudoclaspers”. The new specimens now additionally obtained from the area support the presence of two species, with D. nudigena most reliably distinguished from D. mizolepis by the few small, non-imbricate scales on the upper cheek only (versus continuous imbricate scale patch on upper and lower cheek), the pseudoclasper with the short anterior and hockey-stick bent posterior supporters (versus straight and almost equal in length), the curved penis (versus straight) and the lower V in D (1.9–2.3 versus 2.2–2.6), while the previously mentioned meristic differences include a large area of overlap. Didymothallus nudigena is distinguished from the other species of the genus, D. criniceps and D. pruvosti, by the higher number of dorsal fin rays (78–90 versus 69–77), the reduced scale patch on the upper cheek, the hockey-stick shaped posterior supporter of the outer pseudoclasper and the long sulcus (otolith length to sulcus length 1.9–2.1 vs 2.6).

Distribution. Didymothallus nudigena is known from northwestern Australia from 24°S and 113°E to about 16°S and 122°E, where it may overlap geographically with D. mizolepis known from 18°S and 122°E to the Cape York (Fig. 7).

Etymology. A combination from nudes (Latin = naked) and gena (Latin = cheek) owing to the reduced squamation of the cheeks. The name is intended as a noun in apposition.

Majungaichthys Schwarzhans & Moller, 2007

Gender masculine. Type species, by original designation, Majungaichthys simplex Schwarzhans & Moller, 2007. Recent. Type locality: 16°21’S, 43°59’E, off Cape Saint-Andre, Madagascar.

Majungaichthys agalegae sp. nov.
(Figs. 8–10; Table 2)

Majungaichthys simplex Schwarzhans & Moller 2007: 75 (pars: tentatively assigned specimens, Fig. 31 G, non Fig. 31 A–F = Majungaichthys simplex).

Material examined. (6 specimens, 26–40 mm SL).

Holotype – WAM P.32017-008, male, 40 mm SL, 12°49’S, 48°35’E, Nosy Fisaka, northwestern Madagascar, outer reef on west side, depth 4–5 m, coll. G.R. Allen, 13 January 2002. Paratypes – USNM 374164, 1 female, 26 mm SL, 10°19’S, 056°35’E, Agalega Islands (North Island), Mauritius; USNM 374174, 3 females, 30–35 mm SL, 10°19’S, 056°35’E, Agalega Islands (North Island), Mauritius; USNM 374175, 1 female, 32 mm SL, 10°2US, 056°35’E, Agalega Islands (North Island), Mauritius.

Diagnosis. Vertebræ 12+30–32=42, pleural ribs on vertebrae 2–11, dorsal fin rays 71–75, anal fin rays 55–62, D/A 20–21. Distance from base of ventral fin to base of anal fin 25.5–28. Head with rounded snout, scale patch on cheeks with 4 or 5 rows on upper cheek and 2 or 3 rows on

1 cm

![Fig. 8. Majungaichthys agalegae sp. nov. Holotype. WAM P.32017-008, male, 40 mm SL.](image)
lower cheek. Pseudoclaspers almost equally large, 2 pairs, outer flap-shaped with broadened tip, inner narrower with anteriorly inclined tip. Otolith with indistinctly divided sulcus with extremely small cauda, ostium length to cauda length about 7:1, sulcus slightly inclined, otolith length to otolith height 2.1, otolith length to sulcus length 1.8–1.9.

Description (Figs 8, 9). The principle meristic and morphometric characters of *Majungaichthys agalegae* are shown in Table 2. Body moderately slender, mature at about 35 mm SL. Head with rounded front and with scale patch on cheek containing 4 or 5 vertical rows of scales on upper part and 2 or 3 vertical rows on lower part (Fig. 9 A). Horizontal diameter of scales on body about 2% SL, in 22 horizontal rows. Maxillary ending far behind eyes, dorsal margin of maxillary covered by upper lip dermal lobe, posterior end slightly expanded, with small knob. Anterior nostril positioned low, 1/4 the distance from upper lip to anterior margin of eye. Posterior nostril small, about 1/4 the size of eye. Opercular spine with free tip, pointed. Anterior gill arch with 13 short and 3 long rakers. Pseudobranchial filaments 2.

Head sensory pores (Fig. 9 A,B). Supraorbital pores 2 or 3. Infracrinal pores 6 (3 anterior and 3 posterior): three posterior pores about 0.25 size of 3 anterior pores. Mandibular pores 6 (3 anterior and 3 posterior); first anterior mandibular pore without cirrus. Preopercular pores: 3 lower, first and second with joined opening; third non-tubular, tubular upper preopercular pore.

Dentition (of holotype). Premaxilla with 4 outer rows of granular teeth and one inner row of larger teeth anteriorly. Anteriormost teeth in inner row up to 0.5 diameter of pupil. Vomer horseshoe-shaped, with one outer row of small teeth and one inner row of large teeth up to 0.3 diameter of pupil. Palatine with 2 rows of small teeth up to 0.3 diameter of pupil. Dentary with 4 outer rows of granular teeth and 1 inner row of larger teeth anteriorly, up to about 0.6 diameter of pupil.

Otolith (Fig. 9 E,F). Elongate in shape, length to height 2.1 (35–40 mm SL) and moderately thin (otolith height to otolith thickness about 2.0). Anterior tip slightly pointed, short, posterior rim expanded. Dorsal rim with rounded pre- and angular postdorsal angles, section in between nearly
straight, small concavity towards anterior and posterior tips; ventral rim gently curved, deepest anterior of the middle. Inner face moderately convex, outer face flat to slightly concave, both smooth. Otolith length to sulcus length straight, small concavity towards anterior and posterior tips; inner pseudoclaspers narrower with small knob at rear margin and middle stretch of pseudoclaspers and forward inclined pointed tip. Penis curved, slightly longer than pseudoclaspers, with broad base.

**Colour.** Preserved holotype uniformly chocolate brown. Live colour unknown.

**Comparison.** Majungaichthys agalegae was first noted in Schwarzhans and Moller (2007) from the Agalega Islands, but was tentatively placed in *M. simplex* found along the central western coast of Madagascar. The new find of an adult male from the northwestern coast of Madagascar not far from the Agalega Islands, however confirmed the presence of a second species in the area. *Majungaichthys agalegae* differs from *M. simplex* in the lower number of dorsal fin rays (71–75 versus 78 or 79), pleural ribs on vertebrae 2–11 (versus 2–10), lower D/A (20 or 21 versus 24), the distance of the base of the ventral fin to the anal fin origin (25.5–28 versus 30–30.5) and the presence of a very small caudal colliculum (ostium length to cauda length about 7:1) in an indistinctly divided sulcus of the otolith. The pseudoclaspers pattern however does not differ significantly between the two species.

**Distribution.** Known from the Nosy Mitsio Archipelago off northwestern Madagascar to the Agalega Islands.

**Etymology.** Named after the Agalega Islands, where this species was observed first. The name is intended as a noun in apposition.

*Mascarenichthys* Schwarzhans & Moller, 2007


**Mascarenichthys heemstraï** Schwarzhans & Moller, 2007

(Fig. 10)


**Remarks on distribution.** The additional material confirms the presence of *M. heemstraï* at Mauritius and extends the distribution of the species to mainland East Africa along the shores of Mozambique.

Diagnosis. Vertebrae 12+30 or 31=42 or 43, dorsal fin rays 76 or 77, anal fin rays 62 or 63. Head with scale patch on cheeks with 4 rows on upper cheek and 2 rows on lower cheek. Two pairs of pseudoclaspers, outer pseudoclasper flap-shaped, bent outwards, with pointed tip and symmetrical fleshy expansions anterior and posterior, inner pseudoclasper small, narrow, anteriorly inclined, not hidden in below isthmus in resting position. Otolith with sulcus with separate small cauda and large ostium, otolith length to otolith height 2:1.

Description (Figs 11, 12). The principle meristic and morphometric characters of *Mascarenichthys remotus* are shown in Table 3. Body slender, mature at about 25 mm SL, probably not growing much larger. Head with moderately pointed snout and with scale patch on cheek containing 4 vertical rows of scales on upper part and 2 vertical

| Table 3. Meristic and morphometric characters of *Mascarenichthys remotus* sp. nov. |
|---------------------------------|-----------------|-----------------|
| Holotype | Paratype |                   |
| SAIAB 68756 | SAIAB ex. 68756 |                   |
| Standard length in mm | 30 | 28 |
| Dorsal fin rays | 77 | 76 |
| Caudal finrays | - | - |
| Anal fin rays | 63 | 62 |
| Pectoral fin rays | 20 | 19 |
| Precaudal vertebrae | 12 | 30 |
| Caudal vertebrae | 12 | 31 |
| Total vertebrae | 42 | 43 |
| Rakers on anterior gill arch | 9+2-1+2 | 9+2-1+3 |
| Pseudobranchial filaments | 2 | 2 |
| D/V | 6 | 6 |
| D/A | 22 | 21 |
| V/A | 14 | 14 |
| Head length | 25.2 | 25.9 |
| Head width | 12.0 | 11.3 |
| Head height | 14.5 | 14.4 |
| Snout length | 5.5 | 5.8 |
| Upper jaw length | 13.3 | 13.4 |
| Diameter of pigmented eye | 3.2 | 2.9 |
| Diameter of pupil | 2.0 | 1.8 |
| Interorbital width | 6.6 | 6.8 |
| Posterior maxilla height | 3.9 | 4.1 |
| Postorbital length | 16.7 | 18.1 |
| Preanal length | 46.4 | 46.9 |
| Predorsal length | 31.5 | 30.8 |
| Body depth at origin of anal fin | 14.2 | 15.1 |
| Pectoral fin length | 15.8 | 16.8 |
| Pectoral fin base height | 5.2 | 5.7 |
| Ventral fin length | 26.6 | 25.7 |
| Base ventral fin - anal fin origin | 27.7 | 28.6 |

rows on lower part (Fig. 12 A, C). Horizontal diameter of scales on body about 1.5% SL, in about 20 horizontal rows. Maxillary ending far behind eyes, dorsal margin of maxillary covered by upper lip dermal lobe, posterior end expanded, angular. Anterior nostril positioned low, 1/4 the distance from upper lip to anterior margin of eye. Posterior nostril very small, less than 1/8 size of eye. Opercular spine with free tip, pointed. Anterior gill arch with 14 rakers, 3 elongate. Pseudobranchial filaments 2.

Fig. 11. *Mascarenichthys remotus* sp. nov. Holotype. SAIAB 68756, male, 30 mm SL.
New Dinematichthyini (Teleostei: Bythitidae) from the Indo-west Pacific

**Head sensory pores** (Fig. 12 A–C). Supraorbital pores 3. Infraorbital pores 6 (3 anterior and 3 posterior); three posterior pores about 1/3 the size of three anterior pores. Mandibular pores 6 (3 anterior and 3 posterior); first anterior mandibular pore without cirrus. Preopercular pores: 3 lower, first and second with joined opening; third non-tubular; tubular upper preopercular pore.

**Dentition** (of holotype). Premaxilla with 3 outer rows of granular teeth and one inner row of larger teeth anteriorly. Anteriormost teeth in inner row up to 1/2 diameter of pupil. Vomer horseshoe-shaped, with 1 outer row of small teeth and 1 inner row of larger teeth up to 1/3 diameter of pupil. Palatine with an outer row of small teeth and an outer row of larger teeth up to 1/3 diameter of pupil. Dentary with 4 outer rows of granular teeth and 1 inner row of larger teeth, up to about 1/2 diameter of pupil.

**Otolith** (Fig. 12 H). Elongate in shape, length to height 2.1 (30 mm SL). Anterior tip rounded, short, posterior rim expanded. Dorsal rim with rounded pre- and angular postdorsal angles, section in between nearly straight, small concavity towards posterior tips; ventral rim gently curved (poorly preserved). Inner face moderately convex. Otolith length to sileus length 1.9. Sileus positioned slightly towards anterior, with separated colliculi, slightly inclined. Ostium much larger than cauda (ostium length to cauda length about 5.5). Ventral furrow indistinct.

**Axial skeleton.** Neural spine of vertebra (3) inclined and 5–8 depressed. Parapophyses present from vertebrae 7 to 12. Pleural ribs on vertebrae 2 to 11. First anal fin pterygophore elongate, reaching tip of last precaudal parapophysis.

**Male copulatory organ** (Fig. 12 D–G). Two pairs of pseudoclaspers; outer pseudoclasper flap-shaped, bent outwards, with broad basis and pointed tip, anterior and posterior margins expanded at about mid-section; inner pseudoclasper small, narrower, anteriorly inclined, connected with a ligament to isthmus, but otherwise free from isthmus. Penis curved, slightly longer than pseudoclaspers, with broad base and pointed tip.

**Colour.** Preserved colour uniformly pale. Live colour unknown.

**Comparison.** Mascarenichthys remotus is easily distinguished from the widespread M. heemstrai and the
South African endemic *M. microphthalmus* by the presence of 12 precaudal vertebrae (versus 11), the high number of dorsal fin rays (76 or 77 versus 63–73) and anal fin rays (62 or 63 versus 47–57), the shape of the pseudoclaspers with the inner pseudoclasper not hidden in a pocket of the isthmus in the resting position and the slightly more compressed otolith (length to height 2.1 vs 2.3–2.5).

**Distribution.** Endemic to the Rodrigues Islands in the southern Indian Ocean.

**Etymology.** From remotus (Latin = far away, distant, remote) referring to the remote location of this endemic species. The name is intended as a noun in apposition.

*Nielsenichthys* gen. nov.

(Figs 2, 13, 14; Table 4)


**Diagnosis.** A genus of Dinematichthyini with the following combination of characters: anterior nostril placed high on snout (nearly half the distance from upper lip to anterior margin of eye). Male copulatory organ with 2 pairs of equally large pseudoclaspers connected by thin ligament. Both pseudoclaspers slender, each with single straight supporter, inner pseudoclasper positioned anterior of outer pseudoclasper. Fish small, up to about 40 mm SL length. Precaudal vertebrae 12; dorsal fin rays 84–90, anal fin rays 59–67. Head with scale patch on cheek only, no scales on opercle. Upper preopercular pore present. Maxilla expanded posteriorly. Otolith elongate (otolith length to height 2.2–2.3), colliculi separated, ostium approaching close to anterior rim of otolith, ostium length to cauda length 3.3–3.8.

**Comparison.** *Nielsenichthys* belongs to the Dinematichthyini with a high position of the anterior nostril, like *Alionematichthys* Moller & Schwarzhans, 2008, *Dinematichthys* Bleeker, 1855 and *Porocephalichthys* Moller & Schwarzhans, 2008. (Certain species of the genera *Diancistrus* Ogilby, 1898, *Eusurculus* Schwarzhans & Moller, 2007 and *Lapitaichthys* Schwarzhans & Moller, 2007 may also have elevated anterior nostrils, but not less than 1/2 the distance from the upper lip to the anterior margin of the eye.) From these three genera, *Nielsenichthys* shares the head squamation being restricted to the cheeks with *Alionematichthys* while in the other two genera the entire head is covered by scales. *Nielsenichthys* differs from all genera mentioned above by the pseudoclasper pattern consisting of a pair of equally long and slender inner and outer pseudoclaspers, the inner being positioned anteriorly of the outer and connected to it by a thin ligament (versus inner pseudoclasper much smaller than outer pseudoclasper and inserted at the same level than the outer pseudoclasper). The otoliths of *Nielsenichthys* differ from those of all other known Recent Dinematichthyini by the very close approach of the ostium to the anterior rim of the otolith, almost as if opening to it.

**Species.** *Nielsenichthys* is a monospecific genus with *N. pullus* described below from Nusa Penida near Bali, Indonesia.

**Etymology.** Named in honour of Jorgen Nielsen, Copenhagen, ZMUC, in recognition of his many contributions to the biology and systematics of the Ophidiiformes.

*Nielsenichthys pullus* sp. nov.

(Figs 2, 13, 14; Table 4)


**Diagnosis.** See generic diagnosis.

**Description** (Figs 13, 14). The principle meristic and morphometric characters of *Nielsenichthys pullus* are shown in Table 4. Body slender, mature at about 35 mm SL. Head with rounded snout and with scale patch on cheek containing 4 or 5 vertical rows of scales on upper part and 3 vertical rows on lower part (Fig. 14 A); no scales on opercle. Horizontal diameter of scales on body about 1.7% SL, in 24 horizontal rows. Maxillary ending far behind eyes, dorsal margin of maxillary covered by upper lip dermal lobe, posterior end expanded, angular. Anterior nostril positioned...
New Dinematichthyini (Teleostei: Bythitidae) from the Indo-west Pacific

Fig. 14. *Nielsenichthys pullus* sp. nov. Holotype: A, lateral view of head; B, ventral view of head; C, ventral view of male copulatory organ; D, inclined lateral view of male copulatory organ; E, view of left pseudoclasper from inside; F, median view of right otolith; G, ventral view of right otolith.

Fig. 14. *Nielsenichthys pullus* sp. nov. Holotype: A, lateral view of head; B, ventral view of head; C, ventral view of male copulatory organ; D, inclined lateral view of male copulatory organ; E, view of left pseudoclasper from inside; F, median view of right otolith; G, ventral view of right otolith.

high, nearly at half the distance from upper lip to anterior margin of eye. Posterior nostril very small, less than $\frac{1}{6}$ size of eye, with fleshy flap anteriorly. Opercular spine with free tip, pointed. Anterior gill arch with 12–14 rakers, thereof 3 elongate. Pseudobranchial filaments 2.

*Head sensory pores* (Fig. 14 A,B). Supraorbital pores 3. Infraorbital pores 6 (3 anterior and 3 posterior): three posterior pores about half the size of three anterior pores, two most posterior pores tubular. Mandibular pores 6 (3 anterior and 3 posterior); first anterior mandibular pore with cirrus. Preopercular pores: 3 lower, first and second with joined opening; third non-tubular; tubular upper preopercular pore.

*Dentition* (of holotype). Premaxilla with 3 outer rows of granular teeth and one inner row of larger teeth anteriorly. Anteriormost teeth in inner row up to $\frac{1}{2}$ diameter of pupil. Vomer horseshoe-shaped, with 3 outer rows of small teeth and one inner row of large teeth up to $\frac{1}{3}$ diameter of pupil. Palatine with 1 outer row of small teeth and 1 inner row of larger teeth up to $\frac{1}{3}$ diameter of pupil. Dentary with 3 outer rows of granular teeth and 1 inner row of larger teeth anteriorly, up to about $\frac{2}{5}$ diameter of pupil.

*Otolith* (Fig. 14 F,G). Elongate in shape, length to height 2.2–2.3 (34–38 mm SL). Anterior tip slightly pointed, posterior rim expanded. Dorsal rim with angular pre- and postdorsal angles, section in between long, nearly straight, small concavity towards anterior and posterior tips; ventral rim gently curved, deepest anterior of its middle. Inner face markedly convex, particularly posterior, outer face slightly concave. Sulcus long, close approaching anterior rim of otolith and nearly opening to it, otolith length to sulcus length 1.5–1.6. Sulcus positioned slightly towards anterior, with clearly separated colliculi, with ventrally incised collum, not inclined. Ostium larger than cauda (ostium length to cauda length 3.3–3.8). Ventral furrow
Table 4. Meristic and morphometric characters of *Nielsenichthys pullus* sp. nov.

<table>
<thead>
<tr>
<th>Character</th>
<th>Holotype</th>
<th>Holotype + 2 paratypes</th>
<th>N</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean (range)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Standard length in mm</td>
<td>37</td>
<td>32.0 (25-37)</td>
<td>3</td>
</tr>
<tr>
<td><strong>Meristic characters</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dorsal fin rays</td>
<td>90</td>
<td>87.7 (84-90)</td>
<td>3</td>
</tr>
<tr>
<td>Caudal fin rays</td>
<td>13</td>
<td>13.7 (13-14)</td>
<td>3</td>
</tr>
<tr>
<td>Anal fin rays</td>
<td>67</td>
<td>63.3 (59-67)</td>
<td>3</td>
</tr>
<tr>
<td>Pectoral fin rays</td>
<td>21</td>
<td>21.7 (21-22)</td>
<td>3</td>
</tr>
<tr>
<td>Precaudal vertebrae</td>
<td>12</td>
<td>12</td>
<td>3</td>
</tr>
<tr>
<td>Caudal vertebrae</td>
<td>31</td>
<td>30.7 (30-31)</td>
<td>3</td>
</tr>
<tr>
<td>Total vertebrae</td>
<td>43</td>
<td>42.7 (42-43)</td>
<td>3</td>
</tr>
<tr>
<td>Rakers on anterior gill arch</td>
<td>9+2-1+2</td>
<td>13.0 (12-14)</td>
<td>3</td>
</tr>
<tr>
<td>Pseudobranchial filaments</td>
<td>2</td>
<td>2</td>
<td>3</td>
</tr>
<tr>
<td>D/V</td>
<td>5</td>
<td>5.3 (5-6)</td>
<td>3</td>
</tr>
<tr>
<td>D/A</td>
<td>28</td>
<td>28.7 (28-30)</td>
<td>3</td>
</tr>
<tr>
<td>V/A</td>
<td>15</td>
<td>14.7 (14-15)</td>
<td>3</td>
</tr>
<tr>
<td><strong>Morphometric characters in % of SL</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Head length</td>
<td>25.5</td>
<td>26.3 (25.5-27.7)</td>
<td>3</td>
</tr>
<tr>
<td>Head width</td>
<td>14.9</td>
<td>13.7 (13.1-14.9)</td>
<td>3</td>
</tr>
<tr>
<td>Head height</td>
<td>16.2</td>
<td>15.6 (14.7-16.2)</td>
<td>3</td>
</tr>
<tr>
<td>Snout length</td>
<td>5.7</td>
<td>6.0 (5.7-6.3)</td>
<td>3</td>
</tr>
<tr>
<td>Upper jaw length</td>
<td>13.1</td>
<td>13.2 (13.1-13.4)</td>
<td>3</td>
</tr>
<tr>
<td>Diameter of pigmented eye</td>
<td>2.9</td>
<td>2.9 (2.9-3.1)</td>
<td>3</td>
</tr>
<tr>
<td>Diameter of pupil</td>
<td>1.6</td>
<td>1.8 (1.6-1.8)</td>
<td>3</td>
</tr>
<tr>
<td>Interorbital width</td>
<td>6.8</td>
<td>7.1 (6.8-7.4)</td>
<td>3</td>
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<td>Postorbital length</td>
<td>17.2</td>
<td>17.5 (17.2-17.7)</td>
<td>3</td>
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<tr>
<td>Pracanal length</td>
<td>49.9</td>
<td>47.6 (44.5-49.9)</td>
<td>3</td>
</tr>
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<td>Predorsal length</td>
<td>30.7</td>
<td>30.9 (30.7-31.2)</td>
<td>3</td>
</tr>
<tr>
<td>Body depth at origin of anal fin</td>
<td>17.3</td>
<td>15.8 (14.6-17.3)</td>
<td>3</td>
</tr>
<tr>
<td>Pectoral fin length</td>
<td>14.4</td>
<td>14.9 (14.4-15.3)</td>
<td>3</td>
</tr>
<tr>
<td>Pectoral fin base height</td>
<td>6.1</td>
<td>6.6 (6.1-7.3)</td>
<td>3</td>
</tr>
<tr>
<td>Ventral fin length</td>
<td>26.6</td>
<td>25.8 (23.8-27.1)</td>
<td>3</td>
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</table>

**Axial skeleton.** Neural spine of vertebra 4 inclined and 5–8 (–9) depressed. Parapophyses present from vertebrae 7 to 12. Pleural ribs on vertebrae 2 to 11. First anal fin pterygophore elongate, reaching tip of last precaudal parapophysis in males but not in females.

**Male copulatory organ** (Fig. 14 C–E). Two pairs of large and equally long, slender pseudoclaspers, each with single straight supporter; outer pseudoclasper with blunt tip; inner pseudoclasper positioned slightly in front of outer pseudoclasper, with pointed tip and thin fleshy flaps at anterior and posterior margins. Pseudoclaspers connected with thin ligament along entire length, which however disintegrates easily to result in apparently free inner and outer pseudoclaspers (see Fig. 14 E). Penis straight, longer than pseudoclaspers, with pointed tip.

**Colour.** Dark brown after a short period of preservation.

**Comparison.** See comparison between *Nielsenichthys* and other genera.

**Distribution.** Known only from the coast around Nusa Penida near Bali.

**Etymology.** From *pullus* (Latin = dark) referring to the dark colour of the fishes. The name is adjectival.

*Paradiancistrus* Schwarzhans, Moller & Nielsen, 2005


*Paradiancistrus christmasensis* sp. nov. (Figs 15–17; Table 5)


**Diagnosis.** Vertebrae 11+32=43, dorsal fin rays 78, anal fin rays 67. Head with narrow scale patch on cheeks with 3 rows on upper cheek and 2 rows on lower cheek; no scales on operculum. Stubby snout profile. Lower preopercular pore 1. Otolith with undifferentiated, short sulcus, dorsal rim distinct, long, terminating close to anterior and posterior tips of sulcus.

**Fig. 15.** *Paradiancistrus christmasensis* sp. nov. Holotype. WAM P.29004-006, female, 68 mm SL.
anteriorly expanded, posteriorly depressed, otolith length to otolith height 2.15; otolith length to sulcus length 2.3.

Description (Figs. 15, 16). The principle meristic and morphometric characters of Paradiancistrus christmasensis are shown in Table 5. Body with massive head and stubby snout. Head with narrow scale patch on cheek containing 3 vertical rows of scales on upper part and 2 vertical rows on lower part (Fig. 16 A). Horizontal diameter of scales on body about 1.7% SL, in about 25 horizontal rows. Maxillary ending far behind eye, dorsal margin of maxillary covered by upper lip dermal lobe, posterior end expanded, angular. Anterior nostril positioned low, 0.2 the distance from upper lip to anterior margin of eye. Posterior nostril small, about 0.25 the size of eye. Opercular spine with free tip, pointed. Anterior gill arch with 17 rakers, 3 of which are elongate. Pseudobranchial filaments 2.

Dentition (of holotype). Premaxilla with 4 outer rows of granular teeth and one inner row of larger teeth anteriorly. Anteriormost teeth in inner row up to same diameter as pupil. Vomer horseshoe-shaped, with 3 outer rows of small teeth and one inner row of large teeth up to same diameter as pupil. Palatine with 3 rows of 10+6+10 teeth up to 0.5 diameter of pupil. Dentary with 4 outer rows of granular teeth and 1 inner row of larger teeth anteriorly, up to about same diameter as pupil.

Otolith (Fig. 16 C–D). Elongate in shape, length to height 2.15 (68 mm SL). Anterior tip pointed, short, posterior rim expanded. Dorsal rim with expanded predorsal area and depressed postdorsal area, section in between nearly inclined; ventral rim gently curved, deepest at about its middle. Inner face moderately convex, outer face flat. Otolith length to sulcus length 2.3. Sulcus positioned slightly towards anterior and inferior, undivided with fused colliculi, inclined by about 10°. Ventral furrow distinct, close to ventral rim of otolith, anteriorly bent upward to anterior tip of sulcus.

Axial skeleton. Neural spine of vertebrae 4–5 inclined and 6–8 depressed. Parapophyses present from vertebrae 7 to 11. Pleural ribs on vertebrae 2 to 10. First anal fin
Table 5. Meristic and morphometric characters of *Paradiancistrus christmasensis* sp. nov.

<table>
<thead>
<tr>
<th>Character</th>
<th>Holotype WAM 29004-006</th>
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<tbody>
<tr>
<td>Standard length in mm</td>
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</tr>
<tr>
<td>Dorsal fin rays</td>
<td>78</td>
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<td>Caudal finrays</td>
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<td>Total vertebrae</td>
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<td>Rakers on anterior gill arch</td>
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<td>Pseudobranchial filaments</td>
<td>2</td>
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<td>D/V</td>
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<td>D/A</td>
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<tr>
<td>Pectoral fin base height</td>
<td>5.6</td>
</tr>
<tr>
<td>Ventral fin length</td>
<td>15.6</td>
</tr>
<tr>
<td>Base ventral fin - anal fin origin</td>
<td>27.4</td>
</tr>
</tbody>
</table>

pterygophore elongate, not quite reaching tip of last precaudal parapophysis.

**Male copulatory organ.** Not known.

**Colour.** Preserved colour pale. Live colour not known.

**Biology.** The holotype is a gravid female, containing embryos 2.6 mm long with a yolk sac.

**Comparison.** *Paradiancistrus christmasensis* is the fourth species that has become known of this genus, which is readily recognised by the presence of only a single lower preopercular pore, a character shared only with *Pseudogilbia* Moller, Schwarzhans & Nielsen, 2004 from the tropical western Atlantic. In body shape and size, *P. christmasensis* resembles best *P. cuyoensis* Schwarzhans, Moller & Nielsen, 2005 from the northern Philippines, but differs in the narrower scale patch on the cheeks, the higher number of anal fin rays (67 versus 62–65) combined with a smaller preanal length (47% of SL versus 51–52%) and differences in shape and proportions of the otolith. *Paradiancistrus christmasensis* is thus well defined and differentiated from other *Paradiancistrus* species despite the lack of a male and the lack of knowledge of the pseudoclasper pattern.

**Distribution.** The species of *Paradiancistrus* are all rare, presently being known from one or two specimens each occurring at widely separated locations such as northern Philippines, Vanuatu, Lombok Island of Indonesia, and now the Christmas Island in the southeastern Indian Ocean.

**Etymology.** Referring to the type locality. The name is adjectival.

**DISCUSSION**

The identification and description in this work of five new species of Dinematichthyini from the Indo-west Pacific demonstrate that despite the intensive review published by the authors in four parts between 2005 and 2008, the faunal inventory of the group is still incomplete. Two of the newly established species come from remote islands (Christmas Island in the northeastern Indian Ocean and Rodrigues Island), one originates from the Indonesian Archipelago, and two stems from refinements in the definition of previously described species. Another blind eave-living dinematichthyine has recently been described from Sulawesi, Indonesia—*Diancistrus typhlops* Nielsen, Schwarzhans & Hadiyat, 2009. We postulate that particularly the Indonesian Archipelago is very likely to yield further undescribed dinematichthyine species. Other, still underrepresented regions are East Africa and Madagascar, as well the Andaman Islands and the shores of Myanmar and Thailand.

**ACKNOWLEDGEMENTS**

We wish to thank the following people for helping us with material and information: Gerald R. Allen (WAM), Eric Anderson (SAIAB), Mark Erdman (Conservation International), Philipp C. Heemstra (SAIAB), Sue Morrison (WAM). We also thank the following colleagues at ZMUC: Jørgen Nielsen for discussions and advice, Marcus Krag for producing the photos and Tammes Menne for helping with x-raying and pausing. Ronald Friske is thanked for his careful review of the manuscript.

**REFERENCES**


New Dinematichthyini (Teleostei: Bythitidae) from the Indo-west Pacific


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Low genetic diversity in Nurseryfish, *Kurtus gulliveri* (Perciformes: Kurtidae), and an appraisal of its breeding system using microsatellite loci

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ABSTRACT

The Nurseryfish, *Kurtus gulliveri*, is a freshwater fish distributed in northern Australia and southern New Guinea that exhibits forehead brooding, a unique form of male parental care. Microsatellite markers were developed for paternity analysis to study its reproductive life history in a population from the Adelaide River, Northern Territory, Australia. In 20 microsatellite loci tested, only two polymorphic markers were found. The microsatellite data are mostly consistent with the hypotheses that the putative egg-carrying male sired the egg mass and no multiple paternity occurred in the population examined. However, caution should be taken in interpreting the results, given the low genetic diversity and limited analytical power. The extremely low genotype diversity was also corroborated by mitochondrial DNA, the most variable fragment in the piscine mitogenome. Eighteen individuals from the Adelaide River were sequenced, revealing four polymorphic sites in the control region and five haplotypes in total, with an average p-distance of 0.001. Additional individuals from three other isolated populations in the Northern Territory (Daly River, South Alligator River and East Alligator River) were sequenced and found to be identical to one of the common haplotypes from the Adelaide River. Four specimens collected from New Guinea represent a single haplotype that had 24.5 substitutions, on average, relative to the Australian populations.

Keywords: Nurseryfish, *Kurtus gulliveri*, low genetic diversity, microsatellites, control region, breeding system.

INTRODUCTION

The Nurseryfish, *Kurtus gulliveri* Castelnau, 1878, is known for its unusual method of parental care. Weber (1910, 1913) and Beaufort (1914) reported that the male carries the egg mass on a supraoccipital hook, a method termed forehead brooding by Balon (1975). Virtually nothing had been published on the biology of this unique species in the subsequent 90 years until a life history study was begun in 2001 at the Adelaide River near Darwin in the Northern Territory of Australia (Berra 2003).

*Kurtus gulliveri* is known from northern Australia and southern New Guinea (Fig. 1). It is distinct from the only other member of the family Kurtidae, *K. indicus* Bloch, 1786, which occurs from India to Borneo (Berra 2003, 2007). Recent studies of functional morphology and population assessments (Berra 2003; Carpenter et al. 2004; Berra et al. 2007) provide a basis to explore the unique spawning habits of *K. gulliveri*. The anatomy and histology of the male’s supraoccipital hook has been examined, and Berra & Humphrey (2002) speculated that engorgement with blood in the highly vascularised dermis of the hook may help hold egg masses in place. This species feeds on arthropods and teleosts (Berra & Wedd 2001), and has a significantly skewed sex ratio of 65 percent male to 35 percent female (Berra et al. 2007), although skew might be caused by the male’s hook increasing vulnerability to gill netting. It possesses very small chromosomes with a karyotype 2n = 44 (Ezaz et al. 2006).
Recent investigations in fish reproductive behaviours have included genetic analysis of parentage with molecular markers. In 21 percent of all teleost families, there is parental care of offspring; of those families, 70 percent of the species’ parental care is provided entirely by the male (Avise et al. 2002). Although male parental care is common, the novel mode of care in Nurseryfish elicits many questions about its reproductive behaviour. Is the egg mass carried by a male the product of a single female? Conversely, is the egg-carrying male the only sire, or is there competition among males to fertilise egg masses before or after lodging them on their forehead, thus resulting in multiple paternity? Does this mode of reproduction yield any aberrant patterns in terms of population-genetic structure? Instances of multiple paternities are unknown, as molecular data have never been collected in the species. At the most basic level, how genetically diverse is Kurtus gulliveri within a river and among different rivers? Considering the difficulty of observing behaviours in nature and the paucity of information on the genetic diversity and reproductive natural history of this obscure species, microsatellite loci were developed and the mitochondrial control region was sequenced in order to: 1) survey genetic diversity in the species, 2) determine whether egg-carrying males sire the egg mass they carry, and 3) test for multiple paternity in egg masses. Multiple paternity and alternative life history strategies are well documented in fishes (Breder & Rosen 1966; reviewed in Avise et al. 2002), and microsatellite paternity analysis is a widely used tool to test hypotheses about these behaviours (Bruford et al. 1996). If K. gulliveri uses alternative reproductive tactics such as sneaking (Avise et al. 2003) or satellite fertilisations (Neff 2001), multiple paternity should be detectable in the eggs masses.

MATERIALS AND METHODS

Collection sites and materials examined. The majority of specimens utilised for this study were collected by gill netting in Marrakai Creek (12°40.950’S, 131°20.030’E), a major freshwater tributary of the Adelaide River about 65 km east of Darwin (Fig. 1). Three additional samples provided by the Museum and Art Gallery of the Northern Territory from other isolated populations in northern Australia (Daly River, South Alligator River and East Alligator River) and four specimens from New Guinea were acquired from the Kansas University Biodiversity Institute tissue collection for comparison with the Adelaide River population (Fig. 1). Tissue samples of adults and egg masses were preserved in 98 percent ethanol immediately upon capture. Collections were made in 2001, 2003, 2004 and 2009 during the dry season between late June and early November, coinciding with Nurseryfish spawning season (Berra & Neira 2003; Berra et al. 2007).

Forty-one adults from the Adelaide River (Table 1) were used to estimate allelic frequencies and other parameters for the microsatellite loci. Seven egg masses (EM-01 to EM-07) in varying stages of development and colouration caught at varying distances from the most proximate male...
Table 1. Description of specimens used in this study. All samples from Marrakai Creek were collected between 2001 and 2004. Lab codes denote adults (AD), including males associated with egg masses. EM-01 to EM-06 correspond to masses associated with adult males with matching numbers (EM-07 is not an associated mass but was tested for association to AD-06 male found 60 cm away in net). EM-08 to EM-14 are unassociated masses. U = sex unknown. Pink = fertilised.

<table>
<thead>
<tr>
<th>Lab code</th>
<th>Sex</th>
<th>Tissue type</th>
<th>Description</th>
<th>Berra field code</th>
<th>Year</th>
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<tr>
<td>EM-01</td>
<td>male</td>
<td>egg mass</td>
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<td>TMB01-7 #1</td>
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<td>female</td>
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<td>Pink mass assoc, w/ male</td>
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<td>female</td>
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<td>Pink mass assoc, w/ male</td>
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<td>EM-14</td>
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<td>adult</td>
<td>Associated w/ mass</td>
<td>TMB01-50</td>
<td>2001</td>
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</table>
in the net were analysed (see Fig. 2 and Table 1 for field codes and sample descriptions). In cases where the egg mass was lying next to the male in the gill net, it presumably dislodged when the male struck the net, which has been observed sometimes in the field (Berra et al. 2004). Our working hypothesis is that males collected either touching or in close proximity (<5 cm) to an egg mass, e.g., male AD-06 (Fig. 2A) and AD-05 (Fig. 2B), carried the egg mass on their supraocciptal hook as they struck the net and sired any embryos they carried (EM-06 and EM-05, respectively). The extreme difficulty of catching males with an intact egg mass is described by Berra et al. (2004). Three additional pink egg masses with eyed embryos trapped in the net without a male nearby (EM-10, EM-11, and EM-12) and four white egg masses that did not show any obvious signs of development (EM-08, EM-09, EM-13 and EM-14) were also analysed.

Microsatellite marker development. Total genomic DNA was extracted from a single adult (AD-12), and microsatellite loci were isolated using the method described by An et al. (2004). Isolation of targeted genomic fragments, the method of enrichment-capture with stringency washes, and buffer composition followed Hammond et al. (1998). A total of 475 colonies containing inserts was amplified and sequenced in one direction using BigDye Terminator chemistry (Applied Biosystems) and M13F primer to screen for microsatellite inserts. Forty-six positive clones (that contained microsatellites) were sequenced in the opposite direction with M13R. Complementary forward and reverse sequences were assembled using Sequencer 3.0 (Gene Codes Corp.). Twenty-four of the 46 possessed adequate flanking regions and a repeat section ≥12 base pairs. PCR conditions for the newly designed primers were optimised using a temperature gradient with annealing temperatures ranging from 48–62°C to determine optimum amplification conditions. Each reaction contained the following: 2.0 µl 10 mM dNTPs, 1 µl of 10x PCR buffer, 0.4 µl of 50 mM MgCl₂, 0.4 µl 10 mM F primer, 0.4 µl 10 mM R primer, 0.1 µl (0.5U) Taq polymerase (Invitrogen), 4.7 µl ddH₂O and 1.0 µl (50 ng) genomic DNA. Thermo-cycling conditions used an initial denaturation step at 94°C for 2 minutes followed by 30 cycles of 94°C (30 seconds), optimal annealing temperature (30 seconds), 72°C (60 seconds) followed by a final extension at 72°C for 10 minutes. Of the 24 primer-pairs tested, only three failed to amplify a product of the predicted size and one was a duplicate microsatellite. Sequences of the 20 loci were deposited in GenBank (Table 2). Sequences were assembled using Scquencher 3.0 (Gene Codes Corp.).

Marker screening and parentage analyses. Berra & Neira (2003) described egg masses as being individually attached to a fibrous raecme (Fig. 3), as originally described by Guitel (1913). Therefore, we made the assumption that each intact mass originates from a single female, as observed in the closely related apogonids (Vagelli 1999). To test this assumption, we attempted to extract DNA and amplify the control region (D-loop) from ‘maternal’ fibrous material (Fig. 3) holding the eggs together, but the results were
negative. Most likely, the fibrous material contained no DNA and our assumption remains tentative but reasonable.

Parental genotype reconstruction was performed with the program Gerud 2.0 (Jones 2005), which uses an algorithm to describe a minimum number of parental genotypes contributing to an array of typed offspring. This approach is based on Mendelian rules of inheritance but assumes that parental genotypes are unknown. In addition, Gerud 2.0 calculates exclusion probabilities for this ‘neither parent known’ model. The assumption of a single dam meets the criteria of the program Gerud 2.0 to accurately reconstruct parental genotypes by assuring that the progeny are full or half sibs. In addition, for those egg masses with net-associated males, we confirmed paternity by matching genotypes in the mass and in the adjacent male. We tested how powerful our microsatellite markers were at detecting multiple paternity by using PrDM (Probability to Detect Multiple matings) (Neff & Pitche 2002). Following similar simulations used in Chapman et al. (2004), several mating scenarios were run with: 1) two males with equal mating success contributing to the mass; 2) two males with skewed mating success to simulate cuckoldry or sneaker fertilisations (66.7 percent and 33.3 percent); 3) three males with equal success contributing to the mass; and 4) three males with a skewed ratio (60 percent, 25 percent and 15 percent) of mating success. Several brood sizes were tested due to the variability in the sampled egg masses.

Mitochondrial DNA analysis. To further assess genetic diversity, the mtDNA Dloop was partially sequenced (780 bp) in 17 adults and one larva collected from the Adelaide River, three individuals from the Daly River, South Alligator River and East Alligator River (from the Northern Territory, Australia), and four individuals from New Guinea. Amplification conditions followed Sivasundar et al. (2001). Cycle sequencing reactions were performed with BigDye Terminator sequencing reaction kit (Applied Biosystems) and products were visualised with a MJ Research 5100 Basestation sequencer (MJ research, CA). Complementary sequences were edited with Sequencher 3.0 (Gene Codes Corp.) and aligned with Bioedit (Hall 1999) using Clustal W (Thompson et al. 1997). All mtDNA haplotypes were deposited in Genbank (EU262420-EU262436).

Mitochondrial Dloop data were used to estimate relevant demographic parameters for the Adelaide River population. The average p-distance among individuals was calculated using MEGA 3.1 (Kumar et al. 2004) and statistical parsimony (SP) networks were constructed using TCS 1.21 (Clement et al. 2000). Subsequently, the software package LAMARC (Kuhner & Smith 2007) was used to estimate historical demographic parameters (θ and g) under a Bayesian approach. Simulations were performed under a coalescent model with exponential growth to estimate the population parameters g (the exponential growth rate) and θ; θ = 2Nμ, where N is effective population size for females and μ is the mutation rate. MCMC chains were run with the following settings: one initial chain with 500 trees sampled, sampling increment = 20, trees discarded = 1000; one final chain with 10000 trees sampled, sampling increment = 100, trees discarded = 1000. Three independent runs (with different speeds) were performed and the results were consistent. A molecular clock of Dloop calculated for trans-isthmian geminate species of Chromis damselfishes (8.24 x 10-8 to 9.30 x 10-8 substitutions per site per generation, Domingues et al. 2005) was used to calibrate the effective number of females in the population.

RESULTS

Microsatellite loci. Genetic assays reveal that variation is unexpectedly low in this population: among 20 microsatellite loci screened for variation (n = 41 adult individuals) only two loci were polymorphic (Table 2). To confirm that there was no non-homologous amplification, all monomorphic loci were bidirectionally sequenced to confirm the presence of a microsatellite. The two polymorphic loci (Kg019 and Kg275) are suitable for paternity analyses, exhibiting 6 and 5 alleles respectively (Table 2). Tests of genotypic linkage disequilibrium were performed in Arlequin v3.0 (Excoffier et al. 2007) with 10,000 permutations using the EM algorithm. No linkage disequilibrium was detected (Chi-squared test value = 21.086, p = 0.687).

We sought to determine whether a male found in close proximity to an egg mass in the net during capture could have sired and carried the eggs. Five males and five
Table 2. Name and Genbank accession number of 20 microsatellite loci for Kurtus gulliveri developed for this study. PCR primer sequences (bp) including priming sites and optimal annealing temperature (T) are given for each locus. The number of distinct alleles (k), observed and expected heterozygosities, and Hardy-Weinberg Equilibrium test results (H_0, H_e, and HWE) are given for the only two polymorphic loci found in a sample of 41 adult Nurseryfish.

<table>
<thead>
<tr>
<th>Locus-Accession no.</th>
<th>Primer Sequence (5'-3')</th>
<th>Sequence motif</th>
<th>T (°C)</th>
<th>Size (bp)</th>
<th>k</th>
<th>H_0</th>
<th>H_e</th>
<th>HWE</th>
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<tbody>
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<td>Kg054</td>
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<td>58.4</td>
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<td>RTGAAGTCCAGATTTTGGAGAG</td>
<td>(GT)_8</td>
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<td>-</td>
<td>-</td>
</tr>
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<td>(GT)_5(GC)_2</td>
<td>57.4</td>
<td>243</td>
<td>1</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
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<td>(CT)_5(GT)_3</td>
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<td>401</td>
<td>1</td>
<td>-</td>
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<td>0.68</td>
<td>p=0.3395</td>
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<td>-</td>
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<td>-</td>
<td>-</td>
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<td>Kg026</td>
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<td>(GA)_1</td>
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<td>1</td>
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<td>-</td>
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<td>RCACCTGAGGACAAGAGACG</td>
<td>(GA)_1</td>
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<td>-</td>
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<td>-</td>
</tr>
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<td>(GA)_1</td>
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<td>-</td>
</tr>
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<td>(GA)_1</td>
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<td>(GA)_1</td>
<td>60.5</td>
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<td>(CA)_1</td>
<td>58.6</td>
<td>222</td>
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<td>0.61</td>
<td>0.68</td>
<td>p=0.3395</td>
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<td>-</td>
<td>-</td>
</tr>
<tr>
<td>EF349645</td>
<td>RTGTGCTTGGAGGACCTTGAGG</td>
<td>(CA)_1</td>
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<td>-</td>
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<tr>
<td>EF349646</td>
<td>RGCTCTGTGACATTACGAGG</td>
<td>(CA)_1</td>
<td>58.6</td>
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<td>-</td>
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<tr>
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<td>FCAGACTCAACAGTGCCAGC</td>
<td>(GA)_1</td>
<td>60.5</td>
<td>255</td>
<td>5</td>
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<td>0.69</td>
<td>p=0.4806</td>
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<td>(GA)_1</td>
<td>60.5</td>
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<td>(GA)_1</td>
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</table>

Table 3. Allele frequencies for two microsatellite loci estimated from the adult specimens (n=41); exclusion probabilities calculated under a ‘neither parent known’ model.

<table>
<thead>
<tr>
<th>Locus</th>
<th>Exclusion Probabilities</th>
<th>Allele size</th>
<th>Allele frequency</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kg019</td>
<td>0.2477</td>
<td>219</td>
<td>0.354</td>
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<td></td>
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<td>221</td>
<td>0.171</td>
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<td>223</td>
<td>0.012</td>
</tr>
<tr>
<td></td>
<td></td>
<td>229</td>
<td>0.415</td>
</tr>
<tr>
<td></td>
<td></td>
<td>231</td>
<td>0.012</td>
</tr>
<tr>
<td></td>
<td></td>
<td>233</td>
<td>0.037</td>
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<tr>
<td>Kg275</td>
<td>0.26311</td>
<td>236</td>
<td>0.462</td>
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<td></td>
<td></td>
<td>240</td>
<td>0.244</td>
</tr>
<tr>
<td></td>
<td></td>
<td>244</td>
<td>0.205</td>
</tr>
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<td></td>
<td></td>
<td>248</td>
<td>0.051</td>
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<td></td>
<td></td>
<td>252</td>
<td>0.038</td>
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</table>

Associated egg masses were consistent with this scenario (Table 4). Our results report an absence of multiple paternity in all egg masses when assessed independently of an associated male. This is consistent with the breeding scenario described by Berra et al. (2007). The masses that were captured without any associated males were genotyped to screen for multiple paternity, and we did not find evidence for more than two parents contributing to a mass (Table 5). However, in Table 4, EM-02 is consistent with being sired by AD-02. If AD-02 did sire EM-02, assuming Mendelian inheritance, we would see allele 240 present in the mass. Therefore, we can conclude that AD-02 did not contribute to the mass although the presence of the 236 allele is consistent or AD-02 was not the only male to contribute to the mass due to the absence of the 240 allele.
The two microsatellite loci are powerful enough to detect multiple paternity according to the PrDM analysis (Table 6). The results indicate that probability increased as the brood size increased, and the probability of detecting multiple paternity increased as the number of sires increased. However, there was still a 58.9 percent chance that multiple paternity can be detected with these markers with the small brood size of 10 when two males contribute to the mass with a skewed ratio (Table 6).

### Variation in sequences of control region
DNA sequence data from 780 base pairs of mtDNA control region revealed only four variable sites, defining five distinct haplotypes, among all individuals sampled in northern Australia (Fig. 4). The haplotype of three individuals

Table 4. Genotypes of egg masses with associated males. Genotype of male is compared to genotypes of multiple embryos in each mass. * = number of eggs/embryos that successfully amplified, having that genotype, at the given locus. ** = white egg mass

<table>
<thead>
<tr>
<th>Male</th>
<th>Locus</th>
<th>Genotype of male</th>
<th>Associated egg mass(es)</th>
<th>Genotypes found in mass</th>
<th>n</th>
<th>Consistent with male?</th>
</tr>
</thead>
<tbody>
<tr>
<td>AD-01</td>
<td>Kg019</td>
<td>221/229</td>
<td>EM-01</td>
<td>221/229</td>
<td>5</td>
<td>Yes</td>
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<td></td>
<td>Kg275</td>
<td>236/240</td>
<td>EM-01</td>
<td>236/236, 236/240</td>
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<td>AD-02</td>
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<td>EM-02</td>
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<td>EM-02</td>
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<td>EM-03*</td>
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<td>EM-07</td>
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Table 5. Egg masses with no associated males. Parental reconstruction performed in Gerud2.0. ** = white egg masses

<table>
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<tr>
<th>Egg Mass</th>
<th>Locus</th>
<th>Parent 1 genotype deduced</th>
<th>Class 1</th>
<th>n</th>
<th>Class 2</th>
<th>n</th>
<th>Class 3</th>
<th>n</th>
<th>Parent 2 genotype deduced</th>
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<td>EM-08*</td>
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from three Northern Territory river systems disjunct from the Adelaide River were identical to one of the common haplotypes in the Adelaide River population. The four individuals from New Guinea are identical but have on average 24.5 nucleotide substitutions relative to the haplotypes in Australia (Fig. 4). The average p-distance among sampled individuals in northern Australia is extremely low at 0.001. The demographic analyses performed in LAMARC estimated a population growth rate \( g = 875.1 \), which is consistent with population expansion.

**DISCUSSION**

Our study is the first to address questions about the life history of *K. gulliveri* utilising genetic markers. *Kurtus gulliveri* is found in very turbid waters where river levels fluctuate up to eight metres daily due to strong tidal surges. They also co-occur with saltwater crocodiles (*Crocodylus porosus* Schneider, 1801), which make field observations of their behaviours dangerous, if not impossible (Berra 2003). However, the nature of the male supraoccipital hook brooding behavior and the structure of the egg masses provide grounds to study this intriguing reproductive strategy as a unique form of paternal care. We tested paternity of specific males with associated egg masses, along with analysis of egg masses collected without associated males, to address questions in the forehead brooding in *K. gulliveri*, and potentially identify patterns that will lead to further studies.

Microsatellites are excellent markers for paternity studies (Tautz 1989; Goldstein & Schlötterer 1999; DeWoody & Avise 2000) because they are highly variable, codominant, easily amplified, and species-specific. They have proven to be a valuable tool for parentage analyses with as little as two (Kellogg et al. 1995) and three variable loci (Zane et al. 1999; McCoy et al. 2001), and even when few repeat motifs are found using similar techniques (Feldheim et al. 2001). However, the extremely low variation among microsatellite markers (with few alleles at high frequencies) found in this study severely limited our ability to provide robust conclusions regarding the hypotheses tested.

The evidence gleaned from the genotypes suggests, but does not prove, that physical proximity during capture means that the male sired or carried the associated mass. One of the males assayed (AD-06, Fig. 2A) produced evidence that rejects the hypothesis of paternity for both masses shown in Fig. 2A. Genotypes at locus Kg275 among the embryos (Table 4) are inconsistent with the genotype of the male. Therefore, close proximity alone is not a sufficient indicator that the male has sired and was carrying the mass. In addition, Male AD-02 (Table 4) is consistent as the sire of EM-02, however this male could not be the only sire contributing to this mass if we assume Mendelian inheritance.

Discovering the mode of fertilisation will greatly augment our knowledge of the mating system of this species. For instance, although it is a common taxon in the rivers where it occurs, it is still unknown how and when a male acquires an egg mass. Berra et al. (2007) suggested that the male might spawn by directly pulling the mass from the female, similar to the behaviours seen among apogonid fishes (Vagelli 1999), putative close relatives of Nurseryfish (Johnson 1993; Smith & Wheeler 2006; Thacker 2009). Our samples consist of egg masses associated with putative brooding males (Table 4), in most cases providing consistent evidence to suggest paternity. However, we
cannot reject the idea that males may carry unfertilised egg masses. Unfortunately, we cannot ascertain whether the egg mass was unfertilised without direct observation of previtellogenic space and a fertilisation membrane in the field. Failure to amplify microsatellite loci from EM-13 and EM-14 (Table 1) could be due to several factors, among them that the eggs are fertilised but that adequate quantities of DNA could not be recovered. However, recovery of DNA could be hindered by preservation or contamination as well, so the status of these eggs cannot be determined. Since we did not find any egg masses that were homozgyous at both loci for all eggs sampled, we cannot definitively say whether any of the white egg masses were actually unfertilised (Table 5).

While addressing these hypotheses, it was surprising to find extremely low genetic variation, given that microsatellites are one of the most highly variable types of genetic markers (DeWoody & Avise 2000). The lack of diversity in the D-loop region – again, one of the more highly variable molecular markers used for population studies – is consistent with this observation which has also been documented in populations of Esox lucius (Jacobsen et al., 2005). The estimated female effective population size (approx. 12,000) for K. gulliveri is comparable to that of a genetically depauperate population killfish, Fundulus sciadicus Cope, 1865 in streams of Nebraska (N_e approx. 7000) (Li et al., 2009), and significantly less than a highly abundant and fecund characin, Prochilodus nigricans Six & Agassiz, 1829 (N_e approx. 600,000) from a single South American drainage (Orti et al. unpublished data). It is often acknowledged that freshwater fishes exhibit lower genetic variation and increased population structure in comparison to marine fishes (e.g. Ward et al. 1994), which was reinforced by the genetic data observed in the Nurseryfish. However, individuals sampled from disjunct drainages in Australia did not show any divergence from each other while samples from New Guinea were very different from the Australian fish. In addition, the genotypes of the New Guinea specimens revealed novel genotypes not found in the Australian populations (data not shown). A possible explanation for this phenomenon could be historical bottleneck and range expansion events caused by Late Pleistocene sea level fluctuations (Voris 2000), but these all are only speculative given the limited power of the current data set. More samples from the entire range are necessary to test this hypothesis. Other variable markers such as amplified fragment length polymorphism (AFLPs) and single-nucleotide polymorphism (SNPs) may be needed to address the unanswered questions concerning historical demography and the therefore clandestine mating system in these fascinating fishes.

ACKNOWLEDGEMENTS

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REFERENCES


The natural history of mudskippers in northern Australia, with field identification characters

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ABSTRACT

We provide field identification characters and report on the natural history of mudskippers (Gobiidae: Oxudercinae) in Cairns, Darwin, Derby and Broome, northern Australia. Nine species in four genera are recorded (Boleophthalmus birdsongi, B. caeruleomaculatus, Periophthalmodon freycineti, Periophthalmus argentilineatus, P. darwini, P. minutus, P. novaeguineaeus, P. takila and Scartelaos histophorus). The intertidal zonation of mudskippers conforms to previously reported patterns, but subtle differences in habitat preference are observed at both intraspecific and intrageneric levels, underlining the need for in-depth investigation of habitat selection by mudskippers. Although most species inhabit littoral mudflats, some show possible habitat expansion: juvenile Periophthalmodon freycineti are found occasionally in pools on a sandy shore, and a population of Periophthalmus minutus is found to be established in a marginal mangrove habitat (a salt flat behind a pioneer mangrove assemblage). Burrow confinement during high tide is confirmed for both species of Boleophthalmus, two Periophthalmus (P. minutus and P. novaeguineaeus) and Scartelaos, but not for Periophthalmodon or the other Periophthalmus species. Territory formation is described for S. histophorus.

KEYWORDS: mudskipper, Oxudercinae, northern Australia, field identification, distribution, habitat condition, natural history

INTRODUCTION

The term mudskipper usually refers to those amphibious gobies that move about actively on the exposed mudflats of creeks, estuaries and coastal areas during low tide (Clayton 1993; Graham 1997; Graham et al. 2007). These fishes belong to the gobiid subfamily Oxudercinae, which includes 40 species in 10 genera (Murdy 1989; Lee et al. 1995; Murdy & Takita 1999; Darumas & Tantichodok 2002; Larson & Takita 2004; Jaafar & Larson 2008; Jaafar et al. 2009) and are distributed from eastern Asia, the South Pacific islands and northern Australia, westward across South-east Asia and the Arabian Peninsula to both the east and west coasts of Africa (Murdy 1989).

Mudskippers are often one of the dominant ecological components on tidal flats, and they play an important ecological role as carnivores and as preferred prey for many avian predators (Clayton 1993). As such, these fishes contribute to the maintenance of the integrity and health of mudflat ecosystems, which are often very vulnerable to negative human impacts, but offer significant ecological services (Reise 1985; Costanza et al. 1997). For these reasons and because of their biological peculiarity as amphibious fish, mudskippers have been investigated from various aspects; for example, their life on mud, locomotory mechanics, air-breathing capabilities, burrowing and reproductive behaviour (e.g. Atkinson & Taylor 1991; Harris 1960; Ishimatsu et al. 1998, 2007, 2009; MacNae 1968; Takeda et al. 1996; Tamura et al. 1976; Zhang et al. 2003). Recently their ability to produce vocalisations has been confirmed (Polgar et al. 2011). In addition, mudskippers are an invaluable source of information for insights into vertebrate invasion from an aquatic to terrestrial environment (Ishimatsu & Gonzales 2011).

Twelve species of oxudercine gobies belonging to six genera are known from tropical and subtropical northern Australia, where numerous mudflats and other soft substrates are located in sheltered bays, estuaries and areas protected by coral reefs or mangrove forests (Murdy 1989; Larson & Williams 1997; Larson & Takita 2004; Hoese & Larson 2006; Jaafar & Larson 2008). Notwithstanding the abundance of mudskippers in these habitats, biological data are scarce and generally restricted to species inhabiting the east coast of Australia. Milward (1974) studied the morphology, physiology, distribution, food and feeding habits, and habitat conditions of five mudskipper species in areas from Cairns to Brisbane, Queensland. Nursall (1981) provided notes on the behaviour and habitat of one Periophthalmodon and four Periophthalmus species near...
Townsville, Queensland. Townsend & Tibbetts (1995) studied the distribution and the seasonal occurrence of *Scartelaos histophorus* (Valenciennes) in Brisbane, and Townsend & Tibbetts (2005) reported the behaviour and sexual dimorphism of *S. histophorus*.

Thus, the aim of this study was to collect natural history information on the distribution, habitat conditions and lifestyle of mudskippers in four locations of northern Australia, from the east coast of Queensland through the Northern Territory to northern Western Australia. Key characters useful for field identification of mudskippers are also provided to aid further investigations of mudskippers in these regions.

**MATERIALS AND METHODS**

**Study Sites.** Field surveys were conducted on tidal flats along the coasts of Cairns in Queensland, Darwin in the Northern Territory, and Derby and Broome in Western Australia, from 2000 through 2004 (Table 1). The mudflats
The natural history of mudskippers in northern Australia

in Darwin were the most extensively and frequently investigated. All localities are tropical with monthly mean temperature being around 30°C (26–38°C depending on locality) throughout the year, and highest rainfall during the months of November/December through February/March (a monsoonal climate; http://www.bom.gov.au/climate/data/index.shtml).

In Queensland mudskippers were surveyed at Yorkeys Knob (Site A, Fig. 1A), near Cairns Airport (Site B, Fig. 1B) and at Esplanade Beach, Cairns (Site C, Fig. 1C). In the Northern Territory the study sites around Darwin included a beach in Darwin Harbour (Site D, Fig. 1D), Ludmilla Creek (Site E, Fig. 1E), mudflats in the Howard River estuary (Site F, G, H, Site F, G, H), a sloping muddy boulder-strewn shore at Channel Island (Site I, Fig. 1I) and two mudflats (Site J, K, Fig. 1J, K) on the right bank of Middle Arm, Port Darwin. In Western Australia the study sites were a beach facing Roebuck Bay in Broome (Site L, Fig. 1L) and three locations in and outside of Derby Harbour (Site M, N, O, Fig. 1M, N, O) in the Fitzroy River estuary. Macrotidal conditions existed at all sites, reaching more than 8 and 10 m in Port Darwin and Derby, respectively.

Field Observations. Living mudskippers were photographed in their habitats to record body shape and colour patterns. Body colour and shape of freshly caught fish were also recorded immediately after fixation in 10% formalin solution to assist with field identification criteria. Their behaviour was observed and recorded with binoculars.

Table 1. Study sites and times for mudskipper surveys in northern Australia.

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<td><strong>Cairns, Queensland</strong></td>
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<tr>
<td>Yorkeys Knob</td>
<td>Site A: Narrow mud banks of the Moon River estuary (Fig. 1A 16°48'07&quot;S, 145°42'49&quot;E).</td>
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<td>Cairns Airport</td>
<td>Site B: Mangrove forest reserve by airport (Fig. 1B), crossed by Middle Creek (not shown in photograph 16°52'46&quot;S, 145°45'34&quot;E).</td>
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<td>Esplanade Beach</td>
<td>Site C: Open muddy beach and mudflats, Cairns (Fig. 1C), partially covered by sand (not shown in photograph 16°54'50&quot;S, 145°46'21&quot;E).</td>
<td>X</td>
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<td><strong>Darwin, Northern Territory</strong></td>
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<td>Darwin Harbour</td>
<td>Site D: Mud and sandy boulder-strewn tidal flats, bordered landward by mangrove forest (Fig. 1D 12°26'50&quot;S, 130°51'07&quot;E).</td>
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<td>Ludmilla Creek</td>
<td>Site E: Narrow mud banks along Ludmilla Creek mouth, bordered by mangrove forest (Fig. 1E 12°24'44&quot;S, 130°50'14&quot;E).</td>
<td>X</td>
<td>X</td>
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<td>Howard River estuary</td>
<td>Site F: Open, level mudflats on the left bank of Howard River mouth (Fig. 1F 12°21'39&quot;S, 131°01'21&quot;E).</td>
<td>X</td>
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<td>Site G: Landward mangrove border of Site F, with 1–2 m tall mud mounds present, adjacent to eucalypt forest (Fig. 1G 12°21'39&quot;S, 131°01'21&quot;E).</td>
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<td>Site H: Muddy ditches running from adjacent fish ponds, sparsely covered by the halophyte, Suaeda arbusculoides (Fig. 1H 12°21'39&quot;S, 131°01'21&quot;E).</td>
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<td><strong>Channel Island</strong></td>
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<td></td>
<td>Site I: Open boulder-strewn muddy shore on west coast of Channel Island (Fig. 1I 12°33'24&quot;S, 130°51'43&quot;E).</td>
<td>X</td>
<td>X</td>
<td>X</td>
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<tr>
<td><strong>Middle Arm</strong></td>
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<td>Site J: Open mudflat (Fig. 1J) separated by approx. 150 m width mangrove belt from right bank of Middle Arm; mudflat sparsely vegetated by S. arbusculoides and surrounded by mangroves, mainly Avicennia marina and Ceriops australis (12°33'41&quot;S, 130°52'56&quot;E).</td>
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<td>Site K: Narrow mudflat on right bank opposite Channel Island, densely covered by aerial roots of A. marina and strewn with boulders (Fig. 1K 12°33'12&quot;S, 130°52'35&quot;E).</td>
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<tr>
<td><strong>Broome, Western Australia</strong></td>
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<td>Roebuck Bay</td>
<td>Site L: Open muddy beach, with muddy lower zone and sandy upper zone (Fig. 1L 17°58'16&quot;S, 122°14'09&quot;E).</td>
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<td><strong>Derby, Western Australia</strong></td>
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<tr>
<td>Fitzroy River estuary</td>
<td>Site M: Boulder-strewn mudflat within Derby Harbour (Fig. 1M 17°17'33&quot;S, 123°56'29&quot;E).</td>
<td>X</td>
<td>X</td>
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<td></td>
<td>Site N: Open mudflat bordered landward by mangrove forest, outside Derby Harbour (17°17'33&quot;S, 123°36'29&quot;E).</td>
<td>X</td>
<td>X</td>
<td>X</td>
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<td></td>
<td>Site O: Small mudflat bordered by mounds in mangroves at Site N (17°17'33&quot;S, 123°36'29&quot;E).</td>
<td>X</td>
<td>X</td>
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</table>
and a video camera. Field surveys were usually conducted around times of low spring tides when the habitats were exposed, while some surveys were undertaken at high tide to confirm whether mudskippers remained emerged or confined in their burrows. Mudskipper emergence or burrow confinement at high tide was judged from a comparison of fish numbers in the same habitat at high and low tide, and when possible from observation of mudskippers emerging from burrows at ebb tide. Burrow water salinity was measured with a hand-held salinometer (S/Mill-E; ATAGO, Japan).

**Fish Collection.** For collecting *Boleophthalmus*, cylindrical pitfall traps (PVC pipe with one end closed at an angle) were used; hook and line with bait for *Periophthalmus* and *Scartelaos* were collected by dip net or by hand. Collected mudskippers were identified following Mundy (1989), Larson & Takita (2004) and Jaafar & Larson (2008). Voucher specimens are deposited at the Museum and Art Gallery of the Northern Territory, Australia and the National Museum of Nature and Science, Tokyo, Japan.
RESULTS

Species Collected. A total of nine mudskipper species was collected in this study (Fig. 2). This included two skipper species of Bokophthalmus (B. birdsongi Murdy, Fig. 2A,B and B. caeruleomaculatus McCulloch & Waite, Fig. 2C,D), one species of Periophthalmodes (P. freycineti Valenciennes, Fig. 2E), five species of Periophthalmus (P. argenteilineatus Valenciennes, Fig. 2F, P. darwini Larson & Takita, Fig. 2G, P. minutus Eggert, Fig. 2H, I, P. novaeguineensis Eggert, Fig. 2J, K and P. taka Jafaar & Larson, Fig. 2L) and one species of Scartelaos (S. histophorus Valenciennes, Fig. 2M). Their distribution in the sites surveyed is provided in Table 2.

Field Identification. The key characters most useful for field identification of species collected in this study are summarised in Table 3. It should be noted that in this paper ‘juvenile’ refers to small, clearly immature individuals with an indistinct colour pattern.

Adult B. birdsongi (Fig. 2A) and B. caeruleomaculatus (Fig. 2C) are distinguishable by body size, dorsal fin morphology and fin and body colour pattern as given in Table 3. The largest B. caeruleomaculatus we collected measured 144 mm in standard length (SL) and 185 mm in total length (TL), in comparison to 115 mm SL and 138 mm TL of the largest B. birdsongi specimen. Smaller individuals of the two species showed different colour pattern and morphology from adults. Juvenile B. birdsongi (Fig. 2B) was wholly greyish in body colour with dark-brown irregularly-shaped vertical bars, but had no horizontal dark stripe laterally on the body. One juvenile B. caeruleomaculatus (73 mm TL, Fig. 2D) was grey in body colour and had no particular pattern on the body (note that the photograph of Fig. 2D was taken several days after specimen preservation so that it does not represent the colour pattern of the live fish).

Periophthalmodes freycineti specimens (Fig. 2E) are discernible from Periophthalmus species by their larger maximum size, evenly grey-brown body colour and the dorsal fins without a distinct pattern. The black stripe coursing posteriorly from the eye to the caudal peduncle described by Murdy (1989) is conspicuous in juveniles but not always visible in adults.

Periophthalmus argenteilineatus (Fig. 2F) has a distinct colour pattern and a first dorsal fin (DF1) morphology as given in Table 3. Vertical white lines on the side of the body, which are also present in P. minutus (Fig. 7A, D), are distinctive in P. argenteilineatus. Periophthalmus darwini (Fig. 2G) is distinguished from other species of Periophthalmus by the very small DF1 and the space between the DF1 and the second dorsal fin (DF2) being greater than the DF1 basal length. Periophthalmus minutus (male Fig. 2H, female Fig. 2I) shows sexual dichromatism: the dorsal fins are brighter red in colour (and a little larger between the DF1 and the second dorsal fin (DF2) being greater than the DF1 basal length.

Table 2. Habitat characteristics of nine species of mudskippers in northern Australia. BR, Broome; CA, Cairns; DA, Darwin; DE, Derby; a, adults; j, juvenile. Letters in parentheses correspond with labels in site photographs, Figure 1.

<table>
<thead>
<tr>
<th>Species</th>
<th>Occurrence confirmed</th>
<th>Topography*</th>
<th>Height in intertidal</th>
<th>Substrate</th>
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<tbody>
<tr>
<td>Bokophthalmus birdsongi (a)</td>
<td>DA(D,E,F), DE(N)</td>
<td>level or sloping, with smooth or irregular surface</td>
<td>low</td>
<td>mud or muddy sand</td>
</tr>
<tr>
<td>B. birdsongi (j)</td>
<td>DA (IJ)</td>
<td>level; smooth</td>
<td>highest</td>
<td>mud</td>
</tr>
<tr>
<td>Bokophthalmus caeruleomaculatus</td>
<td>DA (F), DE(N)</td>
<td>level; smooth</td>
<td>low</td>
<td>mud</td>
</tr>
<tr>
<td>Periophthalmodes freycineti (a)</td>
<td>CA (B,C), DA (E)</td>
<td>level or sloping</td>
<td>low</td>
<td>mud</td>
</tr>
<tr>
<td>Periophthalmodes freycineti (j)</td>
<td>CA (B,C)</td>
<td>mangrove forest floor or shallow water pool</td>
<td>middle</td>
<td>mud or sand</td>
</tr>
<tr>
<td>Periophthalmus argenteilineatus</td>
<td>CA (A,B), DA (D,E), BR (L)</td>
<td>level or sloping, mangrove forest floor sloping or with mounds with surface inequalities available for refuges (e.g., rocks, pneumatophores)</td>
<td>high and low</td>
<td>mud</td>
</tr>
<tr>
<td>Periophthalmus darwini</td>
<td>DA (E,G,K), DE (O)</td>
<td>sloping or with mounds with surface inequalities available for refuges (e.g., rocks, pneumatophores)</td>
<td>highest</td>
<td>mud</td>
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<tr>
<td>Periophthalmus minutus</td>
<td>DA (F,H,J)</td>
<td>level and smooth</td>
<td>highest</td>
<td>mud</td>
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<tr>
<td>Periophthalmus novaeguineensis</td>
<td>DA, DE (M,O)</td>
<td>sloping or with mounds with surface inequalities available for refuges (e.g., rocks, pneumatophores)</td>
<td>highest</td>
<td>mud</td>
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<tr>
<td>Periophthalmus sakita</td>
<td>DA (E,F)</td>
<td>level or sloping</td>
<td>low</td>
<td>mud</td>
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<tr>
<td>Scartelaos histophorus</td>
<td>CA (C), DA (F), DE (N), BR (L)</td>
<td>level or sloping</td>
<td>low</td>
<td>mud</td>
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<tr>
<td>Species</td>
<td>Body morphology and colour pattern</td>
<td>Dorsal fin (DF) morphology and colour pattern</td>
<td>Figure</td>
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<tr>
<td>Boleophthalmus birdsongi</td>
<td>Maximum size smaller than <em>B. caeruleomaculatus</em>, horizontal black band on mid-side of body usually visible.</td>
<td>Black, paler proximally. Spines usually shorter than in <em>B. caeruleomaculatus</em> (i.e. less than body depth).</td>
<td>2A</td>
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<tr>
<td>Boleophthalmus caeruleomaculatus</td>
<td>Body greyish brown with bright blue speckles. Blue skin at base of eyeball.</td>
<td>Greyish background colour, covered with small blue spots and speckles. 4th spine may be elongated and filamentous; entire fin height greater than body depth in large adults.</td>
<td>2C</td>
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<tr>
<td>Periophthalmodon freycineti</td>
<td>Large body size (can be over 200 mm SL). Dark grey to brownish grey body colour, paler ventrally, small pale blue to whitish spots scattered over side of head; broad black horizontal stripe running from behind eyes to upper part of caudal fin base (stripe not always displayed).</td>
<td>Short fin base; wide interdorsal space. Grey in colour, with whitish to dull yellow margin.</td>
<td>2E</td>
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<tr>
<td>Periophthalmus argentilineatus</td>
<td>White speckling on side of head. Side of body with numerous narrow silvery white vertical stripes, most conspicuous on ventral half of body (fading quickly under stress or after fixation).</td>
<td>Tall and pointed anteriorly. Sub-marginal white-edged black stripe; rest of fin dull red to reddish brown with many white spots.</td>
<td>2F</td>
<td></td>
</tr>
<tr>
<td>Periophthalmus darwini</td>
<td>Small and slender; maximum size 45 mm SL.</td>
<td>Reduced in size, with interdorsal space very wide. Dull brown with pale margin.</td>
<td>2G</td>
<td></td>
</tr>
<tr>
<td>Periophthalmus minutus</td>
<td>Snout steeper than other <em>Periophthalmus</em>. Light brown body with widely scattered small dark brown speckles; many vertical white lines on side of body (fading quickly after fixation).</td>
<td>Fin triangular. In male, fin reddish with broad white margin, with small dark red to red-brown spots and streaks on membranes. Female with submarginal brown to reddish band, rest of fin duller than in male.</td>
<td>2H</td>
<td></td>
</tr>
<tr>
<td>Periophthalmus novaeguineensis</td>
<td>Grey to brown body, lighter ventrally. Head and body covered with numerous dark brown and blue spots and speckles.</td>
<td>White fin margin (brighter in male) with inframarginal red-brown to dark brown stripe; rest of fin bright red.</td>
<td>2I</td>
<td></td>
</tr>
<tr>
<td>Periophthalmus takita</td>
<td>Body grey to greyish brown, with conspicuous orange, red brown and dark brown spots (and smaller white spots) on side of body.</td>
<td>Fin large, with somewhat rounded margin. Reddish brown to dark brown with pale spines.</td>
<td>2J</td>
<td></td>
</tr>
<tr>
<td>Scartelaos histophorus</td>
<td>Slender body, light blue-grey in colour with fine blackish speckles and narrow vertical lines on side.</td>
<td>Dark brown, elongate and 'must-like'; interdorsal space much wider than DFI base.</td>
<td>2K</td>
<td></td>
</tr>
</tbody>
</table>
The natural history of mudskippers in northern Australia

Fig. 3. Boleophthalmus species in their habitats. A, B. caeruleomaculatus on Derby coastal mudflat (Site N, July 2002); B, two B. birdsongi fighting on a sloping mudflat in Darwin Harbour (Site D, Nov. 2000); C, B. birdsongi juvenile in a pool in Middle Arm, Port Darwin (Site J, March 2003).

in size) in males than in females. The margins of these fins are white in both sexes, but become semi-transparent immediately after fixation.

Periophthalmus novaeguineaeensis also shows sexual dichromatism (male Fig. 2J, female Fig. 2K): it has reddish dorsal fins, with the white colour of the DF1 and DF2 margins brighter in males (Fig. 2J). The species is easily recognisable in the field. The body colour becomes darker in males when mating (Fig. 8C). The anal fin is dark in larger males (Fig. 2J) and paler in females (Fig. 2K).

Periophthalmus takita (Fig. 2L) differs from its congeners in having a large DF1 and two distinct horizontal dark stripes on the DF2. The anal fin and the ventral edge of the caudal fin are yellow in colour. All species of Periophthalmus usually show some oblique dark bars on the side of the body, though these markings are occasionally faint or indiscernible.

Scartelaos histophorus (Fig. 2M) is easily identified in the field on the basis of the body morphology and colouration (Table 3). The fish frequently erect the mast-like DF1. Males are larger than females.

Habitat conditions and lifestyle.

Boleophthalmus birdsongi and B. caeruleomaculatus. The distribution of B. birdsongi was observed to be wider than that of B. caeruleomaculatus (Table 2). Boleophthalmus birdsongi occurred on every mudflat in the low intertidal zone in Darwin and Derby, inhabiting either sloping and rough (Fig. 3B) or level and smooth mudflats and muddy sandflats (see Table 2 for definition of topographical terms). Boleophthalmus caeruleomaculatus was restricted to mudflats that were always wet, smooth, comparatively level and more extensive than other mudflats studied (Fig. 3A, Table 2). Adults of both species of Boleophthalmus maintained a burrow for retreat when frightened or when the tide covered the habitat (Table 4). Deduced from the distinctive side to side movement of the head on exposed mudflats, both B. birdsongi and B. caeruleomaculatus likely foraged for surficial algae and diatoms, as known for all other congeners studied (Clayton 1993), during low tide within a territory around the burrow. Both species performed an aggressive display (Fig. 3B) when protecting the territory or chasing away approaching conspecifics. Courtship displays were observed in July (B. caeruleomaculatus) and August and November (B. birdsongi) (Table 4).

Habitat separation with growth was confirmed for B. birdsongi but not for B. caeruleomaculatus. Juveniles of B. birdsongi measuring from 22 to 66 mm TL (Figs 2B and 3C) were found in the intertidal zone close to the high water line of spring tide (HWS) during spring tide in March, July and November at Sites H and J; two sites where adult B. birdsongi were never observed. The juveniles of B. birdsongi disappeared from these high locations during neap tide when the habitat remained exposed by the tide and became dry. Unlike B. birdsongi, juvenile B. caeruleomaculatus of about 70 mm TL and smaller (Fig. 2D) occurred together with adults in March and July in the Howard River estuary (Fig. 1F; Site F) and on the Derby coast (Fig. 1N; Site N).

Periophthalmus freycineti. Adults of P. freycineti (Fig. 4A) inhabited open mudflats as in site C but also occurred on stream banks in Sites B and E. Juveniles were found in March in small shallow pools in the sandy part of Site C (Fig. 4B) or on the forest floor of the Red Mangrove, Rhizophora stylosa, at Site B (Table 2); both areas of which were landward of the adult’s habitat. This suggests that P. freycineti showed a clear habitat separation between different size classes (Table 2). Adults of P. freycineti were often found beside or near their burrows irrespective of
seasons (Fig. 4A). During habitat inundation by the tide, numerous if not all *P. freycineti* were seen along the water’s edge. In November 2000 we observed at Site C, that pairs of *P. freycineti* alternately gulped air and dove into their burrows (Table 4) as observed for *P. schlosseri* (Ishimatsu et al. 1998, 2009), suggesting air storage in egg chambers (Ishimatsu et al. 2009) and biparental embryonic care in both species. HKL confirmed the occurrence of this behaviour in Cairns during December 2006 and March 2010.

*Periophthalmus argentilineatus.* *Periophthalmus argentilineatus* migrates across tidal flats with changing tides. At high tide, this species rested on exposed sediment, rocks (Fig. 5B) or roots of the Red Mangrove *Rhizophora stylosa*, as observed at Sites D, E, and L (Table 2). As the tide ebbed, the fish followed the receding water down to the mudflats. A similar seaward migration during ebb tide was seen along the creek bank at Site A. The fish returned to the higher zones or the mangrove forest with the rising tide, probably after foraging on open tidal flats. Burrows with two or three turreted openings (Fig. 5A) were abundant at Site B throughout the year, even though only a few *P. argentilineatus* were observed near their burrows at low tide. We were unable to confirm use and function of their burrows, located abundantly on the mangrove forest floor (Table 4).

*Periophthalmus darwini.* *Periophthalmus darwini* was usually found in the highest intertidal zone (Table 2), although some individuals were occasionally observed on lower areas. It inhabited steep mounds present on mud at Sites G and O, a rock-strewn muddy shore at Site I, or a sloping mudflat covered by the pneumatophores of the mangrove *Avicennia marina*, at Site K. Fish were seen to forage high on the mud mound surfaces, at the seaward front of the forest floor above mounds or among dense aerial roots of the mangrove (Fig. 6A). At Site I, *P. darwini* foraged on mud or sand accumulating between rocks. Individuals of *P. darwini* resting on a mud mound would swiftly climb up it (Fig. 6B) and take refuge in the mangrove vegetation when frightened. Burrow excavation behaviour was confirmed only once in July, 2001, at Site I (Fig. 6C). The burrow opening was about 1 m below HSW. A comparison of the number of presumed *P. darwini* burrows and the number of fish foraging during low tide suggests that the majority of, if not all, *P. darwini* did not possess a burrow and remained on land during high tide (Table 4). In fact, *P. darwini* was seen to remain on land or on exposed aerial Red Mangrove roots among rocks during high tide (Fig. 6D). Courtship has not been observed, although abundant juvenile *P. darwini* of about 10 mm TL were found in February 2003 and 2004 at Site I (Table 4).

*Periophthalmus minutus.* As with *P. darwini*, *P. minutus* (Fig. 7A) inhabited the highest intertidal zone at Sites F, H and J. Site J was inundated by the tide for only a few days in each tidal cycle and remained un-inundated for more than 10 days during neap tide, resulting in extreme dehydration of the surface mud. Site F was similar to Site J only in its.
The natural history of mudskippers in northern Australia

Fig. 6. *Periophthalmus darwini*. A, *P. darwini* crawling between dense aerial roots of *Avicennia marina*, Middle Arm, Port Darwin (Site K, Jan. 2002); B, *P. darwini* (arrow) climbing up a steep mud mound, Howard River estuary, Darwin (Site G, Jan. 2002); C, burrow of *P. darwini* excavated in mud accumulated between rocks, Channel Island (Site I, July 2001); D, *P. darwini* perching on an exposed aerial root of *Rhizophora stylosa*, Channel Island (Site I, July 2001).

Fig. 7. *Periophthalmus minutus*. A, *P. minutus* on wet mudflat, Middle Arm, Port Darwin (Site J, Feb. 2004); B, turreted burrow openings on mudflat, Howard River estuary, Darwin (Site H, Mar. 2001), with individual (arrow) emerging; C, *P. minutus* (arrow) about to emerge from its burrow before the ebbing tide uncovers the burrow opening, Middle Arm, Port Darwin (Site J, July 2001); D, *P. minutus* sitting on relatively dry mud, Middle Arm, Port Darwin (Site J, Nov. 2000).
landward border. Site H was also high but was subjected to an unpredictable emersion/submersion cycle due to discharge from nearby fish-ponds. Juvenile *B. birdsongi* were often observed together with *P. minutus* in shallow tidepools remaining after the ebb tide. Burrows of *P. minutus* had two or three turrets above the mud surface (Fig. 7B) as did those of *P. argentilineatus* (Fig. 5A). *Periophthalmus minutus* moved around the habitat during the low tide period; some travelled 5 m or more from their burrow, but most individuals stayed closer. *Periophthalmus minutus* confined themselves in burrows during habitat submersion, and came out of the burrows when the water receded to the depth of 1 to 2 cm (Table 4, Fig. 7C), although a few individuals remained perched on mangrove trunks during high tide. During neap tide in the dry season when the *P. minutus* habitat remained exposed and dry for more than 10 days, very few *P. minutus* were observed on the mudflat (Fig. 7D); most remained within their burrows until the next spring tide or rain inundated the habitat. The water salinity of *P. minutus* burrows measured as high as 75 ppt in November 2000, when daily maximum temperature was 30–35°C and the rainy season was about to start toward the end of the month (http://www.bom.gov.au/climate/data/index.shtml). Courtship behaviour was seen in February 2003 (by Dr. K. Soyano of Nagasaki University) and many juveniles of 30 mm TL or less were present on the mudflat in February 2003 and March 2001 (Table 4).

*Periophthalmus novaeguineaeensis. Periophthalmus
ovaeguineaeensis* also inhabited the highest intertidal location, but in areas of irregular topography (Table 2).

**Table 4.** Burrow confinement during high tide and months when reproductive behaviour and the occurrence of juvenile fish were observed for nine species of mudskippers collected in northern Australia. CA, Cairns; DA, Darwin; DE, Derby; *Courtship display, #Biparental burrow tending.

<table>
<thead>
<tr>
<th>Fish Species</th>
<th>Burrow confinement of adult fish during high tide</th>
<th>Reproductive behaviour confirmed</th>
<th>Juvenile fish occurrence</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Boleophthalmus birdsongi</em></td>
<td>Yes</td>
<td>*Aug. and Nov. (DA)</td>
<td>Mar., Jul., and Nov. (DA)</td>
</tr>
<tr>
<td><em>Boleophthalmus caeruleomaculatus</em></td>
<td>Yes</td>
<td>*Jul. (DE)</td>
<td>Mar. (DA) and Jul. (DA, DE)</td>
</tr>
<tr>
<td><em>Periophthalmodon freycineti</em></td>
<td>Probably no</td>
<td>#Nov. (CA)</td>
<td>Mar. (CA)</td>
</tr>
<tr>
<td><em>Periophthalmus argentilineatus</em></td>
<td>Probably no</td>
<td>?</td>
<td>?</td>
</tr>
<tr>
<td><em>Periophthalmus darwini</em></td>
<td>Probably no</td>
<td>?</td>
<td>Feb. (DA)</td>
</tr>
<tr>
<td><em>Periophthalmus minutus</em></td>
<td>Yes</td>
<td>*Feb. (DA)</td>
<td>Feb. and Mar. (DA)</td>
</tr>
<tr>
<td><em>Periophthalmus novaeguineaeensis</em></td>
<td>Yes</td>
<td>*Feb. (DE)</td>
<td>?</td>
</tr>
<tr>
<td><em>Periophthalmus takita</em></td>
<td>Probably yes</td>
<td>*Jul. (DA)</td>
<td>?</td>
</tr>
<tr>
<td><em>Scartelaos histophorus</em></td>
<td>Yes</td>
<td>*Mar. and Nov. (CA), Jul. (DE)</td>
<td>?</td>
</tr>
</tbody>
</table>
The natural history of mudskippers in northern Australia

Periophthalmus novaeguineaeensis changed its distribution during our survey of the Derby coast: the species inhabited a muddy beach at Site M in July, 2002, where boulders of various sizes were strewn in the mud (Fig. 1M), but was rare in February 2003 and 2004. Due to this rarity, we searched nearby areas and found that this species was abundant at Site O (Fig. 1O) in a mangrove forest, only about 200 m from Derby Harbour. Burrows of P. novaeguineaeensis were found mainly under boulders but also in mud several metres away from them at Site M in July (Fig. 8A) and on steep mud mounds at Site O in February (Fig. 8B). Individuals foraged around their burrows and retreated into the burrow when frightened and while the burrows were flooded during high tide (Table 4). In February, some males exhibited a dark body colour (Fig. 8C) and performed courtship displays typical among Periophthalmus species, were observed in July, 2001, on the mudflat in Site F (Table 4).

Scartelaos histophorus. This species inhabited soft, wet and level mudflats located low in the intertidal zone along the shore or on estuarine banks (Table 2). All individuals take refuge in burrows to shelter from predators and during high tide (Table 4). This species was often syntopic with Periophthalmodon freycineti at Site C and with B. birdsongi, B. caeruleomaculatus and Periophthalmus takita at Site F. It is possible to discriminate the sex of paired individuals on the basis of the male’s larger body size and longer DF1 length (Fig. 10D; Townsend & Tibbetts 2005). Often, individuals of S. histophorus, smaller than territorial males and presumably consisting of females and young males, aggregated in pools, but it was not possible to determine their sex by field observation. Larger males were territorial, but paired females were not observed to defend territories. These large males kept territories of approx. 50–80 cm in diameter around the burrow. Male S. histophorus were observed to form a peripheral mud rim around their territories when density was high at Site C in November, 2000 (Fig. 10B). A territory owner repeatedly twisted his body on the mud, pushing the softened mud behind him by his tail (Fig. 10C), piling up the mud on the periphery of the territory. The mudflat area containing mud-rimmed territories extended more than 100 m along the shore. The frequency of rimmed territories decreased as the population density decreased, and they had completely disappeared.
by January 2002. Territorial males performed a unique courtship display (‘tail-standing’; Fig. 10A), a jump that lifts most of the body up onto the tail; these displays were sighted in March, November (and December, HKL pers. obs.) in Cairns and in July in Derby (Table 4). Male *S. histophoradus* frequently had violent confrontations with neighboring males, repeatedly performing the courtship display.

**DISCUSSION**

**Species Occurrence.** All nine mudskipper species identified in this study had previously been reported from northern Australia (Murdy 1989; Larson & Takita 2004; Hoese & Larson 2006; Jaafar & Larson 2008). The species reported as *Periophthalmodon schlosseri*, *Periophthalmus vulgaris* Eggert and *Periophthalmus expeditionimus* Whitley by Milward (1974) and Nursall (1981) have been identified by us as *Periophthalmodon frcycineti*, *Periophthalmus argentilineatus* (see Murdy 1989) and *P. novaeguineaensis*, respectively (but this is not absolutely certain as no specimens are available from these early studies). *Periophthalmus darwini* was described as a new species on the basis of specimens collected in the early part of this study (Larson & Takita 2004). *Periophthalmus mordyi* is a junior synonym of *P. novaeguineaensis* (Jaafar & Larson 2008).

On the other hand, the species which had been identified as *P. novaeguineaensis* by Murdy (1989) and Larson & Takita (2004), was found to be a new species and subsequently named as *P. takita* (Jaafar & Larson 2008). Four oxudercine species previously reported from northern Australia were not found during this study, i.e., *Apocryptodon madurensis* (Bleeker), *Oxudercia wizzi* (Koumans), *Periophthalmus kalolo* Lesson and *Periophthalmus weberi* Eggert (Milward 1974; Nursall 1981; Murdy 1989; Larson & Williams 1997; Larson 2008). The first two species inhabit very specific soft mud habitats (they ‘swim’ through soft mud with only the eyes exposed); the record is a misidentification of *P. kalolo* Eggert (Milward 1974; Townsend & Tibbetts 1995). The habitat shift observed for *Periophthalmus novaeguineaensis* seems not to be attributed to any apparent environmental alterations. Investigations into detailed analyses of physicochemical conditions, recruitment changes and distribution of prey and predator organisms in mudskipper habitats may give a clue to the answer to these questions.

These factors possibly explain our failure in sampling some species previously known from Northern Territory (see above). In addition, mudflats are extremely dynamic habitats, being continually influenced by weather conditions and human activities (Nursall 1981; Takita *et al.* 1999). The transient and sometimes ephemeral nature of mudflats may also be responsible for some inconsistent records of mudskipper distribution in the literature, while settlement and recruitment dynamics may cause frequent population changes as previously observed for some mudskippers (Milward 1974; Townsend & Tibbetts 1995). The habitat distribution and/or juvenile stages (e.g. Kobayashi *et al.* 1972), but they rarely refer to live body colour. Drawings of fixed specimens are of limited use for field identification of juveniles. Baeck *et al.* (2008) illustrated species-specific differences in the fin colour between juveniles of two Korean *Periophthalmus* species (*P. magnespinatus* Lee, Choi & Ryu and *P. modestus* Cantor), which can be distinguished only when the fish are 40 mm or greater in body length.

Our data on the mudskipper distribution in northern Australia may have been biased, for the following reasons. Firstly, there were differences in the frequency and duration of our field surveys between localities; the surveys were mainly conducted in well-developed mangrove forests and mudflats in or near Darwin, but less frequently in Cairns and Western Australia (Table 1) due to greater difficulties in sampling. Secondly, investigations in soft mudflat habitat, which is often located between or beside thick mangrove forests, are usually difficult to conduct, as discussed in a study on mud-dwelling amblyopine fish (Murdy & Shibukawa 2000). On the relatively isolated coasts of northern Australia, access is often not easily gained for mudskipper (or any other) surveys. Lastly, the behaviour of mudskippers of rapidly retreating in response to any disturbance renders fish collection a difficult task.

The most useful feature for identifying congeneric mudskipper species is the colour pattern of the fins and body (Murdy 1989). However, information on mudskipper colour pattern is usually not provided in sufficient detail in taxonomic papers, as they usually deal with fixed specimens that have lost their live colouration soon after fixation. For this reason, knowledge of live adult mudskippers presented in this paper is crucial for field biologists investigating mudskipper ecology and behaviour in their natural habitat, where collecting study material for species identification is often very difficult. An important source of information that we are unable to provide is the colour pattern of juveniles for most species. In fact, juveniles of *Periophthalmus* species were quite difficult to identify, unless the distribution of the species was geographically isolated, as diagnostic colour patterns are not exhibited by juveniles. A few publications describe the morphology of mudskippers during early development and/or juvenile stages (e.g. Kobayashi *et al.* 1972), but they rarely refer to live body colour. Drawings of fixed specimens are of limited use for field identification of juveniles. Baeck *et al.* (2008) illustrated species-specific differences in the fin colour between juveniles of two Korean *Periophthalmus* species (*P. magnespinatus* Lee, Choi & Ryu and *P. modestus* Cantor), which can be distinguished only when the fish are 40 mm or greater in body length.

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**Habitat Condition.** Habitat conditions of the mudskippers studied are summarised in Table 2. Similar accounts on habitat topography and zonation in intertidal zones have also been provided for Australian (Nursall 1981) and Malaysian mudskippers (e.g. Polgar & Croa 2009). Habitat separation of mudskippers in the intertidal zone
The natural history of mudskippers in northern Australia

may be explained by different physiological capacity to withstand prolonged emersion, different tactics of predator avoidance (Polgar & Crosa 2009), the need for water after prey capture (Stebbins & Kalk 1961; Gordon et al. 1978), preference for substrate characteristics, different feeding preference (i.e., herbivory, omnivory versus carnivory), or different environmental requirements with development. The general pattern of mudskipper vertical distribution in tidal flats has been assumed to be: "Species of Apoecyptes and Scartelaos are considered to live in very soft mud while Boleophthalmus spp. are found higher on the shore. The distributions of Periophthalmus and Periophthalmodon spp. are at the level of the highest tides and beyond" (Clayton 1993). However, some of our observations are in conflict with this generalised pattern: juvenile B. birdsongi co-occupied the highest intertidal zones together with P. minutus, while P. takita inhabited the lower zones where Boleophthalmus usually dominate.

Through analysis of seven mudskippers in Malaysia, Polgar & Crosa (2009) found that the habitats of Periophthalmus chrysospilos, Boleophthalmus, and Periophthalmodon (Linnaeus) and S. histophorus, than to the habitats of other Periophthalmus and Periophthalmodon species that they studied (Periophthalmus gracilis Eggert, P. variabilis Eggert and Periophthalmodon schlosseri). It seems likely that no single factor can explain spatial distributions of different mudskippers, but rather a combination of local biotic and abiotic factors would have significant influence on how different species segregate their habitats in an environmental gradient of mudflats (e.g. Clayton 1993).

Of the nine mudskipper species collected in this study, Periophthalmus darwini, P. minutus and P. novaeguineaensis occupied the highest intertidal zone and therefore are presumed to have the highest capacity for life under semi-terrestrial conditions. Unfortunately, comparative physiological data are unavailable for these three Periophthalmus species, but they are presumably capable of maintaining respiratory, acid-base and osmoregulatory homeostasis with limited access to water. Preliminary evidence we obtained for mudskippers' tolerance to high salinity is that the water salinity in P. minutus burrows was as high as 75 ppt during a hot dry season. Thus, this species, and possibly also P. darwini and P. novaeguineaensis, is thought to have the osmoregulatory capacity to withstand these extreme hypersaline conditions. Unpublished data by Takeda et al. in fact demonstrated that P. minutus can maintain plasma sodium concentration during a 9 to 14 day exposure to 200% seawater. Burrows were only partially filled with water during neap tide in the dry season and most individuals remained above the water table in globular chambers 3 to 6 cm deep from the burrow openings during that period (Takeda et al. unpublished). This observation indicates that individuals of P. minutus avoid exposure to high salinities inside their burrows. However, such tactics may further stress the physiological status of the fish when emersion is prolonged.

Habitat preference differs even among the three species living in the highest intertidal zone. Periophthalmus darwini and P. novaeguineaensis inhabited mudflats with rough topography whereas P. minutus always occurred on flat, exposed and relatively smooth mudflats. This difference may be due to behavioural, rather than physiological, differences in species-specific tactics they employed to avoid predators. Periophthalmus darwini and P. novaeguineaensis occupied areas where suitable shelters were abundant and the fishes took refuge under stones or moved quickly into the mangrove vegetation when an observer came near. In contrast, P. minutus inhabited open mudflats, where avian predation risk may be higher. The species' high affinity for burrows may be an adaptation for survival in open mudflats. Where habitats were covered by halophytes or located near a mangrove forest, P. minutus often remained under cover of the vegetation or moved well into the forest when alarmed.

Where P. novaeguineaensis and P. darwini were syntopic, they occupied different microhabitats. At Site O in Derby, P. novaeguineaensis occurred evenly over the surface of a mud mound, while P. darwini was restricted to the higher part of the mound. This may be explained by the need for water access immediately after feeding, as described for some Periophthalmus species (Stebbins & Kalk 1961; Gordon et al. 1978; Sponder & Lauder 1981). Periophthalmus novaeguineaensis was seen to visit pools on the flat wet surface after each capture of a prey item on the mud mound, whereas P. darwini, foraging high on the mud mound, was not seen to make a descent to water after feeding. The highest area of the mud mound and the mangrove forest floor inhabited by P. darwini was relatively dry, apparently with very limited water availability. Similarly, water availability seemed limited during low tide in the P. darwini habitat on the rocky shore at Channel Island. Where P. darwini was the only Periophthalmus species present (Howard River estuary), they occupied the entire surface of a mud mound, suggesting that larger Periophthalmus species may limit the distribution of the smaller P. darwini.

Reproduction of Periophthalmus darwini, P. minutus and P. novaeguineaensis is inferred to occur during the rainy season, as the occurrence of juveniles was confirmed for the former two species and courtship displays were sighted for the last species only during the middle of the rainy season, although P. novaeguineaensis habitat was visited only in February and July. These mudskippers spend their whole life at the highest location where environmental conditions are presumably more formidable for embryo incubation and early development.

The habitat separation observed for juvenile and adult B. birdsongi (Table 2) is puzzling. Polgar et al. (2010) also reported that juvenile Boleophthalmus sp. (possibly a new species) were found in more terrestrial conditions than adults. It is unlikely that juveniles have a higher capacity
for sub-aerial existence than adults. Habitat separation with development was proposed for both Periophthalmodon freycineti and P. schlosseri by Murdy (1989). Nursall (1981) observed smaller sized P. freycineti (as P. schlosseri) avoiding larger individuals.

**Lifestyles and Burrowing.** Table 4 summarises occurrence of burrow confinement of adult fish during high tide, reproductive behaviour (courtship display or biparental care) and the months that we confirmed the occurrence of juvenile individuals for the nine mudskipper species. All Boleophthalmus species appear to maintain a burrow (Boleophthalmus boddarti (Pallas) (Murdy 1986); B. pectiniostris (Dotsu & Matoba 1977); Boleophthalmus dissuniemi Valenciennes (Clayton & Vaughan 1988; as B. boddarti). Boleophthalmus birdsong and B. caeruleonaculatus emerged from their burrows when the tide receded, and performed territorial behaviour on mudflats, similar to that known for B. dissuniemi (Clayton & Vaughan 1982; as B. boddarti) and B. pectiniostris (Dotsu & Matoba 1977; Chen et al. 2007). Male S. histophorus also dig and maintain burrows and arc territorial. Neither burrow excavation nor territorial behaviour were observed for female S. histophorus.

Periophthalmus species are more diverse with respect to burrow behaviour and confinement therein during high tide (Table 4). Those species that make burrows and confine themselves during high tide include P. minitus and P. novaeguineensis. Periophthalmus takita also takes refuge in burrows, which may or may not be ‘owned’ by the fish. It is unlikely that P. darwini uses its burrows as refuges during high tide. Burrow confinement was not confirmed for P. argentilineatus, which was often seen in an exposed position on the substrate or perched on a rock. Periophthalmus argentilineatus was seen to migrate across the tidal flat during incoming tides in Cairns, Darwin and Broome, as was observed for the same species on east African mudflats (Gordon et al. 1968; Colombini et al. 1995: as Periophthalmus sobrismis Eggert) and for other Periophthalmodon species, Periophthalmus modestus (Matoba & Dotsu 1977; as Periophthalmodon cantonensis (Osebeck)) and P. chrysospilos (see Polgar & Crosa 2009).

At Okinawa, Japan, tidal migration of P. argentilineatus was presumed on the basis of burrow locations on the mangrove floor 27.9 ± 1.2 cm high above standard sea level (Oshiro et al. 2005). The lack of burrow confinement in P. argentilineatus (as P. sobrins) observed by Colombini et al. (1995) on the mangrove banks of the Tana River delta in Kenya, where it was recorded that “…the mudskippers always abandoned the occasional burrows on the incoming spring tide...and never remain submerged during high tide” has not been verified in this study. On the basis of the mean hourly zonation at spring and neap tide, these authors stated “The data show that at spring tide the mudskippers escape from the water but tend to remain under cover of the vegetation”. Polgar & Crosa (2009) observed that Periophthalmodon chrysospilos, P. gracilis and P. varibalis from Malaysia formed a group that avoids water when reached by the incoming tide, together with Periophthalmodon schlosseri. Periophthalmodon modestus, a temperate mudskipper, appears to spend the high tide period on the ground when the air temperature is high (Ikebe & Oishi 1996, 1997; Bueck et al. 2008).

Tropical or subtropical mudskippers that take refuge in burrows during high tide under high temperature conditions may store air as an oxygen reservoir to survive severely hypoxic burrow conditions, as inferred from air storage for embryonic development demonstrated for Periophthalmodon schlosseri (Ishimatsu et al. 1998, 2009) and Periophthalmodon modestus (Ishimatsu et al. 2007). Burrow confinement was not confirmed for Periophthalmodon freycineti (Table 4). The lifestyle of P. freycineti observed in this study is similar to that of P. schlosseri with respect to burrowing, foraging, swimming and conspecific confrontation (Horn 1936; MacNac 1968; Murdy 1986). MacNac (1968) speculated that P. schlosseri confined itself in its own burrow during high tide. Periophthalmodon freycineti was often found during high tide hiding itself under grasses along the water’s edge on the shore or stream bank.

**Territory of Scartelaos histophorus.** Territories with mud rims have been known in S. histophorus (as Scartelaos viridis (Hamilton)) in southern China, although their structure or construction behaviour has not been described (Yang et al. 2003). The mud rims in the territories of S. histophorus were constructed by males when fish density was extremely high. Since frequent confrontations took place between neighbours while territory owners repeatedly performed typical courtship jumps, there is no doubt that S. histophorus constructs the mud rims as ‘fences’ to protect the mating space from invasion by neighbouring males. Townsend & Tibbetts (2005) reported territoriality of S. histophorus in shallow water pools with descriptions of agonistic and tail-stand behaviour. These authors also reported body motion displacing the substratum as we observed, but did not mention mud rims, probably because of low fish population. The construction of territories with mud rims is known also in B. dissuniemi, but with different building behaviour (Clayton & Vaughan 1982; as B. boddarti). Boleophthalmus dissuniemi discharges mouthfuls of mud onto the territorial periphery, presumably to secure food and to reduce agonistic confrontations with conspecific neighbours when fish density is high (Clayton 1987). Territories with peripheral mud walls are also known in B. pectiniostris cultured in ponds (Chen et al. 2007), although construction behaviour was not described.

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CONTENTS

BROCKWELL, S., BOURKE, P., CLARKE, A., CRASSWELLER, C., FAULKNER, P., MEEHAN, B., O’CONNOR, S., SIM, R. and WESLEY, D. - Holocene settlement of the northern coastal plains, Northern Territory, Australia ......................................................... 1

JACKES, B.R. - The vine Embelia tiviensis (Angiospermae: Myrsinaceae), a new species from the Northern Territory, Australia .................................................................................... 23

COWIE, I.D. - New taxa and notes on Helicteres L. (Malvaceae: Helicteroideae) from the Northern Territory, Australia ........................................................................................................ 27

ALVAREZ, B. and HOOPER, J.N.A. – Taxonomic revision of the order Halichondrida (Porifera: Demospongiae) of northern Australia. Family Halichondriidae. ............................................... 55

BRABY, M.F. - New larval food plant associations for some butterflies and diurnal moths (Lepidoptera) from the Northern Territory and eastern Kimberley, Australia ........................................................................ 85

BROWN, G.R. - Dimorphothynnus (Hymenoptera: Thynnidae: Rhagigasterini) newly recorded from the Northern Territory, Australia .......................................................................................... 107

BRUCE, A.J. - Periclimenaeus pulitzerfinali sp. nov., a new pontoniine shrimp (Crustacea: Decapoda: Palaemonidae) from East Africa ................................................................................................... 113

DAVIE, P.J.F. - A new species and new records of Oncinopus (Crustacea: Brachyura: Inachidae) from northern Australia ...................................................................................................................... 123

REID, A. - Euprymna pardalota sp. nov. (Cephalopoda: Sepiolidae), a new dumpling squid from northern Australia .................................................................................................................... 135

NIELSEN, J.G. and SCHWARZHANS, W. - A new genus and species of Bythitidae (Teleostei: Ophidiiformes) from northwestern Australia .................................................................................... 143

SCHWARZHANS, W. and NIELSEN, J.G. - Revision of the genus Microbrotula (Teleostei: Bythitidae), with description of two new species and a related new genus ...................................................................... 147

SCHWARZHANS, W. and MÖLLER, P.R. - New Dinematichthyini (Teleostei: Bythitidae) from the Indo-west Pacific, with the description of a new genus and five new species ........................................................................................................ 161

SOMMER, J.A., LI, C., BROZEK, J., BESSERT, M.L., ORTÍ, G. and BERRA, T.M. - Low genetic diversity in Nurseryfish, Kurtus gulliveri (Perciformes: Kurtidae), and an appraisal of its breeding system using microsatellite loci ............................................................................. 179

TAKITA, T., LARSON, H.K. and ISHIMATSU, A. - The natural history of mudskippers in northern Australia, with field identification characters .................................................................................... 189

ABSTRACTED IN ZOOLOGICAL RECORD AND BIOSIS