*RAFFLES BULLETIN OF ZOOLOGY* **68**: 891–994
Date of publication: 23 December 2020
DOI: 10.26107/RBZ-2020-0097
http://zoobank.org/urn:lsid:zoobank.org:pub:815E4670-B063-4FD8-B31E-3AD89B3A7942

# Revision of the intertidal and semiterrestrial crab genera *Chiromantes* Gistel, 1848, and *Pseudosesarma* Serène & Soh, 1970 (Crustacea: Brachyura: Sesarmidae), using morphology and molecular phylogenetics, with the establishment of nine new genera and two new species

Christoph D. Schubart[1] & Peter K. L. Ng[2*]

**Abstract.** The phylogeny of two heterogeneous Indo-West Pacific and African sesarmid genera, *Chiromantes* Gistel, 1848, and *Pseudosesarma* Serène & Soh, 1970, is investigated using morphological and molecular methods. The two genera look superficially very similar, lack stridulatory ridges and tubercles on the chela, and have previously been separated by the presence or absence of an epibranchial tooth on the lateral margin of the carapace. Related members of *Bresedium* Serène & Soh, 1970, *Sesarmops* Serène & Soh, 1970, and allied genera are included in this revision. The analyses reveal a complex evolutionary history with numerous monophyletic clades supported by consistent morphological apomorphies. These clades are here described as nine new genera for which diagnoses are given and the constituent species described, figured, and compared. Two new species of a new genus are also described from Indonesian Papua and Papua New Guinea. This revision is a major step in the process of establishing a taxonomic system taking into account monophyletic units within the Sesarmidae.

**Key words.** Sesarmidae, intertidal, freshwater, systematics, genetics, morphology, revision

## TABLE OF CONTENTS

---

*Accepted by: Jose Christopher E. Mendoza*

[1] Zoology & Evolution, University of Regensburg, 93040 Regensburg, Germany; Email: christoph.schubart@ur.de

[2] Lee Kong Chian Natural History Museum, Faculty of Science, National University of Singapore, 2 Conservatory Drive, Singapore 117377, Republic of Singapore; Email: peterng@nus.edu.sg (*corresponding author)

ISSN 2345-7600 (electronic) | ISSN 0217-2445 (print)

## INTRODUCTION

The Sesarmidae Dana, 1851, is the most diverse crab family of the marine inter- and supratidal zones. Its members are especially common in tropical and subtropical areas, where they are mostly found in vegetated soft-sediment habitats like mangroves, marshes, and estuaries. Several lineages have also invaded successfully and independently into freshwater and terrestrial habitats, most often accompanied by an abbreviation or reduction of larval development. As such, the Sesarmidae constitute a good case study to investigate recent to current colonisation of land and the corresponding adaptations to a secondary terrestrial or freshwater lifestyle (see Schubart et al., 1998, 2000a).

The Sesarmidae was elevated to full family level and redefined by Schubart et al. (2000a, 2002), Ng et al. (2008a), and Shahdadi & Schubart (2017). It currently consists of 35 genera with 314 recognised species (updated from Ng et al., 2008a). The generic composition of the group has undergone dramatic changes over the last 40 years. Until Serène & Soh (1970), the bulk of species were all included in one genus, *Sesarma* Say, 1817 with four subgenera. Their landmark paper introduced a major new generic system that was designed to bring some taxonomic order to the group. Since then, numerous additional genera have been established. Sesarmidae is primarily an Indo-West Pacific family, with only seven genera (*Aratus* H. Milne Edwards, 1853, *Armases* Abele, 1992, *Chiromantes* Gistel, 1848, *Guinearma* Shahdadi & Schubart, 2017, *Metagrapsus* H. Milne Edwards, 1853, *Metopaulias* Rathbun, 1896, *Sesarma* Say, 1817), and less than 40 species known from the Atlantic Ocean and East Pacific (Abele, 1992). After the revision of Serène & Soh (1970), *Sesarma* was restricted to the Americas, so *Chiromantes* Gistel, 1848 (= *Holometopus* H. Milne Edwards, 1853, previous to clarification by Holthuis, 1977) and *Perisesarma* De Man, 1895 (= *Chiromantes* previous to Holthuis, 1977) were the only genera to include Atlantic as well as Indo-West Pacific species. Abele (1992) established *Armases* for all the American and one West African species formerly classified under *Chiromantes*. With this action, the presence of *Chiromantes* in the Atlantic was restricted to two West African species, viz. *C. angolensis* (Brito Capello, 1864) and *C. buettikoferi* (De Man, 1883). Recently, the revision and re-definition of *Perisesarma* and *Parasesarma* De Man, 1895 by Shahdadi & Schubart (2017) led to the transfer of the three African representatives, *Perisesarma alberti* (Rathbun, 1921), *P. huzardi* (Desmarest, 1825), and *P. kamermani* (De Man, 1883) to their own genus, *Guinearma*, as a sister taxon to the exclusively West African *Metagrapsus*

H. Milne Edwards, 1853. Since then, *Chiromantes* remained as the only sesarmid genus occurring in Atlantic and Indo-Pacific waters.

A pivotal key character for earlier classifications had been the presence or absence of an anterolateral (epibranchial) carapace tooth (see Serène & Soh, 1970). There is, however, increasing evidence that the presence of this epibranchial tooth has minimal phylogenetic value. Already in 1978, von Hagen noted that the American species *Sesarma rectum* should be classified within the subgenus *Sesarma* and not *Holometopus* (= *Armases* Abele, 1992), despite the absence of such an epibranchial tooth. Early molecular phylogenies by Fratini et al. (2005) and Schubart et al. (2006) revealed that the genera *Perisesarma* (until then including species with epibranchial teeth) and *Parasesarma* (without such teeth) did not represent monophyletic units, resulting in the taxonomic revisions by Shahdadi & Schubart (2017) and Shahdadi et al. (2020). In the present paper, the taxonomy of *Chiromantes* is revised based on a combination of morphological and molecular characters. In doing so, it became necessary to include *Pseudosesarma* Serène & Soh, 1970, in the revision, and partially treat some of the species now in *Sesarmops* Serène & Soh, 1970. We have also looked at most of the species now referred to *Bresedium* Serène & Soh, 1970, and *Stelgistra* Ng & Liu, 1999. As a result of this revision, the taxa previously classified in *Chiromantes* and *Pseudosesarma* are reorganised and now referred to 12 genera, nine of which are new. Two species of *Sesarmops* are also transferred to one of these new genera.

There are still many systematic problems and uncertainties associated with the Indo-West Pacific Sesarmidae. At the generic level, despite the substantial changes brought on by Serène & Soh's (1970) system, many of the genera and even species remain heterogeneous. The number of species in *Parasesarma* and the recently described *Leptarma* Shahdadi, Fratini & Schubart, 2020, continues to grow as new areas are explored and more pseudocryptic taxa uncovered (see Davie & Pabriks, 2010; Shahdadi & Schubart, 2017; Shahdadi et al., 2017, 2018a, b; Li et al., 2018, 2019a; Shih et al., 2019; Ng & Devi, 2020). The same is true for *Geosesarma* De Man, 1892, which currently includes over 50 species and awaits a systematic revision. Naruse & Ng (2020) reappraised what is today called *Labuanium* Serène & Soh (1970) (with 13 species) and showed that the species should be separated into six genera, three of which are new to science. There is clear polyphyly in *Sesarmops* and *Bresedium*, and the limits of these genera are unclear (Li et al., 2020; Ng et al., 2020; see also discussion later). In addition, there are several species-complexes like those in *Chiromantes dehaani* and *C. haematocheir* that will need more material from additional areas to better understand of how many species they consist. Ideally, all these generic and species problems should be resolved in one revision, as the connections among some of these genera are obvious. Such a comprehensive exercise, however, will simply take too much time; for example, the present revision has taken almost 20 years. We thus believe that a revised system for *Chiromantes* and *Pseudosesarma* needs to be published first. This is especially important, since many of the comprised taxa are common intertidal species and the names will need to be used for a host of systematic, phylogenetic, genomic, faunistic, biogeographical, and ecological studies being undertaken with sesarmids in Asia and Africa.

## MATERIAL AND METHODS

We have used a large suite of characters in this study, and in general the terminology follows that in Davie et al. (2015). The use of the female gonopores (vulvae) in addition to the standard study of male gonopods has proven useful, because many of the recognised generic groups have distinct vulva types. The nomenclature of the vulvar features follows Guinot et al. (2013). The structure of the male pleonal locking mechanism on the sternopleonal cavity is also a useful character to differentiate some groups (see Guinot & Bouchard, 1998). The abbreviations G1 and G2 are used for the male first and second pleopods, respectively. Measurements provided, in millimetres, are of the maximum carapace width and length, respectively.

Specimens examined are deposited in Natural History Museum and Institute, Chiba (CBM); Cochin University of Science & Technology, Kerala, India (CUSAT); Naturhistorisches Museum Basel, Switzerland (NMBA); Muséum national d'Histoire naturelle, Paris, France (MNHN); Muséum national d'Histoire naturelle, Geneva, Switzerland (MNHG); Museo Zoologico Universitá di Firenze, Italy (MZUF); The Natural History Museum, London (previously British Museum (Natural History)) (NHM); National Museum of Marine Biology and Aquarium, Checheng, Pingtung, Taiwan (NMMBA); Naturhistorisches Museum, Wien, Austria (NHMW); National Museum of Natural Science, Taichung, Taiwan (NMNS); Osaka Museum of Natural History, Osaka, Japan (OMNH); Queensland Museum, Brisbane, Australia (QM); Nationaal Natuurhistorisch Museum – Naturalis, Leiden, The Netherlands (previously Rijksmuseum van Natuurlijke Historie, RMNH); Ryukyu University Museum, Fujukan, Okinawa, Japan (RUMF); Senckenberg Museum und Forschungsinstitut, Frankfurt am Main (SMF); Wakayama Prefectural Museum of Natural History, Wakayama, Japan (WMNH); Florida Museum of Natural History, USA (UF-FLMNH); University of Louisiana Zoological Collection, Lafayette, USA (ULLZ); Zoological Reference Collection of the Lee Kong Chian Natural History Museum (previously Raffles Museum of Biodiversity Research), National University of Singapore (ZRC); and Zoological Collections of the University of Tehran, Iran (ZUTC).

The specimens used for the genetic work originate from field work in Singapore, Malaysia, Thailand, Indonesia, Philippines, and Taiwan between 1999 and 2017, as well as from alcohol-preserved material in the ZRC, SMF, NHMW and RMNH, resulting in a total of 56 new sesarmid samples to be used for DNA analyses. In addition, available sequences from GenBank were incorporated, including the correspoding DNA regions of the complete mitochondrial genomes of

*Chiromantes haematocheir* NC_047209 (as *C. eulimene*), *C. dehaani* NC_041212, *C. neglectus* NC_031851 (as *Sesarma neglectum*), *Sesarmops sinensis* NC_030196 and NC_042142 (the second as *Chiromantes haematocheir*), *Parasesarma tripectinis* NC_030046, *Parasesarma affine* NC_039990, and *Parasesarma pictum* NC_038066. Samples collected in the field were killed on ice or in a freezer, preserved in 100% ethanol, after one of the ambulatory legs of the specimen was removed or punctured with a sterile needle to ensure fast penetration of the ethanol.

Genomic DNA was isolated using the Puregene method (Gentra Systems, Minneapolis). We used an approximately 1,250 basepair (bp) region, including the following contiguous mitochondrial genes: the 16S rRNA gene (16S), the tRNA Leucine, and part of the protein coding gene NADH1 (ND1). The following primers were used to obtain the target DNA fragment by combining two PCR products: 16L29 (5'-YGCCTGTTTATCAAAAACAT-3') with 16H37 (5'-CCGGTYTGAACTCAAATCATGT-3), 16H11 (5'-AGATGAAACCRACCTGG-3'), 16H10 (5'-AATCCTTTCGTACTAAA-3') or 16HLeu (5'-CATATTATCTGCCAAAATAG-3') and 16L6 (5'-TTGCGACCTCGATGTTGAAT-3') or 16L37 (5'-TTACATGATTTGAGTTCARACCGG-3') with NDH5 (5'-GCYAAYCTWACTTCATAWGAAAT-3') (summarised in Schubart, 2009).

The PCR profile consisted of 40 cycles with 45 seconds at 94°C, 1 minute at 48–50°C, and 1 minute at 72°C, for denaturing, annealing, and extension, respectively. PCR products were purified with the Quick-Clean kit (Bioline), cycle sequenced with the Big Dye Terminator v. 1.1 (AB Applied Biosystems), and analysed with an automated capillary DNA sequencer ABI PRISM® 310 Genetic Analyzer (Applied Biosystems) or outsourced to Macrogen Europe. Several 16S rDNA sequences originate from previous studies (e.g., Schubart et al., 2000a, 2002).

The final dataset consisted of 93 sequences and an alignment of 1,239 bp, corresponding to the contiguous DNA region comprising parts of two (16S, ND1) mitochondrial genes and one complete one (tRNA Leu) (see Discussion). In the case of the coding gene ND1, the third positions were removed from the final analyses, as they showed signs of saturation (often resulting in back mutations or homoplasy), when comparing clades that split at the base of the tree. Consequently, the effective alignment size consisted of 1,096 basepairs. Sequences were aligned using the software BioEdit v.7.0.5.3 (Hall, 1999), including four species of the genus *Parasesarma* and defining the type species *Parasesarma plicatum* (Latreille, 1806) as outgroup. This selection was done in accordance to preliminary trees embarking a wider variety of representatives of the families Sesarmidae and Varunidae, showing that the genus *Parasesarma* is phylogenetically close enough, but always holding a basal position with respect to all members of the target genera *Chiromantes* sensu lato (s. lat.) and *Pseudosesarma* s. lat. The alignment was converted with FaBox (Villesen, 2007) to a Nexus file that was used as input for evolutionary model testing and for phylogenetic analyses. The best fitting evolutionary model was determined with jModelTest v.2.1.10 (Darriba et al., 2012) based on the Akaike information criterion (Posada & Buckley, 2004). Bayesian inference (BI), as implemented in MrBayes (v.3.2.7) (Huelsenbeck & Ronquist, 2001) was used to carry out phylogenetic reconstructions and to calculate posterior probabilities. We ran 4 million generations with four chains (one heated) and a sample frequency of one tree per 1,000 generations, removing as burn-in the first 25%. New sequences were submitted to NCBI and are available from GenBank under the accession numbers given in Table 1. Homologous sequences from previous studies were also recovered from GenBank and included in our analyses (Table 1).

## SYSTEMATICS

### Family Sesarmidae Dana, 1852

**Historical and nomenclatural issues associated with *Chiromantes* and allied genera**. *Chiromantes* Gistel, 1848, has had a long and often confused history that is not restricted to the species level. Until 40 years ago, members of *Chiromantes* were still classified in *Holometopus* H. Milne Edwards, 1853, but Holthuis (1977: 170) argued that their respective type species had been incorrectly assigned. He showed that both *Chiromantes* Gistel, 1848, and *Holometopus* H. Milne Edwards, 1853, share the same type species, *Grapsus* (*Pachysoma*) *haematocheir* De Haan, 1833, and as such, were objective synonyms, with *Chiromantes* Gistel, 1848, having priority. Holthuis (1977: 170) also noted that all the species that had been assigned to *Chiromantes* by workers up to that point should instead be referred to *Perisesarma* De Man, 1895 (type species *Sesarma dusumieri* H. Milne-Edwards, 1853, subsequent designation of Campbell, 1967).

Serène & Soh (1970) completely reorganised the generic and subgeneric classification of the Indo-West Pacific Sesarmidae (when still considered a subfamily, Sesarminae) and established many new genera and subgenera. However, they did not change the concept of what had previously been the subgenus *Chiromantes* (as *Holometopus*). *Chiromantes* has continued to include all those species with an entire lateral carapace margin (no trace of an epibranchial tooth), the dorsal margin of the cheliped palm with no (or only one oblique) pectinated ridge, and orbits that include the antennal peduncle (Serène & Soh, 1970: 388–392). *Chiromantes* thus remained one of the larger and better-known Indo-West Pacific sesarmid genera. In his 1968 checklist, Serène recognised 13 species (under subgenus *Holometopus*): *C. boulengeri* Calman, 1920, *C. dehaani* (H. Milne Edwards, 1853), *C. elongatus* (A. Milne-Edwards, 1869), *C. eulimene* (De Man, in Weber, 1897), *C. eydouxi* (H. Milne Edwards, 1853), *C. granosimanum* (Miers, 1880), *C. haematocheir* (De Haan, 1833), *C. obesus* (Dana, 1851), *C. obtusifrons* (Dana, 1851), *C. ortmanni* (Crosnier, 1965), *C. stormi* (De Man, 1895), *C. tangi* (Rathbun, 1931), and *C. villosus* (A. Milne-Edwards, 1869). Subsequently, Soh (1978) described a new species, *C. serenei*, from Hong Kong.

An appraisal of *Chiromantes* by Ng & Liu (1999) noted that two major groups could be discerned in *Chiromantes*. One group had a single ridge of tubercles on the dorsal margin of the palm and differentiated granules on the dorsal margin of the dactylus. Included species were *C. elongatus* and *C. villosus* (both with a single longitudinal pectinated ridge), *C. eydouxi* (with one longitudinal tuberculate ridge), and *C. eulimene* and *C. ortmanni* (both with an oblique to transverse single pectinated ridge). Members of the second group, also including *C. tangi* and *C. stormi*, have no ridge on the dorsal margin of the palm and the dorsal margin of the dactylus has no, or only weakly differentiated, granules. These two species were discussed in detail by Ng & Liu (1999), with *C. tangi* provisionally retained in *Chiromantes*, while *C. stormi* was referred to a new genus, *Stelgistra* Ng & Liu, 1999. Significantly, Ng & Liu (1999: 230) commented (but did not elaborate) that "*C. haematochir* [sic] is distinct in several features (especially in the structure of the anterior male thoracic sternum) and should be generically separated from the other species in the group". Since *C. haematocheir* is the type species of *Chiromantes*, this would imply that all the other species in the genus would need to be moved to other genera.

Ng & Liu (1999) referred *Sesarma villosum* to *Clistocoeloma* A. Milne-Edwards, 1873 and suggested that *Sesarma obesum* could be a species of *Metasesarma* H. Milne Edwards, 1853. In a molecular study, Schubart et al. (2006: 197) supported the placement of *Sesarma villosum* within *Clistocoeloma*. Ng & Schubart (2003) showed that *Sesarma obesum* Dana, 1851, is a senior subjective synonym of *Metasesarma rousseauxi* H. Milne Edwards, 1853, and designated a neotype for Dana's species. They also demonstrated that *Sesarma eydouxi* H. Milne Edwards, 1853 (type locality supposedly Vietnam), is not a species of *Chiromantes*, but a junior synonym of the American *Sesarma rectum* Randall, 1840. Schubart & Ng (2002) transferred *Chiromantes tangi* (Rathbun, 1931), to *Neosarmatium* Serène & Soh, 1970, noting that it is close to *N. laeve* (A. Milne-Edwards, 1869). A recent reappraisal of *C. tangi* by Ng et al. (2019), however, showed that it is not closely related to *Neosarmatium*, and was transferred to its own genus, *Sinosesarma*.

Some results of the present study have been foreshadowed by Ng et al. (2008a: 223–225), notably in regard to the taxonomic complexities of *Bresedium*, *Chiromantes*, *Pseudosesarma*, and *Sesarmops*. Ng et al. (2008a) listed eight species in *Chiromantes*: *C. boulengeri* Calman, 1920, *C. dehaani* (H. Milne Edwards, 1853), *C. eulimene* (De Man, in Weber, 1897), *C. haematocheir* (De Haan, 1833), *C. neglectum* (De Man, 1887), *C. obtusifrons* (Dana, 1851), and *C. ortmanni* (Crosnier, 1965); placing *Sesarma granosimana* Miers, 1880, provisionally in *Pseudosesarma* Serène & Soh, 1970, but without explanation. However, they added on the observations of Ng et al. (2001: 41) that *Sesarma neglecta* De Man, 1887, was a valid species allied to *C. dehaani*. Ng et al. (2008a) also noted that *Sesarma serenei* Soh, 1978, should be considered a junior subjective synonym of *C. haematocheir* (see treatment in Naruse & Ng, 2008). Ng et al. (2008a) commented that ongoing revisions of *Chiromantes* and related taxa, like *Sesarmops* and *Pseudosesarma*, would substantially change the generic classification of the species in these genera. In fact, the only species they anticipated to remain in *Chiromantes* sensu stricto (s. str.) was *Sesarma haematocheir* De Haan, 1833. Naruse & Ng (2008) later described *C. ryukyuanus* as a sister species of *C. haematocheir* from the Ryukyu Islands in Japan. In their revision of a number of Indo-Pacific taxa with a longitudinal pectinated crest, Schubart et al. (2009) referred *Chiromantes elongatus* (A. Milne-Edwards, 1869) to *Selatium* Serène & Soh, 1970. Comparative morphological and genetic studies also revealed that some representatives of *Pseudosesarma* and *Sesarmops* have close affinities to *Chiromantes* s. lat. and would need to be revised simultaneously.

With regard to *Pseudosesarma*, Serène & Soh (1970) established the genus for species with the following characteristics: a) medium-sized species with an epibranchial tooth and the antennal peduncle being inside the orbit, but without pectinated crests on male chelar palm; b) carapace slightly convex and shorter than wide, with lateral border of carapace weakly or not diverging posteriorly; c) anterior frontal margin with feeble median concavity, postfrontal lobes not remarkably salient. They made *Sesarma edwardsii* De Man, 1887, the type species and included seven species: *Sesarma bocourti* A. Milne-Edwards, 1869, *Sesarma crassimanum* De Man, 1887, *Sesarma edwardsii* De Man, 1887 (spelled incorrectly as "*edwarsi*"), *Sesarma johorensis* Tweedie, 1940, *Sesarma laevimanum* Zehntner, 1894, *Sesarma modestum* De Man, 1902, and *Sesarma moeschii* De Man, 1892. Soh (1978) added a new species, *Pseudosesarma patshuni*, from Hong Kong.

Ng et al. (2008a: 222, 225) listed nine species in *Pseudosesarma*, thereby including *P. granosimanum* (Miers, 1880), a species previously classified in *Chiromantes* due to the lack of anterolateral carapace teeth, without detailed elaboration (see above). They noted that *Pseudosesarma crassimanum*, *P. johorense*, *P. moeschii*, and *P. patshuni* may need to be referred to other genera in the future (see also Ng & Schubart, 2017). The present revision of *Chiromantes* thus requires the simultaneous reappraisal of *Pseudosesarma*.

Serène & Soh (1970) clearly had reservations about their generic assignments of several species, recognising some of the unresolved generic problems. In their remarks on *Pseudosesarma*, they wrote: "The genus has several characters close to those of *Sesarmops* and the separation of the two genera needs to be improved. As it is, *Pseudosesarma* is still heterogeneous. Perhaps a new genus would have to be established giving priority to the shape of the male pleopod and grouping *bocourti* with the species of *Sesarmops* which, like *intermedium* have the same type of male pleopod. The species *moeschi* and *johorensis* with their smooth shining carapace and other characters are also a few aberrant in[to] *Pseudosesarma*" (Serène & Soh, 1970: 400). As these issues have never been resolved, it is necessary to include *Sesarmops* Serène & Soh, 1970, as part of the present revision.

*Sesarmops* was established for six species: *Sesarma atrorubens* Hess, 1865, *Sesarma impressus* H. Milne Edwards, 1837 (type species by original designation), *Sesarma intermedius* De Haan, 1835, *Sesarma mindanaoensis* Rathbun, 1914, *Sesarma sinensis* H. Milne Edwards, 1853, and *Sesarma weberi* De Man, 1892. Ng et al. (2008a) continued to include these species, but commented that *Sesarmops intermedius*, *S. sinensis*, and *S. weberi* need to be transferred to other genera. This was already noted by Serène & Soh (1970: 401): "If priority is given to the shape of the male pleopod, *intermedium*, *sinensis* can hardly be considered as congeneric with *impressum*. However, the type of the male pleopod of *weberi* is identical with that of *intermedium* and the fact that De Man (1902) considered *intermedium* as a synonym of *impressum* is at least an indication to support the present position. *S. sinensis* by its carapace clearly shorter than breadth between the external orbital angles and with lateral border nearly parallel seem to be aberrant in the genus. At least by the ornamentation of the dactylus of male cheliped *weberi* is somewhat aberrant into *Sesarmops*".

The present study demonstrates that *Pseudosesarma patshuni*, *Sesarmops intermedius*, and *S. sinensis* are morphologically and phylogenetically close to *Chiromantes dehaani* and *C. neglectus*, while *Pseudosesarma moeschii* and *P. johorense* share a unique set of morphological characters. *Sesarma edwardsi* var. *laevimana* Zehntner, 1894 (often placed in *Pseudosesarma*) is here recognised as the senior synonym of *Bresedium sediliense* (Tweedie, 1940), and remains in *Bresedium* for the moment (see Remarks for that genus). *Pseudosesarma* s. str. is here restricted to *P. edwardsii*, *P. crassimanum*, and allies, now also including *Chiromantes boulengeri* (see Ng & Schubart, 2017). *Pseudosesarma bocourti* and *P. granosimanum* are referred to two new genera.

With the present reorganisation and recent reappraisal of the type species by Ng et al. (2020), *Sesarmops* now contains *S. angustifrons* (A. Milne-Edwards, 1869), *S. atrorubens* (Hess, 1865), *S. imperator* Ng, Li & Shih, 2020, *S. impressus* (H. Milne Edwards, 1837), *S. indicus* Ng, Li & Shih, 2020, *S. mindanaoensis* (Rathbun, 1914), *S. similis* Hess, 1865, and *S. weberi* (De Man, 1892) (see also Paulay & Starmer, 2011; Naruse & Ng, 2020). The genus is not monophyletic and will be revised at a later date.

The new taxonomic structure provided here, including the nine new genera proposed, is based on newly recognised morphological characters, supported by a phylogenetic analysis, and clearly shows that the presence or absence of an epibranchial tooth is not useful in systematics (see General Discussion).

**Outline of the new generic structure**. The type species of *Chiromantes*, *Grapsus* (*Pachysoma*) *haematocheir* De Haan, 1833, is markedly different from the other species currently placed in the genus, with the exception of *C. ryukyuanus* and the already synonymised *C. serenei*, because its adult male thoracic sternites 2 to 4 are relatively broader and the sternopleonal cavity reaches only to the median point of sternite 4 (Fig. 9A, B). All other species assigned to *Chiromantes* have thoracic sternites 2 to 4 proportionately narrower and the sternopleonal cavity longer, reaching to just before the anterior margin of sternite 2 (Fig. 9C–H).

With *Chiromantes haematocheir* and *C. ryukyuanus* separated, the remaining species fall into several discrete groups that will be given genus rank: *Chiromantes eulimene* (De Man, in Weber, 1897) and *C. ortmanni* (Crosnier, 1965) are in one group, while *C. dehaani* (H. Milne Edwards, 1853), *C. neglectum* (De Man, 1887), and *C. magnus* Komai & Ng, 2013, are in another. *Chiromantes obtusifrons* (Dana, 1851) and four species described as new in the revision of this group of species by Davie & Ng (2013) belong to a third group. *Chiromantes angolensis* (Brito Capello, 1864) and *C. buettikoferi* (De Man, 1883) belong to their own respective groups. *Chiromantes boulengeri* Calman, 1920, belongs in *Pseudosesarma*, while *C. granosimanum* (Miers, 1880) possesses sufficient unique morphological characters to justify its placement in a monotypic genus. Similarly, *Pseudosesarma bocourti* (A. Milne-Edwards, 1869) is also referred to a new genus, and its former synonym *Sesarma cheirogona* Targioni Tozzetti, 1877, is here regarded as a valid species.

*Chiromantes dehaani* s. str., *C. neglectus*, and *C. magnus* are characterised by their chelipedal palm lacking a longitudinal ridge on its dorsal margin and the dactylus not possessing any distinctly shaped or regularly arranged granules or tubercles along its dorsal margin. On the other hand, the inner surface of the male palm has a prominent transverse ridge of rounded granules that are positioned on the most swollen part of the palm; and the outer surface of the palm has a clearly discernible short and smooth median longitudinal ridge (although sometimes low or partially obscured by a granular surface). In addition, these species have a septum separating the basal antennal and antennular articles (absent in *C. haematocheir* and *C. ryukyuanus*). The structure of the cristae on the postfrontal margin also differs in the two groups. In *C. haematocheir* and *C. ryukyuanus*, the epigastric and postfrontal cristae are sharp and almost confluent, with shallow grooves separating them (Figs. 1A, B, 3A). In *C. dehaani* s. str., *C. neglectus* and *C. magnus*, the epigastric and postfrontal cristae are rounded and separated by deep and broad grooves (e.g., Figs. 1C, D, 3B). In addition, the vulvae are slightly different, with that of *C. haematocheir* and *C. ryukyuanus* just touching the margin of sternite 5 (Fig. 43A), while in *C. dehaani* s. str., *C. neglectus*, and *C. magnus*, the vulva is pressed against sternite 5, causing a slight indentation (Fig. 43B). As such, these three species are here referred to their own new genus, *Orisarma*. This new genus will also accommodate two species that had previously been placed in *Sesarmops* (*S. sinense* and *S. intermedius*) and one from *Pseudosesarma* (*P. patshuni*). The characters noted above for *C. dehaani* s. str., *C. neglectus*, and *C. magnus* also apply to them, including the form of the vulva (Fig. 43C, D), but the epigastric and postorbital cristae are less prominently rounded and the grooves more narrow in *Sesarmops sinensis* and *S. intermedius* (Fig. 2I, J).

The East African *C. eulimene* and *C. ortmanni* are unique in that the dorsal margin of the male palm has a distinct oblique pectinated ridge and the dorsal margin of the chelar dactylus has differentiated granules, presumably for stridulation. These characters are consistent and are here considered to be generically significant. To this effect, we propose to establish a new genus, *Cristarma*, for these two species. With regard to these two characters, *Cristarma* is similar to the two known species of *Selatium* Serène & Soh, 1970, viz. *S. brockii* (De Man, 1887) and *S. elongatum* (A. Milne-Edwards, 1869) (cf. Schubart et al., 2009). *Cristarma* can easily be distinguished from species of *Selatium* in that the pectinated ridge on the male palm is markedly oblique to almost transverse in orientation (Fig. 15D, F) (versus longitudinal), the outer lower surface of the palm has two short, smooth, submedian oblique ridges (Fig. 15C, E) (versus absent), the lateral margins of the ambulatory dactyli are not lined by dense short black setae (Fig. 13E, F), and the surfaces between the first to third ambulatory coxae have dense tufts of long setae (Fig. 18C, D) (versus very short, scattered, or no setae). In addition, the vulva is very low, with the two sternal vulvar covers bracketing the non-projecting opening (Fig. 43G, H). Our molecular phylogenetic tree also shows that there is no close relationship between *Selatium* and *Cristarma* or those genera with two transverse pectinated crests, e.g., *Parasesarma* and *Perisesarma* (Fig. 59).

The other two species endemic to Africa, but from the Atlantic coast, *C. angolensis* and *C. buettikoferi*, are referred to the new genera, *Trapezarma* and *Platychirarma*, respectively. Like *Chiromantes* s. str., their epigastric and postfrontal crests are sharp and almost continuous (Figs. 13G, H, J, 14G, H), a character shared with no other group of species. Unlike the West African *C. eulimene* and *C. ortmanni* that have pectinated crests on their chelae and granules on the dactylar fingers, the chelae of *C. angolensis* and *C. buettikoferi* are smooth and not specially ornamented. What is unusual about their adult male chelae is that the outer surface is gently convex to flat (including the pollex) (Figs. 16, 17), being most extreme in *C. buettikoferi*. The prominently flattened outer surface of the chela of *C. buettikoferi* (Fig. 17) is a character shared only with *Pseudosesarma bocourti* and *C. cheirogonum* from Southeast Asia (Fig. 28) (both referred to a new genus, see later). The carapaces of *C. angolensis* and *C. buettikoferi* are quite distinct with a more trapezoidal appearance, with a wider frontal margin and strongly converging lateral margins towards the posterior carapace margin (Fig. 13G, H, J). While the two species are genetically defined as sister species (despite long individual branches, Fig. 59), the suite of cheliped, male pleonal and G1 characters argue against including them in the same genus (see discussion under *Trapezarma*). This gains further support from the very differently shaped vulvae, those of *Trapezarma* widely spaced and the projecting opening directed obliquely posteriorly (Fig. 43I), while the ones of *Platychirarma* are closer together and the slightly projecting opening is directed obliquely anteriorly (Fig. 43J).

Ng & Liu (1999: 230) had noted that the generic placement of *Chiromantes obtusifrons* should be reappraised. The trapezoidal carapace of this species is diagnostic, although it shares other characters with *Orisarma*, new genus. However, *C. obtusifrons* has a peculiar frontal margin that is very broad and bends downwards so strongly that the antennae and antennules are effectively covered (Fig. 14A–D), the outer surface of the palm has no longitudinal ridge (Fig. 15A), and the surfaces between the first to third ambulatory coxae have distinct dense tufts of long setae (Fig. 18A, B) (a character otherwise only present in *C. eulimene* and *C. ortmanni*). In addition, the vulvae have a totally different structure, with the sternal vulvar covers being plate-like and the opening not projecting (Fig. 43E, F). Davie & Ng (2012) re-examined *Chiromantes obtusifrons* and recognised four new closely allied species from the Indian Ocean and Western Pacific, and also commented on their generic status. All five species are here referred to a new genus, *Danarma*.

Ng & Liu (1999) had already described *Sesarma* (*Sesarma*) *stormi* De Man, 1895, in detail and explained at length why it should be placed in its own genus *Stelgistra* Ng & Liu, 1999. There is no need to elaborate here, as all the characters discussed then are still valid in defining *Stelgistra*. *Stelgistra stormi* has since been found in Guam (Paulay et al., 2003: 508).

The revised classification of the above-discussed species is summarised in Table 2.

## *Chiromantes* Gistel, 1848

**Type species.** *Grapsus* (*Pachysoma*) *haematocheir* De Haan, 1833 (subsequent designation by Holthuis, 1977: 170). Gender masculine.

**Diagnosis**. Carapace squarish; frontal margin almost entire or gently bilobed, gently deflexed, subequal to posterior carapace margin; lateral margin entire, posterolateral part gently convex to subparallel; regions of carapace poorly demarcated; postfrontal and epigastric crests separated by relatively shallow grooves, margin relatively sharp, almost straight, appearing contiguous; basal articles of antenna and antennules adjacent to each other, not separated by septum; dorsal margin of palm without longitudinal pectinated ridge, inner surface not swollen, without granulated ridge, outer surface of palm and pollex convex, outer surface of palm smooth; dorsal margin of cheliped dactylus smooth in adult males, juveniles with row of uniformly sized small granules; inner distal margin of merus of cheliped not lamelliform; inner surfaces of first to third ambulatory coxae with only scattered short setae, not arranged into dense tufts; male thoracic sternites 2–4 relatively narrow in adults, suture between sternites 3 and 4 distinct; male sternopleonal cavity reaching to midlength of sternite 4; male thoracic sternite 5 smooth, without depression on anterior part; G1 relatively stout, chitinous part short. Vulva on anterior part of sternite 6, anterior edge just touching sternite 5; anterior and posterior sternal vulvar covers low; opening short, cylindrical, directed obliquely anteriorly.

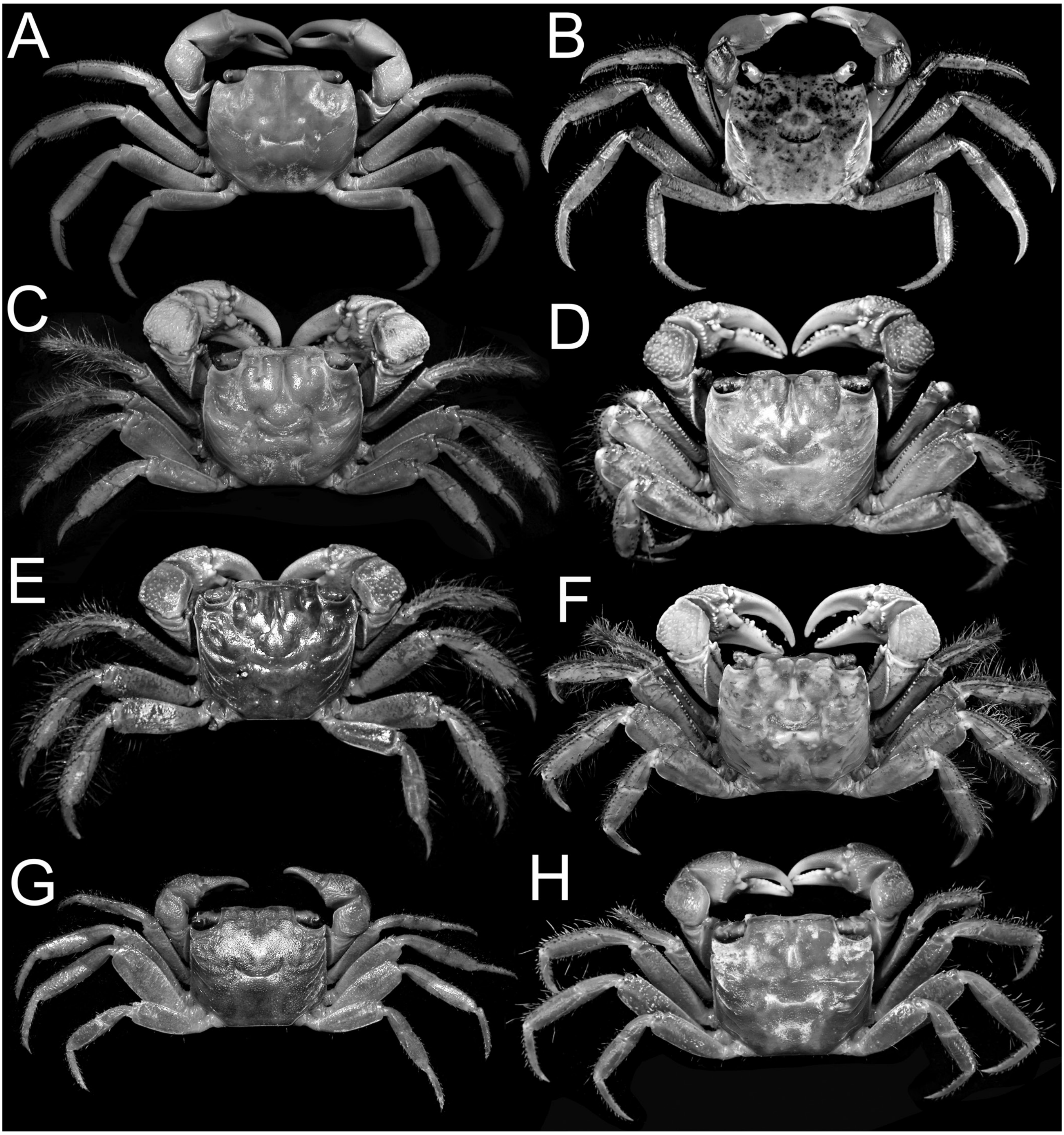

Fig. 1. Overall habitus. A, *Chiromantes haematocheir*, lectotype male (33.7 × 29.7 mm) (RMNH-D160), Japan; B, *C. ryukyuanus*, holotype male (33.1 × 29.6 mm) (RUMF-ZC-539), Okinawa Island, Japan; C, *Orisarma dehaani*, lectotype male (39.5 × 35.7 mm) (RMNH-D157), Japan; D, *O. dehaani*, male (36.4 × 34.4 mm) (ZRC 2011.1027), Kumejima Island, Japan; E, *O. neglectum*, neotype male (35.6 × 31.8 mm) (ZRC 1998.310), Shanghai, China; F, *O. magnum*, paratype male (50.6 × 45.6 mm) (ZRC 2013.0173), Ogasawara Island, Japan; G, *O. patshuni*, male (14.2 × 13.0 mm) (ZRC 1998.345), Hong Kong; H, *O. patshuni*, male (20.4 × 18.2 mm) (ZRC 2012.0032), Hong Kong.

**Included species**. *Chiromantes haematocheir* (De Haan, 1833); *Chiromantes ryukyuanus* Naruse & Ng, 2008.

**Remarks**. As discussed earlier, *Chiromantes* s. str. is uniquely defined by having the adult male thoracic sternites 2–4 relatively broader than other related taxa, and the sternopleonal cavity being shorter, reaching only to the median point of sternite 4 (Fig. 9A, D).

### *Chiromantes haematocheir* (De Haan, 1833)
(Figs. 1A, 3A, 5A–C, 7A–D, 9A, 10A–I, 43A)

*Grapsus* (*Pachysoma*) *haematocheir* De Haan, 1833: 62, pl. 7 fig. 4.

*Holometopus haematocheir* – H. Milne Edwards, 1853: 188; Stimpson, 1858: 106 (part); Heller, 1865: 66; Stimpson, 1907: 137 (part); Takeda, 1975: 146; Soh, 1978: 9, 10, pl. 2e; Takeda, 1982: 219, fig. 650.

*Sesarma haematocheir* – Herklots, 1861: 17; De Man, 1887: 642; Bürger, 1893: 614, pl. 21 fig. 3; Ortmann, 1894: 717 (part);

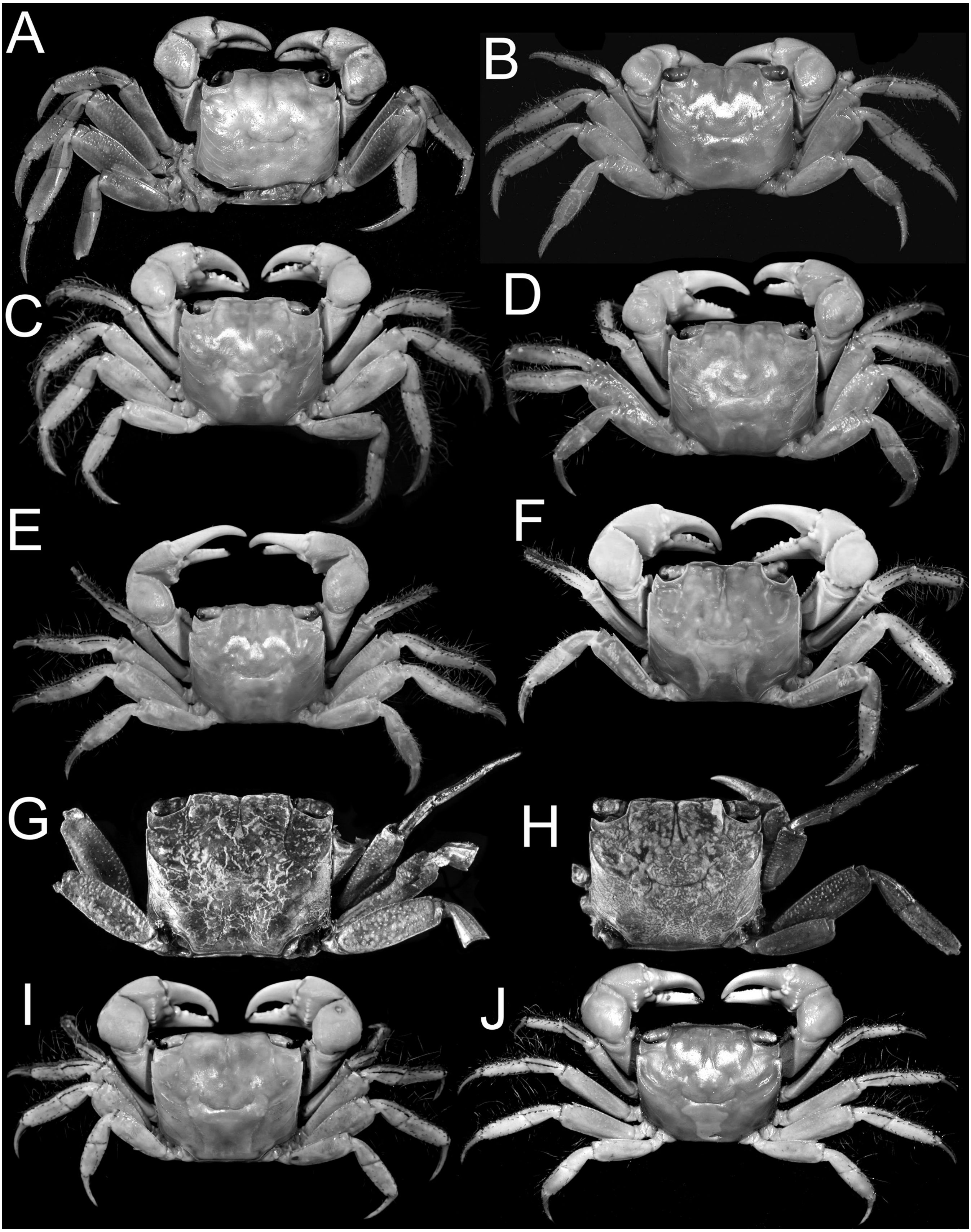

Fig. 2. Overall habitus. A, *Orisarma intermedium*, lectotype male (23.0 × 19.9 mm) (RMNH-D165), Japan; B, *O. intermedium*, male (27.1 × 25.2 mm) (ZRC 1970.2.23.6), Japan; C, *O. intermedium*, male (27.0 × 25.0 mm) (ZRC 2013.0140), Kyushu, Japan; D, *O. intermedium*, male (29.5 × 26.5 mm) (ZRC 2001.0034), Pingtung, Taiwan; E, *O. intermedium*, male (34.2 × 30.7 mm) (ZRC 2001.0034), Pingtung, Taiwan; F, *O. intermedium*, male (37.5 × 35.8 mm) (ZRC 2014.0265), Kumejima Island, Japan; G, *O. sinense*, lectotype male (19.0 × 16.6 mm) (MNHN-BP3635a), China; H, *O. sinense*, paralectotype female (18.8 × 16.9 mm) (MNHN-BP3635b), China; I, *O. sinense*, male (30.7 × 26.7 mm) (ZRC 2010.0421), China; J, *Orisarma sinense*, male (29.6 × 25.4 mm) (ZRC 1998.1204), Shanghai, China.

Yamaguchi & Baba, 1993: 473, fig. 180c; Fransen et al., 1997: 129.

*Sesarma* (*Holometopus*) *haematocheir* – Tesch, 1917: 156; Balss, 1922: 155; Urita, 1926: 19; Shen, 1932: 199, text-figs. 124, 125, pl. 9 fig. 2; Sakai, 1936: 234, pl. 64, fig. 3; Sakai, 1939: 681, pl. 77, fig. 3; Shen, 1940a: 97; Shen, 1940b: 237; Kamita, 1941: 214, text-fig. 118; Shen & Dai, 1964: 134, unnumbered fig.; Sakai, 1965: 202, pl. 97, fig. 1; Serène, 1968: 107; Kim, 1973: 486, text-fig. 216, pl. 45 fig. 166; Sakai, 1976: 655 (part), pl. 224 fig. 1; Matsuzawa, 1977: pl. 110 fig. 1; Dai et al., 1986: 487, text-fig. 274(1), pl. 68(6); Dai & Yang, 1991: 534, text-fig. 274(1), pl. 68(6); Huang, 1994: 597; Muraoka, 1998: 53.

*Chiromantes haematochir* – Liu & Ng, 1999: 229, 230.

*Chiromantes haematocheir* – Miyake, 1983: 179, pl. 60-1; Minemizu, 2000: 297; Kobayashi, 2000: 122, fig. 2p; Ng et al., 2001: 41 [includes references for this species from Taiwan up to 2001]; Schubart et al., 2002: 30; Ho, 2003: 38; Kwok & Tang, 2005: 3, fig. 8; Schubart et al., 2006: 195; Takeda & Ueshima, 2006: 94; Oh et al., 2007: 9; Ng et al., 2008a: 220; Yang et al., 2008: 801; Naruse & Ng, 2008: figs. 1–4, 5b; Lee, 2008: 134; Naderloo & Schubart, 2009: 61, 67; Liu & Wang, 2010: 58; Komai & Ng, 2013: 4, figs. 1–3, 4a, b, 5b; Toyota & Seki, 2014: 188; Ng et al., 2017b: 103 [for other local references for Taiwan].

*Holometopus serenei* Soh, 1978: 13, fig. c, d, pl. 1b, e, pl. 2f; Lee, 1995: 3.

Chiromantes serenei – Kwok & Tang, 2005: 3, fig. 9.

**Material examined**. Lectotype: male (33.7 × 29.65 mm) (RMNH D160), Japan, coll. Ph. v. Siebold. Paralectotypes: 1 female (27.5 × 23.5 mm) (RMNH D 158), Japan, coll. Ph. F. von Siebold, 1823–1829; paralectotypes, 4 males (16.9–28.9 × 14.8 × 25.3 mm), 1 female (26.7 × 22.0 mm) (RMNH D 159), Japan, coll. Ph. F. von Siebold, 1823–1829; 1 male (29.6 × 25.3 mm) (MNHN B-12475), Japan, coll. Ph. F. von Siebold, 1823–1829. Others: JAPAN – 2 males (larger 31.7 × 27.4 mm) (ZRC 1964.9.8.12–13), coll. S. Miyake; 1 male (26.4 × 22.9 mm), 1 female (26.6 × 22.4 mm) (ZRC 1970.8.27.7), Sagami Bay, Kamakura, coll. T. Sakai, 1968; 7 females (smallest 18.5 × 15.6 mm, largest 28.3 × 24.5 mm) (ZRC 2002.0225), river mouth, Izaku River, Satsuma Peninsula, Kagoshima Prefecture, coll. H. Suzuki, 30 August 2000; 1 male, 1 female (ZRC 2017.1004), stream about 50 m before coastline, Kamenoko-jima, Sasebo, Kyushu, 33.125941°N 129.678348°E, coll. P.K.L. Ng, T. Naruse, M. Deki et al., 30 October 2017. TAIWAN – 1 male (26.7 × 24.2 mm), 2 females (22.8 × 19.6 mm, 13.9 × 11.9 mm) (ZRC), Yan Liau, coll. J.-F. Huang, 16 October 1985; 5 males (35.6 × 31.2 mm, 29.1 × 25.4 mm, 25.4 × 22.9 mm, 17.7 × 15.6 mm, 15.6 × 13.7 mm), 1 female (23.4 × 20.0 mm) (ZRC), Lion Museum, Peikuan, Toucheng town area, northeastern Taiwan, coll. H.-C. Liu & P.K.L. Ng, 21 June 2002; 3 males (ZRC 2009.0153), coastal area behind Lion Mountain, Pei Kuan, Ilan County, coll. N.K. Ng & P.-H. Ho, 25 June 2000; 1 juvenile male (ZRC 2009.0669), among grass, supralittoral zone, Hsinchu wetlands, Hsinchu, northwest coast, coll. P.K.L. Ng, 6 June 2009; 1 male (ZRC 2002.0472), Hualien County, mouth of Meilun stream, Hualien city, eastern Taiwan, 23°58′54″N 121°36′37″E, coll. P.K.L. Ng & H.-C. Liu, 22 June 2002. CHINA – 1 male (ZRC 2002.0558), Chao Pu-Tou mangroves, You Long village, mainland, outside Xiamen island, Xiamen, Fujian province, China, coll. P.K.L. Ng & S.H. Fang, 22 September 2002. HONG KONG – 1 male (18.2 × 16.6 mm) (NHM 1978.107) (lectotype of *Holometopus serenei* Soh, 1978), Tai Po ricefield, coll. C.L. Soh, 8 June 1975; 1 male (35.3 × 30.6 mm) (ZRC), in aquarium, coll. H.H. Tan, July 2000; 7 females (largest 12.0 × 10.7 mm, smallest 24.5 × 21.1 mm) (ZRC 1997.761), salt marsh, Tai Tam, south coast of Hong Kong Island, immediately downstream of Tai Tam Dam, coll. P.K.L. Ng & S.Y. Lee, 6 June 1996; 1 male (30.8 × 26.9 mm) (ZRC), salt marsh, Tai Tam, south coast of Hong Kong Island, immediately downstream of Tai Tam Dam, coll. K. Wong, 3 October 2010; 15 males (smallest 9.8 × 11.2 mm, largest 27.8 × 23.9 mm), 6 females (smallest 11.1 × 9.5 mm, largest 21.1 × 18.4 mm) (ZRC 2012.1221), salt marsh, Tai Tam, south coast of Hong Kong Island, immediately downstream of Tai Tam Dam, coll. K. Wong, 27 March 2012; 4 males (10.2 × 8.7 mm, 10.8 × 9.4 mm, 11.6 × 9.6 mm, 14.3 × 13.0 mm), 1 female (17.5 × 15.1 mm) (ZRC 2012.1222), salt marsh, Tai Tam, south coast of Hong Kong Island, immediately downstream of Tai Tam Dam, coll. K. Wong, 17 September 2012.

**Diagnosis**. Ambulatory legs relatively stouter, shorter, distal end of second ambulatory merus just reaches frontal margin when folded; row of granules on dorsal margin of cheliped dactylus only distinct in smaller specimens, very low or undiscernible in large males; male pleonal somite 6 is relatively narrower.

**Colour**. The carapace of adult *C. haematocheir* is usually dark green with the anterior parts and margins yellowish to red (see also Miyake, 1983; Minemizu, 2000; Lee, 2008: 134; Liu & Wang, 2010: 58; Toyota & Seki, 2014).

**Remarks**. There are 25 type specimens (and a set of dried mouthparts) of this species in RMNH (Fransen et al., 1997), with the lectotype designated by Yamaguchi & Baba (1993). The lectotype male is a specimen in excellent condition, despite its age.

Soh (1978) described *Holometopus serenei* from Hong Kong. Shen (1940a: 237) had earlier recorded *C. haematocheir* from Hong Kong from a site called Wong Chuk Hang, a small village near Aberdeen, but Soh (1978: 10) noted that he could not find the species there as the area had since been developed. Examination of the lectotype of *Holometopus serenei* Soh, 1978, as well as numerous specimens from various locations around Hong Kong, confirms that it is only a junior synonym of *C. haematocheir*. All specimens reported or here examined are only juveniles or subadults of *C. haematocheir* (see also Ng et al., 2008a; Naruse & Ng, 2008). The holotype male of *H. serenei* is not fully mature, as evidenced by its poorly developed chelae. The G1 of the type of *H. serenei*, however, is relatively well developed and is almost identical to that of *C. haematocheir*. The male pleon of *H. serenei* has the telson and somite 6 relatively more elongate than adult *C. haematocheir*, but this is also clearly associated with size and age. Medium-sized specimens of *C. haematocheir* from Japan have male pleons intermediate in form between the holotype of *H. serenei* and adult *C. haematocheir*. The paratype females of *H. serenei*

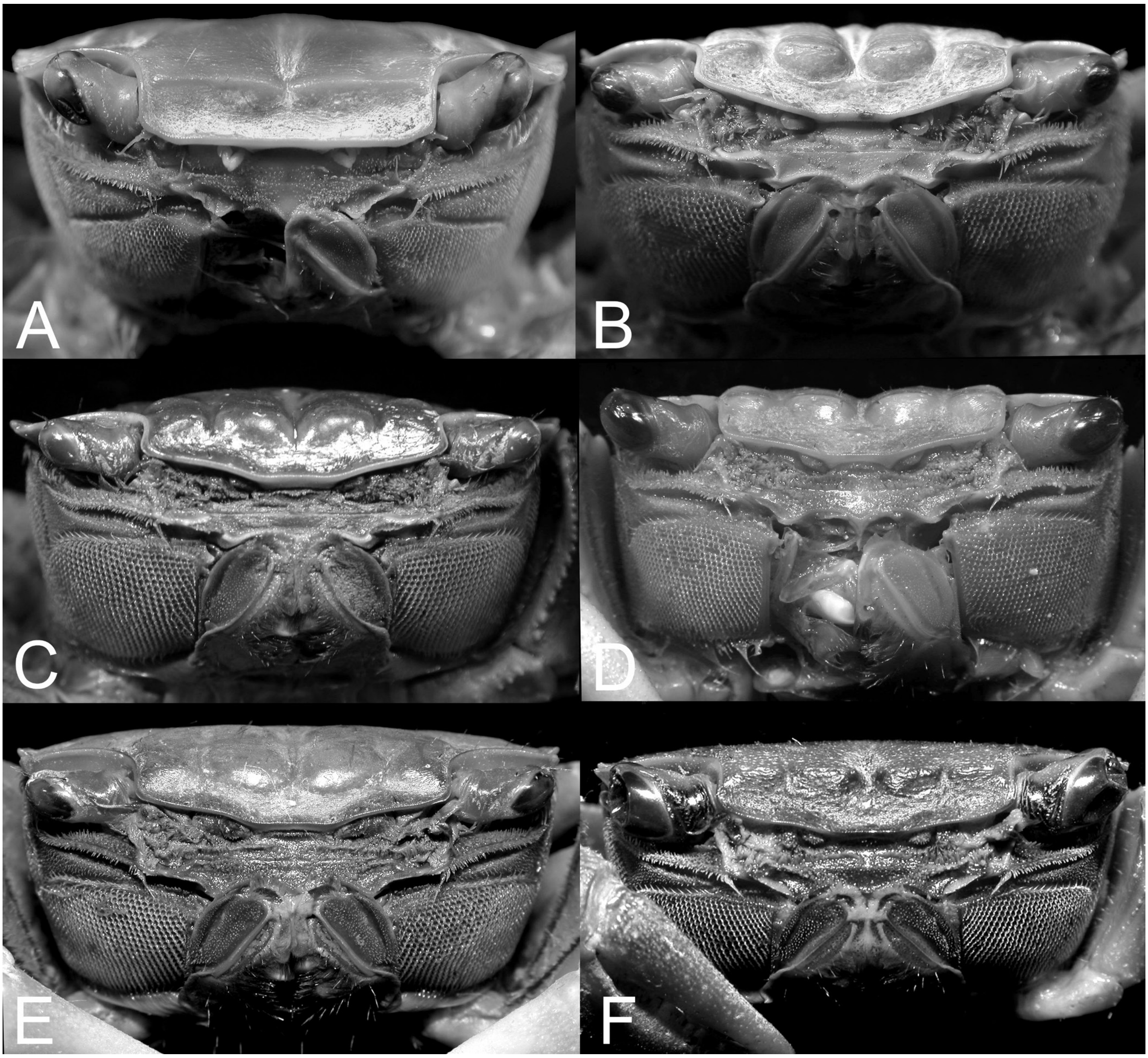

Fig. 3. Frontal view of cephalothorax. A, *Chiromantes haematocheir*, lectotype male (33.7 × 29.7 mm) (RMNH-D160), Japan; B, *Orisarma dehaani*, lectotype male (39.5 × 35.7 mm) (RMNH-D157), Japan; C, *O. neglectum*, neotype male (35.6 × 31.8 mm) (ZRC 1998.310), Shanghai, China; D, *O. intermedium*, male (27.1 × 25.2 mm) (ZRC 1970.2.23.6), Japan; E, *O. sinense*, male (29.6 × 25.4 mm) (ZRC 1998.1204), Shanghai, China; F, *O. patshuni*, male (14.2 × 13.0 mm) (ZRC 1998.345), Hong Kong.

are already mature despite being relatively small, but such early maturity is not abnormal—we similarly have a good series of small adult females of *C. haematocheir* from Taiwan and Japan. Direct comparisons of specimens of *C. haematocheir* comparable in size from Taiwan to the male holotype of *H. serenei* do not show any major differences.

The good series of specimens from Hong Kong has allowed us to estimate the size at which males and females of this species mature. Two small female specimens (11.1 × 9.5 mm, 14.1 × 11.8 mm) (ZRC 2012.1221) are not fully mature with the pleon not completely covering the thoracic sternum, although a slightly larger specimen (14.5 × 12.1 mm) from the same locality is already mature. The species therefore can mature at a relatively small size. The males also appear to be able to reach maturity at smaller sizes. As noted above, the small lectotype male of *H. serenei* (18.2 × 16.6 mm) is already mature, with the G1 fully developed. Surprisingly, an even smaller male (9.8 × 11.2 mm) (ZRC 2012.1222) is also mature. The structure of the male thoracic sternum also varies with size. Small specimens (10.8 × 9.4 mm) (ZRC 2012.1222) have a sternite 4 that is relatively wider, becoming gradually longer as they increase in size (Fig. 7A–D). Why some specimens from Hong Kong can mature at these smaller sizes is not known, some of the specimens we have from there are larger and agree with what we know from other parts of its range (e.g., in Japan and Taiwan). We are also uncertain if this phenomenon occurs in other parts of its range.

The lateral carapace margin of *C. haematocheir* is usually entire, especially in adults and males. In smaller female specimens, however, the margin has two very broad and low lobiform teeth separated by very short and very narrow fissures, which are just discernible under magnification.

Although most of the literature describes the dactylar finger of adult males of *C. haematocheir* as unarmed, this is actually not the case. As discussed at length by Naruse & Ng (2008), the dorsal margin of the dactylar finger is actually lined with a row of regularly shaped low subrectangular granules that are especially prominent in smaller specimens (Fig. 5C), becoming very low or undiscernible in large individuals (Fig. 5B). In fact, *Holometopus serenei* Soh, 1978, was partially diagnosed on this basis. Specimens of the closely related *C. ryukyuanus* of a comparable size to *C. haematocheir* have proportionately larger granules, that are distinct even in large specimens.

Although we do not have morphological support, our phylogenetic reconstruction (Fig. 59) does suggest the possibility that there could still be more than one species within *Chiromantes haematocheir* as defined here. If this is the case, it remains possible that *C. serenei* may still be recognised in the future as a valid cryptic or pseudocryptic species. A more detailed study with a larger series of samples (both morphological and molecular) across the known range of *Chiromantes haematocheir* will need to be undertaken before this problem can be resolved.

The record of "*Chiromantes haematocheir*" by Liu & He (2007: 162) from China is actually *Parasesarma affine* (De Haan, 1837) (cf. Rahayu & Ng, 2010).

**Biology**. This species is found in supralittoral habitats, usually some distance from the sea, often adjacent to or near freshwater habitats. They may be found several kilometres inland if the area is flat and still subjected to some tidal influence. The larval development has been reported by Fukuda & Baba (1976) and Oh et al. (2007). Nematode parasites have been reported on by Yoshimura (1990).

**Distribution**. Widely distributed in East Asia, from Korea to mainland Japan, Taiwan, and mainland China, including Hong Kong.

### *Chiromantes ryukyuanus* Naruse & Ng, 2008

(Figs. 1B, 9B, 10J–L)

*Sesarma haematocheir* – Ortmann, 1894: 717 (part). [not *Grapsus* (*Pachysoma*) *haematocheir* De Haan, 1833]

*Holometopus haematocheir* – Stimpson, 1858: 106 (part); Stimpson, 1907: 137 (part). [not *Grapsus* (*Pachysoma*) *haematocheir* De Haan, 1833]

*Sesarma* (*Holometopus*) *haematocheir* – Sakai, 1976: 655 (part); Nagai & Nomura, 1988: 42; Kishino et al., 2001: 127; Naruse, 2005: 221. [not *Grapsus* (*Pachysoma*) *haematocheir* De Haan, 1833]

*Chiromantes ryukyuanum* [sic] Naruse & Ng, 2008: 2–12, figs. 5a, 6–9; Toyota & Seki, 2014: 189.

**Material examined**. Holotype: male (33.1 × 29.6 mm) (RUMF-ZC-539), Taminato, Ohgimi Village, Okinawa Island, Ryukyu Islands, Japan, coll. T. Naruse, 29 July 2007. Paratypes: 1 female (30.8 × 26.9 mm) (RUMF-ZC-540), east of Funaura Bay, Iriomote Island, coll. T. Nagai, 20 October 2005; 1 female (28.0 × 24.7 mm) (RUMF-ZC-541), west of Mt. Tomori, Funaura Bay, Iriomote Island, coll. T. Naruse & T. Nagai, October 2005; 1 female (29.0 × 25.2 mm) (RUMF-ZC-542), Iriomote Island, coll. S. Shokita, 1980s; 1 female (33.8 × 30.2 mm) (ZRC 2007.0641), near Fukari River mangrove, Komi, Iriomote Island, coll. T. Naruse, 28 September 2002; 6 males (5.4–13.0 × 5.1–11.9 mm), 1 female (6.5 × 5.9 mm) (RUMF-ZC-543), Oura River, Nago City, Okinawa Island, coll. T. Maenosono, 9 June 2007; 1 male (34.1 × 31.3 mm) (ZRC 2007.0640), data same as holotype; 1 male (34.6 × 31.0 mm) (CBM-ZC), Kijoka, Ohgimi Village, Okinawa Island, coll. H. Kimura, 24 June 2007; 1 female (WMNH-Na-Cr-1131), Ohara, Iriomote Island, coll. S. Nagai, March 1982; 1 female (26.2 × 22.7 mm) (OMNH Ar 4809), Ura River, Takigo, Amami-Ohshima Island, coll. T. Kishino et al., 2 May 2000. All localities in Ryukyu Islands, Japan.

**Diagnosis**. Ambulatory legs relatively longer, more slender, distal end of merus of second ambulatory leg reaching distinctly beyond level of frontal margin when folded; row of granules on dorsal margin of cheliped dactylus distinct even in large male adults; male pleonal somite 6 relatively broader.

**Colour**. The carapace of adult *C. ryukyuanus* is green with the anterior parts marbled or uniformly red (see Naruse & Ng, 2008; Toyota & Seki, 2014).

**Remarks**. Naruse & Ng (2008) named the species "*Chiromantes ryukyuanum*" after the Ryukyu Islands, but they did not elaborate on its etymology. Since the gender of *Chiromantes* is masculine, the specific name should be amended to "*C. ryukyuanus*".

The differences between *C. ryukyuanus* and *C. haematocheir* s. str. were discussed at length by Naruse & Ng (2008) and there is no need to elaborate on them here. The main differences are: the carapace of adult of *C. ryukyuanus* is green with the anterior parts marbled or uniformly red in life (versus dark green with the anterior parts and margins yellowish to red in *C. haematocheir*); the relatively longer and more slender ambulatory legs, with the distal end of the merus of the second ambulatory leg reaching distinctly beyond the level of the frontal margin (versus the distal end of the second ambulatory merus just reaching the frontal margin in *C. haematocheir*); the granules on the dorsal margin of the cheliped dactylus are distinct even in large male adults (versus barely visible or absent in *C. haematocheir*); and the male pleonal somite 6 is relatively broader.

As discussed by Naruse & Ng (2008), many of the old records of "*Chiromantes haematocheir*" from the various islands in the Ryukyus Chain by Stimpson (1858), Ortmann (1894), Sakai (1976), Shokita (1990), Shokita et al. (2002), and Shokita et al. (2003) are almost certainly *C. ryukyuanus*. *Chiromantes haematocheir* s. str. therefore has a distribution

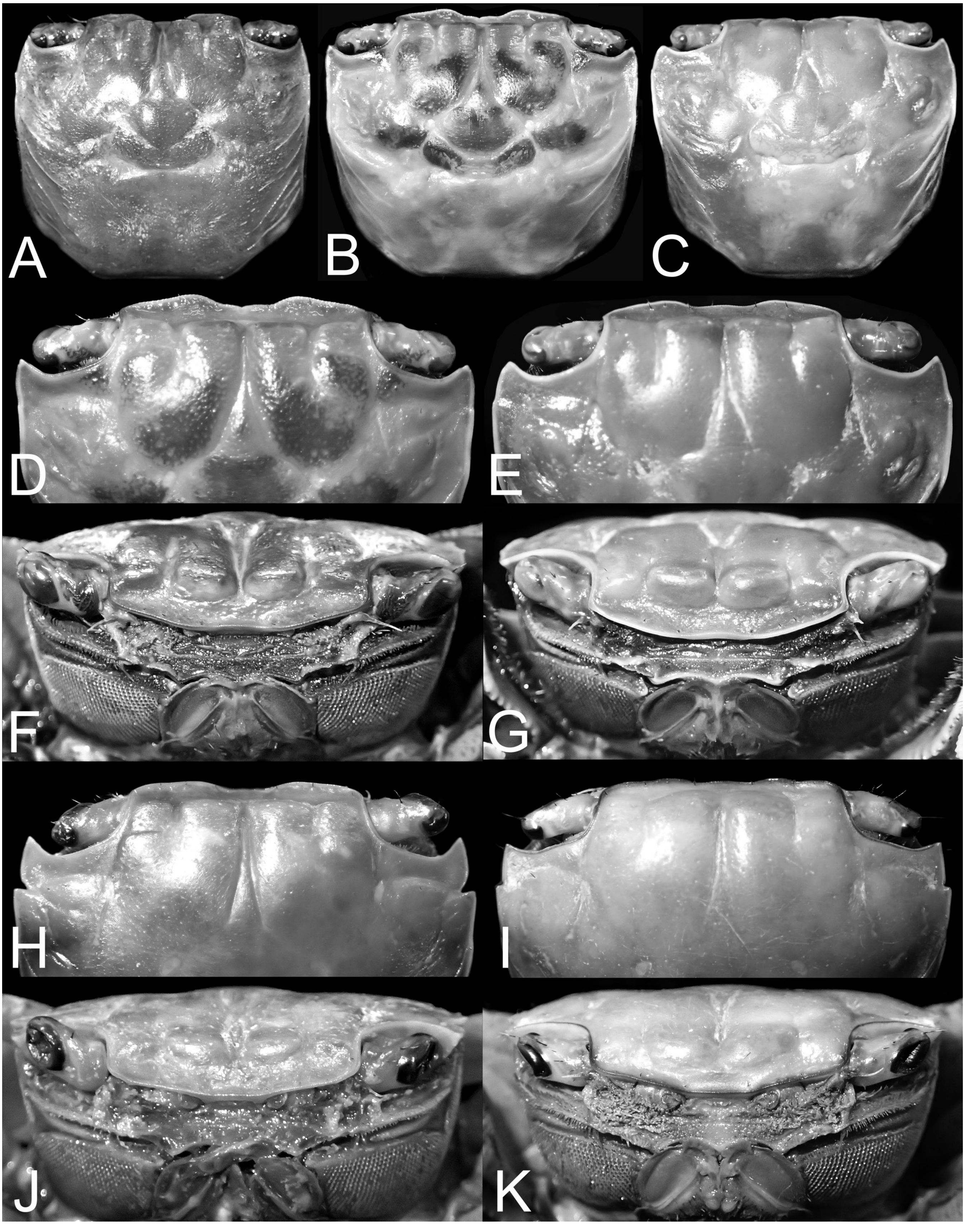

Fig. 4. A, F, *Orisarma dehaani*, male (36.4 × 34.4 mm) (ZRC 2011.1027), Kumejima Island, Japan; B, D, *O. dehaani*, male (27.6 × 29.6 mm) (ZRC 2002.0223), Hong Kong; C, E, G, *O. neglectum*, male (31.7 × 28.0 mm) (ZRC 1998.309), Shanghai, China; H, J, *O. intermedium*, male (29.5 × 26.5 mm) (ZRC 2001.0034), Pingtung, Taiwan; I, K, *O. sinense*, male (30.7 × 26.7 mm) (ZRC 2010.0421), China. A–C, dorsal view of carapace; D, E, H, I, frontal and anterolateral margins; F, G, J, K, frontal view of cephalothorax.

restricted to the mainland or larger continental islands, including Korea, the main island of Japan, mainland China and Taiwan.

**Biology**. According to Naruse & Ng (2008: 9), *C. ryukyuanus* is "found near small hills which are located just beside coastlines of bays".

**Distribution**. Thus far only known from the Ryukyu Islands (Naruse & Ng, 2008).

## *Orisarma*, new genus

**Type species**. *Sesarma dehaani* H. Milne Edwards, 1853, by present designation. Gender neuter.

**Diagnosis**. Carapace squarish to transversely subrectangular; frontal margin distinctly bilobed, gently deflexed, as wide as or slightly wider than posterior carapace margin; lateral margins of carapace entire, gently lobulated or with one epibranchial tooth, posterolateral part gently convex to subparallel; regions of carapace distinct to prominently demarcated; postfrontal and epigastric crests separated by relatively deep or distinct grooves, margin usually relatively rounded, regions clearly separated; basal articles of antenna and antennules clearly separated by septum formed by extension of front; dorsal margin of palm without any longitudinal pectinated ridge; in adult males, inner surface with prominent submedian transverse swelling, highest point with transverse ridge of granules, outer surface of palm and pollex convex, outer surface of palm usually with short longitudinal median smooth ridge (sometimes very low, obscured by granules); dorsal margin of chelipedal dactylus smooth, if small granules present, scattered, never in distinct row or of regular shape; inner distal margin of merus of cheliped not lamelliform; inner surfaces of first to third ambulatory coxae with only scattered short setae among them, not arranged into dense tufts; male thoracic sternites 2–4 relatively narrow in adults, suture between sternites 3 and 4 shallow, sometimes appearing medially interrupted; male sternopleonal cavity reaching two-thirds length of sternite 4 to just before anterior margin of sternite 2; male thoracic sternite 5 smooth, without depression on anterior part; G1 relatively slender, long or short, stout, chitinous part relatively short. Vulva on anterior part of sternite 6, anterior edge presses against sternite 5; anterior sternal vulvar cover very low, posterior sternal vulvar cover low, rim-like; opening projecting, directed anteriorly to obliquely anteriorly.

**Etymology**. The name is derived from the arbitrary combination of the term for East Asia, "Oriental", and the genus name *Sesarma*. The gender is neuter.

**Included species**. *Sesarma dehaani* H. Milne Edwards, 1853 (= *Sesarma hanseni* Rathbun, 1897); *Sesarma neglecta* De Man, 1887; *Chiromantes magnus* Komai & Ng, 2013; *Grapsus* (*Pachysoma*) *intermedius* De Haan, 1835; *Sesarma sinensis* H. Milne Edwards, 1853; *Pseudosesarma patshuni* Soh, 1978.

**Remarks**. The major differences between *Orisarma* and *Chiromantes* s. str. have been discussed under the latter genus. In addition to *Chiromantes dehaani* (H. Milne Edwards, 1853) and *C. neglectus* (De Man, 1887), two species of *Sesarmops* and one species of *Pseudosesarma* also need to be placed in *Orisarma*. As Serène & Soh (1970) had suspected (see Introduction), *Sesarmops intermedius* (De Haan, 1835) and *S. sinensis* (H. Milne Edwards, 1853) are more closely related to each other and to species of *Orisarma*. Surprisingly, we also find that all the morphological characters of the small species, *Pseudosesarma patshuni* Soh, 1978, also agree with *Sesarmops intermedius* and *S. sinensis*, including the form of the thoracic sternum, male chela with a low median longitudinal ridge, relatively wide male pleons, proportionately long ambulatory legs, structure of their G1s (Figs. 1G, H, 3F, 5H, I, 9H, 12K–O) and even in the structure of the vulvae (Fig. 43D). The closest genus to *Orisarma* may be *Manarma*, new genus, which consists of two species, *M. moeschii* (De Man, 1892) and *M. johorensis* (Tweedie, 1940). These two species, as already highlighted by Serène & Soh (1970), are characterised by their shiny carapaces, narrow thoracic sterna, narrow male pleons, and form of their G1s (cf. Figs. 24C, D, 26A, B, 29B, C, 33A, B, D, E, 58).

The remaining species of *Sesarmops* Serène & Soh, 1970 (type species *Sesarma impressa* H. Milne Edwards, 1837), have more trapezoidal carapaces and a relatively stout G1 with a very long chitinous distal process. One species still in *Sesarmops*, *S. weberi* (De Man, 1902), does not belong to this genus on account of its short G1 and a male chelipedal dactylar finger that has a row of stridulatory granules on the dorsal margin (see Ng et al., 2008a: 224; Naruse & Ng, 2020). Ng et al. (2008a) suggested the species was close to *Labuanium trapezoideum* (H. Milne Edwards, 1837) but Naruse & Ng (2020) showed otherwise. The systematic position of this species should be dealt with when *Sesarmops* is completely revised.

### *Orisarma dehaani* (H. Milne Edwards, 1853)

(Figs. 1C, D, 3B, 4A, B, D, F, 5D–F, 7E–G, 9C, 11A–G, 43B, 53A–E)

*Grapsus* (*Pachysoma*) *quadratus* – De Haan, 1835: 62, pl. 8 fig. 3.

*Sesarma dehaani* H. Milne Edwards, 1853: 184; Stimpson, 1858: 106 (part); De Man, 1887: 642; Bürger, 1893: 615; Ortmann, 1894: 718; Stimpson, 1907: 134 (part); Yamaguchi & Baba, 1993: 478, fig. 18b; Fransen et al., 1997: 128; Wang & Leung, 2001: 31, unnumbered figure.

*Sesarma hanseni* Rathbun, 1897: 92; Abele, 1975: 48, figs. 1, 2.

*Sesarma* (*Holometopus*) *dehaani* – Tesch, 1917: 158; Balss, 1922: 154 (part); Sakai, 1936: 234, pl. 65, fig. 1; Sakai, 1939: 682, pl. 77, fig. 1; Shen, 1940a: 97; Kamita, 1941: 217, text-fig. 120; Sakai, 1965: 202, pl. 97, fig. 2; Serène, 1968: 107; Baba & Miyata, 1971: 54; Kim, 1973: 487, text-fig. 217, pl. 95 fig. 167a, b, pl. 96 fig. 167c, d; Sakai, 1976: 655, pl. 224 fig. 2; Matsuzawa, 1977: pl. 110 fig. 2; Dai et al., 1986: 488, text-fig. 274(2), pl. 68(7); Nagai & Nomura, 1988: 43; Dai & Yang, 1991: 534, text-fig. 274(2), pl. 68(7); Huang, 1994: 597; Muraoka, 1998: 53.

*Holometopus dehaani* – Takeda, 1975: 147; Soh, 1978: 9, 10, pl. 2d; Takeda, 1982: 220, fig. 651.

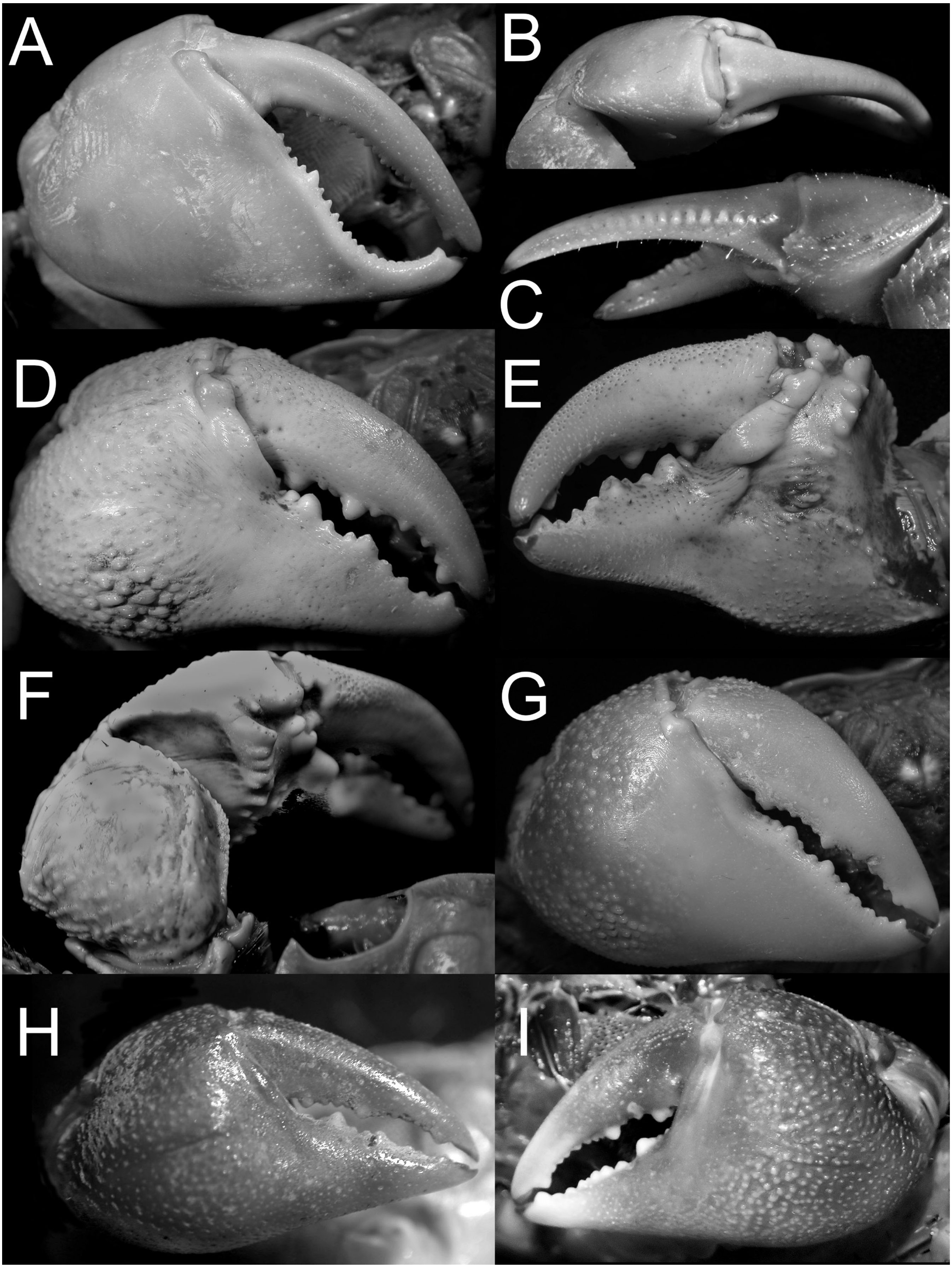

Fig. 5. Chela. A, B, *Chiromantes haematocheir*, lectotype male (33.7 × 29.7 mm) (RMNH-D160), Japan; C, *C. haematocheir*, male (18.6 × 20.7 mm) (RUMF-ZC-544), Japan; D–F, *Orisarma dehaani*, lectotype male (39.5 × 35.7 mm) (RMNH-D157), Japan; G, *O. neglectum*, neotype male (35.6 × 31.8 mm) (ZRC 1998.310), Shanghai, China; H, *O. patshuni*, male (14.2 × 13.0 mm) (ZRC 1998.345), Hong Kong; I, *O. patshuni*, male (20.4 × 18.2 mm) (ZRC 2012.0032), Hong Kong. A, D, G, H, I, outer view; B, C, F, dorso-lateral view; E, inner view.

*Chiromantes dehaani* – Miyake, 1983: 179, pl. 60-2; Liu & Ng, 1999: 229; Minemizu, 2000: 298; Kobayashi, 2000: 122, fig. 2n; Ng et al., 2001: 41 [includes references for this species from Taiwan up to 2001]; Kwok & Tang, 2005: 3, fig. 7; Takeda & Ueshima, 2006: 93; Lee, 2008: 135; Yang et al., 2008: 801; Naderloo & Schubart, 2009: 61–63, 67; Hong et al., 2010: 259; Liu & Wang, 2010: 57; Huang et al., 2011: 732; Li & Chiu, 2013: 40; Komai & Ng, 2013: 540, figs. 1B, 6A, 7A–C, G; Toyota & Seki, 2014: 190; Ng et al., 2017b: 102 [for other local references for Taiwan].

"*Chiromantes*" *dehaani* – Ng et al., 2008a: 220.

**Material examined**. Lectotype male (39.5 × 35.7 mm) (RMNH D 157), Japan, coll. v. Siebold. Others: JAPAN – 1 male (35.0 × 38.5 mm) (CBM-ZC 165), Obitsu River estuary, Kisarazu, Chiba Prefecture, July 1990, coll. T. Furota; 1 male (31.0 × 28.3 mm) (CBM-ZC 169), Hanami River, Chiba, Chiba Prefecture, coll. Nakano, 5 October 1990; 1 male (28.3 × 25.4 mm) (CBM-ZC 11406), Yahata Channel, Ichihara, Chiba Prefecture, coll. J. Takayama, 30 August 2012; 6 males (23.9 × 22.0 mm to 42.0 × 37.7 mm), 3 females (23.9 × 22.0 mm to 29.5 × 26.9 mm) (CBM-ZC 11458), Kaneda, Kisarazu, coll. T. Komai, May 2009; 1 male (27.3 × 24.5 mm) (ZRC 1968.4.22.12), coll. T. Sakai, 1968; 1 female (24.3 × 21.5 mm) (ZRC 1970.8.27.1), Kamakura, Kanagawa Prefecture, Sagami Bay, coll. T. Sakai, 1968; 2 males (22.0 × 20.2 mm, 23.5 × 21.1 mm) (CBM-ZC 7576), Tatara River, Fukuoka, Fukuoka Prefecture, coll. Y. Matsuzawa, March 2003; 1 ovigerous female (21.4 × 19.4 mm) (ZRC 2002.0226), river mouth, Izaku River, Satsuma Peninsula, Kagoshima Prefecture, coll. H. Suzuki, 30 August 2000; 2 males (larger 23.4 × 20.8 mm), 2 females (larger 25.2 × 22.0 mm) (ZRC 2012.0057), Koutsuki River, Kagoshima City, coll. P.K.L. Ng et al., 24 October 2011; 1 male (25.6 × 23.0 mm), 1 ovigerous female (27.4 × 23.9 mm) (CBM-ZC 3129), Tomari, Kume Island, Ryukyu Islands, coll. T. Komai, 12 June 1995; 1 male (38.3 × 36.6 mm) (ZRC 2011.1026), Zenda Forest Park, Kume Island, Ryukyu Islands, coll. T. Naruse et al., 15 November 2009; 3 males (largest 38.4 × 35.5 mm), 1 female (26.6 × 23.7 mm) (ZRC 2011.1027), Zenda Forest Park, Kume Island, Ryukyu Islands, coll. P.K.L. Ng et al., 17 November 2006; 1 female (36.2 × 31.7 mm) (CBM-ZC 9870), Ohtomi, Iriomote Island, Yaeyama Islands, coll. N. Shikatani, 29 April 1998; 1 male (35.4 × 32.4 mm) (ZRC 2000.2263), Iriomote Island, Ryukyu Islands, coll. Y. Cai & N.K. Ng, 15 June 2000. TAIWAN – 1 male (28.3 × 25.7 mm) (ZRC 2001.0025), near Tashi, northern Taiwan, coll. K.-X. Lee, 2000; 1 male (26.2 × 23.9 mm) (ZRC 2009.0871), Meilun stream, Hualien, coll. H.-C. Liu, 27 January 2002; 1 male, 1 female (ZRC 2000.1847), Hsinfeng mangroves, Hsinchu, coll. H.-C. Liu & C.D. Schubart, 17 September 1999; 1 male (ZRC 2002.0414), Lion Museum, Peikuan, Toucheng town area, coll. H.-C. Liu, 21 June 2002. CHINA – 2 males (ZRC 2010.0326), purchased, aquarium trade, supposedly from Guangzhou, China, coll. P.K.L. Ng, 2010. HONG KONG – 2 males (29.6 × 27.6 mm, 30.0 × 26.8 mm) (ZRC 2002.0223), coll. H.H. Tan, July 2000; 2 males (24.7 × 21.5 mm, 22.5 × 19.5 mm), 1 female (24.8 × 21.2 mm) (ZRC 1975.6.30.12–14), Tai Po, New Territories, coll. C.L. Soh, 8 June 1975; 6 males, 2 females (ZRC 2019.0539), back mangroves, ca. 22.492306°N 114.036169°E, Mai Po Nature Reserve, coll. S. Cannici, K. Wong, et al. 24 May 2019.

**Diagnosis**. Carapace distinctly quadrate to transversely rectangular; lateral margin crenulated to entire but no trace of epibranchial tooth; posterolateral margins subparallel or gently converging towards posterior carapace margin; dorsal surface relatively lower, gastric region less swollen, grooves separating regions deep, prominent; frontal lobes separated by deep, broad concavity; ambulatory merus relatively broader; chitinous part of G1 with basal part slightly constricted, distal part relatively broader. In life, carapace dark grey to brown, often with dark median patches, chelae grey to white, with proximal parts sometimes purplish.

**Colour**. The dorsal carapace surface of fresh *O. dehaani* is grey to dark purplish-brown, often with black or dark blotches on the gastric and adjacent areas (Fig. 53A, C). The chelipeds vary from white to pale purple (see also Miyake, 1983; Minemizu, 2000; Liu & Wang, 2010; Li & Chiu, 2013; Toyota & Seki, 2014).

**Remarks**. The type series is represented by 11 specimens (Fransen et al., 1997), and the lectotype was selected by Yamaguchi & Baba (1993). This well-known species has a wide range from Japan to southern China. The distribution is interesting as it seems to bracket the range of *O. neglectum* from Shanghai and Taiwan. The present specimens from Hong Kong are all easily referrable to *O. dehaani* as presently defined, confirming the reports of Soh (1978).

The record of *S. hanseni* Rathbun, 1897, from the West Indies is clearly incorrect (Abele, 1975: 48, figs. 1, 2), and from her description, it seems clear that this species is conspecific with *S. dehaani*.

**Biology**. *Orisarma dehaani* is typically associated with coastal rocky supralittoral habitats, living under rocks, or more often in deep burrows in the soil. They may be present in habitats over 100 metres from the shore or along coastal streams. This contrasts with the closely related *O. neglectum* that appears to prefer muddier and more open littoral habitats. Nara et al. (2006) discussed the social behaviour in this species in Japan, with Hong et al. (2010) commenting on its ecology from Korea. The larval development has been described by Baba & Miyata (1971). Nematode parasites have been reported on by Yoshimura (1990).

**Distribution**. Korea to Japan, Ryukyus, Taiwan, southern part of mainland China.

### ***Orisarma neglectum* (De Man, 1887)**

(Figs. 1E, 3C, 4C, E, G, 5G, 7H, 11H–L, 36D, 53F)

*Sesarma dehaani* – Heller, 1865: 62. [not *Sesarma dehaani* H. Milne Edwards, 1853]

*Sesarma neglecta* De Man, 1887: 643, 661.

*Sesarma* (*Sesarma*) *neglecta* – Tesch, 1917: 178.

*Sesarma* (*Holometopus*) *dehaani* – Balss, 1922: 154 (part); Shen, 1932: 195, text-figs. 121–123. [not *Sesarma dehaani* H. Milne Edwards, 1853]

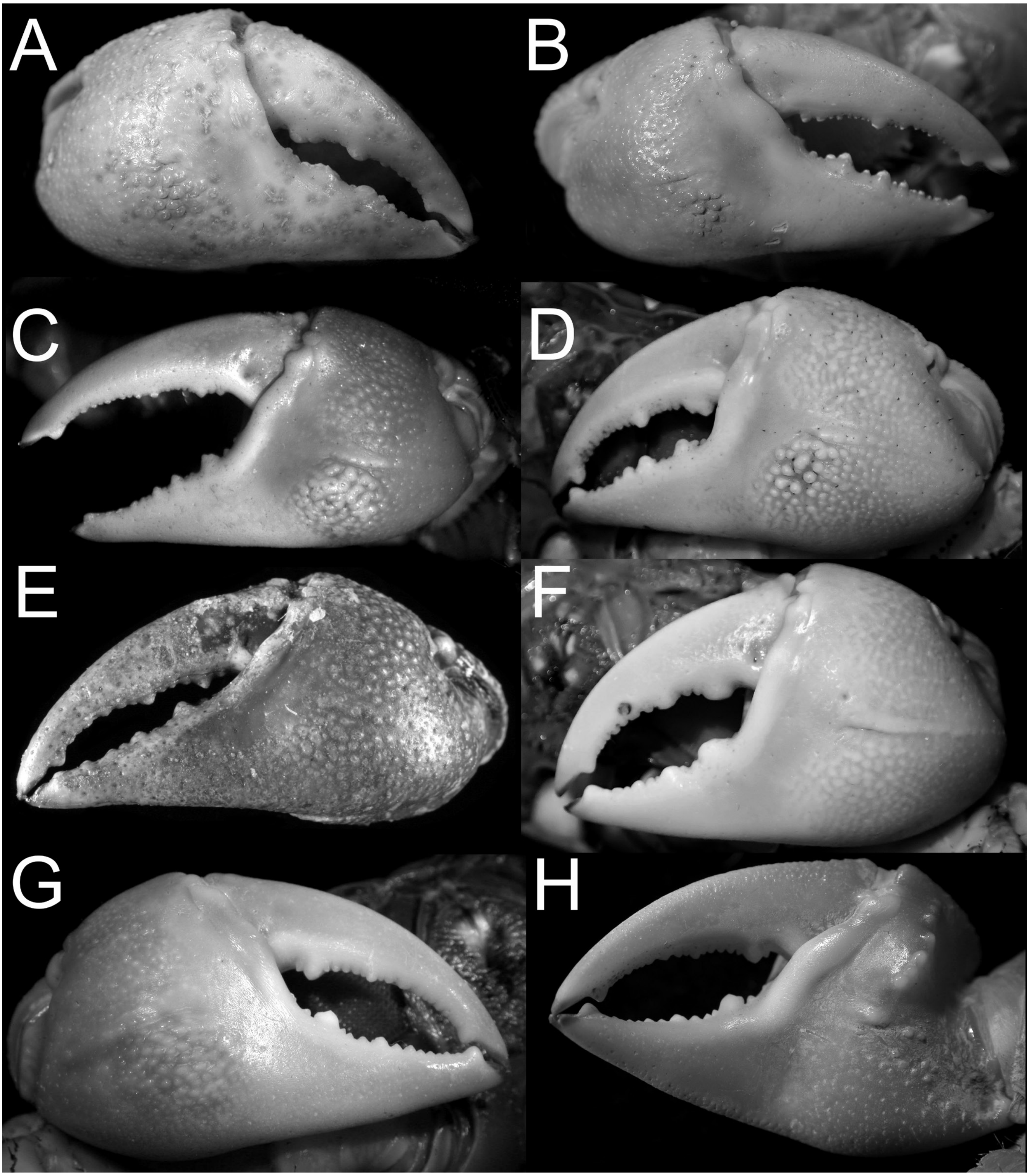

Fig. 6. Chela. A, *Orisarma intermedium*, lectotype male (23.0 × 19.9 mm) (RMNH-D165), Japan; B, *O. intermedium*, male (27.1 × 25.2 mm) (ZRC 1970.2.23.6), Japan; C, *Orisarma intermedium*, male (34.7 × 31.6 mm) (ZRC 2001.0034), Pingtung, Taiwan; D, *O. intermedium*, male (37.5 × 35.8 mm) (ZRC 2014.0265), Kumejima Island, Japan; E, *O. sinense*, lectotype male (19.0 × 16.6 mm) (MNHN-BP3635a), China; F, *O. sinense*, male (30.7 × 26.7 mm) (ZRC 2010.0421), China; G, H, *O. sinense*, male (29.6 × 25.4 mm) (ZRC 1998.1204), Shanghai, China. A–G, outer view; H, inner view.

?*Sesarma* (*Holometopus*) *neglecta* – Shen, 1940a: 97.
*Chiromantes dehaani* – Liu & He, 2007: 161. [not *Sesarma dehaani* H. Milne Edwards, 1853]
*Chiromantes neglectum* – Ng et al., 2001: 41; Komai & Ng, 2013: 540, figs. 6B, 7D–F, H.
"*Chiromantes*" *neglectum* – Ng et al., 2008a: 220.

**Material examined**. Neotype (here designated): male (35.6 × 31.8 mm) (ZRC 1998.310a), Shanghai, Qidong, Jiangsu Province, China, coll. Y.Y. Li, 2 May 1996. Others: CHINA – 15 males (smallest 22.7 × 20.0 mm, largest 35.5 × 32.5 mm), 6 females (smallest 16.7 × 14.5 mm, largest 27.2 × 23.7 mm) (ZRC 1998.310b), 1 male (30.2 × 25.5 mm), 1

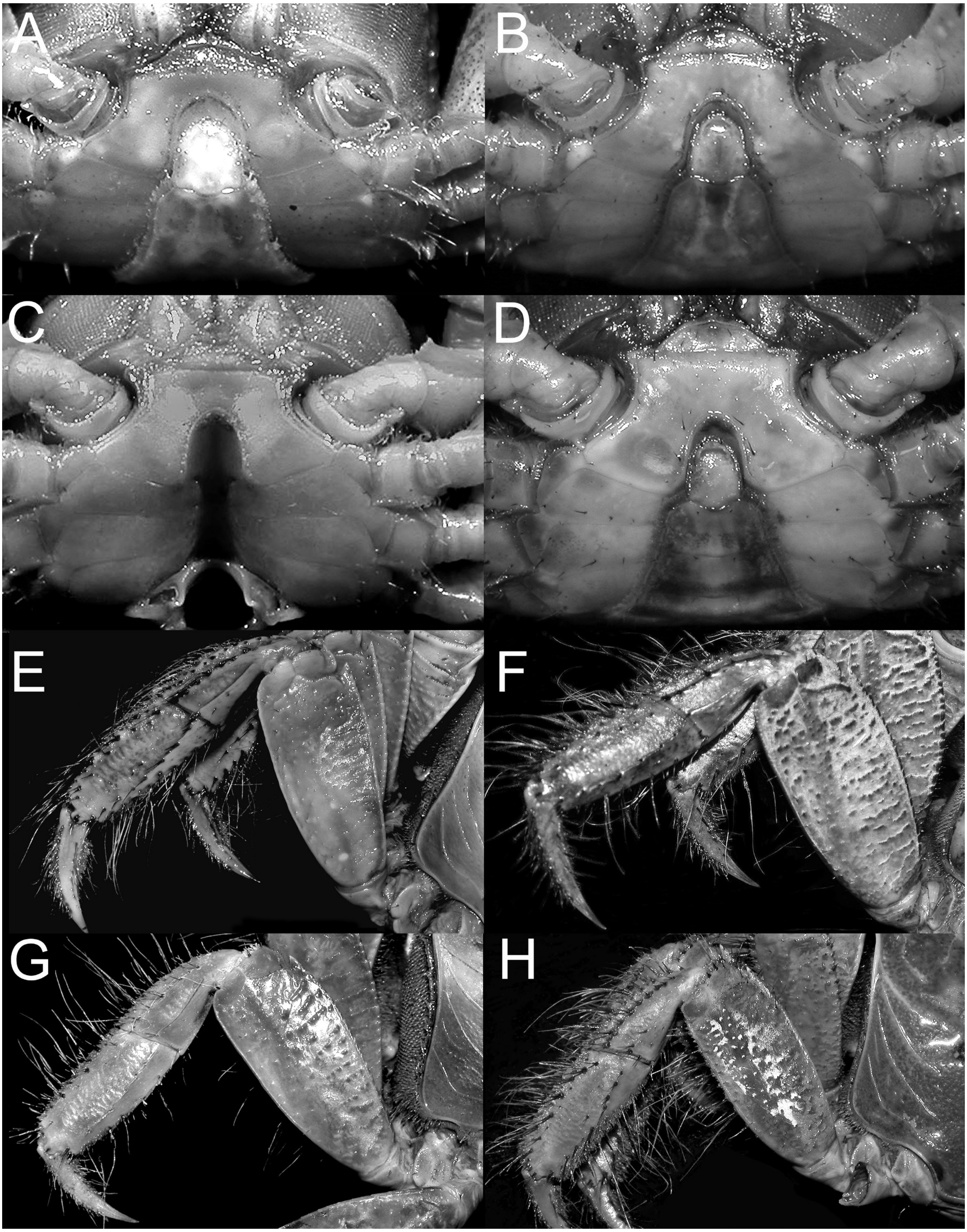

Fig. 7. A–D, *Chiromantes haematocheir*, anterior male thoracic sternum; A, male (10.8 × 9.4 mm) (ZRC 2012.1222), Hong Kong; B, male (14.3 × 13.0 mm) (ZRC 2012.1222), Hong Kong; C, male (18.4 × 16.6 mm) (lectotype of *Holometopus serenei*) (NHM 1978.107), Hong Kong; D, male (27.8 × 23.9 mm) (ZRC 2012.1221), Hong Kong. E–H, left third ambulatory legs; E–G, *Orisarma dehaani*: E, lectotype male (39.5 × 35.7 mm) (RMNH-D157), Japan; F, male (35.4 × 32.4 mm) (ZRC 2000.2263), Iriomote Island, Japan; G, male (29.6 × 27.6 mm) (ZRC 2002.0223), Hong Kong; H, *O. neglectum*, neotype male (35.6 × 31.8 mm) (ZRC 1998.310), Shanghai, China.

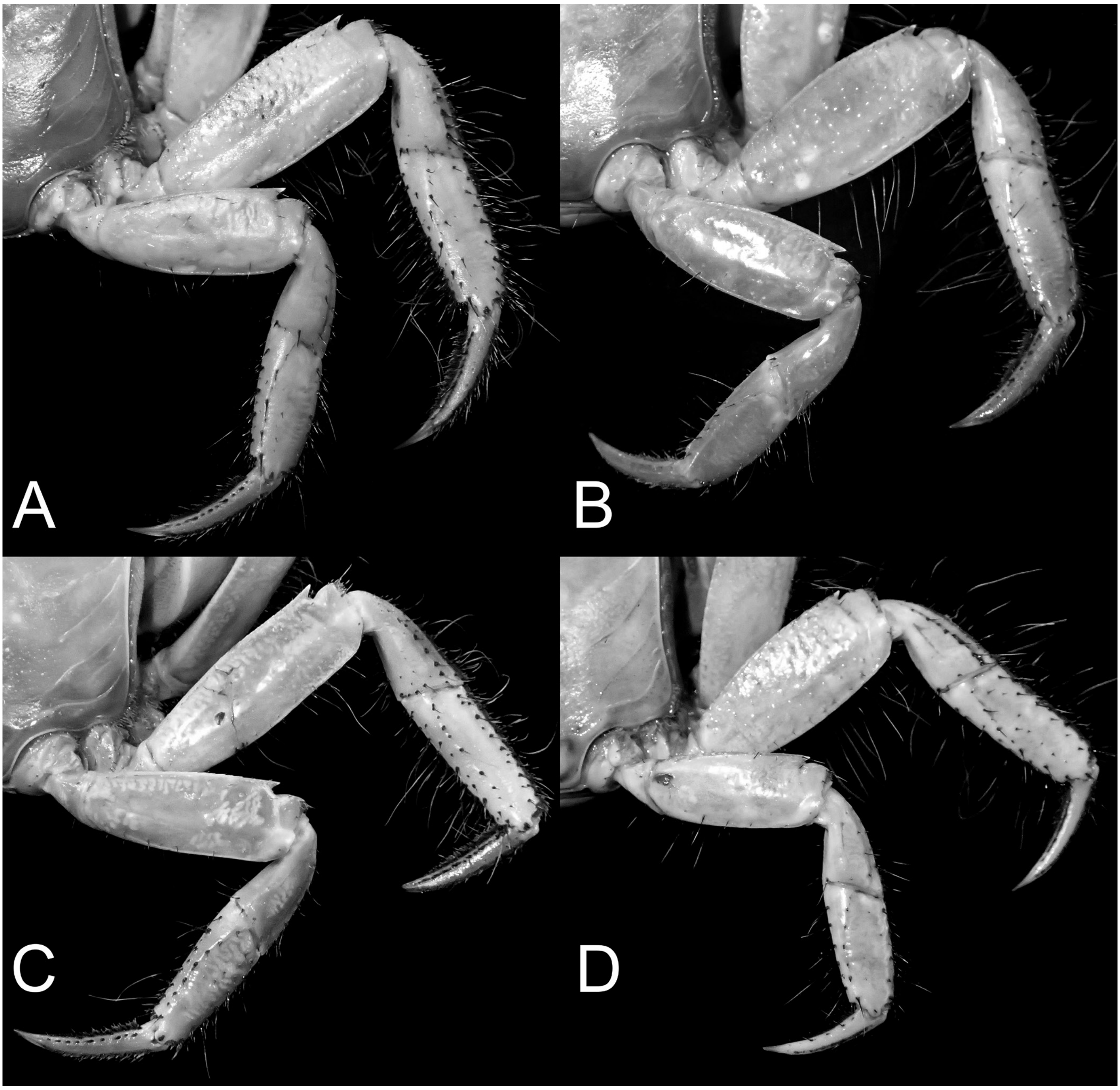

Fig. 8. Right third and fourth ambulatory legs. A, *Orisarma intermedium*, male (27.0 × 25.0 mm) (ZRC 2013.0140), Kyushu, Japan; B, *O. intermedium*, male (29.5 × 26.5 mm) (ZRC 2001.0034), Pingtung, Taiwan; C, *O. intermedium*, male (37.5 × 35.8 mm) (ZRC 2014.0265), Kumejima Island, Japan; D, *O. sinense*, male (30.7 × 26.7 mm) (ZRC 2010.0421), China.

female (25.0 × 21.5 mm) (CBM-ZC 11459), Qidong, Lusi, Shanghai, coll. Y.Y. Li, 1 May 1996; 1 male (31.7 × 28.0 mm) (ZRC 1998.309), Qi Dong, Lusi, Shanghai, coll. Y.Y. Li, 1 May 1996; 3 males (ZRC), Chongming Island, Chongming Dao Bird Sanctuary, Shanghai, coll. N.K. Ng & L.K. Wang, 10 June 2005; 1 male (ZRC 2010.0420), Chongming, west of Shiqiao River, 31°38.37′N 121°21.496′E, coll. B.Y. Au, 15 July 2010.

**Diagnosis**. Carapace subtrapezoidal to quadrate; lateral margin entire, no trace of epibranchial tooth; posterolateral margins clearly converging towards posterior carapace margin; dorsal surface relatively higher, gastric region more swollen, grooves separating regions shallow, not prominent; frontal lobes relatively lower, median concavity between lobes shallow; ambulatory merus usually relatively more slender; chitinous part of G1 evenly cylindrical. In life, carapace grey, sometimes with dark median patches, chelae white and grey.

**Colour**. The dorsal carapace surface of fresh *O. neglectum* is generally a uniform grey to dark grey or brown, often with the gastric regions sometimes with symmetrically arranged dark grey blotches (Fig. 53F). The chelae are whitish with the granules grey, never purple (Fig. 53F).

**Remarks**. This species has long been regarded as a junior synonym of *O. dehaani*. In comparing *O. neglectum* with *O. dehaani*, De Man (1887) noted that one of the main differences was the higher carapace. Tesch (1917: 145) noted that the proportions of the carapace width, form of the lateral carapace margins and front were also different, and the inner surface of the palm of *O. neglectum* does not have a transverse row of granules, but it seems he did not have specimens and based this comparison primarily from De Man's (1887) description.

We have examined a good series of *O. neglectum* specimens from the type locality, Shanghai in China, and we are confident it is distinguishable from *O. dehaani*. Most of the characters enumerated by De Man (1887) and Tesch (1917) are not valid, varying too much to be useful, although the difference in height of the carapace is valid. Smaller specimens of *O. neglectum* have lower transverse ridges on the inner surface of the palm, certainly much lower than in very large males. The major difference which distinguishes *O. neglectum* immediately from *O. dehaani* is its relatively higher carapace, with the gastric region more distinctly swollen, and the grooves separating the regions shallower and less prominent (Figs. 1E, 3C, 4C, E, G versus Figs. 1C, D, 3B, 4A, B, D, F). The shape of the carapace is different: in *O. dehaani*, the carapace is distinctly quadrate to transversely rectangular, with the posterolateral margins subparallel or gently converging (Fig. 4A, B) whereas it is subtrapezoidal to quadrate in *O. neglectum*, with the posterolateral margins clearly converging towards the posterior carapace margin (Fig. 4C). The structure of the frontal margin is quite different. In *O. dehaani*, the two prominent frontal lobes are separated by a deep and broad concavity (Fig. 4D). In *O. neglectum* on the other hand, the two frontal lobes are relatively lower and the median concavity is shallow (Fig. 4E). The G1s of the two species differ slightly with the chitinous part of *O. dehaani* having the basal part slightly constricted and the distal part broader (Fig. 11C–F). In *O. neglectum*, the distal chitinous part is evenly cylindrical (Fig. 11I–L). The relative length of the chitinous part varies slightly with size, being slightly longer in smaller specimens. The ambulatory legs of *O. neglectum* (especially the merus) are also typically more slender (Fig. 7H), with those of *O. dehaani* relatively broader (Fig. 7E–G); although it does vary and the difference is less easy to appreciate in smaller specimens. The live colours are also different. The dorsal carapace surface of freshly preserved or live *O. dehaani* often have large dark brown to black blotches medially (Fig. 53A, C), while in *O. neglectum*, it is usually a uniform grey, with the gastric regions sometimes with dark grey blotches (Fig. 53F).

*Orisarma neglectum* is only known with certainty from and around Shanghai, China, for the moment. As noted earlier, *O. dehaani* is now known from many parts of mainland China, Hong Kong, south of Taiwan, etc. (see Shen, 1940a, b; Dai et al., 1986; Dai & Yang, 1991), and detailed surveys of the southern coast of China are needed to establish the actual distributions of both taxa, especially since *O. neglectum* has long been regarded as a junior synonym. Shen (1940a: 97) actually recognised *O. neglectum* as a good species (as a *Sesarma* (*Holometopus*)) on the basis of specimens from Shanghai and southern China, but only commenting that "The specimens from Canton are not likely the young forms of *Sesarma* (*Holometopus*) *dehaani* H. MILNE-EDWARDS". The characters he used were not stated, and considering that he had specimens of what he regarded as *O. dehaani* from many parts of China (Shen, 1940a: 97), all the old material will need to rechecked to ascertain their identities. Certainly most of the older records will need to be re-examined (e.g., Stimpson [1907] recorded what was supposedly *O. dehaani* from Whampoa in southern China). It is possible that the uncertain identity of *O. neglectum* s. str. has contributed to the confusion. Fresh collections will also be needed to establish their actual distributions and where they may overlap. From what we have observed thus far at least, we have not seen any specimens or photographs/figures clearly referable to *O. neglectum* from south of Shanghai in China.

The whereabouts of the solitary type specimen of *O. neglectum* is not known. It is neither in Leiden, Amsterdam nor Paris, and we believe it is no longer extant (see also Ng et al., 2001). Since it is close to *S. dehaani* and can easily be confused (and has been), we feel that it is necessary to select a neotype for the species to stabilise its taxonomy. We hereby designate a male specimen 35.6 × 31.8 mm from Shanghai (ZRC 1998.310) as the neotype of *Sesarma neglecta* De Man, 1887.

**Biology**. Not much is known about the biology of *O. neglectum* s. str. except that it is common in mudflats and associated areas in mainland China, mainly in locations north of Fujian. Yang et al. (2014) reported on an interesting habit of some individuals from populations in Chongming Island outside Shanghai in China climbing shrubs to attack bird nests. We are confident these are *O. neglectum* as photographs of this species sent to us by W. Liu confirm this, and we have a specimen from near this location.

**Distribution**. From what is known, *O. neglectum* is found north of Fujian, China. Specimens we have examined from Hong Kong and southern China are all *O. dehanni* s. str. so far. Stefano Cannicci (pers. comm.), however, notes that it has been found in small numbers in Hong Kong. This is a pattern of distribution shared with other thoracotreme taxa like *Eriocheir japonica*, *E. sinensis*, and *E. hepuesis* (Varunidae, e.g., see Xu et al., 2009; Naser et al., 2012).

### *Orisarma magnum* (Komai & Ng, 2013)
(Figs. 1F, 11M–P)

*Sesarma dehaani* – Stimpson, 1858: 106 (part); Stimpson, 1907: 134 (part); Parisi, 1918: 111 (part); Asakura et al., 1993: 10.
*Holometopus dehaani* – Takeda & Miyake, 1976: 113 (list).
*Sesarma* (*Holometopus*) *dehaani* – Ooishi, 1970: 95.
*Chiromantes dehaani* – Marumura & Kosaka, 2003: 66 (part); Takeda & Ueshima, 2006: 93 (part); Komatsu, 2011: 277 (list).
*Chiromantes magnus* Komai & Ng, 2013: 539, figs. 1A, 2–5; Toyota & Seki, 2014: 191.

**Material examined.** Holotype: male (52.2 × 47.2 mm) (CBM-ZC 11452), Renju Valley, Chichi-jima Island, Ogasawara Islands, coll. H. Tachikawa, 23 September 2008. Paratypes: 1 male (50.1 × 44.4 mm) (CBM-ZC 11456), 1 male (50.6 × 45.6 mm) (ZRC 2013.0173), same data as holotype; 1 male (41.8 × 37.9 mm) (CBM-ZC 11453),

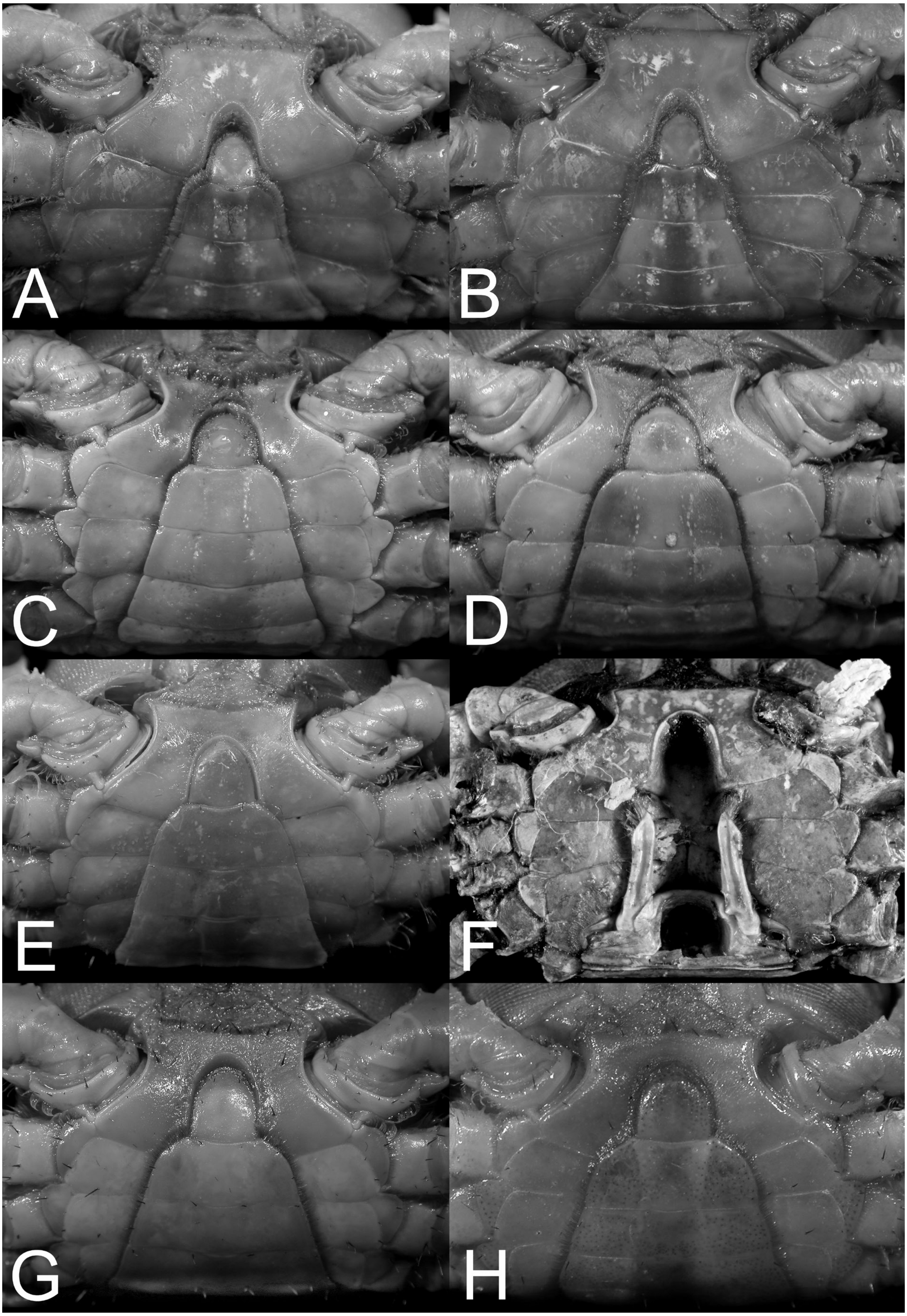

Fig. 9. Male anterior thoracic sternum and pleon. A, *Chiromantes haematocheir*, lectotype male (33.7 × 29.7 mm) (RMNH-D160), Japan; B, *C. ryukyuanus*, holotype male (33.1 × 29.6 mm) (RUMF-ZC-539), Okinawa Island, Japan; C, *Orisarma dehaani*, lectotype male (39.5 × 35.7 mm) (RMNH-D157), Japan; D, *O. neglectum*, neotype male (35.6 × 31.8 mm) (ZRC 1998.310), Shanghai, China; E, *O. intermedium*, lectotype male (23.0 × 19.9 mm) (RMNH-D165), Japan; F, *O. sinense*, lectotype male (19.0 × 16.6 mm) (MNHN-BP3635a), China; G, *O. sinense*, male (29.6 × 25.4 mm) (ZRC 1998.1204), Shanghai, China; H, *O. patshuni*, male (14.2 × 13.0 mm) (ZRC 1998.345), Hong Kong.

Kominato, Chichi-jima Island, coll. T. Komai, 10 December 2005; 1 male (28.2 × 25.5 mm) (CBM-ZC 11454), Kopepe Beach, Chichi-jima Island, coll. T. Komai, 11 December 2005; 1 male (45.2 × 40.8 mm) (RUMF-ZC 2160), same locality, coll. Y. Fujita, 22 June 2010; 1 ovigerous female (43.5 × 40.2 mm) (RUMF-ZC 2362), same data as above; 1 male (49.8 × 44.0 mm) (RUMF-ZC 2360), same locality as above, coll. Y. Fujita, 27 June 2010; 4 males (smallest 18.2 × 15.8 mm, largest 28.5 × 26.1 mm), 1 female (27.9 × 25.2 mm), CBM-ZC 11455, Chichi-jima Island, coll. K. Iwasaki et al., August 2008; 1 male (50.3 × 45.5 mm) (CBM-ZC 11457), Okumura River, river mouth, coll. H. Tachikawa, 28 September 2008; 1 female (CBM-ZC 11600), Kiyose, Chichi-jima Island, coll. T. Komai, 14 July 2009; 1 male (28.3 × 25.3 mm) (RUMF-ZC 2361), same locality as above, coll. Y. Fujita, 25 June 2010.

**Diagnosis**. Carapace subquadrate; lateral margin entire, no trace of epibranchial tooth; posterolateral margins gently diverging towards posterior carapace margin; dorsal surface relatively lower, gastric region less swollen, grooves separating regions deep, prominent; frontal lobes separated by deep, broad concavity; ambulatory merus relatively long; chitinous part of G1 evenly cylindrical. In life, carapace with mottled pattern of black-brown and gray-brown or yellowish gray; chelae light olive or yellowish gray.

**Colour**. Komai & Ng (2013: 547) noted that in life "the carapace has a mottled pattern of black-brown and gray-brown or yellowish gray with scattered whitish spots; the carpus and the dorsal part of chela are light olive or yellowish gray; striae on the ambulatory meri are dark brown".

**Remarks**. The taxonomy of this species was treated at length by Komai & Ng (2013). The main differences between *O. magnum* and the related *O. dehaani* and *O. neglectum* (other than its much larger adult size) are gently diverging posterolateral margins which give it a more subtrapezoidal appearance (Fig. 1F) and the proportionately longer and more slender ambulatory meri (Fig. 1F). Their colours in life also differ, with that of *O. magnum* being unusually mottled.

In the current genetic dataset, there are no obvious genetic differences between *O. magnum*, *O. neglectum*, and *O. dehaani*, which should normally be expected for intraspecific relationships. We see a similar pattern for the closely related *O. intermedium* and *O. sinense*. The morphological differences, however, are such that all three of them must be recognised as distinct species. The relative gigantism of *O. magnum* may be due to the effects of island life as the Ogasawara Islands are very isolated and over 1000 km away from mainland Japan, but this is probably not enough to explain its much larger size.

**Biology**. Komai & Ng (2013: 547) comment that "Individuals occur in estuarine areas to middle parts of rivers or streams where tidal influence is completely absent, sometimes extending to adjacent marsh areas, and sometimes found in burrows under rocks". This is not dissimilar to *O. dehaani* which has also been found some distance from the sea. Nevertheless, the water table (which they can reach through their burrows) is probably still at least brackish in content.

**Distribution**. Known only from the Ogasawara Islands thus far (Komai & Ng, 2013).

### *Orisarma intermedium* (De Haan, 1835)

(Figs. 2A–F, 3D, 4H, J, 6A–D, 8A–C, 9E, 12A–E, 33C, F, 43C, 54A–C)

*Grapsus* (*Pachysoma*) *intermedius* De Haan, 1835: 61, pl. 16 fig. 5.

*Sesarma intermedia* – H. Milne Edwards, 1853: 186; Stimpson, 1858: 105; Herklots, 1861: 17; De Man, 1880: 25; Miers, 1880: 314; De Man, 1887: 649; De Man, 1892: 337; Ortmann, 1894: 721; Stimpson, 1907: 133.

*Sesarma intermedius* – Fransen et al., 1997: 130.

*Sesarma* (*Sesarma*) *intermedia* – Tesch, 1917: 162; Balss, 1922: 155 (part); Sakai, 1936: 235, pl. 65 fig. 3; Sakai, 1939: 684, pl. 78 fig. 3; Shen, 1940a: 95; Shen, 1940b: 236; Kamita, 1941: 224, fig. 124; Sakai, 1965: 202, pl. 97 fig. 3; Kim, 1973: 489, text-fig. 218, pl. 94 fig. 168.

*Sesarma* (*Sesarma*) *intermedium* – Serène, 1968: 105.

*Sesarmops intermedium* – Serène & Soh, 1970: 401; Sakai, 1976: 659, pl. 224 fig. 3; Matsuzawa, 1977: pl. 111 fig. 1; Soh, 1978: 11, pl. 4b; Takeda, 1982: 221, fig. 655; Miyake, 1983: 179, pl. 60-3; Nagai & Nomura, 1988: 44; Muraoka, 1998: 54; Minemizu, 2000: 298; Kobayashi, 2000: 122, fig. 2o; Tsai et al., 2000: 61; Ng et al., 2001: 43 [includes references for this species from Taiwan up to 2001]; Ho, 2003: 32, 33; Cuesta et al., 2006: 162, fig. 13A–E; Takeda & Ueshima, 2006: 99; Yang et al., 2008: 802; Lee, 2008: 133; Liu, 2009: 49, fig. 19; Naderloo & Schubart, 2009: 62, 63, 67; Liu & Wang, 2010: 62, 63; Rademacher & Mengedoht, 2011: 31; Huang & Liu, 2012: 267; Li & Chiu, 2013: 57; Toyota & Seki, 2014: 192, 193; Ng et al., 2017b: 106 [for other references for Taiwan].

"*Sesarmops*" *intermedius* – Ng et al., 2008a: 220.

*Sesarmops intermedius* – Hong et al., 2010: 259, fig. 3b; Lee et al., 2012: 183; Lee, 2015: 321.

**Material examined**. Lectotype male (23.0 × 19.9 mm) (RMNH D 165), Japan, coll. H. Bürger. Paralectotype: 1 female (RMNH D 165), same data as lectotype. Others: JAPAN – 1 male (27.1 × 25.2 mm) (ZRC 1970.2.23.6), coll. T. Sakai, 1968; 1 female (22.7 × 20.0 mm) (ZRC 1970.8.27.3), Manazuru, Sagami Bay, coll. T. Sakai, 1968; 1 female (23.0 × 20.4 mm) (ZRC), river mouth, Izaku River, Satsuma Peninsula, Kagoshima Prefecture, coll. H. Suzuki, 30 August 2000; 4 males (largest 27.0 × 25.0 mm), 4 females (largest 32.1 × 29.3 mm) (ZRC 2013.0140), in brackish water stream, Tomioka, Amakusa, Shikizuki, Japan, coll. J. Lai, 2 September 2002; 1 male (36.4 × 32.4 mm), 2 females (largest 29.0 × 26.9 mm, smallest 33.5 × 30.4 mm) (ZRC 2000.2262), Iriomote Island, Ryukyu Islands, coll. Y. Cai & N.K. Ng, 15 June 2000; 1 female (ZRC 2000.2265), Japan, Nagama river second site from headwaters, Okinawa, coll. Y.X. Cai & N.K. Ng, 15 June 2000; 1 female (ZRC 2000.2266), Japan, along the track to the headwaters of Nagama River, found in dead fallen tree trunk, Okinawa, coll. Y.X. Cai & N.K. Ng, 15 June 2000; 1 male (29.3 × 26.8 mm) (ZRC), Yenbaru, Okinawa, coll. B.Y. Lee, 18 September 2012; 1 male (37.5 × 35.8 mm) (ZRC 2014.0265), Zenda Forest Park, Kume Island, Ryukyu Islands, coll. P.K.L. Ng et al., 17 November 2006. TAIWAN – 1 female (ZRC 2001.0033),

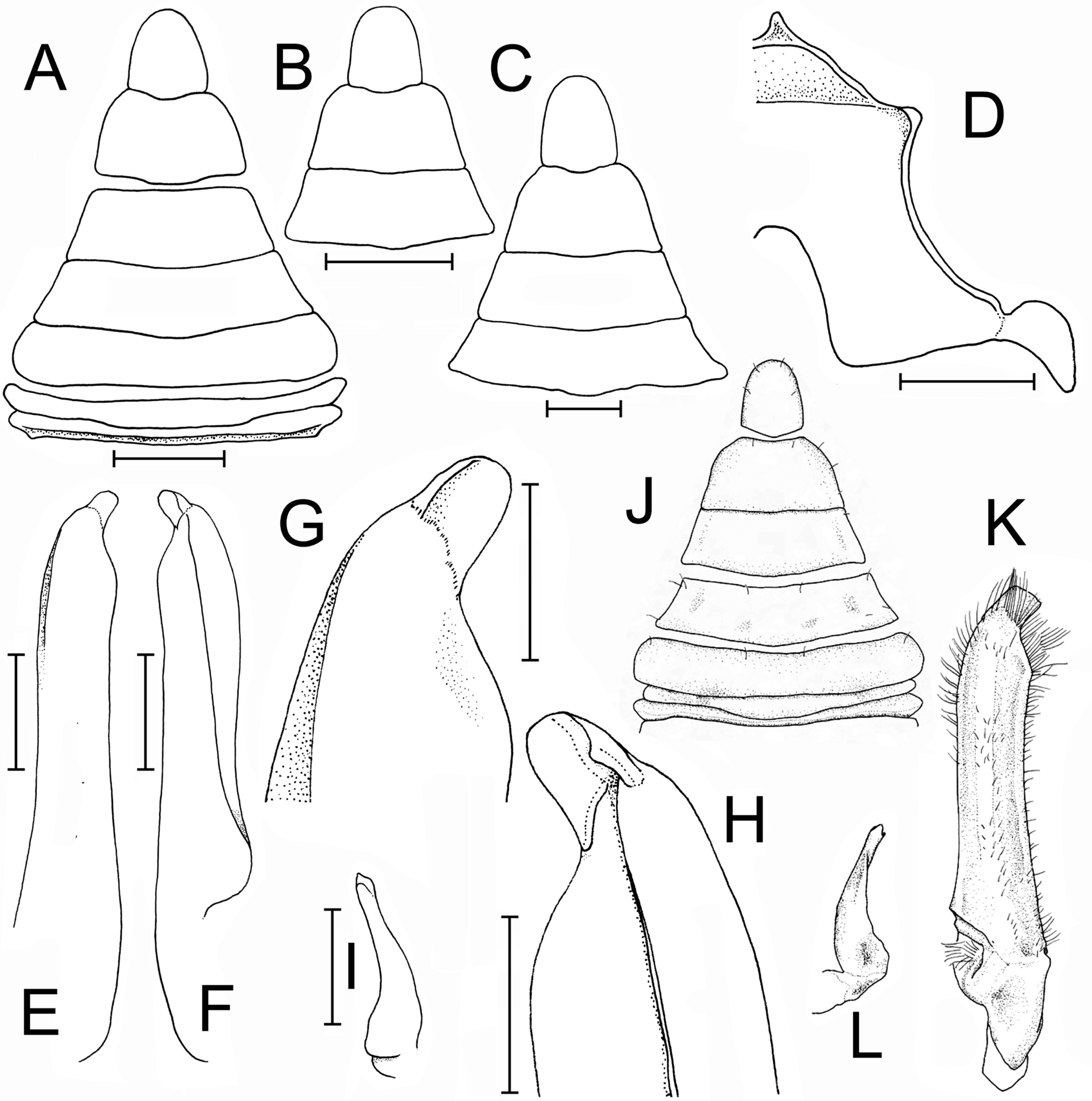

Fig. 10. A, D, E–I, *Chiromantes haematocheir*, lectotype male (33.7 × 29.7 mm) (RMNH-D160), Japan; B, male (26.4 × 22.9 mm) (ZRC 1970.8.27.7), Sagami Bay, Japan; C, *C. haematocheir*, male (lectotype of *Holometopus serenei*) (18.4 × 16.6 mm) (NHM 1978.107), Hong Kong; J–L, *C. ryukyuanus*, holotype male (33.1 × 29.6 mm) (RUMF-ZC-539), Okinawa Island, Japan. A, J, male pleon; B, male pleonal somite 6 and telson; male pleonal somites 4–6, telson; D, anterior thoracic sternites 1–4; E, left G1 (ventral view, denuded); F, left G1 (dorsal view, denuded); G, left distal part of G1 (ventral view, denuded); H, left distal part of G1 (dorsal view, denuded); I, L, left G2 (denuded); K, left G1. Scales: A, B, D = 5.0 mm; C, E, F, I = 2.0 mm; G, H = 1.0 mm. J–L, after Naruse & Ng (2008: fig. 8).

northeastern Taiwan, Ilan county, Tahsi, coll. K.X. Lee, 2000; 1 ovigerous female, 1 juvenile male, 1 juvenile female (ZRC), Hualien county, Hualien city, mouth of Meilun stream, 23°58′54″N 121°36′37″E, eastern Taiwan, coll. P.K.L. Ng & H.-C. Liu, 22 June 2002; 1 male, 1 female, 1 juvenile (ZRC 2000.1834), Rangkon river mouth, coll. H.-C. Liu & C.D. Schubart, 14 September 1999; 4 males (largest 23.5 × 21.2 mm, smallest 29.0 × 25.8 mm), 6 females (largest 23.9 × 20.7 mm, smallest 28.0 × 24.2 mm) (ZRC 1999.527), Tung Kou stream, Kenting National Park, Pingtung, Hengchun Peninsula, coll. P.K.L. Ng et al., 2000; 1 male, 5 females (ZRC 2002.0477), Kang Kou Hsi, Kentin Park, Pingtung, southern Taiwan, coll. P.K.L. Ng & C.-H. Wang, 5 August 2002; 2 males (29.5 × 26.5 mm, 34.2 × 30.7 mm) (ZRC 2001.0034), Pingtung, Hengchun, Chang-Wai, coll. P.K.L. Ng, 7 November 2000; 1 male, 1 female (ZRC 2007.0208), purchased from aquarium trade, supposedly from Taiwan, coll. S.H. Tan, 7 May 2007; 2 females (17.8 × 15.8 mm, 15.5 × 13.4 mm), rice field mouth, Checheng-Pingtung, southern Taiwan, coll. H.-C. Liu & C.D. Schubart, 15 September 1999.

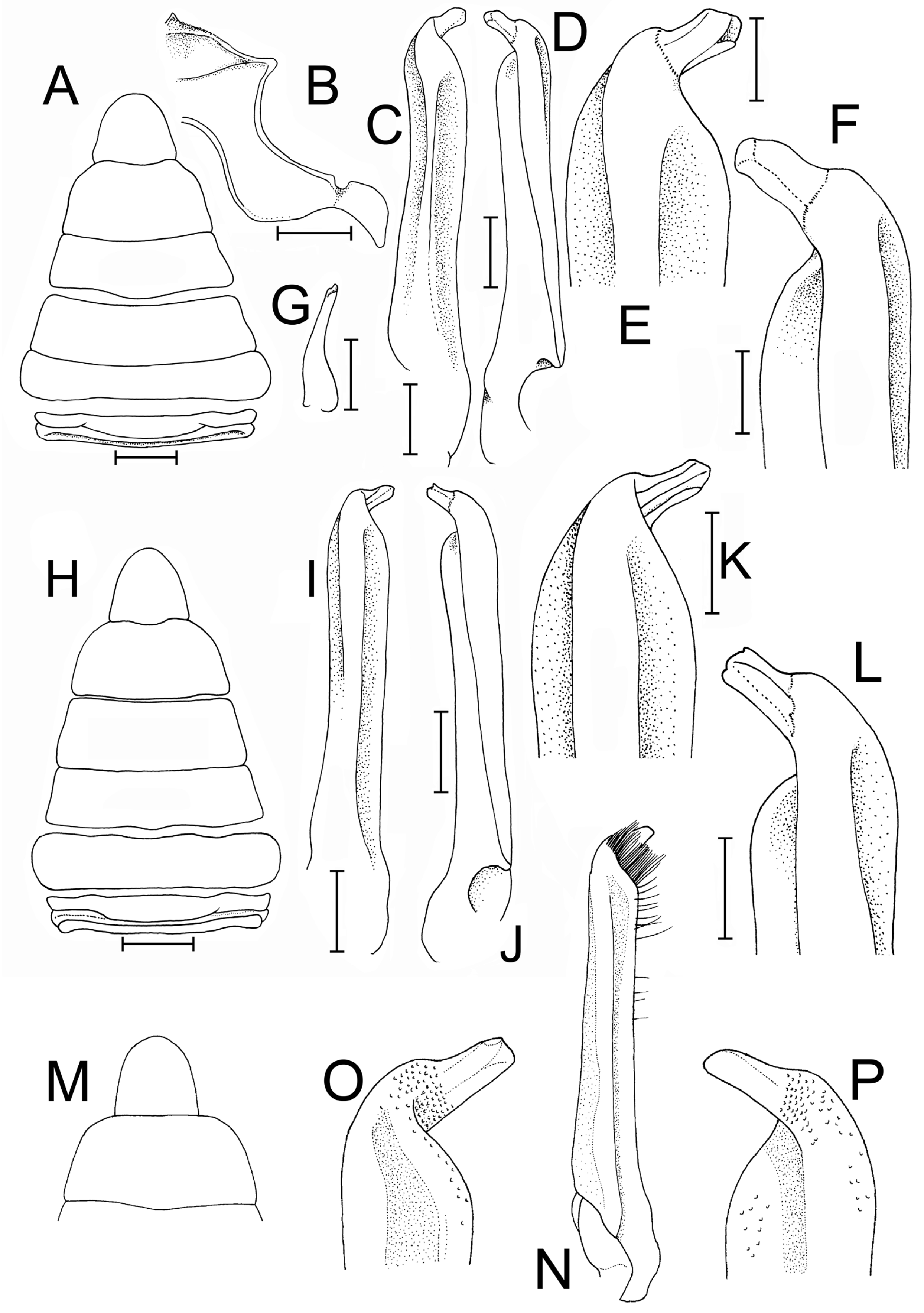

Fig. 11. A–G, *Orisarma dehaani*, lectotype male (39.5 × 35.7 mm) (RMNH-D157), Japan; H–L, *O. neglectum*, neotype male (35.6 × 31.8 mm) (ZRC 1998.310), Shanghai, China; M–P, *O. magnum*, holotype male (47.2 × 52.2 mm) (CBM-ZC 11452), Ogasawara Island, Japan. A, H, male pleon; B, anterior thoracic sternites 1–4; C, I, N, left G1 (ventral view, denuded); D, J, left G1 (dorsal view, denuded); E, K, O, left distal part of G1 (ventral view, denuded); F, L, P, left distal part of G1 (dorsal view, denuded); G, left G2 (denuded); M, male pleonal somite 6 and telson; M–P, after Komai & Ng (2013: fig. 5A, C, D, E). Scales: A, B, H = 5.0 mm; C, D, G, I, J = 2.0 mm; E, F, K, L = 1.0 mm.

HONG KONG – 1 male, 2 females (ZRC 2019.0540), back mangroves, ca. 22°29′44.6″N 114°02′49.7″E, Mai Po Nature Reserve, coll. S. Cannici et al., 24 May 2019.

**Diagnosis**. Dorsal surface of carapace relatively less convex, surfaces usually slightly more rugose, with scattered stiff setae on anterior and branchial regions; frontal lobes separated by deep median concavity; epibranchial tooth distinct even in small specimens, always separated by deep notch; posterolateral margins subparallel; granules on outer surface of palm (especially those below longitudinal ridge) rounded, prominent; merus of ambulatory legs relatively longer; chitinous distal part of G1 short, tip truncate. In life, carapace and chelae red, sometimes yellow.

**Colour**. In life, the dorsal surfaces of the carapace, chelipeds, and ambulatory legs are bright red with the fingers white (Fig. 54A) (see also Miyake, 1983; Lee, 2008; Liu, 2009; Liu & Wang, 2010; Rademacher & Mengedoht, 2011), although some orangish-red specimens are sometimes observed in southern Taiwan. There is an interesting large male collected from the Ryukyus which is bright yellow (Fig. 54B), but this specimen was obtained over a kilometre from the sea on a muddy patch up on a hill, and its colour may be a result of fading. Its morphology is identical to more typically coloured specimens. Smaller specimens and some females may have a dark tranverse band across their frontal margin (Fig. 54C).

**Remarks**. *Orisarma intermedium* is very close to *O. sinense* in general carapace form and smaller specimens are not easy to separate. Many of the old records of these two species in the literature (especially those on mainland China) will need to be rechecked. In an unpublished key, which was the basis of the more recent identifications of Serène (1968), Serène & Soh (1970), and Soh (1978), the primary characters were whether the epibranchial tooth is clearly demarcated (present in *O. intermedium* versus absent in *O. sinense*), whether the outer surface of the chela was strongly granulated, and the presence of a low longitudinal median ridge (strongly granulated with a ridge in *O. intermedium* versus low granules and no ridge in *O. sinense*), the relative proportions of the fingers of the chela (dactylar finger longer than height of palm in *O. intermedium* versus dactylar finger shorter in *O. sinense*) and ambulatory merus (merus of third ambulatory leg 2.5 times longer than broad in *O. intermedium* versus 3 times in *O. sinense*), and proportions of the chitinous distal part of G1 (shorter in *O. intermedium* versus longer in *O. sinense*).

Examination of the present material reveals that smaller specimens of *O. sinense* do have the epibranchial tooth relatively low and while it may appear to be absent and/or almost confluent with the rest of the margin, it is nevertheless always visible (as in the case of small specimen from Hong Kong, ZRC 1975.6.30.10). In medium-sized specimens, the epibranchial tooth is distinct but demarcated from the rest of the margin by a weak notch (Fig. 2I). Only in the largest specimen is the epibranchial tooth really prominent, and with a deeper notch separating it from the rest of the margin (Figs. 2J, 4I). In *O. intermedium*, the epibranchial tooth is distinct even in small specimens and always separated by a deep notch (e.g., Figs. 2A–F, 4H). Soh (1978) suggested that the cheliped of *O. sinense* has relatively shorter fingers but this is not a useful character and was probably due to the small size of the specimens he examined. Larger specimens of *O. sinense* (Fig. 6E–H) have the same kind of fingers as those of *O. intermedium* (Fig. 6A–D). The outer surface of the adult male chela of the two species is slightly different, but the low longitudinal median ridge is present on both species (Fig. 6A–G). In adult *O. intermedium*, the granules on the outer surface of the palm, especially those below the longitudinal ridge, are rounded and prominent (Fig. 6A–D). In the case of *O. sinense*, the granules are lower and more flattened (Fig. 6E–G). The proportions of the ambulatory legs are not useful, and in *O. intermedium* (which supposedly has longer legs), this character is too variable to be reliable. There seems to be a tendency (but not always) for the merus of the ambulatory legs to be relatively wider and shorter in smaller specimens (e.g., Fig. 8A, B), with those of large specimens becoming longer and more slender (Fig. 8C). In fact, on the basis of the specimens of both species available, the ambulatory meri of *O. sinense* actually appear proportionately shorter (Fig. 8D versus Fig. 8A–C) when specimens of similar size are compared. The G1 differences, however, are valid and reliable (Fig. 12G–J versus Fig. 12B–E).

In addition to the epibranchial tooth, chela, and G1 differences noted above, adults of the two species can be separated by the form of the frontal margin and carapace physiognomy. In *O. intermedium*, the two frontal lobes are separated by a deep median concavity (Fig. 4H) but in *O. sinense*, this concavity is distinctly shallower (Fig. 4I). The dorsal surface of the carapace of *O. intermedium* is relatively less convex, with the surfaces usually slightly more rugose and with scattered stiff setae all over the anterior and branchial regions (Figs. 2A–F, 4H, J). In *O. sinense*, the dorsal surface of the carapace is more convex (notably the branchial), smoother, and the setae are more scattered and sparser on the branchial regions (Figs. 2I, J, 4I, K). These characters are valid for both sexes as well as for small and subadult specimens.

De Man's (1888: 182) "*Sesarma intermedia*" from Mergui is a misidentification of *Manarma moeschii* (De Man, 1892). The specimen figured by Soh (1978: pl. 4b) is almost certainly *O. intermedium* on the basis of his photograph, and we have also examined material from Hong Kong. Thus, both *O. intermedium* and *O. sinense* occur sympatrically in Hong Kong.

Hoang et al. (2012: 75, 78) reported "*Sesarmops intermedius*" from southern Vietnam but their record is dubious as the species is not known to be present that far south; and it is more likely their material was confused with a species of *Pseudosesarma*.

**Biology**. This species is common in freshwater streams and waters near the sea, which may still be subject to some tidal influence, although they can also be found several hundreds of metres away on hilly areas. They normally

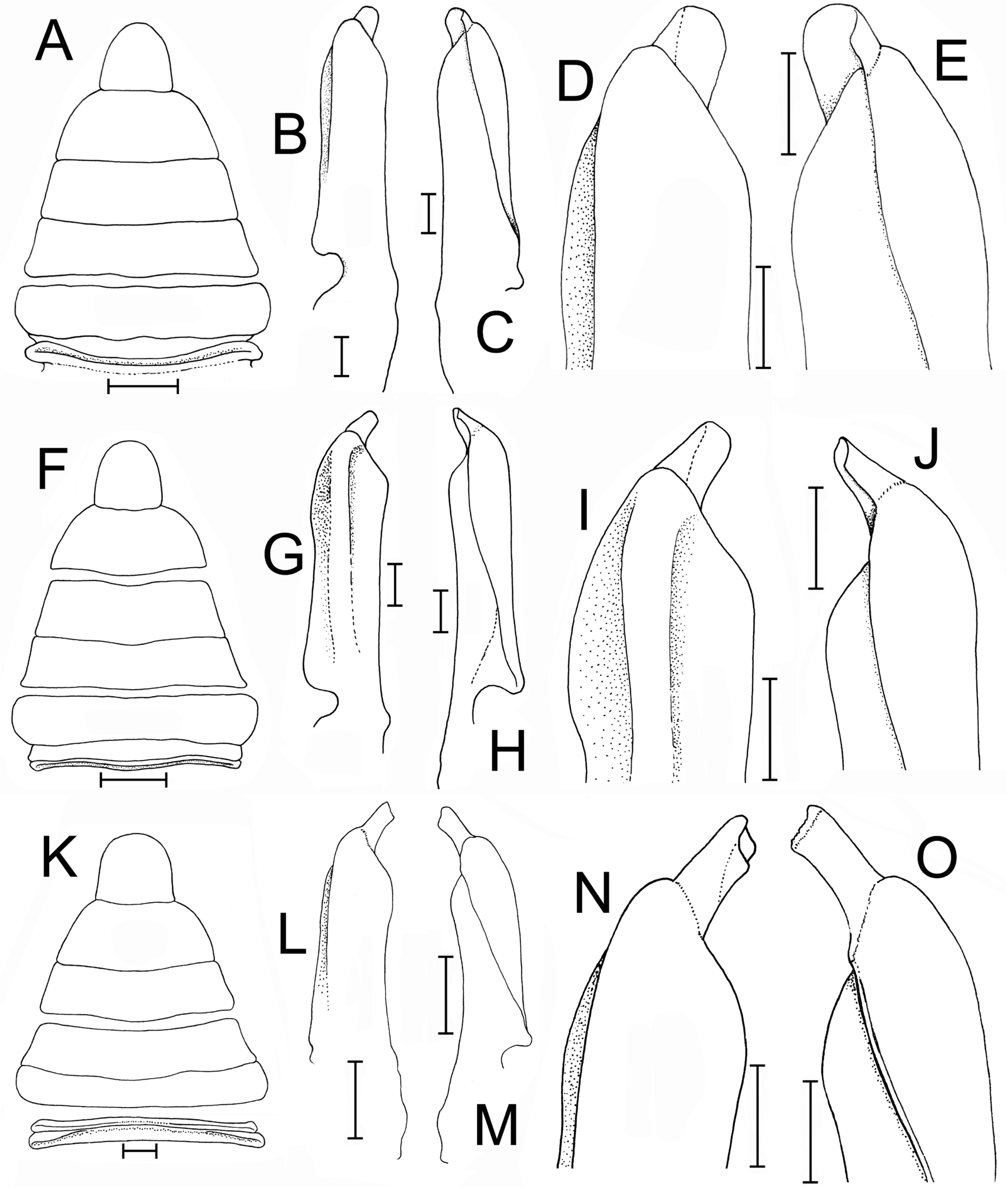

Fig. 12. A–E, *Orisarma intermedium*, male (27.1 × 25.2 mm) (ZRC 1970.2.23.6), Japan; F–J, *O. sinense*, male (29.6 × 25.4 mm) (ZRC 1998.1204), Shanghai, China; K–O, *O. patshuni*, male (14.2 × 13.0 mm) (ZRC 1998.345), Hong Kong. A, F, K, male pleons; B, G, L, left G1 (ventral view, denuded); C, H, M, left G1 (dorsal view, denuded); D, I, N, left distal part of G1 (ventral view, denuded); E, J, O, left distal part of G1 (dorsal view, denuded). Scales: A, F = 5.0 mm; B–E, G–J, K–M = 1.0 mm; N, O = 0.5 mm.

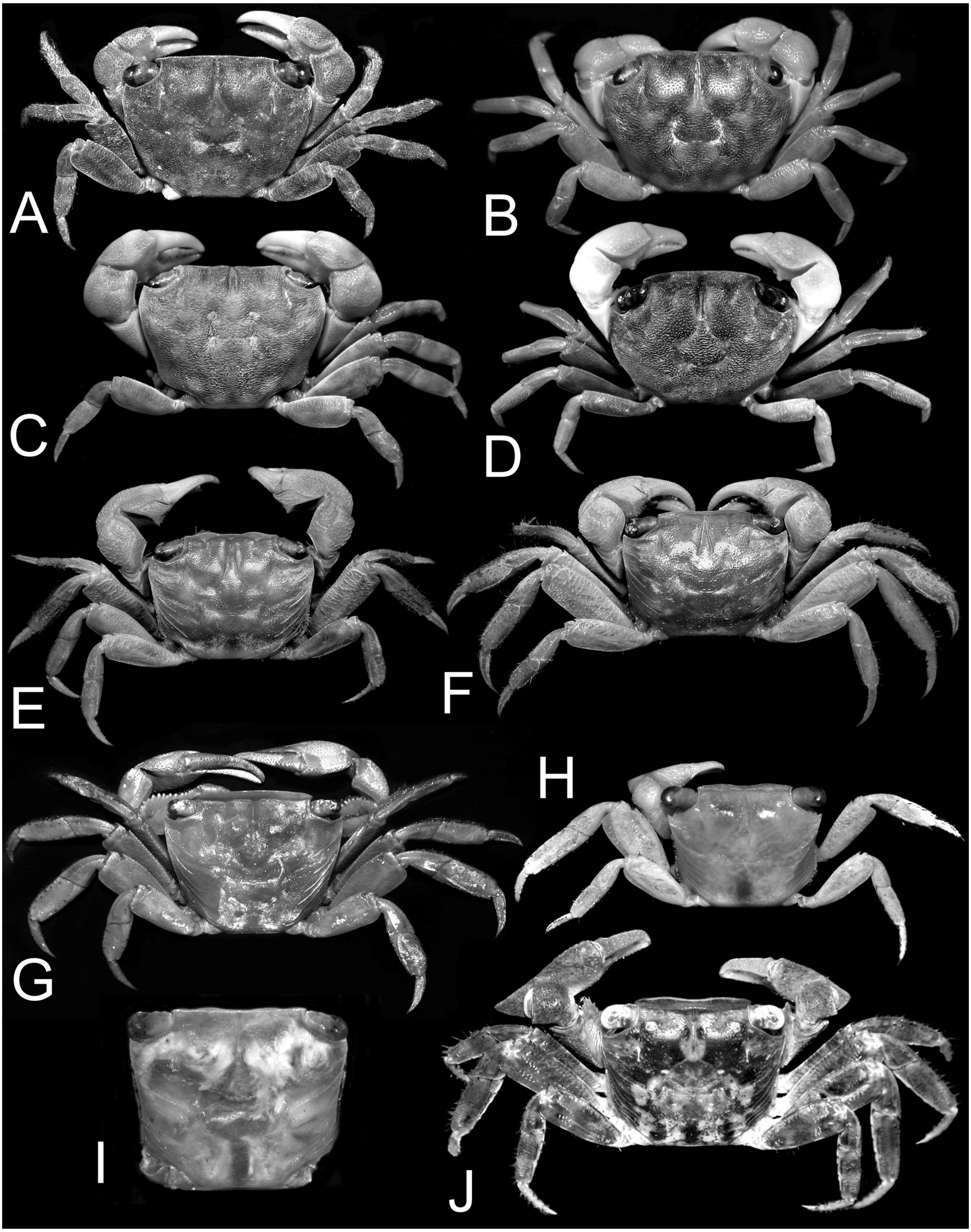

Fig. 13. Overall habitus. A, *Danarma obtusifrons*, male (17.7 × 13.2 mm) (UF-FLMNH 14837), Oahu, Hawaii; B, *Danarma silus*, holotype male (16.3 × 12.8 mm) (ZRC 2012.0787), Guam; C, *Danarma eurymerus*, holotype male (18.7 × 14.8 mm) (NMNS-7028-002), Lanyu Island, Taiwan; D, *Danarma garfunkel*, holotype male (17.0 × 13.0 mm) (QM), Greta Beach, Christmas Island; E, *Cristarma eulimene*, male (22.2 × 17.2 mm) (ZRC 1968.1.22.2), Inhaca Island, Mozambique; F, *Cristarma ortmanni*, male (20.0 × 15.5 mm) (ZRC 1968.1.22.1), Inhaca Island, Mozambique; G, *Trapezarma angolense*, neotype male (39.3 × 32.7 mm) (SMF-ZMG 635), Benguella, Angola; H, *Platychirarma buettikoferi*, paralectotype male (10.0 × 8.7 mm) (SMF-ZMG 636), Fisherman Lake, Liberia; I, *Platychirarma buettikoferi*, lectotype male (14.1 × 11.6 mm) (RMNH D 148), Liberia; J, *Platychirarma buettikoferi*, male (12.6 × 10.4 mm) (ZRC 2015.0298), Cameroon.

occur among dense vegetation along these bodies of water, coming out at night to forage on the sand- and mudflats. They are primarily herbivores and scavengers. Hong et al. (2010) discussed its ecology in Korea. The physiology of the species in Taiwan was studied by Tsai et al. (2000) while the visual orientation and habits was done by Huang & Liu (2012). The reproductive behaviour of this species in Japan was discussed by Kyomo (1986). The larvae have been reported on by Fukuda & Baba (1976), Cuesta et al. (2006), and Lee (2015). The microsatellite markers of the species were studied by Lee et al. (2012). Nematode parasites have been reported on by Yoshimura (1990). In Taiwan, *O. intermedium* is collected in large numbers from southern Taiwan for the aquarium trade (as a freshwater crab), and many populations have been seriously depleted.

**Distribution**. Despite the lack of genetic differentiation in the current genetic dataset, we are confident *O. intermedium* and *O. sinense* are separate species on the basis of their morphology. However, we are less sure about their distribution. In Japan, Korea, and Taiwan, only one species, *O. intermedium*, is known for certain. On mainland China, notably southern China, both species have been reported (Shen, 1940a, b; Dai et al., 1986; Dai & Yang, 1991). Certainly, both species appear to be present in Hong Kong (see Soh, 1978). The older material will need to be re-examined and fresh collections made to determine their actual distributional limits. In the most recent treatments of the Chinese fauna (Dai et al., 1986; Dai & Yang, 1991), *O. intermedium* is not treated at all, even though this species is certainly present in Taiwan and Hong Kong, whereas *O. sinense* is treated as a species of *Sesarmops* (see Dai & Yang, 1991: 539, text-fig. 277(2), pl. 69(6); with their figures of the carapace and G1 leaving no doubt of the identity of this species).

### ***Orisarma sinense*** **(H. Milne Edwards, 1853)**

(Figs. 2G–J, 3E, 6E–H, 8D, 9F, G, 12F–J, 54D)

*Sesarma sinensis* H. Milne Edwards, 1853: 186; Stimpson, 1858: 105; De Man, 1887: 648, 669; Stimpson, 1907: 133; Wang & Leung, 2001: 31, unnumbered figure.

*Sesarma* (*Sesarma*) *sinensis* – Tesch, 1917: 199; Shen, 1931: 196, text-fig. 13, pl. 14 figs. 2, 3; Shen, 1940a: 96; Serène, 1968: 105.

*Sesarma* (*Sesarma*) *intermedia* – Balss, 1922: 155 (part). [not *Grapsus* (*Pachysoma*) *intermedius* De Haan, 1835]

*Sesarmops sinensis* – Serène & Soh, 1970: 401; Soh, 1978: 11, pl. 4c; Kwok & Tang, 2005: 3, figs. 15, 18a, 20; Yang et al., 2008: 802; Huang et al., 2011: 732, 733; Tang et al., 2017: e0179800.

*Sesarma* (*Sesarmops*) *sinensis* – Dai et al., 1986: 492, text-fig. 277(2), pl. 69(6); Dai & Yang, 1991: 539, text-fig. 277(2), pl. 69(6); Huang, 1994: 597.

"*Sesarmops*" *sinensis* – Ng et al., 2008a: 220.

*Sesarmops intermedium* – Sulieman & Pengsakul, 2013: 1. [not *Grapsus* (*Pachysoma*) *intermedius* De Haan, 1835]

**Material examined**. Lectotype male (19.0 × 16.6 mm) (MNHN-BP3635a), China. Paralectotype: 1 female (18.8 × 16.9 mm) (MNHN-BP3635b), same data as lectotype. CHINA – 5 males (largest 30.0 × 25.9 mm, smallest 28.6 × 25.5 mm), 1 female (ZRC 1998.1204), Shanghai, Qidong, Jiangsu Province, coll. Y.Y. Li, 2 May 1996; 4 females (smallest 22.9 × 20.3 mm, largest 31.8 × 26.6 mm) (ZRC), Qi Dong, Lusi, Shanghai, coll. Y.Y. Li, 1 May 1996; 1 male (30.7 × 26.7 mm), 1 female (ZRC 2010.0421), southern Chongming, 31°30.135′N 12°42′E, coll. H. Cao, 15 July 2010. HONG KONG – 1 female (22.0 × 18.5 mm) (ZRC 1975.6.30.10), Shiu Hau, Lantau Island, coll. C.L. Soh, 2 June 1975.

**Diagnosis**. Dorsal surface of carapace relatively more convex, surfaces usually slightly smoother, with very few stiff setae on anterior and branchial regions; frontal lobes separated by relatively more shallow concavity; epibranchial tooth relatively low, almost confluent with rest of margin in small specimens, separated from rest of lateral margin by gentle notch; posterolateral margins subparallel; granules on outer surface of palm (especially those below longitudinal ridge) relatively lower, more flattened; merus of ambulatory legs relatively shorter; chitinous distal part of G1 long, tip truncate. In life, carapace and chelae red.

**Colour**. In life, the species is pale to bright red overall (Fig. 54D).

**Remarks**. The identity of this species from somewhere in China has been hampered by the fact that H. Milne Edwards (1853: 186) described the species very briefly, without any figures and no indication of size, sex, or number of specimens used. Even when the types were apparently re-examined (e.g., De Man, 1887: 648), no figures were provided. The type specimens consist of two small, dried specimens in poor condition (Fig. 2G, H). However, they clearly show the key characters for the species, including the diagnostic G1 structure (Fig. 9F). Both specimens are syntypes and the male is here designated the lectotype of *Sesarma sinensis* H. Milne Edwards, 1853.

The key differences between *O. sinense* and *O. intermedium* have been discussed under the latter species.

The small female from Hong Kong (ZRC 1975.6.30.10) examined here is probably the same specimen figured by Soh (1978: pl. 4c) and agrees with *S. sinense* as presently defined.

**Biology**. The biology of *O. sinense*, is probably similar to *O. intermedium* but little is known. Sulieman & Pengsakul (2013) recorded "*Sesarmops intermedium*" as a potential biological control for pomatiopsid snails in Jiangxi Province, China, but based on the distribution, their species is almost certainly *O. sinense* instead. Specimens of this species from Shanghai were observed climbing several metres up trees at night foraging for food (W. Liu, pers. comm., Fig. 54D). This is a behaviour that has been observed in other sesarmids from Southeast Asia (notably *Episesarma* De Man, 1895) (see Sivasothi, 2000; Sivasothi et al., 1993; Ng et al., 2008b). Tang et al. (2017) obtained the complete mitochondrial genome of the species from China.

**Distribution**. See comments for *O. intermedium.*

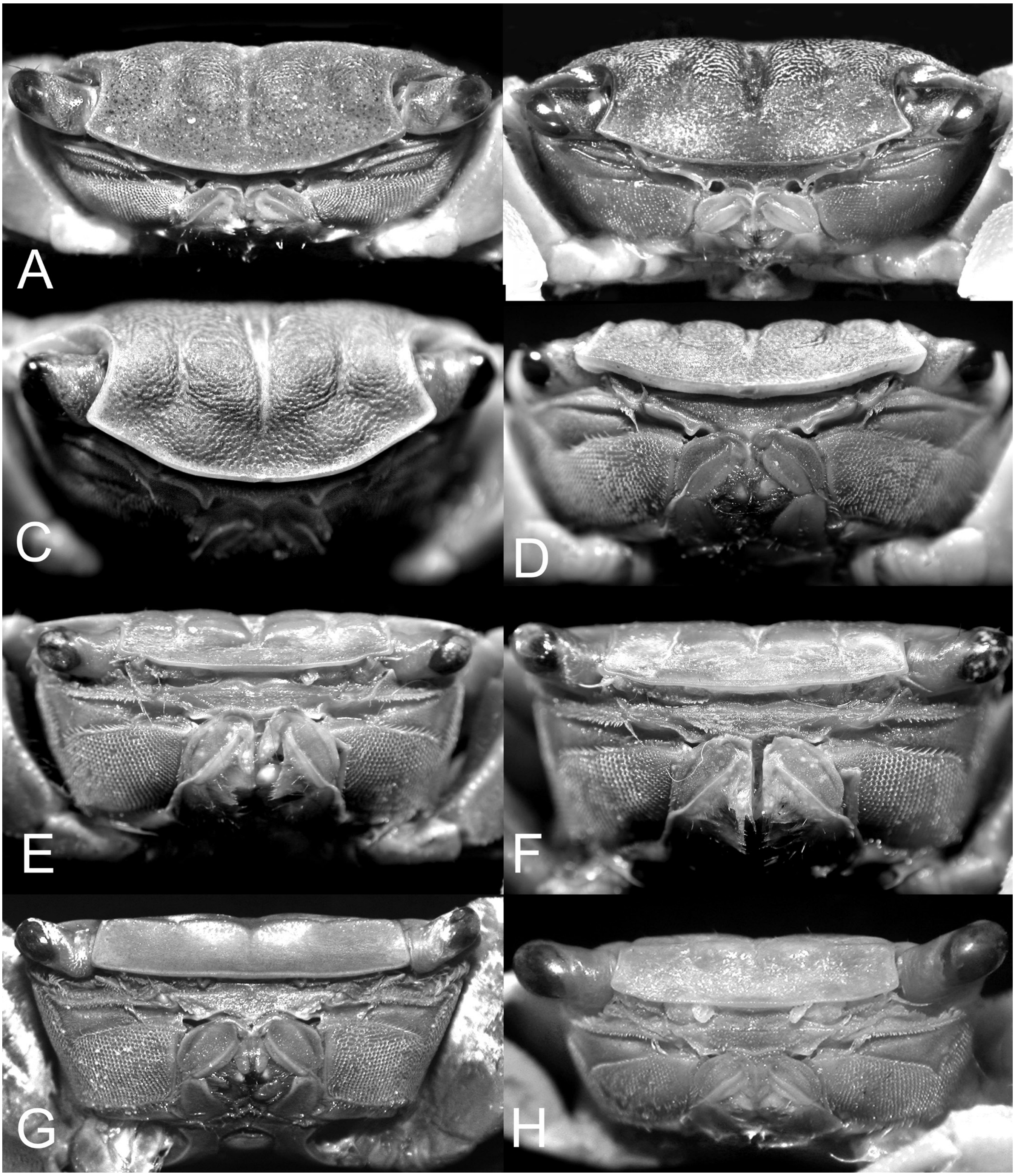

Fig. 14. Frontal view of cephalothorax. A, *Danarma obtusifrons*, male (17.7 × 13.2 mm) (UF-FLMNH 14837), Hawaii; B, *Danarma garfunkel*, holotype male (17.0 × 13.0 mm) (QM, ex ZRC 2009.0822), Christmas Island; C, D, *Danarma eurymerus*, holotype male (18.7 × 14.8 mm) (NMNS-7028-002), Lanyu Island, Taiwan; E, *Cristarma eulimene*, male (22.2 × 17.2 mm) (ZRC 1968.1.22.2), Inhaca Island, Mozambique; F, *Cristarma ortmanni*, male (20.0 × 15.5 mm) (ZRC 1968.1.22.1), Inhaca Island, Mozambique; G, *Trapezarma angolense*, neotype male (39.3 × 32.7 mm) (SMF-ZMG 635), Benguella, Angola; H, *Platychirarma buettikoferi*, paralectotype male (10.0 × 8.7 mm) (SMF-ZMG 636), Fisherman Lake, Liberia.

### ***Orisarma patshuni*** **(Soh, 1978)**

(Figs. 1G, H, 3F, 5H, I, 9H, 12K–O, 33G, 43D, 55)

*Pseudosesarma patshuni* Soh, 1978: 14, fig. e, f, pl. 1c, f, pl. 3f; Lee, 1995: 3; Kwok & Tang, 2005: 3, fig. 16; Yang et al., 2008: 802.
*Sesarma impressum* – Wang & Leung, 2001: 31, unnumbered figure. [not *Sesarma impressa* H. Milne Edwards, 1837]
"*Pseudosesarma*" *patshuni* – Ng et al., 2008a: 220.

**Material examined**. Paratypes: 5 males (largest 13.5 × 11.9 mm, smallest 10.8 × 9.6 mm), 2 females (16.9 × 14.7 mm, 16.4 × 14.0 mm) (ZRC 1975.7.1.2–8), Shiu Hau at Lantau Island, Hong Kong, coll. C.L. Soh, 2 June 1975. Others: HONG KONG – 1 male (14.2 × 13.0 mm) (ZRC 1998.345), Hong Kong Island, south coast, Tai Tam immediately downstream of Tai Tam Dam, salt marsh and remnant mangroves, coll. P.K.L. Ng & S.Y. Lee, 6 June 1996; 7 males (largest 23.2 × 20.7 mm), 12 females (largest 20.2 × 17.2 mm) (ZRC 2012.0032), 2 males, 3 females (ZRC 2014.0817), on banks of small freshwater steam next to Tai Tam Dam, under rocks, Tai Tam immediately downstream of salt marsh and remnant mangroves, south coast of Hong Kong Island, coll. P.K.L. Ng et al., 25 December 2011; 2 males (ZRC 2019.1067), on low shrubs on hard mud, back mangroves, ca. 22°29′44.6″N 114°02′49.7″E, Mai Po Nature Reserve, coll. S. Cannicci et al., 24 May 2019.

**Diagnosis**. Dorsal surface of carapace gently convex, surfaces relatively smooth; frontal lobes separated by distinct concavity; epibranchial tooth distinct, always separated by deep notch; posterolateral margins subparallel; granules on outer surface of palm small but distinct; merus of ambulatory legs relatively slender; chitinous distal part of G1 short but with tip flared. In life, carapace brown; chelae bright purple.

**Colour**. In life, the carapace and ambulatory legs are dark brown to pale purplish-brown, with the chela violet to purple (Fig. 55), even in females and subadults.

**Remarks**. Soh (1978) described *Pseudosesarma patshuni* from one holotype male (14.5 × 13.0 mm, NHM 1976.108) as well as seven males and six females from Lantau Island in Hong Kong. The present material from Hong Kong Island, just east of Lantau Island, agrees very well with the types, except that there are many much larger specimens. The large males agree in almost all aspects with the smaller ones, except that the chelae are stouter and relatively larger. While the smaller males have more delicate chelae, resembling those of many other species of *Pseudosesarma* (Figs. 1G, 5H), in the large males, the chelae more closely resemble those of other species of *Orisarma*, being prominently inflated with a distinct longitudinal ridge on the outer surface and a strong transverse ridge on the inner surface (Figs. 1H, 5I).

Soh (1978) noted that it was the only *Pseudosesarma* species in which the palm of the chela lacked tubercles. This is not strictly correct as the outer surface of the palm of *P. patshuni* is covered with small granules (Fig. 5H, I), albeit relatively lower and less prominent than those of other *Pseudosesarma* species. The form of the chela of *P. patshuni* is close to the condition seen in other *Orisarma* species, with the possession of median longitudinal ridge on the outer surface and a strong transverse ridge on the inner surface (Figs. 1G, H, 5H, I); and it also shares the same kind of male thoracic sternum and male pleon (Fig. 9H). The characteristically short G1 is also similar in form to those seen in *O. intermedium* and *O. sinense*, except that its tip is more distinctly flared (Fig. 12L–O). The above characters are not those now diagnostic for the redefined *Pseudosesarma* (see later). In the form of the carapace and chelae, *P. patshuni* actually is intermediate in form between what is observed for one group of species containing *O. dehaani*, *O. neglectum*, and *O. magnum*; and the other with *O. intermedium* and *O. sinense*. As such, *P. patshuni* should be transferred to *Orisarma*. Compared to other *Orisarma* species, *O. patshuni* is also relatively small in adult size, Soh's (1978) largest specimen was only 14.5 mm in carapace width, and even our largest specimen here only measures 23.2 mm; smaller than the other *Orisarma* species in which adults average 30 mm in width.

**Biology**. Soh (1978: 15) noted that the species was found "underneath stones, driftwood and among grasses in the sandy mud zone near the sea" on Lantau Island. On Hong Kong island, it was found under rocks in a wholly freshwater stream adjacent to a salt marsh near a dam, and is probably subjected to some subterranean saline intrusion, although the stream itself is not affected except by the highest tides. They are semiterrestrial in habit.

**Distribution**. Known from Lantau and Hong Kong islands (Soh, 1978; present data); the species has also been reported from Macau (incorrectly as *Sesarmops impressum*) by Wang & Leung (2001).

## ***Danarma*, new genus**

**Type species**. *Sesarma obtusifrons* Dana, 1851, by present designation. Gender neuter.

**Diagnosis**. Carapace ovate-trapezoidal, broader than long; frontal margin entire, prominently deflexed, almost completely shielding antennules from frontal view, margin much longer than posterior carapace margin; lateral margins of carapace entire, posterolateral part distinctly converging; regions of carapace poorly demarcated; postfrontal and epigastric crests separated by relatively deep grooves, margin relatively rounded, regions clearly separated; basal articles of antenna and antennules separated by septum; dorsal margin of palm smooth; outer surface of palm smooth, inner surface with prominent transverse submedian swelling, highest point with transverse ridge of granules, outer surface of palm and pollex convex, outer lower surface of palm smooth; dorsal margin of chelipedal dactylus smooth; inner distal margin of merus of cheliped not lamelliform; inner surfaces of first to third ambulatory coxae with numerous long setae between them; male thoracic sternites 2–4 relatively narrow in adults, suture between sternites 3 and 4 distinct; male sternopleonal cavity reaching two-thirds length of sternite

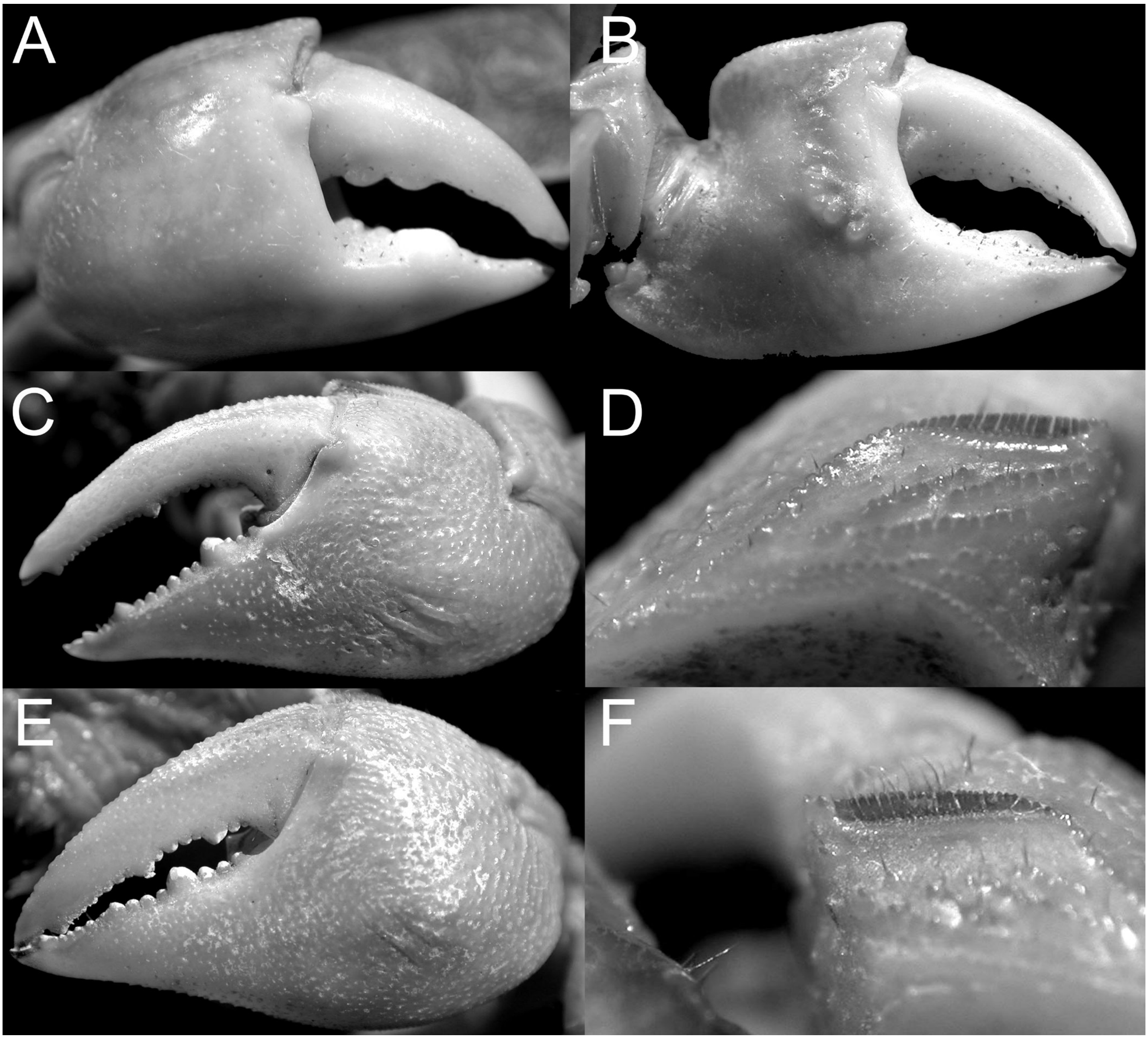

Fig. 15. Chela. A, B, *Danarma eurymerus*, holotype male (18.7 × 14.8 mm) (NMNS-7028–002), Lanyu Island, Taiwan; C, D, *Cristarma eulimene*, male (22.2 × 17.2 mm) (ZRC 1968.1.22.2), Inhaca Island, Mozambique; E, F, *Cristarma ortmanni*, male (20.0 × 15.5 mm) (ZRC 1968.1.22.1), Inhaca Island, Mozambique. A, C, E, outer view; B, inner view; D, F, dorso-lateral view showing pectinated ridge on palm.

4 to just before anterior margin of sternite 2; male thoracic sternite 5 smooth, without depression on anterior part; G1 slender or relatively stout, chitinous part short or relatively long. Vulva on anterior part of sternite 6, anterior edge presses against sternite 5; anterior and posterior sternal vulvar covers flat, triangular, tips overlapping; opening not projecting, below sternal vulvar covers.

**Etymology**. The genus name is derived from James D. Dana (1813–1895), who described the type species, in arbitrary combination with the genus name *Sesarma*. The gender is neuter.

**Included species**. *Sesarma obtusifrons* Dana, 1851; *Chiromantes silus* Davie & Ng, 2013; *Chiromantes leptomerus* Davie & Ng, 2013 *Chiromantes eurymerus* Davie & Ng, 2013; *Chiromantes garfunkel* Davie & Ng, 2013.

**Remarks**. As discussed earlier, what used to be called *Chiromantes obtusifrons* is now a group of five species (Davie & Ng, 2013), all sharing a peculiar frontal margin that is very broad and prominently bent downwards such that much of the antennae and antennules are completely covered in frontal view. The broad front also results in a pecular carapace shape—clearly trapezoidal with the posterolateral margins strongly converging towards the posterior carapace margin, but with the lateral margins arcuate, resulting in a transversely subovate form (Figs. 13A–D, 14A–D). The outer surface of the palm is also smooth, with no longitudinal ridge, the dactylar finger completely unarmed on the dorsal margin (Fig. 15A, B), and the surfaces between the first to third ambulatory coxae have distinct dense tufts of long setae (Fig. 18A, B). The presence of strongly setose ambulatory coxae is a feature shared with species of *Cristarma*, new genus, from East Africa (see later). This suite of distinctive characters shared by five similar species is strong support for the establishment of a new genus, here named *Danarma*.

### *Danarma obtusifrons* (Dana, 1851)

(Figs. 13A, 14A, 18A, 19A–C, F–I, 43E)

*Sesarma obtusifrons* Dana, 1851: 250; Dana, 1852: 355, pl. 22, fig. 9; H. Milne Edwards, 1853: 183; De Man, 1887: 644; Lenz, 1901: 472; Titcomb et al., 1979: 367; Godwin & Bolick, 2006: 39, 49.
*Sesarma* (*Holometopus*) *obtusifrons* – Rathbun, 1906: 840; 1907: 35; Tesch, 1917: 179 (part); Edmondson, 1946: 306, fig. 183e; Edmondson, 1959: 185, figs. 13c, 17c; Serène, 1968: 107 (part).
*Chiromantes obtusifrons* – Ng & Liu, 1999: 230.
"*Chiromantes*" *obtusifrons* – Ng et al., 2008a: 220, 224 (part); Castro, 2011: 120; Davie & Ng, 2013: 2, figs. 1, 4A, 5A, B, 6A, B, 7A, B, 8A, 9A, B, 10A, 11.
*Incertae sedis* [see remarks later] (see Davie & Ng, 2013: 7)
*Sesarma* (*Sesarma*) *obtusifrons* – De Man, 1895: 161; De Man, 1898: pl. 29, fig. 31.

**Material examined**. 2 males (16.8 × 12.9 mm, 19.7 × 14.7 mm) (ZRC 2002.0220, ex. BPBM-266), Malaikahana, Oahu, Hawaii, C.M. Cooke et al., 8 July 1916; 1 male (17.7 × 13.2 mm), 1 female (15.7 × 11.6 mm) (UF-FLMNH 14837), 21.2833°N 157.667°E, Coco Head, Oahu, Hawaii, coll. G. Paulay et al., October 2006.

**Diagnosis**. Carapace transversely rectangular, ca. 1.3 times broader than long; dorsal carapace, lateral branchial regions weakly convex, not prominently swollen; external orbital tooth with outer margin broadly convex so greatest carapace width clearly posterior to external orbital tooth; front ca. 0.65 times carapace width, margin broadly convex in frontal view with medial part relatively straight in dorsal view, beaded with row of small but distinct granules, with pair of low lateral swellings behind margin; supraorbital margin entire, semicircular; dorsal surface of cheliped carpus covered in small but conspicuous granules; ambulatory legs relatively short; third ambulatory merus ca. 2.2 times longer than wide; fifth ambulatory merus ca. 2.3 times longer; fourth ambulatory propodus ca. 2.2 times longer; male pleon moderately broad; somite 6 with distolateral margins strongly divergent, relatively straight over distal two-thirds; somite 3 width 2.9 times basal width of telson; G1 relatively slender, weakly tapering to obtusely angled subdistal shoulder; distally slender, strongly bent to 45° angle; distal chitinous process long, with slender narrow apex, dorsal margin slightly concave. (After Davie & Ng, 2013: 2).

**Colour**. "Background colour of carapace, legs fawn to bluish gray, covered in fine darker speckling with scattering of slightly larger irregular spots. Legs with darker, broad transverse bands that are more noticeable on the carpi and meri. Chelipeds dorsally similar in colour to carapace and legs but becoming greyish white in frontal and ventral view. Ocular peduncles and corneas pale, similar to carapace in colour." (Davie & Ng, 2013: 5; fig. 1).

**Remarks**. This characteristic species has been reported from a wide area from the eastern Indian Ocean to Hawaii (type locality). Davie & Ng (2013) revised the taxonomy of the species and recognised four new species. All these species share the diagnostic generic features of the genus. Although the type(s) of *Sesarma obtusifrons* Dana, 1851, are almost certainly lost, Davie & Ng (2013) argued that there was no need to designate a neotype as the species is distinctive and easily distinguished for all known congeners.

**Biology**. "Edmondson (1959) noted that *C. obtusifrons* was found intertidally and "even above the high water mark", and Paulay & Starmer (2011: 11) reported finding it living in a supratidal boulder field on O‘ahu." (Davie & Ng, 2013: 7).

**Distribution**. Known only from Hawaii (Davie & Ng, 2013).

### *Danarma silus* (Davie & Ng, 2013)

(Fig. 13B)

*Chiromantes obtusifrons* – Paulay et al., 2003: 508; Paulay & Starmer, 2011: 2, 11.
*Chiromantes silus* Davie & Ng, 2013: 14; figs. 3A–C, 4B, 5C, 6C, 7C, 8B, 9C, 13A–E.

**Material examined**. Holotype male (16.3 × 12.8 mm) (ZRC 2012.0787), Tangulsson, Guam, 10–20 m from shore, 5–8 m elevation, under limestone rocks, coll. G. Paulay, 5 October 1997. Paratypes – 1 male (15.1 × 11.3 mm), 1 female (14.9 × 11.2 mm) (ZRC 2012.0788), same data as holotype; 1 male (15.7 × 11.7 mm) (ZRC 2001.0742), Hapato Beach, Guam, coll. P.K.L. Ng, 3 August 2001; 1 ovigerous female (15.2 × 11.6 mm) (with zoea 1) (ZRC 2001.0743), Hapato Beach, Guam, coll. P.K.L. Ng, 4 August 2001; 1 female (15.2 × 11.2 mm) (ZRC 2000.0573), Pago Bay, outside of University of Guam Marine Laboratory, Guam, coll. P.K.L. Ng & C.-H. Wang, 15–18 April 2000.

**Diagnosis**. Carapace transversely subovate, ca. 1.3 times broader than long; dorsal carapace, lateral branchial regions markedly swollen; external orbital tooth weakly oblique, forming rounded obtuse angle posteriorly marking widest point of carapace, especially in larger specimens; front ca. 0.65 times carapace width, margin straight or slightly concave in dorsal view, appearing smooth but microscopically granular, with pair of low lateral swellings behind margin; supraorbital margin entire, semicircular; dorsal surface of cheliped carpus conspicuously granular; ambulatory legs relatively short; third ambulatory merus ca. 2.3 times longer than wide; fourth ambulatory merus similar, 2.4 times longer; third ambulatory propodus ca. 2.6 times longer than wide; fourth ambulatory merus ca. 2.3 times; male pleon moderately broad, somite 6 with lateral margins broadly divergent with margins relatively evenly convex, somite 3 width 3.2 times basal width of telson; G1 relatively slender, weakly tapering to broadly convex subdistal shoulder; distally slender, strongly bent to 45° angle; distal chitinous process long, with dorsal margin concave, apically pointed. (After Davie & Ng, 2013: 16).

**Colour**. "Background colour of carapace typically maroon, with coarse paler orange to yellow-green blotching. Legs

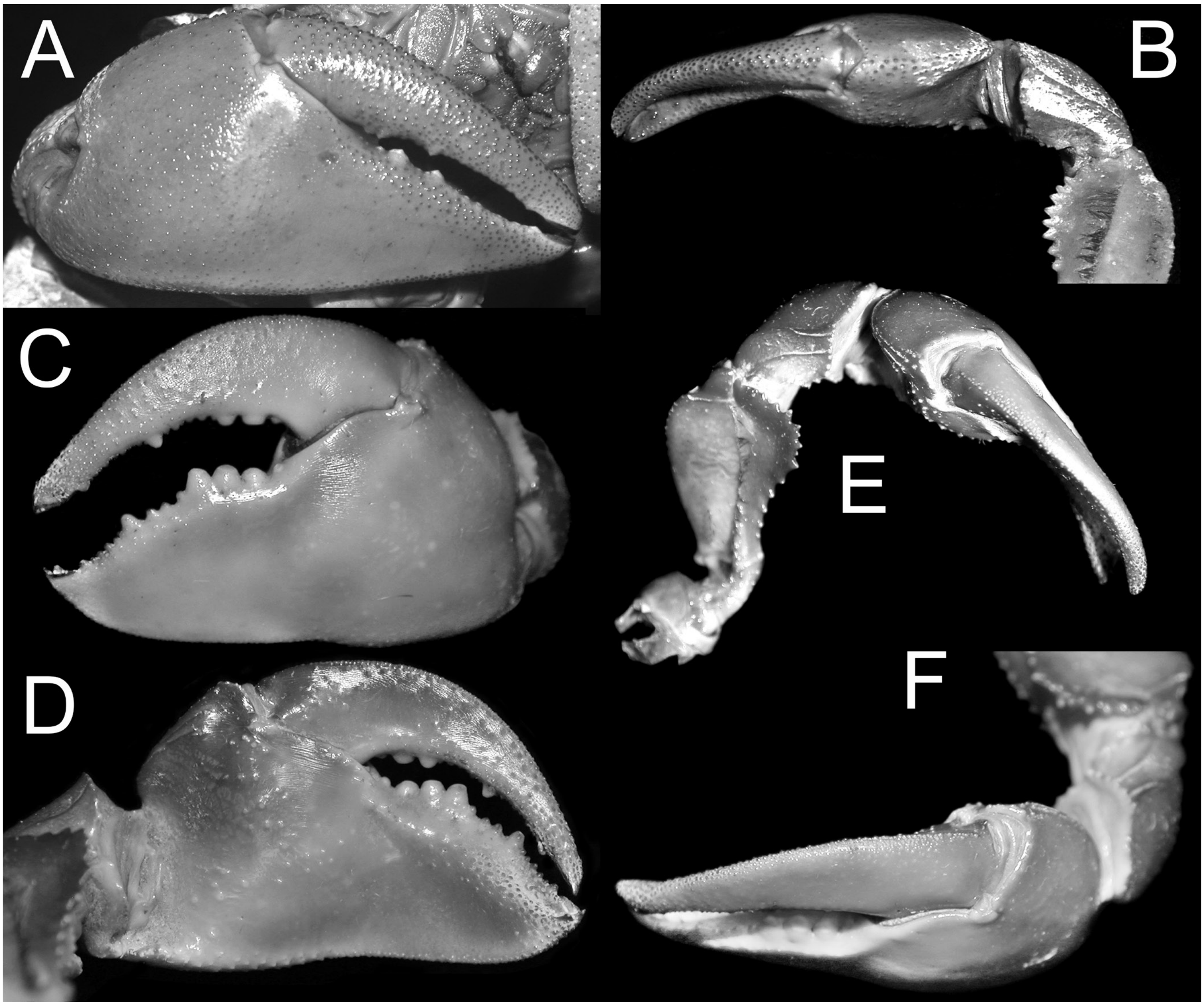

Fig. 16. Chela of species of *Trapezarma angolense*. A, B, neotype male (39.3 × 32.7 mm) (SMF-ZMG 635), Benguella, Angola; C–F, male (35.2 × 28.6 mm) (ZRC 2015.0297), Cameroon. A, C, outer view; D, inner view; B, E, F, dorso-lateral view.

speckled with some indication of transverse banding. Legs and chelipeds dorsally reddish brown to dark orange, becoming paler orange in frontal and ventral view. Ocular peduncles speckled similar to carapace; corneas darker." (Davie & Ng, 2013: 17, fig. 3A–C).

**Remarks**. The taxonomy of this species has been treated by Davie & Ng (2013).

**Biology**. Lives under rocks and in karstic crevices in sparsely vegetated coastal platforms, up to ca. 50 m inland and ca. 10 m elevation (Paulay & Starmer, 2011: 11; Davie & Ng, 2013: 17).

**Distribution**. Known only from Guam (Davie & Ng, 2013).

### *Danarma leptomerus* (Davie & Ng, 2013)

*Chiromantes obtusifrons* – Lin et al., 2011: 45 (with colour photographs).

*Chiromantes leptomerus* Davie & Ng, 2013: 19, figs. 3D–F, 4C, 5D, 6D, 7D, 8C, 9D, 13F–J; Li & Chiu, 2013: 41; Ng et al., 2017b: 103.

**Material examined**. Holotype male (16.8 × 12.7 mm) (NMNS 7028-001 part of ex ZRC 2000.1823), Pingtung County, Hsiang Chiaowan, Taiwan, coll. H.-C. Liu, 25 August 1999.

Paratypes – 2 males (13.4 × 10.3 mm, 16.4 × 12.7 mm) (ZRC 2000.1860), 1 male (16.2 × 12.4 mm), 1 female (18.1 × 13.4 mm) (QM-W25699), west coast of Lanyu Island, Taiwan, calcareous rock terraces, spray zone, coll. C.D. Schubart & H.-C. Liu, 20–21 September 1999; 2 males (23.0 × 18.3 mm, 16.7 × 13.0 mm) (NMMBA 3504a), coll. Hsiang-Chiau-Wan, Kenting, Pingtung County, Taiwan, coll. C.C. Li, 23 August 2012; 2 females (21.0 × 15.7 mm, 20.0 × 14.9 mm) (ZRC 2012.0958), Siatanzai, Kenting, Pingtung County, 21°55′55.8″N 120°44′37.4″S, Taiwan, coll. J.-H. Lee & W.-J. Wang, 6 August 2012; 1 male (17.1 × 13.0 mm), 1 female (20.5 × 15.6 mm) (NMNS), Siatanzai, Kenting, Pingtung

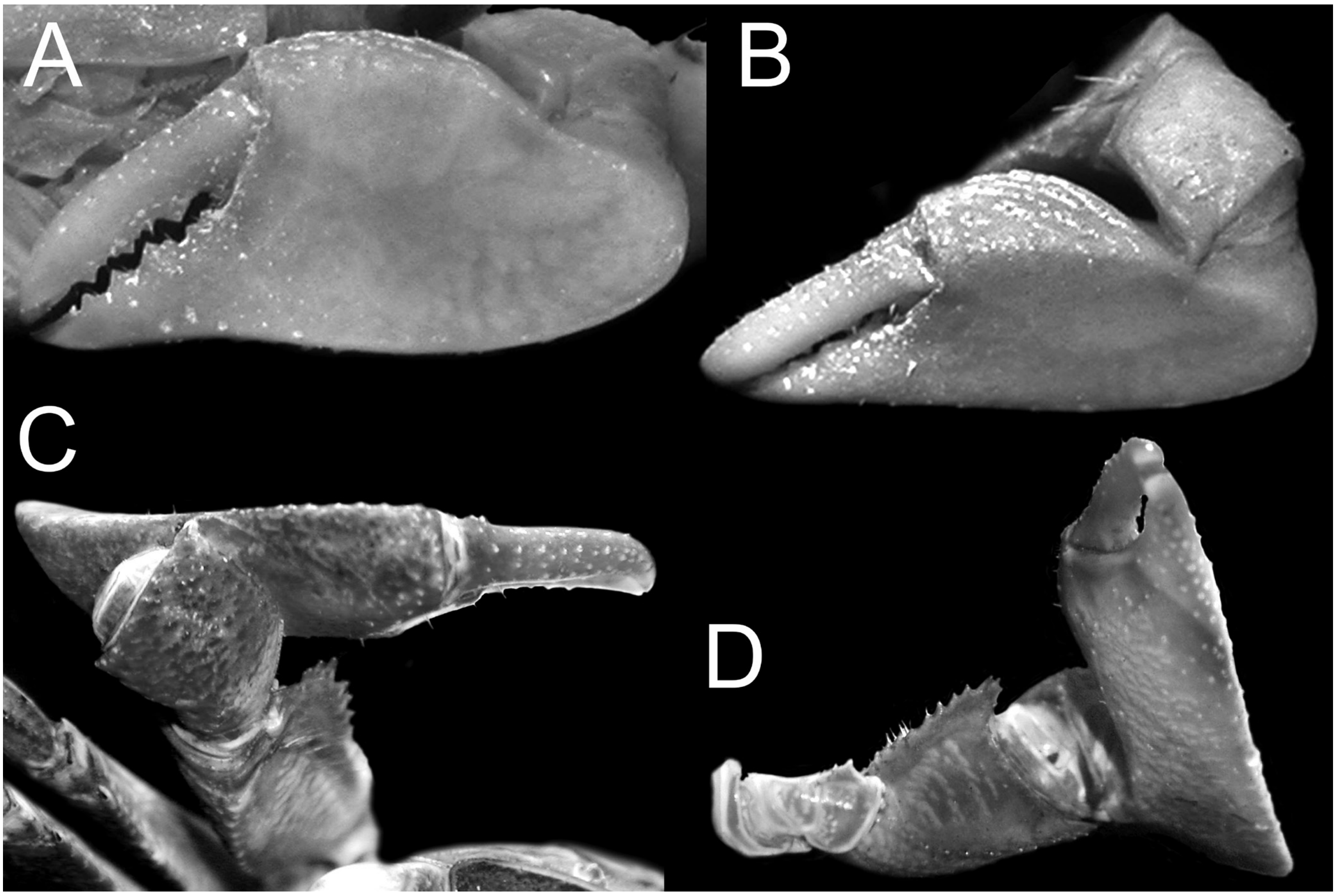

Fig. 17. Chela of species of *Platychirarma buettikoferi*. A, paralectotype male (10.0 × 8.7 mm) (SMF-ZMG 636), Fisherman Lake, Liberia; B–D, male (12.6 × 10.4 mm) (ZRC 2015.0298), Cameroon. A, outer view; B, C, dorso-lateral view; D, ventro-marginal view.

County, 21°55′36.6″N 120°44′21.8″S, Taiwan, coll. J.-H. Lee & W.-J. Wang, 17 August 2012; 1 male (18.1 × 13.9 mm) (ZRC 2012.0959), Siatanzai, Kenting, Pingtung County, 21°55′36.6″N 120°44′21.8″S, Taiwan, coll. J.-H. Lee & W.-J. Wang, 31 August 2012; 1 male (17.8 × 13.9 mm), 1 ovigerous female (18.8 × 14.2 mm) (ZRC 2012.0960), Siatanzai, Kenting, Pingtung County, 21°55′36.6″N 120°44′21.8″S, Taiwan, coll. J.-H. Lee & W.-J. Wang, 31 August 2012; 1 female (22.3 × 16.6 mm) (ZRC 2012.0961), Hsiang-Chiau-Wan, Kenting, Pingtung County, Taiwan, coll. P.K.L. Ng & C.-W. Lin, 1 October 2012. Others: JAPAN – 1 male (16.1 × 12.4 mm) (RUMF-ZC-1351), Gazuda Beach, Hateruma Island, Ryukyu Islands, coll. Y. Fujita, 2 May 2009; 2 males (15.5 × 11.1 mm, 13.2 × 9.9 mm) (RUMF-ZC-1386), beside Hateruma Port, Hateruma Island, Ryukyu Islands, coll. Y. Fujita, 19 April 2009; 1 male (16.9 × 13.0 mm) (RUMF-ZC-2075), Dannu Beach, Yonagun Island, Ryukyu Islands, coll. Y. Fujita, 15 November 2007; 1 male (19.7 × 14.6 mm) (RUMF-ZC-2076), Honba Coast, Minamidaito Island, coll. Y. Fujita, 2 September 2008; 1 male (18.5 × 13.9 mm) (RUMF-ZC-2077), Honba Coast, Minamidaito Island, coll. Y. Fujita, 2 September 2008; 1 male (10.9 × 8.2 mm) (RUMF-ZC-2078), Ubama Beach, Yonaguni Island, Ryukyu Islands, coll. Y. Fujita, 16 November 2007; 1 male (17.2 × 12.8 mm) (RUMF-ZC-2079), Dannu Beach, Yonaguni Island, Ryukyu Islands, coll. Y. Fujita, 15 November 2007; 1 male (12.5 × 9.5 mm) (RUMF-ZC-2080), Dannu Beach, Yonaguni Island, Ryukyu Islands, coll. Y. Fujita, 15 November 2007; 1 female (16.9 × 12.9 mm) (RUMF-ZC-2082), Shimoji Island, Miyako Group, Ryukyu Islands, coll. Y. Fujita, 23 September 2012; 1 female (15.6 × 12.1 mm) (RUMF-ZC-2083), Shimoji Island, Miyako Group, Ryukyu Islands, coll. Y. Fujita, 23 September 2012; 1 female (18.0 × 13.1 mm) (RUMF-ZC-2089), Giza Banta, Okinawa Island, Ryukyu Islands, coll. T. Maenosono, 2007; 2 males (16.0 × 12.2 mm, 14.1 × 11.0 mm), 1 female (14.8 × 11.6 mm) (RUMF-ZC-2090), Kori Island, off Nakijin Village of Okinawa Island, Ryukyu Islands, coll. T. Maenosono, 9 June 2010; 2 males (17.5 × 13.7 mm, 17.4 × 12.9 mm), 1 female (15.7 × 12.1 mm) (RUMF-ZC-2104), Muigah, Miyako Island, Ryukyu Islands, coll. Y. Fujita, 4 May 2005; 6 males (largest 18.9 × 14.5 mm, smallest 14.3 × 10.8 mm), 5 females (largest 15.2 × 11.3 mm, smallest 8.3 × 7.1 mm) (ZRC), Muigah, Miyako Island, Ryukyu Islands, coll. Y. Fujita, 4 July 2005; 1 female (12.0 × 15.7 mm) (RUMF-ZC-819), Giza Banda, Yaese Town, Okinawa Island, Ryukyu Islands, coll. T. Maenosono, 22 May 2007.

**Diagnosis**. Carapace transversely subovate, ca. 1.3 times broader than long; dorsal carapace, lateral branchial regions markedly swollen; external orbital tooth moderately oblique, forming slight angle posteriorly marking widest point of carapace, most prominent in larger specimens; front ca. 0.6 times carapace width, margin slightly to broadly concave in dorsal view, appears smooth but microscopically granular, with pair of prominent lateral swellings behind margin; supraorbital margin entire, semicircular; dorsal surface of

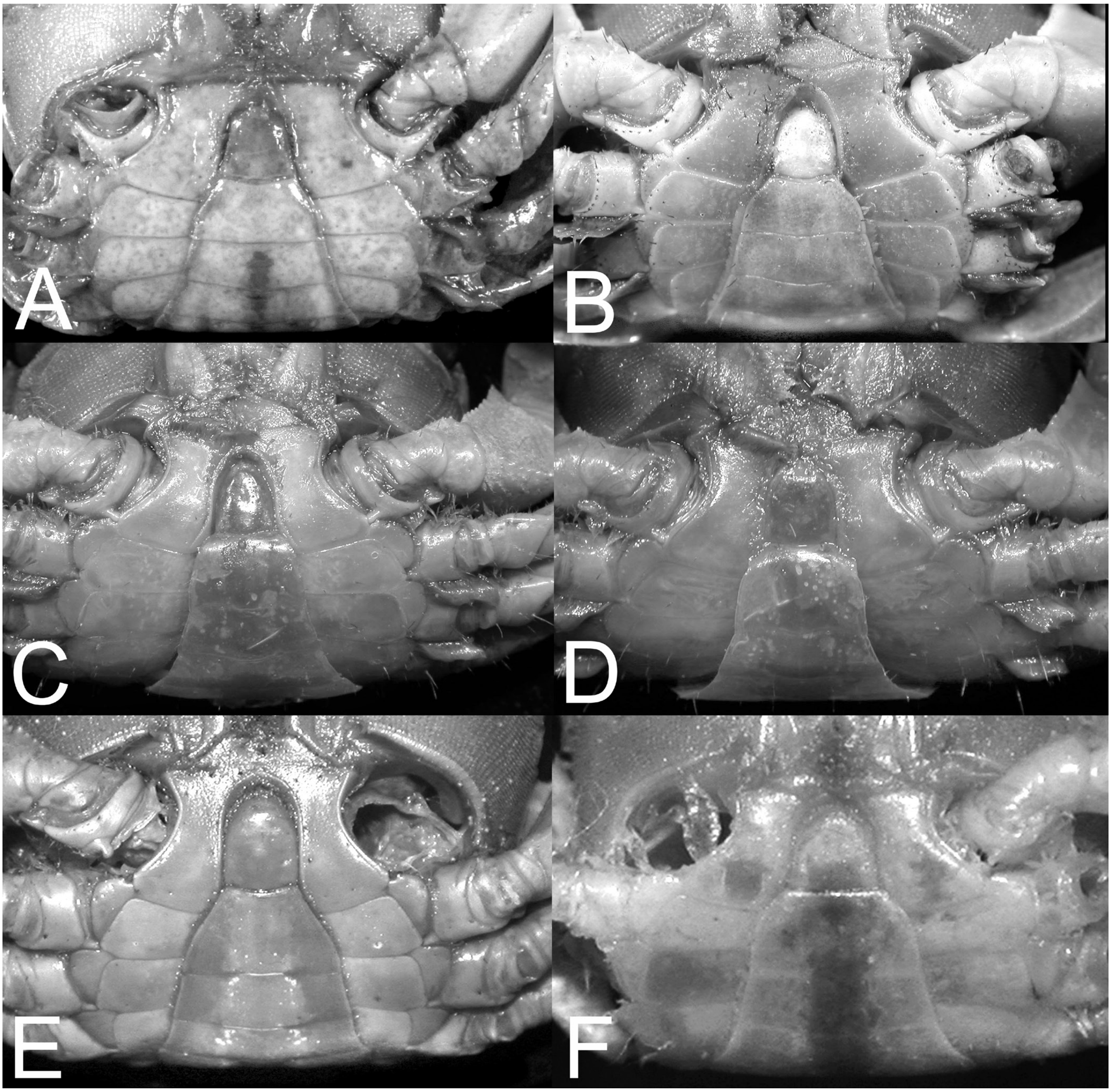

Fig. 18. Male anterior thoracic sternum and pleon. A, *Danarma obtusifrons*, male (19.7 × 14.7 mm) (ZRC 2002.0220), Oahu, Hawaii; B, *Danarma eurymerus*, holotype male (18.7 × 14.8 mm) (NMNS-7028-002), Lanyu Island, Taiwan; C, *Cristarma eulimene*, male (22.2 × 17.2 mm) (ZRC 1968.1.22.2), Inhaca Island, Mozambique; D, *Cristarma ortmanni*, male (20.0 × 15.5 mm) (ZRC 1968.1.22.1), Inhaca Island, Mozambique; E, *Trapezarma angolense*, neotype male (39.3 × 32.7 mm) (SMF-ZMG 635), Benguella, Angola; F, *Platychirarma buettikoferi*, paralectotype male (10.0 × 8.7 mm) (SMF-ZMG 636), Fisherman Lake, Liberia.

cheliped carpus conspicuously granular; ambulatory legs relatively short; third ambulatory merus ca. 2.3 times longer than wide; fourth ambulatory merus similar, 2.2–2.3 times longer; third ambulatory propodus ca. 2.8 times longer than wide; fourth ambulatory propodus 2.4 times; male pleon moderately broad; somite 6 with divergent lateral margins, margins relatively evenly convex; somite 3 width 2.8 times basal width of telson; G1 relatively slender, weakly tapering to broadly convex subdistal shoulder; distally slender, strongly bent to 45° angle; distal chitinous process long, with dorsal margin concave, apex slightly flanged. (After Davie & Ng, 2013: 19).

**Colour**. "Carapace background colour of adult males varying from pale brown to a darker grey-green; females and smaller males mottled greyish white, sometimes yellowish. Upper surface of carapace and legs with some course blotches and streaks; a distinctive pattern of large dirty yellow to green blotches across anterior part of carapace. Chelae of adult males reddish-pink to purplish red overall, especially on dorsal surfaces and dactylus; smaller males and females with palm whitish to whitish-pink, dactylus always clearly tinged with red to pink in part or whole. Ocular peduncles similar to carapace; corneas light green to yellowish green." (Davie & Ng, 2013: 20, fig. 3D–H).

**Remarks**. The taxonomy of this species has been treated and discussed by Davie & Ng (2013).

**Biology**. The species lives among supralittoral karst areas, usually under rocks or in crevices, often in exposed areas (Davie & Ng, 2013: 21). It occurs sympatrically with *D. eurymerus* and thus must have different ecological adaptations, but this has not been studied.

**Distribution**. Known only from Taiwan and Ryukyus, Japan (Davie & Ng, 2013).

### *Danarma eurymerus* (Davie & Ng, 2013)

(Figs. 13C, 14C, D, 19D, E, J–N, 43F)

*Chiromantes obtusifrons* – Liu, 2009: 41, fig. 10. [not *Sesarma obtusifrons* Dana, 1851]
*Chiromantes eurymerus* Davie & Ng, 2013: 21, figs. 3I, J, 4D, 5E, 6E, 7E, 9E, 14; Li & Chiu, 2013: 39; Ng et al., 2017b: 103.

**Material examined**. Holotype male (18.7 × 14.8 mm) (NMNS 7028-002), west coast of Lanyu Island, Taiwan, calcareous rock terraces, spray zone, coll. C.D. Schubart & H.-C. Liu, 20–21 September 1999 [DNA voucher taken but needs to be checked against *C. leptomerus*] (ex ZRC 2000.1860). Paratypes: 1 male (20.0 × 15.4 mm) (QM-W29171), same data as holotype; 1 male (18.2 × 14.0 mm), 2 females (17.0 × 13.2 mm, 19.9 × 15.0 mm) (ZRC 2000.1823), Pingtung County, Hsiang Chiaowan, Taiwan, coll. H.-C. Liu, 25 August 1999; 1 male (13.3 × 10.2 mm) (ZRC 2000.1822), Pingtung County, Hsiang Chiaowan, Taiwan, coll. H.-C. Liu, 5 July 1999; 1 male (19.3 × 14.8 mm), 1 female (22.6 × 16.7 mm) (NMMBA 3504b), coll. Hsiang-Chiau-Wan, Kenting, Pingtung County, Taiwan, coll. C.C. Li, 23 August 2012; 2 males (17.5 × 13.4 mm, 16.7 × 12.3 mm) (NMNS), Siatanzai, Kenting, Pingtung County, 21°55′36.6″N 120°44′21.8″S, Taiwan, coll. J.-H. Lee & W.-J. Wang, 17 August 2012; 1 male (15.4 × 12.3 mm), 1 ovigerous female (18.0 × 13.4 mm) (ZRC 2012.0956), 1 female (18.8 × 13.6 mm) (NMNS), Siatanzai, Kenting, Pingtung County, 21°55′36.6″N 120°44′21.8″S, Taiwan, coll. J.-H. Lee & W.-J. Wang, 31 August 2012. Others: TAIWAN – 1 dried female exuvium (24.8 × 18.7 mm) (ZRC 2012.0957), Dingtanzai, near nuclear power station, Kenting, Pingtung County, coll. P.K.L. Ng, 4 October 2012.

**Diagnosis**. Carapace transversely subovate, ca. 1.3 times broader than long; dorsal carapace, lateral branchial regions markedly swollen; external orbital tooth with outer margin broadly convex marking widest point of carapace; front ca. 0.65–0.7 times carapace width, margin broadly convex in frontal view, but medial part relatively straight in dorsal view, appears smooth but microscopically granular, with pair of low lateral swellings behind margin; supraorbital margin entire, semicircular; dorsal surface of carpus of cheliped covered in small granules; ambulatory legs relatively short; merus of third ambulatory leg ca. 2.0 times longer than wide; that of fourth ambulatory leg similar at 2.0–2.1 times longer; fourth ambulatory propodus 2.1–2.2 times; male pleon moderately broad; somite 6 with distolateral margins relatively straight, strongly divergent, margins convex overall; somite 3 width 3.1 times basal width of telson; G1 markedly stout, with margins subparallel to obtusely angled subdistal shoulder; distally slender, strongly bent to 45° angle; distal chitinous process short, not projecting past line of gonopod shaft, moderately tapering. (After Davie & Ng, 2013: 21).

**Colour**. “Carapaces of adult males and females are generally pale grey and white to yellowish-brown to yellowish-grey; with chelae of both sexes, notably dactylus, white, without obvious pink or red; eyes blue to bluish-green.” (Davie & Ng, 2013: 22, fig. 3I, J).

**Remarks**. The taxonomy of this species has been treated by Davie & Ng (2013). As observed by Davie & Ng (2013: 7, 22), *D. eurymerus* is markedly different from all congeners in having a G1 that is proportionately much stouter, with the distal chitinous part short and subtruncate (Fig. 15J–M). In all other *Danarma* species, the G1 is slender and the distal chitinous part is long (Fig. 15F–I). It is most unusual for congeners to have such a dissimilar G1, and it may be a consequence of natural selection by character displacement to reduce or prevent hybridisation (see General discussion). In any case, the genetic data supports the monophyly of all the *Danarma* species.

The record of “*Stelgistra stormi*” by Lee (2008: 137) from Taiwan is mixed. One photograph is *S. stormi* (De Man, 1895) while the other with blue eyes is clearly a specimen of *D. eurymerus*.

**Biology**. This species lives in crevices or under rocks in the supralittoral karst zone. It has been found together with *D. leptomerus* (Davie & Ng, 2013: 24).

**Distribution**. Known only from Taiwan and Ryukyus, Japan (Davie & Ng, 2013).

### *Danarma garfunkel* (Davie & Ng, 2013)

(Figs. 13D, 14B)

*Sesarma* (*Holometopus*) *obtusifrons* – Balss, 1934: 229.
*Sesarma obtusifrons* – Gibson-Hill, 1947: 44; Tweedie, 1947: 33; George, 1978: 13 (unnumbered pages); Hicks et al., 1984: 22, 65, with colour photograph.
*Chiromantes obtusifrons* – Davie, 2002: 221; Ng & Davie, 2012: 18; Orchard, 2012: 198, 199.
*Chiromantes garfunkel* Davie & Ng, 2013: 7, figs. 2, 4E, 5F, 6F, 7F, 8D, 9F, 10B, 12; Aw & Low, 2020: 8.

Material examined. Holotype male (17.0 × 13.0 mm) (QM, ex ZRC 2009.0822), Greta Beach, Christmas Island, coll. H.H. Tan, 8 December 2007. Paratypes – 4 males (13.5 × 10.2 mm, 15.2 × 11.6 mm, 18.2 × 14.7 mm, 17.9 × 14.0 mm), 4 females (13.0 × 9.6 mm, 14.3 × 10.8 mm, 14.7 × 11.2 mm, 17.5 × 13.6 mm) (ZRC 2012.0778), station CI-06, Grotto, Waterfall Road, 10°25.386′S 105°42.127′E, weathered cave, tidal sump, coll. 23 January 2010; 1 female (12.1 × 9.1 mm) (ZRC 2012.0780), station CI-04, Merrial Beach, 10°28.455′S 105°33.551′E, sandy beach, beach forest,

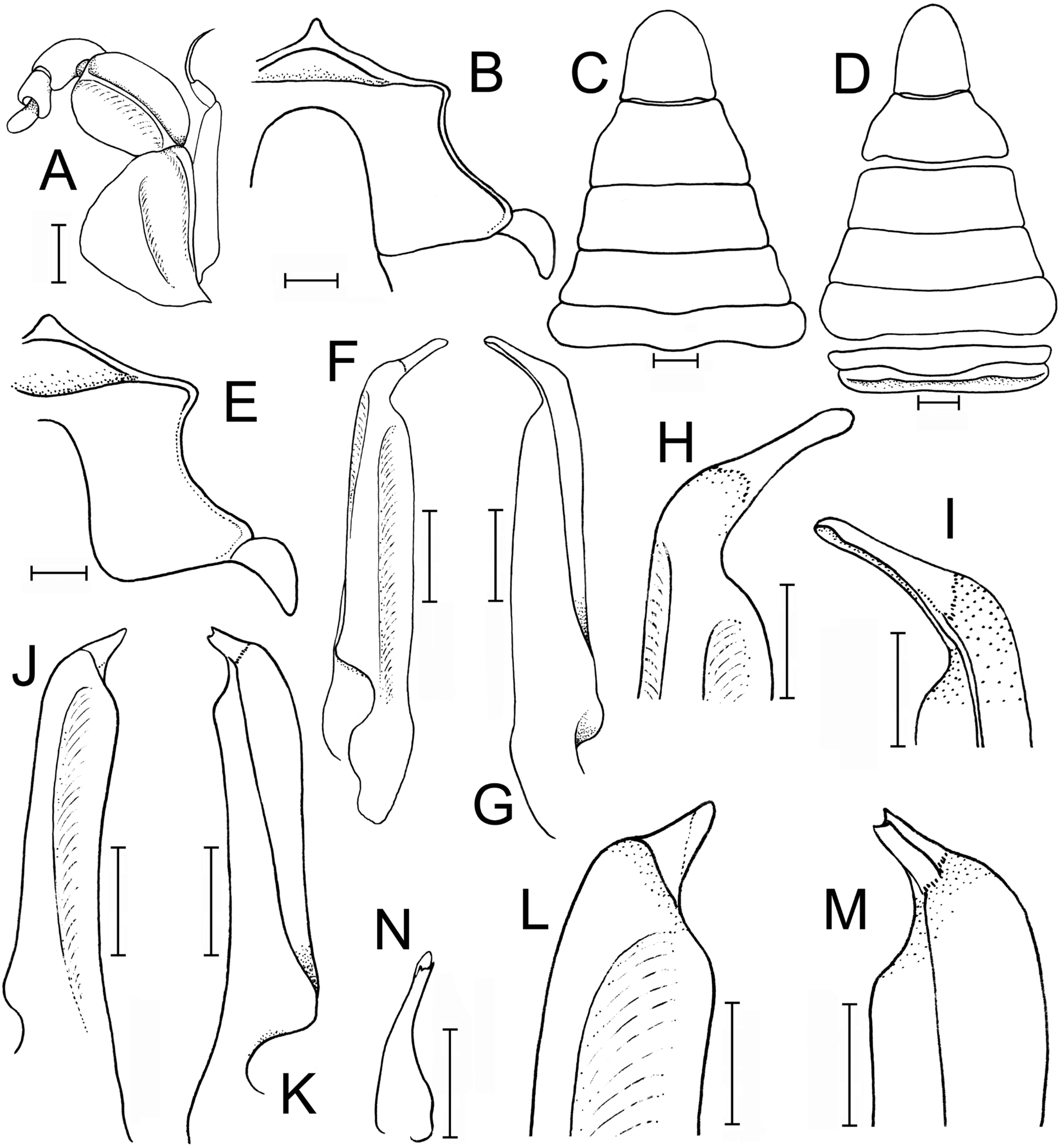

Fig. 19. A–C, F–I, *Danarma obtusifrons*, male (19.7 × 14.7 mm) (ZRC 2002.0220), Oahu, Hawaii; D, E, J–N, *Danarma eurymerus*, holotype male (18.7 × 14.8 mm) (NMNS-7028-002), Lanyu Island, Taiwan. A, left third maxilliped (denuded); B, E, anterior thoracic sternites 1–4; C, D, male pleon; F, J, left G1 (ventral view, denuded); G, K, left G1 (dorsal view, denuded); H, L, left distal part of G1 (ventral view, denuded); I, M, left distal part of G1 (dorsal view, denuded); N, left G2 (denuded). After Davie & Ng (2013: figs. 11, 14). Scales: A–G, J, K, N = 1.0 mm; H, I, L, M = 0.5 mm.

limestone base rock, coll. 20 March 2011; 1 male (13.5 × 10.2 mm) (ZRC 2012.0781), Ethel Beach, 10°27.805′S 105°42.443′E, sandy beach, beach forest, limestone base rock, station CI-09, coll. 21 March 2011; 1 female (13.3 × 12.0 mm) (ZRC 2012.0776), Greta Beach, 10°30.127′S 105°40.475′E, station CI-33, coll. 27 March 2011; 1 female (11.1 × 8.3 mm) (ZRC 2012.0782), Flying Fish Cove, 10°25.815′S 105°40.180′E, rocky, gravel beach, station CI-01, coll. 22 January 2010; 1 ovigerous female (11.4 × 8.6 mm) (ZRC 2012.0783), Flying Fish Cove, 10°25.815′S 105°40.180′E, rocky, gravel beach, station CI-01, coll. 22 January 2010; 1 female (10.8 × 8.2 mm) (ZRC 2012.0785), Lily Beach, 10°28.011′S 105°42.688′E, sandy beach, beach forest, limestone base rock station CI-02, coll. 22 January 2010; 1 male (13.9 × 10.6 mm) (ZRC 2012.0777), Greta Beach, 10°30.127′S 105°40.475′E, limestone cliff, sandy beach, limestone bedrock, station CI-12, coll. 24 January 2010; 1 male (14.0 × 10.8 mm) (ZRC 2012.0784), Flying Fish Cove, 10°25.815′S 105°40.180′E, rocky, gravel beach, 22 January 2010; 2 males (10.8 × 9.8 mm, 14.5 × 13.2 mm) (ZRC 2012.0779), Waterfall Bay, Christmas Island Resort, 10°27.54′S 105°42.30′E, freshwater stream, sandy beach, limestone base rock, station CI-07, coll. 23 January 2010; 1 female (11.6 × 8.6 mm) (ZRC 2012.0786), Lily Beach, 10°28.011′S 105°42.688′E, sandy beach, beach forest, limestone base rock, station CI-02, coll. 22 January 2010; 1 male (13.7 × 10.4 mm) (ZRC 1965.7.29.153), no specific location, coll. 1932; 2 paratype males (larger 11.5 × 8.8 mm), 7 paratype females (largest 20.4 × 16.2 mm) (ZRC 1965.7.29.154–163), shore terrace along east and north coasts, and Isabel Beach, Christmas Island, coll. M.W.F. Tweedie, 2 March 1932. All locations on Christmas Island.

**Diagnosis**. Carapace transversely subovate, ca. 1.3 times broader than long; dorsal carapace, lateral branchial regions prominently swollen; external orbital tooth at widest point only projecting slightly more than external orbital tooth; front ca. 0.6 times carapace width, margin broadly convex in dorsal view, appearing smooth but microscopically granular, with pair of weak lateral swellings behind margin; supraorbital margin entire, straight, obliquely sloping posteriorly; outer surface of cheliped carpus moderately granular; ambulatory legs relatively short; third ambulatory merus ca. 2.3 times longer than wide; fourth ambulatory merus relatively narrower than third ambulatory merus, ca. 2.6 times longer; third ambulatory propodus ca. 2.8 times longer than wide; fourth ambulatory propodus ca. 2.7 times longer; male pleon (moderately broad; somite 6 with lateral margins diverging, slightly concave over distal half, more subparallel over proximal half; somite 3 width 3.0 times basal width of telson; G1 relatively slender, weakly tapering to prominent subdistal shoulder; distal chitinous process long, with slender narrow apex, dorsal margin slightly sinuous. (After Davie & Ng, 2013: 9).

**Colour**. "Carapace and legs of adults rich, dark purple to maroon; without prominent speckling or splotching. Legs uniform in colour, without transverse banding. Chelipeds relatively uniform in colour, not clearly darker dorsally; off-white to white porcelain in adults, markedly contrasting with purple carapace. Ocular peduncles same as carapace in colour; corneas bright yellow. Female specimens from more exposed supralittoral areas behind beaches can be paler in coloration, with the carapace and legs beige with streaks of purple and brown. Their eyes, however, are still bright yellow." (Davie & Ng, 2013: 12, 13, fig. 2).

**Remarks**. The taxonomy of this species has been treated at length by Davie & Ng (2013).

**Biology**. This species is typically found in the supralittoral, usually among limestone or similar formations. Crabs have been observed to climb many metres up on karst cliffs. They are primarily nocturnal, apparently feeding on the algae growing on the rocks. Gibson-Hill (1947: 44) states that the preferred spawning period is between January to April, with broods estimated at 5,500 eggs. See also Davie & Ng (2013: 14).

**Distribution**. Known only from Christmas Island (Davie & Ng, 2013).

### *Cristarma*, new genus

**Type species**. *Sesarma* (*Sesarma*) *eulimene* De Man, in Weber, 1897, by present designation. Gender neuter.

**Diagnosis**. Carapace transversely rectangular, distinctly broader than long; frontal margin gently bilobed, gently deflexed, subequal to posterior carapace margin; lateral margins of carapace entire in adults, posterolateral part subparallel; regions of carapace demarcated; postfrontal and epigastric crests separated by relatively deep grooves, margin relatively rounded, regions clearly separated; basal articles of antenna and antennules separated by septum; dorsal margin of palm with oblique pectinated ridge near base of finger; inner surface of palm with prominent submedian transverse swelling, highest point with transverse ridge of granules, outer surface of palm and pollex convex, lower surface of palm with 2 short, smooth, submedian oblique ridges; dorsal margin of chelipedal dactylus with differentiated or prominently shaped row of stridulatory granules; inner distal margin of merus of cheliped not lamelliform; inner surfaces of first to third ambulatory coxae with numerous long setae between them; male thoracic sternites 2–4 relatively narrow in adults, suture between sternites 3 and 4 distinct; male sternopleonal cavity reaching two-thirds length of sternite 4 to just before anterior margin of sternite 2; male thoracic sternite 5 smooth, without depression on anterior part; G1 relatively slender, chitinous part relatively short. Vulva on anterior part of sternite 6, anterior edge presses against sternite 5; anterior sternal vulvar cover very low, posterior sternal vulvar cover forming low rim; opening projecting obliquely anteriorly.

**Etymology**. The name is derived from the Latin term for "crest" (crista) with the genus name *Sesarma*. The gender is neuter.

**Included species**. *Sesarma* (*Sesarma*) *eulimene* De Man, in Weber, 1897; *Sesarma ortmanni* Crosnier, 1965.

**Remarks**. The two species included in *Cristarma*, new genus, have been well described and discussed by De Man (1895) and Crosnier (1965). Although they have been treated as species of *Chiromantes* s. lato because their lateral carapace margins are entire, they have more features in common with *Parasesarma* De Man, 1895, i.e., absence of an epibranchial tooth, presence of pectinated crest on the dorsal margin of the chela, and possession of distinct tubercles on the dorsal margin of the cheliped dactylus. *Parasesarma* species, however, have a relatively wider male thoracic sternum, a proportionately much broader pleon, the tubercles on their cheliped dactylus are almost always more distinctively structured, and the inner surface of the chela has a prominent

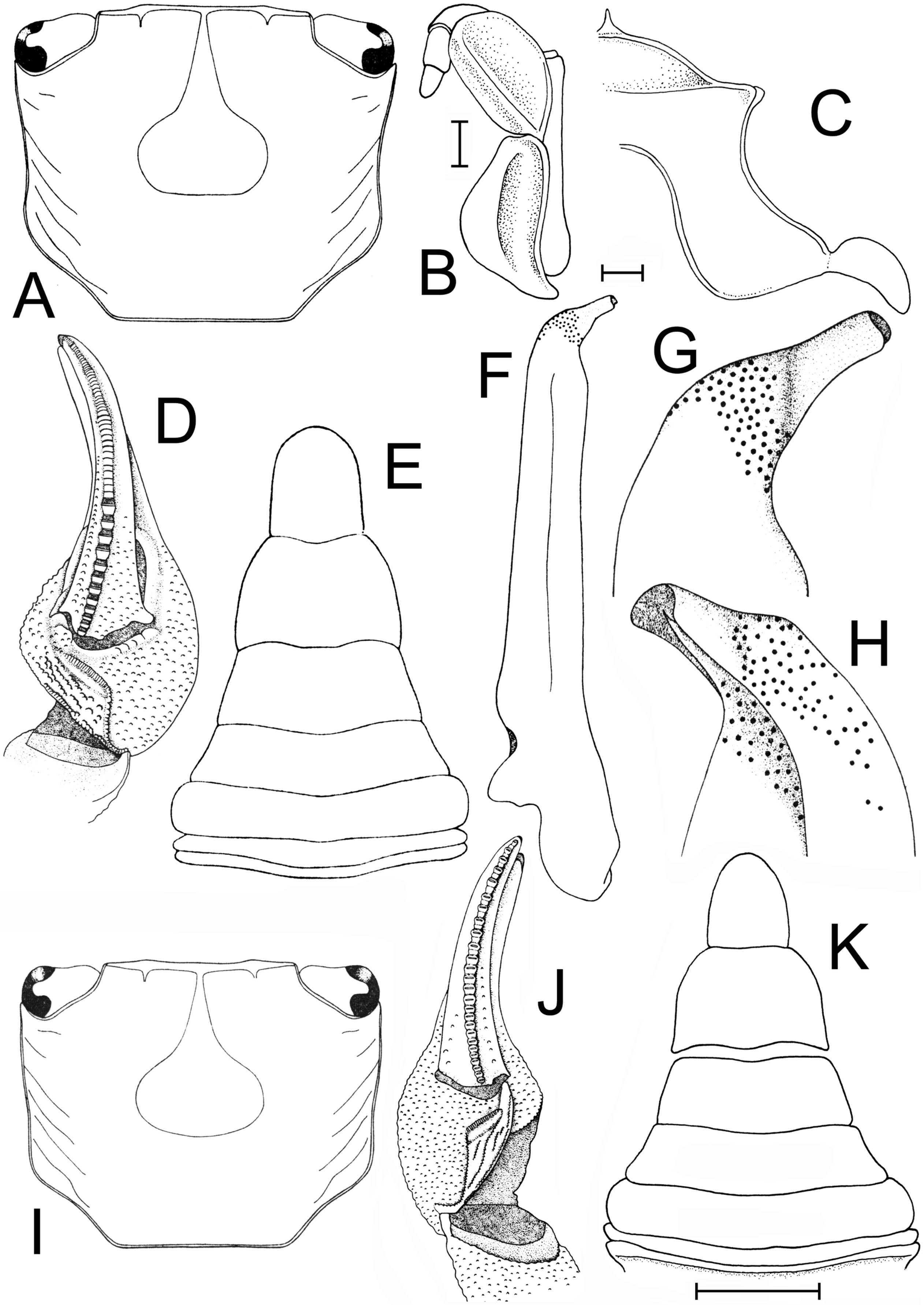

Fig. 20. A, D–H, *Cristarma eulimene*, male, Tamatave, Madagascar; B, C, *C. eulimene*, male (22.2 × 17.2 mm) (ZRC 1968.1.22.2), Inhaca Island, Mozambique; I, J, *C. ortmanni*, male, Tuléar, Madagascar; K, *C. ortmanni*, male (20.0 × 15.5 mm) (ZRC 1968.1.22.1), Inhaca Island, Mozambique. A, I, carapace; B, left third maxilliped (denuded); C, anterior thoracic sternites 1–4; D, J, dorso-lateral view showing ridge on chela and dactylus; E, K, male pleon; F, left G1 (ventral view, denuded); G, left G1 (dorsal view, denuded); H, left distal part of G1 (ventral view, denuded). A, D–H, I, J, after Crosnier (1965: figs. 68–71, 73, 85, 107, 108). Scales: B, C = 1.0 mm; K = 5.0 mm.

transverse granulated ridge (low or not as prominent in species of *Parasesarma*). In addition, *Cristarma eulimene* and *C. ortmanni* have two short parallel oblique ridges on the outer surface of their chelae, a character absent in all known *Parasesarma* species. The combination of characters on the chela is unique for these two species, and combined with the fact that the male palm is oblique to almost transverse in orientation, the glabrous lateral margins of the ambulatory dactyli, the presence of dense setae between the first to third ambulatory coxae and the vulva is very low, with two sternal vulvar covers bracketing the opening, we believe a new genus is warranted. The molecular tree also supports this, with the two species clustering in a distinct clade far from all the other genera (Fig. 59).

### *Cristarma eulimene* (De Man, in Weber, 1897)

(Figs. 13E, 14E, 15C, D, 18C, 20A–H, 43G)

*Sesarma* (*Sesarma*) *eulimene* De Man, in Weber, 1897: 157, pl. 15 fig. 1.
*Sesarma eulimene* – Stebbing, 1910: 322; Fourmanoir, 1953: 90.
*Sesarma* (*Holometopus*) *eulimene* – Tesch, 1917: 150; Crosnier, 1965: 51, figs. 68, 69, 73, 77b, 85, 107, 108; Guinot, 1967: 288; Serène, 1968: 107.
*Holometopus eulimine* (sic) – Hartnoll, 1975: 308, 311, 316.
*Chiromantes eulimene* – Naderloo & Schubart, 2009: 67.
"*Chiromantes*" *eulimene* – Ng et al., 2008a: 220; Emmerson, 2016: 235, unnumbered colour fig.

**Material examined**. MOZAMBIQUE – 1 male (22.2 × 17.2 mm), 1 adult female (15.6 × 12.8 mm) (ZRC 1968.1.22.2–3), Inhaca Island, coll. W. McNae, April 1967. SOUTH AFRICA – 2 males (22.0 × 17.8 mm, 22.2 × 18.5 mm) (ZRC 2017.0168), mangrove creek, Mngazana, Eastern Cape Province, coll. S. Cannici, 9–10 March 2017.

**Diagnosis**. Carapace quadrate; lateral margin sinuous; dorsal margin of male cheliped dactylus with about 15 symmetrical tubercles on proximal half, followed by 10 asymmetrical tubercles on distal half; male pleon proportionately narrower, longer.

**Colour**. In life, the species was described as with a brown carapace and red male chela (Crosnier, 1965: 51). In larger males, the centre of the chela becomes more faded (Emmerson, 2016: 235, unnumbered colour fig.).

**Remarks**. The authorship for this species should be "De Man, in Weber, 1897". Weber wrote the chapter on decapod crustaceans in his paper but noted that some contributions were by De Man (Weber, 1897: 156). In the new species description for *Sesarma eulimene*, it was clearly stated that the work was by De Man: "(Beschrieben von Herrn Dr. J. G. de Man.)" (Weber, 1897: 157). The year of publication is usually cited as 1898 but this is incorrect. While volume 10 of "Zoologische Jahrbücher, Abtheilung für Systematik, Geographie und Biologie der Thiere" was dated as 1898, the articles actually appeared in parts. Weber's paper appeared in part 2 of volume 10, and this was stated to be published on 21 May 1897. This species was described from two males and four females from Umbilo River in Natal (present day KwaZulu-Natal, South Africa), and he gave measurements for the two males (17 × 14.25 mm, 15 × 12 mm) and two larger females (15.3 × 12.5 mm, 12.25 × 9.7 mm). It is not known where this material is now and whether it is still extant; it is not in Leiden (Fransen et al., 1997). Crosnier (1965: 51) commented that he had compared his specimens to the syntypes but he did not elaborate if he had actually seen the specimens or based it on the publication only. In any case, the material reported by Crosnier (1965) from Madagascar and the present specimens agree well with De Man's (1897) detailed description and good figures and we have no doubt of their conspecificity.

Crosnier (1965) redescribed *C. eulimene* with good figures and compared it in detail with *C. ortmanni*. While both species have superficially a similar G1, their carapace shapes are quite different: *C. eulimene* is more squarish, with the lateral carapace margins sinuous (Figs. 13E, 20A), while *C. ortmanni* is distinctly more transversely rectangular with the lateral margins almost straight (Figs. 13F, 20I). In addition, *C. ortmanni* has 25 tubercles on the dorsal margin of the male cheliped dactylus, with half of them larger and relatively symmetrical (Figs. 15E, 20J), while *C. eulimene* has only 12 slightly asymmetrical tubercles (Figs. 15C, 20D). The male pleon of *C. ortmanni* is also slightly wider and shorter (Figs. 18D, 20K) compared to that of *C. eulimene* (Figs. 18C, 20E).

**Biology**. The best account of the ecology of this species is by Hartnoll (1975: 316) who notes that it occurs only in the terrestrial vegetation above the supralittoral zone. *Neosarmatium africanum* Ragionieri, Fratini & Schubart, 2012 [as *N. meinerti* (De Man, 1887)] and *C. ortmanni* also occur in this zone, with both species also found elsewhere in the mangroves. Emmerson (2016: 237, 238) provides a detailed summary of the known ecology and biology of the species.

**Distribution**. From Tanzania and Mozambique to South Africa and Madagascar (Crosnier, 1965: 51; Hartnoll, 1975; Emmerson, 2016).

### *Cristarma ortmanni* (Crosnier, 1965)

(Figs. 13F, 14F, 15E, F, 18D, 20I–K, 43H)

*Sesarma quadrata* – Hilgendorf, 1869: 90, pl. 3 fig. 3c, pl. 4 fig. 3 [not *Cancer quadratus* Fabricius, 1798].
*Sesarma erythrodactyla* var. *africana* – Ortmann, 1894: 56 [not *Sesarma africana* H. Milne Edwards, 1837].
*Sesarma ortmanni* Crosnier, 1965: 51, figs. 70, 71.
*Sesarma* (*Holometopus*) *ortmanni* – Serène, 1968: 107.
*Holometopus ortmanni* – Hartnoll, 1975: 308, 311, 316.
*Chiromantes ortmanni* – Naderloo & Schubart, 2009: 67.
"*Chiromantes*" *ortmanni* – Ng et al., 2008a: 220; Emmerson, 2016: 240, unnumbered colour fig.

**Material examined**. Lectotype (here designated): male (10.7 × 8.2 mm) (MNHN B16741a), Nosy Be, Tuléar, Madagascar, coll. A. Crosnier, 1960s. Paralectotypes: 1 male (8.6 × 6.7 mm), 2 females (10.9 × 8.6 mm, 12.7 × 9.8 mm) (MNHN B16741b), same data as lectotype. KENYA – 2 males (19.4

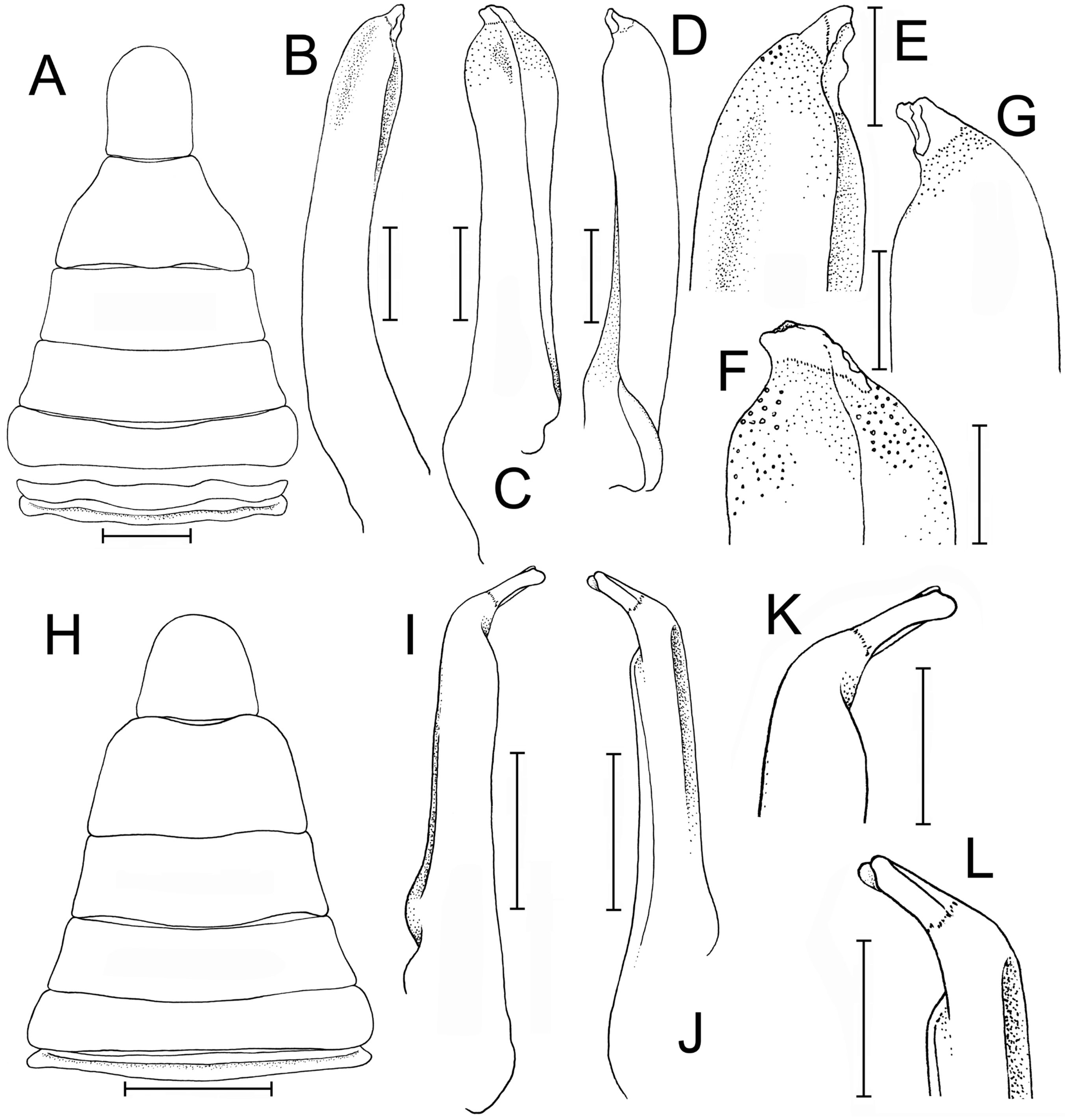

Fig. 21. A–G, *Trapezarma angolense*, neotype male (39.3 × 32.7 mm) (SMF-ZMG 635), Benguella, Angola; H–L, *Platychirarma buettikoferi*, 1 male (10.7 × 8.8 mm) (SMF 25980), West Nimbe Cameroon. A, H, male pleon; B, I, left G1 (ventral view, denuded); C, left G1 (dorso-lateral view) (denuded); D, J, left G1 (dorsal view, denuded); E, K, left distal part of G1 (ventral view, denuded); G, L, left distal part of G1 (dorsal view, denuded); F, left distal part of G1 (dorso-lateral view) (denuded). Scales: A = 5.0 mm; B–D, H = 2.0 mm; E–G, I, J = 1.0 mm; K, L = 0.5 mm.

× 14.4 mm, 15.1 × 11.9 mm), 2 females (13.1 × 10.2 mm, 10.9 × 8.6 mm) (ZRC 2000.1783), Gazi, coll. M. Vannini, November 1991. MOZAMBIQUE – 1 male (20.0 × 15.5 mm) (ZRC 1968.1.22.1), Inhaca Island, coll. MacNae, April 1967.

**Diagnosis**. Carapace proportionately broader, transversely rectangular; lateral margin almost straight; dorsal margin of male cheliped dactylus with about 12 slightly asymmetrical tubercles which get progressively smaller distally; male pleon proportionately broader, shorter.

**Colour**. According to Crosnier (1965: 53), the carapace is green with the ambulatory legs yellowish. Emmerson (2016: 240, unnumbered colour fig.) depicts a specimen with bright red chelae and a beige transverse faceband on the carapace.

**Remarks**. Some nomenclatural notes on this species are necessary. In describing *Sesarma* (*Holometopus*) *ortmanni*, Crosnier (1965) suggested that it may be the same as *Sesarma erythrodactyla* var. *africana* Ortmann, 1894. Crosnier (1965: 53) commented that "le type de *Sesarma erythrodactyla*

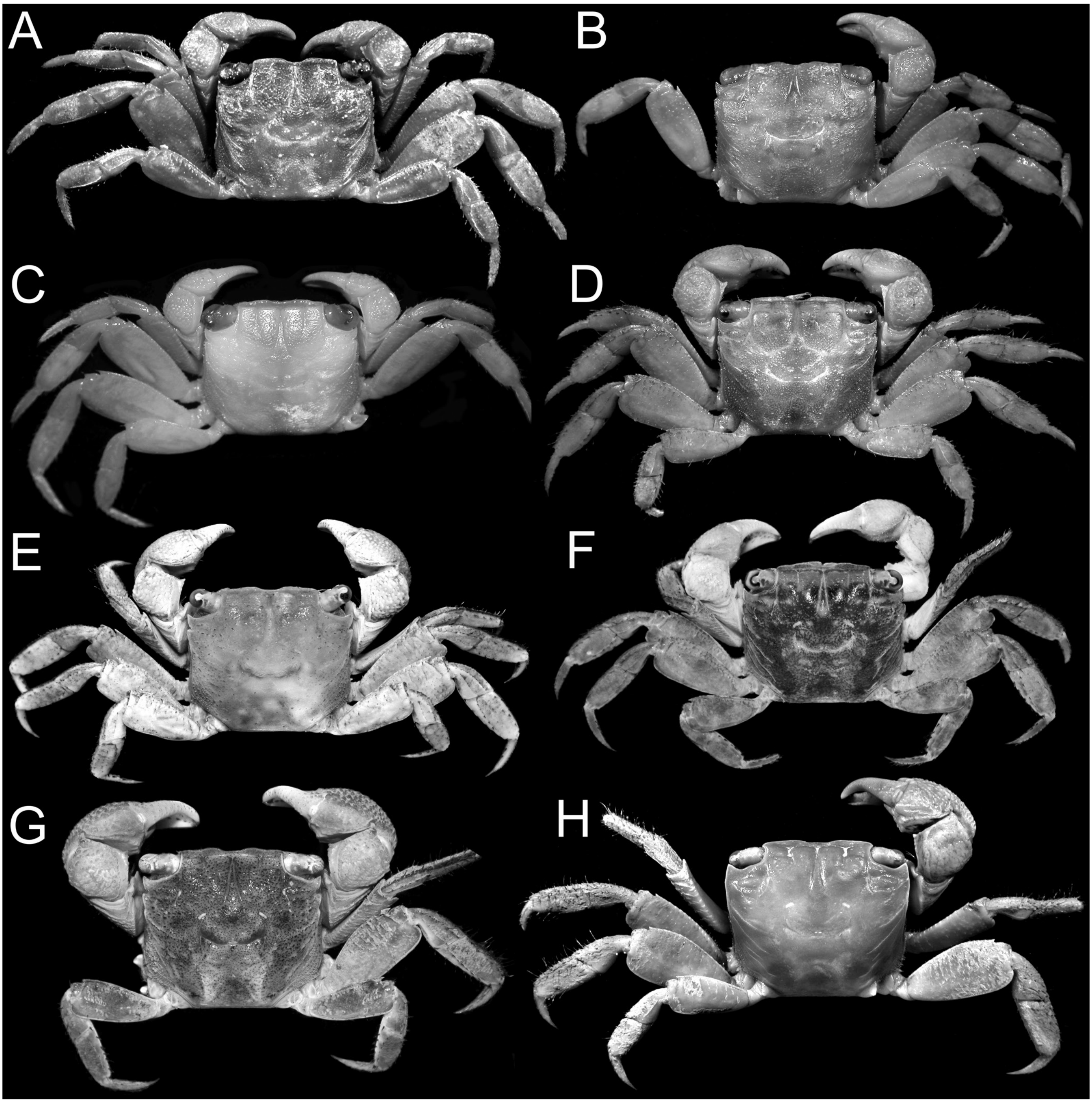

Fig. 22. Overall habitus, *Pseudosesarma* species. A, *P. edwardsii*, lectotype male (17.5 × 16.1 mm) (RMNH-D17a), Mergui Archipelago; B, *P. edwardsii*, male (13.4 × 11.9 mm) (ZRC 1965.8.2.81), Pulau Pawai, Singapore; C, *P. edwardsii*, male (12.9 × 11.8 mm) (ZRC 1971.9.24.9), Singapore; D, *P. crassimanum*, male (15.9 × 14.5 mm) (RMNH-D23313), Singapore; E, *P. anteactum*, holotype male (16.7 × 14.7 mm) (ZRC 2016.0602), Sri Lanka; F, *P. glabrum*, holotype male (13.8 × 12.0 mm) (CUSAT 2016-1), Kerala, India; G, *P. brehieri*, holotype male (17.4 × 15.7 mm) (ZRC 2016.0593), Myanmar; H, *P. boulengeri*, lectotype male (26.9 × 23.5 mm) (NHM 1919.11.14.1), Basra, Iraq.

var. *africana* ne se trouve pas au Muséum de Strasbourg où est déposée la collection d'ORTMANN. La description de cette espèce est, d'autre part, assez sommaire. Il est donc impossible de savoir avec certitude si l'espèce que nous considérons ci-dessus est la même que celle décrite par ORTMANN. Nous pensons toutefois qu'il y a de fortes chances qu'il en soit ainsi et c'est pour cela que nous dédions notre espèce à ORTMANN. L'examen de spécimens des espèces de *Sesarma* existant à Dar es Salam (localité du type d'ORTMANN) permettrait vraisemblablement d'éclaircir le problème. *Sesarma erythrodactyla* Hess appartient au sous-genre *Parasesarma*; l'espèce que nous appelons *S. ortmanni* au sous-genre *Holometopus*. Si donc *S. ortmanni* et *S. erythrodactyla* var. *africana* sont identiques, l'espèce d'ORTMANN ne doit pas être considérée comme une variété de *S. erythrodactyla* mais comme une espèce distincte. Il n'est pas possible de l'appeler *S. africana*, ce nom ayant déjà été donné par H. MILNE EDWARDS à une espèce de *Sesarma* de la côte oust de l'Afrique. *Sesarma ortmanni* est donc soit une espèce nouvelle, soit simplement, si son

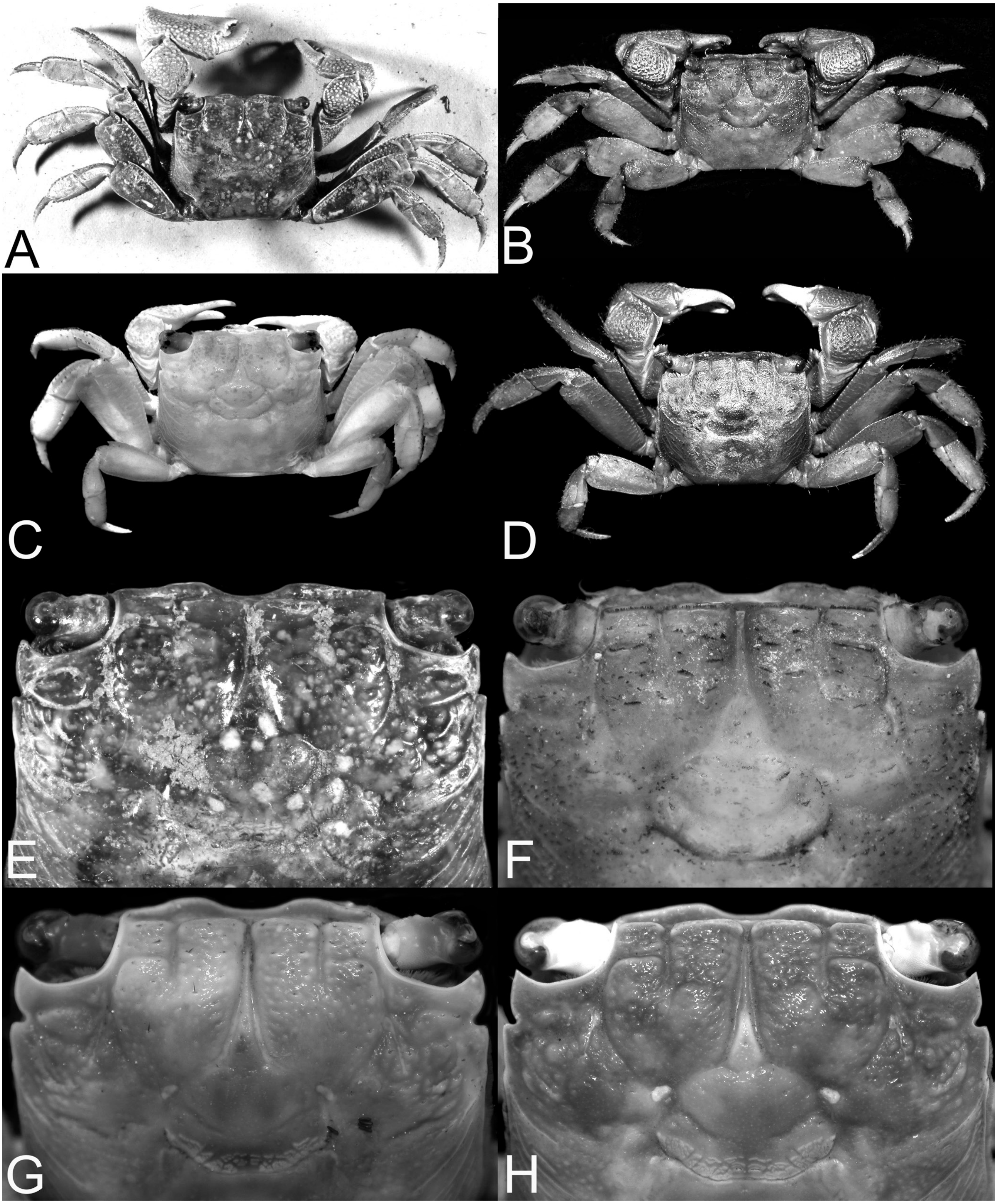

Fig. 23. A, E, *Contusarma bocourti*, lectotype male (24.0 × 27.2 mm) (MNHN D-10965), Bangkok, Thailand; B, F, *C. bocourti*, male (25.3 × 23.3 mm) (ZRC 2000.0952), Bangkok, Thailand; C, *C. bocourti*, female (21.1 × 19.0 mm) (ZRC 2019.1114), Bangkok, Thailand; D, H, *C. cheirogonum*, neotype male (24.5 × 21.5 mm) (ZRC 1995.225), Bako National Park, Sarawak; G, *C. cheirogonum*, male (23.0 × 20.7 mm) (ZRC 2000.2018), Pulau Ubin, Singapore. A–D, overall habitus; E–H, anterior half of carapace.

identité avec l'espèce d'ORTMANN peut être clairement établie, une nouvelle désignation de *S. erythrodactyla* var. *africana*". *Sesarma erythrodactyla* var. *africana* Ortmann, 1894, is clearly a junior primary homonym of *Sesarma africana* H. Milne Edwards, 1837, and according to article 57.2 of the current zoological code (ICZN, 1999), the name needs to be replaced. Although Article 23.9.5 allows for a junior primary homonym to be retained, it states that "When an author discovers that a species-group name in use is a junior primary homonym [Art. 53.3] of another species-group name also in use, but the names apply to taxa not considered congeneric after 1899, the author must not automatically replace the junior homonym; the case should be referred to the Commission for a ruling under the plenary power and meanwhile prevailing usage of both names is to be maintained [Art. 82]". The requirements of Article 23.9.5 are not fulfilled because even after 1899, H. Milne Edwards' and Ortmann's names were used together in the same genus by some authors. For example, Tesch (1917) uses both "*Sesarma* (*Chiromantes*) *africana* H. Milne Edwards" (p. 129) and "*Sesarma* (*Parasesarma*) *erythrodactyla africana* Ortmann" (p. 140); and although he has them in different subgenera and species-groups, the fact remains that both taxa were placed in "*Sesarma*" and the zoological code (Article 57.1) treats species and subspecies as species-group names and therefore of equal status. As such, *Sesarma erythrodactyla* var. *africana* Ortmann, 1894, is not an available name. This situation remains even if *Sesarma africana* H. Milne Edwards, 1837, is currently regarded as a junior subjective synonym of *Perisesarma huzardi* (Desmarest, 1825). As discussed by Crosnier (1965), it is likely that *Sesarma erythrodactyla* var. *africana* Ortmann, 1894, is conspecific with *Sesarma* (*Holometopus*) *ortmanni* Crosnier, 1965. In the event they are not, then Ortmann's (1894) name must be replaced if there is no senior synonym.

In naming this species, Crosnier (1965: 51) stated he had two males and two females but did not specify a holotype. As such, all his specimens are syntypes. The largest male (10.7 × 8.2 mm) (MNHN B16741a) is here designated the lectotype of *Sesarma ortmanni* Crosnier, 1965.

**Biology**. Hartnoll (1975: 316) records this species as occurring in terrestrial vegetation above the supralittoral zone all the way down to the sand flats and *Avicennia* mangrove zone.

**Distribution**. Along the eastern and southern coasts of Africa (Crosnier, 1965; Hartnoll, 1975; Emmerson, 2016). Emmerson (2016: 241–243) provides a detailed summary of the known ecology and biology of the species.

### *Trapezarma*, new genus

**Type species**. *Sesarma angolensis* Brito Capello, 1864, by present designation. Gender neuter.

**Diagnosis**. Carapace trapezoidal, distinctly broader than long; frontal margin entire or slightly bilobed, gently deflexed, wider than carapace margin; lateral margins of carapace gently convex, entire in adults, posterolateral part prominently converging; regions of carapace demarcated; postfrontal and epigastric crests separated by relatively shallow grooves, margin relatively sharp, almost straight, appearing contiguous; basal articles of antenna and antennules separated by septum; dorsal margin of palm without longitudinal pectinated ridge, inner surface not swollen, without granulated ridge, outer surface of palm and pollex gently convex to almost flat, smooth or with small granules, palm and pollex high in adult males, outer margin of palm rounded, without elbow-like projection; dorsal margin of chelipedal dactylus lined with irregularly arranged small granules of various sizes; inner margin of the chelipedal merus rounded, inner distal margin not lamelliform or with distal part partially expanded into projection; inner surfaces of first to third ambulatory coxae with only scattered short setae between them, not arranged into dense tufts; male thoracic sternites 2–4 relatively narrow, suture between sternites 3 and 4 distinct; male sternopleonal cavity reaching three-quarters length of sternite 4 to just before anterior margin of sternite 2; male thoracic sternite 5 smooth, without depression on anterior part; male pleonal somite 6 proportionately more narrow, telson linguiform; G1 relatively stout, subdistal part dilated, chitinous part short. Vulva on median part of sternite 6; sternal vulvar covers lateral, anterior sternal vulvar cover low, lobiform, posterior sternal cover very low; opening short, projecting, directed obliquely posteriorly.

**Etymology**. The genus name alludes to the trapezoidal shape of the carapace of the type species, in combination with the genus name *Sesarma*. The gender is neuter.

**Included species**. *Sesarma angolensis* Brito Capello, 1864.

**Remarks**. The two West African species, *Sesarma angolense* Brito Capello, 1864, and *Sesarma buettikoferi* De Man, 1883, form a discrete genetic clade in the molecular analysis, indicating they are sister taxa. They both possess relatively trapezoidal carapaces, a broad frontal margin, flattened to relatively flattened adult male chela and a sternopleonal cavity that reaches the junction between sternites 3 and 4, however they differ markedly in many features. *Sesarma angolense* is a much larger species with a more trapezoidal carapace (Fig. 13G) compared to *S. buettikoferi* (Fig. 13H–J). Adult males of *S. buettikoferi* also have a prominently flattened outer face of the chela with the outer angle elbow-like (Fig. 17G–J), while that of *S. angolense* is rounded and there is no elbow-like structure laterally, even if the pollex is enlarged and laterally flattened (Fig. 16A–F). The inner margin of the merus of the cheliped of *S. angolense* is also rounded (Fig. 16B, E) while that of *S. buettikoferi* has the distal part expanded and somewhat wing-like (Fig. 17I, J). In *S. angolense*, the male anterior thoracic sternum is relatively narrower and the male pleon has somite 6 proportionately narrower and a linguiform telson (Figs. 18E, 21A). The male anterior thoracic sterum of *S. buettikoferi* is relatively broader and the male pleon has a proportionately broader somite 6 with the telson more rounded (Figs. 18F, 21H). The G1 of *S. angolense* is also obviously stouter with the

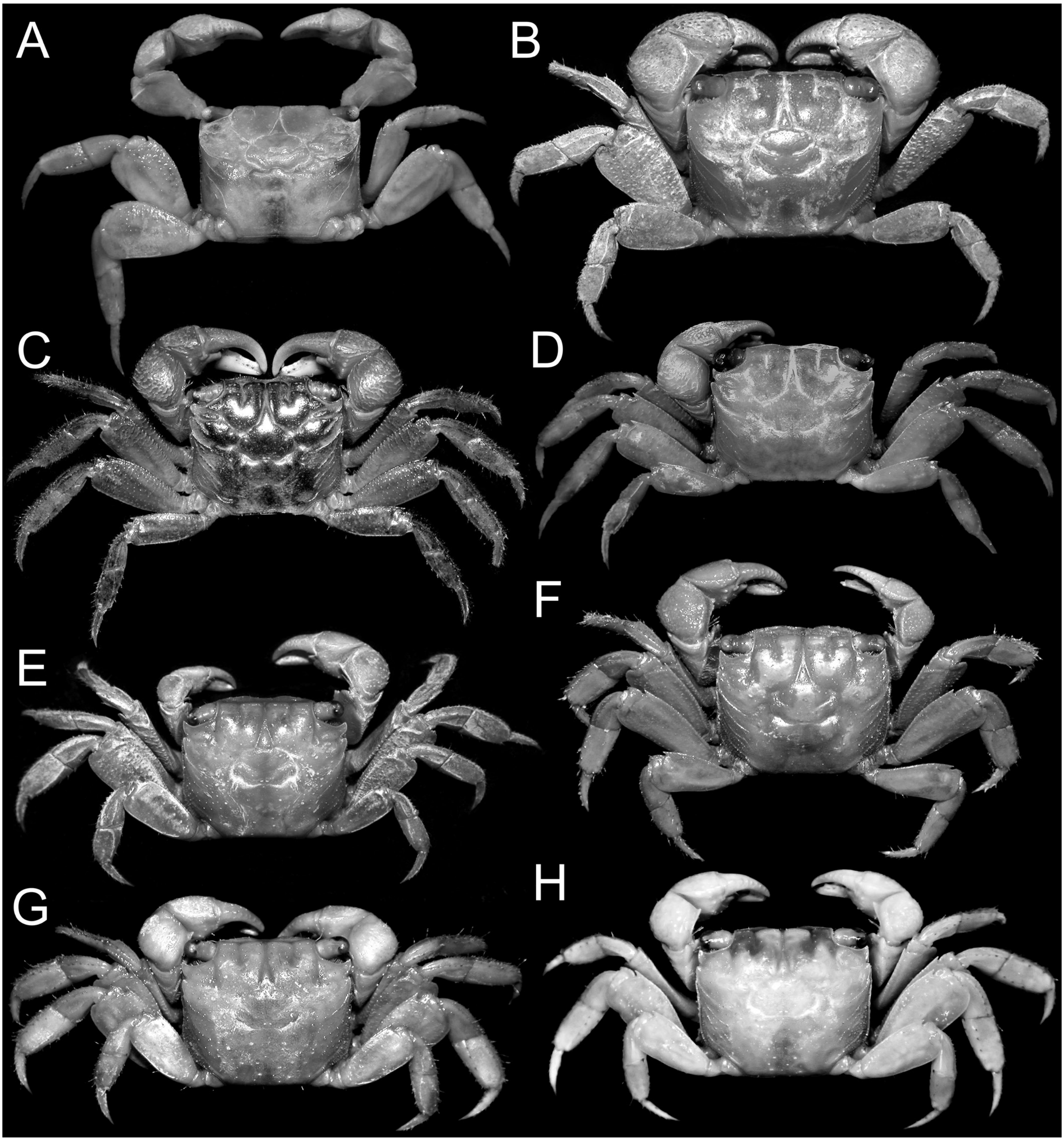

Fig. 24. Overall habitus. A, *Miersarma granosimanum*, lectotype male (16.9 × 14.8 mm) (NHM 1880.6), Borneo; B, *Miersarma granosimanum*, male (22.5 × 19.2 mm) (ZRC 1965.7.29.164), Sedili River, Johor, Malaysia; C, *Manarma moeschii*, male (18.2 × 16.3 mm) (ZRC 2000.1926), Thailand; D, *Manarma johorense*, male (14.6 × 12.6 mm) (ZRC 1971.9.24.14), Seletar River, Singapore; E, *Bresedium laevimanum*, lectotype male (20.0 × 17.6 mm) (MNHG), Borneo; F, *Bresedium laevimanum*, male (26.3 × 23.7 mm) (NHM) (lectotype of *Sesarma sediliensis*), Johor, Malaysia; G, *Bresedium laevimanum*, male (18.1 × 16.4 mm) (ZRC 1972.3.7.25), Sarawak, Borneo; H, *Bresedium laevimanum*, male (21.2 × 18.2 mm) (ZRC 1965.7.29.121), Johor, Malaysia.

distal chitinous tip short and truncate (Fig. 21B–G), while that of *S. buettikoferi* is slender with the distal chitinous part elongate and subspatuliform (Fig. 21I–L). Most remarkably, their vulvae are completely different—that of *S. angolense* is positioned on the median part of sternite 6 and spaced far apart, almost to the edge of the sternopleonal cavity (Fig. 43I) while that of *S. buettikoferi* is positioned more medially and at the anterior edge of sternite 6, touching sternite 5 (Fig. 43J). These are very substantial differences and argue for separating the two species into separate genera. While the two species are in one clade, the branches are long, suggesting they have been separated for a substantial period of time, which would explain the morphological differences observed. As such, *Trapezarma*, new genus, and *Platychirarma*, new genus, are established for *Sesarma angolense* Brito Capello, 1864, and *Sesarma buettikoferi* De Man, 1883, respectively.

Schubart et al. (2009) retained two morphologically different arboreal species in one Indo-West Pacific *Selatium* Serène & Soh, 1970, but in this case, the differences were mainly with carapace shape and leg proportions. Unlike the case of *Selatium*, however, the differences between *S. angolense* and *S. buettikoferi* are far more substantial, and the different position of the vulvae on sternite 6 is a compelling generic level difference.

### *Trapezarma angolense* (Brito Capello, 1864)

(Figs. 13G, 14G, 16, 18E, 21A–G, 43I)

*Sesarma angolensis* Brito Capello, 1864: 4, fig. 2; De Man, 1883: 161; Büttikofer, 1890: 487; Johnston, 1906: 861; Longhurst, 1958: 88; Gauld, 1960: 71.

*Sesarma* (*Holometopus*) *angolensis* – De Man, 1900: 59, pl. 2 fig. 11; Tesch, 1917: 130; Dartevelle, 1950: 48; Monod, 1956: 445, fig. 605; Rossignol, 1962: 120.

*Sesarma* (*Holometopus*) *angolense* – Rathbun, 1921: 451, pls. 43, 45 fig. 1; Dartevelle, 1950: 50; Capart, 1951: 191, fig. 76; Rossignol, 1957: 92, 122 [key]; Jordan, 1957: 198; Humes, 1957: 186, 187, 189.

*Sesarma* (*Parasesarma*) *angolensis* – Rathbun, 1900: 280.

*Sesarma* (*Chiromantes*) *angolense* – Manning & Holthuis, 1981: 243.

"*Chiromantes*" *angolense* – Ng et al., 2008a: 220.

**Material examined**. ANGOLA – Neotype (here designated): male (39.3 × 32.7 mm) (SMF-ZMG 635a), Benguella, river mouth of Catumbella near Benguella, coll. M.P. Kammerman; 1 ovigerous female (39.6 × 33.8 mm) (SMF-ZMG 635b), same data as neotype; 1 male, 2 females (RMNH D 1200), Lobito, coll. P. Kamerman, 1899. CAMEROON – 1 juvenile male (SMF 25982), West Nimbe (Limbe or Victoria), Mile 6, north of Nimbe, between pieces of basalt, coll. C.H. Otto, 7 January 1984; 2 males (35.2 × 28.6 mm, 21.2 × 16.3 mm), 1 female (18.2 × 14.3 mm) (ZRC 2015.0297), Lokoundjié mangrove, coll. P.A. Mvogo-Ndongo, 21 June 2015. LIBERIA – 2 females (RMNH D 1937), coll. J. Demery, 1890–1897.

**Diagnosis**. Carapace distinctly trapezoidal; frontal margin entire; lateral margins of carapace strongly converging to posterior carapace margin; cheliped merus with inner margin serrated but not expanded; adult male chela stout, outer surface gently convex, in large males, pollex may be expanded, shear-like, more flattened; male thoracic sternites 2–4 narrow in adults, suture between sternites 3 and 4 distinct; male sternopleonal cavity reaching three-quarters length of sternite 4 to just before anterior margin of sternite 2; male thoracic sternite 5 smooth, without depression on anterior part; male pleon elongate, narrow, telson linguiform; G1 relatively stout, chitinous part short.

**Colour**. The colour was described in detail by Rossignol (1957: 92): carapace blue-green with a yellow margin; ambulatory legs of the same colour as the carapace with a red dot to the joints, end dactylus yellow-orange dactyls; pincers colour of yellow leather with a red spot at the joint of the chela and fingers; eyes with light blue or gray-blue peduncle; cornea brown with a red dot; pleon dirty yellow with a blue median transverse line spanning somite 1; thoracic articles yellow and blue (translated from the French).

**Remarks**. In naming this species, Brito Capello did not indicate how many specimens he had. All he stated was that the species was from "mares de Angola" (Brito Capello, 1864: 4). Unfortunately, all of Brito Capello's material in the Lisbon Museum were lost in a fire in 1978, and the types of this species are no longer extant. While the identity of this species is currently not in doubt, because it is here designated as the type species for *Trapezarma*, new genus, it is important to ensure a stable taxonomy. As such, we designate a large male specimen in the Senckenberg Museum (SMF-ZMG 635a) as the neotype of *Sesarma angolensis* Brito Capello, 1864.

There is considerable variation in the form of the male chela. The largest male from Angola (the neotype male) has a more typical chela in which the pollex is relatively slender and the dactylus gently curved (Fig. 16A). In the smaller but clearly adult male from Cameroon, the pollex is strongly expanded, very broad, the outer surface more flattened, and the dactylus is strongly curved (Fig. 16C, D). The specimen figured by Brito Capello (1864: fig. 2c) shows a chela which is more intermediate in form. Other than this, the specimens from Cameroon and Angola are very similar and we have no reason to suspect they are different species. The characteristic male chela (Fig. 16C, D) noted above may be a feature of dominant males.

**Biology**. The best account of the biology of this species is given in Rathbun (1921: 451–452), who observes that it prefers the more freshwater sections of the river.

**Distribution**. Sierra Leone to Angola (Monod, 1956; Manning & Holthuis, 1981).

### *Platychirarma*, new genus

**Type species**. *Sesarma büttikoferi* De Man, 1883, by present designation. Gender neuter.

**Diagnosis**. Carapace trapezoidal, distinctly broader than long; frontal margin slightly bilobed, gently deflexed, wider than carapace margin; lateral margins of carapace almost straight, entire in adults, posterolateral part prominently converging; regions of carapace demarcated; postfrontal and epigastric crests separated by relatively shallow grooves, margin relatively sharp, almost straight, appearing contiguous; basal articles of antenna and antennules separated by septum; dorsal margin of palm without longitudinal pectinated ridge, inner surface not swollen, without granulated ridge, outer surface of palm and pollex almost flat, smooth, outer margin of palm with prominent elbow-like projection; dorsal margin of chelipedal dactylus lined with irregularly arranged small granules of various sizes; inner margin of the chelipedal merus with distal part expanded, wing-like; inner surfaces of first to third ambulatory coxae with only scattered short setae between them, not arranged into dense

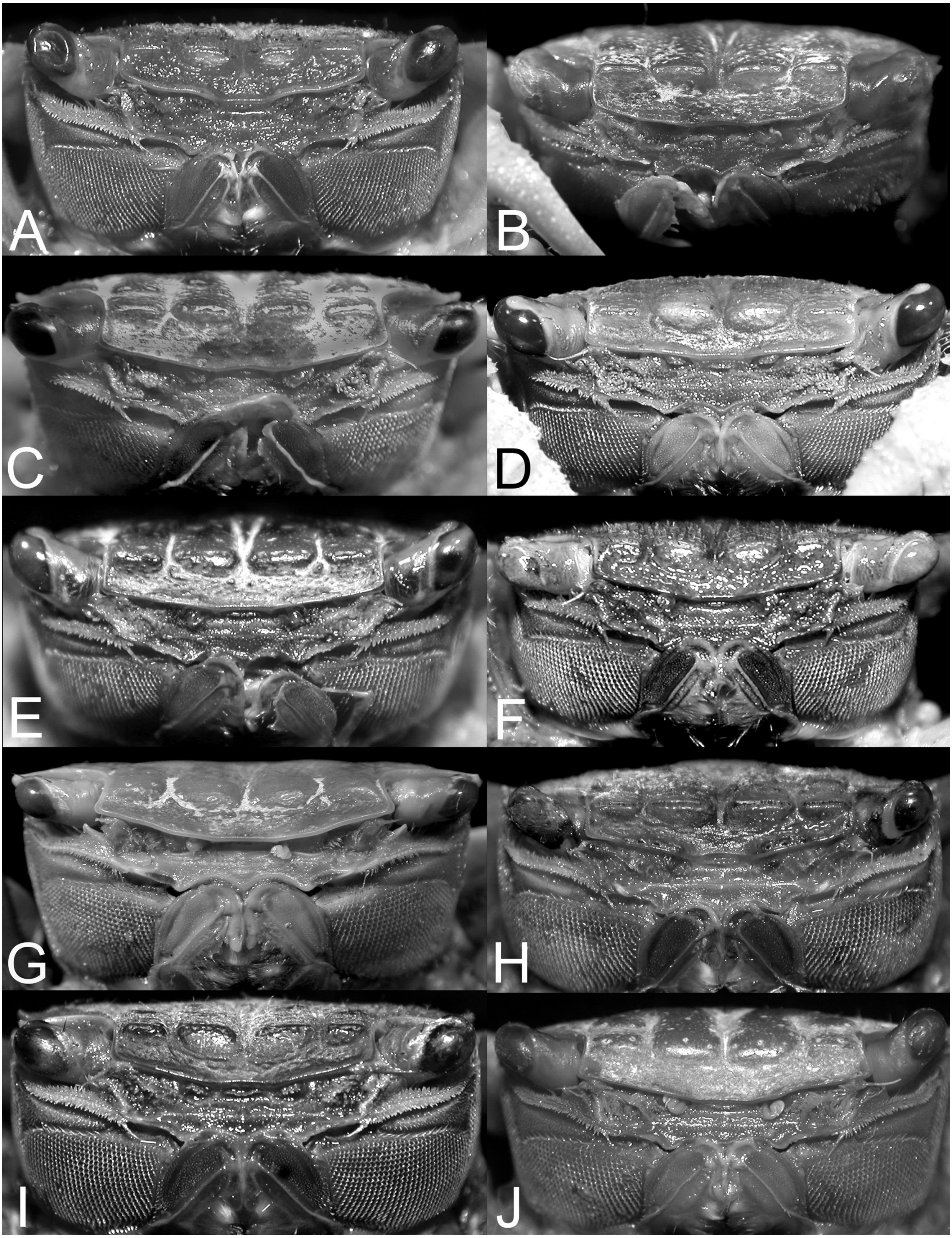

Fig. 25. Frontal view of cephalothorax of *Pseudosesarma*. A, *P. edwardsii*, lectotype male (17.5 × 16.1 mm) (RMNH-D17a), Mergui Archipelago; B, *P. edwardsii*, male (13.4 × 11.9 mm) (ZRC 1965.8.2.81), Pulau Pawai, Singapore; C, *P. crassimanum*, male (15.9 × 14.5 mm) (RMNH-D23313), Singapore; D, *P. anteactum*, holotype male (16.7 × 14.7 mm) (ZRC 2016.0602), Sri Lanka; E, *P. glabrum*, holotype male (13.8 × 12.0 mm) (CUSAT 2016-1), Kerala, India; F, *P. brehieri*, holotype male (17.4 × 15.7 mm) (ZRC 2016.0593), Myanmar; G, *P. boulengeri*, lectotype male (26.9 × 23.5 mm) (NHM 1919.11.14.1), Basra, Iraq; H, *Contusarma bocourti*, male (25.3 × 23.3 mm) (ZRC 2000.0952), Bangkok, Thailand; I, *Contusarma cheirogonum*, neotype male (24.5 × 21.5 mm) (ZRC 1995.225), Bako National Park, Sarawak; J, *Miersarma granosimanum*, lectotype male (16.9 × 14.8 mm) (NHM 1880.6), Borneo.

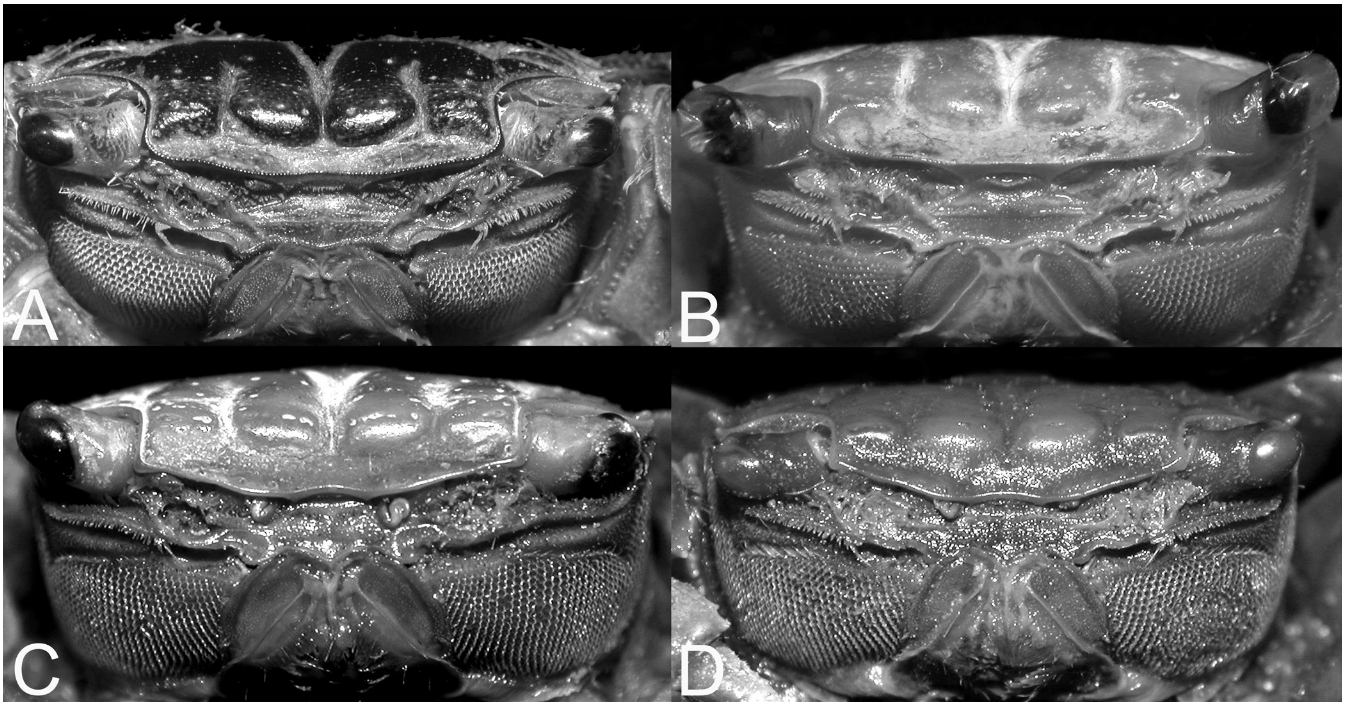

Fig. 26. Frontal view of cephalothorax. A, *Manarma moeschii*, male (18.2 × 16.3 mm) (ZRC 2000.1926), Thailand; B, *Manarma johorense*, male (14.6 × 12.6 mm) (ZRC 1971.9.24.14), Seletar River, Singapore; C, *Bresedium laevimanum*, lectotype male (20.0 × 17.6 mm) (MNHG), Borneo; D, *Bresedium laevimanum*, male (26.3 × 23.7 mm) (NHM) (lectotype of *Sesarma sediliensis*), Johor, Malaysia.

tufts; male thoracic sternites 2–4 relatively broader, suture between sternites 3 and 4 distinct; male sternopleonal cavity reaching three-quarters length of sternite 4 to just before anterior margin of sternite 2; male thoracic sternite 5 smooth, without depression on anterior part; male pleonal somite 6 proportionately broader, telson more rounded; G1 slender, distal chitinous part elongate, subspatuliform. Vulva on anterior part of sternite 6, anterior edge presses against sternite 5; anterior and posterior sternal vulvar covers low, opening short, cylindrical, projecting, directed obliquely anteriorly.

**Etymology**. The genus name is derived from the characteristic flattened outer surface of the chelae of the type species, in combination with the genus name *Sesarma*. The gender is neuter.

**Included species**. *Sesarma büttikoferi* De Man, 1883.

**Remarks**. See earlier discussion for *Trapezarma*, new genus.

### *Platychirarma buettikoferi* (De Man, 1883)

(Figs. 13H–J, 14H, 17, 18F, 21H–L, 43J)

*Sesarma büttikoferi* De Man, 1883: 163; De Man, 1891: 50; Thallwitz, 1892: 37; Aurivillius, 1889: 11, pl. 3 figs. 1–4; Fransen et al., 1997: 128.
*Sesarma* (*Parasesarma*) *büttikoferi* – Rathbun, 1900: 280.
*Sesarma buettikoferi* – Johnston, 1906: 861.
*Sesarma buttikoferi* – Büttikofer, 1890: 464, 487; Rossignol, 1957: 91, text-fig. 6, pl. 2: fig. 5.
*Sesarma* (*Holometopus*) *buttikoferi* – Dartevelle, 1950: 48.
*Sesarma* (*Holometopus*) *buettikoferi* – Tesch, 1917: 140; Rathbun, 1921: 449, pl. 47 figs. 5–9; Monod, 1956: 447, figs. 606, 607; Rossignol, 1962: 121.
*Sesarma* (*Holometopus*) *buttikoferi* – Rossignol, 1957: 91, 122 [key].
*Sesarma* (*Chiromantes*) *buettikoferi* – Manning & Holthuis, 1981: 243.
"*Chiromantes*" *buettikoferi* – Ng et al., 2008a: 220.

**Material examined**. Lectotype (here designated): male (14.1 × 11.6 mm) (RMNH D 148), Liberia, coll. J. Büttikofer & J.A. Sala, January 1881. Paralectotypes: 1 male (10.0 × 8.7 mm), 1 female (9.1 × 7.9 mm) (SMF-ZMG 636), Fisherman Lake, Liberia, coll. Büttikofer, 1881. LIBERIA – 1 male (RMNH D 147), Grand Cape Mountain, coll. Büttikofer, 1882; 2 males (10.1 × 8.1 mm, 9.4 × 7.6 mm), 1 female (10.4 × 8.7 mm) (MNHN B16229), Junk River, coll. Stamplli, 1886. CAMEROON – 1 male (10.7 × 8.8 mm) (SMF 25980), West Nimbe (Limbe or Victoria), Mile 6, north of Nimbe, between pieces of basalt, coll. C.H. Otto, 7 January 1984; 2 males (12.6 × 10.4 mm, 11.9 × 9.4 mm), 1 ovigerous female (11.3 × 9.1 mm) (ZRC 2015.0298), Mouang Ko, mangrove area recently destroyed, coll. P.A. Mvogo-Ndongo, 22 July 2015.

**Diagnosis**. Carapace distinctly wider than long, trapezoidal; frontal margin gently bilobed; lateral margins of carapace converging to posterior carapace margin; cheliped merus with inner margin serrated with distal angle expanded into projection; adult male chela more slender, outer surface distinctly flattened, with lateral part of chela prominently expanded laterally, elbow-like; male thoracic sternites 2–4 relatively wider in adults, suture between sternites 3 and 4 distinct; male sternopleonal cavity reaching three-quarters length of sternite 4 to just before anterior margin of sternite 2; male thoracic sternite 5 smooth, without depression on anterior part; male pleon relatively wider, telson more rounded; G1 relatively slender, long, chitinous part long.

**Colour**. The colour in life was described by Rossignol (1957: 91): carapace reddish-brown with patches of lighter colour; chelae violet-purple, pollex reddish-orange; ventral surfaces greyish (translated from the French).

**Remarks**. In naming this species, De Man (1883: 163, 164) did not indicate how many specimens he had. All he stated was that he described one male measuring 13.5 by 11.0 mm from Fisherman's Lake in Liberia collected by Büttikofer in January 1881. He did not state if this was the holotype or if he had other specimens. In RMNH is a male specimen which corresponds very closely to the measurements and data specified by De Man and was regarded as the holotype of *Sesarma buettikoferi* De Man, 1883, by Fransen et al. (1997: 128). Article 72.4.1.1 of the code (ICZN, 1999), however, notes that "for a nominal species or subspecies established before 2000, any evidence, published or unpublished, may be taken into account to determine what specimens constitute the type series". In this case, SMF also has two specimens (labelled as types) collected by Büttikofer from the same type locality with the same date. As such, they were almost certainly also examined by De Man (1883), but being smaller, were probably just not listed in his description. We here regard all three specimens as syntypes and designate the male specimen from Leiden (RMNH D 148) as the lectotype of *Sesarma buettikoferi* De Man, 1883.

The flattened outer face of the adult male chela of *P. buettikoferi* is very distinctive and is even apparent on smaller specimens (Figs. 13J, 17). In larger males, it is more prominent, with the ventral margin blade-like and the outer margin of the chela prominently expanded laterally, forming a distinct "elbow" (Figs. 13J, 17). This is less developed in smaller males (Figs. 13H, 17B). The form of this chela closely resembles that of two species now included in the new genus *Contusarma*, viz. *C. bocourti* and *C. cheirogonum* from Southeast Asia (Fig. 28), but in these species, the outer surface of the chela is prominently granulated and the lateral edge is never expanded to form an elbow-like structure.

**Biology**. Rathbun (1921: 449–451) describes the biology of this species at length, noting that it prefers the brackish areas of the supralittoral back mangroves. Rathbun (1921: 450) also observed that the flattened chelae of *P. buettikoferi* is used for display to attract females. The species appears to be common among the leaf axils of plants in the mangroves (Stefano Cannicci, pers. comm.).

**Distribution**. Liberia to Angola (Monod, 1956; Manning & Holthuis, 1981).

### *Pseudosesarma* Serène & Soh, 1970

**Type species**. *Sesarma edwardsii* De Man, 1887, by original designation. Gender neuter.

**Diagnosis**. Carapace squarish to transversely subrectangular; frontal margin bilobed, gently deflexed, subequal to posterior carapace margin; lateral margins of carapace entire in adults or with one tooth, posterolateral part subparallel; regions of carapace clearly demarcated; postfrontal and epigastric crests separated by relatively deep grooves, margin relatively rounded, regions clearly separated; basal articles of antenna and antennules separated by septum; dorsal margin of palm without longitudinal pectinated ridge, inner surface may be gently swollen, but without prominent granulated ridge, outer surface and pollex convex or almost flat, covered with small granules; dorsal margin of chelipedal dactylus smooth in adult males or lined with irregularly arranged small granules of various sizes; inner distal margin of merus of cheliped not lamelliform; inner surfaces of first to third ambulatory coxae with only scattered short setae between them, not arranged into dense tufts; male thoracic sternites 2–4 relatively narrow in adults, suture between sternites 3 and 4 distinct or obsolete; male sternopleonal cavity reaching two-thirds length of sternite 4 to just before anterior margin of sternite 2; pleonal locking mechanism formed by small angular projection on posterior edge of sternite 4 of sternopleonal cavity, no trace of tubercle on sternite 5; male thoracic sternite 5 usually with slight depression on anterior part for tip of G1 when pleon closed; G1 very stout or if more slender, subdistal part distinctly swollen, much wider than base; chitinous part almost absent to relatively short or long. Vulva on submedian part of sternite 6 or more anterior, close to margin with sternite 5; sternal vulvar covers small, rounded, flat, tips sometimes partially overlapping, opening not projecting or small, sometimes extending beyond sternal vulvar covers.

**Included species**. *Sesarma edwardsii* De Man, 1887; *Sesarma edwardsii* var. *crassimana* De Man, 1887; *Pseudosesarma anteactum* Ng & Schubart, 2017; *Pseudosesarma glabrum* Ng, Rani & Nandan, 2017; *Pseudosesarma brehieri* Ng, 2018; *Chiromantes boulengeri* Calman, 1920.

**Remarks**. As discussed earlier, Serène & Soh (1970) had already realised their genus was heterogeneous, which is confirmed in the present study. Of the nine species recognised by Ng et al. (2008a), five (*P. modestum*, *P. patshuni*, *P. moeschii*, *P. johorensis*, *P. laevimanum*) need to be transferred to other genera (see later). Instead, one other species, *Chiromantes boulengeri*, is here transferred into *Pseudosesarma*.

*Pseudosesarma* species are characterised by their G1 being stout, with the distal part (before the chitinous tip) being very wide; this has necessitated the anterior part of sternite 5 of the sternopleonal cavity developing a complementary concavity to accommodate this structure (Fig. 32A, B). In addition, the species have two kinds of vulva; one in which it is positioned submedially on sternite 5 with a distinctive plate-like covering and the opening is not projecting, and the other has the vulva closer to the margin of sternite 6 with two low sternal vulvar covers and a short projection (Fig. 44A–F).

The variation in the form of the vulva in *Pseudosesarma* species merits discussion. The type species, *P. edwardsii*, is the only one where the vulva is submedian in position on

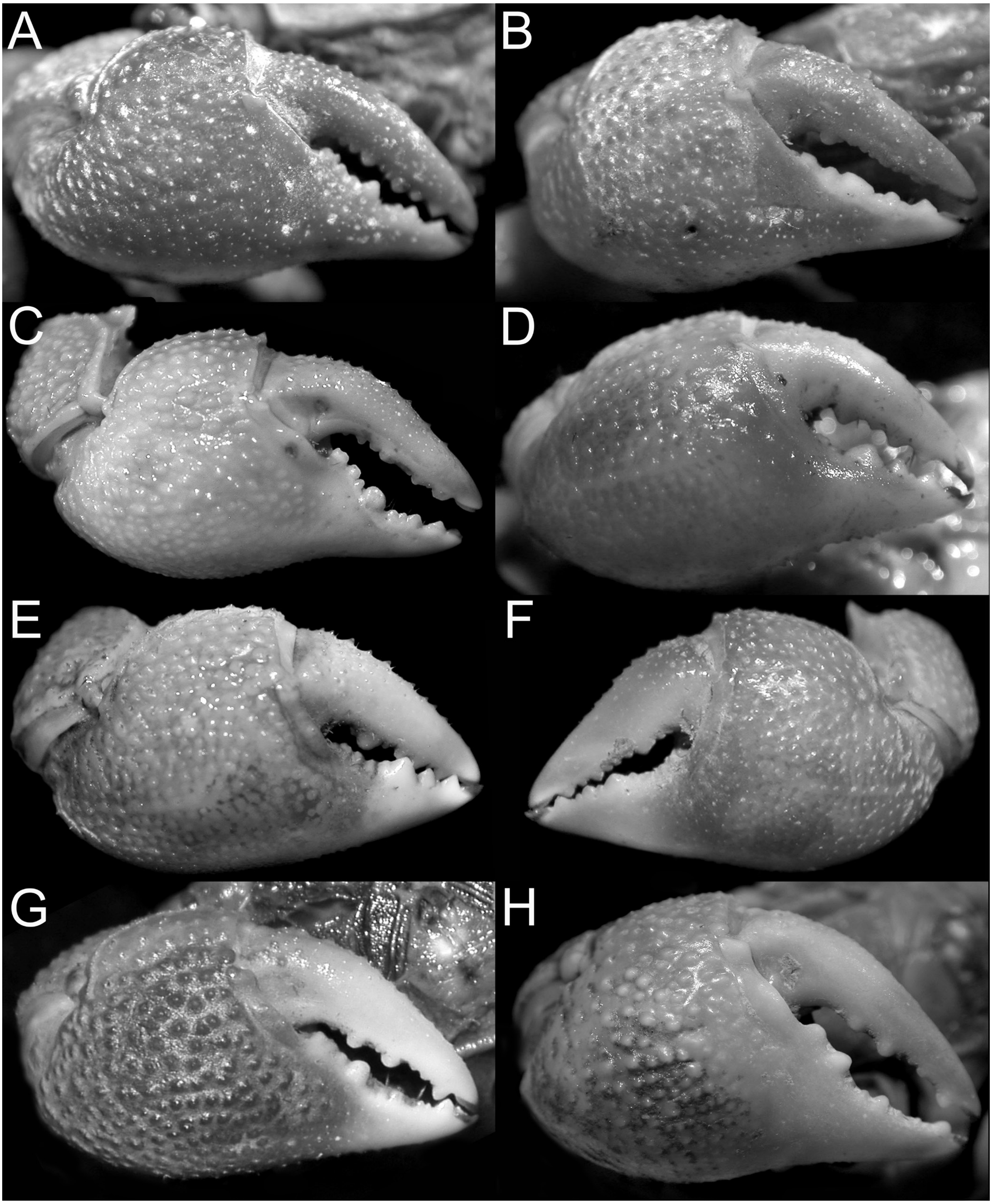

Fig. 27. Outer view of chela of *Pseudosesarma*. A, *P. edwardsii*, lectotype male (17.5 × 16.1 mm) (RMNH-D17a), Mergui Archipelago; B, *P. edwardsii*, male (13.4 × 11.9 mm) (ZRC 1965.8.2.81), Pulau Pawai, Singapore; C, *P. edwardsii*, male (19.4 × 17.3 mm) (ZRC 1971.9.24.8), Singapore; D, *P. crassimanum*, male (15.9 × 14.5 mm) (RMNH-D23313), Singapore; E, *P. anteactum*, holotype male (16.7 × 14.7 mm) (ZRC 2016.0602), Sri Lanka; F, *P. glabrum*, holotype male (13.8 × 12.0 mm) (CUSAT 2016-1), Kerala, India; G, *P. brehieri*, holotype male (17.4 × 15.7 mm) (ZRC 2016.0593), Myanmar; H, *P. boulengeri*, lectotype male (26.9 × 23.5 mm) (NHM 1919.11.14.1), Basra, Iraq.

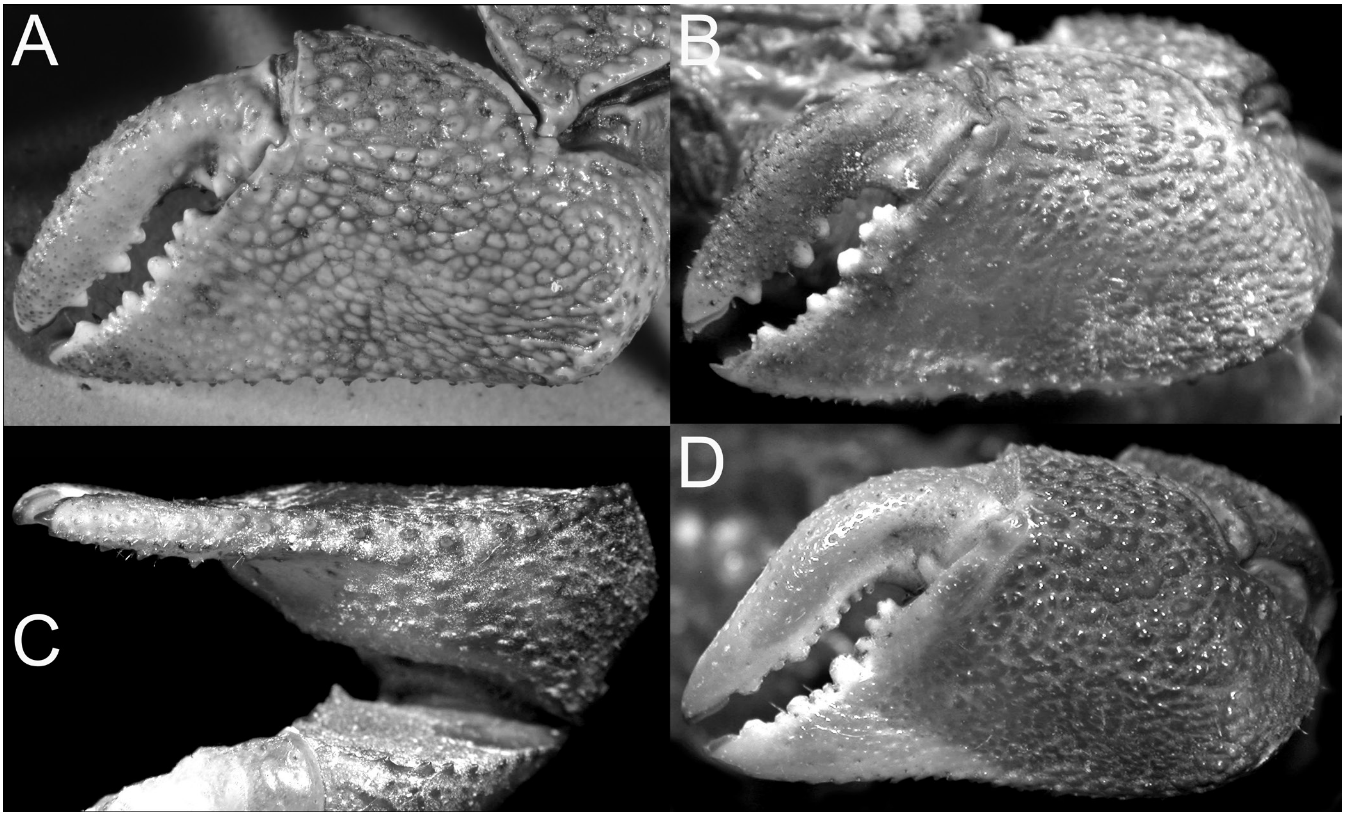

Fig. 28. Chela of *Contusarma*. A, *C. bocourti*, lectotype male (24.0 × 27.2 mm) (MNHN D-10965), Bangkok, Thailand; B, C, *C. bocourti*, male (25.3 × 23.3 mm) (ZRC 2000.0952), Bangkok, Thailand; D, *C. cheirogonum*, neotype male (24.5 × 21.5 mm) (ZRC 1995.225), Bako National Park, Sarawak. A, B, D, outer view; C, ventro-marginal view.

sternite 6 and the opening does not project at all (Fig. 44A). In all the other species examined, the vulvae are positioned more anteriorly, and are closer or adjacent to the margin with sternite 5 (Fig. 44B–F). In these other species, the opening is also visible as a short projection that may be directed obliquely anteriorly (Fig. 44B, D, F) or obliquely posteriorly (Fig. 44E). In one large specimen of *P. crassimanum*, the right vulva appears to have a short opening protruding above the posterior sternal vulvar cover but on the left side, only a very low opening is visible (Fig. 44C). In any case, the opening in *P. crasssimanum* is low (Fig. 44B), so some degree of variation is to be expected. In all the *Pseudosesarma* species examined, the relative position of the vulvae is the same, i.e., they are all submedially positioned in the female sternopleonal cavity.

*Pseudosesarma patshuni* Soh, 1978, is quite different from the species now recognised in *Pseudosesarma* in the form of the chela, male pleon, proportionately longer ambulatory legs, and having a short, straight, and stout G1. As discussed earlier, it has been transferred to *Orisarma*, new genus, with two other *Sesarmops* species. Its vulva is similar to those of *Orisarma* species (Fig. 43D).

The placement of *Sesarma* (*Sesarma*) *modesta* De Man, 1902 (type locality Ternate) in *Pseudosesarma* is incorrect. We have examined the type specimen and it is better placed in a new genus, *Migmarma* (see later). Its subtrapezoidal carapace shape resembles many species of *Pseudosesarma* but its G1 is unlike any of those species, being more slender and without the subdistal part of the structure swollen (Figs. 45G–J, 46C–H), and the surface of thoracic sternite 5 does not have a depression (see discussion on this species later).

*Pseudosesarma bocourti* (A. Milne-Edwards, 1869) is here referred to a new genus, *Contusarma*. The chelae have the outer surface characteristically flattened (Fig. 28); the G1 is relatively slender and straight (Figs. 38D–H, 39F–J, L–M) and the vulvae are small with the sternal vulvar covers poorly developed, and the opening small and slightly projecting (Fig. 44G, H).

*Pseudosesarma granosimanum* (Miers, 1880) previously transferred to *Chiromantes* by Ng et al. (2008a) is also here referred to a new genus, *Miersarma*. It is unusual in having the anterolateral margins entire, the suture between thoracic sternites 3 and 4 almost undiscernible; press-button for the normal pleonal locking mechanism absent from sternite 5 (Fig. 32D); no depression on the anterior part of male sternite 5 for the G1 tip (Fig. 32D); an elongate, slender, and straight G1 (Fig. 40B–E, F–J); and a small vulva pushing prominently into the margin with sternite 5, and with the sternal vulvar covers and opening small (Fig. 44I).

Interestingly, the genetic data strongly supports a monophyletic lineage for *P. bocourti* and places it as sister to *P. granosimanum* (Fig. 59). This is despite the two taxa being morphologically very different.

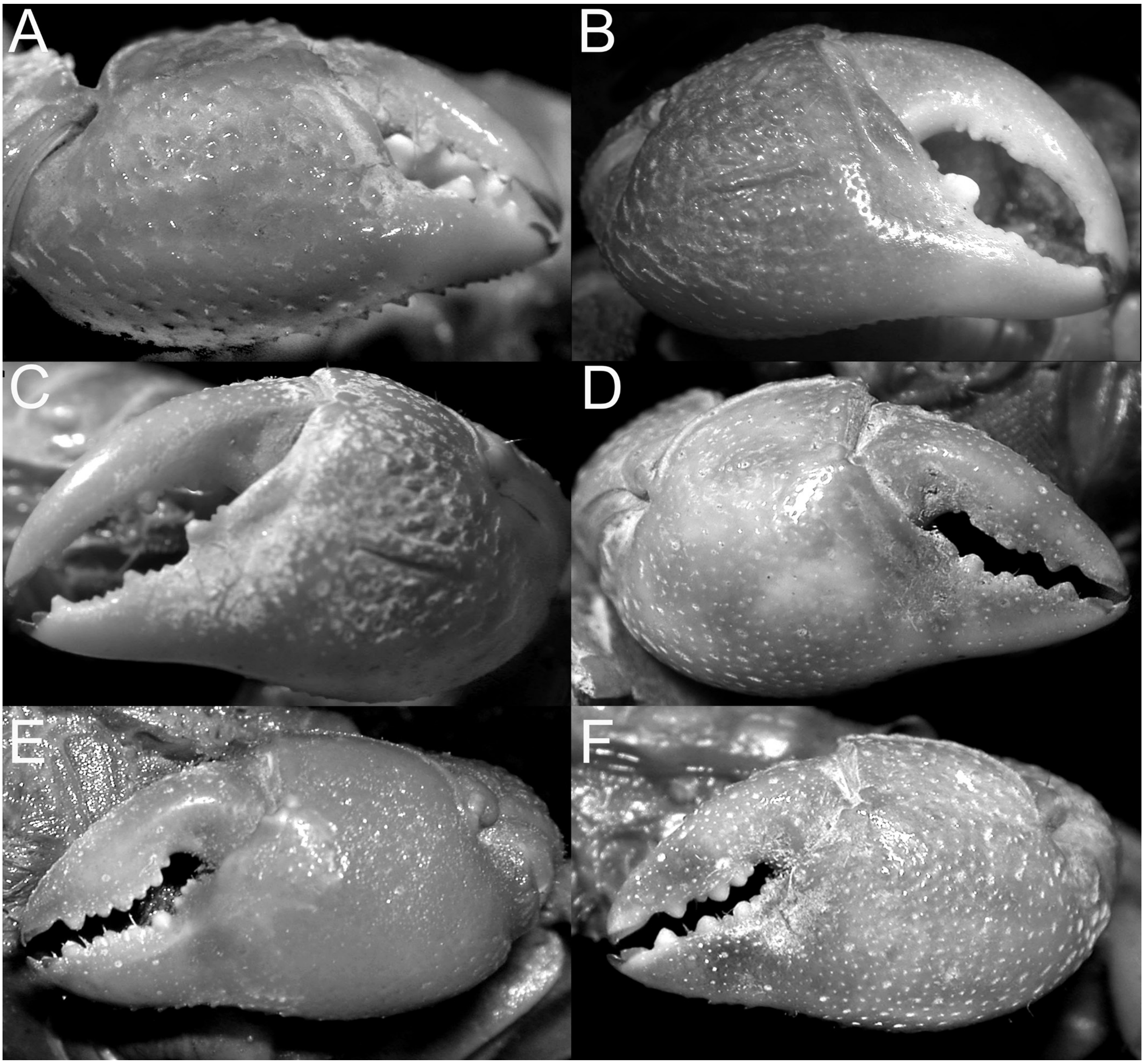

Fig. 29. Outer view of chela. A, *Miersarma granosimanum*, lectotype male (16.9 × 14.8 mm) (NHM 1880.6), Borneo; B, *Manarma moeschii*, male (18.2 × 16.3 mm) (ZRC 2000.1926), Thailand; C, *Manarma johorense*, male (14.6 × 12.6 mm) (ZRC 1971.9.24.14), Seletar River, Singapore; D, *Bresedium laevimanum*, lectotype male (20.0 × 17.6 mm) (MNHG), Borneo; E, *Bresedium laevimanum*, male (26.3 × 23.7 mm) (NHM) (lectotype of *Sesarma sediliensis*), Johor, Malaysia; F, *Bresedium laevimanum*, male (18.1 × 16.4 mm) (ZRC 1972.3.7.25), Sarawak.

Two species of *Pseudosesarma*, originally highlighted by Serène & Soh (1970: 400) as atypical of the genus, *P. moeschii* (De Man, 1892) and *P. johorense* (Tweedie, 1940), are also referred to a new genus *Manarma* (see Remarks for that genus). In addition to differences in the chelae, male thoracic sternum, male pleon and G1, this genus is distinct from *Pseudosesarma* in that its vulvae are located on the anterior edge of sternite 6 (rather than median) and have a different structure (Fig. 44J).

A re-examination of the types of *Pseudosesarma laevimanum* (Zehntner, 1894) show that it should be placed in *Bresedium* Serène & Soh, 1970, instead, and as a senior synonym of *B. sediliensis* (Tweedie, 1940). It is redescribed and figured later in this paper.

The remaining species historically recognised in *Pseudosesarma*, viz. *Sesarma edwardsii* De Man, 1887 and *Sesarma crassimana* De Man, 1887, are closely related with the three new species described since 1970 (Ng & Schubart, 2017). This also holds for *Sesarma boulengeri* Calman, 1920, despite the fact that it has no epibranchial tooth. The male pleonal somites 5 and 6 in all six species are proportionately broader when compared to those of *Chiromantes*, *Orisarma*, or *Manarma*, rendering the pleon a relatively broader appearance (widest in *P. edwardsii* and narrowest in *P. boulengeri*). The G1s are generally stocky, being shortest and stoutest in the type species, *P. edwardsii*. The distal chitinous part is generally short (e.g., *P. crassimanum*) or even absent (e.g., *P. edwardsii*). In species of *Pseudosesarma* s. str. (as in *Contusarma* species),

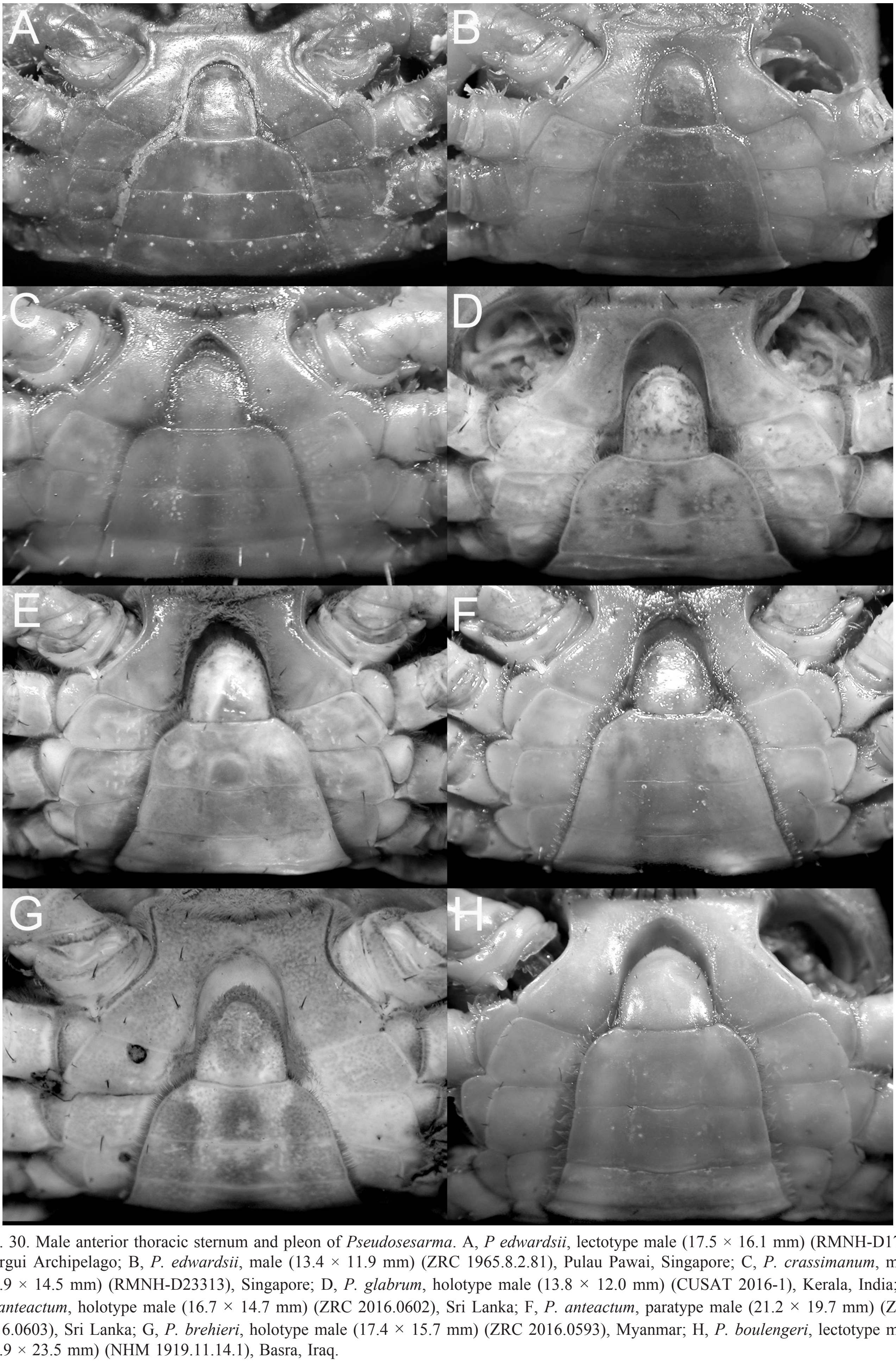

Fig. 30. Male anterior thoracic sternum and pleon of *Pseudosesarma*. A, *P edwardsii*, lectotype male (17.5 × 16.1 mm) (RMNH-D17a), Mergui Archipelago; B, *P. edwardsii*, male (13.4 × 11.9 mm) (ZRC 1965.8.2.81), Pulau Pawai, Singapore; C, *P. crassimanum*, male (15.9 × 14.5 mm) (RMNH-D23313), Singapore; D, *P. glabrum*, holotype male (13.8 × 12.0 mm) (CUSAT 2016-1), Kerala, India; E, *P. anteactum*, holotype male (16.7 × 14.7 mm) (ZRC 2016.0602), Sri Lanka; F, *P. anteactum*, paratype male (21.2 × 19.7 mm) (ZRC 2016.0603), Sri Lanka; G, *P. brehieri*, holotype male (17.4 × 15.7 mm) (ZRC 2016.0593), Myanmar; H, *P. boulengeri*, lectotype male (26.9 × 23.5 mm) (NHM 1919.11.14.1), Basra, Iraq.

there is also a shallow but distinct depression on sternite 5, just posterior to the ledge on sternite 4 that locks the pleon (Fig. 32A, B). In this depression sits the dilated distal part of the G1. In *P. boulengeri*, however, there is no trace of a depression, with the entire lateral surface of sternite 5 weakly convex.

It is interesting that *Pseudosesarma* and its related genera have only a very weak or even absent press-button pleonal locking system as described by Guinot & Bouchard (1998). Even when present, the press-button on sternite 5 is at most a small, low rounded granule. Instead, the male pleon appears to lock onto a small ledge on each side of sternite 4. The press-button on *P. edwardsii* is the most anteriorly positioned of the species studied, being just before sternal suture 4/5, and just below the ledge of sternite 4 (Fig. 32A). In *P. crassimanum* and *P. boulengeri*, the press-button is on the anterior third of sternite 4 (Fig. 32B, C). As noted above, *P. granosimanum* completely lacks any locking mechanism on sternite 4 (Fig. 32D).

### *Pseudosesarma edwardsii* (De Man, 1887)

(Figs. 22A–C, 25A, B, 27A–C, 30A, B, 32A, 34, 44A, 56A–E)

*Sesarma edwardsii* De Man, 1887: 649.
*Sesarma edwardsi* – De Man, 1888: 185, pl. 13 figs. 1–4; Lanchester, 1900: 757.
*Sesarma* (*Sesarma*) *edwardsi* – Tesch, 1917: 147 (part?).
?*Sesarma* (*Sesarma*) *edwardsii* – Calman, 1925: 166.
*Sesarma* (*Sesarma*) *edwarsi* (sic) – Serène, 1968: 105.
*Pseudosesarma edwarsi* (sic) – Serène & Soh, 1970: 399, 406.
*Pseudosesarma edwardsii* – Tan & Ng, 1994: 82; Fransen et al., 1997: 127; Ng et al., 2008a: 222; Ng & Schubart, 2017: 655, figs. 1A–C, 2A, B, 3–7, 12.
Not *Sesarma edwardsi* Ortmann, 1894: 721 = *Bresedium brevipes* (De Man, 1889).

**Material examined**. Lectotype (here designated): male (17.5 × 16.1 mm) (RMNH-D17a), Mergui Archipelago, Myanmar, coll. J. Anderson, 1886. Paralectotypes: 1 female (RMNH-D17b), same data as lectotype; 1 young male (7.9 × 7.0 mm), 8 females (20.3 × 17.7 mm, 14.9 × 13.2 mm, 13.8 × 12.7 mm, 13.7 × 12.5 mm, 12.3 × 11.6 mm, 12.3 × 11.3 mm, 10.9 × 10.2 mm, 8.8 × 7.9 mm) (NHM 1886.52a), same data as lectotype. Others: SINGAPORE – 1 male (19.4 × 17.3 mm) (ZRC 1971.9.24.8), Sungei Seletar, coll. C.L. Soh, 29 March 1966; 1 male (ZRC 1965.7.29.50), Pulau Aya, Merban, coll. F.N. Chasen, 1931; 1 male (ZRC 1971.9.24.9), Sungei Seletar, coll. C.L. Soh, 29 March 1966; 1 male (ZRC 2003.0083), Pulau Ubin, vicinity of Asam mangroves (pitfall trap), coll. R. Teo, 20 September 2001; 1 male, 1 female (ZRC 2000.2019), Pulau Ubin, coll. C.D. Schubart, July 2000; 3 males (ZRC), swamp along dirt road to Chek Jawa, Pulau Ubin, coll. C.D. Schubart, 25 November 2011; 1 male (ZRC 2003.0084), culvert beside reservoir, Pulau Tekong, Singapore, coll. B.Y. Lee, 16 November 2001; 1 female (11.5 × 10.0 mm) (ZRC 2013.1116), near stream, northern axis of Pulau Tekong, coll. T.M. Leong, 31 January 2002; 1 ex-ovigerous female (19.1 × 17.8 mm, first zoeae reared and preserved) (ZRC), in secondary forest, 300 m from coast, coll. M. Chua, 24 March 2012. PENINSULAR MALAYSIA – 1 male (ZRC 1984.8031), Pangkor Island, Straits of Malacca, coll. 13 August 1967; 1 male, 1 female (ZRC 2010.0035), Pulau Langkawi, Temurun waterfall, coll. P.K.L. Ng, 17 June 1998; 1 male (13.9 × 12.9 mm), 1 female (13.1 × 11.6 mm) (ZRC), Sungei Temurun Datai, Langkawi, Kedah, Malaysia, coll. Universiti Sains Malaysia, 1 April 2003; 1 male (19.4 × 18.2 mm), 1 female (19.3 × 17.7 mm) (NHMW 26842), Pulau Langkawi, Air Temurun waterfall and stream, coll. C.D. Schubart et al., 15 March 2006; 8 males (1 post-molt, badly damaged), 3 females (ZRC 2016.0608), Temurun waterfall, at base of waterfalls, under rocks at side of stream, near bank, about 200 m from sea, Langkawi, Peninsular Malaysia, coll. P.K.L. Ng & P.Y.C. Ng, 18 December 2016.

**Diagnosis**. Carapace transversely rectangular; frontal margin less wide, median concavity separating lobes relatively more shallow; epibranchial tooth distinct, separated from rest of margin by deep notch; posterolateral margins subparallel; outer surface of chela gently convex, covered with small rounded granules, ventral margin of palm sinuous, unarmed; suture between male thoracic sternites 3 and 4 distinct; male pleon broadly triangular; male sternopleonal cavity with press-button of pleonal locking mechanism on sternite 5; distal part of G1 bifurcated or bilobed, with chitinous part very short. In life, chelae red, pigmentation extending to midway of white fingers.

**Colour**. The carapace of fresh *P. edwardsii* is brown to reddish-brown, with many specimens having the posterior part of the carapace slightly to much darker in colour (Fig. 56A, C), with the outer surface of the chela red, the colour extending to at least the middle of both fingers, with the distal half white (Fig. 56B, D, E) (see also Ng & Schubart, 2017).

**Remarks**. The taxonomy of this species has been discussed at length by Ng & Schubart (2017) and there is no need to further elaborate. The date of publication for this species (and *P. crassimanum*) follows Ng et al. (2015). Ng & Schubart (2017) clarified the differences with *P. crassimanum* (De Man, 1887) and further realised that *P. edwardsii* s. lat. was harbouring a number of closely related species, including *P. anteactum* Ng & Schubart, 2017, from Sri Lanka, *P. glabrum* Ng, Rani & Nandan, 2017, from western India, and *P. brehieri* Ng, 2018, from Myanmar.

Ng & Schubart (2017) observed that the proportions of the male pleon varies with size. In the largest male, the lectotype, from the Mergui (17.5 × 16.1 mm, RMNH-D17), the pleon is very wide (Figs. 30A, 34B) but it is narrower in smaller males (Figs. 30B, 34C). Larger males also have proportionately stouter G1s, with the distal part distinctly bilobed (Fig. 34D, E) while those of smaller males are more slender with the distal part less obviously bilobed.

The identity of "*Sesarma* (*Sesarma*) *edwardsii*" from Pasir Ganing in western Sumatra by Calman (1925: 166) cannot be confirmed. It is within the range of variation of the present species, so it is here retained within its synoymy. The specimens should be re-examined when possible.

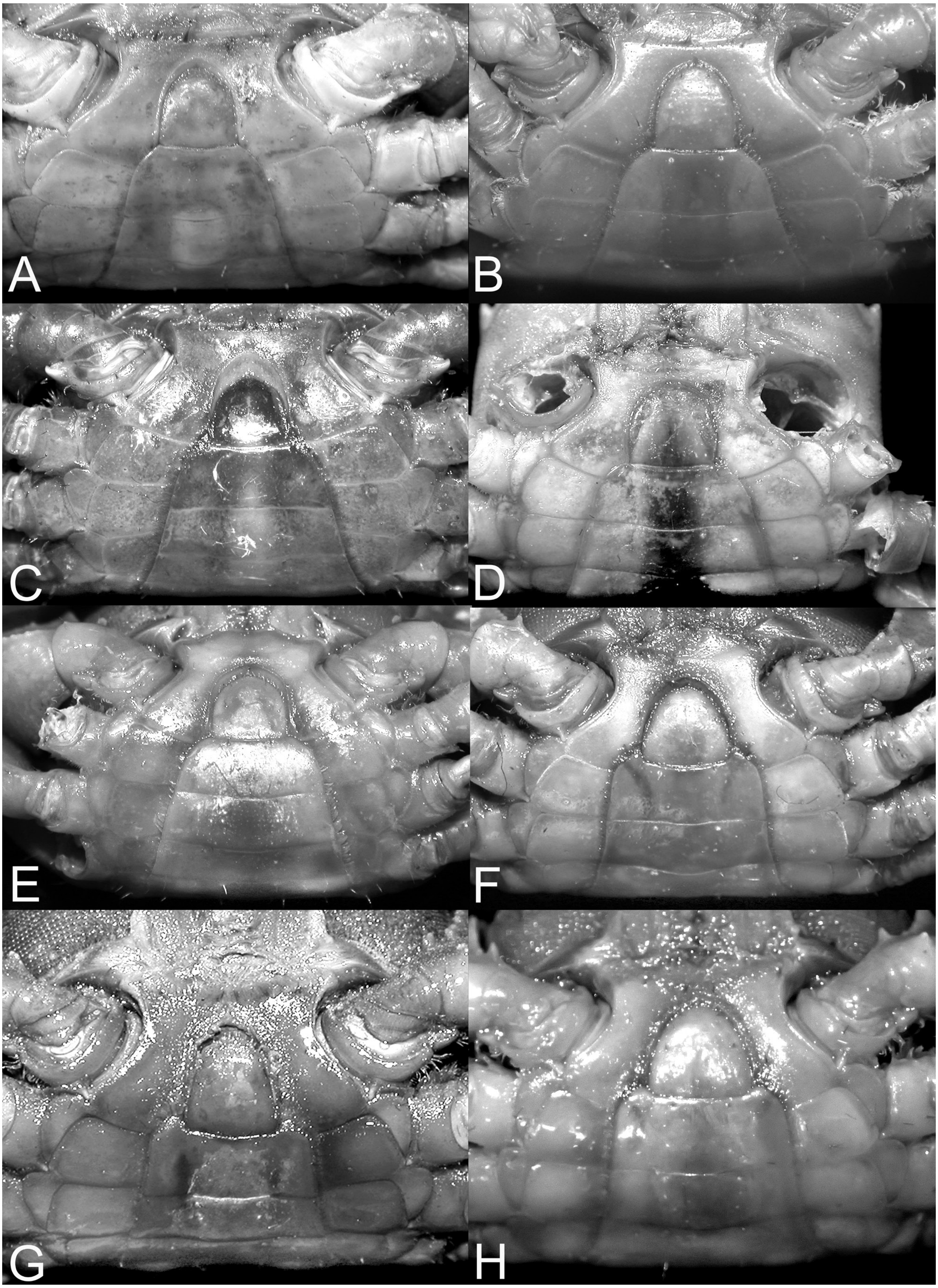

Fig. 31. Male anterior thoracic sternum and pleon. A, *Contusarma bocourti*, male (25.3 × 23.3 mm) (ZRC 2000.0952), Bangkok, Thailand; B, *Contusarma cheirogonum*, male (15.3 × 14.0 mm) (ZRC 2011.0924), Pulau Tioman, Malaysia; C, *Contusarma cheirogonum*, neotype male (24.5 × 21.5 mm) (ZRC 1995.225), Bako National Park, Sarawak; D, *Miersarma granosimanum*, lectotype male (16.9 × 14.8 mm) (NHM 1880.6), Borneo; E, *Miersarma granosimanum*, male (22.5 × 19.2 mm) (ZRC 1965.7.29.164), Sedili River, Johor, Malaysia; F, *Bresedium laevimanum*, lectotype male (20.0 × 17.6 mm) (MNHG), Borneo; G, *Bresedium laevimanum*, male (26.3 × 23.7 mm) (NHM) (lectotype of *Sesarma sediliensis*), Johor, Malaysia; H, *Bresedium laevimanum*, male (21.2 × 18.2 mm) (ZRC 1965.7.29.121), Johor, Malaysia.

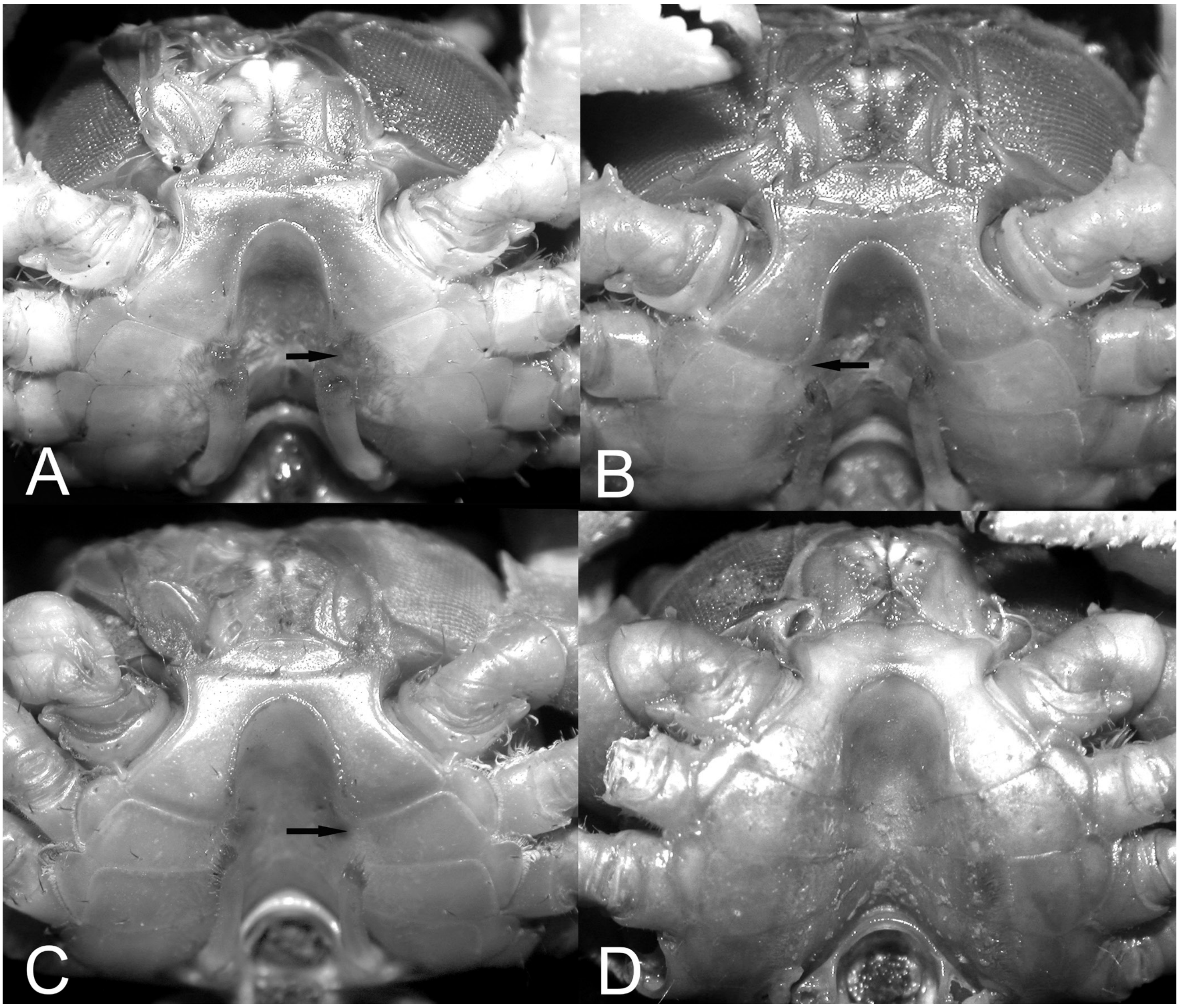

Fig. 32. Male sternopleonal cavity. A, *Pseudosesarma edwardsii*, male (20.8 × 18.6mm (ZRC 2003.0084), Pulau Tekong, Singapore; B, *Pseudosesarma crassimanum*, male (15.1 × 13.3 mm) (ZRC 2000.1768), Sungei Benut, Johor, Malaysia; C, *Contusarma cheirogonum*, male (15.3 × 14.0 mm) (ZRC 2011.0924), Pulau Tioman, Malaysia; D, *Miersarma granosimanum*, male (22.5 × 19.2 mm) (ZRC 1965.7.29.164), Sedili River, Johor, Malaysia. Arrow indicates shallow depression on somite 5 to accept G1 tip when pleon closed (depression absent in *Miersarma*, D).

Specimens reported as "*Sesarma edwardsi*" and "*Pseudosesarma edwardsii*" from many parts of Burma, India, Andamans, Bangladesh, Sri Lanka by Alcock (1900: 416), Mandal & Nandi (1989: 25), Kathirasan (2000: 193), Dev Roy & Nandi (2001: 18), Dev Roy & Bhadra (2007: 143, pl. 4 fig. 5), Dev Roy (2008: 131), Paul et al. (2012: 193), Holmes et al. (2014: 160) and Shet et al. (2016: 8, 12, fig. 2) (see Trivedi et al., 2018: 73); as well as Java, Sulawesi, and New Guinea by Tesch (1917: 147) probably belong to other species. The material from Sri Lanka by Alcock (1900) was referred to *P. anteactum*; while specimens from Kerala in West India probably belong to *P. glabrum*; as does most western Indian material. Specimens from northeastern India belong to *P. brehieri* and we have some specimens from West Bengal that confirm this (Fig. 37F–I). The precise identities of all these records can only be determined after re-examining the specimens. Ortmann's (1894: 721) record of "*Sesarma edwardsi*" from Australia is probably *Bresedium brevipes* (De Man, 1889) (see also Laurie, 1906; McNeill, 1968; Davie, 2002).

**Biology**. *Pseudosesarma edwardsii* is typically found in well-forested coastal freshwater or brackish water habitats. They are semiterrestrial and live on the banks of streams as well as swamps, and are often found under rocks and vegetation. They are sometimes found several hundred metres from the sea, even at the base of waterfalls. They have small eggs and it is clear their larval development remains tied to the open sea.

**Distribution**. Mergui Archipelago and Andamans to Peninsular Malaysia and Singapore, possibly to Java and Sulawesi (De Man, 1887; Tesch, 1917; Ng & Schubart, 2017).

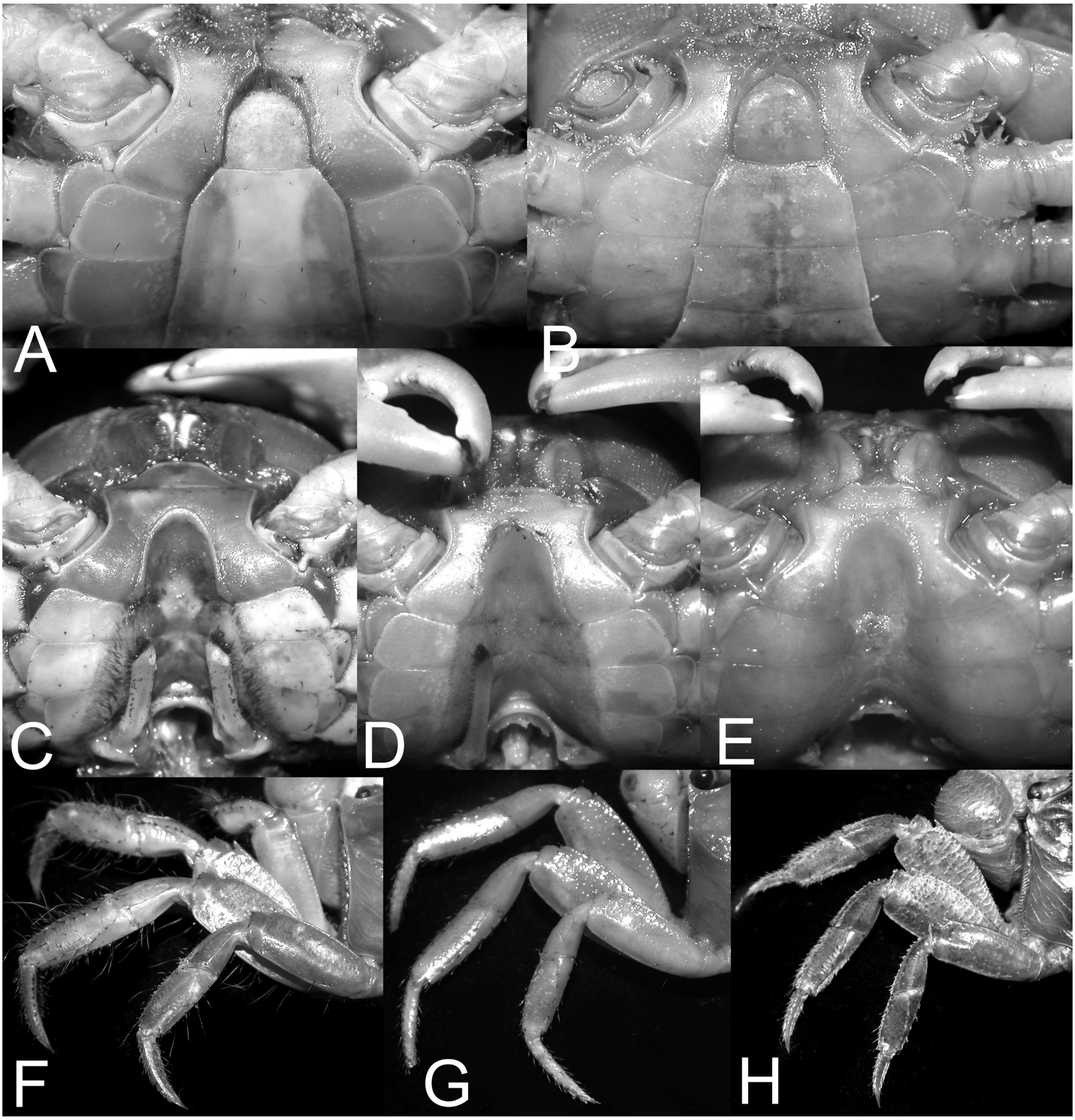

Fig. 33. A–E, male anterior thoracic sternum and pleon; F–H, left ambulatory leg. A, D, H, *Manarma moeschii*, male (18.2 × 16.3 mm) (ZRC 2000.1926), Thailand; B, E, *M. johorense*, male (14.6 × 12.6 mm) (ZRC 1971.9.24.14), Seletar River, Singapore; C, F, *Orisarma intermedium*, male (34.7 × 31.6 mm) (ZRC 2001.0034), Pingtung, Taiwan; G, *O. patshuni* (, male (14.2 × 13.0 mm) (ZRC 1998.345), Hong Kong.

### ***Pseudosesarma crassimanum* (De Man, 1887)**
### (Figs. 22D, 25C, 27D, 30C, 32B, 35, 44B, C, 56F, G)

*Sesarma edwardsii* var. *crassimana* De Man, 1887: 649.
*Sesarma edwardsi* var. *crassimana* – De Man, 1888: 188, pl. 13 figs. 5, 6; Zehntner, 1894: 180; Lanchester, 1900: 757.
*Sesarma* (*Episesarma*) *edwardsi* var. *crassimana* – De Man, 1895: 174.
*Sesarma* (*Sesarma*) *edwardsi crassimana* – Tesch, 1917: 148.
*Sesarma crassimana* – Tweedie, 1940: 92; Tweedie, 1950: 343, fig. 2b.
*Sesarma* (*Sesarma*) *crassimanum* – Serène, 1968: 105.
*Pseudosesarma crassimanum* – Serène & Soh, 1970: 399, 406; Tan & Ng, 1994: 82; Naiyanetr, 1998: 102; Cuesta et al., 2006: 160, fig. 9A–E; Naiyanetr, 2007: 115; Rademacher & Mengedoht, 2011: 29; Ng & Schubart, 2017: 661, figs. 1D, E, 2C, D, 8–11, 13.
"*Pseudosesarma*" *crassimanum* – Ng et al., 2008a: 222.

**Material examined**. Lectotype: male (16.3 × 14.6 mm) (NHM 1886.52b), mangrove swamps at Zediwon, Mergui Archipelago, Myanmar (= Burma), coll. J. Anderson, 1886. Paralectotypes: 1 male (18.8 × 16.7 mm), 2 females (16.6 ×

14.3 mm, 12.5 × 11.0 mm) (NHM 1886.52c), same data as lectotype. THAILAND – 1 male (15.9 × 14.3 mm) (ZRC 2008.0442), Ranong Province, King Amphoe Suk Sam Lan, Ton Roi waterfall, 9°27′29.2″N 98°30′31″E, Thailand, coll. D.C.J. Yeo et al., 12 August 1997; 2 males (21.9 × 19.5 mm, 18.5 × 16.3 mm), 2 females (larger 18.0 × 15.9 mm) (ZRC 2017.0169), Gulf of Thailand, coll. aquarium trade, April 2017. SINGAPORE – 1 male, 2 females (ZRC 1985.422–424), Sungei Seletar, coll. C.L. Soh, 23 September 1959; 1 male (17.5 × 15.0 mm) (ZRC 1967.7.21.4), Sungei Seletar, coll. C.L. Soh, 31 December 1966; 1 male (15.9 × 14.5 mm) (RMNH-D23313), probably from Singapore, don. R. Serène; 1 female (ZRC 1967.7.10), Sungei Seletar, coll. C.L. Soh, 6 May 1966; 2 males (ZRC 1967.7.10.40), Sungei Seletar, coll. C.L. Soh, 18 July 1966; 1 male (ZRC number), Simpang River, Mak Wai, coll. C.L. Soh, 18 February 1966; 2 females (ZRC 1973.11.2.493–494), Sungei Seletar, 29 March 1966; 1 male (ZRC 1967.7.10.39), coll. C.L. Soh; 1 male (ZRC 1971.9.22.10), no other data, coll. C.L. Soh; 1 male, 3 females (ZRC), no other data. PENINSULAR MALAYSIA – 1 male (ZRC 2003.0054), Johor, Mawai, Sungei Ulu Sedili, coll. T.M. Leong, 30 August 2002; 4 males, 3 females (ZRC 2010.1768), Johor, Sungei Benut Cintom, coll. C.D. Schubart et al., 30 September 1999; 2 males, 1 female (ZRC 1964.9.25.210–212), Sedili River, Johor, coll. M.W.F. Tweedie, 1938; 1 male (ZRC 1999.990), Pulau Tioman, Sungei Keliling, coll. H.H. Tan, 25 June 1999; 1 male, 8 females (largest 20.2 × 17.0 mm) (ZRC 2011.1012), Pulau Tioman, Sungei Keliling, coll. P.K.L. Ng et al., 27–28 January 1996; 1 male (12.6 × 10.5 mm) (ZRC), 1 female (ZRC 2016.0276), small freshwater stream at beginning of mangroves, Pulau Tioman, Sungei Keliling, coll. P.K.L. Ng, 19 August 2003; 1 male (ZRC 1985.425), coll. D.S. Johnson, 31 July 1959; 5 males, 3 females (ZRC 1999.957), Pulau Tioman, Sungei Keliling, coll. H.H. Tan et al., 25 June 1998. SARAWAK – 1 male (14.0 × 11.9 mm) (MNHG), coll. Bedot & Pichet, 1800s; 14 males, 10 females (ZRC 1964.9.25.368–379), Kuching, coll. M.W.F. Tweedie, 1950; 1 male (18.9 × 16.7 mm) (ZRC 1999.851), stream 3 km before turn off to Cape Pelandok and Kampung Pandan, after Landa town, drains from Sungei Gading, coll. H.H. Tan, 2 September 1996; 3 males (ZRC 1964.9.28.14–16), Stambak, Saribas, coll. L.K. Charles, 1950. INDONESIA – 2 males (17.2 × 15.0 mm, 14.3 × 12.3 mm) (ZRC 1999.503), Tanjung Reolep, Sungai Berau, riverbank, Kalimantan, coll. R. Diesel, 2 September 1995. THAILAND – 2 males, 1 female (ZRC 2017.1045), from aquarium trade, coll. P.K.L. Ng, 2017. CAMBODIA – 1 male, 1 female (ZRC 1965.7.29.52), Tonle Sap, Siam, coll. N. Annandale, 1918.

**Diagnosis**. Carapace transversely rectangular; frontal margin relatively wider, median concavity separating lobes more distinct; epibranchial tooth distinct, separated from rest of margin by deep notch; posterolateral margins subparallel; outer surface of chela gently convex, covered with small rounded granules, ventral margin of palm sinuous unarmed; suture between male thoracic sternites 3 and 4 distinct; male pleon broadly triangular; male sternopleonal cavity with press-button of pleonal locking mechanism on sternite 5; distal part of G1 gently swollen with chitinous part forming beak-like structure. In life, chela purplish red to yellow, pigmentation reaching to base of yellowish-white fingers.

**Colour**. In life, smaller specimens have a darker brown carapace with purple chelae and yellowish fingers (Fig. 56F, G). Larger specimens have carapaces which are lighter brown, with the chelae purplish-red to yellow (Rademacher & Mengedoht, 2011: 29) (see also Ng & Schubart, 2017).

**Remarks**. The differences between *P. edwardsii* and *P. crassimanum* have been discussed at length by Ng & Schubart (2017).

Li et al. (2020: 3, 29, 30) list "*Pseudosesarma crassimanum*" for the molecular tree they used in a study of *Sesarmops impressus* (H. Milne Edwards, 1837). Its genetic data, however, aligns with what is here regarded as *Manarma moeschii* (De Man, 1892) (see later). The material that was used for the study by Li et al. (2020) originated from the aquarium trade and was misidentified, they are actually *M. moeschii* (H.-T. Shih, pers. comm.).

**Biology**. This species seems to prefer to hide under small rocks and vegetation along the banks of coastal freshwater streams leading to the sea, but they have also been found in the rearward mangrove zones. They appear to be mainly nocturnal. On Pulau Tioman in Malaysia, they have been observed to climb up shrubs and small trees at night, apparently foraging for young shoots and buds. The larvae have been reported on by Cuesta et al. (2006).

**Distribution**. Known only from Thailand, Peninsular Malaysia, Singapore, and Borneo (Tweedie, 1940, 1950).

### *Pseudosesarma anteactum* Ng & Schubart, 2017

(Figs. 22E, 25D, 27E, 30F, 36A–G, 44D)

*Sesarma edwardsii* – Alcock, 1900: 416 (part). [not *Sesarma edwardsii* De Man, 1887]

*Sesarma* (*Sesarma*) *edwardsi crassimana* – Ingle & Fernando, 1963: 101, figs. 1, 2a, b. [not *Sesarma edwardsii* var. *crassimana* De Man, 1887]

*Pseudosesarma crassimanum* – Bouillon et al., 2004: 84; Dahdouh-Guebas et al., 2011: 192. [not *Sesarma edwardsii* var. *crassimana* De Man, 1887]

*Pseudosesarma anteactum* Ng & Schubart, 2017: 664, figs. 14–17.

**Material examined**. Holotype male (16.7 × 14.7 mm) (ZRC 2016.0602), Colombo, Sri Lanka, coll. R. Serène, 12 October 1972. Paratypes: 3 males (21.2 × 19.7 mm, 17.2 × 15.9 mm, 14.1 × 12.2 mm), 2 females (17.5 × 15.4 mm, 15.7 × 14.2 mm) (ZRC 2016.0603), same data as holotype.

**Diagnosis**. Carapace transversely rectangular; frontal margin relatively wide, median concavity separating lobes distinct; epibranchial tooth distinct, separated from rest of margin by deep notch; posterolateral margins subparallel; outer surface of chela gently convex, covered with closely packed rounded granules, ventral margin of palm gently convex, lined with rounded granules, not denticulate, fingers relatively short; suture between male thoracic sternites 3 and 4 distinct;

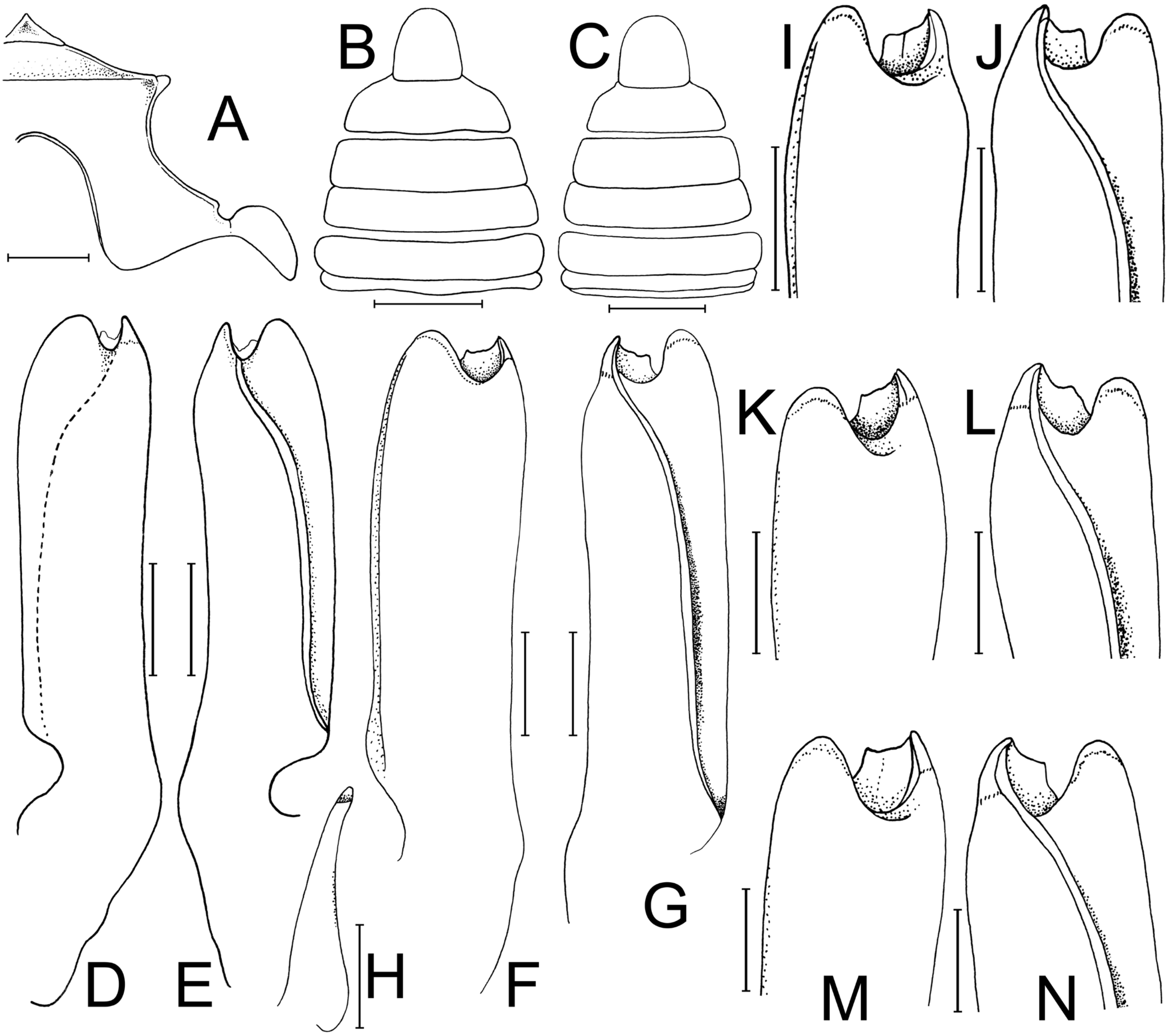

Fig. 34. *Pseudosesarma edwardsii*. A, B, D, E, lectotype male (17.5 × 16.1 mm) (RMNH-D17a), Mergui Archipelago; C, male (13.3 × 12.9 mm) (ZRC 2000.2019), Pulau Ubin, Singapore; F–H, male (20.5 × 19.3 mm) (ZRC 2016.0608), Langkawi; I, J, male (21.3 × 18.7 mm) (ZRC 2003.0084), Singapore; K, L, male (17.8 × 16.3 mm) (ZRC 2016.0608), Langkawi; M, N, male (12.5 × 10.4 mm) (ZRC 2016.0608), Langkawi. A, anterior thoracic sternites 1–4; B, C, male pleon; D, H, I, K, M, left G1 (dorsal view, denuded); E, G, J, K, N, left G1 (ventral view, denuded); H, left G2. Scales: A–C = 2.0 mm; D–J = 1.0 mm; K–N = 0.5 mm. (After Ng & Schubart, 2017: figs. 6, 7).

male pleon broadly triangular; male sternopleonal cavity with press-button of pleonal locking mechanism on sternite 5; distal half of G1 gently swollen, wider than proximal part, median part appears gently constricted, chitinous part forming relatively wide beak-like structure. In life, chela red, not extending beyond base of fingers.

**Colour**. Ingle & Fernando (1963: 102) described the palm of the cheliped as red but with the colour not extending beyond the base of the fingers.

**Remarks**. The species was described and figured in detail by Ng & Schubart (2017). The species is most similar to *P. crassimanum* in most of its external features but the ventral margin of the palm of *P. anteactum* is gently convex rather than concave (Fig. 27E versus Fig. 27D); and the median part of the G1 gently constricted with the proximal and subdistal parts dilated, the distal chitinous part being relatively wider and more truncate (Fig. 36A–G) (versus the G1 subdistal part is more dilated than the relatively more slender proximal parts, and the distal chitinous part is proportionately narrower, being more acute and beak-like in *P. crassimanum*; Fig. 35B–F, H–L, O–R).

**Biology**. The specimens of Ingle & Fernando (1963: 101) were from a brackish water canal in Kirillapone, a low-lying area just 5–6 km west of the main coastal city of Colombo. The types were from somewhere in Colombo. This fits the general habitat preference for many *Pseudosesarma* species.

**Distribution**. The species is known only from Sri Lanka thus far (Ng & Schubart, 2017).

### ***Pseudosesarma glabrum*** **Ng, Rani & Nandan, 2017**
(Figs. 22F, 25E, 27F, 30D, 36H–L)

*Pseudosesarma edwardsii* – Shet et al., 2016: 8, 12, fig. 2 (not *Sesarma edwardsii* De Man, 1887).

*Pseudosesarma glabrum* Ng, Rani & Nandan, 2017: 265, figs. 2–5; Trivedi et al., 2018: 73; Apreshgi & Abraham, 2018: 96; Pati et al., 2020: 139, figs. 2–4.

**Material examined**. Holotype: male (13.8 × 12.0 mm) (CUSAT 2016-1), mangrove forest (mixed mangrove zone with human settlements), Aroor, Cochin estuary, part of Vembanad wetland, RAMSAR site, Kerala, India, coll. V. Rani et al., 16 January 2016. Paratypes: 1 male (12.2 × 10.3 mm) (CUSAT 2016-2), same data as holotype; 1 male (16.5 × 14.5 mm) (CUSAT 2016-3), same location as holotype, coll. 3 March 2017. Others: INDIA – 2 males, 1 female (ZRC 2019.0487), Thejaswini River, near Palayi Kadavu, Kasaragod district, Kerala, 12.261°N 75.165°E, coll. students, 10 October 2018.

**Diagnosis**. Carapace slightly wider than long, width to length ratio 1.15–1.18; dorsal surface, including anterior part almost glabrous, without setae, with only short, barely visible scattered setae on posterolateral regions; frontal margin wide, median concavity separating lobes shallow; lateral margin with 1 distinct low epibranchial tooth, posterolateral margins subparallel; chela short, stout, fingers just shorter than palm, outer surface of palm with numerous small rounded granules, ventral margin of fixed finger and distal half of palm straight; suture between male thoracic sternites 3 and 4 distinct, straight; male pleon broadly triangular, somite 6 wide with distinctly convex lateral margins; male sternopleonal cavity with press-button of pleonal locking mechanism on anterior edge of sternite 5; G1 stout, distal part dilated forming bulbous structure, chitinous tip relatively broad, appearing bifurcated. In life, chela purple, not extending beyond base of fingers.

**Colour**. In life, the carapace is dark grey to brown with patches of lighter grey and brown; with the merus of the cheliped orange and the palm purple to dark orangish-brown and fingers white. The ambulatory legs are light brown with some parts orange (Ng et al., 2017a: 267, fig. 5; Pati et al., 2020: fig. 2).

**Remarks**. *Pseudosesarma glabrum* was described and figured in detail by Ng et al. (2017a). It closely resembles *P. crassimanum*, but can easily be separated by the median cleft of the frontal margin being relatively more shallow (Fig. 22F), the anterior part of the dorsal surface of the carapace is almost glabrous except for a few very small scattered setae on the posterolateral regions (Fig. 22F), the ventral margin of the pollex and distal half of the palm of the adult chela is almost straight (Fig. 27F), the male pleon is relatively wider (Fig. 30D), and the G1 distal chitinous process is relatively shorter, wider, and appears bifurcated (Fig. 36I–K) (versus the median cleft of the frontal margin deeper, most of dorsal carapace surface covered with scattered but distinct stiff setae, the ventral margin of the pollex and distal half of the palm of the adult chela is distinctly concave, the male pleon is relatively narrower and the G1 distal chitinous process is beak-like, longer, and narrower in *P. crassimanum*; Figs. 22D, 27D, 30C, 35B–F, H–L, O–R).

**Biology**. *Pseudosesarma glabrum* is semi-terrestrial in habits, occurring in the intertidal mixed mangrove forests of Aroor in the Cochin estuary, Kerala, India. Sympatric sesarmids include *Parasesarma plicatum* (Latreille, 1803) and *Neosarmatium malabaricum* (Henderson, 1893) (Ng et al., 2017a: 269).

**Distribution**. The species was described from northern Kerala (Ng et al., 2017a) but has since been found in other parts of Kerala state as well as in Karnataka and Maharashtra in western India (Pati et al., 2020).

### ***Pseudosesarma brehieri*** **Ng, 2018**
(Figs. 22G, 25F, 27G, 30G, 37A–I, 44E)

*Pseudosesarma brehieri* Ng, 2018: 191, figs. 4–6, 7D–I; Trivedi et al., 2020: 4, fig. 3.

**Material examined**. Holotype: male (17.4 × 15.7 mm) (ZRC 2016.0593), Nathack Gu (Two Level Cave), near Saddan Sin Gu, Mawlamyine (Moulmein), Mon State, 16°31′33.5″N 097°42′48.8″E, Myanmar, coll. F. Bréhier et al., 26 November 2016. Paratype: 1 female (14.9 × 13.4 mm) (ZRC 2016.0594), same data as holotype. Others: INDIA – 5 males (11.9 × 10.4 mm, 12.4 × 10.9 mm, 13.6 × 11.7 mm, 14.5 × 13.0 mm, 15.0 × 13.6 mm) (ZRC 2013.0209), river bank, Bhagirath, Nabadiwip, Nadia, West Bengal, coll. Z. Jaafar et al., 26 December 2004.

**Diagnosis**. Carapace quadrate, slightly wider than long, width to length ratio 1.1; frontal margin wide, median concavity separating lobes relatively shallow; external orbital tooth short, not reaching to level of front, lateral margin with 2 epibranchial teeth; posterolateral margins subparallel; chela short, stout, fingers shorter than palm, outer surface of chela covered with numerous granules, ventral margin of palm almost straight or gently convex; suture between male thoracic sternites 3 and 4 distinct; male pleon triangular, somite 6 wide; male sternopleonal cavity with press-button of pleonal locking mechanism on sternite 5; G1 stout, distal part prominently dilated forming bulbous structure, chitinous tip short, broad, truncate, fan-like.

**Colour**. Not known.

**Remarks**. The species was described and figured in detail by Ng (2018). *Pseudosesarma brehieri* most closely resembles *P. crassimanum* but can easily be separated by the ventral margin of its adult male chela being almost straight (Fig. 27G) and the distal half of the G1 being proportionately more dilated with the chitinous distal part very wide and fan-like (Fig. 37B–D, F–I) (versus ventral margin of adult male chela gently concave, and the G1 distal part less dilated with the chitinous distal part narrow and beak-like in *P. crassimanum*; Figs. 27D, 35B–F, H–L, O–R).

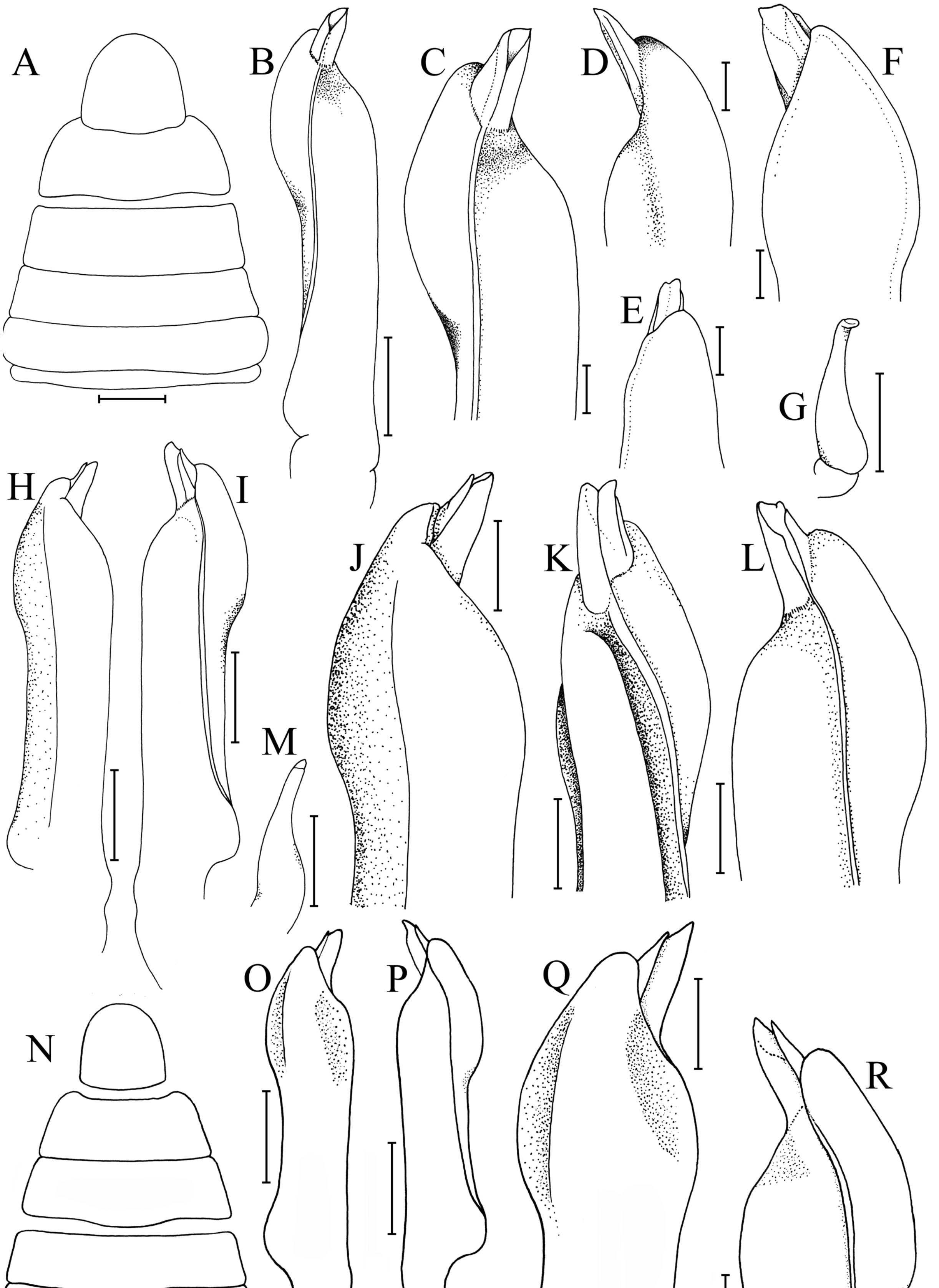

Fig. 35. A–E, *Pseudosesarma crassimanum*. A–G, lectotype male (16.3 × 14.6 mm) (NHM 1886.52b), Myanmar; H–M, male (15.9 × 14.3 mm) (ZRC 2008.0442), Ranong; N–R, male (15.9 × 14.5 mm) (RMNH-D23313), Singapore. A, N, pleon; B–F, right G1; G, right G2; H–L, O–R, left G1; M, left G2. Scales: A = 2.0 mm; B, G, H, I, M, O, P = 1.0 mm; N = 5.0 mm; C–F, J–L, Q, R = 0.5 mm. After Ng & Schubart (2017: fig. 11).

**Biology**. Ng (2018: 193, 195) observed that the type specimens of *P. brehieri* were found in a small upper chamber of a cave at the foot of the hill not far from Saddan Sin Gu in southern Myanmar. The water in the cave was completely fresh. The site is not far from the sea and the species is clearly not an obligate cave species with well developed eyes and normal colouration. Trivedi et al. (2020: 4) recorded the species from India, noting that the material was "collected from [the] muddy shore of Hooghly River at Barrackpore city of West Bengal state which is considered as upper reaches of Hooghly-Matla estuary, where tidal effects usually occur with a low salinity (0.5 to 4 ppm) of interstitial waters". The present specimens from India were collected from the side of a riverbank in an estuarine habitat in West Bengal, India.

**Distribution**. The species was described from Myanmar and we now also have specimens from Bengal in eastern India (ZRC 2013.0209).

### *Pseudosesarma boulengeri* (Calman, 1920)

(Figs. 22H, 25G, 27H, 30H, 37J–O, 44F)

*Chiromantes boulengeri* Calman, 1920: 63, fig. A.
*Sesarma* (*Holometopus*) *boulengeri* – Serène, 1968: 107.
*Chiromantes boulengeri* – Ng & Liu, 1999: 229; Apel & Türkay, 1999: 133; Apel, 2001: 116; Naderloo & Schubart, 2009: 61; Naderloo, 2011: 15, figs. 6a–f, 7a, b; Naderloo & Turkäy, 2012: 47; Naderloo, 2017: 348, figs. 31.1, 31.2, 31.6, 31.11a.
"*Chiromantes*" *boulengeri* – Ng et al., 2008a: 220.

**Material examined**. Lectotype male (26.9 × 23.5 mm) (NHM 1919.11.14.1), Basra, Ashar Creek, Iraq (Mesopotamia), coll. C.L. Boulenger. Paralectotypes – 1 male (21.0 × 17.8 mm), 1 ovigerous female (23.8 × 20.4 mm, 26.7 × 22.4 mm) (NHM 1919.11.14.2–4) (same data as lectotype). Others: IRAQ – 1 male, 1 female (NHM 1892.9.16.7.20), Fao; 1 male (NHM 1999.124), Fao. IRAN – 3 males (ZUTC Brach 1151), Bahmanshir River, coll. E. Gholinezhad, summer 2006; 1 male, 1 female (ZUTC Brach 1153), Bahmanshir River, coll. E. Gholinezhad, summer 2006; 16 males, 25 females (16 ovigerous), 3 juveniles (SMF 33818), 2 males, 2 females (ZRC 2014.0335), Abadan, Bahmanshir River, Pole Tanki Abolhassan, 30°21′01.5″N 48°18′35.9″E, coll. R. Naderloo & A. Kazemi, 20 May 2008.

**Diagnosis**. Carapace squarish; epibranchial tooth absent, lateral margin entire; posterolateral margins gently converging towards posterior carapace margin; outer surface of chela gently convex, covered with large rounded granules in adults, ventral margin of palm sinuous, unarmed; male pleon triangular, appears more elongate; suture between male thoracic sternites 3 and 4 distinct; male sternopleonal cavity with press-button of pleonal locking mechanism on sternite 5; distal part of G1 gently swollen with main chitinous part forming beak-like structure and smaller projection basally. In life, chelae beige to cream.

**Colour**. In life, the carapace and appendages are cream to buff, with the dorsal surface of the carapace possessing darker blotches (Fig. 56H) (see also Naderloo, 2011: 7a, b; Naderloo, 2017: fig. 31.1).

**Remarks**. The taxonomy of this species has been treated at length by Naderloo & Schubart (2009).

**Biology**. In Iran, the species lives in burrows along the muddy banks of rivers subject to tidal influence (Naderloo & Schubart, 2009). The type from Iraq, however, was found in Ashar Creek, 96 km from the sea, and presumably freshwater (Calman, 1920).

**Distribution**. Iraq and Iran, Persian Gulf (Calman, 1920; Naderloo & Schubart, 2009).

### *Contusarma*, new genus

**Type species**. *Sesarma bocourti* A. Milne-Edwards, 1869, by present designation. Gender neuter.

**Diagnosis**. Carapace subrectangular; frontal margin bilobed, gently deflexed, as wide as or slightly wider than posterior carapace margin; lateral margins of carapace with small epibranchial tooth, posterolateral part subparallel; regions of carapace clearly demarcated; postfrontal and epigastric crests separated by distinct grooves, margin straight, sharp or gently convex, regions clearly separated; basal articles of antenna and antennules clearly separated by septum formed by extension of front; dorsal margin of palm without any longitudinal pectinated ridge; outer surfaces of both chelae prominently flattened, covered with numerous squamate or low sharp granules; chelipedal dactylus relatively broad; inner surfaces of first to third ambulatory coxae with only scattered short setae between them, never arranged into dense tufts; male thoracic sternites 2–4 relatively narrow in adults, shallow but just visible suture between sternites 3 and 4; male sternopleonal cavity reaching three-quarters length of sternite 4 but not reaching sternite 2; pleonal locking mechanism formed by small angular projection on posterior edge of sternite 4 of sternopleonal cavity, no trace of tubercle on sternite 5; male thoracic sternite 5 smooth, without depression on anterior part; G1 relatively slender, long, chitinous part bent obliquely, relatively long. Vulva on anterior part of sternite 6, anterior edge just touching sternite 5; rim-like anterior and posterior sternal vulvar covers; opening short, cylindrical, slightly projecting, directed obliquely posteriorly.

**Etymology**. The name is derived from the combination of the Latin "contusus" for flattening surface, with the genus name *Sesarma*. This alludes to the flat chelae that the two included species use to help in burrowing. The gender is neuter.

**Included species**. *Sesarma bocourti* A. Milne-Edwards, 1869; *Sesarma cheirogona* Targioni Tozzetti, 1877.

**Remarks**. The genus contains two species, *Sesarma bocourti* A. Milne-Edwards, 1869, and *Sesarma cheirogona* Targioni

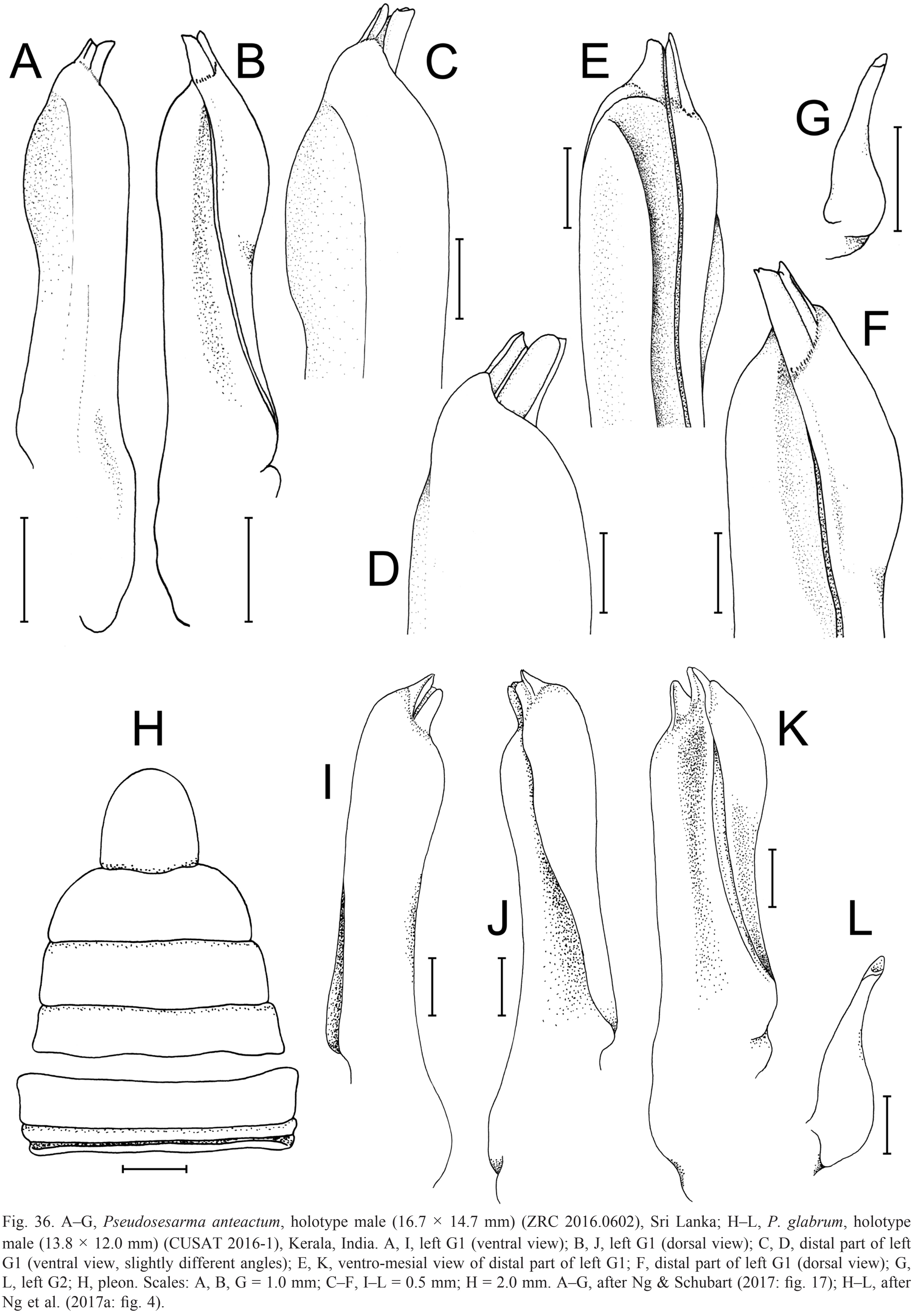

Fig. 36. A–G, *Pseudosesarma anteactum*, holotype male (16.7 × 14.7 mm) (ZRC 2016.0602), Sri Lanka; H–L, *P. glabrum*, holotype male (13.8 × 12.0 mm) (CUSAT 2016-1), Kerala, India. A, I, left G1 (ventral view); B, J, left G1 (dorsal view); C, D, distal part of left G1 (ventral view, slightly different angles); E, K, ventro-mesial view of distal part of left G1; F, distal part of left G1 (dorsal view); G, L, left G2; H, pleon. Scales: A, B, G = 1.0 mm; C–F, I–L = 0.5 mm; H = 2.0 mm. A–G, after Ng & Schubart (2017: fig. 17); H–L, after Ng et al. (2017a: fig. 4).

Tozzetti, 1877. The latter has been treated as a junior synonym of *S. bocourti* for over a century, but a suite of small morphological characters as well as genetic data allow it to be recognised as a separate taxon (Fig. 59). The differences between these two species are discussed under *Contusarma bocourti* below.

### ***Contusarma bocourti*** **(A. Milne-Edwards, 1869)**

(Figs. 23A–C, E, F, 25H, 28A–C, 31A, 38, 44G, 57A)

*Sesarma bocourti* A. Milne-Edwards, 1869: 28.
*Sesarma* (*Sesarma*) *bocourti* – Tesch, 1917: 135 (part).
*Pseudosesarma bocourti* – Naiyanetr, 1998: 101; Naiyanetr, 2007: 17 (unnumbered fig.), 115; Ng et al., 2008a: 222; Hoang et al., 2012: 75, 78.

**Material examined**. Lectotype (here designated): male (24.0 × 27.2 mm) (MNHN D-10965), Bangkok, Thailand. Paralectotype: male (19.1 × 21.5 mm) (MNHN D-10965), same data as lectotype. THAILAND – male (25.3 × 23.3 mm) (ZRC 2000.0952), Silom, Chao Phraya at cemetery, Hotel Mae-Noon, Bangkok, coll. Pongsathron, 1 August 1998; 1 female (ZRC 2019.1114), Bangkok, Thailand, from aquarium trade, via C. Lukhaup, 9 January 2007.

**Diagnosis**. Anterior dorsal carapace regions with relatively dense short black setae; outer surface of adult chela covered with large flattened granules, those on margins large, sharp; margins of ambulatory segments with dense short setae; male pleon relatively transversely more narrow; G1 relatively stouter, chitinous distal part gently curved, proportionately wider.

**Colour**. Carapace relatively dark, gastric regions almost black; distal margins of ambulatory merus, carpus, and propodus with darker bands (Fig. 57A) (see also Naiyanetr, 2007: 17, unnumbered fig.).

**Remarks**. *Sesarma bocourti* was described briefly by A. Milne-Edwards (1869) from an unspecified number of specimens from Bangkok, Thailand. The extant specimens (all dried) are therefore syntypes. The largest male (24.0 × 27.2 mm, MNHN D-10965) is here selected as the lectotype of the species (Fig. 23A). *Sesarma cheirogona* Targioni Tozzetti, 1877, was described on the basis of a single male (22.0 × 20.0 mm) supposedly collected from Yokohama in Japan. Nobili (1900: 507) apparently examined the holotype of *Sesarma cheirogona* and commented that there were no significant differences from his specimens of *Sesarma bocourti* from Sumatra collected by the Siboga Expedition and synonymised both species. Tesch (1917) agreed with the synonymy but noted there were two types of male pleons for what had been called *S. bocourti* in Southeast Asia; one relatively more narrow (Tesch, 1917: fig. 2a; from an unspecified location in Borneo and Deli, Sumatra) and one relatively wider (Tesch, 1917: fig. 2b; from Balikpapan, Borneo). He, however, recognised just one species as he commented that they were otherwise similar externally. Urita (1926: 20) recorded *S. bocourti* from "near coast of Kagosima, Satuma" in Japan, but no material was indicated, and no figure was provided so its identity cannot be confirmed. Sakai (1939: 685; 1976: 661) listed the species for the Japanese fauna but noted that it was based on Targioni Tozzetti's (1877) record and he had no specimens. Tweedie (1940) discussed this and commented that broader pleons are generally associated with smaller specimens and the differences were probably due to variation. Tweedie (1940: 91) also commented that "If *Sesarma cheirogona* Targioni Tozzetti from Yokohama (1877, p. 141) is really identical with *bocourti*, I am inclined to think that the specimen was wrongly localised. It was collected during the world cruise of the 'Magenta', which included visits to Borneo and Sumatra". There have thus been no reliable confirmed records of this species north of Thailand, despite intensive collecting and study of crabs in Japan. This supports Tweedie's suggestion that the type locality is likely to have been from the Indo-Malayan region rather than Yokahama.

Examination of the present extensive collection has revealed differences between the specimens from Thailand and the rest of Southeast Asia (southern Peninsular Malaysia, Singapore, and Sarawak). Most significantly, their G1s are slightly different, with those from Thailand being relatively stouter, with the chitinous distal part gently curved and proportionately wider (Fig. 38D–H). Those from the rest of Southeast Asia are relatively more slender, and the chitinous distal part is straight and proportionately narrower (Fig. 39F–J, L–N). In addition, while the male pleon does have a degree of natural variability in proportions, as discussed by Tweedie (1940), that of Thai specimens is still relatively transversely narrower (notably somite 6) (Fig. 38C) compared to those from the rest of Southeast Asia (Fig. 39E, O–Q). The adult male from Thailand is also distinctly more setose over the whole carapace and ambulatory legs (Fig. 23B, F), with the granules on the chelae proportionately stouter and larger (Fig. 28A–C). Those from the rest of Southeast Asia have sparsely setose to almost glabrous carapaces and legs (Fig. 23G, H), and the granules on the chelae are smaller (Fig. 28D). The degree of setation is not discernible on the types of *C. bocourti* (Fig. 23A, E), but the setae may have fallen off due to their age and dried condition. The phylogenetic tree supports this, with a sister-group relationship between the two species (Fig. 59).

While we have no doubt that the Thai material is *Contusarma bocourti* s. str., Hoang et al.'s (2012) material of "*Pseudosesarma bocourti*" from southern Vietnam should be re-examined if possible. It is provisionally identified as *C. bocourti*. The identity of the Malaysian, Singapore, and Bornean specimens is more problematic. This is because the real origin of *Sesarma cheirogona* is unclear, as discussed above. Tweedie (1940) commented that Targioni Tozzetti's (1877) material of *S. cheirogona* could have originated from Borneo or Sumatra, but that expedition also visited Singapore, Java, and Vietnam; before the vessel reached Japan. Comparing the figures given in Targioni Tozzetti (1877), however, it seems likely his material came from Singapore or Borneo (or adjacent areas) as his figure (Fig. 39C; Targioni Tozzetti, 1877: fig. 2d) shows a proportionately wider pleon similar to those from this area (Fig. 39E, O–Q). For this reason, we refer all the present

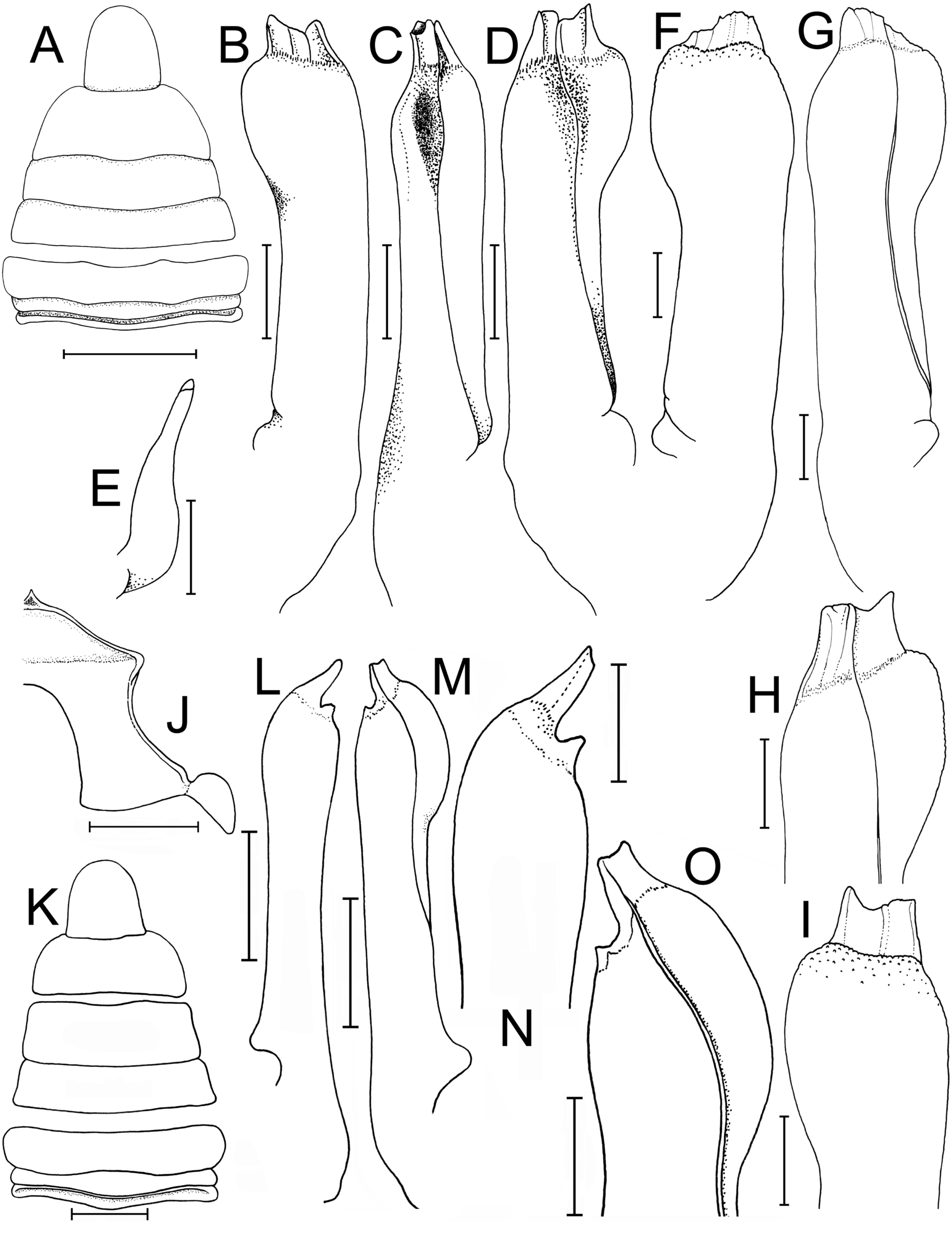

Fig. 37. A–G, *Pseudosesarma brehieri*, paratype female (14.9 × 13.4 mm) (ZRC 2016.0594), Myanmar; F, G, *P. brehieri*, male (15.0 × 13.6 mm) (ZRC 2013.0209), West Bengal, India; H, I, *P. brehieri*, male (14.5 × 13.0 mm) (ZRC 2013.0209), West Bengal, India; J–O, *P. boulengeri*, lectotype male (26.9 × 23.5 mm) (NHM 1919.11.14.1), Basra, Iraq. A, K, male pleon; B, F, L, left G1 (ventral view, denuded); D, G, M, left G1 (dorsal view, denuded); E, left G2; H, O, left distal part of G1 (dorsal view, denuded); I, N, left distal part of G1 (ventral view, denuded); J, anterior thoracic sternites 1–4. Scales: A = 4.0 mm; B–E, N, O = 1.0 mm; F–I = 0.5 mm; J, K = 5.0 mm; L, M = 2.0 mm. A–E, after Ng (2018: fig. 7E–I).

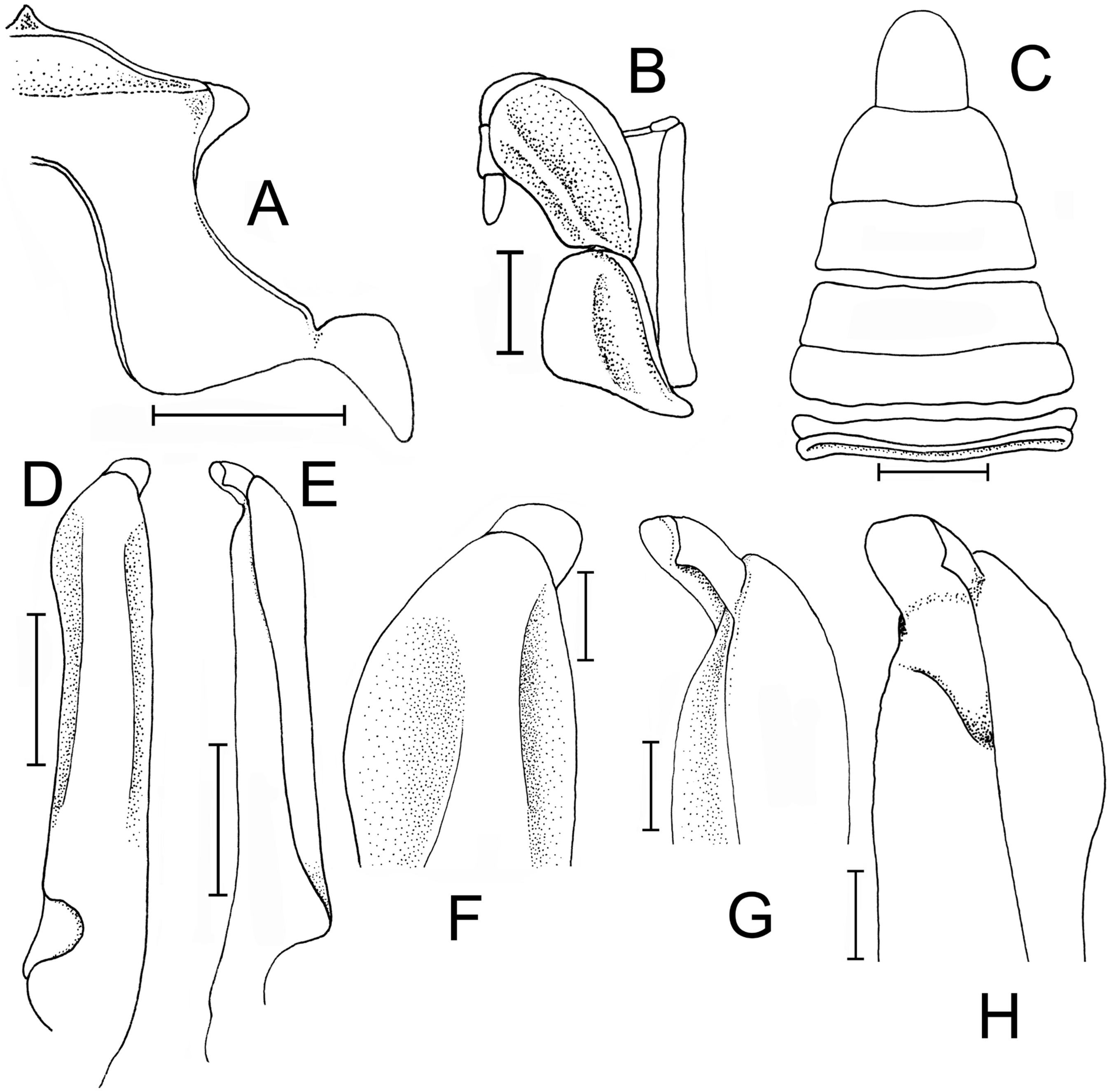

Fig. 38. *Contusarma bocourti*, male (25.3 × 23.3 mm) (ZRC 2000.0952), Bangkok, Thailand. A, anterior thoracic sternites 1–4; B, left third maxilliped (denuded); C, male pleon; D, left G1 (ventral view, denuded); E, left G1 (dorsa view); F, left distal part of G1 (ventral view, denuded); G, left distal part of G1 (dorsal view, denuded); H, left distal part of G1 (mesial view). Scales: A, C = 5.0 mm; B = 2.5 mm; D, E = 1.0 mm; F–H = 0.5 mm.

material from Peninsular Malaysia, Singapore, and Sarawak to *C. cheirogonum*. The identity of the specimen figured by Tesch (1917: 138, fig. 2b) with a very wide male pleon from Balikpapan in eastern Kalimantan in Borneo cannot be ascertained without a re-examination at a future date. This may simply be intraspecific variation because one specimen from Sarawak has a similarly proportioned male pleon (Fig. 31C), with the other male specimens from this location having narrower pleons. The records from the rest of Borneo and Sumatra by De Man (1880, 1895), Miers (1880), Nobili (1900), Tesch (1917), and Roux (1933) are also provisionally referred to *C. cheirogonum*.

The types of Targioni Tozzetti (1877) are lost. Lucas (1981: 200) notes that "The type specimens which were kept in the Museo Zoologico de "La Specola", Firenze, Italy, are not extant; they were lost during World War II (M. Poggesi, pers. comm.)". Gianna Innocenti (Universitá di Firenze) conducted a fresh search in 2019 but also came to the conclusion the type of *Sesarma cheirogona* is no longer extant. To stabilise the taxonomy of the two species in *Contusarma*, we here select a male (24.5 × 21.5 mm) (ZRC 1995.225) from Bako National Park, Sarawak, as the neotype of *Sesarma cheirogona* Targioni Tozzetti, 1877. This is necessary to stabilise the taxonomy of the species.

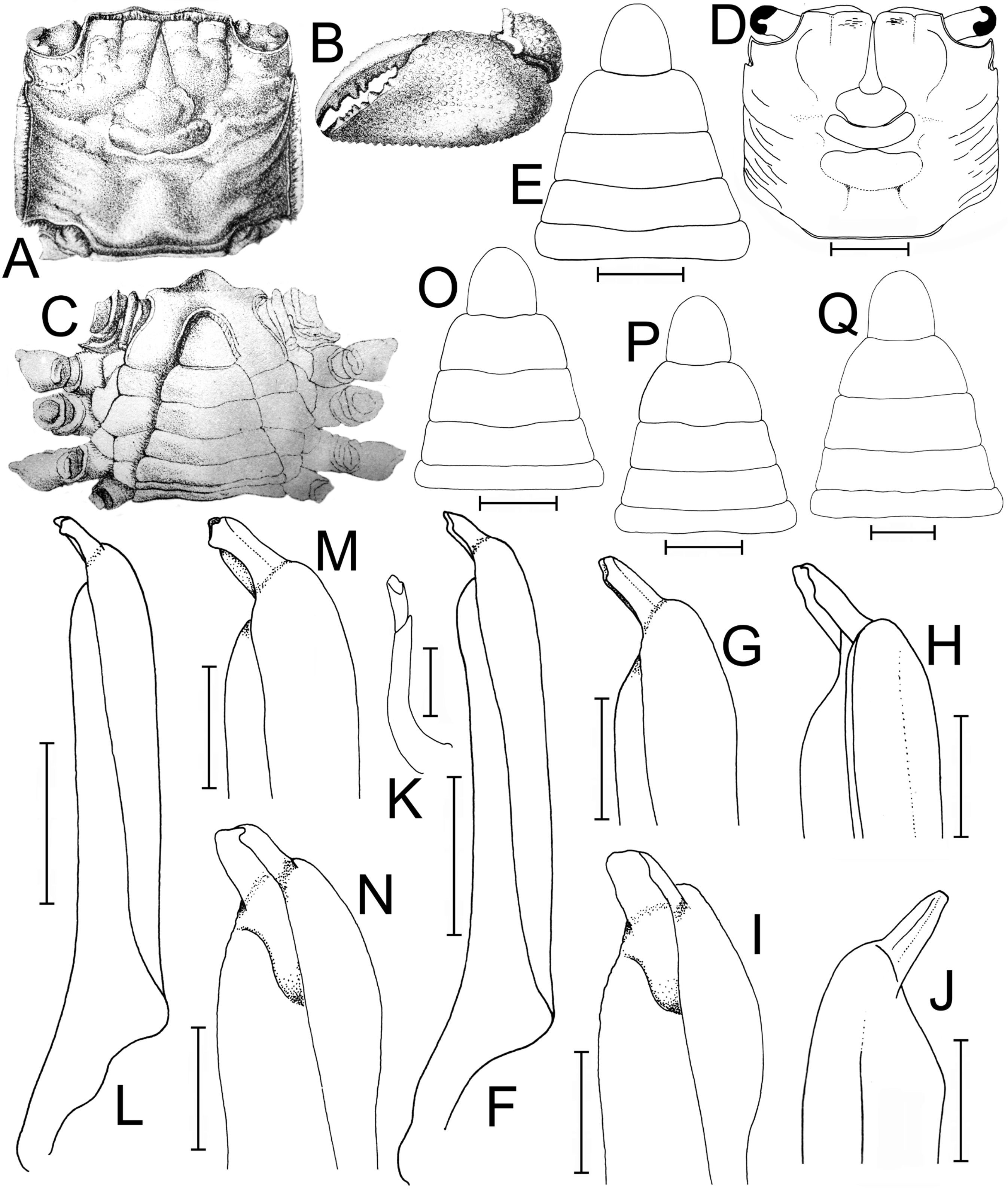

Fig. 39. *Contusarma cheirogonum*. A–C, holotype male of *Sesarma cheirogona* (after Targioni Tozzetti, 1877: pl. 9 fig. 2); D, E, F–J, K, male (26.3 × 23.0 mm) (ZRC 1995.226), Bako National Park, Sarawak; L–N, neotype male (24.5 × 21.5 mm) (ZRC 1995.225), Bako National Park, Sarawak; O, male (24.5 × 21.3 mm) (ZRC 1964.9.28.140), Johor, Malaysia; P, male (22.3 × 20.5 mm) (ZRC 1964.9.28.127), Saribas, Sarawak; Q, male (28.8 × 25.5 mm) (ZRC 1964.9.28.126), Saribas, Sarawak. A, D, carapace; B, outer view of left chela; C, thoracic sternites and pleon; E, O–Q, pleon; F, L, left G1 (dorsal view, denuded); M, G, H, left distal part of G1 (dorsal view, denuded); N, I, left distal part of G1 (mesial view); J, left distal part of G1 (ventral view, denuded); K, left G2 (denuded). A–C, after Targioni Tozzetti (1877: pl. 9 fig. 2); D, H, J, K, after Ng (1995: fig. 14). Scales: D, E, K, O–Q = 5.0 mm; F, L = 2.0 mm; G–K, M, N = 1.0 mm.

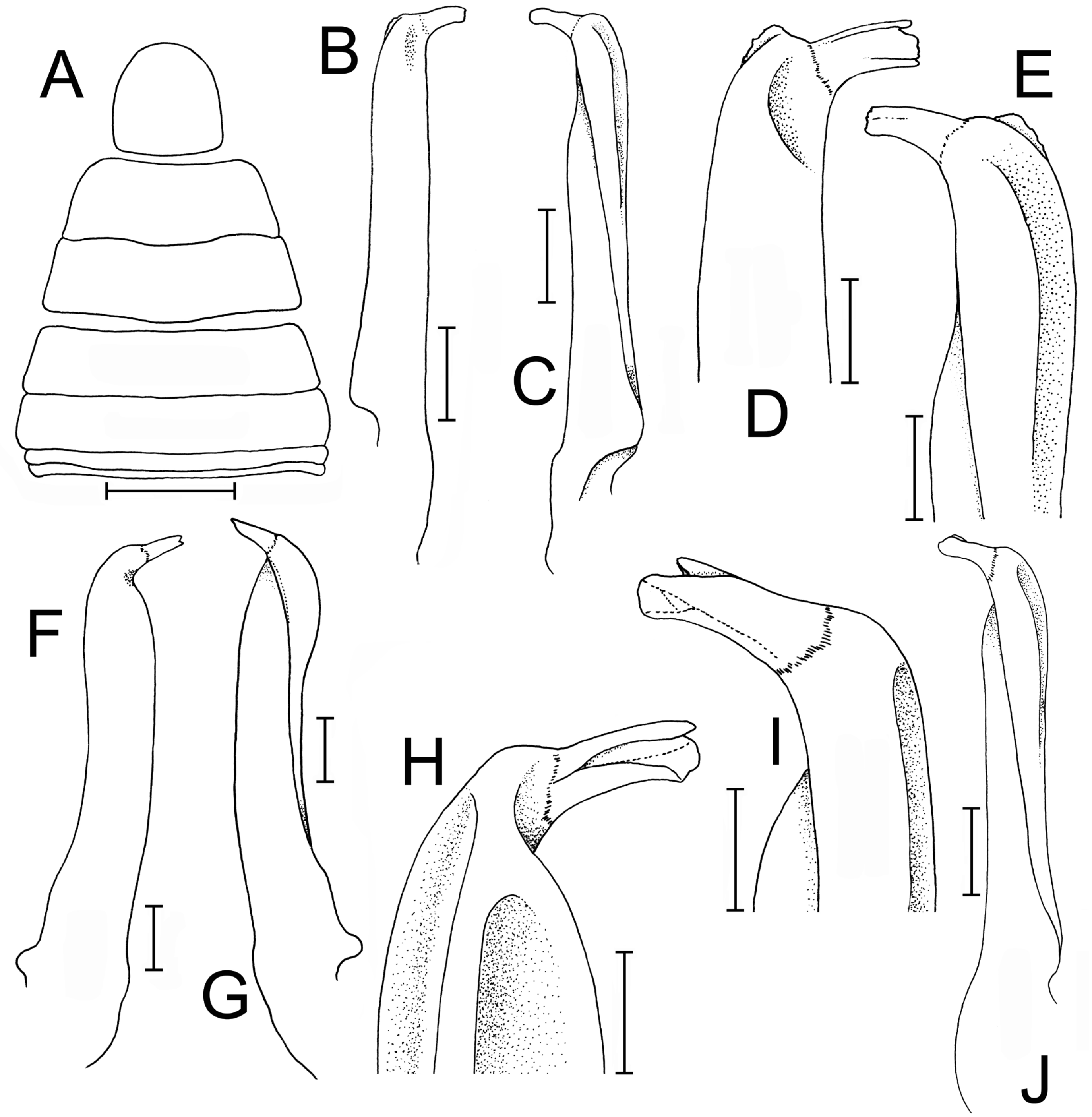

Fig. 40. *Miersarma granosimanum*. A–E, lectotype male (16.9 × 14.8 mm) (NHM 1880.6), Borneo; F–I, male (22.5 × 19.2 mm) (ZRC 1965.7.29.164), Sedili River, Johor, Malaysia; J, male (19.5 × 16.7 mm) (ZRC 1965.7.29.165), Sedili River, Johor, Malaysia. A, male pleon; B, F, left G1 (ventral view, denuded); C, G, J, left G1 (dorsal view, denuded); D, H, left distal part of G1 (ventral view, denuded); E, I, left distal part of G1 (dorsal view, denuded). Scales: A = 5.0 mm; B, C, F, G, J = 1.0 mm; D, E, H, I = 0.5 mm.

**Biology**. Probably very similar to *Contusarma cheirogonum* (see below), but detailed data or field observations are not available. One recent specimen (ZRC 2000.0952) was obtained from along the Chao Phraya River, from Silom, a site about 20 km from the sea. This is in the main city area of Bangkok but there is still strong tidal influence.

**Distribution**. Known only from western coast of Thailand, Indian Ocean.

### *Contusarma cheirogonum* (Targioni Tozzetti, 1877)

(Figs. 23D, G, H, 25I, 28D, 31B, C, 32C, 39, 44H, 57B–H)

*Sesarma cheirogona* Targioni Tozzetti, 1877: 141–145, pl. 9, fig. 2a–g.

*Sesarma bocourti* – De Man, 1880: 28; Miers, 1880: 313; Zehntner, 1894: 182; Tweedie, 1940: 90.

*Sesarma* (*Sesarma*) *bocourti* – Nobili, 1900: 507; Tesch, 1917: 135, figs. 1, 2a; Balss, 1922: 155; Roux, 1933: 13.

*Sesarma* (*Episesarma*) *bocourti* – De Man, 1895: 169.

*Pseudosesarma bocourti* – Tan & Ng, 1994: 82; Ng, 1995: 200, fig.

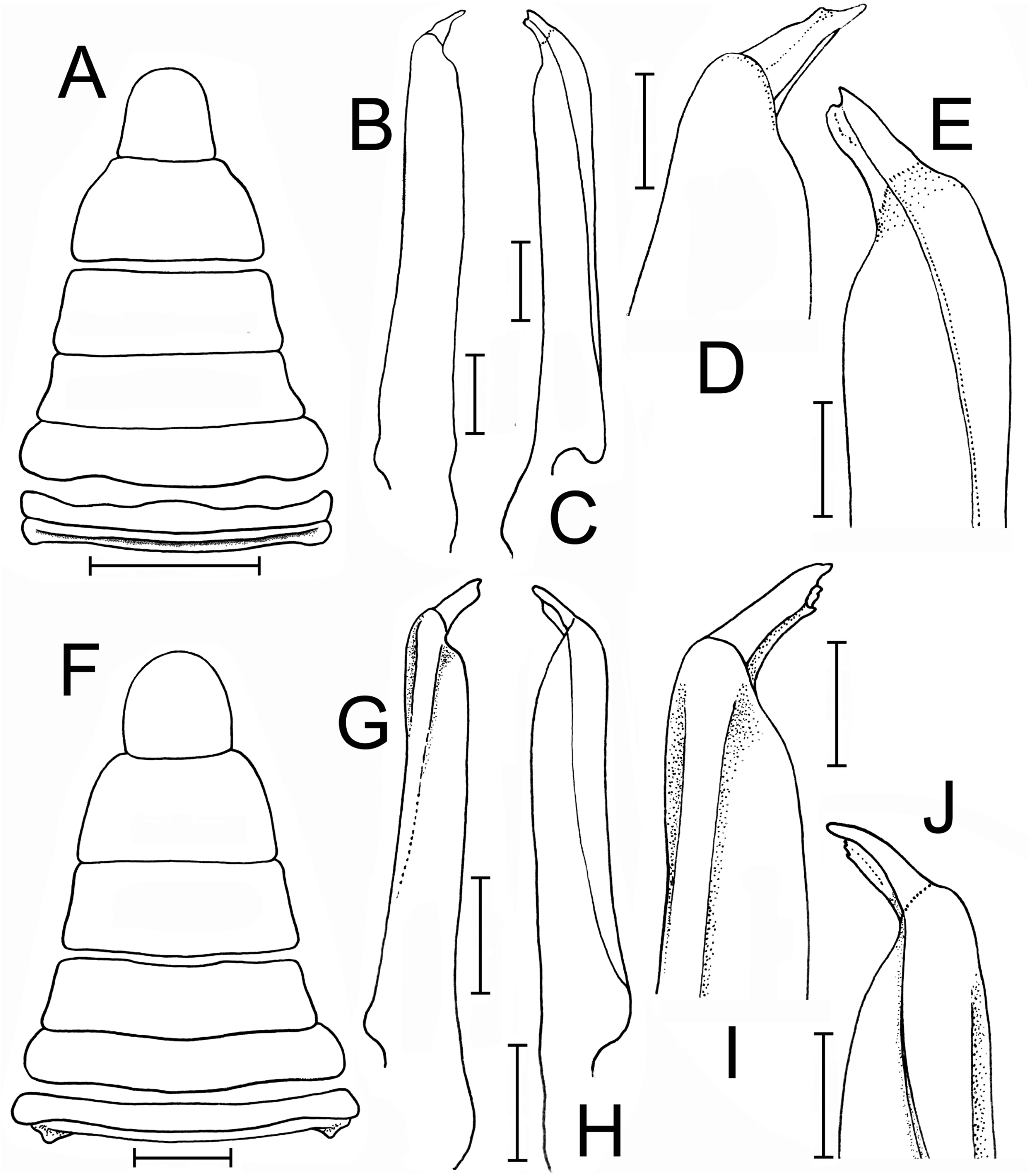

Fig. 41. A–E, *Manarma moeschii*, male (20.2 × 18.0 mm) (ZRC 2000.1926), Thailand; F–J, *M. johorense*, male (14.6 × 12.6 mm) (ZRC 1971.9.24.14), Seletar River, Singapore. A, F, male pleon; B, G, left G1 (ventral view, denuded); C, H, left G1 (dorsal view, denuded); D, I, left distal part of G1 (ventral view, denuded); E, J, left distal part of G1 (dorsal view, denuded). Scales: A = 5.0 mm; B, C, G, H = 1.0 mm; F = 2.0 mm; D, E, I, J = 0.5 mm.

14; Ng et al., 2008a: 222; Rademacher & Mengedoht, 2011: 30; Lim & Chua, 2015: 18; Ribero et al., 2020: 3.

**Material examined**. Neotype (here designated): male (24.5 × 21.5 mm) (ZRC 1995.225), peat swamp beginning of Ulu Assam trail, Bako National Park, Sarawak, Malaysia. coll. P.K.L. Ng & M. Lateef, 29 June 1994. SARAWAK – 3 males, 1 female (ZRC 1964.9.28.126–130), Stambak, Saribas, Sarawak, coll. L.K. Charles, 1950; 6 males, 2 females (ZRC 1964.9.28.131–139), Stambak, Saribas, coll. L.K. Charles, 1950; 1 male (26.3 × 23.0 mm) (ZRC 1995.226), peat swamp, beginning of Ulu Assam trail, Bako National Park, coll. P.K.L. Ng, 28 June 1994; 2 females (ZRC 2010.0063), Bako National Park trail, coll. rangers, May 2002. PENINSULAR MALAYSIA – 1 male (ZRC 1971.9.22.11), Kota Tinggi, Johor, Malaysia, coll. M.W.F. Tweedie, 1940; 5 males, 3 females (ZRC 1964.9.28.140–149), Kota Tinggi, Johor, coll. M.W.F. Tweedie, 1950; 16 males, 18 females (ZRC 1964.9.28.150–183), Kota Tinggi, Johor, coll. M.W.F. Tweedie, 1950; 4 males, 3 females (ZRC 1996.1724), Pulau Tioman, Sungei Ayer Besar, stream along beginning of Tekok Juara trail (Tekek side), coll. P.K.L. Ng et al., 29 June 1996; 1 male (ZRC 1999.890), Pulau Tioman, Juara tributary of Sungei Keliling, ca 500 m south after Sungei Keliling, coll. H.H. Tan, 18 June 1999; 3 males (ZRC 1999.611), Pulau Tioman, coll. P.K.L. Ng, 1996; 1 male (ZRC 1996.1726), Pulau Tioman, Kampung Genting, Sungei Ayer Raja, 2°45′36.7″N 104°07′21″E, coll. P.K.L. Ng et al., 15 September 1995; 3 females, 2 males (ZRC 2011.0924), stream from Tekek Bay, Pulau Tioman, coll. P.K.L. Ng, 23 June 1983; 7 males, 7 females (ZRC 1996.1725), Pulau Tioman, Sungei Keliling, coll. P.K.L. Ng, 27–28 June 1996; 1 male (ZRC 1998.850), Pulau Tioman, Sungei Keliling, coll. P.K.L. Ng et al., 26 June 1997; 1 male (ZRC 1998.851), Malaysia, Sungei Paya, Pulau Tioman, coll. P.K.L. Ng et al., 25 June 1997; 2 males, 1 female (ZRC 2019.1115), Sungei Paya, Tioman, Malaysia, coll. R. Diesel, 1995. SINGAPORE – 1 male (ZRC 1967.7.10.29), Sungei Seletar, coll. C.L. Soh, 15 January 1967; 1 female (ZRC 1967.7.10.33), Sungei Seletar, coll. C.L. Soh, 18 April 1968; 1 male (ZRC 1967.7.10.32), Sungei Seletar, coll. C.L. Soh, 31 December 1966; 1 male (ZRC 1967.7.10.28), Sungei China, coll. C.L. Soh, 15 January 1967; 1 male (ZRC 1967.7.10.30), Sungei Seletar, coll. C.L. Soh, 31 December 1966; 1 female (ZRC 1967.7.10.31), Sungei Seletar, coll. C.L. Soh, 21 March 1966; 1 male (ZRC 1973.11.2.492), Sungei Seletar, coll. C.L. Soh, 6 May 1966; 1 male (ZRC 2000.2018), Singapore, Pulau Ubin, caught dead, coll. C.D. Schubart, July 2000; 1 young female (ZRC), freshwater swamp, Belang, Pulau Tekong, Singapore, coll. K.K.P. Lim, 17 November 2012.

**Diagnosis**. Anterior dorsal carapace regions with scattered short black setae to almost glabrous; outer surface of adult chela covered with relatively smaller flattened granules, those on margins especially smaller, sharper; margins of ambulatory segments with scattered short setae; male pleon relatively transversely broader; G1 relatively more slender, chitinous distal part almost straight, proportionately more narrow.

**Colour**. In life, the carapace is dark purplish-black, with the posterior part sometimes lighter grey; lateral margins yellow to orange; outer surface of chela purple with orange to almost red fingers (Fig. 57B–H) (see also Rademacher & Mengedoht, 2011: 30).

**Remarks**. Targioni-Tozzetti (1877: 141) used the name "*Sesarma cheirogona*" for the species without any explanation of the etymology. The name is derived from the Greek Χειρός (cheira) for hand, and γωνία (gonía) for angle or joint; clearly alluding to the distinctive chela of the species. Targioni-Tozzetti (1877) probably did not intend to use the name as a noun as it should then have been spelled "*cheirogonia*". Like most workers during that time, the gender of the name *Sesarma* was regarded as a feminine, and as such, he probably used "*cheiragona*" to reflect this.

For differences with *C. bocourti*, see Remarks for that species.

**Biology**. Ng (1995: 202) summarises the following observations about its ecology (as *Pseudosesarma bocourti*): "In the ZRC is a large series of this species from freshwater swamps in Kota Tinggi, Johor which had been collected by the late Michael Tweedie. I have also obtained specimens from coastal peat swamps in Pekan (Pahang) and Sarawak. The present specimens agree very well with these specimens. They dig burrows in the peat substrate, often among roots and debris, and emerge only late at night to feed on dead leaves and other vegetable matter. The crabs are terrestrial in habits and have been obtained several hundred metres from the nearest water source. The habitat (a coastal peat swamp) where they were collected, the beginning of the Ulu Assam trail, is only about 300 metres from the sea".

**Distribution**. Sumatra, Borneo, Peninsular Malaysia, and Singapore.

### *Miersarma*, new genus

**Type species**. *Sesarma granosimana* Miers, 1880, by present designation. Gender neuter.

**Diagnosis**. Carapace squarish or just wider than long; frontal margin weakly bilobed, gently deflexed, wider than posterior carapace margin; lateral margins of carapace straight, unarmed, posterolateral part subparallel; regions of carapace demarcated; postfrontal and epigastric crests separated by distinct but relatively shallow grooves, margin relatively straight, regions separated; basal articles of antenna and antennules clearly separated by septum formed by extension of front; dorsal margin of palm without any longitudinal pectinated ridge; in adult males, inner surface with submedian transverse swelling, highest point with granules, outer surface of palm and pollex convex, outer surface of palm with squamose granules and striae, ventral margin with sharp granules, appears serrate, dorsal margin of chelipedal dactylus with small granules; inner distal margin of merus of cheliped not lamelliform; inner surfaces of first to third ambulatory coxae with scattered short setae between

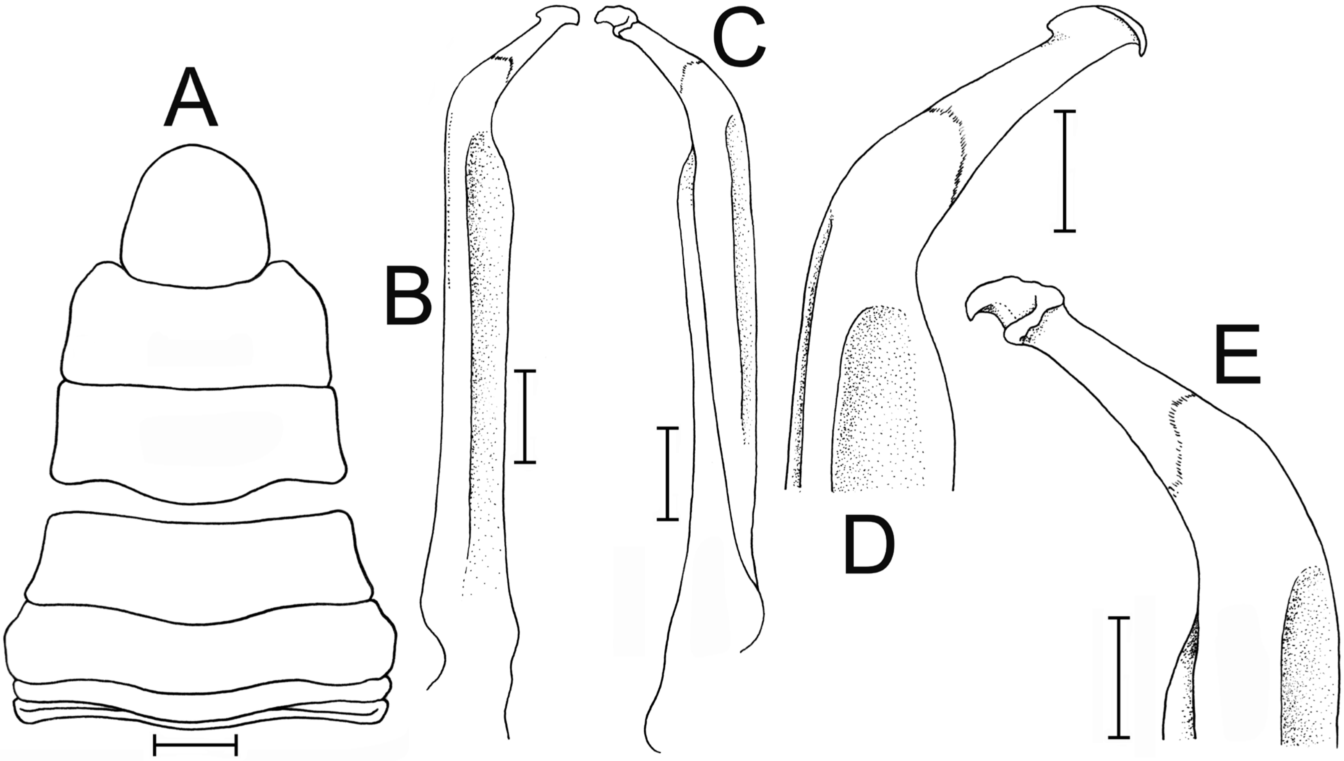

Fig. 42. A–E, *Bresedium laevimanum*, lectotype male (20.0 × 17.6 mm) (MNHG), Borneo. A, male pleon; B, left G1 (ventral view, denuded); C, left G1 (dorsal view, denuded); D, left distal part of G1 (ventral view, denuded); E, left distal part of G1 (dorsal view, denuded). Scales: A = 2.0 mm; B, C = 1.0 mm; D, E = 0.5 mm.

them, not arranged into dense tufts; male thoracic sternites 2–4 relatively narrow in adults, shallow suture between sternites 3 and 4 barely visible; male sternopleonal cavity reaching three-quarters length of sternite 4 to just before anterior margin of sternite 2; male thoracic sternite 5 smooth, without depression on anterior part; male sternopleonal cavity without trace of press-button on sternite 5, posterior edge of sternite 4 not expanded, no trace of obvious pleonal locking mechanism; G1 slender, straight, relatively long chitinous distal part bent at almost right angles. Vulva on anterior part of sternite 6, anterior edge presses against sternite 5; low and rim-like anterior and posterior sternal vulvar covers; opening low, rounded, not projecting.

**Etymology**. The genus name is derived from Edward J. Miers (1851–1930), who described the type species, in combination with the genus name *Sesarma*. The gender is neuter.

**Included species**. *Sesarma granosimana* Miers, 1880.

**Remarks**. Differences between this genus and *Pseudosesarma* s. str. have been discussed under that genus.

### *Miersarma granosimanum* (Miers, 1880)
(Figs. 24A, B, 25J, 29A, 31D, E, 32D, 40, 44I)

*Sesarma granosimana* Miers, 1880: 24, pl. 14 fig. 3; De Man, 1887: 644; Tweedie, 1940: 92; Tweedie, 1950: 343, fig. 2a.
*Sesarma* (*Sesarma*) *granosimana* – De Man, 1895: 143.
*Sesarma* (*Holometopus*) *granosimana* – Tesch, 1917: 155; Roux, 1933: 10; Serène, 1968: 107.
*Pseudosesarma granosimanum* – Ng et al., 2008a: 222.

**Material examined**. Lectotype (here designated): male (16.9 × 14.8 mm) (NHM 1880.6), Borneo, purchased by E. Gerrard from Dr. P. Bleeker collection. PENINSULAR MALAYSIA – 5 males, 8 females (ZRC 2002.0162), Malaysia, Johor, Muar, Tanjong Olak, Bukit Pasir, coll. Y.Y. Goh, 28 May 1998; 46 females, 33 males (ZRC 1973.11.2.191–268), near Sedili River, Johor, Sungei Kayu, swamp forest, coll. 1937; 7 males, 2 females (ZRC 1965.7.29.164–173), Sungei Kayu, swamp forest near Sedili River, Johor, coll. February 1937; 1 male (ZRC 1965.7.29.174), Sedili River, Johor, coll. October 1937; 2 males, 2 females (ZRC 1965.7.29.175–178), Kota Tinggi, Johor, no date. SARAWAK – 4 males, 2 females (ZRC 1965.7.29.179–184), Kuching, freshwater ditch, coll. M.W.F. Tweedie, December 1948.

**Diagnosis**. Carapace squarish; no epibranchial tooth present, lateral margin entire; posterolateral margins subparallel; outer surface of chela gently convex, covered with small squamiform granules, ventral margin of palm sinuous, serrated; suture between male thoracic sternites 3 and 4 undiscernible; male pleon broadly triangular; male sternopleonal cavity without press-button of pleonal locking mechanism on sternite 5; G1 slender, straight, relatively long chitinous distal part bent at almost right angles.

**Colour**. Not known.

**Remarks**. In *Miersarma granosimanum*, the entire surface of sternites 1–4 appears almost contiguous, without any trace of a ridge or suture. However, this surface is uneven and when dried, the separation between sternites 2 and 3 can just about be discerned.

The G1 is characteristically long and slender, with an elongate distal part. The G1 is somewhat twisted; viewed from one angle, it appears almost straight (e.g., Fig. 40B, C, J), but when slightly adjusted, it appears distinctly sinuous (Fig. 40F, G). In the lectotype male, the G1 is in poor condition and slightly shrivelled, the subdistal part of the G1 appears slightly damaged, with a small flange visible (Fig. 40D, E).

Roux' (1933) record of the species from Palembang in Sumatra cannot be confirmed. It is retained as a synonym of *M. granosimanum* until the specimens can be re-examined.

**Biology**. Tweedie (1940: 92) writes that he obtained a "good series from fresh-water swamp-forest near the river Sedili, Johor. A single specimen from among nipah palms beside the river Sedili, where the water is slightly saline". The more recent specimens from Muar (ZRC 2002.0162) were collected from behind a mangrove.

**Distribution**. Known from Peninsular Malaysia, Borneo, and Sumatra (Roux, 1933; Tweedie, 1940, 1950).

## ***Manarma*, new genus**

**Type species**. *Sesarma moeschii* De Man, 1892, by present designation. Gender neuter.

**Diagnosis**. Carapace transversely rectangular; frontal margin bilobed, gently deflexed, as wide as or slightly wider than posterior carapace margin; lateral margins of carapace with epibranchial tooth, posterolateral part subparallel; regions of carapace prominently demarcated; postfrontal and epigastric crests separated by relatively deep or distinct grooves, margin relatively rounded, regions clearly separated; basal articles of antenna and antennules clearly separated by septum formed by extension of front; dorsal margin of palm without longitudinal pectinated ridge; in adult males, inner surface with prominent submedian transverse swelling, highest point with transverse ridge of granules, outer surface of palm and pollex convex, outer surface of palm with short longitudinal median smooth ridge; dorsal margin of chelipedal dactylus almost smooth, if small granules present, scattered, never in distinct row or of regular shape; inner distal margin of merus of cheliped not lamelliform; inner surfaces of first to third ambulatory coxae with only scattered short setae among them, not arranged into dense tufts; male thoracic sternites 2–4 relatively narrow in adults, suture between sternites 3 and 4 shallow, sometimes appearing medially interrupted; male sternopleonal cavity reaching three-quarters length of sternite 4 to just before anterior margin of sternite 2; pleonal locking mechanism formed by low angular projection on posterior edge of sternite 4 of sternopleonal cavity, no trace of tubercle on sternite 5; male thoracic sternite 5 smooth, without depression on anterior part; G1 relatively slender, long, chitinous part relatively long. Vulva on anterior part of sternite 6, anterior edge presses against sternite 5; anterior sternal vulvar cover low, rim-like, posterior sternal vulvar cover slightly raised; opening low, tip flattened, uneven, not projecting.

**Etymology**. The name is derived by combining the name of the carcinologist Johannes Govertus de Man (1850–1930) with the genus name *Sesarma*. This honours the substantial contributions he has made to our knowledge of sesarmid diversity in the Indo-West Pacific. The gender is neuter.

**Included species**. *Sesarma moeschii* De Man, 1892; *Sesarma johorensis* Tweedie, 1940.

**Remarks**. *Pseudosesarma moeschii* (De Man, 1892) and *P. johorense* (Tweedie, 1940) differ markedly from other species of *Pseudosesarma* in having a carapace that is distinctly transversely rectangular, the regions on the dorsal surface are prominent and glossy, the outer surface of the adult male chela has a distinct longitudinal ridge with the inner surface possessing a strong transverse submedian granulated ridge, the male pleon is relatively narrow and the G1 is elongated and slender. In addition, adult male specimens of most *Pseudosesarma* species have a slight depression on the anterior part of thoracic sternite 5 in which the tip of the G1 rests when the pleon is closed (see Remarks for *Pseudosesarma*). This depression is absent in *P. moeschii* and *P. johorense*. It is also not discernible in members of the other genera studied here. The characters discussed are significant enough to warrant the removal of *P. moeschii* and *P. johorense* to their own new genus, *Manarma*. This decision is also well supported by the genetic data which shows these two species to be in their own deep clade basal to *Pseudosesarma*, *Bresedium*, and *Sesarmops* (Fig. 59). While *Manarma* superficially resembles *Orisarma*, new genus, in many of the above characters, it is nevertheless easy to distinguish them. The male pleon of species of *Manarma* is proportionately more slender and elongate (Fig. 33A, B) (versus proportionately broader in *Orisarma* species, e.g., Fig. 9C–H) and the ambulatory dactylus is relatively shorter (Fig. 33H) (versus distinctly longer in *Orisarma* species, e.g., Fig. 33F, G).

### ***Manarma moeschii* (De Man, 1892)**

(Figs. 24C, 26A, 29B, 33A, D, H, 41A–E, 44J, 58)

*Sesarma intermedia* – De Man, 1888: 182. [not *Grapsus* (*Pachysoma*) *intermedius* De Haan, 1835]

*Sesarma moeschii* De Man, 1892: 331, pl. 20 fig. 14; Tweedie, 1940: 92, fig. 3, pl. 24-1.

*Sesarma intermedium* – Alcock, 1900: 416. [not *Grapsus* (*Pachysoma*) *intermedius* De Haan, 1835]

*Sesarma* (*Sesarma*) *moeschii* – Tesch, 1917: 177.

*Sesarma* (*Sesarma*) *moeschi* – Serène, 1968: 105.

*Pseudosesarma moeschi* – Naiyanetr, 1998: 102; Naiyanetr, 2007: 116; Rademacher & Mengedoht, 2011: 28; Ribero, 2020: 3, 6.

"*Pseudosesarma*" *moeschi* – Ng et al., 2008a: 220.

*Pseudosesarma crassimanum* – Li et al., 2020: 3, 29–30. [not *Sesarma edwardsii* var. *crassimana* De Man, 1887: 649]

**Material examined**. BRUNEI – 1 male (13.6 × 12.2 mm) (ZRC 2016.0405), Sungei Belayang, coll. G. Polgar & L. Ribero, 15 October 2013. THAILAND – 8 males (largest 20.2 × 18.0 mm, smallest 15.8 × 14.5 mm), 2 females (17.5 × 15.4 mm, 15.9 × 14.3 mm) (ZRC 2000.1926), probably central Thailand, Thailand, purchased from Bangkok market,

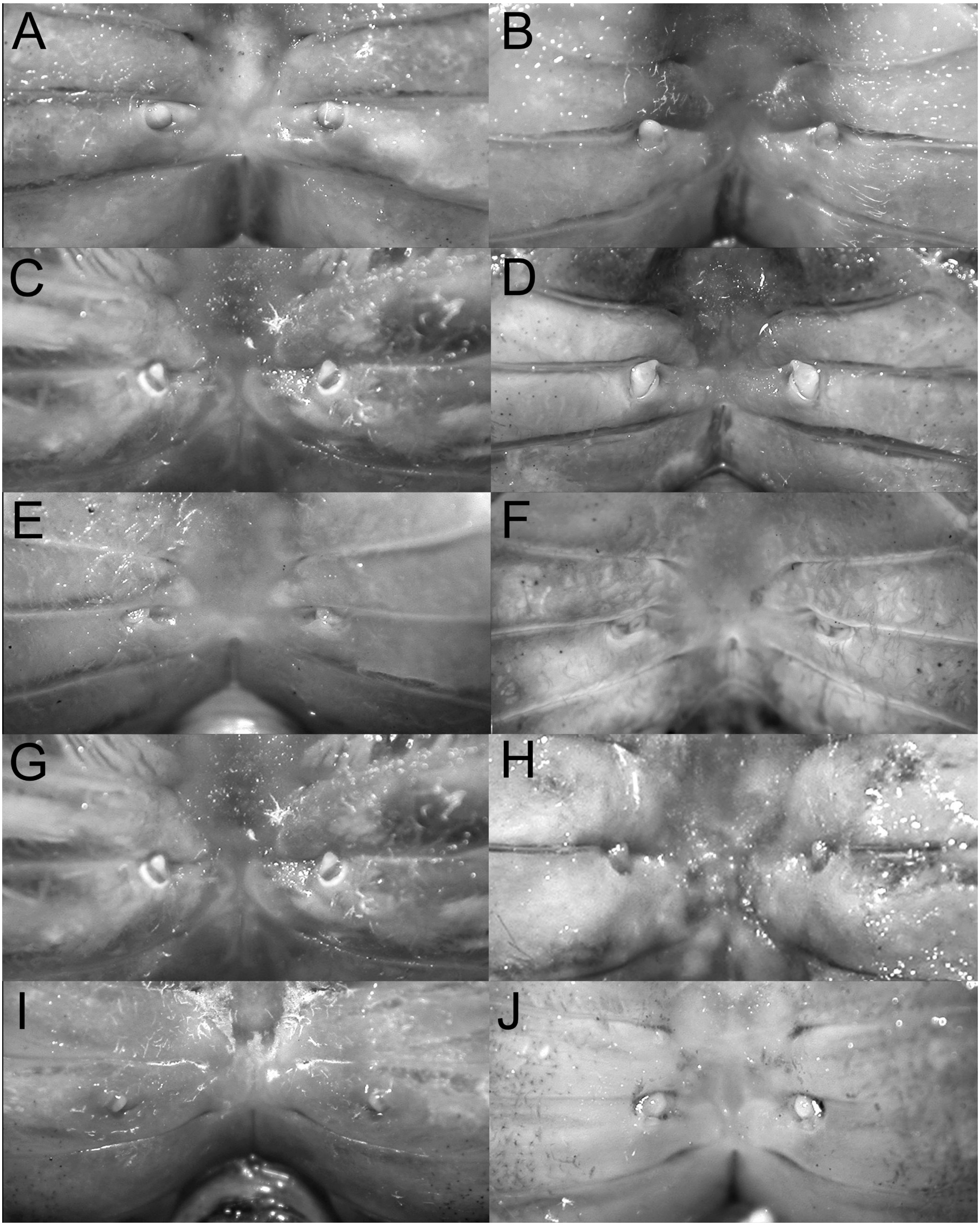

Fig. 43. Vulva. A, *Chiromantes haematocheir*, female (27.0 × 23.7 mm) (ZRC 2002.0225), Japan; B, *Orisarma dehaani*, female (20.4 × 17.8 mm) (ZRC 2012.0057), Japan; C, *Orisarma intermedium*, female (31.8 × 28.4 mm) (ZRC 2013.0140), Japan; D, *Orisarma patshuni*, female (20.5 × 18.1 mm) (ZRC 2014.0817), Hong Kong; E, *Danarma obtusifrons*, female (15.7 × 11.6 mm) (UF-FLMNH 14837), Hawaii; F, *Danarma eurymerus*, paratype ovigerous female (18.0 × 13.4 mm) (ZRC 2012.0956), Taiwan; G, *Cristarma eulimene*, female (15.6 × 12.8 mm) (ZRC 1968.1.22.3), Mozambique; H, *Cristarma ortmanni*, female (13.1 × 10.2 mm) (ZRC 2000.1783), Kenya; I, *Trapezarma angolense*, female (18.2 × 14.3 mm) (ZRC 2015.0297), Cameroon; J, *Platychirarma buettikoferi*, ovigerous female (11.3 × 9.1 mm) (ZRC 2015.0298), Cameroon.

coll. P.K.L. Ng & C.D. Schubart, 20 February 2000; 5 males (largest 19.7 × 17.1 mm), 2 females (larger 19.3 × 17.3 mm) (ZRC 2017.0170), Gulf of Thailand, coll. aquarium trade, April 2017.

**Diagnosis**. Dorsal surface of carapace relatively more swollen, regions prominent; fingers of cheliped relatively longer in adult males; male pleonal somite 6 relatively shorter, telson more triangular; distal chitinous part of G1 relatively straighter, more tapering. In life, carapace dark grey to almost black with a gentle marbling.

**Colour**. The carapace is dirty brown with scattered blotches and spots of light brown and grey, giving it a "marbled" appearance. The chelae are bright red (Rademacher & Mengedoht, 2011: 28).

**Remarks**. De Man (1892: 331) described *Sesarma moeschii* on the basis of two males (15.75 × 13.25 mm, 15.25 × 13.5 mm) from the Batak territories in Deli, northern Sumatra. The depository for this material is uncertain. Fortunately, the specimens on hand from Peninsular Malaysia and Thailand agree very well with the type description and excellent figures in De Man (1892: 331–333, pl. 20 fig. 14) and we have little doubt they are conspecific.

*Manarma moeschii* can be distinguished from *M. johorense* by the dorsal surface of the carapace being more swollen (Figs. 24C, 26A) (flatter and the regions relatively less prominent in *M. johorense* due to the shallow grooves, Figs. 24D, 26B); the fingers of the cheliped being relatively longer in adult males (Fig. 29B) (relatively shorter in *M. johorense*, Fig. 29C); male pleonal somite 6 being relatively shorter with the telson more triangular (Fig. 41A) (relatively longer with the telson more rounded in *M. johorense*, Fig. 41F); and the distal chitinous part of the G1 being relatively straighter and more tapering (Fig. 41B–E) (distally gently curved distally in *M. johorense*, Fig. 41G–J). Their live colours are also different, with the carapace of *M. moeschii* dark grey to almost black with a gentle marbling (Fig. 58C, D) whilst that of *M. johorense* is a uniform dark brown (Tweedie, 1940: 105). In addition, the chela is red in *M. moeschii* (Fig. 58B, E, G, H) but yellow in *M. johorensis* (cf. Tweedie, 1940: 105).

Tweedie (1940: 92) commented that the male pleon of his specimen from Peninsular Malaysia (Tweedie, 1940: fig. 3a) has a relatively more slender pleonal somite 6 compared to that from the Bay of Gorontalo in Sulawesi (Tweedie, 1940: fig. 3b). This was the same specimen reported by Tesch (1917). Tweedie, however, noted that the differences do not appear to be substantial.

**Biology**. Tweedie (1940: 92) commented that he had "one adult male from among nipah palms beside the river Sedili, Johore". Ribero et al. (2020: 6) found that the species was mainly associated with dense *Nipah* forests in Brunei. The species is, however, widely collected for the aquarium trade (see Rademacher & Mengedoht, 2011). One source is from the back mangroves of Chonburi in central Thailand in the Gulf of Thailand; and we have specimens from this area obtained by local collectors.

**Distribution**. Sumatra, Peninsular Malaysia, Thailand, and Sulawesi (De Man, 1892; Tesch, 1917; Tweedie, 1940; Naiyanetr, 1998, 2007).

### *Manarma johorense* (Tweedie, 1940)

(Figs. 24D, 26B, 29C, 33B, E, 41F–J)

*Sesarma johorensis* Tweedie, 1940: 103, fig. 9, pl. 24-3; Tweedie, 1950: 342.
*Sesarma* (*Sesarma*) *johorensis* – Serène, 1968: 105.
*Pseudosesarma johorense* – Tan & Ng, 1994: 82.
"*Pseudosesarma*" *johorense* – Ng et al., 2008a: 220.

**Material examined**. Paratypes: male (10.0 × 8.5 mm), 1 female (9.6 × 8.3 mm) (ZRC 1965.7.29.189–190), Pendas River, southern Johor, Peninsular Malaysia, coll. M.W.F. Tweedie, February 1937; 1 female (11.2 × 9.1 mm) (ZRC 1970.3.13.2), Pendas River, southern Johor, Peninsular Malaysia, coll. M.W.F. Tweedie, February 1937. Others: SINGAPORE – 1 male (14.6 × 12.6 mm) (ZRC 1971.9.24.14), Sungei Seletar, coll. C.L. Soh, 31 December 1966; 1 female (ZRC 1971.9.24.13), Simpang River, Mak Wai, Singapore, coll. C.L. Soh, 3 March 1966; 1 female (ZRC 1971.9.22.8), Simpang River, Mak Wai, coll. C.L. Soh, 20 December 1966; 1 female (ZRC 1973.11.2.496), Sungei Seletar, coll. 14 June 1967; 3 males (ZRC 1971.9.24.12), Sungei Seletar, coll. C.L. Soh, 31 December 1966; 1 juvenile (ZRC 1970.2.23.4), Sungei Seletar, coll. C.L. Soh, 31 December 1966; 1 female (ZRC 1970.2.23.1), Sungei Seletar, coll. C.L. Soh, 11 December 1966; 1 male (ZRC 1971.9.22.9), Sungei Seletar, coll. C.L. Soh, 31 December 1966; 1 female (ZRC 1971.9.24.11), Sungei Seletar, coll. C.L. Soh, 31 December 1966. PENINSULAR MALAYSIA – 1 female (ZRC 1965.7.29.57), Sedili River, Johor, March 1938. LABUAN – 4 males (ZRC 1965.7.29.185–188), coll. M.W.F. Tweedie, 1938. VIETNAM – 1 male (ZRC 1969.10.1.4), Cantho, coll. Nguyen Thi Lai, August 1969; 2 juveniles (ZRC 1970.2.23.2–3), Cantho, coll. Institute of Oceanography, Nhatrang, 1958.

**Diagnosis**. Dorsal surface of carapace relatively flatter, regions relatively less prominent; fingers of cheliped relatively shorter in adult males; male pleonal somite 6 relatively longer, telson more rounded; distal chitinous part of G1 gently curved distally. In life, carapace uniform dark brown.

**Colour**. According to Tweedie (1940: 105), the "colour of the carapace is very dark greenish brown and of the chelae, pale yellow".

**Remarks**. The differences between *M. johorensis* and *M. moeschii* have been discussed under the latter species.

**Biology**. The species lives in mangrove swamps near the main river (Tweedie, 1940: 103).

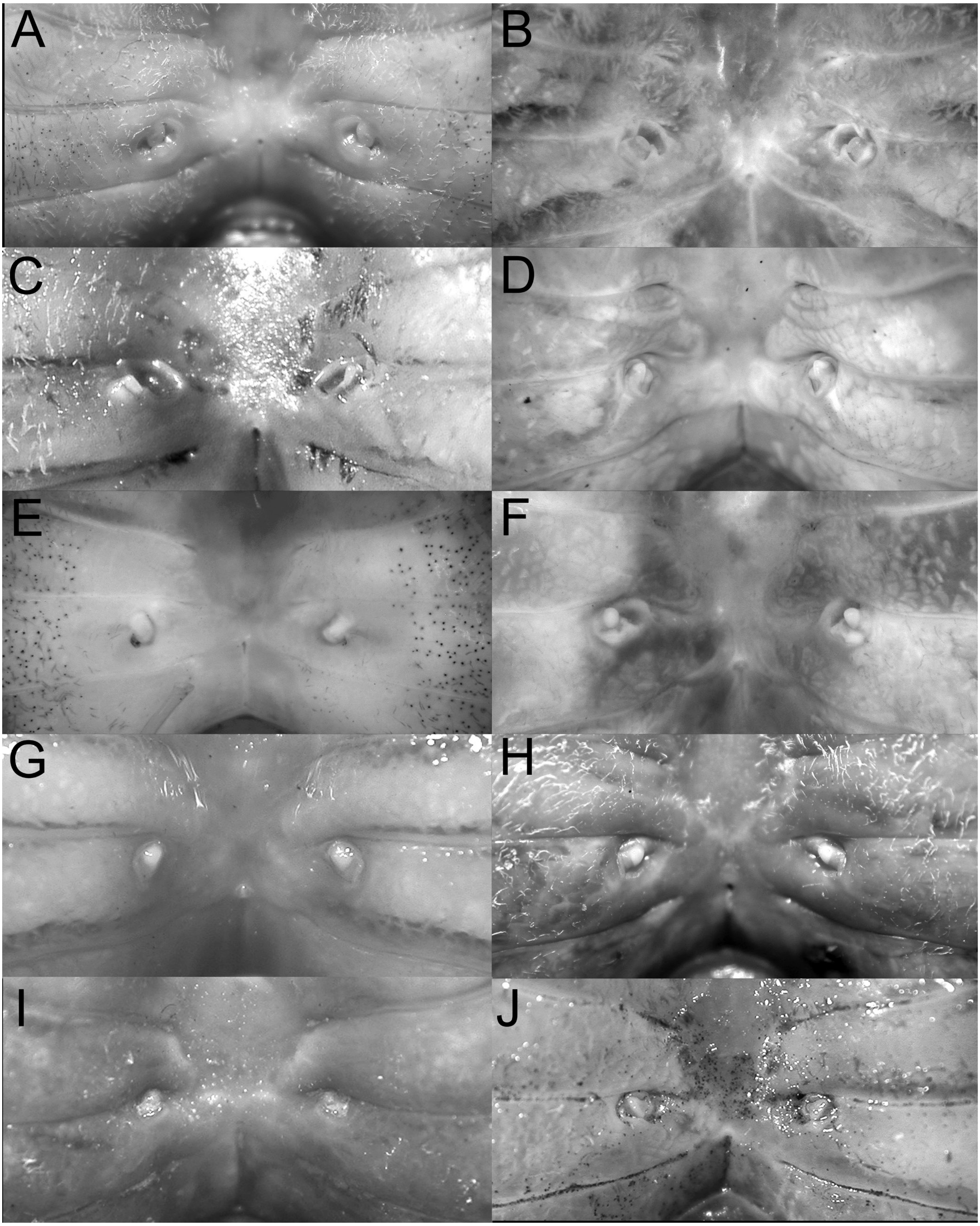

Fig. 44. Vulva. A, *Pseudosesarma edwardsii*, female (16.5 × 15.3 mm) (ZRC 2016.0608), Malaysia; B, *Pseudosesarma crassimanum*, female (15.9 × 13.8 mm) (ZRC 2000.1768), Malaysia; C, *Pseudosesarma crassimanum*, female (18.0 × 15.7 mm) (ZRC 2017.1045), Thailand; D, *Pseudosesarma anteactum*, paratype female (17.5 × 15.4 mm) (ZRC 2016.0603), Sri Lanka; E, *Pseudosesarma brehieri*, paratype female (14.9 × 13.4 mm) (ZRC 2016.0594), Myanmar; F, *Pseudosesarma boulengeri*, female (24.2 × 20.0 mm) (ZRC 2014.0335), Iran; G, *Contusarma bocourti*, female (21.1 × 19.0 mm) (ZRC 2019.1114), Thailand; H, *Contusarma cheirogonum*, female (26.6 × 23.0 mm) (ZRC 1964.9.28.127), Sarawak; I, *Miersarma granosimanum*, female (20.1 × 16.4 mm) (ZRC 1965.7.29.166), Malaysia; J, *Manarma moeschii*, female (19.3 × 17.3 mm) (ZRC 2017.0170), Thailand.

**Distribution**. Known only from southern Peninsular Malaysia, Sarawak, and Vietnam (Tweedie, 1940, 1950; present data).

### *Bresedium* Serène & Soh, 1970

**Type species**. *Sesarma edwardsii brevipes* De Man, 1889, by original designation. Gender neuter.

**Diagnosis**. Carapace transversely rectangular; frontal margin bilobed, gently deflexed, wider than posterior carapace margin; lateral margins of carapace with epibranchial tooth, posterolateral part subparallel; regions of carapace demarcated; postfrontal and epigastric crests separated by relatively deep or distinct grooves, margin rounded, regions clearly separated; basal articles of antenna and antennules clearly separated by septum formed by extension of front; dorsal margin of palm without longitudinal pectinated ridge; in adult males, inner surface with submedian transverse swelling, outer surface of palm and pollex convex, with low striae or flattened granules; dorsal margin of chelipedal dactylus almost smooth; inner distal margin of merus of cheliped not lamelliform; inner surfaces of first to third ambulatory coxae with scattered short setae, not arranged into dense tufts; male thoracic sternites 2–4 relatively narrow in adults, suture between sternites 3 and 4 shallow; male sternopleonal cavity reaching three-quarters length of sternite 4 to just before anterior margin of sternite 2; without trace of press-button on sternite 5, posterior edge of sternite 4 not expanded, no trace of obvious pleonal locking mechanism; male thoracic sternite 5 without depression on anterior part; G1 slighty stout to relatively slender, chitinous part elongate, tip dilated to some degree. Vulva on anterior part of sternite 6, anterior part presses against sternite 5; anterior sternal vulvar cover low, posterior sternal vulvar cover low; opening cylindrical, projecting with tip rounded, directed obliquely anteriorly.

**Included species**. *Sesarma edwardsii brevipes* De Man, 1889 (= *Sesarma* (*Sesarma*) *edwardsi philippinense* Rathbun, 1914); *Sesarma Edwardsi* var. *laevimana* Zehntner, 1894 (= *Sesarma sediliensis* Tweedie, 1940); *Bresedium eurypleon* Li, Shih & Ng, 2020.

**Remarks**. Three species are now recognised in *Bresedium* Serène & Soh, 1970: *B. brevipes* (De Man, 1889), *B. sediliense* (Tweedie, 1940), and *B. eurypleon* Li, Shih & Ng, 2019. *Bresedium sediliense* is the only one known from the Sunda Shelf, and its generic position is not certain, although it does have a characteristic male pleon which has the telson distinctly sunken into the distal margin of somite 6 and the tip of the distal chitinous part of the G1 flared. Li et al. (2020) revised the *Sesarmops* and *Bresedium* species from Taiwan, Philippines, and Sulawesi and commented on the problems with the two genera. They showed that *B. philippinense* is a junior subjective synonym of *B. brevipes*; recognised a new species, *B. eurypleon*, with a diagnostic G1 structure with an elongate distal chitinous part; described a new species of *Sesarmops* (*S. mora*); and redescribed *Sesarmops mindanaoensis* s. str.

Serène & Soh (1970) noted that both *Sesarmops* and *Bresedium* were related in having the male telson sunken into the distal margin of somite 6. They separated *Sesarmops* as having a more trapezoidal carapace versus a rectangular carapace for *Bresedium*. Ongoing studies now show that neither the carapace shape, nor the male telson are reliable characters at the generic level. Both genera are very close, and some species now placed in these genera do not possess the distinctive telson-somite 6 feature. There are also several kinds of G1 structures present, and it is clear that a full revision of both genera will be needed. This is beyond the scope of the present paper and will have to be undertaken at a future time.

For the present work, only one species is treated as it had been placed in *Pseudosesarma* previously—*Sesarma edwardsi* var. *laevimana* Zehntner, 1894—and we find that it is actually a senior subjective synonym of *Bresedium sediliense* (Tweedie, 1940). Specimens from Lorentz River in New Guinea which have been identified as "*Sesarma laevimana*" in NMBA are here identified as a new species of *Migmarma*, *M. lorentzi* (see later). The placement of *B. sediliense* in *Bresedium* as presently diagnosed is mainly because of the male telson being prominently sunken into the distal margin of somite 6 and the G1 having the distal chitinous part elongate. In the phylogenetic tree (Fig. 59), *B. sediliense* is not part of but adjacent to the main clade of *Bresedium* and *Sesarmops*, although the bootstrap support is not considered strong enough to be definitive.

### *Bresedium laevimanum* (Zehntner, 1894)

(Figs. 24E–H, 26C, D, 29D–F, 31F–H, 42)

*Sesarma Edwardsi* var. *laevimana* Zehntner, 1894: 181, 182.
*Sesarma edwardsi* var. *laevimana* – Lanchester, 1900: 757.
*Sesarma* (*Sesarma*) *edwardsi laevimana* – Tesch, 1917: 148.
*Sesarma sediliensis* Tweedie, 1940: 100, fig. 8, pl. 24-2; Tweedie, 1950: 342.
*Sesarma* (*Sesarma*) *edwarsi laevimanum* – Tan & Ng, 1994: 82; Serène, 1968: 105.
*Pseudosesarma laevimanum* – Ng et al., 2008a: 222.
*Pseudosesarma laevimana* – ?Naiyanetr, 1998: 102; ?Naiyanetr, 2007: 116.
*Bresedium sediliensis* – Ng & Tan, 1994: 82.
*Bresedium sedilensis* [sic] – Ng et al., 2008a: 220.

**Material examined**. Lectotype (here designated): male (20.0 × 17.6 mm) (MNHG), coll. "Indes Neerlandische", Bedot & Pichet, 1800s. Paralectotypes: 2 males (16.7 × 15.3 mm, 10.5 × 9.3 mm), 2 females (10.4 × 9.3 mm, 6.8 × 5.8 mm) (MNHG), Sarawak, coll. Bedot & Pichet, 1800s. Others: PENINSULAR MALAYSIA – 1 male (26.3 × 23.7 mm) (NHM) (lectotype of *Sesarma sediliensis* Tweedie, 1940, here designated), Sedili River, Johor, coll. M.W.F. Tweedie, March 1938; 1 female (22.8 × 19.7 mm) (NHM) (paralectotype of *Sesarma sediliensis* Tweedie, 1940), Sedili River, Johor, coll. M.W.F. Tweedie, March 1938; 37 males (largest 21.2 × 18.2 mm), 22 females (largest 20.3 × 17.8 mm) (ZRC 1965.7.29.121–133), Sedili River, Johor, coll. M.W.F. Tweedie, March 1938. SARAWAK – 19 males (largest 20.1 × 17.9 mm), 17 females (largest 19.2 × 16.7 mm, 2 ovigerous) (ZRC 1972.3.7.25–35), water ditch, Kuching, coll. M.W.F. Tweedie, January 1949.

**Diagnosis**. Carapace transversely rectangular; epibranchial tooth distinct, separated by deep notch; posterolateral margins subparallel; outer surface of chela relatively smooth, punctate, or with scattered low granules, ventral margin of palm sinuous, smooth; suture between male thoracic sternites 3 and 4 visible; ambulatory merus short, broad; male pleon somewhat elongate, subrectangular, telson distinctly sunken into distal margin of somite 6; G1 very slender, straight, chitinous distal part long, with tip prominently flared.

**Colour**. "In life the chelipeds are bright red and the carapace dark brown, more or less variegated with greenish." (Tweedie, 1940: 102).

**Remarks**. The identity of this species has been uncertain since its original description as no figures were provided. Zehntner (1894) regarded it as a variety of *Sesarma edwardsii*, and most subsequent workers have followed this association. Comparison of the types of *Sesarma edwardsi* var. *laevimana* from the Muséum national d'Histoire naturelle, Geneva, with type material of *Sesarma sediliensis*, leave no doubt that Zehntner's (1894) variety is identical with *Bresedium sediliensis* (Tweedie, 1940). The broadly rectangular carapace (Figs. 24E–H), subrectangular male pleon with the telson sunken into somite 6 (Figs. 31F–H, 42A) and the characteristic G1 with the tip expanded (Fig. 42B–E) are typical for members of this genus. *Sesarma sediliensis* Tweedie, 1940, was transferred to *Bresedium* by Serène & Soh (1970).

Tweedie (1940: 100–103, fig. 8, pl. 24-2) described *Sesarma sediliensis* from one male and one female which he labelled as cotypes and "a series of sub-adult specimens from the type locality". The way this sentence is phrased means he only regarded the male and female specimens mentioned (both of which are now in NHM) as syntypes, and the rest are not types. The male (26.3 × 23.7 mm) is here designated as the lectotype of the species to stabilise the taxonomy. In the ZRC are two lots, ZRC 1965.7.29.121–133 (from Johor) and ZRC 1972.3.7.25–35 (from Sarawak), both of which are listed as paratypes. They are therefore not types, even though the Johor material was collected at the same time by Tweedie as the syntypes. The Johor lot (ZRC 1965.7.29.121–133), however, are not sub-adults, with most of the specimens large and fully adult, even though none of the females are ovigerous.

**Biology**. According to Tweedie (1940: 103), "These crabs were found among the stems of nipah palms (*Nipah fruticans*) growing in mud on the banks of the river Sedili. The water in the part of the river where the palms grow is slightly brackish with incursions of fresh water when the river floods. Its salinity never approaches that of the open sea."

**Distribution**. Known from Southern Peninsular Malaysia and Sarawak, and perhaps Thailand (Tweedie, 1940, 1950; Naiyanetr, 1998, 2007).

## *Migmarma*, new genus

**Type species**. *Sesarma* (*Sesarma*) *modesta* De Man, 1902, by present designation. Gender neuter.

**Diagnosis**. Carapace squarish to trapezoidal, wider than long; frontal margin weakly bilobed, gently deflexed, wider than posterior carapace margin; lateral margins of carapace with one tooth, posterolateral part subparallel or gently diverging; regions of carapace demarcated; postfrontal and epigastric crests separated by relatively deep grooves, margin relatively distinct, regions clearly separated; basal articles of antenna and antennules separated by septum; dorsal margin of palm without longitudinal pectinated ridge, inner surface gently convex, without prominent granulated ridge, outer surface and pollex gently convex or almost flat, covered with small granules; dorsal margin of chelipedal dactylus smooth in adult males or lined with small granules of various sizes; inner distal margin of merus of cheliped not lamelliform; inner surfaces of first to third ambulatory coxae with only scattered short setae between them, not arranged into tufts; male thoracic sternites 2–4 relatively narrow in adults, suture between sternites 3 and 4 shallow but visible; male sternopleonal cavity reaching two-thirds length of sternite 4 to before anterior margin of sternite 2; without trace of press-button on sternite 5, posterior edge of sternite 4 not expanded, no trace of obvious pleonal locking mechanism; G1 stout to relatively slender, subdistal part slightly swollen or subequal to width of base; chitinous part short to relatively long. Vulva is on anterior part of sternite 6, anterior edge presses against sternite 5; anterior sternal vulvar cover very low, posterior sternal vulvar cover low, rim-like; opening cylindrical, projecting, tip rounded, directed obliquely anteriorly.

**Etymology**. The name is derived from the Latin "migma" for mixture, with the ending of the genus name *Sesarma*. This alludes to the mix of characters present in the type species. The gender is neuter.

**Included species**. *Sesarma* (*Sesarma*) *modesta* De Man, 1902; *Migmarma lustrum*, new species; *Migmarma lorentzi*, new species.

**Remarks**. *Migmarma*, new genus, is established for three species with a mix of characters that make their assignment to *Pseudosesarma* or *Bresedium* difficult; but which are nevertheless genetically related (Fig. 59). The carapaces of *M. modestum* and *M. lustrum*, new species, are similar, being trapezoidal but clearly much wider than long (Figs. 45B, 47B); while that of *M. lorentzi*, new species, is distinctly quadrate (Fig. 50B). Their male pleons are triangular but the telson is normal in *M. modestum* and *M. lustrum* (Figs. 45D, 46B, 47H), but slightly sunken into somite 6 in *M. lorentzi* (Fig. 50E). Their G1s are relatively stout to more slender with the chitinous distal part relatively short or more elongate (Figs. 46C, D, 49A, B, 51A, B). None of them can be placed in *Pseudosesarma* as defined at present as the G1 is not sufficiently stout and the inner surface of sternite 5 of the sternopleonal cavity does not have a depression for the G1 (Figs. 45E, 48A, B). In *B. brevipes* and *B. laevimanum*, the male telson is prominently sunken into the distal margin of somite 6 (see Li, 2014: fig. 1B; unpublished data), distinct from the condition in *M. lorentzi* which is only slightly so (Fig. 50E) and not at all apparent in *M. modestum* and *M. lustrum* (Figs. 45D, 46B, 47H). In any case, the G1 of species in *Bresedium* s. str. are either stout with the chitinous distal process very long and straight, or the G1 is more slender with the distal process long and the tip dilated (Fig. 42B–E; Li, 2014: fig. 2A, B). Like *Pseudosesarma*, the inner surface of sternite 5 of the sternopleonal cavity in *Bresedium* species also do not have a depression for the G1.

### ***Migmarma modestum* (De Man, 1902)**

(Figs. 45, 46)

*Sesarma* (*Sesarma*) *modesta* De Man, 1902: 511, pl. 19 fig. 8; Tesch, 1917: 175; Roux, 1917: 619.
*Sesarma* (*Sesarma*) *modestum* – Serène, 1968: 105.
*Pseudosesarma modestum* – Serène & Soh, 1970: 400; Ng et al., 2008a: 222.

**Material examined**. Holotype: male (25.0 × 20.9 mm) (SMF 1989), Ternate, Moluccas, Indonesia, coll. W. Kükenthal, 26 December 1893–11 June 1894.

**Diagnosis**. Carapace trapezoidal, wider than long; dorsal carapace surface uneven but not setose; epibranchial tooth distinct, separated by deep notch; posterolateral margins slightly divergent; outer surface of chela covered with rounded granules, those on margins relatively larger, outer surface almost flat, ventral margin of palm almost straight; suture between male thoracic sternites 3 and 4 distinct; ambulatory merus short, broad; male pleon triangular, telson relatively elongate, not sunken into distal margin of somite 6; male pleonal somite 6 relatively broader; G1 relatively stout, almost straight, chitinous distal part relatively short, stout, tip subtruncate.

**Remarks**. The identity of this species has long been uncertain. Serène & Soh (1970) referred it to *Pseudosesarma* where it has remained since, and the type has never been redescribed or refigured. Roux (1917) identified a female specimen from New Guinea to this species, but this cannot be confirmed until it can be re-examined. It is also possible that his specimen belongs to *M. lustrum*, new species, which is close to *M. modestum* but differs markedly in the form of the G1 (see next species).

### ***Migmarma lustrum*, new species**

(Figs. 47–49)

**Material examined**. Holotype: male (15.7 × 13.9 mm) (ZRC 2010.0021), in base of leaf of sago palm (*Metroxylon sagu*), inland sago swamp, moist secondary lowland forest, village of Lilinta, Misool Barat, Raja Ampat Province, Irian Jaya, Indonesia, D. Telmov & K. Cureke, 1 April 2009.

**Diagnosis**. Carapace somewhat trapezoidal; dorsal carapace surface uneven but not setose; epibranchial tooth distinct, separated by deep notch; posterolateral margins slightly divergent; outer surface of chela covered with small granules, those on margins relatively sharper, outer surface gently convex, not flat, ventral margin of palm concave; suture between male thoracic sternites 3 and 4 distinct; ambulatory merus short, broad; male pleon triangular, telson relatively elongate, not sunken into distal margin of somite 6; male pleonal somite 6 broad; G1 slender, gently curved, chitinous distal part long, relatively slender, subspatuliform, tip subtruncate.

**Etymology**. The name is derived from the Latin word for swamp or bog, "lustrum". The name is used as a noun in apposition.

**Remarks**. *Migmarma lustrum*, new species, is morphologically similar to *M. modestum* except that the ventral margin of the cheliped palm is gently concave and the outer surface is not flat (Fig. 47E, F) (versus ventral margin almost straight and the outer surface flat in *B. modestum*; Fig. 45F); the male pleonal somite 6 is less broad (Fig. 47G, H) (versus proportionately broader in *B. modestum*; Figs. 45D, 46B); and most significantly, the G1 is more slender with the chitinous distal part distinctly more elongate (Figs. 48C–G, 49A–E) (versus G1 stouter with the chitinous distal part short and stout in *B. modestum*; Figs. 45G–K, 46C–H).

### ***Migmarma lorentzi*, new species**

(Figs. 50–52)

**Material examined**. Holotype: male (15.8 × 14.0 mm) (NMBA 625IIa), Noord River (= present day Lorentz River), New Guinea, ca. 4°15′S 138°40′E, coll. Lorentz Expedition 1909 (donated Zoological Museum Amsterdam, 1920). Paratype: 1 female (13.4 × 11.8 mm) (NMBA 625IIa), same data as holotype.

**Diagnosis**. Carapace squarish, slightly longer than wide; dorsal carapace surface smooth, glabrous; epibranchial tooth distinct, separated by deep notch; posterolateral margins subparallel; outer surface of chela gently rugose, smooth flattened granules, outer surface gently convex, not flat, ventral margin of palm gently concave; suture between male thoracic sternites 3 and 4 distinct; ambulatory merus short, broad; male pleon subrectangular, telson rounded, slightly sunken into distal margin of somite 6; G1 slender, gently curved, chitinous distal part long, tapering, relatively slender, subspatuliform, tip appears bifurcated.

**Etymology**. The species is named after Hendrikus Albertus Lorentz, the Dutch explorer for whom its type locality river is also named.

**Remarks**. In having the male telson only slightly sunken into somite 6, *Migmarma lorentzi*, new species, superficially

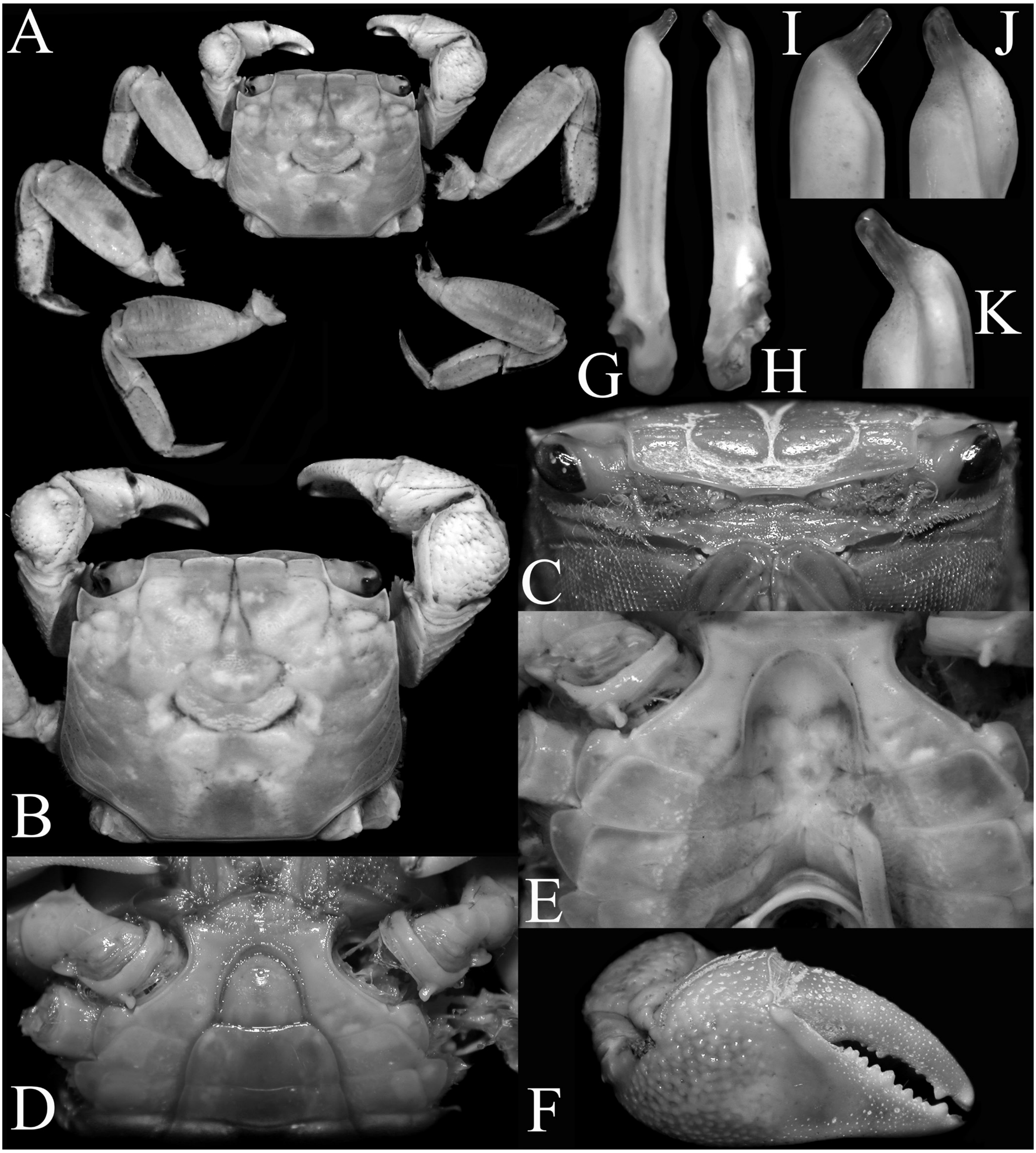

Fig. 45. *Migmarma modestum*, holotype male (25.0 × 20.9 mm) (SMF 1989), Indonesia. A, overall habitus; B, dorsal view of carapace; C, frontal view of cephalothorax; D, anterior thoracic sternum and pleon; E, sternopleonal cavity; F, outer view of right chela; G, H, left G1; I–K, distal part of left G1.

resembles species of *Bresedium*, notably *B. laevimanum*, but can easily be separated by the male telson being rounded and the pleonal somite 6 less broad (Fig. 50E) (versus telson more elongate and somite 6 is wider and more rectangular in shape in *B. laevimanum*; Figs. 31F–H, 42A); and the G1 is also proportionately stouter and the tip of the chitinous distal part is tapering and sharp (Figs. 50F–K, 51A–E) (versus G1 proportionately more slender and the tip of the chitinous distal part is flared in *B. laevimanum*; Fig. 42B–E).

## MOLECULAR PHYLOGENETICS

The obtained phylogenetic tree is based on an alignment with 1,096 bp of mitochondrial DNA that in living cells is transcribed to three contiguous genes with very different functions, and thus different molecular characteristics and degree of potential variability. The longest section with 706 bp corresponds to the 5' end of the commonly used gene 16S rRNA (16S), which is transcribed to the ribosomal

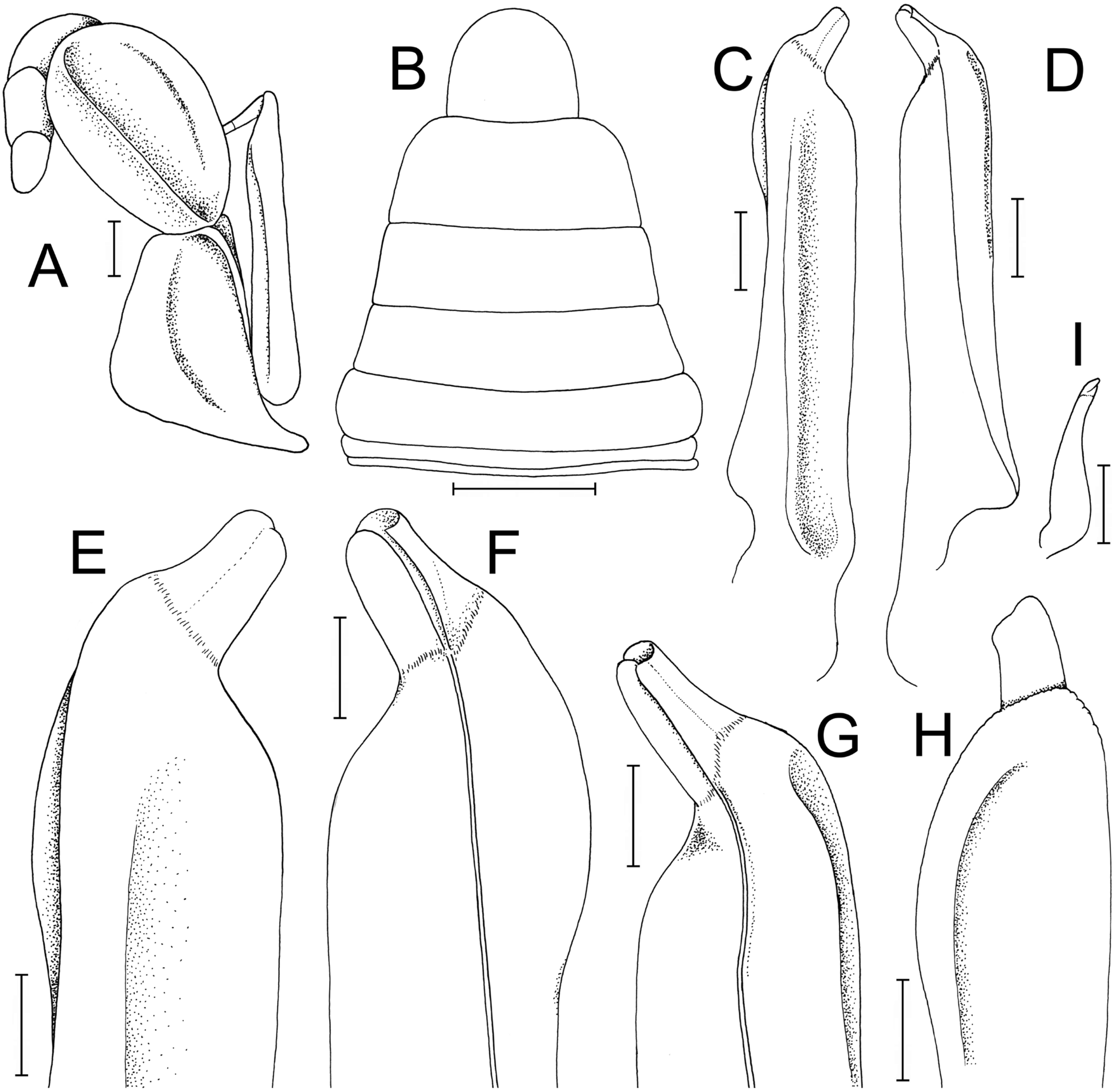

Fig. 46. *Migmarma modestum*, holotype male (25.0 × 20.9 mm) (SMF 1989), Indonesia. A, left third maxilliped (denuded); B, pleon; C, left G1 (ventral view); D, left G1 (dorsal view); E, distal part of left G1 (ventral view); F, distal part of left G1 (mesial view); G, distal part of left G1 (dorsal view); H, distal part of left G1 (mesial view); I, left G2. Scales: A, C, D, I = 1.0 mm; B = 5.0 mm; E–H = 0.5 mm.

RNA of the large subunit of mitochondrial ribosomes. It is thus not a protein-coding gene. However, it does play an active and important role for the independent biosynthesis and DNA-translation in the mitochondrial organelles, by determining and conserving the shape of the ribosomes with the skeletal function of the folded rRNA in its secondary structure. Furthermore, it supplies the active binding sites for tRNAs and nucleotides during the process of mRNA translation into amino acid sequences and proteins. The consequent advantages of this gene as a phylogenetic marker have already been emphasised in a review by Schubart et al. (2000b). Variable regions in the loops of the secondary structure alternate with highly conserved DNA regions in the stem regions. The latter ones are important to recover phylogenetic signals in the older splits of the tree. Next to the 5' end of the 16S is a relatively small gene of up to 80 bp (or 110 including flanking regions), which corresponds to the tRNA of the amino acid leucine (tRNA-Leu). It is relatively conserved, but its evolution allows for insertions and/or deletions (indels), thus gaining some variability. The third gene in this complex is the NADH dehydrogenase subunit 1 (ND1), of which 423 bp of the 5' end constitute the protein-coding DNA section of this analysed region. As the third position of the DNA triplet in protein-coding genes can often mutate without resulting in an amino acid change (silent mutations), mitochondrial protein-coding genes tend to be quite variable and are often used for intraspecific genetic comparisons. However, when comparing taxa that have been separated by extended evolutionary time intervals (several million years), the phylogenetic signal of these

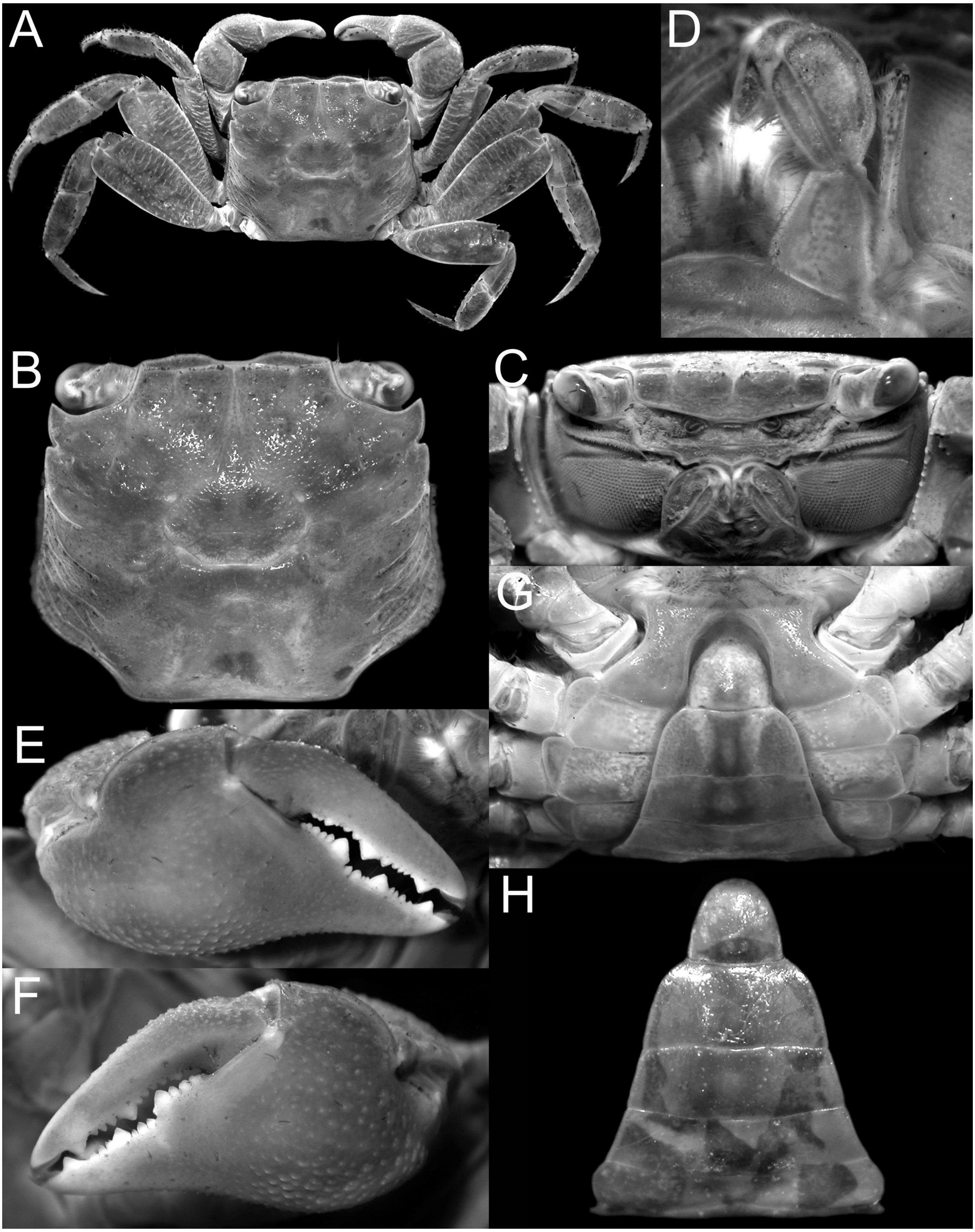

Fig. 47. *Migmarma lustrum*, new species, holotype male (15.7 × 13.9 mm) (ZRC 2010.0021), Irian Jaya, Indonesia. A, overall habitus; B, dorsal view of carapace; C, frontal view of cephalothorax; D, left third maxilliped; E, outer view of right chela; F, outer view of left chela; G, anterior thoracic sternum and pleon; H, pleon.

Fig. 48. *Migmarma lustrum*, new species, holotype male (15.7 × 13.9 mm) (ZRC 2010.0021), Irian Jaya, Indonesia. A, thoracic sternites 1–4; B, sternopleonal cavity; C, frontal view of cephalothorax; D, outer view of right chela; E, anterior thoracic sternum and pleon; C, D, left G1; E–G, distal part of left G1.

third positions is saturated, and it is often better to remove them from the analyses. This was done in the present case, resulting in the omission of 141 nucleotides corresponding to third positions of the ND1 gene.

The treatment of these three genes as a combined molecular marker, resulted in GTR+I+G as the best fitting model to reconstruct the evolution of the complete dataset, as well as for the resulting partitions, if each of the genes were tested separately with jModelTest. This substitution model was then used for running a Bayesian phylogenetic analysis with MrBayes v.3.2.7 and 4 million generations, leading to a total of 4,000 trees. After removing a burn-in of 25%, 3,000 trees were used to calculate the maximum clade credibility tree with FigTree v.1.3.1, a midpoint rooting topology, and *Parasesarma plicatum* as outgroup.

The resulting phylogenetic tree is shown in Fig. 59 and depicts the complex relationships within this very diverse and relatively young group of coastal crab genera and species. Support values for the different nodes are expressed as posterior probabilities (pp), shown to the left of the corresponding node. After applying a midpoint rooting to the phylogenetic tree, the four included species of *Parasesarma* cluster together with maximal support (pp = 1), so that all the other species included are likewise recovered as a clean monophylum (pp = 1). Within this monophylum, *Tiomanium indicum* (H. Milne Edwards, 1837) holds a basal position, whereas the next taxon to split off already represents a species that used to be a member of the genus *Chiromantes*, i.e., *Stelgistra stormi*, emphasising even more the monophyletic character (pp = 1) of all other analysed taxa. Also, the following steps of diversification can be described as dichotomous bifurcation events, in which always one or two of the newly defined genera (formerly belonging to *Chiromantes*) separate from the remaining taxa. These separations occur in the order: 1. the new genus *Danarma* (pp = 1); 2. the two West African species (pp = 1) that remained

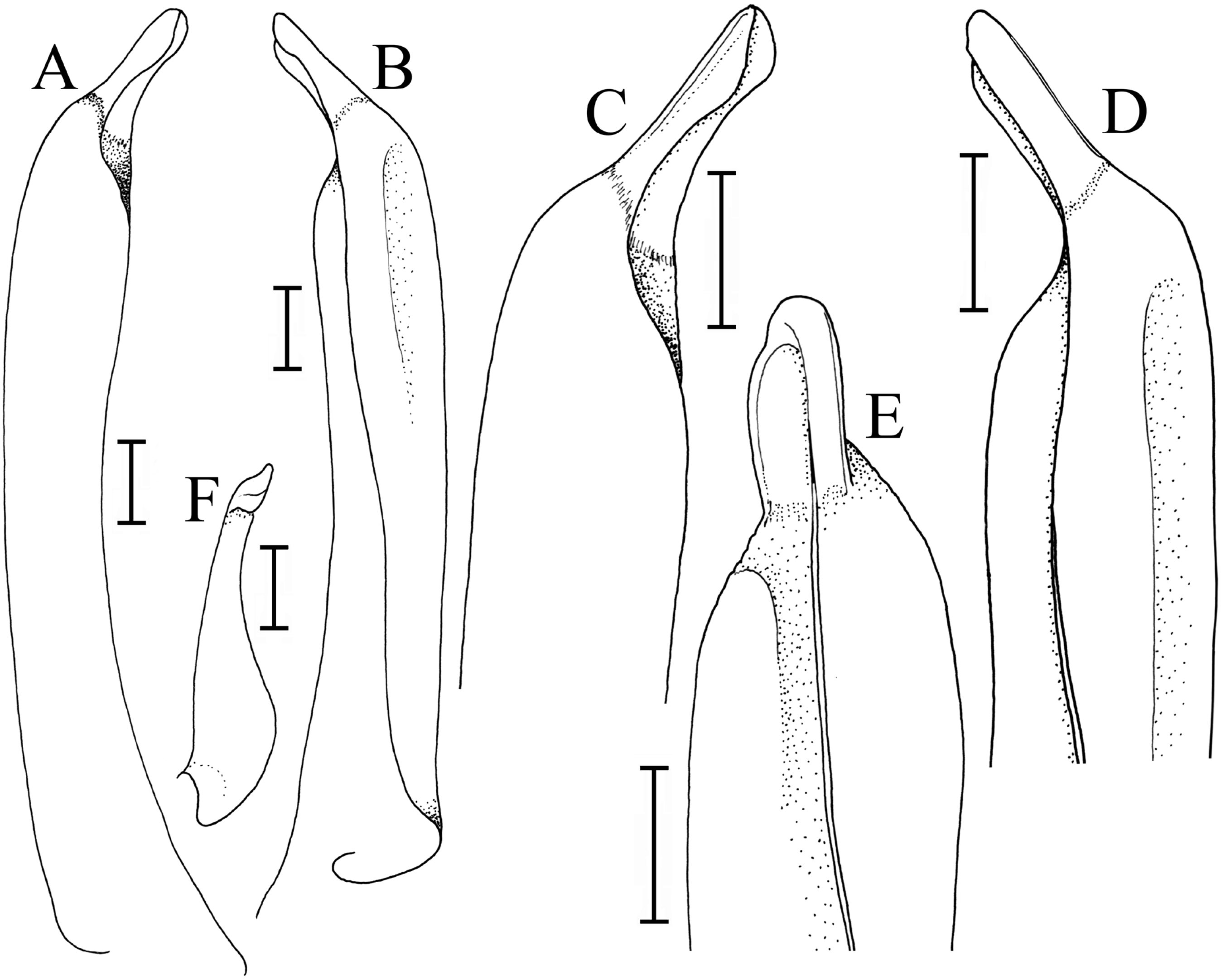

Fig. 49. *Migmarma lustrum*, new species, holotype male (15.7 × 13.9 mm) (ZRC 2010.0021), Irian Jaya, Indonesia. A, left G1 (ventral view); B, left G1 (dorsal view); C, distal part of left G1 (ventral view); D, distal part of left G1 (dorsal view); E, distal part of left G1 (mesial view); F, left G2. Scales = 0.5 mm.

in *Chiromantes* after Abele (1992) moved *C. elegans* to the genus *Armases*, and are now placed in their own monotypic new genera, *Platychirarma* and *Trapezarma*; 3. the new genus *Cristarma* (pp = 1) containing the two former members of *Chiromantes* from East Africa. The separation of the latter genus has a lower support (pp = 0.51), but the following monophyletic groups are strongly supported again (pp = 1).

Within the next clade, there is an early split of an interesting monophyletic assemblage (pp = 0.99) consisting of *Sinosesarma tangi* (included in *Chiromantes* until 2003) and a representative of the terrestrial genus *Geosesarma*, i.e., *G. hednon*. The remaining main cluster (pp = 0.95) includes all the species that are more closely related to the type species of *Chiromantes*, *Pseudosesarma*, *Bresedium*, and *Sesarmops*, within which a small cluster (pp = 1) includes the type of *Chiromantes*, *C. haematocheir*, together with two other species (of which one has been synonymised). These are the only remaining representatives of this formerly large genus. The GenBank sequence NC_047209 labelled as '*Chiromantes eulimene*' (Zhang et al., 2020) within this clade must be due to an erroneous identification or a mixup of samples in the laboratory.

After the split of two species of *Scandarma* (pp = 1), the next highly supported monophyletic assemblage (pp = 0.93) consists of two branches, of which the first one (pp = 0.88) includes six species that are here referred to the new genus *Orisarma*, with the type species *O. dehaani*. Here again an obviously misidentified species is unmasked: the GenBank sequence of NC_042142 labelled as '*Chiromantes haematocheir*' (Li et al., 2019b) from Fushun City (in Liaoning Province, northern China) cannot possibly belong to that species. Li et al.'s (2019b) species is most likely *O. sinense*, which is known from that area. The second branch (pp = 1) is mostly composed of former representatives of *Pseudosesarma*, *Bresedium*, and *Sesarmops*. It can be subdivided again in two branches, of which the first one (pp = 1) gathers *Pseudosesarma* sensu stricto (pp = 1) on one hand, and the closely related (pp = 0.96) new genera *Contusarma* and *Miersarma* on the other. The second of these branches (pp = 0.97) includes the remaining taxa, of which the new

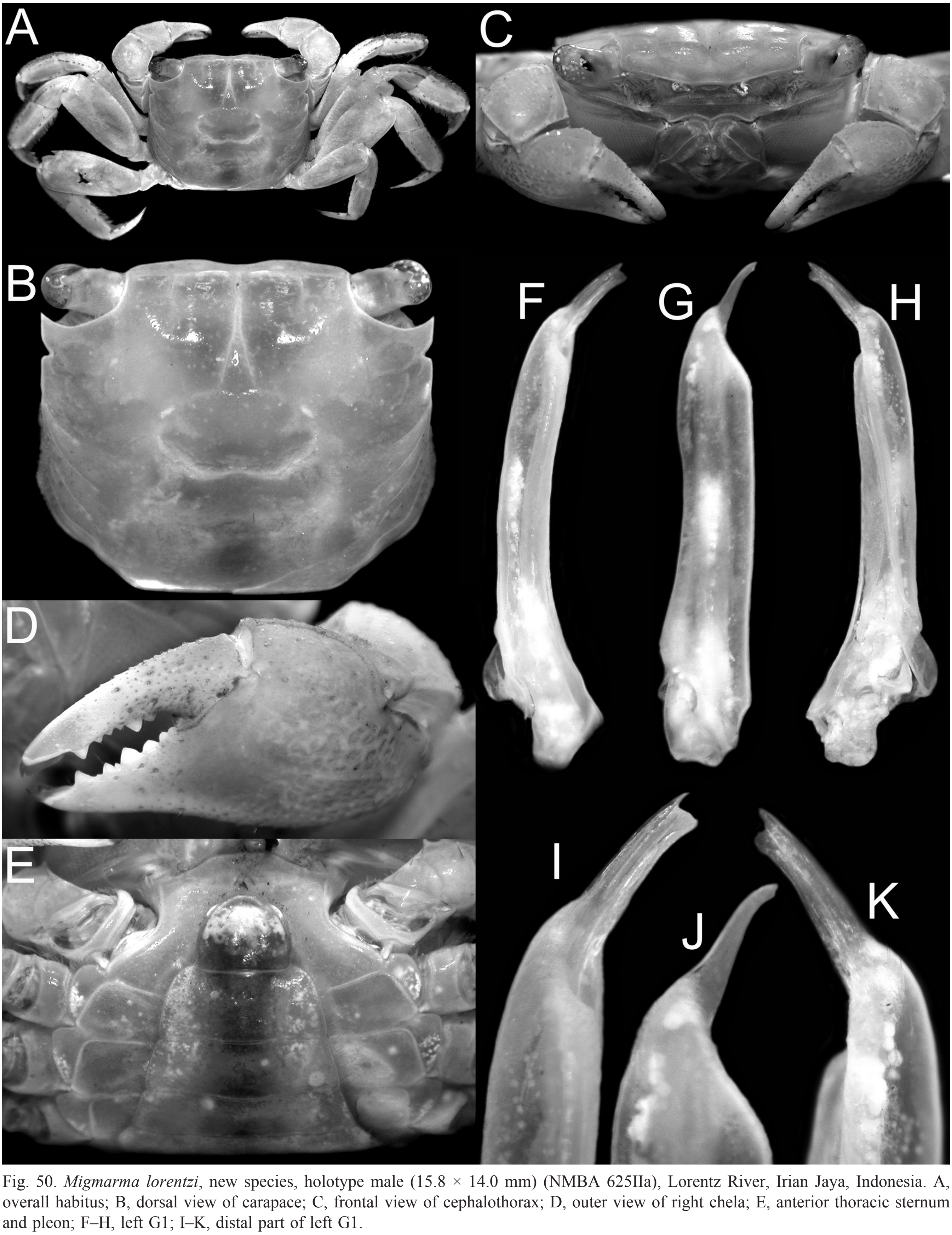

Fig. 50. *Migmarma lorentzi*, new species, holotype male (15.8 × 14.0 mm) (NMBA 625IIa), Lorentz River, Irian Jaya, Indonesia. A, overall habitus; B, dorsal view of carapace; C, frontal view of cephalothorax; D, outer view of right chela; E, anterior thoracic sternum and pleon; F–H, left G1; I–K, distal part of left G1.

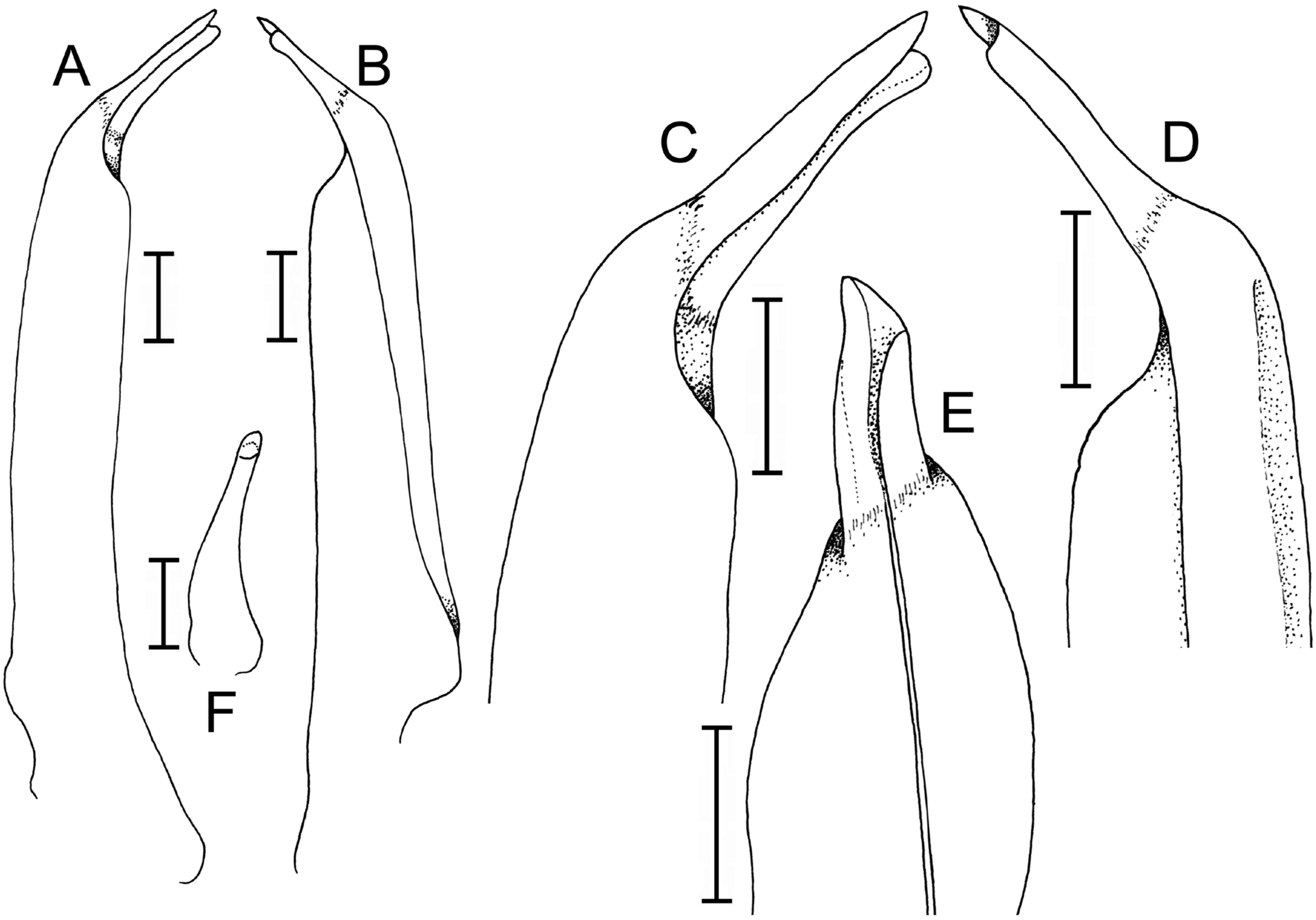

Fig. 51. *Migmarma lorentzi*, new species, holotype male (15.8 × 14.0 mm) (NMBA 625IIa), Lorentz River, Irian Jaya, Indonesia. A, left G1 (ventral view); B, left G1 (dorsal view); C, distal part of left G1 (ventral view); D, distal part of left G1 (dorsal view); E, distal part of left G1 (mesial view); F, left G2. Scales = 0.5 mm.

genus *Manarma* (pp = 1) splits first, whereas the species of *Bresedium* and *Sesarmops* cannot be currently separated according to their generic assignments. However, the three species now assigned to the new genus *Migmarma* (two of them new to science), which also belong into this phylogenetic vicinity, form a weakly supported (pp = 0.66) monophylum, completing the series of molecular phylogenetic evidences for all of our here newly defined genera.

## GENERAL DISCUSSION

The present phylogenetic revision of *Chiromantes* and *Pseudosesarma* shows that several key morphological characters commonly used in the definition of sesarmid genera are of limited and questionable value. The anterolateral epibranchial tooth is perhaps one of the most important of those presumed key characters, and in most keys to the Sesarmidae one of the first steps in the separation of major groups. The absence or presence of an epibranchial tooth has long been considered to be diagnostic, but its appearance is actually too variable to be useful, with several recent studies demonstrating this, for example in the recent revision of *Parasesarma* and *Perisesarma* by Shahdadi & Schubart (2017). In the present study, most examined specimens of adult *C. haematocheir* have the lateral carapace margin unarmed, but in many of the smaller specimens, the fissures of at least two teeth are indicated, even if very low. In *Orisarma dehaani* and *O. neglectum*, the anterior part of the lateral carapace margin has a low lobe, corresponding to the epibranchial tooth, but it is so poorly developed and with an often not discernible fissure, that it cannot be regarded as a true tooth. In some specimens, there is even an indication of a second epibranchial tooth. Therefore, the presence or absence of an epibranchial tooth should not be considered anymore a valid key character in defining genera. Confirming this, the newly described or redefined genera *Orisarma* and *Pseudosesarma* now comprise representatives with and without epibranchial teeth.

The separation of *Chiromantes* from *Pseudosesarma* and *Sesarmops* was also mainly based on the presence of an epibranchial tooth. *Pseudosesarma* and *Sesarmops* are actually morphologically close, and the other characters used to distinguish them (size, carapace shape, leg form, and G1 structure) (sensu Serène & Soh, 1970) are not always reliable. The presence of a row of regularly arranged granules on the dactylar fingers of young male *Chiromantes haematocheir* is remarkable, as they are lost when the specimens grow larger and the mature chela takes on a very different appearance. They closely resemble the typical stridulatory granules found in genera like *Perisesarma*, *Parasesarma*, and *Leptarma*,

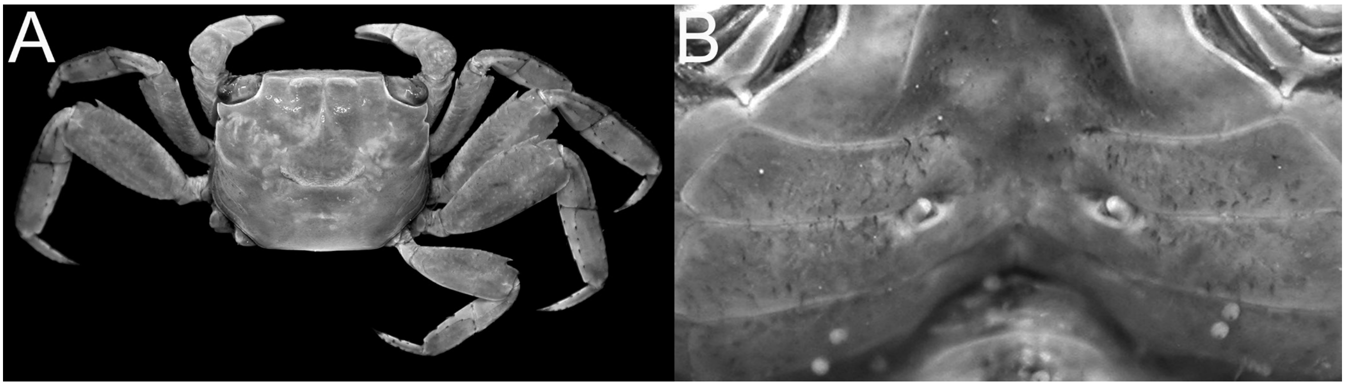

Fig. 52. *Migmarma lorentzi*, new species, paratype female (13.4 × 11.8 mm) (NMBA 625IIa), Lorentz River, Irian Jaya, Indonesia. A, overall habitus; B, vulvae.

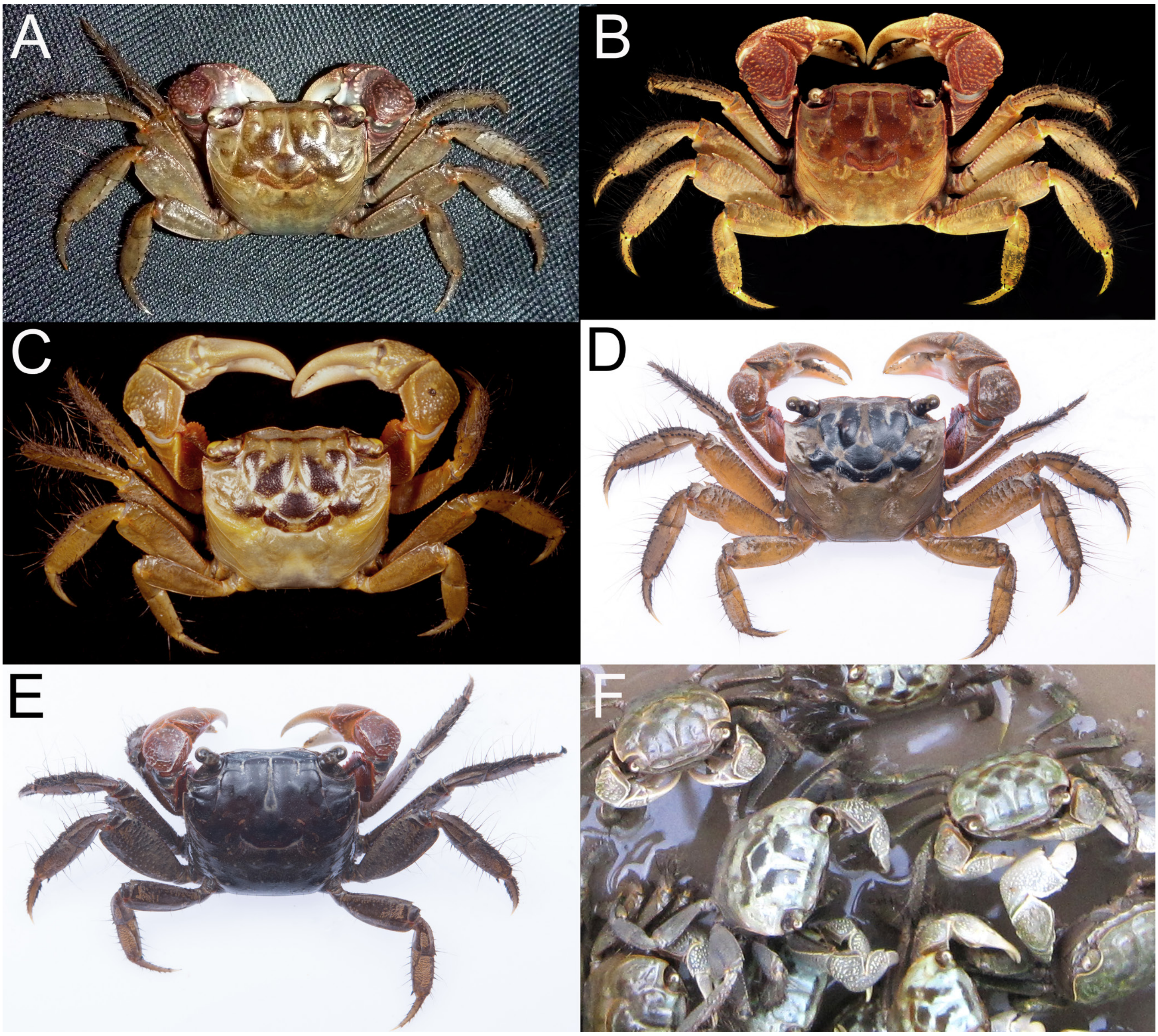

Fig. 53. Colour in life. A, *Orisarma dehaani*, male (23.4 × 20.8 mm) (ZRC 2012.0057), Kagoshima, Japan [photograph: PKL Ng]; B, *O. dehaani*, male (36.4 × 34.4 mm) (ZRC 2011.1027), Kumejima Island, Japan; C, *O. dehaani*, male (27.6 × 29.6 mm) (ZRC 2002.0223), Hong Kong [photograph: Tan Heok Hui]; D, *O. dehaani*, male (26.5 × 24.0 mm) (ZRC 2019.0539), Hong Kong [photograph: Paul Ng]; E, *O. dehaani*, female (20.2 ×17.6 mm) (ZRC 2019.0539), Hong Kong [photograph: Paul Ng]; F, *O. neglectum*, Shanghai, China, specimens not preserved [photograph: Liu Wenliang].

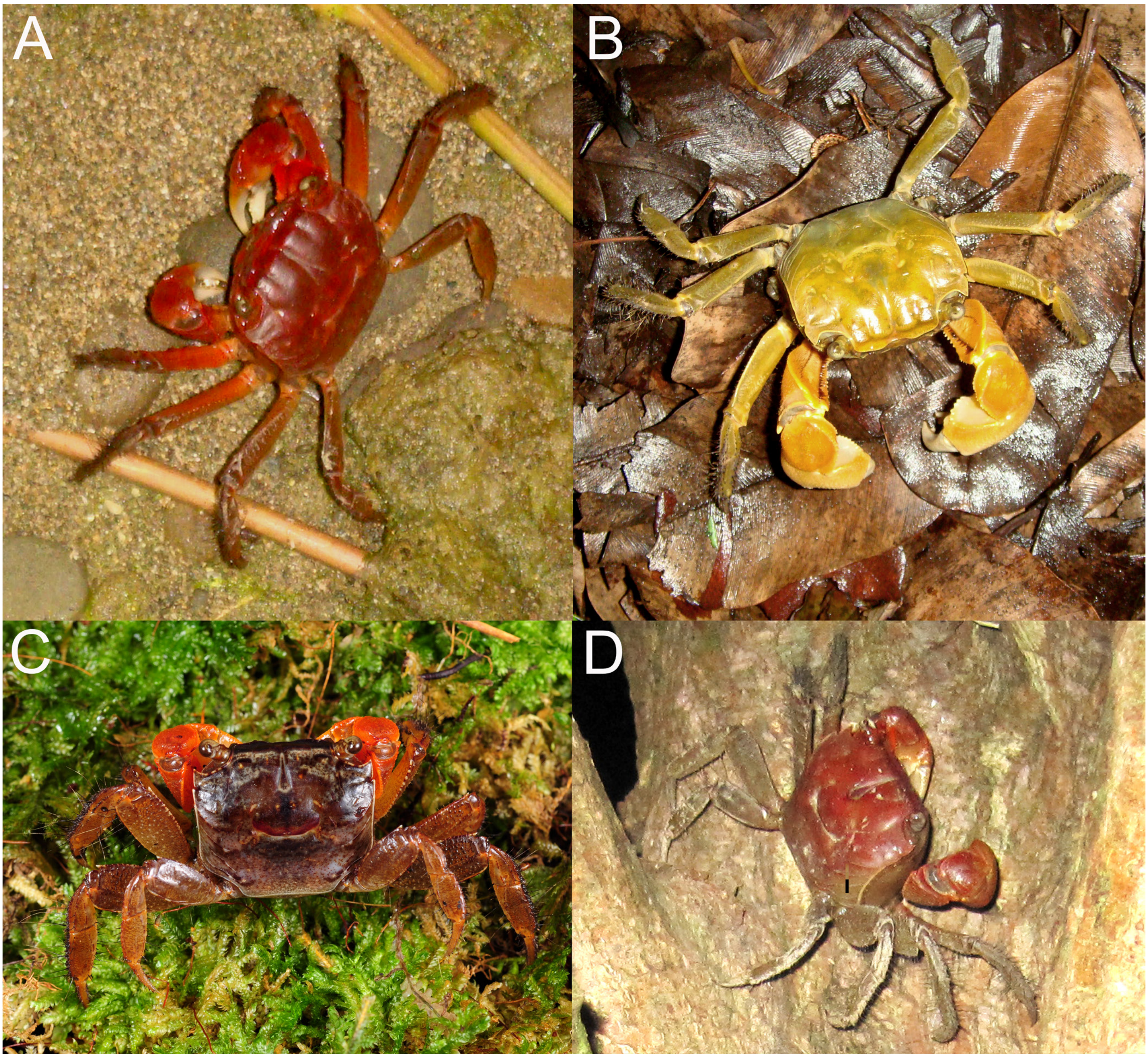

Fig. 54. Colour in life. A, *Orisarma intermedium*, Pingtung, Taiwan, specimen not collected [photograph: PKL Ng]; B, *O. intermedium*, female (37.5 × 35.8 mm) (ZRC 2014.0265), Kumejima Island, Japan [photograph: PKL Ng]; C, *O. intermedium*, male (23.2 × 20.0 mm) (ZRC 2019.0540), Hong Kong [photograph: Paul Ng]; D, *O. sinense*, Shanghai, China, specimen not collected [photograph: Liu Wenliang].

except that they are less well-formed and less complex in structure. However, they are most likely not used in the same way as in stridulating sesarmid species (see Godsall & Smallegange, 2011; Chen et al., 2014, 2017), as a pectinated crest on the dorsal carpus is missing. Such a row of granules is not known in any of the species now assigned to *Orisarma*, even in smaller subadult specimens. On the other hand, the pectinated crests (here used as a diagnostic and name-giving character) found in the East African genus *Cristarma* are a clear indication for likely stridulatory behaviour in this genus.

While the G1 structure is relatively conservative in sesarmid crabs, it does vary somewhat among the newly defined genera with convergent changes in shape and length. In *Orisarma*, new genus, the G1 may be relatively long and slender (e.g., *O. dehaani*; Fig. 11C, D), becoming stouter and shorter (e.g., *O. intermedium*; Fig. 12B, C) to very short and stout (e.g., *O. patshuni*; Fig. 12L, M). In *Danarma*, new genus, the differences in G1 structure can be extreme, from long and slender (e.g., *D. obtusifrons*; Davie & Ng, 2013: fig. 11D, E) to very stout (e.g., *D. eurymerus*; Davie & Ng, 2013: fig. 14D, E). In *Pseudosesarma*, two types of G1 can be distinguished, one is evenly stout with a symmetrical structure and a short chitinous distal part (e.g., *P. edwardsii*; Fig. 34D, E); the other being less stout, but with the distal part dilated, and the chitinous distal part more elongate and beak-like (e.g., *P. crassimanum*; Fig. 35B, H, I, O, P). Otherwise, brachyuran congeners almost always have similarly structured G1 (it is very often a diagnostic character for genera), and the very different structures seen in *Danarma*, and to some degree in *Pseudosesarma*, are surprising. This has previously been reported in other sesarmid genera like *Selatium* and *Leptarma* (see Schubart et al., 2009; Shahdadi et al., 2020). The genetic data, however, unambiguously shows these genera

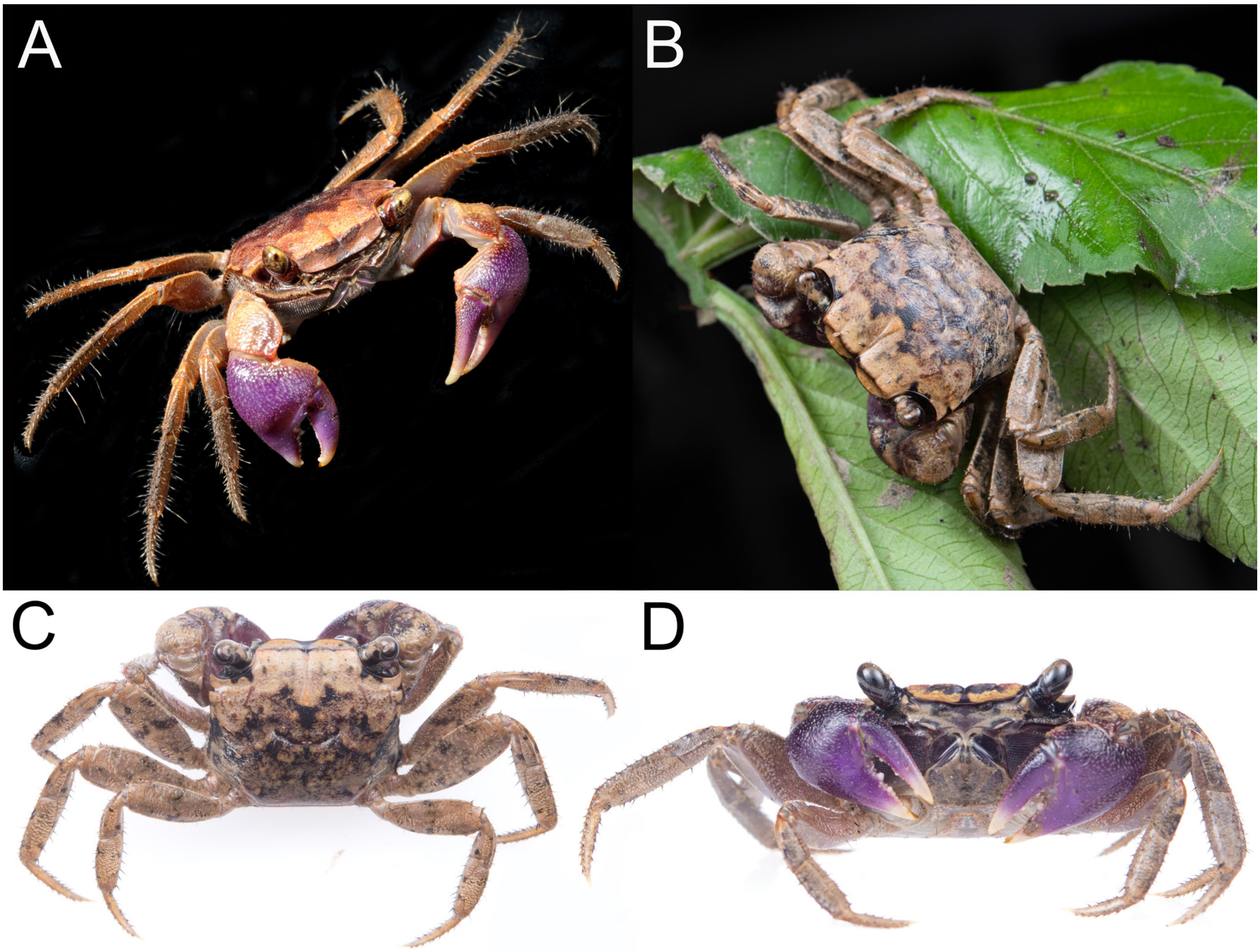

Fig. 55. Colour in life. A, *Orisarma patshuni*, male (14.2 × 13.0 mm) (ZRC 1998.345), Hong Kong [photograph: PKL Ng]; B–D, *O. patshuni*, male (13.8 × 12.3 mm) (ZRC 2019.1067), Hong Kong [photograph: Paul Ng].

to be monophyletic units. The very different G1 structures observed in members from one genus can only be explained by intrageneric character displacement to reduce the chances for subsequent hybridisation.

Matching the G1 structure to the conspecific vulva is not easy, and there does not seem to be any discernible pattern. Nevertheless, the general structure of the vulva is still very useful as a taxonomic character. In other cases, notably in *Pseudosesarma*, there are different conformations in the vulvar structure, but more or less following a general pattern in which it is positioned on the submedian or anterior part of sternite 6, with the opening low or not projecting outward. How variable the structures of the opening and sternal vulvar covers are (with regard to size and shape) is not known, but some variability can be expected and observed (e.g., in *P. crasssimanum*, Fig. 44C). It is noteworthy that only *P. edwardsii* has the tip of the G1 clearly bifurcated (Fig. 34D, E) and its vulva is submedian in position, with the two sternal vulvar covers forming flaps (Fig. 44A). Almost all other species of *Pseudosesarma* have a more beak-like chitinous distal part of the G1 (e.g., Figs. 35A, H, 36A, B, I, J, 37L, M), and their vulvae are positioned anteriorly on sternite 6 with a more distinctly protruding opening (Fig. 44B–F). Only *P. brehieri*, where the chitinous distal part is also very broad (Fig. 37B, D), has another unusual vulva, with the opening directed obliquely posteriorly (Fig. 44E). On the other hand, the relative position of the vulvae (whether they are spaced far apart or closer to the median part of the sternopleonal cavity) is a constant character. In *Trapezarma* (Fig. 43I) and *Platychirarma* (Fig. 43J), the vulvae are positioned so differently on sternite 6, that it provides strong support for their placement into two separate genera, despite being sister taxa (Fig. 59).

The region of mitochondrial DNA used for this study has the advantage of combining information of a conserved gene (16S), suitable for resolving relatively old intrageneric relationships, with few hundred basepairs of a variable protein coding gene (ND1) that often allows to distinguish between closely related species (if complete lineage sorting has taken place), and sometimes even isolated populations within species when third positions are included in the analyses. Consequently, this mtDNA region has previously been used to reconstruct phylogenetic relationships and postulate a new taxonomic system among families of the superfamily Portunoidea (Schubart & Reuschel, 2009), but also to uncover intraspecific differentiation within freshwater crabs, resulting in the description of a cryptic species of *Potamon* (Potamidae) (see Jesse et al., 2010). Therefore,

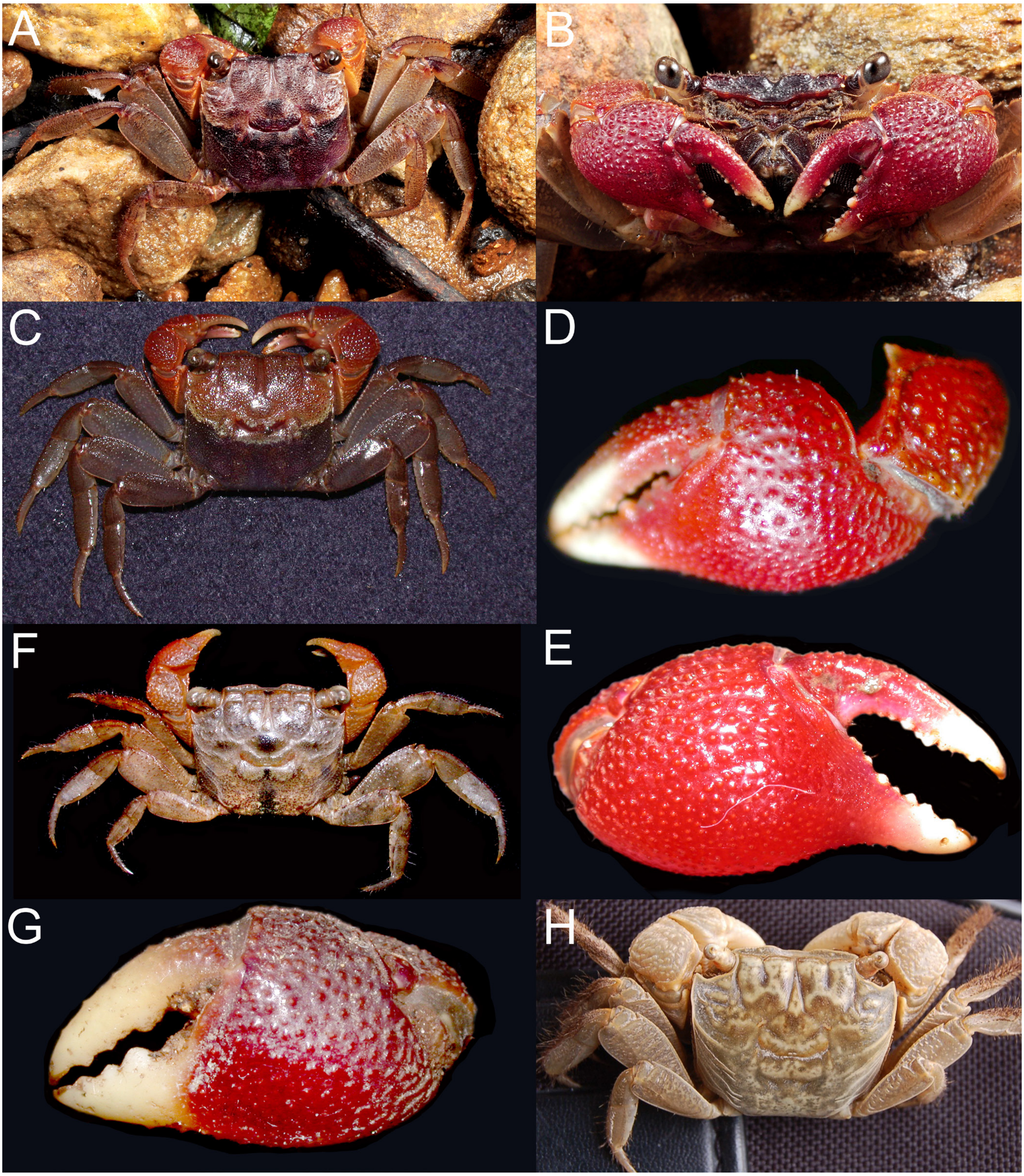

Fig. 56. Colour in life. A, B, *Pseudosesarma edwardsii*, male (20.5 × 19.3 mm) (ZRC 2016.0608), Langkawi [photograph: Paul Ng]; C–E, *P. edwardsii*, male (19.4 × 18.2 mm) (SMF), Langkawi, Peninsular Malaysia [photograph: CD Schubart]; F, G, *P. crassimanum*, (12.6 × 10.5 mm) (ZRC 2010.0035), Tioman, Peninsular Malaysia [photograph: PKL Ng]; H, *P. boulengeri*, specimen not preserved [photograph: Reza Naderloo].

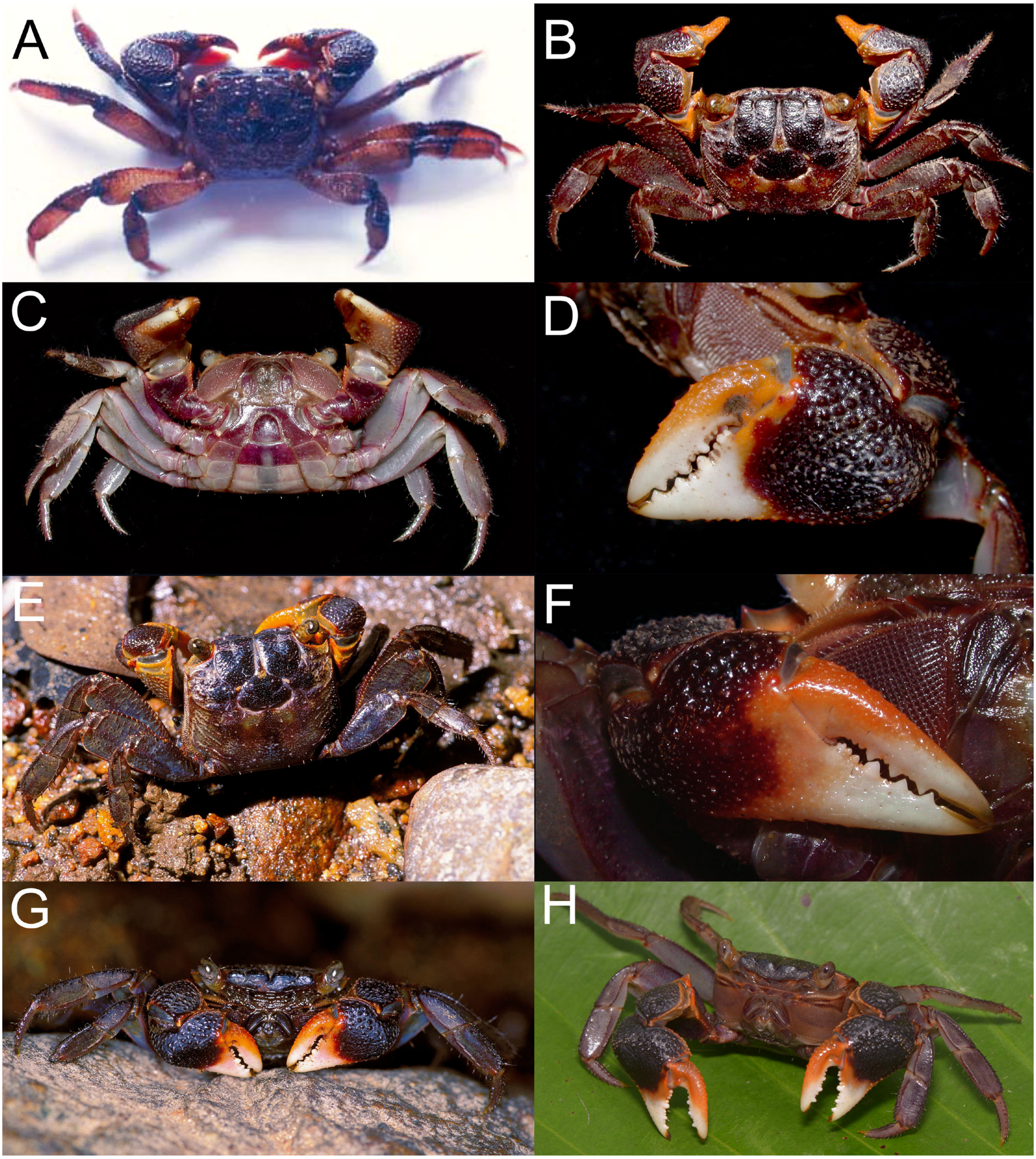

Fig. 57. Colour in life. A, *Contusarma bocourti*, male (25.3 × 23.3 mm) (ZRC 2000.0952), Bangkok, Thailand [photograph: Phaibul Naiyanetr]; B–D, *C. cheirogonum*, male (26.3 × 23.0 mm) (ZRC 1995.0226), Bako, Sarawak [photograph: PKL Ng]; E, G, *C. cheirogonum*, male, Tioman, Peninsular Malaysia, specimen not collected [photograph: Chua Ee Kiam]; F, *C. cheirogonum*, Tioman, Peninsular Malaysia, female (specimen not collected); H, *C. cheirogonum*, specimen not collected, Bako, Sarawak [photograph: Jongkar Grinang].

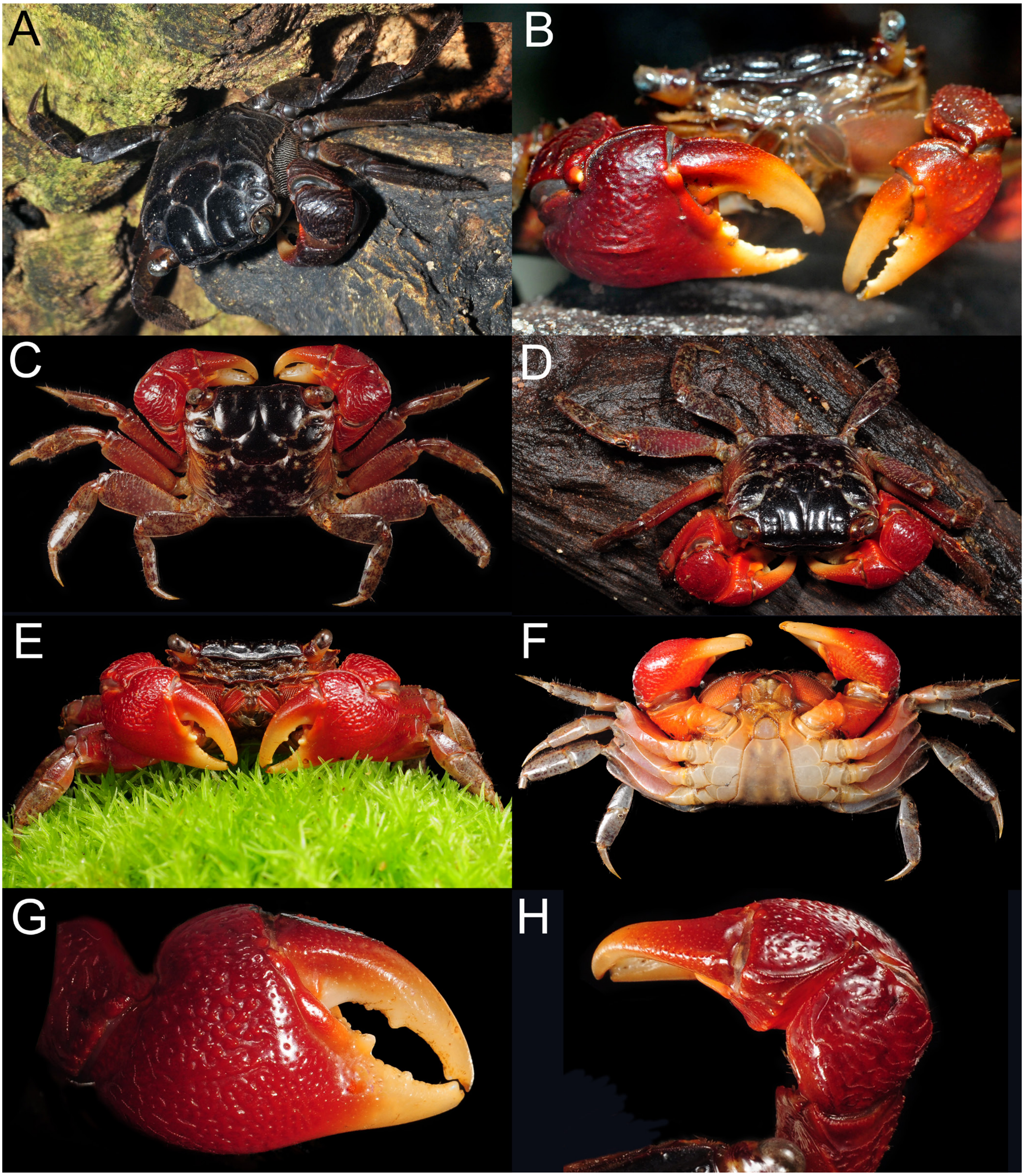

Fig. 58. Colour in life. *Manarma moeschii*. A, B, male, Thailand, specimen not preserved [photograph: Oliver Mengedoht]; C–H, male (19.7 × 17.1 mm) (ZRC 2017.0170), Thailand [photograph: Paul Ng].

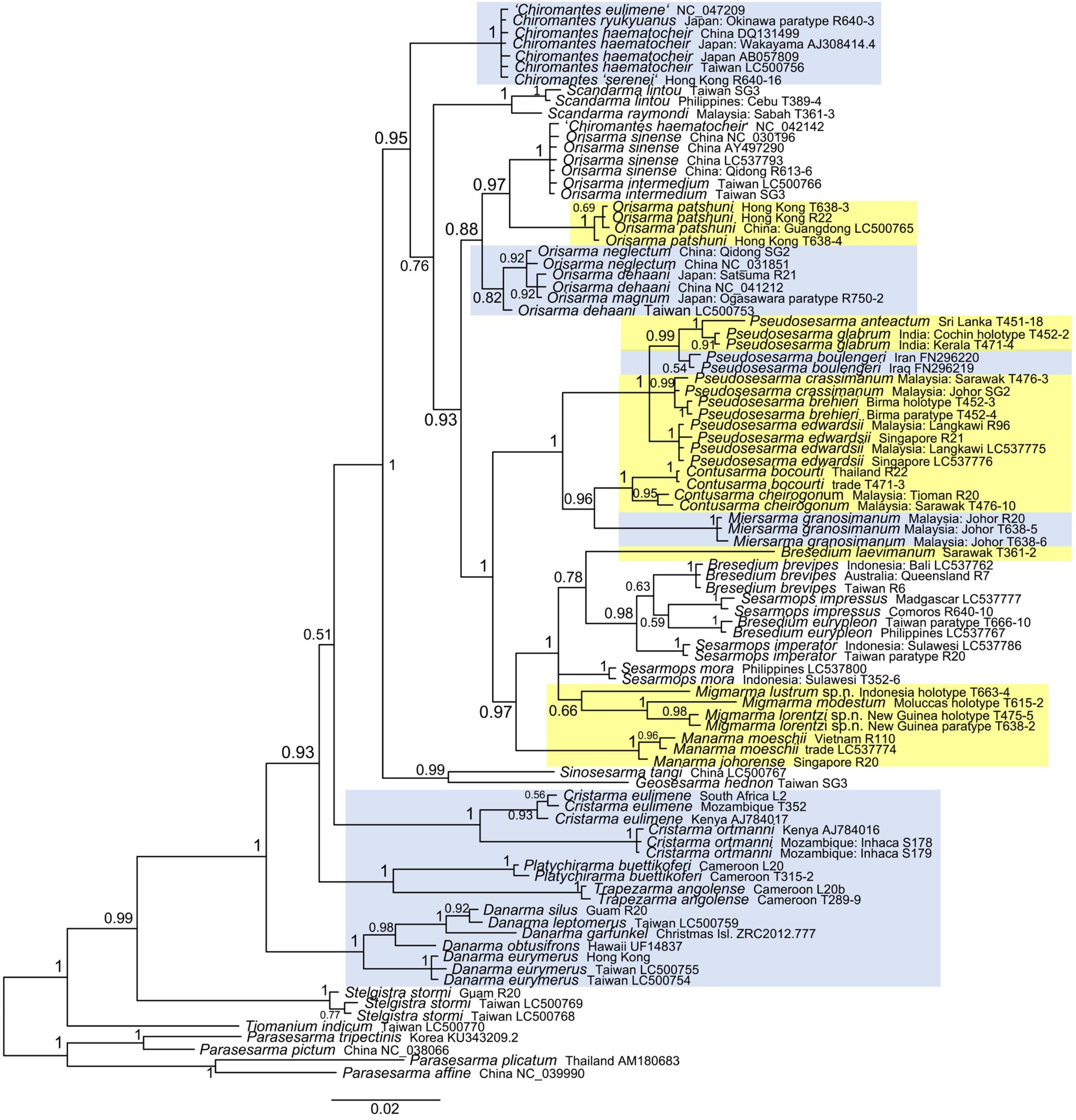

Fig. 59. Phylogenetic relationships among selected taxa of Sesarmidae (91 OTUs), including all representatives of *Chiromantes* and *Pseudosesarma* previous to current revision of these genera. In addition, several species of *Bresedium* and *Sesarmops* are considered, as the revision also involves some of their former members. Topology and confidence values were determined by means of a phylogenetic reconstruction based on 1,096 basepairs of mtDNA (16S-tRNALeu-ND1), conducted with MrBayes, GTR+I+G as substitution model, and *Parasesarma plicatum* as outgroup (midpoint rooting). Posterior probabilities were determined after 4 million generations with a burn-in of 25%. All species so far classified within *Chiromantes* (without obvious anterolateral teeth) are shaded in blue, whereas those species that used to be classified in *Pseudosesarma* (carrying at least one pair of anterolateral teeth) are shaded in yellow.

Table 1. List of specimens from which DNA was sequenced and used for phylogenetic reconstruction, excluding GenBank sequences from other authors.

| **Species & code** | **New classification** | **Collection locality & date** | **Collection #** | **GenBank accession #** |
|---|---|---|---|---|
| *Bresedium brevipes* R6 | | Taiwan: Hualien, 12.12.2000 | NHMW 26837 | MW014860 |
| *Bresedium brevipes* R7 | | Australia: Queensland, Flame Tree Creek, 2.6.1997 | QM W22085 | MW014859 |
| *Bresedium eurypleon* T666-10 | | Taiwan: Pingtung: Gangkou R. (paratype) | ZRC 2019.1652 | MW014861 |
| *Bresedium sediliense* T361-2 | *Bresedium laevimanum* | Sarawak: Kuching, January 1949 | ZRC 1972 3.7.25–35 | MW014858 |
| *Chiromantes angolense* L20b | *Trapezarma*, new genus | Cameroon: north of Victoria, 7.1.1984 | SMF 25982 | MW014877 |
| *Chiromantes angolense* T289 | *Trapezarma*, new genus | Cameroon: Lokoundje mangrove, 2015 | NHMW 26838 | MW014878 |
| *Chiromantes boulengeri* R195 | *Pseudosesarma* | Iran: Abadan: Buhmanshir R., 20.5.2008 | SMF 33818 | FN296220 |
| *Chiromantes boulengeri* R21 | *Pseudosesarma* | Iraq: Basra, Ashar Creek, 1919 | BMNH 2002.298 | FN296219 |
| *Chiromantes buettikoferi* L20 | *Platychirarma*, new genus | Cameroon: north of Victoria, 7.1.1984 | SMF 25980 | MW014875 |
| *Chiromantes buettikoferi* T315 | *Platychirarma*, new genus | Cameroon: Mouang Ko mangrove, 2015 | NHMW 26839 | MW014876 |
| *Chiromantes dehaani* R21 | *Orisarma*, new genus | Japan: Satsuma Peninsula, Izaku River, 30.8.2000 | ZRC 2002.226 | MW014837 |
| *Chiromantes eulimene* S42 | *Cristarma*, new genus | Kenya: Mida Creek, April 1997 | MZUF 2501 | AJ784017 |
| *Chiromantes eulimene* L2 | *Cristarma*, new genus | South Africa: Natal, 1997 | tissue only | MW014871 |
| *Chiromantes eulimene* T352 | *Cristarma*, new genus | Mozambique: Bilene, Dec. 2009 | ZRC 2014.130 | MW014872 |
| *Chiromantes eurymerus* | *Danarma*, new genus | Hong Kong | CUHK | MW014880 |
| *Chiromantes garfunkel* | *Danarma*, new genus | Christmas Island: Greta Beach, 24.1.2010 | ZRC 2012.777 | MW014881 |
| *Chiromantes granosimanum* R20 | *Miersarma*, new genus | Malaysia: Johor, Bukit Pasir, 28.5.1998 | ZRC 2002.0162 | MW014855 |
| *Chiromantes granosimanum* T638-5 | *Miersarma*, new genus | Malaysia: Johor, Bukit Pasir, 28.5.1998 | ZRC 2002.0162 | MW014856 |
| *Chiromantes granosimanum* T638-6 | *Miersarma*, new genus | Malaysia: Johor, Bukit Pasir, 28.5.1998 | ZRC 2002.0162 | MW014857 |
| *Chiromantes haematocheir* L19 | | Japan: Wakayama, Samusaura, 11.6.1998 | SMF 25989 | AJ308414 |
| *Chiromantes magnus* R750-2 | *Orisarma*, new genus | Japan: Ogasawara Isl., Renju Valley (paratype) | ZRC 2013.173 | MW014838 |
| *Chiromantes neglectus* SG2 | *Orisarma*, new genus | China: Jiangsu: Qui Dong: Lusi, 1.5.1996 | ZRC 1998.310 | MW014836 |
| *Chiromantes obtusifrons* | *Danarma*, new genus | Hawaii: Oahu, Coco Head, Oct. 2006 | FMNH 14837 | MW014882 |
| *Chiromantes ortmanni* S29 | *Cristarma*, new genus | Kenya: Gazi, July 1997 | MZUF 2523 | AJ784016 |
| *Chiromantes ortmanni* S178 | *Cristarma*, new genus | Mozambique: Inhaca, Feb. 2006 | MZUF 2994 | MW014873 |
| *Chiromantes ortmanni* S179 | *Cristarma*, new genus | Mozambique: Inhaca, Feb. 2006 | MZUF 2995 | MW014874 |
| *Chiromantes ryukyuanus* R640-3 | | Japan: Okinawa Isl.: Ohgimi, 2007 (paratype) | ZRC 2007.640 | MW014828 |
| *Chiromantes "serenei"* R640-16 | *Chiromantes haematocheir* | Hong Kong: South coast: Tai Tam | ZRC 1997.761 | MW014829 |
| *Chiromantes silus* R20 | *Danarma*, new genus | USA: Guam: Hapato Bay, August 2001 | ZRC 2001.742 | MW014879 |
| *Geosesarma hednon* SG3 | | Taiwan: Pingtung: Kangkou R. | SMF 28108 | MW014830 |
| *Migmarma lustrum* T663-4 | | Indonesia: Irian Jaya: Raja Ampat, April 2009 | ZRC 2010.21 | MW014865 |
| *Parasesarma plicatum* SG1 | | Thailand: Phuket, 23.8.1999 | ZRC 2000.1913 | AM180683 |
| *Pseudosesarma anteactum* T451 | | Sri Lanka: Sri Lanka: Galle, 14.11.2002 | NHMW 26840 | MW014842 |

| Species & code | New classification | Collection locality & date | Collection # | GenBank accession # |
|---|---|---|---|---|
| *Pseudosesarma bocourti* R22 | *Contusarma*, new genus | Thailand: Bangkok, Silom, 1.8.1998 | ZRC 2000.952 | MW014851 |
| *Pseudosesarma bocourti* T471 | *Contusarma*, new genus | Thailand: Bangkok (from trade), 9.1.2007 | ZRC 2019.1114 | MW014852 |
| *Pseudosesarma bocourti* R20 | *Contusarma cheirogonum* | Malaysia: Tioman: Sungei Paya, 1995 | NHMW 26841 | MW014853 |
| *Pseudosesarma bocourti* T476-10 | *Contusarma cheirogonum* | Malaysia: Sarawak: Bako NP, 8.6.1994 | ZRC 1995.226 | MW014850 |
| *Pseudosesarma brehieri* T452-3 | | Myanmar: Moulmein: Nathack Gu (holotype) | ZRC 2016.593 | MW014847 |
| *Pseudosesarma brehieri* T452-4 | | Myanmar: Moulmein: Nathack Gu (paratype) | ZRC 2016.594 | MW014848 |
| *Pseudosesarma crassimanum* SG2 | | Malaysia: Johor: Sungei Benut, 30.9.1999 | ZRC 2000.1768 | MW014846 |
| *Pseudosesarma crassimanum* T476-3 | | Malaysia: Sarawak: Kuching, 1950 | ZRC1964.9.25.368–79 | MW014845 |
| *Pseudosesarma edwardsii* R21 | | Singapore: Pulau Ubin, July 2000 | ZRC 2000.2019 | MW014850 |
| *Pseudosesarma edwardsii* R96 | | Malaysia: Langkawi: Temurun Falls, March 2006 | NHMW 26842 | MW014849 |
| *Pseudosesarma glabrum* T452-2 | | India: Cochin Estuary, 16.1.2016 (holotype) | CUSAT 2016-1 | MW014843 |
| *Pseudosesarma glabrum* T471 | | India: Kerala: Pazhayangadi mangrove, 2017 | NHMW 26843 | MW014844 |
| *Pseudosesarma johorense* R20 | *Manarma*, new genus | Singapore: Mandai mangrove, 25.7.2000 | CDS pers. collection | MW014870 |
| *Pseudosesarma laevimanum* T475-5 | *Migmarma lorentzi*, new species | New Guinea: Lorentz River, 1909 (holotype) | NMBA 625IIa | MW014867 |
| *Pseudosesarma laevimanum* T638-2 | *Migmarma lorentzi*, new species | New Guinea: Lorentz River, 1909 (paratype) | NMBA 625IIa | MW014868 |
| *Pseudosesarma modestum* T615-2 | *Migmarma*, new genus | Indonesia: Moluccas: Ternate 1893 (holotype) | SMF 1989 | MW014866 |
| *Pseudosesarma moeschii* R20 | *Manarma*, new genus | Thailand: Bangkok (trade) | ZRC 2000.1926 | MW014869 |
| *Pseudosesarma patshuni* R22 | *Orisarma*, new genus | China: Hong Kong, Tai Tam salt marsh 1996 | ZRC 1998.345 | MW014841 |
| *Pseudosesarma patshuni* R638-3 | *Orisarma*, new genus | China: Hong Kong, Tai Tam salt marsh 1996 | ZRC 1998.345 | MW014839 |
| *Pseudosesarma patshuni* R638-4 | *Orisarma*, new genus | China: Hong Kong, Tai Tam salt marsh 1996 | ZRC 1998.345 | MW014840 |
| *Scandarma lintou* SG3 | | Taiwan: Pingtung: Kangkou R., 14.9.1999 | ZRC 2000.1830 | MW014831 |
| *Scandarma lintou* T389-4 | | Philippines: Cebu: Moalboal, 21.2.2003 | NHMW 26844 | MW014832 |
| *Scandarma raymondi* T361-3 | | Malaysia: Sabah: Kota Kinabalu, 1.11.1990 | ZRC 2013.614 | MW014833 |
| *Sesarmops impressus* R640-10 | | Comoros, 11.10.2000 | ZRC 2011.004 | MW014863 |
| *Sesarmops imperator* R20 | | Taiwan: Lanyu Isl.: Taitung, 20.9.1999 (paratype) | ZRC 2000.1858 | MW014862 |
| *Sesarmops intermedius* SG3 | *Orisarma*, new genus | Taiwan: Pingtung: Kangkou R., 14.9.1999 | ZRC 2000.1834 | MW014835 |
| *Sesarmops mora* T352-6 | | Indonesia: Sulaweis: Manado | ZRC 2019.1661 | MW014864 |
| *Sesarmops sinensis* R613-6 | *Orisarma*, new genus | China: Jiangsu Province: Qidon, 2.5.1996 | ZRC 1998.1204 | MW014834 |
| *Stelgistra stormi* R20 | | USA: Guam, 5.8.2001 | CDS pers. collection | MW014882 |

BMNH: British Museum of Natural History, London; CDS: personal collection CD Schubart; CUHK: Chinese University of Hong Kong tissue collection; CUSAT: Cochin University of Science & Technology, India; FMNH: Florida Museum of Natural History, Gainesville, USA; NMBA: Naturhistorisches Museum Basel, Switzerland; MZUF, Museo Zoologico Universitá di Firenze, Italy; NHMW, Naturhistorisches Museum, Vienna, Austria; SMF, Forschungsinstitut und Museum Senckenberg, Frankfurt a.M., Germany; ULLZ, University of Louisiana Zoological Collection, Lafayette, USA; QM, Queensland Museum, Brisbane, Australia; UF-FLMNH: Florida Museum of Natural History; ZRC, Zoological Reference Collection, National University of Singapore, Singapore.

Table 2. List of taxa discussed in present study. The first species listed under each genus is the type species.

| Taxon | Original genus | Current genus (2008-present) | Synonym | Authority |
|---|---|---|---|---|
| ***Chiromantes*** **Gistel, 1848** | | | | |
| *Chiromantes haematocheir* (De Haan, 1833) | *Grapsus* (*Pachysoma*) | *Chiromantes* | *Holometopus serenei* Soh, 1978 | Ng & Liu (1999) |
| *Chiromantes ryukyuanus* Naruse & Ng, 2008 | *Chiromantes* | *Chiromantes* | | Naruse & Ng (2008) |
| ***Stelgistra*** **Ng & Liu, 1999** | | | | |
| *Stelgistra stormi* (De Man, 1895) | *Sesarma* (*Sesarma*) | *Stelgistra* | | Ng & Liu (1999) |
| ***Clistocoeloma*** **A. Milne-Edwards, 1873** | | | | |
| *Clistocoeloma villosus* (A. Milne-Edwards, 1869) | *Sesarma* | *Clistocoeloma* | | Ng & Liu (1999) |
| ***Sinosesarma*** **Ng, Shih & Cannicci, 2019** | | | | |
| *Sinosesarma tangi* (Rathbun, 1931) | *Sesarma* (*Holometopus*) | *Sinosesarma* | | Ng et al. (2019) |
| ***Orisarma*, new genus** | | | | |
| *Orisarma dehaani* (H. Milne Edwards, 1853) | *Sesarma* | *Chiromantes* | *Sesarma hanseni* Rathbun, 1897 | Present study |
| *Orisarma intermedium* (De Haan, 1835) | *Grapsus* (*Pachysoma*) | *Sesarmops* | | Present study |
| *Orisarma magnum* (Komai & Ng, 2013) | *Chiromantes* | *Chiromantes* | | Present study |
| *Orisarma neglectum* (De Man, 1887) | *Sesarma* | *Chiromantes* | | Present study |
| *Orisarma patshuni* (Soh, 1978) | *Pseudosesarma* | *Pseudosesarma* | | Present study |
| *Orisarma sinense* (H. Milne Edwards, 1853) | *Sesarma* | *Sesarmops* | | Present study |
| ***Danarma*, new genus** | | | | |
| *Danarma obtusifrons* (Dana, 1851) | *Sesarma* | *Chiromantes* | | Present study |
| *Danarma eurymerus* (Davie & Ng, 2013) | *Chiromantes* | *Chiromantes* | | Present study |
| *Chiromantes garfunkel* (Davie & Ng, 2013) | *Chiromantes* | *Chiromantes* | | Present study |
| *Danarma leptomerus* (Davie & Ng, 2012) | *Chiromantes* | *Chiromantes* | | Present study |
| *Danarma silus* (Davie & Ng, 2013) | *Chiromantes* | *Chiromantes* | | Present study |
| ***Cristarma*, new genus** | | | | |
| *Cristarma eulimene* (De Man, in Weber, 1897) | *Sesarma* (*Sesarma*) | *Chiromantes* | | Present study |
| *Cristarma ortmanni* (Crosnier, 1965) | *Sesarma* | *Chiromantes* | | Present study |
| ***Trapezarma*, new genus** | | | | |
| *Trapezarma angolense* (Brito Capello, 1864) | *Sesarma* | *Chiromantes* | | Present study |
| ***Platychirarma*, new genus** | | | | |
| *Platychirarma büttikoferi* (De Man, 1883) | *Sesarma* | *Chiromantes* | | Present study |
| ***Pseudosesarma*** **Serène & Soh, 1970** | | | | |
| *Pseudosesarma edwardsii* (De Man, 1887) | *Sesarma* | *Pseudosesarma* | | Serène & Soh (1970) |
| *Pseudosesarma anteactum* Ng & Schubart, 2017 | *Pseudosesarma* | *Pseudosesarma* | | Ng et al. (2017) |
| *Pseudosesarma boulengeri* (Calman, 1920) | *Chiromantes* | *Chiromantes* | | Naderloo & Schubart (2009) |
| *Pseudosesarma brehieri* Ng, 2018 | *Pseudosesarma* | *Pseudosesarma* | | Ng (2018) |
| *Pseudosesarma crassimanum* (De Man, 1887) | *Sesarma* | *Pseudosesarma* | | Serène & Soh (1970) |

| Taxon | Original genus | Current genus (2008-present) | Synonym | Authority |
|---|---|---|---|---|
| *Pseudosesarma glabrum* Ng, Rani & Nandan, 2017 | *Pseudosesarma* | *Pseudosesarma* | | Ng et al. (2017) |
| ***Contusarma*, new genus** | | | | |
| *Contusarma bocourti* (A. Milne-Edwards, 1869) | *Sesarma* | *Pseudosesarma* | | Present study |
| *Contusarma cheirogonum* (Targioni Tozzetti, 1877) | *Sesarma* | *Pseudosesarma* | | Present study |
| ***Miersarma*, new genus** | | | | |
| *Miersarma granosimanum* (Miers, 1880) | *Sesarma* | *Pseudosesarma* | | Present study |
| ***Manarma*, new genus** | | | | |
| *Manarma moeschii* (De Man, 1892) | *Sesarma* | *Pseudosesarma* | | Present study |
| *Manarma johorense* (Tweedie, 1940) | *Sesarma* | *Pseudosesarma* | | Present study |
| ***Bresedium* Serène & Soh, 1970** | | | | |
| *Bresedium brevipes* (De Man, 1889) | *Sesarma* | *Bresedium* | *Sesarma* (*Sesarma*) *edwardsi philippinense* Rathbun, 1914 | Serène & Soh (1970) |
| *Bresedium eurypleon* Li, Shih & Ng, 2020 | *Bresedium* | *Bresedium* | | Li et al. (2020) |
| *Bresedium laevimanum* (Zehntner, 1894) | *Sesarma* | *Pseudosesarma* | *Sesarma sediliensis* Tweedie, 1940 | Present study |
| ***Migmarma*, new genus** | | | | |
| *Migmarma modestum* (De Man, 1902) | *Sesarma* (*Sesarma*) | *Pseudosesarma* | | Present study |
| *Migmarma lustrum*, new species | *Migmarma* | *Migmarma* | | Present study |
| *Migmarma lorentzi*, new species | *Migmarma* | *Migmarma* | | Present study |
| ***Sesarmops* Serène & Soh, 1970** | | | | |
| *Sesarmops impressus* (H. Milne Edwards, 1837) | *Sesarma* | *Sesarmops* | | Ng et al. (2020) |
| *Sesarmops imperator* Ng, Li & Shih, 2020 | *Sesarmops* | *Sesarmops* | | Ng et al. (2020) |
| *Sesarmops mora* Li, Shih & Ng, 2020 | *Sesarmops* | *Sesarmops* | | Li et al. (2020) |
| *Sesarmops weberi* (De Man, 1892) | *Sesarma* | *Sesarmops* | | Naruse & Ng (2020) |

we are convinced that its resolution is sufficient to reveal true phylogenetic relationships within this widely radiated complex of littoral crab genera and species. However, going further back in time and addressing phylogenetic relationships in the early evolution of sesarmid crabs and other related families within the Thoracotremata will require the additional support of nuclear genes (Tsang et al., in preparation). On the other hand, even the more variable regions of this stretch of mitochondrial DNA sequence are apparently too short to detect distinction of very recently separated taxa, as can be seen in the cases of *Chiromantes haematocheir* versus *C. ryukyuanus*, *Orisarma dehaani* versus *O. neglectum* and *O. magnum*, and *O. intermedium* versus *O. sinense* (see also Li et al., 2020: 29). In these cases, the inclusion of a longer fragment of the protein coding genes ND1 and/or cytochrome oxidase c subunit 1 (CO1) should be considered and are currently being applied to solve phylogenetic and phylogeographic relationships within these species complexes.

In all nine cases of newly described genera, our results from genetic comparisons of the mitochondrial DNA agree very well with the morphological characters defining them. Although this should be expected, as both sets of characters are influenced by the same factor, i.e., evolutionary time of separation of different lineages, there are enough cases in which convergences (mostly morphological) result in apparent contradictions of this logical conclusion and blur the corresponding picture. A quick and superficial look at morphological characters can be responsible for that, as could be relying on easily visible characteristics (e.g., anterolateral tooth) of for example otherwise very similar-looking squarish littoral crabs that are encountered in a similar habitat. However, the present study serves as another documentation that in-depth morphological analyses have a good chance to reveal much more cryptic but consistent characters that will allow to recognise exactly those lineages that have been shown to evolve independently over relatively long time spans. We therefore would like to use our results to conclude with an advisory to invest the necessary time, when identifying and/or classifying living organisms for genetic studies. Incorrect identifications may lead to wrong clusterings as in the two cases unveiled by this study, involving two sesarmid crabs for which the entire mitochondrial genome has been sequenced, and thus have the potential to serve as suitable genetic model organisms: '*Chiromantes haematocheir*' most likely corresponding to *Orisarma sinense* (NC042142, Li et al., 2019b) and '*Chiromantes eulimene*' corresponding to *C. haematocheir* (NC047209, Zhang et al., 2020). Unfortunately, we must conclude that they were wrongly identified and therefore all future studies using the corresponding DNA should correct for this in order to avoid wrong assignments.

## ACKNOWLEDGEMENTS

The authors are very grateful to many friends and colleagues for their kind help with specimens, material, and enquires over the years: Stefano Cannicci (University of Hong Kong); Paul Clark (NHM); Charles Fransen and the late Lipke Holthuis (RMNH); Sara Fratini and Gianna Innocenti (Universitá di Firenze); Danièle Guinot and Paula Martin-Lefèvre (MNHN); Joe S.Y. Lee and Kingsley Wong (University of Hong Kong and Chinese University of Hong Kong); Liu Wen Liang (Shanghai University); Chris Lukhaup (Germany); Brent Newman (South Africa); Pierre A. Mvogo-Ndongo (Cameroon); Phaibul Naiyanetr (Chulalongkorn University, Bangkok, Thailand); Peter Schweizinger (MNHG); Shih Hsi-Te (National Chung-Hsing University, Taiwan); Kingsley Wong (University of Hong Kong); Ng Ngan Kee (ZRC) and Tohru Naruse (University of the Ryukyus), the latter two for help to check and photograph MNHN material. For colour photographs, we thank Paul Ng, Oliver Mengedoht, Jongkar Grinang, Reza Naderloo, Liu Wen Liang, Phaibul Naiyanetr, Chua Ee Kiam, and Tan Heok Hui. We also thank Elena Gavetti (Museo Regionale di Scienze Naturali, Torino) for her help in searching for the types of Targioni Tozzetti, Martin Schwentner (NHMW) for last minute cataloguing material, and Theodor Poettinger, Adnan Shahdadi, Fabian Flücken, and Theresa Süß for their support in Regensburg. We are especially grateful to Peter Davie and Shih Hsi-Te for their detailed comments, which helped to improve the manuscript.

## LITERATURE CITED

Abele LG (1975) The identity of *Sesarma hanseni* Rathbun, 1897, a supposedly West Indian species, with *S. dehaani* H. Milne Edwards, 1853, from the West Pacific (Decapoda, Grapsidae). Crustaceana, 28(1): 48–52.

Abele LG (1992) A review of the grapsid crab genus *Sesarma* (Crustacea: Decapoda: Grapsidae) in America, with the description of a new genus. Smithsonian Contributions to Zoology, 527: 1–60.

Alcock A (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.

Apel M (2001) Taxonomie und Zoogeographie der Brachyura, Paguridea und Porcellanidae (Crustacea: Decapoda) des Persisch-Arabischen Golfes. Unpublished doctoral thesis, Johann Wolfgang Goethe-Universität, Frankfurt a. M., 268 pp.

Apel M & Türkay M (1999) Taxonomic composition, distribution and zoogeographic relationships of the grapsid and ocypodid crab fauna of intertidal soft bottoms in the Persian Gulf. Estuarine, Coastal and Shelf Science, 49 (Supplement A): 131–142.

Apreshgi KP & Abraham KM (2018) Brachyuran Mangrove Crab Diversity of Puthuvype Mangrove Belt, Cochin, Kerala. In: Proceedings of the International Conference on Innovations and Sustainable Research in Environment and Life Sciences. 7–9th August 2018, PG and Research Department of Zoology, Fatima Mata National College, Kollam, Kerala. Pp. 93–97.

Asakura A, Nishihama S & Kondo Y (1993) Studies on the biology and ecology of the intertidal animals of Chichijima Island in the Ogasawara (Bonin) Islands. I. List of collected species with comments on some species. Atoll Research Bulletin, 383: 1–17.

Aurivillius CWS (1893) Die Beziehungen der Sinnesorgane amphibischer Dekapoden zur Lebensweise und Athmung. Eine vergleichend biologisch-morphologische Studie. Nova Ada Regiae Societatis Scientiarum Upsaliensis, series 3, 16: 1–48, pls. 1–3.

Aw J & Low MEY (2020) L. Stories of Labour and Love. Lee Kong Chian Natural History Museum, National University of Singapore, 88 pp.

Baba K & Miyata K (1971) Larval development of *Sesarma* (*Holometopus*) *dehaani* H. Milne Edwards (Crustacea, Brachyura) reared in the laboratory. Memoirs of the Faculty of Education, Kumamoto University, Natural Science, 19: 54–64.

Balss H (1922) Ostasiatische Decapoden, IV. Die Brachyrhynchen (Cancridea). Archiv für Naturgeschichte, 88A(11): 94–165, figs. 1, 2, pls. 1, 2.

Balss H (1934) Die Krabben der Reise J. W. Harms' nach der Christmas-Insel und dem Malaiischen Archipel. Zoologischer Anzeiger, 106(10): 225–237.

Bouillon S, Moens T, Overmeer I, Koedam N & Dehairs F (2004) Resource utilization patterns of epifauna from mangrove forests with contrasting inputs of local versus imported organic matter. Marine Ecology Progress Series, 278: 77–88.

Brito Capello F de (1864) Descripção de tres especies novas de crustaceos da Africa Occidental e observações ácerca do *Penoeus* [sic] *bocagei*. Johnson. Especie nova dos mares de Portugal. Typographia da Academia, Lisboa. 11 + [1 unnumbered page of errata] pp., 1 unnumbered plate with 10 figures.

Bürger O (1893) Beiträge zur Kenntniss der Gattung *Sesarma*. Zoologischen Jahrbücher, Abtheilung für Systematik, Geographie und Biologie der Thiere, 7(4): 613–632, pl. 21.

Büttikofer J (1890) Reisebilder aus Liberia: Resultate geographischer, naturwissenschaftlicher und ethnographischer Untersuchungen während der Jahre 1879–1882 und 1886–1887, 2. Brill, Leiden, viii + 510 pp.

Calman WT (1920) A new crab of the genus *Sesarma* from Basra. Annals and Magazine of Natural History, Series 9, 5(25): 62–65, figs. A, B.

Calman WT (1925) X. Crustacea Decapoda. Collected in Korinchi and on the West Sumatran Coast, by Messrs. H. C. Robinson and C. Boden Kloss. Results of an Expedition to Korinchi Peak, Sumatra. Journal of the Federated Malay States Museums, 8(3): 166–167.

Campbell BM (1967) The Australian Sesarminae (Crustacea: Brachyura): Five species of *Sesarma* (*Chiromantes*). Memoirs of the Queensland Museum, 15(1): 1–19, pls. 1–5.

Capart A (1951) Crustacés Décapodes Brachyures. In: Expedition Océanographique Belge dans les Eaux Côtières Africaines de l'Atlantique Sud (1948–1949), Résultats Scientifiques, 3(1): 11–205, figs. 1–80, pls. 1–3.

Castro P (2011) Catalog of the anomuran and brachyuran crabs (Crustacea: Decapoda: Anomura, Brachyura) of the Hawaiian Islands. Zootaxa, 2947: 1–154.

Chen PZ, Carrascoa LR & Ng PKL (2014) Post-contest stridulation used exclusively as a victory display in mangrove crabs. Ethology, 120(6): 532–539.

Chen PZ, Carrascoa LR & Ng PKL (2017) Mangrove crab uses victory display to "browbeat" losers from re-initiating a new fight. Ethology, 123(12): 885–988.

Crosnier A (1965) Crustacés Décapodes, Grapsidae et Ocypodidae. Faune de Madagascar, Tananarive, 18: 1–143, pls. 1–11, textfigs. 1–260.

Cuesta JA, Guerao G, Liu H-C & Schubart CD (2006) Morphology of the first zoeal stages of eleven Sesarmidae (Crustacea, Brachyura, Thoracotremata) from the Indo-West Pacific, with a summary of familial larval characters. Invertebrate Reproduction & Development, 49(3): 151–173.

Dahdouh-Guebas F, Koedam N, Satyanarayana B & Cannicci S (2011) Human hydrographical changes interact with propagule predation behaviour in Sri Lankan mangrove forests. Journal of Experimental Marine Biology and Ecology, 399: 188–200.

Dai AY & Yang SL (1991) Crabs of the China Seas. China Ocean Press, Beijing and Berlin, xxi + 681 pp., pls. 1–74.

Dai AY, Yang SL, Song YZ & Chen GX (1986) Crabs of the China Seas. China Ocean Press, Beijing, 17 + 642 pp., figs. 1–295, pls. 1–74.

Dana JD (1851) Conspectus crustaceorum quae in orbis terrarum circumnavigatione, Carolo Wilkes e classe Reipublicae Foederatae Duce, lexit et descripsit J. D. Dana. Crustacea Grapsoidea, (Cyclometopa, Edwardsii). Proceedings of the Academy of Natural Sciences of Philadelphia, 5: 247–254.

Dana JD (1852) Crustacea, Part I. United States Exploring Expedition, During the Years 1838, 1839, 1840, 1841, 1842, Under the Command of Charles Wilkes, U.S.N., 13(2): 686–1618. C. SHERMAN, Philadelphia. Atlas [1855]. Vol. 14, 27 pp., pls. 1–96.

Darriba D, Taboada GL, Doallo R & Posada D (2012) jModel-Test 2: more models, new heuristics and parallel computing. Nature Methods, 9: 772.

Dartevelle E (1950) La côte et l'estuaire du Congo. Mémoires de l'Institut Royal Colonial Belge, Section de Sciences Naturelles et Médicales, 19(2): 1–58, figs. 1–8.

Davie PJF (2002) Crustacea: Malacostraca: Eucarida (Part 2: Anomura, Brachyura). In: Wells A & Houston WWK (eds.) Zoological Catalogue of Australia. Vol. 19.3b. CSIRO Publishing, Melbourne, 641 pp.

Davie PJF, Guinot D & Ng PKL (2015) Anatomy and functional morphology of Brachyura. In: Castro P, Davie PJF, Guinot D, Schram FR & von Vaupel Klein JC (eds.) Treatise on Zoology – Anatomy, Taxonomy, Biology. The Crustacea. Volume 9C-I. Decapoda: Brachyura (Part 1). Pp. 11–163.

Davie PJF & Ng PKL (2013) A review of *Chiromantes obtusifrons* (Dana, 1851) (Decapoda: Brachyura: Sesarmidae), with descriptions of four new sibling-species from Christmas Island, Guam and Taiwan. Zootaxa, 3609(1): 1–25.

Davie PJF & Pabriks L (2010) A new species of *Parasesarma* (Crustacea: Brachyura: Sesarmidae) from the mangroves of Western Australia. Zootaxa, 2564: 62–68.

Desmarest AG (1825) Considérations génerales 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. FG Levrault, Paris, xix + 446 pp., 56 pls.

Edmondson CH (1946) Reef and Shore Fauna of Hawaii. Special Publications. Bernice Pauahi Bishop Museum, 22: i–iii, 3–381, figs. 381–223.

Edmondson CH (1959) Hawaiian Grapsidae. Occasional Papers of the Bernice Pauahi Bishop Museum, Honolulu, 22: 153–202, figs. 1–27.

Emmerson WD (2016) A guide to, and checklist for, the Decapoda of Namibia, South Africa and Mozambique. Volumes 1–3. Cambridge Scholars Publishing, Cambridge. Vol. 1: 590 pp., Vol. 2: 650 pp., Vol. 3: 720 pp.

Fourmanoir P (1953) Notes sur la faune de la mangrove dans la région de Manjunga. Naturaliste Malgache, 5(1): 87–92.

Fransen CHJM, Holthuis LB & Adema JPHM (1997) Type-catalogue of the Decapod Crustacea in the collections of the Nationaal Naturhistorisch Museum, with appendices of pre-1900 collectors and material. Zoologische Verhandelingen, Leiden, 311: i–xvi, 1–344.

Fratini S, Vannini M, Cannicci S & Schubart CD (2005) Tree-climbing mangrove crabs, a case of convergent evolution. Evolutionary Ecology Research, 7(2): 219–233.

Fukuda Y & Baba K (1976) Complete larval development of the sesarminid crabs, *Chiromantes bidens*, *Holometopus haematocheir*, *Parasesarma plicatum*, and *Sesarmops intermedius*, reared in the laboratory. Memoirs of the Faculty of Education, Kumamoto University, Natural Science, 25: 61–75.

Gauld DT (1960) Brachyura: An annotated check-list of the Crustacea of Ghana, IV. Journal of the West African Science Association, 6(1): 68–72.

George RW (1978) The Land and Freshwater Crabs of Christmas Island. Unpublished report commissioned by the Australian National Parks and Wildlife Service, 22 pp.

Gibson-Hill CA (1947) Field notes on the terrestrial crabs. Bulletin of the Raffles Museum, 18: 43–52.

Gistel JNFX (1848) Naturgeschichte des Tierreichs, für höhere Schulen. 216 + xvi pp., (4), pls. 1–32.

Godsall B & Smallegange IM (2011) Assessment games and competitive behaviour of the mangrove tree-dwelling crab, *Selatium brockii* (De Man, 1887) (Decapoda, Grapsidae). Crustaceana, 84(14): 1697–1718.

Godwin S & Bolick H (2006) Inventory of Intertidal and Shallow Subtidal Marine Invertebrates at Kalaupapa National Historical Park, Moloka'i], Hawai'i. Final Report Prepared for the U.S. Department of Interior, National Park Service, Pacific Islands Coral Reef Program, Honolulu, 58 pp.

Guinot D (1967) La faune carcinologique (Crustacea Brachyura) de l'Océan Indien occidental et de la Mer Rouge. Catalogue, remarques biogéographiques et bibliographie. In: Réunion de Spécialistes C.S.A. sur les Crustacés, Zanzibar 1964. Mémoires de l'Institut Fondamental d'Afrique Noire, Ifan-Dakar, (77), 1966 (1967): 237–352.

Guinot D & Bouchard J-M (1998) Evolution of the abdominal holding systems of brachyuran crabs (Crustacea, Decapoda, Brachyura). Zoosystema, 20(4): 613–694, figs. 1–27, tabs. 1–3.

Guinot D, Tavares M & Castro P (2013) Significance of the sexual openings and supplementary structures on the phylogeny of brachyuran crabs (Crustacea, Decapoda, Brachyura), with new nomina for higher-ranked podotreme taxa. Zootaxa, 3665(1): 1–414.

Haan W De (1833–1849) Crustacea. In: Siebold PF (ed.) Fauna Japonica sive Descriptio Animalium, quae in Itinere per Japoniam, Jussu et Auspiciis Superiorum, Qui Summum in India Batava Imperium Tenent, Suscepto, Annis 18231830 Collegit, Notis, Observationibus et Adumbrationibus Illustravit, (Crustacea). LugduniBatavorum. Pp. ixvii + ixxxi + iixxvi + 1–243, pls. A–J, L–Q, 1–55, circ. table 2.

Hagen HO von (1978) The systematic position of *Sesarma* (*Sesarma*) *rectum* Randall and a new definition of the subgenus *Sesarma* (Brachyura, Grapsidae). Crustaceana, 34(1): 45–54.

Hall TA (1999) BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. Nucleic Acids Symposium Series, 41: 95–98.

Hartnoll RG (1975) The Grapsidae and Ocypodidae (Decapoda: Brachyura) of Tanzania. Journal of Zoology, 177: 305–328.

Heller C (1865) Crustaceen. In: Reise der Österreichischen Fregatte Novara um die Ede in den Jahren 1857, 1858, 1859 unter den Befehlen des Commodores B. von Wüllerstorf-Urbair. Zoologischer Theil. Zweiter Band, Volume 3(1). Pp. 1–280, 25 pls.

Henderson JR (1893) A contribution to Indian carcinology. Transactions of the Linnean Society of London, Series 2, Zoology, 5(10): 325–458, pls. 36–40.

Herklots JA (1861) Symbolae Carcinologicae. I. Catalogue des Crustacés qui ont servi de base au système carcinologique de M. W. de Haan, rédigé d'après la collection du Musée des Pays- Bas et les Crustacés de la Faune du Japan. Tijdschrift voor Entomologie uitgegeven door de Nederlandische Entomologische Vereeniging, Leyden, 1861: 1–43.

Hess W (1865) Beiträge zur Kenntnis der Decapoden-Krebse Ost-Australiens. Archiv für Naturgeschichte, 36: 127–173, pls. 1, 2.

Hicks J, Rumpff H & Yorkston H (1984) Christmas Crabs. Second Edition. Christmas Island Natural History Association, 81 pp.

Hilgendorf F (1869) Crustaceen. In: Peters WCH, Cabanis J, Hilgendorf F, von Martens E & Semper C (eds.) Baron Carl Claus von der Decken's Reisen in Ost-Afrika in den Jahren 1859–1865. C. F. Winter'sche, Leipzig and Heidelberg. Volume 3(1). Pp. 69–116, 147 [Appendix], pls. 1–6.

Ho P-H (2003) Land crabs in the coastal forest of Kenting National Park. Kenting National Park, Pingtung, 47 pp.

Hoang NK, Do VN, Nguyen TT & Nguyen TTH (2012) Preliminary data of three zoobenthos groups (Brachyura, Gastropoda and Bivalviva) found in the mangrove forest ecosystems of the Tran De Estuary, Soc Trang Province. Journal of Science of HNUE (Hanoi National University of Education), Chemical and Biological Sciences, 57(8): 72–80.

Holthuis LB (1977) The Grapsidae, Gecarcinidae and Palicidae (Crustacea: Decapoda: Brachyura) of the Red Sea. Israel Journal of Zoology, 26: 141–192.

Hong J-S, Choi J-W & Tsutsumi H (2010) Concluding remarks on the joint survey of macrobenthic fauna on Suncheon Tidal Flats by the participants of "Korea and Japan Joint Symposium on Biology of Tidal Flats 2009". Plankton Benthos Research, 5 (Supplement): 255–263.

Huang H-D & Liu H-C (2012) Comparison of visual orientation between two land crabs *Sesarmops intermedium* and *Scandarma lintou* in Kenting National Park, southern Taiwan. Integrative and Comparative Biology, 52: 267–267.

Huang J, Liu Q, Zhao Y, Dou B, Li L, Liu W & Lin J (2011) The crab fauna in the mangrove of the Qi'Ao Island, Zhuhai. Ecology and Environmental Sciences, 20(4): 730–736.

Huang Z-G (ed.) (1994) Brachyura. In: Marine species and their distributions in China's Seas. Department of Ocean Management and Monitoring State Oceanic Administration. China Ocean Press, Beijing. Pp. 576–600.

Huelsenbeck JP & Ronquist F (2001) MRBAYES: Bayesian inference of phylogenetic trees. Bioinformatics, 17: 754–755.

Humes AG (1957) The genus *Cancrincola* (Copepoda, Harpacticoida) on the West Coast of Africa. Bulletin de l'Institut Français d'Afrique Noire, (A) 19(1): 180–194, pls. 1–3.

ICZN, International Commission on Zoological Nomenclature (1999) International Code of Zoological Nomenclature. International Commission of Zoological Nomenclature. Fourth Edition. Adopted by the XXI General Assembly of the International Union of Biological Sciences. International Trust for Zoological Nomenclature, in association with the British Museum (Natural History), London, 338 pp.

Ingle RW & Fernando CH (1963) On some fresh and brackish water crustaceans from Ceylon. Crustaceana, 6(2): 101–109.

Jesse R, Schubart CD & Klaus S (2010) Identification of a cryptic lineage within *Potamon fluviatile* (Herbst) (Crustacea: Brachyura: Potamidae). Invertebrate Systematics, 24(4): 348–356.

Johnston 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 (ed.) Liberia with an appendix on the flora of Libera by Dr. O. Stapf. Volume 2. Hutchinson & Co., London. Pp. 860–883.

Jordan HD (1957) Crabs as pests of rice on tidal swamps. Empire Journal of Experimental Agriculture, 25(99): 197–206.

Kamita T (1941) Studies of the decapod crustaceans of Chosen. Pt. 1. Crabs. The Fisheries Society of Chosen, Keijo, 289 pp., 146 text-figs., 1 map.

Kim HS (1973) Anomura and Brachyura. In: Illustrated Encyclopaedia of Fauna and Flora of Korea. Vol. 14. Ministry of Education, Sam Wha Publishing Co., Republic of Korea, 694 pp., 112 pls.

Kishino T, Nomoto A, Kimura S, Yonezawa T & Wada K (2001) Brachyuran crab species recorded in the brackish waters of Amami-Oshima Island, Kagoshima Prefecture, Japan. Nankiseibutu, 43: 125–131.

Kobayashi S (2000) Distribution pattern and ecology of brachyuran crabs in the riverine environment: their significance in the ecosystem and present condition. Ecological Civil Engineering, 3(1): 113–130.

Komai T & Ng PKL (2013) A new species of sesarmid crab of the genus *Chiromantes* (Crustacea: Decapoda: Brachyura) from the Ogasawara Islands, Japan. Zootaxa, 3681(5): 539–551.

Komatsu H (2011) Crabs dredged off the Ogasawara Islands (Crustacea, Decapoda, Brachyura). Memoirs of the National Museum of Nature and Science, 47: 219–277.

Kwok WPW & Tang W-S (2005) An Introduction to Common Sesarmine Crabs of Hong Kong. Hong Kong Biodiversity, Agriculture, Fisheries and Conservation Department Newsletter, 9: 1–6.

Kyomo J (1986) Reproductive activities in the sesarmid crab *Sesarma intermedia* in the coastal and estuarine habitats of Hakata, Japan. Marine Biology, 91: 319–329.

Lanchester WF (1900) On a collection of crustaceans made at Singapore and Malacca. Part I. Crustacea Brachyura. Proceedings of the Zoological Society of London, 1900(3): 719–770, pls. 44–47.

Latreille PA (1803) Histoire naturelle, générale et particulière des Crustacés et des Insectes. Ouvrage faisant suite aux oeuvres de Leclerc de Buffon, et partie du cours complet d'histoire naturelle rédigé par C. S. Sonnini, membre de plusieurs sociétés savantes. Vol. 5. F. Dufart, Paris, 468 pp.

Latreille PA (1806) Genera Crustaceorum et Insectorum secundum Ordinem naturalem in Familias disposita, iconibus, exemplisque plurimis explicata. Apud Amand Koenig Bibliopolam, Paris, 302 pp.

Laurie RD (1906) Report on the Brachyura collected by Professor Herdman, at Ceylon, in 1902. In: Herdman WA (ed.) Report to the Government of Ceylon on the Pearl Oyster Fisheries of the Gulf of Manaar with Supplementary Reports Upon the Marine Biology of Ceylon by Other Naturalists, 5 (Supplemental Reports No. 40): 349–432, figs. 1–12, pls. 1, 2.

Lee HJ (2015) First zoea of *Sesarmops intermedius* (De Haan, 1835) (Crustacea: Decapoda: Brachyura: Sesarmidae). Fisheries & Aquatic Sciences, 18(3): 321–324.

Lee J-H (2008) A Field Guide to Crabs in Taiwan. Bigtrees Company, Taipei, 174 pp.

Lee S-K, Jung J, Kang S & Kim W (2012) Isolation and characterization of microsatellite markers for the endangered crab species *Sesarmops intermedius*. Conservation Genetics and Resources, 4: 183–185.

Lee SY (1995) Endemic sesarmine crabs rediscovered. Porcupine, 12: 3.

Li J-J (2014) Redescription of two poorly known sesarmid crabs from Taiwan. Platax, 11: 83–93.

Li J-J & Chiu Y-W (2013) Land crabs of Hengchun Peninsula. National Museum of Marine Biology & Aquarium, Pingtung, 95 pp.

Li J-J, Rahayu DL & Ng PKL (2018) Identity of the tree-spider crab, *Parasesarma leptosoma* (Hilgendorf, 1869) (Decapoda: Brachyura: Sesarmidae), with seven new species from the West Pacific. Zootaxa, 4482(3): 451–490.

Li J-J, Shih H-T & Ng PKL (2019a) Three new species and two new records of *Parasesarma* De Man, 1895 (Crustacea: Brachyura: Sesarmidae) from Taiwan and the Philippines, from morphological and molecular evidence. Zoological Studies, 58: 40. doi: 10.6620/ZS.2019.58-40, 23 pp.

Li J-J, Shih H-T & Ng PKL (2020) The Taiwanese and Philippine species of the terrestrial crabs *Bresedium* Serène and Soh, 1970 and *Sesarmops* Serène and Soh, 1970 (Crustacea: Decapoda: Brachyura), with descriptions of two new species. Zoological Studies, 59: 16. doi: 10.6620/ZS.2020.59-16, 32 pp.

Li Q, Xu C, Wang C & Liu G (2019b) The complete mitochondrial genome of the red-clawed crab *Chiromantes haematochir* (Sesarmidae: Grapsidae). Mitochondrial DNA B Resources, 4(1): 53–54.

Lim KKP & Chua MAH (2015) Swamp crab *Pseudosesarma bocourti* on Pulau Tekong. Singapore Biodiversity Records, 2015: 18.

Lin D-R, Chao R-F, Lu C-Y & Hsieh L-C (2011) Guide to the Land Crabs of Lyudao (Green Island), Taiwan. Taitung County Government, Taitung, 57 pp.

Liu H-C (2009) Diversity, population biology and managements of land crabs in the Kenting National Park. The National Kenting Headquarters, Kenting, 77 pp.

Liu H-C & Wang C-H (2010) Taiwan Coastal Wetland Crabs. Wild Bird Society of Taipei, Taipei, 79 pp.

Liu W & He W (2007) The benthic macro-invertebrates in Yangtze Estuary. Shanghai Scientific & Technical Publisher, Shanghai, 203 pp.

Longhurst AR (1958) An Ecological Survey of the West African Marine Benthos. Colonial Office, Fishery Publications, Issue 11. H.M. Stationery Office, London, 102 pp., 11 figs.

Lucas JS (1981) Spider crabs of the family Hymenosomatidae (Crustacea: Brachyura) with particular reference to Australian species: Systematics and biology. Records of the Australian Museum, 1980, 33(4): 148–247, figs. 1–10.

Man JG De (1880) On some species of the genus *Sesarma* Say and *Cardisoma* Latr. Notes Leyden Museum, 2(5): 21–36.

Man JG De (1883) Carcinological Studies in the Leyden Museum. No. 3. Notes from the Leyden Museum, 5(3): 150–169.

Man JG De (1887) Übersicht der Indopacifischen Arten der Gattung *Sesarma* Say nebst einer Kritik der von W. Hess und E. Nauck in den Jahren 1865 und 1880 beschrieben Decapoden. Zoologische Jahrbücher, Abtheilung für Systematik, Geographie und Biologie der Thiere, 2: 639–722.

Man JG De (1888) 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 IV. Journal of the Linnean Society of London (Zoology), 22(139): 177–240, pls. 13–15.

Man JG De (1889) Ueber einige neue oder seltene indopacifische Brachyuren. Zoologische Jahrbücher, Abteilung für Systematik, Geographie und Biologie der Thiere, Jena, 4(2): 409–452, pls. 9, 10.

Man JG De (1891) Carcinological studies in the Leyden Museum. No. 5. Notes from the Leyden Museum, 13: 1–61, pls. 1–4.

Man JG De (1892) Carcinological studies in the Leyden Museum, No. 6. Notes Leyden Museum, 14(36): 225–264, pls. 7–10.

Man JG De (1895) Bericht über die von Herrn Schiffscaptän Storm zu Atjeh, an den westlichen Küsten von Malakka, Borneo und Celebes sowie in der JavaSee gesammelten Decapoden und Stomatopoden. Zweiter Theil. Zoologische Jahrbücher, Abtheilung für Systematik, Geographie und Biologie der Thiere, 9: 75–218.

Man JG De (1900) Note sur une petite collection de Crustacés décapodes provenant de la côte d'Angola (Afrique occidentale). Mémoires de la Société Zoologique de France, 13: 31–65, 2 pls.

Man JG De (1902) Die von Herrn Professor Kükenthal im Indischen Archipel gesammelten Dekapoden und Stomatopoden. In: Kükenthal W (ed.) Ergebnisse einer Zoologischen Forschungsreise in den Molukken und Borneo, in Aufträge der Senckenberg. Naturforsch. Gesellschaft ausgeführt von Dr. Willy Kükenthal. Abhandlungen der Senckenbergischen naturforschenden Gesellschaft, 25(3): 467–929, pls. 19–27.

Manning RB & Holthuis LB (1981) West African brachyuran crabs (Crustacea: Decapoda). Smithsonian Contributions to Zoology, 306: i–xii, 1–379, figs. 1–88, table 1.

Marumura M & Kosaka A (2003) Catalog of the Brachyuran and Anomuran Crabs Donated by the Late Mr. Seiji Nagai to the Wakayama Prefectural Museum of Natural History. Wakayama Prefectural Museum of Natural History, Kainan, 74 pp.

Matsuzawa K (1977) Sea Shore Animals of Muroto. Kansai-Insatsu-Kogyi, Japan, unnumbered pages, 126 pls.

McNeill FA (1968) Crustacea, Decapoda & Stomatopoda. Great Barrier Reef Expedition 1928–29. Scientific Reports, 7(1): 1–98

Miers EJ (1880) On a collection of Crustacea from the Malayan Region. Part II. Telphusidea, Catometopa and Oxystomata. Annals and Magazine of Natural History, Series 5, 5(28): 304–317, pl. 14.

Milne-Edwards A (1869) Notes sur quelques nouvelles espèces du genre *Sesarma* (Say). Nouvelle Archives du Muséum d'Histoire Naturelle, Paris, 5: 25–31.

Milne-Edwards A (1873) Recherches sur la faune carcinologique de la NouvelleCalédonie. Deuxième Partie. Groupe des Cyclometopes Neptunens. Nouvelles Archives du Muséum d'Histoire naturelle, Paris 9: 155–332, pls. 4–18.

Milne Edwards H (1834–1837) Histoire naturelle des Crustacés comprenant l'anatomie, la physiologie et la classification de ces animaux. Paris, Librairie Encyclopédique de Roret. Vol. 1: i–xxxv, 1–468. Vol. 2: 1–531. Atlas (1837): 1–32, pls. 1–42. Vol. 3, 1840: 1–638.

Milne Edwards H (1853) Mémoires sur la famille des Ocypodiens, suite. Annales de Sciences Naturelle, Zoology, Paris, Serie 3 (Zoologie) 20: 163–228, pls. 6–11. [A continuation of H. Milne Edwards, 1852, and reprinted with it in the undated Mélanges Carcinologiques pp. 129–196]

Minemizu R (2000) [Marine decapod and stomatopod crustaceans mainly from Japan]. Bun-Ichi Sogo Shuppan, Tokyo, 344 pp.

Miyake S (1983) Japanese Crustacean Decapods and Stomatopods in Color, vol. II. Brachyura (Crabs). First Edition. Hoikusha, Osaka, viii + 277 pp., 64 pls., unnumbered figs.

Monod T (1956) Hippidea et Brachyura ouest-africains. Mémoires de I'Institut Français d'Afrique Noire, 45: 1–674, 884 figs.

Muraoka K (1998) Catalogue of the Brachyuran and Anomuran Crabs donated by Prof. Dr. Tune Sakai to the Kanagawa Prefectural Museum. Catalogue of the Collection in the Kanagawa Prefectural Museum of Natural History, Odawara, Kanagawa, Japan, No. 11: 1–67.

Naderloo R (2011) Grapsoid crabs (Decapoda: Brachyura: Thoracotremata) of the Persian Gulf and the Gulf of Oman. Zootaxa, 3048: 1–43.

Naderloo R (2017) Atlas of crabs of the Persian Gulf. Springer, 440 pp.

Naderloo R & Schubart CD (2009) Redescription and mitochondrial identification of *Chiromantes boulengeri* (Calman, 1920) (Decapoda: Brachyura: Sesarmidae) based on fresh material from the Persian Gulf, Iran. Zootaxa, 2128: 61–68.

Naderloo R & Türkay M (2012) Decapod crustaceans of the littoral and shallow sublittoral Iranian coast of the Persian Gulf: Faunistics, Biodiversity and Zoogeography. Zootaxa, 3374: 1–67.

Nagai S & Nomura K (1988) Crustacea (Brachyura), [The guide book of marine organisms of Okinawa]. No. 7. Shinsei Tosho, Okinawa, 250 pp.

Naiyanetr P (1998) Checklist of Crustacean Fauna in Thailand (Decapoda, Stomatopoda, Anostraca, Myodocopa and Isopoda). Office of Environmental Policy and Planning, Bangkok, 161 pp.

Naiyanetr P (2007) Checklist of Crustacean Fauna in Thailand (Decapoda, Stomatopoda, Anostraca, Myodocopa and Isopoda). Office of Natural Resources and Environmental Policy and Planning, Bangkok, 196 pp.

Nara Y, Kitaura J & Wada K (2006) Comparison of social behaviors among six grapsoid species (Brachyura) of different habitat conditions. Crustacean Research, 35: 56–66.

Naruse T (2005) *Chiromantes haematocheir* (De Haan, 1833). In: Nature Conservation Division (Department of Cultural and Environmental Affairs, Okinawa Prefectural Government) (ed.) Threatened Wildlife in Okinawa, 2nd edition (Animals) —Red Data Okinawa. Nature Conservation Division (Department of Cultural and Environmental Affairs, Okinawa Prefectural Government), Okinawa, 221 pp.

Naruse T & Ng PKL (2008) A new species of *Chiromantes* s. str. (Decapoda: Brachyura: Sesarmidae) from the Ryukyu Islands, Japan, with a note on the identity of *Holometopus serenei* Soh, 1978. Crustacean Research, 37: 1–13.

Naruse T & Ng PKL (2020) Revision of the sesarmid crab genera *Labuanium* Serène and Soh, 1970, *Scandarma* Schubart, Liu and Cuesta, 2003, and *Namlacium* Serène and Soh, 1970 (Crustacea: Decapoda: Brachyura: Grapsoidea), with descriptions of four new genera and three new species. Journal of Natural History, 54(7–8): 445–532.

Naser MD, Page TJ, Ng NK, Apel M, Yasser AG, Bishop JM, Ng PKL & Clark PF (2012) Invasive records of *Eriocheir hepuensis* Dai, 1991 (Crustacea: Brachyura: Grapsoidea: Varunidae): implications and taxonomic considerations. BioInvasions Records, 1(1): 71–86.

Ng PKL (1995) The freshwater crabs and prawns (Crustacea: Decapoda) of Bako National Park, Sarawak, Malaysia, with descriptions of one new genus and three new species. Raffles Bulletin of Zoology, 43(1): 181–205.

Ng PKL (2018) On two new species of potamid and sesarmid crabs (Decapoda, Brachyura) from caves in Myanmar. Crustaceana, 91(2): 185–197.

Ng PKL & Davie PJF (2012) Christmas Island – a very crabby history. In: Orchard M (ed.) Crabs of Christmas Island. Christmas Island Natural History Association. Pp. 8–19.

Ng PKL & Devi SS (2020) A new tree-spider crab of the genus *Leptarma* (Brachyura, Sesarmidae) from mangroves in Kerala, India. Crustaceana, 93(7): 759–768.

Ng PKL, Guinot D & Davie PJF (2008a) Systema Brachyurorum: Part I. An annotated checklist of extant brachyuran crabs of the world. Raffles Bulletin of Zoology, Supplement 17: 1–286.

Ng PKL, Lee BY & Tan HH (2015) Observations on the taxonomy and ecology of *Labuanium politum* (De Man, 1887) (Crustacea: Decapoda: Sesarmidae), an obligate arboreal crab on the nipah palm, *Nypa fructicans* (Arecales: Arecaceae). Raffles Bulletin of Zoology, Supplement 31: 216–225.

Ng PKL, Li J-J & Shih H-T (2020) What is *Sesarmops impressus* (H. Milne Edwards, 1837) (Crustacea: Brachyura: Sesarmidae)? Zoological Studies, 59: 27, pp. 1–39. doi: 10.6620/ZS.2020.59-27

Ng PKL & Liu HC (1999) The taxonomy of *Sesarma tangi* Rathbun, 1931 and *S. stormi* De Man, 1895 (Crustacea: Decapoda: Brachyura: Grapsidae: Sesarminae), with establishment of a new genus for *S. stormi*. Zoological Studies, 38(2): 228–237.

Ng PKL, Rani V & Nandan B (2017a) A new species of *Pseudosesarma* Serène & Soh, 1970 (Crustacea: Brachyura: Sesarmidae) from Cochin in southwest India. Zootaxa, 4311(2), 263–270.

Ng PKL & Schubart CD (2003) On the identities of *Sesarma obesum* Dana, 1851, and *Sesarma eydouxi* H. Milne Edwards, 1853 (Crustacea: Decapoda: Brachyura: Sesarmidae). Zoosystema, 25(3): 425–437.

Ng PKL & Schubart CD (2017) On the taxonomy of *Pseudosesarma edwardsii* (De Man, 1887) and *P. crassimanum* (De Man, 1887) (Crustacea: Decapoda: Brachyura: Sesarmidae), with description of a new species from Sri Lanka. Raffles Bulletin of Zoology, 65: 655–669.

Ng PKL, Shih H-T & Cannicci S (2019) A new genus for *Sesarma* (*Holometopus*) *tangi* Rathbun, 1931 (Decapoda: Brachyura: Sesarmidae) from mangrove forests, with notes on its ecology and conservation. Journal of Crustacean Biology, 40(1), 89–96. doi: 10.1093/jcbiol/ruz078

Ng PKL, Shih H-T, Ho P-H & Wang C-H (2017b) An updated annotated checklist of brachyuran crabs from Taiwan (Crustacea: Decapoda). Journal of the National Taiwan Museum, 70(3–4): 1–185.

Ng PKL, 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 Series, 11: 1–86, 8 colour pls.

Ng PKL, Wang LK & Lim KKP (eds.) (2008b) Private Lives. An Exposé of Singapore's Mangroves. Raffles Museum of Biodiversity Research, National University of Singapore, Singapore, 249 pp.

Nobili G (1900) Decapodi e stomatopodi Indo-Malesi. Annali del Museo Civico di Storia Naturale di Genova, Series 2, 20(40): 473–523, figs. 1–4.

Oh SM, Chung DE & Ko HS (2007) Complete larval development of *Chiromantes haematocheir* (Crustacea: Decapoda: Brachyura: Grapsidae), with a key to seven sesarminid zoeas in Korea. Korean Journal of Systematics and Zoology, 23(1): 9–20.

Ooishi S (1970) Marine invertebrate fauna of the Ogasawara and volcano islands collected by S. Ooishi, Y. Tomida, K. Izawa and S. Manabe. Report on the Marine Biological Expedition to the Ogasawara (Bonin) Islands, 1968, 102 pp., 25 pls.

Orchard M (2012) Crabs of Christmas Island. Christmas Island Natural History Association, 287 pp.

Ortmann AE (1894) Abtheilung: Brachyura (Brachyura genuina Boas), III. Unterabtheilung: Cancroidea. 2. Section: Cancrinea, 2. Gruppe: Catametopa. 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 [= Part 8]. Zoologische Jahrbücher, Abtheilung für Systematik, Geographie und Biologie der Thiere, 7(5): 683–772, pl. 23.

Parisi B (1918) I decapodi giapponese del Museo di Milano VI. Catometopa e Paguridea. Atti della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano, 57: 90–115, pl. 8.

Pati SK, Sujila PS & Sudha Devi AR (2020) Crab out of its shell: multiple records of the sesarmid crab, *Pseudosesarma glabrum* Ng, Rani & Bijoy Nandan, 2017 (Decapoda: Brachyura:

Sesarmidae), confirm species' wide distribution along the west coast of India. In: Nandan SB, Priyaja P & Jayachandran PR (eds.) Frontiers in Benthic Science. Cochin University of Science and Technology, Kochi, India. Pp. 139–146.

Paulay G, Kropp R, Ng PKL & Eldredge LG (2003) The crustaceans and pycnogonids of the Mariana Islands. Micronesica, 35–36: 456–513.

Paulay G & Starmer J (2011) Evolution, insular restriction, and extinction of oceanic land crabs, exemplified by the loss of an endemic *Geograpsus* in the Hawaiian Islands. PLoS ONE, 6(5): e19916. doi: 10.1371/journal.pone.0019916

Posada D & Buckley TR (2004) Model selection and model averaging in phylogenetics: advantages of Akaike information criterion and Bayesian approaches over likelihood ratio tests. Systematic Biology, 53: 793–808.

Rademacher M & Mengedoht O (2011) Krabben-Fibel. Die schönsten Krabben für das Aquaterrarium. Dähne Verlag, Ettlingen, Germany, 95 pp.

Ragionieri L, Fratini S & Schubart CD (2012) Revision of the *Neosarmatium meinerti* species complex (Decapoda: Brachyura: Sesarmidae), with descriptions of three pseudocryptic Indo-West Pacific species. Raffles Bulletin of Zoology, 60(1): 71–87.

Rahayu DL & Ng PKL (2010) Revision of the *Parasesarma plicatum* (Latreille, 1803) species-group (Crustacea: Decapoda: Brachyura: Sesarmidae). Zootaxa, 2327: 1–22.

Randall JW (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 Science of Philadelphia, 8: 106–147, pls. 1–5.

Rathbun MJ (1897) Synopsis of the American Sesarmæ, with description of a new species. Proceedings of the Biological Society of Washington, 11: 89–92.

Rathbun MJ (1900) The decapod crustaceans of West Africa. Proceedings of the United States National Museum, 22(1199): 271–316.

Rathbun MJ (1906) The Brachyura and Macrura of the Hawaiian Islands. Bulletin of the United States Fish Commission, 23(3): 827–930, figs. 1–73, pls. 1–24.

Rathbun MJ (1914) New species of crabs of the families Grapsidae and Ocypodidae. Proceedings of the United States National Museum, 47(2044): 69–85.

Rathbun MJ (1921) The Brachyuran crabs collected by the American Museum Congo Expedition, 1909–1915. In: Scientific results of the American Museum Congo Expedition. General Invertebrate Zoology, No. 6. Bulletin of the American Museum of Natural History, 43: 379–484, figs. 1–22, pls. 15–44.

Rathbun MJ (1931) New and rare Chinese crabs. Lingnan Science Journal (1929), 8: 75–125, pls. 5–15.

Ribero L, Lim PE, Ramli R & Polgar G (2020) Assemblage structure, distribution and habitat type of the grapsoid crabs (Brachyura: Grapsoidea) of the coastal forested swamps of northern Borneo. Regional Studies in Marine Science, 37: 101323, 11 pp. doi: 10.1016/j.rsma.2020.101323

Rossignol M (1957) Crustacés Décapodes marins de la region de Pointe-Noire. In: Collignon J, Rossignol M & Roux C (eds.) Mollusques, Crustacés, Poissons Marins des côtes d'A.E.F. en collection au Centre d'Océanographie de d'Institut d'Études Centrafricaines de Pointe-Noire. Paris. Pp. 71–136, figs. 1–20, pls. 1–3.

Rossignol M (1962) Catalogue de Crustacés Décapodes Brachyoures, Anomoures et Macroures littoraux en collection au centre d'océanographie de Pointe-Noire. Travaux du Centre Océanographique de Pointe-Noire, 2: 111–138, pls. 1–4.

Roux J (1917) Crustacés (Expédition de 1903). In: Résultats de l'Expédition scientifique Néerlandaise à la Nouvelle-Guinée en 1903. Nova Guinea, Zoologie, 5: 589–621, pls. 27, 28.

Roux J (1933) Crustacés Décapodes d'eau douce. In: Résultats Scientifiques du Voyage aux Indes Orientales Néerlandaises de LL. AA. RR. le Prince et la Princesse Léopold de Belgique. Memoires du Musée Royal d'Histoire Naturelle de Belgique, Hors Série [= Supplement] 3, No. 14 [= 3(14)]: 1–18, figs. 1, 2.

Sakai T (1936) Crabs of Japan. 66 plates in life colours with descriptions. Sanseido, Tokyo, 239 pp., 12 pp. [literature cited], 27 pp. [bibliography and index], 66 pls. [dated 1935 but published in 1936]

Sakai T (1939) Studies on the Crabs of Japan. IV. Brachygnatha, Brachyrhyncha. Yokendo Co., Ltd., Tokyo. Pp. 365–741 + 1–23 [= Index], figs. 1–129, pls. XLII–CXI, tables 1–6.

Sakai T (1965) The Crabs of the Sagami Bay collected by His Majesty the Emperor of Japan. Maruzen Co., Tokyo. xvi + 206 pp. [English section], figs. 1–27, pls. 1–100, pp. 1–92 [in Japanese] + 1–26 [Bibliography and Index in English] + 27–32 [Index in Japanese], 1 map.

Sakai T (1976) Crabs of Japan and the Adjacent Seas. Kodansha Ltd., Tokyo. In three volumes. xxix + 773 pp. [English Text], 461 pp. [Japanese Text]. Pp. 1–16, pls. 1–251 [Plates volume].

Say T (1817–1818) An account of the Crustacea of the United States. Journal of the Academy of Natural Science of Philadelphia, 1(1–2): 57–63, 65–80 (pl. 4), 97–101, 155–160, 161–169 [1817]; 235–253, 313–319, 374–380, 381–401, 423–441 [1818].

Schubart CD (2009) Mitochondrial DNA and decapod phylogenies; the importance of pseudogenes and primer optimization. In: Martin JW, Crandall KA & Felder DL (eds.) Crustacean Issues 18: Decapod Crustacean Phylogenetics. Taylor & Francis/CRC Press, Boca Raton, Florida. Pp. 47–65.

Schubart CD, Cannicci S, Vannini M & Fratini S (2006) Molecular phylogeny of grapsoid crabs and allies based on two mitochondrial genes and a proposal for refraining from current superfamily classification. Journal of Zoological Systematics and Evolutionary Research, 44(3): 193–199.

Schubart CD, Cuesta JA, Diesel R & Felder DL (2000a) Molecular phylogeny, taxonomy, and evolution of non-marine lineages within the American grapsoid crabs (Crustacea: Brachyura). Molecular Phylogeny and Evolution, 15(2): 179–190.

Schubart CD, Cuesta JA & Felder DL (2002) Glyptograpsidae, a new brachyuran family from Central America: larval and adult morphology, and a molecular phylogeny of the Grapsoidea. Journal of Crustacean Biology, 22(1): 28–44.

Schubart CD, Diesel R & Hedges SB (1998) Rapid evolution to terrestrial life in Jamaican crabs. Nature, 393: 363–365.

Schubart CD, Liu H-C & Cuesta JA (2003) *Scandarma lintou*, a new genus and new species of tree-climbing crab (Crustacea: Brachyura: Sesarmidae) from Taiwan with notes on its ecology, larval morphology and phylogeny. Raffles Bulletin of Zoology, 51(1): 49–63.

Schubart CD, Liu H-C & Ng PKL (2009) Revision of *Selatium* Serène & Soh, 1970 (Crustacea: Brachyura: Sesarmidae), with description of a new genus and two new species. Zootaxa, 2154: 1–29.

Schubart CD, Neigel JE & Felder DL (2000b) The use of the mitochondrial 16S rRNA gene for phylogenetic and biogeographic studies of Crustacea. In: The Biodiversity Crisis and Crustacea. Proceedings of the Fourth International Crustacean Congress, Amsterdam, Netherlands, 20–24 July 1998, Vol. 2. Crustacean Issues, 12: 817–830.

Schubart CD & Ng PKL (2002) The sesarmid genus *Neosarmatium* (Decapoda: Brachyura): new distribution records and a new species from Sulawesi. Crustacean Research, 31: 28–38.

Schubart CD & Reuschel S (2009) A proposal for a new classification of Portunoidea and Cancroidea (Brachyura: Heterotremata) based on two independent molecular phylogenies. In: Martin JW, Crandall KA & Felder DL (eds.) Crustacean Issues 18: Decapod Crustacean Phylogenetics. Taylor & Francis/CRC Press, Boca Raton, Florida. Pp. 533–549.

Serène R (1968) The Brachyura of the Indo Pacific Region. In: Prodromus for a check list of the nonplanctonic marine fauna of South East Asia. Singapore National Academy of Science, Special Publication No. 1: 33–112.

Serène R & Soh CL (1970) New IndoPacific genera allied to *Sesarma* Say 1877 (Brachyura, Decapoda, Crustacea). Treubia, 27: 387–416.

Shahdadi A, Davie PJF & Schubart CD (2017) *Perisesarma tuerkayi*, a new species of mangrove crab from Vietnam (Decapoda, Brachyura, Sesarmidae), with an assessment of its phylogenetic relationships. In: Magalhães C, Becker C, Davie PJF, Klimpel S, Martínez-Arbizu P & Sonnewald M (eds.) Special Issue dedicated to the memory of Michael Türkay (1948–2015). Crustaceana, 90(7–10): 1155–1175.

Shahdadi A, Davie PJF & Schubart CD (2018a) Systematics and phylogeography of the Australasian mangrove crabs *Parasesarma semperi* and *P. longicristatum* (Decapoda: Brachyura: Sesarmidae) based on morphological and molecular data. Invertebrate Systematics, 32: 196–214.

Shahdadi A, Fratini S & Schubart CD (2020) Taxonomic reassessment of *Parasesarma* (Crustacea: Brachyura: Decapoda: Sesarmidae) based on genetic and morphological comparisons, with description of a new genus. Zoological Journal of the Linnean Society, 190(4): 1123–1158. doi: 10.1093/zoolinnean/zlaa025/5825211

Shahdadi A, Ng PKL & Schubart CD (2018b) Morphological and phylogenetic evidence for a new species of *Parasesarma* De Man, 1895 (Crustacea: Decapoda: Brachyura: Sesarmidae) from the Malay Peninsula, previously referred to as *Parasesarma indiarum* (Tweedie, 1940). Raffles Bulletin of Zoology, 66: 739–762.

Shahdadi A & Schubart CD (2017) Taxonomic review of *Perisesarma* (Decapoda: Brachyura: Sesarmidae) and closely related genera based on morphology and molecular phylogenetics: new classification, two new genera and the questionable phylogenetic value of the epibranchial tooth. Zoological Journal of the Linnean Society, 182(3): 517–548. [First online 24 August 2017; doi: 10.1093/zoolinnean/zlx032]

Shen C (1931) The crabs of Hong Kong. Part II. Hong Kong Naturalist, 2(3): 185–197, Addenda, figs. 1–13, pls. 12–14.

Shen C (1932) The Brachyuran Crustacea of North China. Zoologica Sinica, Series A (Invertebrates of China), Vol. 9, Fasc. 1. The Fan Institute of Biology, Peking [= Beijing], China, x + 321 pp., 171 figs., 10 pls., 1 map.

Shen CJ (1940a) The brachyuran fauna of Hong Kong. Journal of the Hong Kong Fisheries Research Station, 1: 211–242.

Shen C (1940b) On the collection of crabs of south China. Bulletin of the Fan Memorial Institute of Biology, Zoology Series, Peiping, 10(2): 69–104.

Shen J & Dai A (1964) [Illustrations of Animals in China (Crustacea Part II)]. Peking, 142 pp., 277 figs.

Shet GN, Subash Chandran MD & Ramachandra TV (2016) Brachyuran crabs of Aghanashini Estuary, South Indian West Coast, Karnataka. In: Proceedings of the Lake 2016: Conference on Conservation and Sustainable Management of Ecologically Sensitive Regions in Western Ghats, 2016, 17 pp.

Shih H-T, Hsu P-Y, Shahdadi A, Schubart CD & Li J-J (2019) The synonymy of the supratidal crab species *Parasesarma cognatum* Rahayu & Li, 2013 with *P. liho* Koller, Liu & Schubart, 2010 (Decapoda: Brachyura: Sesarmidae) based on morphological and molecular evidence, with a note on *P. paucitorum* Rahayu & Ng, 2009 Zoological Studies 58: 21. doi: 10.6620/ZS.2019.58-21, pp. 1–13.

Shokita S (1990) Inland-water decapods and their distribution in Iriomotejima Island of the Ryukyu Islands. In: Nature Conservation Bureau, Environment Agency (ed.) Study of Essential Factors for Preservation of Wildlife in Nansei Islands, Nature Conservation Bureau, Environment Agency, Tokyo. Pp. 305–317.

Shokita S, Fujita Y, Nagai T, Salim MI & Shinjo K (2003) Distribution and abundance of crustaceans in the mangrove swamp and upper reaches of the Sumiyou River and Yakugachi River, Amami-ohshima Island, Japan. In: Research Institute for Subtropics (ed.) A Comprehensive Study for Mangrove Ecosystem in Okinawa, Research Institute for Subtropics, Okinawa. Pp. 113–124.

Shokita S, Nagai T, Fujita Y, Naruse T, Ito A, Nagamatsu, T Yamzaki, T, Shinjo K & Nagata Y (2002) Distribution and abundance of crustaceans in the Ohura River Mangrove Swamp of Okinawa Island, Japan. In: Research Institute for Subtropics (ed.) A Comprehensive Study for Mangrove Ecosystem in Okinawa, Research Institute for Subtropics, Okinawa. Pp. 73–86.

Sivasothi N (2000) Niche preferences of tree-climbing crabs in Singapore mangroves. Crustaceana, 73: 25–38.

Sivasothi N, Murphy DH & Ng PKL (1993) Treeclimbing and herbivory of crabs in the Singapore mangroves. In: Sasekumar A (ed.) Mangrove Fisheries and Connections. ASEANAustralia Marine Science Project: Living Resources (Malaysia), Kuala Lumpur. Pp. 220–237.

Soh CL (1978) On a collection of sesarmine crabs (Decapoda, Brachyura, Grapsidae) from Hong Kong. Memoirs of the Hong Kong Natural History Society, 13: 9–22.

Stebbing TRR (1910) General Catalogue of South African Crustacea (Part V. of S. A. Crustacea, for the Marine Investigations in South Africa). Annals of the South African Museum, 6(4): 281–593, pls. 15–21.

Stimpson W (1858) Crustacea Ocypodoidea. Prodromus descriptionis animalium evertebratorum, quae in Expeditione ad Oceanum Pacificum Septentrionalem, a Republica Federata missa, Cadwaladaro Ringgold et Johanne Rodgers Ducibus, observavit et descripsit. Pars V. Proceedings of the Academy of Natural Sciences of Philadelphia, 10: 93–110.

Stimpson W (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.

Sulieman Y & Pengsakul T (2013) Laboratory and semi-field evaluation on the biological control of *Oncomelania hupensis* snail (Gastropoda: Pomatiopsidae), using *Sesarmops intermedium* Crab (Decapoda: Grapsidae). Asian Transactions on Basic and Applied Sciences, 3(1): 1–5.

Takeda M (1975) Brachyura. In: Utinomi H (ed.) Aquatic Invertebrates. First Edition. Gakken Chukosei zukan, 9: 120–149 (fig. with Latin names), 188–331 (descriptions).

Takeda M (1982) Keys to the Japanese and foreign crustaceans fully illustrated in colors. Hokuryukan, Tokyo, vi + 285 pp., 58 pp. (keys).

Takeda M & Miyake S (1976) Crabs of the Ogasawara Islands I. List of the known species. Researches on Crustacea, 7: 101–115.

Takeda M & Ueshima R (2006) Crabs preserved in the Department of Zoology, the University Museum, the University of Tokyo. In: Ueshima R (ed.) Catalogue of Invertebrate Collection Deposited in the Department of Zoology, The University Museum, the University of Tokyo. The University Museum, the University of Tokyo Materials Reports, 62: 61–105. [In Japanese]

Tan CGS & Ng PKL (1994) An annotated checklist of mangrove brachyuran crabs in Malaysia and Singapore. Hydrobiologia, 285: 75–84.

Tang B-P, Xin Z-Z, Liu Y, Zhang D-Z, Wang Z-F, Zhang H-B, Chai X-Y, Zhou C-L & Liu Q-N (2017) The complete mitochondrial genome of *Sesarmops sinensis* reveals gene rearrangements and phylogenetic relationships in Brachyura. PLoS ONE, 12(6): e0179800. doi: 10.1371/journal.pone.0179800, pp. 1–16.

Targioni Tozzetti A (1877) Crostacei brachyuri e anomuri. Zoologia del viaggio intorno al Globo della R. Pirocorvetta Magenta durante gli anni 1865–1868. Pubblicazioni del R Istituto di Studi Superiori Pratici e di Perfezionamento in Firenze, Sezione di Scienze fisiche e naturali, Successori le Monnier, Firenze, 1: i–xxix + 1–257, pls. 1–12.

Tesch JJ (1917) Synopsis of the genera *Sesarma*, *Metasesarma*, *Sarmatium* and *Clistocoeloma*, with a key to the determination of the IndoPacific species. Zoologische Mededelingen, 3: 127–260, pls. 15–17.

Thallwitz J (1892) Decapoden-Studien, inbesondere basirt auf A. B. Meyer's Sammlungen im ostindischen Archipel, nebst einer Aufzählung der Decapoden und Stomatopoden des Dresdener Museums. Abhandlungen und Berichte aus dem Königlichen Zoologischen und Anthropologisch-Ethnographischen Museums zu Dresden, R. Friedländer und Sohn, Berlin, 1890–91(3): 1–56, pl. 1.

Titcomb M, Fellows DB, Pukui MK & Devaney DM (1979) Native use of marine invertebrates in old Hawaii. Pacific Science, 32(4): 325–386.

Toyota K & Seki S (2014) Shrimps and Crabs. Nature Watching Guidebook, Freshwater Shrimps and Crabs in Japan. Seibundo Shinkosha Publishing, 256 pp.

Trivedi JN, Trivedi DJ, Vachhrajani KD & Ng PKL (2018) An annotated checklist of marine brachyuran crabs (Crustacea: Decapoda: Brachyura) of India. Zootaxa, 4502(1): 1–83.

Trivedi J, Mitra S & Patel P, Gosavi S & Vachhrajani K (2020) Four new records of brachyuran crabs (Crustacea: Decapoda: Brachyura) from India. Thalassas (2020). doi: 10.1007/s41208-020-00252-6, pp. 1–8.

Tsai M-L, Li J-J & Dai C-F (2000) Is large body size always advantageous for terrestrial adaptation? A study of water balance in a semi-terrestrial crab, *Sesarmops intermedium* (Crustacea: Grapsidae). Evolutionary Ecology, 14: 61–78.

Tweedie MWF (1940) New and interesting Malaysian species of *Sesarma* and *Utica* (Crustacea, Brachyura). Bulletin of the Raffles Museum, 16: 88–113, figs. 1–12, pl. 24.

Tweedie MWF (1947) On the Brachyura of Christmas Island. Bulletin of the Raffles Museum, 18: 27–42, textfig. 1.

Tweedie MWF (1950) Grapsoid crabs from Labuan and Sarawak. Sarawak Museum Journal, 5(2): 338–369, figs. 1–9.

Urita T (1926) A check list of Brachyura found in Kagoshima Pref., Japan. The Tsingtao Times, Tsingtao, 40 pp.

Villesen P (2007) FaBox: an online toolbox for Fasta sequences. Molecular Ecology Notes, 7: 965–968.

Wang ZH & Leung V (2001) Fauna and flora of Macau. Câmara Municipal de Ilhas Provisória, Macau, 139 pp.

Weber M (1897) Beiträge zur Kenntniss der Fauna von Süd-Afrika. Ergebnisse einer Reise von Prof. Max Weber im Jahre 1894. 3. Die Decapoden Crustaceen des Süsswassers von Süd-Afrika. (Mit Beiträgen von Dr. J.C.H. de Meijere und Dr. J.G. de Man). I. Zoologische Jahrbücher, Abtheilung für Systematik, Geographie und Biologie der Thiere, (Part VI) 10: 156–180, 1 pl.

Xu J, Chan T-Y, Tsang LM & Chu KH (2009) Phylogeography of the mitten crab *Eriocheir* sensu stricto in East Asia: Pleistocene isolation, population expansion and secondary contact. Molecular Phylogeny and Evolution, 52: 45–56.

Yamaguchi T & Baba K (1993) Crustacean specimens collected in Japan by Ph. F. von Siebold and H. Bürger and held by the Nationaal Natuurhistorisch Museum in Leiden and other Museums. In: Yamaguchi T (ed.) Ph.F. von Siebold and Natural History of Japan Crustacea. The Carcinological Society of Japan, Tokyo. Pp. 145–570.

Yang C, Møller AP, Ma Z, Li F & Liang W (2014) Intensive nest predation by crabs produces source-sink dynamics in hosts and parasites. Journal of Ornithology, 155: 219–223.

Yang S, Chen H & Jiang W (2008) Crustacea: Decapoda Brachyura. In: Liu R (ed.) Checklist of Marine Biota of China Seas. Institute of Oceanology, Chinese Academy of Sciences. Pp. 761–810.

Yoshimura K (1990) Two new species of the genus *Monhystrium* Cobb, 1920 (Monhysteridae: Nematoda) from terrestrial crabs of subfamily Sesarminae (Brachyura) in Japan. Zoological Science, 7(4): 755–761.

Zehntner L (1894) Crustacés de l'Archipel Malais. Voyage de MM. M. Bedot et C. Pictet dans l'Archipel Malais. Revue Suisse de Zoologie et Annales du Musée d'Histoire Naturelle de Genève, 2: 135–214, pls. 7–9.

Zhang Y, Gong L, Lu X, Jiang L, Liu L, Lü Z, Li P & Zhang X (2020) Gene rearrangements in the mitochondrial genome of *Chiromantes eulimene* (Brachyura: Sesarmidae) and phylogenetic implications for Brachyura. International Journal of Biological Macromolecules, 162(1): 704–714.