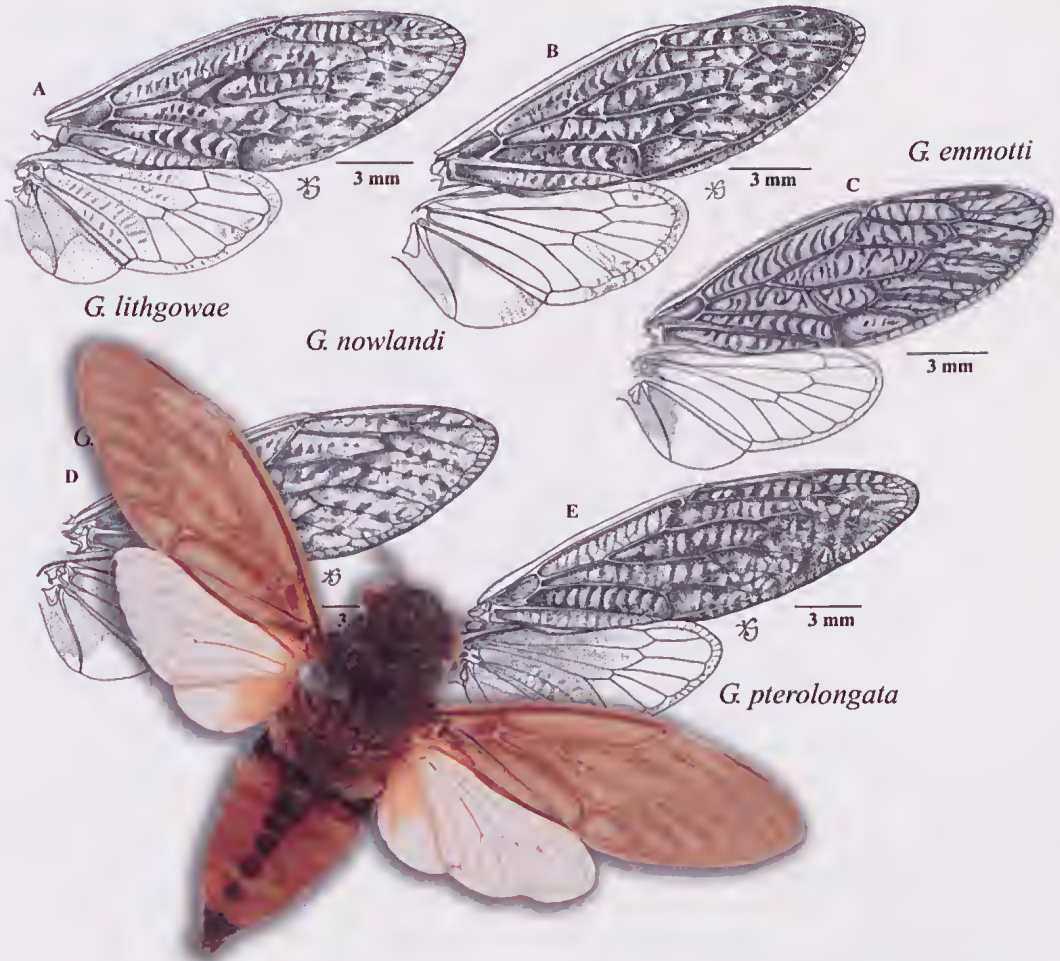


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COVER: Colour image, *Gudanga lithgowae* by Geoff Thompson.
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The reproductive cycle of the Asian House Gecko (*Hemidactylus frenatus*) in Brisbane, south-eastern Queensland: a tropical invader of a subtropical, seasonal environment.

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ABSTRACT

The Asian House Gecko, *Hemidactylus frenatus*, is a successful invader of much of the tropical habitat of the world. It has also colonised many subtropical, seasonal areas, including Brisbane, Queensland, where it has become abundant, further from the equator than any other known breeding population. The reproductive cycle of this population was investigated and, in contrast to equatorial populations, it was found to be strongly seasonal, with females generally ceasing breeding activity in March to August and males also reducing reproductive effort May to June. □ *Asian House Gecko, Hemidactylus frenatus, invasive species, Queensland.*

The biology of invasive species is an increasingly urgent topic of research as more and more species successfully colonise new areas with human assistance, deliberate or otherwise. A relatively small number of animal and plant species are spreading throughout large parts of the globe. The effects of the new settlers can be dramatic, such as the smothering of all other plants by rubber vine (*Cryptostegia grandiflora*) or more subtle, but all tend towards the reduction of the distinctiveness of disparate ecosystems, a process that has been styled as “McDonaldisation” of the world’s biodiversity (Holmes 1998; Lövei 1997; Low 2001). A better understanding of the factors permitting invasive species to reproduce and adapt successfully to new environments is crucial to either reducing the impact or, more hopefully, preventing invasions.

The Asian House Gecko, *Hemidactylus frenatus* Duméril and Bibron, 1836, is one such invader. Its original distribution is uncertain but thought to centre on south-east Asia, from India to

Indonesia (Case *et al.* 1994). It has now spread in a broad band around the equator, being known from central America to the islands of the Indian and Pacific Oceans (Case *et al.* 1994; Cole 2005; Rödder *et al.* 2008). It was first recorded in Australia at Port Essington, Northern Territory, in the 1840s. This colony was thought to have died out when humans abandoned this early settlement (Cogger & Lindner 1974) but the species was re-collected on Coburg Peninsula in 1990 (Fisher & Calaby 2009). The species’ next appearance was in Darwin in the 1960s where they have since become abundant and have spread into native bushland outside the city (Cook 1990; Covacevich *et al.* 2001; Keim 2002; Newbery & Jones 2007). Asian House Geckos were first recorded in Brisbane in 1983 when specimens from the wharves were donated to the Queensland Museum (Covacevich *et al.* 2001). They are now one of the commonest reptiles to be encountered in this city, being found in abundance on buildings from the inner city to the outer suburbs and outlying towns. This spectacular success is all the more intriguing given that the

Brisbane population is the furthest from the equator known to be reproductively successful. In Java (6° S from the equator and within its presumptive native range), *H. frenatus* is a continuous breeder, with no apparent seasonal pattern in males or females (Church 1962). This strategy is understandable in an equatorial climate, where there is little temperature or humidity change through the year. However, *H. frenatus* has now spread to more subtropical parts of the world which are distinctly seasonal and where year-round reproduction would seem to be disadvantageous. Populations living in the Ryukyu Islands (politically part of Japan, 25° 57' N) and Taiwan (24° 10' N) are strongly seasonal with reproductive activity confined to the spring and summer months (Cheng 1988; Cheng & Lin 1977; Lin & Cheng 1984; Ota 1994). However, females in a Mexican population (19° 30' N) are reported to be aseasonal (Ramírez-Bautista *et al.* 2006).

Hemidactylus frenatus has been in Taiwan and the Ryukyus for a considerable time (a synonym of *H. frenatus*, *H. inornatus* Hallowell, was described from the Ryukyus in 1861) and some adaptation to the environment would be expected. The species has been present in Brisbane for a much shorter time frame and Brisbane is further from the equator than any other breeding population (27° 28' S). In order to better understand why *H. frenatus* has been so successful in such a different environment to that of its native range, the annual reproductive cycle of the Brisbane population was examined to determine whether it remains aseasonal like its tropical ancestral population, has become strongly seasonal like established Northern Hemisphere subtropical populations or is somewhere in between.

METHODS

The population of *Hemidactylus frenatus* from south-eastern Queensland was sampled by hand collecting specimens from sites around suburban Brisbane (between 27° 20' S and 27° 31' S) monthly between October 2009 and September 2010. On capture, specimens were euthanased, preserved and accessioned into the collection

of the Queensland Museum. Geckos were handled following procedures approved by the Queensland Museum Ethics Committee (permit no. 09-02). Additional specimens were donated by the public to the Queensland Museum.

Snout-vent length (SVL) of specimens was measured with Mitutoyo electronic callipers. A small abdominal incision was made to allow determination of gender. If male, the epididymis was classed as Not Visible, Visible or Full. If female, the width of the largest ovarian follicle was measured and the ovary was classed as Non-vitellogenic (all follicles small and white), Vitellogenic (an enlarged, yellow follicle present) or Gravid (ovulated ovum present in the oviduct). If gravid, the width of the ovulated ovum and the largest ovarian follicle were both measured. Previous workers have classed a specimen as fecund if they had yolked ovarian follicles of 2 mm (Cheng 1988), 2.5 mm (Lin & Cheng 1984) or 3 mm (Church 1962). However, the smallest yolked follicle in this study was found to be 1.47 mm in diameter, so it was decided to use follicle colour (yellow rather than white) rather than size as the determinant of reproductive condition.

Specimens smaller than the smallest individual found to be reproductively active in each sex were classed as immature. The assumption was made that individuals larger than this with no reproductive activity were non-reproductive, rather than immature.

Uncertainty regarding size at sexual maturity at time of collection meant that a proportion of captures turned out to be sexually immature. Unfortunately, this impacted sample size significantly, so that lower numbers of mature individuals than hoped were collected, and no mature females were collected in January and no mature males in March. Therefore months were combined for statistical analysis (Dec-Jan, Feb-Mar, Apr-May, Jun-Jul, Aug-Sep, Oct-Nov). The data were analysed using Excel and Systat 11.

Reproductive cycle of the Asian House Gecko

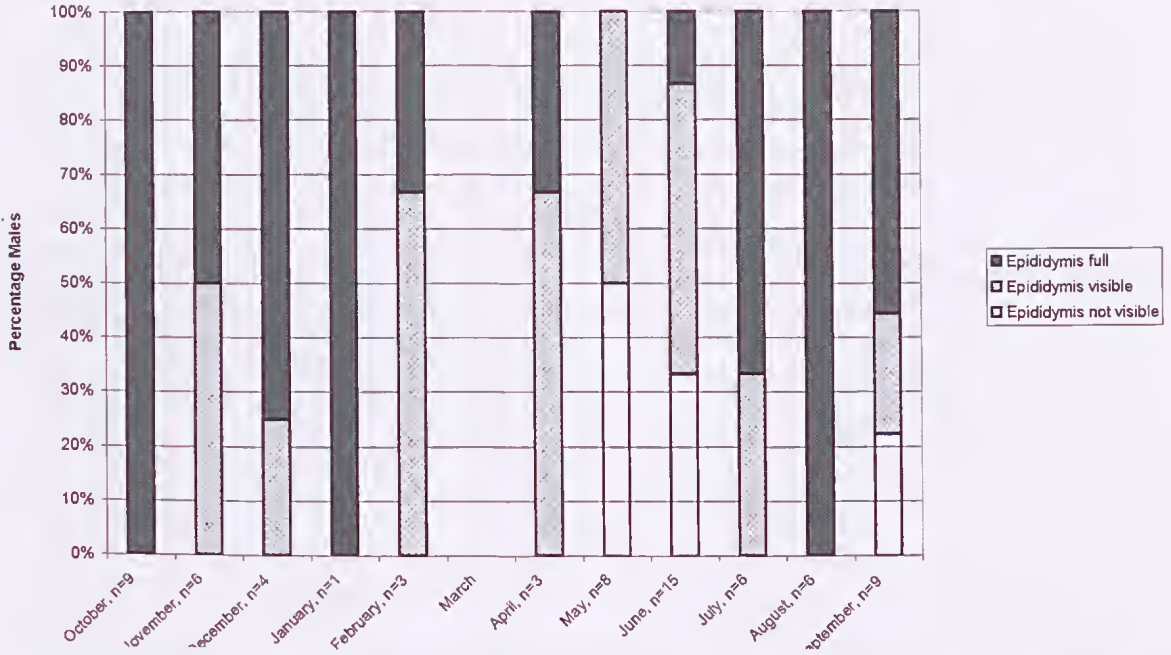


FIG. 1. Reproductive activity of female *Hemidactylus frenatus* in Brisbane between October 2009 and September 2010.

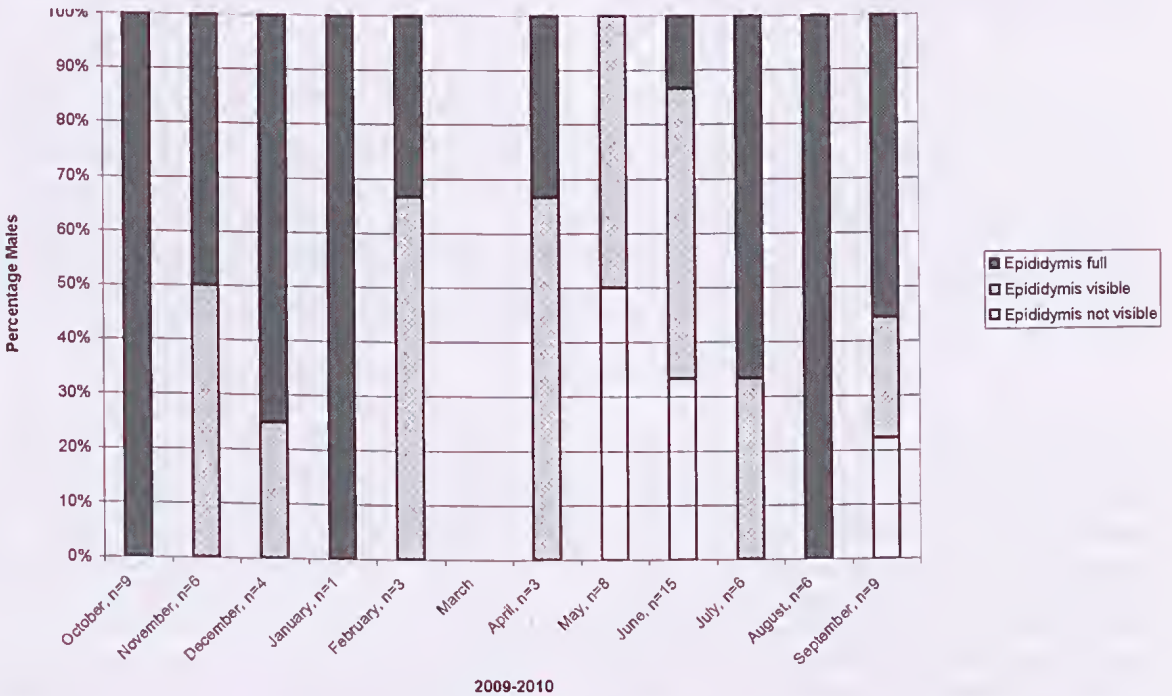


FIG. 2. Reproductive activity of male *Hemidactylus frenatus* in Brisbane between October 2009 and September 2010.

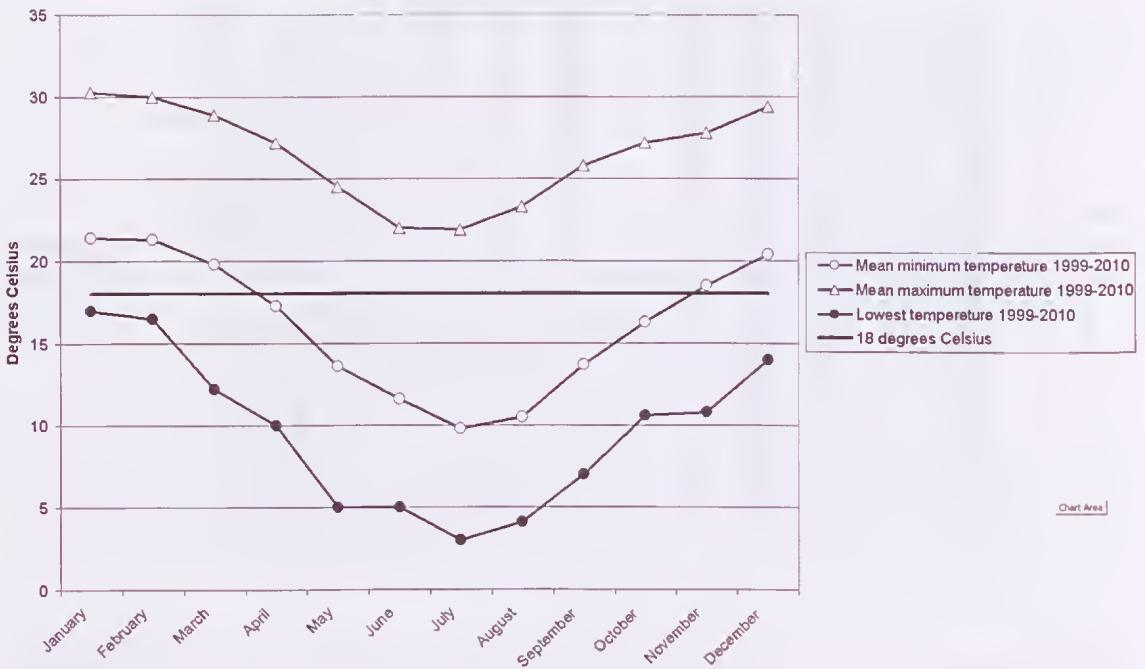


FIG. 3. Temperature ranges recorded in Brisbane between 1999 and 2010. Data from Australian Bureau of Meteorology website Climate Data Online (<http://www.bom.gov.au/climate/data>, accessed 26 July 2010).

RESULTS

A significant size difference between the sexes was observed (t -test, $t = -3.535$, $df = 112$, $p = 0.001$). Mature males averaged 55.05 mm snout-vent length ($SE = 0.52$, $n = 59$) while females averaged 51.03 mm ($SE = 0.36$, $n = 45$). The largest specimen collected in this study (62.72 mm) was male, whereas the largest female was 57.42 mm. The smallest vitellogenic female was 44.58 mm SVL while the smallest male with a visible epididymis was 42.10 mm SVL.

Females were clearly reproductively seasonal. Months differed significantly in numbers of reproductive females (vitellogenic and gravid combined; $\chi^2 = 33.945$, $df = 5$, $p = 0.000$) with markedly reduced reproductive activity around April when no vitellogenic or gravid individuals were collected (Fig. 1). Some reproductive activity was seen June to August, but it was not until September that the majority of females were reproductively active. Gravid females were not vitellogenic in any month.

Males showed a less pronounced peak in reproductive activity (Fig. 2) with little significant difference between months in number of reproductive males (epididymis Visible or Full classes combined; $\chi^2 = 7.615$, $df = 5$, $p = 0.179$). Males with turgid testes and enlarged epididymides were observed in all months except May but reproductive activity seemed somewhat reduced May to June.

DISCUSSION

The reproductive cycle of *H. frenatus* in Brisbane, the furthest population from the equator known to be reproducing successfully, is similar to that of populations in Taiwan and the Ryukyu islands, where breeding is strongly seasonal (Cheng 1988; Cheng & Lin 1977; Lin & Cheng 1984; Ota 1994), rather than that of Java, where breeding occurs year round (Church 1962). The selective pressure to reduce breeding effort in the cooler months is understandable given the temperature sensitivity of *H. frenatus*. Metabolism

of this species is impaired below 26° C and eggs die if they are exposed to temperatures below 18°C, according to studies carried out on populations in Brunei (Snyder & Weathers 1976) and the Ryukyus (Ota 1994) respectively. Figure 3 shows that air temperatures lower than 18° C are possible at any time of year in Brisbane, but are to be expected April-October. Although egg temperature is likely to more closely follow substrate, rather than air, temperature, this still suggests that keeping eggs consistently warm enough is likely to be challenging during a Brisbane winter. The oviposition site selected by the female no doubt has a large role in buffering environmental variation and protecting the eggs from extremes of temperature, especially in human-modified environments where lights, water heaters and other powered devices can provide heat. Such heat sources are unavailable in more natural environments, which could preclude successful incubation. This may be a factor limiting the expansion of *H. frenatus* into the bushland surrounding Brisbane. While this species is known to have colonised natural environments around Darwin in the Northern Territory (Keim 2002), no such observations have been made in Brisbane. However, it must be borne in mind that the Darwin population has been in existence for considerably longer than that in Brisbane and eventual adaptation and invasion of Brisbane's natural environment cannot be ruled out.

Data presented in this paper show that females are not simply suspending vitellogenesis in response to lower temperatures and resuming once conditions improve. If this were the case, suspended but vitellogenic follicles should have been observed in the winter months. This observation suggests an adaptive response anticipating the cooler temperatures of winter. A cessation of reproduction as winter approached was also observed in Taiwan, well before food availability, a potentially limiting factor, declined (Lin & Cheng 1984).

While size at maturity for females in Brisbane is the same as in Taiwan (Lin & Cheng 1984), an interesting difference between the Brisbane population and other subtropical populations is the apparent lower reproductive effort of *H.*

frenatus living in Brisbane. 100% of females in Taiwan were reproductive in June (n = 23) and many gravid females were also vitellogenic, that is, the next clutch was already developing (Lin & Cheng 1984). A maximum of 75% of Brisbane females were vitellogenic or gravid at any one time and none were both. Whether this is a consequence of poorer adaptation to Brisbane conditions or an acute response to the conditions of 2009-2010, when Brisbane was experiencing a severe drought, cannot be determined from the present data.

The cooler temperatures experienced in the middle of the year also appear to affect male reproductive activity, but males do not show as strong a response as females. While a reduction in reproductive effort is discernible May-June, some reproductive activity was observed year round. Although spermatogenesis was not assessed in this study, it is likely that males in Brisbane are behaving similarly to those in Taiwan, which were defined as 'confined acyclic' because, although testis weight varied seasonally, spermatogenic activity was constant (Chen *et al.* 1987; Cheng 1988). This is in keeping with ideas of male reproductive strategy, where the cost of maintaining spermatogenic activity is small enough to be compensated for by the reduced chances of securing a successful mating outside the normal breeding period (Wilhoft 1963). This is especially the case in species where females are capable of storing sperm, which has been documented in *H. frenatus* (Murphy-Walker & Haley 1996; Yamamoto & Ota 2006). In support of this, a mating pair was observed during collection of specimens in the Brisbane winter (8 June 2010).

There are three possibilities to explain the adaptation of *H. frenatus* to Brisbane conditions. Firstly, selection could have acted on acyclic founders to create a cyclic population. Secondly, the founding population could be derived from cyclic populations, such as those in Taiwan. It certainly seems likely that Taiwan has supplied a significant proportion of the geckos that have invaded Brisbane, given the volume of shipping traffic between the two. Even in a mix of founders from cyclic and acyclic populations, those from cyclic populations would be expected to out-

compete those less well-adapted. The third possibility is that individual *Hemidactylus frenatus* are capable of adjusting their reproductive activity to the environment they find themselves in. This 'facultatively cyclic' hypothesis was favoured by Lin and Cheng (1984). Such adaptability may be a critical factor in the invasive success of this gecko. This idea could be tested by taking specimens from a population and subjecting them to conditions different from their usual experience (for example, Brisbane geckos in a constant temperature and humidity environment) and observing whether they adjust their reproductive behaviour accordingly.

In summary, the invasive success of the tropical, aseasonally breeding gecko *Hemidactylus frenatus* into different climates such as that of Brisbane can be partly attributed to its ability to readily become a seasonal breeder by reducing breeding activity in the cooler months. This effect is more marked in females than males, presumably because of sperm storage by females.

ACKNOWLEDGEMENTS

Thanks to Patrick Couper for assistance in collecting geckos and to the residents of McGregor St in Clayfield; Denise and Stephen Keim, Maree and Mark Leith and Ruth and Nick Kennedy, for tolerating our monthly night time intrusions of their homes. Glenn Shea and Simon Blomberg gave useful and much appreciated comments on the manuscript.

LITERATURE CITED

- Case, T.J., Bolger, D.T. & Petren, K. 1994. Invasions and competitive displacement among house geckoes in the tropical Pacific. *Ecology* 75: 464-77.
- Chen, R.H., Lin, J.Y., Yu, Y.L. & Cheng, H.Y. 1987. Annual changes in plasma and testicular androgen in relation to reproductive cycle in a Japalura lizard in Taiwan. *Zoological Science* 4(2): 323-9.
- Cheng, H.Y. 1988. Gonad condition and fat stores of the house gecko, *Hemidactylus frenatus*, in Taiwan during winter. *Journal of the Taiwan Museum* 41(1): 93-97.
- Cheng, H.Y. & Lin, J.I. 1977. Comparative reproductive biology of the lizards, *Japalura swinhonis formosensis*, *Takydromus septentrionalis* and *Hemidactylus frenatus* in Taiwan. *Bulletin of the Institute Of Zoology, Academica Sinica* 16(2): 107-120.
- Church, G. 1962. The reproductive cycles of the Javanese house geckos, *Cosymbotus platyurus*, *Hemidactylus frenatus*, and *Peropus mutilatus*. *Copeia* 1962(2): 262-9.
- Cogger, H.G. & Lindner, D.A. 1974. Frogs and reptiles. Pp. 67-107. In, Frith, H.J. & Calaby, J.H. (eds) *Fauna Survey of the Port Essington District, Coburg Peninsula*. (CSIRO).
- Cole, N. 2005. The new noisy neighbours. Impacts of alien house geckos on endemics in Mauritius. *Aliens* 22: 8-10.
- Cook, R.A. 1990. Range extension of the Darwin house gecko *Hemidactylus frenatus*. *Herpetofauna* 20(1): 23-27.
- Covacevich, J.A., Buffet, A.F., Couper, P.J. & Amey, A.P. 2001. Herpetological "foreigners" on Norfolk Island, an external territory of Australia. *Memoirs of the Queensland Museum* 46(2): 408.
- Duméril, A.M.C. & Bibron, G. (1836) *Erpétologie Générale, ou Histoire Naturelle Complète des Reptiles*. (Roret: Paris).
- Fisher, C. & Calaby, J. 2009. The top of the Top End: John Gilbert's manuscript notes for John Gould on vertebrates from Port Essington and Cobourg Peninsula (Northern Territory, Australia); with comments on specimens collected during the settlement period 1838 to 1849, and subsequently. *The Beagle, Records of the Museum and Art Galleries of the Northern Territory Supplement* 4: 1-239.
- Hallowell, E. 1861. Report upon the Reptilia of the North Pacific Exploring Expedition, under command of Capt. John Rogers, U.S.N. *Proceedings of the Academy of Natural Sciences of Philadelphia* 1860: 480-510.
- Holmes, B. 1998. Day of the sparrow. *New Scientist* 158(2140): 32-35.
- Keim, L.D. 2002. The spatial distribution of the introduced Asian House Gecko (*Hemidactylus frenatus*) across suburban/forest edges. Honours thesis, Zoology & Entomology. (The University of Queensland: Brisbane).
- Lin, J.Y. & Cheng, H.Y. 1984. Ovarian cycle in the house gecko, *Hemidactylus frenatus*, in Taiwan with reference to food stress in winter. *Bulletin of the Institute Of Zoology, Academica Sinica* 23(1): 21-28.
- Lövei, G. 1997. Global change through invasion. *Nature* 388(6643): 627.
- Low, T. 2001. *Feral Future*. (Penguin Books: Ringwood).
- Murphy-Walker, S. & Haley, S.R. 1996. Functional sperm storage duration in female *Hemidactylus frenatus* (Family Gekkonidae). *Herpetologica* 52(3): 365-73.

Reproductive cycle of the Asian House Gecko

- Newbery, B. & Jones, D.N. 2007. Presence of Asian House Gecko *Hemidactylus frenatus* across an urban gradient in Brisbane: influence of habitat and potential for impact on native gecko species. Pp. 59-65. In, Lunney, D., Eby, P., Hutchings, P. & Burgin, S. (eds) *Pest or Guest: the Zoology of Overabundance*. (Royal Zoological Society of New South Wales: Mosman).
- Ota, H. 1994. Female reproductive cycles in the northernmost populations of the two gekkonid lizards *Hemidactylus frenatus* and *Lepidodactylus lugubris*. *Ecological Research* 9(2): 121-30.
- Ramírez-Bautista, A., Hernández-Salinas, U. & Leyte-Manrique, A. 2006. *Hemidactylus frenatus* (Common House Gecko). Reproduction. *Herpetological Review* 37(1): 85-86.
- Rödger, D., Solè, M. & Böhme, W. 2008. Predicting the potential distributions of two alien invasive Housegeckos (Gekkonidae: *Hemidactylus frenatus*, *Hemidactylus mabouia*). *North-Western Journal of Zoology* 4(2): 236-246.
- Snyder, G.K. & Weathers, W.W. 1976. Physiological responses to temperature in the tropical lizard, *Hemidactylus frenatus* (Sauria: Gekkonidae). *Herpetologica* 32(3): 252-256.
- Wilhoft, D.C. 1963. Gonadal histology and seasonal changes in the tropical Australian lizard, *Leiolepis rhomboidalis*. *Journal of Morphology* 113(2): 185-204.
- Yamamoto, Y. & Ota, H. 2006. Long-term functional sperm storage by a female common house gecko, *Hemidactylus frenatus*, from the Ryukyu Archipelago, Japan. *Current Herpetology* 25(1): 39-40.

A revision of the carabid tribe Migadopini in Australia (Insecta: Coleoptera: Carabidae: Migadopini)

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ABSTRACT

The Australian members of the carabid tribe Migadopini are revised. A new genus and four species and one additional subspecies are newly described: *Dendromigadops* gen. nov. with the species *D. alticola* sp. nov. from mountains on Atherton Tableland in North Queensland and *D. gloriosus* sp. nov. from Mt. Glorious in South-east Queensland, *Stichonotus decoloratus* sp. nov. from Tasmania, *Calyptogonia lynetteae* sp. nov. from north-western Tasmania, and *Calyptogonia atra occidentalis* subsp. nov. from western Tasmania. The genera *Nebriosoma* Castelnau, 1867, *Stichonotus* Sloane, 1910, *Decogmus* Sloane, 1915, and *Calyptogonia* Sloane, 1920 are partly redescribed and the male genitalia and female gonocoxites of all species are figured. Keys to the genera of the Australian Migadopini and to the species of *Dendromigadops*, *Stichonotus*, and *Calyptogonia* are provided. According to the structure of their female gonocoxites *Dendromigadops* belongs in the subtribe Migadopina and is related to *Decogmus* and *Calyptogonia*, but in body shape it is quite distinct from all described Australian genera of the subtribe. □ *Coleoptera, Carabidae, Migadopini, Dendromigadops, new genus, new species, Stichonotus, new species, Calyptogonia, new species, Nebriosoma, Stichonotus, Decogmus, Calyptogonia, partial redecriptions, key to Migadopine genera, keys to the species of Dendromigadops, Stichonotus, and Calyptogonia, Australia.*

While searching through the unidentified material of Carabid beetles in the Australian National Insect Collection, Canberra (ANIC), for additional material for a projected key to the genera of Australian Carabidae, I detected two strangely shaped, large specimens of the tribe Migadopini that did not seem to fit into any of the described Australian genera of this tribe. On closer examination of the specimens at home, I remembered that I had seen a similar specimen years earlier in the Queensland Museum, Brisbane. I had postponed an examination on initial advice that Geoff Monteith (former Curator, Queensland Museum) had informed me of similar specimens located at ANIC, these are those specimens. On my request

Geoff kindly loaned the QM specimen which agree well with one of the ANIC specimens. Since the enigmatic species *Nebriosoma fallax* Castelnau, 1867, the only Australian migadopine genus that I had not yet seen, had not been studied by modern workers, I suspected that these specimens might be related to it. On my request, the holotype, and apparently single recorded specimen, was loaned to me by R. Poggi of the Genoa Museum. However, examination showed that *Nebriosoma fallax* is completely different in body shape and structure from the specimens mentioned above, so these represent an additional new genus. Examination of the specimens further revealed some differences in body shape and

surface structure between the specimens from North and South Queensland, respectively. Therefore two new species are described, even though all available specimens are females.

While seeking additional information about *Nebriosoma* I discovered that another putative 'holotype' exists in Museum of Victoria, Melbourne, which was not noted by B. P. Moore in his catalogue of the Australian Carabidae (Moore et al. 1987). Examination revealed it to be a male which gives me the opportunity now to figure male and female genitalia of all Australian Migadopini except those of *Dendromigadops* and one species of *Migadopidiella* Baehr, the latter genus belonging in the subtribe Amarotypina.

In the course of dissecting male and female genitalia of all known Australian migadopine species I also detected that the material previously identified as *S. leai* Sloane is composed of two different species and that *Calyptogonia atra* Sloane includes three different taxa, two of which are represented in the type series. These new species and subspecies are described in the present paper.

Different authors do not agree about the taxonomical status of the migadopine beetles. For the present paper I prefer to recognise Migadopini as a tribe, not as a subfamily. At present Migadopini includes 17 genera with about 40 species and a couple of subspecies. The tribe is famous for its circumantarctic distribution, occurring in the southern part of South America north to Uruguay, on Falkland Islands, Auckland Island, in Tasmania and south-eastern Australia, and in New Zealand (Sloane 1920, Jeannel 1938, Lorenz 1998, 2005, Laroche & Larivière 2001, 2007, Roig-Juñent (2004), Baehr 2009, Johns 2010). However, undescribed species (and perhaps even genera) may occur throughout the range of the tribe, and for New Zealand Laroche & Larivière (2001) and Johns (2010) explicitly stated the occurrence of several additional undescribed species.

Based mainly on structures of the female genitalia, Migadopini had been split into two subtribes: Migadopina which include almost

all described genera, and Amarotypina which so far includes only two genera: *Amarotypus* Bates, 1872 with the single presently described species *Amarotypus edwardsii* Bates, 1872 from New Zealand (Erwin 1985, Liebherr & Will 1998, Laroche & Larivière 2007), and *Migadopidiella* Baehr, 2009 from Tasmania with the two species *Migadopidiella convexipennis* Baehr, 2009 and *M. octoguttata* Baehr, 2009. In New Zealand other species of *Amarotypus* are also known and await description (Johns 2010).

Migadopini *s. l.* combines several characters: presence of a single supraorbital seta, absence of lateral pronotal setae, presence of an additional 10th stria (probably resulting from the parascutellary stria being complete), closed procoxal cavities, disjunct mesocoxal cavities, simple antenna cleaner on the protibia, and large parameres of which at least the right one is densely setose. A couple of these character states are very plesiomorphic and hence Migadopini, in all phylogenetic surveys, are believed to have their position near the base of the carabid phylogenetic tree. Commonly they are ranked near Elaphrini, but according to Liebherr & Will (1998) the female genitalia of only *Amarotypus* are similar to those of Elaphrini, whereas those of all other genera (= the subtribe Migadopina) are quite different.

The absence of any discal elytral setae, formerly thought to be another character common to all migadopine species, must be removed from the general diagnosis, because *Nebriosoma* and *Decognus* have a distinct puncture in the basal third of the 4th interval but apparently no seta.

In Amarotypina not only the female genitalia differ from those of the Migadopina *s. str.*, but the male aedeagus is also different: it has the orifice (i.e. the apical ostium) situated on the left side of the apex, while in Migadopini it is situated on the right side; and the left paramere is quite differently shaped and aetose, while in most other migadopine genera it is setose at the apex. Migadopina and Amarotypina hence may represent quite different groups which are similar only in a number of plesiomorphic

characters states that cannot serve as evidence of close relationship of both subtribes. Hence they have been ranked by some authors, and probably should be ranked, as separate and not too closely related tribes.

From Australia five migadopine genera were recorded so far, namely in Migadopina s. str.: *Nebriosoma* Castelnau, 1867, with the single species *N. fallax*, Castelnau, 1867 from south-eastern NSW, *Stichouotus* Sloane, 1910, with three species living in Tasmania and southern Victoria, *Decognuus* Sloane, 1915 with the single species *D. chalybaeus* Sloane, 1915 from central-eastern NSW, and *Calyptogonia* Sloane, 1920 with the single species *C. atra* Sloane, 1920, from Tasmania; and in Amarotypina: *Migadopidiella* Baehr, 2009, with two species from central Tasmania. Sloane (1915, 1920) provided keys for the then known genera of Australian Migadopini.

No migadopine species hitherto was recorded from north of Comboyne Plateau in central near-coastal NSW. Hence the discovery of a species as far north as the mountain ranges at the margins of the Atherton Tableland in north-eastern Queensland is surprising.

MATERIAL AND METHODS

About 300 specimens were examined in the course of this study. However, the overwhelming number belongs to two species of the genus *Stichouotus*, whereas of most other species only single or few specimens were available, and actually are recorded.

The holotypes of the new species are shared with the Australian National Insect Collection, Canberra (ANIC), Queensland Museum, Brisbane (QM), and Forestry Tasmania Insect Collection, Hobart (FTIC). Other types and material are shared with Museo Civico di Storia Naturale 'Giacomo Doria', Genoa (MCSN), Museum of Victoria, Melbourne (NMV), The Natural History Museum, London (NHM), South Australian Museum, Adelaide (SAMA), ANIC, FTIC, and the working collection of the author in Zoologische Staatssammlung, München (CBM).

Measurements were taken using a stereo microscope with an ocular micrometer. Body length was measured from apex of labrum to apex of elytra, length of pronotum along midline, length of elytra from the most advanced part of the humerus to the very apex.

For dissection of the genitalia of both sexes specimens were softened for a night in a jar under moist atmosphere, then the genitalia were removed and subsequently cleaned for a short while in hot KOH. The habitus photographs were obtained with a digital camera using AutoMontage and subsequently were worked with Corel Photo Paint X4.

ABBREVIATIONS

NSW	New South Wales
Vic	Victoria
Qld	Queensland
Tas	Tasmania
C	central
CE	central eastern
E	eastern
NE	north-eastern
NW	north-western
S	southern
SE	south-eastern
SW	south-western
>	larger or longer than
<	smaller or shorter than

KEY TO THE AUSTRALIAN GENERA OF THE TRIBE MIGADOPINI

1. Apical angles of pronotum acute, much protruded, head deeply retracted in the prothorax (Figs 18, 22-25)..... 2
 - Apical angles of pronotum obtuse, little or not protruded, head not imbedded in the prothorax (Figs 19-21)..... 3
2. Large, relatively elongate, body length >11 mm; eye very large; pronotum with wide, thick lateral margin (Figs

- 26, 27); elytra elongate, parallel-sided, striae distinctly crenulate (Fig. 18); aedeagus unknown; female gonocoxite 1 odd shaped and very densely setose, gonocoxite 2 asymmetrically inserted (Figs 1, 2). E QLD. *Dendromigadops* gen. nov.
- Small, relatively wide, body length <8.5 mm; eye smaller; pronotum with narrow lateral margin; elytra obovate, striae not or little crenulate (Figs 22-25); aedeagus very narrow and elongate (Figs 14-17), female gonocoxites straight, more or less densely setose, gonocoxite 1 inserted at apex (Figs 6-9). Tas., S. Vic. . . *Stichonotus* Sloane, 1910
 - 3. Small, body length < 5 mm; elytra markedly oval, striae punctate (see figs 1, 2 in Baehr 2009); aedeagus compact, orifice on the left side, internal sac with several complexly coiled, denticulate sclerites, left paramere asetose at apex (see fig. 3 in Baehr 2009). Tas. *Migadopidiella* Baehr, 2009
 - Large, body length > 8 mm; elytra not or far less oval-shaped, striae impunctate (Figs 19-21); aedeagus variously shaped but orifice on the right side, left paramere setose at apex (Figs 10-13) 4
 - 4. Dorsal surface greenish-violaceous, slightly metallic; mandibles elongate, straight; elytra elongate, parallel-sided (Fig. 20); aedeagus elongate, narrower, lower surface less concave, apex not much enlarged, nor with a markedly denticulate sclerite, both parameres rather similarly shaped (Fig. 11). CE NSW *Decomus* Sloane, 1915
 - Dorsal surface brown or black, not metallic; mandibles shorter, rounded; elytra either shorter (Fig. 19) or slightly oviform (Fig. 21); aedeagus stouter, wider, lower surface very concave, either apex much enlarged, or with a markedly denticulate sclerite; parameres quite dissimilar (Figs 10, 12, 13). 5
 - 5. Large, body length >11 mm; eye depressed; pronotum not cordiform, lateral margin thick; elytra oblong, slightly oval, striae rather superficial (Fig. 21); aedeagus regularly curved on lower surface, with wide, leaf-like apex (Figs 12, 13); female gonocoxite 1 very densely setose with elongate, nematiform setae, gonocoxite 2 small, narrow, parallel sided (Fig. 5). Tas. . . *Calyptogonia* Sloane, 1920
 - Small, body length c. 8 mm; eye laterally protruded; pronotum very cordiform, lateral margin narrow, but marginal sulcus wide; elytra short and wide, not oviform, striae deep (Fig. 19); aedeagus irregularly curved on lower surface, apex with a markedly denticulate sclerite (Fig. 10); female gonocoxite 1 sparsely setose with short and stout setae, gonocoxite 2 large, obliquely triangular (Fig. 3). SE NSW *Nebriosoma* Castelnau, 1867

Dendromigadops Gen. Nov.

Type species. *Dendromigadops alticola*, sp. nov., by present designation.

Etymology. The name is a combination of the Greek word '*dendron*' which means 'tree' and the noun *Migadops*, and refers to the putative arboricolous habits of the species of this genus. Masculine.

Diagnosis. Genus of the tribe (or subfamily) Migadopini (-inae) and the subtribe Migadopina, characterised by the following features which are not repeated in full length in the descriptions of the species: head deeply retracted into in the prothorax; eye very large, immediately touching the apex of the pronotum; clypeus bisetose; labrum short and transverse, apex slightly excised, 6-setose; mandibles short and wide, depressed, regularly curved, with wide and deep scrobe; both palpi impilose, the apical palpomere of the maxillary palpus narrow, slightly widened apicad and slightly transverse; the apical palpomere of the labial palpus in the female securiform; mentum with wide, apically transverse tooth, bisetose; glossa elongate, narrow, apicad acute, with one or two elongate apical setae; paraglossae hyaline, much shorter than glossa; lacinia large, with sparse, elongate spines and hairs; antenna fairly elongate, just surpassing base of pronotum; median antennomeres 2-2.5 × as long as wide; four basal antennomeres impilose, antenna densely pilose from 5th antennomere; a single supraorbital seta present, located at middle of eye; pronotum wide, depressed; apex very deeply excised, apical angles far protruded and acute; base bisinuate; lateral margin wide and thick,

asetose; elytra elongate and rather depressed; humerus angulate, apex oblique-convex, not sinuate; completely striate, striae more or less crenulate; disk asetose; microreticulation extremely fine and dense, consisting of very fine transverse lines; metathoracic wings fully developed; terminal abdominal sternum in female bisetose; 4th tarsomeres not widened nor excised; lower surface of 5th tarsomeres asetose; 1st – 3rd tarsomeres of female protarsus and mesotarsus biserially squamose; tarsal claws large; aedeagus unknown; female gonocoxites remarkably odd-shaped: gonocoxite 1 curved, with very wide, convex apex, a hyaline area at median margin at the insertion of gonocoxite 2, at apex and in apical part of the ventral surface densely setose with short and stout, at apex obtuse setae, the remainder of the ventral surface, and the median part of the dorsal surface densely setose with elongate nematiform setae; gonocoxite 2 very asymmetrically inserted at subapical lateral margin of gonocoxite 1, small, narrow, slightly curved, at apex with 1 nematiform seta which originates from a circular groove.

Distribution. Mountains near the coast in both northeastern and southeastern Queensland.

Relationships. Because the male genitalia are unknown, the relationships of the genus remain somewhat obscure. However, the markedly deeply excised apex of the prothorax and the deeply retracted head are similar to the structure of head and prothorax of species in the genus *Stichonotus*. Shape and structure of the female gonocoxites, on the other hand, in particular the narrow gonocoxite 2, the presence of short apically obtuse hairs on the apical part of gonocoxite 1, and in the very dense and elongate setosity of gonocoxite 2, is most similar to those of species of *Decogmus* and *Calypogonia*. These, however, in their external morphology have little in common with *Dendromigadops*. Nevertheless, because the female genitalia in Carabidae commonly better depict relationships than many other character sets, I believe that these two genera are the closest relatives of *Dendromigadops*.

Dendromigadops alticola sp. nov.
(Figs 1, 18, 26)

Material. Holotype: ♀, Mt Bartle-Frere, N. Qld. NW/Centre Peak ridge 7-8.xi.1981, 1400–1500 m Earthwatch/Qld.Mus. / Coll. G. Monteith on tree trunk at night (QMT183295). – Paratype: ♀, 17.27S 145.29E Qld GS3 Hugh Nelson Ra 2 Oct-1 Nov 1995 L. Umback, 1150 m Malaise trap (ANIC).

Etymology. The species name is a masculine noun and reflects the occurrence high up in mountains.

Diagnosis. Distinguished from *Dendromigadops gloriosus* sp. nov. from southeastern Queensland by larger body size, wider, towards apex more incurved pronotum, wider lateral margin of the pronotum, posterior transverse sulcus and basal groove united by a transverse sulcus, more acute humeral angle, more distinctly crenulate elytral striae, and slightly differently shaped female gonocoxites.

Description. *Measurements.* Length: 12.2–12.85 mm; width: 5.3–5.55 mm. Ratios. Width/length of pronotum: 1.92–1.96; width base/apex of pronotum: 1.54–1.57; width widest diameter/base of pronotum: 1.07; width of pronotum/width of head: 1.76–1.80; length/width of elytra: 1.57–1.58; width elytra/pronotum: 1.18–1.20.

Colour. (Fig 18) Black, lateral margin of pronotum piceous; mouth parts and antenna reddish-piceous, legs and lower surface dark piceous to black.

Head. (Figs 18, 26) Medium sized; frons in middle with a shallow, horseshoe-shaped impression; in middle of frons with some fine, transverse wrinkles, orbits laterally rather rugose. Surface of head with very dense, distinct but extremely fine, isodiametric microreticulation, with scattered, fine punctures which are almost invisible within the dense microreticulation; surface moderately dull.

Pronotum. (Fig. 18, 26) Very wide, widest at about basal third. Apex very deeply excised, anterior angles acute; lateral margin convex throughout, also markedly incurved to middle posteriad, basal angle very small, dentiform. Apex distinctly margined, base not margined. Lateral margin very wide, with a narrow sulcus in anterior half which suddenly widens posteriad and meets

the oblique, linear lateral basal groove at a less than 90° angle. Disk depressed, median line distinct though shallow, neither reaching apex nor base. Anterior transverse sulcus shallow, posterior transverse sulcus deep but shortly interrupted in middle. Median basal groove linear and meeting the posterior transverse sulcus which is connected by a shallow but distinct sulcus with the marginal groove and the lateral basal groove. Surface with extremely fine and very superficial microreticulation which is composed of very irregularly transverse meshes, and with extremely fine, rather sparse punctures only visible under very high magnification. Surface moderately glossy.

Elytra. (Fig. 18) Rather elongate, parallel-sided, dorsal surface convex in middle, wide at humerus which is angulate. Lateral margin straight in basal three fifths, then evenly convex towards suture. Base not margined, marginal channel narrow throughout. Striae complete, rather deep, all distinctly crenulate almost to apex, intervals gently convex. Parascutellary pore located at meeting point of 2nd and 3rd striae, seta short. Disk asetose. 14–15 marginal punctures present, series slightly interrupted in middle, an additional puncture and seta at apex of 2nd stria, setae rather short. Microreticulation on intervals extremely fine and very superficial, composed of very dense, very transverse meshes and transverse lines, no distinct punctures visible. Surface rather glossy and slightly iridescent.

Lower surface. Prosternal process at apex carinate and produced. Metepisternum moderately elongate, c. 1.5 × as long as wide at apex. Lateral parts of prosternum and the proepimeron finely punctate-rugose, the lateral parts of mesosternum and metasternum, the metepimeron, and the anterior, widened part of the elytral epipleura coarsely punctate. Abdomen laterally irregularly and very coarsely punctate. Microreticulation very fine though distinct, composed of irregular, slightly transverse meshes.

Male genitalia. Unknown.

Female gonocoxites. (Fig. 1) As in genus diagnosis. Gonocoxite 1 laterally below insertion of gonocoxite 2 angulate, ventral surface also in

middle rather densely setose, setae elongate; gonocoxite 2 small, moderately narrow, slightly curved, widened towards apex.

Variation. Very little variation noted. In the paratype the crenulation of the lateral elytral striae is slightly coarser.

Distribution. Mountains at the margins of Atherton Tableland in northeastern Queensland.

Collecting circumstances. According to information from Geoff Monteith the holotype was collected at night running on the bark of a living tree trunk, about 4m from the ground, at high altitude in montane rain forest. The paratype was also sampled at high altitude, but in a ground-based Malaise trap.

Dendromigadops gloriosus sp. nov.
(Figs 2, 27)

Material. HOLOTYPE ♀, SE. Qld; 27.3219°S, 152.7502°E, Mt Glorious, Daguilar NP, 700 m, 1988–89, canopy intercept trap in *Argyrodendron actinophyllum* in subtropical rainforest, Y. Basset/Co/Car.19/ Migadopinae genus ?? det. T.A. WEIR 2010 (ANIC).

Etymology. The species name reflects the occurrence on Mt Glorious near Brisbane.

Diagnosis. Distinguished from *Dendromigadops alticola* sp. nov. from northeastern Queensland by smaller body size, narrower, towards apex less incurved pronotum, narrower lateral margin of the pronotum, the basal transverse sulcus and the basal groove separated by a low boss, less acute humeral angle, less distinctly crenulate elytral striae, and slightly differently shaped female gonocoxites.

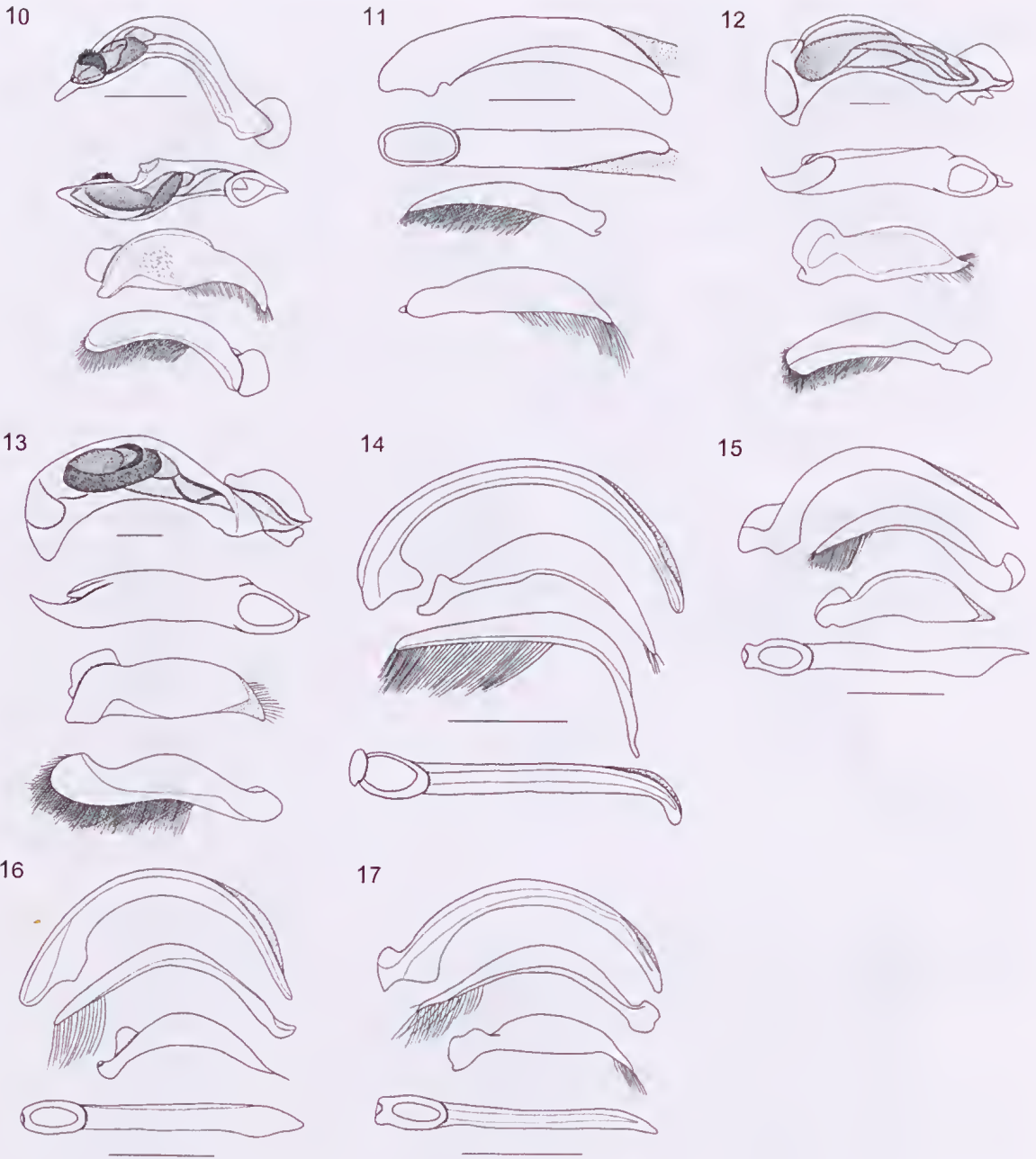
Description. Measurements. Length: 11.0 mm; width: 4.75 mm. Ratios. Width/length of pronotum: 1.79; width base/apex of pronotum: 1.48; width widest diameter/base of pronotum: 1.06; width of pronotum/width of head: 1.60; length/width of elytra: 1.56; width elytra/pronotum: 1.25.

Colour. (Fig. 27) Black, lateral margin of pronotum piceous; mouth parts and antenna reddish-piceous, legs and lower surface dark piceous to black.

Revision of Migadopini in Australia



FIGS 1-9. Female gonocoxites (scale bars: 0.25 mm). 1. *Dendromigadops alticola* sp. nov. 2. *D. gloriosus* sp. nov. 3. *Nebriosoma fallax* Castelnau. 4. *Decogmus chalybaeus* Sloane. 5. *Calyptogonia atra atra* Sloane. 6. *Stichonotus leai* Sloane. 7. *S. piceus* Sloane. 8. *S. limbatus* Sloane. 9. *S. decoloratus* sp. nov.



FIGS 10-17. Male aedeagus and parameres (scale bars: 0.5 mm). 10. *Nebriosoma fallax* Castelnau. 11. *Decogmus chalybaeus* Sloane. 12. *Calyptogonia atra atra* Sloane. 13. *Calyptogonia lynetteae* sp. nov. 14. *Stichonotus leai* Sloane. 15. *S. piceus* Sloane. 16. *S. limbatus* Sloane. 17. *S. decoloratus* sp. nov.

Head. (Fig. 27) Medium sized; frons in middle with a very shallow, about horse-shoe impression; in middle of frons with some extremely fine, transverse wrinkles, orbits laterally rather rugose. Surface of head with very dense, distinct but extremely fine, isodiametric microreticulation, with scattered, fine punctures which are almost invisible within the dense microreticulation; surface moderately dull.

Pronotum. (Fig. 27) Very wide, widest about at basal third. Apex very deeply excised, anterior angles acute; lateral margin in convex throughout, also markedly incurved to middle posteriad, basal angle very small, dentiform. Apex distinctly margined, base not margined. Lateral margin rather wide, with a narrow sulcus in anterior half which suddenly widens posteriad and meets the oblique, linear lateral basal groove in a less than 90° angle. Disk depressed, median line distinct though shallow, neither reaching apex nor base. Anterior transverse sulcus shallow, posterior transverse sulcus deep but shortly interrupted in middle. Median basal groove linear and meeting the posterior transverse sulcus. The space between median and lateral basal grooves slightly convex, both grooves not connected. Surface with extremely fine and very superficial microreticulation which is composed of very irregularly transverse meshes, and with extremely fine, rather sparse punctures which are visible only under very high magnification. Surface moderately glossy.

Elytra. Rather elongate, parallel-sided, dorsal surface convex in middle, wide at humerus which is obtusely angulate. Lateral margin straight in basal three fifths, then evenly convex towards suture. Base not margined, marginal channel narrow throughout. Striae complete, rather deep, all striae distinctly crenulate in basal half, smooth in apical half, intervals gently convex. parascutellary pore located at meeting point of 2nd and 3rd striae, seta short. Disk asetose. 15 marginal punctures present, series slightly interrupted in middle, an additional puncture and seta at apex of 2nd stria, setae rather short. Microreticulation on intervals extremely fine and very superficial, composed of very dense, moderately transverse meshes, no distinct

punctures visible. Surface rather glossy and slightly iridescent.

Lower surface. Prosternal process at apex carinate and produced. Metepisternum moderately elongate, c. 1.5 × as long as wide at apex. Lateral parts of prosternum and the proepimeron moderately coarsely punctate-rugose, the lateral parts of mesosternum and metasternum, the metepimeron, and the anterior, widened part of the elytral epipleura very coarsely punctate. Abdomen laterally irregularly and very coarsely punctate. Microreticulation very fine though distinct, composed of irregular, slightly transverse meshes.

Male genitalia. Unknown.

Female gonocoxites. (Fig. 2) As in genus diagnosis. Gonocoxite 1 more curved than in *D. alticola*, laterally below insertion of gonocoxite 2 not angulate, ventral surface in middle more sparsely setose and setae shorter; gonocoxite 2 longer and narrower than in *D. alticola*, less widened towards apex.

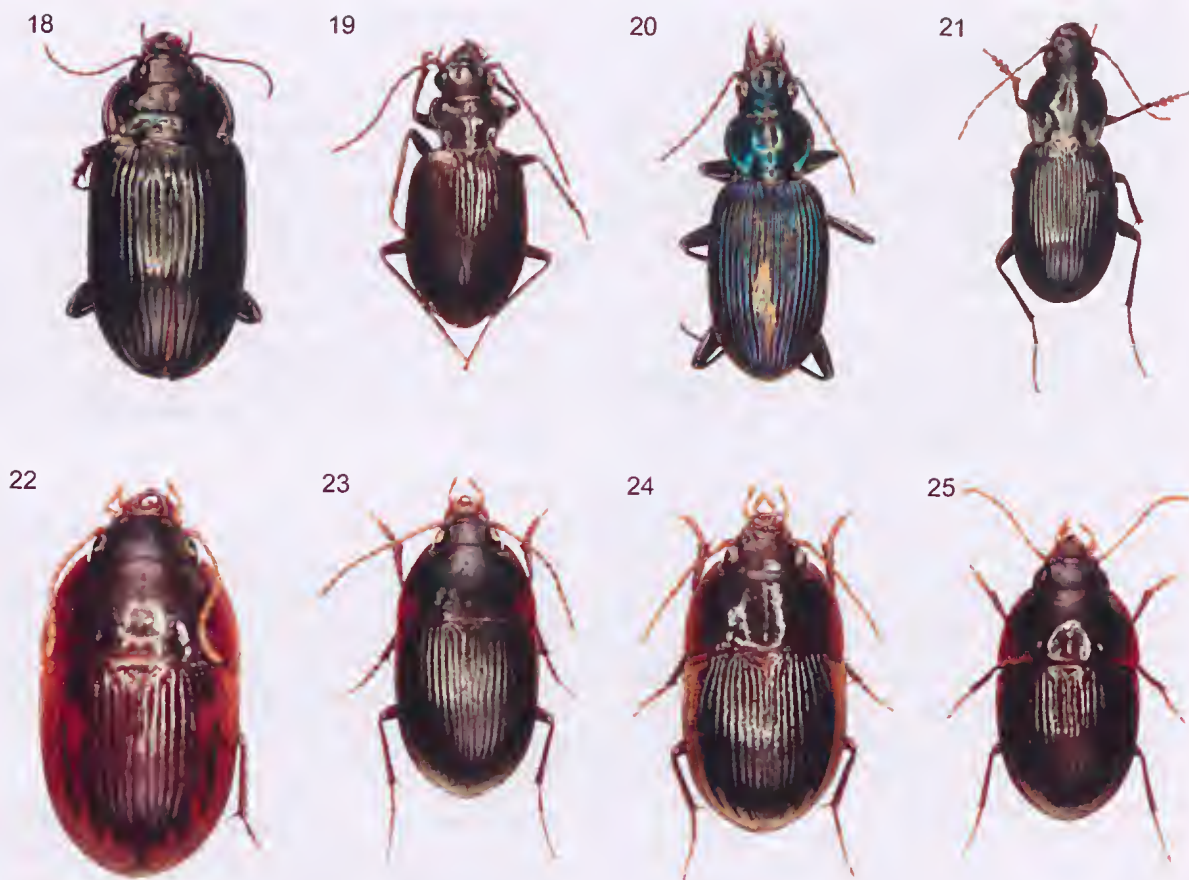
Variation. Unknown.

Distribution. Mountains slightly west of Brisbane, southeastern Queensland. Known only from type locality.

Collecting circumstances. The holotype was collected in a special canopy flight intercept trap (Basset 1988) designed and used by Yves Basset in a study of the canopy fauna of the tall rainforest tree *Argyrodendron actinophyllum* (F.M. Bailey) Edlin (Sterculiaceae) in rainforest at Mt Glorious which is 30 km NW of Brisbane (Basset 1991).

Key to species of *Dendromigadops* gen. nov.

1. Body size large, >12 mm; pronotum relatively wide, ratio width/length >1.90, towards apex more incurved, ratio width of base/width of apex >1.54, wider in relation to the head, ratio width of pronotum/width of head >1.75; lateral margin of pronotum wider; basal transverse sulcus and basal groove united by a transverse sulcus (Fig. 26); humeral angle of the elytra more acute; lateral elytral striae more distinctly crenulate; gonocoxite 1 latero-



FIGS 18-25. Habitus (body lengths in brackets). 18. *Dendromigadops alticola* sp. nov. (11.8 mm). 19. *Nebriosoma fallax* Castelnau (8.0 mm). 20. *Decognmus chalybaeus* Sloane (12.4 mm). 21. *Calyptogonia atra atra* Sloane (11.8 mm). 22. *Stichonotus leai* Sloane (5.6 mm). 23. *S. piceus* Sloane (7.1 mm). 24. *S. limbatus* Sloane (5.9 mm). 25. *S. decoloratus* sp. nov. (5.6 mm).

apically excised, gonocoxite 2 shorter and less curved (Fig. 1). NE QLD. . . *D. alticola* sp. nov.

- Body size smaller, 11 mm; pronotum narrow, ratio width/length 1.79, towards apex less incurved, ratio width of base/width of apex 1.48, narrower in relation to the head, ratio width of pronotum/width of head 1.60; lateral margin of pronotum narrower; basal transverse sulcus and basal groove separated by a low boss (Fig. 27); humeral angle of the elytra less acute; lateral elytral striae less distinctly crenulate; gonocoxite 1 not latero-apically excised, gonocoxite 2 longer and more curved (Fig. 2). SE QLD *D. gloriosus* sp. nov.

Nebriosoma Castelnau, 1867

Nebriosoma Castelnau, 1867: 93. – Castelnau 1868: 179; Sloane 1905: 703; 1915: 442; Csiki 1927: 443; Moore *et al.* 1987: 65, Lorenz 1998: 118.

Type species. *Nebriosoma fallax* Castelnau, 1867, by monotypy.

Diagnosis. Medium sized, rather short and wide, non metallic, piceous species; head wide, with large, laterally produced eye; prothorax clearly cordiform with barely excised apex and rectangular basal angles, pronotum with wide marginal sulcus; elytra rather short and wide but not oviform, striae shallow, 4th interval at basal fourth with a puncture; metathoracic wings reduced; aedeagus odd-shaped, very

26

27



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29

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FIGS 26-30. Head and Pronotum. 26. *Dendromigadops alticola* sp. nov. 27. *D. gloriosus* sp. nov. 28. *Calyptogonia atra atra* Sloane. 29. *Calyptogonia atra occidentalis* subsp. nov. 30. *Calyptogonia lynetteae* sp. nov.

curved, with a sclerotized fold at anterior part of the internal sac that bears two rows of short, stout, transverse setae at tip; both parameres markedly curved and coiled, both with dense fringe of setae at least in apical half of their lower surfaces; gonocoxites straight, rather stout, gonocoxite 1 with about 12 short, stout setae in apico-median half of lower surface; gonocoxite 2 large, obtusely triangular, with two very short nematiform setae at apex.

Distribution. A single species, known only from Kiama, southeastern NSW.

Nebriosoma fallax Castelnau, 1867
(Figs 3, 10, 19)

Nebriosoma fallax Castelnau, 1867: 93. – Castelnau 1868: 179; Sloane 1905: 703; 1915: 442; Csiki 1927: 443; Moore et al. 1987: 65, Lorenz 1998: 118 .

Note. Curiously, the two recorded specimens are both labeled ‘Holotype’, although both labels were added long after the description. However, both bear determination labels in Castelnau’s handwriting. One specimen is a male and since it is better preserved, it is herein designated the lectotype. The female specimen becomes the paralectotype.

Material. LECTOTYPE (by present designation): ♂, Kiama/Type (red)/*Nebriosoma fallax* Cast. (Castelnau’s hand) / HOLOTYPE T-18464 *Nebriosoma fallax* Castelnau (red) (NMV). – PARALECTOTYPE: ♀, *Nebriosoma fallax* Cast Kiama (Castelnau’s hand) / NSW Kiama leg. Howitt Coll. CASTELNAU/HOLOTYPUS *Nebriosoma fallax* Castelnau, 1867 (red) (MCSN).

No additional specimens recorded.

Diagnosis. As for genus.

Partial redescription. *Measurements.* Length: 7.3-8.0 mm; width: 3.35-3.5 mm. Ratios. Width/length of pronotum: 1.46-1.48; width base/apex

of pronotum: 0.93-0.96; width widest diameter/ base of pronotum: 1.39-1.43; width of pronotum/ width of head: 1.25-1.26; length/width of elytra: 1.45-1.48; width elytra/pronotum: 1.55-1.57.

Male genitalia. (Fig. 10) Rather thickly sclerotized. Genital ring short and wide, oval. Aedeagus remarkably odd-shaped, moderately wide, rather stout, rather sinuate; lower surface remarkably concave; in middle on right side suddenly narrowed, apex short, convexly tapering, with obtusely convex tip. Orifice rather elongate, situated on the right side. Internal sac on the right side in the anterior part of the orifice with a large, sclerotized fold which at apex bears two rows of short, stout, at tip transverse setae. Both parameres large, markedly sinuate, coiled, and curved down at apex; left paramere wider than right one, angulate in middle of upper margin, with convexly triangular, bent down apex; basal part in middle less sclerotized, inner surface with a field of very short setae; apical half of lower surface and outer surface of apex with dense, uniseriate fringe of elongate setae; right paramere moderately narrow, with wide, obtusely rounded apex, lower surface in apical two thirds with two very dense fringes of very elongate hairs.

Female gonocoxites. (Fig. 3) Gonocoxite 1 elongate, straight, fairly wide, with a large hyaline area at upper lateral margin, with about 12 short, stout setae in apical median half of lower surface; gonocoxite 2 wide, short, straight, triangular, with a fold on the medio-dorsal surface, with obtuse apex which bears two very short nematiform seta originating close to apex.

Variation. Very little variation noted.

Distribution. Known only from the type locality Kiama, extreme southeastern NSW.

Collecting circumstances. Not recorded.

Decogmus Sloane, 1915

Decogmus Sloane 1915: 441 – Csiki 1927: 443; Moore et al. 1987: 65, Lorenz 1998: 118.

Type species. *Decogmus chalybaeus* Sloane, 1915, by monotypy.

Diagnosis. Moderately large, rather elongate, greenish species; head wide, with rather small but laterally produced eye and elongate, straight mandibles; prothorax slightly cordiform with barely excised apex and rectangular basal angles, pronotum with moderately wide marginal sulcus and very deep basal grooves; elytra rather elongate, incurved towards humerus, striae deep, smooth, 4th interval at basal fourth with a puncture; metathoracic wings fully developed; aedeagus rather large, straight, gently curved with a denticulate fold in the internal sac; both parameres densely setose at least in apical half; gonocoxite 1 with wide, convex apex; in apical part with many short and stout setae and the whole ventral surface and the median half of the dorsal surface with very dense, very elongate nematiform setae; gonocoxite 2 short, straight, inserted in middle of apex of gonocoxite 1, with one short nematiform seta originating from a circular pit at the very apex.

Distribution. A single species which is known from central eastern NSW.

Decogmus chalybaeus Sloane, 1915 (Figs 4, 11, 20)

Decogmus chalybaeus Sloane 1915: 441 – Csiki 1927: 443; Moore et al. 1987: 65, Lorenz 1998: 118.

Material. Holotype in ANIC, seen 2011.

New records. ♂, ♀, Carrai Plateau, via Kemsey, NSW. 14-15. iv. 1968 G. Monteith / *Decogmus chalybaeus* Sl. det. B. P. Moore '69 and '74 (ANIC, QM).

Diagnosis. As for genus.

Partial redescription. Measurements. Length: 12.4-13.0 mm; width: 4.6-4.7 mm. Ratios. Width/length of pronotum: 1.32-1.35; width base/apex of pronotum: 1.20-1.22; width widest diameter/ base of pronotum: 1.27-1.28; width of pronotum/ width of head: 1.40-1.42; length/width of elytra: 1.68-1.73; width elytra/pronotum: 1.34-1.37.

Male genitalia. (Fig. 11) Rather thickly sclerotized. Genital ring short and wide, oval. Aedeagus moderately wide, rather stout, very slightly sinuate; lower surface gently concave throughout; apex wide, convexly tapering, with obtusely convex tip, slightly curved to left. Orifice rather elongate, situated on the right side. Internal sac in

the single available specimen completely everted; apparently simply structured, with one elongate, slightly sclerotized fold which is shortly but densely setose at apex. Both parameres large; left paramere much wider than right one, with triangular tip, obtuse, very slightly bent down apex, lower surface in apical half with dense, uniseriate fringe of elongate setae which at extreme apex are extremely elongate; right paramere rather narrow, very slightly curved, with obtusely tapering apex, lower surface in apical two thirds with two very dense fringes of very elongate hairs.

Female gonocoxites. (Fig. 4) Gonocoxites remarkably odd-shaped: gonocoxite 1 elongate, curved, with very wide, convex apex, with a large hyaline area on the latero-apical margin; at the margin of the hyaline area with several stout but elongate setae, and the whole apex with many short and stout setae; and the whole ventral surface and the median half of the dorsal surface with very dense, very elongate nematiform setae which are even longer at the median margin of the base; gonocoxite 2 stout, short, straight, almost parallel-sided, inserted in middle of apex of gonocoxite 1, with transverse apex which bears one rather short nematiform seta originating from a circular pit at the very apex.

Variation. Very little variation noted.

Distribution. Known from the type locality, Comboyne Plateau, and the Carrai Plateau (30.888°S, 152.267°E) which is 80 km N of the type locality, central eastern NSW.

Collecting circumstances. According to Sloane (1915) the types were found 'under the bark of a decaying tree fallen in the thick brush by the side of the road on the Bulli Mountain (north-western slope) near the village of Comboyne, in July'. According to the collector, the two specimens from Carrai Plateau were collected together under a log on the ground in temperate rainforest.

Calyptogonia Sloane, 1920

Calyptogonia Sloane 1920: 121 – Csiki 1927: 443; Moore *et al.* 1987: 65, Lorenz 1998: 118.

Type species. *Calyptogonia atra* Sloane, 1920, by monotypy.

Diagnosis. Moderately large, rather elongate, black species; head fairly wide, with eyes rather small and little produced laterally, and with short, curved mandibles; antenna pilose from apical fifth of 4th antennomere; surface of head with fine, isodiametric microreticulation; prothorax not cordiform with barely excised apex, basally incurved lateral margins, and obtuse basal angles; pronotum with narrow, posteriad widened marginal sulcus and shallow basal grooves; surface of pronotum with fine, isodiametric or very slightly transverse microreticulation; elytra moderately elongate, oval shaped, 3rd interval impilose; striae shallow, smooth; microreticulation varied; metathoracic wings reduced, metepisternum quadrate; aedeagus large, slightly sinuate, deeply curved with very large, axe-shaped apex; internal sac with a large, sclerotized fold in the posterior part of the orifice; parameres very dissimilar, the right one densely setose in apical two thirds, the left one acute at tip and more sparsely setose; gonocoxites straight, elongate, gonocoxite 1 very densely setose; gonocoxite 2 small, parallel sided, situated at apex of gonocoxite 1, with four short nematiform setae at apex.

Distribution. Two species and one additional subspecies which occur in western and central Tasmania.

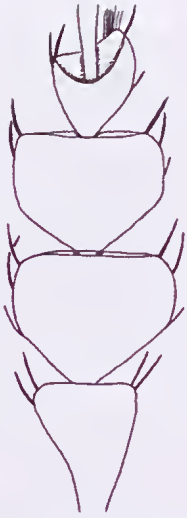
Calyptogonia atra Sloane, 1920

Calyptogonia atra Sloane 1920: 121 – Csiki 1927: 443; Moore *et al.* 1987: 65, Lorenz 1998: 118, 2005.

Note. This species is known from two areas in Tasmania: Cradle Mt National Park and environments in the Central Highland and Mt Weld in south-western Tasmania. Both populations differ slightly in width of prothorax and length of elytra and therefore also in the ratios of pronotum/head and pronotum/elytra. The male and female genitalia, however, are quite similarly shaped. Because of these morphological differences and the separation of both populations by a wide corridor of rather dry lowland running between their ranges these are provisionally described as subspecies.

Diagnosis. Distinguished from *Calyptogonia lyuetteae* sp. nov. by narrower pronotum with narrower base, laterad less projected eye with

31



32



FIGS 31-32. Male protarsus. 31. *Calyptogonia atra atra* Sloane. 32. *C. lynetteae* sp. nov.

longer orbit, isodiametric microreticulation of the elytra, narrower and longer 2nd-4th tarsomeres of the male protarsus, and sinuate upper margin of the aedeagus.

Calyptogonia atra atra Sloane, 1920
(Figs 5, 12, 21, 28, 31)

Material. LECTOTYPE: ♂, Cradle Mt T.H.J.C. 1.18 T/Type./*Calyptogonia atra* Sl. Id. by T.G. Sloane/Lectoholo-*C. ater* Sl. PJD (red)/J. 10829 *Calyptogonia atra* Sl. Tasmania, TYPE (SAMA). - PARALECTOTYPES: 1 ♀, Cradle Mt, T.H.J.C. 1.18 / Co-Type. / *Calyptogonia atra* Sl. Id. by T.G. Sloane (SAMA); ♂, Cradle Mt Tasmania Carter & Lea / Co-type / 19686 *Calyptogonia atra* Sl. Tasmania Cotype (SAMA); ♂, Cradle Mt Tasmania Carter & Lea / Co-type / *Calyptogonia atra* Sl. Id. by T.G. Sloane (SAMA); ♂, Cradle Mt Tasmania Carter & Lea / Co-type / Cotype (green) / Tribe Migadopini *Calyptogonia* n. g. (1918) *ater* Sl. (1918) Id. by T. G. Sloane / 2823 Paratype (blue) (NMV 2011-14L); ♂, Cradle Mt, Tasmania, Carter & Lea / Co-type / Cotype (green) / H.J. Carter Coll. P. 20.4.22 / 2824 Paratype (blue) (NMV 2011-14L); ♂, Cradle Mt, T.H.J.C. 1.18 / Co-type / Cotype (green) / H. J. Carter Coll. P. 20.4.22 / 2825 Paratype (blue) (NMV 2011-14L); ♂, Cradle Mt, Tasmania, Carter & Lea / Cotype 2568 (blue) / F. E. Wilson Collection (NMV 2011-14L); 1 (?sex, defect, head and prothorax missing, abdomen eaten by dermestid larva), Tasmania, H.J.C. 1918/Co-Type / *Calyptogonia ater* Sl. Id. by T. G. Sloane/PARATYPE (blue) (ANIC); ♂ (abdomen eaten), Co-type (yellow)

/Australia 1921. 125/Cradle Mt T.H.J.C. 1.18/*Calyptogonia atra* Sl. Id. by T. G. Sloane (NHM).

New records. ♂, ♀, Tasmania Hartnett 2.ii.77 J. Sedlacek (ANIC); ♀, AUSTRALIA: Waldheim Tas. 20.iii.77 B. P. Moore / *Calyptogonia ater* Sl. det. B. P. Moore'77 (ANIC); ♀, AUSTRALIA, C-TASMANIA Lake St. Clair Narcissus Bay 750 m, 27 I 1998 (Lok 11/52) Lars Hendrich leg/Coll (CBM); ♀, Cradle Mt. T H J. C. 1.18 / *Calyptogonia ater* Sl. (ANIC) ; ♀, Tas., Lake Sydney 690 m 2 Feb. 1994 R. Mesibov 55GDN686070 / Databased 201534 PBMcQ (FTIC); ♂, Dorrigo, NSW Jan. 1931. C. Oke/*Calyptogonia atra* Sloane Tasmanian sp. !! Det. B.P. Moore'61 (NMV).

Diagnosis. Distinguished from *Calyptogonia atra occidentalis* subsp. nov. by narrower pronotum and slightly longer elytra.

Partial redescription. *Measurements* (ratios of a specimen with exceptionally wide pronotum and narrow elytra in brackets). Length: 11.6-12.6 mm; width: 4.3-4.7 mm. Ratios: Width/length of pronotum: 1.26-1.34 (1.37); width base/apex of pronotum: 1.17-1.22; width widest diameter/base of pronotum: 1.26-1.33; width of pronotum/width of head: 1.40-1.45; length/width of elytra: 1.58-1.61; width elytra/pronotum: (1.13)1.29-1.38.

Legs. (Fig. 31) 2nd-4th tarsomeres of male protarsus moderately wide.

Male genitalia. (Fig. 12) Very heavily sclerotized. Genital ring short and wide, oval, very thickly sclerotized. Aedeagus large, narrow, markedly curved; lower surface in apical two thirds very concave; apex large, somewhat axe-shaped, tip directed down. Upper margin near apex distinctly incised. Orifice situated completely on the right side, oval. Internal sac with several, thickly sclerotized folds. Both parameres large and wide, markedly hollowed on the inner surface; left paramere with acute, slightly upturned apex, with many moderately elongate setae at apical third of lower surface and some setae on upper surface immediately at apex; right paramere longer than left, slightly boomerang-shaped, with wide, slightly rounded apex, apex with moderately short setae, lower surface in apical three fifth with very dense, double fringe of elongate hairs.

Female gonocoxites. (Fig. 5) Gonocoxite 1 elongate, moderately narrow, widened towards

apex, medially at the base with a hook-shaped plate, with a large hyaline area on the latero-apical margin; with many short and stout, at apex obtuse, setae at the median and lateral apical margins, and the whole ventral surface and the median half of the dorsal surface with very dense, very elongate nematiform setae; gonocoxite 2 narrow, rather short, straight, almost parallel-sided, inserted at apex of gonocoxite 1, with transverse apex which bears three or four moderately elongate nematiform setae originating from a circular pit at the very apex.

Variation. Generally little variation noted. One old specimen from Cradle Mt, however, has a slightly wider pronotum than usual (ratio width/length 1.37) and remarkably narrow and less oviform elytra, hence the ratio width of elytra/width of pronotum is exceptionally small (1.13). Therefore, this specimen is only tentatively ascribed to the nominate subspecies.

Distribution. Central Tasmania. The single 'Dorrigo' specimen is certainly wrongly labeled.

Collecting circumstances. Not recorded, but probably collected at rather high altitude of 800 m or even higher.

Calypogonia atra occidentalis subsp. nov.
(Fig. 29)

Material. HOLOTYPE: ♂, Tas.: Mt Weld, 146.58E x 43.01S Warra-Mt Weld, alt. transect Pitfall trap WD1300P45L N. Doran & R. Bashford, 18 Dec 2001 FT5823 (FTIC). - PARATYPES: ♂, ♀, same data (FTIC); ♂, Tas.: Mt Weld, 146.58E x 43.01S Warra-Mt, Weld alt. transect Pitfall trap WD1300P25L N. Doran & R. Bashford, 22 Jan 2001 FT5912 (FTIC); ♂, 2♀, Tas.: Mt Weld 146.59E x 43.01S Warra-Mt. Weld, alt. transect Pitfall trap WD1100P45L N. Doran & R. Bashford, 22 Jan 2001 FT5901 (FTIC); ♂, Tas.: Mt Weld, 146.58E x 43.01S Warra-Mt Weld, alt. transect Pitfall trap WD1300P5L N. Doran & R. Bashford, 26 Feb 2001 FT97 (FTIC); 2♂♂, ♀, Tas.: Mt Weld 146.58E x 43.01S Warra-Mt Weld alt. transect Pitfall trap WD1300P45U N. Doran & R. Bashford, 22 Jan 2001 FT5916 (FTIC); 2♂♂, Tas.: Mt Weld, 146.60E x 43.00S Warra-Mt Weld, alt. transect Pitfall trap WD900P45L N. Doran & R. Bashford, 26 Feb 2001 FT5978 (FTIC); ♀, Tas.: Mt Weld, 146.59E x 43.01S Warra-Mt Weld, alt. transect Pitfall trap WD1100P45L N. Doran & R. Bashford, 18 Dec 2001 FT5811 (FTIC); ♀, Tas.: Mt Weld, 146.58E x 43.01S Warra-Mt Weld, alt. transect Pitfall trap

WD1200P5U N. Doran & R. Bashford, 26 Feb 2001 FT5998 (FTIC); ♀, Tas.: Mt Weld, 146.60E x 43.00S Warra-Mt Weld, alt. transect Pitfall trap WD900P45U N. Doran & R. Bashford, 22 Jan 2001 FT5891 (FTIC); ♀, Tas.: Mt Weld, 146.58E x 43.01S Warra-Mt Weld, alt. transect Pitfall trap WD1300P5L N. Doran & R. Bashford, 22 Jan 2001 FT5911 (FTIC); ♀, Tas.: Mt Weld, 146.58E x 43.01S Warra-Mt Weld, alt. transect Pitfall trap WD1300P5U N. Doran & R. Bashford, 22 Jan 2001 FT5914 (FTIC); ♀, Tas.: Mt Weld, 146.59E x 43.01S Warra-Mt Weld, alt. transect Pitfall trap WD1100P25U N. Doran & R. Bashford, 22 Jan 2001 FT5903 (FTIC); ♀, Tas.: Mt Weld, 146.58E x 43.01S Warra-Mt Weld, alt. transect Pitfall trap WD1300P5L N. Doran & R. Bashford, 18 Dec 2001 FT5821 (FTIC); ♀, Tas.: Mt Weld, 146.58E x 43.01S Warra-Mt Weld, alt. transect Pitfall trap WD1200P45L N. Doran & R. Bashford, 22 Jan 2001 FT5907 (FTIC); 2♀♀, Tas.: Mt Weld, 146.58E x 43.01S Warra-Mt Weld, alt. transect Pitfall trap WD1200P5L N. Doran & R. Bashford 22 Jan 2001 FT5905 (FTIC); ♂, Tas.: Mt Weld, 146.59E x 43.01S Warra-Mt Weld, alt. transect Pitfall trap WD1100P45L N. Doran & R. Bashford, 26 Feb 2001 FT87 (CBM); ♂, Tas.: Mt Weld, 146.60E x 43.00S Warra-Mt Weld, alt. transect Pitfall trap WD900P45U N. Doran & R. Bashford, 26 Feb 2001 FT77 (CBM); ♀, Tas.: Mt Weld, 146.58E x 43.01S Warra-Mt Weld, alt. transect Pitfall trap WD1200P45U N. Doran & R. Bashford 26 Feb 2001 FT276 (CBM); ♂, Tas.: Mt Weld, 146.58E x 43.01S Warra-Mt Weld, alt. transect Pitfall trap WD1300P25U N. Doran & R. Bashford, 26 Feb 2001 FT6005 (FTIC).

Etymology. The species name refers to the occurrence of the subspecies in western Tasmania.

Diagnosis. Distinguished from *Calypogonia atra atra* Sloane by wider pronotum and slightly shorter elytra.

Description. Measurements. Length: 11.8-13.2 mm; width: 4.55-5.0 mm. Ratios. Width/length of pronotum: 1.39-1.43; width base/apex of pronotum: 1.19-1.22; width widest diameter/base of pronotum: 1.29-1.33; width of pronotum/width of head: 1.58-1.60; length/width of elytra: 1.52-1.56; width elytra/pronotum: 1.21-1.25.

Colour. Similar to that of the nominate subspecies.

Head. (Figs 29) Rather similar to those of the nominate subspecies.

Pronotum. (Fig. 29) Fairly similar to those of the nominate subspecies, but wider and also wider in relation to the head and the elytra.

Elytra. Surface structure similar to those of the nominate subspecies, but elytra slightly shorter.

Lower surface. Similar to that of the nominate subspecies.

Legs. Similar to those of the nominate subspecies.

Male genitalia. Rather similar to those of the nominate subspecies.

Female gonocoxites. Similar to those of the nominate subspecies.

Variation. Very little variation noted.

Distribution. South-western Tasmania, recorded only from the area around Mt. Weld.

Collecting circumstances. All specimens were sampled in pitfall traps in montane rain forest.

Calyptogonia lynetteae sp. nov.
(Figs 13, 30, 32)

Calyptogonia atra Sloane 1920: 121 (part).

Material. HOLOTYPE: ♂, Magnet Tasmania/Lea/Tribe Migadopini Gen. ? sp. nov. Id by T. G. Sloane / PARATYPE *Calyptogonia ater* Sl. (blue) (ANIC) (paratype label written by Darlington!). - PARATYPE: ♂, CP890910 NW Tas., Animal Creek. 740 m. 24 JAN. 1992 A. Mesibov / Databased 201635 PBMcQ (FTIC).

Etymology. The species name is a patronym in honour of Lynette Forster of Tasmania Forestry Insect Collection, in gratitude for her kind assistance to me in many respects during my visit at that collection and because she independently recognised this as a new species.

Diagnosis. Distinguished from *Calyptogonia atra* Sloane by wider pronotum with much wider base, laterad more projected eye with shorter orbit, very transverse microreticulation of the elytra, wider and shorter 2nd–4th tarsomeres of male protarsus, and not sinuate upper margin of the aedeagus.

Description. Measurements. Length: 10.7–11.2 mm; width: 4.15–4.25 mm. Ratios. Width/length of pronotum: 1.51–1.54; width base/apex of pronotum: 1.39–1.47; width widest diameter/base of pronotum: 1.09–1.15; width of pronotum/width of head: 1.49–1.54; length/width of elytra: 1.51; width elytra/pronotum: 1.15–1.19.

Colour. (Fig. 30) Black, only tarsi and apical antennomeres piceous.

Head. (Fig. 30) Of average size. Labrum slightly excised at apex. Eye slightly larger than in *C. atra*, laterad rather projected, orbit very short, c. 1/10 of length of eye.

Pronotum. (Fig. 30) Wide, at base much wider than at apex; lateral border evenly convex; lateral margin moderately wide, and of almost equal width throughout. Marginal sulcus shallow, widened and explanate behind middle. Both apex and base gently sinuate. Apical angles slightly produced, basal angles rectangular but obtuse. Median line comparatively deep. Both transverse sulci very shallow. Basal impressions rather shallow, the inner one rather narrow, elongate, and sinuate.

Elytra. Comparatively short, with rather wide base, lateral borders evenly convex to suture. Striae complete, deep, impunctate, intervals moderately convex. Parascutellary pore at junction of 2nd and 3rd stria. Marginal series consisting of 13–14 punctures which are quite regularly arranged. Microreticulation composed of very fine, rather superficial, very transverse meshes and lines; surface rather iridescent.

Lower surface. With fine, isodiametric to slightly transverse microreticulation. Metepisternum quadrate. Terminal sternum in male bisetose.

Legs. (Fig. 32) Of average size. 2nd–4th tarsomeres of male protarsus very wide and densely squamose.

Male genitalia. (Fig. 13) Very heavily sclerotized. Genital ring short and wide, oval, very heavily sclerotized. Aedeagus large, narrow, markedly curved; lower surface in apical two thirds very concave; apex large, somewhat axe-shaped, tip directed down. Upper margin evenly convex. Orifice situated completely on the right side, oval. Internal sac with several, thickly sclerotized folds. Both parameres large and wide, markedly hollowed on the inner surface; left paramere with acute, slightly down-curved, hyaline apex, with several moderately elongate setae at apical part of upper surface; right paramere longer than left, slightly boomerang-shaped, with wide, evenly rounded apex, apex with moderately short hairs, lower surface in apical three fifths with very dense, double fringe of elongate hairs.

TABLE 1. Measurements and ratios of the species of *Calyptogonia* sloane, 1920. N = number of specimens measured; body length in mm; w/l pr = ratio width/length of pronotum; b/a pr = ratio width of base/width of apex of pronotum; dia/b pr = ratio widest diameter/width of base of pronotum; pr/h = ratio width of pronotum/width of head; l/w el = ratio length/width of elytra; el/pr = ratio width of elytra/width of pronotum.

	N	body	w/l	b/a	dia/b	pr/h	l/w	el/pr
		length	pr	pr	pr		el	
<i>atra atra</i>	12	11.6-12.6	1.26-1.34	1.17-1.22	1.26-1.33	1.40-1.45	1.58-1.61	1.29-1.38
<i>atra occidentalis</i>	8	11.8-13.2	1.39-1.43	1.19-1.22	1.29-1.33	1.58-1.60	1.52-1.56	1.21-1.25
<i>lynetteeae</i>	2	10.7-11.2	1.51-1.54	1.39-1.47	1.09-1.15	1.49-1.54	1.51	1.15-1.19

Female gonocoxites. Unknown.

Variation. The paratype has a wider pronotum with a relatively wider base.

Distribution. North-western Tasmania.

Collecting circumstances. Not recorded.

and wider in comparison to the head, ratio width of pronotum/width of head >1.58 (Fig. 29); elytra slightly shorter, ratio length/width 1.52-1.56. SW Tas
.....*atra occidentalis* subsp. nov.

***Stichonotus* Sloane, 1910**

Stichonotus Sloane, 1910: 378. – Sloane 1915: 439; 1920: 122; Csiki 1927: 443; Moore et al. 1987: 65, Lorenz 1998: 118.

Type species. *Stichonotus leai* Sloane, 1910, by monotypy.

Diagnosis. Small, oval-shaped, more or less brightly coloured species with wide, at apex deeply excised pronotum and far produced apical angles; head deeply imbedded into the prothorax; eye of normal size; elytra short, oviform, impunctate; metathoracic wings reduced; aedeagus very narrow and remarkably elongate, conspicuously curved at least in basal part; right paramere also narrow and elongate, curved, densely setose in apical third; left paramere stouter than right one, asetose or sparsely setose at apex; gonocoxites narrow and elongate, gonocoxite 1 more or less densely setose, gonocoxite 2 small, narrow, straight, with a single short nematiform seta at apex.

Distribution. Four species, three of which occur in Tasmania, one in southern Victoria.

Note. The three described species of *Stichonotus* are rather similar in shape and structure. The key given by Sloane (1915: 439) is still reasonably useful, but not all specimens, in particular of the two recorded Tasmanian species, do fit the characters enumerated in the key. Therefore colleagues of Tasmanian Forestry requested

KEY TO SPECIES OF CALYPTOGONIA

1. Pronotum very wide, ratio width/length >1.50, base much wider than apex, ratio width of base/ width of apex >1.39; eye more convex, orbit shorter (Fig. 30); 2nd-4th tarsomeres of male protarsus wider and shorter (Fig. 32); microreticulation of elytra composed of very transverse meshes and lines, surface slightly iridescent; upper margin of aedeagus not sinuate (Fig. 13). NW Tas.....*lynetteeae* sp. nov.
- Pronotum narrower, ratio width/length >1.43, base comparatively narrower, ratio width of base/ width of apex <1.22; eye less convex, orbit longer (Figs 28, 29); 2nd-4th tarsomeres of male protarsus narrower and longer (Fig. 31); microreticulation of elytra isodiametric, surface dull; upper margin of aedeagus distinctly sinuate (Fig. 12). C, SW Tas.....2.
2. Pronotum narrower, ratio width/length < 1.34, and narrower in comparison to the head, ratio width of pronotum/width of head < 1.45 (Fig. 28); elytra slightly longer, ratio length/width 1.58-1.61. C Tas
.....*atra atra* Sloane, 1920
- Pronotum wider, ratio width/length >1.39,

that I examine the genitalia to achieve additional distinguishing characters. Hence the male genitalia and female gonocoxites of all species were examined and are figured. This examination revealed an additional species from Tasmania which is also different in some characters of external morphology. Therefore a new key to all species is provided.

Stichonotus leai Sloane, 1910
(Figs 6, 14, 22)

Stichonotus leai Sloane, 1910: 379. – Sloane 1915: 439; 1920: 122; Csiki 1927: 443; Moore *et al.* 1987: 65, Lorenz 1998: 118.

Material. HOLOTYPE: ♀, *Stichonotus leai*, Sl. Type / Magnet, Tas. Rec. from A.M. Lea / Holotype *Stichonotus leai* Sl. PJD / ANIC Database 25 054362 (ANIC).

New Records. (4 ex.) ♂, 42.06S 146.10E Lake St. Clair 750 m Tas. 25-27 Jan. 1980 Lawrence & Weir / Berlesate ANIC 664 litter under tree ferns & *Nothofagus* (ANIC); ♀, Waratah Tas: Lea & Carter / H. J. Carter Coll. P. 20.4.22 / *Stichonotus leai* Sl. (1910) Id. by T.G. Sloane (NMV 3476); ♂, Waratah Tas Mar.'57 Darlington / *Stichonotus leai* Sl. Darlington 63 (NMV 3477); ♀, Magnet Tas./1155 S *Stichonotus oodiformis* Sl. Tas. (SAMA 25-033391).

Note. This species includes all those Tasmanian specimens that are smaller and shorter than *S. piceus* Sloane and possess a wide, uninterrupted, pale elytral margin. It is unclear why this was done, as Sloane's description explicitly states that the 7th interstice (which is the 8th when the first interval is included) is dark over most of its length. This is not the case in most specimens determined as *S. leai*. These specimens are described as the new species *S. decoloratus* in the present paper.

Diagnosis. A rather small and short, distinctly coloured species, with a wide, reddish margin of the elytra which bears a distinct, longitudinal, dark stripe on the 8th interval. Further distinguished from all small, short species by the markedly curved apex of the aedeagus and the strongly curved basal part of the right paramere. Further distinguished from *S. limbatus* Sloane by the margin of the elytra not crenulate, and from the most similar *S. decoloratus* by slightly longer elytra and much larger and more regularly curved aedeagus.

Partial redescription. *Measurements.* Length: 5.4-5.9 mm; width: 2.7-2.9 mm. Ratios. Width/length of pronotum: 1.92-1.97; width base/apex of pronotum: 1.74-1.82; width widest diameter/base of pronotum: 1.01-1.012; width of pronotum/width of head: 1.80-1.86; length/width of elytra: 1.19-1.21; width elytra/pronotum: 0.99-1.01.

Colour. (Fig. 22) Conspicuous. Head and pronotum more or less dark brown, palpi, antennae, and legs reddish. Pronotum with wide pale reddish margin which is widened towards base. Elytra more or less dark brown, this colour covers the six median intervals, at base even the eight median ones; lateral margin from 7th interval contrastingly yellow or pale reddish, but the 8th interval over most of its length again contrastingly dark. Apex widely pale, except the sutural interval.

Male genitalia. (Fig. 14) Genital ring short and wide, oval. Aedeagus very narrow and elongate, barely sinuate except in apical part; lower surface regularly and markedly concave throughout; apex rather narrow, obtuse, very much curved to left. Orifice elongate, largely situated on the right side. Internal sac very simply structured, with one elongate, slightly sclerotized fold. Both parameres large; left paramere shorter than right one, moderately wide, markedly boomerang-shaped, with narrow, obtusely triangular apex, lower surface with a few moderately elongate setae immediately at apex; right paramere longer than left, rather narrow, in basal third extremely curved, in apical two thirds straight, with obtuse, slightly tapering apex, lower surface in apical half with two very dense fringes of extremely elongate hairs.

Female gonocoxites. (Fig. 6) Gonocoxite 1 elongate, moderately wide, the complete lower surface and part of the upper surface very densely setose with elongate nematiform setae; apical part and along the border of the hyaline area with several short and stout setae; gonocoxite 2 narrow, short, elongate, with obtuse apex which bears one short nematiform seta originating close to apex from a circular pit.

Variation. Little variation noted. In particular the colouration is very characteristic and barely varied.

Distribution. North-western and central Tasmania.

Collecting circumstances. Specimens were collected by Berlese extraction in 'litter under tree ferns & *Nothofagus*' at rather high altitude.

Stichonotus piceus Sloane, 1915
(Figs 7, 15, 23)

Stichonotus piceus Sloane 1915: 439, 440. – Sloane 1920: 122; Csiki 1927: 443; Moore *et al.* 1987: 65, Lorenz 1998: 118.

Material. HOLOTYPE: in ANIC, seen 2011.

New records. Many specimens from central and western Tasmania.

Diagnosis. A comparatively large, predominantly dark species, easily distinguished from the three other species by longer elytra, comparatively wider base of the pronotum in relation to apex, and the distinct, isodiametric microreticulation of the elytra which give these a somewhat dull appearance. Further distinguished by the less curved aedeagus and the stout left paramere which is impilose at apex.

Partial redescription. *Measurements.* Length: 6.5–8.2 mm; width: 3.0–3.85 mm. Ratios. Width/length of pronotum: 1.78–1.85; width base/apex of pronotum: 2.04–2.15; width widest diameter/base of pronotum: 1.0; width of pronotum/width of head: 2.18–2.26; length/width of elytra: 1.30–1.33; width elytra pronotum: 1.01–1.03.

Colour. (Fig. 23) Head and pronotum dark piceous to almost black, palpi, antennae, and legs dark reddish. Pronotum with inconspicuous, moderately wide dark reddish margin which is widened towards base. Elytra dark piceous to black, with or without an inconspicuous, narrow, dark reddish margin which is widened in only apical fourth.

Male genitalia. (Fig. 15) Genital ring short and wide, oval. Aedeagus very narrow and elongate, very slightly sinuate; lower surface in basal half very concave, in apical half almost straight;

apex narrow, asymmetrically situated on the right side, slightly curved. Orifice elongate, largely situated on the right side. Internal sac very simply structured, with one elongate, slightly sclerotized fold. Both parameres large; left paramere short and wide, with triangular, slightly obtuse apex, without any setae; right paramere longer than left, narrow, markedly curved, with triangularly tapering apex, lower surface with two very dense fringes of elongate hairs in apical third.

Female gonocoxites. (Fig. 7) Gonocoxite 1 elongate, moderately wide, the complete lower surface very densely setose with rather short nematiform setae; gonocoxite 2 narrow, short, elongate but slightly triangular, with obtuse apex which bears one short nematiform seta originating close to apex from a circular pit.

Variation. Considerable variation is noted in body size and in degree of light colour of the margins of pronotum and elytra, less so in shape of pronotum and elytra.

Distribution. Widely distributed in western and central Tasmania.

Collecting circumstances. A common, ground living species which occurs in open to dense forest. According to information kindly received from Lynette Forster and Simon Grove of Forestry Tasmania, this species is most common in somewhat disturbed environments.

Stichonotus limbatus Sloane, 1915
(Figs 8, 16, 24)

Stichonotus limbatus Sloane 1915: 439, 440. – Csiki 1927: 443; Moore *et al.* 1987: 65, Lorenz 1998: 118.

Material. SYNTYPES: 1 (?sex, damaged, head and prothorax missing, abdomen eaten by dermestid larva), Beech Forest Vict. J.E.D. / *Stichonotus limbatus* Sl. cotype / PARATYPE (*blue*) (ANIC); other syntypes in NMV, seen 2007.

New records. (16 ex.) Mt. Sabine Otway Ranges, Vic 22-23.i.1967, G. Monteith (CBM, QM); Lorne Vic 25.i.59 B. P. Moore (ANIC); Beech Forest Vict, 13.ii.60 B.P. Moore (ANIC, CBM); Beech Forest Vic, 11 – 19 Jan. 1932 F.E. Wilson (QM); 38.47S 143.37E Vic Otway NP Elliot R. 5.5 km W Marengo. 80 m, 828, 8 Feb 1987 A. Newton & M. Thayer (ANIC); 38.43S 143.35E Vic Otway NP 390m Binn Rd, 4.3km N.Cape Horn 808, 25 Jan–8 Feb 1987 A. Newton & M. Thayer (ANIC);

38.39S 143.42E VIC Haines Junct. 525 m, 1.9 km W.on Turtons Track. 809 25Jan-8Feb 1987 A. Newton & M. Thayer (ANIC).

Diagnosis. A rather small and short, distinctly coloured species, distinguished from other two small, short species by crenulate margin of the elytra and the unisetose apex of the left paramere; further from *S. leai* by more curved aedeagus and right paramere; and from *S. decoloratus* by straight apex of the aedeagus and right paramere far less curved basally.

Partial redescription. Measurements. Length: 5.9-6.8 mm; width: 2.9-3.15 mm. Ratios. Width/length of pronotum: 1.93-2.0; width base/apex of pronotum: 1.76-1.80; width widest diameter/base of pronotum: 1.0-1.01; width of pronotum/width of head: 1.86-1.90; length/width of elytra: 1.20-1.28; width elytra/pronotum: 1.01-1.03.

Colour. (Fig. 24) Rather conspicuously contrasting pattern. Head and pronotum piceous to almost black, palpi and antennae reddish, legs brown to piceous. Pronotum with rather distinct, pale reddish margin which in anterior half is narrow but is widened towards base. Elytra piceous to almost black, with narrow but conspicuous reddish margin which extends from the lateral half of 9th interval to the margin, but is widened in apical fifth or sixth. At apex only the sutural interval is dark.

Male genitalia. (Fig. 16) Genital ring short and wide, oval. Aedeagus very narrow and elongate, straight, slightly widened near apex; lower surface very concave throughout, in apical third even slightly bent down; apex rather wide, triangularly tapering, straight. Orifice elongate, largely situated on the right side. Internal sac very simply structured, with one elongate, slightly sclerotized fold. Both parameres large but comparatively narrow; left paramere shorter than right one, moderately wide, with narrow, triangular, slightly up-curved apex, with a single, fairly elongate seta at apex; right paramere longer than left, very narrow, markedly curved, even slightly boomerang-shaped, with narrow, triangularly tapering apex, lower surface in apical third with two very dense fringes of extremely elongate hairs.

Female gonocoxites. (Fig. 8) Gonocoxite 1 elongate, rather narrow, with a hyaline area at the apical-lateral part of the ventral surface; at the border of the hyaline area with a series of stout but elongate setae, the medio-apical margin with some shorter, stout setae; the whole lateral and ventral surfaces densely clothed with elongate nematiform setae; gonocoxite 2 narrow, moderately short, straight, almost parallel-sided, with slightly rounded apex which bears one short nematiform seta originating close to apex from a circular pit.

Variation. Little variation noted in relative length of the elytra.

Distribution. Recorded only from the Otway Ranges in south-western Victoria.

Collecting circumstances. A ground living species which occurs in closed forest. Some specimens were collected in 'wet sclero. forest in leaf and log litter'.

Stichonotus decoloratus sp. nov.
(Figs 9, 17, 25)

Material. HOLOTYPE: ♂, AUSTRALIA: 12 km NE of Corinna Tas. 22.iii.77 B.P. Moore / *Stichonotus leai* Sl. det. B.P. Moore'77 (ANIC). - PARATYPES: ♂, AUSTRALIA: Waldheim Tas. 20.iii.77 B.P. Moore (ANIC); ♂, SW Tasmania, Lower Gordon R. 42.48.5S 145.51E 42.48.5S 145.51E Howard, Hill... / H.E.C. Survey 5L. 720 Mar 1977 litter (ANIC); ♂, SW Tasmania Lower Gordon R. 42.31-56S 145.42-56E Howard, Hill... / H.E.C. Survey 5R. 500 Mar 1977 litter / *Stichonotus leai* Sl. det. B.P. Moore'77 (CBM); ♀, SW Tasmania Lower Gordon R. 42.31-56S 145.42-56E Howard, Hill... / H.E.C. Survey 5R. 500 Mar 1977 litter (ANIC); ♂, SW Tasmania Lower Gordon R. 42.43 S 45 145.43 E50 Howard, Hill... / H.E.C. Survey 2R. 860 12R 850 litter / *Stichonotus leai* Sl. det. B.P. Moore'77 (ANIC); ♂, 43.22S 146.09E Tas. Celery Top Island Bathurst Harbour 15 Mar.-15Apr.1991 E. Edwards, J. Berry F.I.T. #2/F.I.T. ANIC 1180 closed forest (ANIC); ♀, 12 km E of Strahan Tas. 21 Jan 1982 G. Bornemissza / Berlesate ANIC 9125 (ANIC); ♂, Cradle Mt Tas. H.J.C. 1.18 T. (ANIC); ♂, Waldheim, Cradle Mt Tas. 12-14.ii.1967. G. Monteith (QM); ♂, AUST Tas. Cradle Mt NP, Waldheim Forest. *Nothofagus* & King Billy Pine: Litter. 145.57'E. 41.39'S. 1000 m. R. Raven & J. Gallon 1 Feb 1987 (QM); ♂, Warra LTER: Manuka Rd Tas.: 43.07 S x 146.67 E SSTCON338 Pit 02 of 10 Apr 2007 Control R. Bashford FT FT40131 (FTIC); ♂, Warra LTER: Manuka Rd Tas.: 43.07 S x 146.67 E SSTBIG1/U Pit 1 of 6 Apr-2002 Post-logging

- R. Bashford FT11/43 (FTIC); ♂, Tas, Warra LTER, Manuka Rd, 43.07S x 145.67E, SSTMID, 160 Pit 4 of 6, Mar 2002, Post logging, R. Bashford, FT11670 (FTIC); ♀, Tas, Warra LTER, Manuka Rd, 43.07S x 145.67E, SSTMID160, Pit 5 of 6, Feb 2002, Post logging, R. Bashford, FT11535 (FTIC); ♂, Warra LTER: Manuka Rd Tas.: 43.07 S x 146.67 E SSTTOP070 Pit 6 of 10 Sep 2002 Post-logging R. Bashford FT FT26594 (FTIC); ♀, Warra LTER: Manuka Rd Tas.: 43.07 S x 146.67 E SSTTOP070 Pit 3 of 10 Jun 2002 Post-logging R. Bashford FT FT14496 (CBM); ♀, Warra LTER: Manuka Rd Tas.: 43.07 S x 146.67 E SSTTOP070 Pit 6 of 10 May 2002 Post-logging R. Bashford FT FT11914 (FTIC); ♀, Warra LTER: Manuka Rd Tas.: 43.07 S x 146.67 E SSTTOP070 Pit 7 of 10 May 2002 Post-logging R. Bashford FT FT11915 (FTIC); ♀, Warra LTER: Manuka Rd Tas.: 43.07 S x 146.67 E SSTNEW058 Pit 03 of 10 Feb 2005 Pre-logging R. Bashford FT35391 (FTIC); ♀, Warra LTER: Manuka Rd Tas.: 43.07 S x 146.67 E SSTTOP070 Pit 1 of 10 Series 17 16-Feb-99 R. Bashford FT8647 (FTIC); ♂, Warra LTER: Manuka Rd Tas.: 43.07 S x 146.67 E SSTCON338 Pit 04 of 10 May 2007 Control R. Bashford FT FT40238 (CBM); ♂, Warra LTER: Manuka Rd Tas.: 43.07 S x 146.67 E SSTSMA254 Pit 10 of 10 Apr 2000 Post-logging R. Bashford FT FT9790 (CBM); ♂, Tas, Warra LTER, Manuka Rd, 43.07S x 145.67E, SSTMID160, Pit 9 of 10, Jan 2005, Post logging, R. Bashford, FT35016 (FTIC); ♂, Tas., Warra LTER, Manuka Rd, 43.07S x 145.67E, SSTTOP070, Pit 2 of 10, Sep 2001, Post-logging, R. Bashford, FT10922 (FTIC); ♂, Tas, Warra LTER, Manuka Rd, 43.07S x 145.67E, SSTCON338, Pit 9 of 10, Apr 2006, Control, R. Bashford, FT37217 (FTIC); ♂, Tas, Warra LTER, Manuka Rd, 43.07S x 145.67E, SSTBIG106, Pit 6 of 6, Oct 2001, Post logging, R. Bashford, FT10962 (FTIC); ♀, Tas, Warra LTER, Manuka Rd, 43.07S x 145.67E, SSTNEW058, Pit 1 of 10, Feb 2005, Pre-logging, R. Bashford, FT35389 (FTIC); ♀, Tas, Warra LTER, Manuka Rd, 43.07S x 145.67E, SSTBIG254, Pit 2 of 6, Aug 2001, Post logging, R. Bashford, FT10752 (FTIC); ♂, Tas, Warra LTER, Manuka Rd, 43.07S x 145.67E, SSTSMA663, Pit 10 of 10, Sep 1999, Post logging, R. Bashford, FT9266 (FTIC); ♀, Tas, Warra LTER, 43.07S x 145.67E, Log decay Invert project, Emergence trap 5 lower, OG log 1 May 2002 R. Bashford FT14166 (FTIC); ♀, Tas, Warra LTER, 43.07S x 145.67E, Log decay Invert project, Emergence trap 1 lower, OG log 6 Oct 2006 R. Bashford FT32232 (FTIC); ♂, Tarraleah: Homes Dam area Tas.: 42.272S x 146.361 E Tarraleah WHS fauna proj. Pit # 2.3 WHS Apr 2003 M. McDonald FT23196 (FTIC); ♂, Tarraleah: Homes Dam area Tas.: 42.372S x 146.361 E Tarraleah WHS fauna proj. Pit # 2.2 WHS Apr 2003 M. McDonald FT23195 (CBM); ♀, Tas. Tarraleah: Homes Dam 42.275 S x 146.3583 E Tarraleah WHS 7.4 Pitfall trap 19-Feb-92 R. Brereton FT21283 (FTIC); ♀, Tas, Tarraleah Homes Dam area, 42.272S x 146.361E, Tarraleah WHS fauna project, Pit 2.3, Jun 2003, M. McDonald, FT23520 (FTIC); ♂, Tas, Tarraleah Homes Dam area, 42.329S x 146.359E, Tarraleah WHS fauna project, Pit WHS 9.4, Feb 1992, R. Brereton, FT21295 (FTIC); ♀, Tas, Tarraleah Butlers Rd area, 42.304S x 146.3612E, Tarraleah WHS fauna project, Pit A6 CON, Jun 2003, M. McDonald, FT23649 (FTIC); ♀, Tas, Tarraleah Butlers Rd area, 42.304S x 146.3612E, Tarraleah WHS fauna project, Pit 1.4, Mar 2003, M. McDonald, FT23029 (FTIC); ♀, Tas., Hartz Road 43.1601 S 146.8021 E Yee Log Invertebrate Study Hand collection HS3.5 16-May-00 M. Yee FT29187 (CBM); ♀, Tas., Harz Road 43.1601 S 146.8021 E Yee Log Invertebrate Study Hand collection HL1.5 13-Mar-00 M. Yee FT29121 (FTIC); ♀, Tas., Harz Road 43.1601 S 146.8021 E Yee Log Invertebrate Study Hand collection HS3.3 16-May-00 M. Yee FT29185 (CBM); ♀, Tas. Hartz Rd, 43.1601S x 146.8021E, Yee Log Invertebrate Study, Hand collection, HL2.4 Mar 2000 M. Yee FT29130 (FTIC); ♂, Tas. Hartz Rd, 43.1601S x 146.8021E, Yee Log Invertebrate Study, Hand collection, HL1.5 Mar 2000 M. Yee FT29121 (FTIC); ♂, Tas.: West Picton Road 43.1672 S x 146.6869 E Yee Log Invertebrate Study Log emergence trap PR2LET3 15-Nov-00 M. Yee FT29604 (FTIC); ♂, 2♀, Tas, West Picton Rd, 43.1672S x 146.6869E, Yee Log Invertebrate Study, Log emergence trap, PR2SET2 Nov 2000 M. Yee FT29635 (x3) (FTIC); ♂, Tas, West Picton Rd, 43.1672S x 146.6869E, Yee Log Invertebrate Study, Log emergence trap, PR2SET1 Nov 2000 M. Yee FT29619 (FTIC); ♀, Tas. South West Road Spur 43.0826 S 146.7223 E Yee Log Invertebrate Study Log emergence trap SLET3 13-Dec-00 M. Yee FT29776 (FTIC); ♀, Tas Scotts Peak Rd, 42.5807S x 146.228E, Driscoll rainforest patch survey, pitfall site B2B, Mar 2003, D. Driscoll, FT44093 (FTIC); ♂, Tas Scotts Peak Rd, 42.5807S x 146.228E, Driscoll rainforest patch survey, pitfall site B3A, Mar 2003, D. Driscoll, FT44095 (FTIC).

Diagnosis. A rather small and short, more or less distinctly coloured species, distinguished from *S. limbatus* by margin of the elytra not crenulate, less curved aedeagus, and multisetose apex of the left paramere; and from *S. leai* by less vividly coloured elytra, in particular without dark 8th interval, smaller aedeagus with little curved apex, and basally far less curved right paramere.

Description. Measurements. Length: 5.1-6.1 mm; width: 2.55-3.15 mm. Ratios. Width/length of pronotum: 1.93-1.95; width base/apex of pronotum: 1.79-1.85; width widest diameter/base of pronotum: 1.0-1.01; width of pronotum/width of head: 1.83-1.88; length/width of elytra: 1.09-1.14; width elytra/pronotum: 1.0-1.02.

Colour. (Fig. 25) Inconspicuous. Head and pronotum piceous to almost black, palpi and antennae reddish, legs brown to piceous. Pronotum with

TABLE 2. Measurements and ratios of the species of *Stichonotus* Sloane, 1910. N = number of specimens measured; body length in mm; w/l pr = ratio width/length of pronotum; b/a pr = ratio width of base/width of apex of pronotum; dia/b pr = ratio widest diameter/width of base of pronotum; pr/h = ratio width of pronotum/width of head; l/w el = ratio length/width of elytra; el/pr ≈ ratio width of elytra/width of pronotum.

	N	body length	w/l pr	b/a pr	dia/b pr	pr/h	l/w el	el/pr
<i>decoloratus</i>	6	5.1-6.1	1.93-1.95	1.79-1.85	1.0-1.01	1.83-1.88	1.09-1.14	1.00-1.02
<i>leai</i>	4	5.4-5.9	1.92-1.97	1.74-1.82	1.01-1.02	1.80-1.86	1.19-1.21	0.99-1.01
<i>limbatus</i>	6	5.9-6.8	1.93-2.00	1.76-1.80	1.0-1.01	1.86-1.90	1.20-1.28	1.01-1.03
<i>piceus</i>	6	6.5-8.2	1.78-1.85	2.04-2.15	1.0-1.01	2.18-2.26	1.30-1.33	1.01-1.03

rather inconspicuous, reddish margin which in anterior half is narrow but is widened towards base. Elytra piceous to almost black, with inconspicuous, narrow reddish margin which is widened in apical fifth or sixth. At apex only the sutural interval is dark.

Head. (Fig. 25) Of average size and shape, more than half as wide as the prothorax. Surface slightly impressed anterior-medially of the eye. Head not widened behind eye. Surface with fine, distinct, isodiametric microreticulation.

Pronotum. (Fig. 25) Of average size and shape. Apex deeply excised, apical angles acute. Lateral margins evenly convex, pronotum widest at base. Base less than twice as wide as apex, rather deeply excised, basal angles acute, far less than 90°. Apex margined, base not margined, median line rather impressed. Surface comparatively convex. Basal impression comparatively deep, rather punctiform.

Elytra. (Fig. 25) Short and wide, shorter than in all other species, upper surface comparatively convex. Lateral margins convex throughout, even in basal third barely straight. Humeral angle comparatively obtuse. Striae complete, rather deep, impunctate, interval convex. Scutellary puncture situated at junction of 2nd and 3rd striae. Marginal series consisting of 12 rather regularly spaced punctures. Microreticulation composed of fine, very superficial, very transverse meshes and lines, surface rather glossy and iridescent.

Lower surface. Metepisternum quadrate. Microreticulation very fine and highly superficial,

slightly transverse, surface glossy. Terminal abdominal sternum bisetose in both sexes.

Legs. Of average size and shape. 1st-4th tarsomeres of the male protarsus slightly widened and squamose.

Male genitalia. (Fig. 17) Genital ring short and wide, oval. Aedeagus very narrow and elongate, barely sinuate; lower surface regularly concave throughout; apex triangularly tapering, slightly curved to left. Orifice elongate, largely situated on the right side. Internal sac very simply structured, with one elongate, slightly sclerotized fold. Both parameres large; left paramere shorter than right one, moderately wide, with narrow, triangular, slightly bent down apex, lower surface with some elongate setae immediately at apex; right paramere longer than left, narrow, moderately curved, with triangularly tapering apex, lower surface in apical third with two very dense fringes of very elongate hairs.

Female gonocoxites. (Fig. 9) Gonocoxite 1 elongate, rather narrow, with many rather elongate nematiform setae at median margin and in median half of lower surface, also with some short nematiform setae on the median part of the apex and on the apical part of the lower surface along the border of the hyaline area; gonocoxite 2 narrow, short, straight, almost parallel-sided, with slightly rounded apex which bears one short nematiform seta originating close to apex from a circular pit.

Variation. Little variation noted.

Distribution. Widely distributed mainly in western and southern Tasmania.

Collecting circumstances. A common, ground living species which occurs in open to dense forest. According to information kindly received from Lynette Forster and Simon Grove of Forestry Tasmania this species is most common in somewhat disturbed environments.

KEY TO SPECIES OF *STICHONOTUS*

1. Elytra longer, slightly oviform, almost parallel-sided in basal third (Fig. 23); intervals rather depressed; microreticulation of intervals distinct, isodiametric, therefore surface rather dull; lateral margins of pronotum very convex, apex comparatively narrow, ratio base/apex >2.05; basal margin of pronotum less concave (Fig. 23); aedeagus less curved, apex asymmetric and acute; both parameres stouter, left paramere asetose at apex (Fig. 15); gonocoxite 1 densely setose, but without distinct stout setae in apical part (Fig. 7). Tas. *piceus* Sloane, 1915
 - Elytra shorter, more oviform, slightly convex in basal third (Figs 22, 24, 25); intervals fairly convex; microreticulation of intervals superficial, consisting of very fine, transverse lines, therefore surface rather glossy; lateral margins of pronotum less convex, apex wider, ratio base/apex <1.85; basal margin of pronotum more concave (Figs 22, 24, 25); aedeagus more curved, apex less asymmetric and less acute; both parameres narrower, left paramere with more than one seta at apex (Figs 14, 16, 17); gonocoxite 1 with distinct stout setae in apical part (Figs 6, 8, 9). 2
2. Elytra short, but not markedly oviform, almost parallel-sided in basal third; marginal channel distinctly crenulate; elytral striae perceptibly crenulate (Fig. 24); aedeagus markedly but regularly curved, apex straight; both parameres regularly curved, left paramere narrow, with a single seta at apex (Fig. 16); gonocoxite 1 completely setose, with very elongate stout setae in apical part (Fig. 8). SW Vic *limbatus* Sloane, 1915
 - Elytra short and quite oviform, marginal channel not crenulate; elytral striae not

crenulate (Figs 22, 25); aedeagus less curved, apex either asymmetric or slightly curved to the right; left paramere wider, with several elongate setae at apex (Figs 14, 17); gonocoxite 1 variously setose, but with less elongate stout setae in apical part (Figs 6, 9) Tas 3

3. Colouration of elytra less bright, 8th interval without distinct dark stripe (Fig. 25); aedeagus smaller, >1.25 mm long, far less curved, apex less curved to the right; parameres less curved and less odd-shaped, left paramere stouter, with several elongate setae at apex, right paramere regularly curved (Fig. 17); gonocoxite 1 not completely setose, with much smaller stout setae in apical part (Fig. 9) *decoloratus* sp. nov.
 - Colouration of elytra brighter, 8th interval with distinct dark stripe (Fig. 22); aedeagus larger, c. 1.5 mm long, far more curved, apex much more curved to the right; parameres markedly curved and odd-shaped, left paramere narrower, with a few short setae at apex, right paramere irregularly curved, rather boomerang-shaped (Fig. 14); gonocoxite 1 completely setose, with much larger stout setae in apical part (Fig. 6) *leai* Sloane, 1910

Migadopidiella Baehr, 2009

Migadopidiella Baehr, 2009: 32.

Type species. *Migadopidiella convexipennis* Baehr, 2009, by original designation.

Diagnosis. Small species, either unicolourous black or blackish-piceous with eight indistinct reddish spots on the elytra; elytral striae punctate; aedeagus short and compact with the orifice on the left side and several complexly folded and denticulate sclerites inside the internal sac; parameres large and rather similarly shaped, left asetose at apex, right densely setose along most of the lower surface.

Distribution. Two species, *M. convexipennis* Baehr, 2009 and *M. octoguttata* Baehr, 2009, both recorded from the Central Highlands, Tasmania.

Note. For additional information, description of the species, and figures of habitus and male

and female genitalia see Baehr (2009). This genus belongs in the subtribe (Amarotypina which presently also includes only *Amarotypus edwardsii* Bates, 1872 from New Zealand. According to Laroche & Larivière (2007) and Johns (2010) that genus includes additional undescribed species in New Zealand.

REMARKS

With respect to body shape and the female gonocoxites, the new genus *Dendromigadops* can be placed in the subtribe Migadopina, but as the male genitalia are unknown, its systematic position among the Australian and New Zealand genera remains obscure. Certainly the species of this genus are outstanding in their body shape and the extremely large eyes. However, the dense setosity of the female gonocoxite 1 and the small, parallel sided gonocoxite 2 are quite similar to those of the genera *Decognus* from NSW and to those of the Tasmanian genus *Calyptogonia*, less so to those of *Stichonotus*. In external features, however, *Dendromigadops* lacks compelling similarities with *Decognus* and *Calyptogonia*, whereas the wide prothorax, deeply excised at the apex, and the retracted head are rather similar to those of *Stichonotus*. In view of the strange shape of body, female gonocoxites, its putative arboricolous habits, and its unusual distribution, this genus seems to occupy a somewhat separate systematic position because of apparent lack of clear synapomorphies, and indeed, it may represent one of the most derived genera of Migadopini.

Dendromigadops extends the range of the tribe Migadopini far north into the tropics. This is surprising, because the tribe is regarded as a circumantartic that in Australia belongs to the cool adapted, so-called Bassian faunal element. Species of this group usually occur in the wet and cool south-east of Australia and Tasmania, and a few species are found in the extreme south-west. However, a number of species of certain tribes or genera which are believed to represent true Bassian elements, range far north into the so-called Torresian zone along the east coast of Australia (Baehr 1995, 2003a). But in south-eastern and even more

so in north-eastern Queensland, they almost exclusively occur on tablelands and on the summits of high mountains, where they inhabit temperate or subtropical montane rain forests and are typically found in *Nothofagus* forest. Baehr (2003a, 2003b) therefore stressed the superposition of such Bassian over Torresian environments and their inhabitants along the Great Dividing Range over almost the whole east coast of Queensland, except Cape York Peninsula. Most probably this was caused by the drift of the Australian plate through most of Tertiary to the north, the uplift of the Great Dividing Range along the east coast, and the resulting retreat of southern, temperate, Bassian environments to the highest tops of mountains and tablelands. At the same time, this drift facilitated the immigration of northern, Torresian floral and faunal elements into the lowlands of eastern Australia. Accordingly to their Bassian origin the two species of the genus *Dendromigadops* were found only at high altitude in montane rain forest.

Another problem is the apparent rarity of these species, the montane rain forests of eastern Australia have been reasonably well collected by a number of keen collectors during the last century. Why have these large and impressive species escaped the notice of collectors for so long? It seems that the apparent arboricolous, and most probably nocturnal, habits answer this question. To capture beetles with this habit and in this habitat require targeted collecting methods not frequently used. Both holotypes of the new species were collected arboreally whereas the paratype of *Dendromigadops alticola* was captured in a Malaise trap, which means that this species flies.

For this reason, I suggest that the species are not as rare as they seem to be, and, moreover, that additional species may occur in the vast area between the ranges of the southern and northern populations. Either the species may occur in the canopy of rain forest trees and the few recorded specimens are only serendipitously collected stragglers, which forayed down the trees instead of staying in the crowns where they normally remain, or they may live inside hollow trunks or branches of rain forest

trees. In the latter case they may leave these only occasionally and at night. The speculation that they live in tree-hollows is supported by the quite similar body shape of the species of *Dendromigadops* and certain melisoderine species of the tribe Psydrini which are known to occur inside hollow trunks and branches presumably feeding on beetle larvae in decaying wood (Baehr 2011). These tree-hollow beetles include species of *Melisodera* Westwood and *Moriodemna* Castelnau, which share with *Dendromigadops* the short broad, powerful body with wide pronotum, short, strong legs, large eyes and short broad mandibles. This body-form and features may equip them for this lifestyle. All these taxa are extremely rarely collected possibly indicating how infrequently these putatively arboreal, cavity-living forms come to ground level.

The very large eyes of both species of *Dendromigadops*, in comparison to the eyes of other migadopine species, and the fact that the holotype of *D. alticola* was definitely collected at night, suggest a strictly nocturnal way of life. This again would explain the rarity of the species in collections.

This short review of the described Australian genera and species of Migadopini reveals a surprisingly high level of diversity in body shape and structure, including diversity of shape and structure in both male and female genitalia. Usually, such morphological diversity is noted in old, relict groups which have lost most of their relatives within geological time, so that only a few, markedly diverse genera have survived. It is well known that Migadopini are plesiomorphic in many respects, so that they usually are arranged quite near the roots of the phylogenetic tree of Carabidae. Their high level of diversity, therefore, may corroborate their old age and their relict status.

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and Max Barclay and Beulah Garner, The Natural History Museum, London, for the loan of types and specimens and for their kind assistance during my previous and recent visits at their institutions; and to Roberto Poggi, Museo Civico di Storia Naturale, Genoa, for the kind loan of one of the types of *Nebriosoma fallax* from the Castelnau Collection. To Geoff Monteith I am also indebted for important information about collecting circumstances and presumable habits. To the Deutsche Forschungsgemeinschaft (DFG) I am indebted for supporting the recent visits at ANIC, FTIC, and SAMA by the grant No. BA 856/11-1.

LITERATURE CITED

- Baehr, M., 1995. Revision of *Philipis* (Coleoptera: Carabidae: Bembidiinae), a genus of arboreal tachyine beetles from the rainforests of eastern Australia. Taxonomy, phylogeny, and biogeography. *Memoirs of the Queensland Museum* 38: 315-381.
- 2003a. Australia's subantarctic Tropics - a contradiction? Abstract of a talk held at Forum Herbulot, 2003. *Spixiana* 26: 206.
- 2003b. Psydrine ground beetles (Coleoptera: Carabidae: Psydrinae) excluding Amblytelini, of eastern Queensland rainforests. *Memoirs of the Queensland Museum* 49: 65-109.
2009. A new genus and two new species of the subfamily Migadopinae from Tasmania (Coleoptera: Carabidae). *Folia Heyrovskyana*, ser. A: 17: 95-103.
2011. New species of the Genera *Melisodera* Westwood, *Rhaebolestes* Sloane, and *Moriodemna* Castelnau from Australia (Coleoptera, Carabidae, Psydrini). *Australian Entomologist* 38: 129-144.
- Basset, Y. 1988. A composite interception trap for sampling arthropods in tree canopies. *Journal of the Australian Entomological Society* 27:213-219.
1991. The taxonomic composition of the arthropod fauna associated with an Australian rainforest tree. *Australian Journal of Zoology* 39: 171-190.
- Castelnau, F.L. de 1867. Notes on Australian Coleoptera. *Royal Society of Victoria*. 139 pp
1868. Notes on Australian Coleoptera. *Transactions of the Royal Society of Victoria* 8: 95-225.
- Csiki, E. 1927. Coleopterorum Catalogus. Carabidae: Carabinae II. (92): 317-621. *De Gruyter, Berlin*.
- Erwin, T.L. 1985. The taxon pulse: a general pattern of lineage radiation and extinction among carabid beetles. Pp: 437-472. *In*, Ball, G.E. (ed.):

- Taxonomy, phylogeny, and zoogeography of beetles and ants. *Junk, Dordrecht*.
- Jeannel, R. 1938. Les Migadopides (Coleoptera Adepaga), une lignée subantarctique. *Revue française d'Entomologie* 5: 1-55.
- Johns, P.M. 2010. Migadopini (Coleoptera: Carabidae: Migadopinae) of New Zealand. *Records of the Canterbury Museum* 24: 39-63.
- Larochelle, A. & M.-C. Larivière, 2001. Carabidae (Insecta: Coleoptera): catalogue. *Fauna of New Zealand* 43. Lincoln, Canterbury: 285 pp.
2007. Carabidae (Insecta: Coleoptera): synopsis of supraspecific taxa. *Fauna of New Zealand*. 60. (Lincoln: Canterbury) 188 pp.
- Liebherr, J.K. & K.W. Will, 1998. Inferring phylogenetic relationships within Carabidae (Insecta, Coleoptera) from characters of the female reproductive tract. In, Ball, G.E., A. Casale & A. Vigna Taglianti (eds): Phylogeny and classification of Caraboidea (Coleoptera: Carabidae). *Atti di Museo Regionale di Scienze Naturali Torino* 5: 107-170.
- Lorenz, W., 1998. *Systematic List of extant Ground Beetles of the World (Insecta Coleoptera 'Geadephaga': Trachypachidae and Carabidae incl. Paussinae, Cicindelinae, Rhysodidae)*. Tutzing, printed by the author. 502 pp.
2005. *Systematic List of extant Ground Beetles of the World (Insecta Coleoptera 'Geadephaga': Trachypachidae and Carabidae incl. Paussinae, Cicindelinae, Rhysodidae)*. (2 ed) Tutzing: printed by the author. 530 pp.
- Moore, B.P., T.A. Weir & J.E. Pyke, 1987. Rhysodidae and Carabidae. In, *Zoological Catalogue of Australia*. 4: 17-320. (Australian Government Publication Service: Canberra).
- Roig-Juñent, S., 2004 South American Migadopini (Coleoptera: Carabidae): description of male and female genitalia and phylogenetic and biogeographic considerations. *Acta entomológica chilena*. 28: 7-29.
- Sloane, T. G. 1905. Revisional notes on Australian Carabidae. Part I. Tribes Carabini, Pamborini, Pseudomorphini, Clivinini, and the genus *Nebriosoma*. *Proceedings of the Linnean Society of New South Wales*. 29: 699-733.
1910. Studies in Australian entomology, No. xvi. New species of Carabidae. *Proceedings of the Linnean Society of New South Wales*. 35: 378-406.
1915. Studies in Australian entomology, No. xvii. New Genera and Species of Carabidae. (Pamborini, Migadopini, Briscini, Cuneipectini, Nomiini, Pterostichini, Platynini, Oodini, Harpalini, and Lebiini). *Proceedings of the Linnean Society of New South Wales*. 40: 438-473.
1920. The Carabidae of Tasmania. *Proceedings of the Linnean Society of New South Wales*. 45: 113-178.

A second species of *Tristichopterus* (Sarcopterygii: Tristichopteridae), from the Upper Devonian of the Baltic Region

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ABSTRACT

A review of the osteology of the tristichopterid sarcopterygian *Eusthenopteron kurshi* Zupinš, 2008, from the Lower Frasnian of Latvia, indicates that it should be placed in the genus *Tristichopterus*, and a new combination *Tristichopterus kurshi* Zupinš is proposed. The features that support this include: the number of coronoid fangs, proportions of the coronoids and the skull roof, and the relatively small epichordal lobe of the caudal fin. Recognition of a second species of *Tristichopterus* extends the stratigraphic range of the genus to the Upper Devonian, and its geographic range to the Baltic Region in northern Europe. □ *Eusthenopteron*, *Tristichopterus*, *Tristichopteridae*, *Devonian*.

Following excavation of well preserved sarcopterygian material from the Lower Frasnian, Lode clay quarry (Lode Formation) in Latvia; Zupinš (2008) erected the taxon *Eusthenopteron kurshi* on the basis of a complete individual and 12 partial remains. The species was interpreted to be the most primitive within the genus *Eusthenopteron*, on the basis of its more asymmetric caudal fin, and remarkably low parietal to postparietal shield length ratio: 1.57, compared to 1.7–1.85 in *E. foordi* Whiteaves, 1881, 1.85 in *E. traquairi* Westoll, 1937, and 1.95 in *E. savesoderbergi* Jarvik, 1937 (Jarvik 1950). A revision of the original description of the material, however, suggests that the material assigned to *E. kurshi* does not belong to *Eusthenopteron*, but to the genus *Tristichopterus*. Here I review the features that support referral of this species to *Tristichopterus*.

OBSERVATIONS

Several features of the material assigned to *Eusthenopteron kurshi* by Zupinš (2008) clearly suggest affinities to *Tristichopterus*, and also distinguish it from other species of *Eusthenopteron*. These are:

1. The posterior coronoid possesses a single pair of fangs. The only genus of tristichopterid that possesses a single pair of fangs on the posterior coronoid is *Tristichopterus* (Snitting 2008a).
2. In *Eusthenopteron* (and more derived tristichopterids), the posterior coronoid is around twice the length of the other two coronoids, whereas in *Tristichopterus* it is only approximately 35–40% longer (Snitting 2008a, b). In *E. kurshi*, the posterior coronoid is about half as long again as the anterior and middle coronoids (Zupinš 2008).
3. The available material of *E. kurshi* suggests a maximum length of 55 cm (Zupinš 2008). This small size corresponds better to a maximum length of 40 cm for *Tristichopterus* (Ahlberg & Johanson 1997). *Eusthenopteron* typically measures more than 60 cm long, sometimes more than 100 cm, and one specimen, W.661, figured by Andrews & Westoll (1970), is estimated to have measured about 1.5 m long.
4. The proportion of the epichordal lobe to the total height of the caudal fin in *Tristichopterus* is one quarter to one third

(Egerton 1861; Jarvik 1937), whereas in *Eusthenopteron* it is three sevenths (Jarvik 1937) (Fig. 1). In the holotype of *E. kurshi*, the epichordal lobe is comparable to that of *Tristichopterus alatus* Egerton, 1864 in terms of its proportions. Caution must be used when interpreting this feature, however, because taphonomic distortion can cause fin lepidotrichia to spread out to different degrees (Zupinš 2008).

5. The parietal to postparietal shield length ratio in *E. kurshi* is 1.57. This is closer to the shield length ratio in *T. alatus* which

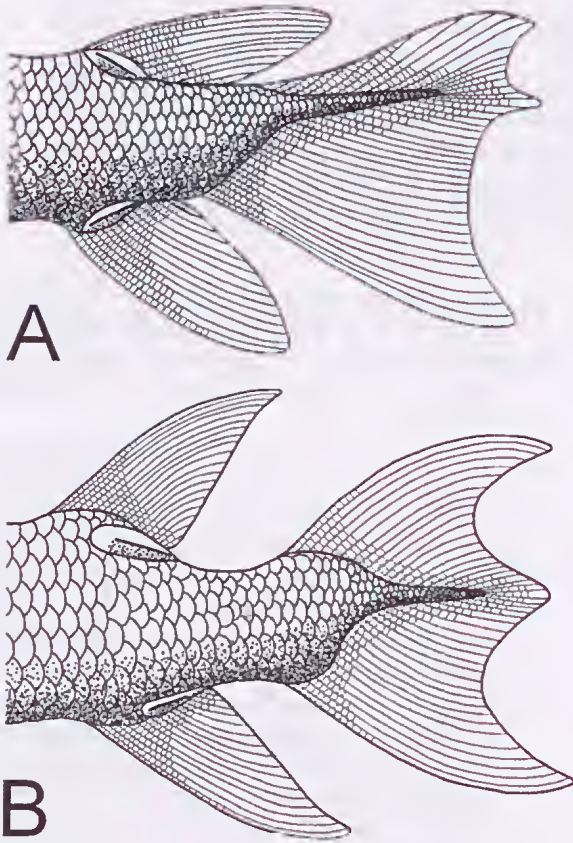


FIG. 1. Reconstructions of the morphology of the caudal region in left lateral view. A, morphology of *Tristichopterus*, characterised principally by a strongly heterocercal caudal fin; after Egerton (1861). B, morphology of *Eusthenopteron*, characterised principally by a near-homocercal caudal fin; after Jarvik (1980). Reconstructions not to scale.

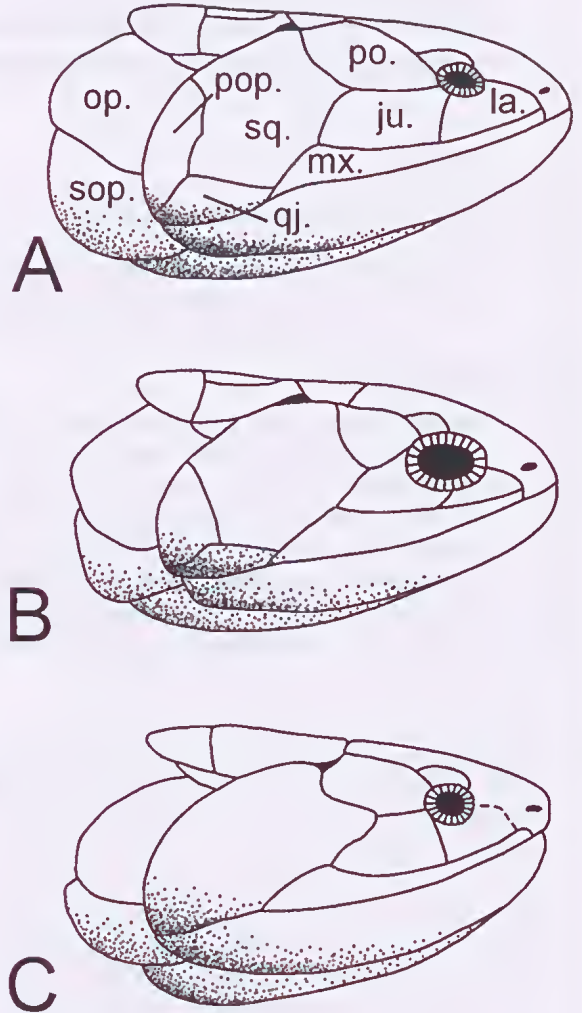


FIG. 2. Reconstructions of the skull, lower jaws and operculogular series in right lateral view. A, *Eusthenopteron foordi*, after Jarvik (1944). B, *Tristichopterus alatus*, mostly after Traquair (1875). C, *Tristichopterus kurshi*, based on the holotype, after Zupinš (2008); sutures of posterior cheek plate, parietal shield and postparietal shield unknown. Reconstructions not to scale. Abbreviations: ju., jugal; la., lacrimal; mx., maxilla; op., opercular; po., postorbital; pop., preopercular; qj., quadratojugal; sop., subopercular; sq., squamosal.

is 1.4–1.49 (Jarvik 1937; Westoll 1937); in *Eusthenopteron*, it is 1.7–1.95 (Jarvik 1950).

6. The pineal foramen of *Eusthenopteron foordi*, and probably also *E. savesoderbergii*, is approximately level with the posterior margin of the orbits (Jarvik 1937, 1944). In both *E. kurshi* and *Tristichopterus* however, it is positioned behind the posterior margin of the orbits, by at least ten percent of the length of the parietal shield (Snitting 2008a; Zupinš 2008).
7. In *E. foordi*, the opercular is of about the same height as the subopercular (Jarvik 1944), whereas in *Tristichopterus*, the former bone is around 1.5 times as high as the latter (Traquair 1875). In *E. kurshi*, the opercular is around twice as high as the subopercular (Zupinš 2008; Fig. 2).

Notwithstanding the many similarities to *Tristichopterus* and differences to *Eusthenopteron*, *E. kurshi* does show affinities with the latter genus. As in *E. foordi*, the orbits of *E. kurshi* are relatively small compared to the size of the head, in contrast to *Tristichopterus* where the orbits are large, relative to the size of the head (Traquair 1875; Jarvik 1944). The shapes of the postorbital and jugal in *E. kurshi* are different to those bones in *Tristichopterus*, but quite similar to those of *E. foordi* (Fig. 2; Traquair 1875; Jarvik 1944). Interestingly, the dorsal, pelvic and anal fins of *E. kurshi* are positioned more posteriorly than those of both *Tristichopterus* and *Eusthenopteron*, particularly the anterior dorsal and pelvic fins (Zupinš 2008), and in this regard it is distinguished from both genera.

On the basis of the above observations, *E. kurshi* is better placed in *Tristichopterus* than in *Eusthenopteron*. *Eusthenopteron kurshi* differs from the type species, *T. alatus*, in adult size, relative orbit size, cheek bone shape, fin positioning and vomer morphology (Snitting 2008a; Zupinš 2008) and a new combination *Tristichopterus kurshi* (Zupinš, 2008) is thus proposed.

SYSTEMATIC PALAEOLOGY

Class Sarcopterygii Romer, 1955

Order Osteolepiformes Berg, 1937

Family Tristichopteridae Cope, 1889

Genus *Tristichopterus* Egerton, 1861

Type species. *Tristichopterus alatus* Egerton, 1861.

Emended generic diagnosis. Small cosmine-free tetrapodomorph. Caudal fin heterocercal, trifurcate, epichordal lobe one quarter to one third the total height of the fin. Extratemporal bone posteriorly displaced, in 'postspiracular' position. Pineal foramen slightly posterior to posterior margin of orbit. Opercular greater in height (by at least fifty percent) than subopercular. One fang pair present on ectopterygoid and posterior coronoid. Posterior coronoid slightly (35–50%) longer than anterior and middle coronoids. Parasymphyseal dental plate small and drop-shaped, failing to contact anterior coronoid. Vomer possesses long posterior process, suturing with much of lateral edge of parasphenoid. Ethmosphenoid and otico-occipital of equal length. Crista parotica extended posteriorly; posterior margin of floor of fossa bridgei transverse, forming distinct posterolateral corner to otico-occipital.

Remarks. Since the discovery and original description of *E. foordi* (Whiteaves 1881), the great similarity between *Eusthenopteron* and *Tristichopterus* has been well recognised; indeed, the two are considered the most basal tristichopterid genera known (Clément *et al.* 2009). Doubt has previously surrounded the validity of the genus *Eusthenopteron* and whether it should be synonymised with the earlier named *Tristichopterus*, with several attempts to distinguish the two genera having been made (e.g. Traquair 1890; Jarvik 1937; Zupinš 2008). Only recently has the matter been satisfactorily resolved, in favour of their separation (Snitting 2008a). *Eusthenopteron* can be distinguished from *Tristichopterus inter alia* by the possession of two fang pairs on the ectopterygoid and posterior coronoid, a very long posterior coronoid (around twice as long as the anterior and middle coronoids), an ethmosphenoid which is longer than the otico-occipital and a more symmetric caudal fin. *Eusthenopteron* is also a distinctly larger fish than *Tristichopterus*; species of the former are typically longer than 60 cm (and often reach

considerably more, in excess of 1 m), whilst *Tristichopterus* is the smallest member of the Tristichopteridae, measuring less than 60 cm, and generally much less.

Tristichopterus kurshi (Zupiņš, 2008)
comb. nov.

Eusthenopteron kurshi Zupiņš, 2008: p. 40–46, figs 1–5.

Holotype. LDM G 291/23, complete skeleton, squamation and fins, as well as counterpart of posterior part of body. Lower Frasnian Lode Formation, Lode clay quarry, Latvia. LDM G denotes the Geology Collections, Natural History Museum of Latvia, Riga.

Material. Material of Zupiņš (2008).

Emended specific diagnosis. Tristichopterid of small size. Orbits relatively small compared to size of head. Vomers fused medially, their anteromedial corners extend anteriorly so as to form slightly convex anterior margin of vomer pair. Parietal shield approximately 1.6 times as long as postparietal shield. Dorsal margin of postorbital more or less straight, jugal-postorbital suture straight. Jugal forms near right angle around its contribution to orbit margin, formed from jugal-postorbital and jugal-lacrimal sutures; jugal contribution to orbit margin minimal. Squamosal extends significantly anterior to joint between parietal and postparietal shields. Opercular twice as high as subopercular. Dorsal, pelvic and anal fins positioned well posterior on body. Caudal fin heterocercal, epichordal lobe one third of total height of fin.

Remarks. Previously *Tristichopterus* was known only from the Middle Givetian of Scotland (Marshall *et al.* 2010). *Tristichopterus kurshi* now extends the stratigraphic range of the genus into the Lower Frasnian (but see Forey *et al.* 2000, who assigned a Late Givetian age to the Lode Formation), and also extends its geographic range to Latvia in northern Europe.

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LITERATURE CITED

- Ahlberg, P.E. & Johanson, Z. 1997. Second tristichopterid (Sarcopterygii, Osteolepiformes) from the Upper Devonian of Canowindra, New South Wales, Australia, and phylogeny of the Tristichopteridae. *Journal of Vertebrate Paleontology* 17(4): 653–673.
- Andrews, S.M. & Westoll, T.S. 1970. The postcranial skeleton of *Eusthenopteron foordi* Whiteaves. *Transactions of the Royal Society of Edinburgh* 68(9): 207–329.
- Berg, L.S. 1937. A classification of fish-like vertebrates. *Bulletin of the Academy of Sciences of USSR, Class of Mathematics and Natural Sciences, Biological Series* 1937: 1237–1277. [In English and Russian].
- Clément, G., Snitting, D. & Ahlberg, P.E. 2009. A new tristichopterid (Sarcopterygii, Tetrapodomorpha) from the Upper Famennian Evieux Formation (Upper Devonian) of Belgium. *Palaeontology* 52(4): 823–836.
- Cope, E.D. 1889. Synopsis of the families of Vertebrata. *American Naturalist* 23: 849–877.
- Egerton, P.deM.G. 1861. *Tristichopterus alatus*. Figures and Descriptions Illustrative of British Organic Remains. *Memoirs of the Geological Survey of the United Kingdom*. Tenth Decade. 51–55.
- Forey, P.L., Ahlberg, P.E., Lukševičs, E. & Zupiņš, I. 2000. A new coelacanth from the Middle Devonian of Latvia. *Journal of Vertebrate Paleontology* 20(2): 243–252.
- Jarvik, E. 1937. On the species of *Eusthenopteron* found in Russia and the Baltic States. *Bulletin of the Geological Institution of Uppsala* 27: 64–127.
1944. On the dermal bones, sensory canals and pit-lines of the skull in *Eusthenopteron foordi* Whiteaves, with some remarks on *E. säve-söderberghi* Jarvik. *Kunglia Svenska Vetenskapsakademiens Handlingar, 3rd Series* 21(3): 1–48.
1950. On some osteolepiform crossopterygians from the Upper Old Red Sandstone of Scotland. *Kunglia Svenska Vetenskapsakademiens Handlingar, 4th Series* 2(2): 1–35.
1980. *Basic Structure and Evolution of the Vertebrates, Volume 1*. (Academic Press: London).
- Johanson, Z. & Ahlberg, P.E. 1997. A new tristichopterid (Osteolepiformes: Sarcopterygii) from the Mandagery Sandstone (Late Devonian, Famennian) near Canowindra, NSW, Australia. *Transactions of the Royal Society of Edinburgh: Earth Sciences* 88(1): 39–68.
- Marshall, J.E.A., Brown, J.F. & Astin, T.R. 2010. Recognising the Taghanic Crisis in the Devonian terrestrial environment and its implications for understanding land-sea interactions. *Palaeogeography, Palaeoclimatology, Palaeoecology* 304(1/2): 165–183.

Tristichopterus kurshi

- Romer, A.S. 1955. Herpetichthyes, Amphibioidei, Choanichthyes or Sarcopterygii? *Nature* **176**: 126.
- Snitting, D. 2008a. *Morphology, Taxonomy and Interrelationships of Tristichopterid Fishes (Sarcopterygii, Tetrapodomorpha)*. PhD Thesis, Uppsala University: Uppsala.
- 2008b. A redescription of the anatomy of the Late Devonian *Spodichthys buetleri* Jarvik, 1985 (Sarcopterygii, Tetrapodomorpha) from East Greenland. *Journal of Vertebrate Paleontology* **28**(3): 637–655.
- Traquair, R.H. 1875. On the structure and affinities of *Tristichopterus alatus* Egerton. *Transactions of the Royal Society of Edinburgh* **27**: 383–396.
1890. Note on the Devonian Fishes of Scaumenac Bay and Cambelltown in Canada. *Geological Magazine (Decade III)* **7**(1): 15–22.
- Westoll, T.S. 1937. On a specimen of *Eusthenopteron* from the Old Red Sandstone of Scotland. *Geological Magazine* **74**(11): 507–524.
- Whiteaves, J.F. 1881. On some remarkable fossil fishes from the Devonian rocks of Scaumenac Bay, Province of Quebec, with descriptions of a new genus and three new species. *Canadian Naturalist* **10**: 27–35.
- Zupiņš, I. 2008. A new tristichopterid (Pisces, Sarcopterygii) from the Devonian of Latvia. *Proceedings of the Latvian Academy of Sciences, Section B* **62**(1/2): 40–46.

FANG HISTOLOGY OF THE LATE DEVONIAN TRISTICHOPTERID *HYNERIA LINDAE* THOMSON, 1968

Memoirs of the Queensland Museum – Nature 56(2): 311–311. 2013:– Tooth and fang histology in many Palaeozoic amphibians is characterised by infolding of pleats of orthodontine (plicidentine), giving the tooth or fang a labyrinthodont structure (Schultze 1969, 1970; Warren & Davey 1992; Warren & Turner 2005). Folded orthodontine also occurs in some sarcopterygian fish, including osteolepiforms, porolepiforms, and rhizodonts (Schultze 1969, 1970; Ahlberg & Johanson 1998; Warren & Turner 2005). The tooth and fang histology of many members of the Tristichopteridae Cope, 1889, a Middle to Late Devonian osteolepiform clade, has been studied previously (e.g. Vorobyeva 1959, 1962, 1977; Schultze 1969; Lelièvre & Janvier 1986; Clément 2002). Currently, two distinct folding morphologies are recognised in tristichopterids, the simpler polyplocodont type, and the more complex eusthenodont type, the latter characterised by more extensive orthodontine infolding and a pulp cavity filled with osteodentine (Schultze 1969, 1970).

The large, derived tristichopterid *Hyneria lindae* Thomson, 1968 was first described on the basis of limited material from the Upper Devonian (Famennian) Catskill Formation of Pennsylvania, United States of America, from a site now known as ‘Red Hill’. Renewed excavations at the site since 1993 have yielded additional material of this taxon, which is yet to be described (Daeschler & Shubin 2007). This note describes the histology observed in a fang of *H. lindae*. Fangs are distinguished from teeth in their large size relative to adjacent teeth (Bolt & Lombard 2001), and also in their unique pattern of development and replacement: they occur in distinct pairs, with eruption and replacement occurring in an alternating pattern (Fox *et al.* 1995; Snitting 2008; Clément *et al.* 2009).

Material and Methods. A near complete (missing only the tip) fang of *H. lindae*, measuring 35 mm long with a maximum basal diameter of 15 mm, was provided to me by Dr E. B. Daeschler for examination. The isolated fang is laterally compressed, carinated both anteriorly and posteriorly, curved posteromesially and probably came from the dermopalatine or ectopterygoid (E.B. Daeschler, pers. comm. 2011). The orthodontine is well preserved in part of the fang, but has undergone significant alteration in other parts. In the poorly preserved parts the orthodontine folds have turned dark brown or been obliterated completely, leaving a crumbly brown residue which renders the fang too fragile for thin sectioning. To permit sectioning the fang was embedded in resin (Renlam 100), and two polished sections one 8 mm from the base, the other 14 mm from the base were made. The specimen, QMF 56172, is now housed in the Geosciences Collection of the Queensland Museum.

Description. Orthodontine folds are most clearly observed near the base of the fang (Fig. 1). Orthodontine is very intensely folded into both first- and second-order folds (*sensu* Vorobyeva 1962). The total number of first-order folds in the specimen cannot be exactly determined (but is estimated to be approximately 30 at the base). The number of second-order folds per first-order fold could not be determined. Folded orthodontine extends about 3 mm in toward the centre of the fang; the remaining central region consists of osteodentine, with small vascular canals still visible despite the alteration (Fig. 1A). Dentine tubules are not visible, due to the specimen being a polished section examinable only under reflected light.

Orthodontine folding is extremely tight, with individual second-order folds pressed against each other such that there is little or no room for osteodentine or bone in between. This produces a ‘branched zig zag’ geometry in individual folds (Warren & Turner 2005). The overall histology of the orthodontine thus presents itself as a very regular ‘hexagonal’ pattern, resulting from the tightly compressed second-order folds (Fig. 1B).

Comparison to other Taxa. *Hyneria lindae* displays a peculiar and unique fang histology which combines features observed in a number of different sarcopterygian groups. The pulp cavity is filled with osteodentine, a eusthenodont characteristic observed in the tristichopterids *Eusthenodon* (Schultze 1969), *Langlieria* (Clément 2002; Clément *et al.* 2009), *Platycephalichthys* and *Jarvikinia* (Vorobyeva 1959, 1962, 1977), as well as the osteolepiform *Litoptychus* (Schultze 1969). However, the hexagonal folding pattern of orthodontine in *H. lindae* is far more regular and complex than in any known tristichopterid (cf. Vorobyeva 1959, 1962, 1977; Schultze 1969; Clément 2002); the fang histology in the genera *Mandageria* and *Cabonnichthys* cannot be described from the existing material (P.E. Ahlberg, pers. comm. 2011).

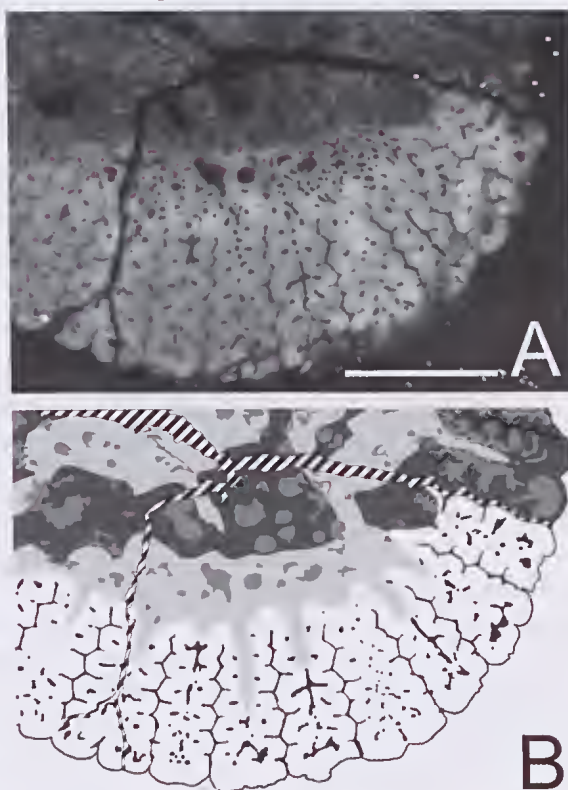


FIG. 1. Histology of *Hyneria lindae* fang, showing the distinctive ‘hexagonal’ orthodontine folding pattern. A, microphotograph of 8 mm parabal section of QMF 56172; scale bar is 3 mm. B, interpretive drawing of the section in A. In B, white represents more or less unaltered orthodontine, black represents natural spaces between orthodontine folds, dark grey represents areas of significant alteration, medium grey represents dissolution cavities formed possibly through diagenesis, light grey indicates more or less unaltered osteodentine and diagonal hatching represents fractures.

It is more similar to the dendrodont pattern observed in porolepiforms (Schultze 1969, 1970; Holland 2010) and in some temnospondyls (Schultze 1969; Warren & Davey 1992), although in all of these forms it is less regular and complex than observed in *H. lindae*. Additionally, there does not appear to be any bone of attachment extending between the folds in *H. lindae*, at least as can be determined from the section near the base, which is also a dendrodont characteristic (Schultze 1969, 1970). This combination of characters prevents *H. lindae* being assigned to a distinct type of fang histology, although it is most similar to the dendrodont pattern. It is clear, however, that it is not of the polyplocodont type, which within the Tristichopteridae is considered to be restricted to more primitive members, namely *Eusthenopteron*, *Tristichopterus* (Schultze 1969, 1970) and *Notorhizodon* (Young *et al.* 1992), as well as an incomplete specimen from Morocco (Lelièvre & Janvier 1986).

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Literature Cited

- Ahlberg, P.E. & Johanson, Z. 1998. Osteolepiformes and the ancestry of tetrapods. *Nature* 395: 792–794.
- Bolt, J.R. & Lombard, R.E. 2001. The mandible of the primitive tetrapod *Greerpeton*, and the early evolution of the tetrapod lower jaw. *Journal of Paleontology* 75(5): 1016–1042.
- Clément, G. 2002. Large Tristichopteridae (Sarcopterygii, Tetrapodomorpha) from the Late Famennian Evieux Formation of Belgium. *Palaeontology* 45(3): 577–593.
- Clément, G., Snitting, D. & Ahlberg, P.E. 2009. A new tristichopterid (Sarcopterygii, Tetrapodomorpha) from the Upper Famennian Evieux Formation (Upper Devonian) of Belgium. *Palaeontology* 52(4): 823–836.
- Cope, E.D. 1889. Synopsis of the families of Vertebrata. *American Naturalist* 23: 849–877.
- Daeschler, E.B. & Shubin, N.H. 2007. New data on *Hyeria lindae* (Sarcopterygii; Tristichopteridae) from the Late Devonian of Pennsylvania, USA. P. 65A. Abstracts of Papers from the 67th Annual Meeting of the Society of Vertebrate Paleontology, Austin, 17–20 October, 2007.
- Fox, R.C., Campbell, K.S.W., Barwick, R.E. & Long, J.A. 1995. A new osteolepiform fish from the Lower Carboniferous Raymond Formation, Drummond Basin, Queensland. *Memoirs of the Queensland Museum* 38(1): 97–221.
- Holland, T. 2010. Upper Devonian osteichthyan remains from the Genoa River, Victoria, Australia. *Memoirs of Museum Victoria* 67: 35–44.
- Lelièvre, H. & Janvier, P. 1986. L'Eusthénopteridae (Osteichthys, Sarcopterygii) du Famennien (Dévonien supérieur) du Tafilalet (Maroc): nouvelle description. *Bulletin du Muséum National d'Histoire Naturelle, Paris, Section C, Série 4* 8(3): 351–365. [In French].
- Schultze, H.-P. 1969. Die faltenzähne der rhipidistien crossopterygier der tetrapoden und die actinopterygier gattung *Lepisosteus*; nebst einer beschreibung der zahnstruktur von *Onychodus* (struniiformer crossopterygier). *Palaeontographica Italica, Neue Series* 35: 63–136.
1970. Folded teeth and the monophyletic origin of Tetrapoda. *American Museum Novitates* 2408: 1–10.
- Snitting, D. 2008. A redescription of the anatomy of the Late Devonian *Spodichthys buetleri* Jarvik, 1985 (Sarcopterygii, Tetrapodomorpha) from East Greenland. *Journal of Vertebrate Paleontology* 28(3): 637–655.
- Thomson, K.S. 1968. A new Devonian fish (Crossopterygii: Rhipidistia) considered in relation to the origin of the Amphibia. *Postilla* 124: 1–13.
- Vorobyeva, E.I. 1959. A new genus of crossopterygian fish *Platycephalichthys* from the Upper Devonian of the River Lovat'. *Paleontologicheskii Zhurnal* 3: 95–106. [In Russian].
1962. Rhizodontid crossopterygian fishes from the Devonian rocks of USSR. *Trudy Paleontologicheskogo Instituta, Academia Nauk SSSR* 44: 1–139. [In Russian].
1977. Morphology and peculiarities of evolution of crossopterygian fish. *Trudy Paleontologicheskogo Instituta, Academia Nauk SSSR* 163: 1–239. [In Russian].
- Warren, A.A. & Turner, S. 2005. Tooth histology patterns in early tetrapods and the presence of 'dark dentine'. *Transactions of the Royal Society of Edinburgh: Earth Sciences* 96(2): 113–130.
- Warren, A.A. & Davey, L. 1992. Folded teeth in temnospondyls – a preliminary study. *Alcheringa* 16(2): 107–132.
- Young, G.C., Long, J.A. & Ritchie, A. 1992. Crossopterygian fishes from the Devonian of Antarctica: systematics, relationships and biogeographic significance. *Records of the Australian Museum, Supplement* 14: 1–77.
- Peter J. Bishop Queensland Museum, Ancient Environments Program, 122 Gerler Rd, Hendra, Qld 4011, Australia. Accepted: 12 November 2012.

Arboreality, excavation, and active foraging: novel observations of radiotracked woma pythons *Aspidites ramsayi*

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ABSTRACT

Novel wild behaviours were observed during a 21 month intensive radiotracking study of the woma python *Aspidites ramsayi* (Macleay, 1882) in south-western Queensland, Australia. Arboreal behaviour was unexpected in this terrestrial and burrow-dwelling species, with no previous anecdotal or published reports. Arboreal activity occurred strictly at night during warm weather and was associated with sleeping reptile predation, particularly predation upon bearded dragons *Pogona barbata* (Cuvier, 1829). Excavation behaviour in wild womas was predicted from captive specimens in 1981, but has not been reported to date. Two observations of radiotracked womas excavating in alluvial clay soils are detailed with comments on the function of this behaviour. Finally, brief descriptions and a summary of all thirteen feeding observations are given. Bearded dragons *P. barbata*, sand goannas *Varanus gouldii* (Gray, 1838) and yakka skinks *Egernia rugosa* (De Vis, 1888) were the most commonly observed prey items; however predation and ingestion of one large mammal - an adult hare *Lepus capensis* (Linnaeus, 1758) - was also observed. Pre- and post-feeding movements indicate an active foraging strategy predominates; however ambush behaviour was also observed. Here I outline and summarise these novel wild behavioural observations and discuss them in the context of known snake ecology and physiology. These observations greatly enhance the behavioural and ecological understanding of this large, yet elusive python. □ *Reptile, feeding, snake, radio-tracking, arid, temperature, caudal luring*

Aspidites ramsayi is a large (up to 2.5 m SVL) and rarely observed python found throughout arid and semi-arid central Australia (Wilson & Swan 2010). Sightings of this widely distributed species are rare due to a combination of sparse human population (Tobler, Deichmann *et al.* 1995; Australian Government 2006; Wilson & Swan 2010), fossorial and nocturnal habits (Bruton, unpub. data), and excellent camouflage (pers. obs.). Consequently the few published observations of wild woma behaviour are anecdotal and most pertain to sightings of disturbed pythons (e.g. Pearson 1993; Covacevich & Couper 1996; Maryan 2002; Borsboom 2008).

Despite a paucity of wild *A. ramsayi* behavioural observations, indigenous knowledge (Pearson 1993), information from research programs (Read 2010; Bruton, unpub. data; Dave Pearson pers. comm.) and observations of captive specimens (Richard Jackson pers. comm.) all indicate that the woma is a terrestrial/fossorial species that shelters predominately in underground burrows and occasionally moves overland between shelter sites. It is generally accepted that *A. ramsayi* is a terrestrial species with no previous reports or indications of arboreal behaviour, either in the wild or in captivity.

Aspidites ramsayi shelter in pre-excavated burrows created by varanids, rabbits *Oryctolagus cuniculus* (Linnaeus, 1758), hopping mice *Notomys alexis* (Thomas 1922), bilbies *Macrotis lagotis* (Reid 1837), and natural tunnel erosion (Covacevich & Couper 1996; Cogger 2000; Read 2010; Wilson & Swan 2010) in both sandy and clay soils. In captivity, womas have been observed using the head as a scoop to dig in sandy substrates (Fyfe & Harvey 1981; Richard Jackson pers. comm.), indicating they may be capable of burrow excavation in sandy areas. Womas are generally associated with sandy areas (Fyfe & Harvey 1981; Smith 1981; Pearson 1993; Maryan 2002; Read 2010) and in captivity they are rarely provided with finer clay substrates found in the east of their range. Although excavation behaviour has not been reported in the wild, Fyfe and Harvey (1981) predicted that ‘...this technique would be used to enlarge existing burrows for shelter or while hunting’.

Analysis of woma python stomach contents throughout Australia identified mammal and reptile prey items in approximately equal proportions (Slip & Shine 1990; Shine 1999). Specific reptile prey items include ring-tailed dragons *Ctenophorus caudicinctus* (Gunther 1875), dwarf bearded dragons *Pogona minor* (Sternfeld 1999), other agamids, gekkonids, blue tongue lizards *Tiliqua scincoides* (White 1790), other scincids, *V. gouldii*, other varanids, and ‘snakes’, whilst reported mammalian prey include rabbits *O. cuniculus*, hares *L. capensis*, bandicoots *Isodon spp.*, rats *Rattus spp.*, mice *Mus domesticus* (Rutty 1772), and other murids (Slip & Shine 1990; Covacevich & Couper 1996; Read 2010). The wide variety of both reptilian and mammalian prey items suggests a generalist diet but gives no indication of the hunting and prey capture strategies that wild womas employ.

In captivity, womas generally use typical boid coiling constriction when feeding (Fyfe & Harvey 1981; pers. obs.), indicative of a predominately ambush feeding strategy. However Fyfe and Harvey (1981) also describe a second ‘most unusual’ method in which womas do not utilise the mouth in a strike but instead squash prey against the side of the vivarium

with the body. Similar squashing behaviour has also been observed in a captive woma population held at Australia Zoo (Richard Jackson pers. comm.). This ‘squashing’ method is likely to be effective in the confined spaces of the burrows *A. ramsayi* inhabit (Fyfe & Harvey 1981) and could be used in either active foraging or ambush prey capture situations. Another feeding strategy reported in captive womas is caudal (tail) luring (Fyfe & Harvey 1981); again indicative of an ambush hunting strategy. Whilst these captive behaviours give insight into potential hunting strategies, there are no known reports or descriptions of wild *A. ramsayi* foraging and food capture behaviours and it was not previously known if *A. ramsayi* is ambush predator or an active forager.

Here I report the first known observations of arboreal behaviour, wild burrow excavation, and wild prey capture and feeding behaviours in a population of eastern woodland inhabiting womas, and discuss these behaviours in the context of snake ecology and physiology.

METHODS

Twelve adult (5F:7M) eastern ‘Brigalow’ womas were radiotracked on a conservation reserve near the town of St George in southern Queensland. The location is sub-tropical semi-arid (rainfall \approx 540 mm/year) with summer rain and generally dry winters. During this study, the mean ambient temperatures at the field site ranged from 1.7 - 18.6°C (July) to 18.8 - 30.8°C (January). Historic wool and beef production has resulted in a mosaic of remnant, cleared and regrowth woodland areas at the study site. Geology consists of low sedimentary rock ridges dominated by *Acacia catenulata* and *Acacia aneura* woodlands that slope down to clay alluvial soils dominated by open *Eucalyptus populnea* woodlands.

Each woma python was radiotracked for approximately one year (mean = 331 days, range = 199 - 480 days) from Oct 2010 - Jun 2012. The womas were radiotracked on foot approximately every 55 hrs (2 days + 7 hrs) during the summer active seasons and approximately every 79 hrs during the winter

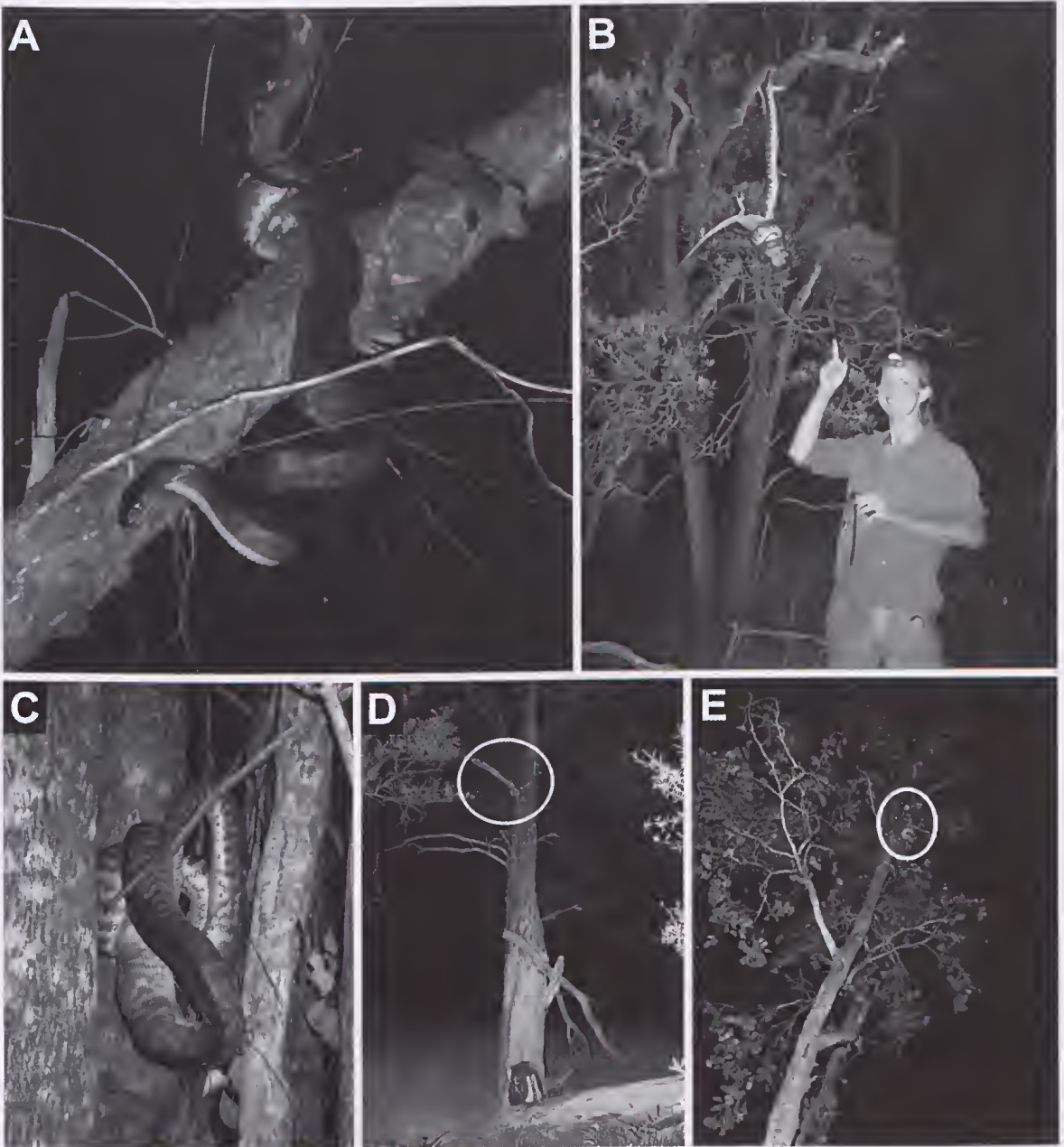


FIG. 1. Novel arboreal woma python *Aspidites ramsayi* behaviours: A, An adult male python pauses 5 m high in a poplar box *Eucalyptus populnea* tree. Coiling of the caudal section of the body indicates recent prey stalking/ingestion behaviour; B, An adult male python coils a bearded dragon *Pogona barbata* in a false sandalwood *Eremophila mitchelli* tree, the first observed arboreal behaviour; C, An adult male python hangs precariously 1.5 m high on a thin twig wedged between regrowth *E. populnea* trunks; D, A small female adult python 4 m high in a mulga *Acacia aneura* tree, hunting a sleeping *P. barbata* (not in frame); E, A small male adult python hangs from a branch 10 m high in a thin regrowth *E. populnea* tree whilst consuming an adult *P. barbata* captured in his coils.

TABLE 1: Summary of novel arboreal behaviours observed during a 21 month radiotracking program of twelve adult woma pythons *Aspidites ramsayi* in semi-arid Queensland, Australia.

*Radiotracking commencement date in parentheses. M = Male, F = Female

^Size at transmitter implantation (snout-vent length and mass)

#Height of python, height of prey (on arrival)

% Previous day maximum temperature and afternoon cloud cover

Python Id*	Size^	Date & Time	Observed Activity	Ht (M)#	Tree Species	T _b (°C)	T _a (°C)	Daily Max% (°C)	Notes
HU - M (27-10-11)	1.6 m 1.48 kg	28-10-11 23:12	Stalked, captured and ate a sleeping <i>P. barbata</i>	3, 3	<i>E. mitchelli</i>	24	24	29.3 patchy	Full cloud, 65% humidity, high winds
DC - M (15-3-11)	1.45 m 1.48 kg	14-11-11 03:11	Stationary, facing down trunk of tree	5, NA	<i>E. populnea</i>	24.5	23	33.5 patchy	No cloud, 55% humidity, light wind
DC - M (15-3-11)	1.45 m 1.48 kg	20-11-11 22:58	Stalked a sleeping sub-adult <i>P. barbata</i>	2, 1.8	<i>E. mitchelli</i>	25.5	24.5	35.7 clear	No cloud, 60% humidity, light wind
EL - F (27-4-11)	1.25 m 1.06 kg	22-11-11 23:05	Stalked a small adult <i>V. gouldii</i>	2, 4	<i>E. populnea</i> - dead	29	26.5	33.9 patchy	Min. cloud, 60% humidity, mod. winds
EL - F (27-4-11)	1.25 m 1.06 kg	6-1-12 21:34	Stalked a sleeping adult <i>P. barbata</i>	5, 4	<i>A. aneura</i>	30.5	27	35.4 clear	No cloud, 60% humidity, no wind
KT - F (4-1-11)	1.85 m 3.05 kg	6-1-12 23:36	Moved swiftly down trunk; head almost on ground on arrival	1, NA	<i>E. mitchelli</i>	26	24.5	35.4 clear	No cloud, 70% humidity, no wind
RM - M (23-5-11)	1.55 m 1.75 kg	11-2-12 2:11	Stalked, caught and ate a sleeping adult <i>P. barbata</i>	1.5, 1.5	<i>E. populnea</i>	20.5	19	32.9 clear	No cloud, 85% humidity, no wind
MX - M (20-3-11)	1.70 m 2.3 kg	20-2-12 3:52	Stalked, caught and ate a sleeping adult <i>P. barbata</i>	2, 3.5	<i>A. aneura</i>	23.5	23.2	36.8 clear	Minimum cloud, 70% humidity, no wind
KT - F (4-1-11)	1.85 m 3.05 kg	5-3-12 21:43	Stalked a sleeping adult <i>P. barbata</i>	3, 2	<i>A. aneura</i>	28	25.2	34.3 cloudy	Moderate cloud, 60% humidity, light wind
RM - M (23-5-11)	1.55 m 1.75 kg	5-3-12 23:00	Ate an adult <i>P. barbata</i>	10, 10	<i>E. populnea</i>	26.5	24.2	34.3 cloudy	Moderate cloud, 60% humidity, light wind

inactive season. The time interval between radiotracking sessions resulted in alternating nocturnal and diurnal observations and allowed all periods of the day to be observed.

The pythons were located using conventional VHF signals from implanted temperature sensitive transmitters (Holohil SI-2T, 11g), using the method of Reinert and Cundall (1982). Locations were recorded using a global positioning system (Garmin E-trex) with 3 - 5 m accuracy. Body temperatures were calculated from a calibrated

transmitter pulse rate recorded at each observation. Ambient temperature, humidity and wind speed were recorded using a portable weather meter (Kestrel 3000) suspended 1 - 1.5 m above the ground in the nearest shade. Daily ambient temperatures were recorded every ten minutes at a permanent weather meter (Kestrel 4500) installed at the field base; within six kilometres of all radiotracked woma python locations. The womas were radiotracked with minimal disturbance; however disturbance was occasionally unavoidable due to excellent



FIG. 2: An adult male woma python *Aspidites ramsayi* excavates a large burrow in alluvial clay soil.

camouflage. The observations reported here were all recorded on still camera and several behaviours were also captured on motion camera. A genetic tissue sample of each radiotracked woma python is held at the Queensland Museum.

RESULTS

Arboreal Behaviour. *Aspidites ramsayi* demonstrated ten arboreal behaviours out of 1680 radiotracking events during this study (Fig 1, Table 1, with further descriptions in Appendix 1). Six of the twelve radiotracked individuals demonstrated arboreal behaviour, including the smallest (EL - 125 cm SVL, 1.06 kg) and one of the largest (KT - 185 cm SVL, 3.05 kg). Both sexes demonstrated arboreal behaviour equally. The three most common tree species at the study site were utilised with equal frequency during arboreal activity - *E. populnea* (n = 4), *A. aneura* (n = 3), and *Eremophila mitchelli* (n = 3). Pythons were observed up to 10 m high in these trees, with 2 - 4 m being more common.

All arboreal observations commenced at night and were completed by dawn (range 21:30 to 04:00, mean observation time 24:00). Eight of ten arboreal observations were confirmed prey stalking behaviours and the remaining two observations occurred as the womas were descending the trees. Arboreal prey items consisted of *P. barbata* - the largest reptile species regularly sighted sleeping in trees and shrubs on warm nights at the study site (pers. obs.) - and one sleeping *V. gouldii*.

All arboreal observations occurred during warm weather in the austral summer seasons. During arboreal activity, woma body temperature was warmer than ambient air temperature during 9/10 observations (Table 1). Mean snake temperature on arrival at an arboreal observation was 25.8°C and ranged from 20.5 - 30.5°C, whilst mean ambient temperature on arrival was lower at 24.1°C, ranging from 19 - 27°C. The maximum daily temperature prior to a nocturnal arboreal sighting was higher than the midsummer mean maximum January

TABLE 2. Summary of novel observed feeding behaviours and subsequent movements of adult woma pythons *Aspidites ramsayi* during a 21 month radiotracking program in semi-arid southern Queensland, Australia.

*Radiotracking commencement date in parentheses. M = Male, F = Female

^Size at transmitter implantation (snout-vent length and mass)

§Time taken to ingest prey

#Distance from previous location, 55 hrs earlier

%Distance at next location, 55 hrs later.

Python Id*	Size^	Date, Time	Prey	Activity On Arrival	Time§	Dist. Prior#	Dist. After%	Immobile Period
1. CH - M (12-10-10)	1.8 m 1.45 kg	15-1-11 9:45	<i>V. gouldii</i> Adult	Head swallowed	35 mins	925 m	145 m	12 days
2. KT - F (11-1-11)	1.85 m 3.05 kg	15-3-11 10:07	<i>L. capensis</i> Adult	Capturing, killing	65 mins	70 m	60	8 days
3. GA - F (1-6-11)	1.35 m 1.3 kg	27-5-11 15:30	<i>E. rugosa</i> Adult	Basking. Regurgitated	NA	NA	NA	NA
4. HU - M (27-10-11)	1.6 m 1.48 kg	28-10-11 23:12	<i>P. barbata</i> Adult	Stalking 30 cm away	130 mins	430 m	420 m	6 days
5. DC - M (15-3-11)	1.45 m 1.48 kg	20-11-11 22:58	<i>P. barbata</i> Subadult	Stalking 20 cm away	NA	450 m	1,240 m	15 days
6. EL - F (27-4-11)	1.25 m 1.06 kg	22-11-11 23:05	<i>V. gouldii</i> Adult	Stalking 2 m away	NA	555 m	NA	NA
7. JA - M (20-4-11)	1.8 m 3.5 kg	13-12-11 19:50	<i>V. gouldii</i> Adult	Stalking 1 m away	>240 mins	1,160 m	400 m	12 days
8. EL - F (27-4-11)	1.25 m 1.06 kg	6-1-12 21:34	<i>P. barbata</i> Adult	Stalking 3.5 m away	NA	265 m	495 m	Nil
9. JA - M (20-4-11)	1.8 m 3.5 kg	18-1-12 12:25	<i>V. gouldii</i> Adult	Ensnared in hollow log	55 mins	0 m	325 m	10-15 days
10. RM - M (23-5-11)	1.55 m 1.75 kg	11-2-12 2:11	<i>P. barbata</i> Adult	Stalking 30 cm away	80 mins	165 m	60 m	15 days
11. MX - M (20-3-11)	1.70 m 2.3 kg	20-2-12 3:52	<i>P. barbata</i> Adult	Stalking 1.5 m away	70 mins	1,070 m	520 m	27 days
12. KT - F (11-1-11)	1.85 m 3.05 kg	5-3-12 21:43	<i>P. barbata</i> Adult	Stalking, 15 m from tree	NA	475 m	50 m	Nil
13. RM - M (23-5-11)	1.55 m 1.75 kg	5-3-12 23:00	<i>P. barbata</i> Adult	Hanging, prey in coils	~50 mins	580 m	80 m	Nil

temperature (2012) of 30.8°C, and ranged from 29.3 - 36.8°C with a mean of 34.2°C.

Excavation Behaviour. *Aspidites ramsayi* were observed excavating soil twice during this study. The first digging observation occurred early in the afternoon (2pm, 18 Dec 2011) on a hot summer day with full cloud cover and storms developing ($T_{max} = 35^{\circ}C$, $T_a = 32.7^{\circ}C$, ground temp. = 34-39°C, *A. ramsayi* $T_b = 36.6^{\circ}C$). An adult male python (160 cm SVL) was located with the

anterior portion of his body approximately 30 cm inside a wide burrow entry. A pile of loose soil was present outside the burrow (Fig 2). Ten minutes after arrival the python began to scoop more soil out of the burrow with his head and continued to do this for approximately twelve scoops before reversing out of the burrow and investigating the loose soil. The python then braced against the base of a hopbush *Dodonaea viscosa* shrub located 30 cm from the burrow entry, using it to loosen soil deep in the burrow. After leveraging



FIG. 3. An adult female woma python *Aspidites ramsayi* enlarges an existing burrow entry close to a sand goanna *Varanus gouldii* (potential prey) sighting moments earlier.

against the shrub for a further five minutes, the python slowly moved down into the burrow entry and disappeared. This woma had moved 400 m from its last known burrow and 55 hours after the digging observation, had moved a further 260 m to shelter in a well-established ground burrow system.

The second digging observation was of a small adult female python (SVL = 135 cm) at sunset late in summer (24 Feb 2012). It was a warm day with some cloud present ($T_{max} = 31.6^{\circ}\text{C}$, $T_a = 27.4^{\circ}\text{C}$, ground temp. = 27–28°C, $A. ramsayi$ $T_b = 28.0^{\circ}\text{C}$). Whilst locating the python, an adult *V. gouldii* (a known prey item) was observed retreating from the top of a hollow log within one metre of the subsequently determined location of the python. On arrival the head of the python was deep inside a slender burrow and the tail was jerking erratically from side to side, a behaviour identical to that observed previously during a prey attack (Appendix 1: Feeding Observation 7). The python proceeded to scoop dirt out of the burrow using her head in the same manner as described by Fyfe and Harvey (1981) and observed in the earlier *A. ramsayi* excavation. The scooping movement

exposed a small amount of loose soil at the burrow entry, indicating the woma had just commenced digging (Fig 3). The python continued to scoop out dirt for another two minutes before (without being disturbed) abandoning the excavation to enter a very small burrow 1 m away and underneath the log from which the *V. gouldii* had retreated. Eight minutes later, the python slowly exited this same burrow, stopping intermittently, and then moved back past the excavated burrow before exiting the area. This python had moved 125 m from her previous (exposed) location and 55 hrs later she had moved 250 m further to a hollow log shelter.

Feeding Behaviour. Twelve feeding behaviours from nine individual *A. ramsayi* and one occurrence of a regurgitated prey item were recorded during the radiotracking program (Fig 2, Table 2, with descriptions in Appendix 1). Feeding behaviours occurred both night and day, but occurred more often at night (9/12 observations). The nine ingested prey items included three adult *V. gouldii*, one adult *L. capensis*, four *P. barbata*, and a regurgitated adult *E. rugosa*. Stalking (without

TABLE 3. Radiotracked adult woma python *Aspidites ramsayi* body temperatures and weather conditions during thirteen feeding observations (semi-arid southwest Queensland, Australia). * M = Male, F = Female

Python Id*	Date & Time	T _b (Oc) Start	T _b (Oc) End	T _a (Oc) Start	T _a (Oc) End	Weather
1. CH - M	15-1-11 9:45	36.5 sun	41.8 sun	27	30	Minimal cloud, 60% humidity, light wind
2. KT - F	15-3-11 10:07	33 shade	31.7 shade	29.3	32.3	No cloud, 50% humidity, light wind
3. GA - F	27-5-11 15:30	NA sun	NA	19	NA	No cloud, 45% humidity, light wind
4. HU - M	28-10-11 23:12	24 night	23.4 night	24	24	Full cloud, 65% humidity, high winds
5. DC - M	20-11-11 22:58	25.5 night	NA	24.5	NA	No cloud, 60% humidity, light wind
6. EL - F	22-11-11 23:05	29 night	NA	26.5	NA	Min. cloud, 60% humidity, mod. winds
7. JA - M	13-12-11 19:50	26 night	32 night	23.9	16.2	No cloud, 65-90% humidity, no wind
8. EL - F	6-1-12 21:34	30.5 night	NA	26.9 night	NA	No cloud, 60% humidity, light wind
9. JA - M	18-1-12 12:25	26 log	35.5 shade	32.3	33.5	Minimal cloud, 50% humidity, light wind
10. RM - M	11-2-12 2:11	20.5 night	19.8 night	18.9	18.9	No cloud, 85% humidity, no wind
11. MX - M	20-2-12 3:52	23.5 night	23.9 night	23.2	22.5	Minimal cloud, 70% humidity, no wind
12. KT - F	5-3-12 21:43	28 night	NA	25.2 night	NA	Moderate cloud, 60% humidity, light wind
13. RM - M	5-3-12 23:00	26.5 night	NA	24.2 night	NA	Moderate cloud, 60% humidity, light wind

prey capture) of a further three *P. barbata* and a *V. gouldii* were observed. Eight prey stalking behaviours were observed, though not all were successful. Seven of the eight observed prey stalking behaviours occurred in trees at night and prey included five adult *P. barbata*, a subadult *P. barbata*, and a small adult *V. gouldii*. The thirteen feeding records were dominated by reptilian prey (92%).

The pythons travelled an average of 506 m (range 70 - 1160 m) from their last recorded position to capture prey (Table 2). Following successful ingestion of prey (n = 8), the womas

moved an average of 250 m (range 60-520 m) to a shelter and remained immobile for an average of 11.3 (range = 0-27) days before departing the shelter (Table 2).

All feeding observations occurred during the austral warm season, between October and March. However, regurgitation of the *E. rugosa* occurred in late autumn (Table 2, Appendix 1: Feeding Observation 3). Mean *A. ramsayi* body temperature on arrival at a feeding observation (27.4°C, range 20.5-36.5°C) was higher than mean ambient temperature (25.5°C, range 18.9 -32.3°C, Table 3). On most occasions, body

temperature either increased or decreased according to the trend in ambient temperature during prey capture and ingestion (Table 3).

DISCUSSION

Arboreal Behaviour: These are the first recorded observations of arboreal behaviour in a species that has formerly been recorded as exhibiting only terrestrial and fossorial tendencies both in captivity and in the wild. Whilst there are records of *A. ramsayi* from sparsely treed habitats, including mulga *A. aneura* and desert sheoak *Allocasuarina decaisneana* sand dunes near Uluru (Fyfe & Harvey 1981), the eastern woma population is the only population known to inhabit an area where large stands and continuous tracts of woodlands create a tall and semi-closed canopy. Other reported habitats include shrubby myrtaceous heath, (Smith 1981), shrubby Banksia heathland (Maryan 2002), cleared farmland (Maryan 2002), hummock grass and spinifex (Fyfe & Harvey 1981; Pearson 1993), and chenopod vegetation (Read 2010); all associated with more western *A. ramsayi* populations in South Australia, Western Australia and the Northern Territory. Therefore it is likely that for the majority of *A. ramsayi* populations, arboreal activity is restricted by an absence or scarcity of trees, and arboreality may be behaviour specific to eastern woma populations. Further reporting of wild woma sightings (including habitat and behaviour) in western locations is necessary to confirm this.

Although arboreal behaviour has not been reported in western *A. ramsayi* populations, captive raised womas from northern South Australia demonstrated that all womas may have at least some capacity to climb. Read (2010) reports that during a trial woma soft-release program, all four of the 5 year old pythons breached the 900 mm high netting fence within two months. No other examples of woma climbing behaviour either in the wild or in captivity have been reported.

Arboreal snakes have evolved physiological adaptations to withstand gravitational pressure in the circulatory system (Lillywhite &

Henderson 1993). Therefore it is remarkable that the terrestrial *A. ramsayi* is not only capable of climbing to reasonable heights but is also able to spend over an hour consuming prey whilst hanging vertically from a tree limb (see Appendix 1: Feeding Observations 11 & 13), all without demonstrating adverse effects. Arboreal behaviour in adult womas is even more unusual considering they possess none of the typical arboreal snake external body shape adaptations of slenderness, a laterally compressed cross section, and a long tail (Lillywhite & Henderson 1993). However it is interesting to note that juvenile womas are more slender and laterally compressed in cross section than adults (pers. obs.) and may also be quite capable climbers. Further investigation into the physiological capacity of eastern womas for arboreal activity may uncover cardiovascular and/or other physiological adaptations to assist in coping with short-term gravitational stress.

Arboreal behaviour in *A. ramsayi* was observed exclusively at night during warm months and was strongly linked to feeding activity (Table 1). Behavioural observations of the most commonly recorded woma python prey items at the study site help explain this behaviour. On warm nights *P. barbata* were regularly observed sleeping horizontally on exposed tree and shrub limbs, as well as vertically on tree trunks. These 'roosting' adult *P. barbata* are a bountiful summer food supply that adult woodland inhabiting eastern woma pythons are able to exploit through an arboreal behavioural adaptation.

Two smaller agamids *Amphibolurus burnsi* (Wells & Wellington, 1985) and *Diporiphora nobbi* (Witten 1972) were also regularly observed sleeping on limbs of trees and shrubs on warm nights at the study site. *Amphibolurus burnsi* and *D. nobbi* 'roosted' in greater densities than *P. barbata* (pers. obs.), however they were not observed prey for adult womas. Based on movements from this radiotracking program and typical observed prey size, actively searching for and ingesting small agamids may result in a net energy loss for larger womas (see Arnold 1993 for snake predator-prey size and energy discussion), making such prey items

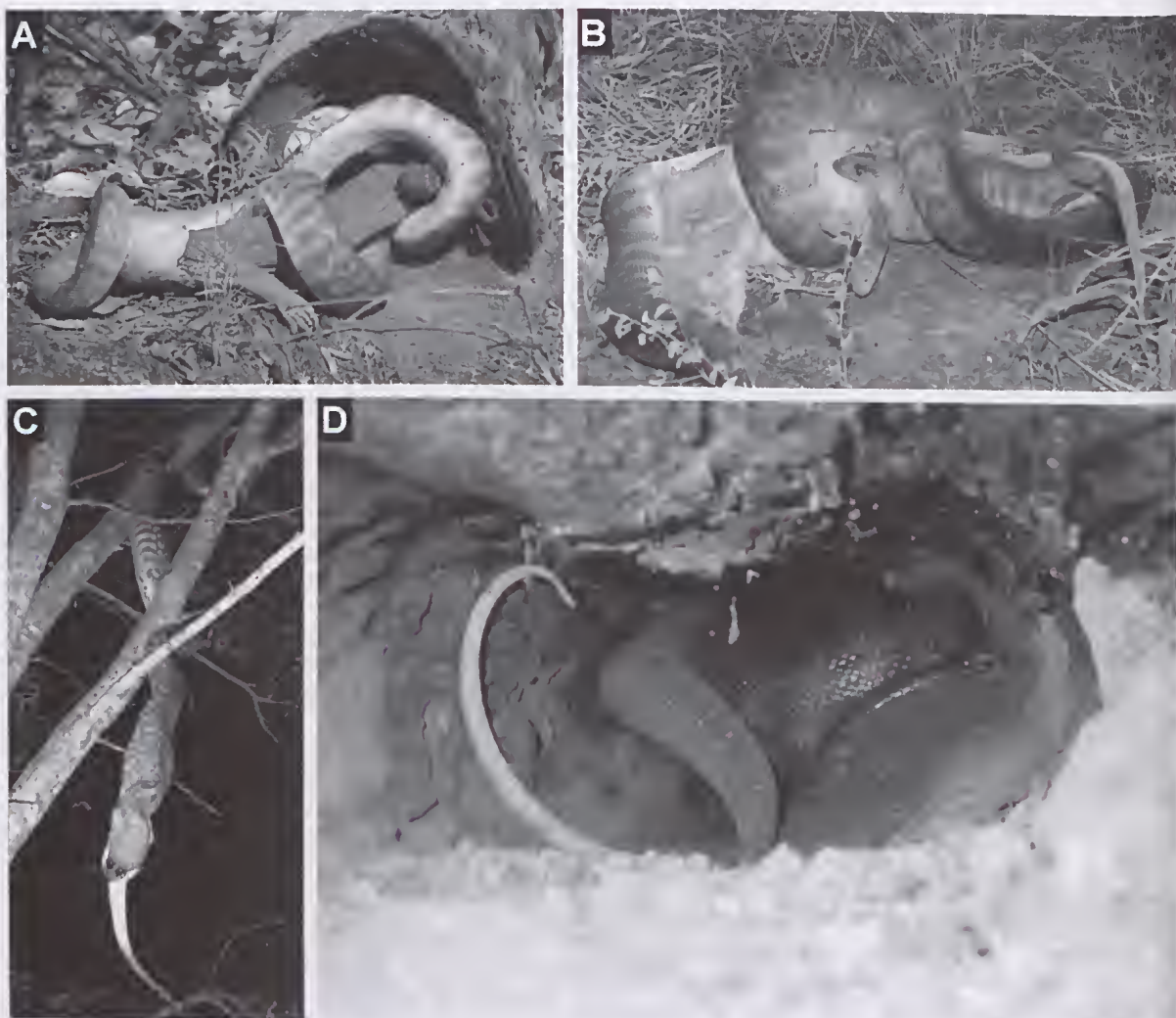


FIG. 4. Novel *Aspidites ramsayi* feeding behaviours and prey: A, An adult male python ingests an adult sand goanna *Varanus gouldii*, captured inside a single-ended hollow log; B, An adult female python consumes an adult hare *Lepus capensis* captured in long grass; C, An adult male python swallows a bearded dragon *Pogona barbata* whilst hanging vertically from a 4 m high mulga *Acacia aneura* tree limb; D, An adult male python traps and 'squashes' an adult *V. gouldii* inside a single-ended hollow log.

unviable. However, if juvenile womas are also capable of arboreal behaviour, it is conceivable that they would prey on 'roosting' *A. burusi* and *D. nobbi*. Juvenile woma pythons were not radiotracked during this study and were rarely sighted at the study site.

Aspidites ramsayi were not observed using trees for shelter. There were no womas observed in arboreal resting positions during this study.

The only python observed stationary in a tree (Table 1: python DC 15-3-11) was facing down the main trunk with his posterior end coiled tightly around a branch - a characteristic boid post-prey ingestion position rather than a coiled resting boid position (Fig 1A, pers. obs.). All observed arboreal woma pythons immediately began to descend following prey ingestion; therefore it is likely that this python had just

completed ingestion and was beginning to descend before 'freezing' after being disturbed by an initially fruitless and extensive search on the ground. *Aspidites ramsayi* appear to use trees exclusively for prey capture and ingestion and the limited amount of time that the pythons were observed in trees helps to explain why arboreal behaviour has not been previously reported for this species.

The two largest radiotracked womas were not observed engaging in arboreal activity. This includes the longest (Python BB - 210cm SVL) and the heaviest (Python JA - 180 cm, 3.5 kg). However large python KT (185cm, 3.05kg) was observed engaging in arboreal activity twice. Although it is reasonable to assume that the larger radiotracked womas may have engaged in unobserved arboreal activity, it is noteworthy that there may be a physiological size limit that restricts arboreal activity in very large woma pythons.

Despite greater thermal exposure of snakes in arboreal environments (Lillywhite & Henderson 1993), all except one of the womas were warmer than ambient temperature on arrival at an arboreal observation. Daily maximum temperatures preceding nocturnal arboreal activity were unusually hot on almost all occasions, indicating that either active basking or passive heat retention occurred prior to arboreal activity. Active basking cannot be presumed because warmer body temperatures during arboreal activity could be an artefact of faster ambient cooling rates than *A. ramsayi* body cooling rates at night (thermal hysteresis). Regardless of the mechanism, particularly warm days appear to stimulate active foraging activity, which increases the chance of woma pythons encountering prey scent trails leading to arboreal behaviour (for chemosensory perception discussion see Ford & Burghardt 1993).

Excavation Behaviour. Whilst womas have been observed excavating sandy soils in captivity, these are the first known observations of wild *A. ramsayi* digging behaviours, and they occurred in harder alluvial clay soils. Ehmann (1993) reports that python burrowing behaviour is unique to the *Aspidites* genus -

A. ramsayi and the similarly sized, but more northerly distributed black-headed python *A. melanocephalus* (Krefft 1864). The digging descriptions for captive *A. ramsayi* (Fyfe & Harvey 1981), wild *A. ramsayi* (this study), and captive *A. melanocephalus* (Murphy, Lamoreaux *et al.* 1981) are all consistent - using the head as a scoop to excavate loose substrate. Murphy, Lamoreaux *et al.* (1981) reported four captive *A. melanocephalus* were able to excavate gravel using this technique, indicating that members of the *Aspidites* genus are capable of digging in a wide range of soil types.

Fyfe & Harvey (1981) were correct in surmising the digging behaviour they observed in captive *A. ramsayi* would likely be used for enlarging existing burrows for shelter or during hunting. In this study, the male excavating *A. ramsayi* (first observation) appeared to use the excavated burrow as a temporary shelter, and post-excavation behaviour indicates he was enlarging an existing burrow. The excavating female (second observation) also enlarged an existing burrow, as determined by a discrepancy between the amount of excavated soil and the burrow depth. The presence of known prey (*V. gouldii*) at this digging site combined with rapid caudal jerking motions consistent with a previous prey capture observation also indicate that she was actively hunting prey. Although we cannot rule out the possibility that *A. ramsayi* dig new burrows for shelter, it seems more likely that they modify existing burrows as a hunting, and possibly also as a sheltering strategy in all soil types.

Feeding Behaviour. *Aspidites ramsayi* are very secretive, spending 74 % of the time underground and 95% of the time in inaccessible shelters such as hollow logs, mounds of dirt, and large piles of woody debris (Bruton, unpub. data). Subsequently it is not surprising that wild *A. ramsayi* feeding observations have not been previously reported. It is likely that womas regularly feed in both underground and above ground shelters, and occasionally out in the open. Therefore it is important to note that the observed feeding behaviours presented here are only a brief glimpse of potential woma python foraging activity.

Museum records throughout Australia demonstrated that woma pythons consume mammals and reptiles in equal proportions, with birds also recorded (Shine 1999). Whilst it is unclear if ground-dwelling or flying birds were consumed, the observations of arboreal behaviour during this study indicate that roosting birds may be taken at night; however roosting birds are unlikely to leave a scent trail for the pythons to follow from the ground. Feeding observations indicate that prey for the eastern population of womas may be strongly biased towards reptiles; especially bearded dragons *P. barbata* and sand goannas *V. gouldii*. Whilst only one woma was observed feeding on a hare *L. capensis*, two other potential hare stalking behaviours were also observed. Unfortunately both hares were unwittingly disturbed whilst pinpointing the exact position of the python. No other mammalian prey foraging or feeding was observed despite the presence of numerous hares and rabbits *O. cuniculus* at the study site.

Although capture and ingestion of yakka skinks *E. rugosa* was not observed, it is likely that this species also constitutes a significant proportion of the diet of eastern woma python populations. *Aspidites ramsayi* utilised a high proportion of ground burrow systems at the study site that are confirmed or suspected yakka skink colonies (Bruton, unpublished data). In addition, the regurgitation of a yakka skink by a woma captured basking outside a known yakka skink colony (Appendix 1: Feeding Observation 3) confirms that *E. rugosa* are preyed upon within their colonial shelters. *Aspidites ramsayi* not only shelter in yakka skink colonies but also feed on the inhabitants.

Whilst it cannot be observed with current technology, it is feasible that many *E. rugosa* are captured within the confines of the communal burrow system tunnels using the prey 'squashing' method described by Fyfe and Harvey (1981). Whilst one radiotracked woma was observed using this 'squashing' method to capture a *V. gouldii* inside a hollow log (Appendix 1: Feeding Observation 7), no other 'squashing' behaviours were observed during this radiotracking program. However

this was not unexpected due to the limited viewing opportunities in such confined spaces.

Aspidites ramsayi often travelled long distances both prior to and after prey capture (Table 2), indicating an active foraging mode. Supporting this, throughout the active season the womas regularly moved >300 m between shelter sites (49% of moves) and were capable of moving up to 2 700 m in 55 hrs (Bruton, unpub. data). However, one python demonstrated that womas are also opportunistic and will attack prey from an ambush position. In Feeding Observation 9 (Appendix 1), the sand goanna *V. gouldii* prey was familiar with the hollow log it sought refuge in and the python responded rapidly as it entered the log, indicating a set ambush. It is also likely that womas ambush yakka skinks in the tunnels of the ground burrow systems they shelter in. These observations suggest *A. ramsayi* are predominantly active foragers (intercepting and following prey scent trails), but are also capable of ambush tactics to capture prey.

Caudal luring is an ambush tactic employed by snakes from different phylogenetic lineages, e.g. Viperidae (Heatwole & Davison 1976), Elapidae (Carpenter, Murphy *et al.* 1978), Colubridae (Leal & Thomas 1994), and Boidae (Murphy, Carpenter *et al.* 1978). Caudal luring involves wriggling the slender and differentially marked tail tip like a grub to tempt prey within striking distance (Heatwole & Davison 1976; Carpenter, Murphy *et al.* 1978). The snake may make very rapid caudal movements once prey has been detected, as vividly described for the death adder (Carpenter, Murphy *et al.* 1978). Fyfe and Harvey (1981) report second hand observations of 'caudal luring' in captive womas, however this species lacks the differentiated tail tip and predominantly ambush foraging strategy typical of most species that employ this ambush technique (Heatwole & Davison 1976; but see Leal & Thomas 1994). During this study, erratic tail movements that could potentially be interpreted as caudal luring were observed twice: whilst digging near known prey and whilst 'rushing' forwards to capture cornered prey (see Results section and Appendix 1: Feeding Observation 7). These rapid caudal movements

have also been observed in captive womas when they scent imminent food (pers. obs.). During burrow excavation, the rapid caudal tail movements occurred when the head of the python was deep inside the burrow (Fig 3), so luring prey within striking range could not be the purpose of these movements. The head of the python was also not within sensory range of the tail during Feeding Observation 7 (Appendix 1): this python attacked a cornered *V. gouldii* with his head inside a short single-ended log and his tail outside the log. The rapid caudal movements observed are best described as analogous to the tail wag or twitch of a stimulated dog or predatory cat. The stimulus for captive *A. ramsayi* is the scent of food, and imminent prey capture also appears to be the stimulus in the two wild observations. It is not clear if these tail movements have a purpose or are an artefact of hunting. Whilst superficially similar to caudal luring and associated with prey capture, the caudal behaviour observed in wild *A. ramsayi* during this study was not 'luring'.

CONCLUSION

As with all burrowing animals, *A. ramsayi* are very difficult to observe hence there is very limited information on basic ecology and behaviour of this species. This is accentuated by the fact that despite having a vast distribution, womas inhabit an area very sparsely populated by humans (Tobler, Deichmann *et al.* 1995): only 10 towns within the extensive woma python distribution have a population of >1000 people (Australian Government 2006). Therefore it is not surprising that information regarding the natural history and ecology of this elusive species is so limited. Reporting and description of the novel *A. ramsayi* behaviours encountered during this radiotracking study has increased our knowledge of woma python natural history and assisted in understanding python behaviour and ecology.

ACKNOWLEDGMENTS

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LITERATURE CITED

- Arnold, S.J. 1993. Foraging Theory and Prey-size-Predator-size Relations in Snakes. *In*, Pp. 87-112. Seigel, R.A. & Collins, J.T. (eds). *Snakes: Ecology & Behaviour*. (The Blackburn Press: New Jersey).
- Australian Government. 2006. 2006 Census Data by Location. Retrieved 5 May, 2012, from www.censusdata.abs.gov.au/ABSNavigation/prenav/LocationSearch.
- Borsboom, A. 2008. Nomination to re-classify the 'rare' *Aspidites ramsayi* to 'near threatened' under the *Nature Conservation Act 1992*. Environmental Protection Agency.
- Carpenter, C.C., Murphy, J.B. *et al.* (1978). Tail luring in the death adder, *Acanthophis antarcticus* (Reptilia, Serpentes, Elapidae). *Journal of Herpetology* 12(4): 574-577.
- Cogger, H.G. 2000. *Reptiles & Amphibians of Australia*. Sydney, Reed New Holland.
- Covacevich, J.A. & Couper, P.J. 1996. *Aspidites ramsayi* (Boidae) in the brigalow biogeographic region of Queensland: occurrence, conservation status and possible bilby associations. *Memoirs of the Queensland Museum* 39(2): 243-246.
- Ehmann, H. 1993. 33. Family Boidae. *Fauna of Australia*. C.G. Glasby, G.J.B. Ross & P.L. Beesley. Canberra, AGPS. Vol. 2A.
- Ford, N.B. & Burghardt, G.M. 1993. Perceptual mechanisms and the behavioral ecology of snakes. *In*, Pp. 117-164, Seigel, R.A. & Collins, J.T. (eds) *Snakes: Ecology & Behaviour*. (The Blackburn Press: New Jersey).

- Fyfe, G. & Harvey, C. 1981. Some observations on the woma (*Aspidites ramsayi*) in captivity." *Herpetofauna* 13: 23-25.
- Heatwole, H. & Davison, E. 1976. A review of caudal luring in snakes with notes on its occurrence in the Saharan sand viper, *Cerastes vipera*. *Herpetologica* 32(3): 332-336.
- Leal, M. & Thomas, R. 1994. Notes on the feeding behavior and caudal luring by juvenile *Alsophis portoricensis* (Serpentes: Colubridae). *Journal of Herpetology* 28(1): 126-128.
- Lillywhite, H.B. & Henderson, R.W. 1993. Behavioral and Functional Ecology of Arboreal Snakes. In, Pp. 1-42, Seigel, R.A & Collins, J.T. (eds) *Snakes: Ecology and Behavior*. (The Blackburn Press: Caldwell).
- Maryan, B. 2002. Status of the woma, *Aspidites ramsayi*, in south-west Western Australia. *The Western Australian Naturalist* 23(3): 167-172.
- Murphy, J.B., Carpenter, C.C. *et al.* 1978. Caudal luring in the gree tree python, *Chondropython viridis* (Reptilia, Serpentes, Boidae). *Journal of Herpetology* 12: 117-119.
- Murphy, J.B., Lamoreaux, W.E. *et al.* 1981. Miscellaneous notes on the reproductive biology of reptiles. 4. Eight species of the family Boidae, Genera *Acrantophis*, *Aspidites*, *Candoia*, *Liasis* and *Python*. *Transactions of the Kansas Academy of Sciences* 84(1): 39-49.
- Pearson, D. 1993. Distribution, status and conservation of pythons in Western Australia. In, D. Lunney & D. Ayers (eds). *Herpetology in Australia: A diverse discipline*. (Royal Zoological Society of NSW: Mosman).
- Read, J. L. 2010. Predation by snakes thwarts trial reintroduction of the Endangered woma python *Aspidites ramsayi*. *Oryx* 45(4): 506-512.
- Reinert, H.K. & Cundall, D. 1982. An improved surgical implantation method for radio-tracking snakes. *Copeia* 1982(3): 702-705.
- Shine, R. 1999. *Australian Snakes: A Natural History*. (Reed New Holland: Sydney).
- Slip, D. J. & Shine, R. 1990. Biological aspects of the adaptive radiation of Australasian pythons (Serpentes: Boidae). *Herpetologica* 46(3): 283-290.
- Smith, L.A. 1981. A revision of the python genera *Aspidites* and *Python* (Serpentes: Boidae) in Western Australia. *Records of the Western Australian Museum* 9: 211-226.
- Tobler, W., Deichmann, V. *et al.* 1995. Map Historical Population Density - 1994. Santa Barbara, California, USA, National Center for Geographic Information Analysis.
- Wilson, S. & Swan, G. 2010. *A Complete Guide to Reptiles of Australia*. (New Holland Publishers Pty Ltd: Sydney).

APPENDIX 1: BRIEF DESCRIPTIONS OF WOMA PYTHON *ASPIDITES RAMSAYI* FEEDING BEHAVIOUR OBSERVATIONS

Feeding Observation 1. A large woma swallowed an adult sand goanna *V. gouldii* (Fig 4A). On arrival, python CH was partially visible at the entrance to a single-ended fallen hollow log. An adult *V. gouldii* was trapped in his coils and the head was already swallowed. Python CH extricated himself and his prey from the hollow log during ingestion and finished swallowing whilst exposed to full sun on hot bare dirt, 1 m from the log entrance. Although the prey item was large, the ingestion time was short (Table 2). Python CH used typical snake 'jaw walking' motions to ingest the body of the *V. gouldii*, and oesophageal contractions only to swallow the long tail. Upon completion of the meal, python CH immediately returned to the hollow log.

Feeding Observation 2. A large woma caught, killed and swallowed an adult hare *L. capensis*

(Fig 4B). On arrival, python KT was not visible in the long grass. After triangulating her position, a furtive attempt was made to observe her activity. However this approach startled the hare, which screamed and bounded away with python KT dragged along behind, clinging onto the hind foot with her mouth. Python KT overwhelmed and coiled the hare within 30 m. There was no movement from the hare after three minutes of constriction. Python KT found the head of the hare very quickly and began to swallow. Ingestion took an hour and occurred in the shade of a Dean's wattle *Acacia deanei*.

Feeding Observation 3. A small adult woma regurgitated an adult yakka skink *E. rugosa* two hours after her initial capture. Python GA was found basking outside a ground burrow system containing a radiotracked python (JA), with a large bulge in her stomach. Whilst every effort was made to gently capture her for transmitter implantation, she later regurgitated her meal in captivity. As this was the initial capture of python GA no snake temperatures are

available. The prey item was easily identifiable with limited breakdown of the integument.

Feeding Observation 4. A medium-sized woma stalked, caught, killed and ate an adult bearded dragon *P. barbata* sleeping on an outer limb of a false sandalwood *E. mitchelli* tree (Fig 1B). This was the first arboreal observation, so a futile ground search took place over several minutes before the python and prey were located. On discovery python HU was stretched out from the trunk of the tree with his head 30 cm from the head of the sleeping *P. barbata*. The dragon did not respond despite the noise and light from the initial search. It took python HU 15 mins to stalk the final 30 cm along the branch to strike and capture the sleeping bearded dragon by the head in typical boid manner. The bearded dragon immediately inflated its body. Whilst capturing the prey, the cranial end of python HU fell from the branch, but he held on with the caudal end of his body to hang one metre below the branch. Python HU then coiled the prey upwards into his body and began consuming it whilst hanging vertically from the branch. After 20 mins python HU lost his grip and fell two metres to the ground with the *P. barbata* head already swallowed. He then re-coiled the prey in situ and continued to ingest it over the following 90 mins. The bearded dragon took a comparatively long time to ingest (Table 2), possibly due to its puffed-up profile. Python HU had been implanted with a transmitter only 4 days prior to this encounter and had been released only 37 hrs previously.

Feeding Observation 5. An unsuccessful attempt by a medium-sized adult woma to capture a subadult bearded dragon *P. barbata* sleeping in a small *E. mitchelli* shrub. On arrival python DC was stretched vertically up the trunk of the tree with his head 20 cm from the tail of the sleeping bearded dragon. Five minutes later the bearded dragon unexpectedly jumped down to the ground and ran away, possibly due to disturbance. Python DC made no attempt to follow but continued to slowly stalk slowly up the shrub for another five minutes before observations were ceased.

Feeding Observation 6. An unsuccessful attempt by a small adult woma to capture a small adult sand goanna *V. gouldii* four metres high in a burnt eucalyptus *E. populnea* tree stump. On arrival python EL was two metres high on the smooth outer edge of the stump and beginning to disappear into the hollow inner trunk. The *V. gouldii* had not been sighted at this time and the correlation between arboreal behaviour and prey stalking had not yet been established. Python EL had not been sighted since her release six months earlier and it was vital that her transmitter implantation wound site be checked for infection and antenna protrusion. As she was being extricated from the hollow the torch beam illuminated the head of the sand goanna in a hollow two metres higher than python EL. It is likely that python EL had been stalking the sand goanna. A slightly protruding antenna necessitated a short stay in captivity so her next movements could not be observed.

Feeding Observation 7. A large woma attacked a large adult sand goanna *V. gouldii* ensconced in a single-ended hollow log (Fig 4E). On arrival, python JA had approximately 30 cm of his anterior end inside the log and was rapidly entering it. He appeared very animated with the posterior section of his body jerking erratically from side to side as he moved. Once inside, there was an audible scrabbling of claws and commotion. Several moments later the tip of a *V. gouldii* tail was visible twitching underneath the coils of python JA. Over the following four hours there was little movement from python JA as he squashed the sand goanna against the end, the bottom, and the sides of the log. At 01:00 the sand goanna was still alive and python JA showed no evidence of attempting to kill it but kept it pinned within the log. The following morning (09:40), python JA was sighted moving 340 m away from the attack site with a large goanna-shaped bulge in his stomach.

Feeding Observation 8. An attempt by a small woma to stalk and capture an adult bearded dragon *P. barbata* sleeping in a mulga tree *A. aneura* (Fig 1D). On arrival python EL was

extended horizontally from the tree trunk with an adult bearded dragon sleeping 3.5 m away on the outer reaches of the same branch. Due to time constraints and fatigue, the stalking behaviour was not able to be observed and it is not known if the hunt was successful.

Feeding Observation 9. A large woma caught, killed, and swallowed an adult sand goanna *V. gouldii*. On arrival, the position of python JA was identified as approximately 1.5 m inside a slightly raised fallen hollow poplar box *E. populnea* log. Also noted was a sand goanna basking two metres away from the log. Despite slowly backing away, the sand goanna took fright and ran under the hollow log before doubling back to the log entry and pausing momentarily to scent it. The sand goanna then entered the log rapidly and was immediately attacked by python JA. The sand goanna then dragged python JA out of the log where he overpowered it in the shade of a mulga *A. aneura* tree, 1.5 m from the burrow entry. Python JA remained tightly coiled around the sand goanna for 20 mins before releasing his hold and locating the head for swallowing. Following ingestion, python JA immediately retreated back into the hollow log and settled in his original position.

Feeding Observation 10. A medium-sized woma caught, killed, and swallowed a bearded dragon *P. barbata* (Fig 1C). On arrival, python RM was stretched vertically up a multi-stemmed regrowth poplar box *E. populnea* tree. Whilst no prey item was initially located, python RM was observed continuously tongue flicking between a thick trunk of the tree and a nearby *E. mitchelli* shrub. Five minutes later python RM attacked and coiled the adult bearded dragon, along with a thin stick lodged horizontally 1.5 m above the ground in the midst of the multiple stems of the *E. populnea* tree (Fig 1C). The prey ceased moving within five minutes of capture and python RM proceeded to ingest it whilst hanging precariously in the tree. After 70 mins the stick slanted too far resulting in python RM sliding and tumbling 1.5 m to the ground with the head and body of the bearded dragon

already swallowed. Python RM took a further 10 mins to complete ingestion and move away.

Feeding Observation 11. A large woma stalked, killed, and swallowed an adult bearded dragon *P. barbata* sleeping on an inner vertical stem of a mulga *A. aneura* tree (Fig 4C). On arrival python MX was climbing vertically up the tree with his head approximately 1.5 m below the tail of the sleeping bearded dragon. Over the following 30 mins python MX stalked up past the prey and attacked it directly on the head from above. Python MX then coiled the puffed up bearded dragon whilst suspended from a limb one metre higher than the original bearded dragon position. After 15 mins, python MX began to ingest the dragon whilst hanging vertically from one limb with his tail anchored down to a second limb, providing a stable position approximately four metres above the ground (Fig 4C). Python MX completely ingested the prey whilst hanging vertically. After ingestion, python MX immediately began to descend the tree.

Feeding Observation 12. A large woma stalked an adult bearded dragon *P. barbata* sleeping on a very slender outer twig of a three metre long horizontal mulga *A. aneura* branch. On arrival python KT was cruising slowly along the ground 15 m from the base of the mulga tree. The position of the sleeping bearded dragon was noted and it was realised that python KT may be following its scent trail. Five minutes after the initial location, a very dim light was used to locate python KT four metres from the base of the tree in a direct line from her previous position. She did not respond during either of the observations. Over the following 45 minutes the silhouette of python KT was followed using moonlight as she reached the base of the tree and proceeded to climb it. During the following 35 mins python KT explored the central trunk area up to a height of three metres. She did not attempt to climb out onto the limb containing the sleeping bearded dragon but spent much time exploring the trunk area. Observations were ceased at this point to radiotrack the remaining *A. ramsayi*.

Four hours later both woma python KT and the *P. barbata* were absent.

Feeding Observation 13. A medium-sized woma ate an adult bearded dragon *P. barbata* ten metres high in a thin regrowth poplar box *E. populnea* tree (Fig 1E). On arrival python RM could not be pinpointed. Eventually he was sighted hanging vertically down from a high limb of a straight trunked tree, anchored up and over a branch, with a bearded dragon in his coils, swallowing the head. To avoid disturbing him (and potentially a ten metre fall), RM was left alone to complete ingestion. Fifty minutes later python RM had just finished swallowing the bearded dragon and was lifting the anterior portion of his body up from a vertical hanging position. Over the following 25 mins python RM slowly descended the straight, narrow tree trunk using a concertina method typically employed by arboreal snakes. On descending to a height of 2.5 m, python RM was left to continue onto a shelter undisturbed.

A RECORD OF REPRODUCTION IN ANTHOPS ORNATUS (CHIROPTERA: HIPPOSIDERIDAE), YSABEL ISLAND, SOLOMON ISLANDS.

Memoirs of the Queensland Museum - Nature 56(2): 331-331. 2013:- The Solomons Leaf-nosed (or Fower-faced) Bat (*Anthops ornatus* Thomas 1888a) belongs to a monotypic genus of hipposiderid bats endemic to the Solomon Islands and Bougainville (Flannery 1995). The nose-leaf is complex with two secondary leaflets and three upward projections that rise to form backward facing spherical cups. The tail is short, comprising four transparent vertebrae that terminate less than mid-way to the external edge of the membrane. The nose-leaf and lower jaw are orange; hairs of the dorsum have black bases changing to silver then tipped with black; and ventral hairs are black-based tipped with silver (Thomas 1888a, b; Flannery 1995).

Records of the species are extremely rare. Its description was based on six specimens collected from Aola on Guadalcanal Island by C.M. Woodford. Subsequently, Sanborn (1931) reported a specimen from Choiseul during the Whitney South Seas expedition in 1929, and Troughton (1936) reported a specimen from Bougainville and remarked on a second specimen collected from Ysabel by N. S. Heffernan in 1924. More recently, Flannery (1995) recorded a male at Balani Village on the southern coast of Guadalcanal and Bowen-Jones *et al.* (1997) recorded an individual on Choiseul. In addition to these locations, the Bernice Pauahi Bishop Museum (Honolulu) holds one specimen collected from Ngella in 1964. This distribution comprises islands that were connected as the *Greater Bukida* landmass during the Pleistocene (Mayr & Diamond 2001), plus Guadalcanal.

On 12 November 2011, we captured a female *A. ornatus* carrying a neonate. The capture occurred on Ysabel Island (Fig. 1) in a mist net positioned within the understorey of lowland forest at an elevation of 411 m a.s.l. As we approached the net, the female managed to free itself, however the neonate had become entangled and remained behind. We had deployed 168 m² of mist net over two nights (total 14 hours) for the single capture. Nets were 12 m long by 2.8 m high and constructed of 38 mm mesh.

Vegetation at the site was ultrabasic/ultramafic forest. This forest type is distinct from typical Solomon Island lowland forest but does share some similarities in species composition and structural characteristics. Dominant canopy trees are *Xanthostemon melanoxylon*, *Gymnostoma papuana*, *Metrosideros salomonensis*, *M. collina*, *Gnetum gnemon*, *Podocarpus salomonensis* and *Fagraea obtusifolia*. The palms *Actinorhynchus calapparia* and *Hydriastele hollrungii* are also common. The understorey contains *Nastus obtusus*, *Lycopodium cernuum*, *Gleichenia linearis*, *G. oceanica*, and *Capitularia involucreata*.

The specimen was lodged with the Queensland Museum, Brisbane, Australia (QM JM19844). Weight was not recorded in the field, however, body measurements

with comparative dimensions of existing museum specimens are given below in Table 1.

The age of the specimen is likely to have been less than two weeks, as this is typically the upper time limit for which other hipposiderid bats carry their young before depositing them in roosts (Churchill 2008). The forearm was approximately 40% of adult length. Short, dark hair was present over much of the body, the eyes were closed, ears were erect and an umbilical scar was evident. In China, juvenile *Hipposideros cineraceus* Blyth, 1853 with such attributes have been determined to be approximately five days old (Jin *et al.* 2010). Tate (1941) identified one of the

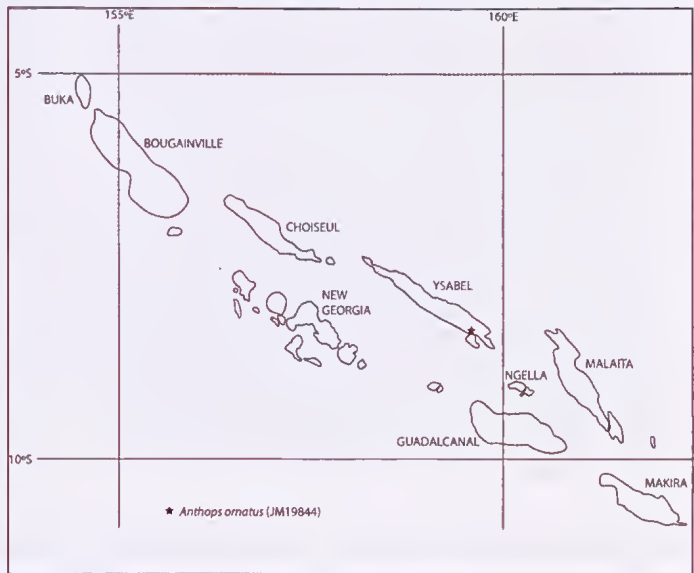


FIG 1. The geographical Solomon Islands and location of *Anthops ornatus* record (JM19844).

TABLE 1. Comparisons of external measurements (mm) between adult *Anthops ornatus* museum specimens and the captured juvenile.

Source	Specimen	Island	Sex	HB	FA	EA	TIB
Thomas, 1888a	B.M.88.1.5.16*	Guadalcanal	F	51	51	17	22
Tate, 1941	B.M.88.1.5.1	Guadalcanal	F	-	51	-	-
Flannery, 1995	-	-	F	46.6	49.3	18.5	22.4
Thomas, 1888b	-	Guadalcanal	M	53	50	16.5	23
Flannery, 1995	-	Guadalcanal	M	49	48.6	19	23.2
Tate, 1941	B.M.88.1.5.28	Guadalcanal	M	-	48.5	-	-
Tate, 1941	B.M.89.4.3.5#	Guadalcanal	M	-	37	-	-
Lavery <i>et al.</i> , 2013	BPBM-24473	Ngella	M	52	51	21	23
Lavery <i>et al.</i> , 2013	JM19844	Ysabel	F	31	19.9	8.7	10.3

HB head-body length; FA forearm length; TL tail length; EA ear length from tip to ear notch; TIB tibia length. *Holotype. #Specimen regarded as a juvenile by Tate (1941).

specimens collected by C.M. Woodford (Thomas 1888a) as being a juvenile, however, JM19844 is the first record of a neonate for the species. *Anthops ornatus* is believed to be a foliage-gleaning insectivore (Bonaccorso 1998; Flannery 1995). All previous specimens have been captured within primary lowland forest below 200m a.s.l (Bonaccorso 1998). This capture thus extends the upper known altitudinal limit of the species to 411 m a.s.l.

Most published records of this species do not specify collection localities. We have completed extensive searches of caves within the species' range but are yet to encounter an *A. ornatus* roost. Given this, and the apparent rarity of captures, it is possible *A. ornatus* does not roost in caves but instead utilises hollow trees or strangler figs (*Ficus* spp.). In northern Queensland, Australia, the rainforest hipposiderid *Hipposideros semoni* Matschie, 1903 is a non-obligate cave roosting species and single individuals or small groups have been encountered in hollow trees (Van Deusen 1975; Churchill 2008; G. Hoyer personal communication).

The apparent rarity of *A. ornatus* and the rapid loss of its primary lowland forest habitat raise concern for the species' conservation. It was previously listed as *Vulnerable* under the IUCN *Red List of Threatened Species* (Baillie & Groombridge 1996) but at present is listed as data deficient (IUCN 2011). Only five records of the species have been published since the original specimens were collected in 1888 and we identified only 19 museum specimens in a review of major museum collection databases. All records have come from primary lowland forest, a habitat type predicted to face exhaustion from commercial logging by the year 2015 (URS 2006)

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Literature Cited

- Baillie, J. & Groombridge, B. (eds). 1996. 1996 IUCN Red List of Threatened Animals. IUCN, Gland, Switzerland.
- Blyth, E. 1853. Report of the curator, Zoological Department. *Journal of the Asiatic Society of Bengal* 22: 408-417.
- Bonaccorso, F. 1998. 'Bats of Papua New Guinea.' (Conservation International: Washington, D.C.)
- Bowen-Jones, E., Abrutat, D., Markham, B. & Bowe, S. 1997. Flying foxes on Choiseul (Solomon Islands) - the need for conservation action. *Oryx*, 31: 209-217.
- Churchill, S. 2008. 'Australian Bats.' (Allen & Unwin: Crows Nest).
- Flannery, T. 1995. 'Mammals of the South-west Pacific and Moluccan Islands.' (Reed Books: Chatswood).
- IUCN 2011. 'IUCN Red List of threatened species (Version 2011.2).' Available at: www.iucnredlist.org [accessed 28 March 2012].
- Jin, L., Lin, A., Sun, K., Liu, Y. & Feng, J. 2010. Postnatal growth and age estimation in the ashy leaf-nosed bat, *Hipposideros cineraceus*. *Acta Chiropterologica* 12: 155-160.
- Matschie, P. 1903. Die Chiropteren, Insectivoren und Muriden der Semon'chen Forschungsreise. *Denkschriften der Medicinisch-Naturwissenschaftlichen Gesellschaft zu Jena* 8: 771-778.
- Mayr, E. & Diamond, J. 2001. 'The birds of Northern Melanesia: speciation, ecology & biogeography.' (Oxford University Press: New York.)
- Sanborn, C. 1931. Bats from Polynesia, Melanesia and Malaysia. *Field Museum of Natural History Publications, Zoological Series*, 2: 7-29.
- Tate, G. 1941. Results of the Archibold expeditions. No. 36. Remarks on some old world leaf-nosed bats. *American Museum Novitates*, 1140.
- Thomas, O. 1888a. Diagnoses of six new mammals from the Solomon Islands. *The Annals and Magazine of Natural History* 1: 155-158.
- 1888b. The mammals of the Solomon Islands, based on the collections made by Mr. C.M. Woodford during his second expedition to the archipelago. *Proceedings of the Zoological Society of London*, 56: 470-484.
- Troughton, E.L.G. 1936. The mammalian fauna of Bougainville Island, Solomons Group. *Records of the Australian Museum* 19: 341-353.
- URS Sustainable Development. 2006. Solomon Islands Forestry Management Project (SIFMP11). National Forest Resource Assessment Update 2006. Honiara, Solomon Islands.
- Van Deusen, H.M. 1975. History of Semon's horse-shoe bat in Australia. *The North Queensland Naturalist*. 42: 4-5.
- Tyrone Lavery, School of Agriculture and Food Sciences, The University of Queensland, Gatton, Queensland Qld 4343, Email: tyrone.lavery@uq.edu.au; Patrick Pikacha and Myknee Sirikolo, Solomon Islands Community Conservation Partnership, Honiara, Solomon Islands. Accepted: 30 October 2012.

The genus *Terepsalta* Moulds (Insecta: Cicadidae: Cicadettinae: Cicadettini) in Queensland, including the description of a new species

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ABSTRACT

The new genus *Terepsalta* Moulds, 2012, has recently been described with type species *Cicada infans* Walker. The original types now representing this species are *Cicada infans* Walker 1850 and *C. abbreviata* Walker 1862, the latter a later synonym with *C. infans*, both held in the British Museum of Natural History, and labelled as collected from Adelaide. No further specimens are known from South Australia. Cicadas collected from semi-arid grasslands of southern-central and southwestern Queensland, however, correspond closely to the types and are here identified as *T. infans*. A new species, *T. leichhardti*, is described from Mt Isa, north-western Queensland. The calling songs of both species are documented. □ *Cicadas, calling songs, song structures, song analyses, Queensland, taxonomy, semi-arid grasslands.*

This work results from the ongoing systematic collection of cicadas throughout Queensland. Such surveys continue to uncover previously undescribed species, especially smaller species, occurring in a wide range of woodland, heath and grassland habitats (e.g. Ewart & Marques, 2008). An important adjunct of the collection of specimens is the aural recording of their songs, which are valuable taxonomic tools (e.g. Young, 1972; Simmons & Young, 1978; Ewart, 1988, 1989, 1998, 2005; Simões *et al.*, 2000; Ewart & Popple, 2001; Sueur, 2002; Popple & Strange, 2002; Popple, 2003; Sueur & Aubin, 2004; Pinto-Juma *et al.*, 2005; Quartau & Simões, 2006; Seabra *et al.*, 2006). In fact, in the field, calling songs provide an efficient means for identifying known species, and for recognising new species and species complexes.

In this paper, I redescribe *Terepsalta infans* and describe a new species belonging to this genus, including documenting their calling songs.

Abbreviations. *Institutions and collections.* ANIC, Australian National Insect Collection, Canberra; AE, private collection of A. Ewart, Caloundra; BMNH, the Natural History Museum, London; LWP, private collection of L.W. Popple, Brisbane; MSM, private collection of M.S. Moulds, Kuranda; QM, Queensland Museum, Brisbane. *Collectors and general.* NP, National Park; EP, Environmental Park; Rd, Road; H.S., Hstd., Homestead (agricultural property); Hwy, highway; Rec, recorded (= aural/electronic song recording); sp, species; spec, specimen; AE, A. Ewart; I.R., I. Rattray; J.N., Jack Nowland; SWQ, south-western Queensland; NWQ, north-western Queensland; PS refer to Queensland Museum photographic numbers.

MATERIALS AND METHODS

Anatomical terminology follows Moulds (2005, 2012) for general body shape and wing characters, Dugdale (1972) and Moulds (2005, 2012) for genitalia; de Boer (1999) for opercula,

and Simmons and Young (1978), Dugdale (1972) and Bennet-Clark (1997) for timbals. The timbal long ribs are referred to sequentially as ribs numbered 1 to 5, with rib 1 being the most distal (adjacent to timbal plate). The higher classification adopted in this paper follows Moulds (2012).

Measurements (in mm) are given as ranges and means (in parentheses) and include the largest and smallest specimens available. Head width is across the outer margins of the compound eyes; pronotum width across the lateral margins (excluding amplified lateral angles); abdomen width across the outer edges of the auditory capsules. Abbreviations used are: BL, total body length; FWL and FWB, forewing length and maximum breadth; HW, head width; PW, pronotum width; AW, abdomen width; FWL/BR, forewing length/breadth ratio.

Song Recordings and Analyses. Details of aspects of the methods used for acoustic song recordings, and the accompanying analyses are outlined in Ewart & Marques (2008). Field recordings are generally preferred for detailed analyses of the finer scale syllable structures of the songs and for frequency analyses using amplitude and power spectra. In the case of the *Terepsaltas*, their very small size, the low amplitude and relatively high frequency of their songs necessitates that the recording microphone be placed close to the singing insects, ideally within 1 to 2 m (thus parabolas should not be used). One option used was to use open net cages placed in the field locations of the cicadas. Container recordings, in contrast, allow very low-background noise recordings illustrating subtleties within their temporal characteristics, but commonly distort the finer pulse structures of the songs. Recordings of *T. infans* were made with a Marantz PMD660 Solid State recorder, and for the new species a Sony Walkman cassette recorder WM-D6C (with upper frequency response limited to 18 kHz), both in conjunction with a Sennheiser model K6/ME66 microphone. For the Marantz PMD660, recordings were made in PCM mode at sampling rate of 48 kHz. Although manufacture specifications indicate frequency responses of microphone and recorder to 20.0 kHz (-3.0dB) at 44.1 kHz sampling rate, bat detector comparisons

indicate frequency responses to 24 kHz. Processing of recordings was undertaken with Avisoft SAS LabPro software. Amplitude spectra were produced using a 556-point Fast Fourier Transform with Hamming window. As the amplitude spectra of the *Terepsalta* species exhibit broad band frequencies, a "dominant frequency" parameter is used, this being the mean (or inferred mean) frequency of the total amplitude dominant frequency envelope as seen in the amplitude and power spectra. The extents of this envelope are shown in the amplitude spectra presented.

Terepsalta Moulds, 2012

Type species: *Terepsalta infans* (Walker, 1850)

Included species. *infans* (Walker, 1850), comb.n. Moulds, 2012: *leichhardti* sp. nov.

Diagnosis (slightly modified after Moulds, 2012). Small cicadas, total body lengths <13 mm. Head width, including compound eyes slightly wider than thorax, but not as wide as abdomen across auditory capsules; supra-antennal plate meeting eye; compound eyes separated from pronotum along outer ventral margin; distance between lateral ocelli slightly less than between lateral ocelli and eyes; rostrum clearly reaching mid coxae but not beyond. Postclypeus rounded transversely across ventral midline, also as seen in anterior and dorsal view; lateral margins of pronotum in dorsal view approximately parallel sided; pronotal collar width less than diameter of eyes; paranota confluent with adjoining pronotal sclerites; no mid lateral tooth; cruciform elevation wider than longer; metanotum clearly visible at dorsal midline. Abdomen broadly cylindrical between tergites 1 to 5, tapering posteriorly on tergite 6, more strongly tapered on tergites 7 and 8; widest part of abdomen across auditory capsules; epipleurites not reflexed to ventral surface; tergite 1 narrowed across dorsal midline; tergite 2 usually wider than tergite 3 along dorsal midline; sternites III to VII in cross-section weakly convex laterally, often somewhat flattened ventrally, not unusually swollen.

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Fore wings hyaline, relatively short and broad (length/breadth ratios 2.3-2.6), similar in length to body; 8 apical cells; no subapical cells; ulnar cell 3 angled to radial cell; basal cell long and narrow; costal veins translucent and slightly higher than the R+Sc; costa parallel-sided to node, uncurved to gently curved (male); vein CuA weakly bowed so that the cubital cell of similar width to medial cell; veins M and CuA not touching or fused at basal cell; vein RA₁ not closely aligned with Sc, but vein RA is aligned with Sc; vein CuA₁ divided by cross vein m-cu such that the proximal portion may be shorter or nearly equal to distal segment; veins CuP and 1A fused in part; distance between cross veins r and r-m similar to distance between r-m and m; apical cells 3-6 approximately equal to ulnar cells (some longer, some shorter); radial cell clearly shorter than distance from its apex to wing tip; 3 distal vein sections of M that form inner margin of radial cell are of unequal length; basal cell slightly translucent, hyaline; infuscation absent; wing outer margin developed for its whole length, never reduced to be contiguous with ambient vein. Hind wings hyaline; most commonly with 5, but varying from 3 to 6 apical cells; no infuscation; width of 1st cubital cell at distal end about twice that of 2nd cubital cell; anal lobe moderately broad with 3A vein curved, long and separated from wing margin; veins RP and M fused basally. Fore legs with 3 erect spines. Male operculae reaching margin of tympanal cavity, directed towards disto-medial margin of tympanal cavity; broadly rounded along distal and lateral margins, more linear along medial margin; gently domed across dist-medial area; operculae not meeting medially; clearly raised above tympanal cavity along its outer margin; developed asymmetrically around meracanthae, these located towards midline; meracantha spikes well developed, just overlapping operculae. Timbals with 5 long ribs, rib 5 shortest, rib 4 not continuous medially, ribs 1 to 3 fused ventrally, and also dorsally with basal spur; basal dome on timbal plate elongated, relatively prominent; anterior part of timbal plate mostly occupied by ribs; posterior margin of timbal cavity ridged on lower half; timbals not extended below wing

bases; 2 to 3 small inter-rib sclerites; timbal covers absent.

Male genitalia; pygofer in ventral view sub-ovoid to ovoid in shape; distal portion of upper pygofer lobes not widest point; pygofer with distal shoulders not developed; upper lobes flat, moderately developed, set well away from dorsal beak, moderately acutely terminated distally; basal lobes undivided, moderately developed, broadly rounded in lateral view, abutted against pygofer margin, slightly indented at distal terminations; dorsal beak present, relatively sharp apex, part of chitinized pygofer; uncas relatively small, flattened, more or less duck-billed shape; claspers well developed, dominant, restraining aedeagus, slightly flattened, outer face with an overhanging lip along margin, unfused, lacking an inward facing swelling on proximal half of inner margins and diverging gently towards distal ends, their apices not widely separated; aedeagus with basal plate in lateral view undulated, weakly depressed on dorsal midline, in dorsal view as long or longer than broad, apically broadened with 'ears'; basal portion directed forwards away from thecal shaft; junction with theca and basal plate with a functional 'hinge' that poses a chitinous back; thecal shaft relatively straight; pseudoparameres present, dorsal of theca and originating distal of thecal base, unfused throughout their length, in dorsal view slightly undulated and diverging apically, in lateral view aligned with thecal shaft; endotheca exposed, soft, entirely fleshy; endothecal ventral support present, shorter than pseudoparameres; thecal apex chitinized.

Terepsalta infans (Walker, 1850

(Figs 1-5, 8, Plates 1A-D, 2A-B, Table 1)

Cicada infans Walker, 1850: 201 (*nec* Walker 1862:304)

Tibicen infans (Walker): Stål, 1862: 485

Cicada abbreviata Walker 1862: 303-304

Melampsalta abbreviata (Walker): Goding and Froggatt, 1904: 649-650

Quintilia infans (Walker): Distant, 1906: 144 (*nec* Froggatt, 1907:352)

Terepsalta infans (Walker): Moulds, 2012: 216-219

Distant (1906) synonymised *C. infans* (type is a female held in BMNH) and *C. abbreviata* (Walker), type is a male also held in the BMNH.

Moulds (2012) has accepted this synonymy, and this is followed here. Plate 1 illustrates these two type specimens. As documented in Moulds (2012), both the type specimen locations are labelled as 'Adelaide'. No further specimens of this species are known from Adelaide, or indeed from South Australia.

Collecting in central and south-western Queensland has, however, revealed the presence at multiple locations of small dark grass cicadas which very closely match the characters of the types of *T. infans* and are here specifically identified as *T. infans*. The following descriptions are based on representative specimens from central and south-western Queensland, together with analyses of their calling songs. Until such time when further specimens of *T. infans* are captured in South Australia, and their calling songs documented, there could remain some doubt about the true identity of this species, but the overall similarities with the type specimens are noteworthy. Nevertheless, comparison of Plates 1, 2 and 4 indicates that the type specimens have more extensive darker pigmentation of the tergites than the Queensland specimens. The semi-arid grassland habitats in which the Queensland specimens occur suggests that the types may actually have come from dryer grassland areas north or northeast of Adelaide, rather than Adelaide City.

Material. Queensland: 14♂, 35 km W. Barcaldine, C.Q., grass, A.E., 15.i.2002, 23°31.94'S 144°56.51'E; 10♂, 2♀, ~8.2 km E Longreach, C.Q., grass, A.E., 16.i.2002, 23°26.67'S 144°19.19'E; 1♂, "Big Hole", Vergemont Cks, Tonkoro Rd, W. of Noonbah H.S., SWQ, A.E., 30.i.2009, 24°05'14.8"S 143°07'45.2"E; 2♂, 3♀, Dam, Milroy Hst, ~70 km N. Quilpie, SWQ, grass, A.E., I.R., J.N., 13.i.2000; 26°02.85'S 144°20.81'E; 2♂, 6.7 km E. Longreach airport, along Hwy, C.Q., grassland, A.E. 10.i.2008, flood plain, 23°26.73'S 144°20.18'E; 1♂, 2♀, Buffel grass, Blackall, C.Q., early.ii.1979, after rains, Qld. Dept. of Primary Industries; 10♂, 7.7 km N. Milroy Hstd, ~70 km N Quilpie, SWQ, grass, A.E., I.R., 9.i.2000; 25°59.98'S 144°24.37'E; 1♂, 10 km ESE Blackall, W.Q., grassland, 25.ii.2007, A.E., 24°27.56'S 145°33.27'E; 1♂, 51 km NNW Blackall, C.Q., grass, A.E., 15.i.2002, 24°04.27'S 145°19.94'E; 1♂, 42 km NNW Blackall, SWQ, grass, A.E., 15.i.2002, 24°08.38'S 145°20.72'E; 2♂, 23 km NW Longreach, CQ., grass, A.E., 17.i.2002, 23°14.54'S 144°06.39'E; 2♂, Bulloo R. crossing, Milroy/Bulls Gully Hstds., ~70 km N. Quilpie, SWQ, A.E., I.R., 9.i.2000, 25°59.38'S 144°25.79'E; 1♂, 11.7 km E. Noonbah H.S., Tonkoro Rd, Lochern N.P.,

SWQ, Mitchell grassland, A.E., 19.ii.2009, 24°06.46'S 143°18.11'E (AE). 1♂, 7.7 km N. Milroy Hstd, ~70 km N Quilpie, SWQ, grass, A.E., I.R., 9.i.2000; 25°59.98'S 144°24.37'E (LWP). 1♂, (molecular voucher 09.AU. QL.VER.01), Vergemont R. channels, Noonbah Stn, 24° 05.327'S 143° 08.773'E, 30.i.2009, K. Hill, D. Marshall, A Emmott; 1♂, 1♀, (teneral), Noonbah Stn, Vergemont R. channels, 24° 5.327S 143° 8.773'E, 14.i.2002, Cooley, Hill, Cowan, Marshall, Moulds; 2♂, 2♀, Noonbah Stn, 24° 07'S 143° 11'E, 17.i.2002, A.J. Emmott & R. Ballard (MSM). 1♂, 7.7 km N. Milroy Hstd, ~70 km N Quilpie, SWQ, grass, A.E., I.R., 9.i.2000; 25°59.98'S 144°24.37'E; 1♀, ~8.2 km E Longreach, C.Q., grass, A.E., 16.i.2002, 23°26.67'S 144°19.19'E (QM). 1♂, 7.7 km N. Milroy Hstd, ~70 km N Quilpie, SWQ, grass, A.E., I.R., 9.i.2000; 25°59.98'S 144°24.37'E (ANIC)

Description. (Male). Fig. 1, Plates 1C, D, 2A, B. Specimens exhibit continuous variability in the extent and intensity of the darker pigmentation of especially the thorax and abdomen. The darker forms are more prevalent, but in the following descriptions, note is made of the deviations of pigmentation in the paler specimens.

Head. Supra-antennal plate, vertex and frons generally shiny black, small pale brown patches adjacent to pedicels; mandibular plate and gena shiny black to deep brown, covered by silvery-yellow pubescence; sandy brown along the depressed epicranial suture, extending between the lateral ocelli, and joining with the pronotal central fascia; ocelli pale red; compound eyes dark brown. Postclypeus shiny black to deep brown medially and dorsally, extending outwards along transverse ridges into the pale brown outer margins; diffuse dorso-medial pale brown spot; anteclypeus deep brown, paler towards rostrum; rostrum brown, darker apically.

Thorax. Pronotum in most specimens predominantly deep brown to black, paler brown along and adjacent to paramedian fissures; central fascia narrow, pale brown, not quite reaching pronotal collar, with black margins widening along the anterior and posterior pronotal margins; pronotal collar mostly black, lateral margin ampliate; in paler specimens, pronotum has extensive but broken black colouration between paramedian and lateral fissures, extending to pronotal collar, the remainder brown, central fascia off-white to pale brown with more prominent narrow black margins widening along anterior and posterior

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TABLE 1. Summary of song parameters of calling song of *Terepsalta infans*.

Location within phrase	Vergemont channels Noonbah, 135 km SW Longreach, S.W. Q.(1)	6.7 km E. Longreach, central Queensland(2)
1. Phrase lengths (seconds) ⁽³⁾	13.9±4.0 [7.1-25.0] n=28	14.6±2.8 [10.9-20.8] n=8
2. Initial echeme element Durations of closed macrosyllables Mean (ms)	222±59 [114-339] n=46 (4.5Hz) (8.8-3.0Hz)	171±40 [81-314] n=33 (5.8Hz) (12.3-3.2Hz)
First 3 sets (ms)	150±29 [114-205] n=15	136±28 [81-154] n=6
Final 3 sets (ms)	275±36 [205-337] n=15	232±49 [193-314] n=6
3. Repetition Rates of ticks within closed macrosyllables Mean (ms)	9.4±1.1 [8.0-13.9] n=98 (106Hz) (125-72Hz)	10.1±1.7 [8.4-13.7] n=53 (99Hz) (119-73Hz)
First 2 ticks	11.5±1.3 [9.3-13.9] n=10 (87Hz) (108-72Hz)	13.4±2.4 [9.9-17.5] n=6 (74Hz) (101-57Hz)
Final 5 ticks	8.6±0.4 [8.0-9.1] n=25 (116Hz) (116-110Hz)	8.7±0.3 [8.4-9.1] n=15 (115Hz) (119-110Hz)
Primary-secondary pulse durations within ticks (ms)	2.79±0.13 [2.6-3.0] n=62 (358Hz) (385-333Hz)	3.49±0.29 [3.1-3.9] n=39 (358Hz) (323-256Hz)
4. Open macrosyllables – tick repetition rates Mean (ms)	37.8±6.2 [20-51] n=53 (26Hz) (50-20Hz)	47.9±8.6 [23-75] n=47 (21Hz) (43-13Hz)
Primary-secondary pulse durations within ticks (ms)	2.77±0.17 [2.5-3.1] n=41 (361Hz) (400-323Hz)	3.32±0.10 [3.1-3.5] n=21 (301Hz) (323-286Hz)
5. Post-echeme microsyllable element Number of microsyllables Microsyllable repetition rates (ms)	23.2±8.1 [9-42] n=30 323±24 [298-382] n=34 (3.1Hz) (3.4-2.6Hz)	26.0±4.4 [16-32] n=9 267±19 [246-315] n=28 (3.7Hz) (4.1-3.2Hz)
Tick repetition rates within microsyllables (Hz)	136±3 [129-140] n=29 (7.4ms) (7.8-7.4ms)	126±3 [119-131] n=26 (7.9ms) (8.4-7.6ms)
Number of ticks per microsyllable	3-5	4-5
Primary-secondary pulse durations within ticks (ms)	2.87±0.12 [2.6-3.1] n=54 (348Hz) (385-323Hz)	3.74±0.15 [3.3-4.0] n=34 (267Hz) (303-250Hz)

(1) Recorded in open net, in the field with microphone, 30.i.2009, 24°05.25'S, 143°07.75'E, Mitchell grassland.

(2) In situ field recording with microphone, 10.i.2008, 23°26.73'S, 144°20.18'E, Mitchell grassland.

(3) Figures represent: Mean; ± 1s; range (in square brackets); n=number of measurements; and equivalent Hz (or ms) in pa.

TABLE 2. Summary of song parameters of calling song of *Terepsalta leichhardti* (1)

Location in phrase	Mean	σ	n	Range
1. Phrase lengths (seconds)	15.5	6.5	12	3.5-25.5
2. Echeme				
A. Initial microsyllables				
Number of ticks per microsyllable	5.3	1.6	39	2-8
Primary-secondary pulse duration within ticks (ms)	3.96	0.40	60	3.0-4.4
Tick repetition rate within each microsyllable (Hz)	120 (8.3ms) ⁽²⁾	4	32	112-129 (8.9-7.8ms)
B. Macrosyllable ticking phase				
Number of ticks	31	7	10	17-40
Tick repetition rates (ms)	41.1 (24Hz)	4.1	88	32.2-53.6 (31-19Hz)
Primary-secondary pulse durations (ms)	3.22 (311 Hz)	0.14	68	2.9-3.7 (345-270Hz)
3. Post-echeme microsyllable phase				
Number of microsyllables	44	19	12	14-76
Number of ticks per microsyllable	3.3	0.6	207	2-5
Microsyllable repetition rates (all data) (ms)	323 (3.1Hz)	71	140	149-436 (6.7-2.3Hz)
Microsyllable repetition rates - First 20 microsyllables (ms)	262 (3.8Hz)	49	60	149-346 (6.7-2.9Hz)
Microsyllable repetition rates - Final 20 microsyllables (ms)	361 (2.8Hz)	42	60	279-436 (3.6-2.3Hz)
Tick repetition rates within each microsyllable (Hz)	129 (7.8ms)	6	52	114-135 (8.9-7.4ms)
Primary-secondary pulse durations within ticks (ms)	3.59 (278Hz)	34	119	3.0-4.1 (333-244Hz)

(1) Container recordings, specimens from 2.2 km south of Mt Isa town, NW Queensland, 22.i.2002, 20°44.62'S, 139°29.72'E.

(2) Figures in parentheses are equivalent values in Hz or ms, as appropriate.

pronotal margins. Mesonotum predominantly dark brown to black, often obscuring the outlines of the sigilla; parapsidal sutures pale brown extending distally as thin, diffuse brown lines along inner margins of lateral sigilla; lateral sigilla extend to just beyond anterior cruciform elevation arms; cruciform elevation translucent pale brown, dark brown to black between anterior and lateral arms; pale brown along and between wing grooves; in paler specimens, the sigilla are more clearly defined,

the intervening colouration varying from pale yellow to brown.

Wings. Fore wing costal vein very pale brown tending to translucent; remaining venation colour medium brown proximally, becoming paler brown apically; basal membrane translucent pale grey-brown. Hind wing mostly very pale brown, darker proximal to mesonotum; weakly developed off-white plaga around anal cell 3 and adjacent to veins 3A and 2A; 5 apical cells most common, but a few

Terepsalta Moulds

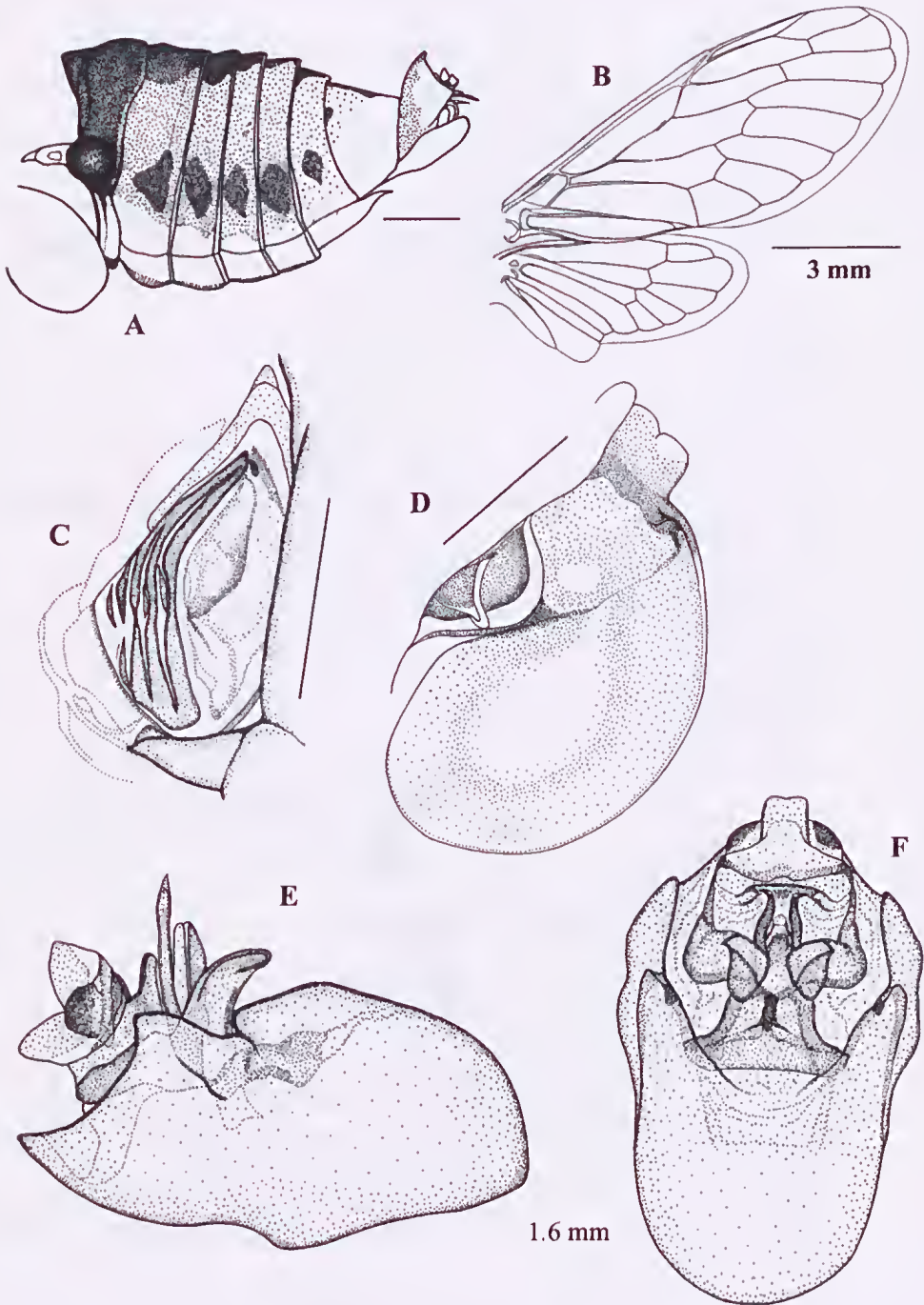


FIG.1. *Terepsalta infans*. 7.7 km N. Milroy H.S., ~ 80 km N. of Quilpie, SW Queensland. (A), lateral abdomen view; (B), fore and hind wings; (C), timbal (posterior margin at right, dorsal edge at top); (D), right operculum; (E) and (F), pygofer and male genitalia, lateral and ventral views, respectively. Scale bars 1 mm, except wings (3 mm).

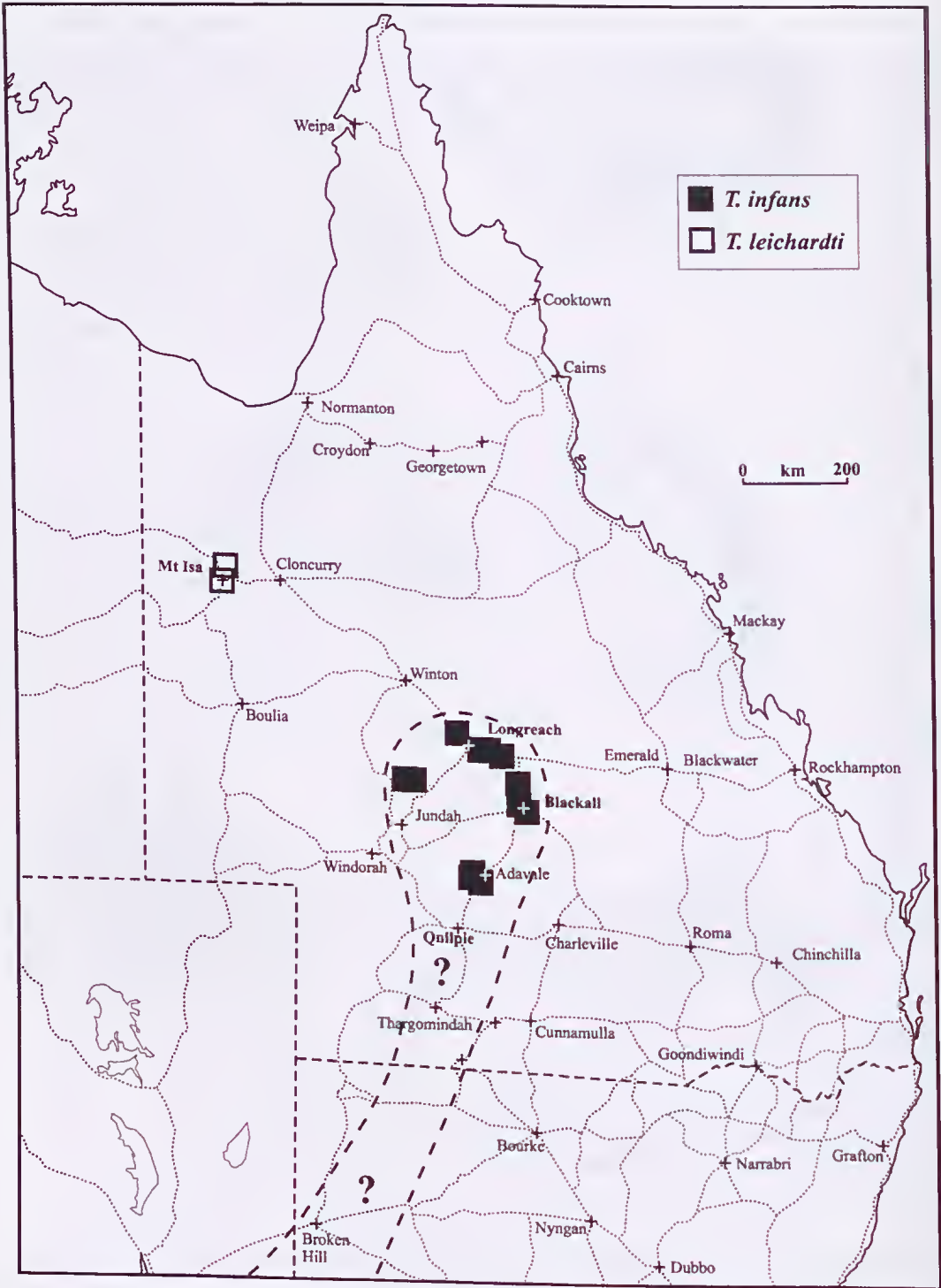


FIG. 2. Distribution records of the two known *Terepsalta* species in Queensland.

Terepsalta Moulds

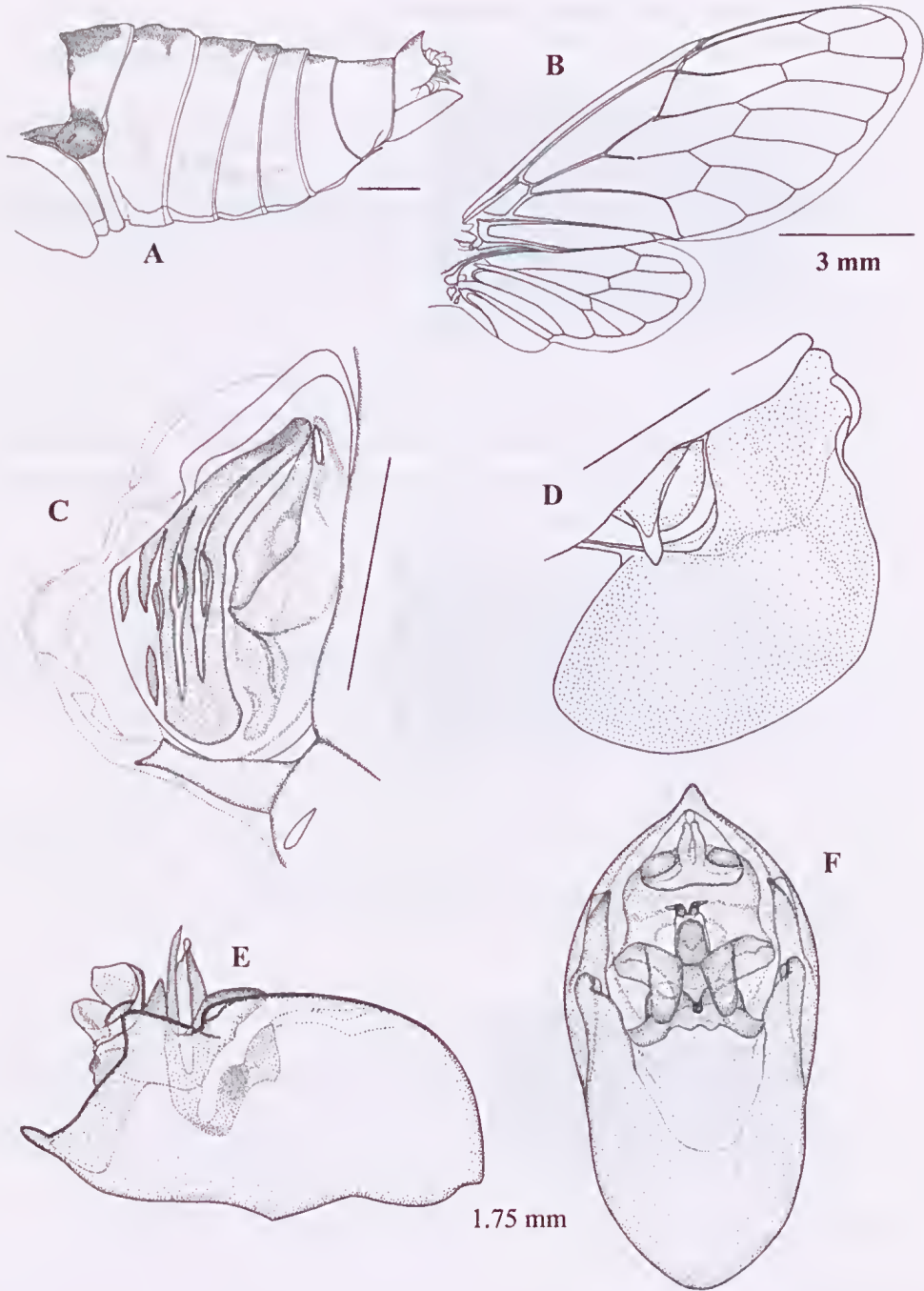


FIG. 3. *Terepsalta leichhardti* sp.nov., 2.2 km S. of Mt Isa and 6 km NE Mt Isa. (A), lateral abdomen view; (B), fore and hind wings; (C), timbal (posterior margin at right, dorsal edge at top); (D), right operculum; (E) and (F), pygofer and male genitalia, lateral and ventral views, respectively. Scale bars 1 mm, except wings (3 mm).

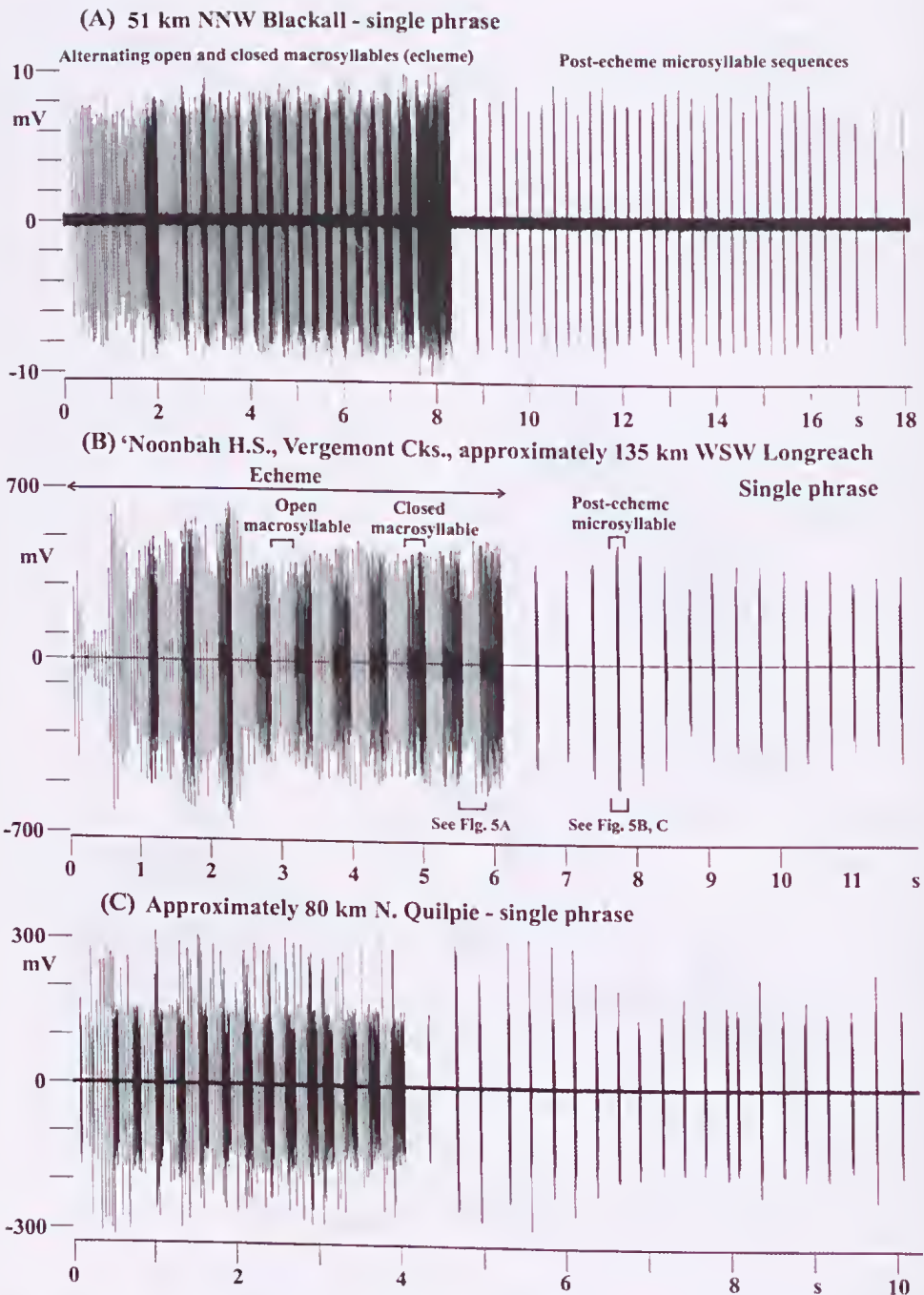


FIG. 4. *Terepsalta infans*. Waveform plots of calling songs showing the gross temporal structures of the phrases, specifically the echeme and post-echeme microsyllable elements. (A), 51 km NNW of Blackall, Central Queensland, container recording, 15.i.2002, filtered to 14 kHz. (B), 'Noonbah' H.S., Vergemont Creeks, approximately 135 km WSW of Longreach, SW Queensland, field recording in open cage, 30.i.2009, filtered to 14 kHz. (C), 80 km N. of Quilpie, SW Queensland, container recording, 9.i.2000, filtered to 1 kHz.

Terepsalta Moulds

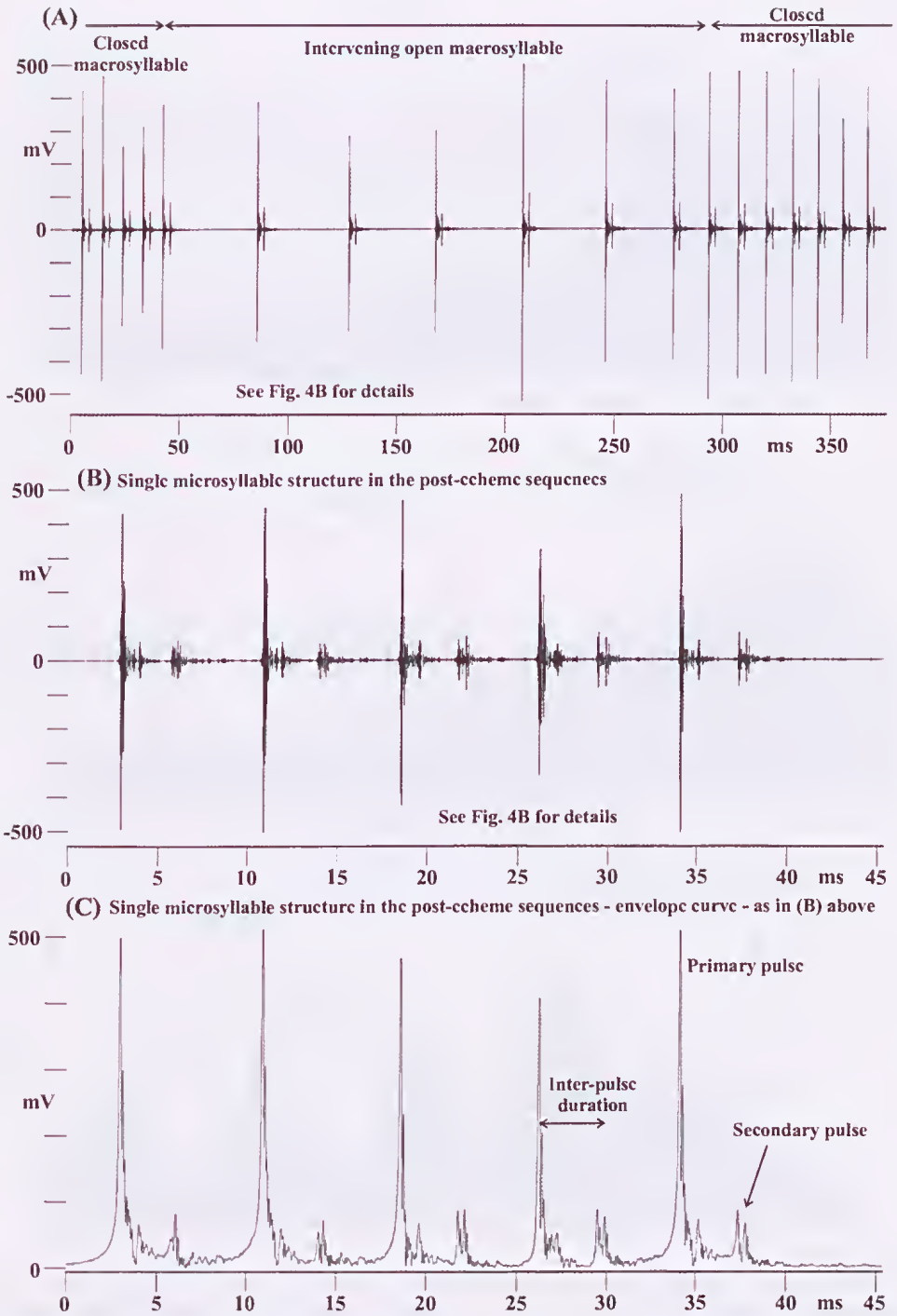


FIG. 5. *Terepsalta infans*. (A), time expanded waveform plots showing the tick structures within the closed macrosyllables and the intervening open macrosyllable. (B), higher resolution waveform plot of the tick structures within a single post-echeme microsyllable. (C), envelope curve plot of the same tick sequence shown in (B). The precise locations of these plots within each recording is shown in Fig. 4B.

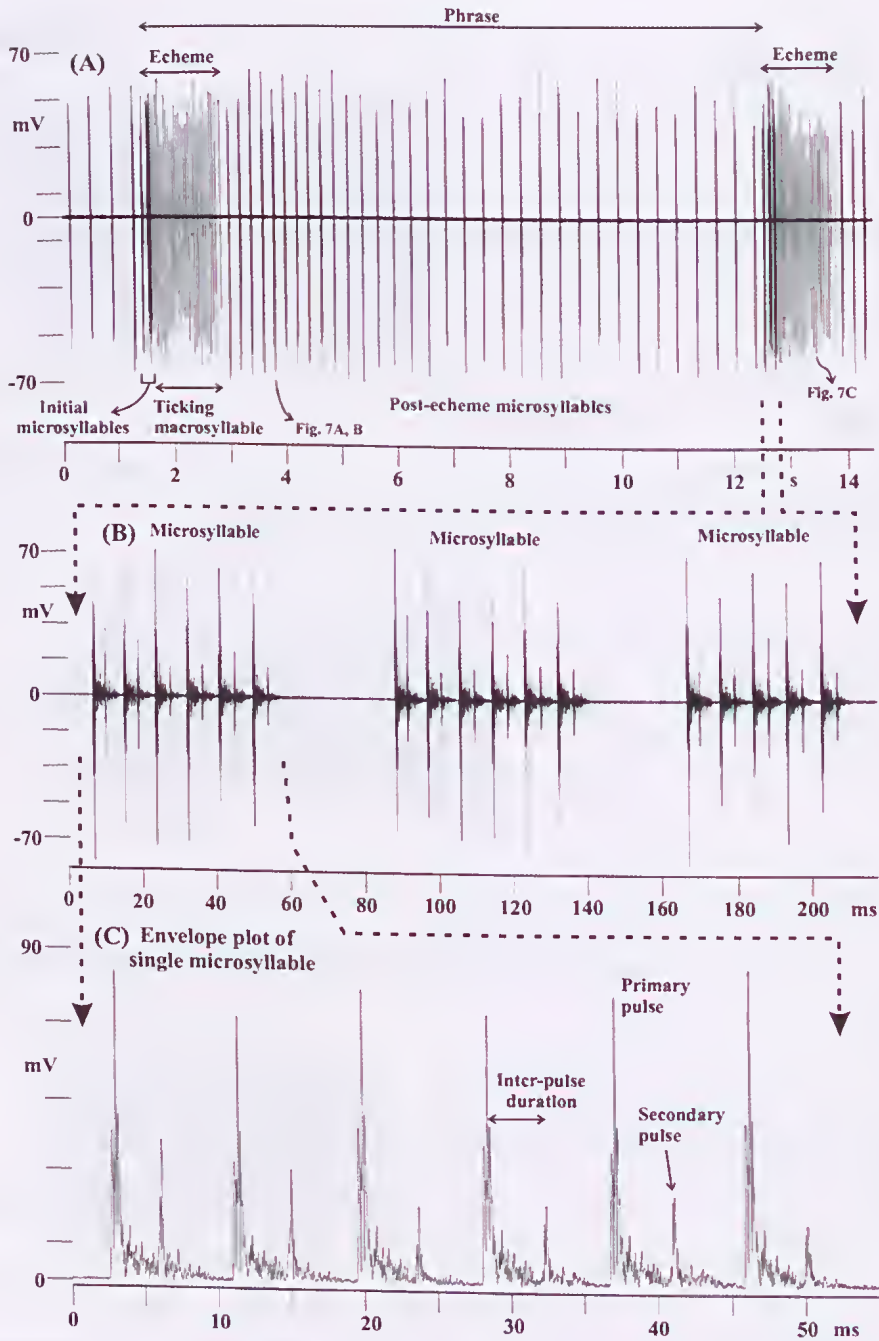


FIG. 6. Waveform plots of the calling song of *Terepsalta leichhardti* sp. nov., from 2.2 km S. of Mt Isa, container recording, 22.i.2002, filtered to 1 kHz. (A), plot of one complete phrase and segments of adjacent phrases, illustrating the echeme and the post-echeme microsyllable elements. (B), time expanded plot of three discrete microsyllables marking the beginning of a phrase, showing the detailed structures of the coalesced ticks. (C), higher resolution envelope curve plot of a single microsyllable shown in (B), revealing greater detail of the pulses and inter-pulse intervals.

Terepsalta Moulds

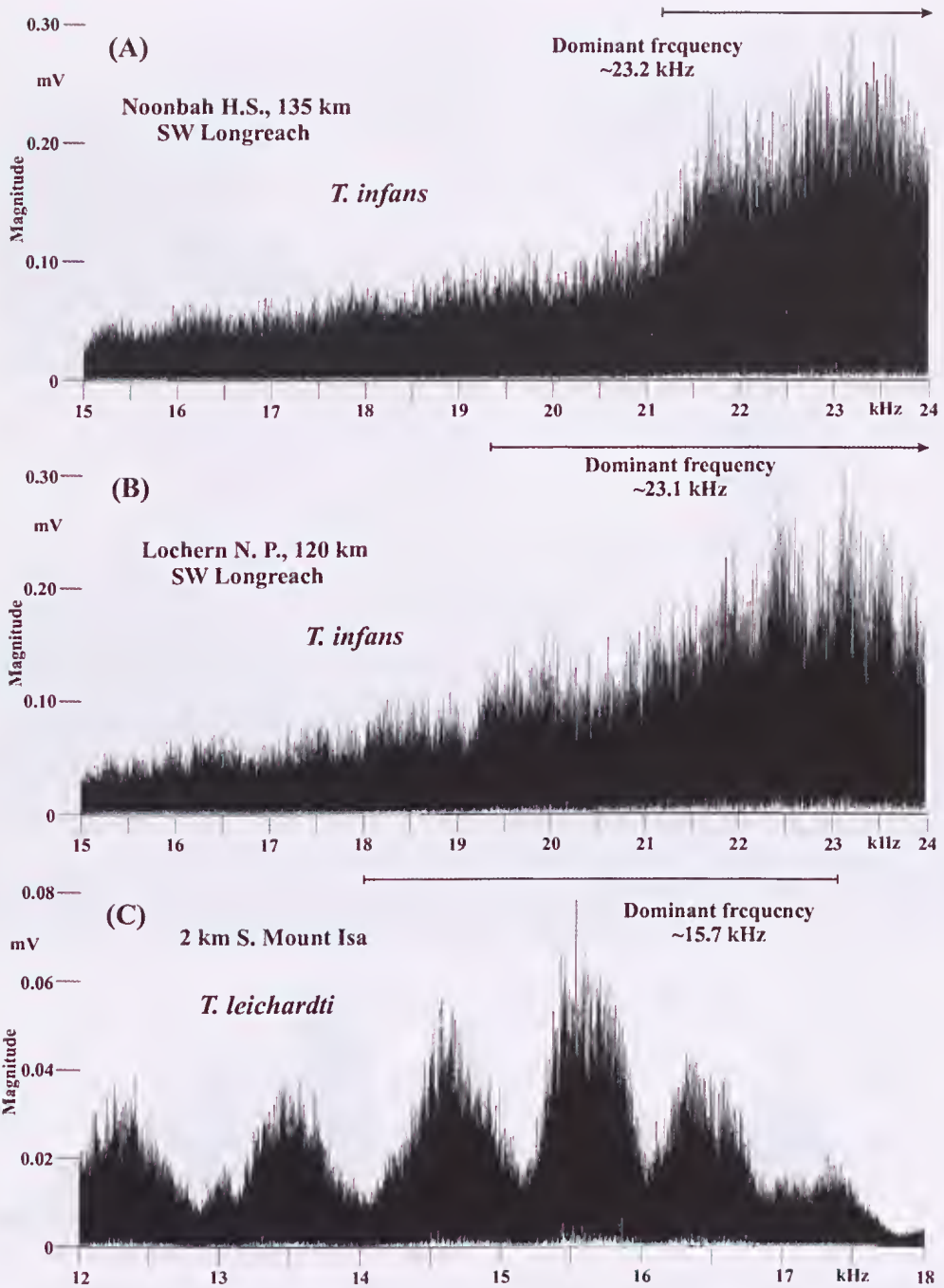


FIG. 7. Higher resolution plots in waveform and envelope curve of the calling song of *Terepsalta leichardti* sp.nov., details as in Fig. 6 caption. (A) Waveform plot of the tick structures within a single post-echeme microsyllable (location shown in Fig. 6A). (B), envelope curve of the tick structures illustrated in (A), defining more clearly the pulse structures. (C), two single ticks within the ticking macrosyllable phase of the echeme (see Fig. 6A). Note the identical tick structures in the different segments of the song.

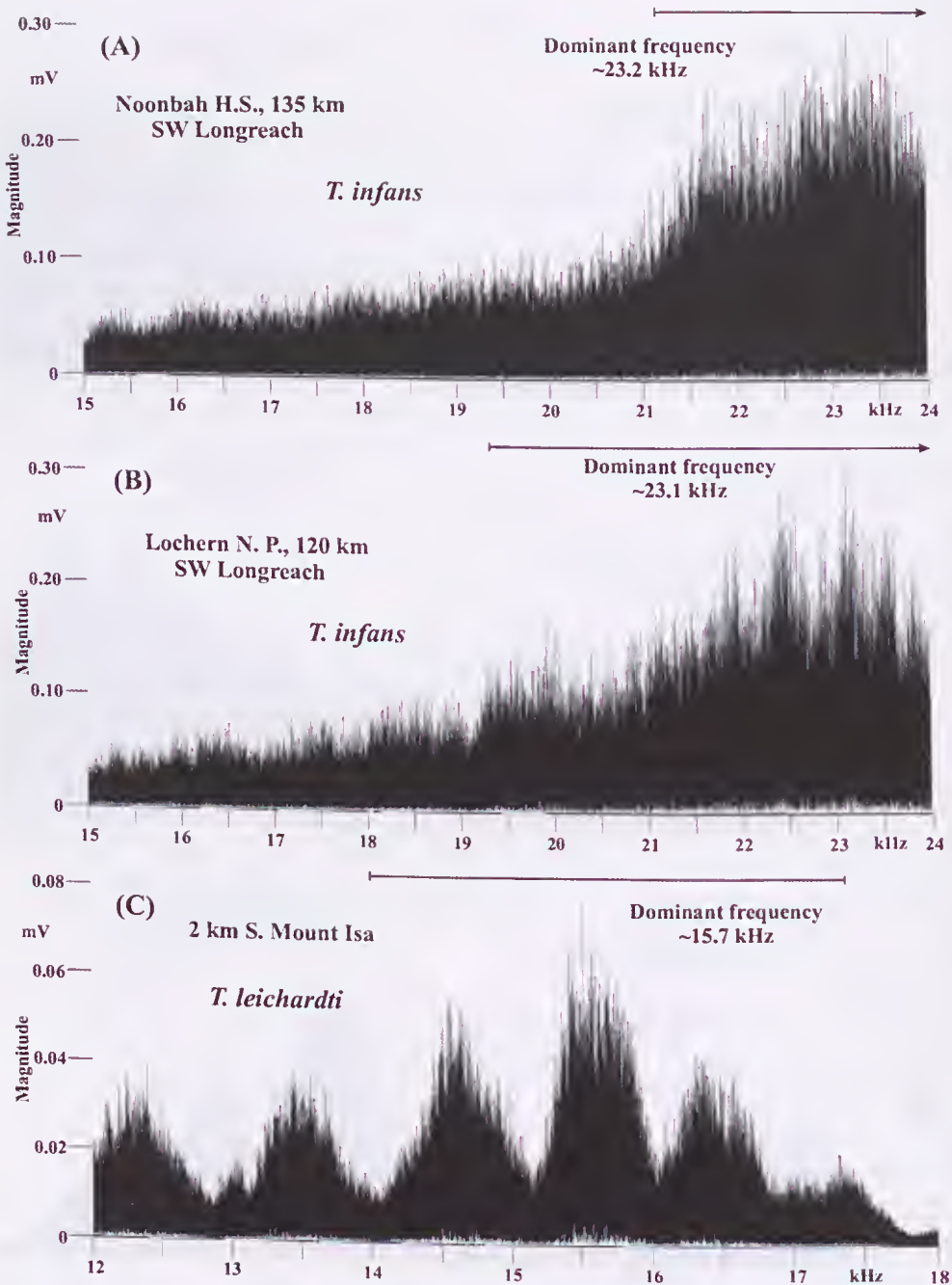


FIG. 8. *Terepsalta infans* (A,B) and *Terepsalta leichardti* sp. nov. (C); amplitude spectra of songs from (A), Noonbah H.S., ~135 km SW Longreach, SW Queensland, field recording in open net, 30.i.2009. (B), Lochern N.P., 120 km SW Longreach, in situ field recording, 20.ii.2009. (C), 2.2 km S Mt Isa, container recording, 22.i.2002. The horizontal bars indicate the inferred high amplitude envelope of each spectrum, used to estimate (in part) the dominant frequency. Note in A, B, that the higher amplitude envelope extends to >24 kHz, but this is limited by the higher frequency resolution (24 kHz) of the recorder used.



PLATE 1. Holotypes of *Cicada infans* Walker (♀) and *C. abbreviata* Walker (♂), dorsal and ventral views, also with label data. Photos by Dr. M.S. Moulds. Fore wing and total body lengths (mm) marked on photos.

specimens have 4, very rarely 3 apical cells; even in specimens with 5 apical cells, some of the cells are small and poorly developed.

Legs. Coxae medium brown with darker brown fasciae on anterior and lateral faces; fore femora medium brown with broad fasciae on lateral faces; mid and hind femora pale brown with thin darker brown fasciae on anterior and dorsal faces, tending paler on hind femora; trochanters brown; tibiae and tarsi of fore legs medium dark brown, pale brown on mid and hind legs; claws brown; spines black to deep brown.

Opercula. Pale brown, black around crest at disto-lateral corner and adjoining lateral margin; black on meracantha, meracantha spikes brown; gently domed in disto-medial area. Shape as in diagnostic details.

Timbals. As in diagnostic details.

Abdomen. Colouration variable in detail. Tergite 1 dominantly black between timbals; tergite 2 is normally dominantly black, in some specimens grading to deep brown distally, extending ventrally to, and on the auditory capsules; tergite 3 deep brown to black, with small



PLATE 2. Males of *Terepsalta infans* from: A, (PS1942), 35 km W. Barcaldine, C.Q., 15.i.2002, 23°31.94'S 144°56.51'E; total body length 10.7 mm; example of slightly paler colouration. B, (PS1943), 10 km ESE Blackall, W.Q., 25.ii.2007, 24°27.56'S 145°33.27'E; total body length 10.7 mm; example of slightly darker colouration.

paler brown area developed laterally; tergites 4 and 5 deep brown to black dorsally, along distal margins (excluding the narrow paler intersegmental membranes), and ventrally grading from medium to dark brown antero-laterally; tergites 6 and 7 usually with reduction of dorsal darker pigmentation which may tend towards dark brown, with dark brown patches ventrally; remaining colouration medium to dark brown, sometimes with faint greenish tinge, usually paler on tergite 7; tergite 8 pale to medium brown with small black area dorsally along distal margin. In paler specimens, a distinct reduction in the extent of the darkest pigmentation is evident, for example, tergite 2 is dominantly black grading to brown on the disto-medial area; tergites 3 to 7 mainly medium brown with black dorso-medial



PLATE 3. Males of *Terepsalta leichhardti*: A, (PS1946), male holotype; total body length 11.5 mm; example of paler colouration: B, example of darker colouration; total body length 12.2 mm. Both specimens from Duchess Rd, 2.2 km S. Mt Isa, NWQ, 22.i.2002, 20°44.62'S 139°29.72'E.

areas, broadest on tergite 3, becoming notably smaller on tergites 4 through to 7; in addition, darker brown ventro-lateral areas extend from near anterior margins distally to intersegmental membranes, but not reaching the ventral tergite margins; tergite 8 is uniformly pale brown. Sternites are pale brown and in most specimens with a well-defined darker brown ventro-medial area (not crossing intersegmental membranes), darkest in sternites II and III, paler and progressively smaller from sternites IV through to VI, forming only a thin fascia in sternite VII, and absent on sternite VIII; these darker dorso-medial areas give general appearance of a dark venter in ventral view; in the paler specimens, the sternites are pale yellow-brown, and the darker ventro-medial areas are more weakly developed, rarely even absent.



PLATE 4. A. Female *Terepsalta infans* (PS1944) from ~8.2 km E Longreach, C.Q., 16.i.2002, 23°26.67'S 144°19.19'E; total body length 11.4 mm. B. Female *Terepsalta leichhardti* (PS1947) from Duchess Rd, 2.2 km S. Mt Isa, NWQ, 22.i.2002, 20°44.62'S 139°29.72'E; total body length 12.5 mm.

Genitalia. Pygofer pale brown laterally, darker brown dorsally, becoming black on beak. Details as in diagnosis.

Female. (Plates 1A, B, 4A) Generally comparable to male, but with a consistent reduction of the extents of the areas of darker pigmentation. Supra-antennal plate pale sandy-brown, vertex and frons pale brown around and between ocelli, extending to pronotal margin; mandibular plate and gena pale sandy brown, silvery pubescence; postclypeus pale brown with darker brown transverse ridges, midline pale yellow; anteclypeus pale brown, brown medial spot; rostrum pale brown, darker apically; ocelli pink; dark brown compound eyes. Pronotum pale brown with some darkening along the paramedian and lateral fissures, and darker thin margin to the central fascia, itself pale brown; mesonotum pale sandy-brown to brown with short, dark brown sub-

medial sigilla; lateral sigilla well defined, with a broken, discontinuous dark brown colour. Legs similar to male. Abdomen: tergite 1 pale yellow-brown; tergites 2-7 pale brown with darker brown dorso-medial areas, broadest on tergites 2 and 3, but progressively narrowing on tergites 4 through to 7, these areas extending across widths of tergites excepting tergites 6 and 7; auditory capsules (tergite 2) pale to medium brown; additionally, small brown patches present ventro-laterally on tergites 3 to 7, extending across widths of tergites to inter-segmental membranes but not reaching ventral tergite margins; tergite 8 pale yellow-brown; tergite 9 pale sandy-brown to pale brown with a pair of paramedial dark brown fasciae which extend distally for three-quarters of length of tergite, to stigma. Sternites uniformly pale sandy-brown with darker ventro-medial pigmentation either weak or absent; ovipositor sheath brown, darker apically, extending 1-2 mm beyond apex of tergite.

Measurements. N = 12♂, 7♀. Ranges and means (in parentheses), mm; BL: ♂ 10.2-11.3 (10.7); ♀ 10.5-11.7 (11.1). FWL: ♂ 10.1-11.2 (10.5); ♀ 10.7-11.3 (10.9). HW: ♂ 3.0-3.4 (3.2); ♀ 3.1-3.3 (3.3). PW: ♂ 2.8-3.1 (2.9); ♀ 2.8-3.1 (3.0). AW: ♂ 3.5-4.0 (3.8); ♀ 3.3-3.8 (3.6). FWL/BR: ♂ 2.32-2.50 (2.40); ♀ 2.38-2.60 (2.47).

Distribution, Habitat and Behaviour. (Fig. 2) Distributed through southern central and south-western Queensland. Specific locations include Blackall (easternmost location), areas between Barcaldine and Longreach, and around Longreach, locations approximately 70-80 km north of Quilpie, and locations in and west of the Lochern National Park extending westwards to the Noonbah HS region, all some 120-135 km southwest of Longreach. It has not been found further north than approximately 25 km north-west of Longreach, or other westerly locations including Windorah, Boulia or further west in the desert areas. The habitat is grassland, sometimes open Mitchell grassland, or grassland within open forest. In all locations, these cicadas occur within the proximity of seasonal water, including near rivers and shallow gullies, dams, ephemeral ponds, and on flood plains. The populations are localised although the cicadas are very mobile within these areas. The relatively high frequency and soft songs

(below), plus their small size make these species inconspicuous in the field. The occurrence of the types in South Australia suggests that this species should occur through the far southwest of Queensland (e.g. Thargomindah and south), far western NSW into South Australia, but peripheral to the desert regions.

Terepsalta leichhardti sp.nov.

(Figs 2, 3, 6-8, Plate 3A, B, Plate 4B, Table 2)

Material. HOLOTYPE: ♂, QMT183443, Duchess Rd, 2.2 km S. Mt Isa, NWQ, grassland, A.E., 22.i.2002, 20°44.62'S 139°29.72'E, PS1946 (QM).

Paratypes. 21♂, 3♀, Duchess Rd, 2.2 km S. Mt Isa, NWQ, grassland, A.E., 22.i.2002, 20°44.62'S 139°29.72'E; 2♂, 2.1 km N. along Moondarra Rd, via Mt Isa, N.W.Q., A.E., 23.i.2002, 20°40.42'S 139°30.52'E. (AE). 1♀, Duchess Rd, 2.2 km S. Mt Isa, NWQ, grassland, A.E., 22.i.2002, 20°44.62'S 139°29.72'E, PS1947 (QM). 1♂, Duchess Rd, 2.2 km S. Mt Isa, NWQ, grassland, A.E., 22.i.2002, 20°44.62'S 139°29.72'E (MSM). 1♂, Duchess Rd, 2.2 km S. Mt Isa, NWQ, grassland, A.E., 22.i.2002, 20°44.62'S 139°29.72'E (LWP). 1♂, Duchess Rd, 2.2 km S. Mt Isa, NWQ, grassland, A.E., 22.i.2002, 20°44.62'S 139°29.72'E (ANIC). 1♂, Duchess Rd, 2.2 km S. Mt Isa, NWQ, grassland, A.E., 22.i.2002, 20°44.62'S 139°29.72'E (BMNH).

Description. (Male) Fig. 3, Plate 3A, B. Specimens exhibit variability in the detail of the extent and intensity of the areas of darker pigmentation of especially the thorax and abdomen.

Head. Supra-antennal plate pale sandy-brown anteriorly; vertex black adjacent to compound eyes, dark brown on frons and adjacent to median ocellus, in part the area anterior of lateral ocelli, and two small areas distally to each lateral ocellus and adjacent to pronotum; remaining areas between and distal to lateral ocelli, including epicranial suture, pale sandy-brown; ocelli pale pink to yellow-brown; compound eyes dark brown. Postclypeus predominantly pale sandy to yellow-brown, black on dorsal surface, with short segments of brown colouration on transverse ridges adjacent to midline; anteclypeus pale yellow-brown, narrow brown along midline; rostrum pale brown, darker brown apically.

Thorax. Pronotum dominantly pale brown, darker in proximity to paramedian and especially lateral fissures, with pale yellow-brown central fascia

extending distally from anterior pronotal margin, not quite reaching pronotal collar; deep brown to black margin on either side of central fascia, broadening anteriorly and splaying outwards along anterior margin; pronotal collar pale yellow-brown, lateral margins ampliate. Mesonotum variable in colour between specimens with broken pale brown to black submedian sigilla and broken pale brown to continuous black colouration defining the lateral sigilla which extend to just beyond the anterior cruciform elevation arms; parapsidal suture defined by a thin golden line; remaining colouration pale to medium sandy brown; cruciform elevation very pale yellow, tending translucent; pale yellow to yellow-brown along and between wing grooves.

Wings. Fore wing costal vein very pale yellow, translucent; venation pale yellow-brown; basal membrane translucent, off-white to very pale yellowish. Hind wing venation very pale yellow-brown; very weakly developed off-white plaga around anal cell 3 and adjacent veins 3A and 2A; 5 apical cells most common, but a significant number of specimens have 4, very rarely 3 or even 6 apical cells; apical cells often variable in size.

Legs. Coxae and trochanters pale yellow-brown; femora pale brown with narrow darker brown longitudinal fasciae; fore tibiae and tarsi brown, darker apically; mid and hind tibiae and tarsi paler brown, darker apically; spines and claws dark brown.

Opercula. Main opercula plate is off-white to pale yellow; remainder, including meracantha and spike are pale yellow-brown; gently domed from disto-lateral to disto-medial margins.

Timbals. As in diagnosis.

Abdomen. Tergite 1 pale sandy brown, some specimens with brown submedian patches, other specimens extensively dark brown to black between timbals; tergite 2 sandy brown with broad black area dorso-medially, not extending to distal margin, and black to deep brown area dorso-medially on, and immediately surrounding and extending anteriorly from auditory capsule; tergites 3 to 7 dominantly sandy

brown with dorso-lateral brown to black patches (varying between specimens), not always extending distally to intersegmental membranes, becoming progressively paler and smaller from tergites 3 to 7; tergite 8 sandy brown, usually with small brown to black area dorsally. Sternites uniformly sandy brown.

Genitalia. Pygofer sandy brown, medium brown dorsally extending to beak. Otherwise as in diagnosis.

Female. (Plate 4B). Similar to male, but without any well-defined darker markings or colouration. Head, including postclypeus pale sandy brown, ocelli pink, eyes dark brown; rostrum sandy-brown, darker apically. Pronotum pale sandy brown, mesonotum uniformly off-white to very pale brown, tending to translucent. Wings as in male. Legs, pale yellow-brown, slightly darker brown apically and on spines; claws dark brown. Tergites uniformly yellow-brown, intersegmental membranes pale brown. Sternites similarly pale yellow-brown; ovipositor sheath brown, paler apically, extending approximately 1 mm beyond apex of tergites.

Measurements. N = 16♂, 4♀. Ranges and means (in parentheses), mm; BL: ♂ 11.2-12.7 (11.9); ♀ 12.1-12.9 (12.6). FWL: ♂ 11.1-12.6 (11.8); ♀ 12.0-13.1 (12.4). HW: ♂ 3.0-3.5 (3.2); ♀ 3.3-3.4 (3.3). PW: ♂ 2.9-3.3 (3.1); ♀ 3.1-3.3 (3.2). AW: ♂ 3.9-4.5 (4.1); ♀ 3.7-4.1 (3.9). FWL/BR: ♂ 2.29-2.51 (2.43); ♀ 2.50-2.60 (2.53).

Distribution, Habitat and Behaviour. (Fig. 2) Known only from Mt Isa, at two locations, one approximately 2.2 km S of the town along the Duchess Road, and the second on the Lake Moondarra Road, approximately 6.4 km NNE of Mt Isa town. Habitats are grassland associated with sparse open woodland, both locations being in proximity to seasonal streams. The populations are apparently relatively localised, and the cicadas wary. Notably, this species has not been found east of Mt Isa, including the Cloncurry region.

Etymology. From the Leichhardt River which runs through Mt Isa and areas to the north and northeast. The grassland localities of this cicada are proximal to this river system.

CALLING SONGS. (Figs. 4-8, Table 1)

T. infans: Song recordings were made from six locations, three being container recordings, and three field recordings. Measurements of the songs parameters were performed on two of each of these sets of recordings, the data closely comparable. Table 1 presents the measured data on the two field recordings.

The songs are clearly separated into recognisable phrases, varying in length between 7-25 seconds. Each phrase consists of two distinct elements (Figs. 4A-C), an initial echeme followed by a repetitive sequence of microsyllables ('chirps').

The echemes are characterised by two well defined, but alternating sets of tick (strictly 'syllable', but term not used for clarity) arrangements, each termed here as macrosyllables; an 'open ticking' macrosyllable arrangement (referred to hereafter as 'open macrosyllables'), with mean ticking repetition rates of 21-28 Hz (four recording sets). These open macrosyllables alternate with clearly defined 'closed ticking' macrosyllables (referred to hereafter as 'closed macrosyllables'), characterised by ticks, identical in structure to those in the open macrosyllables, but with mean repetition rates between 99-113 Hz (four recording sets). The initiation of each echeme commences with an open macrosyllable. The number of closed macrosyllables per echeme range from 6-18 (mean 11). The durations of each of the closed macrosyllables increases during echeme emission, as seen by comparing the mean values for the initial and final 3 sets of closed macrosyllables (Table 1). Within each of the closed macrosyllables, a corresponding increase in tick repetition rates is also observed during emission of each macrosyllable. Time expanded plots of the individual ticks (Fig. 5) show each to consist of a high amplitude primary pulse, followed by a low amplitude secondary pulse. The inter-pulse mean durations range from between 2.8-3.5 ms (four recording sets), the values overlapping for both the open and closed macrosyllables. The alternating open and closed macrosyllables within each echeme are always terminated by a closed macrosyllable.

The post echeme microsyllable sequences within each phrase comprise between 9-47 (mean values 23-32; four recordings) discrete microsyllables, the individual microsyllables comprising sets of between 2-5 individual coalesced ticks. The number of ticks per microsyllable decreases towards the end of the echeme. Mean microsyllable repetition rates range from 267-323 ms (3.7-3.1 Hz), the repetition rates tending to decrease at the end of each of the complete microsyllable sequences. Mean pulse repetition rates of the ticks within the microsyllables range between 126-147 Hz. Mean inter-pulse durations within the individual ticks range between 2.9-3.7 ms, similar to those in the echeme, with a small but distinct increase in inter-pulse duration occurring during emission of each microsyllable.

T. leichhardti sp. nov.: Two sets of container recordings were made, both from Mt Isa. The song is again divided into readily identifiable phrases, which range from 3.5 to >25 seconds in duration. The initial part of each phrase commences with a set of 2 to 4 microsyllables, followed by a well-developed ticking macro-syllable element, which together define an echeme, similar to, but simpler than in *T. infans* (Fig. 6). The initial sets of microsyllables of each echeme comprise from 2-8 (mean 5.3) coalesced ticks, with mean ticks repetition rates of 120 Hz. Immediately following is the ticking macro-syllable phase, consisting entirely of repeated single discrete ticks, from 17-40 in number, with repetition rates that clearly decrease through the emissions of the ticking sequence (Fig. 6-7) from 31 to 19 Hz (mean 24 Hz), similar in magnitude to those in the *T. infans* song.

The post-echeme microsyllables vary in number from 14-76 (mean 44), and exhibit a decreasing repetition rate with progressive emission, from mean rates of 3.8 Hz early in each sequence, to 2.8 Hz late in each sequence. The microsyllables comprise between coalesced 2-5 ticks, tending to reduce in number during the progressive emission of the microsyllables. Tick repetition rates within the microsyllables range from 114-135 Hz, similar to those in the initial microsyllables of the echeme. Inter-pulse

durations are also similar to those within the initial macro-syllable and microsyllable phases of the echemes.

Comparative notes on the temporal song structures. The *T. infans* and *T. leichhardti* songs are clearly different, but nevertheless do share a number of structural and temporal characteristics. These include the echeme elements comprising repeated single tick macro-syllables, followed by the extended or extended post-echeme microsyllables. Additional similarities include the detailed syllable structures (Figs. 5-7), inter-pulse intervals within the ticks, and the microsyllable repetition rates and tick repetition rates within the post-echeme microsyllables (Tables 1 and 2). A significant difference is the development of the alternating open and closed macro-syllable elements, marked by mean tick repetition rates of 21-28 Hz and 99-113 Hz respectively, in the echemes of the *T. infans* song.

Song frequencies. These are illustrated by the amplitude spectra (Fig. 8). Both the *T. infans* songs illustrated (Fig. 8A, B), based on field recordings from separate locations, indicate a broadband frequency emission with the dominant frequencies lying between 23.1 to 23.2 kHz. These are within the ultrasonic range and account for the very soft audible song. In both these recordings, the upper frequency resolution limit of the recorder used is 24 kHz, thus cutting off the highest frequency components of the songs. Use of a bat detector suggests that the dominant frequency envelope probably extends to 28-30 kHz, and further, when close to the insects, extremely weak frequency components extending to 60 kHz.

The amplitude spectrum of the *T. leichhardti* song shows frequency splitting which often characterises container recordings. The song again appears to be broadband with an apparent dominant frequency of 15.5 kHz. The recorder used in this recording (see above) has an upper frequency resolution limit of 18 kHz, and thus the dominant frequency of this song could realistically be even higher.

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LITERATURE CITED

- Bennet-Clark, H.C. 1997. Tymbal mechanics and the control of song frequency in the cicada *Cyclochila australasiae*. *The Journal of Experimental Biology* 200: 1681-1694.
- de Boer, A.J. 1999. Taxonomy and biogeography of the New Guinean Cicadettini (Hemiptera, Tibicinidae). *Mitteilungen Museum Naturkunde Berlin: Deutsche entomologische Zeitschrift* 46(2): 115-147.
- Distant, W.L. (1906). *A synonymic catalogue of Homoptera. Part 1. Cicadidae*. (British Museum: London) 207 pp.
- Dugdale, J.S. 1972. Genera of New Zealand Cicadidae (Homoptera). *New Zealand Journal of Science* 14(4): 856-882.
- Ewart, A. 1988. Cicadas (Homoptera). Pp 180-201 In, Scott, G. (ed) *Lake Broadwater. The natural history of an inland lake and its environs*. (Lake Broadwater Natural History Association and Darling Downs Institute Press: Toowoomba).
1989. Revisionary notes on the genus *Pauropsalta* Goding and Froggatt (Homoptera: Cicadidae) with special reference to Queensland. *Memoirs of the Queensland Museum* 27(2): 289-375.
1998. Cicadas, and their songs of the Miles-Chinchilla region. *The Queensland Naturalist* 36(4-6): 54-72.
2005. New genera and species of small ticking and 'chirping' cicadas (Hemiptera: Cicadidae) from Queensland, with descriptions of their songs. *Memoirs of the Queensland Museum* 51(2): 439-500.
- Ewart, A. & Marques, D. 2008. A new genus of grass cicadas (Hemiptera: Cicadoidea: Cicadidae) from Queensland, with descriptions of their songs. *Memoirs of the Queensland Museum* 52(2): 149-202.
- Ewart, A. & Popple, L.W. 2001. Cicadas, and their songs, from south-western Queensland. *The Queensland Naturalist* 39(4-6): 52-71.
- Froggatt, W.W. (1907) *Australian insects*. William Brooks, Sydney, 449 pp.
- Goding, F.W. & Froggatt, W.W. 1904. Monograph of the Australian Cicadidae. *Proceedings of the Linnean Society of New South Wales* 29(3): 561-670, pls XVIII, XIX.
- Moulds, M.S. 2005. An appraisal of the higher classification of cicadas (Hemiptera: Cicadoidea) with special reference to the Australian fauna. *Records of the Australian Museum* 57: 375-446.
2012. A review of the genera of Australian cicadas (Hemiptera: Cicadoidea). *Zootaxa*, Monograph 3287, 262pp.
- Pinto-Juma, G., Simões, P.C., Seabra, S.G. & Quartau, J.A., 2005. Calling song structure and geographic variation in *Cicada orni* Linnaeus (Hemiptera: Cicadidae). *Zoological Studies* 44: 81-94.
- Popple, L.W., 2003. Intraspecific variation or species specificity in cicada songs: the *Pauropsalta annulata* species complex (Auchenorrhyncha: Cicadidae). Honours Research Thesis, Department of Zoology and Entomology, The University of Queensland, pp. 70.
- Popple, L.W. & Strange, A.D. 2002. Cicadas, and their songs, from the Tara and Waroo Shires, southern central Queensland. *The Queensland Naturalist* 40(1-3): 15-30.
- Quartau, J.A. & Simões, P.C., 2006. Acoustic evolutionary divergence in cicadas: The species of *Cicada L.* in Southern Europe. Pp. 227-237. In, Droupopoulos, S. & Claridge, M.F. (eds) *Insect Sounds and Communication. Physiology, Behaviour and Evolution*. Taylor & Francis.
- Seabra, S.G., Pinto-Juma, G. & Quartau, J.A., 2006. Calling songs of sympatric and allopatric populations of *Cicada barbara* and *C. orni* (Hemiptera: Cicadidae) on the Iberian Peninsula. *European Journal of Entomology* 103: 843-852.
- Simões, P.C., Boulard, M., Rebelo, M.T., Drosopoulos, S., Claridge, M.F., Morgan, J.C. & Quartau, J.A., 2000. Differences in the male calling songs of two sibling species of *Cicada* (Hemiptera: Cicadoidea) in Greece. *European Journal of Entomology* 97: 437-440.
- Simmons, P. & Young, D., 1978. The tymbal mechanism and song patterns of the Bladder Cicada *Cystosoma*

- saundersii*. *The Journal of Experimental Biology* **76**: 27-45.
- Sueur, J., 2002. Cicada acoustic communication: potential sound partitioning in a multispecies community from Mexico (Hemiptera: Cicadomorpha: Cicadidae). *Biological Journal of the Linnean Society* **75**: 379-394.
- Sueur, J. & Aubin, T. 2004. Acoustic signals in cicada courtship behaviour (order Hemiptera, genus *Tibicina*). *Journal of Zoology* **262**: 217-224.
- Young, D., 1972. Analysis of songs of some Australian cicadas (Homoptera: Cicadidae). *Journal of the Australian Entomological Society* **11**: 237-243.

Three new cicada species of the genus *Gudanga* Distant (Insecta: Cicadidae: Cicadettinae: Cicadettini) from Queensland; comparative morphology, songs, behaviour and distributions

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ABSTRACT

Three additional cicada species belonging to the genus *Gudanga* are described from Queensland. *G. lithgowae* sp. nov. from south east Queensland, and *G. nowlandi* sp. nov. and *G. emmotti* sp. nov., both from south west Queensland, bringing the total of described Queensland species to five. Detailed comparisons are presented of the morphologies, colourations, distributions and calling songs of the five Queensland *Gudanga* species. The calling songs are shown to also be characteristic for each of these species. These comprise two distinct song types, those with two echemes per song phrase and those with three echemes per song phrase. The latter type is characteristic of the three new species described in this paper, the specificity of the songs of each of these three species confirmed by detailed statistical analyses. A revised key is presented for the nine known Australian species. □ *Cicadettini*, *cicadas*, *taxonomy*, *Gudanga*, *calling songs*, *song specificity*, *acoustic analyses*, *Queensland*, *acacias*.

The cicadas belonging to the genus *Gudanga* Distant are distinctive medium-sized insects (15–26 mm body lengths), with black to brown pigmented, semi-opaque to opaque fore wings and usually with orange to crimson pigmentation on at least part of the hind wings. These wing colourations are quite unlike other Australian cicadas. Moulds (1996) reviewed the genus, adding four additional new species (*G. adamsi*, *G. aurea*, *G. solata*, *G. kalgoorliensis*), to the two previously known species (*G. browni* Distant, *G. boulayi* Distant); five of these species are from Western Australia, with one from Queensland (*G. adamsi*). Olive (2007)

described an additional species from northern Queensland (*G. pterolongata*). Moulds (2012) has provided, in his comprehensive review of the genera of Australian cicadas, an updated diagnosis of the genus *Gudanga* Distant. Three additional new Queensland species are described here, along with comparisons of the occurrences, distributions, calling songs and taxonomic characteristics of all five Queensland species. A revised key for the identification of the nine Australian *Gudanga* species is also included. The dark fore wing pigmentation ensures that these cicadas are superbly cryptic, in Queensland, within the Mulga (*Acacia*

aneura), Creepline Mineritchie (*A. cyperophylla*), Brigalow (*A. harpophylla*), Gidyea (*A. cambagei*), or Lancewood (*A. shirleyi*) woodlands in which they most frequently inhabit. This, together with their highly wary nature and fast flight, results in their being visually very inconspicuous cicadas, typically heard far more frequently than seen. Although the songs of the Queensland species are mainly sharp repetitive 'chirping' songs, this work presents detailed aural analyses of their songs which show that each Queensland species has distinctive calling song characteristics.

Documentation of the calling songs is now an important adjunct to the collection of cicadas, proving to be valuable taxonomic tools, and in the field, providing efficient means for identifying known species, and for recognising new species and species complexes, even possible hybridisation (e.g. Ewart, 1998, 2005; Ewart & Popple, 2001; Ewart & Marques, 2008, Marshall *et al.*, 2011; Popple & Strange, 2002; Popple, 2003; Popple *et al.*, 2008; Simões *et al.*, 2000; Seabra *et al.*, 2006; Sueur, 2002; Sueur & Aubin, 2004).

MATERIALS AND METHODS

Abbreviations. *Institutions and collections.* ANIC, Australian National Insect Collection, Canberra; AE, private collection of A. Ewart, Caloundra; BMNH, the Natural History Museum, London; LWP, private collection of L.W. Popple, Brisbane; JM, private collection of J. Moss, Brisbane; MSM, private collection of M.S. Moulds, Kuranda; QM, Queensland Museum, Brisbane. *Collectors and general.* Hstd, Homestead; NP, National Park; EP, Environmental Park; Rd, Road; Rec, recorded (= aural/electronic song recording); sp, species; spec, specimen; PS, prefix to Queensland Museum photo number; Sta, cattle station; CB, C.J. Burwell; AE, A. Ewart; BJM, B.J. Moulds; MSM, M.S. Moulds; LWP, JM, J. Moss; L.W. Popple. *Morphological.* Measurements (in mm) are given as ranges and means (in parentheses) and include the largest and smallest specimens available. BL, total body length; FWL and FWW, fore wing length and width; HW, head width

(across the outer margins of the compound eyes); PW, pronotum width (across the lateral margins, excluding amplified lateral angles); AW, abdomen width (across the outer edges of the auditory capsules); FWL/WR, fore wing length/width ratio.

Anatomical terminology follows Moulds (2005, 2012) for body and wings, Dugdale (1972) and Moulds (2005, 2012) for genitalia, de Boer (1999) for opercula, and Simmons and Young (1978), Dugdale (1972) and Bennet-Clark (1997) for timbals. The long timbal ribs are referred to sequentially as ribs numbered 1 to 5, with rib 1 being the most posterior (adjacent to timbal plate). The higher classification adopted in this paper follows Moulds (2012).

Song Recordings and Analysis. Although field recordings are generally preferred, a number of earlier song recordings in this project were made of single insects placed within plastic containers, in which small quantities of the relevant vegetation were inserted, as detailed in Ewart & Marques (2008). The primary reasons for use of containers relates to the wary nature, and sometimes erratic singing behaviour of cicadas which can make it difficult to place a microphone in the field environment close enough, for long enough, to directly record meaningful song segments. These container recordings utilised a recording microphone (Sennheiser model K6/ME66) in conjunction with a Sony Walkman cassette recorder WM-D6C model; this recorder responds to near 18 kHz, with a linear response to at least 15 kHz. Container recordings provide very low-background noise recordings illustrating subtleties within temporal song characteristics, and can avoid higher frequency filtering which may affect some field recordings. They do, nevertheless, suffer problems with reverberation effects causing some broadening and blurring of pulses, and enhanced splitting of the dominant frequency peaks into discontinuous frequency bands as seen in amplitude and power spectra.

Later recordings were all made in the field, commonly using a parabola (Telinga model with Telinga PRO 5 "Classic" and PRO 6

microphones) allowing direct field recordings, when appropriate direct recordings with a hand held microphone, or by use of a microphone with a collapsible net cage (38cm long by 30cm diameter) hung from convenient vegetation in the field in the habitats of the cicadas in question. Such field recordings are preferred for obtaining long song sequences, detailed analyses of the finer syllable structures of the songs and for frequency analyses using amplitude and/or power spectra. One common problem is background and other interference noise, which can be removed, at least in part, by digital filtering.

The field recordings (AE) were made with a Marantz PMD660 Solid State recorder in conjunction with a Sennheiser model K6/ME66 microphone, in PCM mode at sampling rate of 48 kHz. Manufacture specifications indicate frequency responses of microphone and recorder to 20.0 kHz (-3.0dB) at 44.1 kHz sampling rate. Other recordings (LWP) utilised a Marantz PMD670 (sampling rate and frequency response as per PMD 660) with a Telinga Pro 6.0 parabolic reflector microphone (frequency response to >18 kHz), or a Tascam DR-07 Compact Flash recorder with an Audio Technica ATR-55 cardioid condenser shotgun microphone (frequency response to 18 kHz). Some additional field recordings were provided by David Marshall, University of Connecticut, using Sony TCD_D8 DAT, Marantz PMD-660 and/or 670 recorders, with Sennheiser ME-62 microphone with Sony 330 parabola. Processing of all recordings was undertaken with Avisoft SAS LabPro software. Two sets of amplitude spectra were run, one with 556-point Fast Fourier Transform with Hamming window on extended song sequences (e.g.20-60 seconds), and a second set on 10 second sequences with 1024-point FFT with Hamming window. Only very minor differences were noted between the data sets, and the latter parameters are used in the plots presented in this paper. Filtering employed the time domain IIR procedure. Amplitude spectra of the *Gudanga* songs exhibit broad band frequency structures, the mean frequency (referred to here as the “dominant frequency”) is represented by the mean

frequency of the main frequency envelope of each recording as determined by the amplitude and power spectra. The inferred extents of this envelope are shown in the amplitude spectra presented. In addition to dominant frequencies, the amplitude spectra illustrated also list measured sideband frequencies (e.g. Bradbury and Vehrencamp, 1998). These are derived manually from frequency expanded segments of the spectra, using the automatic measuring cursors available in the Avisoft software. Sideband frequencies below about 300 Hz are reproducible in spectra from the same species. Above this frequency, the measured frequencies become progressively less reliable due to uncertainties in their correct identification and significance.

A modified terminology of Ragge and Reynolds (1998) is adapted for the description and analyses of the songs (Ewart, 2005). Although the Ragge-Reynolds terminology was designed for orthopteran insects, there are sufficient similarities in song structures to warrant extending the terminology to the cicada songs described here. The term *syllable* is used for discrete but relatively short (≤ 2 ms) groups of pulses; where, however, a small but distinct time gap does occur within short grouping of syllables, the term *diplosyllable* is used for these syllable pairs. The term *echeme* is applied to the first order assemblage of syllables produced during continuous phases of repetitive buckling of the timbal pairs. Where a smaller number of syllables are clearly juxtaposed, these are termed *macrosyllables*, and are identified as basic echeme components in most songs described here. Time expanded analysis of syllables and macrosyllables allows the resolution of individual pulses and therefore the fundamental frequency carrier waves of the song.

KEY TO SPECIES OF *GUDANGA*

The following key is based on modifications to the original key by Moulds (1996) with the additions by Olive (2007):

1. Abdominal tergites 1-6 black (entirely lacking areas of orange pigmentation)... 9

- Abdominal tergites 1-6 with obvious areas of orange pigmentation 2
- 2. Hind wing predominantly hyaline, orange at base 3
 - Hind wing entirely orange or red basally, remainder fuscous as on forewing 8
- 3. Orange pigmentation covering basal half of hind wing; remainder hyaline; anal lobe orange with outer half semi-opaque fuscous as on fore wing (northern Qld) *pterolongata* Olive
 - Hind wing without fuscous area on anal lobe 4
- 4. Hind wing with orange colouration clearly extending beyond anal lobe; weak brown infuscation extending along hind wing margin outside ambient vein. 5
 - Hind wing orange colouration almost entirely confined to anal lobe 6
- 5. Hind wing with orange restricted to proximal half to two-thirds of anal lobe, along 2A vein, and within proximal quarters of anal cell 1 through to radial cells, slightly more extensive on costal cell (eastern-central Qld) *adamsi* Moulds
 - Hind wing with extensive orange covering the anal cells through to all but the most distal segments of the cubital to costal cells; very weak orange-brown infuscation on apical cells (south eastern Qld) *lithgowae* sp.n.
- 6. Hind wing with orange confined almost entirely to the plaga in anal cell 3 and the area between the plaga and inner margin (southern WA) *kalgoorliensis* Moulds
 - Hind wing with orange colouration confined to proximal three-quarters of anal cell 3, proximal half of anal cell 2, extending along 3A and 2A veins; pale orange-brown proximal infuscation on hind wing adjacent to proximal terminations of cubital, medial and costal cells, often extending weakly adjacent to costal and subcostal veins (south western Qld) 7
- 7. Pygofer secondary basal lobe weakly developed, not markedly swollen and not easily visible except with dissection . . *nowlandi* sp.n.
- Pygofer secondary basal lobe relatively swollen and visible in lateral and dorsal view *eumotti* sp.n.
- 8. Pigmentation of hind wing apical cells 1-5 paler than forewing and showing slight orange suffusion (clearly visible when specimen is held approximately 10 cm above a white background); abdomen of male in dorsal view nearly parallel-sided for much of its length (south western WA) *aurca* Moulds
 - Pigmentation of hind wing apical cells 1-5 similar to that of forewing; abdomen of male in dorsal view tapering from base to apex (southern WA) *browni* Distant
- 9. Base of hind wing crimson; remainder of hind wing usually hyaline but sometimes fuscous (south western WA) . . *boulayi* Distant
 - Base of hind wing reddish-orange; remainder of hind wing always fuscous, never hyaline (south western WA) *solata* Moulds

To facilitate comparison of the new *Gudanga* species with previously described species from Queensland, new drawings (Figs 1-6), and photographs (Plates 1-4) illustrating the morphological features of all five Queensland species are included in this paper.

SYSTEMATICS

Family CICADIDAE Latreille, 1802

Subfamily CICADETTINAE Buckton, 1889

Tribe CICADETTINI Buckton, 1889

Gudanga lithgowae sp. nov.

(Figs 1A-6A, 7, 8B, 10C, 11A, 15A-E, 16D, 18, 19, 20, Plates 1, 4A, Table 1)

Gudanga sp.: Ewart, 1988: 185.

Gudanga adamsi: Ewart, 1998: 62-63, Fig. 8.

Gudanga sp. nr *adamsi*: Popple and Strange, 2002: 28.

Material. HOLOTYPE: ♂, QMT156218, Jct. Auburn-Warrego Rds., Chinchilla, S. Qld, 9-10.i.1994, A.E. 26° 43.64'S 150° 36.76'E (QM).

PARATYPES: Southern Queensland: 1♀, 'Allinga' dam, Chinchilla District, 26° 40'S 150° 38'E, 7.i.1994, G. Lithgow; 4♂, 'Allinga', Lithgow Rd, 26° 39.79'S

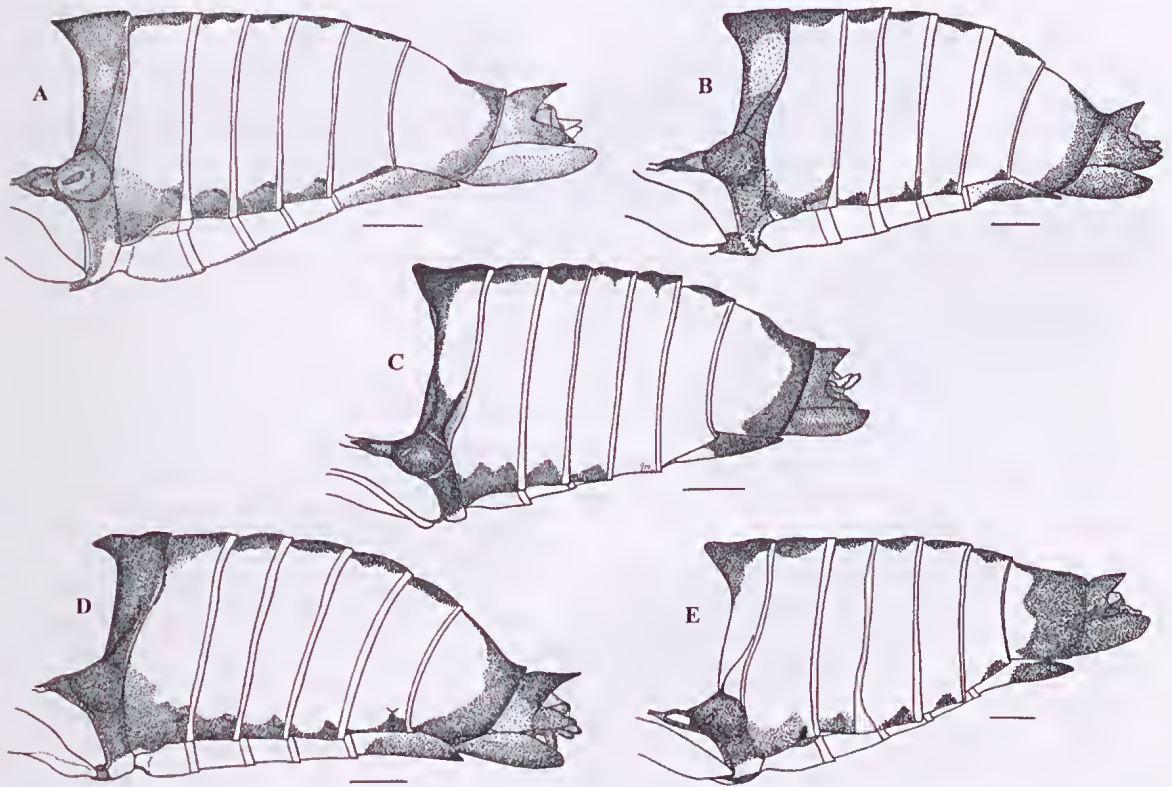


FIG. 1. Lateral abdomen views of males of the five Queensland *Gudanga* species showing the areas of dark pigmentation. A, *G. lithgowae*; B, *G. nowlandi*; C, *G. emmotti*; D, *G. adamsi*; E, *G. pterolongata*. Scale bars are 1 mm.

150° 38.06'E, Chinchilla, 8.i.1994, brigalow, AE; 1♂, 1♀, 'Coo-ee (Stock)Yards', Red Hill Rd, Chinchilla, 26° 38.96'S 150° 38.54'E, 9.i.1994, AE; 14♂, 2♀, Jct. Auburn-Warrego Rds., Chinchilla, 26° 43.64'S 150° 36.76'E, 9-10.i.1994, AE; 2♂, same data, 10.i.1995, AE; 1♂, same data, recorded, 13.xii.1997, AE; 1♂, same data, recorded, 4.i.2000, AE; 3♂, 1♀, same data, 22.xii.2001, AE; 1♂, 1♂ (recorded), 'Allinga' Pty, Chinchilla, brigalow, 26° 39.79'S 150° 38.06'E, 9.i.2002, AE (AE). The following paratypes were listed in Moulds (1996) under *G. adamsi*; 1♂, 2♀, "Allinga", Chinchilla, i.1984, 26.xi.1984, 11.xii.1984, G. Lithgow; 3♂, 1♀, "Allinga", Chinchilla, 8.i.1984, J. Moss; 1♀, Allinga Dam, Chinchilla District, 7.i.1994, G. Lithgow; 19♂, 8♀, Auburn Rd, Chinchilla, 8.xii.1987, 9.i.1994, J. Moss (JM). 1♀, Chinchilla, 8.xii.1987, J. Moss, 138-0001; 1♂, Auburn Rd, 2 km W. Chinchilla, 1-3.xii.1999, J. Moss, L. Popple, mv lamp, 139-0002; 3♂, Myall Park, 8 km N. Glenmorgan, 27-28.xii.2001, m.v. lamp, L. Popple, R. MacSloy, 139-0003 to 5; 1♂, same data, on minidisc, L.W. Popple, 139-0006; 1♀, 3 km E. Kindon, 10.i.2004, 28° 05'S 150° 47'E, L. Popple, R. MacSloy, 139-0007; 1♂, Southwood N.P. via Moonie, 5-10.

xii.2005, 27° 49'51"S 150° 06'14"E, L. Popple, A.E., 139-0009 (LWP). 2♂, AU.QL.SWN, N. edge of Southwood N.P., 27° 48.429'S 150° 05.101'E, 254 m, 31.xii.2008, Hill, Marshall, Moulds, Owen; 1♂, as previously, 1.i.2009; 1♀, as previously, 2.i.2009 (MSM). 1♀, Jct. Auburn-Warrego Rds., Chinchilla, 26° 43.64'S 150° 36.76'E, 9-10.i.1994, AE (QM). 1♂, 1♀, Jct. Auburn-Warrego Rds., Chinchilla, 26° 43.64'S 150° 36.76'E, 9-10.i.1994, AE; (ANIC). 1♂, Jct. Auburn-Warrego Rds., Chinchilla, 26° 43.64'S 150° 36.76'E, 9-10.i.1994, AE; (BMNH). NEW SOUTH WALES: 1♀, ca.16 km SE of Boggabilla, 28° 44.673'S 150° 25.050'E, 235 m, 1.i.2005, Hill, Marshall, Moulds (MSM). 1♂, Bundemar Sta., N.E. Trangie, 14.xii.1947, L.J. Chinnick (ANIC).

Description of Male (Figs 1A-6A, Pl. 1A, 4A).

Head. Compound eyes separated from pronotum along their outer ventral margins; distance between lateral ocelli similar to distance between lateral ocellus and compound eyes. Vertex black, mandibular plate and genae black with

narrow sandy-brown narrow ridged margins, covered by mostly short golden pubescence; supra-antennal plate black with pale sandy-brown anterior margins; pale triangular sandy-brown, slightly depressed fascia extending posteriorly from near median ocellus, narrowing towards and extending to pronotal margin. Ocelli rose red. Compound eyes dark brown. Postclypeus black with narrow sandy-brown margin and small dorso-medial pale brown spot. Anteclypeus black; rostrum brown grading to black apically; extends to between mid and hind coxae. Antennae medium brown, darker brown pedicels. Head across outer margins of compound eyes slightly wider than width of pronotum across lateral margins (excepting amplified lateral angles of pronotal collar).

Thorax. Pronotum predominantly reddish-brown, sometimes dark brown, with irregular black patches adjacent to, and between the paramedian and lateral fissures; sandy-brown central fascia extending posteriorly from near anterior margin, splaying out towards, and fusing with pronotal collar where the sandy-brown core is replaced by black colouration, from which lateral triangular pale sandy-brown extensions run, dorsally to submedially, along the posterior pronotal margin; pronotal collar predominantly black with very narrow pale sandy-brown dorso-lateral posterior margins; narrow pale sandy brown anterior margin; lateral angles of pronotal collar clearly amplified. Mesonotum predominantly black with the outlines of the black submedial and lateral sigillae largely obscured except for the thin brown line incompletely defining the parapsidal suture, in some specimens extending posteriorly to outer arms of cruciform elevation; lateral mesonotal margins adjacent to wing grooves predominantly pale orange-brown; central dorsal area of cruciform elevation pale to medium brown, remainder, including areas between lateral cruciform elevation arms, black; short, sparse golden pubescence, most pronounced near wing grooves.

Wings. (Fig. 2A). Fore wings commonly black in relatively freshly emerged specimens, evidently fading to semi-opaque, brown colour

in older insects and in most dried specimens, always darker immediately adjacent to all veins; conspicuous undulations on the wings between veins; lengths similar to total body length with relatively high length/width ratios (2.6-2.9); costal vein relatively even in width, with minor thickening proximally and with gentle anterior curvature towards node; sclerotised zone along anterior costal vein margin similar in width to costal vein; costal and R+Sc veins fused, but each clearly distinct; nodal line clearly visible in some specimens (as seen in Figs 2C, D); CuA vein not intersecting M vein, but directly intersects arculus of basal cell; 3 distal vein sections of M that form the inner margin of radial cell are of approximately equal length, slightly variable between specimens; medial cell significantly larger than cubital cell; 8 apical cells that are mostly shorter than the adjacent ulner cells; basal membrane orange and opaque; radial cell normally shorter than distance from its apex to wing tip (ratio 0.89-1.04); venation pale to medium brown. Hind wings predominantly hyaline; bright orange opaque plaga covering most of anal cell 3, except for small, apical, well defined, oval-shaped area; approximately one half to two-thirds of anal cell 2 covered by bright orange opaque plaga, the border sharply defined, the plaga extending to and along 2A vein to its distal termination; strong orange infuscation covering the distal hyaline areas of anal cells 2 and 3, and all anal cell 1; deep orange infuscation, almost appearing semi-opaque, fills much of the cubital, medial, radial and costal cells, weakening in intensity in each towards and almost reaching the adjacent apical cells; apical cells with weak orange-brown infuscation also fading towards wing margin; hind wing margin outside ambient vein with weak to distinct brown infuscation, variable between specimens, which just extends into the distal edge of anal cell 2; 6 apical cells; anal lobes clearly broader than cubital cell 1; venation yellow-orange.

Legs. Fore coxae predominantly black with short brown longitudinal fasciae located centrally on lateral and anterior faces; mid and hind coxae predominantly dark brown; fore femora with

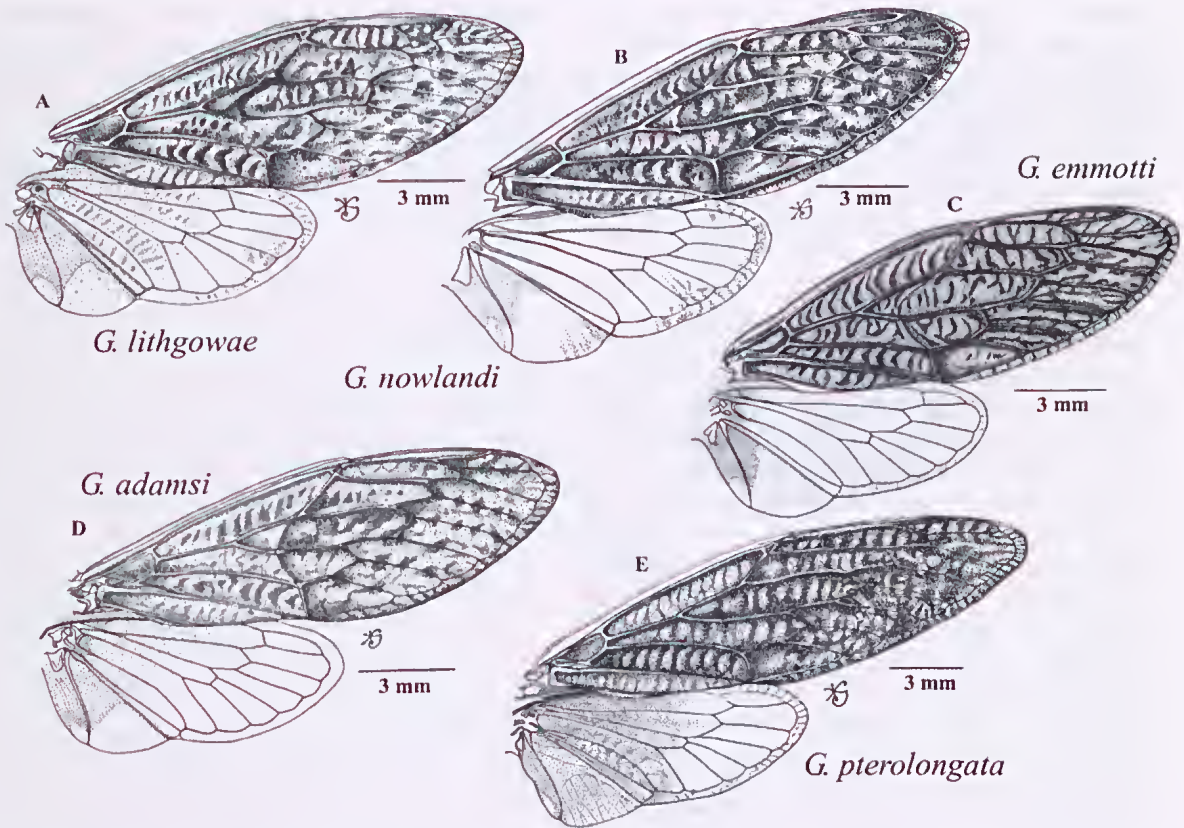


FIG. 2. Fore and hind wings of males of the five Queensland *Gudanga* species, showing the well developed undulations on the fore wings. A, *G. lithgowae*; B, *G. nowlandi*; C, *G. emmotti*; D, *G. adamsi*; E, *G. pterolongata*. Scale bars are 3 mm. Drawings A, B, D, E by Katie Schuler.

alternate longitudinal sandy-brown and dark brown fasciae on each face; mid and hind femora similar but fasciae thinner; trochanters medium to dark brown, being paler brown on hind trochanters; tibiae, tarsi and claws medium brown, pale brown on hind tibiae; tarsi and claws darker apically; 3 black semi-erect spines on fore femora.

Opercula. (Fig. 3A). Relatively elongated roughly parallel to abdomen, although slightly inwardly curved towards abdominal midline in the disto-medial areas of operculum; disto-medial margins rounded; medial margin reaching beyond tympanal cavity margins; distal margin and crest not reaching lateral tympanal cavity margins; inner margins of opercula well separated; opercula developed

asymmetrically around meracantha; meracantha spike overlapping timbal plate; broad shallow dome developed across basal and distal areas extending towards crest; domed area medium to dark brown colouration, remaining operculum colouration sandy-brown; opercula usually just reach anterior margin of sternite II in lateral view.

Timbals. (Fig. 4A). Five long ribs, the anterior long rib shortest sometimes barely reaching the adjacent short rib, sometimes clearly overlapping dorsal termination of short rib; long ribs 1 and 2 fused ventrally, long ribs 1 to 3 fused dorsally to basal spur; four well developed short ribs; well developed, elongated dome on timbal plate with shallow grooves oriented along the top of the dome.

Abdomen (Fig. 1A). Width across auditory capsules greater than across lateral pronotal and mesonotal margins, and also across outer margins of compound eyes; in dorsal view, tergites usually gently tapered posteriorly to tergite 6, more strongly curved and tapered along tergites 7 and especially 8, giving a slightly bulbous appearance to abdomen; tergite 2 predominantly black, deep brown on auditory capsules, and with a small orange area developed submedially; black colouration extending anteriorly from tergite 2 to tergite 1, filling area between timbals; tergites 3 to 8 predominantly bright orange, each with a well defined black dorsal area, not extending across intersegmental membranes, and decreasing in size from tergites 3 through to 8; black areas on ventro-lateral margin of each tergite, progressively decreasing in size from tergites 3 to 8, also not extending across intersegmental membranes; the sequence of dorsal black areas give the overall impression of a black fascia extending along the dorsal abdominal surface. Sternites predominantly yellowish sandy-brown; sternite II with small dark median depression; a diffuse brown venter occurs on sternites III to VI, becoming darker in colour and broader on sternites VII and VIII; sternites convex, normally projecting below tergites in lateral view.

Genitalia. (Figs 5A-6A) Pygofer predominantly black including dorsal beak, tending to dark orange colour around anterior margins; prominent upper lobes extending to or beyond anal styles, relatively acutely rounded terminations as seen in lateral view, which dominate the pygofer between the basal lobes and dorsal beak; angle between dorsal margin of upper lobe and its extension to dorsal beak near or slightly less than orthogonal; prominent sharp dorsal beak; well developed basal lobes with rounded apices, visible in lateral view; relatively small but clearly developed, rounded secondary basal lobes; well developed robust claspers, sharply-pointed with hooked terminations; median lobe of uncus conspicuous and duck-bill shaped; aedeagus with theca that is short, simple and tubular which in lateral view has a slanting termination

with the posterior rim most prominent; a pair of prominent curved pseudoparameres, sharply pointed apices, much longer than theca and originating closer to theca than its base; theca with short sclerotised ventral support; aedeagal basal plate undulated in lateral view, with broad Y-shape in dorsal view, and functional membranous 'hinge'.

Description of Female. (Pl. 1B) Similar in general colouration and patterning to male, but with reduction in some specimens in the extent of black pigmentation, sometimes partially replaced by deep brown pigmentation on head, thorax and legs; similar variation occurs in the extent of black or dark brown pigmentation dorsally on abdomen. Slightly larger in size compared to male, with head width across outer margins of compound eyes slightly less than abdominal width across auditory capsules, and both greater than pronotum width across lateral margins. Supra-antennal plate, vertex, mandibular plate, genae and anteclypeus predominantly black to deep brown, with localised brown areas adjacent to pedicels; rostrum brown, black at apex; slightly depressed pale sandy-brown triangular fascia extending from near median ocellus to pronotal margin; ocelli, compound eyes, and postclypeus as in male. Pronotum as in male. Mesonotum with reduced black, and increased brown pigmentation allowing the black short submedial sigillae to be clearly visible, fused anteriorly, rounded posterior terminations; a pair of broadly triangular-shaped lateral sigillae are likewise more clearly visible, with rounded posterior terminations which do not quite reach anterior cruciform elevation arms; areas between and around sigillae medium to dark brown, becoming pale brown around and adjacent to wing grooves; cruciform elevation brown, patchy black areas between anterior and lateral arms. Fore and hind wing pigmentation as in male. Fore coxae and femora similar to male, but with more extensive pale brown fascia; mid and hind coxae predominantly pale brown with localised dark brown patches and thin fasciae anteriorly; fore femora pale brown with dark brown, often irregular fasciae on dorsal and lateral faces; mid and hind femora

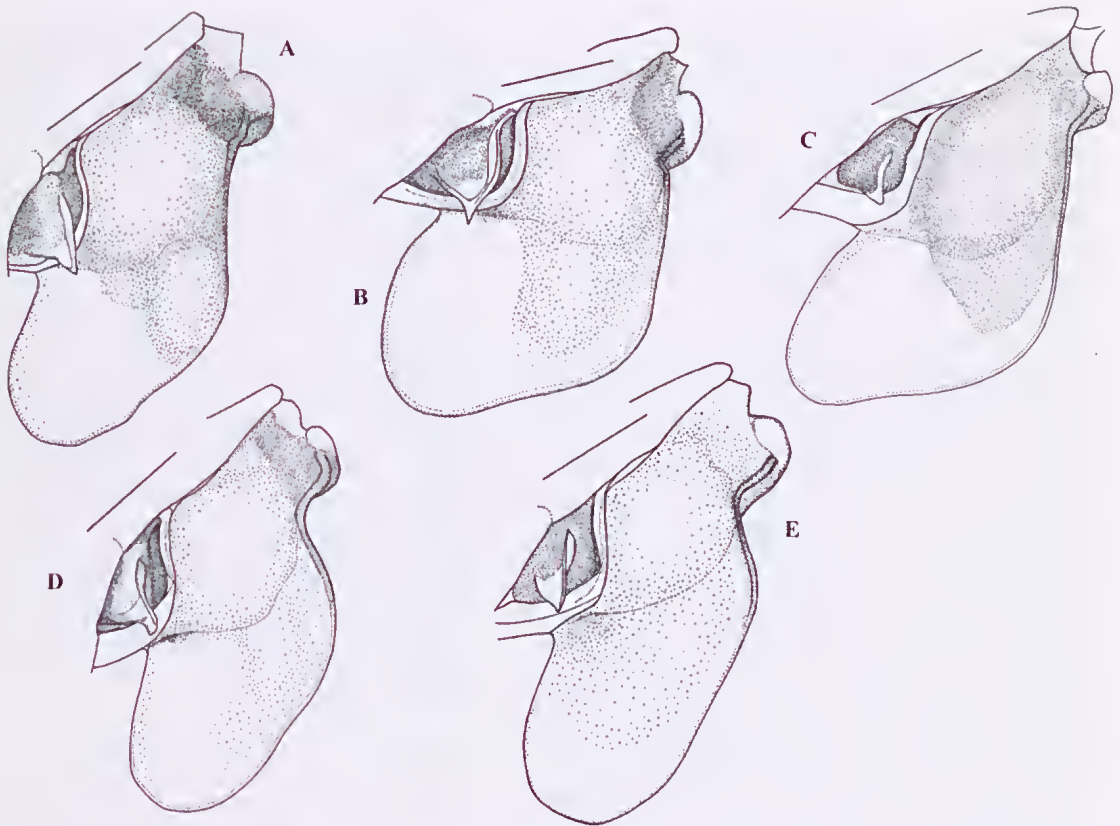


FIG. 3. Left opercula of males of the five Queensland *Gudanga* species. A, *G. lithgowae*; B, *G. nowlandi*; C, *G. emmotti*; D, *G. adamsi*; E, *G. pterolongata*. Scale bars are 1 mm.

pale brown with well developed, narrow dark brown fasciae along anterior and posterior faces; trochanters, tibiae and tarsi medium to pale brown; apices of claws, and spines on fore femora dark brown. Abdomen; tergites 1 and 2 black or dark brown dorsally, tending to brown or light brown ventrally towards the ventro-lateral margins; tergites 3 to 7 with black or deep brown dorsal patches, which on tergite 3 extend submedially along anterior margins; these dorsal black or brown patches extend across intersegmental membranes and decrease sequentially in width towards tergite 7; as viewed dorsally, these dorsal dark patches appear as a prominent longitudinal black fascia running along the abdomen, splaying out strongly anteriorly towards, and within, tergite 2, which in some specimens are much more

conspicuous than in the males; dark brown to black patches also occur along ventro-lateral tergite margins of tergites 3 to 7, usually not extending across intersegmental membranes; remaining tergite colouration orange; tergite 8 orange with or without thin discontinuous black patches along posterior margin, a diffuse narrow brown dorsal fascia across tergite, and small dark brown patch on ventro-lateral margin; tergite 9 predominantly orange grading to sandy-brown posteriorly, with a pair of distinct to diffuse (specimen dependent), brown dorso-medial fasciae, each narrowing, darkening, and fusing towards posterior tergite margin; dorsal to dorso-lateral anterior tergite margin with or without darker brown irregular pigmentation; a diffuse spot occurs posterior-laterally. Sternites sandy-brown to medium

brown with a median darker brown venter, variable in darker pigmentation intensity between specimens. Ovipositor sheath extends 0.4–0.8 mm beyond apex of tergite 9.

Measurements. N=24♂, 8♀. Ranges and means (in parentheses): *BL*: ♂ 15.1–18.7 (16.80); ♀ 16.2–20.2 (17.77). *FWL*: ♂ 14.5–17.0 (15.85); ♀ 15.8–19.7 (17.36). *FWW*: ♂ 5.3–6.3 (5.87); ♀ 5.7–7.3 (6.22). *HW*: ♂ 4.5–5.2 (4.84); ♀ 5.0–5.9 (5.19). *PW*: ♂ 4.2–4.8 (4.50); ♀ 4.6–5.5 (4.97). *AW*: ♂ 4.8–5.7 (5.39); ♀ 5.0–6.2 (5.49). *FWL/AWR*: ♂ 2.57–2.88 (2.71); ♀ 2.69–2.98 (2.79).

Distribution, Habitat and Behaviour. (Fig. 7) Occurs in inland southeastern and southern Queensland; specific localities include the Chinchilla area; Southwood National Park; Myall Park, 8 km N. of Glenmorgan; near Kindon. Additional southeast Queensland aural records and recordings (LWP) include: 8 and 20 km ENE. of Goondiwindi; Barakula State Forest, N. of Chinchilla; Cameby Downs, between Miles and Chinchilla; 6 km W. of Glenmorgan; Hannaford, between Miles and Moonie; and Wyaga Creek, approximately 60 km NE. Goondiwindi. In N.S.W., specimens are available from ~16 km SE. of Boggabilla and northeast of Trangie. It is a localised species occurring within or associated with Brigalow (*A. harpophylla*) woodland, often where disturbed with dense regrowth. Available records are from mid December to mid January. It is an elusive, cryptic and wary species. The song is a sharp, rapid chirping, described in detail below.

Etymology. Named after Grace Lithgow, (of "Allinga" homestead, Chinchilla) who collected some of the first specimens of the species, and who has also contributed so much to the documentation of the natural history of the Chinchilla region (where the species is locally abundant).

Gudanga nowlandi sp. nov.

(Figs 1B–6B, 7, 9A, 10A, 11 to 13, 16A–C, 18, 19, 20, Plates 2, 4B, Tables 1, 3)

Gudanga species B: Ewart and Popple, 2001: 62, 70, Fig. 8C.

Material. TYPES. HOLOTYPE: ♂, QMT156219, 1♂, 'Bulls Gully' lagoon, Adavale, 14.i.1999, 25° 58.11'S 144° 28.39'E, A.E. (QM).

PARATYPES. SOUTHWESTERN QUEENSLAND: 15♂, 3♀, 'Bulls Gully', Adavale, 13.i.1999, 25° 57.70'S 144° 30.03'E, A.E.; 3♂ recorded, same data; 1♀, same data, 16.i.1999; 1♂, 'Bulls Gully', ~70 km N. Quilpie, 16.iii.1999, 25° 57.74'S 144° 29.19'E,

S. & G. Nowland; 1♀, 1.5 km E. 'Bulls Gully', Adavale, 15.i.1999, 25° 57.84'S 144° 29.90'E, A.E.; 2♂, 2.7 km S.W. 'Bulls Gully' Hstd, Adavale, gidyea, 16.ii.1999, 25° 57.91'S 144° 27.88'E, A.E.; 1♂, ~75 km N. Adavale, mulga, 11.xii.2000, 25° 25.07'S 144° 56.97'E, A.E., I.Ratray; 5♂, 1♀, 'Milroy', ~70 km N. Quilpie, mulga, 11.i.2000, 26° 02.58'S 144° 21.60'E, A.E., I.Ratray; 5♂, 2♀, same data, 8.i.2000; 4♂, same data, 9.i.2000; 1♂, Dam 'Milroy Hstd', ~70 km N. Quilpie, gidyea, 15.i.2000, 26° 02.85'S 144° 20.81'E, A.E., I.R., J.N. (AE). 1♂, Mt. Slowcombe, 3 miles (=5 km) N. of Yaraka, 21.ix.1990, G. Lithgow (listed as paratype of *G. adamsi* in Moulds, 1996) (JM). 5♂, 2♀, Currawinya N.P., 29.x.1998, branches of *Acacia aneura*, Colin Dollery; 2♂, AU.QL.WIN, approx. 63 km SW of Eromanga, 3.ii.2009, 153 m, 27° 2.573'S 142° 53.274'E, K. Hill, D. Marshall; 1♂, AU.QL.DMR, 50 km SE of Windorah, 2.ii.2009, 25° 36.028'S 143° 0.936'E, 140 m, K. Hill, D. Marshall (MSM). ♀, 17.3 km N.E. 'Milroy Hstd', ~90 km N. Quilpie, mulga & turkey bush, 15.i.2000, 25° 56.21'S 144° 22.75'E, A.E., I.Ratray (QM). 1♂, 'Bulls Gully', Adavale, 13.i.1999, 25° 57.70'S 144° 30.03'E, A.E.; 1♀, 17.3 km N.E. 'Milroy Hstd', ~90 km N. Quilpie, mulga & turkey bush, 15.i.2000, 25° 56.21'S 144° 22.75'E, A.E., I.Ratray; (ANIC). 1♂, 'Bulls Gully', Adavale, 13.i.1999, 25° 57.70'S 144° 30.03'E, A.E.; 1♀, 'Milroy', ~70 km N. Quilpie, mulga, 9.i.2000, 26° 02.58'S 144° 21.60'E, A.E., I.Ratray (BMNH).

Description of Male. (Figs 1B–6B, Pl. 2A, 3B) *Head.* Dark brown compound eyes separated from pronotum along their outer ventral margins; distance between lateral ocelli similar to distance between lateral ocellus and compound eyes; width of head across outer margins of compound eyes greater than across lateral pronotal margins (i.e. excluding amplified lateral angles of pronotal collar). Supra-antennal plate and vertex black; mandibular plate and genae black with narrow pale brown raised edges, covered by silvery-yellow pubescence, usually longest on mandibular plate and genae; poorly defined and slightly depressed small pale fascia extending posteriorly from near median ocellus to pronotal margin; small brown patches adjacent to pedicels and along narrow anterior margin of supra-antennal plate, the colour variable from light to dark brown in different specimens. Ocelli pale rose red. Postclypeus shiny black with narrow, pale brown margin; small to very small pale sandy-brown dorso-medial spot. Anteclypeus black; rostrum brown, black apically, extending to beyond the mid coxae, not always quite reaching anterior edges of hind coxae. Antennae brown.

Thorax. Pronotum predominantly black with reddish-brown or deep brown patches between the paramedian fissures, between the paramedian and lateral fissures, and postero-laterally to lateral fissures; central fascia predominantly black with a small, discontinuous median pale sandy-brown fascia; posterior part of central fascia splays out and merges with the mainly black pronotal collar, except for small sub-medial pale brown patches; the black colour of the pronotal collar continues around the ventro-lateral pronotal margins; anterior pronotal margin pale brown; lateral angles of pronotal collar ampliate. Mesonotum with black submedial and lateral sigillae just visible against the deep brown colouration of the mesonotal areas between and enclosing the sigillae; submedial sigillae relatively short and fused with broad rounded, rounded posterior terminations; lateral sigillae extend posteriorly to anterior arms of cruciform elevation and into area between lateral arms of cruciform elevation; cruciform elevation pale sandy-brown, black along apices of arms; lateral mesonotal margins proximal to wing grooves pale brown; mesonotum with sparse silvery-yellow pubescence, more pronounced adjacent to wing grooves.

Wings. (Fig. 2B) Fore wings semi-opaque, black to brown (apparently browner in worn and dried specimens), relatively darker brown adjacent to all the veins, with conspicuous undulations on the wings between the veins; lengths similar to total body length, with relatively high length/width ratios (2.8-3.1); costal vein very gently curved anteriorly towards node, degree of curvature slightly variable between individuals; sclerotised zone along anterior costal vein margin similar in width to costal vein width; costal and R+Sc veins fused, but each clearly distinct; nodal line clearly visible in some specimens; CuA vein not intersecting M vein, but directly intersects arculus of basal cell; the three distal vein sections of M that form inner margin of radial cell are of unequal length; medial cell larger in size than cubital cell; 8 apical cells that are shorter than adjacent ulnar cells; basal membrane opaque orange; radial cell normally

shorter than distance from its apex to wing tip (ratio 0.85-1.00); fore wing venation pale to medium brown. Hind wing predominantly hyaline with variably weak to very weak yellow colouration, always weaker distally; semi-opaque orange plaga covering proximal three-quarters of anal cell 3, the distal margin strongly concavely curved, also covering the proximal third to half of anal cell 2 with obliquely curved or straight margin extending towards vein 2A and further extending adjacent to the vein as narrow colouration to vein termination; the detailed shapes and extents of these areas of orange plaga in anal cells 2 and 3 is variable between individuals; paler orange infuscation variably developed within proximal terminations of cubital cell 1, medial, radial and costal cells, often partially extending weakly adjacent to cubitus, median, subcostal and costal veins; minor weak brown infuscation at distal termination of 2A vein extending very weakly to adjacent margin of anal cell 2; weak but distinct brown infuscation developed along wing margin may be present; 6 apical cells; anal cells 1+2+3 much broader than cubital cell 1+2; hind wing venation orange-brown grading to medium-brown apically.

Legs. Fore coxae predominantly black with short brown longitudinal fasciae located centrally on lateral and anterior faces and three erect black spines; mid and hind coxae dark brown, tending to medium brown distally on hind coxae; fore femora predominantly black with relatively thin brown longitudinal fasciae on each face; mid and hind femora predominantly pale brown with narrow dark brown longitudinal fasciae; fore trochanters, tibiae and tarsi dark brown; mid and hind trochanters, tibiae and tarsi pale brown with diffuse darker brown longitudinal fascia on anterior trochanter faces; claws brown, darker apically.

Opercula. (Fig. 3B) Relatively broad, oriented roughly parallel to abdomen, slightly curved inwards towards abdominal midline in disto-medial area; disto-medial operculum margins broadly rounded; medial margins reaching beyond margin of tympanal cavity while distal margins and crests not reaching lateral

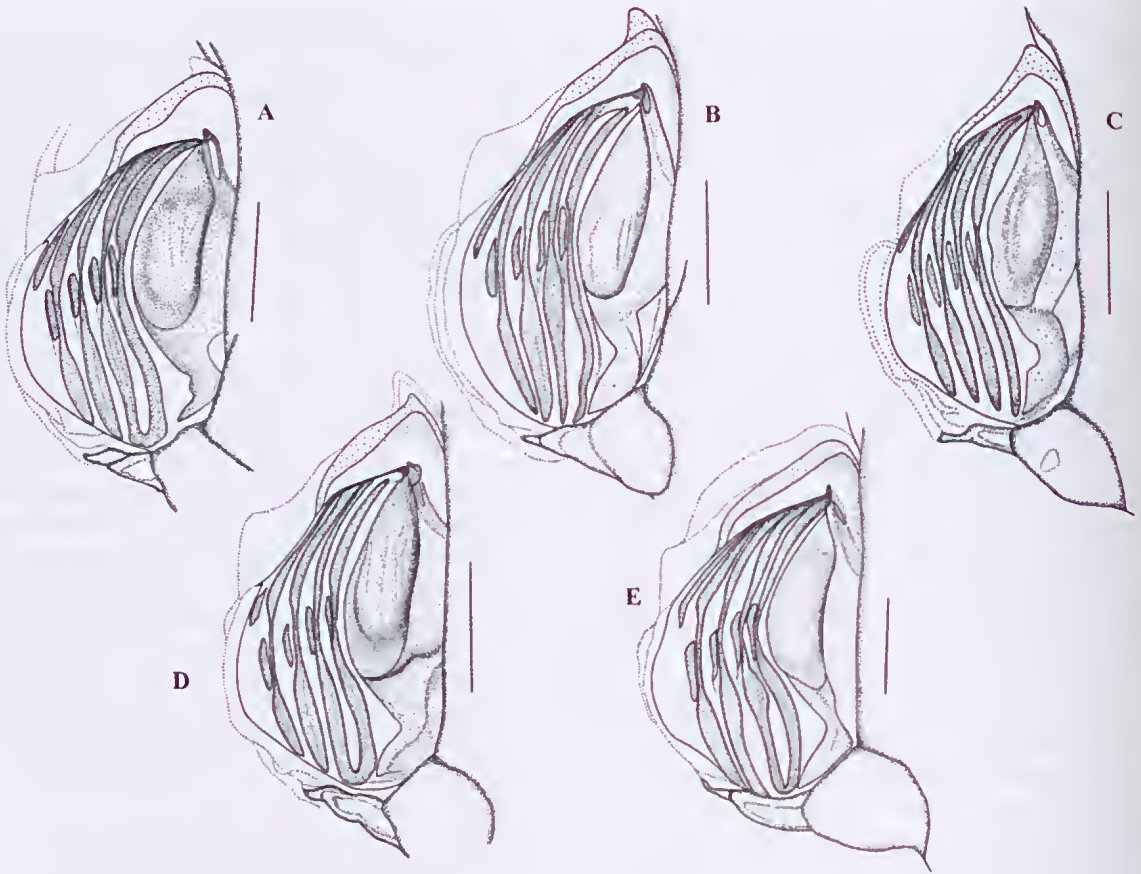


FIG. 4. Timbals of males of the five Queensland *Gudanga* species, with posterior margin at right, dorsal edge at top. A, *G. lithgowae*; B, *G. nowlandi*; C, *G. emmotti*; D, *G. adamsi*; E, *G. pterolongata*. Scale bars are 1 mm.

tympanal cavity margins; inner margins of opercula well separated; opercula developed asymmetrically around meracantha; meracantha spikes overlap operculum plate; broad dome developed across distal and basal areas of opercula extending towards crests; dome areas marked by dark brown colouration, remaining colouration sandy-brown; opercula do not reach anterior margin of sternite II in lateral view.

Timbals. (Fig. 4B) Five long ribs, the anterior long rib shortest, in some specimens overlapping, in other specimens not quite reaching, dorsal termination of adjacent anterior short rib; four well developed short ribs; long ribs 1 to 4 fused dorsally to basal spur, but are not fused ventrally

at their terminations; well developed elongated dome on timbal plate with shallow grooves across top of dome.

Abdomen. (Fig. 1B) Width across auditory capsules greater than head width across compound eyes; in dorsal view, tergites gently tapered posteriorly to tergite 6, more strongly curved and tapered along tergites 7 and especially 8, giving a slight bulbous shape to abdomen; tergite 2 black dorsally, the black colouration extending submedially along anterior margin and expanding laterally and ventro-laterally on to, and enclosing the auditory capsules, further extending ventrally along the anterior margin of sternite II; submedial area orange-brown; black dorsal pigmentation of tergite 2 extends

anteriorly to tergite 1, filling area between timbals; tergites 3 to 7 predominantly bright orange, each with well defined black dorsal areas not extending across the intersegmental membranes, and decreasing in size from tergite 3 through to 7, with additional dark brown pigmentation along ventro-lateral margins; the black dorsal areas give the overall impression of a black fascia extending dorsally along the abdomen; relatively small, irregular black areas on ventro-lateral margins of tergites 3 to 7, most not extending across intersegmental membranes; tergite 8 orange with broad area of black pigmentation occurring posteriorly and extending to pygofer and dorso-laterally to ventro-laterally around posterior margin. Sternites pale sandy-brown, convex, projecting below tergites in lateral view; abdominal venter with a diffuse and usually weakly developed brown central fascia on sternites II to VI, more strongly developed on sternites VII and VIII; a small black medial depression on sternite II.

Genitalia. (Figs 5B-6B) Pygofer predominantly deep brown to black including dorsal beak; prominent upper lobes extending to anal styles, relatively acutely rounded (although variable) terminations in lateral view which dominate pygofer between basal lobes and dorsal beak; along the dorsal margin of the upper lobe, in some specimens is developed a gentle convex curvature as seen in outline; angle between dorsal margin of upper lobe and its extension to dorsal beak approximately orthogonal; prominent sharp dorsal beak; well developed basal lobes with rounded apices, visible in lateral view; secondary basal lobes present but not strongly developed; robust claspers, sharply pointed, with hooked terminations, roughly parallel; median lobe of uncus conspicuous, somewhat duck-bill shaped; aedeagus with tubular theca which in lateral view has a slanting termination, the posterior rim most prominent; a pair of slightly curved and undulatory pseudoparameres, sharply pointed apices, much longer than theca, originating closer to theca than its base; theca with short sclerotised ventral support; aedeagus basal plate undulated in lateral view,

Y-shape in dorsal view, and with functional membraneous 'hinge'.

Female. (Pl. 2B) Similar to male, commonly with subtle reduction in extents of black pigmentation on head, thorax and legs, but generally increased extent of dorsal black pigmentation on abdomen. Head; supra-antennal plate and vertex predominantly black, narrow pale-brown dorso-anterior margin extending to pedicels, even to compound eye; distinct short yellow-brown fascia extending from near median ocellus to pronotal margin; mandibular plate and genae black with pale brown narrow ribbed lateral margins and prominent silver-yellow pubescence; ocelli rose to pale red; postclypeus predominantly black to deep brown with narrow pale brown margin, partially extending between transverse ridges, distinct pale brown dorso-medial spot; anteclypeus black; rostrum brown, darker brown to black apically, reaching beyond mid-coxae but not always hind coxae; antennae dark brown, pale brown apically. Pronotum predominantly black with reddish-brown or dark brown areas occurring between the lateral and paramedian fissures and on to the lateral margins; central fascia pale brown to yellow-brown, splaying out along posterior pronotal margins; pronotal collar black, thin pale brown posterior margin; remaining pronotal colouration as in male. Mesonotum; similar to male, with submedian sigillae more clearly defined and medium to dark brown pigmentation between sigillae covering mesonotum. Wings as in male, relatively high length/width ratios (2.8-3.1); radial cell shorter than distance from its apex to wing tip (ratios 0.86-0.97). Legs similar to male, but with general reduction of black pigmentation, replaced by dark to medium brown colouration on fore legs; mid and hind legs similar to male. Abdomen, tergites 1 and 2 black or brown dorsally, grading to brown submedially, orange-brown laterally, brown or black on, and enclosing the auditory capsules, but not extending to sternite II; tergites 3 to 8 predominantly bright orange, each with variable dorsal black to brown patches, which are irregular in shape, mostly extending across intersegmental membranes, and showing an

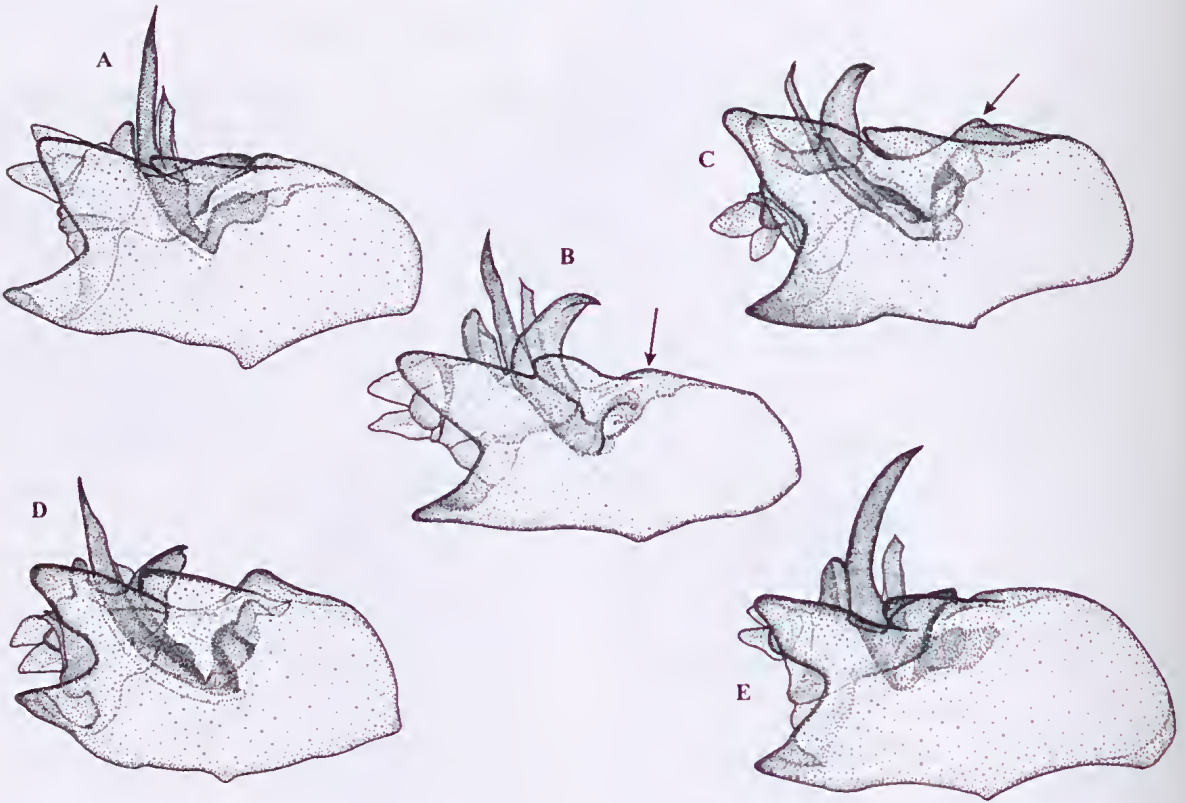


FIG. 5. Pygofer and male genitalia of the five *Gudanga* species illustrated in lateral view. Lengths of pygofers are: 2.3 mm, *G. adamsi*; 2.4 mm, *G. lithgowae*; 2.6 mm, *G. nowlandi*; 2.7 mm *G. emmotti*; 2.5 mm, *G. pterolongata*. Arrows indicate the relatively swollen secondary basal lobes of *G. emmotti* compared to *G. nowlandi*. A, *G. lithgowae*; B, *G. nowlandi*; C, *G. emmotti*; D, *G. adamsi*; E, *G. pterolongata*.

overall narrowing posteriorly towards tergite 8, in addition to a posterior narrowing also evident within each tergite; in dorsal view, these dorsal patches give the appearance of a prominent dark fascia running longitudinally along abdomen, conspicuously splaying out anteriorly towards, and within, tergite 2, more prominent than in the males; deep brown to black diffuse patches also present on ventro-lateral margins of tergites 3 to 8; tergite 9 pale sandy-brown sometimes with an ill-defined broad brown median fascia extending from approximately one-quarter of length of tergite to posterior margin, becoming darker distally, and continuing along submedial posterior margins; in specimens without the median fascia, a pair of submedial, diffuse, slightly curved deep

brown to black fasciae occur which extend from anterior tergite margin distally; anterior margin of tergite 9 typically has a deep brown irregular zone, extending and narrowing from the submedial fasciae ventrally towards the ventro-lateral margins; another broad, diffuse zone of brown pigmentation continues partially along ventro-lateral margin; a weak diffuse spot occurs posterior-laterally. Sternites pale yellow to off-white colouration, with or without darker median longitudinal fascia. Ovipositor sheath extends between 0.5-1.3 mm beyond apex of tergite 9.

Measurements. N = 29♂♂, 10♀. Ranges and means (in parentheses): *BL*: ♂ 16.2-20.0 (18.46); ♀ 16.8-20.7 (18.93). *FWL*: ♂ 15.4-18.5 (17.08); ♀ 16.3-20.3 (18.52). *FWW*: ♂ 5.4-6.5 (5.95); ♀ 5.5-

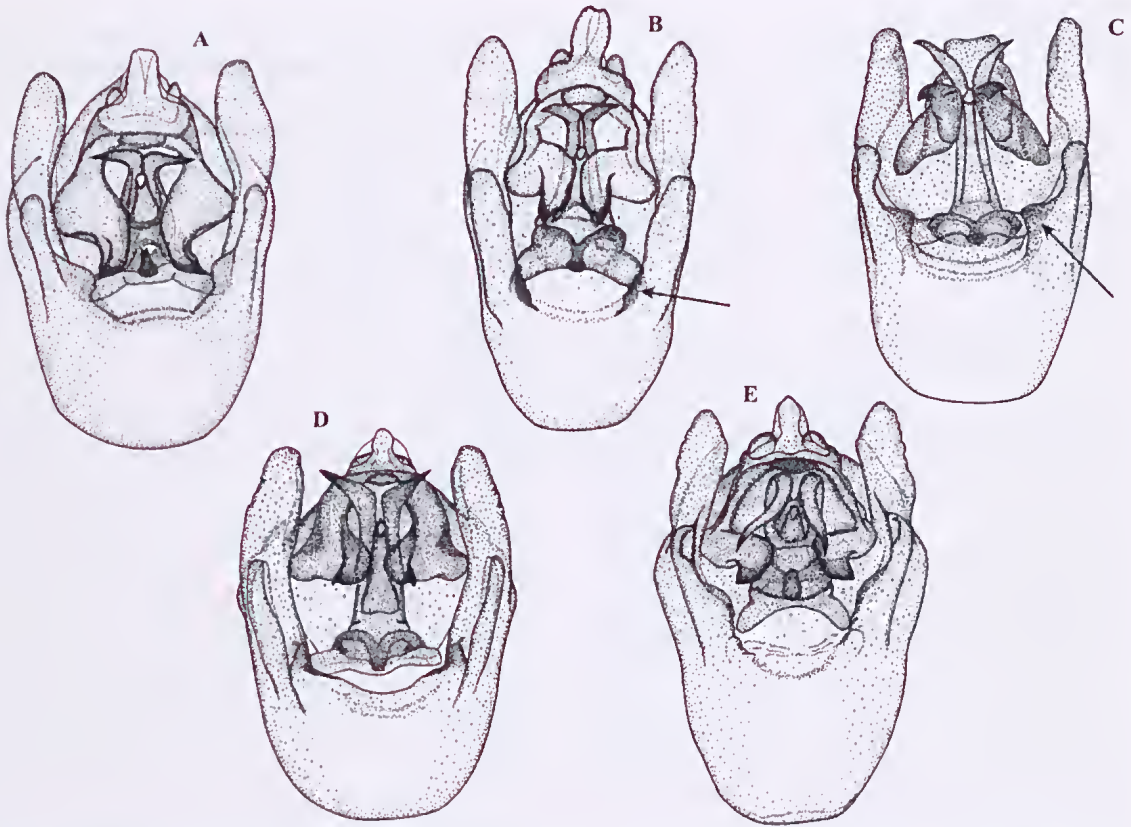


FIG. 6. Pygofer and male genitalia of the five Queensland *Gudanga* species illustrated in ventral view. A, *G. lithgowae*; B, *G. nowlandi*; C, *G. emmotti*; D, *G. adamsi*; E, *G. pterolongata*. Pygofer lengths are listed in Fig. 5 caption. Arrows indicate the relatively swollen secondary basal lobes of *G. emmotti* compared to *G. nowlandi*.

6.8 (6.18). HW: ♂ 4.5-5.4 (5.00); ♀ 4.7-5.7 (5.29); PW: ♂ 4.2-5.0 (4.68); ♀ 4.5-5.5 (4.94). AW: ♂ 5.2-6.3 (5.96); ♀ 5.3-6.1 (5.71). FWL/WR: ♂ 2.69-3.02 (2.87); ♀ 2.81-3.14 (3.00).

Distribution, Habitat and Behaviour. (Fig. 7) Known only from the semi-arid region of southwestern Queensland, associated with Mulga (*A. aneura*) woodlands, more rarely Gidyea (*A. cambagei*) woodlands when relatively high populations are present. A localised species, although sometimes locally very common, superbly cryptic, wary and fast flying. Specific localities include: 34 km E Bulloo River crossing at Quilpie (aural records); Mt. Slowcombe, 5 km N of Yaraka; region extending from approximately 70 km N of Quilpie to Adavale, including especially the 'Milroy' and 'Bulls

Gully' properties; Boss's Gorge, approximately 75 km N of Adavale, and intervening mulga areas through to Adavale (aural records); the Eulo and Currawinya National Park region; 63 km SW of Eromanga; and 43 km SE of Windorah (near Jundah-Quilpie road junction). The sharp chirping and 'buzzing' song is described below. Available records range from September to March, the optimum months being January to March.

Etymology. Named after J. Nowland, the youngest son of the Nowland families who managed and owned the 'Milroy' and 'Bulls Gully' properties during the time of this study. J. Nowland was active in finding many cicadas, known and undescribed, within the area.

Similar species. *G. nowlandi* is closely similar in morphology and colour patterning to *G. emmotti*, differences being detailed below.

Gudanga emmotti sp. nov.

(1C-6C, 7, 9B, 10B, 11A, 14A-F, 17, 18, 19, 20, Plates 3, 4C, Table 1)

Material. TYPES. HOLOTYPE: ♂, (QMT165702), 200 m W Green Ck, Bald Hills Sta., Tonkoro Rd, SWQ, mulga, 30.i.2009, 24° 05'59.0"S 143° 01'07.2", K. Hill, A.E. (QM).

PARATYPES. Southwestern Queensland: 1♂, 200 m W Green Ck, Bald Hills Sta., Tonkoro Rd, SWQ, mulga, 30.i.2009, 24° 05'59.0"S 143° 01'07.2"E., K. Hill, AE. (AE). 1♂, 3♀, "Hickleton", SW of Longreach, 27.ii.2004, 23° 59'19"S 143° 03'17"E, A.J. Emmott, P. Kleinschmidt; 5♂, 2♀, Bald Hills Stn nr Noonbah Stn, 18.iii.2003, A.J., F.F. & A.M.M. Emmott, in *Acacia cyperophylla*; 1♀ "Noonbah" Stn, SW of Longreach, 18.iii.2003, 24° 04'S 143° 11'E, A.J. Emmott, P. Kleinschmidt; 6♂, 1♀, c.20 km S of Stonehenge, 24° 31'55"S 143° 15'23"E, M.S. & B.J. Moulds; 5♂, 4♀, AU.QL.SSD, 68 km N of Windorah, 1.ii.2009, 24° 56.688'S 142° 51.096'E, 147 m, K. Hill, D. Marshall; 6♂, AU.QL.BHS, Green Ck, 18 km W of Noonbah Hsd., 30.i.2009, 24° 06.071'S 143° 01.054'E, K. Hill, D. Marshall, A. Emmott. (MSM). ♂, 200 m W Green Ck, Bald Hills Sta., Tonkoro Rd, SWQ, mulga, 30.i.2009, 24° 05'59.0"S 143° 01'07.2"E, K.Hill, AE. (BMNH). ♂, 200 m W Green Ck, Bald Hills Sta., Tonkoro Rd, SWQ, mulga, 30.i.2009, 24° 05'59.0"S 143° 01'07.2"E, K. Hill, AE. (ANIC).

Description of Male (1C-6C, Pl. 3A, 4?). *Head.* Dark brown compound eyes separated from pronotum along their outer ventral margins; distance between lateral ocelli similar to distance between lateral ocellus and compound eyes; width of head across outer margins of compound eyes greater than across lateral pronotal margins (i.e. excluding amplified lateral angles of pronotal collar). Supra-antennal plate and vertex black; mandibular plate and genae black with narrow pale brown raised margins, covered by silvery pubescence, usually longest on mandibular plate and genae; poorly defined and slightly depressed small pale fascia extending posteriorly from near median ocellus to pronotal margin; pale brown margin adjacent to pedicels extending along the dorso-anterior margin of supra-antennal plate, usually continuing in part across vertex to compound eyes. Ocelli pale red. Postclypeus shiny black with narrow, pale brown margin;

small to very small diffuse pale sandy-brown dorso-medial spot. Anteclypeus black; rostrum brown, black apically, extending beyond mid coxae, usually just reaching anterior margin of hind coxae. Antennae brown.

Thorax. Pronotum predominantly black with conspicuous reddish-brown, less often deep brown areas between the paramedian fissures, between the paramedian and lateral fissures, and postero-laterally to lateral fissures; central fascia pale brown anteriorly, the posterior end pale sandy brown, centrally black, and splaying out and merging with the mainly black pronotal collar; the black pronotal collar colouration continues around the ventro-lateral pronotal margins with a very narrow pale margin visible; narrow anterior pronotal margin pale brown; lateral angles of pronotal collar amplified. Mesonotum predominantly black, with submedial sigillae deep brown merging to black medially, lateral sigillae black and merging into deep brown to black mesonotum; only the dark brown along and adjacent to parapsidal suture is more clearly defined; lateral sigillae extend posteriorly to anterior arms of cruciform elevation; area between anterior arms of cruciform elevation black to deep brown; cruciform elevation pale sandy-brown to darker brown, becoming darker towards apices of arms, scutal depressions black; lateral mesonotal margins proximal to, and within wing grooves pale brown; mesonotum with sparse silvery to silvery-yellow pubescence, more pronounced adjacent to wing grooves.

Wings. (Fig. 3B). Fore wings semi-opaque black to brown, relatively darker brown adjacent to all the veins, with conspicuous undulations on the wings between the veins; lengths similar to total body length, with relatively high length/breadth ratios (2.6-3.0); costal vein very gently curved anteriorly towards node; sclerotised zone along anterior costal vein margin similar in width to costal vein width; costal and R+Sc veins fused, but each clearly distinct; nodal line clearly visible in some specimens; CuA vein not intersecting M vein, but directly intersects arculus of basal cell; the three distal vein sections of M that form inner margin of radial cell are generally of unequal length; medial cell larger

in size than cubital cell; cubital cell and clavus of similar maximum width; 8 apical cells shorter than adjacent ulnar cells; basal membrane orange and opaque; fore wing venation pale to medium brown; radial cell normally shorter than distance from apex to wing tip (ratios 0.85–1.01). Hind wing predominantly hyaline with variably weak to very weak yellow colouration, always weaker distally; semi-opaque orange plaga covering proximal three-quarters of anal cell 3, the distal margin strongly concavely curved, also covering the proximal third to half of anal cell 2 with obliquely curved or straight margin extending towards vein 2A and further extending adjacent to the vein as narrow colouration to vein termination; the detailed shapes and extents of these areas of orange plaga in anal cells 2 and 3 is variable between individuals; paler orange infuscation variably developed within proximal terminations of cubital cell 1, medial, radial and costal cells, often partially extending weakly adjacent to cubitus, median, subcostal and costal veins; minor weak brown infuscation at distal termination of 2A vein extending very weakly to adjacent margin of anal cell 2; weak but distinct brown infuscation developed along wing margin is commonly present; 6 apical cells; anal cells 1+2+3 much broader than cubital cell 1+2; hind wing venation orange-brown grading to medium-brown apically.

Legs. Fore coxae predominantly black with pale sandy-brown longitudinal fasciae on lateral and posterior faces, and three erect black spines; mid and hind coxae similar but with more extensive pale sandy-brown colouration, especially on posterior faces; fore and mid femora, trochanters, tibiae and tarsi predominantly black, in some specimens dark brown with pale sandy-brown longitudinal fasciae; hind femora dark brown with pale sandy-brown posterior faces; hind trochanters, tibiae and tarsi medium brown with darker brown longitudinal fasciae; claws dark brown, darker apically; three spines on fore femora.

Opercula. (Fig. 3C). Relatively broad, oriented roughly parallel to abdomen, angled inwards towards abdominal midline in disto-medial area; disto-medial operculum margins rounded,

the degree of rounding variable between specimens; medial margins reaching margins of tympanal cavity while distal margins and crests not reaching lateral tympanal cavity margins; inner margins of opercula well separated; opercula developed asymmetrically around meracantha; meracantha spikes overlap operculum plate; broad dome developed across distal and basal areas of opercula extending towards crests; dome areas marked by dark brown colouration, remaining colouration pale sandy-brown; opercula may just extend to anterior margin of sternite II in lateral view.

Timbals. (Fig. 4C). Five long ribs, the anterior long rib shortest, commonly not reaching dorsal termination of adjacent anterior short rib, but in some specimens just overlapping the termination; four well developed short ribs; long ribs 1 to 4 fused dorsally to basal spur, but not fused at their ventral terminations; well developed elongated dome on timbal plate with shallow grooves across top of dome.

Abdomen (Fig. 1C). Width across auditory capsules greater than head width across compound eyes; in dorsal view, tergites gently tapered posteriorly to tergite 6, more strongly curved and tapered along tergites 7 and especially 8, giving a slightly bulbous shape to abdomen; tergite 2 black dorsally, the black colouration extending submedially along anterior margin and expanding laterally and ventro-laterally on to, and enclosing the auditory capsules, further extending ventrally along the anterior margin of sternite II; submedial area orange to orange-brown; black dorsal pigmentation of tergite 2 extends anteriorly, becoming deep brown, to tergite 1, filling area between timbals; tergites 3 to 7 predominantly bright orange, each with well defined black dorsal areas not extending across intersegmental membranes, and decreasing in size from tergite 3 through to 7; deep brown pigmentation along ventro-lateral margins to at least tergites 3 to 5; the black dorsal area on tergite 8 posteriorly located and extends to pygofer and around whole of posterior margin, with remaining colouration orange. Sternites pale sandy-brown to pale orange-brown, convex but not always fully visible in lateral view; a diffuse

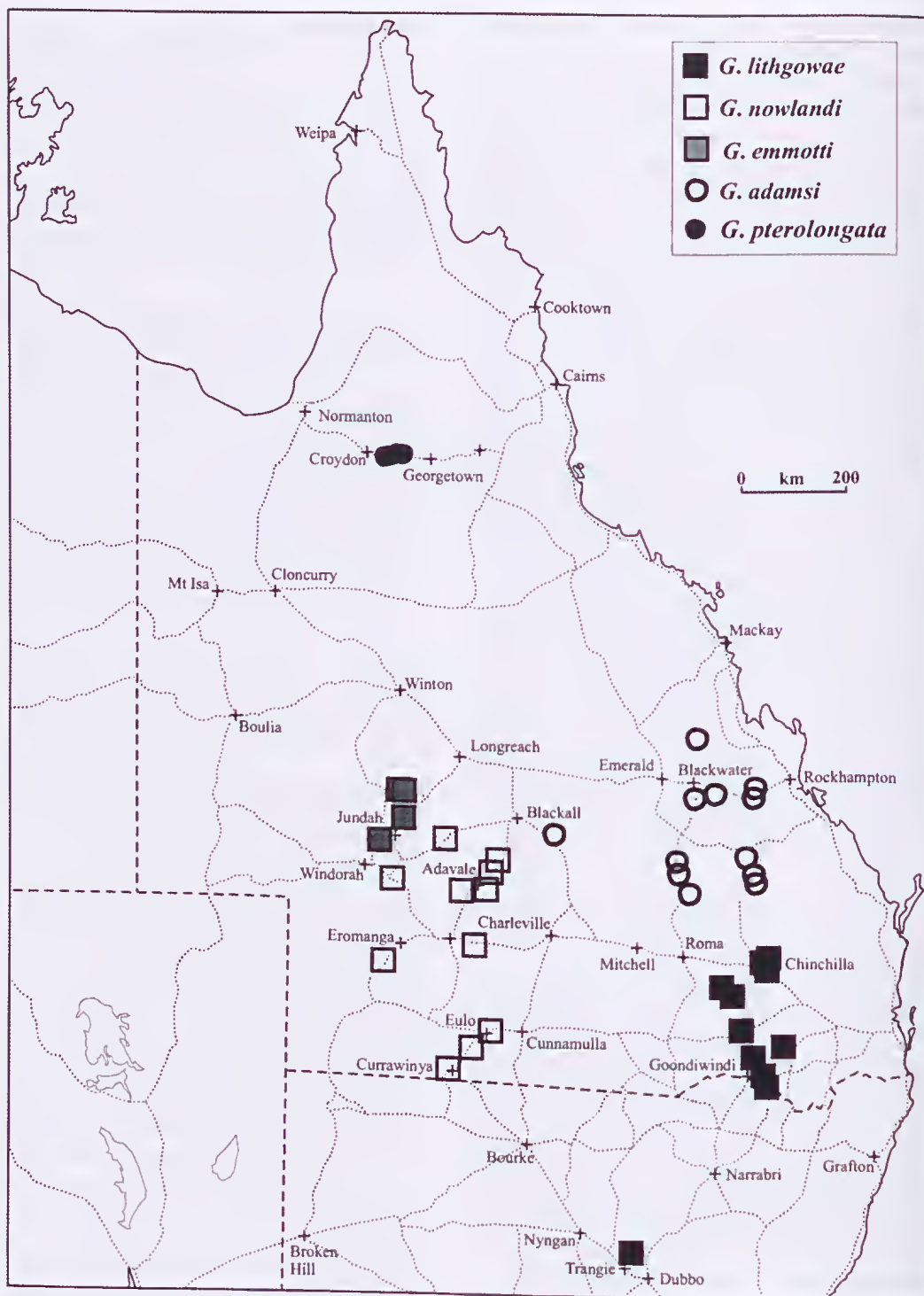


FIG. 7. Distribution records of the five described *Gudanga* species in Queensland and New South Wales based on collected specimens, and aural records and recordings as listed in the text.

and weakly developed brown spot or short fascia on shallow medial depression adjacent to posterior margin of sternite II; diffuse and weakly developed brown abdominal venter on sternites III to V may be present; posterior half of sternite VII black to deep brown, extending to sternite VIII.

Genitalia. (Figs 5C-6C). Pygofer predominantly black to deep brown including dorsal beak; prominent upper lobes extending to anal styles, relatively acutely rounded terminations in lateral view, variable between specimens, which dominate pygofer between basal lobes and dorsal beak; dorsal and especially ventral margins of upper lobe with gentle convex outlines as seen in lateral view; angle between margins of upper lobe and their extension to dorsal beak normally greater than orthogonal (i.e. relatively gently rounded); prominent sharp dorsal beak; well developed basal lobes with rounded apices, visible in lateral view; secondary basal lobes well developed and clearly seen in dorsal and lateral views; robust claspers, sharply pointed, with hooked terminations, tending slightly outwardly pointing; median lobe of uncus conspicuous; aedeagus with tubular theca which in lateral view has a slanting termination, the posterior rim most prominent; a pair of pseudoparameres, slightly curved apically in lateral view, sharply pointed apices, longer than theca, originating closer to theca than its base; theca with short ventral support; aedeagus basal plate undulated in lateral view, Y-shape in dorsal view, and with functional membranous 'hinge'.

Female (Pl. 3B). Generally similar to male in patterning and colour, with some colour variation between specimens. Head and pronotum very close to male colours and patterning; mesonotum varies from specimens which are similar to male, to those with medium brown colouration of submedial sigillae and enclosing mesonotum area; in such specimens, lateral sigillae dark brown to black, with parapsidal suture visible due to sharply defined paler brown colours. Wings as in male; relatively high length/width ratios (2.8-3.0); radial cells shorter than distance from their apices to wing tip (ratios 0.90-0.96). Legs similar

to colour patterning of males, but with reduced areas of black and brown pigmentation and generally paler brown pigmentation replacing the darker male colours. Abdomen: Tergite 1 medium to dark brown; tergite 2 with dorsal dark brown to black patches, not extending submedially in some specimens, grading submedially and laterally to brown or black in other specimens; auditory capsules brown to black; black to brown dorsal patches on tergites 2 to 8 progressively reduce in size posteriorly, variably cross intersegmental membranes, with additional posterior narrowing of individual patches occurring within each tergite; overall appearance of the darker dorsal areas is that of a longitudinal dark fascia, commonly with a conspicuous splaying out anteriorly towards, and within, tergite 2; colour of main areas of tergites 2 to 8 is orange, with narrow brown areas extending along ventro-lateral margins of tergites; tergite 9 pale brown to orange-brown with an ill-defined slightly darker brown broad median fascia not always extending along length of tergite; in addition, a pair of submedial brown diffuse fasciae that extend from anterior tergite margin distally to stigma are present in some but not all specimens; anterior margin of tergite 9 commonly has a zone of brown pigmentation extending and narrowing from submedial to ventro-lateral margins, again not always present; a weak to pronounced brown or black spot occurs posterior-laterally. Sternites uniformly pale sandy-brown to orange-brown, usually with a diffuse and weakly developed brown central fascia, which tends to darken on sternites VII and VIII. Ovipositor sheath extends between 0.6-1 mm beyond apex of tergite 9.

Measurements. N = 27♂, 12♀. Ranges and means (in parentheses): *BL*: ♂ 15.8-20.1 (17.98); ♀ 16.7-20.4 (18.42). *FWL*: ♂ 15.7-18.4 (17.03); ♀ 17.0-18.8 (18.06). *FWW*: ♂ 5.6-6.9 (6.21); ♀ 5.9-6.6 (6.20). *HW*: ♂ 4.5-5.3 (4.94); ♀ 4.8-5.2 (5.06); *PW*: ♂ 4.1-5.0 (4.61); ♀ 4.5-5.0 (4.76). *AW*: ♂ 5.5-6.4 (5.89); ♀ 4.9-5.8 (5.46). *FWL/WR*: ♂ 2.59-2.87 (2.75); ♀ 2.80-3.00 (2.91).

Distribution, Habitat and Behaviour. (Fig. 7) Known only from a restricted region within far south-western Queensland which

TABLE 1. Comparative summary of calling song parameters of the three Queensland *Gudanga* species emitting three echemes per phrase.

Species	Localities	Phrase repetition rates	Intra-phrase repetition rates			Echeme durations (ms)			Inter-echeme intervals (ms)		Macro-syllable durations (ms)	Female response flick intervals (ms)	Extended echeme durations (sec)
			Echemes 1 to 2	Echemes 2 to 3	Echemes 1 to 3	Echeme 1	Echeme 2	Echeme 3	Echemes 1 to 2	Echemes 2 to 3			
<i>G. emmotti</i> (1) Short echeme 1 lengths (<190 ms)	Bald Hills, Hickleton and Noonbah stations*	Mean = 514±46 ms (1) = 1.95 Hz [298-711] (2) (n=216) (3)	185±22 ms = 5.4 Hz [141-255] (n = 219)	108±13 ms = 9.3 Hz [63-218] (n=217)	108±28 [22-184] (n=230)	33.5±8.4 [22-118] (n=217)	26.9±8.8 [10-107] (n=217)	74.5±12.3 [30-127] (n=217)	75.2±10.6 [27-118] (n=217)	(Coalesced) 4.23±0.38 [3.61-5.00] (n=25)	-	Single 'buzz' only recorded (and heard) = 1.16 sec	
(2) Long echeme 1 lengths (<190 ms)	As above	Mean = 633±55 ms = 1.58 Hz [542-772] (n=80)	323±42 ms = 3.1 Hz [261-412] (n=81)	113±15 = 8.8 Hz [70-205] (n=78)	259±38 [196-349] (n=82)	35.5±14.0 [112-131] (n=78)	28.4±6.4 [10-49] (n=78)	65.4±13.0 [41-88] (n=78)	77.7±13.4 [38-100] (n=78)	(Non-coalesced) 4.92±0.40 [4.02-5.33] (n=48)	-	None recorded	
<i>G. emmotti</i> (1) Short echeme 1 lengths (<190 ms)	68 km N. Windorah*	Mean = 564±71 ms = 1.77 Hz [446-672] (n=20)	211±34 ms = 4.7 Hz [130-276] (n=22)	113±6 ms = 8.8 Hz [105-124] (n=2)	129±34 [66-180] (n=22)	31.0±3.0 [26-38] (n=22)	24.4±5.5 [4-37] (n=22)	83.3±18.0 [59-115] (n=22)	82.5±6.9 [73-98] (n=22)	Combined with above	46.4 ±3.5 [40-55] (n=21)	None recorded	
(2) Long echeme 1 lengths (≥ 190 ms)	As above	Mean = 644±49 ms = 1.69 Hz [591-794] (n=44)	310±37 ms = 3.2 Hz [276-405] (n=45)	114±11 = 8.8 Hz [93-136] (n=45)	243±36 [190-373] (n=45)	27.3±2.7 [18-30] (n=45)	23.7±5.1 [8-31] (n=45)	69.7±9.8 [53-87] (n=45)	87.2±10.8 [74-115] (n=45)	Combined with above	-	Mean = 1.25±0.23 sec [0.98-1.40] (n=3)	
<i>G. nowlandi</i>	Milroy & Bulls Gully Stations, Nr. Adavale, 74 km NNE Adavale (Boss's Gorge)	Mean = 388±37 ms = 2.58 Hz [252-525] (n=59)	126±13 ms = 7.9 Hz [60-153] (n=66)	62±5 = 16.1 Hz [38-76] (n=66)	46.2±10.3 [32-69] (n=66)	28.5±3.1 [21-37] (n=66)	14.2±4.2 [6-21] (n=66)	79.7±11.6 [28-110] (n=66)	34.6±4.4 [26-43] (n=66)	(Coalesced) 4.41±0.52 [3.3-5.3] (n=36)	-	Mean = 1.18±0.31 sec [0.43-2.22] (n=142)	
<i>G. nowlandi</i>	Eulo-Currawinya region	Mean = 411±51 ms (1) = 2.43 Hz [315-643] (2) (n=262) (3)	159±27 = 6.29 Hz [120-363] (n=266)	64±8 = 15.6 Hz [56-162] (n=265)	78.8±24.6 [34-300] (4) (n=266)	33.4±4.8 [25-50] (n=266)	22.3±3.5 [12-40] (n=265)	82.3±16.4 [59-146] (n=266)	31.4±5.2 [12-46] (n=265)	Combined with above	-	Mean = 1.17±0.16 sec [0.90-1.39]	
<i>G. nowlandi</i>	63 km SW Eromanga*	Mean = 373±20 ms = 2.68 Hz [341-482] (n=110)	126±5 = 7.9 Hz [88-146] (n=113)	60±2 = 16.7 Hz [55-70] (n=120)	54.0±7.3 [26-79] (n=115)	25.9±3.4 [21-37] (n=121)	18.0±2.9 [13-29] (n=120)	71.9±8.5 [49-108] (n=121)	35.0±3.4 [23-42] (n=120)	Combined with above	-	Mean = 1.17±0.16 sec [0.90-1.39]	

TABLE 1. Continued ...

Species	Localities	Phrase repetition rates	Intra-phrase repetition rates	Echeme durations (ms)		Inter-echeme intervals (ms)	Macro-syllable durations (ms)	Female response flick intervals (ms)	Extended echeme durations (sec)
<i>G. nowlandi</i>	50 km SE Windorah (Jundah-Quilpie Rd Jct)	Mean = 484±33 ms = 2.07 Hz [436-602] (n=155)	154±7 = 6.5 Hz [136-184] (n=165)	77.7±5.1 [64-91] (n=165)	25.7±2.0 [23-36] (n=165)	76.6±8.8 [62-118] (n=165)	Combined with above	49.2±3.9 [39-61] (n=33)	None recorded
<i>G. lithgowae</i>	Chinchilla; 20 km E Moorie; 15 km SW Goondiwindi; Southwood N.P. (All data)	Mean = 739±111 ms = 1.35 Hz [531-1143] (n=154)	196±51 = 5.1 Hz [146-412] (n=165)	127±52 [76-346] (n=165)	36.5±4.9 [25-58] (n=165)	69.7±6.6 [51-88] (n=165)	(Coalesced) 4.04±0.59 [2.4-5.1] (n=38) (lowest values tend to occur at end or start of echemes)	43.9±4.8 [30-54] (n=60)	None recorded
<i>G. lithgowae</i>	As above, with echeme 1 <150 ms only	Mean = 721±89 ms = 1.39 Hz [531-934] (n=138)	181±17 = 5.5 Hz [146-212] (n=148)	112±18 [76-145] (n=148)	36.2±4.3 [25-49] (n=148)	69.9±6.4 [51-88] (n=148)	-	-	-

(1) Mean ± 1σ, with equivalent Hz values; (2) Range of values; (3) Number of data (4) Includes atypical longer echemes
 * Recordings by D. Marshall; + recordings by D. Marshall, L.W. Poppo, A. Ewart.

extends from approximately 68 km north of Windorah (aural records), northward through Stonehenge and further northwest into areas some 15-25 km west of the Lochern National Park, specifically the Noonbah (aural records), Bald Hills and Hickleton Stations. Associated with Mulga (*A. aneura*) and Creekline Mineritchie (*A. cyperophylla*) woodlands. Apparently does not extend west of Windorah into the inter-dune mulga woodlands of the eastern Simpson Desert. A localised species, wary and cryptic. Available records range from January to March. Current distribution records indicate no overlap with *G. nowlandi*.

Etymology. Named after Angus Emmott of Noonbah Station, well known for his extensive and systematic insect collecting through the region, together with his wide natural science contributions to inland Australia.

Similar Species. *G. emmotti* is very similar in morphology and pigmentation to *G. nowlandi*. Subtle differences in their calling songs provided the first indications of complexity and led ultimately to the recognition of their status as sibling species. Both species exhibit variability in their detailed morphology and colouration, enough to preclude most external characters as being uniquely diagnostic.

The most consistent character differences are seen in the respective development of the secondary basal lobes within the pygofer (Figs 5B, C and 6B, C). In *G. emmotti* these are relatively swollen and clearly visible in lateral and dorsal view. In *G. nowlandi*, these are much reduced in size, not markedly swollen and not easily visible. To evaluate these characters require either that the pygofer is very well exposed in preserved specimens, or else requires pygofer dissection.

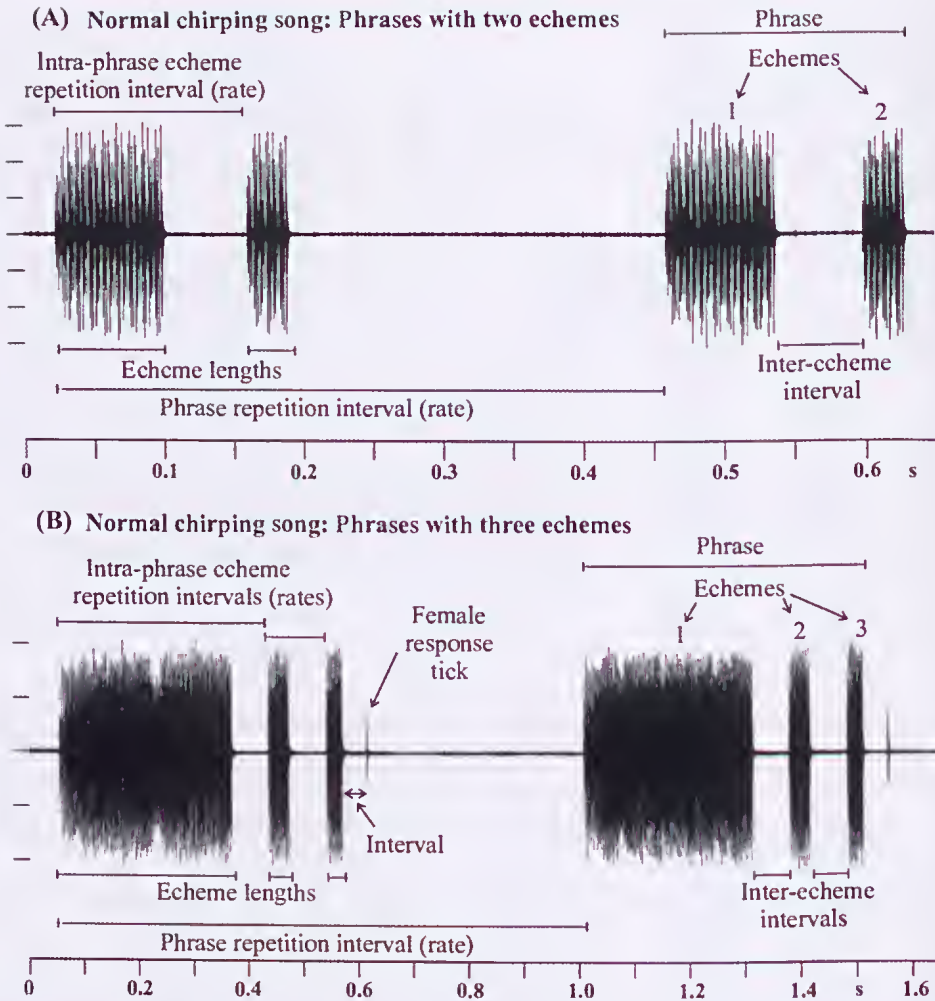


FIG. 8. Waveform plots of the two basic types of normal chirping song of the Queensland *Gudanga* species: (A) Two echemes per phrase (*G. adamsi*), and (B) three echemes per phrase (*G. lithgowae*). The song parameters measured and documented in Tables 1 to 3 are illustrated on the Figure. The vertical scales are linear relative amplitude scales in this and all following waveform plots.

The following, less obviously distinct characters provide useful guides to identification when they are considered in combination and when dissection of the pygofer is not practical:

- (i) Upper pygofer lobe shape (as seen in lateral view; Figs 5B, C); *G. emmotti* with relatively more acutely rounded posterior termination, and with gently undulated outlines along dorsal and ventral margins. *G. nowlandi* with more broadly rounded posterior termination, and with slight or even no curvature in outline

along dorsal and ventral margins.

- (ii) Angle between dorsal margin of upper lobe and its extension towards dorsal beak (as seen in lateral view; Figs 5B, C): For *G. emmotti*, this is broadly rounded and greater than orthogonal; for *G. nowlandi*, it is near orthogonal.
- (iii) Opercula shape (Figs 3B, C). For *G. emmotti*, the disto-medial margin tends to be more acutely rounded. For *G. nowlandi*, the disto-medial margin is more broadly rounded and the opercula generally broader in outline.

New cicada species of the genus *Gudanga* Distant

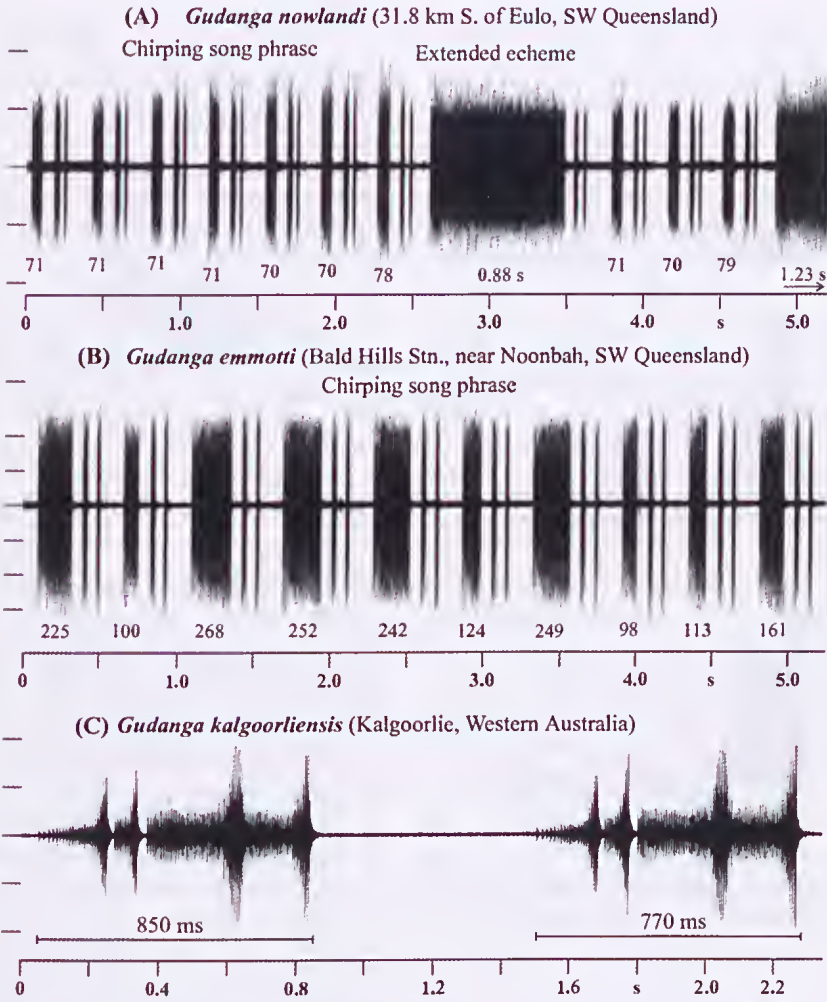


FIG. 9. Waveform plots comparing the similarities and characteristic differences between the calling songs of the three morphologically very similar *Gudanga* species, *G. nowlandi* and *G. emmotti* from south west Queensland and *G. kalgoorliensis* from Western Australia (recording by D. Marshall). The figures beneath the echemes in (A), (B), are the durations (ms), and seconds for the two extended (buzz) echemes in (A).

(iv) Timbal ribs (Figs 4B, C). In *G. emmotti*, the anterior long rib (no. 5) typically does not reach the dorsal termination of the adjacent anterior short rib. In *G. nowlandi*, the anterior long rib more commonly extends to, and overlaps with, the adjacent anterior short rib.

Song differences are detailed below.

SONGS OF THE QUEENSLAND
GUDANGA SPECIES (FIGS 8-17).

General Characteristics. The calling songs of each of the five species are predominantly complex chirping songs, with an additional interspersed extended 'buzz' echeme commonly emitted within the calling songs of *G. pterolongata* and *G. nowlandi*, most conspicuously during the warmer parts of the day (later morning through to later afternoon), and when the cicada populations

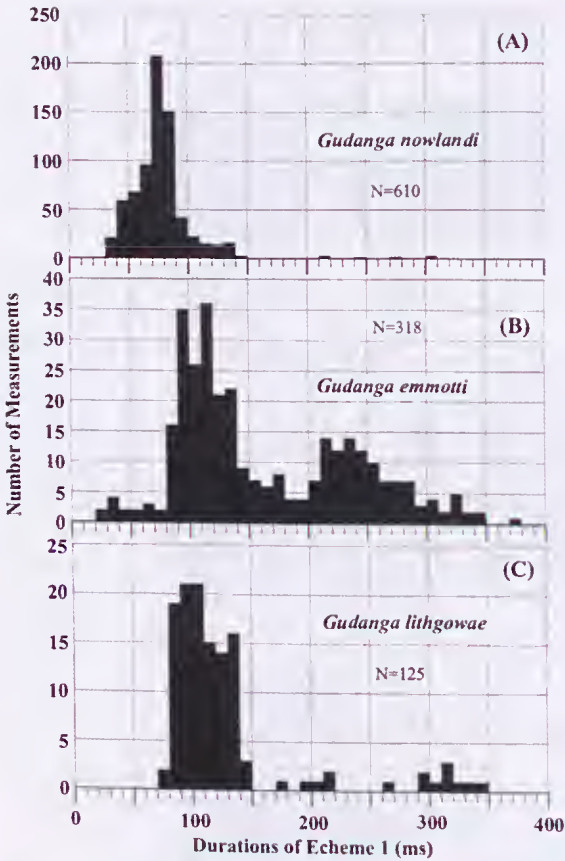


FIG. 10. Histograms comparing the distributions of the echeme 1 durations in the three-echeme chirping song types emitted by *G. lithgowae*, *G. nowlandi* and *G. emmotti*.

are relatively high. The chirping song consists of repeated chirp phrases, each phrase comprising either two or three echemes depending on species. These song differences provide a clear division between the five *Gudanga* species occurring in Queensland; the three-echeme song types include *G. lithgowae*, *G. nowlandi* and *G. emmotti*, while the two-echeme song types include *G. adamsi* and *G. pterolongata*. Fig. 8 illustrates the detailed nomenclature and the specific temporal parameters used to describe the songs in this paper.

The Three-Echeme Song Types

The echemes are simply labelled 1, 2 and 3. The initial echeme (echeme 1) is the longest,

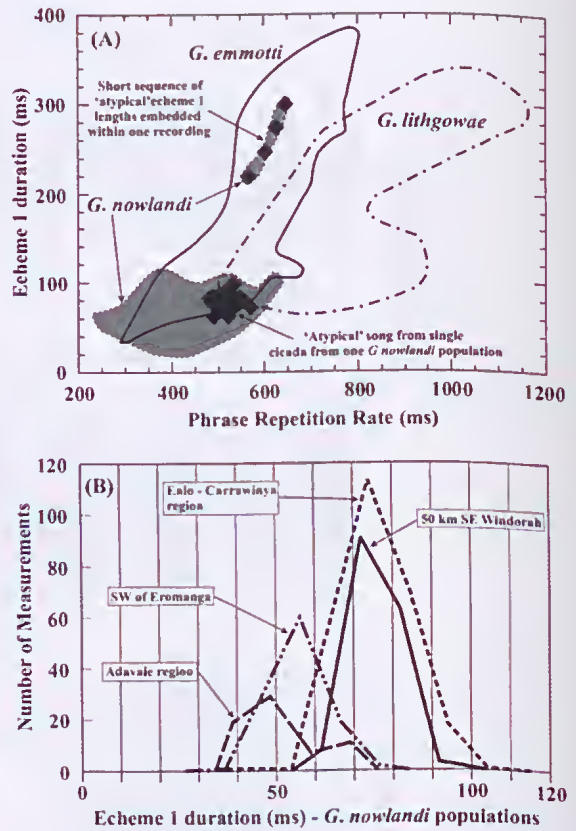


FIG. 11. (A), echeme 1 duration versus phrase repetition rate within the three species emitting the 'three-echeme' chirping song types. Also shown are two sets of 'atypical' song data recognised by statistical analyses within the *G. nowlandi* songs. (B), distribution of echeme 1 durations within four major population groupings of *G. nowlandi*, illustrating subtle inter-population shifts.

echeme 3 is normally the shortest, and echeme 2 intermediate in duration (Table 1). Differences in the durations of the echemes, the phrase repetition rates, the inter-echeme intervals and the intra-echeme repetition rates (Fig. 8) between the species, shown below, are assumed to be sufficient to allow female cicadas to recognise conspecifics. They also facilitate taxonomic identification.

As indicated by the morphological descriptions given above, *G. nowlandi* and *G. emmotti* are sibling species, not easily distinguished by colour or morphology. Figs 9A,

B, illustrate the gross temporal structures of their calling songs. The chirping song phases of these two species are characterised by differences in the durations of echeme 1. Additionally, *G. nowlandi* commonly emits extended buzz echemes, between 0.43–2.25 seconds in length, which are very rare in the *G. emmotti* songs. It is noted that the longest measured echeme 1 (0.38 second) in a *G. emmotti* song is shorter than the shortest measured buzz echeme in *G. nowlandi*. A third morphologically very similar species is described from Western Australia, *G. kalgoorliensis* Moulds, whose calling song is shown for comparison in Fig. 9C. Not only is this song very different from the two Queensland sibling species, but it exhibits quite different temporal phrase structures from all of the known Queensland *Gudanga* species.

The complexities of the *G. emmotti* song are illustrated in Figs 10B, 11A and 14 (see Table 1). The variability of echeme 1 durations is noted above, the distribution of the durations being broadly bimodal, with the critical dividing duration lying at approximately 190 ms. These echeme 1 durations range between the extremes of 22 to 373 ms. There is a tendency, observed qualitatively in the field, for a larger proportion of longer examples of echemes 1 to be emitted on hotter days. In any given recording, however, the shorter and longer versions of echeme 1 may roughly alternate (e.g. Fig. 14A), or occur in groups of longer or shorter echeme lengths. There is no clear correlation between the lengths of echeme 1 and the lengths of the associated second and third echemes within each phrase.

For *G. nowlandi*, echeme 1 durations are more closely constrained (Fig. 10A) and typically even shorter than the short examples of echeme 1 produced by *G. emmotti*. Nevertheless, in a single recording from the Eulo-Currawinya area, a small number of unusually extended versions of echemes 1 are found, as discussed below (apparently a rare case of song variation for this species). The echeme 1 durations do, however, show small differences between the main *G. nowlandi* populations for which data are available (Fig. 11B; Table 1). In addition to echeme 1 durations, four other temporal

song parameters vary between these two sibling species, namely phrase repetition rates, echeme 1 to 2 repetition rates (noting that the definition of these two parameters partially correlate them with echeme 1 length; Figs. 8B, 9A), echeme 2 to 3 repetition rates and to a less extent, inter-echeme 2 to 3 intervals. The other very important characteristic difference is the presence of extended 'buzz' echemes that are present in most, but not all, *G. nowlandi* song sequences (Figs 12B–C, 13A). These, however, are emitted most strongly and frequently in hot weather and where high population densities of this cicada occur. At lower population densities, even in hot weather, the 'buzz' phrases are typically absent. The points of insertion of the extended 'buzz' echemes into the normal chirping song are generally consistent. When emitted, they occur between echemes 1 and 2 (Figs 12C, 13A), with echeme 1 typically clearly defined and produced just prior to the 'buzz', and with echemes 2 and 3 following thereafter. In some records, echeme 1 is partially or fully coalesced into the following 'buzz' echeme (Fig. 12B). As also seen in Figs 12B and C, echeme 1 durations that immediately precede the extended 'buzz' phrases are usually of slightly longer duration than those emitted elsewhere in the chirping songs. As noted, the emission of extended 'buzz' echemes by *G. emmotti* is very rare, with only one recorded (Table 1).

The song of *G. lithgowae* shares broad characteristics with that of both *G. nowlandi* and *G. emmotti*, but is statistically distinct (see below). Echeme 1 durations are longer on average than in *G. nowlandi*, with some sporadically produced longer echemes being more closely similar to *G. emmotti* (Figs 10C, 15A, B). Further differences within the *G. lithgowae* song, compared to *G. nowlandi* and *G. emmotti*, include phrase repetition rates (Fig. 11A), intra-echeme repetition rates, and slightly longer echeme 2 and 3 durations (Table 1).

Finer Scale Macrosyllable Structures. The chirp and extended 'buzz' echemes comprise sequences of partially to completely coalesced macrosyllables in the songs of each species. Figs 14B–D illustrate a rare example, occurring at the initiation of a chirping song sequence of

TABLE 2. Comparative summary of calling song parameters of the two Queensland *Gudanga* species emitting two echemes per phrase

Species	Localities	Phrase repetition rates	Intra-phrase echeme repetition rates		Echeme durations (ms)		Inter-echeme intervals (ms)	Macro-syllable durations (ms)	Extended echeme durations (sec)
			Echemes 1 to 2	Echeme 1	Echeme 2				
<i>G. adamsi</i>	35 km S. Blackwater, (Central Queensland)+	Mean = 457±33 ms = 2.19 Hz [357-601 ms] (n=142)	119±7 ms = 8.38 Hz [103-176 ms] (n=32)	43.7±6.2* [31-58] (n=145)	17.8±4.8 [7-40] (n=147)	75.0±6.7 [14-87] (n=147)	4.47±0.67 [3.95-5.89] (n=42) (1.72-3.97 at echeme ends)	No aural record	
<i>G. adamsi</i>	Blackdown, Wyseby+ Tambo+, Isla N.P., (Central Queensland)	Mean = 496±36 ms = 2.02 Hz [426-612 ms] (n=114)	142±7 ms = 7.04 Hz [125-154 ms] (n=122)	65.8±9.0 [45-83] (n=122)	25.1±4.1 [16-33] (n=122)	76.9±7.9 [56-89] (n=122)	Combined with above	No aural record	
<i>G. pterolongata</i>	41 and 60 km E. Croydon, (Northern Queensland)	Mean = 457±32 ms = 2.19 Hz [394-553 ms] (n=181)	121±10 ms = 8.26 Hz [99-138] (n=119)	55.1±5.4 [40-77] (n=119)	38.6±6.5 [31-61] (n=119)	66.9±8.4 [46-83] (n=119)	'Double' Macro-syllables: 10.06±0.80 (n=72) [9.11-12.7] (3.8-7.7 at echeme ends): Single macro-syllables 5.36±0.85 (n=49) [3.8-7.2]	2.55±1.61 [0.65-5.16] N=36	

Figures in square brackets are minimum and maximum measured values.

* Excludes two high values of 112 and 127 ms.

+ Recordings by D. Marshall

TABLE 3. Comparison of calling song parameters between the 'anomalous' song of a single recording and the normal songs of *G. nowlandi*, all from the Eulo-Currawinya area (see text for explanation)

Species	Phrase repetition rates (ms)	Intra-phrase echeme repetition rates (ms)		Echeme lengths (ms)			Inter-echeme intervals (ms)	
		Echemes 1 to 2	Echemes 2 to 3	Echeme 1	Echeme 2	Echeme 3	Echemes 1 to 2	Echemes 2 to 3
Normal song type (excluding two sets of anomalous songs)	397±35(1) [315-622](2) n= 233(3)	153±11 [120-205] n=235	63±7 [56-162] n=235	76±9 [34±103] n=235	33±5 [25-50] n=235	22±3 [15-40] n=235	78±9 [59-146] n=235	30±5 [12-46] n=235
Anomalous song type comprising whole of recording (representative subset)	518±21 [479-568] n=26	199±7 [178-210] n=27	77±2 [73-82] n=27	79±8 [64-99] n=27	38±2 [34-42] n=27	23±5 [12-29] n=27	122±9 [103-138] n=27	40±3 [35-45] n=27

(1) Mean ±1σ (2) Range of values (3) Number of data

G. emmotti, in which the macrosyllables comprising each echeme are not coalesced, being clearly separate, thereby showing details of their structures, each macrosyllable comprising four discrete syllables. The frequency structures within the macrosyllables and syllables shown in Fig. 13B-C (*G. nowlandi*), and 14D (*G. emmotti*) are not, however, constant. In the case of *G. emmotti*, the frequencies of the first three syllables lie between ca. 8245-9910 Hz, the final syllables >10,600 Hz. This frequency structure is consistent within all macrosyllables examined and facilitates the recognition of macrosyllables structures when strongly coalesced. Figs 14E, F illustrate the progressive processes of syllable and macrosyllable coalescence in the *G. emmotti* songs, in which the syllables are initially still clearly defined (Fig. 14C, E), becoming more compacted as coalescence increases. At a more advanced stage, the microsyllables become segregated into pairs (Fig. 14F), with consequent decrease in the macrosyllable lengths (relative to uncoalesced macrosyllables). When examined in time expanded detail, each coalesced macrosyllable is still seen to terminate with a syllable of higher frequency.

Very similar macrosyllable and syllable structures and their frequency variations are observed in the time expanded echeme structures within the songs of *G. nowlandi* (Figs 13B, C) and *G. lithgowae* (Figs 15C). The songs of the latter species appear to be more variable, with syllable structures often less easily resolved, syllables apparently varying between three to five per macrosyllable. Nevertheless, as in the previous songs, rapid frequency modulations are apparent at time expanded detail with an increase in frequency occurring at the termination of each macrosyllable. In the specific example illustrated (Fig. 15C) of an echeme 3 structure, the measured waveform frequencies range between 5.2-9.4 kHz (in fact, even wider, due to greater pulse frequency variability that occurs within the time scales even finer than the time divisions shown). The measured frequency range is consistent with that of the accompanying amplitude spectrum for this same echeme 3 (Fig. 15D). Corresponding macrosyllable durations (and ranges) are similar for the each of the three described species (Table 1), mean values being 4.0, 4.4 and 4.2 ms, respectively, in the *G. lithgowae*, *G. nowlandi*, and *G. emmotti* songs.

TABLE. 4. Results of statistical analyses of non-parametric song parameters, calculated according to Chi-Square Kruskal-Wallis procedure

Phrase Repetition Rates	Intra-phrase echeme repetition rates			Echeme durations (ms)			Inter-echeme intervals (ms)		
	Echemes 1 to 2	Echemes 2 to 3	Echeme 3 to end of phrase	Echeme 1	Echeme 2	Echeme 3	Echemes 1 to 2	Echemes 2 to 3	Echeme 3 to end of phrase
Raw song parameter comparisons									
<i>G. emmotti</i> vs <i>G. nowlandi</i>									
Chi-Square	465.8	570.3	81.6	509.3	72.9	326.4	35.1	475.7	30.7
Asymp. Sig.	.000	.000	.000	.000	.000	.000	.000	.000	.000
<i>G. emmotti</i> vs. <i>G. lithgowae</i>									
Chi-Square	51.1	187.2	246.0	25.6	36.1	8.25	3.69	220.9	246.0
Asymp. Sig.	.000	.000	.000	.000	.000	.004	.055	.000	.000
<i>G. nowlandi</i> vs <i>G. lithgowae</i>									
Chi-Square	192.3	165.4	287.1	278.3	138.6	230.1	65.9	73.4	286.6
Asymp. Sig.	.000	.000	.000	.000	.000	.000	.000	.000	.000
Comparisons between recordings with female wing-flick responses following each phrase									
<i>G. emmotti</i> vs. <i>G. nowlandi</i>									
Chi-Square	33.7	38.3	0.59	34.3	22.3	28.8	9.39	36.9	1.69
Asymp. Sig.	.000	.000	.445	.000	.000	.000	.002	.000	.194
<i>G. emmotti</i> vs. <i>G. lithgowae</i>									
Chi-Square	39.25	10.9	43.5	12.1	37.5	9.23	7.03	43.5	43.5
Asymp. Sig.	.000	.001	.000	.001	.000	.002	.008	.000	.000
<i>G. nowlandi</i> vs <i>G. lithgowae</i>									
Chi. Square	47.1	48.0	47.1	48.0	48.4	48.3	1.20	21.1	47.1
Asymp. Sig.	.000	.000	.000	.000	.000	.000	.274	.000	.000

All data shown with 1 degree of freedom. Grouping variable: (Category). Asymp. Sig., asymptotic significance, represents critical ($p(0.5)$) for these statistics.

Gudanga nowlandi

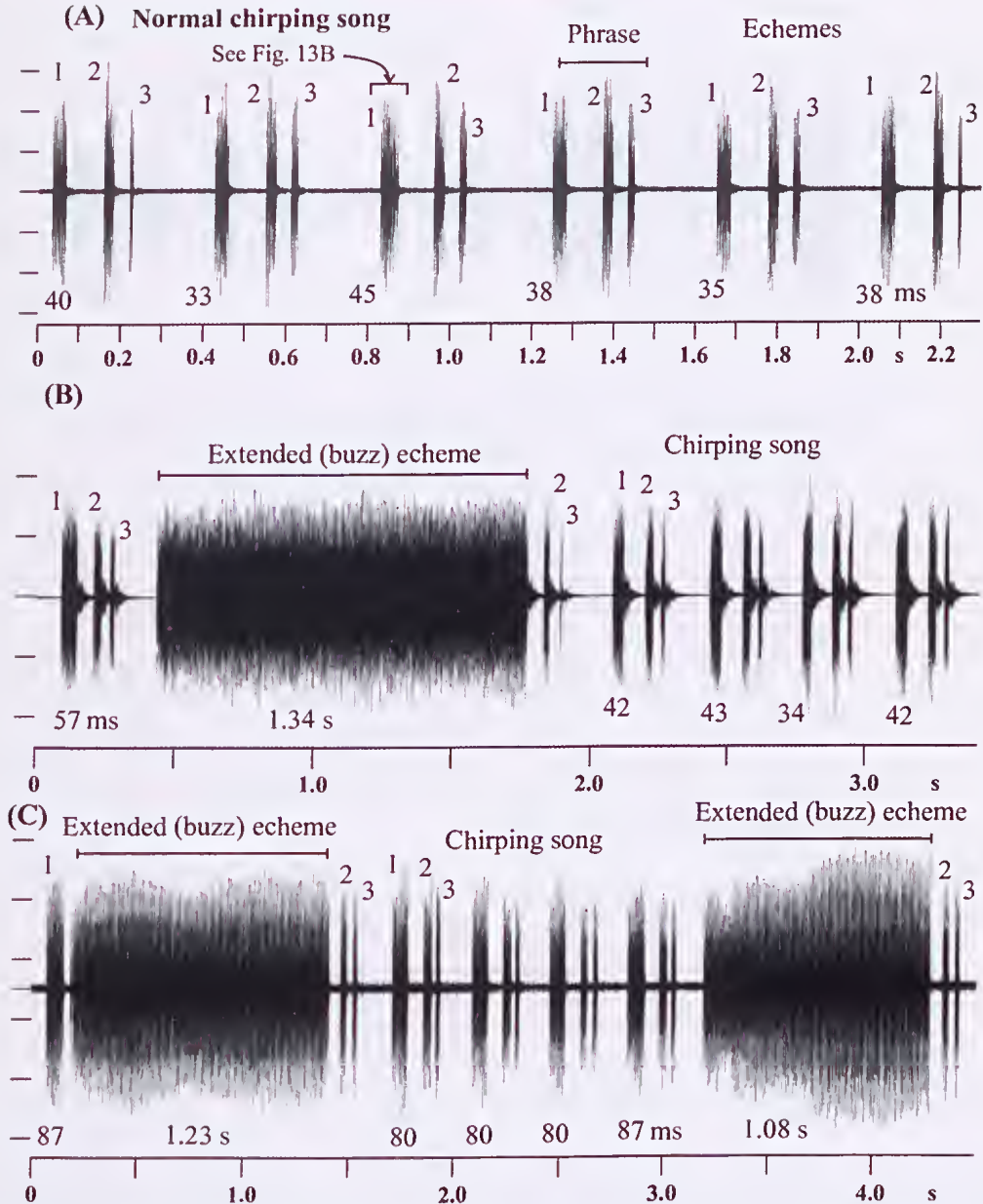


FIG. 12. *Gudanga nowlandi*. Waveform plots showing; (A) the chirping song phase, each phrase consisting of 3 echemes of variable but generally short durations. (B) Chirp phrases with an interspersed extended ('buzz') echeme, and (C) chirp phrases with two interspersed extended echemes. The numbers 1, 2, and 3 indicate the echeme number; numbers beneath the echeme 1's are durations in ms, those beneath the extended echemes are in seconds; A, field recording from Boss's Gorge, 1.xii.1995, ~75 km N. Adavale, south west Queensland. B, container recording at Milroy H.S., near Adavale, 9.i.2000. C, field recording, 31.8 km south of Eulo (Hungerford Road), 18.i.2010, south west Queensland. These were filtered to 1 kHz to improve visualisation.

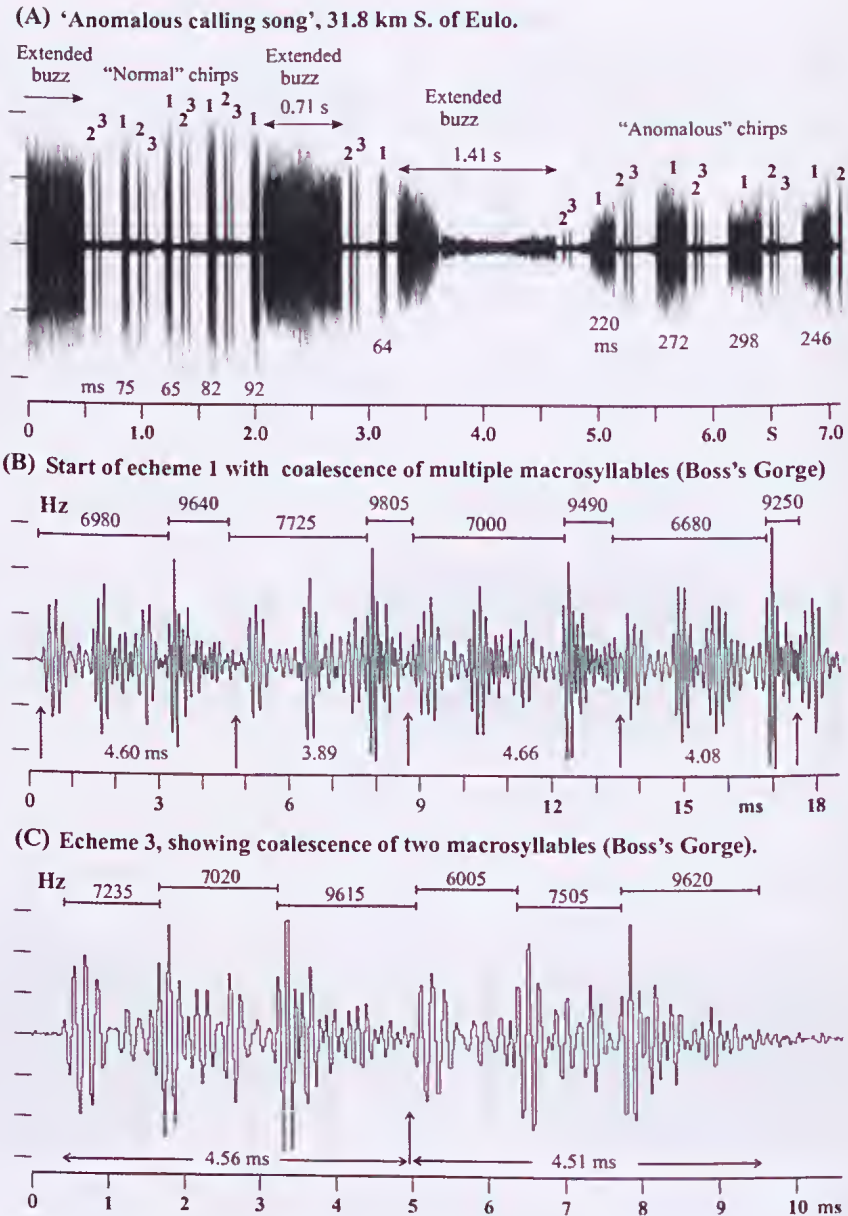


FIG. 13. *Gudanga nowlandi*. Waveform plots showing; (A), complete recording showing a transition from an initial typical chirping song with extended 'buzz' echemes, to an 'atypical' chirping song in which, following the third extended echeme, the first echemes are of longer than normal duration. Numbers above echemes are the echeme numbers, those beneath the echeme 1's are durations (ms). Between 3.5 to 5.0 seconds, the recorded cicada moved its singing position, resulting in the temporary amplitude drop. (B), (C), time expanded plots of detailed syllable-macrosyllable structures within the initial segment of an echeme 1, and a complete echeme 3, respectively. Frequencies measured on these plots from within the syllable segments are shown above the waveforms. Vertical arrows mark the inferred limits of each macrosyllable, with durations in ms. Field recordings from south west Queensland, (A), 31.8 km south of Eulo, 18.i.2010; (B), (C), Boss's Gorge, ~75 km north of Adavale, 1.xii.1998. These were filtered to 2 kHz to improve visualisation.

It is noted, however, that in the *G. lithgowae* songs, slightly shorter than normal syllables commonly mark the beginning and end of each macrosyllable, a distinction from the songs of the other two species.

Amplitude Spectra (Figs 16, 17). The linear frequency spectra of all three species are broadband, with multiple maxima, exhibiting a crude periodicity in some of the *G. nowlandi* and *G. emmotti* spectra. The dominant frequency ranges and means shown by these spectra for each of the three species are very close, lying between approximately 5.4–11 kHz, also representing various localities for *G. nowlandi* and *G. emmotti*. The wide frequency range of the songs is suggested to be an adaptation to their mobile and fast moving behaviour, and the relatively dense acacia woodland in which they occur, thereby facilitating more effective transmission of at least part of the emitted signals. The apparent sidebands, based on detailed measurements of the spectra, reveal a series of low frequency sidebands most likely correlated with repetition rates of the phrases, while the higher frequency sidebands (>200 Hz) possibly reflect the macrosyllable and syllable structures. The inter- and intra-phrase echeme repetition rates broadly correlate with the sidebands in the 6–18 Hz range.

Female Response Clicks. Figs 8B, 15A show an example of female response wing-flicks to the male chirping song of *G. lithgowae*. The response flicks occur 30–54 ms (mean 44 ms) following the emission of the final (third) echeme of each phrase. This behaviour comprises an acoustic duet, the female responding to the structured phrases with wing-flick signals emitted at specific points during the end of each phrase (Sueur & Aubin 2004). It has been described as the 'cueing' (Cooley & Marshall 2001) or 'tilting' (Popple *et al.* 2008) song components. They are believed to facilitate the localisation of the females by the males. Comparable response flicks have been recorded in *G. emmotti* songs from 68 km north of Windorah, and in *G. nowlandi* songs from 43 km southeast of Windorah. The mean response intervals measured are 46 and 50 ms respectively (Table 1), each wing flick following the termination of echeme 3 as in *G. lithgowae*.

Statistical Analyses of Song Specificity within the Three Echeme Song Types.

Methodology. The statistics were based on the measurements of eight song parameters (see Table 4; Fig. 8): echeme 1, 2 and 3 durations, inter-echeme gap 1 duration, inter-echeme gap 2 duration, phrase repetition rate, intra-phrase gap 1 repetition rate, and intra-phrase gap 2 repetition rate.

Some of these parameters are not, however, entirely independent; specifically the repetition rate parameters are dependent on echeme and gap durations (Fig. 8). The data have therefore been subdivided into two subsets, one based on rates and the other based on durations of all echemes and gaps. There were six parameters in the durations analyses (comprising the three echemes and each of the gaps between them; Fig. 8) and three in the rates analyses (each of the three echemes in combination with their subsequent gap). The duration of the silence at the end of each phrase was obtained by summing the durations of the echemes and gaps and then subtracting these from phrase repetition rates (i.e. total phrase lengths).

These measurements were taken from all available replicates ($n=2-63$) in each recording, across 54 separate recording instances ($n=7$ for *G. emmotti*, $n=33$ for *G. nowlandi*, and $n=14$ for *G. lithgowae*). The recording instances were sourced from several sites across the geographical distributions of these three closely related *Gudanga* species (Fig. 7). For each recording instance, the measurements of each song parameter were averaged and the data were formatted into a song parameters matrix. Within this matrix, song instances were treated as objects and the nine sets of measurements were the attributes.

Data were analysed using PC-Ord software (McCune and Mefford 2006). The outlier analysis, as well as the object and attribute summaries, did not reveal any outliers in the data matrix, which indicated that data exclusion and/or transformation were not required. The Sørensen (Bray Curtis) distance measure was used to generate the distance matrix, as it emphasises absolute differences between individual instances across each of the measures and is

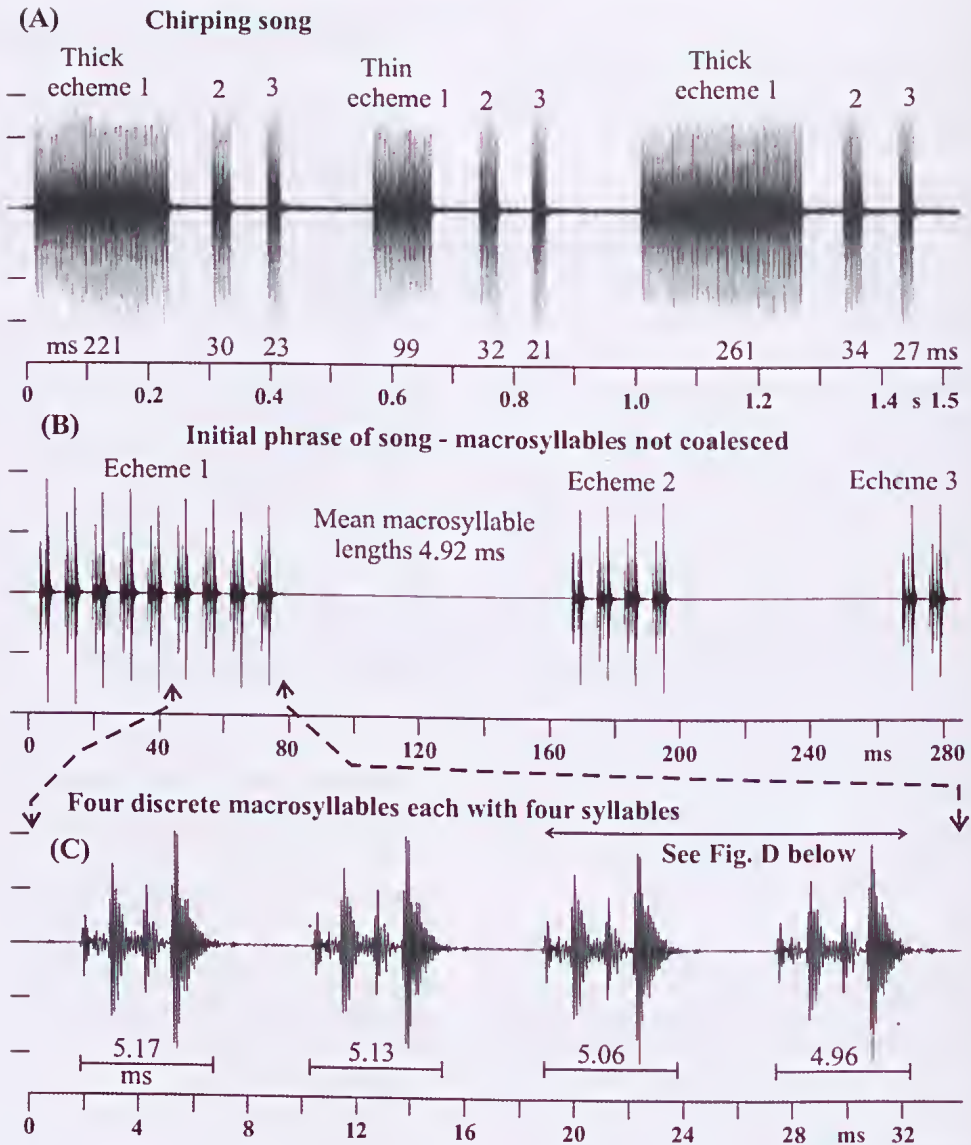
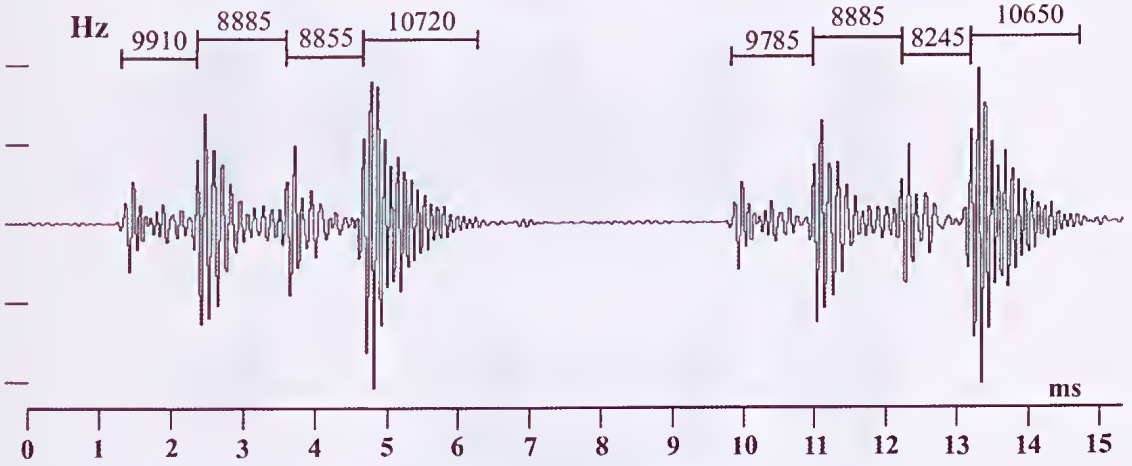
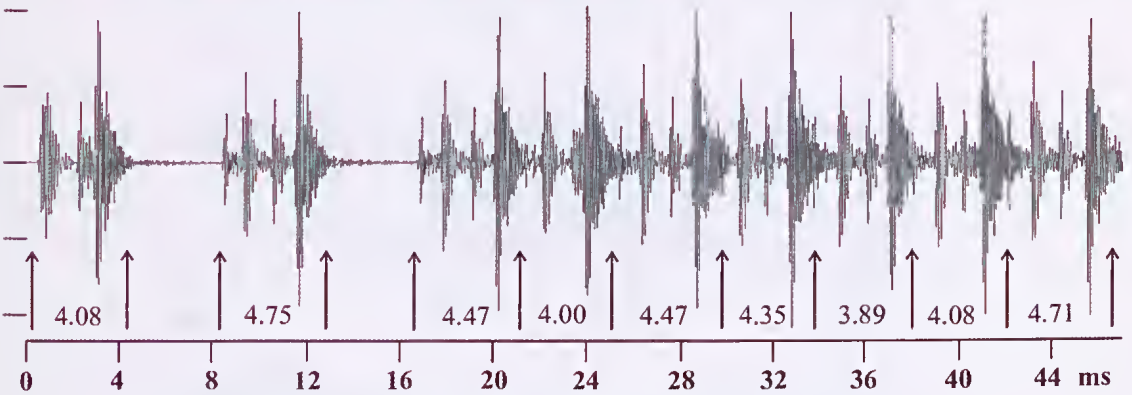


FIG. 14. (Above & opposite) *Gudanga emmotti*. Waveform plots showing, (A) short segment of chirping song illustrating the variable echeme 1 durations. Numbers above echeme are the echeme number, the numbers below the echemes are durations (ms). (B), (C), (D) are time expanded waveform plots of an echeme 1 from the opening phrase segment showing a set of three completely uncoalesced echemes, not commonly seen, illustrating their detailed macro-syllable and syllable structures. (C), (D) show more detailed time expansion revealing the syllable structures and frequencies measured within the pulses of the final two echeme 1 macro-syllables (D). (E), initiation of another echeme 1 from within the same set of recordings showing the progressive process of macro-syllable coalescence, the initial two macro-syllables still separated, the following macro-syllables coalesced into a continuous echeme sequence. (F), final echeme 1 segment, from same song sequence, showing a more advanced stage of macro-syllable coalescence, in which macro-syllables themselves merge into doublets, forming distinctive sets of double macro-syllables. Recordings taken from cicada placed in an open net, in the field, Bald Hills Station, 200 m west of Green Creek, 30.i.2009, south west Queensland. Recording filtered to 2 kHz to improve visualisation.

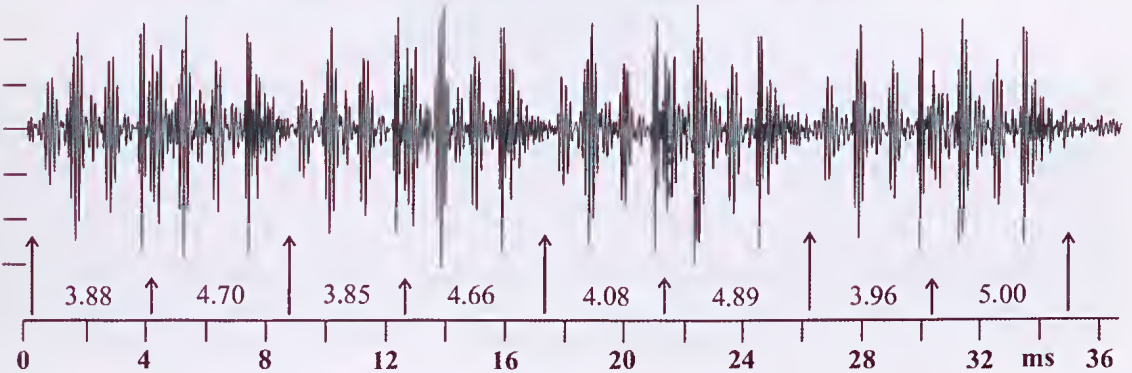
(D) Final two discrete macrosyllables of echeme 1 (see Fig. C).



(E) Start of an echeme 1 showing the initiation of the coalescence of the macrosyllables



(F) End segment of an echeme 1 with partially coalesced macrosyllables, arranged into sets of doublet macrosyllables



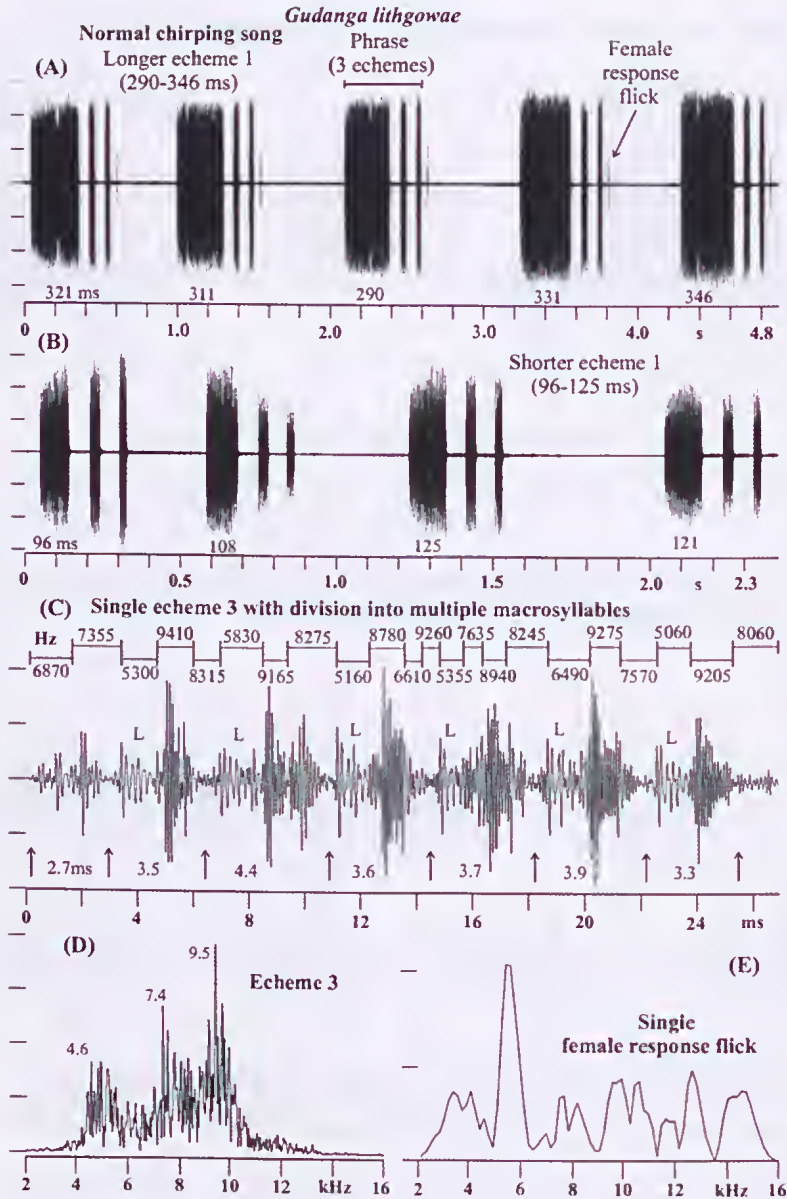


FIG.15. *Gudanga lithgowae*. Waveform plots of (A, B) the gross chirp song structures, each phrase consisting of 3 echemes (1, 2, and 3 in order of emission), with female “wing-flick” responses punctuating the silent intervals following echeme 3 (A only); numbers beneath each echeme 1 are durations in ms. (C) Time expanded detail of a selected complete echeme 3 showing the macro-syllable and syllable structures, and the frequencies measured within the constituent syllables; the upward pointing arrows define the inferred individual macro-syllable limits, with their durations in ms; the symbols ‘L’ indicate segments of lower frequency. Each macro-syllable is interpreted to consist of three syllables, in some macro-syllables exhibiting variable degrees of syllable coalescence. (D) Amplitude spectrum of the echeme 3 shown in (C). (E) Amplitude spectrum of a single female response flick. Field recordings, filtered to 1 kHz, taken (A, B, E) at the ‘Allinga’ Property, Chinchilla, south east Queensland, 9.i.1994; (C, D) taken at Southwood National Park, southern Queensland, by D. Marshall, 31.xii.2008.

New cicada species of the genus *Gudanga* Distant

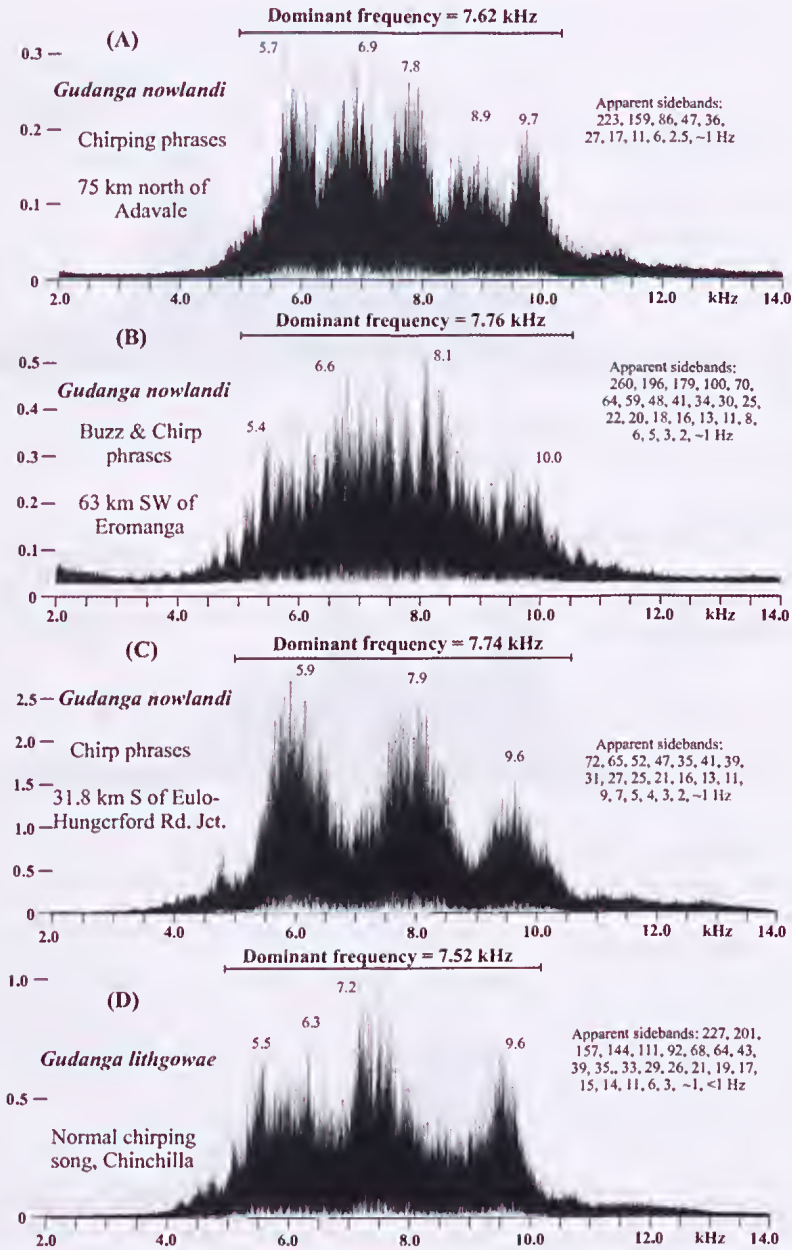


FIG. 16. Amplitude spectra showing, (A) to (C) the frequency distributions within the calling songs of *G. nowlandi* from three widely separated locations within south west Queensland; and (D), *G. lithgowae* from Chinchilla, south east Queensland. The dominant frequency is defined by the mean frequency of the main frequency envelope in each plot, shown by the horizontal lines. The numbers against the various peak concentrations are the maximum frequency (kHz) shown by each main peak. Also listed are the apparent sidebands as measured within each spectrum. Each spectrum is based on field recordings; (A), Boss's Gorge, ~75 km north of Adavale, 1.xii.1998; (B), 63 km south west of Eromanga, 3.ii.2009, D. Marshall; (C), 31.8 km south of Eulo, 18.1.2010; (D), 'Allinga' Property, Chinchilla, 9.1.1994. The vertical scales are linear relative amplitude scales.

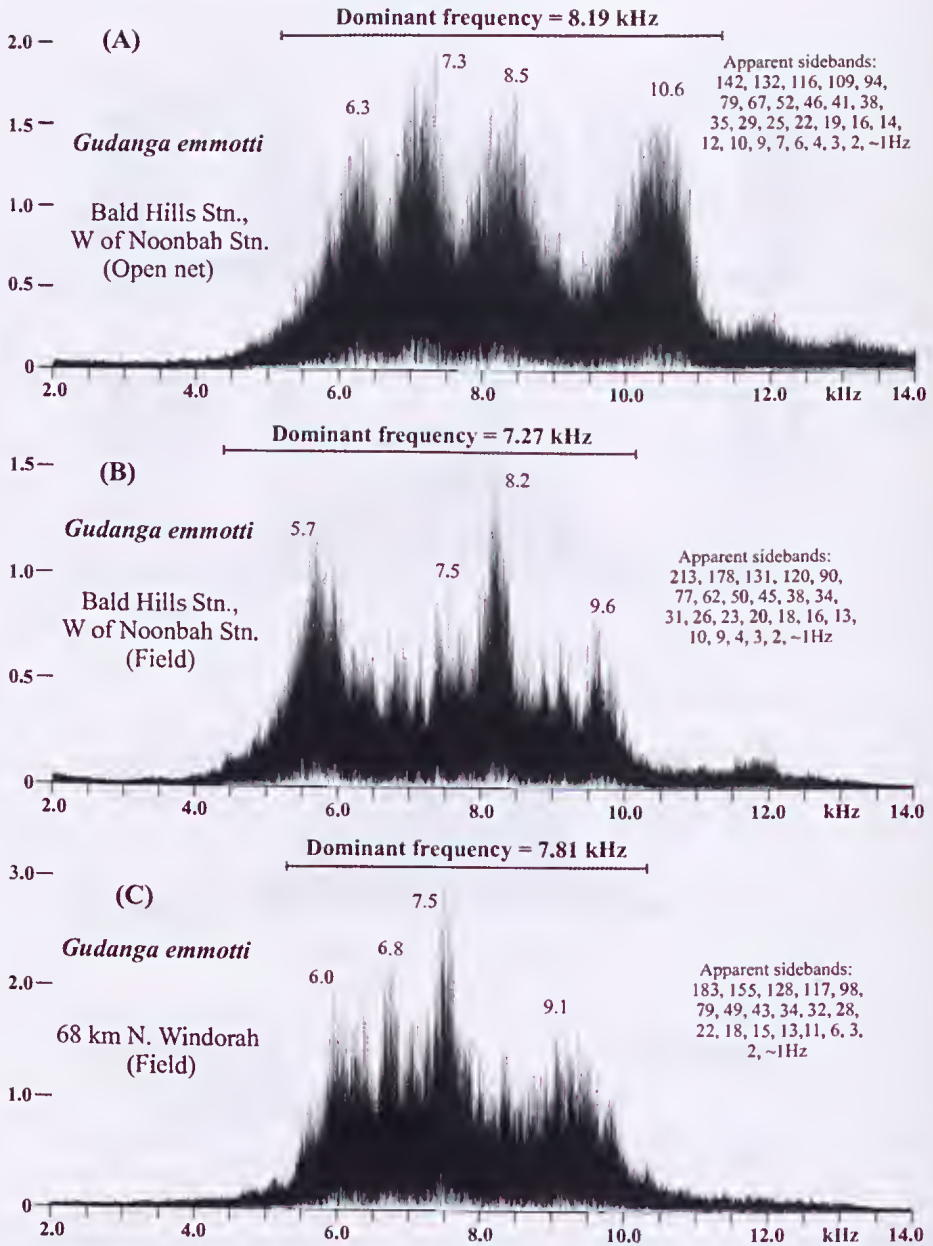


FIG. 17. Amplitude spectra showing, (A) to (C), the frequency distributions within the calling songs of *G. emmotti* from two separate locations within south west Queensland. The dominant frequency is defined by the mean frequency of the main frequency envelope in each plot, shown by the horizontal lines. The numbers against the various peak concentrations are the maximum frequency (kHz) shown by each peak concentration. Also listed are the apparent sidebands as measured within each spectrum. (A), Recording taken from cicada placed in an open net, in the field, from Bald Hills Station, 200 m west of Green Creek, 30.i.2009, south west Queensland. (B), (C), Field recordings, respectively, taken at Bald Hills Station, 200 m west of Green Creek, 30.i.2009, D. Marshall, and 68 km north of Windorah, 1.ii.2009, D. Marshall. Each recording filtered to 2 kHz. The vertical scales are linear relative amplitude scales.

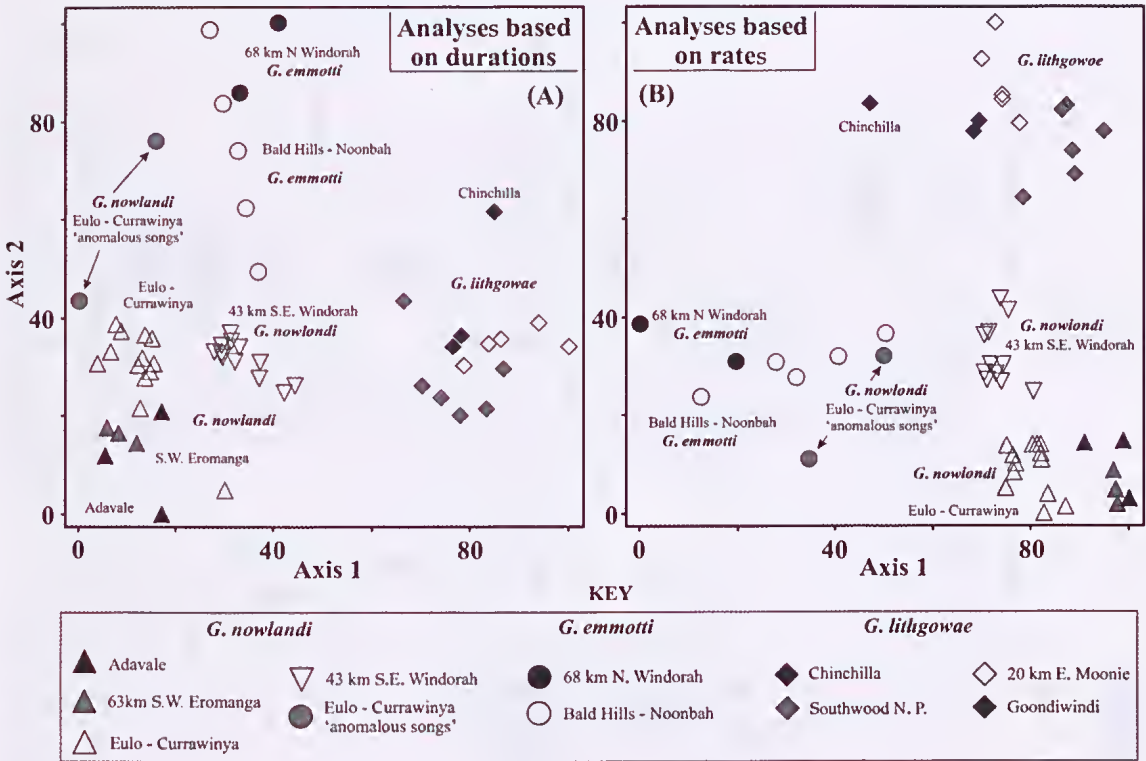


FIG. 18. Results of non-metric multidimensional scaling (NMDS), projected in two dimensions, of the chirping songs of *G. lithgowae*, *G. nowlandi* and *G. emmotti*. (A) Analyses based on durations data; (B) based on repetition rates data (see text for details). The results distinguish the three species, and the main population groupings within each species. The two divergent results identified within *G. nowlandi* songs, both from Eulo-Currawinya area, are discussed in the text.

considered to be robust (Faith et al. 1987). Both clustering and ordination procedures were performed on the distance matrix. Cluster analyses (not shown) employed a flexible beta algorithm ($\beta=0.25$), which is known to exhibit low chaining (Legendre and Legendre 1998). Non-metric multidimensional scaling (NMDS) was conducted on both data subsets. Preliminary runs were performed using four axes, followed thereafter by runs with reduced dimensionality. A scree plot, comparing relative stress vs number of dimensions, and a Shepard plot, showing distance versus dissimilarity, were both used to evaluate the desirable number of dimensions. Stress reduced to acceptable levels (<15%) at two dimensions, so the NMDS ordination procedure was rerun with two dimensions. The ordination of

recording instances was then plotted with the original species assignments and groupings identified overlaid onto the plot. These NMDS plots (Fig. 18) provide clearly visible measures of relative similarity between the sets of data. The cluster plots, which are not illustrated, showed very similar patterns of discrimination as those seen in the NMDS plots. The analyses are specifically applied to the chirping phrases, common to each of the three species, and do not incorporate the extended 'buzz' echemes which are effectively confined to *G. nowlandi*.

Kruskal-Wallis analyses and boxplots were used to evaluate differences in specific song parameters between the three-echeme producing species of *Gudanga*. Both of these approaches were chosen because they accom-

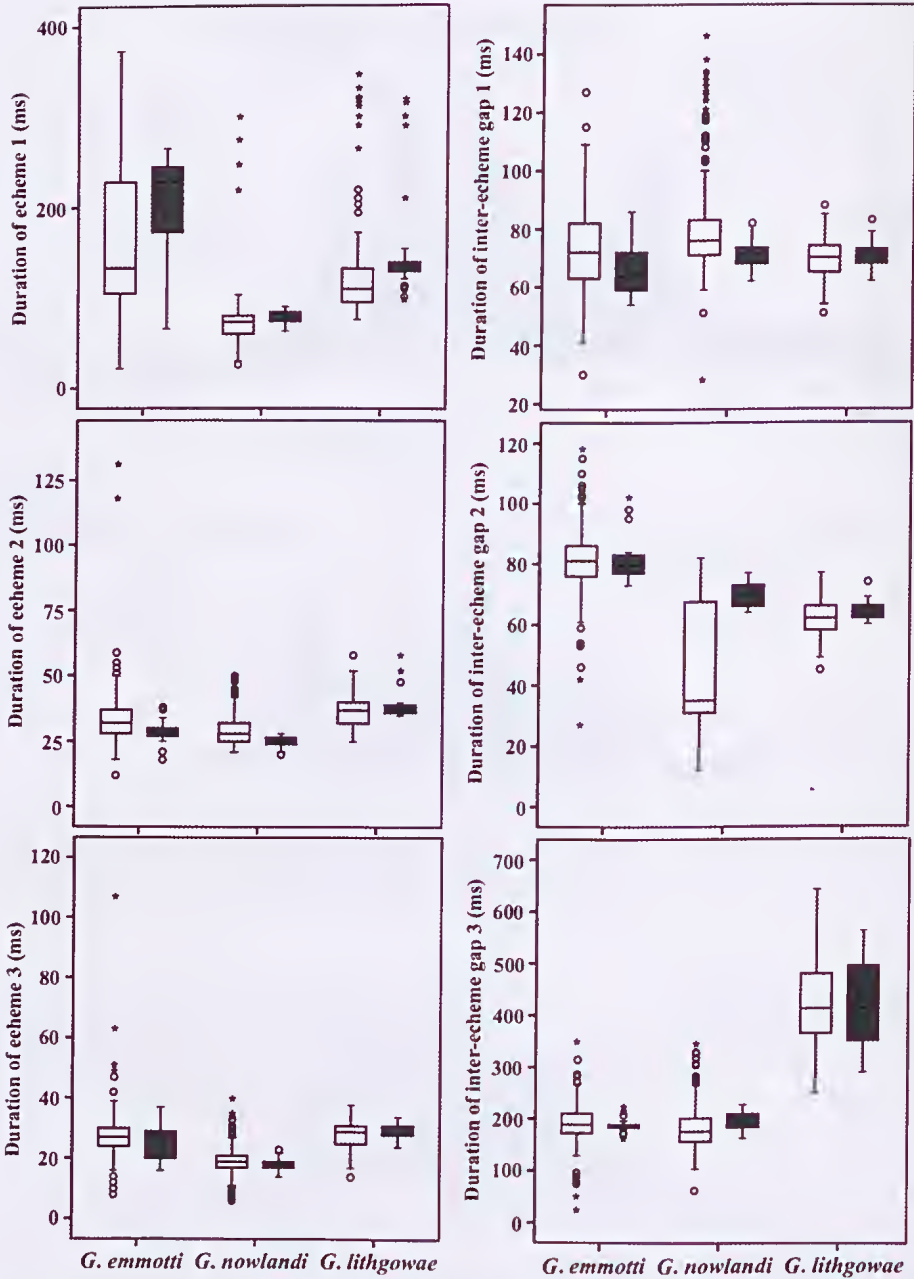


FIG. 19. Boxplots comparing the properties of six song parameters based on durations of the stated parameters for *G. nowlandi*, *G. emmotti*, and *G. lithgowae*. The horizontal bars represent median values and the boxes themselves represent the interquartile range (50% of the distribution of the data). The extended bars cover 75% of the distribution of the data, with the circles being outliers that project between 0.5-3 box lengths from either side of the box. Asterisks represent extreme values (>3 box lengths from either side of the box). The boxes without shading are those representing analyses of the total raw data (as in the NMDS analyses). The shaded boxes represent specifically the data for which the male phrases were followed by female wing-flicks.

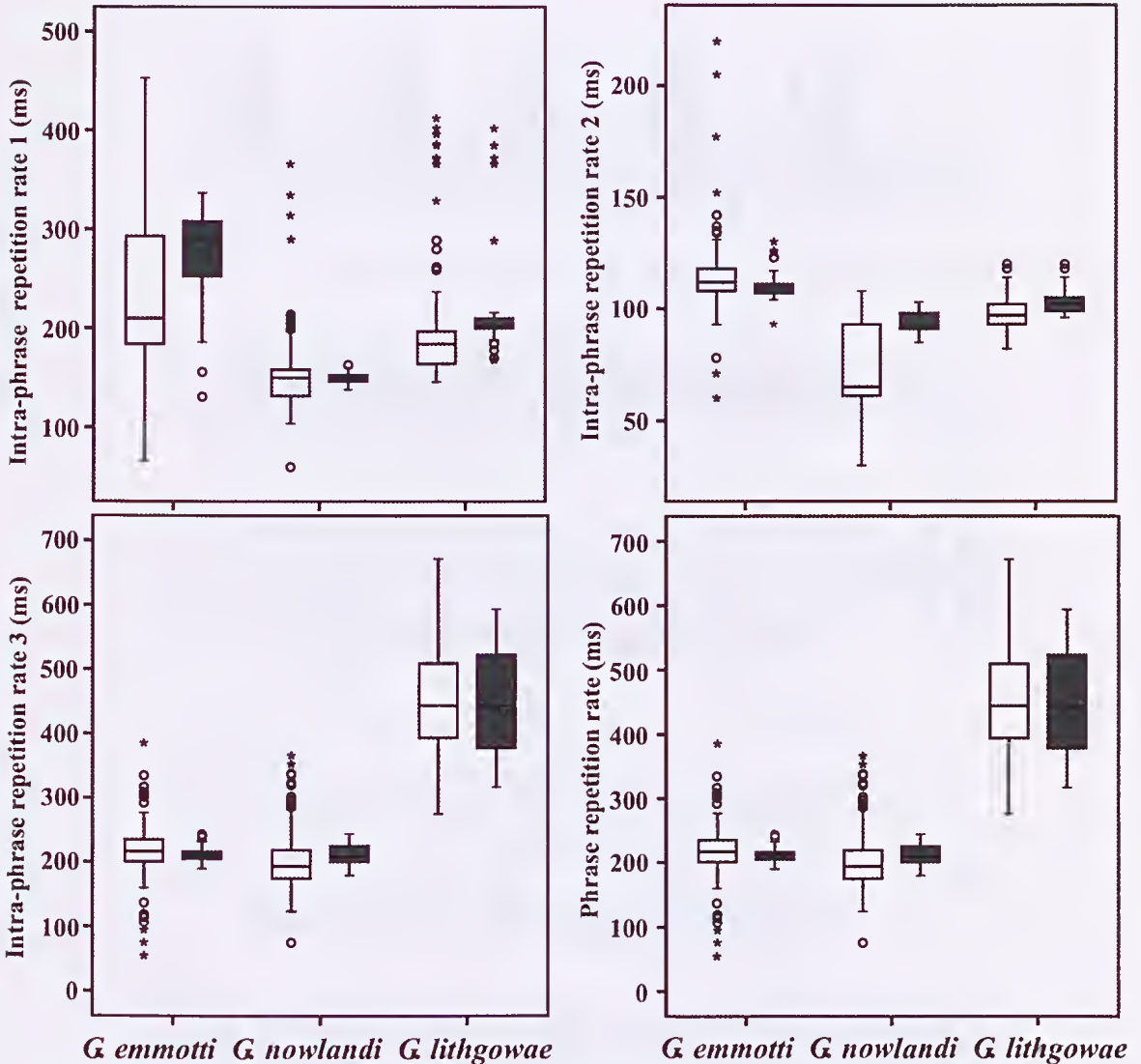


FIG. 20. Boxplots comparing the properties of four song parameters based on repetition rates for *G. nowlandi*, *G. emmotti*, and *G. lithgowae*. Symbols and shading as in Fig. 19 caption.

moderate the non-linear distributions within the song data. Raw song parameter measurements were sourced from all available recordings from each of the three species of *Gudanga* (rather than averages of recording instances, as used in the NMDS analyses; $n=318$ for *G. emmotti*, $n=609$ for *G. nowlandi*, and $n=126$ for *G. lithgowae*). Phrases that elicit female response flicks were analyzed and plotted separately for comparison, based upon the same parameters

described above (Fig. 8) ($n=26$ for *G. emmotti*, $n=31$ for *G. nowlandi*, and $n=34$ for *G. lithgowae*). It is important to note that these represent recordings were made from single localities only (the only such data available).

Results. (Figs 18 to 20, Tables 3, 4). The results show that the songs of the three species are separated on both the NMDS plots, one based on duration data, the other based on rate data.

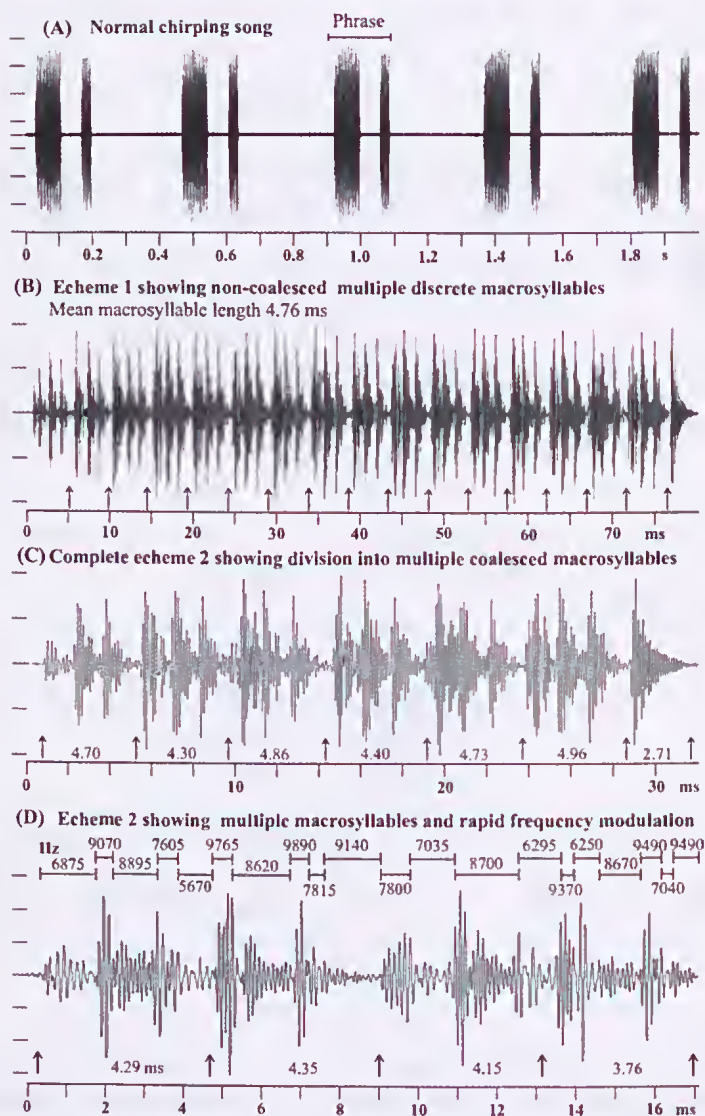


FIG. 21. (Left) *Gudanga adamsi*. Waveform plots showing, (A) gross structure of chirp phrases, each consisting of two echemes with the initial echeme being of longer duration, (B) time expanded detail of a selected complete echeme 1, showing the macro-syllable and syllable structures, the final part of the echeme consists of a single, exponentially decaying syllable of relatively longer duration; (C) a selected single complete echeme 2 showing the individual macro-syllable and syllable structures. Each macro-syllable comprises three syllables, the final segment of the echeme again appears to comprise an exponentially decaying single syllable of greater than normal duration; (D) higher resolution time expansion of segment of an echeme 2 showing greater detail of the syllable structures. The frequencies, measured within the plots from within the different syllable segments, are shown above the waveform. The upward pointing arrows in B to D, show the inferred macro-syllable limits, each of which comprise three (more rarely four) syllables; macro-syllable durations are indicated in ms. (A) to (C), field recordings, filtered to 1 kHz, from the base of the Blackdown Tableland, along Charlevue Creek in eastern-central Queensland, recorded on 17.xii.1985; (D), field recording, filtered (IIR) to 3 kHz, south of Wysby road junction (91.7 km north of Injune), central Queensland, 29.xii.2005, recorded by D. Marshall.

New cicada species of the genus *Gudanga* Distant

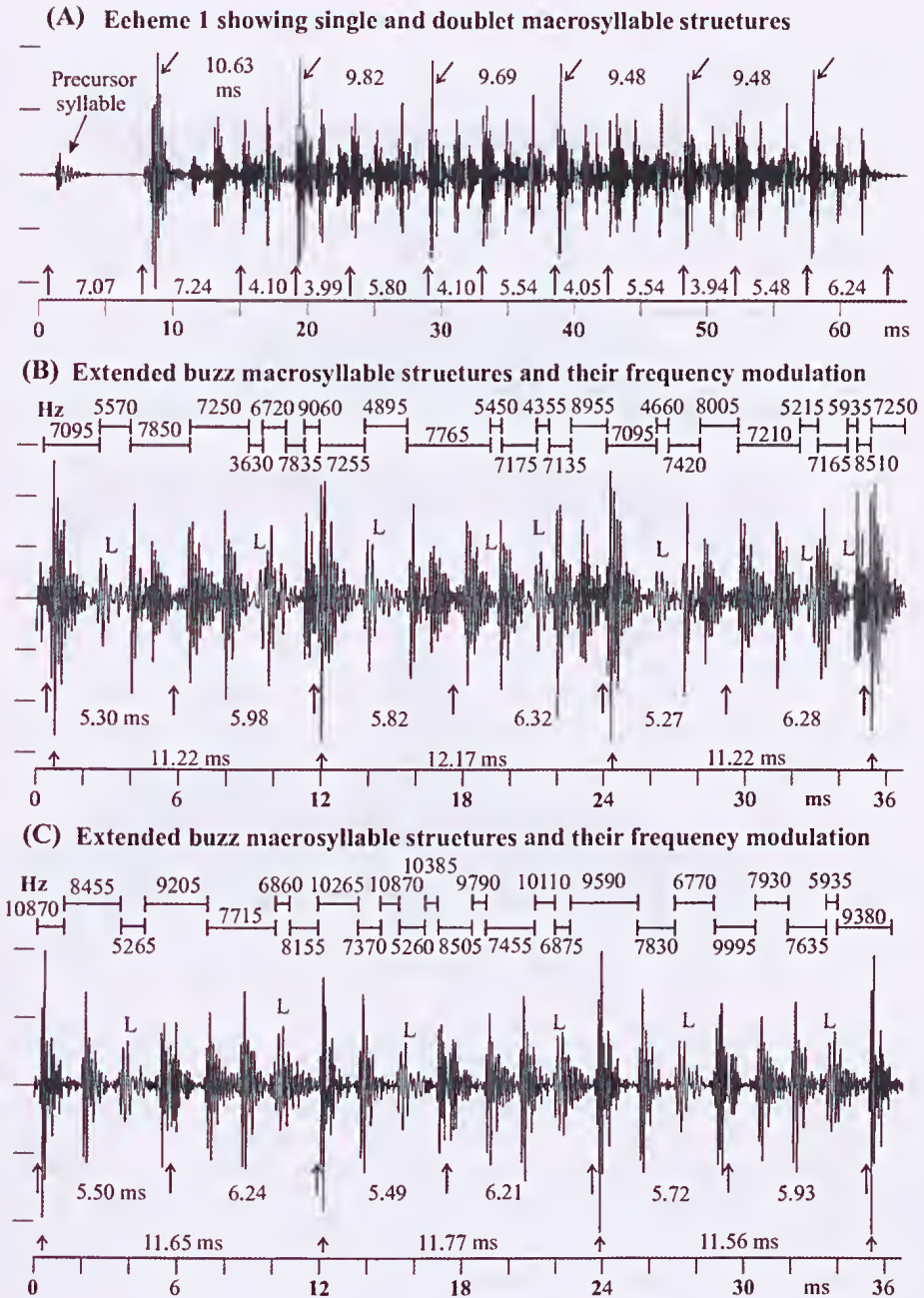


FIG. 22. (Above left) *Gudanga pterolongata*. Waveform plots of (A), (B), the chirping and interspersed extended 'buzz' echeme' phrases. (A) exhibits two extended echemes, (B) a single extended echeme, in both cases followed by short chirp echemes, usually two in number, but varying between one and three; (C) time expanded plot showing more detail of the syllable and inferred macrosyllable structures (macrosyllable limits shown by vertical arrows), including the low amplitude precursor syllable preceding each echeme. Field recordings, filtered to 1 kHz, from 41 km E of Croydon, northern Queensland, taken on 27.i.2005.

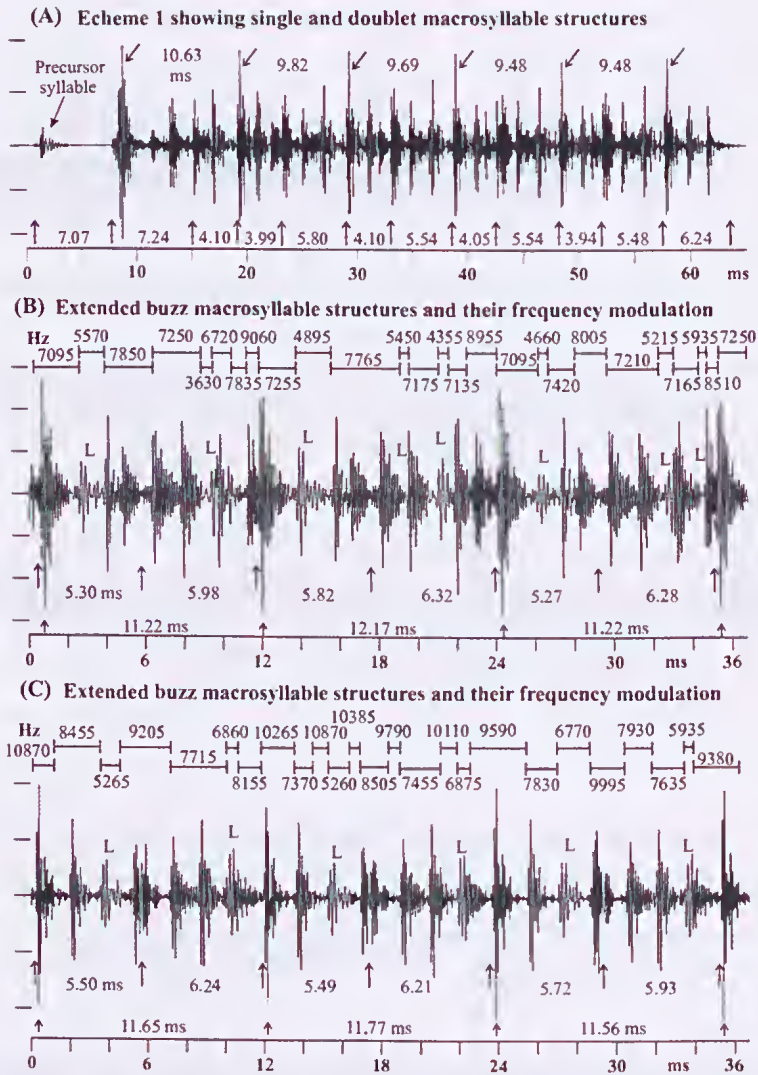


FIG. 23. (Above right) *Gudanga pterolongata*. Waveform plots of; (A), time expansion showing details, from the start of an echeme 1, of syllable and macrosyllable structures, including the precursor syllable and the strongly developed syllable marking the beginning of the echeme. The inclined arrows mark the higher amplitude pulses repeating at 9.5-10.6 ms intervals. These are inferred to define sets of coalesced macrosyllable doublets, the limits of each single macrosyllable indicated by the vertical arrows; number between each vertical arrow are durations in ms. Four syllables occur within each single macrosyllable. (B), (C), further time expanded waveform plots of macrosyllable and syllable structures within extended echemes from separate localities, four (to five) syllables comprising each macrosyllable. The frequencies measured within these plots between and within the syllables are shown above each waveform. The inferred single and doublet macrosyllable limits (and lengths in ms) are indicated by the upper set of vertical arrows. The short segments of lower frequencies are emphasised by the letter 'L', there being one such lower frequency syllable within each macrosyllable, usually the second or third syllable within each. The doublet macrosyllable limits, marked by the higher amplitude pulses, are shown by the lower set of short vertical arrows, noting that these doublet macrosyllable durations are slightly longer than those within the chirp echemes. Field recordings, (A, B), 41 km east of Croydon, northern Queensland, 27.i.2005, unfiltered; (C) 60 km east of Croydon, 30.i.2002, filtered to 2 kHz.

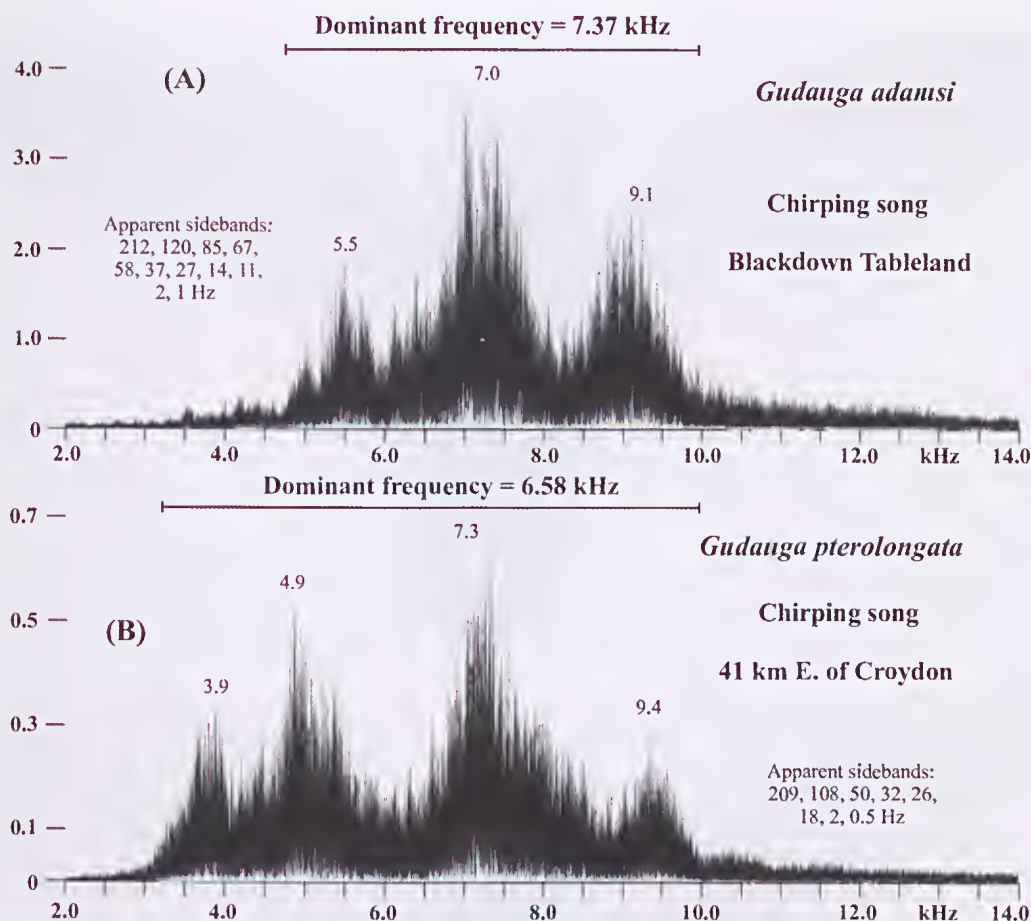


FIG. 24. Amplitude spectra showing the frequency distributions of the calling songs of *G. adamsi* and *G. pterolongata*. The dominant frequency is defined by the mean frequency of the main frequency envelope in each plot, shown by the horizontal lines. The numbers shown against the various peak concentrations within the dominant frequency envelope are the maximum frequency (kHz) shown by each of the peaks. Also listed are the apparent sidebands as measured within each spectrum. Field recordings from, (A), base of Blackdown Tableland, along Charlevue Creek, 27.xii.1985; (B), 41 km east of Croydon, northern Queensland, 27.i.2005. The vertical scales are linear relative amplitude scales.

These plots therefore provide support for the specificity of the calling songs of each of the three species considered, with two cases of partial misclassification within the *G. nowlandi* songs discussed below. Secondly, results point to subtle differences in song properties between regional population groupings, most notable in those of *G. nowlandi*. These populations represent those from ~43 km southeast of Windorah; from the Adavale region; the Eulo-Currawinya region; and ~63 km southwest of Eromanga, this latter data set strongly

separated from the Adavale populations although geographically well separated (Fig. 7).

The case of the *G. nowlandi* population ~43 km southeast of Windorah is significant in at least two ways. First, the distinct separation of its song parameters from the other studied *G. nowlandi* populations, and secondly, the closer proximity of its song vectors in the NMDS plots to those of *G. emmotti* (Fig. 18). This population is, in fact, the closest geographically to the known areas of *G. emmotti* distribution



Plate 1. *Gudanga lithgowae*. A. male, from Warrego-Auburn Road junction, Chinchilla, southeast Queensland, body length 15.6 mm. B. female, from same locality, body length 18.5 mm.

New cicada species of the genus *Gudanga* Distant

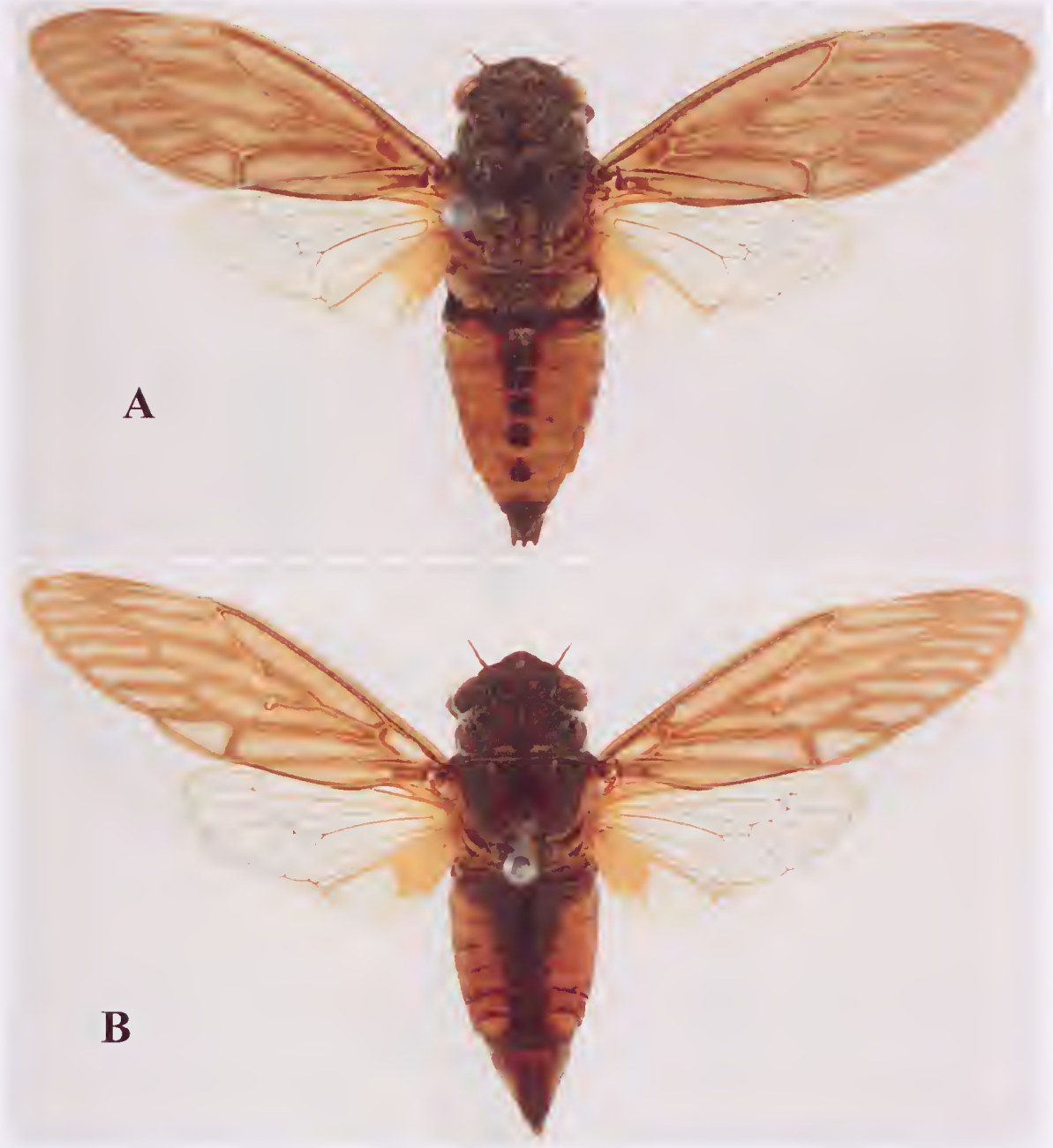


Plate 2. *Gudanga nowlandi*. A. male, 'Bulls Gully H.S.', lagoon, Adavale, southwest Queensland, body length 17.3 mm. B. female, 17 km northeast of 'Milroy H.S.', near Adavale, southwest Queensland, body length 18.5 mm.



A



B

Plate 3. *Gudanga emmotti*. A. male from 200 m west of Green Creek, Bald Hills Station, southwest Queensland, body length 18.1 mm. B. female, from 68 km north of Windorah, southwest Queensland, body length 18.5 mm.

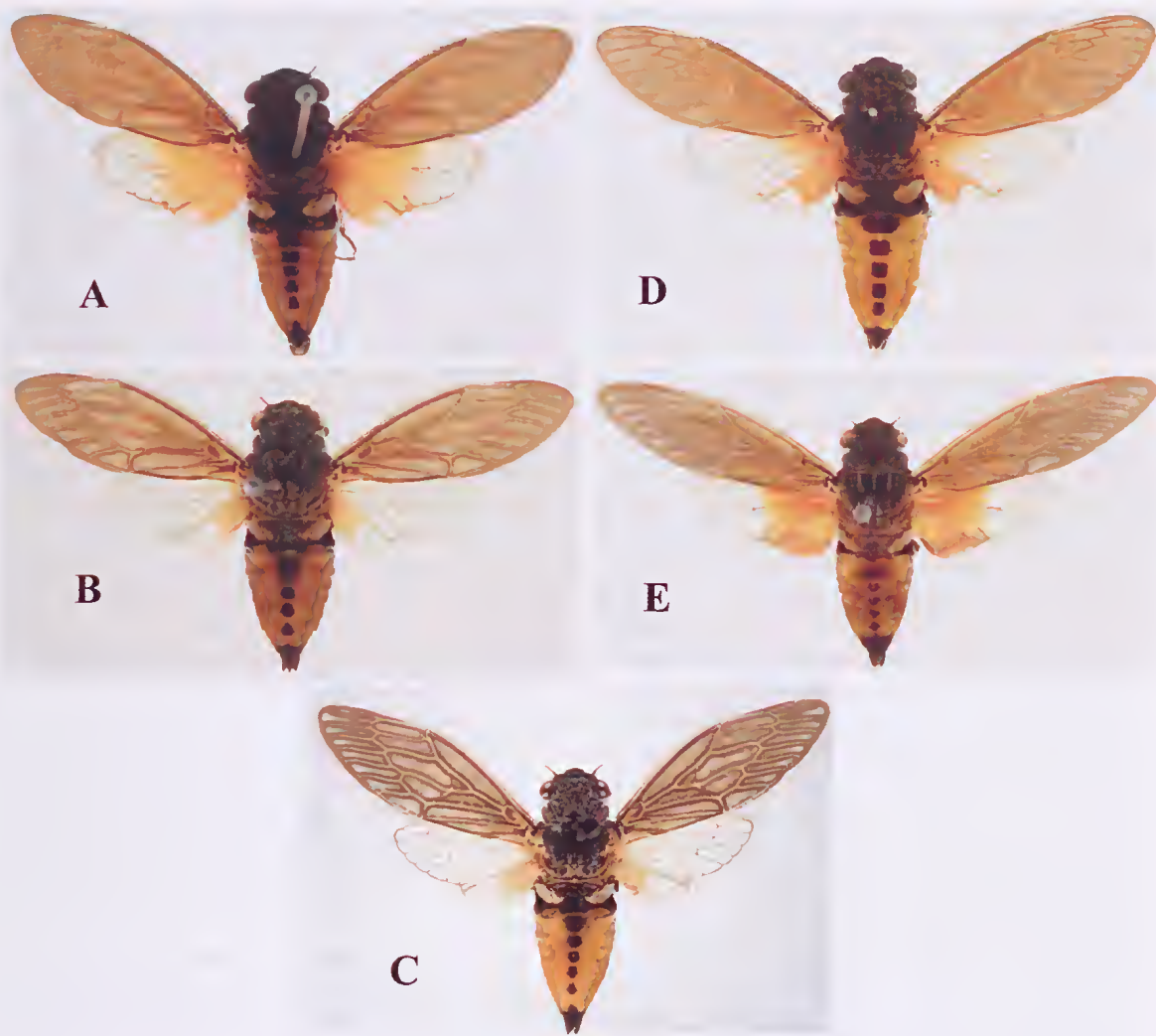


Plate 4. Comparison of males of: A, *Gudanga lithgowae*, details as in Plate 1 caption. B. *Gudanga nowlandi*, details as in Plate 2 caption. C. *Gudanga emmotti*, details as in Plate 3 caption. D. *Gudanga adamsi*, base of Blackdown Tableland, Charlevue Creek, east-central Queensland, body length 16.6 mm. E. *Gudanga pterolongata*, 60 km east of Croydon, Georgetown Road, north Queensland, body length 18.3 mm.

(Fig. 7) and therefore suggestive of possible introgression between the two species within this population. However, morphological characters in this population, including pygofer morphology (single specimen only; see taxonomy above) were found to be consistent with *G. nowlandi*.

The two cases of *G. nowlandi* partial misclassification require explanation, both

examples occurring in cicadas in relatively close geographical proximity within the Eulo-Currawinya region, specifically 29.5 and 31.8 km south of Eulo (fifteen separate insects recorded from the general locality). The data in one case diverge markedly away from typical *G. nowlandi*, and project towards the *G. emmotti* vector fields in both NMDS plots. This case occurs in a single recording in which a number

of atypically long echeme 1's are embedded within otherwise normal sets of phrases and phrase lengths (shown in full in Fig. 13A; see also Fig. 11), though apparently influencing the mean duration of echeme 1. This recording, however, also exhibits multiple instances of extended 'buzz' echemes characteristic of *G. nowlandi*, including one at the commencement of the 'atypical' segment. Overall, apart from the anomalies involving some extended variations of echeme 1, the recorded song matches recordings typical of *G. nowlandi*.

The second anomalous case has resulted in the projected song data diverging from the *G. nowlandi* fields, although not projecting especially close to the *G. emmotti* field, most clearly seen in Fig. 18B. The anomalous characters within this song occur throughout a single recording (38s duration), of a single insect. All other recordings from this same locality show no similar anomaly. The anomaly results from subtle but consistently elevated inter-echeme 1 to 2 repetition rates and inter-echeme 1 to 2 intervals, which further result in similarly elevated phrase repetition rates (documented in Table 3). Within the plot of the echeme 1 durations versus phrase repetition rates (Fig. 11), the 'anomalous' data set represented in this recording clearly plot within the *G. nowlandi* song field. Additional evidence that this recording is that of *G. nowlandi* is provided again by the presence of the characteristic, multiple extended 'buzz' echemes in the recording. Although isolated 'anomalous' song parameters do occur in many recordings of individual cicadas (as shown by the minimum-maximum parameter limits shown in Table 3), the 'atypical' parameters described previously differed in being persistent throughout the recording in question.

The statistical results illustrate several aspects of the song properties of these three very similar species: (i) The chirping songs are, with the two previously noted *G. nowlandi* anomalies from the Eulo-Currawinya region, clearly separated by the statistical methodology used, based on the duration and rate song parameters. The emission of extended 'buzz' echemes in many *G. nowlandi* songs is an additional characteristic parameter that

refines the recognition of the songs of this species, specifically removing the uncertainty of the two 'atypical' cases discussed. The recordings of multiple songs at these localities in particular suggests that as more song data are collected, inevitably more 'atypical' song parameters will be encountered. (ii) Inherent calling song variability between the main *G. nowlandi* populations sampled is shown by the cluster and NMDS plots, by the compiled data for each population (Table 1), and even by simple echeme 1 duration comparisons (Fig. 10B, 11B), all indicating song parameter shifts within the different regional populations. The songs of the populations from Adavale and the Eulo-Currawinya areas are relatively similar in both NMDS plots. The songs of the population from 63 km southwest of Eromanga are very similar to the Adavale songs, notwithstanding the significant geographic separation involved. It is the population from 43 km southeast of Windorah that is the most divergent, as previously noted, perhaps indicative of more persistent isolation. This area lies near the eastern limit of the Simpson sand dune systems and is certainly relatively arid, probably more so than the other areas from which the *G. nowlandi* populations were sampled. (iii) The statistical results also highlight some systematic song variability within and between populations of both *G. emmotti* and *G. lithgowae*. Although not sufficient to break down the specificity of the calling songs, such variability does appear to be characteristic of southern Queensland *Gudanga* songs, presumably a key to their song evolution.

Boxplots (Figs 19, 20), based on statistical comparisons (Table 4) of the total raw song parameter measures reveal a number of differences between the three *Gudanga* species with the three-echeme song type. Differences, at high levels of significance, are seen across most of the parameters (Kruskal-Wallis, $p < 0.01$) between the three species, as also illustrated in the boxplots. Exceptions are noted in the inter-echeme gap 1 data between *G. emmotti* and *G. lithgowae* ($p > 0.05$). The statistically strongest differences that are evident between the three species are the echeme durations, the inter-

echeme gaps 2 and 3, the phrase repetition rates and each of the intra-phrase repetition rates, the distribution of which can be seen in the respective boxplots.

The statistical results again show that the differences between the three species based on song phrases followed by female wing-flicks are similarly highly significant ($p < 0.01$), important as these parameters are specifically recognised by the females. The least significant parameters are the inter-echeme gap 3 and intra-phrase repetition rate 3 ($p > 0.19$) between *G. emmotti* and *G. nowlandi*, and the inter-echeme gap 1 ($p > 0.27$) between *G. nowlandi* and *G. lithgowae*. These statistical analyses again emphasise the importance of song recognition in differentiating these morphologically very similar three species. An additional aspect is the comparison of individual parameters between the total raw data and the data in which song phrases are followed by female wing-flicks. The box plots suggest that for most parameters, there is significant overlap. Differences are more readily apparent when independent song parameters are treated in combination (Fig. 18). A notable exception, seen in the *G. nowlandi* data, are those of inter-echeme gap 2 and the partially interdependent intra-phrase repetition rate 2, which are revealed to be quite distinct in duration (Figs 19, 20).

The Two-Echeme Song Types.

The chirping calling song phrases of *G. adamsi* and *G. pterolongata* consist of two echemes, the initial echeme (echeme 1) longer in duration than the following echeme (echeme 2; Figs 8A, 21 to 24; Table 2). Extended 'buzz' echeme phrases are also commonly emitted by *G. pterolongata*, between 0.65–5.5 seconds in duration, interspersed within the normal chirp phrases (Figs 22A, B; Table 2), similar to those emitted by *G. nowlandi*. These extended 'buzz' echemes are not always emitted, being most commonly emitted when the cicada populations are relatively high. The timing of insertion of these extended echemes into the chirping song occurs in three different ways; (a) between the two echemes within a single chirp phrase, in some cases with coalescence of echeme 1 into

the start of the following extended echeme (the second extended echeme in Fig. 22A). (b), insertion between separate chirp phrases (Fig. 22B), in which case they are followed by sets of two, rarely three short echemes; and (c) emitted at the end of a long series of chirping phrases, thereby terminating a given song sequence. There is no evidence of any systematic changes of echeme durations, inter-echeme intervals or intra-echeme repetition rates immediately preceding or following extended echeme emission. Extended 'buzz' echemes have not been recorded within the *G. adamsi* calling songs.

The chirping songs are described by five temporal parameters (Table 2; Fig. 8). Comparison of these between *G. adamsi* and *G. pterolongata* show extensive overlap, the echeme 2 durations tending to be slightly longer in *G. pterolongata*. The extended echemes and finer scale macrosyllable structures (see below) distinguish the *G. pterolongata* songs.

The chirping songs of *G. adamsi* exhibit similar temporal properties in the various localities for which song recordings have been made, with the exception of the localities 30–35 km south of Blackwater. Here, a subtle but consistent reduction is recognised in the echeme 1 durations compared to all other locations sampled, as documented in Table 2. These are not accompanied by readily discernible morphological or colour differences. Research in progress sequencing mitochondrial DNA within Australian cicadas, including the *Gudanga* species, has identified a distinctive genetic divergence within this particular *G. adamsi* population (K. Hill, pers. comm.).

Fine-scale macrosyllable structures. The chirp and extended 'buzz' echemes comprise multiple discrete macrosyllables which typically vary in their degree of coalescence. Figs 21B–D illustrate examples of discrete macrosyllables within echemes 1 and 2 of *G. adamsi*. Each macrosyllable, the mean lengths of which are 4.5 ms (Table 2), comprises three syllables. The terminating syllable within the echemes is characterised as a single exponentially decaying syllable, longer than the remaining syllable durations within the echemes, although shorter than the macrosyllable

lengths (Fig. 21C). A comparable feature is seen within the terminations of echemes within the *G. lithgowae* songs. When viewed in more detail in time expanded waveform plots (Figs 21D), measured frequencies of the syllables and pulses within the macrosyllables of the *G. adamsi* song show very rapid and sharply defined modulations, both between and within syllables. The highest amplitude groups of pulses typically mark the initiation of most syllables, and are characterised by relatively elevated frequencies, usually >9 kHz. The wide range of measured frequencies measured in these detailed waveform plots is consistent with the broad frequency range limits shown by the amplitude spectrum (Fig. 24A).

The detailed structures of the chirp and extended echemes within the *G. pterolongata* songs differ from those of *G. adamsi*. One clearly defined feature is the presence of an exponentially decaying precursor syllable, followed after an interval of some 7-7.5 ms, by the initial syllable of the echeme itself (Figs 22C, 23A). This initial echeme syllable is itself distinctive, being sharply defined, with higher amplitude and slightly longer duration than the following syllables comprising the macrosyllable sequences (Fig. 23A). A conspicuous character of the macrosyllable structures within this species is their regular repetition, marked by single high amplitude pulses, with repeat intervals of near 10 ms (9.1-12.2 ms), i.e. ~ 100 Hz (Figs. 23A-C; Table 2). Each of these 10 ms segments, on detailed examination, is seen to represent coalesced double macrosyllables, each macrosyllable comprising four to five syllables. These exhibit rapid and marked frequency modulations in which the second or third syllable are of lower frequency. The final syllable of each macrosyllable is typically of relatively higher frequency (≥ 9 kHz), as illustrated in Figs 23B, C. The range of frequencies measured in the waveform plots are consistent with the amplitude spectrum determined from a larger sampling of the song (Fig. 24B).

Amplitude spectra. (Figs 24A, B) The spectra of the calling songs of *G. adamsi* and *G. pterolongata* are comparable to those previously described for the three-echeme song types. They again

exhibit very broad band frequencies, also evident in the above described time expanded waveform plots. The dominant frequencies exhibit similar ranges and magnitudes as observed for the songs of *G. lithgowae*, *G. emmotti* and *G. nowlandi*. A crude periodicity is present within the *G. adamsi* and *G. pterolongata* spectra of the individual peaks within the dominant frequency envelopes, on scales of ~ 1.5 -2 kHz, possibly reflecting very fine scale syllable structures. The complex sideband ranges must reflect the complexities inherent in the syllable, macrosyllable, echeme and phrase structures of the calling songs, those in the ~ 100 Hz range in the *G. pterolongata* songs probably correlating with the doublet, repetitive macrosyllables.

Distribution (Fig. 7). *Gudanga adamsi*. (Figs 1D-6D; Pl. 4D). Additional localities to those listed in Moulds (1996) include brigalow woodland in the north eastern corner of the Isla Gorge National Park ($25^{\circ} 10.02'S$ $150^{\circ} 00.73'E$), AE; the Brigalow Research Station, approximately 30 km northwest of Theodore ($24^{\circ} 48.85'S$ $149^{\circ} 47.48'E$), AE, LWP; the boggomoss site near Glebe Weir, Dawson River, north east of Taroom, $\sim 25^{\circ} 28'S$ $150^{\circ} 02'E$, QM; 31 km south of Blackwater ($23^{\circ} 52.14'S$ $148^{\circ} 53.65'E$), MSM; 44.4 km south of Rolleston ($24^{\circ} 50.28'S$ $148^{\circ} 31.81'E$); 91.7 km north of Injune ($25^{\circ} 08.14'S$ $148^{\circ} 34.95'E$), MSM; Little Windeyer Creek crossing, 28 km north of Tambo ($24^{\circ} 40.19'S$ $146^{\circ} 22.19'E$), MSM; Lonesome National Park, 47 km northeast of Injune, $25^{\circ} 29.40'S$ $148^{\circ} 49.92'E$, QM reference numbers T189497, 8, 9, QM. These localities are all in central and eastern central Queensland.

G. pterolongata (Figs 1E-6E, Pl. 4E). This species has been observed in extensive lancewood (*Acacia shirleyi*) forest areas, extending from 23 km E of Croydon, eastwards to near, and probably just east of the Gilbert River crossing, approximately 70 east of Croydon, adjacent to the Croydon-Georgetown road, north Queensland. It occurs in both disturbed and undisturbed lancewood forest, which occur along the top of laterite plateau (the western margin of which is 23 km E. Croydon), but is apparently absent from mixed woodland with only minor lancewood presence. Distri-

butional data presented by Beadle (1981, p. 461) for lancewood woodlands in this region indicate that they extend in a broad band for approximately 200 km northwest of the Croydon-Gilbert River localities, and in a narrow belt south-eastwards for a comparable distance. It is therefore anticipated that the distribution of *G. pterolongata* will at least partially follow these broader regional lancewood occurrences, depending on appropriate soil and climatic conditions.

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LITERATURE CITED

Beadle, C.W. 1981. The vegetation of Australia. Cambridge University Press, Cambridge, New York, Melbourne: Gustav Fischer Verlag, Stuttgart, 690pp.

- Bennet-Clark, H.C. 1997. Timbal mechanics and the control of song frequency in the cicada *Cycloclitula australasiae*. *The Journal of Experimental Biology* 200: 1681-1694.
- Bradbury, J.W. & Vehrencamp, S.L., 1998. Principles of animal communication Sunderland Mass.: Sinauer Associates, 882pp, plus bibliographical references and index.
- Cooley, J.R. & Marshall, D.C. 2001. Sexual signalling in periodical cicadas, *Magicalcicada* spp. (Hemiptera: Cicadidae). *Behaviour* 138: 827-855.
- de Boer, A.J. 1999. Taxonomy and biogeography of the New Guinean Cicadettini (Hemiptera, Tibicinidae). *Mitteilungen Museum Naturkunde Berlin: Deutsche entomologische Zeitschrift* 46(2): 115-147.
- Dugdale, J.S. 1972. Genera of New Zealand Cicadidae (Homoptera). *New Zealand Journal of Science* 14(4): 856-882.
- Ewart, A. 1998. Cicadas, and their songs of the Miles-Chinchilla region. *The Queensland Naturalist* 36(4-6): 54-72.
2005. New genera and species of small ticking and 'chirping' cicadas (Hemiptera: Cicadidae) from Queensland, with descriptions of their songs. *Memoirs of the Queensland Museum* 51(2): 439-500.
- Ewart, A. & Marques, D. 2008. A new genus of grass cicadas (Hemiptera: Cicadoidea: Cicadidae) from Queensland, with descriptions of their songs. *Memoirs of the Queensland Museum* 52(2): 149-202.
- Ewart, A. & Popple, L.W. 2001. Cicadas, and their songs, from south-western Queensland. *The Queensland Naturalist* 39(4-6): 52-71.
- Faith, D.P., Minchin, P.R. & Belbin, L. 1987. Composition dissimilarity as a robust measure of ecological distance. *Vegetatio* 69: 57-68.
- Legendre, P. & Legendre, L. 1998. *Numerical ecology*. (Elsevier Scientific Publishing Company: Amsterdam) 853pp.
- Marshall, D. C., Hill, K.B.R., Cooley, J.R. & Simon, C. 2011. Hybridization, mitochondrial DNA phylogeography, and prediction of the early stages of reproductive isolation: Lessons from New Zealand cicadas (genus *Kikihia*). *Systematic Biology* 60: 482-502.
- Mccune, B. & Mefford, M.J. 2006. PC-ORD. Multivariate analysis of ecological data, version 5.05. MjM Software Design, Gleneden Beach, Oregon.
- Moulds, M.S. 1996. Review of the Australian genus *Gudanga* Distant (Hemiptera: Cicadidae) including new species from Western Australia and Queensland. *Australian Journal of Entomology* 35: 19-31.
- Moulds, M.S. 2005. An appraisal of the higher classification of cicadas (Hemiptera: Cicadoidea) with special reference to the Australian fauna. *Records of the Australian Museum* 57: 375-446.
- Moulds, M.S. 2012. A review of the genera of Australian cicadas (Hemiptera: Cicadoidea). *Zootaxa* 3287, Monograph, 1-262.

- Olive, J.C. 2007. A new species of *Gudauga* Distant (Hemiptera: Cicadidae) from Northern Queensland. *Australian Entomologist* **34**: 1-6.
- Popple, L.W. & Strange, A.D. 2002. Cicadas, and their songs, from the Tara and Waroo Shires, southern central Queensland. *The Queensland Naturalist* **40**(1-3): 15-30.
- Popple, L.W., Walter, G.H. & Raghu, S. 2008. The structure of calling songs in the cicada *Pauropsalta annulata* Goding and Froggatt (Hemiptera: Cicadidae): evidence of diverging populations? *Evolutionary Ecology* **22**: 203-215.
- Ragge, D.R. & Reynolds, W.J., 1998. *The songs of the grasshoppers and crickets of Western Europe*. Harley Books, Colchester, in association with The Natural History Museum, London, 591pp.
- Seabra, S.G., Pinto-Juma, G. & Quartau, J.A. 2006. Calling songs of sympatric and allopatric populations of *Cicada barbara* and *C. orni* (Hemiptera: Cicadidae) on the Iberian Peninsula. *European Journal of Entomology* **103**: 843-852.
- Simmons, P. & Young, D. 1978. The tymbal mechanism and song patterns of the Bladder Cicada *Cystosoma saundersii*. *The Journal of Experimental Biology* **76**: 27-45.
- Simões, P.C., Boulard, M., Rebelo, M.T., Drosopoulos, S., Claridge, M.F., Morgan, J.C. & Quartau, J.A. 2000. Differences in the male calling songs of two sibling species of *Cicada* (Hemiptera: Cicadoidea) in Greece. *European Journal of Entomology* **97**: 437-440.
- Sueur, J. 2002. Cicada acoustic communication: potential sound partitioning in a multispecies community from Mexico (Hemiptera: Cicadomorpha: Cicadidae). *Biological Journal of the Linnean Society* **75**: 379-394.
- Sueur, J. & Aubin, T. 2004. Acoustic signals in cicada courtship behaviour (order Hemiptera, genus *Tibicina*). *Journal of Zoology* **262**: 217-224.

A revision of *Hypselosoma* Reuter (Insecta: Heteroptera: Schizopteridae) from New Caledonia

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ABSTRACT

The identity of *Hypselosoma oculatum* Reuter is clarified and 19 new species are described from New Caledonia. The new species are *H. hypselosomatum*, *H. amieuensis*, *H. bleuensis*, *H. koghiensis*, *H. mandjeliensis*, *H. mouensis*, *H. rhinatum*, *H. elytratum* (the preceding eight forming *H. hypselosomatum* group), *H. chorizobregmatum*, *H. dicroum*, *H. gephyrobregmatum*, *H. haplacanthatum*, *H. ndouaensis*, *H. nordiensis*, *H. onceronotatum*, *H. rembaiensis*, *H. touhoensis*, *H. trachyacanthatum* and *H. triacanthatum*. Lack of sympatry in relation to tentative clades is suggested. Related fossil genera are mentioned and dispersal via oceanic drift briefly discussed. Aspects of subfamily morphology are reviewed and compared with *Cryptostemma* Herrich-Schaeffer (Dipsocoridae). Sympatry of *Hypselosoma* Reuter and *Pateena* Hill in Tasmania is reported. □ *Schizopteridae*, *Hypselosoma*, *Hypselosoma oculatum*, *New Caledonia*, *Pateena*.

The family Schizopteridae has a tropical distribution with distinct genera in the eastern and western hemispheres and few genera in temperate zones (Štys, 1970). *Hypselosoma* Reuter is distributed around the western Pacific rim and Madagascar with many species described by Wygodzinsky (1959). It contains 18 described species from mainland China (2), Honshu, Shikoku, Kyushu and Amami-Oshima Islands in Japan (2), Marinduque Island in Philippines (1), the northern coast of mainland New Guinea (4), Garove Island near New Britain (1), Guadalcanal in the Solomons (1), Grande Terre in New Caledonia (1), Queensland and New South Wales in Australia (4), Tasmania in Australia (1), south island of New Zealand (1) and Madagascar (1) (Fig. 24). Several undescribed species from the Oriental region and Australia await description. *Hypselosoma* has not been found in Fiji or on Norfolk and Lord Howe Islands despite considerable collecting there by the Queensland Museum or Australian Museum. None have been recorded from Vanuatu. Most recently, Ren and Zheng (1992) recorded *H.*

matsumurae Horvath 1905, originally described from Japan, in China.

Recent collecting by Queensland Museum revealed 19 new species from New Caledonia and specimens of the type species, *H. oculatum* Reuter, 1891. *Hypselosoma* was erected by Reuter (1891) for *H. oculata* (sic) in a brief Latin description based on a single elytrous female from 'monte Kogui, m. Maji', New Caledonia. Poppius (1909) briefly described a macropterous male from Mt Koghis, New Caledonia as *H. oculata* including a figure of its forewing and said the locality was the same as the type locality of Reuter. Wygodzinsky (1959) described in detail a male from 7 miles southeast of La Foa, New Caledonia (80 km NW from Mt Koghis) as *H. oculatum* and emended the gender of Reuter's specific epithet to be neuter. The 19 new species include eight that can be distinguished only by male genitalia and one of these is from the generic type locality. However, another species best fits the description by Reuter and also matches the description by Wygodzinsky as discussed below.

The genus belongs to the Hypselosomatinae (Esaki and Miyamoto, 1959; Emsley, 1969) whose other extant members are *Glyptocombus saltator* Heidemann, 1905 from the USA including Michigan, Georgia and Arkansas (Heidemann, 1905; Allen & Carlton, 1989), the poorly known *Onmatides insignis* Uhler, 1894 from the Lesser Antilles, the Australian genera *Pateena* Hill, 1980, *Ordirete* Hill, 1984, *Macromannus* Hill, 1984, *Cryptomannus* Hill, 1984, *Lativena* Hill, 1984, *Duonota* Hill, 1984 and *Rectilamina* Hill, 1984, (Hill, 1980, 1984, 1985a, 1985b) and *Williamsocoris ornatus* Carpintero and Dellapé, 2006 from Argentina. Perrichot *et al.* (2007) described two new fossil Hypselosomatinae, *Buzinia* and *Tanaia* from mid-Cretaceous amber (100 Ma) from France and Burma. Azar and Nel (2010) described *Libanohypselosoma* from Lower Cretaceous amber of Lebanon. Some comments on the fossil genera are made in the discussion.

METHODS

Specimens were obtained in 75% ethanol or glued to cards. Some specimens were cleared in cold sodium hydroxide and divided into several mounts such as a vial of 75% ethanol and several Euparal® slides. Drawings of small slide-mounted structures such as genitalia were done by freehand under a compound microscope while larger structures were drawn using a gradicule eyepiece and squared paper under a stereomicroscope. Montaged photographs of forewings on microscope slides were taken with a stereomicroscope while other photographs are montaged images from a compound microscope.

Terminology. The postnotal flange is a lamina projecting posteriorly from the metanotum. It has a continuously curved margin in all pteromorphs of all species described here and is termed arcuate (Fig. 6E) rather than segmental as in Hill (1984, 1987a, 1991). Hill (1987a) used the terms truncate and trapezoidal for some Queensland species in which the margin is briefly straight and (Hill, 1984) used the term rectangular for species of *Rectilamina* Hill in which most of the margin is straight.

Descriptions of the tumidity of the base of the labrum in profile are tentative but may reward further study by scanning electron microscopy. The diagnostic value of male T8 was not investigated but setation of its posterolateral projections may prove useful.

In light of comments by Rédei (2007) the terminology for wing venation is changed from Emsley's system (Emsley, 1969; Hill, 1987a) to that in Figure 6I. The anterior marginal vein is regarded as C, the deflexed margin anterior to C as the hypocostal lamina, the thick submarginal basal vein as Sc+R+M, the posterior membranous vein as 1AN so that Cu runs a direct path and joins M only apically. The identities of the intervening distal veins remain uncertain. The cell on the clavus is termed the anal cell.

Abbreviations. In the text a.s.l. is above sea level, S is sternum, T is tergum and LT is laterotergite (appendage articulating with T9). In lists of material female is f, male is m, collectors are C. Burwell, CB; D. Cook, DC; P. Grimbacher, PG; G. B. Monteith, GBM; R. Raven, RR; S. Wright, SW and habitat and methods of collecting are rainforest, R; berlesate, B; pyrethrum knockdown, P and flight intercept trap, FIT. Lists include Queensland Museum sample numbers (QM prefix) for precision given the large number of sympatric species and papers by other authors treating material collected in the numerous samples collected by Queensland Museum.

Depositories. All specimens except one of *H. oculatum* were collected by and deposited in the Queensland Museum, Brisbane (QM) other than the holotypes which were deposited in the Muséum national d'Histoire naturelle, Paris (MNHN(EH)). QM registration numbers have a T prefix. One specimen of *H. oculatum* was borrowed from the American Museum of Natural History (AMNH).

SYSTEMATICS

Order HETEROPTERA

Family SCHIZOPTERIDAE Reuter, 1891

Subfamily HYPSELOSOMATINAE Esaki and Miyamoto, 1959

Hypselosoma Reuter, 1891

Type Species. *H. oculata* Reuter, 1891 [emended *oculatum* Wygodzinsky, 1959.]

HOLOTYPE not seen ('D. A. Montadon (Coll. auctoris)' in Reuter, 1891).

Hill (1987) enlarged and qualified the definition of *Hypselosoma* in Wygodzinsky (1959). In brief, *Hypselosoma* has the very large eyes, four-segmented labium and well developed gonapophyses typical of Hypselosomatinae. It is differentiated most notably on the structure of the male genitalia and preceding segments from all other hypselosomatine genera which, as far as documented, share a different and more asymmetric plan. In *Hypselosoma*, T8 has no non articulated laterotergal processes, T9 bears two articulated laterotergites, T10 (anophore) is a simple complete or incomplete ring without processes; the male conjunctival complex is linked to the basal plate by a Y-shaped sclerite; the membranous wall of the conjunctiva bears discrete anterior, right and left sclerites; the last two sclerites often bear prominent processes (see discussion). In the female the anterior gonapophyses bear 5-7 teeth rather than 2-4. In addition, in *Hypselosoma* the labrum bears 1+4 macrosetae but only 4 in males when a male labral organ is present; the male clypeus (or rarely labrum) bears a special organ (rather than pronotal collar or clavus); the labial segments never bear pairs of long, ventrolateral macroseta (equal to or greater than labial diameter); the bucculae do not bear a prominent pair of ventrolateral macrosetae although 0-4 short, procurved macrosetae occur on each side; spiracles are present only on segments 6-8 and a sclerotized spermatheca is absent.

SHARED CHARACTERS OF NEW CALEDONIAN HYPSELOSOMA

All the species described below have: five labral macrosetae (Fig. 6B); an unmodified labrum (unlike *H. oncerochilotum* Hill of Queensland, Australia); mesosternum with simple anteroventral face and domed process on posteroventral face (Fig. 6C); metasternum with only a curved, fin-like process; scutellum impunctate; metanotum bearing a large, arcuate postnotal flange (Fig. 6E) (arc not truncated); full hind wings in macropterous males; no medial concavity on posterior margin of T9 for reception of a digit that arises ventrally and at midlength on right LT9 (unlike Queensland species) except *H. touhoensis* in which a medial concavity receives the apex of left LT9.

KEY TO MALES OF NEW CALEDONIAN HYPSELOSOMA

(Male of *H. onceronotatum* is unknown)

1. Elytrous 2
 - Macropterous or submacropterous 5
2. Clypeal organ absent *H. elytratum* sp. nov.
 - Clypeal organ present 3
3. Clypeal organ recessed between clypeal fused lobes which form a bridge between organ and labrum, without erect setae reaching anterior margin of clypeus *H. geophyrobregmatum* sp. nov.
 - Clypeal organ marginal, erect setae reaching margin (Fig. 4F) 4
4. Elytral apices lobate, highly convex profile *touhoensis* sp. nov.
 - Elytral apices simple, moderately convex profile *rembaiensis* sp. nov.
5. Clavus mostly punctate, anal cell obliterated 6
 - Clavus not or weakly punctate, small anal cell 9
6. Three anterior corial cells between Sc and M mostly punctate 7
 - Three anterior corial cells impunctate

- except vein margins 8
7. Left process T9 has non serrate apex (Fig. 18A) *H. haplacanthatum* sp. nov.
 – Left process T9 has serrate apex (Fig. 21A) *H. trachyacanthatum* sp. nov.
8. Clypeal organ bilobate (Figs 4B, C), disc impunctate, 1.4 mm labrum to wing apex
H. chorizobregmatum sp. nov.
 – Clypeal organ weakly elevated hole (Fig. 4E), disc punctate, 1.8 mm labrum to wing apices *H. nordiensis* sp. nov.
9. Habitus highly convex (Figs 1A, 1G), medium-large (1.7-2.4 mm), clypeal organ absent or strongly salient cone, costal cell not concave, margin not explanate, lateral margins of disc smoothly rounded in dorsal view (Figs 1A, 1E) 10
 – Habitus less convex (Figs 1C, 1E, 1K), small-medium (1.2-1.6 mm), clypeal organ present (flat with erect setae or pit with adpressed setae and pale bridge), costal cell concave, margin explanate, lateral margins of disc sinuate in dorsal view (Figs 3C, 3I) 17
 – Large (2.4 mm), clypeal organ in salient cone (Fig. 5) *H. oculatum* Reuter
 – Medium (1.7-2.0 mm), clypeal organ absent (Fig. 4A) 11
10. Macropterous 12
11. Submacropterous 16
12. Vesical process 60% as long as vesica, only one (long) right conjunctival process *H. koghiensis* sp. nov.
 – Vesical process less than 50% as long as vesica, 2-3 right conjunctival processes. . . 13
13. Two right conjunctival processes, left process of T9 short. 14
 – Three right conjunctival processes, left process of T9 long 15
14. Vesical process 5% as long as vesica *H. hypselosomatum* sp. nov.
 – Vesical process 33% as long as vesica *H. bleuensis* sp. nov.
15. Left process of T9 not bifid, vesical process 150% as long as second right conjunctival process, second right conjunctival process 40% as long as first right conjunctival process. *H. mandjeliensis* sp. nov.
 – Left process of T9 bifid, vesical process 100% as long as second right conjunctival process, second right conjunctival process 75% as long as first right conjunctival process *H. mouensis* sp. nov.
16. Length 1.71 mm, vesical process 200% as long as second right conjunctival process, two right conjunctival process. *H. rhinatum* sp. nov.
 – Length 1.90 mm, vesical process 100% as long as second right conjunctival process, three right conjunctival process *H. amieuensis* sp. nov.
17. Small (1.3 mm), strongly flattened (Fig. 1E), submacropterous (Fig. 8E), clypeal organ flat with erect setae . *H. ndouaensis* sp. nov.
 – Medium (1.5-1.6 mm), less flattened (Figs 1C, 1K), macropterous 19
18. Claval vein 1AN and corial veins R and M bordered by punctuation, clypeal organ with adpressed setae and pale bridge *H. triacanthatum* sp. nov.
 – Veins not bordered by punctuation, clypeal organ flat with erect setae. . . *H. dicroum* sp. nov.

HYPSELOSOMATUM-SPECIES GROUP

The following eight species are similar externally but they can be readily identified by male genitalia (Table 2). These eight species are referred to here as the *H. hypselosomatum* group which is defined in detail under the discussion. Species in this group share similarly small distributions, at a variety of elevations, but as a group are spread the entire length of Grande Terre.

Hypselosoma hypselosomatum sp. nov.
 (Figs 4A, 7A, 9F, 10A-B, 22A,
 Tables 1-2)

Etymology. Greek, provided with a high body.

Material. HOLOTYPE male: 22°17'0"S x 166°54'46"E, Pic du Grand, Kaori, site 1, 250 m, GBM, 21.xi.2001-

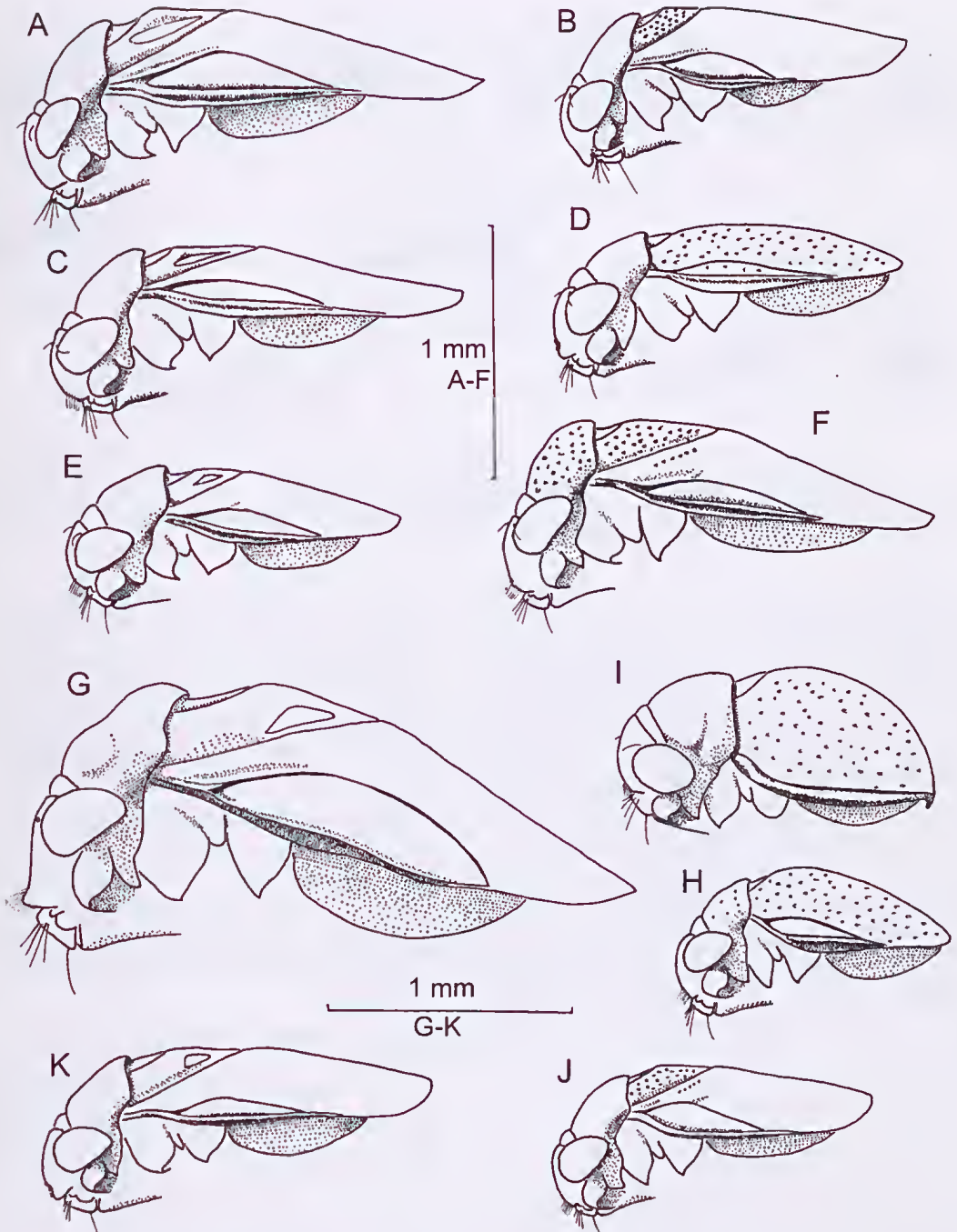


FIG. 1. Left lateral view of 11 New Caledonian male *Hypselosoma*. A, *H. bleuensis* sp. nov.; B, *H. chorizobregmatum* sp. nov.; C, *H. dicroum* sp. nov.; D, *H. gephyrobregmatum* sp. nov.; E, *H. ndouaensis* sp. nov.; F, *H. nordiensis* sp. nov.; G, *H. oculatum* Reuter; H, *H. rembaiensis* sp. nov.; I, *H. touhoensis* sp. nov.; J, *H. trachyacanthatum* sp. nov.; K, *H. triacanthatum* sp. nov.

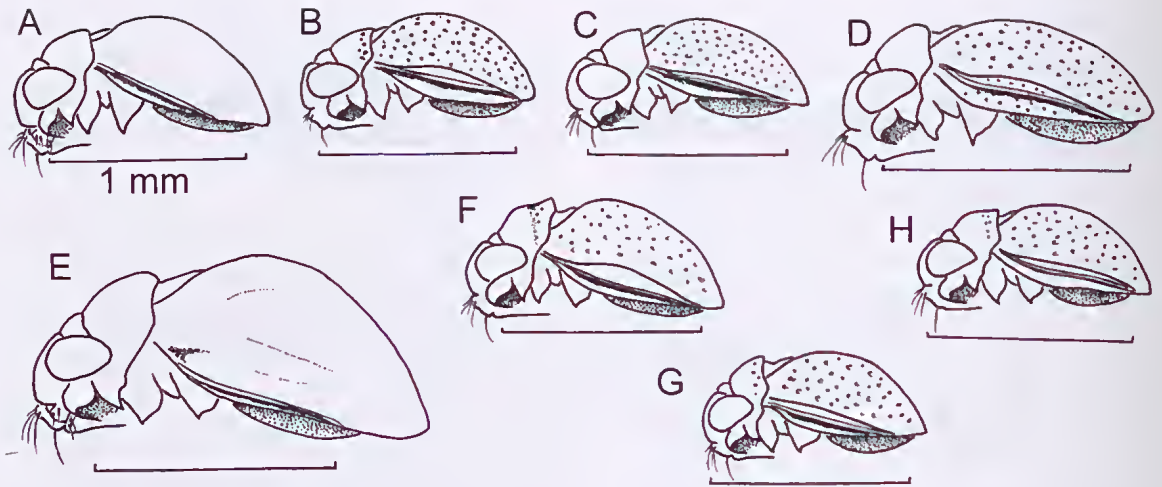


FIG. 2. Left lateral view of 8 New Caledonian female *Hypselosoma*. A, *H. bleuensis* sp. nov.; B, *H. dicroum* sp. nov.; C, *H. ndouaensis* sp. nov.; D, *H. nordiensis* sp. nov.; E, *H. oculatum* Reuter; F, *H. onceronotatum* sp. nov.; G, *H. trachyacanthatum* sp. nov.; H, *H. triacanthatum* sp. nov.

29.i.2002, RFIT, QM8919, 3 slides and vial, 16353 (MNHN(EH)). Paratypes: 2 m as for holotype, T165619-20. Other material: 1 m T165726, 4 f, T165727-30, same site, GBM & PG, 22.xi.2004, RB, QM11767; 2 f, T165731-2, same site, GBM, 22.xii.2004, RB, QM12021; 3 m, 1 f, T165733-6, same site, GBM & PG, 22.xii.2004-12.i.2005, RFIT, QM11847; 1 f, T165737, same site, GBM & PG, 22.xii.2004-12.i.2005, R pitfall trap, QM11848; 1 f, T165738, same site, CB & SW, 22-23.xi.2004, R yellow pans, QM11760; 1 m, T165739, 2 f, T165740-1, 22°17'7"S x 166°54'54"E, Pic du Grand, Kaori site 2, 250 m, QM party, 22.xi.2004, R mercury vapour light, QM11774; 1 m, T165742, vial & 3 slides, same site, GBM & PG, 22.xi.2004, RB, QM11777; 1 m, T165743, 22°19'23"S x 166°54'55"E, Foret Nord, site 2, 200 m, GBM & PG, 22.xii.2004-9.i.2005 FIT, QM11889 (QM).

Diagnosis. Colour, high convexity and absence of male clypeal organ as for all members of *H. hypselosomatum* group. See Table 2 for diagnostic characters.

Description. *Macropterous male.* Black except frons sometimes uniformly a little paler than clypeus (but without pair of red patches), antennae, labrum, maxillary plates, labium and legs mostly dark brown but tibial apices light brown, forewing membrane black-brown proximally becoming brown distally, costal cell black. Profile convex like Fig. 1A.

Base of labrum tumid in profile, salient above plane of clypeus; maxillary plates tumid rather than gently convex, with two short, erect macrosetae aligned with the basal macrosetae of labrum; bucculae with very short macroseta mounted below a tubercle bearing two minor setae like Fig. 6B; clypeal organ absent.

Disc finely punctate (indistinct at 80x magnification); lateral margins convexly convergent (not sinuous, disc not weakly constricted anteriorly), calli not tumid; posterior margin convex; medial ends of mesosternal transverse carinae taper rather than end abruptly (squarely or acutely).

Forewing (Fig. 7A) not explanate; costal cell sclerotized, not depressed or concave (hence margin not explanate), impunctate but coarsely granulate ventrally; hypocostal lamina narrow, about as wide as hind femoral width; a glabrous furrow along posterior margin of costal cell; corium mostly membranous, darker around anterior margin of trapezoidal cell perhaps from incipient sclerotization; anal cell twice or more as large as trapezoidal cell, bases of 1AN and 2AN sclerotized and finely granulate ventrally.

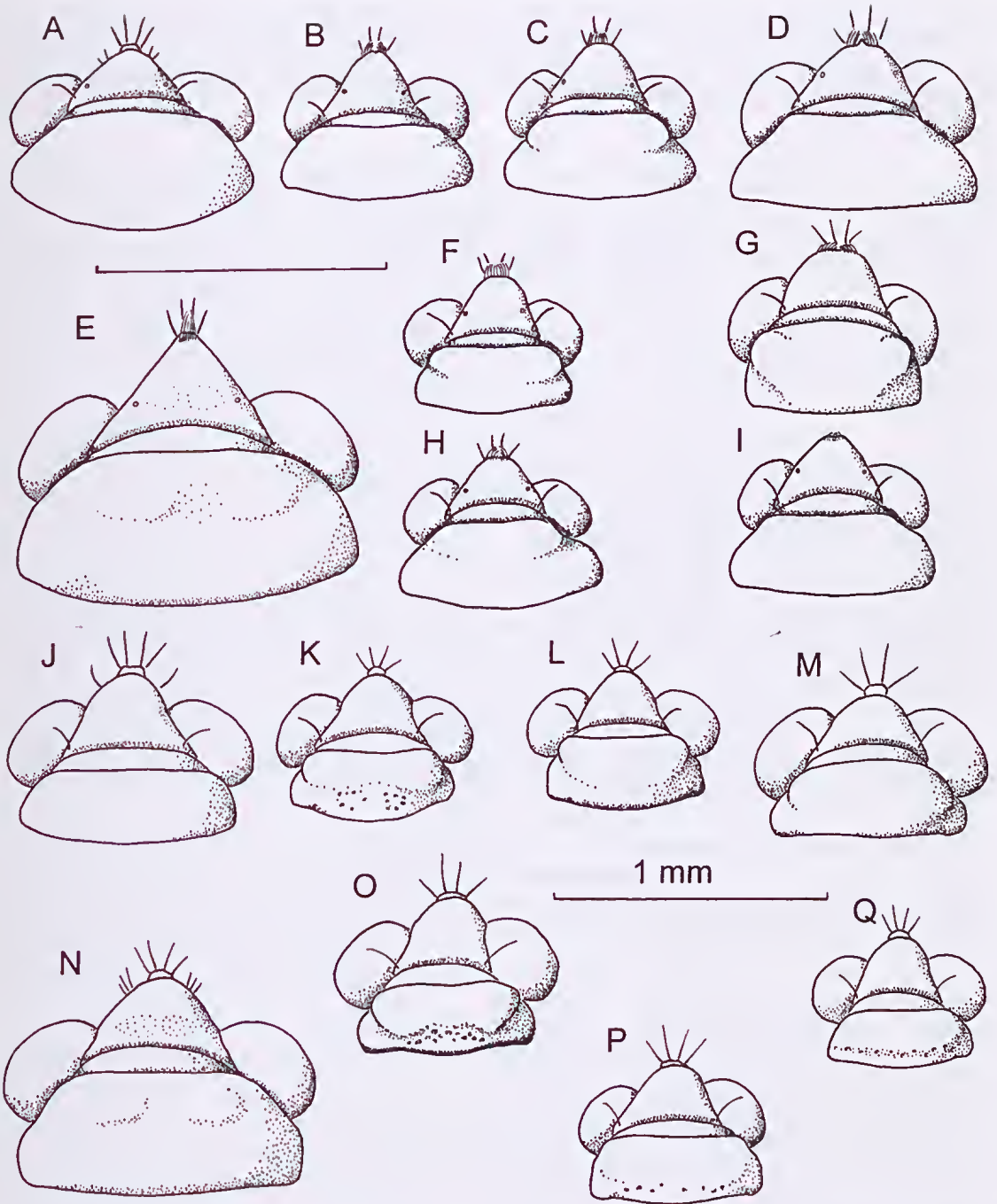


FIG. 3. Dorsal view of head and pronotum, A-I male ; J-Q female *Hypselosoma*. A, *H. bleuensis* sp. nov.; B, *H. chorizobregmatum* sp. nov.; C, *H. ndouaensis* sp. nov.; D, *H. nordiensis* sp. nov.; E, *H. oculatum* Reuter; F, *H. rembaiensis* sp. nov.; G, *H. touhoensis* sp. nov.; H, *H. trachyacanthatum* sp. nov.; I, *H. triacanthatum* sp. nov. J, *H. bleuensis* sp. nov.; K, *H. dicroum* sp. nov.; L, *H. ndouaensis* sp. nov.; M, *H. nordiensis* sp. nov.; N, *H. oculatum* Reuter; O, *H. onceronotatum* sp. nov.; P, *H. trachyacanthatum* sp. nov.; Q, *H. triacanthatum* sp. nov.

TABLE 1. Dimensions of New Caledonian *Hypselosoma* in millimetres. The first eight species form a group and are arranged alphabetically after *H. hypselosomatum* sp. nov. except for the elytrous *H. elytratum* sp. nov. Remaining species are arranged alphabetically. LHT length hind tibia; WP width pronotum; LP length pronotum; DAE distance across eyes; LAH, length from labrum to apex of hemelytra; N, number of specimens measured.

Species	Males						Females					
	LHT	WP	LP	DAE	LAH	N	LHT	WP	LP	DAE	LAH	N
<i>Hypselosoma hypselosomatum</i>	0.74	0.87	0.48	0.88	1.77	9	0.72	0.76	0.38	0.89	1.47	10
<i>amieuensis</i>	0.82	0.99	0.53	0.97	1.90	2	0.80	0.86	0.41	1.02	1.66	7
<i>bleuensis</i>	0.84	0.87	0.50	0.88	1.89	2	0.82	0.77	0.36	0.93	1.48	4
<i>koghiensis</i>	0.88		0.54		2.00	2	0.84	0.89	0.42	1.02	1.70	3
<i>mandjeliensis</i>	0.67	0.81		0.83	1.89	2	0.74	0.80	0.39	0.94	1.60	2
<i>mouensis</i>	0.76		0.53		1.96	1						
<i>rhinatum</i>	0.81	0.83		0.87	1.71	1	0.72	0.77	0.36	0.89	1.57	6
<i>elytratum</i>	0.66	0.78	0.41	0.88	1.51	1	0.74	0.83	0.38	0.98	1.68	1
<i>chorizobregmatum</i>	0.56	0.70	0.36	0.69	1.37	1						
<i>dicroum</i>	0.62	0.75	0.41	0.75	1.57	2	0.56	0.60	0.29	0.72	1.19	10
<i>gephyrobregmatum</i>	0.60	0.69	0.34	0.70	1.33	1						
<i>halploacanthatum</i>	0.56	0.71	0.35	0.67	1.40	1	0.55	0.60	0.27	0.70	1.19	1
<i>ndouaensis</i>	0.55	0.67	0.36	0.70	1.26	1	0.53	0.63	0.28	0.73	1.25	1
<i>nordiensis</i>	0.79	0.85	0.46	0.91	1.84	7	0.82	0.76	0.37	0.92	1.58	16
<i>oculatum</i> Reuter	1.27	1.20	0.69	1.20	2.38	9	1.21	1.09	0.55	1.20	2.08	5
<i>onconotatum</i>						0	0.73	0.68	0.34	0.84	1.38	3
<i>rembaiensis</i>	0.54	0.59	0.29	0.67	1.14	9						
<i>touhoensis</i>	0.59	0.68	0.39	0.77	1.26	3						
<i>trachyacanthatum</i>	0.56	0.74	0.37	0.71	1.42	4	0.55	0.64	0.28	0.74	1.16	2
<i>triacanthatum</i>	0.59	0.77	0.39	0.71	1.61	1	0.56	0.61	0.29	0.71	1.18	1

S3 organ (Fig. 10A) granulate oval with single, peripheral row of long setae anteriorly and a cluster of long setae posteriorly on a tumid area of S3, no setae within oval area (like Fig. 10E).

Genitalia. left process of T9 short, decurved spine projecting laterally over base of left LT9 (possibly sharing common base with blunter, shorter medially directed process); left LT9 a medially procurved arm (Fig. 12A); right LT9 gently curved with hyaline, digitate apex and triangular rather than digitate subapical process on ventral margin (Fig. 12C); distal lobe of right paramere barely longer than colinear proximal lobe; left paramere curved, spine-like with broader, lamellate base bearing short spinous process (Fig. 12D); left conjunctival process spatulate, apically serrate and proximally tuberculate (Figs 10B, 12D, 12E); right

conjunctival sclerite with two long, curved processes, one 80% as long as other, lacking third very short, spinous process basally; base of vesica has very short, thick, acute process barely 5% as long as vesica; vesical process 20% as long as second right conjunctival process (see Table 2 for *H. hypselosomatum* group comparison).

Elytrous female. Colour like male, elytra black.

Base of labrum tumid in profile, more salient than clypeal apex; maxillary plates tumid rather than gently convex, with 1-3 short, erect macrosetae; bucculae with a very short macroseta mounted below a tubercle bearing two minor setae.

Disc finely punctate (indistinct at 80x magnification), lateral margins of disc parallel in posterior half, roundly converging anteriorly; posterior margin straight, posterior angles not tumid (not projecting posteriorly and not

TABLE 2. Diagnostic characters for males of *H. hypselosomatum* group which are defined in the discussion. LT: laterotergite; RCjPr1 and 2: major and secondary processes of right conjunctival sclerite; T: tergum.

Species	Left T9	Right LT9 apex	Vesical process of vesica	Vesical process of R Cj Pr2	Right conjunctival processes	R CjPr 2 of 1
<i>hypselosomatum</i>	Short spine	digit	5%	20%	2	80%
<i>mandjeliensis</i>	Long spine	digit	33%	150%	3	40%
<i>amieuensis</i>	Short spine	digit	25%	100%	3	50%
<i>mouensis</i>	Long bifid spine	Spinous	25%	100%	3	75%
<i>koghiensis</i>	Short spine	digit and lobe	60%	Na	1 (long)	0%
<i>bleuensis</i>	Short apically serrate	digit	33%	400%	2	25%
<i>rhinatum</i>	Possibly very short apically serrate	digit	33%	200%	2 (striate)	40%
<i>elytratum</i>	Short spine	digit	10%	25%	3	75%

causing lateral margins to become tumid posteriorly); medial ends of transverse, mesosternal carinae taper rather than end acutely or squarely.

Elytra highly convex in profile and in section (vertical sides), surface appearing irregular at 80x magnification but finely punctate in cleared material (Fig. 9F); no glabrous furrow marking path of vein Sc; costal cell not abruptly changing plane from remainder of elytra; vein C present as a sharp carina, as high as its width, extending only 75% to apices; hypocoelal lamina finely punctate, barely wider than hind femoral width; most venation weakly evident as several raised lines (and in cleared material); elytra overlap in distal half, variably right on left and vice versa.

Gonapophyses with six teeth. Spermatheca absent.

Distribution. Known from two localities at 200-250 m a.s.l. at the southern tip of Grande Terre (Fig. 22A).

Notes. A male from nearby at Forêt Nord, 200 m a.s.l. has the abdomen missing. It may be conspecific but its hind tibiae are shorter (0.63 mm). It is lodged in QM.

Hypselosoma amieuensis sp. nov.
(Figs 6F-G, 7B, 11A, 13A-C, 22A,
Tables 1-2)

Etymology. From the type locality.

Material. HOLOTYPE male: 21°35'33"S x 165°48'19"E, Col d'Amieu, sawmill, 350-400 m, GBM & CB, 14.xi.2002, RP, trees & logs, QM11183, 7 slides, 16354 (MNHN(EH)). Paratypes: 4 f as for holotype, 3 slides T165624; 3 points T165621-3. Other material: 1 m, T165703, 7f, same site T165705-165711, GBM, 25.xi.2003-27.i.2004, RFIT, QM11476; 1 m, T165712, 21°33'15"S x 165°46'21"E, Table Unio summit, 1000 m, GBM & DC, 10.v.1984, QM7197 (male transposed by author with male of *H. oculatum* from Forêt de la Thi Reserve in labeled vials but probable error rectified) (QM).

Diagnosis. Colour, high convexity and absence of male clypeal organ as for all members of *H. hypselosomatum* group but submacropterous like *H. rhinatum*. See Table 2 for diagnostic characters.

Description. *Submacropterous male.* Like *H. hypselosomatum* (no setae within oval of S3 organ) except head dark brown; fore tibiae, apical quarter to whole of mid tibiae and sometimes apical quarter of hind tibiae brown. Fore wing (Fig. 10B) membrane reduced to width equal to that between Cu and 1AN; forewing otherwise like *H. hypselosomatum*; male genitalia (Figs 13A-C) like *H. hypselosomatum* except vesical process is 25% (not 5%) as long as vesica, vesical process 100% (not 20%) as long as second right conjunctival process; three (not two) processes present on right conjunctival sclerite; second right conjunctival process is 50% (not 80%) as long as first.

Elytrous female. Like *H. hypselosomatum* (including finely punctate disc and elytra which may not appear distinctly punctate at 80x magnification), except head dark brown; fore tibiae, apical quarter to all of mid tibiae and sometimes apical quarter of hind tibiae brown.

Distribution. Known from two adjacent localities at 400-1000 m a.s.l. At Table Unio it is sympatric with *H. rembaiensis*. At Col d'Amieu it is sympatric with *H. gephyrobregmatum* (Fig. 22A).

Notes. Reduction of the forewing membrane is marginally less than in *H. rhinatum* (compare Figs 6B, 6E).

Hypselosoma bleuensis sp. nov.
(Figs 1A, 2A, 3A, 6C, 7B, 13D,
14A-G, 22A, Tables 1-2)

Etymology. From the type locality.

Material. HOLOTYPE male: 22°4'33"S x 166°37'12"E, Rivière Bleue, Kauri Track, 250 m, SW, 21.xi.2002, RP, trees, QM11206, 4 slides, 16255 (MNHN(EH)). Paratypes: 1 m, 4 f, as for holotype, T165625-9 (QM).

Diagnosis. Colour, high convexity and absence of male clypeal organ as for all members of *H. hypselosomatum* group. See Table 2 for diagnostic characters.

Description. *Macropterous male.* Fig. 1A. Like *H. hypselosomatum* except male genitalia (Fig. 13D, 14A-C) as follows: left process of T9 short and apically serrate; vesical process 33% (not 5%) as long as vesica; vesical process 400% (not 20%) as long as second conjunctival process and second right conjunctival process 25% (not 80%) as long as first. Fore wing membrane fully developed.

Elytrous female. Fig. 2A. Like *H. hypselosomatum* except head black brown, elytra smoother at 80x magnification.

Distribution. Known from one locality at 250 m a.s.l. at Rivière Bleu (Fig. 22A).

Notes. The granulation of the ventral surface of male costal cell is apparently finer than in *H. hypselosomatum*. Pale dots (possibly micro-

tubercles) of similar size to those at the bases of setae on veins occur along the margins of fore wing veins in this species, *H. mouensis*, *H. rhinatum* and possibly in all species of *H. hypselosomatum* group but not so conspicuously.

Hypselosoma koghiensis sp. nov.
(Figs 7C, 10C, 14D-F, 22A, Tables 1-2)

Etymology. From the type locality.

Material. HOLOTYPE male: 22°10'39" x 166°30'32"E, Mt Koghis track entrance, 500 m, RR & N. Platnik, 23-30.v.1987, R pitfall, QM7135, 3 slides and 1 vial, 16356 (MNHN(EH)). Paratypes: 1 m, 2 f, as for holotype, T165630-2. Other material: 1 f, same site, GBM, 5.ii.2004, RB, QM11533, T165633 (QM).

Diagnosis. Colour, high convexity and absence of male clypeal organ as for all members of *H. hypselosomatum* group. See Table 2 for diagnostic characters.

Description. *Macropterous male.* Like *H. hypselosomatum* (including bare S3 organ) except head dark brown; male genitalia as for *H. hypselosomatum* except apex right LT9 provided with short hyaline digit and broad, well-defined subapical lobe (Fig. 14D); vesical process 60% (not 5%) as long as vesica; one (not two) process present on right conjunctival sclerite (Fig. 14F). Fore wing membrane fully developed (Fig. 7C).

Elytrous female. Like *H. hypselosomatum* except head brown, legs with same pattern but overall paler; elytra smoother, venation less discernable and most conspicuous as two parallel lines in proximal half in dorsal view.

Distribution. Known from one locality at 500 m a.s.l. at Mt Koghis (Fig. 22A).

Notes. The pattern of the vestigial venation of female elytra is one character excluding this species from consideration as *H. oclatum*.

Hypselosoma mandjeliensis sp. nov.
(Figs 6B, 15A-C, 22C, Tables 1-2)

Etymology. From the type locality.

Material. HOLOTYPE male: 20°24'15"S x 164°31'13"E, Mandjélia sawmill, 700 m, GBM & DC, 12.v.1984, RB, QM4263, 4 slides, 16357

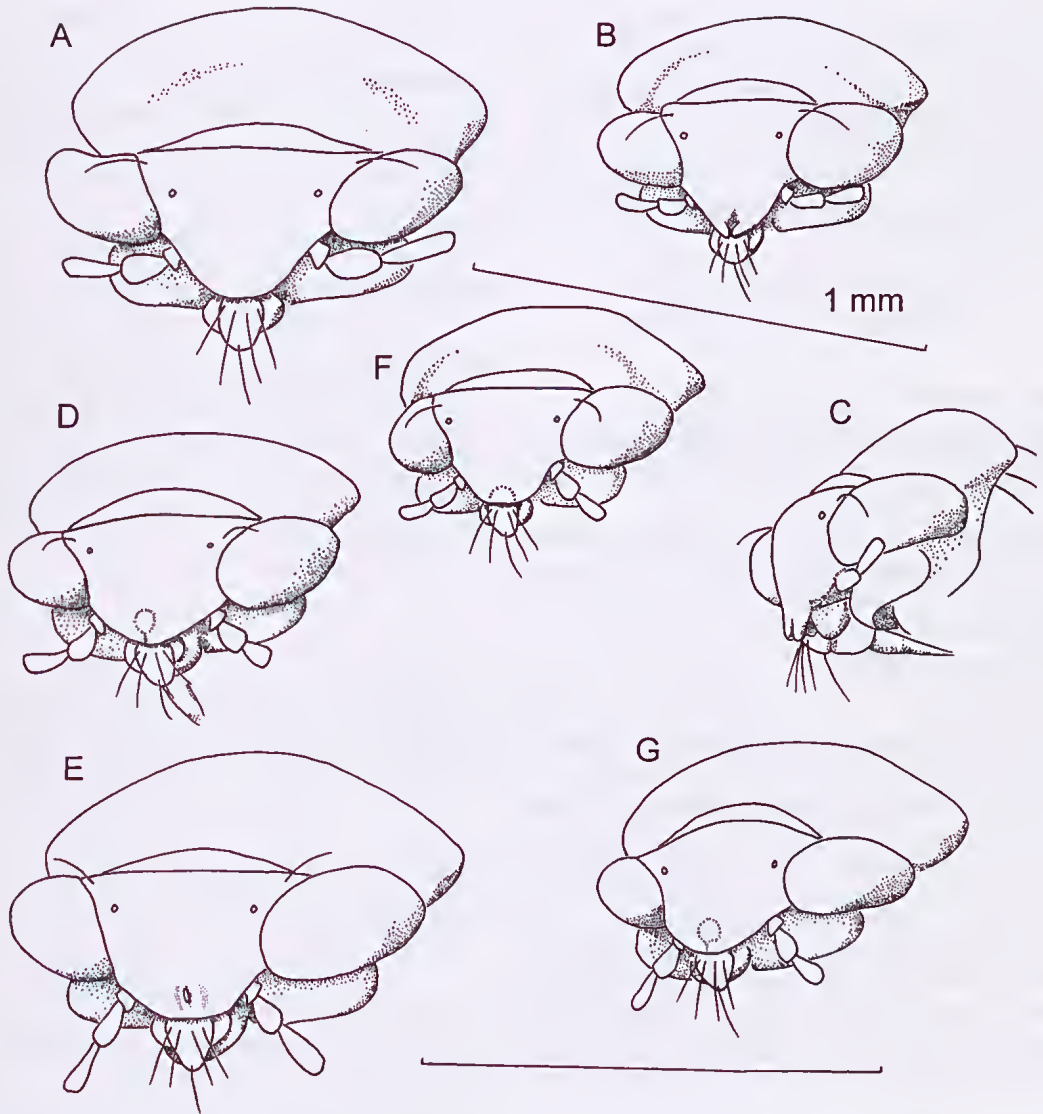


FIG. 4. Left anterolateral view of head and pronotum of 6 male *Hypselosoma*. A, *H. hypselosomatum* sp. nov.; B-C, *H. chorizobregmatum* sp. nov.; D, *H. gephyrobregmatum* sp. nov.; E, *H. nordiensis* sp. nov.; F, *H. trachyacanthatum* sp. nov.; G, *H. triacanthatum* sp. nov.

(MNHN(EH)). Other material: 1 m, same site, GBM & DC, 12.v.1984, RB, QM4265, T165693 (QM).

Diagnosis. Colour, high convexity and absence of male clypeal organ as for all members of *H. hypselosomatum* group. See Table 2 for diagnostic characters.

Description. *Macropterous male.* Like *H. hypselosomatum* except male genitalia as follows: left process of T9 present as long not short spine (Fig. 15B), vesical process 33% (not 5%) as long as vesica; vesical process 150% (not 20%) as long as second right conjunctival process; three (not two) processes present on right conjunctival sclerite (Fig. 15A); second right conjunctival

process 40% (not 80%) as long as first (Fig. 15C). Fore wing membrane fully developed.

Elytrous female. Not described but two specimens from Mt Panié may fit here.

Distribution. Known from two localities at 700-900 m a.s.l. at the northwestern end of Grande Terre (Fig. 22C).

Hypselosoma mouensis sp. nov.
(Figs 6A, 6E, 6I, 15D-H, 22A,
Tables 1-2)

Etymology. From the type locality.

Material. HOLOTYPE male: 22°4'31"S × 166°19'52"E, Mt Mou base, 200 m, GBM, 7.xii.2003-2.ii.2004, RFIT, QM11468, 6 slides, 16358 (MNHN(EH)).

Diagnosis. Colour, high convexity and absence of male clypeal organ as for all members of *H. hypselosomatum* group. See Table 2 for diagnostic characters.

Description. *Macropterous male*. External morphology as for *H. hypselosomatum* except setae present within oval of S3 organ (like Fig. 11H), maxillary plates with 1 macroseta (Fig. 6A). Male genitalia as for *H. hypselosomatum* except left process of T9 present as long bifid spine (Fig. 15D-E); apex of right LT9 spinous (not digitate); vesical process 25% (not 5%) as long as vesica, vesical process 100% (not 20%) as long as second right conjunctival process; three (not two) processes present on right conjunctival sclerite; second right conjunctival process 75% (not 80%) as long as first (Fig. 15F). Fore wing membrane fully developed.

Elytrous female. Unknown.

Distribution. Known from one rainforest locality at 200 m a.s.l. at Mt Mou (Fig. 22A).

Hypselosoma rhinatum sp. nov.
(Figs 7E, 16A-B, 16D, 16E, 22A, Tables 1-2)

Etymology. Greek, provided with a rasp (on the left conjunctival sclerite).

Material. HOLOTYPE male: 21°34'47"S × 165°49'0"E, 4km N Col d'Amieu, 300 m, GBM & DC, 8.v.1984, RB, QM4257, 4 slides, 16359 (MNHN(EH)). Paratypes: 5 f as for holotype, 1 vial T165635-8, pin T165634. Other material: 1 f, 21°34'22"S × 166°6'42"E, Col de

Petchecara, 350 m, GBM, 28.i.2004, RB, QM11541, T165694 (QM).

Diagnosis. Colour, high convexity and absence of male clypeal organ as for all members of *H. hypselosomatum* group but submacropterous like. See Table 2 for diagnostic characters.

Description. *Submacropterous male*. As for *H. hypselosomatum* (no setae within oval of S3 organ) except male genitalia as follows: left process of T9 possibly very short and apically serrate; vesical process 33% (not 5%) as long as vesica; vesical process 200% (not 20%) as long as second right conjunctival process; first right conjunctival process broad and striate not spinous; second right conjunctival sclerite 40% (not 80%) as long as first (Fig. 16A). Fore wing membrane is reduced to a thin band half as wide as distance between Cu and 1AN (Fig. 7E).

Elytrous female. Like *H. hypselosomatum* except head dark brown.

Distribution. Known from two rainforest localities at 300-350 m a.s.l. and 30 km apart (Fig. 22A). At Col d'Amieu it is sympatric with *H. haplacanthatum*.

Notes. The degree of reduction of the fore wing membrane is a little greater than in *H. amieuensis* (compare Figs 6B, 6E).

Hypselosoma elytratum sp. nov.
(Figs 7F, 16C, 22A, Tables 1-2)

Etymology. Greek, provided with elytra.

Material. HOLOTYPE male: 22°3'44"S × 166°20'41"E, Mt Mou summit, 1150 m, GBM & DC, 24.v.1984, RB, QM4276, 3 slides and 1 vial, 16360 (MNHN(EH)). Paratype: 1 f, as for holotype, 1 vial, T165639 (QM).

Diagnosis. The highly convex elytrous form and absence of male clypeal organ distinguish this species.

Description. *Elytrous male*. Mostly black; antennae, labrum, maxillary plates, labium and legs mostly dark brown but tibial apices paler.

Profile moderately convex.

Base of labrum tumid in profile, salient above plane of clypeus; maxillary plates tumid, with 2

short, erect macrosetae aligned with four basal macrosetae of labrum; bucculae with 1 short macroseta below tubercle bearing two minor setae; clypeal organ absent.

Disc of pronotum impunctate; lateral margins convexly convergent (not sinuous, disc not weakly constricted anteriorly); calli not tumid; posterior margin straight, posterior angles not tumid; medial ends of mesosternal transverse carinae rounded (not ending acutely).

Elytra moderately convex, weakly overlapping distally; costal margin not explanate; costal cell sclerotized, flat, appearing impunctate at 80x magnification but see Fig. 7F; hypocostal lamina little wider than depth of hind femora, extending 75% to apices; glabrous furrow along posterior margin of costal cell; venation faint.

S3 organ as in *H. hypselosomatum*.

Genitalia. As in *H. hypselosomatum* except: right LT9 has clearly digitate process subapically on ventral margin; vesical process 10% (not 5%) as long as vesica; vesical process 40% (not 20%) as long as second conjunctival sclerite (Fig. 16C).

Elytrous female. Colour like male.

Base of labrum tumid in profile, more salient than clypeal apex; maxillary plates with 2 short, erect macrosetae, bucculae with tubercle and 1 short, erect macroseta.

Disc appears impunctate at 80x magnification; lateral margins of disc roundly converging anteriorly, parallel posteriorly; posterior margin straight, posterior angles not tumid.

Elytra highly convex in profile, finely punctate; no glabrous furrow marking path of vein Sc and costal cell not abruptly changing plane from remainder of elytra; vein C present as sharp carina, high as wide, extending 75% to apices; hypocostal lamina barely wider than hind femoral depth; venation faint; elytra barely overlapping in distal half.

Distribution. Known from one locality at 1200 m a.s.l. on Mt Mou which is the highest involved in this paper (Fig. 22A).

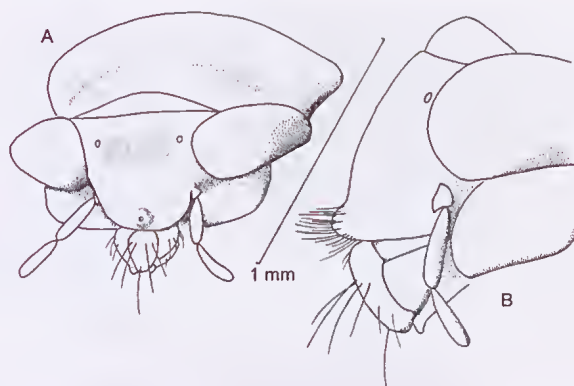


FIG. 5. Left anterolateral and lateral views of head and pronotum of male *Hypselosoma oculatum* Reuter.

Notes. This species belongs to *H. hypselosomatum* group but differs in having an elytrous male (minor submacroptery occurs in *H. amieuensis* and *H. rhinatum*). The genitalia are most similar to *H. hypselosomatum* (compare values in Table 2).

Hypselosoma chorizobregmatum sp. nov.
(Figs 1B, 3B, 4B-C, 8A, 10D, 11B, 17A-B, 22B, Table 1)

Etymology. Greek, provided with a split front part of the head.

Material. HOLOTYPE male: 22°4'31"S x 166°19'52"E, Mt Mou base, 200 m, GBM, 7.xii.2003-2.ii.2004, RFIT, QM11468, 3 slides and 1 vial, 16362 (MNHN(EH)).

Diagnosis. The convex rather than flattened form and pair of clypeal lobes obscuring the labral base (Fig. 4C) distinguish males of this species.

Description. *Macropterous male.* Black except antennae, labrum, maxillary plates, labium and legs mostly dark brown but tibial apices light brown, forewing membrane black-brown proximally becoming brown distally, costal cell black.

Profile convex but less than macropterous males of *H. hypselosomatum* group (compare Figs 1A-B).

Base of labrum not tumid, obscured by lobes of clypeal organ; maxillary plates without macrosetae; bucculae with tubercle, without macroseta;

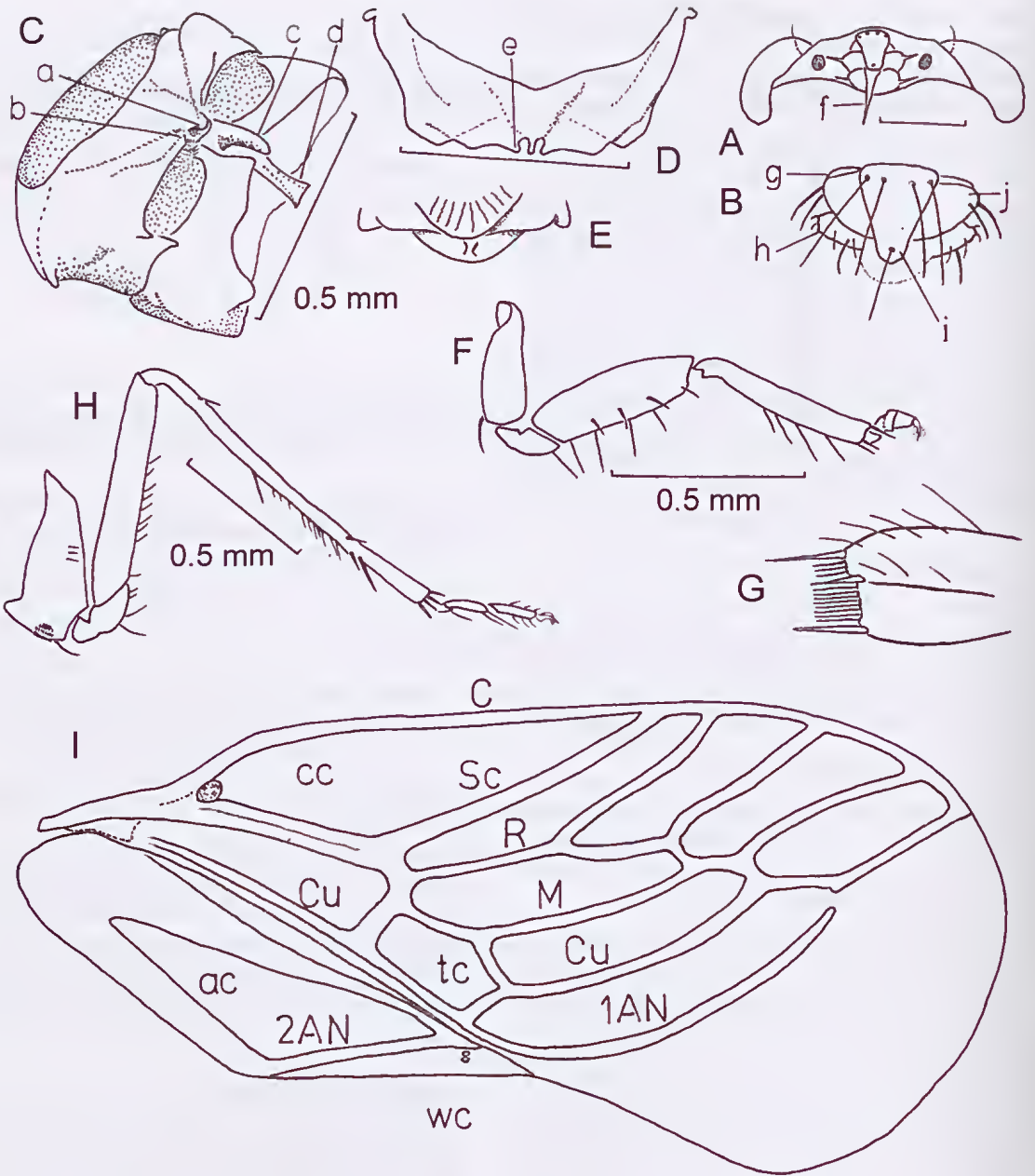


FIG. 6. *Hypselosoma* species. A, head on slide, labium removed, anterior, *H. mouensis* sp. nov.; B, labrum, bucculae, mandibular and maxillary plates on slide, dorsal, *H. mandjeliensis* sp. nov.; C, male pterothorax, ventrolateral, *H. bleuensis* sp. nov.; D, mesosternal carinae, anterior, *H. trachyacanthatum* sp. nov.; E, arcuate postnotal flange, dorsal, *H. mouensis* sp. nov.; F-G, *H. amieuensis* sp. nov. F, male left fore leg, anterior; G, apex fore tibia, ventrolateral; H, left hind leg, anterior, *H. oculatum* Reuter; I, fore wing terminology, *H. mouensis* sp. nov. a, mesosternal process; b, medial end of mesosternal carina; c, metasternal process; d, metendosternite; e, medial end of mesosternal carina; f, epipharyngeal projection; g, mandibular plate; h, bucculae; i, labrum; j, maxillary plate; ac, anal cell; cc, costal cell; tc, trapezoidal cell; wc, wing coupling.

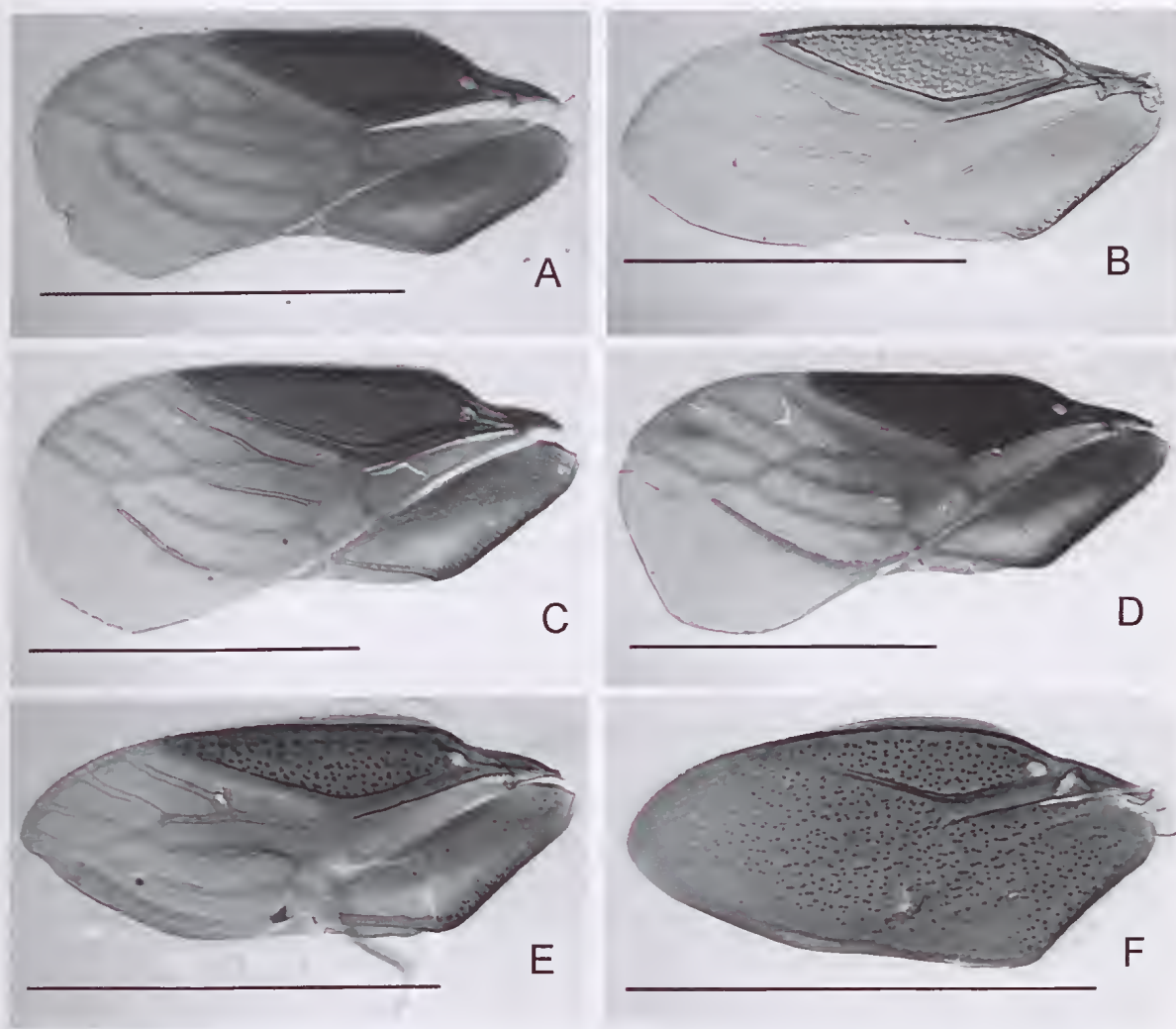


FIG. 7. Male fore wings, dorsal, *H. hypselosomatum* species group. A, *H. hypselosomatum* sp. nov.; B, *H. amieuensis* sp. nov.; C, *H. koghiensis* sp. nov.; D, *H. mouensis* sp. nov.; E, *H. rhinatum* sp. nov.; F, *H. clytratum* sp. nov. Scale lines 1 mm.

apex of clypeus with pair of prominent lobes embracing a setigerous organ (Figs 4B-C).

Disc of pronotum impunctate, weakly constricted anteriorly, lateral margins sinuously convergent (indistinct in view used in Fig. 3B), calli not tumid, posterior margin sinuously convex; medial ends of mesosternal transverse carinae acute.

Forewing (Fig. 8A) distinctly explanate; costal cell sclerotized, impunctate or ventrally

granulate, flat but depressed between vein Sc and inclined, explanate costal margin which is 3-4 membranul-vein widths in dorsal view; hypocostal lamina 1.5 hind femoral widths; glabrous furrow along posterior margin of costal cell; five corial cells including trapezoidal cell wholly sclerotized (in addition to costal cell) except base of cell Sc+R+M, impunctate except posterodistal margin of cell Sc+R+M; clavus sclerotized and coarsely punctate, cell obscure but venation discernible.

S3 organ semicircular, with straight, sclerotized posterior margin extending beyond lateral angles, right projection wide basally and longer than left, semicircular anterior margin without peripheral long setae, many long setae posteriorly on tumidity of S3 and medially on S4 (setae omitted in Fig. 10D).

Genitalia. left process of T9 blunt, triangular, projecting over base of left LT9; left LT9 present as a medially procurved arm; right LT9 provided with a short, hyaline, apical lobe (not digitate), short, dorsal, subapical spine and a large, broad ventral process near midlength (Fig. 17B); left paramere curved, tapering spine-like, with bulbous base lacking subbasal lamella and spine; right paramere with spinous, distal lobe twice as long as broad basal lobe; left conjunctival sclerite with two short spines (fractured in slide preparation, Fig 17A); right conjunctival sclerite with (probably) one short spine; vesica with one short, basal, spinous process a little longer than conjunctival spines; vesica abruptly bent near midlength into loop, widening at bend and near three-quarters from base (Fig. 17A).

Elytrous female. Unknown

Distribution. Known from one locality at 200 m a.s.l. on Mt Mou where it is sympatric with *H. mouensis*, whereas *H. elytratum* is known only from the summit (Fig. 22B).

Notes. *H. triacanthatum* and *H. gephyrobregmatum* have the clypeal organ recessed between what are possibly fused lobes of the clypeus but *H. chorizobregmatum* is the only species in which the lobes are salient, obscure the base of the labrum and are clearly discrete although contiguous (Figs 4B-D, 4G).

Hypselosoma dicroum sp. nov.

(Figs 1C, 2B, 3K, 8B, 11C, 17C-D, 23A, Table 1)

Etymology. Greek, forked (apex of right conjunctival process).

Material. HOLOTYPE male: 22°5'49"S x 166°40'40"E, Rivière Bleue main forest, Kaori Track, 120 m, RR., 21.v.1987, RB, QM4352, 3 slides, 16362 (MNHN(EH)). Paratypes: 11 f, same as holotype,

T165640-50. Other material: 1f, same site, GBM & DC, 25.v.1984, RB, QM4278, T165725; 1f, same site, 120 m, GBM, 12.xi.2000, forest B, QM4447, T165723; 5f, same site, 160 m, GBM, 17.xi.2001, RB, QM8969, T165718-22; 1 m, 22°14'52"S x 166°49'51"E, Pic du Pin, East base site 1, 280 m, GBM & PG, 25.xi.2004-12.i.2005, RFIT, QM11859, T165724 (QM).

Diagnosis. The convex rather than flattened form, flat, setigerous clypeal organ, lack of corial sclerotization and punctation, lack of claval punctation and presence of an anal cell distinguish males of this species.

Description. *Macropterous male.* Black except antennae, labrum, maxillary plates, labium and legs mostly dark brown, forewing membrane black-brown proximally becoming brown distally (anal cell brown, costal cell black).

Profile convex but less than *H. hypselosomatum* group (compare Figs 1A, 1C).

Base of labrum not tumid in profile, more salient than flat clypeal apex, less salient than setae of clypeal organ; maxillary plates without erect macrosetae; bucculae without macroseta, with tubercle; clypeal organ present in flat, semicircular area on anterior margin bearing many erect, incurved setae.

Disc of pronotum finely punctate (indistinct at 80x magnification); disc weakly constricted anteriorly, lateral margins of disc sinuously convergent, calli not tumid, posterior margin sinuously convex; medial ends of mesosternal transverse carinae acute.

Forewing strongly explanate; costal cell sclerotized, impunctate, concave, merging with wide, inclined, explanate, subcostal margin creating a broad furrow one third from costal edge; hypocostal lamina subequal to width of hind femora; glabrous furrow present along posterior margin of costal cell; clavus sclerotized in proximal half, impunctate, anal cell present, 1AN and 2AN clearly evident in distal half. Vein Cu absent on left forewing of holotype (Fig. 8B).

S3 organ (Fig. 11C) semicircular to oval, possibly without sclerotized posterior rim, with short sclerotized projections from lateral angles, right larger than left, without peripheral row

of long setae, with many long setae adjacently posteriorly on tumidity of S3 and on S4.

Genitalia. left process of T9 short, broad, with rounded apex; left LT9 present as a medially procurved arm; right LT9 with broadly bilobate apex (Fig. 17D); distal lobe of right paramere slender, spinous, more than twice as long as proximal lobe; left paramere long, with bulbous base lacking any spine or lamella; left conjunctival sclerite without process (perhaps with a very short spine only); right conjunctival sclerite with curved, apically bifid spine longer than left paramere; vesical base with recurved, slender spine one third length of right conjunctival spine (Fig. 17C); vesica with slight rounded expansion near midlength.

Elytrous female. Head dark brown, elytra black, legs dark brown with femoral apices, tibiae and tarsi light brown.

Profile highly convex (Fig. 2B).

Base of labrum not tumid in profile, salient above clypeal plane; maxillary plates without erect macrosetae; bucculae with tubercle, without macroseta.

Disc punctate along faint, transverse impression posterior to calli; lateral margins of disc roundly converging anteriorly, tumid in posterior half; posterior margin straight except angles tumid and projecting a little posteriorly (Fig. 3K).

Elytra highly convex in profile, punctate (including clavus), venation faint, no overlap; glabrous furrow along vein Sc extending roughly 90% to elytral apices demarcating costal cell which is inclined at roughly 30° below horizontal to form a sloping, tapering shelf a little wider than depth of hind femora; hypocostal lamina at least 1.5 times width of hind femora and inclined at roughly 45°, extending 90% to elytral apices.

Gonapophyses provided with 5 teeth.

Distribution. Known from two localities about 25km apart and at 120-280 m a.s.l. near the southern end of Grande Terre (Fig. 23A).

Notes. The colour of the legs of the female is unlike that of the male. Male S3 organ is like in *H. nordiensis* in apparently lacking a sclerotized posterior rim and possessing a tiny fragmentary sclerite on left side. The holotype has the vein Cu missing on remigium of the left wing (Fig. 8B). The hind tibiae have five not four non-apical macrosetae (3-4 distally and 1-2 near midlength).

Hypselosoma gephyrobregmatum sp. nov.

(Figs 1D, 4D, 8C, 11D,
17E-G, 22B, Table 1)

Etymology. Greek, provided with a bridge on front part of head.

Material. HOLOTYPE male: 21°35'33"S x 165°48'19"E, Col d'Amieu, sawmill, 400 m, GBM, 25.xi.2003-27.i.2004, RFIT, QM11476, 3 slides and 1 vial, 16363 (MNHN(EH)).

Diagnosis. The flat, elytrous form and recessed clypeal organ lacking erect setae (Fig. 4D) distinguish males of this species.

Description. *Elytrous male.* Head, pronotum and elytra black; antennae, labrum, maxillary plates, labium and legs dark brown except apices of fore and mid femora and tibiae lighter, hind tibiae lighter except basally; tarsi not lighter.

Overall profile very flat with distinctly explanate costal margins (Fig. 1D).

Base of labrum not tumid in profile, less salient than bridging lobes of clypeal organ; maxillary plates smoothly convex, without erect macrosetae; bucculae without erect macroseta, with tubercle; clypeal organ present, separated from anterior margin by a pair of partly fused lobes forming a bridge (not pale) anterior to circular pit surrounded by many short, incurved, adpressed setae (Fig. 4D).

Disc of pronotum impunctate, gradually constricted anteriorly, lateral margins sinuously convergent, calli not tumid, posterior margin straight, angles weakly tumid; medial ends of transverse mesosternal carinae acute.

Forewing (Fig. 8C), elytrous, punctate, strongly explanate, venation not evident,

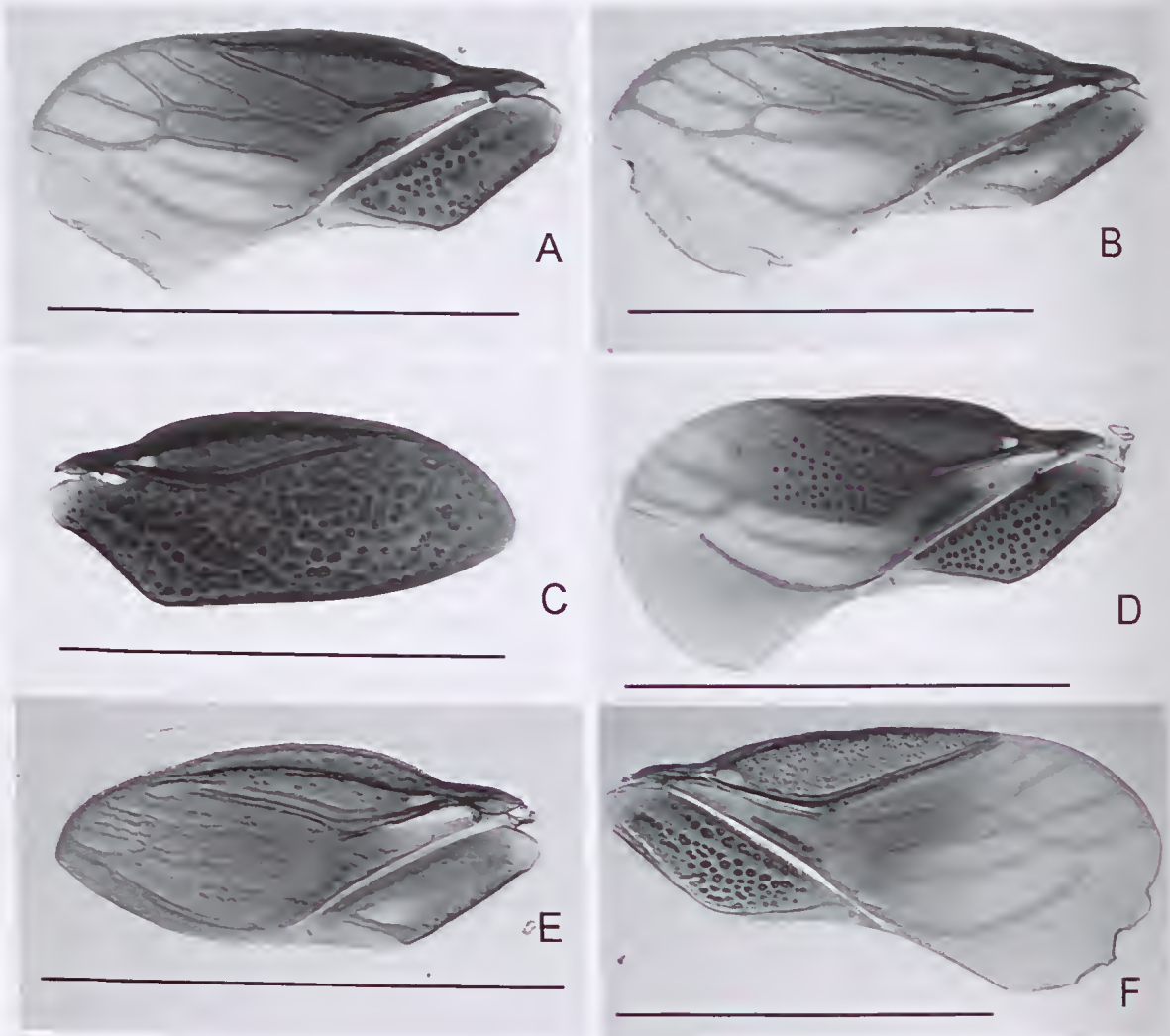


FIG. 8. Male fore wings, dorsal, *Hypselosoma* species. A, *H. chorizobregmatum* sp. nov.; B, *H. dicroum* sp. nov. (aberrant, Cu missing); C, *H. gephyrobregmatum* sp. nov.; D, *H. haplacanthatum* sp. nov.; E, *H. udouaensis* sp. nov.; F, *H. nordiensis* sp. nov. Scale lines 1 mm.

elytra weakly overlap in distal half; costal cell less punctate, weakly concave, merging with upturned costal vein; glabrous furrow along posterior margin of costal cell extending 75–80% to apex; hypocostal lamina twice width of hind femora, extending 90% to apex.

S3 organ (Fig. 11D) semicircular, with straight, sclerotized posterior margin extending beyond lateral angles, right projection widening basally and longer than left, semicircular anterior margin without peripheral row of long setae,

many long setae posteriorly on tumidity of S3 and medially on S4.

Genitalia. left process of T9 short tapering process; left LT9 present as a medially procurved arm; right LT9 with spherical lobate apex, with subapical spine and with a spine on ventral margin at midlength (Fig. 17E); distal lobe of right paramere slender, spinous, twice as long as proximal lobe; left paramere curved, spine-like, with bulbous base lacking lamella or spine (Fig. 17F); left conjunctival sclerite with two

short, curved spines; right conjunctival sclerite with one long curved spine subequal to left paramere; base of vesica provided with one curved spine adjacent to and shorter than those of left conjunctival sclerite (this spine possibly originates from left conjunctival sclerite) (Fig. 17G); vesica abruptly bent near midlength into loop, with short expansion at bend and second abrupt widening near three-quarters from base.

Female. Unknown.

Distribution. This species is known from one locality at 400 m a.s.l. at Col d'Amieu where it is sympatric with *H. amieuensis* (Fig. 22B).

Notes. The right LT9 is like in *H. triacanthatum*. The short, trispinous configuration (Fig. 17G) of the left conjunctival sclerite and vesical base is shared with *H. triacanthatum* (Fig. 21D), *H. nordiensis* (Fig. 19C) and perhaps *H. chorizobregmatum*.

Hypselosoma haplacanthatum sp. nov.

(Figs 8D, 11E, 18A-C,
22B, Table 1)

Etymology. Greek, provided with a single spine (left conjunctival process).

Material. HOLOTYPE male: 21°34'47"S x 165°49'0"E, 4km N Col d'Amieu, 300 m, GBM & DC, 8.v.1984, RB, QM4257, 2 slides and 1 vial, 16364 (MNHN(EH)). Paratype: 1 f, as for holotype, 1 vial, T165651 (QM).

Diagnosis. The convex form, flat, setigerous clypeal organ, sclerotized and punctate corium and clavus and absence of anal cell distinguish males of this species.

Description. *Macropterous male.* Black to dark brown; antennae, labrum, maxillary plates, labium dark brown; coxae and femora dark brown, femoral apices, tibiae and tarsi light brown; forewing membrane black to dark brown proximally becoming brown distally (costal cell black).

Profile convex but less than in members of *H. hypselosomatum* group.

Base of labrum not tumid in profile but salient above plane of flat clypeal apex and less salient than setae of clypeal organ; maxillary plates without erect macrosetae; bucculae

without erect macroseta, with tubercle; clypeal organ present in flat, semicircular area on anterior margin and bearing many (12-20) erect, incurved setae.

Disc of pronotum punctate (not as clearly as forewings), weakly constricted anteriorly, lateral margins sinuously convergent, calli not tumid, posterior margin sinuously convex; medial ends of mesosternal transverse carinae acute.

Forewing (Fig. 8D) moderately explanate, costal cell sclerotized, weakly punctate (in slide mounted material), flat but depressed between vein Sc and inclined, explanate costal margin which is 2-3 membranal-vein widths in dorsal view; hypocostal lamina about 1.5 hind femoral widths; glabrous furrow along posterior margin of costal cell; four corial cells (additional to costal cell) wholly or partly sclerotized and punctate; trapezoidal cell with one puncture in posterobasal angle; clavus sclerotized and punctate, cell obscured, 1AN and 2AN barely discernible.

S3 (Fig. 11E) organ subcircular, with curved, sclerotized posterior margin lacking lateral projections, with peripheral row of long setae anteriorly and cluster of long setae posteriorly on S3 as well as long setae medially on S4.

Genitalia. left process of T9 short, broad, with non serrate, rounded apex; left LT9 present as a medially procurved arm; right LT9 possibly without an apical hyaline digit, provided with two spinous processes subapically (Fig. 18A); distal lobe of right paramere almost twice as long as broad, bilobate proximal lobe (Fig. 18B); left paramere curved, tapering spine-like, with bulbous base bearing spine but no lamella; left conjunctival sclerite with short straight spine; right conjunctival sclerite with one short and one long, curved spines; base of vesica with a short spinous process (unless a second spine of left conjunctival process has been confused); vesica bent abruptly at midlength to form incomplete loop, with short digit at bend (Fig. 18C).

Elytrous female. Colour like male, elytra black.

Base of labrum not tumid in profile but salient above apex of clypeus; maxillary plates without erect macrosetae or tubercle; bucculae with tubercle, without macroseta.

Disc of pronotum punctate, lateral margins of disc roundly convergent anteriorly, tumid posteriorly; posterior margin mostly straight but tumid at angles.

Elytra highly convex in profile, punctate (including clavus), venation indistinct except faint 1AN, no overlap; a glabrous furrow along path of vein Sc extending roughly 90% to elytral apices demarcating the costal cell which is inclined at roughly 30° below horizontal to form a sloping, tapering shelf a little wider than depth of hind femora; hypocostal lamina at least 1.5 times width of hind femora and inclined at roughly 45°, extending 90% to elytral apices.

Gonapophyses provided with with five teeth.

Distribution. Known from a single locality at 300 m a.s.l. near Col d'Amieu where it is sympatric with *H. rhinatum* (Fig. 22B).

Notes. The S3 organ seems subcircular but may have a sclerotized posterior rim. It may be intermediate between the subcircular or oval form lacking a sclerotized posterior rim but possessing anterior peripheral setae (*H. hypselosomatium* group) and the semicircular form with a sclerotized posterior margin and lateral projections of most other species. The presence of a spine but no lamella at the base of left paramere is also intermediate.

Hypselosoma ndouaensis sp. nov.

(Figs 1E, 2C, 3C, 3L, 8E, 11F,
18D-G, 22B Table 1)

Etymology. From the type locality.

Material. HOLOTYPE male: 22°23'11"S x 166°55'3"E, Cape Ndoua, site 2, 50 m, GBM & PG, 28.xi.2004-8.i.2005, RFIT, QM11877, 2 slides and 1 vial, 16365 (MNHN(EH)). Paratype: 1 f, as for holotype, T165652 (QM).

Diagnosis. The small size, flat submacropterous form, flat, setigerous clypeal organ, remigial punctuation limited to margins of veins and

presence of an anal cell distinguish males of this species.

Description. *Submacropterous male.* Head dark brown, pronotal collar brown, disc dark brown, clavus and costal cell brown, remainder of fore wing black-brown becoming paler apically; antennae, labrum, maxillary plates, labium and legs dark brown except tarsi and apices of femora and tibiae lighter.

Overall profile flat with distinctly explanate costal margins (Fig. 1E).

Base of labrum not tumid in profile, equal to clypeal plane, less salient than setae of clypeal organ; maxillary plates without erect macrosetae; bucculae without erect macroseta, with tubercle; clypeal organ present, pit near anterior margin in flat area bearing many erect, incurved setae, flat area not coplanar with labrum in profile because clypeus protrudes gently at posterior margin of clypeal organ.

Disc of pronotum finely punctate (indistinct at 80x magnification), gradually constricted anteriorly, lateral margins sinuously convergent, calli not tumid, posterior margin straight, angles not tumid (Fig. 3C); medial ends of transverse mesosternal carinae acute.

Forewing (Fig. 8E) strongly explanate; costal cell sclerotized, impunctate, flat but merging with wide, inclined, explanate, subcostal margin creating a broad furrow midway between vein Sc and costal edge; hypocostal lamina 1.5 times depth of hind femora; glabrous furrow along posterior margin of costal cell extending 80% to apex; fine punctuation along remigial veins; membrane reduced to width equal to that between 1AN and Cu; clavus sclerotized in proximal half, impunctate, anal cell present, 1AN and 2AN clearly evident in distal half. Hindwing reduced, reaching T9.

S3 organ (Fig. 11F) semicircular, with sclerotized posterior margin, with short sclerotized projections from lateral angles, right larger than left, without anterior peripheral row of long setae, with many long setae adjacently posteriorly on tumidity of S3 and on S4.

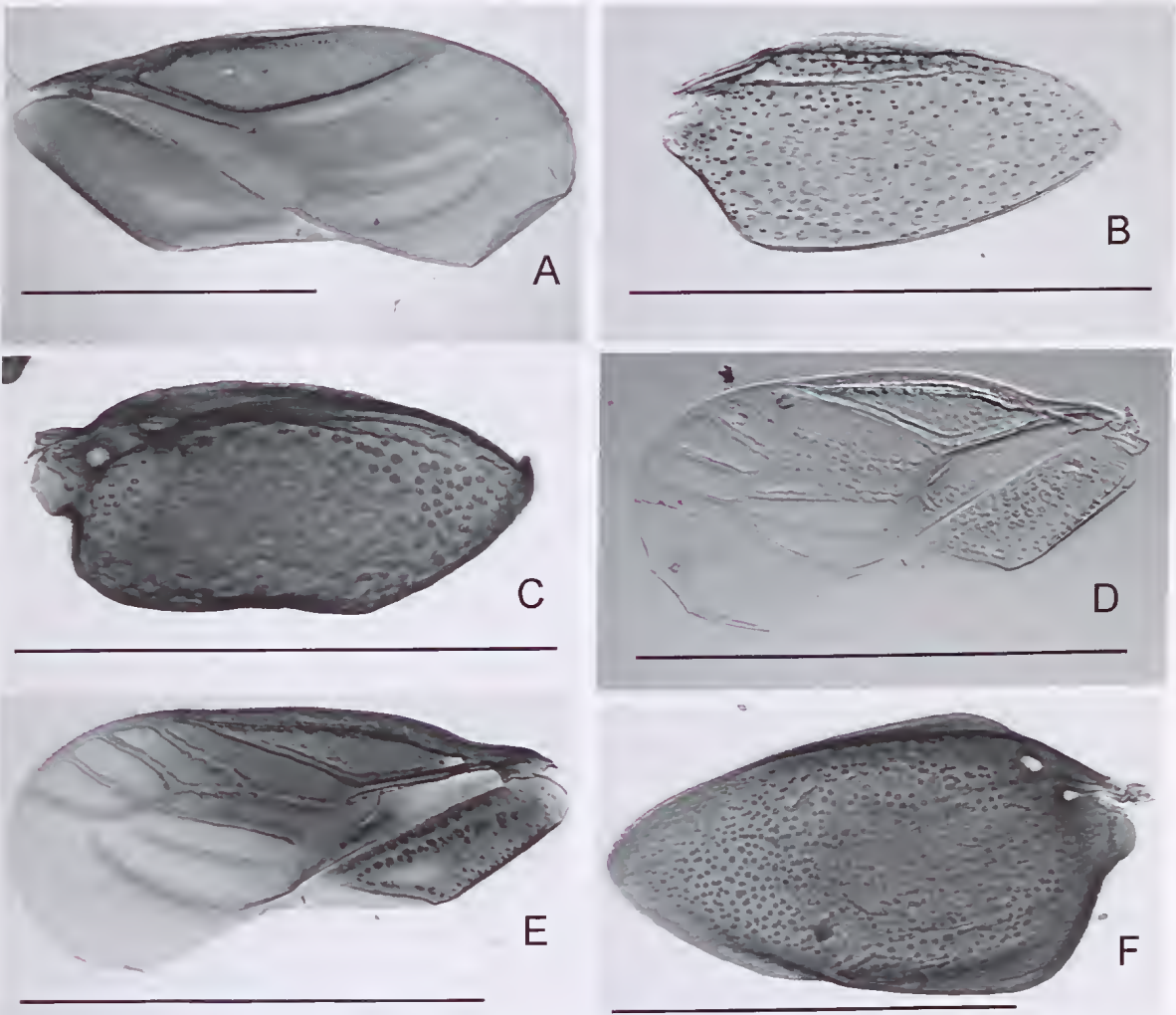


FIG. 9. Fore wings, dorsal, *Hypselosoma* species, A-E, male, F, female. A, *H. oculatum* Reuter; B, *H. rembaiensis* sp. nov.; C, *H. touhoensis* sp. nov.; D, *H. trachyacanthatum*, sp. nov.; E, *H. triacanthatum* sp. nov.; F, *H. hypselosomatum* sp. nov. Scale lines 1 mm.

Genitalia. left process of T9 short, tapering to round apex; left LT9 present as a medially procurved arm with expanded apex; right LT9 with blunt apex lacking hyaline digit, with blunt subapical lobe (Fig. 18D); distal lobe of right paramere slender, spinous, twice as long as proximal lobe (Fig. 18E); left paramere very long (twice as long as spinous lobe of right paramere), spine-like, with bulbous base lacking both lamella and spine (Fig. 18F); left conjunctival sclerite with minute spine; right conjunctival sclerite with very long, thick,

spinous process bearing four serrations subapically; base of vesica with short spinous process (one third left paramere); vesica sinuous, with rounded expansion before midlength (Fig. 18G).

Elytrous female. Colour black except head uniformly dark brown, antennae, labrum, maxillary plates, labium and legs dark brown but tarsi and apices of femora lighter.

Moderately convex in profile (Fig. 2C).

Base of labrum not tumid in profile, equal to clypeus; maxillary plates without erect macrosetae; bucculae with tubercle, without erect macroseta.

Disc of pronotum impunctate, constricted at midlength, lateral margins roundly converging anteriorly in association with tumid calli, straight and parallel in posterior half (not roundly tumid); posterior margin straight (Fig. 3L), not tumid except angles projecting a little posteriorly.

Elytra moderately convex in profile, punctate (including clavus), venation not evident, no overlap; glabrous furrow along path of vein Sc extending 90% to elytral apices demarcating costal cell as an almost horizontal, concave, tapering shelf subequal to hind femoral depth; hypocostal lamina 1.5-2 times depth of hind femora, inclined at roughly 45°, extending 90% to elytral apices.

Distribution. Known from one locality at 40 m a.s.l. at the southern tip of Grande Terre (Fig. 22B).

Hypselosoma nordiensis sp. nov.
(Figs 1F, 2D, 3D, 3M, 4E, 8F,
11G, 19A-C, 23B, Table 1)

Etymology. From the type locality.

Material. HOLOTYPE male: 22°19'23"S x 166°54'55"E, Forêt Nord, site 2, 200 m, GBM & CB, 2.xii.2004, RP, QM11832, 4 slides 16366 (MNHN(EH)). Paratype: 5 m, T165660-4 and 7f, T165653-9, as for holotype. Other material: 1 m, 22°5'49"S x 166°40'40"E, Rivière Bleue, main forest Kaori track, 160 m, GBM, 17.xi.2001, RP, trees & logs, QM8731, T165747; 3f, same site, GBM, 11.xi.2000, RP, QM9954, T165744-6; 5f, same site, GBM, 19.xi.2002, RP, trees and logs, QM11202, T165756-60; 3 m, 5f, 22°14'52"S x 166°49'51"E, Pic du Pin, site 1, 280 m, GBM & CB, 26.xi.2004, RP, QM11782, T165748-55 (QM).

Diagnosis. The convex form, weakly elevated, setigerous clypeal organ, sclerotized and punctate clavus without an anal cell, mostly unsclerotized and non punctate corium and two pale sections on all legs distinguish males of this species.

Description. *Macropterous male.* Black to dark brown, apex of scutellum sometimes pale; antennae, labrum, maxillary plates and labium dark brown; legs dark brown except apices

of tibiae and basal tarsomeres light brown; forewing membrane black to dark brown proximally becoming brown distally (costal cell dark) as well as pale triangular area at base of remigium between costal cell and clavus.

Profile convex but less than in members of the *H. hypselosomatum* group (Fig. 1F).

Base of labrum not tumid in profile but salient above plane of (unflattened) clypeal apex and less salient than setae of clypeal organ; maxillary plates without erect macrosetae; bucculae without macroseta, with tubercle; clypeal organ small, weakly elevated, submarginal hole surrounded by many erect, incurved setae (Fig. 4E).

Disc of pronotum coarsely and finely punctate, weakly constricted anteriorly, lateral margins sinuously convergent, calli not tumid, posterior margin sinuously convex (Fig. 3D); medial ends of mesosternal transverse carinae acute.

Forewing (Fig. 8F) moderately explanate, costal cell sclerotized, impunctate (ventrally granulate in slide mounts), flat but depressed between vein Sc and inclined, explanate subcostal margin which is 2 membranous-vein widths in dorsal view; hypocostal lamina about 1.5 hind femoral depths; glabrous furrow along posterior margin of costal cell; corial cells (other than costal cell) not sclerotized except cell Sc+R+M posterodistally (with about six punctures), trapezoidal cell not sclerotized but with one puncture posterobasally; clavus sclerotized and punctate, cell obscured, 1AN and 2AN barely discernible.

S3 organ (Fig. 11G) oval, with (probably) sclerotized posterior margin projecting briefly from lateral angles, right projection T-shaped and larger than left, without peripheral row of long setae anteriorly, with many long setae posteriorly on tumidity of S3 and on S4.

Genitalia. left process of T9 short, tapering, with rounded apex; left LT9 present as a medially procurved arm; right LT9 with lobate apex lacking hyaline digit, provided with a triangular process on ventral margin at two thirds from base (Fig. 19B); spinous distal lobe

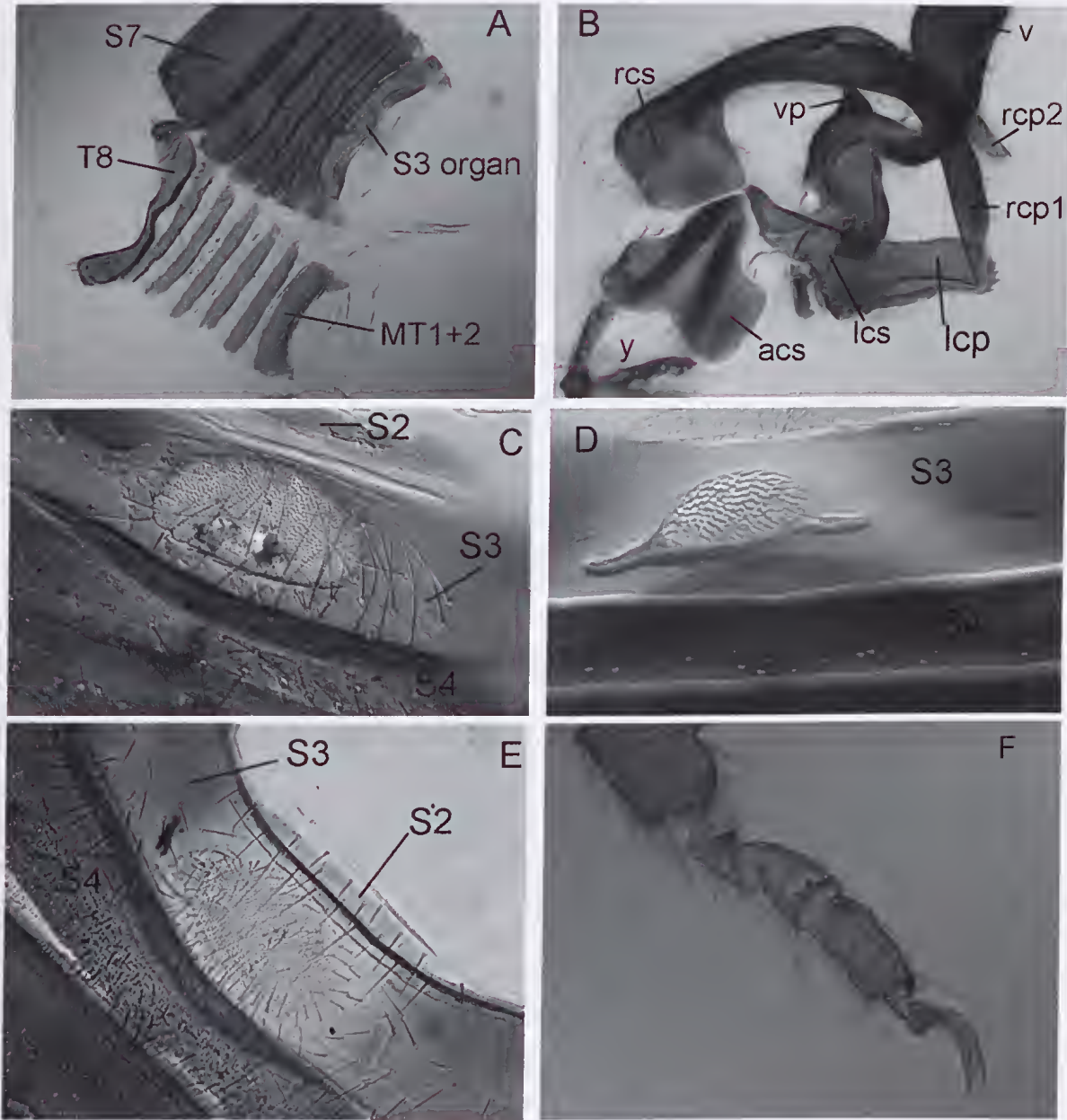


FIG. 10. Males. A-B, *H. hypselosomatum* sp. nov.; A, dissected pregenital abdomen on slide, B, conjunctival sclerites; C, organ on third abdominal sternum, *H. koghiensis* sp. nov.; D, *H. chorizobregmatum* sp. nov., same; E, *H. oculatum* Reuter, same; F, unswollen midtarsus, *H. touhoensis* sp. nov. acs, anterior conjunctival sclerite, lcp, left conjunctival process; lcs, left conjunctival sclerite, rcp, right conjunctival processes; rcs, right conjunctival sclerite, v, vesica, vp, vesical process; y, y sclerite.

of right paramere twice as long as proximal lobe; left paramere curved, tapering, spine-like, with bulbous base bearing a spine but no lamella (Fig. 19A); left conjunctival sclerite with two short processes, longer process spinous and proximally curved, shorter process half as long, spinous, bearing a biserrate basal flange (Fig. 19C); right conjunctival sclerite provided with one process, subequal in length to left paramere, stout and spiculate proximally, abruptly constricted at midlength into broadly tapering spine; vesical base with spinous process subequal to longer process of left conjunctival sclerite (Fig. 19C); vesica bent abruptly near midlength into loop, with short widening or projection at bend.

Elytrous female. Mostly black; labrum, maxillary plates and labium dark brown; legs dark brown except apices of tibiae and basal tarsomeres light brown. Moderately convex in profile (Fig. 2D).

Base of labrum tumid in profile and salient above apex of clypeus; maxillary plates without erect macrosetae; bucculae with tubercle, without macroseta.

Disc of pronotum punctate, lateral margins roundly convergent anteriorly, tumid posteriorly; posterior margin mostly straight, not tumid except at angles (Fig. 3M).

Elytra moderately convex in profile, coarsely punctate (including clavus), venation faint, no overlap; glabrous furrow along path of vein Sc extending roughly 90% to elytral apices demarking costal cell which is inclined at roughly 30° below horizontal to form a sloping, tapering shelf a little wider than width of hind femora; hypocostal lamina at least 1.5 times depth of hind femora and inclined at roughly 45°, extending 90% to elytral apices.

Gonapophyses provided with 5 teeth.

Distribution. Known from three localities (four sites) about 35km apart and at 120-210 m a.s.l. near the southern end of Grande Terre. It is sympatric with *H. bleuensis*, *H. dicroum*, *H. oculatum*, *H. onceronotatum* and possibly *H. hypselosomatum* at various localities (Fig. 23B).

Notes. The colour of the male legs is distinctive in that the pale femoral apices and basal (but not apical) tarsomeres form two pale spots on each leg. The vesica, vesical process, left conjunctival sclerite and right paramere are similar to those of *H. triacanthatum*. The clypeal organ hole is submarginal but not embraced by salient lobes nor in a flat area. In this, it is similar but less elevated than the clypeal organ of *H. oculatum*. The male S3 organ may not be strictly semicircular and may share a fragmentary sclerite (perhaps an artifact) on left side with *H. dicroum*. The presence of a basal spine but no lamella of the left paramere also occurs in *H. haplacanthatum* and may be intermediate between *H. hypselosomatum* group and other species.

Hypselosoma oculatum Reuter, 1891
(Figs 1G, 2E, 3E, 5, 6H, 9A, 10E,
11H, 19D-G, 23C, Table 1)

Material. HOLOTYPE not seen. 1 m on slide, 5 miles (sic) SE La Foa, C.L. Remington, 9 April 1945 (AMNH). 1 m, 22°5'15"S x 166°26'41"E, Dzumac Road, GBM, 5.xii.2003-26.i.2004, RFIT, QM11467, T165678; 1 m, 1 nymph, T65714-5, 22°11'3"S x 166°31'59"E, Forêt de la Thy Reserve, M&C, 21.v.1984; 5 m, 5 f, T165668-0, T165672-6, T165716, 22°19'23"S x 166°54'55"E, Forêt Nord site 2, QM party, 200 m, 3.xii.2004, R handpicking, QM11829; 1 m T165677, 20°57'22"S x 165°17'27"E, Pic d'Amoa, N slopes, 500 m, GBM, 27.xi.2003-30.i.2004, RFIT, QM11482, T165677 (QM).

Diagnosis. The large size, convex profile, strongly elevated setigerous clypeal organ and reddish spots on the frons distinguish males of this species.

Redescription. *Macropterous male.* Mostly black; head black except for pair of reddish spots which sometimes merge to form a band across frons; antennae, labrum, maxillary plates, labium and legs mostly dark brown but tibiae and tarsi paler (fore tibiae wholly pale, mid tibiae mostly pale and hind tibiae distally pale), forewing membrane black proximally becoming black-brown distally (costal cell black). Profile highly convex (Fig. 1G).

Base of labrum not tumid in profile, equal to clypeal apex but less salient than setae of clypeal organ; maxillary plates with 2-3 macro-

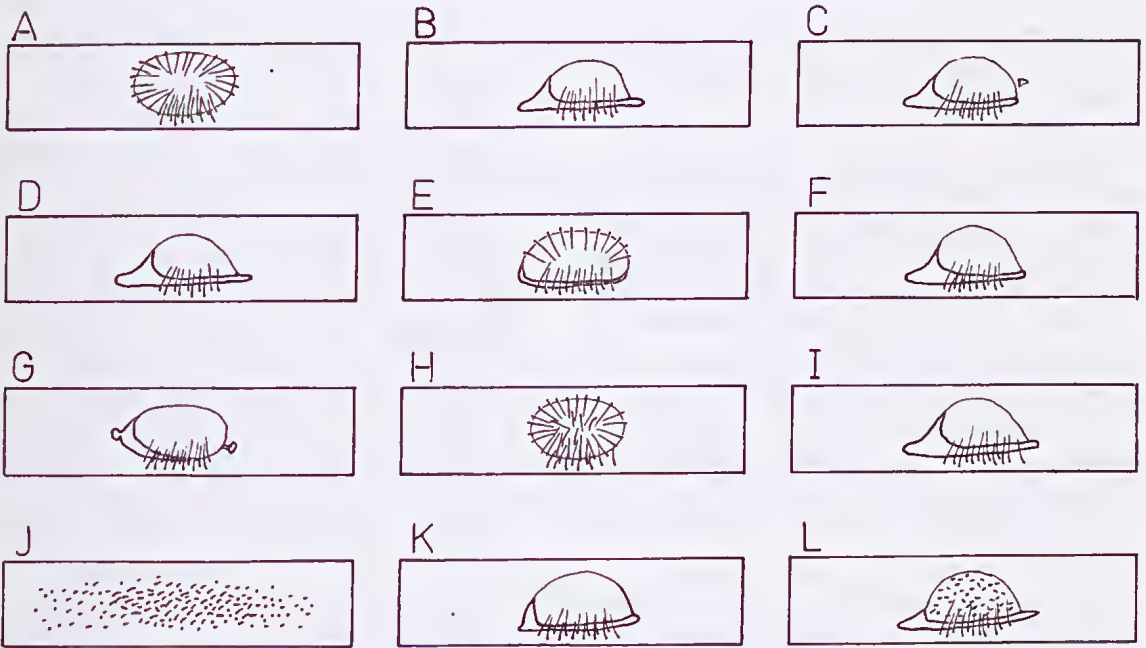


FIG. 11. Male third abdominal sternum with medial organ, schematic, anterior margin upper, *Hypselosoma* species. A, *H. amieuensis* sp. nov.; B, *H. chorizobregmatum* sp. nov.; C, *H. dicroum* sp. nov.; D, *H. gephyrobregmatum* sp. nov.; E, *H. haplacanthatum* sp. nov.; F, *H. ndouaensis* sp. nov.; G, *H. nordiensis* sp. nov.; H, *H. oculatum* Reuter; I, *H. rembaiensis* sp. nov.; J, *H. loulioensis* sp. nov.; K, *H. trachyacanthatum* sp. nov.; L, *H. triacanthatum* sp. nov.

setae setae aligned with basal macrosetae of labrum; bucculae with 2-3 macroseta and rugose tubercle; clypeal organ present as small submarginal hole elevated on a conical prominence surrounded by many erect incurved setae (Fig. 5); ocular setae absent.

Disc of pronotum finely punctate (not easily observed); lateral margins convexly and smoothly convergent (not sinuous), calli tumid, posterior margin convex (Fig. 3E); medial ends of mesosternal, transverse carinae square (perhaps acute but not tapering).

Forewing (Figs 9A, 10E, 11H) not explanate; costal cell sclerotized, not concave (hence margin not explanate), impunctate but finely granulate ventrally; hypocostal lamina as wide as hind femoral width; glabrous furrow along posterior margin of costal cell; corium mostly membranous, with some dark areas perhaps indicating incipient sclerotization associated with fine punctation on margins of

veins immediately distal to trapezoidal cell; membrane fully developed; anal cell reduced to area of trapezoidal cell, remainder sclerotized and finely granulate ventrally.

Hind tibiae with anterodorsal macroseta at 10% from base and posteroventral macroseta at 40% from base in addition to 2-3 distal non-apical macrosetae (Fig. 6H).

S3 organ is oval granulate area with a single peripheral row of long setae plus shorter seta within oval area; with cluster of long setae adjacently on posterior tumidity of S3.

Genitalia. left process of T9 absent; left LT9 is present as a medially bent arm; right LT9 with round non-hyaline apex, with pair of lobate processes subapically, lacking spinous process at midlength (Fig. 19F); distal lobe of right paramere digitate (not spinous), longer than proximal lobe (Fig. 19D); left paramere stout, tapering (but not spinous) arm with bifid apex, without subbasal spine and lamella (Fig. 19G);

left conjunctival sclerite without process; right conjunctival sclerite with very long, sinuously recurved, spinous process; vesica recurved, without basal process, with short branch distally (Fig. 19E).

Elytrous female. Mostly black; head black except for pair of reddish spots which sometimes merge to form a band across frons; antennae, labrum, maxillary plates, labium and legs mostly dark brown but tibiae and tarsi paler (fore tibiae wholly pale, mid tibiae mostly pale and hind tibiae distally pale); elytra black. Profile highly convex (Fig. 2E).

Base of labrum not tumid in profile, barely more salient than clypeus; maxillary plates with 2-3 short, erect macrosetae; bucculae with tubercle bearing 1-2 erect macrosetae; ocular setae absent.

Disc of pronotum impunctate, lateral margins of disc linearly converging anteriorly (truncate not rounded), parallel posteriorly; posterior margin straight, posterior angles not tumid.

Elytra highly convex in profile and in section (with vertical sides), impunctate; no glabrous furrow marking path of vein Sc and costal cell not abruptly changing plane from remainder of elytra; costal margin (vein C) with low (as high as wide), rounded carina extending 60% to apices; hypocostal lamina a little wider than width of hind femora, extending 60% to apices; venation weakly evident distally as several raised parallel lines in dorsal view; elytra overlap in distal half, variably right on left and vice versa.

Distribution. This species is known from five, disjunct localities at 150-700 m a.s.l. mostly in the southern half of Grande Terre. It is sympatric with *H. nordiensis*, *H. rembaiensis*, *H. hypselosomatum* (or a close relative at Forêt Nord) and perhaps *H. koghiensis* (Mt Koghi) (Fig. 23C).

Notes. It is believed that the male from Forêt de la Thy listed above was transposed with a male of *H. amieuensis* from Table Unio in labeled vials during observations for this paper but this error was rectified.

The absence of ocular setae (arising on the frons and overlying the eyes) is very unusual in Hypselosomatinae and was observed in several specimens.

The holotype of *H. oculatum* was listed as 'D.A. Montadon (Coll. auctoris)' in Reuter (1891) and as 'Holotype brachypterous female [Reuter], Mt Kogui, New Caledonia (D.A. Fennel)' in Emsley 1969. It was not found through enquiries at Hensinki and London Museums. The author does not know whether Wygodzinsky saw the type of Reuter or the macropterous male described by Poppius. Of the latter, Emsley (1969) wrote 'Macropterous male, Mt Kogui (probably lost)'. The holotype may be with other material of Montadon in Bucharest Museum (Rédei, pers. comm.). Wygodzinsky's (1959) material was listed as '7 miles southeast of Foa, New Caledonia, under a stone, 22.iv.1945, collector C.L. Remington' which is not precisely the same as the material from AMNH examined here.

The Queensland Museum specimens listed above match the slide of a dissected male used by Wygodzinsky in his description, including dimensions of appendages. They also match the description by Wygodzinsky (1959), particularly the diagnostic male genitalia and red frons but dimensions are smaller. Wygodzinsky gave the length of his male as 3.2 mm, which is 35% larger than the males studied here (2.38 mm, range 2.17-2.51, n = 9), larger than the 19 species newly described here or any previously described species although Wygodzinsky said the elytrous female of *H. pauliana* Wygodzinsky is 2 mm suggesting the male, if macropterous, is 2.4 mm. However, in the same paper Wygodzinsky made an error when describing *H. hickmani* Wygodzinsky, 1959, the only species in Tasmania, as explained by Hill (1980). In essence, Wygodzinsky gave a length of 2.45 mm for *H. hickmani* when the true length is closer to 1.8 mm, an overestimate of 36%. Measurement of the holotype in the British Museum confirmed the error. Hence it is concluded that some of the dimensions in Wygodzinsky (1959) are erroneous and that the specimen described by him is conspecific with the Queensland Museum material listed above.

Reuter said the head of *H. oculatum* has a 'furrugineis' band between the eyes, rostrum and antennae. In the other 19 species described here the head is concolourous (black, black-brown or brown) or the frons and vertex are slightly paler than the clypeus. However, this difference in colour is slight and variable whereas in the material examined above two well-defined reddish patches (sometimes coalescing) consistently occur on the otherwise black head. In *H. koghiensis*, from the generic type locality of Mt Koghis, the head is entirely and uniformly brown in contrast to the remainder of the body being black. The only other species known to have a red frons is *H. hirashimai* Esaki and Miyamoto, 1959. Esaki and Miyamoto (1959) described a red area on the frons of the female and paler area in males.

On locality, size, convexity and lack of elytral punctation, two species among the 20 studied here were strong contenders to be *H. oculatum*, namely that described above and *H. koghiensis*. The latter occurs at Mt Koghis while the former occurs nearby at Forêt de la Thy Reserve. However, seven other species occur in a 20km radius, namely *H. bleuensis*, *H. chorizobregmatum*, *H. dicroum*, *H. elytratum*, *H. mouensis*, *H. nordiensis* and *H. rembaiensis*.

Reuter's figure 16A, a dorsal view of his elytrous female, indicates three parallel longitudinal lines distally on each elytra (traces of veins M, Cu and 1AN), linearly rather than roundly truncated anterior angles on the pronotal disc, straight parallel lateral margins of the posterior half of the disc and a relatively acute, prominent rather than bluntly rounded clypeus. These four characters best match the specimens described above among the 20 species studied here. *H. koghiensis* has two parallel lines proximally on the relatively shiny elytra not three distally, roundly truncated anterior angles on the disc, convex lateral margins on the disc posteriorly and a less prominent clypeus.

Reuter gave the overall length of his elytrous female as 1.8 mm compared with 2.08 mm observed here for the specimens described above (12% longer or a possible error by Reuter of -7.8%). All the other species described

here have shorter elytrous females with the closest being *H. amieuensis*, *H. elytratum* and *H. koghiensis* at 1.7 mm and *H. nordiensis* at 1.6 mm. The convexity in lateral profile of *H. nordiensis* is much less than Reuter's figure 16B and it has inflated posterior angles on the disc and more rounded anterior angles in dorsal view. Although *H. elytratum* and *H. amieuensis* have strong convexity in profile they lack the four characters mentioned in the preceding paragraph and have concolourous heads.

It is concluded that the specimens described above and that described by Wygodzinsky belong to *H. oculatum* while *H. koghiensis* from Mt Koghis, the generic type locality, is a sympatric species. Many examples of sympatry in New Caledonia *Hypselosoma* species are listed below.

H. oculatum differs from *H. hypselosomatum* group in the following characters: presence of clypeal organ; linear not round truncation of anterior disc angles; greater male claval sclerotization (small anal cell); left paramere is apically bifid and lacks a lamella and associated spine basally; distal lobe of right paramere is much longer than proximal lobe; left conjunctival sclerite lacks a spatulate process; vesica branches distally and lacks a subbasal process; left process of T9 is absent (although it is small in some members of *H. hypselosomatum* group); and apex of right LT9 is not hyaline and digitate.

The left paramere was observed acting as a wing clip restraining the left wing in one male. The vesical branch may act as a scribe against the margin of genital capsule.

Hypselosoma onceronotatum sp. nov.
(Figs 2F, 23D, Table 1)

Etymology. Greek, provided with a swollen back (pronotum).

Material. HOLOTYPE female: 22°5'49"S x 166°40'40"E, Rivière Bleue, main forest, Kaori track, 120 m, RR, 21.v.1987, QM4352, carded, 16367 (MNHN(EH)). Other material: 1f, same site, GBM & DC, 25.v.1984, RB, QM4278, T165761; 1f, 22°17'0"S x 166°53'46"E, Pic du Grand, Kaori W base, site 1, 250 m, GBM & PG, 23.xi.2004, RB, QM11767, T165762 (QM).

Diagnosis. The pronotal disc has distinctively complex topography derived from a faint transverse depression and tumid muscles scars (calli), posterior angles and margin.

Description. *Male.* Unknown

Elytrous female. Colour black except head uniformly dark brown, antennae, labrum, maxillary plates, labium and legs mostly dark brown but tarsi and apices of femora and tibiae lighter.

Overall profile is moderately convex (Fig 2F).

Base of labrum not tumid in profile, salient above clypeal plane; maxillary plates without erect macrosetae; bucculae with tubercle, without erect macroseta; clypeal organ absent as in all female *Hypselosoma*.

Disc of pronotum impunctate except in faint, transverse impression posterior to calli; constricted anteriorly; lateral margins of disc roundly convergent anteriorly, straight and parallel posteriorly; calli tumid; posterior margin straight and thick (abruptly rather than roundly deflexed), posterior angles tumid and squarely deflexed.

Elytra highly convex in profile, punctate (excluding base of clavus), venation not evident, no overlap; glabrous furrow along path of vein Sc demarcating costal cell which is inclined at roughly 45° below horizontal to form a sloping, tapering shelf a little wider than depth of hind femora and extending roughly 90% to elytral apices; hypocostal lamina at least 1.5 times depth of hind femora and inclined at roughly 45°.

Distribution. Known from two localities about 30 km apart and at 120-250 m a.s.l. near the south end of Grande Terre. It is sympatric with *H. nordiensis* and *H. dicroum* at Rivière Bleu and with *H. hypselosomatum* at Pic du Grand (Fig. 23D).

Hypselosoma rembaiensis sp. nov.
(Figs 1H, 9B, 11I, 20A-F, 23E, Table 1)

Etymology. From the type locality.

Material. HOLOTYPE male: 21°34'46"S x 165°50'34"E, Mt Rembai, 750 m, GBM & DC,

9.v.1984, RB, QM4259, 4 slides, 16368 (MNHN(EH)). Other material: 1 m, 21°36'36"S x 165°48'37"E, Col d'Amieu west slope, 470 m, GBM, 25.xi.2003-27.1.2004, RFIT, QM11475, T16571, 3 slides and vial; 1 m, 21°24'59"S x 165°28'11"E, Col de Rousettes, forestry track, 490 m, RR, 29.v.1987, RB, QM4353, T165692; 4 m, 22°1'54"S x 166°27'59"E, Dzumac Rd junction, 950 m, GBM, 5.xii.2003-26.i.2004, RFIT, QM11465, T165685-8; 1 m, same site, GBM, 26.i.2004, RB, QM11534, T 165691; 2 m, Forêt Nord summit, site 1, 480 or 600 m, GBM & PG, 1.xii.2004-9.i.2005, RFIT, QM11883, T 16589-90; 1 m, 21°33'15"S x 165°46'21"E, Table Unio summit, 1000 m, GBM & DC, 10.v.1984, RB (moss), QM4261, T165717 (QM).

Diagnosis. The convex, elytrous form and flat setigerous clypeal organ distinguish males of this species.

Description. *Elytrous male.* Black except antennae, labrum, maxillary plates, labium and legs dark brown; tarsi and apices of femora marginally paler in some individuals.

Overall profile is moderately convex (Fig. 1H).

Base of labrum not tumid in profile, more salient than flat clypeal apex, less salient than setae of clypeal organ; maxillary plates smoothly convex, without erect macrosetae; bucculae without erect macroseta, with tubercle (rugose apically); clypeal organ present in flat, subcircular area on anterior margin bearing many erect, incurved setae. Ocelli present.

Disc of pronotum punctate (indistinct at 80x magnification), abruptly constricted anteriorly, anterior halves of lateral margins roundly convergent, calli not tumid, posterior halves tumid; posterior margin straight, posterior angles tumid.

Medial ends of mesosternal transverse carinae acute.

Elytra (Fig. 9B) moderately convex in profile, punctate (including costal cell and hypocostal lamina), venation not evident, no overlap; glabrous furrow along path of vein R extending almost 90% to elytral apices demarcating costal cell which is inclined at roughly 45° below horizontal to form a sloping, tapering shelf a little wider than depth of hind femora; hypocostal lamina at least 1.5 times width of hind femora and inclined at roughly 45°, extending 90% to elytral apices.

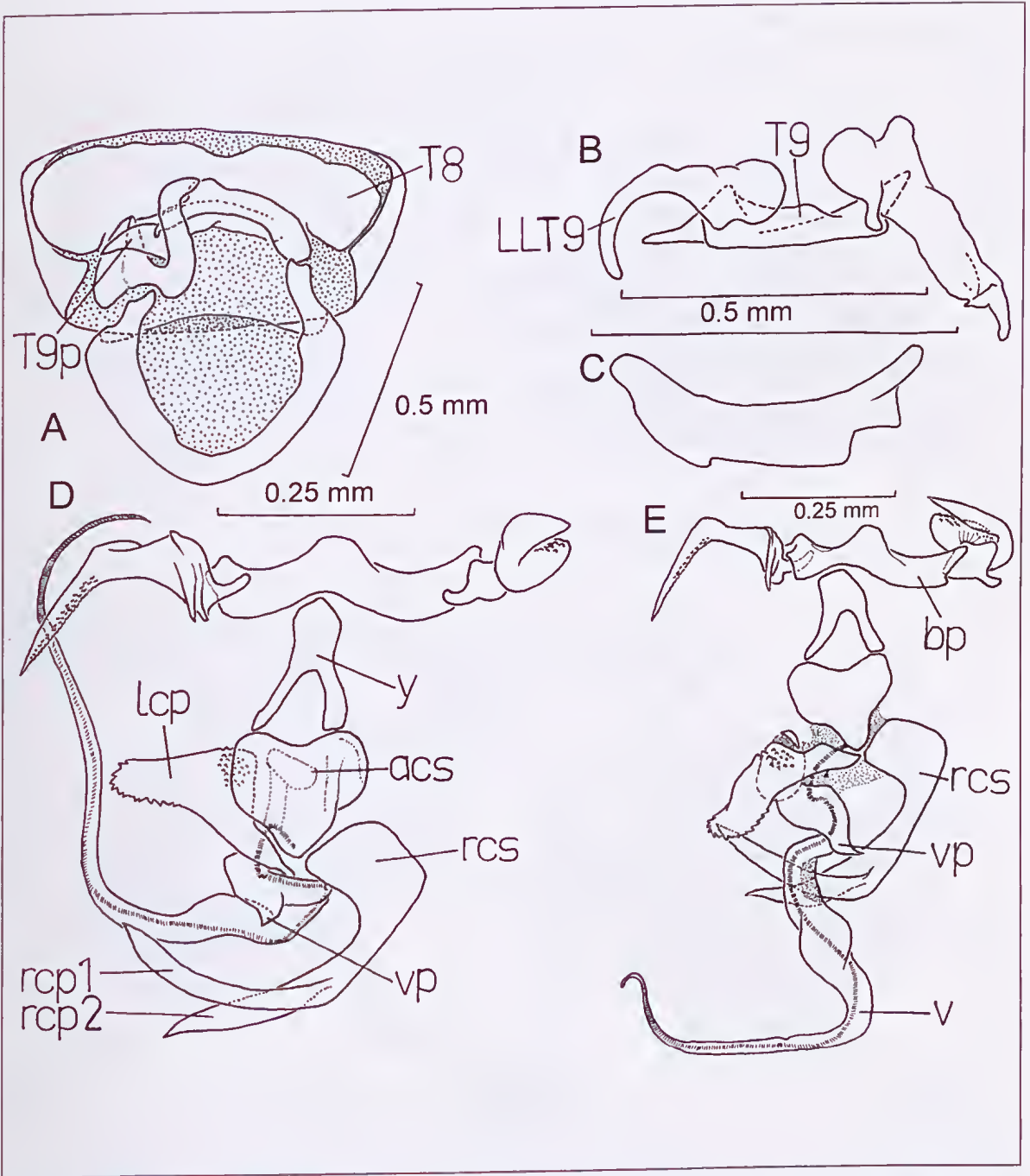


FIG. 12. Male genitalia *Hypselosoma hypselosomatum* sp. nov. A, caudum with aedeagus removed; B, T9 and laterotergites; C, right ninth laterotergite; D, aedeagus, basal plate and parameres (Pic du Grand Kaori site); E, same, another male. acs, anterior conjunctival sclerite; bp, basal plate; lcp left conjunctival process; LLT9, left ninth laterotergite; rcp, right conjunctival process; rcs, right conjunctival sclerite; T8, eighth tergum; T9, ninth tergum; T9p, left process of ninth tergum; v, vesica; vp, vesical process; y, y-sclerite.

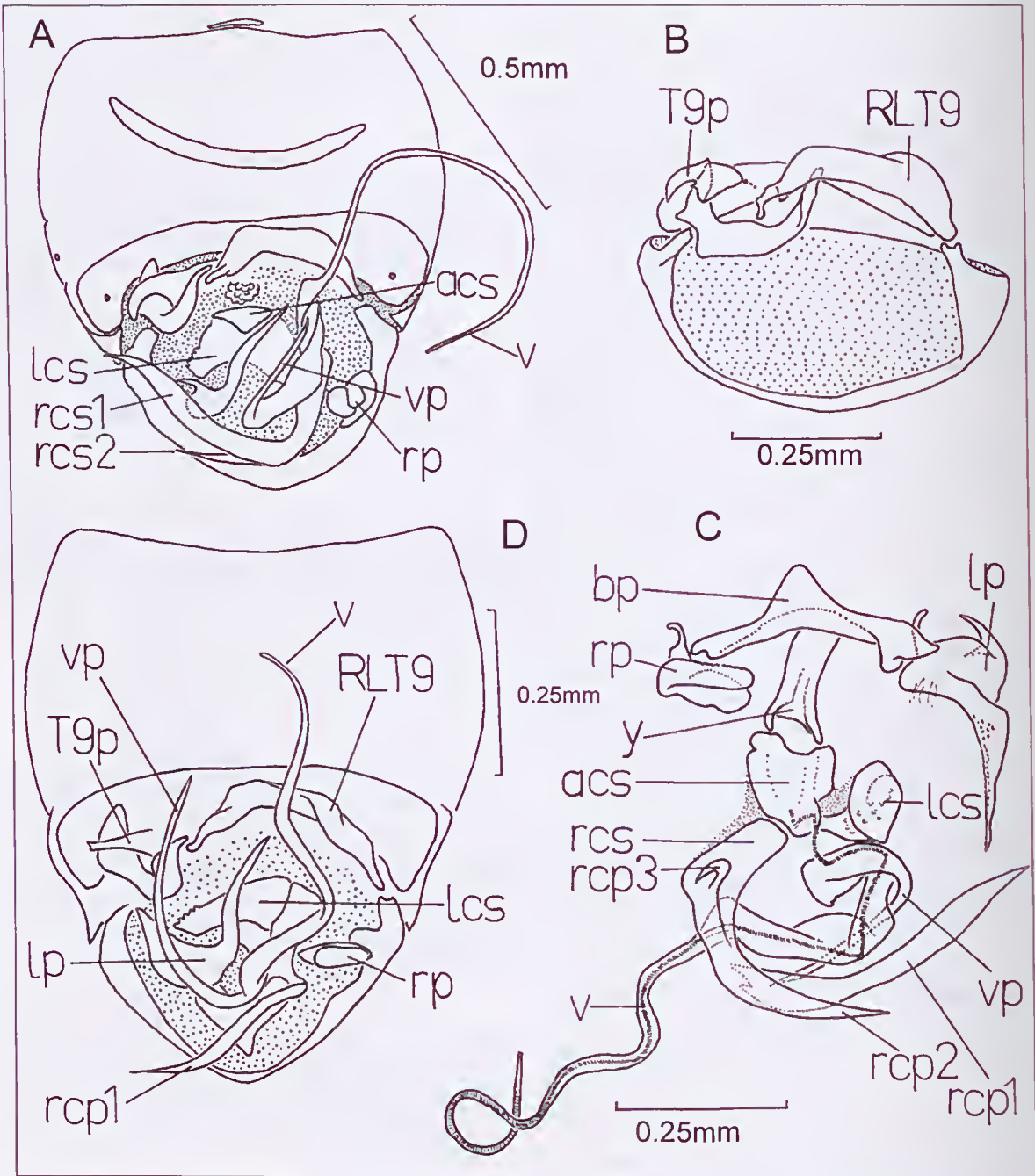


FIG. 13. Male genitalia, A-C, *Hypselosoma amieuensis* sp. nov. A, abdomen, dorsal; B, genital capsule and T9, dorsal; C, aedeagus, basal plate and parameres; D, *H. bleuensis* sp. nov., abdomen, dorsal. acs, anterior conjunctival sclerite; bp, basal plate; lcs, left conjunctival sclerite; lp, left paramere; RLT9, right ninth laterotergite; rcp, right conjunctival process; rcs, right conjunctival sclerite; rp, right paramere; T8, eighth tergum; T9, ninth tergum; T9p, left process of ninth tergum; v, vesica; vp, vesical process; y, y-sclerite.

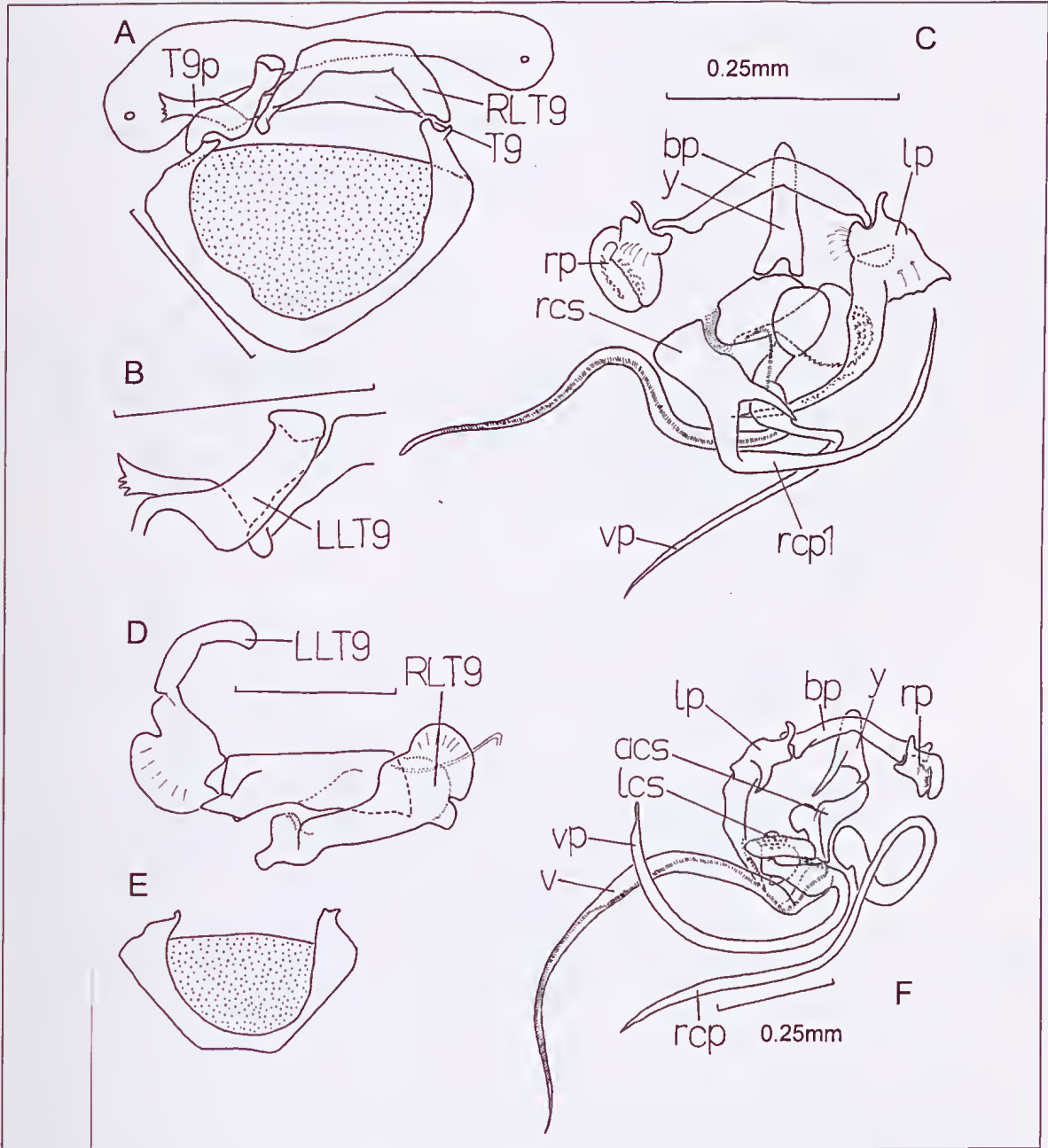


FIG. 14. Male genitalia. A-C, *Hypselosoma bleuensis* sp. nov.; A, T8-9 and genital capsule with aedeagus removed, dorsal; B, left ninth laterotergite and left process of T9; dorsal; C, aedeagus, basal plate and parameres. D-F, *H. koghiensis* sp. nov. D, T9 and laterotergites; E, genital capsule, aedeagus removed, dorsal; F, aedeagus, basal plate and parameres. acs, anterior conjunctival sclerite; bp, basal plate; lcs, left conjunctival sclerite; lp, left paramere; LLT9, left ninth laterotergite; RLT9, right ninth laterotergite; rcp, right conjunctival process; rcs, right conjunctival sclerite; rp, right paramere; T9, ninth tergum; T9p, left process of ninth tergum; v, vesica; vp, vesical process; y, y-sclerite. All scale lines 0.25 mm.

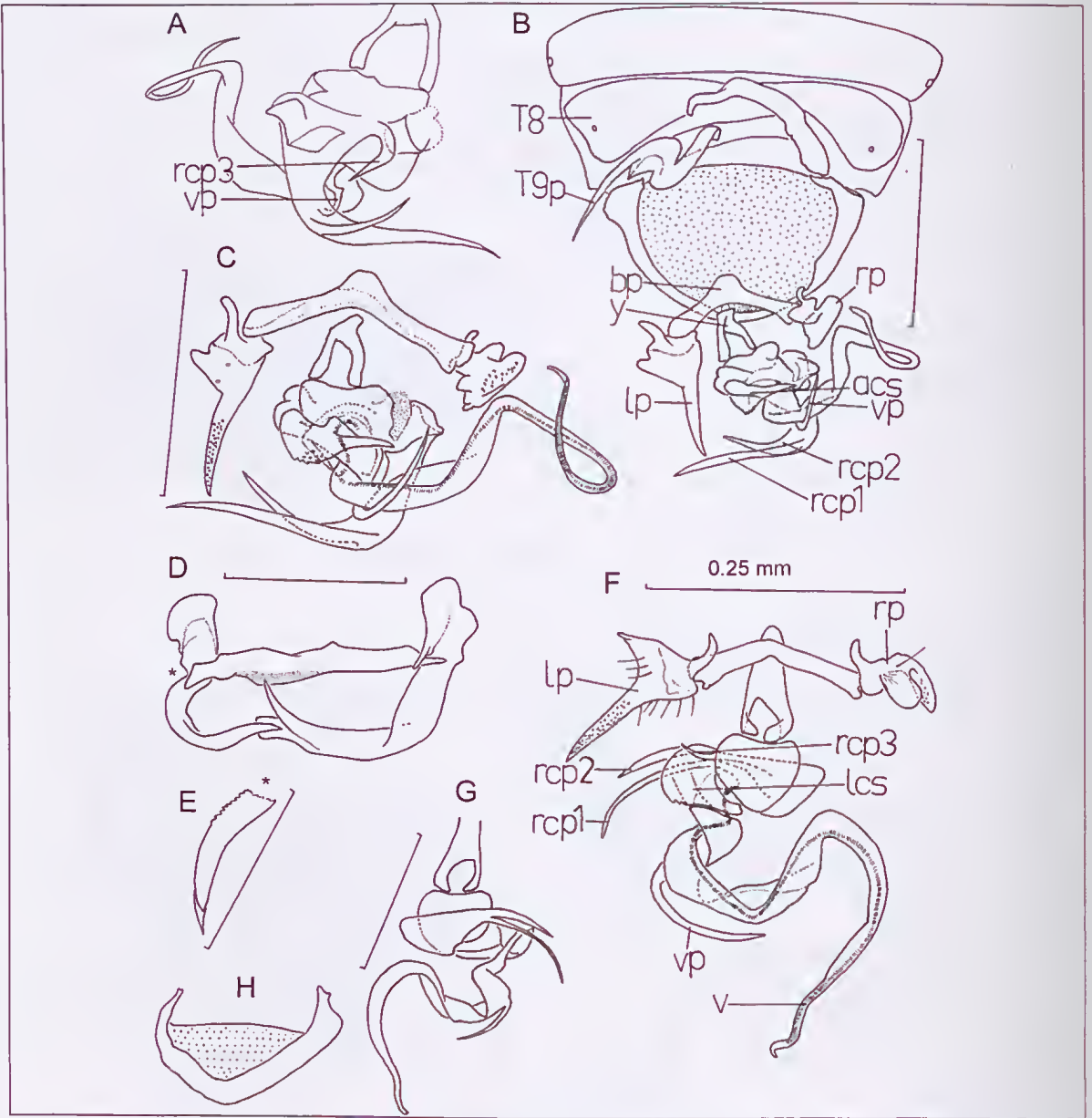


FIG. 15. Male genitalia. A-C, *Hypselosoma mandjeliensis* sp. nov. A, y-sclerite, conjunctiva and vesica with right conjunctival sclerite dorsal; B, caudum, dorsal, aedeagus folded out; C, aedeagus, basal plate and parameres, left conjunctival sclerite dorsal. D-H, *H. mouensis* sp. nov. D, T9 and laterotergites with fracture of left process asterisked; E, fractured apex of left process of T9; F, aedeagus, basal plate and parameres with right conjunctival sclerite ventral; G, aedeagus with right conjunctival sclerite dorsal. acs, anterior conjunctival sclerite; bp, basal plate; lcs, left conjunctival sclerite; lp, left paramere; LLT9, left ninth laterotergite; RLT9, right ninth laterotergite; rcp, right conjunctival process; rcs, right conjunctival sclerite; rp, right paramere; T8, eighth tergum; T9, ninth tergum; T9p, left process of ninth tergum; v, vesica; vp, vesical process; y, y-sclerite. All scale lines 0.25 mm.

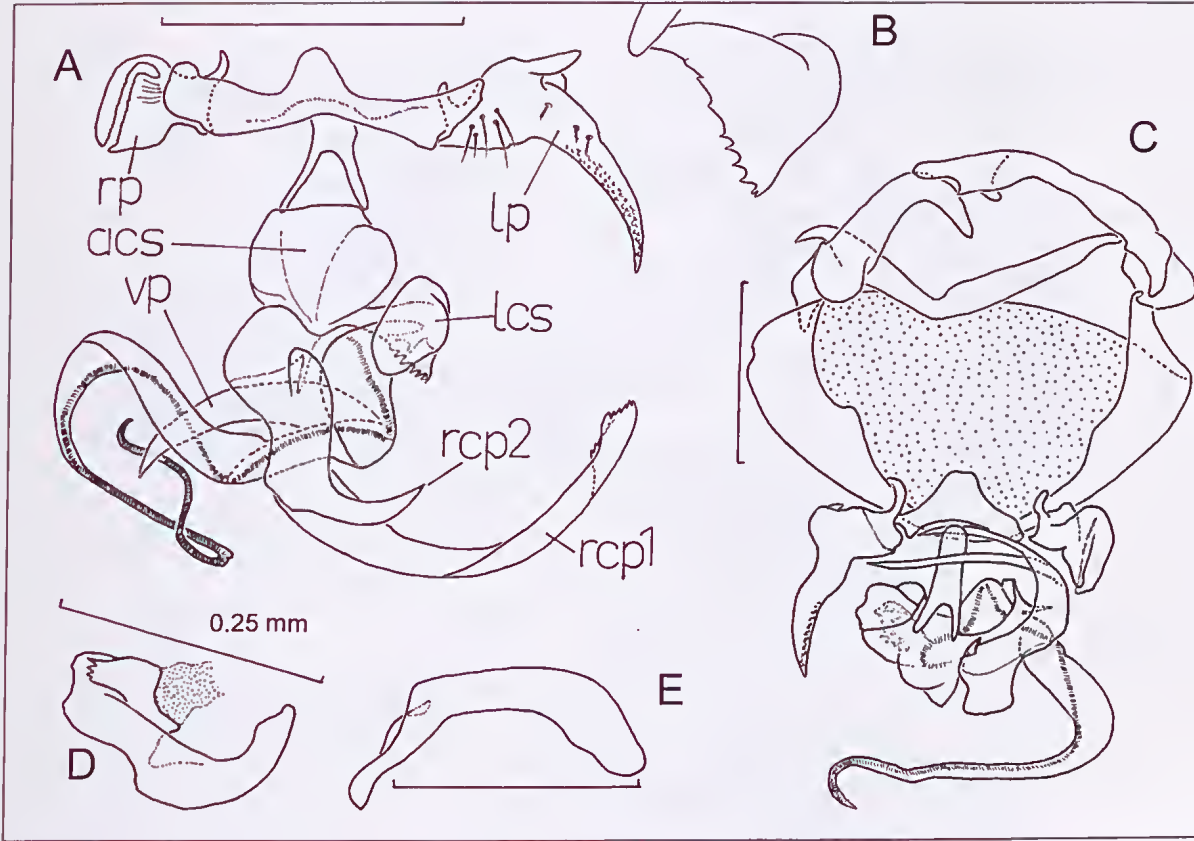


FIG. 16. Male genitalia. A, B, D and E, *Hypselosoma rhinatum* sp. nov. A, aedeagus, basal plate and parameres; B, apex left conjunctival process; D, left process of T9 and laterotergite; E, right ninth laterotergite. C, *H. elytratum* sp. nov., T9 and laterotergites and genital capsule with aedeagus folded out. acs, anterior conjunctival sclerite; lcs, left conjunctival sclerite; lp, left paramere; rcp, right conjunctival process; rp, right paramere; vp, vesical process. Scale lines 0.25 mm.

S3 organ (Fig. 11I) semicircular, with sclerotized posterior margin and projections from lateral angles, right projection widening basally and longer than left, semicircle without anterior peripheral row of long setae, many long setae posteriorly on tumidity of S3 and medially on S4.

Genitalia. left process of T9 short and broad with finely serrate apex; left LT9 present as a medially procurved arm; right LT9 with lobate apex (no hyaline digit), with distal, digitate process on ventral margin (Figs 20A, 20E); distal lobe of right paramere slender, spinous, more than twice as long as proximal lobe (Fig. 20D); proximal lobe of right paramere bilobate with short secondary lobe projecting perpendicular

to axis of distal lobe; left paramere long, with bulbous base, lacking spine and lamella (Fig. 20F); left conjunctival sclerite bearing a short, recurved spine; right conjunctival sclerite bearing a curved, spatulate process with spiculate apex (Fig. 20C), process equal in length to left paramere and four times as long as spine on left conjunctival sclerite (Fig. 20A); base of vesica bearing a spine equal in length to left conjunctival spine (Fig. 20B); vesica stout, with short projection (apex of spiral sheath?) at midlength, probably not abruptly bent at midlength (Fig. 20F).

Female. Unknown.

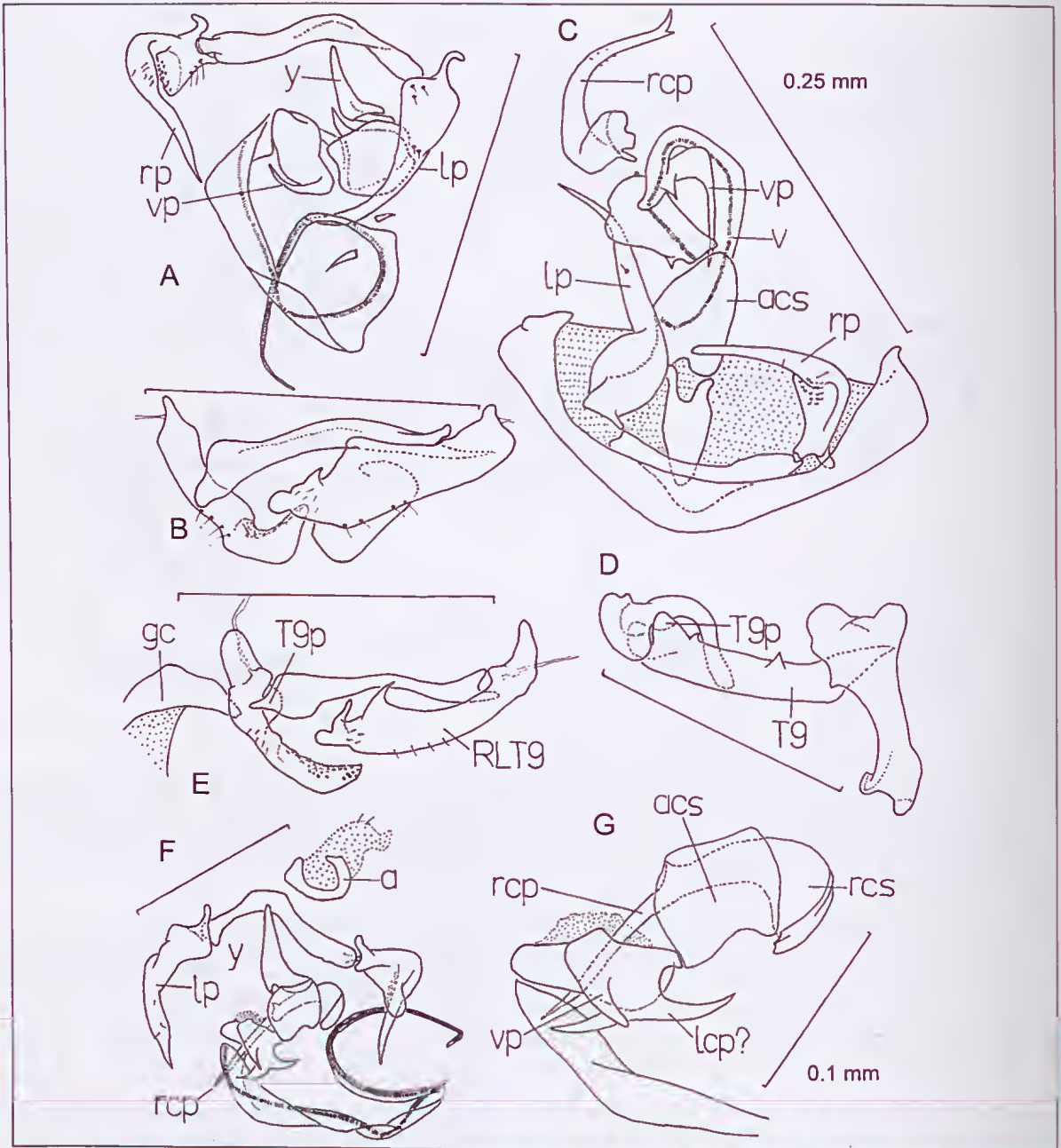


FIG. 17. Male genitalia. A-B, *Hypselosoma chorizobregmatum* sp. nov.; A, aedeagus, basal plate and parameres; B, T9 and laterotergites. C-D, *H. dicroum* sp. nov.; C, genital capsule, aedeagus, basal plate and parameres; D, T9 and laterotergites. E-G, *H. gefhyrobregmatum* sp. nov.; E, T9 and laterotergites; F, aedeagus, basal plate and parameres; G, conjunctiva and base of vesica with left conjunctival sclerite dorsal. acs, anterior conjunctival sclerite; lcp, left conjunctival process; lp, left paramere; RLT9, right ninth laterotergite; rcp, right conjunctival process; rcs, right conjunctival sclerite; rp, right paramere; T9, ninth tergum; T9p, left process of ninth tergum; v, vesica; vp, vesical process; y, y-sclerite. Scale lines 0.25 mm except G.

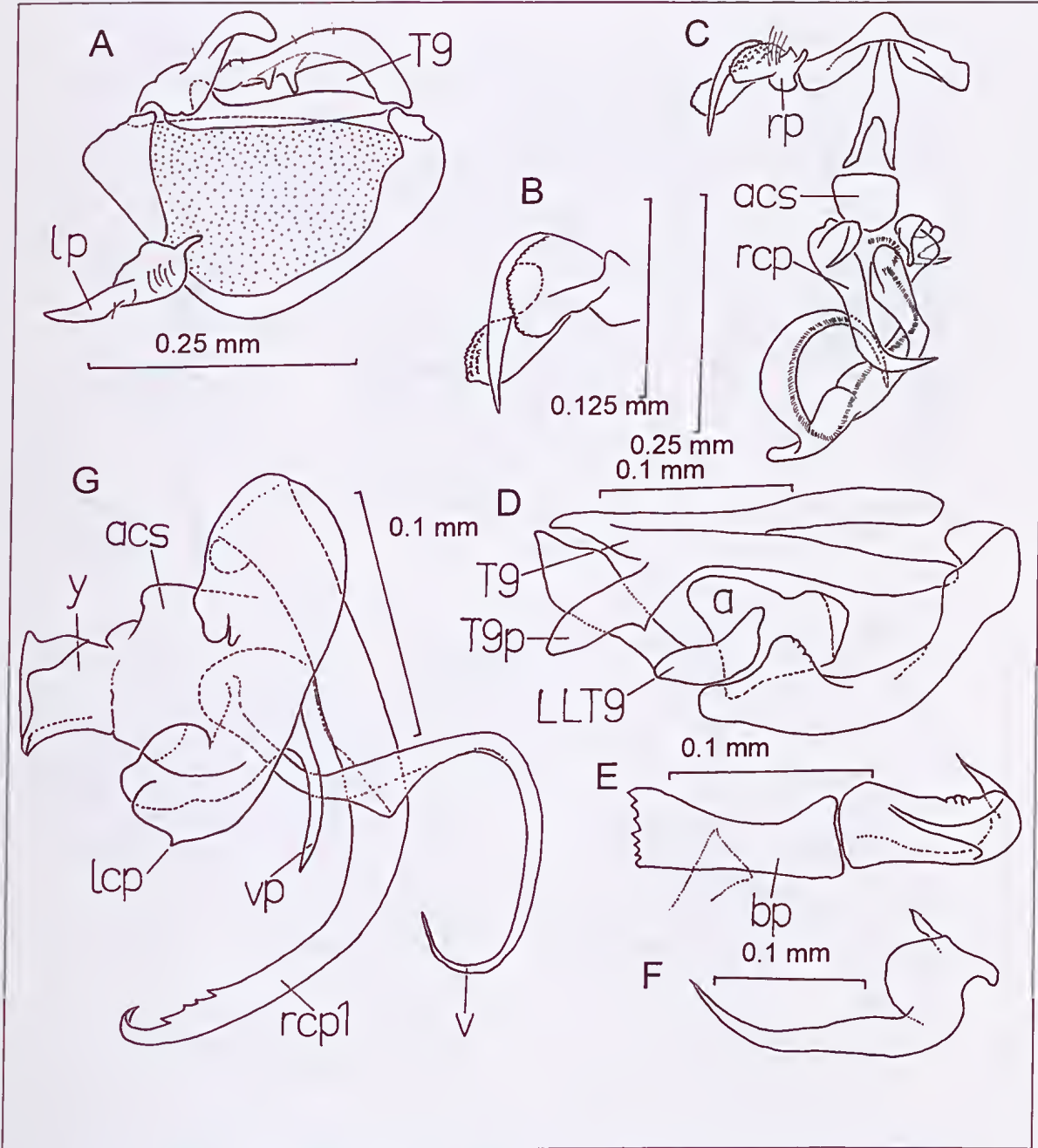


FIG. 18. Male genitalia. A-C, *Hypselosoma haplacanthatum* sp. nov.; A, T9, genital capsule and left paramere, aedeagus removed; B, right paramere; C, aedeagus, basal plate and right paramere. D-G, *H. ndouaensis* sp. nov.; D, T9, laterotergies and anophore, dorsal; E, right paramere and half of basal plate; F, left paramere; LLT9, left ninth laterotergite; rcp, right conjunctival process; rp, right paramere; T9, ninth tergum; T9p, left process of ninth tergum; v, vesica; vp, vesical process; y, y-sclerite.

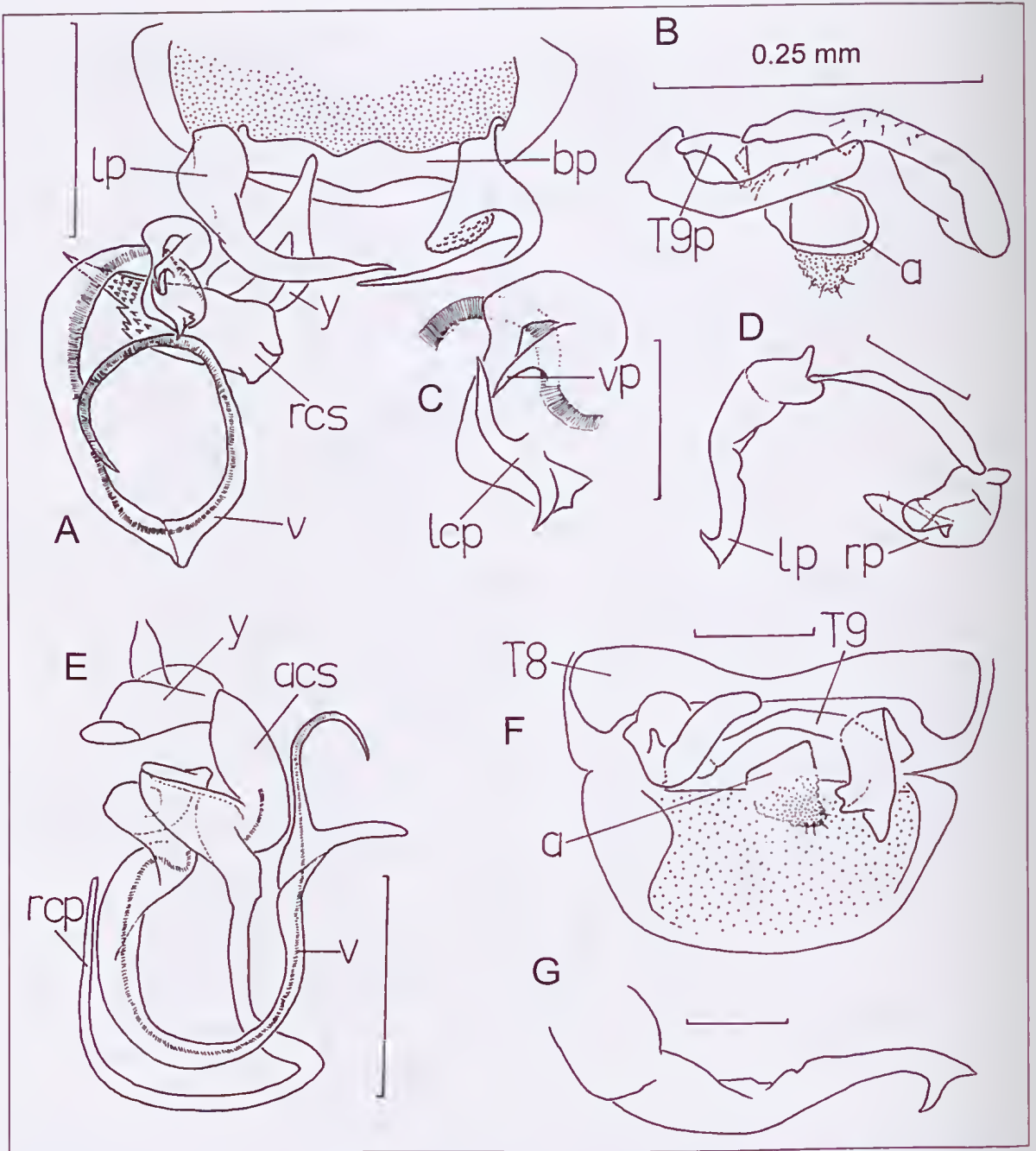


FIG. 19. Male genitalia. A-C, *Hypselosoma nordiensis* sp. nov.; A, genital capsule with aedeagus folded out; B, T9, laterotergites and anophore; C, processes at base of vesica and left conjunctival sclerite. D-G, *H. oculatum* Reuter; D, basal plate and parameres; E, aedeagus; F, T9, laterotergites and genital capsule with aedeagus removed; G, apex left paramere. acs, anterior conjunctival sclerite; bp, basal plate; lcp, left conjunctival sclerite; lp, left paramere; rcp, right conjunctival sclerite; rcs, right conjunctival sclerite; T8, eighth tergum; T9, ninth tergum; T9p, left process of ninth tergum; v, vesica; y, y-sclerite. Scale lines 0.25 mm.

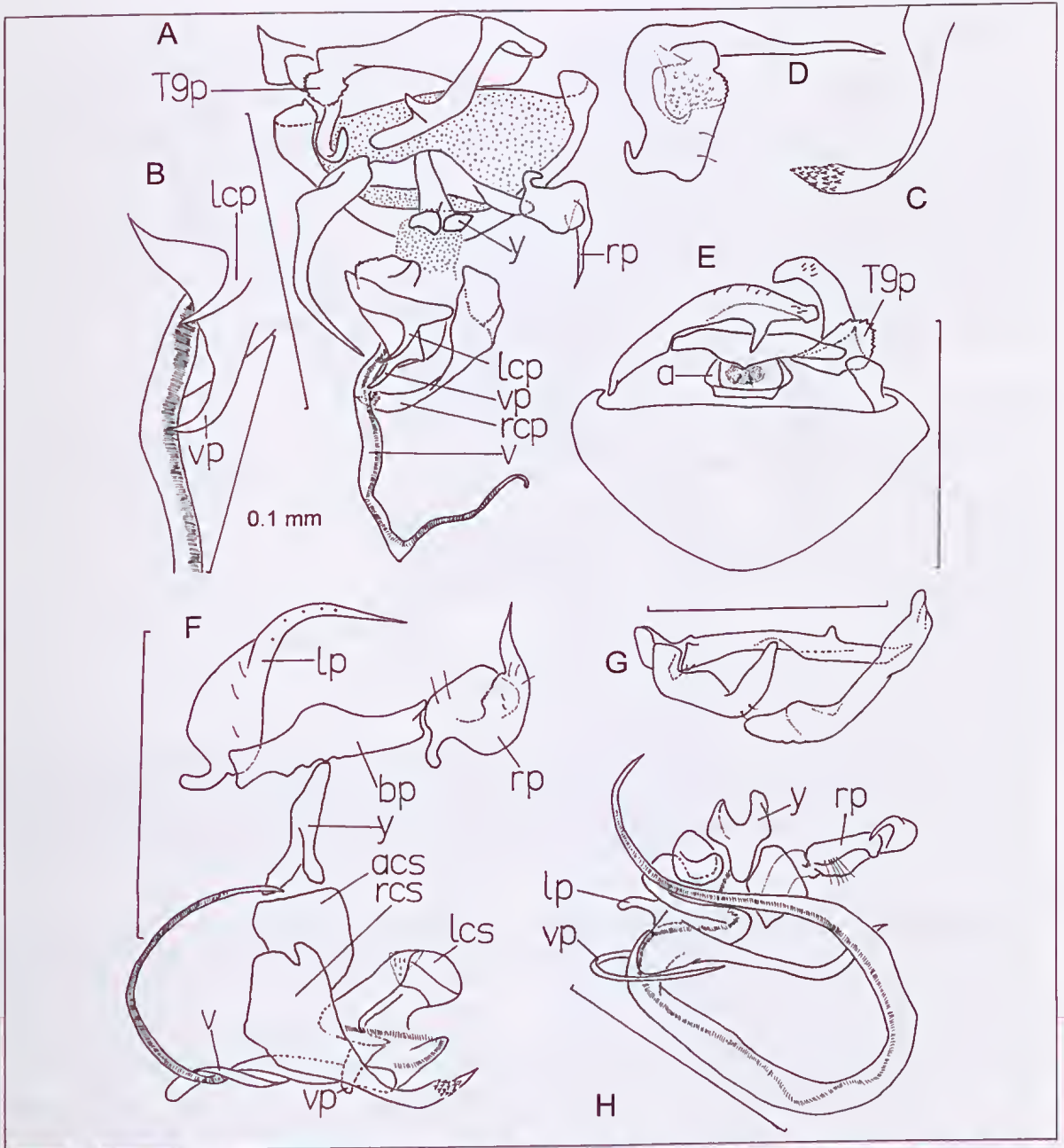


FIG. 20. Male genitalia. A-F, *Hypselosoma rembaiensis* sp. nov.; A, caudum with aedeagus folded out and left conjunctival sclerite dorsal; B, base of vesica; C, apex right conjunctival process; D, right paramere; E, caudum, anterior view; F, aedeagus, basal plate and parameres with right conjunctival sclerite dorsal. G-H, *H. touhoensis* sp. nov.; G, T9 and laterotergites; H, aedeagus, basal plate and parameres. acs, anterior conjunctival sclerite; bp, basal plate; lcp, left conjunctival process; lcs, left conjunctival sclerite; lp, left paramere; rcp, right conjunctival process; rcs, right conjunctival sclerite; rp, right paramere; T9p, left process of ninth tergum; v, vesica; vp, vesical process; y, y-sclerite. Scale lines 0.25 mm except B.

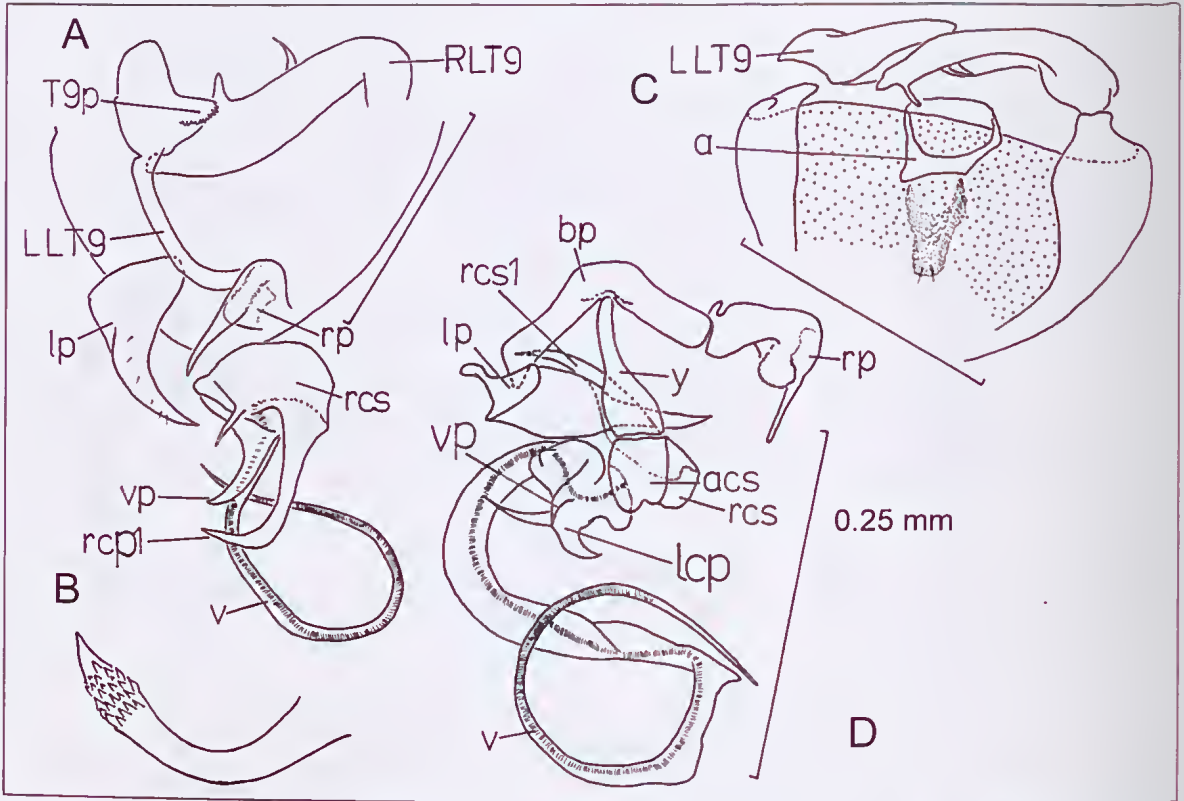


FIG. 21. Male genitalia. A-B, *Hypselosoma trachyacanthatum* sp. nov.; A, caudum with aedeagus folded out; B, apex right conjunctival process. C-D, *H. triacanthatum* sp. nov.; C, T9, appendages, anophore and genital capsule, dorsal; D, aedeagus, basal plate and parameres. acs, anterior conjunctival sclerite; bp, basal plate; lp, left paramere; LLT9, left ninth laterotergite; RLT9, right ninth laterotergite; rcp, right conjunctival process; rcs, right conjunctival sclerite; rp, right paramere; T9p, left process of ninth tergum; v, vesica; vp, vesical process; y, y-sclerite. Scale lines 0.25 mm.

Distribution. Known from six disjunct localities at 470-1000 m a.s.l. in the southern half of Grande Terre (Fig. 23E). It is sympatric with *H. triacanthatum* and *H. oculatum*.

Notes. The presence of ocelli in an elytrous male is unusual in Hypselosomatinae but occurs in *Pateena* (Hill, 1980) whose males are pterygodimorphic with macropters being rare.

***Hypselosoma touhoensis* sp. nov.**
(Figs 11, 10F, 20G-H, 22B, Table 1)

Etymology. From the type locality.

Material. HOLOTYPE male: 20°47'56"S x 165°13'50"E, Touho TV tower, 400 or 470 m, GBM, 28.xi.2003-30.i.2004, RFTT, QM11485, 5 slides, 16369

(MNHN(EH)). Paratype: 1 m as for holotype, T165666. Other material: 1 m, same site, GBM, 30.i.2004, RP, trees & logs, QM 11507, T165667, vial + 2 slides (QM).

Diagnosis. The slender tarsi, highly convex and rotund, elytrous form and apical lobes on the elytra distinguish males of this species.

Description. *Elytrous male.* Black except antennae, labrum, maxillary plates, labium and legs dark brown.

Overall form is distinctively cylindrical because of the tumid, horizontal pronotal disc and abruptly rounded elytral apices each with a drooping lobe (Fig. 11).

Base of labrum not tumid in profile but salient above plane of flat clypeal apex and less salient

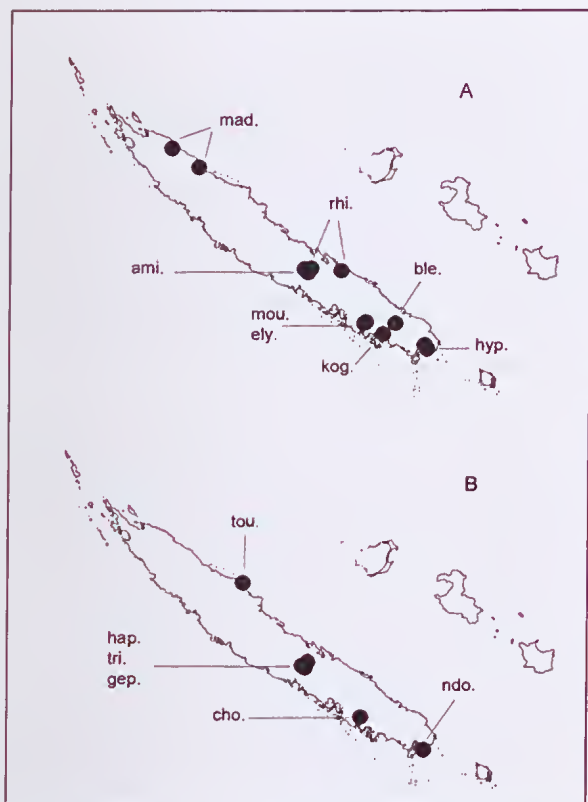


FIG. 22. Localities in Grande Terre, New Caledonia from which *Hypselosoma* species have been described. A, *H. hypselosomatum* group; B, six species with few localities. ami. *H. amieuensis* sp. nov.; ble. *H. bleuensis* sp. nov.; cho. *H. chorizobregmatum* sp. nov.; ely. *H. elytratum* sp. nov.; gep. *H. gephyrobregmatum* sp. nov.; hap. *H. haplacanthotum* sp. nov.; kog. *H. koghiensis* sp. nov.; mad. *H. mandjeliensis* sp. nov.; mou., *H. mouensis* sp. nov.; ndo., *H. ndouaensis* sp. nov.; rhi. *H. rhinatum* sp. nov.; tou., *H. touhoensis* sp. nov.; tri., *H. triacanthatum* sp. nov.

than setae of clypeal organ; maxillary plates smoothly convex, without erect macrosetae; bucculae without erect macroseta, with tubercle; clypeal organ present in flat, semicircular area on anterior margin and bearing many erect, incurved setae.

Disc of pronotum impunctate, abruptly constricted, anterior halves of lateral margins roundly convergent, calli tumid, posterior halves straight and parallel, posterior margin straight and declivent, posterior angles not tumid.

Scutellum sparsely, finely punctate; medial ends of mesosternal transverse carinae acute.

Fore and mid tarsi not swollen (Fig. 10F).

Elytra highly convex in profile, no overlap, punctate, venation not evident; glabrous furrow along path of vein Sc extending 95% to elytral apices demarcating costal cell which is inclined at roughly 30° below horizontal to form a sloping, tapering shelf a little wider than width of hind femora; hypocostal lamina at least 1.5 times depth of hind femora and inclined at roughly 45°, extending to elytral apices and joining small, apical lobe.

S3 organ not well defined but possibly elongate, transverse, medial depression bearing dense spicules adjoined posteriorly by long setae.

Genitalia. left process of T9 short and tapering; left LT9 present as a medially procurved arm; right LT9 with broad, rounded apex, without digitate process on ventral margin at midlength (Fig. 20G); distal lobe of right paramere very slender, spinous, twice as long as proximal lobe; left paramere slender, curved, spine-like, with bulbous base lacking spine and lamella; left and right conjunctival sclerites possibly without processes; vesical process slender, recurved, spine shorter than left paramere; vesica stout, recurved at midlength (Fig. 20H).

Elytrous female. Unknown

Distribution. Known from one locality at 400 m a.s.l. in northern Grande Terre and sympatric with *H. trachyacanthatum* (Fig. 22B).

Notes. The male has female facies in convex elytra and unswollen fore and mid tarsi which are rare in the subfamily (see Discussion). The rudimentary S3 organ has similarity with *H. acantheen* Hill, 1991 of New Zealand.

***Hypselosoma trachyacanthatum* sp. nov.**
(Figs 1J, 2G, 3H, 3P, 4F, 6D, 9D, 11K, 21A-B, 23F, Table 1)

Etymology. Greek, provided with a rough spine (spiculate right conjunctival process).

Material. Holotype male: 20°47'56"S x 165°13'50"E, Touho TV tower, 470 m, GBM, 30.i.2004, RP, trees & logs, QM11507, 4 slides, 16370 (MNHN(EH)). Paratype: 1 f,

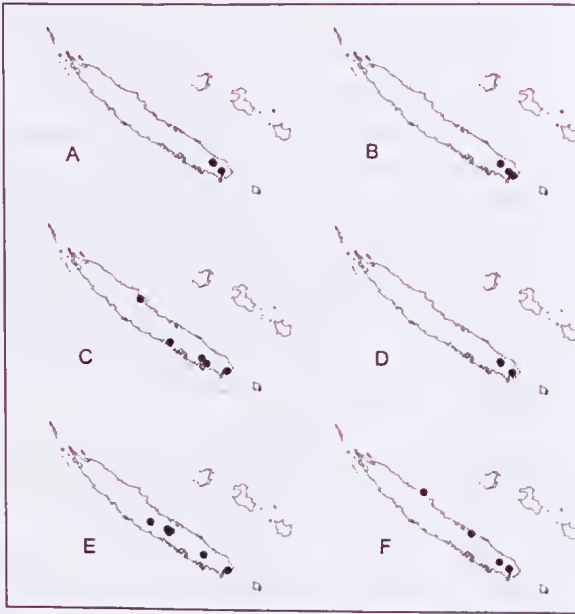


FIG. 23. Localities in Grande Terre, New Caledonia from which *Hypselosoma* species have been described. A, *H. dicroum* sp. nov.; B, *H. nordiensis* sp. nov.; C, *H. oculatum* Reuter (including Reuter, Poppius and Wygodzinsky sites); D, *H. onceronotatum* sp. nov.; E, *H. rembaiensis* sp. nov.; F, *H. trachyacanthatum* sp. nov.

as for holotype, 4 slides, T165665. Other material: 1 m, 21°34'35"S x 166°7'24"E, Col de Petchecara, 250 m, GBM, 22.xi.2003-28.i.2004, RFTI, QM11473, T165681; 1 m, 22°14'16"S x 166°50'1"E, Pic du Pin site 2, 250 m, GBM & PG, 26.xi.2004, RB, QM11797, T165682; 2 m, 22°6'41"S x 166°38'51"E, Rivière Bleue, Mois de Mai, 400 m, GBM, 19.xi.2001, RB, QM8968, T165683-4 (QM).

Diagnosis. The convex form, flat setigerous clypeal organ, sclerotized and punctate corium and absent anal cell distinguish males of this species and *H. haplacanthatum*. The former has a serrate process on the left side of T9 while the latter does not.

Description. *Macropterous male.* Black to dark brown, frons sometimes uniformly a little paler than clypeus (but without pair of red patches), antennae, labrum, maxillary plates, labium dark brown; coxae and femora dark brown, femoral apices, tibiae and tarsi light brown (not so in *H. hypselosomatum* group); forewing membrane black to dark brown proximally becoming brown distally (costal cell black) as well as pale

triangular area at base of remigium between costal cell and clavus.

Profile convex but less than in members of the *H. hypselosomatum* group (Fig. 1J).

Base of labrum not tumid in profile but salient above plane of flat apex of clypeus and less salient than setae of clypeal organ; maxillary plates smoothly convex, without erect macrosetae; bucculae without macroseta, with tubercle; clypeal organ present in flat, semicircular area on anterior margin and bearing many erect, incurved setae (Fig. 4F).

Lateral margins of disc of pronotum (Fig. 3H) sinuously convergent, disc weakly constricted anteriorly, calli not tumid, disc punctate (less coarsely than forewings), posterior margin sinuously convex; medial ends of mesosternal transverse carinae acute (Fig. 6D).

Forewing (Fig. 9D) with substantial corial punctation as for *H. haplacanthatum*.

S3 organ (Fig. 11K) semicircular with straight, sclerotized, posterior margin projecting a little on left but not right side and anterior margin lacking peripheral setae.

Genitalia. left process of T9 short, broad, with serrate apex; left LT9 present as a medially procurved arm; right LT9 with lobed, possibly hyaline apex (not hyaline digit), digitate process on ventral margin at midlength (Fig. 21A); distal lobe of right paramere twice as long as broad, proximal lobe; left paramere curved, tapering, spine-like, with bulbous base lacking lamella and spine; left conjunctival sclerite with short, straight spinous process; right conjunctival sclerite with long curved spine bearing tumid, spiculate apex (Fig. 21B); base of vesica with curved, spinous process half as long as right conjunctival spine; vesica abruptly recurved beyond midlength (Fig. 21A).

Elytrous female. (Fig. 2G). Colour like male, elytra black.

Base of labrum not tumid in profile but salient above apex of clypeus; maxillary plates without erect macrosetae; bucculae with tubercle, without macroseta.



FIG. 24. World distribution of *Hypselosoma* showing number of species at localities including one undescribed species at each of the asterisked localities and including New Caledonian species described here.

Disc punctate, lateral margins of disc roundly convergent anteriorly, tumid posteriorly; posterior margin mostly straight but tumid at angles (Fig. 3P).

Elytra highly convex in profile, punctate (including clavus), venation not evident except 1AN faintly, no overlap; glabrous furrow along path of vein Sc extending roughly 90% to elytral apices demarcating costal cell which is inclined at roughly 30° below horizontal to form a sloping, tapering shelf a little wider than depth of hind femora; hypocoastal lamina at least 1.5 times depth of hind femora and inclined at roughly 45°, extending 90% to elytral apices.

Distribution. Known from four disjunct locations at 250–400 m a.s.l. mostly in the southern half of Grande Terre (Fig. 23F). It is sympatric with *H. touhoensis* in the north and *H. rhinatum* in the south.

Hypselosoma triacanthatum sp. nov.
(Figs 1K, 2H, 3Q, 4G, 9E, 11L,
21C–D, 22B, Table 1)

Etymology. Greek, provided with three spines (three short spines arising from left conjunctival process and base of vesica).

Material. HOLOTYPE male: 21°36'36"S x 165°48'37"E, Col d'Amieu, west slope, upper, 470 m, GBM, 27.i.2003, RB, QM11546, 4 slides, 16371 (MNHN(EH)). Paratype: 1f, as for holotype, T165679. Other material: 1f, 21°35'6"S x 165°47'44"E, Col d'Amieu, 2km W (or 3.5km NNW), GBM & DC, 8.v.1984, RB, QM4258 (vial, translucent), T165680 (QM).

Diagnosis. The flat, macropterous form, recessed, non-setigerous clypeal organ bounded anteriorly by a pale bridge, sclerotized corium with punctuation limited to veins, similarly limited claval punctuation and presence of an anal cell distinguish males of this species.

Description. *Macropterous male.* Black, head uniformly dark brown, antennae, labrum, maxillary plates, labium dark brown; legs dark brown proximally, femoral apices and tibiae light brown but tarsi darker; forewing membrane black to dark

brown proximally becoming brown distally (costal cell black) as well as pale triangular area at base of basal cell.

Overall profile weakly convex (Fig. 1K).

Base of labrum not tumid in profile and less salient than 'bridge' lying anterior to clypeal organ; maxillary plates without erect macrosetae; bucculae without erect macroseta, with tubercle; clypeal organ present, separated from anterior margin by pair of fused lobes forming a pale bridge anterior to circular pit surrounded by many short, adpressed, incurved setae (Fig. 4G).

Disc of pronotum punctate; gradually constricted anteriorly, lateral margins sinuously convergent, calli not tumid, posterior margin sinuously convex, angles not tumid; medial ends of transverse mesosternal carinae acute.

Forewing (Fig. 9E) moderately explanate; costal cell sclerotized (faintly punctate or granulate on ventral surface in slide preparation), flat, depressed below inclined, explanate costal margin which is 2-3 membranal-vein widths in dorsal view forming a broad furrow about 25% from edge; hypocostal lamina about 1.5 hind femoral widths; glabrous furrow along posterior margin of costal cell; possible ventral carinae on Sc+R+M (proximal posterior edge of costal cell); five corial cells (in addition to costal cell) wholly (cell R and trapezoidal cell) or partly sclerotized and veins marginally punctate; clavus sclerotized and veins marginally punctate but small anal cell present, venation discernible.

S3 organ (Fig. 11L) semicircular, with straight, sclerotized posterior margin extending beyond lateral angles, right projection longer than left and widening basally, semicircle without peripheral row of long setae anteriorly, with many long setae adjoining posteriorly on tumidity of S3 and medially on S4.

Genitalia. left process of T9 not observed; left LT9 present as a medially procurved arm; right LT9 with round, decurved, hyaline apex (no hyaline digit), with spine subapically, with spine on ventral margin at midlength (Fig. 21C); distal lobe of right paramere slender, spinous, twice as long as proximal lobe; left paramere

curved, spine-like with bulbous base lacking lamella and spine; left conjunctival sclerite with two short, curved spines; right conjunctival sclerite with one long, curved spine subequal to left paramere; vesical base with one curved spine adjacent to and shorter than those on left conjunctival sclerite (or perhaps this spine also originates on left conjunctival process); vesica abruptly bent near midlength into loop, with short projection at bend and second widening near three-quarters from base (Fig. 21D).

Elytrous female. Colour black except head uniformly dark brown, antennae, labrum, maxillary plates, labium and bases of legs dark brown, tarsi, tibiae and apices of femora lighter.

Moderately convex in profile (Fig. 2H).

Base of labrum not tumid in profile, salient above clypeal plane; maxillary plates without erect macrosetae; bucculae with tubercle, without erect macroseta.

Disc of pronotum impunctate except transverse line of punctures posteriorly, disc constricted anteriorly, anterior halves of lateral margins roundly convergent, posterior halves tumid, posterior margin weakly convex, not tumid except angles projecting a little posteriorly (Fig. 3Q).

Elytra moderately convex in profile, no overlap, punctate (including clavus), venation not evident except 1AN faintly; glabrous furrow along path of vein Sc extending 80-90% to elytral apices demarking costal cell which is inclined at roughly 30° below horizontal to form a sloping, tapering shelf a little wider than width of hind femora; hypocostal lamina at least 1.5 times depth of hind femora and inclined at roughly 45°, extending 90% to elytral apices.

Distribution. Known from two adjacent localities at 400-470 m a.s.l. near Col d'Amieu where it is sympatric with *H. reumbaiensis* (Fig. 22B).

Notes. The ocular macrosetae of the holotype appeared to be absent but perhaps were destroyed during preservation whereas their absence in several specimens of *H. oculatum* is less likely an artefact. The fused clypeal lobes

form a pale bridge anterior to clypeal organ. *H. gephyrobregmatum*, which is elytrous, has a similar bridge but it is not pale and the lobes seem less completely fused as indicated by a probable sulcus visible at 80X magnification. In *H. chorizobregmatum* the lobes are contiguous but apparently not fused and project over the labrum. *H. triacanthatum* shares a trispinous configuration of left conjunctival and vesical processes (Fig. 21D) with *H. gephyrobregmatum* (Fig. 17G) and *H. nordiensis* (Fig. 19C). The vesical form is like *H. chorizobregmatum* (Fig. 17A), *H. haplacanthatum* (Fig. 18C) and *H. nordiensis* (Fig. 19A) in having an abrupt bend and widening at midlength with a lesser widening distally.

DISCUSSION

Definition of the *Hypselosomatum* Species Group.

Eight species of *Hypselosoma* are separable mainly by details of male genitalia as tabulated in Table 2 and hereby defined as the *H. hypselosomatum* group. Characters for recognition of this group are as follows: male and female relatively highly convex; male clypeal organ absent; male pronotal disc smoothly rounded and tapering anteriorly (lateral margins not sinuous in dorsal view), lacking weak transverse impression; male costal margin not explanate, hypocostal lamina narrow; costal cell impunctate (but perhaps granulate ventrally), flat not concave; female costal cell in same plane as surrounding area; male claval veins impunctate (granulate ventrally); female elytra smooth; male S3 organ subcircular, with single row of peripheral setae, without sclerotized posterior rim; spatulate left conjunctival process; 1-3 right conjunctival processes; hyaline digit on the apex of the right LT9 (except *H. elytratum*) and with lamella and spine near base of the left paramere.

The males are macropterous except for *H. elytratum* which occurs at the highest locality for the genus in New Caledonia (summit of Mt Mou, 1200 m). No members of the *H. hypselosomatum* group occur sympatrically, although *H. amieuensis* and *H. rhinatum* occur closely near Col d'Amieu. *H. oculatum* has similar convexity, fore wings, elytra and male S3 organ but possesses

a clypeal organ and has dissimilar conjunctival sclerites.

Trends in wing sclerotization. The species show a variety of states of sclerotization of the forewing but without a simple progressive trend. Among macropterous and submacropterous species, two (*H. haplacanthatum* and *H. trachyacanthatum*) have the clavus and three corial cells entirely or almost entirely sclerotized and punctate (Figs 8D, 9D). Another two species (*H. chorizobregmatum* and *H. nordiensis*) have the clavus sclerotized and punctate and the corial cells are partly sclerotized but impunctate except adjacent to the claval suture (Figs 8A, F). In the preceding four species the anal cell on the clavus is totally obliterated. In *H. triacanthatum* (Fig. 9E) the sclerotized and partly punctate clavus retains a small anal cell but the corial sclerotization has progressed to punctation along the vein margins. In the submacropterous *H. ndouaensis* (Fig. 8E) the sclerotized and weakly punctate clavus retains a small anal cell while the corial cells are sclerotized and possess punctation along the veins. In *H. dicroum* (Fig. 8B) the clavus is impunctate and retains an anal cell while the sclerotization of the corium is less than the preceding species and lacking any punctation. In all the preceding species the costal cell is depressed and the margin weakly to strongly explanate. In *H. oculatum* (Fig. 9A) and macropterous species of the *H. hypselosomatum* group (Figs 7A-E) the costal cell is flush with the corial plane and the margin not explanate while the sclerotization of the corium and clavus is comparable to *H. dicroum* and without signs of punctation. Among the three elytrous species *H. touhoensis* (Fig. 9C) seems most specialised with a highly convex form and lobate apices on the elytra.

Male S3 organ and male clypeal organ.

Wygodzinsky (1959) described a variety of male S3 organs (S2 in his terminology). The New Caledonian species contain a subset of these forms and separate into three groups on this character. One form is a subcircular area with a single, anterior, peripheral row of setae and no sclerotized posterior rim (Figs 10A, C, E, 11A, H). The second form is a semicircular

area lacking anterior setae but possessing a sclerotized posterior margin that projects laterally, especially on right side (Figs 10D, 11B-D, 11F, 11I-K, 11L). The third form is an ill-defined setigerous impression (Fig. 11J). The S3 organ of *H. haplacanthatum* (Fig. 11E) is assigned here to the first form but seems to possess a sclerotized posterior margin. The S3 organ of *H. nordiensis* (Fig. 11G) is assigned to the second form although it seems more subcircular than semicircular. Otherwise, among New Caledonian species, only *H. oculatum* (Fig. 11H) and the *H. hypselosomatum* group (Fig. 11A) share the first form of S3 organ but it occurs in all Australian species. The second form possibly does not occur outside New Caledonia while the third form probably does occur elsewhere, judging by Wygodzinsky (1959).

The male clypeal organ has several forms: (1) absent (Fig. 4A); (2) a flat, setigerous area perhaps embracing a pore (Fig. 4F); (3) a weakly or strongly elevated, setigerous area embracing a pore (Figs 4E, 5) and (4) a pit embraced by fused or unfused lobes (Figs 4B, C, D, G). The flat and salient forms have not been described outside New Caledonia but the organ is absent in several species outside New Caledonia and the lobate form occurs in *H. schizobregmatum* Hill, 1987 (Queensland), *H. hickmani* (Tasmania), *H. acantheen* (New Zealand) and *H. hirashimai* Esaki and Miyamoto, 1959 (Japan). One Queensland species (*H. oncerochilotum* Hill, 1987) that lacks a clypeal organ possesses a unique and probably analogous structure on the labrum. Males of other Australian hypselosomatine genera often possess an analogous organ on the pronotum (*Rectilamina* and *Cryptomannus*) or the clavus (*Duonota*) (Hill, 1984). In the Ogeriinae, *Kaimon* Hill possesses a probably analogous structure on the male vertex (Hill, 2004).

Among Australian, New Zealand and New Caledonian *Hypselosoma* the male S3 organ occurs in species with or without a clypeal organ. These two characters occur among the New Caledonian species as follows:

H. hypselosomatum group have a subcircular S3 organ and no clypeal organ.

H. oculatum has a subcircular S3 organ and strongly salient clypeal organ (not mentioned by Wygodzinsky, 1959).

H. haplacanthatum has a probably subcircular S3 organ and a flat clypeal organ.

H. dicroum, *H. ndouaensis*, *H. rembaiensis* and *H. trachyacanthatum* have a semicircular S3 organ and flat clypeal organ.

H. chorizobregmatum, *H. gephyrobregmatum*, and *H. triacanthatum* have a semicircular S3 organ and a lobate or bridged clypeal organ.

H. nordiensis has a sub- to semicircular S3 organ and weakly salient clypeal organ.

H. touhuensis has an ill-defined setigerous impression on male S3 (perhaps no S3 organ) and flat clypeal organ.

Distribution and microendemism. The comparative richness of New Caledonian *Hypselosoma* indicated in Figure 24 is exceeded by *Schizoptera* Fieber in Trinidad with 32 species of which 29 occurred at one site (Emsley, 1969).

Two broad localities in New Caledonia seem particularly rich in *Hypselosoma* species, namely Rivière Bleue and Col d'Amieu with five and six species respectively, occurring within a few kilometers at each locality. Seven species occur within a 20 km radius of Mt Koghis, the type locality of *H. oculatum*. Other localities have 1-3 species each and many species have small distributions usually in the southern half of Grande Terre. *H. rembaiensis*, *H. trachyacanthatum* and *H. oculatum* have relatively broad distributions (Fig. 23). Sites visited by Queensland Museum collectors that did not yield *Hypselosoma* species include: Col de Mouirange, Rivière des Pirogues, Bois du Sud on Yaté to Nouméa Road, Mt Do, La Koua stream and Ningua Reserve on road southwest from Thio, Tontouta River (perhaps near La Foa, a site of *H. oculatum*), Farino sites near Col d'Amieu, Aoupinié sites, Ateou, Pwanaki, Tiea Reserve, Forêt Plate, Pindaï Peninsula, Forêt Francis and Grottes d'Adio. The main absences occur in the northwest coast. The distributions are summarised as follows from northwest to south east along the axis of Grande Terre:

1. Mandjéla sawmill, 700 m: macropterous *H. mandjeliensis*.
2. Mt Panié refuge 900-1330 m: macropterous *H. mandjeliensis*.
3. Touho TV tower, 400-470 m: macropterous *H. trachyacanthatum* and elytrous *H. touhoensis*.
4. Pic de Amoa north slope, 500 m: macropterous *H. oculatum*.
5. Col de Rousettes, forestry track: elytrous *H. rembaiensis*.
6. Table Unio summit, 1000 m: submacropterous *H. amieuensis* and elytrous *H. rembaiensis*.
7. Col d'Amieu, 2 km W (3.5km NNW), 400 m: macropterous *H. triacanthatum*.
8. Col d'Amieu sawmill, 400 m: submacropterous *H. amieuensis* and elytrous *H. gephyrobregmatum*.
9. Col d'Amieu upper west slope, 470 m: elytrous *H. rembaiensis* and macropterous *H. triacanthatum*.
10. Col d'Amieu, 4 km N, 300 m: submacropterous *H. rhinatum* and macropterous *H. halploacanthatum*.
11. Mt Rembai 750 m: elytrous *H. rembaiensis*.
12. Cape de Petchecara: macropterous *H. rhinatum* and *H. trachyacanthatum*.
13. La Foa (site of Wygodzinsky, 1959): macropterous *H. oculatum*.
14. Mt Mou base, 200 m: macropterous *H. chorizobregmatum* and *H. monensis*.
15. Mt Mou summit, 1150 m: elytrous *H. elytratum*.
16. Dzumac Road: macropterous *H. oculatum* and elytrous *H. rembaiensis*.
17. Mt Koghis track entrance, 500 m: macropterous *H. koghiensis* (possibly site of *H. oculatum* in Reuter 1890 and Poppius 1910).
18. Forêt de la Thy Reserve: macropterous *H. oculatum*.
19. Rivière Bleue main forest, 120-160 m: macropterous *H. dicroum* and *H. nordiensis*, and *H. onceronotatum* (male pteromorph unknown).
20. Rivière Bleue main forest 250 m: macropterous *H. bleuensis* and *H. nordiensis*.
21. Rivière Bleue, Mois de Mai, 400 m: macropterous *H. trachyacanthatum*.
22. Pic du Pin, site 1, 280 m: macropterous *H. dicroum* and *H. nordiensis*.
23. Pic du Pin, site 2, 280 m: macropterous *H. trachyacanthatum*.
24. Pic du Grand 250 m: macropterous *H. hypselosomatum* and *H. onceronotatum* (male pteromorph unknown).
25. Forêt Nord summit, 480-600 m: elytrous *H. rembaiensis*.
26. Forêt Nord site 2 200 m: macropterous *H. sp.* near *hypselosomatum*, *H. oculatum* and *H. nordiensis*.
27. Cape Ndoua, 50 m: macropterous *H. ndouaensis*.

In summarising the distribution of *Kaimon* species in the wet tropics of North Queensland, Australia, Hill (2004) found that many localities had one endemic non-macropterous species supplemented by one or two widespread macropterous species. This pattern was not strongly evident in New Caledonian *Hypselosoma* although sympatric pairs often include a member of the mostly macropterous *H. hypselosomatum* group and a species (macropterous or elytrous) not from that group. Grandcolas *et al.* (2008) cited evidence that sympatry of New Caledonian plants, insects, snails and lizards usually involves different clades. Other than the *H. hypselosomatum* group, it is not possible to properly define clades of *Hypselosoma* here but of the 27 'sites' recognised above 13 have one species, 13 have two species and one has three species. None of the pairs at the 13 sympatric sites share the same form of both clypeal and S3 organ although at one site each, a pair shares either a circular S3 organ (site 17), a semicircular S3 organ (site 9) or a flat clypeal organ (site 3). At the site with three species (site 26), at least one pair shares a circular S3 organ. In addition, no two members of the *H. hypselosomatum* group occur sympatrically.

Dispersal. The Hypselosomatinae show elements of relictual distribution but also recent dispersal and radiation. Hill (1984) suggested radiation in the Miocene-Pliocene to explain the diversity of Australian genera. However, Hill (1991) also implied *H. hickmani* of Tasmania and *H. acantheen* of New Zealand were relicts dating from the separation of those places 80M y.a. They are very similar while *H. hickmani* is unlike other Australian *Hypselosoma*, which occur in Queensland and northern New South Wales but are absent in Victoria and the remainder of New South Wales. Previously, Wygodzinsky (1959) explained the disjunct distribution of *Hypselosoma* in Madagascar as the result of the transport of vegetative material on the equatorial current from the Pacific rim across the Indian Ocean. Citing Millot (1952), he said 'forest fauna is particularly apt to be transported' by ocean currents. Figure 24 suggests the possibility of transoceanic dispersal of *Hypselosoma* westwards around the Pacific rim. Grandcolas *et al.* (2008) questioned the relictual nature of New Caledonian fauna suggesting it had colonised since 37 Ma and that much microendemism arose 2-3Ma. Perrichot *et al.* (2007) said of the Hypselosomatinae that the occurrence 'of isolated genera in Madagascar and North America, together with the French amber fossils ... merely reflects a relict distribution'. Their omission of *Ommatides insignis* on the volcanic, oceanic Lesser Antilles adjoining South America and *Williamsocoris ornatus* in Argentina does not detract from this statement. Nevertheless, the diversity of *Hypselosoma* in New Caledonia and hypselosomatine genera in Australia suggests they have an ancient but active lineage.

Most Hypselosomatinae live in wet forests but some occupy other moist habitats that seldom burn (Hill, 1984 and 1991, Schuh and Slater, 1995). *Pateena* Hill typically occurs in wet, tussock grassland. Hill found *H. hickmani* within hollow forest logs but it is not restricted to forest habitats and occurs from sea level to 1000 m in Tasmania. Perrichot *et al.* (2007) said that in 'the mangroves of Singapore, schizopterids ... shelter under dead wood during high tide' and reported tanaidacan

crustaceans, occupants of marine and brackish habitats, included in French amber with *Buzinia*. Two species of *Hypselosoma* live in intertidal habitats, namely *H. hirashimai* Esaki and Miyamoto of Japan 'among grasses and rushes ... where the ground is submerged under sea water at the time of high tide' (Esaki and Miyamoto, 1959) and an undescribed species from Queensland in graminoid coastal saltpan sward near Seaforth (Hill, 1987). These observations suggest that some Hypselosomatinae survive periodic immersion and occur in habitats where dispersal within vegetation by oceanic currents is likely so that the disjunct distributions of Hypselosomatinae may not be entirely relictual.

Notable Characters of Hypselosomatinae. Esaki and Miyamoto (1959) defined the Hypselosomatini as possessing four-segmented, male fore and mid tarsi among other characters. Emsley (1969) showed these were swollen but not truly tetramerous. In *Semanganamus* Štys the intermediate and distal tarsomeres increase in diameter where they connect and the intermediate tarsomere has an internal apodeme adjacent to a slight constriction which create the impression of a segmental division (Štys, 1974). However, these tarsi are not swollen in the hypselosomatine *Glyptocombus*, *Williamsocoris* and *H. touhoensis* while apparently similarly swollen tarsi occur in the ceratocombid genus *Kvamula* Štys, 1982.

The pronotal collar is absent in *Williamsocoris* and overlapped by the disc in *Cryptomammus*. Hill (2004) noted that in genera allied to *Ogeria* (not Hypselosomatinae) the collar is present or absent suggesting this character has little value in defining subfamilies.

Despite Emsley's statement (1969) in support of the primitiveness of *Hypselosoma*, it has three pairs of spiracles whereas most other genera of Hypselosomatinae such as *Glyptocombus*, *Williamsocoris*, *Pateena* and allied Australian genera have 5-6 pairs. Esaki and Miyamoto (1959) said the first to fifth abdominal spiracles were reduced in *H. hirashimai* but no vestigial spiracles have been observed on those segments in Australian, New Zealand and New Caledonian species by this author.

Perhaps the presence of a setigerous pore at the base of the costal cell (Fig. 9F), which overlies the thoracic spiracle, in *Hypselosoma* and its absence in *Pateena* is correlated with fewer abdominal spiracles in the former. Nevertheless, *Hypselosoma* has the most plesiomorphic male genitalia among Hypselosomatinae and perhaps all Schizopteridae.

Despite Carpintero and Dellapé's statement (2006), the spermatheca (at least, a sclerotized spermatheca) is absent in *Hypselosoma*.

Perrichot *et al.* (2007) and Azar and Nel (2010) provide valuable figures of the venation of fossil Hypselosomatinae but also include some misunderstandings of characters of the subfamily. *Glyptocombus*, *Williamsocoris* and the Australian Hypselosomatinae have four not three marginal cells beyond the costal cell (Fig. 6I) although the most distal cell is sometimes lost by fusion of distal veins as in *Rectilamina oblonga* Hill, 1984, *R. illacuna* Hill, 1984 and an undescribed clytrous *Glyptocombus* noted by Hill (1980). In these two *Rectilamina* species the costal cell is sclerotized and the wing has a wide hypocostal lamina giving greater rigidity (Hill, 1984). The costal cell is also sclerotized in two other *Rectilamina* species, *Duonota decoricuada* Hill, 1984, *Pateena elimata*, Hill, 1980 and all *Hypselosoma* (some of which also have sclerotized corial cells). Three rather than four marginal cells arise in *Libanohypselosoma* because the most proximal cell (adjacent to the costal cell) is absent rather than a distal cell. The very unusual path of their vein R is unlike modern Hypselosomatinae in departing the associated vein well proximally of the level of the trapezoidal cell and rejoining their vein M1 rather than travelling independently to the costal margin. It takes a curved path in reverse to all other veins. This possibly stiffens the basal, costal part of the wing as does the sclerotization of the costal cell in many modern species. Some modern non-hypselosomatine Schizopteridae also stiffen the proximal costa by a sclerotized costal cell (*Voccoroda* Wygodzinsky, 1950) or lobate 'costal' vein (*Pachyplagia* Gross, 1951, *Ogeria* Distant, 1913 and *Humpatanannus* Wygodzinsky, 1950).

Azar and Nel mention a 'claval depression' in *Libanohypselosoma*. This is possibly a sensory organ otherwise only known in males of *Duonota*. Probable analogous organs occur on the clypeus of some *Hypselosoma* and the pronotal collar of *Cryptomannus* and *Rectilamina*.

The three labral macrosetae of *Libanohypselosoma*, *Buzinia* and *Tanaia* do distinguish them from *Hypselosoma* but also allign them with adult *Duonota*, *Pateena*, *Ordirete* and *Macromannus*. Three labral macrosetae are typical of intermediate instar nymphs of all Australian genera whether 0, 1, 3 or 5 occur on the adult labrum. The fourth and fifth macrosetae appear in late instar nymphs of *Hypselosoma* (Hill, 1984).

The three labial segments described for *Libanohypselosoma* and *Buzinia* do not link these genera more with Hypselosomatinae than with Ogeriinae (Perrichot *et al.*, 2007) because the labium is three-segmented in Schizopterinae and four-segmented in both Hypselosomatinae and Ogeriinae. The third and fourth segments often appear connate so that miscounting is possible, particularly in amber fossils.

The articulated male laterotergites of *Cryptostemma* (Dipsocoridae) may be homologous with those of *Hypselosoma*. The asymmetrical appendages in *Hypselosoma*, here termed LT9, do not bear spiracles but these are present on T8. The appendages articulate subbasally with the anterodorsal angles of the genital capsule and the ends of a large, discrete T9, which bridges the open genital capsule anteriorly, but their bases project into segment 8 as expansions for the attachment of muscles (Figs 14A, D, 15B, D). During dissection of *H. geophyrobregmatum* a ligamentary connection was observed between the left LT9 and a sclerite torn from posterior margin of S8, perhaps an internal S9. A similar broken connection to the right LT9 was also observed (Fig. 17E). These ligaments join the laterotergites subbasally, that is distal of expanded area for muscle attachment. The asymmetrical appendages in *Cryptostemma*, termed LT8 in Hill (1987b), bear spiracles while T8 does not. The appendages articulate subbasally with a slender rudimentary T9 sclerite that lies anterior to the closed genital

capsule and articulate basally with the ends of T8. Processes at the bridge of the genital capsule guide movements of the laterotergites. Both genera have a long, spinous left paramere and compact right paramere but the vesical form differs considerably, being long and coiled in *Cryptostemma*.

Some other comparisons with *Cryptostemma* warrant consideration. The non-sheathing vesical sclerite of *Cryptostemma* (Hill, 1987b) may be homologous with the vesical process of *Hypselosoma*. Conjunctival sclerites 1, 2 and 3 of *Cryptostemma* (Hill, 1987b) may be homologous with the anterior conjunctival sclerite, left conjunctival sclerite(s) and right conjunctival sclerite, respectively of *Hypselosoma* (Hill, 1987a). The two struts connecting the basal plate to the conjunctival complex of *Cryptostemma* appear in *Hypselosoma* as the Y-sclerite (Hill, 1987a). This sclerite may be homologous with the U-sclerite or circular sclerite which is partly overlapped by the arcuate basal plate in *Pateena*, allied Australian genera and *Glyptocombus*. In these genera the anterior and lateral conjunctival sclerites may be represented by the rigid 'spermathecal bulb' which fills the opening of the U-sclerite to transform it into a circular sclerite. In *Glyptocombus* there appear to be elongate, conjunctival processes but in the Australia genera these are absent.

The medial, sometimes asymmetric S3 organ of male *Hypselosoma* may be analogous with the asymmetrical pocket on the left side of S3 in male *Cryptostemma*.

In some preserved specimens of *Hypselosoma* the bifid right paramere is positioned like a peg or clip restraining the right forewing and perhaps does the same during copulation. In a specimen of *H. oculatum* the left paramere was observed restraining the forewing.

ERRATA

In Hill (1980) the first couplet of the key should be transposed and for *H. hickmani* the male S8 is longer on left than right not vice versa. In the differential diagnosis for *Pateena* in Hill (1980) it should be understood that *Hypselosoma* also has stout antennal lamellae (shaped like a elephant's

ear) and four marginal cells on the forewing while *Glyptocombus* does not. Hill (1985) stated that *Pateena* is allopatric to *Hypselosoma* in Tasmania. Subsequent collecting confirm this is true for most localities, with *Hypselosoma* present in the south and northeast of the island and *Pateena* in the northwest and central east of the island. However, the genera meet at the montane Black Bog Creek near Cradle Mountain where two *Pateena* species occur sympatrically with *H. hickmani*. At this site, the microhabitats appear to be partitioned with *Hypselosoma* typically found among *Gleichenia* ferns on stream edges, *P. elimata* in wet heath adjacently and *P. polymitarior* Hill, 1980 more remotely on higher and comparatively drier ground in wet *Poa* tussock grassland.

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LITERATURE CITED

- Allen, R.T. & Carlton, C.E. 1989. New records of Ceratocombidae and Schizopteridae from Arkansas (Heteroptera: Schizopteridae). *Journal of the Kansas Entomological Society* 62(1): 125-126.
- Azar, D. & Nel, A. 2010. The earliest fossil schizopterid bug (Insecta: Heteroptera) in the Lower Cretaceous amber of Lebanon. *Annales de la Société Entomologique de France (nouvelle série)* 46(1-2): 193-197.
- Carpintero, D.L. & Dellapé, P.M. 2006. *Williamsocoris*, a new genus of Schizopteridae (Heteroptera) from Argentina. *Zoological Science* 23(7): 653-655.
- Esaki, T. & Miyamoto, S. 1959. A new or little known *Hypselosoma* from Anami-Oshima and Japan, with the proposal of a new tribe for the genus (Hemiptera). *Sieboldia Acta Biologica* 2(2): 109-120, plates 14-17.
- Emsley, M. G. 1969. The Schizopteridae (Hemiptera: Heteroptera) with the description of new species from Trinidad. *Memoirs of the American Entomological Society* 25: 1-154.

- Grandcolas, P., Muriene, J., Robillard, T., Desutter-Grandcolas, L., Jourdan, H., Guilbert, E. & Deharveng, L. 2008. New Caledonia: a very old Darwinian island? *Philosophical Transactions of the Royal Society (B)* 363: 3309-3317.
- Heidemann, O. 1905. A new genus and species of the hemipterous family Ceratocombidae from the United States. *Proceedings of the entomological Society of Washington* 7: 192-194.
- Hill, L. 1980. Tasmanian Dipsocoroidea (Hemiptera: Heteroptera). *Journal of the Australian Entomological Society* 19: 107-127.
1984. New genera of Hypselosomatinae (Heteroptera: Schizopteridae) from Australia. *Australian Journal of Zoology*, Supplementary Series 103:1-55.
- 1985a. New records and species of *Duonota* (Heteroptera: Schizopteridae) *Australian Journal of Zoology* 33: 263-271.
- 1985b. New records and species of *Pateena* (Heteroptera: Schizopteridae) *Australian Journal of Zoology* 33: 273-281.
- 1987a. Four new Australian species of *Hypselosoma* Reuter (Heteroptera: Schizopteridae). *Journal of the Australian Entomological Society* 26: 265-276.
- 1987b. First record of Dipsocoridae (Hemiptera) from Australia with the descriptions of four new species of *Cryptostemma* Herrich-Schaffer. *Journal of the Australian Entomological Society* 26: 129-139.
1991. *Hypselosoma acantheen* n. sp. (Heteroptera: Schizopteridae), first record of the family in New Zealand. *New Zealand Journal of Zoology* 18: 75-81.
2004. *Kaimon* (Heteroptera: Schizopteridae), a new, speciose genus from Australia. *Memoirs of the Queensland Museum* 49(2): 603-647.
- Perrichot, V., Nel, A. & Néraudeau, D. 2007. Schizopterid bugs (Insecta: Heteroptera) in mid-Cretaceous ambers from France and Myanmar (Burma). *Paleontology* 50(6): 1367-1374.
- Poppius, B. 1910. Neue Ceratocombiden. Öfversigt af Finska Vetenskaps-Societetens Förhandlingar, 52 Afd. A (1): 1-14.
- Rédei, D. 2007. A new species of the family Hypsipterygidae from Vietnam, with notes on the hypsipterygid fore wing venation (Heteroptera, Dipsocoromorpha). *Deutsche Entomologische Zeitschrift* 54(1): 43-50.
- Ren, S. & Zheng, L. 1992. New species and new records of Dipsocoromorpha (Hemiptera: Heteroptera) from China. *Entomotaxonomia* 14(3):187-186.
- Reuter, O. M. 1891. Monographia Ceratocombidarum orbis terrestris. *Acta Societatis Scientiarum fennicae* 19(6): 1-27, 1 plate.
- Schuh, R.T. & Slater, J.A. 1995. *True Bugs of the World*. (Cornell University Press: Ithaca and London).
- Štys, P. 1970. On the morphology and classification of the family Dipsocoridae s. lat., with particular reference to the genus *Hypsipteryx* Drake (Heteroptera). *Acta Entomologica Bohemoslovaca* 67: 21-46.
1974. *Semanganianus mirus* gen. n., sp. n. from Celebes - a bug with accessory male genitalia (Heteroptera, Schizopteridae). *Acta Entomologica Bohemoslovaca* 71:382-397.
- Uhler, P.R. 1894. A list of the Hemiptera-Heteroptera of the families Anthocoridae and Ceratocombidae collected by Mr. H.H. Smith in the island of St Vincent (B), Descriptions of new genera and species. *Proceedings of the Zoological Society of London* 1894: 157-160.
- Wygodzinsky, P. 1959. Un nouvel *Hypselosoma* de Madagascar, avec la description d'autres especes et des observations sur le genre (Schizopterinae, Dipsocoridae, Hemiptera). *Mémoires de Institut Scientifique de Madagascar* (E) 11: 509-539.

Gastric nematodes from the Plains Goanna, *Varanus spenceri* (Reptilia: Varanidae), from central Queensland.

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ABSTRACT

Three species of nematode, *Abbreviata hastaspicula*, *A. tumidocapitis* and *Hastospiculum* sp. were recovered from *Varanus spenceri*. The two species of *Abbreviata* occur commonly in related varanid species which inhabit the dry hot interior of Australia. Despite differences in habitat and behavioral ecology between *V. spenceri* and other large sympatric species of *Varanus*, the wide range of prey taken by large species of *Varanus* lizards precludes inferring the arthropod intermediate hosts of these nematodes. □ *Varanus spenceri*, *Abbreviata*, *Hastospiculum*, locusts, Australia.

Varanus spenceri is a large lizard with a total length in adults of 1.0 to 1.25 m (Cogger, 1992), and, despite its size, is probably the least known of the large Australian varanid lizards (Lemm & Bedford, 2004). It is confined to the black soil country of western Queensland and the Barkly Tablelands of the Northern Territory, where perennial Mitchell Grass (*Astrebla* spp.) is the dominant vegetation. *Varanus spenceri* is a shy species which readily takes refuge in deep cracks in the dry soil. Studies on the parasites of other large species of *Varanus* from the arid Australian inland have shown that *Abbreviata hastaspicula* is the dominant gastric nematode (Jones, 1983a, 1983b, 1988). Apart from an identification of *A. hastaspicula* from a road-killed *V. spenceri* (Woolley *et al.*, 2010), there have been no reports on the helminth parasites of this large species. I undertook this study to determine whether the nematode fauna differed significantly from that in related species (*V. gouldii*, *V. panoptes*), and to investigate whether its restricted and specialised habitat, and hence its diet, exercised a discernible influence on this fauna.

MATERIALS AND METHODS

The gastro-intestinal tracts of 14 *Varanus spenceri* held in the Queensland Museum were dissected (QM Accession nos. J15694, J15695, J21656*, J24535, J41654, J47127, J58096, J60593, J60712, J63898, J66732, J74893*, J75043 and J86146*; the three marked with an asterisk had no gastric nematode infection). Nematodes from another three specimens provided by Dave Spratt, Ian Beveridge and Pat Woolley. Nematodes recovered were cleaned and cleared in lactophenol and examined under a BA series Olympus microscope. Ecological terms used follow the definitions of Bush *et al.* (1997). All specimens (nematode accession numbers: G233510-G233526) have been returned to the Queensland Museum.

RESULTS

Three species of nematode were recovered. Nematode infections occurred in 14 out of 17 specimens examined (88%). Adult *Abbreviata hastaspicula* occurred in 14 hosts (82%), at an

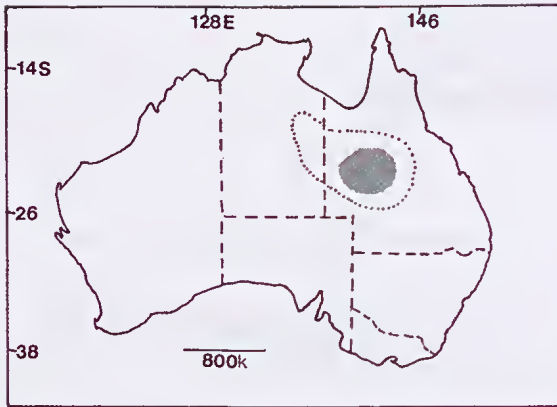


FIG. 1. Map of mainland Australia, showing distribution of *Varanus spenceri* (dotted outline), and area from which specimens studied were collected (shaded area).

intensity of between 1 and 213 (mean 56), and *A. tumidocapitis* in four (23.5%; intensity 2-5). In addition one host was infected with 15 immature *A. tumidocapitis*. One host contained one male and three incomplete female *Hastospiculum* sp. Four specimens infected with *A. hastaspicula* also contained physalopterid larvae in the stomach lumen; there were no larvae encysted in host tissues. All four infections with *A. tumidocapitis* occurred concurrently with *A. hastaspicula*, which with one exception was present at a higher prevalence than *A. tumidocapitis*.

Host Size and Infection. Lizard snout-vent length (SVL) ranged from 205-510 mm (mean, 360 mm). Three lizards had a snout-vent length <300 mm. There were no relationships between host size and intensity of either *A. hastaspicula* (significant regression, $p=0.2283$), or *A. tumidocapitis* ($p=0.1928$).

Host Diet. Ten of 14 stomachs contained food residues. Four contained scanty plant material (grass stems and one ball of plant fibers), six contained orthopteran remains; spur-throated locusts, *Austracris* sp, and *Lagoonia* or *Yrrhapta* spp. were identified in one host each, and one contained a large centipede and a caterpillar. One contained immature bird feathers, and the lizards *Tympanocryptis* sp. and *Ctenotus* sp. and

scanty vertebrate bones were identified from one host stomach.

Locality (Fig. 1). All 17 *V. spenceri* were recovered from central-western Queensland, where Mitchell grass (*Astrebla* spp.) is the dominant vegetation.

DISCUSSION

Abbreviata hastaspicula and *A. tumidocapitis* have been reported from ten other species of tropical and arid-zone *Varanus* lizards, and appear to be confined to this host genus (Jones, unpub.). They are most frequent in *V. gouldii*, *V. acanthiurus* and *V. panoptes* (Jones, 1983a, 1983b, 1988, 1995). The gastric nematode fauna of *V. spenceri* is thus similar to that of other large, closely-related *Varanus* spp. which inhabit the same climatic region, and in which these nematode species occur at comparable prevalence and intensity; five of six *V. gouldii* and one *V. panoptes* examined from Mitchell grassland areas of central Queensland, sympatric with *V. spenceri*, were infected with 9-248 adult *A. hastaspicula*; that with the highest infection was also infected with a single *A. tumidocapitis* (Jones, unpublished). Valentic & Turner (1997), in examining a road-killed *V. spenceri*, recorded a number of small live transparent nematodes (20-25 mm in length) located inside the oesophagus, on the *Ctenotus joanae* (Scincidae) prey items, and in the intestines; these were not identified, but may have been *A. hastaspicula*.

Varanus spenceri is a burrowing species confined to relatively treeless *Astrebla* spp. grasslands in central Queensland and the adjacent Northern Territory, where it feeds on other smaller reptiles, small mammals such as *Rattus villosissimus*, and invertebrates (Pengilley 1981; Jackson & Lemm 2009). Orthoptera, including plague locust species, are frequently reported in the diet of *V. spenceri* (Valentic & Turner 1997; Woolley *et al.* 2010). They occurred in 6/14 lizards dissected in the present study, often as the sole prey species.

Astrebla spp. grasslands (Mitchell Grass) cover about 450 000 km² of inland tropical and subtropical Australia, primarily in western and central Queensland (Orr 1975). These grassy plains are the primary habitat of the Australian

plague locust (*Chortoicetes terminifera*) (Anon. 2009a), from where most plagues originate (Wright *et al.* 1988). Nine of ten lizards whose date of collection was recorded (1971 to 1998), were collected in seasons of localised or major outbreaks (Anon. 2009b). There was no discernible relationship between locust plague years and intensity of *A. hastaspicula*. Neither the time to reach maturity nor the longevity of *Abbreviata* spp. nematodes are known, and in view of the wide range of prey taken by *V. spenceri*, the relevance of the periodic preponderance of migratory locusts in the diet of these lizards cannot be determined. Orthoptera can be intermediate hosts for *Abbreviata kazachstanica* (Kabilov, 1980), and the cockroach *Blatella germanica* for *Abbreviata caucasica* (Poinar & Quentin 1972), but no life cycles of physalopterid nematodes in Australia have yet been elucidated. In the Great Victoria Desert only 7% of *V. gouldii* contained identifiable orthopterans in the stomach (Jones 1995), and in that study epidemiological evidence suggested that termites may have a role as intermediate hosts for arid-zone species of larger species of *Varanus* lizards. However, the black soil country which *V. spenceri* inhabits is almost devoid of termites (Watson & Gay 1991). Larger *Varanus* lizards are opportunistic feeders and take a wide range of largely vertebrate prey (Pianka 1994), many smaller reptiles acting as paratenic hosts for physalopterid nematodes (Jones 1995). Therefore, despite marked differences between the behavioral biology of *V. spenceri* and other species of large sympatric species of *Varanus*, a relatively wide range of arthropod species may be implicated as intermediate hosts for these nematodes.

The third nematode species, recovered from a road-killed lizard, comprised one complete male and three incomplete female *Hastospiculum* sp., but they were in poor condition and could not be confidently identified to species. *Hastospiculum gouldi* has been recorded from several species of *Varanus* in Australia (Yorke & Maplestone 1926; Baylis 1930; Jones 1988) and *H. drysdaliae* from the elapid snake *Drysdalia coronata* (Jones 1980). This is the first report of *Hastospiculum* sp. from *V. spenceri*.

These observations illustrate that despite the discrete and specialised habitat of *V. spenceri* and the preponderance of species of plague locusts in the diet, many other prey species may be taken, and thus nothing can be firmly inferred as to the intermediate hosts of these nematodes.

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LITERATURE CITED

- ANON. 2009a. *Locust habitats*. Department of Agriculture, Fisheries and Forestry, Australian Government. 2pp.
- ANON. 2009b. *History of locust and grasshopper outbreaks in Australia*. Department of Agriculture, Fisheries and Forestry, Australian Government. 4pp.
- Baylis, H.A. 1930. *Filaria macrophallos*, Parona, and the genus *Hastospiculum*, Skrjabin (Nematoda). *Annals and Magazine of Natural History*, 6: 672-677.
- Bush, A.O., Lafferty, K.D., & Shostak, A.W. 1997. Parasitology meets ecology on its own terms: Margolis *et al.* revisited. *Journal of Parasitology* 83: 575-583.
- Cogger, H.G. 1992. *Reptiles and Amphibians of Australia*. (Reed Books: Chatswood).
- Jackson, R. & Lemm, J.M. 2009. Stomach contents note for a road-killed *Varanus spenceri*. *Biawak* 3: 18-20.
- Jones, H.I. 1980. Observations on nematodes from West and Central Australian snakes. *Australian Journal of Zoology* 28: 423-433.
- 1983a. *Abbreviata* (Nematoda: Physalopteridae) in lizards of the *Varanus gouldii* complex (Varanidae) in Western Australia. *Australian Journal of Zoology* 31: 258-298.
- 1983b. Prevalence and intensity of *Abbreviata Travassos* (Nematoda: Physalopteridae) in the Ridge Tailed Monitor *Varanus acanthurus* Boulenger in Northern Australia. *Records of the Western Australian Museum* 11: 1-9.
1988. Nematodes from nine species of *Varanus* (Reptilia) from tropical northern Australia, with

- particular reference to the genus *Abbreviata* (Physalopteridae). *Australian Journal of Zoology* 36: 691-708.
1995. Gastric nematode communities in lizards from the Great Victoria Desert, and an hypothesis for their evolution. *Australian Journal of Zoology* 43: 141-164.
- Kabilov, T.K. 1980. The life cycle of *Abbreviata kazachstanica*. *Parazitologiya* 14: 263-270 [in Russian].
- Lemm, J.M. & Bedford, G.S. 2004. *Varanus spenceri*. In, *Varanoid Lizards of the World*, (eds) E.R. Pianka, D.R. King & R.A. King, (Indiana University Press: Indiana).
- Orr, D.M. 1975. A review of *Astrebla* (Mitchell Grass) pastures in Australia. *Tropical Grasslands* 9: 21-36.
- Pengilley, R. 1981. Notes on the biology of *Varanus spenceri* and *V. gouldii*, Barkly Tablelands, Northern Territory. *Australian Journal of Herpetology* 1: 23-26.
- Pianka, E.R. 1994. Comparative ecology of *Varanus* in the Great Victoria Desert. *Australian Journal of Ecology* 19: 395-408.
- Poinar, G.O. Jr & Quentin, J-C. 1972. The development of *Abbreviata caucasica* (von Linstow) (Spirurida: Physalopteridae) in an intermediate host. *The Journal of Parasitology* 58: 23-28.
- Valentic, R.A. & Turner, G. 1997. Diet and reproductive status of a road-killed Spencer's Monitor *Varanus spenceri*. *Herpetofauna* 27: 43-45.
- Watson, J.A.L., & Gay, F.J. 1991. Isoptera. Pp: 330-347, In, CSIRO, *The Insects of Australia*. (Melbourne University Press: Carlton).
- Woolley, P., Steinbauer, M.J., & Mifsud, G. 2010. *Varanus spenceri*: a last supper of grasshoppers (Acrididae). *Biawak* 4: 24-25.
- Wright, D.E. Hunter, D.M. & Symmons, P.M. 1988. Use of pasture growth indices to predict survival and development of *Chortoicetes terminifera* (Walker) (Orthoptera: Acrididae). *Journal of the Australian Entomological Society* 27:189-192.
- Yorke, W. & Maplestone, P.A. 1926. *The Nematode Parasites of Vertebrates*. London.

A review of *Polyrhachis gravis* and *P. micans* species-groups of the subgenus *Campomyrma* Wheeler (Insecta: Hymenoptera: Formicidae: Formicinae)

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ABSTRACT

Polyrhachis gravis and *micans* species-groups of the subgenus *Campomyrma* Wheeler are reviewed. Ten species in the *gravis*-group are recognised, including two previously described, *Polyrhachis gravis* Clark and *P. pseudothrinax* Hung, and eight species are described as new: *P. bispinosa* sp. nov., *P. capillata* sp. nov., *P. captiva* sp. nov., *P. curtospinosa* sp. nov., *P. hespera* sp. nov., *P. opacita* sp. nov., *P. palmerae* sp. nov. and *P. unicornis* sp. nov. Five species are recognised in the *micans*-group, with three species previously described, *P. incerta* Kohout, *P. micans* Mayr and *P. prometheus* Santschi, and two species are described as new: *P. eureka* sp. nov. and *P. shattucki* sp. nov. A key to the species of both groups is included. All species are illustrated and their known distribution summarised. □ *Polyrhachis gravis*, *micans*, *Formicidae*, *Campomyrma*, *Australia*, *systematics*, *new species*.

The subgenus *Campomyrma* was established by Wheeler, (1911) as a replacement of the Emery's (1896) 'cohors *Polyrhachides camponotiformes*'. He designated *Polyrhachis clypeata* Mayr, 1862 (= *Polyrhachis exercita* Walker, 1859) as the type species, but did not provide a description of the subgenus. Forel (1915) elaborated on Emery's classification by subdividing several of the *Polyrhachis* subgenera established by Wheeler. Within the subgenus *Campomyrma* he included Emery's 'manipulus *clypeata*' and 'manipulus *femorata*', but excluded 'manipulus *thrinax*', which he formally established as subgenus *Myrmothrinax*. A description of *Campomyrma* was eventually provided by Emery (1925), who also subdivided the subgenus into two species-groups, with most species included in the *clypeata-femorata* group and two species from south-east Asia placed in the *halidayi*-

group. An additional, *inconspicua*-group, was listed by Andersen & Burbidge (1991), but the authors did not give any further details. Later, Andersen (2000) recognised six species groups within *Campomyrma* - *creusa*, *gravis*, *inconspicua*, *micans*, *schwiedlandi* and 'Group A', most of them pertinent to the monsoonal and arid zones of northern Australia. He provided a key for their separation and portrayed three of these groups (*gravis*, *micans* and *schwiedlandi*) as composed of 'some of the most spectacular-looking of all *Campomyrma*'. Andersen (2000) characterised the species comprising the *gravis*-group as 'hairy and conspicuously striate species (although often rather shiny), often with contrasting reddish legs. They typically have a scale-like petiolar node, with four erect, approximately equal teeth or small spines'. Two exceptions are *P. pseudothrinax* Hung, 1967

and *P. unicornis* sp. nov., described below, both featuring a *Myrmotherinx*-like petiole with a single, long, central spine. Besides *P. gravis* Clark, 1930 and *P. pseudothrinax*, the *gravis*-group presently includes 8 newly described, closely similar species differentiated mostly by the sculpturation of the mesosoma and the configuration of the petiolar spines. Most species of the group are relatively rare, with many known only from a short original series or single specimens collected during recent environmental surveys of poorly known and isolated parts of the country. Andersen (2000) characterised species of the *micans*-group as 'easily recognised by their *Myrma*-like petiole, with a central pair of long, sharp spines'. The only relatively common species of this group are *P. micans* Mayr, 1876 and *P. prometheus* Santschi, 1920, the latter also being the most widespread species of the group. As perceived here, the *micans*-group includes the two latter species, the recently described *P. incerta* Kohout, 2008 and two new species described below. The third, *schwiedlandi*-group, according to Andersen (2000), is 'extremely rich' in species which are 'distributed primarily throughout the arid zone'. It includes rather 'large, bulky species with highly distinctive, curled petiolar node, with strongly curved carinae running between the central and lateral teeth' (Andersen, 2000). The taxonomy of the *schwiedlandi*-group will be dealt with in a separate paper. While this framework is being followed here, it is anticipated that further studies on this subgenus will result in refinements and changes to the groups recognised by Andersen (2000). This will be undertaken in a future study.

METHODS

Photographs of specimens were taken with a digital camera attached to a stereomicroscope and processed using Auto-Montage (Syncroscopy, Division of Synoptics Ltd, USA) and Adobe Photoshop CS2 (Adobe Systems Inc., USA). Unless otherwise indicated, images of new species depict the primary types. Those of previously described species are mostly of

type-compared voucher specimens from ANIC or QM collections.

The standard measurements and indices follow those of Kohout (2008): TL = Total length (the necessarily composite measurement of the outstretched length of the entire ant measured in profile); HL = Head length (the maximum measurable length of the head in perfect full face view, measured from the anterior-most point of the clypeal border or teeth, to the posterior-most point of the occipital margin); HW = Head width (width of the head in perfect full face view, measured immediately in front of the eyes); CI = Cephalic index ($HW \times 100 / HL$); SL = Scape length (length of the antennal scape, excluding the condyle); SI = Scape index ($SL \times 100 / HW$); PW = Pronotal width (greatest width of the pronotal dorsum, including the pronotal teeth, or across the humeri in species without teeth); MTL = Metathoracic tibial length (maximum measurable length of the tibia of the hind leg). All measurements were taken using a Zeiss (Oberkochen) SR stereomicroscope at 20x and 32x magnifications with an eyepiece graticule calibrated against a stage micrometer. All measurements are expressed in millimetres (mm).

Abbreviations for specimen data. acc. – accession; Ck – Creek; for. – forest; Mt – Mount; NP – National Park; Pdk – paddock; rf – rainforest; stn – station; w – worker/s; xing – crossing. Standard abbreviations are used for the states and territories.

Abbreviations for collectors name. ANA – A.N. Andersen; BBL – B.B. Lowery; CJB – C.J. Burwell; RJK – R.J. Kohout.

Abbreviations for institutions and depositories (with names of cooperating curators). AMNH – American Museum of Natural History, New York, NY, USA. (Dr J.M. Carpenter); AMSA – Australian Museum, Sydney, NSW, Australia (Drs D. Britton, D. Smith); ANIC – Australian National Insect Collection, CSIRO Entomology, Canberra, ACT, Australia (Dr S.O. Shattuck); BMNH – The Natural History Museum, London, UK (S. Ryder); CASC – California Academy of Sciences, San Francisco, CA., USA (Dr B.L. Fisher); CURT – Curtin University of Technology, Perth, WA, Australia (Drs J.D. Majer, B.E. Heterick); MCZC – Museum of Comparative Zoology, Harvard University, Cambridge, MA., USA (Dr S.P. Cover);

MHNG – Muséum d’Histoire Naturelle, Geneva, Switzerland (Dr B. Merz); MNHU – Museum für Naturkunde, Humboldt-Universität, Berlin, Germany (Dr F. Koch); MLAC - Natural History Museum, Los Angeles, CA, USA (Dr R.R. Snelling); MVMA – Museum of VIC, Melbourne, VIC., Australia (Dr K. Walker); NHMB – Naturhistorisches Museum, Basel, Switzerland (Dr D.H. Burckhardt); NHMW - Naturhistorisches Museum, Vienna, Austria (Dr H. Zettel; D. Zimmermann); NMNH – National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (Drs T.R. Schultz, D.R. Smith); OXUM – University Museum, Oxford, UK (Dr D.J. Mann); QM – QLD Museum, Brisbane, QLD, Australia (Dr C.J. Burwell); SAMA – SA Museum, Adelaide, SA, Australia (A. McArthur); TERC – Tropical Ecosystems Research Centre, CSIRO Sustainable Ecosystems, Darwin, NT, Australia (Dr A.N. Andersen); WAMP – WA Museum Perth, WA, Australia (Dr T. Houston).

SYSTEMATICS

Polyrhachis Fr. Smith, 1857

Polyrhachis Fr. Smith, 1857: 58. Type species: *Formica bihamata* Drury, 1773: 73, pl. 38, figs 7, 8, worker; by original designation.

Campomyrma Wheeler, 1911

Campomyrma Wheeler, 1911: 860 (as subgenus of *Myrma* Billberg, 1820 = *Polyrhachis* Fr. Smith, 1857). Type species: *Polyrhachis clypeata* Mayr, 1862 (junior synonym of *Polyrhachis exercita* Walker, 1859), by original designation.

POLYRHACHIS GRAVIS
SPECIES-GROUP

Description. *Worker:* Medium-sized to relatively large ants (HL > 2.30) with general characteristics of the genus and subgenus. Mandibles with 5 or 6 teeth; anterior clypeal margin widely truncate medially, with truncate portion mostly irregularly denticulate. Head with sides in front of eyes rounded towards mandibular bases; behind eyes sides with short, postocular lateral ridges, forming distinct, narrowly rounded occipital corners, before converging into relatively narrow occipital margin. Eyes mostly moderately large (except in *P. hespera*) and convex; ocelli lacking. Pronotal humeri angular (as in *P. capillata* or *P. opacita*) (e.g. Figs 1G; 4E), or narrowly

rounded with pronotal lateral margins behind more-or-less emarginate (as in *P. curtospinosa*, *P. palmerae* or *P. unicornis*) (e.g. Figs 2G; 4G; 5G). Mesonotal and propodeal dorsa strongly converging posteriorly with lateral margins of propodeal dorsum terminating in short, upturned teeth. Petiole scale-like, with four spines or teeth of various configurations, or with a pair of dorsal spines and lateral teeth greatly reduced (as in *P. bispinosa*), or with a single dorsal spine and two lateral teeth (as in *P. pseudothrinax* and *P. unicornis*). Gaster in side view with anterior face straight; dorsoanterior margin of first gastral tergite with a distinct carina in most species, except *P. captiva* and *P. opacita*, where carina is only poorly indicated.

Queen. Apart from sexual characters, including three ocelli, complete thoracic structure and wings, very similar to worker. Armament of pronotum, propodeum and petiole distinctly reduced with spines and teeth shorter and stouter. Sculpturation, pilosity and colour virtually identical to worker. The only known queen is that of *P. pseudothrinax* described below.

Male. Males and immature stages unknown.

Distribution and biology. Species of the *P. gravis*-group are distributed primarily throughout the arid and monsoonal zones of central and northern Australia. Most are relatively rare and only occasionally collected in poorly known and isolated parts of the country. From a few know records, they are terrestrial nesters, building their nests under the ground with entrances covered by a rock, piece of wood, or simply concealed by a tuft of grass.

KEY TO WORKERS OF THE
P. GRAVIS SPECIES-GROUP

1. Dorsum of petiole armed with single spine 2
- Dorsum of petiole armed with pair of spines 3
2. Pronotal humeri simply angular; eyes smaller, distinctly convex; dorsal petiolar spine long and acute (Fig. 5B,E-F) *P. pseudothrinax* Hung

- Pronotal humeri produced into short, distinct teeth; eyes larger, moderately convex; dorsal petiolar spine short and blunt (Fig. 5D,G-H). *P. unicornis* sp. nov.
- 3. Petiolar node in profile distinctly swollen at base (Fig. 1F) *P. bispinosa* sp. nov.
 - Petiolar node in profile slender, scale-like (e.g. Figs 1H; 3H) 4
- 4. Pilosity generally long, hair-like, rather abundant. 5
 - Pilosity generally short, bristle-like, less abundant 6
- 5. Large species (HL 2.68); pilosity very long, abundant; lateral margins of propodeal dorsum barrel-shaped (VIC). . . *P. captiva* sp. nov.
 - Smaller species (HL < 2.50); pilosity shorter, more sparse, notably on dorsum of mesosoma; lateral margins of propodeal dorsum converging posteriorly (WA) . . . *P. capillata* sp. nov.
- 6. Petiole high and slender in frontal view; dorsolateral margins steeply raised, strongly converging dorsally, forming single base for two slender dorsal spines (Fig. 4D,G); body black, somewhat semipolished, with appendages light orange (WA, Kimberley) *P. palmerae* sp. nov.
 - Petiole about as long as wide in frontal view; dorsolateral margins less steep and less strongly converging dorsally; bases of dorsal pair of spines more widely separated (e.g. Figs 2D; 4B); body rather dull black, opaque, with appendages black or dark reddish-brown 7
- 7. Dorsal petiolar spines tooth-like, distinctly shorter and stouter than lateral spines (Fig. 2D); bristle-like pubescence very sparse, virtually lacking from dorsum of mesosoma and petiole *P. curtospinosa* sp. nov.
 - Dorsal petiolar spines slender, distinctly longer than lateral spines (e.g. Figs 3B,D; 4B); bristle-like pubescence present on most body surfaces, including dorsum of mesosoma and petiole 8
- 8. Anterior margin of first gastral tergite with strongly raised carina 9
 - Anterior margin of first gastral tergite with only poorly indicated carina (WA) *P. opacita* sp. nov.
- 9. Antennal scapes longer (Sl >125); eyes more-or-less normal, moderately convex; pronotal humeri narrowly rounded with pronotal margins behind shallowly emarginated; greatest width of pronotal dorsum at middle of segment (NT, QLD) *P. gravis* Clark
 - Antennal scapes shorter (Sl 115); eyes distinctly smaller, strongly convex; pronotal humeri distinctly angular; greatest width of pronotal dorsum across humeri (WA) *P. hespera* sp. nov.

***Polyrhachis bispinosa* sp. nov.**
(Figs 1A-B, E-F)

Etymology. Name derived from the combination of the Latin words *bi-*, meaning two and *spina*, meaning thorn, spine, with reference to the twin dorsal petiolar spines.

Material. HOLOTYPE: NT: Kakadu NP, Nourlangie Rock, 12°51'S, 132°49'E, 12.i.1991, open sclerophyll forest, A.N. Andersen (worker). PARATYPES: NT: Kakadu NP, ii.2004, A. Fisher, PFS (worker); Bradshaw Stn, Yambaron Plateau, vii.1997 (A.L. Hertog) (worker). QLD: Mt Isa, xi.1997 (B. Hoffmann) (2 workers); Mt Isa Mines, xii.1997 (T. Griffiths) (worker); Mt Isa Mines, v.2005 (T. Griffiths) (worker). Type deposition: Holotype in ANIC; 2 paratype workers each in QM and TERC; 1 paratype worker each in BMNH and MCZC.

Description. *Worker:* Dimensions (holotype cited first): TL c. 8.72, 7.51-8.72; HL 2.21, 1.93-2.21; HW 1.93, 1.68-1.93; CI 87, 86-89; SL 2.28, 2.06-2.28; Sl 118, 113-123; PW 1.62, 1.40-1.62; MTL 2.93, 2.34-2.93 (4 measured).

Mandibles with 5 teeth distinctly reducing in length towards base. Anterior clypeal margin widely medially truncate with truncate portion distinctly denticulate. Clypeus with blunt, poorly defined median carina; weakly sinuate in profile with weakly impressed basal margin. Frontal carinae sinuate with weakly raised margins; central area almost flat with poorly indicated frontal furrow. Sides of head in front

of eyes rounding into mandibular bases in weakly convex line; behind eyes sides forming distinct, narrowly rounded, almost right-angled occipital corners, before converging into relatively narrow occipital margin. Eyes convex, in full face view clearly breaking lateral cephalic outline. Ocelli lacking. Pronotal humeri distinctly angular with margins converging anteriorly towards pronotal collar; lateral margins of pronotal dorsum converging into well impressed promesonotal suture. Dorsum of mesonotum with lateral margins strongly converging posteriorly towards distinct metanotal groove, forming almost straight line with lateral margins of propodeum and terminating in closely approximated, rather blunt, propodeal teeth; margins of teeth continued for short distance downwards into steeply concave propodeal declivity. Petiole with base distinctly swollen in lateral view (Fig. 1F); sides strongly convex towards dorsum armed with pair of closely approximated, dorso-posteriorly directed, slender spines; lateral petiolar spines reduced to mere angles. Anterior face of first gastral segment flat in lateral view, widely rounding onto dorsum; anterodorsal margin of first gastral tergite with blunt transverse carina.

Mandibles very finely striate with numerous piliferous pits. Head between frontal carinae and eyes distinctly, rather regularly, longitudinally striate; sculptural pattern distinctly less regular towards sides and on vertex where it is rugose with numerous piliferous pits. Dorsum of mesosoma generally longitudinally striate, with striae on pronotal dorsum somewhat posteriorly diverging and curving towards posterior corners of segment. Sides of mesosoma finely, more-or-less uniformly, wrinkled. Propodeal declivity and petiole finely, transversely striate. Gaster with base and sides of first tergite rather polished, intensity of sculpture increasing dorsally, becoming very finely, longitudinally striate towards posterior margin of segment; subsequent tergites finely reticulate-punctate.

Mandibles with numerous curved, golden hairs. Anterior clypeal margin with several, anteriorly directed, unequal length golden setae

medially and shorter setae fringing margin laterally. Numerous erect to semierect hairs on head, mesosoma, gaster and legs, hairs longest on clypeus and gastral venter and shortest on dorsum of mesosoma; antennae with numerous short, bristle-like, semierect hairs.

Black; mandibles medium reddish-brown with teeth black. Clypeus dark reddish brown with anterior margin narrowly bordered black. Antennal scapes dark reddish-brown with funiculi a shade lighter. Legs, including middle and hind coxae distinctly orange, tarsi a shade darker.

Sexuals and immature stages unknown.

Remarks. The characteristic distinctly swollen base of the petiole makes this species easily recognisable (Fig. 1F). The distribution of *P. bispinosa* appears to be restricted to the northern parts of the NT and the Mt Isa basin in north-western QLD.

Polyrhachis capillata sp. nov.
(Figs 1C-D, G-H)

Etymology. Derived from the Latin *capillus*, meaning hair, in reference to the relatively long hair distributed over most body surfaces.

Material. HOLOTYPE: WA: Kalgoorlie, WA, Museum, No. 50-1804/51 (worker). PARATYPE: data as for holotype, except WA, Museum No. 50-1812/41 (worker). Type deposition: Holotype in WAMP; paratype in ANIC.

Description. *Worker:* Dimensions. (holotype cited first) TL c. 9.68, 10.89; HL 2.28, 2.50; HW 1.96, 2.21; CI 86, 88; SL 2.56, 2.74; SI 131, 124; PW 1.87, 2.02; MTL 3.38, 3.83 (2 measured).

Mandibles with 6 teeth, distinctly reducing in length towards base. Anterior clypeal margin widely truncate medially, truncate portion bluntly and irregularly denticulate. Clypeus without distinct median carina; clypeus in profile very shallowly convex with raised anterior margin, virtually flat posteriorly. Frontal triangle only shallowly impressed. Frontal carinae sinuate with moderately raised margins; central area with flat frontal furrow. Sides of head in front of eyes converging towards mandibular bases in straight line; behind eyes sides converging

into rather narrow occipital margin. Eyes convex, in full face view clearly breaking lateral cephalic outline. Ocelli lacking. Pronotal humeri produced into distinct, laminate, triangular teeth, lateral pronotal margins behind teeth converging posteriorly into promesonotal suture. Mesonotal dorsum with anterior corners rounded; lateral margins converging posteriorly towards flat metanotal groove. Propodeal dorsum distinctly longer than wide with lateral margins converging posteriorly and terminating in short, upturned, divergent, acute teeth; dorsum curving into shallowly concave declivity in medially uninterrupted line. Petiole scale-like, virtually triangular in lateral view; dorsum armed medially with a pair of relatively short and slender, acute spines; inner margins of spines continuous medially, forming rather narrow, 'U' shaped dorsum of petiole; outer margins of spines steeply descending towards distinct, acute lateral spines that are only marginally shorter than dorsal pair (Fig. 1D). Gaster in lateral view with anterior face flat; anterior margin of first gastral tergite with blunt transverse carina.

Mandibles finely, longitudinally striate with numerous piliferous pits. Clypeus reticulate-punctate; head and dorsum of mesosoma reticulate-punctate with sculpture distinctly organised in mostly longitudinal striae, except on pronotal dorsum where striae are distinctly divergent towards lateral margins of segment; sides of mesosoma finely wrinkled. Anterior face of petiole rather coarsely reticulate-punctate with sculpture distinctly finer dorsally; posterior face more finely, transversely wrinkled. Gaster very finely reticulate, opaque.

Mandibles with numerous, curved, golden hairs at masticatory borders and along outer margins; truncate median portion of anterior clypeal margin with numerous, relatively long, golden setae; numerous shorter setae fringing margin laterally. All body surfaces, including appendages, with semierect to erect and variously curved, moderately long, golden hairs; hairs distinctly shorter and much diluted on pronotal and mesonotal dorsa; apical portion of propodeal dorsum with tuft of variously curved, medium length hairs. Hairs on head anteriorly

inclined, those on dorsum of mesosoma, petiole and dorsum of gaster mostly erect, hairs on gastral venter distinctly posteriorly curved. Diluted, closely appressed, greyish pubescence present only on coxae, virtually absent from rest of body.

Mandibles distinctly reddish-brown towards masticatory borders, with bases and teeth dark reddish-brown; antennae virtually black with only apical funicular segments reddish-brown; Legs medium reddish-brown, with tibiae a shade darker; tarsi black. Venter and apex of gaster very dark, reddish-brown.

Sexuals and immature stages unknown.

Remarks. *Polyrhachis capillata* is characterised by its relatively long hairs, notably on the front of the head, antennal scapes and legs, the distinct tuft of variously curved, medium length hairs on the posterior portion of propodeal dorsum around the propodeal teeth and the rather distinct, somewhat laminate humeral teeth (Fig. 1G). Only two specimens of *P. capillata* are known, both collected at Kalgoorlie in the Goldfields region of WA.

Polyrhachis captiva sp. nov.
(Figs 2A-B, E-F)

Etymology. Derived from the Latin *captivus*, meaning 'taken prisoner' in reference to the unique holotype being caught in a pitfall trap.

Material. HOLOTYPE: VIC, Nowingi, 34°36'S, 142°13'E, 20-23.xi.2004, top of sand dune, pitfall trap, DPI PIRVic Knoxfield (worker). Unique holotype in ANIC.

Description. *Worker:* Dimensions. TL c. 11.79; HL 2.68; HW 2.34; CI 87; SL 3.06; SI 131; PW 2.09; MTL 4.03 (1 measured).

Mandibles with 6 teeth, distinctly reducing in length towards base. Anterior clypeal margin widely truncate; truncate portion irregularly denticulate, with angular corners. Clypeus with blunt, poorly defined median carina; straight in profile with flat basal margin. Frontal triangle shallowly impressed. Frontal carinae sinuate with only moderately raised margins; central area with rather flat frontal furrow. Sides of head in front of eyes converging towards mandibular bases in straight line; behind eyes

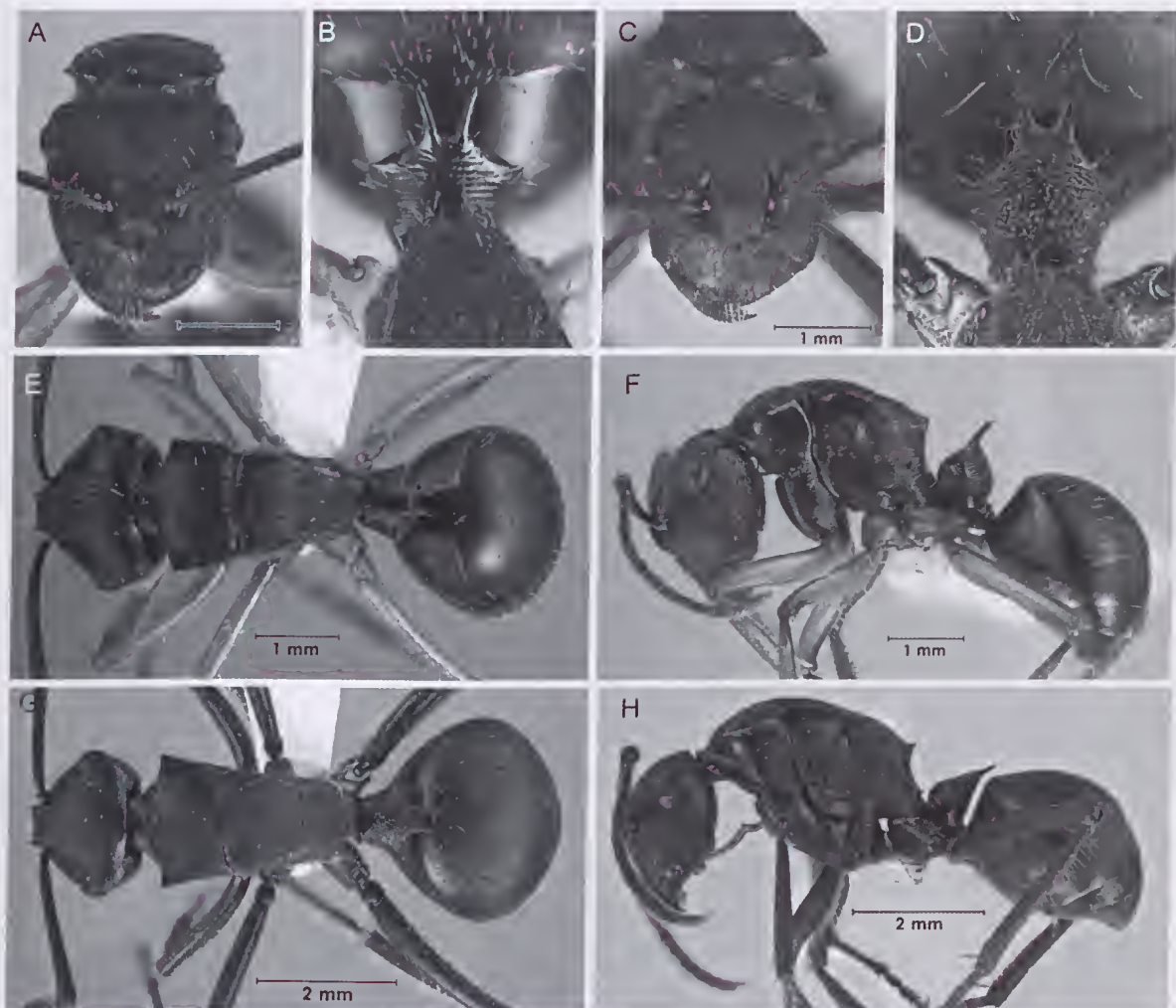


FIG. 1. *Polyrhachis gravis* species-group. Head in full-face view (A, C), petiole in frontal view (B, D), dorsal habitus (E, G), lateral habitus (F, H): *P. bispinosa* sp. nov. (holotype) (A-B, E-F); *P. capillata* sp. nov. (holotype) (C-D, G-H).

sides rounding into only moderately convex occipital margin. Eyes convex, in full face view clearly breaking lateral cephalic outline. Ocelli lacking. Pronotal humeri armed with distinct triangular, laminate, teeth; lateral margins behind humeri weakly emarginate and converging posteriorly in weakly convex line into distinct promesonotal suture. Mesonotal dorsum with anterior corners widely rounded; lateral margins converging posteriorly towards distinct metanotal groove. Propodeal dorsum with lateral margins barrel-shaped and

terminating posteriorly in short, upturned, acute teeth; dorsum curving into shallowly concave declivity in medially uninterrupted line. Petiole scale-like, virtually triangular in lateral view; dorsum armed medially with a pair of relatively short and slender, weakly divergent, acute spines; inner margins of spines continuous medially, forming rather narrow, 'U'-shaped dorsum of petiole; outer margins of spines steeply descending into distinct lateral angles, produced into short, acute spines (Fig. 2B). Gaster in lateral view with anterior face

flat; anterior margin of first gastral tergite with blunt, transverse carina.

Mandibles distinctly, longitudinally striate-rugose with numerous piliferous pits. Clypeus reticulate-punctate; head and dorsum of mesosoma reticulate-punctate with sculpture distinctly organised into relatively fine, mostly longitudinal striae; sides of mesosoma finely wrinkled. Petiole with anterior face rather coarsely, transversely reticulate-punctate; posterior face more finely, transversely wrinkled. Gaster very finely shagreened, somewhat semipolished.

Very hairy; mandibles with numerous, curved, golden hairs; truncate median portion of anterior clypeal margin with numerous, relatively long, pale golden setae; numerous shorter setae fringing margin laterally. All body surfaces, including appendages, with semierect to erect, generally long, pale golden or silvery hairs, some almost as long as greatest diameter of eyes. Hairs on head anteriorly inclined, those on dorsum of mesosoma and petiole mostly erect, those on gaster distinctly posteriorly curved. Closely appressed, greyish pubescence present only on anterior face of fore coxae, virtually absent from rest of body.

Mandibles distinctly reddish-brown towards masticatory borders; antennae virtually black with only apical funicular segments reddish-brown; Legs very dark reddish-brown; tarsi black with apical segments rather light reddish-brown. Venter and apex of gaster dark reddish-brown.

Sexuals and immature stages unknown.

Remarks. The unique holotype is a rather large specimen, distinguished from the other species of the group by its relatively large size, a pronotal dorsum with humeri produced into distinct, laminate, triangular teeth and weakly convex lateral margins (Fig. 2E) and a barrel-shaped propodeal dorsum. Postocellar process lacking and carina of dorsoanterior margin of first gastral segment only very weakly indicated. Pilosity very distinct, notably on dorsa of head, mesosoma, appendages and gaster, the later with hairs almost reaching in length the greatest diameter of eye; hairs

are virtually absent from sides of mesosoma. *Polyrhachis captiva* is the only species of the group known from VIC. The single known specimen was collected in a pitfall trap on the top of an inland sand dune.

Polyrhachis curtospinosa sp. nov.
(Figs 2C-D, G-H)

Etymology. Derived from the combination of the Latin *curtus*, meaning shorten and *spina*, meaning thorn or spine, in reference to the distinctly shortened dorsal petiolar spines.

Material. HOLOTYPE: NT: 6.5 km WNW of Yuendumu Mission, 10.iv.1963, McInnes & Dowsie (worker). PARATYPES: data as for holotype (worker). QLD: Mt Isa, CRC MIM study site, xii.1997 (T. Griffiths) (2 workers). Type deposition: Holotype in ANIC; 1 paratype each in BMNH, MCZC and QM.

Description. *Worker.* Dimensions: TL c. 9.22, 9.22-9.78; HL 2.31, 2.28-2.36; HW 2.12, 2.09-2.15; CI 92, 91-92; SL 2.43, 2.40-2.50; SI 115, 114-116; PW 1.84, 1.65-1.84; MTL 2.93, 2.87-2.96 (1+3 measured).

Mandibles with 6 teeth. Anterior clypeal margin widely truncate, with truncate portion irregularly denticulate. Clypeus smoothly curved without median carina; weakly sinuate in profile with flat base. Frontal triangle distinct. Frontal carinae sinuate with moderately raised margins; central area with rather indistinct frontal furrow. Sides of head in front of eyes weakly convex towards mandibular bases; behind eyes sides narrowly rounding into moderately convex occipital margin. Eyes convex, in full face view clearly breaking lateral cephalic outline. Ocelli lacking. Pronotal humeri bluntly angular, with lateral margins behind emarginate, before converging posteriorly towards well impressed promesonotal suture. Mesonotal lateral margins converging posteriorly, virtually forming a continuous line with margins of propodeum; metanotal groove flat. Propodeal dorsum strongly narrowed posteriorly with lateral margins terminating in upturned, somewhat medially flattened teeth; dorsum somewhat medially and posteriorly concave before curving through narrow gap between closely approximated teeth into steeply descending declivity. Petiole scale-like in lateral view;

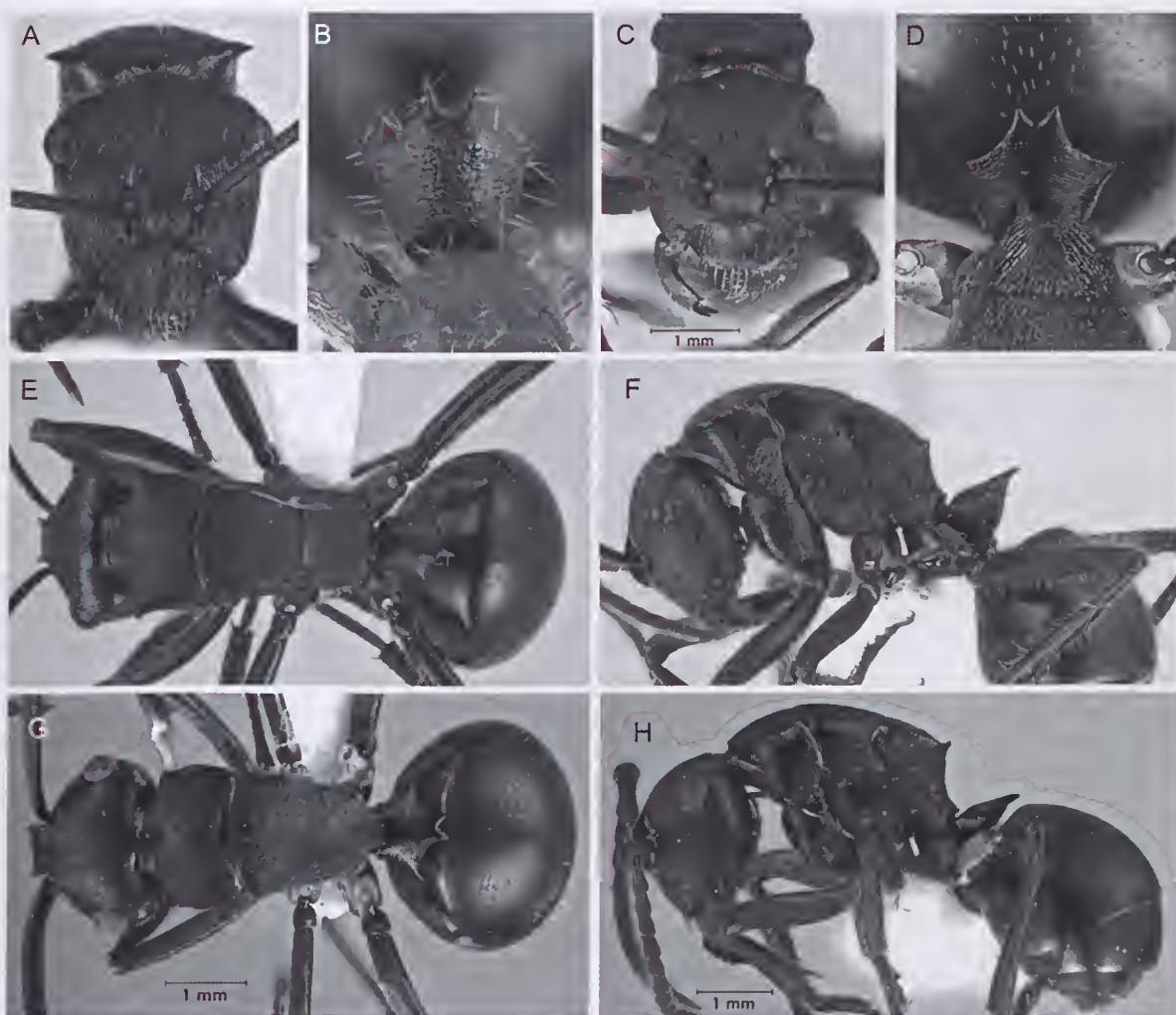


FIG. 2. *Polyrhachis gravis* species-group. Head in full-face view (A, C), petiole in frontal view (B, D), dorsal habitus (E, G), lateral habitus (F, H): *P. captiva* sp. nov. (holotype) (A-B, E-F); *P. curtospinosa* sp. nov. (holotype) (C-D, G-H).

dorsum armed with a pair of tooth-like spines, hardly longer than their basal width; outer margins of spines descending into slender, acute, lateral spines (Fig. 2D). Gaster in lateral view with anterior face flat; anterior margin of first gastral tergite with blunt transverse carina.

Mandibles finely, longitudinally striate with numerous piliferous pits. Clypeus reticulate-punctate; head distinctly, mostly longitudinally striate. Pronotal dorsum with distinctly finer striae that curve medially from humeral angles towards centre, before turning towards

promesonotal suture and posterior corners of segment. Dorsa of mesonotum and propodeum mostly longitudinally striate, striae on propodeum strongly converging posteriorly towards narrow gap between propodeal teeth. Sides of mesosoma and petiole finely wrinkled. Gaster very finely and closely reticulate, somewhat semipolished.

Mandibles with numerous, curved, golden hairs at masticatory and outer borders; anterior clypeal margin with numerous, relatively long, golden setae medially and fringe of shorter

setae laterally. Several semierect, rather short, golden hairs on clypeus; only a few, very short, bristle-like hairs along frontal carinae and on vertex, none breaking cephalic outline in full face view. Only a few, very short, anteriorly inclined hairs evident on pronotal dorsum of some specimens, no hairs on mesonotal and propodeal dorsa and petiole. Dorsum of gaster with only a few, very short, golden hairs along posterior margins of segments; hairs distinctly longer and posteriorly curved on vertex and gastral apex. Closely appressed, golden pubescence in various densities on most body surfaces, virtually absent from dorsum of mesosoma.

Head, mesosoma and petiole generally black. Mandibles, mandibular bases and anterior portion of clypeus distinctly orange or light reddish-brown, narrowly bordered brown or black. Antennae black or very dark brown with funicular segments progressively lighter reddish-brown towards apices. Legs, including coxae, light to medium reddish-brown with basal portion of tibiae and tarsi black; apical tarsal segments reddish-brown. Dorsum of gaster black with dorsoanterior margin, sides, venter and apex progressively lighter reddish-brown.

Sexuals and immature stages unknown.

Remarks. *Polyrhachis curtospinosa* is very similar to *P. gravis* but differs in having distinctly shorter antennal scapes (SI 114-116 in *curtospinosa* versus 125-131 in *gravis*), very short, tooth-like dorsal petiolar spines and mesosomal dorsum that completely lacks the short, bristle-like pilosity seen in *P. gravis*. The distribution of *P. curtospinosa* is similar to that of *P. bispinosa* and appears to be restricted to the northern parts of the NT and the Mt Isa basin in north-western QLD.

Polyrhachis gravis Clark, 1930
(Figs 3A-B, E-F)

Polyrhachis (*Campomyrma*) *gravis* Clark, 1930: 15, fig. 1, nos 12, 12a. Holotype and paratype workers. Type locality: NT: Burt Plain (C. Barrett), MVMA (examined).

Dimensions (holotype cited first, paratype second): TL c. 10.58, 8.77, 8.72-10.58; HL 2.43, 2.25, 2.18-2.48; HW 2.17, 1.93, 1.93-2.20; Cl 89, 86, 86-92; SL 2.74, 2.53,

2.49-2.81; SI 126, 131, 125-131; PW 1.72, 1.56, 1.56-1.72; MTL 3.28, 3.09, 3.09-3.38 (1+1+14 measured).

Material. WA: 147.1 km SSE Newman, 24°34'28"S, 120°18'28"E, iv.1997, calcrete mulga woodland, pitfall trap (S.van Leeuwen & R.N. Bromilow (w)). NT: 6.5 km WNW of Yuendumu Mission, 10.iv.1963 (McInness & Dowse) (w); c. 56 km E of Sandy Blight Junct., 5.iv.1963 (McInness & Dowse) (w); Kunoth Pdk, nr Alice Springs, 24.x.1974 (P.J.M. Greenslade) (w). QLD: Mitchell Hwy, 11 km S Charleville, 26°30'S, 146°11'E, 13-22.v.1991 (T. Dahms & G. Sarnes) (w); 'Gumbardo' site 8, 26°4.4'S, 144°45.9'E, iv.2001, mulga pitfall trap (T. Beutel) (w); ditto, site 4, 26°5.8'S, 144°45.0'E, iv.2001, mulga pitfall trap (T. Beutel) (w).

Sexuals and immature stages unknown.

Remarks. Based on the original description, it appears that both available specimens of *P. gravis* were regarded by Clark as equals, i.e. syntypes. However, one of the specimens is furnished with a red tag which reads: T-6238, Type. When Dr Robert W. Taylor examined both specimens, he evidently considered this specimen to be the holotype and added a new red tag reading 'HOLOTYPE, T-6238, *Polyrhachis gravis* Clark'. I am following Taylor's decision and accept this specimen as the holotype of *P. gravis*, with the second specimen labelled with 'PARATYPE, T-9088' on a blue tag, considered a paratype.

Polyrhachis gravis is a characteristic species of the dry, mulga and spinifex clad country of the central Australia. It has been collected in the Pilbara region in WA and across the NT to western QLD. In spite of being widely distributed, *P. gravis* is relatively morphologically uniform with only minor variations from the types detected in some specimens from WA and QLD. These are manifest mostly in the direction of the body sculpturation, the apical width of the propodeal dorsum and the length of the dorsal petiolar spines that can vary even in specimens of a single nest series (e.g. specimens from Kunoth Pdk, nr Alice Springs).

Polyrhachis hespera sp. nov.
(Figs 3C-D, G-H)

Etymology. Derived from the Latin *hesperius*, meaning western, referring to its WA origin.

Material. HOLOTYPE: WA, RGC Eneabba, c. 29°49'S, 115°16'E, iii.1998, Paul West (worker). Type distribution: Unique holotype in ANIC.

Description. *Worker.* Dimensions: TL c. 9.42; HL 2.25; HW 2.03; CI 90; SL 2.34; SI 115; PW 1.65; MTL 2.99 (1 measured).

Mandibles with 6 teeth. Anterior clypeal margin widely truncate, truncate portion irregularly denticulate, laterally delimited by blunt angles. Clypeus without distinct median carina; straight in profile with flat base. Frontal triangle weakly impressed. Frontal carinae sinuate with moderately raised margins; central area with rather indistinct frontal furrow. Sides of head in front of eyes evenly convex towards mandibular bases; behind eyes sides narrowly rounding into distinct occipital corners. Eyes strongly convex, in full face view clearly breaking lateral cephalic outline. Ocelli lacking. Pronotal humeri bluntly angular, with lateral margins converging posteriorly towards weakly impressed promesonotal suture. Mesonotal and propodeal lateral margins weakly sinuate, converging posteriorly and terminating in upturned teeth; propodeal dorsum curving through narrow gap between teeth into steep, weakly concave declivity. Petiole scale-like in lateral view; dorsum armed with a pair of closely approximate spines; outer margins of spines descending into acute, shorter and slender, lateral spines (Fig. 3D). Gaster in lateral view with anterior face flat; anterior margin of first gastral tergite with distinct transverse carina.

Mandibles finely, longitudinally striate with numerous piliferous pits. Clypeus reticulate-punctate; head distinctly irregularly rugose, with sculpture on vertex and along frontal carinae somewhat longitudinally striate-rugose. Pronotal dorsum mostly longitudinally striate; dorsa of mesonotum and propodeum mostly longitudinally striate-rugose. Sides of mesosoma and petiole finely wrinkled. Gaster very finely and closely reticulate-striate.

Mandibles with numerous, curved, golden hairs at masticatory and outer borders; anterior clypeal margin with numerous, relatively long, somewhat reddish-golden setae medially

and fringe of shorter setae laterally. Several semierect, rather short, golden hairs, on clypeus; very short, bristle-like hairs on head and mesosomal dorsum, metapleura and a few hairs along lateral margins of petiole. Dorsum of gaster with numerous, very short, golden hairs, hairs increasing in length towards gastral apex and on venter, where they are distinctly longer and posteriorly inclined. Antennae and legs with numerous, very short, bristle like hairs on all surfaces. Closely appressed, rather grey or silvery pubescence very sporadic on various body surfaces, virtually absent from dorsum of head, mesosoma and petiole.

Mandibles light reddish-brown at masticatory borders, distinctly darkening towards bases; teeth and outer edges bordered black. Antennal scapes black; basal funicular segments black at bases, subsequent funicular segments progressively lighter, reddish-brown towards apices. Most of body, including fore coxae and petiole black; middle and hind coxae and femora medium reddish-brown; tibiae and tarsi black. Gaster black with gastral segments bordered reddish-brown; apex of gaster reddish-brown.

Sexuals and immature stages unknown.

Remarks. *Polyrhachis hespera* is quite similar to *P. gravis*. They share a distinctly raised carina on the anterior margin of first gastral tergite and have quite similar configurations of the petiole. It differs from the latter by its shorter antennal scapes (SI 115 in *hespera* versus 125-131 in *gravis*), distinctly smaller and strongly convex eyes, and by having the pronotal dorsum widest across the humeri. In contrast, the eyes in *P. gravis* are comparatively larger and less convex and the pronotal dorsum is widest at about its midlength. *Polyrhachis hespera* is known only from a single specimen collected at Eneabba in the Batavia Coast region of WA.

Polyrhachis opacita sp. nov.
(Figs 4A-B, E-F)

Etymology. Derived from the Latin *opacus*, meaning shady, obscure, in reference to its very finely striate, opaque gaster.

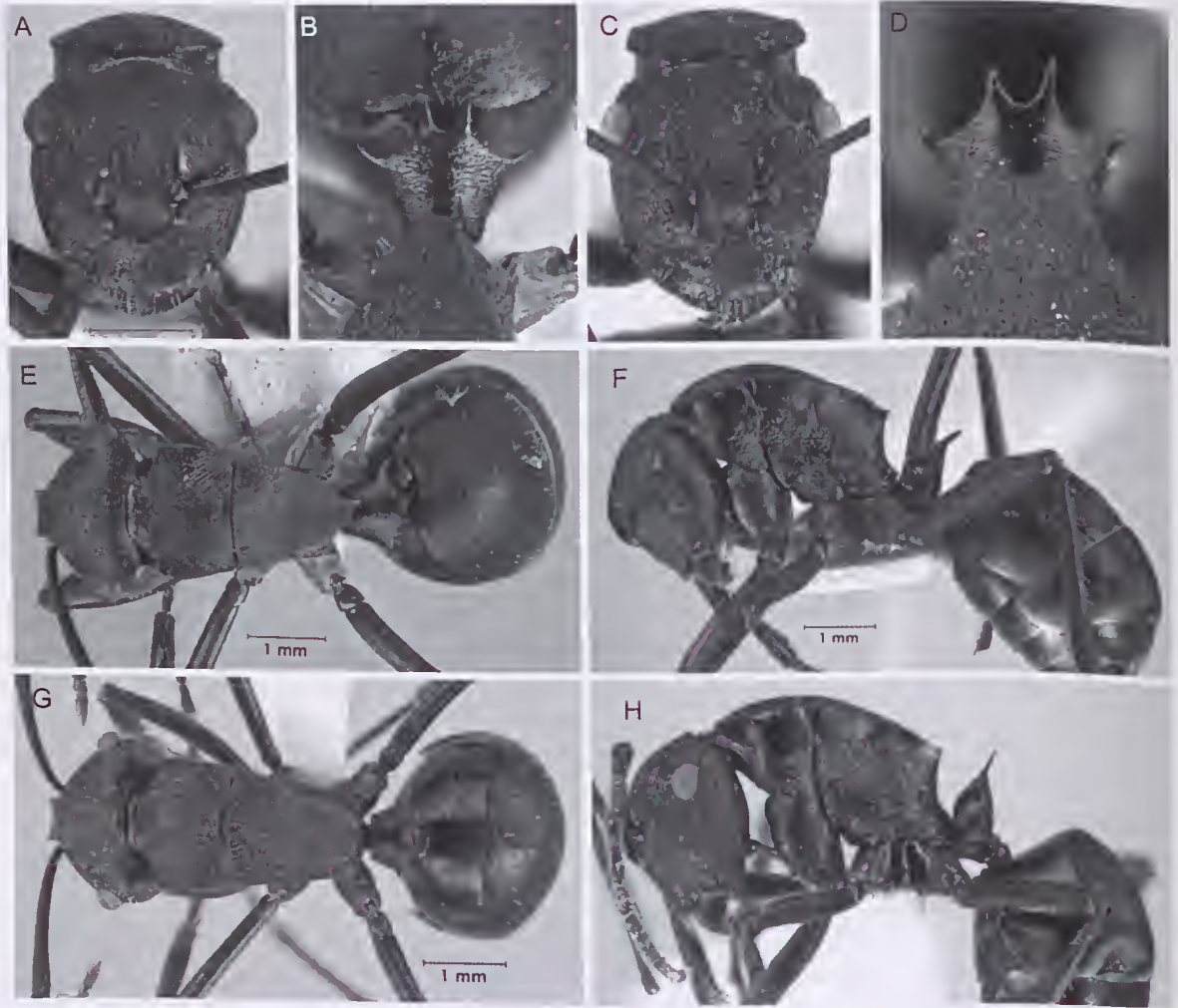


FIG. 3. *Polyrhachis gravis* species-group. Head in full face view (A, C), petiole in frontal view (B, D), dorsal habitus (E, G), lateral habitus (F, H): *P. gravis* Clark (holotype) (A-B, E-F); *P. hespera* (holotype) (C-D, G-H).

Material. HOLOTYPE: WA, Coral Bay, vi.1991, I. & G. Grose (worker). PARATYPE: data as for holotype (1 worker). Type deposition: Holotype in ANIC; 1 paratype in WAMP.

Description. *Worker:* Dimensions (holotype cited first): TL c. 9.52, 9.78; HL 2.28, 2.31; HW 1.96, 2.06; CI 86, 89; SL 2.46, 2.50; SI 125, 121; PW 1.81, 1.81; MTL 3.28, 3.22 (2 measured).

Mandibles with 6 teeth. Anterior clypeal margin widely truncate, truncate portion denticulate medially. Clypeus without distinct median carina; straight in profile with flat base.

Frontal triangle distinct. Frontal carinae sinuate with moderately raised margins; central area with rather indistinct frontal furrow. Sides of head in front of eyes weakly convex towards mandibular bases; behind eyes sides narrowly rounding into distinct occipital corners. Eyes convex, in full face view clearly breaking lateral cephalic outline. Ocelli lacking. Pronotal humeri bluntly angular; lateral margins of pronotum converging posteriorly towards moderately impressed promesonotal suture. Mesonotal and propodeal lateral margins converging posteriorly in single, weakly

sinuate line; metanotal groove flat. Propodeal dorsum strongly narrowed posteriorly with lateral margins terminating in upturned, somewhat dorsomedially flattened teeth; dorsum curving through narrow gap between closely approximate teeth into steeply descending declivity. Dorsum of petiole armed with a pair of slender spines; outer margins of spines descending into distinctly shorter, acute, lateral spines (Fig. 4B). Gaster in lateral view with anterior face flat; anterior margin of first gastral tergite with poorly indicated carina.

Mandibles finely, longitudinally striate with numerous piliferous pits. Head, including clypeus, reticulate-striate. Pronotal dorsum with rather irregular, somewhat obliquely directed striae; mesonotal dorsum longitudinally striate with sculpture on propodeal dorsum rather irregularly rugose. Sides of mesosoma and petiole finely wrinkled. Gaster very finely and closely reticulate-striate, opaque.

Mandibles with numerous, curved, golden hairs; anterior clypeal margin with numerous, relatively long, reddish-golden setae medially and fringe of shorter setae laterally. Numerous, medium length hairs on clypeus; rather abundant, distinctly shorter, bristle-like hairs on rest of head; distinctly less abundant, short, bristle-like hairs, on dorsum of mesosoma and along lateral margins of petiole. Dorsum of gaster with numerous, short, posteriorly inclined hairs, with hairs distinctly increasing in length towards apex; venter of gaster with numerous, medium to rather long, golden hairs. Closely appressed, greyish or silvery pubescence in various densities on most body surfaces, virtually absent from dorsum of mesosoma.

Whole body, including fore coxae and dorsum of gaster, black. Mandibles black, with teeth and bases reddish-brown; narrow band along masticatory borders light reddish-brown. Antennae black with only apical funicular segments light reddish-brown. Femora and middle and hind coxae medium reddish-brown; tarsi black. Venter of gaster and apex reddish-brown.

Sexuals and immature stages unknown.

Remarks. *Polyrhachis opacita* is characterised by the very finely striate, opaque gaster with the carina on anterior margin of the first gastral tergite only poorly developed. This is another species evidently restricted to WA, with both known specimens collected on a single occasion at Coral Bay.

Polyrhachis palmerae sp. nov.
(Figs 4C-D, G-H)

Etymology. Named after the collector, Ms Carol Palmer, a researcher with the Biodiversity Conservation Division of the NT Department of Natural Resources, Environment, Arts and Sport, who collected many ants, including several new species of *Polyrhachis*, during a broader fire project in the Kimberley region of WA.

Material. HOLOTYPE: WA: Kimberley area, Bachesten Ck, vii.2001, Carol Palmer (Kimberley Fire Project 8.3L) (worker). PARATYPES: data as for holotype (except Kimberley Fire Project 4.3L) (2 workers); Kimberley, Mitchell Plateau, vi.2007, J. Lanoue (Fire Study sp. B) (worker). Type deposition: Holotype in ANIC; 1 paratype worker each in BMNH, MCZC, QM, WAMP.

Description. *Worker:* Dimensions (holotype cited first): TL c. 9.07, 8.52-9.27; HL 2.28, 2.18-2.31; HW 2.00, 1.81-2.03; CI 88, 87-89; SL 2.25, 2.12-2.34; SI 112, 109-117; PW 1.72, 1.62-1.84; MTL 2.81, 2.71-3.12 (1+4 measured).

Mandibles with 6 teeth. Anterior clypeal margin widely truncate, truncate portion irregularly denticulate. Clypeus with short, poorly defined, median carina towards base; very weakly sinuate in profile. Frontal triangle distinct. Frontal carinae sinuate with weakly raised margins; central area with indistinct frontal furrow. Sides of head in front of eyes convex towards mandibular bases; behind eyes sides rounding into distinct occipital corners. Eyes convex, in full face view clearly breaking lateral cephalic outline. Ocelli lacking. Pronotal humeri bluntly angular, somewhat laminate, with rather distinct anterior margins converging towards pronotal collar. Lateral pronotal margins converging towards moderately impressed promesonotal suture. Mesonotal lateral margins converging posteriorly into rather flat, metanotal groove. Propodeal lateral margins strongly converging posteriorly and terminating in relatively short,

upturned teeth; dorsum descending into steep, weakly concave declivity in medially uninterrupted line. Dorsum of petiole strongly raising medially and dorsally, terminating in two, closely approximate, divergent spines; outer margins of spines steeply descending into slender, acute, lateral spines (Fig. 4D). Gaster in lateral view with anterior face flat; anterior margin of first gastral tergite with distinct transverse carina.

Mandibles very finely, longitudinally striate with numerous piliferous pits. Clypeus reticulate-punctate anteriorly, striate towards base; head distinctly, longitudinally reticulate-striate. Pronotal dorsum mostly longitudinally striate, striae distinctly curving towards posterior angles of segment; mesonotal dorsum longitudinally striate; propodeal dorsum with striae distinctly directed posteriorly and medially. Sides of mesosoma below lateral margins of segment very smooth and polished, sculpture becoming wrinkled ventrally. Petiole finely wrinkled. Dorsum of gaster very finely, longitudinally striate, somewhat polished.

Mandibles with several, curved, golden hairs at masticatory borders and along outer margins; truncate median portion of anterior clypeal margin with a few, relatively long, golden setae and shorter setae fringing margin laterally. Clypeus with several, medium length hairs, hairs on rest of head distinctly shorter, bristle-like. Dorsum of mesosoma with numerous, rather short, variously inclined hairs; numerous hairs lining lateral margins of petiole. Antennae and legs with numerous, bristle-like hairs on all surfaces. Gaster with semierect, mostly posteriorly inclined, medium length hairs, distinctly longer on gastral venter and apex. Closely appressed, rather sparse, golden pubescence variously distributed on most body surfaces, virtually absent from dorsa of head, mesosoma and petiole.

Mandibles, including bases, distinctly light reddish-brown, teeth very dark, almost black. Clypeus medium reddish-brown anteriorly, anterior border lined black. Body, including fore coxae, black, distinctly polished. Antennal scapes medium reddish-brown with apices

a shade lighter; funiculi rather light reddish-brown at bases, segments progressively lighter, yellow, towards apices. Legs, including middle and hind coxae, very distinctly light orange; tarsi a shade darker.

Sexuals and immature stages unknown.

Remarks. The black body with light orange appendages and rather polished appearance makes *P. palmerae* easily recognisable. The petiole is also very characteristic, with its highly and steeply raised dorsum which virtually forms a single base for two, slender, divergent spines (Fig. 4D). *Polyrhachis palmerae* is known only from the Kimberley region in WA where it appears to be endemic.

Polyrhachis pseudothrinax Hung, 1967
(Figs 5A-B, E-F)

Polyrhachis pseudothrinax Hung, 1967: 199, figs 1-6. Holotype & paratype worker. Original localities: NT, Daly River (H. Wesselmann) (holotype), MLAC (examined); QLD, Cape York Pen., Coen (P.F. Darlington) (paratype), MCZC (examined).

Material. WA, 12 km N of Broome, 10.x.1993, savannah woodland/spinifex (B.B. Lowery) (w); 35 km E of Kununurra, 25.v.1994, savannah woodland/spinifex (B.B. Lowery) (w); Glenelg R., 15°48'S, 124°44'E, vi.1988, woodland (ANA) (w); Mirima, nr Kununurra, 7.iv.2004 (ANA) (w); Kimberley region, Cape Bernier, 14°07'S, 127°31'E, vi.1988, woodland (ANA) (w); ditto, King Edward R., 15°09'S, 126°09'E, vi.1988 (ANA) (w); ditto, Bachesten Ck., vii.2001 (C. Palmer) (w); ditto, Yampi 2 Stn, v.2002 (C. Palmer) (w). NT, Melville I., Maxwell Ck., 27.vi.2008 (B. Hoffmann) (w); Groote Eylandt, 16-19.ix.1991 (G. Webb) (w); ditto, 10-12.iv.1992 (G. Webb) (w); Kakadu NP, Border Store, S of Ubirr, 23.v.1994, savannah woodland (B.B. Lowery) (w); ditto, Kapalga, 12°33'S, 132°19'E, 31.i.1991 (S.O. Shattuck #2240.5) (w); ditto, Kapalga, 1991 (ANA) (q); ditto, Nanguluwurr, 4-5.xii.1988 (R.R. Snelling) (w); ditto, Ranger Uranium lease site, vii.1999 (ANA) (w); ditto, ii.1993 (ANA) (q); ditto, Baroalba Springs, 31.xii.1989 (ANA) (w); Douglas Hot Springs, 4.vii.1985 (B.B. Lowery) (w); Douglas Daly, vii.1998 (O. Price) (w); Auvergne Stn, 27.vii.1999 (S. Eldridge) (w); Umbruwarr Gorge, SW of Pina Ck., 30.iii.1997 (B. Hoffmann) (w); Borrook Stn, Pine Ck, 10.x.1995 (ANA) (w); Hayfield, vi.1996 (A. Fisher) (q); Bradshaw Stn, VIC R. area, vi.1997 (A.L. Hertog) (w); Katherine Gorge NP, 14°19'S, 132°28'E, 25.xi.1993, sav. woodland (RJK acc. 93.62) (w). QLD, 10 km SE of Croydon, nr Alehvale Stn, 18°15'S, 142°19'E, 3-5.x.1977 (RJK acc. 77.13) (w); Mt Isa, xi.1997 (B. Hoffmann) (w); Mt Isa Mines, v.2005 (T. Griffiths, Plume Outfall Study) (w);

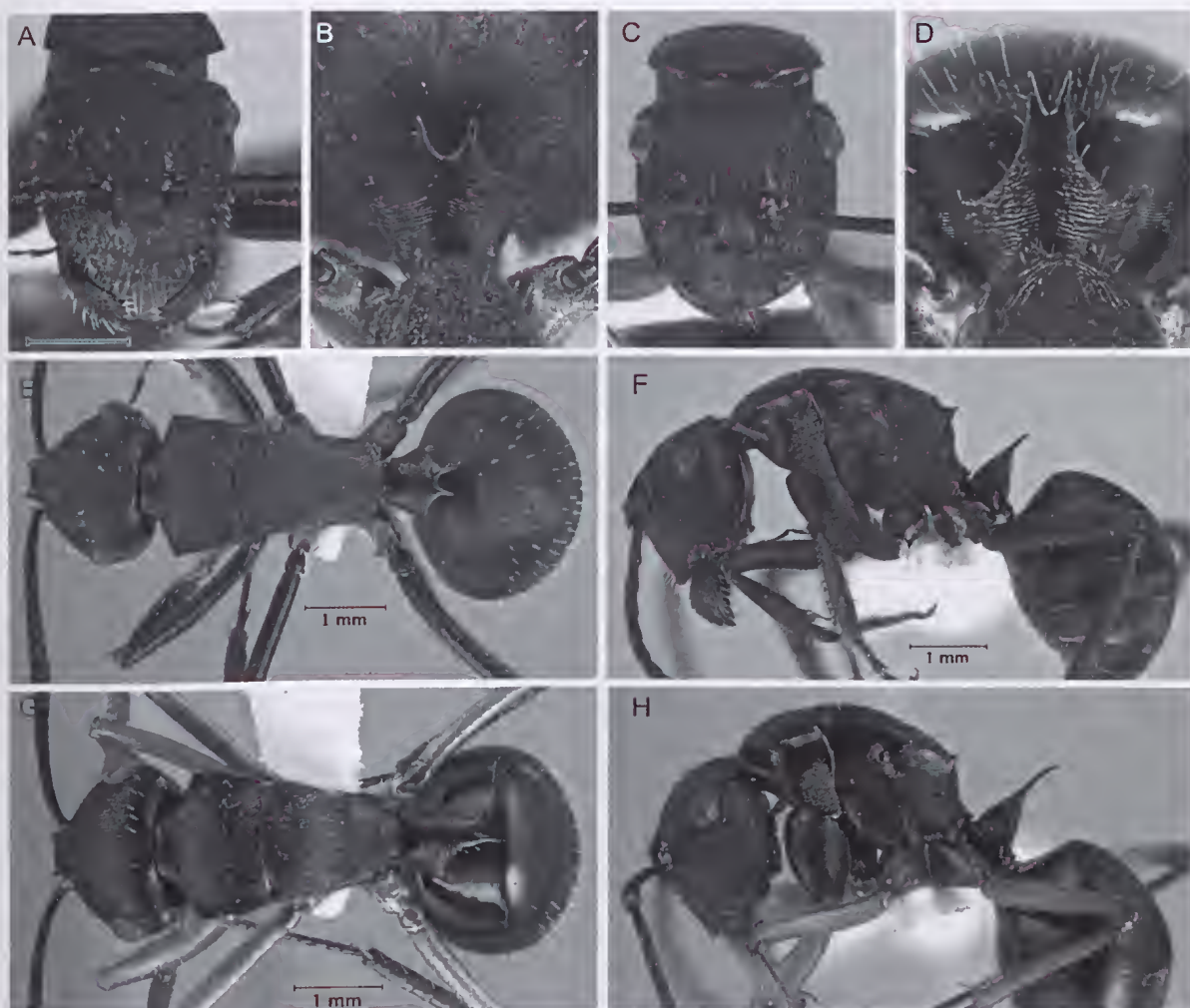


FIG. 4. *Polyrhachis gravis* species-group. Head in full-face view (A, C), petiole in frontal view (B, D), dorsal habitus (E, G), lateral habitus (F, H): *P. opacita* sp. nov. (holotype) (A-B, E-F); *P. palmerae* sp. nov. (holotype) (C-D, G-H).

30mi N of Tambo, 14.xii.1972 (BBL) (w); German Ck mine, nr Middlemount, 200 km NW of Rockhampton, 23°00'S, 148°30'E, 1997 (ANA) (w); Monklands Stn. 2(2), xi.1999 (K. Schneider 4/00, Tree Clearing Project) (w); Byganna Stn 56(3), vii.1999 (K. Schneider 3/00, TCP) (w); Townsville, Field Training area/Tabletop, 19°27'S, 146°24'E, vii.1999 (J. Woinarski) (w); ditto, vii.1999 (J. Woinarski) (w).

Description. *Worker*: Dimensions (holotype cited first, paratype second): TL c. 8.37, 8.47, 7.00-9.22; HL 2.06, 2.06, 1.72-2.25; HW 1.75, 1.72, 1.43-2.01; CI 85, 83, 83-90; SL 2.09, 2.12, 1.81-2.34; SI 119, 123, 112-127; PW 1.62, 1.62,

1.31-1.87; MTL 2.65, 2.65, 2.25-2.90 (1+1+18 measured).

Queen. (not previously described) Dimensions: TL c. 9.42; HL 2.21; HW 1.81; CI 82; SL 2.15; SI 119; PW 2.06; MTL 2.81 (1 measured).

Queen very similar to worker with usual characters identifying full sexuality, including three ocelli, complete thoracic structure, wings and distinctly larger eyes. Pronotal humeri armed with distinct, somewhat dorsally flattened teeth. Mesoscutum marginally wider

than long with widely rounded anterior margin in dorsal view; median line distinct; parapsides flat; anterior face in profile rounding onto relatively low, flat dorsum. Mesoscutellum only marginally elevated above dorsal plane of mesosoma. Propodeal dorsum with lateral margins strongly converging posteriorly, terminating in upturned, dorsolaterally directed, acute teeth; dorsum between them descending into steep declivity in medially uninterrupted line. Petiole very similar to worker, only median spine distinctly shorter. Sculpturation, pilosity and colour scheme virtually as in worker.

Male and immature stages unknown.

Remarks. *Polyrhachis pseudothrinax* appears to be somewhat more common than other species of the *P. gravis*-group. It ranges from north QLD westwards across the NT to the Kimberley region of WA. Throughout its distribution, *P. pseudothrinax* is relatively morphologically uniform, however, the QLD populations appear to have a longer antennal scapes (SI 118-126 versus 112-120 in NT populations), with the exception of a single specimen from Melville Island (SI 127). When describing this species, Hung (1967) also noted differences in sculpturation of the propodeal dorsum, however, following examination of numerous specimens across the whole range of this species it is apparent that the variability in striation is similar to that displayed by other species of the *P. gravis*-group. Some specimens also appear to differ in the shape and length of the propodeal dorsum (Andersen, Pers. comm.), however, subsequent examination failed to reveal any other associated taxonomically important characters and I consider they represent only variants from the 'prototype' of this species.

With its single middle petiolar spine, *P. pseudothrinax* is easily recognised. Only *P. unicornis*, described below, shares this character, however, it differs in having the spine less acute and shorter (Fig. 5D, G) and in some specimens weakly emarginate apically. They also differ in the shape of their eyes which, in *P. unicornis*, are larger and distinctly less convex (Fig. 5C). In addition, the sculpturation on the pronotal

dorsum is distinctly transverse in *P. unicornis*, while it is more-or-less longitudinal in *P. pseudothrinax* and the bristle-like pubescence is distinctly longer and rather abundant in *P. pseudothrinax*, while it is much shorter and rather sporadic in *P. unicornis*. Their colour patterns are very similar with a black body and very distinct, light reddish-brown or orange-coloured legs, however, the anterior portion of clypeus in *P. unicornis* is distinctly lighter reddish-brown, while it is black throughout in the other species.

Polyrhachis unicornis sp. nov.
(Figs 5C-D, G-H)

Etymology. Derived from the combination of the Latin *unicus*, meaning sole, and *cornu*, meaning horn, in reference to the single dorsal petiolar spine.

Material. HOLOTYPE: WA: Kimberley area, Joonjoo Stn, v.2002, C. Palmer (worker). PARATYPES: data as for holotype (3 workers); Beagle Bay, vi.2001 (C. Palmer) (1 worker); 12 km N of Broome, savannah woodland, 10.x.1993 (B.B. Lowery) (2 workers). Type deposition: Holotype in WAMP; 2 paratypes in ANIC; 1 paratype each in BMNH, MCZC, QM and TERC.

Description. *Worker.* Dimensions: TL c. 8.62, 6.90-8.62; HL 2.06, 1.72-2.06; HW 1.81, 1.51-1.81; CI 88, 86-89; SL 2.12, 1.84-2.12; SI 117, 117-126; PW 1.56, 1.26-1.56; MTL 2.81, 2.25-2.81 (1+6 measured).

Mandibles with 5 teeth, distinctly reducing in length towards base. Anterior clypeal margin widely truncate, truncate portion bluntly denticulate, laterally delimited by blunt corners. Clypeus without distinct median carina; very shallowly concave in profile with flat basal margin. Frontal triangle distinct. Frontal carinae sinuate with only moderately raised margins; central area with poorly distinct frontal furrow. Sides of head in front of eyes converging towards mandibular bases in virtually straight line before rounding into mandibular bases; behind eyes sides rounding into distinct occipital corners. Eyes relatively large, only moderately convex, in full face view breaking lateral cephalic outline. Ocelli lacking. Pronotal humeri armed with distinct blunt teeth, lateral margins behind narrowly emarginate (Fig. 5G) before converging posteriorly and rounding into relatively shallow promesonotal suture.

Mesonotal dorsum with anterior lateral margins converging posteriorly towards flat, indistinct metanotal groove. Propodeal dorsum with lateral margins converging posteriorly and terminating in upturned, somewhat dorsomedially flattened, acute teeth; dorsum shallowly concave medially, before curving into steeply descending declivity in medially uninterrupted line. Petiole scale-like, virtually triangular in lateral view; dorsum armed with relatively short, weakly posteriorly curved, median spine; in some specimens, including holotype, spine is weakly emarginate apically; lateral petiolar spines distinct, acute. Gaster in lateral view with anterior face flat, distinctly lower than full height of petiole; anterior margin of first gastral tergite with blunt transverse carina.

Mandibles very finely striate with numerous piliferous pits. Clypeus reticulate-punctate; head along frontal carinae and on sides and vertex rather regularly, longitudinally striate. Pronotal dorsum transversely striate, striae somewhat medially bowed and curving towards posterior corners of segment. Mesonotal and propodeal dorsa finely striate, striae converging posteriorly along lateral margins of segments. Propodeal declivity, petiole and anterior face of gaster finely, transversely striate. Dorsum and sides of gaster very finely, longitudinally striate.

Mandibles at masticatory borders and along outer margins with numerous, medium length, curved, golden hairs. Anterior clypeal margin with several, anteriorly directed, relatively long, golden setae medially and shorter setae fringing margin laterally. Head with numerous, erect to semierect, bristle-like, short hairs, only few hairs breaking lateral cephalic outline at occipital corners in full face view. Dorsum of mesosoma virtually without hairs, except a few, very short, erect hairs towards propodeal teeth and declivity. Dorsum of first gastral tergite without hairs; medium length, posteriorly directed hairs rather abundant on subsequent tergites, venter and apex of gaster. Antennae and legs, including coxae, with numerous short, bristle-like, semierect hairs.

Black; mandibles and anterior portion of clypeus distinctly light reddish-brown; teeth,

mandibular borders and anterior clypeal margin narrowly bordered black. Antennae reddish-brown with funiculi towards apices a shade lighter. Fore coxae dark, reddish-brown, in some specimens somewhat blotched light brown. Legs, including mid and hind coxae, distinctly orange, tarsi a shade darker. Gastral apex reddish-brown.

Sexuals and immature stages unknown.

Remarks. Similar to *P. pseudothrinax* with which it shares the single median spine on the petiole. However, the spine in *P. unicornis* is distinctly shorter and blunt and in some specimens, including the holotype, its apex is shallowly emarginate. Most of the characters distinguishing the species are given above in the remarks section of *P. pseudothrinax*.

POLYRHACHIS MICANS SPECIES-GROUP

CHARACTERS OF THE *P. MICANS* SPECIES-GROUP

Description. *Worker:* Medium-sized to relatively large ants (HL > 2.14) with general characteristics of the genus and subgenus. Head triangular in frontal view, sides in front of eyes rounding towards mandibular bases; sides in most species distinctly wider behind eyes with postocular and lateral ridges extending on each side towards occipital corners. Eyes relatively large, situated close to occipital corners. Dorsum of mesosoma relatively wide and short with pronotal humeri bluntly angular (distinctly angular in some *P. prometheus* specimens). Mesonotal dorsum with lateral margins converging posteriorly (as in *P. micans* or *P. incerta*) or distinctly posteriorly rounded (as in *P. prometheus*). Metanotal groove rather flat, poorly indicated, except in *P. prometheus* where it is short and clearly impressed. Propodeal dorsum strongly converging posteriorly in most species, except in *P. prometheus* where it is very narrow, about 1.5 times longer than wide, with virtually parallel lateral margins. Petiole scale-like, armed with four subequal spines (as in *P. micans*), or two distinctly elongated dorsal



FIG. 5. *Polyrhachis gravis* species-group. Head in full-face view (A, C), petiole in frontal view (B, D), dorsal habitus (E, G), lateral habitus (F, H): *P. pseudothrinax* Hung (paratype) (A-B, E-F); *P. unicornis* sp. nov. (holotype) (C-D, G-H).

spines and two lateral teeth, usually reduced to mere angles (e.g. *P. incerta* or *P. shattucki*). Gaster in side view with anterior face straight, rather narrowly rounding onto dorsum of first gastral tergite.

Queen. Apart from sexual characters, including three ocelli, complete thoracic structure and wings, very similar to worker. Armament of pronotum, propodeum and petiole distinctly reduced with spines and teeth shorter and

stouter. Sculpturation, pilosity and colour virtually identical to worker. The only known queens are those of *P. micans* and *P. prometheus* and description of the latter is given below under that species heading.

Male. Males and immature stages mostly unknown and not dealt with in this paper.

Distribution and biology. The known distribution of the *P. micans*-group ranges from

central coastal QLD to the Gulf Country and westwards across the NT as far as the Kimberley region in northern WA. With a few exceptions, the species are relatively rare and only occasionally collected. They appear to be terrestrial nesters, building nests under the ground with entrances usually covered with a rock, piece of wood, or simply under a tuft of grass.

KEY TO WORKERS OF THE
P. MICANS SPECIES-GROUP

1. Petiole with four, almost subequal spines . . 2.
 - Petiole with two large dorsal spines; lateral spines greatly reduced or obsolete 3.
2. Petiole with dorsal margin strongly raised dorsomedially towards closely approximated dorsal spines (Fig. 6B, E); propodeal teeth rather massive, long and broad (Fig. 46); legs medium reddish-brown *P. eureka* sp. nov.
 - Petiole with dorsal margin less strongly raised; dorsal spines situated further apart (Fig. 7B); propodeal spines relatively short, more acute and slender (Fig. 7F); legs very dark reddish-brown or black *P. micans* Mayr
3. Body distinctly reddish-brown; lateral petiolar spines reduced to short acute teeth (NT, QLD) *P. incerta* Kohout
 - Body uniformly black; lateral petiolar spines reduced to blunt angles, or obsolete 4.
4. Propodeal dorsum very narrow, about 1.5 times longer than basal width, with parallel lateral margins; dorsal petiolar spines long and slender (WA, NT, QLD) *P. prometheus* Santschi
 - Propodeal dorsum distinctly wider than long, with strongly posteriorly converging lateral margins; dorsal petiolar spines relatively short (QLD) . . . *P. shattucki* sp. nov.

Polyrhachis eureka sp. nov.
(Figs 6A-B, E-F)

Etymology. Derived from a Greek word *heurēka*, meaning 'I have found it' (an exclamation of discovery).

Material. HOLOTYPE: QLD, Alehvale Stn., 9 km SE of Croydon, 18°15'S, 142°18'E, 16.x.1976, R.J. Kohout acc. 76.59 (worker). PARATYPES: data as for holotype (4 workers). Type deposition: Holotype (QMT 169998) and paratype in QM; 1 paratype each in ANIC, BMNH and MCZC.

Description. *Worker:* Dimensions (holotype cited first): TL c. 8.87, 8.87-9.58; HL 2.21, 2.14-2.25; HW 2.00, 1.87-2.03; CI 90, 87-90; SL 2.34, 2.31-2.37; SI 117, 117-123; PW 1.75, 1.63-1.78; MTL 2.74, 2.65-2.78 (1+4 measured).

Mandibles with 5 teeth. Anterior clypeal margin widely medially truncate, truncate portion more-or-less regularly denticulate, laterally delimited by distinct teeth. Clypeus with rather blunt median carina; virtually straight in profile, basal margin flat. Frontal triangle distinct. Frontal carinae sinuate with weakly raised margins; central area shallowly concave with flat frontal furrow. Sides of head in front of eyes rounding towards mandibular bases; behind eyes sides with a short, postocular lateral ridges and narrowly rounded occipital corners. Eyes distinctly convex, in full face view breaking lateral cephalic outline. Ocelli lacking. Pronotal dorsum distinctly wider than long; humeri bluntly angular with rather distinct anterior margins converging towards occipital collar; lateral pronotal margins converging towards moderately impressed, anteriorly bowed promesonotal suture. Mesonotal lateral margins converging posteriorly into flat metanotal groove. Propodeal margins raised, converging posteriorly and terminating in very distinct, somewhat dorsomedially flattened, broad-based, propodeal teeth with rounded tips; basal width of teeth about as wide as distance between their bases; propodeal dorsum curving in medially uninterrupted line into steep, shallowly concave declivity. Petiole with dorsal margin strongly rising medially and dorsally, terminating in a pair of closely approximate, slender, divergent spines; inner margins of spines continuous medially

into open 'U'-shaped dorsum of petiole (Fig. 6B); outer margins of spines descending into distinctly shorter, slender, lateral spines. Anterior face of first gastral segment virtually flat, lower than full height of petiole, narrowly rounding onto dorsum of gaster.

Mandibles closely and finely, longitudinally striate with piliferous pits. Clypeus reticulate-punctate. Head reticulate-punctate with sculpturation on vertex organised into more-or-less longitudinal striae. Pronotal dorsum very finely striate, median striae somewhat barrel-shaped. Dorsa of mesonotum and propodeum more distinctly, somewhat irregularly, longitudinally striate; sides of mesosoma wrinkled. Petiole, including spines, very finely reticulate. Gaster very closely and finely reticulate-punctate, semiopaque.

Mandibles towards masticatory borders with numerous curved, medium length, golden hairs. Anterior clypeal margin with several, anteriorly directed, longer golden setae medially and numerous shorter setae fringing margin laterally. A pair of medium length golden hairs near anterior clypeal margin and pair of shorter hairs near base; a few hairs on fore coxae and venter of middle and hind coxae and femora. Hairs absent from dorsum of head, mesosoma, petiole and dorsum of gaster. Venter and apex of gaster with relatively long, posteriorly inclined, golden hairs. Very short, appressed, golden pubescence in various densities over most body surfaces, except dorsum of mesosoma, most abundant on dorsum of gaster.

Mandibles medium reddish-brown at masticatory borders, becoming progressively darker towards bases; teeth dark, reddish-brown. Clypeus reddish-brown with rest of head black. Antennal scapes and basal funicular segments black or very dark reddish-brown, subsequent segments progressively lighter towards apices. Coxae and femora relatively light reddish-brown with tibiae a shade darker; tarsi very dark, almost black, with apical segments very light orange. Petiole reddish-brown, lateral borders and teeth almost black. Gaster, including venter and apex, distinctly reddish-brown.

Sexuals and immature stages unknown.

Remarks. *Polyrhachis eureka* is very similar to *P. micans* but differs in several characters including distinctly coarser and less regular sculpturation of the mesosomal dorsum. The eyes in *P. eureka* are more convex (Fig. 6A) and the propodeal teeth distinctly longer and wider (Fig. 6F), about as wide as the distance between their bases. In contrast, the eyes in *P. micans* are relatively flat (Fig. 7A) and the propodeal spines shorter, more acute and relatively slender (Fig. 7F), with their basal width about half of the distance between their bases. Dorsal margin of petiole strongly rising medially and dorsally, armed with a pair of closely approximate dorsal spines that are dorsoposteriorly directed and form, in lateral view, a single continuous line with anterior face of petiole (Fig. 6F). In contrast, the dorsal petiolar spines in *P. micans* are distinctly longer, more widely separated and distinctly more dorsally directed in lateral view (Fig. 7F).

The type series of *P. eureka*, from the Gulf Country of north-western QLD, are the only specimens known of this apparently rare species. The specimens were collected foraging on the ground in savannah woodland.

Polyrhachis incerta Kohout, 2008 (Figs 6C-D, G-H)

Polyrhachis incerta Kohout, 2008: 163, figs 1, 3-4. Holotype and paratype workers. Type locality: NT, Kakadu NP, Nourlangie Rock, 12°51'S, 132°49'E, 18.xi.1993, open sclerophyll forest, strays on ground and low vegetation (RJK acc. 93.50), QM (QMT 152088), ANIC, BMNH and MCZC (examined).

'*Polyrhachis (Campomyrma) micans* r. *ops* var. *rufa*' Crawley, 1921: 97. Original material: QLD, Townsville, 11-12.xii.1902 (F.P. Dodd) (workers), ANIC, BMNH, MCZC, OXUM, QM (examined) (unavailable name).

Material. NT: Kakadu NP, Ranger Uranium lease site, vii.1993 (ANA) (w); Groote Eylandt, i.1983 (G. Barrett) (w); ditto, G. Webb Pty Ltd site, 16-19. ix.1991 (G. Webb) (w).

Description. *Worker*: Dimensions (holotype cited first): TL c. 7.96, 7.56-8.32; HL 2.00, 1.87-2.03; HW 1.81, 1.68-1.84; CI 90, 87-92; SL 2.09, 2.00-2.15; SI 115, 115-123; PW 1.47, 1.34-1.50; MTL 2.43, 2.28-2.50 (9 measured).



FIG. 6. *Polyrhachis micans* species-group. Head in full-face view (A, C), petiole in frontal view (B, D), dorsal habitus (E, G), lateral habitus (F, H): *P. eureka* sp. nov. (holotype) (A-B, E-F); *P. incerta* Kohout (holotype) (C-D, G-H).

Sexuals and immature stages unknown.

Remarks. *Polyrhachis incerta* appears to be a very rare species currently known from two widely separated regions. The type series specimens were collected in Kakadu National Park in the NT, with additional specimens collected on Groote Eylandt. The only specimens recorded from QLD were collected on a single occasion by F.P. Dodd at Townsville in 1902.

***Polyrhachis micans* Mayr, 1876**
(Figs 7A-B, E-F)

Polyrhachis micans Mayr, 1876: 76. Syntype workers, queen. Original localities: QLD, Rockhampton, Peak Downs (A. Dietrich), NHMW (examined).

Polyrhachis (Camponyrrna) micans Mayr; Santschi, 1920: 185. Combination in *P. (Camponyrrna)*.

'*Polyrhachis (Camponyrrna) micans* st. ops var. *dentinasis*' Santschi, 1920: 185. Original locality: QLD, Townsville, 11.ii.1902 (F.P. Dodd) (workers, queen), NHMB (examined) (unavailable name) (Taylor, 1986: 34).

'*Polyrhachis (Camponyrrna) micans* st. ops var. *dentinasis*' Santschi; Kohout, 2008: 167. Material referred to *P. micans*.

Material. QLD: Mt Pollux, SW base, 22°28.7'S, 147°52.2'E, 13.i.2006, 380 m, eucalypt w'land (CJB #12601) (w, ♀); Lords Table, SE base, 22°40.7'S, 148°01.3'E, 440 m, 10.i.2006, eucalypt w'land (CJB #12566, 12567, 12568) (w, ♀); ditto, 4-6.iii.2006 (QM Party #13380, 13382) (w); Lords Table, SE base, 22°40.7'S, 148°01.3'E, 460m, 13.i-4.iii.2006, eucalypt w'land, intercept (CJB #13374) (w); ditto, malaise (CJB #13373) (w); ditto, dung/pitfall (CJB #13376) (w); Lords Table, W base, 22°39.6'S, 148°00.5'E, 500 m, eucalypt w'land (QM Party #13350, 13352) (w, ♀); Lords Table plateau, 22°39.4'S, 148°00.9'E, 640 m, 7.iii.2006, eucalypt w'land (CJB, S. Wright #13359) (♀); Scotts Peak, SE base, 22°34.6'S, 148°13.7'E, 420 m, 4&9.iii.2006, eucalypt woodland (CJB, S. Wright #13339) (w); ditto, 22°51.7'S, 148°13.5'E, 440 m, 3&9.iii.2006, lancewood (CJB, G.B. Monteith #13341) (w); 6.5 km NNW of Clermont, 22°46.2'S, 147°37.6'E, 260 m, 13.i-5.iii.2006, open forest, pitfall trap (CJB #12665) (w); Britton Ra., 6 km NNE of Homevale, 21°23'S, 148°33'E, 1-6.iv.1975 (RJK accs 75.155, 156/1); German Ck mine, nr Middlemount, 200 km NW of Rockhampton, 23°00'S, 148°30'E, 1997 (ANA) (w); nr Rockhampton, 6 km N of Mt Archer, 23°17'S, 150°34'E, 4.i.1979 (RJK acc. 79.16); Rundle Ra., 36 km NW of Gladstone, 23°39'S, 150°58'E, 24-30.iii.1975 (RJK acc. 75.136/2).

Description. *Worker.* Dimensions (syntypes cited first): TL c. 9.42-9.93, 8.67-10.63; HL 2.31-2.43, 2.21-2.40; HW 2.09-2.18, 1.95-2.09; CI 90, 87-89; SL 2.37-2.46, 2.31-2.50; SI 113, 115-120; PW 1.93-2.06, 1.84-2.03; MTL 2.90-2.96, 2.71-2.96 (2+6 measured).

Queen. Dimensions (syntype queen): TL c. 10.03; HL 2.37; HW 2.00; CI 84; SL 2.25; SI 112; PW 2.28; MTL 2.87 (1 measured).

Male and immature stages unknown.

Remarks. *Polyrhachis micans* is the oldest known species of the group, apparently first collected by Amelia Dietrich, a collector 'extraordinaire' for the former Museum Godeffroy in Hamburg. In spite of being a well known species occurring in an easily accessible part of the country, from about Mackay south to Gladstone, *P. micans* is poorly represented in most collections examined. It has apparently become a relatively rare species, perhaps due to the clearance of its natural habitat for vast areas of sugar cane plantations.

Polyrhachis micans is characterised by a petiole armed with four, almost uniformly distributed spines of subequal length. It is rather similar

to *P. eureka*, described above, sharing with that species the very finely, mostly longitudinally striate head and mesosoma, however, the sculpturation in *P. eureka* is distinctly coarser, notably on the mesosomal dorsum. Additional characters separating the species are given in the remarks section of *P. eureka*.

Polyrhachis prometheus Santschi, 1920 (Figs 7C-D, G-H)

Polyrhachis (Campomyrma) prometheus Santschi, 1920: 566.
Syntype workers. Type locality: QLD, Townsville, F.P. Dodd, NHMB (examined).

Material. WA: Kununurra, i.1986 (JDM) (w); Purnululu NP, 17°38'S, 128°26'E, spinifex uplands, 1.ix.2004 (L. Barrow) (w); Marandoo, Mt Bruce, xii.1991 (P.A. Warns) (w); Pilbara, Ethel Ck Stn, nr Newman, 1993 (P.A. Varris) (w). NT: Tiwi I., v-vi.2001 (J. Woinarski, PWCNT Fauna Survey) (w); Groote Eylandt, vi.1982 (JDM) (w); ditto, G. Webb Pty Ltd site, 16-19 ix 1991 (G. Webb) (w); ditto, 18 km S of Milikapiti, 19.xii.1994 (B. Hoffmann) (w); Darwin R., 2.xi.1997 (ANA) (w); Kalkaringi, 22-29.iv.1997 (A. Salvarani) (w); Kidman Springs, 8-14.v.1997 (B. Hoffmann) (w, q); ditto, 21.iv.1998 (Ben Hoffmann) (q); ditto, 13.vi.1996 (ANA) (w); Killarney Stn, VIC R. Distr., 2002 (A. Fisher) (w); Broadshaw Stn, Timber Ck area, ix.1999 (A.L. Hertog) (w); ditto, ?15°38'S, 130°25'E?, 2.vi.1999 (S. Eldridge) (w); Sherwin Ck, Roper R. region, v.1997 ((A.L. Hertog) (w); Threeways Roadhouse, 22.x.1993, savannah w'land (B.B. Lowery) (w); Mainoru Stn, 250 km E of Katherine, iv.1996 (B. Hoffmann) (w, q). QLD: Floraville Stn, Leichard R. x-ing, 18°13'S, 139°53'E, 19-22.x.1976 (RJK acc. 76.65) (♀); Alehvale Stn, 10 km SE of Croydon, 18°15'S, 142°19'E, 3-5.x.1977 (RJK acc. 77.12) (w); Mt Isa, CRC MIM study, xii.1992 (T. Griffiths) (w); Lawn Hill Stn, 18°30'S, 138°10'E, iv.1991 (ANA, CRA Century Project) (w); Townsville, 15.xii.1902 (F.P. Dodd) (2 syntypes); Townsville Field Training Area/Tabletop, 19°27'S, 146°24'E, ii 1999 (A. Ash #76) (w); Cardigan Stn, nr Charters Towers, viii.1997 (B. Hoffmann) (w); 2.5 km of N Fanning Riv HS, 19°42.6'S, 146°25.9'E, 280 m, 10.ii.2007, open forest (CJB #14790) (w); Rochford Scrub, 20°07.0'S, 146°37.8'E, 270 m, 10.xii.2006, vinescrub (S. Wright #14684) (w);

Description. *Worker.* Dimensions (syntypes cited first): TL c. 7.46-8.82, 7.46-9.02; HL 1.79-2.09, 1.79-2.15; HW 1.62-1.93, 1.62-1.93; CI 90-92, 87-92; SL 1.84-2.03, 1.84-2.15; SI 105-113, 105-116; PW 1.43-1.68, 1.43-1.68; MTL 2.31-2.37, 2.31-2.74 (3+11 measured).

Queen. (not previously described) Dimensions: TL c. 9.52-9.98; HL 2.12-2.25; HW 1.81-1.93; CI 82-88; SL 1.96-2.06; SI 107-110; PW 2.00-2.15; MTL 2.65-2.74 (3 measured).

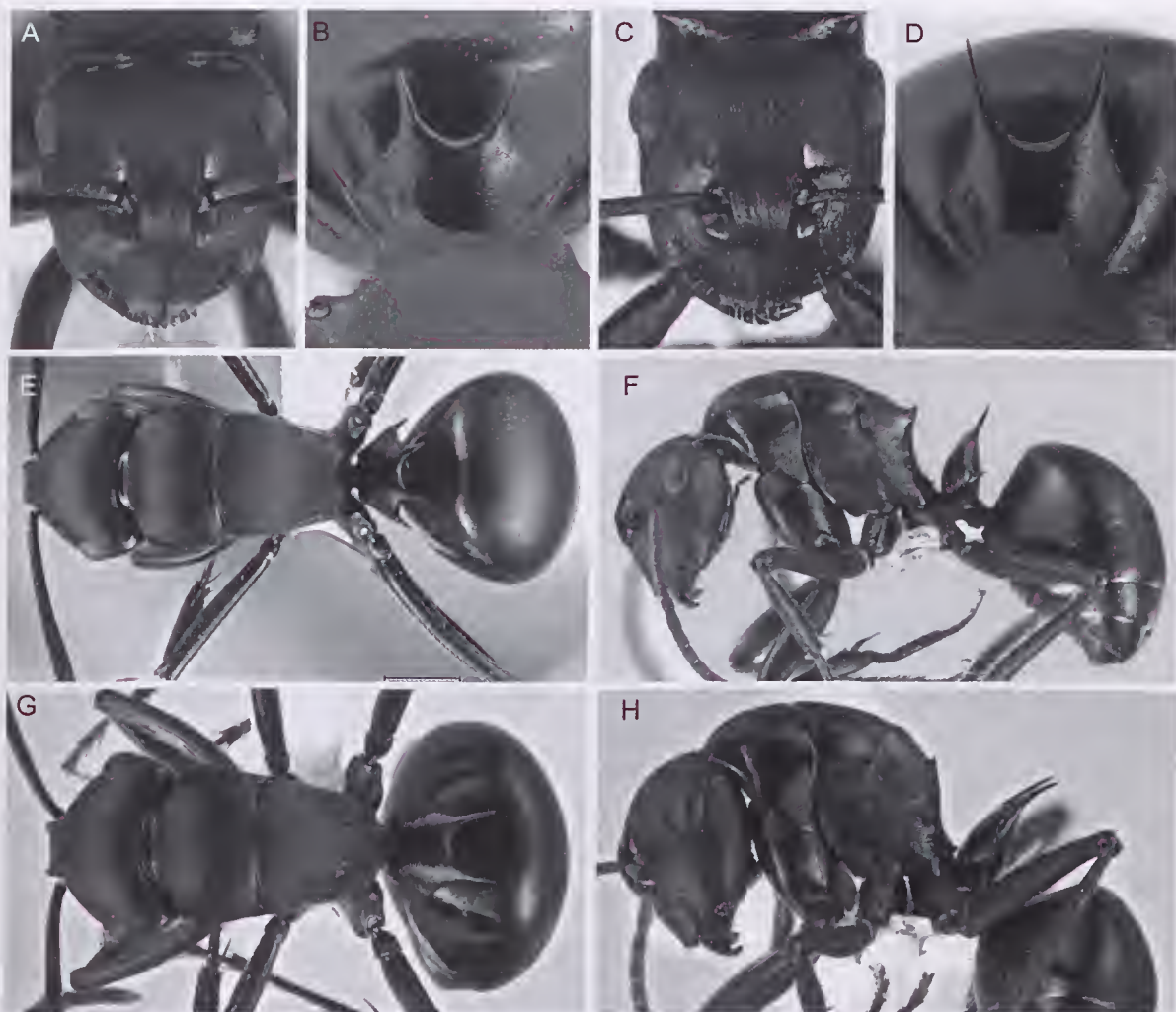


FIG. 7. *Polyrhachis micans* species-group. Head in full-face view (A, C), petiole in frontal view (B, D), dorsal habitus (E, G), lateral habitus (F, H): *P. micans* Mayr (A-B, E-F); *P. prometheus* Santschi (C-D, G-H).

Queen with usual characters identifying full sexuality, including three ocelli, complete thoracic structure and wings. Pronotal humeri bluntly angular; mesoscutum in dorsal view virtually as long as wide, anterior margin widely rounded; median line distinct; parapsides flat, only weakly raised posteriorly; mesoscutum in profile with relatively low anterior face and flat dorsum. Mesoscutellum weakly convex, marginally elevated above dorsal plane of mesosoma. Propodeal dorsum with lateral margins poorly defined, strongly converging posteriorly and terminating in short, upturned,

somewhat dorsolaterally directed teeth; propodeal dorsum between them rounding in uninterrupted line into steeply oblique declivity. Petiole rather similar to worker, spines distinctly shorter. Sculpturation similar to worker with head and mesoscutum finely, mostly longitudinally striate; propodeal dorsum finely reticulate-punctate; propodeal declivity and petiole very finely wrinkled, somewhat semipolished. Dorsum of gaster very finely reticulate-punctate. pilosity similar to worker, mandibles towards masticatory borders with numerous, relatively long, curved golden

hairs; anterior clypeal margin medially with rather long, somewhat reddish-golden setae and numerous shorter setae fringing margin laterally. A pair of very short, bristle-like hairs on mesoscutum, venter of middle and hind coxae and femora; distinctly longer hairs on fore coxae and gastral venter and apex. Very short, silvery or pale golden, closely appressed pubescence sparingly distributed over most body surfaces. Colour identical to worker.

Male and immature stages unknown.

Remarks. With its narrow, parallel-sided propodeal dorsum and long petiolar spines, *P. prometheus* is easily recognised. It has the widest distribution of all the *P. micans*-group species, ranging from the Pilbara and Kimberley regions of WA and across the NT to QLD, where it has been recorded as far south as Gladstone.

Polyrhachis shattucki sp. nov.
(Figs 8A-D)

Etymology. Named in honour of Dr Steve O. Shattuck of the ANIC, CSIRO Division of Entomology, Canberra, in appreciation of his support and encouragement towards my work on *Polyrhachis* and for invaluable help in providing many of the excellent digital images that illustrate my continuing work on these highly interesting ants.

Material. HOLOTYPE: QLD: Undara Lava Lodge, 18°12'S, 144°34'E, savannah woodland, nocturnal strays on ground, R.J. Kohout acc. 03.43 (worker). PARATYPES: data as for holotype (68 workers). Type deposition: Holotype (QMT 169999) and most paratypes in QM; 6 paratype workers in ANIC; 2 paratype workers each in AMNH, BMNH, CASC, MCZC, MHNG, MNHU and NHMW.

Other Material. QLD: 4 km E of Charters Towers, 13.xiii.1976, dry sclerophyl (B.B. Lowery) (w, ♀).

Description. *Worker:* Dimensions (holotype cited first): TL c. 9.07, 7.66-9.07.87; HL 2.12, 1.93-2.18; HW 1.93, 1.72-2.06; CI 91, 89-94; SL 1.90, 1.75-1.90; SI 98, 92-103; PW 1.68, 1.59-1.81; MTL 2.34, 2.12-2.34 (1+15 measured).

Mandibles with 5 teeth. Anterior clypeal margin widely medially truncate, truncate portion more-or-less regularly denticulate. Clypeus with flat, rather indistinct median carina; virtually straight

in profile, only very weakly raised towards anterior margin; basal margin flat. Frontal triangle distinct. Frontal carinae sinuate with only very weakly and narrowly raised margins; central area wide with poorly indicated frontal furrow. Sides of head in front of eyes virtually straight, only weakly rounding towards mandibular bases; behind eyes sides forming short, narrowly rounded occipital corners. Eyes only moderately convex, in full face view breaking lateral cephalic outline. Ocelli lacking. Pronotal dorsum distinctly wider than long; humeri bluntly angular with rather distinct anterior margins converging towards occipital collar; lateral pronotal margins converging towards well impressed, anteriorly bowed promesonotal suture. Mesonotal lateral margins converging posteriorly into poorly indicated, shallowly impressed, metanotal groove. Propodeal margins weakly raised, converging posteriorly and terminating in short, upturned, somewhat dorso-anteriorly flattened, acute teeth; propodeal dorsum between them curving into steep, almost vertical declivity. Petiole scale-like, very slender in lateral view; dorsum armed with a pair of slender, medium length, subparallel spines; inner margins of spines continuous medially, forming 'U'-shaped dorsum of petiole; outer margins of spines steeply descending into rather blunt, lateral angles. Anterior face of first gastral segment virtually flat, lower than full height of petiole, narrowly rounding onto dorsum of gaster.

Mandibles closely and finely, longitudinally striate with piliferous pits. Clypeus reticulate-punctate. Head reticulate-punctate with sculpturation on vertex and along frontal carinae organised into longitudinal striae. Dorsum of mesosoma somewhat more finely, longitudinally, reticulate-striate with sides finely wrinkled. Petiole, including spines, very finely wrinkled. Gaster very closely and finely reticulate-punctate, semiopaque.

Mandibles towards masticatory borders with numerous curved, golden hairs. Anterior clypeal margin medially with several, anteriorly directed, uneven length golden setae and very short setae fringing margin laterally. A pair of medium length golden hairs near anterior

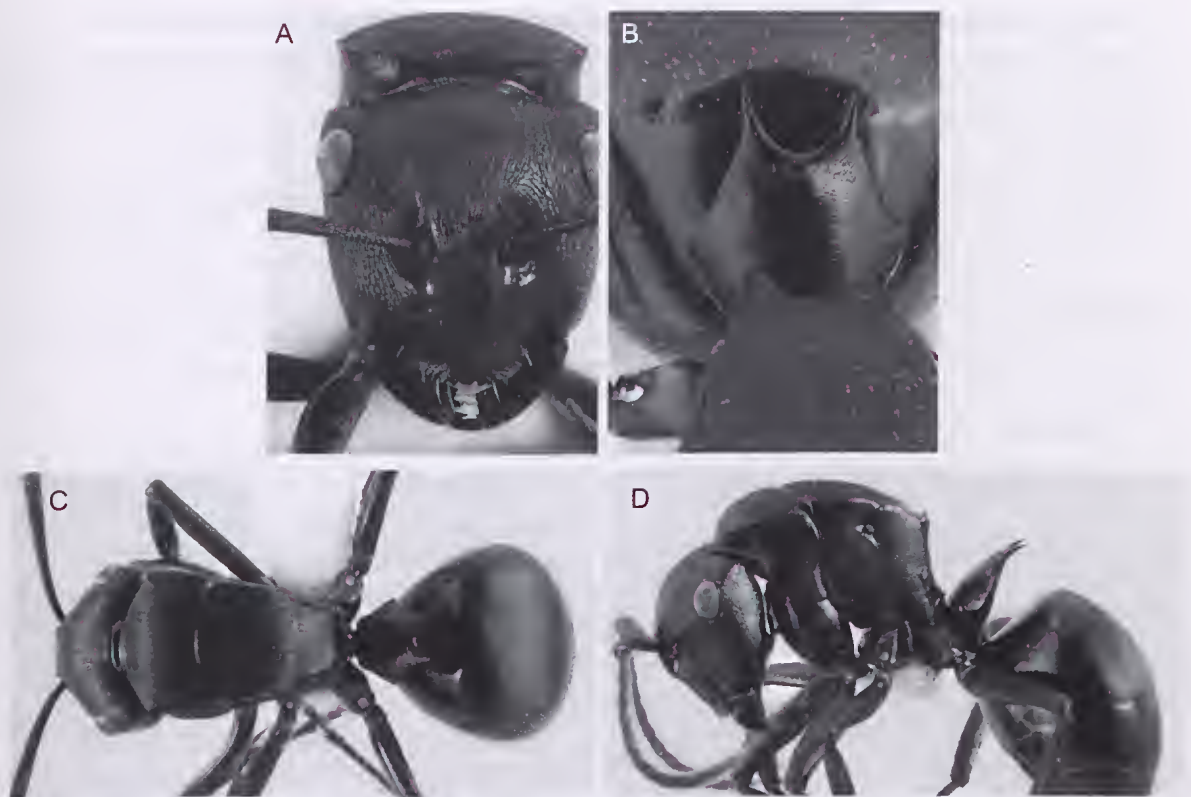


FIG. 8. *Polyrhachis micans* species-group. Head in full-face view (A), petiole in frontal view (B), dorsal habitus (C), lateral habitus (D): *P. shattucki* sp. nov. (holotype) (A-D).

clypeal margin laterally and a few hairs on fore coxae and venter of femora. Gaster with rather long, posteriorly inclined, golden hairs on venter and around apex, some as long as greatest diameter of eyes. Very short, appressed, silvery pubescence in various densities over most body surfaces, most abundant on dorsum of gaster.

Black; mandibles medium reddish-brown, light red band at masticatory borders, teeth black. Antennal scapes and basal funicular segments very dark reddish-brown; apical funicular segments progressively lighter towards apices. Middle and hind coxae, femora and fore tibiae medium reddish-brown; middle and hind tibiae a shade darker; tarsi very dark, almost black. Dorsum of gaster black; sides and venter reddish-brown, with margins of segments lined

with very dark reddish-brown or black; apex a shade lighter.

Queen. Dimensions: TL c. 9.22; HL 2.12; HW 1.87; CI 88; SL 1.84; SI 98; PW 2.06; MTL 2.25 (1 measured).

Queen very similar to worker and apart from characters identifying full sexuality, including three ocelli, complete thoracic structure and wings, differing as follows: clypeus with blunt, anteriorly distinct, median carina; eyes larger; pronotal humeri bluntly angular with anterior margins less distinct and shorter. Mesoscutum with anterior margin widely rounded in dorsal view, distinctly wider than long; median line very short; parapsides flat; mesoscutum in profile with relatively low anterior face, widely rounding onto flat dorsum. Mesoscutellum not elevated above dorsal plane of mesosoma, weakly

convex, posteriorly rounded into well impressed metanotal groove; propodeum wider than long with lateral margins strongly converging posteriorly, terminating in upturned teeth. Petiole with dorsal spines distinctly shorter. Sculpturation, pilosity and colour scheme virtually identical to worker.

Male and immature stages unknown.

Remarks. *Polyrhachis shattucki* is apparently a rare and has been collected only twice. It has been listed earlier (Kohout, 2008: 165) in a key to species of the *P. micans*-group as '*P. 'Campo 12'* (undescribed)'.

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I am very grateful to Dr Alan Andersen, CSIRO Darwin, for supplying the specimens from the monsoonal and arid zones of northern Australia and his generous support that allowed me to visit and study the *Polyrhachis* ants at the TERC collection. I am much indebted to Dr Steve Shattuck, ANIC, CSIRO, Canberra, for producing the excellent digital images used for illustrations. I would also like to thank to Dr Ken Walker, MVMA, Melbourne, for loan of the type specimens of *P. gravis*, lodged in the Museum VIC. To my colleagues, Dr Chris Burwell, Ms Susan Wright and Karin Koch, all QM, I thank for their continuous support during the course of this study. My special thanks go to Dr Chris Burwell, QM, for reading and commenting on a draft of the manuscript.

LITERATURE CITED

- Andersen, A.N. 2000. *The Ants of Northern Australia*. A guide to the monsoonal fauna. CSIRO Publishing, Melbourne, 106 pp.
- Andersen, A.N. & Burbidge, A.H. 1991. The ants of a vine thicket near Broome: a comparison with the northern Kimberley. *Journal of the Royal Society of Western Australia* 73(3): 79-82.
- Clark, J. 1930. New Formicidae, with notes on some little known species. *Proceedings of the Royal Society of VIC* 43: 2-25.
- Emery, E. 1896. Saggio di un catalogo dei generi *Camponotus*, *Polyrhachis* e affini. *Memorie della R. Accademia delle Scienze dell'Istituto di Bologna* (5)5: 363-383 (pp. 761-780 in separate).
- Forel, A. 1915. Results of Dr. E. Mjöberg's Swedish scientific expedition to Australia, 1910-1913. 2. Ameisen. *Arkiv för Zoologi* 9(16): 1-119.
- Hung, A.C.F. 1967. A new species and two names of the *Polyrhachis* ants. *Mushi* 40: 199-202.
- Kohout, R.J. 2008. Two new species of *Polyrhachis* Fr. Smith (Hymenoptera: Formicidae: Formicinae) from Australia, based on formerly quadrinomial taxa. *Australian Entomologist* 35(4): 161-171.
- Wheeler, W.M. 1911. Three formicid names which have been overlooked. *Science*. New York (N.S.) 33: 858-860.

Revision of *Polyrhachis* (*Hagiomyrma*) Wheeler, 1911 (Insecta: Hymenoptera: Formicidae: Formicinae)

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ABSTRACT

The subgenus *Hagiomyrma* Wheeler, 1911, of the genus *Polyrhachis* Fr. Smith, 1857, is revised. Forty-eight species are recognised, including sixteen previously described species: *P. ammon* (Fabricius), *P. ammonoeides* Roger, *P. angusta* Forel, *P. crawleyi* Forel, *P. denticulata* Karavaiev, *P. lachesis* Forel, *P. lydiae* Forel, *P. metella* Fr. Smith, *P. paxilla* Fr. Smith, *P. penelope* Forel, *P. schenkii* Forel, *P. semiaurata* Mayr, *P. semiobscura* Donisthorpe, *P. thusnelda* Forel, *P. trapezoidea* Mayr and *P. tubifera* Forel. Thirty-two species are described as new: *P. anderseni*, *P. archeri*, *P. aurora*, *P. bohemia*, *P. brisbanensis*, *P. brutella*, *P. burwelli*, *P. callima*, *P. capeyorkensis*, *P. clarki*, *P. conciliata*, *P. cracenta*, *P. darlingtoni*, *P. diversa*, *P. dougcooki*, *P. electra*, *P. elegantula*, *P. feehani*, *P. hoffmanni*, *P. injinooi*, *P. isolata*, *P. melanura*, *P. nourlangie*, *P. pilbara*, *P. placida*, *P. seducta*, *P. stricta*, *P. tanami*, *P. tenebra*, *P. uncaria*, *P. vernoni* and *P. weiri*. Six species-groups are recognised: *P. ammon*-group, *metella*-group, *penelope*-group, *schenkii*-group, *trapezoidea*-group and *tubifera*-group. Three species, *Polyrhachis sokolova* Forel, *P. trophima* Fr. Smith and *P. xiphias* Fr. Smith, formerly placed in *Hagiomyrma* are excluded and placed in different subgenera. A key based on the worker caste is provided. All species are illustrated and their known distributions and biology and ecology summarised. □ *Polyrhachis*, *Hagiomyrma*, Australia, New Guinea, systematics, new species, distribution.

This is the fourth in a series of papers reviewing the Australian ants of the genus *Polyrhachis* (Kohout 2006, 2010, 2012). It deals with the species of the subgenus *Hagiomyrma* which is confined to the Australasian Region with the majority of species restricted to Australia. In terms of the Australian fauna, *Hagiomyrma* is the third most speciose subgenus of *Polyrhachis* with only *Charionomyrma* and *Caupomyrma* containing more Australian species.

In 1775 Johann Christian Fabricius described *Formica ammon*, one of the first Australian ants collected at Botany Bay by Joseph Banks during the *Endeavour* voyage of discovery under Captain James Cook. However, it was not until almost a century later that Frederick Smith (1860 and 1863) and Julius Roger (1863) described

five more species that were later considered members of the subgenus *Hagiomyrma*. In the following years (1866, 1870 and 1876) Gustav Mayr described a further thirteen *Polyrhachis* species and subspecific forms, mostly from the material in the Godeffroy Museum in Hamburg, two of which now belong to *Hagiomyrma*. However, the work of Auguste Forel had the greatest impact on the taxonomy of the *ammon*-group, that later (see Wheeler, 1911) become known as the subgenus *Hagiomyrma*. Except for two species, one he described in 1886 from Darnley Island in Torres Strait and the other in 1907 from the north-west of Western Australia, all the specimens he worked on were collected and sent to him by Gilbert Turner, a retired farmer from Mackay in Queensland

(see Turner, 1897). From this material, between 1895 and 1916, Forel described a vast number of new species and subspecies of Australian ants, including ten which were considered members of the subgenus *Hagiomyrma*. Only two more species, *P. denticulata* Karavaiev, 1927, and *P. semiobscura* Donisthorpe, 1944, were later described, raising the number of *Hagiomyrma* species to twenty-two. This situation remained unchanged until Kohout (1988, 1994) synonymised the subspecies *P. animon angustata* Forel and *P. sokolova degenier* Forel with their nominal forms and *P. chalcas* Forel with *P. ammonoeides* Roger, reducing the number of species to nineteen. Finally, with the transfer of three species to different subgenera (see below), I consider only sixteen previously described species to be valid members of the subgenus *Hagiomyrma*.

MATERIAL AND METHODS

Photographs of specimens were taken with a digital camera attached to a stereomicroscope. The images were then processed using Helicon Focus (Mac OSX version) or Auto-Montage (Syncoscopy, Division of Synoptics Ltd, USA) and Adobe Photoshop CS2 (Adobe Systems Inc., USA) software. Unless otherwise indicated, illustrations are of the holotypes of the new species or critically compared specimens (mostly topotypes) of previously described species.

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

Lists of synonymies presented here are not always comprehensive and for full synonymic citations see Bolton (1995), Bolton *et al.* (2007) and Dorow (1995). Publication dates and the spelling of species' and authors' names generally follow Bolton *et al.* (2007). Where a holotype specimen is mentioned as 'unique',

this infers that this was the only specimen available and no syntype or paratype specimens are known to exist.

Names of the most frequently listed collectors are abbreviated as follows: ANA = A.N. Andersen; BDH = B.D. Hoffmann; CJB = C.J. Burwell; DJC = D.J. Cook; DKY = D.K. Yeates; GIT = G.I. Thompson; H&C = H. Heatwole & E. Cameron; JDM = J.D. Majer; JEF = J.E. Feehan; JPH = J. & P. Hasenpusch; PMR = P.M. Room; RJK = R.J. Kohout; BBL = B.B. Lowery; GBM = G.B. Monteith; SKR = S.K. Robson; RWT = R.W. Taylor; TAW = T.A. Weir. Other abbreviations used in specimen data are: Arch. = Archipelago; Bch = Beach; c. = about (*L. circa*); CALM = Department of Conservation and Land Management, Western Australia; Ck = Creek; CURT = Curtin University of Technology, Perth, Western Australia; DPI = Department of Primary Industries; Hmsd = Homestead; I. = Island; Is = Islands; Mt = Mount; Mtn = Mountain; Mts = Mountains; NP = National Park; nr = near; Pen. = Peninsula; Pltn = Plantation; PNG = Papua New Guinea; Prov. = Province; Pt = Point; R. = River; Ra. = Range; Rd = Road; rf. = rainforest; SF = State Forest; Stn = Station; Tblnd = Tableland; TERC = CSIRO, Tropical Ecosystems Research Centre, Darwin, Northern Territory; w = worker/s; x-ing = crossing. Australian states and territories are abbreviated as follows: ACT = Australian Capital Territory; NSW = New South Wales; NT = Northern Territory; QLD = Queensland; SA = South Australia; TAS = Tasmania; VIC = Victoria; WA = Western Australia.

Abbreviations for institutions and depositories (with the names of co-operating curators) are: AMNH - American Museum of Natural History, New York, NY, USA. (Dr J.M. Carpenter); AMSA - Australian Museum, Sydney, NSW, Australia (Drs D. Britton, D. Smith); ANIC - Australian National Insect Collection, CSIRO Ecosystem Sciences, Canberra, ACT, Australia (Drs S.O. Shattuck, R.W. Taylor, N. Barnett); BMNH - The Natural History Museum, London, UK (Barry Bolton, K. Goodger, S. Ryder); BPBM - Bernice P. Bishop Museum, Honolulu, HI, U.S.A. (Dr G.M. Nishida, K.T. Arakaki); CASC - California

Academy of Sciences, San Francisco, CA., U.S.A. (Dr B.L. Fisher, K.J. Ribardo); CURT - Curtin University of Technology, Perth, WA, Australia (Drs J.D. Majer, B.E. Heterick); HNHM - Hungarian Natural History Museum, Budapest, Hungary (Dr J. Papp); IZAS - Institute of Zoology, Ukrainian Academy of Sciences, Kiev, Ukraine (Dr A.G. Radchenko); MCZC - Museum of Comparative Zoology, Harvard University, Cambridge, MA., USA (Dr S.P. Cover); MHNG - Muséum d'Histoire Naturelle, Geneva, Switzerland (Drs C. Besuchet, I. Löbl, B. Merz); MNHA - Museum of Nature and Human Activities, Sanda, Hyogo, Japan (Dr Yoshiaki Hashimoto); MNHN - Muséum National d'Histoire Naturelle, Paris, France (Dr J. Casevitz Weulersse); MNHU - Museum für Naturkunde, Humboldt-Universität, Berlin, Germany (Dr F. Koch, A. Kleine-Möllhoff); MSNG - Civic Museum of Natural History 'G. Doria', Genova, Italy (Drs R. Poggi, F. Penati); MVMA - Museum of Victoria, Melbourne, VIC., Australia (Dr A. Neboiss, K. Walker); NHMB - Naturhistorisches Museum, Basel, Switzerland (Drs M. Brancucci, D.H. Burckhardt); NHMW - Naturhistorisches Museum, Vienna, Austria (Drs M. Fischer, S. Schödl, H. Zettel); NHRS - Naturhistoriska Riksmuseet, Stockholm, Sweden (Drs K.-J. Hedquist, F. Ronquist); NMNH - National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (Drs T.R. Schultz, D.R. Smith); OXUM - University Museum, Oxford, UK (Drs C. O'Toole, D.J. Mann); QM - Queensland Museum, Brisbane, QLD, Australia (Drs C.J. Burwell, G.B. Monteith); SAMA - South Australian Museum, Adelaide, SA, Australia (A. McArthur); TERC - Tropical Ecosystems Research Centre, CSIRO Sustainable Ecosystems, Darwin, NT, Australia (Dr A.N. Andersen); WAMP - Western Australian Museum, Perth, WA, Australia (Dr T. Houston); ZMSG - Zoologische Staatssammlung, München, Germany (Dr E. Diller).

The following standard measurements and indices are used: TL - Total length (the necessarily composite measurement of entire ant measured in profile); HL - Head length

(maximum measurable length of the head in perfect full face view, measured from the anteriormost point of the clypeal border or teeth, to the posteriormost point of the occipital margin); HW - Head width (width of the head in perfect full face view, measured immediately in front of eyes); CI - Cephalic index ($HW \times 100/HL$); SL - Scape length (length of the antennal scape, excluding the condyla); SI - Scape index ($SL \times 100/HW$); PW - Pronotal width (maximum width of the pronotal dorsum measured in dorsal view); MTL - Metathoracic tibial length (maximum measurable length of the tibia of the hind leg).

Because of variability in the shape of the promesonotal dorsum, resulting from the posterior convergence of the lateral margins of the pronotum and mesonotum, MW, the minimum width of the mesonotal dorsum measured along the metanotal groove when viewed from behind, was added to the standard set of measurements. Its comparison with the greatest width of the pronotal dorsum, using the formula $PW \times 100/MW$ (= PMI, the promesonotal index) provides a valuable tool to compare the shape of the promesonotal dorsum between species. The PMI proved to be one of the important identification characters for species of *Hagiomyrma*. However, for a number of types examined in the early stages of this study the MW was not measured and consequently PMI is not available for those specimens.

All measurements were taken using a Zeiss SR stereomicroscope at 20x and 32x magnifications with an eyepiece graticule calibrated against a stage micrometer. All measurements are expressed in millimetres (mm).

SYSTEMATICS

Polyrhachis Fr. Smith, 1857

Polyrhachis Fr. Smith, 1857: 58. Type species: *Formica bhamata* Drury, 1773: 73, pl. 38, figs 7, 8, worker; by original designation.

Hagiomyrma Wheeler, 1911

Hagiomyrma Wheeler, 1911: 860 (as subgenus of *Myrma* Billberg, 1820 [sensu Wheeler, 1911: 859] = *Polyrhachis*)

Fr. Smith, 1857). Type species: *Formica ammon* Fabricius, 1775: 394, worker; by original designation.

Hagiomyrma Wheeler; Forel, 1915: 106. As subgenus of *Polyrhachis* Fr. Smith, 1857.

Hagiomyrma Wheeler; Wheeler, 1922: 702. Diagnosis in a key. As subgenus of *Polyrhachis* Fr. Smith, 1857.

Hagiomyrma Wheeler; Emery, 1925: 184. Diagnosis of subgenus. As subgenus of *Polyrhachis* Fr. Smith, 1857.

Hagiomyrma Wheeler; Hung, 1967: 398; Dorow, 1995: 24; Bolton, 1995: 30. As subgenus of *Polyrhachis* Fr. Smith, 1857.

Hagiomyrma was originally established by Wheeler (1911a: 860) as the fourth subgenus within the genus *Myrma* Billberg, 1820 (see Dorow *et al.* 1997: 236-241). Wheeler used the subgeneric combination of *Myrma* (*Polyrhachis*) repeatedly (Wheeler 1911b, 1912) and proposed several new combinations, e.g. *Formica sexspinosa* Latreille (1802) or *Formica ammon* Fabricius (1775), that he cited as '*Myrma* (*Polyrhachis*)' and '*Myrma* (*Hagiomyrma*)' respectively. Forel (1915) strongly objected to Wheeler's proposed nomenclature and claimed support from then prominent myrmecologists Emery and Santschi. Subsequently, without explanation, Wheeler (1915: 821-823) evidently abandoned his position and cited *Polyrhachis* at generic rank in all his following papers (Wheeler 1919, 1922 *etc.*).

Diagnosis. *Hagiomyrma* is one of the relatively well-defined subgenera of the genus *Polyrhachis*. A marginate mesosomal dorsum, mostly rounded pronotal humeri and more-or-less horizontal, posteriorly directed propodeal spines, make most members of this subgenus easily recognisable (see a key to workers of the Australian subgenera of *Polyrhachis* in Kohout 2010: 169-171, fig. 1).

Description. *Worker*: Small to moderately large ants (HL 1.30-2.80) with general characteristics of the genus. Anterior clypeal margin usually with distinct, denticulate, median flange (as in *P. ammon*), simply truncate (as in *P. anderseni* sp. nov.) or with deep, open, 'V'-shaped emargination (as in *P. metella* Fr. Smith). Clypeus with median, longitudinal carina; sinuate or straight in profile. Frontal carinae sinuate with moderately raised margins at midlength; central area relatively wide with more-or-less distinct frontal furrow or weakly raised carina. Dorsum of mesosoma distinctly

laterally marginate along its entire length. Pronotal dorsum generally near quadrate with lateral margins subparallel or converging posteriorly (as in *P. schenkii* Forel, *P. trapezoidea* Mayr or *P. weiri* sp. nov.); more rarely margins anteriorly converging (strongly as in *P. metella* Fr. Smith or weakly as in *P. darlingtoni* sp. nov., *P. dougcooki* sp. nov. and *P. feehani* sp. nov.). Pronotal humeri unarmed with margins weakly to moderately laminate, often dilated, widely or narrowly rounded or more rarely bluntly angular (as in *P. schenkii* Forel and *P. vernonii* sp. nov.). Promesonotal suture distinct; metanotal groove often distinct laterally, but weakly impressed dorsally, or virtually lacking. Propodeum armed with a pair of more-or-less horizontal, subparallel or divergent, acute spines. Petiole scale-like or rarely columnar (as in *trapezoidea*-group species), armed with a pair of acute spines that can be subparallel or divergent, horizontal or curved downwards (as in *P. uncaria* sp. nov.), upwards (as in *P. stricta* sp. nov.), or re-curved and hook-like (as in *P. ammonooides* Roger); dorsum narrowly rounded or rarely with flat platform that can be horizontal (as in *P. thusnelda* Forel) or sloping posteriorly (as in *P. trapezoidea* Mayr, *P. darlingtoni* sp. nov. and *P. nourlangie* sp. nov.).

Queen. Very similar to worker, with usual characters identifying full sexuality, including three ocelli and complete thoracic structure with wings. Besides larger size (except in *P. semiaurata* Mayr), differing in distinctly larger eyes and distinctly shorter propodeal and petiolar spines. Sculpturation, pilosity, pubescence and colour virtually identical to that in worker.

Male. Males are unknown for most of the species and as such their treatment was not attempted here. However, where known, their presence in collections is indicated under each species.

Distribution and biology. *Hagiomyrma* can be considered the most 'Australian' subgenus of *Polyrhachis*, with almost all of its constituent species endemic to Australia. Only four of the presently recognised 48 species were originally described from beyond the Australian

mainland, with three of them, *P. denticulata* Karavaiev, *P. schenkii* Forel and *P. semiobscura* Donisthorpe, reported from Australia in recent years (Kohout & Taylor 1990: 514, 519), while the fourth species, *P. metella* Fr. Smith, appears to be endemic to New Guinea. The distributions of most *Hagiomyrma* species are centred on coastal Queensland, however, some (e.g. *P. ammonoides* Roger, *P. pilbara* sp. nov.) occur only in north-western Western Australia, while the ranges of several others (e.g. *P. crawleyi* Forel, *P. schenkii* Forel) extend along the northern Australian coastline from the Kimberley region in the west to Cape York Peninsula in the east. Only four species follow the eastern Australian seaboard from Queensland south to central New South Wales, with two (*P. ammon* and *P. semiaurata* Mayr) reaching as far south as Victoria and one of them (*P. ammon*) extending westwards to the Australian Capital Territory.

Most species seemingly prefer open *Eucalyptus* forests and savannah woodlands. However, two new species were most recently recorded from the spinifex grasslands of central Australia, with one from the Tanami Desert and the other from the MacDonnell Ranges. In stark contrast, two species, *P. diversa* sp. nov. and *P. vernoni* sp. nov., are rainforest dwelling species. Virtually all known species of the subgenus, except the apparently lignicolous *P. semiobscura* Karavaiev, are ground-nesting (both terrestrial and subterranean) and their nesting habits were discussed in detail by Kohout (1997) and Robson & Kohout (2007). The lithocolous nesting habit of *P. thusnelda* Forel was reported by Robson & Kohout (2005) and a similar nesting habit inside rock crevices has recently been discovered in *P. anderseni* sp. nov. (Kohout unpublished).

TAXA EXCLUDED FROM *P. HAGIOMYRMA*

The following three species that have been previously included within the subgenus *Hagiomyrma* are here excluded and placed in different subgenera.

Polyrhachis (*Chariomyrma*) *sokolova* Forel, 1902 comb. nov.

Polyrhachis sokolova Forel, 1902: 522. Syntype workers.
Type locality: AUSTRALIA, QLD, Mackay (G. Turner), MHNG (examined) (transferred to subgenus *P. (Chariomyrma)* Forel), New combination.

Remarks. When describing *Polyrhachis sokolova*, Forel indicated that it belonged to the *ammon*-group and, consequently, Emery (1925) and all subsequent authors treated it as a member of the subgenus *Hagiomyrma*. However, *P. sokolova* features laminate pronotal margins with acutely spinose humeri, a character common to species of the subgenus *Chariomyrma* Forel. In fact, small specimens of *P. sokolova* ('var. *degener*') are remarkably similar to *Polyrhachis constricta*, described by Emery from Australia in 1897, and subsequently placed by him in the subgenus *Chariomyrma* (Emery 1925: 186). *Polyrhachis sokolova* is a quite common species that also occurs beyond the Australian mainland, with records from the Aru Islands, the southern coast of Papua and New Caledonia. Specimens from the Northern Territory differ in several characters from those from Queensland and were earlier considered a separate, undescribed species (see Kohout 1988: 436; Nielsen 1997: 16). However, subsequent examination and comparison of Northern Territory specimens with others from throughout the range of *P. sokolova*, has shown no taxonomically significant variability to justify their separate specific status. At many localities in the Northern Territory, *P. sokolova* is sympatric with *P. constricta* and their undeniable similarity resulted in Andersen (2000) correctly listing both species under the subgenus *Chariomyrma*.

Polyrhachis (*Hedomyrma*) *trophima* Fr. Smith, 1863 comb. nov.

Polyrhachis trophimus Fr. Smith, 1863: 14. Holotype worker.
Type locality: INDONESIA, Seram I. (A.R. Wallace), OXUM (examined) (transferred to subgenus *P. (Hedomyrma)* Forel).
New combination.

Remarks. *Polyrhachis trophima* was placed by Dalla Torre (1893: 271), Emery (1925: 185) and Chapman & Capco (1951: 267) in the subgenus *Hagiomyrma* and by Donisthorpe (1932: 469), Bolton (1995: 359) and Dorow (1995: 21) in the subgenus *Chariomyrma*. I have examined

the unique holotype of *P. trophima* and found it remarkably similar to *P. calliope* Emery, a species described in 1900 from New Guinea. It features pronotal humeri armed with short, but distinct spines and a petiole with a flat dorsum, a combination of characters identifying members of the subgenus *Hedomyrma* Forel.

Polyrhachis (Campomyrma) xiphias Fr.
Smith, 1863 comb. nov.

Polyrhachis xiphias Fr. Smith, 1863: 16. Holotype queen. Type locality: INDONESIA, Waigiou I. (= Pulau Waigeo) (A.R. Wallace), OXUM (examined) (transferred to subgenus *P. (Campomyrma)* Wheeler). New combination.

Remarks. *Polyrhachis xiphias* was described from a single queen and subsequently placed by Emery (1925: 185) in the subgenus *Hagiomyrma*. Only following the recent identification of worker specimens was *P. xiphias* recognised as a member of the subgenus *Campomyrma* Wheeler. It became the name-bearing species of the *Polyrhachis xiphias*-group (Kohout 2007: 7), a small group of species within *Campomyrma*, which also includes *P. hashimotoi* Kohout from Borneo and *P. shixingensis* Wu & Wang from China. The members of this group differ from other *Campomyrma* species by having the petiolar node columnar and the dorsum armed with two, more-or-less horizontal, posteriorly directed spines, in contrast to the scale-like petiole of all other known *Campomyrma* species.

THE SPECIES-GROUPS

The subgenus *Hagiomyrma* had never been formally subdivided (Emery 1925; Dorow 1995) until Andersen (2000) introduced four species-groups pertinent to his work on the ants of monsoonal Australia. He recognised the *ammon*-group, *schenkii*-group, *trapezoidea*-group and an unnamed 'Group A', that he distinguished mostly by the shape of the petiolar dorsum, the comparative length of the petiolar and propodeal spines, the length of the antennal scapes and the colour of the body. Three more species-groups are proposed here, the *metella*-group, the *penelope*-group and the *tubifera*-group, with Andersen's 'Group A' incorporated within the *trapezoidea*-group. Most of these groups intergrade on morphological

grounds and within the groups the species tend to polarise into several complexes.

Andersen (2000) included two species, *P. ammon* and *P. angusta*, within the *ammon*-group which is expanded here to incorporate 16 species. It includes most of the larger species of the subgenus (generally HL > 1.90) which have promesonotal lateral margins that are only weakly converging posteriorly (PMI < 160) and generally hairless scapes. The species have uniformly black ground colour which is often obscured by golden or silvery pubescence. The dorsum of the gaster is usually covered with rich, golden pubescence (except in *P. semiaurata* Mayr) with a rather distinct, very dark, reddish-brown, median patch in the species of the *calliina*-complex (e.g. Fig. 2G-H), or without a dark patch in the species of the *ammon*-complex (e.g. Fig. 1A-B). Most species of the *ammon*-group have a scale-like petiolar node, however, *P. burwelli* sp. nov. has a columnar petiole with a widely rounded dorsum (Fig. 2F). The majority of *ammon*-group species tend to be stoutly built, but some species closely related to *P. ammonooides* Roger and *P. angusta* Forel (*ammonooides*-complex) are more slender and elongate and feature distinctly dilate pronotal humeri and rather long, widely divergent, propodeal spines (e.g. Fig. 3C-D). *Polyrhachis ammonooides* has hairs along the antennal scapes and somewhat more distinct sculpturation, and so is intermediate between the *ammon*-group and the *pilbara*-complex of the newly proposed *penelope*-group (see below).

Polyrhachis tubifera Forel, previously placed in the *ammon*-group by Andersen (2000), is here included, with *P. diversa* sp. nov., in a new *tubifera* species-group characterised by a distinctly short and broad mesosomal dorsum, propodeal spiracles situated on relatively long, laterally projecting tubercles and very short propodeal and petiolar spines (Fig. 14A-B, C-D).

The *schenkii*-group, as conceived by Andersen (2000), includes mostly reddish-coloured species with the leading edge of the antennal scapes fringed with short, bristle-like hairs (except in *P. bohemia* sp. nov.) and relatively

coarsely reticulate or vermiculate-punctate body sculpturation. Besides *P. schenkii* Forel, *P. lachesis* Forel and *P. lydiae* Forel, listed by Andersen (2000), the group also includes *P. paxilla* Fr. Smith and several newly described species. Within the group species tend to polarise into two complexes, centring on either *P. schenkii* or *P. lachesis*. Species allied to *P. schenkii* are smaller (HL < 1.90), with strongly posteriorly converging promesonotal margins (PMI \pm 200) and finer sculpturation. In contrast, the species more closely related to *P. lachesis*, are larger (HL \pm 2.00), with the promesonotal margins less strongly converging posteriorly (PMI < 185) and with more-or-less distinct, vermiculate-rugose sculpturation.

The *trapezoidea*-group was proposed by Andersen (2000) to accommodate *P. trapezoidea* and 'a few species of *Hagiomyrma*' with a 'dorsally flattened petiolar node'. Besides *P. trapezoidea* Mayr, only two other species, *P. thusnelda* Forel and the more distantly related *P. metella* Fr. Smith, feature a high columnar petiole with a distinctly flat dorsum. Two other species, *P. darlingtoni* and *P. nourlangie*, feature a distinctly low and broad petiole with a somewhat flat dorsum and very short petiolar spines (Fig. 13A-B, C-D). These latter species also agree with Andersen's (2000) definition of his 'Group A', that constituted mostly 'smaller, more gracile species with very reduced petiolar spines'. *Polyrhachis nourlangie* is 'endemic to sandstone escarpments of the northern Top End' and is undoubtedly the species Andersen was referring to when proposing his new group. *Polyrhachis darlingtoni* and *P. nourlangie* are closely related and form a distinct *darlingtoni*-complex within the *trapezoidea*-group.

Polyrhachis metella has always been a difficult species to place. With its strongly anteriorly converging pronotal margins, rather long and slender propodeal and petiolar spines, very high declivity and flat-topped petiole (Figs 5A-B), it resembles some members of *Hedomyrma* and can be considered an intermediate between that subgenus and *Hagiomyrma*. It is clearly unrelated to other species of the *trapezoidea*-group and is consequently placed into a newly proposed *metella*-group.

Most of the smaller species of the subgenus (HL < 1.90) are incorporated into the newly proposed *penelope*-group. Besides their smaller size and black body colour, most species have golden or silvery pubescence fairly evenly distributed over the gastral dorsum (except *P. electra* sp. nov.) or have virtually no gastral pubescence (e.g. Fig. 6E). Consequently most species lack a median patch on the gastral dorsum as seen in species within the *ammon*-group. The species of the *penelope*-group can be divided into three complexes. Species in the *pilbara*-complex are characterised by bristle-like hairs along the antennal scapes and rather coarsely reticulate-punctate body sculpturation (e.g. Fig. 8C). In contrast, species of the *anderseni*- and *penelope*-complexes lack antennal hairs and their body sculpture is distinctly more finely, reticulate-punctate. Also, species in the *anderseni*-complex have the bases of petiolar spines closely approximate and the dorsum of petiole transversely narrow and medially concave (Fig. 6A). Species in the *penelope*-complex, feature widely divergent petiolar spines and a transversely wide and virtually straight petiolar dorsum (e.g. Figs 6E, 8A).

CHECKLIST OF HAGIOMYRMA SPECIES

The following list includes all described *Hagiomyrma* species, with their synonyms indented.

POLYRHACHIS (HAGIOMYRMA)
AMMON SPECIES-GROUP

- ammou* (Fabricius, 1775)
ammon angustata Forel, 1902
ammonoeides Roger, 1863
chalchas Forel, 1907
augusta Forel, 1902
aurora sp. nov.
brisbanensis sp. nov.
brutella sp. nov.
burwelli sp. nov.
callima sp. nov.
couciliata sp. nov.
cracenta sp. nov.
dougcooki sp. nov.
elegantula sp. nov.
feehani sp. nov.
semiaurata Mayr, 1876
uncaria sp. nov.
vernoni sp. nov.

POLYRHACHIS (HAGIOMYRMA) METELLA
SPECIES-GROUP

metella Fr. Smith, 1860

POLYRHACHIS (HAGIOMYRMA) PENELOPE
SPECIES-GROUP

- anderseni* sp. nov.
archeri sp. nov.
clarki sp. nov.
crawleyi Forel, 1916
denticulata Karavaiev, 1927
electra sp. nov.
hoffmauii sp. nov.
melanura sp. nov.
penelope Forel, 1895
pilbara sp. nov.
placida sp. nov.
seducta sp. nov.
semiobscura Donisthorpe, 1944
stricta sp. nov.
tanami sp. nov.
tenebra sp. nov.
weiri sp. nov.

POLYRHACHIS (HAGIOMYRMA) SCHENKII
SPECIES-GROUP

- bohemia* sp. nov.
capeyorkensis sp. nov.
injinoi sp. nov.
isolata sp. nov.
lachesis Forel, 1897
lydiae Forel, 1902
paxilla Fr. Smith, 1863
schenkii Forel, 1886

POLYRHACHIS (HAGIOMYRMA) TRAPEZOIDEA
SPECIES-GROUP

- darlingtoni* sp. nov.
nourlaugie sp. nov.
thusnelda Forel, 1902
trapezoidea Mayr, 1876

POLYRHACHIS (HAGIOMYRMA) TUBIFERA
SPECIES-GROUP

- diversa* sp. nov.
tubifera Forel, 1902

KEY TO SPECIES OF POLYRHACHIS
(HAGIOMYRMA)

(based on worker caste)

- Generally larger species (HL > 2.20) 2.
 – Generally medium-sized or small species (HL < 2.15) 14.
- Pronotal dorsum with margins strongly converging anteriorly (Fig. 5A); occipital corners with distinct postocular carinae; anterior clypeal margin deeply emarginate medially (New Guinea and Bismarck Archipelago). *P. metella* Fr. Smith
 – Pronotal dorsum more-or-less quadrate or only weakly converging anteriorly (e.g. Figs 2E, 4A); occipital corners simply rounded, without postocular carinae; anterior clypeal margin medially with denticulate flange or simply truncate. . . . 3
- Gaster with pubescence very much diluted, virtually lacking; head and

- mesosoma with long, rich golden pubescence (Fig. 4C-D) (QLD, NSW, VIC) *P. semiaurata* Mayr
- Gaster with golden or silvery pubescence identical or similar to that on dorsum of head and mesosoma 4
4. Pronotal humeri distinctly angular (Fig. 4G); dorsum of first gastral tergite strongly transverse, laterally produced into narrowly rounded prominences (Cape York Pen., Mt Tozer, QLD) *P. vernoni* sp. nov.
 - Pronotal humeri narrowly or widely rounded (e.g. Fig. 2C, E); dorsum of first gastral tergite less transverse, with sides widely rounded 5
 5. Petiolar node relatively thick in profile with dorsum widely rounded or forming more-or-less flat platform; petiolar spines short, bases situated well below summit of dorsal convexity (Figs 2F, 13B) 6
 - Petiolar node in profile with anterior and posterior face converging towards narrowly rounded dorsum; petiolar spines longer, bases situated at lateral corners of dorsal summit (e.g. Fig. 1B, H) 7
 6. Pronotal dorsum with margins weakly converging anteriorly; propodeal spines subparallel (Fig. 13A); head in full face view with numerous hairs fringing lateral outline between eyes and mandibular bases (Cape York Pen., McIlwraith Range, QLD) *P. darlingtoni* sp. nov.
 - Pronotal dorsum more-or-less quadrate; propodeal spines divergent (Fig. 2E) head in full face view with no hairs fringing lateral outline between eyes and mandibular bases (Mt Abbott, QLD) *P. burwelli* sp. nov.
 7. Dorsum of gaster with golden or silvery pubescence and more-or-less distinct, dark reddish-brown, median patch, extending from dorsum of first gastral tergite towards apex (e.g. Fig. 2C, G) 8
 - Dorsum of gaster with widely diffused patch of golden pubescence extending towards apex; reddish-brown median patch on gaster not evident (e.g. Figs 1A-B, 4E-F) 2
 8. Median patch on gastral dorsum very dark and prominent (Figs 2G, 3A) 9
 - Median patch on gastral dorsum lighter and less prominent (e.g. Figs 2C, 4A) ... 10
 9. Dorsum of pronotum with only a few, relatively short, erect hairs; hairs completely absent from mesonotum, propodeum, including declivity, and propodeal spines (Fig. 3A-B) (central QLD) ... *P. conciliata* sp. nov.
 - Dorsum of mesosoma, including bases of propodeal spines, with numerous erect or semierect, long or medium length hairs (central QLD) *P. callima* sp. nov.
 10. Pronotal dorsum with margins weakly converging anteriorly (Fig. 4A) (Cooktown district, QLD) *P. feelhani* sp. nov.
 - Pronotal dorsum more-or-less quadrate or weakly converging posteriorly (e.g. Fig. 2A, C) 11
 11. Smaller species (HL 2.18-2.37); clypeus virtually straight in profile; dorsa of head and mesosoma with rich golden pubescence, radiating towards midline of mesosoma (Fig. 2A-B) (Brisbane district, QLD) *P. brisbanensis* sp. nov.
 - Larger species (HL 2.28-2.62); clypeus sinuate in profile; dorsa of head and mesosoma with pubescence mostly silvery, diffused into pale golden along midline of mesosoma (Fig. 2C-D) (central QLD) *P. brutella* sp. nov.
 12. Petiolar spines subparallel, shorter than distance between their bases; dorsa of head and mesosoma with evenly distributed golden pubescence 13.
 - Petiolar spines divergent, about as long as or longer than distance between their bases; body pubescence unevenly distributed with head distinctly less pubescent than dorsum of mesosoma (Fig. 1A-B) (QLD, NSW, VIC) *P. ammon* (Fabricius) (in part).
 13. Smaller species (HL 2.02-2.24); propodeal spines widely divergent; petiolar spines strongly downturned (Fig. 4E-F) (QLD) *P. uncaria* sp. nov. (in part).
 - Larger species (HL 2.21-2.40); propodeal spines subparallel; petiolar spines more-

- or-less horizontal (Fig. 3E-F) (Hann Tblld, QLD) *P. dougcooki* sp. nov.
14. Dorsum of mesosoma distinctly short and wide; propodeal spiracles situated on prominent, laterally projecting tubercles; petiolar dorsum strongly transverse, armed with very short spines 15
- Dorsum of mesosoma more-or-less elongated; propodeal spiracles relatively flat, not situated on prominent tubercles; petiolar dorsum armed with spines of various lengths 16
15. Head and mesosoma with distinct, closely appressed, golden pubescence; dorsum of gaster with only a few, medium length hairs and no pubescence (Fig. 14A-B) (Cape York Pen., QLD).....*P. diversa* sp. nov.
- Head and mesosoma without appressed pubescence; dorsum of gaster with very fine, closely appressed, pale golden pubescence (Fig. 14C-D) (QLD) *P. tubifera* Forel
16. Head and mesosoma generally black, with only mouthparts, pronotal collar, spines and appendages occasionally reddish-brown 24.
- Head and mesosoma not black, coloured or multi-coloured (e.g. Figs 11E-F, 12C-D) .. 17
17. Lateral margins of promesonotum strongly converging posteriorly (PMI > 190) (e.g. Fig. 12G) 18
- Lateral margins of promesonotum less strongly converging posteriorly (PMI < 180) (e.g. Fig. 11C) or subparallel 20
18. Generally smaller species (HL 1.31-1.56); antennal scapes virtually circular in cross-section; dorsum of gaster with distinct, thick silvery or golden, appressed pubescence (Fig. 12G-H) (New Guinea, WA, NT, QLD) *P. schenkii* Forel.
- Generally larger species (HL 1.53-1.75); antennal scapes somewhat flattened, oval in cross-section; appressed pubescence on dorsum of gaster very sparse or lacking 19
19. Antennal scapes relatively short (Sl 123); greatest width of pronotal dorsum near its mid-length; propodeal spines obliquely elevated from bases (Fig. 11G-H) (NT) *P. isolata* sp. nov.
- Antennal scapes relatively long (Sl 134-143); greatest width of pronotal dorsum across humeri; propodeal spines horizontal (Fig. 11E-F) (Cape York Pen., QLD) *P. injinooi* sp. nov.
20. Head, mesosoma and gaster metallic green, with front of head, anterior portion of pronotum and appendages orange or reddish-brown (Fig. 12C-D) (QLD) *P. lydiae* Forel
- Head, mesosoma and gaster not metallic green, mostly medium to dark reddish-brown or red with gaster distinctly darker 21
21. Head and mesosoma conspicuously red or orange-red; gaster very dark brown; appendages reddish-brown (Fig. 11A-B) (WA, NT, QLD) *P. bohemia* sp. nov.
- Head and mesosoma almost uniformly medium to dark reddish-brown with gaster usually a shade lighter; appendages reddish-brown 22
22. Pronotal humeri produced into dilated, dorsally shallowly concave, rounded prominences (Fig. 12A, E); head and mesosoma with more-or-less distinct, vermiculate sculpturation 23.
- Pronotal humeri narrowly rounded; body sculpturation reticulate-punctate, not vermiculate (Fig. 11C) (Cape York Pen., QLD) *P. capeyorkensis* sp. nov.
23. Head and mesosoma reticulate-punctate, shallowly vermiculate-rugose on vertex of head and dorsum of mesosoma; colour almost uniformly medium reddish-brown, appendages and spines a shade lighter (Fig. 12A-B) (QLD) *P. lachesis* Forel
- Head and mesosoma with very distinct, vermiculate-rugose sculpturation; colour mostly black or very dark reddish-brown on most dorsal surfaces; appendages and spines distinctly lighter (Figs 12E-F) (Indonesia, New Guinea, Cape York, QLD) *P. paxilla* Fr. Smith (in part).

24. Antennal scapes with at least a few short, bristle-like hairs along leading edge ... 25
 – Antennal scapes without any hairs along leading edge.....35
25. Promesonotal lateral margins only very weakly converging posteriorly (PMI < 140); petiole in lateral view rather low with very short, curved spines (Fig. 13C-D) (NT)*P. nourlangie* sp. nov.
 – Promesonotal lateral margins more strongly converging posteriorly (PMI > 150); petiole in lateral view distinctly higher with longer spines of various configurations26
26. Outline of head in full face view with numerous, bristle-like hairs fringing margin between eyes and mandibular bases28
 – Outline of head in full face view without hairs, or at most with only a few, inconspicuous, very short hairs fringing margin between eyes and mandibular bases27
27. Head, mesosoma and petiole very distinctly and evenly, rather coarsely, reticulate-punctate; petiole in profile with posterior face distinctly convex and swollen towards base (Fig. 19G-H) (Nth QLD).....*P. tenebra* sp. nov.
 – Head, mesosoma and petiole finely reticulate-punctate with sculpture somewhat longitudinally rugulate-striate on vertex of head; petiole in profile with posterior face only weakly convex (Fig. 9A-B) (New Ireland, New Guinea, Cape York Pen.).....*P. semiobscura* Donisthorpe.
28. Petiolar spines distinctly downcurved, hook-like (Fig. 1D) (only WA)*P. ammonoëides* Roger.
 – Petiolar spines more-or-less horizontal or obliquely elevated, never hook-like (e.g. Figs 9D, 10B).....29
29. Promesonotal lateral margins distinctly converging posteriorly (PMI > 190) (e.g. Figs 9C, 10A) 30
 – Promesonotal lateral margins less strongly converging posteriorly (PMI < 180) (e.g. Fig. 12E)31
30. Antennal scapes relatively short (SI < 141); petiole in profile with posterior face only weakly convex towards base (Fig. 9C-D) (Nth QLD) *P. stricta* sp. nov.
 – Antennal scapes relatively long (SI > 154); petiole in profile distinctly swollen towards base (Fig. 10A-B) (NT)..... *P. weiri* sp. nov.
31. Pronotal dorsum with humeri produced into dilated, distinctly rounded prominences (Fig. 12E-F); head and mesosoma with distinct, vermiculate sculpturation (Indonesia, New Guinea, Cape York) *P. paxilla* Fr. Smith (in part).
 – Pronotal dorsum with humeri rounded or subangular, not distinctly dilated; head and mesosoma reticulate-punctate.....32
32. Petiolar node in profile with posterior face distinctly swollen towards base (Fig. 10B); clypeus in profile virtually straight or only very shallowly impressed anteriorly ... 33
 – Petiolar node in profile with posterior face not distinctly swollen, descending towards base in weakly convex line; clypeus in profile distinctly sinuate (Fig. 8E-F) (Nth QLD)*P. placida* sp. nov.
33. Dorsum of gaster with distinct, closely appressed, golden pubescence, completely hiding underlying sculpturation (Fig. 8C-D) (Pilbara, WA) *P. pilbara* sp. nov.
 – Dorsum of gaster with much diluted, silvery or golden, appressed pubescence (Fig. 11A-B).....34
34. Dorsum of mesosoma with very short, erect, bristle-like hairs (Fig. 8G-H) (Barrow l., WA)*P. seducta* sp. nov.
 – Dorsum of mesosoma with distinctly longer, posteriorly directed hairs that are up to half greatest diameter of eyes in length (Fig. 9E-F) (Tanami Desert, NT)*P. tanami* sp. nov.
35. Promesonotal lateral margins strongly converging posteriorly (PMI > 185) (e.g. Figs 1G, 13G)..... 36
 – Promesonotal lateral margins less strongly or weakly converging posteriorly (PMI < 180) (e.g. Fig. 3C, 13E).....37

36. Dorsum of petiole with flat, strongly posteriorly sloping, triangular platform; petiolar spines obliquely elevated; propodeal spines subparallel or only weakly divergent; antennal scapes relatively short (SI < 142) (Fig. 13G-H) (NT, QLD) *P. trapezoidea* Mayr.
 – Dorsum of petiole narrowly rounded, without flat platform; petiolar spines horizontal; propodeal spines widely divergent; antennal scapes longer (SI > 160) (Fig. 1G-H) (Paluma, Mt Elliot).....*P. aurora* sp. nov.
37. Propodeal spines strongly divergent and long, distinctly longer than distance between their bases (Fig. 3C)..... 38.
 – Propodeal spines less strongly divergent or subparallel, distinctly shorter than distance between their bases (Fig. 13E)..... 39.
38. Dorsum of body without hairs, except a few, short hairs on apical gastral tergites; closely appressed pubescence very diluted with whole body superficially glabrous (Fig. 3C-D) (NT, Nth QLD) *P. cracenta* sp. nov.
 – Dorsum of mesosoma with rather sporadic hairs of various lengths; gaster with hairs more abundant, notably on venter; appressed, golden pubescence diluted on most body surfaces, except rather dense on gastral dorsum (Fig. 6G-H) (WA, NT, Nth QLD) *P. crawleyi* Forel.
39. Dorsum of petiole with flat, transversely wide platform; dorsum of body with very abundant, long silvery hairs that are distinctly longer than greatest diameter of eyes; antennal scapes very short (Fig. 13E-F) (SI < 125) (Cape York Pen., Nth QLD) *P. thusnelda* Forel.
 – Dorsum of petiole narrowly rounded without flat platform; body with relatively short, erect hairs or, at most, with only sporadic, variously curved, longer hairs (as in *P. hoffmanni* and *P. denticulata*); antennal scapes longer (SI > 125) 40
40. Dorsum of head and mesosoma with distinct, rather abundant, mostly golden, medially radiating pubescence 41.
 – Dorsum of head and mesosoma with rather diluted, mostly silvery, variously scattered pubescence 45
41. Petiolar node in side view with anterior and posterior faces subparallel towards base; antennal scapes rather short (Fig. 7C-D) (SI < 137) (Nth QLD) ... *P. electra* sp. nov.
 – Petiolar node in side view with anterior and posterior faces converging dorsally; posterior face descending towards base in oblique, almost straight line 42
42. Dorsum of mesosoma distinctly slender (PMI > 167); propodeal spines obliquely elevated from bases; petiolar spines widely divergent, very slender and long, about as long as distance between their bases (Fig. 1E-F) (QLD, NSW)..... *P. angusta* Forel.
 – Dorsum of mesosoma not distinctly slender (PMI < 167); propodeal spines more-or-less horizontal or weakly downturned; petiolar spines subparallel or only weakly divergent, distinctly shorter than distance between their bases..... 43
43. Petiolar spines divergent, obliquely elevated from bases; propodeal spines virtually parallel along entire length (Fig. 3G-H) (Nth QLD) *P. elegantula* sp. nov.
 – Petiolar spines only weakly divergent or subparallel, horizontal or downturned; propodeal spines weakly divergent with tips curved outwards 44
44. Petiolar spines horizontal; dorsum of gaster with wide median patch of golden pubescence, laterally diffused into pale golden and silvery on sides and venter (Fig. 1A-B). *P. ammon* (Fabricius) (in part).
 – Petiolar spines strongly downturned from bases; whole dorsum of gaster with distinct, reddish-golden pubescence, lined with silvery pubescence on sides and venter (Fig. 4E-F)..... *P. uncaria* sp. nov. (in part)
45. Dorsum of mesosoma with rather long, variously curved, scattered hairs; hairs more abundant and posteriorly directed on gaster..... 46
 – Dorsum of mesosoma virtually lacking hairs or with only very short, much diluted hairs on dorsal body surfaces, including

- gaster.....47
46. Promesonotal lateral margins strongly converging posteriorly (PMI > 170); body with variously curved, scattered hairs that are longer than half of greatest diameter of eyes; posterior face of petiolar node convex, but not distinctly swollen (Fig. 7A-B) (Indonesia, New Guinea, Bismarck Archipelago, Torres Strait) *P. denticulata* Karavaiev.
- Promesonotal lateral margins rather weakly converging posteriorly (PMI < 145); body with variously curved hairs, most longer than greatest diameter of eyes; posterior face of petiolar node distinctly swollen towards base (Fig. 7E-F) (Nth western QLD) *P. hoffmanni* sp. nov.
47. Dorsum of petiole transversely narrow, rather deeply concave between closely approximated bases of spines 48
- Dorsum of petiole flat or very weakly concave; bases of spines separated by transversely wide dorsum of segment 50
48. Petiolar spines widely divergent, highly obliquely elevated; propodeal spines very slender, divergent; posterior face of petiolar node convex but not distinctly swollen (Fig. 6E-F) (Geraldton, WA) *P. clarki* sp. nov.
- Petiolar spines parallel or only weakly divergent, moderately elevated; propodeal spines subparallel; posterior face of petiolar node distinctly swollen towards base . 49.
49. Smaller species (HL < 1.62); anterior clypeal margin truncate medially; bases of petiolar spines very closely approximated, spines subparallel; body sculpture very finely reticulate-punctate, semi-polished (Fig. 6A-B) (WA, NT) *P. anderseni* sp. nov.
- Larger species (HL > 1.62); anterior clypeal margin with denticulate median flange; bases of petiolar spines more widely separated, spines weakly; body sculpture closely reticulate-punctate, distinctly opaque (Fig. 6C-D) (NT, Gulf Country, QLD) *P. archeri* sp. nov.
50. Petiole with posterior face distinctly swollen towards base; petiolar spines

elevated from bases; head and mesosoma with rather sporadic, very short, bristle-like hairs, no hairs on dorsum of petiole; body sculpture closely reticulate-punctate, distinctly opaque (Fig. 7G-H) (WA, NT, QLD) *P. melanura* sp. nov.

- Petiole with posterior face only moderately convex towards base; petiolar spines horizontal; head, mesosoma and petiole with more abundant, marginally longer hairs; body sculpture finely reticulate-punctate, semi-polished (Fig. 8A-B) (Nth and Central QLD) *P. penelope* Forel.

**POLYRHACHIS (HAGIOMYRMA)
AMMON SPECIES-GROUP**

Polyrhachis (*Hagiomyrma*) *ammon*
(Fabricius, 1775)
(Fig. 1A-B)

Formica ammon Fabricius, 1775: 394. Holotype worker. Type locality: AUSTRALIA (as 'Nova Hollandia') (J. Banks), BMNH (examined).

Polyrhachis ammon (Fabricius). Fr. Smith, 1858: 73 (combination in *Polyrhachis*); Mayr, 1876: 72 (descriptions of queen and male).

Myrma (*Hagiomyrma*) *ammon* (Fabricius). Wheeler, 1911: 860 (combination in *Myrma* (*Hagiomyrma*)); Forel, 1915: 108.

Polyrhachis ammon var. *angustata* Forel, 1902: 525. Kohout, 1988: 430 (junior synonym of *P. ammon*).

Material. Australia (no further data) (w). QLD: Bakers Blue Mtn, 17 km W of Mt Molloy, 12.ix.1981 (GBM & DJC) (w); Kanervo Rd., W of Kuranda, 16°53'S, 145°32'E, 400 m, iii.1996 (C. Reid) (w); 16 km E of Mareeba, 400 m, 29.i.1964 (J. Sedláček) (w); Millstream Falls NP, 17°39'S, 145°26'E, xii.1985 (H.T. Imai HI85-299) (w, ♀); Kirrama Ra., c. 600 m, 18°10'S, 145°44'S, 26.ix.1987 (RJK acc. 87.97) (w); Hervey Ra., Turtle Rock area, 19°24'S, 146°31'E, c. 500 m, 3.vi.1996 (RJK & SKR acc. 96.11) (w); Proserpine, N of Airport Drive, 20°29'15"S, 148°33'45"E, 7.xi.2007 (also 10-16.ii.2007, 13.ii-12.iii.2008, 15.viii-5.ix.2007, 2-10.v.2007) (CJB, C. Lambkin, N. Starick, R. Raven, J. Stanisic) (w); Cape Hillsborough NP, 20°55'S, 149°02'E, 2.i.1979 (RJK acc. 79.11) (w); Mt Blackwood NP, 21°02'S, 148°56'E, 14.iv.1981 (RJK acc. 81.102) (w); Eungella NP, Finch Hatton Gorge, 21°04'S, 148°38'E, 7-13.iv.1975 (RJK acc. 75.171) (w); ditto, Broken R., 21°10'S, 148°30'E, 29.ix.1976 (RJK acc. 76.101) (w); Britton Ra., 6 km NNE of Homevale, 21°23'S, 148°33'E, 1-6.iv.1975 (RJK acc. 75.159) (w); Lords Table Plateau, 22°39'23"S, 140°0'51"E, 10.i.2006 (also 7-8.iii.2006 (CJB, GBM, QM Party) (w); Lorna Vale Hmsd, nr Marlborough, 22°43'S, 149°46'E, 8.iv.1981 (RJK acc. 81.44) (w); 7.5km E of Clermont, 22°49'21"S,

- 147°42'46"E, 13-14.i.2006 (CJB) (w); Scotts Peak, SE base, 22°51'35"S, 148°13'41" | E, 9.iii.2006 (S. Wright, CJB) (w); Palm Park, 5.6 km ESE of Byfield, 24.v.1969 (T.G. Campbell & R. Jealous) (w); 6 km N of Mt Archer, nr Rockhampton, 23°17'S, 150°34'E, 4.i.1979 (RJK acc. 79.17) (w); Expedition Ra., Blackdown Tblld, 23°45'S, 149°07'E, 4-6.iv.1981 (RJK accs 81.6, 34) (w); ditto, 1-6.ii.1981 (GBM) (w); Rundle Ra., 36 km NW of Gladstone, 23°39'S, 150°58'E, 24-30.iii.1975 (RJK accs 75.116, 120, 122) (w); Mt Moffat NP, Marlong Arch, 23.ix.1986 (GBM, GIT & DKY) (w); ditto, Top shelter shed, 1000 m, 10-12.xii.1987 (GBM, GIT & DKY) (w); ditto, The Chimneys, 14.xii.1987 (GBM, GT & DKY) (w); Kroombit Tops, 29.ix.1985 (GBM) (w); Moolayember Ck NP, 25°14'28"S, 148°37'20"E, 3-10.iii.2006 (CJB, S. Wright) (w); Fraser I., Urang Ck, 25°19'S, 153°03'E, 14.xii.1984 (RJK acc. 84.446) (w); ditto, Lake McKenzie, 25°27'S, 153°03'E, 12.xii.1984 (RJK acc. 84.445) (w); Taroom Distr., Boggomoss, 25°29'0"S, 150°8'0"E, 14.xi.1996 (QM Survey) (w); Taroom Distr., 9 km N of Ooline Scrub, 25°35'0"S, 149°46'0"E, 15.vi.1996 (H. Janetzki) (w); Cooloola SF, Rainbow Bch, 25°57'S, 153°05'E, 18-25.i.1975 (RJK acc. 75.48) (w); ditto, Searay Scrub, 25°57'S, 153°06'E, 31.viii.1974 (RJK acc. 74.48) (w); ditto, Camp Milo Rd, i.1985 (C. Wallace) (w); Peregrine Bch, 6 km N of Coolool, 26°29'S, 153°05'E, 12.iv.1974 (RJK acc. 74.23) (w); Landsborough, 10.xi.1981 (MJH); Beerwah, 4.xi.1980 (MJH) (w); Bunya Mts NP, 26°51'S, 151°34'E, 1-6.iii.1976 (P. Filewood) (w); Dunmore, W of Toowoomba, 22-23.xii.1981 (MJH & M. de Baar) (w); Stanley R., Environ. Edu. Centre, 27°0'45"S, 152°33'9"E, 31.viii.2006 (B. Renton, S. Clarke, CJB) (w); Bribie I. Rd, 9 km E of Caboolture, 27°05'S, 153°02'E, 19.x.1974 (RJK acc. 74.118) (w); Bribie I., 27°05'S, 153°02'E, 6.vii.1974 (RJK acc. 73.37) (w); Kogan Ck, Braemar Forest Stn, 27°11'S, 150°47'E, 5-6.ii.1980 (RJK acc. 80.2) (w); D'Aguilar Ra., Lacey's Ck Rd, 27°14'S, 152°43'E, 15-20.xii.1974 (RJK acc. 74.157) (w); Moreton I., 27°17'S, 153°25'E, 23.vii.1980 (V. Salanitri) (w); Crows Nest NP, Perseverance sect., 27°18'53"S, 152°6'51"E, 4.xii.2003 (CJB, S. Wright, O. Seeman) (w); Boondall Wetlands, 27°20'21"S, 153°4'27"E, 11.xi.2003 (also 20.ii.2004) (S. Wright, QM Party) (w); Perseverance Ck For. Res., 27°20'57"S, 152°6'18"E, 4.xii.2003 (CJB, S. Wright, O. Seeman) (w, ♀); Brisbane Airport, 27°22'16"S, 153°6'46"E, 6.x.2003 (CJB, E. Vanderduys) (w); Mt Nebo Rd, 27°26'S, 152°54'E, 21.ix.1974 (RJK acc. 74.106) (w); Mt Coot-tha Park, Brisbane, 27°29'S, 152°57'E, 12.iii.1974 (RJK acc. 74.12) (w); ditto, 16.viii.2003 (CJB) (w); Ransome Reserve, 27°29'34"S, 153°11'5"E, 10.xi.2003 (also 27.v-30.vi.2003, 24.ii.2004) (S. Wright, E. Volschenk, QM Party) (w); Belmont Hills Bushlands, 27°30'47"S, 153°7'5"E, 22.iv.2003 (CJB, S. Wright, E. Volschemk) (w); Brisbane, Kingston, 29.ix.1981 (MJH) (w); Bulimba Ck, Carindale, 27°30'9"S, 153°6'34"E, 3.xi.2003 (also 1.ix-10.x.2003, 30.x-1.xii.2003, 19.ii.2004) (QM Party) (w); North Stradbroke I. (27/153), x.1982 (JDM) (w); ditto, 27°37'S, 153°27'E, 10.i.2002 (CJB) (w); 3.5 km SSE of Dunwich, 27°31'41"S, 153°25'1"E, 7-8.i.2002 (D. Cook) (w); Redlands, Hilliards Ck, 27°32'52"S, 153°14'28"E, 20.i.2009 (QM Party) (w); Enterprise Mine, Blackbutt, 27°33'23"S, 153°27'34"E, 9.i.2002 (CJB, QM Party) (w); ditto, Mallee, 27°34'27"S, 153°26'20"E, 7-11.i.2002 (CJB, QM Party) (w); ditto, Scribbly Gum, 27°36'44"S, 153°26'27"E, 10.i.2002 (CJB, QM Party) (w); Gold Ck Reservoir, 27°27'53"S, 153°52'32"E, 29.iv.2003 (also 26.v.2003, 4.xi.2003, 23.ii.2004) (CJB, GBM, E. Volschenk, QM Party) (w); Chelsea Rd Bushlands Res., 27°28'58"S, 153°11'15"E, 23.iv.2003 (also 10.xi.2003, 24.ii.2004) (E. Volschenk, S. Wright, CJB, QM Party) (w); Buhot Ck, Burbank, 27°35'27"S, 153°10'19"E, 6.xi.2003 (also 18.ii.2004) (QM Party) (w); Doolandella, Paradise Rd, 27°36'9"S, 153°1'22"E, 1-15.ii.2002 (CJB, S. Wright) (w); Karawatha For., 27°37'24"S, 153°4'38"E, 25-26.i.2004 (also 17.iv.2003, 25-26.v.2003, 5.xi.2003) (CJB, GBM, S. Wright, QM Party) (w); Illaweena St, Drewvale, 27°38'39"S, 153°3'47"E, 17.iv.2003 (CJB, S. Wright) (w); Spring Mtn, 27°43'17"S, 152°52'42"E, 19.iii.2005 (GBM, QM Party) (w); Mt French, lookout, 27°59'9"S, 152°37'11"E, 13.viii.2003 (CJB) (w); Upper Tallebudgera Ck, 10-11.iii.1989 (GBM) (w); Lake Moogerah, 15 km SW of Boonah, 28°04'S, 152°32'E, 1.i.1975 (RJK acc. 75.2) (w); Stanthorpe, 13.xi.1985 (DKY) (w); Girraween NP, 28°50'S, 151°55'S, 9-10.i.1982 (RJK acc. 82.2) (w); Nundubbermere Falls, 25 km SW of Stanthorpe, 1-4.iv.1988 (GBM) (w); Texas Caves, nr Russenden Hmsd, 28°56'S, 151°27'E, 24-28.ii.1975 (RJK acc. 75.98) (w); Mt Barney, 5.x.1962 (E. Exley) (w). NSW (including ACT): Avoca Beach, 28.x.1985 (L. Hunter) (w); Manning Pt, 20 km E Taree, 7.i.1991, rf. (G. & T. Williams) (w); 4 km NE Harrington, 6.iii.1992, rf. (G. Williams) (w); Myvall Lakes, 32°30'S, 152°21'E, 15.xi. & 14.xii.1996 (L. Wilkie) (w); Wyrabalong NP, 33°16'S, 151°32'E, 15.xii.1996 (L. Wilkie) (w); Richmond Ra. SF, Wattle Ck Rd., 28°38'S, 152°46'E, 130 m, (M. Gray & G. Cassis) (w); Doubleduke SF, 29°12'S, 153°15'E, 4.ii-9.iv.1993 (M. Gray & G. Cassis) (w); Bodella SF, Reservoir Link Rd., 9.iii.1999 (L. Wilkie et al) (w); Athol (W.M. Mann) (w); nr Taree, 25.ix.1981 (M. de Baar) (w); 32 km N of Newcastle, 9.xii.1960 (E.B. Webb) (w); Olney SF, 33°06'S, 151°25'E, 23.ii.1991 (T. Gush) (w); McPherson SF, 33°13'S, 151°11'E, 7.x.1990 (T. Gush) (w); Mooney Mooney, 33°32'S, 151°12'E, 25.xii.1990 (T. Gush) (w); Maroota SF, 33°33'S, 150°58'E, 10.vi.1990 (T. Gush) (w); Gosford, x.1914 (W.M. Wheeler) (w); Woy Woy, 14.vi.1959 (BBL) (w); Castlereagh SF, 33°40'S, 150°45'E, 6.vii.1991 (T. Gush) (w); Galston Gorge, 25 km NNW of Sydney, 33°40'S, 151°05'E, 22.i.1982 (RJK acc. 82.44) (w); Sydney (W.M. Mann) (w); Royal NP, Garie Bch, 34°09'S, 151°04'E, 22.i.2004 (C. Reid) (w); Canberra, Black Mtn, 35°16'S, 149°06'E, 1973 (RJK acc. 73.106) (w); Jerrabomberra Hill, nr Queanbeyan, 35°22'S, 149°13'E, 2.xi.1985 (H.T. Imai HI85-204) (w); Kioloa, ANU Field Stn, 35°32'S, 150°23'E, 50 m, 12.viii.1990 (S. Shattuck #1687) (w); 5 km W of Nellingen, 35°39'S, 150°08'E, 7.xi.1985 (H.T. Imai HI85-218, 238, 240) (w, ♀); Mt Gladstone NP, nr Cooma, 36°15'S, 149°04'E, c. 1110 m, 11.ii.1974 (RJK acc. 74.12) (w); Rosedale, SE of Batemans Bay, 7.xii.1975 (BBL) (w); Bungonia Lookout, 17.v.1978

Revision of *Polyrhachis* (*Hagiomyrma*)



POLYRHACHIS (HAGIOMYRMA) AMMON SPECIES GROUP

- | | | |
|-------|--------------------------|-------------------------|
| Map 1 | ● <i>P. ammon</i> | ▼ <i>P. ammonooides</i> |
| Map 2 | ● <i>P. angusta</i> | ▼ <i>P. aurora</i> |
| Map 3 | ● <i>P. brisbanensis</i> | ▼ <i>P. brutella</i> |
| Map 4 | ● <i>P. burwelli</i> | ▼ <i>P. callima</i> |
| Map 5 | ● <i>P. conciliata</i> | ▼ <i>P. cracenta</i> |
| Map 6 | ● <i>P. dougcooki</i> | ▼ <i>P. fehani</i> |
| Map 7 | ● <i>P. elegantula</i> | ▼ <i>P. semiaurata</i> |
| Map 8 | ● <i>P. uncaria</i> | ▼ <i>P. veroni</i> |

(BBL) (w); Booti Booti NP, 32°14'S, 152°32'E, 12.xii.1996 & 31.v.1997 (L. Wilkie) (w); Munmorah State Rec., 33°13'S, 151°34'E, 23.v.1998 (L. Wilkie) (w); Second gully N of Wonga Gully, 30°48'S, 152°07'E, 4.ii-9.iv.1993 (M. Gray & G. Cassis) (w); Crown Res., 31°18'S, 151°9'E, 24.xi-15.xii.2002 (L. Wilkie et al.) (w); Attunga SF, 30°56'S, 150°54'E, 15.xi-6.xii.2001 (G. Carter) (w); Oaky Ck NR, NE side of Figtree Mt, 31°6'S, 150°36'E, 17.xi-8.xii.2001 (L. Wilkie & D. Smith) (w); W of Flagstaff Mtn, nr Tamworth, 31°5'S, 150°58'E, 15.xi-6.xii.2001 (H. Doherty & M. Elliott) (w); Tamworth, Moore Ck area, 14.v.1987 (BBL) (w); Linton NR, 30°26'S, 150°51'E, 18.xi-9.xii.2001 (H. Doherty & M. Elliott) (w); Mt Kaputar NP, base at N side of Mt Yulludunida, 30°16'S, 150°4'E, 20.xi-11.xii.2001 (H. Doherty & M. Elliott) (w); Kaputar, Narrabri, Gravel Pit Ck (PMR) (w). VIC: Mt Ida, nr Heathcote, 29.v.1961 (BBL) (w); You Yangs, nr Geelong, 1.ii.1958 (BBL) (w).

Description. *Worker.* Dimensions. (holotype cited first): TL c. 9.07, 7.91-9.83; HL 2.22, 1.96-2.31; HW 1.78, 1.56-1.91; CI 80, 78-85; SL 2.67, 2.42-2.97; SI 150, 141-159; PW 1.51, 1.39-1.72; MW 0.94-1.09; PMI 135-159; MTL 3.17, 2.81-3.43 (37 measured).

Median flange of anterior clypeal margin with distinct, acute teeth medially, laterally flanked by acute angles. Clypeus with median, posteriorly raised, longitudinal carina; sinuate in profile. Frontal carinae with only moderately raised margins; central area relatively wide with flat frontal furrow. Sides of head in front of eyes converging anteriorly in virtually straight line, behind eyes sides rounding into moderately convex occipital margin. Eyes situated close to occipital corners, convex, marginally breaking lateral cephalic outline in full face view. Ocelli lacking. Pronotal dorsum wider than long, humeri distinctly rounded, weakly dilated and shallowly concave dorsally; lateral margins behind humeri usually shallowly emarginate or notched, weakly converging towards promesonotal suture. Mesonotum with lateral margins converging posteriorly into dorsally indistinct metanotal groove. Propodeum with lateral margins divergent, terminating in broad-based, horizontal, subparallel or weakly divergent acute spines, tips weakly turned outwards; declivity steep, convex in profile. Petiole armed with a pair of horizontal, divergent, acute spines.

Mandibles finely longitudinally striate with numerous piliferous pits towards bases. Head

and mesosoma finely reticulate-punctate, sculpturation on vertex and sides of head more distinct and organised into more-or-less longitudinal striae. Gaster finely shagreened.

Mandibles with medium length, curved, golden hairs at masticatory and outer borders; numerous closely appressed, shorter hairs towards mandibular bases. Only a few anteriorly directed setae fringing anterior clypeal margin. Several short to medium length, erect hairs on clypeus, along frontal carinae and vertex, no hairs breaking lateral outline of head in full face view. Numerous, medium length, erect golden hairs on most body surfaces, including upper part of propodeal declivity; hairs somewhat longer and posteriorly inclined on gaster, notably around apex and on venter. Closely appressed, mostly silvery or pale golden pubescence rather sparse on head, more abundant on sides of mesosoma, propodeal dorsum, petiole and venter of gaster. Rather abundant, mostly rich golden, with distinct brassy hue, somewhat medially radiating pubescence along promesonotal midline and on gastral dorsum where it virtually hides underlying sculpturation.

Black with only mandibular teeth and condylae reddish-brown.

Queen. Dimensions. TL c. 9.78-11.14; HL 2.12-2.37; HW 1.75-1.96; CI 81-86; SL 2.37-2.77; SI 133-148; PW 2.02-2.37; MTL 2.87-3.22 (17 measured).

Queen similar to worker with usual characters identifying full sexuality. Pronotal dorsum with humeri widely rounded, shallowly concave dorsally along narrowly raised margins. Mesoscutum almost as long as wide; anterior margin evenly rounded; median line distinct, parapsides rather flat; mesoscutum and mesoscutellum uniformly flat in lateral view. Propodeal and petiolar spines similar to those in worker, but distinctly shorter. Sculpturation, pilosity, pubescence and colour virtually identical to worker.

Males and immature stages present in the QM and ANIC collections.

Remarks. *Polyrhachis ammon* closely resembles *P. uncaria* described below, however, they

differ in numerous characters, discussed in the remarks section under *P. uncaria*. *Polyrhachis ammon* is a widespread and relatively common, ground-nesting species, mostly occurring in open eucalypt forests along the eastern Australian seaboard. It ranges from northern Queensland south to Victoria and as far inland as the Australian Capital Territory, however, it becomes rather uncommon towards the northern limit of its distribution. Throughout its range *P. ammon* forms numerous, more-or-less overlapping populations that often, to some extent, differ morphologically from the holotype. However, when specimens from across the entire distribution were compared, no taxonomically significant variability was evident and I believe that all the examined populations are conspecific.

Polyrhachis (*Hagiomyrma*) *ammonoides*
Roger, 1863
(Fig. 1C-D)

Polyrhachis ammonoides Roger, 1863: 157. Lectotype and paralectotype workers (1+2) (designated by Kohout, 1994). Type locality: AUSTRALIA (as 'Neu-Holland, Port Jackson') (locality evidently in error - see Kohout, 1994: 135), MNHN, NHMW (examined).

Polyrhachis ammon r. *ammonoides* Roger. Forel, 1879: 116 (reduced in rank to race of *ammon*).

Polyrhachis ammonoides Roger. Dalla Torre, 1893: 258 (revived status as species).

Polyrhachis (*Hagiomyrma*) *ammonoides* Roger. Forel, 1915: 108 (combination in *P. (Hagiomyrma)*).

Polyrhachis chalthas Forel, 1907: 307. Kohout, 1994: 135 (junior synonym of *ammonoides*).

Material. WA: Montebello Is, Northwest I., 20°22'S, 115°32'E, 22.x.2000 (D. Edinger) (w); Barrow I., 20°46'S, 115°24'E, ii.1977 (H. Heatwole) (w); Dampier, 11.vi.1975 (JDM) (w); Yardie Ck, 29.vii.1975 (R.P. McMillan) (w); 20 km S of Minderoo, 17.x.1970 (JEF) (w); Blowholes, N of Carnarvon, ii-viii.1983 (BBL) (w); Kalbarri, Shellhouse Head, vi.1991 (I. & G. Grose) (w); Kalbarri NP, 1.viii.1983, coastal scrub (BBL) (w, ♂); Kalbarri, 1.x.1998 (ANA) (w); Cervantes, 4.x.1998 (ANA) (w); Easter Group Is, Abrolhos I., 1.ix.1972 (Aquinas College) (w, ♀); Geraldton (J. Clark) (w); ditto, 18-19.xi.1963 (J. Sedláček) (w); 3.2 km SSW of Dongara, 15.x.1970 (JEF) (w); Exmouth, 22.ix.1985 (R.P. McMillan) (w); Enderby I., 20°36'S, 116°29'E, 31.vii-1.viii.1985 (R.P. McMillan) (w); Shark Bay, 20.vii.1985 (R.P. McMillan) (w); Rosemary I., 20°29'S, 116°35'E, 6.viii.1985 (R.P. McMillan) (w); Dirk Hartog I, Turtle Bay, 3.ix.2006 (G. Wright) (w); ditto, S of Sandy Pt., 16.ix.2006 (G. Wright) (w, ♀); ditto, Surf Pt., 21.ix.2006 (G. Wright) (w); Useless Loop, 26°08'S, 113°25'E, 1.viii.1998 (R.P. McMillan) (w); ditto, 11.xi.1998 (R.P. McMillan) (w, ♀); Coolimba Bay,

29°51'S, 114°59'E, xii.1989 (R.P. McMillan) (w); John Forrest NP (E of Perth), 1973 (G.H. Lowe) (w); Beekeeper Res., Leeman, 16.vii.2001 (R.P. McMillan) (w).

Description. *Worker:* Dimensions of *P. ammonoides* (lectotype cited first): TL c. 8.0, 6.65-8.52; HL 1.98, 1.65-2.09; HW 1.53, 1.34-1.65; CI 77, 77-82; SL 2.28, 2.09-2.56; SI 149, 146-164; PW 1.34, 1.05-1.50; MW 0.81-0.88; PMI 147-164; MTL 2.65, 2.46-3.12 (25 measured).

Median flange of anterior clypeal margin irregularly jagged with one central tooth and rather blunt lateral angles. Clypeus with median, longitudinal carina, sinuate in profile. Frontal carinae with distinctly raised margins; central area relatively wide, weakly raised medially. Sides of head in front of eyes converging anteriorly in virtually straight line; behind eyes, sides widely rounding into convex occipital margin. Eyes convex, marginally breaking lateral cephalic outline in full face view. Ocelli lacking, only rudimentary lateral ocelli indicated in some specimens. Pronotal dorsum wider than long; humeri narrowly rounded with shallow depression dorsally; lateral margins behind humeri sinuate, distinctly raised and only weakly converging towards promesonotal suture. Lateral margins of mesonotum converging posteriorly in gentle curve towards metanotal groove indicated by weakly impressed, posteriorly bowed line. Propodeum with lateral margins terminating in distinctly divergent, slender, acute spines. Petiole armed with pair of divergent, hook-shaped, acute spines.

Mandibles finely longitudinally striate with numerous piliferous pits towards bases. Head and mesosoma reticulate-punctate; sculpturation on vertex somewhat coarser with numerous shallow pits. Gaster finely shagreened.

Mandibles with medium length, curved, golden hairs at masticatory and outer borders; numerous closely appressed, shorter hairs towards mandibular bases. Several anteriorly directed, longer setae arising from median anterior clypeal margin, shorter setae fringing margin laterally. Long and medium length, golden, mostly erect hairs, some longer than greatest diameter of eyes, on clypeus, along frontal carinae and on vertex, numerous hairs

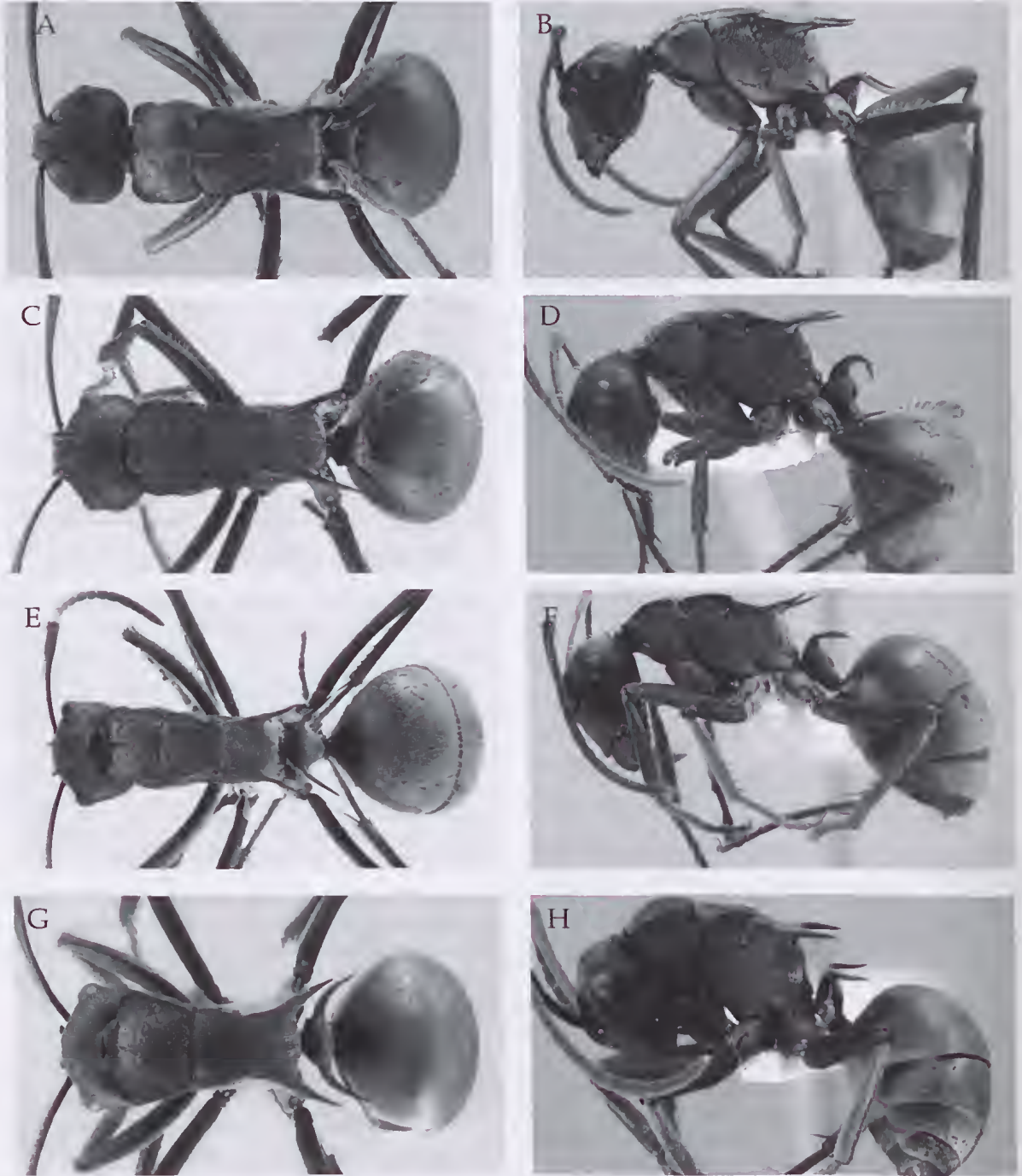


FIG. 1. *Polyrhachis (Hagiomyrma) ammon* species-group – dorsal (left) and lateral (right) view. A-B, *P. ammon* (Fabricius); C-D, *P. ammonoides* Roger; ; E-F, *P. angusta* Forel; G-H, *P. aurora* sp. nov. (not to scale).

fringing lateral outline of head in full face view. Short, erect hairs along leading edge of antennal scapes. Rather long, golden hairs abundant on most body surfaces, including propodeal declivity and spines, except apices. Hairs somewhat longer and posteriorly inclined on gaster, notably around apex and on venter. Closely appressed, rather sparse, mostly silvery pubescence on head, mesosoma, petiole and venter of gaster; longer, rich golden pubescence on gastral dorsum, completely hiding underlying sculpturation.

Black with only mandibular teeth, apical funicular segments and legs dark to very dark reddish-brown.

Queen. Dimensions: TL c. 9.68-10.43; HL 2.18-2.21; HW 1.68-1.75; CI 76-79; SL 2.37-2.56; SI 139-149; PW 1.96-2.12; MTL 2.93-2.99 (4 measured).

Apart from sexual characters, closely resembling worker except: pronotal dorsum with humeri rounded and indication of blunt humeral angles. Mesoscutum in dorsal view virtually as long as wide; anterior margin widely rounded in dorsal and lateral views; median line distinct, parapsides rather flat; mesoscutum and mesoscutellum uniformly flat in lateral view. Propodeal and petiolar spines similar to those in worker, but distinctly shorter.

Males in ANIC spirit collection. Immature stages unknown.

Remarks. Forel was apparently misled by the original type locality given by Roger as Port Jackson and redescribed *P. ammonooides* from Western Australia as *P. chalchas*. He also misinterpreted the short description given by Roger and considered a series of specimens collected by E. Mjöberg at Laura, Queensland (MNHU) to be *P. ammonooides*. However, after examining these specimens, I consider they represent a new species described below as *P. cracenta*. *Polyrhachis ammonooides* is a ground-nesting species with its distribution limited to a relatively narrow band of coastal north-western Australia, from Dampier in the north almost to Perth in the south.

Polyrhachis (*Hagiomyrma*) *angusta* Forel, 1902 (Fig. 1E-F)

Polyrhachis ammon r. *angusta* Forel, 1902: 524. Syntype workers, queens, males. Type locality: QLD, Mackay (G. Turner), MHNG, QM (examined).

Polyrhachis (*Hagiomyrma*) *ammon* r. *angusta* Forel. Forel, 1915: 108 (combination in *P. (Hagiomyrma)*).

Polyrhachis angusta Forel. Kohout, 1988: 431 (raised to species).

Material. QLD: Eungella NP, Broken R., 21°10'S, 148°30'E, 20.xi.1976 (RJK acc. 76.101) (w); Mon Repos Conserv. Pk, 24°48'7"S, 152°26'25"E, 25-26.i.2003 (J. Haines) (w); Taroom Distr., Boggomoss, 25°26'0"S, 150°1'0"E, 11.xi.1996-31.i.1997 (also 9.viii.-11.xi.1996) (CJB, P. Lawless, QM Party) (w); Landsborough, 10.xi.1981 (MJH) (w); Obi Obi Ck, Blackall Ra., 26.v.1962 (RWT acc. 62.1229) (w); Fraser I., Lake Wabby, 8.i.1994 (B. Hoffmann) (w); ditto, Kingfisher Resort, 19.iii.2004 (A. Andersen) (w); Boreen Point, Lake Cootharaba, 26°17'S, 153°00'E, 13.xi.1976 (RJK acc. 76.87) (w); Somerset Dam, 27°06'S, 152°33'E, 12.i.1975 (RJK acc. 75.35) (w); Boondall Wetlands, 27°20'21"S, 153°4'27"E, 22.iv.2003 (also 11.xi.2003, 20.ii.2004) (CJB, S. Wright, E. Volschenk, QM Party) (w); Brisbane Airport, 27°23'38"S, 153°5'54"E, 2-31.x.2003 (CJB, E. Vanderduys) (w); Illaweena St, Drewvale, 27°38'39"S, 153°3'47"E, 9.ix.2003 (also 5.xi.2003, 17.ii.2004) (S. Wright, QM Party) (w); Brisbane, Mt Gravatt, i.1987 (J. Gallon) (w); Moggill Farm, W of Brisbane, 23-27.i.1961 (J.L. Gressitt) (w); Lake Moogerah, 28°04'S, 152°32'E, 11.i.1975 (RJK accs 75.1, 5, 25) (w); Lamington NP, Binna Burra, 28°12'S, 153°11'E, 1.i.1974 (RJK acc. 74.1) (w). NSW: nr Taree, 25.ix.1981 (M. de Baar) (w).

Description. *Worker.* Dimensions (syntypes cited first): TL c. 8.12-8.52, 7.41-9.17; HL 2.07-2.12, 1.81-2.15; HW 1.69-1.71, 1.42-1.72; CI 81-82, 77-82; SL 2.52-2.57, 2.18-2.62; SI 149-152, 148-159; PW 1.06-1.25, 1.15-1.33; MW 0.62-0.70, 0.64-0.75; PMI 167-178, 172-180; MTL 2.97-3.07, 2.67-3.17 (3 + 17 measured).

Median flange of anterior clypeal margin usually with three acute teeth along its shallowly emarginate margin; laterally flange delimited by acute angles. Clypeus with distinct, median carina; sinuate in profile with relatively shallow basal margin. Frontal carinae with moderately raised margins; central area with rather flat frontal furrow. Sides of head in front of eyes converging anteriorly in almost straight line before rounding into mandibular bases; behind eyes, sides rounding into moderately convex occipital margin. Eyes situated close to occipital corners, convex,

clearly breaking lateral cephalic outline in full face view. Ocelli lacking. Pronotal dorsum virtually quadrate, only marginally wider than long; humeri dilated, rounded and dorsally shallowly concave with margins narrowly raised dorsally; lateral margins subparallel, distinctly emarginate at midlength. Promesonotal suture distinct; mesonotal dorsum with lateral margins rather strongly converging posteriorly towards dorsally indistinct metanotal groove. Propodeum with lateral margins diverging posteriorly, terminating in relatively long, slender, moderately elevated, acute spines with tips weakly turned outwards. Petiole with pair of slender, horizontal, divergent, acute spines.

Mandibles finely longitudinally striate with numerous piliferous pits towards bases. Mesosoma and petiole finely reticulate-punctate with sculpturation on head, notably on vertex and sides, somewhat coarser and organised into more-or-less distinct longitudinal pattern. Gaster finely shagreened.

Mandibles with numerous, medium length, curved, golden hairs at masticatory and outer borders; only a few closely appressed, very short hairs towards mandibular bases. Several anteriorly directed setae arising from median clypeal flange and a few very short setae fringing anterior clypeal margin. Several medium length, erect hairs on clypeus, along frontal carinae and vertex, with a few breaking occipital outline in full face view. Numerous, relatively long, erect golden hairs on most body surfaces, some almost as long as greatest diameter of eye. Hairs more numerous, but marginally shorter and posteriorly inclined on gaster. Closely appressed, rather sparse, mostly silvery pubescence on head, sides of mesosoma, petiole and venter and sides of gaster; pubescence rich golden with distinct reddish hue along midline of mesosoma and on gaster, where it forms a relatively wide, laterally diffused patch in centre of first gastral tergite that virtually hides underlying sculpturation.

Black with only mandibular teeth and condylae reddish-brown.

Queen. Dimensions (syntype queen cited first): TL c. 9.93, 9.83-10.43; HL 2.27, 2.18-2.27; HW 1.81, 1.72-1.81; CI 80, 78-82; SL 2.57, 2.46-2.57; SI 142, 140-144; PW 2.17, 1.87-2.17; MTL 3.02, 2.97-3.06 (8 measured).

Apart from sexual characters, very similar to worker except: pronotal humeri widely rounded with lateral margins only very narrowly raised; mesoscutum only marginally wider than long or subquadrate; anterior margin rather narrowly rounded with distinct medial line; parapsides flat. Mesoscutum virtually flat, mesoscutellum only weakly convex, not elevated above dorsal plane of mesosoma in lateral view. Propodeal dorsum evenly rounded into weakly convex declivity. Propodeal and petiolar spines slender, but distinctly shorter than in worker. Body sculpturation similar to that in worker, sculpturation on vertex and sides of head somewhat coarser. Pilosity and pubescence on head and gaster similar to that in worker, but more sporadic and shorter on dorsa of mesosoma and petiole.

Males and immature stages present in the QM collection.

Remarks. *Polyrhachis angusta* is very similar to *P. annuon*, however it is consistently separable by its distinctly more slender body and longer spines and hairs. The reddish-golden midline patch on dorsum of the first gastral tergite is rather narrow in dorsal view and widely bordered with very distinct, silvery, appressed pubescence. In contrast, the patch in *P. annuon* is distinctly wider, covering most of the dorsum, and is only narrowly diffused into pale golden pubescence on the sides and venter of the gaster. *Polyrhachis angusta* appears to be much less common and also more localised than the widespread *P. annuon*.

Polyrhachis (Hagiomyrma) aurora sp. nov.
(Fig. 1G-H)

Etymology. Derived from the Latin word *aurora*, meaning dawn or morning, in reference to the distinctly bright reddish colour of the gastral pubescence.

Material. HOLOTYPE: QLD, Mt Elliot NP, N ridge, 790 m, 19°29'S, 146°58'E, 5.vii.1977, R.W. Taylor

acc. 77.240 (worker). PARATYPES: data as for holotype (8 workers); Mt Elliot NP, North Ck, 500-800 m, 2.xii.1986, G.B. Monteith, G.I. Thompson & S. Hamlet (8 workers). Type deposition: Holotype and 2 paratypes in ANIC; 2 paratypes each in BMNH, MCZC, MHNG, QM.

Other Material. QLD: 12 km W of Paluma, 3.xi.1980 (BBL) (w); Mt Spec NP, Little Crystal Ck, 14.xii.1988 (R.R. Snelling & J. Grey #88-159) (w); Mt Elliot NP, Margaret Ck, 23.ix.1995 (SKR #11) (w); Paluma Ra., Crystal Ck NP, 19°01'S, 146°16'E, 6.ix.2001 (RJK acc. 01.11) (w).

Description. *Worker:* Dimensions (holotype cited first): TL c. 7.41, 6.80-7.71; HL 1.87, 1.75-1.93; HW 1.40, 1.37-1.47; CI 75, 75-80; SL 2.34, 2.28-2.40; SI 165, 159-167; PW 1.40, 1.28-1.45; MW 0.65, 0.62-0.75; PMI 215, 185-215; MTL 2.53, 2.43-2.71 (11 measured).

Anterior clypeal margin with denticulate, median flange. Clypeus with raised median carina, sinuate in profile, posteriorly rounding into well impressed basal margin. Frontal carinae sinuate with moderately raised margins; central area with weakly impressed frontal furrow. Sides of head in front of eyes straight, before rounding into mandibular bases; behind eyes, sides widely rounding into convex occipital margin. Eyes convex, in full face view clearly breaking lateral cephalic outline. Ocelli lacking. Pronotal dorsum flat anteriorly, convex towards promesonotal suture; humeri rounded with distinctly raised margins, shallowly concave dorsally; lateral margins of promesonotum distinctly converging posteriorly (PMI >185) and weakly raised before rounding into poorly indicated metanotal groove. Propodeum with lateral margins terminating in horizontal, distinctly divergent, acute spines. Petiole with anterior face straight, posterior face strongly convex; dorsum shallowly concave with pair of laterally elevated and posteriorly curved, acute spines. Anterior face of first gastral segment widely rounding onto dorsum of gaster.

Mandibles finely, longitudinally striate with numerous piliferous pits. Clypeus very closely punctate; head reticulate-punctate, genae distinctly more coarsely sculptured. Mesosoma and petiole more finely reticulate-punctate; gaster finely shagreened.

Mandibles with numerous, semierect, short, golden hairs near masticatory borders and closely appressed hairs towards bases. Anterior clypeal margin with several anteriorly directed setae. Clypeus, frontal carinae and vertex with a few pairs of rather short, erect hairs; several longer hairs on fore coxae and distinctly short hairs on venter of trochanters and femora. Numerous short, erect, golden hairs on dorsum of gaster; longer hairs around apex and on gastral venter. Closely appressed, mostly golden pubescence with distinctly brassy hue in various densities over most dorsal body surfaces but not hiding underlying sculpturation, except on gaster where it is rather abundant and with distinct reddish tint over most of gastral dorsum; pubescence more silvery on sides of head, mesosoma, petiole and gastral venter.

Black, with only mandibular masticatory borders, condylae, extreme tip of apical funicular segments and gastral apex, reddish brown.

Sexuals and immature stages unknown.

Remarks. *Polyrhachis aurora* is characterised by distinctly posteriorly converging lateral margins of the promesonotal dorsum and strongly divergent propodeal spines. It closely resembles *P. trapezoidea* which shares posteriorly contracted ('trapezoidal') pronotal and mesonotal dorsa and relatively dark, somewhat brassy-coloured pilosity and pubescence. *Polyrhachis aurora* differs from *P. trapezoidea* in having the propodeal spines more divergent and the petiole with a very narrowly rounded dorsum (Fig. 1G-H). In contrast, the propodeal spines in *P. trapezoidea* are only weakly divergent and the dorsum of petiole is a relatively wide, posteriorly sloping platform (Fig. 13G-H). Also, the bright red pubescence that covers most of the gastral dorsum in *P. aurora*, is limited to a rather narrow median patch in *P. trapezoidea*.

Polyrhachis aurora is only known from two closely situated localities, Mt Elliot NP and the Paluma Ra., with all collections made in grassy open forests. Its nesting habit is unknown, but as all known specimens were collected foraging on the ground it can be assumed that *P. aurora*

is a ground-nesting species, as are most other Australian *Hagiomyrma*. *Polyrhachis aurora* was listed as *P. 'Hagio 21'* by Kohout (2000: 200).

Polyrhachis (Hagiomyrma) brisbanensis sp. nov.
(Fig. 2A-B)

Etymology. Named after the city of Brisbane, which lies in the centre of the distribution of *P. brisbanensis*.

Material. HOLOTYPE: QLD, D'Aguiar Ra., Lacey's Ck Rd, 27°14'S, 152°43'E, 15.xii.1974, R.J. Kohout acc. 74.158, QM T174500 (worker). PARATYPES: data as for holotype (61 paratype workers, 1 paratype dealate queen, 10 paratype males from the holotype colony); ditto, except RJK acc. 74.159 (55 paratype workers and 1 paratype dealate queen). Type deposition: Holotype, most paratypes and paratype queen in QM, 3 paratype workers and paratype queen in ANIC; 2 paratype workers each in AMNH, BMNH, CASC, MCZC, MNHU, MHNG and NMNH.

Other Material. QLD: Fraser I., Central Stn, 25°29'S, 153°03'E, 11-12.xii.1984 (RJK acc. 84.444) (w); Cooloola SF, 23.ii.1977 (P.J.M. Greenslade) (w); 10 km N of Yarraman, 20.ix.1979 (BBL) (w); Woodford, NW of Caboolture, 31.vii.1981 (MJH) (w); Jolly's Lookout, Mt Nebo Rd, 13.v.1962 (RWT acc. 1024) (w); Brisbane, Mt Coot-tha Park, 11-19.iii.1973 (RJK accs 73.5, 15, 16, 18, 20, 41) (w, ♀); Brisbane, One Tree Hill, 12.xii.1925 (A. Musgrave) (w); Brisbane, 20.vii & 3.viii.1915 (H. Hacker) (w); Hampton-Esk Rd, 27°19'S, 153°11'E, 15.ii.1975 (RJK acc. 75.84) (w); Perseverance Ck For. Res., 27°20'57"S, 152°6'18"E, 4.xii.2003 (CJB, S. Wright, O. Seeman) (w); Buhot Ck, Burbank, 27°35'27"S, 153°10'19"E, 17.iv.2003 (also 26.v.2003, 6.xi.2003, 18.ii.2004) (CJB, S. Wright, QM Party) (w); White Rock, 27°41'50"S, 152°51'38"E, 19.iii.2005 (QM Party) (w); Spring Mtn, 27°43'17"S, 152°52'42"E, 19.iii.2005 (GBM) (w); Darlington Ra., Cedar Ck, 27°54'S, 153°11'E, 10-15.ix.1974 (RJK accs 74.87, 94, 99) (w); Mt Tambourine, x.1924 (A. Musgrave & C. Geissmann) (w); Beaudesert (S.H. Parlett) (w); Lamington NP, Binna Burra, 28°13'S, 153°11'E, c. 850m, 30.xii.1973 (RJK acc. 73.247) (♀); McPherson Range, NP, xii.1925 (A. Musgrave) (w).

Description. *Worker:* Dimensions (holotype cited first): TL c. 10.43, 9.42-10.58; HL 2.21, 2.15-2.37; HW 1.81, 1.65-1.87; CI 82, 76-82; SL 2.90, 2.87-3.12; SI 160, 158-174; PW 1.47, 1.40-1.72; MW 1.00, 0.97-1.15; PMI 147, 133-150; MTL 3.48, 3.38-3.68 (21 measured).

Median flange of anterior clypeal margin with usually three teeth, flanked by acute angles laterally. Clypeus with distinct, longitudinal carina, straight in profile, narrowly rounding into weakly impressed basal margin. Frontal

carinae sinuate, distinctly raised in midlength; central area with distinct frontal furrow. Sides of head in front of eyes converging towards mandibular bases in straight line; behind eyes, sides narrowly rounding into moderately convex occipital margin. Eyes convex, clearly breaking lateral cephalic outline in full face view. Ocelli lacking. Pronotal dorsum almost quadrate, only slightly wider than long; humeri widely rounded, dorsally shallowly concave, lateral margins behind humeri usually notched or shallowly emarginate and subparallel towards promesonotal suture. Mesonotal lateral margins converging posteriorly, weakly raised and rounding into poorly indicated metanotal groove. Propodeal dorsum with lateral margins subparallel, terminating in more-or-less horizontal, weakly sinuate, acute spines. Petiole armed with pair of parallel, horizontal, posteriorly directed, acute spines.

Mandibles finely longitudinally striate with numerous piliferous pits. Head and mesosoma reticulate-punctate, sculpturation on front of head and pronotal dorsum organised into somewhat longitudinally striate rugulations. Spines smooth and polished towards tips. Gaster finely shagreened.

Mandibles at masticatory borders with numerous, curved golden hairs. Anterior clypeal margin with two longer setae medially and only a few very short setae fringing margin laterally. A few, paired, medium length, erect hairs on clypeus, along frontal carinae and on vertex, no hairs breaking lateral cephalic outline. Dorsum of mesosoma and petiole, fore coxae and ventral surfaces of femora with numerous, erect and variously curved, relatively long golden hairs, longest hairs almost equal to greatest diameter of eye. Gaster with numerous, moderately long, posteriorly inclined golden hairs. Relatively abundant, appressed, golden pubescence with distinct brassy tint, somewhat medially radiating on pronotal and mesonotal dorsa; pubescence silvery and distinctly more diluted on head and sides of mesosoma. Gastral dorsum with abundant, golden-brassy pubescence virtually hiding underlying sculpturation; first gastral tergite with distinct, reddish-coloured, rather

small, median patch, surrounded by golden and diffused into silvery pubescence on sides and venter of gaster.

Black; mandibles very dark reddish-brown with narrow, transverse, light reddish band at bases of mandibular teeth. Appendages black or very dark reddish-brown.

Queen. Dimensions: TL c. 10.38-10.89; HL 2.09-2.15; HW 1.59-1.68; CI 76-78; SL 2.71-2.78; SI 163-172; PW 2.25- 2.37; MTL 3.33-3.53 (6 measured).

Apart from sexual characters, very similar to worker except: longitudinal clypeal carina less distinct; eyes more convex, virtually protuberant. Pronotal humeri subangular; mesoscutum as long as wide, anterior margin evenly rounded; median line distinctly bifurcate; dorsum flat with parapsides only weakly raised posteriorly. Mesoscutellum with dorsum convex, distinctly raised above dorsal plane of mesosoma. Propodeum with spines parallel, shorter than in worker; dorsum rounding evenly into virtually vertical declivity. Petiole armed with very short, posteriorly curved spines. Sculpturation, pilosity, pubescence and colour identical to that in worker.

Males and immature stages present in the QM and ANIC collections.

Remarks. *Polyrhachis brisbauensis* is similar to several species, notably *P. annon* and *P. brutella*. It differs from the former by its almost quadrate pronotal dorsum, closely spaced, parallel petiolar spines and the narrow patch of dark reddish pubescence on the gastral dorsum. In contrast, in *P. annon* the pronotal dorsum is rectangular and wider than long, the petiolar spines are distinctly divergent and rich golden pubescence is distributed over most of the gastral dorsum. Besides its generally smaller size (HL 2.15-2.37 in *P. brisbauensis* versus 2.28-2.56 in *P. brutella*), *P. brisbauensis* differs from *P. brutella* in several other characters, including the straight profile of the clypeus, the weakly sinuate propodeal and parallel petiolar spines and the abundant, brassy golden pubescence of the body. In contrast, the clypeus in *P. brutella* is shallowly, but distinctly concave in profile, the tips of the propodeal and petiolar spines are

curved outwards and the rather sporadic body pubescence is mostly pale silvery. Differences between the queens of the species are even more pronounced. The queen of *P. brutella* features an exceptionally massive mesosoma, which lacks any pilosity or pubescence.

Polyrhachis brisbauensis is a relatively common species in open eucalypt forests and woodlands of the greater Brisbane region. Its distribution extends north to Fraser Island and the Cooloola coast and south to the Queensland-New South Wales border and almost reaches the Great Dividing Range in the west. It is a ground-nesting species with nest entrances usually hidden under pieces of wood or rock. Colonies are relatively small with examined nests containing about 50-60 workers and one dealate queen.

Polyrhachis (*Hagiomyrma*) *brutella* sp. nov.
(Fig. 2C-D)

Etymology. Derived from the Latin word *brutus*, meaning rough, in reference to the harsh conditions under which the nest of the type series was excavated from stony ground.

Material. HOLOTYPE: QLD, Mt Archer, nr Rockhampton, 23°20'S, 150°35'E, 6-7.iv.1981, R.J. Kohout acc. 81.35, QM T174501 (worker). PARATYPES: data as for holotype (245 workers and 1 dealate queen). Type deposition: Holotype, most paratype workers and paratype queen in QM; 2 paratype workers each in AMNH, ANIC, BMNH, CASC, MCZC, MNHU, MHNG and NMNH.

Other material. QLD: Hervey Ra., Turtle Rock, 19°24'S, 146°31'E, 3.vi.1996, open forest, ex nest under large rock (RJK & SKR accs 96.10, 11) (w); ditto, 24.ix.1995 (SKR #18, 19) (w); Eungella NP, 17.xii.1972 (BBL) (w); ditto, Broken R., 700 m, 21°10'S, 148°31'E, 10-12.xi.1976 (RWT & TAW acc. 76.165) (w); Britton Ra., 6 km NNE of Homevale, 21°23'S, 148°33'E, 1-6.iv.1975 (RJK accs 75.158, 161, 166) (w); 20 km S of Sarina, 18.viii.1975 (BBL) (w); Lords Table Plateau, 22°39'23"S, 148°0'51"E, 10.i-7.iii.2006 (CJB, GBM) (w); Scotts Peak, SE base, 22°51'35"S, 148°13'41"E, 9.iii.2006 (GBM, CJB) (w); Roper Ck via "Coomburragee", 22°54'5"S, 148°20'0"E, 11.i.2006 (CJB) (w); Lorna Vale, nr Marlborough, 23.v.1974 (O. Rakemann) (w); Byfield, x.1924 (H.J. Carter & A. Musgrave) (w); Palm Park, c. 5 km ESE of Byfield, 24.v.1969 (T.G. Campbell & R. Jealous) (w); 15 km SbyE of Byfield, 22°59'S, 150°41'E, 26.x.1976 (RWT & TAW acc. 76.218) (w); Mt Archer, nr Rockhampton, 23°20'S, 150°35'E, 4.xii.1976 (RJK accs 76.111, 113) (w); ditto, 6-7.iv.1981 (RJK acc. 81.36) (w, dealate ♀, larvae and pupae); Cania, 24°38'S, 150°58'E, 27.v.1972

(S.A. Harrington) (w); Carnarvon Ra., ix.1940 (S.R. Mitchell) (w); Carnarvon Gorge, 24.v-2.vi.1954 (E. Exley) (w).

Description. *Worker.* Dimensions (holotype cited first): TL c. 10.89, 10.28-11.54; HL 2.50, 2.28-2.62; HW 2.02, 1.84-2.12; CI 81, 78-82; SL 3.43, 3.12-3.53; SI 170, 155-181; PW 1.72, 1.53-1.72; MW 1.25, 1.15-1.31; PMI 138, 125-142; MTL 4.03, 3.88-4.28 (26 measured).

Anterior clypeal margin with median flange, laterally flanked by blunt angles. Clypeus with distinct longitudinal carina, sinuate in profile, posteriorly narrowly rounding into weakly impressed basal margin. Frontal carinae sinuate with moderately raised margins. Sides of head in front of eyes converging towards mandibular bases in virtually straight line; behind eyes, sides abruptly rounding into only moderately convex occipital margin. Eyes convex, clearly breaking lateral cephalic outline in full face view. Ocelli lacking. Pronotal dorsum almost quadrate, only marginally wider than long, lateral margins more-or-less parallel, usually narrowly emarginated or notched at midlength; humeri emarginated with raised margins, weakly concave dorsally. Mesonotal margins weakly raised, converging into weakly indicated, posteriorly bowed metanotal groove. Propodeal dorsum relatively short, rounding into steep, convex declivity; lateral margins terminating in long, slender spines, with tips bent outwards. Petiolar spines sinuate, subparallel or even weakly posteriorly converging, with tips bent weakly outwards and upwards.

Mandibles longitudinally striate with numerous piliferous pits. Head and mesosoma finely reticulate-punctate, with sculpturation irregularly longitudinal along frontal carinae and on vertex; more coarsely sculptured on sides of head. Gaster finely shagreened.

Mandibles with numerous curved, golden hairs at masticatory borders and along outer borders. Anterior clypeal margin with only a few, anteriorly directed setae medially and very short setae laterally. Several pairs of medium length, golden hairs on clypeus, along frontal carinae and on vertex. Numerous, relatively long hairs on dorsum of mesosoma and

petiole, fore coxae and along ventral surfaces of femora. Gaster with numerous, posteriorly inclined, medium length, golden hairs. Closely appressed, mostly silvery pubescence in various densities over most body surfaces, with somewhat pale golden hue along median line of mesosoma; first gastral tergite with distinct, reddish-brown coloured, median patch of pubescence, diffused laterally into rich golden pubescence that blends into silvery on sides and venter of gaster.

Black, with only mandibles dark reddish-brown.

Queen. Dimensions: TL c. 10.84-12.25; HL 2.25; HW 1.72; CI 76; SL 2.92-3.03; SI 170-176; PW 2.59-2.84; MTL 3.73-3.88 (2 measured).

Apart from sexual characters and larger size, similar to worker, except: longitudinal clypeal carina indistinct; sides of head in front of eyes subparallel, very weakly concave; eyes distinctly more convex, virtually protuberant. Pronotal humeri subangular; mesoscutum rather massive, as long as wide with anterior margin widely rounded; median line distinctly bifurcate; dorsum flat with parapsides only weakly raised posteriorly. Mesoscutellum with dorsum convex, distinctly raised above dorsal plane of mesosoma. Propodeum with spines weakly divergent, shorter than in worker; dorsum rounding evenly into virtually vertical declivity. Petiole armed with very short, posteriorly and weakly inwardly curved spines. Sculpturation, pilosity, pubescence and colour identical to that in worker, except virtual lack of pilosity and pubescence on dorsum of mesoscutum.

Males and immature stages (eggs, larvae and pupae from holotype colony) present in the QM collection.

Remarks. *Polyrhachis brutella* is similar to *P. brisbanensis* but is generally larger (HL 2.28-2.56 in *P. brutella* versus HL 2.15-2.37 in *P. brisbanensis*), with most of the distinguishing characters given in the remarks section under the latter. Other characters specific to *P. brutella* include the lack of a light band at the bases of mandibular teeth, the blunt lateral angles of the

anterior flange of the clypeus, the subparallel, undilated lateral margins of the pronotal dorsum, the distinctly sinuate petiolar spines with their tips bent outwards, the distinctly shorter pilosity and the very short, rather diluted body pubescence, notably on the pronotal and mesonotal dorsa. The gastral pubescence in both species is pale gold or silvery, with an almost identical median patch on first gastral tergite.

The distribution of *P. brutella* extends from Eungella National Park south to Rockhampton and as far west as Canarvon National Park, with an apparently isolated population at Turtle Rock in the Hervey Range near Townsville. Specimens from the latter population closely resemble those from Mt Archer, except in having marginally shorter antennal scapes (SI 156-164 in specimens from Turtle Rock versus 167-181 in other specimens) and a wider petiolar dorsum with divergent petiolar spines that have their base more widely separated. *Polyrhachis brutella* inhabits open eucalypt forests, seemingly preferring rocky ground in which to build their nests. Two of the nests dug up at the type locality had their tunnels excavated along and under large boulders with the lowest chambers reaching a depth of about 50-70cm. The Turtle Rock population of *P. brutella* was listed earlier as '*Hagio 16*' by Kohout, 2000: 200).

Polyrhachis (*Hagiomyrma*) *burwelli* sp. nov.
(Fig. 2E-F)

Etymology. Named in honour of my colleague, Dr Chris Burwell of the Queensland Museum, in appreciation of his continuing support of my work on Australian *Polyrhachis*.

Material. HOLOTYPE: QLD, Mt Abbot, summit area, 20°06'S, 147°45'E, 750-1000 m, 8-10.xii.1996, G.B. Monteith & I. Cook, QM T174502 (worker). PARATYPES: data as for holotype (2 workers). Type deposition: Holotype and 1 paratype worker in QM; 1 paratype worker in ANIC.

Other material. QLD: Mt Abbot, Nova Ridge, 20.098°S, 147.756°E, 850 m, 28.ix.2011, B. Nolan #34970 (1 worker).

Description. *Worker:* Dimensions (holotype cited first): TL c. 9.98, 9.73-10.68; HL 2.31, 2.18-2.34; HW 1.96, 1.81-1.96; CI 85, 82-85; SL 3.09, 2.87-3.12; SI 158, 157-159; PW 1.56, 1.47-1.68;

MW 1.18, 1.09-1.25; PMI 132, 132-135; MTL 3.83, 3.63-3.83 (3 measured).

Anterior clypeal margin with median, shallowly emarginate, denticulate flange, laterally delimited by acute teeth. Clypeus with median longitudinal carina; weakly sinuate in profile, posteriorly gently rounding into moderately impressed basal margin. Frontal carinae sinuate with distinctly raised margins; central area with shallowly impressed frontal furrow. Sides of head in front of eyes converging towards mandibular bases in very weakly convex line; behind eyes, sides rather narrowly rounding into shallowly convex occipital margin. Eyes convex, situated near occipital corners; in full face view clearly breaking lateral cephalic outline. Ocelli lacking. Pronotal dorsum virtually quadrate with humeri rounded, dorsally shallowly concave; lateral margins narrowly raised, distinctly emarginate at midlength, widely rounding into laterally deeply impressed promesonotal suture. Mesonotum with lateral margins converging posteriorly towards shallow, but distinct metanotal groove. Propodeal dorsum with lateral margins subparallel, widening posteriorly and terminating in relatively broad-based, divergent, acute spines; spines weakly dorso-posteriorly raised at bases and gently turned downwards at midlength. Petiolar node relatively broad in profile with anterior face weakly and posterior face distinctly convex; spines relatively short, widely divergent, with bases situated well below apex of dorsal convexity; length of spines less than one third of distance between tips. Anterior face of first gastral segment widely rounding onto dorsum of gaster.

Mandibles longitudinally striate-rugose with numerous piliferous pits. Mesosoma and petiole finely, head somewhat more coarsely, reticulate-punctate. Gaster shagreened.

Mandibles with numerous, semierect, curved, golden hairs. Medium length, erect hairs on clypeus, along frontal carinae and on vertex, no hairs evident on sides of head between occipital corners and mandibular bases in full face view. Numerous long, erect, golden hairs on dorsum of mesosoma, coxae,



FIG. 2. *Polyrhachis* (*Hagiomyrma*) *ammon* species-group - dorsal (left) and lateral (right) view. A-B, *P. brisbanensis* sp. nov.; C-D, *P. brutella* sp. nov.; E-F, *P. burwelli* sp. nov.; G-H, *P. callima* sp. nov. (not to scale).

venter of femora, petiole and gaster, most hairs longer than greatest diameter of eyes. Silvery or pale golden, appressed pubescence in various densities over most body surfaces, with golden tint on pronotal and mesonotal dorsa. Gastral dorsum with pubescence virtually hiding underlying sculpturation; pubescence rich golden with reddish hue along midline, silvery on gastral sides and venter.

Black with only condylae and apical tarsal segments reddish-brown.

Sexuals and immature stages unknown.

Remarks. *Polyrhachis burwelli* is a very distinctive species, characterised by its broad petiolar node with a widely rounded dorsum. It is known only from the type locality and, in spite of two extensive surveys at Mt Abbot and neighbouring Mt Aberdeen (west of Bowen), the types are the only known specimens of this apparently rare species.

A single worker (see under 'Other material') differs from the specimens of the type series in a virtual lack of any hairs on head, mesosoma and petiole and with only relatively short, erect hairs lining abdominal segments. The closely appressed, silvery pubescence completely absent from the head, dorsum and sides of mesosoma, with only diluted, silvery pubescence on propodeal declivity, petiole and sides and venter of gaster. Gastral dorsum with rich golden with reddish hue, similar to that in specimens of the type series.

Polyrhachis (*Hagiomyrma*) *callima* sp. nov.
(Fig. 2G-H)

Etymology. Derived from the Greek word *kalos*, meaning beautiful.

Material. HOLOTYPE: QLD, Expedition Ra., Blackdown Tbl, nr Lookout Pt, 23°45'S, 149°07'E, 4.iv.1981, R.J. Kohout acc. 81.12, QM T174503 (worker). PARATYPES: data as for holotype (126 workers, 1 dealate queen, 1 male from holotype colony). Type deposition: Holotype, most paratype workers, paratype dealate queen and male in QM; 4 paratype workers in ANIC, 2 paratype workers each in BMNH, CASC, MCZC, MHNG and NMNH.

Other Material. QLD: Expedition Ra., Blackdown Tbl, nr Lookout Pt, 23°45'S, 149°07'E, 4-6.iv.1981

(RJK accs 81.3, 4, 30) (w); Blackdown Tbl, SEbyE of Blackwater, Horseshoe Lookout, 23°46'S, 149°06'E, 4.vii.1980 (Balderson & Vickery) (w); Mt Moffatt NP, Peawaddy Gorge, 12.xii.1987 (J. Gallon) (w); ditto, Park Headquarters, 25°01'S, 147°47'E, 740 m, 17.xi.1995 (CJB) (w); Mahogany Forest, 1000 m, 11-12.xii.1987 (GBM, GIT & DKY) (w); Marlong Arch, 23.ix.1986 (GBM, GIT & DKY) (w); Top shelter shed, 1000 m, 10-12.xii.1987 (GBM, GIT & DKY) (w, ♀); The Chimneys, 14.xii.1987 (GBM, GIT & DKY) (w); Carnarvon Gorge NP, 24.v-2.vi.1954 (E. Exley) (w).

Description. *Worker.* Dimensions (holotype cited first): TL c. 12.20, 10.89-12.20; HL 2.71, 2.56-2.71; HW 2.06, 1.93-2.06; CI 76, 74-79; SL 3.73, 3.43-3.73; SI 181, 171-183; PW 1.65, 1.53-1.65; MW 1.31, 1.25-1.31; PMI 126, 124-130; MTL 4.89, 4.54-4.89 (21 measured).

Anterior clypeal margin with median, denticulate flange, flanked laterally by acute angles. Clypeus with median carina; in profile distinctly concave anteriorly, straight posteriorly towards virtually flat basal margin. Frontal triangle shallowly impressed. Frontal carinae with raised margins; central area relatively wide and flat with frontal furrow replaced with weakly raised ridge. Sides of head in front of eyes converging towards mandibular bases in virtually straight line; behind eyes, sides converging into weakly convex occipital margin. Eyes situated close to occipital corners, convex, in full face view clearly exceeding lateral cephalic outline. Ocelli lacking. Pronotal dorsum with humeri moderately dilated, rounded, with upturned margins; lateral margins behind humeri weakly notched, parallel towards promesonotal suture. Mesonotal dorsum with posteriorly converging margins; metanotal groove distinct. Propodeum with lateral margins terminating in moderately divergent acute spines, tips weakly turned outwards; propodeal dorsum widely rounding into distinctly convex propodeal declivity. Petiole with dorsum narrowly rounded, armed with divergent, acute spines. Anterior face of first gastral segment widely rounding onto dorsum.

Mandibles finely longitudinally striate with numerous piliferous pits. Head and mesosoma very finely and closely reticulate-punctate. Gaster finely shagreened.

Mandibles with numerous medium length, golden hairs, distinctly longer at masticatory borders, shorter towards mandibular bases. Numerous, anteriorly directed setae fringing anterior clypeal margin. Several, rather long hairs on clypeus, along frontal carinae and vertex, but no hairs breaking lateral outline of head in full face view. Numerous, pale golden or silver, erect and somewhat undulated hairs, longer than greatest diameter of eyes on dorsum of mesosoma, front coxae and petiole; somewhat shorter hairs on middle and hind coxae. Gaster with numerous, golden, posteriorly inclined hairs, longest on gastral venter and around apex where they exceed greatest diameter of eyes. Very sparse, closely appressed, mostly silvery pubescence on dorsum of mesosoma; pubescence more abundant on sides of mesosoma and petiole. Abundant, closely appressed, somewhat medially radiating pubescence over all gastral surfaces, obscuring underlying sculturation; pubescence silvery on venter, rich golden with distinct, dark reddish-brown, median patch on gastral dorsum (Fig. 2G).

Black with only mandibles very dark reddish brown; condylae medium reddish-brown.

Queen. Dimensions: TL c. 12.25-12.60; HL 2.37-2.40; HW 1.81; CI 75-76; SL 3.12-3.28; SI 172-181; PW 2.96-3.18; MTL 4.08-4.38 (3 measured).

Apart from sexual characters, very similar to worker except: pronotal dorsum with humeri subacute, widely rounded posteriorly. Mesoscutum distinctly wider than long; anterior margin evenly rounded; median line distinct, bifurcate; parapsides rather flat; dorsum of mesoscutum flat in lateral view; mesoscutellum convex, distinctly raised above dorsum of mesoscutum. Propodeal and petiolar spines similar to those in worker, but distinctly shorter. Pale golden and silvery, erect hairs over most body surfaces, rather short on dorsum of mesoscutum, distinctly longer on mesoscutellum; appressed pubescence very similar to worker with identical patch on gastral dorsum.

Male and immature stages (larvae and pupae from holotype colony) present in the QM spirit collection.

Remarks. At the type locality, *Polyrhachis callima* was sympatric with *P. conciliata* described below. These species are superficially very similar and I originally considered them to represent a single species. However, closer examination revealed several characters clearly separating them. The most apparent difference is their pilosity which, in *P. callima*, is distributed almost evenly over the entire dorsum of the body, with the longest hairs reaching or exceeding the greatest diameter of the eyes in length. In contrast, the pilosity in *P. conciliata* is distinctly shorter and completely absent from the mesonotal and propodeal dorsa. Nests of *P. callima*, which are identical to those of *P. conciliata*, are excavated in soil with entrances under pieces of wood, stone, or beneath tufts of grass. The holotype colony, which was almost completely excavated, contained 129 ants, including a dealate queen and a male.

Polyrhachis (Hagiomyrma) conciliata sp. nov.
(Fig. 3A-B)

Etymology. Derived from the Latin word *concilium*, meaning assembly, meeting, referring to its close association with *P. callima* described above.

Material. HOLOTYPE: QLD, Expedition Ra., Blackdown Tld, 23°48'S, 149°04'E, 4.iv.1981, R.J. Kohout acc. 81.11, QM T174504 (worker). PARATYPES: data as for holotype (92 workers and 1 dealate queen from holotype colony). Type deposition: Holotype, most paratype workers and paratype queen in QM; 4 paratype workers in ANIC; 2 paratype workers each in AMNH, BMNH, MCZC, MHNG and NMNH.

Other Material. QLD: Expedition Ra., Blackdown Tld, 23°48'S, 149°04'E, 1-6.ii.1981 (GBM) (w, ♀); ditto, nr Lookout Pt, 23°45'S, 149°07'E, 4-6.iv.1981 (RJK accs 81.10, 14), (w); ditto, Mimosa Ck x-ing, 5.iv.1981 (RJK accs 81.15, 17, 19, 22, 24, 27) (w, ♀); Mt Moffat NP, Dargonelly Rockhole, 20-27. ix.1986 (GBM, DKY & GIT) (w); Kenniff's Lookout, 13.xii.1987 (GBM, DKY & GIT) (w); Claravale, 45 km NE of Mitchell, xi.2002 (T. Hardaker) (w).

Description. *Worker:* Dimensions (holotype cited first): TL c. 11.09, 10.28-11.24; HL 2.56, 2.37-2.56; HW 2.03, 1.81-2.06; CI 79, 76-82; SL

3.33, 3.07-3.33; SI 164, 157-178; PW 1.68, 1.48-1.68; MW 1.27, 1.15-1.28; PMI 132, 122-139; MTL 4.33, 3.93-4.33 (26 measured).

Anterior clypeal margin with median, denticulate flange, laterally flanked by acute, laterally directed teeth. Clypeus with median carina; in profile shallowly concave anteriorly, straight posteriorly towards virtually flat basal margin. Frontal triangle shallowly impressed. Frontal carinae with raised margins; central area relatively wide and flat with frontal furrow replaced with weakly raised ridge. Sides of head in front of eyes converging towards mandibular bases in virtually straight line; behind eyes, sides converging into weakly convex occipital margin. Eyes situated close to occipital corners, convex, in full face view clearly exceeding lateral cephalic outline. Ocelli lacking. Pronotal dorsum with humeri moderately dilated, rounded with upturned margins; lateral margins behind humeri weakly notched in some specimens, parallel towards promesonotal suture. Mesonotal dorsum with posteriorly converging margins. Propodeum with lateral margins divergent, terminating in subparallel, acute spines, tips weakly turned outwards; propodeal dorsum widely rounding into distinctly convex propodeal declivity. Petiole with dorsum narrowly rounded, weakly convex medially, armed with divergent, acute spines. Anterior face of first gastral segment widely rounding onto dorsum.

Mandibles finely longitudinally striate with numerous piliferous pits. Head and mesosoma very finely and closely reticulate-punctate with sculpturation on sides of head somewhat more distinct. Gaster finely shagreened.

Mandibles with numerous medium length, golden hairs, distinctly longer at masticatory borders, shorter towards mandibular bases. Numerous, anteriorly directed setae fringing anterior clypeal margin. Several medium length hairs on clypeus, along frontal carinae and vertex, but no hairs breaking lateral outline of head in full face view. Several, medium length, semierect golden hairs on pronotal dorsum; long hairs, almost reaching greatest diameter of eyes in length, on anterior aspect of

front coxae; somewhat shorter hairs on middle and hind coxae, below propodeal spiracles and on petiolar dorsum. Mesonotal and propodeal dorsa completely without hairs. Gaster with numerous, golden, posteriorly inclined hairs, longest on gastral venter and around apex, almost reaching greatest diameter of eyes in length. Very sparse, closely appressed, mostly silvery pubescence on dorsum of mesosoma; pubescence more abundant on head, sides of mesosoma and petiole. Abundant, closely appressed, somewhat medially radiating pubescence over all gastral surfaces, obscuring underlying sculturation; pubescence silvery on venter, rich golden with distinct, dark reddish-brown, median patch on gastral dorsum (Fig. 3A).

Black with only mandibles very dark reddish brown; condylae medium reddish-brown.

Queen. Dimensions: TL c. 12.20-12.65; HL 2.18-2.25; HW 1.75-1.68; CI 74-79; SL 2.87-2.91; SI 164-174; PW 2.70-2.74; MTL 3.83-3.88 (3 measured).

Apart from sexual characters, similar to worker except: pronotal dorsum with humeri narrowly rounded, margins shallowly emarginate posteriorly. Mesoscutum virtually as long as wide; anterior margin evenly rounded; median line distinct, bifurcate anteriorly; parapsides rather flat; mesoscutum flat in lateral view, mesoscutellum convex, distinctly elevated above dorsal plane of mesoscutum. Propodeal and petiolar spines similar to those in worker, but distinctly shorter. Pale golden and silvery, very short, erect hairs on most body surfaces; appressed pubescence very similar to worker with identical patch on gastral dorsum.

Males unknown. Immature stages (eggs, larvae and pupae) in QM spirit collection.

Remarks. *Polyrhachis conciliata* is very similar to *P. callima* described above, with distinguishing characters given under the latter species. Workers of both species have been collected in close proximity and, at the type locality, their nests were located only a few metres apart. They nest in soil with the entrances covered by a stone or piece of wood.



FIG. 3. *Polyrhachis (Hagiomyrma) ammon* species-group – dorsal (left) and lateral (right) view. A–B, *P. conciliata* sp. nov.; C–D, *P. cracenta* sp. nov.; E–F, *P. dougcooki* sp. nov.; G–H, *P. elegantula* sp. nov. (not to scale).

Polyrhachis (*Hagiomyrma*) *cracenta* sp. nov.
(Fig. 3C-D)

Etymology. Derived from the Latin word *cracens*, meaning graceful, for its elegant appearance.

Material. HOLOTYPE: QLD, Mt Elliot NP, 22 km SW of Giru, 25.v.1980, B.B. Lowery (worker). PARATYPES: data as for holotype (30 paratype workers, 2 paratype alate queens). Type deposition: Holotype, most paratype workers and 1 paratype queen in ANIC; 3 paratype workers and 1 paratype queen in QM; 2 paratype workers each in AMNH, BMNH, CASC, MCZC, NMNH; 1 paratype worker in MSNG, MHNG, MNHU and NHMW.

Other Material. WA: Kimberley Distr., Mitchell Plateau, 4 km SbyW of Mining Camp, 14°52'S, 125°50'E, 13.v.1983 (D.C.F. Rentz & J. Balderson) (♀). NT: Arnhem Land, Birany Birany, 10.xi.2004 (BDH) (w); ditto, Balkbalkbuy, 53 km SW of Nhulunbuy 12°35'S, 136°31'E, 1.xi.2005 (BDH) (w); Gorathiya, 90 km SW of Nhulunbuy, 12°35'S, 136°33'E, 11.xi.2007 (BDH) (w); Virginia, E of Darwin, 25.ii.1992, at light (BDH) (♀). QLD: Cape York Pen., Laura (E. Mjöberg) (w); Mareeba, 16.vi.1937 (T. Greaves) (w); 5 km N of Innisfail, 5.viii.1975, on tree (BBL) (w); Townsville, 25.ix.1919 (G.F. Hill) (w, ♀); Townsville, 30.i.1902 (F.P. Dodd) (w); Mackay (W.W. Froggatt) (w); Mackay, viii.1894 (G. Turner) (w).

Description. *Worker.* Dimensions (holotype cited first): TL c. 8.97, 7.81-9.02; HL 2.09, 1.93-2.12; HW 1.81, 1.62-1.81; CI 87, 83-89; SL 2.59, 2.34-2.62; SI 143, 143-149; PW 1.28, 1.18-1.31; MW 0.84, 0.75-0.84; PMI 152, 152-160; MTL 3.09, 2.78-3.09 (19 measured).

Anterior clypeal margin medially with shallow, truncate, denticulate flange, flanked by rather blunt teeth. Clypeus with distinctly raised median carina; sinuate in profile with shallowly impressed basal margin. Frontal triangle poorly indicated. Frontal carinae sinuate with moderately raised margins; central area relatively wide with rather flat frontal furrow. Sides of head in front of eyes very weakly convex towards mandibular bases; behind eyes, sides rounding into convex occipital margin. Eyes moderately convex, in full face view marginally breaking lateral cephalic outline. Ocelli lacking; their position indicated by minute elevations in cephalic sculpture. Pronotal humeri distinctly dilated, rounded with raised lateral margins, dorsally shallowly concave; pronotal dorsum with lateral margins distinctly emarginate or

notched at about midlength, weakly divergent towards promesonotal suture. Lateral margins of mesonotum converging posteriorly and weakly raised towards laterally impressed, medially flat metanotal groove. Propodeal dorsum with margins terminating in broad-based, very long and slender, widely divergent, acute spines. Anterior face of petiole in profile rounding dorsally into long, slender, widely divergent spines; propodeal dorsum deeply concave between spines. Base of first gastral segment widely rounding onto dorsum.

Mandibles distinctly longitudinally striate with numerous piliferous pits. Head and mesosoma very finely and closely reticulate-punctate with sculpturation on sides of head somewhat more distinct; spines highly polished. Gaster finely shagreened.

Mandibles with several medium length, golden hairs at masticatory borders. Only a few anteriorly directed setae fringing anterior clypeal margin medially. Posterior face of fore coxae, gastral venter and apex with medium length, semierect, golden hairs. Whole dorsum of body, including head, mesosoma, petiole and gaster without hairs, except a few, short hairs on apical gastral tergites. Very short, closely appressed, silvery pubescence rather sporadic on venter of head, propodeal declivity, venter and sides of gaster; pubescence completely absent from most dorsal surfaces, except dorsum of gaster, where it is uniformly golden and rather abundant, completely hiding underlying sculpturation.

Black; narrow band across mandibular teeth and condylae reddish-brown.

Queen. Dimensions: TL c. 9.42-9.52; HL 2.00-2.09; HW 1.62-1.72; CI 80-82; SL 2.28-2.40; SI 137-143; PW 2.03-2.21; MTL 2.74-2.90 (5 measured).

Apart from sexual characters, very similar to worker except: pronotal dorsum with humeri subacute, margins widely rounded posteriorly. Mesoscutum distinctly wider than long; anterior margin evenly rounded; median line distinct, bifurcate dorsally; parapsides flat anteriorly, weakly raised posteriorly; dorsum of

mesoscutum and mesoscutellum forming very weakly convex line in lateral view. Propodeal and petiolar spines similar to those in worker, but distinctly shorter. Sculpturation, pilosity, pubescence and colour virtually identical to worker.

Male and immature stages unknown.

Remarks. *Polyrhachis cracenta* is very similar to *P. crawleyi* but is easily separated by its consistently larger size (HL 1.93-2.12 in *P. cracenta* versus 1.66-1.84 in *P. crawleyi*) and its unique superficially glabrous appearance. It is evidently a rare species that has been collected only on a few occasions. Specimens collected by Mjöberg near Laura on Cape York Peninsula, were erroneously identified by Forel (1915) as *P. ammonoeides* Roger and as a result, he described a closely similar species, *P. crawleyi*, as a variety of *ammonoeides*. Like most *Hagiomyrma* species, it is a ground-nesting species, apparently preferring the bases of trees as nesting sites ('nest at base of small sapling' [G.F. Hill]; 'extensive diggings all round small paperbarks' [B.B. Lowery]).

Polyrhachis cracenta is one of several *Polyrhachis* species which were originally collected at Townsville and other north Queensland localities by F.P. Dodd and other early collectors (see above) and were subsequently located in the Northern Territory (i.e. *P. lysistrata* Santschi, *P. prometheus* Santschi and *P. incerta* Kohout (= '*P. micans ops rufa*' Crawley). *Polyrhachis cracenta* was listed as *P. 'Hagio 03'* by Kohout (2000: 199).

Polyrhachis (Hagiomyrma) dougcooki sp. nov.
(Fig. 3E-F)

Etymology. Named in honour of the collector, Doug Cook, a long time associate of the Queensland Museum, who collected many species of *Polyrhachis* and other insects on numerous collecting trips to remote localities in Queensland.

Material. HOLOTYPE: QLD, Hann Tbl'd (Nth End), 16°48'S, 145°10'E, 950-1000 m, 11-14.xii.1995, G.B. Monteith, G.I. Thompson & D.J. Cook, QM T174505 (worker). PARATYPES: data as for holotype (10 workers, 1 alate ♀). Type distribution: Holotype, 3 paratype workers and paratype ♀ in QM; 2 paratypes each in ANIC, BMNH, MCZC; 1 paratype worker in MHNG.

Description. *Worker:* Dimensions (holotype cited first): TL c. 10.03, 9.37-10.23; HL 2.31, 2.21-2.40; HW 1.81, 1.72-1.86; CI 78, 76-78; SL 3.07, 2.95-3.12; SI 170, 168-173; PW 1.53, 1.47-1.59; MW 1.03, 1.03-1.15; PMI 148, 135-150; MTL 3.73, 3.53-3.78 (8 measured).

Anterior clypeal margin with denticulate median flange, laterally flanked by acute teeth. Clypeus with median carina, sinuate in profile, posteriorly rounding into moderately impressed basal margin. Frontal triangle distinct. Frontal carinae sinuate with moderately raised margins. Sides of head in front of eyes converging towards mandibular bases in straight line; behind eyes, sides widely rounding into occipital margin. Eyes moderately convex, in full face view marginally exceeding lateral cephalic outline. Ocelli lacking. Pronotal dorsum quadrate; pronotal humeri rounded, lateral margins weakly emarginate behind humeri and subparallel towards well impressed promesonotal suture. Mesonotal dorsum with lateral margins converging posteriorly; metanotal groove indistinct. Propodeal margins terminating in rather strong, subparallel spines, with bases weakly elevated and sinuate towards tips in side view. Petiole armed with pair of horizontal, weakly divergent spines. Anterior face of first gastral tergite higher than full height of petiole, widely rounding onto dorsum.

Mandibles finely and densely striate-rugose with numerous piliferous pits. Head and mesosoma reticulate-punctate, sculpturation almost completely hidden by overlying pubescence. Spines rugose with tips rather smooth and polished. Gaster finely shagreened.

Mandibular masticatory borders with numerous, medium length golden hairs. Anterior clypeal margin medially with several longer setae and fringe of shorter setae laterally. Numerous medium length hairs on clypeus, along frontal carinae and vertex, but no hairs breaking lateral cephalic outline. Somewhat longer, more abundant, variously curved hairs on dorsum of mesosoma, petiole and spines, excluding extreme tips. Gaster with abundant, erect or posteriorly inclined, golden

hairs, longest hairs reaching greatest diameter of eyes in length. Relatively long, closely appressed, golden pubescence with somewhat reddish hue, over most dorsal body surfaces; pubescence more abundant and distinctly medially radiating on mesosomal dorsum, silvery on sides. Gastral pubescence somewhat longer and more abundant dorsally where it completely hides underlying sculpturation; pubescence silvery on gastral venter and sides, rich golden with distinct reddish hue on dorsum.

Black throughout.

Queen. Dimensions: TL c. 10.68; HL 2.23; HW 1.78; CI 76; SL 2.93; SI 165; PW 2.34; MTL 3.68 (1 measured).

Apart from sexual characters, very similar to worker except: mesoscutum only marginally wider than long with anterior margins widely rounded; medial line bifurcate dorsally; dorsum relatively low and virtually flat in lateral view with parapsides only weakly raised posteriorly. Mesoscutellum not elevated above dorsal plane of mesosoma. Spines similar to those in worker, but marginally shorter. Sculpturation, pilosity, pubescence and colour virtually identical to worker, except mandibles in single available queen dark reddish-brown.

Male and immature stages unknown.

Remarks. *Polyrhachis dougcooki* closely resembles *P. ammon* but differs by its distinctly longer antennal scapes (SI 168-173 in *P. dougcooki* versus 145-155 in *P. ammon*) and relatively small, virtually quadrate pronotal dorsum. The pilosity in *P. dougcooki* is distinctly longer and the somewhat brassy golden pubescence is denser and covers the whole body, including the head. In contrast the pilosity in *P. ammon* is distinctly shorter and the more appressed golden pubescence is virtually absent from the head. *Polyrhachis dougcooki* was listed earlier by Kohout (2000: 200) as '*Hagio 20*'.

Polyrhachis (*Hagiomyrma*) *elegantula* sp. nov.
(Fig. 3G-H)

Etymology. Derived from the Latin word *elegantulus*, meaning fine, graceful, in reference to the species

somewhat elegant appearance, given by the very tidy, closely appressed pubescence.

Material. HOLOTYPE: QLD, Cape York Pen., Iron Ra., 12°43'S, 143°18'E, 26-31.vii.1981, R.J. Kohout acc. 81.203, QM T174506 (worker). PARATYPES: data as for holotype (33 workers); Type deposition: Holotype and most paratypes in QM; 2 paratypes each in AMNH, ANIC, BMNH, CASC, MCZC, MHNG and NMNH.

Other Material. QLD: Cape York, Somerset, 10°45'S, 142°36'E, 7-12.vii.1976 (E. Cameron) (w); Cape York Pen., 10 km N of Bamaga, 25.viii.1972 (R. Jenkins) (w); Bamaga, 10°53'S, 142°23'E, 10-24.iii.1987 (RJK accs 87.76, 79) (w); Andoom, nr Weipa, 12°29'S, 141°50'E, ii.1975 (GBM) (w); Iron Ra., 12°42'S, 143°18'E, 9-15.vi.1971 (RWT & JEF acc. 71.244) (w); ditto, 1-9.vi.1971 (GBM) (w); Mt Lamond, 12°44'S, 143°18'E, 9-15.vi.1971 (RWT & JEF acc. 71.257) (w); Tozer's Gap, 12°45'S, 143°12'E, 9-15.vi.1971 (RWT & JEF acc. 71.273) (w); McIlwraith Ra., 13°45'S, 143°21'E, c. 510 m, 22-27.vii.1977 (RWT acc. 77.557) (w); 3.5 km SWbyS of Mt Baird, 15°10'S, 145°07'E, 3-5.v.1981 (JEF) (w); 1 km N of Rounded Hill, 15°17'S, 145°13'E, 5-7.v.1981 (JEF) (w); Isabella Falls, 45 km NW of Cooktown, 21.vii.2002 (ANA) (w); Black Mtn, NW base, 15°40'S, 145°13'E, 10.vi.1996 (CJB) (w); Mt Cook, nr Cooktown, 17.vii.2002 (ANA) (w); Home Rule, 15°45'S, 145°17'E, c. 200 m, 9-11.vi.1996 (RJK acc. 96.43) (w); Mt Hartley, 15°46'S, 145°19'E, 200-500 m, 11.vi.1996 (CJB) (w); c. 10 km NW of Ellis Bch, 16°40'S, 145°34'E, <20 m, 8.vi.1996, open forest (RJK & CJB acc. 96.33) (w); Cairns, 7.x-2.xi.1914 (W.M. Wheeler) (w); c. 6 km W of Sth Mission Beach, 17°56'S, 146°02'E, 18-19.vii.1980 (RJK acc. 80.62) (w); Porter Ck, 23 km SE of Cardwell, 18°26'S, 146°08'E, 26.ii.2000 (RJK acc. 2000.66) (w); Hinchinbrook I., v.1998 (A.D. Cutter) (w).

Description. *Worker:* Dimensions (holotype cited first) TL c. 8.16, 7.51-8.72; HL 2.03, 1.84-2.15; HW 1.62, 1.47-1.68; CI 80, 78-81; SL 2.59, 2.34-2.73; SI 160, 155-162; PW 1.43, 1.31-1.56; MW 0.94, 0.84-1.03; PMI 152, 140-167; MTL 2.87, 2.59-3.06 (19 measured).

Anterior clypeal margin with obtusely denticulate median flange. Clypeus with median carina, sinuate in profile, with moderately impressed basal margin. Frontal furrow poorly indicated. Frontal carinae sinuate with weakly raised margins; central area with rather flat frontal furrow. Sides of head in front of eyes almost straight towards mandibular bases; behind eyes, sides rounding into convex occipital margin. Eyes moderately convex, in full face view reaching or marginally exceeding lateral cephalic outline. Ocelli lacking.

Pronotal humeri rounded with raised lateral margins, dorsally shallowly concave; pronotal dorsum with lateral margins behind humeri emarginate or notched, weakly converging towards promesonotal suture. Lateral margins of mesonotum converging posteriorly and weakly raised towards medially flat metanotal groove. Propodeal dorsum with margins terminating in slender, horizontal, subparallel, acute spines. Anterior face of petiole in side view rounding dorsally into long, slender, elevated, weakly divergent spines with tips curved upwards. Anterior face of first gastral tergite widely rounding onto dosum.

Mandibles densely and closely longitudinally striate with numerous piliferous pits. Head, mesosoma and petiole very finely reticulate-punctate. Tips of spines smooth and polished. Gaster shagreened.

Mandibles at masticatory and outer borders with numerous, curved, golden hairs. Anterior clypeal margin with a few, anteriorly directed setae and several short setae fringing margin laterally. Numerous relatively short, erect, golden hairs on dorsum of head, mesosoma and petiole, with several hairs on coxae and venter of femora. Gaster with numerous, erect, posteriorly inclined hairs dorsally; somewhat longer hairs around apex and on venter of gaster. Closely appressed, somewhat medially radiating, golden pubescence with somewhat reddish hue, rather abundant on dorsum of head and mesosoma, completely hiding underlying sculpturation; pubescence distinctly more pale golden or silvery along lateral margins and sides of mesosoma, on propodeal dorsum, bases of spines and gaster. Dorsum of gaster with very fine, closely appressed, golden pubescence and distinct, reddish, laterally diffused, median patch; pubescence more silvery on sides and venter of gaster.

Black, with mandibular teeth very dark reddish-brown.

Sexuals and immature stages unknown.

Remarks. *Polyrhachis elegantula* is somewhat similar to several *Hagiomyrma* species, but not

to any of them in particular. It is characterised by its exceptionally tidy appearance, rather slender body and the lightly diffused reddish patch on the gastral dorsum. It is a relatively common species throughout lowland open eucalypt forests, *Melaleuca* dominated coastal plains and savannah woodlands. Its distribution extends from Cape York (Somerset, Bamaga), south to about Ingham. *Polyrhachis elegantula* was listed earlier by Kohout (2000: 199) as '*Hagio* 10'.

Polyrhachis (Hagiomyrma) feehani sp. nov.
(Fig. 4A-B)

Etymology. Named in honor of the collector of the type series specimens, J. Feehan of the ANIC, CSIRO Ecosystem Sciences, Canberra.

Material. HOLOTYPE: QLD, Cape York Pen., 14 km WbyN of Hope Vale Mission, 15°16'S, 144°59'E, 7-10.v.1981, J.E. Feehan (worker). PARATYPES: data as for holotype (36 paratype workers). Type deposition: Holotype and most paratypes in ANIC; 2 paratypes each in BMNH, MCZC and QM.

Other Material. QLD: Shipton's Flat, S of Cooktown, vi.1958 (P.J. Darlington) (w); Cooktown (E.A.G. Clive) (w).

Description. *Worker.* Dimensions (holotype cited first): TL c. 11.24, 10.78-11.79; HL 2.65, 2.56-2.74; HW 2.06, 1.96-2.12; CI 78, 73-80; SL 3.53, 3.33-3.68; SI 171, 164-176; PW 1.75, 1.71-1.90; MW1.28, 1.21-1.31; PMI 137, 137-154; MTL 4.18, 4.03-4.43 (13 measured).

Anterior clypeal margin with shallow, emarginate, obtusely denticulate, median flange. Clypeus with median carina, weakly sinuate in profile, posteriorly rounding into shallow basal margin. Frontal carinae sinuate with distinctly raised margins. Sides of head in front of eyes almost straight towards mandibular bases; behind eyes, sides rounding into convex occipital margin. Eyes moderately convex, in full face view only reaching, or marginally exceeding lateral cephalic outline. Ocelli lacking. Pronotal dorsum with humeri rounded; lateral margins notched and weakly divergent towards promesonotal suture. Mesonotum with lateral margins converging towards poorly indicated metanotal groove. Propodeal dorsum armed with rather strong,

weakly divergent spines, with tips curved upwards and outwards. Petiole armed with pair of weakly divergent, acute spines. Anterior face of first gastral tergite widely rounding onto dorsum. First gastral tergite somewhat transverse with sides produced into blunt prominences, somewhat similar to, but less distinct than those in *P. vernoni* described below.

Mandibles closely longitudinally striate with numerous piliferous pits. Head, mesosoma and petiole distinctly reticulate-punctate, with sculpturation between eyes and frontal carinae organised into fine, longitudinal striae, converging anteriorly and obliquely on clypeus and meeting along median carina. Mesosomal dorsum with reticulae somewhat organised more regularly into striate rugulations, anteriorly directed along promesonotal suture, bowed and forming more-or-less incomplete semicircles on mesonotal and propodeal dorsa. Gaster shagreened.

Mandibles at masticatory borders and towards bases with numerous golden hairs. Anterior clypeal margin with several, anteriorly projecting setae medially and fringe of short setae laterally. Clypeus and sides of head with very short, appressed, silvery hairs arising from numerous shallow pits. Medium length, anteriorly inclined, silvery hairs between frontal carinae, increasing in density on vertex. Dorsa of mesosoma and petiole with rather dense cover of mostly erect or variously curved, long hairs, most longer than greatest diameter of eyes. Gaster with long, posteriorly directed hairs, silvery on venter and sides, golden on dorsum. Somewhat untidy, silvery, appressed pubescence in various densities over most body surfaces. Dorsum of gaster with distinctly longer, golden, appressed pubescence and very distinct, dark reddish-brown, laterally diffused, median patch; pubescence more silvery on sides and venter of gaster.

Black; mandibles black with narrow, reddish-brown band along masticatory border; teeth black. Appendages and venter of gaster reddish-brown.

Sexuals unknown. Immature stages present in the ANIC collection.

Remarks. *Polyrhachis feehani* is superficially similar to several species, including *P. brisbanensis*, *P. brutella*, *P. burwelli*, *P. darlingtoni* and *P. dougcooki*, which are all large and have a very obvious, reddish-golden, median patch on the gastral dorsum. It differs from most of them by its weakly anteriorly converging pronotal margins, a character shared only with *P. darlingtoni*. Both species are easily distinguished by the shape of their petioles (see Figs 4A-B and 13A-B). *Polyrhachis feehani* appears to be rather rare and has been collected only on a few occasions. Its distribution is apparently limited to the wider Cooktown area.

Polyrhachis (*Hagiomyrma*) *semiaurata*
Mayr, 1876
(Fig. 4C-D)

Polyrhachis semiaurata Mayr, 1876:71. Syntype workers.
Type locality: NSW, Sydney, NHMW (examined).

Polyrhachis (*Hagiomyrma*) *semiaurata* Mayr. Forel, 1915:108
(combination in *P. (Hagiomyrma)*).

Other Material. QLD: Expedition Ra., Blackdown Tbl, 23°48'S, 149°04'E, 1-6.ii.1981 (GBM) (w); ditto, 4-6.iv.1981 (RJK accs 81.9, 32) (w); Mt Moffat NP, Kenniffs Lookout, 13.xii.1987 (J. Gallon) (w); ditto, 13.xii.1987 (GBM, GT & DKY) (w); Marlong Arch, 23.ix.1986 (GBM, GT & DKY) (w); Consuelo Tbl, 1000 m, 20-27.ix.1986 (GBM, GT & DKY) (w); Beerwah, 10.xi.1981 (M.J. Hockey) (w); Toorbul, ENE of Caboolture, 27.x.1981 (M.J. Hockey) (w); 9 km E of Caboolture, 27°05'S, 153°02'E, 19.x.1974 (RJK acc. 74.115) (w); Crows Nest MP, Perseverance sec., 27°18'53"S, 152°6'51"E, 4.xii.2003 (CJB, S. Wright, O. Seeman) (w); Hampton-Esk Rd, 27°19'S, 152°16'E, 15.ii.1975 (RJK acc. 75.85) (w); Perseverance Ck For. Res., 27°21'8"S, 152°6'5"E, 4.xii.2003 (CJB, S. Wright, O. Seeman) (w); Mt Nebo Rd, 27°26'S, 152°54'E, 21.ix.1974 (RJK acc. 74.105) (w); ditto, 15.xii.1974 (RJK acc. 74.160) (w); Brisbane, Mt Coot-tha, 14.i.1961 (BBL) (w); ditto, iv-v.1962 (RWT acc. 663) (w); Chelsea Rd Bushland Res., 27°28'58"S, 153°11'15"E, 10.xi.2003 (QM Party) (w); Rafting Ground Res., 27°31'17"S, 152°55'30"E, 13-17.viii.2003 (CJB) (w); Redlands, Hilliards Ck, nr Weippin Rd, 27°32'6"S, 153°14'54"E, 19.i.2009 (QM Party) (w); Enterprise Mine, 27°33'37"S, 153°27'6"E, 9.i.2002 (QM Party) (w); Illaweena St, Drewvale, 27°38'39"S, 153°3'47"E, 9.ix.2003 (QM Party) (w); 0.8km SE of Spring Mtn, 27°43'36"S, 152°52'58"E, 19.iii.2005 (QM Party) (w); Darlington Ra., Thunderbird Park, 27°54'S, 153°11'E, 15.ii.1976 (RJK acc. 76.4) (w); Mt French, lookout area, 27°59'9"S, 152°37'11"E, 13.viii.2003 (CJB) (w);

Lamington NP, Binna Burra, 28°13'S, 153°11'E, c. 850 m, 30.xii.1973 (RJK acc. 73.244) (♀); Stanthorpe, 13.xi.1985 (DKY) (w); Girraween NP, 28°50'S, 151°55'E, 9-10.i.1982 (RJK acc. 82.1) (w). NSW: Barraba-Bundarra Rd, 30°17'S, 150°47'E, 18.xi-9.xii.2001 (L. Wilkie & H. Smith) (w); Eastwood SF, nr Armidale, 30°24'S, 151°43'E, 1981-82 (Y. Sakurai) (♀); 'Warrane', nr Armidale, iv.1980 (K. Jackques) (w); Coffs Harbour distr., Pine Ck SF, 25.vi.1967 (RWT) (w); Olney SF, 33°08'S, 151°24'E, 30.vi.1990 (T. Gush) (w); Castlereagh SF, 33°40'S, 150°45'E, 6.vii.1991 (T. Gush) (w); Tamworth, 800 m, 29.iv.1987 (BBL) (w); Galston Gorge, 25 km NNW of Sydney, 33°40'S, 151°05'E, 22.i.1982 (RJK acc. 82.42) (w); Kurragong, 20.iv.1975 (K. Stante) (w); Brisbane Water NP, Gurracool, 16.xii.1977 (BBL) (w); Killarney Gap, Narrabri, iii.1978 (PMR) (w); Woy Woy, 15.viii.1976 (BBL) (w); Kioloa, ANU Field Stn, 35°32'S, 150°23'E, 50 m, 12.viii.1990 (S.O. Shattuck #1683) (w); Narrabri, Gravel Pit Ck, Kaputar, 1.xi.1975 (P. Room) (w); Urbenville (J. Armstrong) (w). VIC: Glenaladale NP, Bull Ck, 3 iii 1983 (ANA) (w).

Description. *Worker.* Dimensions (syntypes cited first): TL c. 9.47-9.63, 9.02-10.38; HL 2.34-2.40, 2.21-2.43; HW 1.84-1.93, 1.72-1.96; CI 79-80, 78-84; SL 2.81-2.87, 2.62-2.92; SI 149-153, 144-153; PW 1.61-1.65, 1.50-1.65; MW 1.13-1.18, 1.13-1.25; PMI 140-142, 131-142; MTL 3.63-3.68, 3.38-3.68 (2+16 measured).

Anterior clypeal margin with obtusely denticulate, median flange, laterally flanked by blunt angles. Clypeus with median carina, straight or very weakly sinuate in profile, rounding posteriorly into well impressed basal margin. Frontal carinae with moderately raised margins. Sides of head in front of eyes converging towards mandibular bases in almost straight line; behind eyes, sides rounding into convex occipital margin. Eyes convex, in full face view clearly exceeding lateral cephalic outline. Ocelli lacking. Pronotal dorsum with humeri rounded; lateral margins emarginate or notched at about midlength, widely rounding into well impressed promesonotal suture. Mesonotal dorsum with lateral margins weakly raised towards medially flat, metanotal groove. Propodeal dorsum armed with horizontal, divergent spines, distinctly curved outwards from midlength. Petiole in lateral view with anterior face rounded into elevated, sinuate spines, with tips curved upwards; dorsum concave medially, spines only weakly

divergent in dorsal view. Anterior face of first gastral tergite widely rounding onto dorsum.

Mandibles finely, irregularly, striate-rugose with piliferous pits. Head, mesosoma and gaster reticulate-punctate; basal half of propodeal spines sculptured, smooth and polished towards tips; petiolar spines smooth and polished along full length. Gaster finely shagreened, smooth and rather polished.

Mandibular masticatory and outer borders with curved, golden hairs. Anterior clypeal margin with a few longer, golden setae medially and fringe of shorter setae laterally. Head, mesosoma, petiole and gaster with abundant, golden, erect and/or variously curved, hairs, distinctly longer than greatest diameter of eyes, except: clypeus with only a few paired, long hairs along anterior and basal borders; leading edge of antennal scapes with fringe of short, semierect, bristle-like hairs; head in full face view with a few shorter hairs between occipital corners and mandibular bases; hairs on gaster more posteriorly inclined. Abundant, rather long, rich golden, appressed pubescence on most body surfaces, except clypeus, appendages and gaster; pubescence denser and distinctly medially radiating on dorsum of mesosoma, completely hiding underlying sculpturation. Very diluted, pale golden or silvery pubescence on gaster, lacking in some specimens.

Black throughout, only mandibles reddish-brown.

Queen. Dimensions: TL c. 9.17-9.42; HL 1.96-2.06; HW 1.59-1.65; CI 80-81; SL 2.42-2.50; SI 151-153; PW 1.86-1.96; MTL 2.96-3.06 (3 measured).

Apart from sexual characters and generally smaller size (HL 1.96-2.06 in queen, versus 2.21-2.43 in worker), very similar to worker, except: mesoscutum with dorsum flat, as wide as long; median line bifurcate; parapsides flat, only marginally raised posteriorly. Mesoscutellum very weakly convex, not elevated above dorsal plane of mesosoma. Propodeal spines very slender, divergent; petiolar spines similar to those in worker, but shorter. Pilosity generally

much shorter and less dense on head and dorsum of mesosoma, head in full face view without fringing hairs between eyes and mandibular bases. Pubescence similar to worker, except for dorsum of mesoscutum where it is rather diluted, with only a patch of closely appressed hairs along midline. Sculpturation and colour virtually identical to worker.

Males and immature stages present in the QM collection.

Remarks. With its rich golden pubescence on the head and mesosoma, combined with a black, polished and virtually pubescence free gaster, *Polyrhachis semiaurata* is one of the most easily recognisable species. It ranges from Blackdown Tableland in central Queensland, south to northern Victoria and as far west as Carnarvon National Park in central Queensland. In its nesting habits, *P. semiaurata* is both lignicolous and terrestrial, with some colonies found nesting in the partly burned trunks of felled trees.

Polyrhachis (*Hagiomyrma*) *uncaria* sp. nov.
(Fig. 4E-F)

Etymology. Formed by the latinization of a modern word, *uncared-for*, meaning neglected.

Material. HOLOTYPE: QLD, Expedition Ra., Blackdown Tbl, 23°48'S, 149°04'E, 1-6.ii.1981, G.B. Monteith, QM T174507 (worker). PARATYPES: data as for holotype (5 workers); Mt Moffat NP, 25.ix.1995, G.B. Monteith (2 workers). Type distribution: Holotype and 1 paratype in QM; 2 paratypes each in ANIC, BMNH and MCZC.

Other Material. QLD: Windsor Tbl, 28 km NNW of Mt Carbine, 15-18.iv.1982 (GBM, DKY & DLC) (w); Taroom Distr., Cabbage Tree Ck, Nathan Gorge, 25°27'0"S, 150°10'0"E, 20.vi.1996 (H. Janetzki) (w); ditto, Nathan Gorge Camp, 25°27'0"S, 150°8'0"E, 14.xi.1996 (QM Survey) (w).

Description. *Worker.* Dimensions (holotype cited first): TL c. 8.82, 8.12-8.82; HL 2.15, 2.02-2.24; HW 1.90, 1.76-1.97; CI 88, 84-88; SL 2.78, 2.52-2.78; SI 146, 141-147; PW 1.68, 1.56-1.76; MW 1.12, 1.01-1.15; PMI 151, 141-158; MTL 3.22, 3.02-3.38 (6 measured).

Anterior clypeal margin with denticulate, medially notched, median flange, laterally

flanked by obtuse angles. Clypeus with weakly raised median carina; in profile virtually straight with only very shallow depression anteriorly; basal margin very weakly impressed. Frontal triangle indistinct. Frontal carinae sinuate with moderately raised margins; central area rather flat with shallowly impressed frontal furrow. Sides of head in front of eyes converging towards mandibular bases in weakly convex line; behind eyes, sides rounding into rather low, weakly convex, occipital margin. Eyes convex, in full face view not or only marginally exceeding lateral cephalic outline. Ocelli lacking; relative position of posterior pair indicated by sculptural tubercle in most specimens. Pronotal humeri rounded with raised margins; pronotal lateral margins weakly emarginate or notched at about midlength. Promesonotal suture distinctly impressed. Mesonotum with margins converging towards weakly impressed, medially flat, metanotal groove. Propodeal margins terminating in weakly divergent, somewhat downwards and outwards directed spines. Anterior face of petiole in lateral view rounding dorsally into downward curved spines with distinctly upturned tips. Petiolar spines in dorsal view subparallel with tips curved outwards; posterior face of petiole distinctly convex towards base.

Mandibles very finely, longitudinally striate with numerous piliferous pits. Head, mesosoma and petiole finely and closely reticulate-punctate, sculpture on vertex somewhat more longitudinally directed. Spines sculptured at bases, smooth and polished towards tips. Gaster finely shagreened.

Mandibles at masticatory borders with numerous, golden, curved hairs. Anterior clypeal margin with a few, anteriorly projecting longer setae medially and several shorter setae fringing margin laterally. Clypeus, central area and vertex with numerous, medium length, erect and anteriorly directed, golden hairs. Dorsum of mesosoma with numerous, erect or variously curved, golden hairs, some almost as long as greatest diameter of eyes. Several hairs on dorsum of petiole, anterior face of fore coxae and venter of middle and hind coxae and femora. Gaster with

abundant, posteriorly directed, golden hairs on dorsum; hairs marginally longer on apex and venter. Closely appressed, medium length pubescence, in various densities over most body surfaces; pubescence silvery on front and sides of head, sides of mesosoma, coxae and petiole, more golden on vertex of head and dorsum of mesosoma where it is medially radiating. Dorsum of gaster with very distinct, reddish-golden pubescence completely hiding underlying sculpturation; pubescence somewhat laterally diffused to more silvery on gastral sides and venter.

Black; mandibles dark reddish-brown towards masticatory borders.

Sexuals and immature stages unknown.

Remarks. *Polyrhachis uncaria* is very similar to *P. ammon* but they can be separated by the following characters: clypeus in *P. uncaria* with median carina only weakly raised; clypeus virtually straight in profile, with only a very shallow depression behind anterior margin, terminating posteriorly in an almost flat basal margin; propodeal spines in lateral view directed downwards, following the curved outline of the mesosomal dorsum; petiole with spines subparallel; anterior face of petiole in lateral view rounding dorsally into rather strongly downwardly curved spines; posterior face of petiole distinctly swollen towards base; pubescence on dorsum of head virtually the same density as that on dorsum of mesosoma; very distinct, reddish-golden pubescence covering most of the dorsum of the gaster. In contrast, the clypeus in *P. ammon* has a distinctly raised median carina and is strongly sinuate in profile with a distinctly impressed basal margin, the propodeal spines are horizontal and aligned with the main axis of the body in lateral view, the anterior face of the petiole is straight and its posterior face is obliquely descending, the petiolar spines are distinctly divergent and horizontal in side view, pubescence is virtually lacking from the dorsum of head which is distinctly black in appearance and strongly contrasts with the pubescent dorsum of the mesosoma, and the reddish-golden patch of appressed gastral

pubescence is limited to a median dorsal strip that extends posteriorly from the base of first gastral tergite but does not reach the apex of the gaster.

Polyrhachis uncaria appears a rather rare species known only from a few localities in central Queensland, with an apparently isolated population on Windsor Tableland, just north-west of Mossman. However, since the species is rare, the apparent gaps in its distribution may be reduced through additional surveys. It inhabits open forests and often occurs together with *P. ammon*. The nesting habit of *P. uncaria* is unknown, but it probably nests in the ground like most other *Hagiomyrma* species.

Polyrhachis (Hagiomyrma) vernoni sp. nov.
(Fig. 4G-H)

Etymology. Named in honour of the collector of the holotype, Donald P. Vernon, formerly of the Queensland Museum, Brisbane, who was the only Australian member of the 1948 Archbold Expedition to Cape York.

Material. HOLOTYPE: QLD, Cape York Pen., Mt Tozer, 12°45'S, 143°13'E, 24.vi.1948, D.P. Vernon, QM T174508 (worker). PARATYPES: data as for holotype (1 worker); Mt Tozer, summit, 12°45'S, 143°13'E, 545 m, 8.xii.1985, G.B. Monteith & D.L. Cook (10 workers). Type deposition: Holotype and 2 paratypes in QM; 2 paratypes each in ANIC, BMNH, MCZC, 1 paratype in MHNG.

Other Material. QLD: West Claudie R., 12°44'S, 143°14'E, 500 m, rf., 3-10.xii.1985 (GBM & DJC) (w).

Description. *Worker*: Dimensions (holotype cited first): TL c. 11.04, 11.04-11.74; HL 2.56, 2.56-2.78; HW 1.84, 1.84-2.00; CI 72, 70-73; SL 3.17, 3.17-3.48; SI 172, 167-178; PW 1.68, 1.68-1.84; MW 1.12, 1.12-1.22; PMI 150, 146-160; MTL 3.88, 3.88-4.28 (12 measured).

Anterior clypeal margin with shallow, obtusely denticulate, median flange, laterally flanked by blunt angles. Clypeus with median carina; sinuate in profile, posteriorly rounding into well impressed basal margin. Frontal triangle indistinct. Frontal carinae sinuate with distinctly raised margins; central area relatively wide with distinct median carina. Sides of head in front of eyes converging towards mandibular bases in straight line; behind eyes, sides

Revision of *Polyrhachis* (*Hagiomyrma*)



FIG. 4. *Polyrhachis* (*Hagiomyrma*) *ammon* species-group – dorsal (left) and lateral (right) view. A-B, *P. feehani* sp. nov.; C-D, *P. semiaurata* Mayr; E-F, *P. (H.) uncaria* sp. nov.; G-H, *P. vernoni* sp. nov. (not to scale).

rounding into highly convex occipital margin. Eyes convex, in full face view exceeding lateral cephalic outline. Ocelli lacking. Pronotal humeri produced into dilated, angular prominences with distinctly raised margins; lateral margins behind humeri weakly raised, subparallel towards well impressed promesonotal suture. Mesonotal lateral margins weakly raised for most of length; posteriorly converging towards indistinct metanotal groove. Propodeal margins terminating in rather strong, divergent spines, obliquely raised from bases in side view and sinuate towards weakly upturned tips. Petiole with dorsum shallowly concave medially, armed with divergent, horizontal spines. First gastral tergite distinctly transverse, in dorsal view with sides produced into somewhat bluntly elevated, shoulder-like prominences.

Mandibles finely, longitudinally striate with numerous piliferous pits. Head, mesosoma and petiole reticulate-punctate; spines sculptured at bases, smooth and polished towards tips. Gaster shagreened.

Mandibular masticatory borders with numerous, curved, golden hairs and short, appressed hairs towards bases. Anterior clypeal margin with a few longer, anteriorly projecting setae medially and numerous, short setae, fringing margin laterally. Clypeus with only a few, paired, rather short, semierect hairs; central area and vertex with numerous, medium length, anteriorly directed, golden hairs, but no hairs breaking lateral cephalic outline between eyes and mandibular bases in full face view. Leading edges of antennal scapes with a few, semierect, short, bristle-like hairs. Dorsum of mesosoma, gaster and anterior face of fore coxae, with numerous, erect or variously curved, golden hairs, some as long as greatest diameter of eyes; somewhat shorter hairs on dorsum of petiole, mid and hind coxae and venter of femora; hairs more diluted and anteriorly directed on venter of gaster. Relatively long, appressed, somewhat untidy, golden pubescence on dorsum of head, mesosoma and petiole; pubescence distinctly shorter and much diluted on clypeus and sides of head and mesosoma. Dorsum of gaster with abundant, golden pubescence and very

distinct, dark, reddish-brown median patch, extending posteriorly along first and second tergite; pubescence more diluted and silvery on gastral venter.

Black; mandibular masticatory borders, appendages and venter of gaster medium to dark reddish-brown.

Sexuals and immature stages unknown.

Remarks. *Polyrhachis vernoni* is a very distinct species, easily separated from all other *Hagiomyrma* by the unique, distinctly raised, angular margins of pronotal humeri and the strongly transverse first gastral tergite with blunt lateral prominences. It is one of only a few rainforest dwelling members of the subgenus, with most specimens known collected foraging on the ground and large boulders at the summit and slopes of Mt Tozer in Iron Range National Park.

**POLYRHACHIS (HAGIOMYRMA)
METELLA SPECIES-GROUP**

***Polyrhachis (Hagiomyrma) metella* Fr. Smith,
1860
(Fig. 5A-B)**

Polyrhachis metella Fr. Smith, 1860: 99, pl. 1, figs 20, 29. Holotype worker. Type locality: NEW GUINEA, Dory (= INDONESIA, IRIAN JAYA, Manokvari) (A.R. Wallace), OXUM (examined).

Other Material. INDONESIA: Waigeu (= Pulau Waigeo), Camp Nok, 2500', v.1938 (L.E. Cheesman, BM 1938-593) (w). IRIAN JAYA (as Dutch New Guinea): Lordberg (Mt Burgers), c. 5°N, 143°S (Kais, Augustall Exp.) (w); above Ikar, 500-750 m, 23.vi.1959 (J.L. Gressitt) (w). NEW GUINEA: (no further data) (P. Hossfeld) (w). BISMARCK ARCHIPELAGO, NEW BRITAIN, Baining Mts (G.F. Hill) (♀). PAPUA NEW GUINEA: Western Prov., Muller Ra., 45 km SW of Kopiago, -5.72914, 142.2633, 495 m, rf., 4.& 9.ix.2010 (A. Lucky) (w); West Sepik Prov.(Kais, Wilhelmisland), Torricelli Mts, (Dr Schlaginhausen) (w); (D. Neuginea) Wareo (w); Adelbert Mts, Wanuma, 800-1000 m, 25-26.x.1958 (J.L. Gressitt) (w); Tsanga, Upper Jimmi Valley, 840 m, 13.vii.1958 (J.L. Gressitt) (w); Wum, Upper Jimmi Valley, 840 m, 17.vii.1955 (J.L. Gressitt) (w); Upper Jimmi V., 15.vii.1955 (J.L. Gressitt) (w); Finschhafen (as Finsch Haven) (L. Wagner) (w); Gulf Prov.: Ivinka Camp, Lakekamu basin (07°7'S, 146°8'E), 120 m, 4.xii.1996, lowland wet forest (R.R. Snelling #96.405) (w).



POLYRHACHIS (*HAGIOMYRMA*) *METELLA*
SPECIES-GROUP

Map 1 ● *P. metella*

Description. *Worker:* Dimensions (holotype cited first): TL c. 10.13, 9.42-11.14; HL 2.52, 2.28-2.65; HW 1.74, 1.59-1.93; CI 69, 69-74; SL 3.43, 3.17-3.73; SI 197, 189-204; PW (greatest width measured along promesonotal suture) 1.36, 1.31-1.55; MTL 4.18, 3.93-4.43 (12 measured).

Mandibles with 5 teeth. Anterior clypeal margin with open 'U'-shaped emargination, laterally flanked by distinct, strong teeth; clypeus with rather blunt median carina, virtually straight in profile; basal margin shallow. Frontal triangle indistinct. Frontal carinae weakly sinuate, very strongly raised, almost vertical; central area very narrow, deeply excavated, with poorly indicated frontal furrow. Sides of head in front of eyes subparallel, straight or very weakly convex towards mandibular bases; behind eyes, sides merging into distinct, postocular ridges running on each side from narrow occipital margin along occipital corners, terminating before reaching posterior margin of eyes. Eyes relatively small, moderately convex, in full face view not reaching lateral cephalic outline. Median ocellus present in some specimens; lateral ocelli lacking. Pronotal dorsum with lateral margins strongly converging anteriorly; pronotal humeri with high, almost vertically raised, somewhat angular margins; promesonotal suture deeply impressed laterally. Mesonotal dorsum disc-shaped in dorsal view, lateral margins raised posteriorly; metanotal groove distinctly impressed. Propodeal lateral margins strongly raised for short distance before terminating in long, subparallel or divergent, somewhat sinuate

spines, apical third of spines usually weakly curved outwards; propodeal dorsum between somewhat flattened, bases of spines rather short and narrow, abruptly rounding into high, obliquely descending, weakly convex, declivity. Hind coxae dorsoposteriorly carinate with dorsally projecting blunt processes. Petiole with anterior and posterior faces subparallel, or distinctly concave in some specimens; dorsum with posteriorly sloping platform, laterally armed with long, slender, divergent spines with tips weakly curved outwards. Anterior face of first gastral tergite only marginally higher than full height of petiole, widely rounding onto dorsum.

Mandibles densely longitudinally striate at bases, smooth and polished towards masticatory borders with numerous piliferous pits. Head and mesosoma closely reticulate-punctate. Spines sculptured at bases, smooth and polished towards tips. Petiole with anterior face smooth and polished, posterior face finely reticulate. Gaster finely shagreened.

Mandibles at masticatory borders with numerous, rather short, curved, golden hairs. Anterior clypeal margin medially with a few, rather long, anteriorly projecting setae and fringe of shorter setae laterally. Clypeus with a few paired, medium length, golden hairs. A few erect hairs on venter of coxae, fringe of hairs on venter of fore and mid femora. Apex and venter of gaster with numerous posteriorly directed hairs, longest hairs almost reaching greatest diameter of eyes in length. Hairs completely lacking from sides and vertex of head, mesosoma, petiole and most of gastral dorsum. Closely appressed, relatively long, silvery pubescence on sides of head, mesosoma, petiole and venter of gaster; pubescence distinctly golden on vertex of head and dorsum of mesosoma where it is somewhat medially radiating. Dorsum of gaster with rather abundant, medially radiating, golden pubescence, virtually identical to that in members of the *Polyrhachis sexspinosa*-group of subgenus *Myrmihopla*.

Black; mandibular masticatory borders, appendages, excluding coxae, and gaster medium

reddish-brown. Antennal scapes towards bases and tarsi a shade darker.

Queen. Dimensions: TL c. 11.19; HL 2.56; HW 1.84; CI 72; SL 3.53; SI 192; PW 2.00; MTL 4.28 (1 measured).

Apart from sexual characters similar to worker, except: eyes more convex, clearly exceeding lateral cephalic outline. Mesoscutum wider than long with lateral margins converging into narrowly rounded anterior margin; dorsum relatively low, weakly convex in lateral view; median line distinct; parapsides flat. Mesoscutellum only marginally elevated above dorsal plane of mesosoma. Propodeal spines horizontal, relatively short, about as long as distance between bases. Petiole similar to that in worker with spines divergent and distinctly shorter. Sculpturation, pilosity, pubescence and colour identical to those in worker.

Male and immature stages unknown.

Remarks. *Polyrhachis metella* is a very unusual species that combines several unrelated characters, such as the deeply medially emarginate anterior clypeal margin, rather peculiar, disc-shaped mesonotal dorsum, extremely long and slender propodeal spines and appendages, very high declivity and flat topped petiole. Such a combination of characters suggests that *P. metella* may be allied with species in the subgenus *Hedomyrma*. However, when Vichmeyer (1912) redescribed the worker of *P. metella*, he considered its unarmed pronotal shoulders a sufficient character to place it in the *ammon*-group. His decision was followed by Emery (1925) and all subsequent authors have included *P. metella* in the subgenus *Hagiomyrma*.

Polyrhachis metella is one of only two *Hagiomyrma* species that does not occur on the Australian mainland (the other is *P. denticulata* Karavaiev). It is evidently a rare species, manifestly missing from most recent collections.

POLYRHACHIS (HAGIOMYRMA)
PENELOPE SPECIES-GROUP

Polyrhachis (Hagiomyrma) anderseni sp. nov.
(Fig. 6A-B)

Etymology. Named in honor of Dr Alan N. Andersen of the CSIRO, TERC in Darwin, who has discovered many new species of *Polyrhachis* and other ants throughout the monsoonal and arid zones of the northern Australia.

Material. HOLOTYPE: WA, Kimberley region, Cape Bernier, 14°07'S, 127°31'E, vi.1988, A.N. Andersen, (worker). PARATYPES: data as for holotype (5 workers); Mirima (Hidden Valley) NP, 15°45'S, 128°45'E, c. 54 m, 10-11.vi.2008, ex nest in rock crevice, R.J. Kohout & S.K.A. Robson acc. 2008.5 (51 workers). Type deposition: Holotype and 2 paratypes in ANIC; most paratypes in QM, 2 paratypes each in BMNH, CURT, MCZC, MHNG, TERC and WAMP.

Other Material. WA: Kimberley region, CALM site 28/3, 15°38'S, 128°15'E, 16.vi.1988 (TAW) (w); Wyndham, 6.iv.2004 (ANA) (w); 10 km NE of Kununurra, 2.v.1989 (DKY) (w); Mirima (Hidden Valley) NP, 12.ix.1998 (ANA) (w); ditto, 10-11.vi.2008, ex nest in rock crevice (RJK & SKR acc. 2008.8) (w); Yampi 1 Stn, v.2002 (C. Palmer) (w); Glenelg R., 15°48'S, 124°44'E, vi.1988 (ANA) (w); Kununurra-Purnululu NP, 11.vi.2001 (A. Chapman) (w); Purnululu NP, Gorge, 2.ix.2004 (L. Barrow) (w); Osborne I. SW, vi.1988 (JDM) (w). NT: Keep R. NP, E of Kununurra (WA), 15.vii.1990 (R.P. McMillan) (w); Keep River NP, Gurrandalng, 15°52'S, 129°03'E, 12.vi.2008 (RJK & SKR accs 2008.12, 13) (w); Keep R. NP, Keep R. Escarpment, 15°51'S, 129°07'E, 9.v.1990 (S. Mann) (w); Cannon Hill, 6 km NNW of Cahills x-ing, 12°23'S, 132°57'E, 8.vi.1973 (JEF) (w); Podocarpus Canyon, Arnhem Land, 12°39'S, 133°27'E (H. Reichel) (w); 22 km WSW of Borooloa, 16°08'S, 136°06'E, 16.iv.1976 (JEF) (w); Gregory NP, Jasper Gorge, xi.1999 (K. Nash) (w); Alligator Ck/ Reynolds R. junct., 25.iv.1994 (BDH) (w).

Description. *Worker*: Dimensions (holotype cited first): TL c. 6.80, 5.90-6.80; HL 1.62, 1.43-1.62; HW 1.43, 1.23-1.43; CI 88, 86-92; SL 2.09, 1.87-2.12; SI 146, 138-153; PW 1.28, 1.09-1.31; MW 0.76, 0.70-0.81; PMI 168, 149-168; MTL 2.25, 2.00-2.28 (14 measured).

Anterior clypeal margin truncate medially without distinct median flange; truncate portion denticulate, laterally delimited by acute teeth. Clypeus with distinct median carina; weakly convex in profile, posteriorly rounding into moderately impressed basal margin. Frontal triangle indistinct. Frontal carinae with weakly

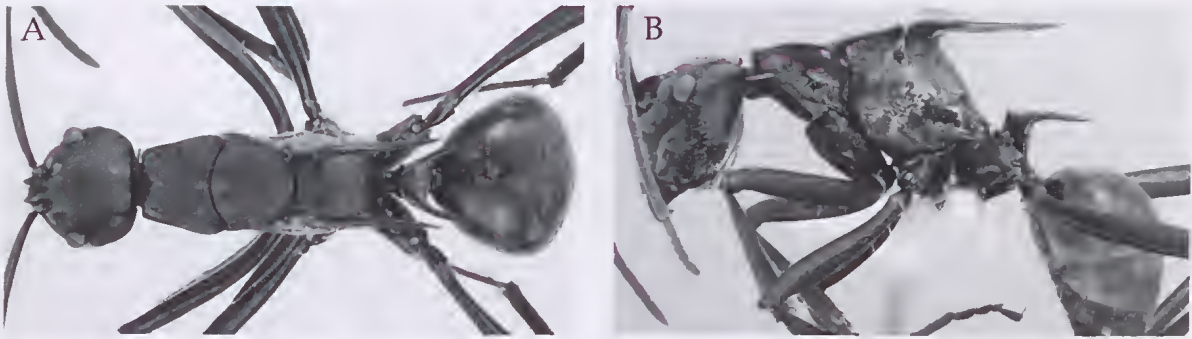


FIG. 5. *Polyrhachis* (*Hagiomyrma*) *metella* species-group – dorsal (left) and lateral (right) view. A-B, *P. metella* Fr. Smith (not to scale).

raised margins; central area relatively wide, flat. Sides of head in front of eyes converging towards mandibular bases in straight line; behind eyes, sides widely rounding into convex occipital margin. Eyes moderately convex, in full face view not or only marginally exceeding lateral cephalic outline. Ocelli lacking. Pronotal dorsum distinctly wider than long, widest at about midlength; humeri widely rounded, with shallow depression dorsally along narrowly raised, posteriorly converging lateral margins. Mesonotal dorsum with lateral margins shallowly emarginate towards poorly indicated metanotal groove. Propodeal margins terminating posteriorly in relatively short, horizontal and subparallel, acute spines; spines about half as long as distance between tips. Anterior face of petiole rounding dorsally into upturned, subparallel, or weakly divergent, acute spines; bases of spines closely approximated, petiolar dorsum between them deeply concave, forming open 'U' when viewed from behind. Posterior face of petiole distinctly swollen towards base. Anterior face of first gastral segment widely rounding onto dorsum.

Mandibles finely, longitudinally striate with numerous piliferous pits. Head, mesosoma and petiole finely and uniformly reticulate-punctate. Gaster shagreened.

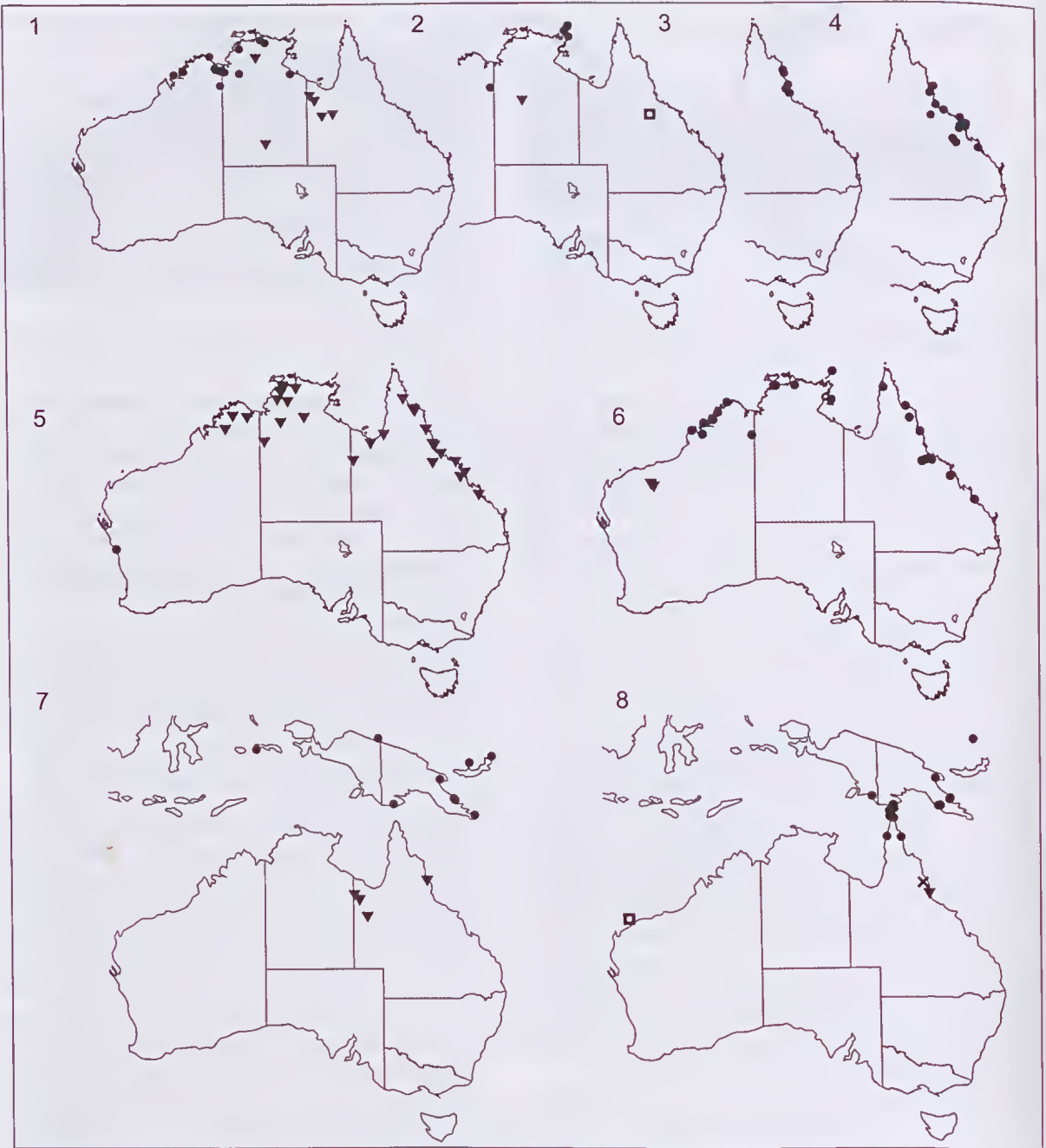
Mandibular masticatory and outer borders with curved golden hairs and closely appressed shorter hairs towards bases. Anterior clypeal margin medially with several, medium length

setae and a few short setae fringing margin laterally. Rather sporadic, relatively short, erect hairs on dorsum of head and body, hairs on gaster distinctly longer and more abundant. Silvery, appressed pubescence in various densities over most dorsal body surfaces; pubescence silvery or pale golden and more abundant on gastral dorsum, partly hiding underlying sculpturation.

Black, with mandibular teeth, condylae and apical funicular segments medium to dark reddish-brown. Legs, including coxae, dark to very dark reddish-brown.

Sexuals and immature stages unknown.

Remarks. *Polyrhachis anderseni* is an easily recognisable species, featuring very closely approximated, upturned, petiolar spines. It somewhat resembles *P. archeri*, however, in that species the anterior clypeal margin is produced into a median denticulate flange, while it is simply medially truncate in *P. anderseni*. The bases of the petiolar spines in *P. archeri* are more distant and the propodeal spines in lateral view are directed downwards, forming a continuous line with the arching profile of the mesosomal dorsum (Fig. 6C-D). In contrast, the bases of petiolar spines in *P. anderseni* are closer and the propodeal spines are more horizontal. *Polyrhachis anderseni* is one of only a few lithocolous *Polyrhachis* species (the others are *P. thusnelda* Forel and *P. turneri* Forel) that build their nests inside rock crevices or on the sides of rock walls (Robson & Kohout 2005).



POLYRHACHIS (HAGIOMYRMA) PENELOPE SPECIES GROUP

- Map 1 ● *P. anderseni* ▼ *P. archeri*
- Map 2 ● *P. weiri* ▼ *P. tanami* □ *P. tenebra*
- Map 3 ● *P. electra*
- Map 4 ● *P. penelope*

- Map 5 ● *P. clarki* ▼ *P. crawleyi*
- Map 6 ● *P. melanura* ▼ *P. pilbara*
- Map 7 ● *P. denticulata* (PNG) ▼ *P. hoffmanni*
- Map 8 ● *P. semiobscura* ▼ *P. stricta*
 □ *P. seducta* × *P. placida*

Polyrhachis (*Hagiomyrma*) *archeri* sp. nov.
(Fig. 6C-D)

Etymology. Named in honour of Prof. Michael Archer, formerly of the Queensland Museum, whose name is closely associated with the famous palaeontological site at Riversleigh which is near the type locality of the species.

Material. HOLOTYPE: QLD, c. 6 km NW of Riversleigh Hmsd, 19°00'S, 138°41'E, 18-26.x.1977, R.J. Kohout acc. 77.27, QMT174509 (worker). PARATYPES: data as for holotype (4 workers); Gregory R., nr Riversleigh Hmsd, 19°01'S, 138°43'E, 23-24.x.1976, RJK acc. 76.71 (2 workers). Type deposition: Holotype and 1 paratype in QM, 1 paratype each in ANIC, BMNH, MCZC, MHNG and TERC.

Other Material. QLD: Lawn Hill Stn, 18°30'S, 138°10'E, ix.1991 (ANA, CRA Century Project) (w); Mt Isa, xii.1997 (T. Griffiths, CRC MIM Study) (w, ♀); Mt Fort Constantine, 20°29'8"S, 140°36'35"E, 7.iii.2004 (M. Sanders) (w). NT: Katherine Gorge escarpment, 14°19'S, 132°28'E, 25.xi.1993 (H. Reichel) (w); Standley Chasm, West MacDonnell Ranges, 23°44'S, 133°28'E, c. 750 m, 14.iii.2002 (CJB & C.M. Rodriguez acc. 51022) (w); ditto, 9.vi.2002 (RJK & SKR acc. 02.32).

Description. *Worker.* Dimensions (holotype cited first): TL c. 6.65, 6.55-6.96; HL 1.65, 1.62-1.72; HW 1.31, 1.28-1.34; CI 79, 78-81; SL 1.93, 1.93-2.00; SI 147, 145-153; PW 1.23, 1.22-1.28; MW 0.72, 0.72-0.84; PMI 171, 149-171; MTL 2.03, 2.03-2.15 (8 measured).

Anterior clypeal margin medially with acutely denticulate flange. Clypeus with distinct median carina; straight in profile, posteriorly rounding into weakly impressed basal margin. Frontal carinae with weakly raised margins; central area relatively wide, flat. Sides of head in front of eyes converging towards mandibular bases in straight line; behind eyes, sides widely rounding into convex occipital margin. Eyes weakly convex, marginally exceeding lateral cephalic outline in full face view. Ocelli lacking. Pronotal dorsum distinctly wider than long, widest at about midlength; humeri widely rounded, with shallow depression dorsally along narrowly raised margins. Lateral margins of pronotum and mesonotum converging posteriorly. Metanotal groove indistinct. Propodeal margins terminating posteriorly in relatively short, acute spines; length of spines

distinctly less than half distance between tips. Anterior face of petiole rounding dorsally into upturned, divergent, acute spines; bases of spines relatively close together, dorsum between them concave. Posterior face of petiole distinctly swollen. Anterior face of first gastral segment widely rounding onto dorsum.

Mandibles finely, longitudinally striate with numerous piliferous pits. Head, mesosoma and petiole finely and uniformly reticulate-punctate, opaque. Gaster shagreened.

Mandibular masticatory and outer borders with curved golden hairs and closely appressed shorter hairs towards bases. Anterior clypeal margin medially with a few, medium length setae. Several short and medium length, erect hairs on clypeus, along frontal carinae and on vertex; distinctly shorter and more sparse hairs on dorsum of mesosoma; gaster dorsally with numerous short, posteriorly inclined, pale golden hairs, hairs on gastral venter distinctly longer and more abundant. Silvery, appressed pubescence in various densities over most dorsal body surfaces, except gastral dorsum with golden and more abundant pubescence, completely hiding underlying sculpturation.

Black; mandibles, clypeus, frontal area, antennae and legs, including coxae, medium to dark reddish-brown. Mandibular teeth and anterior clypeal margin bordered with black.

Queen. Dimensions: TL c. 7.91-8.32; HL 1.72-1.81; HW 1.37-1.40; CI 77-80; SL 1.87-1.93; SI 136-138; PW 1.62-1.68; MTL 1.96-2.15 (2 measured).

Apart from sexual characters very similar to worker except: mesoscutum wider than long with dorsum weakly convex in lateral view; median line distinct; parapsides flat. Mesoscutellum weakly convex, not elevated above dorsal plane of mesosoma. Propodeal spines very short, bases broad; petiolar spines shorter than in worker, distinctly obliquely elevated, divergent. Sculpturation, pilosity, pubescence and colour virtually identical to worker.

Male and immature stages unknown.

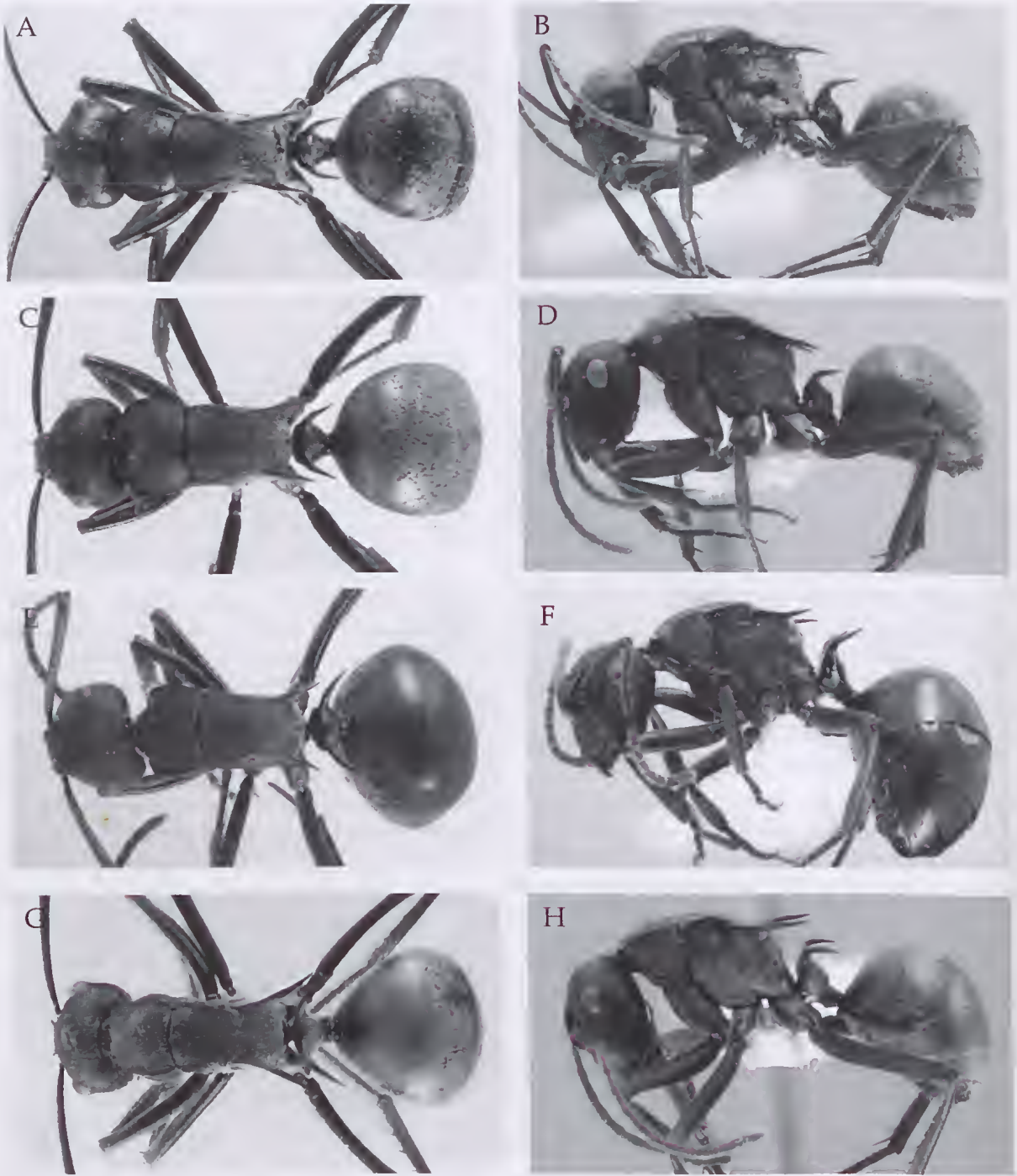


FIG. 6. *Polyrhachis (Hagiomyrma) penelope* species-group - dorsal (left) and lateral (right) view. A-B, *P. anderseni* sp. nov.; C-D, *P. archeri* sp. nov.; E-F, *P. clarki* sp. nov.; G-H, *P. crawleyi* Forel (not to scale).

Remarks. *Polyrhachis archeri* is very similar to *P. anderseni*, with most of the distinguishing characters listed in the remarks on the latter species. It is also similar to *P. hoffmanni*, which shares the same type locality with *P. archeri*. *Polyrhachis hoffmanni* is easily separated by the presence of relatively long hairs over most body surfaces which are completely absent in both the other species. *Polyrhachis archeri* is a ground-nesting species, with the type series specimens collected foraging near a nest entrance hidden under a small rock. The distribution of *P. archeri* appears to be centred on the Gulf Country in north-western Queensland, however, it has recently been collected in the Northern Territory at Nitmiluk (Katherine Gorge) Nat. Park and Standley Chasm in the West MacDonnell Ranges.

Polyrhachis (*Hagiomyrma*) *clarki* sp. nov.
(Fig. 6E-F)

Etymology. Named in honour of the collector, the late John Clark, former entomologist at the Museum of Victoria, Melbourne.

Material. HOLOTYPE: WA, Geraldton, J. Clark (worker). PARATYPES: data as for holotype (12 workers). Type deposition: Holotype and 8 paratypes in MVMA; 1 paratype each in ANIC, BMNH, MCZC and QM.

Description. *Worker.* Dimensions (Holotype cited first): TL c. 7.31, 7.31-7.91; HL 1.78, 1.78-1.93; HW 1.47, 1.47-1.59; CI 82, 81-85; SL 1.96, 1.93-2.18; SI 133, 131-140; PW 1.25, 1.22-1.31; MW 0.72, 0.72-0.81; PMI 174, 162-174; MTL 2.18, 2.15-2.43 (6 measured).

Mandibles with 5 teeth, outer tooth distinctly short and blunt. Anterior clypeal margin with denticulate flange medially, flanked by acute teeth. Clypeus with distinctly raised median carina, shallowly sinuate in profile (almost straight in some specimens); basal margin virtually flat. Frontal triangle distinct. Frontal carinae sinuate with weakly raised margins; central area relatively wide, raised medially with rather short frontal furrow. Sides of head in front of eyes weakly convex, rounding into mandibular bases; behind eyes, sides rounding into convex occipital border. Eyes convex, exceeding lateral cephalic outline. Ocelli

lacking. Pronotal humeri subacute or narrowly rounded in some specimens, margins weakly raised; pronotal dorsum widest at midlength. Pronotal and mesonotal dorsa with lateral margins converging posteriorly; metanotal groove indistinct medially. Propodeal dorsum with margins weakly divergent posteriorly, terminating in slender, acute, divergent, downturned spines. Petiole with anterior face straight, posterior face weakly convex; dorsum deeply concave medially, armed laterally with pair of distinctly elevated, divergent, acute spines. Anterior face of first gastral tergite widely rounding onto dorsum.

Mandibles distinctly longitudinally striate with numerous piliferous pits. Head and mesosoma very finely and closely reticulate-punctate with sculpturation on sides of head and mesosoma somewhat more distinct. Gaster finely shagreened.

Mandibles with several medium length, golden hairs at masticatory borders, distinctly shorter and closely appressed hairs towards mandibular bases. Only a few anteriorly directed setae fringing anterior clypeal margin. Fore coxae and gastral venter and apex with medium length, semierect, golden hairs. Whole dorsum of body, including head, mesosoma, petiole and gaster without hairs, except a few, short hairs on apical gastral tergites. Closely appressed, silvery pubescence sporadically scattered on venter of head, propodeal declivity, venter and sides of gaster; pubescence completely lacking over most dorsal body surfaces, including gaster.

Black; mandibular masticatory borders, condylae and subpetiolar process medium reddish-brown; antennae and tarsi dark reddish-brown.

Sexuals and immature stages unknown.

Remarks. The type series are the only specimens known of *P. clarki*. Apart from the holotype, which is in relatively good condition, most of the types are poorly preserved with various legs, antennae and/or gasters missing. *Polyrhachis clarki* is distinguished from other *Hagiomyrma* species by the lack of hairs on the dorsum of the body, the rather short, very

slender, downturned and outwardly directed propodeal spines and the strongly upturned petiolar spines with a deeply concave dorsum between their bases. There is some variation in the form of the pronotal humeri which are either subacute (as in the holotype and some paratypes) or narrowly rounded (in the remaining paratypes).

Polyrhachis (Hagiomyrma) crawleyi Forel, 1916
(Fig. 6G-H)

Polyrhachis (Hagiomyrma) ammonoecoides var. *crawleyi* Forel, 1916:447. Syntype workers. Type locality: 'NORTH AUSTRALIA', MHNG, QM (examined).

Polyrhachis crawleyi Forel. Kohout, 1988 (raised to species).

Other Material. WA: Kimberley region, King Edward R., vi.1988 (ANA) (w); ditto, 10 km S of Beverley Springs Hmsd, v.1979 (B.G. Muir #29) (w); Jack's Waterhole, Duract River Hmsd, 15°50'S, 127°24'E, 7.v.1992 (S.O. Shattuck #3435-3) (w). NT: Kakadu NP, Alligator R., 19-23.vi.1982 (W. Houston) (w); 130 km S of Darwin, 11.ii.1964 (J. Sedláček) (w); Koolpinyah track, c. 24 mi SE of Darwin, 12°23'S, 131°10'E, 9.vii.1951 (W.L. Brown) (w); Batchelor (G.F. Hill) (w); Daly R. (H. Wesselmann) (w); Kidman Springs, v.1999 (A.J. Fisher) (w); Fog Dam, 20.viii.1996 (BDH) (w); Bunda Stn, Victoria R. Distr., v.1994 (A.J. Fisher) (w); Larimah, 10.vii.1985, savannah woodland (BBL) (w). QLD: Cape York Pen., Coen Aerodrome, 26.vi.1960 (C.N. Smithers) (w); Lakefield NP, 14°59'S, 144°15'E, 19-29.vi.1980 (RJK acc. 80.42) (w); ditto, 17 km N Lakefield, 21.vii.2002 (ANA) (w); ditto, White Lily lagoon, 14 km N Lakefield, 19.vii.2002 (ANA) (w); 5-15 mi N of Mareeba, 15.ii.1958 (P.F. Darlington) (w); 15 km N of Maggieville Hmsd, N of Normanton, 11.iv.1962 (J.E. Dowse) (w); Floraville Hmsd, Leichard R. x-ing, 18°13'S, 139°52'E, 7-17.x.1977 (RJK acc. 77.16) (w); Cardwell, 14.ii.1992 (C.J. Hill) (w); 25 km S of Cardwell, 16.iv.1976 (P.J.M. Greenslade) (w); Camooweal, 25.vii.1981 (BBL) (w); Townsville, 3.& 13.xii.1901 (F.P. Dodd) (w, ♀, ♂); Townsville, 11.xi.1948 (Sr Conleth) (w); 6 km NWbyN of Powlathanga, 20°10'S, 146°00'E, c. 350 m, 16.vii.1977 (RWT acc. 77.366) (w); Ayr-Proserpine Hwy, 6-7.ii.1964 (J. Sedláček) (w); Mackay (Turner) (w); 10 km N of Nebo, 16.viii.1975, under log (BBL) (w); Rockhampton, 9.ii.1964 (J. Sedláček) (w).

Description. *Worker.* Dimensions (syntypes cited first): TL c. 6.20-6.60, 6.65-8.01; HL 1.53-1.69, 1.53-1.90; HW 1.25-1.31, 1.25-1.47; CI 77-82, 76-82; SL 1.93-2.12, 1.93-2.34; SI 154-162, 154-170; PW 0.87-0.91, 0.87-1.06; MW 0.59, 0.59-0.69; PMI 147, 147-164; MTL 2.25-2.47, 2.25-2.75; (3+25 measured).

Anterior clypeal margin medially with shallow, truncate, denticulate flange, flanked by blunt teeth. Clypeus with distinctly raised median carina; sinuate in profile with moderately impressed basal margin. Frontal triangle poorly indicated. Frontal carinae sinuate with moderately raised margins; central area relatively wide with rather flat frontal furrow. Sides of head in front of eyes converging towards mandibular bases in almost straight line; behind eyes, sides rounding into convex occipital margin. Eyes convex, in full face view clearly breaking lateral cephalic outline. Ocelli lacking. Pronotal humeri dilated, distinctly rounded with weakly raised margins; dorsum with lateral margins distinctly emarginate or notched at about midlength, subparallel or weakly diverging towards promesonotal suture. Lateral margins of mesonotum converging posteriorly and weakly raised towards laterally impressed, medially flat metanotal groove. Propodeal dorsum with margins terminating in broad-based, long, slender, widely divergent, acute spines. Anterior face of petiole in side view rounding dorsally into long, slender, widely divergent spines, dorsum between spines deeply concave. Base of first gastral segment widely rounding onto dorsum.

Mandibles longitudinally striate with numerous piliferous pits. Head and mesosoma closely reticulate-punctate; spines sculptured for most of length, tips smooth. Gaster finely shagreened.

Mandibles with numerous medium length, golden hairs at masticatory borders; distinctly shorter and closely appressed hairs towards mandibular bases. Only a few anteriorly directed setae fringing anterior clypeal margin. Several paired, medium length hairs on clypeus, along frontal carinae and vertex. Somewhat longer, variously inclined hairs on dorsum of mesosoma and fore coxae; distinctly shorter hairs on venter of mid and hind coxae and femora. Gaster with numerous, posteriorly directed golden hairs, rather short on dorsum, distinctly longer and more abundant on venter and around apex. Closely appressed, somewhat medially radiating golden pubescence with somewhat brassy hue, over most dorsal body

Revision of *Polyrhachis* (*Hagiomyrma*)

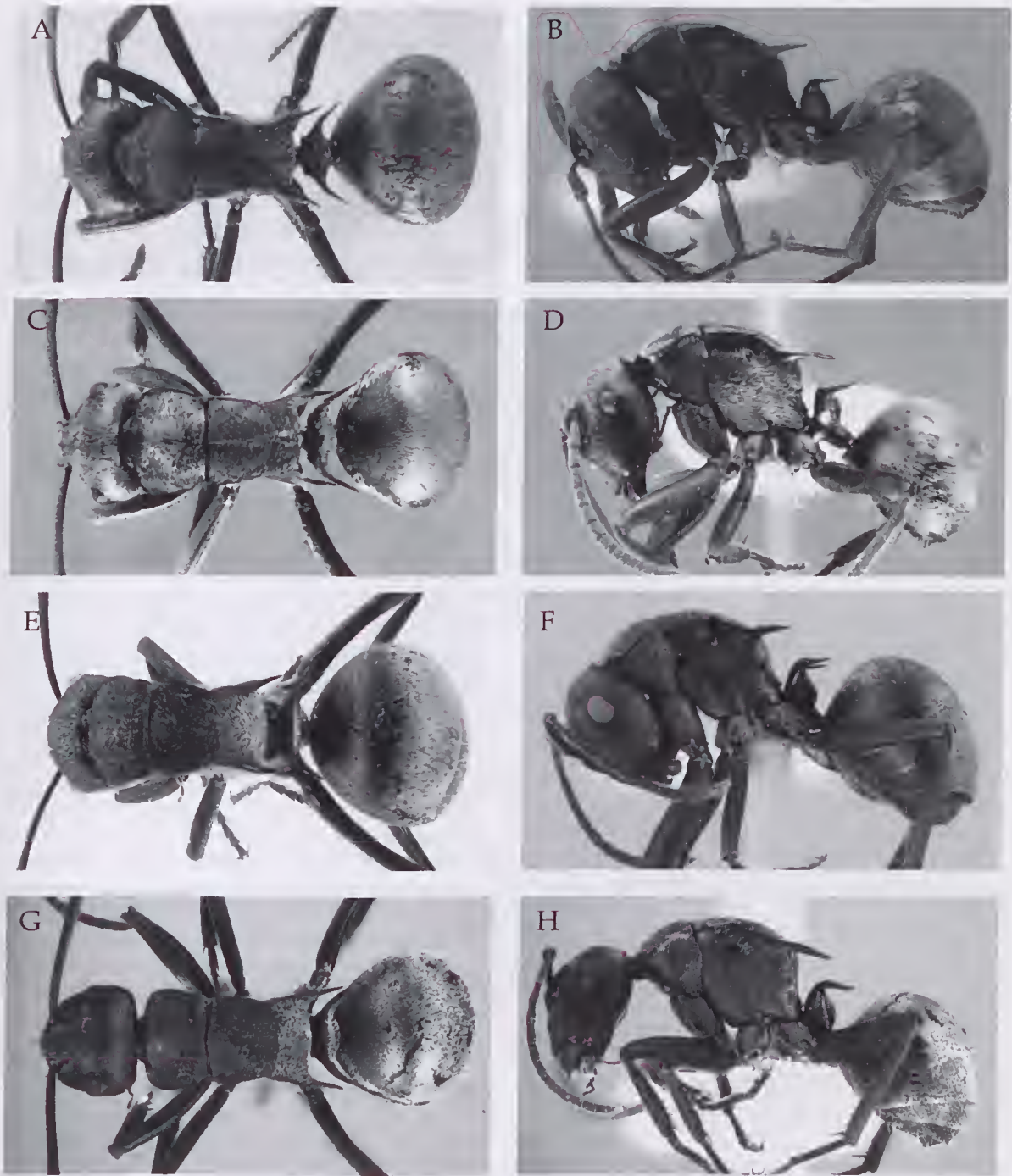


FIG. 7. *Polyrhachis* (*Hagiomyrma*) *penelope* species-group – dorsal (left) and lateral (right) view. A-B, *P. denticulata* Karavaiev; C-D, *P. electra* sp. nov.; E-F, *P. hoffmanni* sp. nov.; G-H, *P. melanura* sp. nov. (not to scale).

surfaces, including dorsum of gaster, where it is rather abundant, completely hiding underlying sculpturation; pubescence more sporadic and mostly silvery on sides of head, mesosoma and venter of gaster.

Black; mandibular teeth and appendages usually very dark reddish-brown.

Queen. Dimensions: TL c. 9.83; HL 2.03; HW 1.57; CI 77; SL 2.15; SI 137; PW 1.81; MTL 2.82 (1 measured).

Apart from sexual characters very similar to worker, except: pronotal dorsum with humeri subacute, margins widely rounded behind. Mesoscutum marginally wider than long; median line distinct, bifurcate anteriorly; parapsides flat anteriorly, weakly raised posteriorly; anterior margin of mesoscutum evenly rounded; dorsum relatively low and very weakly convex in lateral view; mesoscutellum only weakly elevated above dorsal plane of mesoscutum. Propodeal and petiolar spines similar to those in worker, but distinctly shorter. Sculpturation, pilosity, pubescence and colour virtually identical to worker.

Male and immature stages were reported in F.P. Dodd's collection, however, their location is unknown and the material is probably lost.

Remarks. *Polyrhachis crawleyi* is rather similar to *P. cracenta*, but is separable by its consistently smaller size and closely reticulate-punctate sculpturation of the body, with distinguishing characters provided in the remarks of the latter species. *Polyrhachis crawleyi* is uncommon with a rather patchy distribution across northern Australia. It is apparently restricted to open eucalypt forests and savannah woodlands, preferring patches of bare ground without a covering of grass to excavate their nests.

Polyrhachis (Hagiomyrma) denticulata
Karavaiev, 1927
(Fig. 7A-B)

Polyrhachis (Hagiomyrma) denticulata Karavaiev, 1927e:13, fig. 4.
Syntype workers. Type locality: INDONESIA, Ambon I. (= Amboina) (V. Karavaiev #3008), IZAS, QM (examined).

Other Material. INDONESIA, IRIAN JAYA: Hollandia, 02°32'S, 140°42'E, 24.i.1960 (T.C. Maa) (w). PAPUA NEW GUINEA: Bismarck Archipelago

(no further data) (w); East New Britain Prov., Ralum, 2.x.1896 (F. Dahl) (w, ♀); Morobe Prov., Lae, 4.viii.1972 (D.H. Messersmith) (w); Northern Prov., Oro Bay, 6.i.1973 (PMR) (w); Buna, 23.iii.1972 (PMR) (w); Milne Bay, 14-23.ii.1969 (J. & M. Sedláček) (w). AUSTRALIA, QLD: Torres Strait, Mabuiag I., 1974 (H&C) (w).

Description. *Worker.* Dimensions (syntypes cited first): TL c. 6.20-6.70, 6.00-7.43; HL 1.50-1.59, 1.50-1.75; HW 1.22-1.31, 1.22-1.43; CI 81-82, 80-83; SL 1.68-1.78, 1.68-2.00; SI 136-138, 136-146; PW 1.14-1.25, 1.12-1.34; MW 0.65-0.69, 0.62-0.89; PMI 175-181, 172-185; MTL 1.90-2.00, 1.90-2.37 (2+9 measured).

Mandibles with 5 teeth, distinctly reducing in length towards base. Anterior clypeal margin medially truncate and denticulate, without clearly defined median flange. Clypeus with distinct median carina; sinuate in profile, posteriorly rounding into moderately impressed basal margin. Frontal carinae sinuate with weakly raised margins; central area relatively wide, with medially raised ridge. Sides of head in front of eyes converging towards mandibular bases in straight line; behind eyes, sides rounding into convex occipital margin. Ocelli indistinct. Pronotal dorsum distinctly wider than long; humeri widely rounded with raised, posteriorly converging margins; promesonotal suture distinctly impressed. Mesonotal margins converging posteriorly into medially flat metanotal groove. Propodeal dorsum with lateral margins terminating in more-or-less horizontal, divergent, acute spines. Petiole with anterior face straight, posterior face distinctly swollen; dorsum shallowly concave medially, armed with pair of divergent, weakly elevated, acute spines. Anterior face of first gastral tergite widely rounding onto dorsum.

Mandibles longitudinally striate with numerous piliferous pits; head, mesosoma and petiole reticulate-punctate. Gaster shagreened.

Mandibular masticatory and outer borders with medium length, golden hairs. Anterior clypeal margin medially with several, medium length, golden setae. Numerous, semierect, anteriorly inclined hairs on clypeus, front and vertex of head, a number of hairs fringing outline of head in full face view. Mesosoma

and petiole with numerous erect or semierect hairs; gaster with rather abundant, posteriorly inclined, golden hairs, some longer than half of diameter of eyes. Rather sparse and long, silvery, appressed pubescence, covering most body surfaces; pubescence more abundant on gaster, pale golden on dorsum and silvery on sides and venter.

Head and mesosoma black or very dark reddish-brown; mandibles, clypeus, anterior portion of pronotum, appendages and gaster medium reddish-brown. Colour scheme in older specimens, including syntypes, is generally light, reddish-brown, while more recently collected specimens are distinctly darker, with head and mesosoma almost black.

Queen. Dimensions: TL c. 7.15-7.41; HL 1.62; HW 1.31; CI 81; SL 1.78; SI 136; PW 1.51-1.59; MTL 2.09-2.12 (2 measured).

Apart from sexual characters very similar to worker, except: mesoscutum in lateral view relatively low with anterior margin rounding onto flat dorsum; median line bifurcate anteriorly; parapsides flat. Mesoscutellum weakly convex, not elevated above dorsal plane of mesosoma. Propodeal spines very short, subparallel, with tips weakly curved downwards. Petiolar spines very short, divergent. Sculpturation, pilosity, pubescence and colour virtually identical to worker.

Males and immature stages were apparently collected by F. Dahl at Ralum (Bismarck Archipelago) and should be lodged in the MNHU. However, in a recent visit I failed to locate the material and consider it lost.

Remarks. *Polyrhachis denticulata* is rather similar to *P. penelope* which resulted in specimens collected by F. Dahl at Ralum, being identified as *P. penelope* by Forel (1901:31). However, the differences separating the species are rather obvious and are discussed in the remarks section under the latter species.

Polyrhachis (*Hagiomyrma*) *electra* sp. nov.
(Fig. 7C-D)

Material. HOLOTYPE: QLD, Mt Finnigan, summit, 15°49'S, 145°16'E, 1100 m, 28-30.xi.1985, G.B.

Monteith, D.J. Cook & L. Roberts, QMT174510 (worker). PARATYPES: data as for holotype (20 workers); data as for holotype, except 3-5.xii.1990 (41 workers, 8 ♀, 4 ♂). Type deposition: Holotype, most paratype workers and paratype queens in QM, 3 paratype workers and paratype ♀ in ANIC; 2 paratype workers each in AMNH, BMNH, CASC, MSNG, MCZC, MHNG, MNHU and NMNH.

Other Material. QLD: Mt Finnigan, summit, 15°49'S, 145°16'E, 1100 m, 19-21.iv.1982 (GBM, DJC & L. Roberts) (w); Cape Tribulation, Thornton Peak, 16°10'S, 145°23'E, 1374 m, ix.1984 (GBM) (w); Mt Bartle Frere, Sth Peak, 1622 m, 17°24'S, 145°49'E, 8.xi.1981 (GBM & Earthwatch Exp.) (w); 2.5 km WSW of Koombulooma T'ship, 17°50'S, 145°34'E, 740 m, 4.ii-15.iv.1999 (GBM & S.R. Monteith) (w); Cardwell Ra., Macalister Mtn, 18°18'S, 145°55'E, 800-900 m, 13-16.i.1987 (S. Hamlet) (w); Cardwell Ra., Upper Broadwater Ck, 7-21.xii.1986 (GBM, GIT & S. Hamlet) (w).

Description. *Worker.* Dimensions (holotype cited first): TL c. 7.06, 6.45-7.51; HL 1.81, 1.56-1.84; HW 1.50, 1.33-1.56; CI 83, 81-88; SL 2.00, 1.75-2.03; SI 133; 127-137; PW 1.37, 1.22-1.47; MW 0.87, 0.81-0.87; PMI 157, 157-178; MTL 2.18, 1.96-2.28 (23 measured).

Anterior clypeal margin with median, obtusely denticulate flange, laterally flanked by acute angles. Clypeus with distinct longitudinal carina, sinuate in profile; basal margin only weakly impressed. Frontal triangle indistinct. Frontal carinae sinuate with weakly raised margins anteriorly, flat posteriorly; central area wide with poorly indicated frontal furrow. Sides of head in front of eyes converging towards mandibular bases in straight line; behind eyes, sides rounding into weakly convex occipital margin. Eyes moderately convex, in full face view marginally breaking lateral cephalic outline. Ocelli lacking, positions of lateral ocelli indicated by weakly raised tubercles in cephalic sculpture. Pronotal dorsum wider than long with humeri distinctly rounded, dorsally shallowly concave; lateral margins converging posteriorly towards well impressed promesonotal suture. Mesonotal dorsum with margins converging posteriorly; metanotal groove weakly indicated laterally, indistinct medially. Propodeum with margins divergent, terminating in slender, subparallel spines with tips weakly turned outwards. Propodeal spiracles situated on laterally projecting

tubercles. Petiole with anterior face straight, rounding dorsally into slender, divergent, elevated spines with tips curved upwards; dorsum descending posteriorly towards base in convex line. Anterior face of first gastral tergite widely rounding onto dosum.

Mandibles with numerous piliferous pits, closely and finely longitudinally striate at their bases, more polished towards masticatory borders. Head, mesosoma and petiole reticulate-punctate; spines sculptured at bases, smooth and polished towards tips. Gaster finely shagreened.

Mandibular masticatory borders with several, anteriorly inclined, golden hairs. Anterior clypeal margin with only a few anteriorly directed setae medially and fringe of shorter setae laterally. Several paired, relatively short hairs on clypeus, along frontal carinae and on vertex, no hairs exceeding lateral cephalic outline. Dorsum of mesosoma, coxae and venter of femora with several erect or suberect, short to medium length hairs. Gaster with a number of medium length hairs dorsally; hairs distinctly longer and more abundant around apex and venter of gaster. Rather abundant, closely appressed, golden pubescence on dorsum of head, mesosoma and petiole; more diluted, silvery pubescence on sides of body and base of petiole. Gaster dorsally with rich golden pubescence, completely hiding underlying sculpturation; pubescence distinctly less dense and silvery on gastral venter.

Black; mandibular teeth reddish-brown, apendages and apex of gaster dark to very dark reddish-brown.

Queen. Dimensions: TL c. 8.57-8.82; HL 1.90-1.95; HW 1.62-1.65; CI 84-85; SL 2.00-2.03; SI 123-125; PW 1.84-1.93; MTL 2.31-2.37 (4 measured).

Apart from sexual characters very similar to worker except: pronotal humeri widely rounded. Mesoscutum marginally wider than long; median line bifurcate anteriorly; dorsum flat in profile with parapsides only weakly raised posteriorly. Mesoscutellum flat, not elevated above dorsal plane of mesosoma.

Propodeal and petiolar spines similar to worker, but shorter. Sculpturation, pilosity, pubescence and colour identical to worker.

Males present in QM spirit collection. Immature stages unknown.

Etymology. Name derived from *Electra*, a daughter of Agamemnon and Clytemnestra, of Greek mythology.

Remarks. *Polyrhachis electra* is somewhat similar to *P. penelope*, but differs in having the propodeal spiracles situated on laterally projecting tubercles. However, the spiracular tubercles are shorter and less conspicuous than those in *P. diversa* and *P. tubifera*. *Polyrhachis electra* differs from *P. penelope* in the shape of the petiolar spines which are longer and obliquely elevated in *P. electra*, and horizontal in *P. penelope*. In addition, the pubescence in *P. electra* is rather golden and abundant over all dorsal body surfaces, while it is much diluted and more silvery or pale golden in *P. penelope*.

Polyrhachis electra appears to be restricted to the Wet Tropics region of northern Queensland with all specimens having been collected at high altitude localities above 700 m in elevation. It is a ground-nesting species with entrances usually hidden under a rock. *Polyrhachis electra* was listed earlier by Kohout (2000: 199) as 'Hagio 04'.

Polyrhachis (Hagiomyrma) hoffmanni sp. nov.
(Fig. 7E-F)

Etymology. Named in honour of one of the collectors, Ben Hoffmann, of the CSIRO, TERC, Darwin, who has collected extensively across the Northern Territory, including Arnhem Tableland and adjacent islands.

Material. HOLOTYPE: QLD, Riversleigh Stn, c. 6 km NW of, 19°00'S, 138°41'E, 18-26.x.1977, R.J. Kohout acc. 77.22, QMT174511 (worker). PARATYPES: data as per holotype (4 workers); Lawn Hill Stn, CRA Century Project, 18°30'S, 138°10'E, iv.& ix.1991 (A.N. Andersen) (2 workers). Type deposition: Holotype and 1 paratype in QM; 1 paratype each in ANIC, BMNH and MCZC.

Other Material. QLD: Mt Isa, xi.1997 (BDH) (w, ♀); Mt Isa, CRC MIM study, xii.1997 (T. Griffiths) (w); Mt Isa, Plume Outfall Study, v.2005 (T. Griffiths) (w); 3 km along Davies Ck Rd, nr Mareeaba, 3.viii.1975 (B.B. Lowery) (w).

Description. *Worker.* Dimensions (holotype cited first): TL c. 6.60, 5.81-6.69; HL 1.62, 1.53-1.62; HW 1.34, 1.25-1.34; CI 83, 82-83; SL 1.87, 1.75-1.87; SI 139, 133-142; PW 1.31, 1.20-1.31; MW 0.87, 0.78-0.87; PMI 150, 149-156; MTL 2.09, 1.93-2.09 (5 measured).

Anterior clypeal margin with denticulate median flange, laterally flanked by distinct, acute teeth. Clypeus with median carina; almost straight in profile, posteriorly rounding into shallow basal margin. Frontal triangle distinct. Frontal carinae with weakly and narrowly raised margins anteriorly, flat posteriorly; central area relatively wide with distinct frontal furrow. Sides of head in front of eyes converging in straight line towards mandibular bases; behind eyes, sides widely rounding into convex occipital margin. Eyes moderately convex, in full face view clearly exceeding lateral cephalic outline. Ocelli lacking. Pronotal humeri widely rounded; dorsum distinctly wider than long, widest near mid-length. Promesonotal suture distinct; mesonotal lateral margins converging posteriorly towards medially indistinct metanotal groove. Propodeum armed with relatively short, weakly divergent spines. Petiolar dorsum distinctly concave medially, armed with divergent, weakly elevated, acute spines; posterior face of petiole strongly convex (Fig. 7F). Anterior face of first gastral tergite distinctly higher than full height of petiole, widely rounding onto dorsum.

Mandibles densely longitudinally striate with piliferous pits towards masticatory borders. Head, mesosoma and petiole closely reticulate-punctate. Spines sculptured from bases, tips smooth and polished. Gaster shagreened with sculpture distinctly coarser on dorsum.

Mandibles at masticatory and along outer borders with several, anteriorly inclined, golden hairs. Anterior clypeal margin medially with a few, anteriorly directed setae and fringe of shorter setae laterally. Several, mostly paired, rather long, curved hairs on clypeus, along frontal carinae, vertex and occipital corners; no hairs breaking lateral cephalic outline between eyes and mandibular bases in full frontal view. Long, variously curved hairs, as long as or

longer than greatest diameter of eyes, scattered over most body surfaces. Gaster with abundant, long, posteriorly inclined, silvery hairs. Relatively long, silvery, appressed pubescence, generally untidy and rather diluted on dorsum of head and mesosoma; pubescence somewhat denser on pronotal shoulders and propodeal declivity. Gaster with abundant, golden, appressed pubescence on dorsum, completely hiding underlying sculpturation; pubescence silvery and much diluted on gastral venter.

Black; mandibles relatively light, reddish-brown, with teeth and outer borders lined with black. Clypeus, central area and appendages medium to dark reddish-brown; anterior clypeal margin and frontal carinae with narrow black margins. Gaster distinctly reddish-brown on venter.

Queen. Dimensions: TL c. 8.01; HL 1.78; HW 1.43; CI 80; SL 1.90; SI 133; PW 1.72; MTL 2.15 (1 measured).

Apart from sexual characters very similar to worker except: mesoscutum wider than long with virtually flat dorsum in lateral view; median line distinct; parapsides flat. Mesoscutellum weakly convex, only marginally elevated above dorsal plane of mesosoma. Propodeal spines very short, bases broad; petiolar spines shorter than in worker, distinctly obliquely elevated, divergent. Sculpturation, pilosity and pubescence identical to worker. Colour generally as in worker, with only mandibles and appendages very dark, reddish-brown.

Males and immature stages unknown.

Remarks. *Polyrhachis hoffmanni* is very similar to the sympatric *P. archeri* and *P. anderseni* but differs in the shape of the petiolar node, as discussed in the remarks section of *P. archeri*. *Polyrhachis hoffmanni* can also be easily separated by the relatively long hairs on most body surfaces which are completely absent in the two other species.

Polyrhachis (*Hagiomyrma*) *melanura* sp. nov.
(Fig. 7G-H)

Etymology. Derived from the Greek word *melanos*, meaning black, for its uniformly black colour.

Material. HOLOTYPE: QLD, Britton Ra., 6 km NNE of Homevale, 21°23'S, 148°33'E, 1-6.iv.1975, ex nest in ground, R.J. Kohout acc. 75.154, QMT174512 (worker). PARATYPES: data as for holotype (69 paratype workers). Type distribution: Holotype and most paratypes in QM; 2 paratype workers each ANIC, BMNH, MCZC.

Other Material. WA: Kimberley region, Cape Bougainville, 14°05'S, 126°08'E, vi.1988 (ANA) (w); Boongarree I., 15°05'S, 125°11'E, vi.1988 (ANA) (w); Glenelg R., 15°48'S, 124°44'E, vi.1988 (ANA) (w); JoonJoo Stn, v.2002 (C. Palmer) (w); Yampi 1 & 2 Stns, v.2002 (C. Palmer) (w); Beagle Bay, vi.2001 (C. Palmer) (w); Purnululu NP, 5.ix.2004 (L. Barrow) (w). NT: Wessel Is, Rimbija I., 11°01'S, 136°45'E, 3-14.ii.1977 (TAW) (w); Groote Eylandt, UmbaKumba, 11-22.vi.1948 (R.R. Miller) (w); Groote Eylandt, vi.1982 (JDM) (w); Kakadu NP, Ubirr, 3.vi.1986 (ANA) (w); ditto, x.1988-vi.1989 (ANA) (w, ♀); Holmes Jungle, 15 km NE of Darwin, 12°25'S, 130°58'E, 11-12.ii.1994, ex nest in ground (RJK accs 94.9, 13) (w, ♀); Darwin region, 'Pethericks', 9.vii & 25.x.1986 (ANA) (w); Howard Springs, 1.xi.1990 (BDH) (w). QLD: Cape York Pen., Weipa, MRRP study site N3b, v-vi.1995 (ANA) (w); Split Rock, 12 km SE of Laura, 15°38'S, 144°30'E, c. 120m, 4.xii.1985 (RJK acc. 85.1) (w); Jane Table Hill, Princess Charlotte Bay, 14°30'S, 144°08'E, 28.vi.1980 (RJK acc. 80.48) (w); Davis Ck, 15 km E of Mareeba, 17°00'S, 145°34'E, 15.vi.1980 (RJK acc. 80.25) (w); 2.5 km N of Fanning R. Hmsd, 19°42'36"S, 146°25'53"E, 10.ii.2007 (GBM) (w); Lolworth NP, 19°49'41"S, 146°5'26"E, 13.xii.2006 (S. Wright) (w); ditto, 19°49'42"S, 146°5'26"E, 28.ix-12.xii.2006 (QM Party) (w); 14 km E of Mingela, 5.i.1977 (BBL) (w); Red Falls, basalt, 19°55'33"S, 145°44'1"E, 16.xii.2006 (GBM) (w); Britton Ra., 6 km NNE of Homevale, 21°23'S, 148°33'E, 1-6.iv.1975, ex nest in ground (RJK acc. 75.153, 165/1) (w); Rundle Ra., 36 km NW of Gladstone, 23°39'S, 150°58'E, 24-30.iii.1975 (RJK acc. 75.116/3) (w).

Description. *Worker.* Dimensions (holotype cited first): TL c. 6.70, 5.85-6.77; HL 1.65, 1.50-1.72; HW 1.37, 1.22-1.43; CI 84, 80-84; SL 2.06, 1.81-2.06; SI 150, 144-151; PW 1.28, 1.12-1.31; MW 0.97, 0.81-0.97; PMI 132, 129-145; MTL 2.12, 1.87-2.25 (15 measured).

Anterior clypeal margin with denticulate, median flange, laterally flanked by acute angles. Clypeus with median carina; weakly sinuate in profile (almost straight in some specimens), posteriorly rounding into moderately impressed basal margin. Frontal triangle indistinct. Frontal carinae sinuate with weakly raised margins; central area flat. Sides of head in front of eyes converging towards mandibular bases in very weakly convex

line; behind eyes, sides rounding into convex occipital margin. Eyes only moderately convex, in full face view not or only marginally exceeding lateral cephalic outline. Ocelli lacking, position of median ocellus indicated by shallow pit in some specimens. Pronotal humeri widely rounded with anterior margins weakly raised; pronotal dorsum widest at mid-length, lateral margins weakly emarginate medially before terminating in distinctly impressed promesonotal suture. Mesonotal dorsum with lateral margins converging towards indistinct metanotal groove. Propodeal dorsum armed with slender, moderately long, subparallel spines with tips weakly curved outwards. Petiole with posterior face distinctly swollen; dorsum weakly concave medially, laterally armed with pair of slender, obliquely elevated, divergent spines with tips curved upwards. Anterior face of first gastral tergite widely rounding onto dorsum.

Mandibles densely and closely longitudinally striate with piliferous pits. Head, mesosoma and petiole very densely, reticulate-punctate; sculpturation rather flat with distinctly matt-opaque appearance, including on spines. Gaster very closely shagreened, opaque.

Mandibles at masticatory borders with numerous, curved, golden hairs. Anterior clypeal margin with only a few, anteriorly directed setae medially. Dorsa of head and mesosoma with several, rather scattered, very short, bristle-like, pale golden hairs; only a few short hairs on anterior face of fore coxae and venter of mid and hind coxae and femora; no hairs fringing lateral outline of head or antennal scapes. Gastral dorsum with several, very short, posteriorly inclined hairs; somewhat more abundant, marginally longer and posteriorly inclined, pale golden or silvery hairs around apex and on venter of gaster. Rather short, appressed, silvery pubescence in various densities over most body surfaces; pubescence pale golden and denser, hiding underlying sculpturation medially, on dorsum of gaster.

Black; mandibles and appendages black or very dark reddish-brown.

Queen. Dimensions: TL c. 7.16-7.71; HL 1.68-1.75; HW 1.31-1.40; CI 78-80; SL 1.90-1.93; SI 138-1.47; PW 1.68-1.72; MTL 2.15-2.18 (3 measured).

Apart from sexual characters, very similar to worker except: pronotal humeri widely rounded with indication of blunt humeral angles. Mesoscutum wider than long, with relatively low and virtually flat dorsum in lateral view; anterior margin evenly rounded in dorsal view; median line distinct; parapsides flat. Mesoscutellum only marginally elevated above dorsal plane of mesosoma. Propodeal spines shorter than in worker, tips weakly curved outwards. Petiolar spines short, weakly elevated and divergent. Sculpturation, pilosity, pubescence and colour identical to worker.

Males unknown; immature stages (larvae in various stages of development and pupae from holotype colony) present in the QM spirit collection.

Remarks. *Polyrhachis melanura* is one of several species that is very similar to *P. penelope*, but can be easily separated by its distinctly dull appearance, the swollen posterior face of its petiole (Fig. 7H) and its obliquely elevated petiolar spines. In contrast, the sculpturation in *P. penelope* is somewhat more lucid and semi-polished, the oblique posterior face of the petiole is only weakly convex (Fig. 8B) and the petiolar spines are horizontal.

Polyrhachis melanura is a widespread and relatively common species along the northern and northeastern Australian seaboard. It ranges from the Kimberley region in the north-west, to Cape York Peninsula in the east, and south to Rundle Range near Gladstone. It seems to prefer open forests and savannah woodlands, where it builds nests in the ground with the entrances usually hidden under a rock or piece of wood. *Polyrhachis melanura* was listed as *P. 'Hagio 11'* by Kohout (2000: 199).

Polyrhachis (*Hagiomyrma*) *penelope* Forel, 1895
(Fig. 8A-B)

Polyrhachis penelope Forel, 1895:46. Syntype workers. Type locality: QLD, Mackay (G. Turner), MHNG, ANIC, QM (examined).

Polyrhachis (*Hagiomyrma*) *penelope* Forel. Forel, 1915:108 (combination in *P. (Hagiomyrma)*).

Other Material. QLD: Stratford-Cairns, 2.viii.1975 (BBL) (w); Cairns, 2.viii.1975 (BBL) (w); Yarrabah, c. 9 km E of Cairns, 16°54'S, 145°51'E, 22-24.vii.1980 (RJK acc. 80.121) (w); Millstream NP, nr Ravenshoe, 6.viii.1975 (BBL) (w); Jourama Falls, Paluma NP, 5.viii.2002 (ANA) (w); Mt Elliot NP, Alligator Ck, 19°26'S, 146°57'E, 11.vi.1987 (RJK acc. 87.88) (w); Toomba, 19°58'5"S, 145°34'49"E, 14-16.xii.2006 (S. Wright) (w); 20 km S of Bowen, 17.viii.1975 (BBL) (w); Brampton I., 20°49'S, 149°16'E, 1.i.1979 (RJK acc. 79.1) (w); Cape Hillsborough NP, 20°55'S, 149°01'E, 2.i.1979 (RJK accs 79.4, 10) (w); ditto, 12.iv.1981 (RJK acc. 81.82) (w, ♀); ditto, 22.x.1995 (SKR #42, 45, 50, 51) (w); 1.5 km SE of Mt Ossa, 20°58'S, 148°50'E, 28.xi.1976 (RJK acc. 76.93) (w); Eungella NP, Finch Hatton Gorge, 21°04'S, 148°38'E, 7-13.iv.1975 (RJK acc. 75.171) (w); Mt Blackwood NP, 21°02'S, 148°56'E, 14.iv.1981 (RJK accs 81.99, 109) (w); Britton Ra., 6 km NNE of Homevale, 21°23'S, 148°33'E, 1-6.iv.1975 (RJK acc. 75.169) (w); Mt Pollux, SW base, 22°28'43"S, 147°52'9"E, 12-13.i.2006 (CJB) (w); Lords Table, W base, 22°39'35"S, 148°0'27"E, 8.iii.2006 (GBM) (w); ditto, SE base, 22°40'29"S, 148°1'13"E, 13.i-9.iii.2006 (CJB, GBM) (w); Scotts Peak, SE base, 22°51'44"S, 148°13'31"E, 9.iii.2006 (CJB, GBM) (w); Mt Archer, nr Rockhampton, 23°20'S, 150°34'E, 4.xii.1976 (RJK acc. 76.112) (♀).

Description. *Worker*: Dimensions (syntypes cited first): TL c. 6.65-7.61, 6.50-7.61; HL 1.68-1.75, 1.65-1.78; HW 1.40-1.46, 1.34-1.59; CI 80-81, 80-85; SL 2.03-2.09, 2.03-2.15; SI 145-149, 135-151; PW 1.28-1.40, 1.28-1.47; MW 0.90-1.03, 0.84-1.03; PMI 139-142, 139-154; MTL 2.06-2.18, 2.06-2.34 (5+10 measured).

Anterior clypeal margin with denticulate median flange, laterally flanked by acute angles. Clypeus with distinct median carina; sinuate in profile, posteriorly rounding into moderately impressed basal margin. Frontal triangle weakly indicated. Frontal carinae sinuate with only weakly raised margins; central area flat. Sides of head in front of eyes converging towards mandibular bases in weakly convex line; behind eyes, sides rounding into convex occipital margin. Eyes moderately convex, in full face view marginally exceeding lateral cephalic outline. Ocelli lacking. Pronotal humeri widely rounded with anterior margins weakly raised; pronotal margins weakly emarginate medially before terminating at well impressed promesonotal suture. Mesonotal dorsum with lateral margins converging towards indistinct

metanotal groove. Propodeal dorsum armed with moderately long, weakly divergent spines with tips weakly curved outwards. Petiole with posterior face descending towards base in weakly convex line; dorsum weakly concave medially, laterally armed with pair of broad-based, horizontal, divergent spines. Anterior face of first gastral tergite distinctly higher than full height of petiole, widely rounding onto dorsum.

Mandibles longitudinally striate with numerous piliferous pits. Head, mesosoma and petiole distinctly, more-or-less regularly reticulate-punctate, with punctures very smooth, polished. Spines sculptured at bases, smooth and polished towards tips. Gaster finely shagreened.

Mandibular masticatory borders with numerous, curved, golden hairs. Anterior clypeal margin with a few, anteriorly projecting setae medially and several very short setae fringing margin laterally. Dorsa of head, mesosoma and petiole with numerous, rather short, erect, bristle-like hairs; a few hairs fringing anterior face of fore coxae and venter of mid and hind coxae and femora. Gaster with more abundant, golden hairs on dorsum; distinctly longer, posteriorly directed hairs around apex and on venter. Rather diluted, closely appressed, silvery pubescence on dorsa of head and mesosoma; pubescence more abundant on sides of mesosoma, declivity and petiole, except its smooth and polished anterior face. Gaster with abundant golden pubescence on dorsum, hiding underlying sculpturation; pubescence much diluted and silvery on venter of gaster.

Black; mandibular teeth reddish-brown.

Queen. Dimensions: TL c. 8.52; HL 1.81; HW 1.53; CI 84; SL 2.03; SI 133; PW 1.72; MTL 2.18 (1 measured).

Apart from sexual characters, very similar to worker except: mesoscutum as wide as long; relatively low in lateral view, anteriorly rounding onto very weakly convex dorsum; median line bifurcate anteriorly; parapsides weakly raised. Mesoscutellum only marginally

raised above dorsal plane of mesosoma. Propodeal and petiolar spines similar to worker, but shorter. Sculpturation, pilosity, pubescence and colour identical to worker, except pilosity on dorsum of mesoscutum completely lacking.

Male unknown. Immature stages present in the QM collection.

Remarks. *Polyrhachis penelope* is an uncommon species with its distribution centred on Mackay and extending along the Queensland coast from about Rockhampton as far north as Cairns. It is an inhabitant of open eucalypt forests and woodlands that mostly nests in the ground although one nest was located in a rotten tree stump.

Polyrhachis (Hagiomyrma) pilbara sp. nov.
(Fig. 8C-D)

Etymology. After the type locality, the Pilbara region in the north-west of Western Australia.

Material. HOLOTYPE: WA, Pilbara region, Hamersley Ra., Dales Gorge, 24.iv.1963, McInnes & Dowse (worker). PARATYPES: data as for holotype (4 workers); Wittenoom, c. 20 km N of, 23.iv.1963, McInnes & Dowse (6 workers). Type deposition: Holotype and 2 paratypes in ANIC; 2 paratypes each in QM, BMNH, MCZC and WAMP.

Other Material. WA: Barlee Ra., vi.1994 (S.van Leeuwin) (2w in CURT - Heterick #816 and JDM #901 collection identified and labelled as '*Hagio* 22').

Description. *Worker*: Dimensions (holotype cited first): TL c. 7.76, 6.85-8.16; HL 1.87, 1.65-1.90; HW 1.47, 1.34-1.50; CI 79, 76-81; SL 2.28, 2.06-2.34; SI 155, 150-159; PW 1.37, 1.28-1.43; MW 0.81, 0.73-0.87; PMI 169, 164-175; MTL 2.40, 2.09-2.50 (11 measured).

Anterior clypeal margin with shallow, denticulate flange, flanked laterally by acute teeth. Clypeus with median carina; virtually straight in profile, posteriorly rounding into shallow basal margin. Frontal triangle poorly indicated. Frontal carinae sinuate with only weakly raised margins. Sides of head converging towards mandibular bases in almost straight line; behind eyes, sides rounding into convex occipital margin. Eyes only moderately convex; in full face view not or only marginally exceeding lateral cephalic outline. Ocelli lacking. Pronotal humeri rounded with

weakly raised margins; pronotum widest at mid-length. Promesonotal suture distinctly impressed. Lateral margins of mesonotum converging towards indistinct metanotal groove. Propodeal margins terminating in weakly divergent spines; spines horizontal from bases and weakly curving downwards at midlength. Petiole rather broad at base in lateral view; dorsum weakly concave medially, armed with divergent spines elevated from bases, tips upturned. Anterior face of first gastral tergite distinctly higher than full height of petiole, widely rounding onto dorsum.

Mandibles longitudinally striate with piliferous pits. Head, mesosoma and petiole reticulate-punctate, sculpturation mostly longitudinal on vertex and dorsum of mesosoma. Spines distinctly sculptured for most of length, only tips smooth and polished. Gaster closely reticulate-punctate.

Mandibular masticatory and outer borders with numerous, curved, golden hairs. Anterior clypeal margin with several anteriorly projecting longer setae medially and a few short setae fringing margin laterally. Numerous, medium length, erect, golden hairs on most body surfaces, including appendages; antennal scapes, sides of head in full face view and pronotal humeri in dorsal view distinctly fringed with short bristle-like hairs. Gaster with hairs somewhat longer and posteriorly directed, notably around apex and on venter. Dorsum of gaster with closely appressed, golden pubescence, completely hiding underlying sculpturation; pubescence much diluted on gastral venter.

Black; mandibles, appendages, including coxae and gaster medium reddish-brown.

Sexuals and immature stages unknown.

Remarks. Rather coarsely reticulate-punctate sculpturation and the bristle-like hairs along the antennal scapes, make *P. pilbara* a very characteristic representative of the *pilbara*-complex within the *penelope*-group. It appears restricted to the mulga and spinifex clad hills of the Pilbara region of north-western Western

Australia. Nothing is known about its biology or nesting habits.

Polyrhachis (*Hagiomyrma*) *placida* sp. nov.
(Fig. 8E-F)

Etymology. Derived from the Latin *placidus*, meaning quiet, tranquil, in reference to the peaceful and serene western slope of the Atherton Tableland that surrounds the type locality.

Material. HOLOTYPE: QLD, Herberton, 10 km W, 15.ix.1981, savannah woodland, B.B. Lowery (worker). PARATYPES: data as for holotype (2 workers). Type deposition: Holotype and 1 paratype in ANIC; 1 paratype in QM.

Description. *Worker.* Dimensions (holotype cited first): TL c. 6.80, 6.60-6.80; HL 1.59, 1.56-1.59; HW 1.23, 1.22-1.25; CI 77, 77-79; SL 1.78, 1.75-1.78; SI 145, 142-146; PW 1.09, 1.03-1.09; MW 0.65, 0.62-0.65; PMI 168, 163-168; MTL 2.09, 1.93-2.09 (3 measured).

Anterior clypeal margin with acutely denticulate, median flange. Clypeus with median carina; distinctly sinuate in profile with moderately impressed basal margin. Frontal carinae sinuate with weakly raised margins at midlength, flat posteriorly; central area relatively wide, flat with poorly indicated frontal furrow. Sides of head in front of eyes converging towards mandibular bases in straight line; behind eyes, sides widely rounding onto convex occipital margin. Eyes convex, in full face view clearly exceeding lateral cephalic outline. Ocelli lacking. Pronotal dorsum with weakly raised, bluntly angular humeri; lateral margins converging towards distinct promesonotal suture. Mesonotal margins converging posteriorly; metanotal groove indistinct. Propodeal margins terminating in divergent, relatively short, weakly curved, spines. Petiole with anterior face straight, posterior face convex; dorsum shallowly concave medially, armed with slender, divergent, weakly elevated spines. Anterior face of first gastral tergite distinctly higher than full height petiole, widely rounding onto dorsum.

Mandibles finely striate at bases, rather smooth with numerous piliferous pits towards masticatory borders. Head, mesosoma and

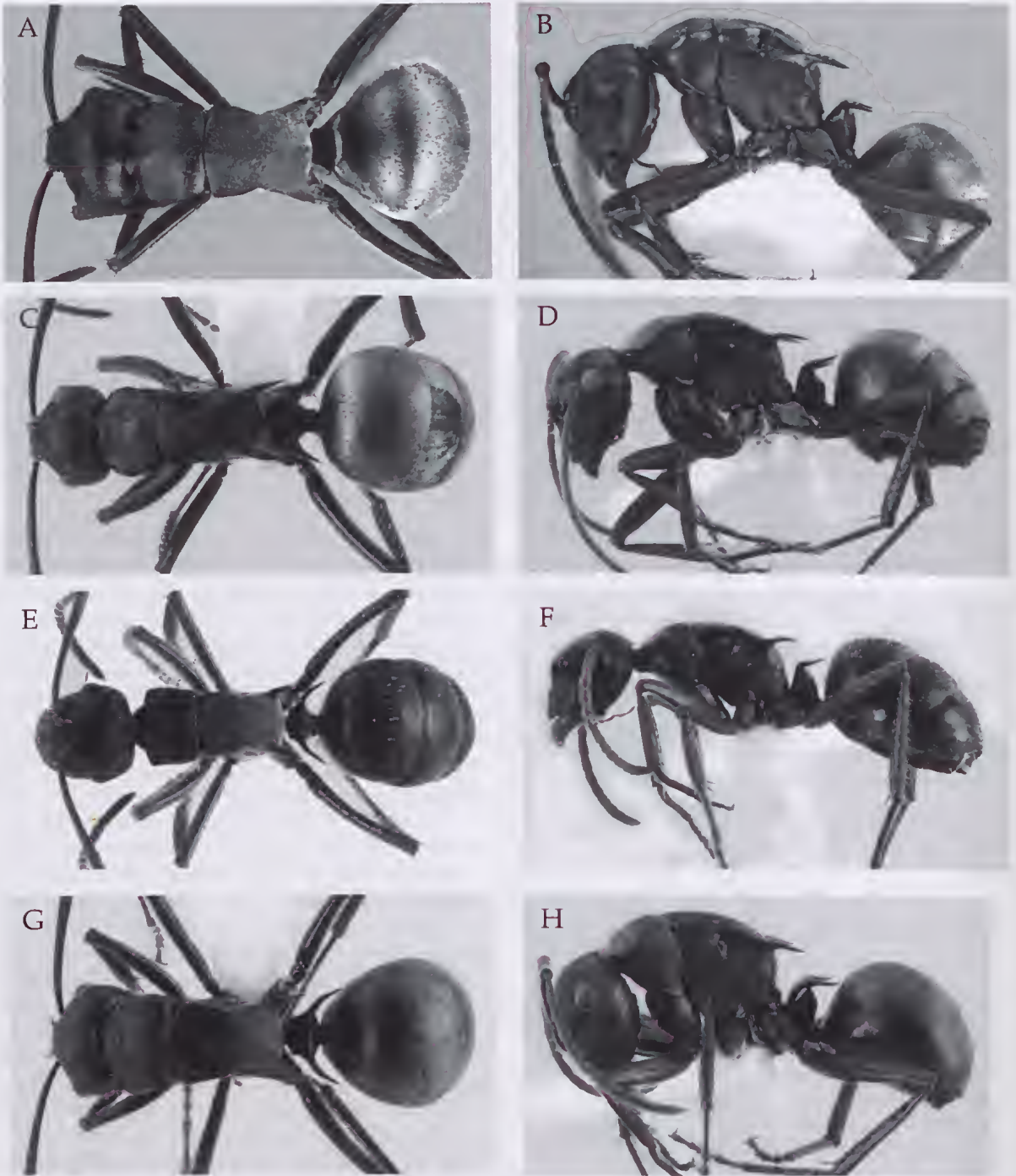


FIG. 8. *Polyrhachis* (*Hagiomyrma*) *penelope* species-group – dorsal (left) and lateral (right) view. A-B, *P. penelope* Forel; C-D, *P. pilbara* sp. nov.; E-F, *P. placida* sp. nov.; G-H, *P. seducta* sp. nov.; (not to scale).

petiole distinctly reticulate-punctate. Spines sculptured from bases up to midlength, smooth and polished towards tips. Gaster shagreened.

Mandibles with numerous, curved, golden hairs and closely appressed hairs towards bases. Anterior clypeal margin with several longer setae medially and fringe of shorter setae laterally. Numerous, mostly medium length, erect, golden hairs on most body surfaces, including appendages; antennal scapes with very short, bristle-like hairs; head in full face view with a few short hairs between eyes and mandibular bases and numerous, distinctly longer hairs fringing occipital margin. Gastral pubescence posteriorly directed and somewhat longer around apex and on venter.

Black; mandibles and legs, including coxae, light to medium reddish-brown; antennae and gaster dark reddish-brown.

Sexuals and immature stages unknown.

Remarks. *Polyrhachis placida* is similar to *P. lydiae*, but has a virtually black body while in *P. lydiae* the body is bright metallic green with the front of head and anterior portion of the pronotum distinctly light reddish-brown. It also closely resembles *P. stricta* described below, however they differ in numerous characters, including the more strongly posteriorly converging promesonotal margins in *P. stricta* (PMI >190 versus PMI <168 *P. placida*). *Polyrhachis placida* is apparently a ground-nesting species with the known specimens collected from under a rock in savannah woodland. *Polyrhachis* 'Hagio 17' listed by Kohout (2000: 200) actually consisted of two species, *Polyrhachis placida* and *P. stricta*.

Polyrhachis (*Hagiomyrma*) *seducta* sp. nov.
(Fig. 8G-H)

Etymology. Derived from the Latin *seductus*, meaning remote, distant, in reference to the species rather isolated occurrence on Barrow Island.

Material. HOLOTYPE: WA, Barrow Island., 20°47'S, 115°26'E, 24.iv.2005, S. Callan (worker). PARATYPE: data as for holotype (1 worker). Type deposition: Holotype in WAMP, paratype in QM.

Other Material. WA, Barrow I., 20°47'S, 115°27'E, 24.iv.2005 (S. Callan) (w); ditto, 17.v.2005 (S. Callan) (w); ditto, 20°46'S, 115°24'E, ii.1977 (H. Heatwole) (w).

Description. *Worker:* Dimensions (holotype cited first) TL c. 6.85, 5.64-7.31; HL 1.75, 1.47-1.75; HW 1.40, 1.18-1.40; CI 80, 80-83; SL 2.06, 1.68-2.06; SI 147, 140-150; PW 1.28, 1.09-1.28; MW 0.82, 0.65-0.84; PMI 156, 156-174; MTL 2.21, 1.72-2.28 (6 measured).

Anterior clypeal margin with denticulate, median flange. Clypeus with median carina, weakly sinuate in profile, posteriorly rounding into moderately impressed basal margin. Frontal triangle indistinct. Frontal carinae sinuate with weakly raised margins; central area flat with distinct frontal furrow. Sides of head in front of eyes converging in virtually straight line towards mandibular bases; behind eyes, sides rounding into convex occipital margin. Eyes moderately convex, in full face view marginally exceeding lateral cephalic outline. Ocelli lacking. Pronotal humeri rounded with anterior margins weakly raised; pronotal dorsum widest at midlength, lateral margins converging into distinctly impressed promesonotal suture. Mesonotal dorsum with lateral margins converging towards indistinct metanotal groove. Propodeal dorsum armed with moderately long, weakly divergent spines. Petiole with posterior face distinctly swollen (Fig. 8H); dorsum armed with pair of slender, divergent spines with tips weakly curved upwards. Anterior face of first gastral tergite widely rounding onto dorsum.

Mandibles finely longitudinally striate with piliferous pits. Clypeus closely punctate. Head reticulate-punctate, sculpturation on vertex distinctly coarser and more-or-less regularly, longitudinally striate. Dorsum of mesosoma reticulate-punctate; sculpturation on mesonotum organised into rather uneven, longitudinal striae, curved obliquely towards lateral margins on propodeal dorsum. Sides of mesosoma, declivity and petiole reticulate-punctate. Spines sculptured at bases, smooth and polished towards tips. Gaster closely shagreened, opaque.

Mandibles with numerous, relatively short, curved hairs at masticatory and outer borders. Anterior clypeal margin medially with a few, anteriorly directed setae. Dorsa of

head, mesosoma and petiole with numerous, short, bristle-like, golden hairs, many fringing lateral and dorsal outline of head; appendages, including antennal scapes, with very short, erect hairs. Gaster with abundant, posteriorly inclined, marginally longer, golden hairs, distinctly longer around apex and on venter. Very sporadic, short, appressed, silvery pubescence in various densities over most body surfaces; pubescence golden and denser on dorsum of gaster but not hiding underlying sculpturation.

Black; mandibular masticatory borders and appendages dark to very dark reddish-brown.

Sexuals and immature stages unknown.

Remarks. *Polyrhachis seducta* is somewhat similar to *P. melanura*. However, *P. seducta* can be distinguished by the distinctly deeper body sculpturation, more strongly posteriorly converging promesonotal lateral margins and short, bristle-like hairs on antennal scapes. *Polyrhachis seducta* is also very similar to *P. tanami* described below, with both having numerous short hairs on the antennal scapes and a distinctly swollen posterior face of the petiole. They differ mainly by the hairs on dorsum of mesosoma that are erect and very short in *P. seducta*, while they are longer and distinctly posteriorly directed in *P. tanami*.

Polyrhachis seducta is known only from Barrow Island. All specimens were collected foraging on the ground and it is highly probable that the species is a terrestrial nester like most other *Hagiomyrma* species.

Polyrhachis (Hagiomyrma) semiobscura
Donisthorpe, 1944
(Fig. 9A-B)

Polyrhachis (Hagiomyrma) semiobscura Donisthorpe, 1944:65. Holotype worker. Type locality: BISMARCK ARCHIPELAGO, NEW IRELAND, Kavieng (L.E. Cheesman), BMNH (examined).

Polyrhachis semiobscura Donisthorpe. Kohout & Taylor, 1990.

Other Material. INDONESIA, IRIAN JAYA: (as New Guinea: Neth.) Eramboe, 80 km ex Marauke, 5.ii.1960 (T.C. Maa) (w). PAPUA NEW GUINEA: Morobe Prov., Atzera Ra., Bubia Research Stn, 30-100 m, 06°40'S, 146°55'E, 23-26.viii.1984 (RJK acc. 84.357) (w); Northern Prov., Buna, 15.iii.1972 (PMR) (w);

Girua, 3.vii.1973 (PMR) (w). Central Prov., Varirata Rd, c. 500 m, 3 km WSW of Sogeri, 09°26'S, 147°23'E, 4.ix.1984 (RJK acc. 84.429) (w); Port Moresby, Boroko, 6-7.xi.1960 (J.L. Gressitt) (w). AUSTRALIA, QLD: Torres Strait, Saibai I., nr Saibai village, 09°23'S, 142°37'E, 10-21.vi.1975 (H&C) (w); Dauan I., nr Dauan village, 09°25'S, 142°32'E, 30-31.vii.1975 (H&C #DAU.6) (w); Mabulag (= Jarvis I.), 09°58'S, 142°11'E, 3.viii.1975 (H&C #MAB.1) (w); Wednesday I., 10°32'S, 142°19'E, 2-3.vii.1977 (E. Cameron) (w); Thursday I., 10°35'S, 142°13'E, 3.vii.1974 (H&C) (w); Horn I., 10°37'S, 142°17'E, 10-27.vi.1974 (H&C #HOR.23) (w); Gabba I., 09°46'S, 142°38'E, 30-31.vii.1975 (H&C) (w); Cape York, 10°41'S, 142°31'E, 25.iii.1987 (RJK acc. 87.85) (w); Cape York, Somerset, 10°45'S, 142°36'E, 7-12.vii.1976 (E. Cameron) (w); Cape York Pen., Weipa, MRRP study site N2a, v-vi.1995 (ANA) (w); Iron Ra., 12°43'S, 143°18'E, 26-31.vii.1981 (RJK accs 81.176, 179, 203) (w, ♀).

Description. *Worker.* Dimensions (holotype cited first): TL c. 7.00, 5.04-7.62; HL 1.71, 1.31-1.84; HW 1.51, 1.09-1.64; CI 88, 83-89; SL 1.91, 1.53-1.96; SI 126, 119-140; PW 1.28, 0.94-1.37; MW 0.68, 0.59-0.78; PMI 188, 151-188; MTL 2.12, 1.68-2.37 (1+9 measured).

Anterior clypeal margin with denticulate, median flange. Clypeus with distinct median carina; straight, or very weakly sinuate in profile with shallowly impressed basal margin. Frontal triangle poorly indicated. Frontal carinae sinuate with weakly raised margins. Sides of head in front of eyes weakly convex towards mandibular bases; behind eyes, sides rounding into convex occipital border. Eyes moderately convex, in full face view not or only marginally exceeding lateral cephalic outline. Ocelli lacking. Pronotum with humeri dilated (distinctly less dilated in Australian specimens), rounded, with lateral margins somewhat emarginate behind, subparallel or weakly converging into well impressed promesonotal suture. Mesonotum with lateral margins converging into medially indistinct, flat, metanotal groove. Propodeal spiracles situated on moderately projecting tubercles. Propodeal margins terminating in more-or-less horizontal, subparallel, acute spines with tips weakly curved outwards. Petiole with divergent, slender spines, weakly elevated in lateral view. Anterior face of first gastral segment higher than full height of petiole, widely rounding on dorsum.

Mandibles finely, longitudinally striate with piliferous pits. Head, mesosoma and petiole reticulate-punctate; vertex with more-or-less regular, rather distinct, longitudinal striae, extending anteriorly between eyes and frontal carinae and along sides of head; sculpturation rather smooth with distinctly polished appearance. Dorsum of mesosoma with reticulae more irregular and less distinct; spines finely sculptured along entire length. Gaster finely shagreened.

Mandibular masticatory borders with several curved, golden hairs and a few short, erect hairs along outer borders towards bases. Anterior clypeal margin medially with only a few, anteriorly directed setae. All body surfaces with rather short, mostly erect hairs, barely as long as half greatest diameter of eyes. Only a few, very short, bristle-like hairs lining leading edge of antennal scapes. Hairs distinctly longer and more posteriorly directed around apex and on venter of gaster. Closely appressed, mostly silvery or pale golden pubescence in various densities on head, mesosoma and petiole; pubescence distinctly more abundant and more golden on mesonotal and propodeal dorsa in Australian specimens. Gaster with somewhat longer, golden pubescence on dorsum, silvery on venter.

Black; mandibular teeth dark reddish-brown.

Queen. Dimensions: TL c. 8.06; HL 1.72; HW 1.43; CI 83; SL 1.81; SI 126; PW 1.62; MTL 2.12 (1 measured).

Apart from sexual characters very similar to worker, except: dorsum of mesoscutum wider than long with widely rounding anterior margin in dorsal view; flat in lateral view; median line bifurcate anteriorly; parapsides weakly raised. Mesoscutellum flat, not elevated above dorsal plane of mesosoma. Spines distinctly shorter than in worker. Sculpturation, pilosity, pubescence and colour similar to worker.

Male unknown. Immature stages present in the QM collection.

Remarks. *Polyrhachis semiobscura* is one of only four *Hagiomyrma* species originally described from specimens from outside the Australian

mainland, the others being *P. denticulata*, *P. metella* and *P. schenkii*. In *P. semiobscura*, Australian specimens have distinctly less dilated pronotal humeri and more abundant dorsal pubescence, notably on mesonotum and propodeum, compared to their New Guinean counterparts. However, considering their uniformity in other characters, such as the longitudinal striation of the head, the position of the propodeal spiracles on short, laterally projecting tubercles and the rather remarkable differences in the size of the workers (HL 1.31–1.84) from both populations, I am hesitant to consider them separate species. The known distribution of *P. semiobscura* ranges from New Ireland in the Bismarck Archipelago to Papua New Guinea and south across the Torres Strait islands as far as Iron Range on Cape York Peninsula. *Polyrhachis semiobscura* appears to be lignicolous in its nesting habit. The only known colony was found nesting in two adjacent galls attached to a twig of a small sapling in the open forest at Iron Range Nat. Park. At Varirata Range in Papua New Guinea numerous workers of *P. semiobscura* were collected from the rims of the pitchers of a species of *Nepenthes*. Despite the large numbers of workers and their rather busy activity around the rims, none were found trapped in the liquid at the bottom of the pitchers.

Polyrhachis (*Hagiomyrma*) *stricta* sp. nov.
(Fig. 9C–D)

Etymology. Derived from the Latin *strictus*, meaning drawn together, tight, in reference to its distinctly posteriorly constricting promesonotal dorsum.

Material. HOLOTYPE: QLD, Porter Ck, 23 km SE of Cardwell, 18°26'S, 146°08'E, 26.ii.2000, *Melaleuca* swamp, R.J. Kohout acc. 2000.67, QMT174513 (worker). PARATYPE: data as for holotype (1 worker). Type distribution: Holotype in QM; paratype in ANIC.

Description. *Worker.* Dimensions (holotype cited first): TL c. 6.35, 5.95; HL 1.65, 1.56; HW 1.31, 1.22; CI 79, 78; SL 1.84, 1.72; SI 140, 141; PW 1.12, 1.09; MW 0.59, 0.56; PMI 190, 195; MTL 2.03, 1.90 (2 measured).

Anterior clypeal margin with denticulate median flange. Clypeus with distinct median

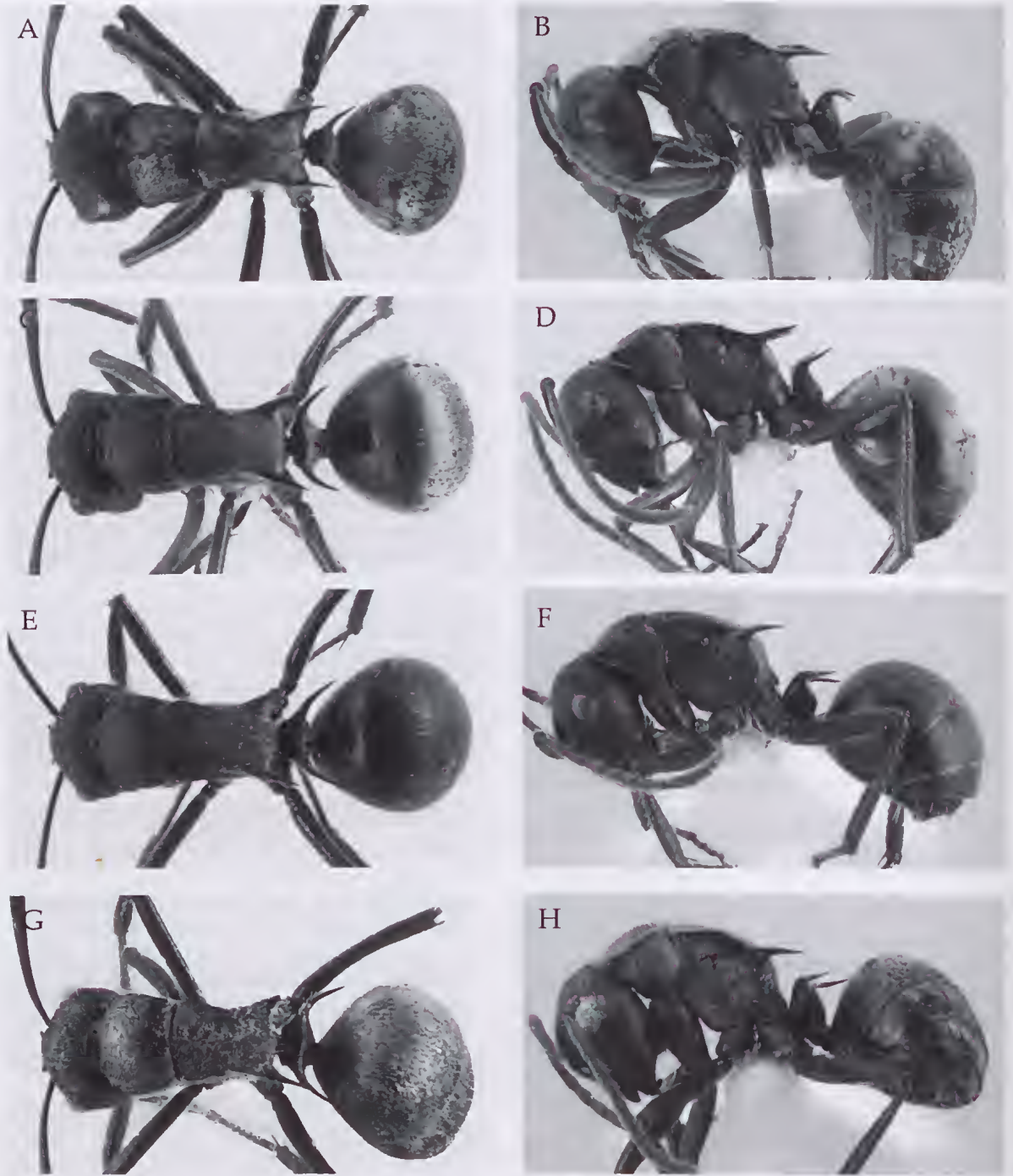


FIG. 9. *Polyrhachis* (*Hagiomyrma*) *penelope* species-group – dorsal (left) and lateral (right) view. A–B, *P. semiobscura* Donisthorpe; C–D, *P. stricta* sp. nov.; E–F, *P. tanami* sp. nov.; G–H, *P. tenebra* sp. nov. (not to scale).

carina; almost straight in profile with basal margin only very shallowly impressed. Frontal carinae sinuate with narrowly raised margins; central area with rather flat frontal furrow. Sides of head in front of eyes only weakly converging towards mandibular bases; behind eyes, sides widely rounding into convex occipital margin. Eyes convex, in full face view clearly breaking lateral cephalic outline. Ocelli lacking. Pronotal dorsum with humeri bluntly angular; promesonotal lateral margins narrowly raised, distinctly converging posteriorly. Promesonotal suture distinctly impressed; metanotal groove indicated by a notch in lateral margins, indistinct dorsally. Propodeal lateral margins terminating in distinctly divergent, weakly upturned, acute spines; dorsum descending into declivity in weakly convex line. Petiole with a pair of slender, divergent, upturned, acute spines. Anterior face of first gastral segment widely rounding onto dorsum.

Mandibles finely striate with numerous piliferous pits. Head, mesosoma and petiole distinctly and closely, rather uniformly, reticulate-punctate. Gaster finely shagreened.

Mandibles at masticatory and outer borders with curved, golden hairs and closely appressed shorter hairs towards bases. Anterior clypeal margin with several longer setae medially and fringe of shorter setae laterally. Numerous, mostly erect hairs on clypeus and along frontal carinae; distinctly shorter hairs on sides of head and vertex. Dorsum of mesosoma with numerous erect or suberect hairs, hairs on propodeum half as long as greatest diameter of eye. Gaster dorsally and ventrally with numerous posteriorly directed, relatively long, golden hairs. Rather sparse pale golden or silvery, closely appressed pubescence on head and mesosoma, more abundant on meso- and metapleura, propodeal declivity and petiole. Gastral dorsum with rich golden pubescence almost hiding underlying sculpturation; pubescence silvery and less abundant on gastral venter.

Black; mandibles, clypeal flange (except narrow anterior margin), antennae, pronotal

collar, legs, including coxae, light to medium reddish-brown; tibiae and gastral venter distinctly darker reddish-brown.

Sexuals and immature stages unknown.

Remarks. *Polyrhachis stricta* is known only from two specimens found foraging on the ground and low vegetation at the type locality. *Polyrhachis stricta* somewhat resembles *P. placida* as they have similar colour patterns. However, the clypeus in *P. stricta* is almost straight in lateral view with the basal margin only shallowly impressed, while in *P. placida* the profile of the clypeus is distinctly sinuate and the basal margin deeper. The promesonotal lateral margins in *P. stricta* are strongly converging posteriorly (PMI >190) with the propodeal spines weakly upturned. In contrast, in *P. placida* the promesonotal margins cover less strongly (PMI <168) and the propodeal spines curve downwards from their midlength. The pilosity in *P. placida* is also distinctly longer and mostly silvery with the pubescence somewhat less tidy, notably over the gastral dorsum. *Polyrhachis stricta* and *P. placida* were both listed earlier as 'Hagio 17' by Kohout (2000: 200).

Polyrhachis (*Hagiomyrma*) *tanami* sp. nov.
(Fig. 9E-F)

Etymology. From the type locality, the Tanami Desert in the Northern Territory.

Material. HOLOTYPE: NT, Central Tanami Desert, 152 km E of Lajamanu, 19°03'S, 131°51'E, 26.vii.2001, A.L. Hertog (worker). PARATYPE: data as for holotype (1 worker). Type distribution: Holotype in ANIC; paratype in QM.

Description. *Worker:* Dimensions (holotype cited first): TL c. 6.10, 6.65; HL 1.59, 1.59; HW 1.22, 1.28; CI 77, 80; SL 1.87, 1.87; SI 153, 146; PW 1.15, 1.18; MW 0.65, 0.67; PMI 177, 176; MTL 2.03, 2.09 (2 measured).

Anterior clypeal margin with shallow, denticulate, median flange. Clypeus with distinct median carina; almost straight in profile, posteriorly rounding into shallowly impressed basal margin. Frontal carinae sinuate, with only weakly and narrowly raised margins. Sides of head converging towards mandibular bases in virtually straight line; behind eyes, sides

rounding into convex occipital margin. Eyes convex, in full face view clearly exceeding lateral cephalic outline. Ocelli lacking. Pronotal humeri rounded with narrowly raised margins; lateral margins converging towards well impressed promesonotal suture. Mesonotum with margins converging towards poorly indicated metanotal groove. Propodeal dorsum armed with slender, horizontal, divergent spines, weakly curved outwards and downwards from midlength. Petiolar spines widely divergent, raised obliquely from bases, continued horizontally towards weakly upturned tips. Anterior face of first gastral tergite widely rounding onto dorsum.

Mandibles very finely, closely, longitudinally striate with piliferous pits. Head, mesosoma and petiole very distinctly, rather coarsely reticulate-punctate; sculpturation on vertex distinctly, mostly longitudinally striate. Sculpturation less coarse on dorsum of mesosoma, pronotal sculpture consisting of somewhat irregular, anteriorly converging, rather flat striae. Gaster shagreened; sculpturation on dorsum more distinct with numerous shallow pits.

Mandibular masticatory and outer borders with numerous, curved, golden hairs, hairs suberect towards bases. Anterior clypeal margin with a few longer setae medially and fringe of shorter setae laterally. Most body surfaces, including appendages, with numerous, short to medium length, mostly erect hairs; gaster with hairs marginally longer and more posteriorly directed. Very diluted short, silvery, closely appressed pubescence on head, mesosoma and petiole; pubescence somewhat more abundant and golden on dorsum of gaster.

Black; mandibles reddish-brown. Appendages black or very dark reddish-brown.

Sexuals and immature stages unknown.

Remarks. *Polyrhachis tanami* is characterised by its small size and distinctly and rather deeply sculptured body. It is relatively similar to *P. tenebra*, with which it shares rather strongly posteriorly converging margins of the promesonotal dorsum (PMI 176-177 in *P. tanami* versus 172 in *P. tenebra*) and virtually

identically shaped petiolar spines. However, *P. tenebra* has the dorsum of the head and mesosoma more finely reticulate-punctate with the sculpture on the anterior pronotum, including the humeri, and most of mesonotum and propodeum partially hidden by relatively long, appressed, pale golden pubescence. *Polyrhachis tanami* is known only from a single locality in the Tanami Desert and nothing is known of its nesting habits.

Polyrhachis (Hagiomyrma) tenebra sp. nov.
(Fig. 9G-H)

Etymology. Derived from the Latin *tenebrosus*, meaning dark, darkness, in reference to its virtually black appearance.

Material. HOLOTYPE: QLD, 5 km E of Pentland (20°32'S, 145°24'E) 3.i.1977, B.B. Lowery (worker). Type deposition: Unique holotype in ANIC.

Description. *Worker.* Dimensions: TL c. 6.35; HL 1.62; HW 1.31; CI 81; SL 1.75; SI 133; PW 1.12; MW 0.65; PMI 172; MTL 2.00.

Anterior clypeal margin with shallow, acutely denticulate, median flange. Clypeus with median carina; almost straight in profile, weakly elevated posteriorly; basal margin very shallowly impressed. Frontal carinae sinuate, with narrowly raised margins. Sides of head in front of eyes converging towards mandibular bases in weakly convex line; behind eyes, sides rounding into convex occipital margin. Eyes convex, in full face view marginally exceeding lateral cephalic outline. Ocelli lacking. Pronotal humeri rounded with narrowly raised anterior margins; promesonotal suture distinct. Mesonotum with margins converging towards poorly indicated metanotal groove. Propodeal dorsum armed with slender, horizontal, divergent spines, with tips weakly curved outwards. Petiolar spines widely divergent, obliquely elevated from bases and continued horizontally towards weakly upturned tips. Anterior face of first gastral tergite widely rounding onto dorsum.

Mandibles finely, longitudinally striate with piliferous pits. Head, mesosoma and petiole reticulate-punctate with sculpturation relatively fine and uniform. Spines sculptured

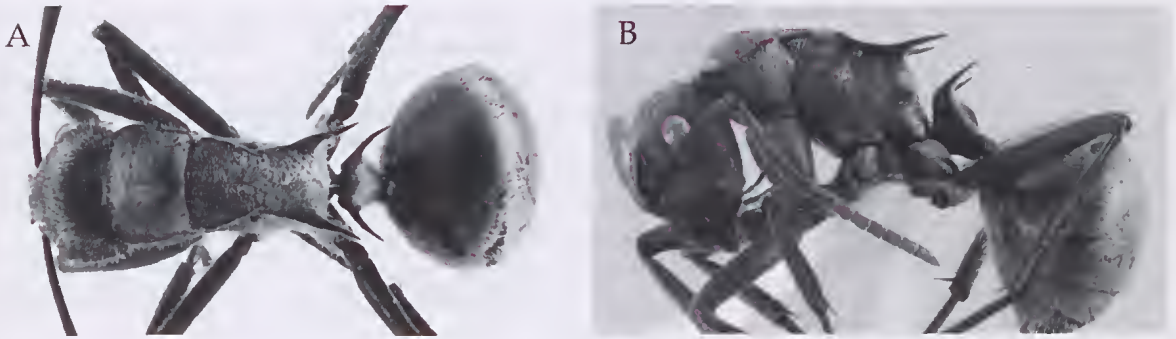


FIG. 10. *Polyrhachis* (*Hagiomyrma*) *penelope* species-group – dorsal (left) and lateral (right) view. A-B, *P. weiri* sp. nov. (not to scale).

at bases, smooth and polished towards tips. Gaster shagreened.

Mandibular masticatory and outer borders with numerous, curved, golden hairs; hairs shorter and suberect towards bases. Anterior clypeal margin with a few longer setae medially and fringe of shorter setae laterally. Most body surfaces, including appendages, with numerous, rather short, golden hairs; marginally longer and variously directed hairs on dorsum of mesosoma. Gaster with posteriorly directed hairs on dorsum; somewhat longer hairs on apical segments and venter. Mostly silvery, closely appressed pubescence on head, mesosoma and petiole; pubescence distinct, somewhat longer and pale golden on anterior portion of pronotal dorsum, including humeri. Gastral dorsum with rather abundant, golden pubescence, almost hiding underlying sculpturation; much diluted, silvery pubescence on gastral venter.

Black; mandibles reddish-brown.

Sexuals and immature stages unknown.

Remarks. *Polyrhachis teuebra* is somewhat similar to *P. tananii* with their differences discussed in remarks section of the latter species. The unique holotype of *P. teuebra* was collected foraging on the ground in savannah woodland. Like most other *Hagiomyrma* species inhabiting this kind of habitat, it is most likely a ground-nesting species.

Polyrhachis (*Hagiomyrma*) *weiri* sp. nov.
(Fig. 10A-B)

Etymology. After the collector of the type series specimens, Tom Weir of the ANIC of the Ecosystem Sciences, Canberra.

Material. HOLOTYPE: NT, Wessel Is, Rimbija I., 11°01'S, 136°45'E, 3-14.ii.1977, T.A. Weir acc. 77.7 (worker). PARATYPES: data as for holotype (5 workers); Wessel Is, Marchinbar I., 11°09'S, 136°42'E, vii.1993, sandstone slope, CCNT Survey M3/4 (2 workers); Wessel Is, Emu I., ix.1994, S. Morrison (3 workers); Rainbow Cliff nr Nhulunbuy, 12°12'S, 136°49'E, 1.v.2004, B. Hoffmann (worker). Type deposition: Holotype and 2 paratypes in ANIC; 2 paratypes each in BMNH, MCZC and QM; 1 paratype each in CASC, MHNG and WAMP.

Other Material. WA: Kimberley region, Cathedral NP, ix.1993 (S. Morrison) (w).

Description. *Worker:* Dimensions (holotype cited first): TL c. 6.85, 5.59-7.36; HL 1.75, 1.40-1.78; HW 1.34, 1.06-1.34; CI 76, 74-76; SL 2.09, 1.72-2.12; SI 156, 154-166; PW 1.22, 0.90-1.22; MW 0.53, 0.37-0.53; PMI 230, 212-259; MTL 2.34, 1.77-2.34 (13 measured).

Anterior clypeal margin with denticulate, median flange. Clypeus sinuate in profile, posteriorly rounding into moderately impressed basal margin. Frontal triangle poorly indicated. Frontal carinae sinuate with narrowly raised margins; central area relatively wide with distinct frontal furrow. Sides of head in front of eyes moderately convex towards mandibular bases; behind eyes, sides widely rounding into convex occipital margin. Eyes convex, in full face view exceeding lateral cephalic outline.

Ocelli lacking. Pronotal dorsum with humeri rounded; lateral margins converging towards distinctly impressed promesonotal suture. Mesonotum with margins strongly converging posteriorly; metanotal groove only weakly impressed. Propodeal margins terminating in rather slender, horizontal, divergent spines with tips weakly turned outwards. Petiole with anterior face straight, rounding dorsally into very slender, distinctly obliquely raised, divergent spines; posterior face of petiole distinctly swollen towards base.

Mandibles finely, longitudinally striate with numerous piliferous pits. Head and mesosoma closely reticulate-punctate; spines sculptured at bases, smooth and polished towards tips. Gaster finely shagreened.

Mandibles at mastitatory borders with numerous, curved, pale golden hairs and short, more appressed hairs towards bases. Anterior clypeal margin with several anteriorly projecting longer setae medially and fringe of short setae lining margin laterally. Head, including clypeus, mesosoma, petiole, gaster and appenages with numerous, mostly erect, relatively short hairs; head in full face view with numerous short hairs breaking lateral cephalic outline; antennal scapes with numerous, very short, semierect, bristle-like hairs. Gastral dorsum with abundant, somewhat longer, semierect, pale golden hairs; hairs distinctly longer and posteriorly directed on venter and around apex of gaster. Silvery, appressed pubescence in various densities over most of head and body surfaces; pubescence more pale golden on dorsum of first gastral tergite and somewhat laterally diffused into more silvery towards sides and on venter.

Vertex of head, dorsum of mesosoma, petiole, dorsum of gaster and spines, black; mandibles, front, sides and venter of head, sides of pronotum, venter of gaster and appendages medium to dark reddish-brown.

Sexuals and immature stages unknown.

Remarks. *Polyrhachis weiri* is characterised by the strongly posteriorly converging lateral margins of the promesonotum (PMI ca. 250).

Polyrhachis weiri is apparently restricted to the extreme north of the Northern Territory, including its adjacent islands, and to the Kimberley region of Western Australia. Nothing is known about the species' biology, but as the type series specimens were collected foraging on the ground it is reasonable to suggest that their nesting habit is terrestrial or subterranean.

POLYRHACHIS (HAGIOMYRMA) SCHENKII
SPECIES-GROUP

Polyrhachis (Hagiomyrma) bohemia sp. nov.
(Fig. 11A-B)

Etymology. After the type locality, Bohemia Downs, in the southern Kimberley region.

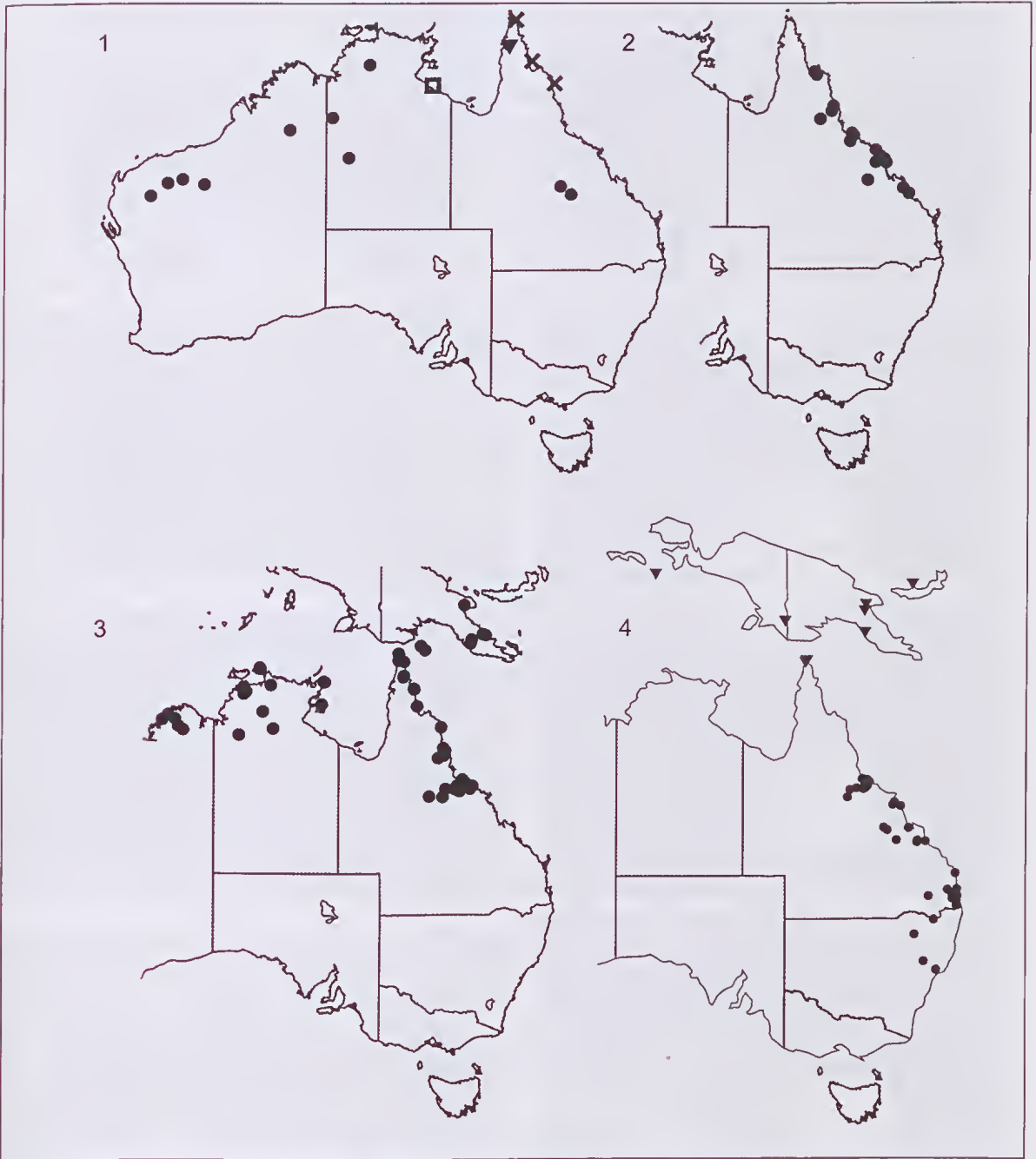
Material. HOLOTYPE: WA, Bohemia Downs Stn, 18°53'S, 126°14'E, v.2001, C. Palmer (worker). PARATYPES: data as for holotype (2 workers); Karijini NP, Fortescue Falls, 22°28'S, 118°33'E, 22.ix.1998, A.N. Andersen (worker). NT, 45 km NW of Katherine, 7.iv.1978, P.J.M. Greenslade (worker); Tanami Desert, 20.v.1986, P.J.M. Greenslade (worker); Bunda Stn, Victoria R. distr., v.1994, A.J. Fisher (1 dealate queen). QLD, Texas Cattle Stn, c. 30 km NNW of Jericho, vi.1999, K. Schneider #3/00 (2 workers); nr Alpha, Desert Uplands, v.2007, J. Bennett (1 worker). Type deposition: Holotype and 1 paratype in ANIC; 2 paratypes in QM; 1 paratype each in BMNH, MCZC and WAMP.

Other Material. WA: Pilbara region, 24.4 km S of Tom Price, Nanutarra-Wittendom Rd., 22°46'S, 117°30'E, 5.vi.2004 (M. Bulbert, N. Tartarnic & S. Lassau) (w); Ethel Ck, ii.1996 (F.K. Singarayar) (w); Barlee Ra., ix.1995 (S.van Leeuwin) (w) (CURT-JDM #900).

Description. *Worker.* Dimensions (holotype cited first): TL c. 6.65, 6.65-7.56; HL 1.62, 1.59-1.81; HW 1.27, 1.27-1.47; CI 78, 78-81; SL 1.93, 1.87-2.03; SI 152, 138-152; PW 1.22, 1.15-1.43; MW 0.72, 0.64-0.84; PMI 169, 155-181; MTL 2.28, 2.21-2.43 (9 measured).

Median flange of anterior clypeal margin with acute teeth medially, laterally delimited by acute angles. Clypeus with median, rather acute longitudinal carina; straight in profile. Frontal carinae with moderately raised margins; central area relatively wide with blunt, weakly elevated longitudinal carina. Sides of head in front of eyes weakly convex towards mandibular bases; behind eyes, sides rounding into convex

Revision of *Polyrhachis* (*Hagiomyrma*)



POLYRHACHIS (HAGIOMYRMA) SCHENKII SPECIES GROUP

- Map 1 ● *P. bohemia* ▼ *P. capeyorkensis* □ *P. isolata* × *P. injinooi*
 Map 2 ● *P. lachesis*
 Map 3 ● *P. schenkii*
 Map 4 ● *P. lydiae* ▼ *P. paxilla*

occipital margin. Eyes convex, clearly breaking lateral cephalic outline in full face view. Ocelli lacking. Pronotal dorsum distinctly wider than long; humeri widely rounded, weakly concave dorsally with moderately raised margins; lateral margins virtually parallel. Mesonotum with lateral margins weakly converging posteriorly; metanotal groove indistinct dorsally. Propodeal lateral margins divergent, terminating in mostly horizontal, subparallel, acute spines with tips weakly turned outwards in some specimens. Petiole with posterior face distinctly inflated towards base; dorsum armed with pair of horizontal, posteriorly curved, divergent spines.

Mandibles finely longitudinally striate with piliferous pits towards bases. Head, mesosoma and gaster closely reticulate-punctate. Spines distally smooth and highly polished.

Mandibles with medium length, curved, golden hairs near masticatory borders. Only a few, relatively short setae fringing anterior clypeal margin. Numerous relatively long, erect or variously curved, golden hairs arising from all dorsal body surfaces, some hairs almost as long as greatest diameter of eyes. Pale golden and silvery appressed pubescence in various densities over most of body; pubescence most dense and longest on gaster, with rich golden hue dorsally, silvery on gastral venter.

Head and mesosoma light to medium red; gaster distinctly darker, reddish-brown. Mandibular teeth dark brown, legs light to medium brown. Anterior clypeal margin, frontal carinae, lateral margins of mesosoma and spines narrowly bordered with brown.

Queen. Dimensions: TL 7.96; HL 1.78; HW 1.43; CI 80; SL 1.87; SI 131; PW 1.68; MTL 2.31 (1 measured).

Apart from sexual characters very similar to worker, except: pronotal humeri subangular. Mesoscutum almost as long as wide, anterior margin evenly rounded; dorsum flat in lateral view; median line distinct, parapsides rather flat; mesoscutellum flat, only marginally raised above dorsal plane of mesosoma. Propodeal spines distinctly shorter than in worker,

horizontal and parallel; propodeal dorsum sloping posteriorly into steeply oblique declivity. Sculpturation similar to worker, sides of mesoscutum and mesoscutellum distinctly finer, almost polished. Pubescence, pilosity and colour scheme virtually as in worker.

Male and immature stages unknown.

Remarks. With its bright red head and mesosoma and dark reddish-brown gaster, *P. bohemia* is a very characteristic and easily recognised species. Despite of its wide distribution across arid and semi-arid regions of northern tropical Australia, it appears to be rare. Like most other *Hagiomyrma* species, it nests in the ground.

Polyrhachis (Hagiomyrma) capeyorkensis sp.
nov.
(Fig. 11C-D)

Etymology. After the type locality Cape York Peninsula in Queensland.

Material. HOLOTYPE: QLD, Cape York Pen., Embley Ra. (Nth end), Rock Slab Hill, 24.x.1958, J.L. Wassell #381 (worker). PARATYPES: data as for holotype (15 workers). Type deposition: Holotype and 5 paratypes in ANIC; 4 paratypes in QM, 2 paratypes each in BMNH, MCZC and MHNG.

Description. *Worker.* Dimensions (holotype cited first): TL c. 7.31, 6.50-7.81; HL 1.78, 1.65-1.90; HW 1.47, 1.31-1.59; CI 82, 78-84; SL 2.03, 1.89-2.12; SI 138, 131-149; PW 1.31, 1.12-1.37; MW 0.75, 0.64-0.78; PMI 175, 175-184; MTL 2.40, 2.18-2.50 (16 measured).

Anterior clypeal margin with denticulate flange medially, flanked by acute denticles. Clypeus with distinctly raised median carina; sinuate in profile; basal margin moderately impressed. Frontal triangle distinct. Frontal carinae sinuate with weakly raised margins; central area rather flat with distinct frontal furrow. Sides of head in front of eyes only weakly convex, rounding into mandibular bases; behind eyes, sides widely rounding into convex occipital border. Eyes marginally exceeding lateral cephalic outline in full face view. Ocelli lacking. Pronotal humeri narrowly rounded with weakly raised margins. Promesonotal dorsum with lateral margins

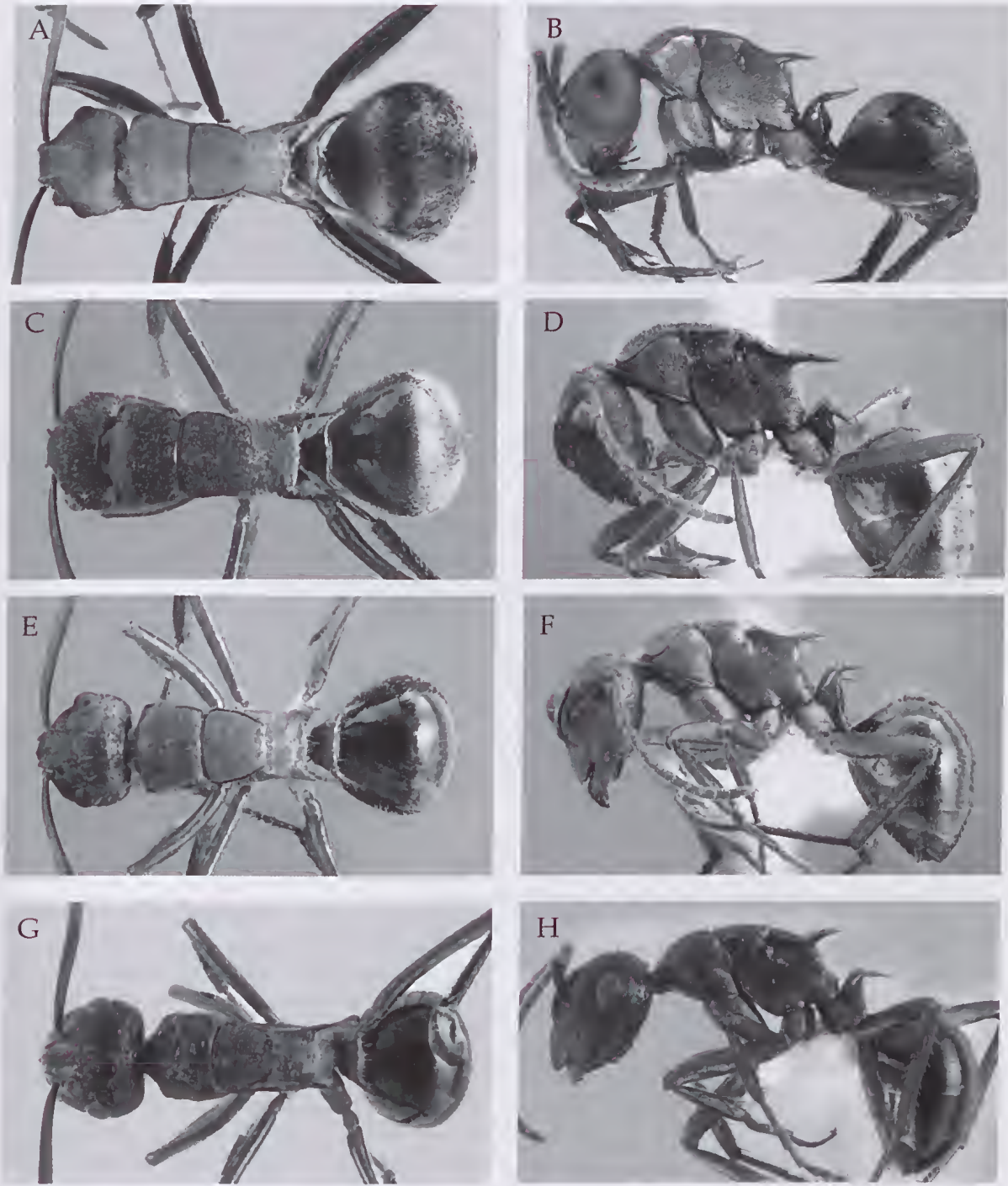


FIG. 11. *Polyrhachis* (*Hagiomyrma*) *schenkii* species-group - dorsal (left) and lateral (right) view. A-B, *P. bohemia* sp. nov.; C-D, *P. capeyorkensis* sp. nov.; E-F, *P. injinooi* sp. nov.; G-H, *P. isolata* sp. nov. (not to scale).

converging posteriorly into medially indistinct metanotal groove. Propodeal dorsum with margins weakly divergent, terminating in horizontal, subparallel, acute spines. Petiole with anterior face straight, posterior face convex, laterally bordered with distinct carina; dorsum with shallow notch medially, armed laterally with pair of divergent, weakly downturned, acute spines. Anterior face of first gastral segment higher than full height of petiole, straight, widely rounding onto dorsum.

Mandibles very finely longitudinally striate. Head and mesosoma very closely reticulate-punctate. Petiole and gaster finely shagreened, rather smooth and polished.

Mandibles with medium length, curved hairs at masticatory borders and shorter hairs along outer borders. Anterior clypeal margin with a few longer setae medially and fringe of shorter setae lining margin laterally. Short to medium length, erect, bristle-like hairs abundant over whole body, including appendages, with distinctly longer, more posteriorly directed hairs on gaster. Rather untidy, relatively long, appressed and semierect pubescence variously distributed over most body surfaces, more abundant and somewhat medially radiating on dorsum of gaster, where it forms a poorly defined midline.

Relatively dark, reddish-brown or rusty red with mandibles, clypeus, central area, anterior portion of pronotum, gaster and appendages distinctly lighter.

Sexuals and immature stages unknown.

Remarks. *Polyrhachis capeyorkensis* is similar to several species, but most notably to *P. lachesis*, which is also a characteristic reddish-brown colour and clothed with bristle-like hairs. It differs by its generally smaller size (HL 1.65-1.90 in *P. capeyorkensis* versus 1.84-1.96 in *P. lachesis*), the form of its pronotal humeri which lack distinctly dilated, rounded prominences and the vertical carina running along the lateral margin of the posterior face of the petiole that is lacking in *P. lachesis*.

Polyrhachis (Hagiomyrma) injinooi sp. nov.
(Fig. 11E-F)

Etymology. After the Injinoo Aboriginal Community, the traditional owners of the land on which the type locality of *P. injinooi* is located.

Material. HOLOTYPE: QLD, Cape York Pen., Bamaga, 10°53'S, 142°23'E, 24.iii.1987, R.K. Kohout acc. 87.80, QMT174514 (worker). PARATYPES: data as for holotype (44 workers). Type deposition: Holotype and most paratypes in QM; 2 paratypes each in ANIC, BMNH, CASC, MCZC, MHNG and MNHU.

Other Material. QLD: Cape York Pen., Leo Kitchen Camp, 17.x.1958 (J.L. Wassell) (1 w); 3 km SE of Annan R. x-ing, 15°33'S, 145°14'E, c. 40 m, 10.vi.1996 (RJK acc. 96.35) (4 w).

Description. *Worker:* Dimensions (holotype cited first): TL c. 7.11, 5.74-7.16; HL 1.75, 1.53-1.75; HW 1.36, 1.15-1.36; CI 78, 75-85; SL 1.87, 1.65-1.87; SI 137, 134-143; PW 1.17, 0.97-1.20; MW 0.56, 0.50-0.59; PMI 209, 190-209; MTL 2.25, 1.87-2.25 (15 measured).

Anterior clypeal margin with median denticulate flange, flanked by acute angles. Clypeus with distinctly raised median carina; virtually straight in profile (medially shallowly concave in some specimens), narrowly rounding into moderately impressed basal margin. Frontal triangle poorly indicated. Frontal carinae sinuate with weakly raised margins; central area flat with frontal furrow replaced anteriorly by distinct carina. Sides of head in front of eyes converging towards mandibular bases in virtually straight line; behind eyes, sides widely rounding into convex occipital margin. Eyes convex, in full face view marginally breaking lateral cephalic outline. Ocelli lacking; position of median ocellus indicated by shallow pit in cephalic sculpture. Antennal scapes distinctly flattened dorsally for most of length. Pronotal humeri narrowly rounded with indication of blunt angles in some specimens. Lateral margins of promesonotal dorsum narrowly raised, strongly converging posteriorly (PMI 190-209). Metanotal groove poorly defined medially. Propodeal dorsum with lateral margins divergent, terminating in weakly sinuate, acute spines. Anterior face of petiole straight, posterior face descending towards base in oblique, straight line; dorsum

concave medially, laterally rounding into horizontal, divergent, acute spines, with tips weakly curved outwards.

Head and mesosoma finely reticulate-punctate, with interspaces between reticulae, notably on dorsum of mesosoma, rather smooth and polished; spines, petiole and gaster very smooth, highly polished.

Mandibles with masticatory and outer borders with curved, rather short, golden hairs. Anterior clypeal margin with a few longer setae medially and fringe of short setae lining margin laterally. Antennal scapes and legs with numerous short, bristle-like hairs. Head, mesosoma, petiole and gaster with relatively long, mostly erect or suberect hairs, longest hairs more than half greatest diameter of eyes. Pubescence absent from most body surfaces, except for patches of short, closely appressed hairs on fore coxae, propodeal declivity and posterior face of petiole. Gaster with more abundant, somewhat longer, appressed pubescence on venter, very sparse on dorsum.

Reddish-brown to rusty-red. Mandibles, anterior clypeal margin, frontal carinae, occipital margin, lateral margins of mesosoma and outer borders of spines narrowly lined with black. Gaster and tarsi a shade darker.

Sexuals and immature stages unknown.

Remarks. *Polyrhachis injinooi* is very similar to *P. schenkii* and in addition to their virtually identical colour patterns, they both have a strongly posteriorly narrowed pro-mesonotal dorsum (PMI 190-209 in *P. injinooi* and 210-250 in *P. schenkii*). However, *Polyrhachis injinooi* is generally larger (HL 1.53-1.75 versus 1.31-1.56 in *P. schenkii*) and has somewhat flattened antennal scapes, distinctly longer body hairs and very sparse, closely appressed pubescence on the dorsum of gaster. In contrast, *P. schenkii* has antennal scapes that are virtually circular in cross section, distinctly shorter, bristle-like hairs and silvery or golden, appressed pubescence on the gastral dorsum. The eyes are also distinctly smaller in *P. injinooi* than in *P. schenkii*.

All known specimens of *P. injinooi* were collected foraging on the ground in open forest and savannah woodland, together with specimens of *P. schenkii*. Both species have similar nesting habits, building nests in the ground with the entrances hidden under pieces of wood or stones. However, the distribution of *P. injinooi* is much more restricted than that of *P. schenkii*, with the species known only from Cape York Peninsula as far south as Cooktown.

Polyrhachis (*Hagiomyrma*) *isolata* sp. nov.
(Fig. 11G-H)

Etymology. Derived from the neo-Latin word *isolatus*, meaning detached in reference to the species rather isolated occurrence on North Islet, West Island.

Material. HOLOTYPE: NT, North Islet, West I., Sir Edward Pellew Group, 15°32'S, 136°31'E, 20.iv.1976, J.E. Feehan (worker). Unique holotype in ANIC.

Description. *Worker:* Dimensions of holotype: TL c. 6.40; HL 1.72; HW 1.40; CI 81; SL 1.72; SI 123; PW 1.06; MW 0.53; PMI 200; MTL 2.03.

Mandibles with 5 blunt teeth of equal length. Anterior clypeal margin with median, denticulate flange. Clypeus with very strongly raised median carina; virtually straight in profile, posteriorly rounding into well impressed basal margin. Frontal triangle indistinct. Frontal carinae sinuate with moderately raised margins; central area relatively wide, with distinctly anteriorly raised, longitudinal ridge replacing frontal furrow. Sides of head in front of eyes converging towards mandibular bases in weakly convex line; behind eyes, sides widely rounding into convex occipital border. Eyes convex, clearly exceeding lateral cephalic outline in full face view. Ocelli lacking. Pronotal humeri only narrowly rounded with indication of blunt angles; pronotal dorsum widest just behind humeri; promesonotal suture distinct. Mesonotal lateral margins distinctly converging into laterally distinct, medially somewhat obscure metanotal groove. Propodeum with subparallel lateral margins terminating in sinuate, acute spines with tips curved outwards. Petiole armed with very slender, divergent, acute spines; posterior face of petiole obliquely descending towards base

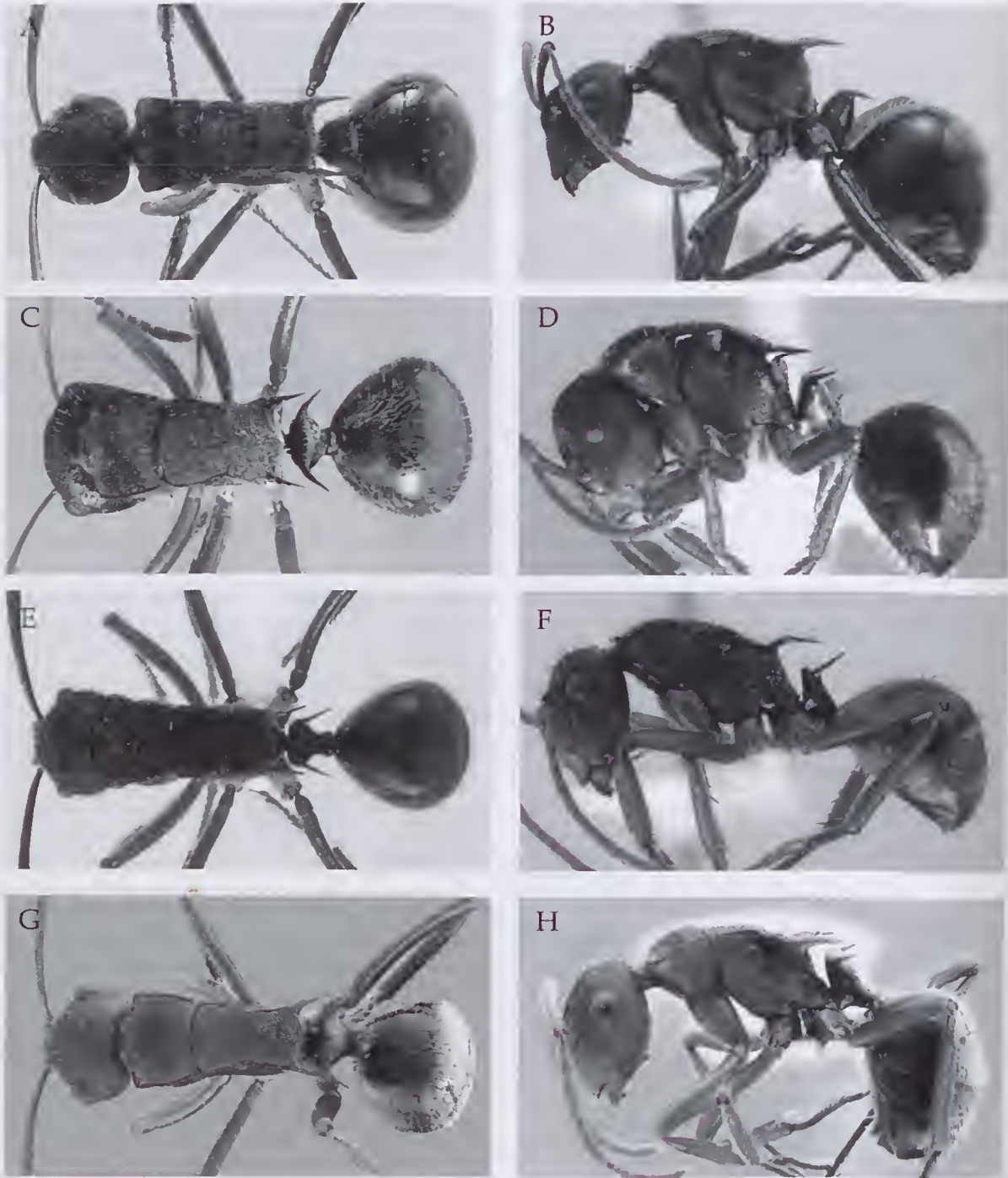


FIG. 12. *Polyrhachis* (*Hagiomyrma*) *schenkii* species-group – dorsal (left) and lateral (right) view. A-B, *P. lachesis* Forel; C-D, *P. lydiae* Forel; E-F, *P. paxilla* Fr. Smith; G-H, *P. schenkii* Forel (not to scale).

in straight line. Anterior face of first gastral tergite straight at base, rounding onto dorsum.

Mandibles at bases with very fine, rather flat, longitudinal striae and a few, shallow pits, rather polished towards masticatory borders. Clypeus reticulate-punctate, sculpture somewhat wrinkled and obliquely directed towards median carina. Head reticulate-punctate, reticulae more longitudinally organised on sides and between eyes and frontal carinae. Sculpturation on vertex of head and mesosomal dorsum forming rather irregular, more-or-less vermiculate pattern that is superimposed over irregularly spaced, shallow punctures, giving dorsum somewhat polished appearance. Sides of mesosoma and posterior face of petiole reticulate; spines, anterior face and dorsum of petiole rather smooth and polished; gaster highly polished.

Mandibles with a few, relatively short, golden hairs. Anterior clypeal margin with several, very short setae medially and laterally. Head, mesosoma and petiole with numerous, bristle-like, short and medium length hairs, many hairs fringing lateral outline of head; appendages, including antennal scapes, with very short to medium length, erect hairs. Gaster with abundant, posteriorly inclined, golden hairs, longest more than half greatest diameter of eyes. Very sporadic, short, appressed pubescence on sides of mesosoma, petiole, coxae and venter of gaster; pubescence virtually absent from all dorsal surfaces.

Distinctly light to medium reddish-brown; mandibular teeth and outer borders, anterior and basal margins of clypeus, frontal carinae, occipital margin, pronotal, mesonotal and mesopleural margins very narrowly lined with black.

Sexuals and immature stages unknown.

Remarks. With its distinct reddish-brown colour scheme and short, bristle-like pilosity, *P. isolata* resembles *P. lachesis* and *P. schenkii*. It differs from both in the outline of the pronotal humeri, the orientation of the propodeal spines and the body sculpturation. In *P. isolata* the lateral pronotal margins are narrowly rounded

with the humeri indicated by poorly defined blunt angles, and the pronotal dorsum widest near its midlength. The pronotal dorsum in both other species is distinctly widest across the humeri, with the lateral pronotal margins strongly posteriorly converging. In *P. lachesis*, the humeri are produced into distinctly dilated, rounded, dorsally shallowly concave prominences, while in *P. schenkii* the humeri are bluntly angular. In *P. isolata*, the propodeal spines in profile are oblique to the main axis of the body, while in the other two species they are more-or-less horizontal. The sculpturation of the head and mesosomal dorsum consists of a relatively fine, somewhat vermiculate-rugose pattern, superimposed over irregularly spaced, shallow and rather polished punctures. In both the other species the head and body are finely reticulate-punctate. The gaster in *P. isolata* and *P. lachesis* is very smooth, highly polished, while in *P. schenkii* the gastral dorsum is finely shagreened with relatively abundant, closely appressed pubescence.

Polyrhachis (*Hagiomyrma*) *lachesis* Forel, 1897
(Fig. 12A-B)

Polyrhachis lachesis Forel (in Emery), 1897:582 (footnote).
Syntype workers. Type locality: QLD, Mackay (G. Turner), MHNG, QM (examined).

Polyrhachis lachesis Forel. Emery, 1925:185 (combination in *P. (Hagiomyrma)*).

Other Material. QLD: Lakefield NP, 14°59'S, 144°15'E, 19-29.vi.1980 (RJK acc. 80.36) (w); ditto, White Lily Lagoon, 14 km N Lakefield, 19.vii.2002 (ANA) (w); Atherton (E.H. Bourne) (w); Archer Ck, nr Ravenshoe, 23.v.1935 (T. Greaves) (q); Undara Lava Lodge, 8.vii.2002 (ANA) (w); 14 km E of Mingela, 5.i.1977 (BBL) (w); Townsville, 18.x.1902 (F.P. Dodd) (w); Mt Elliot NP, Alligator Ck, 19°26'S, 146°57'E, 11.vi.1987 (RJK acc. 87.94) (w); Proserpine, Airport Drive, 20°29'17"S, 148°33'55"E, 7.xi.2007 (CJB) (w); Mt Blackwood NP, 21°02'S, 148°56'E, 14.iv.1981 (RJK acc. 81.100) (w); Surprise Ck, Mt Ossa-Seaforth Rd, 20°56'S, 148°53'E, 15.iv.1981 (RJK acc. 81.114) (w); Sarina Beach, 20 mi S of Mackay, 19.xii.1972 (BBL) (w); Britton Ra., 6 km NNE of Homevale, 21°23'S, 148°33'E, 1-6.iv.1975 (RJK accs 75.159, 160, 165) (w); Lords Table, W base, 22°39'35"S, 148°0'27"E, 8.iii.2006 (GBM) (w); 6 km N of Mt Archer, nr Rockhampton, 23°17'S, 150°34'E, 4.i.1979 (RJK acc. 79.18) (w); Rundle Ra., 36 km NW of Gladstone, 23°39'S, 150°58'E, 24-30.iii.1975 (RJK acc. 75.116, 143) (w); Callide Dam, nr Biloa, 19.xii.1972 (BBL) (w).

Description. *Worker.* Dimensions (syntypes cited first): TL c. 7.56-7.96, 7.06-8.21; HL 1.87-1.90, 1.84-1.96; HW 1.43-1.47, 1.40-1.53; CI 76-77, 76-79; SL 2.18-2.21, 2.14-2.34; SI 150-152, 148-155; PW 1.25-1.34, 1.22-1.34; MW 0.78, 0.69-0.81; PMI 160-172, 175-185; MTL 2.53-2.56, 2.50-2.74 (2+10 measured).

Anterior clypeal margin with acutely denticulate median flange, laterally flanked by widely obtuse teeth. Clypeus with distinct median carina; sinuate in profile, posteriorly rounding into moderately impressed basal margin. Frontal triangle indistinct. Frontal carinae sinuate with narrowly raised margins. Sides of head in front of eyes weakly convex towards mandibular bases; behind eyes, sides rounding into convex occipital margin. Eyes moderately convex, in full face view only reaching (in some modern specimens) or exceeding (in syntypes) lateral cephalic outline. Ocelli lacking. Pronotal humeri produced into dilated, dorsally shallowly concave, rounded prominences with distinctly raised margins; lateral margins behind humeri emarginate or notched, subparallel and rounding into laterally deeply impressed promesonotal suture. Mesonotum with lateral margins very narrowly raised, posteriorly converging into poorly indicated metanotal groove; propodeal margins terminating in slender, subparallel spines, obliquely elevated at bases and sinuate in side view. Petiole armed with pair of slender, divergent, acute spines with tips weakly curved outwards. Anterior face of first gastral tergite straight at base, widely rounding onto dorsum.

Mandibles longitudinally striate with pili-ferous pits. Clypeus closely punctate; vertex, sides of head and dorsum of mesosoma reticulate-punctate with sculpture forming weakly impressed vermiculate pattern, somewhat more distinct on vertex of head. Sides of mesosoma and posterior face of petiole finely reticulate. Anterior face of petiole, spines and gaster very smooth and highly polished.

Mandibles with curved, golden hairs at masticatory borders and shorter hairs along outer margins. Anterior clypeal margin with several setae medially and fringe of shorter

setae laterally. Dorsa of head, mesosoma, and petiole with numerous, short, bristle-like hairs, many hairs fringing lateral and dorsal outline of head; appendages, including antennal scapes, with very short, erect hairs. Gaster with abundant, posteriorly inclined, short golden hairs; hairs marginally longer around apex and on venter of gaster. Very sporadic, short, appressed, golden pubescence in various densities over most body surfaces; pubescence denser and silvery on propodeal declivity and venter of gaster.

Generally light to medium reddish-brown with vertex and mesosomal dorsum a shade darker; mandibular teeth, anterior margin of clypeus, frontal carinae, lateral margins of mesosoma, including spines, and mesopleural margins very narrowly lined with black.

Queen. Dimensions: TL c. 8.37; HL 1.81; HW 1.37; CI 76; SL 1.93; SI 141; PW 1.62; MTL 2.28 (1 measured).

Apart from sexual characters very similar to worker, except: pronotal humeri widely rounded with margins somewhat weakly, irregularly, notched. Mesoscutum marginally longer than wide, rather low anteriorly and flat in lateral view; median line distinct; parapsides flat. Mesoscutellum flat, marginally elevated above dorsal plane of mesosoma. Propodeal spines short, subparallel; petiolar spines shorter than in worker, obliquely elevated, divergent. Sculpturation distinctly coarser than in worker, notably on dorsa of mesoscutum and mesoscutellum, which are rather deeply rugose, without any regularity in pattern. Pilosity, pubescence and colour virtually identical to worker.

Male and immature stages unknown.

Remarks. *Polyrhachis lachesis* is very similar to *P. paxilla*, with most distinguishing characters given under the latter species. It is also relatively close to *P. schenkii* and it seems that Forel originally considered *P. lachesis* to be a subspecies of the latter (the original labels on syntype specimens read '*P. Schenki* For. r. *Lachesis* For.'). However, they are easily separated by differences in their size (HL 1.31-1.56 in *P. schenkii* versus 1.84-1.96 in *P. lachesis*),

the shape of the promesonotal dorsum (PMI 210-250 in *P. schenckii* versus 160-185 in *P. lachesis*) and the outline of the pronotal humeri that, in *P. lachesis*, are produced into dilated, dorsally shallowly concave, rounded prominences (Fig. 12A), while they are narrowly rounded or subangular in *P. schenckii* (Fig. 12G).

Polyrhachis lachesis inhabits open eucalypt forests and savannah woodlands, seemingly preferring bare ground without a grass cover as their nesting sites. It is not a very common species which occurs from Lakefield on Cape York Peninsula, south to about Gladstone.

***Polyrhachis* (*Hagiomyrma*) *lydiae* Forel, 1902**
(Fig. 12C-D)

Polyrhachis schencki r. *lydiae* Forel, 1902:523. Syntype workers, queen. Type locality: QLD, Mackay (G. Turner), MHNG, QM (examined).

Polyrhachis schencki subsp. *lydiae* Forel, Emery, 1925:185 (variant spelling, combination in *P. (Hagiomyrma)*).

Polyrhachis lydiae Forel, Kohout, 1988:434 (raised to species).

Other Material. QLD: 6 km W of Mingela, 7.i.1977 (BBL) (w); 14 km E of Mingela, 5.i.1977 (BBL) (w); 40 km N of Townsville, 11.i.1977 (BBL) (w); Turtle Rock, Harvey Ra., 24.ix.1995 (SKR #20) (w); Townsville (G.F. Hill) (w); 40 km N of Charters Towers, 4.i.1977 (BBL) (w); Mt Elliot NP, Alligator Ck, 19°26'S, 146°57'E, 11.vi.1987 (RJK acc. 87.93) (w); 4 km S of Calcium, 19°41'S, 146°50'E, c. 150 m, 18.vii.1977 (RWT acc. 77.429) (w); Toomba, 19°58'43"S, 145°35'25"E, 14.ii.2007 (CJB) (w); Lords Table, W base, 22°39'35"S, 148°0'27"E, 8.iii.2006 (GBM) (w); ditto, SE base, 22°40'29"S, 148°1'13"E, 13-14.iii.2006 (CJB) (w); Scotts Peak, SE base, 22°51'35"S, 148°13'41"E, 9.iii.2006 (S. Wright, CJB) (w); Blackwater, Bowen Basin mines, iv.1994 (A.V. Spain) (w); 5 km E of Pentland, 3.i.1977 (BBL) (w); Calen, 17.xii.1972 (BBL) (w); Mackay, vi.1899 (E. Turner) (w); Eungella NP, Finch Hatton Gorge, 21°04'S, 148°38'E, 7-13. iv.1975 (RJK acc. 75.171) (w); ditto, 23.x.1995 (SKR #60) (w); Lorna Vale, nr Marlborough, 22°43'S, 149°46'E, 8.iv.1981 (RJK acc. 81.42) (w); 5 km NbyE of Mt Morgan, 23°37'S, 150°24'E, 27.x.1976 (RWT & TAW acc. 76.250) (w); Mt Morgan, 23°43'S, 150°22'E, 15.vi.1972 (S.A. Harrington) (w); Rundle Ra., 36 km NW of Gladstone, 23°39'S, 150°58'E, 24-30.iii.1975 (RJK acc. 75.116) (w); Cooloola SF, Rainbow Bch, 25°57'S, 153°05'E, 18-25.i.1975 (RJK acc. 75.43) (w); Darling Downs, E of Cecil Plains, 17.v.1966 (K.E. Lee) (w); Somerset Dam, 27°06'S, 152°33'E, 12.i.1975 (RJK accs 75.15, 27, 33) (w); Bribie I., Woorim, 27°04'S, 153°12'E, 28.xii.1976 (RJK acc. 76.114) (w); Boondall Wetlands, 27°20'21"S, 153°4'27"E, 11.xi.2003 (also 20.ii.2004) (QM Party) (w); Brisbane, 3.viii.1915 (H. Hacker) (w); Gold Ck Reservoir,

27°27'53"S, 152°52'32"E, 4.xi.2003 (QM Party) (w); Chelsea Rd Bushlands Res., 27°28'58"S, 153°11'15"E, 10.xi.2003 (QM Party) (w); Chapel Hill, Cassandra St, 27°29'43"S, 152°57'20"E, 15-16.iii.2003 (CJB) (w); Brisbane, Ithaca Ck, 18.ix.1979 (BBL) (w); Redlands, Hilliards Ck, nr Weippin Rd, 27°32'6"S, 153°14'54"E, 19-28.i.2009 (BAAM/QM Party) (♀); Karawatha For., 27°37'24"S, 153°4'38"E, 25-26.v.2005 (CJB) (w); Illaweena St, Drewvale, 27°38'39"S, 153°3'47"E, 17.ii.2004 (QM Party) (w); 0.8km SE of Spring Mtn, 27°43'36"S, 152°52'58"E, 19.iii.2005 (QM Party) (w); c. 7 km E of Jimboomba, 27°50'S, 153°06'E, 18.v.1975 (RJK acc. 75.190) (w); Darlington Ra., Cedar Ck, 27°54'S, 153°11'E, 10-15.ix.1974 (RJK acc. 74.84) (w); Mt Devlin, 7 km NE of Maryvale, 28°01'S, 152°17'E, 6-24.xi.1978 (RJK acc. 78.8) (w); Lamington NP, Binna Burra, 28°12'S, 153°11'E, 1.i.1974 RJK acc. 74.2) (w); Texas Caves, 28°56'S, 151°28'E, 14.viii.1975 (RJK acc. 75.193) (w). NSW: Mt Warning, 30.viii.1965 (BBL) (w); Anthony Pik, Upper Hunter Valley, 32°22'S, 150°56'E (ANA) (w); Raymond Terrace, 20.viii.1976 (BBL) (w).

Description. *Worker:* Dimensions (syntypes cited first): TL c. 5.80-6.50, 5.64-6.65; HL 1.55-1.70, 1.47-1.75; HW 1.22-1.37, 1.14-1.42; CI 79-81, 76-83; SL 1.50-1.65, 1.50-1.78; SI 117-123, 120-134; PW 1.14-1.22, 1.00-1.25; MW 0.69-0.70, 0.59-0.78; PMI 165-174, 160-174; MTL 1.60-1.85, 1.65-2.03 (6+30 measured).

Anterior clypeal margin with obtusely denticulate, median flange. Clypeus with posteriorly elevated, median carina; distinctly sinuate in profile and rounding into well impressed basal margin. Frontal triangle poorly indicated. Frontal carinae sinuate with moderately raised margins; central area rather flat with distinct frontal furrow. Sides of head in front of eyes converging towards mandibular bases in virtually straight line; behind eyes, sides rounding into weakly convex occipital margin. Eyes convex, in full face view clearly exceeding lateral cephalic outline. Ocelli lacking. Pronotal humeri rounded with margins weakly raised anteriorly; pronotal dorsum widest near midlength; lateral margins converging into distinctly impressed promesonotal suture. Mesonotum with lateral margins converging posteriorly; metanotal groove indistinct. Propodeal margins divergent, terminating in relatively short, horizontal, acute spines, with tips curved weakly outwards. Petiole with anterior face straight, posterior face descending towards base in weakly convex line; dorsum

armed with horizontal, divergent, acute spines. Anterior face of first gastral tergite straight at base, widely rounding onto dorsum.

Mandibles longitudinally striate at bases, rather smooth with piliferous pits towards masticatory borders. Head, mesosoma and petiole closely reticulate-punctate. Spines weakly rugose, tips smooth and polished. Gaster very finely shagreened, polished.

Mandibular masticatory and outer borders with a few curved, golden hairs. Anterior clypeal margin with a few anteriorly directed setae medially. Whole body, including appendages, with numerous, rather short, mostly erect, bristle-like, golden hairs, somewhat longer and posteriorly directed on gaster. Appressed, rather diluted, pale golden or silvery pubescence on head and mesosoma; more abundant, somewhat longer, medially radiating golden pubescence with distinct reddish hue on dorsum of gaster; pubescence much diluted on gastral venter.

Mandibles, clypeus, condylae, sides of head at mandibular bases, outer borders of frontal carinae, anterior and lateral pronotum, appendages, including coxae, and subpetiolar process mostly light or medium reddish-brown; clypeus and central area with somewhat purplish hue. Pronotal dorsum, except anteriorly, mesosoma and petiole distinctly metallic green. Gaster medium reddish-brown.

Queen. Dimensions (syntypes cited first): TL c. 6.90-7.00, 7.21-7.51; HL 1.70-1.75, 1.65-1.75; HW 1.35, 1.29-1.35; CI 77-79, 77-79; SL 1.55-1.60, 1.55-1.62; SI 115-119, 115-125; PW 1.50-1.55, 1.50-1.59; MTL 1.80-1.85, 1.80-1.87 (2+6 measured).

Apart from sexual characters very similar to worker, except: mesoscutum virtually as wide as long, anterior margin evenly rounded in dorsal view; relatively low with flat dorsum in lateral view; median line distinct; parapsides flat. Mesoscutellum only marginally elevated above dorsal plane of mesosoma. Propodeal spines very short, subparallel. Petiolar spines short, divergent. Sculpturation identical to worker; pilosity shorter with appressed pubescence generally more abundant. Colour scheme virtually identical to

that in worker, with additional reddish-brown patches on meso- and metapleura.

Males and immature stages present in the QM collection.

Remarks. *Polyrhachis lydiae* is a very easily recognised species due to its characteristic colour pattern. The metallic green colour is unusual and, apart from *P. lydiae*, occurs in only one another Australian *Polyrhachis* species, *P. hookeri* Lowne of the subgenus *Chariomyrma*. However, the combination of metallic green and reddish-brown in *P. lydiae* is unique.

Polyrhachis lydiae is a relatively common species, frequently encountered in open eucalypt forests and savannah woodlands. They build nests in the ground with their entrances usually hidden under stones or tufts of grass. *Polyrhachis lydiae* ranges along the eastern Australian seaboard from about Townsville in north Queensland to just north of Newcastle in New South Wales.

Polyrhachis (Hagiomyrma) paxilla Fr. Smith,
1863
(Fig. 12E-F)

Polyrhachis paxillus Fr. Smith, 1863:17. Holotype worker. Type locality: INDONESIA, Martabello (= Matabello I.) (A.R. Wallace), OXUM (examined).

Polyrhachis paxilla Fr. Smith, Emery, 1925:188 (combination in *P. (Chariomyrma)*); Kohout, 1988:435 (combination in *P. (Hagiomyrma)*).

Polyrhachis lachesis ssp. *maeandrifera* Emery, 1897:582. Holotype worker. Type locality: NEW GUINEA, Paumotu R. (= Angabanga R.) (L. Loria), MSNG (examined). Synonymy by Kohout (1988).

Other Material. INDONESIA, IRIAN JAYA: (as New Guinea: Neth.), Eramboe, 07°56'S, 140°56'E, 80 km ex Merauke, 29.i.1960 (T.C. Maa) (w). PAPUA NEW GUINEA: Morobe Prov., nr Vampit, c. 50 m, 06°45'S, 146°40'E, 24-27.viii.1984 (RJK acc 84.368) (w); Bulolo, 16.xii.1967 (BBL) (w). BISMARCK ARCHIPELAGO, NEW BRITAIN, Linga Linga, W of Willaumez Pen., 11.iv.1956 (L.J. Gressitt) (w). AUSTRALIA, QLD: Cape York Pen., Lockerbie Scrub, 23-27.iv.1973 (GBM) (w); ditto, 10°46'S, 142°29'E, 19-23.iii.1987 (RJK accs 87.18, 63) (w); Bamaga, 10°53'S, 142°23'E, 18.iii.1987 (RJK acc. 87.7) (w).

Description. *Worker*: Dimensions (holotype cited first): TL c. 8.92, 7.36-8.92; HL 2.17, 1.90-2.17; HW 1.66, 1.47-1.66; CI 76, 75-79; SL 2.47, 2.12-2.47; SI 149, 141-149; PW 1.54, 1.31-1.54; MW 0.86, 0.78-

0.86; PMI 179, 159-180; MTL 3.02, 2.50-3.02 (10 measured).

Anterior clypeal margin with obtusely denticulate median flange. Clypeus with median carina distinctly raised towards basal margin; strongly sinuate in profile. Frontal triangle distinct. Frontal carinae sinuate with margins distinctly raised at midlength. Sides of head in front of eyes converging towards mandibular bases in weakly convex line; behind eyes, sides widely rounding into convex occipital margin. Eyes moderately convex, in full face view only marginally breaking lateral cephalic outline. Ocelli lacking. Pronotal dorsum with raised lateral margins; pronotal humeri distinctly dilated, forming rounded or bluntly angular, laminate prominences. Mesonotum with posteriorly converging lateral margins; metanotal groove indistinct medially. Propodeal dorsum with margins subparallel, terminating in slender, acute spines, obliquely elevated from bases, sinuate at midlength, tips curved outwards. Petiole with anterior face terminating dorsally in jagged, transverse ridge, merging laterally into slender, acute, divergent spines with bases situated well below apex of dorsal convexity.

Mandibles longitudinally striate with piliferous pits. Clypeus finely punctate. Dorsa of head, mesosoma and petiole with characteristic vermiculate-rugose sculpturation; sides of mesosoma more finely reticulate. Gaster finely shagreened.

Mandibles with numerous golden, curved hairs at masticatory borders and shorter appressed hairs towards mandibular bases. All body surfaces, including outline of head and appendages, with numerous bristle-like, mostly erect hairs, shorter than maximum diameter of eyes. Hairs dark brown to black on dorsum, golden to golden-brown and generally shorter on ventral surfaces. Silvery, appressed pubescence in various densities over most body parts, denser with distinct rusty tint on gastral dorsum.

Black or very dark reddish-brown; mandibles, clypeus, antennae and spines medium to dark reddish-brown. Legs, including coxae distinctly

lighter, medium reddish-brown. Apex and venter of gaster blotched reddish-brown.

Queen. Dimensions: TL c. 8.77; HL 2.03; HW 1.47; CI 72; SL 2.28; SI 155; PW 1.78; MTL 2.81 (1 measured).

Apart from sexual characters very similar to worker, except: sides of head converging towards mandibular bases in straight line; eyes distinctly more convex, in full face view clearly exceeding lateral cephalic outline. Humeral angles of pronotum with narrowly rounded and weakly raised margins; mesoscutum distinctly wider than long with anterior margin widely rounded; median line distinct, parapsides flat. Anterior margin of mesoscutum in profile widely rounding onto virtually flat dorsum; mesoscutellum marginally elevated above dorsal plane of mesoscutum, weakly convex. Propodeal and petiolar spines shorter than in worker. Sculpturation, pilosity, pubescence and colour identical to worker.

Male unknown; single pupa in QM spirit collection.

Remarks. With its characteristic, vermiculate-rugose sculpturation, *P. paxilla* is easily recognised. It bears some similarity to *P. lachesis* and Forel (1897) redescribed it as *P. lachesis maeandrifera*. It is apparently a lignicolous species with a single nest collected from a dry, hollow bamboo internode. The nest was located on the edge of a small patch of lowland rainforest within swampy grassland in Papua New Guinea, a similar habitat to that on Cape York Peninsula where the Australian specimens of *P. paxilla* were collected. They were found foraging together with *P. bamaga* Kohout, a species of similar appearance and almost identical body sculpturation that belongs to the recently erected subgenus *Hirtomyrma* Kohout.

Polyrhachis (*Hagiomyrma*) *schenkii* Forel, 1886
(Fig. 12G-H)

Polyrhachis schenkii Forel, 1886:198. Syntype workers.
Type locality: Australia, QLD, Torres Strait, Darnley I., MHNG (examined).

Polyrhachis schenki Forel, 1902:523. Variant spelling.

Polyrhachys (*Hedomyrma*) *schenkii* Forel. Santschi, 1920:569
(variant spelling, combination in *P. (Hedomyrma)*).

Polyrhachis schencki Forel. Emery, 1925:185 (variant spelling, combination in *P. (Hagiomyrma)*).

Polyrhachis schenkii Forel. Dorow, 1995:26.

Polyrhachis schenckii Forel. Bolton, 1995:356 (variant spelling).

Other Material. Papua New Guinea: Morobe Prov., Aztera Ra., Bubia Research Stn, 06°40'S, 146°55'E, 23-26.viii.1984 (RJK acc. 84.357) (w). Northern Prov., Oro Bay, 6.i.1973 (PMR) (w); Buna, 30.iv.1972 (PMR) (w); Girua, 4.xii.1971 (PMR) (w); Popondetta, 18.xii.1972 (PMR) (w). Central Prov., 3 km WSW of Sogeri, c. 500 m, 09°26'S, 147°23'E, 4 ix 1984 (RJK acc. 74.430) (w). WA, Kimberley area, Old Doongan, 15°19'S, 126°32'E, 2.viii.1975 (I.F.B. Common & M.S. Upton - Drysdale Survey 1975 Base) (w); Mitchell Plateau, 6 km E of Surveyor's Pool Camp, 14°38'S, 125°46'E, 4.v.1992 (S.O. Shattuck #33892-6) (w); 1.5 km W of King Edward R. x-ing, 14°53'S, 126°12'E, 5.v.1992 (S.O. Shattuck #3413-9) (w); Boongarree I., 15°05'S, 125°11'E, vi.1988 (ANA) (w). King Edward R., 15°09'S, 126°09'E, vi.1988 (ANA) (w). NT: Coburg Pen., Black Point, 11°09'S, 132°09'E, 31.i.1977 (E.D. Edwards) (w); ditto, 15-23.ii.1977 (TAW) (w); Coburg Pen., Cai man Ck, 11°15'S, 132°13'E, 19.ii.1977 (TAW) (w); Gove, Nhulumbuy, 1.xi.1972 (RWT acc. 72.824) (w); Obiri Rock, 12°25'S, 132°57'E, 7.vi.1973 (RWT acc. 73.473) (w); Gove Pen., 24-29.vi.1982 (JDM) (w); Grootte Eylandt, vi.1982 (JDM) (w); Larrimah, 15°35'S, 133°12'E, 16.vii.1981 (BBL) (w); Howard Springs, 12°27'S, 131°03'E, 14.vii.1981 (BBL) (w); ditto, 5.iii.1991 (BDH) (w); Lake Bennett, 20.ii.1992 (BDH); Berry Springs, 7.ii.1993 (BDH) (w); Virginia, E of Darwin, 11.i.1993 (BDH) (w); Batchelor, 22.v.1993 (BDH) (w); Katherine Gorge, 21.x.1977 (P.J.M. Greenslade) (w); Nitmiluk (Katherine) NP, Dunlop Swamp, 10.iv.1993 (BDH) (w). QLD: Torres Strait, Murrav I., 09°55'S, 144°05'E, vii.1974 (H&C) (w); Prince of Wales I., 10°40'S, 142°10'E, 6-15.ii.1975 (H&C #POW20) (w); Horn I., 2-8.xii.1986 (J. Gallon) (w); Badu I., 18.ii.1984 (J.H. Sedláček) (w); Cape York Pen., Lake Wicheura, 10°46'S, 142°34'E, 23.x.1993 (P. Zborowski & D. Rentz) (w); Heathlands, 11°45'S, 142°35'E, v.1993 (P. Zborowski & J. Lyon) (w); Bertie Ck, 11°50'S, 142°30'E, 21.x.1992 (P. Zborowski & T. Weir) (w); Iron Ra., 16.viii.1971 (R. Jenkins) (w); ditto, Mt Lamond, 12°44'S, 143°18'E, 9-15.vi.1971 (RWT & JEF acc. 71.257) (w); ditto, 12°43'S, 143°18'E, 1-3.vii.1976 (P. Filewood) (w); Silver Plains, Station Ck, 21.vi.60 (C.N. Smithers) (w); Cooktown, 20.vi.1955 (J. Beauglehole) (w); Davies Ck Rd, nr Mareeba, 3.viii.1975 (BBL) (w); Mareeba, 7.vi.1937 (T. Greaves) (w); Tinaroo Dam, 3.viii.1975 (BBL) (w); c. 8 km SW of Mt Garnet, 750 m, 3.vii.1971 (RWT & JEF) (w); Millstream NP, nr Ravenshoe, 6.viii.1975 (BBL) (w); 3.2km SE of Fanning R. Hmsd, 19°45.1'S, 146°27.1'E, 9.xii.2006-10.ii.2007 (S. Wright) (♀); 4 km NE by N of Mingela, c. 220m, 19°53'S, 146°38'E, 18.vii.1977 (RWT acc. 77.411) (w); 14 km E of Mingela, 5.i.1977 (BBL) (w, ♀); Townsville, 4.viii. & 21.x.1902 (F.P. Dodd) (w); Flinders Hwy - 7 Mile Ck xing, 19°50.3'S, 146°43.6'E, 9.ii.2007 (CJB) (w); Toomba, 19°58.1'S, 145°34.8'E

Gregory Dev. Rd - Sardine Ck xing, 20°06.7'S, 146°26.5'E, 7-19.xii.2006 (GBM, DJC) (w); "Myola", 20°04.3'S, 146°28.0'E, 29.ix.-17.xii.2006 (QM Party) (w); Rochford Scrub, 20°07.0'S, 146°37.8'E, 10.xii.2006 (S. Wright) (w); 18 km N of Charters Towers, 4.i.1977 (BBL) (w, ♀); 10 km SW of Giru, 7.iii.1980 (BBL) (w); Porcupine Gorge NP, 20°30'S, 144°25'E, 13.v.1980 (BBL) (w); 5 km E of Pentland, 3.i.1977 (BBL) (w, ♀); 25 km SW of Ayr, 15.viii.1979 (BBL) (w); 60 km S of Ayr, 14.viii.1975 (BBL) (w).

Description. *Worker.* Dimensions (syntype cited first): TL c. 5.2, 4.99-6.50; HL 1.45, 1.31-1.56; HW 1.15, 0.97-1.20; CI 79, 74-79; SL 1.55, 1.43-1.78; SI 135, 135-159; PW 1.00, 0.81-1.06; MW 0.40-0.47; PMI 210-250; MTL 1.65, 1.53-2.00 (1+36 measured).

Anterior clypeal margin with emarginate, irregularly denticulate, median flange, flanked by acute angles. Clypeus with distinct median carina; sinuate in profile. Frontal triangle poorly indicated. Frontal carinae sinuate with weakly raised margins; central area rather flat with weakly impressed frontal furrow. Sides of head in front of eyes converging towards mandibular bases in almost straight line; behind eyes, sides rounding into convex occipital margin. Eyes relatively large, convex, in full face view clearly exceeding lateral cephalic outline. Ocelli lacking. Pronotal humeri narrowly rounded or bluntly angular (distinctly angular in some PNG specimens). Lateral margins of promesonotal dorsum with very narrowly raised margins, strongly converging posteriorly. Metanotal groove weakly impressed. Propodeal dorsum with lateral margins terminating in horizontal, divergent, acute spines. Petiole with posterior face sloping in even, moderately convex line; dorsum armed with horizontal, widely divergent, acute spines. Anterior face of first gastral segment higher than full height of petiole, evenly rounding onto dorsum.

Mandibles very finely, longitudinally striate with piliferous pits. Head, mesosoma and petiole distinctly reticulate-punctate; spines smooth and polished. Gaster shagreened.

Mandibular masticatory and outer borders with numerous, yellowish or golden, curved hairs. Anterior clypeal margin with a few longer setae medially and short setae fringing margin laterally. Numerous, mostly short,

erect hairs on all body surfaces, including antennal scapes and outline of head in full face view; rather longer, somewhat posteriorly directed hairs on gaster. Rather diluted, closely appressed, golden pubescence over most body surfaces; pubescence usually more abundant, somewhat longer and mostly pale golden or silvery on dorsum of gaster, but almost lacking in some specimens.

Yellowish- to rusty-red, with distinctly darker patches variously on vertex of head, dorsum of mesosoma and petiole. Mandibles with teeth dark reddish-brown; spines light reddish-brown. Anterior clypeal margin, frontal carinae and lateral margins of mesosoma narrowly lined with dark brown or black. Appendages, including coxae, light to medium reddish-brown; tarsi a shade darker. Gaster mostly dark, reddish-brown.

Queen. Dimensions: TL c. 6.85-7.16; HL 1.56-1.59; HW 1.18-1.22; CI 74-78; SL 1.56-1.59; SI 128-135; PW 1.40-1.47; MTL 1.81-1.84 (6 measured).

Apart from sexual characters, very similar to worker except: pronotal humeri narrowly rounded or bluntly angular in some specimens; mesoscutum as wide as long, lateral margins converging anteriorly into moderately rounded anterior margin; median line weakly indicated; parapsides flat; mesoscutum in profile widely rounded onto flat dorsum. Mesoscutellum flat, only marginally raised above dorsal plane of mesosoma. Propodeum armed with pair of horizontal, acute spines; dorsum rounding medially into virtually vertical declivity. Petiole with posterior face weakly convex; spines rather short, widely divergent. Sculpturation, pilosity, pubescence and colour identical to worker.

Males and immature stages in ANIC spirit collection.

Remarks. *Polyrhachis schenkii* is easily recognised by its small size, light-red or reddish-brown colour and the strongly posteriorly converging lateral margins of the promesonotal dorsum. It is one of the most widely distributed *Hagiomyrma* species, ranging from Papua New Guinea south across the Torres Strait to northern

Australia. *Polyrhachis schenkii* forms a number of variable populations. The pronotal humeri are very narrowly rounded or bluntly angular in Australian specimens, while they are distinctly angular in most specimens from Papua New Guinea. The antennal scapes of specimens from the Northern Territory are somewhat longer than those of other populations (SI 151-159 in specimens from the Northern Territory versus 138-149 in Queensland and PNG specimens). Also, the posterior face of the petiolar node is rather evenly convex in specimens from New Guinea and Cape York Peninsula, while in specimens from north Queensland and the Northern Territory the posterior face is uneven, with the base somewhat broader and swollen in lateral view. However, when specimens across the whole distribution are compared, no other significant differences are evident and I consider them to represent a single, albeit variable, species.

Polyrhachis schenkii is rather common in suitable localities in open eucalypt forest and savannah woodland. It is a ground nesting species with nest entrances usually hidden under a stone, piece of wood or a tuft of grass.

POLYRHACHIS (HAGIOMYRMA)
TRAPEZOIDEA SPECIES-GROUP

Polyrhachis (Hagiomyrma) darlingtoni sp. nov.
(Fig. 13A-B)

Etymology. Named in honour of the late Philip J. Darlington, former professor at Harvard University, Cambridge and eminent entomologist and biogeographer, who collected many *Polyrhachis* species and other insects during the 1932 and 1956-1958 Australia Harvard Expeditions.

Material. HOLOTYPE: QLD, Cape York Pen., McIlwraith Ra., 28 km NNE of Coen, 13°43'S, 143°19'E, 400 m, 25.viii.2004, *Araucaria* forest, under stone, P.S. Ward #15330 (worker). PARATYPES: data as for holotype (11 workers); ditto, 13°46'S, 143°19'E, c. 395 m, 24.vii.1977, low mixed forest, R.W. Taylor acc. 77.576 (9 workers); ditto, Lankelly Ck, vi.1932, P.J. Darlington, Aust. Harvard Exp. (14 workers). Type deposition: Holotype and 6 paratypes in ANIC; 4 paratypes each in MCZC and QM, 2 paratypes each in AMNH, BMNH, CASC, MHNG and NMNH.

Description. *Worker.* Dimensions (holotype cited first): TL c. 11.79, 10.50-11.79; HL 2.68, 2.52-2.68; HW 1.90, 1.79-1.96; CI 71, 71-73; SL 3.58, 3.28-3.58; SI 188, 180-189; PW 1.56, 1.46-1.66; MW 1.09, 1.06-1.16; PMI 143, 142-152; MTL 4.33, 4.08-4.43 (9 measured).

Mandibles with 5 teeth, progressively reducing in length towards base. Anterior clypeal margin with median, shallowly emarginate, bluntly denticulate flange, laterally flanked by rather obtuse angles. Clypeus with median longitudinal carina; distinctly sinuate in profile, posteriorly rounding into impressed basal margin. Frontal carinae sinuate with moderately raised margins; central area with rather flat frontal furrow. Sides of head in front of eyes converging towards mandibular bases in very weakly convex line; behind eyes, sides rounding into occipital margin. Eyes convex, in full face view marginally breaking lateral cephalic outline. Ocelli lacking, positions indicated in some specimens by shallow pits in cephalic sculpture. Pronotal humeri narrowly rounded; dorsum almost quadrate with lateral margins very weakly converging anteriorly in some specimens and somewhat irregularly notched before their midlength; promesonotal suture deeply impressed. Mesonotum with lateral margins converging posteriorly towards distinct metanotal groove. Propodeal dorsum with lateral margins terminating in subparallel, somewhat sinuate, acute spines. Petiolar node markedly broad and low in lateral view, with anterior face rounding onto flat, strongly posteriorly descending triangular dorsum; spines very short, weakly divergent, bases situated well below apex of dorsal convexity. Anterior face of first gastral segment widely rounding onto dorsum.

Mandibles finely longitudinally striate with numerous piliferous pits. Head and mesosoma finely reticulate-punctate, vertex of head and pronotal dorsum somewhat polished, mesonotum and propodeum opaque; tips of spines highly polished. Gaster shagreened.

Mandibles with numerous, semierect, curved, golden hairs. Medium length, erect hairs on clypeus, along frontal carinae and on vertex, numerous erect hairs fringing outline of head in full face view. Long, erect or semierect, rather abundant, golden hairs on dorsum of

mesosoma, coxae, venter of femora, petiole and gaster, most hairs as long as greatest diameter of eyes. Silvery appressed pubescence in various densities over most body surfaces, except vertex of head and pronotal dorsum where it is golden and sporadic; distinctly medially radiated pubescence with brassy tint abundant on mesonotal dorsum. Gastral dorsum with pubescence virtually hiding underlying sculpturation, golden with reddish hue along midline, silvery on sides and venter of gaster.

Black throughout with only mandibular teeth and condylae dark reddish-brown.

Sexuals unknown. Immature stages (larva and eggs) in QM spirit collection.

Remarks. *Polyrhachis darlingtoni* is easily identified by its low petiole with a strongly posteriorly descending, triangular dorsum and the bases of its rather short spines situated well below its widely rounded summit (Fig. 13B). The petiolar node of *P. darlingtoni* resembles that of *P. nourlangie* described below, however in the latter species the petiolar dorsum is flat, laterally marginate, with the margins terminating in the bases of short, curved spines on the petiolar summit (Fig. 13D). The species also differ in their size, with *P. darlingtoni* consistently larger (HL 2.59-2.67 versus 1.62-2.09 in *P. nourlangie*), and in the colour of their pubescence which, in *P. nourlangie* is uniformly golden, lacking the brassy and reddish hues of *P. darlingtoni*.

Polyrhachis darlingtoni is only known from two closely situated localities in the McIlwraith Range, along Leo Creek Road and at Lankelly Creek, near Coen on Cape York Peninsula.

Polyrhachis (Hagiomyrma) nourlangie sp. nov.
(Fig. 13C-D)

Etymology. After the type locality, Nourlangie Rock in Kakadu National Park, Northern Territory.

Material. HOLOTYPE: NT: Kakadu NP, Nourlangie Rock, 12°51'S, 132°49'E, 18.xi.1993, R.J. Kohout acc. 93.50, QMT174515 (worker). PARATYPES: data as for holotype (28 workers). Type deposition: Holotype and most paratypes in QM, 2 paratypes each in AMNH,



POLYRHACHIS (HAGIOMYRMA) TRAPEZOIDEA SPECIES GROUP

Map 1 ● *P. nourlangie* ▼ *P. thusnelda* ■ *P. darlingtoni*
 Map 2 ● *P. trapezoidea*

ANIC, BMNH, CASC, MCZC, MHNG, MLAC and NMNH.

Other Material. NT: Wessell Is, Rimbija I., 11°01'S, 136°45'E, 3-14.ii.1977 (TAW) (w); Arnhem Land, Dhallwuy, 5.x.2002 (BDH) (w); NE Arnhem Land, Cape Arnhem, 7.x.2002 (BDH) (w); ditto, nr Mt Dundas, 5.x.2002 (BDH) (w); Baroalba Springs, 12°47'S, 132°51'E, 16-17.xi.1972 (RWT & JEF acc. 72.1043) (w); Kakadu NP, Nourlangie Rock, 12°51'S, 132°49'E, 21.iii.1987 (ANA) (w); ditto, Koolpin Gorge, 3.viii.1997 (ANA) (w); Sawcut Gorge, 12°55'S, 132°56'E, 19.xi.1972 (RWT & JEF acc. 72.1087) (w); 46 km SSW of Borroloola, 16°28'S, 136°09'E, 23.iv.1976 (JEF) (w); Lake Bennett, 20.ii.1992 (BDH) (w); Litchfield NP, Sandy Ck Falls, 14.vii.1992 (BDH) (w); ditto, Wangi Falls, 13°10'S, 130°41'E, 13.ii.1994 (RJK acc. 94.16) (w); Kakadu NP, Bukbukluk, 13°29'S, 132°15'E, 23.xi.1993 (RJK acc. 93.60) (w); Nitmiluk NP, Dunlop Swamp, 10.iv.1993 (BDH) (w); ditto, 8th Gorge, 11.xi.1992 (BDH) (w); ditto, 11.vii.1976 (R. Mercer) (w); ditto, Amphitheatre-Crystal Falls track, 15-16.iii.1995 (GBM & H. Janetzki) (w); ditto, 14°19'S, 132°28'E, 25.xi.1993 (RJK acc. 93.62) (w).

Description. *Worker*: Dimensions (holotype cited first): TL c. 7.61, 6.6-8.3; HL 1.84, 1.62-2.09; HW

1.53, 1.36-1.75; CI 83, 81-86; SL 2.46, 2.25-2.71; SI 161, 152-165; PW 1.18, 1.06-1.40; MW 0.86, 0.84-1.00; PMI 137, 125-137; MTL 2.78, 2.43-3.03 (17 measured).

Anterior clypeal margin shallowly emarginate and obtusely denticulate medially, without clearly defined median flange. Clypeus with median carina; sinuate in profile, posteriorly rounding into moderately impressed basal margin. Frontal triangle indistinct. Frontal carinae sinuate with moderately raised margins; central area relatively wide, flat with distinct frontal furrow. Sides of head in front of eyes converging towards mandibular bases in weakly convex line; behind eyes, sides rounding into convex occipital margin. Eyes moderately convex, in full face view, only marginally exceeding lateral cephalic outline. Ocelli lacking. Pronotal dorsum with humeri rounded; lateral margins emarginate at midlength; promesonotal suture distinctly impressed. Mesosomal dorsum with posteriorly converging lateral margins; metanotal groove

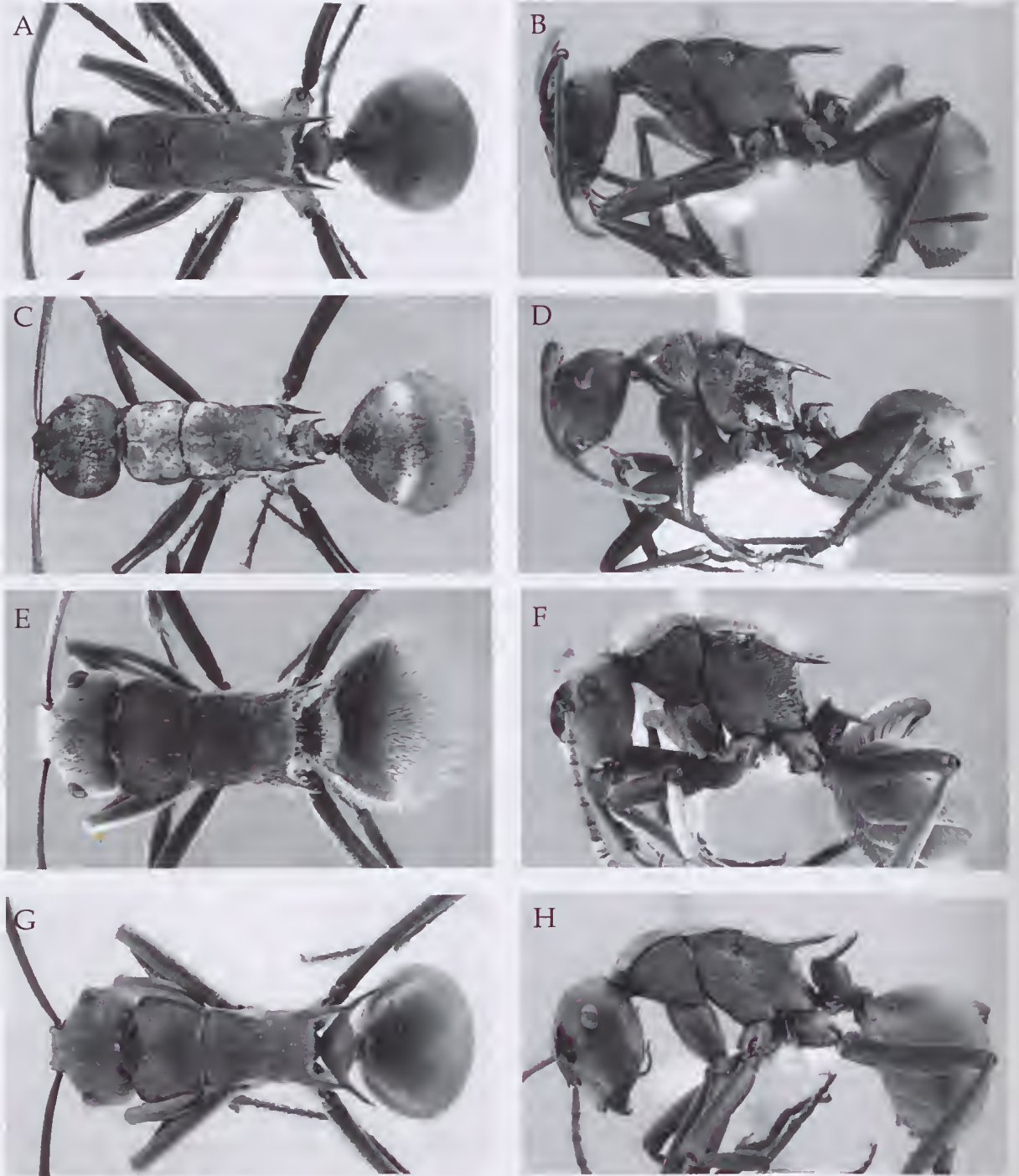


FIG. 13. *Polyrhachis* (*Hagiomyrma*) *trapezoidea* species-group – dorsal (left) and lateral (right) view. A-B, *P. darlingtoni* sp. nov.; C-D, *P. nourlangie* sp. nov.; E-F, *P. thlusnelda* Forel; G-H, *P. trapezoidea* Mayr (not to scale).

indistinct. Propodeal margins subparallel; spines moderately long with inner margins parallel, outer margins sinuate, with extreme tips weakly curved outwards. Petiole markedly low and broad at base in lateral view, anterior face inclined forwards before rounding onto virtually flat, laterally marginate dorsum, margins terminating in bases of short, curved spines (Fig. 13D). Anterior face of first gastral segment widely rounding onto dorsum.

Mandibles finely, longitudinally striate with piliferous pits. Head, mesosoma and petiole closely reticulate-punctate. Spines sculptured at bases, rather smooth and polished towards tips. Gaster finely shagreened.

Mandibles at masticatory and along outer borders with numerous, curved, golden hairs. Anterior clypeal margin with several anteriorly projecting setae medially. Clypeus, central area and vertex with several short to medium length, erect hairs; outline of head in full face view with numerous, erect, relatively short hairs. Leading edge of antennal scapes with several, very short, erect hairs. Dorsum of mesosoma with numerous, somewhat posteriorly inclined hairs, those on propodeum and petiole marginally longer. Several, medium length hairs on coxae and venter of femora. Gaster with relatively abundant, distinctly longer, posteriorly inclined, golden hairs. Closely appressed, rich golden, pubescence, rather diluted on vertex of head and sides of mesosoma; pubescence somewhat medially radiating and dense on mesosomal dorsum and petiole, completely hiding underlying sculpturation. Gaster with dense, somewhat longer, golden pubescence on dorsum; pubescence less dense, pale golden on sides and silvery on venter.

Black; mandibular teeth reddish-brown.

Sexuals and immature stages unknown.

Remarks. *Polyrhachis nourlangie* is somewhat similar to *P. darlingtoni* with the main distinguishing characters given in the remarks section of the latter. The distribution of *Polyrhachis nourlangie* is centred on the northern parts of the Northern Territory, including the islands adjacent to Arnhem Land. It is locally

common in open eucalypt forest, extending into savannah woodland in Nitmiluk National Park at the southern limit of its distribution.

Polyrhachis (*Hagiomyrma*) *thusnelda* Forel,
1902
(Fig. 13E-F)

Polyrhachis thusnelda Forel, 1902:509. Syntype workers, queen, males. Type locality: QLD, Mackay (G. Turner), MHNG, QM (examined).

Other Material. QLD: Cape York Pen., Weipa, vii.1982 (JDM) (w); Hann Tbl'd (Nth Base), 16°48'S, 145°12'E, c. 500 m, 11-14.xii.1995 (GBM, GIT, DJC) (w); 10 km N of Cairns, 9.viii.1975 (BBL) (w); Davies Ck, 15 km E of Mareeba, 17°00'S, 145°34'E, 15.vi.1980 (RJK accs 80.26, 29) (w); Almaden, SE of Chillagoe, 17°21'S, 144°41'E, 4.v.1990, savannah woodland (BBL) (w); Townsville, 9.x.1902 (F.P. Dodd) (w); Mt Stuart, nr Townsville, 19°10'S, 146°47'E, 12.iii.1993 (GBM) (w); Cape Hillsborough NP, 20°55'S, 149°03'E, 10-11. iv.1981 (RJK accs 81.56, 67, 70, 73) (w).

Description. *Worker.* Dimensions (syntypes cited first): TL c. 8.62-8.92, 8.16-9.12; HL 2.00-2.03, 1.93-2.15; HW 1.81-1.84, 1.75-2.00; CI 90-91, 90-94; SL 2.25-2.28, 2.21-2.46; SI 124, 118-125; PW 1.78-1.84, 1.72-2.01; MW 1.09-1.12, 1.00-1.28; PMI 159-169, 156-172; MTL 2.56-2.59, 2.43-2.84 (6+16 measured).

Anterior clypeal margin with very shallow, denticulate, median flange, laterally flanked by acute teeth. Clypeus straight in profile with only weakly raised median carina; basal margin flat. Frontal triangle indistinct. Frontal carinae sinuate, with moderately raised margins; central area wide with distinct frontal furrow. Sides of head in front of eyes converging towards mandibular bases in weakly convex line; behind eyes, sides narrowly rounding into weakly convex occipital margin. Eyes convex, in full face view not or only marginally exceeding lateral cephalic outline. Ocelli lacking. Pronotal humeri shallowly concave; pronotal dorsum with moderately raised margins converging into distinct promesonotal suture. Mesosomal margins converging into weakly impressed metanotal groove. Propodeum armed with broad-based, relatively short, divergent spines. Petiole with anterior and posterior faces subparallel; dorsum with distinct, flat platform, laterally armed with horizontal, divergent, acute spines. Anterior

face of first gastral tergite widely rounding onto dorsum.

Mandibles finely longitudinally striate with numerous piliferous pits. Head and mesosoma very closely, distinctly reticulate-punctate; pronotal dorsum with sculpture distinctly coarser, somewhat vermiculate-rugose in some specimens. Bases of spines sculptured, tips smooth and polished. Petiole with anterior face polished, posterior face deeply sculptured; dorsal platform distinctly reticulate. Gaster shagreened with dorsum more distinctly sculptured.

Mandibles at masticatory and outer borders with numerous curved, golden hairs. Anterior clypeal margin with a few longer, anteriorly projecting setae medially and several short setae fringing margin laterally. Head, mesosoma, petiole, gaster and venter of femora with numerous, mostly erect and variously curved, long silvery hairs, many distinctly longer than greatest diameter of eyes. Hairs on head more anteriorly directed with none breaking lateral cephalic outline between eyes and mandibular bases in full face view. Hairs lacking on antennal scapes, dorsal surfaces of femora, most of propodeal declivity and sides of mesosoma, except a few hairs on metapleurae. Closely appressed, silvery pubescence in various densities over most body surfaces, partly hiding underlying sculpturation; pubescence on gaster somewhat longer, silvery on sides and venter, rich golden on dorsum, completely hiding underlying sculpturation.

Black; mandibular teeth narrowly reddish-brown; antennal segments progressively lighter reddish-brown towards apices.

Queen. Dimensions: TL c. 9.47-10.18; HL 2.12-2.21; HW 1.84-2.00; CI 87-90; SL 2.21-2.28; SI 114-120; PW 2.15-2.20; MTL 2.62-2.68 (4 measured).

Apart from sexual characters, very similar to worker except: pronotal humeri more-or-less subangular. Mesoscutum wider than long with anterior margin widely and evenly rounded in dorsal view; median line bifurcate towards flat dorsum; parapsides flat, only weakly raised posteriorly. Mesoscutellum flat,

not elevated above dorsal plane of mesosoma. Spines distinctly shorter than in worker. Sculpturation, pilosity, pubescence and colour virtually identical to worker.

Males evidently in MHNG collection. Immature stages present in the QM spirit collection.

Remarks. *Polyrhachis thusnelda* is easily recognised by a combination of a flat-topped petiolar dorsum, most of the body covered with long hairs and a black body strongly contrasting with rich golden pubescence on the gastral dorsum. It is a relatively widespread species with a patchy distribution from Cape York Peninsula south to about Mackay, Queensland. However, it becomes rather uncommon towards the northern limits of its range. It inhabits open eucalypt forests, but has also been collected from the canopy of lowland tropical rainforest. For information on the lithocolous nesting habit of *P. thusnelda*, see Robson & Kohout (2005: 164-169).

Polyrhachis (Hagiomyrma) trapezoidea Mayr,
1876
(Fig. 13G-H)

Polyrhachis trapezoidea Mayr, 1876:72. Syntype workers, queen, male. Original localities: QLD, Rockhampton, Peak Downs (A. Dietrich, E. Dämel), NHMW (examined).

Polyrhachis (Hagiomyrma) ammon r. *trapezoidea* Mayr. Forel, 1915:108. (combination in *P. (Hagiomyrma)* and race of *P. ammon*).

Polyrhachis trapezoidea Mayr. Emery, 1925:185 (revived status as species).

Other Material. NT: Litchfield NP, nr Tolmer Falls, 13°12'S, 130°42'E, 10.viii.1991 (ANA) (w). QLD: Torres Strait, Horn Island, 10°37'S, 142°17'E, 10-27.vi.1974 (H&C) (w); Prince of Wales Is., 10°40'S, 142°10'E, 6-15.ii.1975 (H&C) (w); Cape York Pen., Moreton Telegraph Stn, 1958 (G. Hall) (w); Leo Kitchen Camp, 17.x.1958 (J.L. Wassel) (w); 6 km E of Heathlands, 18-22.iv.1992 (G. Cassis) (w); Weipa, vii.1982 (JDM) (w); Weipa, MRRP study site N1b, v-vi.1995 (ANA) (w); Merluna turnoff, 20.viii.1958 (E. Exley) (w); Iron Ra., 12°43'S, 143°18'E, 1-3.vii.1976 (P. Filewood) (w); ditto, 26-31.vii.1981 (RJK acc. 81.203) (w); McIlwraith Ra., Peach Ck, 13°46'S, 143°18'E, c. 170 m, 24.vii.1977 (RWT acc. 77.583) (w); Leo Ck, 10-20.vii.1976 (P. Filewood) (w); Battlecamp Rd, 21.vii.2002 (ANA) (w); 1 km N of Rounded Hill, 15°75'S, 145°13'E, 5-7.v.1981 (JEF) (w); Bakers Blue Mtn, 17 km W of Mt Molloy, 12.ix.1981 (GBM & DLC) (w); Mareeba, 3.viii.1975 (BBL) (w); Townsville, James Cook University

Campus, 4.vi.1993 (C.J. Hill) (w); Harvey Ra, nr Townsville, 24.ix.1995 (SKR #15) (w); Mt Elliot NP, Alligator Ck, 19°26'S, 146°57'E, 2.x.1977 (RJK accs 77.5, 9) (w); ditto, 11.vi.1987 (RJK acc. 87.96) (w); Toomba, 19°58'43"S, 145°35'25"E, 14.ii.2007 (CJB) (w); ditto, 19°58'5"S, 145°34'49"E, 14-16.xii.2006 (GBM, DJC) (w); 30 km SbyW of Charters Towers, 20°05'S, 146°16'E, c. 330 m, 17.vii.1977 (RWT acc. 77.390) (w); Mt Abbott, E base, Finley Ck, 20°06'S, 147°49'E, 13.iv.1997 (CJB) (w); Proserpine, nr Kelsey Substation, 20°23'23"S, 148°32'26"E, 11-17.ii.2007 (C. Lambkin, N. Starick) (w); Proserpine, 20°29'14"S, 148°34'19"E, 8.xi.2007 (CJB) (w); ditto, Airport Drive, 20°29'17"S, 148°33'55"E, 7.xi.2007 (CJB) (w); Rochford Scrub, 20°6'59"S, 146°37'48"E, 10-11.xii.2006 (S. Wright) (w); Cape Hillborough NP, 20°55'S, 149°02'E, 2.i.1979 (RJK acc. 79.11) (w); ditto, 10-11.iv.1981 (RJK accs 81.57, 80, 81, 85) (w); 1.5 km SE of Mt Ossa, 20°58'S, 148°50'E, 28.xi.1976 (RJK acc. 76.92) (w); Mt Blackwood NP, 21°02'S, 148°56'E, 14.iv.1981 (RJK acc. 81.101) (w); Eungella NP, Broken R., 21°10'S, 148°30'E, 29.xi.1976 (RJK acc. 76.101) (w); Britton Ra., 6 km NNE of Homevale, 21°23'S, 148°33'E, 1-6.iv.1975 (RJK accs 75.159, 164) (w); Mt Castor, 22°28'6"S, 147°52'32"E, 6.iii.2006 (QM Party) (w); Lords Table, 22°40'29"S, 148°1'13"E, 13.i-4.iii.2006 (CJB) (w); Lorna Vale, nr Marlborough, 22°43'S, 149°46'E, 8.iv.1981 (RJK acc. 81.40) (w); c. 4-10 km N of Marlborough, 22°45'S, 149°54'E, 9.iv.1981 (RJK acc. 81.49) (w); 6.5km NNW of Clermont, 22°46'12"S, 147°37'35"E, 13.i-7.iii.2006 (CJB, GBM) (w); Scotts Peak, SE base, 22°51'35"S, 148°13'41"E, 9.iii.2006 (S. Wright, CJB) (w); 6 km N of Mt Archer, nr Rockhampton, 23°17'S, 150°34'E, 4.i.1979 (RJK acc. 79.17) (w); Bouldercombe, 23°32'S, 150°25'E, 22.iv-19.vii.1990 (D. Wallace & R. Raven, DW15) (w); Rundle Ra., 36 km NW of Gladstone, 23°39'S, 150°59'E, 24-30.iii.1975 (RJK accs 75.116, 119, 129) (w); Gladstone, xi.1925 (A. Musgrave) (w); Taroom Distr., Boggomoss, 25°29'0"S, 150°8'0"E, 14.xi.1996 (QM Survey) (w).

Description. *Worker.* Dimensions (syntypes cited first): TL c. 8.92-9.07, 7.61-9.42; HL 2.18-2.21, 1.87-2.21; HW 1.84, 1.53-1.90; CI 83-84, 80-85; SL 2.50-2.53, 2.15-2.71; SI 136-137, 128-140; PW 1.68, 1.37-1.78; MW 0.72-0.84; PMI 197-221; MTL 2.87-3.03, 2.50-3.21 (2+13 measured).

Anterior clypeal margin with denticulate, shallowly 'V'-shaped emarginate, median flange. Clypeus with blunt median carina; almost straight in profile with virtually flat basal margin. Frontal carinae sinuate with weakly raised margins; central area relatively wide with distinct frontal furrow. Sides of head in front of eyes converging towards mandibular bases; behind eyes, sides narrowly rounding into weakly convex occipital margin. Eyes

convex, in full face view marginally breaking lateral cephalic outline. Ocelli lacking. Pronotal and mesonotal dorsa distinctly converging posteriorly; pronotal humeri rounded with raised margins; promesonotal suture distinctly impressed, metanotal groove poorly indicated. Lateral margins of propodeum weakly divergent, terminating in more-or-less horizontal, acute spines with tips bent slightly outwards and upwards. Petiole with relatively wide, posteriorly sloping dorsum and horizontal, widely divergent, acute spines.

Mandibles finely, longitudinally striate with numerous piliferous pits. Head and mesosoma finely reticulate-punctate; gaster finely shagreened.

Mandibular masticatory borders with medium length, variously curved, golden hairs. Very short, erect, bristle-like golden hairs on dorsa of head, mesosoma and petiole; gaster with somewhat longer hairs, notably around apex and on venter. Mostly golden, closely appressed pubescence in various densities on most dorsal surfaces; pubescence distinctly medially radiating, denser and with somewhat brassy hue along dorsal midline of mesosoma, completely hiding underlying sculpturation. Dorsum of gaster with abundant, rather pale golden pubescence, progressively more silvery towards sides and venter; first gastral tergite medially with rather narrow, rich golden median patch that widens posteriorly.

Black, with only narrow reddish-brown band along mandibular masticatory borders.

Queen. Dimensions (syntype cited first): TL c. 9.68, 9.63-11.09; HL 2.18, 2.18-2.31; HW 1.72, 1.72-1.84; CI 79, 79-80; SL 2.31, 2.31-2.46; SI 134, 132-138; PW 1.96, 1.96-2.21; MTL 2.77, 2.81-2.90 (5 measured).

Apart from sexual characters, very similar to worker except: pronotal humeri bluntly angular; lateral margins slightly raised and weakly rounded posteriorly. Mesoscutum with dorsum flat, as wide as long in dorsal view; median line bifurcate anteriorly; parapsides only slightly raised posteriorly. Mesoscutellum flat, not elevated above dorsal plane of



POLYRHACHIS (HAGIOMYRMA) TUBIFERA
SPECIES-GROUP

Map 1 ● *P. diversa*

Map 2 ● *P. tubifera*

mesosoma. Propodeal dorsum convex with spines shorter than worker, subparallel and slightly bent downwards. Petiole as in worker with spines shorter. Sculpturation, pilosity, pubescence and colour virtually identical to worker.

Male evidently in NHMW. Immature stages (eggs, larvae in various stages of development and pupae) in QM spirit collection.

Remarks. *Polyrhachis trapezoidea* is very similar to *P. aurora* with the main distinguishing characters given in the remarks under the latter species. The known distribution of *P. trapezoidea* extends from Torres Strait south to about Gladstone, with reports of its occurrence in the northern part of the Northern Territory (Andersen, 2000). *Polyrhachis trapezoidea* is relatively common in open eucalypt forests and savannah woodlands and, like most of other *Hagiomyrma* species, nests in the ground.

POLYRHACHIS (HAGIOMYRMA) TUBIFERA
SPECIES-GROUP

Polyrhachis (Hagiomyrma) diversa sp. nov.
(Fig. 14A-B)

Etymology. Derived from the Latin word *diversus*, meaning different, in reference to several characters separating *P. diversa* from the very similar *P. tubifera*.

Material. HOLOTYPE: QLD, Cape York Pen., Mt Tozer summit, 12°45'S, 143°13'E, 8.xii.1985, G.B. Monteith & D.J. Cook, QMT174516 (worker).

PARATYPES: data as for holotype (6 workers); Mt Lamond, 12°44'S, 143°18'E, 19-15.vi.1971, RWT & JEF accs 71.259, 266 (3 workers); Iron Ra., 12°43'S, 143°18'E, 26-31.vii.1981, RJK acc. 81.203 (1 worker). Type deposition: Holotype and 2 paratype workers in QM, 2 paratype workers each in ANIC, BMNH and MCZC.

Other Material. QLD: Cape York Pen., Captain Billy Ck, 11°40'S, 142°50'E, 9-13.vii.1975 (GBM) (w).

Description. *Worker.* Dimensions (holotype cited first): TL c. 6.35, 5.80-6.65; HL 1.56, 1.50-1.68; HW 1.31, 1.28-1.47; CI 84, 84-89; SL 1.75, 1.70-1.90; SI 133, 127-136; PW 1.50, 1.34-1.62; MW 1.03; PMI 145; MTL 1.75, 1.68-1.96 (10 measured).

Anterior clypeal margin medially widely truncate and denticulate, without clearly defined median flange. Clypeus with median, anteriorly elevated carina; sinuate in profile with rather flat basal margin. Frontal carinae sinuate with weakly raised margins anteriorly, virtually flat posteriorly; central area relatively wide with flat frontal furrow. Sides of head converging anteriorly towards mandibular bases in straight line; behind eyes, sides rounding into relatively low occipital margin. Eyes weakly convex, in full face view almost reaching lateral cephalic outline. Ocelli lacking, relative positions indicated by shallow pits in cephalic sculpture. Mesosoma relatively broad and short, strongly convex in lateral view. Pronotal dorsum with humeri rounded; lateral margins weakly raised, converging towards deeply laterally impressed promesonotal suture. Metanotal groove indistinct; mesonotal and propodeal dorsa in lateral view forming uninterrupted, convex line before rounding into vertical declivity. Propodeal spiracles prominent, situated on laterally projecting tubercles. Lateral margins of propodeum strongly divergent, terminating in broad-based, relatively short, acute, spines. Petiole very narrow in lateral view with anterior face straight, posterior face weakly convex; dorsum transversely wide, armed with very short, divergent spines. Anterior face of first gastral tergite distinctly higher than full height of petiole, widely rounding onto dorsum.

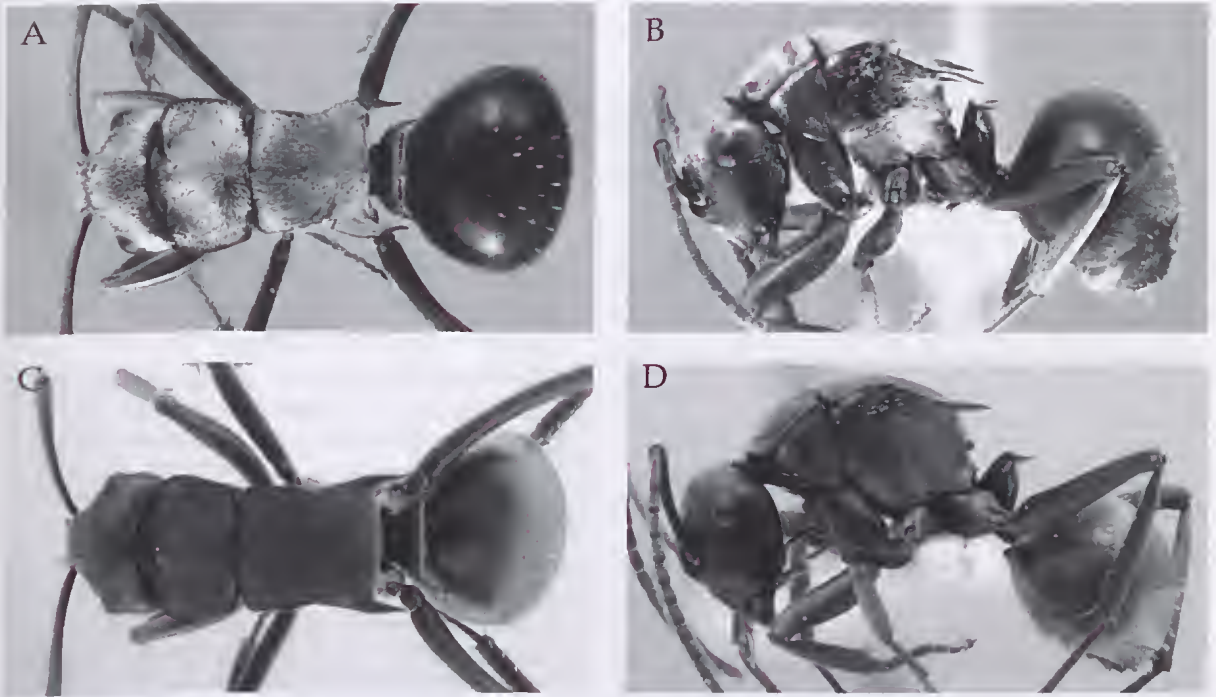


FIG. 14. *Polyrhachis* (*Hagiomyrma*) *tubifera* species-group – dorsal (left) and lateral (right) view. A–B, *P. diversa* sp. nov.; C–D, *P. tubifera* Forel (not to scale).

Mandibles very finely, longitudinally striate with numerous piliferous pits. Head, mesosoma and petiole closely reticulate-punctate. Gaster very finely shagreened.

Mandibles at masticatory borders and along outer borders with numerous golden hairs. Anterior clypeal margin medially with several medium length, golden setae. Several short to medium length, mostly erect hairs on clypeus, along frontal carinae, vertex, anterior face of front coxae and venter of mid and hind coxae and femora; only a few very short, erect hairs on dorsum of pronotum and mesonotum. Dorsum of gaster with a few short hairs; apical segments and venter with numerous, medium length, posteriorly directed, golden hairs. Abundant closely appressed, rich golden pubescence on dorsum of head, mesosoma and petiole, completely hiding underlying sculpturation; pubescence less dense and pale golden or silvery on clypeus and sides of head, mesosoma and petiole. Short, silvery, closely appressed pubescence on venter of gaster; pubescence virtually absent from gastral dorsum.

Black; mandibular teeth and appendages dark reddish-brown; gaster medium reddish-brown, semi-polished.

Sexuals and immature stages unknown.

Remarks. *Polyrhachis diversa* is very similar to *P. tubifera* and they share a relatively short and wide, evenly arched mesosoma, distinctly elongated propodeal spiracles and very short petiolar spines that are separated by the transversely wide dorsum of the petiole. However, *P. diversa* features rich, closely appressed, golden pubescence that is absent in *P. tubifera*. In contrast, *P. diversa* has virtually no pubescence on the dorsum of the gaster, while in *P. tubifera* the gastral dorsum is covered with rich golden pubescence that completely hides the underlying sculpturation.

Polyrhachis diversa differs from most other *Hagiomyrma* species by inhabiting rainforest, where it has been collected upon the trunks and foliage of trees.

Polyrhachis (Hagiomyrma) tubifera Forel,
1902
(Fig. 14C-D)

Polyrhachis tubifera Forel, 1902:517. Syntype workers, males. Type locality: QLD, Mackay (G.Turner), MHNG (examined).

Polyrhachis tubifera Forel. Emery, 1925:185 (combination in *P. (Hagiomyrma)*).

Other Material. QLD: Cape York Pen., 13 km E by S of Weipa, 12°40'S, 143°00'E, 15-19.ii.1994 (P. Zborowski) (w); Weipa, Uningan Nature Reserve, 1.vi.1995 (ANA) (w); Weipa, MRRP study site N2a, v-vi.1995 (ANA) (w); Iron Ra., 12°43'S, 143°18'E, 26-31.vii.1981 (RJK acc. 81.203) (w); Lizard I., 14°40'S, 145°28'E, 14 & 22.ii.1992 (H. Reichel) (w); Mt Cook, nr Cooktown, 17.vii.2002 (ANA) (w); Barratt Ck, 4 km ESE of Daintree, 15°15'S, 145°21'E, 21.vii.1980 (RJK acc. 80.100) (w); Davies Ck Falls, nr Mareeba, 29.vi.1971 (RWT & JEF acc. 71.781) (w); ditto, 3.viii.1975 (BBL) (w); Herberton, 7.viii.1975 (BBL) (w); Wallaman Falls, 18°38'S, 145°48'E, 28.ix.1987 (RJK acc. 87.99) (w); Mt Elliot NP, Alligator Ck, 19°26'S, 146°57'E, 11.vi.1987 (RJK acc. 87.89) (w); Red Falls, basalt, 19°55'33"S, 145°44'1"E, 15.ii.2007 (CJB, GBM) (w); Toomba, 19°58'1"S, 145°34'46"E, 14.ii.2007 (CJB) (w, ♀); Gregory Dev. Rd, 14km NW Clarke R., 19°7'53"S, 145°20'14"E, 17.xii.2006-15.ii.2007 (GBM, DJC) (w); Mt Abbott, SE slopes, 20°07'S, 147°46'E, <500 m, 9-12.iv.1997 (CJB) (w); Proserpine, 20°29'14"S, 148°34'19"E, 10-16.ii.2007 (C. Lambkin, N. Starick) (w); ditto, Airport Drive, 20°29'17"S, 148°33'55"E, 7.xi.2007 (CJB) (w); ditto, Deadman Ck, 20°30'18"S, 148°33'22"E, 10.xi.2007 (CJB) (w); Brampton I., 20°49'S, 149°16'E, 1.i.1979 (RJK acc. 79.1) (w); Newry I., 20°51'S, 148°55'E, 31.xii.1978 (RJK acc. 78.19) (w); Cape Hillsborough NP, 20°55'S, 149°03'E, 10-11.iv.1981 (RJK acc. 81.54) (w); ditto, 22.x.1995 (SKR #45) (w); Mt Blackwood NP, 21°02'S, 148°56'E, 14.iv.1981 (RJK acc. 81.98) (w); Eungella NP, Finch Hatton Gorge, 21°04'S, 148°38'E, 7-13.iv.1975 (RJK acc. 75.171) (w); ditto, 16.iv.1981 (RJK acc. 81.122) (w); 18 km SW of Walkerston, 16.8.1975 (BBL) (w); Britton Ra., 6 km NNE of Homevale, 21°23'S, 148°33'E, 1-6.iv.1975 (RJK acc. 75.159) (w); Sarina, 16.viii.1975 (BBL) (w); 30 km S of Sarina, 30.vii.1975 (BBL) (w); Cooloola SF, Rainbow Beach Rd, 25°47'S, 153°05'E, 7.xii.1974 (RJK acc. 74.144) (w); ditto, 18-25.i.1975 (RJK acc. 75.68) (w); Chelsea Rd Bushlands Res., 27°28'58"S, 153°11'15"E, 24.ii.2004 (QM Party) (w, ♀); Ransome Res., 27°29'34"S, 153°11'5"E, 23.iv.2003 (E. Volschenk, S. Wright) (w); Enterprise Mine, 27°34'27"S, 153°26'20"E, 11.i.2002 (QM Party) (w); Karawatha For., 27°37'33"S, 153°5'24"E, 17.ii.2004 (QM Party) (w).

Description. *Worker*: Dimensions (syntypes cited first): TL c. 6.0-7.25, 5.49-7.25; HL 1.6, 1.40-1.6; HW 1.37-1.4, 1.15-1.4; CI 86-87, 82-89; SL 1.8, 1.56-1.81; SI 128-131, 125-141; PW 1.45, 1.15-1.45; MW 1.12, 0.90-1.12; PMI 129, 120-139; MTL 1.9, 1.64-1.93 (2+16 measured).

Anterior clypeal margin truncate medially, truncation obtusely denticulate. Clypeus with rather flat carina; weakly sinuate in profile, basal margin shallowly impressed. Frontal triangle distinct. Frontal carinae sinuate, with moderately raised margins. Sides of head in front of eyes converging towards mandibular bases in almost straight line; behind eyes, sides rounding into rather low, weakly convex occipital margin. Eyes weakly convex, in full face view not or only marginally reaching lateral cephalic outline. Ocelli lacking. Dorsum of mesosoma markedly broad and short, strongly convex in lateral view. Pronotal dorsum with humeri rounded; lateral margins converging towards deeply laterally impressed promesonotal suture. Metanotal groove indistinct; mesonotal and propodeal dorsa in lateral view forming interrupted line before rounding into vertical declivity. Propodeal spiracles prominent, situated on laterally projecting tubercles. Lateral margins of propodeum divergent, terminating in broad-based, short, subparallel, acute, spines. Petiole very narrow in lateral view with anterior face straight, posterior face very weakly convex; dorsum transversely wide, armed with very short, divergent, weakly upturned spines. Anterior face of first gastral tergite widely rounding onto dorsum.

Mandibles very finely, longitudinally striate with numerous piliferous pits. Head, mesosoma and petiole very finely and closely reticulate-punctate with characteristic opaque appearance. Gaster very finely shagreened.

Mandibles at masticatory borders with numerous, curved, golden hairs. Anterior clypeal margin medially with a few, medium length, golden setae. Several short to medium length, mostly suberect hairs on clypeus, along frontal carinae, vertex, anterior face of front coxae and venter of mid and hind coxae and femora; only a few, very short, erect hairs on dorsum of pronotum and mesonotum. Dorsum of gaster with several short hairs, more abundant posteriorly; apical segments and venter of gaster with numerous, medium length, posteriorly directed, golden hairs. Closely appressed, silvery pubescence, very

short and diluted on dorsum of mesosoma, more abundant and somewhat longer on head, propodeal declivity, metapleurae and dorsum of petiole. Abundant, mostly pale golden, closely appressed pubescence on dorsum of gaster, completely hiding underlying sculpturation; sides and venter of gaster with rather diluted, silvery pubescence.

Black; mandibles and appendages medium to dark, reddish-brown. Antennae with funicular segments progressively lighter towards apices.

Queen. Dimensions: TL c. 7.31-7.36; HL 1.65-1.68; HW 1.34; CI 80-81; SL 1.70-1.73; SI 127-129; PW 1.68-1.78; MTL 1.87-1.96 (2 measured).

Apart from sexual characters, very similar to worker except: clypeus in lateral view distinctly sinuate. Eyes more convex, exceeding lateral cephalic outline. Pronotal humeri with widely rounded, weakly raised margins. Mesoscutum distinctly wider than long, with widely rounded anterior margin in dorsal view; dorsum relatively low, weakly convex in lateral view; median line short, bifurcate; parapsides flat. Dorsum of mesoscutellum very weakly convex, not raised above dorsal plane of mesosoma. Propodeal and petiolar spines shorter than in worker. Sculpturation, pilosity, pubescence and colour virtually identical to those in worker.

Males in MHNG. Immature stages (larvae and pupae) in QM spirit collection.

Remarks. With its short and broad mesosoma, *P. tubifera* resembles *P. diversa* described above, with most distinguishing characters listed in remarks of the latter species. *Polyrhachis tubifera* is relatively common, ranging from Cape York Peninsula south to Brisbane, south-east Queensland. It occurs mostly in open eucalypt forests and woodlands, however, it is also occasionally encountered along the edges of lowland rainforests. *Polyrhachis tubifera* is evidently a ground-nesting species, with a few, rather shallowly excavated, leafmould covered nests found at the bases of trees.

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LITERATURE CITED

- Andersen, A.N. 2000. *The Ants of Northern Australia. A guide to the monsoonal fauna.* CSIRO Publishing, Collingwood, Melbourne 106 pp.
- Billberg, G.J. 1820. *Enumeratio Insectorum in Museo Gust. Joh. Billberg:* Stockholm, 138 pp.
- Bolton, B. 1995. *A new general Catalogue of the Ants of the World.* Harvard University Press, Cambridge, Mass. 504 pp.
- Bolton, B., Alpert, G.D., Ward, P.S. & Naskrecki, P. 2007. *Bolton's Catalogue of Ants of the World: 1758-2005.* Harvard University Press, Cambridge, Mass., CD-ROM.
- Chapman, J.W. & Capco, S.R. 1951. Check list of the ants of Asia. *Monographs of the Institute of Science and Technology, Manila* 1: 327 pp.

- Dalla Torre, C.G.de. 1893. *Catalogus Hymenopterorum, hucusque descriptorum systematicus et synonymicus* 7: 289 pp. Lipsiae.
- Donisthorpe, H. 1938. On the identity of Smith's types of Formicidae collected by Alfred Russell Wallace in the Malay Archipelago, with description of two new species. *Annals and Magazine of Natural History*. London (10) 10: 441-476.
1944. A new subgenus and three new species of *Polyrhachis* F.Smith (Hym., Formicidae). *Entomologist's Monthly Magazine*. London 80: 64-66.
- Dorow, W.H.O. 1995. Revision of the ant genus *Polyrhachis* Smith, 1857 (Hymenoptera: Formicidae: Formicinae) on subgeneric level with keys, checklist of species and bibliography. *Courier Forschungsinstitut Senckenberg* 185: 1-113.
- Dorow, W.H.O., Kohout, R.J. & Taylor, R.W. 1997. *Polyrhachis* Smith, 1857 (Insecta, Hymenoptera): proposed precedence over *Myrma* Billberg, 1820. Case 3009. *Bulletin of Zoological Nomenclature* 54(4): 236-241. December 1997.
- Emery, C. 1895. Descriptions de quelques fourmis nouvelles d'Australie. *Annales de la Société entomologique de Belgique*. Bruxelles 39: 345-358.
1897. Viaggio di Lamberto Loria nella Papuaasia orientale 18. Formiche raccolte nelle Nuova Guinea dal Dott. Lamberto Loria. *Annali del Museo Civico di Storia Naturale Giacomo Doria di Genova* 18(38): 546-594, pl.1.
1898. Descrizioni di Formiche nuove Malesi e Australiane; note sinonimiche. *Rendiconti delle sessioni dell'Accademia delle scienze dell'Istituto di Bologna* (ns) 2: 231-245, figs 1-16.
1925. In, Wytzman, *Genera Insectorum*. Hymenoptera, Fam. Formicidae, subfam. Formicinae. Fasc. 183: 302 pp., 4 pls. Brussels.
- Fabricius, J.C. 1775. *Systema Entomologiae*, sistens insectorum classes, ordines, genera, species, adiectis, synonymis, locis, descriptionibus, observationibus. Flensburgi et Lipsiae. 832 pp.
- Forel, A. 1879. Etudes myrmécologiques en 1879 (deuxième partie [1re partie en 1878]). *Bulletin de la Société Vaudoise des Sciences Naturelles* 16: 53-128.
1886. Études Myrmécologiques en 1886. *Annales de la Société Entomologique de Belgique* 30: 131-215.
1895. Nouvelles fourmis de diverses provenances, surtout d'Australie. *Annales de la Société entomologique de Belgique* 39: 41-49.
1901. Formiciden aus dem Bismarck-Archipel, auf Grundlage des von Prof. Dr. F. Dahl gesammelten Materials bearbeitet. *Mitteilungen aus dem Zoologischen Museum in Berlin* 2: 1-37.
1902. Fourmis nouvelles d'Australie. *Revue Suisse de Zoologie* 10: 405-548, Geneve.
1907. Formicidae. In: Michaelsen, W. & Hartmeyer, R. (eds.). *Die Fauna Südwest Australiens*. Ergebnisse der Hamburger südwest-australischen Forschungsreise 1905. Band 1(7): 263-310, Jena.
1907. Formicides du Musée National Hongrois. *Annales historico-naturales Musei nationalis Hungarici* 5: 1-142.
1915. Results of Dr E. Mjöberg's Swedish Scientific Expeditions to Australia, 1910-1913. 2. Ameisen. *Arkiv för Zoologi* 9: 1-119.
1916. Fourmis du Congo et d'autres provenances récoltées par MM. Hermann Kohl, Lujá, Mayné, etc. *Revue Suisse de Zoologie* 24: 397-460.
- Hung, A.C.F. 1967. A revision of the ant genus *Polyrhachis* at the subgeneric level (Hymenoptera: Formicidae). *Transactions of the American Entomological Society*. Philadelphia 93: 395-422.
- Karavaiev, W. 1927. Ameisen aus dem Indo-Australischen Gebiet III. Académie des Sciences de l'Ukraine. *Memoires de la Classe des Sciences Physiques et Mathématiques* 7(1). *Travaux du Musée Zoologique* 3: 3-52. Kiev.
- Kohout, R.J. 1988. Nomenclatural changes and new Australian records in the ant genus *Polyrhachis* Fr. Smith (Hymenoptera: Formicidae: Formicinae). *Memoirs of the Queensland Museum* 25(2): 429-438, 3 figs.
1990. A review of the *Polyrhachis vielmeyeri* species-group (Hymenoptera: Formicidae: Formicinae). *Memoirs of the Queensland Museum* 28(2): 499-508, 7 figs.
1994. New synonymy of three Australian ants (Formicidae: Formicinae: *Polyrhachis*). *Memoirs of the Queensland Museum* 35(1): 135-136.
1997. Australian *Polyrhachis* and their nesting habits (Formicidae: Formicinae). *Proceedings of the International Colloquia on Social Insects*. Russian Language Section, Socium, St Petersburg (1997) 3-4: 217-222, 1 fig.
2000. A review of the distribution of the *Polyrhachis* and *Echinopla* ants of the Queensland Wet Tropics (Hymenoptera: Formicidae: Formicinae). *Memoirs of the Queensland Museum* 46(1): 183-209, 1 tbl., 4 figs.
2006. Review of *Polyrhachis* (*Cyrtomyrma*) Forel (Hymenoptera: Formicidae: Formicinae) of Australia, Borneo, New Guinea and the Solomon Islands with descriptions of new species. *Memoirs of the Queensland Museum* 52(1): 87-146, 12 figs.
2007. A review of the subgenus *Polyrhachis* (*Camponyrma*) Wheeler from Borneo with descriptions of new species (Hymenoptera: Formicidae: Formicinae). *Asian Myrmecology* 1: 7-17, 12 figs.

2010. A review of the Australian *Polyrhachis* ants of the subgenera *Myrmhopla* Forel and *Hirtonomyrma* subgen. nov. (Hymenoptera: Formicidae: Formicinae). *Memoirs of the Queensland Museum - Nature* 55(1): 167-204, 10 figs.
2012. A review of the Australian *Polyrhachis* ants of the subgenera *Myrma* Billberg, *Myrmatopa* Forel, *Myrnothrinax* Forel and *Polyrhachis* Fr. Smith (Hymenoptera: Formicidae: Formicinae). *Memoirs of the Queensland Museum - Nature* 56(1): 25-59, 8 figs.
- Kohout, R.J. & Taylor, R.W. 1990. Notes on Australian ants of the genus *Polyrhachis* Fr. Smith, with a synonymic list of the species (Hymenoptera: Formicidae: Formicinae). *Memoirs of the Queensland Museum* 28(2): 509-522.
- Mayr, G. 1870. Neue Formiciden. *Verhandlungen der Zoologisch-Botanischen Gesellschaft in Wien* 20(Abhand.): 939-996.
1876. Die australischen Formiciden. *Journal des Museum Godeffroy. Hamburg* 12(5): 56-115.
- Nielsen, M.G. 1997. Nesting Biology of the mangrove mud-nesting ant *Polyrhachis sokolova* Forel (Hymenoptera: Formicidae) in northern Australia. *Insectes Sociaux* 44: 15-21.
- Robson, S.K.A. & Kohout, R.J. 2005. Evolution of nest-weaving behaviour in arboreal nesting ants of the genus *Polyrhachis* Fr. Smith (Hymenoptera: Formicidae). *Australian Journal of Entomology* 44: 164-169, fig.
2007. A review of the nesting habits and socioecology of the ant genus *Polyrhachis* Fr. Smith. *Asian Myrmecology* 1: 81-99.
- Roger J. 1863. Die neu aufgeführten Gattungen und Arten meines Formiciden- Verzeichnisses, nebst Ergänzung einiger früher gegeben Beschreibungen. *Berliner entomologische Zeitschrift* 7: 131-214.
- Santschi, F. 1920. Quelques nouveaux Camponotinae d'Indochine et Australie. *Bulletin de la Société Vaudoise des Sciences Naturelles* 52: 565-569.
- Shattuck, S.O. 1999. *Australian Ants. Their Biology and Identification*. Monographs on Invertebrate Taxonomy 3, CSIRO Publishing, Collingwood, Melbourne 226 pp.
- Smith, Fr. 1860. Catalogue of hymenopterous insects collected by Mr. A.R. Wallace in the Islands of Bachian, Kaisaa, Amboyna, Gilolo, and at Dory in New Guinea. *Journal of the Proceedings of the Linnean Society, Zoology* 5 (supplement to vol. 4): 93-143, pl. 1.
1863. Catalogue of hymenopterous insects collected by Mr. A.R. Wallace in the Islands of Mysol, Ceram, Waigiou, Bouru and Timor. *Journal of the Proceedings of the Linnean Society, Zoology* 7: 6-48.
- Turner, G. 1897. Notes upon the Formicidae of Mackay, Queensland. *Proceedings of the Linnean Society of New South Wales* 22: 129-144.
- Viehmeyer, H. 1912. Ameisen aus Deutsch Neuguinea gesammelt von Dr. O. Schlaginhaufen. Nebst einem Verzeichnisse der papuanischen Ameisen. *Abhandlungen und Berichte des Königl. Zoologischen und Anthropologisch-Ethnographischen Museums zu Dresden* 14: 1-26, pl. 1.
- Wheeler, W.M. 1911a. Three formicid names which have been overlooked. *Science (NS)* 33: 858-860.
- 1911b. A list of the type species of the genera and subgenera of Formicidae. *Annals of the New York Academy of Sciences* 21: 157-175.
1912. New names for some ants of the genus *Formica*. *Psyche* 19: 90.
1915. Scientific notes on an expedition into the north-western regions of South Australia. Hymenoptera. *Transactions and Proceedings of the Royal Society of South Australia* 39: 805-823.
1919. The Ants of Borneo. *Bulletin of the Museum of Comparative Zoology* 63: 43-147.
1922. Ants of the American Museum Congo Expedition. A contribution to the myrmecology of Africa. Part 7. Keys to the genera and subgenera of ants. *Bulletin of the American Museum of Natural History* 45: 631-710.
1927. Chinese ants collected by Professor S.F. Light and Professor N. Gist Gee. *American Museum Novitates* 255: 1-12.
1935. Check list of the ants of Oceania. *Occasional Papers of the Bernice P. Bishop Museum* 11(11): 1-56.

CLUTCH TRAITS AND CLUTCH SIZE-BODY SIZE RELATIONSHIPS IN THE GECKO *OEDURA MONILIS*

Memoirs of the Queensland Museum - Nature 56(2): 579-579. 2013:- Resources allocated to reproduction are determined by costs and benefits associated with current versus future reproductive potential. Life history theory posits that the optimal balance between egg size and number should maximize offspring survivorship, and in turn, female life-time reproductive success (Stearns 1992). In most squamate reptiles, larger females produce both larger and more offspring (Dunham *et al.* 1988). However, for invariant clutch species, which produce a fixed clutch size, this relationship may break down, because females are unable to change clutch size even as body size increases. As an invariant clutch is phylogenetically constrained for geckos (Doughty 1997), they provide an excellent opportunity to examine relationships between maternal body size (snout-vent length and post-oviposition mass) and egg-size and clutch mass. This paper reports clutch traits, and examines the relationship between maternal size (snout-vent length and post-oviposition mass) and egg size (mass) in the gecko *Oedura monilis* de Vis, 1888, a medium-sized (snout-vent length to 85 mm) arboreal and rock-inhabiting gecko that occurs in dry timber habitats from northern New South Wales to northern Queensland (Bustard 1971). Gravid *O. monilis* were sampled intermittently from October-December 1995 from the Townsville district of north-east Queensland, Australia. Individuals were maintained separately in plastic containers (350 L x 130 W x 100 H mm), with a potting mix substrate, bark refuge, water bowl and a heating element that produced a thermal gradient within each box (range 45-23° C) and enabled lizards to thermoregulate. Lizards were fed 2-3 mealworms or crickets three-four times weekly; water was always available. All females and their eggs were weighed (± 0.1 g) and measured (females: snout-vent length, SVL; eggs, length and width; ± 0.1 mm), within eight hours of oviposition. All gravid females laid eggs within 3 weeks of collection. We calculated relative clutch mass (RCM) as the ratio of total wet clutch mass to post-oviposition mass (Shine 1980). Maternal size-clutch trait relationships were examined using regressions and correlations. All data were log-transformed to achieve normality. Female body condition (mass per unit length) and reproductive investment (as clutch mass) were assessed by comparing wet clutch mass against residuals of the regression of post-oviposition mass against snout-vent length.

All females produced clutches of two eggs (Table 1). Total wet clutch mass was significantly correlated with maternal post-oviposition mass ($r = 0.64$, $n = 11$, $P < 0.035$), indicating that heavier females produced heavier clutches. However, snout-vent length was unrelated to total wet clutch mass ($r = 0.15$, $P > 0.65$), indicating that longer females did not produce heavier clutches. Maternal body condition was significantly positively related to clutch mass ($r = 0.72$, $P < 0.05$), suggesting females in better condition produce heavier clutch masses.

The relationship between post-oviposition mass and clutch mass indicates that egg size and maternal mass increase as abdominal space and/or resources become available. The lack of a relationship between snout-vent length and pelvic aperture, between snout-vent length and clutch mass, and between snout-vent length and egg size may indicate egg diameter is less than that of the pelvic aperture (Congdon & Gibbons 1987), and is therefore, unconstrained. However, it must be acknowledged that

the size range of females examined in this study was relatively small, therefore, to definitively test this idea would warrant a larger sample of females. The relationship between maternal body condition and clutch mass suggests that females in better condition produce heavier clutches, and have a higher reproductive investment. Mixed reports on relationships between body size and clutch mass (Vitt 1986; Doughty 1997), suggests other factors (e.g. food availability) may determine egg size, and therefore, clutch mass. Moreover, species that produce multiple clutches per season, as has been shown for a population of *O. monilis* (Bustard 1971), may show considerable variation in such traits as clutch size. For instance, clutch size is reduced and egg size is increased in clutches produced later in the season in several North American lizard species (Nussbaum 1981; Demarco 1989). However, it is difficult to assess whether this is likely to be an issue for invariant clutch-size species, such as the species examined in this study, as all females were collected over a two month period (Mid-October to mid-December).

The relationship between body condition and clutch mass may suggest that females in better condition increase their allocation to reproduction. This pattern of condition-dependent reproductive investment is more frequently observed in relatively long-lived species that are likely to experience more than a single reproductive season within a lifetime (Tinkle *et al.* 1970). Clearly, more data on seasonal variation in food availability, longevity, demography and age-specific reproductive investment in *O. monilis* is required (e.g. Bustard 1967), to determine whether *O. monilis* shows a pattern of condition-dependent reproductive investment.

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Literature cited

Bustard, R.H. 1967. Reproduction in the Australian gekkonid genus *Oedura* (Gray 1842). *Herpetologica*, 23:276-284.
 1971. A population study of the eyed gecko, *Oedura ocellata* Boulenger, in Northern New South Wales, Australia. *Copeia* 1971: 658-669.
 Congdon, J.D. & Gibbons, J.W. 1987. Morphological constraint on egg size: a challenge to optimal egg size theory? *Proceedings of the National Academy of Science USA*, 84:4145-4147.
 Demarco, V.G. 1989. Annual variation in the seasonal shift in egg size and clutch size in *Sceloporus woodi*. *Oecologia*, 80: 525-532.
 Doughty, P. 1997. The effects of "fixed" clutch sizes on lizard life-histories: reproduction in the Australian velvet gecko, *Oedura lesueurii*. *Journal of Herpetology*, 31:266-272.
 Dunham, A.E., D.B. Miles, & D.N. Reznick. 1988. Life history patterns in squamate reptiles. Pp.441-522. In: Gans, C. & Huey, R.B. (eds) *Biology of the Reptilia*. (Alan R. Liss, Inc.: New York).
 Nussbaum, R.A. 1981. Seasonal shifts in clutch size and egg size in the side-blotched lizard, *Uta stansburiana* Baird and Girard. *Oecologia* 49:8-13.

TABLE 1. Clutch traits for *Oedura monilis*. Shown are mean \pm standard error (N = 11).

TRAIT	Mean \pm S.E.	Range
Snout-vent length (mm)	95.18 \pm 0.829	90.0 – 99.0
Post-oviposition mass (g)	13.07 \pm 0.387	11.01 – 14.81
Clutch size	2	2
Clutch mass (g)	2.50 \pm 0.095	2.049 – 3.083
Relative clutch mass	0.192 \pm 0.006	0.175 – 0.244
Egg length (mm)	19.35 \pm 0.330	17.3 – 21.5
Egg width (mm)	10.56 \pm 0.150	9.60 – 11.55

- Shine, R. 1980. 'Costs' of reproduction in reptiles. *Oecologia*. 46:92-100.
- Stearns, S.C. 1992. *The evolution of life histories*. (Oxford University Press: Oxford).
- Tinkle, D.W., Wilbur, H.M. & Tilley, S.G. 1970. Evolutionary strategies in lizard reproduction. *Evolution*. 24:55-74.
- Vitt, L.J. 1986. Reproductive tactics of sympatric Gekkonid lizards with a comment on the evolutionary and ecological consequences of invariant clutch size. *Copeia*. 1986:773-786.
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Morphological data show that *Hyla dayi* Günther, 1897 (Amphibia: Anura: Hylidae) should never have been assigned to *Nyctimystes*

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ABSTRACT

The treefrog described as *Hyla dayi* Günther and now known as *Litoria dayi* is restricted to the Wet Tropics of northern Queensland and has long been a source of taxonomic confusion. For many years this species was placed in *Nyctimystes*, but here I show that this frog never met the morphological criteria for assignment to that genus, which has long been defined by the combination of a vertically oriented pupil and the presence of a reticulum of coloured lines on the palpebrum. In particular, this species lacks the diagnostic vertical pupil on the basis of which *Nyctimystes* was originally erected. This is important because recent molecular studies have used this species and its erroneous generic assignment to provide misleading phylogenetic “tests” purporting to refute the monophyly of *Nyctimystes*. Recognising that *L. dayi* was never properly placed within *Nyctimystes* obviates these claims. Morphological and more recent molecular evidence both support a monophyletic *Nyctimystes* restricted to the Papuan region. I note an additional cranial character that, upon broader taxonomic investigation, may further support the monophyly of that genus. □ *Litoria dayi*, *Nyctimystes*, *Pelodyadinae*, *Queensland*, *Treefrog*, *Wet Tropics*.

The pelodyadine hylid frog originally described by Günther (1897) as *Hyla dayi* and currently known as *Litoria dayi* is restricted to a small area of the northern Queensland Wet Tropics and has been the source of considerable taxonomic confusion, the ramifications of which continue to the present. The holotype is lost (Tyler, 1968) and the original description was not particularly detailed, and this led to confusion as to which frog species the name properly applied. Liem (1974), in a review of northern Queensland small-eared treefrogs, showed that Günther’s name *H. dayi* was not properly assigned to the frog previously referred to as *Litoria dayi* by Loveridge (1935), Copland (1957), and Tyler (1968). He showed instead that the original description better accorded with frogs then placed in the genus *Nyctimystes*, but he

could not clearly assign the name to any of the three Queensland *Nyctimystes* species then recognised. Liem (1974) then provided a name for the frog erroneously treated as *L. dayi* by Loveridge (1935), Copland (1957), and Tyler (1968), describing it as *L. nyakalensis*. It is this early assignment of *Hyla dayi* to *Nyctimystes* that continues to provide problems for modern taxonomy.

Frogs placed in *Nyctimystes* were first distinguished from all other Australo-Papuan hylids on the basis of having the long axis of the pupil oriented vertically instead of horizontally. Boulenger (1882) erected the genus *Nyctimantis* for an Ecuadorian hylid having a vertical pupil and then later assigned new treefrog species from New Guinea to that genus on the basis of sharing that same feature (Boulenger,

1897, 1914). Stejneger (1916) pointed out the improbability of frogs from those two continents being directly related phylogenetically, noted that the South American species had the skin co-ossified with the skull whereas the Papuan species did not, and provided the replacement name *Nyctimystes* for the Papuan species. That name was then used for additional Papuan species having a vertical pupil (Parker 1936). The first comprehensive review of *Nyctimystes* described seven additional species, transferred two species to and removed four species from the genus, and provided a re-definition that included more characters (Zweifel 1958). Since that time, *Nyctimystes* has been defined as having the unique combination of (1) the contracted pupil forming a vertical slit, (2) a reticulum of pigmented lines on the transparent membrane of the lower eyelid, (3) the tip of the first toe not reaching the disc of the second, and (4) the skin not co-ossified with the skull. The last two characters serve to distinguish *Nyctimystes* from unrelated American forms having a vertical pupil and/or palpebral reticulum, such as *Agalychnis* and *Nyctimantis* (Zweifel 1958), leaving the combined presence of a vertical pupil and a palpebral reticulum as the definitive character combination distinguishing *Nyctimystes* among the Australo-Papuan pelodyadine hylids.

Nyctimystes was first thought to be represented in Australia when Tyler (1964) described *N. hosmeri* and *N. vestigea*, each on the basis of a single specimen. He later (Tyler 1968) transferred *Hyla tympanocryptis* (Andersson 1916), also known only from the holotype, to *Nyctimystes*. These generic assignments were based on the presence in all examined specimens of the palpebral reticulum characteristic of *Nyctimystes*, but the second diagnostic feature – vertical orientation of the pupil – was left unremarked. As noted above, Liem (1974) later showed that frogs referable to *Hyla dayi* also belonged with these three presumptive *Nyctimystes* species. Czechura *et al.* (1987) examined 174 specimens of *Nyctimystes* from Queensland, including all extant type material, and showed that all four of these names apply to only one

variable species, for which *Hyla dayi* (Günther 1897) was the oldest available name. Since that time, *Nyctimystes dayi* has been considered the sole Australian representative of the genus, which has two dozen additional species described from New Guinea and one known from Halmahera, Indonesia. On the basis of a phylogeny derived from DNA sequence data, Frost *et al.* (2006) synonymised *Nyctimystes* with *Litoria*; therefore, this frog is currently referred to as "*Litoria dayi*".

During a casual examination of specimens of *Litoria dayi* in the collection of the Australian Museum, Sydney, I noticed that some specimens clearly had the contracted pupil oriented horizontally instead of vertically. To assess the generality of this surprising finding, I later examined the much larger collection of specimens of the same species in the Queensland Museum to determine whether intraspecific variation occurred in this feature. I report my findings and their taxonomic implications here.

MATERIALS AND METHODS

I examined pupil shape and long-axis orientation in all 394 specimens of *Litoria dayi* in the collections of the Australian Museum, Sydney (AMS) and the Queensland Museum (QM). Examined specimens included topotypic material of all named forms, all but three specimens (the three extant holotypes) examined by Czechura *et al.* (1987), and 223 additional specimens collected since that study. I confirmed that specimens were correctly assigned to *L. dayi* by verifying the presence of the palpebral reticulum in each; *L. dayi* is the only Australian hylid to have this feature. Because of the large number of specimens involved, the brief duration of my visits, and the fact that my findings were uniform and unambiguous with respect to pupil morphology I did not record catalogue numbers for each specimen involving each of the three pupil states: widely dilated, contracted and horizontally oriented, or contracted and vertically oriented.

Material Examined. *Litoria dayi* ($n=394$). Australia: Queensland: Alexandra Creek, McDowall Range, 16° 6' 45" S, 145° 20' 50" E (QM J66037-38); Atherton, 17° 16' S, 145° 29' E (AMS R39722); Atherton Rd, just before Mt Hypipamee National Park, 17° 26' 0" S, 145° 29' 0" E (QM J29524-25); Atherton Tableland, 17° 16' S, 145° 29' E (QM J25080, J25084-85); Babinda Creek, Babinda, 17° 22' S, 145° 55' E (QM J55599-607, J55617-25, J55627, J56145-47); Barron River, 17° 3' S, 145° 26' E (QM J13012, J43620-23, J55842-43); Bartle Frere, 17° 27' S, 145° 52' E (QM J30914, J32072, J32093-94, J32099, J32113, J32119, J32124, J32133-34, J32170-72); Beatrice River, near Millaa Millaa, 17° 33' S, 145° 39' E (QM J54923-25, J55628-32, J56182-85, J56493-94, J56496-97); Behana Gorge, 17° 10' S, 145° 49' E (QM J61844); Big Tableland, 15° 42' 30" S, 145° 16' 30" E (QM J60914); Billy Creek, 17° 49' 25" S, 145° 47' 5" E (QM J48220-21); 16 km from Bloomfield River, 16° 2' S, 145° 15' E (QM J36324-25); Broadwater Creek National Park, 11 km S Mt McAlister, 18° 23' 30" S, 145° 56' 30" E (QM J61211-12); Bushy Creek, near Julatten, 16° 36' S, 145° 20' E (QM J55626); Cairns Intake, Lake Placid Station, 16° 52' S, 145° 40' E (QM J55580-82); Cape Tribulation, 16° 5' S, 145° 29' E (QM J36323, J36326-29, J41322, J52165); Charappa Creek, Walter Hill Range, 17° 42' 20" S, 145° 40' 20" E (QM J66040-42, J67192); Charmillan Creek, Tully Falls Rd, 17° 42' S, 145° 31' E (QM J56144, J56492); Crystal Cascades, 16° 58' 0" S, 145° 40' 40" E (AMS R55967, QM J62086); Dalrymple Gap, 18° 24' 45" S, 146° 4' 58" E (QM J86782-83); Davies Creek, Kuranda-Mareeba, 17° 3' S, 145° 33' E (QM J56181); Dinner Falls, 10 km SE Herberton, 17° 26' S, 145° 28' E (AMS R53954); Dirran Creek, 13 km S Malanda, 17° 28' S, 145° 33' E (QM J55572-79, J56108-22, J56127, J56178-80, J56498-99); Gap Creek, Mt Finlay, 15° 48' 45" S, 145° 19' 5" E (QM J57832); Goolagan Creek, 27 km W Innesfail, 17° 36' S, 145° 48' E (AMS R85587); Helenvale, 15° 42' S, 145° 13' E (AMS R56702); Henrietta Creek, Palmerston Hwy, 17° 36' S, 145° 45' E (QM J25570-71, J36332-37, J41085-94, J54926, J56188-90, J65538, J66039, J66045-49); Home Rule Camp, via Wallaby Creek, 15° 44' S, 145° 18' E (QM J24857); Home Rule, 4 km E "The Granites", 15° 45' 40" S, 145° 20' 55" E (QM J25277); Home Rule, Slaty Creek, 15° 44' S, 145° 18' E (AMS R26778-79); Home Rule, Wallaby Creek, 15° 44' S, 145° 15' E (QM J25147-50, J25180, J25219); Home Rule Falls, 15° 44' S, 145° 18' E (QM J25261-62, J75830); 34 km W Innisfail, 17° 34' S, 145° 45' E (QM J29717-24); Jira Cave, Russell River, 5.8 km SW Mt. Bartle Frere, 17° 26' 39" S, 145° 47' 10" E (QM J74726-29); Koombooloomba Dam, 17° 50' S, 145° 36' E (QM J29559-62, J29573-75); Little Forks, via Shiptons Flat, 15° 49' S, 145° 13' E (QM J27151, J27163, J27259); Maalan State Forest, via Millaa Millaa, 17° 37' S, 145° 38' E (QM J31181); Malanda Creek, near Malanda Falls, 17° 21' S, 145° 36' E (QM J55844-45); McDowall Range, 16° 6' 45" S, 145° 20' 50" E (QM J66035-36); McHugh Bridge, 42.8 km E Ravenshoe, 17° 34' S, 145° 41' E (QM J29600, J29670-76); Meunga Creek, Cardwell, 18° 16' 30" S, 145° 52' 30" E (QM J48320-21); Millaa Millaa Falls, 17° 31' S, 145° 37' E (QM J55608-15, J56123-26); Millstream National Park, 17° 38' 35" S, 145° 27' 25" E (QM J67198); Mossman Gorge, 16° 28' 15" S, 145° 19' 40" E (AMS R26603-05, QM J52164, J52167, J60942); Mt Fox State Forest, 18° 34' 48" S, 145° 47' 1" E (QM J66044); Mt Hypipamee National Park, 17° 25' 40" S, 145° 29' 15" E (QM J24529-30, J66108, J66127-28); Mt Lewis, 16° 35' S, 145° 15' E (QM J43618); Mt Spec, 18° 57' S, 146° 11' E (QM J36309-11, J36318-20, J41084); Mt Spurgeon, 16° 26' S, 145° 12' E (QM J56186-87, J56700); northern Queensland (QM J41321); O'Keefe Creek, Big Tableland, 15° 42' 30" S, 145° 16' 30" E (QM J63708-09); Palmerston, 17° 37' S, 145° 40' E (QM J32066-67); Palmerston Hwy, 17° 34' S, 145° 42' E (QM J31966); Palmerston Hwy, near Millaa Millaa, 17° 34' S, 145° 42' E (QM J32080, J32098, J32131-32, J32139); Palmerston National Park, 17° 35' 58" S, 145° 45' 27" E (AMS R33423, QM J63702); Palmerston National Park, Boulder Creek, 17° 37' S, 145° 40' E (QM J36314-17, J36338-47); Palmerston Rocks National Park, 17° 34' 30" S, 145° 53' 30" E (QM J61320, J87114); Paluma, 19° 0' S, 146° 12' E (QM J29593-96, J30899, J32097, J32122, J32173); Parrot Creek, Shiptons Flat, 15° 48' S, 145° 16' E (QM J13158, J40547); South Johnston River, near Millaa Millaa, 17° 40' S, 145° 48' E (QM J56139-43); Stallions Pocket, Mulgrave River, 17° 12' S, 145° 45' E (QM J30905-06, J30908-12, J32068, J32091, J32096, J32101-02, J32130, J32166, J32168); The Boulders, Babinda, 17° 20' S, 145° 54' E (QM J36330-31, J41076-78, J41081-83); The Crater, 17° 26' S, 145° 29' E (QM J30700, J30917-19, J32095); Thiaki Rd, 6 km E Mt Hypipamee National Park, 17° 25' S, 145° 32' E (QM J32164-65); Tully, 17° 46' 30" S, 145° 38' 30" E (QM J60922); Tully Falls, 17° 46' S, 145° 34' E (QM J29258, J32065, J32092, J32100, J32169, J32174, J36308, J36312-13, J36321-22, J41079-80, J56161-70); Tully River, H Rd, 1 km from Tully River bridge, 17° 46' 45" S, 145° 39' 40" E (QM J48195-98); Tully River, 1st Creek E of bridge, 17° 47' 30" S, 145° 40' 30" E (QM J60950); Tully River, 2nd Creek E of bridge, 17° 48' 30" S, 145° 41' 30" E (QM J60913, J60948); Upper Russell River, W slope Mount Bartle Frere, 17° 23' S, 145° 42' E (AMS R61388, QM J56148-49); Wallaman Falls National Park, 18° 34' 30" S, 145° 47' 30" E (QM J61292-93, J61299-300); Walsh Falls, 3 km from Atherton, 17° 18' S, 145° 25' E (QM J56150-53); West Mulgrave River, W side Mt Bellenden Ker, 17° 17' S, 145° 48' E (QM J56128-38, J56154-60, J56171-77, J56495); Windsor Tableland State Forest, 16° 12' 30" S, 144° 58' 30" E (QM J52166, J57847); Wongabel area, 17° 19' S, 145° 26' E (QM J43684-87); Yuccabine Creek, Kirrama State Forest, 18° 12' 30" S, 145° 45' 50" E (QM J71258).

RESULTS

Most specimens examined had the pupil so widely dilated that it appeared either round or diamond-shaped, with neither axis unambiguously narrower than the other. Many of these also had a white flocculant material beneath the cornea that made determining the pupil's outline difficult. Nonetheless, in several dozen specimens with clearly viewable, nicely contracted pupils, these were invariably oriented with the long axis on the horizontal plane, as seen in any other *Litoria* species. AMS 26604, 39722, and 61388 serve as exemplars illustrating this character state. No specimen had the vertical pupil characteristic of *Nyctimystes* and observed by me in hundreds of specimens of more than 20 species in that genus (partial list provided in Kraus (2012)).

DISCUSSION

The significance of a horizontal pupil in *Litoria dayi* is that previous assignment of these frogs to the genus *Nyctimystes* was in error, being based solely on possession of a palpebral reticulum, a feature that comprises only one of the two characters that *in combination* define the genus and which was first used to assist in diagnosing the genus more than 40 years after it was defined on the basis of pupil shape. How is it that the failure of *Litoria dayi* to meet both morphological criteria for valid membership in *Nyctimystes* could be overlooked for approximately 50 years? Tyler (1964) first placed his *N. hosmeri* and *N. vestigea* in *Nyctimystes* based on their possessing the characteristic palpebral reticulum of that genus. However, both species were described from single specimens, each of which had a widely dilated pupil whose orientation could not be distinguished as either vertical or horizontal; hence, the second diagnostic character for membership in the genus could not be assessed. Similarly, Tyler (1968) transferred *Hyla tympanocryptis* to *Nyctimystes* on the basis of examining the holotype (and sole known specimen) but without noting the character state for the pupil, a point on which Andersson (1916) was also silent. Liem (1974)

used adult body size, extent of finger webbing, and dorsal color pattern in determining that *Hyla dayi* should be referred to *Nyctimystes*; he also made no mention of pupil shape in his specimens. More problematically, Czechura *et al.* (1987) stated in their summary description of *N. dayi* "Pupil vertically elliptical". But, even though they examined a large series of specimens, their claim is directly contradicted by my observations of the same material (Appendix I). Hence, it would appear to be not an empirical assessment of the character so much as a pro forma statement of expectation based on judging that the species belonged in *Nyctimystes* given its obvious palpebral reticulum. The similar claim for a vertical pupil in Cogger (1975) should also be viewed as non-empirical inasmuch as that is a secondary literature source. Thus, the origin of this easily observed error and its persistence for almost 50 years likely derives from original allocation of these frogs to *Nyctimystes* solely based on presence of the palpebral reticulum, correlation of that feature with a vertical pupil in other Australo-Papuan hylids, assumption that this correlation applied as well in Australian frogs having a palpebral membrane, and failure of subsequent researchers to critically evaluate prior literature claims. Interestingly, Davies and Richards (1990, fig. 3) illustrated a horizontal pupil in the tadpole of *L. dayi* but did not remark upon the feature.

The discovery that *Hyla dayi* and its synonyms do not fit with *Nyctimystes* on morphological grounds conforms with recent molecular evidence indicating that the species rightly belongs in *Litoria* and not with *Nyctimystes* (e.g. Frost *et al.* 2006; Rossauer *et al.* 2009; Faivovich *et al.* 2010; Wiens *et al.* 2010). Indeed, *L. dayi* appears closely related to the same species group (*L. nannotis*, *L. nyakalensis*, *L. rheocola*) from which Liem (1974) originally distinguished it (Rossauer *et al.* 2009). That a palpebral reticulum could evolve multiple independent times within Pelodyadinae is unsurprising, given that it has clearly done so as well in two distantly related American hylid genera as well as in unrelated rhacophorid treefrogs. In this regard, it is worth noting that some other *Litoria* have pigmented

patterns on the palpebrum (e.g., *Litoria saurouii* [Richards & Oliver, 2006] and an undescribed *Litoria* in possession of the author), although these do not form a reticulum, so *Litoria* is clearly more variable in palpebral pigmentation than earlier thought. Future study of fresh material of the Halmaheran *N. rueppelli* (Boettger, 1895) may show that species to provide another such instance inasmuch as it too was assigned to *Nyctimystes* solely on the basis of presence of a palpebral reticulum and it represents the only species assigned to *Nyctimystes* having a darkened animal pole to the eggs (Zweifel 1958); hence, it may also prove to be unrelated to the Papuan species that otherwise comprise the genus.

That placement of *Hyla dayi* in *Nyctimystes* was not justified morphologically might seem a trivial discovery except that it impacts on recent interpretations of the monophyly of *Nyctimystes*. In their large study of lissamphibian phylogeny, Frost *et al.* (2006) included ten species as exemplars of pelodyadine hylid frogs, including two putative members of *Nyctimystes*: “*N.*” *dayi* and *N. pulcher*. They found the latter two species to not group together, concluded on that basis that *Nyctimystes* was paraphyletic, and accordingly synonymised that genus with *Litoria*. Doing this created a *Litoria* with 197 species that is synonymous with the already recognised presumptive clade Pelodyadinae (Tyler 1971; Savage 1973). Frost *et al.* (2006) expressed some surprise at their finding of paraphyly in *Nyctimystes*, noting that “morphological evidence would suggest that *Nyctimystes* is monophyletic”. That conundrum is readily explained, however, when one recognises that *Hyla dayi* was improperly assigned to *Nyctimystes* to begin with and that, accordingly, Frost *et al.* (2006) did not actually provide a test of the monophyly of *Nyctimystes*.

Subsequent to Frost *et al.* (2006), more comprehensive molecular-phylogenetic surveys of pelodyadine hylids have (depending on the study) included 6–12 Papuan exemplars of *Nyctimystes* and consistently recovered that genus as monophyletic (Rossauer *et al.*, 2009; Faivovich *et al.*, 2010; Wiens *et al.*, 2010). These findings, coupled with recognition that *L.*

dayi was improperly included in *Nyctimystes*, support taxonomic revalidation of *Nyctimystes* as a clade of distinctive Papuan stream-breeding frogs. Of course, recognising *Nyctimystes* as a valid clade once again leaves *Litoria* paraphyletic, pending additional resolution of relationships within Pelodyadinae and taxonomic action on those findings. However, that unsatisfactory situation has long been recognised anyway, at least by implication (e.g. Tyler & Davies 1979; Hutchinson & Maxson 1987), is merely provisional until a well-supported monophyletic taxonomy is available for the group, and has the advantage of meanwhile identifying two clades (Pelodyadinae, *Nyctimystes*) instead of the single clade (*Litoria* = Pelodyadinae) proposed by Frost *et al.* (2006). Since identifying and taxonomically recognising distinctive clades is a major goal of modern systematics, reinstatement of *Nyctimystes* as a valid genus meets this goal better than the current pelodyadine taxonomy (Frost *et al.* 2006; Frost 2012).

Lastly, removal of *Litoria dayi* from association with *Nyctimystes* suggests an additional morphological feature that may add to the diagnosis of *Nyctimystes*. All eight species of *Nyctimystes* osteologically examined in detail by Tyler & Davies (1979) have the pars facialis of the maxilla well developed and (in all but one species) in contact with the maxillary process of the nasal. In *Litoria*, the pars facialis varies from shallow to deep but is not in contact with the nasal, except in the *L. aurea* group (Tyler & Davies 1978, 1979). Should this finding be confirmed across a broader taxonomic sample of pelodyadine frogs and should nasal-maxilla contact prove derived within pelodyadines, it would provide further support for monophyly of *Nyctimystes*.

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LITERATURE CITED

- Andersson, L.G. 1916. Results of Dr. E. Mjöberg's Swedish scientific expeditions to Australia 1910-1913. IX. Batrachians from Queensland. *Königliche Svenska Vetenskaps-Akademiens Handlingar* (new series) 52(9): 1-20.
- Boettger, O. 1895. Liste der Reptilien und Batrachier der Insel Halmahera nach den Sammlungen Prof. Dr. W. Kükenthal's. *Zoologischer Anzeiger* 18: 129-138.
- Boulenger, G.A. 1914. An annotated list of the batrachians and reptiles collected by the British Ornithologists' Union Expedition and the Wollaston Expedition in Dutch New Guinea. *Transactions of the Zoological Society of London* 20: 247-274.
1897. Descriptions of new lizards and frogs from Mount Victoria, Owen Stanley Range, New Guinea, collected by Mr. A. S. Anthony. *Annals and Magazine of Natural History*, 6th series 19: 6-13.
1882. *Catalogue of the Batrachia Salientia s. Ecaudata in the collection of the British Museum*, 2nd ed. (Taylor & Francis: London).
- Cogger, H.G. 1975. *Reptiles and amphibians of Australia*. (Ralph Curtis Books: Hollywood, Florida, USA).
- Copland, S.J. 1957. Australian tree frogs of the genus *Hyla*. *Proceedings of the Linnean Society of New South Wales* 83: 9-108.
- Czechura, G.V., Ingram, G.J. & Liem, D.S. 1987. The Genus *Nyctimystes* (Anura: Hylidae) in Australia. *Records of the Australian Museum* 39: 333-338.
- Davies, M., & Richards, S.J. 1990. Developmental biology of the Australian hylid frog *Nyctimystes dayi*. *Transactions of the Royal Society of South Australia* 114: 207-211.
- Faivovich, J., Haddad, C.F.B., Baêta, D., Jungferd, K.-H., Álvares, G.F.R., Brandão, R.A., Sheil, C., Barrientos, L.S., Barrio-Amorós, C.L., Cruz, C.A.G. & Wheeler, W.C. 2010. The phylogenetic relationships of the charismatic poster frogs, Phyllomedusinae (Anura, Hylidae). *Cladistics* 26: 227-261.
- Frost, D.R. 2012. Amphibian species of the world: an online reference, version 5.5. Available at <http://research.amnh.org/vz/herpetology/amphibia/index.html>. American Museum of Natural History, New York, USA.
- Frost, D.R., Grant, T., Faivovich, J., Bain, R.H., Haas, A., Haddad, C.F.B., de Sá, R.O., Channing, A., Wilkinson, M., Donnellan, S.C., Raxworthy, C.J., Campbell, J.A., Blotto, B.L., Moler, P., Drewes, R.C., Nussbaum, R.A., Lynch, J.D., Green, D.M. & Wheeler, W.C. 2006. The amphibian tree of life. *Bulletin of the American Museum of Natural History* 297: 1-370.
- Günther, A. 1897. Descriptions of new species of lizards and of a tree-frog from north-eastern Queensland. *Novitates Zoologicae* 4: 403-406.
- Hutchinson, M.N. & Maxson, L.R. 1987. Phylogenetic relationships among Australian treefrogs (Anura: Hylidae: Pelodyadinae): an immunological approach. *Australian Journal of Zoology* 35: 61-74.
- Kraus, F. 2012. A new species of *Nyctimystes* (Anura: Hylidae) from Papua New Guinea. *Herpetologica* 68: 541-550.
- Liem, D.S. 1974. A review of the *Litoria nannotis* species group, and a description of a new species of *Litoria* from northern Queensland, Australia (Anura: Hylidae). *Memoirs of the Queensland Museum* 17: 151-168.
- Loveridge, A. 1935. Australian amphibia in the Museum of Comparative Zoology, Cambridge, Massachusetts. *Bulletin of the Museum of Comparative Zoology, Harvard* 78: 1-62.
- Parker, H.W. 1936. A collection of reptiles and amphibians from the mountains of British New Guinea. *Annals and Magazine of Natural History*, 10th series 17: 66-93.
- Richards, S.J. & Oliver, P.M. 2006. Two new species of large green canopy-dwelling frogs (Anura: Hylidae: *Litoria*) from Papua New Guinea. *Zootaxa* 1295: 41-60.
- Rossauer, D., Laffan, S.W., Crisp, M.D., Donnellan, S.C. & Cook, L.G. 2009. Phylogenetic endemism: a new approach for identifying geographical concentrations of evolutionary history. *Molecular Ecology* 18: 4061-4072.
- Savage, J.M. 1973. The geographic distribution of frogs: patterns and predictions. Pp. 351-445. In Vial, J.L. (ed.) *Evolutionary biology of the anurans: contemporary research on major problems*. (University of Missouri Press: Columbia).
- Stejneger, L. 1916. New generic name for a tree-toad from New Guinea. *Proceedings of the Biological Society of Washington* 29: 85.
- Tyler, M.J. 1971. The phylogenetic significance of vocal sac structure in hylid frogs. *University of Kansas Museum of Natural History Occasional Papers* 19: 319-360.
1968. An additional species of the hylid frog genus *Nyctimystes* with notes on *Hyla dayi* Gunther. *Arkiv för Zoologi* 20(22): 501-504.
1964. Two new species of Australian frogs of the hylid genus *Nyctimystes*. *Transactions of the Royal Society of South Australia*. 88: 111-114.
- Tyler, M.J. & Davies, M. 1979. Redefinition and evolutionary origin of the Australopapuan hylid frog genus *Nyctimystes* Stejneger. *Australian Journal of Zoology* 27: 755-772.

1978. Species-groups within the Australopapuan hylid frog genus *Litoria* Tschudi. *Australian Journal of Zoology, Supplementary Series* **63**: 1–47.
- Wiens, J.J., Kuczynski, C.A., Hua, X. & Moen, D.S. 2010. An expanded phylogeny of treefrogs (Hylidae) based on nuclear and mitochondrial sequence data. *Molecular Phylogenetics and Evolution* **55**: 871–882.
- Zweifel, R.G. 1958. Results of the Archbold Expeditions. No. 78. Frogs of the Papuan hylid genus *Nyctimystes*. *American Museum Novitates* **1896**: 1–51.

PERICLIMENES BURRUP BRUCE, 2008, AN ADDITION TO THE PONTONIINE SHRIMP FAUNA OF HERON ISLAND, QUEENSLAND

Memoirs of the Queensland Museum – Nature 56(2): 588. 2013:- The pontoniine shrimp fauna of Heron Island, one of the Capricorn Island group, on the southern Great Barrier Reef, was intensively studied from 1975–1980 and the presence of 100 species was recorded (Bruce 1981) and recently extended by the CReefs Heron Island Biodiversity Expedition 2009 (Bruce 2010a, 2010b, 2011), increasing the number of species now known to 113. Re-examination of some old collections provided specimens of a further species, *Periclimenes burrup* Bruce, 2007, which is now added to the Heron Island and Queensland fauna, the second report of the species and the first for the east coast of Australia. The shrimps were found in association with a soft coral, *Dendronephthya* sp., which constitutes a new host record.

Periclimenes burrup Bruce, 2007 (Fig. 1)

Periclimenes burrup Bruce, 2007: 113–116, figs 5–7.

Material Examined. 6 ♂, 8 ovig. ♀, 1 ♀, north Wistari Reef, Heron Island, coll D. Fisk, stn. DF.64, scuba, 24.5 m, 8 April 1978, QM W29141.

Diagnosis. A species of the *Periclimenes incertus* group (Bruce 1969). Rostral dentition 8–11/1–2 (Fig. 1A), first pereiopod with carpus longer than chela, second pereiopods robust, markedly unequal, major pereiopod dactyl (Fig. 1C) with single small subacute, slightly recurved tooth, proximal half of cutting edge of fixed finger with small subacute, slightly recurved tooth distally and 3–4 smaller rounded teeth proximally, minor pereiopod dactyl unarmed, ambulatory dactyls slender with long unguis and very slender accessory tooth.

Colouration. Not previously reported. Body and appendages mainly transparent, cornea white, fingers of major second pereiopod chalky white, colour not in chromatophores, ovary pale grey, sparsely speckled with small red chromatophores.

Host. *Dendronephthya* sp. [Alcyonacea, det. P.N. Alderslade].

Remarks. The specimens agree well with the original description except the articulated posterior rostral teeth are

not discernible. Ten *Periclimenes* species are now referred to the *incertus* species group (Bruce 2008). Of these six are known from Australian waters but only two, *P. incertus* Borradaile, 1915, and *P. toloensis* Bruce, 1969, have been found on Heron Island. *Periclimenes burrup* is readily distinguishable from these by the form of the fingers of the major second pereiopod. It has been suggested that the report of *P. sinensis* Bruce from the Northern Territory by Bruce & Coombes (1995) may also be referable to *P. burrup* (Bruce 2007).

Distribution. Known only from the type locality, the Burrup Peninsula, and Enderby Island and Roly Rock, Dampier Archipelago, Western Australia, and now Heron Island, Queensland.

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Literature Cited

Bruce, A.J. 1981. Pontoniine shrimps of Heron Island. *Atoll Research Bulletin*, 245: 1–33.
 2007. Palaemonoid shrimps from the Dampier Archipelago (Crustacea: Decapoda). In: Diana S. Jones, (ed.), *Crustaceans collected by the Western Australian Museum/Woodside Energy Ltd. Partnership to explore the Marine Biodiversity of the Dampier Archipelago, Western Australia, 1998–2002. Records of the Western Australian Museum Supplement* 73: 97–129, figs 1–7
 2010a. Pontoniine shrimps (Crustacea: Decapoda: Palaemonidae) from the CReefs 2009 Heron Island Expedition, with a review of the Heron Island pontoniine fauna. *Zootaxa*, 2541: 50–68, figs 1–8.
 2010b. More pontoniine shrimps (Crustacea: Decapoda: Palaemonidae) from the CReefs 2009 Heron Island Expedition. *Zootaxa*, 2604: 20–36, figs 1–11.
 2011. Notes on some Indo-Pacific Pontoniinae, XLVIII. *Onyccaris nieli* sp. nov., a new pontoniine shrimp from Heron Island, Queensland, *Crustaceana*, 84 (3): 319–330, figs 1–5.
 Bruce, A.J., & K.E. Coombes. 1995. The palaemonoid shrimp fauna (Crustacea: Decapoda: Caridea) of the Cobourg Peninsula, Northern Territory. *The Beagle, Records of the Museums and Art Galleries of the Northern Territory*, 12: 101–144, figs 1–12.
 A.J. Bruce, *Queensland Museum, PO Box 3300, South Brisbane, Queensland, 4101 Australia. email: aBruce@broad.net.au. Accepted: 13 December 2011.*

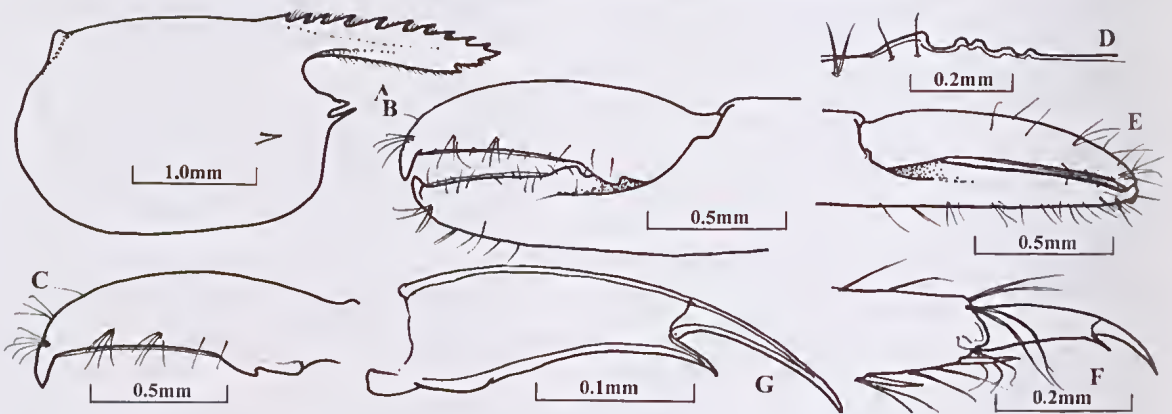


FIG. 1. *Periclimenes burrup* Bruce, 2008. Ovigerous female, postorbital carapace length 1.7 mms, Heron Island, QM W29141. A, carapace and rostrum. B, major second pereiopod, fingers. C, same, dactyl. D, same, fixed finger, proximal cutting edge. E, minor second pereiopod, fingers. F, third pereiopod, distal propod and dactyl. G, same, dactyl.

Survival of a Laughing Kookaburra (*Dacelo novaeguineae*) after the predation of a Cane Toad (*Rhinella Marina*)

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ABSTRACT

Australian wildlife is highly susceptible to poisoning from bufotoxins in the tissues of the introduced Cane Toad *Rhinella marina* (Linnaeus 1758. Formerly *Bufo marinus*). While the outcomes of predation attempts are well documented in Australian mammals and reptiles, the susceptibility of birds is less well known. In a series of incidental observations, an adult Laughing Kookaburra *Dacelo novaeguineae* (Hermann 1783) was seen to survive the predation and ingestion of cane toads on two occasions with no ill effects. □ *survival, predation, Rhinella marina, Dacelo novaeguineae*

The Cane Toad *Rhinella marina*, was introduced to Australia in 1935 as a biological control against agricultural pests (Lever 2001; Shine, 2010). It now occupies much of the east coast and the tropical north, continuing to spread rapidly into Western Australia (Urban *et al.* 2007; Scott-Virtue 2012). The parotoid glands and ovaries of cane toads contain high concentrations of toxic bufadienolides which act as an antipredator defence mechanism (Lever 2001). As Australia has no naturally occurring bufonid species, bufadienolides are novel toxins to many of the predatory vertebrate species that occur there (Cogger 2000). While some predatory vertebrates that co-evolved with bufonids exhibit resistance to their toxins (Phillips *et al.*, 2003), many evolutionarily naive species are highly susceptible to their effects.

Attempts to prey on cane toads by frog-eating snakes, varanids, crocodiles and carnivorous marsupials often have fatal consequences for the predator (Burnett 1997). Hence, some predatory species have adapted behaviourally by avoiding tissues with the highest toxicity (Beckmann & Shine 2011). While the effects of Cane Toad predation by Australian

reptiles and mammals is relatively well documented (Burnett 1997), much less is known about predation attempts by Australian birds (Beckmann & Shine 2009). Herein, I report an observation of successful Cane Toad predation by a Kookaburra. This observation is a response to the specific request from Beckmann and Shine (2009) to publish anecdotal observations of predation attempts on cane toads made by Australian birds.

PREDATION OBSERVATION

The observation commenced at approximately 1700 hrs on the 8th of October 2012 in suburbia in the Greater Brisbane region (-27.5464S, 153.1939E). An adult Laughing Kookaburra, was observed to have secured a prey item, identified as a Cane Toad. From photographs of the event, the toad was estimated to be approximately 75 mm s-v length and to be of poor condition.

The Kookaburra despatched the toad by repeated thrashing against a branch. At 1708 hrs the Kookaburra flew down to a clothes line (Fig 1A) and continued to beat the Toad against



FIG. 1. A sequence of photographs documenting the predation of a cane toad *Rhinella marina* by a Laughing Kookaburra *Dacelo novaeguineae*.

its perch. This manipulation continued until 1711 hrs until the Cane Toad had become limp and pliable (Fig. 1A). The intact Cane Toad was then swallowed whole (Fig. 1B). At 1718 hrs,

seven minutes after swallowing the Cane Toad, the Kookaburra flew away with no ill effects observed. This individual Kookaburra was a member of a resident family group, being identifiable from other members by an unusual patch of pale feathers on its back (Fig. 1C). The same bird was observed on the following two days having survived its encounter and exhibiting no ill effects. Furthermore, the same bird was observed on the 24th of December 2012 preying upon another cane toad under similar circumstances.

Unlike other predatory birds which have been reported to ingest only parts of cane toads (Beckmann & Shine 2011), this Kookaburra was observed to ingest the entire toad. It is likely that, given the bill morphology and feeding strategy of Laughing Kookaburras, partial consumption of non-toxic parts is not possible. I cannot rule out that the Kookaburra did not regurgitate the toad following the initial encounter. However, it is clear from this observation that the species is resilient enough to survive mouthing and ingesting a Cane Toad. Further, that the same Kookaburra was observed taking another Toad at a later date does strongly suggest that Toads are a feature of its diet. The emaciated condition of the Cane Toad on both occasions may have played some part in its predation and consumption, as well as the survival of the Kookaburra.

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LITERATURE CITED

- Beckmann C. & Shine R. (2009). Impact of Invasive Cane Toads on Australian Birds. *Conservation Biology*. **23**: 1544-1549.
- Beckmann C. & Shine R. (2011). Toad's tongue for breakfast: exploitation of a novel prey type, the invasive cane toad, by scavenging raptors in tropical Australia. *Biological Invasions*. **13**: 1447-1455.
- Burnett S. (1997). Colonizing cane toads cause population declines in native predators: reliable

Rh. Predation of Cane Toad by a Kookaburra

- anecdotal information and management implications. *Pacific Conservation Biology*. 3: 65.
- Cogger H. (2000). *Reptiles and Amphibians of Australia*. (Reed New Holland: Sydney).
- Lever C. (2001). *The cane toad: the history and ecology of a successful colonist*. (Westbury: Otley).
- Phillips B.L., Brown G.P. & Shine R. (2003). Assessing the potential impact of cane toads on Australian snakes. *Conservation Biology*. 17: 1738-1747.
- Shine R. (2010). The ecological impact of invasive cane toads (*Bufo marinus*) in Australia. *The Quarterly review of biology*. 85: 253-291.
- Scott-Virtue L. (2012). Kimberly toad busters newsletter 46. URL <http://www.canetoads.com.au/hewslet46.htm>
- Urban M.C., Phillips B.L., Skelly D.K. & Shine R. (2007). The cane toad's (*Chaunus* [*Bufo*] *marinus*) increasing ability to invade Australia is revealed by a dynamically updated range model. *Proceedings of the Royal Society B: Biological Sciences*. 274: 1413-1419.

A new description and association of a larva with the adult male of *Pliocaloca fidesria* Shackleton (Insecta: Trichoptera: Calocidae) from eastern Australia.

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ABSTRACT

The genus *Pliocaloca* Neboiss consists of five species, of which the larva of only one, *P. kleithria* Shackleton, is known. Here we associate the larva of *P. fidesria* Shackleton. The larva is associated with adult males based on molecular and geographical data. Adult males and larvae were collected from the same location at Saddle Tree Creek, Bunya Mountains National Park (NP), southern Queensland. A 657 base pair (bp) fragment of the mitochondrial gene cytochrome oxidase sub unit 1 (COI) was used to verify species association. Two larvae and two adult males successfully yielded COI sequences. Sequences of the larvae and one of the adult males were identical. The other adult male differed from these by only one nucleotide. The larva of *P. fidesria* can be distinguished from *P. kleithria* by the presence of 9 setae in setal area 1 of the metanotum, the posterior margin of the pigmentation on the mesonotum being well defined, and the pigmentation of the metanotum being round. □ *Bunya Mountains National Park, Caddisfly, COI, idase, Larva, Pliocaloca, Taxonomy.*

Pliocaloca Neboiss, 1984 is an Australian endemic genus of caddisfly occurring in the north-east of the country. Neboiss (1984) established the genus initially with the description of three species from around the Cairns region: *P. fastigiata* Neboiss, 1984, *P. dasodes* Neboiss, 1984, and *P. mucronata* Neboiss, 1984. Jackson (1998 pp 12-13) provided a description of a larva of *Pliocaloca* (sp. AV1) in a preliminary key to the larvae of Calocidae Ross, 1967. She cited a pharate male pupa as the basis of this association and indicated that this undescribed species occurred in southern Queensland (QLD) and northern New South Wales (NSW). Shackleton (2010) described the adult males of *P. fidesria* Shackleton, 2010 from southern

Queensland and the adult males, pupa, and larva of *P. kleithria* Shackleton, 2010 from northern New South Wales. At the time, it was not apparent if the larva illustrated in Jackson (1998) corresponded to the larva described in Shackleton (2010), but the setation and shape and size of sclerites of the mesonotum in *P. kleithria* appeared to differ from her illustrations. The larva Jackson used for these illustrations, along with her other Calocidae material, can no longer be located for comparative purposes.

Cartwright *et al.* (2013) noted that detailed larval descriptions were few for Australian taxa. In the current paper, the larva of *P. fidesria* is described and associated. This association reveals that the larval range for the *Pliocaloca*

sp. AV1 specimens in Jackson (1998) is a combined range of two species. Furthermore, the specimen illustrated in Jackson (1998) is likely to belong to *P. fidesria* as it shares diagnostic characters with this species.

Association of the larval and adult stages of trichopteran species has, in the past, primarily either been made through rearing larval specimens into adults, as in Drecktrah (1984), or examining the genitalic characters of pharate male pupae (Milne 1938). When pupae have not been able to give a reliable indication of association, some authors have inferred associations based on local occurrences, i.e. males, females, and larvae collected in the same location, as in Neboiss (1979). More recently, genetic data have been employed to associate life stages (Miller *et al.* 2005, Zhou *et al.* 2007).

Here morphological characters and population segregation are used to infer species delimitation. This inference is tested using sequences of the mitochondrial gene cytochrome oxidase sub unit 1 (COI). Association is inferred through sequence homology of the COI gene within the species and supported by the occurrence of larvae and adults existing together at the same site. This association will enhance the capabilities of studies, such as river health monitoring programs, which depend on accurate identifications of larval specimens.

MATERIALS AND METHODS

All material was collected into 100% ethanol and is deposited in the Queensland Museum, Brisbane (QM). Shackleton (2010) was used to identify the adult specimens and the keys of Jackson (1998) and Shackleton (2013) to identify the larval specimens. Material was examined using a Leica MZ16 stereo microscope. Photographs were taken using a Leica DFC320 camera mounted on a Leica MZ16 microscope. Photographs were edited using GIMP 2.6.11.

A small amount of tissue (usually a leg) was taken from each specimen and used to obtain a 657 base pair (bp) fragment of the mitochondrial gene cytochrome oxidase sub unit 1 (COI).

Methods for extraction and amplification of this gene fragment are detailed below.

Extraction method. Deoxyribonucleic acid was extracted using a 5% Chelex solution and Proteinase K mix. A 657 base pair (bp) fragment of the mitochondrial gene cytochrome oxidase sub unit 1 (COI) was amplified. For all specimens of *P. fidesria* and 3 specimens of *P. kleittria*, DNA extraction, amplification, and sequencing were conducted at the Canadian Centre For DNA Barcoding (CCDB, Guelph, Ontario, Canada). Protocols used by the CCDB are available at www.dnabarcoding.ca. For the remaining specimens, DNA extraction and amplification were performed at La Trobe University (LTU) (Wodonga, Australia). Sequencing of these specimens was conducted by MacroGen Inc (Seoul, Korea). The LTU methods consisted of amplifying COI using the primers LCO1490 and HCO2198 (Folmer *et al.* 1994); primers were M13-tailed to facilitate sequencing. The Polymerase Chain Reaction (PCR) cocktail for reactions consisted of 4µl buffer, 20µl 10% w/v trehalose, 0.8µl deoxynucleotide triphosphates (dNTPs), 2µl 50mM MgCl₂, 0.8µl of each primer, 0.1µl taq polymerase (Invitrogen), 0.01–5µl of DNA template, and water to 40µl. PCR conditions consisted of 1 min at 94° C; 5 cycles of 1 min at 94° C, 1.5 min at 45° C, 1.5 min at 72° C; 35 cycles of 1 min at 94° C, 1 min at 50° C, 1 min at 72° C; and 4 min at 72° C.

For the resultant data, contigs were assembled in DNABaser 2.75 (www.DnaBaser.com) and aligned with default settings in Clustal X as implemented in MEGA5 (Tamura *et al.* 2011). All sequences were examined for the presence of double peaks, frame shifts, and stop codons. Sequences were submitted to GenBank under the accession numbers given in Table 1. A search for similar sequences on GenBank was conducted using the Basic Local Alignment Search Tool (BLAST) and the resultant sequences were added to the data set.

A sequence of *Tamasia variegata* Mosely, 1936 was added to the data set as an outgroup. The data set was partitioned into three categories, according to the position of base pairs with the codon (COI1, COI2, COI3), and the best

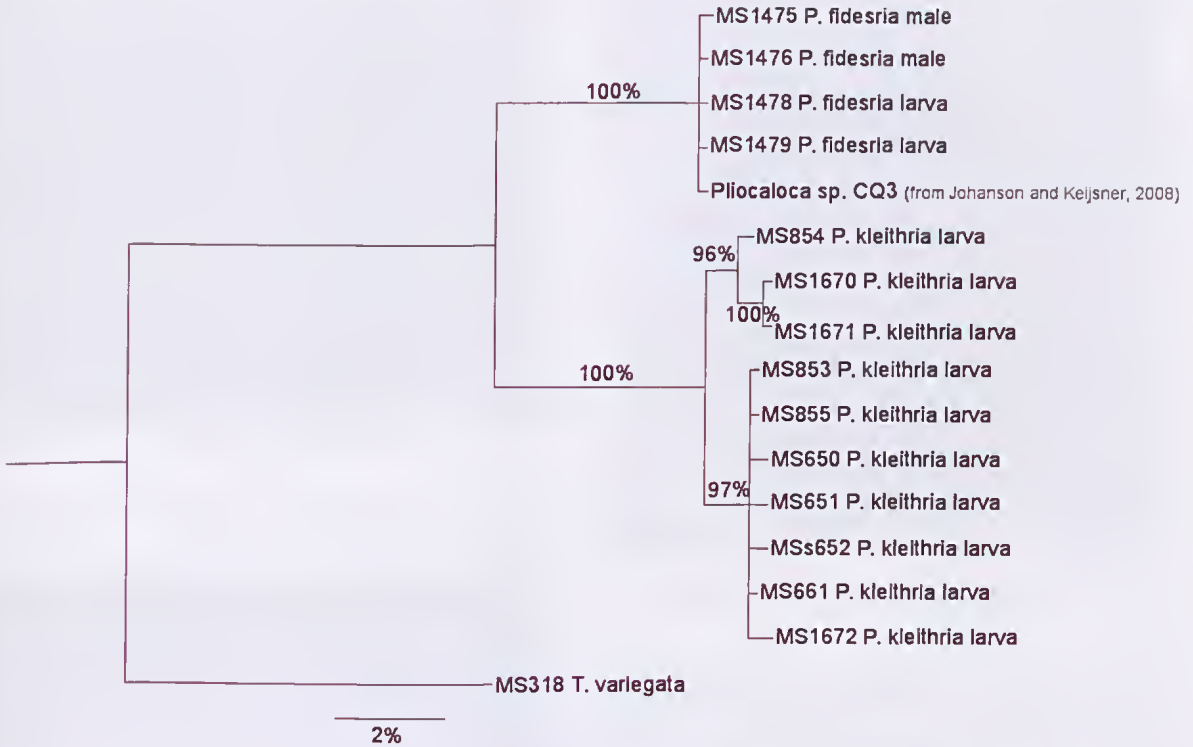


FIG. 1. Bayesian inference of 657 bp barcoding region of cytochrome oxidase subunit 1 including 4 specimens of *P. fidesria*, 8 specimens of *P. kleithria*, and an outgroup specimen of *T. variegata*. Posterior probabilities are indicated on branches. Scale bar represents percent divergence.

model of evolution was determined for each partition using MrModeltest (Nylander 2004) and Phylogenetic Analysis Using Parsimony (PAUP) (Swofford 1999). Evolutionary models were selected from the Akaike Information Criterion (AIC) given in the MrModeltest (Nylander 2004) outputs. A Bayesian analysis was performed using MrBayes 3.1 (Ronquist & Huelsenbeck 2003), in which ten million generations were run and a sample taken every one thousand generations. The first 25% (2500) of the trees generated were deleted from the statistical summary as a 'burn in'. The resultant tree (Fig. 1) was rooted using the sequence of *T. variegata*. Pairwise p-distances were calculated in MEGA5 (Tamura *et al.* 2011) and were used to calculate minimum inter-specific divergence and the maximum intra-specific divergence. Specimens collected for this study and used for molecular analysis are indicated by the accession

numbers of the senior author with the prefix 'MS'. The sole sequence obtained through GenBank is indicated by the accession number assigned by the author of that sequence followed by the publication in which the sequence was first published.

RESULTS

Four specimens of *Pliocaloca fidesria* (two males and two larvae) successfully yielded 657 bp long COI sequences. The BLAST search retrieved one sequence from an undescribed *Pliocaloca* species (sp. CQ3), with 90% query coverage and 99% percent similarity. The sequence was originally published in Johanson and Keijsner (2008). For all specimens of *P. fidesria* the COI sequences were identical except that in specimen MS1475 a thiamine was present at position 216 as opposed to a cytosine in the



FIG. 2. *Pliocaloca fidesria* Shackleton. Larva, dorsal views. Head.

other specimens. Sequences of COI were also obtained from 10 larval specimens of *P. kleithria*. The maximum p-distance, calculated using pairwise deletion, within *P. fidesria* was 0.17% and within *P. kleithria* was 2.85%. The minimum distance between the two species was 6.76%.

The AIC returned the following models: GTR for first codon position, HKY for second codon position, and HKY+I for third codon position. After ten million generations in MrBayes 3.1 (Ronquist and Huelsenbeck 2003), the standard deviations of split frequencies fell below 0.01, stationarity was assumed to have been reached, and the analysis was stopped. The resultant tree (Fig. 1) indicated a large distance between the two *Pliocaloca* species with 100% posterior probability support for the separation of the two species. Three larval specimens of *P. kleithria* occurred as a sister clade to the rest of the *P. kleithria* specimens. The specimens of *P. fidesria* formed a monophyletic clade with 100% posterior probability support.

DISCUSSION

Analysis of the COI gene indicates that the *Pliocaloca* larvae found at Saddle Tree Creek,



FIG. 3. *Pliocaloca fidesria* Shackleton. Larva, dorsal view pronotum.

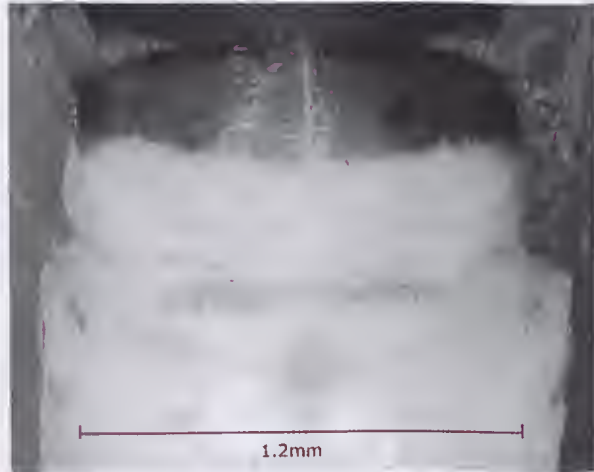


FIG. 4. *Pliocaloca fidesria* Shackleton. Larva, dorsal view, mesonotum and metanotum.

Bunya Mountains National Park, belong to the species *P. fidesria*. The larvae shared an identical COI sequence with one of the males collected and differed by only one base pair from the other male adult. It is unlikely that our result is a product of a shared ancestral polymorphism between two species, as recent studies suggest that COI sequences shared between species is rare. Hebert *et al.* (2009) found only 9 cases of shared COI sequences between 1327 species of Lepidoptera, and then

Pliocaloca fidesria

TABLE 1. Specimen details for sequenced specimens including GenBank, BOLD, and La Trobe University (LTU) accession numbers and processing institutions. CCDB=Canadian Centre for DNA Barcoding.

Species	Life stage	Locality	Date collected and collector	LTU accession number	COI GenBank reference	Amplification and sequencing institute	BOLD specimen id
<i>Pliocaloca fidesria</i>	male	Saddle tree creek, Bunya Mtns NP, southern QLD	23 Nov 2011 J. Mynott and M. Shackleton	MS1475	KC860488	CCDB	LTUT470-11
<i>Pliocaloca fidesria</i>	male	Saddle tree creek, Bunya Mtns NP, southern QLD	23 Nov 2011 J. Mynott and M. Shackleton	MS1476	KC860491	CCDB	LTUT471-11
<i>Pliocaloca fidesria</i>	larva	Saddle tree creek, Bunya Mtns NP, southern QLD	23 Nov 2011 J. Mynott and M. Shackleton	MS1478	KC860490	CCDB	LTUT473-11
<i>Pliocaloca fidesria</i>	larva	Saddle tree creek, Bunya Mtns NP, southern QLD	23 Nov 2011 J. Mynott and M. Shackleton	MS1479	KC860489	CCDB	LTUT474-11
<i>Pliocaloca kleithria</i>	larva	Coppernook ck, Dorrigo NP, northern NSW	10 Nov 2011 J. Mynott and M. Shackleton	MS836	KC860498	LTU / Macrogen	
<i>Pliocaloca kleithria</i>	larva	Tributary Wilson River, 70m along Falls walk track, Willi Willi NP, northern NSW	04 Dec 2007 A. Glaister, J. Dean, and R. St. Clair	MS650	KC860496	LTU / Macrogen	
<i>Pliocaloca kleithria</i>	larva	Tributary Wilson River, 70m along Falls walk track, Willi Willi NP, northern NSW	04 Dec 2007 A. Glaister, J. Dean, and R. St. Clair	MS651	KC860495	LTU / Macrogen	
<i>Pliocaloca kleithria</i>	larva	Tributary Wilson River, 70m along Falls walk track, Willi Willi NP, northern NSW	04 Dec 2007 A. Glaister, J. Dean, and R. St. Clair	MS652	KC860494	LTU / Macrogen	
<i>Pliocaloca kleithria</i>	larva	Eight mile ck, Bullock rd, northern NSW	04 May 2010 NSW Department of Environment and Climate Change	MS661	KC860487	LTU / Macrogen	
<i>Pliocaloca kleithria</i>	larva	Williams River at rest area beneath 1st bridge along walking track, Barrington Tops NP, northern NSW	09 Nov 2011 J. Mynott and M. Shackleton	MS853	KC860493	CCDB	LTUT035-11
<i>Pliocaloca kleithria</i>	larva	Williams River at rest area beneath 1st bridge along walking track, Barrington Tops NP, northern NSW	09 Nov 2011 J. Mynott and M. Shackleton	MS854	KC860500	CCDB	LTUT036-11
<i>Pliocaloca kleithria</i>	larva	Williams River at rest area beneath 1st bridge along walking track, Barrington Tops NP, northern NSW	09 Nov 2011 J. Mynott and M. Shackleton	MS855	KC860499	CCDB	LTUT037-11
<i>Pliocaloca kleithria</i>	larva	Creek at waterfall above Darraboola falls, Lamington National Park, QLD	17 Nov 2011 J. Mynott and M. Shackleton	MS1670	KC860492	La Trobe / Macrogen	
<i>Pliocaloca kleithria</i>	larva	Creek at waterfall above Darraboola falls, Lamington National Park, QLD	17 Nov 2011 J. Mynott and M. Shackleton	MS1671	KC860497	La Trobe / Macrogen	
<i>Tamasia variegata</i>	larva	Unnamed River on Racecourse trail @ brushy mt picnic area, Werrikimbe NP, northern NSW	12 Nov 2011 J. Mynott and M. Shackleton	MS823	KC860501	La Trobe / Macrogen	

only between congeneric and morphologically similar species. Webb *et al.* (2012) found no shared COI sequences between Ephemeroptera species of Northern America. Among studies involving caddisflies, Hogg *et al.* (2009) found no sequences shared between 61 New Zealand species and Zhou *et al.* (2011) found no shared COI sequences between 209 species from the Great Smoky Mountains National Park, USA.

In the past, association of these two forms would have been made based on the occurrence of the two forms occurring at the same site with no other similar species occurring close to the site. *Pliocaloca fidesria* appears to be an isolated species with no other *Pliocaloca* species existing within its range. The range of its closest neighbouring species is not known to extend within around 300 km from *P. fidesria*. Furthermore, the larvae and adults, collected for this project, were collected from the same site. This indicates that *P. fidesria* is a candidate for an association based on geographic data alone. However, the COI data also provide strong evidence in support of this association. The present study indicates that analysis of molecular data alone may serve as a reliable method for associating life stages in other species. This method is particularly useful when pharate male pupae, which have traditionally used to infer associations, but are difficult to collect or rear out, are not available.

The *P. sp.* AV1 larva depicted in Jackson (1998, figs. 1.12-1.17) resembles the larva of *P. fidesria*. Her illustration (fig. 1.16) clearly shows that the pigmentation on the metanotum has a strongly demarcated and relatively straight posterior margin. Also, on the metanotum the pigmentation patch is rounded and 9 pairs of setae are present anteriorly on the segment. These characters are all present on our larvae of *P. fidesria* associated with male adults. Given that only two species are known to exist in the northern NSW and southern QLD region (Shackleton 2013) it is likely that the *Pliocaloca* sp. AV1 larva depicted in Jackson (1998) belongs to *P. fidesria*.

The findings here provide the ability to place a species identity to larval specimens of *P.*

fidesria, which is important for those conducting river health monitoring programs and other scientific enquiries involving larval specimens. Furthermore, it allows researchers to distinguish between the larvae of *P. fidesria* and *P. kleithria*, which has, until now, not been possible.

SYSTEMATICS

Family CALOCIDAE

Pliocaloca Neboiss, 1984

Type species. *Pliocaloca mucronata* Neboiss, 1984, by original designation, from northern Queensland.

Pliocaloca fidesria Shackleton

Material examined. Queensland. Saddle Tree Creek at Festoon Falls. Bunya Mountains National Park (-26.848611S, 151.56166E) 23 November 2011: MS1475 1 male (QM - T183456); MS1476 1 male (QM - T183457); MS1478 1 larva (QM - T183458); MS1479 1 larva (QM - T183459); MS1480 1 larva (QM - T183460); MS1481 1 larva (QM - T183461).

Diagnosis. *Pliocaloca* larvae are distinguishable from other Calocidae larvae in that the setae of the head are large and flattened; the pronotum is covered in short, dense, papillose setae; and the metanotum has a pigmented patch anteriorly, which is not raised. In *Pliocaloca* and *Calocoides* Neboiss, but no other Calocidae, the foretrochantin is not fused to the propleuron. The larva of *P. fidesria* differs from *P. kleithria* in that the pigmentation of the mesonotum is more defined along the posterior margin; in *P. kleithria* this posterior margin is encroached by unpigmented areas, especially along the midline where the unpigmented area extends anteriorly about half way into the pigmentation. In the metanotum of *P. fidesria* setal area 1 contains about 9 setae as opposed to *P. kleithria* which has around 6 setae. The pigmented patch on the metanotum appears more rounded in *P. fidesria* than in *P. kleithria*, which is somewhat more elongate and pointed towards the posterior (see Shackleton 2010, Fig. 23). In the original description of *P. kleithria* (Shackleton 2010) the pigmented patch on the metanotum is incorrectly described as being rounded.

Description. *Male:* as described in Shackleton (2010).

Female. Unknown.

Pupa. Unknown

Larva. Length: 9.4-9.9 mm. Head (Fig. 2): dorsum papillate, with conspicuous, mesially directed, flattened setae; antennae situated half way between eye and anterior margin of head capsule. Pronotum (Fig. 3): dorsum covered with spinules, with dense, short setae; anterior margin with dense, short setae; each sclerite with anterior margin curved forward between medial suture and lateral margin; lateral carina present, not extending to dorsum, with fringe of setae on dorsal margin; foretrochantin not fused to propleuron. Metanotum (Fig.4): posterior margin of pigmentation relatively straight and well defined. Mesonotum (Fig.4): setal area 1 with about 9 setae closely spaced; pigmentation patch rounded. Abdomen: abdominal segment I spiny patch present without lateral sclerite; abdominal gills absent; lateral sclerite of segment X with many setae; anal claws each with 1 accessory tooth. Case: curved cylinder of sand grains, posterior aperture round.

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LITERATURE CITED

- Cartwright, D., Wells, A., Dean, J., St Clair, R., & Shackleton, M. 2013 Taxonomic status and distribution of Australian caddisflies (Insecta: Trichoptera). *Aquatic macroinvertebrates 2013 Taxonomic Workshop*, La Trobe University, Albury-Wodonga.
- Drecktrah, G. 1984. Descriptions of the immature stages of *Alloecella grisea* Banks (Trichoptera: Helicophidae) and morphological characteristics used to distinguish between larvae of Australian Calocidae, Conoesucidae and Helicophidae. In: J.C. Morse (ed.) *Proceedings of the 4th International Symposium on Trichoptera*, Clemson 1983 (Series Entomologica 30: 267-276) W. Junk, The Hague. Pp 115-122.
- Folmer, O., Black, M., Hoeh, W., Lutz, R. & Vrijenhoek, R. 1994. DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology*. 3: 294-299.
- Hebert, P.D.N., deWaard, J.R., & Landry, J. 2009. DNA barcodes for 1/1000 of the animal kingdom. *Biology letters*. 6: 359-362.
- Hogg, I.D., Smith, B.J., Banks, J.C., DeWaard, J.R., & Hebert, P.D.N. 2009. Testing use of mitochondrial COI sequences for the identification and phylogenetic analysis of New Zealand caddisflies (Trichoptera). *New Zealand Journal of Marine and Freshwater Research*. 43: 1137-1146.
- Jackson, J. 1998. *Preliminary guide to the identification of late instar larvae of Australian Calocidae, Helicophidae, and Conoesucidae (Insecta: Trichoptera)*. Cooperative Research Centre for Freshwater Ecology Identification Guide No. 16. Cooperative Research Centre for Freshwater Ecology: Albury, Australia.
- Johanson, K.A. & Keijsner, M. 2008. Phylogeny of the Helicophidae (Trichoptera), with emphasis on the New Caledonian species of *Helicophia*. *Systematic Entomology*. 33(3): 451-483.
- Miller, K.B, Alarie, Y, Wolfe, G.W, & Whiting, M.F. 2005. Association of insect life stages using DNA sequences: the larvae of *Phylodytes umbrinus* (Motschulsky) (Coleoptera: Dytiscidae). *Systematic Entomology*. 30: 499-509.
- Milne, M.J. 1938. The "metamorphotype method" in Trichoptera. *Journal of New York entomological Society*. 46:435-437.
- Neboiss, A. 1979. A Terrestrial caddis-fly larva from Tasmania (Calocidae: Trichoptera). *Australian Entomological Magazine*, 5: 90-93.
- Neboiss, A. 1984. Calocidae of Northern Queensland (Calocidae: Trichoptera). In, Morse, J.C. (ed) Pp. 267-276. *Proceedings of the 4th International Symposium on Trichoptera*. Junk, The Hague.

- Nylander, J.A.A. 2004. Mr Modeltest v2. Program distributed by the author. Evolutionary Biology Centre, Uppsala University.
- Ronquist, F. & Huelsenbeck, J.P. 2003. MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics*. **19**: 1572-1574.
- Ross, H.H. 1967. The evolution and past dispersal of the Trichoptera. *Annual Review of Entomology*. **12**: 169-206.
- Shackleton, M. 2010 Two new species of *Pliocaloca* Neboiss (Trichoptera: Calocidae) from eastern Australia, with descriptions of the immature stages of one species. *Zootaxa* **2476**: 30:38.
- Shackleton, M. 2013 Preliminary keys to the larvae of Australian Calocidae (Trichoptera: Insecta). *Aquatic macroinvertebrates 2013 Taxonomic Workshop*, La Trobe University, Albury-Wodonga.
- Swofford, D.L. 1999. PAUP 4.0: Phylogenetic Analysis Using Parsimony (And Other Methods). Sunderland, MA, Sinauer Associates, Inc.
- Tamura, K., Peterson, D., Peterson, N., Stecher, G., Nei, M. & Kumar, S. 2011. MEGA5: Molecular Evolutionary Genetics Analysis using Maximum Likelihood, Evolutionary Distance, and Maximum Parsimony Methods. *Molecular Biology and Evolution* **28**(10): 2731-2739.
- Webb, J.M., Jacobus, L.M., Funk, D.H., Zhou, X., Kondratieff, B., Geraci, C.J., DeWalt, R.E., Baird, D.J., Richard, B., Phillips, I., & Hebert, P.D.N. 2012. A DNA barcode library for North American Ephemeroptera: progress and prospects. *PLoS ONE*. **7**(5): e38063 doi:10.1371/journal.pone.0038063.
- Zhou, X., Kjer, K.M. & Morse, J.C. 2007. Associating larvae and adults of Chinese Hydropsychidae caddisflies (Insecta:Trichoptera) using DNA sequences. *Journal of the North American Benthological Society* **26**(4): 719-742.
- Zhou, X., Robinson, J.L., Geraci, C.J., Parker, C.R., Flint Jr, O.S., Etnier, D.A., Ruitter, D., DeWalt, E., Jacobus, L.M., & Hebert, P.D.N. 2011. Accelerated construction of a regional DNA-barcode reference library: caddisflies (Trichoptera) in the Great Smoky Mountains National Park. *Journal of the North American Benthological Society*. **30**(1): 131-162.

A ziphodont crocodile from the late Pleistocene King Creek catchment, Darling Downs, Queensland.

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ABSTRACT

A well preserved reptilian tooth recovered from late Pleistocene fluvial sediments along King Creek on the Darling Downs, south eastern Queensland, displays a suite of characters including lateral compression and curvature, lenticular cross section, length/width ratio >1.3, slight anterior/posterior recurve and distinct, strongly serrate carinae, that enable it to be attributed to a ziphodont crocodile (*Quinkana* sp.). It is the first record of a ziphodont in the King Creek ecosystem and only the second for the eastern Darling Downs in over 150 years of fossil collecting. This tooth as well as previously documented fossils from Tea Tree Cave (N. Qld) and Texas Caves (S. Qld) provides the youngest records of ziphodont crocodiles globally. □ *Ziphodont, Crocodile, Quinkana, King Creek, Darling Downs, Pleistocene.*

A high diversity of large bodied reptilian carnivores, including varanids and crocodylians, inhabited the late Pleistocene ecosystems of south eastern Queensland. Within the fossil collections of the Queensland Museum, the giant varanid *Varanus priscus* (formerly *Megalania prisca*) is the most abundant having been recorded in deposits from several sub-catchments throughout the Darling Downs, but being best known from the intensively studied King Creek catchment (Molnar & Kurz 1997; Price & Sobbe 2005; Price & Webb 2006). Crocodiles, principally *Pallimnarchus pollens* and *Crocodylus porosus*, have also been recorded from a range of Darling Downs localities (Molnar & Kurz 1997; Price & Webb 2006).

In their review of eastern Darling Downs Pleistocene vertebrates in the collection of the

Queensland Museum, Molnar & Kurz (1997) concluded that ziphodont crocodiles seem to have been absent from the region during the Pleistocene, although an earlier paper (Molnar 1981) listed a single ziphodont tooth crown from either Westbrook Creek or Gowrie Creek, northwest of Toowoomba in the collection of the Australian Museum (AMF2876). A newly collected fossil is the first record of a ziphodont crocodile in the King Creek catchment. The purpose of this paper is to report the palaeontological significance of this specimen.

MATERIALS AND METHODS

The specimen as collected was robust and did not require special preparation or preservation techniques. All measurements are in metric

units using digital callipers or calibrated eyepiece micrometer. Higher systematics follow Molnar (1981) and Willis *et al.* (1993). Institutional abbreviations include: AMF, Fossil collection of the Australian Museum, Sydney. QMF, Fossil collection of the Queensland Museum, Brisbane.

SYSTEMATIC PALAEOONTOLOGY

Family CROCODYLIDAE Cuvier, 1807

Subfamily MEKOSUCHINAE Willis, Molnar and Scanlon 1993

Quinkana Molnar, 1981

Quinkana sp.

Material. QMF57032. (Fig. 1A-C) An isolated tooth crown from fluvial sediments exposed in the naturally eroded bank of King Creek, west of Pilton, eastern Darling Downs, Queensland. Specific locality details are recorded in the Queensland Museum fossil register.

Geological Age. QMF57032 has not been directly dated but is considered to be late Pleistocene based on the abundance of other late Pleistocene deposits in the King Creek catchment (see Price & Sobbe 2005; Price & Webb 2006; Price *et al.* 2011) and the presence of other late Pleistocene species such as *Diprotodon optatum*, *Macropus ferragus*, *Macropus titan*, *Protemnodon anak*, *Troposodon minor*, *Varanus priscus* in the adjacent area (Molnar & Kurz 1997). The oldest geological age of sediments containing fossils of megafauna, currently recorded in the King Creek catchment is an optically stimulated luminescence age of 122 ± 22 ka. (Price *et al.* 2011).

Description. The tooth crown is 29.9 mm long, tapers distally, and is laterally compressed and lenticular in cross section. The surface texture of the enamel is well detailed with little evidence of stream abrasion although several small post mortem chips are present and there is evidence of chemical corrosion from plant roots. The enamel shows no evidence of vertical



Fig. 1. A - C. QMF57032, ziphodont crocodilian tooth (*Quinkana* sp.). A, Lateral view of lingual surface; B, Posterior surface; C, Lateral view of buccal surface. At right, a magnified view of portion of carina showing the serrate edge. An occlusal wear facet is visible on the tip of the tooth in A and B.

TABLE 1. Comparative features of the teeth of large late Pleistocene reptilian carnivores and the King Creek ziphodont crocodile (QMF57032).

Character	<i>Varanus priscus</i>	<i>Crocodylus porosus</i>	<i>Crocodylus johnstoni</i>	<i>Pallimnarchus pollens</i>	<i>Quinkana</i> sp.	QMF57032
Tooth crown shape	Laterally compressed elongate	Robust conical	Slender conical (small)	Robust conical laterally curved	Laterally compressed and curved	Laterally compressed and curved
Crosssectional shape	Tear shaped	Ovoid to Round	Ovoid	Ovoid	Lenticular	Lenticular
Lateral shape	Strong recurve posterior margin concave	Blunt tapering Slightly curved	Long slender evenly tapering	Blunt Evenly tapered	Tapered Slightly recurved	Tapered Slightly recurved
Length / Width Ratio	> 1.3	< 1.3	Not measured	< 1.3	> 1.3	1.36 to 1.59
Fluting / Ridging	Strong basal Irregular	Weak	Weak	Absent	Absent	Absent
Carinae	Anterior - Distal 30% only Posterior 100%	Poorly developed	Poorly developed	Distinct	Distinct	Distinct
Carinae Serrations	Strongly serrate	Non serrate	Non serrate	Serrate	Strongly serrate	Strongly serrate

fluting or ridging. The tooth measures 13.6 mm x 10 mm in greatest basal dimensions (length /width ratio = 1.36) and at approximately 50% of the crown height it measures 12.1 mm x 7.6 mm (length/width ratio = 1.59) thus becoming increasingly laterally compressed dorsally. It has pronounced lateral curvature with slight anterior/posterior recurve, with well developed carinae along the complete anterior and posterior margins. Both carinae are finely serrate along their entire length (25–26 serrations per 5 mm). There is a cup in the base of the crown in the shape of an oval cone, 8 mm in depth. A small occlusal wear facet 7 mm x 3.2 mm is present postero-distally.

Remarks. Willis and Molnar (1997) provided a set of characters that aided identification of isolated large reptilian teeth. These characters

are observable on QMF57032 allowing it to be confidently identified (Table 1). For comparative photographs of the teeth of other large reptilian taxa discussed below, see Willis and Molnar (1997).

QMF57032 is not referable to *Varanus priscus* because their teeth are much more distally tapered and heavily recurved making the posterior margin concave. Additionally *V. priscus* has pronounced basal fluting and the anterior carina is serrate only for the distal third of its length.

QMF57032 differs from *Crocodylus porosus* because their teeth are ovoid and less flattened in cross section and have poorly developed, non serrate carinae. Willis and Molnar (1997) described *C. porosus* teeth as smooth and only rarely having basal ridging. However all

specimens examined for this study including the photos in Willis and Molnar (1997, p. 83) showed distinct basal ridging and thus differs from QMF57032.

Crocodylus johnstoni teeth are much smaller and more slender than QMF57032 and have poorly developed carinae with no serrations. They also commonly have weak basal ridging or fluting.

Teeth of *Pallimnarchus pollens* have a more symmetrical profile than QMF57032, are rounder in cross section (length / width ratio < 1.3), but have distinct carinae that are occasionally serrate.

In contrast, teeth of *Quinkana* are laterally curved with slight posterior recurve, laterally compressed (length / width ratio > 1.3) with well developed carinae that are serrate along their entire length. QMF57032 shares these characters and is accordingly referred of this genus of ziphodont crocodile. The holotype specimen (AMF57844) of the type species of the genus, *Q. fortirostrum* from Tea Tree Cave, is edentulous (teeth are missing) thus not allowing for direct comparison with QMF57032. The only other Pleistocene ziphodont with retained dentition, (QMF7898, *Quinkana* sp.) from 'The Joint', Texas Caves is poorly preserved (Molnar 1981) and only allows superficial comparison of the dentition; however it appears at least superficially morphologically similar to QMF57032.

QMF57032 differs from *Quinkana meboldi* (Late Oligocene) in that unlike other species of *Quinkana*, *Q. meboldi* teeth have carinae without serrations (Willis 1997). QMF57032 differs from *Quinkana timara* (Miocene) because *Q. timara* teeth are much smaller (approx. 50% of linear dimensions) and the carinae are more finely serrate (Megirian 1994). Compared to QMF57032, the teeth of *Quinkana babarra* (Early Pliocene) appear broader, less laterally curved and slightly more antero- posteriorly recurved (Willis and Mackness 1997). A small terrestrial mekosuchine crocodile has also been recorded from the middle Pleistocene Mt. Etna caves system (Hocknull 2005). The tooth varies from QMF57032 in that it is much smaller, relatively

broader and the carinae serrations are much coarser.

QMF57032 appears morphologically closest to *Quinkana* sp. cf. *Q. fortirostrum* teeth described by Willis & Molnar (1997). However, all species of *Quinkana* are described from specimens with limited retained teeth or only associated teeth. Until additional, more complete specimens are available for study, assignment of single teeth such as QMF57032 to a specific species seems premature.

DISCUSSION

QMF57032 represents the first record of a ziphodont crocodilian in the late Pleistocene King Creek catchment and only the second for the entire (Pleistocene) eastern Darling Downs in over 150 years of fossil collecting. Given the high replacement rate of crocodilian teeth (Willis & Molnar 1997) and the paucity of the fossil record, we conclude that ziphodont crocodiles were a very rare component of late Pleistocene Darling Downs ecosystems. In contrast, ziphodont teeth are much better represented in the Pliocene fossil deposits at Chinchilla on the western Darling Downs (Molnar 1981) possibly indicating a post-Pliocene decline in abundance on the Darling Downs.

Outside of Australia, the youngest records of crocodiles with ziphodont morphologies are Miocene, while within Australia the ziphodont (or semi-ziphodont) record ranges from the Eocene to Pleistocene (Molnar 1981; Willis et al. 1993; Willis & Mackness 1996). Thus, recognition of QMF57032 as *Quinkana* sp. on the late Pleistocene Darling Downs as well as *Q. fortirostrum* from the undated but probably Pleistocene Tea Tree Cave of north Queensland and *Quinkana* sp. from the probably middle Pleistocene (Price et al. 2009) Texas Caves in south Queensland, represent the youngest known records of crocodiles with ziphodont morphologies not only for Australia, but globally.

Molnar (1981), Flannery (1994) and Willis & Mackness (1996) noted the preponderance of large-bodied terrestrial reptilian carnivores in Pleistocene Australia is unlike that of

most modern faunas which typically contain markedly more diverse large-bodied terrestrial mammalian carnivores. The three largest-bodied mammalian carnivores recorded in the late Pleistocene King Creek catchment include *Thylacoleo carnifex* (ca. 100–150 kg), *Thylacinus cynocephalus* (ca. 15–35 kg) and *Sarcophilus laniarius* (ca. 10–20 kg). Such species were dwarfed in size by Pleistocene reptilian counterparts including *Quinkana* sp. (ca. 200 kg) and *Varanus priscus* (ca. 600 kg), as well as the semi-aquatic *Pallimnarchus* sp. (ca. 1000 kg). Interestingly, such a dominance of large-bodied non-mammalian carnivores is not evident in older fossil deposits, such as those from the Miocene. Rather, most Miocene deposits, such as those from Riversleigh, are dominated, in terms of diversity, by relatively large-bodied mammalian carnivores (Wroe *et al.* 1999). Pliocene deposits, such as those from Chinchilla (western Darling Downs) are more similar to those from the Pleistocene King Creek catchment in that they are dominated by large-bodied reptilian carnivores (*Pallimnarchus pollens*, *P. gracilis*, *Quinkana* sp., *Varanus priscus* and *V. komodoensis* which are each 200 kg or greater, versus the largest known mammalian carnivore *T. crassidentatus* which was likely <100 kg). Thus, there must have been an unprecedented ‘taxonomic-ecological shift’ in the makeup of large-bodied carnivores sometime after the Miocene, shifting from dominantly mammals to dominantly reptiles. Such a shift appears to have been in place from at least the Pliocene, and lasting as recently as the late Pleistocene. A cause of such a marked transition is unclear.

Palaeohabitats appear to have changed markedly in south-eastern Queensland between the Pliocene and late Pleistocene, principally reflecting the contraction of closed woodlands and expansion of grasslands, driven by an overall trend towards an increasingly arid climate (Price 2012). The late Pleistocene King Creek ecosystems also underwent significant changes in the early part of the last glacial cycle (i.e., from ca. 120–80 ka) with significant forest and vine scrub thicket contractions giving way to more markedly open systems dominated by grasslands with environmental conditions that

were punctuated by repeated and prolonged droughts (Price *et al.* 2005; 2011; Price & Webb 2006; Price 2012). The later changes at least may explain the extinction of taxa such as *Quinkana* locally.

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LITERATURE CITED

- Flannery, T.F. 1994. *The future eaters: an ecological history of the Australasian lands and people*, 1st ed. (Reed Books: Sydney)
- Hocknull, S.A. 2005. Ecological succession during the late Cainozoic of central eastern Queensland: extinction of a diverse rainforest community. *Memoirs of the Queensland Museum* 51(1): 39–122.
- Megirian, D. 1994. A new species of *Quinkana* Molnar (Eusuchia: Crocodylidae) from the Miocene Camfield Beds of northern Australia. *The Beagle, Records of the Museums and Art Galleries of Northern Territory* 11: 145–166.
- Molnar, R.E. 1981. Pleistocene ziphodont crocodylians of Queensland. *Records of the Australian Museum* 33(19): 803–834.
- Molnar, R.E. & Kurz, C. 1997. The distribution of Pleistocene vertebrates on the eastern Darling Downs, based on the Queensland Museum collections. *Proceedings of the Linnean Society of New South Wales* 117: 107–133.
- Price, G.J. 2012. Plio-Pleistocene climate and faunal change in central eastern Australia. *Episodes* 35(1): 160–165.
- Price, G.J. & Sobbe, I.H. 2005. Pleistocene palaeoecology and environmental change on the Darling Downs, southeastern Queensland, Australia. *Memoirs of the Queensland Museum* 51(1): 171–201.
- Price, G.J., Tyler, M.J. & Cooke, B.N. 2005. Pleistocene frogs from the Darling Downs, south-eastern Queensland, and their palaeoenvironmental significance. *Alcheringa* 29: 171–182.

- Price, G.J. & Webb, G.E. 2006. Late Pleistocene sedimentology, taphonomy and megafauna extinction on the Darling Downs, southeastern Queensland. *Australian Journal of Earth Sciences* 53: 947–970.
- Price, G.J., Zhao, J.-x., Feng, Y.-x. & Hocknull, S.A. 2009. New U/Th ages for Pleistocene megafaunal deposits of southeastern Queensland, Australia. *Journal of Asian Earth Sciences* 34: 190–197.
- Price, G.J., Webb, G.E., Zhao, J.-x., Feng, Y.-x., Murray, A.S., Cooke, B.N., Hocknull, S.A. & Sobbe, I.H. 2011. Dating megafaunal extinction on the Pleistocene Darling Downs, eastern Australia: the promise and pitfalls of dating as a test of extinction hypotheses. *Quaternary Science Reviews* 30: 899–914.
- Willis, P.M.A. 1997. New crocodylians from the late Oligocene White Hunter Site, Riversleigh, northwestern Queensland. *Memoirs of the Queensland Museum* 41: 423–438.
- Willis, P.M.A. & Mackness, B.S. 1996. *Quinkana babarra*, a new species of ziphodont mekosuchine crocodile from the early Pliocene Bluff Downs local fauna, northern Australia with a revision of the genus. *Proceedings of the Linnean Society of New South Wales* 116: 143–151.
- Willis, P.M.A. & Molnar, R.E. 1997. Identification of large reptilian teeth from Plio-Pleistocene deposits of Australia. *Journal and Proceedings of the Royal Society of New South Wales* 130 (3–4): 79–92.
- Willis, P.M.A., Molnar, R.E., Scanlon, J.D. 1993. An early Eocene crocodylian from Murgon, southeastern Queensland. *Kaupia Darmstädter Beiträge zur Naturgeschichte* 3: 27–33.
- Wroe, S., Myers, T.J., Wells, R.T., Gillespie, A. 1999. Estimating the weight of the Pleistocene marsupial lion, *Thylacoleo carnifex* (Thylacoleonidae: Marsupialia): implications for the ecomorphology of a marsupial super-predator and hypotheses of impoverishment of Australian marsupial carnivore faunas. *Australian Journal of Zoology* 47: 489–498.

Range extension of the Cubozoan, *Tripedalia binata* Moore (Cnideria: Carybdeida: Carybdeidae) from far north Queensland, Australia.

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ABSTRACT

The occurrence of *Tripedalia binata*, a small species of carybdeid jellyfish previously known in Australia only from specimens collected in the Northern Territory, is recorded from three new locations in North Queensland. Photographic documentation of the morphology of *T. binata* is also presented herein. □ *Tripedalia binata*, cubozoan, range, jellyfish, carybdeid, morphology.

Box jellyfish of the order Carybdeida, are defined as having a single tentacle per pedalium with the majority of species having one pedalia on the each corner of the bell. However, notable exceptions are members of the bitypic genus *Tripedalia*, which display additional interradial pedalia, each extending to a single tentacle. The first species attributed to the genus, and after which it is aptly named, is *Tripedalia cystophora* Conant, 1897, with three undivided pedalia per corner. This species has been recorded from tropical mangrove areas world-wide (Conant 1897; Stiasny 1926; Werner 1973), the most recent record from Lake Wyman in Florida, USA (Orellana & Collins 2011). In 1988, a second species within the genus was identified as *Tripedalia binata* Moore due to its characteristic paired interradial pedalia (Moore 1988). To date, records for *T. binata*

indicate a limited species distribution within Australia, with all known samples collected from the near-shore waters around the Darwin region (Moore 1988). Two additional samples have been recorded from the Jambu River in India (Moore 1988).

In this paper we detail five new records of *T. binata* from the north Queensland areas of Cairns, Innisfail and Weipa (Fig.1) thus increasing the known range of this species for Australia. Two of these specimens have been lodged at the Tropical Museum of Queensland, Townsville (MTQ G66685). In addition, we verify and supplement the original species description and drawings by Moore (1988) with photographs of morphological characteristics. We further highlight the types of environment in which *T. binata* is found,



FIG. 1. Distribution map for *Tripedalia binata* in Australia showing previously known records (◆) and documenting new distributional records (●).

suggesting that its actual distribution is considerably wider than is currently described.

AUSTRALIAN DISTRIBUTION

Record 1. In October 2002, a single male specimen was found in a mangrove lined creek approximately 13 km from the mouth of the Barron River, Cairns (16°52'24.96"S, 145°41'9.99"E). The specimen had an interpedalia distance (IPD, Fig.1) of 7.5 mm and a niche-bell height (NB, Fig.1) of 7.5 mm.

Record 2. A single female specimen (IPD: 9mm, NB:8.5mm) was collected at Thomatis Creek, Cairns approximately 5km from the river mouth (16°51'4.93"S, 145°43'3.44"E) on the 15th October 2002.

Record 3. One of the authors was called to an aquaculture facility in Mourilyan, 5k south of Innisfail, QLD (17°35'56.53"S, 146

°6'7.63"E), on 14th October 2008 to identify a number of box-shaped jellyfish. The animals had been found in an aquaculture pond following drainage of the facility. The pond in question had initially been filled 5 months previously, with water pumped directly into the pond from an adjacent tidal creek. Given that the incoming water had been pumped through a 200 micron mesh filter, we believe that the planula or polyp stage of *T. binata* rather than the medusae were introduced into the pond from the external water source. A total of 5 animals were collected and identified as *T. binata* (IPD (mm), NB (mm); 7,7; 9,9; 9,10; 10.5,12; 11,11; 8.5,9; 8,9, respectively). As the specimens did not display developed gametes, sex determination was not possible.

Record 4. In November 2011 a single female specimen (IPD 13.5 mm, NB 11 mm) was collected in the shallows of Red Beach, Mapoon (GPS

12°01'6.28"S, 141°54'16.5"E) on the western side of Cape York. The following November, three additional *T. binata* specimens (IPD(mm), NB(mm); 13,10; 10,9; 9,8.5 respectively) were collected at the same location. Sex determination was not possible due to lack of gonad material, possibly through spawning prior to collection or during transportation back to the lab. The specimens were observed swimming within a large aggregation of another cubozoan species, *Chironex fleckeri*, located in knee-deep water within 1 meter of the shore-line, at the southern end of a sandy beach near mangrove habitat.

MORPHOLOGY

The following characteristics observed in the collected specimens are concurrent with the published description (Moore 1988): pedalia arranged in pairs at each of the 4 interradial corners of the bell (Figs 2, 3) ending in a single tentacle (Figs 2, 3); velarium with 7-8 velarial canals per quadrant (Fig. 4); the bell is covered in randomly dispersed bell warts of nematocyst type atrichous isorhizas (Figs 1, 5, 6); nematocyst on the tentacles were identified as stenoteles and atrichous isorhizas; 4 rhopalial niches on the bell containing visual sensory structures (Figs 2, 5); the stomach is located in the bell apex connecting to the perradial canals (Fig. 6); brush-like bundles of gastric phacellae are present in the 4 corners of the stomach (Fig. 6); gonad sheathes extend from the top of the bell to the velarium (Figs 2, 6). The manubrium extends mid-way down the centre of the bell and in contraction is double cruciform in appearance (Figs 4, 6). However, on further dissection and in a more relaxed state it proves to be a single piece of tissue or a simple cruciform as originally described (Moore 1988) The pattern of nematocyst banding on the tentacles is of one larger band then one smaller band repeated along the length of the tentacle (Fig.7).

Maximum tentacle length could not be accurately measured due to contraction during

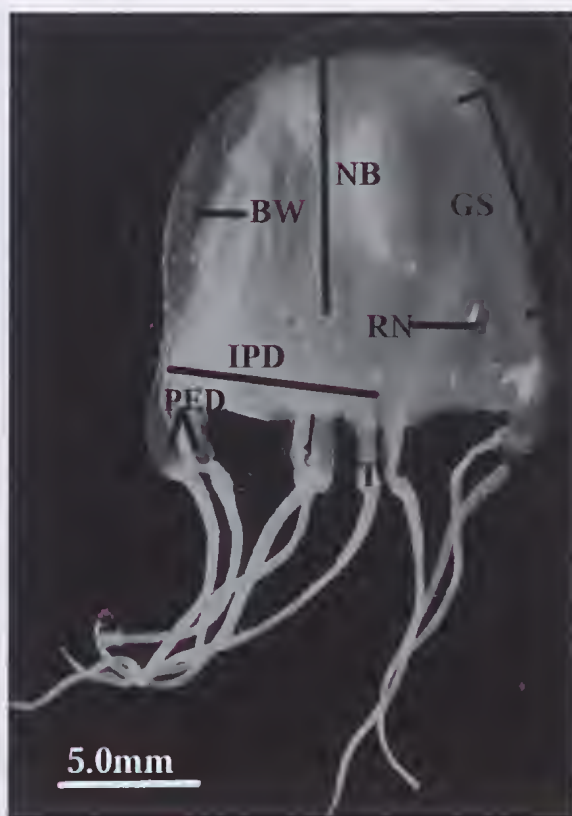


FIG. 2. Whole preserved specimen of *Tripedalia binata*. Lateral view. NB, niche-bell height; IDP, inter-pedalian distance; BW, bell warts containing nematocysts; RN, rhopalial niche containing sensory structures; GS, gonad sheathes (undeveloped in this specimen); T, tentacles containing bands of nematocysts; PED, pedalia.

preservation of the specimens. In the specimen identified as female, eggs could be seen throughout the bell (Fig. 3) including behind the rhopalial niche and extending into the velarial and pedalial canals. In the male specimens, gonad material also filled most of the interior of the animal (Fig. 8). Although sexual dimorphism is a defining characteristic of the family Tripedalidae (Conant 1897), to which *T. binata* belongs, there is no evidence of male seminal vesicles in *T. binata* as evident in the two other species of this family, *T. cystophora* and *Copola sivickisi*. Additional male specimens are needed to verify this.

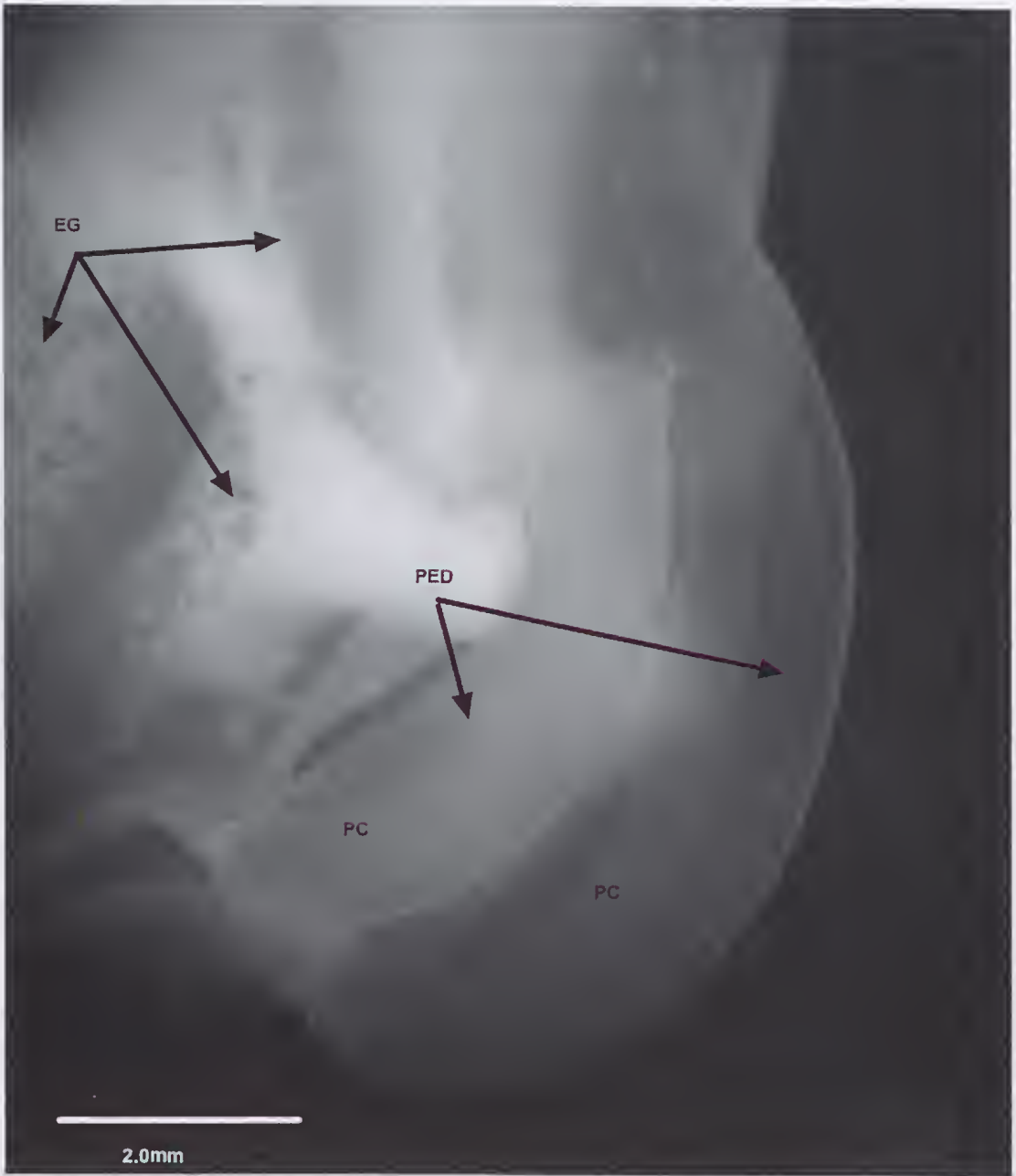


FIG. 3. Paired pedalia of mature female *Tripedalia binata*. PED, pedalia; PC, pedial canal; EG, eggs.

ECOLOGY AND DISTRIBUTION

In the original description of *Tripedalia binata*, it was stated that this species was found in mangrove-lined creeks and beaches (Moore

1988). The location of the new specimens recorded above appears to substantiate this observation, with the majority of specimens closely associated with mangrove habitats.

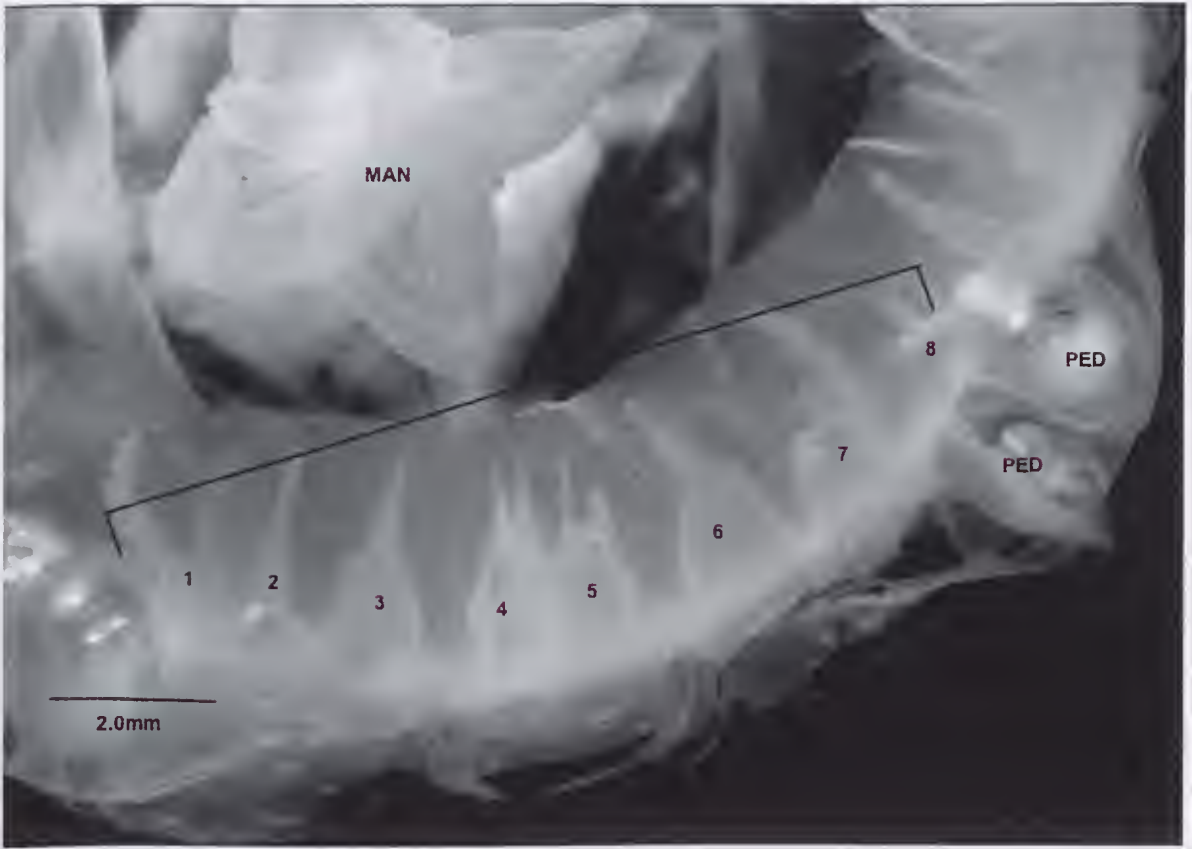


FIG. 4. Velarium and interior of bell of *Tripedalia binata*. MAN, manubrium; P, location of pedalia (removed at base in specimen for enhanced visibility of internals); VC, velarial canals. Numbers 1-8 indicate the number of velarial canals per quadrant.

Even where the specimens were collected from aquaculture ponds, the water in which they were found had been pumped directly from a mangrove-lined creek adjacent to the facility. Given this extended range, it would be reasonable to assume that *T. binata* should be present in other localities of Tropical Australia under similar habitat conditions. However, as with the majority of cubozoan species, this could be problematic to verify given the difficulty in visually spotting these small, transparent and highly mobile animals.

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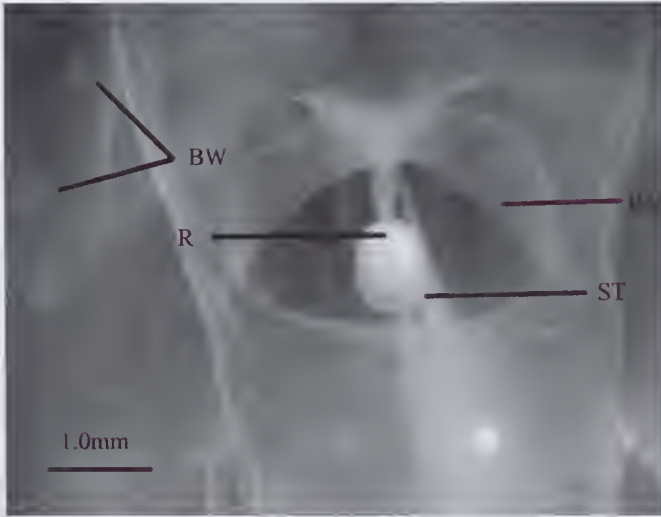


FIG. 5. Sensory structures of *Tripedalia binata*. RN, rhopial niche; R, rhopalia; ST, statolith; RH, viking-like rhopial horns; BW, bell warts containing nematocysts.



FIG. 6. Dorsal view of internal structures of *Tripedalia binata*; MAN, maubrium; GS, gonad sheaths; GP, gastric phacellae.



LITERATURE CITED

- Conant, F.S. 1897. Notes on the Cubomedusae. *Johns Hopkins University Circulars* 132:8-10.
- Moore, S.J. 1988. A new species of cubomedusan (Cubozoa: Cnidaria) from northern Australia. *The Beagle, Records of the Northern Territory Museum of Arts and Sciences* 5(1): 1-4.
- Orellana, E.R. & Collins, A.G. 2011. First report of the box jellyfish *Tripedalia cystophora* (Cubozoa: Tripedaliidae) in the continental USA, from Lake Wyman, Boca Raton, Florida. *Marine Biodiversity Records* 4(54): 1-3.
- Stiasny, G. 1926. Ueber einige Scyphomedusen von Puerto Galera, Mindoro (Philippinen). *Zoologische Mededelingen* 9: 239-248.
- Werner, B. 1973. Spermatozeugment und Paarungsverhalten bei *Tripedalia cystophora* (Cubomedusae). *Marine Biology* 18: 212-217.

FIG. 7. Tentacles of *Tripedalia binata* displaying nematocyst banding pattern of consecutive small and larger bands.



FIG. 8. Sexually mature male *Tripedalia binata*.

Additional information on *Ramphotyphlops aspina* Couper, Covacevich & Wilson 1998 (Reptilia: Typhlopidae), a poorly known blind snake from the Mitchell Grass Downs of Queensland

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ABSTRACT

Blind snakes (Typhlopidae: *Ramphotyphlops*) are relatively poorly known compared to most other Australian reptiles. One quarter of Australia's species are known from one specimen or one location only. *Ramphotyphlops aspina* Couper, Covacevich and Wilson is known from two specimens collected within 22 km of each other in the Mitchell Grass Downs Bioregion of Queensland. A third specimen is discussed here, from a location 470 km from the previous specimens, also within the Mitchell Grass Downs. The collection localities of all *R. aspina* specimens suggest it may be a Mitchell Grass Downs endemic. □ blind snake, *Ramphotyphlops aspina*, Mitchell Grass Downs, Queensland.

A *Ramphotyphlops* specimen collected near Julia Creek in the Mitchell Grass Downs bioregion of central Queensland is described. This specimen closely conforms morphologically to *Ramphotyphlops aspina* Couper, Covacevich & Wilson, 1998. Prior to this specimen, only two individuals of *R. aspina* were known, both from near Barcaldine, also in the Mitchell Grass Downs. These are the holotype (QMJ51541) and a paratype (QMJ7). This third specimen represents a known-range extension of 470 km for *R. aspina*. It is in the collection of the Queensland Museum, registered as QMJ91822.

MATERIALS AND METHODS

Measurements were taken with a Sontax Digital caliper. As well as comparing QMJ91822 with the original description of *Ramphotyphlops aspina* (Couper *et al.* 1998), direct comparison was made with the holotype and paratype, to see if any obvious differences could be discerned. Length, and width at widest point,

of rostral scales of all specimens were measured from above.

QMJ91822 was collected under a small rock from relatively featureless open plains, south of Julia Creek at approximately 20.77°S, 141.74°E (GDA94). Collection locations for all specimens of *Ramphotyphlops aspina* were checked against Regional Ecosystem (RE) mapping in the Queensland Regional Ecosystem Description Database (Environmental Protection Agency 2005).

Area calculations for minimum convex polygon and RE extents were calculated using XTools Pro in ESRI ArcMap 10.0. For area calculations, Geoscience Australia Lambert projection in GDA 1994 was used.

RESULTS

Specimen QMJ91822 conforms closely to the description given in Couper *et al.* (1998) as follows: lacks a caudal spine (Fig. 1); 18 midbody scale



FIG. 1. *Ramphotyphlops aspina* tail tip showing lack of terminal spine. Arrow shows position of vent QMJ91822 after preservation.

rows; 437 ventrals scales; 14 subcaudal scales, not including terminal scale; SVL 226 mm; tail length 6mm (2.6% SVL); body width 3.7 mm (1.6% SVL); head width 2.5 mm (1.1% SVL); a bluntly rounded snout when viewed from above; head slightly flattened when viewed

from the side; rostral scale elongate, tapering slightly caudally both above and below (38% of head width, as measured at widest dorsal part of rostral); rostral narrower underneath the head (23.5% of head width as measured at the level of the eye) and with parallel margins; rostral length/width from above = 1.44 (QM J51541 = 1.44, QMJ7 = 1.36); nasals broadly separated by prefrontal; prefrontal larger than frontal; supraoculars broadly separated by frontal; nostrils inferior and near snout apex with nasal cleft extending to second supralabial, and also extending dorsally so that it is visible from above; eye small and distinct in life but almost indistinguishable in preservative, located below ocular/supraocular junction; caudally, the ocular overlaps two postoculars and parietal; first supralabial the smallest, overlapped by rostral lobe of nasal; second supralabial larger, overlapped by rostral lobe and caudal lobe of nasal and preocular; third supralabial slightly larger than second, overlapped by preocular, and overlapping



FIG. 2. *Ramphotyphlops aspina*, QMJ91822 colour in life.

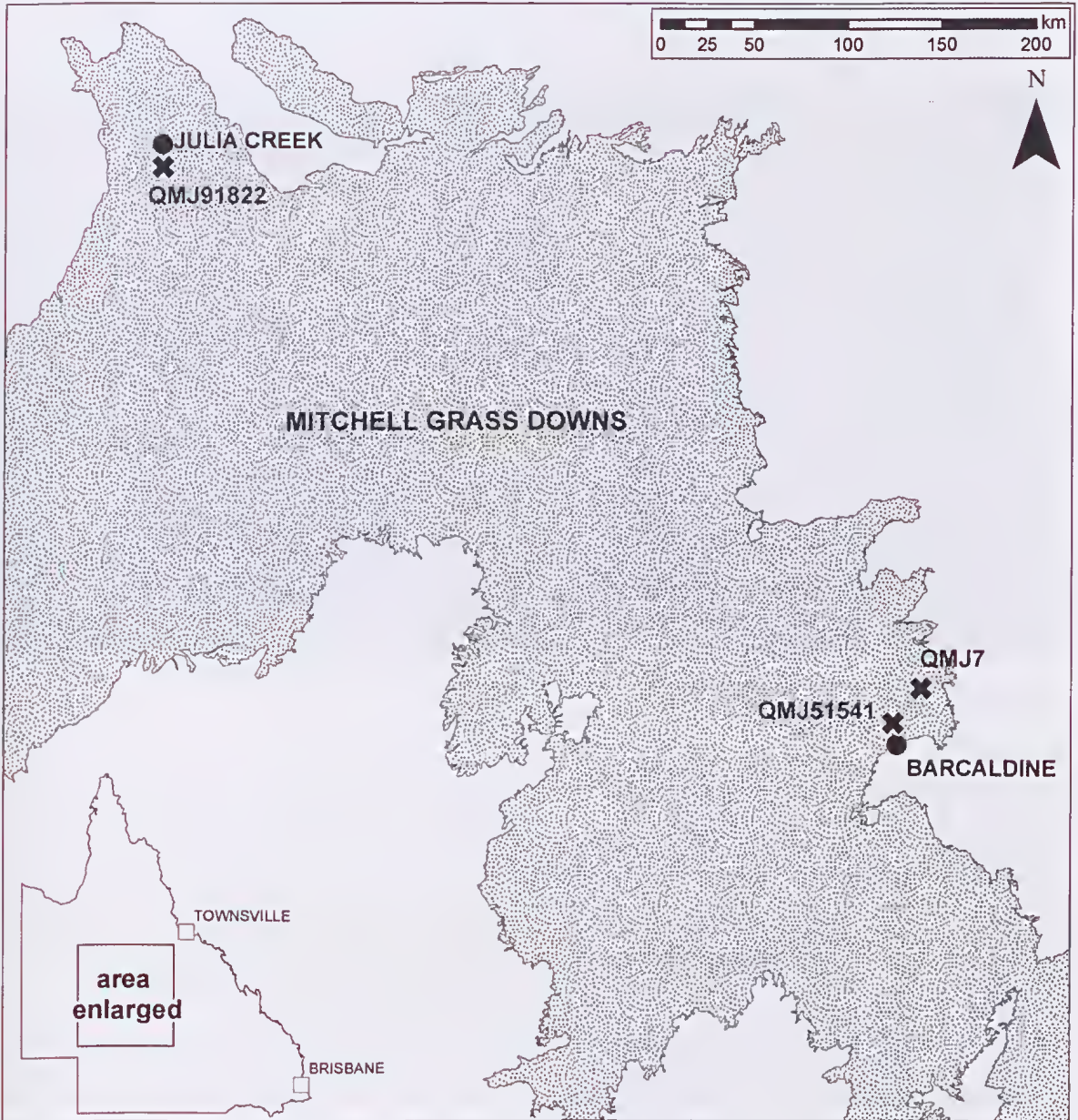


FIG. 3. Map showing locations of all known specimens (QMJ numbers) of *Ramphotyphlops aspina*.

ocular for about 1/3 of supralabial's height; fourth supralabial much the largest, elongate, overlapped by ocular; mental the same width as postmental; infralabials three, with the third being slightly larger than the first two; microtubercles of head sparse, but most

abundant on lower surfaces of nasals, but none visible on lower surface of rostral; glands not visible along margins of head shields.

Colour in Life. The overall appearance of the live specimen was a light pink colour



FIG. 4. *Astrebla* grassland south of Julia Creek, where QMJ91822 was collected. Photo courtesy Stephen Malone Photography.

(Fig. 2). The scales towards the anterior and posterior of the animal have a pattern of a curved darker band around the base, which is visible through the overlying scale. This gives the appearance of posterior scales overlapping those anterior to them, when the opposite is the case. The pattern is present, but much reduced, in the midbody region. This pattern is present, but much faded, in QMJ7 and QMJ51541. Colour is slightly paler ventrally, with some internal organs visible as darker patches under the scales. The eyes are visible as small and distinct dark spots beneath the margin of the supraocular and ocular scales. The tongue is a uniform translucent cream.

DISCUSSION

Ramphotyphlops aspina is a poorly known species, but distinctive for being the only Australian Typhlopidae snake lacking a terminal tail spine (Couper *et al.* 1998). Unfortunately, genetic material is not available for the two

previous museum specimens. Specimen QMJ7 was donated to the Queensland Museum in 1911 (Couper *et al.* 1998) and is not well preserved. Specimen QMJ51541 was donated in 1990 and was formalin fixed with no genetic vouchers taken. Thus, identification of QMJ91822 is entirely reliant upon morphological characters. However, given the close conformity of QMJ91822 to the original description there can be little doubt that it is *R. aspina*.

The location of QMJ91822 represents a known-range extension of approximately 470 km to the northwest of the previous specimens (Fig. 3).

Mitchell Grass grasslands, which dominate the Mitchell Grass Downs bioregion, have relatively low vertebrate richness (Sattler & Williams 1999). Despite its vast area, approximately 13.8% of Queensland, there are relatively few endemic species. Among the reptiles there are five specialists of Mitchell Grass grasslands on cracking clay soil (*Ctenotus agrestis*, *C. schevilli*, *Pogona henrylawsoni*, *Varanus spenceri*, *Pseudechis colletti*, Sattler & Williams 1999; Wilson 2005), that

are endemic, or nearly so, to the Mitchell Grass Downs bioregion. The three known specimens of *Ramphotyphlops aspiua* were collected within the Mitchell Grass Downs bioregion (Fig. 3; Sattler & Williams, 1999), suggesting *R. aspiua* may be a Mitchell Grass Downs endemic. QMJ91822 was collected from open treeless plains south of the town of Julia Creek. Ground layer vegetation was dominated by Mitchell Grasses *Astrebala* spp. The area is mapped as regional ecosystem 4.9.1; "*Astrebala lappacea* ± *Aristida latifolia* ± *Panicum decompositum* grassland on fresh cretaceous sediments. Deep grey and brown cracking soil." (Sattler & Williams, 1999), and this is consistent with the ground layer species composition observed at the point of collection (Fig. 4). QMJ51541 was from mixed REs 4.9.2 and 4.9.1 which are both *Astrebala* spp. grasslands on cracking clay soils. QMJ7 was from near the boundary of RE 4.9.1 and a mix of several REs which include open woodlands of *Eucalyptus* spp. and *Acacia cambagei*, and *Atriplex* spp. or *Astrebala* spp. grasslands in an alluvial landzone.

Ramphotyphlops aspiua is not listed under Australian or Queensland legislation (Australian Government, 1999; Queensland Government, 2006) or the IUCN Red List (IUCN, 2012). With three known specimens, *R. aspiua* could reasonably be listed as Data Deficient. However, it seems likely that *R. aspiua* fits the criteria for classification as Least Concern. A minimum convex polygon between the three records gives an area of 5284 km². A reasonable estimate of suitable habitat area is probably the extent of REs 4.9.1 and 4.9.2, both of which have greater than 30% of original extent remaining and are subject to little on-going clearing (Accad *et al.* 2006; Sattler & Williams 1999). The estimated area dominated by either of these REs is 79634 km², which is approximately 33% of the area of the Mitchell Grass Downs bioregion.

QMJ91822 was notable because it did not, despite a significant amount of handling (including close observation with a hand lens to attempt identification), emit the foul-smelling liquid from its anal gland that is the usual behaviour in *Ramphotyphlops* (pers. obs.; Cogger, 2000). It also did not dig the tail tip into the author's hand, a common behaviour in blind snakes when captured (pers. obs.). This second

point was what initially alerted the author to the fact that the snake was *R. aspiua*.

Blind snakes are an extremely secretive group, with 10 of Australia's 42 species (*R. batillus*, *howi*, *longissimus*, *margaretae*, *micromma*, *nema*, *robertsi*, *splendidus*, *yampiensis*, *yirrikalae*) being known from one specimen or one location only. For many of these species it is highly likely that targeted surveys will uncover more records and locations that will extend the known extents of occurrence as has happened with *R. aspiua*.

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LITERATURE CITED

- Accad A., Neldner V. J., Wilson B. A. & Niehus R. E. (2006) *Remnant Vegetation in Queensland. Analysis of remnant vegetation 1997-1999-2000-2001-2003, including regional ecosystem information.* (Queensland Herbarium, Environmental Protection Agency, Brisbane).
- Australian Government. (1999) *Environment Protection and Biodiversity Conservation Act 1999.*
- Cogger H. G. 2000. *Reptiles and Amphibians of Australia.* (Reed New Holland, Sydney).
- Couper P. J., Covacevich J. A. & Wilson S. K. 1998. Two new species of *Ramphotyphlops* (Squamata: Typhlopidae) from Queensland. *Memoirs of the Queensland Museum* 42: 459-64.
- Environmental Protection Agency. (2005) *Regional Ecosystem Description Database (REDD).*
- IUCN. (2012) *IUCN Red List of threatened species.* <http://www.iucnredlist.org/>. Species Survival Commission, Gland, Switzerland.
- Queensland Government. (2006) *Nature Conservation (Wildlife) Regulation 2006.*
- Sattler P. & Williams R. (1999) *The Conservation Status of Queensland's Bioregional Ecosystems.* (Environmental Protection Agency, Brisbane, Queensland).
- Wilson S. (2005) *A Field Guide to Reptiles of Queensland.* (Reed New Holland Sydney).

A significant range extension for the Australian wet tropics skink *Eulamprus frerei* (Reptilia: Squamata: Scincidae)

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ABSTRACT

The known range of *Eulamprus frerei* is extended approximately 110 km north-northwest to Mt Lewis (16.510°S, 145.269°E) on the Mt Carbine Tableland, North Queensland. This record is from 200 m lower than the reported minimum elevation for the species. Despite extensive surveys throughout the Australian Wet Tropics, this is the first record for *E. frerei* outside the Bellenden Ker Range. Additional details are given for a previously reported record from Mt Bellenden Ker. □ *Mt Lewis, Bellenden Ker Range, Mt Carbine Tableland, Queensland.*

Eulamprus frerei Greer, 1992 is a rainforest skink known only from elevations above 1400 m on Mt Bartle Frere and the adjacent Mt Bellenden Ker (the two highest mountains in Queensland) (Cogger 2000; Goodman 2012; Williams *et al.* 2010; Wilson & Swan 2010). It is a heliothermic, presumably viviparous lizard considered to be largely dependent upon rock and boulder habitats and occasionally on tree trunks, but otherwise little is known of its ecology (Goodman 2012; Turner 2007). It is listed as vulnerable under the Queensland Nature Conservation Act 1992 due to its presumed localised distribution. Because it appears to be restricted to cool montane rainforest, the potential for climate change to negatively affect the distribution and biology of *E. frerei* is considered to be high (Williams *et al.* 2003).

On 7th December 2012, a specimen of *E. frerei* was collected by one of us (BRS) during canopy surveys at approximately 1200 m elevation on Mt Lewis (16.510°S, 145.269°E), located west of Mossman on the Mt Carbine Tableland, North Queensland (Figs 1–2). The skink was found protruding from a tree hollow approximately 15 m up the trunk of a canopy tree (Fig. 3). The tree possessed extensive insect damage and appeared to be dying. The specimen was identified by the following characters using the key to *Eulamprus* in Wilson (2005): third pair of enlarged chin scales separated by 3 longitudinal rows of small scales; no supranasal scale; prefrontal scales in point contact; lower secondary temporal scale overlaps upper; 72 paravertebral scales. Examination of the holotype (QMJ47985) and paratype (QMJ39531) of *E. frerei* by one of us (SMZ) confirmed identification, which was further supported by



FIG. 1. *Eulamprus frerei* (QMJ92282) collected from Mt Lewis, North Queensland.

molecular data (CJH unpublished data). The specimen is now lodged at the Queensland Museum (QMJ92282).

The known distribution of *E. frerei* was determined by searching all Australian museum collections as well as consulting relevant literature (Cogger 2000; Goodman 2012; Greer 1992; Williams *et al.* 2010; Wilson 2005; Wilson & Swan 2010). Searches of museum collections revealed only the two type specimens, both collected near the Mt Bartle Frere summit. Williams *et al.* (2010) showed a single locality for *E. frerei* near the summit of Mt Bellenden Ker but did not provide any additional information. We elaborate on this record here: The record was obtained on 1st January 2000 by SEW. This individual was found on the side of a tree 1.5 m above the ground at an elevation of approximately 1437 m. Mt Bellenden Ker is Queensland's second highest mountain, reaching an elevation of 1593 m. It is separated from the adjacent Mt Bartle Frere by a lowland divide lying at 320 m elevation. All known localities

FIG. 2. Map illustrating known localities of *Eulamprus frerei*, including the 2012 Mt Lewis and 2000 Mt Bellenden Ker records.

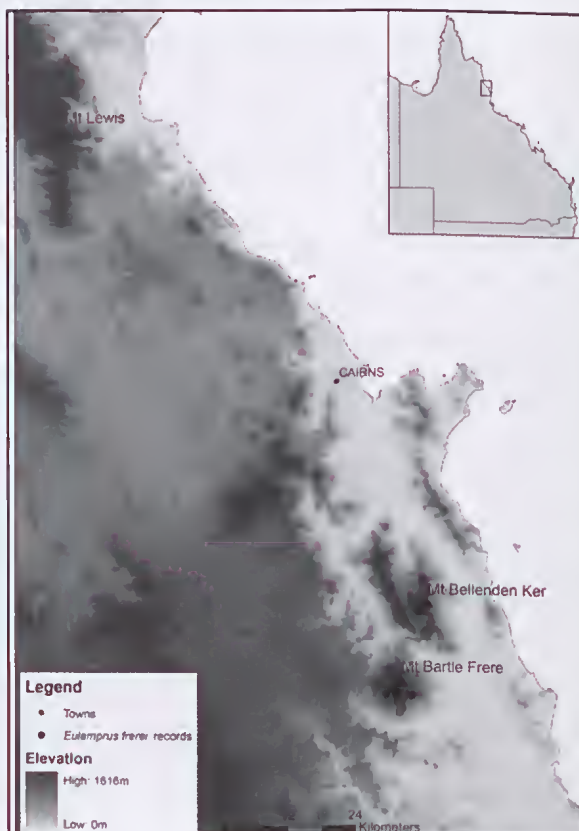




FIG. 3. The tree on Mt Lewis from which QMJ92282 was captured.

of *E. frerei*, including the Bellenden Ker and Mt Lewis animals, are presented in Fig. 2.

Once thought to exist on a single mountaintop, these observations demonstrate that *E. frerei* occurs on at least three separate mountains in the Australian Wet Tropics. The discovery of this species on the Mt Carbine Tableland extends the known range approximately 110 km north-northwest and confirms the existence of *E. frerei* north of the Black Mountain Corridor (BMC), a significant biogeographic barrier to rainforest fauna (Schneider *et al.* 1998). Furthermore, this record is 200 m lower than the reported minimum elevation for the species (>1400 m; Goodman 2012). Notably, the records from Mt Bellenden Ker and the Mt Carbine Tableland are from areas lacking boulder habitats, which are extensive near the summit of Mt Bartle Frere and typically regarded as the preferred habitat of *E. frerei* (Goodman, 2012). This suggests that the species is not reliant upon boulders and can occupy arboreal habitats. The ability to use a variety of habitats, its existence on opposite sides of the BMC, and a broader altitudinal range than previously thought indicates that *E. frerei* might be even more widespread than reported here.

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LITERATURE CITED

- Cogger, H.G. 2000. *Reptiles and Amphibians of Australia*. (Reed New Holland: Sydney).
- Goodman, B.A. 2012. Bartle Frere Barsided Skink. Pp 226–227. In, Curtis, L.K., Dennis, A.J., McDonald, K.R., Kyne, P.M. & Debus, S.J.S. (eds) *Queensland's Threatened Animals*. (CSIRO Publishing: Melbourne).
- Greer, A.E. 1992. Revision of the species previously associated with the Australian scincid lizard *Eulamprus tenuis*. *Records of the Australian Museum* 44: 7–19.
- Schneider, C.J., Cunningham, M. & Mortiz, C. 1998. Comparative phylogeography and the history of endemic vertebrates in the Wet Tropics rainforests of Australia. *Molecular Ecology* 7: 487–498.
- Turner, G. 2007. Notes on the habits of three skinks from the Mt Bartle Frere summit, North Queensland. *Herpetofauna* 37: 2–6.
- Williams, S.E., Bolitho, E.E. & Fox, S. 2003. Climate change in Australian tropical rainforests: an impending environmental catastrophe. *Proceedings of the Royal Society of London B* 270: 1887–1892.
- Williams, S.E., VanDerWal, J., Isaac, J., Shoo, L.P., Storlie, C., Fox, S., Bolitho, E.E., Moritz, C., Hoskin, C.J. & Williams, Y.M. 2010. Distributions, life-history specialization, and phylogeny of the rain forest vertebrates in the Australian Wet Tropics. *Ecology* 91: 2493.
- Wilson, S. 2005. *A Field Guide to Reptiles of Queensland*. (Reed New Holland: Sydney).
- Wilson, S. & Swan, G. 2010. *A Field Guide to Reptiles of Australia*. (Reed New Holland: Sydney).

A remarkable new jellyfish (Cnidaria: Scyphozoa) from coastal Australia, representing a new suborder within the Rhizostomeae

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ABSTRACT

A new genus and species of rhizostome jellyfish, which cannot be placed in any known family or suborder, is described from central eastern Australia. The Ptychophorae suborder nov., can be separated from the two recognised suborders of the Rhizostomeae in having hooded rhopalia rather than open pits, unbranched evenly-spaced radial canals, and a large circular stomach. It also possesses a unique combination of some of the primary diagnostic characters of rhizostome families in both current suborders. Moreover, *Bazinga rieki* gen. nov., sp. nov. is unique among all rhizostomes in its very small mature size. It is probable that this species has been previously mistaken for juveniles of other species. □ Scyphozoa, Rhizostomeae, Bazingidae, blubber jelly, new species, taxonomy.

Rhizostome jellyfish are typically the most obvious of all gelatinous life-forms, often being large and brightly coloured, and often having bizarre exumbrellar morphology or conspicuous trailing clubs and filaments. Most rhizostomes are relatively large, and certain edible species support a significant commercial fishery. The biggest in the group is the infamous 2 m wide, 200 kilogram *Nemopilema nomurai* Kishinouye, 1922, which has been plaguing Japanese fishing grounds by the billions, particularly since 2000 (Kawahara *et al.* 2006). While there are a few rhizostomes in the 35–50 mm range, such a small size is exceptional.

The present work documents an intriguing little jellyfish that is particularly striking by reaching maturity at below 20 mm. It is also significantly different from other rhizostomes by its unusual combination of morphological characters, and by having a suite of unique features that have not otherwise been observed in any rhizostome family or suborder.

While *Bazinga rieki* gen. nov., sp. nov. is likely to be relatively common, it has probably been

overlooked because its small size makes it easily mistaken for a juvenile of other species. In particular it is superficially similar to the common *Catostylus mosaicus* (Quoy & Gaimard, 1824), and similar sized juveniles of that species were also collected at the same time at one location.

MATERIALS AND METHODS

Specimens were fixed in a solution of about 5% concentrated formalin in seawater. Measurements were made on preserved specimens with digital calipers. Character evaluations were made on preserved specimens examined under a dissecting scope and from photographs and video of live specimens.

Peripheral portions of the radial canals were studied by dissecting away the subumbrellar circular muscles and exumbrellar warts.

All type material has been deposited in the Queensland Museum. Abbreviations: QM, Queensland Museum; BD, bell diameter; RC, radial canals.

SYSTEMATICS

Order RHIZOSTOMEAE Cuvier, 1799

Ptychophorae suborder nov.

Diagnosis. Body globular. Oral arms coalesced into a single short, ridged column; without scapulets. Rhopalia hooded, lacking typical pits. Velar lappets 4 per octant; 2 asymmetrical ocular lappets per octant. Annular muscles conspicuous. Subgenital ostia very small, round. Stomach circular, large. Radial canals 4 per octant, proximally unbranched, fluted; peripherally coalesced into vast open sinus with patchwork of jelly matrix.

Etymology. From the Greek *ptychos* (fold, leaf, layer) and *phoras* (bearing), in reference to the hooded rhopalia.

Bazingidae fam. nov.

Diagnosis. As for the suborder.

Bazinga gen. nov.

Type species. *Bazinga rieki* sp. nov. by present designation.

Diagnosis. As for the suborder.

Etymology. The name *Bazinga* has been conferred for two reasons. Firstly, *bazinga* is a slang term in present popular culture, meaning 'fooled you!' or 'stung you!' (e.g., the fictional Dr Sheldon Cooper in the television series *The Big Bang Theory*), and this is appropriate as the type species, *B. rieki*, is so small that it has probably been overlooked in the past as a juvenile of a larger species. Secondly, a seven-string harp is also called a *bazinga* (Cuppy 1950), and the straight radial canals of this new species are reminiscent of such strings.

Bazinga rieki sp. nov.

(Figs 1, 2)

Material examined. HOLOTYPE: QM-G331996, male (18.7 mm BD), Brunswick River, NSW, high tide in shallow water, Denis Riek, 04.12.2011.

PARATYPES: QM-G331997, male (15.5 mm BD), gravid female (14.0 mm BD), Cudgen Creek, Hastings Point, NSW, high tide, under road bridge, Denis Riek, 16.11.2011. QM-G331998, gravid female (16.4 mm BD), male (13.7 mm BD), Seagull Rocks, Brunswick Heads, NSW, rock pools, low tide, Denis Riek, 14.11.2011.

Description. Body thick, globular, rounded, tending to flattened above; small, reaching maturity at less than 20 mm BD (Fig. 1A). Exumbrella without any form of central hump or papillae clusters. Entire aboral surface evenly and densely covered in minute warts; each minute wart resembles small spherical sessile tag with yellowish core, possibly filled with zooxanthellae. Peripheral region of bell turned vertically downward parallel to body axis.

Oral arms (Fig. 1B) coalesced into single short column, ridged along column wall; arms formed into narrow folded sheets with mouthlets arranged along distal margin. Sheets contain scattered zooxanthellae throughout. Column wall and arm sheets finely granulated with many minute warts. Filaments, clubs, knobs, and other appendages lacking (Fig. 1F).

Subumbrellar surface (Fig. 1C) evenly covered with fine warts from oral arm column to just before edge of stomach; warts mostly longer proximally and rounder and smaller distally. Gastrogonadal cavity open to outside only at 4 small, round, perradial holes (Fig. 1D) located on subumbrellar portion of stomach wall very close to margin of stomach, about midway between oral arm column and proximal muscle bands. Circular muscle bands numbering about 12; in form of broad flat lamellae; richly impregnated with zooxanthellae.

Stomach circular in outline, large, occupying more than half body diameter; margin plainly visible through subumbrellar wall. Stomach extends via broad, evenly spaced, irregular flute-shaped radial canals, 4 per octant; peripherally coalesced into a broadly open circular sinus, punctuated with an irregular patchwork of jelly matrix (Fig. 2A). All radial canals arise at same level and are of same length. No radial canals reach bell margin, and no specifically differentiated rhopalian canal; radial canals dissipate in circular sinus. Proximal straight portions of canals clearly visible in live animal (Fig. 1E), but precise nature of peripheral gastrovascular system otherwise obscured by surface warting and subumbrellar muscle bands. Defined ring canal lacking.

Gonads comprised of heavily folded tissue sheets, plainly visible through subumbrellar wall as dark masses rich with zooxanthellae.

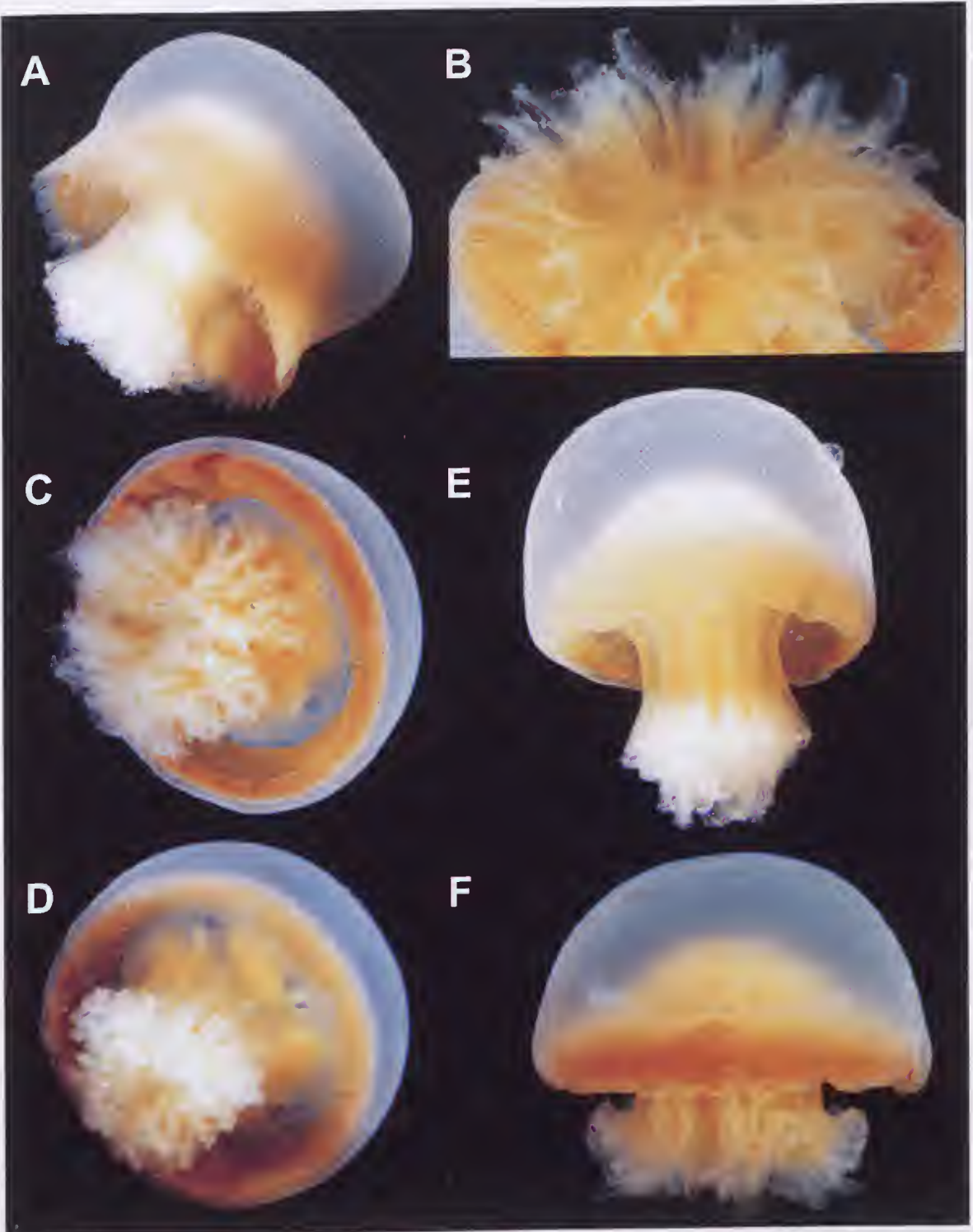


FIG. 1. *Bazinga rieki* gen. nov., sp. nov., in life. A, habitus; B, oral arms; C, subumbrellar view; D, gastrogonadal pores; E, bell on power stroke (note straight radial canals visible through bell); F, bell relaxed.

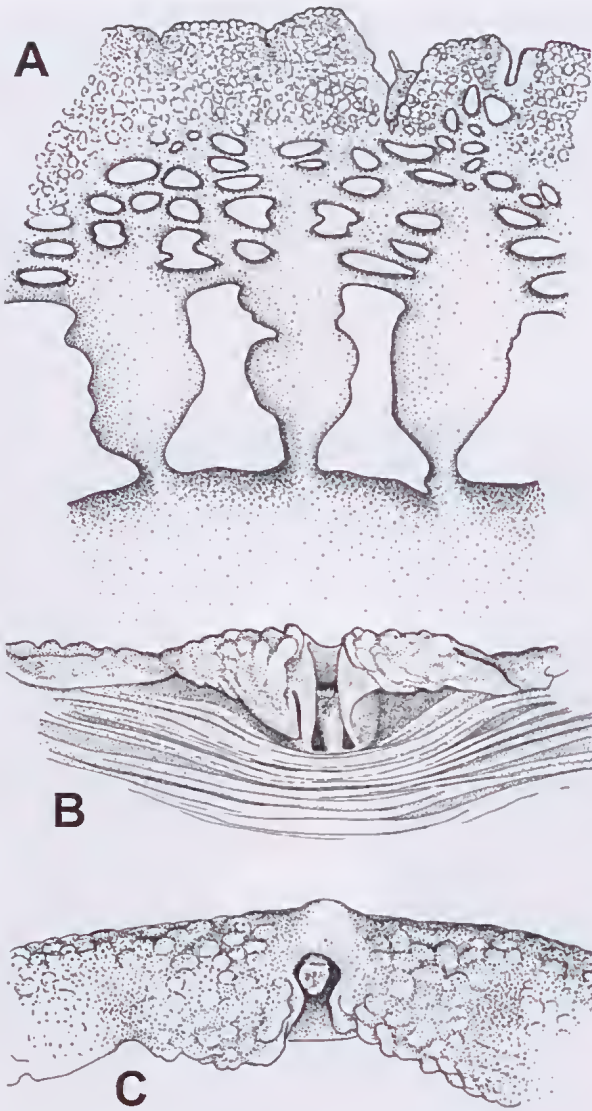


FIG. 2. *Bazinga rieki* gen. nov., sp. nov. A, peripheral canal sinus with subumbrellar muscles dissected away; B, subumbrellar view of rhopaliar niche (note asymmetrical lappets); C, exumbrellar view of rhopaliar niche (note protective hood in place of open pit).

Velar lappets 4 per octant, short, squared off, not as long as ocular lappets, defined from one another proximally by narrow region without warts. Ocular lappets two per octant, long and pointed, asymmetrical in preserved specimens, with right-hand lappets in ventral view folding to point obliquely along bell margin, left-hand lappets folding axially (Fig. 2B); bases of right

and left ocular lappets folded axially to create a straight-sided gap between, slightly rounded marginally (Fig. 2C). All lappets heavily granulated with fine warts.

Rhopalia 8; 4 perradial and 4 interradial; deeply embedded under exumbrellar hood, in cavity formed by large fold on axial side of each ocular lappet (Figs 2B, C). Typical rhizostome exumbrellar smooth or radially ridged, rhopaliar pits lacking.

Colour in life. Bell jelly translucent and colourless; subumbrellar muscle folds golden brown due to zooxanthellae; gonads darker brown; after 2–3 months preserved in formalin solution, whole animal pale yellowish with brownish gonads.

Variation. Smaller paratypes have the radial canals in the shape of a simple broad straight line, without the flared sides of the holotype; mid-size specimens have the sides of the canals somewhat more divergent like a funnel.

Observations on live animals. Video taken by Denis Riek in both natural and laboratory settings accompanies the type series. The swimming pattern consists of continuous rapid pulsations at a rate of more than 200 per minute, and even though the bell is being continually flexed, there appears to be little effective propulsion. In an aquarium these pulsations were insufficient to lift it off the substrate. Thus it would seem that *Bazinga rieki* is largely at the mercy of currents.

Etymology. The species name, *rieki*, is to honour Mr Denis Riek, whose keen interest in photographing and identifying the sea-life of northern New South Wales led to the discovery of this most intriguing species.

Distribution. *Bazinga rieki* is only known from coastal waters off northern New South Wales. However, having been found at three different collecting sites on three different dates it seems likely to be relatively common, and could be expected to be found more widely along the central east Australian coast, particularly south of the Tropic of Capricorn.

DISCUSSION

The order Rhizostomeae was divided into two suborders by Stiasny (1921), based on a suite of structural features. Members of the Dactylio-

phorae are characterised by having radial folds on the surface of the rhopaliar pits; subgenital pits narrowed by conspicuous papillae; annular subumbrellar muscles; oral arms that are three-winged and may have scapulets; and by the anastomosing network of canals not being in communication with the gastric cavity.

In contrast, the Kolpophorae has smooth-surfaced rhopaliar pits; subgenital ostia without papillae; muscles variable in form from radial and straight to annular to feather-like arcs; anastomosing canals in communication with the gastric cavity; and oral arms that lack scapulets and are dichotomous, triangular, or three-winged. The primary diagnostic features for both suborders are summarised and compared in Table 1.

Bayha *et al.* (2010) constructed a phylogeny for the scyphozoan families using sequence data from 18S and 28S rDNA nuclear genes. Their results were largely consistent with prior morphological hypotheses, but importantly they concluded that the dactyliophorids were paraphyletic with respect to the kolpophorids. Since *Bazinga* falls well outside both of these groups morphologically, it seems likely that it is either the sister group to, or basal to, all other rhizostomes. Moreover, its hooded rhopalia are more reminiscent of some semaestomes than of the rhizostomes, again suggesting a basal affinity. Obtaining DNA and testing these hypotheses should be considered a high research priority.

Rhizostomes are famously large, some reaching diameters of 350–500 mm or even more, and while there are a few small species in the size range 35–50 mm, e.g., *Cassiopea udrosia* Agassiz & Mayer, 1899 (50 mm, Fiji), *Mastigias gracilis* (Vanhöffen, 1888) (35 mm, Red Sea), and *Acromitus taukahikei* Light, 1924 (45 mm, China), this is unusual. However, *Bazinga rieki* is mature at less than 20 mm, making it by far the smallest rhizostome yet discovered. While this is noteworthy in itself, *Bazinga rieki* is also unique in its morphology, differing in major ways from all other rhizostomes.

The ocular lappets of *Bazinga rieki* are remarkable in being asymmetrically folded, and this is consistent across all specimens. Such an occurrence has apparently not been described in any other rhizostome.

The unusual canal system is also utterly unlike any other rhizostome, and can only be

awkwardly described using standard terminology. In most rhizostomes, the radial canals arise at different levels along the cross-shaped stomach, with those arising from the interradii (i.e., the arms of the cross) being the shortest, those arising from the perradii (i.e., between the arms of the cross) being the longest, and those in between being midway in length. In *Bazinga* the arms are all the same length because they arise from the same level off the circular stomach. Moreover, rhizostomes are taxonomically separated based on a) how many radial canals extend past the ring canal to reach the margin, and b) whether the anastomosing network communicates with the stomach. However, *Bazinga* has no ring canal, and no radial canals extend to the margin, but rather, the coelenteric region covered by the circular muscles consists of a vast open sinus with scattered small patches of jelly matrix, giving the impression of a reversed meshwork, where the swollen and coalesced area of the anastomosed canals is far greater than the area between.

If one looks at individual families within the Rhizostomeae, irrespective of suborder, then *Bazinga rieki* does share some important characters with particular families. Like Cassiopeidae, the stomach of *Bazinga* is circular; however, in the only described cassiopeid genus, *Cassiopea*, it is very small compared to the whole diameter, whereas in *Bazinga* it is very broad, spanning more than half the bell diameter. *Bazinga* further differs from *Cassiopea* in all other primary diagnostic characters such as the number of rhopalia, the form of the subumbrellar muscles, the form of the oral arms, the form and number of the radial canals, and the general habits of the live animal.

Bazinga is reminiscent of Cepheidae in having small subgenital ostia; however, the Cepheidae is characterised by a large central dome on the exumbrella which often bears conspicuous papillae or sometimes a large knob. Even in *Cotylorhiza*, which lacks papillae or a knob, the central dome is well defined and dominates the bell. *Bazinga* has no such central dome; instead, the bell is globular and often somewhat flattened in life. Species in the Cepheidae are also characterised by having appendages on the oral arms such as filaments, stalked suckers, or spindles, whereas *Bazinga* completely lacks any

such appendages. Furthermore, the oral arms of *Bazinga* are coalesced whereas those of cepheids are not. Finally, the conspicuous annular muscles of *Bazinga* compared to the fine radial muscles of the cepheids, the circular stomach of the former compared with the octagonal stomach of the latter, and the completely different radial canal pattern between the two groups convincingly separates them.

Like some Kolpophorae families such as Mastigiidae, Versurigidae, and Thysanostomidae, *Bazinga* has well developed annular muscles on the subumbrella. However, along with many other structural features, the continuous subgenital porticus and separate oral arms of these other families would serve to immediately distinguish them from *Bazinga*.

Similarly, the Dactyliophorae families have annular muscles, but they have conspicuous papillae in the subgenital ostia, whereas *Bazinga* does not.

Even the families with coalesced oral arms would not be easily mistaken for *Bazinga*, with both the Rhizostomatidae and Stomolophidae also having scapulets, whereas *Bazinga* does not.

One of the key features that separates the two orders, Kolpophorae and Dactyliophorae, is the surface texture of the horseshoe-shaped rhopalial pits, being smooth in the former and decorated by radial folds in the latter. However, the rhopalia of *Bazinga* are completely different, i.e., completely covered by an exumbrellar hood and embedded in a subumbrellar cavity formed by the folded lappets.

Therefore, while *Bazinga* does share some features with other Rhizostomeae suborders and families, its large circular stomach, unbranched evenly spaced radial canals, and hooded rhopalia are unique, and warrant new subordinal status. This decision is further reinforced by its unusual combination of other primary diagnostic characters such as coalesced oral arms and lack of scapulets and subgenital papillae, that also make it wholly unlike any other known family or suborder.

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LITERATURE CITED

- Agassiz, A. & Mayer, A.G. 1899. Acalephs from the Fiji Islands. *Bulletin of the Museum of Comparative Zoology at Harvard University* 32(9): 157–189, 17 pls.
- Bayha, K.M., Dawson, M.N., Collins, A. G., Barbeitos, M.S., & Haddock, S.H.D. 2010. Evolutionary relationships among scyphozoan jellyfish families based on complete taxon sampling and phylogenetic analyses of 18S and 28S ribosomal DNA. *Integrative and Comparative Biology* 50: 436–455.
- Cuppy, W. 1950. *The Decline and Fall of Practically Everybody*. (Dorset Press: New York).
- Cuvier, G. 1799. Sur l'organisation de l'animal nommé méduse. *Journal de Physique, de Chemie, d'Histoire Naturelle et des Arts* 49: 436–440.
- Kawahara, M., Uye, S.-I., Ohtsu, K. & Izumi, H. 2006. Unusual population explosion of the giant jellyfish *Neupilema nomurai* (Scyphozoa: Rhizostomeae) in East Asian waters. *Marine Ecology Progress Series* 307: 161–173.
- Kishinouye, K. 1922. On a new rhizostome medusa. *Neupilema nomurai* ng. nsp. *Dobutsugaku Zasshi* 34: 343–346. [In Japanese].
- Kramp, P.L. 1961. Synopsis of the medusae of the world. *Journal of the Marine Biological Association of the United Kingdom* 40: 1–469.
- Light, S.F. 1924. A new species of scyphomedusan jellyfish in Chinese waters. *The China Journal of Science and Arts* 2(5): 449–450, 1 pl.
- Mayer, A.G. 1910. *Medusae of the World. Vol. 3, The Scyphomedusae*. (Carnegie Institution: Washington)
- Quoy, J.R.C. & Gaimard, J.P. 1824. *Voyage autour du monde ... exécuté sur l'Uranie et la Physicienne, pendant ... 1817–20. Zoologie. Voyage de l'Uranie. M. L. d. Freycinet*. Paris: 712 pp., plus Atlas.
- Stiasny, G. 1921. Studien über Rhizostomeen. *Capita Zoologica* 1(2): viii, 1–179, 5 plates.
1923. Das Gastrovascularsystem als Grundlage für ein neues System der Rhizostomeen. *Zoologischer Anzeiger* 57(9/13): 241–247.
- Vanhöffen, E. 1888. Untersuchungen ueber Semaestome und Rhizostome Medusen. *Bibliotheca zoologica Stuttgart* 1(3): 51 pp., 6 pls., 1 map.

A new record of *Dardanus australis* Forest & Morgan, 1991 (Crustacea: Anomura: Diogenidae) from off northern New South Wales, eastern Australia

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ABSTRACT

Dardanus australis Forest & Morgan, 1991, is reported from off Nambucca Heads, New South Wales, markedly increasing its known distribution in Australian waters. It was captured in a deep water lobster trap at 137 m. It is diagnosed and refigured, and notes on variation in colour and morphology are given. It is characterised by its pattern of spination, subequal chelipeds, proportions of the ocular peduncles, colour pattern, and its large size (to at least 36.5 mm shield length). □ *Decapoda, Diogenidae, Dardanus, New South Wales, Australia, deep water, new record.*

In Australia, particularly New South Wales (NSW), the majority of by-catch recorded by eastern rock lobster (*Jasus verreauxi*) fishermen is taken from deep water traps greater than 50 m. A large component of this by-catch is predominantly hermit crab species, particularly *Strigopagurus striguanus* (White 1847) and *Dardanus arrosor* (Herbst 1796). The implementation of the NSW Department of Primary Industries Eastern Rock Lobster Fishery Management Strategy (FMS) in 2007 recognised the need to identify by-catch species associated with lobster catches and to assess the impacts of rock lobster fishing activities on hermit crab populations. During 2008 and 2009, as part of an observer based research program with the eastern rock lobster fishery, collections of hermit crabs were taken from numerous deep water lobster traps at depths ranging from 50–220 m along the entire NSW coast.

Daniel Stewart, a commercial fishermen from Coffs Harbour, on the board the vessel *Flo Baby*, set deep water lobster traps off Nambucca Heads (30°38' S) on 20 April 2009 in 137 m, on the edge

of a patchy coralline reef, running down a gentle slope to 146 m to a muddy/gravel sea bed. Traditional traps (rectangular hard wood frame of 1.8×1.4×0.8 m, with three 25 cm nozzles) were baited with a combination of fish wastes and salted shark/cow hide, and set for a period of approximately six weeks. With the retrieval of the traps on 1 June, all hermit crabs captured were removed from the traps, packed into foam boxes with ice, labeled and sent to the NSW Industry and Investment Cronulla Fisheries Research Centre for processing in the laboratory. All hermit crabs and shells were identified to species, crabs were removed from their shells, sexed, measured and weighed. The present specimen could not be initially recognised, and so was set aside for further examination. After processing it was frozen before being placed into 95% ethanol and forwarded to the Queensland Museum where it was formally identified as *Dardanus australis* Forest & Morgan, 1991, after comparison with specimens from Western Australia, from where it was originally described.

Dardanus currently contains 43 species (see McLaughlin *et al.* 2010), of which 30 are Indo-West Pacific in distribution. The most recent additions to the genus have been four new species described by Asakura & Hirayama (2002) and Asakura (2006).

Abbreviations. All measurements were taken using dial calipers, and are in millimeters (mm). Measurements are of cephalothoracic shield length (SL); cephalothoracic shield width (SW), claw length (CL), chela length, including fixed finger (CHL), chela width (CHW), and total weight (g). Specimens examined are deposited in the Queensland Museum, Brisbane (QM); Western Australian Museum, Perth (WAM); Museum of Victoria, Melbourne (MOV).

SYSTEMATICS

Dardanus australis Forest & Morgan, 1991 (Figs 1–3)

Dardanus australis Forest & Morgan, 1991: 204–208, fig. 1; Poupin, 1996a: 17, 76, 96; 1996b: 16, pl. 7h. *Dardanus* sp. — Poore, McCallum & Taylor, 2008: 25, un-numbered colour fig.

Material examined. QM-W29182, male (SL 29.0 mm, SW 24.2 mm, CL 95.8 mm, CHL 59.6 mm, CHW 25.9 mm, fresh weight 155.02 g), off Nambucca Heads, northern NSW, 137 m depth, D. Stewart, 1.06.2009. WAM-C20215, paratype male (SL 34.3 mm, SW 28.7 mm), off Hamelin Bay, Augusta, Western Australia, 34°12'S, 115°01'E, coll. Mrs Wynne, Dec 1964. MOV-J54960, ovig. female, SL 12.2 mm, SW 10.6 mm, off Zuytdorp, Western Australia (27°03'07"S–27°02'53"S, 113°04'52"E–113°04'48"E), 106 m, beam trawl, *Southern Surveyor*, stn SS10-2005-110, G.C.B. Poore *et al.*, 6.12.2005. MOV-J54961, female (SL 3.4 mm, SW 3.0 mm), female (SL 5.0 mm, SW 4.4 mm), off Mentelle, Western Australia (33°58'48"S–33°59'01"S, 114°44'02"E–114°44'06"E), 96–123 m, *Southern Surveyor*, stn SS10-2005-15, coll. G.C.B. Poore *et al.*

Diagnosis. Shield (Fig. 1C, D) 1.13–1.33 times longer than broad, proportionately longer with increasing size. Rostrum broadly triangular, blunt or rounded distally; not projecting as far as lateral projections; lateral projections strongly projecting, apex blunt or rounded. Shield unarmed except for small spines and tubercles anterolaterally. Ocular peduncles (Fig. 1C), moderately stout; shorter than front of shield, and less than half length; peduncles weakly inflated distally and proximally; corneal length about 0.25 total length of peduncle. Ocular

acicles with 3–6 distal spinules; acicles about 1/3 length of ocular peduncles, as broad as long. Antennular peduncles long, over-reaching ocular peduncles by 1/2 to 2/3 length of ultimate segment; unarmed except for 6–10 spinules on distolateral margin of proximal segment. Antennal peduncles as long as or slightly longer than ocular peduncles. Antennal acicles reaching at most 1/3 length of ultimate peduncular segment; acicles with 2 distal spines, 1 dorsal spine posterior to these, 3–4 mesial spines. Antennal flagella as long as or slightly longer than carapace. Third maxilliped merus with 1 distodorsal and 3–5 ventral spines; ischium with strong crista dentata, 1–3 ventral spines; basis with about 12 distoventral spines. Chelipeds (Fig. 1A, B) subequal; dactyl about 0.5 times length of propodus, covered with strong corneous-tipped spines on dorsal and lateral faces; mesial face with some spines dorsally. Propodus twice as long (or slightly less) maximum width (excluding spines); fixed finger deflexed ventrally; finger and palm covered on lateral, dorsal and ventral faces with strong mostly corneous-tipped spines (on large specimens spines tend to lose corneous tips and become distally blunted); propodus less spinose mesially, with more scattered and usually blunter spines. Carpus slightly broader than long; numerous corneous-tipped spines on lateral and dorsal faces; spines largest dorsally; mesial face almost smooth. Merus dorsal edge with several large spines distally and on distolateral edge; spines and tubercles along ventrolateral and ventromesial edges, especially large proximally on ventromesial edge. Second pereopods (Fig. 1E) longer than chelipeds; dactyl long and recurved ventrally, bearing numerous corneous-tipped spines dorsally and laterally in irregular rows; mesial and ventral surfaces with few scattered spines; lateral longitudinal sulcus along most of length. Propodus shorter, stouter than dactyl, with numerous corneous-tipped spines, largest and most numerous dorsally; mesial face with few spines dorsally. Carpus with large spines dorsally; some smaller more scattered spines laterally; 1–2 ventral spines; mesial surface almost smooth. Merus with non-corneous spines only along ventral margin. Third pereopods (Fig. 1F) similar to second. Dactyl longer than

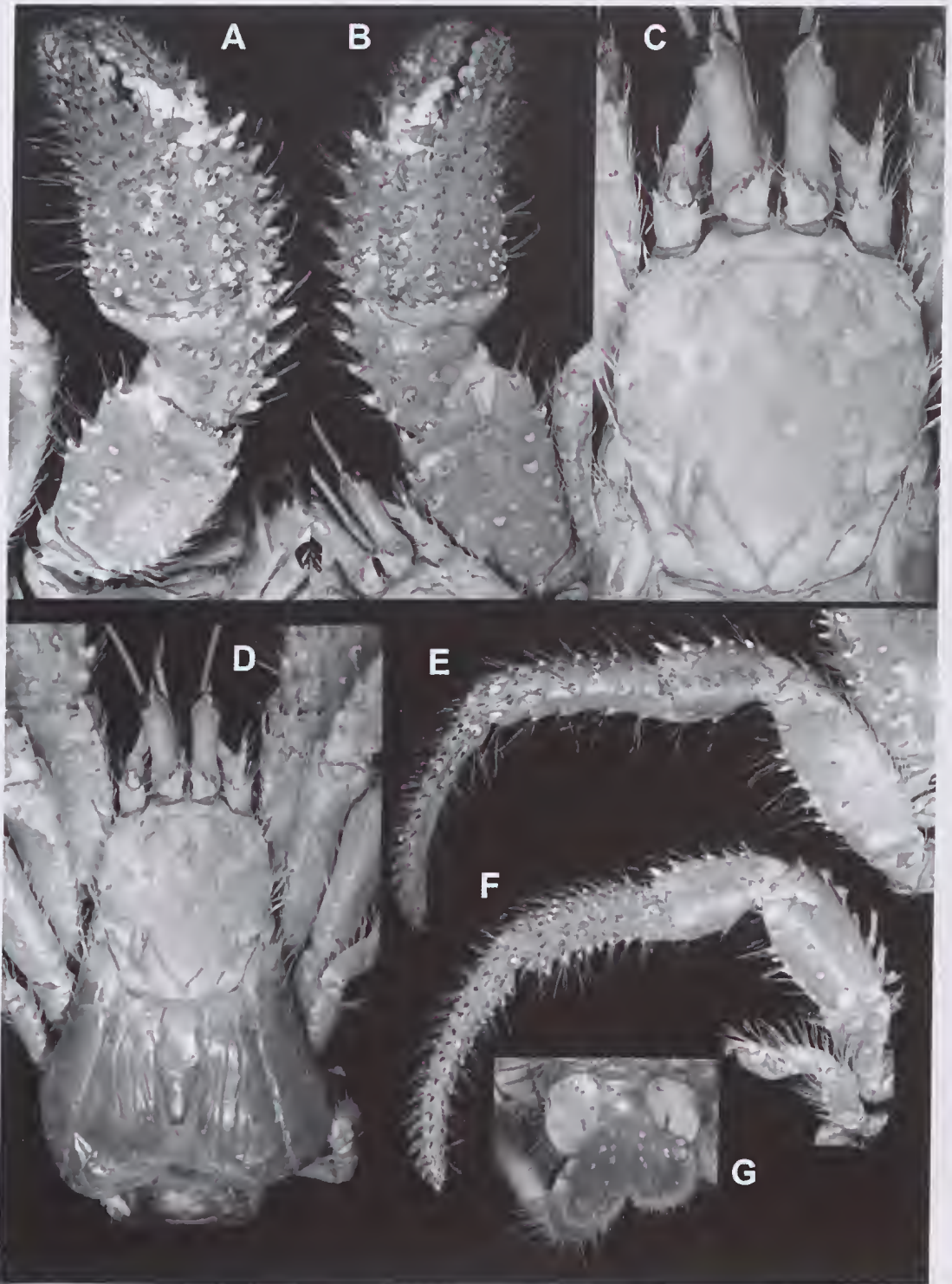


FIG. 1. *Dardanus australis* Forest & Morgan, 1991. QM-W29182, male (SL 29.3 mm), off Nambucca Heads, northern NSW. A, left cheliped; B, right cheliped; C, dorsal view of carapace shield and eyestalks; D, dorsal view of cephalothorax; E, second left pereopod; F, third left pereopod; G, telson.

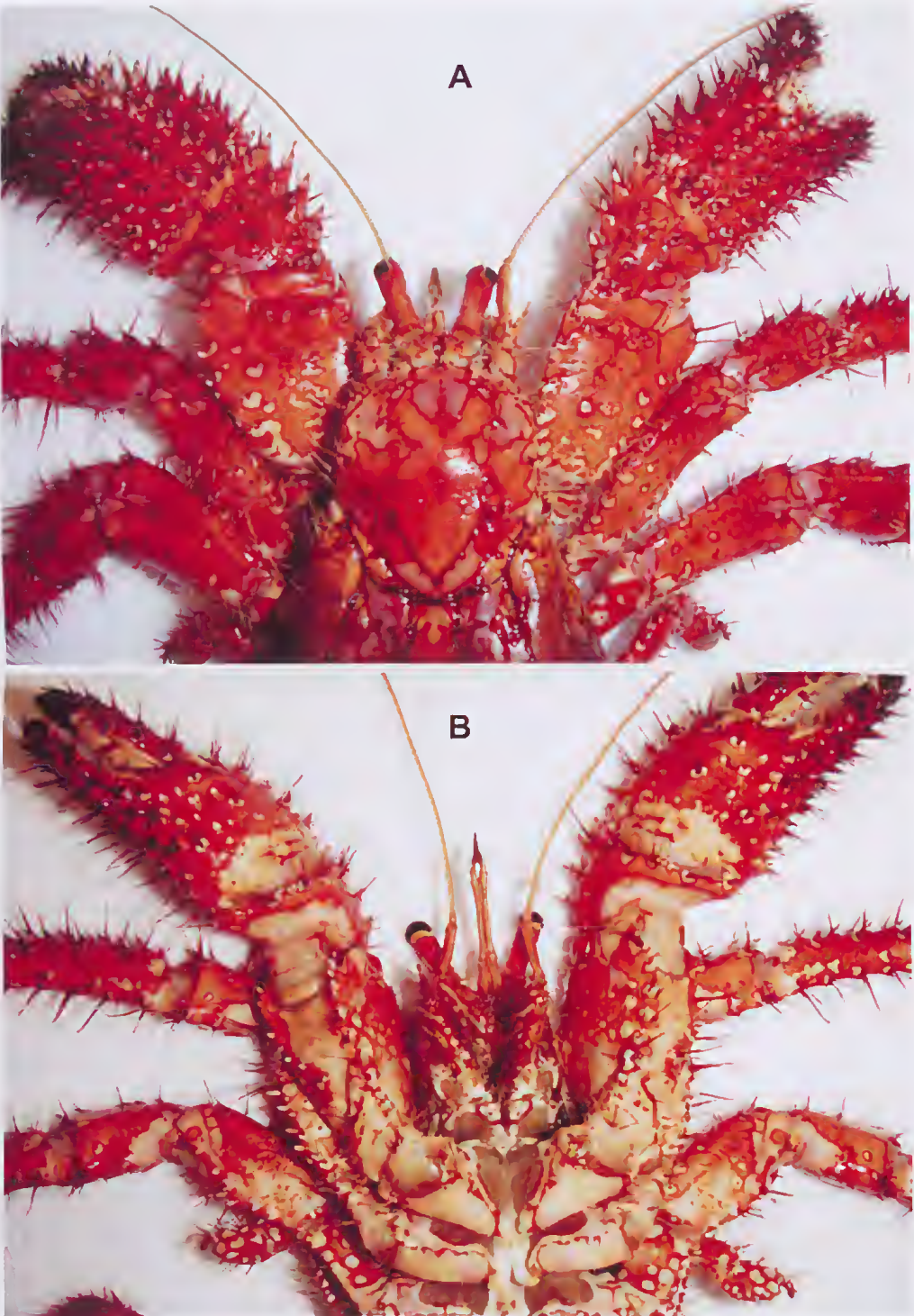


FIG. 2. *Dardanus australis* Forest & Morgan, 1991: QM-W29182, male (SL 29.3 mm), off Nambucca Heads, northern NSW. A, dorsal view of anterior carapace and claws; B, ventral view of same. Photographs by Marcus Miller.



FIG. 3. *Dardanus australis* Forest & Morgan, 1991, A, off SW Western Australia, precise locality not recorded (photograph by Gary Morgan); B, off SW Western Australia, coll. *Southern Surveyor*, SS10-2005 (photograph by Karen Gowlett-Holmes); C, Rapa, Austral Islands, French Polynesia, BENTHAUS Exped., stn CP1906, trawl 110–127 m (photograph by Joseph Poupin); D, Marotiri, Austral Islands, French Polynesia, male SL 9.5 mm, in shell of *Malia* sp. (photograph by Joseph Poupin); E, off SW Western Australia, precise locality not recorded (photograph by Gary Morgan).

second; spines more numerous ventrolaterally. Propodus similar length to second, but broader and more spinose especially ventrolaterally. Tailfan markedly asymmetrical; left uropods much larger than right. Telson (Fig. 1G) length similar to width, or slightly longer; left posterior lobe slightly larger than right, each bearing 5–8 corneous spines along posterior margins (sometimes reduced).

Colouration. The original colour description is a little misleading as it fails to take into account some of the variation in colour and pattern shown by this species, particularly at different stages of maturity. Figure 3A is of a specimen from Western Australia photographed by Gary Morgan, and may have been that upon which he based his original colour description, as it matches almost exactly ... 'Shield predominantly red-brown with large semi-symmetrical patches of cream ... Ocular peduncles uniformly pale red-brown except for diffuse darker areas proximally and at base of corneas. Ocular acicles and antennal peduncles with patches of red-brown. Chelipeds and pereopods 2 and 3 with dactyl and propodus mostly deep red or red-brown, non-corneous spines tipped with cream or white; carpus and merus paler with darker red-brown band under corneous tips of most spines and areas of cream especially on tubercles and non-corneous spines; cream patches usually bordered by thin band of dark red-brown.' (Forest & Morgan 1991). However, large specimens are overall orange rather than red-brown (Figs 2, 3C, D), and the large semi-symmetrical patches are more typically pale mauve. Ocular peduncles are also not always uniformly pale red or orange, but can have even paler almost yellow tonings only, becoming darker distally (Fig. 3C).

There are also conspicuous mauve to cream patches baso-proximally on the carpi and meri of the chelipeds and pereopods 1 and 2, which can be particularly broad and prominent next to the mero-carpal joint (especially in juveniles); no such colouration is mentioned by Forest & Morgan (1991), but which are indeed also visible on the photographs of the Western Australian specimens (Fig. 3A, B). In small specimens (Fig. 3B) the chelae are less uniformly coloured, with red-brown colour mostly on

fingers, and extending a variable distance laterally onto palm.

Not previously mentioned is the marked mottling or spotting on the abdomen. Juveniles appear strongly mottled with white and reddish brown over the entire abdomen (Fig. 3B), but this gradually becomes white irregular blotching or spotting (Fig. 3A), gradually fading posteriorly until it almost disappears in large adult specimens (Fig. 3C).

Habitat. The present specimen was taken in a lobster pot at a depth of 137 m, on the edge of a patchy coralline reef, beside a gentle slope descending to a muddy/gravel bottom at 146 m. It occupied the shell of *Charonia lampas rubicunda* (total length, 185.1 mm; aperture width, 45.2 mm; weight 145.7 g). The shell had encrusting epibiotic and endolithic species, covering greater than 50% of the shell. Forest & Morgan (1991) recorded: '*Dardanus australis* has been dredged or caught in rock lobster pots at recorded depths of 10–188 m. The 10 m record might be regarded with suspicion as the next shallowest report is from 40 m, with most specimens taken at depths exceeding 50 m, most frequently between 130–150 m. Shells utilised by the species are large and voluminous and include *Angaria delphinus* (Linnaeus, 1758), *Monodonta labio* (Linnaeus, 1758) and *Turbo jourdani* Kiener, 1839.' A record from the Austral Is. in French Polynesia (see Legall & Poupin 2013) recorded it living in a shell of an unidentified *Malia* sp (Fig. 3D).

Distribution. *Dardanus australis* was originally described from southwestern Australia between about Dirk Hartog I., Shark Bay (25°31' S, 112°29' E) in the north, and Albany (35°02' S, 117° 53' E) in the south. A further specimen (a male SL 35.0 mm) in the Muséum national d'Histoire naturelle, Paris, that was trawled from 47 fathoms off Kingscliff, northern NSW, in June 1961, was considered to most probably have been an error as it was otherwise unknown from localities eastward across southern Australia. However, Poupin (1996a, b) recorded specimens from Rapa in the Austral Islands, French Polynesia, which were identified by Jacque Forest after comparison with paratypes in the MNHN, Paris. There have also now been further records from the Austral Is (Marotiri and Neilson Reef;

Legall & Poupin 2013). Thus the present record collected off Nambucca Heads, NSW, indicates that the unconfirmed record from off Kingscliff, is likely to have been accurate, and thus this species can be considered to extend up the eastern Australian coast to about 28°15' S.

Remarks. *Dardanus australis* Forest & Morgan, 1991 (maximum recorded shield length of 36.5 mm) is most closely related to *D. hessii* (Miers, 1884), and *D. brachyops* Forest, 1962. All are similarly spinose species, and all have subequal chelipeds which is rare for *Dardanus* species. *D. australis* can be immediately separated by 1) its longer ocular peduncles with feebly inflated corneas; 2) by the shape and spination of the chelae that have a much more enlarged palm, that bears slightly shorter, more numerous, and more closely set spines on the dorsal and lateral faces; and 3) more extensive spination on the lateral surfaces of the second and third pereopods.

Dardanus hessii, is known from the Red Sea to Vietnam, the Arafura Sea, and north-western Australian waters down to depths of 15–73 m (see Forest & Morgan, 1991). It also occurs across northern Australian waters and down the east coast to about Innisfail, north Queensland (Davie unpublished). However its range is more tropical and apparently does not overlap with that of *D. australis*. It also differs in colour in having dark lateral and mesial longitudinal bands on the ocular peduncles, and by having deep red coloration confined to the fingers of the chelae (Fize & Serène, 1955: fig. 34; Forest & Morgan, 1991). Adult *Dardanus hessii* are also much smaller, only reaching about 15.0 mm in shield length.

The only species comparable in size to *Dardanus australis* is *D. brachyops* Forest, 1962, known from Hawaii in the Pacific, and from Madagascar, the Marquesas and La Réunion in the Indian Ocean. Both are typically found at depths from 50–190 m. They are also similar in spination, however, in *D. brachyops* the right cheliped is obviously smaller than the left, and the ocular peduncles are much shorter and stouter, and bear three transverse dark red bands (Forest 1962: fig. 1; Forest & Morgan 1991).

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LITERATURE CITED

- Asakura, A. 2006. *Dardanus sanguinocarpus* Degener, 1925 (Crustacea: Decapoda: Anomura: Diogenidae) species complex: A redescription of *D. sanguinocarpus* and descriptions of three new species. *Zootaxa* 1230: 1–54.
- Asakura, A. & Hirayama, A. 2002. *Dardanus jacquesi*, a new species of hermit crab from the Indo-west Pacific, with the redescription of a little known species, *Dardanus dearmatus* (Henderson, 1888). *Crustaceana* 75(3–4): 213–230.
- Fize, A. & Serène, R. 1955. Les Pagures du Vietnam. *Institut Océanographique Nhatrang, Note* 45: ix, 1–228.
- Forest, J. 1962. Sur un *Dardanus* des Hawaï et de Madagascar, *D. brachyops* sp. nov. *Bulletin du Muséum national d'Histoire naturelle, Paris*, (2) 34(5): 365–370.
- Forest, J. & Morgan, G. J. 1991. A large new species of *Dardanus* (Crustacea, Decapoda, Diogenidae) from southwestern Australia. *Bulletin du Muséum national d'Histoire naturelle, Paris*, (4)13, sect. A(1–2): 203–208.
- Legall, N. & Poupin, J. 2013. Internet – CRUSTA: Database of Crustacea (Decapoda and Stomatopoda), with special interest for those collected in French overseas territories. At <http://crustiesfroverseas.free.fr/> [consulted 2 March 2013].

- McLaughlin, P.A., Komai, T. Lemaitre, R. & Rahayu, D.L., 2010. Annotated checklist of anomuran decapod crustaceans of the world (exclusive of the Kiwaoidea and families Chirostylidae and Galathidae of the Galatheoidea) Part I – Lithodoidea, Lomisoidea and Paguroidea. *The Raffles Bulletin of Zoology Supplement* **23**: 5-107.
- Poore, G.C.B., McCallum A.W. & Taylor, J. 2008. Decapod Crustacea of the continental margin of southwestern and central Western Australia: preliminary identifications of 524 species from FRV Southern Surveyor voyage SS10-2005. *Museum Victoria Science Reports* **11**: 1-106
- Poupin, J., 1996a. Crustacea Decapoda of French Polynesia (Astacidea, Palinuridea, Anomura, Brachyura). *Atoll Research Bulletin*, April 1996, **442**: 1-114.
- Poupin, J., 1996b. Atlas des crustacés marins profonds de Polynésie française. Récoltes du navire Marara, 1986/1996. *Rapport Scientifique du Service Mixte de Surveillance Radiologique et Biologique, SMSRB, Montlhéry, France*: 1-59, pl. 1-20.

The distribution, ecology and conservation status of *Euastacus urospinosus* Riek, 1956 (Crustacea: Decapoda: Parastacidae), a dwarf freshwater crayfish from the Mary and Brisbane River drainages, south-eastern Queensland

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ABSTRACT

The Maleny Crayfish *Euastacus urospinosus* has previously only been recorded from Booloumba and Obi Obi Creeks, Mary River, Queensland. Recent biological surveys of the region have extended its known distribution to include rainforested streams draining both sides of the Conondale Range into the Mary and Brisbane Rivers. In the Brisbane River drainage *E. urospinosus* was found from 415 to 613 m elevation at 15 sites in 5 creek systems, and was abundant at each site. New observations on burrowing and ecological preferences are presented. *E. urospinosus* appears to be dependant on the presence of bangalow palm trees (*Archontophoenix cunninghamiana*). The newly extended distribution, along with an assessment of current threats, suggests that the current IUCN listing of 'Endangered' could potentially be downgraded to 'near threatened', but only after a genetic analysis to assess the possible isolation of populations between catchments. □ *conservation, crayfish, distribution, ecology, Conondale Range, Mary River, Brisbane River, Euastacus urospinosus.*

As part of the ongoing Australian Crayfish Project (ACP), research was conducted in the upper Brisbane River catchment between Nanango, Kilcoy and Jimna in late July 2011. That survey was centred on *Cherax* crayfish in the Brisbane River drainage, however as part of the investigation, several specimens of a *Euastacus* species were observed that were clearly not *E. hystricosus* Riek, 1951, the species that would normally be expected. One specimen was collected and later identified as *Euastacus urospinosus* Riek, 1956 (Fig. 1). *E. urospinosus* was originally described from one small male specimen collected from a cleared section of Obi Obi Creek, Maleny, Queensland. Morgan (1988) redescribed the species in detail with

additional specimens from a tributary of Obi Obi Creek above Mapleton Falls. Borsboom (1998) conducted a detailed study on the species ecology and biology based on specimens from North Booloumba and Bundaroo creeks, both tributaries of Booloumba Creek. Then Shull *et al.* (2005) collected specimens from two sites north of Maleny in tributaries of Obi Obi Creek. Until now all species records have been in the Mary River drainage. To confirm the extension of its distribution into the Brisbane River catchment system, another limited survey was conducted in January 2012, and its presence was confirmed in another two nearby creek systems. Finally, in May 2012 we undertook a more extensive survey, using our new found



FIG. 1. *Euastacus urospinosus* in life. West Kilcoy Creek, Brisbane River drainage.

knowledge of the species' habitat preferences, to effectively find the limits of distribution in the new catchment.

METHODS

The upper part of the Brisbane River catchment was surveyed from Beerwah westwards to Jimna, Johnstown, Nanango, and to the mountains behind Yarraman. The coordinates of collection sites were recorded using a Global Positioning System. The presence of crayfish was assessed by physically lifting rocks and logs, by excavating burrows, both by hand and with the assistance of spades, and by visually finding the entrances to active burrows. Large deep burrows were carefully excavated so as to document the direction and shape of the burrow, and the presence of branch tunnels. Specimens were preserved in 70% ethanol.

Voucher numbers refer to the collection currently maintained by Robert McCormack as part of the Australian Crayfish Project (ACP). Abbreviations: AM, Australian Museum, Sydney; Ck, Creek; OCL, Occipital Carapace Length, the

oblique distance from the posterior radius of the eye socket to the posterior mid-dorsal carapace (see Morgan 1997); QM, Queensland Museum, Brisbane; R., River; Trib., Tributary.

RESULTS

DISTRIBUTION

Euastacus urospinosus was recorded from 15 sites across five streams in the headwaters of the Brisbane River catchment: West Kilcoy, East Kilcoy, Mary Smokes, Sandy and Stony Creeks (Fig. 2, Table 1). In streams further to the east we were unable to locate *E. urospinosus*, even though suitable habitat seemed to be present, so future surveying in this direction may well increase the distribution eastwards. In Monsildale Creek catchment, further to the west, we were also unable to locate *E. urospinosus*, but the preferred rainforest conditions do not seem to occur around Monsildale Creek, or further west, so this lack of suitable habitat is likely to be the limiting factor. Two other similar species also occur in the Brisbane River catchment, *E. setosus* (Riek, 1956) replaces *E. urospinosus* in the

Table 1. Locality details for records of *Euastacus urospinosus* collected as part of the Australian Crayfish Project. Latitudes and longitudes are provided as decimal degrees. All specimens were collected by Robert B. McCormack & Paul Van der Werf.

Voucher Record #	Sex	Weight (g)	OCL (mm)	LOCALITY	LATI-TUDE	LONGI-TUDE	ALT (m)	COLL. DATE
ACP-3783	♂	22	35.1	West Kilcoy Ck, Conondale National Park (Brisbane R.)	26.75637	152.54637	552	29.07.2011
AM-P89667	♂	6	25.1	Trib. Mary Smokes Ck, Bellthorpe State Forest (Stanley-Brisbane R.)	26.85342	152.67299	514	13.01.2012
ACP-3855	♂	4	20.5	Trib. Mary Smokes Ck, Bellthorpe State Forest (Stanley-Brisbane R.)	26.85342	152.67299	514	13.01.2012
QM-W52160	♀	6	22.4	Trib. Mary Smokes Ck, Bellthorpe State Forest (Stanley-Brisbane R.)	26.85342	152.67299	514	13.01.2012
QM-W52161	♂	7	23.9	Trib. of east Kilcoy Ck, Conondale National Park (Brisbane R.)	26.74352	152.56852	613	13.01.2012
AM- P89668	♀	13	30.3	Trib. of east Kilcoy Ck, Conondale National Park (Brisbane R.)	26.74320	152.57012	594	14.01.2012
ACP-3903	♂	2	16.0	East Kilcoy Ck, Conondale National Park (Brisbane R.)	26.74103	152.57092	600	14.01.2012
ACP-3904	♀	7	23.5	East Kilcoy Ck, Conondale National Park (Brisbane R.)	26.74593	152.57165	580	14.01.2012
ACP-4003	♂	2	15.5	Branch Ck, Bellthorpe State Forest (Stoney Ck-Stanley-Brisbane R.)	26.85773	152.67763	524	20.05. 2012
ACP-4004	♂	6	24.7	Trib. of Mary Smokes Ck, Bellthorpe State Forest (Mary Smokes-Brisbane R.)	26.85247	152.67386	522	20.05.2012
ACP-4005	♂	2	16.2	Trib. of Flagstone Ck, Bellthorpe State Forest (Kilcoy Ck-Mary R.)	26.81774	152.67783	528	20.05.2012
ACP-4006	♂	0.71	11.6	Trib. West Kilcoy Creek, Bellthorpe National Park (Kilcoy-Brisbane R.)	26.76307	152.55459	515	20.05.2012
QM-W52162	♂	3	17.0	Stoney Ck (Stanley-Brisbane R.)	26.85790	152.72030	468	21.05.2012
ACP-4028	♀	3	20.8	Stoney Ck (Stanley- Brisbane R.)	26.85790	152.72030	468	21.05.2012
ACP-4029	♂	3	17.6	Branch Ck (Stoney Ck-Stanley-Brisbane R.)	26.86087	152.70772	415	21.05.2012
QM-W52163	♂	5	21.2	Branch Ck, (Stoney Ck-Stanley-Brisbane R.)	26.86087	152.70772	415	21.05.2012
ACP-4031	Juv.	1	13.8	Branch Ck (Stoney Ck-Stanley-Brisbane R.)	26.85818	152.70112	466	21.05.2012
QM-W52164	♂	12	28.7	Branch Ck (Stoney Ck-Stanley-Brisbane R.)	26.85818	152.70112	466	21.05.2012

Table 1. Continued ..

QM-W52165	♀	22	35.1	Trib. of Branch Ck (Stoney Ck–Stanley–Brisbane R.)	26.65668	152.69635	470	21.05.2012
ACP-4034	♀	18	31.1	Trib. of Branch Ck (Stoney Ck–Stanley–Brisbane R.)	26.65668	152.69635	470	21.05.2012
ACP-4035	♂	2	16.4	Trib. of Branch Ck (Stoney Ck–Stanley–Brisbane R.)	26.86317	152.68970	467	21.05.2012
QM-W52166	♂	8	24.4	Trib. of Goodla Ck (Sandy Ck–Stanley–Brisbane R.)	26.82267	152.67718	584	22.05.2012
ACP-4037	♀	36	43.5	Trib. of Goodla Ck (Sandy Ck–Stanley–Brisbane R.)	26.82267	152.67718	584	22.05.2012

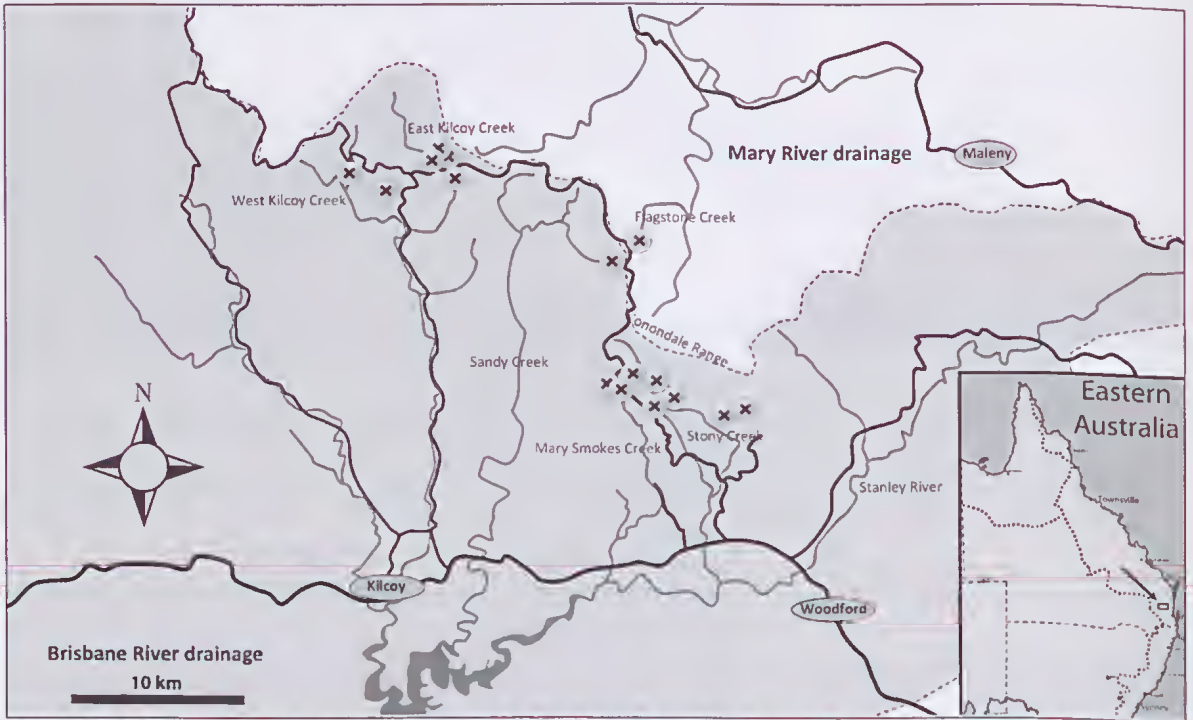


FIG. 2. Distribution of *Euastacus urospinosus* in the Brisbane River Catchment. *E. urospinosus* was newly recorded from 15 sites in the Brisbane River catchment and one site in the Mary River drainage. All sites were above 415 m, and the species was abundant at all sites.

southeast, and *E. jigara* Morgan, 1988, is found further to the south-west.

This survey did not target the Mary River drainage, however, we did observe large numbers of burrows, and vouchered one specimen for laboratory analysis, from a tributary of Flagstone Creek a tributary of the Mary River. This also greatly increases the known distribution of the species in the Mary River drainage.

ECOLOGY

This study did not target the larger giant spiny crayfish, *Euastacus hystricosus*, that also lives in the area, though they were plentiful, especially juveniles under rocks in the creeks. *E. hystricosus* is a species best sampled with baited traps which we did not use. The focus of our study was *E. urospinosus* and *Cherax* crayfish. Our *Euastacus urospinosus* specimens ranged in size from 11.6–43.5 mm OCL, and were found

at elevations of 415–613 m. Berried females were observed only in May, and a female of 36 grams, and 43.5 mm OCL, had 67 eggs. *Cherax* crayfish specimens sampled ranged from 10.0–31.9 mm OCL, and occurred from the lowest of our sites at 256 m above sea level up to 566 m (*Cherax* species occurs down to the coastal plain). Many specimens of *E. urospinosus* had abundant colonies of small white commensal temnocephalans (Platyhelminthes: Turbellaria) covering their bodies, and ectocommensal worms (Phreodrilid oligochaetes) were also observed on specimens from the Brisbane River drainage.

Euastacus urospinosus is a burrowing crayfish preferring cryptic habitat. It typically makes two types of burrows. Smaller crayfish less than 28 mm OCL make relatively rudimentary burrows with only one or two entrances under rocks or other structures, and which usually extend no more than 300 mm into creek banks. They were always in wet areas, but burrows did not always reach water and many were just in wet sandy/rock areas along the stream edges or gravel bars. Larger adults, conversely, make deep burrows that are not connected to the creek and range deep into the rainforest adjacent to the creeks, or along ephemeral drainage gullies. Small drainage gullies through the rainforest that were dry on the surface during our survey, but would hold flowing water during rain events, were favoured areas. Burrows were also found in riparian rainforest that would only have water coverage during major flood events, and in such cases, burrows typically went down to the water table. These could be as deep as 1 m or more, but where the water table was at as little as 300 mm depth, the burrows would still be long. Most of the smaller adult burrows we managed to excavate were generally 0.85–1.2 m in total depth with an average of three (occasionally 2–5) surface entrances, several blind tunnels, and a chamber at the bottom. The lower tunnels and chamber were usually flooded. Most adult burrows were in the rainforest floor adjacent to small flowing streams, with a particular concentration of burrows around palm tree roots (Fig. 3). It was common for the whole forest floor in palm valleys to be riddled with burrows (McCormack 2012).

Two important factors governing the presence of *Euastacus urospinosus* became apparent during our work: 1) bangalow palm trees (*Archontophoenix cunninghamiana*) must be present; and 2) *Cherax* crayfish must be absent. Streams without palms scattered along the banks did not seem to support *E. urospinosus*, and even at over 500 m elevation invariably contained a *Cherax* species. Additionally, when we encountered *Cherax* crayfish in a stream with palms, only *E. hystricosus* was co-occurred. Conversely, when *Cherax* was absent but *E. hystricosus* present, the two *Euastacus* species cohabited, with *E. hystricosus* in the large main streams, while *E. urospinosus* preferred the stream margins and banks as well as the smaller feeder streams that penetrate deep into the rainforest. Only *E. urospinosus* is found at the top of the catchment in the smaller feeder streams flowing through the rainforest, but then as the streams widen and deepen, both species begin to be found together. Lower down the stream again, *E. urospinosus* disappears, and *Cherax* species begin to co-occur with *E. hystricosus*, and then lower down still, a species of *Cherax* becomes the only crayfish present. From our observations there are some grounds to speculate that the dominance of *E. urospinosus* over *Cherax* spp. is directly linked to the prosperity of *E. hystricosus*. It seems possible that if *E. hystricosus* disappeared from a stream then there would be no obstacle to the upstream dispersal of *Cherax*, and if that occurred then *E. urospinosus* may be ultimately displaced from the area.

Euastacus urospinosus, like many species of its genus, are aggressive and will whip around to face any threat, raising their claws and snapping whilst rapidly retreating backwards, seeking to retreat under shelter or down their burrow. No crayfish were observed wandering the creeks or forest floor during the day, however, occasionally the tips of crayfish claws could be seen at the entrance to the burrow in the late afternoon. Our limited surveys did not include any night time field work.

We observed areas where creeks in both the Mary and Brisbane River drainages came within 100 m of each other, with *E. urospinosus* occurring in both, and only separated by low-lying ground that would be inundated during



FIG. 3. Flags signalling the entrances of adult *E. urospinosus* burrows in the rainforest floor on a tributary of Goodla Ck (Site ACP-4036; precise locality data in Table 1) at 584 m in the Brisbane River drainage. In this case there were as many as 25 in a 3×3 m quadrat. In the background are the authors, Rob McCormack (left) and Paul Van der Werf (right).

storms and prolonged wet periods. As *E. urospinosus* is known to construct burrows in the forest floor at least 20 m from the stream, and is also recorded to travel over 20 m to find a mate (Borsboom 1998), it seems feasible that there could be regular gene flow between the two catchment populations. Morphologically, specimens from both drainages show no obvious differences. We are not aware of any genetic studies having been conducted on this species, and studies into population genetics and gene flow would be desirable.

CONSERVATION STATUS

All *Euastacus* species are classed as 'no take' and protected in Queensland. Currently *E. urospinosus* is listed as Endangered on the

IUCN Red List, but has no specific state conservation listing. The current IUCN (2012) listing is based on: IUCN Status: EN B1+2(a), (b)iii based on EOO <5,000 km², severely fragmented distribution (two fragmented localities), and anticipated decline in area, extent and/or quality of habitat and EOO due to climate change (Coughran & Furse 2010). This assessment was based on a species' distribution of two geographically separate areas around 15 km apart and regarded as fragmented with an overall Extent of Occurrence (EOO) of approximately 200 km². Original listed threats included illegal or recreational fishing, localised impacts, climate change, cane toads and other exotic species (cats, foxes pigs, goats).

The new information presented here, increases the EOO for *E. urospinosus* to 600 km², and increases the number of known locations from two to eight, with new populations recorded at 16 new sites. Morgan (1988) listed the species distribution as above 240 m. The lower reaches of the independent creek systems in the Brisbane River drainage all connect to the main river at approximately 100 m altitude, and although this would be too low (and thus warm) to establish viable populations, perhaps migration up and down the creek systems during cold wet winter periods, by a few individuals at least, could be responsible for occasional dispersal into different creek systems.

Within the Brisbane River drainage *Euastacus urospinosus* occurs almost entirely within State Forests and National Parks, and often in remote inaccessible locations that offer excellent protection for this species. It is abundant at all sites. From our own research in the area, and after consultation with other researchers, we believe *E. urospinosus* is not generally susceptible to illegal or recreational fishing. The juveniles are rarely captured in traps, and the adults spend the majority of time away from the streams where illegal fishing occurs, so this is encouraging for the species long term survival.

Additionally, we did not identify any significant current threat by exotic species that normally impact on freshwater crayfish (pigs, goats, foxes, cats, cane toads, fish and invasive crayfish), within the Brisbane River drainage. In Queensland, feral pigs (*Sus scrofa*) are declared Class 2 animals under the Land Protection (Pest and Stock Route Management) Act 2002 (Queensland Government 2010), and are indeed a serious threat to similar crayfish species. *Euastacus yigara* Short & Davie, 1993, for example, is a similar dwarf crayfish from the Mistake Mountains area further north, that we consider is dramatically impacted by wild pigs that are devastating the juvenile population. However, *E. urospinosus* adults are secure in their deep forest burrows, and the juveniles that live within the creek and stream margins are also well protected by the nature of the very rocky geology of the area that provides protection from the pigs normal feeding activities. We found no evidence of widespread habitat

degradation by pigs in the survey area. We found no evidence of threats from foxes, goats and cats, and we do not consider these a particular threat to this group of dwarf crayfish generally. We did not observe any cane toads in the area. No exotic fish species or invasive crayfish were found in the Brisbane River drainage during our surveys, however, we did record exotic *Cherax destructor* in the Mary River drainage (Tributary of Yabba Creek, Jimna State Forest 26.59854°S, 152.38082°E, 566 m). This species has the potential to out-compete the native species in a short period of time (Coughran *et al.* 2009), and must be considered a potential threat to *Euastacus urospinosus* in the Mary River drainage.

The current IUCN listing of Endangered for *Euastacus urospinosus* is predicated on there being only two fragmented populations, and a continuing decline in extent and/or quality of habitat. However, given the present new data this is no longer valid, and a listing of 'near threatened' may be more appropriate. Based on the present survey work, we consider the species is unlikely to be facing a high risk of extinction in the wild within the next 20 years. Nevertheless, we currently have no genetic data on the populations of either catchment, and it is possible that they may be highly divergent with little or no gene-flow occurring. If this is the case, then a higher conservation category would still be applicable. Longer term population monitoring would also be appropriate, as the hotter and drier climate predicted to come is likely to have severe impacts on the viability of this and many other *Euastacus* species.

Large areas of the upper Brisbane River catchment have been cleared for agriculture, and this has clearly restricted the available habitat for *E. urospinosus*. Population numbers could be increased and reestablished by remediation of the small creeks that drain through the cleared agricultural areas. Fencing off riparian strips along the creeks and allowing native vegetation to regenerate would provide the shade, and coolness the species requires, and in particular, the replanting of palms would favour *E. urospinosus* and help deter *Cherax* crayfish invasions. Conservation measures

generally should be centred on retaining palm coverage around the smaller creeks as this appears pivotal to the survival of the species.

Future conservation or management initiatives for *E. urospinosus* will be greatly facilitated by further research. This should include: further distribution mapping (especially of the Mary River catchment that remains mostly unsurveyed); an assessment of population genetics; a better understanding of habitat requirements relating to palm trees; a better understanding of the potential interdependence with *E. hystricosus*; temperature monitoring of streams and investigations into thermal tolerance; and finally, investigations into the impacts of exotic species such as *Cherax destructor*.

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LITERATURE CITED

Borsboom, A. 1998. Aspects of the biology and ecology of the Australian freshwater crayfish, *Euastacus urospinosus* (Decapoda: Parastacidae). *Proceedings of The Linnean Society of New South Wales* **119**: 87–100.

Coughran, J. & Furse, J. 2010. *Euastacus urospinosus*. In: IUCN 2011. IUCN Red List of Threatened Species. Version 2011.2. <www.iucnredlist.org>. Downloaded 10 June 2012.

Coughran, J., McCormack, R.B. & Daly, G. 2009. Translocation of the Yabby, *Cherax destructor*, into eastern drainages of New South Wales, Australia. *Australian Zoologist* **35**(1): 100–103.

McCormack, R.B. 2012. *The spiny freshwater crayfish of Australia – A guide to the Euastacus freshwater crayfish of Australia*. (CSIRO Publishing: Melbourne).

Morgan, G.J. 1988. Freshwater crayfish of the genus *Euastacus* Clark (Decapoda: Parastacidae) from Queensland. *Memoirs of the Museum of Victoria* **49**(1): 1–49.

1997. Freshwater crayfish of the genus *Euastacus* Clark (Decapoda: Parastacidae) from New South Wales, with a key to all species of the genus. *Records of The Australian Museum Supplement* **23**: 1–110.

Queensland Government 2010. Fact Sheet – Declared class 2 pest animal. Control of feral pigs. The State of Queensland, Department of Employment, Economic Development and Innovation, 2010.

Riek, E.F. 1956. Additions to the Australian freshwater crayfish. *Records of the Australian Museum* **24**(1): 1–6, pl. 1.

Shull, H.C. Pérez-Losada, M., Blair, D., Sewell, K., Sinclair, E.A., Lawler, S., Ponniah, M. & Crandall, K.A. 2005. Phylogeny and biogeography of the freshwater crayfish *Euastacus* (Decapoda: Parastacidae) based on nuclear and mitochondrial DNA. *Molecular Phylogenetics and Evolution* **37**: 249–263.

Identification aid for the Indo-West Pacific species of *Periclimenaeus* Borradaile, 1915 (Crustacea: Decapoda: Caridea: Pontoniinae) using ambulatory dactyli

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ABSTRACT

Species of the Indo-West Pacific shrimp genus *Periclimenaeus* Borradaile, 1915, can be preliminarily identified using the morphology of the dactylus of the third ambulatory pereopods. The dactyli of the 60 currently recognised species are illustrated, and are placed into seven discrete groupings. Data is provided on major morphological reports, hosts, type material and general distribution. □ *Periclimenaeus*, *Palaemonidae*, *dactyli*, *morphology*, *commensal*, *Indo-Pacific Ocean*

Periclimenaeus Borradaile, 1915, is the second most speciose genus of Pontoniinae, with some 60 Indo-West Pacific species (and a further 14 in the East Pacific and Atlantic regions). The first species to be described was *Periclimenaeus tridentatus* (Miers, 1884), as *Coralliocaris? tridentatus*, from Thursday Island, Torres Strait, collected on the voyage of H.M.S. *Alert*, 1881–1882. A number of undescribed species exist in collections, and undoubtedly numerous further species of these small cryptic shrimps, found in association with sponge and ascidian hosts, remain to be described and discovered. Most commonly found in shallow tropical waters and particularly on coral reefs, they may also occur in deeper water, with *P. jeaucharcoti* Bruce, 1991, reaching a depth of 375–450 m.

One of the impediments to easy identification of *Periclimenaeus* species is the facility with which they autotomize their second pereopods when disturbed, and especially on collection. These appendages are frequently essential for the precise identification of species, although the morphologies of the rostrum, scaphocerite, the other ambulatory pereopods, and the caudal fan are all important. However, I have also found that a most useful character for the preliminary identification of *Periclimenaeus* species is the dactyl of the third ambulatory

pereopod, an appendage that is relatively rarely autotomized. Some species, e.g. *Periclimenaeus arthro-dactylus* Holthuis, 1952, can be identified on that character alone. Experience has shown that, where numerous specimens are collected simultaneously, for example *P. rhodope* (Nobili, 1904) or *P. quadrangularis* (Rathbun, 1906), the morphology of this character is highly consistent. The initial examination of the third ambulatory dactyl will readily indicate a small number of possible identifications. The identity of the specimens then needs to be confirmed by detailed comparisons with the appropriate species descriptions and illustrations available in the literature. Details particularly of the rostrum, presence or absence of supraorbital teeth or tubercles, inferior orbital angle and antennal tooth, presence of an anterior mediodorsal lobe on the first abdominal tergite, of the first segment of the antennular peduncle, carapocerite and scaphocerite, fingers of the first pereopod chelae, major and minor second pereopod chelae, tuberculation of the proximal segments, spinulation of the ambulatory propods and the armament of the uropodal exopod, will probably provide an identification without the necessity of removal of any mouthparts, although these can provide useful confirmatory details.

Discrepancies from these may suggest that an undescribed species is involved, and comparison with type material may be necessary when descriptions and illustrations are insufficiently detailed. The wide range of morphological variation in the ambulatory dactyls may well be related to details of host structure, either sponge skeletal or ascidian pharyngeal details. Many species are still poorly known, often from the type material only, frequently from a single sometimes incomplete specimen. In addition to details concerning type material, data is provided on descriptive reports, nomenclatorial changes, host preferences and general distributions. Major references to the literature of *Periclimenaeus* are Holthuis (1952), Bruce (1975), Fransen (2006) and Marin (2007). Several species of *Periclimenaeus* have recently been transferred into new genera, such as *Anisomenaeus spinimanus* (Bruce, 1969), *Climeniperæus orbitospinatus* (Bruce, 1969), *Isopericlimenes gorgonidarum* (Balss, 1913), *Orthopontonia ornata* (Bruce, 1969), *Paraclimenæus fimbriatus* (Borradaile, 1915) and *P. spinicauda* (Bruce, 1969). All these closely resemble *Periclimenaeus* species and may need care in separation. Keys for generic identification are available in Holthuis (1993). It is likely that further changes can be expected as well as the discovery of numerous more undescribed species.

To facilitate further study of this interesting genus, figures of the third ambulatory dactyl of all Indo-West Pacific species are provided, grouped by easily observable characters, together

with details of the original descriptions, more detailed reports on morphological details, institutions where type material is held, host animals and general geographical distributions.

Abbreviations: BMNH, The Natural History Museum; London; BPBM, Bishop Museum, Oahu; ION, Institute of Oceanography, Nha Trang, Vietnam; LACM, Los Angeles County Museum, Los Angeles; LEMMI, Laboratory of Ecology and Morphology of Marine Invertebrates, A.N. Svertzov Institute of Ecology and Evolution, Moscow; MNHN, Muséum National d'Histoire Naturelle, Paris; NHM, The Natural History Museum, London; NTM, Northern Territory Museum of Arts & Sciences, Darwin; QM, Queensland Museum, Brisbane; RMNH, Netherlands Centre for Biodiversity Naturalis, Leiden; SAM, South African Museum, Capetown; USNM, Smithsonian Institution, National Museum of Natural History, Washington; WAM, Western Australian Museum, Perth; ZMA, Zoological Museum, Amsterdam, now with RMNH; ZLKU, Zoological Laboratory, Faculty of Agriculture, Kyushu University, Kyushu; ZMC, Zoology Museum, Cambridge; ZMMSU, Zoological Museum, Moscow State University, Moscow; ZMUC, Zoological Museum, University of Copenhagen.

SYSTEMATICS

Palaemonidae Rafinesque, 1815: 98.

Pontoniinae Kingsley, 1879: 64.

Periclimenaeus Borradaile, 1915: 207.

Group 1: Species with simple ambulatory dactyli (4 species)

Periclimenaeus calmani Bruce 2012

Periclimenes calmani Bruce, 2012a: 525–528, figs 6–7.

Host. *Didemnum psammotode* (Sluiter, 1895) [Asciacea],

Distribution. Known only from the holotype male from East Point, Darwin, 12°25.0'S, 130°39.0'E, 8–10 m, Northern Territory (NTM-Cr. 000326).



P. calmani Bruce 2012, from Bruce (2012a).

***Periclimentaenus hecate* (Nobili, 1904)**

Coralliocaris hecate Nobili, 1904: 232; 1906: 58, pl. 3, fig. 2.
Periclimentaenus hecate – Bruce, 1975: 1574–1577, figs 11–12, 13e.

Host. *Diplosoma* ? *modestum*. Michaelsen, 1920 [Asciadiacea].

Distribution. Known from male and ovigerous female syntypes (MNHN-Na1911) from Djibuti (type locality), and reported also from Kenya, Comoro Islands, Seychelle Islands, Réunion, Maldiv Islands, Indonesia, China, Western Australia, Queensland and Society Islands, to 60 m.



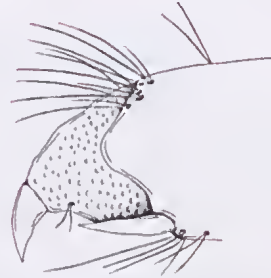
P. hecate (Nobili, 1904), from Bruce (1974).

***Periclimentaenus serenei* Bruce, 2012**

Periclimentaenus hecate – Marin, Britaev & Anker, 2004: 205–207, fig. 5a–h.
Periclimentaenus serenei Bruce, 2012a: 528–529.

Host. Probably from ascidian.

Distribution. Known only from the ovigerous female holotype, Tam Island, Nha Trang Bay, Vietnam, LEMMI, un-numbered.



P. serenei Bruce, 2012, from Marin *et al.* (2004).

***Periclimentaenus serrula* Bruce & Coombes, 1995**

Periclimentaenus serrula Bruce & Coombes, 1995: 111–115, figs 3–5.

Host. *Leptoclinoides incertus* Sluiter, possibly a *lapsus* for *Leptoclinoides dubius* (Sluiter, 1909) [Asciadiacea].

Distribution. Known only from the ovigerous female holotype and male allotype, (NTM-Cr 004174AB). Type locality Orontes Reef, Port Essington, Northern Territory, 12 m.



P. serrula Bruce & Coombes, 1995, from Bruce & Coombes (1995).

Group 2: Species with distal accessory tooth only (10 species)

***Periclimentaenus ardeae* Bruce, 1970**

Periclimentaenus ardeae Bruce, 1970: 310–312: 2005a: 397, fig. 5AB.

Host. *Asteropus simplex* (Carter, 1879) [Porifera] (Bruce, 1976a).

Distribution. Known only from the ovigerous female holotype (RMNH-D45526), type locality Heron Island, Queensland, and from Mombasa, Kenya.



P. ardeae Bruce, 1970, from Bruce (2005a).

Periclimentaenus bouvieri (Nobili, 1904)

Typton bouvieri Nobili, 1904: 233; 1906: 67, pl. 3, fig. 4.
Periclimentaenus bouvieri – Holthuis, 1952: 131–134, fig. 56.

Host. Unknown.

Distribution. 'Several syntypes' (MNHN-Na1926, *vide* Paula Martin-Lefevre, 12 April 2012). Five syntypes (2 ovig. females), in collections of the Istituto e Museo di Zoologia della Università, Turin (Holthuis 1952), from Djibouti (type locality). Also known only from Suez. Nobili (1906) reports on 15 syntypes, but the whereabouts of the additional specimens is unknown.



P. bouvieri (Nobili, 1904), from Holthuis (1952).

Periclimentaenus sp. 1

Periclimentaenus stylirostris – Marin, Britayev & Anker, 2004: 307, figs 7–8.

Host. Uncertain, probably sponges.

Distribution. Known only from Vietnam as reported by Marin *et al.* (2004). Material presently housed in the Laboratory of Ecology and Morphology of Marine Invertebrates, Moscow.

Remarks. To be described as a new species in Bruce (2013).



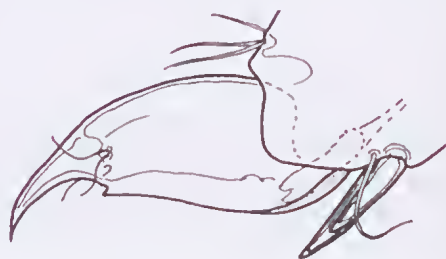
Periclimentaenus sp. 1, from Marin *et al.* (2004).

Periclimentaenus orontes Bruce, 1986

Periclimentaenus orontes Bruce, 1986: 151–158, figs 1B, 6–10.

Host. *Jaspis stellifera* (Carter, 1879) [Porifera].

Distribution. Known only from the ovigerous female holotype (NTM-Cr000272), from Orontes Reef, Port Essington, Northern Territory, 3.0 m.



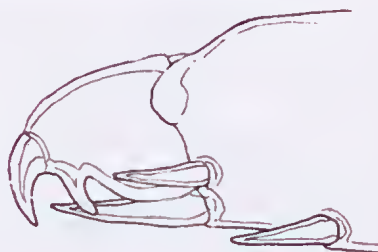
P. orontes Bruce, 1986, from Bruce (1986)

Periclimentaenus pachydentatus Bruce, 1969

Periclimentaenus pachydentatus Bruce, 1969: 162–163; 1993: 834, fig. 3a; 2005b: 338–341, figs 9–10.

Hosts. *Hypodistoma deerratum* (Sluiter, 1885), *Botrylloides leachi* (Savignyi, 1816) [Ascidiacea].

Distribution. Ovig. female holotype and male allotype (BMNH-1971.152, BMNH-1971.153), from Gulf of Carpentaria, Queensland, 14°12'S, 142°48'E. Also from Western Australia, Heron Island, Qld, Papua New Guinea and the Philippines.



P. pachydentatus Bruce, 1969, from Bruce (2005b).

Periclimanaeus palauensis Miyake & Fujino,
1968

Periclimanaeus palauensis Miyake & Fujino, 1968: 417–420, fig. 5.

Host. Uncertain.

Distribution. Known only from the ovigerous female holotype (ZLKU-2773) from Ngadarak Reef, Palau, Caroline Islands.

Periclimanaeus quadridentatus (Rathbun, 1906)

Coralliocaris quadridentatus Rathbun, 1906: 920, fig. 69, pl. 24, fig. 1.

Periclimanaeus quadridentatus – Bruce, 2012a: 515–519, figs 1–2; 2013 [in press].

Host. Unidentified yellow sponge [Porifera].

Distribution. Holotype female (USNM-30552) from Auau Channel, between Maui and Lanai Is, Hawaiian Is, 51–79 m. Known with certainty only from holotype. Also reported from Kenya, La Réunion?, Marianna? and the Hawaiian Is. Some records may be confused with *P. stylirostris*.

Periclimanaeus robustus Borradaile, 1915

Periclimanaeus robustus Borradaile, 1915: 213; 1917: 324, 278, pl. 55, fig. 20; Bruce, 2005a: 390–395, figs 1–3.

Host. *Asteropus simplex* (Carter, 1879) [Porifera].

Distribution. Reported only from the male holotype (ZMC-I.1953.1) from Amirante Is, Seychelle Is, 52–71 m and Kenya, 119–141 m.

Periclimanaeus stylirostris Bruce, 1969

Periclimanaeus stylirostris Bruce, 1969: 165–166; 1972: 68–75, figs 2–6.

Host. Unidentified sponge [Porifera].

Distribution. Known from holotype female (RMNH-D25612) and male paratype (BMNH), from South China Sea, 20°34.0'N, 113°30.5'E – 20°30.3'N, 113°29.0'E, 89–91 m. Also reported from Fiji. Possibly from Northern Territory, Queensland (Coral Sea), and New Caledonia.

Periclimanaeus usitatus Bruce, 1969

Periclimanaeus usitatus Bruce, 1969: 172–174; 2010b: 28–29, fig. 6.

Host. Unidentified sponge [Porifera].

Distribution. Known only from ovig. holotype female (RMNH-D25614) and male allotype (NHM-2010.291) from off Unguja, Zanzibar, 7°46'48"S. 39°42'36"E, at 20 m.



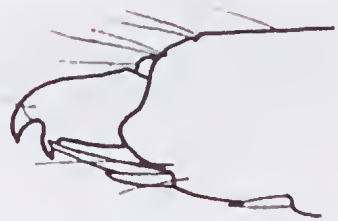
P. palauensis Miyake & Fujino, 1968, from Miyake & Fujino (1968).



P. quadridentatus (Rathbun, 1906), from Bruce (2012a).



P. robustus Borradaile, 1915, from Bruce (2005a).



P. stylirostris Bruce, 1969, from Bruce (1972).



P. usitatus Bruce, 1969, from Bruce (2010b).

Group 3: Species with distal accessory tooth and corpus with ventral denticles (17 species)

Periclimenaeus bidentatus Bruce, 1969

Periclimenaeus bidentatus Bruce, 1970: 305–307; 1991b: 257–258, figs 20.

Hosts. *Dysidea fragilis* (Montagu, 1818), *Hyatella intestinalis* (Lamarck, 1814), *Liosina paradoxa* Thiele, 1899 [Porifera].

Distribution. Reported first from the ovigerous female holotype (RMHH-D45527) from Heron I., Qld at 18.2–27.4 m. Now known from Kenya, Zanzibar, Papua New Guinea, Western Australia, Northern Territory, and New Caledonia. To 33 m.



P. bidentatus Bruce, 1969, from Bruce (1991b).

Periclimenaeus djiboutensis Bruce, 1969

Periclimenaeus djiboutensis Bruce, 1970: 307–308; 1975: 1568–1572, figs 8, 9, 13AD; Bruce, 1978: 256–259, figs 28–29; Marin, 2007: 227–228, fig. 11.

Host. *Spongia officinalis* var. *ceylonica* Dendy [Porifera].

Distribution. Known from the ovig. female holotype (MNHN-Na17812) and male and two ovig. female paratypes (MNHN-Na11053) from Djibuti (type locality, 80–85 m). Now known from Israel, Zanzibar, Madagascar, Vietnam and Queensland.



P. djiboutensis Bruce, 1969, from Bruce (1978).

Periclimenaeus garthi Bruce, 1976

Periclimenaeus garthi Bruce, 1976b: 443–447, figs 2–4.

Host. Unknown.

Distribution. Known only from the ovigerous female holotype (LACM-CR1964-001.1), from Dunidu, Malé Atoll, Maldive Islands.



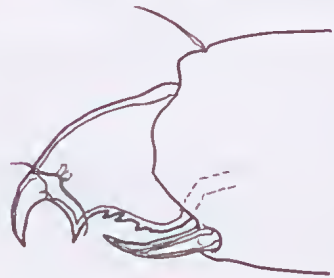
P. garthi Bruce, 1976, from Bruce (1976).

Periclimenaeus hebedactylus Bruce, 1969

Periclimenaeus hebedactylus Bruce, 1970: 308–310; 2012b: 472–481, figs 1–58.

Host. Unidentified sponge [Porifera].

Distribution. Known only from the male holotype (RMNH-D51597) and ovigerous female allotype (RMNH-D53333) from off Makunduchi, Unguja, Zanzibar, at 91.5 m.



P. hebedactylus Bruce, 1969, from Bruce (2012b).

***Periclimenaeus heronensis* Bruce, 2010**

Periclimenaeus heronensis Bruce, 2010b: 21–28, figs 1–5.

Host. Sponge ?

Distribution. Known only from the male holotype (QM-W31919), from Heron Island, Capricorn Islands Queensland, at 12 m.



P. heronensis Bruce, 2010, from Bruce (2010b).

***Periclimenaeus leptodactylus* Fujino & Miyake, 1968**

Periclimenaeus leptodactylus Fujino & Miyake, 1968: 90–95, figs 3–5.

Host. *Desmacidon* sp. [Porifera].

Distribution. Reported only from the ovig. female holotype (ZLKU-9276) and ovig. female paratype (ZLKU-9277) from Kasari-cho, Amami Is, Japan, and from Kenya, Tanganyika and Zanzibar. The Zanzibar material (QM-W29194), Mazizini Bay, Unguja Ukuu, Zanzibar, intertidal sponge), has been compared with the type by Dr Fujino and is considered conspecific.



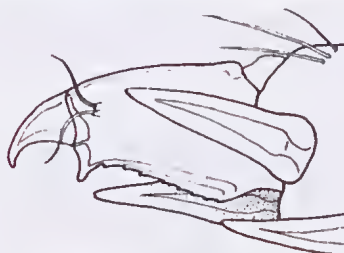
P. leptodactylus Fujino & Miyake, 1968, ♂ from Zanzibar (QM-W29194) [original].

***Periclimenaeus lobiferus* Bruce, 1978**

Periclimenaeus lobiferus Bruce, 1978: 260–269, figs 30–35.

Host. Unknown.

Distribution. Known only from the female holotype (MNHN-Na2582) from the Mozambique Channel, 15°21.7'S, 46°12.6'E, at 80–85 m



P. lobiferus Bruce, 1978, from Bruce (1978).

***Periclimenaeus matheri* Bruce, 2005**

Periclimenaeus matherae Bruce, 2005b: 331–338, figs 4–8.

Host. *Hypodistoma deerata* (Sluiter, 1895) [Ascidiacea].

Distribution. Known only from the male holotype (NTM-Cr013631), from Ashmore Reef, Western Australia, at 4–7 m.



P. matheri Bruce, 2005, from Bruce (2005b).

***Periclimenaeus mortenseni* Bruce, 1994**

Periclimenaeus mortenseni Bruce, 1993: 829–833, figs 1–2.

Host. Unknown.

Distribution. Known only from adult female holotype specimen (ZMUC-CRU-007399), from Tual, Pulau Kai Dulah, Indonesia, at 2 m.



P. mortenseni Bruce, 1994, from Bruce (1993).

***Periclimeneaus nufu* Āuriš, Horká, & Hoc, 2009**

Periclimeneaus nufu Āuriš, Horká, & Hoc, 2009: 453–464, figs 1–5.

Host. Found in coral rubble, presumably from a sponge host [Porifera].

Distribution. Known only from the holotype female (ION.R.4254/E54104), from Van Phong Bay, Vietnam, 12°36'25"N, 109°19'58"E, at 5 m.



P. nufu Āuriš, Horká & Hoc, 2009, from Āuriš *et al.* (2009).

***Periclimeneaus pachyspinosus* Marin, 2007**

Periclimeneaus pachyspinosus Marin, 2007: 239–235, figs 12–15.

Host. Unidentified sponge (Porifera).

Distribution. Known only from the male holotype specimen (RMNH-D51752), from Nok Island, Nhatrang Bay, Vietnam, 15–20 m.



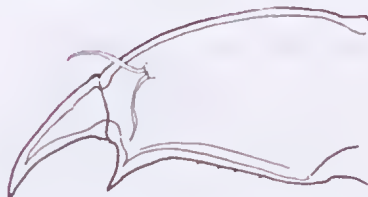
P. pachyspinosus Marin, 2007, from Marin (2007).

***Periclimeneaus pulitzerfinali* Bruce, 2011**

Periclimeneaus pulitzerfinali Bruce, 2011: 113–121, figs 1–5.

Host. Unknown.

Distribution. Known only from the ovigerous female holotype (NTM-Cr.17287), from Shelly Beach, Mombasa, Kenya, at 16 m.



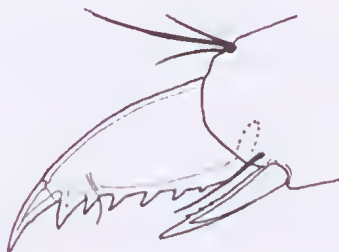
P. pulitzerfinali Bruce, 2011, from Bruce (2011).

***Periclimeneaus rastrifer* Bruce, 1980**

Periclimeneaus rastrifer Bruce, 1980a: 27–33, figs 12, 13 A, B.

Hosts. *Mycale philippinensis* Dendy, 1896, *Tedania anhelans* (Lieberkuhn, 1859). Also *Siphonochalina*, *Dysidea* and *Ulosa* spp. [Porifera].

Distribution. Reported from male holotype (MNHN-Na3696) from Ilôt Maitre, Nouméa, New Caledonia. Also known from Hong Kong, Vietnam, and Queensland. To 33 m.



P. rastrifer Bruce, 1980, from Bruce (1980).

***Periclimeneaus solitus* Bruce & Coombes, 1995**

Periclimeneaus solitus Bruce & Coombes, 1995: 115–119, figs 6–7.

Host. *Jaspis stellifera* (Carter, 1879) [Porifera].

Distribution. Only known from ovig. female holotype and male allotype (NTM-Cr.000277) from Orontes Reef, Port Essington, Cobourg Peninsula, Northern Territory, at 3 m.



P. solitus Bruce & Coombes, 1995, from Bruce & Coombes (1995).

***Periclimenaeus spongicola* Holthuis, 1952**

Periclimenaeus spongicola Holthuis, 1952: 13–140, figs 60–62; Fransen, 2006: 741, fig. 18.

Host. Unidentified sponge [Porifera].

Distribution. Known only from ovig. female holotype (RMNH-D4751), from the Java Sea, Indonesia, at 4°41'S. 113°2'E, 28–32 m.

Remarks. See also, *Periclimenaeus* aff. *spongicola* Fransen, 2006: 738–740, fig. 17.



P. spongicola Holthuis, 1952, from Fransen (2006).

***Periclimenaeus tchesunovi* Đuriš, 1990**

Periclimenaeus tchesunovi Đuriš, 1990: 615–620, figs 1–2.

Host. Uncertain.

Distribution. Reported from female holotype (ZMMSU-Ma2520) only. Type locality: Genego Island, North Nilandu Atoll, Maldive Islands, at 20 m.



P. tchesunovi Đuriš, 1990, from Đuriš (1990).

***Periclimenaeus tuamotae* Bruce, 1969**

Periclimenaeus tuamotae Bruce, 1969: 170–172.

Host. *Acarinus ternatus* Ridley 1844; *Acanthostrongylophora ingens* (Thiele, 1899) (Fransen 2013). [Porifera].

Distribution. From the type locality, Mururoa Atoll, Tuamotu Is, and from Kenya, Tanganyika, Northern Territory and Queensland, and Sabah.

Remarks. The type material was originally sent to MNHN, Paris, but recent enquiries reveal it was either not received or subsequently misplaced. However, one ovig. ♀ paratype was retained in the author's collection and is now deposited in the Queensland Museum (W29193).



P. tuamotae Bruce, 1969, ovig. ♀ paratype, Mururoa (QM-W29193) [original].

Group 4: Species with distal accessory tooth and corpus with basal ornamentation, without ventral denticles (6 species)

***Periclimenaeus creefi* Bruce, 2010**

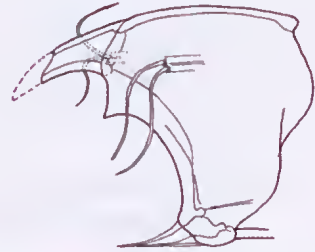
Periclimenaeus creefi Bruce, 2010b: 29–35, figs 7–11.

Host. Ascidian ?

Distribution. Known only from ovig. ♀ holotype (QM-W31437), from Heron Island, Capricorn Islands, Queensland.



P. creefi Bruce, 2010, from Bruce (2010b).

Periclimenaens fawatu Bruce, 2006*Periclimenaens fawatu* Bruce, 2006a: 33–41, figs 1–6.**Host.** Unidentified sponge [Porifera].**Distribution.** Known only from the holotype male and ovigerous female allotype specimens (RMNH-D51593), from Fungu Fawatu, Unguja, Zanzibar, 33–36.5 m.*P. fawatu* Bruce, 2006, from Bruce (2006a).*Periclimenaens manihinei* Bruce, 1976*Periclimenaens manihinei* Bruce, 1976c: 138–142, figs 29–30.**Host.** Unknown: found in coral debris.**Distribution.** Known only from ovigerous female holotype specimen (BMNH-1976.69) from Baie Sainte Anne, Praslin, Seychelle Islands, at 4 m.*P. manihinei* Bruce, 1976, from Bruce (1976).*Periclimenaens parkeri* Bruce, 2012*Periclimenaens parkeri* Bruce, 2012c: 289–298, figs 1–5.**Host.** Unidentified ascidian [Ascidiacea].**Distribution.** Known only from the adult female holotype specimen (WAM-40281) from Cassini Island, Western Australia, 13°55.926'S 125°37.094'E, at 12 m.*P. parkeri* Bruce, 2012, from Bruce (2012c).*Periclimenaens tridentatus* (Miers, 1884)*Coralliocaris?* *Tridentatus* Miers, 1884: 2946, pl. 32, fig C.
Periclimenaens tridentatus — Holthuis, 1952: 14, 140–146, figs 63–65 (*partim*); Bruce, 2002: 566–577, figs 1–7.**Hosts.** *Diplosoma* sp. [Ascidiacea].**Distribution.** Ovig. female holotype (BMNH-81.31). Type locality Thursday Island, Queensland. Also reported from Moçambique, Singapore (?), Vietnam, China (?), Northern Territory, Marianas Islands, Society Islands.*P. tridentatus* (Miers, 1884), from Bruce (2002).*Periclimenaens wolffi* Bruce, 1993*Periclimenaens wolffi* Bruce, 1993: 833–839, figs 3–4.**Host.** Unknown.**Distribution.** Known from ovigerous female holotype specimen only (ZMUC-CRU-008631), from Tai-Wan Hai-Hsia, Taiwan, 23°20'N, 118°30'E, at 31 m.*P. wolffi* Bruce, 1994, from Bruce (1993).

Group 5: Species with unguis as well as corpus ventrally dentate (8 species)

***Periclimenaeus arabicus* (Calman, 1939)**

Periclimenaeus (*Periclimenaeus*) *arabicus* Calman, 1939: 210–211, fig. 4.

Periclimenaeus arabicus – Holthuis, 1952: 13, 130.

Periclimenaeus ohslimai – Miyake & Fujino, 1967: 275–279, fig. 1.

Hosts. *Gellius*, *Toxochalina*, *Callyspongia*, *Acarinus* spp. [Porifera].

Distribution. Known from the female holotype (BMNH-1939.10.9) from off Oman, at 13.5 m. Also from 'Cotes d'Arabie', Djibuti, Kenya, Zanzibar, Tanganyika, Seychelles, Maldives, Vietnam, China, Hong Kong, Japan, Northern Territory, Queensland, New Caledonia, Fijian Islands.



P. arabicus Calman, 1939, from Bruce (1975).

***Periclimenaeus arthroductylus* Holthuis, 1952**

Periclimenaeus arthroductylus Holthuis, 1952: 122–125, figs 51–53; Bruce, 2006b: 14–15, fig. 7G–I; Bruce, 2010a: 51–53, fig. 1.

Host. Unknown.

Distribution. Known from ovig. female holotype (ZMA-De.102518), from Pulau Sailus ketjil, Indonesia, to 18 m, and from Heron Island, Qld.



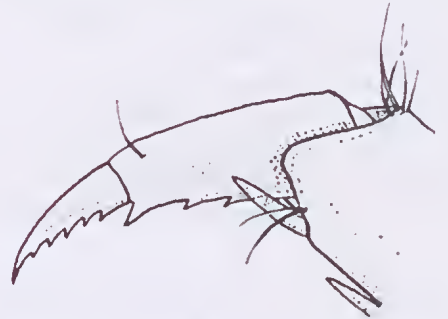
P. arthroductylus Holthuis, 1952, from Bruce (2010a).

***Periclimenaeus echinimanus* Đuriš, Horká, & Al-Horani, 2011**

Periclimenaeus echinimanus Đuriš, Horká, & Al-Horani, 2011: 56–65, figs 1–6.

Host. Unident. sponges [Demospongia: Porifera].

Distribution. Known only from holotype male and allotype female (RMNH-D.53450, D.53452) and 13 paratypes from Aqaba, Jordan, from 2–9 m.



P. echinimanus Đuriš, Horká, & Al-Horani, 2011, from Đuriš, et al. (2011).

***Periclimenaeus holthuisi* Bruce, 1969**

Periclimenaeus rhodope – Holthuis, 1952: 125–129, figs 54–55 bis.

Periclimenaeus holthuisi – Bruce, 1969: 159–160; 2006b: 12–14, fig. 7A–F.

Host. Unknown.

Distribution. Known only from the ovigerous female holotype (ZMA-De.102519), from Rumah-lusi, Tiour Island, Kepulauan Banda, Indonesia, at uncertain depth.



P. holthuisi Bruce, 1969, from Bruce (2006b).

***Periclimenaeus nielbrucei* Bruce, 2006**

Periclimenaeus nielbrucei Bruce, 2006b: 1–12, figs 1–6.

Hosts. Unidentified sponge [Porifera].

Distribution. Known only from ovig. female holotype and male allotype (QM-W27987, QM-W27988), from Wreck I., and female paratype from Heron I., Capricorn Is, Qld.



P. nielbrucei Bruce, 2006, from Bruce (2006b).

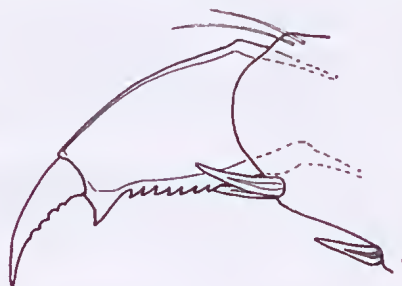
***Periclimenaeus rhodope* (Nobili, 1904)**

Coralliocaris (*Onycocaris*) *rhodope* Nobili, 1904: 233; 1906: 61, pl. 2 fig. 8.

Periclimenaeus rhodope – Holthuis, 1952, 125–129, figs 54, 55, 55bis; Bruce, 1975: 1558–1562, figs 1–2, 3A, B, 7A, B; Marin, Britaev & Anker, 2004: 207, fig. 6a–l.

Hosts. *Haliclona* sp.; *Siphonochalina* sp. [Porifera].

Distribution. Known from male lectotype (MNHN-Na2766) and male and two ovig. female paralectotypes (MNHN-Na2767) from Djibouti; also reported from Somalia, Kenya, Zanzibar, Tanganyika, Seychelle Islands, China (South China Sea) ?, and Queensland.



P. rhodope (Nobili, 1904), from Bruce (1975).

***Periclimenaeus uropodialis* Barnard, 1958**

Periclimenaeus uropodialis Barnard, 1958: 18–20, fig. 6.

Host. *Callyspongia* sp. [Porifera].

Distribution. Adult female holotype from Delagoa Bay, Mozambique (present whereabouts unknown; not in SAM). Also from Kenya, Zanzibar, Tanganyika, and Queensland.



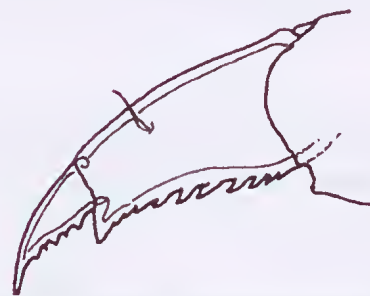
P. uropodialis Barnard, 1958, from Barnard (1958).

***Periclimenaeus zanzibaricus* Bruce, 1969**

Periclimenaeus zanzibaricus Bruce, 1969: 174–175: Bruce, 2006b: 15–20, figs 8–9.

Host. *Haliclona* sp. [Porifera].

Distribution. Known only from 15 specimens including the type material, ovigerous female holotype (RMNH-D.25615 and male allotype RMNH-D.51673?), 1 paratype (BMNH-2006.407-408), from Uroa, Unguja, Zanzibar, intertidal. Further specimens from Ras Iwatine and Mombasa I., Kenya.



P. zanzibaricus Bruce, 1969, from Bruce (2006b).

Group 6: Species with unguis dorsally dentate (3 species)

Periclimenaeus jeancharcoti Bruce, 1991

Periclimenaeus jeancharcoti Bruce, 1991a: 371–378, figs 50–55; Fransen, 2006: 727–731, figs 9–10.

Hosts. *Leptoclinides uniorbis* Monniot & Monniot, 1996; *Didemnum granulatum* Tokioka, 1954; *D. subviridis* (Sluiter, 1909) (Asciadiacea).

Distribution. Holotype female from 375–450 m off New Caledonia: 21°31'S, 166°21'E, (MNHN-Na12023); also from Papua New Guinea and Philippines, at 3–37 m.

Remarks. Also see *Periclimenaeus* aff. *jeancharcoti* Bruce, 1991, Palau, 1 juv., 10 m, in *Leptoclinides madara* Tokioka, 1953, (Fransen 2006, fig. 12).



P. jeancharcoti Bruce, 1991, from Bruce (1991a).

Periclimenaeus minutus Holthuis, 1952

Periclimenaeus minutus Holthuis, 1952: 134–137, figs 57–59; Fransen, 2006: 730–731, fig. 11; Bruce, 2010c: 386–387 fig. 6.

Hosts. Unidentified sponges.

Distribution. Known from two syntypes (male, ovig. female) (ZMA-De.101.630) from Banda I., Indonesia, at 73–80 m; also from Somalia, Zanzibar, Tanganyika, Indonesia, Philippines and (?) Western Australia.



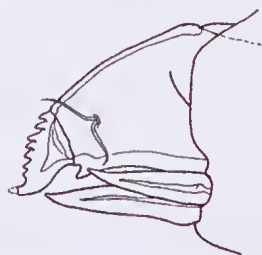
P. minutus Holthuis, 1952, from Fransen (2006).

Periclimenaeus trispinosus Bruce, 1969

Periclimenaeus trispinosus Bruce, 1969: 169–170; 2001: 147–152, figs 1–3.

Host. Unidentified sponge [Porifera].

Distribution. Known from ovig. female holotype and male allotype only, from Mkokotoni, Unguja, Zanzibar (RMNH-D.25613, BMNH, number uncertain), from 25.5–27.5 m.



P. trispinosus Bruce, 1969, from Bruce (2001).

Group 7: Species with corpus bearing acute proximal tooth, without ventral denticles or distal accessory tooth (12 species)

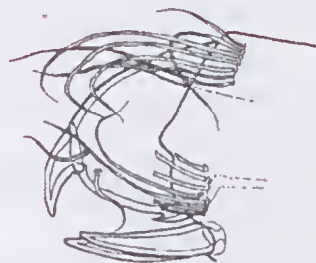
Periclimenaeus colodactylus Bruce, 1996

Periclimenaeus colodactylus Bruce, 1996: 222–226, figs 9–10.

Host. *Diplosoma versicolor* F. Monniot, 1994 [Asciadiacea].

Distribution. Known from male holotype, female allotype (MNHN-Na12926; 12927) and two paratypes, from Uatio Islet, New Caledonia at 20–25 m.

Remarks. See also *P.* aff. *colodactylus* — Fransen (2006: 726, fig. 7).



P. colodactylus Bruce, 1996, from Bruce (1996).

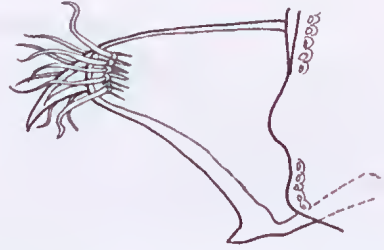
Perclimenaeus crassipes Calman, 1939

Perclimenes (*Ancylocaris*) *crassipes* Calman, 1939: 211–215, fig. 5.

Perclimenaeus tridentatus – Holthuis, 1952: 14, 141.
Perclimenaeus crassipes – Bruce, 2012a, 520–524, figs 3–5.

Host. Unknown.

Distribution. Known only from two ovig. female syntypes (NHMUK-1939.10.9.304–305) from Oman, 18°03.5'N, 57°02.5'E, at 38 m.



P. crassipes Calman, 1939, from Bruce (2012a).

Perclimenaeus dactylodon Bruce, 2012

Perclimenaeus dactylodon Bruce, 2012d: 51–60, figs 1–7.

Host. Unidentified ascidian [Ascidiacea].

Distribution. Known only from type specimens, an ovig. female holotype (QM-W29142), male allotype (QM-W29143) and ovig. female paratype (QM-W29144), from Wistari Reef, Heron I., Queensland at 24.5 m.



P. dactylodon Bruce, 2012, from Bruce (2012d)

Perclimenaeus devaneyi Bruce, 2010

Perclimenaeus devaneyi Bruce, 2010c: 380–386, figs 1–5.

Host. Uncertain, probably sponge or ascidian associated with *Pocillopora*.

Distribution. Known only from the type locality, Kahe Point, Oahu, Hawai'an Islands, at about 3.0 m, with ovigerous female holotype and allotype male (BPBM-S14815; S148140); ovigerous female paratype (QM-W28904).



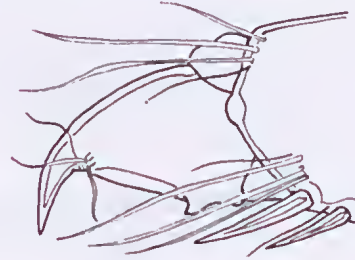
P. devaneyi Bruce, 2010, from Bruce (2010c).

Perclimenaeus diplosomatis Bruce, 1980

Perclimenaeus diplosomatis Bruce, 1980b: 39–51, figs 1–6.
Perclimenaeus djiboutensis – Fransen, 2006: 726–727, fig. 8.

Host. *Diplosoma inflatum* F. Monniot, 1994 [Ascidiacea].

Distribution. Known only from ovig. female holotype (AM-P24817) and male allotype (AM-P24818) from Heron I., Queensland, and New Caledonia, to 27 m.



P. diplosomatis Bruce, 1980, from Bruce (1980).

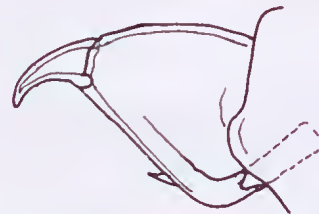
Perclimenaeus sp. 2

Coralliocaris tridentata – Edmondson, 1925: 7.

Host. Unknown.

Distribution. Known only from one female and one male (BPBM-S1026), from Pearl & Hermes Reef, Hawaiian Islands.

Remarks. To be described as a new species in Bruce (2013).



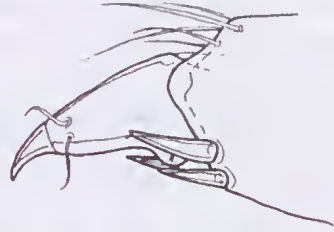
Perclimenaeus sp. 2, from Bruce (2013).

***Periclimentaenus kottae* Bruce, 2005**

Periclimentaenus kottae Bruce, 2005b: 325–331, figs 1–3.

Host. *Didemnum membranaceum* Sluiter, 1909 [Ascidiacea].

Distribution. Known only from the ovig. female holotype (WAM-174.93) from Ashmore Reef, Western Australia, at 6–16 m.



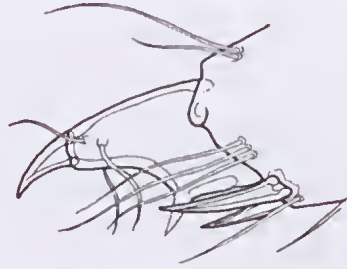
P. kottae Bruce, 2005, from Bruce (2005b).

***Periclimentaenus myora* Bruce, 1998**

Periclimentaenus myora Bruce, 1998: 394–398, figs 4–5.

Host. 'Unidentified, presumably a tunicate.'

Distribution. Known only from the ovig. female holotype (QM-W21706) from Myora, North Stradbroke I., Qld, 27°29'S. 153°25'E, at 3m.



P. myora Bruce, 1998, from Bruce (1998).

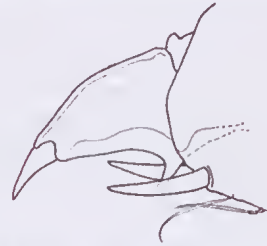
***Periclimentaenus nobilii* Bruce, 1975**

Periclimentaenus nobilii Bruce, 1975: 1577–1581, figs 13f, 14; 1991b, 354–256, fig. 19.

Host. *Lissoclinum* sp. [Ascidiacea].

Distribution. Holotype female from 'Red Sea', MNHN number not reported. Also from La Réunion, Papua New Guinea and New Caledonia.

Remarks. *Periclimentaenus* sp. aff. *nobilii* reported from Socotra, Yemen (Bruce, 2006c).



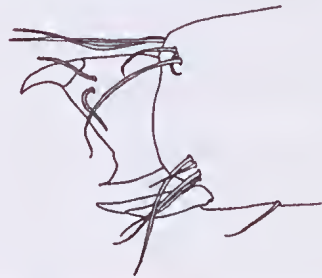
P. nobilii Bruce, 1974, from Bruce (1974).

***Periclimentaenus orbitocarinatus* Fransen, 2006**

Periclimentaenus orbitocarinatus Fransen, 2006: 732–737, figs 13–15.

Hosts. *Lissoclinum verrilli* (Van Name, 1902) and *Didemnum* sp. [Ascidiacea].

Distribution. Known from ovig. female holotype (MNHN-Na.15253), from Loyalty Is, 20°22.25'S 166°10.00'E, and paratypes from Madagascar (RMNH-D51002), and from Indonesia and Society Islands.



P. orbitocarinatus Fransen, 2006, from Fransen (2006).

***Periclimentaenus storchi* Bruce, 1989**

Periclimentaenus storchi Bruce, 1989b: 181–183, fig. 5.

Host. *Didemnum molle* (Herdmann, 1886) [Ascidiacea].

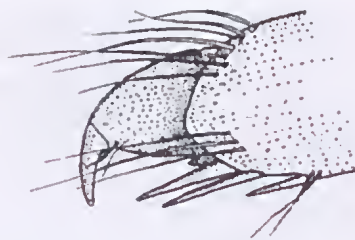
Distribution. Ovig. female holotype and male allotype (NTM-Cr.006473), from Cuaming I., Bohol, Philippines. Also reported from Indonesia and Vietnam.



P. storchi Bruce, 1989, from Bruce (1989).

Periclimenaeus zarenkovi Đuriš, 1990*Periclimenaeus zarenkovi* Đuriš, 1990: 620–624, figs 3–4.

Host. Unknown.

Distribution. Known only from male holotype (ZMMSU-Ma2519) from 0.7 m, Genego Islet, North Nilandu Atoll, Maldive Islands.*P. zarenkovi* Đuriš, 1990, from Đuriš (1990).

REMARKS

Of the 60 species of *Periclimenaeus* 25 are known from only a single specimen, six from the male holotype (*P. calmani*; *P. heronensis*; *P. matheri*; *P. pachyspinosus*; *P. robustus*; *P. zarenkovi*) and 19 from the female holotype (*P. ardaea*; *P. creffi*; *P. gartlii*; *P. holthuisi*; *P. kottae*; *P. lobiferus*; *P. manihinei*; *P. mortenseni*; *P. myora*; *P. nufu*; *P. orontes*; *P. palauensis*; *P. parkeri*; *P. pulitzerfuiali*; *P. quadridentatus*; *P. serenei*; *P. spongicola*; *P. tchesunovi*; *P. wolffi*), with 11 known from a single heterosexual pair (*P. diplosomatis*; *P. echininaeus*; *P. sp. 2*; *P. fawatu*; *P. hebedactylus*; *P. nielbrucei*; *P. serrula*; *P. solitus*; *P. stordii*; *P. trispinosus*; *P. usitatus*). Two species are known each from a pair of female syntypes (*P. bouvieri*; *P. crassipes*). The remaining twenty two species are known from multiple localities (*P. arabicus*; *P. arthroactylus*; *P. bidentatus*; *P. colodactylus*; *P. dactylodon*; *P. devaneyi*; *P. djiboutensis*; *P. hecate*; *P. jeaucharcoti*; *P. leptodactylus*; *P. sp. 1*, *P. minutus*; *P. nobilii*; *P. orbitocarinatus*; *P. pachydentatus*; *P. stylirostris*; *P. rastrifer*; *P. rhodope*; *P. tuamotae*; *P. tridentatus*; *P. uropodialis*; *P. zauzibaricus*).

Further information on hosts is needed. *Periclimenaeus* species have been found only in association with poriferan or ascidian hosts. So far, 24 species have been confirmed as poriferan associates, 16 confirmed as ascidian associates, and the remainder are of uncertain or unknown origin. In many cases the hosts are just unidentified sponges or ascidians, without generic or specific determinations. This is unfortunate as it seems likely that a high degree of specificity may exist in these associations together with species complexes of the shrimps.

LITERATURE CITED

- Barnard, K.H. 1958. Further additions to the crustacea fauna list of Portuguese East Africa. *Memorias do Museu Dr. Alvaro de Castro* 4: 3–23, figs 1–7.
- Borradaile, L.A. 1915. Notes on Carides. *Annals and Magazine of Natural History* (8)15: 205–213.
- Bruce, A.J. 1969. Preliminary descriptions of ten new species of the genus *Periclimenaeus* Borradaile, 1915 (Crustacea, Decapoda Natantia, Pontoniinae). *Zoologische Mededelingen* 44(12): 159–175.
1970. Further preliminary descriptions of new species of the genus *Periclimenaeus* Borradaile, 1915 (Crustacea, Decapoda Natantia, Pontoniinae). *Zoologische Mededelingen, Leiden* 44(21): 305–315.
1972. A report on a small collection of pontoniid shrimps from Fiji, with the description of a new species of *Coralliocaris* Stimpson. *Pacific Science* 26(1): 63–86, figs 1–11.
1975. Observations upon some specimens of the genus *Periclimenaeus* Borradaile (Decapoda Natantia, Pontoniinae) originally described by G. Nobili. *Bulletin du Muséum national d'Histoire naturelle* (3)258, *Zool.* 180: 1557–1583, figs 1–15.
- 1976a. A Synopsis of the Pontoniid Shrimp Fauna of central East Africa. *Journal of the Marine Biological Association of India* 16(2)(1974): 462–490.
- 1976b. A report on a small collection of pontoniine shrimps from the northern Indian Ocean. *Journal of the Marine Biological Association of India* 17(1974): 437–454.
- 1976c. A report on some pontoniid shrimps collected from the Seychelle Islands by the F.R.V. *Manihine*, 1972, with a review of the Seychelles pontoniid shrimp fauna. *Journal of the Linnean Society of London, Zoology* 59: 89–153, tabs 1–8, figs 1–30.
1978. A report on a collection of pontoniine shrimps from Madagascar and adjacent seas. *Zoological Journal of the Linnean Society* 62: 205–290, figs 1–44.
- 1980a. On some pontoniine shrimps from Nouméa, New Caledonia. *Cahiers de l'Indo-Pacifique* 2(1): 1–39, figs 1–14.
- 1980b. Notes on some Indo-Pacific Pontoniinae, XXXIII. *Periclimenaeus diplosomatis* sp. nov., an ascidian associate from Heron Island, Australia. *Crustaceana* 39(1): 39–51, figs 1–6.
1986. Three new species of commensal shrimp from Port Essington, Arnhem Land, Northern Australia

- (Crustacea: Decapoda: Pontoniinae). *The Beagle, Records of the Northern Territory Museum of Arts and Sciences* 3: 143–166, figs 1–15.
1989. A report on some coral reef shrimps from the Philippine Islands. *Asian Marine Biology* 6: 173–192, figs 1–6.
- 1991a. Crustacea Decapoda: Further deep-sea Palaemonid shrimps from New Caledonian waters. In: A. Crosnier (Ed.), *Résultats des Campagnes MUSORSTOM, 9. Mémoires du Muséum national d'Histoire Naturelle (A) Zoologie* 152: 299–411, figs 1–75.
- 1991b. Shallow water Palaemonoid shrimps from New Caledonia (Crustacea: Decapoda). In: Richer de Forges, B., (Ed.), *Le Benthos des fonds meubles des lagons de Nouvelle-Calédonie, 1. Études et Thèses; Paris, ORSTOM*: 221–279, figs 1–31.
1993. Pontoniine shrimps from the Zoological Museum, Copenhagen. *Journal of Natural History* 28: 829–840, figs 1–6.
1996. Crustacea Decapoda: Palaemonid shrimps from the Indo-West Pacific region, mainly from New Caledonia. In: A. Crosnier (Ed.), *Résultats des Campagnes MUSORSTOM, 15. Mémoires du Muséum National d'Histoire Naturelle* 168: 197–267, figs 1–31.
1998. Pontoniine shrimps from Moreton Bay, Queensland (Crustacea: Decapoda: Pontoniinae). *Memoirs of the Queensland Museum* 42(2): 387–389, figs 1–5.
2001. A re-examination of *Periclimenaeus trispinosus* Bruce and *P. orbitospinatus* Bruce (Crustacea: Decapoda: Pontoniinae). *Zoologische Mededelingen, Leiden* 75(9): 147–158, figs 1–4, tab.1.
2002. A re-description of *Periclimenaeus tridentatus* (Miers, 1884), based on specimens from Port Essington, Northern Territory, and a note on *P. laeate* (Nobili, 1904) (Crustacea: Decapoda: Pontoniinae), with a key for the preliminary identification of the tunicate-associated species of *Periclimenaeus* Borradaile. *Journal of Natural History* 35: 565–584, figs 1–8.
- 2005a. A re-description of *Periclimenaeus robustus* Borradaile, the type species of the genus *Periclimenaeus* Borradaile, 1915 (Crustacea: Decapoda: Pontoniinae). *Cahiers de Biologie Marine* 46: 389–398, figs 1–5.
- 2005b. New species of *Periclimenaeus* Borradaile (Crustacea: Decapoda: Pontoniinae) from Ashmore Reef, Western Australia, with remarks on *P. pachydentatus* Bruce, 1969. *Records of the Western Australian Museum* 22: 325–343, figs 1–10.
- 2006a. *Periclimenaeus fawatu* spec. nov. (Crustacea: Decapoda: Pontoniinae), from Zanzibar. *Zoologische Mededelingen, Leiden* 80-4 (3): 33–43, figs 1–6.
- 2006b. *Periclimenaeus uelbrueei* sp. nov. (Crustacea: Decapoda: Pontoniinae), a new sponge associate from the Capricorn Islands, Queensland, with notes on related *Periclimenaeus* species. *Zootaxa* 1224: 1–22, figs 1–5.
- 2006c. Pontoniine shrimps (Decapoda: Palaemonidae) from the island of Socotra, with descriptions of new species of *Daetylonia* Fransen, 2002 and *Periclimenoides* Bruce, 1990. *Zootaxa* 1137: 1–36, figs 1–9.
- 2010a. Pontoniine shrimps (Crustacea: Decapoda: Palaemonidae) from the CReefs 2009 Heron Island Expedition, with a review of the Heron Island pontoniine fauna. *Zootaxa* 2541: 50–68, figs 1–8.
- 2010b. More pontoniine shrimps (Crustacea: Decapoda: Palaemonidae) from the CReefs 2009 Heron Island expedition. *Zootaxa* 2604: 20–36, figs 1–11.
- 2010c. *Periclimenaeus devaneyi* sp. nov., from Oahu, Hawai'i (Crustacea: Decapoda: Pontoniinae). *Zootaxa* 2372: 339–388, figs 1–5.
2011. *Periclimenaeus pulitzerfinali* spec. nov. (Crustacea: Decapoda: Pontoniinae), from Mombasa, Kenya. *The Beagle, Records of the Museums and Art Galleries of the Northern Territory* 27: 113–122, figs 1–5.
- 2012a. Notes on some Indo-Pacific Pontoniinae, LI. *Periclimenaeus quadridentatus* (Rathbun, 1906) and *P. crassipes* (Calman, 1939) (Crustacea: Decapoda: Pontoniinae), with the designation of *P. ealmani* and *P. serenei* spp. nov. *Crustaceana* 85(4–5): 513–531, figs 1–7.
- 2012b. A re-description of *Periclimenaeus hebdaetylus* Bruce, 1970 (Crustacea: Decapoda: Palaemonidae). *Zoologisches Mededelingen* 86(2): 471–484, figs 1–58.
- 2012c. *Periclimenaeus parkeri* sp. nov. (Crustacea: Decapoda: Pontoniinae) from the Kimberley, Western Australia. *Cahiers de Biologie Marine* 53(2): 289–298, figs 1–5.
- 2012d. *Periclimenaeus daetylodon* sp. nov. (Decapoda: Pontoniinae), from Heron Island, Queensland, Australia. *Zootaxa* 3436: 51–60, figs 1–7.
2013. Notes on some Indo-Pacific Pontoniinae, LIII. *Periclimenaeus* species from the Hawai'ian region, *Crustaceana* [In Press].
- Bruce, A.J. & Coombes, K.E. 1995. The palaemonoid shrimp fauna (Crustacea: Decapoda: Caridea) of the Cobourg Peninsula, Northern Territory. *The Beagle, Records of the Museums and Art Galleries of the Northern Territory* 12: 101–144, figs 1–12.
- Calman, W.T. 1939. Crustacea: Caridea. *The John Murray Expedition 1933–34, Scientific Reports* 6: 183–224, figs 1–8.
- Đuriš Z. 1990. Two new species of the commensal shrimp genus *Periclimenaeus* Borradaile, 1915, (Decapoda, Palaemonidae) from the Maldives

- Islands. *Journal of Natural History* 24: 615–625, figs 1–4.
- Đuriš, Z., Horká, I. & Hoc, Dan Tan, 2009. *Periclimenaeus nifu*, a new species of shrimp (Crustacea: Decapoda: Pontoniinae) from Vietnam. *The Raffles Bulletin of Zoology* 57(2): 453–464, figs 1–5.
- Đuriš, Z., Horká, I. & Al-Horani, F. 2011. *Periclimenaeus echinimanus* sp. nov. (Crustacea: Decapoda: Pontoniinae), a new species from the Gulf of Aqaba, Red Sea. *Zootaxa* 2983: 57–68, figs 1–7.
- Edmondson, C.H. 1925. Crustacea. Marine Zoology of Tropical central Pacific. (Tanager Expedition Publ. 1). *Bulletin of the Bishop Museum, Honolulu* 27: 3–62, pls 1–4.
- Fransen, C.H.J.M. 2006. On Pontoniinae (Crustacea, Decapoda, Palaemonidae) collected from ascidians. *Zoosystema* 28(3):713–746, figs 1–18.
2013. A new species of the sponge-associated pontoniine shrimp genus *Nippontonia* Bruce & Bauer, 1997 (Decapoda, Caridea, Palaemonidae) from Sabah, Malaysia. *Zootaxa* [In Press].
- Fujino, T. & Miyake, S. 1968. Descriptions of two new species of pontoniid shrimps (Crustacea, Decapoda, Palaemonidae) commensal with sponges. *Occasional Papers of the Zoological Laboratory, Faculty of Agriculture, Kyushu University* 1(3): 85–96, figs 1–5.
- Holthuis, L.B. 1952. The Decapoda of the *Siboga* Expedition. Part XI. The Palaemonidae collected by the *Siboga* and *Snellius* Expeditions with remarks on other species. II. Subfamily Pontoniinae. *Siboga Expedition Monograph* 39a10: 1–252, figs 1–110, tab. 1.
1993. *The recent genera of the caridean and stenopodidean shrimps (Crustacea, Decapoda) with an appendix on the order Amphionidacea*. (Nationaal Natuurhistorisch Museum, Leiden). 1–328, figs 1–312.
- Marin, I. 2007. Pontoniine shrimps (Decapoda: Caridea: Palaemonidae) inhabiting boring sponges (Porifera: Demospongia) from Nhatrang Bay, Vietnam, with descriptions of three new species. *Zoologische Mededelingen, Leiden* 81: 217–240, figs 1–18.
- Marin, I.N., Britayev, T.A. & Anker, A. 2004. Pontoniine shrimps associated with cnidarians: new records and list of species from coastal waters of Viet Nam. *Arthropoda Selecta* 13(4): 199–218, figs 1–13.
- Miers, E.J. 1884. Part II. Collections from the Western Indian Ocean. Crustacea. In: Report of the Zoological Collections made in the Indo-Pacific Ocean during the Voyage of H.M.S. 'Alert' 1881–82., 513–575, pls. 46–52. (British Museum of Natural History, London).
- Miyake, S. & Fujino, T. 1967. On four species of Pontoniinae (Crustacea, Decapoda, Palaemonidae) found in Porifera inhabiting the coastal regions of Kyushu, Japan. *Journal of the Faculty of Agriculture, Kyushu University* 14: 275–291, figs 1–7, pl. 3.
1968. Pontoniinid shrimps from the Palau Islands (Crustacea, Decapoda, Palaemonidae). *Journal of the Faculty of Agriculture, Kyushu University* 10(3): 339–431, figs 1–8.
- Nobili, G. 1904. Diagnoses préliminaires de vingt-huit espèces nouvelles de Stomatopodes et Décapodes Macroures de la Mer Rouge. *Bulletin du Museum d'Histoire Naturelle, Paris* 10: 228–238.
1906. Faune Carcinologique de la Mer Rouge. Décapodes et Stomatopodes. *Annales des Sciences naturelles, Zoologie* (9)4(1–3): 1–347, text figs 1–12, pls 1–11.
- Rafinesque, C.S. 1815. *Analyse de la Nature ou Tableau de l'Univers et des Corps organisés* (Palermo). 224 pp.
- Rathbun, M.J. 1906. The Brachyura and Macrura of the Hawaiian Islands. *Bulletin of the U.S. Fisheries Commission* 23(3): 827–930, figs 1–79, pls 3–24.

Revision of the genus *Ocypode* with the description of a new genus, *Hoplocypode* (Crustacea: Decapoda: Brachyura)

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ABSTRACT

A taxonomic revision of *Ocypode* Weber, 1795, has resulted in the recognition of a new genus, *Hoplocypode* containing a single species *H. occidentalis* (Stimpson, 1860) that is endemic to the East Pacific. *Ocypode* is now recognised to contain 21 valid species. Of these, one eastern Pacific, one western Atlantic, and two eastern Atlantic species tend to have widespread distributions within their respective regions. Conversely, many of the 17 Indo-Pacific species exhibit relatively restricted ranges. Only three of them, *O. cordimanus*, *O. ceratophthalma* and *O. pallidula* are widespread. Morphological features and their importance in identification are discussed, and a key to all species is provided. □ *Ocypode*, taxonomy, new genus, biogeography, Indian Ocean, Pacific Ocean, Atlantic Ocean.

Species in the genus *Ocypode* are a common and conspicuous feature of tropical and subtropical sandy beaches worldwide. This is the reason why specimens have been collected since early times, and there has been so much interest in studying them. However, there have long been problems in identifying some species, and there has been considerable confusion over the correct names to use. Some species were described from very few specimens and types have been subsequently lost, some have had confusion over their original labeling, or were attributed to vague or even wrong localities. Thus, the present world revision has, by necessity, attempted to carefully re-examine all earlier published specimens, including the types, as well as the extensive collections of the Senckenberg Forschungsinstitut und Naturmuseum in Frankfurt am Main, and a number of other museums from around the world. We give complete keys, descriptions, and figures of all the species of the genus known to date to finally resolve problems in identification. Detailed

descriptions and figures of the male Go1, and the female genital opening, have been provided for the first time for many species, and these have proved very important in helping to define species and genera, and in helping to understand their phylogenetic relationships.

Abbreviations. *c.* = *ca.*; Car = carapace; Go1 = Gonopod 1; Mxp3 = Maxilliped 3; P1 = pereopod 1; P2–5 = pereopods 2–5. The measurements of carapace length and width (CL/CW) in the descriptions of the species and the material lists are given in mm. AMS = Australian Museum, Sydney; IRSNB = Institut Royal des Sciences Naturelles de Belgique, Bruxelles; MCM = Museo Civico di Storia Naturale di Milano; MCG = Museo Civico di Storia Naturale di Genova; MZT = Museo e Istituto di Zoologia sistematica dell'Università di Torino; MBL = Museu Bocage Lisboa; MCZ = Museum of Comparative Zoology, Cambridge, Massachusetts; MHNG = Museum d'Histoire naturelle, Genève; MI = Mauritius-Institute, Port Louis, Mauritius;

MNHN = Muséum national d'Histoire naturelle, Paris; MW = Museum Wiesbaden, Naturwissenschaftliche Sammlungen; MZUT = Zoological Museum of the Turin University; NHM = Natural History Museum, London; NHMB = Naturhistorisches Museum Basel; NHCY = National Natural History Collection Yemen (collection presently at Senckenberg, Frankfurt); NHMW = Naturhistorisches Museum Wien; NHRS = Naturhistoriska Riksmuseet Stockholm; QM = Queensland Museum, Brisbane; RMNH = Rijksmuseum van Natuurlijke Historie, Leiden [now 'Naturalis']; SMF = Senckenberg Museum, Frankfurt am Main; SNMNH = Saudi National Museum of Natural History (collection presently at Senckenberg, Frankfurt am Main); USNM = U.S. National Museum, Washington, D.C.; UZMK = Universitetets Zoologiske Museum, København; WAM = Western Australian Museum, Perth; ZRCNUS = Zoological Reference Collections, National University of Singapore; ZSI = Zoological Survey of India, Calcutta; ZSM = Zoologische Staatssammlung, München; ZMA = Zoologisch Museum Universiteit van Amsterdam; ZMG = Zoologisches Museum Göttingen (on Permanent loan to Senckenberg); ZMH = Zoologisches Museum Hamburg; ZMK = Zoologisches Museum Kiel.

TERMINOLOGY

The terminology we use for the body-parts is based on the thorough descriptions of Balss (1940, 1941), and Pesta (1918) and is explained in detail by Sakai *et al.* (2006).

Morphological features and their importance

A number of characters can be used for discriminating species within this genus, however these are not necessarily useful for creating natural groupings, and a discussion of their adaptive and phylogenetic value is necessary. In *Ocypode*, classifications simply based on the most obvious morphological characters result in different groupings depending on the primary feature used. This was the case in the past, and very different and incompatible relationships have been suggested. Therefore, the character complexes used in this paper are here discussed one by one, with regard to their

usefulness in defining a natural phylogenetic classification.

Stridulating ridge. A stridulating ridge is found on the inner surface of the palm of the larger cheliped in all species except for *O. cordimannus*, and its morphology differs among species. It may be composed of tubercles, of tubercles with striae, of tubercles and tubercles with striae, of tubercles and striae, or solely of striae. It is one of the most important characters for distinguishing species, because it can be found even in juveniles. The difference in the structure of the stridulating ridge is closely related to the sound produced for communication, on which interspecific separations are based (Popper *et al.* 2001). We have observed that the stridulating ridge is often absent on regenerated claws (easily recognisable as abnormal because the larger cheliped is similar in size to the smaller one). As this would make sound production impossible, normal communication with other individuals must be severely impaired.

As stated, the morphology of the stridulating ridge is very useful for separating species, however this feature may not be useful in helping to define relationships between species. Selection pressures may actually promote diversification between species in order to avoid introgression. Furthermore the detection of plesiomorphies and apomorphies is rendered difficult, as even species without stridulating ridges exhibit a similar mode of sound production (Horch 1975; for *Gecarcinus*, see Klassen 1973). Von Hagen (1975) postulated that the existence of a stridulating ridge is a synapomorphy, however the one species lacking this character, *Ocypode cordimannus*, stridulates quite efficiently (Horch 1975), so it is difficult to know if the lack of a stridulating ridge in *O. cordimannus* is plesiomorphic, or if the ridge has been secondarily lost.

The suggestion that diversification plays a major role in determining the morphology, and sound patterns generated, is further supported by the fact that stridulating ridges of sympatric species are typically very different, while geographically distant species can be very similar. For example, the stridulating ridge of *O. occidentalis* (= *H. occidentalis*) from the eastern Pacific is

almost identical with that of *O. convexa* from Western Australia, though those two species are now classified under different genera according to the form of Go1. Thus it is apparent that a classification based on the shape of the stridulating ridge would be artificial.

The stridulating ridges of *Hoplocypode* and *Ocypode* species are characterised as follows:

1. *Hoplocypode occidentalis* (Fig. 1A). Stridulating ridge composed of *c.* 21–22 tubercles.
2. *Ocypode africana* (Fig. 1B). Stridulating ridge composed of 11–13 interspaced tubercles with striae in dorsal half and 21–26 closely spaced tubercles with striae in ventral half.
3. *Ocypode brevicornis* (Fig. 1C). Stridulating ridge composed of 23–28 tubercles.
4. *Ocypode ceratophthalma* (Figs 1D–I). Stridulating ridge composed of 10–11 interspaced tubercles in dorsal third, 8 thick striae in middle third, and 20–30 closely spaced striae in ventral third.
5. *Ocypode convexa* (Fig. 2A). Stridulating ridge composed of 19–24 tubercles.
6. *Ocypode cordimannus*. Stridulating ridge absent.
7. *Ocypode cursor* (Fig. 2B). Stridulating ridge composed of 69–96 tubercles with striae [*c.* 23 tubercles with striae in dorsal third and *c.* 46 closely pressed tubercles with fine striae in ventral two-thirds (SMF 9296)].
8. *Ocypode fabricii* (Fig. 2C). Stridulating ridge composed of 126–133 regularly and closely spaced fine striae.
9. *Ocypode gaudichaudii* (Fig. 2D). Stridulating ridge composed of 18 tubercles in dorsal half and 36–38 striae in ventral half.
10. *Ocypode jousseauui* (Fig. 3A). Stridulating ridge composed of at least 41 (SMF 24530), 72 (NHMW) or at most 79 (Holotype) elements [15 tubercles in dorsal third and 26 closely spaced tubercles with striae in ventral two thirds (SMF 24530)].
11. *Ocypode kuhlii* (Fig. 3B). Stridulating ridge composed of *c.* 10 interspaced tubercles.
12. *Ocypode macrocera* (Fig. 3C). Stridulating ridge composed of 36–56 elements [9 slightly interspaced tubercles with striae in dorsal third and 27 closely pressed elongate tubercles with striae in ventral two-thirds (SMF 6772)]
13. *Ocypode madagascariensis* (Fig. 3D). Stridulating ridge composed of 20–30 closely spaced tubercles with striae.
14. *Ocypode mortoni* (Fig. 3E). Stridulating ridge composed of 35–71 striae.
15. *Ocypode nobilii* (Fig. 4A). Stridulating ridge composed of 99–120 closely spaced fine striae.
16. *Ocypode pallidula* (Fig. 4B). Stridulating ridge composed of 30–42 interspaced thick striae.
17. *Ocypode pauliani* (Fig. 4C). Stridulating ridge composed of 7–13 irregularly spaced tubercles.
18. *Ocypode quadrata* (Fig. 4D). Stridulating ridge composed of 15–18 interspaced tubercles.
19. *Ocypode rotundata* (Fig. 5A). Stridulating ridge composed of 10–15 irregularly spaced elongate tubercles with striae.
20. *Ocypode ryderi* (Fig. 5B). Stridulating ridge composed of *c.* 15 irregularly arranged tubercles.
21. *Ocypode saratan* (Fig. 5C). Stridulating ridge composed of 67–87 fine striae.
22. *Ocypode stimpsoni* (Fig. 5D). Stridulating ridges composed of 44–57 narrow striae, extending ventrally over midline of fixed finger to near ventral margin.

Eyestalks. Eyestalks are elongate throughout *Ocypode*, with the cornea located distally. In seven species the eyestalks are prolonged beyond the cornea (exophthalmy), and this appears to occur randomly within the genus. Its function is not yet known (von Hagen 1970). All species with exophthalmy have an associated reduction of the external orbital tooth, and the anterolateral corner of the carapace is more or less rounded. Exophthalmy is clearly apomorphic, but it is not clear if it can be regarded as a synapomorphic relationship among all species in which it occurs. Instead, it may have developed several times independently. In consequence, we feel this feature cannot be used, on its own, to define monophyletic groups within the genus.

Carapace, pereopods and thoracic sternum. Most of these features are relatively homogeneous in morphology. This applies especially to the carapace which shows only minor variation in shape, although the granulation may vary among species. This is also true of the shape of the front. The sternum is that of a typical thoracotreme crab (see Guinot 1969), and again there are only minor variations in granulation

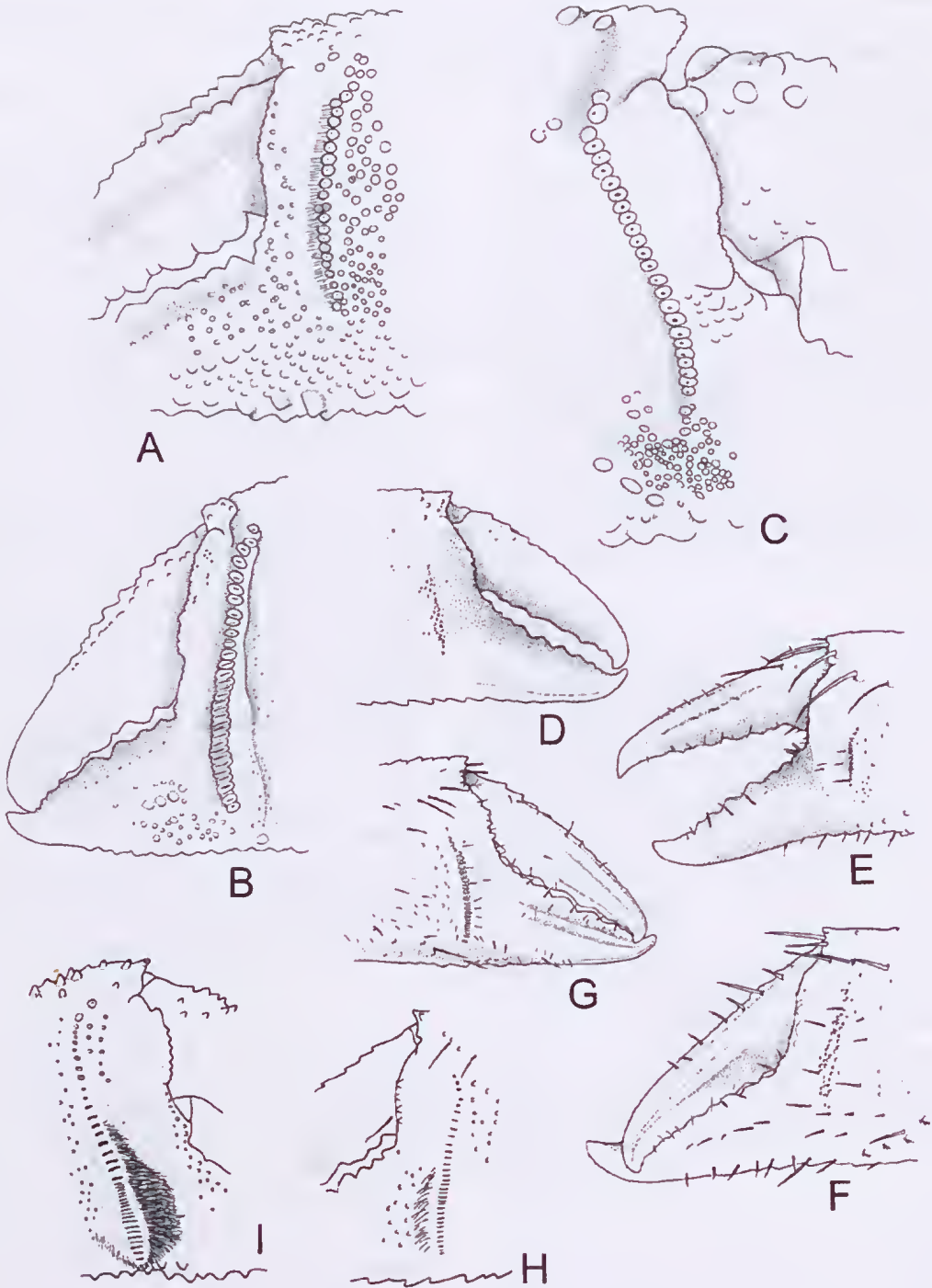


FIG. 1. Stridulating ridges: A, *Hoplocypode occidentalis*, SMF-2191; B, *Ocypode africana*, SMF-4364; C, *Ocypode brevicornis*, SMF-24536; D, *Ocypode ceratophthalma*, RMNH 30272, CW 9.5 mm; E, same, CW 6.3 mm; F, same, 6.2×5.8 mm; G, same, CW 13.3 mm; H, same, CW 17.5 mm; I, same, adult male specimen.

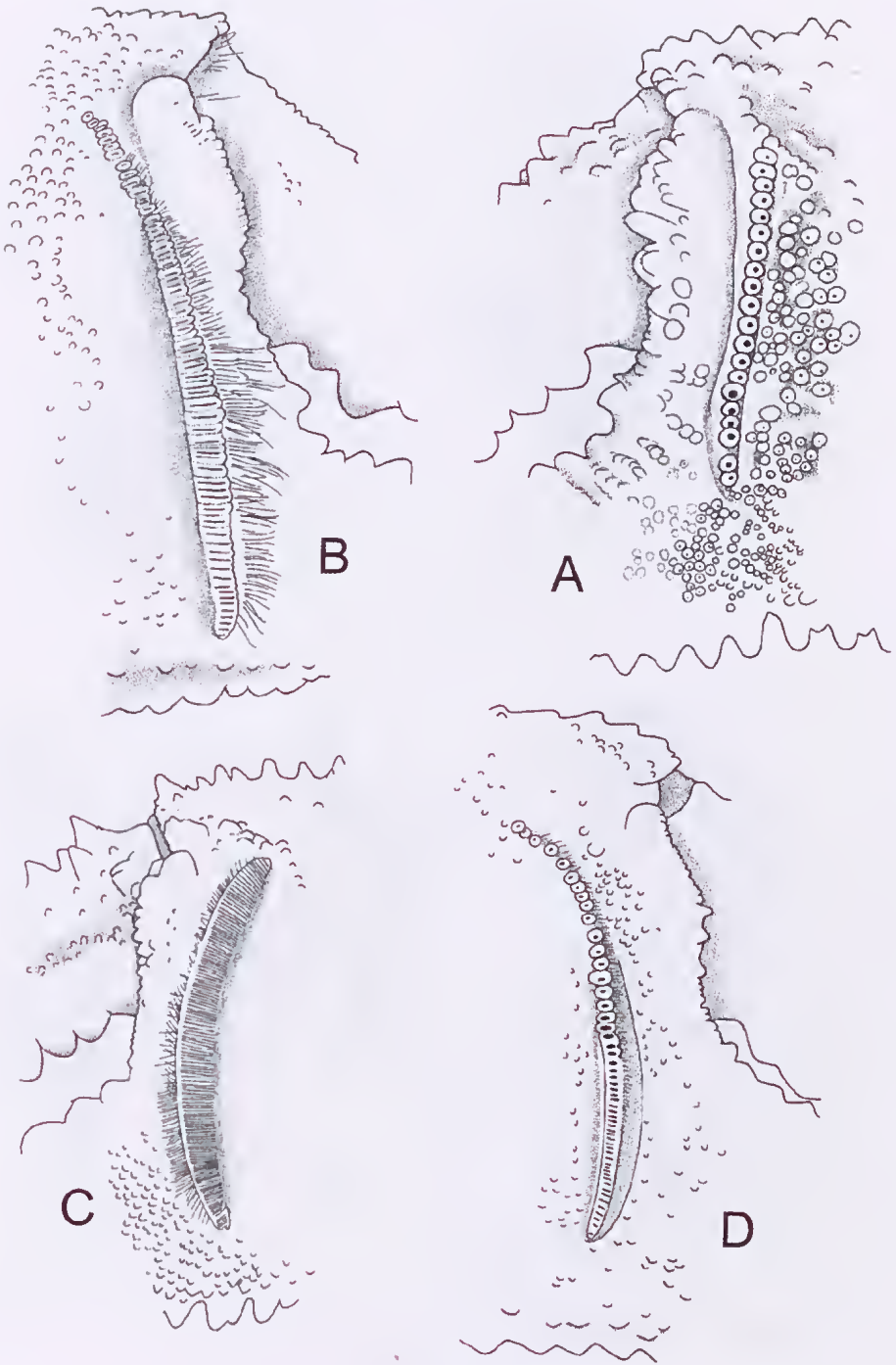


FIG. 2. Stridulating ridges: A, *Ocypode convexa*, SMF-7609; B, *Ocypode cursor*, SMF-9269; C, *Ocypode fabricii*, SMF-7612; D, *Ocypode gaudichaudii*, SMF-11443.

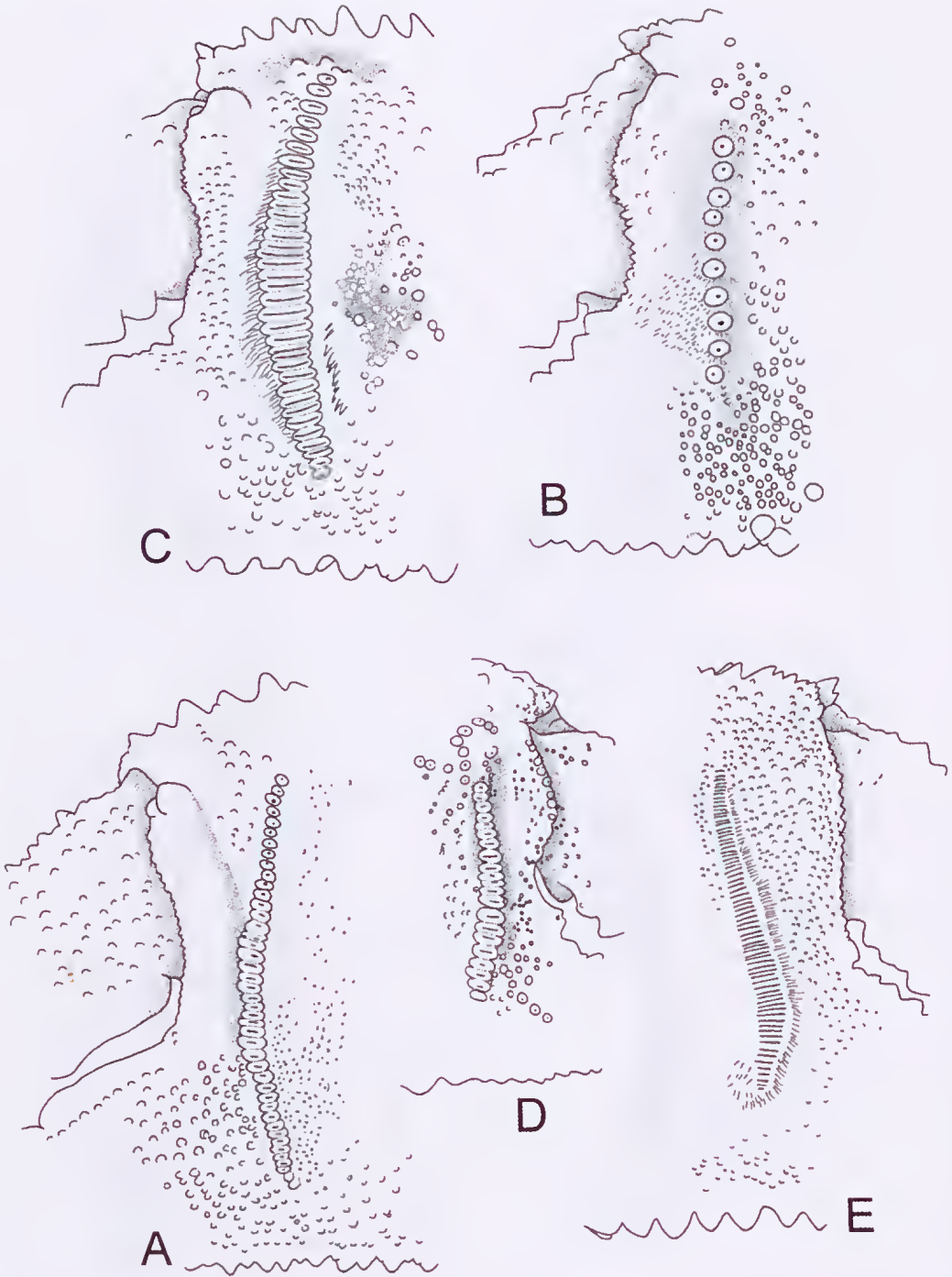


FIG. 3. Stridulating ridges: A, *Ocypode jousseaumei*, SMF-24530; B, *Ocypode kuhlii*, SMF-23298; C, *Ocypode macrocera*, SMF-6772; D, *Ocypode madagascariensis*, SMF-7274; E, *Ocypode mortoni*, SMF-36912.

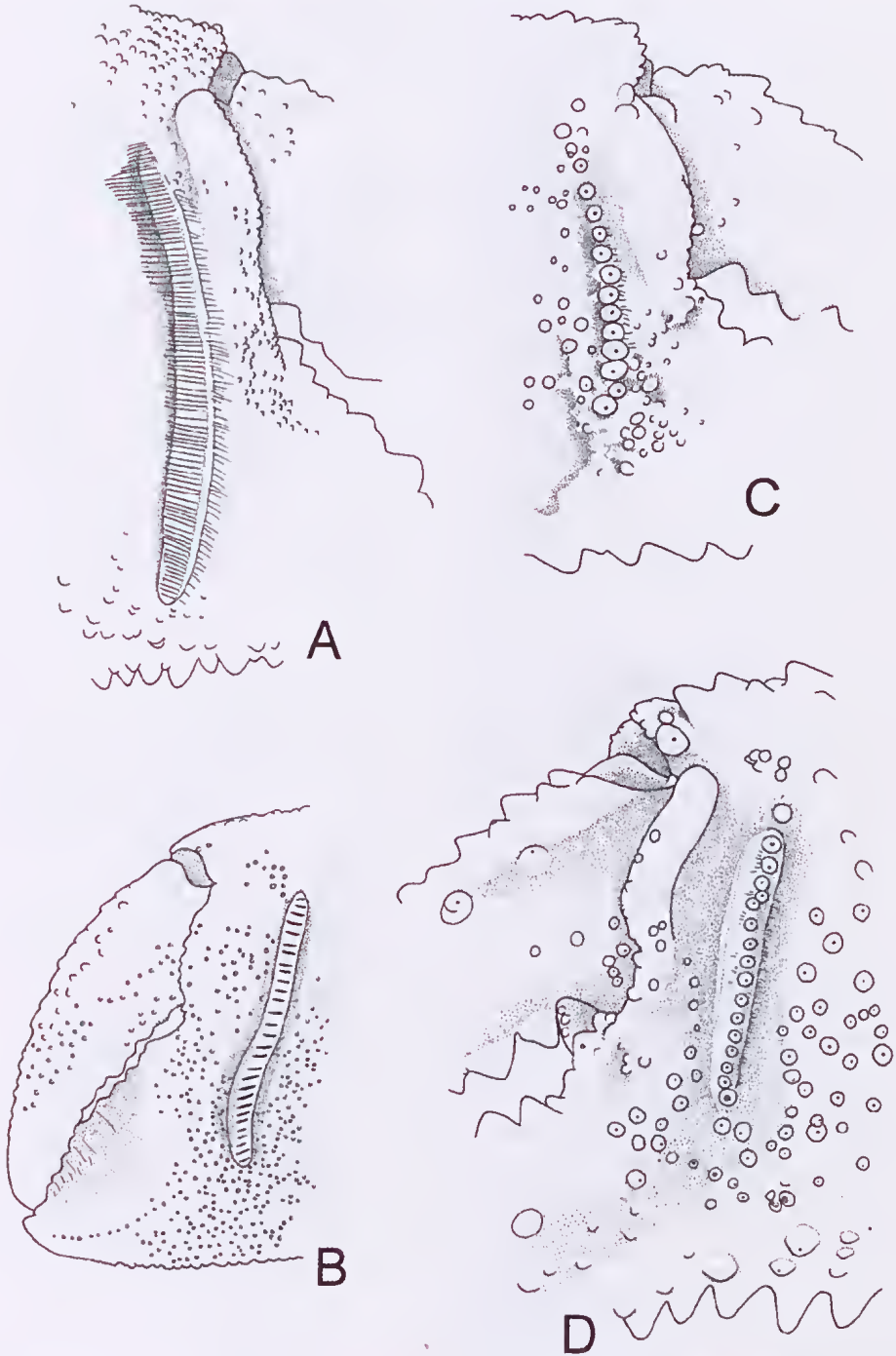


FIG. 4. Stridulating ridges: **A**, *Ocypode nobilii*, SMF-5412; **B**, *Ocypode pallidula*, SMF-10924; **C**, *Ocypode pauliani*, SMF-1958; **D**, *Ocypode quadrata*, SMF-16595.

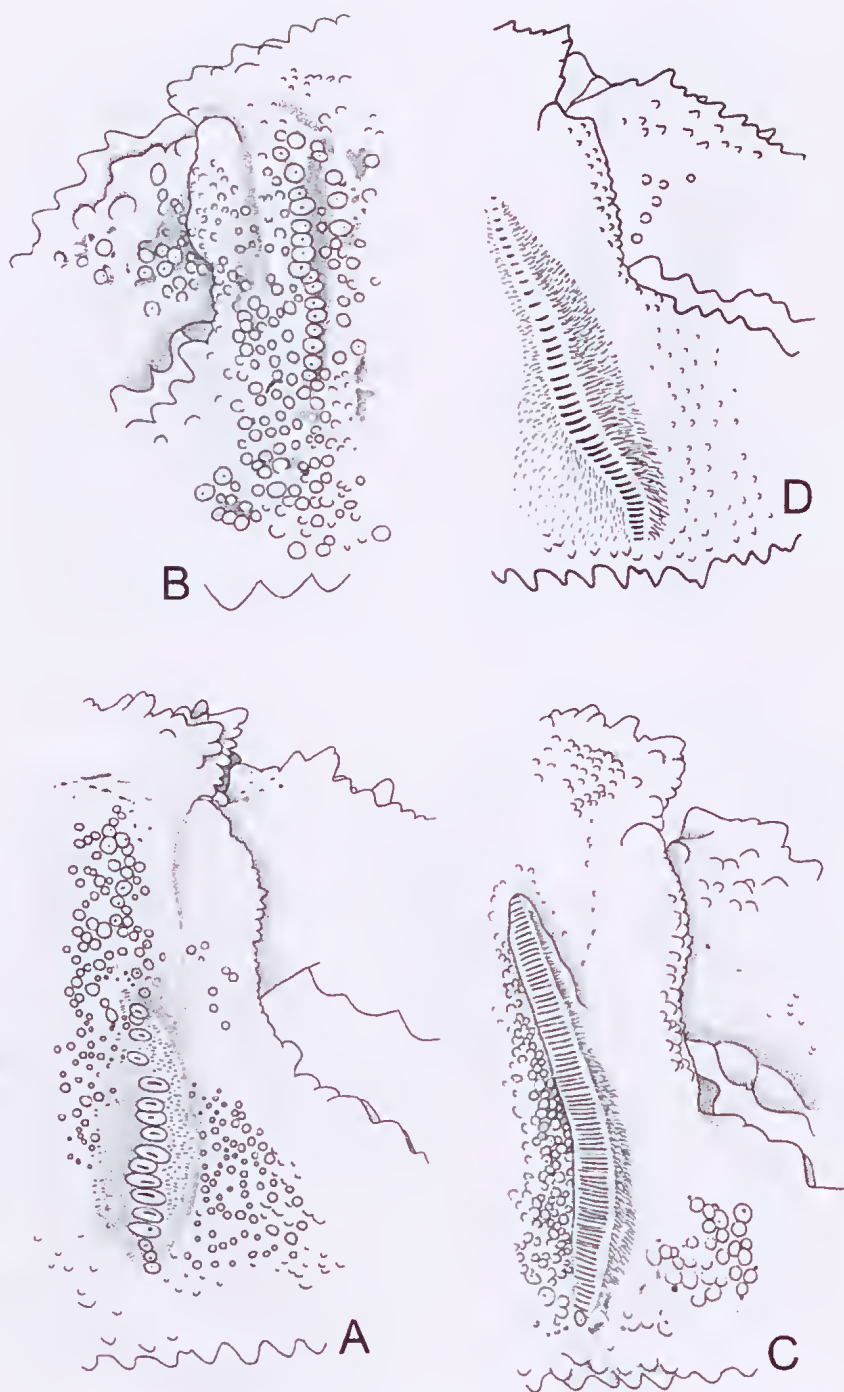


FIG. 5. Stridulating ridges: A, *Ocypterus rotundata*, SMF-24535; B, *Ocypterus ryderi*, NHCY-86; C, *Ocypterus saratan*, SMF-36171; D, *Ocypterus stimpsoni*.

Revision of *Ocypode*

Table 1. The distribution of the species in the genera *Hoplocypode* and *Ocypode*.

Atlantic Ocean and Mediterranean Sea	
Mediterranean Sea	<i>Ocypode cursor</i>
Eastern Atlantic	<i>O. cursor</i> <i>O. africana</i>
Western Atlantic	<i>O. quadrata</i>
Eastern Pacific Ocean	
Eastern Pacific	<i>Hoplocypode occidentalis</i> <i>O. gaudichaudii</i>
Indo-West Pacific Ocean	
Hawaii, Central and Southern Pacific, and Eastern Australia	<i>O. ceratophthalma</i> <i>O. cordimanus</i> <i>O. pallidula</i>
China and Japan	<i>O. ceratophthalma</i> <i>O. cordimanus</i> <i>O. mortoni</i> <i>O. pallidula</i> <i>O. stimpsoni</i>
Sarawak, Gulf of Thailand	<i>O. ceratophthalma</i> <i>O. cordimanus</i> <i>O. nobilii</i>
Indonesia	<i>O. ceratophthalma</i> <i>O. cordimanus</i> <i>O. kuhlii</i> <i>O. pallidula</i>
Northern and Western Australia	<i>O. fabricii</i> <i>O. ceratophthalma</i> <i>O. convexa</i> <i>O. cordimanus</i> <i>O. pallidula</i>
India and Indian Ocean	<i>O. brevicornis</i> <i>O. ceratophthalma</i> <i>O. cordimanus</i> <i>O. macrocera</i> <i>O. pallidula</i> <i>O. rotundata</i>
Persian Gulf and Gulf of Oman	<i>O. rotundata</i>
Gulf of Aden	<i>O. jousseaucei</i> <i>O. saratan</i>
Red Sea	<i>O. cordimanus</i> <i>O. saratan</i>
Madagascar	<i>O. ceratophthalma</i> <i>O. cordimanus</i> <i>O. madagascariensis</i> <i>O. pallidula</i> <i>O. pauliani</i>
Eastern and Southern Africa	<i>O. ceratophthalma</i> <i>O. cordimanus</i> <i>O. madagascariensis</i> <i>O. ryderi</i>

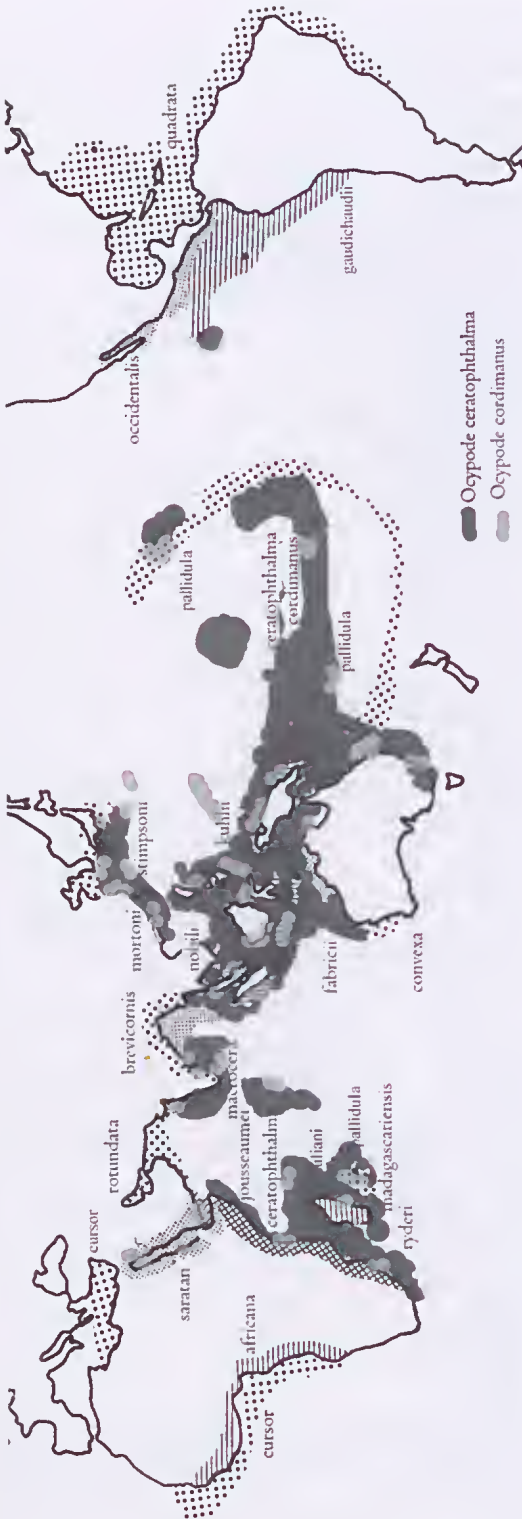


FIG. 6. Distribution map of *Ocypode*.

and armature among species. However, as an agile runner, the ghost crabs have a very particularly broad sternum to provide support for increased leg musculature. The arrangement of setae on the merus and propodus of the walking legs is very characteristic for individual species, but again similarities in pattern are just as likely to be ecotypically convergent, as they are to be synapomorphic.

Gonopod. The significance of gonopod morphology for detecting relationships in brachyuran crabs has been dealt with in several publications (Türkay 1975, Magalhães & Türkay 1996, Brandis *et al.* 1999). The main argument is that evolutionary selection pressure determining the morphology of the copulatory apparatus favors efficient functioning during sperm transfer, and thus is less likely to be impacted by environmental factors. Functionally, the copulatory organ of both sexes must be complementary, and therefore there should be very low variability. This means that a significant change in morphology must occur in both sexes simultaneously, and thus it is highly improbable that closely related species would have very different copulatory structures. Only a gradual change is possible, much slower than in non-sexual characters, and thus these organs are of major significance for determining relationships. Of course, some minor characters, such as slight changes in the length of the palp, can still show some intraspecific variability.

Family OCYPODIDAE Rafinesque, 1815

- Ocypodia Rafinesque, 1815: 96.
- Ucainae Dana, 1851: 289.
- Gelasimiden Nauck, 1880: 8, 17, 23, 64, 66 [unavailable as not in Latin].
- Gelasimidae Miers, 1886: viii.
- Ocypodidae, Manning & Holthuis, 1981: 192; Davie, 2002: 345; Ng, Guinot & Davie, 2008: 240.

Subfamily OCYPODINAE Rafinesque, 1815

Type genus: *Ocypode* Weber, 1795.
 Genera included: *Hoplocypode* gen. nov.; *Ocypode* Weber, 1795.

Remarks. The distribution list shows that many species occur in the Indo-Pacific region, but only three species, *Ocypode ceratophthalma*, *O. cordimanus*, and *O. pallidula* are widely distributed. Interestingly, only *O. ceratophthalma* and

O. cordimanus are sympatric throughout nearly their entire ranges (Fig. 6).

KEY TO THE GENERA OF OCYPODINAE

1. Go1 complex at distal end, hoof-shaped in mesial view. *Hoplocypode* gen. nov.
- Go1 simple at distal end.
. *Ocypode* Weber, 1795

Hoplocypode gen. nov.

Diagnosis. Body deep. Carapace quadrate, regions ill-defined, front deflexed. Eye-stalks large, cornea occupying most of ventral surface of stalk. A1 long; inner antennal-septum broadened. Chelipeds unequal in both sexes, palm of larger chela usually provided with a stridulating ridge of tubercles. P1-4 strong; P5 weaker than others. Most part of male sternite 8 not covered by abdomen. Go1 complex in shape at distal end, hoof-shaped in mesial view.

Type species. *Ocypoda occidentalis* Stimpson, 1860, by present designation and monotypy.

Distribution. Eastern Pacific; Gulf of California to Colombia.

Etymology. *Hoplocypode* is derived from the Greek 'hoplē', meaning a hoof (horseshoe), and refers to the hoof-shaped Go1 of the type species when seen in distal mesial view. Gender is feminine.

Hoplocypode occidentalis (Stimpson, 1860) (Figs 1A, 7, 29)

Ocypoda occidentalis Stimpson, 1860: 229.

Ocypode occidentalis — Rathbun, 1899: 74; 1918: 372, tab. 129, figs 2-3; 1923: 632; Boone, 1929: 580, text-fig. 16; Glassell, 1934: 302; Crane, 1940: 65, figs 3-8; 1941: 308, figs 3, 4E-F, 5A, C, E, 6A, C, 7A, B, pl. 1 fig. 2, pl. 2 fig. 5; Garth, 1948: 59, pl. 4, fig. 2; Buitendijk, 1950: 279 [in part]; Holthuis, 1954a: 40; 1954b: 162; Bott, 1955: 67; Bright & Hogue, 1972: 9; Ng *et al.*, 2008: 240.

Ocypode gaudichaudii — Lockington, 1877: 145 [not *Ocypode gaudichaudii* H. Milne Edwards & Lucas 1843].

Ocypoda Kuhlilii — Miers, 1882: 385 [in part], tab. 17, fig. 8b [not *Ocypode kuhlilii* De Haan, 1835].

Material examined. Mexico. No exact locality, male (MHNG); male (ZMH-2798); 3 males, 2 females (ZMH-2941); — Baja California: no exact locality, male, female, 1 juv. female, 6 juvs. (MNHN); female (NHMW); — Estado Baja California Sur: Todos Santos, 2 females (RMNH-7561, Buitendijk, 1950); — La Paz, male

(NHMW-1401); 9 males, 6 females (MNHN); — El Mogote near La Paz, female (AMS-P 5495); — Cape St. Lucas, male, female (syntype of Stimpson, 1860, MNHM); female (UZMK); 2 juvs. (UZMK); — Estado Sinaloa: Las Copas, Topolobampo, 1 juv. (RMNH-7611); — Mazatlan (23°16.59'N, 106°28.07'W), 10.i.1974, W. Baumeister; beach at northern end of town, male (SMF-7497), 23.viii.1984, A. Allspach; male, 6 juvs. (SMF-12999); — Estado Guerrero: Acapulco, male (RMNH-7560, Buitendijk, 1950); 4 juvs. (RMNH-7559). Guatemala. male (NHMB-564a); 5 males, 4 females (ZMH-2865); 2 males, female (ZMH-2923); male, female (ZMH-2924). El Salvador. Depto. Ahuachapán: El Zapote (13°42.7'N, 90°01.9'W), 2 juvs. (SMF-6858), 23.iv.1953, O. Schuster; — Depto. Sonsonate: Metallo (13°37.9'N, 89°53.5'W), 2 juvs. (SMF-5414), O. Schuster; — Acajutla (13°35.3'N, 89°50.03'W), male, female, 1 juv. (SMF-2210), O. Schuster; — Las Salinas de Cachapa (13°33.5'N, 89°41.5'W), 1 juv. male, 2 juvs. (SMF-2199), O. Schuster; — Las Salinas (13°32.0'N, 89°41.0'W), 11 juvs. (RMNH-9650); Playa de las Piedras (13°31.9'N, 89°40.0'W), 3 juvs. (SMF-6855), 13.ii.1952, O. Schuster; — Depto. La Libertad: Playa Zunzal near La Libertad (13°15.6'N, 89°23.5'W), 2 juvs. (SMF-6857), 27.ii.1953, O. Schuster; — La Libertad (13°29.0'N, 89°19.6'W), 9 males, female (SMF-2191), 2 males (RMNH-9655), O. Schuster; — Playa de las Flores near La Libertad (13°29.1'N, 89°17.7'W), male (SMF-2200), 1 juv. (SMF-16173), O. Schuster; — Toluca (13°27.1'N, 89°13.0'W), 3 juvs. (SMF-6859), 10.xii.1952, O. Schuster; — Depto. La Paz: Playa las Hojas (13°21.48'N, 89°2.65'W), 1 juv. (SMF-16172), 28.xi.1952, O. Schuster; — Amate de Campo (13°21.3'N, 89°02.2'W), male, female, 13 juvs. (SMF-2204), O. Schuster; — Los Blancos (13°20.0'N, 88°58.9'W), 1 juv. (SMF-6853), 17.x.1952, O. Schuster; — Depto. Usulután: La Pita, mouth of Rio Lempa (13°15.6'N, 88°50.0'W), 2 juvs. (SMF-6856), 19.iii.1953, O. Schuster; — Coral de Mula, Peninsula San Juan del Gozo (13°12.2'N, 88°31.8'W), 2 juvs. (SMF-6854), 17.xii.1952, O. Schuster; — SE tip of Peninsula San Juan del Gozo (13°10.7'N, 88°27.6'W), male, female (SMF-2076), H.M. Peters; — La Chepona, (13°11.0'N, 88°21.0'W), 1 juv. (RMNH-9658); — *ibid.*, male (SMF-2205), O. Schuster; — Estero, 5 juvs. (RMNH-9657). Panama. No exact locality. Incorrect localities. Mexico: Is. Sacrificio, male (MCM-2340). Honduras. 4 males, 3 females (SMF-4104), H. M. Peters. Venezuela, female (UZMK).

Diagnosis. Middle-sized species. Eyestalks not prolonged distally beyond cornea. Lateral half of orbital margin distinctly concave. Exorbital angles triangular and distinctly protruding anteriorly. Stridulating ridge composed of c. 21-22 tubercles. P2-3 propodi setose on dorsal half of anterior surface. Go1 complex in shape at distal end, hoof-shaped. Female genital opening membranous and slightly calcified.

Description. Carapace (Fig. 29) wider than long and covered densely with coarse tubercles. Lateral half of orbital margin distinctly concave. Exorbital angles acutely triangular and directed anteriorly. Lateral margins of carapace directed slightly outward from base of exorbital angle in anterior half of carapace, and then directed mesially in posterior half, and carapace broadest in middle. Pterygostomial region distinctly tuberculate, except around buccal cavern. P1 thoracic sternite (Fig. 7A) sparsely tuberculate medially, bearing tuberculate carinae on anterior and lateral margins. Palm of larger cheliped elongate and distinctly serrated on ventral margin, bearing coarse tubercles on anterior surface. Stridulating ridge (Fig. 1A) composed of c. 21–22 tubercles. Smaller cheliped tapering to pointed distal end. Male P2–3 propodi (Fig. 7B–C) with setae on dorsal margin; bearing transverse rows of setae on dorsal half and two median rows (in P2), or one indistinct row of setae (in P3) on anterior surface. P4 propodus with setae only on dorsal margin. P5 propodus naked. In female P4–5 propodi naked on anterior surface. Go1 (Fig. 7D–E) three-sided proximally; hoof-shaped at distal end. Operculum of female genital duct (Fig. 7F) quadrate, membranous, and slightly calcified. Slit of genital opening narrow and mesial with respect to operculum; directed along longitudinal axis of sternum.

Juvenile specimens. In a specimen from El Salvador (4.8×5.8 mm, SMF-2204) carapace distinctly wider than long and covered with fine tubercles on dorsal surface. Exorbital angles located far backward, but already acutely triangular as in adult specimens. Palm of larger cheliped flat on mesial surface. Stridulating ridge composed of short row of tubercles in median third on inner surface of palm. P2–3 propodi setose on dorsal half of anterior surface. In a specimen from El Salvador

(6.3×6.4 mm, SMF-6859) stridulating ridge composed of a longer row of irregularly arranged tubercles.

Distribution. Gulf of California to Colombia in the Eastern Pacific Ocean. Type locality: Cape San Lucas, Baja California peninsula, Mexico.

Remarks. *Hoplocypode occidentalis* is very similar to *Ocypode quadrata* from the western Atlantic coast, and has sometimes been regarded as its Pacific Ocean sister species. However, those two species are clearly distinguished from each other by significant differences not only in the structure of the Go1, but also in the arrangement pattern of setae on the anterior surfaces of the P2–3 propodi. Moreover, the difference in distribution between the two species prevents them from being confused; *H. occidentalis* is distributed on the eastern Pacific coast, whereas *O. quadrata* is on the western Atlantic coast. *H. occidentalis* is also similar to the eastern Pacific *O. gaudichaudii* in the pattern of setae on the anterior surfaces of the P2–3 propodi, and they could therefore be confused with each other. However, those two species are easily distinguishable by the differences shown in Table 2. It is very difficult to distinguish juvenile specimens of those two species when they are smaller than CL×CW 5.0×6.0 mm, and this has led to some past confusion in identifications.

Based on the characters given in Table 2, all reports of *Ocypode occidentalis* (= *Hoplocypode occidentalis*) from Peru are incorrect, because they were made, without exception, on the basis of juvenile specimens of *O. gaudichaudii*.

The report of *O. urvillei* from Peru by Doflein (1899), based on a juvenile specimen, has also caused subsequent confusion because his diagnosis was not clear enough for identification, and his only specimen was later lost. Rathbun (1918) considered Doflein's record to refer to *O.*

Table 2. Differences between *H. occidentalis* and *O. gaudichaudii*.

	<i>H. occidentalis</i>	<i>O. gaudichaudii</i>
Eyestalks	Not prolonged distally.	Prolonged distally.
Both chelae	Pointed distally.	Truncate distally.
Stridulating ridge	Short, composed of 21–22 tubercles.	Long, composed of 18 tubercles and 38 striae.
P1 palm	Flat on mesial surface.	Distinctly convex on mesial surface.

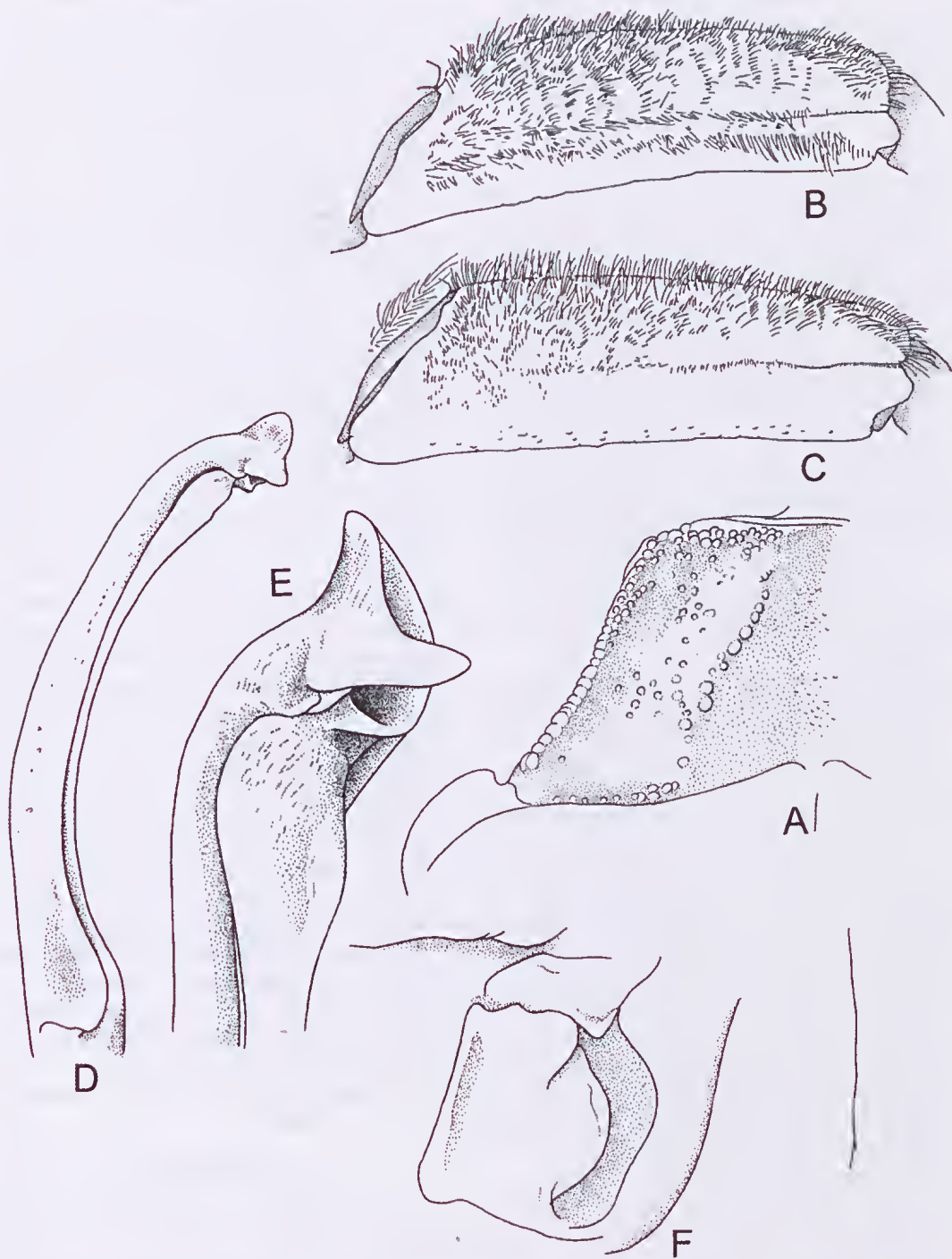


FIG. 7. *Hoplocypode occidentalis*: A, P1 thoracic sternite; B, C, P2-3 propodi; D, E, Go1; F, female operculum.

occidentalis (= *H. occidentalis*), but with hesitation. It is logical to assume, however, that Doflein's record must be of the eastern Pacific *O. gaudichaudii*, because *O. urvillei* (= *O. ceratophthalma*) only occurs in the Indo-West Pacific.

Ocypode Weber, 1795

- Ocypode* Weber, 1795: 92 [type species: *Cancer ceratophthalmus* Pallas, 1772, subsequent designation by Latreille, 1810: 95, 422; gender feminine] [ICZN (1964), Opinion 712; name 1637 on Official List].
- Ocypode* Fabricius, 1798: 312, 347 [a junior objective homonym of *Ocypode* Weber, 1795; type species: *Cancer ceratophthalmus* Pallas, 1772, by selection by Latreille, 1810: 95, 422; gender feminine] [ICZN Opinion 712; name 1738 on the Official Index of Rejected and Invalid Generic Names in Zoology].
- Ocypoda* Lamarck, 1801: 149 [an incorrect subsequent spelling for *Ocypode* Weber, 1795] [ICZN (1964), Opinion 712; name 1737 on the Official Index of Rejected and Invalid Generic Names in Zoology].
- Monolepis* Say, 1817: 155 [type species: *Monolepis inermis* Say, 1817, a subjective junior synonym of *Cancer quadratus* Fabricius, 1787, by selection by Fowler, 1912: 457; gender feminine].
- Ceratophthalma* MacLeay, 1838: 64 [type species: *Cancer cursor* Linnaeus, 1758, by monotypy; gender feminine].
- Parocypoda* Neumann, 1878: 26 [junior objective synonym of *Ocypode* Weber, 1795; gender feminine. Type species: *Cancer ceratophthalmus* Pallas, 1772 by monotypy].

Diagnosis. Body deep. Carapace subquadrangular, regions ill-defined, front deflexed. Eye-stalks large, cornea occupying most of ventral surface of stalk which is often produced beyond cornea like a horn. A1 long; inner antennal septum broadened. Chelipeds unequal in both sexes, palm of larger chela usually with a stridulating ridge of tubercles, tubercles with streae, or striae. P1–4 strong; P5 weaker than others; dactylus fluted. A cavity, connecting with branchial chamber, between bases of P3–4, its edges fringed with long setae. Greater part of male thoracic sternite 8 not covered by carapace. Go1 simple distally. (Revised after Barnard, 1950: 83).

Remarks. *Ocypode* Weber, 1795 is most closely related to *Uca* Leach, 1814, but differs in numerous characters. In *Ocypode*, the carapace is subquadrate; the eyestalks are stout; the chelipeds are unequal in both sexes; the palm of the larger chela is usually provided with a

stridulating ridge of tubercles, striae, or both; and the male Go1 is incurved distally. In *Uca*, the carapace is wider than long; the eyestalks are slender; the chelipeds are unequal in males, but equal in females; there is no stridulating ridge on the palm of the larger chela; and the male Go1 is slightly incurved.

Species included: *Ocypode africana* De Man, 1881; *O. brevicornis* H. Milne Edwards, 1837; *O. ceratophthalma* (Pallas, 1772); *O. convexa* Quoy & Gaimard, 1824; *O. cordimanus* Latreille, 1818; *O. cursor* Linnaeus, 1758; *O. fabricii* H. Milne Edwards, 1837; *O. gaudichaudii* H. Milne Edwards & Lucas, 1843; *O. jousseauinei* (Nobili, 1905); *O. kulilii* De Haan, 1835; *O. macrocera* H. Milne Edwards, 1837; *O. madagascariensis* Crosnier, 1965; *O. mortoni* George, 1982; *O. nobilii* De Man, 1902; *O. pallidula* Hombron & Jacquinot, 1846; *O. pauliani* Crosnier, 1965; *O. quadrata* (Fabricius, 1787); *O. rotundata* Miers, 1882; *O. ryderi* Kingsley, 1881; *O. saratani* (Forskål, 1775); *O. stimpsoni* Ortmann, 1897.

There are two other available names, *Ocypode minuta* Fabricius, 1798, and *Ocypode laevis* Fabricius, 1798, however these species have not been reported since the type description, the type specimens appear to have been lost, and the descriptions are so short and ambiguous that they are inadequate for recognising any species. Ng *et al.* (2008: 240) listed them as *incertae sedis*, and we here treat them as a *nomen dubium*. The identity of another Fabricius species, *Ocypode rhombea* Fabricius, 1798, has also been confused in the past, and often treated as a junior subjective synonym of *Ocypode quadratus* (Fabricius, 1787) (see Ng *et al.* 2008: 240). However, in this case, there is a presumed juvenile type specimen in the ZMUC, and based on examination of this, we are confident that *O. rhombea* Fabricius, 1798, is a junior synonym of *O. ceratophthalma* (Pallas, 1772) (see later).

KEY TO SPECIES OF OCYPODE

Key works best with adults. In juveniles the eyestalks are not sufficiently developed to be useful; in this case choices should be first restricted according to the region of occurrence (Table 1), and then the stridulating ridges compared to reach a determination.

1. Eyestalks prolonged distally beyond cornea in a stylus, or eyestalks with a setal brush at distal end of cornea. 2
 - Eyestalks neither prolonged distally beyond cornea in a stylus, nor bearing setal brush at distal end of cornea. 9
2. Eyestalks with a setal brush at distal end of cornea. Stridulating ridge composed of *c.* 69–96 fine striae [about 23 striae on interspaced tubercles in dorsal half and about 46 closely arranged fine striae in ventral half]. *O. cursor*
 - Eyestalks prolonged distally beyond cornea in a stylus. 3
3. P2–3 propodi naked on anterior surface. Stridulating ridge composed of 23–28 tubercles. *O. brevicornis*
 - P2–3 propodi with setae, or P2 propodus with setae and P3 propodus naked. 4
4. P2 propodus with setae, and P3 propodus naked. 5
 - P2–3 propodi with setae. 6
5. Stridulating ridge composed of 10–15 irregularly spaced elongate tubercles with striae. *O. rotundata*
 - Stridulating ridge composed of 67–87 fine striae. P2 propodus with a wide median row of setae on anterior surface. *O. saratan*
6. Both chelipeds pointed distally. Stridulating ridge composed of 10–11 interspaced tubercles in dorsal third, 8 thick striae in middle third, and 20–30 closely spaced striae in ventral third. *O. ceratophthalma*
 - Both chelipeds truncate distally, or larger cheliped pointed distally but smaller cheliped rounded to truncate distally. 7
7. Both chelipeds truncate distally. Stridulating ridge composed of *c.* 18 tubercles in dorsal half and *c.* 38 striae in ventral half. *O. gaudichaudii*
 - Larger cheliped pointed distally but smaller cheliped rounded to truncate distally. 8
8. Stridulating ridge composed of 35–71 striae. not extending ventrally beyond middle of fixed finger. *O. mortouii*
 - Stridulating ridge composed of 36–56 tubercles with striae; 9 slightly interspaced tubercles with striae in dorsal third and 27 closely arranged elongate tubercles with striae in ventral two thirds. *O. macrocera*
9. Mesial surface of palm of larger cheliped without a stridulating ridge. P2 propodus with setae along dorsal margin and transverse rows of setae on dorsal half, bearing a median row of setae on anterior surface. P3 propodus with thick setae along dorsal margin. *O. cordimanus*
 - Mesial surface of palm of larger cheliped always bearing a stridulating ridge. 10
10. P2–3 propodi with median rows of setae on anterior surface, bearing long setae on and along dorsal and ventral margins. Stridulating ridge composed of 15–18 interspaced tubercles. *O. quadrata*
 - P2–3 propodi with setae on anterior surface, or either P2–3 propodi naked or P2 propodus with setae but P3 propodus naked on anterior surface. 11
11. P2–3 propodi naked, or P2 propodus with setae but P3 propodus naked. 12
 - P2–3 propodi with setae on anterior surface. 16
12. P2–3 propodi naked. 13
 - P2 propodus with setae, but P3 propodus naked. 15
13. Stridulating ridge composed of *c.* 11–13 interspaced stout tubercles with striae in dorsal half and 21–26 closely spaced tubercles with striae in ventral half. *O. africana*
 - Stridulating ridge composed of interspaced tubercles. 14
14. Stridulating ridge composed of *c.* 10 interspaced tubercles. Greatest width of carapace near midline. *O. kuhli*
 - Stridulating ridge composed of *c.* 15 irregularly arranged tubercles. Greatest width of carapace at anterior 1/3. *O. ryderi*
15. Stridulating ridge composed of 41–79 elements, which gradually transformed from tubercles into tubercles with striae from above downwards. P2 propodus with a median row of setae on anterior surface. Exorbital tooth directed obliquely forward. Carapace with coarse granulations. *O. jousseaumei*
 - Stridulating ridge composed of 126–133 regularly and closely spaced fine striae. Exorbital tooth directed obliquely forward. P2 propodus with transverse rows of

- tubercles on dorsal half of anterior surface, bearing one median row of setae and another one on ventral half. . . . *O. fabricii*
16. Stridulating ridge composed of striae. . . 17
 – Stridulating ridges composed of tubercles, or tubercles with striae. 19
17. Stridulating ridge composed of 99–120 closely spaced fine striae. P2 propodus setose along dorsal margin, bearing a median row of long setae and another short row of long setae just below on anterior surface. P3 propodus with transverse rows of setae on dorsal half of anterior surface, bearing a median row of setae. . . . *O. nobilii*
 – Stridulating ridge composed of 17–57 striae. 18
18. Stridulating ridge composed of 30–42 (in male), or 17–29 (in female) rather interspaced thick striae, extending to ventral fourth of palm. Ventral margin of palm of larger chela granulate. P2 propodus sparsely setose on anterior surface, bearing a short median row of scanty setae, and setae along dorsal margin. P3 propodus sparsely setose on dorsal half of anterior surface, bearing setae and spinules on dorsal margin. *O. pallidula*
 – Stridulating ridge composed of 44–57 narrow striae, extending to near ventral margin of palm. Ventral margin of palm of larger chela distinctly serrate. P2 propodus with a median row of thick setae on anterior surface. P3 propodus with transverse rows of setae on dorsal half of anterior surface, bearing a median row of setae. *O. stimpsoni*
19. Stridulating ridge composed of 20–30 closely arranged tubercles with striae. P2–3 propodi setose on dorsal half of anterior surface. Go1 strongly crooked laterally in distal part. *O. madagascariensis*
 – Stridulating ridge composed of tubercles. 20
20. Stridulating ridge composed of 7–13 tubercles. P2–3 propodi with setae on and along dorsal margin, which are expanding distally onto anterior surface. *O. pauliani*
 – Stridulating ridge composed of 19–24 tubercles. P2 propodus with setae on dorsal margin, and P3 propodus with a row of setae along dorsal margin on anterior surface. Go1 smoothly curved in distal part. . . . *O. convexa*

Ocypode africana De Man, 1881

(Figs 1B, 8, 30)

- Ocypode africana* De Man, 1881: 253; Büttikofer, 1890: 465, 487; Ortmann, 1897: 365; Rathbun, 1900: 275; 1921: 462, pl. 53; Bouvier, 1922: 74; Rossignol, 1957: 86; Guinot-Dumortier & Dumortier, 1960: 136, 148, tab. 3; Bott, 1964: 30; Forest & Guinot, 1966: 89; Kensley, 1970b: 180; Penrith & Kensley, 1970: 252, 260; Manning & Holthuis, 1981: 218; Antia, 1989: 264; Ng, Guinot & Davie, 2008: 240.
- Ocypode hexagonura* Hilgendorf, 1882: 23.
 ? *Ocypode africana* – Miers, 1882: 386.
- Ocypode africana* – De Man, 1883: 155; Doflein, 1904: 127; Nobili, 1906c: 318; Bouvier, 1906a: 199; 1906b: 187; 1907: 497; Sandler, 1912: 190–191; Balss, 1914: 106; 1922: 80; Odhner, 1923: 23; Monod, 1927: 612; Roux, 1927: 238; Irvine, 1932: 7, fig. 19; 1947: 286, fig. 192; Bruce-Chwatt & Fitz-John, 1951: 117; Capart, 1951: 176, fig. 67; Monod, 1956: 395, figs 555–558; Gauld & Buchanan, 1956: 295, 296, 299; Dubois, 1957: 7; Sourie, 1957: 14, 31 [footnote], 45; Rossignol, 1957: 119 [key]; 1962: 119; Longhurst, 1958: 53, 88; Gauld, 1960: 71; Guinot & Ribeiro, 1962: 66; Uschakov, 1970: 447, 455 [listed]; Via Boada, 1980: 59, pl. 1 figs 7, 8, 8a.
- Ocypode Edwardsi* Osório, 1890: 48, 49; 1895a: 253; 1895b: 57; 1898: 193 [a junior subjective synonym of *Ocypode africana* De Man, 1881].
- Ocypode edwardsii* – De Man, 1896: 90.
- Material examined.** No exact locality. Africa, male (NHMW), iii.1885, 'Helgoland Expedition'; – West-Africa, 4 males, female [det. Balss] (ZMH-2746); – West-Africa, 3 juvs. [det. Th. Monod] (MNHN), 1910, A. Gruvel. **Sierra Leone.** No exact locality, female (NHM-1955.10.7.32); – Freetown, Lumley beach, 1 damaged juv. (NHM-1957.5.26.66); – *ibid.*, male [det. Th. Monod] (MNHN), 1882, Chaper. **Liberia.** Monrovia, 1 juv. (USNM-20577), Cook & Collins; – *ibid.*, Mouth of Mesurado River, male, female, 1 juv. (USNM-20667), Cook; – *ibid.*, Ocean Beach in front of Camp Johnson, 1 specimen (USNM-105883), 1 specimen (USNM-105881), 21.vii.1952, G.C. Miller; – Kap Mesurado near Monrovia, 11 males, female (ZSM), 1908, Scherer; – Paynesville, c. 9 km SE of Monrovia, beach of ELWA-hospital (6°15.55'N, 10°43.04'W), 3 males, 3 females (SMF-9823), 12.iv.1981, J. Voelker; – Mouth of Junk River, from mud under beach roots, 2 males (USNM-125758), 20.vii.1968, T. C. Rutherford. **Cote d'Ivoire.** Abidjan, 4 males, 6 females (MNHN), 1959, Rancurel; – surroundings of Sassandra (4°56.58'N, 6°5.23'W), 1 juv. male (SMF-9391), 19.iii.1976; – Assinie, female [det. Th. Monod] (MNHN), 1896, Alluaud. **Ghana.** No exact locality, male [det. Th. Monod] (MNHN), 1882, Chaper; – Accra, 2 males, 1 juv. female (NHM); – *ibid.*, Christiansborg beach, male, female (MNHN), 1948, R. Bassindale;

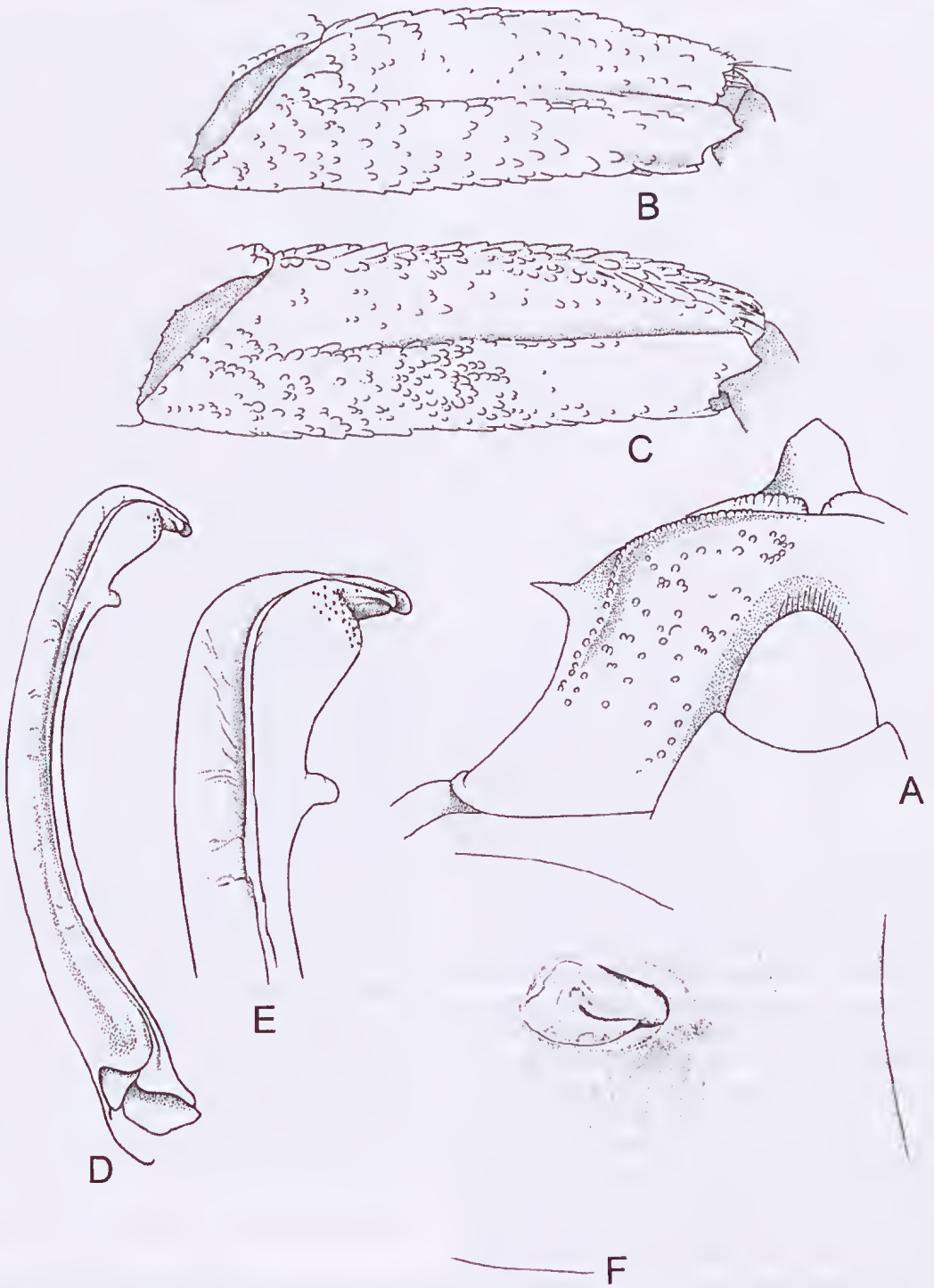


FIG. 8. *Ocypode africana*: A, P1 thoracic sternite; B, C, P2-3 propodi; D, E, Go1; F, female operculum.

Prampram, 2 males (NHM-1940.4.9.3). Togo. No exact locality, male, female (ZMH-2749); – Aného (= Anecho), male (ZMH-5566); – Lomé, 2 juvs. (ZMH-5567). Benin. Cotonou, 1 juv. (ZMH-29771), vi.1967 ‘Afrika-Expedition’. Nigeria. Lagos, female (NHM-1891.4.1.46–47). Cameroon. Douala (4°3.06'N, 9°41.34'E), 6 males (SMF-4364), 16.xii.1913, A. Haas; – Souelaba, 2 males, 2 females [det. Th. Monod] (MNHN), 1932–36, Th. Monod; – Rocher du loup (2°36.16'N, 9°50.37'E), S of Kribi, beach, 3 males (SMF-11714), 16.ii.1980, F. Ferrara. Equatorial Guinea. Mbini (= Benito) (1°35.48'N, 9°37.07'E), 3 males, female (SMF-6120), H. Eidmann; – Bata, 2 males [det. Th. Monod] (MNHN), 2 males, 2 females [det. Th. Monod] (MNHN), 1892, Pobéguin; – Bioko (= Fernando Poo), male (NHMW), 7.iii.1885, ‘Helgoland-Expedition’; – *ibid.*, male, female (NHMW), 13.iii.1885, ‘Helgoland-Expedition’, Sta. 184; – Annobón, 3 juvs. (NHM-1960.10.3.1–3). São Tomé and Príncipe. São Tomé, 2 males (ZMH-2751); – *ibid.*, 2 juv. males, 1 juv. female, 5 juvs. (MNHN), 1906, A. Gravier. Gabon. No exact locality, male, female (NHMW), 5.iii.1886, Herrman; – Cape López, 3 males (ZMH-2747); – *ibid.*, 1 dry female [det. as *Ocypode nitida*] (MNHN-3305S); 1 dry female [det. as *Ocypode nitida*] (MNHN-3306S), 1865, Duparquet; – *ibid.*, 1 dry male [det. as *Ocypode nitida*] (MNHN), Oeuvre de la Ste-Enfance; Cape Lopez, NW of Port Gentil, 1 juv. male, 1 juv. female, 5 juvs. [det. Th. Monod] (MNHN), 1907, Ronbaud & Weiss. Republic Congo. No exact locality, 3 males, 5 females [det. Th. Monod] (MNHN), 1892, Dybowski. Democratic Republic of Congo. Banana (5°59.38'S, 12°23.1'E), male, 1 ovig. female (SMF-1960), 12.v.1886, P. Hesse; – *ibid.*, 2 juvs. (USNM-54244); 5 males, 2 females (USNM-54245), viii.1915, H. Lang; – *ibid.*, beach, 1 juv. [det. A. Capart] (IRSNB), 10.viii.1948; – Muanda (= Moanda-Tonda) (5°56.1'S, 12°20.54'E), 2 females, 2 juvs. (SMF-6757), viii.1947, Darteville. Angola. Cabinda, female (ZMH-2748); – Benguella, 4 juvs. (NHM-1906.2.5.11–14).

Diagnosis. Middle-sized species. Eyestalks neither prolonged distally beyond cornea nor bearing a brush at distal end of cornea. Lateral half of orbital margin concave. P2–3 propodi naked. Stridulating ridge composed of 11–13 interspaced tubercles with striae in dorsal half and 21–26 closely spaced tubercles with striae in ventral half. Go1 strongly crooked laterally at distal end with broad bulge, bearing a thumb-like palp. Operculum of female genital opening protruding mesially, bearing strong lateral rim.

Description. Carapace (Fig. 30) wider than long, and covered with fine tubercles on dorsal surface. Lateral half of orbital margin slightly concave. Exorbital angles broadly triangular,

and protruding slightly forward. Lateral margins of carapace directed slightly outward from tip of exorbital angle in anterior third of carapace, and then directed mesially in posterior two-thirds, and carapace broadest at anterior third. Pterygostomial region with sparsely scattered fine tubercles except along each lateral side of buccal cavern. P1 thoracic sternite (Fig. 8A) sparsely tuberculate in anterior half, but smooth in posterior half, bearing triangular protrusion at anterolateral angle, and tuberculate carina on anterior to anterolateral margin. Palm of larger cheliped relatively broad, finely tuberculate on anterior surface, and finely serrated on ventral margin. Smaller cheliped pointed distally. Stridulating ridge (Fig. 1B) composed of 11–13 interspaced tubercles with striae in dorsal half and 21–26 closely spaced tubercles with striae in ventral half. P2–5 propodi (Fig. 8B–C) naked on anterior surface. Go1 (Fig. 8D–E) three-sided proximally, and crooked laterally at distal end with a broad bulge, bearing a thumb-like palp. Operculum of female genital opening (Fig. 8F) protruding mesially, bearing strong lateral rim.

Distribution. West coast of Africa from Mauritania to Namibia. Type locality was reputed to be the Congo, but according to Manning & Holthuis (1981), this is erroneous and the specimen would have come from Musserra, Angola.

Remarks. *Ocypode africana* from the eastern Atlantic is similar to *O. gaudichaudii* from the eastern Pacific in the morphology of the Go1, however differs from the latter, because in *O. africana* both chelipeds are distally pointed, and the P2–3 propodi are naked on the anterior surface. In *O. gaudichaudii* both chelipeds are truncate distally, and the P2–3 propodi are setose on the dorsal half of the anterior surface. *Ocypode cursor* also occurs in the eastern Atlantic, but differs from *O. africana*, because in *O. cursor* the eyestalks bear a brush at the distal end of the cornea, and the Go1 lacks a palp.

Ocypode brevicornis H. Milne Edwards, 1837
(Figs 1C, 9, 31)

Ocypode brevicornis H. Milne Edwards, 1837: 48; Ng *et al.*, 2008: 240.

Ocypode platytarsis H. Milne Edwards, 1852: 141; Guinot-Dumortier & Dumortier, 1960: 135, figs

15a-c; Guinot-Dumortier, 1961: 85, fig. 8; Veerannan, 1974: 36-42, tabs 1-4, figs 1-2; Serène, 1968: 97; Paulraj *et al.*, 1982: 115-128, tabs 1, 3-7. Nadarajalingam & Subramoniam, 1987: 43-53, tabs 1, 3, 4; Ng *et al.*, 2008: 240.

Ocypode platytarsis — Heller, 1865: 42 [in part]; Kingsley, 1880: 180; Miers, 1882: 383, pl. 17, figs 5, 5a; Henderson, 1893: 380; Alcock & Anderson, 1894: 202; Ortmann, 1897: 359, 363; Alcock, 1900: 345, 348; Laurie, 1906: 426; Kemp, 1915: 218; Gravelly, 1941: 105; Pillai, 1951: 27; Raja Bai Naidu, 1954: 89-95, 98-100, figs 1-17; Sarojini, 1962: 189, tab. 1, fig. 1 G; Thampy & John, 1970: 203-210; Ramadevi *et al.*, 1990: 261-265, tab. 1, figs 1-5; Chhapparg, Desai & Patel, 2004: 185.

Ocypode neglecta Ortmann, 1894a: 766, pl. 23, fig. 18.
Ocypode platytarsus — Clayton, 2001: 37-55.

Material examined. Oman. Khawr Al-Milh southern part (20°23'N, 58°17'E), tongue of land Bar Al Hikman, Gulf of Masirah, male (SMF-24536); male (SMF-24537), 31.v.1995, D. Clayton; — Al Ashkirah, S Ras el Hadd (21°48'N, 59°32'E), male (SMF-24538), 1.vi.1995, D. Clayton. India. Malankara (= Malabar), 2 males, 2 females, 2 juvs. (NHM-1898.6.17.77-81); male, female (ZSM from ZSI), Investigator-Expedition; male (MNHN-3308S); 2 males (MNHN-3309S); — Eastern coast, 3 males (ZMK-1536); — Tharangambadi (= Tranquebar), 1 juv. male, female (UZMK); — Puducherry (= Pondichery), male [lectotype of *Ocypode brevicornis*] (MNHN-4028S); male [holotype of *Ocypode platytarsis*] (MNHN); 6 males (MNHN); — Puri, 1 juv. (NHM-1956. 1.14.16); — Krakatau, Kolkata (= Calcutta), 1 juv. (NHMB-561b); — Nicobars, without exact locality, male [from Heller, 1865] (NHMW), 'Novara Expedition'. Sri Lanka (Ceylon). Without exact localities, 2 males (NHM-52); female, 1 juv. (NHM-1907.5.22.381-383); 1 juv. male, 1 juv. female (NHM-75.14); — Colombo, male, 1 juv. (ZMH-2968), 1901; — *ibid.*, 2 males [17.0×25.5, 10.6×17.4 mm], ix.1900, G. Duncker; female [32.8×44.2 mm] (ZSM-1442/1), 9.ix.1900, G. Duncker; — Dehiwala-Mount Lavinia (6°49.87'N, 79°51.73'E), 10 juvs. (SMF-6754), 23.iii.1974; — Kuchchaveli (8°49.09'N, 81°6.15'E), 2 juvs. (SMF-5427), 9-10.xi.1962, Brinck, Anderson & Cederholm, Lund Univ. 'Ceylon Expedition'; — Trincomalee, male (NHMB, 561a); 2 females (NHMW); — Trincomalee & Pamban (= 'Paumben'), 2 males, 6 juv. males, 1 juv. female (UZMK). **Missing or uncertain localities.** Without localities: male (ZMH-30357); 1 juv. male (NHM-60.15); 1 juv. (SMF-5425); 2 juvs. (SMF-5426); 3 juvs. (SMF-5428); 3 dry specimens (UZMK). — Tahiti, male [from Heller, 1865] (NHMW-1957), 'Novara Expedition'.

Diagnosis. Large-sized species. Eyestalks prolonged distally beyond cornea in a stylus. Carapace almost trapezoid. Lateral half of orbital margin directed obliquely backward.

Exorbital angles rectangular. Stridulating ridge composed of 23-28 tubercles. P2-5 propodi naked on anterior surface. Go1 slender and slightly curved laterally in distal part, bearing broad and flat palp distant from distal end. Female genital opening lengthwise and almost parallel with sternum. Operculum with anterior thick rim directed obliquely backward.

Description. Carapace (Fig. 31) distinctly wider than long and scattered dorsally with coarse tubercles, becoming larger from middle toward lateral sides. Lateral half of orbital margin directed obliquely backward. Exorbital angles rectangular. Lateral margins of carapace directed slightly outwards from base of exorbital angle in anterior third of carapace, and then directed mesially in posterior two-thirds, carapace broadest at anterior third. Pterygostomial region beset with distinct tubercles, becoming smaller and indistinct toward each side of buccal cavern. P1 thoracic sternite (Fig. 9A) with a pair of low humps with fine tubercles anteriorly near base of Mxp3, bearing distinct tuberculate transverse carina at anterior third, which continuous with tuberculate lateral carina, and fine tubercles along mesial and posterior margins. Palm of larger cheliped elongate, scattered with coarse tubercles on anterior surface, distinctly serrated on ventral margin and coarsely tuberculate on dorsal margin. Stridulating ridge (Fig. 1C) composed of 23-28 tubercles. Smaller cheliped narrowing to pointed distal end. P2-5 propodi (Fig. 9B-C) naked, and tuberculate on anterior surface, bearing denticles on dorsal margin. Go1 (Fig. 9D-E) stemlike and three-sided proximally, and slightly curved laterally in distal part, bearing a broad and flat palp distant from distal end. Female genital opening (Fig. 9F) lengthwise and almost parallel with sternum. Operculum also lengthwise, bearing anteriorly a thick and straight rim directed obliquely backward.

Juvenile material. In a small specimen (10.0×13.0 mm, SMF-6754) carapace distinctly wider than long and covered with coarse tubercles on dorsal surface. Eyestalks not yet prolonged distally beyond cornea, but cornea broadened at distal end. Palm of larger cheliped long. Stridulating ridge already composed of tubercles as in adult specimens. P2-3 propodi with a smaller number of spinules on dorsal margin of

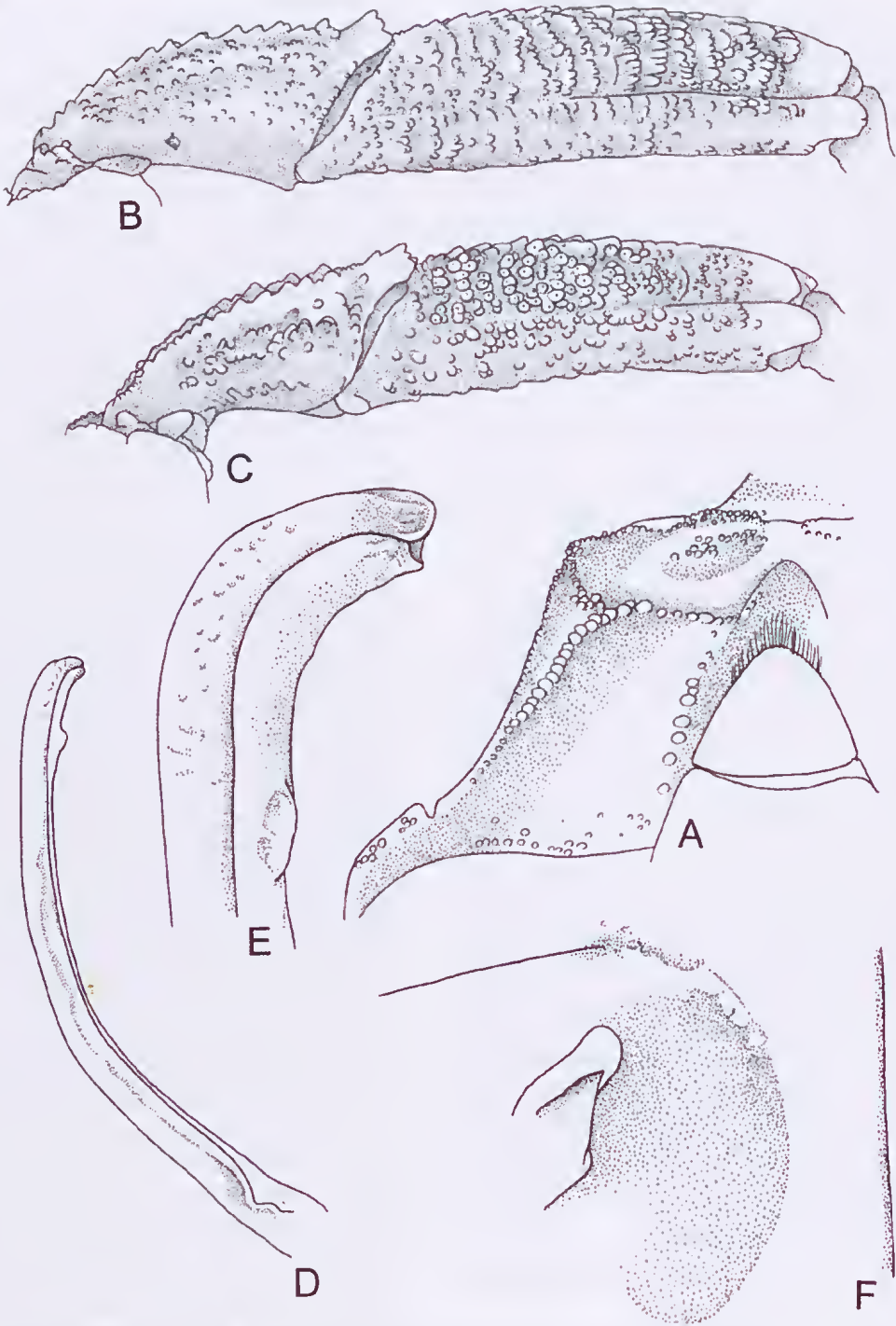


FIG. 9. *Ocypode brevicornis*: A, P1 thoracic sternite; B, C, P2-3 carpi and propodi; D, E, Go1; F, female operculum.

anterior surface than in adult specimens. In a slightly larger specimen (11.5×14.6 mm, SMF-6754) eyestalks already bearing a small distal protrusion. Lateral half of orbital margin slightly concave, therefore exorbital angles tooth-shaped and located backward. This small tooth at exorbital angle develops fully in course of growth. Palm of larger cheliped elongate. Stridulating ridge composed of tubercles as in adult specimens. P2–3 propodi with tubercles on anterior surface as in adult specimens.

Distribution. Oman, India; Nicobars; Sri Lanka. Type locality: East coast of India.

Remarks. H. Milne Edwards (1837) originally described *Ocypode brevicornis* based on two juvenile specimens from Pondichery, India, however subsequently the same author also described *O. platytarsis* H. Milne Edwards, 1852, based on adult specimens from the same locality. Kingsley (1880: 180) synonymised *O. brevicornis* with *O. ceratophthalma*, and since then *O. platytarsis* has been considered to be the fourth Indian species besides *O. ceratophthalma*, *O. cordimanus*, and *O. macrocera*. Our careful re-examination of the holotype of *O. platytarsis* in the MNHN, Paris, has shown it to be identical with *O. brevicornis*, and, therefore, *O. platytarsis* is here synonymised with *O. brevicornis*. In order to stabilise the usage, one of the syntypes of *O. brevicornis* (CB 26.0 mm, MNHN-4028S) is selected here as the lectotype.

Ocypode brevicornis is clearly distinguished from all other Indian Ocean *Ocypode* species by the following characters; the P2–3 propodi are naked, the stridulating ridge is composed of 23–28 tubercles, the Go1 bears a broad, flat palp distant from the distal end, and the female genital opening is located longitudinally below the operculum developed lengthwise on the lateral side of the concavity. The record of *O. platytarsis* (= *O. brevicornis*) from Tahiti, in the Pacific, by Heller (1865: 42) is presumed to be a misidentification, because *O. brevicornis* is now considered to be restricted to the Indian Ocean.

Ocypode ceratophthalma (Pallas, 1772)

(Figs 1D–I, 10, 32)

Cancer cursor Linnaeus, 1758: 625 [in part]; 1767a: 1038 [in part]; 1767b: 1038 [in part]; Herbst, 1782: 74, pl. 1, figs 8–9 [in part].

Cancer arenarius Toreen in Osbeck 1765: 479 [a *nomen oblitum*, a subjective synonym of *Ocypode ceratophthalma* (Pallas, 1772); see Low & Ng 2012: 43–46].
Cancer ceratophthalmus Pallas, 1772: 83; (9); pl. 5, figs 7–8; Fabricius, 1781: 499; 1787: 315; 1793: 439 [nomen protectum, see Low & Ng 2012: 46].

Cancer caninus Herbst, 1782: 78.

Ocypode ceratophthalma – Weber, 1795: 92; Fabricius, 1798: 347; Bosc, 1801–1802: 194; Latreille, 1803: 47, pl. 45, figs 1–2; Leach, 1814: 393 [in part]; Latreille, 1818: 252, pl. 274, fig. 1; Latreille, 1818: pl. 274, fig. 1; Bosc, 1830: 247; De Haan, 1835: 58; H. Milne Edwards, 1837: 66, pl. 17; Kraus, 1843: 41; Adams & White, 1848: iii; H. Milne Edwards, 1852: 141; H. Milne Edwards, 1852: 105; Stimpson, 1858: 100; A. Milne-Edwards, 1868: 71; Hilgendorf, 1869: 82; A. Milne-Edwards, 1873: 270; Hoffmann, 1874: 13; Miers, 1877: 135; Hilgendorf, 1879: 802; Miers, 1880: 308; De Man, 1881: 245; Ortmann, 1894a: 762, 767, pl. 23, fig. 20; Ortmann, 1894a: 767; Borradaile, 1900: 595; Lanchester, 1900b: 751; Lanchester, 1900a: 258 [in part; *O. nobili*]; Borradaile, 1901: 67, 96; Rathbun, 1902b: 123; Rathbun, 1906: 833; Borradaile, 1907: 65; Stimpson, 1907: 108, pl. 12, fig. 12; Borradaile, 1910: 408; Rathbun, 1910a: 321 [in part]; Laurie, 1915: 416; Maki & Tsuchiya, 1923: 202, pl. 23, fig. 2; Edmondson, 1923: 8; McNeill, 1926: 316; Urita, 1926a: 421–438, 1 fig; Balss, 1934: 226; Takahashi, 1934a: 8–14; Miyake, 1936: 511; Estampador, 1937: 542; Balss, 1938: 76; Miyake, 1939: 221; Horikawa, 1940: 21–31; Chace, 1942: 202; Barnard, 1950: 86, fig. 17c–d; Suvatti, 1950: 153; Tweedie, 1950: 321; Fourmanoir, 1953: 88; Holthuis, 1953: 28; Altevogt, 1959: 130–133, figs 2, 4; Stephenson, Endean & Bennett, 1958: 269; Guinot-Dumortier & Dumortier, 1960: 135, 146, 148, tab. 3; Edmondson, 1962: 15, figs 6a, 7a; Shen & Liu, 1963: 141; Garth, 1965: 37, figs 23–26; George & Knott, 1965: 17, fig. 1A, B, 2B; McNeill, 1968: 85; Allender, 1969: 63, tabs 1–3; Bright & Hogue, 1972: 11; Sakai, T., 1976: 600, text-fig. 327b, pl. 207; Berry, 1976: 35–37, 1 unnumbered text-fig; Yang, 1986: 153, fig. 2; Dai *et al.*, 1986: 419, text-fig. 231; Poupin, 1996: 73; Yu *et al.*, 1996: 58, fig. 58; Jeng, 1997: 87; Carpenter, 1998: 1152, fig.; Davie *et al.*, 1998: 19; Wang *et al.*, 1998: 69, figs 60–62; Rosenberg & Langer, 2001: 345–353, tab. 2, fig. 2; Davie, 2002: 357; Marumura, M. & Kosaka, A., 2003: 69; Yodo *et al.*, 2006: 2, 4, 5, figs 3, 5; Mano *et al.*, 2008: 2, 5, 6, 7, 8, tabs 1–2, figs 2–7; Seike & Nara, 2008: 594, tab. 2; Ng *et al.*, 2008: 240; Poupin, 2011: 18, fig. 8F.

Ocypode rhombea Weber, 1795: 92 [Nomen nudum].

Ocypode rhombea Fabricius, 1798: 348; Olivier, 1811: 418; Desmarest, 1825: 122; Audouin, 1826: 80, pl. 1, fig. 2 [in part]; Lucas, 1840: 58.

Ocypode cursor – Olivier, 1811: 416 [not *Cancer cursor* Linnaeus 1758].

- Ocypode ceratophthalma* — Latreille, 1817: 16; Lamarck, 1818: 252; Desmarest, 1825: 121, pl. 12, fig. 1; H. Milne Edwards, 1838: 463; Stebbing, 1910: 326; Day, Millard & Broekhuysen, 1954: 140, 153; Millard & Harrison, 1954: 166; Taramelli, 1955: 31; 1963: 73; Michel, 1964: 11; Green, 1964: 407–413; Crosnier, 1965: 93, figs 152, 160, 167–168, pl. 8, fig. 1, pl. 10, fig. 3; Serène, 1968: 97; Kensley, 1970a: 104; Horch & Salmon, 1972: 1–2, 6–10, tab. 2, figs 2–6; Jones, 1972: 31–43, tab. 1, figs 3, 4a, 4c, 4e, 4g, 5; Horch, 1975: 193; Dai & Yang, 1991: 458, text-fig. 231, pl. 58 (4); Jackson, Smale & Berry, 1991: 280–286; Huang *et al.*, 1992: 143, fig. 2, pl. 1B, tab. 1; Ng *et al.*, 2001: 35.
- Ocypode Urvillei* Guérin, 1829: pl. 1, fig. 1; 1838: 9; H. Milne Edwards, 1852: 141 [in part]; A. Milne-Edwards, 1868: 71 [in part].
- Ocypodes* — Audouin & H. Milne Edwards, 1829: 143, pl. 14, fig. 1.
- Ocypoda* (*Ocypode*) *ceratophthalma* — Voigt, in Cuvier, 1836: 119.
- Ocypoda ceratophthalma* — H. Milne Edwards, 1837: 48; Lucas, 1840: 57, pl. 1, fig. 1; Heller, 1865: 42 [in part]; Streets, 1877: 114; Richters, in Moebius, 1880: 155; Kingsley, 1880: 179 [in part]; Lenz & Richters, 1881: 423; Miers, 1882: 379, pl. 17, fig. 1; 1884: 237, 542, 573; 1886: 238 [in part]; Osório, 1888: 238; De Man, 1887–1888c: 107; 1888b: 351; Pfeffer, 1889: 30; Walker, 1890: 107; Thallwitz, 1891: 42; Henderson, 1893: 387; Aurivillius, 1893: 17, pl. 2, figs 1–6; Zehntner, 1894: 178; De Man, 1895: 570; Ortmann, 1897: 362, 364; Alcock & Anderson, 1894: 202; Alcock, 1900: 345; Andrews, 1900: 164; Calman, 1900: 24; Doflein, 1900: 144; Lancheater, 1901: 548; De Man, 1902: 477, pl. 19, fig. 1; Nobili, 1903: 20; Doflein, 1904: 126; Nobili, 1905a: 494; Lenz, 1905: 365; Laurie, 1906: 426; Nobili, 1906b: 310; Calman, 1909: 705; Lenz, in Voeltzkow 1910: 558; Pesta, 1911: 54 [in part]; Bouvier, 1915: 122; Parisi, 1918: 96; Tesch, 1918: 36; Balss, 1922a: 141; Sendler, 1923: 21; Calman, 1925: 166; Nakazawa, 1927: 1123, fig. 2165; Gravely, 1927: 148; Cott, 1929: 755, pl. 1, fig. 1; De Man, 1929: 2; Gordon, 1931: 528; 1934: 9; Takahashi, 1934b: 74; Balss, 1935: 140; Takahashi, 1935: 78; Tweedie, 1937: 141; Chopra & Das, 1937: 418, fig. 17a–a'; Sakai, T., 1939: 614, pl. 104, fig. 5; 1940: 32; Ward, 1942: 103; Tweedie, 1947: 27; Buitendijk, 1947: 280; Sakai, T. & Nakazawa, 1947: 664, fig. 1915; Lin, 1949: 26; Tweedie, 1950: 127; Fourmanoir, 1954: 1, fig. 1; Sakai, T., 1956: 53; Chhapparg, 1957: 44, pl. 13a–c; Sarojini, 1962: 191, tab. 1, fig. 1 H; Sankarankutty, 1961: 125; Hashmi, 1963: 240; Baksi, Ray & De, 1980: 184–187, pl. 1 figs 6–7, pl. 2, figs 1–2.
- Ceratophthalma cursor* — MacLeay, 1838: 64.
- Ocypode urvillei* — Owen, 1839: 80; Borradaile, 1900: 595; Stebbing, 1917: 11.
- Ocypoda urvillei* — Lucas, 1840: 57; Kingsley, 1880: 181; Doflein, 1904: 406; Bouvier, 1915: 122.
- Ocypode cursor* — White, 1847: 35 [in part].
- Ocypoda pallidula* — Dana, 1852: 324, pl. 20, fig. 1.
- Ocypoda Urvillii* — Dana, 1852: 328; 1855: pl. 20, fig. 5.
- Ocypoda brevicornis* var. *longicornuta* Dana, 1852: 327; 1855: pl. 20, fig. 4a, e.
- Ocypoda brevicornis* — Dana, 1852: 326; 1855: pl. 20, fig. 3.
- Ocypode cordimanus* — Jacquinet & Lucas, 1853: 64; Heller, 1865: 42; Ooishi, 1970: 94, pl. 16, fig. 2.
- Ocypoda Macleayana* Hess, 1865: 143, pl. 4, fig. 8; Haswell, 1882: 95.
- Ocypode Fabricii* — Hilgendorf, 1869: 82.
- Ocypode aegyptiaca* — Hoffmann, 1874: 13.
- Parocypoda ceratophthalma* — Neumann, 1878: 26.
- Ocypoda cordimanus* — Kingsley, 1880: 185 [in part]; Lenz, 1901: 476.
- Ocypoda fabricii* — Kingsley, 1880: 182.
- Ocypoda macleayana* — De Man, 1887a: 696.
- Ocypoda Kulilii* — Pfeffer, 1889: 30.
- ? *Ocypoda ceratophthalma* — Matsuura, 1894: 55; Schenkel, 1902: 581.
- Ocypoda Urvillei* — Nobili, 1907: 407; Bouvier, 1921: 57.
- Ocypode* sp. — Tu *et al.*, 1923: 819.
- Ocypoda* sp. — Gordon, 1934: 9 [in part].
- Ocypode gaudichaudii* — Estampador, 1937: 542.
- Cancer francisci* Curtiss, 1938: 175; Ng, Eldredge & Evenhuis, 2011: 45, 51.
- ? *Ocypode longicornuta* — Ng *et al.*, 2008: 240.
- Material examined. Unknown locality:** — 1 juv. male [syntype of *Ocypode rhombea* Fabricius] (UZMK); 2 juvs. (SMF-6732); 6 males, 2 females, 2 juvs., 2 damaged specimens (SMF-1934). These specimens were labelled as from the Red Sea, coll. Rüppell. Indeed the handwritten 1832 catalogue includes such a sample, but without any numbers of specimens. As the species has never again been found in the Red Sea and the label with the specimens was written around 1912, most of the Rüppell material usually having labels written in 1832, this Red Sea record must be considered doubtful; 4 males (SMF-36204, ex. T. Sakai coll.); 3 females (SMF-36206); 1 juv. male, 2 juvs. (SMF-36207); 2 juvs. (SMF-36208); 1 juv. male (SMF-36238, probably from Japan, but not definitely, as the T. Sakai collection also includes specimens from other regions); male (ZMG-129); male (ZMG-130, possibly from the Philippines, as locality numbers contained in the vials are similar to those written by Semper); — 'South Seas' (= Micronesia, Melanesia), 1 juv. (ZMG-128), purchased Capt. Pöhl; no further data, 1 juv. male, 1 juv. female, 3 juvs, 1 ovig. female [det. Balss as *Ocypode affinis nobilii*] (NHM-85.18), Dr. Millot. East Africa. No further data, female (ZMH-2809); 1 juv. [16.9×19.8 mm] (ZMH-2824). Somalia. Migiurtina [a former sultanate, now part of the region of Bari], Ras Hafun, female (MCG-144). Kenya. No further data, 1 juv.

female [det. Bouvier 1921] (MNHN); — Lamu Island, male (NHM-1983.11.9.3); — Mida Creek S of Watamu, Swatami Mangrove (3°24.05'S, 39°57.95'E), 2 males (SMF-18276); — Kilifi Creek (3°38.27'S, 39°51.58'E) between Malindi and Mombasa, female (SMF-18287), xii.1985, W. Baumeister; — 7 miles North of Mombasa, Bamburi beach, 10 males, female (RMNH-26016); — Mombasa, Kikambala (3°49.65'S, 39°49.71'E), female (SMF-6111); female (SMF-6112), 20.iii.-5.iv.1971, Z. Štević. **Tanzania.** Zanzibar: No exact locality, 1 juv. female (ZMH-2966); female (USNM-72530); male (MNHN-B 32715); 1 specimen with many legs of *O. ryderi* [det. A. Milne-Edwards, 1868] (MNHN-B33125); female, 1 juv. (NHM-1964.7.1.81); 2 males, female (ZMH-2816); male (ZMH-2820); female [det. Pfeffer, 1889] (ZMH-2961); 26 juvs. [det. Pfeffer, 1889] (ZMH-2965); 1 juv. (MNHW); 2 juvs. (NHMW); 1 juv. male, 2 juvs. (NHMW); male (NHMW); — close to Zanzibar town, male (NHMW), St. Paulay, 'Saida Expedition'; — NW-coast, Mkokotoni, 1 juv. female [det. Lenz, 1905] (ZSM); — East coast, 2 males, 4 females, 6 juvs. (NHM-1964.7.1.74-80); — Dar es Salam, 9 males, 9 females, 3 juvs., 1 damaged specimen (NHM-1973.51). **Mozambique.** Beira, 2 males, 3 juv. males, female, 2 juv. females, 1 juv. (ZMH-K-2824), 21.vi.1912, P. Timm; — Inhambane, mud flat, female (ZMH-29789); 2 males (ZMH-29831); — Inhambane, Praia do Tofo, male (ZMH-29810); — Costa do Sol, N of Maputo, female (RMNH-27421); — Maputo (= Lourenço Marques), 4 males, 4 females, 3 juvs. (ZMH-29808); — *ibid.*, Polana coast, 1 juv. (RMNH-16279-16281). **South Africa.** Kwa Zulu Natal: Boteler Point (27°1.0'S, 32°51.92'E), 3 males, 2 females (SMF-10930), 2-3.i.1976, S. Alexander; — Durban, 1 molted male (ZMH-2962); Durban Bay, male (NHM-1917.6.19.31); — *ibid.*, Salisbury Island, male, 2 juv. males, 3 juv. females, 6 juvs. (RMNH); — Eastern Cape: Port Alfred, 2 specimens (NHMW); — Port Elisabeth, 1 juv. (ZMH-11845). **Madagascar.** No exact locality, male, larger cheliped (MNHN); 13 juv. males, 6 juv. females, 58 juvs. (SMF-1933); female (SMF-1958); female (SMF-6750); 1 juv. male, 1 juv. female (NHM-88.5); male, 2 females (MNHN); male [det. Crosnier, 1965] (MNHN); 4 males, 4 females, 7 juvs. (MNHN); male (MNHN); male [det. Crosnier, 1965] (MNHN); — Nosy Bé (13°23.78'S, 48°12.33'E), 2 males, 2 females (SMF-1936), 7.vi.1883, A. Stumpf; 5 males, female [det. Hoffmann, 1874] (RMNH-229); — South-West of Morombe, 3 males, 2 females (MNHN); — St. Augustin (= Ianantsy), 8 males, female (MNHN); — East coast, Fenerive (= Fenoarivo), male (MNHN). **Réunion.** No further data, male (MHNG); — St. Paul (21°0.54'S, 55°16.09'E), beach, 2 males (SMF-18274), 1.ii.1989, H. G. Müller; — Beach at Caphomard (21°20'S, 55°13.25'E), 1 juv. (SMF-18272), 30.i.1989, H. G. Müller; — N l'Etang-Sale-les-Bains, Pnte. Des Avirons (21°14.21'S, 55°18.39'E), beach, from burrows, male (SMF-18273), 31.i.1989, H. G. Müller. **Mauritius.** No exact locality, male (NHMW); 3 males, female (NHMW); 2 males [det. Pesta, 1911] (NHMW); female [det. Pesta, 1911] (NHMW); 5 males [det. Bouvier, 1915] (MNHN); 3 males (MNHN-B3274S); 2 males (MNHN-B3273S); female (MNHN-B3291S); 2 specimens (MNHN-B3279S); 3 specimens (MNHN-B3289S); 1 specimen (MNHN-B3290S); 2 males (MHNG); — Flic en Flac, female (MI); — Tamarin, male, female (MI); — Fouquets I., 2 males [det. Richters, 1880] (ZMK-1520); male [det. Richters, 1880] (ZMK-1541); male, female [det. Richters, 1880] (ZMK-1543). **Republic of Seychelles.** No exact locality, 2 juvs. (NHM-1974.552); — La Digue, in front of Choppy's Bungalow (4°21.16'S, 55°49.57'E), male, 4 females (SMF-12909), 7.v.1979, M. Ackermann; — *ibid.*, male, female, 3 juvs. (SMF-12917), 8.v.1979; male (SMF-12919); — Mahé, male (NHMW); — Wizard I., Cosmoledo Is, male (NHM-1969.11.13); — Ile des Roches, Amirantes, male [det. Miers, 1880] (NHM-82.24); — Amirante Is, Poive-Atoll (5°45.0'S, 53°18.0'E), 4 juvs. (SMF-18271), I. Eibl-Eibesfeldt. **Chagos Archipelago.** No further data, 1 juv. (ZMH-2821); — Diego Garcia (7°15.5'S, 72°22.52'E), male (NHM-1968.803); 1 juv. (NHM-1969.1172); 1 juv. (SMF-5389); 1 juv. male, 1 juv. female (SMF-1939); female (NHMW). **Maldives.** No further data, male (NHM-1960.12.5.2); male (NHM-1966.2.1.61-62); — Addu Atoll, Gan Island, male (NHM-1965.7.20.6-7); — Addu Atoll, Beach of Hithadoo I. (0°36.51'S, 73°5.1'E), 2 males (SMF-6730), 1.i.1958, W. Klausewitz; — Rasdoo-Atoll NW of Ari (= Alifu) Atoll, Kuramathi (4°15.72'N, 72°57.96'E), male (SMF-24953), 15.vii.1999, D. Kovac; 2 females (SMF-24954). **India.** No further data, 2 juvs. (ZMH-2866); — Western coast, without more data, 8 males, 3 females (ZMH-26973); Western coast between Colachel and Goa, 1 juv. male (SMF-36253), 1984, W. Bee; — Maharashtra: Mumbai (= Bombay), male (MNHN-B3270S); 1 juv. male (NHMW-2081); — Alibag, South of Mumbai, many juvs. (ZMH-26906); — Karnataka: Karwar, specimen(s) (ZMH-26991); — Kerala: Malabar, 4 juvs. (NHM-1898.6.17.77-81); — *ibid.*, 4 males, female, 2 damaged specimens (ZMH-2803), Capt. Schwinghammer; — Badagara, Azhitala, Murat River (11°33.4'N, 75°35.7'E), female (SMF-36257), 26.vi.1984, W.H. Bee; — Chaliyar River, Beypore, ferry beach to Chaliyam (11°9.91'N, 75°48.33'E), 1 juv. (SMF-36252), 6.v.1984, W. Bee; — Chaliyam, Forest office (11°9.67'N, 75°48.54'E), 1 juv. male (SMF-36254), 21.v.1984, W. Bee; — *ibid.*, 1 juv. male (SMF-36251), 20.vi.1984, W. Bee; — Pondicherry: Malabar, Mahé, 4 juv. males, 1 juv. female (MZT-1100); — Tamil Nadu: Southern coast, 1 juv. male, 1 juv. female (NHM); — Pamban, 2 males (NHM-1890.10.20.4-5); — Lakshadweep: Agatti (10°51.51'N, 72°11.45'E), male (SMF-6727), 18.x.1974, Krammig; — Kalputhi (= Kalipatti): S of Agatti (10°48.83'N, 72°10.13'E), 2 males, 2 juv. males, female, 2 juv. females (SMF-6728), 13.x.1974, Krammig; — Bangaram (10°56.35'N, 72°17.38'E), male, female (SMF-6729), 15.x.1974, Krammig. **Nicobar Islands:**

No further data, female [det. Heller 1865] (NHMW), 'Novara Expedition'; 1 juv. male, 1 juv. female [det. Heller, 1865] (NHMW), 'Novara Expedition'. **Sri Lanka.** No further data, 1 juv. (NHM-1907.5.22.380); male (BMN-1974.152). — Colombo (6°55.41'N, 79°50.67'E), male (ZSM); 1 juv. (SMF-6737); — Mount Lavinia (6°49.87'N, 79°51.73'E), male, 7 females, 18 juvs. (SMF-6731), 29.iii.1974, Z. Števíč; — Moragalla Beruwela Beach (6°26.85'N, 79°58.98'E), c. 50 km S of Colombo, male (SMF-18275), 6-16.v.1989, H.G. Müller; — Weligama, male (NHMW); — Trincomalee, male, female (NHM-1934.1.16.159); male (NHMW-1156). **Myanmar.** Yangon (= Rangoon), 2 juv. males, 1 juv. female (USNM-106702). **Thailand.** No further data, 1 juv. [19.0×22.7 mm] (SMF-19319); male, 4 females (USNM-210884); 3 males, 2 females (USNM-210884); 1 juv. female (USNM-112170); — 'Eastern coast', male (USNM-230087); — Phuket: Pa Tong Bay (7°53.89'N, 98°17.75'E), 4 juv. males, 1 juv. female, 2 juvs. (SMF-11020), 1-4.ii.1983, Z. Števíč; — West coast, male (USNM-127110); — NW point, 1 juv. male, 1 juv. female (RMNH-24991); — Satun: Koh Terutao, beach (6°37.84'N, 99°36.99'E), male [exchange with UZMK] (SMF-7845), 1.iii.1966, 5th Thai Danish expedition; — Songhka: Songhka city, male (USNM-230087); — Surat Thani: Koh Tao, 2 females (USNM-107725); 1 juv. (USNM-104216); — Chon Buri: Sriracha N of Koh Samet Island, 2 juvs. (RMNH-27750); — Trat: Koh Chang, female (USNM-63656); 2 juvs. (NHM-1898.11.18); — probably around Koh Chang, 3 juv. males, 1 juv. female (RMNH-27118). **Singapore.** Beach (1°17.73'N, 103°53.93'E), male (SMF-1945), E. Marx; 5 males, 2 females, 6 juvs. [det. Lanchester, 1900] (NHM-1900.10.22.183-190); 3 males (NHMW-2079), i.1910, M. Pfister; — no further data; 1 juv. (NHMW). **Vietnam.** Con Son (= Poulo Condore), male (MNHN); female (MNHN). **China.** Exact locality unknown, male (MNHN-B32695); — Hongkong, male, female (NHM-1935.3.19.9); female, 1 juv. female (NHM-1930.12.2.194); male (ZMH-2802); — Amoy (= Xiamen), female (MNHN). **Taiwan.** male, 2 females [det. Balss, 1922] (ZMH); — *ibid.*, female (SMF-8809), J. Dörjes; — Mai Liao (23°47.9'N, 120°10.6'E), 2 males, female (SMF-8807), 27.viii.1977, J. Dörjes; 1 juv. female (SMF-8810); — Tainan-city, Anping district, male [det. Balss, 1922] (ZSM); male, female, 1 juv. female [det. Parisi, 1917] (MCM-1614); — Hainan, Qukou (20°1.07'N, 110°32.85'E), sandy beach, male [36.2×41.7 mm]; female [31.4×34.4 mm] (SMF-36228), 14.iii.1992, H. L. Chen & M. Türkay; — Hainan, Sanya (18°16.65'N, 109°28.09'E), male, female [exchange with Institute of Oceanology, Academia Sinica Qingdao] (SMF-36191), 14.iii.1955. **Japan.** No further data: 2 males [coll. T. Sakai] (SMF-24527); — 'unknown, but possibly Okinawa', female [coll. T. Sakai] (SMF-36225). — Shizuoka-Prefecture: Izu-Shirahama, Shimoda, Sagami Bay (34°41.46'N, 138°58.38'E), 2 juv. males, 2 juv. females (SMF-6751), 14.ix.1974, H. Suzuki. — Kochi Prefecture: Ikumi-kaigan (33°31.68'N, 134°17.06'E), Toyo-cho, 25 males [20.6×24.1 – 12.9×15.8 mm]; 15 females [19.4×24.5 – 14.5×17.6 mm] (SMF-36222), 11.ix.1998, I. Mano; — Shirahama, North of Ikumi-kaigan, Toyo-cho, 3 juvs. (SMF-36237), 5.viii.1992, Hirata; — Usa bay off Ryu Village (33°25.92'N, 133°27.19'E), 1 damaged male (SMF-36232), 2.ix.2004, K. Sakai; — Tosa-shi, Usa-Inoshiri, Entrance of Uranouchi Inlet (33°26.0'N, 133°26.19'E), 4 juv. males (SMF-16608), 19.x.1979, M. & H. Türkay, K. Sakai; — Okinohama (32°57.34'N, 132°59.57'E), Ogata-cho, 3 juvs. (SMF-36230), 21.viii.1994, T. Shimeno; — Kagoshima-Prefecture: Manose-gawa B. (31°26.72'N, 130°17.29'E), 2 females [15.3×18.1, 15.0×17.6 mm] (SMF-36234), 26.v.1996, M. Sato; — Ibusuki, northern beach (31°15.99'N, 130°39.7'E), 1.xi.1979, M. & H. Türkay, K. Sakai; — Amami-Oshima: Akagina (28°27.38'N, 129°40.33'E), 4 females, 1 damaged specimen (SMF-6741), 20-24.vii.1966, K. Sakai; — Yoron I. (27°3.11'N, 128°24.9'E), male (SMF-6734), 18-24.viii.1966, K. Sakai; — *ibid.*, Kori (27°2.17'N, 128°24.47'E), male [19.9×23.9 mm] (SMF-36233), 27.vii.1966, K. Sakai; — Chabana (27°3.11'N, 128°24.9'E), male [17.1×20.0 mm] (SMF-36231), 3.xi.1966, K. Sakai; — Okinawa, female [coll. T. Sakai] [27.2×32.2 mm] (SMF-36225); — Okinawa-honto, 1 juv. [coll. T. Sakai] [8.2×10.0 mm] (SMF-36239); — Kushi (26°42.56'N, 127°49.54'E), Nago-City, Okinawa, 2 females [20.8×26.1, 11.9×13.8 mm] (SMF-36220), viii.1987, R. Higa; — Onna Coast (26°27.32'N, 127°48.47'E), 3 males [34.3×38.0 – 9.1×11.4 mm], 2 females [25.7×30.0, 25.6×26.0 mm] (SMF-36221), 23.viii.1992, W. Shimabukuro; — Nakadomari (26°16.9'N, 127°49.0'E), upper tidal zone, 2 males [14.6×17.7, 6.2×7.3 mm], 1 juv. (SMF-36235), viii.1983, R. Higa; — Hentona (26°44.89'N, 128°10.78'E), male, 2 females (USNM-171693); — Tokashiki-jima, West of Okinawa-honto, Awaren (26°10.23'N, 127°20.72'E), 4 females (SMF-6733), 24.ix.1973, K. Sakai; — Ishigaki Island (24°20.0'N, 124°11.33'E), 2 males (MCM) [det. ? Parisi, 1917]; male, female (SMF-6740); female (ZMH-2811); — Taketomi-jima (24°20.13'N, 124°5.63'E), 1 juv. female (SMF-6735) [ded. K. Sakai], 1-8.v.1973, Uchida & Uda; — Ogasawara Is: Chichijima, male (MCM-1613). **Philippines.** No exact localities, 3 males, female (USNM-109780); 2 males (MNHN-B39375); 2 males (MNHN-B32775); 2 males (MNHN-B32755); male (RMNH-231); 1 juv. male, 1 juv. (NHM-84.31); — *ibid.*, fish market, 2 males (SMF-12495), [det. A. Schreiber], iii-iv.1983; — Luzon: Manila, female (ZMH-2806); — Laguna, 2 juvs. (ZMG-127), 'Blover Expedition' [this locality is very improbable, because the Laguna is a freshwater-lake, it might therefore refer to another locality around Manila], 1876, K. Semper; — Mindoro: No exact locality, 1 juv. (USNM-171315); — Panay: Iloilo, male (USNM-73200); — *ibid.*, beach at Jaro river mouth, 1 juv. male (USNM-73203); — Negros: Victorias, Magnanud River, 1 juv. male (USNM-73272); — Samar: E-coast, surroundings of General MacArthur

- (11°14.63'N, 125°33.27'E), 2 males, female (SMF-9999), viii.1978, W. Lobin; — Mactan I.: Maribago (10°17.16'N, 124°0.09'E), NW coast of Hilutangan Channel, 2 juvs. (SMF-18683), J.J. Janssen. Malaysia. No further data, 1 juv. female, 1 juv. (NHM-1898.11.18); — Pulau Langkawi, Pantai Kok (6°21.62'N, 99°42.03'E), 2 males (SMF-19481), 16-28.iii.1992, H.G. Müller; — Batu Feringgi, Northern coast of Pinang I., 2 males (RMNH-29450); — Pinang, Muka Head (5°27.92'N, 100°14.29'E), beach, 2 juvs. (SMF-36240), 5.iv.1994, B. Hellmund; — Port Dickson, many males & females (RMNH-5323); — Malacca, 1 juv. (NHMW); — Johor, male, female (MHNG); — Pulau Babi Besar, beach (2°25.88'N, 103°58.72'E), male, female (SMF-20287), 9.iv.1981, H. G. Müller; — Sarawak: no further details, male (NHM-1895.10.10.2-3); male (USNM-233139); — Palau Labuan, 1 juv. male (RMNH-15486-15491); male, female (NHMW); 1 juv. male, 2 juv. females, 1 juv. (NHMW); — Baram river, male, female (NHM-1898.10.25.22); — Buntal, Santubong, 2 males (NHM-1900.12.20.21) [det. Lanchester, 1900]. **Indonesia.** No exact locality, male (ZMH-2825); 3 juvs. (ZMH-2972); — Sumatera: No exact locality, female (IRSNB-6729); female (NHM); — Pulau Nias, no exact locality, 3 males, 2 females (RMNH-2061); many males and females (RMNH-15483); — Lahewa (= Luau Vara, Luah Vara), North-West corner of Pulau Nias, male (MCG); — Pulau We, 1 juv. (ZMH-2967) [det. Doflein, 1904]; male (RMNH-15492); 1 juv. male (RMNH-15486-15491); male (RMNH-15507); male (RMNH-15487); male (RMNH-15480); 1 juv. (RMNH-2151); male, 2 females (RMNH-15482); 2 males (RMNH-15483); — Region Pasaman, Batang Tamak, Mangrove North of Airbangis (0°12.92'N, 99°21.94'E), sandy beach, 1 juv. male (SMF-36260), 21.ii.1994, Th. Ziegler; — Padang, female (NHMW-2082); — Bengkulu (= Benkoelen), 1 juv. (USNM-87355); — Jaga Utara I. (= Noordwacher Eiland or Pulo Sebiri) (5°12.0'S, 106°27.0'E), SE of Lampung, Sumatera, 3 males, 6 females (ZMG-124), J. Brock; — Java: No exact locality, 2 males, female, 1 juv. (MHNG); male, female (MHNG); — Java Sea, male, female (RMNH-2002); — North coast of Java, male, 1 juv. male, 1 juv. female (RMNH-2004); — Alkmaar Island in front of Jakarta Bay, 2 juv. males, 1 juv. (RMNH-15486-15491); — Jakarta Bay, 10 juvs. (RMNH-15486-15491); — Jakarta, Tanjung Priok, 3 males (RMNH-15479); 38 juvs. (RMNH-154845); males (RMNH-2367); — Semarang female (MNHN); — Southern coast, Cilacap (= Tjilatjap), male, 3 females (NHMW); — Irian Jaya (0°21.07'S, 132°10.42'E), 1 juv. (RMNH-D 15499), 3.vii.1952, L. D. Brongersma & W. J. Roosdorp; — Nicobar, 2 juvs. (NHMW) [det. Heller, 1865]; — Lesser Sunda Islands: No exact locality, female (NHRM-St5970); 1 juv. female (NHRM-St5971); — Lombok: Ampanan, 1 juv. female (MCZ-7246) [det. Rathbun, 1910]; — Flores: Ende, 3 males, 8 females (RMNH), 'Snellius Expedition'; — Sumba: Rua, about 14 km South of Waikabubak, 1 juv. (NHMB); — near Timor, 2 juv. females (RMNH-15486-15491); — Timor: Kera Island North-West of Kupang, 5 males, 1 juv. female, 1 juv. (RMNH), Snellius Expedition; female, 3 juvs. (RMNH); — Pulau Kisar, north-east of Timor Island, male, 1 ovig. female (RMNH), 'Snellius Expedition'; — Pulau Leti, E of Timor, male (RMNH-10600); — Sabalana (= Postillon) Islands: Sarasa, male (RMNH), 'Snellius Expedition'; — Sapuka-Beser (= Sapoeoka), male, 3 juv. males, 2 females, 1 juv. female (RMNH), Snellius Expedition; — Kepulauan Aru: No exact locality, 1 juv. (NHMW-1886); female, 5 juvs. (NHM-84.31), 'Challenger Expedition'; — Wamar Island, Dobo (5°45.43'S, 134°12.94'E), 4 males, 1 juv. male, 1 juv. (SMF-1941); — Trangan Island, Ngaigoeli coast (6°37.98'S 134° 5.46'E), male (SMF-1938); 1 juv. (SMF-1963); — Kepulauan Kai: no exact locality, male (MCG-135); — Pulau Ut (= Oet), sandy beach (5°35.19'S, 132° 40.77'E), male (SMF-7847) [exchange with Copenhagen Museum], 23.iv.1922, Danish Expedition to Kai Is; — Kalimantan: — Palau Maratua, East of Kalimantan, male, 3 juv. males, 2 females, 1 juv. female (RMNH), 'Snellius Expedition'; — Pulau Karakelong, Maririka (= Meriri) (4°25.88'N, 126°42.87'E), female (SMF-1937); — Talaud-Islands (North of Sulawesi); no exact locality, female (ZMH-14980); male (MNHN-B3272S); female (MNHN-B3285S); male (NHM-80.6); male, 2 females (RMNH-230); — Spermonde Archipelago [off Makassar, SW Sulawesi], all from 'Snellius-Expedition': Samalona, 3 juvs. (RMNH); — Koedingareng Lompo, 1 juv. (RMNH); — Madeang, male, 4 juv. males, 4 juv. females (RMNH); — Lankadea, 8 males, 2 juv. males, 2 females (RMNH); 3 males, 2 females (RMNH); — Gonto Soea, 2 males (RMNH); — Makassar, female (NHM-80.6); 1 juv. female (NHMB-562c) [det. Schenkel, 1902]; — Pulau Butung SE of Sulawesi. Bau-Bau (= Bava Bava) (5°27.38'S, 122°36.03'E), male (SMF-1944), 31.viii.1909, J. Elbert; — Pulau Binongko, South-East of Sulawesi, 1 juv. male, 6 juv. females, 4 juvs. (RMNH) 'Snellius Expedition'; — Sula Archipelago: Pulau Taliabu, 9 males, 5 females (RMNH), 'Snellius Expedition'; female (RMNH); — Moluccas: Ternate (0°45.64'N, 127°21.64'E), 2 males, female, 1 ovig. female, 7 juvs. (SMF-1930), W. Küenthal; — *ibid.*, 2 males, 3 juv. males, 2 females, 3 juv. females (RMNH), 'Snellius Expedition'; 1 juv. male, female, 38 juvs. (RMNH); 2 juvs. (RMNH); 1 juv. (RMNH); 2 juvs. (RMNH); — Bacan (= Batjan), male (NHM-80.6); — Halmahera (1°8.73'N, 127°52.64'E); — No exact locality, male (SMF-1940), W. Küenthal; — Kau Bai, Halmahera, 2 males (RMNH), 'Snellius Expedition'; — Kau Bai, Halmahera, 7 juvs. (MCZ-7245) [det. Rathbun, 1910]; — Pulau Obilatu, 9 males, 2 females (RMNH) 'Snellius Expedition'; — Pulau Buru, male, female (MNHN-B3311S) [det. H. Milne Edwards, 1852]; — Pulau Ambon (= Amboina) (3°37.82'S, 128°15.41'E), 3 males (MCG); 2 males (MNHN); 1

- juv. male (SMF-5423); 5 males, 1 juv. (SMF-1932); male (MHNG); male (RMNH-226); 2 males (NHMW); 1 juv. (NHMW) [det. Pesta, 1911]; — *ibid.*, 5 males, 6 juv. males, 2 females, 6 juv. females, 8 juvs. (RMNH), 'Snellius Expedition'; — Haruru (= Harolo), 11 males (RMNH), 'Snellius expedition'; — Irian Jaya: No exact Locality, 'East Coast', 2 males, 2 females (RMNH-25857); — Misool Island, 1 juv. (NHM) [det. Gordon, 1934]; — Kafal Island near Misool Island, male, 2 juv. males, female (RMNH), 'Snellius Expedition'; — Pulau Miössu (formerly Middelburg Eiland) (0°21.07'S, 132°10.42'E), 1 juv. (RMNH); — Mapia Islands, Pegun-Island, male, female (RMNH); 1 juv. male (RMNH-15493-15500); — East of Manokwari, 2 juvs. (RMNH-15493-15500); 1 juv. male, 1 juv. female, 3 juvs. (RMNH-15493-15500); — Mansinam Island off Manokwari, 3 juv. females (IRTSNB-9223) [det. Gordon, 1934]; — Cenderawasih Bay (formerly Geelvink Bay), Numfoor Island, Kameri, 1 juv. male, 1 juv. female (RMNH-16279-16281); — Cenderawasih Bay (formerly Geelvink Bay), Nabire, many males & females (RMNH-15402); — Cenderawasih Bay (formerly Geelvink Bay), Aropen, 1 juv. female (RMNH-15493-15500); — South of Jayapura (formerly Hollandia), 2 juv. males (RMNH-16279-16281); — North of Jayapura (formerly Hollandia), 1 juv. male, 1 juv. female, 3 juvs. (RMNH-15493-15500); — Papua Province, estuary of Kali Bocaja at Holtekang on South-East coast of Humboldt (= Yos Sudarso) Bay, 2 males (RMNH-15502); male, 1 juv. male, female (RMNH-16283); — Teluk Yautefa (= Jautefa Bay) South of Jayapura, 1 juv. male (RMNH-15493-15500); — Mimika river, South coast of Westirian, male (NHM-1911.8.1.24). **Papua New Guinea.** Mainland Papua; — North-East New Guinea, male (NHMW); — Tarawai Is. (= Bertrand. Is.) (03°12.9'S, 143°15.56'E), female (SMF-1943), Hanseatische Südsee-Expedition, E. Wolf; male, female, 1 juv. female (SMF-3610); — Huon Bay, 'Bukaika 6 km West of Lae' [could refer to Bukaua, 14 km East of Lae, inasmuch 'west' from Lae would be inland]; — Close to Katau-River mouth near Kadawa on South-West coast, female (MCG-131); — Papua Bay, Yule Island (about 100 km NW Port Moresby), female (MZT-1103); 3 males (MCG-133); male (MCG-135); male (MCG-143); — Hula SE of Port Moresby, 20 juvs. (MCG-132); — Beagle Bay, male (MCG-129). **Admiralty-Islands:** North coast, female (ZMH-5771); — Bismarck Archipelago; — No exact localities, male (ZMH-5782); female, 11 juvs. (ZMH-5785); — Duke of York Island, 2 males (NHM-77.8); — New Britain, 7 males, 2 females, 1 juv. (ZMH-5820). **Solomon Islands:** No exact locality, female (NHMW); — Buka Island (5°27.26'N, 154°37.47'E), 1 juv. (SMF-6736); 1 juv. [5.5×6.5 mm] (RMNH-15499). **Australia.** No exact locality, male (ZMG-125); — Western Australia: 'West coast', 3 males (ZMH-11617); — 'Northwest coast', female (NHM-1932.11.30.165); — Thevenard Island, female (NHM-1960.10.6.5); — Onslow, town-beach (21°38.16'S, 115°6.84'E), male, female (SMF-10331), 6.x.1975, G. Hartmann & G. Hartmann-Schroeder; — Point Cloates near Coral Bay, male, female (NHM-1960.10.6.3-4); — Northern Territory: North-West of Cape Arnhem, 5 males, 5 females, 2 juvs. (USNM-178294); — Gulf of Carpentaria at North East end, 1 juv. female (USNM-178294); — *ibid.*, Groote Eylandt, East coast, female (USNM-178294); — *ibid.*, Groote Eylandt, Umba Kumba at north end, female (USNM-178294); — Queensland: Torres Strait, 3 males (NHM-1955.4.22.182-186); 2 juvs. (NHM-1954.9.14.121-122); male, female, 1 damaged specimen (NHM-1954.4.22.182-186); — *ibid.*, Thursday Island, male, 3 females (NHM-82.7) [det. Miers, 1882]; — *ibid.*, Friday Island, female (NHM-84.31) [det. Miers, 1882]; — Cape York, Somerset, male, female (MCG); — Great Barrier Reef, 3 males, female (NHM-1937.9.21.261-263); — *ibid.*, Raine Island, male (NHM-84.31), 'Challenger Expedition'; — *ibid.*, Bunker Group, male (MNH); — *ibid.*, Lady Musgrave Island, 1 juv. (NHM); — Yarrabah (16°54.28'S, 145°51.85'E), North East of Cairns, sandy beach, 2 juvs. (SMF-16561), 6.vi.1980, M. Türkay; — Ellis Beach (16°43.9'S, 145°39.42'E), North of Cairns, 10 males, 5 females (SMF-16562), 8.vi.1980, M. Türkay; — *ibid.*, 3 males, 1 juv. (SMF-16563), 4.vi.1980, M. Türkay; — Green Island (16°45.47'S, 145°58.39'E), 1 juv. (SMF-9855), 15.v.1957, H. Felten; — Brampton Island (20°48.6'S, 149°15.86'E), female (SMF-3610) [vend. S. Kellner]; — North Stradbroke Island, Northern part, beach (27°26.64'S, 153°32.23'E), male, damaged [15.9×19.5 mm] (SMF-36229), 29.ix.1999, M. Türkay; — *ibid.*, central part, beach (27°31.33'S, 153°30.13'E), 3 males [17.1×21.2 - 13.0×16.2 mm], 1 juv. (SMF-36226), 30.ix.1999, M. Türkay; — Bribie Island, Woorim Beach (27°4.03'N, 153°12.28'E), female (SMF-16560), 25.v.1980, M. Türkay; — New South Wales: Sydney municipality: Sydney, no further data, juv. female [holotype of *Ocyropa macleayana* Hess, 1865] (ZMG-126); — Collaroy, Long Reef (33°44.31'S, 151°18.43'E), sandy beach, male [23.0×27.4 mm], female [26.2×32.1 mm], 1 juv., damaged (SMF-36227), 24.v.1980, M. Türkay; — Balmoral Beach, Mosman, 1 juv. (RMNH-10600); Maroubra Bay, 2 juvs. (USNM-17035); — Double Bay, 1 juv. (MCG-127); — Pt. Stephens, Nelson Bay, 2 males, 3 females, 4 juvs. (MNH); — Jervis Bay, 1 juv. (NHM); — Botany Bay, 2 juvs. (NHM-84.31) [det. Miers, 1886], 'Challenger Expedition'; — South Australia: South Australian coast, 2 juvs. (NHM-84.31) [det. Miers, 1886]. **Palau.** No further data, male (NHMW-1623), 'Challenger Expedition'. **Northern Marianas.** Saipan, Garapan, Beach (15°12.51'N, 145°42.94'E), male, 18 juvs. (SMF-19495), x.1990, G. vom Berg; — *ibid.*, 8 juvs. (SMF-19496), 10.viii.1990, A. Allspach. **Guam.** No exact locality, female (USNM-33159), 'Albatross Expedition'; — *ibid.* (appr. 13°28.67'N, 144°45.44'E), male, 20 juvs. (SMF-19494), x.1990, G. vom Berg; — Ritidian Point,

1 juv. (USNM-170990); – Tumon Bay, female (USNM-171477); 1 juv. (USNM-170990); – Piti Bay, female, 2 juvs. (USNM-170990); – Bijia Point, male (USNM-170990); 1 juv. female (USNM-171477); – Cocos Island, male (NHM-1925.2.11.3); male (NHM-1925.2.11.1–2). **Micronesian Federation.** Kapingamarangi Atoll: Hare Island, male (USNM-104979); – Turuaimu Island, male (USNM-104983); – Caroline Islands: No further data, male, female (NHM-1898.11.1.69–71); – Pohnpei (= Ponape) (6°5 0.0'N, 158°19.69'E), male (SMF-22444), 8.vii.1986, K. Sakai; – Woleai Atoll, female (ZSM). **Marshall Islands.** No exact locality, male (USNM-172586); male (USNM-176603); – Enewetak (= Eniwetok) Atoll: No exact locality, male (USNM-172224); – Rigili Island, 7 males, 3 females (USNM-172224); – Aaraanbiru Island, 1 juv. female (USNM-172586); – Bikini Atoll: Uorikku Island, 3 males, female (USNM-17224) [det. Holthuis, 1953]; – Emon Island, female (USNM-176603); – Rongelap Atoll: Rongelap I., 1 juv. (USNM-101144); – Bikar Atoll: Bikar Island, male (USNM-94272) [det. Holthuis, 1953]; 2 males (USNM-94273) [det. Holthuis, 1953]; male (USNM-94274) [det. Holthuis, 1953]; – Taka Atoll: No exact locality, male (USNM-93601) [det. Holthuis, 1953]; – Ailuk Atoll: Ailuk Island, male (NHM-84.31) [det. Holthuis, 1953]; – Ujae Atoll: Enylamij Island, male (USNM-93602) [det. Holthuis, 1953]; – Kwajalein (= Kwadjelinn) Atoll: No exact locality, female (NHRM-St14267); 1 juv. (NHRMSt 14755). **Vanuatu** (= New Hebrides). Ambrym, male, 9 juvs. (MHMG); – Tanna, 1 juv. (NHM-75.69); – Prov. Tafea, Aniwa (= Jmmer) (19°13.84'S, 169°36.8'E), East of Tanna, 2 males (SMF-1929) [det. Sandler, 1923], 'Hanseatische Südsee-Expedition', E. Wolf. **New Caledonia.** No exact locality, female (MNHN-B3287S) [det. A. Milne-Edwards, 1872]; – N-Province, Ponérihouen, beach, (21°3.65'S, 165°24.57'E), 4 juvs. (SMF-36236), 23.iii.1994, T. Ziegler; – South-province, Ile des Pins, southern beach (22°40.49'S, 167°29.02'E), among debris after storm, 2 females [28.5×33.9, 20.3×23.9 mm] (SMF-36223); female [38.6×41.8 mm] (SMF-36224), 28.iii.1994, T. Ziegler. **Loyalty Islands.** Lifou Island, Cap des Pins, 4 males (NHM-1950.12.11.1–2). **Norfolk Islands.** No exact Locality, male (MNHN). **Fiji Islands.** No exact locality, male (USNM-66613); female (NHMW); – *ibid.*, 1 juv. (NHM-84.31) [det. Miers, 1886], 'Challenger Expedition'; – Viti Levu: No exact locality, female (ZMH-2810); male, 1 juv. (ZMH-2957); – Makaluva Island, c. 6 km South-East of Suva (18°11.32'S, 178°31.12'E), 1 juv. male, 3 juv. females (USNM-74486); – Kadavu (=Kandavu): No exact locality, 2 males, female, 7 juvs. (NHM-84.31) [det. Miers, 1886]; female (NHM-84.31) [det. Miers, 1886], 'Challenger Expedition'. **Kiribati.** Gilbert Islands: Onotoa Atoll, male (RMNH-9652); 3 males (USNM-93824) [det. Holthuis, 1953]; 2 males (USNM-94227) [det. Holthuis, 1953]; – Aranuka Atoll, 1 juv. (NHRMSt 14756); – Abemama (= Apamama) Atoll, 3 juvs. (NHRMSt 14266); – Phoenix Islands: Kanton Island (= Abariringa), male (USNM-76921); male (USNM-77268); – Line Islands: Kiritimati (= Christmas Island), 4 males (NHM-1957.11.6.9–10); male (NHM-1896.10.31.21); – Tabuaeran (= Fanning Island), female (USNM-2304) [det. Streets, 1877]. **Hawaiian Islands.** No exact Locality, 2 males (MNHN); – *ibid.*, female (SMF-9838), xii.1980, Sudhaus; – Oahu: No exact locality, 2 juvs. (USNM-171520); male, female (ZMH-27719); 2 males, female (ZMH-27720); – Kaneohe Bay, Coconut I., male (USNM-64175); male (USNM-64176); – Kailua, 20 juvs. (NHMW); 3 juv. females, 8 juvs. (NHMW); – Honolulu, Kahala, 1 juv. male, 4 broken pieces (RMNH-15486–4991); – *ibid.*, Waikiki Beach, 1 juv. (USNM-182729). **Samoa.** No further data, female (NHM-76.17); – No exact locality [but probably western Samoa which was a German and later, until 1962, New Zealand colony, purchased Mus. Goddefroy], male (SMF-1942); many males & females (ZMH-2804); – Upolu, female, 1 juv. female (NHMW) [det. Pesta, 1911]; – *ibid.*, Apia, 6 males, 4 females (USNM-43289); male (NHM-1931.5.26.15). **American Samoa.** Tutuila: Pago Pago, 1 juv. female (USNM-43285). **French Polynesia.** Society Islands: Bora Bora, Motu Babu Cay, 1 juv. male, 1 juv. (USNM-213821); – Raiatea Island, male (USNM-123617); – Tahiti, 1 juv. male (ZMH-2955); 1 juv. female (NHM); – Tahiti, Papeete, 2 juvs. (USNM-89871); – Tahiti, Papeete (17°31.45'S, 149°31.14'W), 4 males, 1 ovig. female (SMF-1931), 'Hanseatische Südsee-Expedition'; – Tuamotu Islands: No exact locality, 2 females (USNM-94563) [det. Holthuis, 1953]; 1 juv. female (USNM-33158), 'Albatross Expedition', Fakarava; – Rangiroa, 2 males, 2 females (UZMK); – Gambier Islands: No exact locality, male (MNHN) [det. Nobili, 1907]; female (MNHN) [det. Nobili, 1907]; – Mangarewa, male (MNHN-B4027S), Zelée Expedition. **Clipperton Island.** – No further data, male, female (USNM-107292); 7 males, 8 females (MNHN).

Diagnosis. Middle- to large-sized species. Eystalks prolonged distally beyond cornea in a stylus. Exorbital angles broadly triangular and protruding laterally in large specimens. Stridulating ridge composed of 10–11 interspaced tubercles in dorsal third, 8 thick striae in middle third, and 20–30 closely spaced striae in ventral third. Smaller cheliped narrowing to pointed distal end. P2–3 propodi setose on dorsal half of anterior surface, bearing one (in female) or two (in male) median rows of setae. Go1 slender, bearing palp. Sternite sunken around round operculum towards genital opening; no discernible lateral rim.

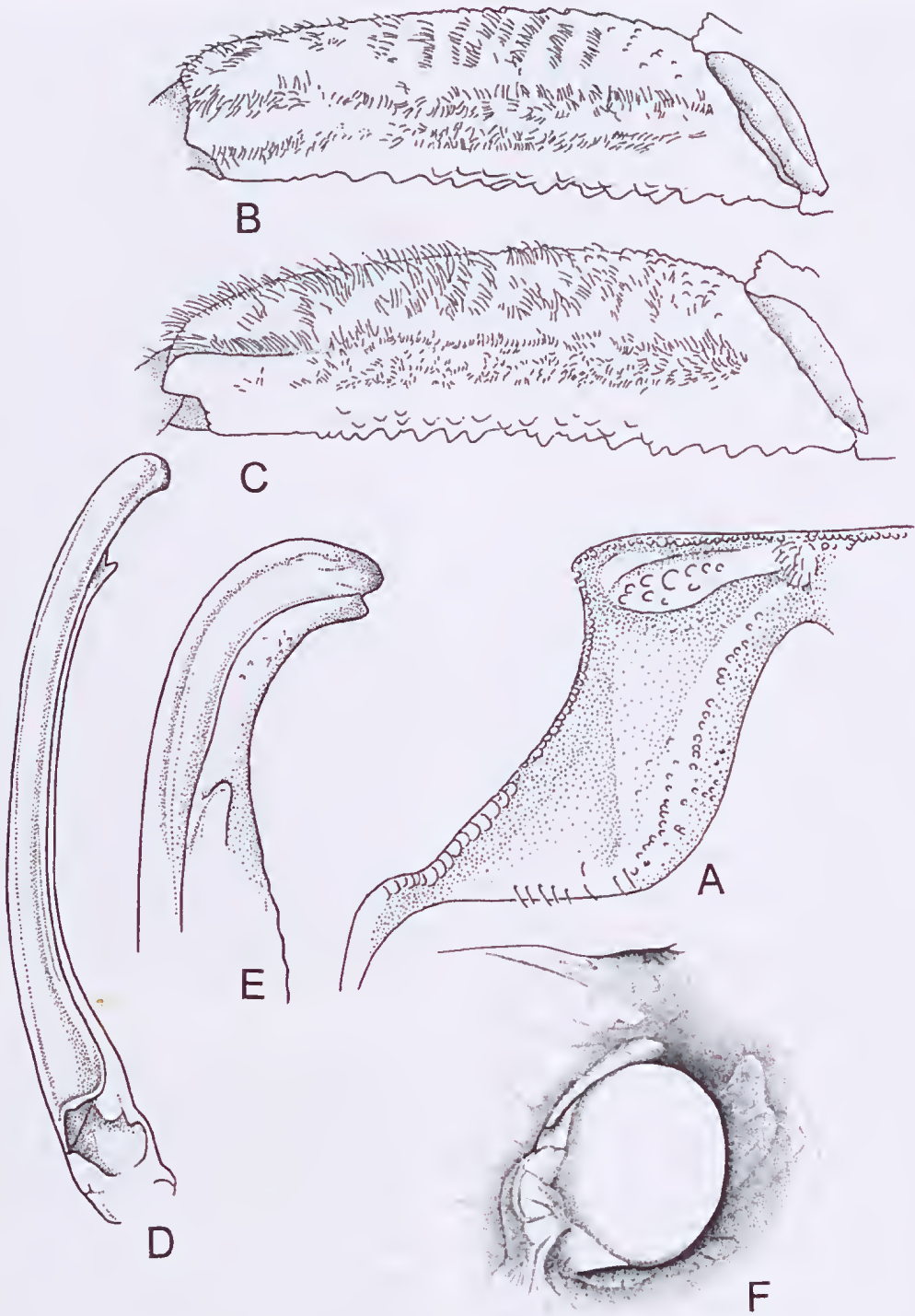


FIG. 10. *Ocypode ceratophthalma*: A, P1 thoracic sternite; B, C, P2-3 propodi; D, E, Go1; F, female operculum.

Description. Carapace (Fig. 32) slightly wider than long and covered with densely arranged fine granules on dorsal surface. Eystalks prolonged distally beyond cornea in a stylus. Lateral half of orbital margin slightly concave, and directed obliquely backward in adult specimens. Exorbital angles broadly triangular and directed laterally. Lateral margins of carapace directed distinctly outward from base of exorbital angle in anterior third of carapace, and then directed inward in posterior two-thirds. Carapace broadest at exorbital angles, or in specimens with smaller exorbital angles, at anterior third. Pterygostomial region entirely tuberculate, but tubercles small along lateral sides of buccal cavity. P1 thoracic sternite (Fig. 10A) smooth and bordered with tubercles, bearing tuberculate humps anteriorly. Palm of larger cheliped broad, covered with coarse tubercles on anterior surface, and distinctly serrated on dorsal and ventral margins. Stridulating ridge (Fig. 1D-I) composed of 10-11 interspaced tubercles in dorsal third, 8 thick striae in middle third, and 20-30 closely spaced striae in ventral third. Smaller cheliped narrowing to pointed distal end. P2-3 propodi (Fig. 10B-C) with oblique rows of setae on dorsal half of anterior surface, bearing one (in female) or two (in male) median rows of setae. Go1 (Fig. 10D-E) slender, three-sided proximally, and slightly curved laterally in distal part, bearing a small protruding palp directed distally and distant from distal end. Sternite sunken around round operculum (Fig. 10F) towards genital opening, no discernible lateral rim.

Juvenile specimens. In a specimen from New Guinea (5.5×6.5 mm, RMNH-15499) eystalks not prolonged distally beyond cornea. Carapace distinctly wider than long and covered with densely arranged fine granules on dorsal surface. Lateral half of orbital margin straight and directed laterally. Exorbital angles rectangular. Palm of larger cheliped much longer than broad, and more sharply serrated on dorsal and ventral margins than in adult specimens. Stridulating ridge distinct and composed of sparsely and irregularly arranged tubercles. P2-3 propodi bearing a median row of setae on anterior surface and setae on dorsal margin, both of which meet distally. In slightly larger

specimens lateral half of orbital margin strongly bent, and exorbital angles directed laterally. In a specimen from eastern Africa (16.9×19.8 mm, ZMH-2824) eystalks not yet prolonged distally beyond cornea in a stylus, but just as a small projection, while in a specimen from Tahiti (19.0×22.7 mm, SMF-1931) distal prolongation completely lacking.

Distribution. Indo-Pacific from the western Indian Ocean (except Red Sea) to Japan, Micronesia, and eastwards to Polynesia and Clipperton Island. Type locality: Unknown.

Remarks. The present species was reported for the first time by Peter Simon Pallas (1772) under the name of *Cancer ceratophthalmus* with his description and figures. It seems, however, that Pallas' species had already been included in a species described as *Cancer cursor* by Linnaeus (1758) based on specimens from Palestine (what we consider now to be the 'true' *cursor*) and India (presumed to be Pallas' species). So, earlier authors often confused *O. ceratophthalma* with *O. cursor*, and even synonymised the former with the latter. Herbst (1782) described *C. cursor* with reference to a specimen from East-India, but largely following Hasselquist's description (1762) of *Cancer anomalus* (= *O. cursor*) based on a specimen from Palestine. He referred to *C. ceratophthalma* Pallas as a synonym of *C. cursor* Linnaeus. However Herbst's specimen has turned out, on examination, to be clearly different from Haaselquist's; in Herbst's specimen the eystalks are prolonged distally beyond the cornea in a stylus (*O. ceratophthalma*), whereas in Haaselquist's they are not prolonged distally beyond the cornea, but bear a brush at the distal end of the cornea (*O. cursor*). McLeay (1838) and White (1847) also synonymised *O. ceratophthalma* with *O. cursor*. Later White went as far as to name his specimen from the Red Sea *O. cursor* rather than *O. saratan*. MacLeay (1838: 64) used the name *Ceratophthalma cursor* for the whole taxon. It is evident that the specimens named *O. cursor* based on the specimens from India and the Red Sea were not correctly identified, because they are clearly different from *O. cursor* from Palestine and Syria.

It is quite difficult to identify juvenile specimens, which were at times even treated as good species. *Ocypode rhombea* described from

the Indo-West Pacific by Fabricius (1798) has turned out to be conspecific with *O. ceratophthalma* as shown by a thorough examination of the type specimen. On the other hand *O. rhombea* reported from the western Atlantic by H. Milne Edwards (1837) and White (1847) has turned out to be conspecific with *O. quadrata*. *O. brevicornis* (Dana, 1852: 326) and *O. brevicornis* var. *longicornuta* (Dana, 1852: 327) were synonymised with *O. ceratophthalma* by Kingsley (1880), however, it has turned out that *Ocypode brevicornis* H. Milne Edwards (1837) is not synonymous with *O. ceratophthalma*, but a valid species distributed in Oman, India and Sri Lanka. *Ocypode macleayana* Hess, 1865 from Sydney was synonymised with *O. ceratophthalma* by De Man (1888c: 351), who had in fact examined Hess' type specimen, and could thus confirm his earlier suggestion (De Man 1887: 696). The reasons for making *Ocypode urvillei* Guerin a junior synonym of *O. ceratophthalma* were explained in detail by Sakai, K. & Türkay (1976: 86). All this shows that access to type specimens is absolutely necessary for sound decisions in *Ocypode*, because juveniles differ so much from adults.

O. ceratophthalma is distributed widely in the Indo-Pacific and although it is easily recognisable by the morphology of the stridulating ridge, the male Go1, and the pointed smaller cheliped, it has nevertheless at sometime been confused with almost all other species of *Ocypode*. This has probably been caused by the uncritical use of growth dependent characters. Tu *et al.* (1923: 819) described *Ocypode* sp., calling it Sandkrabbe (= Sunagani) and indicating its characters as follows; the anterolateral angles of the carapace are sharply pointed; the eyestalks are prolonged, so that the species is most probably determined as *O. ceratophthalma*. Its reference is shown as Zoological Nomenclature (A complete Dictionary of Zoological Terms), however it should be shown as Doubutsugaku-Daijiten [= Zoological Encyclopedia].

Ng *et al.* (2008: 240) questionably included *Ocypode longicornuta* Dana, 1852, from Tonga and Singapore, (originally described as *Ocypode brevicornis* var. *longicornuta* Dana, 1852), as a possible valid species, however *O. brevicornis* var. *longicornuta* had already been synonymised with *O. ceratophthalma* by Kingsley (1880),

and after having examined the figure by Dana, we fully agree with this conclusion. Thus, we treat *Ocypode brevicornis* var. *longicornuta* as a junior synonym of *O. ceratophthalma*.

Ocypode convexa Quoy & Gaimard, 1824

(Figs 2A, 11, 33)

Ocypode convexa Quoy & Gaimard, 1824: 525, pl. 77, fig. 2.

Ocypode bombée — H. Milne Edwards, 1837: 49.

Ocypoda convexus — Kingsley, 1880: 185.

Ocypoda Kuhlii — Miers, 1882: 348, pl. 17, fig. 8-8a [in part].

Ocypoda kuhlii — Miers, 1884: 237 [in part].

Ocypode pygoides Ortmann, 1894a: 766, pl. 23, fig. 19; Montgomery, 1931: 451, pl. 25, fig. 1, pl. 27, fig. 5; Serène, 1968: 97.

Ocypoda pygoides — Ortmann, 1897: 364; Balss, 1935: 140.

Ocypode convexa — George & Knott, 1965: 19, fig. 2D; Allender, 1969: 61, tabs 1-3; Davie, 2002: 357; Ng, Guinot & Davie, 2008: 240.

? *Ocypode convexus* — Serène, 1968: 97.

Material examined. Australia. Western Australia: No exact locality, female (NHM-1931.7.24.131); — *ibid.*, male (ZSM), Hamburger Südwest Australien Expedition; — Wooded I., Houtman Rock, male, 2 females (NHM-1931.7.24.128-9); — Dongara, male (ZMH-11519), 17.vii.1905, W. Michaelsen, Hamburger Südwest-Australien-Expedition; — Barrow Island, 2 males [35.8×43.9, 33.4×40.8 mm], female [33.7×42.0 mm] (ZMH-11339) [det. Balss, 1935 as *O. pygoides*], 1905; — Exmouth Gulf, Carnarvon, exterior part of the Gulf, southern and near low tidal line, male (AMS-P19421), 1972, N. Coleman; — 16 km of North Ningaloo (22°34.63'S, 113°39.66'E), near point Cloates, 3 males (SMF-7609 [ex. WAM]); — Bernier Island, female (AMS-P14964), 25.vii.1959, A. Douglas; — Dorre Island, Quoin Bluff, male (AMS-P14963), 19.vii.1959, N. McLaughlin; — Dorre Island, Shark Bay, female (NHM-1960.10.6.1-2) [det. George & Knott, 1965: 19 as *C. convexa*]; — Harrocks (28°22.77'S, 114°25.72'E), North of Geraldton, beach, male (SMF-10332), 17.x.1975, G. Hartmann & G. Hartmann-Schröder; — Geraldton, male (AMS-P14965), x.1929, A. A. Livingstone; — Cottesloe Beach, female (AMS-P4036); — Cottesloe (= Gotteslow) Beach, male (NHM-1931.7. 24.130).

Diagnosis. Large-sized species. Eyestalks not prolonged distally beyond cornea. Exorbital angles triangular and directed anteriorly. Palm of larger cheliped broadened and covered with coarse tubercles on anterior surface, bearing irregularly arranged spiniform tubercles on dorsal margin and regularly arranged distinct

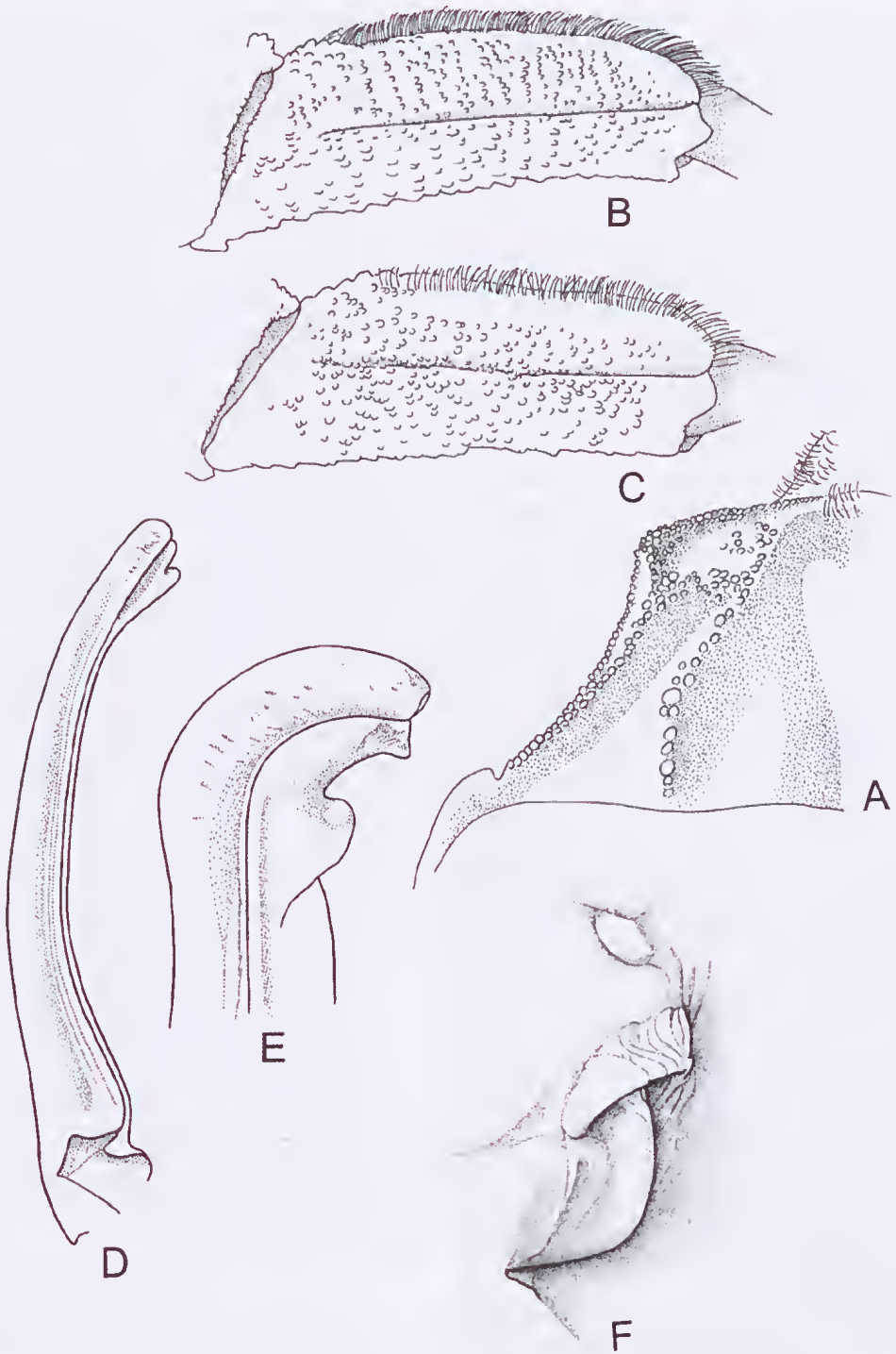


FIG. 11. *Ocypode convexa*: A, P1 thoracic sternite; B, C, P2-3 propodi; D, E, Go1; F, female operculum.

spiniform tubercles on ventral margin. Smaller cheliped tapering to pointed distal end. Stridulating ridge composed of 19–24 tubercles. P2–3 propodi setose on or along dorsal margin on anterior surface. Go1 narrowing distally, and slightly curved laterally at distal end, bearing distinct palp. Lateral rim of female genital opening located anterior to operculum.

Description. Carapace (Fig. 33) slightly wider than long, and covered dorsally with densely arranged tubercles, becoming larger and sparsely distributed towards anterolateral sides. Lateral half of orbital margin regularly concave. Ex-orbital angle triangular and protruding anteriorly. Lateral margins of carapace convex from tip of ex-orbital angle in anterior third of carapace, and then directed inward in posterior two-thirds, carapace broadest at anterior third. Pterygostomial region tuberculate all over its surface. P1 thoracic sternite (Fig. 11A) hemmed with distinct tuberculate carinae except on posterior margin, bearing tuberculate humps anteriorly, and transverse carina with tubercles in anterior third. Palm of larger cheliped slightly longer than broad, and coarsely tuberculate on outer surface, bearing irregularly arranged spiniform tubercles on dorsal margin and regularly arranged distinct spiniform tubercles on ventral margin. Both chelipeds covered with irregularly arranged tubercles of various sizes on anterior surface. Stridulating ridge (Fig. 2A) composed of 19–24 tubercles. P2 propodus (Fig. 11B) with setae on dorsal margin, and P3 propodus (Fig. 11C) with a row of setae along dorsal margin on anterior surface, but P4–5 propodi naked. Go1 (Fig. 12D–E) three-sided proximally, narrowing distally, and curved laterally in distal part, bearing a distinctly bulging palp protruding distolaterally near distal end. Lateral rim of genital opening horn-shaped and located anterior to operculum. Operculum of female genital opening (Fig. 11F) slightly convex mesially and evenly rounded, and terminated at distal end with a strong fold over distolateral rim.

Distribution. Entire coast of Western Australia, from about Broome in the north to south of Perth. Type locality: Dirk Hartog Island, Shark Bay, Western Australia.

Remarks. The present species was generally known as *Ocypode pygoides* Ortmann, 1894,

instead of *Ocypode convexa* Quoy & Gaimard, 1824, because H. Milne Edwards (1837: 49) suppressed *O. convexa* due to uncertainty of the original description and figures. Miers (1882) referred to *O. convexa* as *incertae sedis* and named his material from Shark Bay, Western Australia, Thursday Island, Torres Strait, and Indonesia as *O. kuhlii*. Later Ortmann (1894: 766) introduced *O. pygoides* without paying any attention to Quoy & Gaimard's earlier work, but shortly after his description, Ortmann (1897: 361) suggested that *O. pygoides* might be identical with *O. convexa*. Much later George & Knott (1965) finally showed that *O. pygoides* is identical with *O. convexa* and therefore a synonym of this last species. Since then this usage has been stabilised (Davie 2002). After having re-examined and compared all the species of *Ocypode*, we confirm the synonymies and the current usage. This species is, as can be seen from the figures, delimited from all others by the pattern of setae on the anterior surface of the P2–3 propodi, the shapes of the carapace and the chela of the larger cheliped, as well as the morphologies of the stridulating ridge, the Go1, and the female genital opening.

Ocypode cordimanus Latreille, 1818

(Figs 12, 34)

Ocypode cordimana Latreille, 1818: 198, figs 1–3, 11; Desmarest, 1825: 121; Lucas, 1840: 58; Stimpson, 1858: 100; Hilgendorf, 1869: 82; A. Milne-Edwards, 1873: 271 [in part]; Hoffmann, 1874: 13; Kossmann, 1877: 55; Hilgendorf, 1879: 803; Neumann, 1878: 26; Miers, 1879: 489 [in part]; Miers, 1880: 308; Richters, 1880: 155; De Man, 1881: 248; Lenz & Richters, 1881: 423; Haswell, 1882: 95; Miers, 1882: 387, pl. 17, fig. 9; Miers, 1884: 542, 573; De Man, 1887c: 108; 1888b: 352; Ozório, 1888: 243; Pfeffer, 1889: 30 [in part]; Henderson, 1893: 387; Matsuura, 1894: 55; Alcock & Anderson, 1894: 202; Ortmann, 1894a: 761, 764, pl. 23, fig. 16; Zehntner, 1894: 178; De Man, 1895: 572; Ortmann, 1897: 359, 362; Alcock, 1900: 349; Lanchester, 1900b: 752; Lanchester, 1901: 548; Borradaile, 1901: 67, 96; De Man, 1902: 438; Nobili, 1905a: 494; Nobili, 1906b: 310; Stimpson, 1907: 110, pl. 15, fig. 2; Borradaile, 1907: 65; Borradaile, 1910: 408; Lenz, in Voeltzkow, 1910: 558; Stebbing, 1910: 326; Lenz, 1912: 6; Urita, 1917: 72, fig.; Parisi, 1918: 96; Tesch, 1918: 35; Balss, 1922: 142; Maki & Tsuchiya, 1923: 204; Gravelly, 1927: 148; Gordon, 1934: 9; Sakai, T., 1934: 319; Takahashi, 1932: 329; 1934: 74; 1935: 78; Estampador, 1937:

- 542; Tweedie, 1937: 141; Chopra & Das, 1937: 420, fig. 18; Shen, 1937b: 184; Miyake, 1939: 221; Sakai, T., 1939: 613, pl. 104, fig. 1; Sakai, T., 1940: 32; Shen, 1940: 91; Ward, 1942: 103; Sakai, T. & Nakazawa, 1947: 664, fig. 1916; Lin, 1949: 26; Barnard, 1950: 84, fig. 17a–b; Tweedie, 1950a: 126; 1950b: 323; Pillai, 1951: 27; Holthuis, 1953: 28; Raja Bai Naidu, 1954: 95–100, figs 18–30; Sakai, T., 1955: 111; Sakai, T., 1956: 53; Chhapgar, 1957: 45, pl. 13d–f; Stephenson *et al.*, 1958: 269; Guinot-Dumortier & Dumortier, 1960: 136; Sarojini, 1962: 191, tab. 1, fig. 1; Sankarankutty, 1961: 125; Shen & Liu, 1963: 141; Hashmi, 1963: 240; Inaba, 1963: 170; 1988: 102; Miyake, 1963: 69; George & Knott, 1965: 16, fig. 2A; Sakai, T., 1965: 188, pl. 90, fig. 2; McNeill, 1968: 85; Chakrabati, 1972: 129; Horch, 1975: 193; Sakai, T., 1976: 599, text-fig. 327a, pl. 206, fig. 3; Paulraj, Mullainadhan & Ravindranath, 1982: 115–128, tabs 2–7; Yang, 1986: 153; George, 1982: 187, pl. 1; Dai & Yang, 1991: 455, text-fig. 230, pl. 58 (3); Gamo & Kosakai, 1991: 27, 30, fig. 1; Huang *et al.*, 1992: 142, fig. 1, pl. 1A, tab. 1; Poupin, 1996: 73; Yu *et al.*, 1996: 58, fig. 58; Jeng, M.-S., 1997: 88, fig.; Ng *et al.*, 2001: 36; Bruyn, 2002: 29–30, figs 1, 3, 5, 7; Marumura, & Kosaka, 2003: 69; Ng *et al.*, 2008: 240.
- Ocypoda cordimana* – Sakai, T. & Nakazawa, 1947: 664, fig. 1916.
- Ocypode cordimanus* – Michel, 1964: 11; Crosnier, 1965: 96, figs 154, 162, 171–172, pl. 8, fig. 3; Pretzmann, 1968: 5; Serène, 1968: 97; Sakai, K. & Türkay, 1977a: 478; Sakai, K. & Türkay, 1977b: 97; Dai *et al.*, 1986: 418, pl. 58, fig. 3, text-fig. 230–4; Wang & Liu, 1993: 63, figs 51, 52; Türkay, Sakai & Apcl, 1996: 102, figs 1–3; Davie *et al.*, 1998: 19, fig.; Davie, 2002: 357; Poupin *et al.*, 2011: 18.
- ? *Ocypode cordimana* MacLeay, 1838: 64; Kraus, 1843: 41; White, 1847: 34; Herklots, 1851: 23; Laurie, 1915: 416.
- Ocypoda ceratophthalma* – Pesta, 1911: 55.
- Ocypode albicans* – Estampador, 1937: 542.
- Ocypoda laevis* – Sandler, 1923: 22.
- Ocypode aegyptiaca* – Balss, 1924: 14 [in part].
- Cancer roberti* Curtiss, 1938: 175; Ng, Eldredge & Evenhuis, 2011: 45, 52.
- Ocypode sinensis* Dai *et al.*, 1985: 372, 377, figs 8–14 [in Chinese]; Dai *et al.*, 1986: 418; Dai & Yang, 1991: 456, fig. 230A; Huang *et al.*, 1998: 943, tab. 1; Wang *et al.*, 1998: 64, figs 51, 52; Ng *et al.*, 2001: 36; Yodo *et al.*, 2006: 2, 4, 5, figs 2, 3, 6; Mano *et al.*, 2008: 2, 5, 6, 7, 8, tabs 1–2, figs 2–8; Seike & Nara, 2008: 593, tabs 1–2.
- Material examined.** Locality unknown, male [30.2×3.7 mm], female [27.9×32.8 mm] (SMF-1957); 4 males [12.9×15.1–15.3×17.3 mm] (SMF-36200), T. Sakai; male [25.4×28.9 mm] (SMF-36202); male [17.7×19.7 mm], 2 females [19.0×22.7, 19.6×23.4 mm] (SMF-36203); male [12.8×15.2 mm] (SMF-36218). **China.** Fujian Province: Xiamen (= Amoy), male (MNHN), 1925, C.F. Wang; 15 males, 16 females (RMNH-221) [described by De Man, 1881]. Taiwan (= Formosa): no further data, female (ZMH-2801); – Lan yu (= Koto-syo) Island, 1 juv. male (USNM-73263) [det. as *O. africana*], 1933, T. Kano; – South-coast, Pingdong County, Kenting National Park, male [21.5×26.3 mm], 2 females [20.9×26.0, 19.5×23.6 mm] (SMF-24955) [det. as *O. sinensis*], 31.v.1997, P.K.L. Ng.; – Hainan Province: Hainan Island, male [32.5×35.8 mm] (SMF-36192); male [18.8×23.5 mm] (SMF-36194); male [18.8×23.5 mm] (BNHM-58-0024) [det. Chen as *O. sinensis*]. – Xisha Is, male [31.8×35.0 mm] (SMF-13233), 13.vi.1975; male [20.5×25.0 mm] (SMF-36193). **Japan.** Kanagawa Prefecture: Yokohama, male (MZT1112); – Kochi Prefecture: Tosa, female [17.7×21.7 mm] (SMF-36201), coll. T. Sakai. – Kagoshima Prefecture: Beach north of Tarumizu at river mouth of Honjou-gawa in the northern part of port (31°29.85'N, 130°41.98'E), female [9.8×11.3 mm] (SMF-16607), 2.xi.1979, H. & M. Türkay; – Ryukyu Islands: Yoron Island, north of Okinawa, 3 males (ZMH-2832); 2 males [7.8×9.6, 15.1×17.6 mm]; female [15.0×18.6 mm] (SMF-6745); – *ibid.*, male [8.4×10.1 mm] (SMF-36219), 3.xi.1966, K. Sakai; – Okinawa, Onna Coast, male [15.9×18.3 mm] (SMF-36213), 23.viii.1992, W. Shimabukuro; – Okinawa, 2 juvs. (USNM-171693); – Ishigaki I., female [11.1×13.2 mm] (SMF-7729), T. Sakai; – Ogasawara-Gunto (= Bonin Is.): Chichi-jima, male [20.1×24.7 mm] (SMF-6742), 25.vii.1971, H. Suzuki; – *ibid.*, male [16.5×19.5 mm] (SMF-6743). **Caroline Islands.** Ruck (= Chuuk) Island, 3 males, 2 females (MCM-1610) [described by Paris, 1917]. **W-Carolines.** Fais, Hanseatische Südsee-Expedition, male [21.4×24.4 mm] (SMF-1954) [det. Sandler, 1923 as *O. laevis*], 22–29.ix.1909, E. Wolf. **Palau Islands.** female [22.0×28.7 mm] (ZMG-120) [Capt. Pöhl vend. 1889]. **Philippines.** No further data, male [28.2×30.7 mm] (SMF-13556); – Mariveles near Manila or Guindulman, Luzon, 2 males [17.8×21.6, 21.5×25.1 mm] (ZMG-119), 1876, C. Semper; – General MacArthur (11°15'N, 125°32.5'E), E-Samar, female [19.1×23.9 mm] (SMF-9998), viii. 1978, W. Lobin; – Cebu, E Mactan, Maribago, NW-coast of Hilutangan channels (10°17'N, 124°00'E), female [27.9×31.0 mm] (SMF-19744), A. Schreiber. **Mariana Islands.** Wing Beach, Saipan, N-Mariana, female [6.1×7.3 mm] (SMF-19497), 11.viii.1990, A. Allspach. **Vanuatu.** Prov. Tafea, Aniwa (= Jmmer) (19°13.84'S, 169°36.8'E), East of Tanna, male [30.2×32.5 mm] (SMF-1949) [det. Sandler, 1923 as *O. laevis*], Hanseatische Südsee Expedition, E. Wolf. **New Caledonia.** Sandy beach, female [18.9×22.4 mm] (SMF-36215). **Solomon Is.** Sikaiana (= Stewart Island), male [27.2×30.6 mm] (SMF-1953) [det. Sandler, 1923 as *O. laevis*], Hanseatische Südsee-Expedition, E. Wolf. **Papua New Guinea.** Tarawai Is. (= Bertrand. Is.) (03°12.9'S, 143°15.56'E), male [Neotype of *Ocypode cordimanus*, designated by K. Sakai & M. Türkay, 1977] [33.9×37.2 mm] (SMF-1948) [det. Sandler, 1923 as *O. laevis*]. **Hanseatische Südsee Expedition, E. Wolf.** **Australia.** Queensland: Ellice

- Beach, north of Cairns, male [12.0×13.8 mm] (SMF-16564), 4.vi.1980, M. Türkay; — Rainbow Beach (25°54.28'S, 153°5.74'E), male [13.5×16.2 mm], 5 juvs. [7.0×7.9, 7.7×9.3, 6.5×7.4, 7.1×8.7, 7.0×8.6 mm] (SMF-9897), A. Türkay; 4 males [17.5×20.7–12.5×15.8 mm]; 4 juvs. (SMF-36214); — North Stradbroke I., N coast (27° 25.56'S, 153° 31.58'E), sand flat and sandy beach, 4 males [17.5×20.7–12.5×15.8 mm], 4 juvs. (SMF-36214), 30.ix.1999, M. Türkay; — *ibid.*, northern part, eastern beach (27°26.64'S, 153°32.23'E), 2 males [24.0×27.9, 10.9×12.8 mm], female [17.6×22.0 mm], 5 juvs. (SMF-36217), 29.ix.1999, M. Türkay; — *ibid.*, east coast, central part of island, sandy beach (27°31.33'S, 153°30.13'E), male [13.7×16.6 mm], 2 females [15.0×19.3, 9.0×11.3 mm] (SMF-36216), 30.ix.1999, M. Türkay; — Gold Coast, Southport, ocean beach, sand dunes, 2 males [21.7×24.1, 19.1×23.0 mm], 3 females [20.2×24.3, 17.9×21.0, 14.8×18.2 mm] (SMF-16565), 30.v.1980, M. Türkay; — New South Wales: Sydney, Port Jackson, male [16.9×19.6 mm], female [17.6×21.6 mm] (SMF-3607), May 1951, S. Kellner; — Sydney, Long Reef (33°44'S, 151°19'E), male, female, 1 juv. (SMF-38306), 24.v.1980, M. Türkay. **Malaysia.** Penang, Muka Head Beach (05°28.3'N, 100°11.2'E), male [22.7×27.0 mm] (ZRCNUS-1987-919) [det. as *O. sinensis*], 13.vi.1987, P.K.L. Ng & S. Harminto. **Indonesia.** Riau Archipelago, Pulau Bintan, Tanjung Tondang (01°10.8'N, 104°18.9'E), male [18.0×20.3 mm] (ZRCNUS-1999-0291) [det. as *O. sinensis*], vii.1995, P. K. L. Ng *et al.* — Sumatera: West Sumatera, Sasak, Sandy Beach, male [19.5×23.9 mm] (SMF-36259), 9.ii.1994, T. Ziegler; — Jaga Utara Is. (= Noordwachter Eiland or Pulo Sebiri) (5°12.0'S, 106°27.0'E), South-East of Lampung, Sumatera, male [30.9×33.2 mm] (ZMG-118), J. Brock; — Lesser Sunda Isles: Bali, Sanus, beach, male [16.0×18.5 mm] (SMF-17298), 29.vii.1979, R. König; — Moluccas: Ternate, 2 females [18.3×24.4, 24.7×29.5 mm] (SMF-1956), Kükenthal; — Halmahera, Tobelo, female [27.8×31.2 mm] (SMF-1952), Kükenthal; — Aru Islands, Trangan (= Terangan), Ngaigoeli (= Ngaigulu) coast (6°37.37'S, 134°5.51'E), male [26.5×29.7 mm] (SMF-1951), 6.ii.1908, H. Merton. **Sri Lanka.** Bentota River, 2 males [8.8×7.8, 13.3×10.9 mm] (SMF-5429), 16.i.1914, J. Mastbaum; — Colombo, beach, female [7.0×9.1 mm] (SMF-6738), 12.i.1914, J. Mastbaum; — Lavinia (6°49.87'N, 79°51.73'E), 5 males [16.1×19.0, 14.9×17.8, 15.1×17.9, 15.8×17.7, 12.9×15.4 mm], 2 juvs. [8.8×8.0, 7.5×9.0 mm], male, damaged [15.3×18.6 mm] (SMF-6744), 29.iii.1974, Z. Števičić; — Kuchchaveli (8°49.09'N, 81°6.15'E), 20 km North-west of Trincomalee, 4 males [14.2×17.4, 15.7×17.9, 18.7×21.8, 19.9×23.7 mm]; 3 females [20.2× 23.1, 21.1×26.0, 21.5×26.8 mm] (SMF-5421), 9-10.xi.1962, Brinck, Anderson & Cederholm, Lund Univ. Ceylon Expedition; — Moragalla, c. 50 km South of Colombo, beach of Wormels Reef Hotel, female [18.6×22.6 mm] (SMF-18265), 5-13.v.1989, H.G. Müller. **India.** Kerala Province: Badagara, Azhitala, Murat River (11°33.4'N, 75°35.7'E), female [21.0×25.1 mm] (SMF-36255), 25.vii.1984, W. H. Bee; — *ibid.*, female [13.9×15.8 mm] (SMF-36256), 26.vi.1984, W. H. Bee. **Chagos Archipelago.** Diego Garcia, male [32.7×34.7 mm], female [31.6×35.2 mm] (SMF-1955), 24.ii.1899. **Maldives.** Kuramathi, Rasdhoo Atoll, Alifu (Ari) Atoll, at night, farther away from water line, burrowing in sand, male [39.0×42.8 mm] (SMF-24952), 15.vii.1999, D. Kovac. **Seychelles.** Aldabra Atoll, male [38.0×41.6 mm] (SMF-9983), iii. 1979, M. Vannini; — La Digue (4°20'S, 55°50'E), Choppy's bungalow, beach, male [16.0×18.5 mm] (SMF-12910), 7.v.1979, M. Ackermann; — La Digue (4°20'S, 55°50'E), forest with ground vegetation, 2 males [23.3×25.7, 34.7×37.5 mm] (SMF-12911), 8.v.1979, M. Ackermann; female [21.3×24.6 mm]; — La Digue (4°20'S, 55°50'E), open meadow with trees, 2 females [36.7×40.6, 39.5×43.6 mm] (SMF-12946), 16.v.1979, M. Ackermann. **Mauritius.** Round Island (19°52.84'S, 57°39.98'E) female (SMF-38305), 9.iii.1979, Blaich. **Réunion.** La Saline-les-Bains, beach, from burrows, 2 males [26.8×29.9, 28.8×31.2 mm], female [30.2×34.6 mm] (SMF-18266), 28-30.i.1989, H.G. Müller; — Beach at Caphomard (21°2.0'S, 55°13.25'E), male [21.5×23.1 mm], 3 females [29.3×34.1, 22.5×26.1, 21.5×25.3 mm] (SMF-18267), 30.i.1989, H.G. Müller; — N l'Etang Saleles-Bains, Pnte. Des Avirons (21°14.21'S, 55°18.39'E), beach, from burrows, 3 males [19.5×22.4–23.2×25.7 mm], 4 females [21.2×25.7–29.7×33.5 mm], 2 specimens broken on the lateral margin (SMF-18268), 31.i.1989, H.G. Müller; — Beach at St. Paul, male [28.6×31.4 mm], female [29.7×33.2 mm] (SMF-18269), 1.ii.1989, H.G. Müller; — Harbour of St Gilles les Bains, beach, 4 males [24.0×27.4, 11.3×12.5, 8.1×10.0 mm], female [15.9×18.7 mm] (SMF-18270), 3.ii.1989, H.G. Müller. **Madagascar.** No further data, 3 males [10.5×12.1, 24.9×27.5, 26.3×28.4 mm] (SMF-1950), Ebenau. **Oman.** Khawr Al-Milh, peninsula Barr Al-Hikman, Gulf of Masirah (20°23.0'N, 58°17.0'E), male [20.1×24.1 mm] (SMF-24528), 31.v.1995, D. Clayton; — Maskat, Quam W. Kaskat (23°37.00'N, 58°30.00'E), female [19.7×16.7 mm] (SMF-24529), 31.v.1995, D. Clayton. **Kenya.** Kilifi Creek, between Mombasa & Malindi, female [19.5×23.6 mm] (SMF-18263), W. Baumeister. **Rep. Djibouti.** Djibouti, Plage du Triton, 1 juv. male [8.3×9.6 mm] (SMF-16566), 18.iii.1987, Allspach, Fischer & Türkay. **Yemen.** Aden, male (MCSNM 2158); — Mukalla, female (NHML-1894.10.31.13). **Somalia.** Sar Uanle, 20 km South of Kismayu (= Chisimaio), male [18.7×22.5 mm], female [24.0×27.7 mm] (SMF-9982), vii.1973, M. Vannini. **Eritrea.** Massaua, 2 juvs. (SMF-6749), xii.1965, K.E. Linsenmair; — *ibid.*, female (MZUT-1102), 1903, P. Clivio. **Saudi Arabia.** Naman Island, male (NHMW), 8.x.1896, S.M.S. 'Pola'; male (NHMW), 30.x.1896. **Egypt.** Gulf of Aqaba, Dhahab, 2 males (RMNH-29238), 28.iii.1973, L.B. Holthuis & C. Lewinsohn.

Diagnosis. Middle-sized species. Eyestalks not prolonged distally beyond cornea. Exorbital angles broadly triangular and distinctly protruding anteriorly. Palm of larger cheliped

lacking stridulating ridge. Smaller cheliped narrowing to pointed distal end. P2 propodus setose on dorsal half of anterior surface, bearing a median row of setae. P3 propodus with setae along dorsal margin. Go1 curved laterally over distal part, bearing a distinct protruding palp directed distally. Operculum of female genital opening rounded distally, and protruding mesially. Lateral rim usually distinct distally and then extended mesially.

Description. Carapace (Fig. 34) slightly wider than long, and covered densely with fine tubercles, becoming larger toward lateral sides. Lateral half of orbital margin distinctly concave. Exorbital angles broadly triangular and distinctly protruding anteriorly. Lateral margins of carapace convex from tip of exorbital angle in anterior third of carapace, and then directed inwards in posterior two-thirds, carapace broadest at anterior third. Pterygostomial region distinctly tuberculate except along lateral sides of buccal cavern. P1 thoracic sternite (Fig. 12A) hemmed anteriorly with tuberculate carina and laterally with carina, bearing distinct tuberculate humps anteriorly. Palm of larger cheliped broad, covered densely with fine and coarse tubercles on anterior surface, and distinctly denticulate on ventral margin. Stridulating ridge absent. Smaller cheliped narrowing to pointed distal end. P2 propodus (Fig. 12B) with setae along dorsal margin and transverse rows of setae on dorsal half of anterior surface, bearing a median row of setae. P3 propodus (Fig. 12C) with thick setae along dorsal margin. P4-5 propodi naked. Go1 (Fig. 12D-E) three-sided proximally, narrowing distally, curved laterally in distal part, bearing distinct protruding palp directed distally near distal end. Operculum of female genital opening (Fig. 12F) elongate; rounded distal portion protruding mesially like a bean. Lateral rim usually distinct distally and then extended mesially.

Juvenile specimens: In a small specimen from Okinawa (6.5×7.5 mm, USNM-171693) exorbital angles acutely triangular and distinctly protruding anteriorly. Lateral margins of carapace directed straight downwards from base of exorbital angle in anterior third of carapace; then directed mesially in posterior two-thirds. Palm of larger cheliped broad, finely tuber-

culate on anterior surface; distinctly and regularly serrated on ventral margin. P2 propodus with setae on dorsal margin, bearing median row of longer setae. P3 propodus with setae only present on dorsal margin.

Distribution. From the Western Indian Ocean including the Red Sea and the east coast of Africa throughout the Indo-West Pacific to French Polynesia. Original type locality: 'Indes orientales'; locality of neotype: Tarawai I. (= Bertrand I.) (03°12.9'S, 143°15.56'E) [Papua New Guinea].

Remarks. The exact identity of this widely distributed and common species, remained uncertain for many years, because its original description was based upon more than one species. However, the selection of a neotype by Sakai, K. & Türkay (1977) made it possible to fix its identity. This species is widely distributed in the Indo-Pacific Ocean, although it has only been collected sporadically in the Red Sea.

Urita (1917) reported the present species from Kagoshima under the Japanese name of 'Mizugani', which is now called 'Minami-sunagani', at the same time stating that the larger cheliped bears no stridulating ridge.

Dai *et al.* (1985) established *Ocypode sinensis* based on specimens from Xisha Island, Jinyindao, southern China, whose distribution has later been extended to India, Malaysia Peninsula, the Philippines, Taiwan, and Japan, and distinguished the species *O. sinensis* from *O. cordimanus* which co-occurs in almost the same region, using various external characters as well as the structure of the gastric mill. Later Huang *et al.* (1998: 949, 951, Table 1) listed 11 morphological differences between *O. sinensis* and *O. cordimanus*. These points of difference are evaluated and discussed in the following.

O. sinensis is smaller, stated to reach a smaller maximum size of c. 20.0 mm carapace width in an adult male, while *O. cordimanus* is relatively larger, and an adult male reaches c. 30.0 mm carapace width. However, such a difference in size of the carapace cannot be used on its own as a major character for delimiting species, and even if it were to be true, it is useless for identifying any specimens less than 20 mm carapace width. Also juvenile and smaller specimens tend to take somewhat different morphology

from adults, and this could explain the differences observed by others.

In *O. sineusis* the carapace is said to be weakly arched dorsally, while in *O. cordimanaus* the carapace is strongly arched dorsally. However, the small specimens determined as *O. sineusis* from Hainan Island, China, a male (18.0×20.3 mm, ZRCNUS-1999-0291) and a male (18.8×23.5 mm, BNHM-58-0024), have their carapaces arched just as strongly as larger specimens of *O. cordimanaus*, so it is apparent this character is not consistent.

Huang *et al.* (1998: 949) described 'the median part of the suborbital margin is entire, gently convex, without any trace of a cleft (vs. interrupted with a distinct cleft in *O. cordimanaus*).' However, *O. cordimanaus* is not always characterised as 'interrupted with a distinct cleft, because a male specimen (15.3×18.6 mm, SMF-6744) determined as *O. cordimanaus*, has the median part of the suborbital margin lacking a distinct cleft. In two male specimens (12.6×15.2 mm, ZRC-1999-0291, 15.8×17.7 mm, SMF-6744) from Indonesia determined as *O. cordimanaus*, the median part of the suborbital margin is entire and regularly denticulate as in *O. sineusis*, while in a male specimen (22.7×27.0 mm, ZRC-1987.919) from Malaysia and another male specimen (18.8×23.5 mm, BNHM-58-0024) from Hainan which were both determined as *O. sineusis* by H. Chen, the median part of the suborbital margin is not entire, but shallowly concave as in *O. cordimanaus*, which suggests that these two males might better be determined as *O. cordimanaus*, considering their comparatively larger carapace width, so this character is also clearly difficult to use to discriminate between the two species. The same applies to the gap between the supra- and suborbital margins.

In *O. siuensis*, the urocardiac ossicle has the lateral margins of the peduncle weakly convex, tooth plate relatively smaller, zygo-cardiac ossicle relatively shorter, and premolar longer and more distinctly produced, with about 16 comb-like teeth. This compares with *O. cordimanaus* that has the urocardiac ossicle with the lateral margins of the peduncle distinctly convex, tooth plate relatively larger, zygo-cardiac ossicle relatively longer, premolar shorter and less

distinctly produced, and with about 17 comb-like teeth. We consider, however, those characters to be sufficiently variable that they are not useful for separating the species.

The differences that have been listed between the two species in the morphology of the third maxillipeds, their colour, the immovable finger of the male chela, the movable finger of the minor chela, the anterior thoracic sternum, and the male abdomen, are all variable in our opinion, and cannot be used to reliably distinguish the two species.

In our material some of the characters mentioned by Huang *et al.* (1998) appear to be randomly distributed among the size classes. Also because the differences in the Go1 observed between them are not sufficient to separate one species from the other, and they stated themselves 'the differences observed in the Go1 are difficult to use (for differentiation of two species).' They also remarked that 'Specimens of "*O. Cordimana*" reported and figured by T. Sakai (1976) from Japan are probably *O. siuensis* as well. The figure provided (T. Sakai, 1976, pl. 206, fig. 4) agrees very well with what is defined here as *O. sineusis*. In addition, T. Sakai (1976: 599) noted that the specimens of "*O. cordimana*" from Japan measure only up to 25.5 mm carapace width. This small adult size also strongly suggests that the Japanese specimens are *O. siuensis*.' As already discussed however, it is difficult to separate one species from the other based on their size. Smaller specimens often differ in some external characters from larger specimens of the same species (for example, different size-classes of *O. pallidula* have in the past been regarded as two different species). We consider smaller-sized specimens of *O. cordimanaus* from Japan are not distinguishable from larger-sized *O. cordimanaus* from the continent, though some external differences are observed between the two groups. We here conclude that *O. siuensis* is merely a smaller sized but conspecific form of *O. cordimanaus* that cannot be separated at species level by morphological evidence.

The present species has been extensively dealt with in the literature under the name *Ocyropode cordimana*. However, as 'manus' is a feminine Latin word, and the generic name

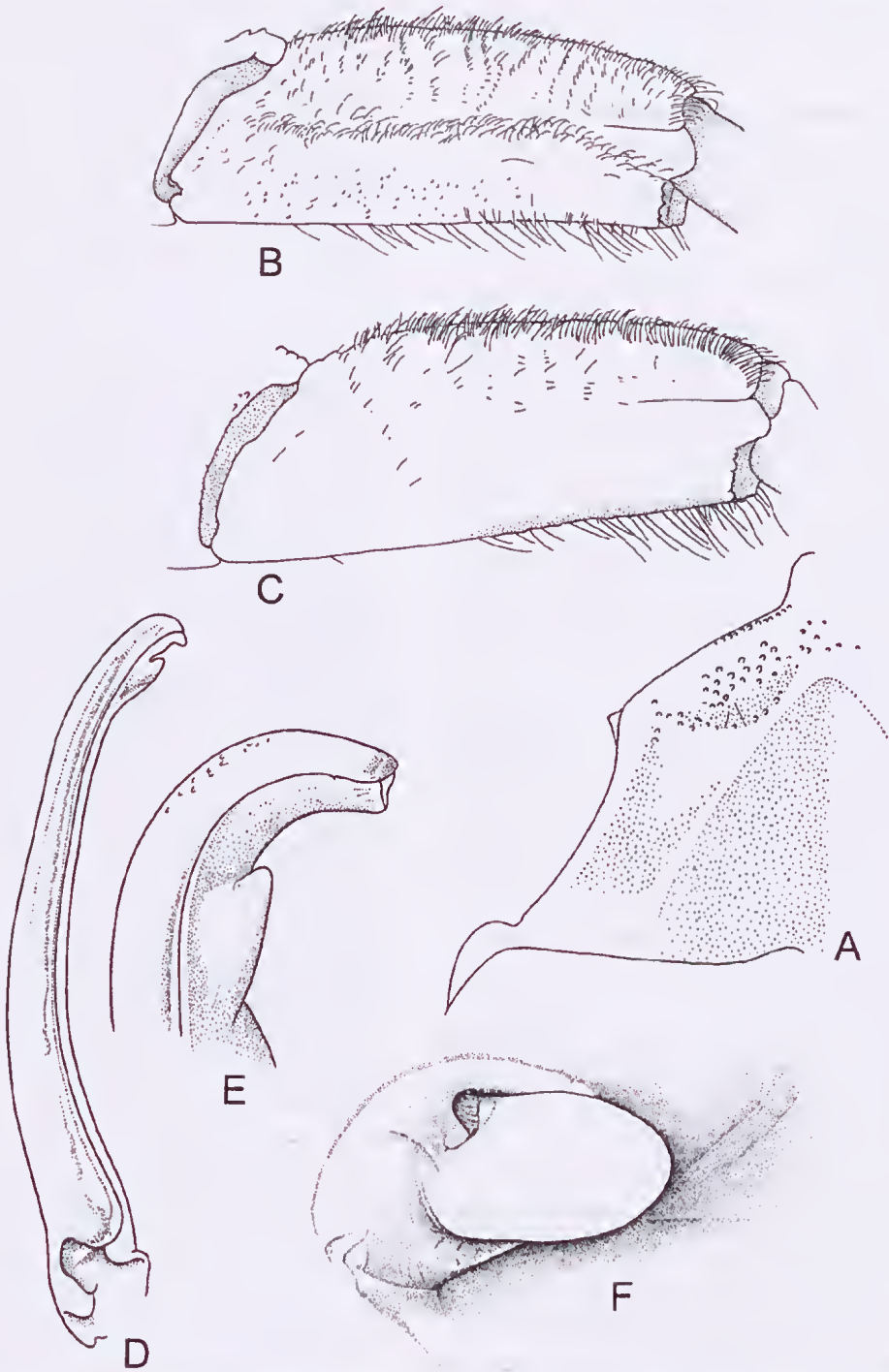


FIG. 12. *Ocypode cordimanus*: A, P1 thoracic sternite; B, C, P2-3 propodi; D, E, Go1; F, female operculum.

Ocypode is also feminine, it should rather be named *Ocypode cordimanus* than *O. cordimana*.

Ocypode cursor Linnaeus, 1758

(Figs 2B, 13, 35)

Cancer cursor Linnaeus, 1758: 625 [in part] [*sensu stricto*]; Müller, 1775: 1098 [in part]; Herbst, 1782: 74 [in part].

Cancer eques Aubert de la Chesnaye des Bois, 1759: 416, 417.

Cancer Cursor – Linnaeus, 1767: 1038 [in part].

Cancer anomalus Hasselquist, 1762: 474.

Ocypoda ippeus Olivier, 1804a: 235, footnote; 1804b: 52, footnote; Ozório (miss-spelling), 1887: 222; Osório, 1889: 133; 1890: 46; 1895a: 249; 1906: 150; Bouvier, 1907: 497; Olivier, 1804: 2: 234, 235, footnote, Pl. 30, fig. 1; 1804c: 52, footnote; Savigny, 1817, Atlas: pl. 1, fig. 1; Lamarck, 1818: 252; Latreille, 1817: 197; Audouin, 1826: 80; Desmarest, 1825: 121; Guérin-Méneville, 1832: 50; H. Milne Edwards, 1835: 47; H. Milne Edwards, 1838: 463; Lucas, 1840: 57; De Man, 1900: 42; Rathbun, 1900: 275; Rathbun, 1921: 461, pl. 52; Monod, 1933: 548.

Cancer hippeus Olivier, 1804b, pl. 30, fig. 1 [an alternative original spelling and considered a *lapsus* of *Ocypoda ippeus*, see Low & Ng 2012: 50].

Ocypoda Ippeus – Olivier, 1811: 416.

Ocypode chevalier – Latreille, 1817: 16; Latreille, 1829: 46; H. Milne Edwards, 1837: 66.

Ocypode rhombea – Audouin, 1826: 80 [in part, Locality Syria = *O. cursor*].

Ocypode (Ocypode) cursor – De Haan, 1835: 29.

Ocypoda (Ocypoda) cursor – Voigt 1835. In: Cuvier, 1836, 4: 119.

Ocypoda cursor – Herklots, 1851: 22; Heller, 1861a: 17; Heller, 1863: 99 [in part]; Kingsley, 1880: 182; Studer, 1883: 13; Miers, 1886: 240; Osório, 1889: 129, 139; Benedict, 1893: 538; Osório, 1898: 193; A. Milne-Edwards & Bouvier, 1900: 107; Doflein, 1904: 127; Odhner, 1923: 23; Bouvier, 1940: 285, text-fig. 178; Capart, 1951: 178, text-fig. 68; Gottlieb, 1953: 441; Monod, 1956: 391, text-figs 552–554; Dubois, 1957: 7, fig. 22; Sourie, 1957: 14, 31, 43, 45; Longhurst, 1958: 53, 88; Gauld, 1960: 71; Nicou, 1960: 140; Guinot & Ribeiro, 1962: 66; Rossignol, 1962: 119; Ribeiro, 1964: 14; Via Boada, 1966: 22–24, 2 figs; Antia, 1989: 264.

Ocypode cursor – H. Milne Edwards, 1852: 142; Stimpson, 1858: 100; Hilgendorf, 1869: 80, 81; Hilgendorf, 1879: 802; 1882: 23; De Man, 1881: 248; Miers, 1882: 380; Büttikofer, 1890: 465, 487; Ortmann, 1894a: 763; Johnston, 1906: 862;

Stimpson, 1907: 108; Stebbing, 1910: 326; Vilela, 1949: 65, fig. 14; Barnard, 1950: 88; Sourie, 1955: 52, figs 15–17; Carmin, 1955: 2; 1957: 4; Rossignol, 1957 in Collignon, Rossignol & Roux, Mollusques, Crustacés Poissons A.E.F.: 86, pl. 2, fig. 1; Holthuis & Gottlieb, 1958: 99; Altevogt, 1959: 129, fig. 1; Guinot-Dumortier & Dumortier, 1960: 135, figs 16a–b; Holthuis, 1961: 58; Guinot-Dumortier, 1961: 85, fig. 9; Bott, 1964: 31; Forest & Guinot, 1966: 89; Voss, 1966: 30; Kunze, 1967: 466–478, figs 1–13; 1968: 568–569, figs 1–4; Desportes, 1968: 201; Kensley, 1970b: 180; Penrith & Kensley, 1970: 252, 261; Kinzelbach, 1970: 318, text-fig. 1; Pretzmann, 1971: 481; Hartmann-Schroeder & Hartmann, 1974: 5–94: 13, 23; Sakai, K. & Turkey, 1977a: 178; Shuchmann & Warburg, 1978: 255–263; Shiber & Izzidin, 1978: 113–127, figs 1–10; Warburg & Schuchmann, 1979: 147–156, tabs 1–4, figs 1–5; Manning & Holthuis, 1981: 219; Ziese, 1985: 123–125, map 1; Turkey, 1989: 186, figs 5–6; Glaubrecht, 1992: 563–567, fig. 1; Erk'akan, 1993: 2; Ewa-Oboho, 1993: 119–127, tab. 2, figs 1–5; Strachan, Smith, Hamilton, Taylor & Atkinson, 1999: 51–60, tabs 1–5, figs 1–4; Rosenberg & Langer, 2001: 345–353; Voultziadou & Vafidis, 2007: 108; Ng, Guinot & Davie, 2008: 240.

Ocypoda [sic] *ippeus* – Moseley, 1879: 48, 1 fig.

Ocypoda [sic!] *cursor* – Vireira, 1886: 238.

Ocypoda hippeus – Ortmann, 1897: 368, pl. 17, fig. 11; Nobili, 1906c: 317; Bouvier, 1906a: 187; 1906b: 199; Sendler, 1912: 190; Balss, 1914: 79; Gravier, 1922: 120, 1 fig.; Roux, 1927: 238; Monod, 1927: 609; Balss, 1936: 42; Gauld & Buchanan, 1956: 295, 296, 298, 301; Gauld & Buchanan, 1959: 127.

Ocypode ceratophthalma – Pesta, 1911: 88: 54 [in part, material from Fernandes].

Ocypoda ceratophthalma – Balss, 1922b [In: Michaelsen, W.: *Beitr. Kennt. Meeres-fauna W. Afrika* 3: 80].

Ocypode hippeus – Balss, 1914: 106.

Ocypoda aegypticae – Monod, 1937: 18 [in part, material from Suez-Canal].

Ocypoda aegyptiaca – Monod, 1938: 148 [in part, material from Suez-Canal].

Ocypoda cordimana – Bodenheimer, 1937: 281.

Ocypode hypeus [sic!] – Sourie, 1954: 22.

Material examined. No exact locality. Probably NW Africa, female (SMF-22927); – Senegambia, 1 dry female (MHNG) [det. as *O. ippeus*]; – *ibid.*, 2 males (NHMW), 1869, F. Steindachner. West Africa. No further locality, 2 males (ZMH-2862); 5 juvs. (ZMH-5570); 3 males, 4 females, 6 juvs. (ZMH-26603) [det. as *O. kuhli*]; – *ibid.*, 2 males (NHMW-1860), 1885, R. Lippe, 'Helgoland-Expedition'. Mauritania. Nuakchott, female (MNHN) [det. Bouvier, 1906 as *O. africana*], 1905, A. Gruvel. Cape Verde Islands. No further data, 2 males (MNHN); – *ibid.*, 2 juvs. (SMF-4363), Lindberg; – São Vicente, female (MNHN-3278S); female, 4 juvs. (NHRS-5625); – *ibid.*, male, 2 females, 2 juvs. (MNHN) [det. A. Milne-Edwards & Bouvier,

1900], 1883, RV 'Talisman Expedition': — *ibid.*, male, 6 juv. males, 3 juv. females, 13 juvs. (NHM-84.31) [det. Moseley, 1879, Miers, 1882, Miers, 1886], 'Challenger Expedition'; — Sal: Santa Maria (16°35.64'N, 22°54.87'W), male (SMF-11058), 3.xi.1981, M. Geisthardt; — *ibid.*, beach in town, 5 juvs. (SMF-19312), 3-7.v.1990, R. Kinzelbach; — Boavista: NE-coast, Punta Rodrigo, beach (16°12.75'N, 22°45.46'W), male, 2 females [1 heavily damaged] (SMF-8954), 26.xii.1978, R. Von Cosel; — São Tiago: male (NHM-84.31) [det. Miers, 1886] 'Challenger Expedition'; — Tarrafal (15°16.84'N, 23°45.18'W), 1 juv. male, 1 juv. (SMF-9636), 18-21.x.1979, K. Groh & W. Lobin; — E-coast, Praia Baixo (15°3.8'N, 23°28.47'W), beach, 18 males, 2 females (SMF-34546), 2-3.iv.2005, M. Türkay, I. Kröncke, K. Pietratus & W. Rosenboom; — Fogo, male, female (MCG-147) [det. as *Ocypode* sp.]; — Porto do Vale de Cavaleiros (14°55.22'N, 24°30.14'W), North of San Felipe, 1 juv. male (SMF-9639), 31.x.1979, K. Groh. **Senegal**. Cape Verde, 3 juv. males, 3 juv. females (NHM-1934.8.17.6-7); — Malika NE of Dakar, male, 3 females (MNHN) [det. Monod, 1956], Monod; — Dakar, 7 juvs (NHMW-9832), 1885, 'Helgoland Expedition', R. Lippe; — Dakar, Tratta, female (MNHW 9834) [det. as *O. ceratophthalma*], 1885, 'Helgoland Expedition', Nr. 73, R. Lippe; — Gorée, 1 juv. male, 1 juv. female (NHMW-9829), 1881, K. Höfler. **Sierra Leone**. No further data, female (NHM-1905.1.31.9); — Freetown, 2 males (NHM); — Tagrin coast, female (NHM-1957.5.26.67). **Liberia**. No exact locality, 6 juvs. (MNHN) [det. Monod, 1956], 1882, Chaper; — Grand Cape Mount, 2 males, 2 females (RMNH-2768), 1882, J. Büttikofer; — Cape Mesurado, female (ZSM) [det. Balss, 1922 as *O. africana*], 1908, Scherer. **Côte d'Ivoire**. Abidjan, 2 males, 2 females (MNHN), 1956, Rancurel; — c. 10 km W of Sassandra (4°54.26'N, 6°10.0'W), male (SMF-25977), 2.xii.1998, J. Reimer. **Ghana**. No further data, 2 males (RMNH-220) [det. De Man, 1881]; — *ibid.*, female (MNHN) [det. Monod, 1956], Chaper; — Akka, female (NHM-1966.2.18.20). **Nigeria**. Lagos, 8 males, 3 females (NHM-1891.4.38.45); — near Lagos, male (RMNH-23407), 28.v.1965, RV 'Pillsbury' Sta. 316; — Nigerdelta between Brass and Port Harcourt, male, female (RMNH-15517), v-viii, 1960, H. J. G. Beets. **Cameroon**. No further data, female (ZMH-2872) [det. Balss, 1922]; — *ibid.*, 20 juvs. (RMNH-21179), 9.iii.1964, B. de Wilde-Duyfjes; — *ibid.*, 6 males, 3 females (RMNH-21146), 8.iii.1964; — Bibundi, 3 males, 3 juv. males, female (ZMH-2873) [det. Balss, 1922]; 2 males, 4 females (NHRS-t5978); — Limbe (= Victoria), female (ZMH-5568); — Bimbia river, male, 2 juv. males, female (MNHN) [det. Monod, 1927], 1925; — Kribi-beach, male (MNHN) [det. Forest & Guinot, 1966], 29.v.1956, RV 'Calypso', Sta. 33 (3°42'N, 9°15'E). **Equatorial Guinea**. 2 males (MNHN) [det. Monod], Pobequin; — Mbini (= Benito) (1°35.48'N, 9°37.07'E), 1 juv. (SMF-6120), Eidmann; — Cogo (= Kokobusch), 20 km upstream Rio Muni from Elobey Island, female (ZMH-5558) [det. Balss, 1922]; — Bioko (= Fernando Poo): no further data, male (NHM-1905.7.19.13); — sandy beach, male (NHMW-9795) [det. as *O. ceratophthalma*], 1885, R. Lippe, 'Helgoland Expedition'; — beach, 2 males (NHMW-9802) [det. as *O. ceratophthalma*], 1885, R. Lippe, 'Helgoland Expedition'; — muddy ground, about 100-150 m off the water, male (NHMW-9784) [det. as *O. ceratophthalma*], 1885, R. Lippe, 'Helgoland Expedition'; female (NHMW-9783) [det. as *O. ceratophthalma*], 1885, R. Lippe, 'Helgoland Expedition'; — beach, male, female (NHMW-9814) [det. as *O. ceratophthalma*], 1885, R. Lippe, 'Helgoland Expedition'; — Annobón: no exact locality, 4 juvs. (RMNH-23788), 20.v.1965, RV 'Pillsbury', Sta. 281; — *ibid.*, 1 juv. (ZMH-5375) [det. Balss, 1914], 1811, Schultze; male (ZSM) [det. Balss, 1914]; — *ibid.*, 2 males, 2 females (MCG-147), iv.1902, L. Fed. **São Tomé and Príncipe**. Príncipe: Pta. Da Mina, sandy beach with rocks, intertidal, 2 males, 1 ovig. female, 2 females (MNHN) [det. Forest & Guinot, 1966], RV 'Calypso', Sta. 112. **São Tomé**: no exact locality, male, female (ZMH-5377) [det. Balss, 1922]; — *ibid.*, male (MNHN) [det. E. L. Bouvier, 1906], A. Gravier; female (MNHN) [det. E. L. Bouvier, 1906]. **Gabon**. No exact locality, 2 males (ZMH-2871) [det. Balss, 1922]; — *ibid.*, male (MNHN-32945) [det. Monod, 1956] 1863, Duparquet. **Cape Lopez**, North of Port Gentil, male (ZMH-2864) [det. Balss, 1922]. **Congo**. No further locality data, female (MCG-147) [det. as *Ocypode* sp.], ii.1986; — *ibid.*, 3 males, 6 juvs. (RMNH-219.3), 1878, P. Kameran; — *ibid.*, female (MNHN) [det. Monod, 1956], 1894, Dybowski; — Pointe-Noire, 4 juvs. (MNHN); — *ibid.*, 3 males (MNHN), 1959, Rossignol; 4 males, female (MNHN); — *ibid.*, estuary of Noumbi river, female (ZSM), 27.v.1964, A. Strauch. **Congo, Democratic Republic**. No exact locality, 2 males, female (NHMW-1659) [det. as *O. ceratophthalma*], 1885, R. Lippe, 'Helgoland Expedition'; male (NHMW-9763) [det. as *O. ceratophthalma*]; 2 juvs. (NHMW-9828) [det. as *O. cordimana*]; — Banana (5°59.38'S, 12°23.1'E), male, 3 juvs. (SMF-1959), 12.v.1886, P. Hesse; — *ibid.*, 2 juvs. (SMF-6756), 1940, Vleeschouwers; — *ibid.*, 2 males (ZSM), 29.vi.1890; — *ibid.*, male, 1 juv. male, female, 4 juvs. (MCM-1974) [det. as *O. ippeus*], 1915; — Muanda (= Moandağ Tonda) (5°56.1'S, 12°20.54'E), male (SMF-6755); 1 juv. (SMF-4108), Darteville. **Angola**. No further data, male (MCM-2111) [det. Catumoele as *O. ippeus*]; female (ZMH-2860); male (ZMH-5443); — *ibid.*, male (ZMNH) [det. De Man, 1900 as *O. ippeus*], 3.vi.1900; — Cabinda: Landana, male (MNHN) [det. Monod, 1956], 1898, Petit; — Zaire: near Musserra, 2 females (RMNH-1571), 1882, P. Kameran; — Luanda: male, 2 females (ZMH, 29825); — *ibid.*, beach at St. Paul de Luanda, 8 juvs. (NHMW-9831), 23.vi.1894, J. Klimesch; — Cuanza Sul: Novo Redondo near Sumbe, 1 juv. male, 1 juv. female (ZMH-29817); — Benguela: Lobito (12°21.45'S,

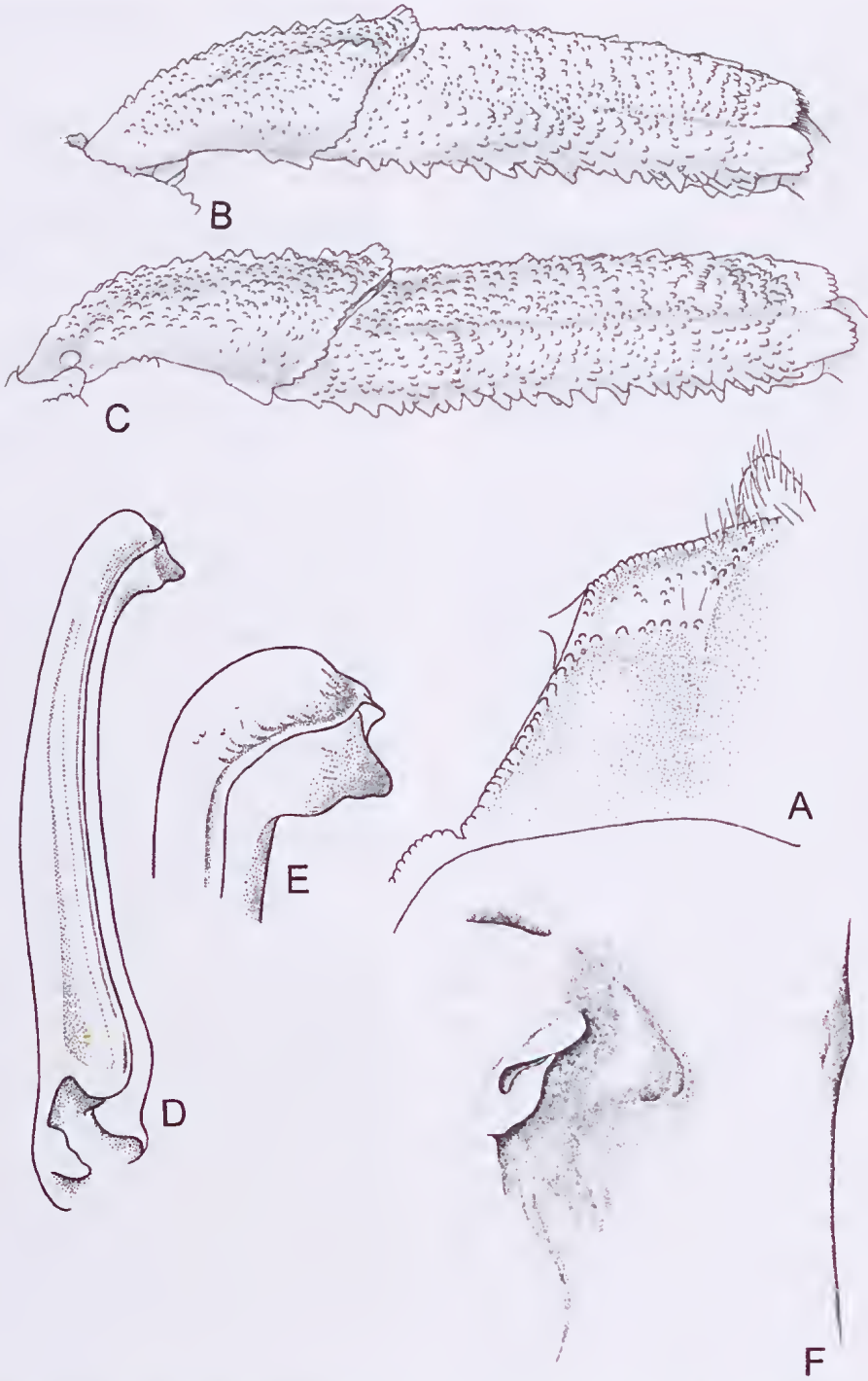


FIG. 13. *Ocyptode cursor*: A, P1 thoracic sternite; B, C, P2-3 carpi and propodi; D, E, Go1; F, female operculum.

13°31.77'E), 3 juvs. (SMF-2671); – *ibid.*, Harbour, male (RMNH-1253) [det. De Man, 1900], Kamerman; – Benguela, male (NHM-1906.2.5.9); 4 juvs. (ZMH-29783); – Namibe: Tombua (= Port Alexander), male (RMNH-27226), 9.vi.1967, G. Hartmann; male (ZMH-29806). Greece. Karpathos, Pigadia-Bay (35°30.98'N, 27°12.01'E), several body parts (SMF-5104), spring, 1966, N. Polemikos & R. Kinzelbach. Turkey. Muğla Province: İztuzu beach (36°47.44'N, 28°37.7'E), SW of Köyceğiz, 2 juvs. (SMF-19311), 17.iv.1989, R. Kinzelbach; – Antalya-Province: Manavgat (36°45.84'N, 31°24.07'E), female, heavily damaged (SMF-2687), Dobal; – İncekum Beach (36°38.33'N, 31°43.58'E) between Alanya and Manavgat, male, female (SMF-4900), 25.v.1966, H. Felten; – Hatay-Province: İskenderun, sandy beach (36°37.24'N, 36°11.87'E), 5 juvs. (SMF-8679), 29.viii.1978, R. Kinzelbach; – Antakya, mouth of Orontes (= Asi nehri) (36°2.91'N, 35°57.73'E) and surroundings, 1 juv. (SMF-23244), 19.ix.1982, R. Kinzelbach; – Samandağ, sandy beach N of Orontes (= Asi nehri) mouth (36°2.79'N, 35°57.78'E), 2 females (SMF-12165), 19.ix.1982; – beach between Samandağ and Orontes mouth (36°3.77'N, 35°57.31'E), male, female, 4 juvs. (SMF-18282); 1 juv. (SMF-20443), 9-10.viii.1988, R. Kinzelbach. Syria. Nahr al Kabir S of Lataqia, river mouth (35°30.04'N, 35°48.6'E), male (SMF-9296), 5.iii.1979, R. Kinzelbach. Lebanon. Khaldé (33°47.27'N, 35°28.55'E), 12 km S of Beirut, sandy beach, male (SMF-9221), 1.v.1973, Lechner; – S of Tyros, sandy beach (33°15.47'N, 35°12.65'E), male, female (SMF-31128), 16.vi.2006, M. Bariche & M. Türkay.

Diagnosis. Large-sized species. Eystalks not prolonged distally beyond cornea, but bearing a brush at distal end of cornea. Lateral half of orbital margin almost straight. Exorbital angles triangular and protruding outward. Propodi of P2-3 naked on anterior surface. Stridulating ridge composed of 69-96 tubercles with striae. Go1 curved laterally at distal end, lacking a palp. Female genital opening with lateral rim continuous lengthwise to elongate operculum, which is directed anteromesially under median rim.

Description. Eystalks with a brush at distal end of cornea. Carapace (Fig. 35) wider than long, and covered with densely arranged fine tubercles on dorsal surface. Exorbital angles triangular and protruding outward. Lateral margins of carapace directed slightly outwards from base of exorbital angle in anterior third of carapace, and then directed inwards in posterior two-thirds. Carapace broadest at its anterior third. Pterygostomial region with regularly arranged tubercles. P1 thoracic sternite (Fig. 13A) with tuberculate carina on anterior to lateral

margin, and a distinct transverse tuberculate carina at anterior third. Palm of larger cheliped slightly longer than broad, naked, and covered with coarse and fine tubercles on anterior surface. Stridulating ridge (Fig. 2B) curved in dorsal third, and composed of 69-96 tubercles with striae; *c.* 23 tubercles with striae in dorsal third, and *c.* 46 closely pressed tubercles with striae in ventral two-thirds (SMF-9296). Smaller cheliped narrowing to pointed distal end. P2-3 propodi (Fig. 13B-C) naked, bearing distinct spiniform tubercles on anterior surface and ventral margin. Go1 (Fig. 13D-E) three-sided proximally, curved laterally at distal end, lacking palp (SMF-9296). Female genital opening (Fig. 13F) sunken; operculum protruding anteromesially, slipped down under median rim.

Juvenile specimens. Carapace much wider than long. Lateral half of orbital margin slightly concave, so that exorbital angles triangular and directed somewhat anteriorly, tip located posterior to median convexity of orbital margin. Stridulating ridge composed of fine striae, and narrowed and distinctly curved in dorsal third. In a specimen (7.9×9.0 mm, SMF-6756) stridulating ridge less developed in dorsal third, only as an indistinct line. In smaller specimens, stridulating ridge not yet developed in dorsal third, but distinctly developed in ventral two-thirds. In a larger specimen (12.5×15.5 mm, SMF-6756) eystalks already provided with a brush at distal end of cornea, but in a slightly smaller specimen (10.0×13.0 mm, MNHN-14096) eystalks not yet provided with a brush. P2 propodus with scanty yellowish spines on dorsal margin. P3 propodus with row of long setae along distal 1/2-2/3 of dorsal margin.

Distribution. Mauritania to Namibia, eastern Mediterranean (from Egypt across the Levant to Turkey and southern Greece). Type locality: 'Mari Mediterranei, Indico'.

Remarks. This species was first described under the name *Cancer cursor* Linnaeus, 1758. Later Hasselquist (1762) described *Cancer anomalus*, and Olivier (1811) listed it under *Ocypode Ippicus*, attributing *O. cursor* to *O. ceratophthalma*. However, all of these species are synonyms of *O. cursor*, because they have the following characters in common: eystalks bear a brush at

the distal end of the cornea, the stridulating ridge is composed of 69-96 closely pressed tubercles with striae and curved in its dorsal third, and the P2-3 propodi are naked and provided with spiniform tubercles, both on the anterior surface and on the ventral margin.

Ocypode fabricii H. Milne Edwards, 1837
(Figs 2C, 14, 36)

Ocypoda fabricii H. Milne Edwards, 1837: 47; Lucas, 1840: 57; Nobili, 1905b: 230, fig. 1-1a.

Ocypode Fabricii – Gibbs, 1850: 180; H. Milne Edwards, 1852: 142.

Ocypode fabricii – Ortmann, 1897: 361; George & Knott, 1965: 18, fig. 2C; Crosnier, 1965: 98, figs 155, 175, pl. 10, figs 1, 4; Serène, 1968: 97; Allender, 1969: 63; Davie, 2002: 358; Ng *et al.*, 2008: 240.

Ocypoda aegyptiaca – Balss, 1935: 140.

Material examined. Exact localities unknown. No data, male, female (MNHN); male (NHMW); female (SMF-6753 [ex. WAM]) [det. George & Knott, 1965]; – ‘Oceania’, male [holotype] (MNHN). **Australia.** Northern Territory. West of Darwin, male, female (USNM-178294), 31.iii.1948, D. H. Johnston; – Western Australia, Broome in Mangrove, male (AMS-P14996); – Crab Creek near Broome, 2 males, female, 1 damaged (ZMH-K32304); – Pretty Pool, Port Hedland (20°18.514'S, 118°38.42'E), 3 males, 3 females (ZMH-K32299), 28.ix.1975, G. Hartmann & G. Hartmann-Schröder; male, female (SMF-10328); – Hersines Cove, 7 km East of Dampier (20°38.384'S, 116°44.662'E), 4 males, 2 females (ZMH-K32281); 2 males (SMF-10329), 2.x.1975, G. Hartmann & G. Hartmann-Schröder; – Nickol Bay, South-East of Dampier, 1 juv. female (NHM-69.38); – Pelican Point, Carnarvon (24°53.908'S, 113°24.533'E), 3 males, female (ZMH-K32294); male (SMF-10330), 13.x.1975, G. Hartmann & G. Hartmann-Schröder; – Shark Bay, male (ZMH-K11338) [det. Balss, 1935 as *Ocypoda aegyptiaca*]; – Small lagoon North of Denham (25°54.089'S, 113°31.933'E), Shark Bay, male, female (SMF-7612 [ex. WAM]) [det. George & Knott, 1965], 12.iii.1964, D.G. Bathgate; – Monkey Mia Beach (25°47.437'S, 113°41.851'E) near Denham, Shark Bay, male (SMF-23858 [ex. WAM]), 15-16.ix.1974, B. Shaw.

Diagnosis. Middle-sized species. Eystalks not prolonged distally beyond cornea. Exorbital angles acutely triangular and protruding outward. Stridulating ridge composed of 126-133 fine striae. Smaller cheliped tapering to pointed distal end. P2 propodus with median row of setae (in female) or median row plus another in ventral half (in male). P3-5 propodi naked. Go1 curved laterally and tri-lobed at distal end, bearing an indistinct palp. Operculum

of female genital opening rounded distally and protruding mesially; vaginal slit directed obliquely at about 45 degrees to sternal median line.

Description. Carapace (Fig. 36) almost quadrate and covered with coarse tubercles, becoming finer towards middle of dorsal surface. Lateral half of orbital margin slightly concave. Exorbital angles acutely triangular and directed outward. Lateral margins of carapace directed slightly outward from base of exorbital angles in anterior third of carapace, and then directed inwards in posterior two-thirds, forming an epibranchial corner, where carapace broadest. Pterygostomial region distinctly tuberculate except along lateral sides of buccal cavern. P1 thoracic sternite (Fig. 14A) concave at its mesial surface, bearing strongly tuberculate carinae on anterior and lateral margins. Palm of larger cheliped broad and covered densely with fine and coarse tubercles on anterior surface, among which coarser tubercles scattered, bearing distinct denticles on dorsal and ventral margins. Stridulating ridge (Fig. 2C) composed of 126-133 regularly and closely spaced fine striae. Small cheliped narrowing to pointed distal end. P2 propodus (Fig. 14B) with transverse rows of tubercles on dorsal half of anterior surface, bearing one median row of setae and another one on ventral half (in male) or one median row of setae (in female). P3 propodus (Fig. 14C) naked. Go1 (Fig. 14D-E) curved laterally and tri-lobed at distal end, bearing a low flat elevation as palp (SMF-7612). Operculum of female genital opening (Fig. 14F) rounded distally, protruding mesially in shape of button; vaginal slit directed obliquely at about 45 degrees to sternal median line.

Juvenile specimens. In a juvenile (11.5×13.5 mm) carapace slightly wider than long and less quadrate than in adult specimens, and rather similar to those of large specimens of other species. Carapace covered with tubercles, becoming finer from lateral sides towards middle of dorsal surface, as in adult specimens. Exorbital angles directed less outwards than in adult specimens. Stridulating ridge composed of 55 striae, much fewer than those in adult ones, but regularly and closely spaced as in adult ones. P2-5 propodi naked except on anterior surface of P2 propodus, which bears a median row of setae.

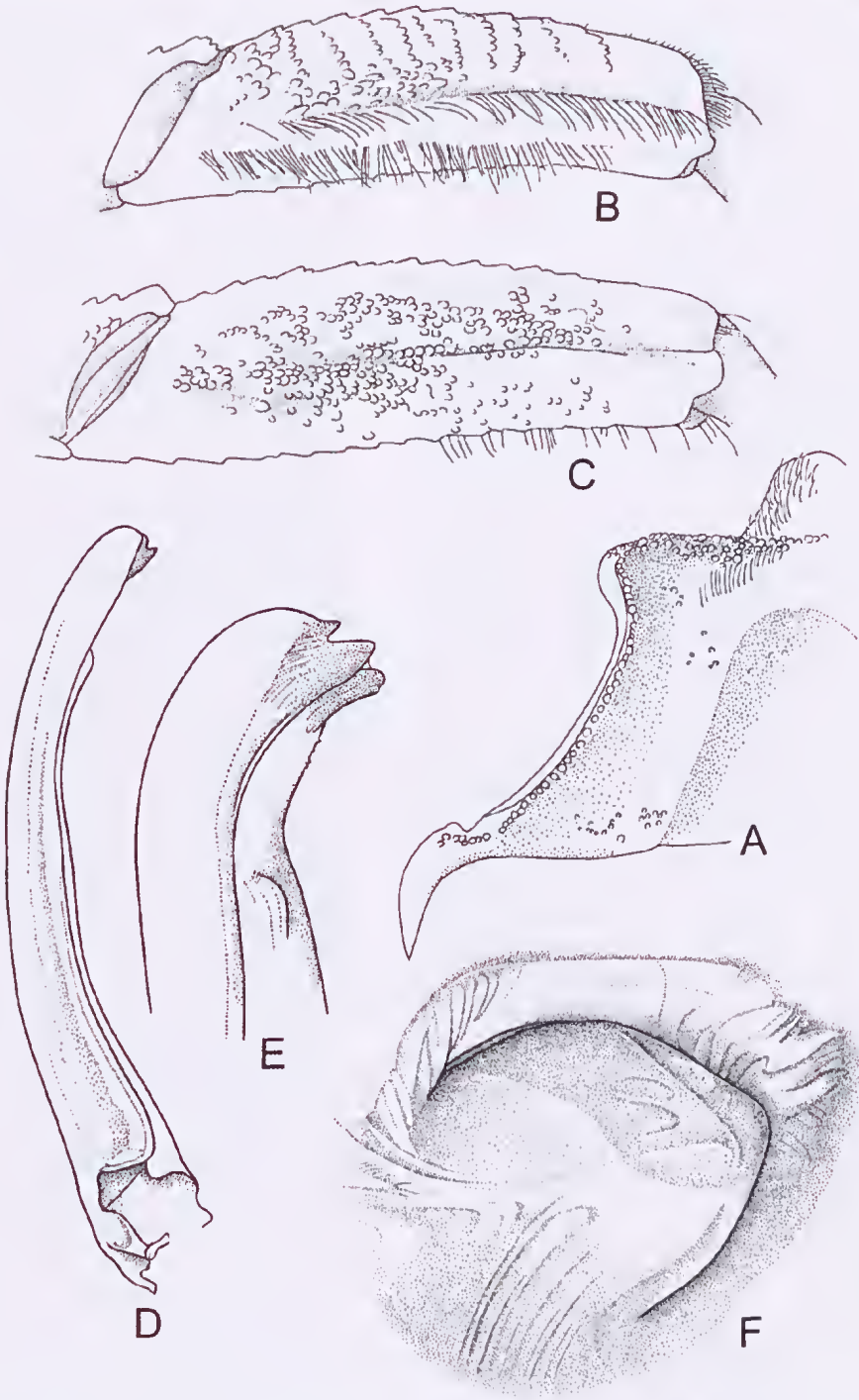


FIG. 14. *Ocypode fabricii*: A, P1 thoracic sternite; B, C, P2-3 propodi; D, E, Go1; F, female operculum.

Distribution. Northern and Western Australia (Darwin to Shark Bay). Type locality: 'Oceanie'.

Remarks. H. Milne Edwards (1837) gave the type locality of *Ocypode fabricii* simply as 'Oceanie' (= Pacific Ocean). Later, Ortmann (1897: 31) remarked that H. Milne Edwards' species is 'unidentificierbar' [sic] (= unidentifiable) because of the imprecise type locality. The identity of a specimen listed by Gibbes (1850) without specific reference to its locality, has also remained unclear, because it was later destroyed by the Philadelphia fire of 1866 (H.S. Feinberg, *in litt.*). Nobili (1905) finally clarified the identity of *O. fabricii* by publishing a thorough redescription of the type specimen, together with a figure of the carapace. He also restricted the type locality to Australia after comparing *O. fabricii* with other species of *Ocypode* collected from the Pacific. The type specimen has also been re-examined by Crosnier (1965), George & Knott (1965), and the present authors, and we all concur that specimens from Northern and Western Australia are *Ocypode fabricii* as described by H. Milne Edwards (1837).

Ocypode fabricii is very similar in morphology to *O. jousseaumei*, but the characters that separate them are discussed under that species account. Juvenile specimens of *O. fabricii* are liable to be confused with those of the sympatric species *O. ceratophthalma*, however, even in the smallest specimen of *O. fabricii* available (carapace width of 13.5 mm) the P2 propodus bears a median row of setae on the anterior surface, but the P3 propodus is naked. In *O. ceratophthalma* the P2-3 propodi are both provided with setae on the dorsal margin, and possess a median row of setae on the anterior surface. Those two species are also different from each other in the morphology of the stridulating ridge; in our juvenile specimen of *O. fabricii* there are 55 regularly and closely spaced striae, whereas *O. ceratophthalma* of the same size has only sparsely and irregularly arranged striae.

***Ocypode gaudichaudii* H. Milne Edwards & Lucas, 1843**

(Figs 2D, 15, 37)

Ocypode Gaudichaudii H. Milne Edwards & Lucas, 1843: Atlas, 9, pl. 11, fig. 4; Lucas 1843: 26; Stimpson, 1860: 61.

Ocypode Gaudichaudi — H. Milne Edwards, 1852: 142.

Ocypoda Gaudichaudii — Nicolet, In Gay, 1852: 163; Dana, 1852: 329; Streets, 1871: 240; Miers, 1882: 383, pl. 17, figs 5, 5a; Cano, 1889: 91, 99, 100, 230; Aurivillius, 1893: 23, pl. 2, figs 7-13.

Ocypoda gaudichaudii — Kingsley, 1880: 181; Ortmann, 1897: 360, 365; Lenz, 1902: 767; Pesta, 1931: 180.

Ocypode gaudichaudi — Ortmann, 1894a: 762, 770, pl. 23, fig. 22; Porter, 1940: 312; Garth, 1957: 105.

Ocypode gaudichaudii — Rathbun, 1898: 603; 1902a: 275; 1906: 834 [no new material, only discussion of record]; 1910b: 550, pl. 43, fig. 2; 1918: 373, pl. 129, fig. 1, pl. 130, fig. 1; Schmitt, 1921: 278, fig. 163, pl. 38, figs 5-6; Boone, 1929: 580, fig. 15; Sivertsen, 1933: 19; Crane, 1940: 65, figs 1, 4, 6-8, and fig. of sternite; 1941: 299, figs 2, 4A-D, 5B, D, F, H, 6B, D, 7E, F; pl. 1, fig. 1; pl. 2, figs 3-4; Garth, 1948: 59, pl. 5, fig. 1; Koepcke, 1953: 1, figs 1-14; Holthuis, 1954a: 40; 1954b: 162; Bott, 1955: 67; Guinot-Dumortier & Dumortier, 1960: 136, 148, tab. 3; Edmondson, 1962: 1, fig. 5a-c; Bright & Hogue, 1972: 9; Horch & Salmon, 1972: 1-2, 4, 10, tab. 1, fig. 1; Full & Herreid, 1983: R530-R536, figs 1-5; Pretzmann, 1983: 315; Robinson, in: Robinson & del Pino, 1985: 182, 183; Trott, 1987a: 213-215, tab. 1; 1987b: 295-303, tab. 1, figs 1-3; 1988: 217-219, fig. 1; 1998: 47-56, tab. 1, figs 1-3; Schober & Christy, 1993: 53-60, tabs 1-3, figs 1-5; Arndt, 1999: 111-114; Quijon, Jaramillo & Contreras, 2001: 91-103, tabs 1-4; Villamar & Cruz, 2007: 142-143, tab. 1; Ng, Guinot & Davie, 2008: 240.

Ocypoda gaudichaudii — Doflein, 1899: 189; 1900: 144 [wrong locality]; Rathbun, 1924: 155, pl. 7; Boone, 1927: 267, fig. 96A [not fig. 96B megalopa, *vide* Crane 1940; Garth 1946 & 1948]; Crane, 1939: 19, 5 figs (no numbering); Garth, 1946: 514, pl. 87, fig. 7; Guinot & Cleva, 2002: 512, fig. 7.

Ocypoda urvillei — Doflein, 1899: 189.

Ocypoda Gaudichaumi [sic] — Nobili, 1901b: 53.

Ocypode occidentalis — Garth, 1957: 104 [material = *O. gaudichaudii*; text = *O. occidentalis*].

Material examined. Guatemala. No further locality data, 5 males (ZMH-2931), Paessler; — Puerto San José de Guatemala, female (ZMH-2842). El Salvador. Depto Sonsonate: Acajutla, male [18.6×22.7 mm] (SMF-2077), 21.x.1951, H. M. Peters; — Depto. Usulután: Mouth of Rio Lempa (13°15.6'N, 88°50.0'W), male [18.6×22.7 mm], 2 females [18.0×23.0 mm] (SMF-2202), O. Schuster; — *ibid.*, female (RMNH-9653), 19.iii.1953, M. Boeseman; — La Chapona (13°11.0'N, 88°21.0'W), male (SMF-2201), 11.iv.1953, O. Schuster; — Depto. San Miguel: El Cuco (13°10.35'N, 88°6.6'W), 1 juv. (RNHM-9654), 19.iv.1953, M. Boeseman; — Depto. San Salvador: San Salvador (wrong locality because San Salvador is far inland), 2 males (ZMH-2846). Nicaragua. No exact locality, 3 males, 3 females (ZMH-2840), Paessler. Costa Rica. No further data, 2 males, 2 females (NHM-1892.6.7.18-20); — Osa Peninsula, Golfo Dulce, male (NHMW) [det.

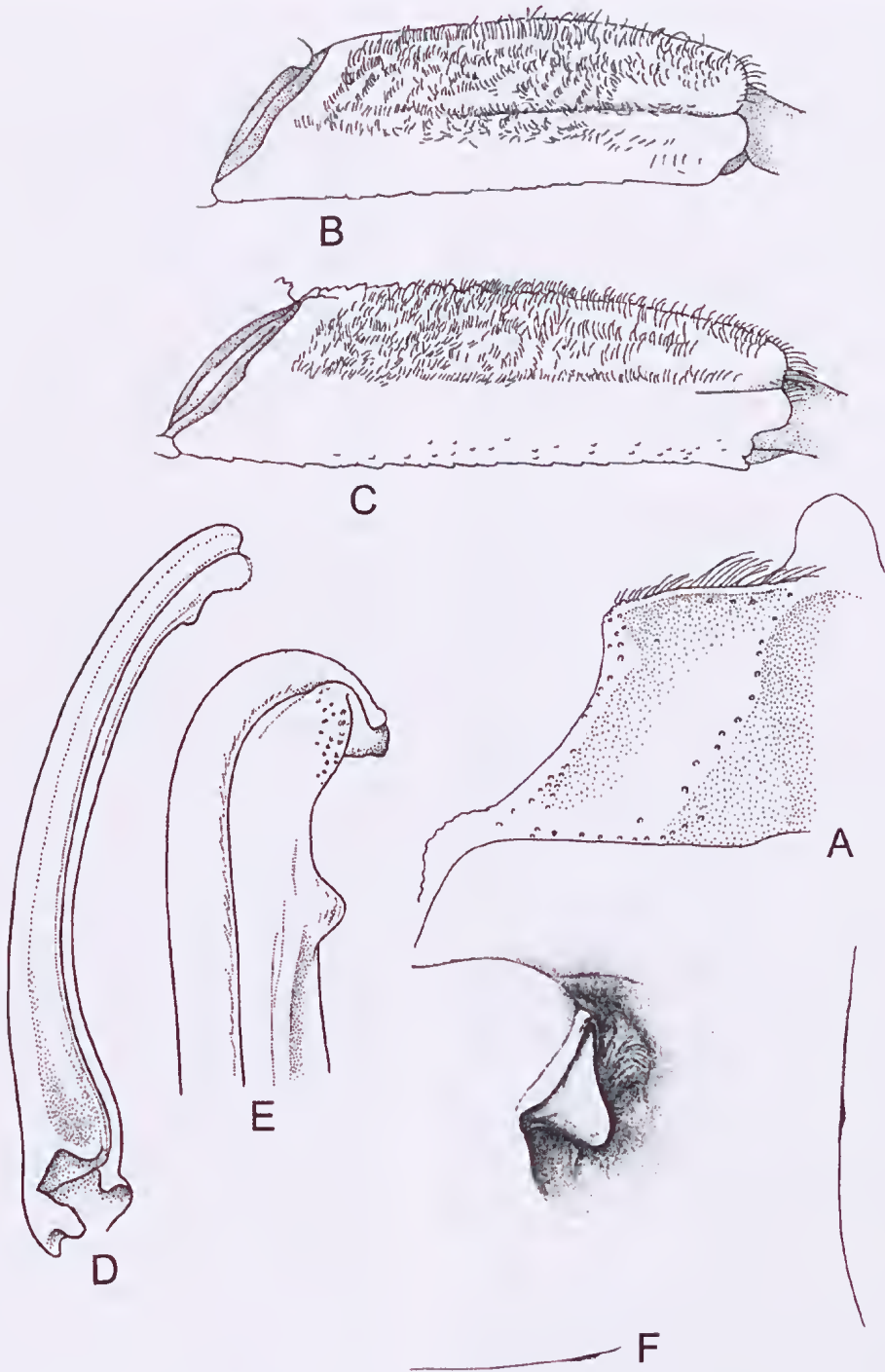


FIG. 15. *Ocypode gaudichaudii*: A, P1 thoracic sternite; B, C, P2-3 propodi; D, E, Go1; F, female operculum.

Pesta, 1931], Costa Rica Expedition, 1930. Panama. No exact locality, 2 males, female (USNM-168826), J.P.E. Morrisson; — Beach at Venado, 2 juvs. (UZMK), 14.xii.1915; — Isla Taboquilla, 13 males, 4 females (UZMK), 8.xii.1915; — Pearl Islands, Isla del Rey (8°27.12'N, 78°56.59'W), 1 juv. female (SMF-2400); — *ibid.*, SE-coast, Bahía San Telmo (8°18.01'N, 78°53.36'W), male (SMF-22178), 16.ii.1954, RV 'Xarifa'. Colombia. Depto. Valle del Cauca: Playa de Choncho in the delta of Rio San Juan (4°5.36'N, 77°29.33'W), male [19.6×24.3 mm] (SMF-9445), 15.ix.1979, H. von Prah; — Depto. Nariño: Mulatos (2°39.27'N, 78°16.97'W), 2 juvs. (SMF-9444), 21.ix.1979, H. Von Prah; — Tumaco (1°48.53'N, 78°22.37'W), male [13.2×16.5 mm], female [18.1×23.5 mm] (SMF-7848 [from UZMK]), 21.vii.1948, E. M. Poulsen; — *ibid.*, 2 males [28.3×34.4, 25.9×33.0 mm], 1 damaged male [CL 24.5 mm], 2 females [23.2×28.9, 21.5×27.6 mm] (SMF-6844), viii.1970, F. Klassen; — *ibid.*, beach of El Morro, male, female (SMF-7844 [from UZMK]), 28.viii.1948, E. M. Poulsen; — Depto. Cauca: Isla Gorgona, Arena (2°56.64'N, 78°11.36'W), 4 males [17.8×33.4 - 24.3×29.5 mm] (SMF-18684), 26.i.1979, E. Wedler; — *ibid.*, 4 males, female [21.9×29.2 mm], 13 juvs. [12.6×15.2 - 6.1×6.7 mm] (SMF-18685), 24.v.1979, E. Wedler; — Isla Gorgonilla (2°56.1'N, 78°13.0'W), male [28.8×32.6 mm] (SMF-18686), 27.i.1979, E. Wedler. Ecuador. District Esmeraldas, Muisne, beach (36°17.25'N, 80°01.57'W), 2 females [24.6×31.4, 22.8×28.9 mm] (SMF-36244), 29.viii.1985, R. Hutterer; — Galápagos, Rábida (= Jervis) (0°23.98'S, 90°42.41'W), male [27.0×32.4 mm] (SMF-2521), 30.vii.1957, Eibl. Peru. Tumbes Province: Surroundings of Puerto Pizarro, Mangrove (3°29.7'S, 80°29.29'W), male (SMF-13157), 15.v.1984, M. Clüsener-Godt; — Surroundings of Bocapán, beach without mangrove (3°43.52'S, 80°44.3'W), 2 females (SMF-13149), 31.vii.1984, M. Clüsener-Godt; — Lima Province: Ventannila, NW of Lima (11°52.31'S, 77°9.43'W), sandy beach, 2 juvs. (SMF-6852), 17.iii.1951, H.W. Koepcke; — Surroundings of Lima, 2 males (SMF-11443), 20.ix.1983, Riede; — Chilca (12°32.15'S, 76°45.22'E), c. 70 km South of Lima, sandy beach, male (SMF-2326), 4.ix.1951, H.W. Koepcke; — Coast near Asia (12°46.37'S, 76°36.26'W), 103 km South from Lima, male [16.7×2 1.0 mm], female [27.5×34.3 mm], 2 juvs. [6.5×7.5, 7.0×8.9 mm] (SMF-13148), 4.iii.1984, M. Clüsener-Godt; — Arequipa Province: Surroundings of Camaná (16°39.1'S, 72°42.6'W), pebble beach, 1 juv. (SMF-2311), 15.vi.1951, H.W. Koepcke. Chile. Arica (18°26.65'S, 90°42.41'W), male [29.3×36.8 mm] (ZMG-121), 1906, Bürger; — Antofagasta, Isla Santa Maria, beach (23°26.29'S, 70°36.16'W), male (SMF-19210), 15.iii.1989, M. Heisig. No locality. 2 males, 3 females (ZMG-122).

Diagnosis. Middle- to large-sized species. Eye-stalks prolonged distally beyond cornea in a slender stylus. Larger and smaller chelipeds

truncate at distal end. Exorbital angles protruding outward. P2-3 propodi setose. Stridulating ridge composed of 18 tubercles in dorsal half and c. 38 striae in ventral half. Go1 curved laterally in distal part and truncate at distal end, bearing conical palp. Operculum of female genital opening protruding mesioposteriorly.

Description. Eye-stalks prolonged distally beyond cornea in a slender stylus. Carapace (Fig. 37) distinctly wider than long and covered densely with fine tubercles on dorsal surface. Lateral half of orbital margin directed obliquely backward. Exorbital angles protruding outward. Lateral margins of carapace directed slightly outward from base of exorbital angle in anterior third of carapace, and then directed inwards in posterior two-thirds. Carapace broadest at exorbital angles. Pterygostomial region tuberculate except around buccal cavern. P1 thoracic sternite (Fig. 15A) shallowly and broadly concave medially; hemmed anteriorly with tuberculate carina with setae; and laterally with tuberculate carina. Palm of larger cheliped comparatively longer than in other species of *Ocyropsis*, and covered densely with fine tubercles on anterior surface, among which are a small number of coarser ones. Ventral margin of palm provided with remarkably stout interspaced denticles. Stridulating ridge (Fig. 2D) composed of c. 18 tubercles in dorsal half and 36-38 striae in ventral half. Larger and smaller chelipeds both truncate at distal end of chela. P2-3 propodi (Fig. 15B-C) setose on dorsal half of anterior surface; in a juvenile specimen (CW 21.0 mm, SMF-13148) P2 propodus with a median row of setae on anterior surface and scanty yellowish spinules along dorsal margin and median line, and P3 propodus setose on dorsal half of anterior surface, bearing scanty yellowish spinules along dorsal margin and median line; in another juvenile one (CW 8.9 mm, SMF-13148) P2 propodus almost naked, bearing scanty yellowish spinules along dorsal and ventral margins, and a median line on anterior surface. P3 propodus also naked on anterior surface, bearing scanty yellowish spinules along dorsal and ventral margins. Go1 (Fig. 15D-E) three-sided proximally, and curved laterally in bulging distal part; truncate at distal end, bearing conical palp. Operculum of female

genital opening (Fig. 15F) protruding mesioposteriorly, and narrow anterior part of operculum surrounded by distinct thick rim.

Juvenile specimens. In our smallest specimen (5.1×5.6 mm, SMF-6852) carapace slightly wider than long. Front broad. Exorbital angles located far backward. Palm of larger cheliped distinctly swollen on inner surface. Chelae of larger and smaller chelipeds both tapering to pointed distal end. Stridulating ridge already distinctly raised and composed of fine granules. P2-3 propodi naked on anterior surface. In a slightly larger specimen (6.1×7.5 mm, SMF-2311) eyestalks not yet prolonged distally beyond cornea. Carapace distinctly wider than long, and smooth on dorsal surface. Front strongly reduced in breadth. Lateral half of orbital margin distinctly concave. Exorbital angles broadly triangular, protruding anteriorly, and located far backward. Stridulating ridge distinctly developed, and composed of sparsely arranged striae in dorsal half, and densely and irregularly arranged striae in ventral half. Larger cheliped already truncate at distal end of chela, while smaller cheliped still pointed at distal end of chela.

In a still larger specimen (13.7×17.7 mm, UMK) eyestalks prolonged distally beyond cornea in a small stylus. Lateral half of orbital margin not concave, but rather straight and directed obliquely backward. Exorbital angles protruding slightly outward as in adult specimens. Larger cheliped truncate at distal end of chela, and smaller cheliped rounded distally. Stridulating ridge distinctly developed; composed of tubercles in dorsal half and striae in ventral half. In a much larger specimen (18.5×24.5 mm) both larger and smaller chelipeds truncate at distal end of chela.

Distribution. Pacific coast of the Americas, from Guatemala to Chile (Valparaiso is the southern-most known locality). Type locality: 'Côtes de Chili'.

Remarks. The present species was introduced through a figure by H. Milne Edwards & Lucas (1843), though its formal description was not published until a year later, in 1844, by Lucas (1844: 17) alone. For practical purposes it is very important to distinguish this species from *H. occidentalis*, because those two species are both

distributed in the eastern Pacific from Central to South America. Adult specimens of *O. gaudichaudii* are distinctly different from those of *H. occidentalis* particularly in the structure of the male Go1 and female genital opening. *O. gaudichaudii* is also differentiated by both chelipeds with truncated chelae, and this is also true of juveniles over a certain size. Although Crane (1941: 302) reported this for specimens with a carapace width as little as 10.0 mm, our examination of a series of specimens suggests that this feature is only reliable for specimens greater than 24.5 mm carapace width. Smaller specimens are best determined by the structure of the stridulating ridge. Other useful characters for adults include the laterally protruding exorbital angles, and the styli extending beyond the cornea, but these are not useful for identifying juveniles. Past confusion in reliably identifying juveniles of *O. gaudichaudii* and *H. occidentalis*, has led mis-identifications and mistakes in distribution records.

Cano (1889) reported *O. gaudichaudii* from Honolulu, Hawaiian Islands, but Rathbun (1906: 834) remarked that his report needed verification. Edmondson (1962: 15) also stated: '... there is no confirmation of its occurrence in the Hawaii Islands or anywhere else in the Central Pacific area.' It is certain that Cano's report of *O. gaudichaudii* from the Hawaiian Islands is incorrect. Rathbun's reports (1910, 1918) of *O. gaudichaudii* from San Pablo, Lower-California are also doubtful, and as Schmitt (1921: 278) commented that 'it is very probable that the label on this lot is either incorrect or the result of an exchange.' The reports of *O. gaudichaudii* by Boone (1927, 1929) are based on Rathbun's reports without mentioning Schmitt's comments. We re-examined Rathbun's specimens and did confirm that her identification was correct, but agree that they were probably mis-labelled as this species has never since been reported from either Hawaii or California. *O. gaudichaudii* was also reported from the Galápagos Islands by Rathbun (1899, 1902, 1918), Boone (1927), Sivertsen (1933), and Garth (1946), but not from Clipperton Island (Garth, 1965: 37). There is, however, an adult male specimen of the present species from Clipperton Island, which was found included in a collection preserved at the Museum National

d'Histoire Naturelle (MNHN) in Paris. The problem is that this adult male is the only specimen from Clipperton Island. So further investigation will be required in order to confirm this locality is correct. Doflein (1900) reported *O. gaudichaudii* from the Atlantic coast of Panama, about which he himself remarked that 'the specimens are from the Atlantic Ocean as described clearly on the label, though this species has been reported only from the Pacific Ocean.' [translation of German text]. The examination of his specimens (male & female, ZSM) shows that they were correctly identified as *O. gaudichaudii*, which suggests that this species may have reached the Atlantic coast of Panama through the Panama Canal. Again, this record needs confirmation before the Atlantic Panama can be safely included in the distribution of the present species. Therefore, the present species has to be regarded as a Pacific American element, with a distribution area ranging from Guatemala to Chile including the Galápagos Islands.

Ocypode jousseaumei (Nobili, 1905)

(Figs 3A, 16, 38)

Ocypoda jousseaumei Nobili, 1905b: 233, fig. 2; 1906b: 310.

Ocypode jousseaumei – Laurie, 1915: 416; Crosnier, 1965: 99, figs 156, 163, 173–174, pl. 10, figs 2, 6; Serène, 1968: 97; Türkay *et al.*, 1996: 102, figs 4–6, 11; Clayton, 2001: 37–55; Clayton, 2005: 53–70, figs 1–9; Ng *et al.*, 2008: 240.

Material examined. Red Sea, male [holotype] (MNHN-B11782). Republic of Djibouti. No further data, 2 males, 1 juv. male, 3 juv. females (ZMB 15639); – Tadjoura, 2 juv. males (ZMH-K2927). Yemen. Aden, 1 juv. male, 2 juv. females, 2 juvs. (ZMB 5878); male (USNM-64745); – Tauwahi (= at-Tawahi), East of Aden (12°47'N, 44°59'E), male (NHMW-24970), 1899, O. Simony. Oman. As Suwadi W of Masqat (23°46.57'N, 57°47.46'E – 12°47'N, 44°59'E), male (SMF-24530); male (SMF-24531); male (SMF-24532); – Golf of Masirah, peninsula Barr Al-Hikman, Khawr Al-Milh, South (20°22.22'N, 58°17.34'E), female (SMF-24533), 31.v.1995, D. Clayton.

Diagnosis. Middle- to small-sized species. Eye-stalks not prolonged distally beyond cornea. Exorbital angles acutely triangular. Stridulating ridge composed of 41–79 tubercles and tubercles with striae. Smaller cheliped narrowing to pointed distal end. P2 propodus with a median row of setae on anterior surface. P3

propodus naked on anterior surface. Go1 narrowing distally, and slightly curved laterally in distal part, bearing a palp. Horny endpiece flat, longer than broad, and rounded at tip. Operculum of female genital opening rounded and protruding mesially.

Description. Carapace (Fig. 38) almost quadrate, and covered densely with fine tubercles on dorsal surface. Lateral half of orbital margin concave. Exorbital angles acutely triangular and protruding outward. Lateral margins of carapace directed slightly outward from base of exorbital angle in anterior third of carapace, and then directed inwards in posterior two-thirds, forming weakly protruding epibranchial angles. Carapace broadest at exorbital angles. Pterygostomial region coarsely tuberculate except along lateral sides of buccal cavern. P1 thoracic sternite (Fig. 16A) smooth and rimmed laterally with tuberculate carina, bearing scantily tuberculate humps. Palm of larger cheliped broad and covered densely with irregularly arranged tubercles on anterior surface, bearing a relatively small number of denticles on ventral margin. Stridulating ridge (Fig. 3A) composed of at least 41 (SMF-24530), 72 (NHMW), or at most 79 (holotype) elements; 15 tubercles in dorsal third and 26 closely spaced tubercles with striae in ventral two-thirds (SMF-24530). Smaller cheliped narrowing to pointed distal end. P2 propodus (Fig. 16B) with a median row of setae on anterior surface. P3 propodus (Fig. 16C) naked on anterior surface. Go1 (Fig. 16D–E) distinctly narrowing distally, and weakly curved laterally in distal part, bearing a distinct palp directed distally and located distant from distal end. Operculum of female genital opening (Fig. 16F) rounded and protruding mesially, posterior to which a large elevation present.

Juvenile specimen. In a young specimen (7.8×9.0 mm, ZMB 5878) carapace tuberculate. Orbital margin directed obliquely backward from front. Exorbital angles located distinctly backward. Stridulating ridge already characterised by elements, which are gradually transformed from tubercles into striae from the upper end downwards. P2 propodus with a median row of long setae on anterior surface. P3 propodus sparsely setose on anterior surface.

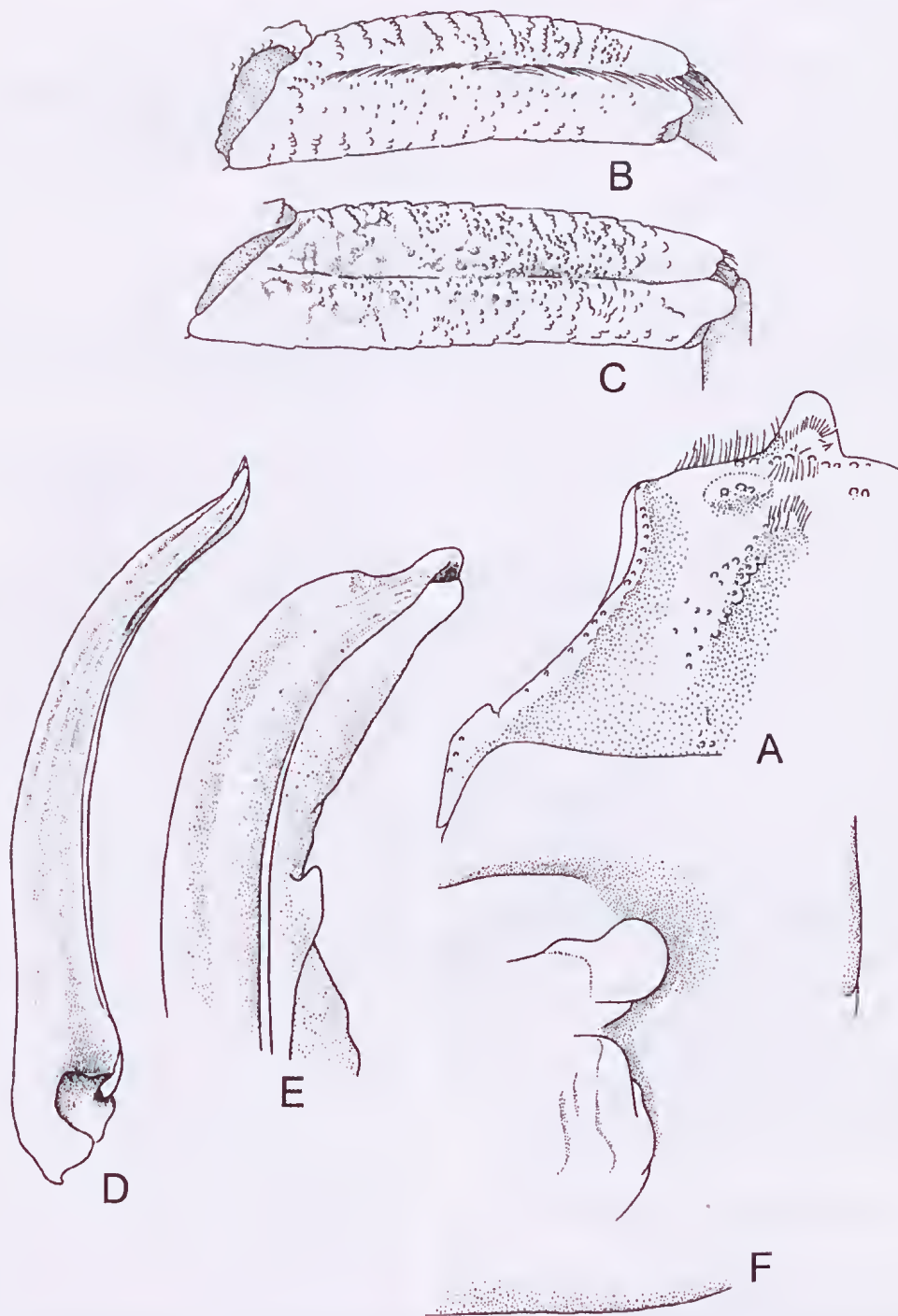


FIG. 16. *Ocypode jousseaumei*: A, P1 thoracic sternite; B, C, P2-3 propodi; D, E, Go1; F, female operculum.

Table 3. Differences between *O. fabricii* and *O. jousseauimei*.

<i>O. fabricii</i>	<i>O. jousseauimei</i>
Carapace covered with coarse tubercles becoming finer toward middle (branchial region).	Carapace covered densely with fine tubercles.
Male P2 propodus with two rows of setae on anterior surface.	Male P2 propodus with one row of setae on anterior surface.
Stridulating ridge composed of fine striae.	Stridulating ridge composed of tubercles and tubercles with striae.
Distributed in northern and western Australia.	Distributed in the Gulf of Aden.

Distribution. Only known from the Gulf of Aden (Yemen and Djibouti) and the Gulf of Oman (surroundings of Masqat). Though the holotype is labelled 'Red Sea', this might refer to the southern-most part, already in the straits of Bab el Mandeb. To date there are no records from the Red Sea proper. Type locality: Obock, Djibouti (Nobili 1906b).

Remarks. *Ocypode jousseauimei* from the Gulf of Aden seems very similar to *O. fabricii* from northern and western Australia. Those two species are, however, easily distinguishable from each other by the differences between them listed in Table 3.

Juvenile specimens of *O. jousseauimei* are also easily distinguishable from the potentially sympatric species *O. saratan* by the length of their stridulating ridge; in *O. jousseauimei* the stridulating ridge extends dorsally past a line corresponding the median line of the movable finger, while in *O. saratan* the stridulating ridge reaches the line but does not extend further.

The type locality of *O. jousseauimei* was corrected by Nobili (1906) from the Red Sea to Obock (now in the Republic of Jibouti), and there has been no evidence since that this species occurs in the Red Sea. The very small number of male specimens recorded from the Gulf of Aden, suggests that it is not well established there.

Ocypode kuhlii De Haan, 1835

(Figs 3B, 17, 39)

Ocypode (*Ocypode*) *kuhlii* De Haan, 1835: Fauna Japon. Crust., 29, 58; Herklots, 1861: 128.

Ocypode kuhlii – De Man, 1881: 250; Miers, 1882: 384 [in part: not pl. 8, 8a = *O. convexa*]; De Man, 1883: 156; Osório, 1888: 238; Crosnier, 1965: 101, figs 157, 164, 176-177, pl. 9, fig. 1; Holthuis, In

Yamaguchi, 1993: 626, fig. 18; Davie, 2002: 358; Ng, Guinot & Davie, 2008: 240.

Ocypode kuhli – De Man, 1895: 570; Ortmann, 1897: 364 [in part]; Tesch, 1918: 36; Gordon, 1934: 9; Tweedie, 1947: 32.

Ocypoda Kuhli – Doflein, 1904: 126.

Ocypode ceratophthalma – Rathbun, 1910a: 321[in part].

? *Ocypode kuhli* – Stephenson, Endean & Benett, 1958: 269.

Ocypode cf. *kuhlii* – McNeill, 1968: 86.

Material examined. India. Kondul (7°12.92'N, 93°42.6'E), Nicobar Islands, 1 juv. (SMF-8341). **Thailand.** NorthWest point of Phuket Is., female (RMNH-24992). **Indonesia.** Sumatera: Aceh, 6 males, 4 females (ZSM, originally from Natur Museum Lübeck) [det. De Man, 1895]; – Storm, male (ZMA-102367); male (RMNH-1615) [det. De Man, 1895]; – Padang, West Sumatera, 2 juv. males, 5 juv. females (RMNH-218); – Lsikin, Simeulue Is., off west coast of Sumatera, 2 juv. males (RMNH-2182); – Nias Island, off west coast of Sumatra, female (ZMA-102.336); – Luau vara, Nias Island, 2 males, 2 juv. females (MCG-147) [det. as *O. sp.*]; – Java: no further data, male [lectotype] (RMNH-D217), male [paralectotype] (RMNH-D 216), 2 dry males [paralectotypes], male, 6 juvs. (UZMK), 1 juv. (SMF-7850); – South coast, male, female (ZMA-102368); – Jakarta, male, female (ZMA-102365); – Semarang, male, dried (MNHN-3286); female (NHMW-1874) [det. as *O. cordiuanus*], Pfason; – Madura I., 1 juv. male, 1 juv. (RMNH-15514-516); – Kangean Islands off East Java, male (ZMA-102363), 'Siboga Expedition', St. 51; – Poelo Pete, 3 males, 5 juvs., 1 broken specimen (IRSNB-9223) [det. Gordon, 1934]; – South coast, Karang Hawoe, 1 juv. male (IRSNB-9223) [det. Gordon, 1934 as *O. sp.*]; – Lesser Sunda Islands: Bali, South-West coast, Batu Belig Beach (8°40.96'N, 115°9.1'E), North-West of Legian, male (SMF-23298), x.1994, C. Tautz-Kopania; – Lombok, Ampenan, 1 juv. female, 2 juv. males (MCZ-7246) [det. Rathbun, 1910 as *O. ceratophthalma*]; – Flores, 7 males, 10 juv. males, 2 females, 19 juv. females (RMNH), 'Snellius Expedition'; – Flores, South coast, female (MS-t11431); – Flores, South-east coast, Paga (8°46.77'N, 122°2.67'E), female (SMF-7611); male (SMF-20288 [ex. WAM]), 2.vi.1973, R.W.

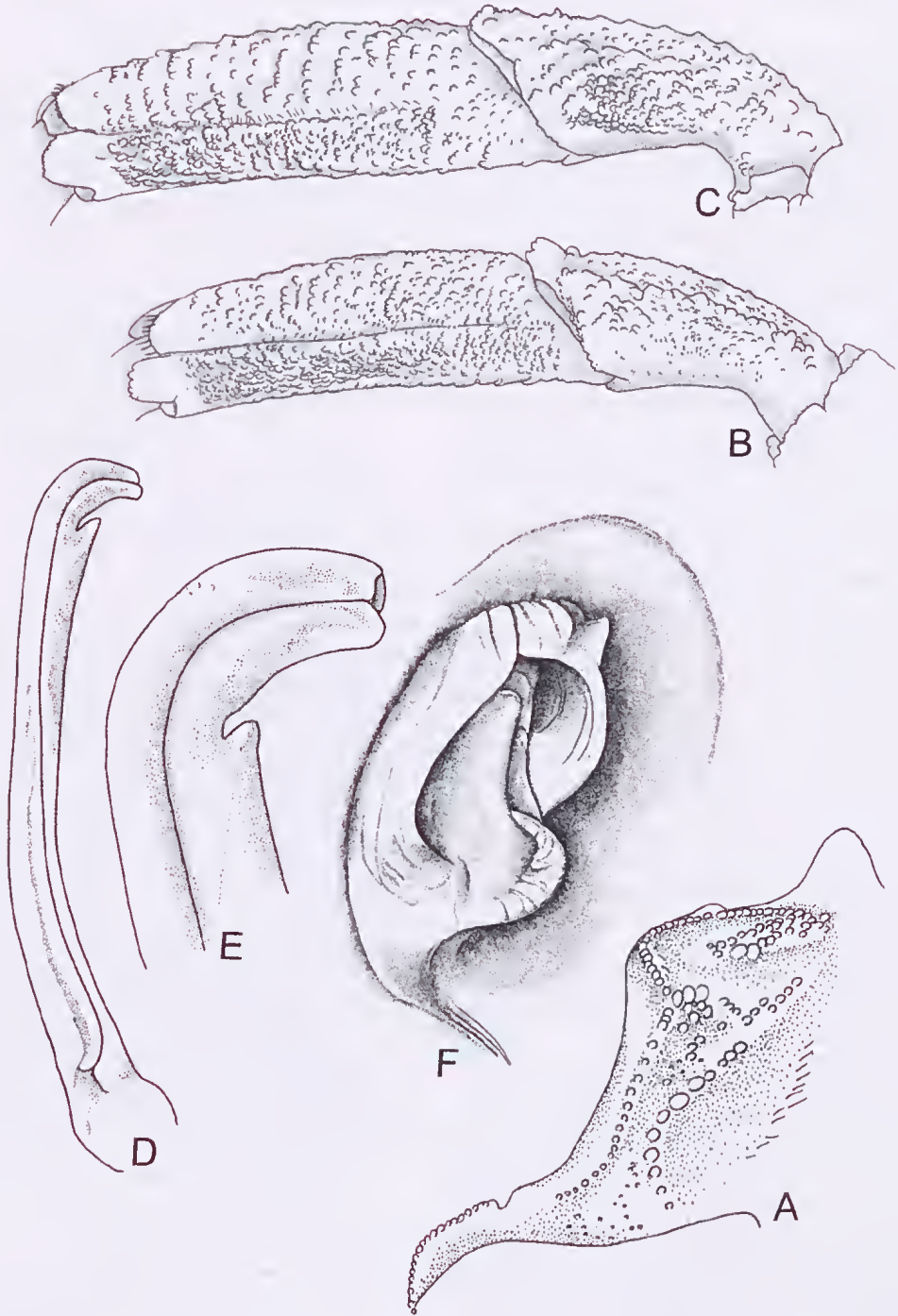


FIG. 17. *Ocypode kuhlii*: A, P1 thoracic sternite; B, C, P2-3 carpi and propodi; D, E, Go1; F, female operculum.

George; – Solor Island, Lamakera, male (ZMA-102.364) [det. Tesch, 1918]; – Timor, female (MBL-1852) [det. Osório, 1887]; – Moluccas: Ternate, 1 juv. (RMNH), ‘Snellius Expedition’; – Irian Jaya, Western New Guinea: Sekru, north-west coast of New Guinea, 1 juv. male (RMNH-15514-516); – Kabupaten Nabire, male (RMNH-15513); – Kali Buaja near Holtekang, East coast of Humboldt Bay (= Yos Sudarso Bay), male (RMNH-16296); 1 juv. male (RMNH-15514-516); – Jayapura, Humboldt Bay (= Yos Sudarso Bay), 5 juv. males, 1 juv. female (RMNH-16297); – Haytefa, Humboldt Bay (= Yos Sudarso Bay), 2 juv. females (RMNH-15493-500). **Papua New Guinea.** Solomon Is, Bougainville, female (ZSM); male (USNM-90874).

Diagnosis. Middle- to large-sized species. Eye-stalks not prolonged distally beyond cornea. Exorbital angles acutely triangular. Stridulating ridge composed of *c.* 10 interspaced tubercles. P2–5 propodi naked on anterior and posterior surfaces. Go1 slightly narrowing distally, and curved laterally in distal part, bearing a palp. Operculum of female genital opening broadened.

Description. Carapace (Fig. 39) wider than long, and covered densely with fine tubercles, becoming larger toward lateral. Exorbital angles acutely triangular and protruding anteriorly. Lateral margins of carapace distinctly directed outwards from base of exorbital angle in anterior half of carapace, and then directed inwards in posterior half, and carapace broadest at its middle. Pterygostomial region with distinct tubercles, becoming smaller and indistinct towards lateral sides of mouth parts. P1 thoracic sternite (Fig. 17A) bearing tuberculate humps near anterior margin, and tuberculate carinae surrounding posterior two-thirds and on anterior margin. Palm of larger cheliped distinctly serrated on ventral margin. Stridulating ridge (Fig. 3B) composed of *c.* 10 interspaced tubercles arranged in a straight row at least in dorsal two-thirds. Smaller cheliped pointed at distal end. P2–3 carpi and propodi (Fig. 17B–C) naked on anterior and posterior surfaces. Go1 (Fig. 17D–E) three-sided proximally, slightly narrowing distally, and curved laterally in distal part, bearing a distinct cone-shaped palp directed distally. Operculum of female genital opening (Fig. 17F) broadened and posterior half of operculum reaching to caudal end of genital opening; median rim broad.

Juvenile specimens. In a specimen (10.0×12.9 mm, IRSNB-9223) stridulating ridge composed

of *c.* 9 irregularly arranged indistinct granules. In a larger specimen (15.1×19.3 mm, MCZ-7246) stridulating ridge composed of distinct tubercles arranged in a straight row as in adult ones. Stridulating ridge easily distinguishable because of its smooth and flat surroundings. P2–3 propodi naked on anterior surface. Epibranchial angles very evident.

Distribution. Nicobars, southern Thailand, throughout Indonesia, Papua New Guinea. Type locality: ‘Mari Indico’.

Remarks. *Ocypode kuhlii* had long been considered to be distributed widely in the Indo-West Pacific region until Sakai, K. & Türkay (1976) showed that the species considered as *O. kuhlii* by earlier authors is in reality heterogeneous. We found that *O. ryderi*, hitherto regarded as a synonym of *O. kuhlii*, was a valid species distributed in the western Indian Ocean. *O. kuhlii* is restricted to an area ranging from N. Sumatera and Timor to New Guinea and Bougainville, North Solomon Islands (Papua New Guinea). Crosnier (1965) stated that one specimen of *O. kuhlii* reported by Miers (1882) from Madagascar had to be considered as belonging to his new species *O. madagascariensis* (Crosnier, 1965: 102). A specimen from New Hebrides, also attributed to *O. kuhlii* by Miers (1882) was identified as part of this study as *O. convexa* because of the number of tubercles on the stridulating ridge. The record of *O. kuhlii* by Stephenson *et al.* (1958) from the Great Barrier Reef is doubtful, because, according to McNeill (1968), the specimen from Low Isles of the Great Barrier Reef recorded by them, could not be traced. A subsequent revision of the *Ocypode* holdings of the Australian and Queensland Museums in 1980 by one of us (M. T.) also failed to find any specimens of *O. kuhlii* from Australia, and therefore, a misidentification of *O. ceratophthalma*, *O. cordimanus*, or *O. pallidula* as *O. kuhlii* is the most probable explanation.

Rathbun (1910b: 305) recorded *O. ceratophthalma* based on 7 juveniles from Lombok. Upon our re-examination her material has turned out to include 3 specimens of *O. kuhlii*, and therefore, only 4 specimens were correctly identified as *O. ceratophthalma*.

Ocypode macrocera H. Milne Edwards, 1837
(Figs 3C, 18, 40)

Ocypoda macrocera H. Milne Edwards, 1837: 49 [in part]; Lucas, 1840: 57; Heller, 1865: 42; Miers, 1882: 381, pl. 17, figs 2, 2a, 2b; Henderson, 1893: 387; Alcock & Anderson, 1894: 202; Ortman, 1897: 360, 368; Alcock, 1900: 345, 347 [in part]; Kemp, 1915: 219, fig. 6; Gravely, 1927: 148; Chopra & Das, 1937: 419 [in part]; Nagabushanam & Rao, 1967: 1109; Nageswara Rao *et al.*, 1986: 1.

Ocypode macrocera — White, 1847: 35; H. Milne Edwards, 1852: 142; Kingsley, 1880: 181 [in part]; Altevogt, 1959: 130–133, fig. 3; Guinot-Dumortier & Dumortier, 1960: 136, 148, tab. 3; Rao, 1966: 257; Rajabai, 1974: 203; Sakai, K. & Türkay, 1977a: 178, Pl. 1; Nadarajalingam & Subramoniam, 1987: 43–53, tabs 2, 3, 5; Ng *et al.*, 2008: 240.

Ocypoda portonovoensis Prem Kumar, 1964: 153, fig. 1, pl. 4, figs 1, 2.

Ocypode portonovoensis — Serène, 1968: 97.

Ocypode macrocerus — Serène, 1968: 97.

? *Ocypoda stimpsoni* — Baksi, Ray & De, 1980: 184–187, pl. 2 fig. 3.

Material examined. Myanmar. Yangon, male (USNM-106702), G. E. Gates. Arakan; — male (NHMW-2168). India. No further data, male (UZMK); — Nicobar Islands, female (NHMW-1627) [det. Heller, 1865], 1857–59, 'Novara Expedition'; — Ganjam, east coast of India, male (NHM); — Ennore, east coast of India, male, 2 females, larger cheliped (NHM-1892.7.15.26–28); — Puducherry (= Pondicherry), male [lectotype], female, dried [syntype] (MNHN-3304) [det. H. Milne Edwards, 1837], Leschenoult; male, dried (MNHN) [det. H. Milne Edwards, 1837], Reynaud; 3 males, 1 juv. male, female, 1 juv. female (MNHN), 1959, ldetmov; — Parangipettai (= Porto Novo), female [type specimen of *C. portonovoensis* Prem Kumar, 1964] (ZSI-C-4351/1); — Tharangambadi (= Tranquebar), 5 males, 4 females (UZMK); — Toothukudi (= Tuticorin) (8°44.64'N, 78°10.21'E), 3 males (NHM-1890.10.20.6–10), E. Thurston; male (SMF-6772). Sri Lanka. Trinkomali, female (UZMK); 2 females (NHMW), ix 1929, Zool. Inst. Wien, Nr. 384; male, dried (MHNG) [det. Sakai, K. & Türkay, 1977]; 2 males (MHNG-563a). Pakistan. Karachi, 3 males (NHM-82.278). Wrong locality. ? Tahiti, 2 males (NHMW) [det. Heller, 1865, locality confused], 1857, 'Novara Expedition'.

Diagnosis. Middle-sized species. Eystalks prolonged distally beyond cornea in a stylus. Exorbital angles protruding laterally. Stridulating ridge composed of 36–56 tubercles with striae. Chela of smaller cheliped truncate distally. P2–3 propodi with setae on dorsal half of anterior surface. Go1 slightly curved laterally in distal part, bearing a palp. Operculum of female genital

opening rounded and protruding mesially; lateral rim distinct.

Description. Carapace (Fig. 40) distinctly wider than long and covered dorsally with fine tubercles, which becoming distinct along anterolateral borders. Lateral half of orbital margin almost straight and directed obliquely backward. Exorbital corners angulate, tooth-shaped, and protruding outward in adult males, but not in females and young males. Lateral margins of carapace directed slightly outwards from base of exorbital corner in anterior third of carapace, and then directed inwards in posterior two-thirds in adult males, and carapace broadest at exorbital corners or anterior third, while in females and young males lateral margins of carapace directed straight backwards and parallel with each other. Pterygostomial region sparsely tuberculate, but smooth around buccal cavern. P1 thoracic sternite (Fig. 18A) smooth, bearing tuberculate carinae on anterior and lateral margins, and a transverse granulous carina at anterior third (SMF-6772). Palm of larger cheliped broad and densely tuberculate on anterior surface, and distinctively serrated on dorsal and ventral margins. Stridulating ridge (Fig. 3C) composed of 36–56 tubercles with striae; 9 slightly interspaced tubercles with striae in dorsal third and 27 closely pressed elongate tubercles with striae in ventral two thirds. Chela of smaller cheliped truncate distally. P2 propodus (Fig. 18B) with numerous short oblique rows of setae on dorsal half of anterior surface, bearing two median rows of setae. P3 propodus (Fig. 18C) with setae on dorsal half of anterior surface, bearing one median row of setae. P4–5 propodi naked. Go1 (Fig. 18D–E) three-sided proximally, slightly narrowing distally, and curved laterally in distal part, bearing protruding palp directed distally. Operculum of female genital opening (Fig. 18F) roundly protruding in mesial half; lateral rim distinct.

Distribution. Pakistan, India (including Nicobars), Sri Lanka, Myanmar. Type locality: 'Les Indes orientales, le Brésil etc.' (in error).

Remarks. As demonstrated by Sakai, K. & Türkay (1977: 178), the type locality of *Ocypode macrocera* is Pondicherry, India. These authors also discussed in detail the synonymy of *O.*

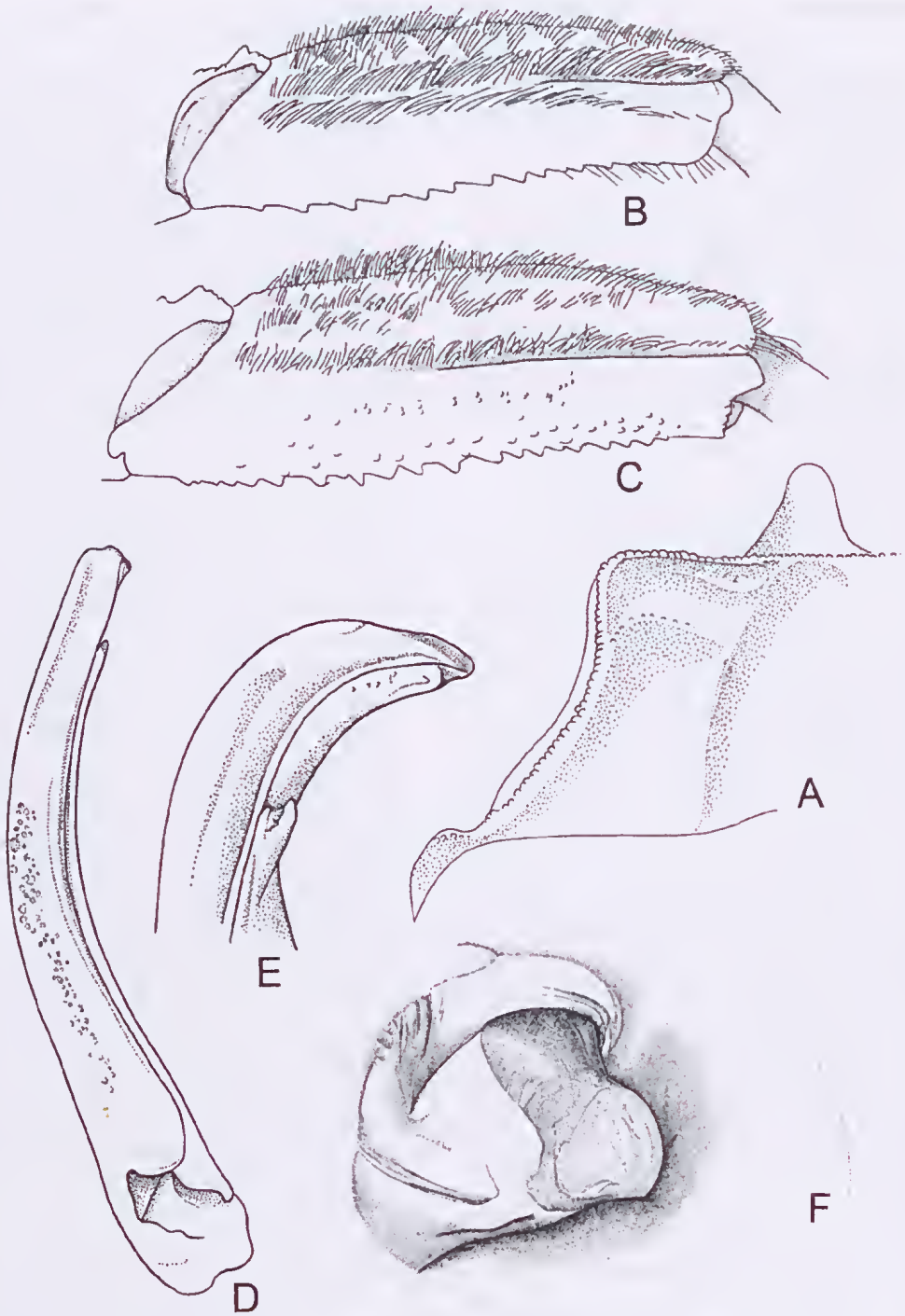


FIG. 18. *Ocypode macrocera*: A, P1 thoracic sternite; B, C, P2-3 propodi; D, E, Go1; F, female operculum.

portonovoensis with *O. macrocera*, and concluded that the former was based on a specimen with regenerated chelipeds. The record of *O. macrocera* from Japan by Urita (1917) refers in reality to *O. stiimpsoni* (see under that species).

Ocypode madagascariensis Crosnier, 1965
(Figs 3D, 19, 41)

Ocypode cordimana – Krauss, 1843: 41.

Ocypoda kuhlii – Miers, 1882: 385 [in part].

Ocypode madagascariensis Crosnier, 1965: 103–105 [in part: only specimen of Petit identified by Balss as *Ocypode* aff. *nobilii*], figs 159, 166, 180–181, pl. 9, fig. 3, pl. 11, fig. 2; Berry, Smale & Jackson, 1976: 29; Berry, 1976: 35–37, 1 unnumbered text-fig.; McLachlan, 1980: 57; Kensley, 1981: 49; Jackson, Smale & Berry, 1991: 280–286, tabs 1–3, text-fig. 1; Ng, Guinot & Davie, 2008: 240.

Material examined. Madagascar. Tuléar [= Toliara], male [holotype] (MNHN) [det. Crosnier]; – Lokaro Island near Fort Dauphin, East coast of Madagascar, male, female (MNHN) [det. Crosnier], 7.iii.1973; – Tamatave, East coast of Madagascar, 1 ovig. female [det. as *O.* sp.]; male, female (NHM-82.6) [det. Miers, 1882 as *O. kuhlii*]; male (NHM) [det. Miers, 1882 as *O. kuhlii*]; female (NHM-1892.7.4.1). Comores. Grand Comore, Ngazidja, male (MNHN) [det. as *O. cordimana*], P. Fournanoir. South Africa. No further data, 1 juv. male (RMNH); female (NHM-1917.6.19.48); – KwaZulu-Natal: No further data, 2 males (SMF-7274); – Kosi Bay, female (NHM-1917.6.19.48); – Boteler Point (27°1.0'S, 32°51.92'E), male, 5 females (SMF-10931). No definite locality. male (ZMH-2969).

Diagnosis. Middle-sized species. Eyestalks not prolonged distally beyond cornea. Exorbital angles broadly triangular and distinctly protruding anteriorly. Stridulating ridge composed of 20–30 tubercles with striae. P2–3 propodi setose on dorsal half of anterior surface. Go1 strongly crooked at distal end, bearing a palp. Operculum of female genital opening broad and rounded; median rim with strong triangular tooth.

Description. Carapace (Fig. 41) slightly wider than long, and covered densely with coarse tubercles on dorsal surface. Eyestalks not prolonged distally beyond cornea. Lateral half of orbital margin regularly concave. Exorbital angles triangular and distinctly protruding forward. Lateral margins of carapace directed outwards from tip of exorbital angle in anterior third of carapace, and then directed inwards in

posterior two-thirds, and carapace broadest at anterior third. Pterygostomial region distinctly tuberculate, but smooth along lateral sides of buccal cavern. P1 thoracic sternite (Fig. 19A) tuberculate irregularly on surface, bearing tuberculate carinae on anterior and lateral margins, and an obliquely running swelling with tubercles at anterior third. Palm of larger cheliped broad, bearing strong denticles on ventral margin and small denticles on dorsal margin. Both chelipeds scattered irregularly with coarse tubercles on anterior surface. Stridulating ridge (Fig. 3D) composed of 20–30 closely spaced tubercles with striae. Smaller cheliped pointed at distal end. P2–3 propodi (Fig. 19B–C) setose on dorsal half of anterior surface. P4–5 propodi naked. Go1 (Fig. 19D–E) three-sided proximally, slightly narrowing distally; strongly crooked at distal end; bearing a bulging, rounded palp at base of distal crook. Operculum of female genital opening (Fig. 19F) broad and rounded; median rim with strong triangular tooth.

Distribution. Madagascar; SE coast of Africa, Mozambique to Natal. Type locality: Tuléar, Madagascar [= Toliara].

Remarks. *Ocypode madagascariensis* Crosnier, 1965, had earlier been reported from Madagascar under the names *O. kuhlii* or *O. cordimana*. Crosnier (1965: 105) remarked that *O. kuhlii* described by Miers (1882: 385) based on a specimen (NHM-82.6) from Madagascar would probably prove to be identical with his species *O. madagascariensis*. Krauss (1843: 41) described two species, *O. cordimana* and *O. ceratophthalma* based on specimens from South Africa. However, his description of *O. cordimana*, especially the following part; 'Die Unterscheidungsmerkmale von letzter (*O. ceratophthalma* – Anm. Verf.) liegen aber hauptsächlich in einem mehr breiten als langen und in einem gewölbten Rückenschild ... [= The characters to distinguish *O. cordimana* from *O. ceratophthalma* lie chiefly in the carapace which is more wider than long and more strongly vaulted ...]' suggests that Krauss' '*O. cordimana*' is not identical with *O. cordimanus* Latreille, 1818, because the carapace of *O. cordimanus* is not more wider than long than that of *O. ceratophthalma* and not strongly vaulted but as flat as *O. ceratophthalma*, so

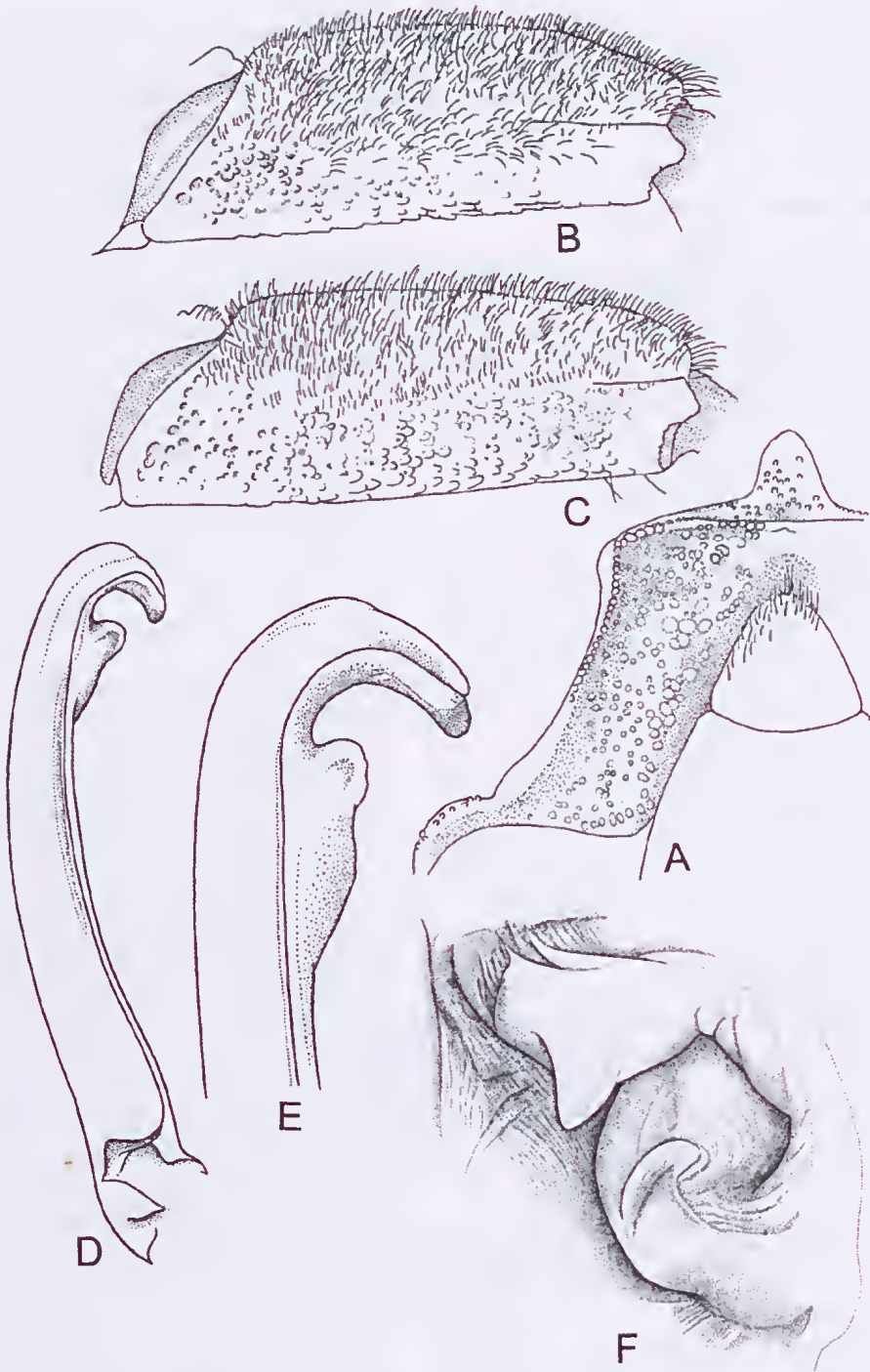


FIG. 19. *Ocypode madagascariensis*: A, P1 thoracic sternite; B, C, P2-3 propodi; D, E, Go1; F, female operculum.

Table 4. Comparison in characteristics among 6 species of *Ocypode*.

	<i>O. cordimanus</i>	<i>O. madagascariensis</i>	<i>O. ceratophthalma</i>	<i>O. pauliani</i>	<i>O. kuhii</i>	<i>O. ryderi</i>
Carapace CW/CL (mm)	1.10	1.19	1.18	1.19	1.23	1.26
Anterolateral margin of carapace.	Rounded.	Rounded.	Straight.	Straight.	Rounded.	Rounded.
Eyestalks.	Not prolonged.	Not prolonged.	Prolonged.	Not prolonged.	Not prolonged.	Not prolonged.
Stridulating ridge.	Absent.	Composed of 20-30 closely spaced tubercles with striae.	Composed of 10-11 interspaced tubercles in dorsal third, 8 thick striae in middle third, and 20-30 closely spaced fine striae in ventral third.	Composed of 7-13 tubercles.	Composed of c. 10 interspaced tubercles.	Composed of c.15 irregularly arranged tubercles.
Pereiopod 2 propodus.	With transverse rows of setae on dorsal half of anterior surface, bearing a median row of setae.	Setose on dorsal half of anterior surface.	With oblique rows of setae on dorsal half of anterior surface, bearing two median rows of setae.	With setae on and along dorsal margin.	Naked on anterior surface.	Naked on anterior surface.
Pereiopod 3 propodus.	With thick setae along dorsal margin.	Setose on dorsal half of anterior surface.	With oblique rows of setae on dorsal half of anterior surface, bearing two median rows of setae.	With setae on and along dorsal margin.	Naked on anterior surface.	Naked on anterior surface.

Krauss' '*O. cordimana*' must be identical with *O. madagascariensis* occurring in almost the same area, whose carapace is always more wider than long and more strongly vaulted than that of *O. ceratophthalma*. Unfortunately Krauss' specimens are lost (H. Janus, Museum Stuttgart, *in litt.*), so this can never be confirmed. Crosnier (1965) indicated that one male of Petit's specimens from Tuléar determined by Balss as *O. affinis nobilii* is identical with *O. madagascariensis*.

O. madagascariensis is best characterised by the shapes of the Go1 and the female genital opening, which are diagnostic (a comparison of six species of *Ocyropode* that have often been misidentified is presented in Table 4). However, it is very difficult to distinguish juvenile specimens of *O. madagascariensis* from *O. pauliani* of the same size, not only because they are very similar to each other in the carapace and the eyestalks, but also because they are both distributed in Madagascar. However, the former is distinguishable from the latter by the structure of the stridulating ridge and the pattern of setae on the anterior surfaces of the P2–3 propodi.

It is also to be added that in a male specimen examined (SMF-7274) the stridulating ridge is composed of as many as 30 closely spaced tubercles with striae, though Crosnier stated that it is composed of 20 tubercles with striae.

Ocyropode mortoni George, 1982

(Figs 3E, 20, 42)

Ocyropode mortoni George, 1982: 187–190, fig. 1C, 2C, pl. 3; Sakai K., 2000:1159, figs 2a–b, 3a–e; Ng, Guinot & Davie, 2008: 240; Wong, Shih. & Chan, 2012: 71–87, figs 1–8.

Ocyropode macrocera – Dai *et al.*, 1985: 370, figs 1–7, pl. 1, figs 1–2; Yang, 1986: 153.

Material examined. **China.** No further data, 2 males (SMF-36912); – Tai Long Wan, Sai Wan, East New Territories, Hong Kong, 2 males, female (WAM-230–80); – Hainan, Sanya, Xishatan, female [23.3×27.5 mm] (SMF-36189, ex. Coll. IOAS), 19.iii.1958. **Japan.** Kochi Prefecture: Cape Muroto, Toyo-cho, sandy beach of Ikumi (33°31.68'N, 134°17.06'E), male [22.0×26.0 mm], female [24.4×28.2 mm] (SMF-36190, ex. BLT-6277), 4.x.1998, I. Mano.

Diagnosis. Small-sized species. Eyestalks prolonged distally beyond cornea in a stylus. Exorbital angles protruding outward. Stridulating ridge composed of 35–71 striae, not extending ventrally over median line of fixed

finger. Smaller cheliped broadly rounded to truncate at distal end. P2–3 propodi with a median row of setae on anterior surface. Go1 slender, slightly narrowing distally, and curved laterally in distal part, bearing a small palp distant from distal end. Operculum of female genital opening directed obliquely forward at an angle of 45° relative to midline, without prominent lateral rims.

Description. Carapace (Fig. 42) slightly wider than long; covered densely with fine tubercles on dorsal surface. Lateral half of orbital margin directed obliquely backwards to exorbital corner. Exorbital corners protruding outward. Lateral margins of carapace directed slightly outward from base of exorbital corner in anterior third of carapace and then directed inward in posterior two-thirds, forming distinct epibranchial angles, where carapace broadest. Pterygostomial region spacious and finely tuberculate except along lateral sides of buccal cavern. P1 thoracic sternite (Fig. 20A) smooth. Palm of larger cheliped broad and beset with regularly arranged coarse tubercles on anterior surface, and serrated regularly on ventral margin and roughly on dorsal margin. Stridulating ridge (Fig. 3E) composed of 35–71 striae, terminating far from ventral margin of palm without extending ventrally over median line of fixed finger. Smaller cheliped rounded to truncate at distal end. P2 propodus (Fig. 20B) with a short row of setae along dorsal margin on anterior surface, bearing a median row of scanty setae. P3. propodus (Fig. 20C) setose on dorsal half of anterior surface, bearing a median row of short setae. Go1 (Fig. 20D–E) slender, slightly narrowing distally; curved laterally at distal end; bearing a small palp distant from distal end. Sperm-channel originating dorsally, running without torsion along distal curve into flat terminal part. Distal opening located terminally. Operculum of female genital opening (Fig. 20F) directed obliquely forward at 45° to sternal median line, without rim. Vagina deep anteriorly; sunken in shape of funnel.

Distribution. S. China (Hongkong, Quandong, Guangxi, and Hainan); southern Japan. Type locality: Sai Wan-Tai Long Wan, E. New Territories, Hongkong.

Remarks. The present species is closely related to the sympatric species *O. stimpsoni*, with

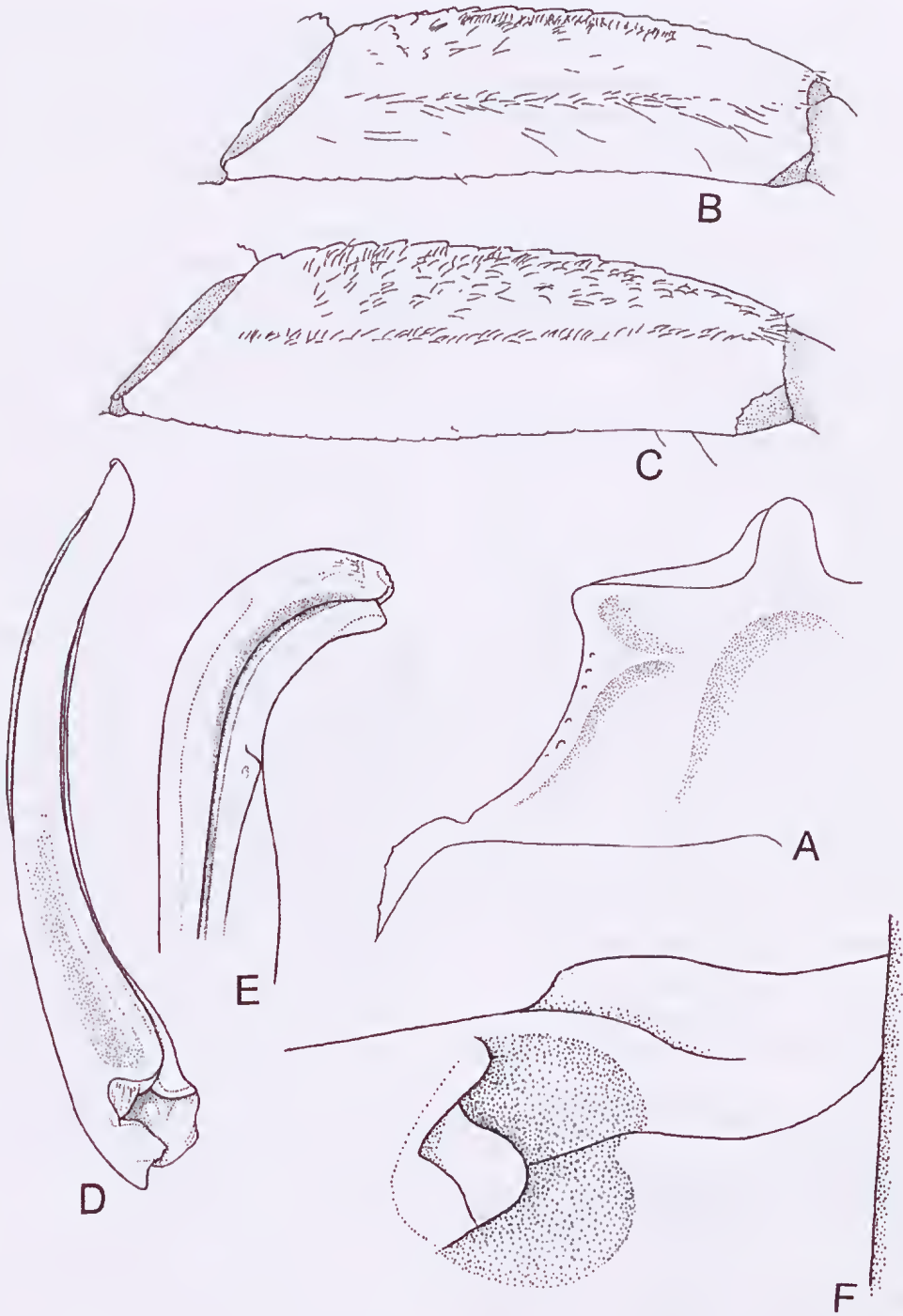


FIG. 20. *Ocypode mortoni*: A, P1 thoracic sternite; B, C, P2-3 propodi; D, E, Go1; F, female operculum.

which it shares an almost identical Go1, however, it differs from that species by having the eyestalks prolonged distally beyond the cornea in a stylus; a rather short stridulating ridge that does not extend over the median line of the fixed finger; and the palm of the larger cheliped coarsely tuberculate on the anterior surface. Conversely, the eyestalks of *O. stimpsoni* are not prolonged distally beyond the cornea, the stridulating ridge is longer, always over-reaching the median line of the fixed finger, or even almost reaching the ventral margin of the palm, and the palm of the larger cheliped is finely tuberculate.

Wong *et al.* (2012) mention that 'It [*O. mortoni*] was always sympatric with the common *O. ceratophthalmus* (Pallas, 1772) at the same tidal level, and there appeared to be no clear habitat/niche distinction. Relative abundance of *O. mortoni* vs. *O. ceratophthalmus* was at most in the ratio of 31:69% based on quantitative transect survey data from Sai Wan', and '... our results do not support George's preliminary ecological hypothesis.' In Toyo-cho, on the sandy beaches of Ikumi, Kochi Pref., Japan, facing the the Pacific Ocean, *O. ceratophthalma* is also common, whereas *O. mortoni* was recorded only once (Sakai, K. 2000). Nevertheless they can also be considered to be sympatric at this locality, and the low incidence of *O. mortoni* may be the result of the lower tidal zone being often effected by typhoons (in litt. Mano).

Ocypode nobilii De Man, 1902

(Figs 4A, 21, 43)

Ocypoda convexa – Nobili, 1900: 518.

Ocypode ceratophthalma – Lanchester, 1900a: 258 [in part].

Ocypode convexa – Lanchester, 1900b: 548.

Ocypoda nobilii De Man, 1902: 47, pl. 19, figs 2-3; Nobili, 1903: 20.

Ocypoda macrocera – Rathbun, 1910a: 322.

Ocypode macrocera – Suvatti, 1950:153.

Ocypode nobilii – Guinot-Dumortier & Dumortier, 1960: 135, fig. 17; Serène, 1968: 97; Ng *et al.*, 2008: 240.

Material examined. Malaysia. Borneo: No further data, 2 males (NHM); – Sarawak, male (NHM-1895 10.10.2-3); 3 males, female (MCSNG) [det. Nobili, 1899]; – estuary of Sarawak River (1°39.7'N, 110°28.72'E), Sarawak, 2 males, female (SMF-7273), 1967, W. Macnae; – Baram River (4°35.68'N,

113°58.93'E), Sarawak, male [holotype] (SMF-5412), W. Kükenthal; 2 females (NHM-1895.7.2.23-24); 4 males, 2 females (NHM-1895.2.7.17-22); – E-Buntal, Santubong Peninsula, Sarawak, male (NHM); – Sarawak, Baka Beach, female (ZRC-199.0683) [det. Lanchester, 1900], vi.1999, P. Ng *et al.*; – Malacca, male (UZMK). Cambodia. Island Kaoh Kong, Gulf of Thailand, female (UZMK) [det. Rathbun, 1910].

Diagnosis. Small-sized species. Eyestalks not prolonged distally beyond cornea. Exorbital angles broadly triangular with tips directed behind. Stridulating ridge composed of 99–120 closely spaced fine striae. Smaller cheliped rounded to truncate at distal end of chela. P2 propodus setose along dorsal margin, bearing two rows of setae on anterior surface. P3 propodus setose on dorsal half of anterior surface, bearing a median row of setae. Go1 strongly curved laterally in distal part; broadened at distal end; bearing a palp. Horny terminal endpiece much wider than long. Operculum of female genital opening protruding mesially; rounded distally. Vaginal slit oval.

Description. Carapace (Fig. 43) distinctly wider than long and beset densely with fine tubercles. Orbital margin with a median bulge, its lateral half directed obliquely backwards. Exorbital angles broadly triangular and directed slightly anterolaterally with tips directed behind, and located clearly posterior to median convexity of orbital margin. Lateral margins of carapace directed outward from base of exorbital angle in anterior third of carapace, and then directed inward in posterior two-thirds, forming epibranchial angle, where carapace broadest. Pterygostomial region with distinct tubercles except along lateral sides of buccal frame. P1 thoracic sternite (Fig. 21A) smooth on surface, bearing tuberculate carinae on anterior and lateral margins. Palm of larger cheliped broad, beset densely with fine tubercles on anterior surface, and finely serrated on ventral margin. Stridulating ridge (Fig. 4A) composed of 99–120 closely spaced fine striae. Smaller cheliped rounded to truncate at distal end of chela. P2 propodus (Fig. 21B) setose along dorsal margin, bearing a median row of long setae and another short row of long setae just below on anterior surface. P3 propodus (Fig. 21C) with transverse rows of setae on dorsal half of anterior surface, bearing a median row

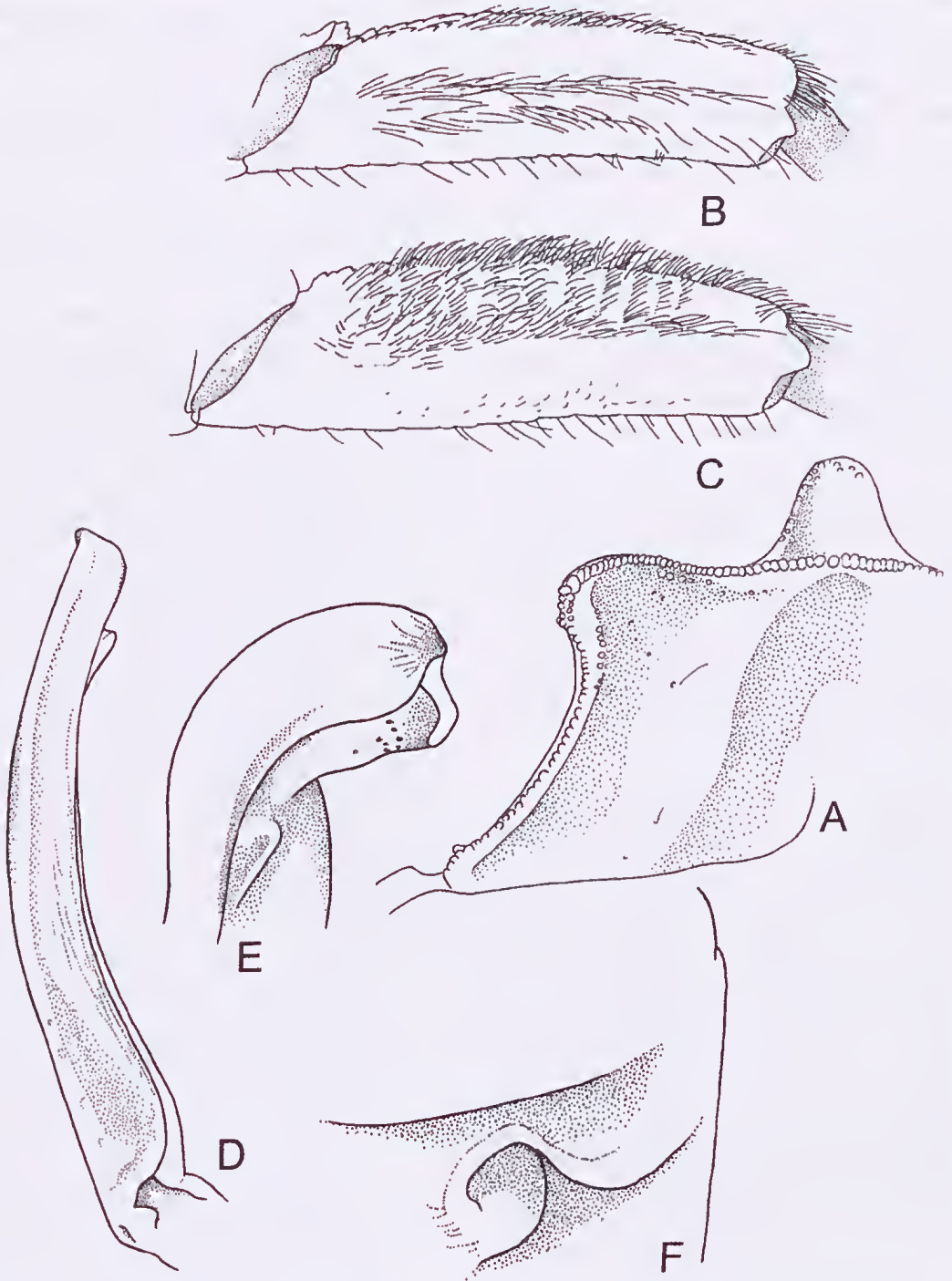


FIG. 21. *Ocypode nobilii*: A, P1 thoracic sternite; B, C, P2-3 propodi; D, E, Go1; F, female operculum.

of setae. Go1 (Fig. 21D–E) strongly curved laterally in distal part; broadened at distal end; bearing a cone-like palp. Sperm-channel originating dorsally and running dorsally without torsion into short, broad terminal endpiece. Distal opening located terminally. Operculum of female genital opening (Fig. 21F) protruding mesially and rounded distally. Vaginal slit oval.

Distribution. Malay peninsula and northern Borneo. Type Locality: Baram River, Sarawak, Malaysia.

Remarks. This species was reported for the first time by Nobili (1899) under the name of *Ocypode convexa*, however, De Man (1902) recognised the earlier record was not a typical *O. convexa* and named it as a separate species *O. nobilii* in honour of the Italian carcinologist. Nevertheless, this species seems to have continued to confuse later authors. Rathbun (1910) recorded *O. macrocera* based on a specimen (UZMK) from Koh Kong, Cambodia in the Gulf of Thailand, but our re-examination shows this was a mis-identification of *O. nobilii*. Thus, it is likely that *O. macrocera* reported from Lem Sing in Thailand by Suvatti (1950) is also *O. nobilii*, because his identification was based on Rathbun's definition.

Ocypode nobilii is very similar to *O. stimpsoni*, as suggested by De Man (1902), especially in the rounded to truncate distal end of the smaller cheliped, and the eyestalks without a distal projection. However they differ from each other in the pattern of setae on the P2–3 propodi, and in the morphology of the stridulating ridge and the sexual organs. *O. nobilii* is sympatric with both *O. ceratophthalma* and *O. cordimanus*, but it appears to prefer a different habitat. *O. nobilii* has been collected on muddy beaches near estuaries (De Man 1902; Sérene 1968), while Rathbun's (1910) '*O. macrocera*' is said to have come from a sandy beach. Further fieldwork is needed to better understand the ecological preferences of this interesting species.

Ocypode pallidula Hombron & Jacquinot, 1846

(Figs 4B, 22, 44)

- Ocypode rhombea* – Randall, 1840: 123 [not *O. rhombea* Fabricius, 1798: 348 a *nomen dubium* – *vide* Rathbun 1906: 834].
- Ocypoda pallidula* Hombron & Jacquinot, 1846, Atlas, pl. 6, fig. 1.
- Ocypoda laevis* – Dana, 1852: 325; Dana, 1855: pl. 20, fig. 2; Stimpson, 1858: 100 [not *Ocypode laevis* Fabricius, 1798: 348 which is here considered *nomen dubium*].
- Ocypoda cordimana* (junior) – Jacquinot & Lucas, 1853: 65 [only locality, not the description; description = *O. ceratophthalma* (Pallas, 1772), not *O. cordimana* Latreille 1818]; Kingsley, 1880: 185 [in part].
- Ocypoda kuhlii* – Miers, 1882: 386 [in part; only material from New Hebrides].
- Ocypoda ceratophthalma* – Miers, 1886: 238–239 [in part; only specimens from Hilo, Hawaii].
- Ocypoda urvillei* – Ortmann, 1897: 366–367; Lenz, 1901 Zool. Jb. Syst., 14: 476–477; Bouvier, 1915: 122 [not *O. urvillei* Guérin, 1829].
- Ocypode laevis* – Rathbun, 1906: 834, pl. 7, fig. 2; Stimpson, 1907: 110; Edmondson, 1962: 16, figs 6–7; Crosnier, 1965: 105; Fellows, 1966: 1–78; Serène, 1968: 97; Horch & Salmon, 1972: 9, fig. 6; Fellows, 1975a: 257–258, fig. 1; 1975b: 1–158.
- Ocypoda Urvillei* – Nobili, 1907: 407 [not *O. urvillei* Guérin, 1829].
- Ocypoda ceratophthalma* – Pesta, 1911: 54–55 [in part; material from Mauritius].
- ? *Ocypode kuhli* – Stephenson, 1958: 269, 273.
- Ocypode urvillei* – Michel, 1964: 12 [not *O. urvillei* Guérin, 1829].
- ? *Ocypode cf. kuhlii* – McNeill, 1968: 86.
- ? *Ocypode cordimana* – Ooishi, 1970: 94.
- Ocypode pallidula* – Sakai, K. & Türkay, 1976: 87–91, figs 14–15, pl. 2; Jones, 1988: 33; Poupin, 1996: 73; Clark & Crosnier, 2000: 417, tab. 4; Holthuis, 2002: 420; Ng, Guinot & Davie, 2008: 240.
- Ocypode aff. pallidula* – Poupin *et al.*, 2011: 18.
- Material examined. Madagascar.** No exact locality, 3 juvs. (SMF-36209), 1971, H. Kurokawa [ex. Sakai, T.]; – West coast, male (MNHN). **Mauritius.** No exact locality, male, 3 females (NHMW); 5 males (MNHN); female (MNHN-B32895); 5 males, female (MI); – Tombeau Bay, 6 males, female (MI); – Flic en Flac, 1 juv. male, 2 females (MI); – Wolmar near Flic en Flac, 2 males, 3 females (MI); – Mahébourg, 2 males (RMNH-16293); male (MI); – Belle Maré, male (MI); – NW-coast Cannoniers Point [often previously cited as 'Cannonius Point' which is a spelling error] (20°0.02'S, 57°33.14'E), sandy beach, 11 males, 1 juv. (UZMK); 2 males, 2 females (SMF-7849), x.1929/Dr. Th. Mortensen's South Africa Expedition 1929/30.
- Réunion.** Beach near La Saline des Bains (21°05.68'S, 55°14.08'E), male, 6 females (SMF-18278), 28–30.i.1989,

H. G. Müller; — Pointe des Avirons, N of l'etang Salé de Bains (21°15.11'S, 55°19.23'E), sandy beach, male, 2 females (SMF-18279), 31.i.1989, H.G. Müller; — St. Paul beach (21°00.53'S, 55°16.1'E), 3 males (SMF-18280), 1.ii.1989, H.G. Müller. **Indonesia.** Pulau Binongko, the Tukangbesi group, Banda See, 5 males (RMNH-30272); — Pulau Wetar near Timor, female (RMNH-15558); — North of Jayapura, Yos Sudarso Bay (formerly known as Humboldt Bay), Western New Guinea (= Irian Jaya), 1 juv. male (RMNH-15493-15500). **Australia.** Queensland: South Inlet, Willis Island off Cairns (16°17.25'S, 149°57.95'E), Coral Sea, female (SMF-10919), viii-ix. 1975, Z. Števecić; female (SMF-10920); female (SMF-10921); male (SMF-10922); male (SMF-10923); male (SMF-10924); male (SMF-10925); — Holmes Reef, Coral Sea, 2 juv. males (AMS-P17033); — Herald Cay, NE Cay (16°56.48'S, 149°11.89'E), Coral Sea, male, female (SMF-6871), 8.xii.1964, McMichael & Yaldwyn; 3 males, 3 females (QM-W2508); — Diamond Island, West Cay (17°26.88'S, 150°58.6'E), 2 males, female (SMF-6870), x.1964, McMichael & Yaldwyn; 8 males, female (AMS-P16888); 4 males, 2 females (AMS-P16889); — Swains Reefs, Great Barrier Reef, 14 males, 5 females (AMS-P16894); female (AMS); — NW-End of Gillett Cay, Swains Reefs, 3 males, 3 females (AMS-P16894); — Lady Musgrave Island, Capricorn Group, 4 males, 2 females (NHM); 5 males, female (AMS-P14969); — N-Riff, Heron Island, male (ZMH-K32283); — South Gladstone, Lady Elliot Island, Great Barrier Reef, male, 3 females (AMS-P17087); — Sand Cay, Wreck Reef, male (AMS-P13511). **Norfolk Island.** male (MNHN); 3 males (AMS-P4099); — Emile Bay, Norfolk Island, sandy coast of upper tidal zone, 2 males (AMS-P17310). **Cook Islands.** Rarotonga, female (NHM-2382); male (NHM-3219); male (BMH-3301); — Manuae, female (NHM-71.201). **French Polynesia.** Rurutu (22°27.25'S, 151°19.71'E), Austral Islands, 2 males, female (MNHN), v.1980, P. Fourmanoir; male (SMF-9408); — Gambier Islands, Tuamotu Archipelago, 5 males (MNHN); — Mangareva I., Gambier Is, Tuamotu Archipelago, male (MNHN); — Rikitea, Mangareva I., Gambier Is, Tuamotu Archipelago, female (MNHN). **Johnston Atoll.** 5 males, 5 females (BMNH 1336). **USA.** Hawaii: 1 juv. (NHM-84.31); — Oahu, Hawaii, 3 males, 2 females (UZMK); 4 juvs. (ZMH-K27846); male (NHM-224); male (NHM-6936); 1 juv. (NHM-223); 6 juvs. (NHM-226); — Waimea, Hawaii, 3 juvs. (USNM-171297); — Paia, Maui, 1 juv. male, 2 juvs. (RMNH-19068). **Midway Island.** male (NHM-4933); — Laysan, 1 damaged specimen (NHM-225); 4 males, female, 2 juvs. (ZMH-K27732).

Diagnosis. Small- to middle-sized species. Eye-stalks not prolonged distally beyond cornea. Ex-orbital angles triangular and distinctly protruding anteriorly. Stridulating ridge composed of 30–42 (in male) or 17–29 (in female) thick striae.

Smaller cheliped pointed at distal end. P2–3 propodi sparsely setose on anterior surface. Go1 slightly narrowing distally; slightly curved laterally in distal part; lacking palp. Terminal part longer than broad. Operculum of female genital opening directed obliquely forward; protruding anteromesially; mesial rim evident at caudal end.

Description. Carapace (Fig. 44) slightly wider than long and beset densely with fine tubercles on dorsal surface. Lateral half of orbital margin distinctly concave. Exorbital angles triangular and directed anteriorly. Lateral margins of carapace directed straight backward from tip of exorbital angle in anterior third of carapace and then directed inwards in posterior two-thirds, forming distinct epibranchial angles where carapace broadest. Pterygostomial region spacious, and distinctly tuberculate except along lateral sides of buccal cavern. P1 thoracic sternite (Fig. 22A) shallowly concave in shape of triangle and rimmed anterolaterally with tuberculate carina. Palm of larger cheliped distinctly wider than long, and scattered coarsely with tubercles of different sizes on anterior surface, bearing denticles on ventral margin. Stridulating ridge (Fig. 4B) composed of 30–42 (in male) or 17–29 (in female) rather interspaced thick striae. Smaller cheliped pointed at distal end. P2 propodus (Fig. 22B) sparsely setose on anterior surface, bearing a short median row of scanty setae, and setae along dorsal margin, which expanded distally onto anterior surface. P3 propodus (Fig. 22C) sparsely setose on dorsal half of anterior surface, bearing setae and spinules on dorsal margin. Go1 (Fig. 22D–E) slightly narrowing distally, slightly curved laterally in distal part, lacking a palp. Sperm channel originating dorsally and running without torsion into flat terminal part. Distal opening located terminally. Operculum of female genital opening (Fig. 22F) directed obliquely forward; protruding anteromesially; mesial entrance sunken and concave, vagina slightly sunken at mesial entrance, mesial side rim evident in caudal half and obscure towards frontal side.

Juvenile specimens. In a juvenile (5.5×6.7 mm, USNM-171297) carapace distinctly wider than long, and beset densely with fine granules.

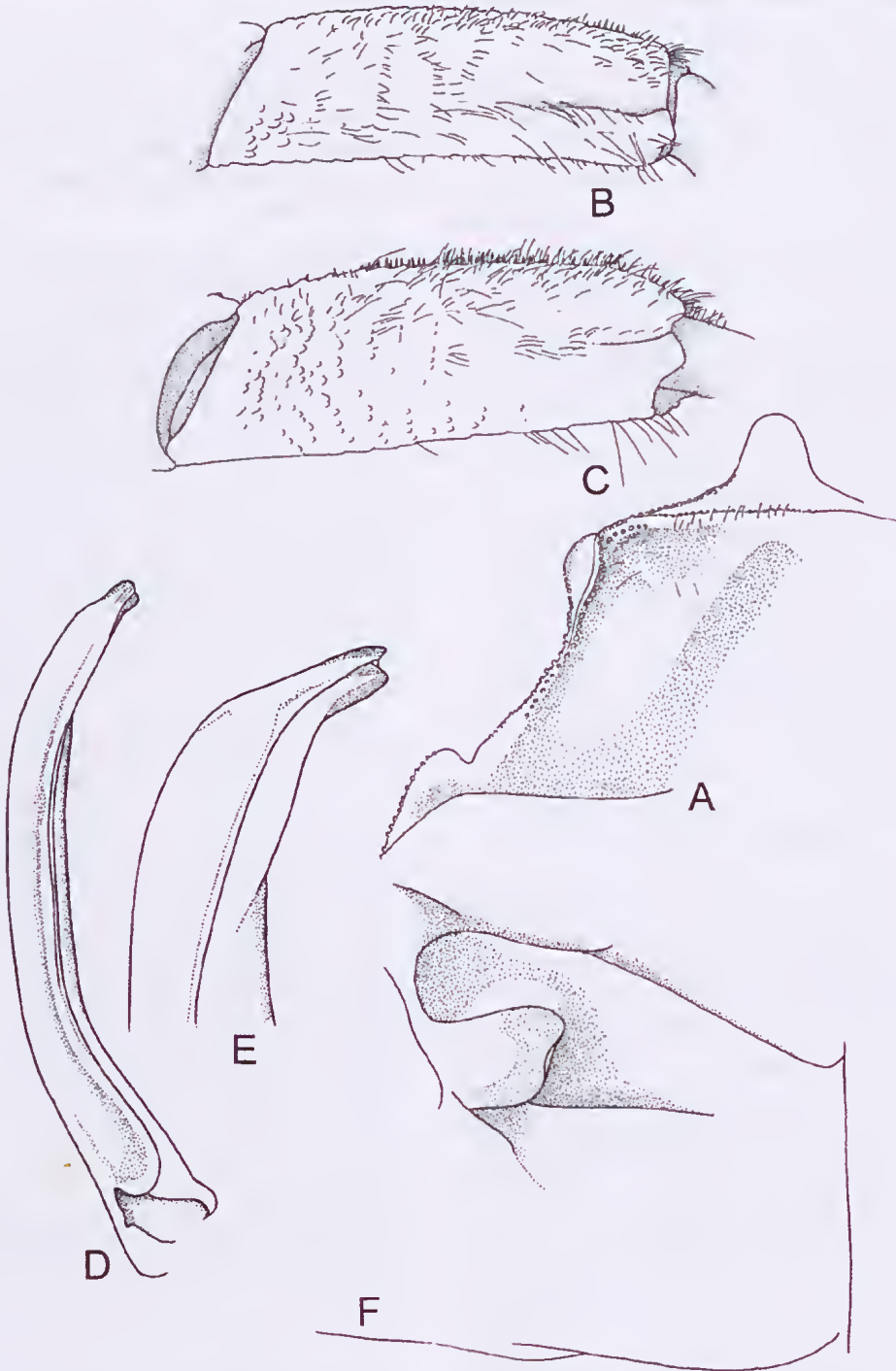


FIG. 22. *Ocypode pallidula*: A, P1 thoracic sternite; B, C, P2-3 propodi; D, E, Go1; F, female operculum.

Exorbital angles broadly triangular and less protruding. Carapace not broadening but keeping same width to epibranchial corners located at short distance from base of exorbital corners, and then narrowing. Palm of larger cheliped less wider than long and scattered more roughly with granules on anterior surface than in adult specimens. Stridulating ridge not yet distinct, but weakly developed as faint elevation. P2–3 propodi with scanty setae on dorsal margin, and P2 propodus with a median row of scanty setae on anterior surface. In a slightly larger specimen (8.0×9.5 mm, RMNH-30272) palm of large cheliped wider. Stridulating ridge already composed of interspaced striae as in adult specimens. P2 propodus with scanty setae on dorsal margin, which already expanded distally onto anterior surface, bearing a median row of setae on anterior surface, while P3 propodus naked on anterior surface.

Distribution. A relatively wide distribution: Hawaii Islands in the Central Pacific, the Great Barrier Reef in Australia (Fellows 1975b), the Cook Islands in the southern Pacific, and also in the Banda Sea, Indonesia, Ogasawara (= Bonin) Is, and Madagascar and Mauritius in the western Indian Ocean. Type locality: Mangareva, Gambier Islands, Tuamotu Archipelago.

Remarks. The taxonomic and nomenclatural problems associated with *Ocypode pallidula* have already been discussed by Sakai, K. & Türkay (1976), showing as *O. pallidula* Jacquinot [? 1842–47], however Holthuis (2002) cited that ‘This name was published on pl. 6. g. 1 by Hombron & Jacquinot (February 1846).’ As noted above this species, as presently conceived, has a wide Indo-Pacific distribution, however it is interesting that there is such a wide gap in distribution in the Indian Ocean from Mauritius to Indonesia. The small size of the Mauritius specimens is not particularly unusual, because specimens from south Pacific are also typically smaller (Fellows 1975; personal observations). Similar sized males from Mauritius and Indonesia have a stridulating ridge composed of more striae than those from Hawaii; however, two male specimens from the Cook Islands are intermediate in the number of striae. There is no obvious geographic differentiation in females, and all the other characters

(gonopods, pereopods, orbits, eyestalks) do not show any geographically meaningful groupings. Therefore, on present evidence we are unable to recognise any obvious consistent geographical populational structure that may indicate there are two cryptic species present, however, further investigation using more sophisticated molecular methods may prove interesting.

Ooishi (1970: 94, pl. 16–1) reported *O. cordimana* from Futami Bay, Bonin (= Ogasawara) Islands, however, in Ooishi’s material, as shown by her photo ‘Pl. 16-1’, the lateral margin of the carapace is directed straight backward from the tip of the exorbital angle in the anterior third of the carapace, and then directed inwards in the posterior two-thirds as in *O. pallidula*, which makes it clear that her specimen belongs neither to *O. cordimana* nor to *O. stimpsoni* which are both distributed in the southern part of the Japanese and Ryukyu Islands, but has to be attributed to *O. pallidula*. In *O. cordimana* the lateral margin of the carapace is not straight but convex from the tip of the exorbital angle in the anterior third of the carapace; and in *O. stimpsoni* the lateral margin of the carapace is directed straight and slightly outward from the base of the exorbital angle in the anterior third of the carapace.

The type specimens of *Ocypode laevis* Fabricius, 1798 and *Ocypode minuta* Fabricius, 1798, are lost (*in litt.*, J. Olesen, Zoological Museum, University of Copenhagen and D. Brandis, Zoological Museum, University of Kiel), so we consider it best to treat these two species as ‘nomen dubium’, because Fabricius’ descriptions are too short and ambiguous for species separation.

Ocypode pauliani Crosnier, 1965

(Figs 4C, 23, 45)

Ocypode fabricii – Lenz & Richters, 1881: 423 [in part].
Ocypode pauliani Crosnier, 1965: 102, figs 158, 165, 178–179, pl. 9, fig. 2, pl. 11, fig. 1; Ng, Guinot & Davie, 2008: 240.

Material examined. Madagascar. Tany Kely Island, male [holotype] (MNHN-B 11776), 1962, A. Crosnier; – Nosy Iranja, 2 males, 4 females [paratypes] (MNHN-B 11823), 25.i.1959, A. Crosnier; – Nosy Bé (13°23.78’S, 48°12.33’E), 2 males, 2 females (SMF-

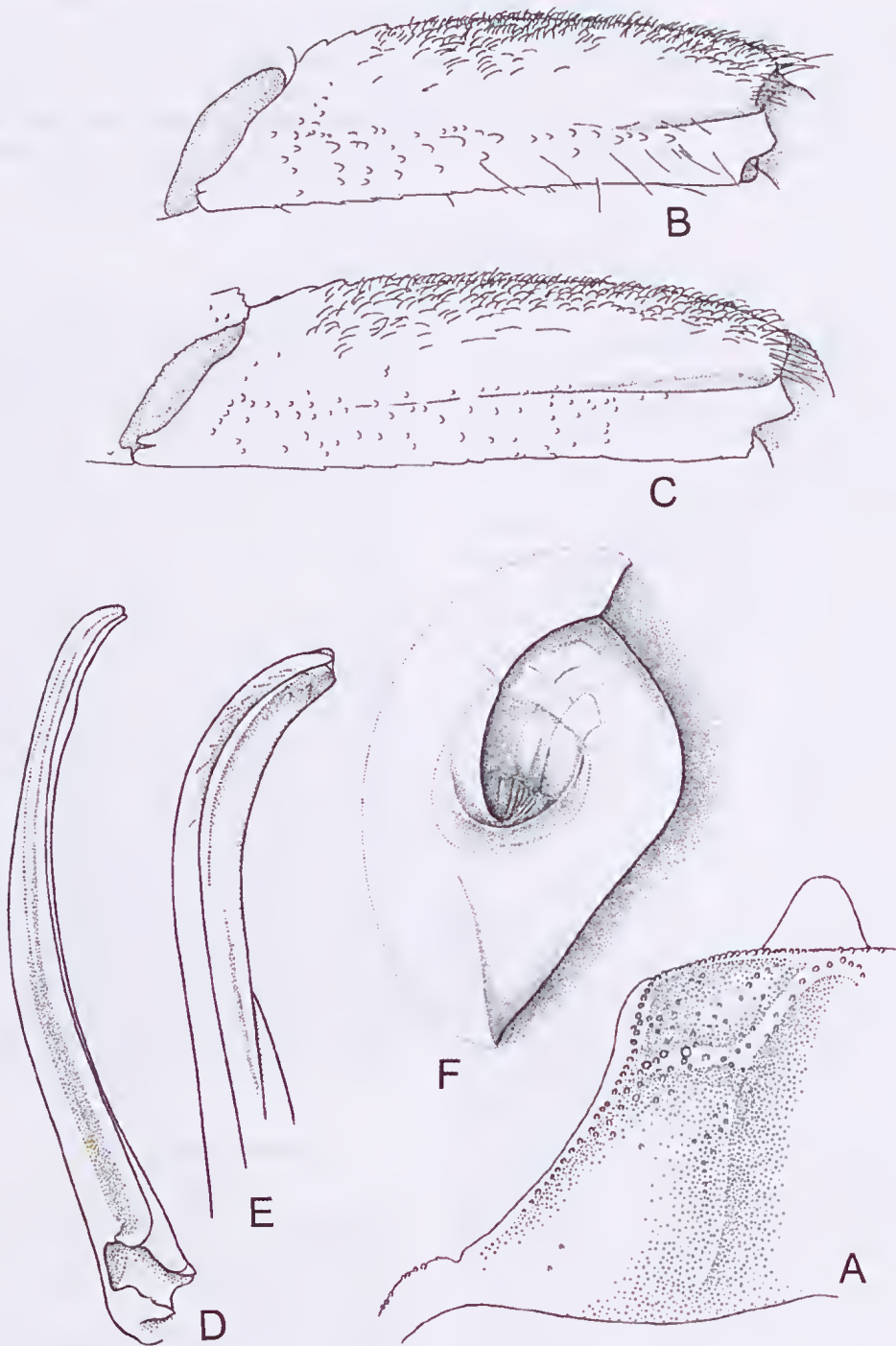


FIG. 23. *Ocypode pauliani*: A, P1 thoracic sternite; B, C, P2-3 propodi; D, E, Go1; F, female operculum.

1958) [det. Lenz & Richters, 1881 as *O. Fabricii*], C. Ebenau. No locality. male (UZMK).

Diagnosis. Middle-sized species. Carapace wider than long. Eyestalks not prolonged distally beyond cornea. Exorbital angles broadly triangular. Stridulating ridge composed of 7–13 tubercles. Smaller cheliped pointed at distal end. P2–3 propodi with setae on and along dorsal margin. Go1 tubelike distally and circular in cross section, bearing no palp. Operculum of female genital opening protruding mesially; median rim curved slightly and regularly.

Description. Carapace (Fig. 45) distinctly wider than long, and densely beset with fine tubercles, becoming larger near anterolateral margin of carapace. Lateral half of orbital margin broad and concave. Exorbital angles broadly triangular. Lateral margins of carapace directed straight backward from tip of exorbital angles in anterior third of carapace, and then directed inwards in posterior two-thirds. Pterygostomial region tuberculate except around buccal cavern. P1 thoracic sternite (Fig. 23A) with a granulated transverse crest at anterior third, to be connected to lateral carina of respective sternite. Palm of larger cheliped broad, and scattered sparsely with tubercles of various sizes on anterior surface as in palm of smaller cheliped; distinctly serrated on ventral margin. Stridulating ridge (Fig. 4C) composed of 7–13 irregularly spaced tubercles. Smaller cheliped pointed at distal end. P2–3 propodi (Fig. 23B–C) with setae on and along dorsal margin, extending distally onto anterior surface. Go1 (Fig. 23D–E) slender and three-sided proximally, tube-like distally, circular in cross section; slightly curved laterally in its distal part; bearing no palp. Sperm-channel originating dorsally and running along distal curve without torsion to terminal part; distal opening terminal. Operculum of female genital opening (Fig. 23F) protruding mesially; median rim curved slightly and regularly, lateral rim narrow.

Distribution. Madagascar. Type locality: Tany Kely Island, NW coast of Madagascar.

Remarks. *Ocypode pauliani* is similar to *O. ryderi* in the shape of the carapace, but they are easily distinguishable by the setae on the P2–3 propodi. *O. pauliani* is also similar to *O. madagascariensis* in the pattern of setae on the P2–3 propodi, but

those two species can be differentiated by the structure of the Go1, the female operculum, the stridulating ridge, and the carapace granulation. In *O. pauliani* the carapace is much more finely and densely tuberculate on the dorsal surface than in *O. madagascariensis*, whose carapace is scattered with coarse and rough tubercles. Lenz & Richters (1881: 3) described *O. fabricii* based on specimens from Madagascar, and their report was supported by Crosnier (1965), who also considered their specimens to belong to *O. fabricii* without examining them. However, we have now re-examined that original material (SMF-1958) and found that they are actually *O. pauliani*, so *O. fabricii* is excluded from the fauna of Madagascar.

Ocypode quadrata (Fabricius, 1787)

(Figs 4D, 24, 46)

- Cancer arenarius* Catesby 1771: 35, pl. 35, caption [ICZN Opinion 262; name 18 on the Official Index of Rejected and Invalid Specific Names in Zoology] [Not *Cancer arenarius* Zimmermann, in Cavolini, 1792 = *Eriphia verrucosa* (Forsåke, 1775); and not *Cancer* (*Gammarellus*) *arenarius* Herbst, 1793 = *Gamarellus homari* (Fabricius, 1779)].
- Cancer albicans minor littoralis* Fermin, 1765: 73.
- Cancer albicans minor* Fermin, 1769: 276; 1770: 249. 'Witte Krab', Hartsinck, 1770: 118.
- Cancer quadratus* Fabricius, 1787: 315; 1793: 439.
- Ocypode quadrata* — Fabricius, 1798: 347; Latreille, 1803: 49; Smith, 1880: 254.
- Ocypoda quadrata* — Bosc, 1801–1802: 194; 1830: 247; Latreille, 1818: 199.
- Ocypode albicans* Bosc, 1802: 196, pl. 4, fig. 1 [in part]; Latreille, 1802: 48; Olivier, 1811: 414, 417; Lamarck, 1818: 253; Latreille, 1818: pl. 285, fig. 1; Latreille, 1818: 198, pl. 15, fig. 4; Desmarest, 1825: 121; H. Milne Edwards, In Lamarck, 1838: 463.
- Ocypode arenarius* — Say, 1817: 69.
- Monolepis inermis* — Say, 1817: 157.
- 'Landkrebse' Sack, 1821: 230.
- Ocypoda albicans* — Bosc, 1830: 249, pl. 4, fig. 1 [in part]; Lucas, 1840: 58.
- Ocypode* (*Ocypode*) *albicans* — De Haan, 1835: 29.
- Ocypode* (*Ocypode*) *quadrata* — De Haan, 1835: 29.
- Ocypoda arenaria* — H. Milne Edwards, 1837: 44, pl. 19, figs 13–14; Lucas, 1840: 58; Guérin-Méneville, 1856: 7; Desbonne & Schramm, 1867: 44; Kingsley, 1878: 322; Kingsley, 1880: 184 [in part]; De Man, 1881: 248; Miers, 1882: 378, 384, pl. 17, fig. 7, 7a, 7b; Miers, 1886: 240; Leidy, 1888: 333; Ives, 1891: 179; Benedict, 1892: 77; Aurivillius, 1893: 24; Ortmann, 1897: 359, 362; Doflein, 1899: 190; Cowles, 1908: 1–41, pl. 1, fig. 10; Luederwaldt,

- 1919: 435; A. Milne-Edwards & Bouvier, 1923: 351; Luederwaldt, 1929: 51.
- Ocypoda rhombea* H. Milne Edwards, 1837: 46; Dana, 1852: 322; Guérin-Méneville, 1856: 7; Saussure, 1858: 440; Heller, 1865: 42; Desbonne & Schramm, 1867: 44; Smith, 1869: 35; Cunningham, 1871: 493.
- Ocypoda macrocera* H. Milne Edwards, 1837: 49; Lucas, 1840: 57 [in part, only material from Brasil].
- Ocypode arenaria* – White, 1847: 34; Gibbes, 1850: 180; H. Milne Edwards, 1852: 143; Gerstäcker, 1856: 136; Hilgendorf, 1869: 81; von Martens, 1872: 103; Gundlach, 1887: 334; Ortman, 1894a: 761, 765; Rathbun, 1898a: 287; 1898b: 603.
- Ocypode rhombea* – White, 1847: 58; Gibbes, 1850: 180; H. Milne Edwards, 1852: 143 [in part]; Gundlach, 1887: 335.
- Monolepis inermis* – White, 1847: 65.
- ? *Ocypoda rhombea* – Streets, 1871: 240.
- Ocypode albicans* – Rathbun, 1901: 6; 1918: 367, pls 127–128; 1919: 342; Pearse, 1915: 555; Crane, 1940: 70, figs 2, 3A, 4B, 4C, 4D, 5A, 6B, 6C, 6D, 7A–7N, 8A–I; 1941: 309, fig. 7C–D, pl. 2 fig. 6; Chace & Holthuis, 1948: 22, 27; Ferguson & Jones, 1949: 442; Buitendijk, 1950: 278; Monod, 1951: 398; Bott, 1955: 67.
- Ocypode arenarius* – Verrill, 1908a: 306, fig. 1; 1908b: 491.
- Ocypoda albicans* – Balss, 1922b: 79.
- Ocypoda quadrata* – Milne, 1946: 362–380; Milne & Milne, 1946: 224–230.
- Ocypode occidentalis* – Jones, 1968: 159, pl. 4.
- Ocypode quadrata* – Chace, 1956: 159; Holthuis, 1959: 259, pl. 9, fig. 3; Schöne, 1964: 107, unnumbered text-fig; Williams, 1965: 225, fig. 208; Jones, 1968: 159, pl. 4; Chace & Hobbs, 1969: 204, fig. 68; Holthuis, 1969: 13; Coêlho, 1971a: 81; 1971b: pl. 1; Coêlho & Ramos, 1972: 198; Bright & Hogue, 1972: 10; Diaz & Costlow, 1972: 120; Gomes-Corrêa, 1972: 12; Haley, 1972: 1; Horch & Salmon, 1972: 10; Henning & Klaassen, 1973: 67; Fates, 1976: 65; Powers, 1977: 141; Wolcott, 1978: 67–82; Fisher & Tevesz, 1979: 31–36; Leber, 1981: 110–112; Robertson & Pfeiffer, 1981: 165–177; Steiner & Leatherman, 1981: 111–122; Hill, 1982: 23–34; Williams, 1984: 468, text-fig. 375; Abele & Kim, 1986: 66, fig. 716a; Melo, Veloso & Oliveira, 1989: 25; Melo, 1996: 484, 1 text-fig.; 1998: 504; Alberto & Fontoura, 1999: 95–108; Weinstein & Full, 2000: 33; Rosenberg & Langer, 2001: 345–353; Fransozo *et al.*, 2002: 189–195; Portell *et al.*, 2003: 712–722; Vallero-Pacheco, *et al.*, 2004: 466–475; Sabine, Meyers & Schweitzer, 2005: 295; Turra, Goncalves & Denadai, 2005: 2163–2177; Blankensteyn, 2006: 870–876; Neves & Bemvenuti, 2006: 431–435; Martin, 2006: 57–67; Maccarone & Mathews, 2006: 51–60; Valero-Pacheco, *et al.*, 2007: 313–325; Hobbs, *et al.*, 2008: 1450–1458; Rosa Da. *et al.*, 2008: 383–388; Souza *et al.*, 2008: 139–145; Ng, Guinot & Davie, 2008: 240; Vilar de Araujo, *et al.*, 2008: 73–80, figs 1–5; López-Greco *et al.*, 2009: 41–50, figs 1–4; Maccarone & Matthews, 2008: 51–60; Teixeira, Torres & Capitoli, 2008: 9, 10, text-figs 9.1, 10A; López-Greco, *et al.*, 2009: 41–50, figs 1–4; McDermott, 2009: 637–646, figs 1–2; Perry *et al.*, 2009: 673–683; Magalhães *et al.*, 2009: 149–152, fig. 2; Arteta-Bonivento, 2009: 149, 1 text-fig.
- Material examined.** Bermuda Islands. No exact locality, female (NHM-84.31), Challenger Expedition. USA. Massachusetts: Harraganserr Pier, Rhode Island, 1 juv. female (USNM-92129), 2.ix.1950, C.J. Fish; – New York: Long Island, 2 juvs. (MNHN) [det. Smith, 1899 as *O. arenaria*]; 2 juvs. (NHM), not registered; – New Jersey: no exact locality; – Carolina: no exact locality, 1 dry female (MNHG) [det. as *O. arenaria*]; – North Carolina: Beaufort, male, female (MZT-1107); – *ibid.*, 1 juv. male (SMF-5507), 1904, Reichard; – Georgia: Sapelo Island, 2 males, 4 females, 5.iv.1964, Mus. Copenhagen; – *ibid.*, 2 males (SMF-6847), J. Dörjes; – *ibid.*, tidal flat, 3 males, 1 juv. (SMF-22177), 23.v.1969, J. Dörjes; – Florida: Cay Biscayne, male (MNHG-147); – Key West, female (NHM-1898.5.7.536–537); – Dry Tortugas, male (ZMH-2800) [det. as *O. arenaria*]; 3 males, female (NHM-1938.3.19.61–63); – Sarasota, Siesta-Key, male (SMF-5404), x.1963, W. Klausewitz; – *ibid.*, male (SMF-6851), ix.1963; – Santa Rosa I. near Pensacola, beach with white sand, 2 juvs. (SMF-22175), 17.ix.1972, J. Dörjes; – Texas: no exact locality, female (NHMW) [det. as *O. rhombea* Fabricius], 20.i.1882, Stind. Mexico. No exact locality, 1 juv. female (NHMW-1957) [det. as *O. occidentalis*], 1884, Bilimek; – East coast of Mexico, 5 males, female, 1 juv. female (NHMW), 5.v.1883, Bilimek; – Estado de Veracruz: Veracruz, male (NHM-81.29); – Barra de Tuxpam (20°58.55'N, 97°18.54'W), male (SMF-7495), 5.xi.1973, E.G. Burmeister; 1 juv. (SMF-7506). Belize. No exact locality, male, 1 ovig. female (NHM-1967.7.1.93–94). Honduras. Puerto Cortés, strand (15°51.92'N, 87°56.54'W), 2 females, 1 juv. (SMF-2341), 19.ix.1951, H.M. Peters; – *ibid.*, 2 males, female (SMF-2075), 21.ix.1951, H.M. Peters; – Coast of Tela (15°46.98'N, 87°27.33'W), 1 juv. female (SMF-2206), 24.i.1953, O. Schuster. Costa Rica. No further data, 3 females (ZMH-2799) [det. as *O. Arenaria*]. Bahamas. No further data, male (MZT-1104). Cuba. No further data, 1 dry female (MNHG) [det. as *O. arenaria*]; male (ZMH-25495); – Cárdenas (23°3.08'N, 81°12.14'W), male, female (ZMH-2742). Cayman Islands. Grand Cayman, 1 juv. (NHM-1955.10.6.34). Jamaica. No exact locality, male (NHMW-1955) [det. *O. albicans* Bosc], xi.1929, Schmarda; – Saint Thomas Parish: near Port Morant, male (NHM-1912.7.13.3); – Trelawny Parish: Falmouth, Mangrove near Glistening Waters (18°29.67'N, 77°40.01'W), 1 juv. female (SMF-19578), 18.ii.1987, R. Diesel. Haiti. No exact locality, male (SMF-1946), 1904, A. Reichardt. Dominican Republic. No exact locality, 1 juv.

female (ZSM), 8.xii.1903, Heitz; – Monte Christi, 3 males, 2 females (ZMH-25171) [det. as *O. arenaria*]; – Beata Island, male (UZMK) [det. as *Ocypode* sp.], 22.iii.1922. USA, Puerto Rico. Mona Island between Dominican Republic and Puerto Rico, male (MNHN) [det. Bouvier, 1907 as *O. areuaria*]. U.S. Virgin Islands. No exact locality, male, 1 juv. male, female (MCZ), 1911; – St. Thomas, male (ZMH-2808) [det. as *O. ceratophthalma*]; 3 males, female, 1 juv. female, 6 juvs. (ZMH-2788); female (MZT-1098); – *ibid.*, Salmin, female (ZSM) [Vend]; – Water Island, St. Thomas, female (MCZ) [det. as *O. sp.*], 3.xii.1910; – Smiths Bay, St. Thomas, male (MCZ) [det. *Ocypode* sp.], 1.xii.1933; – St. Croix, Bay beach, 1 juv. male (SMF-22176), 5.xii.1972, J. Dörjes. St. Kitts and Nevis. St. Kitts, female (NHM-441b); – Nevis I., male, 1 juv. male, 1 juv. female (NHM-1938.3.29.97-99). French Antilles. Martinique: no exact locality, 1 dry male (MNHN-3263) [det. as *O. arenaria*]; – *ibid.*, male, female, dry (MNHN) [det. as *O. arenaria*], Plee; – *ibid.*, male [18.0×23.3 mm], female [27.4×28.4 mm] (SMF-36242), 8-16.i.2004, M. Türkay; – St. Anne, male, female (ZSM), 1898, F. Doflein; – Martinique, Dizac near Diamant (14°28.707'N, 61°1.767'W), sandy beach, taken at night, 2 males [34.0×41.4, 30.4×37.2 mm] (SMF-36241), 13.i.2004, M. Türkay; – Guadeloupe: no exact locality, 1 dry female (MNHN-3264) [det. as *O. areuaria*]; – *ibid.*, female (SMF-9409), 1960, Merkel; – District Basse Terre, NW-coast close to Deshaies (16°1.09'N, 61°47.68'W), 2 males, 2 females (SMF-21573), x.1991, M. Gutmann. Trinidad and Tobago. Mt. Irvine Bay, SW-coast of Tobago Island, 2 juv. males (NHM, unregistered). Colombia. Depto Bolívar: Cartagena, sandy beach near Boca Grande (10°24.21'N, 75°33.41'W), male (SMF-6849), 16.i.1968, Sturm; – Depto Magdalena: Isla de Salamanca, male (SMF-6848), viii-xii.1969, F. Klaassen; – *ibid.*, Pueblo Viejo, cemetery, 2 juv. males (SMF-7036), viii.1969, F. Klaassen; – Beach at Hotel Irotama, 15 km SW Santa Marta (11° 8.94'N, 74° 13.58'W), female (SMF-16597), 12.x.1978, M. & H. Türkay; – Ensenada Grande, N of Santa Marta, sandy beach, male (SMF-16596), 20.x.1978, M. & H. Türkay; – Bahía Concha, c. 10 km NE of Santa Marta (11°17.8'N, 74°9.1'W), sandy beach, 1 juv. male (SMF-5141), 24.ix.1967, F. Riemann; – *ibid.*, male, female (SMF-16593), 7.x.1978, M. & H. Türkay; – *ibid.*, male (SMF-16594), 14.x.1978, M. & H. Türkay; – Bahía Nenguangue c. 25 km NE of Santa Marta (11°18.92'N, 74°4.96'W), muddy mangrove, male (SMF-6861), xii.1974, H. Schmalfuß; – *ibid.*, male (SMF-16595), 8.x.1978, M. & H. Türkay; – *ibid.*, male (SMF-17994), 11.x.1978, M. & H. Türkay; – Playa del Muerto c. 25 km NE of Santa Marta (11°19.65'N, 74°4.63'W), sandy beach, male, 1 juv. (SMF-16598), x.1978, M. & H. Türkay; – *ibid.*, female (SMF-18687), 1.xii.1978, D. Rodriguez; – Rio Buritaca (11°15.81'N, 73°46.14'W), 4 females (SMF-6850), viii-ix.1970, F. Klaassen. Venezuela. No exact locality, male (ZMH-2794); – *ibid.*, male (NHMW-9776) [det. O. Pesta], 1930, Koller, Costa Rica Expedition; – Valencia [This locality is clearly wrong, as Valencia, the capital of the Carabobo State, lies far inland. Probably the collector meant the coast of Carabobo State], female (ZMK-1537), 1815, Werner; – Isla Los Roques (11°51.63'N, 66°45.19'W), female (SMF-2440), 1. Eibl. Republic of Guyana. No exact locality, male, female (MNHN) [det. Guinot as *O. arenaria*], 1953, J. Durand. Brazil. No exact locality, 1 dry male [CL 21 mm] (MNHN) [det. as *O. rhombea* Fabricius]; 1 damaged male (ZMH-2744); 3 males, female (NHMW) [det. *O. rhombea*], Nallere; – North Brazil, female, (ZMH-2786); – Estado de Pará: Belem, female (NHMW-1952); 2 females (NHMW-1632), Nallere; – Estado de Maranhão: Tutoia, 2 ovig. females (ZMH-2785); – Estado de Pernambuco: Fernando de Noronha, 4 males, female (NHM-88.19); – Estado de Bahia: Salvador, male, juv. female, 1 juv. (ZMH-25276); 1 juv. (ZMH-2949); male (NHM-84.31); – Estado de Espírito Santo: no exact locality, 2 males (SMF-9822); – Estado Rio de Janeiro: Rio de Janeiro, male (NHM-69.37); male (NHMW-1951) [det. as *O. albicans*]; female (NHMW-1954) [det. as *O. albicans*]; – *ibid.*, male (NHMW), 1.xi.1931, Ryrk, Kurl & Klelle Son; – *ibid.*, male (NHMW-1399) [det. Heller, 1865 as *O. rhombea*], 'Novara Expedition'; female (NHMW-1434); – Rio de Janeiro, Penha, 6 males, female (SMF-1947), 24.vi.1914, Breslau; – Estado São Paulo: São Paulo, male, 1 damaged female (ZMH-13817) [det. as *O. areuaria*]; – Estado de Santa Catarina: Praia Grande, São Francisco do Sul, 3 males, 2 females (USNM-70947), 6.x.1925, W.L. Schmitt; – Estado de Rio Grande do Sul: Torres, 2 males, female (SMF-5075), 12.ii.1966, Lise; – 7 km N of Tranandai (30°00'S, 50°15'W), 4 males (SMF-21987), 3-4.iii.1993, Ha. Langer; 4 males (SMF-21987); – Pinai (30°10'S, 50°15'W), E of Porto Alegre, 6 males, 2 females (SMF-21988), 9.iii.1993, H. Langer. **Incorrect localities.** Altata, West coast of Mexico, Pacific Ocean, 1 damaged female (ZMH-2743); – West coast of Mexico, Pacific Ocean, female (ZMH-2787); – Indian Ocean, male (ZMK-1538) [det. as *O. Cordimanus*]; – West Africa, 1 damaged female (ZMH-2796). **No locality.** 2 males (ZSM) [from Natur Museum Lübeck 817]; male (ZMH-2797); male (NHM); – 'America', male, female (SMF-7153); male (SMF-36886), J. Dörjes; – 'West Indies', 2 males, 2 females, 1 juv. (ZMH-25373) [det. as *O. arenaria*]; male, 2 females (ZMH-2793); 1 juv. male (NHM-1967.4.4.142); – *ibid.*, male (SMF-16567 [ex. Mus. Heidelberg]), 1865, Salmin.

Diagnosis. Mid-to large-sized species. Eystalks not prolonged distally beyond cornea. Lateral half of orbital margin concave. Exorbital angles acutely triangular and directed anteriorly. Stridulating ridge composed of 15–18 tubercles. P2–3 propodi with median rows of setae on

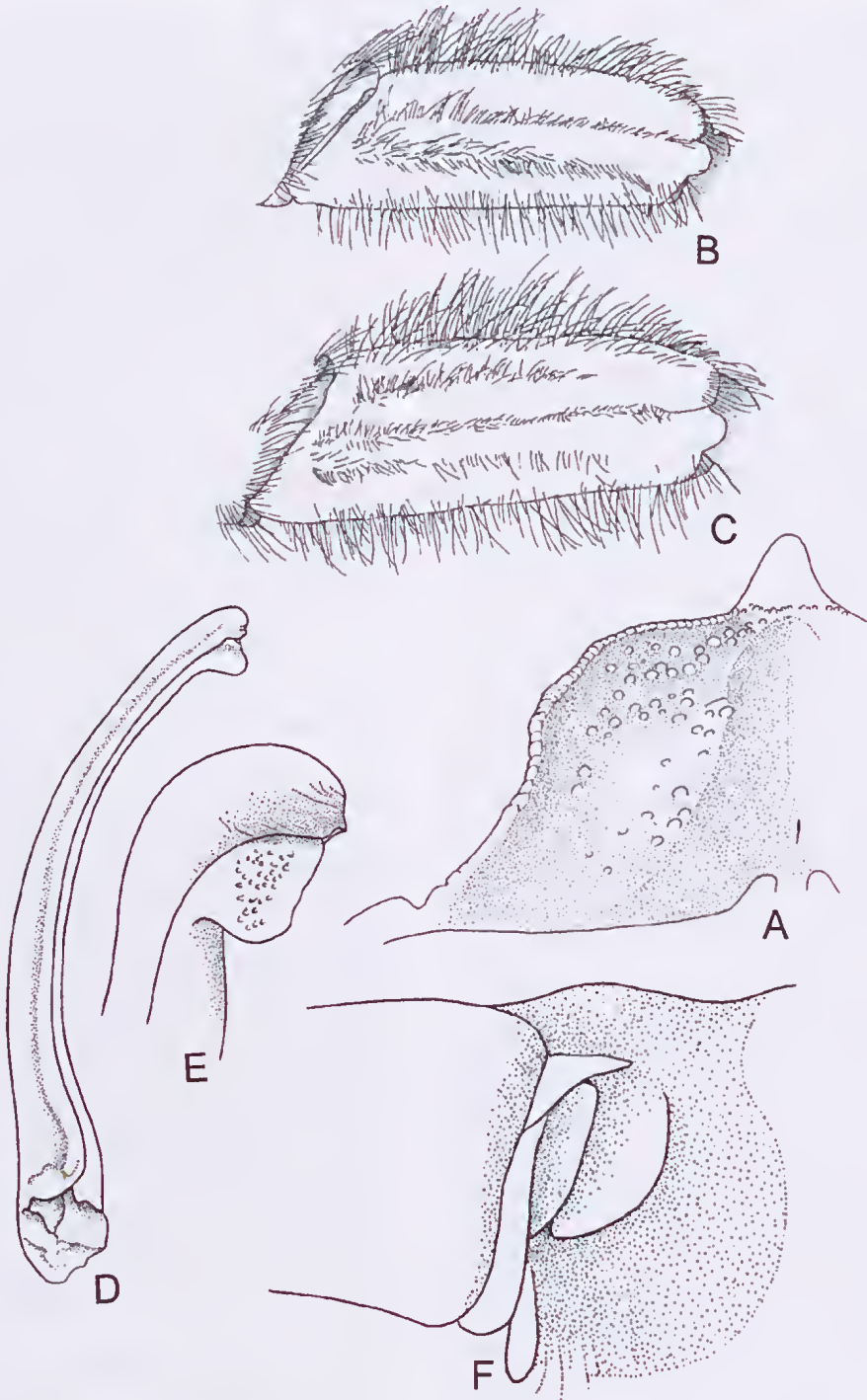


FIG. 24. *Ocypode quadrata*: A, P1 thoracic sternite; B, C, P2-3 propodi; D, E, Go1; F, female operculum.

anterior surface, bearing long setae on dorsal and ventral margins. Go1 deepened on both sides of sperm channel; broadened at distal end; lacking palp. Operculum of female genital opening very narrow and long.

Description. Carapace (Fig. 46) wider than long and beset densely with fine tubercles on dorsal surface, which becoming larger towards lateral sides. Lateral half of orbital margin concave. Exorbital angles acutely triangular and directed anteriorly. Lateral margins of carapace directed slightly outwards from tip of exorbital angle in anterior third of carapace, and then directed mesially in posterior two-thirds, so that carapace broadest at anterior third. Pterygostomial region distinctly tuberculate except along smooth lateral sides of buccal cavern. P1 thoracic sternite (Fig. 24A) rounded at anterolateral angle and slightly sunken around corner, and hemmed anteriorly and laterally with tuberculate carinae, and roughly tuberculate in anterior third. Palm of larger cheliped elongate and scattered sparsely with coarse tubercles on anterior surface, bearing irregularly arranged obtuse teeth on ventral margin and denticles on dorsal margin. Smaller cheliped pointed distally. Stridulating ridge (Fig. 4D) composed of 15–18 interspaced tubercles. P2–3 propodi (Fig. 24B–C) with median rows (two in P2 and three in P3) of setae on anterior surface, bearing long setae on dorsal and ventral margins. P4–5 propodi with long setae on dorsal and ventral margins. Go1 (Fig. 24D–E) three-sided proximally; deepened on both sides of sperm channel; curved laterally at broadened distal end with lateral bulge; lacking palp. Operculum of female genital opening (Fig. 24F) very narrow and long; median rim elevated, acutely triangular.

Distribution. Western Atlantic: From Block I., Massachusetts to Rio Grande do Sul, Brazil. Type locality: Jamaica.

Remarks. The name of the only *Ocypode* species reported from the Atlantic coast of North and South America was settled as *Ocypode quadrata* through ICZN opinion 262 (1954). Which name to apply to the species had been ambiguous and confused before this act, by which most of the historical problems regarding its nomenclature

were solved. It must especially be pointed out that, though *Ocypode rhombea* has been used for Atlantic specimens by a number of authors in the past, after examination of their respective specimens it is clear that this Atlantic material is all *O. quadrata*, and that *O. rhombea* Fabricius, 1798, is restricted to the Pacific. Also, as mentioned earlier, we have examined the holotype of *O. rhombea* in the ZMUC and although it is a juvenile, and in poor condition, we are confident that it is a junior synonym of *O. ceratophthalma* and not *O. quadrata* as has long been supposed.

Ocypode rotundata Miers, 1882

(Figs 5A, 25, 47)

Ocypoda rotundata Miers, 1882: 378, 382, pl. 17, fig. 4; Ortmann, 1897: 360, 364; Alcock, 1900: 348; Chhappargar, 1956: 508; 1957: 46, pl. 13 figs g–i; Hashmi, 1963: 240.

Ocypoda rotundata var. *arabica* Nobili, 1906a: 152, pl. 5, fig. 26; Ng *et al.*, 2008: 240.

Ocypode aegyptiaca – Laurie, 1915: 416 [in part, only record from Persian Gulf].

Ocypoda aegyptiaca – Stephensen, 1945: 188, fig. 55.

Ocypode rotundata – Pretzmann, 1971: 480, pl. 4, figs 8–10; 1974: 453; 1975: 15; Tirmizi, 1980: 109; Titgen, 1982: 152; Tirmizi & Kazmi, 1983: 371, 377; Türkay *et al.*, 1996: 104, text-figs 7–8, 12, pls 1–3; Clayton, 2001: 37–55; Yousuf *et al.*, 2007: 110, figs 7–8; Ng *et al.*, 2008: 240; Hosseini, 2009: 37–46.

Ocypode saratan – Basson *et al.*, 1977: 38, 40, 56, 60, 126, 140, 145, text-fig. 14; Jones, 1986: 157, pl. 42; Hogarth, 1989: 103, 115; Kazemiyan, 2008: 404–409.

Ocypode ceratophthalma – Yousuf *et al.*, 2007: 108, figs 1–2.

Ocypode macleayana – Yousuf *et al.*, 2007: 109, figs 5–6.

Ocypode gaudichaudii – Yousuf *et al.*, 2007: 108, figs 3–4.

Material examined. Pakistan. Karachi, female (NHM-1897.9.12.2); 2 specimens (NHM-1911.1.17.72–73); 1 juv. male (USNM-216684); 1 juv. (UZMK); – Sandy beach at Horst Point, W of Karachi, male (UZMK); – Clifton, Karachi, female (NHM); – Indus-Delta, Waddi Khuddi Creek [= 'Khudi Creek'] (24°34.52'N, 67°12.4'E), 3 males, female (SMF-6748), xii.1970; – *ibid.*, male, female (SMF-17728), i.1974, G. Pilleri. Oman. Island Al Hallaniyah (17°30'N, 56°01'E), Oman, Arabian Sea, male [holotype of *Ocypoda rotundata* var. *arabica*] (MNHN); – Masqat, Gulf of Oman, 2 males (NHM-1898.4.14.3–4); – Al Bustan (23°34.37'N, 58°36.72'E), South of Masqat, male [9.9×12.8 mm] (SMF-36245), 6.ix.1983, P.J. Hogarth; – Al Chasab, male (NHM-1973.167); female (NHM-1973.170); – Al Khuwayr, Batinah (23°36'N, 58°25'E), 1

juv. male, 2 females, 2 juv. females (SMF-18285), 28.vi.1988, M. Gallagher; — Suwadi, West of Masqat (23°47'N, 57°47'E), Sandy shoal, female (SMF-24534), 26.v.1995, D. Clayton; — Seeb, W of Masqat, male (SMF-24535), 29.v.1995, D. Clayton. **Persian Gulf.** No further data, female (NHM-1962.8.30.5). **Iran.** No further data, 4 males, 3 females (NHMW); — Bushehr, Persian Gulf coral reef, 2 males (UZMK) [det. Stephensen, 1945]; — Jazireh-ye Shotur (= Jazireh-ye Shitwar), Persian Gulf (26°47'N, 53°25'E), 2 females (UZMK) [det. Stephensen, 1945]; — Bandar Abbas, male, female (NHMW-3804), 1970, Pretzmann & Bilek; 2 males (NHMW-3805); 1 juv. male, 5 juv. females, 2 juvs. (NHMW-3806); females (NHMW-9870); 5 males, female, 1 juv. (NHMW-10793). **Saudi-Arabia.** Ras at Tannurah, male (RMNH-15616); male (USNM-207674); — Jazirat Abu Ali (27°20'N, 49°33'E), 2 males, 2 females (NHM-1974.386); — *ibid.*, (27°21'N, 49°30'E), North coast, sandy beach, male (SMF-23028), 2.xi.1992, M. Apel; 2 males, 3 females (SMF-23029), 11.vi.1992; male, female (SNMNH-13), 16.v.1995; — *ibid.*, North coast behind ARAMCO-camp, sandy beach covered with tar, male, female (SNMNH-12), 30.x.1992, M. Apel; — *ibid.*, (27°18'N, 49°42'E), eastern tip, close to coast guard camp, male, 2 females (SMF-23030), 29.v.1992; male, 2 females (SMF-23031); 2 males, 2 females (SNMNH-11), 28.vi.1992; — *ibid.*, (27°18'N, 49°41'E), north coast close to eastern tip, sandy beach with scattered rocks, 2 males, 2 females (SMF-23033), 16.v.1995, M. Apel; — *ibid.*, South-West tip, sandy beach, female (SMF-24534); male, 3 females (SNMNH-14), 20.v.1995, M. Apel; — Ras Az Zawr (27°27'N, 49°18'E), sandy beach, female (SMF-23032), 17.v.1995, M. Apel; — Jazirat Karan (27°43'N, 49°48.48'E), sandy beach with scattered rocks, female (SMF-23027), 12.vii.1992, M. Apel; — *ibid.*, 2 males, 2 females (SMF-23034). **Qatar.** Dukhun, male [holotype] (NHM-79.32). **United Arab Emirates.** Ash Shariqah, female (NHM-1971.32); — Jazirat Abu Ali (27°20'N, 49°33'E), 2 males, 2 females (NHM-1974.386); — Fujairah, N of Khor Fakkan (25°30'N, 56°22'E), 4 males, 9 females (SMF-23035).

Diagnosis. Large-sized species. Eystalks prolonged distally beyond cornea in a stylus. Ex-orbital angles rounded. Stridulating ridge composed of 10–15 tubercles with striae. Smaller cheliped pointed at distal end. P2 propodus with two median rows of setae on anterior surface. P3–5 propodi naked. Go1 broadened, curved laterally at distal end, with distinct palp. Operculum of female genital opening rounded distally, protruding mesially in button-shape. Vaginal slit directed lengthwise.

Description. Carapace (Fig. 47) wider than long and beset densely with coarse tubercles, becoming less densely scattered toward lateral sides.

Lateral half of orbital margin directed obliquely backwards, so that exorbital corners located far posterior to median convexity of orbital margin. Exorbital corners broadly rounded. Lateral margins of carapace convex from rounded exorbital corners to anterior third of carapace, and then directed inwards in posterior two-thirds, forming broad and rounded epibranchial corners, at which carapace broadest. Pterygostomial region sparsely tuberculate except along lateral sides of buccal cavern. P1 thoracic sternite (Fig. 25A) triangular at anterolateral corner and slightly sunken mesially, and indistinctly tuberculate in posterior two-thirds, bearing tuberculate carinae on setose anterior and naked lateral margins. Palm of larger cheliped broad and densely beset with fine tubercles on anterior surface, among which scanty coarse tubercles present, and roughly serrated on ventral margin. Stridulating ridge composed (Fig. 5A) of 10–15 irregularly spaced elongate tubercles with striae. Smaller cheliped pointed at distal end. P2 propodus (Fig. 25B) with two median rows of setae on anterior surface, all other surfaces of P3 (Fig. 25C) to P5 propodi naked. Go1 (Fig. 25D–E) broadened with lateral bulge and curved laterally at distal end, bearing thumb-like palp branching from stem near genital opening; sperm channel originating dorsally and running without torsion to broad distal part. Operculum of female genital opening (Fig. 25F) rounded distally; protruding mesially in button-shape. Vaginal slit directed lengthwise, almost parallel to sternal median line. Lateral rim well developed, increasing in height toward median part.

Juvenile specimens. In a small specimen (13.8×15.8 mm, NHMW-3806) eystalks not yet prolonged distally beyond cornea, but in larger specimens (19.7×22.9, 22.5×26.6 mm, NHMW-3806) eystalks already prolonged distally beyond cornea in a short stylus. Lateral half of orbital margin concave, and exorbital angles distinct. Lateral margins of carapace directed straight backwards, and then directed inwards, forming more distinct epibranchial corners than in adult specimens. Palm of larger cheliped more longer than broad than in adult ones. Stridulating ridge composed of 10–11 interspaced striae. P2 propodus with a median

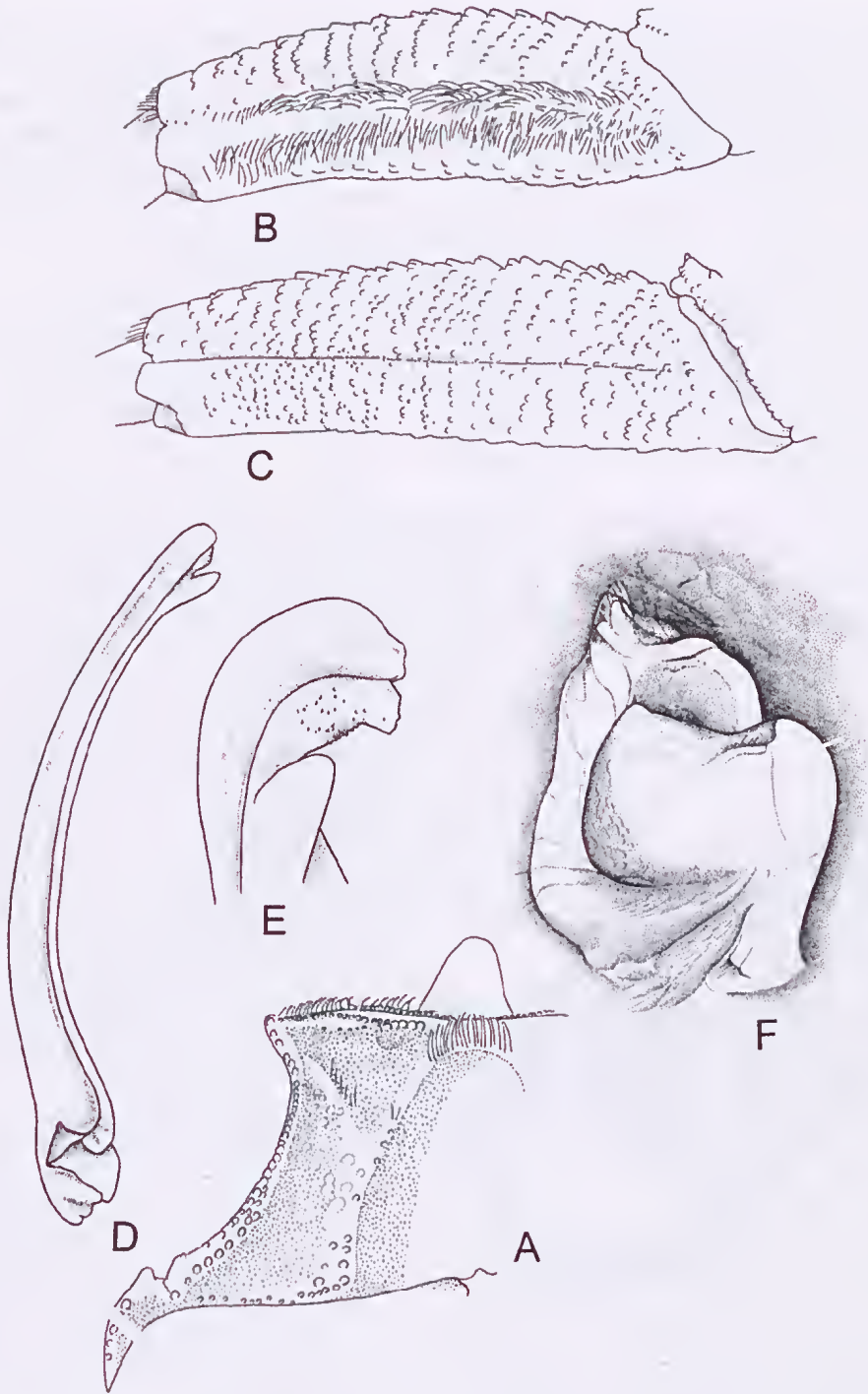


FIG. 25. *Ocypode rotundata*: A, P1 thoracic sternite; B, C, P2-3 propodi; D, E, Go1; F, female operculum.

row of scanty setae on anterior surface, and yellowish setae at distal end of dorsal margin.

Distribution. South coast of Arabian Peninsula (Oman) to North India (Bombay State), including the Persian Gulf. Type locality: 'Dukhun' (probably Dukhan, Qatar, see Remarks)

Remarks. *O. rotundata* is similar in morphology to *O. saratan* from the Red Sea and its adjacent regions, and they have often been confused. However, in *O. rotundata* the stridulating ridge of the chela is composed of 10–15 irregularly spaced elongate tubercles with striae, and the Go1 bears a stout thumb-like palp; whereas in *O. saratan* it is composed of 67–87 fine striae and the Go1 bears a palp which is slenderly triangular in its distal half.

Different names were used by earlier authors, and this caused some confusion. *O. rotundata* var. *arabica* described by Nobili (1906) was characterised by its typical triangular exorbital angles; however, this is also observed in young specimens of *O. rotundata*, and is simply related to growth. We re-examined the type specimen of *O. rotundata* var. *arabica* and here confirmed that it is conspecific with *O. rotundata*. Stephensen (1945) reported *O. aegypticae* from the Persian Gulf, because he considered his specimen to be similar to *O. aegypticae* described by Gerstaecker (1856) (later synonymised with *O. saratan*), however, his specimen too has been re-identified as *O. rotundata*.

Some uncertainty exist regarding the type locality of *O. rotundata*. Miers (1882) stated: 'The specimen, which is much mutilated, is labeled "Dukhun, Col. Sykes" (coll. Indian Museum), and was probably obtained at some locality on the western coast of India.' 'Dukhun' is presumed to be Dukhan located on the coast of Qatar in the Persian Gulf.

Yousuf *et al.* (2007) recorded *Ocypode ceratophthalma*, *O. gaudichaudii*, *O. macleayana*, and *O. rotundata*, based on specimens collected from the sandy beach of Sonmiani on the Makran coast (Baluchistan Province, Pakistan) and published figures of the specimens. However, it is evident from their figures and distribution that the first two species are rather to be identified as *O. rotundata*, because their '*O. ceratoph-*

thalma' and '*O. gaudichaudii*' are shown to have the carapace rounded at the exorbital corners, though *O. ceratophthalma* and *O. gaudichaudii* have the carapace triangular at the exorbital corners. It must also be added that *O. gaudichaudii* is not distributed in Pakistan but in the eastern Pacific. *Ocypode macleayana* is also impossible as it is a synonym of *O. ceratophthalma*, and their '*O. macleayana*' can also be attributed to *O. rotundata*.

Ocypode ryderi Kingsley, 1881

(Figs 5B, 26, 48)

Ocypode Urvillii — A. Milne-Edwards, 1868: 71 [in part].

Ocypode ryderi Kingsley, 1881: 183; Sakai, K. & Türkay, 1976: 82, figs 2, 5, 6, 9, 10, 12, pl. 1; Berry *et al.*, 1976: 29; Berry, 1976: 35–37, 1 un-num. text-fig; Vannini, 1980: 171–183, figs 1–4; McLachlan, 1980: 57–58, fig. 1; Vannini & Valmori, 1981: 206, figs 1C, 2C, 3C, 4C; Kensley, 1981: 49; Rivera & Langner, 1982: 228; Henning & Langner, 1986: 213–214; Jackson *et al.*, 1991: 280–286; Vetter, 1992: 2, 6, 33, 61, 65, 66, 67, 85, fig. 9; Rosenberg & Langner, 2001: 345–353, fig. 1; Rosenberg *et al.*, 2001: 53–70, figs 1–7; Bruyn, 2002: 28–34, figs 1–2, 4, 6–9; Ng *et al.*, 2008: 240.

Ocypoda Kuhlii — Pfeffer, 1889: 30; Lenz, 1912: 6.

Ocypoda Kuhlii — Lenz, in: Voeltzkow, 1910: 558.

Ocypoda cordimana — Pfeffer, 1889: 30 [in part]; Bouvier, 1921: 58.

Ocypode kuhli — Ortmann, 1894a: 761; Stebbing, 1910: 327; Rathbun, 1933: 260, pl. 7, fig. 2; 1935: 26; Chace, 1942: 202; Barnard, 1950: 87, fig. 17e–g; Barrass, 1963: 73; Guinot, 1967: 281; Jones, 1972: 31–43, tab. 1, figs 3, 4b, 4d, 4f, 4h, 5; Evans, 1976: 121–135, tabs 1–4, figs 1–4).

Ocypode Kuhli — Ortmann, 1894b: 59.

Ocypoda kuhli — Ortmann, 1897: 359 [in part]; Lenz, 1905: 365; Cott, 1929: 755.

Material examined. No locality. male (ZMH-K2963). Eastern Africa. No further data, male (ZMH-K25451). Yemen. Suqutra, South coast centre (12°18.7'N, 53°48.29'E), 3 males, female (SMF-36170), 9.iv.1999, M. Apel; 2 males, 2 females (NHCY-86); — Abd el-Kuri island, 3 female, 1 juv. (NHM-1906.5.29.23–25). Somalia. Mogadischu, beach (2°2.68'N, 45°22.1'E), male (SMF-9981), xi–xii.1976, M. Vannini; — Marka, South of Mogadischu, female, 1 juv. female, 3 juvs. (MCSNM); — Sar Uanle, 20 km S of Kisimayo (= Kismaayo), 2 males (RMNH-25852); male, female (AMS-P24831). Kenya. female (MHNG); — Lamu I., male (NHM-1893.11.9.11); — Malindi (3°12.72'S, 40°7.35'E), 2 males (SMF-9831), xii.1980, W. Sudhaus; — Watamu (3°21.2'S, 40°1.5'E), S of Malindi, male (RMNH-15852); — *ibid.*, 1 juv. male, 1 juv. female

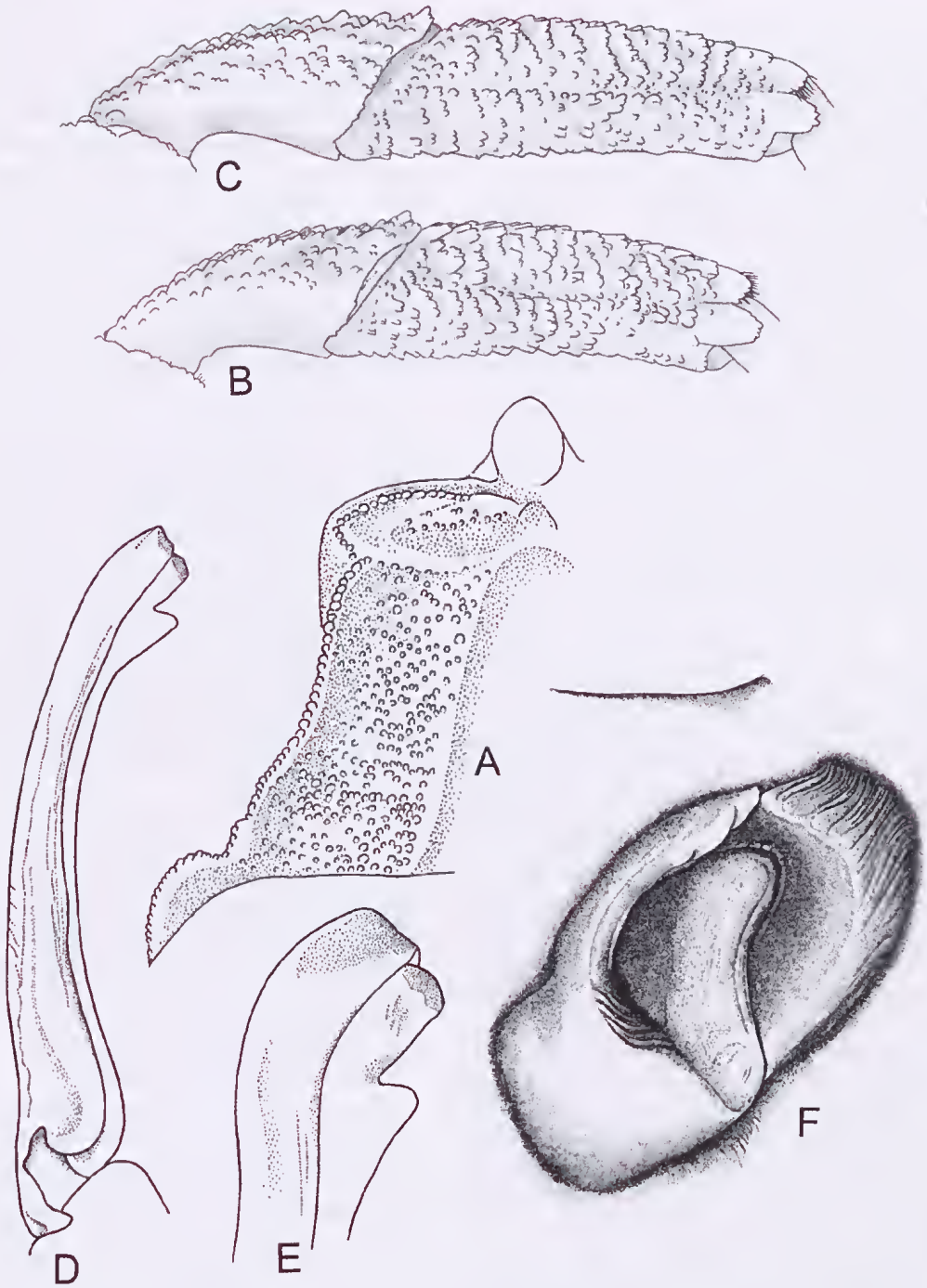


FIG. 26. *Ocypode ryderi*: A, P1 thoracic sternite; B, C, P2-3 propodi; D, E, Go1; F, female operculum.

(SMF-9315), x.1978, M. Grasshoff; — Mida Creek, S of Watamu, Swatami Mangrove (3°24.05'S, 39°57.95'E), 1 juv. (SMF-18281); — Kilifi Creek (3°38.27'S, 39°51.58'E) between Malindi and Mombasa, male (SMF-18286), xii.1985, W. Baumeister; — Kikambala (3°49.65'S, 39°49.71'E), 3 males, female, 4 juvs. (SMF-6110), 20.iii-5.iv.1971, Z. Števičić; — *ibid.*, male (SMF-6354), 1.ix.1973, W. Sudhaus; — Mombasa, 1 juv. male, 2 females (ZSM); female (ZSM); 2 males, 3 females (ZSM); male (NHM); 2 juv. females (NHM-1955.6.9.38-39); — Mombasa, Nyali, male (UZMK); — Mombasa, Bamburi, 10 males, 3 females, 1 juv. (RMNH-26015). Tanzania. Zanzibar, male (ZMH-K2839) [det. Pfeffer, 1888 as *Ocypode cordimana*]; — Zanzibar, Mkokotoni, female (ZSM) [det. Lenz, 1905]; — Dar es Salaam, 2 males, 1 juv. male, female, 2 juvs. (NHM-1973.41); 2 males (NHM-1964.7.10.9-10); male, female (ZMH-K2964). Mozambique. No further data, male (NRMS-t5972); — Inhambane, male, 2 females (ZMH-K29813); — Xai-Xai, 3 males, 2 females (ZMH-K29816). South Africa. Boteler Point (27°1.0'S, 32°51.92'E), Kosi Bay, 2 males, 2 females (SMF-10932); — Durban, male, female (NRMS-t6526); female, 1 juv. female (RMNH-73801); female (ZMUA-102.369); — Amanzimtoti, S of Durban, 1 juv. female (NMG-2235) [det. Lenz, 1912]; — Port Alfred, 1 specimen (NHMW). Seychelles. Mahé, 1 juv. (NHMW-24971) [det. Koelbel as *Ocypode fabricii*], Korvette Frundsberg Expedition.

Diagnosis. Middle-sized species. Eystalks not prolonged distally beyond cornea. Exorbital angles broadly triangular. Stridulating ridge composed of c. 15 tubercles. Smaller cheliped pointed distally. P2-3 propodi naked on anterior surface. P1-5 bases, carpi, and dactyli each bearing a distinct narrow red band along proximal margin. Go1 broadly bulging, slightly curved laterally in distal part, bearing a distinct palp. Operculum of female genital opening strongly protruding anteromesially with distinct rim; vaginal slit directed lengthwise.

Description. Carapace (Fig. 48) slightly wider than long and beset less densely with coarse tubercles than in other species of *Ocypode*, gradually becoming larger toward lateral sides. Lateral half of orbital margin broadly concave. Exorbital angles broadly triangular and directed slightly anteriorly. Lateral margins of carapace directed slightly outwards from base of exorbital angle in anterior third of carapace, and then directed inwards in posterior two-thirds, forming distinct epibranchial angle, and carapace broadest at anterior third. Pterygostomial region distinctly tuberculate except along lateral sides

of buccal cavern. P1 thoracic sternite (Fig. 26A) protruding roundly at anterolateral corner and concave inside, and distinctly tuberculate in posterior two-thirds, bearing a pair of distinct humps with roughly arranged tubercles, and tuberculate carinae on anterior and lateral margins. Palm of larger cheliped longer than broad and scattered with distinct and coarse tubercles on anterior surface, and irregularly denticulate on ventral and dorsal margins. Stridulating ridge (Fig. 5B) composed of c. 15 irregularly arranged tubercles. Smaller cheliped pointed distally. P2-3 carpi and propodi (Fig. 26B-C) naked on anterior surface. P1-5 bases, carpi, and dactyli each bearing a distinct narrow red band along proximal margin. Go1 (Fig. 26D-E) broadly bulging, curved laterally in distal part, bearing distinct cone-like palp; terminal projection wider than long; sperm channel originating dorsally and running without torsion along distal curve to short terminal projection; last part of channel in median line of terminal projection; distal opening located in flat median concavity of distal margin. Operculum of female genital opening (Fig. 26F) strongly protruding anteromesially with rounded distal end; vaginal slit directed lengthwise, almost parallel to sternal median line; lateral rim well developed.

Juvenile specimens. In a small specimen (12.4 × 15.1 mm, NHMW) stridulating ridge not distinguishable among tubercles around. In a slightly larger specimen with a carapace width of 17.5 mm (SMF-9315) stridulating ridge not yet distinguishable either, however in a still larger specimen with a carapace width of 18.0 mm (SMF-6111) stridulating ridge distinguishable. P2-3 propodi naked on anterior surface, bearing sparse setae on dorsal margin.

Distribution. East coast of Africa from Abd El Kuri and South Somalia to Port Elizabeth (South Africa), Seychelles. Type locality: Natal.

Remarks. *O. ryderi* is common on the eastern to southern coasts of Africa. It was identified by earlier authors under such different names as *O. kuhlii*, *O. cordimanus*, or *O. urvillei*, which turned out later, however, to be based upon misidentified specimens. Pfeffer (1889), Ortmann (1894, 1897), Lenz (1905, 910), Barnard (1950), *etc.* identified specimens from eastern to

southern Africa as *O. kuhlii* instead of *O. ryderi*. So *O. ryderi* had remained confused with *O. kuhlii*, until Sakai, K. & Türkay (1976) clarified that they were two species which are clearly separable by their individual distribution area. Specimens examined since 1976 have proven, as suggested by us in 1976, that it is only *O. ryderi* of the two species that occurs on the eastern to southern coasts of Africa (vs. *O. kuhlii* is known to be distributed only in Indonesia), and therefore, there is no doubt that their material from the eastern to southern coasts of Africa is conspecific with the type specimen of *O. ryderi*, which seems to have been lost (S.H. Fuller, *in litt.*).

O. urvillei described by A. Milne-Edwards (1868) based on a specimen from among Grandidier's collection, has turned out to be identical with *O. ceratophthalma*, however the P3 and P5 that have been glued to the left side of the specimen are not those of *O. ceratophthalma*, but of *O. ryderi*, and this has caused confusion.

O. ryderi is easily distinguishable from all the other eastern to southern African species by the morphology of the stridulating ridge, the naked P2-3 propodi, and the structure of the Go1. Recognition in the field is easy because of the striking red band along the proximal margins of the P1-5 bases, carpi, and dactyli, which even persists in ethanol for many years.

Juvenile specimens of *O. ryderi* are characterised by the scanty setae on the pereopods when compared with the sympatrically occurring *O. madagascariensis*, *O. ceratophthalma*, and *O. cordimanus*, which have dense setae on the legs.

Ocypode saratan (Forskål, 1775)

(Figs 5C, 27, 49)

Cancer saratan Forskål, 1775: 87.

Ocypode saratan — Olivier, 1811: 414, 416 [in part, Red Sea except Suez Canal]; Holthuis, 1958: 52; George & Knott, 1965: 19; Crosnier, 1965: 92, 95 [in part], figs 153, 161, 169-170, pl. 8, fig. 2, pl. 10, fig. 5; Linsenmair, 1967: 403-456; Serène, 1968: 97; Carli, 1969: 57, 62, 63-76; Lewinsohn, 1977: 48; Vannini & Valmori, 1981: 205, figs 1 B, 2 B1-2, 3 B, 4B; Eshky, 1985: 1-451; Eshky *et al.*, 1988: 341-358; Al-Waissa *et al.*, 1988: 106P; Al-Waissa *et al.*, 1989: 755-764; Whiteley *et al.*, 1990: 261-273; Eshky *et al.*, 1990: 237-248; Türkay *et al.*, 1996:

107, figs 9-10, pls 4-6; Clayton, 2001: 37-55; Ng *et al.*, 2008: 240.

Ocypode (Ocypode) saratan — De Haan, 1835: 29.

Ocypode Fabricii — White, 1847: 35.

Ocypode cursor — White, 1847: 35 [in part: only material from the Red Sea].

Ocypode aegyptiaca Gerstäcker, 1856: 134; Miers, 1878: 409; De Man, 1881: 247; Ortmann, 1894a: 762, 769; Laurie, 1915: 416, 467 [in part: not material from the Persian Gulf]; Balss, 1924: 14 [material from the Gulf of Aqaba but not the Red Sea]: 14 [in part: including *O. cordimanus* from Noman I.]; Ramadan, 1936: 37; Monod, 1937: 18 [in part]; Monod, 1938: 146 [in part]; Holthuis, 1956: 328; 1960: 316, figs 1-5, 8.

Ocypoda aegyptiaca — Heller, 1861a: 16; 1861b: 361; 1862: 292; Miers, 1882: 381, pl. 17, figs 3, 3a; Ortmann, 1897: 360, 366; Nobili, 1901a: 16; 1906b: 309, 310; Lenz, 1912: 4.

Ocypoda cordimana — Heller, 1861a: 17; 1861b: 361; 1862: 292.

Ocypoda cursor — Heller, 1861a: 17.

Ocypode ceratophthalma — Von Martens, 1866: 381; Kossmann, 1877: 55; Neumann, 1878: 26.

Ocypode ceratophthalma var. *Ceratophthalma-aegyptiaca* — Paulson, 1875: 64.

Ocypoda ceratophthalma var. *aegyptiaca* — Kingsley, 1880: 180.

Ocypoda ceratophthalma — Nobili, 1906b: 310; Parenzan, 1931: 1001, fig. 1, pl. 14, figs 1-6, pl. 15, figs 7-8.

Ocypode aegypticus [sic.] — Serène, 1968: 97.

Material examined. Red Sea (no exact locality). Male, female (MNHN-3296); male (USNM-43333); male (ZMH-K2960); male, 4 juv. females (SMF-1935), Rüppell; female (SMF-6746), Rüppell; female (SMF-1961), Bannwarth; 1 juv. [vend. Kapt. Pöhl], female (MNHN-3295); 2 males (MNHN), 'Companie de l'Isthme Suez'; male (MNHN), 'Calypso'; 1 specimen (MNHN-3281), Clot Bey; 2 specimens (NHN-3282), Clot Bey; 2 specimens (MNHN-3283), Beaudoin; male, female (RMNH-237); 5 males (NHMW); 2 juvs [18.7×21.7, 22.5×25.7 mm] (RMNH-D2720); — Sinai Peninsula, female (RMNH-17722); — *ibid.*, male (SMF-18277), W. Baumeister; — Gulf of Aqaba, male (NHM-78.25). Egypt. Gulf of Suez: No exact locality, 2 males, female, 1 juv. female (NHM-69.49) [det. Miers, 1882]; — El Bilaiyim, female (RMNH-SLR 2672); male (RMNH-SLR 2702); 6 males (RMNH-SLR 2891); 1 juv. female (RMNH-27748); female, 10 juvs. (RMNH-27228); — Et-Tur (28°14.07'N, 33°36.21'E), male [40.7×44.5 mm]; 3 females [42.0×46.8 - 36.0×40.1 mm] (SMF-9711), 1874-75, R. Kossmann; — Et-Tur, 2 males, 2 females (SMF-6747), 21.ix.1967, L. Fishelson; male (ZSF); male (RMNH-SLR 262); male, female (RMNH-1990); female (RMNH-SLR 2156); — At-Tur, Abu Galambo, 4 females (NRMS-t6012); — Kad el Hamden, 2 males (MNHN); — Mersa Tal Kad Yayah, 2 females (MNHN); — Umm el Kyaman, female (MNHN); — Shadwan Island, 2 males, female

(RMNH-21934); male, female (NHMW); – Gulf of Aqaba: Dahab, male, female (RMNH-29236); 1 juv. (NHMW), S.M.S. 'Pola'; – Abu Zabad, 40 km south of Dahab, male (RMNH-12169); female (RMNH-SLR 892); – Sharm el Sheikh, 1 juv. male, 1 juv. female (RMNH-12168); – Ras Muhammad, female (RMNH-SLR 728); male, female (RMNH-11930); – Red Sea coast: Al Ghardaqa (= Hurghada) (27°16.12'N, 33°48.09'E), 4 males, female (UZMK); male, 6 females (RMNH-SLR 2361); – *ibid.*, male (SMF-7154), vii.1965, E. Linsenmayr; – Ras Abu Soma, male (NHMW), S.M.S. 'Pola'; – Beach at c. 20 km South of Safaga (26°30'N, 34°05'E), sand bottom near mangrove, male (SMF-23036), 23.iv.1995, M. Apel; – Al-Qusayr (= Kosseir), many specimens (RMNH-17546); female, 2 juvs. (NHMW), S.M.S. 'Pola'; – Port Berenice (= Barnis), male (MNHW), S.M.S. 'Pola'; – Mersah Dhiba, 2 juv. males (NHMW), S.M.S. 'Pola'. Sudan. No specific locality, 1 specimen (NHM-1934.1.17.118); – Mersa Halaib, male, female (USNM-97952); 5 males, 6 females (NHMW), S.M.S. 'Pola'; – Port Sudan, female, 2 juvs. (NHM-1955.6.9.37). Saudi Arabia. Bir al Mash'i, male, 1 juv. female (NHMW), S.M.S. 'Pola'; male, 5 juvs. (ZSM); – Sanafir-Island, 2 males (NHMW); – Mersah Duba, 2 juv. males (NHMW), S.M.S. 'Pola'; – Habban (26°44'N, 36°32'E), male (MNHW), S.M.S. 'Pola'; – Jeddah, 3 males, 2 juv. females (RMNH-236); 2 juvs. (RMNH-2720); – 50 km South of Jeddah (21°00'N, 39°12'E), 3 males, 4 females, 10 juvs (SMF-23037), 1.iv.1995, M. Apel; – Shoiba Beach, 120 km South of Jeddah (20°48.71'N, 39°25.58'E), male (SMF-10700), 21.viii.1982, W. John; – Farasan Islands, Sarso, 1 juv. (ZMH-K28635) 'Meteor-1 Expedition' 1964, W. Schäfer, W. Klausewitz *et al.*; 1 juv. male (SMF-5417). Eritrea. Difnen Island, 2 males, female (MCSNG); – Mitsiwa (= Massawa, Massaua), male, female (MNHN); 3 males, 4 females (MCSNG-136-142); male, female (MCSNG-147); 2 males (MZT-1108); female (MZT-1111); – Massawa, Adbelkader Peninsula, 2 males, 3 females (MZT-1106); – Shëk Seyd (= Sheikh Sa'id I. = Green I.) near Massawa, 1 juv. male, 1 juv. (RMNH-26863); female (MZT-1101); – Dahlak Archipelago: Shumma-Island, female (MCSNG-147); – Madote Island, male, 3 females (MCSNG); – Dissei Island, Dahlak Archipelago, 3 males (MCSNG-147); – Entedebir Island near W coast of Dahlak Kebir, male, 2 females (RMNH-17822), male, 1 juv. male, 1 juv. female (RMNH-25846); – Cundabulu I. c. 2 km West of Entedebir Island, male (RMNH-24767); – Museri Island near SE point of Dahlak Kebir, 1 juv. male, 2 juv. females (RMNH-25847); 2 females (RMNH-25847); 2 females (RMNH-25849); – Seil Anbar Island, E of Museri, male (RMNH-25848). – Assab (= Aseb), 2 males (MNHN), 1 juv. (RMNH-26864); 2 juv. males, 4 juv. females, 1 juv. (RMNH-25846); 3 males (RMNH-25566). Yemen. Red Sea: Kamaran Island, 2 males (NHMW), S.M.S. 'Pola'; – Jazirat Zabarjad (= Zebayir Island), female (MNHW),

S.M.S. 'Pola'; – Gulf of Aden: Aden, female (USNM-19040); female (USNM-43295); 2 males, 3 females (MNHN); 1 juv. male (RMNH-15504); 3 juvs. (RMNH-15505); male, female (RMNH-15506); 2 juvs. (NHMW); female (MCSNG-143); male, 3 juvs. (MCSNG); – Al-Mukalla, male, 1 juv. female (NHM-1894.10.31.13); female (MNHN); – Suqutra (= Socotra), male, 3 females (NHM-1906.5.18-22); – Suqutra (= Socotra), Soc/It-157a (12°18.698'N, 53°48.285'E) – (12°18.698'N, 53°48.285'E), sandy beach, male cheliped (SMF-36171), 9.iv.199, M. Apel. Republic of Djibouti. Ras Siyahn (12°28.59'N, 43°18.89'E), Mangrove, Lagoon, 4 males, female, 1 juv. (SMF-24495), 24.vi.1996, U. Zajonz & F. Krupp; – Godorayah (12°9.97'N, 43°24.73'E), behind northern Mangrove, male (SMF-24499), 2 juv. males (MZUT-1097); male, 5 juvs. (MNHN), 24.vi.1996, U. Zajonz & F. Krupp; – Gulf of Tadjoura, Obock, Tadjoura, male (MNHN); – Djibouti, male, 2 juvs. (MNHN); male (MNHN). Somalia. Berbera, male (ZMK-1540); – Kasim, male, 4 females (MCSNM-2155). Oman. Gulf of Masirah, peninsula Barr Al-Hikman, Khawr Al-Milh, southern part (20°23'N, 58°17'E), male (SMF-24539), 31.v.1995, D. Clayton; 1 damaged female (SMF-24540).

Diagnosis. Middle- to large-sized species. Eye-stalks prolonged distally beyond cornea in a long slender stylus. Exorbital angles slightly protruding forward. Stridulating ridge composed of 67–87 fine striae. Smaller cheliped pointed distally. P2 propodus with a broad median row of setae on anterior surface. P3 propodus naked. Go1 distinctly curved laterally at bulging distal end, bearing a distinct palp at base of distal curve; terminal projection wider than long. Operculum of female genital opening rounded distally and protruding mesially; vaginal slit directed anteromesially.

Description. Carapace (Fig. 49) wider than long; densely beset with fine tubercles, becoming larger towards sides of carapace. Lateral half of orbital margin directed obliquely backward. Exorbital angles slightly protruding forward as a small pointed tip. Lateral margins of carapace directed distinctly outwards from base of ex-orbital angle in anterior third of carapace, and then directed inwards in posterior two-thirds, so that carapace broadest at anterior third. Pterygostomial region distinctly tuberculate except around buccal cavern. P1 thoracic sternite (Fig. 27A) smooth on surface and triangular at anterolateral corner, bearing tuberculate carina on lateral margin. Palm of larger cheliped broad, densely beset with fine tubercles on

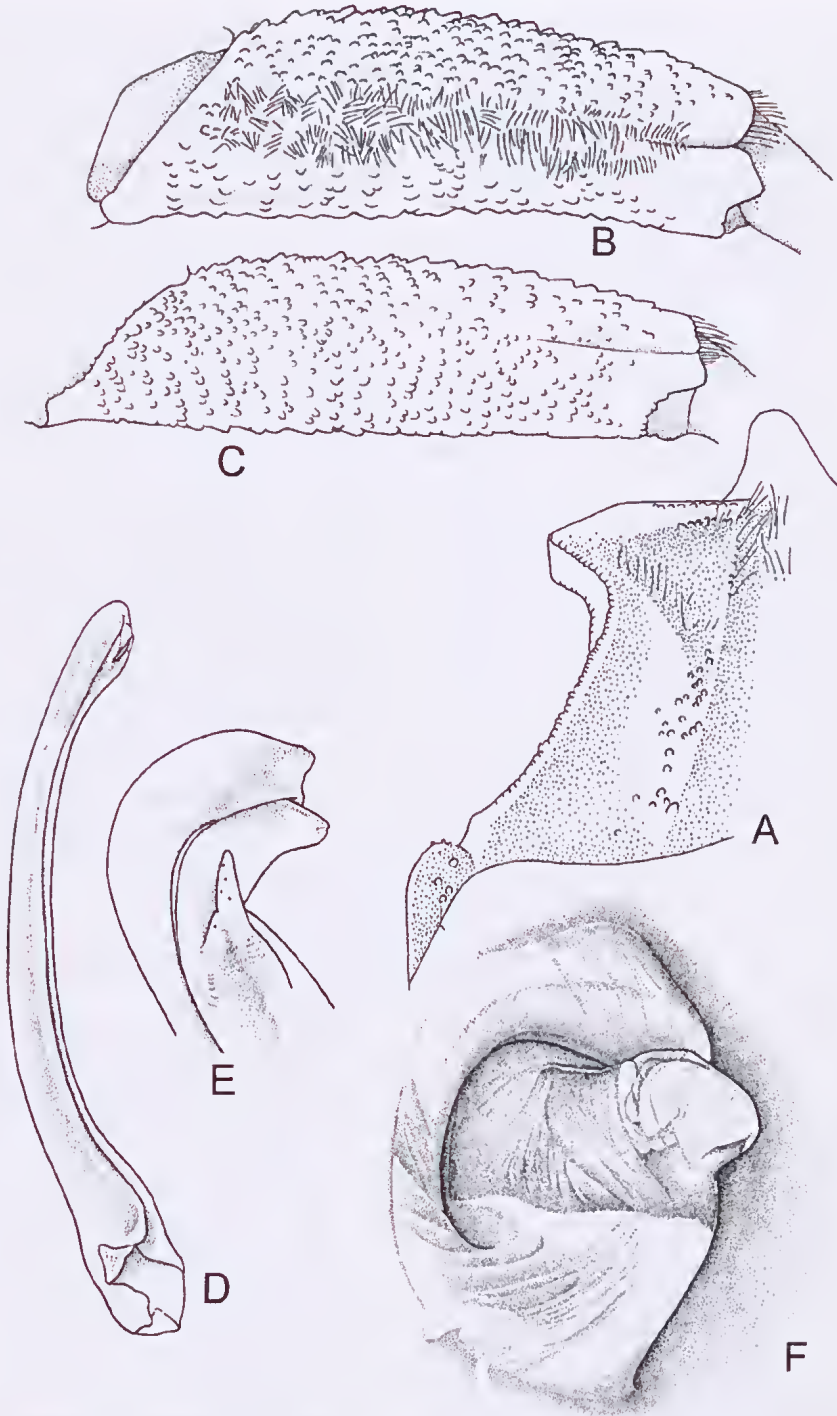


FIG. 27. *Ocypode saratan*: A, P1 thoracic sternite; B, C, P2-3 propodi; D, E, Go1; F, female operculum.

anterior surface. Stridulating ridge (Fig. 5C) composed of 67–87 fine striae. Smaller cheliped pointed distally. P2 propodus (Fig. 27B) with broad median row of setae on anterior surface. P3 propodus (Fig. 27C) naked. Go1 (Fig. 27D–E) three-sided proximally, distinctly curved laterally at bulging distal end, bearing palp with slenderly triangular distal half at base of distal curve. Operculum of female genital opening (Fig. 27F) protruding mesially in globular shape; mesial part of rim distinct.

Juvenile specimens. In a small specimen (5.7×6.3 mm, RMNH-15505) eyestalks not yet prolonged distally beyond cornea. Exorbital angles broadly triangular, located far backward, and slightly protruding forward. Carapace quadrate. Stridulating ridge not yet developed, but low elevation already present. P2–3 propodi with scanty spinules on dorsal margin and yellowish short distal setae at distal end, bearing (only in P2 propodus) a median row of scanty setae on anterior surface. In a larger specimen (18.7×21.7 mm, RMNH-D2720) eyestalks not yet prolonged distally beyond cornea, but slightly protruding at distal end of cornea. In a still larger specimen (22.5×25.7 mm, RMNH-D2720) eyestalks prolonged distally beyond cornea in a small stylus. In those larger specimens lateral margins of carapace curved outwards from base of exorbital angle. P2–3 propodi naked on dorsal margin, but yellowish short setae at distal end, bearing (only in P2 propodus) a median row of scanty setae on anterior surface. Stridulating ridge already composed of more than 50 fine striae.

Distribution. All coasts of the Red Sea, African coast of the Gulf of Aden and northeastern coast of Somalia up to Bedei, southern Arabian coast to southern Oman. Type locality: the Red Sea, but without specific locality.

Remarks. *Ocypode saratan* is common on the coast of the Red Sea and on the African coast of the Gulf of Aden. Another species *O. cordimana* is also found, though rarely, in the Red Sea. Earlier records of some species, especially of *O. ceratophthalma* have turned out to be incorrect, and those records can be considered to be based upon mis-identified specimens, especially of juveniles. Juvenile specimens reported by Von Martens (1866), Kossmann

(1877), Neumann (1878), Kingsley (1880), Nobili (1906) and Parenzan (1931) have all been re-examined and found to be *O. saratan*. Monod (1937, 1938) identified specimens from the Suez Canal as *O. aegyptica*, and this was later cited by Holthuis (1956). However, the reexamination of Monod's specimens shows them to be all *O. saratan*, except one, which we identified as *O. cursor*. A good number of records of *O. saratan* from areas outside the Red Sea and the African coast of the Gulf of Aden exist in the literature. Hoffmann (1874) reported *O. saratan* from Madagascar, and was followed by Miers (1878), Ortmann (1894, 1897), and Nobili (1906). Lipke Holthuis examined Hoffmann's material at our request, and determined it to be *O. ceratophthalma* as suggested by Crosnier (1965). The reports of *O. aegyptiaca* (= *O. saratan*) by Laurie (1915) and Stephensen (1945) based on the material from the Persian Gulf, have turned out to be incorrect, because their material is clearly identifiable as *O. rotundata*. We have also reidentified *O. aegyptiaca* (= *O. saratan*) reported by Balss (1935) from Shark Bay, Western Australia as *O. fabricii*.

Ocypode stimpsoni Ortmann, 1897

(Figs 5D, 28, 50)

Ocypode (*Ocypode*) *cordimana* – De Haan, 1835: 57–58, pl. 15, fig. 4.

Ocypode convexa Stimpson, 1858: 100; 1907: 110, pl. 15, fig. 2 [Junior homonym of *Ocypode convexa* Quoy & Gaimard, 1824]; Ortmann, 1894a: 769, pl. 23, fig. 21.

Ocypoda stimpsoni Ortmann, 1897: 367–368 [Nomen nudum for *Ocypode convexa* Stimpson, 1858. – type locality therefore: Japan, Shimoda]; Sakai, T. 1934: 319; 1935a: 211, pl. 58, fig. 4; 1947: 664, fig. 1915; 1939: 613, pl. 104, fig. 1; 1940: 50; 1956: 53; 1965: 189, pl. 90, fig. 1; Kamita, 1936a: 318; 1936b: 33; Horikawa, 1940: 28; Shen, 1940: 91; Kamita, 1941a: 241; 1941b: 80; 1941c: 154; Lin, 1949: 26; Kim, 1958: 11; 1962: 53; 1970: 18; Ono, 1959: 146; Kikuchi, 1959: 51; Park, 1964: 17; Kim & Rho, 1971: 13; Muraoka, 1974: 48–51, tab. 1, figs 1–2.

Ocypode macrocera, Urita, 1917: 72.

Ocypoda stimpsonii – Balss, 1922a, 88A (11): 142.

Ocypode stimpsoni – Urita, 1926a: 435; 1926b: 27; Shen, 1932: 268–272, figs 164, 166, pl. 9, fig. 3; 1937b: 309; Sakai, T., 1935b: 72; 1976: 599–600, fig. 327a, pl. 206, fig. 3; Shen, 1936: 76; 1937: 184; Miyake *et al.*, 1962: 130; Inaba, 1963: 170; 1988: 102; Utinomi, 1976: 89, pl. 45, fig. 5; Kim, 1977: 206; Miyake & Takeda, 1978: 43; Dörjes, 1978: 121;

Terada, 1979: 58, 60–62, 68, 69, figs 1–2; Fukuda, 1980: 1–8, figs 1–3; Yang, 1986: 153; Dai & Yang, 1991: 454, text-fig. 230, pl. 58 (2); Gamo & Kosakai, 1991: 27, 30, fig. 1; Huang *et al.*, 1992: 144, fig. 3, pl. 1C, tab. 1; Wang *et al.*, 1998: 65, figs 53–59; Kitaura *et al.*, 1998: 627, 628, 630, 632, 633; Ng *et al.*, 2001: 36; Imafuku, Habu & Nakajima, 2001: 197–211, tabs 1–3, figs 1–5; Marumura, & Kosaka, 2003: 69; Yodo *et al.*, 2006: 2–3, figs 2–4; Mano *et al.*, 2008: 2, 5–8, figs 2–8; Ng *et al.*, 2008: 240; Wada, 2009: 1–7, figs 1–3.

Ocypoda cordimana Desmarest, Nakazawa, 1927: 1124, fig. 2166 (misidentified)

Material examined. **China.** Unknown locality (NHM-1935.3.19.8); – Shandong Prov.: Shandong Peninsula, female (MCSNM); – Qingdao, 5 females (ZSM-128/1); – Qingdao, Xuejidao, sandy beach (35°58.54'N, 120°17.68'E), 8 males, 4 females (SMF-18283), 22.viii.1987, M.Türkay & Y.-L. Wang; – Suzhou, 1 juv. (USNM-168468); – Shanghai: Beidaihe District, Gulf of Liaotung, male, 3 females, 1 juv. (USNM-55712); 1 juv. female (USNM-50469); – Fujian Province: Fuzhou, 7 males, 5 females, 3 juv. males, 6 juv. females (ZMH-K2869); 18 males, 11 females, 3 juvs., 2 carapaces (ZMH-K2874); 3 males, 5 females (ZMH, K2887); – Xiamen, male (UZMK); female (RMNH-228); female (RMNH-2007); male (MNHN); – Taiwan: No exact locality, 5 males (SMF-8808); – East coast, no exact locality, 4 males, 5 females (SMF-10674). **Japan.** No exact locality, male (RMNH-227); – Akita Prefecture: Oga (39°52.09'N, 139°49.71'E), 2 juvs. (SMF-36199), T. Sakai; – Niigata Pref.: Sado-Island, Mano Bay, Kawaharada (38°0.1'N, 138°18.87'E), male, female (SMF-36196) [ex. coll. T. Sakai], 24.x.1924; – Tokyo Pref.: Tokyo Bay, 3 specimens (MNHN); – Kanagawa Pref.: Sagami Bay, 2 males, 2 females (SMF-6752); – Enoshima, Sagami Bay, female (NHRMST-6531); – Shizuoka Pref.: Suruga Bay, male (MCSNM); – Hamana-ko, beach (34°40.62'N, 137°36.78'E), 5 males (SMF-36198), T. Sugano; – Tokushima Pref.: Tokushima, Yoshino-gawa, 2 males [21.5×24.3, 20.8×23.1 mm] (SMF-36211), 19.vii.1990, S. Shinomiya, K. Sakai & Yoshida; – Tokushima Pref., Okinosu, Yoshino-gawa, male (SMF-36197) [det. K. Sakai, 1993]; – Kochi Pref.: Toyo-cho, Ikumi (33°31.73'N, 134°17.06'E), female (SMF-37066), 7.vii.1986, K. Matsuzawa; male, 1 juv.; – *ibid.*, male, 1 juv. (SMF-37067), 8.viii.1985; – *ibid.*, 1 juv. (SMF-37068), 23.ix.1986; – Toyo-cho, Noné (33°30.12'N, 134°16.15'E), 4 males, 1 juv. female (SMF-37062), 10.x.1989, K. Matsuzawa; – *ibid.*, male (SMF-37063), 4.xi.1989; – *ibid.*, 3 juv. males (SMF-37064), 24.ix.1984; – *ibid.*, 1 juv. male, 1 juv. female (SMF-37065), 2.xi.1989; – Kochi City, Kagamigawa estuary (33°30.44'N, 133°34.44'E), 2 males, female (SMF-37061), 6.ix.1987, K. Matsuzawa; – Tosa Bay, Tosa city, Usa-Inoshiri (33°26.34'N, 133°26.5'E), inlet-beach, 5 males, 3 females (SMF-6843); – Uranouchi Inlet, South-West area, Nakanoura (33°24.47'N, 133°21.66'E),

sandy beach, male (SMF-16610), 24.x.1979, M. & H. Türkay & K. Sakai; – Susaki-city, Awa (33°21.97'N, 133°15.54'E), female (SMF-37069), 9.viii.1989, K. Matsuzawa; – Ohgata-cho, Irino, Matsubara (33°1.19'N, 133°0.88'E), 5 males [26.4×31.0–18.6×20.9 mm], 3 females [23.7×27.4–24.4×27.4 mm], 5 juvs. (SMF-36210), 6.viii.1994, T. Shimeno; – *ibid.*, 1 juv. female, 1 juv. (SMF-37070), 28.viii.1988, K. Matsuzawa; – Kumamoto Pref.: Amakusa I., Beach near Ushibuka (32°10.79'N, 130°1.14'E), 4.ix.1989, T. Yamaguchi; – Kagoshima Pref.: Kagoshima, male (USNM-48365); female (USNM-48328); – Beach north of Tarumizu at river mouth in the northern part of port (31°29.85'N, 130°41.98'E), male (SMF-16611), 2.xi.1979, H. & M. Türkay & K. Sakai.

Diagnosis. Small-sized species. Eyestalks not prolonged distally beyond cornea. Exorbital angles acutely triangular, directed anterolaterally, located slightly backward. Stridulating ridges composed of 44–57 narrow striae, extending ventrally over mid line of fixed finger. Smaller cheliped broadly rounded to truncate distally. P2–3 propodi with median row of setae on anterior surface. Go1 slightly narrowing distally, curved laterally in flattened distal part. Operculum of female genital opening rounded distally, protruding mesially; rim undeveloped.

Description. Carapace (Fig. 50) slightly wider than long, and densely beset with fine tubercles on dorsal surface. Lateral half of orbital margin concave. Exorbital angles acutely triangular, directed anterolaterally, their tips posterior to median convexity of orbital margin. Lateral margins of carapace directed slightly outwards from base of exorbital angle in anterior third of carapace, then directed inwards in posterior two-thirds, forming broadly rounded, less protruding epibranchial corner, where carapace broadest. Pterygostomial region spacious, weakly tuberculate except along lateral sides of buccal cavern. P1 thoracic sternite (Fig. 28A) smooth, hemmed with tuberculate carinae on anterior and lateral margins, bearing shallow concavity at triangular anterolateral corner. Palm of larger cheliped broad, beset densely with fine tubercles on anterior surface, regularly serrated on ventral margin. Stridulating ridge (Fig. 5D) composed of 44–57 narrow striae, reaching (in most females) or overreaching (in very few females) mid-line of fixed finger, or extending (in males) to near ventral margin of palm. Smaller cheliped broadly rounded to

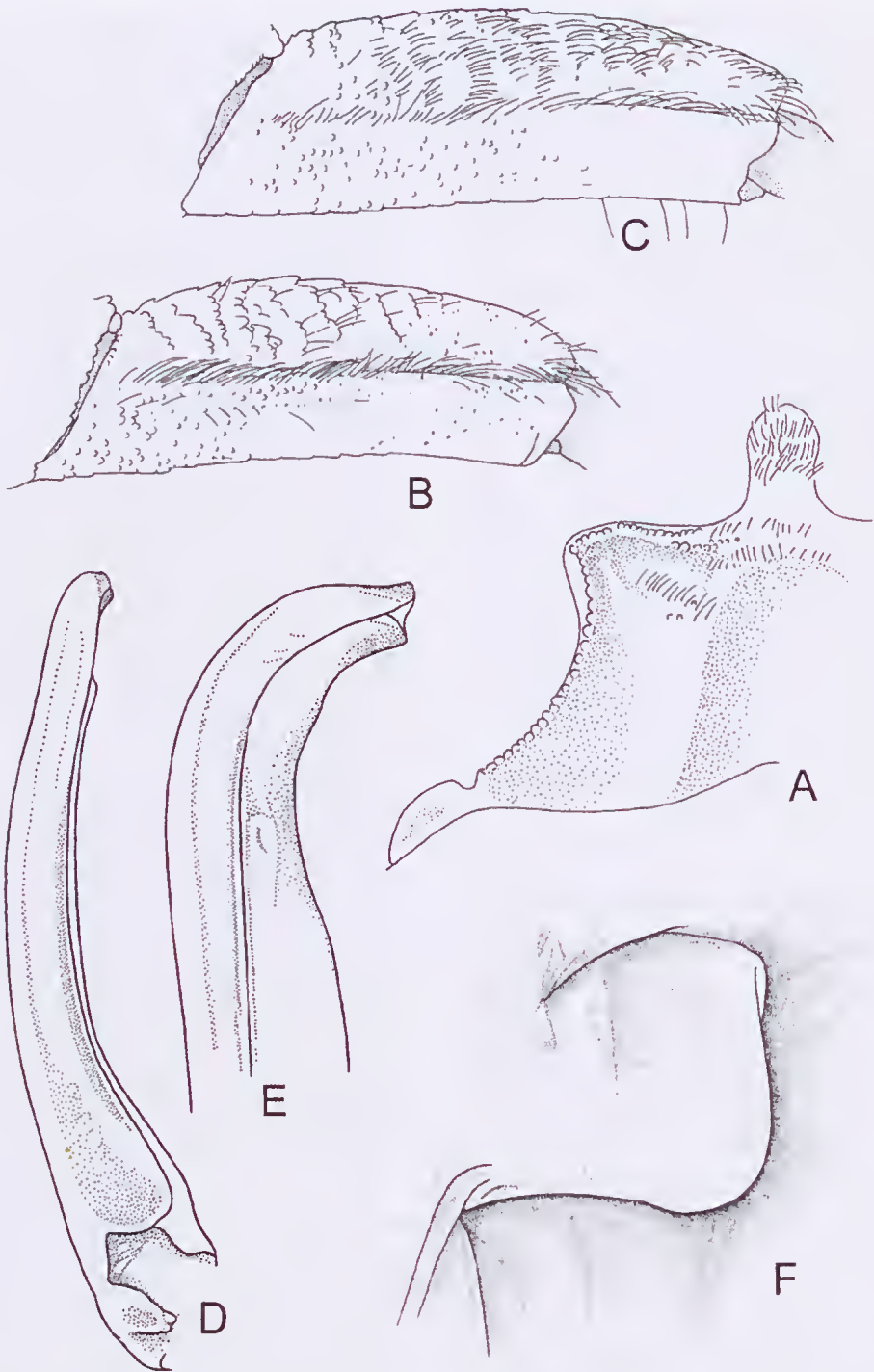


FIG. 28. *Ocypode stimpsoni*: A, P1 thoracic sternite; B, C, P2-3 propodi; D, E, Go1; F, female operculum.

truncate distally. P2 propodus (Fig. 28B) with median row of thick setae on anterior surface. P3 propodus (Fig. 28C) with transverse rows of setae on dorsal half of anterior surface, bearing a median row of setae. Go1 (Fig. 28D-E) slightly narrowing distally, curved laterally in flattened distal part, bearing small palp distant from distal end; groove originating dorsally, running along curved stem without torsion to flattened distal part; sperm-channel in middle line of stem. Operculum of female genital opening (Fig. 28F) rounded distally and protruding mesially in button-shape; rim undeveloped; entrance of vaginal slit sunken, forming deep funnel.

Juvenile specimens. In a small specimen (5.3×6.2 mm, USNM-168468) carapace wider than long, sparsely beset with granules on dorsal surface. Stridulating ridges distinctly developed, composed of striae, becoming finer and curved in S-shape in ventral part. P2 propodus with a median row of interspaced scanty setae on anterior surface. In a larger specimen (9.0×11.0 mm, ZMH-K2869) carapace densely tuberculate on dorsal surface. Stridulating ridge developed as distinctly as in adult specimens. Smaller cheliped pointed distally. In specimens with a carapace width of less than 17 mm, smaller cheliped always pointed distally, but gradually transformed into rounded to truncate adult shape in accordance with growth. In specimens with a carapace breadth of 19 mm, smaller cheliped already beginning to develop into characteristic adult shape, and in specimens with a carapace width of more than 20 mm, smaller cheliped in characteristic adult shape.

Distribution. China, Korea, and Japan. Type locality: Shimoda, Japan.

Remarks. This species was first reported from Japan by De Haan (1835) under the name of *Ocypode* (*Ocypode*) *cordimana*, but due to his precise figures, later authors quickly realised that his specimen did not belong to *O. cordimanus* Latreille, 1818. McLeay (1838: 64) stated: 'O. *cordimana* of De Haan appears to be a different species', and Kraus (1843: 41) also noticed the peculiarity of De Haan's specimen, though he remarked more reservedly that the figures probably represented a juvenile specimen. White (1847: 34) stated very clearly

that 'De Haan's material does not belong to *O. cordimana*.' Stimpson (1858) finally described it as a new species, *Ocypode convexa*, but Ortmann (1897) realised this was a junior homonym of *Ocypode convexa*, Quoy & Gaimard, 1824, and proposed the replacement name *Ocypode stimpsoni* Ortmann, 1897.

Ocypode stimpsoni seems most similar to *O. mortoni*, but the differences between them have already been enumerated under the remarks to *O. mortoni*. Juvenile *O. stimpsoni* are liable to be confused with the sympatric species *O. ceratophthalma* and *O. cordimanus*, however, they are easily identified by their stridulating ridges. *Ocypode stimpsoni* already has its distinctive stridulating ridge of fine striae fully developed from a carapace width as little as 10 mm, whereas in *O. ceratophthalma* of the same size the stridulating ridge is composed of irregularly arranged tubercles, and in *O. cordimanus* it is absent.

Urita (1917: 72) reported *O. macrocera* from Kagoshima, Japan, but his figures of the carapace and the stridulating ridge clearly indicate his specimens are identical with *O. stimpsoni*. Baksi *et al.* (1980) also recorded *O. stimpsoni* from India, where it definitely does not occur, and we suspect that his specimens belong to *O. macrocera*, a species that resembles *O. stimpsoni* in the shape of the smaller chela.

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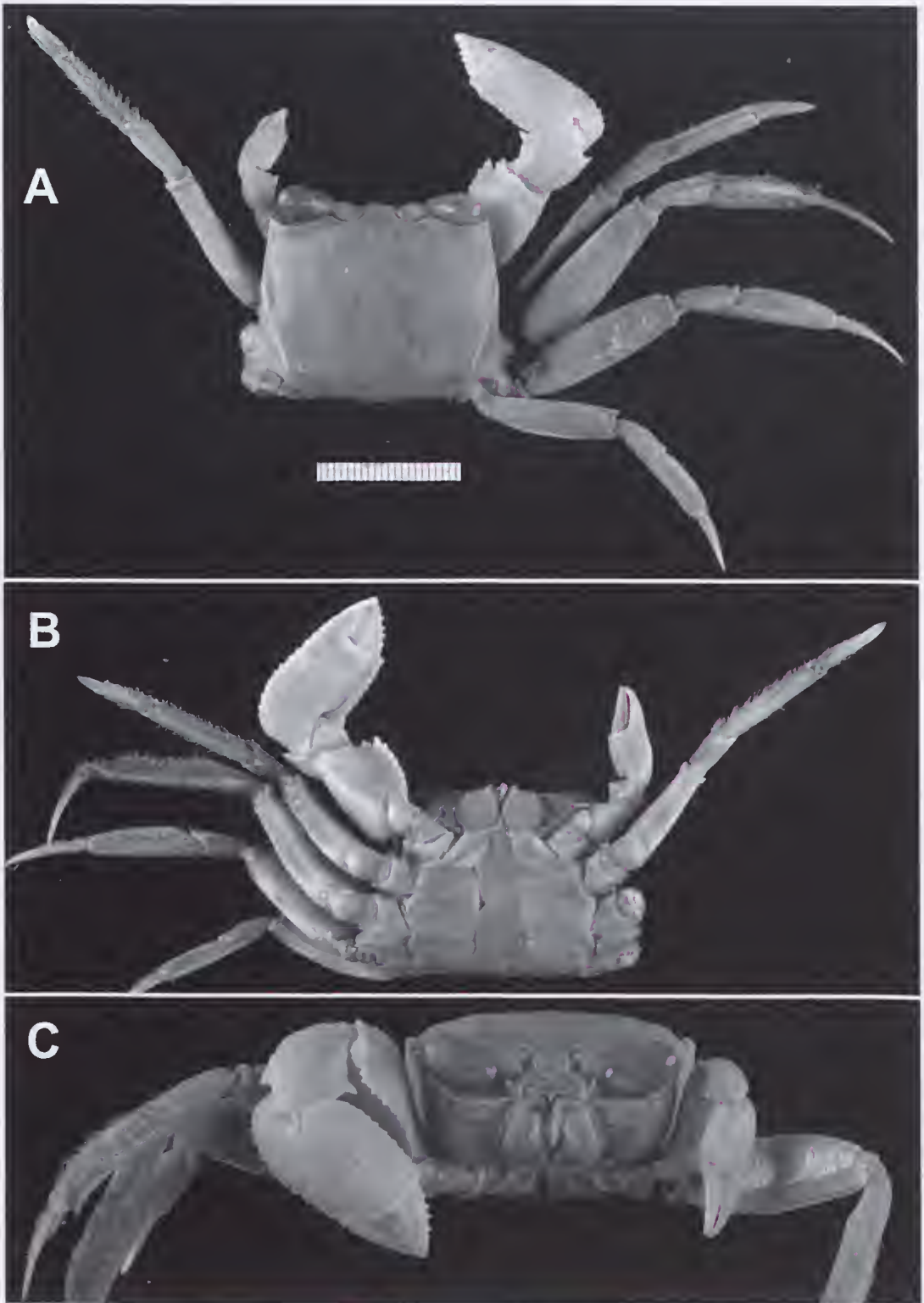


FIG. 29. *Hoplocypode occidentalis* (SMF-4104); dorsal, ventral and frontal aspects.

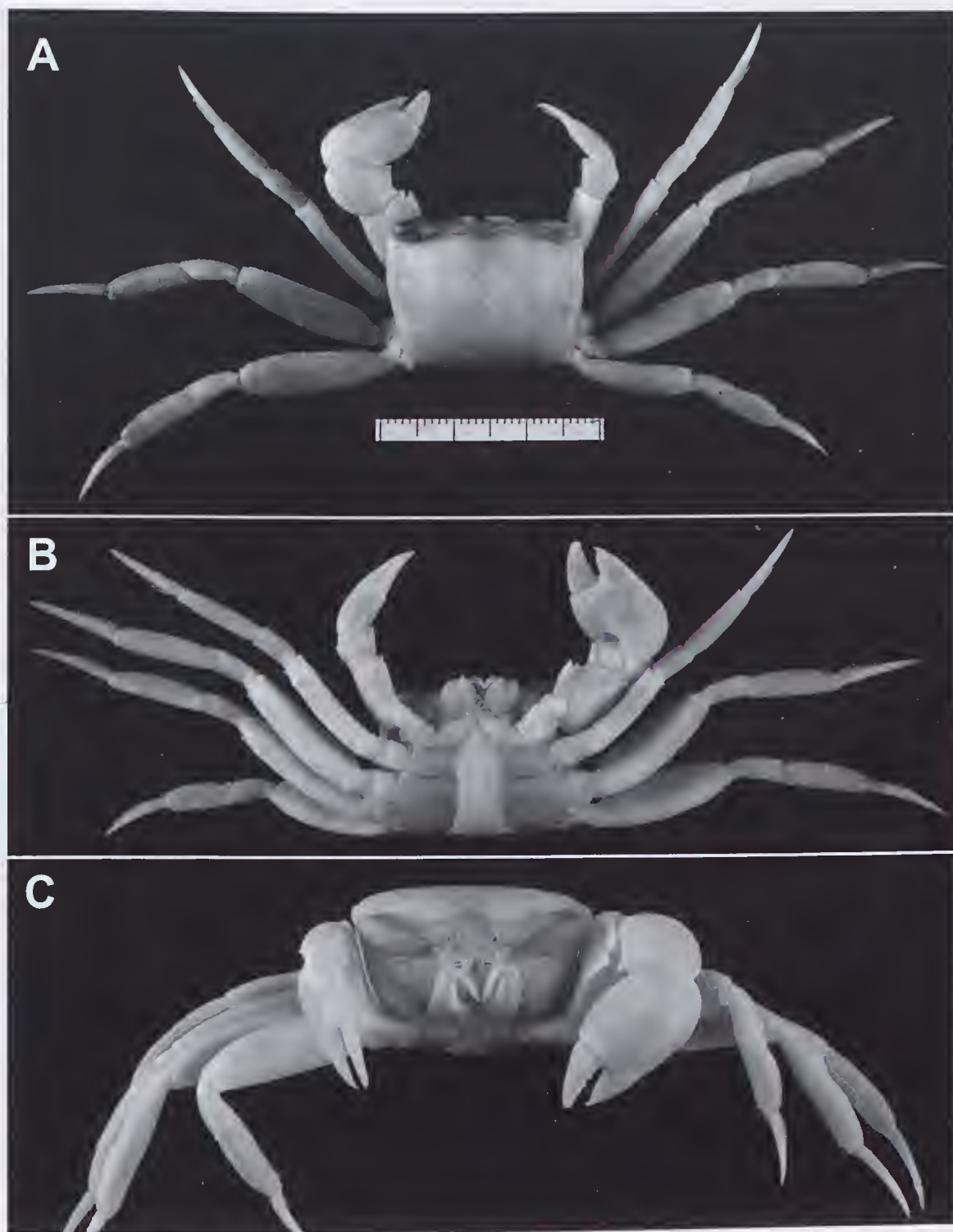


FIG. 30. *Ocypode africana* (SMF-1960); dorsal, ventral and frontal aspects.

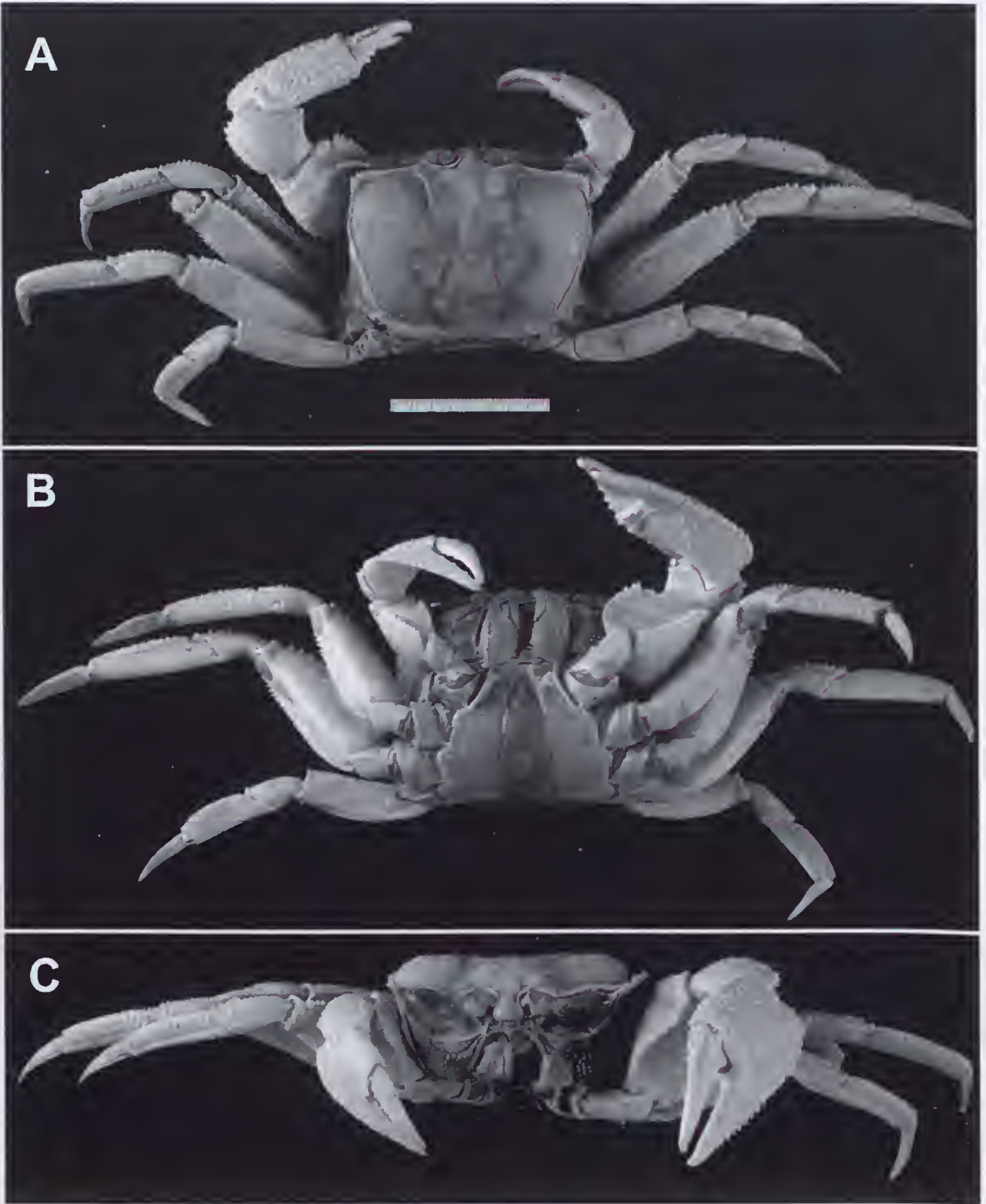


FIG. 31. *Ocypode brevicornis* (SMF-24536); dorsal, ventral and frontal aspects.

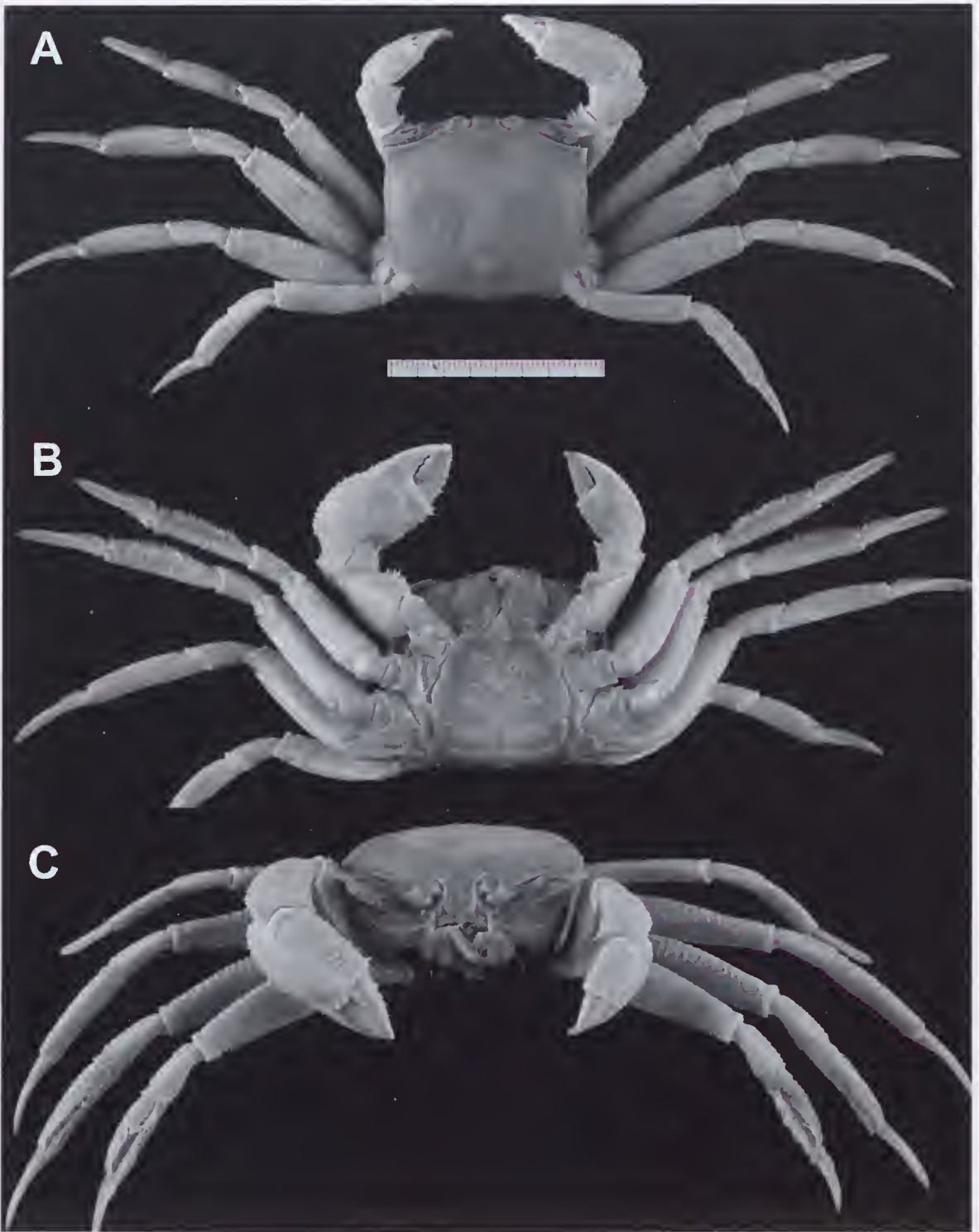


FIG. 32. *Ocypode ceratophthalma* (ZMG-124); dorsal, ventral and frontal aspects.

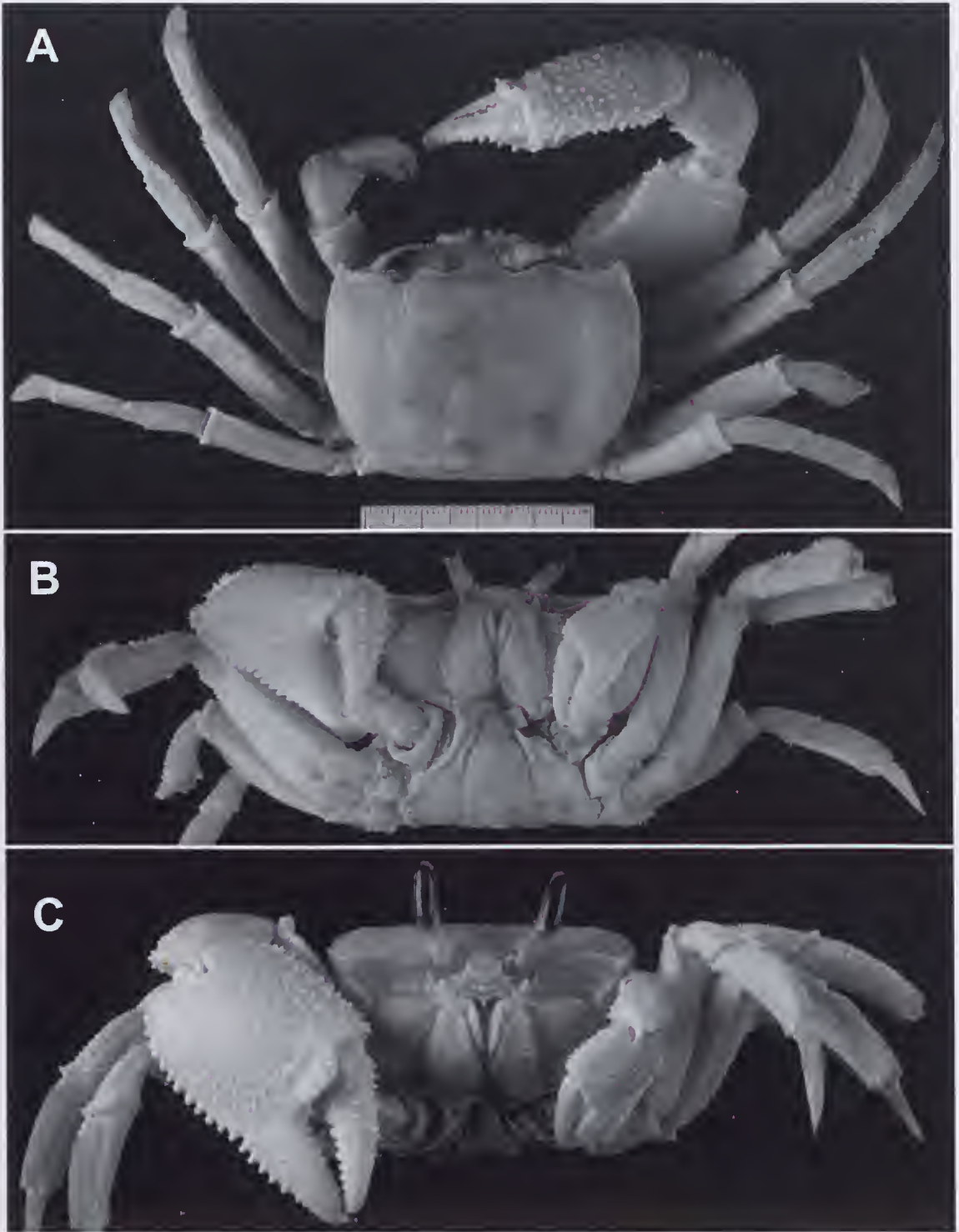


FIG. 33. *Ocypode convexa* (SMF-7609); dorsal, ventral and frontal aspects.

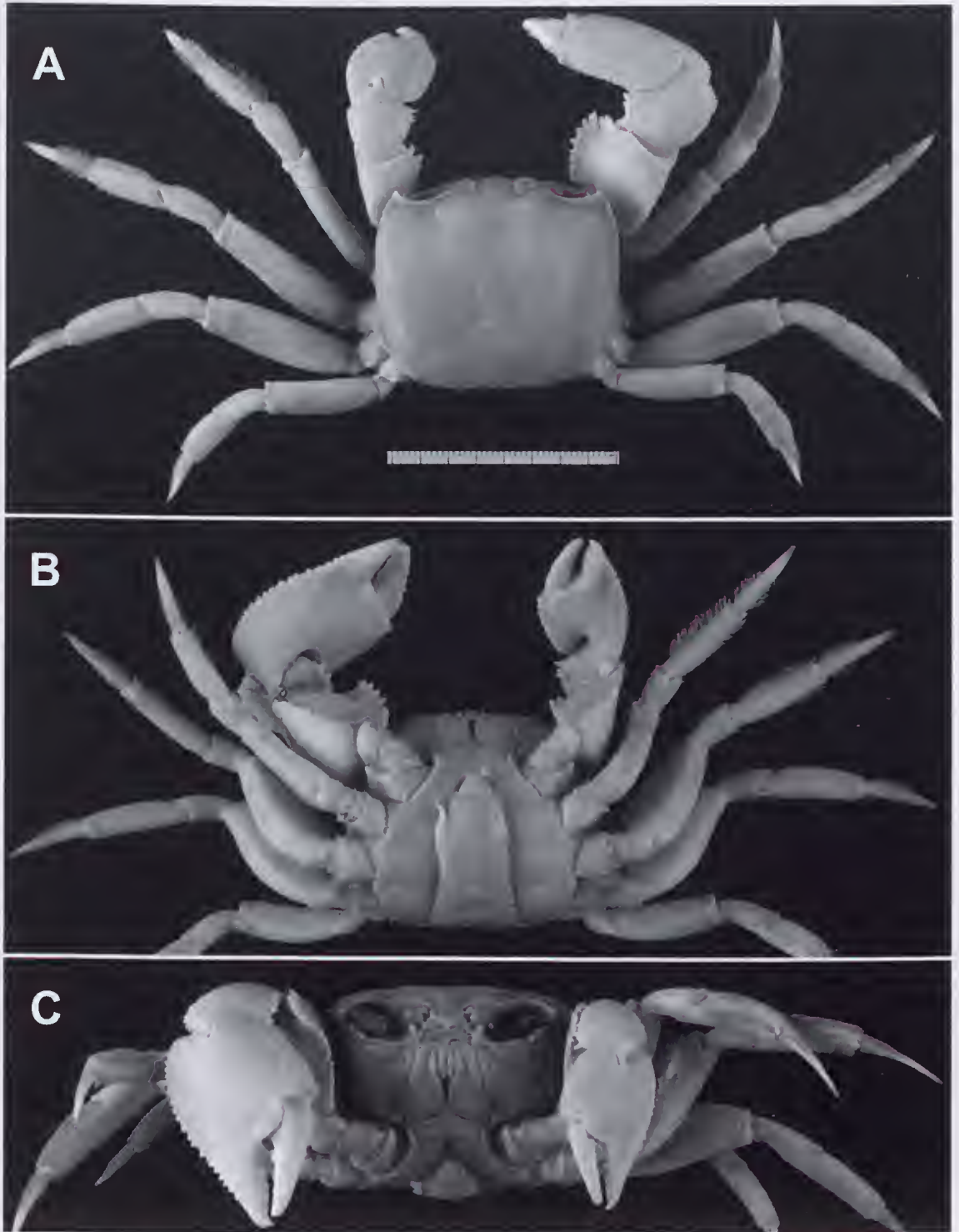


FIG. 34. *Ocypode cordimanus* (SMF-9983); dorsal, ventral and frontal aspects.

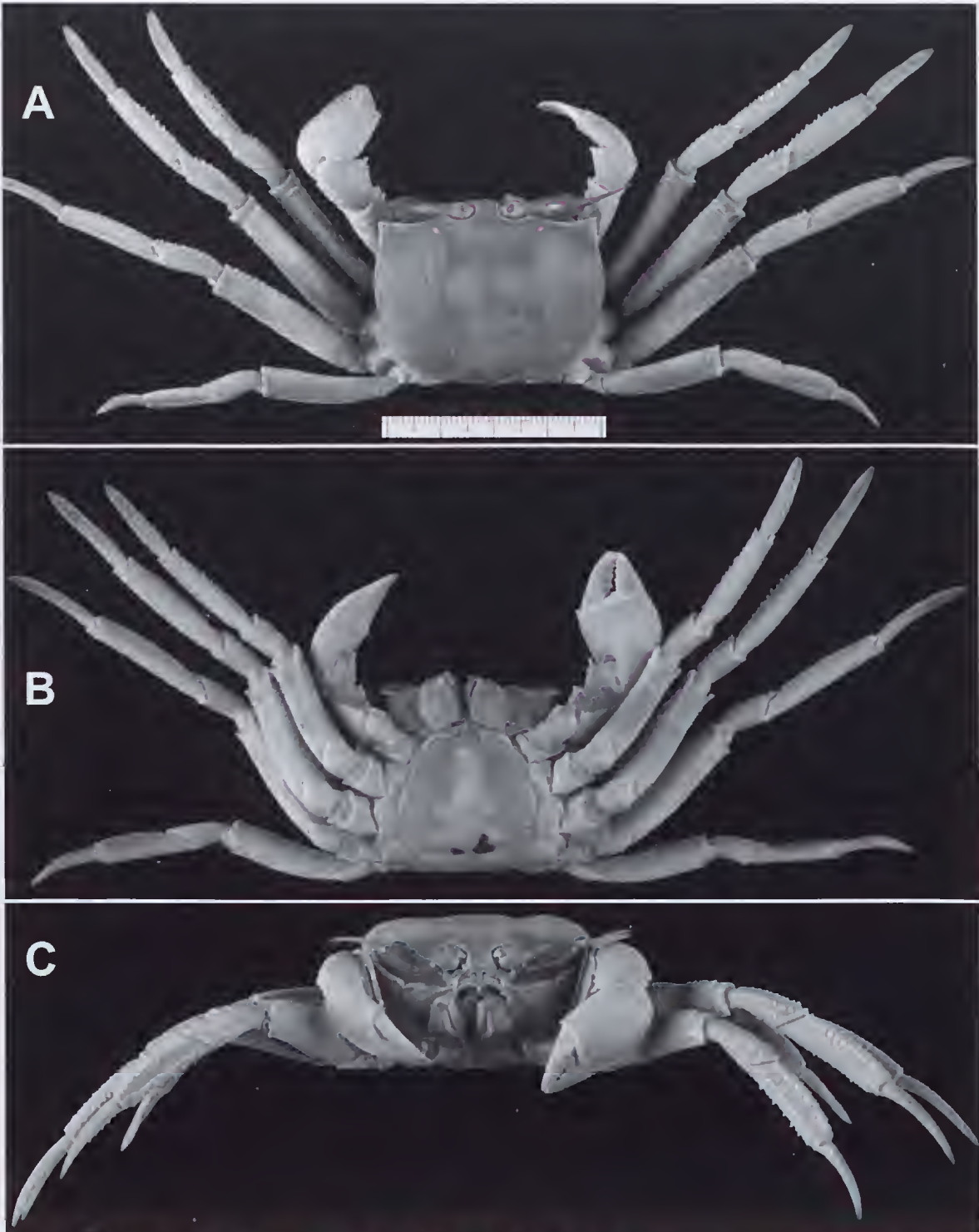


FIG. 35. *Ocypode cursor* (SMF-12165); dorsal, ventral and frontal aspects.

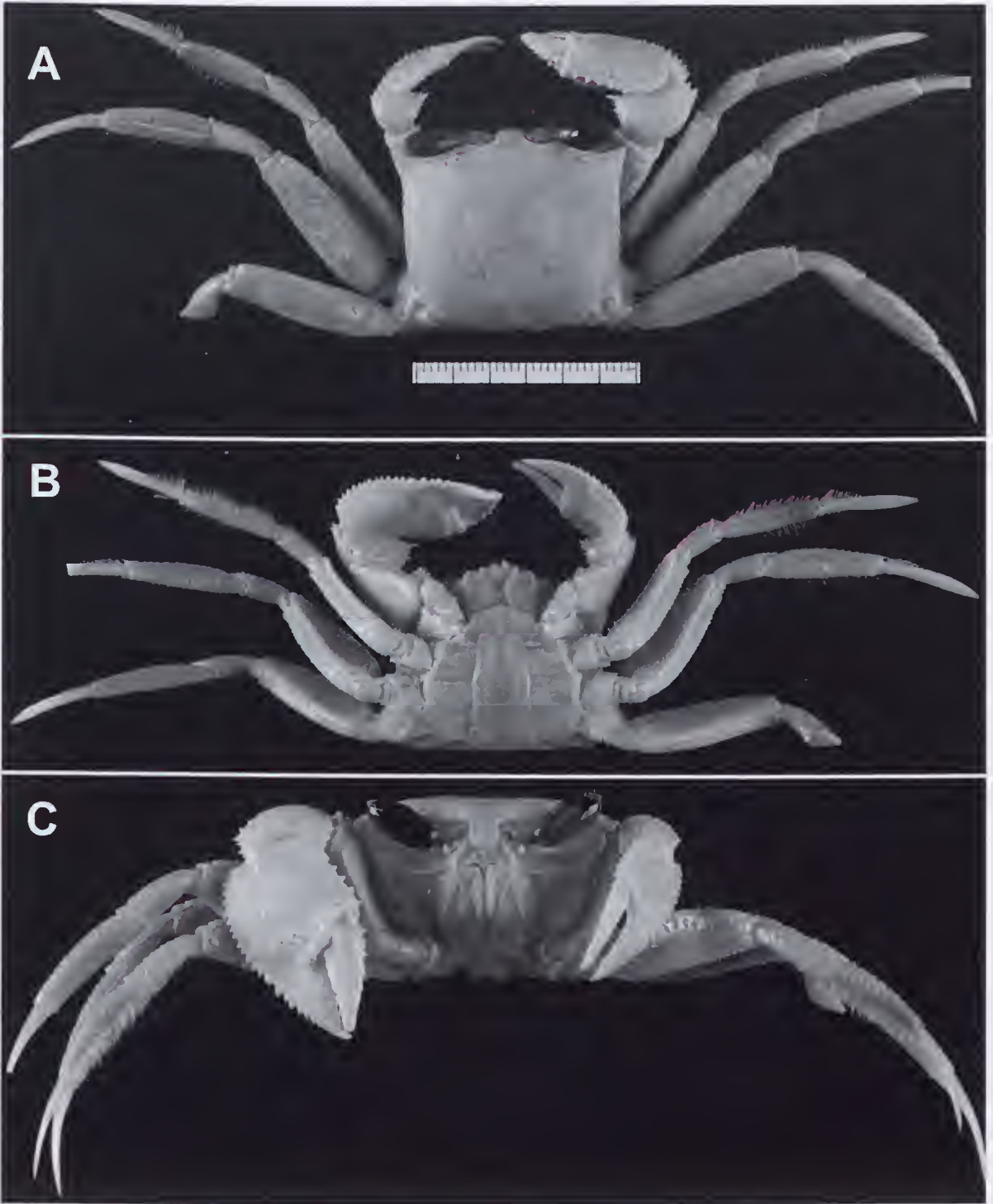


FIG. 36. *Ocypode fabricii* (SMF-10328); dorsal, ventral and frontal aspects.

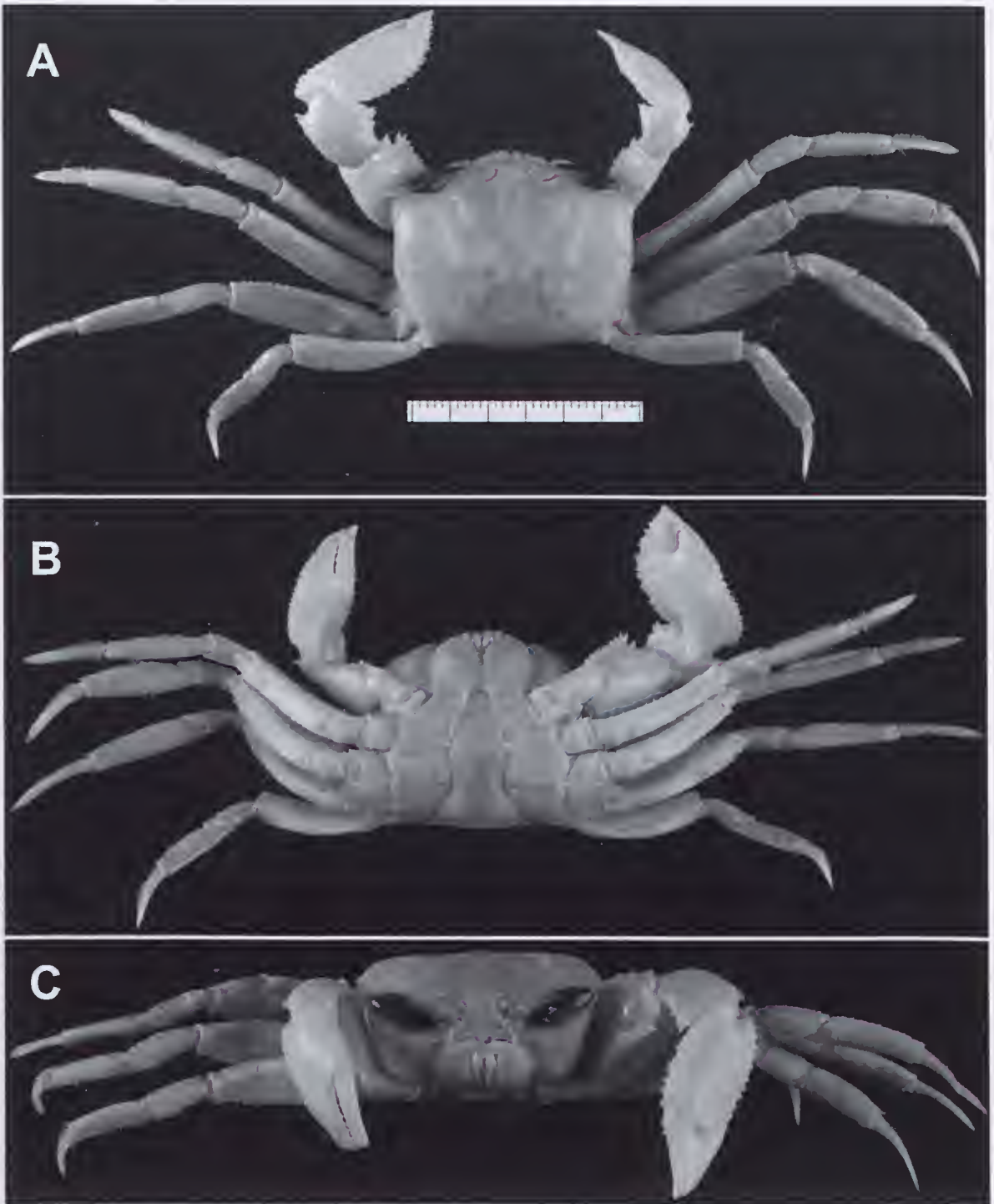


FIG. 37. *Ocypode gaudichaudii* (SMF-18684); dorsal, ventral and frontal aspects.

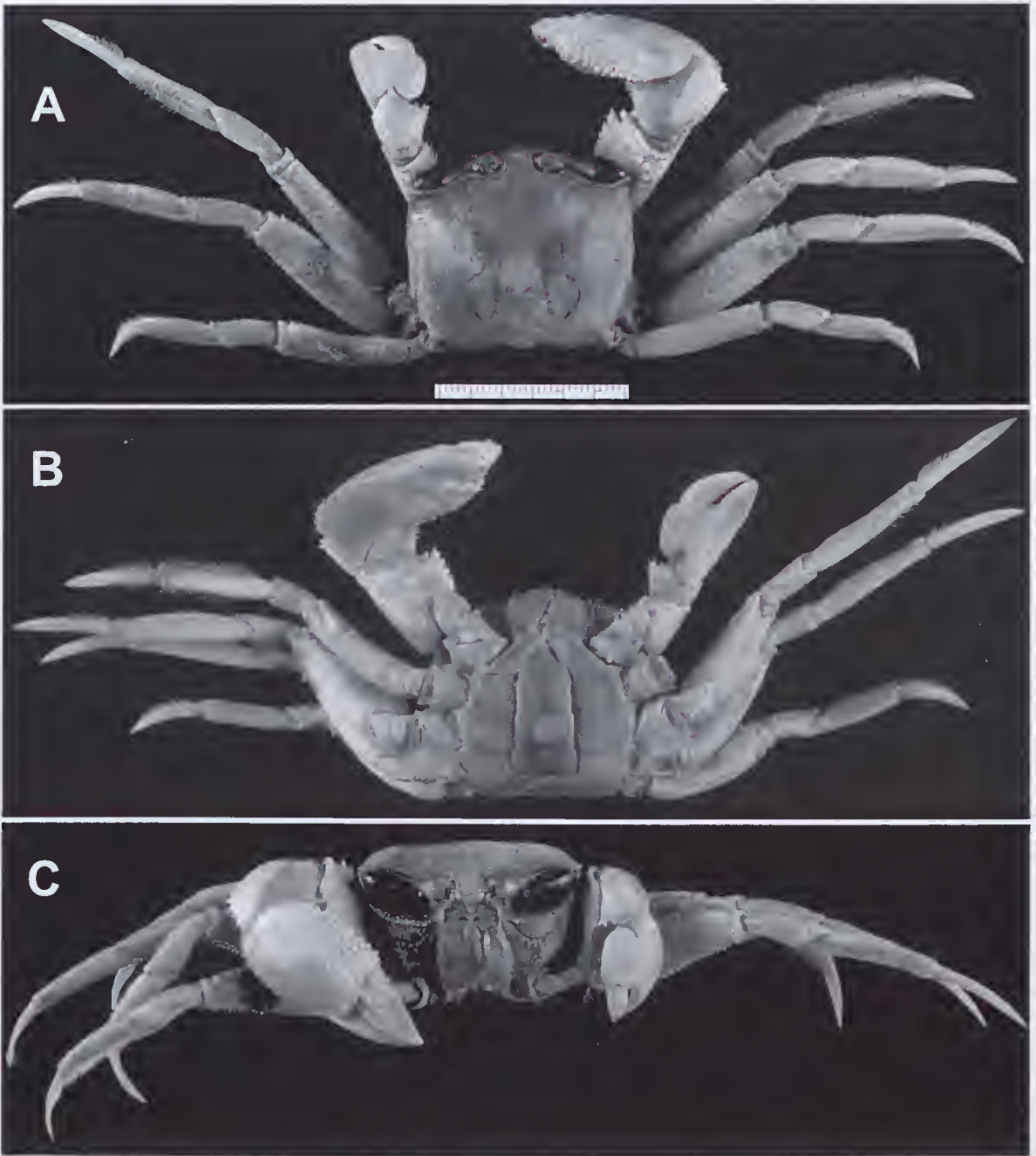


FIG. 38. *Ocypode jousseaumei* (SMF-24530); dorsal, ventral and frontal aspects.

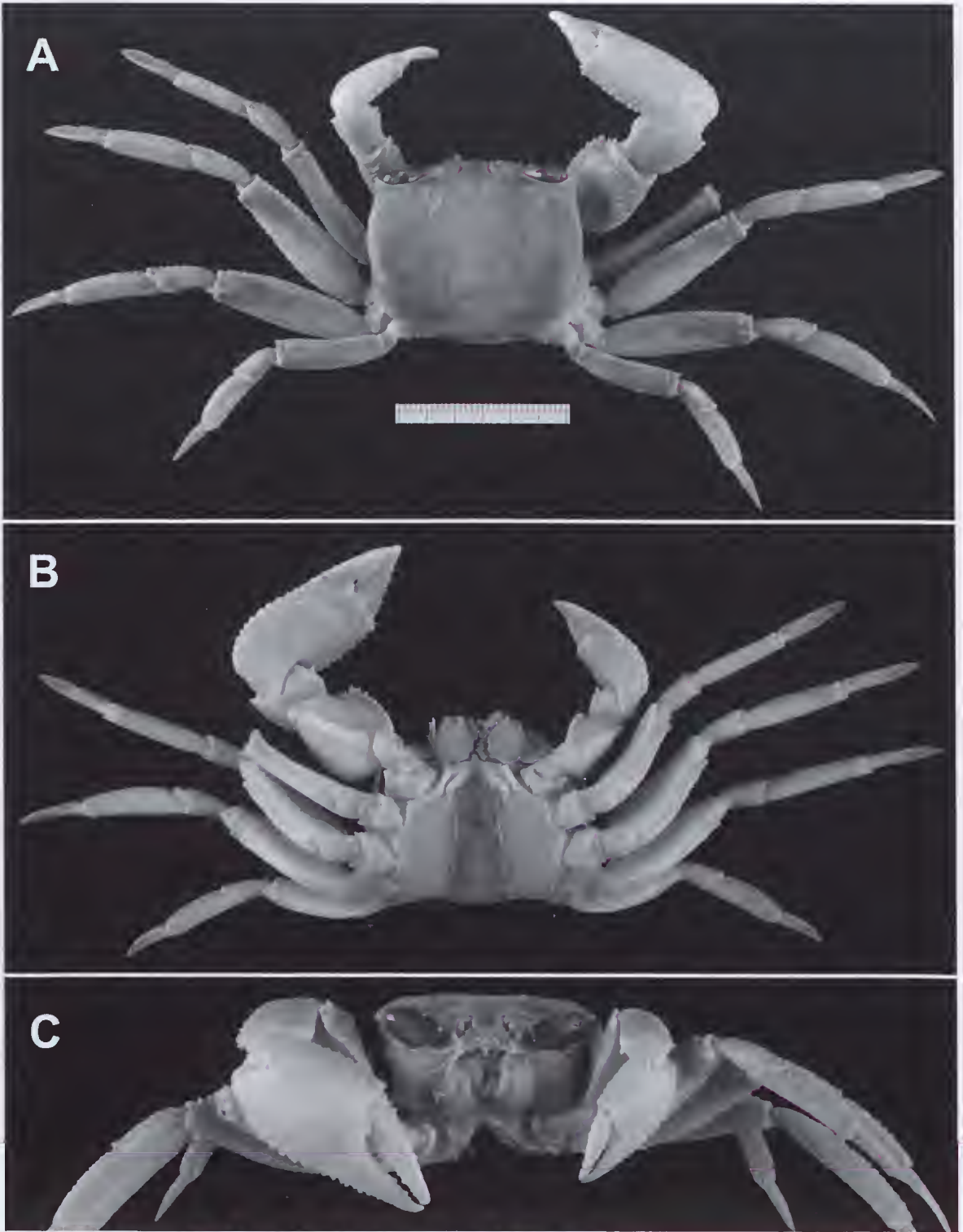


FIG. 39. *Ocypode kuhlii* (SMF-23298); dorsal, ventral and frontal aspects.

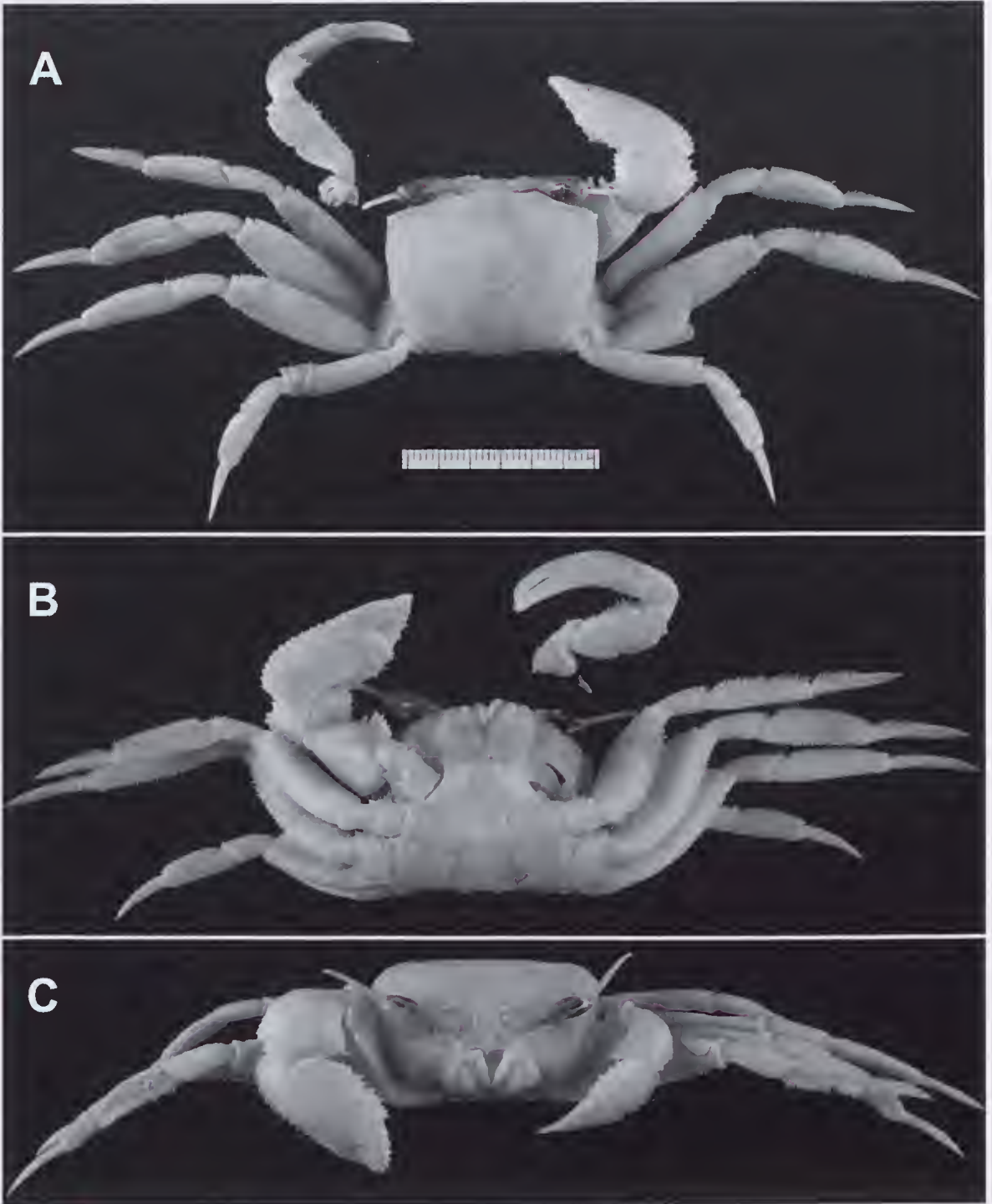


FIG. 40. *Ocypode macrocera* (SMF-6772); dorsal, ventral and frontal aspects.

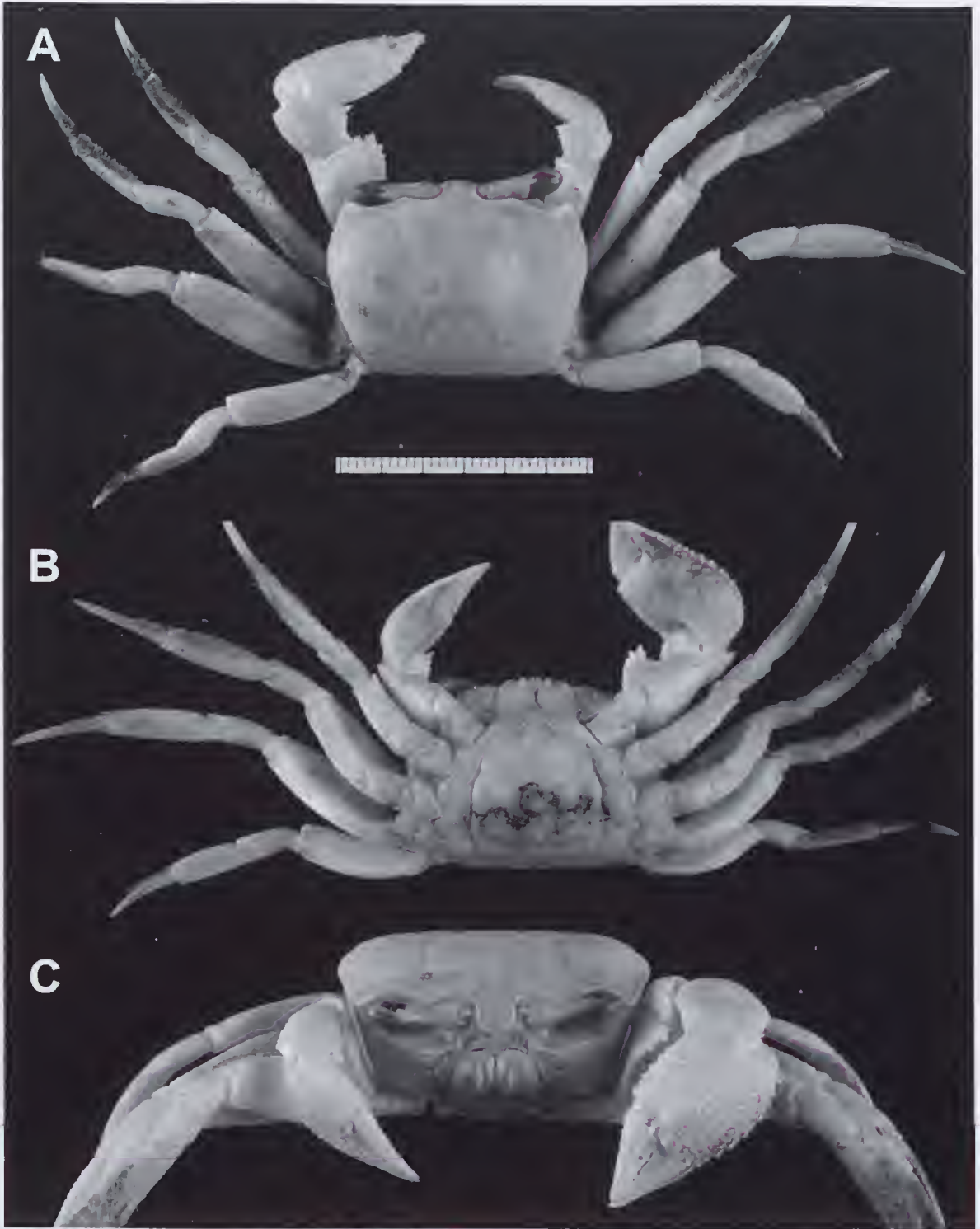


FIG. 41. *Ocypode madagascariensis* (SMF-10931); dorsal, ventral and frontal aspects.

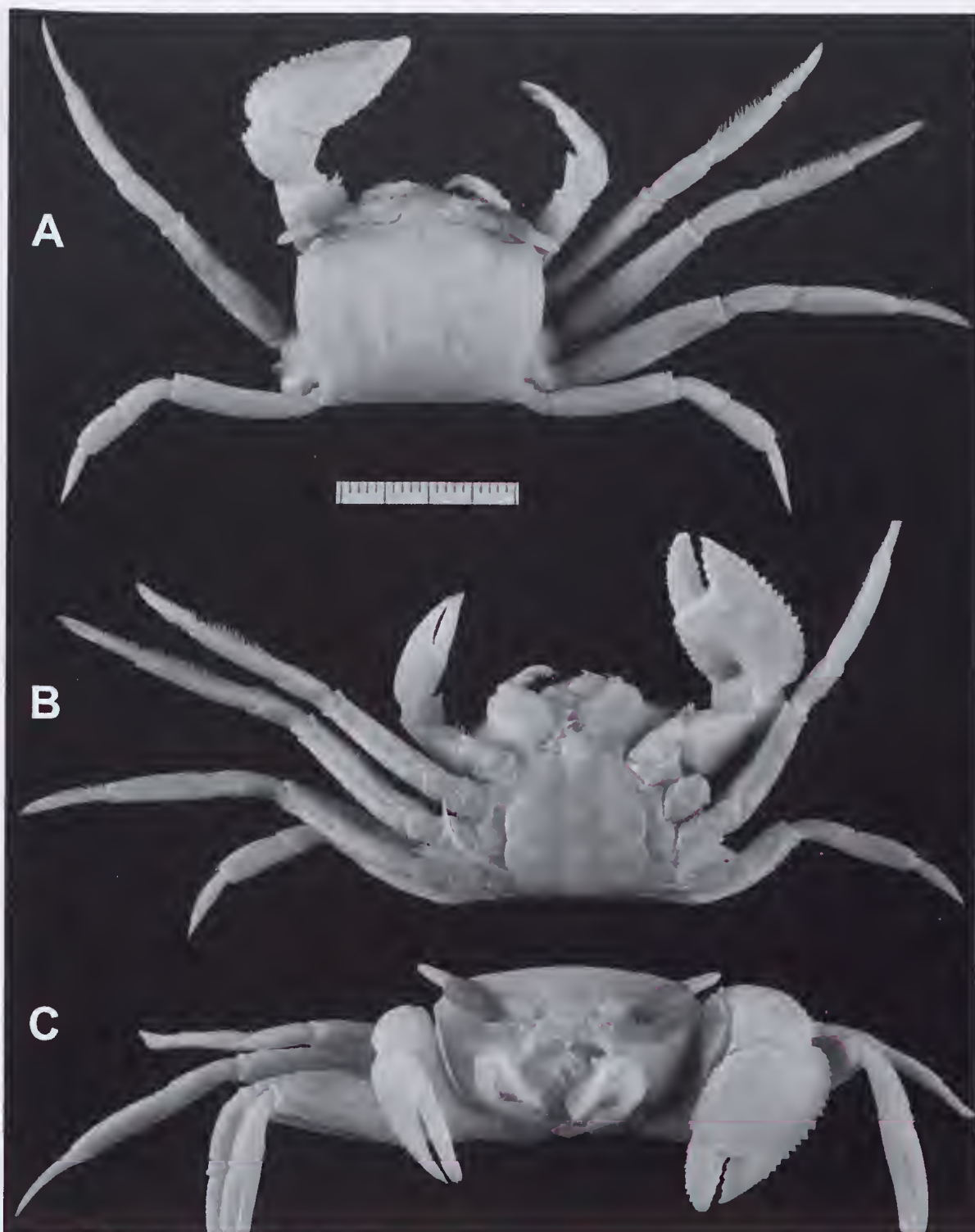


FIG. 42. *Ocypode mortoni* (SMF-36189); dorsal, ventral and frontal aspects.

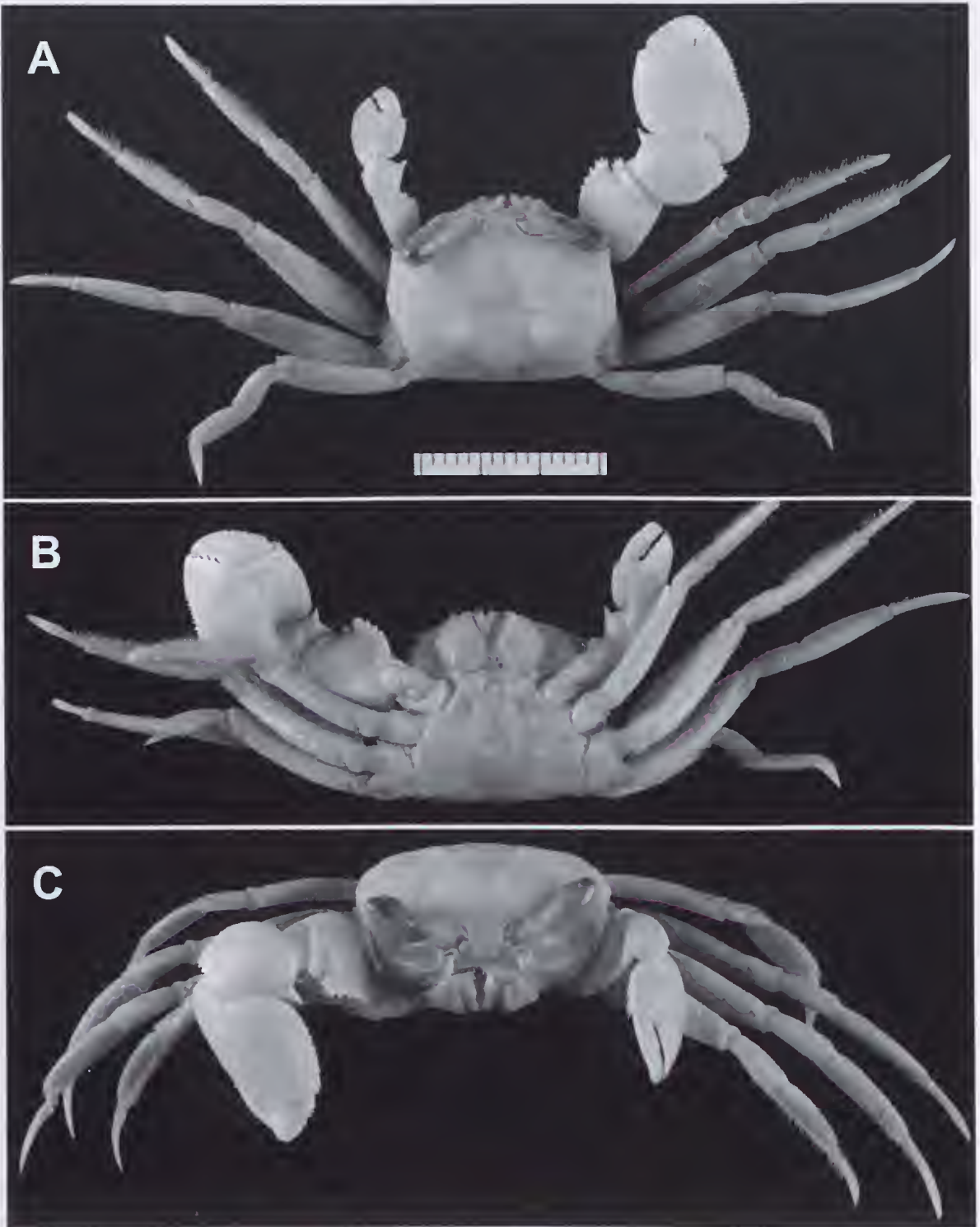


FIG. 43. *Ocypode nobilii* (SMF-7273); dorsal, ventral and frontal aspects.

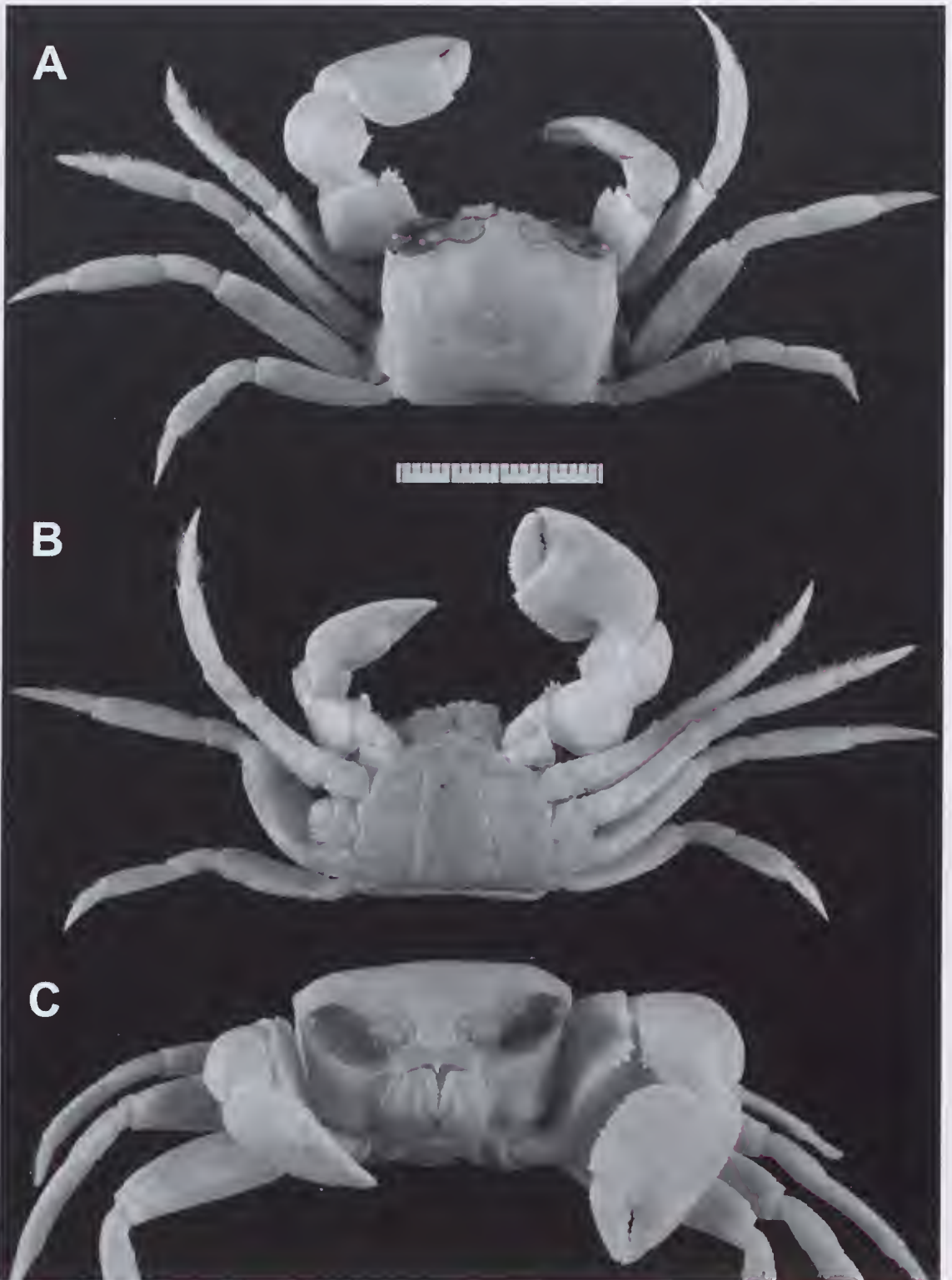


FIG. 44. *Ocypode pallidula* (SMF-6870); dorsal, ventral and frontal aspects.

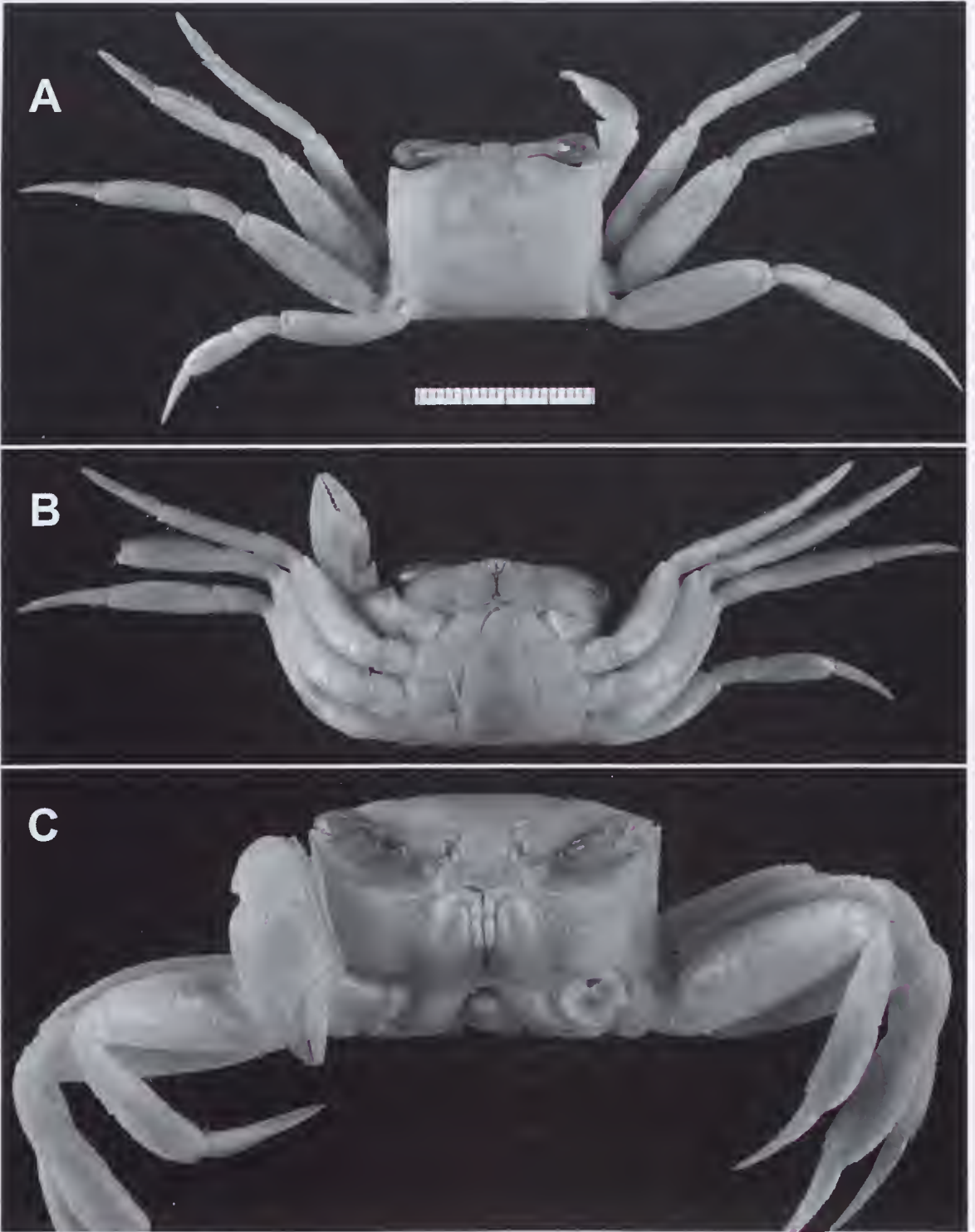


FIG. 45. *Ocypode pauliani* (SMF-1958); dorsal, ventral and frontal aspects.



FIG. 46. *Ocypode quadrata* (SMF-6851); dorsal, ventral and frontal aspects.

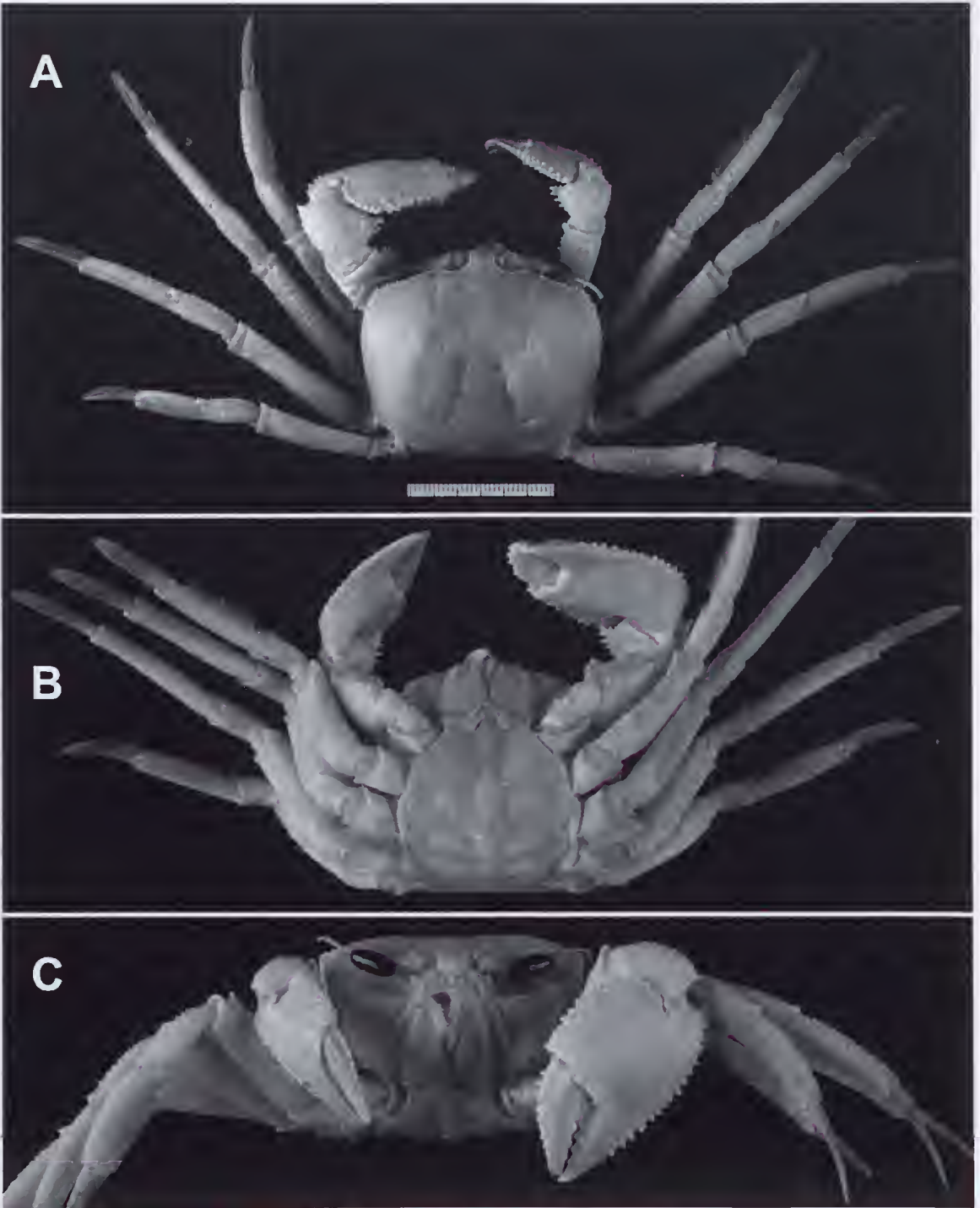


FIG. 47. *Ocypode rotundata* (SMF-23027); dorsal, ventral and frontal aspects.

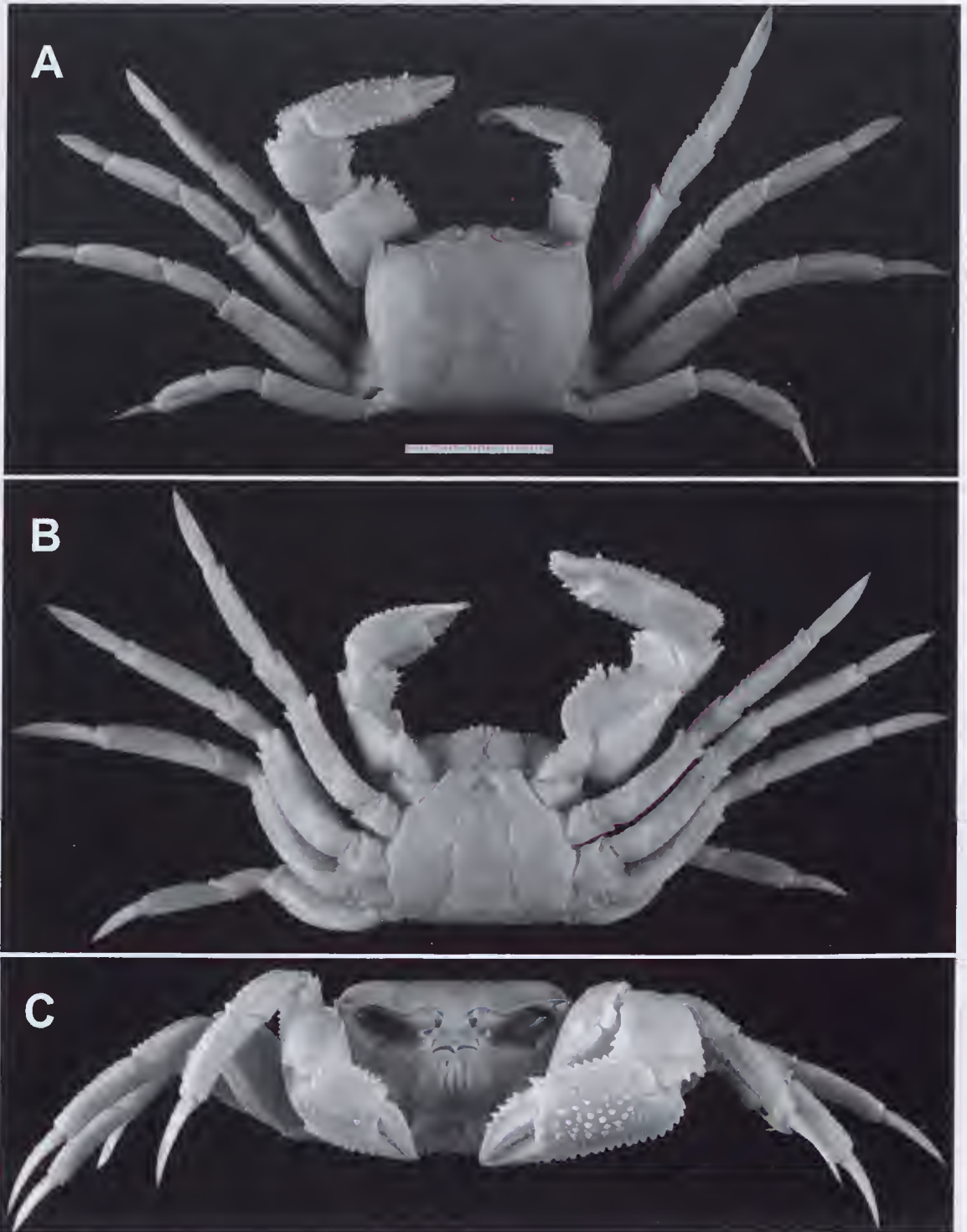


FIG. 48. *Ocypode ryderi* (SMF-10932); dorsal, ventral and frontal aspects.

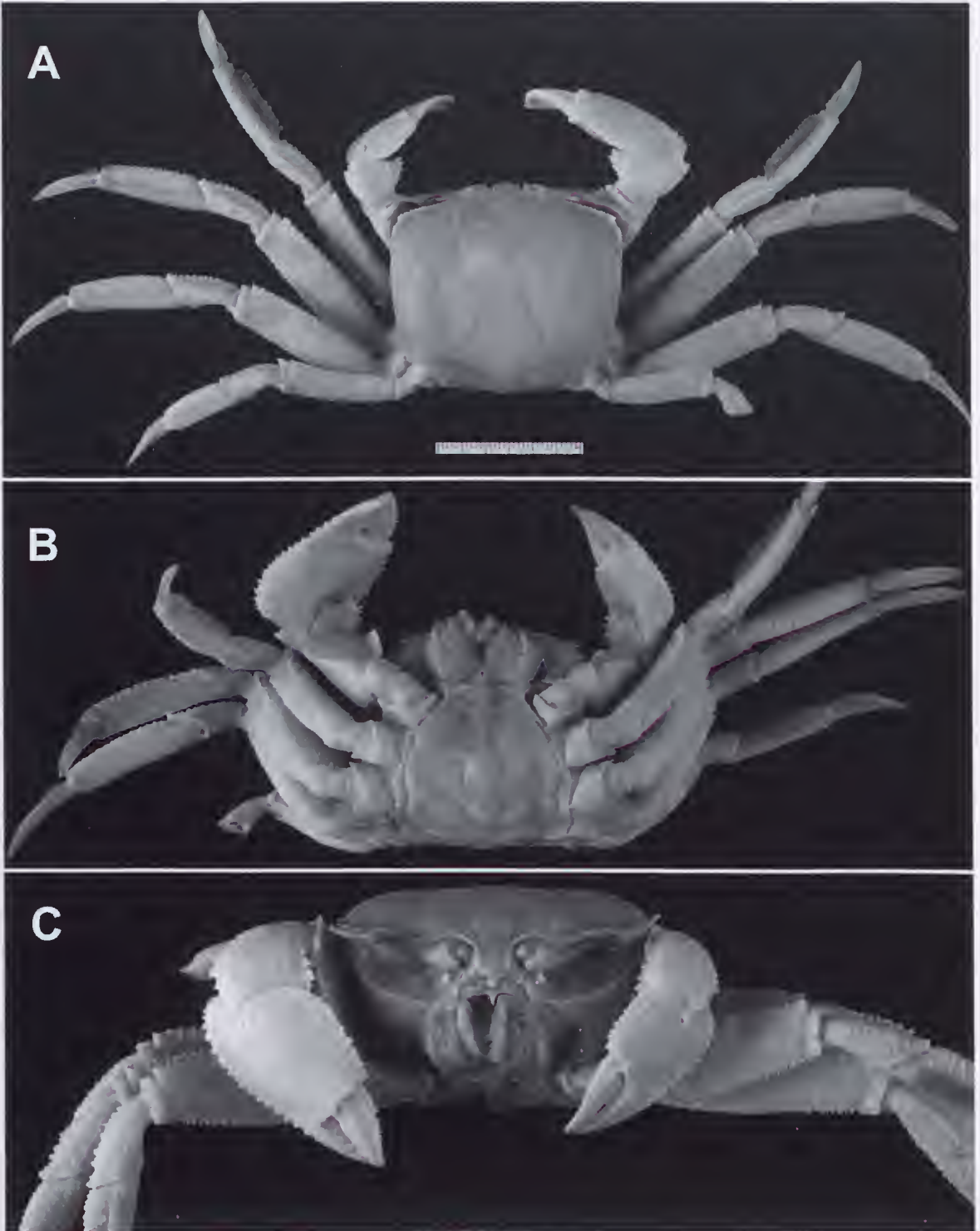


FIG. 49. *Ocypode saratan* (SMF-9711); dorsal, ventral and frontal aspects.

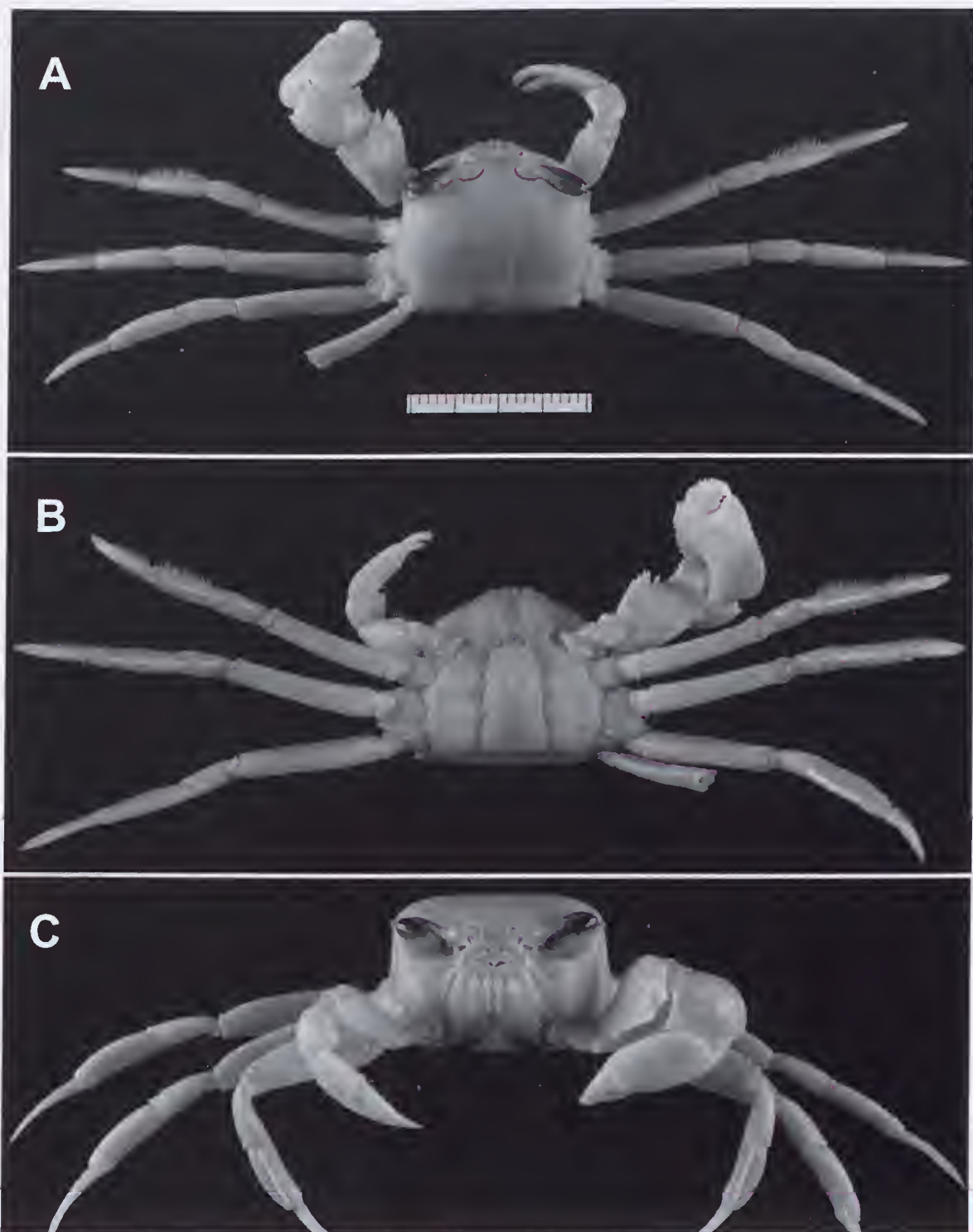


FIG. 50. *Ocypode stimpsoni* (SMF-6843); dorsal, ventral and frontal aspects.

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LITERATURE CITED

- Abele, L.G. & Kim, W. 1986. *An illustrated guide to the marine decapod crustaceans of Florida* 8(1): i–xvii, 1–326 (Part 1), 327–760 (Part 2), pls (Tallahassee, Florida).
- Adams, A. & White, A. 1848. Crustacea. Part 1. In: Adams, A. (Ed.), *The zoology of the voyage of H.M.S. "Samarang", under the command of Captain Sir Edward Belcher, during the years 1843–1846*: i–viii, 1–32, pls 1–6. (London).
- Alberto, R.M.F. & Fontoura, N.F. 1999. Age structure and spatial distribution of *Ocypode quadrata* (Fabricius, 1787) on a sandy beach from the south coast of Brazil (Crustacea, Decapoda, Ocypodidae). *Revista Brasileira de Biologia* 59(1): 95–108.
- Alcock, A.W. 1900. Materials for a carcinological fauna of India. No. 6. The Brachyura Catometopa or Grapsoidea. *Journal of the Asiatic Society of Bengal* 69(3): 279–486.
- Alcock, A. & Anderson, A.R.S. 1894. Natural history notes from H.M. Indian Marine Survey Steamer "Investigator". Ser. II, No. 17. List of the shore and shallow-water Brachyura collected during the season 1893–1894. *Journal of the Asiatic Society of Bengal* 63(2): 197–209.
- Allender, B.M. 1969. The ghost crabs (*Ocypode*) of Dirk Hartog Island. *Western Australian Naturalist* 11: 59–63, tables 1–3, text-fig. 1.
- Altevogt, R. 1959. Rennkrabben. *Natur und Volk* 89(4): 129–133, text-figs 1–4.
- Al-Wassia, A.H., Innes, A.J., Taylor, E.W. & Whiteley, N.M. 1988. Aerial and aquatic respiratory gas exchange in the ghost crab *Ocypode saratan*. *Proceedings of the Physiological Society* 403: 106 pp.
- Al-Wassia, A.H., Innes, A.J., Whiteley, N.M. & Taylor, E.W. 1989. Aerial and aquatic respiration in the ghost crab *Ocypode saratan* – 1. Fine structure of respiratory surfaces, their ventilation and perfusion; oxygen consumption and carbon dioxide production. *Comparative Biochemistry and Physiology (A)* 94(4): 755–764.
- Andrews, C.W. 1900. A monograph of Christmas Island (Indian Ocean): i–xiii, 1–337, 21 pls (London) [Land Crustacea on pp. 163–165].
- Antia, E.E. 1989. Beach cusps and burrowing activity of crabs on a fine-grained sandy beach, south-eastern Nigeria. *Journal of Coastal Research* 5(2): 263–270, table 1, text-figs 1–5.
- Arndt, R.G. 1999. Predation by the black iguana (*Ctenosaura similis*) on the painted ghost crab (*Ocypode gaudichaudii*) in Costa Rica. *Florida Scientist* 62(2): 111–114.
- Araujo, De, C.C.V., Rosa, D. de M. & Fernandes, J.M. 2008. Density and spatial distribution of the crab *Ocypode quadrata* (Fabricius, 1787) (Crustacea, Ocypodidae) on three sandy beaches of Espirito Santo, Brazil. *Biotemas* 21(4): 73–80.
- Arteta-Bonivento, R. 2009. Cangrejos en el delta del Río Rancherfa, Riohacha (Colombia) (Crustacea: Decapoda: Brachyura). *Boletín Científico, Museo de*

- Historia Natural, Universidad de Caldas* 13(1): 140–152, tables 1–3, 9 text-figs.
- Aubert de la Chesnaye des Bois, F.A. 1759. Dictionnaire raisonné et universel des animaux, ou le regne animal, consistant en quadrupedes, cétacées, oiseaux, reptiles, poisson, insectes, vers, zoophytes; ou plantes animales; leurs propriétés en médecine; la classe, la famille, ou l'ordre, le genre, l'espece avec ses variétés, où chaque animal est rangé, suivant les différentes méthodes ou nouveaux systèmes de Messieurs Linnaeus, Klein & Brisson. *Claude-Jean-Baptiste Bauche* 1: i–xxiv, 1–816. (Paris).
- Audouin, J.V. 1826. Explication sommaire des Planches de Crustacés de l'Égypte et de la Syrie, publiées par Jules-César Savigny, membre de l'Institut; offrant un exposé des caractères naturels des genres, avec la distinction des espèces. In, Savigny, J.-C., Description de l'Égypte ou recueil des observation et des recherches qui ont été faites en Égypte pendant l'expédition de l'armée française 1798–1801. *Histoire naturelle* 1(4): 77–98, pl. 1.
- Audouin, J.V. & Milne Edwards, H. 1828–29. *Resumé d'Entomologie ou d'Histoire naturelle des Animaux Articulés, complétée par une Iconographe de 48 planches* 1: 132–157, pl. 4. (Paris).
- Aurivillius, C.W.S. 1893. Eine vergleichend biologisch-morphologische Studie. Die Beziehungen der Sinnesorgane amphibischer Dekapoden zur Lebensweise und Athmung. *Nova Acta Regiae Societatis Scientiarum Upsaliensis* (3)16: 1–48, pls 1–3.
- Baksi, S.K., Ray, T.K. & De, C. 1980. On the workings of some crabs on the sandy beach of western Sundarban, Bengal Delta, India. *Journal of the Geological Society of India* 21: 184–187, pl. 2 fig. 3.
- Balss, H. 1914. Decapode Crustaceen von den Guinea-Inseln, Süd-Kamerun und dem Kongogebiet. *Ergebnisse der Zweiten Deutschen Zentral-Afrika-Expedition 1910–1911 unter Führung Adolf Friedrichs, Herzog zu Mecklenburg* 1 (Zoologie): 97–108, figs 1–12.
- 1922a. Ostasiatische Decapoden. IV. Die Brachyrhynchen (Cancridea). *Archiv für Naturgeschichte* 88A (2): 94–166, figs 1–2, pls 1–2.
- 1922b. Decapoda Brachyura (Oxyrhyncha und Brachyrhyncha) und geographische Übersicht über Crustacea Decapoda. Crustacea VII. In, Michaelson, W., *Beiträge zur Kenntniss der Meeresfauna Westafrikas* 3(3): 69–110, fig. 1–5. (Hamburg).
1924. Decapoden des Roten Meeres. III. Die Parthenopiden, Cyclo- und Catometopen. In, Expedition S.M. Schiff "Pola" in das Rote Meer, nördliche und südliche Hälfte 1895/96–1897/98. Zoologische Ergebnisse. XXXIV. *Denkschriften, Akademie der Wissenschaften in Wien, Mathematisch-Naturwissenschaftliche Klasse, Wien* 99(6):1–18, fig. 1.
1934. Die Krabben der Reise J.W. Harms' nach der Christmas-Insel und dem Malaiischen Archipel. *Anzeiger* 106(10): 225–237, figs 1–12.
1935. Brachyura of the Hamburg Museum Expedition to south-western Australia, 1905. *Journal of the Royal Society of Western Australia* 21: 113–151, figs 1–5, pl. 13.
1936. Decapoda. In, The fishery grounds near Alexandria 7. *Fisheries Research Directorate Notes and Memorirs*. 15: 1–67, 40 figs (Cairo).
1938. Die Dekapoda Brachyura von Dr. Sixten Bock's Pazifik Expedition 1917–1918. *Göteborgs Kungl. Vetenskaps och Vitterhets Samhälles Handlingar* (B) 5(7): 1–85, figs 1–18, pls 1–2.
- 1940–1944. Morphologischer Teil. In, Dr. H.G. Bronns Klassen und Ordnungen des Tierreiches 5(1, 7): 22–667, text-figs 7–740; [1:1–160, 1940; 2: 161–320, 1941; 3: 321–862, 1944] (Akademische Verlagsgesellschaft Geest & Portig K.-G.: Leipzig).
- Barnard, K.H. 1950. Descriptive catalogue of South African Decapod Crustacea (Crabs and Shrimps). *Annals of the South African Museum* 38: 1–837, figs 1–154.
- Barrass, R. 1963. The burrows of *Ocypode ceratophthalmus* (Pallas)(Crustacea, Ocypodidae) on a tidal wave beach at Inhaca Island, Moçambique. *Journal of Animal Ecology* 32: 73–85, text-figs 1–8.
- Basson, P.W., Burchard, J.E., Hardy, J.T. & Price, A.R.G. 1977. *Biotopes of the Western Arabian Gulf*. 284 pp. (ARAMCO: Dhahran).
- Benedict, J.E. 1892. Decapod Crustacea of Kingston Harbour. *Johns Hopkins University Circular* 11: 77.
1893. Notice of the Crustaceans Collected by the United States Scientific Expedition to the West Coast of Africa. *Proceedings of the United States National Museum* 16 (949): 535–541.
- Berry, P.F. 1976. Natal's ghost crabs. *African Wildlife* 30(2): 35–37, 5 unnumbered text-figs.
- Berry, P.F., Jackson, L.F. & Smale, M.J. 1976. Observations on stranded oil on the Natal and Zululand coasts, with reference to its effects on mole crabs (Hippidae) and on sand crabs (Ocypodidae). Council for the Habitat conference on Coastal Conservation. April 2–4, 1976 (Durban).
- Blankensteyn, A. 2006. The use of the ghost crab *Ocypode quadrata* (Fabricius) (Crustacea, Ocypodidae) as an indicator of anthropogenic impact on sandy beaches of Santa Catarina island, Santa Catarina, Brazil. *Revista Brasileira de Zoologia* 23(3): 870–876.
- Bodenheimer, F.S. 1937. *Prodromus Faunae Palaestinae*. Essai sur les éléments zoogéographiques et histor-

- iques du sud-ouest de sous-règne paléarctique. *Memoires presentes a l'Institut d'Egypte* 33: i-iii, 1-286, figs 1-4.
- Boone, L. 1927. The littoral crustacean fauna of Galapagos Islands. Part I. Brachyura. *Zoologica* 8: 127-288, 70 figs (fig. 96A-B). (New York).
1929. A collection of Brachyuran Crustacea from the Bay of Panama and the fresh waters of the Canal Zone. *Bulletin of the American Museum of Natural History* 58(11): 561-583, figs 1-18.
- Borradaile, L.A. 1900. On some Crustaceans from the South Pacific. Part IV. The Crabs. *Proceedings of the Zoological Society of London* 1900: 568-596, pls 40-42.
1901. Land Crustaceans. *The Fauna and Geography of the Maldive and Laccadive Archipelagoes* 1(1): 64-100, figs 12-23, pl. 3.
1907. Land and Freshwater Decapoda (Percy Sladen Trust Expedition to the Indian Ocean in 1905). *Transactions of the Linnean Society of London (Zool.)* (2)12: 63-68.
1910. On the Land and Amphibious Decapoda of Aldabra. *Transactions of the Linnean Society of London (Zool.)* (2)13: 405-409.
- Bosc, L.A.G. 1801-1802. Histoire naturelle des Crustacés, contenant leur description et leurs moeurs, avec figures dessinées d'après nature 1: 1-258, pls 1-8. (Paris).
- 1828-1830. Manuel de l'Histoire naturelle des Crustacés, contenant leur description et leurs moeurs; avec figures dessinées d'après nature. Edition mise au niveau des connaissances actuelles par A.G. Desmarest 1: 1-328, pls 1-9. (Paris).
- Bott, R. 1955. Dekapoden (Crustacea) aus El Salvador. 2. Litorale Dekapoden außer *Uca*. *Senckenbergiana biologica* 36: 45-70.
1964. Decapoden aus Angola unter besonderer Berücksichtigung der Potamidien (Crust. Decapod.), und einem Anhang: Die typen von *Thelplusa petii* Herklots, 1861. *Publicaçôens Cultuais da Compandhia de Diamantes de Angola* 69: 23-34, figs 1-3, pls 1, 2.
- Bouvier, E.L. 1906a. Sur les Crustacés Décapodes marins, recueillis par M. Gruvel en Mauritanie. *Bulletin du Muséum d'Histoire naturelle, Paris* 12: 185-187, 1 fig. [Bouvier, E. L., 1906b. *Actes de la Societe Linneenne de Bordeaux* 61:198-200].
1907. Sur une petite collection de Crustacés (Décapodes et Stomatopodes) recueillis par M. Ch. Gravier à l'île San Thomé (Afrique occidentale). *Bulletin du Muséum d'Histoire naturelle, Paris* 12(7): 491-499.
1915. Décapodes marcheurs (Reptantia) et Stomatopodes recueillis à l'île Maurice par M. Paul Carié. *Bulletin scientifique de la France et de la Belgique* (7)48(3): 178-318 [1-141], figs 1-42, pls 4-7.
1921. Crustacéa III, Décapoda. *Résult. sci. Voyage de Ch. Alluaud et R. Jeannel en Afrique orientale* (1911-1912): 23-62, figs 1-8. (Paris).
1922. Observations complémentaires sur les Crustacés Décapodes (abstraction faite des Caridés), provenants des campagnes de S. A. S. le Prince de Monaco. *Résults des Campagnes Scientifiques accomplies sur son yacht par Alerr 1^{er} Prince Souverain de Monaco* 62: 1-106, 6 pls.
1940. Décapodes marcheurs. *Faune de France* 37: 1-404, figs 1-222, pls 1-14. (Lechevalier: Paris).
- Bruce-Chwatt, L.J. & Fitz-John, R.A. 1951. Mosquitoes in crab-burrows on the coast of West Africa and their control. *The Journal of Tropical Medicine and Hygiene* 54(6): 116-121, 1 fig.
- Brandis, D., Storch, V. & Türkay, M. 1999. Morphology and function of the copulatory system in freshwater crabs of the genus *Potamon*. *Journal of Morphology* 239(2): 157-166, text-figs. 1-4.
- Bright, D.B. & Hogue, C.L. 1972. A synopsis of the burrowing land crabs of the world and list of their arthropod symbionts and burrow associate. *Contributions in Science Los Angeles County Museum of Natural History* 220: 1-58.
- Bruyn, P. De, 2002. Investigations into the occurrence of a previously unrecorded ghost crab (*Ocypode ryderi*) in the Seychelles region. *Phaelsuma* 10: 28-34, text-figs 1-9.
- Buitendijk, A.M. 1947. Zoological notes from port Dickson, III. Crustacea Anomura and Brachyura. *Zoologische Mededeelingen, Leiden* 28: 280-284, fig. 1.
1950. Note on a collection of Decapoda Brachyura from the coasts of Mexico, including the description of a new genus and species. *Zoologische Mededeelingen, Leiden* 30 (17): 269-282, pl. 10.
- Büttikofer, J. 1890. Reisebilder aus Liberia: Resultate geographischer, naturwissenschaftlicher und ethnographischer Untersuchungen während der Jahre 1879-1882 und 1886-1887 2: viii+510 pp. (Leiden).
- Calman, W.T. 1900. On a collection of Brachyura from Torres Straits. *Transactions of the Linnean Society of London (Zool.)* (2) 8(1): 1-50, pls 1-3.
1909. On Decapod Crustacea from Christman Island, collected by Dr. C.W. Andrews F.R.S., F.Z.S. *Proceedings of the Zoological Society of London* 1909: 703-713, pl. 72.
1925. Crustacea Decapoda collected in Kerinchi and on the West Sumatran Coast by Messrs. H. C. Robinson and C. Boden Kloss. *Journal of the Federal Malaysia Museum* 8: 166-167.

- Cano, G. 1889. Crostacei Brachiuri ed Anomuri raccolti nel Viaggio della R. Corvetta "Vettor Pisani" attorno al globo. *Bollettino della Società di Naturalisti in Napoli* (1) 3: 79–105, 169–269, pl. 7.
- Capart, A. 1951. Crustacés Décapodes Brachyures. In, *Résultats Scientifiques de l'expédition océanographique Belge dans les eaux côtières Africaines de l'Atlantique Sud* (1948–1949) 3(1):11–205, figs 1–80, pls 1–3.
- Carli, A. 1969. Osservazioni sistematiche e biologiche su *Ocypode saratan* (Forskal, 1775), raccolto sulle coste della Migiurtinia (speciazione Scortecci, 1953) (Crustacea: Brachyura). *Natura Milano* 60: 57–79.
- Carmin, J. 1955. Some additional notes on the fauna of the tidal zone of our Mediterranean and Red Sea. *Bulletin of the Independent Biological Laboratories, Kefar-Malal* 11(1): 1–4.
1957. Report of the Independent Biological Laboratories Covering the Period May 1953–April 1956. *Bulletin of the Independent Biological Laboratories, Kefar-Malal* 13(1): 1–5.
- Carpenter, K.E. 1998. FAO species identification guide for fishery purposes. In, Niem, V.H. (Ed.), the living marine resources of the Western Central Pacific. *Cephalopods, crustaceans, holothurians and sharks* 2: 687–1396. (FAO: Rome).
- Catesby, M. 1771. The Natural History of Carolina, Florida and the Bahama Islands: Containing the Figures of Birds, Beasts, Fishes, Serpents, Insects and Plants: Particularly, Those not Hitherto Described, or Incorrectly Figured by Former Authors, With Their Descriptions in English and French. To Which is Prefixed, a New and Correct Map of the Countries; With Observations on Their Natural State, Inhabitants, and Productions. Revised by Mr. Edwards, of Royal College of Physicians, London. *To the Whole is Now Added a Linnaean Index of the Animals and Plants*. Volume the Second. [4] + 100 + xlv + [vi] + 2 pp., pls 1–100.
- Cavolini, P. 1792. Abhandlung über die Erzeugung der Fische und der Krebse. Aus dem italienischen übersetzt mit Anmerkungen herausgegeben von E.A.W. Zimmermann. 6 + 192 pp., pls 1–3. (Vossischen Bunchhandlung: Berlin).
- Chace, F.A., Jr. 1942. Decapod Crustacea. In, Scientific results of a fourth expedition to forested areas in eastern Africa. *Bulletin of the Museum of Comparative Zoology of Harvard College* 91: 183–233.
1956. Crustáceos decápodos y estomatópodos del Archipiélago de Los Roques e Isla de La Orchila. *El Archipiélago de Los Rogues y La Orchila, por la Sociedad, de Ciencias Naturales La Salle*: 145–168 pp. (Caracas).
- Chace, F.A. Jr. & Hobbs, H.H. 1969. The Freshwater and Terrestrial Decapod Crustaceans of the West Indies with special reference to Dominica. In, Bredin-Archbold, Smithsonian Biological Survey of Dominica. *United States National Museum Bulletin* 292: i–v, 1–258, figs 1–76, pls 1–5.
- Chace F.A. Jr. & Holthuis, L.B. 1948. Land and freshwater decapods Crustacea from the northern Leeward Group and South America. *Studies on the Fauna of Curaçao, Aruba, Bonaire and the Venezuelan Islands* 12: 21–28.
- Chakrabati A. 1972. Beach structures produced by crab pellets. *Sedimentology* 18: 129–134, figs 1–7.
- Chhapgar, B.F., 1956. On the marine crabs of Bombay State, Part I and II. *Journal of the Bombay Natural History Society* 54: 399–439, 503–549.
1957. On the marine crabs (Decapoda, Brachyura) of Bombay State. Part II. *Journal of the Bombay Natural History Society* 54(3): 503–549, fig. 3, pls B. 12–16, 2 tables. [= Marine crabs of Bombay state Contribution No. 1 of the Taraporevala Marine Biological Station Marine Biological Station: 41–89, pl. 13 & B].
- Chhapgar, B.F., Desai, B.G. & Patel, S.J. 2004. On two interesting marine crabs (Decapoda: Brachyura) from Mandvi, Kutch. *Journal of the Bombay Natural History Society* 101(1): 184–186, text-fig. 1.
- Chopra, B.N. & Das, K.N. 1937. Further notes on Crustacea Decapoda in the Indian Museum. IX. On three collections of crabs from Tavoy and Mergui Archipelago. *Record of the Indian Museum, Calcutta* 39(4): 377–434, figs 1–21, pl. 6.
- Clark, P.F. & Crosnier, A. 2000. The zoology of the "Voyage au pôle sud et dans l'Océanie sur les corvettes l'Astrolabe et la Zélee exécuté par ordre du roi pendant les années 1837–1838–1839–1840 sous le commandement de M. Dumont d'Urville (1842–1854)": titles, volumes, plates, text, contents, proposed dates and anecdotal history of the publication. *Archives of natural history* 27(3): 407–435.
- Clayton, D. 2001. Acoustic calling in four species of ghost crabs: *Ocypode jousseaumei*, *O. platytarsus*, *O. rotundata* and *O. saratan* (Brachyura: Ocypodidae). *Bioacoustics* 12(1): 37–55.
2005. Substrate (acoustic/vibrational) communication and ecology of the ghost crab *Ocypode jousseaumei* (Brachyura: Ocypodidae). *Marine and Freshwater Behaviour and Physiology* 38(1): 53–70, text-figs 1–9.
- Coelho, P.A. 1971a. A distribuição dos crustáceos decapodos reptantes do Norte do Brasil. *Trabalhos Oceanográficos da Universidade Federal de Pernambuco, Recife* 7/8: 71–90.
- 1971b. A distribuição dos crustáceos decapodos reptantes do norte do Brasil. *Trabalhos Oceanográficos da Universidade Federal de Pernambuco, Recife* 7/8: 91–100.

- gráficos da Universidade Federal de Pernambuco, Recife 9/11: 223–238.
- Coelho, P.A. & Ramos, M.A. 1972. A constituição e a distribuição da fauna de decápodos do litoral leste da América do Sul entre as latitudes de 5°N e 39°S. *Trabalhos Oceanográficos da Universidade Federal de Pernambuco* 13: 133–236.
- Cott, H.B. 1929. Observations on the natural history of the racing-crab *Ocypoda ceratophthalma*, from Beira. *Proceedings of the Zoological Society of London* 1929: 755–765, pl. 1, 1 fig.
- Cowles, R.P. 1908. 1. Habits, reactions, and associations in *Ocypoda arenaria*. *Papers from the Tortugas Laboratory of Carnegie Institution of Washington* 2: 1–41, 4 pls, 10 figs.
- Crane, J. 1939. The painted ghosts of Honda Bay. *Bulletine, New York Zoological Society* 42(1): 19–25. 5 unnumbered text-figures.
1940. Eastern Pacific Expedition of the New York Zoological Society XVIII. On the post-embryonic development of Brachyuran crabs of the genus *Ocypode*. *Zoologica, New York Zoological Society* 25(1): 65–82, fig. 1–8.
1941. Eastern Pacific Expeditions of the New York Zoological Society XXIX. On the growth and ecology of Brachyuran crabs of the genus *Ocypode*. *Zoologica, New York Zoological Society* 26(4): 297–310, text-figs 1–7, pls 1–2.
- Crosnier, A. 1965. Crustacés Décapodes. Grapsidae et Ocypodidae. *Faune de Madagascar* 18: 1–143, figs 1–260, pls 1–11.
- Cunningham, R.O. 1871. Notes on the Reptiles, Amphibia, Fishes Mollusca, and Crustacea obtained during the voyage of H.M.S. “Nassau” in the years 1866–69. *Transactions of the Linnean Society of London (Zoology)* 27(4): 465–502, pls 58–59.
- Curtiss, A. 1938. *A short zoology of Tahiti in the Society Islands*. i–xvi, 1–193. (Guide Printing: Brooklyn, New York).
- Cuvier, B. von, 1836. Das Tierreich, geordnet nach seiner Organisation als Grundlage der Naturgeschichte der Thiere und Einleitung in die vergleichende Anatomie. (Dtsche Übersetzung von Voigt, F.S. mit Zusatz) 4: i–xiv, 81–187.
- Dana, J.D. 1851. On the Classification of the Cancroidea. *American Journal of Science and Arts* (2) 12: 283–291.
1852. Crustacea. In, United States Exploring Expedition during the years 1838, 1839, 1840, 1841, 1842, under the command of Charles Wilkes, U.S.N. 13 (1): i–viii, 1–685, pl. 8.
1855. Crustacea. United States Exploring Expedition during the years 1838, 1839, 1840, 1841, 1842 under the command of Charles Wilkes, U.S.N. 14 (Atlas):1–27, pls 1–96.
- Dai, A.-Y., Song, Y.-Z. & Yang, Y.S. 1985. A study on *Ocypode* from China (Crustacea: Decapoda). *Acta Zootaxonomica Sinica* 10(4): 370–378, text-figs 1–14, 1 pl.
- Dai, A.-Y., Yang, S.-L., Song, Y.-Z. & Chen, G.-X., 1986. *Crabs of China Sea*. 11+ 642 pp. (China Ocean Press: Beijing) [in Chinese].
- Dai, A. & Yang, S. 1991. *Crabs of the China Seas*. 1–22 + 1–608 pp., pls 1–74 (English edition (Translation from Chinese original 1986). (China Ocean Press: Beijing; Springer-Verlag: Berlin).
- Diaz, H. & Costlow, J.D. 1972. Larval development of *Ocypode quadrata* (Brachyura : Crustacea) under laboratory conditions. *Marine Biology, Berlin* 15: 120–131.
- Davie, P.J.F. 2002. Crustacea: Malacostraca: Eucarida (Part 2: Anomura, Brachyura). In, Wells, A. & Houston, W.W.K. (Eds), *Zoological Catalogue of Australia* 19.3b: 641 pp. (CSIRO Publishing: Melbourne).
1998. *Wild Guide to Moreton Bay. Wildlife and Habitats of a Beautiful Australian Coast Noosa to the Tweed*: i–xxiv, 1–408. (Queensland Museum: Brisbane).
- Day, J.H., Millard, N.A.H. & Broekhuysen, G.J. 1954. The ecology of South African estuaries. Part IV: The St. Lucia system. *Transactions of the Royal Society of South Africa* 34: 129–156.
- Desbonne, I. & Schramm, A. 1867. Crustacés de la Guadeloupe d’après un manuscrit du Docteur Isis Desbonné compare avec les échantillons de Crustacés de sa collection et les dernières publications de MM. Henri de Saussure et William Stimpson, Brachyures: i–ii, 1–60, pls 1–8 (Imprimerie du Gouvernement, Basse Terre; édité par A. Schramm).
- Desmarest, A.G. 1825. Considérations générales sur la classe des Crustacés et description des espèces de ces animaux, qui vivent dans la mer, sur les côtes, ou dans les eaux douces de la France: i–xix, 1–446, pls 1–56, tabs 1–5. (F.G. Levrault: Paris & Strasbourg, France).
- Desportes, I. 1968. Sur la presence de *Cephaloidophora otivia* (Watson) (Eugregarina, Cephaloidophoridae) chez le crabe *Ocypode cursor* L. (Crustacea, Decapoda) au Liban. *Vie Milieu (A)* 19: 201–202, text-fig. 1.
- Diaz, H. & Costlow, J.D. 1972. Larval development of *Ocypode quadrata* (Brachyura : Crustacea) under laboratory conditions. *Marine Biology, Berlin* 15: 120–131.
- Doflein, F. 1899. Amerikanische Decapoden der k. bayerischen Staatssammlungen. *Sitzungsberichte der Bayerischen Akademie der Wissenschaften zu München, mathematisch-physikalische Klasse* 29: 177–195.

1900. Weitere Mitteilungen über dekapode Crustaceen der K. bayerischen Staatssammlungen. *Sitzungsberichte der Bayerischen Akademie der Wissenschaften zu München, mathematisch-physikalische Klasse* 30: 125–145, figs 1–3.
1904. Brachyura. *Wissenschaftliche Ergebnisse der deutschen Tiefsee-Expedition auf dem Dampfer "Valdivia" 1898–1899* 6: I–XIV, 1–314, 1 map, figs 1–68; Atlas, pls 1–58.
1904. Krebse. In, Schnee, P., Die Landfauna der Marshall-Inseln nebst einigen Bemerkungen zur Fauna der Insel Nauru. *Zoologische Jahrbücher, Abteilung für Systematik, Geographie und Biologie der Tiere* 20: 387–412 (Krebse p. 406).
- Dörjes J. 1978. Sedimentologische und faunistische Untersuchungen an Watten in Taiwan. II. Faunistische und aktuopaläontologische Studien. *Senckenbergiana maritima* 10: 117–138, figs 1–5, pls 1–3, tables 1–5.
- Dubois, L. 1957. Quelques mollusques et crustacés de la côte du Congo Belge. *Zooleo* 40: 3–17, text-figs 1–24.
- Duncan, G.A. 1986. Burrows of *Ocypode quadrata* (Fabricius) as related to slopes of substrate surfaces. *Journal of Paleontology* 60(2): 384–389.
- Edmondson, C.H. 1923. Crustacea from Palmyra and Fanning Islands. *Bulletin of the Bernice Pauahi Bishop Museum* 5: 1–43, figs 1–3, pls 1–2.
1962. Hawaiian Crustacea: Goneplacidae, Pinnotheridae, Cymopoliidae, Ocypodidae, and Gecarcinidae. *Occasional Papers of the Bernice Pauahi Bishop Museum* 23(1): 1–27, figs 1–10.
- Erk'akan, F. 1993. Nesting biology of loggerhead turtles *Caretta caretta* L. on Dalyan beach Mugla-Turkey. *Biological Conservation* 66(1): 1–4, tables 1–4, text-figs 1–3.
- Eshky, A.A. 1985. Aspects of the ecology, behaviour and physiology of the ghost crab *Ocypode saratan* (Forsk.). Doctoral Dissertation, University of Glasgow, 451 pp.
- Eshky, A.A., Al-Wassia, A.H., Atkinson, R.J.A. & Taylor, A.C. 1990. Branchial ventilation in the ghost crab, *Ocypode saratan* (Forsk.). *Marine Behaviour and Physiology* 16(4): 237–248.
- Eshky, A.A., Atkinson, R.J.A. & Taylor, A.C. 1988. Effects of temperature on oxygen consumption and heart rate in the semi-terrestrial crab, *Ocypode saratan* (Forsk.). *Marine Behaviour and Physiology* 13(4): 341–358.
- Estampador, E.P. 1937. A checklist of Philippine crustacean decapods. *Philippine Journal of Science* 62(4): 465–559.
1959. Revised checklist of Philippine crustacean decapods. *Natural and Applied Science Bulletin* 17: 1–127.
- Evans, S.M., Cram, A., Eaton, K., Torrance, R. & Wood, V. 1976. Foraging and agonistic behaviour in the ghost crab *Ocypode kuttlii* de Haan. *Marine and Freshwater Behaviour and Physiology* 4: 121–135, table 1–5, text-figs 1–4.
- Ewa-Oboho, I.O. 1993. Substratum preference of the tropical estuarine crabs, *Uca tangeri* Eydoux (Ocypodidae) and *Ocypode cursor* Linne (Ocypodidae). *Hydrobiologia* 271(2):119–127, tables 1–2, text-figs 1–5.
- Fabricius, J.C. 1781. Species Insectorum exhibentes eorum differentias specificas, Synonyma auctorum, Loca natalia, Metamorphosis adiectis Observationibus, Descriptionibus 1: i–viii, 1–552. (Hamburg & Kilonii).
1787. Mantissa Insectorum sustens eorum Species nuper detectas adiectis Characteribus genericis, Differentiis specificis, Emendationibus, Observationibus 1: i–xx, 1–348. (Hafniae).
1793. Entomologia Systematica emendata et acuta, Secundum Classes, Ordines, Genera, Species, Adiectis Synonymis, Locis, Observationibus, Descriptionibus 2: i–viii, 1–519, pls 1–8. (Hafniae).
1798. Supplementatum Entomologiae Systematicae: 1–572. (Proft & Storch: Hafniae).
- Fates, R.R. 1976. Apparent predation on the mole crab *Emerita talpoida* (Say) by the ghost crab *Ocypode quadrata* (Fabricius) *Chesapeake Science* 17(1): 65.
- Fellows, D.P. 1966. Zonation, and burrowing behaviour of *Ocypode ceratophthalma* and *Ocypode laevis*. M.S. Thesis, University of Hawaii, Pp. 1–78.
1975. On the Distribution of the Hawaiian Ghost Crab, *Ocypode laevis* Dana *Pacific Science* 29(3): 257–258.
1975. Aspects of Ecology, Ethology and Endocrinology of *Ocypode ceratophthalmus* and *Ocypode laevis*. PhD Thesis, University of Hawaii. Pp. 1–158. [fide *Diss. Astr. Intern. (B)*39(1)[1978]: 116–117].
- Ferguson, F.F. & Jones, E.R. 1949. A survey of the shore-line fauna of the Norfolk peninsula. *American Midland Naturalist* 41(2): 436–446.
- Fermin, P. 1765. Histoire naturelle de la Hollande équinoxiale: ou description des animax, plantes, fruits, et autres curiosités naturelles, qui se trouvent dans la colonie de Surinam; avec Leurs Noms différents, tant François, que Latins, Hollandois, Indiens & Nègre-Anglois: i–xii, 1–240, 1 pl. (Amsterdam).
1769. Description générale, historique, géographique et physique de la colonie de Surinam. Contenant. Ce qu'il y a de plus Curieux & de plus Remarquable, touchant sa Situation, ses Rivières, ses

- Forteresses; son Gouvernement & sa Police; avec les moeurs & les usages des Habitants Naturels du Païs, & des Européens qui y sont établis; ainsi que des Eclaircissements sur l'oeconomie générale des Esclaves Negres, sur les Plantations & leurs Produits, les Arbres Fruitiers, les Plantes Medécinales & toutes les diverses Especes d'animaux qu'on y trouve & c., 1, i-xxiv, 1-252, 1 map; vol. 2: 1-352, pls 1-3. (Amsterdam).
1770. Nieuwe algemeene Beschryving van de Colonie van Suriname. Behelzende al het merkwaardige van dezelve, met Betrekkinge tot de Historie, Aardryks-en Natuurkunde 1: i-xx, 1-228, 1 map; 2: 1-323, 3 pp., 3 pls.
- Fisher, J.B. & Tevesz, M.J.S. 1979. Within-habitat spatial patterns of *Ocypode quadrata* (Fabricius) (Decapoda Brachyura). *Crustaceana Supplement* 5: 31-36.
- Forest, J. & Guinot, D. 1966. Campagne de la "Calypso" dans le Golfe de Guinée et aux îles Principe, São Tomé et Annobon (1956). 16. Crustacés Décapodes, Brachyours. In, Résultats scientifiques des campagnes de la Calypso, 7. *Annales de l'Institut Océanographique* 44(1): 23-124, figs 1-19. (Monaco).
- Forskål, P. 1775. Descriptiones Animalium, Avium, Amphibiorum, Piscium, Insectorum, Vermium, quae in itinere orientali observavit Petrus Forskål: 1-19, i-xxxiv, 1-164, 1 map. (Post mortem auct. ed. C. Niebuhr: Hafniae).
- Fourmanoir, P. 1953. Notes sur la faune de la mangrove dans la région de Majunga: Crabs, Crevettes, Poissons. *Le Naturaliste Malgache* 5(1): 87-92.
1954. Crabes de la côte ouest de Madagascar. *Le Naturaliste Malgache* 6(1/2): 1-16, figs 1-12.
- Fowler, H.W. 1912. The Crustacea of New Jersey. *Annual Report of the New Jersey State Museum* (2): 31-650.
- Fransozo, A., Negreiros-Fransozo, A. & Bertini, G. 2002. In, Escobar-Briones, E. & Alvarez, F., eds. Modern Approaches to the study of Crustacea. Morphometric study of the ghost crab *Ocypode quadrata* (Fabricius, 1887) (Brachyura, Ocypodidae) from Ubatuba, São Paulo, Brazil: 189-195.
- Full, R.J. & Herreid, C.F. II. 1983. Aerobic response to exercise of the fastest land crab. *American Journal of Physiology* 244(4): R530-R536, text-figs 1-5.
- Fukuda, Y. 1980. Larval development of the shore crab *Ocypode stimpsoni* Ortmann (Crustacea, Brachyura, Ocypodidae) reared in the laboratory. *Calanus* 7: 1-8, text-figs 1-3.
- Gamo, S. & Kosakai, E. 1991. Some ecological observations of the crabs inhabiting the estuarine regions in northern Sagami and eastern Tokyo Bay. *Reports of the Manazuru Marine Laboratory for Science Education, Faculty of Education, Yokohama University* 7: 25-38. [in Japanese].
- Garth, J.S. 1946. Littoral brachyuran fauna of the Galapagos Archipelago. *Allan Hancock Pacific Expeditions* 5(10): i-iv, 341-601, fig. 1, pls 49-87.
1948. The Brachyura of the "Askoy" Expedition with remarks on carcinological collecting in the Panama Bight. *Bulletin of the American Museum of Natural History* 92(1): 1-66, figs 1-5, pls 1-8.
1957. The Crustacea Decapoda Brachyura of Chile. In, Reports of the Lund University Chile Expedition 1948-49. No. 29. *Lunds Universitets Arsskrift* (2)53(7): 1-130, pls 1-4.
1965. The brachyuran decapod crustaceans of Clipperton Island. *Proceedings of the California Academy of Sciences* 33(1): 1-46, figs 1-26, pls 1.
- Gauld, D.T. 1960. An annotated check-list of the Crustacea of Ghana, IV. Brachyura. *Journal of the West African Science Association* 6(1): 68-72.
- Gauld, D.T. & Buchanan, J.B. 1956. The fauna of sandy beaches in the Gold Coast. *Oikos* 7(2): 293-301, figs 1, 2.
1959. The principal Features of the rock shore fauna in Ghana. *Oikos* 10(1): 121-132.
- George, R.W. 1982. The distribution and evolution of the ghost crabs (*Ocypode* spp.) of Hong Kong with a description of a new species. In, Morton, B.S. & Tseng, C.K. (Eds), *Marine flora and fauna of Hong Kong and southern China* 1(1): 185-194, illustr. (Hong Kong University Press) (with Chinese summary).
- George, R.W. & Knott, M.E. 1965. The *Ocypode* ghost crabs of Western Australia (Crustacea, Brachyura). *Journal of the Royal Society of Western Australia* 48: 15-21, figs 1-3.
- Gerstæcker, A. 1856. Carcinologische Beiträge. *Archiv für Naturgeschichte Berlin* 22(1): 101-162, pls 4-6.
- Gibbes, L.R. 1850. On the carcinological collections of the cabinets of natural history in the United States with an enumeration of the species contained therein, and descriptions of new species. *Proceedings of the Third Meeting of the American Association for Advancement of Science* 3: 167-201.
- Glassell, S.A. 1934. Affinities of the Brachyuran fauna of the Gulf of California. *Journal of the Washington Academy of Sciences* 24: 296-302.
- Glaubrecht, M. 1992. Zur Chorologie der Reiterkrabbe *Ocypode cursor* (Linnaeus 1758) im Osmediterran nebst dem ersten Nachweis in SW-Anatolien. *Zoologische Jahrbücher Abteilung für Systematik*

- Ökologie und Geographie der Tiere* 119(4): 563–567, text-fig. 1.
- Gordon, I. 1931. Brachyura from the coasts of China. *Journal of the Linnean Society of London, Zoology* 37(254): 525–558, figs 1–36.
1934. Crustacea Brachyura. In, Résultats scientifique du voyage aux Indes Orientales Néerlandaises de LL. AA. RR. de Prince et la Princesse Léopold de Belgique. *Memoires du Musée Royal D'Histoire Naturelle Belgique, Hors-série* 3(15): 1–78, figs 1–37.
- Gottlieb, E. 1953. Decapod Crustaceans in the collection of the Sea Fisheries Research Station, Caesarea Israël. *Bulletin of the Research Council of Israel* 2(1–4): 440–41.
- Gravely, F.H. 1927. Decapoda (excl. Paguridea) and Stomatopoda. In, The littoral fauna of the Krusadai Island in the Gulf of Manaar with Appendices on the Vertebrates and Plants. *Bulletin, Madras Government Museum, New Series, Natural History Section* 1(1):135–155, figs 1–2, pls 19–26.
1941. Shells and other animal remains found on the Madras beach. I. Groups other than snails etc. *Bulletin, Madras Government Museum, New Series, Natural History Section* 5(1): 1–112, text-figs 1–31.
- Gravier, Ch. 1922. Observations sur la Locomotion chez l'*Ocypode chevalier* (*Ocypoda Hippeus* Olivier). *Annales des sciences naturelles, Zoologie* (10)5: 119–124, 1 unnumbered text-fig.
- Green, J.P. 1964. Morphological color change in the Hawaiian ghost crab, *Ocypode ceratophthalma* (Pallas). *The Biological Bulletin, Woods Hole* 126: 407–413.
- Guérin-Ménéville, F.E. 1829–1838. Crustacés, Arachnides et Insectes. In, Duperry, L. I., *Voyage autour du monde, exécuté par Ordre du Roi, sur la corvette de sa majesté, La Coquille, pendant les années 1822–1825*. Zool. 22 pls. (Paris).
1832. Crustacés. In, Brullé, A., *Des animaux articulés. Expédition scientifique de Morée. Section des sciences physiques* 3(1), Sect. 2: 30–50, pl. 27.
1838. Crustacés, arachnides. In, Duperrey, L. I., *Voyage autour du monde, exécuté par ordre du Roi, sur la corvette de sa majesté, La Coquille, pendant les années 1822–1825*. Zool. 2(2): 1–47.
1856. Crustacés, arachnides et Insectes. In, *Historia física, política y natural de la isla de Cuba par Ramon de la Sagra* 2 (Hist. nat.) 7: 1–18.
- Guinot, D. 1967. La faune carcinologique (Crustacea Brachyura) de l'Océan Indien Occidental et de la Mer Rouge: Catalogue, remarques biogéographiques et bibliographiques. In, Réunion de Spécialistes C.S.A. sur les Crustacés, Zanzibar 1964. *Mémoires de l'Institut fondamental d'Afrique Noire* 77 [1966]: 235–352, pls 1–26, 1 table.
- Guinot, D. & Ribeiro, A. 1962. Sur une collection de Crustacés Brachyours des îles du Cap Vert et de l'Angola. *Mem. Junta Invest. Ultramar*, (2)40: 8–89, figs 1–33, pls 1–4. (Lisboa).
- Guinot-Dumortier, D. 1960. Sur une collection des Crustacés (Decapoda Reptantia) de Guyane Française, I: Brachyura (*Oxyrhyncha* exclus) (suite). *Bulletin du Musée d'Histoire Naturelle de Paris* (2)31(6)[1959]: 510–515, fig. 10–17.
1961. Crabes, Crevettes et Langoustes ne sont pas toujours silencieux. *La Nature*, 89(3310): 82–89, text-figs 1–16.
- Guinot-Dumortier, D. & Dumortier, B. 1960. La stridulation chez les Crabes. *Crustaceana* 1(2): 117–155, tables 1–3, text-figs 1–22.
- Guinot, D & Cleva, R. 2002. Les crustacés récoltés par d'Orbigny en Amérique du Sud et déposés au Muséum national d'histoire naturelle, Paris. *Comptes Rendus Palevol* 1(7): 499–515, tables 1–2, text-figs 1–8.
- Gundlach, J. 1887. Apuntes para la fauna Puerto-Riqueña. VI. Crustáceos. *Anales de la Sociedad Española de Historia Natural* 16: 325–343.
- Haan, W. de, 1833–1850. Crustacea. In, Ph. F. von Siebold, *Fauna Japonica sive Descriptio Animalium, quae in Itinere per Japoniam, Jussu et Auspiciis Superiorum, qui Summum in India Batava Imperium Tenent, Suscepto, Annis 1823–1830 Collegit, Notis, Observationibus et Adumbrationibus Illustravit: i–xvii, i–xxxii, ix–xvi, 1–243, pls A–J, L–Q, 1–55, circ. tab. 2. [For dates see Sherborn & Jentink, 1895 and Holthuis, 1953].*
- Hagen, H.O. von. 1970. Zur Deutung langgstieliger und gehörnter Augen bei Ocypodiden (Decapoda, Brachyura). *Forma et Functio* 2: 13–57.
1975. Klassifikation und phylogenetische Einordnung der Lautäußerungen von Ocypodiden und Grapsiden (Crustacea, Brachyura). *Zeitschrift fuer Zoologische Systematik und Evolutionsforschung* 13(4): 300–316, 4 tables, 8 pls.
- Haley, S.R. 1972. Reproductive cycling in the ghost crab, *Ocypode quadrata* (Fabr.) (Brachyura, Ocypodidae). *Crustaceana* 23(1): 1–11.
- Hartmann-Schröder, G., & Hartmann, G. 1974. Beschreibung der Lebensräume, Ökologie und Zoogeographie: Zur Kenntnis des Eulitorals der afrikanischen Westküste zwischen Angola und Kap der Guten Hoffnung und der afrikanischen Ostküste von Südafrika und Moçambique unter besonderer Berücksichtigung der Polychaeten und Ostracoden, Teil 1. *Mitteilungen aus dem Hamburgischen zoologischen Museum und Institut* 69 (supplement): 5–94, fig. 1–7.

- Hartsinck, J.J. 1770. Beschryving van Guiana, ob de Wilde Kust, in Zuid-America, Betreffende de Aardrykskunde en Historie des Lands, de Zeeden en Gewoontes der Inwooners, de Dieren, Vogels, Visschen, Boomen en Gewassen, als mede de eerste Ontdekking dier Kust, de Bezittingen der Spanjaarden, Franschen en Portugeezen en voornaamelyk de Volkplantingen der Nederlanderen, als Essequebo, Demerary, Berbice, Suriname, En dezelve Rivieren, met de noodige Kaarten en Afbeelding der Forten. *Waarby komt eene Verhandeling over den Aart en de Gewoontes der Neger-Slaaven* 1: i-xii, 4 pp., pp. 1-520, pls. (Amsterdam).
- Hasselquist, F. 1762. Reise nach Palästina in den Jahren von 1749 bis 1752ⁿ. Auf Befehl Ihro Majestät der Königin von Schweden hrsg. von Carl Linnäus. *Dtsch Ausgabe aus dem schwedischen*: 474-478. (Rostock).
- Hashmi, S.S. 1963. Carcinological Fauna of Karachi. *Agriculture Pakistan* 14(2): 237-243.
- Haswell, W.A. 1882. Catalogue of the Australian stalk-and sessile-eyed Crustacea. The Australian Museum, Sydney: i-xxiv, 1-324 + 2 pp. addenda, figs 1-8, pls 1-4.
- Heller, C. 1861. Synopsis der im Rothen Meer vorkommenden Crustaceen. *Verhandlungen der zoologisch-botanischen Gesellschaft in Wien* 11: 1-30.
1861. Beiträge zur Crustaceen-Fauna des Roten Meeres. I. *Sitzungsberichte der Mathematisch-Naturwissenschaftlichen Classe der Kaiserlichen Akademie der Wissenschaften, Wien* 43: 297-374, pls 1-4.
1862. Beiträge zur Crustaceen-Fauna des Roten Meeres. II. Anomura und Macrura. *Sitzungsberichte der Mathematisch-Naturwissenschaftlichen Classe der Kaiserlichen Akademie der Wissenschaften, Wien* 44(1): 241-295, pls 1-3.
1863. Die Crustaceen des südlichen Europa. Crustacea Podophthalmia, Wien. Mit einer Übersicht über die horizontale Verbreitung sämtlicher europäischer Arten: i-xi, 1-336, pls 1-10.
1865. Die Crustaceen. 1. In, Reise der österreichischen Fregatte "Novara" um die Erde in den Jahren 1857-1859 unter den Befehlen des Commodors B. von Wüllerstorff-Urbair, *Zoologischer Theil* 2(3): 1-280, pls 1-25. (Wien).
- Henderson, J.R. 1893. A Contribution to Indian Carcinology. *Transactions of the Linnean Society of London (Zool.)* 5(1): 325-458, pls 36-40.
- Henning, H.G. & Klaassen, F. 1973. Decapod crustaceans on the Isla de Salamanca (Atlantic Coast, Colombia) (= Dekapode Crustaceen auf der Isla de Salamanca, Atlantik-Küste, Kolumbien). *Boletín de investigaciones marinas y costeras* 7: 63-84 (Mitteilungen aus dem Instituto Colombo-Alelán Invest. Cient. Santa Marta 7: 63-84).
- Henning, U. & Langer, H. 1986. Untersuchungen zum Turnover der Photorezeptormembran im Auge der Krabbe *Ocypode ryderi*. *Verhandlungen der Deutschen Zoologischen Gesellschaft* 79: 213-214.
- Herbst, J.F.W. 1782. *Versuch einer Naturgeschichte der Krabben und Krebse nebst einer systematischen Beschreibung ihrer verschiedenen Arten* 1(1): 1-86, pls 1. (Gottlieb, August & Lange: Berlin Stralsund).
- 1793a. *Versuch einer Naturgeschichte der Krabben und Krebse nebst einer systematischen Beschreibung ihrer verschiedenen Arten* 2(3): 79-98, pls 30-33. (Gottlieb, August & Lange: Berlin Stralsund).
- 1793b. *Versuch einer Naturgeschichte der Krabben und Krebse nebst einer systematischen Beschreibung ihrer verschiedenen Arten* 2(4): 99-146, pls 34-36. (Gottlieb, August & Lange: Berlin Stralsund).
- Herklots, J.A. 1851. *Additamenta ad Faunam Carcinologicam Africae Occidentalis, sive descriptiones specierum novarum e Crustaceorum ordine, quas in Guinea collegit vir strenuus H.S. Pel, praefectus residentiis in hitorre guineae* i-vi, 1-27, 2 pls. (Lugdunibatorum: Leiden).
- Hess, W. 1865. Beiträge zur Kenntnis der Decapoden--Krebse Ost-Australiens. *Archiv für Naturgeschichte, Berlin* 31(1): 127-173, pls 6-7.
- Hill, G.W. 1982. Orientation of ghost crab *Ocypode quadrata* (Fabricius) burrows as an indicator of shoreline position and wind direction. *The Texas Journal of Science* 34(1): 23-34.
- Hobbs, C.H. III., Landry, C.B. & Perry, J.E. III. 2008. Assessing anthropogenic and natural impacts on ghost crabs (*Ocypode quadrata*) at Cape Hatteras National Seashore, North Carolina. *The Journal of Coastal Research* 24(6): 1450-1458.
- Hogarth, P.J. 1989. The marine Crustacea of Dhofar, Southern Oman. *Journal of Oman Studies* 10: 99-124.
- Hoffmann, C.K. 1874. Crustacés et Echinodermes de Madagascar et de l'île de la Réunion. In, Pollen, F.P.L. et Dam, D.C. van. *Recherches sur la faune de Madagascar et de ses dépendances d'après les découvertes de François* 5(2): 1-58, pls 1-10.
- Holthuis, L.B. 1953. Enumeration of the Decapod and Stomatopod Crustacea from Pacific Coral Islands. *Atoll Research Bulletin* 24: 1-66, 2 maps. (Washington D.C.).
1954. On a collection of decapod Crustacea from the Republic of El Salvador (Central America). *Zoologische Verhandlungen* 23: 1-43, 2 pls.
1954. Observaciones sobre los crustaceos decapodos de la Republica de El Salvador. *Comunicaciones. Instituto Tropical de Investigaciones Cientificas* 3: 4159-4166.

1956. Notes on a collection of Crustacea Decapoda from the Great Bitter Lake, Egypt, with a list of species of Decapoda known from the Suez Canal. *Zoologische Mededelingen* 34 (22): 301–330.
1958. Crustacea Decapoda from the northern Red Sea (Gulf of Aqaba and Sinai Peninsula) II. Hippidea and Brachyura (Dromiacea, Oxystemata, and Grapsoidea). *Bulletin of the Sea Fisheries Research Station Haifa* 17: 41–54. (Haifa).
1959. The Crustacea Decapoda of Suriname (Dutch Guiana). *Zoologische Verhandelingen* 44: 1–296, figs 1–68, pls 1–16.
1961. Report on a collection of Crustacea Decapoda and Stomatopoda from Turkey and the Balkans. *Zoologische Verhandelingen* 47: 1–67, pls 1–2.
1969. Thomas Say as a Carcinologist. In, Thomas Say, An Account of the Crustacea of the United States. In, Cramer, J. & H. K. Swann, *Historiae Naturalis Classica* 73: 5–13.
1993. The non-Japanese new species established by W. De Haan in the Crustacea volume of Fauna Japonica (1833–1950). In, Yamaguchi, T. (Ed.), Ph. F. von Siebold and natural history of Japan, Crustacea: 599–642, text-figs 1–27. (Carcinological Society of Japan: Tokyo).
2002. A few notes on the authors and dates of the names of Crustacea collected by the “Voyage au Pole Sud et dans l’Océanie sur les Corvettes l’Astrolabe et la Zélée”. *Crustaceana* 75 (3–4): 413–422, text-figs 1–7.
- Holthuis, L.B. & Gottlieb, E. 1958. An annotated list of the decapod Crustacea of the Mediterranean coast of Israel, with an appendix listing the Decapoda of the eastern Mediterranean. *Bulletin of the Research Council of Israel* 7B (1–2): 126 pp., 3 pls.
- Hombron, J.B. & Jacquinot, H. 1842–1854. Crustacés. In, Atlas d’Histoire Naturelle. Zoologie. Voyage au Pôle Sud et dans l’Océanie sur les corvettes l’Astrolabe et la Zélée pendant les années 1837–1838–1839–1840, pls 1–9.
- Horch, K. 1975. The acoustic behavior of the ghost crab *Ocypode cordimanus* Latreille, 1818 (Decapoda, Brachyura). *Crustaceana* 29(2): 193–205, figs 1–4.
- Horch, K. & Salmon, M. 1972. Responses of the ghost crab, *Ocypode*, to acoustic stimuli. *Zeitschrift Tierpsychol* 30(1): 1–13, tables 1–2, text-figs 1–6.
- Horikawa, Y. 1940. A list of Formosan crabs. *Scientific Taiwan* 8: 21–31.
- Hosseini, S.H. 2009. The intertidal decapods of Bushehr, northern part of the Persian Gulf. *Iranian Journal of Fisheries Sciences* 8(1): 37–46.
- Huang, J.-F., Yang, S.-L. & Ng, P.K.L. 1998. Notes on the taxonomy and distribution of two closely related species of ghost crabs, *Ocypode sinensis* and *O. cordimanus* (Decapoda, Brachyura, Ocypodidae). *Crustaceana* 71(8): 942–954, 1–4 figs.
- Huang J.-F., Yu, H.-P. & Takeda, M. 1992. A review of the ocypodid and mictyrid crabs (Crustacea: Decapoda: Brachyura) in Taiwan. *Bulletin of the Institute of Zoology, Academia Sinica* 31(3): 141–161, figs 1–18, pls 1–2, table 1.
- ICZN, International Commission on Zoological Nomenclature. 1954. Opinion 262. Determination of the specific name of the sand crab (“Opinion” in replacement of “Opinion” 13). Pp. 299–327. In, Hemming, F. (Ed.), *Opinions and declarations rendered by the International Commission on Zoological Nomenclature*. Vol. 5. (International Trust for Zoological Nomenclature: London).
- ICZN, International Commission on Zoological Nomenclature. 1964. Opinion 712. Forty-seven genera of decapod Crustacea: placed on the official list. *Bulletin of Zoological Nomenclature* 21(5): 336–351.
- Imafuku, M., Habu, E. & Nakajima, H. 2001. Analysis of waving and sound-production display in the ghost crab, *Ocypode stimpsoni*. *Marine and Freshwater Behaviour and Physiology* 34(4): 197–211, tables 1–4, text-figs 1–5.
- Inaba, A. 1963. *Fauna and flora of the Inland Sea of Seto*. 170 pp. (Mukaishima Marine Biological Station, Hiroshima University, Japan).
1988. *Fauna and flora of the Inland Sea of Seto*, 2nd ed. 102 pp. (Mukaishima Marine Biological Station, Hiroshima University, Japan).
- Irvine, F.R. 1932. *Gold Coast Crabs and Lobsters*, 20 pp, 19 figs. (Accra).
1947. Crustaceans, turtles, cetaceans, etc. In, *The fishes and fisheries of the Gold Coast*, 283–320 pp, fig. 192. (London).
- Ives, J.E. 1891. Crustacea from the northern coast of Yucatan, the harbor of Vera Cruz, the west coast of Florida and the Bermuda Islands. *Proceedings of the Academy of Natural Sciences of Philadelphia* 43: 176–207.
- Jackson, L.F., Smale, M.J. & Berry, P.F. 1991. Ghost crabs of the genus *Ocypode* (Decapoda, Brachyura, Ocypodidae) of the east coast of South Africa. *Crustaceana* 61(3): 280–286, tables 1–3, text-fig. 1.
- Jacquinot, H. & Lucas, H. 1853. Crustacés. *Voyage au Pôle Sud et dans l’Océanie sur les Corvettes l’Astrolabe et la Zélée; exécuté par ordre du roi pendant les années 1837–1838–1839–1840 sous le commandement de M.J. Dumont d’Urville* 3(3): 1–107 (Text); Atlas, 1842–1853, 9 pls. (Gide et Baudry: Paris).
- Jeng, M.-S. 1997. The Prawns and Crabs of Kenting National Park. 133 pp. *Kenting National Park Hand Guides* No. 14, 133 pp. [in Chinese].

- Johnstone, H. 1906. List of Invertebrate Animals of Liberia Founded on the Collections of Büttikofer, Reynolds, Whicker, H.H. Johnston, A. White, etc. In, Johnston, H., *Liberia* 2: 860–883. (London).
- Jones, D.A. 1972. Aspects of the ecology and behaviour of *Ocypode ceratophthalmus* (Pallas) and *O. kuhlii* De Haan (Crustacea: Ocypodidae). *Journal of Experimental Marine Biology and Ecology* 8: 31–43, table 1, text-figs 1–5.
1986. A Field Guide to the Sea Shores of Kuwait and the Arabian Gulf. 160 pp. University of Kuwait, Blandford Press, U.K.
- Jones, D.S. 1988. The occurrence of *Ocypode pallidula* Jacquinot (Decapoda, Brachyura) in Australia and the Coral Sea. *Crustaceana* 54(1):33–38, table 1.
- Jones, H.G. 1968. Preliminary studies on the brachyuran Crustacea of Barbados. I. *Journal of the Barbados Museum and Historical Society* 32(3): 154–160.
- Kamita, T. 1936. Crabs in Jeju-do. *Zoological Magazine* 48(6): 314–321, figs 1–13. [in Japanese]
1936. Crabs on the coast of Korean Strait. *Journal, Chosen Natural History Society* 21: 30–35, figs 1–2. [in Japanese, Chosen-Kaiku-Engan no Kani-ru].
- 1941a. Distribution of crabs in Korea. *Zoological Magazine* 53(5): 232–244. [in Japanese].
- 1941b. List of crabs in Korea. *Chosen* 309: 61–90. [in Japanese].
- 1941c. Studies on the decapod crustaceans of Chosen, I. Crabs, *Fisheries Society of Chosen, Keijo*: 1–289, pls 1–2.
- Kazemiyani, M. 2008. Aspects of the ecology, behaviour and physiology of the ghost crab *Ocypode saratan* (Forskål). *Pakistan Journal of Biological Sciences* 11(3): 404–409.
- Kemp, S.W. 1915. Crustacea Decapoda. In, Fauna of the Chilka Lake. No.3. *Memoirs of the Indian Museum* 5: 199–325, figs 1–38, pls 12–13. (Calcutta).
- Kensley, B. 1970. A small collection of Decapod Crustacea from Moçambique (Cape Town). *Annals of the South African Museum* 57(5):103–122, figs 1–14.
1970. Some Decapod Crustacea from northern South-West Africa, including a new species of *Hippolyte*. *Cimbebasia* (A)1(8): 179–188, figs 1–2.
1981. On the zoogeography of southern African decapod Crustacea, with a distributional checklist of the species. *Smithsonian Contribution to Zoology* 338: 1–64, figs 1–4, tables 1–2.
- Kikuchi, K. 1959. Decapod crustaceans of Sado Island and adjacent waters. *Bulletin of the Biological Society of Hiroshima University* 26(10): 49–51.
- Kim, H.S. 1958. The crabs in the vicinity of Daichun Sea-Bathing Place. *Journal of Biological Science* 3: 11–13. [in Korean with English summary].
1962. Fauna of the crabs on the coasts of the western Islands of Korea. *Korean Journal of Zoology* 5(2): 51–55.
1970. A checklist of the Anomura and Brachyura (Crustacea, Decapoda) of Korea. *Seoul National University, Journal of the Biology and Agriculture, Series, B*(21): 1–34, pls 1–5.
1977. A fauna-list of the Decapod Crustaceans of Korea. *Commemoration Papers for Prof. M.J. Lee*: 199–208.
- Kim, H.S. & Rho, B.J. 1971. On the distribution of the benthic animals of Korean coastal seas. 1. Jeju Island region. *Report for IBP, Korean National Committee for the IBP*: 7–27.
- Kingsley, J.S. 1878. List of Decapod Crustacea of the Atlantic coast, whose range embraces Fort Macon. *Proceedings of the Academy of Natural Sciences of Philadelphia* 1878: 316–330 [316–328, published 9 Nov 1878; 329–330, published 7 Jan. 1879].
1880. Carcinological notes. No. III. Revision of the genus *Ocypoda*. *Proceedings of the Academy of Natural Sciences of Philadelphia* 1880: 179–186.
- Kinzelbach, R. 1970. Neue Nachweise der Reiterkrabbe, *Ocypode cursor* (Linnaeus, 1758), in der Agäis (Decapoda, Brachyura, Ocypodidae). *Crustaceana* 18(3): 318–320.
- Kitaura, J., Wada, K. & Nishida, M. 1998. Molecular phylogeny and evolution of unique mud-using territorial behavior in ocypodid crabs (Crustacea: Brachyura: Ocypodidae). *Molecular Biology and Evolution* 15(6): 626–637, tables 1–5, text-figs 1–4.
- Klassen, F. 1973. Stridulation und Kommunikation durch Substratschall bei *Gecrcinus lateralis* (Crustacea Decapoda). *Journal of comparative Physiology* 83: 73–79.
- Koepcke, H.W.M. 1953. Contribución al conocimiento de la forma de vida de *Ocypode gaudichaudii* Milne Edwards et Lucas. (Decapoda, Crustacea). *Publicaciones del Museu de Hist. Natural "Javier Prado" Lima, serie A, Zool.* 13:1–46, figs 1–14.
- Kossmann, R. 1877. Malacostraca. 1. Theil: Brachyura. In, *Zoologische Ergebnisse einer Reise in die Küstengebiete des Rothen Meeres* 1(3): 1–66, pls 1–3. (W. Engelmann: Leipzig).
- Krauss, C.F.F. 1843. Die Südafrikanischen Crustaceen. Eine Zusammenstellung aller bekannten Malacostraca, Bemerkungen über deren Lebensweise und geographische Verbreitung, nebst Beschreibung und Abbildung mehrerer neuen Arten. Pp. 1–68, pls 1–4. (Stuttgart).
- Kunze, P. 1967. Histologische Untersuchungen zum Bau des Auges von *Ocypode cursor* (Brachyura). *Zeitschrift für Zellforschung und mikroskopische Anatomie* 82: 466–478, text-figs 1–13.

- Lamarck, J.B.P.A. De. 1801. *Système des animaux sans vertèbres, ou tableau général des classes, des ordres et des genres de ces animaux; présentant leurs caractères essentiels et leur distribution, d'après la considération de leurs rapports naturels et de leur organisation, et suivant l'arrangement établi dans les galeries du Muséum d'Hist. Naturelle, parmi leurs dépouilles conservées; précédé du discours d'ouverture du cours de zoologie, donné dans le Muséum national d'Histoire naturelle l'an 8 de la République.* viii + 432 Pp. (Deterville: Paris).
1818. *Histoire Naturelle des Animaux sans Vertèbres, présentant les caractères généraux et particuliers de ces animaux, leur distribution, leurs classes, leurs familles, leurs genres, et la citation des principales espèces qui s'y rapportent; précédée d'une introduction offrant la détermination des caractères essentiels de l'Animal, sa distinction du végétal et des autres corps naturels, enfin, l'Exposition des principes fondamentaux de la zoologie.* Vol. 5. Pp. 1–612. (Deterville: Paris).
1838. *Histoire Naturelle des animaux sans vertèbres.* 2nd Ed. Vol. 5. [Decapoda, pp. 348–498 by H. Milne Edwards]. 699 Pp. (J.B. Baillière: Paris).
- Lanchester, W.F. 1900. On some Malacostracous Crustaceans from Malaysia in the collection of the Sarawak Museum. *Annals and magazine of natural history* 7(6(33): 249–265, pl. 12.
1900. On a collection of Crustaceans made at Singapore and Malacca. Part I. Crustacea Brachyura. *Proceedings of the Zoological Society of London* 1900: 719–770, pls 44–47.
1901. On the Crustacea collected during the "Skeat Expedition" to the Malay Peninsula, together with a note on the genus *Actaeopsis*. Part I. Brachyura, Stomatopoda and Macrura. *Proceedings of the Zoological Society of London* 1901: 534–574, pls 33–34.
- Latreille P.A. 1803. *Histoire naturelle, générale et particulière, des Crustacés et des Insectes.* Vol. 6: 1–392, pls 1–51. (Paris).
1810. *Considérations générales sur l'ordre naturel des animaux composant les classes des Crustacés, des Arachnides et des Insectes, avec Tableaux méthodiques.* (Paris).
1817. Les crustacés, les arachnides et les insectes. In, Cuvier, *Le Règne Animal distribué d'après son Organisation* 3: i–xxix, 1–653. (Paris)
1818. *Nouveau dictionnaire d'histoire naturelle appliquée aux arts, à l'agriculture, à l'économie rurale et domestique, à la médecine, etc.* Par une société de naturalistes et d'agriculteurs. Nouvelle édition. *Presqu'entièrement refondue et considérablement augmentée; avec des figures tirées des trois règnes de la nature* 23: 1–612. (Paris).
1818. Crustacés, Arachnides et Insectes. *Tableau encyclopédique et méthodique des trois règnes de la nature* 24: pls 268–397. (Paris).
1829. Crustacés, Arachnides et partie des Insectes. In, Cuvier, G., *Le règne animal distribué d'après son organisation, pour servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie comparée.* 2nd edition, Vol. 4: xxvii, 1–584. (Deterville: Paris).
- Laurie, R. D. 1906. Report on the Brachyura collected by Prof. Herdmann at Ceylon in 1902. *Report of the Ceylon Pearl Oyster Fisheries* 5: 349–432, pls 1–2.
1915. Reports on the Marine Biology of the Sudanese Red Sea, from Collections made by Cyril Crossland, M.Z., B.Sc., F.Z.S., XXI. On the Brachyura. *Journal of the Linnean Society of London. Zoology* 31(209): 407–475, figs 1–5, pls 42–45.
- Leach, W.E. 1814. Crustaceology. In, Brewster, D., *The Edinburgh Encyclopaedia* 7: 383–437, pl. 221.
- Leber, K.M. 1981. Spatial patterns of *Ocypode quadrata*: a re-evaluation (Decapoda, Brachyura). *Crustaceana* 41(1): 110–112.
- Leidy, J. 1888. Remarks on the fauna of Beach Haven, New Jersey. *Proceedings of the Academy of Natural Sciences of Philadelphia* 40: 329–333.
- Lenz, H. 1901. Crustaceen. Ergebnisse einer Reise nach dem Pacific (Schauinsland 1896–1897). *Zoologische Jahrbücher Abteilung für Systematik, Ökologie und Geographie der Tiere* 14: 429–482, pl. 32.
1902. Die Crustaceen der Sammlung Plate (Decapoda und Stomatopoda). In, Abhandlungen zur Kenntnis der Zoologie Chiles nach den Sammlungen von Dr. L. Plate. *Zoologische Jahrbücher, Abteilung für Systematik, Ökologie und Geographie der Tiere Suppl.* 5 (Fauna Chilensis 2) 2(3): 731–772, pl. 23.
1905. Ostafrikanische Dekapoden und Stomatopoden, gesammelt von Herrn Prof. Dr. A. Voeltzkow. In, A. Voeltzkow, *Wissenschaftliche Ergebnisse der Reisen in Madagaskar und Ostafrika in den Jahren 1889–1895.* Vol. 3. *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft, Abteilung für Systematik, Ökologie und Geographie der Tiere* 27(4): 341–392, pls 47–48.
1910. Crustaceen von Madagaskar, Ostafrika und Ceylon. In, A. Voeltzkow, *Reise in Ostafrika in den Jahren 1903–1905 mit Mitteln der Hermann und Elise geb. Heckmann Wentzel-Stiftung ausgeführt.* *Wissenschaftliche Ergebnisse, Systematische Arbeiten* 2: 539–576, figs 1–4.
1912. Afrikanische Crustaceen aus schwedischen Sammlungen. *Arkiv för Zoologi* 7(29): 1–10.
- Lenz, H. & Richters, F. 1881. Beitrag zur Crustaceenfauna von Madagaskar. *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft, Abteilung*

- für Systematik, Ökologie und Geographie der Tiere 12: 421–428, figs 20–27, pl. 1.
- Lewinsohn, C. 1977. Die Ocypodidae des Roten Meeres. *Zoologische Verhandlungen* 151: 43–84.
- Lin, C.-C., 1949. A catalogue of Brachyurous Crustacea of Taiwan. *Quarterly Journal of the Taiwan Museum* 2: 10–33.
- Linnaeus, C. 1758. *Cancer: Systema Naturae*, 10 ed., 1: 625–634. (Holmiae).
1767. *Systema Naturae*, 12 ed. 1: 1038–1056.
1767. *Systema Naturae*, 13 ed. 1(2): 1038–1056. (Vindobonae).
- Linsenmair, K.E. 1967. Konstruktion und Signalfunktion der Sandpyramide der Reiterkrabbe *Ocypode saratan* Forskål. (Decapoda Brachyura Ocypodidae). *Zeitschrift für Tierzüchtung und Züchtungsbiologie* 24: 403–456.
- Lockington, W.N. 1877. Remarks on the Crustacea of the West Coast of North America, with a catalogue of the species in the Museum of the California Academy of Science. *Proceedings of the California Academy of Science* 7: 145–156.
- Longhurst, A.R. 1958. An ecological survey of the West African marine benthos. *Colonial Office, Fisheries Publication* 11: 1–102, figs 1–11.
- López-Greco, L.S., Fransozo, V., Negreiros-Fransozo, M.L. & Dos Santos, D.C. 2009. Comparative morphology of the seminal receptacles of *Ocypode quadrata* (Fabricius, 1787) (Brachyura, Ocypodoidea). *Zootaxa* 2106: 41–50, text-figs 1–4.
- Low, M.Y. & Ng, P.K.L. 2012. The identities of *Cancer arenarius* Toren, in Osbeck, 1765, *Cancer arenarius* Zimmermann, in Cavolini, 1792, *Cancer (Mantis) arenarius* Herbst, 1793, and *Cancer (Gamunarellus) arenarius* Herbst, 1793, and other names associated with the genus *Ocypode* Weber, 1795 (Crustacea: Amphipoda, Decapoda, Stomatopoda). *Zootaxa* 3398: 40–57.
- Lucas, H. 1840. Histoire naturelle des Crustacés, des Arachnides et des Myriapodes; Précédée de l'Histoire naturelle des Annelides, par M. le Comte de Castelnau. 1 ed.: 1–600, pls 1–46. (Paris).
- Luederwaldt, H. 1919. Lista dos Crustaceos superiores (Thoracostraca) do Museu Paulista, que foram encontrados no estado de São Paulo. *Revista do Museu Paulista* 11: 429–435.
1929. Resultados de uma excursão científica á Ilha de São Sebastião no litoral do Estado de São Paulo e em 1925. *Revista do Museu Paulista* 16: 3–79.
- Maccarone, A.D. & Mathews, P.L. 2007. Effect of human disturbance on the abundance and spatial distribution of the Atlantic ghost crab (*Ocypode quadrata*) (Fabricius, 1798) on a Texas beach. *Texas Journal of Science* 59(1): 51–60.
- MacLeay, W.S. 1838. On the Brachyurous Decapod Crustacea brought from the Cape by Dr. Smith. In, Dr. A. Smith, Illustrations of the Zoology of South Africa; consisting chiefly of figures and descriptions of the Objects of Natural History, collected during an Expedition into the interior of South Africa, in the years 1834, 1835, and 1836; fitted out by "The Cape of Good Hope Association for Exploring Central Africa": 53–71, pls 2–3. (London).
- Magalhães, W.F., Lima, J.B., Barros, F. & Dominguez, J.M.L. 2009. Is *Ocypode quadrata* (Fabricius, 1787) a useful tool for exposed sandy beach management in Bahia State (Northeast Brazil). *Brazilian Journal of Oceanography* 57(2): 149–152, table 1, text-figs 1–2.
- Maki, M. & Tsuchiya, K. 1923. A monograph of the Decapod Crustacea of Formosa. Report of Department Agriculture, Government Research Institute, Taihoku 3: i–xi, 1–215, pls 1–24. [in Japanese][= Illustrated report of the Crustacea Decapod from Formosa].
- Man, J.G. De, 1881. Carcinological Studies in the Leyden Museum 2. *Notes from the Leyden Museum* 3(38): 245–256.
1883. Carcinological Studies in the Leyden Museum 3. *Notes from the Leyden Museum* 5(15): 150–169.
- 1887a. Übersicht der indo-pacifischen Arten der Gattung *Sesarma* Say nebst einer Kritik der von W. Hess und Nauck in den Jahren 1865 und 1880 beschriebenen Decapoden. *Zoologische Jahrbücher, Abteilung für Systematik, Ökologie und Geographie der Tiere* 2(3–4): 639–722, pl. 17.
- 1887b. Bericht über die von Herrn. Dr. J. Brock im indischen Archipel gesammelten Decapoden und Stomatopoden. *Archiv für Naturgeschichte, Berlin* 53(1): 215–288, pls 7–10. [For dates of publication see Clark, Harrison & Goodman, 1990].
- 1887–1888c. Report on the Podophthalmous Crustacea of the Mergui Archipelago, collected for the Trustees of the Indian Museum, Calcutta, by Dr. John Anderson, F.R.S. Superintendent of the Museum. Part II. *Journal of the Linnean Society of London, Zoology* 22(137): 65–128, pls 4–8. (London).
1888. Bericht über die von Herrn. Dr. J. Brock im indischen Archipel gesammelten Decapoden und Stomatopoden. *Archiv für Naturgeschichte* 53(1): 289–600, pls 11–22a. (Berlin).
1895. Bericht über die von Herrn Schiffscapitän Storm zu Atjeh, an den westlichen Küsten von Malakka, Borneo und Celebes sowie in der Java-See gesammelten Decapoden und Stomatopoden. (In 6 parts). *Zoologische Jahrbücher, Abteilung für Systematik, Ökologie und Geographie der Tiere* 8(1): 485–609, figs 1–15, pls 12–14.

1896. Über neue und wenig bekannte *Brachyurus* des Hamburger und Pariser Museums. *Mitteilungen aus dem Hamburgischen zoologischen Museum und Institut* 13: 73–118, pls 1–3.
1900. Note sur une petit collection de Crustacés Décapodes, provenant de la côte d'Angola (Afrique occidentale). *Mémoires Societe Zoologique de France, Paris* 13: 31–65, pls 1–2.
1902. Die von Herrn Professor Kükenthal im indischen Archipel gesammelten Dekapoden und Stomatopoden. In, W. Kükenthal, Ergebnisse einer zoologischen Forschungsreise in den Molukken und Borneo. *Abhandlungen der Senekenbergischen Naturforschenden Gesellschaft* 25(3): 465–929, pls 19–27.
1929. Decapoda and Stomatopoda from Pulau Berhala. *Miscellanea Zoologica Sumatra* 36: 1–3. (Medan).
- Manning, R.B., & Holthuis, L.B. 1981. West African Brachyuran Crabs (Crustacea: Decapoda). *Smithsonian Contributions to Zoology* 306: 1–379, text-figs 1–88.
- Mano, I., Doura, A., Omori, K. & Yanagisawa, Y. 2008. Seasonal distribution patterns and food habits of three ghost crabs, *Ocypode sinensis*, *O. stimpsoni*, and *O. ceratophthalma*, co-occurring in southern Shikoku. *Japanese Journal of Benthiology* 63: 2–10, tables 1–3, text-figs 1–8.
- Martens, E. von 1866. Verzeichnis der von Dr. E. Schweinfurth im Sommer 1864 auf seiner Reise am rothen Meere gesammelten und nach Berlin eingesandten zoologischen Gegenstände. II. Crustaceen. *Verhandlungen der Zoologisch-Botanischen Gesellschaft in Wien* 16: 377–382.
1872. Über Cubanische Crustaceen nach den Sammlungen Dr. J. Gundlach's. *Archiv für Naturgeschichte* 38(1): 77–147, 257–258, pls 4–5. (Berlin).
- Martin, A.J. 2006. Resting Traces of *Ocypode quadrata* Associated with Hydration and Respiration: Sapelo Island, Georgia, USA. *Ielmos* 13(2): 57–67.
- Marumura, M. & Kosaka, A. 2003. *Catalogue of Brachyuran and Anomuran crabs collection donated by the late Mr. Seiji Nagai to the Wakayama Prefectural Museum of Natural History*. (Wakayama Prefectural Museum of Natural History). Pp. 1–74, 8 pls.
- Matsuura, K. 1894. Brachyura of Japan. *Zoological Magazin Tokyo* 6(23): 51–57.
- McDermott, J.J. 2009. Notes on the unusual megalopae of the ghost crab *Ocypode quadrata* and related species (Decapoda: Brachyura: Ocypodidae). *Northeastern Naturalist* 16(4): 637–646, figs 1–2.
- McLachlan, A. 1980. Occurrence of ghost crabs *Ocypode* spp., in the eastern Cape. *South African Journal of Zoology* 15(1): 57–58, text-fig. 1.
- McNeill, F.A. 1926. The Biology of North-West Islet, Capricorn Group (Queensland). *Australian Zoologist* 4(5): 299–318, figs 1–2, pl. 41.
1968. Crustacea, Decapoda and Stomatopoda. *Scientific Report of the Great Barrier Reef Expedition, 1928–29* 7(1): 1–98, figs 1–2, pls 1–2.
- Melo, G.A.S. 1998. Malacostraca, Eucarida, Brachyura, Oxyrhyncha and Brachyrhyncha. Pp. 455–515. In, Young, P.S. (Ed.), *Catalogue of Crustacea of Brazil*. (Museum Nacional: Rio de Janeiro).
- Michel, C. 1964. Checklist of the Crustacea Brachyura (Crabs) recorded from Mauritius. *Mauritius Institute Bulletin* 6(1): 1–48.
- Miers, E.J. 1877. On a collection of Crustacea made by the Rev. G. Brown on Duke of York-Island. *Proceedings of the Zoological Society of London* 1877: 133–138.
1878. On a small collection of Crustacea made by Major Burton in the Gulf of Akaba. *Annals and magazine of natural history* (5)2: 406–411.
1879. Crustacea. The Collections from Rodriguez. In, An account of the Petrological Botanical and Zoological Collections made in Kerguelen's Land and Rodriguez during the Transit of Venus Expeditions, carried out by order of Her Majesty's Government in the Years 1875–75. *Philosophical Transactions of the Royal Society of London* 168: 485–496, pl. 1.
1880. On a collection of Crustacea from the Malaysian Region. Part II. Thelphusidea, Catometopa, and Oxystomata. *Annals and magazine of natural history* (5)5: 304–317, pl. 14.
1882. On the species of *Ocypoda* in the collections of the British Museum. *Annals and magazine of natural history* (5)10: 376–388, pl. 17.
1884. Crustacea (Brachyura). Part I. The collections from Melanesia. Part II. The collections from the Western Indian Ocean. In, *Report on the Zoological Collections made in the Indo-Pacific Ocean during the Voyage of H.M.S. "Alert" 1881–1882*. 8(1): 178–322, pls 18–32; 8(2): 513–575, pls 46–52. (British Museum (Natural History): London).
1886. Report on the Brachyura collected by H.M.S. "Challenger" during the years 1873–1876. In, C.W. Thompson & J. Murray, *Report on the Scientific Results of the exploring Voyage of H.M.S. "Challenger" during the years 1873–1876, under the command of Captain George S. Nares, R.N., F.R.S. and the Late Captain Frank Tourle Thomson, R.N.* *Zoology* 17(2): i–l, 1–362, pls 1–29.
- Millard, N.A.H. & Harrison, A.D. 1954. The ecology of South African estuaries. Part 5. Richards Bay. *Transactions of the Royal Society of South Africa* 34(1): 157–179.

- Milne-Edwards, A. 1868. Description de quelques Crustacés nouveaux provenant des Voyages de M. Alfred Grandidier à Zanzibar et à Madagascar. *Nouvelles Archives du Museum D'Histoire Naturelle De Paris* 4: 69–92, pls 19–21.
1873. Recherches sur la faune carcinologique de la Nouvelle-Calédonie. Part II. Groupe des Cyclo-métopes Portuniens. *Nouvelles Archives du Museum D'Histoire Naturelle De Paris* 9: 155–332, pls 4–18.
- Milne-Edwards, A. & Bouvier, E.-L. 1900. Crustacés Décapodes. I. Brachyures et Anomoures. In, *Expéditions scientifiques du Travailleur et du Talisman pendant les années 1880, 1881, 1882, 1883*. 6: 1–396, pls 1–32. (G. Masson: Paris).
1923. Reports on the Results of Dredging, under the Supervision of Alexander Agassiz, in the Gulf of Mexico (1877–78), in the Caribbean Sea (1878–79), and along the Atlantic Coast of the United States (1880), by the U.S. Coast Survey Steamer "Blake," Lieut.-Com. C.D. Sigsbee, U.S.N., and Commander J.R. Bartlett, U.S.N., Commanding. XLVII. Les Porcellanides et des Brachyures. *Memoirs of the Museum of Comparative Zoölogy. Harvard College* 47(4): 281–395, figs 1–23, pls 1–12.
- Milne Edwards, H. 1834–1840. Histoire naturelle des Crustacés, comprenant l'anatomie, la physiologie et la classification de ces animaux. *Librairie Encyclopédique de Roret*, vol. 1, i–xxxv; 1–468, titles, 5 tables (April, 1834); vol. 2, 1–532 (July, 1837); vol. 3, pt. 1–348 (January, 1840); pt. 2, 1, ii, 349–638 (October, 1840); Atlas, pt. 1, pls 3, 5, 6, 15, 17, 20, 22, 23, 25 (April, 1834); pt. 2, pls 1, 2, 7, 8, 10, 14, 18, 19, 21, 24 (July, 1837); pt. 3 (+4?), pls 4, 9, 11–13, 14 bis, 25 bis, 26–42 (Oct. 1840) [see Holthuis 1979, for dates of publication].
1838. Arachnides, Crustacés, Annélides, Cirripèdes. In, Lamarck, J.B.P.A. De, *Histoire naturelle des animaux sans vertébrés* (2nd ed.) 5: 1–699.
1852. De la famille des Ocypodides (Ocypodidae). Second Mémoire. In, *Observations sur les affinités zoologiques et la classification naturelle des Crustacés. Annales Des Sciences Naturelles* (3)18: 128–166, pls 3, 4. [Pp. 73–128 in undated reprint, *Mélanges Carcinologiques*].
- Milne Edwards, H. & Lucas, H. 1842–1844. Crustacés. In, d'Orbigny, A., *Voyage dans l'Amérique méridionale (le Brésil, la République orientale de l'Uruguay, la République Argentine, la Patagonie, la République du Chili, la République de Bolivie, la République du Pérou), exécuté pendant les Années 1826–1833*, 6(1): 1–39, + Atlas, pls 1–17. (Strasbourg). [Plates 10–17 possibly published in 1847]. (Date by Sherborn C. D. & Griffin, F. J., Text, pp. 1–8, livr. 69, 1843; pp. 9–16, livr. 71, 1843; pp. 17–24, livr. 72, 1844; pp. 25–32, livr. 73, 1844; pp. 33–39, livr. 74, 1844; pls 1, 3, livr. 62, 1842; pls 4, 6, 13, livr. 67, 184–; pls 2, 10, livr. 68, 184; pls 5, 7, 11, livr. 69, 1843; 8, livr. 71, 1843; pls 7, livr. 73, 1844; pls 9, livr. 74, 1844; pls 14–16, livr. 75, 1844; pl. 17, livr. 77, 1844).
- Miyake, S. 1936. Reports on the Brachyura of Riu-kiu Islands, collected by the Yaeyama expeditions during the years 1932–1934. II. A list of the known species of the Brachyura from Ishigaki-Shima. *Annotationes Zoologicae Japonenses* 15(4): 506–513.
1939. Notes on Crustacea Brachyura collected by Professor Teiso Esaki's Micronesia Expeditions 1937–1938 together with a check list of Micronesian Brachyura. *Records of Oceanographic Works in Japan* 10(2): 168–247, figs 1–13, pls 12–17, 1 table.
1963. On Decapod Crustaceans from the Yaeyama Group, Ryukyu Islands. In, *Reports of the Committee on Foreign Scientific Research, Kyushu University* 1: 61–74, fig. 1, pl. 1.
- Miyake, S. & Takeda, M. 1978. Suborder brachyura. In, Kikuchi, T. & Miyake, S. (Eds), *Fauna and flora of the sea around the Amakusa Marine Biological Laboratory, Part II, Decapod Crustacea*. Revised Ed., *Amakusa Marine Biological Laboratory, Kyushu University, Tomioka*, pp. 32–45.
- Miyake, S., Sakai, K. & Nishikawa, S. 1962. A faunal list of the decapod Crustacea from the coasts washed by the Tsushima Warm Current. *Records of Oceanographic Works in Japan, (Special Number 6)*: 121–131.
- Monod, T. 1927. Crustacea IV. Decapoda (excl. Palaeomonidae, Atyidae et Potamonidae). In, Monod, T. (Ed.), *Contributions a la faune de la region de Yaounde (Cameroun)*. I. *Faune des Colonies françaises* 1: 593–624, figs 1–3.
1933. Sur quelques Crustacés de l'Afrique occidentale. (Liste des Décapodes mauritaniens et de Xanthidés ouest-africaines). *Bulletin du Comité d'Études historiques et scientifiques de l'Afrique Occidentale Française* 15(2–3): 456–548, figs 1–26 [Pages 1–93 on separate].
1937. Crustacés. In, Mission A. Gruvel dans le Canal de Suez. I. *Memoires presentes a l'Institut d'Égypte* 34: 1–19, figs 1–11.
1938. Decapoda Brachyura. In, Mission Robert Ph. Dollfus en Égypte. VIII. *Mémoires présentés a l'Institut d'Égypte* 37: 91–162, figs 1–29.
1951. Contribution à l'étude des peuplements de la Mauritanie. Poissons d'eau douce. *Bulletin de l'Institut Fondamental de l'Afrique Noire*. (A) Sci. Nat. 13: 802–812.
1956. Hippidea et Brachyura ouest-africains. *Mémoires de l'Institut Français d'Afrique Noire* 45:1–674, figs 1–884, 10 tables.

- Montgomery, S.K. 1931. Report on the Crustacea Brachyura of the Percy Sladen Trust Expedition to the Abrolhos Islands under the leadership of Prof. W.J. Dakin, D. Sc., F.L.S., in 1913, along with other crabs from Western Australia. *Journal of the Linnean Society of London. Zoology* 37(253): 405–465, fig. 1, pls 24–30, 1 map.
- Moseley, H.N. 1879. Notes by a naturalist on the “Challenger”, being an account of various observations made during the voyage of H.M.S. “Challenger” around the world, in the years 1872–1876, under the commands of Capt. Sir G. S. Nares and Capt. F. T. Thomson. By H. N. Moseley: 1–620. (London).
- Müller, P.L.S. 1775. In, Linnaeus, C., *Natursystem*, 5(2): 1093–1137, pls 23–36. (Nürnberg).
- Muraoka, K. 1974. Megalopa of *Ocypoda*, carrying stalked barnacle on its back. *Researches on Crustacea, Tokyo* 6: 48–51.
- Nadarajalingam, K. & Subramoniam, T. 1987. Influence of light on endocrine system and ovarian activity in the ocypodid crabs *Ocypode platytarsis* and *O. macrocera*. *Marine Ecology Progress* 36(1): 43–53, tables 1–5.
- Nagabushanam, R. & Rao, K.R. 1967. Studies on the moult cycle in the crab, *Ocypoda macrocera*. In, Symposium on Crustacea. *Marine Biological Association of India, Symposium* 2(3): 1099–1107, table 1.
- Nageswara Rao, C.A., Shyama Sundari, K. & Hanumantha Rao, K. 1986. Reproductive cycle of the crab *Ocypoda macrocera* Milne Edwards (Crustacea: Brachyura) from Visakhapatnam coast. *Proceedings of the Indian Academy of Sciences (Anim. Sci.)* 95(1): 1–6.
- Nakazawa, K. 1927. Brachyura. In, Oka, A. [Ed.], *Illustrated encyclopedia of the fauna of Japan*: 994–1124, figs 1910–2166. (Hokuryu-kan: Tokyo).
- Nauck, E. 1880. Das Kaugerüst der Brachyuren [mit Beschreibung neuer Gattungen und Arten, z. T. von C. Semper]. *Zeitschrift für wissenschaftliche Zoologie* 34(1): 1–69, 2 figs, pl. 1. (Leipzig).
- Neumann, R. 1878. Systematische Übersicht der Gattungen der Oxyrhynchen: Catalog der podophthalmen Crustaceen des Heidelberger Museums. *Beschreibung einiger neuer Arten*: 3–27. (Leipzig).
- Neves, F.M. & Bemvenuti, C.E. 2006. The ghost crab *Ocypode quadrata* (Fabricius, 1787) as a potential indicator of anthropic impact along the Rio Grande do Sul coast, Brazil. *Biological Conservation* 133(4): 431–435.
- Ng, P.K.L., Wang, C.-H., Ho, P.-H. & Shih, H.-T. 2001. An annotated checklist of Brachyuran crabs from Taiwan (Crustacea: Decapoda). *National Taiwan Museum, Special Publication* 11: 1–86, Colour figs 1–8.
- Ng, P.K.L., Guinot, D. & Davie, P.J.F. 2008. Systema Brachyurorum: Part I. An annotated checklist of extant brachyuran crabs of the world. *Raffles Bulletin of Zoology* 17: 1–286, figs 1–198.
- Ng, P.K.L., Eldredge, L.G. & Evenhuis, N.L. 2011. The names of decapod and stomatopod Crustacea from Tahiti, French Polynesia, established by Anthony Curtiss in 1938 and 1944. *Zootaxa* 3099: 43–56.
- Nicolet, H. 1849. Crustaceos y Arachnidios. In, Gay, C., *Historia fisica y politica de Chile segun documentos adquiridos en esta republica durante doce años de residencia en ella y publicada bajo los auspicios del supremo gobierno. Zoologia* 3: 115–318, pls 1–4.
- Nicou, R. 1960. Influence du milieu extérieur sur la teneur en chlorures de l'hémolymphes d'*Uca tangeri* (Eyd.). *Annales de la Faculté des Sciences, Université de Dakar* 5: 135–156, figs 1–4.
- Nobili, M.G. 1900. Decapodi e Stomatopodi Indo-Malesi. *Annali del Museo Civico di Storia Naturale di Genova* (2) 20: 473–523.
- 1901a. Decapodi e Stomatopodi Eritrei del Museo Zoologica dell' Università di Napoli. *Annuario del Museo Zoologico della R. Università di Napoli* (n. ser.) 1(3): 1–20.
- 1901b. Decapodi e Stomatopodi del viaggio del Dr. Enrico Festa nella Repubblica dell' Ecuador e regione vicine. *Bollettino Musei di Zoologia ed Anatomia comparata della R. Università di Torino* 16(415): 1–58.
1903. Contributione alla fauna carcinologica di Borneo. *Bollettino Musei di Zoologia ed Anatomia comparata della R. Università di Torino* 18(447): 1–32, figs 1–3.
- 1905a. Decapodi e Isopodi della Nuova Guinea Tedesca, raccolti dal Sign. L. Biró. *Annales Historico-Naturales Musei Nationalis Hungarici* 3: 480–507, 2 figs, pls 12–13.
- 1905b. Note sur *Ocypoda fabricii* Milne-Edwards. *Bulletin du Muséum d'Histoire Naturelle de Paris* 11(4): 229–235, 3 figs.
- 1906a. Mission J. Bonnier et Ch. Pérez (Golfe Persique 1901). Crustacés Décapodes et Stomatopodes. *Bulletin Scientifique De La France Et De La Belgique* 40: 13–159, figs 1–3, pls 2–7.
- 1906b. Faune carcinologique de la Mer Rouge. Décapodes et Stomatopodes. *Annales des sciences naturelles (Zoologie)* (9)4(1–26): 1–347, figs 1–12, pls 1–11.
- 1906c. Decapodi della Guinea Spagnuola. *Memorias de la Real Sociedad Española de Historia Natural* 1(18): 297–321, figs 1–2, pl. 8.

1907. Ricerche sui Crostacei della Polinesia (Decapodi, Stomatopodi, Anisopodi e Isopodi). *Memorie della Reale Accademia della Scienze Torino* (2)57: 351–430, pls 1–3.
- Odhner, T. 1923. Marine Crustacea podophthalmata aus Angola und Südafrika, gesammelt von H. Skoog 1912. *Meddelanden fran Götheborgs Musei Zoologiska Avdelning* 31: 1–39.
- Olivier, G.A. 1804a. *Voyage dans l'Empire Othoman, l'Égypte et la Perse, fait par ordre du Gouvernement, pendant les six premières années de la République*. 2: i-ii, 1–466. (Agasse, H.: Paris).
- 1804b. *Voyage dans l'Empire Othoman, l'Égypte et la Perse, fait par ordre du Gouvernement, pendant les six premières années de la République* 4: i-iv, 1–456. (Agasse, H.: Paris).
1811. Encyclopédie méthodique. *Histoire Naturelle. Insectes* 8: 414–420. (Paris).
- Ono, Y., The ecological studids on Brachyura in the estuary. *Bulletin of the Marine Biological Station of Asamushi, Tohoku University* 9: 145–148.
- Ooishi, S. 1970. Marine invertebrate fauna of the Ogasawara and Volcano Islands. In, *Report on the Marine Biological Expedition to the Ogasawara (Bonin) Islands, 1968*: 75–104, pls 25.
- Ortmann, A.E. 1894a. Die Decapoden-Krebse des Strassburger Museums mit besonderer Berücksichtigung der von Herrn Dr. Döderlein bei Japan und bei den Liu-Kiu-Inseln gesammelten und zur Zeit im Strassburger Museum aufbewahrten Formen. Theil VIII. Abtheilung: Brachyura (Brachyura genuina Boas), III. Unterabtheilung: Cancroidea. 2. Section: Cancrinea, 2. Gruppe: Catametopa. *Zoologische Jahrbücher, Abteilung für Systematik, Ökologie und Geographie der Tiere* 7: 683/761–772, pl. 23.
- 1894b. Crustaceen. In, Semon, R. (Ed.), *Zoologische Forschungsreisen in Australien und dem Malayischen Archipel ausgeführt in den Jahren 1891–93*. V. *Denkschriften der Medicinisch-Naturwissenschaftlichen Gesellschaft zu Jena* 8: 1–80, pls 1–13.
1897. Carcinologische Studien. *Zoologische Jahrbücher, Abteilung für Systematik, Ökologie und Geographie der Tiere* 10: 358–372, pl. 17.
- Osbeck, P. 1765. Reise nach Ostindien und China. Nebst O. Torens Reise nach Suratte und C. G. Ekebergs Nachricht von der Landwirthschaft der Chineser. Aus dem Schwedischen bersetzt von J. G. George. [3] + xxiv + 1+ 552 + [26] pp., pls 1–13. (Johann Christian Koppe: Rostock).
- Ozório, B. 1887. Liste des Crustacés des possessions Portugaises d'Afrique occidentale dans les collections du Museum d'Histoire naturelle de Lisbonne. *Jornal de ciencias mathematicas, physicas, e naturaes, Lisboa* 12: 220–223.
- Osório, B. 1888. Nota ácerca da collecção de crustaceos provenientes de Maçambique, Timor, Macau, Índia Portuguesa e ilha de S. Miguel (Açotrs) que existem no Museu de Lisboa. *Jornal de ciencias mathematicas, physicas, e naturaes, Lisboa* 12: 236–246.
- 1889–1890. Nouvelle contribution pour la connaissance de la faune carcinologique des îles Saint Thomé et du Prince. *Jornal de ciencias mathematicas, physicas, e naturaes, Lisboa* (2) 1(2): 129–139.
- 1890–1892. Note sur quelques espèces de Crustacés des îles S. Thomé, du Prince et Ilheo das Rolas. *Jornal de ciencias mathematicas, physicas, e naturaes, Lisboa* (2) 2(5): 45–49.
- 1893–1895a. I. Crustaceos da Ilha D'Anno Bom (248–250 pp). II. Crustaceos da Ilah do Principe (251 p). III. Peixes de Dahomey (252–253 pp). *Jornal de ciencias mathematicas, physicas, e naturaes, Lisboa* (2) 3: 248–253.
- 1895b–1897. Peixes e Crustaceos da Ilhade Fernão do Pó e de Elobey. *Jornal de ciencias mathematicas, physicas, e naturaes, Lisboa* (2)4: 55–57.
- 1897–1898. Nota sobre a presença do “*Lycaon pictus*” Temm. No sertão de Benguela. *Jornal de ciencias mathematicas, physicas, e naturaes, Lisboa* (2) 5: 184–193.
1890. Note sur quelques espèces de crustacés des îles S. Thomé, du Prince et Ilheo das Rolas. *Jornal de ciencias mathematicas, Physicas e Naturaes, Publicado sob os auspícios da Academia Real das Ciencias de Lisboa, Lisbon, Portugal* (2) 2(5): 45–49.
- 1903–1910. Uma nova lista de Crustaceos Africanos. *Jornal de ciencias mathematicas, physicas, e naturaes, Lisboa* 7: 149–150.
- Owen, R. 1839. Crustaces. Pp. 77–92, pls 24–28. In, *The zoology of Captain Beechey's voyage; compiled from the collections and notes made by Captain Beechey, the officers and naturalist of the expedition during a voyage to the Pacific and Behrin's Straits performed in his Majesty's ship "Blossom", under the command of Capt. E. W. Beechey, R.N., F.R.SI, &c. in the years 1825, 26, 27 and 28*. (London).
- Pallas, S.P. 1772. Spicilegia zoologica quibus novae imprimis et obscurae animalium species iconibus descriptionibus atque commentariis illustrantur 1(10): 81–84; (9): pl. 5, figs 7–8. (Berlin).
- Parisi, B. 1918. I Decapodi Giapponesi del Museo di Milano. VI. Catometopa e Paguridea. *Atti della Società Italiana di Scienze Naturali e del Museo Civico de Storia Naturale in Milano* 57: 90–115, figs 1–5, pl. 8.
- Paulraj, S., Mullainadhan, P. & Ravindranath, M.H. 1982. Relative growth before and after sexual maturity in *Ocypode platytarsis* (Milne Edwards) and *Ocypode cordimana* (Desmarest) (Crustacea:

- Decapoda). *International Journal of Invertebrate Reproduction* 5(3): 115–128, tables 1–7.
- Paul'son, O.M. 1875. Izledovaniya rakoobraznykh krasnago morya s zametkami otnositel'no rakoobraznykh drugikh morei. Tchasst I. Podophthalmata i Edriophthalmata (Cumacea). [Studies on Crustacea of the Red Sea with notes regarding other Seas, Part I]. Kiev Kul'zhenko: i–xiv, 1–144, pls 1–21. [In Russian] [Paul'son, O.M. 1875. Studies on Crustacea of the Red Sea with notes regarding other seas. Part I. Podophthalmata and Edriophthalmata (Cumacea). (English translation of the original Russian publication for 1875 with different pagination by the Israel Program for Scientific Tranlations, Jerusalem: 1–164, pls 1–21)].
- Pearse, A.S. 1915. An account of the Crustacea collected by the Walker Expedition to Santa Marta, Colombia. *Proceedings of the United States National Museum* 49: 531–556, pls 70–73.
- Penrith, M.-L. & Kensley, B.F. 1970. The constitution of the fauna of rocky intertidal shores of South West Africa, Part II: Rocky Point. *Cimbebasia*, (A) 1(10): 243–268, figs 1–3, pls 1–8.
- Pesta, O. 1911. Crustacea. I. Decapoda Brachyura aus Samoa (Unter Berücksichtigung der Sammlungen des k.k. Naturhistorischen Hofmuseums in Wien). In: K. Rechinger, Botanische und zoologische Ergebnisse einer wissenschaftlichen Forschungsreise nach den Samoa-Inseln, dem Neuguinea-Archipel und den Salomoninseln März bis Dezember 1905. IV. *Denkschriften, Akademie der Wissenschaften in Wien, Mathematisch-Naturwissenschaftliche Klasse* 88: 36–65, figs 1–5, pl. 3.
1918. *Die Decapodenfauna der Adria: Versuch einer Monographie*. x+500 pp., 1 map, text-figs A, B, 1–150. (Leipzig and Wien).
1931. Ergebnisse der Österreichischen Biologischen Expedition nach Cost Rica 1930. I. Crustacea Decapoda aus Costa Rica. *Annalen des Naturhistorischen Museums in Wien* 45: 173–181, 1 fig, pls 5–6.
- Pfeffer, G. 1889. Übersicht der von Herrn Dr. Franz Stuhlmann in Ägypten, auf Sansibar und dem gegenüberliegenden Festlande gesammelten Reptilien, Amphibien, Fische, Mollusken und Krebse. *Mitteilungen aus dem Hamburgischen zoologischen Museum und Institut* 6: 28–35.
- Pillai, N.K. 1951. Decapoda (Brachyura) from Travancore. *Bulletin of the Central Research Institute, University of Travancore, Trivandrum* (C) 2(1): 1–46, figs 1–5.
- Popper, A.N., Salmon, M. & Horch, K.W. 2001. Acoustic detection and communication by decapod crustaceans. *Journal of Comparative Physiology* (A) 187: 83–89, text-figs 1–2.
- Portell, R.W., Turner, R.L. & Beerensson, J.L. 2003. Occurrence of the Atlantic ghost crab *Ocypode quadrata* from the Upper Pleistocene to Holocene Anastasia Formation of Florida. *Journal of Crustacean Biology* 23(3): 712–722.
- Porter, C.E. 1940. Algunos Crustáceos de la costa de Antofagasta. *Revta Univ. Santiago* 25(3): 311–313. [= Porter, C.E. 1941. Algunos Crustáceos de la costa de Antofagasta. *Boletim Museo de Historia Natural Javier Prado* 5: 458–460.]
- Poupin, J. 1996. Crustacea Decapoda of Fench Polynesia (Astacidea, Palinuridea, Anomura, Brachyura). *Atoll Research Bulletin* 442: 1–144, 1 table, 1 map, 1 text-fig.
- Poupin, J., Zubia, M. Gravier-Bonnet, N. Chabanet, P. & Malay, M. 2011. New observations on the crustacean fauna of Europa Island, Mozambique Channel (Crustacea, Decapoda): 1–35 pp, 3 tables, 10 figs.
- Prem Kumar, V.K. 1964. A new species of sandcrab of the genus *Ocypoda* Fabricius, 1798 (Crustacea: Decapoda: Brachyura), from the Coromandel Coast, India. *Proceedings of the Zoological Society (Calcutta)* 17: 153–157, fig. 1, pl. 1.
- Pretzmann, G. 1968. Etudes hydrobiologiques en Nouvelle-Calédonie. VII. Brachyures. *Cahiers de l'O.R.S.T.O.M. Série Hydrobiologie* 2 (2), 3–9, figs 1–4. (Paris).
1971. Ergebnisse einer Sammelreise nach Vorderasien. 2. Teil: Marine Brachyura. *Annalen des Naturhistorischen Museums in Wien* 75: 477–487, pls 1–9.
- 1974a. Bericht über eine Sammelreise nach Iran im Frühjahr 1972. *Annalen des Naturhistorischen Museums in Wien* 78: 453–455.
1975. Verhaltensstudien an Stranddekapoden bei Bandarabbass (Str. v. Hormo). *Anzeiger der mathematisch-naturwissenschaftlichen Klasse der Österreichischen Akademie der Wissenschaften* 1975 (2): 14–18.
- Quoy, J.R.C. & Gaimard, J.P. 1824. Zoologie. In: Freycinet, L.C.D. de (Ed.) *Voyage autour du monde, entrepris par ordre du Roi, sous le Ministère et conformément aux instructions de S. Exc. M. Le Vicomte du Bocage, Secrétaire d'état au Département de la Marine, Exécuté sur les Corvettes de S. M. l'Uranie et al Physicienne, pendant les Années 1817, 1818, 1819 et 1820: i–iv + 1–712, pl. 77. (Paris).*
- Quijon, P., Jaramillo, E. & Contreras, H. 2001. Distribution and habitat structure of *Ocypode gaudichaudii* H. Milne Edwards & Lucas, 1843, in sandy beaches of northern Chile. *Crustaceana* 74(1): 91–103, table 1–4.
- Rafinesque, C.S. 1815. Analyse de la nature ou tableau de l'univers et des corps organisés. 224 pp. (Palermo).

- Rajabai, B.S. 1974. Observations on the behaviour and ecology of *Ocypode macrocera* M. Edwards (Crustacea: Decapoda; Ocypodidae). *Journal of the Zoological Society of India* 24(2): 203–210.
- Raja Bai Naidu, K.G. 1954. The post-larval development of the shore crab *Ocypoda platytarsis* M. Edwards and *Ocypoda cordimana* and Desmarest. *Proceedings of the Indian Academy of Sciences* 40B (4): 89–101, text-figs 1–30.
- Ramadan, M.M. 1936. Report on a collection of Stomatopoda and Decapoda from Ghardaqa, Red Sea. *Bulletin of the Faculty of Science, Egypt University (Cairo)* 6: 1–43, pls 1–2.
- Ramadevi, K.R.L.S., Shyamasundari, K. & Hanumantha Rao, K. 1990. Observation on the hepatopancreas of *Ocypoda platytarsis* (Milne-Edwards) (Crustacea, Brachyura). *Bollettino di Zoologia* 57(3): 261–265, table 1, text-figs 1–5.
- Randall, J.W. 1840. Catalogue of the Crustacea brought by Thomas Nuttall and J. K. Townsend, from the west coast of North America and the Sandwich Islands, with descriptions of such species as are apparently new, among which are included several species of different localities, previously existing in the collection of the Academy. *Journal of the Academy of Natural Sciences of Philadelphia* [1839] 8(1): 106–147, pls 3–7.
- Rao, K.R. 1966. Studies on the influence of environmental factors on growth in the crab *Ocypode macrocera* H. Milne Edwards. *Crustaceana* 11: 257–276, tables 1–5, text-figs 1–5.
- Rathbun, M.J. 1898a. The Brachyura of the Biological Expedition to the Florida Keys and the Bahamas in 1893. *Bulletin from the laboratories of natural history of the State University of Iowa* 4(3): 250–294, pls 1–9.
- 1898b. The Brachyura collected by the U.S. Fish Commission Steamer “Albatross”, on the voyage from Norfolk, Virginia, to San Francisco, California, 1887–1888. *Proceedings of the United States National Museum* 21(1162): 567–616, pls 41–44.
1901. The Brachyura and Macrura of Porto Rico. *Bulletin of the United States Fish Commission* 20(2): 1–127, figs 1–24, pls 1–2.
1902. Crabs from the Maldive Islands. *Bulletin of the Museum of Comparative Zoology of Harvard College* 39(5): 123–238, pl. 1.
1906. The Brachyura and Macrura of the Hawaiian Islands. *Bulletin of the United States Fish Commission* 23(3): i–viii, 827–930, figs 1–79, pls 1–24.
- 1910a. The Brachyura. In, *The Danish Expedition to Siam, 1899–1900. Kongelige Danske Videnskabelnes Selskabs Skrifter, 7 Raekke, Naturvidenskabelig og Mathematisk Afdeling* (7) 5(4): 301–367, figs 1–44, pls 1–2, 1 map. (Kjøbenhavn).
- 1910b. The stalk-eyed Crustacea of Peru and the adjacent coast *Proceedings of the United States National Museum* 38(1766): 531–620, figs 1–3, pls 36–56.
1918. The Grapsoid Crabs of America. *Bulletin of the United States National Museum* 97: i–xxii, 1–461, figs 1–72, 161 pls.
1919. Stalk-eyed Crustaceans of Dutch West Indies. In, J. Boeke, Rapport betreffende een voorloopig onderzoek naar den toestand van de visscherij en de industrie van zeeproducten in de kolonie Curaçao, ingevolge het ministerieel besluit van 22 november 1904 uitgebracht door Prof. D. J. Boeke Hoogleraar aan de Rijks-Universiteit te Utrecht 2: 317–349, figs 1–5.
1921. The Brachyuran Crabs collected by the American Museum Congo Expedition, 1909–1915 (Ecological and other notes by Lang, H.). *Bulletin of the American Museum of Natural History* 43: 379–474, text-figs 1–22, pls 15–64, 1 map.
1923. The Brachyuran Crabs collected by the U.S. Fisheries Steamer “Albatross” in 1911; chiefly on the west coast of Mexiso. *Bulletin of the American Museum of Natural History* 48: 619–637, pls 26–36.
1924. Brachyuran Crabs collected by the Williams Galapagos Expedition, 1923. *Zoologica New York* 5: 153–159, text-fig. 38, pl. 7.
1933. Reports on the scientific results of an expedition to the southwestern highlands of Tanganyika territory. V. Crabs. *Bulletin of the Museum of Comparative Zoology of Harvard College* 75(5): 251–260, pls 1–7.
1935. Scientific results of an expedition to rain forest regions in East Africa. II. Crustacea. *Bulletin of the Museum of Comparative Zoology of Harvard College* 79: 23–28, 2 figs 1–2, pls 1–2.
- Ribeiro, A. 1964. Crustáceos Decápodos Braquiros do Arquipélago de Cabo Verde (Coleção do Centro de Biologia Piscatória). *Notas Mimeografadas do Centro de Biologia Piscatória* 38: 1–27. (Lisboa).
- Richters, F. 1880. Decapoda. In, K. Möbius, Beiträge zur Meeresfauna der Insel Mauritius und der Seychellen, bearbeitet von K. Möbius, F. Richters und E. von Martens nach sammlungen, angelegt auf einer Reise nach Mauritius von K. Möbius, Berlin. Pp. 139–178, pls 15–18.
- Rivera, M.E. & Langer, H. 1982. Enzym-Muster in Facetenaugen und optischen Ganglien von Krebsen. *Verhandlungen der Deutschen Zoologischen* 75: 228, 1 table.
- Robertson, J.R. & Pfeiffer, W.J. 1981. Deposit-feeding by the ghost crab *Ocypode quadrata* (Fabricius). *Journal of Experimental Marine Biology and Ecology* 56(2–3): 165–177.
- Robinson, G. 1985. Influence of the 1982–83 El Niño on Galapagos marine life. Pages 153–190. In,

- Robinson, G. & del Pino, E.M. (Eds), *El Niño en Las Islas Galapagos: El evento de 1982-83*. Pp.153-190, tables 1-4, text-figs 1-4. (Fundacion Charles Darwin para Las Islas Galapagos: Quito, Ecuador).
- Rosa Da, L.C. & Borzone, C.A. 2008. Spatial distribution of the *Ocypode quadrata* (Crustacea: Ocypodidae) along estuarine environments in the Paranagua Bay Complex, southern Brazil. *Revista Brasileira de Zoologia* 25(3): 383-388.
- Rosenberg, J., Henning, U. & Langer, H. 2001. Diurnal changes of fine structure in the compound eyes of the ghost crab *Ocypode ryderi* (Crustacea, Decapoda, Ocypodidae) *Acta Biologica Benrodis* 11(1-2): 53-70, text-figs 1-7.
- Rosenberg, J. & Langer, H. 2001. Ultrastructural changes of rhabdoms of the eyes of *Ocypode* species in relation to different regimes of light and dark adaptation. *Journal of Crustacean Biology* 21(2): 345-353, table 1, text-figs 1-2.
- Rossignol, M. 1957. Crustacés Décapodes marins de la région de Pointe-Noire. In, Collignon, J. Rossignol, M. & Roux, Ch. *Mollusques, Crustacés, Poissons Marins des côte d'A.E.F. en collection au Centre d'Océanographie de l'Institut d'Études Centrafricaines de Pointe-Noire*. Pp. 71-136, figs 1-20, pls 1-3. (Paris).
1962. Catalogue de Crustacés Décapodes Brachyours, Anomours et Macroures littoraux en collection au centre d'oceanographie de Pointe-Noire. *Travaux du Centre Océanographique de Pointe-Noire* 2: 111-138, pls 1-4.
- Roux, J. 1927. Note sur one collection de Crustacés décapodes du Gabon. *Bulletin de la Société vaudoise des sciences naturelles* 56(218): 237-244, fig. 1.
- Sabine, J.B., Meyers, J.M. & Schweitzer, S.H. 2005. A simple, inexpensive video camera setup for the study of avian nest activity. *Journal of Field Ornithology* 76(3): 293-297, text-figs 1-2.
- Sack, B.A. von. 1821. Beschreibung einer Reise nach Surinam und des Aufenthaltes daselbst in den Jahren 1805, 1806, 1807, so wie von des Verfassers Rückkehr nach Europa über Nord-Amerika. (Vol. 2, Beschreibung einer Reise nach Surinam und des Aufenthaltes daselbst in den Jahren 1810, 1811, 1812, so wie von des Verfassers Rückkehr nach Europa über Nord-Amerika.) 1: 230. (Berlin).
- Sakai, K. 2000. On the occurrence of three species of crabs on Shikoku Island Japan and a new species, *Pinnotheres taichungae* nov. spec., from Taiwan (Decapoda, Brachyura). *Crustaceana* 73(9): 1155-1162, text-figs 1-3.
- Sakai, K. & Türkay, M. 1976. Bemerkungen zu einigen *Ocypode*-Arten (Crustacea: Decapoda). *Senckenbergiana biologica* 57(1-3):81-96, 16 figs.
- 1977a. Die Gattung *Ocypode* in der Sammlung des Genfer Naturhistorischen Museums (Crustacea: Decapoda). *Revue Suisse de Zoologie* 84(1): 177-180, pl. 1. [English & French summaries].
- 1977b. Die Deutung von *Ocypode cordimanus* Latreille 1818, mit Festlegung eines Neotypus (Crustacea: Decapoda). *Senckenbergiana biologica* 58(1-2): 97-100.
- Sakai, K., Türkay, M. & Yang, S-L. 1976. Revision of the *Helice/Chasmagnathus* complex (Crustacea: Decapoda: Brachyura). *Abhandlungen* 565: 1-76, 98 text-figs, 3 tables.
- Sakai, T. 1934. Brachyura from the coast of Kyushu, Japan. *Science Reports of the Tokyo Bunrika Daigaku (B)* 1(25): 281-330, text-figs 1-26, pls 17-18 [in colour].
- 1935a. *Crabs of Japan*. Pp. 1-239, front colour pl. 1 + text-figs 1-122, pls 1-66. (Sansei-do: Tokyo). [In colour; Japanese].
- 1935b. List of marine Animals around Shimoda. *Shimoda Marine Biological Station (Tokyo Bunrika Daigaku)*. Pp. 1-89, 6 pls, 2 maps [in Japanese].
1939. Studies on the Crabs of Japan. IV. Brachygnatha, Brachyrhyncha: 365-741+1-23, figs 1-129, pls 42-111, table 1. (Yokendo Co: Tokyo) [in colour].
1940. Bio-geographic review on the Distribution of Crabs in Japanese waters. *Records of Oceanographic Works in Japan* 11(1): 27-63, figs 1-3.
1955. On some rare species of crabs from Japan. *Bulletin of the Biogeographical Society of Japan* 15-16: 106-113, figs 1-6.
1956. Kani (Brachyura); list of Japanese Brachyura: 1-224 + 1-60, pls (Shisei-do, Tokyo)[in Japanese]
1965. *The Crabs of Sagami Bay, collected by His Majesty the Emperor of Japan*. Pp. i-xvi, 1-206 [English text], figs 1-27, pls 1-100: 1-92 [Japanese text]: 1-26 [references and index in English]: 27-32 [index in Japanese], 1 map. (Tokyo).
1976. *Crabs of Japan and the Adjacent Seas*. In three volumes; English Text, pp. xxix+773 pp., Japanese Text, pp. 1-461, Plates volume, pp. 1-16, pls. 1-251. (Kodansha: Tokyo).
- Sakai, T. & Nakazawa, K. 1947. Brachyura. In, Oka, A. (Ed.), *Encyclopedia zoological Illustrated*: 649-730, figs 1-2, 1875-2114, colour pl. 5. [in Japanese] (Hokuryu-kan: Tokyo).
- Sankarankutty, C. 1961. On some crabs (Decapoda-Brachyura) from the Laccadive Archipelago. *Journal of the Marine Biological Association of India* 3 (1 & 2): 120-136, figs 1-2.
- Sarojini, S. 1962. The androgenic organ in some Indian Crustacea I. *Journal of the Zoological Society of India* 13(2): 188-193, text-figs 1-2, table 1.
- Saussure, H. de, 1858. Mémoire sur divers Crustacés nouveaux des Antilles et du Mexique. *Mémoires de*

- la Société de Physique et d'Histoire Naturelle de Genève 14: 417-496, pls 1-6.
- Savigny, J.C. De. 1817. Crustacés. In, *Description de l'Égypte, ou recueil des observations et des recherches qui ont été faites en Égypte pendant l'Expédition de l'Armée Française, publié par les ordres de Sa Majesté l'Empereur Napoléon le Grand: Histoire naturelle, Crustacés. Atlas Crust.*, pls 1-13.
- Say, T. 1817-1818. An account of the Crustacea of the United States. *Journal of the Academy of Natural Sciences of Philadelphia* 1(1)(1817): 57-63, 65-80, 97-101, 155-169; (2)(1818): 235-253, 313-319, 374-401, 423-444, 445-458, pl. 4.
- Schenkel, E. 1902. Beiträg zur Kenntnis der Dekapodenfauna von Celebes. *Verhandlungen der Naturforschenden Gesellschaft in Basel* 13(3): 485-585, pls 7-13.
- Schmitt, W.L. 1921. The marine decapod Crustacea of California with special reference to the decapod Crustacea collected by the United States Bureau of Fisheries Steamer "Albatross" in connection with the Biological Survey of San Francisco Bay during the years 1912-1913. *University of California Publications in Zoology* 23: 1-470, figs 1-165, pls 1-50.
- Schober, U.M. & Christy, J.H. 1993. Sand disposal of the painted ghost crab *Ocypode gaudichaudii* (Decapoda: Ocypodidae): a possible role in courtship. *Marine Biology* 116(1): 53-60, tables 1-3, text-figs 1-5.
- Schöne, H. 1964. Krabben - Ihr Leben und Treiben an tropischen Gestaden. *Neptun* 5(6): 105-108, 6 figs.
- Seike, K. & Nara, M. 2008. Burrow morphologies of the ghost crabs *Ocypode ceratophthalma* and *O. sinensis* in foreshore, backshore, and dune subenvironments of a sandy beach in Japan. *Journal of the Geological Society of Japan* 114: 591-596, tables 1-3, figs 1-6.
- Sendler, A. 1912. Zehnfüßkrebse aus dem Wiesbadener naturhistorischen Museum. *Jahrbücher des Nassauischen Vereins für Naturkunde* 65: 189-207, figs 1-7.
1923. Die Dekapoden und Stomatopoden der Hanseatischen Südsee-Expedition. *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft, Frankfurt am Main* 38: 21-47, figs 1-3, pls 5-6.
- Serène, R. 1968. The Brachyura of the Indo-West Pacific region. In, *Prodromus for a check list of the non-planctonic marine fauna of South East Asia. Unesco Singapore National Academy of the Sciences, Special publication No. 1, Fauna IIIC*: 33-112.
- Shen, C.J. 1932. The Brachyuran Crustacea of North China. *Zoologia Sinica* (A) 9(1): i-x, 1-320, figs 1-171, pls 1-10, 1 map. (Peking)
- 1937a. Second addition to the Fauna of Brachyuran Crustacea of North China, with a check list of the species recorded in this particular region. *Contributions from the Institute of Zoology, National Academy of Peiping* 3(6): 277-313, text-figs 1-11.
- 1937b. On some account of the crabs of North China. *Bulletin of the Fan Memorial Institute of Biology (Zool.)* 7(5): 167-185.
1940. On the collection of Crabs of South China. *Bulletin of the Fan Memorial Institute of Biology (Zool.)* 10(2): 69-104.
- Shen, C.J. & Liu, J.Y. 1963. Preliminary studies on the characteristics of the crab fauna of China Seas. *Oceanologia et Limnologia Sinica* 5(2): 139-153. [In Chinese].
- Shiber, J.G. & Izzidin, S. 1978. The burrow structure of *Ocypode cursor* (Linnaeus 1758) on three shores south of Beirut, Lebanon. *Cercetari Marine* 11: 113-127, text-figs 1-10.
- Shuchmann, E. & Warburg, M.R. 1978. Dispersal, population structure and burrow shape of *Ocypode cursor*. *Marine Biology (Berlin)* 49(3): 255-263, tabs. 1-4, text-figs 1-5.
- Sivertsen, E. 1933. Littoral Crustacea Decapoda from the Galapagos Islands, Part VII. The Norwegian Zoological Expeditions to the Galapagos Islands 1925, conducted by Alf Wollebaek. *Meddelelser fra det Zoologiske Museum, Oslo* 38: 1-23, pls 1-4.
- Smith, S.I. 1869. Notice of the Crustacea Collected by Prof. C. F. Hartt on the Coast of Brazil in 1867. *Transactions of the Connecticut Academy of Arts and Sciences* 2: 1-42, pl. 1. [*American Journal of science* (2) 48: 388-391].
1880. Occasional occurrence of tropical and sub-tropical species of Decapod Crustacea on the Coast of New England. *Transactions of the Connecticut Academy of Arts and Sciences* 4: 254-267.
- Sourie, R. 1954. Contribution à l'étude écologique des côtes rocheuses du Sénégal. *Mémoires de l'Institut Français d'Afrique noire* 38:1-342, figs 1-46, pls 1-23. (Dakar).
1955. Invertébrés. *L'éducation en Afrique (N.S.)* 46(26-27): 49-71, text-figs 1-27.
1957. Étude écologique des plages de la côte Sénégalaise aux environs de Dakar (macrofaune). *Annales de l'École Supérieure des Sciences* 3: 5-10, figs 1-20.
- Stebbing, T.R.R. 1910. General Catalogue of South African Crustacea. Part V of South African Crustacea, for the Marine Investigations in South Africa. *Annals of the South African Museum* 6(4): 281-593, pls 15-22.

1917. The Malacostraca of Natal. I. *Annals of the Durban Museum* 2(1): 1-33, pls 1-6.
- Steiner, A.J. & Leatherman, S.P. 1981. Recreational impacts on the distribution of ghost crabs *Ocypode quadrata* Fab. *Biological Conservation* 20(2): 111-122.
- Stephensen, K. 1945. The Brachyura of the Iranian Gulf with an Appendix: The male pleopod of the Brachyura. In, *Danish Scientific Investigations in Iran* 4: 57-237, figs 1-60. (Copenhagen).
- Stephenson, W., Endean, R. & Bennett, I. 1958. An ecological survey of the marine fauna of Low Isles, Queensland. *Australian Journal of Marine and Freshwater Research* 9: 261-318, pls 1-11.
- Stimpson, W. 1858. Prodromus descriptionis animalium evertibratorum quae in Expeditione and Oceanum Pacificum Septentrionalem, a Republica Feberata Missa, Cadwladaro Ringgold et Johann Rodgers ducibus, observavit et descriptorum. Pars V, Crustacea Ocypoidea. *Proceedings of the Academy of Natural Sciences of Philadelphia* 1858: 93-110 [Pages 39-56 on separate].
1860. Notes on North American Crustacea. No. II. *Annals of the Lyceum of Natural History of New-York* 7: 176-246, pls 2, 5.
1907. Report on the Crustacea (Brachyura and Anomura) collected by the North Pacific Exploring Expedition, 1853-1856. *Smithsonian Miscellaneous Collections* 49(1717): 1-240, pls 1-26.
- Strachan, P.H., Smith, R.C., Hamilton, D.A.B., Taylor, A.C. & Atkinson, R.J.A. 1999. Studies on the ecology and behaviour of the ghost crab, *Ocypode cursor* (L.) in northern Cyprus. *Scientia Marina* 63(1): 51-60, tables 1-5, text-figs 1-4.
- Streets, T.H. 1871. Catalogue of Crustacea from the Isthmus of Panama, collected by J. A. McNeil. *Proceedings of the Academy of Natural Sciences of Philadelphia* 1871: 238-243.
1877. Contributions to the Natural History of the Hawaiian and Fanning Islands and Lower California. *Bulletin of the United States National Museum* 7: 1-172.
- Studer, T. 1883. Verzeichniss der Crustaceen, welche während der Reise S. M. S. "Gazelle" an der Westküste von Afrika, Ascension und dem Cap der guten Hoffnung, gesammelt wurden. *Abhandlungen der Königlichen Akademie der Wissenschaften in Berlin* 2: 1 32, Pls 1-2.
- Suvatti, C. 1950. *Fauna of Thailand*. 2: 1-1100, 1 pl. (Department of Fisheries: Bangkok, Thailand).
- Takahashi, S. 1932. On the burrows of *Ocypode ceratophthalma* Fabricius. *Kagaku (Science)* 2: 329-335, figs 13-16.
- 1934a. An ecological study of the littoral animals near the mouth of Tamsui. *Transactions of the Natural History Society of Formosa* 24: 1-14. [in Japanese].
- 1934b. Ecology of the Ocypodidae at the estuaries of inland water in Taiwan. *Zoological Magazine (Tokyo)* 45: 73-74. [in Japanese].
1935. Ecological notes on the ocypodian crabs (Ocypodidae) in Formosa, Japan. *Annotationes Zoologicae Japonenses* 15: 78-87, pl. 6.
- Taramelli, E. 1955. Crostacei de Zanzibar (Decapodi e Stomatopodi). *Rivista di Biologia Coloniale* 15: 29-47. (Roma).
- Terada, M. 1979. On the zoea larvae of five crabs of the family Ocypodidae. *Zoological Magazine* 88(1): 57-72, tables 1-3, text-figs 1-5. (Tokyo).
- Tesch, J.J. 1918. The Decapoda Brachyura of the Siboga-Expedition. I. Hymenosomidae, Retroplumidae, Ocypodidae, Grapsidae and Gecarcinidae. *Siboga-Expedition Monograph* 39c(82): 1-148, pls 1-6.
- Teixeira, M.F., Torres, S.F. & Capitoli, R.R. 2008. Principais moluscos e crustáceos decapodos da praia do cassino, rs-textos e proposta didática *Cadern Aquatic Ecology* 3(2): 1-18, text-figs 1-14 + 6 un-numbered.
- Thallwitz, J. 1891. Decapoden-Studien, insbesondere basirt auf A.B. Meyer's Sammlungen im Ostindischen Archipel, nebst einer Aufzählung der Decapoden und Stomatopoden des Dresdener Museums *Abhandlungen und Berichte des Königlichen Zoologischen und Anthropologisch-Ethnographischen Museums zu Dresden* 1890-1891 3: 1-55, 1 pl.
- Thampy, D.M. & John, P.A. 1970. On the androgenic gland of the ghost crab *Ocypode platytarsis* M. Edwards. *Acta Zoologica, Stockholm* 51(3): 203-210.
- Tirmizi, N.M. 1980. Marine Crustacea (Decapoda and Stomatopoda) of Pakistan. *Proceedings of the 1st Pakistan Congress of Zoology*: 97-114.
- Tirmizi, N.M. & Kazmi, Q.B. 1983. Carcinological studies in Pakistan, with remarks on species to the Red Sea and the Mediterranean. *Bulletin of the Institute of Oceanography and Fisheries* 9: 347-480.
- Titgen, R.H. 1982. The systematics and ecology of the Decapods of Dubai, and their zoogeographic relationships to the Arabian Gulf and the western Indian Ocean. 291 pp. Dissertation submitted to the Graduate College of Texas A&M University.
- Trott, T.J. 1987a. The prevalence of left-handedness in the painted ghost crab *Ocypode gaudichaudii* H. Milne Edwards & Lucas (Decapoda Brachyura, Ocypodidae). *Crustaceana* 52(2): 213-215, table 1.
- 1987b. Chemoreception by the painted ghost crab *Ocypode gaudichaudii* H. Milne Edwards and Lucas (Brachyura: Ocypodidae): implications for foraging. *Zoologischer Anzeiger* 218(5-6): 295-303, table 1, text-figs 1-3.

1988. Note on the foraging activities of the painted ghost crab *Ocypode gaudichaudii* H. Milne Edwards & Lucas in Costa Rica (Decapoda, Brachyura). *Crustaceana* 55(2): 217–219, text-fig. 1.
1998. On the sex ratio of the painted ghost crab *Ocypode gaudichaudii* H. Milne Edwards & Lucas, 1843 (Brachyura, Ocypodidae). *Crustaceana* 71(1): 47–56, table 1, text-figs 1–3.
- Tu, Y.T., Tu, T.T., Wu, T.L., Ling, C.H. & Hsu, C.C. (Eds). 1923. *Doubutugaku-Daijiten* [= Zoological Encyclopedia]: 1–3, 1–110, 1–2, 1–2635, 1–7, 1–82, 1–135. [Commercial Press Ltd: China] [in Chinese].
- Türkay, M. 1975. Statement: Die Bedeutung des Gonopodenaufbaus für die Aufklärung von Verwandtschaftsverhältnissen bei Dekapoden Crustaceen. *Aufs. Red. senckenb. naturf. Ges.* 27: 114–115. Frankfurt a. M. (= University Doctoral dissertation).
1989. Subtropische und tropische Elemente in der Fauna des östlichen Mittelmeeres. *Natur und Museum* 119(6): 183–189, Abb.1–7.
- Türkay, M., Sakai, K. & Apel, M. 1996. The Ocypode ghost crabs (Crustacea: Decapoda: Brachyura) of the Arabian Peninsula and adjacent regions. *Fauna of Saudi Arabia* 15: 99–117, figs 1–12, pls 1–6.
- Turra, A.M., Goncalves, A.O. & Denadai, M.R. 2005. Spatial distribution of the ghost crab *Ocypode quadrata* in low-energy tide-dominated sandy beaches. *Journal of Natural History* 39(23): 2163–2177.
- Tweedie, M.W.F. 1937. The crabs of the Family Ocypodidae in the collection of the Raffles Museum. *Bulletin of the Raffles Museum, Singapore* 13: 140–170, figs 1–9.
1947. On the Brachyura of Christmas Island. *Bulletin of the Raffles Museum, Singapore* 18: 27–42, 1 fig.
- 1950a. The fauna of the Cocos-Keeling Islands. Brachyura and Stomatopoda. *Bulletin of the Raffles Museum, Singapore* 22: 105–148, figs 1–4, pls 16–17.
- 1950b. Notes on grapsoid crabs from the Raffles Museum. *Bulletin of the Raffles Museum, Singapore* 23: 310–324, fig. 1, pl. 7.
- Urita, T. 1917. Crabs from Kagoshima City and its surrounding area (1). *Rigakukai* 14(12): 67–73, figs [in Japanese].
- 1926a. On macrurous and brachyurous crustaceans around Tsingtao. *Zoological Magazine* 38(458): 421–438, 1 fig. [in Japanese].
- 1926b. A check-list of Brachyura found in Kagoshima Prefecture, Japan. *Tshingtao Times*: i–iii, 1–41, 1 map.
- Uschakov, P.V. 1970. Observations sur la répartition de la faune benthique du littoral Guinéen. *Cahiers de Biologie Marine* 11(4): 435–457, fig. 1–4.
- Valero-Pacheco, E., Alvarez, F., Abarca-Arenas, L.G. & Escobar, M. 2007. Population density and activity pattern of the ghost crab, *Ocypode quadrata*, in Veracruz, Mexico. *Crustaceana* 80(3): 313–325.
- Vallero-Pacheco, E., Alvarez, F., Escobar, M., Abarca-Arenas, L.G. & Arenas, V. 2004. Population density, distribution, and activity pattern of the ghost crab (*Ocypode quadrata*) in Montepio, Veracruz, Mexico. *Proceedings of the Gulf and Caribbean Fisheries Institute* 55: 466–475.
- Vannini, M. 1980. Notes on the behaviour of *Ocypode ryderi* Kingsley (Crustacea, Brachyura). *Marine Behaviour and Physiology* 7(2): 171–183, text-figs 1–4.
- Vannini, M. & Valmori, P. 1981. Researches on the coast of Somalia. The shore and the dune of Sar Uanle. 31. Ocypodidae and Gecarcinidae (Decapoda Brachyura). *Monitore Zoologico Italiano Supplemento* 14(14): 199–226.
- Veerannan, K.M. 1974. Respiratory metabolism of crabs from marine and estuarine habitats: an interspecific comparison. *Marine Biology, Berlin* 26(1): 35–43, tables 1–4, text-figs 1–2.
- Verrill, A.E. 1908. Decapod Crustacea of Bermuda. 1. Brachyura and Anomura. Their distribution, variations, and habits. *Transactions of the Connecticut Academy of Arts and Sciences* 13: 299–474, pls 9–28.
1908. Geographical distribution. Origin of the Bermudian decapod fauna. *American Naturalists* 42: 289–296.
- Vetter, R.-A. 1992. Mechanismen biochemischer Temperaturanpassung. Ein Vergleich der Enzymeigenschaften bei Crustaceen aus verschiedenen Klimazonen. *Berichte aus dem Institut fuer Meereskunde an der Christian-Albrechts Universitaet Kiel* 226: 5 + 93 pp., 9 tables, 25 text-figs.
- Via Boada, L. 1966. Abundantes restos de Ocypoda cursor (crustáceo decápodo) en el Cuaternario de Mallorca. *Acta geologica hispanica* 1: 22–24, 2 text-figs.
1980. Ocypodoidea (Crustacés Décapodes) du Cénozoïque Méditerranéen. Origine et evolution de cette superfamille. *Annales de Paléontologie (Invertébrés)* 66(1): 51–66, table 1, text-figs 1–2, pl. 1.
- Vieira, L. 1886. Crustaceos. In, Notícia acerca dos productos zoológicos trazidos da Ilha de S. Thomé para o Museu zoológico da Universidade de Coimbra, pelo Sr. Adolpho F. Moller, em 1855 (O Instituto, Coimbra (2) 34(5): 1886–1887: 235–241.
- Vilar de Araujo, C.C., de Melo Rosa, D. & Fernandes, J.M. 2008. Densidade e distribuicao espacial do caranguejo *Ocypode quadrata* (Fabricius, 1787) (Crustacea, Ocypodidae) em três praias arenosas do Espirito Sato, Brasil. *Biotemas* 21(4): 73–80, text-figs 1–5.

- Vilela, H. 1949. Crustáceos decápodos et estomatópodos da Guinéa Portuguesa. *Anais da Junta de Investigações Coloniais, Lisboa* 4(16): 47–70.
- Villamar, F. & Cruz, M. 2007. Macrofauna bentónica en la zona intermareal y submareal en Caleta Aeolian, Isla Baltra (Galapagos, Ecuador). *Acta Oceanográfica del Pacífico* 14: 139–145, table 1, text-figs 1–3.
- Voigt, F.S. 1836. In, Cuvier, B. von, *Das Thierreich, geordnet nach seiner Organisation: als Grundlage der Naturgeschichte der Thiere und Einleitung in die vergleichende Anatomie. Bd. 4, Die Anneliden, Crustaceen, Arachniden und die ungeflügelten Insekten enthaltend vom Baron von Cuvier; nach der zweiten, vermehrten Ausgabe übersetzt und durch Zusätze erweitert von F. S. Voigt* 4: i – xiv, 1–502.
- Voss, G.L. 1966. Narrative of the Cruises: The R/V Pillsbury Deep-Sea Biological Expedition to the Gulf of Guinea, 1964–65, 1. *Studies in Tropical Oceanography* 4(1): 1–60, figs 1–17 (Miami).
- Voultsiadou, E. & Vafidis, D. 2007. Marine invertebrate diversity in Aristotle's zoology. *Contributions to Zoology* 76(2): 103–120, table 1, text-figs 1–4.
- Wada, T. 2009. Distribution of the ghost crab *Ocypode stimpsoni* (Crustacea: Brachyura: Ocypodidae) on the sandy beaches of Tottori Prefecture, Honshu, Japan. *Bulletin of the Tottori Prefectural Museum* 46: 1–7, text-figs 1–4.
- Walker, A.O. 1890. Notes on a Collection of Crustacea from Singapore. *Journal of the Linnean Society of London, Zoology* 20(118): 107–117, pls 6–9.
- Wang, C.-H. & Liu, H.-C. 1996. Common seashore crabs of Taiwan. *Taiwan Museum*: 1–138.
1998. *Common Seashore Crabs of Taiwan*. Taiwan Museum (Second edition): 1–136. [in Chinese].
- Warburg, M.R. & Shuchman, E. 1979. Experimental studies on burrowing of *Ocypode cursor* (L.) (Crustacea; Ocypodidae), in response to sand-moisture. *Marine and Freshwater Behaviour and Physiology* 6(2): 147–156, tabs. 1–4, figs 1–5.
- Weber, F. 1795. Nomenclator entomologicus secundum entomologiam systematicam ill. Fabricii adjectis speciebus recens detectis et varietatibus. Pp. i–viii, 1–172. (Chilonii and Hamburgi).
- Weinstein, R.B. & Full, R.J. 2000. Intermittent locomotor behaviour alters total work. In P. Domenici and R. W. Blake [Eds], *Biomechanics in animal behaviour*: 33–48 pp. (BIOS Scientific: Oxford).
- White, A. 1847. List of the specimens of Decapoda Crustacea in the collection of the British Museum. London. *Trustees of British Museum*: i–viii, 1–143.
- Whiteley, N.M., Innes, A.J., Al-Wassia, A.H. & Taylor, E.W. 1990. Aerial and aquatic respiration in the ghost crab, *Ocypode saratan* 2. Respiratory gas exchange and transport in the haemolymph. *Marine Behaviour and Physiology* 16(4): 261–273.
- Williams, A.B. 1965. Marine decapod crustaceans of the Carolinas. *Fishery bulletin. United States Fish and Wildlife Service* 65(1): i– xi, 1–298, fig. 1–252.
1984. *Shrimps, lobsters and crabs of the Atlantic coast of the eastern United States, Maine to Florida*. (Smithsonian Institution Press, Washington, D.C.). 550 pp.
- Wolcott, T.G. 1978. Ecological rôle of ghost crabs, *Ocypode quadrata* (Fabricius) on an ocean beach: scavengers or predators? *Journal of Experimental Marine Biology and Ecology* 31(1): 67–82.
- Wong, K.J.H., Shih, H.-T. & Chan, B.K.K. 2012. The ghost crab *Ocypode mortoni* George, 1982 (Crustacea: Decapoda: Ocypodidae): redescription, distribution at its type locality, and the phylogeny of East Asian *Ocypode* species. *Zootaxa* 3550: 71–87.
- Yang, S.-L. 1986. The diagnostic value of gastric mills, construction as taxonomic character on the classification of crabs (Brachyura: Crustacea). *Acta Zootaxonomica Sinica* 11: 151–159.
- Yodo, S., Watanabe, T., Nakanishi, Y., Sakano, M., Kimura, S., Nomoto, A. & Wada, K. 2006. Distribution of three species of the genus *Ocypode* (Crustacea: Brachyura: Ocypodidae) in Wakayama, Middle Japan in 2000–2003. *Japanese Journal of Benthology* 61: 2–7, text-figs 1–6.
- Yousuf, F., Ali, F. & Kazmi, Q.B. 2007. Some ghost crabs of the genus *Ocypode* (Decapoda: Brachyura: Ocypodidae) from Pakistan's waters (northern Arabian sea). *Turkish Journal of Zoology* 31(2): 107–112, text-figs 1–8.
- Yu, H.-P., Jeng, M.-S., Chan, T.-Y., Ho P.-H. & Shy, J.-Y. 1996. *Studies on the land and aquatic decapod crustacean fauna of the Kenting National Park*. ii + 79 pp. (Ministry of the Interior, Taipei) [in Chinese with English abstract].
- Zehntner, L. 1894. Crustacés de l'Archipel Malais. Voyage de MM. M. Bedot et Ch. Pictet dans l'Archipel Malais. In, *Revue suisse de Zoologie et Annales du Musée d'Histoire Naturelle de Genève* 2: 135–214, pls 7–9.
- Ziese, M. 1985. Weitere Nachweise der Reiterkrabbe *Ocypode cursor* (Linnaeus 1758) im östlichen Mittelmeer (Crustacea: Decapoda: Ocypodidae). *Senckenbergiana biologica* 66 (1–3): 123–125, map 1.

A new species of *Hepthopelta* Alcock, 1899 (Crustacea: Brachyura: Chasmocarcinidae) from deep water off north-eastern Queensland, Australia

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ABSTRACT

A new species of deep water chasmocarcinid, *Hepthopelta potens*, is described from off north-eastern Queensland. It differs from its congeners by a combination of characters, including carapace shape and proportions, the structure of the abdomen and gonopods, and most obviously by the greatly swollen major chela of adult males. □ Crustacea, Brachyura, Chasmocarcinidae, deep water, Indo-West Pacific, new species.

In the late 1980s and early 1990s several cruises were undertaken off northern Queensland investigating deep water faunal community composition and biodiversity. The R.V. *Franklin*, under the direction of Professor Michel Pichon, carried out three cruises, (CIDARIS I–III), and employed beam trawls, Charcot dredges and sledges on the continental slope of the Great Barrier Reef and the Queensland basin (Alongi 1987; Pichon 1987; Richer de Forges 1986). In addition, the CSIRO conducted exploratory deep water trawling off north-eastern Queensland during December 1985 and January 1986, using the stern trawler R.V. *Soela* under the direction of Trevor Ward. Large collections of crustaceans were made during all these cruises and returned to the Queensland Museum. Amongst a number of new species that have been found, is an interesting new species of *Hepthopelta* Alcock, 1899 (family Chasmocarcinidae), and this is described here.

Abbreviations: QM, Queensland Museum, Brisbane; ZRC, Zoological Reference Collection of the Raffles Museum of Biodiversity Research, National University of Singapore. cb, carapace breadth; cl, carapace length; G1, G2, male first and second gonopods.

TAXONOMY

CHASMOCARCINIDAE Serène, 1964
CHASMOCARCININAE Serène, 1964

Hepthopelta Alcock, 1899

Hepthopelta Alcock, 1899: 76–77; 1900: 327; Rathbun, 1914: 149; Tesch, 1918: 232–233; Balss, 1957: 1.658; Serène, 1964: 239–242; Ng, Guinot & Davie, 2008: 76 (in list). [Synonymy not exhaustive].

Type species: *Hepthopelta lugubris* Alcock, 1899, by monotypy; gender feminine) [ICZN Opinion 85, Direction 37].

Hepthopelta potens sp. nov. (Figs 1–4)

Material examined. HOLOTYPE: QM-W16974, ♂ (12.7×10.3 mm), off Tully Heads, 17°59' 02" S, 147°03'01" E, trawled, 260 m, CSIRO, R.V. *Soela*, 13.01.1986. PARATYPES: QM-W16999, ♀ (13.1×10.5 mm), off Yeppoon, 22°56'01"S, 152°41'04"E, trawl, 225–282 m, CSIRO, R.V. *Soela*, 19.11.1985. QM-W17046, ♀ (7.1×6.2 mm), off Babinda, 17° 21' 8" S, 146° 48' 5" E, epibenthic sled, 296–302 m, F.R.V. *Franklin*, 15.5.1986. QM-W17047, ♀ (11.9×9.7 mm), off Tully Heads, 17° 59'09"S, 147°02'09"E, trawl, 250–252 m, CSIRO, R.V. *Soela*, 29.11.1985. QM-W17048, ♀ (7.6×6.6 mm), off Mission Beach, 17°54'03"S, 146°55'07"E, trawl, 212 m, CSIRO, R.V. *Soela*, 09.12.1985. QM-W17049, ♂

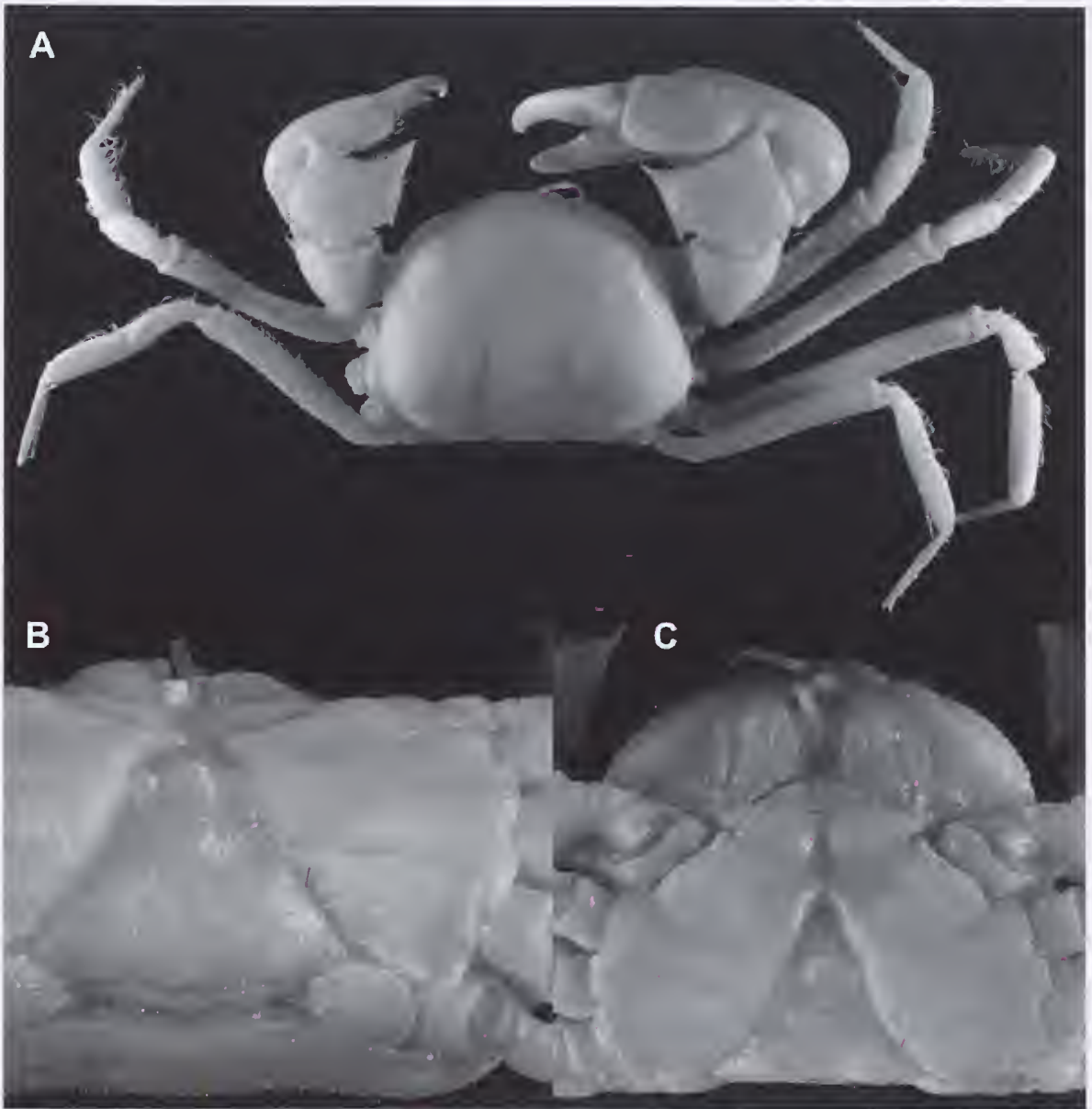


FIG. 1. *Hephthopelta potens* sp. nov., QM-W16974, holotype male (12.7×10.3 mm). A, Dorsal view of crab; B, sternal plastron and abdomen in postero-ventral view; C, sternal plastron and abdomen in ventral view.

(11.0×9.2 mm), off Tully Heads, 18°07'S, 147°02'02"E, trawl, 220 m, CSIRO, R.V. *Soela*, 18.01.1986. QM-W17050, 2 ♀♀ (8.2×7.1, 8.5×7.3 mm), off Tully Heads, 18°02'S, 147°01'06"E, trawl, 220–222 m, CSIRO, R.V. *Soela*, 12.01.1986. QM-W17051, ♂ (11.1×9.1 mm), off Tully Heads, 18°01'S, 147°01'03"E, trawl, 224–228 m, CSIRO, R.V. *Soela*, 09.01.1986.

Description. Carapace (Fig. 1A) semicircular, about 1.2–1.25 times broader than long in adults. Posterior margin costate, broad, very slightly

sinuous in dorsal view, but noticeably concave in posterior view. Carapace broadest at point between coxae of second and third walking legs. Anterolateral and posterolateral borders not distinctly separated, nor demarcated from lateral carapace walls, surface of carapace finely granular laterally, with moderately long setae, particularly anteriorly. Front-orbital width c. 1.9–2.3 times maximum carapace width;

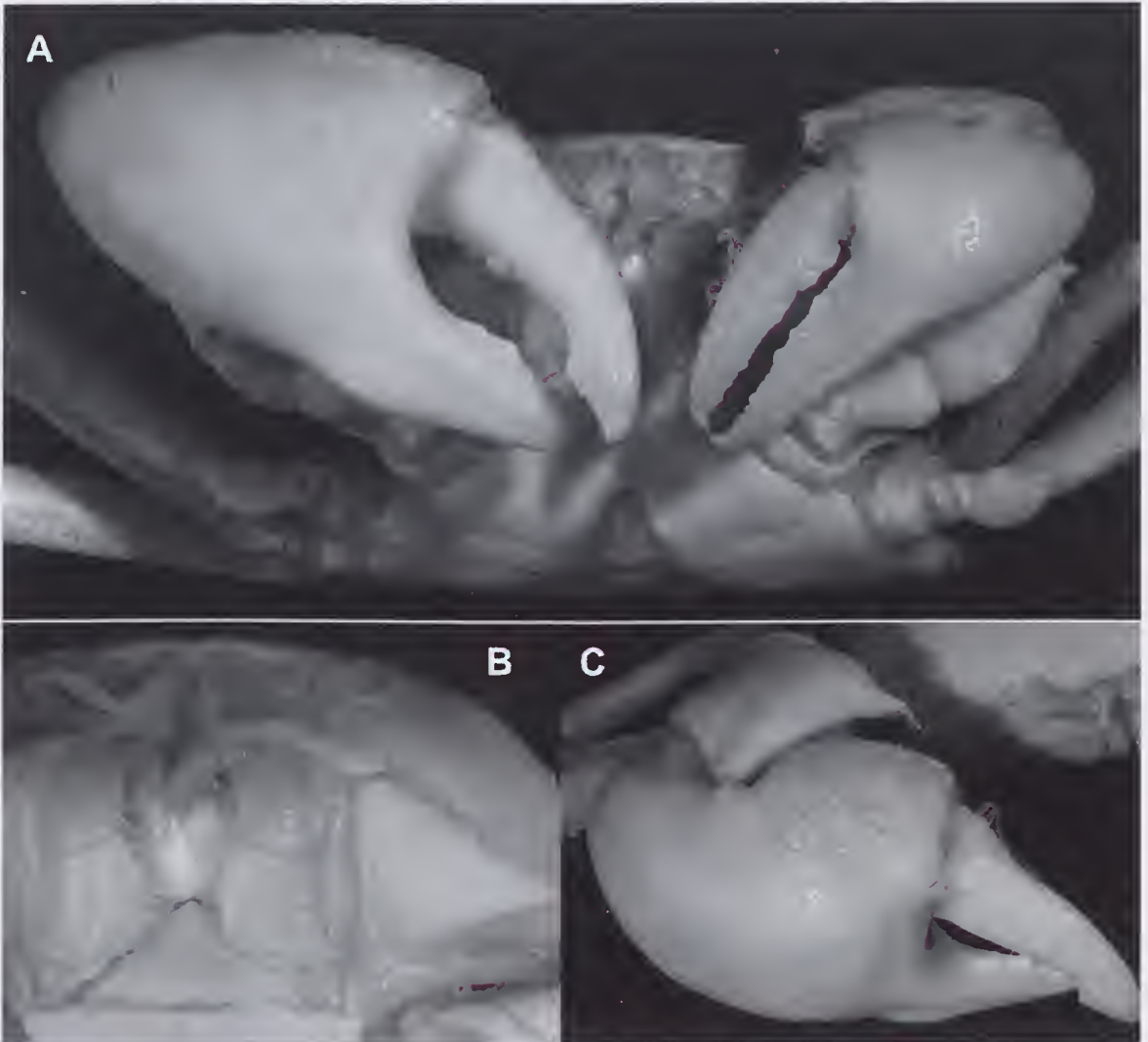


FIG. 2. *Hephthopelta potens* sp. nov., QM-W16974, holotype male (12.7×10.3 mm). A, chelipeds in frontal view; B, third maxillipeds and pterygostome; C, major right chela in antero-dorsal view.

orbits with lateral raised rim, superior inner orbital margin obtusely rounded, infra-orbital margin obliquely sloping with inner tooth developed; frontal margin appearing straight in dorsal view but tri-lobed in frontal view, median lobe smaller than lateral lobes. Eystalk short, moveable, broadest in distal half; cornea darkly pigmented. Dorsal carapace regions poorly defined; gastric, cardiac, and intestinal grooves faintly indicated; posterior branchial groove continues onto lateral carapace walls.

Basal antennular segment globose; completely fills antennular fossa excluding flagellum. Basal

antennal segment slightly longer than wide; does not make contact with front; flagellum lies within orbit, about as long as width of front.

Third maxilliped (Fig. 2B) with ischium slightly longer than wide; merus about as long as at widest point; palp inserted at antero-distal angle; exopod not quite reaching anterior border of merus. Pterygostomian (Fig. 2B) granular at junction with hepatic region; posteriorly with strongly produced crest above broad deep triangular sulcus expanded posteriorly. Male sternal plastron (Fig. 1B, C) broad, oval; sternite eight (Fig. 1B) with distinct broad anterior



FIG. 3. *Hephthopelta potens* sp. nov., QM-W16974, holotype male (12.7×10.3 mm); antero-dorsal view of frontal margin, orbits and pterygostome.

supplementary plate, reaching from base of coxa of legs to sternoabdominal cavity.

Chelipeds (Figs 1A, 2A, C) unequal in males. Merus of larger cheliped relatively short, triangular, with convex posterior face; rounded, unarmed on inner margin but with 3 or 4 spines on outer margin which increase in size distally. Carpus subquadrate in dorsal view, with strong acute spine at inner distal angle; smaller sharp spine, at slightly lower level, at inner proximal angle. Propodus very swollen, especially forming proximal protruding 'elbow', height about half length (including fixed finger) or slightly less; outer face convex; upper surface granular; similar raised, slightly granular patch behind gape on outer surface; fingers pointed, armed with blunt low molariform teeth; in adult males large gape left when fingers closed. Smaller cheliped (Fig. 2A) of similar form but less massive; with flatter fingers armed with sharper teeth; without gape when closed. Female chelipeds less massive, similar to minor cheliped of male.

Walking legs (Fig. 1A) relatively long, slender, unarmed. Second and third very similar, third slightly longer; fourth pair smallest. Total length of third leg twice maximum width of carapace; merus c. 6.6 times longer than wide; dactyl almost straight, acutely pointed, about three-quarters length of propodus. All legs fringed in setae, thicker and longer on distal segments.

Male abdomen (Fig. 4E) with somites 3–5 fused; widest at laterally bulbous somite three, then tapering evenly to rounded telson; somites one and two constricted, narrow, of similar width; telson c. 0.8 times as long as wide at base.

First male gonopod (Fig. 4A, B) very broad, short, tapering to simple pointed tip. G2 (Fig. 4C, D) slender, slightly longer than G1; terminal half of curved flagellum bent at strong angle; flagellum about two-thirds length of basal portion.

Remarks. There are currently ten species recognised within *Hephthopelta* (see Ng *et al.* 2008), viz. *H. apta* Rathbun, 1914; *H. aurita* Rathbun,

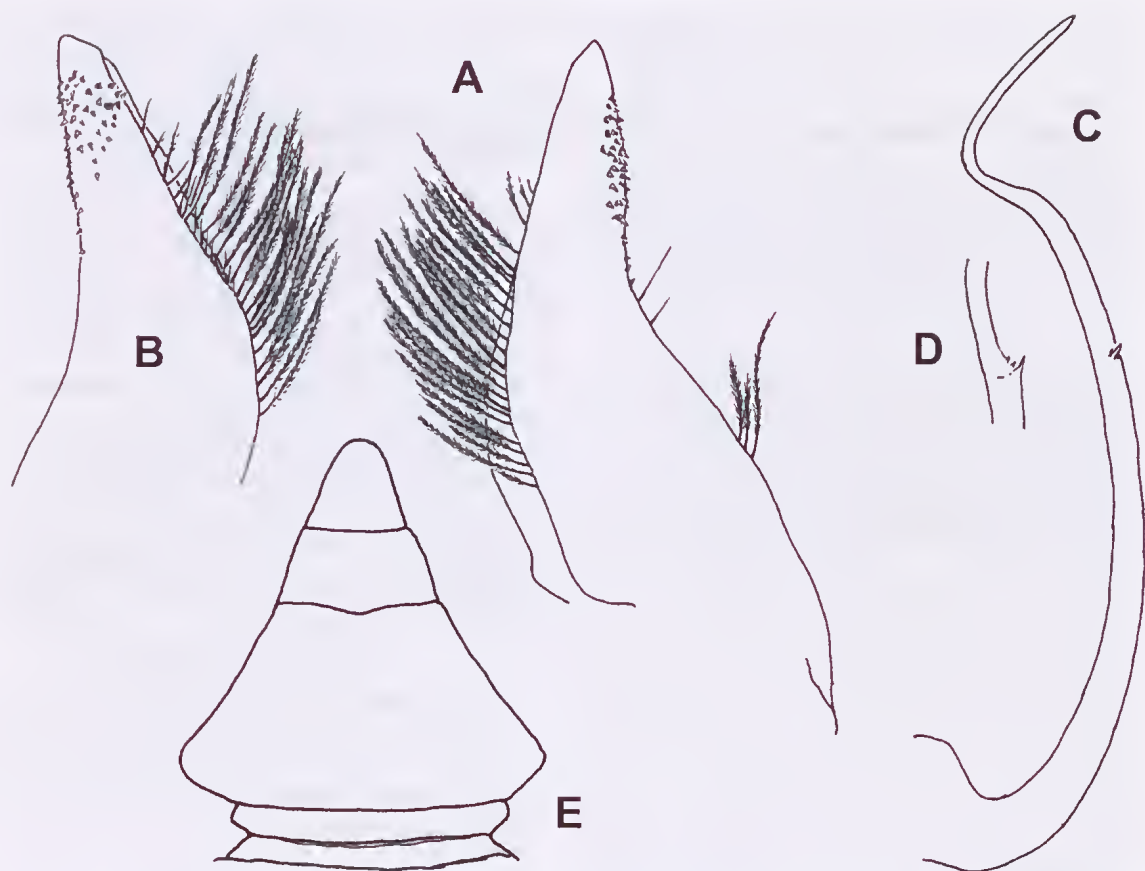


FIG. 4. *Hephthopelta potens* sp. nov., QM-W16974, holotype male (12.7×10.3 mm). A, B, G1 in abdominal and sternal views; C, G2; D, different view of base of palp of G2; E, abdomen. Gonopods 1 & 2 are drawn to the same scale relative to each other.

1932; *H. bruuni* Serène, 1964; *H. cavimana* (Rathbun, 1914); *H. cribrorum* Rathbun, 1932; *H. knudseni* Serène, 1964; *H. littoralis* Tesch, 1918; *H. lugubris* Alcock, 1899; *H. mortenseni* Serène, 1964; and *H. pubescens* Chen, 1998.

Hephthopelta potens sp. nov., by its carapace proportions (cb: cl = 1.15–1.25), is closest to the group including *H. bruuni* (cb: cl = 1.23), *H. apta* (1.21), *H. cribrorum* (1.26), *H. cavimannus* (1.24) and *H. aurita* (1.16) (proportions derived from the type descriptions). *Hephthopelta aurita* Rathbun, 1932, is immediately separable by its large anterolateral spines. *Hephthopelta apta* Rathbun, 1914, differs from other species by having the eyestalks moderately constricted next to the cornea, and in having the pigment spot of the cornea small and dull coloured. It differs partic-

ularly from the present species by the lack of spines on the outer border of the merus of the cheliped.

The male holotype of *Hephthopelta cribrorum* Rathbun, 1932, was supposedly figured by Sakai (1976, text-fig. 298a, b) and is clearly different from the present species in many characters including overall shape, shape of the carpus of the chelipeds, and shape of the front and orbits. However, P.K.L. Ng and P. Castro (*in litt.*) have also examined the type housed in the USNM in Washington, and in their opinion, 'Sakai's figure either shows another species or is a very very young specimen. His figure does not look like the types'. However, from the pictures they supplied me of the holotype, and of another specimen they have from Vanuatu, it

is clear that the above differences in carapace and chela shape still hold true. *Hephthopelta criborum* will be redescribed and discussed as part of the Castro and Ng revision which is currently being undertaken.

Hephthopelta cavimanus (Rathbun 1914) is separable from all other species, including the present one, by the presence on the inside of the palm of the minor cheliped of the male, of a large blunt compressed tooth which fits into a sinus on the inner margin of the arm.

Hephthopelta bruuni Serène, 1964, appears to be the closest relative of the present species. It is only known from the single female type specimen (5×4 mm) from Vietnam, but it can be easily distinguished from *H. potens* sp. nov. by the following differences. 1) The breadth to length ratio of *H. bruuni* is given by Serène (1964) as 1.25; our smallest specimen (~7.1×6.2 mm) is considerably larger than the holotype of *H. bruuni* but relatively narrower with a ratio of 1.15; while our larger specimens (<11 mm c.b.) vary from 1.2–1.25 broader than long. 2) The ratio of fronto-orbital width to carapace width in *H. bruuni* is c. 1.56 whereas in our new species it is approximately twice (1.9–2.26 times). 3) The orbit is relatively wider in relation to the front in *H. bruuni* with the ocular peduncles longer and more obvious dorsally. The lateral edges of the front also meet the supraorbital at an angle whereas in *H. potens* sp. nov., the orbit meets the front in an even curve (Figs 1A, 3). 4) The merus of the third maxilliped is comparatively quadrate in *H. potens*, with its basal width being equal to the anterior width of the ischium (Fig. 2B), whereas in *H. bruuni* it is constricted at the base.

Of the other species currently referred to the genus, *Hephthopelta lugubris* is proportionately narrower, being about as broad as long, but is also readily distinguished from all other species by the spinulose posterior borders of the meri of its first two pairs of walking legs. However, *Hephthopelta* aff. *lugubris* of Komai *et al.* (2012: fig. 7) does appear very similar to *H. potens* sp. nov., but although it was not described by Komai *et al.* in their paper, it clearly has much longer legs than *H. potens* sp. nov., and lacks the characteristic chela shape of our new species. Peter Ng and Peter Castro (pers. comm.) are

currently revising *Hephthopelta* and will split it into several genera. As part of this work *H. aff. lugubris* of Komai *et al.* (2012), will be described as a new, along with a second new species, and it appears likely that our *H. potens* sp. nov. will be included with them in a new genus.

Hephthopelta mortensi, *H. littoralis*, *H. knudseni* and *H. pubescens* are all much broader than long (1.5 times), as well as each differing from *H. potens* sp. nov. in numerous other characters. They have no close affinities with *H. potens*, and thus further comparisons are deemed unnecessary, especially in the light of the Castro and Ng revision currently in progress.

Etymology. The specific name *potens* is Latin for powerful and refers to the markedly swollen claw.

Distribution. Only known from off north-east Queensland, Australia. Bathymetric range: 212–302 m.

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LITERATURE CITED

- Alcock, A. 1899. An account of the deep-sea Brachyura collected by the Indian Marine Survey Ship Investigator. Trustees of the Indian Museum, Calcutta. i-iv + 1-85 pp., Pls I-IV.
1900. Materials for a carcinological fauna of India. No. 6. The Brachyura Catometopa or Grapsoidea. *Journal of the Asiatic Society of Bengal, Calcutta* 69(3): 279–486.
- Alongi, D.M. 1987. The distribution and composition of deep sea microbenthos in a bathyal region of the western Coral Sea. *Deep Sea Research* 34(7): 1245–1254.
- Balss, H. 1957. Decapoda. VIII. Systematik. In: *Dr. H. G. Bronns, Klassen und Ordnungen des Tierreichs*. Leipzig and Heidelberg, Winter. Fünfter Band, I. Abteilung, 7. Buch, 12. Lief.: 1505–1672, figs. 1131–1199.
- Chen, H.-L. 1998. The Goneplacidae (Crustacea: Brachyura) from Nansha Islands and adjacent waters. Pp. 265–316. In: *Studies on Marine Fauna and Flora and Biogeography of the Nansha Islands and*

- Neighbouring Waters* 3. (Academia Sinica: Beijing). [in Chinese with English abstract].
- ICZN, International Commission on Zoological Nomenclature. 1925. Opinion 85. Ninety-five Names in Crustacea placed on the Official Lists of Generic Names. *Smithsonian Miscellaneous Collections* 73(3): 13–18.
- Komai, T., Ng, P.K.L. & Yamada, Y. 2012. A new genus and new species of chasmocarcinid crab (Decapoda, Brachyura, Goneplacoidea) from shallow waters in Japan. In, *Studies on Eumalacostraca: a homage to Takeda Masatsune*. Komatsu, H., Okuno, J. & Fukuoka, K. (Eds). *Crustaceana Monographs, Leiden* 17: 137–154.
- Ng, P.K.L., Guinot, D. & Davie, P.J.F. 2008. Systema Brachyurorum: Part I. An annotated checklist of extant brachyuran crabs of the world. *Raffles Bulletin of Zoology (Supplement)* 17: 1–286.
- Pichon, M. 1987. Deep sea floor fauna samples off North Qld. *AIMS paper*. 1 p.
- Rathbun, M.J. 1914. A new genus and some new species of crabs of the family Goneplacidae. *Scientific Results of the Philippine cruise of the Fisheries Steamer "Albatross," 1907–1910*. No. 32. *Proceedings of the United States National Museum* 48(2067): 137–154.
1932. Preliminary descriptions of new species of Japanese crabs. *Proceedings of the Biological Society of Washington* 45: 29–38.
- Richer de Forges, B. 1986. Mission en Australie du 3 au 25 mai 1986. *Rapport ORSTOM*. 9 pp., 2 maps
- Sakai, T. 1976. *Crabs of Japan and the Adjacent Seas*. In three volumes; English Text, pp. xxix + 773 pp., Japanese Text, pp. 1–461, Plates volume, pp. 1–16, pls. 1–251. (Kodansha Ltd.: Tokyo).
- Serène, R. 1964. Goneplacidae et Pinnotheridae récoltés par le Dr. Mortensen. Papers from Dr. Th. Mortensen's Pacific Expedition 1914–1916, part 80. *Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening i København* 126: 181–282, pls. 16–24.
- Tesch, J.J. 1918. Decapoda Brachyura II. Goneplacidae and Pinnotheridae. *Siboga Expeditie Monographie* 39c1: 149–295, pls 7–18.

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