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Revision of the spider crab genus *Maja* Lamarck, 1801 (Crustacea: Brachyura: Majoidea: Majidae), with descriptions of seven new genera and 17 new species from the Atlantic and Indo-West Pacific

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Abstract. The taxonomy of spider crabs of the genus *Maja* Lamarck, 1801, is revised, and a total of 36 species in 10 genera are now recognised from the eastern Atlantic, Mediterranean and Indo-West Pacific. The present revision describes seven genera and 17 species as new. Two genera previously synonymised under *Maja*: *Paramaya* De Haan, 1837, and *Paramaja* Kubo, 1936, are here treated as valid taxa. The confused nomenclature of *Cancer cornutus* Linnaeus, 1758, is resolved, and the name replaces *Maja capensis* Ortmann, 1894, and *Mamaia queketti* Stebbing, 1908. All genera and species are diagnosed and figured, and keys are provided for their identification.

Key words. Crustacea, Brachyura, *Maja*, taxonomy, revision, new genera, new species, Indo-West Pacific, Atlantic

INTRODUCTION

Spider crabs of the genus *Maja* Lamarck, 1801 (Majoidea: Majidae Samouelle, 1819) are common in the eastern Atlantic, Mediterranean and Indo-West Pacific, occurring in shallow as well as deep waters. Some large species from the Atlantic, e.g., *Maja squinado* (Herbst, 1788) and *M. brachydactyla* Balss, 1922, are valuable as fishery resources and have long been exploited. However, the majority of species occur in the Indo-Pacific and most are small to medium-sized, none of which have commercial value. Ng et al. (2008) listed 19 species of which the identities of two were doubtful. The Atlantic species have been reappraised and revised in recent years (d'Udekem d'Acoz, 1999; Neumann, 1998) and their identities have been clarified. With regard to the Indo-West Pacific taxa, Serène & Lohavanijaya (1973), T. Sakai (1976) and Griffin & Tranter (1986) treated various groups of species and reviewed their taxonomy, providing keys to most or all the species. However, these keys are inaccurate in parts, incomplete and/or difficult to use. Several species have been described from juvenile specimens (e.g., *Maja gibba* Alcock, 1895), and because it was generally believed that carapace spinulation varies with size and geography (e.g., see Griffin, 1976; Griffin & Tranter, 1986), the identities of several taxa remain unclear. The Philippine species named by Rathbun (1916) — *M. suluensis* Rathbun, 1916, *M. linapacanensis* Rathbun, 1916, and *M. bisarmata* Rathbun, 1916, are problematic because they were only briefly described without any figures. Griffin (1976) also treated them in passing but without clear figures or photographs of the types. Overall, the state of taxonomy of *Maja* remains unsatisfactory.

Over the last decade, the authors have obtained numerous *Maja* specimens from many parts of the Indo-West Pacific. This includes a major collection of crabs collected from tangle nets around the island of Balicasag in the Philippines (see Ng et al., 2009; Mendoza et al., 2010). Study of this material in particular has allowed us to resolve many outstanding taxonomic problems with *Maja*.

We can now separate the recognised species of *Maja* into 10 distinct genera, seven of which are new. In addition, we describe 17 new species from the South China Sea, Philippines, Taiwan, Japan, Australia, Papua New Guinea, New Caledonia, Vanuatu, Solomon Islands and Madagascar.

MATERIAL AND METHODS

The terminology used here essentially follows that used by Griffin (1966a) (see also Griffin & Tranter, 1986) (Fig. 1). Some additional comments, however, are necessary. The postorbital spine, as defined by Griffin (1966a) in *Maja* is actually one of two major spines on the hepatic region and the anterior one is here regarded as the actual postorbital spine. Otherwise we follow Griffin's (1966a) system here so that appropriate comparisons can be made when other genera in the Majidae are considered. There is always a marked constriction between the hepatic region and the rest of the carapace, which also marks the start of the convex lateral margin. The lateral margin is always armed with three or four distinct spines, which may be reduced; and there are sometimes smaller ones interspersed between them. The lateralmost spine is usually the largest. There is usually one

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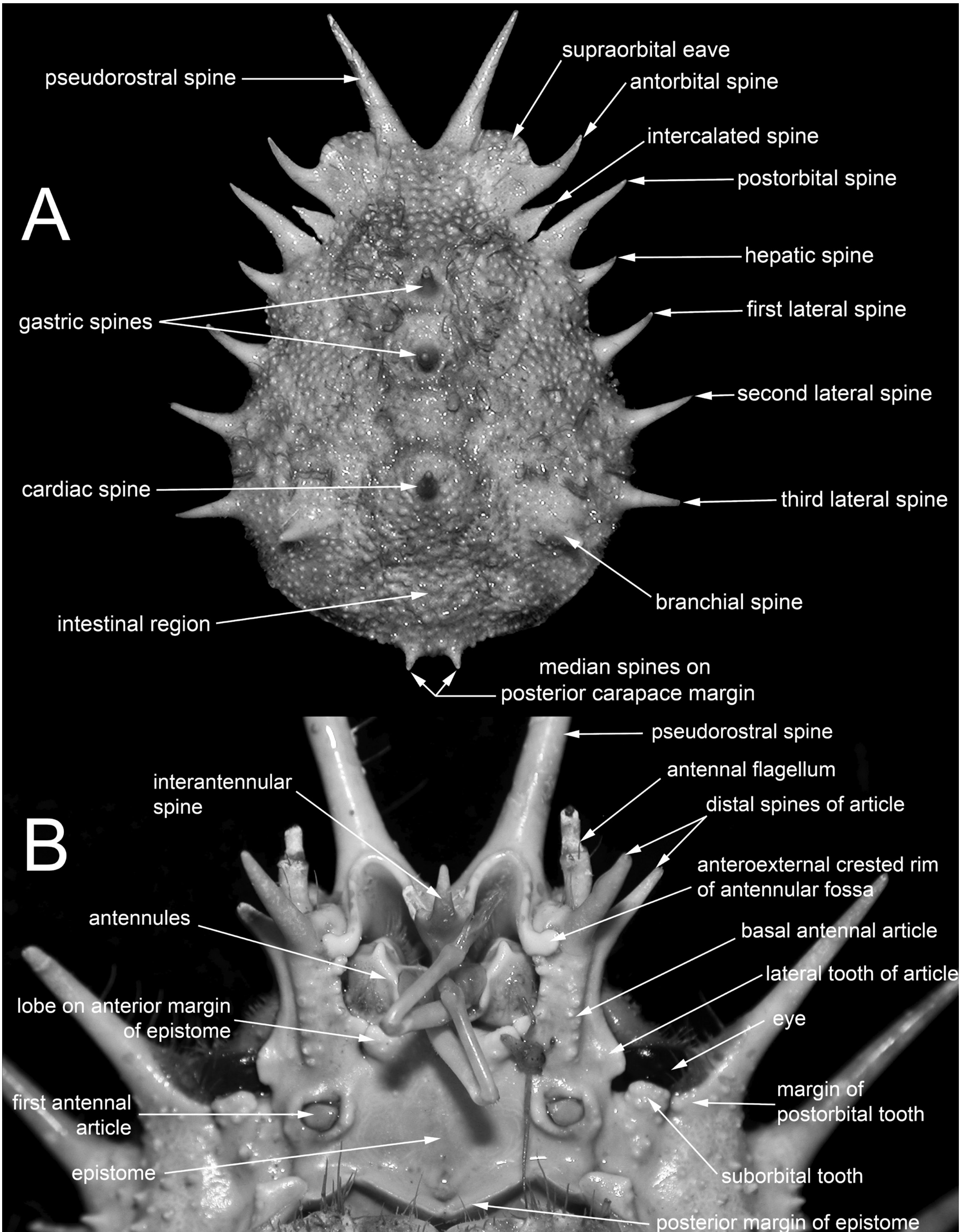

Fig. 1. Nomenclature of spines and other structures. A, dorsal surface of carapace, *Holthuija suluensis*, holotype female (32.4 × 41.2 mm) (USNM 48224a), Philippines; B, frontal surface of carapace, *Paramaya ouch* n. sp., holotype male (76.8 × 60.0 mm) (NMCR), Philippines.

more following spine that is clearly part of the lateral series, but is positioned higher on the branchial region. Herein we refer to this as the branchial spine. The gastric and cardiac regions are usually armed with at least one spine of varying size, although in some species, it is only apparent as a tubercle or large granule in adult specimens. The intestinal region may or may not be armed. The posterior carapace margin is usually lined with granules but in many species, there is a pair of relatively longer and more prominent median spines. The presence of a spine or tubercle on the various regions sometimes poses problems because it is not always discernible. In some species, because the spine is variable in strength (especially with size), it may be reduced and/or eroded to be just a granule, and cannot be separated from the rest of the granules on the surface.

There is some subjectivity with regard to what are here termed spines or teeth, and tubercles or granules. Griffin (1966a) and his subsequent papers generally use these terms relatively interchangeably; with spines being any major projection from the carapace margin surface; and granules for any low small structures present. In brachyurans, the term spine is normally used when the cross-section of an elongated structure is oval or round, and the term tooth is often applied when the structure is distinctly laterally flattened. In majoids, this is not always easy to distinguish. As such, we will generally use the term spine in the descriptions and characterize it with additional terms as necessary. The distinction between an elongated tubercle and low spine is not always clear; and a dorsolaterally flattened spine that is lobiform can just as well be called a tooth. We therefore use the term "spine" whenever possible for any elongated structure that is longer than broad.

The term "basal antennal article" is used for the largest antennal article observed. As discussed by Ng et al. (2008: 11), the "basal antennal article" is actually formed by fusion of the true articles 2 and 3, and is not to be confused with the first article which has the osmoregulatory green gland. Although it can be somewhat misleading, it has been so extensively used that to change terminology now would serve no useful purpose. As such, this term is used here for convenience.

The male anterior thoracic sternum refers to sternites 1–4. Sternites 1 and 2 are always fused and separated from sternite 3 by a groove. The relative width of sternites 3 and 4 are useful characters to separate some genera and species. The male sterno-abdominal cavity refers to the median longitudinal depression in which the abdomen sits. The surfaces surrounding the sterno-abdominal cavity (notably the anterior part on sternite 4) can be armed or structured in different ways and can be used to separate genera and species.

The dorsal margin of the articles of the ambulatory leg refers to the extensor or anterior margin. The male first gonopod (G1) in the species revised here are all more or less straight or curve outwards, i.e. they are directed away from the median part of the thoracic sternum. The ventral surface of the G1s figured is the view of the in situ structure, i.e. the abdominal view. The dorsal surface of the G1 refers to the thoracic sternal view. The structure of the male second gonopod (G2) has not been useful in the taxonomy of the various taxa treated here. All of them have a relatively short G2 that is between 0.15 and 0.20 times the length of the G1, with the distal part subspatuliform to cup-like, and never with a distinct elongated distal segment.

The measurements provided, in millimetres, are of the post-pseudorostral carapace length (from the base of spines to the posterior carapace margin, not including median posterior spines) against the maximum caparace width (at base of spines), respectively. Precise measurements of these dimensions can be problematic in many species as the posterior carapace margin and widest points at the base of spines are often unevenly granular, with the bases of large spines gently sloping, not clearly demarcated and covered with different sized granules. In addition, the base of the pseudorostral spines is also not always distinct as the cleft between them can be deep. Detailed diagnoses are presented for all genera so comparisons can be made. For species, only diagnostic characters useful (or potentially useful) to separate congeners are presented.

Material examined is deposited in the Kanagawa Prefectural Museum of Natural History (KPM), Iriuda, Japan; National Museum of Nature and Science (NSMT), Tsukuba, Tokyo, Japan; Muséum national d'Histoire naturelle (MNHN), Paris, France; The Natural History Museum (NHM), London, U.K.; The Naturalis (ex Rijksmuseum van Natuurlijke Historie, RMNH), Leiden, The Netherlands; Senckenberg Museum Forschunginstitut (SMF), Frankfurt, Germany; Museum of Zoology, Strasbourg (MZS), France; Shirshov Institute of Oceanography (SIO), Russian Academy of Sciences, Moscow, Russia; Crustacean Collection of the Philippine National Museum (NMCR), Manila, Philippines; National Institute of Water & Atmospheric Research (NIWA), Wellington, New Zealand; U.S. National Museum of Natural History (USNM), Smithsonian Institution, Washington D.C., U.S.A.; and Australian Museum (AM), Sydney, Australia; Museum Victoria (NMV), Melbourne, Australia; Institute of Oceanology, Chinese Academy of Science (IOCAS), Qingdao, China; Peikuan Crab Museum (PCM), Tashi, Taiwan; and the Zoological Reference Collection (ZRC), Lee Kong Chian Natural History Museum (formerly Raffles Museum of Biodiversity Research), National University of Singapore.

Much of the examined material is derived from the expeditions to the western Pacific organised by MNHN with colleagues from the area. The names of these expeditions are written in capitals, sometimes with a year after it if there were a series of collections from one area (e.g., PANGLAO 2004). When cruises are named after the research ships used, the name of the vessel is italicised (e.g., *Albatross*).

TAXONOMY

Family Majidae Samouelle, 1819

Subfamily Majinae Samouelle, 1819

Maja Lamarck, 1801

Maja Lamarck, 1801: 154.
Maia – Bouvier, 1940: 319, fig. 195 [incorrect spelling of *Maja*].
Meria Griffith & Pidgeon, 1833: 165 [erroneous spelling of *Maja*].
Mamaia Stebbing, 1905: 23 [substitute name for *Maja;* type species *Cancer squinado* Herbst, 1788].

Diagnosis. Carapace rounded in adults; dorsal surface covered by tubercles, short spines; gastric, branchial regions not distinct, separated by shallow grooves (Figs. 4, 5, 6A, B). Intestinal region with small median spine, not always discernible (Figs. 4, 5, 6A, B). Pseudorostral spines short, divergent, forming a V (Figs. 4, 5, 6A, B). Supraorbital eave usually with anterior part longitudinally narrow, rectangular, not prominently expanded; antorbital spine sharp (Figs. 4, 5, 6A, B). Intercalated spine distinct, separated from supraorbital eave and postorbital spine by narrow gaps; postorbital spine strong; hepatic region with 1 strong spine, much shorter than postorbital spine; 1 smaller spine below (Figs. 36A–E, 39A–D). Lateral carapace margin with 3 large spines, numerous spinules, branchial region with 1 low spine or tubercle (Figs. 4, 5, 6A, B). Posterior carapace margin with 2 short median spines (Figs. 4, 5, 6A, B). Eyes relatively long, thin, slightly curved, with ovoid cornea (Figs. 36A–E, 39A–D). Antennal flagellum short, slender. Basal antennal article as broad as long (quadrate), with 1 long distal spine, 1 blunt median lateral spine; proximal outer angle rounded; inner, outer lateral margins entire; antero-external crested rim of antennular fossa prominently overlapping with subdistal part of basal antennal article as hook-shaped structure by about one-third of its width (Fig. 39A–D). Epistome much wider than long, anterior margin with 2 large round tubercles; posterior margin composed of 4 rectangular plates separated by deep fissures (Figs. 39A–D, 41A–C). Suborbital margin separated from basal antennal article and margin of postorbital tooth by 2 deep fissures (Fig. 39A–D). Outer surface of third maxilliped covered by short setae; ischium squarish to subrectangular; postero-external angle of merus relatively broad, 'inserting' into shallow concavity on outer margin of ischium; antero-internal part of ischium rounded, auriculiform (Figs. 43A–F, 44). Male chelipeds long in adult males, surfaces of merus, carpus covered with distinct tubercles, granules; carpus elongate, with low granulated longitudinal ridge; propodus of palm elongated, curved, smooth, without lateral cristae, slightly enlarged, distinctly longer than fingers; fingers long, slender, gently curved, with narrow basal gape when closed (Figs. 4, 5, 6A, B, 53A–F). Ambulatory legs relatively short, thick; merus without dorsal subdistal spine; dactylus relatively short, curved, usually covered with dense short setae except for corneous distal quarter (Figs. 4, 5, 6A, B, E, 55A–C). Thoracic sternum wide; surfaces of somites 5–8 almost smooth or with scattered very small granules; sternites 3, 4 slightly depressed; margin between sternites 2, 3 demarcated by small notch; anterior margin of sterno-abdominal cavity not forming complete rim (Figs. 47A–G, 52A, B). Male abdomen subrectangular, with 6 free somites and telson; somites 3, 4 distinctly wider than somites 5, 6 and telson; telson subtriangular with convex margins (Fig. 47A–G). Male press-button abdominal locking mechanism submedian in position on sterno-abdominal cavity (Fig. 52A, B). Female abdomen dome-shaped, covering most of thoracic sternum. G1 very long, slender, gently curved throughout length, distal part dilated, subspatuliform, with short but distinct subdistal dorsal process, with scattered very short setae (Fig. 7A–Q).

Type species. *Cancer squinado* Herbst, 1788, by subsequent designation under the plenary powers of the International Commission on Zoological Nomenclature (ICZN) in Opinion 511. Gender of genus feminine; name 1260 on Official List.

Remarks. The complex nomenclatural history of *Maja* Lamarck, 1801, has been discussed at length by Holthuis (1958) and the ICZN has ruled on the validity of the name as well as its associated type species (ICZN Opinion 511). *Mamaia* Stebbing, 1905, is now treated as an unnecessary replacement name. Balss (1957: 1627) spelled the name as "*Mamaja* Stebbing" but this must be regarded as erroneous.

According to Ng et al. (2008), *Maja* Lamarck, 1801, currently contains 19 species, of which *M. brachydactyla* Balss, 1922, *M. capensis* Ortmann, 1894 (= *Mamaia queketti* Stebbing, 1908), *M. crispata* Risso, 1827 (= *Maia verrucosa* H. Milne Edwards, 1834, *Cancer majoides* Nardo, 1847), *M. erinacea* Ninni, 1924, *M. goltziana* d'Oliveira, 1889, and *M. squinado* (Herbst, 1788) (= ?*Cancer cornutus* Fabricius, 1787) are known only from the eastern Atlantic, Mediterranean and/ or South Africa. The other 13 species are only from the Indo-West Pacific. Of these, we are of the opinion *Maja tuberculata* De Haan, 1839, is probably a junior synonym of *M. squinado* (Herbst, 1788) (see discussion for the latter species).

The excellent series of *Maja* specimens and species available for this study allows us to now reappraise the taxonomy of the genus. *Maja* has traditionally been defined for species with an orbital region that has a distinct supraorbital eave, a prominent intercalated spine and a well developed postorbital spine which has the inner surface excavated to form a depression in which the cornea fits; the base of the antenna is inserted inside the orbital hiatus, and the median row of the dorsal carapace surface has small or large spines (see Griffin & Tranter, 1986).

As to the homogeneity of *Maja*, Serène & Lohavanijaya (1973: 50) comment that "further observations could demonstrate that the Indo-Pacific species of *Maja* belong to a different new genus". There is certainly a substantial degree of variety in the general form of the various *Maja* species recognised thus far, but to date, no one has found reliable characters to separate them. A recent molecular study focussing on European *Maja* species by Sotelo et al. (2009) also tested several South African and Asian species (*Maja*

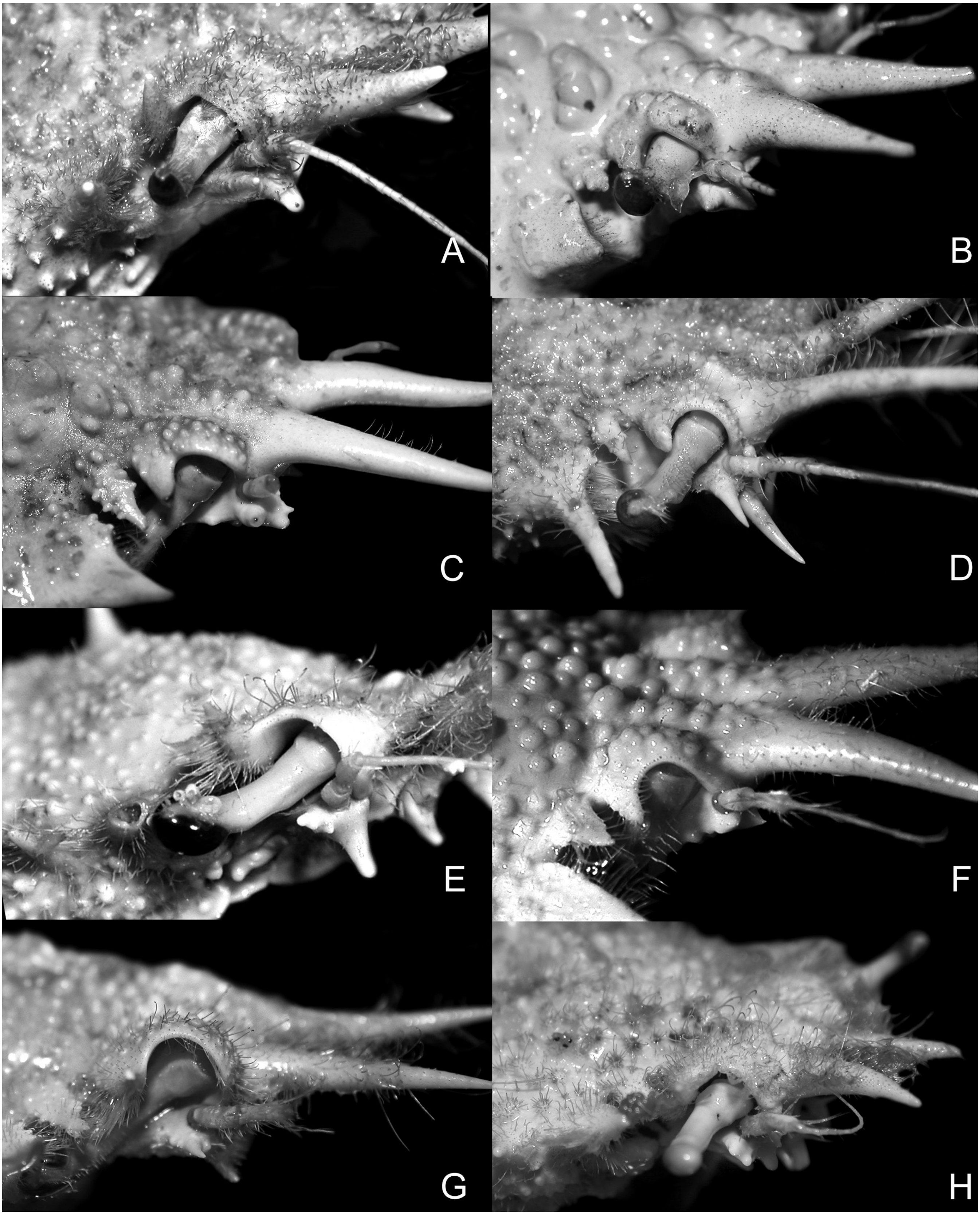

Fig. 2. Basal antennal article and position of flagellum. A, *Maja brachydactyla*, male (98.4 × 89.0 mm) (ZRC 2009.1130), U.K.; B, *Paramaja kominatoensis*, dried male (62.6 × 56.1 mm) (KPM NH0104298), Japan; C, *Alcomaja irrorata* n. sp., holotype male (52.6 × 45.7 mm) (NMCR), Philippines; D, *Paramaya ouch* n. sp., paratype ovigerous female (68.3 × 54.2 mm, with rhizocephala) (ZRC 2013.1317); E, *Holthuija miersi*, male (32.6 × 25.6 mm) (ZRC 2000.1497), Singapore; F, *Sakaija africana*, male (32.2 × 25.4 mm) (MNHN-IU-2010-928), Madagascar; G, *Planaja plana* n. gen. n. sp., holotype male (43.7 × 37.1 mm) (NMCR), Philippines; H, *Ovimaja compressipes*, male (49.6 × 39.6 mm) (ZRC 2008.1318), Taiwan.

"South Africa", "*Maja japonica*" [from Singapore], *Maja spinigera* [from Taiwan] and "*Maja kominatoensis*" [from the Philippines]). The specimens they used from South Africa are here identified as *Maja cornuta* (ex *Maja capensis*); "*Maja japonica*" from Singapore is referred to *Holthuija miersii* (new genus, see below); while "*Maja kominatoensis*" from Philippines is *Alcomaja irrorata* n. sp. (new genus, see below). Interestingly, in the Sotelo et al. (2009) study, the Atlantic species of *Maja* and *M. cornuta* formed one clade, with *Holthuija miersii* and *Paramaya spinigera* forming another, while *Alcomaja irrorata* aligned with another group further away. While this work is preliminary for the Indo-West Pacific species, it nevertheless supports the revised generic system proposed here.

Of the six *Maja* species now recognised from the Atlantic, Mediterranean and South Africa, *M. erinacea* Ninni, 1924, is here regarded as a synonym of *M. crispata* (see discussion under the latter species). Of the five remaining species, three – *M. squinado*, *M. brachydactyla* and *M. cornuta* share the following diagnostic characters: the supraorbital eave has the anterior part longitudinally narrow and rectangular in shape (Fig. 36A–D); each branchial region only has one spine (Figs. 4, 5), the suborbital margin is separated from the basal antennal article and margin of postorbital tooth by distinct fissures (Fig. 39A–C); the antero-external crested rim of the antennular fossa prominently overlaps the surface of article (Fig. 39A–C); the epistome is broader than long (Figs. 39A–C, 41A, B), thoracic sternites 3 and 4 are separated by low broad cleft (Fig. 47A–G); the carpus of the chelipeds is relatively long, covered with distinct tubercles and granules, with the chelae slender, elongate, not prominently inflated (Fig. 53A–E); the merus of the ambulatory legs is unarmed (Figs. 4, 5, 6E); the dactylus of ambulatory legs is short, stout, with most of the surface covered with short, stiff setae except for the pectinated tip (Fig. 55A, B); and the G1 is very long, straight, gently curved, with the distal part slightly expanded and tapering without prominent projections or folds (Fig. 7A–N). They are clearly congeneric.

Maja crispata share the characters of the carapace, orbit, antennae, epistome, male thoracic sternum, male abdomen and gonopods as *M. squinado*, *M. brachydactyla* and *M. cornuta* but possesses several unusual characters that make its placement in *Maja* s. str. more difficult. Its carapace shape is distinctively more pyriform and dorsoventrally flattened (Fig. 6A, B) (versus carapaces that are more rounded and swollen, Figs. 4, 5); the presence of a window-like structure on each side of the gastric region which has no or few granules and marks the area below the carapace where the gastric ossicles are anchored (Fig. 6A, B) (versus no such structure visible, Figs. 4, 5); the ocular peduncle is proportionately longer and more slender (Figs. 36E, 39D) (versus relatively shorter and stouter, Figs. 36A–D, 39A–C); the supraocular eave is relatively much wider and more foliaceous (Fig. 39D) (versus more narrow, Fig. 39A–C); the ischium of the third maxilliped is squarish (Fig. 43F) (versus rectangular, Fig. 43A–E); the carpus of the cheliped is rugose but not tuberculated or granulated (Fig. 53F) (versus prominently tuberculated, Fig. 53A–E); and the dactylus of the ambulatory legs are covered with long coarse setae (Fig. 55C) (versus with short setae, Fig. 55A, B). However, in view of the very similar male thoracic sternal, male abdominal and gonopodal characters shared by *M. squinado*, *M. brachydactyla*, *M. cornuta* and *M. crispata*, we prefer to place all four species in *Maja* s. str. for the time being. This is supported by the genetic study by Sotelo et al. (2009) that showed that *M. crispata* to be the sister species to *M. squinado* s. str. Interestingly, both species are from the Mediterranean Sea.

The fifth Atlantic species, *M. goltziana*, differs significantly from the other four taxa in that the antero-external crested rim of the antennular fossa overlaps further across the surface of the basal antennal article, reaching more than half its width (Fig. 39E, F); its epistome is as long as broad (Figs. 39E, F, 41D), each branchial region only has two spines (Fig. 6C, D), the merus of the ambulatory legs is armed with a strong subdistal dorsal spine (Fig. 6C, D, F), the male anterior thoracic sternum is relatively narrower transversely (Fig. 47H, I), and the distal part of the G1 has a different structure, with the distal part lacking a subdistal dorsal process (Fig. 7R–T). It is here referred to a new genus, *Neomaja*. The genetic study by Sotelo et al. (2009) also shows this species forming a separate clade from the other European *Maja* species.

In Indo-West Pacific species that have been referred to *Maja*, the basal antennal article is distinctly longer than broad, the male thoracic sternites 3 and 4 are separated by a deep V-shaped cleft; the dactylus of the adult ambulatory legs is slender, with scattered long or short setae; the carpus of the chelipeds is short or long with the chelae differently structured (may be inflated); and the G1 is shaped otherwise. With regards to whether the antero-external crested rim of the antennular fossa extends substantially over the basal antennal article, only in a small number of species (here referred to two new genera, *Holthuijia* and *Ovimaja*) have structures similar to that seen in *Maja* s. str. In all other Indo-West Pacific species, the antero-external crested rim of the antennular fossa does not or just slightly overlaps the basal antennal article.

Even then, these Indo-West Pacific "*Maja*" species can still be easily separated into seven groups, which we here recognise as separate genera: *Paramaya* De Haan, 1837, *Paramaja* Kubo, 1936, and five new genera – *Alcomaja*, *Holthuija*, *Sakaija*, *Planaja* and *Ovimaja*.

One species, *Maja bisarmata* Rathbun, 1916, is not a *Maja* as defined at present. Although Rathbun (1916) had defined *Maja* for species in which the antennal flagellum is included inside the orbit, for *M. bisarmata* it is actually just outside the orbit (Fig. 57G, H). While the antennal flagellum for *M. bisarmata* is not prominently excluded from the orbit as in normal *Leptomithrax* Miers, 1876 (Fig. 57A–F), it is also clearly not inside the orbit as in true *Maja* (Fig. 2). In fact, it is just outside the margin of the orbit, but still different from typical *Leptomithrax*. This is in fact the same condition as in *Leptomithrax kiiensis* T. Sakai, 1969. Tune Sakai (1969, 1976) clearly interprets his species as having the antennal flagellum excluded from the orbit, and hence placed it in *Leptomithrax*. *Maja bisarmata* Rathbun, 1916, is very similar to *Leptomithrax kiiensis* T. Sakai, 1969, and both are congeneric. The two species are here referred to a new genus, *Rathbunaja*, together with two new species from the Philippines and Papua New Guinea, respectively.

Much has been written about the position of the antennal flagellum, one of the key characters separating *Maja* s. lato from *Leptomithrax* Miers, 1876. As noted above, all *Maja* s. lato species are supposed to have the antennal flagellum inside the orbit (Fig. 2), while that of *Leptomithrax* species is outside (Fig. 57). However, while this is generally true, it is not always easy to draw a clear line. As discussed, the antennal flagellum of *Rathbunaja* species is just outside the orbit, like the type species *Leptomithrax*, *L. longimanus* (Miers, 1876) (Fig. 57A). In most other species of *Leptomithrax*, the antennal flagellum is positioned far from the orbit (Fig. 57B–F). On the basis of the structure of the antennal flagellum (as well as characters of the third maxillipeds, male abdomen and chelipeds), *Leptomithrax*, as recognised at present, should eventually be separated into three genera (excluding *Rathbunaja*) (see later discussion for the latter genus). In *Maja* s. str., as well as *Neomaja*, *Paramaja*, *Holthuija*, *Planaja* and *Ovimaja*, the antennal flagellum is clearly positioned on the inner surface of the orbit, just before the distal margin of the basal antennal article (Fig. 2A, B, E, G, H). In *Alcomaja*, *Paramaya* and *Sakaija*, the antennal flagellum is positioned right at the margin of the basal antennal article (Fig. 2C, D, F), and it is not possible to state for certain whether it is just inside or outside the orbit.

The intestinal regions of the carapace of all genera are covered with small granules or tubercles, but only in *Paramaya* is there a prominent median spine in all species. In *Maja*, *Neomaja*, *Sakaija* and *Planaja*, the intestinal region has a small spine that may be eroded. In some species in these genera, e.g. *Sakaija africana*, the intestinal spine is always present and is very strong (Fig. 29). Species of *Paramaja*, *Alcomaja*, *Holthuija* and *Ovimaja* do not have visible intestinal spines, but this may be because the whole surface is covered with granules of similar sizes. Species of *Paramaja*, *Alcomaja* and *Planaja* also usually have a pair or several pairs of short spines along the median part of the intestinal region.

The supraorbital eave of *Holthuija* is relatively large and prominently expanded, with the margin of the anterior part foliaceous and the margin convex (Fig. 37D–J). In *Planaja*, the supraorbital eave is expanded (Fig. 38A), but not to the degree observed in *Holthuija*. In all the other genera, the anterior part of the supraorbital eave is relatively narrow longitudinally and more rectangular in general shape (Figs. 36, 37A–C, K–O, 38B, C). In *Paramaya*, the hepatic spine is slightly shorter, as long as or longer than the postorbital spine (Fig. 37A–C). In all other genera, the hepatic spine or tooth is always distinctly smaller than the postorbital spine or tooth (Figs. 36, 37D–O, 38).

The lateral margin of the carapace (excluding the outer branchial spine) always has three or four spines but they are not always easy to enumerate. In *Holthuija* and *Paramaya*, there are always three clearly defined spines since these are large with the granules around them small (Figs. 21, 22, 24, 25). In *Maja* s. str., the lateral margin has three large spines (e.g., Figs. 4B, C, 5C, D), but those in between them are also relatively distinct such that in large specimens, it is not always easy to distinguish these from the other spines (e.g., see Fig. 4D-F). In genera like *Paramaja* and *Alcomaja*, the lateral carapace spines are only clearly discernible in juveniles and smaller specimens (e.g., Figs. 10A, B, 11A-C, 12A), becoming lower and more rounded in adults, so much so that they sometimes cannot be distinguished (e.g., Figs. 9A, B, 10C, D, 11D-G, 12C-E). *Planaja* is interesting because it has about six or seven spines along the lateral margin but these are all relatively small and while distinct, these are only slightly larger than the surrounding spinules and sharp granules (Fig. 34A, B). *Ovimaja* is unusual because only the lateral spines are relatively short, and the number varies between 3 and 4, depending on whether you count sharp tubercles as spines (Fig. 34C, F, G). In general, the same situation applies for the branchial spines for *Ovimaja*.

The posterior carapace margin always has two spines, which vary in size. In some genera (see later), the spines can be short and much eroded to the point that they are indiscernible in larger specimens. In *Maja*, *Neomaja*, *Alcomaja*, *Planaja* and *Ovimaja*, the spines are short and usually visible (Figs. 4, 5, 6A–D), although in very large specimens of *Paramaja*, they are not visible from dorsal view because of their inflated branchial regions (e.g., Figs. 8, 9, 10C, D, 11D, F, G, 12D, E). In some *Sakaija* species, the spines can become so reduced that they are barely visible in larger specimens (Fig. 28A-C). On the other hand, some species of *Sakaija* (e.g. *S. africana* and *S. longispina* n. sp.) always have very long intestinal spines (see Figs. 29, 32A, B). In *Paramaya* and *Holthuija*, the intestinal spines are consistently long and always distinct even in large specimens, with those of *Paramaya* extremely long (Figs. 21, 22, 24, 25).

Paramaya is the only genus that has the proximal outer angle of the basal antennal article as a lobe-like projection that has a sharp or acute tip that may be produced into a spine. This is accentuated by the fact that it is clearly separated from the suborbital margin by a broad cleft (Fig. 40A–C). In *Holthuija*, the proximal angle of the basal antennal article is also dilated and lobiform (never spiniform) but it is more closely appressed against the suborbital margin (Fig. 40D–I). The antero-external crested rim of the antennular fossa projects onto the basal antennal article to various degrees but there is a distinct pattern. In *Maja* s. str. and *Neomaja*, the projection is prominent and extends into and overlaps the article as a prominent hook-like structure (Fig. 39A–F). The same is true for *Paramaya* and *Ovimaja* although the shapes of their basal articles are different (Fig. 40A–C, O). In genera like *Paramaja*, *Alcomaja* and *Sakaija*, the antero-external crested rim of the antennular fossa slightly overlaps the basal antennal article as a simple projection (Figs. 39G–O, 40J–M). In *Holthuija* and *Planaja*, the antero-external crested rim of the antennular fossa extends deeper into the basal antennal article, but the structure is only gently curved and not hooked (Fig. 40D–I, N). The outer edge of the basal antennal article in *Paramaya* is separated from the suborbital margin by a broad U-shaped sinus (Fig. 40A-C). In other genera in which this structure is distinct, it is separated only by a fissure (Figs. 39A–F, 40D–I, N, O). At the same time, the suborbital margin is fused and confluent with the margin of postorbital tooth in *Paramaja*, *Alcomaja* and *Sakaija* (Figs. 39G–O, 40J–M), but in *Maja* s. str., *Neomaja*, *Paramaya*, *Holthuija*, *Planaja* and *Ovimaja*, they are separated by distinct clefts or fissures (Figs. 39A–F, 40D–I, N, O).

The structure of the epistome is distinctive for some genera. Although there is a tendency for the epistome to become slightly broader transversely with increased body size, it generally stays the same shape. In genera like *Maja* s. str. and *Paramaja*, the adult epistome is always rectangular and much broader than long (Figs. 39A–D, G–K, 41A–C, E, F). In *Neomaja* and *Alcomaja*, the epistome is somewhat more quadrangular, being only slightly wider than long (Figs. 39E, F, L–O, 41D, G, H). The same is true for *Holthuija*, *Sakaija*, *Planaja* and *Ovimaja* (Figs. 40D–O, 42C–H). Only in *Paramaya* does the epistome possess a different shape, being distinctly longer than broad (Figs. 40A–C, 42A, B). The anterior margin of the epistome is adjacent to the posterior margin of the antennular fossae and it is usually unarmed or smooth. In *Maja* s. str., *Neomaja* and *Paramaya*, there is a large lobiform structure at the outer margin of the anterior epistomal margin (Figs. 41A–D, 42A, B). In *Ovimaja*, this projection is large and tuberculiform (Fig. 42H). In *Paramaja*, *Alcomaja*, *Holthuija*, *Sakaija* and *Planaja*, the anterior epistomal margin may be cristate or even distinctly raised, but there are no prominent lobes or projections present (Figs. 41E–H, 42C–G). In *Holthuija*, however, there is usually one or a few small tubercles clustered just below the two corners of the anterior margin although the margin itself is not prominently raised (Fig. 42C–E). The posterior margin of the epistome in these genera is generally similar, with four plates separated by distinct fissures; the median ones being relatively broader (Figs. 41, 42C–H). However, in *Paramaya*, the median plates are characteristically more strongly produced downward (Fig. 42A, B).

The form of the third maxilliped is distinct in several genera. In *Paramaya*, the postero-external angle of the merus (which joins the ischium) is very narrow and elongate, and is "inserted" into a deep concavity on the outer margin of the ischium (Fig. 45I–L). As a consequence of this, the antero-internal part of the ischium is acutely triangular (Fig. 45I–L). In all other genera, the postero-external angle of the merus is proportionately broader and the antero-internal part of the ischium is rounded and auriculiform (Figs. 43, 44, 45A–H, 46).

The form of the male anterior thoracic sternum is diagnostic for some genera. In *Paramaya*, the thoracic sternites 1–4 are elongate, with the lateral junction between thoracic sternites 2 and 3 deep (Fig. 50A–C). In *Ovimaja*, while thoracic sternites 1–4 are not elongated, the lateral junction between sternites 2 and 3 is very deep, forming a distinct waist-like structure and the abdominal margins are concave accordingly (Fig. 51I). In *Holthuija*, the depression on thoracic sternite 4 is not evenly rounded like in the other genera but appears as an oblique depression parallel to the outer margin (Fig. 50D–I). The anterior margin of the male sterno-abdominal cavity on thoracic somite 4 of most of the genera is normally slightly raised, with the median part flat (Figs. 47–49, 50A–C, 51A–E, I). Only in *Holthuija* and *Planaja* is the entire margin of the male sterno-abdominal cavity on thoracic somite 4 prominently raised and entire, forming a clear rim (Figs. 50D–I, 51F, G). In *Holthuija*, this rim is distinct but is relatively lower (Fig. 50D–I). In *Planaja*, the rim is very pronounced and distinct (Fig. 51F, G).

The merus and carpus of the cheliped in *Maja* s. str. and *Neomaja* are prominently tuberculate, being covered with prominent short sharp tubercles as well as small granules (Fig. 53A–H). In all the other genera, the merus and carpus are lined with small to very small granules, and while some raised areas appear uneven or crenulated, there are never prominent tubercles covering the surface (Figs. 53I–P, 54). The carpus of *Maja*, *Neomaja* and *Paramaya* is proportionately much longer than those in the other genera (Figs. 4, 5, 6A–D, 21, 22), and these proportions do not appear to change much even after considering size and sex.

The structure of the G1 is important in separating groups of genera. In *Maja* s. str., *Neomaja*, *Paramaja* and *Paramaya*, the G1 is long, slender and gently curved to almost straight long most of its length (Figs. 7, 15, 23). In *Maja* s. str. and *Neomaja*, the distal part lined only with scattered short spinules or very short setae (Fig. 7); it is covered with scattered spinules and spines in *Paramaja* (Fig. 15), and devoid of spines, spinules or setae in *Paramaya*, with a distinct dorsal projection (Fig. 23). In *Alcomaja*, the G1 is generally gently curved with a distinct subdistal flap or projection on the lower margin, and with prominent spines and short setae or spinules present on the distal surface (Figs. 19, 20). In *Ovimaja*, the G1 is very elongated and strongly curved, the distal part has two prominent folds forming a petal-like structure without spines or long setae (Fig. 35F–L). In *Holthuija*, the G1 is relatively stout, curved or straight, but the distal part is slightly to distinctly wider, numerous spines and spinules (Fig. 27). *Planaja* has an atypical curved G1 in which the distal part is partially pectinated and lined with strong spines (Fig. 35A–E), and in this respect, resembles many species of *Leptomithrax* s. lato (see Griffin, 1966b). The G1s of *Sakaija* species are very characteristic, they are relatively slender, curved and the distal part is lined with numerous long setae that are usually weakly or distinctly plumose (Fig. 33). The G1 structures, especially the distal parts, are often curved or gently twisted, and for comparisons between species to be useful, they have to be positioned correctly. In *Maja* s. str. and *Neomaja*, for example, the distal dilated part may appear slender from one view (e.g., with the dorsal or sternal surface horizontal with the flat surface (Fig. 7K) but appears higher and more dilated when it is tilted slightly (Fig. 7M). Interestingly, the G1 structure does not vary substantially even between male specimens substantially different in size (e.g., see *Paramaja turgida* n. sp. and *Planaja plana* n. sp., Figs. 15N–U, 35A–E).

A comment about the names *Paramaya* De Haan, 1837, and *Paramaja* Kubo, 1936, is necessary. The spellings of the two names are nearly identical and were probably intended to be that way. Why De Haan spelled his name "*Paramaya*" (as a subgenus of *Maja*) with a "y" and not a "j" is confusing, but it is clearly intentional. De Haan (1837) used the name *Paramaya* three times in his book, always as a subgenus (but with different generic arrangements) and with the same Japanese species, *spinigera* – "MAJA (MAJA) SPINIGERA, n. sp. T. XXIV. f. 4. ♀. (Paramaya)" (De Haan, 1837: 93), "Maja (Paramaya) spinigera, n." (De Haan, 1837: errata), and "PISA (Paramaya) *spinigera* n." (De Haan, 1837: Pl. 24, fig. 4). *Maja* (*Maja*) *spinigera* De Haan, 1837, is therefore its type species. Some authors (e.g., Manning & Holthuis, 1981: 307; Yamaguchi & Baba, 1993: 359) incorrectly spelled the name as "*Paramaja*" or "*Paramya*" but this must be regarded as an incorrect emendation of *Paramaya*. Rathbun (1905) commented that the name *Paramaya* De Haan, 1837, was available for use. Kubo (1936) later established the name *Paramaja* for a very different species, *Paramaja kominatoensis* Kubo, 1936, also from Japan. Balss (1957: 1628) noted that *Paramaja* Kubo, 1936, was a homonym of De Haan's name and proposed a replacement name, *Paramajella*. This is not the case. Despite the close similarity of the two names, the current zoological code (ICZN, 1999) treats them as separate names, the use of "y" and "j" for the two genera deemed sufficient to differentiate them. This is most unfortunate and can certainly give rise to confusion.

The morphological characters used here agree with the molecular analysis by Sotelo et al. (2009) who showed that *M. squinado*, *M. brachydactyla*, *M. crispata* and *M. cornuta* (as *Maja* SA1 and *Maja* sp. SA2) belonged to one distinct clade. The sister clade to this is *Maja goltziana*, which is here transferred to its own genus, *Neomaja* as it has a suite of distinct morphological characters (see later).

In summary, *Maja* Lamarck, 1801, is now restricted to four primarily Atlantic and Mediterranean species. The other species previously placed in the genus are transferred to nine other genera, seven of which are new:

Maja Lamarck, 1801 – *Maja squinado* (Herbst, 1788), *Maja brachydactyla* Balss, 1922, *Maja cornuta* (Linnaeus, 1758), *Maja crispata* (Risso, 1827)

Neomaja n. gen. – *Neomaja goltziana* (d'Oliviera, 1889)

Paramaja Kubo, 1936 – *Paramaja kominatoensis* Kubo, 1936, *Paramaja gibba* (Alcock, 1895), *Paramaja turgida* n. sp.

Paramaya De Haan, 1837 – *Paramaya spinigera* (De Haan, 1837), *Paramaya ouch* n. sp., *Paramaya coccinea* n. sp.

Alcomaja n. gen. – *Alcomaja irrorata* n. sp., *Alcomaja confragosa* (Griffin & Tranter, 1986), *Alcomaja gracilipes* (Chen & Ng, 1999), *Alcomaja nagashimaensis* (Sakai, 1969), *Alcomaja latens* n. sp., *Alcomaja miriky* n. sp., *Alcomaja desmondi* n. sp.

Holthuija n. gen. – *Holthuija miersii* (Walker, 1887), *Holthuija suluensis* (Rathbun, 1916), *Holthuija cognata* n. sp., *Holthuija aussie* n. sp., *Holthuija pauli* n. sp., *Holthuija poorei* n. sp.

Sakaija n. gen. – *Sakaija japonica* (Rathbun, 1932), *Sakaija sakaii* (Takeda & Miyake, 1969), *Sakaija serenei* n. sp., *Sakaija santo* n. sp., *Sakaija africana* (Griffin & Tranter, 1986); *Sakaija longispinosa* n. sp.

Planaja n. gen. – *Planaja plana* n. sp.

Ovimaja n. gen. – *Ovimaja compressipes* (Miers, 1879)

Rathbunaja n. gen. – *Rathbunaja bisarmata* (Rathbun, 1916), *Rathbunaja kiiensis* (T. Sakai, 1969), *Rathbunaja brevipes* n. sp., *Rathbunaja ursus* n. sp.

Key to genera studied

1. Antennal flagellum positioned just outside of orbit, near rim (Fig. 57G, H); West Pacific .... *Rathbunaja* n. gen.
– Antennal flagellum clearly inside orbit (Fig. 2) 2

2. Ambulatory merus with sharp subdistal spine on dorsal margin (Figs. 6F, G) 3
– Ambulatory merus unarmed on dorsal margin (Fig. 6E, H) 4

3. Basal antennal article as long as broad; epistome as long as broad (Fig. 39E, F); Eastern Atlantic .... *Neomaja* n. gen.
– Basal antennal article longer than broad; epistome longer than broad (Fig. 40A–C); Indo-West Pacific .... *Paramaya* De Haan, 1837

4. Suborbital margin confluent with margin of postorbital tooth, not demarcated by fissure or cleft (Fig. 39G–O) 5
– Suborbital margin clearly separated from margin of postorbital tooth by distinct deep fissures or cleft (Fig. 39A–F) 7

5. Dorsal surface of carapace covered with small uniformly sized small rounded granules (Fig. 28); G1 sinuous with numerous long setae on distal surface (Fig. 33); Indo-West Pacific .... *Sakaija* n. gen.
– Dorsal surface of carapace covered with numerous small and large granules of various types (Figs. 8–12); G1 straight or curved with scattered setae on distal surface (Figs. 15, 19, 20); Indo-West Pacific 6

6. Pseudorostral spines relatively short, stout (Fig. 36G-K); branchial regions of adults very swollen laterally and dorsally, cardiac region prominently swollen, regions poorly demarcated; lateral carapace spines undiscernible in adults (Figs. 8–12); G1 very long, mostly straight, distal part conical (Fig. 15); Indo-West Pacific .... *Paramaja* Kubo, 1936
– Pseudorostral spines long, slender (Fig. 36L–O); branchial regions distinctly less swollen, cardiac region gently convex but not swollen, regions clearly demarcated; lateral carapace spines, even if short, always visible in adults (Figs. 16, 17); G1 proportionately shorter, more curved, part of dorsal fold bends downwards to form a distinct ventral projection (Figs. 19, 20); Indo-West Pacific .... *Alcomaja* n. gen.

7. Basal antennal article as broad as long (Fig. 39A–D); G1 very long, distal part with pad-like folds (Fig. 7A–Q); Eastern Atlantic to Western Indian Ocean .... *Maja* Lamarck, 1801
– Basal antennal article longer than broad (Fig. 40); G1 otherwise 8

8. Carapace ovoid, distinctly longer than broad (Fig. 34C, F, G); basal antennal article with several large rounded granules and tubercles (Fig. 40O); male thoracic sternites 1–4 not elongated, lateral junction between sternites 2 and 3 very deep, forming waist-like structure (Fig. 51I); margin of male sterno-abdominal cavity almost flat, without rim (Fig. 52L); G1 strongly bent, distal part dilated with 2 folds (Fig. 35F–L); West Pacific .... *Ovimaja* n. gen.

– Carapace pyriform, not distinctly ovoid (Figs. 24, 25, 34A, B); basal antennal article with small granules, never large tubercles (Fig. 40N); male thoracic sternites 1–4 elongated, lateral junction between sternites 2 and 3 relatively shallow (Fig. 51F, G); margin of male sterno-abdominal cavity on thoracic somite 4 raised, entire, forming clear rim (Fig. 52K); G1 otherwise..9

9. Lateral carapace margin with 3 spines (Figs. 24, 25); supraocular eave very prominent, large, anterior part prominently foliaceous (Fig. 37D–J); G1 relatively stout, straight or gently bent, distal, part simple, with scattered spinules and short setae (Fig. 27); Indo-West Pacific ....*Holthuija* n. gen.
– Lateral carapace margin with 6 spines (Fig. 34A, B); supraocular eave otherwise (Fig. 38A); G1 slender, curved, distal part sharply tapering, margins distinctly chitinised, line with numerous short spinules (Fig. 35A–E); West Pacific ....*Planaja* n. gen.

Key to species of *Maja* Lamarck, 1801, s. str.

1. Supraorbital eave relatively broad, as wide as long; dorso-anterior surface of carapace with 2 unarmed, relatively smooth dark oval window-like patches, one on each side of gastric region (Figs. 6A, B, 36E); ischium of third maxilliped ca. 1.5 times as long as wide (Fig. 43F); Mediterranean and adjacent Atlantic waters.............................. *Maja crispata* Risso, 1827
– Supraorbital eave relatively narrow, longer than wide; dorso-anterior surface of carapace evenly granulated, without any unarmed or ovate patches (Figs. 4, 36A–D); ischium of third maxilliped twice as long as wide (Fig. 43A–E); eastern Atlantic to western Indian Ocean 2

2. Carapace of adults longer than wide; adult pseudorostral spines subparallel; restricted to Mediterranean (Fig. 36A)................ .... *Maja squinado* (Herbst, 1788)
– Carapace of adults rounded, as long as large; adult pseudorostral spines diverging, forming a V (Fig. 36B–D); Atlantic to South Africa...3

3. Spines of lateral carapace margin relatively short; antorbital spine almost straight (Figs. 4C–F, 36B, C); northern Atlantic to mid-Atlantic .... *M. brachydactyla* (Balss, 1922)
– Spines of lateral carapace margin relatively long; antorbital spine curved (Figs. 5, 36D); southern Atlantic to South Africa ....*M. cornuta* (Linnaeus, 1758)

Maja squinado (Herbst, 1788)

(Figs. 3A, B, 4A, B, 6E, 7A–C, 36A, 39A, 41A, 43A, B, 44, 47A, B, 53A, 55A)

Cancer squinado Herbst, 1788: 214 (in part, Mediterranean) (not *Cancer squinado* Herbst, 1788: pl. 14, figures 84, 85 = *Maja crispata* Risso, 1827).
Maja tuberculata De Haan, 1839: Pl. F.
Maja squinado – d'Udekem d'Acoz, 1999: 189 – Ng et al., 2008: 117 (list).
[For complete synonymy, see Neumann, 1998: 1669; d'Udekem d'Acoz, 1999: 189]

Material examined. Neotype (here designated): male (147.1 × 126.3 mm) (SMF-4548), Rovinj, Croatia, 20–30 m, coll. 21 August 1989. **Croatia** – 1 male (SMF 11088), Rovinj, Croatia, Sorelle, 3–4 m, coll. University of Frankfurt class, August 1981. — 1 male (SMF 40613), west of Figarola, Rovinj, Croatia, 45°5.532'N 13°36.852'E – 45°5.532'N 13°36.852'E, 28.5-30.5 mm, coll. F.B. Burin, 18 September 2009. — 1 male (138.0 × 121.0 mm) (ZRC), 50 m, on mud and sand, Rijeka Bay, near Island of Krk, coll. trawler, 2 April 2014. **Spain** – 1 female (NHM 1954.11.4.178), Rosas. — 1 female (144.5 × 129.0 mm) (ZRC 2013.1126), ca. 70 km north of Barcelona, 41°40'N 2°47'E, northwestern Mediterranean, ca. 5 m, coll. 1960. **Italy** – 1 female (USNM 205743), Mazara del Vallo, Mediterranean, 14–85 m, coll. R.B. Manning, 4 September 1985. **Gilbraltar** – 1 male, 2 females (USNM 57436), Straits of Gilbraltar, coll. March 1923. **Tunisia** – 2 males (USNM 265648), station R28 ST. 10, off Kerkenah, 34°29.5'N 11°40.2'E, coll. Tunisian Marine Decapod Project, RV *Dauphin*, 7 July 1973. **Israel** – 1 male (84.8 × 70.3 mm) (USNM 152563), 31°46.2'N 35°13.8'E, coll. fishermen.

Diagnosis. Large species (adult carapace length in excess of 80–90 mm). Carapace pyriform; dorsal surface strongly convex; uniformly covered with granules and short spines (Fig. 4A, B). Pseudorostral spines long, strong, gently diverging in smaller specimens, subparallel in larger adults (Figs. 4A, B, 36A). Supraorbital eave relatively narrow, antorbital spine sharp, almost straight to gently curved upwards; intercalated spine stout, short, touching postorbital spine; postorbital spine biggest, long, sharp; hepatic spine sharp with 2 accessory spines at base (Figs. 4A, B, 36A). Lateral margin of carapace with 3 spines and several small sharp granules and short spines (Fig. 4A, B). On median row 7 strong spines: 3 gastric, 2 subgastric, 1 cardiac, 1 intestinal, with 1 sharp granule between cardiac and intestinal spines; spines relatively lower in large specimens (Fig. 4A, B). Branchial region with 2 spines; posterior carapace margin with 2 spines (Fig. 4A, B). Basal antennal article very broad with 2 long distal spines; outer margin with proximal spine, appressed on suborbital tooth (Fig. 39A). Ischium of third maxilliped rectangular, much longer than broad (Fig. 43A, B). Carpus of cheliped with distinct tubercles and granules (Fig. 53A). Ambulatory dactyli covered with short setae (Fig. 55A). G1 long, almost straight to slightly curved; distal part straight (Fig. 7A–C).

Remarks. *Maja squinado* (Herbst, 1788) is the type species of the genus (ICZN Opinion 511, see Holthuis, 1958). In a detailed morphological and biometric study using extensive material from the Mediterranean and the Atlantic coast of Europe, Neumann (1998) was able to recognise three species in what had been generally confused under *Maja squinado*: *M. squinado* (Herbst, 1788) s. str. which is restricted to the Mediterranean, *M. brachydactyla* Balss, 1922, which occurs from Ireland to Mauritania (see also Sotelo et al., 2007, 2008, 2009); and *M. capensis* Ortmann, 1894 (present *M. cornuta*), which is found from the Gulf of Guinea to South Africa and just entering southwestern Indian Ocean. He also noted that there is probably overlapping of the distributions of *M. brachydactyla* and *M. cornuta* (as *M. capensis*) along the Senegal coast but more work will have to be done on this.

The excellent study by Neumann (1998), and the series of molecular studies by Sotelo et al. (2007, 2008, 2009) have helped resolve the identity of *M. brachydactyla* Balss, 1922, a large species that has long been regarded as synonymous or merely a subspecies of *M. squinado* (see Manning & Holthuis, 1981: 307). It is clearly a distinct species and the examination of the present material confirms the observations of Neumann (1998). As it turns out, the commercially more valuable species that occurs from Norway to the Atlantic coasts of Spain that had previously been known as "*Maja squinado*" should now be called *M. brachydactyla*. *Maja squinado* s. str. is restricted to the Mediterranean Sea. Even locations immediately outside the Mediterranean Sea such as in Morocco are only known to have *M. brachydactyla*. Interestingly, it seems that *M. brachydactyla* s. str. can also be found in the Mediterranean itself. Recently, Abelló et al. (2014) conclusively recorded this species from the Alboran Sea in western Mediterranean; so it appears at least in this part of the ocean, both species may be sympatric.

Maja squinado and *M. brachydactyla* are close and small specimens are difficult to separate. Large adults, however, can be separated by the shape of their carapaces, with those of *M. squinado* generally more pyriform and elongate (Fig. 4A, B) whereas *M. brachydactyla* is more rounded (Fig. 4C–F). Neumann (1998) uses the shape of the pseudorostral spines as a character – subparallel in *M. squinado* (Fig. 4A) but clearly diverging in *M. brachydactyla* (Fig. 4C–F) and this holds in large specimens, especially males. Smaller specimens of *M. squinado*, however, have pseudorostral spines that are somewhat intermediate in condition, and certainly cannot be described as subparallel (Fig. 4B). As such, both the carapace shape and pseudorostral spine form should be used as characters, with the G1 structure valuable when adult males are available.

There are, however, problems with two names that Neumann (1998) did not treat that have a major bearing on the current nomenclature of *Maja* s. str.: *Cancer cornutus* Linnaeus, 1758, and *Maja tuberculata* De Haan, 1839.

The name *Cancer cornutus* was first used by Linnaeus (1758: 629) who described the species very briefly: "29. C. brachyurus, thorace aculeato : rostro spinis corniformibus barbatis, manibus teretibus. *M. L. U. Habitat in Oceano Indico*." Several years later, Linnaeus (1764: 445) elaborated on this short diagnosis: "Cancer brachyurus, thorace aculeato: rostro spinis corniformibus barbatis, manibus teretibus. Syst. Nat. p. 629· n. 29. Habitat in Mari Indico. Thorax ovatus, adspersus punctis acuto spinosis. Latera utrinque ciliata spinis 6, validis. Disci spinae 3 transversae & una anterior; ommes erectae, reliquis aequales. Spinae 2 minores, erectiusculae, ad basin thoracis. Rostri loco Spinae 2 inter oculos, reliquis majores, erectiusculae, distantes subtus barbatae. Rostrum subtus inter oculos, acutum, reflexum; & duae spinae coadunatae juxta oculos. Cauda inflexa, ovata, articulis 7. linearibus. Brachia teretia, laevia, glabra, nuda. Manus pedibus reliquis minores, basi extrorsum bidentatae." [crab-like, carapace spinate: rostrum spinate, horn-shaped with whiskers, chelipeds smooth. Inhabits Indian Seas. Carapace ovate, covered with sharp spines. Lateral margins each with six large spines. Three transverse and one anterior spine on carapace, all straight, remainder are same length. Two small straight spines at base of carapace. Rostrum with two intraocular spines, other spines short, arranged closely like whiskers. The rostrum bends below eyes, spines concentrated near eyes. Abdomen rigid, ovate, with seven straight segments. Hands smooth, glabrous, without setae. Chelipeds smaller than other articles, base bidentate. Feet fully hirsute. Digits hirsute.]

The relatively detailed description by Linnaeus (1764) matches that of *Maja squinado*, *M. brachydactyla* or *M. cornuta*. The only unusual character seems to be the comment that rostrum bends below the eyes. In *Maja* species, the two most obvious frontal structures are the prominent "rostral horns". As has been discussed earlier, these may not be the true rostral structures (they are referred to here as pseudorostral spines). The actual rostrum is the spine that is between the base of the pseudorostral spines and that is directed sharply downwards. This is almost certainly why Linnaeus (1764) described the rostrum twice. The first time, he described the pseudorostral spines as "rostral intraocular spines", and the second time, he describes the actual rostrum, noting that it "bends below the eyes". Some authors have speculated that Linnaeus (1764) was actually saying that the pseudorostrum bends below the eyes, a character that defines Indo-West Pacific genera like *Micippa* Leach, 1817. Henri Milne Edwards (1834: 331) lists Linnaeus' taxon (as "*Cancer cornatus*") as a species of *Micippa* and Miers (1885: 11, footnote) suggests that *Cancer cornutus* Linnaeus, 1758, may be *Micippa thalia* (Herbst, 1803). The provenance given by Linnaeus (1758: 629) – Indian Seas – is surprising as most *Maja* species are Atlantic. One *Maja* species, however, does enter the western Indian Ocean in South Africa – *M. cornuta*. While it is possible the specimen or specimens of *Cancer cornutus* Linnaeus had on hand may have been mislabelled (and they were actually Atlantic in origin), it is also likely that he had *Maja* material from South Africa as it was part of the then trade routes.

Ng et al. (2008: 117) listed *Cancer cornutus* Fabricius, 1787, as a doubtful synonym of *Maja squinado* (Herbst, 1788). Fabricius (1775: 407) actually first used the name "*Cancer cornutus*" with the following comments: "C. thorace aculeato, rostro spinis corniformibus, barbatis, manibus rotundatis. *Linn. Syst. Nat.* 11. 1047. 46. *Mus. Lud. Ulr.* 445." It is clear from this account that he was citing Linnaeus' (1758) species. In his next publication when he used the name "*Cancer cornutus*", Fabricius (1787: 325) writes: "C. thorace aculeato, rostro spinis corniformibus barbatis, manibus rotundatis. Habitat et in mari Norwagico." This time, he makes no mention of Linnaeus. He also reports the species from Norwegian Seas for the first time. In his next mention of *Cancer cornutus*, however, Fabricius (1798: 356) again refers to Linnaeus, writing: "6. I. thorace aculeato, rostro spinis corniformibus, barbatis, manibus rotundatis. *Cancer cornutus* Ent. Syst. 2. 462. 80. * Linn. Syst. Nat. 2. 1047. 46. Mus. Lud. Ulr. 445. Habitat in mari mediterraneo, Oceano." It is thus very clear from these publications that Fabricius (1787) never intended to use the name "*Cancer cornutus*" as a novel name even though he did not specifically mention Linnaeus in that paper.

Herbst (1788: 214–217, pl. 14 figs. 84, 85) chose to describe a new species, *Cancer squinado*, but also recognised Linnaeus' taxon, *C. cornutus*, as separate. He treated *Cancer squinado* again a few years later with a more detailed description and another figure (Herbst, 1803: 23–27, pl. 56). His detailed descriptions and figures of *Cancer squinado* suggest he had three different taxa. One form, which was relatively smaller was characterised by the presence of two window-like patches on the carapace. This was the form he first figured (Herbst, 1788: pl. 14 figs. 84, 85) (reproduced here as Fig. 3C, D) and is clearly referrable to *Maja crispata* (see also Neumann, 1996a). Herbst's next figure (1803: pl. 56) (reproduced here as Fig. 3E) shows a more rounded animal that can easily be identified with *Maja brachydactyla*. The larger form Herbst (1788, 1803) discusses (depicting *M. brachydactyla*) also certainly includes *M. squinado* as he comments that the species is fished in Napoli (=Naples) in the Mediterranean.

Maja crispata is not only relatively smaller at adult size, it also has two distinct patches on the sides of the gastric region that are not only darker in colour than the other parts of the carapace but are also unarmed. These are evident even in long-preserved specimens. *Maja squinado* (and *M. brachydactyla* as well as *Neomaja goltziana*) does not have these patches. Charpentier (1829: 160–162) discussed at length what he believed were two forms of *Cancer squinado* and opted to recognise them as separate species, treating the smaller form (figured in Herbst's pl. 14 figs. 84 and 85) as "*Inachus cornutus* (Linnaeus, 1758)". Since Herbst (1788) also cited the plates in the non-binomial work (and hence not available for nomenclature purposes) of Seba (1759: pl. 18 figs. 2, 3), the latter's specimen can also be part of his original type series.

The types of *Cancer squinado* Herbst, 1788, are no longer extant (Neumann, 1998). Katushi Sakai (1999: 40) also indicated there are no extant types in the Herbst cabinets in the Museum fur Naturkunde in Berlin; and a recent check of the collection by its curator, Oliver Coleman, and Tan Heok Hui (ZRC) confirmed this. Neumann (1998: 1669) argues that Seba's figures "clearly show an adult male specimen with *squinado*-characters (i.e. comparatively long lateral carapace spines and long, parallel rostral horns)", and as such selected this specimen as the lectotype of *Cancer squinado* Herbst, 1788. These figures (reproduced here in Fig. 3A, B) show a specimen resembling *M. squinado* in general carapace form, although its rostral spines appear to be more divergent than parallel. In any case, there is no extant specimen as Seba's material is lost (see Koh & Ng, 2008: 341). A neotype for *Cancer squinado* Herbst, 1788, is designated here to stabilise the taxonomy of this species (see later).

So what is *Cancer cornutus* Linnaeus, 1758? From all the available evidence, and assuming the original provenance (Indian Ocean) is correct, it can only be what is today known as *Maja capensis* Ortmann, 1894 (= *Mamaia queketti* Stebbing, 1908) (type localities of both species Port Elizabeth in South Africa). Recognising these names as synonyms means Linnaeus' name has priority, and the South African spider crab must hence be known as *Maja cornuta* (Linnaeus, 1758). While the name *Cancer cornutus* Linnaeus, 1758, has actually not been used as an available name since 1900, invoking Article 23.9.1 of the Code (ICZN, 1999: 27) to suppress this name in favour of the younger name, *M. capensis* is not necessary. This is because the name *Maja capensis* Ortmann, 1894, itself is rarely cited, and has been in general use only in recent years since Neumann's (1998) revision.

Linnaeus' specimens of this species are no longer extant and studies of his extant brachyuran material in Uppsala University failed to uncover any specimen of *Maja* (S. H. Tan, pers. comm.) (see also Holm, 1957). Ortmann (1894: 40–41) established the name "*Maja squinado* var. *capensis*" on the basis of three female specimens from Port Elizabeth in South Africa. No measurements were provided for any specimen and all are syntypes. Ortmann compared this variety with *M. squinado* and *M. crispata* (as *M. verrucosa*) and indicated that while he believed it to be intermediate between the two species, he was more inclined to think it was closer to the former species. Neumann (1998) did not indicate if he examined the types. Ortmann's (1894) material is deposited in the Museum of Zoology at Strasbourg (MZS) and two dried specimens were located. To stabilise the taxonomy of the species in question here, we here designate the lectotype female (96.8 × 89.5 mm) of *Maja squinado* var. *capensis* Ortmann, 1894, in the Strasbourg Museum as the neotype of *Cancer cornutus* Linnaeus, 1758. As a result of this action, all three names are synonyms, with the oldest name being *Maja cornuta* (Linnaeus, 1758).

The second outstanding taxonomic problem associated with *M. squinado* s. str. and *M. brachydactyl*a pertains to the identity of *Maja tuberculata* De Haan, 1839. The species was named when De Haan (1839: pl. F) figured two mouthparts of a species he named *Maja tuberculata* but without any description, indication of provenance or diagnostic characters. The name is nevertheless available under the current zoological code (ICZN, 1999). Yamaguchi & Baba (1993: 695, fig. 24) figured some dried and mounted mouthparts still extant in the Leiden Museum (RMNH D 43524, Fig. 44A, B) and suggested they may be the type of *M. tuberculata*. Herklots (1861: 19) in his study of the material of De Haan in the Leiden Museum had indicated that he had a new species of *Maja* (as *Maia* nov. sp.) from "Iles moluques" but he did not formally name it, attribute it to De Haan's "*M. tuberculata*" or refer to the any material or specimens. Whether these dried mouthparts in RMNH formed the basis of Herklots' "*Maia* nov. sp." is not known. There is no other evidence for Yamaguchi & Baba's (1993) suspicion.

Through the courtesy of Charles Fransen, the first author examined the box that supposedly contains the mouthparts of *Maja tuberculata*. The mouthparts remain attached and arranged in a row, and on the original background label is written "*Maja tuberculata*". While this label is old, it is not known if this was written by De Haan or later on by someone else. De Haan (1839: pl. F) figured the various mouthparts of *Maja squinado* (right first to third maxillipeds, right first and second maxillas and right mandible), and only the last two figures (which depicted a right third maxilliped and right first maxilliped) belonged to *Maja tuberculata*. The third maxilliped of *M. tuberculata* figured is smaller than that of *M. squinado* figured on the same plate (both were drawn life-size), and there are no obvious morphological differences between them. In the extant material supposedly of *M. tuberculata*, the various mouthparts are present, but there are two left third maxillipeds in the box (Fig. 44A, B). One is still attached to the box and labelled as *Maja tuberculata*, while the other was loose. No right third maxillipeds were present. The two extant left third maxillipeds, however, are of different sizes; the attached one is 11.1 mm (measured from the anterior margin of the merus to the posterior margin of the basis) (Fig. 44E), the other 17.3 mm (Fig. 44F). They clearly belong to two separate specimens. On the basis of the structure and size, the larger left third maxilliped (Fig. 44F) corresponds well with the size of the right third maxilliped figured as *Maja squinado* by De Haan (1839) (Fig. 44C). The smaller left third maxilliped (Fig. 44E) agrees in size with the right third maxilliped figured as *Maja tuberculata* by De Haan (1839) (Fig. 44C). On this evidence, it would appear that the smaller left third maxilliped, as well as the associated series of mouthparts, are the types of *Maja tuberculata* De Haan, 1839. What happened to the right third maxilliped of *Maja tuberculata* figured by De Haan (1839) is not known – it is probably lost.

The figure of the now missing right third maxilliped of *M. tuberculata* by De Haan (1839) is quite accurate (Fig. 4D) and agrees with the general structure of the extant left third maxilliped. The third maxilliped of *M. tuberculata* measures about 11.1 mm long and on the basis of the *Maja* specimens examined in this study, it would have to belong to a large species measuring about 70–90 mm in carapace length.

Comparing the third maxilliped structure of *M. tuberculata* (Fig. 44) with species of *Maja* sensu lato, it is clear that it almost identical in shape, proportions and setation to *Maja squinado*, *M. brachydactyla* and *M. cornuta* (ex *M. capensis*) from the eastern Atlantic and South Africa. The third maxillipeds of the other two Atlantic species, *Neomaja goltziana* (which can grow to 80 mm in carapace length) (Fig. 43G, H) and *Maja crispata* (which can exceed 60 mm in carapace length) (Fig. 43F), are very different from that of *M. tuberculata* (Fig. 44E). In the Indo-West Pacific, only *Paramaja gibba*, *Paramaja kominatoensis*, *Paramaja turgida*, *Paramaya spinigera* and *Paramaya ouch* are known to grow to 80 mm in carapace length, but their third maxillipeds (Figs. 43L–P, 45I–K) are very different in structure compared to that of *M. tuberculata*. As such, the suggestion by Yamaguchi & Baba (1993) that *Maja tuberculata* may have originated from the "Moluccas" and it is Herklots' (1861) unnamed species seems unfounded.

The available data strongly suggests that De Haan's *Maja tuberculata* was merely based on a small specimen of *M. squinado*, which also tends to be more prominently granulated on the carapace when younger (see Neumann, 1998). Since the distributions of *M. squinado* and *M. brachydactyla* partially overlap (Neumann, 1998), we cannot be sure which of the Atlantic species *M. tuberculata* is actually conspecific with. It poses some potential nomenclatural problems if *Maja tuberculata* De Haan, 1839, is the same as *M. brachydactyla* Balss, 1922, since it is a senior name. *Maja cornuta* (Linnaeus, 1758) and *M. squinado* (Herbst, 1788) are older names. For practical reasons, we regard *Maja tuberculata* De Haan, 1839, as a subjective junior synonym of *Cancer squinado* Herbst, 1788, at least for the time being.

As the types of *Cancer squinado* Herbst, 1788, are lost (K. Sakai, 1999), and even the lectotype selected by Neumann (1998) is no longer extant (see earlier discussion); we here designate a male specimen measuring 147.1 by 126.3 mm (SMF-4548) from Croatia as the neotype of *Cancer squinado* Herbst, 1788 (Fig. 4A). This will stabilise the taxonomy of the genus, the identities of the European species and objectively separate it from the allied *M. brachydactyla* Balss, 1922. As discussed earlier, the types of *Maja tuberculata* De Haan, 1839, may also have to be suppressed in the future by an application to the International Commission for Zoological Nomenclature.

Maja brachydactyla Balss, 1922
(Figs. 2A, 3E, 4C–F, 7D–I, 36B, C, 39B, 41B, 43C, D, 47C, D, 52A, 53B, C, 55B)

Cancer cornutus – Fabricius, 1787: 325 (not *Cancer cornutus* Linnaeus, 1758).
Maja squinado var. *brachydactyla* Balss, 1922: 74.
Maia gigantea Baudouin, 1931: 256.
Maja squinado – Takeda, 1982: 129. – Takeda, 1993: 43. – Muraoka, 1998: 27, pl. 14 fig. 3 (not *Cancer squinado* Herbst, 1788).
Maja brachydactyla – Neumann, 1998: 1672. – d'Udekem d'Acoz, 1999: 188. – Abelló et al., 2014:e77. – Moro et al., 2014: 52.
[For complete synonymy, see Neumann, 1998: 1672; d'Udekem d'Acoz, 1999: 188–189].

Material examined. Spain – 1 male (161.2 × 140.1 mm), 1 ovigerous female (143.2 × 127.6 mm) (ZRC 2008.0179), northwest of Baiona, from fishermen, 25 January 2008. — 1 female (NHM 1956.5.2.49), Lanzarote. — 1 male (USNM 122017), northwestern Spain. **Portugal** – 1 male (NHM 98.1.28.1), Madeira. **England** – 2 males (98.4 × 89.0 mm, 92.6 × 75.5 mm), 1 female (127.8 × 111.9 mm), 1 ovigerous female (119.0 × 103.0 mm) (ZRC 2009.1130), Worbarrow Bay, south Dorset, 5 m, 50°37.06'N 2°11.23'W, U.K., coll. S. De Grave, 5 June 2005. — 1 female (NHM 1983.46), Thorn Island, Pembrokeshire, 10 m, coll. 10 August 1981. — 1 female (NHM 1983.46), Knoll Pins, Lundy, 22 m, coll. 3 September 1982. — 1 female (NHM 1985.11), Eastbourne, coll. 8 August 1984. — 1 female (NHM 1983.44), Littlehampton, 50°39.11'N 00°36.9'W, coll. 29 July 1983. — 1 female (NHM 1959.10.15.1), Langston Harbour, Portsmouth. — 2 males, 2 females (NHM 1965.12), Durdle Door, Dorset, coll. 6 June 1965. — 2 females (NHM 1983.448), Start Bay, Devon. — 2 females (NHM 1983.44), Devon, Start Bay, off Hall Sands, 12 m, 10 May 1981. — 1 female (NHM 1981.54), Devon, Brixham Harbour, 5 m, coll. 9 July 1981. — 1 female (NHM 1902.3.10.2), Plymouth. — 1 female (NHM 1981.237), Plymouth. — 1 male (NHM 98.5.7.264), Falmouth. — 1 male (NHM 1984.454), mouth of Fal river, Trefusis Point, 50°9.8'N 5°3.1'W, coll. 4 July 1984. — 2 females (NHM), Cornwall. — 1 male, 1 female (NHM 1981.37), Belle Creve Bay, Guernsey, coll. 11 June 1981. — 1 male, 3 females (NHM), Guernsey, coll. September 1982. — 1 male (NHM), Rocquaire Bay, Guernsey, coll. 18 August 1982. — 1 male, 4 females (NHM 1951.1.25.134–136), English Channel coast. — 3 males, 4 females (NHM), southern England. — 1 male (USNM 6773), England, from A. M. Norman. — 1 male, 1 female (USNM), Channel Islands, coll. E. Lovett. — 1 male (NSMT 3805), Portsmouth, Devon, English coasts, no other data. **Ireland** – 1 male (NHM 1982.13), Galway Bay, 10 m, coll. 27 August 1981. **Morocco** – 1 male (61.5 × 53.8 mm) (MNHN-IU-2013-4039), coll. Lt. Dyé, 1905.

Diagnosis. Large species (adult carapace length in excess of 90–100 mm). Carapace pyriform, more rounded in large specimens; dorsal surface strongly convex; uniformly covered with granules and short spines (Fig. 4C–F). Pseudorostral spines long, gently curved to almost straight, gently diverging (Figs. 4C–F, 36B, C). Supraorbital eave relatively narrow, antorbital spine sharp, almost straight to gently curved upwards; intercalated spine stout, short, touching postorbital spine basally; postorbital spine largest, long, sharp; hepatic spine sharp with 2 accessory spines basally (Figs. 4C–F, 36B, C). Lateral margin of carapace with 3 spines and several small sharp granules and short spines (Fig. 4C–F). On median row 7 strong spines: 3 gastric, 2 subgastric, 1 cardiac, 1 intestinal, with 1 sharp granule between cardiac and intestinal spines; spines relatively lower in large specimens (Fig. 4C–F). Branchial region with 2 spines; posterior carapace margin with 2 short spines (Fig. 4C–F). Basal antennal article very broad with 2 long distal spines; outer margin with proximal spine, appressed on suborbital tooth (Fig. 39B). Ischium of third maxilliped rectangular, much longer than broad (Fig. 43C, D). Carpus of cheliped with distinct tubercles and granules (Fig. 53B, C). Ambulatory dactyli covered with short setae (Fig. 55B). G1 long, gently curved; distal part gently curved downwards (Fig. 7D–I).

Remarks. Small specimens of *M. brachydactyla* tend to be more spiny overall, with the lateral spines relatively stronger (Fig. 4C) compared to larger ones (Fig. 4D-F). See also discussion for *M. squinado*.

Maja cornuta (Linnaeus, 1758)

(Figs. 5, 7J–N, 36D, 39C, 43E, 47E, F, 53D, E)

Cancer cornutus Linnaeus, 1758: 629. – Linnaeus, 1764: 445.
Maja squinado var. *capensis* Ortmann, 1894: 40.
Mamaia queketti Stebbing, 1908: 3, pl. 27.
Mamaia capensis – Barnard, 1950: 59, fig. 13a.
Maja capensis – Neumann, 1998: 1675.
? *Maja capensis* – Ng et al., 2008: 117 (list).
[For complete synonymy, see Neumann, 1998: 1675, as *Maja capensis* Ortmann, 1894]

Material examined. Lectotype of *Maja squinado* var. *capensis* (here designated) and neotype (here designated) of *Cancer cornutus* Linnaeus, 1758: male (96.8 × 89.5 mm, 110.0 × 100.0 mm with spines) (ZMS), Port Elizabeth, South Africa, obtained from natural history dealer Rolle in Berlin, 1891. **South Africa** – 1 dried female (71.0 × 60.3 mm, 80.0 × 70.0 mm with spines) (ZMS) (paralectotype of *Maja squinado* var. *capensis* Ortmann, 1894), same data as lectotype. — 1 male (88.8 × 86.8 mm) (NHM 1928.12.1.177) (lectotype, here designated, of *Mamaia queketti* Stebbing, 1908), Port Elizabeth, Stebbing Collection, coll. Fitzsimons, 5 November 1907. — 1 female (NHM 1913.3.29.4), Durban, coll. H. C. Chubb. — 2 males (NHM 1928.12.1.178–179), Bird Island, 45 fathoms, coll. H. W. Bek Marley. — 1 ovigerous female (114.9 × 103.8 mm) (ZRC 2005.0014), Kenton on Sea, Bay World, Port Elizabeth, eastern part of Cape of Good Hope, coll. S. Warren, 1 December 2003. — 1 male (115.3 × 103.4 mm) (ZRC 2013.1184), station ACEP 1.4, Transvaal, off Durban, 29°58.56'S 31°04.98'E – 29°57'S 31°06.3'E, 65 m, trawl, coll. S. Fennessy, 18 March 2010. — 2 males (79.8 × 68.9 mm, 53.8 × 45.1 mm) (ZRC 2013.1183), station ACEP 2.4, Transvaal, 29°29.9'S 31°52.8'E – 29°26.56'S 31°53.5'E, 184 m, trawl, coll. S. Fennessy, 19 March 2010.

Diagnosis. Large species (adult carapace length in excess of 80 mm). Carapace pyriform; dorsal surface strongly convex; uniformly covered with granules and short spines (Fig. 5). Pseudorostral spines long, straight, strongly diverging (Figs. 5, 36D). Supraorbital eave relatively narrow, antorbital spine sharp, curved upwards; intercalated spine stout, short, touching postorbital spine basally; postorbital spine largest, long, sharp; hepatic spine sharp with 2 accessory spines basally (Figs. 5, 36D). Lateral margin of carapace with 3 strong spines and several small sharp granules and short spines (Fig. 5). On median row 7 strong spines: 3 gastric, 2 subgastric, 1 cardiac, 1 intestinal, with 1 sharp granule between cardiac and intestinal spines (Fig. 5). Branchial region with 2 spines; posterior carapace margin with 2 spines (Fig. 5). Basal antennal article very broad with 2 long distal spines; outer margin with proximal spine, appressed on suborbital tooth (Fig. 39C). Ischium of third maxilliped rectangular, much longer than broad (Fig. 43E). Carpus of cheliped with distinct tubercles and granules (Fig. 53D, E). Ambulatory dactyli covered with short setae (Fig. 5). G1 long, gently curved; distal part gently curved downwards (Fig. J–N).

Remarks. *Maja cornuta* (previously *M. capensis*) occurs in the sublittoral zone on the Indian Ocean side of South Africa. Compared with *M. brachydactyla*, the carapace of *M. cornuta* is not as inflated, the pseudorostral spines are relatively longer and more slender, the antorbital spine is more distinctly curved anteriorly, there is a relatively wider gap between the intercalated, supra- and postorbital spines (the three spines are closely appressed in *M. brachydactyla*), and all the spines on carapace margin, including the hepatic one, are proportionately longer and sharper. The G1 structures are also slightly different between the two species: in *M. brachydactyla* it is straight with a large terminal opening (Fig. 7D–I), while in *M. cornuta*, it is slender and curved with a more slender tip (Fig. 7J–L). See also discussion for *M. squinado*.

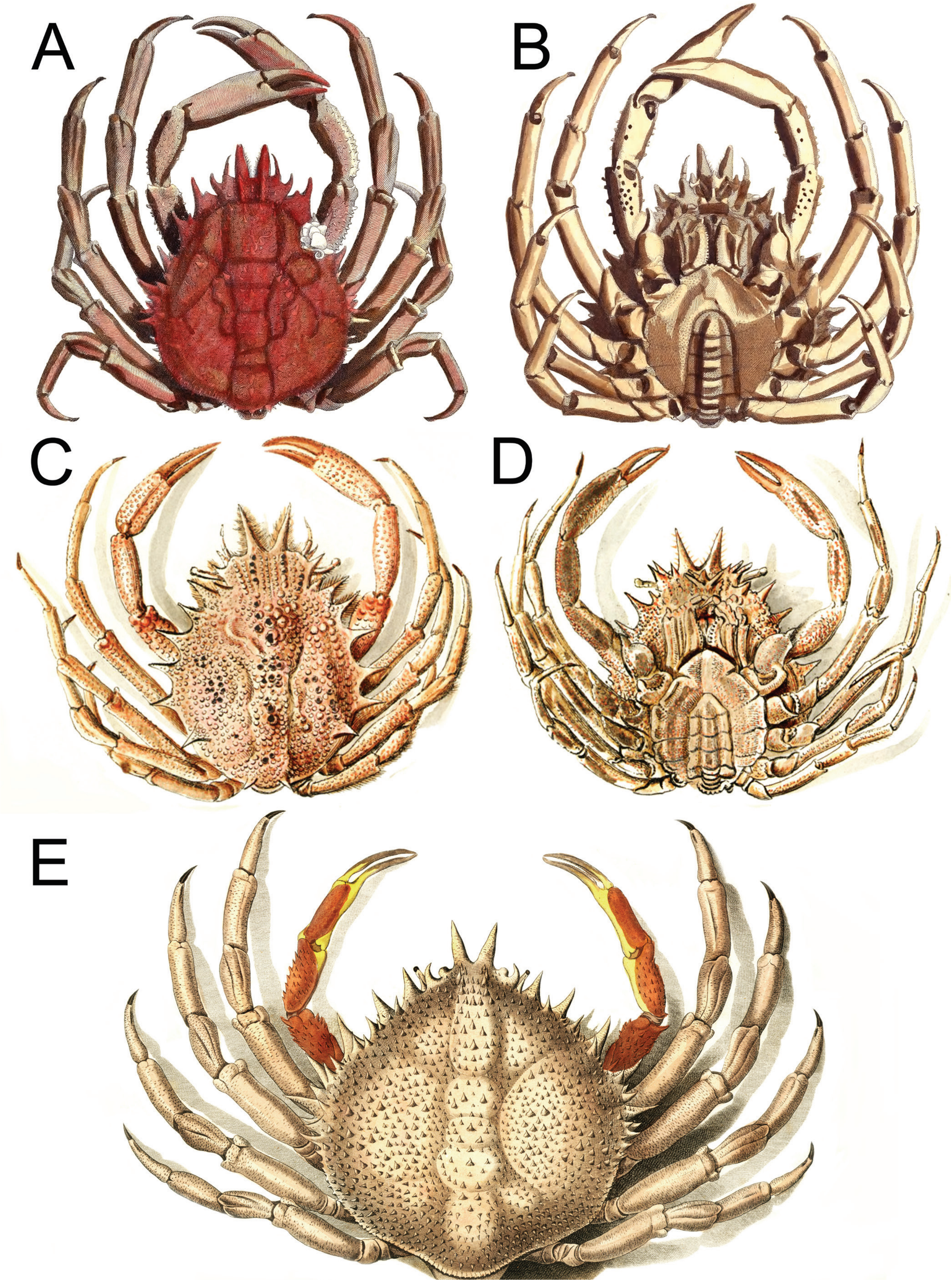

Fig. 3. General habitus. A, B, *Maja squinado* (after Seba, 1759: pl. 18 figs. 2, 3); C, D, *Maja crispata* (after Herbst, 1788: pl. 14, figures 84, 85; as *Cancer squinado*); E, *Maja brachydactyla* (after Herbst, 1803: pl. 56; as *Cancer squinado*).

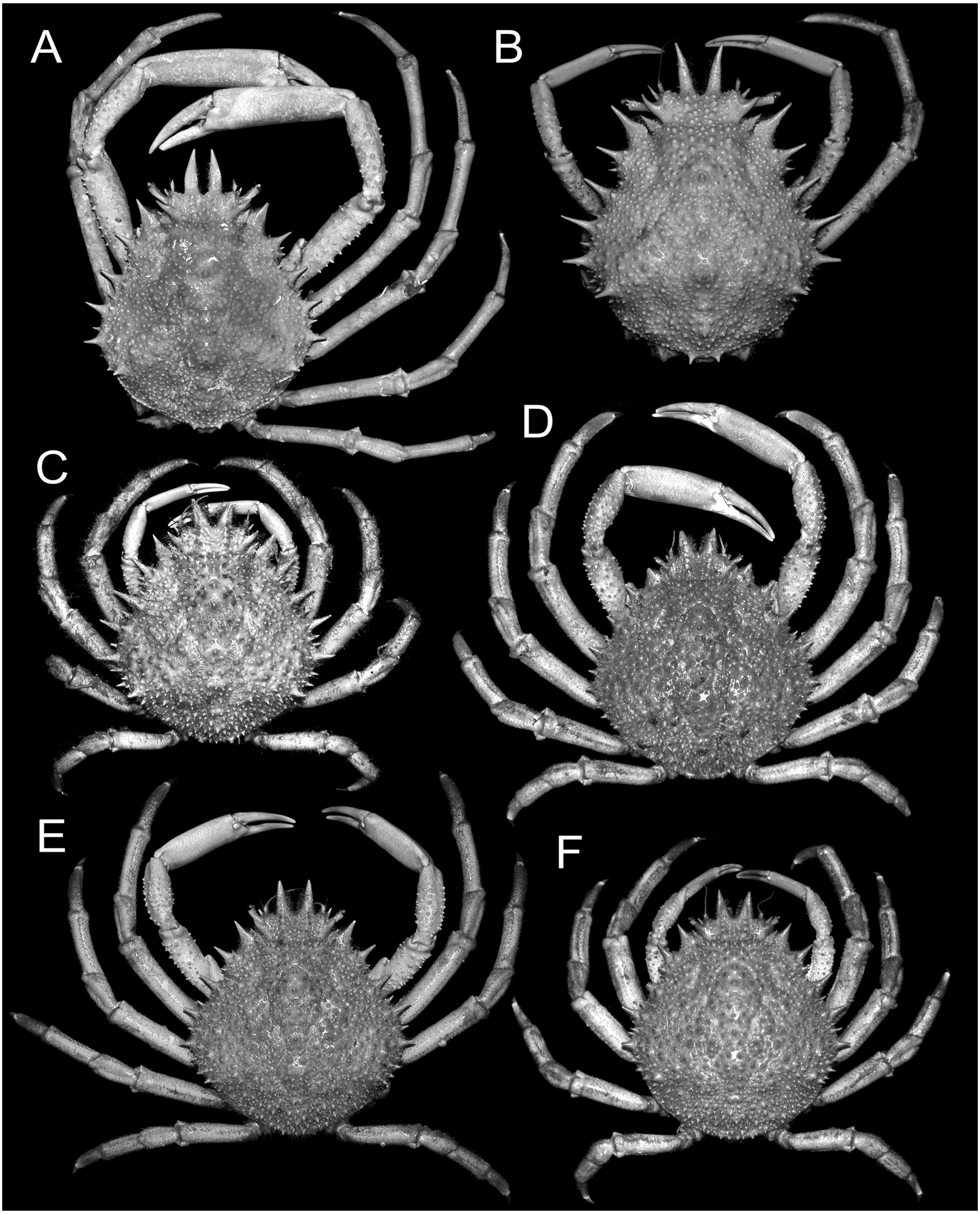

Fig. 4. General habitus, *Maja* species. A, *Maja squinado*, neotype male (147.1 × 126.3 mm) (SMF-4548), Croatia; B, *Maja squinado*, male (84.8 × 70.3 mm) (USNM 152563), Israel; C, *Maja brachydactyla*, male (61.5 × 53.8 mm) (MNHN-IU-2013-4039), Morocco; D, *Maja brachydactyla*, male (161.2 × 140.1 mm), (ZRC 2008.0179), Spain; E, *Maja brachydactyla*, male (98.4 × 89.0 mm) (ZRC 2009.1130), U.K.; F, *Maja brachydactyla*, ovigerous female (119.0 × 103.0 mm) (ZRC 2009.1130), U.K.

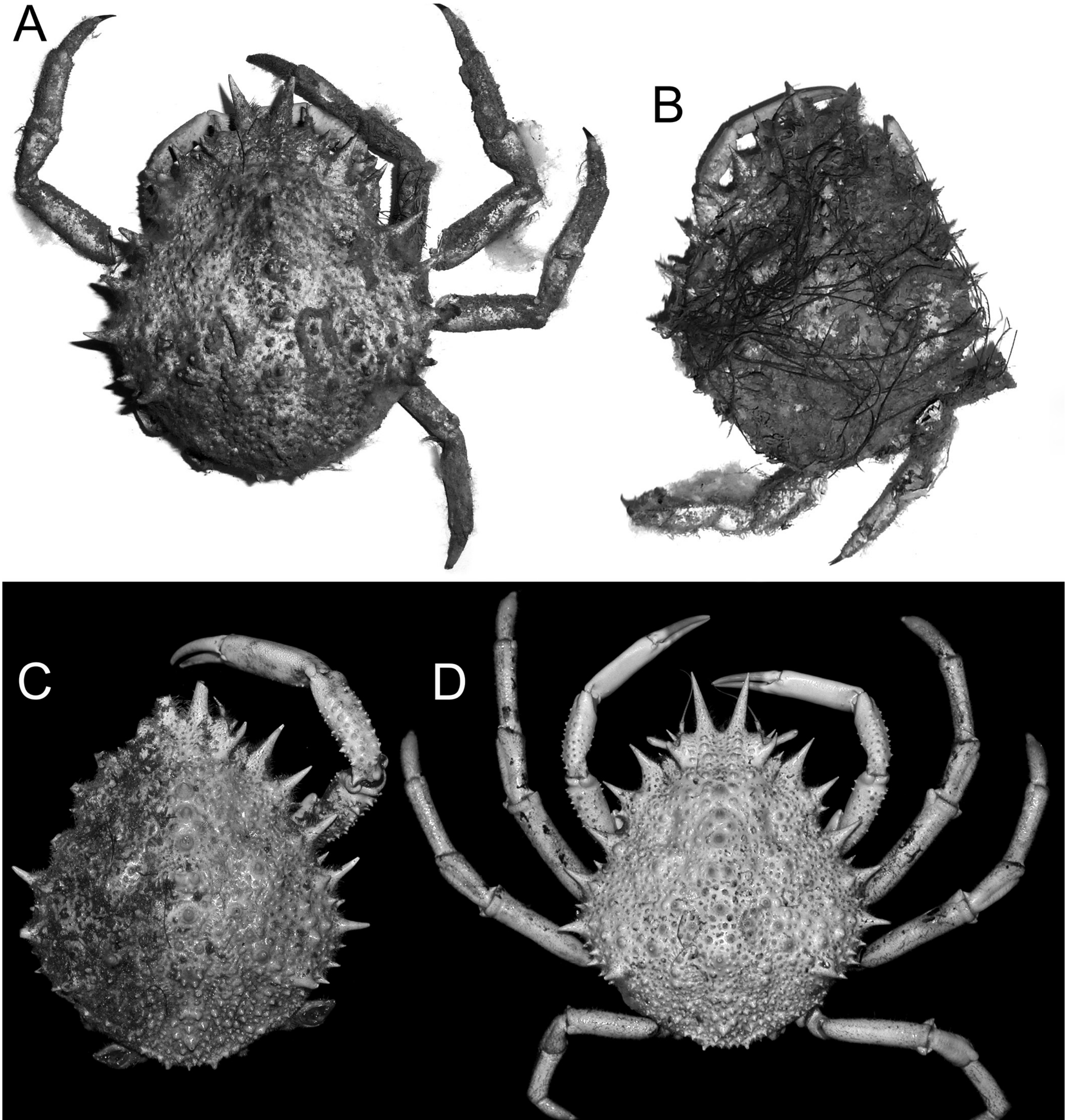

Fig. 5. General habitus, *Maja cornuta*. A, dried female (96.8 × 89.5 mm) (ZMS) (lectotype of *Maja squinado* var. *capensis* Ortmann, 1894, and neotype of *Cancer cornutus* Linnaeus, 1758), South Africa; B, dried female (71.0 × 60.3 mm) (ZMS) (paralectotype of *Maja squinado* var. *capensis* Ortmann, 1894), South Africa; C, male (88.8 × 86.8 mm) (NHM 1928.12.1.177) (lectotype of *Mamaia queketti* Stebbing, 1908), South Africa; D, male (115.3 × 103.4 mm) (ZRC 2013.1184), South Africa.

Maja crispata Risso, 1827
(Figs. 3C, D, 6A, B, 7O–Q, 36E, 39D, 41C, 43F, 47G, 52B, 53F, 55C)

Maja crispata Risso, 1827: 23. – Neumann, 1996b: 828; d'Udekem d'Acoz, 1999: 189.
Maja verrucosa H. Milne Edwards, 1834: 328, pl. 3 figs. 1–14. – Bouvier, 1940: 322. – Monod, 1956: 477. – Zariquiey Alvarez, 1968: 447, figs. 149b, 150a–f, 156a. – Muraoka, 1998: 27.
Cancer majoides Nardo, 1847: 3.
Maja erinacea Ninni, 1924: 49, 50, 2 un-numbered figures.
(see Neumann, 1996b: 828; d'Udekem d'Acoz, 1999: 189, for references)

Material examined. Tunisia – 1 female (NHM), station RBM Tun-303, Sidi Bou Said, Yacht Club, among rocks of jetty, 1 m or less water, coll. R.B. Manning & R. Ingle, 21 February 1974. — 1 male, 1 female (USNM 265589), station R26 ST. 1, 34°29.5'N 11°14.5'E, 34–36 m, coll. Tunisian Marine Decapod Project, RV *El Maghreb*, 18

July 1973. — 1 female (USNM 265651 station), station RBM TUN 184, algae covered boulders above *Posidonia* meadows, isolated cove about 2 km west of Korbous town, coll. Tunisian Marine Decapod Project, 13 July 1973. — 1 male (USNM 265654), station R24 ST. 3, off Kerkenah, 34°25.2'N 11°10.2'E, 37–42 m, coll. Jeddi, 8 July 1973. — 1 male (USNM 265655), station R12 ST. 10, off Zarat, Gabès Governorate, 33°55.2'N 10°31.8'E, 21 m, coll. Tunisian Marine Decapod Project, RV *El Maghreb*, 28 June 1973. — 2 females (USNM 265658), station R28 ST. 3, off Kerkenah, 34°36'N 11°31.5'E, 29–31 m, coll. Tunisian Marine Decapod Project, RV *El Maghreb*, 7 July 1973. — 3 males, 1 female (USNM 265659), station R25 ST. 3, off Kerkenah, 34°28.8'N 11°14.5'E, 40–43 m, coll. Tunisian Marine Decapod Project, RV *El Maghreb*, 9 July 1973. — 1 female (USNM 265660), station R19 ST. 9, off Djerba, 34°13.5'N 10°40.2'E, 36 m, coll. Tunisian Marine Decapod Project, RV *El Maghreb*, 20 July 1973. — 1 male (USNM 265661), station R14 ST. 2, off Gabes, 34°30'N 10°21'E, coll. Tunisian Marine Decapod Project, RV *El Maghreb*, 28 June 1973. — 2 males, 1 juvenile (USNM 265662), station R27 ST. 6, off Kerkenah, 34°31.5'N 11°30.5'E, 40–41 m, coll. Tunisian Marine Decapod Project, RV *El Maghreb*, 8 July 1973. — 1 male (USNM 265868), station RBM TUN 211D, shallow rocky platform with grass and algae, La Marsa, Public Beach at Marsa Plage, coll. R.B. Manning, 21 August 1973. **Spain** – 1 juvenile male (NHM 1957.8.12.53), Barcelona Habour, coll. R. Zariquiey Alvarez. — 1 juvenile female (NHM 1956.3.22.200), Cap l'Abeille, Banyuls, coll. I. Gordon. — 1 male (NHM), Playa Garvet, by Port Bau, coll. I. Gordon. — 1 male (NHM 1955.2.28.241), Cadaqués Bay, coll. I. Gordon. — 2 females (NHM 1953.10.28.77–78), Cadaqués Bay, coll. R. Zariquiey Alvarez. — 1 male (NHM 1965.12.9.164), Vedra Strait, Ibiza, coll. Imperial College, London, 1963. **Portugal** – 1 female (USNM 258341), Armacao De Pera, Algarve, south coast of Portugal, coll. 1 November 1974. **France** – 1 male (NHM 1952.3.18.13), Villefranche, inshore waters, coll. Captain Zotton. **Italy** – 1 female (NHM 1959.5.26.126), Bay of Naples, coll. I. Gordon. — 1 male, 1 female (NHM 1959.5.26.124–125), Bay of Naples, coll. Naples Zoological Station. — 3 males, 1 female (NHM 98.5.7.265/6), Naples, coll. Norman. — 1 male, 2 females (NHM 1954.11.4.175–177), L'Arenella, near Naples, from fishermen, coll. I. Gordon. — 1 male (NHM 1978.209), Santa Marinella, 42°02'N 11°51'E, Roma, coll. M. Gianinotta. — 1 male (63.1 × 51.9 mm) (MNHN-IU-2013-4042), Station Porto Cesareo, Station di Biologia Marina dei Salento, Lecce, no other data. — 1 male (77.1 × 64.3 mm) (MNHN-IU-2013-4040), Messina, coll. M. Vialleton, no date. — 1 male (48.5 × 39.0 mm) (MNHN-IU-2013-4041), Station Porto Cesareo, Costra Neretina Provenance, Lecce, 10–15 m, no other data. — 1 female (USNM 152285), station RBM ITAL12, west side of Bay of Carini, 15 m, Sicily, coll. R.B. Manning, 16 June 1974. — 1 carapace (USNM 152286), station RBM ITAL28, Trapani, rocky flat south of and outside Harbor, Sicily, coll. R.B. Manning, 20 June 1974. — 1 male (USNM 152287), station RBM ITAL36, fish market, Syracuse, Sicily, coll. R.B. Manning, 21 June 1974. — 3 males (USNM 152288), station RBM ITAL36, fish market, Syracuse, Sicily, coll. R.B. Manning, 21 June 1974. — 1 ovigerous female (USNM 205791), Mazara Del Vallo, Sicily, coll. R.B. Manning, 2 September 1985. — **Greece** – 1 male, 1 female (NHM 1968.638), Chios Islands, coll. G. Potts. — 1 male (NHM 1968.637), Chios Islands, coll. G. Potts. — 1 female (NHM 96.5.30.3), Smyrna, coll. Y. Holswood. **Croatia** – 1 male (ZRC), Rovinj, Figarola, coll. Senckenberg Museum class, don. SMF, 23 August 1989. — 1 female (ZRC), Rovinj, coll. Senckenberg Museum class, don. SMF, 20 August 1989. — 1 male (ZRC), Rovinj, coll. Senckenberg Museum class, don. SMF, August 1993. **Slovenia** – 1 male, 1 female (NHM 98.5.7.301), Pirano Adriatic, don. Vienna Museum, coll. Norman. **Macedonia** – 1 female (NHM 1919.19.4.281), coll. Waterston. **Israel** – 1 male (USNM 152564), Mikhmoreth, near rocks, 3–4 m, coll. D. Popper, 12 February 1972.

Diagnosis. Medium-sized species (adult carapace length 60–70 mm). Carapace distinctly pyriform, much longer than broad more rounded in large specimens; dorsal surface gently convex; uniformly covered with granules and short spines except for window-like patch on each side of gastric region which is weakly or not armed (Fig. 6A, B). Pseudorostral spines short, straight, strongly diverging (Figs. 6A, B, 36E). Supraorbital eave relatively wide, antorbital spine sharp, almost straight or gently curved upwards; intercalated spine short, touching postorbital spine basally; postorbital spine largest, long, sharp; hepatic spine slender, sharp with 2 or 3 small spines or tubercles basally (Figs. 6A, B, 36E). Lateral margin of carapace with 3 strong spines and several small sharp granules and short spines (Fig. 6A, B). On median row, no long spines discernible, with 4 sharp tubercles: 2 gastric, 1 cardiac, 1 intestinal (Fig. 6A, B). Branchial region with 2 spines; posterior carapace margin with 2 distinct spines and one small median one (Fig. 6A, B). Basal antennal article very broad with 2 long distal spines, proximal triangular spine passing behind postorbital spine; outer margin with proximal tooth, appressed on suborbital tooth (Fig. 39D). Ischium of third maxilliped squarish, slightly longer than broad (Fig. 43F). Carpus of cheliped with low granules or low, uneven ridges, otherwise almost smooth (Fig. 53F). Ambulatory dactyli covered with relatively long setae (Fig. 55C). G1 long, gently curved; distal part dilated, gently curved downwards (Fig. 7O–Q).

Remarks. For the classification of this species in *Maja* s. str., see Remarks under the genus. The identity of *Maja erinacea* Ninni, 1924, described from the Adriatic, is dubious. Türkay (in Števčić, 1990) had suggested that it was synonymous with *Maja goltziana* d'Oliviera, 1889, but the problem is that the latter species is not known from the Mediterranean Sea. d'Udekem d'Acoz (1999: 189) noted that it is probably not *M. goltziana*. Ninni's (1924) un-numbered figures are rather schematic, but the armature of the carapace spines does bear a marked resemblance to *M. goltziana*. One of the other diagnostic features of *M. goltziana* is that the ambulatory meri are armed with a prominent distal spine on the dorsal margin. Ninni (1924: 49–50) writes that in *M. erinacea*, "La base di quasi tutte le spine è ricoperta da peli, così pure il carapace e tutti I paia di piedi ad eccezione del primo paio. Questo è molto più piccolo degli altri, manca della piccola spina rivolta all' insù e che trovasi invece sul quarto articolo sulla parte superiore di ogni altro paio di piedi" but it is not very clear if he actually says the ambulatory merus has the long sharp spine. In any case, some specimens of *M. crispata* are known to have relatively longer carapace spines (Neumann, 1996a: fig. 2G), and *M. goltziana* is not known from the Mediterranean Sea. As such, we follow Neumann (1996a: 828) in treating *Maja erinacea* Ninni, 1924, as a junior synonym of *M. crispata*, at least for the time being.

Maja crispata is known from Portugal to Mauritania and in the Mediterranean Sea, occurring at depths not deeper than 120 m. The larvae were described by Neumann (1993), with an unusual case of heteromorphosis recorded by Carmona-Suarez (1990).

Neomaja n. gen.

Diagnosis. Carapace pyriform; dorsal surface covered by granules and tubercles, spines large; gastric and branchial regions not distinctly demarcated, separated by shallow grooves; gastric and cardiac regions each with 1 distinct spine (Fig. 6C, D). Intestinal region with distinct median spine (Fig. 6C, D). Pseudorostral spines long, strongly divergent, forming a V (Fig. 6C, D). Supraorbital eave with anterior part longitudinally narrow, rectangular, not prominently expanded; antorbital spine sharp (Fig. 36F). Intercalated spine relatively short, stout, separated from supraorbital eave and postorbital spine by narrow gaps; postorbital spine very strong, long. Hepatic region with 1 strong spine, shorter than postorbital spine; 1 smaller spine below (Fig. 36F). Lateral carapace margin with 3 large spines, branchial region with strong spine (Fig. 6C, D). Posterior carapace margin with 2 median spines (Fig. 6C, D). Eyes relatively long, thin, slightly curved, with ovoid cornea (Fig. 36F). Antennal flagellum short, slender. Basal antennal article as broad as long, quadrate, with 1 long distal spine, 1 low, lobiform proximal lateral tooth; proximal outer angle rounded; inner and outer lateral margins entire; antero-external crested rim of antennular fossa prominently overlaps subdistal part of basal antennal article as hook-shaped structure by more than half its width (Fig. 39E, F). Epistome as long as wide, anterior margin with 2 large rounded tubercles; posterior margin composed of 4 rectangular plates separated by deep fissures (Figs. 39E, F, 41D). Suborbital margin separated from basal antennal article and margin of postorbital tooth by 2 distinct gaps, basally wide but with anterior parts adjoined to form fissures (Figs. 39E, F, 41D). Outer surface of third maxilliped covered by short setae; ischium subrectangular, distinctly longer than broad; postero-external angle of merus relatively broad, "inserted" into shallow concavity on outer margin of ischium; antero-internal part of ischium rounded, auriculiform (Fig. 43G, H). Male chelipeds long in adult males, surfaces of merus and carpus covered with distinct tubercles and granules; carpus elongate, with granulated longitudinal ridge; propodus of palm elongated, curved, smooth, without lateral cristae, slightly enlarged, longer than palm; fingers long, slender, gently curved, with narrow basal gape when closed (Figs. 6C, D, 53G, H). Ambulatory legs relatively short, thick; merus with strong, stout subdistal spine; dactylus relatively short, curved, covered with dense short setae except for corneous distal quarter (Figs. 6C, D, F, 55D). Thoracic sternum wide; surfaces of somites 5–8 almost smooth; sternites 3 and 4 slightly depressed; margin between sternites 2 and 3 demarcated by notch; anterior margin of sterno-abdominal cavity not forming complete rim (Figs. 47H, I, 52C). Male abdomen subrectangular, with 6 free somites and telson; somites 3 and 4 distinctly wider than somites 5, 6 and telson; telson semicircular (Fig. 47H, I). Male press-button abdominal locking mechanism submedian in position on sterno-abdominal cavity (Fig. 52C). Female abdomen dome-shaped, covering most of thoracic sternum. G1 very long, slender, gently curved, distal part dilated, sub-spatuliform, without subdistal process, with scattered very short setae (Fig. 7R–T).

Type species. *Maja goltziana* d'Oliviera, 1889, by present designation.

Etymology. The genus name alludes to the new taxon being different from *Maja* s. str. gender feminine.

Remarks. *Maia goltziana* was compared to *Maja spinigera* De Haan, 1837 (presently in *Paramaya*) by Bouvier (1940: 323, 324) who commented that in the former species, "…une forte épine au bout distal du mérus des pattes ambulatoires". The species is also characterised by possessing relatively shorter antennae (Fig. 39E, F) compared to other *Maja* s. str. species (Fig. 39B, C). The differences in the form of the epistome (relatively longer) (Figs. 39E, F, 41D), presence of distal spines on dorsal margins of the ambulatory meri (Fig. 6C, D, F), and proportionately broader male abdomen (Fig. 47H, I) suggest it should be referred to its own genus, *Neomaja*. Its affinities, however, are clearly with *Maja* s. str., notably in the relatively broad and short basal antennal article (Fig. 39E, F), form of the chelipeds (including the prominent granulation on the carpus) (Fig. 53G, H), and general structure of the G1 (Fig. 7R–T). This taxonomy is consistent with the molecular study of Sotelo et al. (2009) which shows that *M. squinado*, *M. brachydactyla*, *M. crispata* and *M. cornuta* (as *Maja* sp. "SA") form a distinct clade, separate but sister to *M. goltziana*.

Neomaja goltziana (d'Oliveira, 1889)

(Figs. 6C, D, F, 7R–T, 36F, 39E, F, 41D, 43G, H, 47H, I, 52C, 53G, H, 55D)

Maja goltziana d'Oliviera, 1889: 3. – Capart, 1951: 100. – Monod, 1956: 478, Fig. 644–645. – Rossignol, 1957: 116. – Crosnier, 1967: 339, figs. 31, 32. – Longhurst, 1958: 88. – Zariquiey Alvarez, 1968: 447. – Massuti, 1970: 127. – d'Udekem d'Acoz, 1999: 189. –Moro et al., 2014: 52.
Maïa goltziana – Le Loeuff & Intès, 1968.
Maia goltziana – Maurin, 1968a: 30. – Maurin, 1968b: 484.
[see d'Udekem d'Acoz, 1999: 189 for references]

Material examined. Morocco – 1 female (48.0 × 40.5 mm) (MNHN-IU-2013-4037), station 80, 30°21'N 09°56'W, 11–40 m, coll. *Vanneau*, 31 August 1925. **Portugal** – 2 males, 1 female (NHM1966.4.6.62–64), off Malha, Portuguese coast, 3–4 miles offshore, 40 fathoms, coll. G. Palmer,

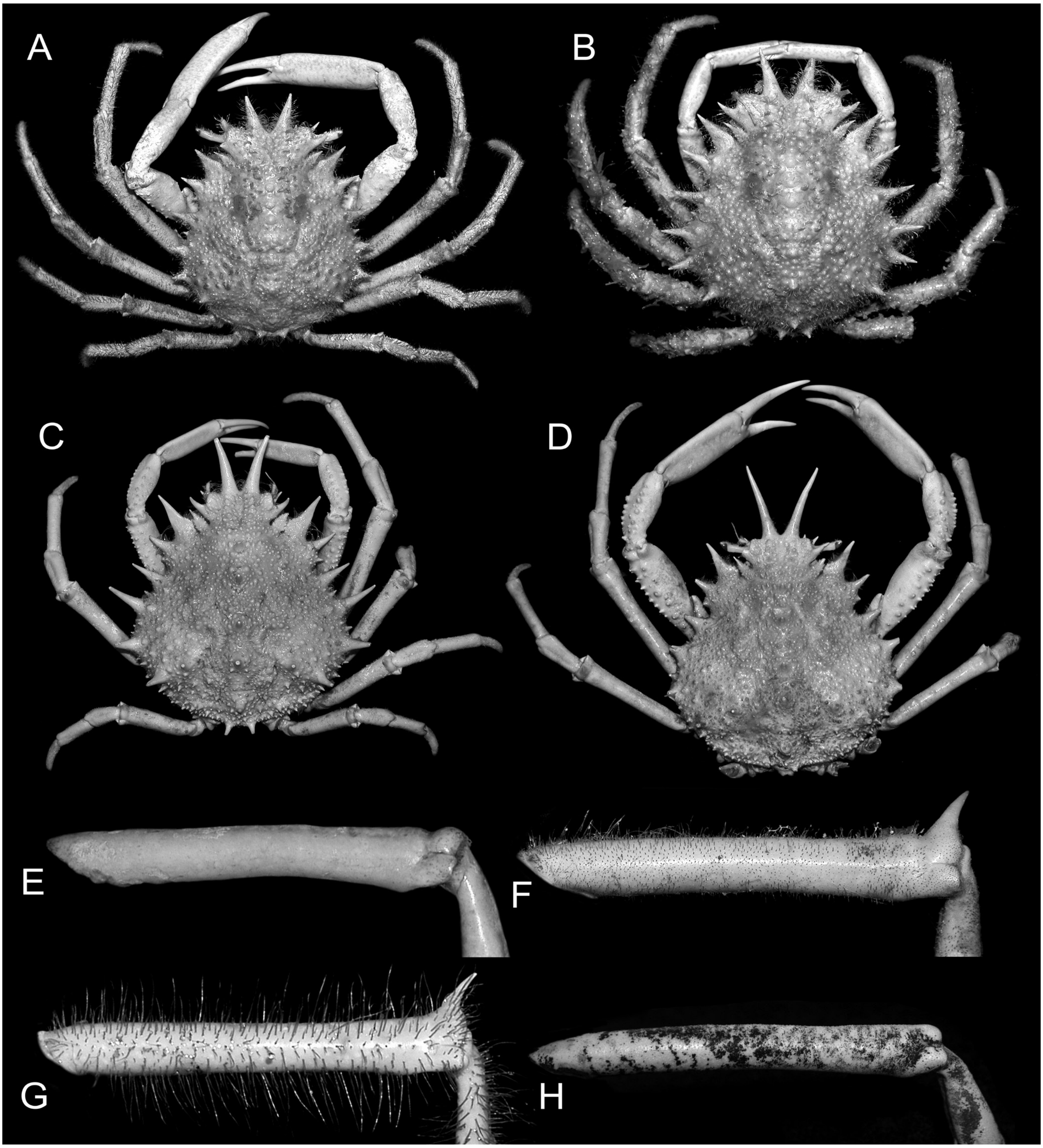

Fig. 6. General habitus and right first ambulatory legs. A, *Maja crispata*, male (63.1 × 51.9 mm) (MNHN-IU-2013-4042), Italy; B, *Maja crispata*, male (48.5 × 39.0 mm) (MNHN-IU-2013-4041), Italy; C, *Neomaja goltziana*, male (73.4 × 65.0 mm) (MNHN-IU-2013-4046), Congo; D, *Neomaja goltziana*, male (90.2 × 83.1 mm) (MNHN-IU-2013-4044), Gabon; E, *Maja squinado*, neotype male (147.1 × 126.3 mm) (SMF-4548), Croatia; F, *Neomaja goltziana*, male (74.7 × 66.7 mm) (MNHN-IU-2013-4043), Senegal; G, *Paramaya spinigera*, male (85.0 × 66.4 mm) (ZRC 1999.738), Taiwan; H, *Paramaja turgida* n. sp., holotype male (74.1 × 66.8 mm) (NMCR), Philippines.

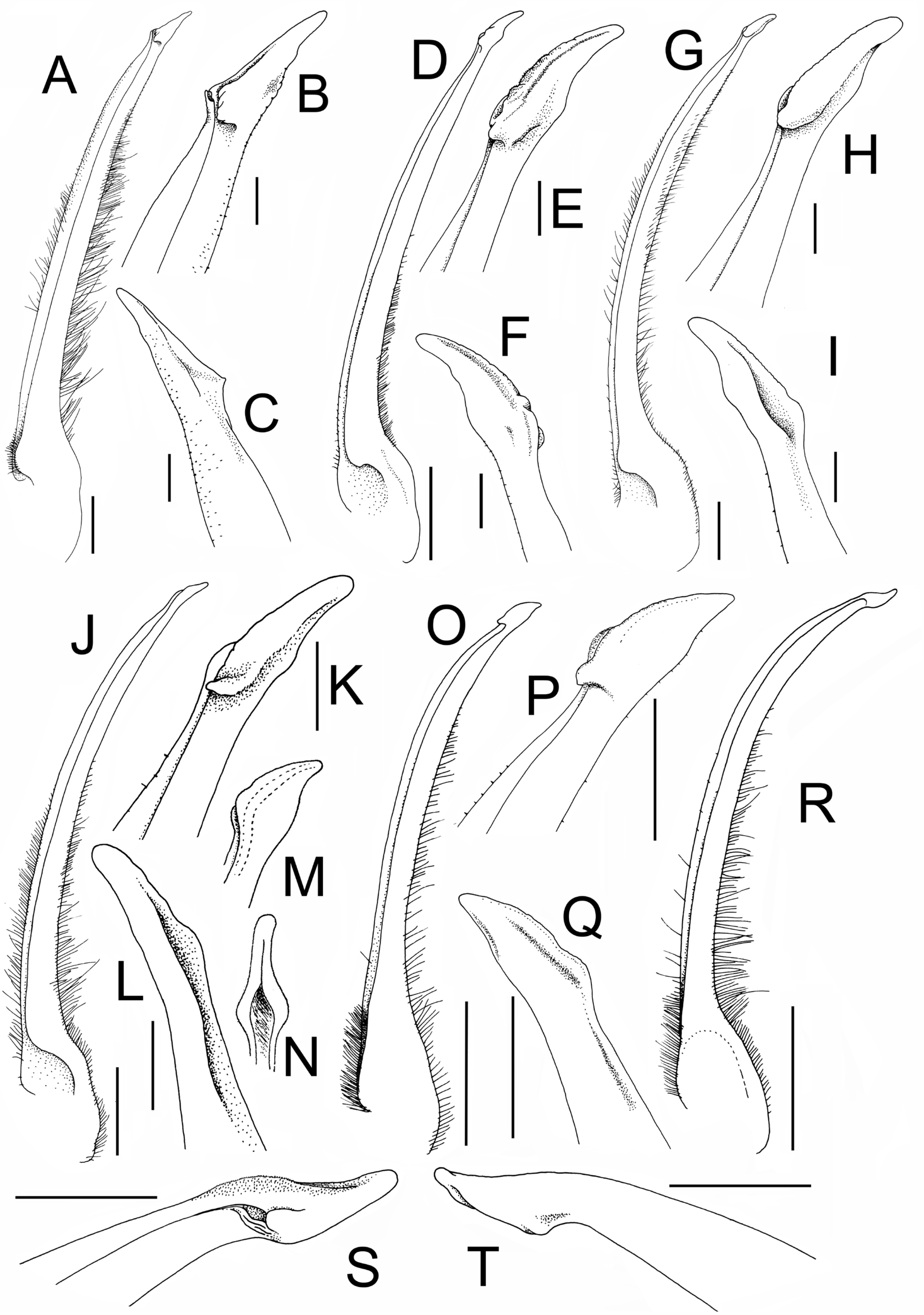

Fig. 7. Left G1s. A–C, *Maja squinado*, neotype male (147.1 × 126.3 mm) (SMF-4548), Croatia [gonopods laterally inverted as left G1 missing, right G1 drawn]; D–F, *Maja brachydactyla*, male (98.4 × 89.0 mm) (ZRC 2009.1130), U.K.; G–I, *Maja brachydactyla*, male (161.2 × 140.1 mm) (ZRC 2008.0179), Spain; J–L, *Maja cornuta*, male (115.3 × 103.4 mm) (ZRC 2013.1184), South Africa; M, N, *Maja cornuta* (as *Mamaia queketti*, after Barnard, 1950: fig. 13a); O–Q, *Maja crispata*, male (63.1 × 51.9 mm) (MNHN-IU-2013-4042), Italy; R–T, *Neomaja goltziana*, male (73.4 × 65.0 mm) (MNHN-IU-2013-4046), Congo. Scale bars = 5.0 mm [A, D, G, J, O, R]; 1.0 mm [B, C, E, F, H, I, K, L, P, Q, S, T].

26–27 August 1965. **Congo** – 1 male (73.4 × 65.0 mm), 1 female (70.9 × 64.6 mm) (MNHN-IU-2013-4046), west of Pointe Noire, 80 m, coll. July 1958. **Senegal** – 1 male (74.7 × 66.7 mm) (MNHN-IU-2013-4043), station 9, 14°27'N 17°35'W, Dakar, 180–220 m, coll. trawl, L. Amaro, 21 February 1981. **Gabon** – 1 male (90.2 × 83.1 mm) (MNHN-IU-2013-4044), 40 m, coll. July 1959. **Cameroon** – 1 male (67.3 × 57.7 mm) (MNHN-IU-2013-4045), coasts, 3°54'N 8°50'E, 65–70 m, coll. 25 August 1963. **Nigeria** – 1 male, 2 females (1 badly damaged) (NHM 1957.5.26.115–117), Afons Deep, coll. A.R. Longhurst. **Azores** – 1 male (SMF 9832), Canary Islands, La Palma, 160 m, coll. E. Santaella, 11 June 1974. — 10 juveniles (SMF 24519), Nilmundung, 32°00.54'N 31°53.70'E – 32°00.55'N 31°52.61'E, 196-199 m, coll. FS *Meteor*, 1 June 1993.

Diagnosis. Medium-sized species (60–70 mm carapace length). Carapace pyriform; dorsal surface gently convex; uniformly covered with granules and short spines, those on posterior part of branchial and intestinal regions spiniform (Fig. 6C, D). Pseudorostral spines long, straight, strongly diverging (Figs. 6C, D, 36F). Supraorbital eave relatively narrow, antorbital spine sharp, gently curved upwards; intercalated spine stout, short, touching postorbital spine basally; postorbital spine largest, long, sharp; hepatic spine sharp with 1 short accessory spines basally (Figs. 6C, D, 36F). Lateral margin of carapace with 3 strong spines, second longest, and several small sharp granules and short spines (Fig. 6C, D). On median row 5 spines: 3 gastric, 1 cardiac, 1 intestinal (Fig. 6C, D). Branchial region with 1 strong spine; posterior carapace margin with 2 long spines (Fig. 6C, D). Basal antennal article very broad with 2 long distal spines; outer margin with proximal lobiform tooth, appressed on suborbital tooth (Fig. 39E, F). Ischium of third maxilliped rectangular, much longer than broad (Fig. 43G, H). Carpus of cheliped with distinct tubercles and granules (Fig. 53G, H). Ambulatory merus with strong subvertical subdistal spine on dorsal margin (Fig. 6F); dactylus covered with short setae (Fig. 55D). G1 long, gently curved; distal part gently curved upwards (Fig. 7R–T).

Remarks. *Neomaja goltziana* was originally described from Portuguese waters (d'Oliviera, 1889). Although the year of publication is usually cited as 1888, volume 36 (where the paper was published) is dated July 1888 to June 1889, and the year "1889" was printed at the bottom of title page of the paper.

Neomaja goltziana is superficially similar to *Paramaya spinigera*, especially with regards to its spiny carapace and the ambulatory meri possessing a strong distal spine on the dorsal margin. Bouvier (1940: 323) comments that "une forte épine au bout distal du mérus des pattes ambulatoires". However, as discussed under the genus, there are many substantial differences between the two species at the generic level.

Neomaja goltziana was described from Portuguese waters. Manning & Holthuis (1981: 307) reported a distribution from Mediterranean to Congo, between 15 to 200 m.

Paramaja Kubo, 1936

Paramaja Kubo, 1936: 361.
Paramajella Balss, 1957: 1628 [unnecessary replacement name for *Paramaja* Kubo, 1936].
Maja – T. Sakai, 1938: 296 (part). – T. Sakai, 1965: 83 (part). (not *Maja* Lamarck, 1801).

Diagnosis. Carapace rounded in adults; dorsal surface evenly inflated, covered by granules or tubercles; gastric and branchial regions clearly delimited by grooves (Figs. 8–12). Intestinal region without distinct median spine (Figs. 8–14). Pseudorostral spines relatively short, diverging, forming a V (Figs. 8–13). Supraorbital eave with anterior part longitudinally narrow, rectangular, not prominently expanded; antorbital spine sharp (Fig. 36G–K). Intercalated spine distinct, separated from supraorbital eave and postorbital spine by distinct gaps; postorbital spine strong, lobiform; hepatic region with 1 strong spine, much shorter than postorbital spine; 1 or more smaller spines below (Fig. 36G–K). Lateral carapace margin with 3 or 4 spines and numerous tubercles, branchial region with larger tubercle, not discernible from other surrounding tubercles in large specimens (Figs. 8–13). Posterior carapace margin with 2 short median spines, not visible from dorsal view when adult due to swollen carapace (Figs. 8–12). Eyes relatively short, slender, with large ovoid cornea (Fig. 36G–K). Antennal flagellum short, slender. Basal antennal article longer than broad, rectangular; surface with several tubercles, with 2 blunt spines distally; inner and outer lateral margins may have low granules or lobes, or entire; proximal outer angle rounded; antero-external crested rim of antennular fossa touches but does not significantly overlap distal part of basal antennal article (Fig. 39G–K). Epistome much wider than long, anterior margin unarmed; posterior margin composed of 4 rectangular plates separated by shallow fissures (Figs. 39G–K, 41E, F). Suborbital margin separated from basal antennal article by short fissure, confluent with margin of postorbital tooth (Fig. 39G–K). Outer surface of third maxilliped covered by short setae in adults; ischium subrectangular, distinctly longer than broad; postero-external angle of merus relatively broad, "inserted" into shallower concavity on outer margin of ischium; antero-internal part of ischium rounded, auriculiform (Fig. 43I–P). Male chelipeds relatively short in adult males, surfaces of merus and carpus almost smooth or with very small granules; carpus short, with low, uneven longitudinal ridge; propodus of palm elongated, curved, smooth, without lateral cristae in young, short, inflated in adults, palm longer than fingers; fingers long, slender, gently curved, with distinct basal gape when closed (Figs. 8–12, 53I–L). Ambulatory legs relatively long, slender; merus without dorsal subdistal spine; dactylus elongate, curved, covered with long setae when young except for corneous tip, almost completely smooth in adults (Figs. 6H, 8–12, 55E–J). Thoracic sternum wide; surfaces of somites 5–8 with numerous prominent rounded tubercles and granules; sternites 3 and 4 slightly depressed; margin between sternites 2 and 3 demarcated by deep notch; anterior margin of sterno-abdominal cavity not forming complete rim (Figs. 48, 52D). Male abdomen subrectangular, with 6 free somites and telson; somites 3–6 and telson subequal in width (Fig. 48). Male press-button abdominal locking mechanism submedian in position on sterno-abdominal cavity (Fig. 52D). Female abdomen dome-shaped, covering most of thoracic sternum. G1 very long, slender, almost straight for most of length, distal part gently curved, subconical with rounded tip, with small, low subdistal dorsal flap, with scattered setae (Fig. 15).

Type species. *Paramaja kominatoensis* Kubo, 1936, by original designation and monotypy. Gender feminine.

Remarks. Kubo (1936: 361) established a new genus for a new species from Kominato, Japan, with the following comments: "The present genus stands somewhat intermediate between the two genera *Maja* and *Majopsis* (sic for *Maiopsis* Faxon, 1893), and it is easily distinguished from the genus *Maja* in lacking any spines on carapace, and from the genus *Majopsis* in having no accessory spine on rostral spines, but two spines on distal margin of basal segment of outer antennae, and fingers of chela not canaliculate within." Although none of these characters work at present to distinguish *Paramaja* from *Maja* s. str. or allied genera, it can still be separated by other features.

Paramaja Kubo, 1936, is here resurrected to accommodate Indo-Pacific species which have a uniformly inflated carapace which has the dorsal surface covered with granules and tubercles: *P. gibba* (Alcock, 1895), *P. kominatoensis* Kubo, 1936, and *P. turgida* n. sp. The genus is also characterised by features of its suborbital margin, epistome, male abdomen and G1 structure.

Paramaja is closest to *Alcomaja* n. gen., with which it shares a suite of carapace, antennal, epistomal, third maxilliped, pereiopodal, thoracic sternal and male abdominal characters. The single most important character separating *Paramaja* from *Alcomaja* is the form of the G1. In *Paramaja*, the G1 is very long and mostly straight, the distal part being conical (Fig. 15). In *Alcomaja*, the G1 is proportionately shorter, more curved, and part of the dorsal fold bends downwards to form a distinct ventral projection (Figs. 19, 20). Species of *Alcomaja* also have relatively longer and more slender pseudorostral spines (Fig. 36L–O) than in *Paramaja* (Fig. 36G–K). Adults of the two genera are easy to separate, with *Paramaja* growing to much larger sizes (over 60–70 mm carapace length) while *Alcomaja* species are smaller. In *Paramaja* specimens, even when small (20–30 mm carapace length), the branchial and cardiac regions are proportionately more inflated and the lateral and branchial spines are relatively shorter (Figs. 10A, B, 11A–C, 12A, B). Specimens of *Alcomaja* of comparable size on the other hand have less inflated branchial and cardiac regions, and the lateral and branchial spines are stronger and longer (Figs. 16, 17). That said, juvenile female specimens of the two species can be difficult to separate.

Key to species of *Paramaja* Kubo, 1936

1. In adults, pseudorostral horns with cross-section rounded (Figs. 8, 9, 13A–C, 36G, H); carapace dorsal surface usually strongly swollen, covered with large rounded or sharp tubercles which may merge basally (Figs. 8, 9, 13A–C, 14A–E); distal part of G1 relatively long, tip gently bent laterally (Fig. 15A–J); Japan, South Korea and Taiwan .... *Paramaja kominatoensis* Kubo, 1936

– In adults, pseudorostral horns dorso-ventrally flattened (Figs. 13D–F, 36I–K); carapace dorsal surface relatively less swollen, with numerous small and large distinct tubercles and granules which are never swollen (Figs. 10–12, 13D–F, 14F–H); distal part of G1 not as above 2

2. Adult carapace rounded (Fig. 12); distal part of G1 relatively shorter, tip in line with rest of G1 (Fig. 15N–U); Philippines, Lesser Sunda Islands and Solomon Islands .... *Paramaja turgida* n. sp.

– Adult carapace ovate (Figs. 10, 11); distal part of G1 relatively longer, tip gently bent laterally (Fig. 15K–M); Indian Ocean .... *Paramaja gibba* (Alcock, 1895)

Paramaja kominatoensis Kubo, 1936
(Figs. 2B, 8, 9, 13A–C, 14A–E, 15A–J, 36G, H, 39G, H, 41E, 43I–K, 48A–E, 53I, J, 55E, F, 68A)

Paramaja kominatoensis Kubo, 1936: 361, figs. 1, 2.
Maja kominatoensis – Miyake, 1936: 418, pl. 28 figs. 1, 2. – T. Sakai, 1938: 300, pl. 38 fig. 3. – Serène, 1968: 57. – Serène & Lohavanijaya, 1973: 50 (key). – T. Sakai, 1976: 240, text fig. 128, pl. 84 fig. 2. – Matsuzawa, 1977: pl. 96 fig. 1. – Miyake, 1983: 47, pl. 16 fig. 2. – Ikeda, 1998: 117, pl. 41. – Muraoka, 1998: 27, pl. 5 fig. 1. – Ng et al., 2001: 12. – Maramura & Kosaka, 2003: 34. – Yang et al., 2008: 780. – Ng et al., 2008: 117 (list).
Maja gibba – T. Sakai, 1976: 239 (part), text fig. 127a, b, pl. 84 fig. 1. – Dai et al., 1986: 137, pl. 18(4). – Dai & Yang, 1991: 152, pl. 18(4). – Huang, 1994: 583. – Muraoka, 1998: 27. – Maramura & Kosaka, 2003: 34. – Yang et al., 2008: 780. (not *Maja gibba* Alcock, 1895).

Material examined. Neotype (here designated): male (56.6 × 40.4 mm) (SMF 47808), None, west of Cape Muroto, Kochi Prefecture, 33°26.617'N 134°16.75'E, Japan, coll. K. Matsuzawa, 13 December 1999. **Japan** – 1 dried male (62.6 × 56.1 mm) (KPM NH0104298), probably Mimase, Tosa Bay, T. Sakai Collection. — 1 dried male (60.4 × 52.5 mm), 1 dried female (61.0 × 54.6 mm) (KPM NH124171), Minabe town, Wakayama Prefecture, Japan, T. Sakai Collection. — 2 males (41.0 × 34.6 mm, 53.1 × 46.8 mm), 1 female (63.5 × 58.5 mm) (SMF 47728), Ashizuri, 200 fathoms, coll. RV *Taisho Maru*, 24 November 1958. — 2 males (50.5 × 44.6 mm, 76.9 × 69.6 mm) (SMF 47738), Tosa Bay, Kochi Prefecture, T. Sakai collection (TS00320), coll. 1970s. — 1 female (62.0 × 58.0 mm) (SMF 47810), None, Kochi Prefecture, 33°26.617'N 134°16.75'E, coll. K. Matsuzawa, 12 November 1988. — 1 female (52.7 × 47.5 mm) (SMF 47736), Tosa Bay, Kochi Prefecture, 190 m, coll. RV *Toyohata-Maru*, 7 April 1989. — 1 female (25.7 × 21.0 mm) (SMF 47744), Tosa Bay, Kochi Prefecture, 250–300 m, coll. K. Sakai, 3–14 November 1963. **South Korea** – 1 female (53.1 × 40.0 mm) (SMF 47605), Cheju Island, 33°32.415'N 126°30.783'E, East China Sea, bottom, coll. M. Matsuo, 7 May 1991. **Taiwan** – 1 dried male (ca. 60 mm carapace length) (PCM), Tashi, northern Taiwan, coll. K.-X. Li, 2000s. — 1 dried male (73.0 × 66.0 mm, 79.0 mm including pseudorostrum) (PCM, one G1 in ZRC

2013.1407), Tashi Port, northern Taiwan, coll. K.-X. Li, from deep-water trawlers, 2000s.

Diagnosis. Adult carapace with branchial and gastric regions rounded; dorsal surface inflated to strongly inflated, covered by large rounded tubercles and/or wart-like or sharp granules, some which may merge basally; those on median row especially large, forming low rounded or sharp crest (Figs. 8, 9, 13A–C, 14A–E). Adult pseudorostral spines gently curved outwards to almost straight, strongly diverging; cross-section circular (Figs. 8, 9, 13A–C, 36G, H). Supraorbital eave relatively narrow, granulated; antorbital spine triangular, sharp; intercalated spine irregular, slightly shorter than supraorbital spine; postorbital spine relatively wide, gently curved anteriorly, triangular with some granules at base of anterior margin; hepatic area prominently inflated with several large sharp tubercles (Figs. 8, 9, 36G, H). Adult male anterior thoracic sternum relatively broad (Fig. 48A–E); lateral margins of anterior edge of male sterno-abdominal cavity almost straight or gently curved (Fig. 48A–E). Distal part of G1 relatively long, tip gently bent laterally (Fig. 15A–J).

Remarks. Kubo (1936) described the species on the basis of a single large male 63.0 by 57.0 mm collected from a depth of 370 m from off Kominato in Chiba, Japan. The extant material of Kubo is in the Tokyo University of Fisheries, and a list of taxa present in this collection was published by Takeda & Ueshima (2006). A recent search there again failed to find his type specimen (T. Komai, pers. comm.). In view of the variation in carapace form observed in the Japanese material, and its close similarity with *P. gibba* (Alcock, 1895) and *P. turgida* n. sp., we have decided to select a neotype for *Paramaja kominatoensis* Kubo, 1936. The neotype selected is a male 56.6 × 40.4 mm in the SMF collected from None in Kochi Prefecture, Japan. Although it not the largest specimen we have examined, it is the most complete and is an adult male.

Kubo's (1936: fig. 1) (Fig. 8A) figure of *P. kominatoensis* shows a specimen with a strongly inflated carapace but the granules on it do not appear to be as swollen, large or wart-like as those illustrated by T. Sakai (1976) or Ikeda (1998) (see present Figs. 8B, C, 68A). The convexity and size of the granules on the carapace varies, as the excellent series of specimens in SMF demonstrate. Smaller specimens all have relatively less swollen carapaces, and the granules are proportionately smaller and sharper (e.g., Fig. 9D, E). Larger specimens vary, with some having the sharper granules (e.g., Figs. 9A–C), some with wart-like granules and having a more swollen carapace (e.g., Figs. 8B, C, E, F), and a few with granules and tubercles intermediate in condition (e.g., Figs. 8D) (like in Kubo's type, Fig. 8A). The lateral margins of anterior edge of the male sterno-abdominal cavity are usually straight or almost so in *P. kominatoensis* (Fig. 48A, B) but can also be gently curved (Fig. 48C–E). This variation in the sterno-abdominal cavity does not seem to be associated with size. The cross-section of the pseudorostral spines in all thes specimens, however, is circular (Fig. 13A–C), not dorsoventrally flattened like in *P. turgida* n. sp. (Fig. 13D–F). Females of *P. kominatoensis* are similar to males in non-sexual characters except that their pereipods are relatively shorter and more slender (Figs. 8E, F, 9B versus Figs. 8A–C, 9A, C).

Paramaja kominatoensis is close to *P. gibba* s. str. (and *P. turgida* n. sp.), and some authors (e.g., Griffin & Tranter, 1986) have suggested that they may be synonymous. The most distinctive feature of *P. kominatoensis* is the presence of large wart-like granules on the median part of the carapace, especially on the gastric, cardiac, intestinal and inner branchial regions (Ikeda, 1998: pl. 41, fig. 1a–f; present Figs. 8B, C, 13A–C, 14A–C); but as discussed above, these characters vary to some degree and cannot be relied on. In *P. gibba* s. str. and *P. turgida* n. sp., these granules are always relatively smaller, sharper and well separated from each other. *Paramaja kominatoensis* also almost always has a proportionately more strongly inflated carapace, especially when viewed frontally or laterally (Ikeda, 1998: pl. 41, figs. 1e, 1f; present Figs. 13A–C, 14A–D), compared to *P. gibba* s. str. or *P. turgida* n. sp. (Figs. 13D–F, 14F–H). This "inflatedness" is attenuated by the large wart-like granules that may be present on the carapace in *P. kominatoensis* (Figs. 13A–C, 14A–C). In addition, in adult *Paramaja kominatoensis*, the pseudorostral spines are circular in cross-section (Figs. 13A–C, 36G, H) (versus dorso-ventrally flattened in *P. gibba* and *P. turgida*, Figs. 13D–F, 36I–K).

The G1 structure of *P. kominatoensis* closely resembles that of *P. gibba*, with the tips of the distal part gently bent laterally (Fig. 15A–J). However, the distal part of the G1 in *P. kominatoensis* is proportionately longer (Fig. 15A, D, H) compared to that of *P. gibba* (Fig. 15L). Compared to the G1 of *P. kominatoensis*, that of *P. turgida* n. sp. is proportionately shorter with the tip in line with the rest of the structure (Fig. 15N–U) (versus longer with the tip gently bent laterally, Fig. 15A–J).

The male specimen from Japan (KPM NH0104298) is one of the two males listed by T. Sakai (1976). Although the attached label does not carry any locality data, T. Sakai (1976: 240) noted he had only two males, both from Tosa Bay. Although generally regarded as a Japanese endemic, the two dried specimens in the Peikuan Crab Museum were supposedly collected from Tashi Fish Port just off northeastern Taiwan. There is also a record of this species from Taiwan (Chou et al., 1999) but the specimen cannot be located so we cannot confirm its identity. The species has also been listed from East China Seas by Yang et al. (2008). It is recorded here for the first time from South Korea.

The color in life is cream with a band of longitudinal big granules bright red (Fig. 68A) (see also Ikeda, 1998: pl. 41).

Paramaja gibba (Alcock, 1895)

(Figs. 10, 11, 13D, 14F, G, 15K–M, 36I, 39I, J, 41F, 43L, M, 48F, G, 52D, 53K, 55H, 68B, C)

Maia gibba Alcock, 1895: 239, pl. 4, fig. 5, 5a. – Alcock & Anderson, 1898: pl. 21 fig. 5. – Alcock, 1899: 56.

Maja gibba – Serène, 1968: 57. – Serène & Lohavanijaya, 1973: 50 (not specimen figured Pl. IX B = *Maja compressipes*). – T. Sakai, 1976: 239 (part). – Griffin & Tranter, 1986: 216 (part). – Poore et al., 2008: 62. – Ng et al., 2008: 117 (list).

Material examined. Lectotype (here designated): juvenile female (25.1 × 21.2 mm) (NHM 1896.5.14.9), code zoo2012-1157T, Andaman Sea, 250 fms, coll. *Investigator*. Others: **India** – 1 male (79.5 × 77.9 mm) (ZRC 2013.1232), Gulf of Bengal, V. Kakati, 2011. **Thailand** – 1 male (65.0 × 59.8 mm) (NSMT-Cr 16618), Andaman Sea, 400 m, coll. Y. Tamura, 5 June 1987. **Australia** – 1 juvenile female (33.9 × 29.4 mm) (NMV J54316), off Point Cloates, 22°37.07'S 113°29.03'E – 22°37.2'S et 113°28.57'E, Western Australia, 355–382 m, coll. G. Poore, CSIRO RV *Southern Surveyor*, 9 December 2005. — 1 female (46.7 × 41.6 mm) (NMV J61055), Kulurnburu L29 Transect, 13°15.9'S 123°22.45'E – 13°16.35'S 123°21.4'E, northwestern Australia, 390–394 m, beam trawl, coll. D. Bray, CSIRO RV *Southern Surveyor*, 6 July 2007. **Madagascar** – 1 male (24.6 × 20.9 mm) (MNHN-IU-2010-61), station CP 3189, 12°30'S 48°18'E, 346–376 m, coll. MIRIKY, 27 June 2009. — 1 ovigerous female (47.6 × 44.1 mm) (ZRC 2013.1405, ex MNHN-IU-2010-508), station CP 3192, 578–580 m, 12°26'S-48°13'E, coll. MIRIKY, 27 June 2009. — 1 ovigerous female (47.1 × 42.6 mm) (MNHN-IU-2010-507), station DW 3198, 440–447 m, 12°05'S-48°59'E, coll. MIRIKY, 28 June 2009. — 1 male (58.6 × 52.2 mm) (ZRC 2013.1406, ex MNHN-IU-2010-63), station CP 3183, 420-436 m, 12°38'S 48°14'E, coll. MIRIKY, 26 June 2009. — 1 male (61.3 × 54.8 mm), 3 ovigerous females (45.1 × 40.6 mm, 46.3 × 43.3 mm, 45.0 × 40.7 mm) (MNHN-IU-2010-467), station CP 3183, 420–436 m, 12°38'S-48°14'E, coll. MIRIKY, 26 June 2009. – 1 male (37.8 × 33.1 mm), 1 ovigerous female (47.1 × 44.3 mm), 1 female (24.4 × 20.3 mm) (MNHN-IU-2010-510), CP 3223, 430–488 m, 12°46'S-48°11'E, coll. MIRIKY, 2 July 2009. — 1 ovigerous female (48.7 × 44.5 mm) (MNHN-IU-2010-506), station DW 3212, 367–369 m, coll. MIRIKY, 30 June 2009. — 2 males (60.4 × 53.4 mm, 62.8 × 57.8 mm), 1 ovigerous female (47.7 × 42.2 mm) (MNHN-IU-2010-926), station DW 3217, 391–438 m, 12°33'S-47°56'E, coll. MIRIKY, 30 June 2009. — 1 ovigerous female (44.6 × 42.2 mm), 1 juvenile male (22.4 × 18.8 mm) (MNHN-IU-2010-927), station CP 3190, 415–416 m, 12°31'S-48°15'E, coll. MIRIKY, 27 June 2009. — 1 male (50.8 × 45.7 mm) (MNHN-IU-2010-509) MIRIKY, CP3289, 332–379 m, 14°29'S-47°26'E, 14 July 2009. — 1 ovigerous female (43.5 × 40.1 mm) (MNHN-IU-2010-58) (specimen barcoded), station CP 3183, 420–436 m, 12°38'S-48°14'E, coll. MIRIKY, 26 June 2009. — 1 female (20.9 × 16.9 mm) (MNHN-IU-2010-931), station CP 3293, 268–408 m, 14°30'S-47°26'E, coll. MIRIKY, 14 July 2009. — 1 juvenile male (16.4 × 12.5 mm) (MNHN-IU-2010-55), station CP 3223, 430–488 m, 12°46'S-48°11'E, coll. MIRIKY, 2 July 2009. — 1 juvenile male (10.6 × 8.1 mm) (MNHN-IU-2010-54) (specimen barcoded), station CP 3223, 430–488 m, 12°46'S 48°11'E, coll. MIRIKY, 2 July 2009. — 1 juvenile male (9.9 × 8.0 mm) (MNHN-IU-2010-56), station CP 3184, 492–524 m, 12°40'S 48°12'E, coll. MIRIKY, 26 June 2009. **Indian Ocean** – 1 male (64.7 × 60.7 mm) (SIO), cruise 17, station 2560, near Socotra Island, Indian Ocean, 12°17.7'N 53°08.9'E 12°21.8'N 53°05.6'E, depth 375–380 m, coll. RV *Vitiaz*, trawl, 27 October 1988. — 1 female (67.7 × 63.2 mm) (SIO), cruise 17, station 2804, Saya de Malha, Indian Ocean, 11°06'S 62°14'E–11°09'S 62°13'E, 235-230 m, coll. RV *Vitiaz*, 7 January 1989.

Diagnosis. Adult carapace with branchial and gastric regions rounded; dorsal surface convex, covered by numerous rounded and sharp granules, those on median row larger, tuberculate, forming low raised crest (Figs. 10, 11, 13D, 14F, G). Adult pseudorostral spines usually almost straight, gently diverging, appears dorso-ventrally flattened (Figs. 10, 11, 13D, 36I, J). Supraorbital eave large, curved with very long, sharp antorbital spine; 1 strong postorbital tooth; 1 intercalated spine large nearly as long as supraorbital spine; short hepatic spine; 3 spines on lateral margin (Figs. 10, 11, 36I, J). Adult male anterior thoracic sternum relatively broad (Fig. 48F, G); lateral margins of anterior edge of male sterno-abdominal cavity gently curved (Fig. 48F, G). Distal part of G1 relatively shorter, tip gently bent laterally (Fig. 15K-M).

Remarks. *Maja gibba* was described by Alcock (1895: 239, pl. 4 fig. 5) from the Andaman Sea (463 m) on the basis of two specimens, supposedly one male 32.0 mm (carapace length, with spines) and one female 41.0 mm, both with relatively short ambulatory legs with all the articles prominently setose. The small figure of Alcock (see also Alcock & Anderson, 1898: pl. 21 fig. 5; present Fig. 10B) shows a posterior carapace margin lined with short spines, a relatively long ocular peduncle; four spines on the lateral carapace margin and the branchial regions separated by deep grooves. The NHM specimen (Fig. 10A) was labelled as a syntype and agrees with the measurements of Alcock (1895) of the male (without the pseudorostrum). Tune Sakai (1976: 240) also noted that he examined this "cotype" male specimen in NHM. However, this NHM specimen is actually a juvenile female, but since the abdomen is subrectangular and resembles that of a male, he (and T. Sakai) probably accidentally misidentified the sex of the specimen. It is here designated as the lectotype of *Maja gibba* Alcock, 1895 (Fig. 10A).

Interestingly, the species has not been reported from the Bay of Bengal area since its original description. Specimens that have been referred to "*Maja gibba*" from the Pacific by various authors after Alcock (1895) should be referred to other taxa. Serène & Lohavanijaya (1973: 50) provided a key to the genus and noted that their *Maja gibba* has spines on the median row of the carapace. The specimen they figured from the South China Sea, however, has a longitudinally ovoid carapace that is covered with flattened tubercles and short, densely setose ambulatory legs which have a large flattened carpus; features diagnostic of *Maja compressipes* (Miers, 1879) (here referred to *Ovimaja* n. gen.).

Tune Sakai (1976: 239) reported the species from Japan and his colour plate depicted a male 54 mm in carapace length with short setose ambulatory legs (T. Sakai, 1976: pl. 84, fig. 1) with his text figure showing a specimen with three lateral spines and two posterior carapace margin spines (T. Sakai, 1976: 240, text-fig. 127). Tune Sakai (1976) commented that he had examined a type specimen in the NHM of *Maja gibba* as well. Griffin (1976: 200) recorded a male as "*Maja gibba*" from between Negros and Siquijor Islands in Philippines; while small specimens were recorded from off Bali and the South China Sea by Griffin & Tranter (1986: 216). In their keys to the genus, T. Sakai (1976: 236) stated that for his "*M. gibba*" and *M. kominatoensis*, the "carapace without median spine". This was also cited by Griffin & Tranter (1986: 210) in their key to *Maja*. Their specimens are here provisionally referred to *P. turgida*.

Tune Sakai (1976: 239–240) had small and large specimens of "*Maja gibba*" from Japan, East China Sea and Philippines and commented that the spines on the carapace median row and lateral margins are relatively sharper and longer in smaller specimens and become very short in large adults, with the granules on the surface also becoming more rounded. Griffin & Tranter (1986) discussed the possible conspecificity of what they regarded as *Maja gibba* Alcock, 1895, with *Paramaja kominatoensis* Kubo, 1936, noting that the large wart-like granules on the carapace supposedly diagnostic of the latter species may be variable once a good series of specimens become available. As discussed under *P. kominatoensis*, this is indeed the case, but the species can still be separated by other characters.

The present study has an excellent series of specimens of various sizes and sexes of *P. turgida* n. sp. from the Philippines and confirms T. Sakai's (1976) observations of changes in the strength and sharpness of the carapace spines and granules – large male and female specimens have almost indiscernible median and lateral spines, and the granules are relatively lower and eroded. The specimens of *P. turgida* from the Philippines are consistent in how they vary in carapace and ambulatory leg form and armature; and specimens of similar sizes do not vary much. Comparing the good series of specimens of *P. turgida* from the Philippines of similar sex and sizes, several other variation patterns are apparent. The eyes are proportionately less elongated in large specimens (also true for *P. gibba*). The proportions of the ambulatory legs, especially the first two, become very long and elongated in large adult males, with the propodus becoming very elongate, almost devoid of setae; and the chelipeds also become enlarged with the palm inflated (Figs. 12, 53L). This is also true for *P. gibba* (Figs. 10, 11, 53K). The rostrums in smaller specimens of *P. gibba* and *P. turgida* form a more distinct V, with the pseudorostral spines gently curved outwards (Figs. 10A, 11A–C, E, 12A–C, 36K). In large specimens, the rostrums become straighter and less curved (Figs. 9C, D, 11D, 12E, 36, I, J). While the lateral margins of male abdominal somites 4–6 are parallel in adult males of *P. gibba* and *P. turgida*, with the abdomen rectangular (Fig. 48G, I), the lateral margins become gently convex in very large males and the abdomen becomes slightly oval (Fig. 48F, H).

The series of specimens of *P. turgida* show that while there is variation in the sharpness and length of the carapace spines and granules, they never reach the degree seen in *P. kominatoensis*, in which the granules can become large and swollen, with those along the median row fused basally (Fig. 8B, C). Nor does the degree of inflation of the carapace vary to the degree seen in *P. kominatoensis*. As discussed earlier, the carapace of *P. kominatoensis* is almost always more swollen and inflated (Figs. 13A–C, 14A–D) than *P. gibba* or *P. turgida* (Fig. 13D–F, 14F–H), and this is obvious from lateral and frontal views. The material of *P. turgida* also demonstrates that the form of the pseudorostrum, male abdomen and G1 structure are relatively constant characters.

Understanding the degree of variation in *P. turgida* also means that we are confident that the material from the Indian Ocean, Japan, Taiwan and Philippines belong to three species. *Paramaja kominatoensis* is clearly a distinct species. The Indian Ocean appears to have only one species, *P. gibba* s. str. The Philippine material is referred to a new species, *Paramaja turgida*. However, most of the characters discussed and regarded as of species-identification value are useful only for adults. Juvenile specimens of these species about 30–40 mm in carapace length cannot be easily separated.

See also remarks for *P. turgida* for discussion of differences with *P. gibba*.

Paramaja turgida n. sp.

(Figs. 6H, 12, 13E, F, 14H, 15N–U, 36J, K, 39K, 43N–P, 48H, I, 53L, 55I, J, 68D–F)

Maja gibba – Griffin, 1976: 200. – T. Sakai, 1976: 239 (part). – Griffin & Tranter, 1986: 216 (part). (not *Maja gibba* Alcock, 1895).

Maja kominatoensis – Ng et al., 2008: 123, Fig. 90. (not *Paramaja kominatoensis* Kubo, 1936).

Material examined. Holotype: male (74.1 × 66.8 mm) (NMCR), Balicasag Island, Panglao, Bohol, Philippines, 200–300 m, coll. fishermen with tangle nets, 28 November 2001. Paratypes: **Philippines** – 1 male (71.4 × 64.4 mm) (NSMT-Cr 22329), 1 male (55.4 × 48.4 mm), 1 ovigerous female (62.9 × 57.2 mm) (AM, ex ZRC 2001.0615), same data as holotype. — 1 young male (26.2 × 21.3 mm) (ZRC 2001.0616b), Balicasag Island, Panglao, Bohol, coll. fishermen with tangle nets, 28 November 2001. — 1 male (69.2 × 64.0 mm), 1 ovigerous female (47.1 × 41.1 mm) (ZRC 2013.1185), Balicasag Island, Panglao, Bohol, 200–300 m, coll. fishermen with tangle nets, June 2002. — 1 ovigerous female (dried) (58.4 × 53.4 mm) (ZRC 2009.0972), Banacon Island, Bohol, coll. local fisherman, 2000. — 3 females (NSMT-Cr 15388), Balicasag Island, Panglao, Bohol, coll. local fisherman via M. Takeda & H. Komatsu, February 2003. — 2 males (34.3 × 29.2 mm, 56.4 × 49.7 mm), 1 female (60.1 × 55.6 mm, with anemone) (ZRC 2013.1239), Balicasag, Panglao, Bohol, 200–300 m, coll. local fishermen with tangle nets, January 2004. — 1 female (61.3 × 56.6 mm) (ZRC 2013.1240), Balicasag, Panglao, Bohol, 200–300 m, coll. local fishermen with tangle nets, February 2004. — 2 males (70.6 × 62.2 mm, 57.8 × 51.5 mm), 2 ovigerous females (60.2 × 53.1 mm, 62.2 × 55.2 mm) (ZRC 2012.1203), Balicasag, Panglao, Bohol,

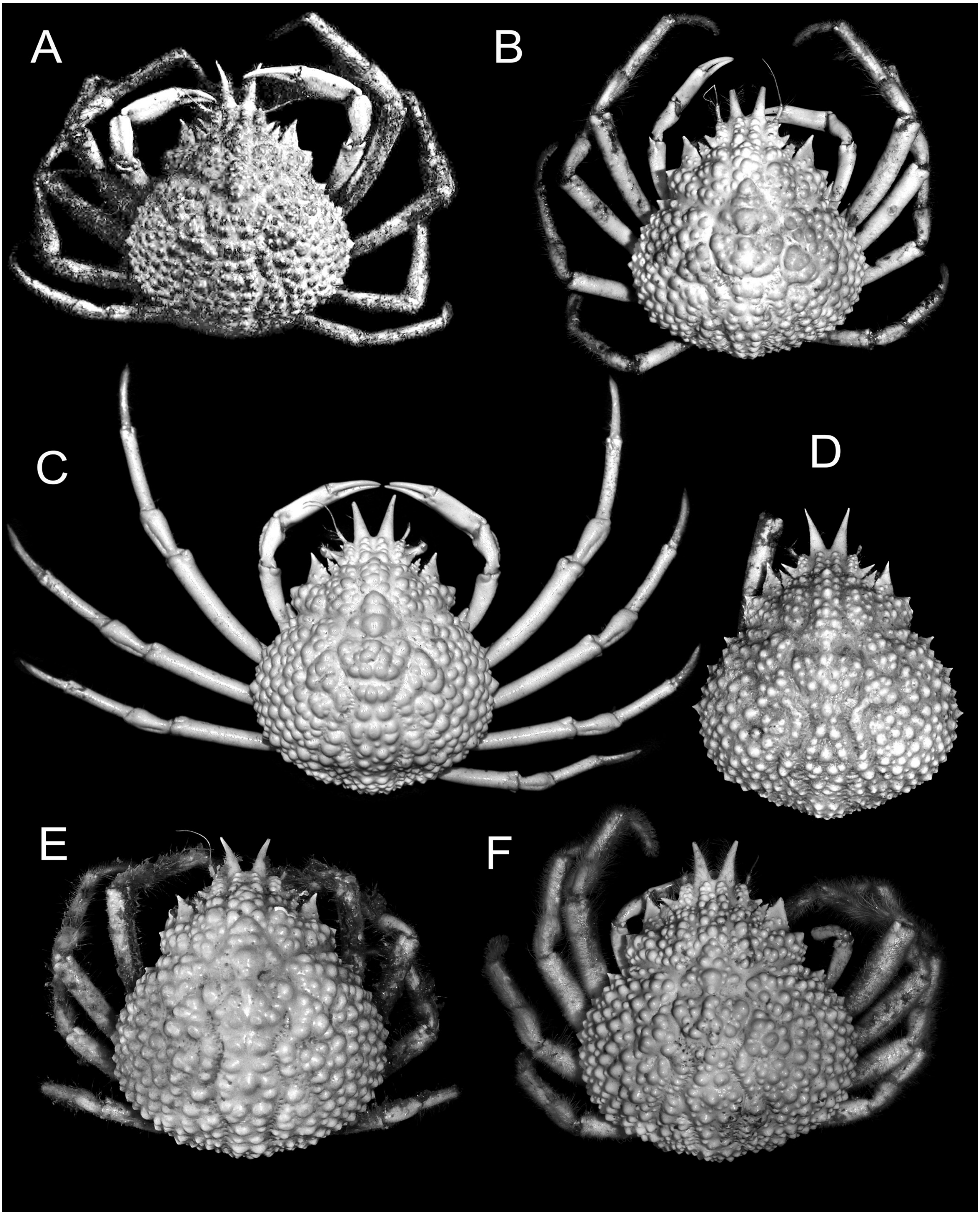

Fig. 8. General habitus, *Paramaja kominatoensis*. A, holotype male (63.0 × 57.0 mm) (after Kubo, 1936: fig. 2); B, neotype male (56.6 × 40.4 mm) (SMF 47808), Japan; C, dried male (62.6 × 56.1 mm) (KPM NH0104298), Japan; D, male (76.9 × 69.6 mm) (SMF 47738), Japan; E, female (52.7 × 47.5 mm) (SMF 47736), Japan; F, female (62.0 × 58.0 mm) (SMF 47810), Japan.

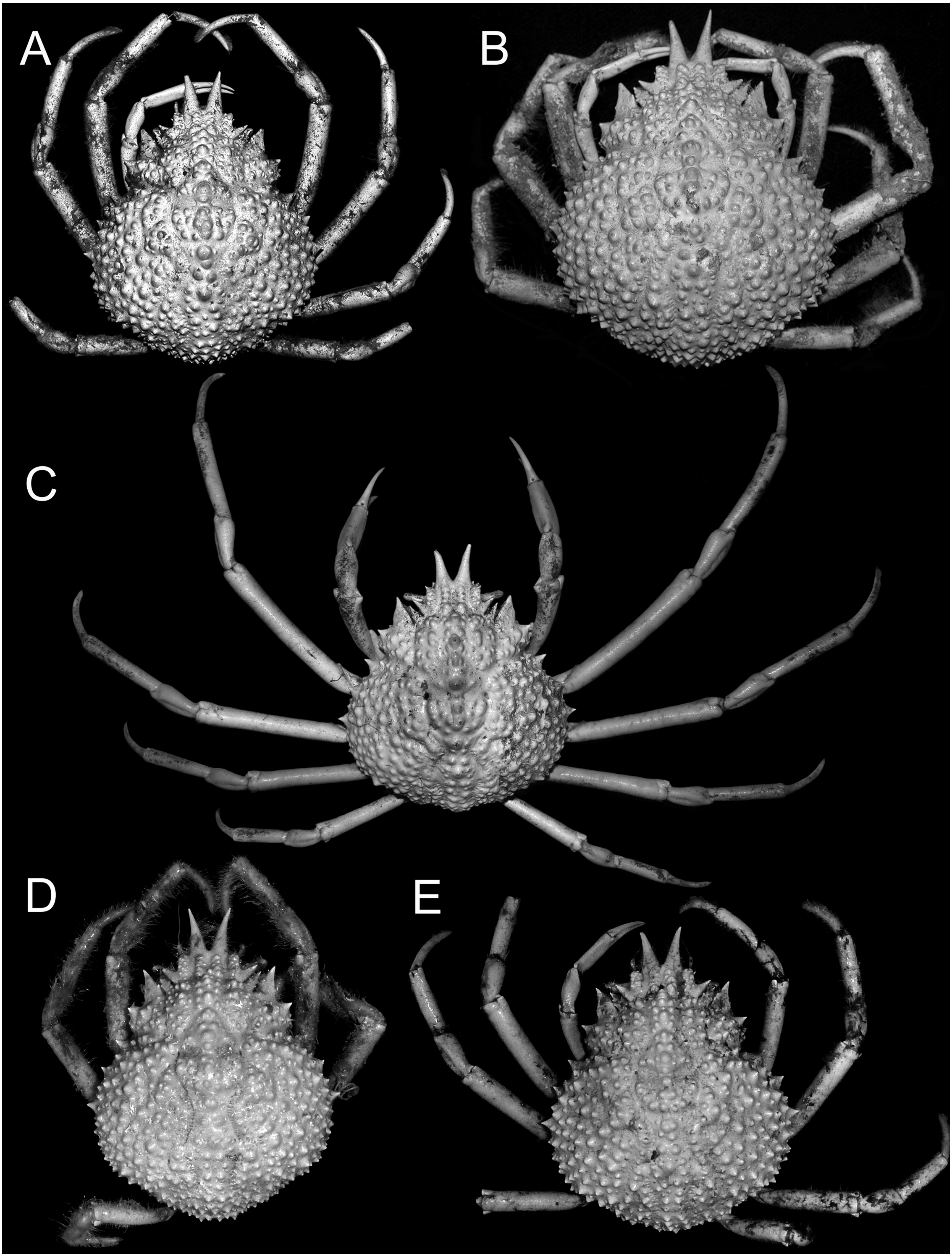

Fig. 9. General habitus, *Paramaja kominatoensis*. A, dried male (60.4 × 52.5 mm) (KPM NH124171), Japan; B, dried female (61.0 × 54.6 mm) (KPM NH124171), Japan; C, male (73.0 × 66.0 mm) (PCM), Taiwan; D, male (53.1 × 46.8 mm) (SMF 47728), Japan; E, male (50.5 × 44.6 mm) (SMF 47738), Japan.

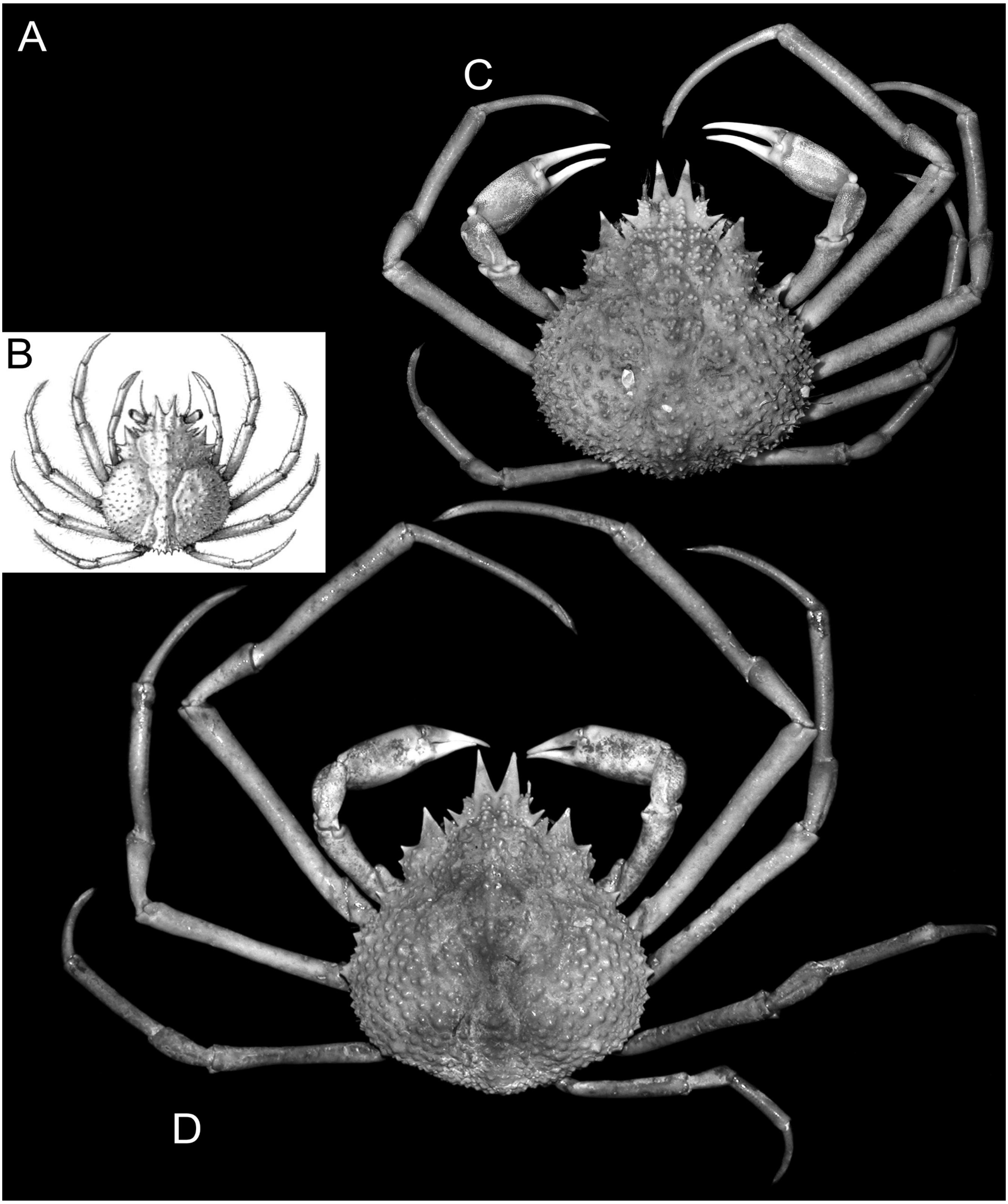

Fig. 10. General habitus, *Paramaja gibba*. A, lectotype female (25.1 × 21.2 mm) (NHM 1896.5.14.9), India; B, as *Maja gibba* (after Alcock & Anderson, 1898: pl. 21 fig. 5); C, male (65.0 × 59.8 mm) (NSMT-Cr 16618), Andaman Sea; D, male (79.5 × 77.9 mm) (ZRC 2013.1232), Bay of Bengal.

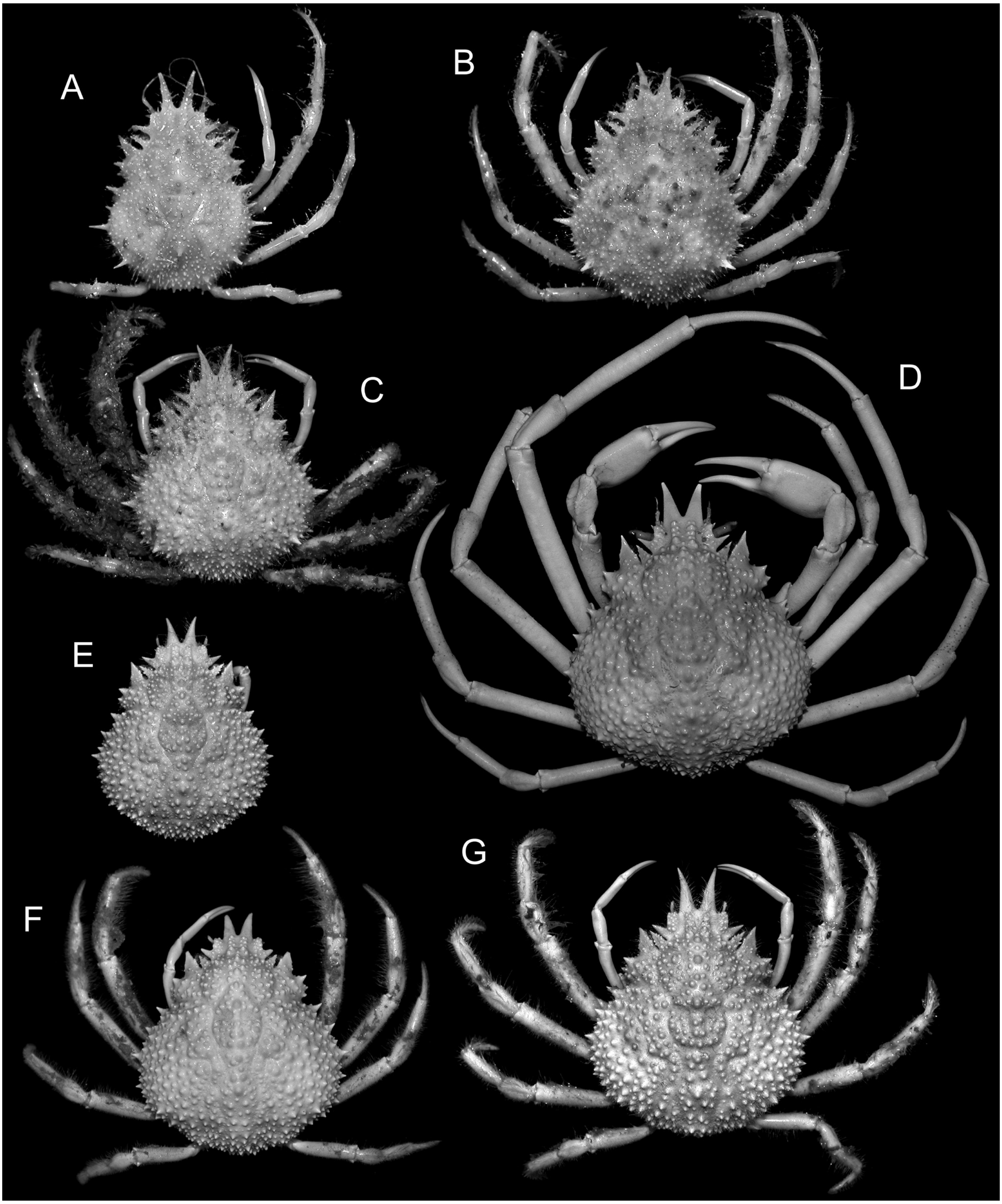

Fig. 11. General habitus, *Paramaja gibba*. A, juvenile male (10.6 × 8.1 mm) (MNHN-IU-2010-54), Madagascar; B, male juvenile (16.4 × 12.5 mm) (MNHN-IU-2010-55), Madagascar; C, male (24.6 × 20.9 mm) (MNHN-IU-2010-61), Madagascar; D, male (58.6 × 52.2 mm) (MNHN-IU-2010-63), Madagascar; E, juvenile female (33.9 × 29.4 mm) (NMV J54316), Australia; F, 1 ovigerous female (45.1 × 40.6 mm) (MNHN-IU-2010-467), Madagascar; G, female (46.7 × 41.6 mm) (NMV J61055), Australia.

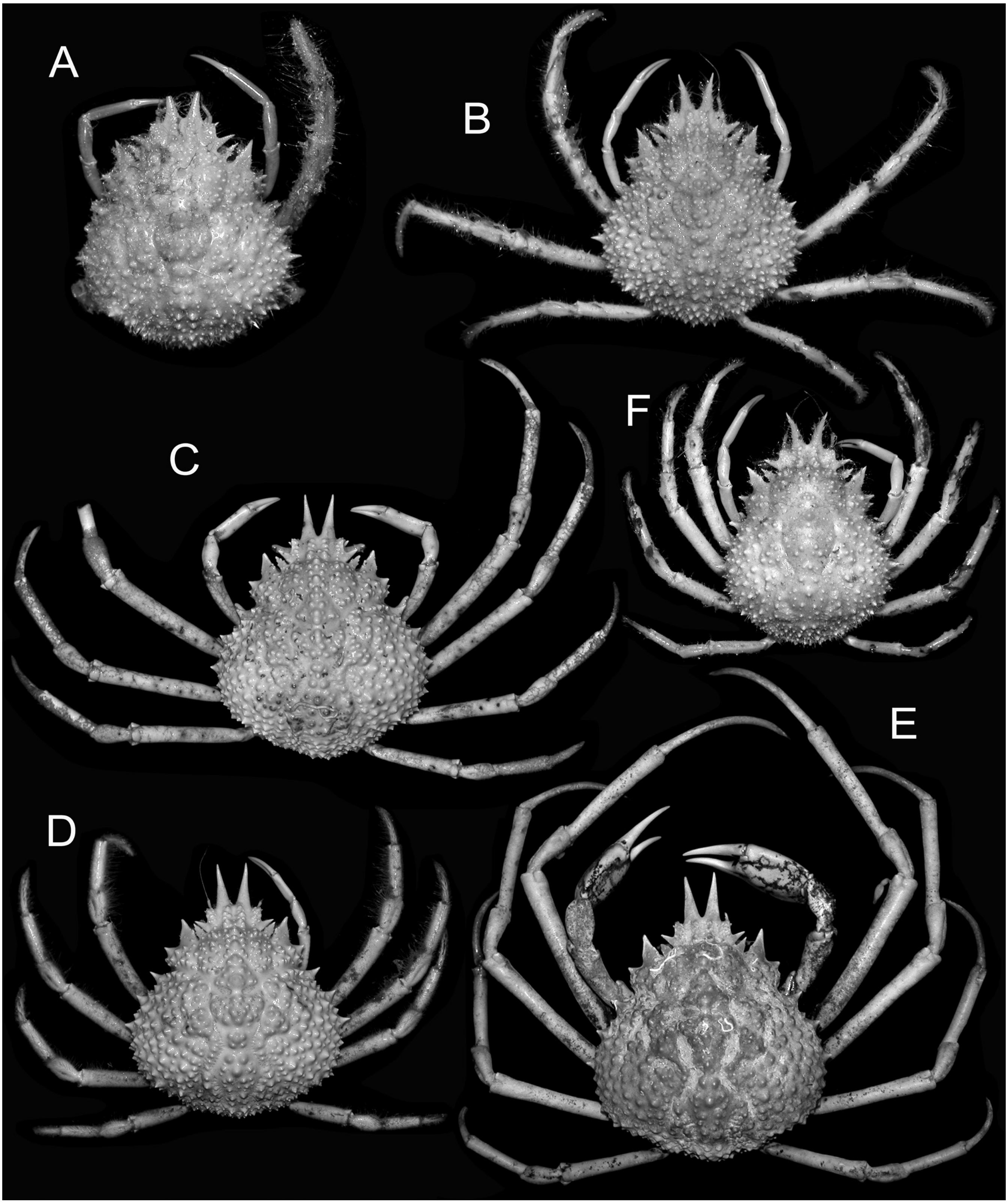

Fig. 12. General habitus, *Paramaja turgida* n. sp. A, paratype male (26.2 × 21.3 mm) (ZRC 2001.0616b); B, paratype female (33.5 × 29.0 mm) (ZRC 2013.1230); C, paratype male (67.9 × 60.5 mm) (MNHN), Philippines; D, paratype female (62.6 × 57.2 mm) (ZRC 2013.1241), Philippines; E, holotype male (74.1 × 66.8 mm) (NMCR), Philippines; F, male (25.1 × 19.6 mm) (MNHN-IU-2013-4051), Solomon Islands.

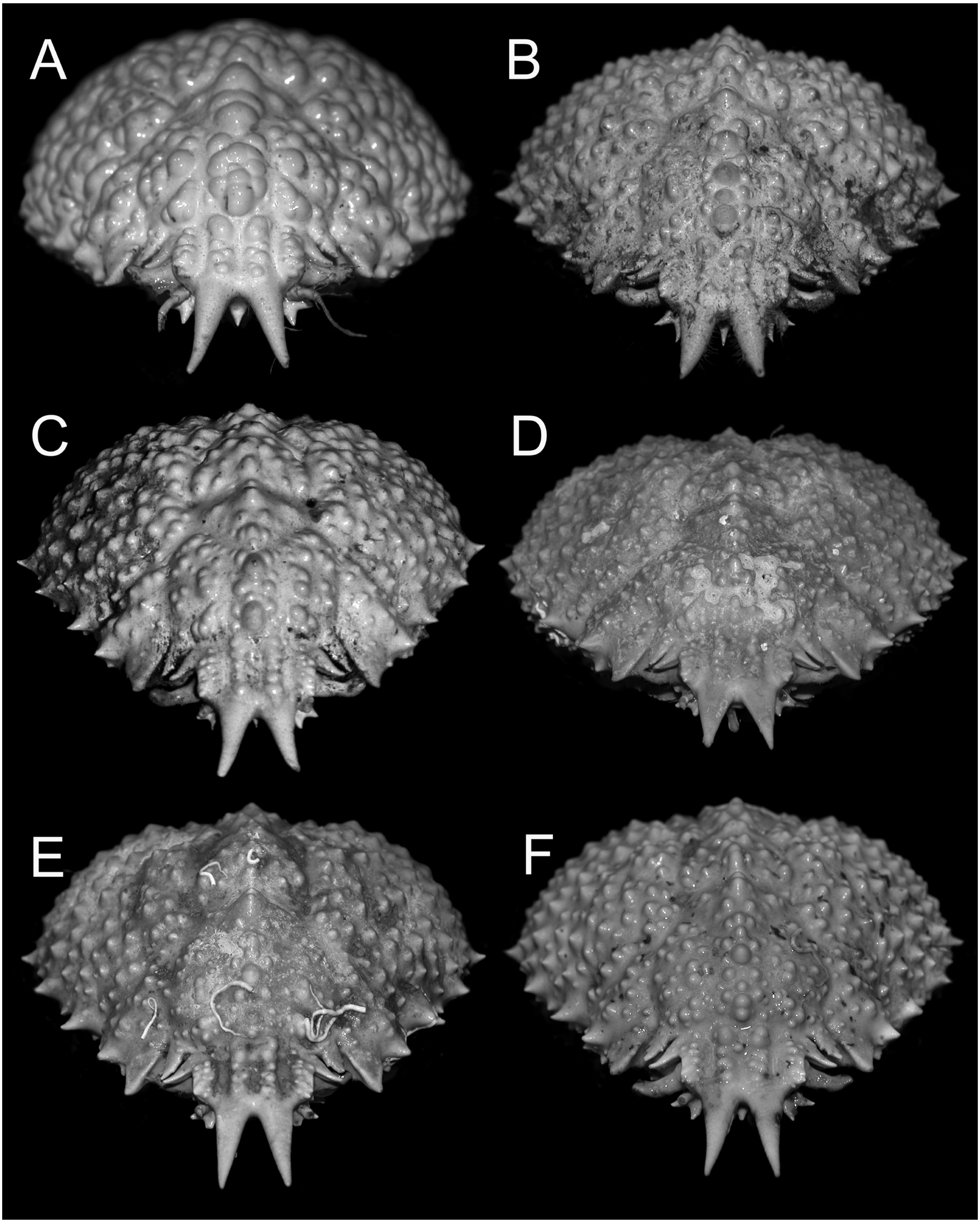

Fig. 13. Frontal views of carapaces, *Paramaja* species. A, *P. kominatoensis*, dried male (62.6 × 56.1 mm) (KPM NH0104298), Japan; B, *P. kominatoensis*, dried male (60.4 × 52.5 mm) (KPM NH124171), Japan; C, *P. kominatoensis*, dried male (73.0 × 66.0 mm) (PCM), Taiwan; D, *P. gibba*, male (79.5 × 77.9 mm) (ZRC 2013.1232), Bay of Bengal; E, *P. turgida* n. sp., holotype male (74.1 × 66.8 mm) (NMCR), Philippines; F, *P. turgida* n. sp., paratype male (67.9 × 60.5 mm) (MNHN), Philippines.

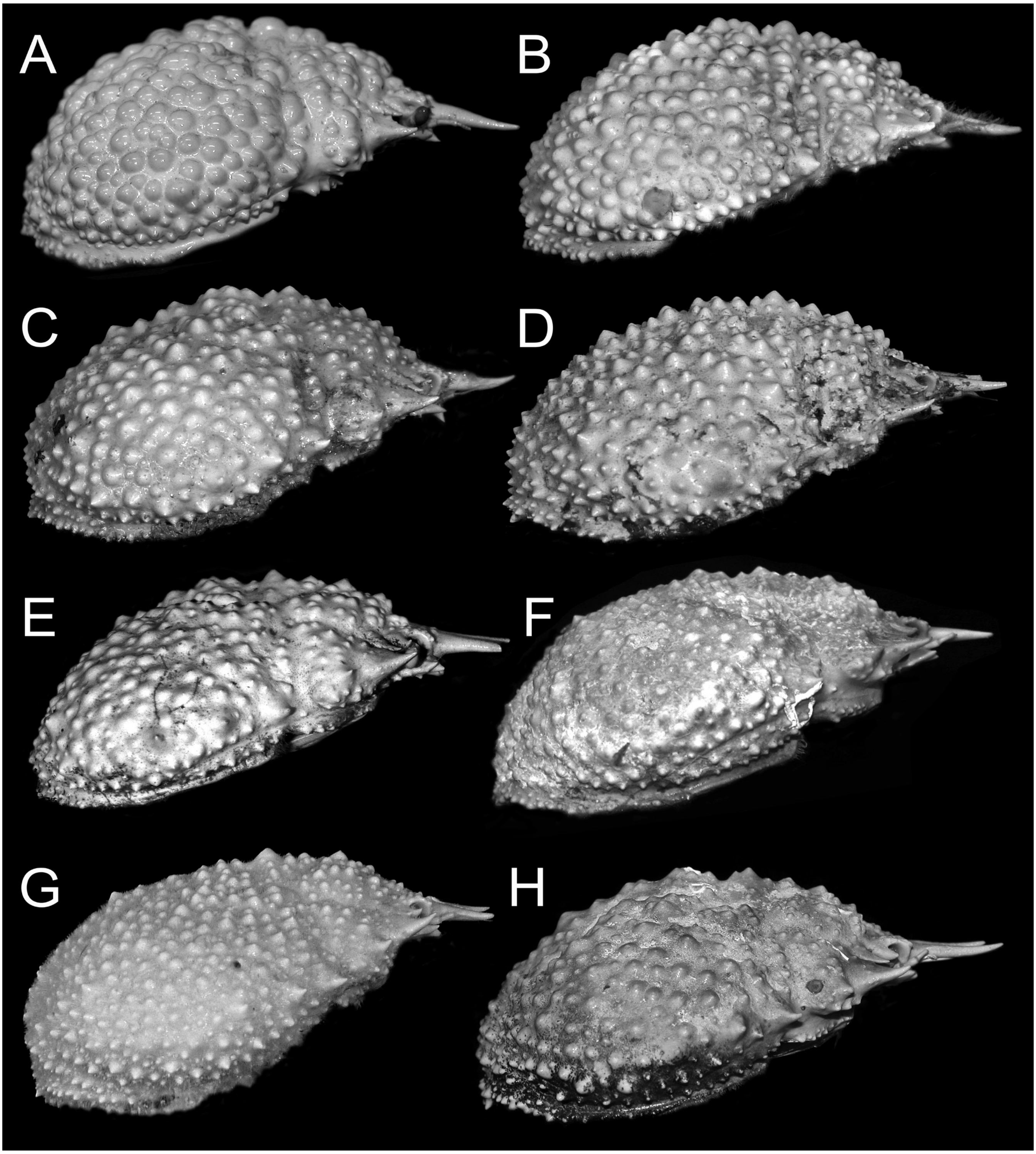

Fig. 14. Lateral views of carapaces, *Paramaja* species. A, *P. kominatoensis*, dried male (62.6 × 56.1 mm) (KPM NH0104298), Japan; B, *P. kominatoensis*, female (62.0 × 58.0 mm) (SMF 47810), Japan; C, *P. kominatoensis*, female (63.5 × 58.5 mm) (SMF 47728), Japan; D, *P. kominatoensis*, male (50.5 × 44.6 mm) (SMF 47738), Japan; E, *P. kominatoensis*, dried male (73.0 × 66.0 mm) (PCM), Taiwan [laterally transposed to match other figures]; F, *P. gibba*, male (79.5 × 77.9 mm) (ZRC 2013.1232), Bay of Bengal; G, *P. gibba*, female (67.7 × 63.2 mm) (SIO), Indian Ocean; H, *P. turgida* n. sp., holotype male (74.1 × 66.8 mm) (NMCR), Philippines.

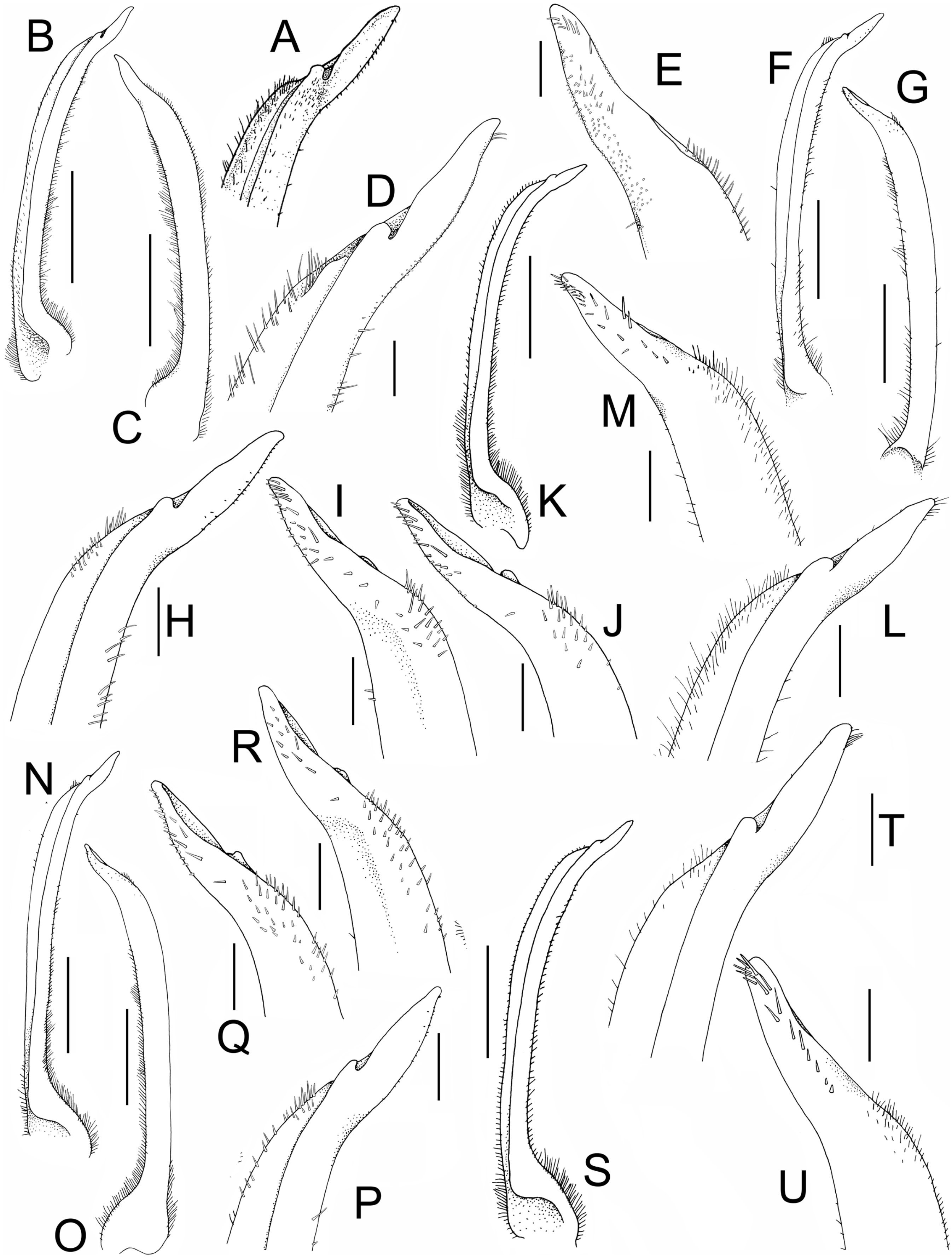

Fig. 15. Left G1s, Paramaja species. A, *P. kominatoensis* (after Kubo, 1936: fig. 1B); B-E, *P. kominatoensis*, male (76.9 × 69.6 mm) (SMF), Japan; F-J, *P. kominatoensis*, dried male (73.0 × 66.0 mm) (PCM), Taiwan; K-M, *P. gibba*, male (79.5 × 77.9 mm) (ZRC 2013.1232), Bay of Bengal; N-R, *P. turgida* n. sp., paratype male (67.9 × 60.5 mm) (MNHN), Philippines; S-U, *P. turgida* n. sp., holotype male (74.1 × 66.8 mm) (NMCR), Philippines. Scales: B, C, F, G, K, N, O, S = 5.0 mm; D, E, H-J, L, M, P-R, T, U = 1.0 mm.

200–300 m, coll. local fishermen with tangle nets, March 2004. — 1 female (61.9 × 58.4 mm) (ZRC 2013.1235), northwest Panglao, Bohol, 120–160 m, tangle nets, coll. J. Arbasto, July 2004–May 2005. — 1 male (70.4 × 63.9 mm) (ZRC 2012.1201), station CP 2332, off Pamilacan Island, Bohol Sea, 9°38.8'N 123°45.9'E, coll. PANGLAO 2005, 22 May 2005. — 1 male (70.9 × 62.2 mm) (ZRC 2012.1202), station CP 2372, Bohol/Sulu Seas, 9°31.4'N 124°00.6'E, PANGLAO 2005, 24 May 2005. — 1 male (70.5 × 63.1 mm) (ZRC 2012.1204), station CP 2397, off Aligbay Island, Maribojoc Bay, Bohol Sea, 9°34.9'N 123°41.7'E, coll. PANGLAO 2005, 31 May 2005. — 1 male (36.4 × 31.2 mm) (MNHN), station CP 2406, rock-sand-coral substrate, 9°38.8'N 123°46.5'E – 9°39.7'N 123°46.6'E, 331–334 m, Bohol Sea, coll. PANGLAO 2005, 1 June 2005. — 1 female (59.6 × 54.5 mm) (MNHN), station CP 2383, sandy substrate, 8°43.1'N 123°19.2'E – 8°44.0'N 123°18.7'E, 253–338 m, Bohol Sea, coll. PANGLAO 2005, 29 May 2005. — 1 male (28.0 × 22.5 mm) (ZRC 2013.1237), station CP 2331, muddy substrate, 9°37.4'N 123°45.9'E – 9°38.9'N 123°46.9'E, 268.2–273 m, Bohol Sea, coll. PANGLAO 2005, 22 May 2005. — 1 female (31.0 × 26.5 mm) (ZRC 2013.1231), station CP 2341, sandy-muddy substrate, 9°26.1'N 123°48.4'E – 9°24.9'N 123°49.3'E, 381–544 m, Bohol Sea, coll. PANGLAO 2005, 23 May 2005. — 1 female (62.6 × 57.2 mm) (ZRC 2013.1241), station CP 2363, sandy substrate, 9°0.1'N 123°26.5'E – 9°0.3'N 123°25.8'E, 439–452 m, Bohol Sea, coll. PANGLAO 2005, 26 May 2005. — 1 female (51.0 × 45.1 mm) (ZRC 2013.1236), station CP 2392, off Balicasag Island, sandy-muddy substrate, 9°30.1'N 123°43.4'E – 9°29.5'N 123°42.6'E, 242–313 m, Bohol Sea, coll. PANGLAO 2005, 30 May 2005. — 1 female (50.5 × 44.8 mm, with rhizocephalan, photographed) (ZRC 2013.1236), station CP 2331, muddy substrate, 9°37.4'N 123°45.9'E – 9°38.9'N 123°46.9'E, 268–273 m, Bohol Sea, coll. PANGLAO 2005, 22 May 2005. — 1 female (33.5 × 29.0 mm) (ZRC 2013.1230), station CP 2396; sandy substrate, 9°37.1N 123°445'E – 9°36.7N 123°42.9'E, 467–609 m, Bohol Sea, coll. PANGLAO 2005, 31 May 2005. — 1 female (ZRC 2013.1234), station CP2405, Maribojoc Bay, Panglao, 9°39.0'N 123°46.1'E, 387–453 m, coll. PANGLAO 2005, 1 June 2005. — 1 male (67.9 × 60.5 mm) (MNHN), station CC 2743, eastern coast of Luzon Island, coll. AURORA 2007, 2 June 2007. — 1 female (42.2 × 37.6 mm) (MNHN-IU-2013-4055), station CP 53, 13°59'N 120°18'E, 215–216 m, coll. RV *Coriolis*, MUSORSTOM 2, 27 November 1980. — 1 male (33.7 × 28.4 mm) (USNM 48508), station 5403, between Leyte and Cebu, 182 fathoms, coll. RV *Albatross*, 16 March 1909. Non-type: Philippines –fragments (USNM 48509), station 5536, 279 fathoms, coll. RV *Albatross*, 19 August 1909. **Solomon Islands** – 1 male (25.1 × 19.6 mm) (MNHN-IU-2013-4051), station CP 1851, 10°28'S 162°00'E, 297–350 m, coll. RV *Alis*, SALOMON 1, 6 October 2001.

Diagnosis. Adult carapace with branchial and gastric regions ovate; dorsal surface convex, covered by numerous rounded and sharp granules, those on median row larger, tuberculate, forming low crest (Figs. 12, 13E, F, 14H). Adult pseudorostral spines almost straight, gently diverging, appears dorso-ventrally flattened (Figs. 12, 13E, F, 36J, K). Supraorbital eave narrow, granulated, with antorbital spine triangular, sharp; intercalated spine irregular, slightly shorter than supraorbital spine; postorbital spine wide, pointing anteriorly, triangular with some granules at base of anterior margin; hepatic area inflated with several granules, largest spiniform, pointing outwards (Figs. 12, 13E, F, 36J, K). Adult male anterior thoracic sternum relatively narrow (Fig. 48H, I); lateral margins of anterior edge of male sterno-abdominal cavity straight (Fig. 48H, I). Distal part of G1 relatively shorter, tip not bent, in line with rest of G1 (Fig. 15N–U).

Etymology. From the Latin "*turgidus*" for swollen, alluding to the carapace appearance of the species.

Remarks. *Paramaja turgida* n. sp. is closest to *P. gibba*, but can be separated by its proportionately narrower male anterior thoracic sternum (Fig. 48H, I) (versus relatively broader in *P. gibba*, Fig. 48F, G) and the distal part of the G1 is relatively shorter with the tip in line with the rest of the structure (Fig. 15N–U) (versus relatively longer with the tip gently bent laterally in *P. gibba*, Fig. 15K–M).

The chelipeds of adult females of *P. turgida* are slender and not inflated, while the ambulatory legs are distinctly shorter and more setose (Fig. 12B, D). The smallest ovigerous female measured 47.1 by 41.1 mm (ZRC 2013.1185).

A young male specimen from the Solomon Islands (25.1 × 19.6 mm, MNHN-IU-2013-4051) (Fig. 12F) is tentatively referred to *P. turgida*. The G1 resembles that of *P. turgida*, but at this size, it is not easy to separate from *P. kominatoensis*. The less inflated carapace shape of the specimen is closest to *P. turgida* and as such, we provisionally refer it here. Adult males will need to be collected to be certain about their identity as the Solomon Islands is some distance from the Philippines.

See also discussion for *P. gibba* and *P. kominatoensis*.

***Alcomaja* n. gen.**

Diagnosis. Carapace ovate; dorsal surface convex, covered by granules or tubercles; gastric and branchial regions delimited by distinct grooves (Figs. 16, 17). Intestinal region without distinct median spine (Figs. 16, 17). Pseudorostral spines long, diverging, forming a V, (Figs. 18, 36L–O). Supraorbital eave with anterior part longitudinally narrow, rectangular, not prominently expanded; antorbital spine sharp (Figs. 18, 36L–O). Intercalated spine distinct, separated from supraorbital eave and postorbital spine by distinct gaps; postorbital spine strong, lobiform; hepatic region with 1 strong spine, much shorter than postorbital spine; 1 or more smaller spines below (Figs. 18, 36L–O). Lateral carapace margin with 3 spines and numerous tubercles or granules, 1 branchial spine or tubercle usually discernible, may be low in large specimens (Figs. 16, 17). Posterior carapace margin with 2 short median spines (Figs. 16, 17). Eyes relatively long, slender, with ovoid cornea (Figs. 18, 36L–O). Antennal flagellum short, slender. Basal antennal article longer than broad, rectangular; surface with several tubercles or granules, with 2 spines distally; inner and outer lateral margins may have low granules or lobes, or entire; proximal outer angle rounded; antero-external crested rim of antennular fossa touches does not substantially overlap basal antennal article (Fig. 39L–O). Epistome as wide as long, anterior margin with low lobes or low swellings; posterior margin composed of 4 rectangular plates separated by shallow fissures (Figs. 39L–O, 41G, H). Suborbital margin separated from basal antennal article by short fissure, confluent with margin of postorbital tooth (Fig. 39L–O). Outer surface of third maxilliped covered by very short setae in adults; ischium subrectangular, distinctly longer than broad; postero-external angle of merus relatively broad, "inserted" into shallower concavity on outer margin of ischium; antero-internal part of ischium rounded, auriculiform (Fig. 45A–H). Male chelipeds relatively short in adult males, surfaces of merus and carpus almost smooth to covered with very small granules, low longitudinal ridges with low tubercles; carpus short, with low, uneven longitudinal ridge; propodus of palm elongated, curved, smooth, without lateral cristae in young, short, inflated in adults, palm longer than fingers; fingers long, slender, gently curved, with distinct basal gape when closed (Figs. 16, 17, 53M–P). Ambulatory legs relatively long, slender; merus without dorsal subdistal spine; dactylus elongate, curved, covered with long setae when young except for corneous tip, almost completely smooth in adults (Figs. 16, 17, 55K–N). Thoracic sternum wide; surfaces of somites 5–8 with numerous prominent rounded tubercles and granules; sternites 3 and 4 distinctly depressed; margin between sternites 2 and 3 demarcated by deep notch; anterior margin of sterno-abdominal cavity not forming complete rim (Figs. 49, 52E–G). Male abdomen subrectangular, with 6 free somites and telson; somites 3 and 4 subequal to or slightly wider than somites 5, 6 and telson (Fig. 49). Male press-button abdominal locking mechanism submedian in position on sterno-abdominal cavity (Fig. 52E–G). Female abdomen dome-shaped, covering most of thoracic sternum. G1 long, slender, gently curved, distal part subconical with rounded tip, dorsal part folding downwards to form ventral projection, with scattered setae on ventral surface and numerous short setae on dorsal surface (Figs. 19, 20).

Type species. *Alcomaja irrorata* n. sp. by present designation.

Etymology. The genus is named after Alfred William Alcock. The name is an arbitrary combination of his family name with *Maja*. Gender feminine.

Remarks. *Alcomaja* n. gen. is established to accomodate *A. irrorata* n. sp., *Maja gracilipes* Chen & Ng, 1999, *M. confragosa* Griffin & Tranter, 1986, *M. nagashimaensis* T. Sakai, 1969, *A. desmondi* n. sp., *A. miriky* n. sp., and *A. latens* n. sp.

In the form of the suborbital margin, basal antennal article, epistome, third maxilliped, pereiopods, thoracic sternum and male abdomen, *Alcomaja* is most similar to *Paramaja* Kubo, 1936. The differences have been discussed under the remarks for that genus.

Key to species of *Alcomaja* n. gen.

1. Dorsal surface of carapace and ambulatory legs densely covered with long, stiff setae (Fig. 17F); G1 almost straight with distinct ventral fold (Fig. 20R–T); Philippines .... *Alcomaja desmondi* n. sp.
– Dorsal surface of carapace and ambulatory legs covered with scattered short, hooked setae, sometimes dense; G1 curved 2

2. Dorsal surface of carapace covered with small rounded granules, lateral and branchial spines strong even as adults, with 2 hepatic spines; adult ambulatory legs relatively short, with first leg of adult males not substantially elongated (Figs. 17A–E) 3
– Dorsal surface of carapace covered with small and large granules, sometimes sharp, lateral and branchial spines distinct but low to absent in adults, with 2 hepatic spines; adult ambulatory legs long, with first leg of adult males prominently elongated (Figs. 16A–E) 5

3. Carapace relatively more elongate; pseudorostral spines long (Figs. 17E, 36O); G1 gently curved with distal part gently curved downwards (Fig. 20O–Q); Madagascar........................ .... *Alcomaja miriky* n. sp.
– Carapace relatively broad; pseudorostral spines relatively shorter (Figs. 17A–D, 36M, N); G1 similar to above or otherwise ..4

4. Intercalated spine acutely triangular (Fig. 36M); G1 strongly curved, with distal part gently curved downwards (Fig. 20A–J); Japan and Taiwan.. ....*Alcomaja nagashimaensis* (T. Sakai, 1969)
– Intercalated spine basally subquadrate (Fig. 36N); G1 gently curved, with distal part gently curved upwards (Fig. 20K–M); Solomon Islands .... *Alcomaja latens* n. sp.

5. Dorsal surface of carapace with distinct small and large sharp and rounded granules; intercalated tooth triangular (Figs. 16D, E,18A, B); G1 gently curved, distal part relatively short (Fig. 19G); Moluccas and Western Australia ....*Alcomaja confragosa* (Griffin & Tranter, 1986)
– Dorsal surface of carapace as above or otherwise (Figs. 16A–C, 18C–F); intercalated tooth subtruncate basally (Fig. 18C–F): G1 gently or strongly curved...6

6. Dorsal surface of carapace with distinct small and large sharp, rounded granules (Figs. 16B, C, 18C, D); pseudorostral spines with rounded cross-section (Fig. 18C, D); ischium of third maxilliped distinctly granular (Fig. 45B, C); G1 gently curved, distal part straight (Fig. 19D–F); South China Sea and Philippines ....*Alcomaja gracilipes* (Chen & Ng, 1999)
– Dorsal surface of carapace with small and large rounded granules, some of which merge basally (Figs. 16A, 18E, F); pseudorostral spines dorsoventrally flattened (Fig. 18E, F); ischium of third maxilliped smooth (Fig. 45A); G1 strongly curved, distal part curved upwards (Fig. 19A–C); Philippines .... *Alcomaja irrorata* n. sp.

Alcomaja irrorata n. sp.

(Figs. 2C, 16A, 18E, F, 19A–C, 39L, 41G, 45A, 49A, 52E, 53M, 55K, L)

Material examined. Holotype: male (52.6 × 45.7 mm) (NMCR), Balicasag, Panglao, Bohol, Philippines, 200–300 m, coll. local fishermen with tangle nets, June 2002. Paratypes: **Philippines** – 1 male (45.5 × 39.5 mm, with rhizocephala), 6 males (47.7 × 43.1 mm, 48.4 × 42.2 mm, 46.7 × 41.5 mm, 44.7 × 39.1 mm, 44.2 × 38.0 mm, 44.7 × 38.4 mm), 2 young males (34.4 × 29.8 mm, 28.7 × 23.9 mm), 2 young females (31.5 × 26.9 mm, 29.7 × 26.1 mm), 10 ovigerous females (43.7 × 38.2 mm, 44.1 × 38.7 mm, 41.1 × 36.9 mm, 44.1 × 36.9 mm, 44.1 × 38.2 mm, 43.7 × 39.2 mm, 45.1 × 40.8 mm, 44.0 × 37.6 mm, 44.1 × 39.2 mm, 41.6 × 36.6 mm), 1 male (28.1 × 23.6 mm, with bopyrid) (ZRC 2013.1229), Balicasag, Panglao, Bohol, Philippines, 200–300 m, coll. local fishermen with tangle nets, June 2002. — 2 ovigerous females (42.6 × 37.4 mm, 43.0 × 38.0 mm) (USNM, ex ZRC 2001.0434), Balicasag, Panglao, Bohol, 200–300 m, coll. local fishermen with tangle nets, Balicasag, Panglao, Bohol, 200–300 m, coll. local fishermen with tangle nets, December 2000. — 12 males (44.6 × 39.7 mm, 44.4 × 39.7 mm, 45.3 × 39.9 mm, 47.5 × 43.4 mm, 46.4 × 40.2 mm, 40.5 × 35.0 mm, 44.4 × 39.0 mm, 43.9 × 38.3 mm, 44.8 × 39.2 mm, 47.0 × 40.4 mm, 46.5 × 40 .1 mm, 44.1 × 39.1 mm); 10 ovigerous females (44.3 × 38.9 mm, 42.5 × 38.1 mm, 39.3 × 34.1 mm, 37.9 × 35.2 mm, 43.7 × 37.7 mm, 45.3 × 39.6 mm, 45.3 × 40.7 mm, 42.9 × 37.9 mm, 40.5 × 35.6 mm, 37.7 × 32.7 mm), 1 young female (32.2 × 26.8 mm) (ZRC 2001.0616), Balicasag, Panglao, Bohol, 200–300 m, coll. local fishermen with tangle nets, 28 November 2001. Others: 1 young female (29.7 × 25.4 mm), 1 ovigerous female (26.2 × 22.5 mm) (ZRC 2013.1222, part ex ZRC 2001.0616), Balicasag Island, Panglao, Bohol, coll. fishermen with tangle nets, 28 November 2001. — 1 male (45.6 × 41.1 mm) (AM), Balicasag Island, Panglao, Bohol, coll. fishermen with tangle nets, July 2003. — 1 male with rhizocephalan (38.9 × 33.5 mm) (ZRC 2013.1221), Balicasag Island, Panglao, Bohol, coll. fishermen with tangle nets, November 2003. — 4 males, 2 females (NSMT-Cr 15387), Balicasag Island, Panglao, Bohol, coll. local fisherman via M. Takeda & H. Komatsu, February 2003. — 1 male (43.0 × 37.2 mm) (ZRC 2013.1223), station CP 2343, off Pamilacan Island, Bohol Sea, 9°27.4'N 123°49.4'E, 273–356 m, coll. PANGLAO 2005, 23 May 2005.

Diagnosis. Carapace pyriform; dorsal surface of carapace and ambulatory legs covered with short, hooked setae; with small and large rounded granules, some of which merge basally (Fig. 16A). Pseudorostral spines dorsoventrally flattened in adults (Fig. 18E, F). Intercalated spine subtruncate basally; antorbital spine gently curved. Lateral and branchial spines strong in juveniles, weak in adults (Fig. 18E, F). Subhepatic region with rugose and unevenly granulated surface (Fig. 39L). Basal antennal article weakly granulated, with 6 small granules, 2 stout spines distally (Figs. 39L, 41G). Ischium of third maxilliped smooth or rugose, without distinct granules (Fig. 45A). Adult male ambulatory legs long, especially merus and propodus first leg which can be twice length of carapace; surfaces almost smooth or with setae when young (Figs. 16A, 55K, L). G1 strongly curved, distal part curved upwards (Fig. 19A–C).

Etymology. The name is derived from the Latin "*irroratus*" which means covered with granules, alluding to the appearance of the species.

Remarks. In general appearance, *A. irrorata* n. sp. is closest to *A. gracilipes* (Chen & Ng, 1999), described from the South China but is now also recorded from the Philippines. However, there are several key differences between the two species. Most significantly, while the G1 structures are superficially similar, it is more strongly curved in *A. irrorata* (Fig. 19A–C) with that of *A. gracilipes* relatively straighter along the median part (Fig. 19D–F). This difference is consistent even for smaller specimens. In addition, the outer surface of the ischium of the third maxilliped is smooth or almost so in *A. irrorata* (Fig. 45A) (distinctly granulous in *A. gracilipes*, Fig. 45B, C); the pseudorostral spines in *A. irrorata* is relatively stouter with the cross-section more dorso-ventrally flattened (Fig. 18E, F) (relatively more slender with a rounded cross-section in *A. gracilipes*, Fig. 18C, D); the postorbital spine is usually relatively wider in *A. irrorata* (Fig. 8E, F) (more slender in *A. gracilipes*, Fig. 18C, D); and the ambulatory legs are relatively longer in adult *A. irrorata* than in *A. gracilipes* (Fig. 16A versus Fig. 16B, C).

Alcomaja irrorata is also similar to *A. confragosa* (Griffin & Tranter, 1986). However, the intercalated spine is more acutely triangular in *A. confragosa* (Fig. 18A, B) (relatively stouter in *A. irrorata*, Fig. 18E, F); the postorbital spine is relatively more narrow in *A. confragosa* (Fig. 18A, B) (relatively stouter in *A. irrorata*, Fig. 18E, F); the basal antennal article is lined with granules on the outer margin in *A. confragosa* (see Griffin & Tranter, 1986: fig. 72d) (with only several granules on the inner margin in *A. irrorata*, Fig. 39L); the ischium of the third maxilliped is relatively shorter with the outer surface is weakly granular in *A. confragosa* (see Griffin & Tranter, 1986: fig. 72c) (ischium relatively longer with the outer surface smooth or almost so in *A. irrorata*, Fig. 45A); and the G1 is relatively shorter with the distal half more prominently curved and the distal part after the subdistal flap proportionately shorter in *A. confragosa* (Fig. 19G, Griffin & Tranter, 1986: 215, fig. 73a, b) (G1 relatively longer with the distal half gently curved and the distal part after the subdistal flap proportionately longer in *A. irrorata*, Fig. 19A–C).

For *A. irrorata*, we observed that male specimens under 35 mm length are still juveniles, with adults possessing inflated chelae only at lengths of 44 mm or longer. In small specimens, the armature is relatively sharper, in particular the three lateral and two branchial spines and the series of large granules along the median row. The smallest ovigerous female, however, is only 26.2 by 22.5 mm (ZRC 2013.1222a). Another slightly larger female specimen from the same site (29.7 × 25.4 mm, ZRC 2013.1222b), however, was still immature.

The spines on the posterior carapace margin and on the lateral margins are always present but get relatively smaller and blunter as the specimens get larger. The ambulatory legs are relatively longer in adult males, with the surfaces generally smooth (Fig. 55K). Smaller male and female specimens, however, have the articles distinctly more setose, particularly the dactylus (Fig. 55L).

Although juveniles of *A. irrorata* (cf. 1 juvenile female 29.7 × 26.1 mm, 1 male 28.7 × 23.9 mm, ZRC 2013.1229) are superficially similar in general form to young *Paramaja* (of *P. gibba* and *P. turgida*), the pseudorostral spines are invariably relatively longer in *A. irrorata*, the carapace is far more granulous but less swollen, the spines are relatively stronger, and the ambulatory legs are proportionately longer.

Alcomaja confragosa (Griffin & Tranter, 1986)

(Figs. 16D, E, 18A, B, 19G)

Maja confragosa Griffin & Tranter, 1986: 213, figs. 72, 73a, b, pl. 16. – Poore et al., 2008: 61. – Ng et al., 2008: 117 (list).

Material examined. Australia – 1 young female (21.5 × 18.2 mm) (NMV J53978), off Point Cloates, 22°37.06'S 113°29.03'E – 22°37.02'S 113°28.56'E, Western Australia, 355–382 m, coll. G. Poore, CSIRO RV *Southern Surveyor*, 9 December 2005.

Diagnosis. Carapace pyriform; dorsal surface of carapace and ambulatory legs covered with short, hooked setae; with small and large rounded granules, some of which merge basally (Fig. 16D, E). Pseudorostral spines with rounded cross-section (Fig. 18A, B). Intercalated spine acutely triangular; antorbital spine gently curved (Fig. 18A, B). Lateral and branchial spines strong in juveniles, weak in adults (Fig. 16D, E). Subhepatic region with distinctly granulated surface. Basal antennal article with numerous distinct granules. Ischium of third maxilliped distinctly granulated, especially on outer margin, with 2 large blunt distal spines. Adult male ambulatory leg condition not known (Fig. 16E). G1 gently curved, distal part relatively short (Fig. 19G).

Remarks. A small female specimen collected from the northern part of Western Australia agrees very well with the type male described in Griffin & Tranter (1986). The holotype of *Maja confragosa* was described from Indonesia, in the Eastern Mollucas. The new material comes from the Tropic of Capricorn near 22°S in the same depth range, around 300 m.

Differences with the allied *A. irrorata* n. sp. and *A. gracilipes* (Chen & Ng, 1999) are discussed under these two species.

Alcomaja gracilipes (Chen & Ng, 1999)

(Figs. 16B, C, 18C, D, 19D–F, 39M, 45B, C, 49B, C, 53N)

Maja gracilipes Chen & Ng, 1999: 754, figs. 1, 2. – Yang et al., 2008: 780. – Ng et al., 2008: 117 (list).

Material examined. Holotype: male (45.4 × 43.5 mm) (IOCAS K33B-34), station 6080, 180 m, on gravel, South China Sea, coll. 21 April 1959. **Philippines** – 1 female (39.8 × 29.2 mm) (MNHN-IU-2013-4049), station CP 27, 14°00'N 120°19'E, 188–192 m, coll. RV. *Vauban*, MUSORSTOM 1, 22 March 1976. — 1 male (31.9 × 25.5 mm) (MNHN-IU-2013-4054), station CP 35, 13°59'N 120°18'E, 186–187 m, coll. RV *Vauban*, MUSORSTOM 1, 23 March 1976. — 1 male (24.8 × 19.4 mm), 1 female (16.3 × 13.2 mm) (MNHN-IU-2013-4048), station CP 61, 184–202 m, 14°02'N 120°18'E, RV *Vauban*, MUSORSTOM 1, 27 March 1976. – 1 female (32.7 × 27.1 mm) (MNHN-IU-2013-4058), station CP 88, 14°00'N 120°17'E, 183–187 m, coll. RV *Coriolis*, MUSORSTOM 3, 31 May 1985. — 1 female (35.7 × 29.8 mm) (MNHN-IU-2013-4056), station CP96, 14°00'N 120°17'E, 190–194 m, RV *Coriolis*, MUSORSTOM 3, 1 June 1985. — 1 male (31.7 × 26.6 mm) (MNHN-IU-2013-4057), station CP 98, 14°00'N 120°18'E, 194–205 m, coll. RV *Coriolis*, MUSORSTOM 3, 1 June 1985. — 1 male (31.7 × 26.6 mm) (ZRC 2001.432), Balicasag Island, Panglao, Bohol, coll. fishermen with tangle nets, December 2000. — 1 male (41.4 × 35.4 mm) (ZRC 2013.1225), Balicasag Island, Panglao, Bohol, coll. fishermen with tangle nets, June 2002. — 1 young female (24.1 × 20.5 mm) (ZRC 2013.1224), Balicasag Island, Panglao, Bohol, coll. fishermen with tangle nets, June 2002. — 1 female (32.1 × 27.5 mm) (ZRC 2013.1227), Balicasag Island, Panglao, Bohol, coll. fishermen with tangle nets, 2003. — 1 female (ZRC 2013.1228), Balicasag Island, Panglao, Bohol, 200–300 m, coll. fishermen with tangle nets, May 2004. — 1 male (NSMT-Cr 22327), Balicasag Island, Panglao, Bohol, coll. local fisherman via M. Takeda & H. Komatsu, February 2003. — 1 female (NSMT-Cr 22326), Balicasag Island, Panglao, Bohol, coll. local fisherman via M. Takeda & H. Komatsu, February 2003. — 1 male (41.9 × 35.2 mm) (ZRC 2013.1226), northwest Panglao, Bohol, coll. J. Arbasto with tangle nets, 2006.

Diagnosis. Carapace pyriform; dorsal surface of carapace and ambulatory legs covered with short, hooked setae; with distinct small and large sharp and rounded granules (Figs. 16B, C, 18C, D). Pseudorostral spines with rounded cross-section (Fig. 18C, D). Intercalated spine subtruncate basally; antorbital spine gently curved (Fig. 18C, D). Lateral and branchial spines strong in juveniles, weak in adults. Subhepatic region with strongly granulated surface (Fig. 39M). Basal antennal article with numerous distinct granules (Fig. 39M). Ischium of third maxilliped distinctly granulated on surface, with 2 distinct distal spines (Fig. 45B, C). Adult male ambulatory legs long, especially merus and propodus first leg which can be twice length of carapace; surfaces almost smooth or with sparse setae (Figs. 16B, C). G1 gently curved, distal part straight (Fig. 19D–F).

Remarks. The specimens from the Philippines agree well with the holotype of *A. gracilipes* (Chen & Ng, 1999) described from the South China Sea. The characters outlined in Chen & Ng (1999) serve to easily distinguish *A. gracilipes* from *A. confragosa* and *A. irrorata* n. sp. (see also discussion of *A. irrorata*).

That both *A. irrorata* and *A. gracilipes* occur in the Philippines (with some specimens sympatric) does pose problems but we know too little about the ecology of these species to speculate further. In the steep slopes along Balicasag, Philippines, the dominant species is clearly *A. irrorata*, with only a few specimens of *A. gracilipes* obtained. On the other hand, only *A. gracilipes* was observed in the trawled material from the French expeditions to the Philippines, albeit there were only a few specimens. The type male was also collected by trawling in the South China Sea. Only one specimen of *A. irrorata* from off Pamilacan Island (male 43.0 × 37.2 mm, ZRC 2013.1223,) was collected by trawling in the Philippines. Whether this suggests they have different habitat preferences is not known.

Alcomaja nagashimaensis **(T. Sakai, 1969)**
(Figs. 17A–C, 20A–J, 36M, 39O, 41H, 45E, F, 49D, E, 52G, 53P, 55N, 69A)

Maja nagashimaensis T. Sakai, 1969: 256, pl. 1, fig. 2, text-fig. 5b, b'. – Serène & Lohavanijaya, 1973: 50 (key). – T. Sakai, 1976: 241, pl. 85, fig. 1, text-fig. 129. – Serène & Vadon, 1981: 129. – Griffin & Tranter, 1986: 217. – Muraoka, 1998: 27. – Ng et al., 2008: 117 (list).
Maja nagasimaensis [sic] – Maramura & Kosaka, 2003: 34.

Material examined. Holotype: male (34.0 × 28.5 mm) (USNM 125886), on rocky shore, Kii Nagashima, Mie Prefecture, Honshu Island, Japan, coll. Y. Yamamoto. Others: **Japan** – 1 male (37.2 × 32.4 mm) (CBM-ZC9928), Ohse-Zaki, Suruga Bay, 35°3.53'N 138°48.26'E, 135–142 m, in 1 m ORI dredge, cruise KT04-6, station OS-1, coll. T. Akiyama, RV *Tansei-Maru*, 4 May 2004. **Philippines** – 2 males (27.3 × 23.3 mm, 28.7 × 23.9 mm), 1 ovigerous female (23.9 × 20.6 mm) (ZRC 2013.1393, ex part ZRC 2001.0435), Balicasag Island, Panglao, Bohol, coll. fishermen with tangle nets, December 2000. — 2 ovigerous females (24.7 × 20.6 mm, 24.6 × 22.3 mm), 3 males (23.4 × 19.5 mm, 21.9 × 18.4 mm, 15.7 × 7.3 mm) (ZRC 2001.0434), Balicasag Island, Panglao, Bohol, coll. fishermen with tangle nets, December 2000. — 1 male (30.5 × 26 mm) (ZRC 2013.1394, ex part ZRC 2001.430), Balicasag Island, Panglao, Bohol, coll. fishermen with tangle nets, 28 November 2000. — 4 males (27.7 × 22.8 mm, 26.8 × 22.1 mm, 22.3 × 17.7 mm, 22.9 × 17.6 mm [with bopyrid], 7 ovigerous females (28.2 × 24.0 mm, 25.1 × 20.8 mm, 22.9 × 18.7 mm, 25.1 × 21.1 mm, 23.1 × 20.0 mm, 22.6 × 19.1 mm) (ZRC 2001.0585a), Balicasag Island, Panglao, Bohol, coll. fishermen with tangle nets, 28 November 2001. — 1 female (ZRC 2013.1389, ex part ZRC 2001.0601), Balicasag Island, Panglao, Bohol, 200–300 m, coll. fishermen with tangle nets, 28 November 2001. — 1 juvenile male (ZRC 2013.1315), Balicasag Island, Panglao, Bohol, 200–300 m, coll. fishermen with tangle nets, June 2002. — 2 males, 2 females (ZRC 2013.1402), Balicasag Island, Panglao, Bohol, coll. fishermen with tangle nets, June 2002. — 2 males (NSMT-Cr 15390a), Balicasag Island, Panglao, Bohol, coll. local fisherman via M. Takeda & H. Komatsu, February 2003. — 3 males (NSMT-Cr 13032), Balicasag Island, Panglao, Bohol, coll. local fisherman via M. Takeda & H. Komatsu, February 2003. — 1 male (20.8 × 16.8 mm), 3 females (23.7 × 19.4 mm, 23.2 × 19.3 mm, 23.1 × 18.2 mm), 1 ovigerous female (23.9 × 19.9 mm) (ZRC 2013.1400), Balicasag Island, Panglao, Bohol, coll. fishermen with tangle nets, July 2003. — 1 male (19.9 × 16.6 mm) (ZRC 2013.1391), Balicasag Island, Panglao, Bohol, coll. fishermen with tangle nets, July 2003. — 1 male (ZRC 2013.1387), Balicasag Island, Panglao, Bohol, 200–300 m, coll. fishermen with tangle nets, 25–30 July 2003. — 1 male, 1 female (ZRC 2013.1392), Balicasag Island, Panglao, Bohol, 200–300 m, coll. fishermen with tangle nets, November 2003. — 1 female (AM), Balicasag Island, Panglao, Bohol, 200–300 m, coll. fishermen with tangle nets, December 2003. — 3 males (22.6 × 18.7 mm, 26.4 × 21.6 mm, 28.3 × 24.1 mm) (ZRC 2013.1381), 19 May 2004. — 1 male (28.9 × 24.8 mm) (ZRC 2013.1388), 28 May 2004. — 1 ovigerous female (ZRC 2013.1386), Balicasag Island, Panglao, Bohol, 200–300 m, coll. fishermen with tangle nets, May 2004. — 1 male (ZRC 2013.1382), Balicasag Island, Panglao, Bohol, 200–300 m, coll. fishermen with tangle nets, 29 May 2004. — 1 male (AM), Balicasag Island, Panglao, Bohol, 200–300 m, coll. fishermen with tangle nets, 4 June 2004. — 1 male (26.1 × 22.0 mm) (ZRC 2013.1390), northwest Panglao, Bohol, 120–160 m, tangle nets, coll. J. Arbasto, 1 December 2007. — 1 male (27.7 × 23.8 mm), 1 ovigerous female (20.9 × 17.4 mm), 1 female (22.2 × 19.2 mm) (ZRC 2013.1399), northwest Panglao, Bohol, 120–160 m, tangle nets, coll. J. Arbasto, 2007. — 1 female (15.0 × 11.2 mm) (MNHN-IU-2013-4053), station CP 31, 14°00'N 120°16'E, 187–195 m, coll. RV *Vauban*, MUSORSTOM 1, 22 March 1976. — 1 ovigerous female (15.8 × 12.7 mm), 1 female (12.1 × 9.1 mm) (MNHN-IU-2013-4052) CP57, 13°53'N-120°13'E, 96–107 m, coll. RV *Vauban*, MUSORSTOM 1, 26 March 1976. **Taiwan** – 1 male (29.5 × 24.2 mm) (ZRC 2013.1385), Tashi fishing port, Ilan Province, sandy mud, 20 m, coll. Hwang 28 April 1989. — 1 male (23.2 × 18.4 mm) (ZRC 2013.1383), Tashi fishing port, Ilan Province, sandy mud, 20 m, coll. Hwang, 4 July 2011.

Diagnosis. Carapace pyriform; dorsal surface of carapace and ambulatory legs covered with short, hooked setae; with small rounded granules (Fig. 17A–C). Pseudorostral spines with rounded cross-section (Fig. 36M). Antorbital spine almost straight; intercalated spine acutely triangular, shorter than supraorbital and postorbital spines, with large open gaps between them; postorbital spine large, longer than others; 1 distinct hepatic spine with small basal spine (Fig. 36M). Lateral and branchial spines strong in juveniles and adults (Fig. 17A–C). Subhepatic region with rugose and weakly granulated surface (Fig. 39O). Basal antennal article with low granules and 2 tubercles, with 2 distal spines (Fig. 39O, 41H). Ischium of third maxilliped almost smooth to slightly rugose (Fig. 45E, F). Ambulatory legs relatively short, first leg never twice length of carapace; surfaces distinctly setose (Figs. 17A–C, 55N). G1 strongly curved, with distal part gently curved downwards (Fig. 20A–J).

Remarks. The type male (Fig. 17A) is very delicate and in poor condition, and appears to have dried up at some stage. The gonopods are still present, although not in a good state. The lateral and branchial spines of the type are relatively stouter (Fig. 17A) compared to the other specimens we have examined from Japan, Taiwan and Philippines (Fig. 17B, C), but this is probably due to variation. The G1 drawn by T. Sakai (1969: text-fig. 5b) (present Fig. 20A, B) appears to have been drawn in situ and the curvature is therefore less strong compared to that when drawn ex-situ (Fig. 20C, D). The subdistal process observed seems to have dried up previously and looks folded, unlike the original condition

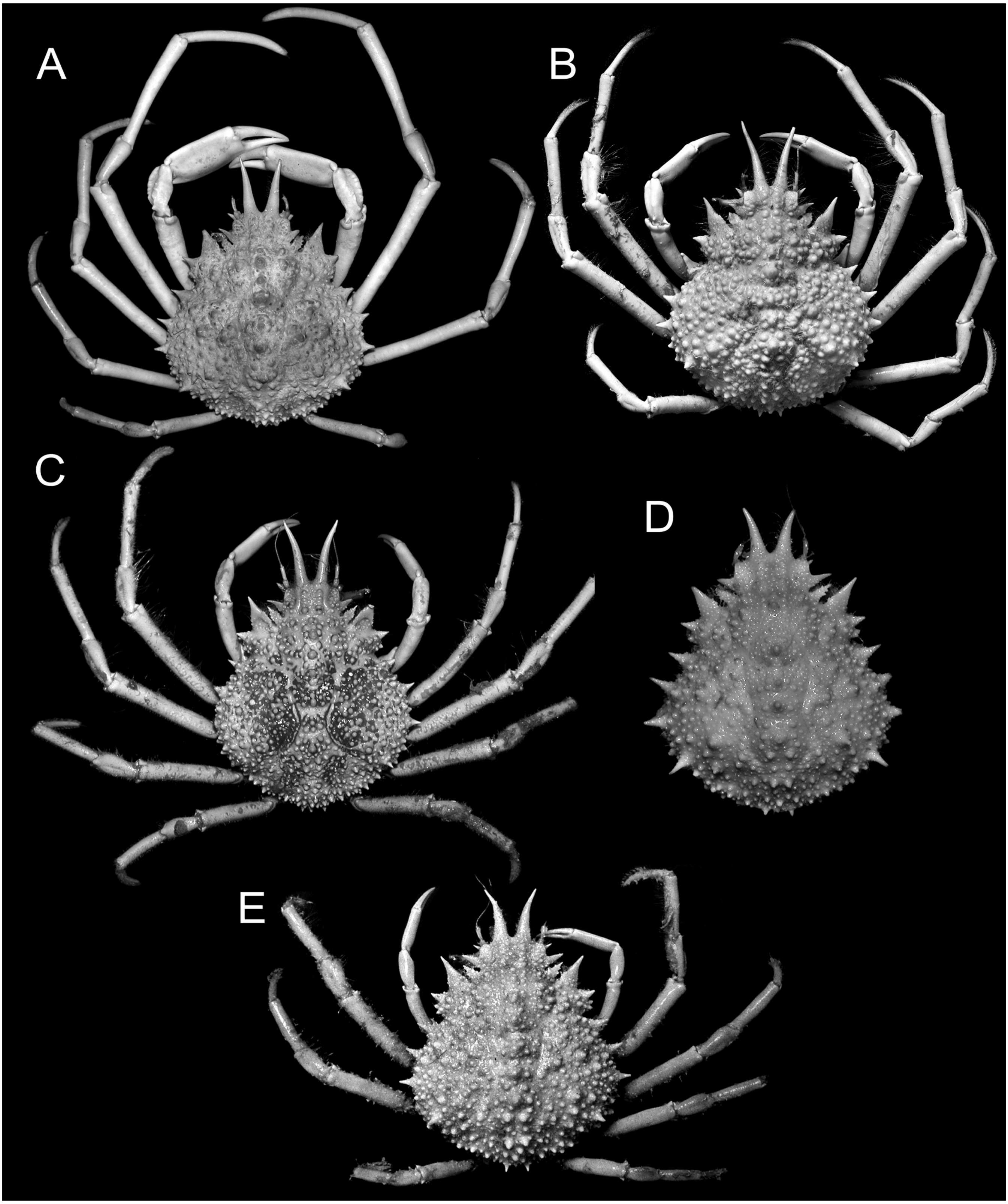

Fig. 16. General habitus, *Alcomaja* species. A, *A. irrorata* n. sp., holotype male (52.6 × 45.7 mm) (NMCR), Philippines; B, *A. gracilipes*, holotype male (45.4 × 43.5 mm) (IOCAS K33B-34), South China Sea; C, *A. gracilipes*, male (41.4 × 35.4 mm) (ZRC 2013.1225), Philippines; D, *A. confragosa*, female (21.5 × 18.2 mm) (NMV J53978), Australia; E, *A. confragosa*, holotype male (as *Maja confragosa*, after Griffin & Tranter 1986: pl. 16a).

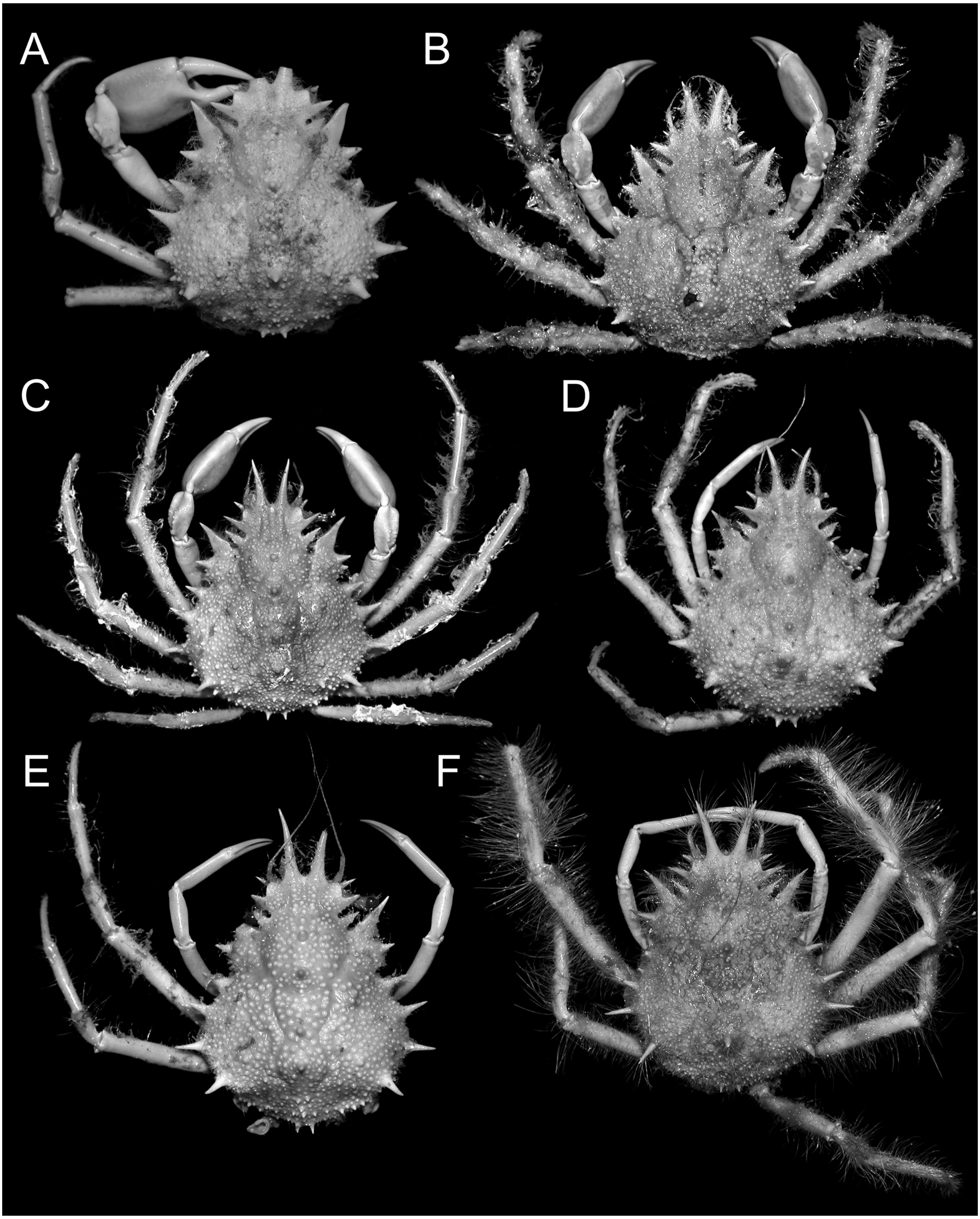

Fig. 17. General habitus, *Alcomaja* species. A, *A. nagashimaensis*, holotype male (34.0 × 28.5 mm) (USNM 125886), Japan; B, *A. nagashimaensis*, male (37.2 × 32.4 mm) (CBM-ZC9928), Japan; C, *A. nagashimaensis*, male (30.5 × 26.0 mm) (ZRC 2001.430), Japan; D, *A. latens* n. sp., holotype male (25.3 × 21.4 mm) (MNHN-IU-2013-4050), Solomon Islands; E, *A. miriky* n. sp., holotype male (26.4 × 20.9 mm) (MNHN-IU-2010-929), Madagascar; F, *A. desmondi* n. sp., holotype male (35.4 × 28.3 mm) (NMCR), Philippines.

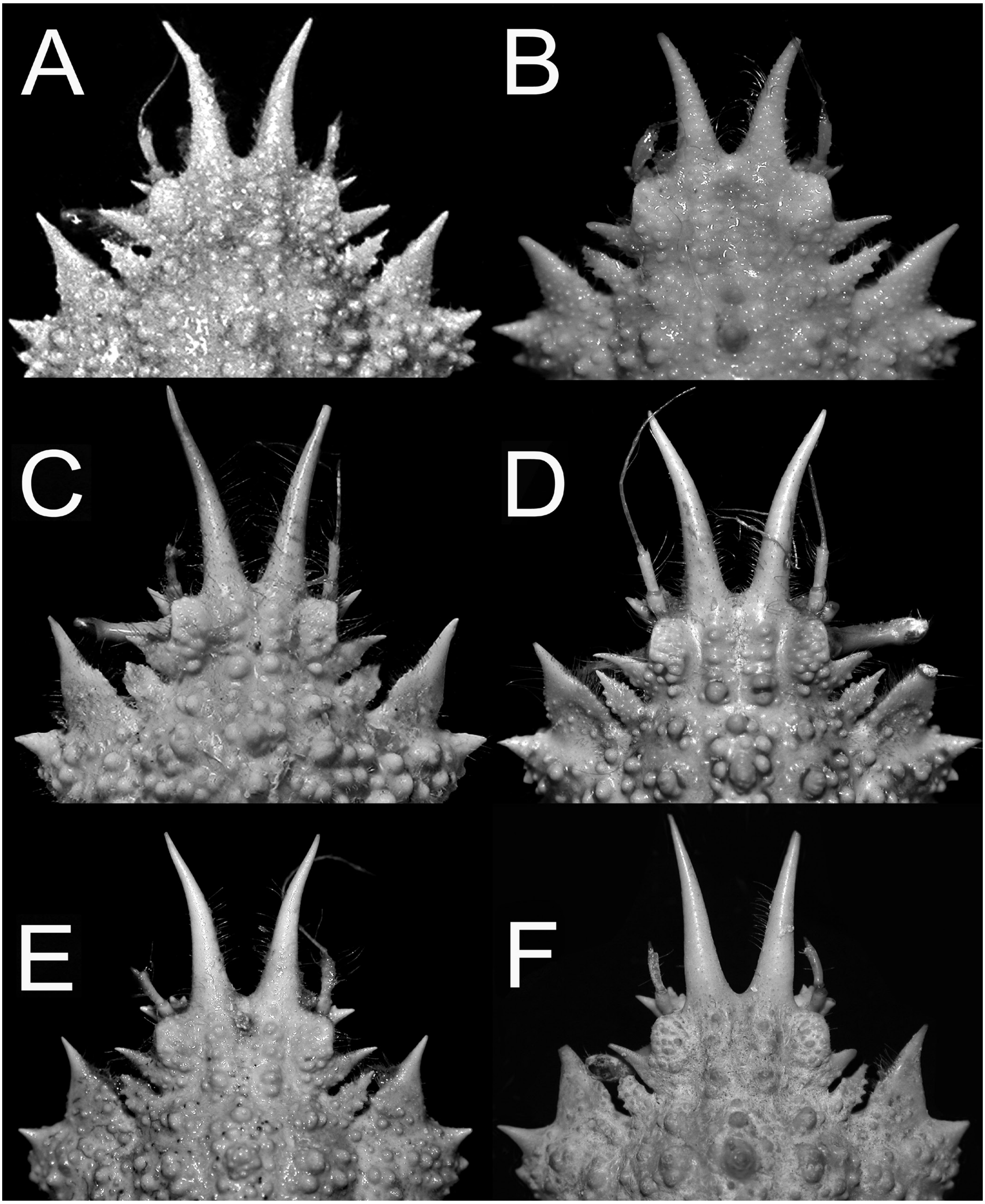

Fig. 18. Frontal regions of carapace showing different structures of intercalated teeth, *Alcomaja* species. A, *A. confragosa*, holotype male (as *Maja confragosa*, after Griffin & Tranter, 1986: pl. 16a); B, *A. confragosa*, female (21.5 × 18.2 mm) (NMV J53978), Australia; C, *A. gracilipes*, holotype male (45.4 × 43.5 mm) (IOCAS K33B-34), South China Sea; D, *A. gracilipes*, male (41.4 × 35.4 mm) (ZRC 2013.1225), Philippines; E, *A. irrorata* n. sp., paratype male (44.7 × 39.1 mm) (ZRC 2013.1229), Philippines; F, *A. irrorata* n. sp., holotype male (52.6 × 45.7 mm) (NMCR), Philippines.

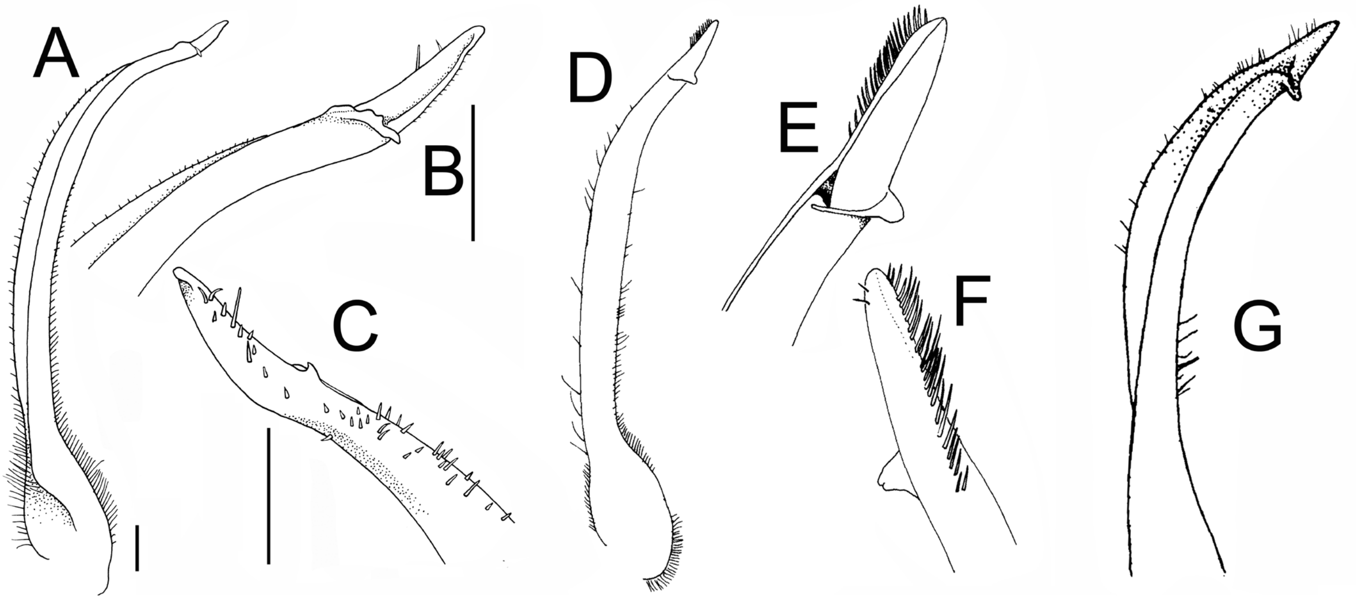

Fig. 19. Left G1s, *Alcomaja* species. A–C, *A. irrorata* n. sp., holotype male (52.6 × 45.7 mm) (NMCR), Philippines; D–F, *A. gracilipes*, holotype male (45.4 × 43.5 mm) (IOCAS K33B-34), South China Sea; G, *A. confragosa* (as *Maja confragosa*, after Griffin & Tranter, 1986: fig. 73a). Scale bars = 1.0 mm [A–C].

figured (T. Sakai, 1969: text-fig. 5b') which is more similar to that in the fresh material on hand. In any case, the shape and structure (Fig. 20C, D) agrees well with the G1s from Philippines and Taiwan and we have no doubt they are conspecific.

The chelae are only enlarged in larger males. Smaller males about 20 mm or less in carapace length (e.g., ZRC 2013.1391) have slender chelae.

Maja nagashimaensis was described from Japan, with Serène & Vadon (1981) reporting this species from the Philippines, and Griffin & Tranter (1986) recording it from the Sulu Islands in the Philippines. It is now also recorded from Taiwan.

Alcomaja latens n. sp.

(Figs. 17D, 20K–N, 36N, 45G, 49F)

Material examined. Holotype: male (25.3 × 21.4 mm) (MNHN-IU-2013-4050), station DW 2190, 8°24'S 159°27'E, 140–263 m, Solomon Islands, coll. RV *Alis*, SALOMON 2, 24 October 2004.

Diagnosis. Carapace pyriform; dorsal surface of carapace and ambulatory legs covered with short, hooked setae; with small rounded granules (Fig. 17D). Pseudorostral spines with rounded cross-section (Fig. 36N). Antorbital spine almost straight; intercalated spine subtruncate basally; postocular spine strong, pointing anteriorly and outwards; 1 distinct hepatic spine with small basal spine (Fig. 36N). Lateral and branchial spines strong in juveniles and adults (Fig. 17D). Subhepatic region with rugose and weakly granulated surface. Basal antennal article with low granules and 2 tubercles, with 2 distal spines. Ischium of third maxilliped almost smooth to slightly rugose (Fig. 45G). Ambulatory legs relatively short, first leg never twice length of carapace; surfaces distinctly setose (Fig. 17D). G1 gently curved, with distal part gently curved upwards (Fig. 20K–N).

Etymology. The name is derived from the Latin for "hidden", alluding to a general absence of external characters to separate the new species from *A. nagashimaensis*.

Remarks. *Alcomaja latens* n. sp. is very close to *A. nagashimaensis* (T. Sakai, 1969) and the two species can only be effectively separated by the form of the G1. In *Alcomaja latens*, the dorsal part is gently bent upwards (Fig. 20K–N) while in *A. nagashimaensis*, it is gently curved downwards (Fig. 20A–J). At around the same size as the holotype of *A. latens*, a male specimen of *A. nagashimaensis* already has distinctly inflated chelipeds.

Alcomaja miriky n. sp.

(Figs. 17E, 20O–Q, 36O, 45H, 49G, 69B)

Material examined. Holotype male (26.4 × 20.9 mm) (MNHN-IU-2010-929), station DW 3215, 12°32'S 47°54'E, 314–433 m, Madagascar, coll. MIRIKY, 30 June 2009. Paratype: **Madagascar** – 1 male (17.3 × 12.7 mm) (ZRC 2013.1409, ex MNHN-IU-2010-60), station CP 3284, 14°51'S 46°59'E, 236–297 m, coll. MIRIKY, 13 July 2009.

Diagnosis. Carapace elongated, pyriform; dorsal surface of carapace and ambulatory legs covered with short, hooked setae; with small rounded granules (Fig. 17E). Pseudorostral spines relatively long, curved, with rounded cross-section (Fig. 36O). Antorbital spine almost straight; intercalated spine acutely triangular; postocular spine very long; 1 distinct hepatic spine (Fig. 36O). Lateral and branchial spines strong in juveniles and adults (Fig. 17E). Subhepatic region with rugose, weakly granulated surface. Basal antennal article

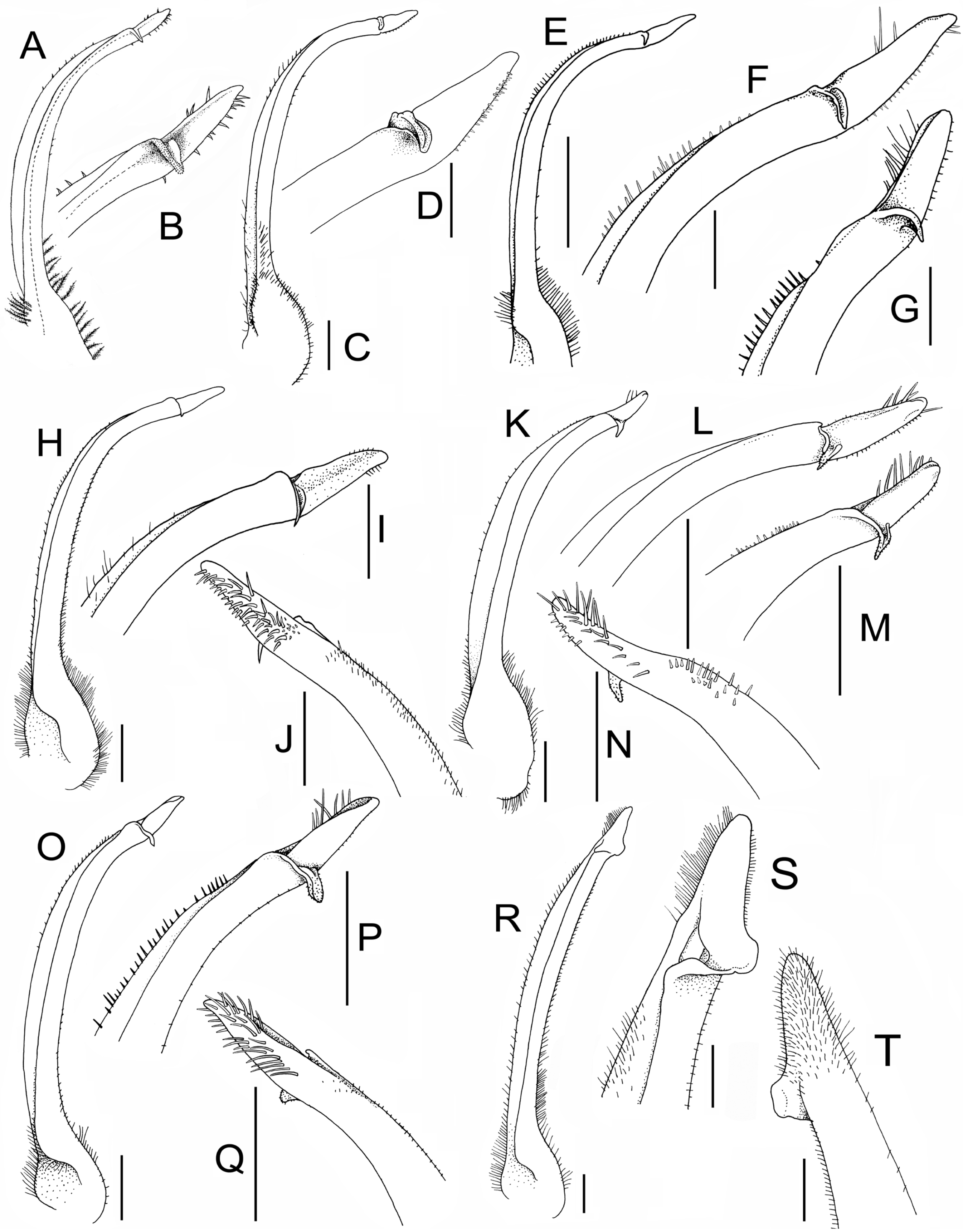

Fig. 20. Left G1s, *Alcomaja* species. A, B, *A. nagashimaensis* (as *Maja nagashimaensis*, after T. Sakai, 1976: text-fig. 129); C, D, *A. nagashimaensis*, holotype male (34.0 × 28.5 mm) (USNM 125886), Japan; E–G, *A. nagashimaensis*, male (37.2 × 32.4 mm) (CBM-ZC9928), Japan; H–J, *A. nagashimaensis*, male (30.5 × 26.0 mm) (ZRC 2001.430), Philippines; K–N, *A. latens* n. sp., holotype male (25.3 × 21.4 mm) (MNHN-IU-2013-4050), Solomon Islands; O–Q, *A. miriky* n. sp., holotype male (26.4 × 20.9 mm) (MNHN-IU-2010-929), Madagascar; R–T, *A. desmondi* n. sp., holotype male (35.4 × 28.3 mm) (NMCR), Philippines. Scale bars = 1.0 mm [H, K–R]; 2.0 mm [E]; 0.5 mm [C, F, G, I, J, S, T]; 0.25 mm [D].

with low granules and 2 tubercles, with 2 relatively long distal spines. Ischium of third maxilliped almost smooth to slightly rugose (Fig. 45H). Ambulatory legs relatively short, first leg never twice length of carapace; surfaces distinctly setose (Fig. 17E). G1 gently curved with distal part gently curved downwards (Fig. 20O–Q).

Etymology. The species is named after the cruise that collected it, MIRIKY. The name is used as a noun in apposition.

Remarks. *Alcomaja miriky* n. sp. is very close to *A. nagashimaensis* (T. Sakai, 1969). The main differences are as follow: the G1 of *A. miriky* is prominently less curved (Fig. 20O–Q versus Fig. 20A–J); the distal spines of the basal antennal article in *A. miriky* are relatively longer and sharper; the overall carapace is proportionately longer (Fig. 17E versus Fig. 17A–C); there is only one hepatic spine in *A. miriky* versus two in *A. nagashimaensis* (Figs. 17E, 36O versus Figs. 17A–C, 36M); there is one accessory spine on the postorbital spine in *A. miriky* which is absent in *A. nagashimaensis* (Figs. 17E, 36O versus Figs. 17A–C, 36M); and the pseudorostral spines of *A. miriky* are relatively longer and more curved (Figs. 17E, 36O versus Figs. 17A–C, 36M).

Alcomaja desmondi n. sp.

(Figs. 17F, 20R–T, 36L, 39N, 45D, 49H, 52F, 53O, 55M)

Material examined. Holotype: male (35.4 × 28.3 mm (NMCR), Balicasag Island, Panglao, Bohol, Philippines, 200–300 m, coll. local fishermen with tangle nets, June 2002. Paratypes: **Philippines** – 2 males (36.6 × 31.7 mm, 27.1 × 23.5 mm) (ZRC 2013.1273), same data as holotype. — 2 males (27.7 × 21.3 mm, 36.6 × 29.1 mm), 1 ovigerous female (38.0 × 32.6 mm) (ZRC 2001.0588), Balicasag Island, Panglao, Bohol, 50–500 m, coll. local fishermen with tangle nets, 28 November 2001. — 1 ovigerous female (37.6 × 32.0 mm) (NSMT-Cr 22328), Balicasag Island, Panglao, Bohol, coll. local fisherman via M. Takeda & H. Komatsu, February 2003.

Diagnosis. Carapace pyriform; dorsal surface of carapace densely covered with long, stiff setae; with small rounded granules (Fig. 17F). Pseudorostral spines with rounded cross-section (Fig. 36L). Antorbital spine strong, curved upwards, appears straight from dorsal view; intercalated spine acutely triangular; postorbital spine very long (Fig. 36L). Lateral and branchial spines strong in juveniles and adults; 3 spines on median row: 2 gastric, 1 cardiac; 2 distinct spines on posterior carapace margin (Fig. 17F). Subhepatic region with numerous very small rounded granules on surface (Fig. 39N). Basal antennal article with numerous granules (Fig. 39N). Ischium of third maxilliped almost smooth to slightly rugose (Fig. 45D). Ambulatory legs relatively short, first leg never twice length of carapace; surfaces strongly setose, covered with long coarse setae (Figs. 17F, 55M). G1 almost straight with distinct ventral fold (Fig. 20R–T).

Etymology. The name is formed to honor Desmond Griffin, a carcinologist who devoted a large part of his life to the taxonomy of Indo-West Pacific majoid crabs.

Remarks. *Alcomaja desmondi* n. sp. superficially resembles *Holthuija suluensis* (Rathbun, 1916), in general shape, especially since both species have strong lateral and branchial spines as well as two gastric spines on the carapace. Excluding the generic level differences, *A. desmondi* has a more rounded carapace, especially on the branchial regions; the pseudorostral spines are more diverging in *Holthuija suluensis;* the first gastric spine is placed more anteriorly in *A. desmondi*; the antorbital spine is straight and directed outwards in *A. desmondi* (versus curved and directed anteriorly in *H. suluensis*), and the setae covering the ambulatory legs in *A. desmondi* are longer and stiffer compared to *H. suluensis*.

Within *Alcomaja*, *A. desmondi* stands out in several features. It is unique among members of the genus in possessing long stiff setae covering its carapace and legs; and the G1 structure is atypical, being almost straight, much stouter with an unusually broad ventral flap (Fig. 20R–T). Since the rest of its characters agree with *Alcomaja* as presently defined, it seems best to leave it in this genus for the time being

The dense stiff setae on the specimens of *A. desmondi* from Balicasag trap a thick layer of silicate sponge spicules, which makes their handling very difficult. It appears to be a species living in the deep sea on the deep steep rocky slopes of Balicasag Island at depths exceeding 300 m.

Paramaya De Haan, 1837

Maja (*Paramaya*) De Haan, 1837: pl. 24, fig. 4.
Maja (*Paramaya*) – De Haan, 1837: errata.
Paramaya – Rathbun, 1905: 73.
Maja – T. Sakai, 1938: 296 (part). – T. Sakai, 1965: 83 (part). (not *Maja* Lamarck, 1801).

Diagnosis. Carapace ovate; dorsal surface convex, covered by granules or tubercles; gastric and branchial regions distinct, clearly delimited by distinct grooves (Figs. 21, 22A–C). Intestinal region with long, distinct median spine (Figs. 21, 22A–C). Pseudorostral spines very long, diverging (Figs. 21, 22A–C, 37A–C). Supraorbital eave with anterior part longitudinally narrow, rectangular, not prominently expanded; antorbital spine sharp (Fig. 37A–C). Intercalated spine distinct, separated from supraorbital eave and postorbital spine by wide gaps; postorbital spine strong; hepatic region with 1 strong spine, slightly shorter or longer than postorbital spine; 1 smaller spine below (Fig. 37A–C). Lateral carapace margin with 3 long spines and numerous granules and spinules, branchial region with 3, sometimes 4 spines (Figs. 21, 22A–C). Posterior carapace margin with 2 long median spines (Figs. 21, 22A–C). Eyes relatively long, slender, with ovoid cornea (Fig. 37A–C). Antennal flagellum short, slender. Basal antennal article longer than broad, rectangular; surface with several low tubercles, with 2 spines distally; inner and outer lateral margins smooth to uneven; proximal outer angle acute, may be produced into spine; antero-external crested rim of antennular fossa overlaps distal part of basal antennal article by about a third of its width, forming hook-like structure (Fig. 40A–C). Epistome rectangular, longer than broad, anterior margin with 2 tubercles; posterior margin composed of 4 rectangular plates separated by shallow fissures (Figs. 40A–C, 42A, B). Suborbital margin separated from basal antennal article by U-shaped cleft, separated from margin of postorbital tooth by deep fissure (Fig. 40A–C). Outer surface of third maxilliped covered by setae; ischium subrectangular, longer than broad; postero-external angle of merus very narrow, elongate, "inserted" into deep concavity on outer margin of ischium; antero-internal part of ischium acutely triangular (Fig. 45I–L). Male chelipeds relatively long in adult males, surfaces of merus and carpus almost smooth; carpus elongate; propodus of palm elongated, may be inflated, curved, smooth, may have lateral cristae, palm longer than fingers (Fig. 54A, C); fingers long, slender, almost straight to gently curved, with or without distinct basal gape when closed (Figs. 21, 22A–C, 54A–C). Ambulatory legs relatively long, slender; merus with long dorsal subdistal spine; dactylus elongate, curved, covered with long setae except for corneous tip (Figs. 6G, 21, 22A–C, 56A, B). Thoracic sternum longer than wide; surfaces of somites 5–8 with small granules; sternites 3 and 4 distinctly depressed; margin between sternites 2 and 3 demarcated by deep cleft; anterior margin of sterno-abdominal cavity not forming complete rim (Figs. 50A–C, 52H). Male abdomen subtriangular, with 6 free somites and telson; somites 3 and 4 wider than somites 5, 6 and telson (Fig. 50A–C). Male press-button abdominal locking mechanism submedian in position on sterno-abdominal cavity (Fig. 52H). Female abdomen dome-shaped, covering most of thoracic sternum. G1 very long, slender, gently curved; distal part with rounded tip, dorsal part folding upwards to form distinct dorsal projection, with scattered very short setae (Fig. 23).

Type species. *Maja* (*Maja*) *spinigera* De Haan, 1837, by monotypy.

Remarks. The genus *Paramaya* was established by De Haan (1837: 24) to accommodate *Maja* (*Maja*) *spinigera*. As discussed earlier (see remarks for *Maja*), the name is available even though it is very similar in spelling to *Paramaja* Kubo, 1936. In the present study, we add two new species to *Paramaya*, *P. ouch* n. sp. from the Philippines and *P. coccinea* n. sp. from Vanuatu.

Members of *Paramaya* are distinctive with their very long carapace spines, elongate epistome and spinose ambulatory meri, and cannot be confused with any other genus. The carapaces of most of the *Paramaya* specimens examined were not extensively covered with animals or debris, and species generally only have sparse stiff setae on their bodies. Their ambulatory legs, however, are densely covered with long stiff setae and these often trap debris.

White (1847: 7) recognised a new species: "PARAMAYA Dehaanii, n. s." but did not provide any data or description. His name is a nomen nudum and is not possible to identify at the moment.

Key to species of *Paramaya* De Haan, 1837

1. Pseudorostral horns relatively short; ambulatory meri in adults relatively stout, short (Fig. 21A–D); G1 gently curved (Fig. 23A–C); Japan and Taiwan .... *Paramaya spinigera* (De Haan, 1837)
– Pseudorostral horns very long; ambulatory meri in adults relatively slender, long (Figs. 21E, F, 22A); G1 otherwise ..2

2. Surface of thoracic sternum relatively smooth, with very low rounded granules (Fig. 50C); G1 gently curved (Fig. 23G–I); Vanuatu... *Paramaya coccinea* n. sp.
– Surface of thoracic sternum distinctly granulated (Fig. 50B); G1 more strongly curved especially distally (Fig. 23D–F); Philippines ....*Paramaya ouch* n. sp.

Paramaya spinigera (De Haan, 1837)
(Figs. 6G, 21A–D, 23A–C, 37A, 40A, 42A, 45I, 50A, 52H, 54A, 56A)

Maja (*Maja*) *spinigera* De Haan, 1837: 93.
Maja (*Paramaya*) *spinigera* – De Haan, 1837: errata.
Maja (*Paramaya*) *spinigera* – De Haan, 1837: pl. 24, fig. 4.
Maia spinigera – Adams & White, 1848: 15. – Parisi, 1915: 289.
Maja spinigera – Ortmann, 1893: 51. – Doflein, 1902: 656. – Ninni, 1924: 47, un-numbered figure on p. 48. – Balss, 1924: 34. – T. Sakai, 1934: 297. – T. Sakai, 1936: 98, pl. 25, fig. 3. – T. Sakai, 1938: 397, pl. 30, fig. 1. – T. Sakai, 1965: 84, pl. 38. – Serène, 1968: 57. – Utinomi, 1969: 77, pl. 39-3. – Holthuis & T. Sakai, 1970: 121, pl. 14. – Nishimura & Suzuki, 1971: 109, pl. 38-2. – Serène & Lohavanijaya, 1973: 50 (key). – Takeda, 1975: 127. – T. Sakai, 1976: 237, pl. 83. – Matsuzawa, 1977: pl. 96 fig. 4. – Takeda, 1982: 128. – Miyake, 1983: 43, pl. 14 fig. 4. – Dai et al., 1986: 136, pl. 18(3). – Matsuda et al., 1986: 130. – Dai & Yang, 1991: 151, pl. 18(3). – Yamaguchi & Baba, 1993: 359, Fig. 116. – Takeda, 1993: 43. – Huang, 1994: 582. – Muraoka & Odawara, 1995: 34. – Muraoka, 1998: 27. – Minemizu, 2000: 216. – Takeda et al., 2000: 139. – Ng et al., 2001: 12. – Maramura & Kosaka, 2003: 34. – Takeda & Ueshima, 2006: 74. – Yang et al., 2008: 780. – Ng et al., 2008: 117 (list).

Material examined. Japan – 1 female (NSMT 5999), Kii-Nagashima, Kaino, Mie Prefecture, coll. M. Saba, 1970s. — 1 carapace only (NSMT 7614), Kii-Nagashima, Kaino, Mie Prefecture, coll. M. Saba, 16 December 1976. — 1 male, 1 female (NSMT 5967), Kii-Nagashima, Kainoura, Mie Prefecture, coll. M. Saba, 1970s. — 1 male (NSMT 6134), Kii-Nagashima, Kainoura, Mie Prefecture, in lobster gill-nets, coll. M. Saba, 25 February 1979. — 1 male (NSMT 10178), Kii-Nagashima, Kaino, Mie Prefecture, coll. M. Saba, 18 December 1978. — 1 female (SMF 47734), Toba, Mie Prefecture, coll. N. Yamashita, 1983. — 1 male, 1 female (SMF 9289), Toba, Mie Prefecture, coll. Nakamura, May 1980. — 1 male (NSMT 6032), Kii-Nagashima, Mie Prefecture, coll. M. Saba, 1970s. — 1 male (NSMT 6752), Kii-Nagashima, Mie Prefecture, coll. M. Saba, 1970s. — 1 female (NHM 1961.11.13.7/9, part), Seto, Shirahama, Japan, coll. I. Gordon. — 1 male, 1 female (NHM 1961.11.13.7/9, part), Seto, Shirahama, Japan, coll. I. Gordon. — 1 male

(64.7 × 51.2 mm) (NHM 1961.6.5.117), Tosa Bay, coll. K. Sakai, April 1961. — 1 male (USNM 18854), Miura, Atami Province, Yokaito coast, Japan, from Mr Sakamoto, from Garrett Droppers. — 1 male (SMF 30766), Katahara, Aichi, 80–150 m, coll. N. Akashi, 1978-1983. — 1 male, 1 female (SMF 7627), Kii Peninsula, coll. K. Sakai. — 2 males, 4 females, 1 ovigerous female (SMF 46532), Kii Minabe, 33°44.944'N 135°19.65'E, coll. K. Sakai, 15 February 1983. — 1 male (SMF 47732), Shikoku, Usa, Ikenoura, Kochi Prefecture, coll. K. Sakai, 18 October 1984. — 1 female (SMF 47747), None, Cape Muroto, Kochi Prefecture, ca. 33°26.617'N 134°16.75'E, coll. K. Matsuzawa, 20 January 1993. — 1 ovigerous female (SMF 47746), Mitsu, Kochi Prefecture, 33°16.6'N 134°10.6'E, coll. 9 February 1974. — 1 ovigerous female (SMF 47748), Mitsu, Kochi Prefecture, 33°16.6'N 134°10.6'E, coll. 13 December 1994. — 1 male (SMF 47757), Mitsu, Muroto City, Kochi Prefecture, 33°16.6'N 134°10.6'E, no other data. — 1 female (SMF 47741), Tokushima, Shikoku, Tsubakidomari, Anan, Kochi Prefecture, 33°51.678'N 134°43.603'E, coll. T. Nakano, 18 April 1983. — 1 female (SMF), Minabe, Wakayama Prefecture, coll. K. Sakai, 18 February 1984. — 1 male (SMF), Minabe, Wakayama Prefecture, T. Sakai Collection. — 1 female (SMF 47742), Honshu, Wakayama Prefecture, Kii Mimase, coll. K. Sakai, 1 March 1988. — 1 male (NSMT 15905), no other data. — 1 dried female (70.1 × 58.8 mm) (KPM NH4195), T. Sakai Collection. — 1 juvenile female (USNM 48486), station 4880, eastern channel of Korean Straits, vicinity of Ohi-Shima, 59 fathoms, coll. RV *Albatross*, 2 August 1906. **Taiwan** – 7 males (85.0 × 66.4 mm, 78.2 × 62.1 mm, 73.6 × 55.3 mm, 68.3 × 53.4 mm, 73.8 × 58.4 mm, 62.8 × 49.0 mm, 72.8 × 57.3 mm), 1 ovigerous female (63.0 × 48.6 mm) (ZRC 1999.738), Longtong, near Keelung, northern Taiwan, in tangle nets for lobsters, coll. S.-H. Wu, May 1999.

Diagnosis. Pseudorostral horns relatively short (Fig. 21A–D). Hepatic, lateral and branchial spines long; median row with 5 spines: 3 gastric, 1 cardiac, 1 intestinal; 2 strong spines on posterior carapace margin (Fig. 21A–D). Surface of thoracic sternum relatively smooth, with very low rounded granules (Fig. 50A). Chela of adult male with distinct carina on dorsal and ventral margins (Fig. 54A). Ambulatory meri in adults relatively stout, short (Fig. 21A–D). G1 gently curved (Fig. 23A–C).

Remarks. Yamaguchi & Baba (1993: 359) recorded two syntype female specimens (87.4 × 72.9 mm, 76.9 × 66.4 mm) in RMNH and selected the larger one as lectotype. The excellent figures in De Haan (1837: pl. 24, fig. 4) and Yamaguchi & Baba (1993: fig. 116) leave no doubt that the present specimens from Taiwan are conspecific with *Paramaya spinigera* s. str.

Alcock (1895: 239) and Alcock & Anderson (1898: pl. 34, fig. 3) recorded "*Maia spinigera*" from a specimen from off Beluchistan (Pakistan) in the Indian Ocean (sex and size not mentioned) (Fig. 22C, D). We also have a photograph of a large specimen (not preserved) collected from Sri Lanka in deeper waters off a reef by aquarium collectors (Fig. 22B). The specimen was collected with a number of other relatively deeper reef animals at night (see Ng, 1994). Alcock's (1895) and Alcock & Anderson's (1898) specimen has relatively short ambulatory legs (notably the merus), suggesting it is unlikely to be real *Paramaya spinigera* (or either of the new species) as presently defined. However, this may be a consequence of its apparently small size (judging by the figure). The specimen is not in the NHM and is probably still in the Indian Museum (present day Zoological Survey of India). The larger specimen photographed from Sri Lanka has proportionately longer legs and a spiny carapace, not unlike *P. coccinea* n. sp. and *P. ouch* n. sp., although on the basis of geography, they are probably different species. For the moment, we do not know their precise identities.

Paramaya ouch n. sp.

(Figs. 1B, 2D, 21E, F, 23D–F, 37B, 40B, 45J, K, 50B, 54B, 70A)

Material examined. Holotype: male (76.8 × 60.0 mm) (NMCR), Balicasag Island, Panglao, Bohol, Philippines, coll. local fishermen in tangle nets, July 2003. Paratypes: **Philippines** – 2 ovigerous females (75.1 × 58.0 mm, 63.2 × 49.3 mm) (ZRC 2013.1312), same data as holotype. — 1 male (NSMT-Cr 16646), Balicasag Island, Panglao, Bohol, coll. local fisherman via T. Kase, 6–10 March 1999. — 2 males, 1 female (NSMT-Cr 15391), Balicasag Island, Panglao, Bohol, coll. local fisherman via T. Kase, 6–10 March 1999. — 2 young females (19.0 × 13.7 mm, 28.0 × 20.6 mm) (ZRC 2013.1282, ex part ZRC 2001.0411), Balicasag Island, Panglao, Bohol, coll. fishermen in tangle nets, December 2000. — 3 males (largest 76.5 × 61.3 mm, one smaller male with rhizocephalan), 2 ovigerous females (larger 60.6 × 74.1 mm), 3 females (ZRC 2001.0577), Balicasag Island, Panglao, Bohol, 200–300 m, coll. fishermen in tangle nets, 28 November 2001. — 4 males (65.0 × 50.4 mm, 53.3 × 40.1 mm, 69.0 × 52.9 mm, 70.7 × 51.7 mm [with rhizocephala], 1 ovigerous female (64.9 × 51.8 mm), 3 ovigerous females (with rhizocephalan) (56.9 × 40.9 mm, 68.9 × 53.5 mm, 58.7 × 42.5 mm), 1 young female (30.0 × 22.5 mm) (ZRC 2013.1187), Balicasag Island, Panglao, Bohol, 200–300 m, coll. fishermen in tangle nets, June 2002. — 1 juvenile male (2013.1313), Balicasag Island, Panglao, Bohol, 200–300 m, coll. fishermen with tangle nets, June 2002. — 1 male (56.1 × 40.5 mm), 1 female (47.7 × 36.1 mm) (AM, ex ZRC 2001.0374), Balicasag Island, Panglao, Bohol, 200–300 m, coll. fishermen in tangle nets, December 2000. — 1 female (46.5 × 36.9 mm) (ZRC 2013.1299), Balicasag Island, Panglao, Bohol, coll. fisherman with tangle nets, 25 October 2003. — 4 males (54.5 × 42.1 mm, 71.4 × 56.5 mm, 75.8 × 62.0 mm, 48.7 × 36.8 mm), 4 females (55.0 × 43.0 mm, 66.5 × 52.5 mm, 57.6 × 44.5 mm, 65.5 × 50.8 mm) (ZRC 2012.1207), Balicasag, Panglao, Bohol, 200–300 m, coll. local fishermen with tangle nets, November 2003 – May 2004. — 1 male (32.7 × 25.2 mm) (ZRC 2013.1283), Balicasag Island, Panglao, Bohol, coll. fisherman with tangle nets, February 2004. — 1 female (42.6 × 34.5 mm) (ZRC 2013.1300), Balicasag Island, Panglao, Bohol, coll. fisherman with tangle nets, May 2004. — 1 male (33.0 × 26.1 mm) (ZRC 2013.1298), station PN 1, Balicasag Island, Panglao,

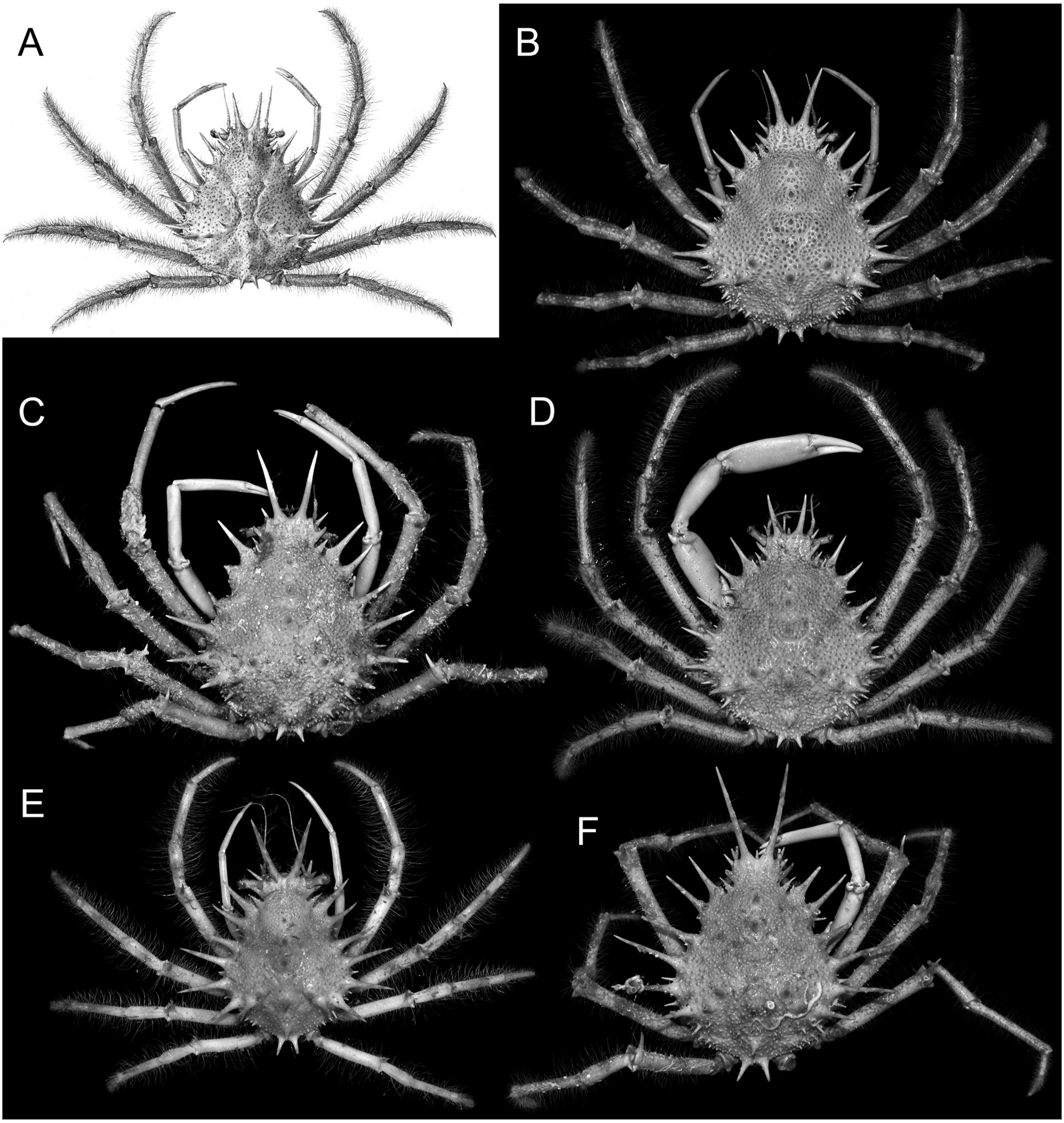

Fig. 21. General habitus, *Paramaya* species. A, *P. spinigera* (as *Maja* (*Paramaya*) *spinigera*, after De Haan, 1837: pl. 24, fig. 4); B, *P. spinigera*, dried female (70.1 × 58.8 mm) (KPM NH4195), Japan; C, *P. spinigera*, male (64.7 × 51.2 mm) (NHM 1961.6.5.117), Japan; D, *P. spinigera*, male (85.0 × 66.4 mm) (ZRC 1999.738), Taiwan; E, *P. ouch* n. sp., paratype male (39.7 × 29.6 mm) (ZRC 2011.0045), Philippines; F, *P. ouch* n. sp., holotype male (76.8 × 60.0 mm) (NMCR), Philippines.

Bohol, 200–300 m, coll. fishermen with tangle nets, January 2004. — 1 young female (ZRC 2013.1281), Balicasag Island, Panglao, Bohol, 200–300 m, coll. fishermen with tangle nets, February 2004. — 1 female (53.3 × 43.4 mm) (ZRC 2013.1305), station PN1, Balicasag Island, Panglao, Bohol, 200–300 m, coll. fishermen with tangle nets, 28 May 2004. — 1 female (53.3 × 43.4 mm) (ZRC 2013.1305), station PN 1, Balicasag Island, Panglao, Bohol, 200–300 m, coll. fishermen with tangle nets, 28 May 2004. — 2 males (37.2 × 29.3 mm, 50.3 × 38.5 mm [damaged]), 1 female (62.7 × 52.0 mm) (ZRC 2013.1306), station P4, Balicasag Island, Panglao, Bohol, 200–300 m, coll. fishermen with tangle nets, 4 June 2004. — 1 male (65.0 × 50.6 mm), 1 female (70.0 × 54.6 mm), 2 ovigerous females (69.4 × 53.6 mm, 71.2 × 56.5 mm) (ZRC 2012.1209), Balicasag, ca. 100 m, 9°31.1'N 123°41.5'E, Panglao, Bohol, 200–300 m, coll. local fishermen with tangle nets, coll. PANGLAO 2004, June 2004. — 1 male (69.5 × 53.7 mm), 1 female (41.5 × 30.6 mm) (ZRC 2012.1208), Maribojoc Bay, Panglao, coll. J. Arbasto, November 2003 – April 2004. — 1 ovigerous female (68.3

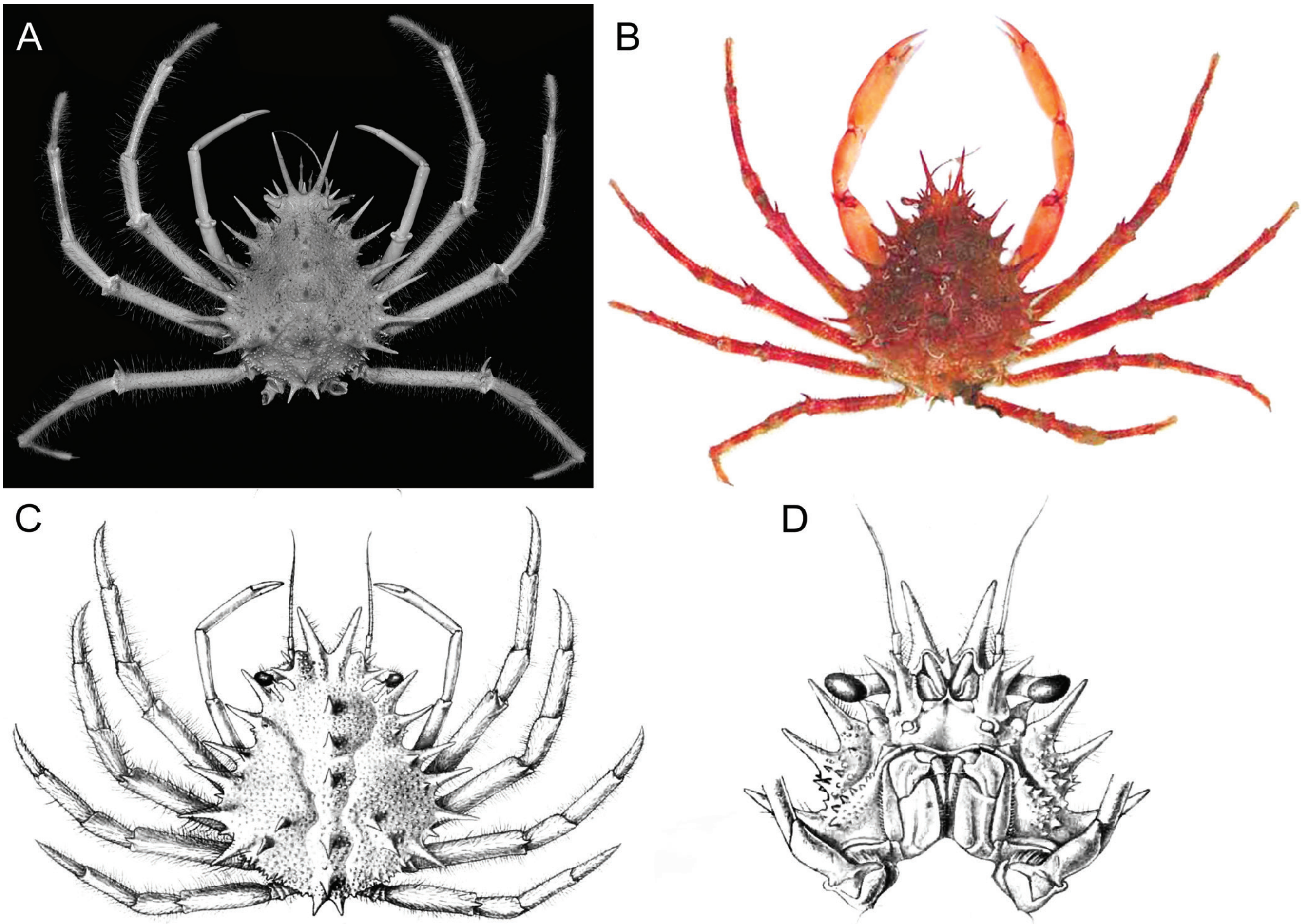

Fig. 22. General habitus. A, *Paramaya coccinea* n. sp., holotype male (69.0 × 55.6 mm) (MNHN), Vanuatu; B, "*Maja spinigera*" (ca. 70 mm carapace length), Sri Lanka, not preserved (photograph: R. Pethiyagoda); C, D, "*Maja spinigera*" (after Alcock & Anderson, 1898: pl. 34, fig. 3).

× 54.2 mm, with rhizocephala) (ZRC 2013.1317), northwest coast of Panglao, Bohol, 120–160 m, coll. J. Arbasto, tangle nets, 1 December 2007. — 1 ovigerous female (63.7 × 50.8 mm, with rhizocephala), 1 young female (56.4 × 44.1 mm) (USNM), northwest coast of Panglao, Bohol, coll. J. Arbasto, tangle nets, 2006. — 1 male (39.7 × 29.6 mm, photographed) (ZRC 2011.0045), northwest coast of Panglao, Bohol, 80–300 m, coll. J. Arbasto, January-March 2011.

Diagnosis. Pseudorostral horns very long (Fig. 21E, F). Hepatic, lateral and branchial spines very long; median row with 4 or 5 spines: 2 or 3 gastric, 1 cardiac, 1 intestinal; 2 strong spines on posterior carapace margin (Fig. 21E, F). Surface of thoracic sternum distinctly granulated (Fig. 50B). Chela of adult male slender, without distinct carina (Fig. 54B). Ambulatory meri in adults relatively slender, long (Fig. 21E, F). G1 more strongly curved especially distally (Fig. 23D–F).

Etymology. The name is derived from the old English word for jewel and ornament, alluding to the beautiful arrangement of red spines and tubercles of the species. It also indirectly alludes to the exclamation for pain, associated with careless handling of the present spiny species. Used as a noun in apposition.

Remarks. The character used in their keys by Serène & Lohavanijaya (1973), T. Sakai (1976) and Griffin & Tranter (1986) concerning a proximal tooth on the outer margin of antenna looks very variable. On some specimens there are only two branchial spines. Even on the juvenile specimens (female 28 mm carapace length, ZRC 2013.1282) the characteristics of *P. ouch* n. sp. are well marked: the pseudorostral spines are long and very divergent but less curved upward than in the adults; and the spines on the lateral margin of the carapace are very long.

Paramaya ouch is superficially similar to *P. spinigera* but can be distinguished easily by the following characters: the spines are proportionately much longer in *P. ouch* than in *P. spinigera* (Fig. 21E, F versus Fig. 21A–D); the antorbital spine is relatively shorter and not as curved as in *P. ouch* (Fig. 37B) than in *P. spinigera* (Fig. 37A); and the G1 of *P. ouch* is more distinctly curved distally (Fig. 23D–F) (versus less curved in P. *spinigera*, Fig. 23A–C).

The structure of the chela is interesting because in *P. spinigera*, the adult male chela is distinctly inflated and the margins are clearly carinated (Fig. 54A). In adult *P. ouch*, the male chela is not inflated and there is no distinct carina, although in some of the largest males, the proximal part appears to be weakly carinated (Fig. 54B). Whether the

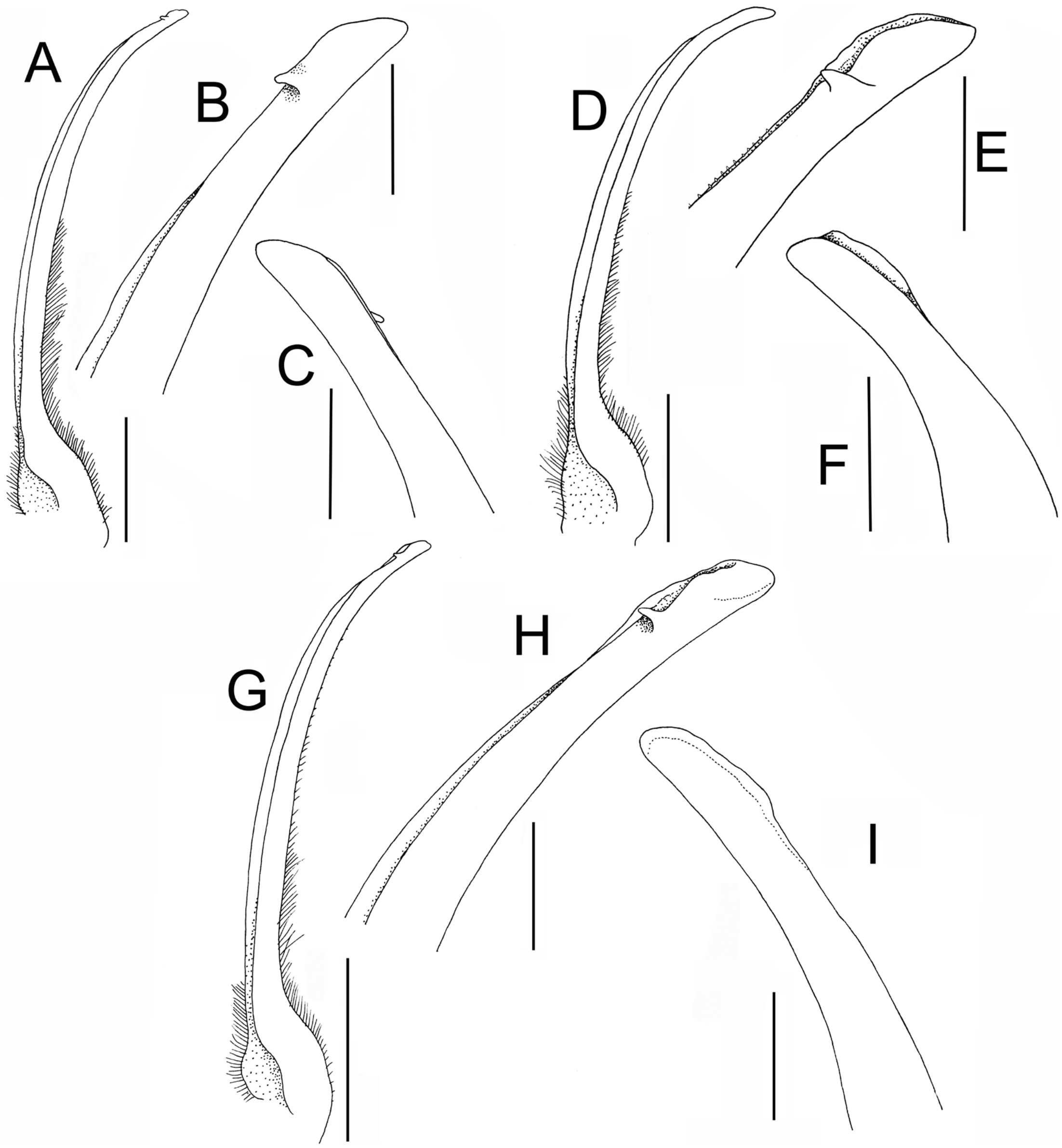

Fig. 23. Left G1s, *Paramaya* species. A–C, *P. spinigera*, male (85.0 × 66.4 mm) (ZRC 1999.738), Taiwan; D–F, *P. ouch* n. sp., holotype male (76.8 × 60.0 mm) (NMCR), Philippines; G–I, *P. coccinea* n. sp., holotype male (69.0 × 55.6 mm) (MNHN), Vanuatu. Scale bars = 5.0 mm [A, D, G]; 1.0 mm [B, C, E, F, H, I].

carina is associated with size or dominance, or is a useful species character cannot be ascertained.

Paramaya ouch is very common on the reef slopes of Balicasag Island. The large series of males, females and juveniles were useful to observe the variation of spines with size.

***Paramaya coccinea* n. sp.**
(Figs. 22A, 23G–I, 37C, 40C, 42B, 45L, 50C, 54C, 56B, 70B)

Material examined. Holotype: male (69.0 × 55.6 mm) (MNHN), northeast of Malo Island, near Santo, 201–212 m, 15°39.0'S 167°15.8'E, Vanuatu, coll. RV *Alis*, SANTO 2006, 5 October 2006.

Diagnosis. Pseudorostral horns very long (Fig. 22A). Hepatic, lateral and branchial spines very long; median row with 5 spines: 3 gastric, 1 cardiac, 1 intestinal; 2 strong spines on posterior carapace margin (Fig. 22A). Surface of thoracic sternum relatively smooth, with very low rounded granules (Fig. 50C). Chela of adult male slender, without carina (Fig. 54C). Ambulatory meri in adults relatively slender, long (Fig. 22A). G1 gently curved (Fig. 23G–I).

Etymology. The name is derived from the Latin for scarlet, alluding to the bright red colour of the species when alive.

Remarks. *Paramaya coccinea* n. sp. is close to *P. ouch* n. sp., with both species having long pseudorostral spines and very long spines on the margins of the carapace. There are several differences. The surfaces of the thoracic sternum are granular in *P. ouch* (Fig. 50B) but smooth to almost smooth in *P. coccinea* (Fig. 50C). The ambulatory legs are also longer and relatively more slender in *P. coccinea* (Fig. 22A) than in *P. spinigera* (Fig. 21A–D). The G1 of *P. coccinea* resembles that of *P. spinigera* (Figs. 23A–D, G–I), and both differ from that of *P. ouch* which is more strongly curved distally (Fig. 23D–F). The live coloration is also different: totally red in *P. coccinea* (Fig. 70B) but red and cream in *P. ouch* (Fig. 70A).

Holthuija n. gen.

Diagnosis. Carapace ovate; dorsal surface inflated, regions distinct, covered by granules or spines; gastric and branchial regions clearly delimited by grooves (Figs. 24–26). Intestinal region without median spine (Figs. 24–26). Pseudorostral spines relatively long, diverging, forming a V (Figs. 24, 25, 37D–J). Supraorbital eave large, anterior part strongly expanded, foliaceous, margin convex; spine; antorbital spine long, sharp (Fig. 37D–J). Intercalated spine distinct, separated from supraorbital eave and postorbital spine by distinct gaps; postorbital spine strong, lobiform; hepatic region with 1 strong spine, much shorter than postorbital spine; 1 tubercle below (Fig. 37D–J). Lateral carapace margin with 3 large spines, 1 branchial spine (Figs. 24, 25). Posterior carapace margin with 2 distinct median spines (Figs. 24, 25). Eyes relatively long, slender, with ovoid cornea (Fig. 37D–J). Antennal flagellum short, slender. Basal antennal article longer than broad, rectangular; surface with several tubercles, with 2 spines distally; inner and outer lateral margins with low granules; proximal outer angle rounded; antero-external crested rim of antennular fossa overlaps distal part of basal antennal article by about a third of its width (Fig. 40D–I). Epistome slightly wider than long, anterior margin with 2 low lobes and granular extension below each; posterior margin composed of 4 rectangular plates separated by shallow fissures (Figs. 40D–I, 42C–E). Suborbital margin separated from basal antennal article and margin of postorbital tooth by fissures (Fig. 40D–I). Outer surface of third maxilliped covered by short setae; ischium subrectangular, slightly longer than broad; postero-external angle of merus relatively broad, “inserted” into shallower concavity on outer margin of ischium; antero-internal part of ischium rounded, auriculiform (Fig. 46A–F). Male chelipeds relatively short in adult males, surfaces of merus and carpus almost smooth; carpus elongate; propodus of palm elongated, not inflated, curved, smooth, palm longer than fingers; fingers long, slender, gently curved, with small basal gape when closed (Figs. 24, 25, 54D–I). Ambulatory legs relatively short, slender; merus without dorsal subdistal spine; dactylus elongate, curved, covered with long setae except for corneous tip (Figs. 24, 25, 56C–G). Thoracic sternum wide; surfaces of somites 5–8 with numerous rounded tubercles and granules; sternites 3 and 4 with obliquely longitudinal depressions; margin between sternites 2 and 3 demarcated by deep notch; anterior margin of sterno-abdominal cavity forming complete rim (Figs. 50D–I, 52I). Male abdomen subrectangular, with 6 free somites and telson; somites 3 and 4 subequal to or wider than somites 6 and telson (Fig. 50D–I). Male press-button abdominal locking mechanism submedian in position on sterno-abdominal cavity (Fig. 52I). Female abdomen dome-shaped, covering most of thoracic sternum. G1 long, relatively stout, almost straight or gently curved, distal part with scattered short setae (Fig. 27).

Type species. *Maia miersii* Walker, 1887, by present designation.

Etymology. The name is derived from an arbitrary combination of the name Holthuis, with the genus name *Maja*. This honours the major contribution by the late Lipke B. Holthuis in resolving the convoluted nomenclature of the genus. Gender feminine.

Remarks. Six species are included in *Holthuija* n. gen. *H. miersii* (Walker, 1887), *H. suluensis* (Rathbun, 1916), *H. pauli* n. sp., *H. cognata* n. sp., *H. aussie* n. sp. and *H. poorei* n. sp. These species are all easily distinguished by their prominently foliate supraorbital eave, which is the most expanded in all the genera treated here. All species also have a strongly granulated carapace surface, epistome, suborbital and pterygostomial regions, third maxilliped, thoracic sternum and abdomen. The suborbital tooth is also sharply separated from the postorbital tooth by a distinct fissure; and the G1 is generally simple, with a simple distal part and only scattered short setae.

Key to species of *Holthuija* n. gen.

1. Carapace with 2 median gastric spines (e.g., Fig. 26A)........2
– Carapace with single median gastric spine (e.g., Fig. 26C)..3

2. Carapace with relatively small lateral spines, 1 cardiac spine (Fig. 24E); pseudorostral spines directed horizontally (Fig. 26A); Philippines............*Holthuija suluensis* (Rathbun, 1916)
– Carapace with relatively long lateral spines, 2 or 3 cardiac spines (Fig. 25B–D); pseudorostral spines gently curved downwards (Fig. 26D); Eastern Indian Ocean........*Holthuija aussie* n. sp.

3. Carapace with relatively short lateral spines, pseudorostral spines almost straight or gently curved outward, appears level from lateral view and not prominently curved upward (Figs. 24A–D, 25A)..4
– Carapace with relatively long lateral spines, pseudorostral spines strongly curved outward and usually distinctly bent or curved upward (Figs. 24F, 25E, F, 26B, E, F)......................5

4. Pseudorostral spines gently curved outward (Fig. 24A–D); G1 strongly curved with small flap distally (Fig. 27A–C); Singapore............................*Holthuija miersii* (Walker, 1887)
– Pseudorostral spines almost straight (Fig. 25A); G1 almost straight with distal part dilated (Fig. 27I–K); Japan................ ....*Holthuija cognata* n. sp.

5. Dorsal surface of carapace with low granules (Fig. 24F); G1 almost straight with distal part slightly dilated (Fig. 27F–H); Philippines, Taiwan...............................*Holthuija pauli* n. sp.
– Dorsal surface of carapace with distinct rounded granules (Fig. 25E, F); G1 curved, distal part simple (Fig. 27L–O); Eastern Indian Ocean..*Holthuija poorei* n. sp.

Holthuija miersii (Walker, 1887)

(Figs. 2E, 24A–D, 27A–C, 37D, E, 40D, E, 42C, 46A, 50D, E, 52I, 54D, 56C, 69C, D)

Maia miersii Walker, 1887: 109, pl. 6, figs 1–3.
Maja miersi – Serène, 1968: 57. – Serène & Lohavanijaya, 1973: 50 (key).
Maja miersii – Rathbun, 1924: 6. – Griffin, 1966a: 284 (key). – Griffin & Tranter, 1986: 217. – Ng et al., 2008: 117.

Material examined. Singapore – 1 female (21.4 × 16.7 mm) (NHM 1900.10.22.13), Pasir Panjang, near Sungei Pandan, sandy mud, 6 fathoms, coll. F.P. Bedford & W.F. Lanchester, 1900. — 1 male (32.6 × 25.6 mm) (ZRC 2000.1497), Southern Islands, dredge, coll. D. Lane, 1991. — 2 females (14.7 × 10.7 mm, 16.5 × 12.2 mm) (ZRC 1995.311), dredged off Pulau Semakau, coll. P.K.L. Ng, 1991. — 1 male (20.1 × 14.7 mm) (ZRC 1985.325), Damar Laut, station B54, 5–8 fms, mud with gorgonians, coll. Singapore Fisheries Research Station, 1955–56. — 1 male (22.3 × 16.5 mm) (CBM-ZC4001), southern Singapore, coll. T. Komai, dredge, 9 May 1997. — 1 ovigerous female (50.2 × 40.4 mm) (ZRC 2013.1272), station 4714-TB2, Semakau Island, dredge, coll. Comprehensive Marine Biodiversity Survey team, RV *Galaxea*, 15 May 2013.

Diagnosis. Carapace covered with small granules (Fig. 24A–D). Pseudorostral spines relatively short, diverging, curved outwards (Fig. 37D, E). Antorbital spine long, sharp; intercalated spine triangular, sharp; postorbital spine very long, sharp, slightly curved upwards; hepatic area with 2 sharp spines pointed outwards, first one longest (Figs. 24A–D, 37D, E). Lateral margin with 3 spines; 1 sharp branchial spine; 2 median spines: 1 gastric, 1 cardiac; 2 spines on posterior carapace margin (Fig. 24A–D). Basal antennal article granulated, with 2 long blunt spines distally (Fig. 40D, E). Epistome with 2 large tubercles on anterior margin (Fig. 40D, E). G1 strongly curved with small flap distally (Fig. 27A–C).

Remarks. Walker (1887) described *Maia miersii* from Singapore on the basis of a male 33 mm in carapace length (excluding pseudorostrum) (Fig. 24A). The largest male from Singapore examined here (ZRC 2000.1497) agrees well with his description and figures. The largest known specimen is a recently collected female specimen and differs from the smaller specimens in several features: the antorbital spine is directed somewhat more upwards, the posterior carapace spines are pointed more upwards, the ocular peduncle is relatively longer and more prominently curved upwards, it has two rows of large rounded granules starting from the basal antennal article to the epistome which are more prominent, the suborbital tooth is more strongly granulated, and the ambulatory legs are more setose. These differences are not significant and probably associated with its large size.

Tune Sakai (1938) first recorded this species as "*Maja miersi*" from Japan, and because material from Singapore (and Southeast Asia) has not been reported since, the Japanese accounts by T. Sakai and his colleagues (see synonymy for next species) are generally the ones used to define this taxon. Comparisons of material from Japan and Singapore show that while they are superficially resemble each other in having a relatively elongate carapace and similar arrangement of spines, their G1 structures are very different. The G1 of *H. miersii* s. str. is medially curved while that of the Japanese material is straight. In addition the two median spines on the posterior carapace margin are always short in the Japanese specimens while it is proportionately longer and stronger in *H. miersii* s. str. In addition, the subhepatic, pterygostomian and thoracic sternal surfaces are relatively more strongly granulated in *H. miersii* s. str. (Fig. 50D, E) compared to the less granulated condition in the Japanese material (Fig. 50H). The Japanese material previously identified as "*Maja miersi*" is here referred to *Holthuija cognata* n. sp. The G1 structure of *H. cognata* actually resembles that of *H. pauli* n. sp., but the two species have different carapace features.

Johnson (1958: 115) had checked on the type specimens of the four decapod species Walker described from Singapore, including *Maia miersii*, and noted that "none of them is present in there at the moment". With Paul Clark, the second author searched the collections of NHM for Walker's type male but could not locate the specimen. It is probably no longer extant, but a neotype is not necessary in light of the distinctive features of the species described here.

The recent specimen of *H. miersii* (ZRC 2013.1272) (Fig. 69C, D) was collected inside a large rock from around 20 m of water, in an area that is very rocky with very strong currents. This may be the preferred habitat of the species.

In life, the species is dull brown with patches of purple. The ambulatory dactyli are reddish brown; with parts of the ventral surfaces and abdomen purple (Fig. 69C, D).

Holthuija cognata n. sp.

(Figs. 25A, 27I–K, 37H, 46D, 50H, 54G, 56E)

Maja miersii – Muraoka, 1998: 27.
Maja miersi – T. Sakai, 1938: 298–299, pl. 38 fig. 2. – T. Sakai, 1976: 237, pl. 82, fig. 3. – Miyake, 1983: 47, pl. 16 fig. 1. – Huang, 1994: 582. – Muraoka, 1998: 27. – Maramura & Kosaka, 2003: 34.

Material examined. Holotype: male (29.5 × 23.7 mm) (CBM-ZC3662a), off Minabe, Kii Peninsula, 10–20 m, Japan, gill net, coll. T. Komai, 28 March 1997. Paratypes: **Japan** – 1 male (32.2 × 24.4 mm), 2 females (36.5 × 27.8 mm, 36.6 × 28.2 mm) (CBM-ZC3662b), same data as holotype. — 1 female (30.2 × 23.6 mm) (CBM-ZC4119), Arita, Kushimoto, Kii Peninsula, in lobster net, coll. S. Yamaguchi, 19 February 1978. — 1 female (26.3 × 19.1 mm) (NSMT-Cr 15470), north of Kuchinoshima Island, 30°5.77'N 130°4.54'E, 96m, coll. H. Saito, 28 May 1999. — 2 males (29.7 × 25.4 mm, 31.0 × 24.7 mm with broken rostrum) (NHM 1961.11.13.5–6), Seto, Shirahama, Japan, coll. gill nets, I. Gordon & Harada, 1950s. — 1 male (ZRC), Honshu, Wakayama, Kii Minabe, 33°45.712'N 135°18.927'E, coll. K. Sakai, 26 October 1988. — 1 male (31.9 × 26.0 mm), 1 female (38.4 × 30.0 mm) (SMF 47733), Honshu, Kii-Minabe, Wakayama, 33°45.712'N 135°18.927'E, coll. K. Sakai, 26 October 1988. — 1 female (42.7 × 33.0 mm) (SMF 47591), Odawara Harbour, 35°14.265'N 139°9.058'E, coll. H. Watabe, 3 August 1970. — 1 male (39.4 × 30.2 mm) (SMF 47737), Shikoku, Tosa Bay, Ashizuri, 32°43.55'N 133°5.028'E, coll. K. Sakai, 13–14 November 1965. — 1 dried male (36.8 × 29.0 mm), 1 dried female (38.0 × 29.6 mm) (SMF 47730), Honshu, Wakayama, Kii Minabe, 33°45.712'N 135°18.927'E, coll. K. Sakai, 15 February 1983.

Diagnosis. Carapace covered with small granules (Fig. 25A). Pseudorostral spines almost straight, diverging (Fig. 37H). Antorbital spine long, curved forwards; intercalated spine short, triangular leaving gaps on each side; postorbital spine strong, straight, enlarged proximally; hepatic spine shorter than postorbital spine, pointed outwards (Figs. 25A, 37H). Lateral margin with 3 low spines, last one longest; 1 branchial spine; median row with 2 spines: 1 gastric, 1 cardiac; 2 small spines on posterior carapace margin (Fig. 25A). Basal antennal article granulated, with 2 long blunt spines distally. Epistome with 2 distinct tubercles on anterior margin. G1 almost straight with distal part dilated (Fig. 27I–K).

Etymology. The species name alludes to the close relationship of the new species with *H. pauli* n. sp. and *H. miersii*.

Remarks. Although the carapace of *H. cognata* n. sp. is close to *H. miersii*, the G1 structure of *H. cognata* (Fig. 27I–K) is closest to *H. pauli* n. sp. (Fig. 27F–H), differing slightly only in proportions. Old records of "*Maja miersi*" from Japan and the East China Sea (Huang, 1994) are almost certainly *H. cognata* instead. See discussion for *H. miersii*.

Holthuija suluensis (Rathbun, 1916)
(Figs. 1A, 24E, 26A, 27D, E, 37F, 40F, 42D, 46B, 50F, 54E, 56D)

Maja suluensis Rathbun, 1916: 552. – Serène, 1968: 57. – Griffin, 1976: 200, Fig. 7a. – Griffin & Tranter, 1986: 210, 218 (part), fig. 71f. – Ng et al., 2008: 117 (list).

Material examined. Holotype: female (32.4 × 41.2 mm) (USNM 48224a), station 5165, Observation Island, Tawi Tawi Group, Sulu Islands, 4°58.33'N 119°50.5'E, Philippines, coll. RV *Albatross*, 24 February 1908. Paratypes: 2 females (22.5 × 30.6 mm, 22.4 × 30.9 mm) (USNM 48224a), same data as lectotype. Others: **Philippines** – 1 male (11.5 × 8.2 mm), 1 young female (26.8 × 20.8 mm) (USNM 48507), station 5557, Jolo Island and vicinity, 19 fathoms, coll. RV *Albatross*, 18 September 1909. — 1 female (36.3 × 27.4 mm) (USNM 49697), station 5163, Tawi Tawi Group, Sulu Archipelago, 28 fathoms, coll. RV *Albatross*, 24 February 1908.

Diagnosis. Carapace covered with small granules (Fig. 24E). Pseudorostral spines straight, strongly diverging (Fig. 37F). Antorbital spine long, curved, directed anteriorly; intercalated spine short, leaving narrow gaps on each side; postorbital spine very long, slightly curved outwards; hepatic spine directed anteriorly, half length of postorbital spine (Figs. 24E, 37F). Lateral margin with 3 long spines; 1 branchial spine; median row with 3 long spines: 2 gastric, 1 cardiac; 2 small spines on posterior carapace margin (Fig. 24E). Basal antennal article broad with median row of granules, 2 sharp distal spines (Fig. 40F). Epistome with 2 granulated lobes on anterior margin (Fig. 40F). G1 almost straight, distal part not dilated or curved [juvenile] (Fig. 27D, E).

Remarks. Rathbun (1916: 553) provided measurements for only one female specimen (the holotype) but did not mention how many more specimens she had. In the bottle are two other female specimens with the same data and they should be treated as paratypes. Rathbun (1916: 552) stated that the specimen was collected from 9 fathoms depth but the label says 46 fathoms. Griffin (1976: 200) said 9 to 28 fathoms.

The record by Griffin & Tranter (1986: 218) from Sulu Islands and Kei Islands (Moluccas) almost certainly contains two species. They comment that the specimen they had from Moluccas has only one gastric spine in contrast to the material from Sulu Islands which has two spines (including the types). They suggested that this character may be variable and used other characters to differentiate *H. suluensis* from *H. miersi*. While the characters they use are valid, we are more inclined to believe that his Moluccas specimen is actually another species, possibly allied to *H. pauli* n. sp. (see below). *Holthuija suluensis* and *H. pauli* are superficially very close, but the large series of *H. pauli* on hand tells us that the position and number of gastric spines (two versus one) is very reliable and not variable, even between sexes or specimens very different in size. Otherwise, they are similar in general carapace form.

Serène & Vadon (1981: 119, 124, 128) records "*Maja miersi*" from the Philippines but their material will need to be checked to see if they are really this species or perhaps the allied *H. pauli* or *H. suluensis*. Maramura & Kosaka's (2003: 35) record of "*Maja* aff. *suluensis*" from Japan will also need to be examined before its identity can be confirmed.

Holthuija pauli n. sp.
(Figs. 24F, 26B, C, 27F–H, 37G, 40G, 46C, 50G, 54F, 69E, F)

Material examined. Holotype: male (37.3 × 28.0 mm) (NMCR), Balicasag Island, Panglao, Bohol, Philippines, 200–300 m, coll. fishermen in tangle nets, July 2003. Paratypes: **Philippines** – 10 males (27.0 × 19.7 mm, 27.6 × 20.2 mm, 27.9 × 20.3 mm, 30.6 × 22.8 mm 32.4 × 24.0 mm, 33.2 × 24.1 mm, 34.2 × 26.1 mm, 34.4 × 25.3 mm, 34.5 × 25.9 mm, 41.0 × 30.8 mm,), 3 females (41.9 × 31.4 mm, 41.9 × 32.4 mm, 34.8 × 26.2 mm), 1 ovigerous female (34.7 × 26.4 mm), 1 damaged female (28.0 × 20.8 mm) (ZRC 2013.1371), same data as holotype. — 1 female (27.8 × 21.5 mm) (ZRC 2001.411), Balicasag Island, Panglao, Bohol, coll. fishermen with tangle nets, December 2000. — 1 male (ZRC 2013.1266, ex part ZRC 2001.0577), Balicasag Island, Panglao, Bohol, coll. fishermen with tangle nets, 28 November 2001. — 4 males (27.5 × 19.9 mm, 28.2 × 20.7 mm, 31.5 × 23.4 mm, 31.9 × 23.8 mm), 1 ovigerous female (35.0 × 26.0 mm) (ZRC 2001.0590), Balicasag Island, Panglao, Bohol, coll. fishermen with tangle nets, 28 November 2001. — 1 female (23.8 × 17.6 mm) (ZRC 2013.1376), Balicasag Island, Panglao, Bohol, coll. fishermen in tangle nets, June 2002. — 1 juvenile female with bopyrid (ZRC 2013.1314), Balicasag Island, Panglao, Bohol, 200–300 m, coll. fishermen with tangle nets, June 2002. — 1 male (35.0 × 27.0 mm) (ZRC 2013.1378), Balicasag Island, Panglao, Bohol, coll. fishermen in tangle nets, June 2002. — 1 male, 2 females (1 ovigerous) (NSMT-Cr 15392), Balicasag Island, Panglao, Bohol, coll. local fisherman via M. Takeda & H. Komatsu, February 2003. — 2 females (33.8 × 25.3 mm, 40.7 × 30.7 [carapace badly damaged]) (ZRC 2013.1375), Balicasag Island, Panglao, Bohol, coll. fishermen with tangle nets, July 2003. — 1 damaged male (19.5 × 15.6 mm) (ZRC 2013.1377), Balicasag Island, Panglao, Bohol, coll. fishermen with tangle nets, July 2003. — 1 female (38.8 × 28.9 mm) (ZRC 2013.1379), Balicasag Island, Panglao, Bohol, coll. fishermen with tangle nets, 25–30 July 2003. — 1 female (35.5 × 27.2 mm) (ZRC 2013.1380), Balicasag Island, Panglao, Bohol, coll. fishermen with tangle nets, November 2003. — 2 males (AM), Balicasag Island, Panglao, Bohol, 200–300 m, coll. fishermen with tangle nets, January 2004. — 1 male (ZRC 2013.1324), Balicasag Island, Panglao, Bohol, 200–300 m, coll. fishermen with tangle nets, February 2004. — 1 female (19.9 × 14.7 mm) (ZRC 2013.1384), Balicasag Island, Panglao, Bohol, coll. fishermen with tangle nets, March 2004. — 1 male, 2 females (ZRC 2013.1222), Balicasag Island, Panglao, Bohol, 200–300 m, coll. fishermen with tangle nets, April 2004. — 1 male (29.0 × 21.9 mm) (ZRC 2013.1373), Balicasag Island, Panglao, Bohol, coll. fishermen with tangle nets, May 2004. — 4 males (smallest 23.4 × 17.4 mm, largest 42.0 × 31.8 mm), 1 female with rhizocephalan (28.2 × 21.4 mm), 2 females (33.4 × 25.7 mm, 45.9 × 35.0 mm) (ZRC 2013.1372), Balicasag Island, Panglao, Bohol, coll. fishermen with tangle nets, 29 May 2004. — 1 female (ZRC 2013.1374), Balicasag Island, Panglao, Bohol, 200–300 m, coll. fishermen with tangle nets, 29 February 2005. Others: 1 badly damaged male (21.5 × 17.8 mm) (ZRC 2013.1323, ex part ZRC 2000.585) Balicasag Island, Panglao, Bohol, coll. fishermen with tangle nets, 28 November 2001.

Diagnosis. Carapace covered with small granules (Fig. 24F). Pseudorostral spines long, strongly diverging and usually curved upwards (Figs. 37G). Antorbital spine curved; intercalated spine triangular with large gaps; postorbital spine very long; hepatic spine relatively small (Figs. 24F, 37G). Lateral margin with 3 long spines, posterior longest; 1 branchial long spine; median row with 2 spines: 1 gastric, 1 cardiac; 2 short spines on posterior carapace margin (Fig. 24F). Basal antennal article broad, granulated, with longitudinal furrow, 2 strong distal spines (Fig. 40G). Epistome with 2 low tubercles on anterior margin (Fig. 40G). G1 almost straight with distal part slightly dilated (Fig. 27F–H).

Etymology. The name honors the memory of Paul Beaudemoulin, father-in-law of the second author, who passed away in October 2012.

Remarks. Of the *Holthuija* species, *H. pauli* n. sp. is distinct in possessing very long carapace spines which are prominently curved obliquely upwards. The large number of specimens we have examined show that the length and orientation of these spines are not variable, even for small specimens and females. It also has proportionately, the longest ambulatory legs (Fig. 24F). In the other species, the ambulatory legs, particularly the merus, are shorter (Figs. 24A–D, 25).

The G1 structure of *H. pauli* most closely resembles that of *H. cognata* n. sp., with the distal part laterally flattened, even though their carapace and legs are quite different (carapace relatively broader with longer and more curved spines, and with proportionately longer legs in *H. pauli*). The G1 of *H. pauli*, however, is relatively more slender than that of *H. cognata* (Fig. 27F–H versus Fig. 27I–K).

Holthuija pauli might be confused with small specimens of *Paramaya spinigera* and *Paramaya ouch*, especially with regard to the relatively long carapace spines which are curved and the very divergent pseudorostral spines. *Paramaya* species, however, have long distal spines on the meri of ambulatory legs (absent in *H. pauli*) as well as many other characters at the generic level (see discussion for *Paramaya*).

In life, *H. pauli* is beige and light reddish-brown overall, with the third maxillipeds and abdomen brighter in colour (Fig. 69E, F).

Holthuija aussie n. sp.

(Figs. 25B–D, 26D, 37I, 40H, 42E, 46E, 54H, 56F)

Maja suluensis – Poore et al., 2008: 62. (not *Maja suluensis* Rathbun, 1916). (not *Maja suluensis* Rathbun, 1916).

Material examined. Holotype: ovigerous female (42.1 × 34.4 mm) (NMV J63752), Arafura Sea, 10°58.03'S 136°47.82'E, 107–108 m, coll. B. A. Glasby, CSIRO RV *Southern Surveyor*, 17 October 2012. Others: 1 juvenile female (14.3 × 11.9 mm [right branchial region with bopyrid parasite) (NMV J61058), Imperieuse L23 Transect, northwestern Australia, 18°27.62'S 120°08.68'E – 18°27.72'S 120°08.68'E, 80–81 m, coll. M. Gomon, CSIRO RV *Southern Surveyor*, 19 June 2007. — 1 juvenile female (11.9 × 9.1 mm) (NMV J63958), off Red Bluff, Western Australia, 24°02.62'S 113°01.62'E – 24°02.83'S 113°01.73'E, 100 m, coll. G. Poore, CSIRO RV *Southern Surveyor*, 8 December 2005.

Diagnosis. Carapace covered with small granules (Fig. 25B–D). Pseudorostral spines long, diverging (Fig. 37I). Antorbital spine long, sharp, strongly curved upwards and anteriorly; intercalated spine triangular, with distinct gaps on each side; postorbital spine long, strong; hepatic spine short; median row with 5 long spines: 2 gastric, 3 cardiac (2 may be small in young specimens) (Figs. 25B–D, 37I). Lateral margin with 3 long spines increasing towards posterior; 1 very long branchial spine; 2 long upwardly directed spines on posterior carapace margin (Fig. 25B–D). Basal antennal article with 2 big blunt distal teeth; on inner margin 2 lobate teeth; external margin serrulated (Fig. 40H). Epistome with 2 tubercles on anterior margin (Fig. 40H). G1 not known.

Etymology. The species is named after a common nickname for Australians – "Aussie". The name is used as a noun in apposition.

Remarks. *Holthuija aussie* n. sp. is the only species of the *Maja* group to possess three cardiac spines. The holotype of the species comes from the northwestern Australian coast, in the Arafura Sea, very close to Indonesian waters.

The identities of two juvenile specimens (J61058 and J53958) collected at 18°S and 24°S, is uncertain as they differ from the type in several aspects. The following differences are observed: the antorbital spine is not as curved in the juveniles as found in the adults; there are wide gaps on each side of the intercalated spine in the juveniles versus narrow gaps in

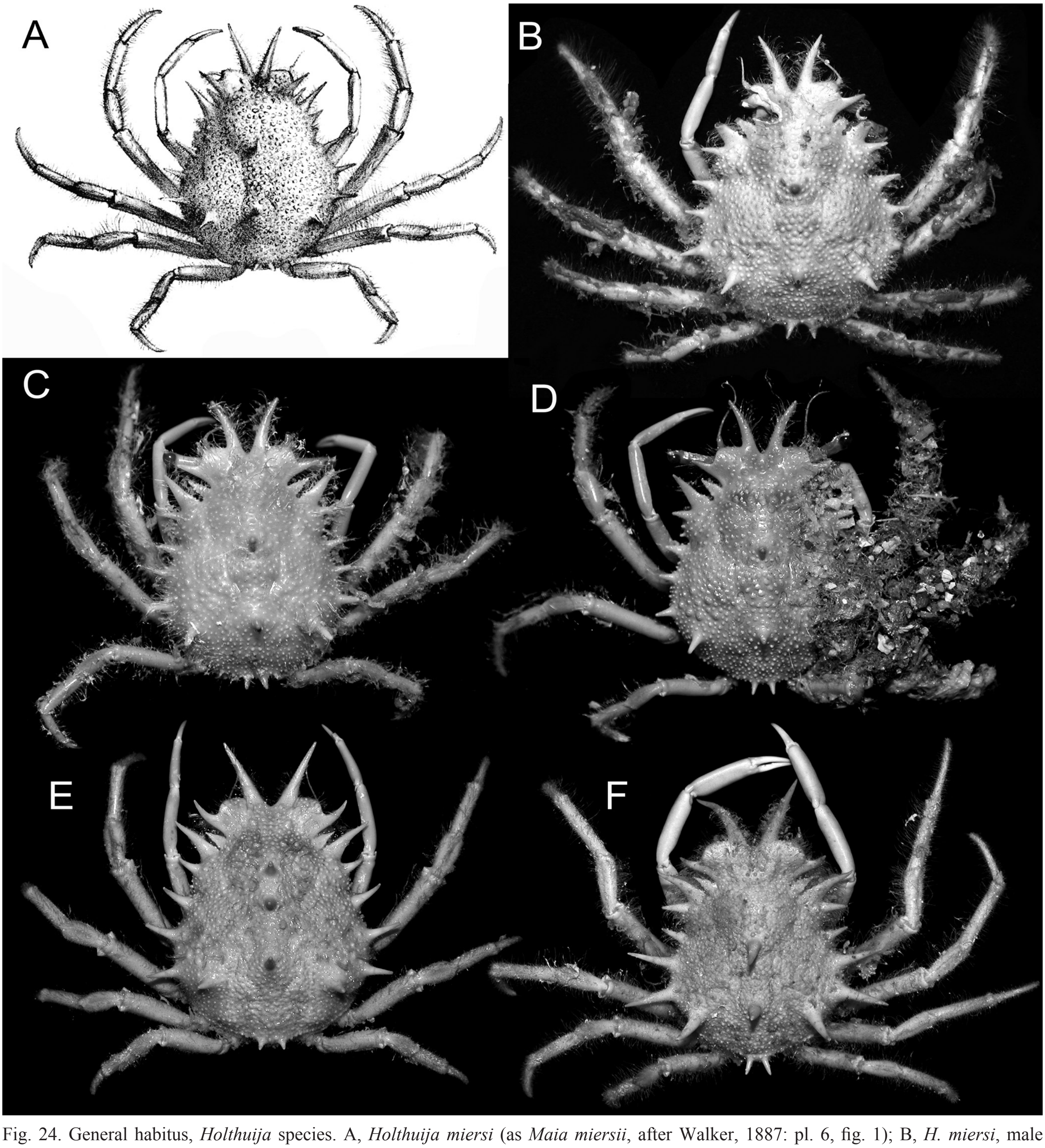

Fig. 24. General habitus, *Holthuija* species. A, *Holthuija miersi* (as *Maia miersii*, after Walker, 1887: pl. 6, fig. 1); B, *H. miersi*, male (32.6 × 25.6 mm) (ZRC 2000.1497), Singapore; C, *H. miersii*, female (16.5 × 12.2 mm) (ZRC 1995.311), Singapore; D, *H. miersii*, female (21.4 × 16.7 mm) (NHM 1900.10.22.13), Singapore; E, *H. suluensis*, holotype female (32.4 × 41.2 mm) (USNM 48224a), Philippines; F, *H. pauli* n. sp., holotype male (37.3 × 28.0 mm) (NMCR), Philippines.

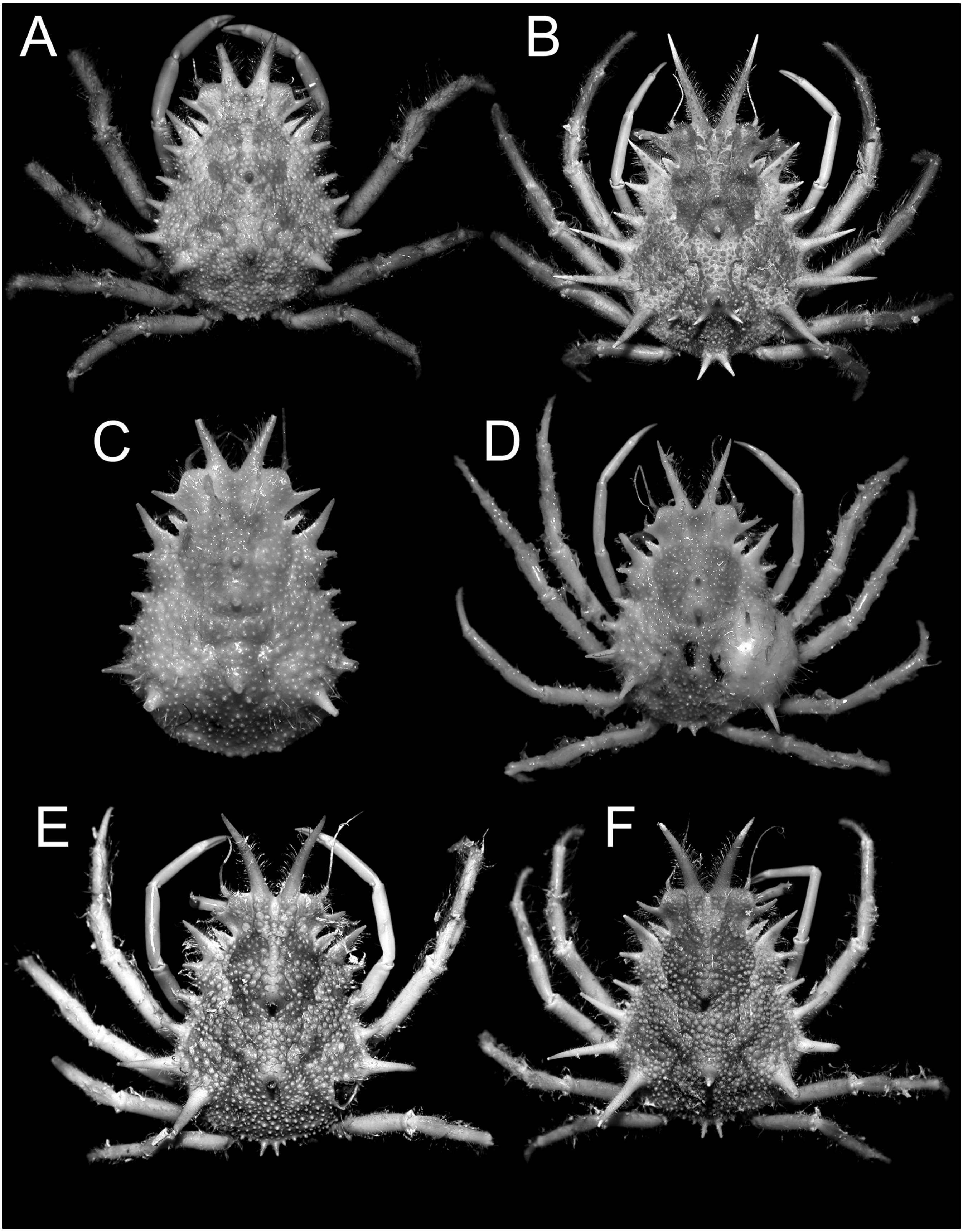

Fig. 25. General habitus, *Holthuija* species. A, *H. cognata* n. sp., holotype male (29.5 × 23.7 mm) (CBM-ZC3662), Japan; B, *H. aussie* n. sp., holotype ovigerous female (42.1 × 34.4 mm) (NMV J63752), Arafura Sea; C, *H. aussie* n. sp., paratype juvenile female (11.9 × 9.1 mm) (NMV J53958), Australia; D, *H. aussie* n. sp., juvenile female (14.3 × 11.9 mm) (NMV J61058), Australia; E, *H. poorei* n. sp., holotype male (24.3 × 18.7 mm) (NMV J63749), Timor Sea; F, *H. poorei* n. sp., paratype female (27.0 × 22.5 mm) (NMV J63751), Arafura Sea.

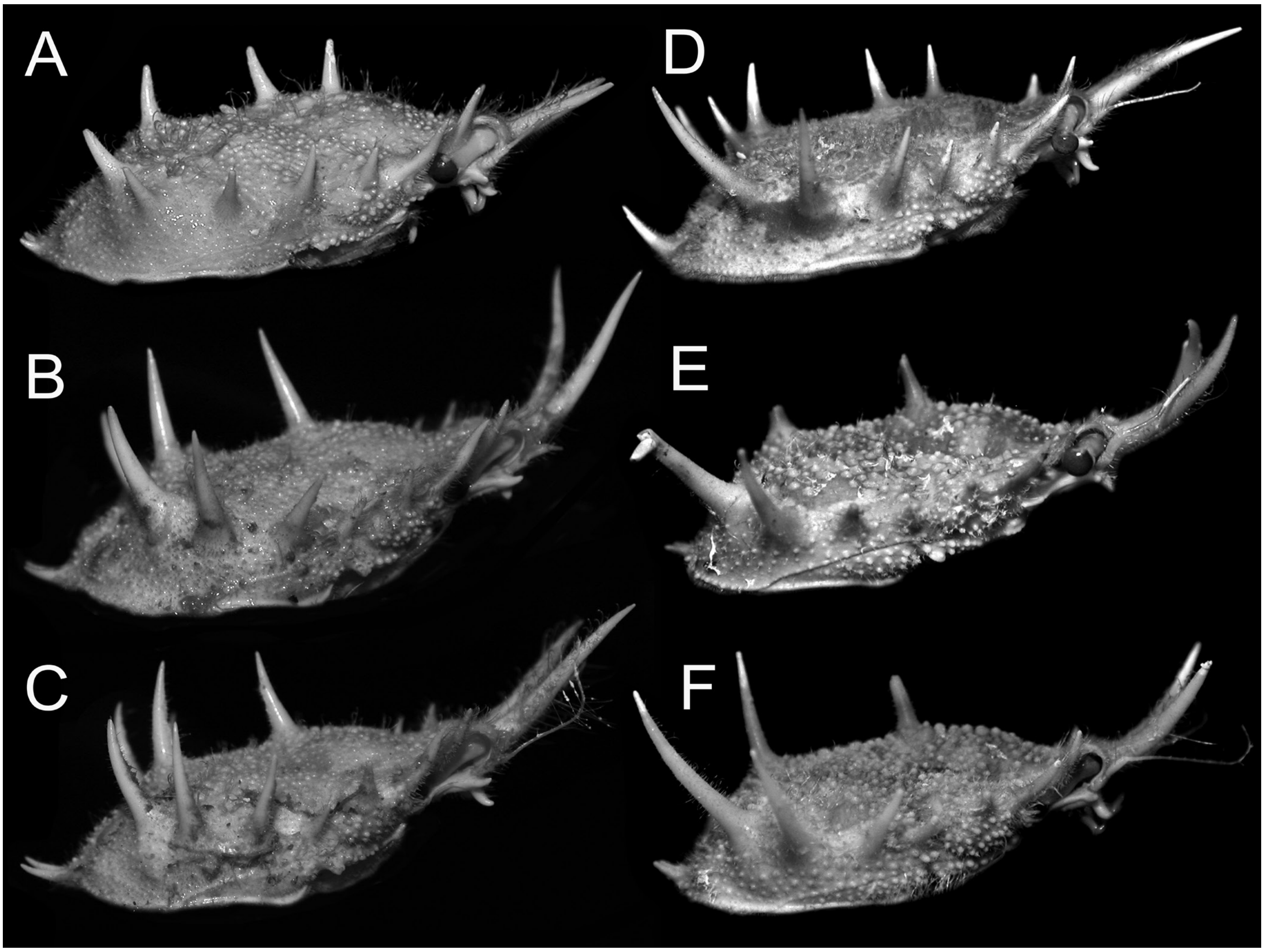

Fig. 26. Lateral views of carapaces, *Holthuija* species. A, *H. suluensis*, holotype female (32.4 × 41.2 mm) (USNM 48224a), Philippines; B, *H. pauli* n. sp., holotype male (37.3 × 28.0 mm) (NMCR), Philippines; C, *H. pauli* n. sp., paratype male (35.0 × 27.0 mm) (ZRC 2013.1378), Philippines; D, *H. aussie* n. sp., holotype ovigerous female (42.1 × 34.4 mm) (NMV J63752), Arafura Sea; E, *H. poorei* n. sp., holotype male (24.3 × 18.7 mm) (NMV J63749), Timor Sea [laterally inverted to match earlier figures]; F, *H. poorei* n. sp., paratype female (27.0 × 22.5 mm) (NMV J63751), Arafura Sea laterally inverted to match earlier figures].

the adults; all the lateral spines are shorter in the juvenile specimens; only one cardiac spine versus 3 in the adult; the distal spines on the basal antennal article are shorter and not so sharp; the cornea shape is different, being more elongate in the juveniles. They could belong to a new species but as neither specimens are adult, it was decided that this was best left to a later date when better material becomes available. They are here provisionally referred to *Holthuija aussie* for convenience.

***Holthuija poorei* n. sp.**

(Figs. 25E, F, 26E, F, 27L–O, 37J, 40I, 46F, 50I, 54I, 56G)

Material examined. Holotype: male (24.3 × 18.7 mm) (NMV J63749), Timor Sea, Ocean Shoals Commonwealth Marine Reserve, 12°04.5'S 127°26.62'E – 12°04.53'S 127°26.62'E, 59–66 m, coll. B.A. Glasby, RV *Solander*, 3 October 2012. Paratypes: 1 male (26.1 × 20.1 mm) (NMV J63196), same data as holotype. — 1 female (27.0 × 22.5 mm) (NMV J63751), Arafura Sea, 10°58.03'S 136°47.82'E, 107–108 m, coll. B.A. Glasby, CSIRO RV *Southern Surveyor*, 17 October 2012.

Diagnosis. Carapace covered with relatively larger rounded granules (Fig. 25E, F). Pseudorostral spines long, strongly diverging (Fig. 37J). Antorbital spine long, straight; intercalated spine strong, with convex margins, with large gaps on each side; postorbital spine long; hepatic spine short, pointed outwards; median row with 2 spines, 1 gastric, 1 cardiac; 2 small spines on posterior carapace margin (Figs. 25E, F, 37J). Lateral margin with 3 large spines, increasing in size towards posterior; 1 long branchial spine, curved upwards (Fig. 25E, F). Basal antennal article with 2 big blunt distal teeth, external margin smooth, carinated, internal margin with one proximal lobate tooth (Fig. 40I). Epistome with 2 low tubercles on anterior margin (Fig. 40I). G1 curved, distal part simple (Fig. 27L–O).

Etymology. The species is named after our "Aussie" friend, Gary Poore, former curator of Crustacea at Museum Victoria.

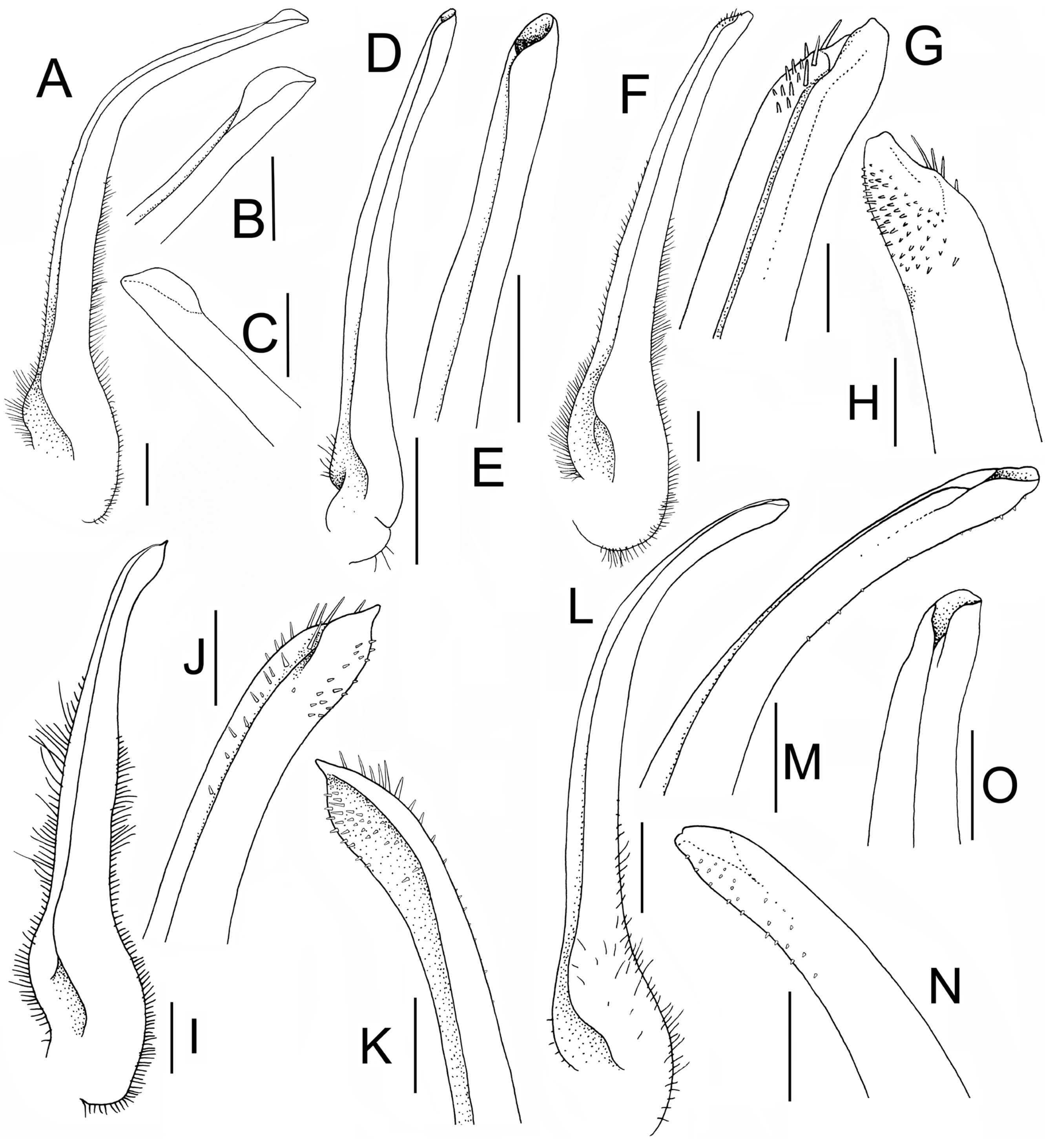

Fig. 27. Left G1s, *Holthuija* species. A–C, *H. miersi*, male (32.6 × 25.6 mm) (ZRC 2000.1497), Singapore; D, E, *H. suluensis*, male (11.5 × 8.2 mm) (USNM 48507), Philippines; F–H, *H. pauli* n. sp., holotype male (37.3 × 28.0 mm) (NMCR), Philippines; I–K, *H. cognata* n. sp., holotype male (29.5 × 23.7 mm) (CBM-ZC3662), Japan; L–O, *H. poorei* n. sp., paratype male (26.1 × 20.1 mm) (NMV J63169), Timor Sea. Scale bars = 1.0 mm [A–F, I, L]; 0.5 mm [D, G, H, J, K, M–O]; 0.25 mm [E].

Remarks. *Holthuija poorei* n. sp. resembles *H. pauli* n. sp. in many aspects, but is easily separated by possessing a distinctly more granular carapace (Fig. 26E, F versus Fig. 25E, F). *Holthuija poorei* also has relatively shorter ambulatory legs (Fig. 25E, F versus Fig. 24F), and the G1 is relatively more elongated and curved with the tip distinctly dilated (Fig. 27L–D versus Fig. 27F–H).

The material of *H. poorei* n. sp. was collected off northwestern Australian coast, in the Timor Sea and Arafura Sea, both at the boundary of Indonesian waters.

Sakaija n. gen.

Diagnosis. Carapace pyriform to rounded in adults; dorsal surface inflated, covered by rounded granules; gastric and branchial regions delimited by grooves (Figs. 28–30, 31A, B, D, E, 32). Intestinal region with small median spine, often reduced to blunt tubercle (Figs. 28–30, 31A, B, D, E, 32). Pseudorostral spines relatively short, diverging,(Figs. 28–30, 32, 37K–O). Supraorbital eave with anterior part longitudinally narrow, rectangular, not prominently expanded; antorbital spine sharp (Fig. 37K–O). Intercalated spine distinct, separated from supraorbital eave and postorbital spine by distinct gaps; postorbital spine strong, lobiform; hepatic region with 1 spine, shorter than postorbital spine; 1 or more smaller spines below (Fig. 37K–O). Lateral carapace margin with 2 short spines and numerous granules, some sharp; branchial region with 1 spine (Figs. 28–30, 31A, B, D, E, 32). Posterior carapace margin with 2 very short median spines, sometimes almost undiscernible in adults (Figs. 28–30, 32). Eyes relatively short, slender, with ovoid cornea (Fig. 37K–O). Antennal flagellum short, slender. Basal antennal article longer than broad, rectangular; surface granulated, with 2 spines distally; inner and outer lateral margins with low granules; proximal outer angle rounded; antero-external crested rim of antennular fossa touches but does not significantly overlap distal part of basal antennal article (Figs. 28F, 40J–M). Epistome slightly wider than long, anterior margin unarmed; posterior margin composed of 4 rectangular plates separated by shallow fissures (Figs. 28F, 40J–M, 42F). Suborbital margin separated from basal antennal article by short fissure, confluent with margin of postorbital tooth (Fig. 40J–M). Outer surface of third maxilliped covered by scattered setae in adults; ischium subrectangular, just longer than broad; postero-external angle of merus relatively broad, "inserted" into shallower concavity on outer margin of ischium; antero-internal part of ischium rounded, auriculiform (Fig. 46G–L). Male chelipeds relatively short in adult males, surfaces of merus and carpus smooth; carpus short, with low longitudinal ridge; propodus of palm smooth, short, inflated in adults, palm longer than fingers; fingers slender, gently curved, with distinct basal gape when closed (Figs. 28–30, 32, 54J–M). Ambulatory legs slender or stout, slender; merus without dorsal subdistal spine; dactylus elongate, curved, covered with long setae except for corneous tip (Figs. 28–30, 31C, F, 56H–J). Thoracic sternum wide; surfaces of somites 5–8 with numerous prominent rounded tubercles and granules; sternites 3 and 4 distinctly depressed; margin between sternites 2 and 3 demarcated by deep notch; anterior margin of sterno-abdominal cavity not forming complete rim (Figs. 51A–E, 52J). Male abdomen subrectangular, with 6 free somites and telson; somites 3–6 and telson subequal in width (Fig. 51A–E). Male press-button abdominal locking mechanism submedian in position on sterno-abdominal cavity (Fig. 52J). Female abdomen dome-shaped, covering most of thoracic sternum. G1 short, slender, gently curved, distal part slightly spatuliform, tip rounded, margins lined with numerous long setae (Fig. 33).

Type species. *Maja japonica* Rathbun, 1932, by present designation.

Etymology. The genus name is derived from an arbitrary combination of the family name Sakai with *Maja*. It honours the significant work done by the late Tune Sakai in advancing our knowledge of Asian Majoidea. Gender feminine.

Remarks. *Sakaija* gen. nov. is established to accommodate the following species: *Sakaija japonica* (Rathbun, 1932) from Japan, *S. sakaii* (Takeda & Miyake, 1969) from Japan, *S. serenei* n. sp. from Philippines, *S. santo* n. sp. from Vanuatu, *S. africana* (Griffin & Tranter, 1986) from South Africa, and *S. longispinosa* n. sp. from the western coast of Australia.

The primary diagnostic feature for members of this genus is the characteristic slender and sinuous or curved G1, the distal part of which is lined with numerous long setae. Members of *Sakaija*, however, can also be recognised by a suite of characters: a distinctly pyriform carapace that has relatively short pseudorostral spines, the suborbital margin confluent with the margin of the postorbital tooth, and shape of the male thoracic sternum and abdomen. Noteworthy is also that all the species are relatively small, the largest being about 30 mm carapace length (*S. africana*), and small species maturing at carapace lengths of only 10 mm (e.g., *S. serenei*).

Key to species of *Sakaija* n. gen.

1. Pseudorostral spines very long; posterior carapace margin with 2 spines and long intestinal spine (Fig. 29); G1 gently curved, distal part with long setae, with low subdistal swelling (Fig. 33N–R); Western Indian Ocean... .... *Sakaija africana* (Griffin & Tranter, 1986)
– Pseudorostral spines not elongate; posterior carapace margin with 2 short spines, sometimes not discernible, intestinal spine short or not visible (Figs. 28, 30, 32); G1 otherwise 2

2. Carapace with very long lateral, branchial and intestinal spines (Fig. 32A, B); Eastern Indian Ocean....................................... .... *Sakaija longispina* n. sp.
– Carapace with relatively short lateral, branchial and intestinal spines (Figs. 28, 30, 32C, D)..3

3. Carapace with 2 subhepatic spines, one of which is small (Fig. 32C, D); G1 sinuous, distal part turned backwards towards median line of sternum, with very long setae (Fig. 33S–U); Vanuatu and New Caledonia ....*Sakaija santo* n. sp.
– Carapace with single visible hepatic spine (Figs. 28, 30); G1 otherwise..4

4. Carapace with posterior part rounded, prominently swollen; lateral spines low; ambulatory legs relatively short, stout (Figs. 28A–C, 31A–C); G1 distinctly curved, distal part long, tapering with very long setae (Fig. 33A–G); Japan and Taiwan........... ....*Sakaija japonica* (Rathbun, 1932)
– Carapace more evenly ovate in appearance; lateral spines short but distinct; ambulatory legs slender, more elongate (Figs. 28D-G, 30); G1 otherwise 5

5. Cardiac spine long, intestinal spine distinct (Fig. 28D, E, G); G1 gently curved, distal part relatively short, subspatuliform, lined with long setae (Fig. 33H–J); Japan............................... ....*Sakaija sakaii* (Takeda & Miyake, 1969)
– Cardiac and intestinal spines very low, almost undiscernible (Figs. 30, 31D, E); G1 gently curved, distal part long, tapering with very long setae (Fig. 33K–M); Philippines, New Britain and Papua New Guinea..........................*Sakaija serenei* n. sp.

Sakaija japonica (Rathbun, 1932)

(Figs. 28A–C, 31A–C, 33A–G, 37K, 40J, 42F, 46G, 51A, B, 52J, 54J, 56H)

Maja sp. – T. Sakai, 1932: 50, pl. 2, fig. 5, text-fig. 5.
Maja japonica Rathbun, 1932: 33. – T. Sakai, 1965: 83, pl. 37, fig. 1. – Serène, 1968: 57. – Takeda & Miyake, 1969: 512, pl. 17, fig. A, B, pl. 18, fig. B. – Takeda, 1973: 42. –Takeda, 1975: 127. – T. Sakai, 1976: 238, pl. 82, fig. 1; text-figs 126a, b. – Miyake, 1983: 44. – Dai et al., 1986: 150, pl. 18(1), text-fig. 76. – Griffin & Tranter, 1986: 216. – Huang, 1989: 339. – Dai & Yang, 1991: 135, pl. 18(1), text-fig. 76. – Takeda, 1993: 43. – Huang, 1994: 582. – Muraoka, 1998: 27. – Ng et al., 2001: 12. – Takeda, 2001: 235. – Maramura & Kosaka, 2003: 34. – Yang et al., 2008: 780. – Ng et al., 2008: 117 (list).
Maja japonica Yokoya, 1933: 157, text-fig. 56.
Maja nipponensis T. Sakai, 1934: 297, text-fig. 11. – T. Sakai, 1936: 100, text-fig. 46. – T. Sakai, 1938: 299, pl. 38, fig. 1, text-fig. 41.
Maja sakaii – Miyake, 1983: 44, pl. 15 fig. 5.

Material examined. Holotype: male (16.2 × 13.0 mm) (USNM 48252), off Honshu, Japan, coll. RV *Albatross*, 7 May 1900. Others: **Japan** – 1 male (18.7 × 14.6 mm) (NHM 1961.6.5.120), Sagami Bay, Japan, coll. T. Sakai. — 1 male (with bopyrid) (15.6 × 13.4 mm), 1 female (20.3 × 15.4 mm) (NSMT-Cr 13177), Tosa Bay, coll. RV *Kotoka-Maru*, 21 January 1998. — 1 male (with bopyrid) (NSMT-Cr 1132), off Tsushima Islands, station 10, 33°57.7’N 129°11.6’E, sand and shell substrate, coll. Tsushima Expedition, 26 July 1968. — 1 male, 1 female (USNM 120722), off Ashizuri Peninsula, Shikoku Island, 300 m, coll. T. Sakai & K. Sakai, 27–31 March 1966. — 1 juvenile female (carapace only) (USNM 48483), station 4893, 10–20 miles southwest of Goto Island, Eastern Seas, 106 fathoms, coll. RV *Albatross*, 9 August 1906. — 1 male, 2 females (SMF), Tosa Bay, Kochi, Usa, coll. RV *Toyohata-Maru*, K. Sakai. **Taiwan** – 1 male (22.3 × 17.8 mm) (ZRC 2013.1267), Tashi fishing port, Ilan County, northern Taiwan, coll. 11 July 1989. — 1 broken male (20.8 × 16.7 mm) (ZRC 2013.2371), Tashi fishing port, Ilan County, northern Taiwan, coll. S.-H. Wu, 1997. — 1 ovigerous female (20.4 × 16.4 mm) (ZRC 2013.1270), Tashi fishing port, Ilan County, northern Taiwan, coll. S.-H. Wu, 23 January 1999. — 1 male (22.6 × 17.9 mm) (ZRC 2013.1269), Tashi fishing port, Ilan County, northern Taiwan, coll. S.-H. Wu, 8 March 1999. — 1 male (18.5 × 13.9 mm) (ZRC 2013.1268), Tashi fishing port, Ilan County, northern Taiwan, coll. Hwang, 18 July 2011.

Diagnosis. Carapace branchial area strongly inflated, rounded; with relatively short lateral and branchial spines (Figs. 28A–C, 31A, B). Pseudorostral spines short, diverging (Fig. 37K). Supraorbital eave strongly curved; antorbital spine short, triangular, sharp; intercalated spine triangular, separated from adjacent spines by large gaps; postorbital spine longest, triangular, pointed anteriorly; hepatic spine short pointed outwards (Figs. 28A–C, 37K). Lateral margin with 2 short spines, posterior one larger (often becoming tubercles in larger specimens); branchial region with 1 low spine or tubercle; median row with 4 low spines or tubercles: 2 gastric (posterior one larger), 1 cardiac, 1 intestinal; 2 short spiniform granules on posterior carapace margin (Figs. 28A–C, 31A, B). Basal antennal article long with several granules, 2 strong distal spines (Fig. 40J). Ischium of third maxilliped weakly granulated (Fig. 46G). Ambulatory legs relatively short (Figs. 31C, 56H). G1 distinctly curved, distal part long, tapering with very long setae (Fig. 33A–G).

Remarks. Despite its age, the type specimen is in a relatively good condition although the G1 appears rather frail and not easy to study. However, it agrees well with those from Japan and Taiwan, and we are confident of their conspecificity.

For a detailed discussion of its taxonomy, see remarks for *S. sakaii*.

In Japan, *S. japonica* has been reported from depths of between 85 and 120 m. Outside Japan, it has been recorded from Hong Kong (Griffin & Tranter, 1986), although their specimens should be re-examined.

Sakaija sakaii (Takeda & Miyake, 1969)

(Figs. 28D–G, 33H–J, 46H)

Maja sp. – T. Sakai, 1932: 50, pl. 2 fig. 5, text fig. 5.
Maja japonica – T. Sakai, 1934: 297, text-figs. 10. – T. Sakai, 1936: 99, pl. 25, fig. 2, text-fig. 45. – T. Sakai, 1938: 299, pl. 30, fig. 2. – Takeda, 1982: 128. (not *Maja japonica* Rathbun, 1932).
Maja sakaii Takeda & Miyake, 1969: 512, pl. 17, fig. C. – Serène & Lohavanijaya, 1973: 50 (key). – T. Sakai, 1976: 237, fig. 125a, b, pl. 85 fig. 2. – Huang, 1989: 339. – Takeda, 1993: 43. – Huang, 1994: 583. – Yang et al., 2008: 780. – Ng et al., 2008: 117 (list).

Material examined. Japan – 1 male (9.0 × 6.6 mm) (NSMT-Cr 8094), station 12, Shimoda, Shizuoka Prefecture, coll. M. Takeda, 9 November 1981.

Diagnosis. Carapace branchial area gently inflated, ovate; with relatively short lateral and branchial spines (Fig. 28D, E, G). Pseudorostral spines short, diverging (Fig. 28D–G). Supraorbital eave gently curved; antorbital spine short, triangular, sharp; intercalated spine triangular, separated from adjacent spines by large gaps; postorbital spine longest, triangular, pointed anteriorly; hepatic spine short, pointed outwards (Figs. 28A–C). Lateral margin with 2 short spines, posterior one larger; branchial region with 1 spine; median row with 4 low spines or tubercles: 2 gastric (very low), 1 cardiac (long), 1 intestinal (low); 2 short spines on posterior carapace margin (Fig. 28D, E, G). Basal antennal article long with several granules, 2 strong distal spines (Fig. 28F). Ischium of third maxilliped weakly granulated (Fig. 46H). Ambulatory legs relatively long, slender (Fig. 28D, G). G1 gently curved, distal part relatively short, subspatuliform, lined with long setae (Fig. 33H–J).

Remarks. The identities of *S. japonica* and *S. sakaii* have been confusing. Tune Sakai (1932) first reported a 14.5 by 13.0 mm male specimen as "*Maja* sp." from Sagami Bay that he thought was close to *Maja japonica* Rathbun, 1932, but believed it to be a juvenile, and hence was uncertain of its identity. Tune Sakai (1934) later realised that there were two forms in Japan and both Rathbun (1932) and

Yokoya (1933) had used the same name "*Maja japonica*" independently of each other. Tune Sakai (1934), however, identified one male specimen from the East China Sea as "*M. japonica* Rathbun, 1932", and another female specimen from Nagasaki as "*M. japonica* Yokoya, 1933". He noted that their carapaces, ambulatory leg and G1 structures were starkly different. Believing that his "*M. japonica*" was conspecific with Rathbun's (1932) species, and since the name *Maja japonica* Yokoya, 1933, was preoccupied by *Maja japonica* Rathbun, 1932, T. Sakai (1934) gave a replacement name, *Maja nipponensis* for Yokoya's species (see also T. Sakai, 1936, 1938). Tune Sakai (1965) examined the type of *Maja japonica* Rathbun, 1932, and realised it was actually conspecific with *Maja japonica* Yokoya, 1933, as was *M. nipponensis* T. Sakai, 1934. He also noted that the species he had identified as "*Maja japonica*" in 1934 was an undescribed species, but he did not name it.

Takeda & Miyake (1969: 512) agreed that what T. Sakai (1934, 1936, 1938, 1965) had originally identified as "*Maja japonica*" was a separate but unnamed species for which they chose a new name, *Maja sakaii*. However, since they also designated an ovigerous female measuring 12.9 by 10.0 mm from the East China Sea as the holotype of *M. sakaii*, they were in effect establishing a new species and not just providing a replacement name.

Sakaija japonica is certainly similar to *S. sakaii*, and most of the distinguishing characters originally highlighted by T. Sakai (1934) still apply (see also Takeda & Miyake, 1969). The shape of the carapace is diagnostic, with *M. japonica* more rounded (Fig. 28A–C) while *S. sakaii* is distinctly pyriform (Fig. 28D, E, G). The difference in carapace shape does not appear to be completely size-dependent in members of this genus. In *S. serenei* n. sp., for which a good series of specimens is available for study, the carapace shape changes only slightly with larger specimens more rounded (Fig. 30) but never reaching the condition of *S. japonica* (Fig. 28A–C). Takeda & Miyake's (1969) adult holotype female of *S. sakaii* measures 12.9 by 10.0 mm but its carapace is still distinctly pyriform. Another key character is the proportions of the ambulatory legs. In *S. japonica*, the merus is notably shorter and stouter (Figs. 28A–C, 31C) while those of *S. sakaii* are relatively more slender and longer (Fig. 28D, G).

The G1 structures are quite different. The G1 structures figured for the two species in T. Sakai (1934: text fig. 11) show two different structures and have been used in all subsequent papers by T. Sakai (1934, 1938, 1976) to separate the two species. The G1 of *S. japonica* provided (as *Maja nipponensis*; T. Sakai, 1934: text fig. 11b) is that of a small male from Sagami Bay, measuring 14.5 by 13.0 mm (cf. T. Sakai, 1932: 50, 51) (Fig. 33G). In larger males, the distal part of the G1 is more elongate and has even more long setae (Fig. 33A–F). The G1 of *S. sakaii* figured (as *Maja japonica*; Sakai, 1934: text fig. 11a), apparently from a small male, is drawn at a marginal view and from a different angle from that of *S. japonica* s. str., and shows an ovate distal part densely lined with setae (Fig. 33H). The young male specimen of *S. sakaii* examined in this study has the same kind of G1 although the distal part is slightly less expanded and has less setae (Fig. 33I, J), differences easily attributed to their size. The kind of G1 in *S. sakaii*, however, is quite different from that of *S. japonica*. While the G1 of *S. japonica* is dorsoventrally flattened, like most of the G1s of this genus (with the exception of *S. santo* n. p.), that of *S. sakaii* is actually more laterally flattened, such that the longitudinal groove is not on the inner margin (as in *S. japonica*, Fig. 33A–F) but is fully exposed from the abdominal (ventral) view (Fig. 33H–J). In the form of the G1, *S. sakaii* is closer to *S. santo* from Vanuatu and New Caledonia (Fig. 33S–U) (see discussion for that species).

Sakaija sakaii (like *S. japonica*) is superficially similar to *Alcomaja nagashimaensis* in being a relatively smaller species in which males have inflated chelipeds. *Alcomaja nagashimaensis* can easily be separated not only by the previously discussed generic characters, it can also be distinguished by the carapace possessing proportionately longer and sharper lateral and median spines; the fingers of the adult chelae are less curved and the basal antennal article is smoother (Figs. 17A–C, 39O, 41H).

The figure of *S. sakaii* in Miyake (1983) more closely resembles *S. japonica* with its rounded carapace and is referred there. Huang's (1989, 1994) records from the East China Sea are probably true *S. sakaii*. Serène & Vadon's (1981) record from the Philippines is here referred to *S. serenei*. Griffin & Tranter's (1986) records from the Lesser Sunda Islands, Moluccas, Ambon and Java Sea are uncertain. Whether their material is really *S. sakaii*, or a separate *Sakaija* species will have to be determined through a re-examination of their material.

Sakaija africana (Griffin & Tranter, 1986)
(Figs. 2F, 29, 33N–R, 37L, 40K, 46I, 51C, 54M, 70C)

Maja africana Griffin & Tranter, 1986: 211, 71a–e, 73c, d, Pl. 14. – Ng et al., 2008: 117 (list).

Material examined. Madagascar – 1 male (28.7 × 22.3 mm) (MNHN-IU-2010-57) (specimen barcoded), station 27, between Nosy Bé and Cap Du Leven, MIRIKY, 12°31'S 48°22'E, 298–301 m, coll. MIRIKY, June 2009. — 1 male (32.2 × 25.4 mm) (MNHN-IU-2010-928), station DW 3228, 260–319 m, 12°55'S 48°11'E, 2 July 2009. — 1 male (26.3 × 19.9 mm), 2 ovigerous females (25.7 × 20.2 mm, 23.8 × 18.4 mm) (MNHN-IU-2010-505), station DW 3211, 12°32' 47°52'E, 244–300 m, coll. MIRIKY, 30 June 2009. — 1 male (27.3 × 21.2 mm) (MNHN-IU-2010-932), no other data, coll. MIRIKY, 25 June–14 July 2009. — 1 male (27.3 × 21.2 mm), 1 ovigerous female (25.7 × 19.9 mm) (ZRC 2013.1408, ex MNHN-IU-2010-504), station CP 3188, 12°31'S 48°22'E, 298–301 m, coll. MIRIKY, 27 June 2009.

Diagnosis. Carapace branchial area gently inflated, ovate; with relatively short lateral and branchial spines (Fig. 29). Pseudorostral spines very long, diverging (Fig. 37L). Supraocular eave narrow, strongly curved; antorbital tooth strong, triangular pointed outwards; intercalated spine basally subtruncate, separated from other spines by narrow gaps; postorbital spine large, pointed anteriorly; hepatic spine low, tuberculiform (Figs. 29, 37L). Lateral margin with 2 short spines, subequal or anterior one slightly smaller; 1 large branchial spine; median row with 3 low spines: 1 gastric, 1 cardiac, 1 long, posteriorly directed intestinal; posterior carapace margin with 2 long spines (Fig. 29). Basal antennal article with 2 large distal spines, external margin with 4 blunt teeth (Fig. 40K). Ischium of third maxilliped almost smooth (Fig. 46I). Adult ambulatory legs relatively long, slender (Fig. 29). G1 gently curved, distal part with long setae, with low subdistal swelling (Fig. 33N–R).

Remarks. *Sakaija africana* was described on the basis of one male specimen, 24 mm in carapace length, collected off Durban, Indian Ocean coast of South Africa. It is the largest known species of *Sakaija*. This species seems common in the Mozambique Channel at a depth of around 300 m.

Male and female specimens smaller than the holotype (Fig. 29B, D) generally have relatively shorter ambulatory legs compared to large males (Fig. 29C); with females also having proportionately shorter pseudorostral spines. The G1 figured by Griffin & Tranter (1986: fig. 73c, d) appears to have been drawn in situ and at an angle and not with the structure lying flat on its dorsal or ventral surfaces. The two lobes depicted on their fig. 73d (present Fig. 33N, O) is where the folds overlap (Fig. 33Q, R). They otherwise agree very well in form and structure.

Sakaija serenei n. sp.

(Figs. 30, 31D–F, 33K–M, 37M, 40L, 46J, 51D, 54K, 56I, 70D)

Maja japonica – Serène & Lohavanijaya, 1973: 50, figs. 93–97, pl. 9 fig. A.
Maja sakaii – Serène & Vadon, 1981: 124.

Material examined. Holotype: male (17.4 × 14.7 mm) (NMCR), Balicasag Island, Panglao, Bohol, Philippines, coll. fishermen with tangle nets, July 2003. Paratypes: **Philippines** – 5 males (18.3 × 14.4 mm, 16.0 × 13.5 mm, 15.3 × 11.8 mm, 16.9 × 13.2 mm, 16.5 × 13.1 mm), 3 ovigerous females (15.2 × 11.6 mm, 14.9 × 11.5 mm, 14.4 × 11.3 mm) (ZRC 2013.1263), same data as holotype. — 3 males, 1 female (ZRC 2001.0413) Balicasag Island, Panglao, Bohol, 200–300 m, coll. fishermen with tangle nets, Balicasag Island, Panglao, Bohol, 200–300 m, coll. fishermen with tangle nets, December 2000. — 2 males, 2 females (ZRC 2001.0601) Balicasag Island, Panglao, Bohol, 200–300 m, coll. fishermen with tangle nets, 28 November 2001. — 1 female (NSMT-Cr 15389), Balicasag Island, Panglao, Bohol, coll. local fisherman via M. Takeda & H. Komatsu, February 2003. — 8 males, 5 females (1 ovigerous) (ZRC 2013.1265), Balicasag Island, Panglao, Bohol, 200–300 m, coll. fishermen with tangle nets, November 2003. — 1 male, 1 female (ZRC 2013.1260), Balicasag Island, Panglao, Bohol, 200–300 m, coll. fishermen with tangle nets, December 2003. — 1 male (ZRC 2013.1257), Balicasag Island, Panglao, Bohol, 200–300 m, coll. fishermen with tangle nets, January 2004. — 6 males (smallest 13.9 × 11.3 mm, 14.6 × 11.1 mm; largest 17.1 × 13.8 mm), 1 female (ZRC 2013.1256), 2 males (larger 18.8 × 15.1 mm), 1 female (NSMT-Cr 22330), Balicasag Island, Panglao, Bohol, 200–300 m, coll. fishermen with tangle nets, March 2004. — 1 ovigerous female (ZRC 2013.1244), Balicasag Island, Panglao, Bohol, 200–300 m, coll. fishermen with tangle nets, Balicasag Island, Panglao, Bohol, 200–300 m, coll. fishermen with tangle nets, May 2004. — 11 males, 14 females (ZRC 2013.1255), Balicasag Island, Panglao, Bohol, 200–300 m, coll. fishermen with tangle nets, May 2004. — 2 males (ZRC 2013.1258), Balicasag Island, Panglao, Bohol, 200–300 m, coll. fishermen with tangle nets, 29 May 2004. — 2 males (ZRC 2013.1259), Balicasag Island, Panglao, Bohol, 200–300 m, coll. fishermen with tangle nets, 29 May 2004. — 3 males, 2 females (ZRC 2013.1243), station P4, 9°31.1'N 123°41.5'E, Panglao, Bohol, coll. tangle nets from local fishermen, 31 May 2004. — 1 male, 1 female (AM), Balicasag Island, Panglao, Bohol, 200–300 m, coll. fishermen with tangle nets, 4 June 2004. — 1 male (19.3 × 15.4 mm), 1 female (15.3 × 12.4 mm) (ZRC 2013.1261), Balicasag Island, Panglao, Bohol, coll. fishermen with tangle nets, June 2004. — 1 male (17.7 × 14.6 mm) (ZRC 2013.1262), station 1, Maribojoc Bay, Bohol, 9°36.1'N 123°45.0'E, 90–200 m, coll. tangle nets from local fishermen, 30 May 2004. — 1 ovigerous female (14.4 × 10.7 mm) (ZRC 2013.1242), northwest Panglao, Bohol, coll. J. Arbasto with tangle nets, 2006. **Papua New Guinea** – 1 ovigerous female (18.2 × 14.8 mm) (MNHN-IU-2011-3898), Jacquinot Bay, New Britain, station DW 3770, 05°34'S 151°32'E, 220–294 m, coll. RV *Alis*, BIOPAPUA, 16 October 2010.

Diagnosis. Carapace branchial area gently inflated, ovate; with relatively short lateral and branchial spines (Figs. 30, 31D, E). Pseudorostral spines short, diverging (Fig. 37M). Supraorbital eave distinctly curved with triangular antorbital spine; intercalated spine shorter, triangular; postorbital spine longest, slightly curved outwards and upwards; hepatic spine short (Fig. 37M). Lateral margin with 2 large tubercles or short spines and several smaller granules; 1 low but strong branchial spine; median row with 3 tubercles: 2 gastric, 1 cardiac, intestinal not easily discernible; posterior carapace margin with 2 low tubercles, sometimes not visible (Figs. 30, 31D, E). Basal antennal article covered with granules, with 2 distal blunt spines (Fig. 40L). Ischium of third maxilliped covered with low granules (Fig. 46J). Adult ambulatory legs relatively long (Figs. 30, 56I). G1 gently curved, distal part long, tapering with very long setae (Fig. 33K–M).

Etymology. The species is named after the renowned French carcinologist Raoul Serène, who first recorded this species as *Maja japonica* from the Philippines.

Remarks. The good series of *S. serenei* on hand shows the variation in carapace shape as the specimens increase in size. The carapace is relatively more pyriform (Fig. 30A, B) in smaller specimens of *S. serenei* (ca. carapace length 12 mm) but as they get larger (ca. carapace length 16 mm), the carapace becomes somewhat more rounded in appearance (Fig. 30C). Even so, it never gets as rounded or as broad as similarly sized specimens of *S. japonica* (Fig. 28A–C). The

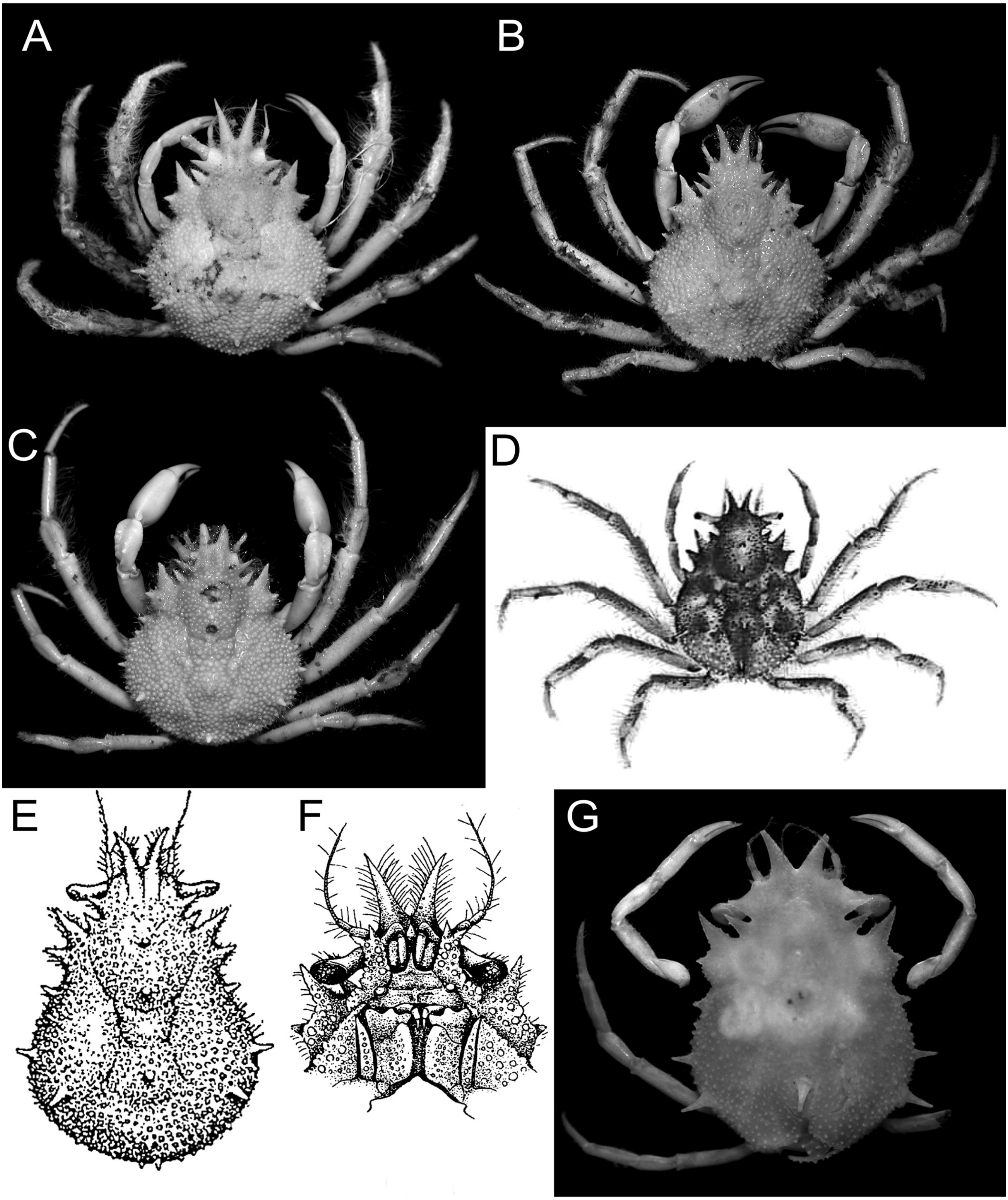

Fig. 28. General habitus, *Sakaija* species. A, *S. japonica*, holotype male (16.2 × 13.0 mm) (USNM 48252), Japan; B, *S. japonica* male (22.6 × 17.9 mm) (ZRC 2013.1269), Tashi fish port, Ilan County, northern Taiwan; C, *S. japonica*, male (22.3 × 17.8 mm) (ZRC 2013.1267), Taiwan; D, *S. sakaii* (as *Maja sakaii*, after T. Sakai 1976: pl. 85 fig. 2); E, *S. sakaii* (as *Maja sakaii*, after T. Sakai, 1976: text-fig. 125a); F, *S. sakaii* (as *Maja* sp., after T. Sakai, 1932: text-fig. 5); G, *S. sakaii*, male (9.0 × 6.6 mm) (NSMT-Cr 8094), Japan.

carapaces are also different in the degree of their inflation and the depth of grooves separating the regions. *Sakaija japonica* differs in having the branchial region more evenly swollen, with the grooves separating it from the gastric, cardiac and intestinal regions visible but shallow and narrow, so much so that the surfaces of all these regions look evenly convex (Figs. 28A–C, 31A, B). In *S. serenei* on the other hand, the grooves separating the branchial region from the gastric, cardiac and intestinal regions are distinct, relatively broader, and the regions are clearly separated (Figs. 30, 31D, E). Since the branchial region is more inflated, the dorsal branchial spine in *S. japonica* is directed obliquely vertically (Figs. 28A–C, 31A, B) while that of *S. serenei* is directly obliquely laterally (Figs. 30, 31D, E). Significantly, the ambulatory legs, notably the meri, are proportionately shorter and stouter in *S. japonica* (Figs. 28A–C, 31C) compared to *S. serenei* where they are relatively more slender and longer (Figs. 30, 31F).

The G1 structures of *S. japonica* and *S. serenei* are superficially similar, both are curved and have the distal part lined with long setae. The G1 of *S. japonica* figured by T. Sakai (1934: text fig. 11b) (as *M. nipponensis*) is that of a small male measuring 14.5 by 13.0 mm, but in larger adult males, the distal part of the G1 is slightly more elongate and more setose (Fig. 33G). However, the G1 structure of adult *S. japonica* clearly differs from that of *S. serenei* by being distinctly more strongly curved outwards (Fig. 33A–F versus Fig. 33K–M).

Serène & Lohavanijaya (1973: 50, figs. 93–97, pl. 9 fig. A) recorded "*Maja japonica*" from off Nhatrang, Vietnam, on the basis of a 16.0 by 11.5 mm male. Their excellent figures leave no doubt that their specimen is *S. serenei*. Serène & Vadon (1981) reported "*Maja sakaii*" from the Philippines, but in view of the present study, their records are almost certainly referrable to *S. serenei* n. sp. instead.

An ovigerous female from Papua New Guinea (MNHN-IU-2011-3898) is tentatively referred to *S. serenei*. Although it was collected some distance from the Philippines, it agrees best with *S. serenei* with regards to the carapace shape and ambulatory leg proportions.

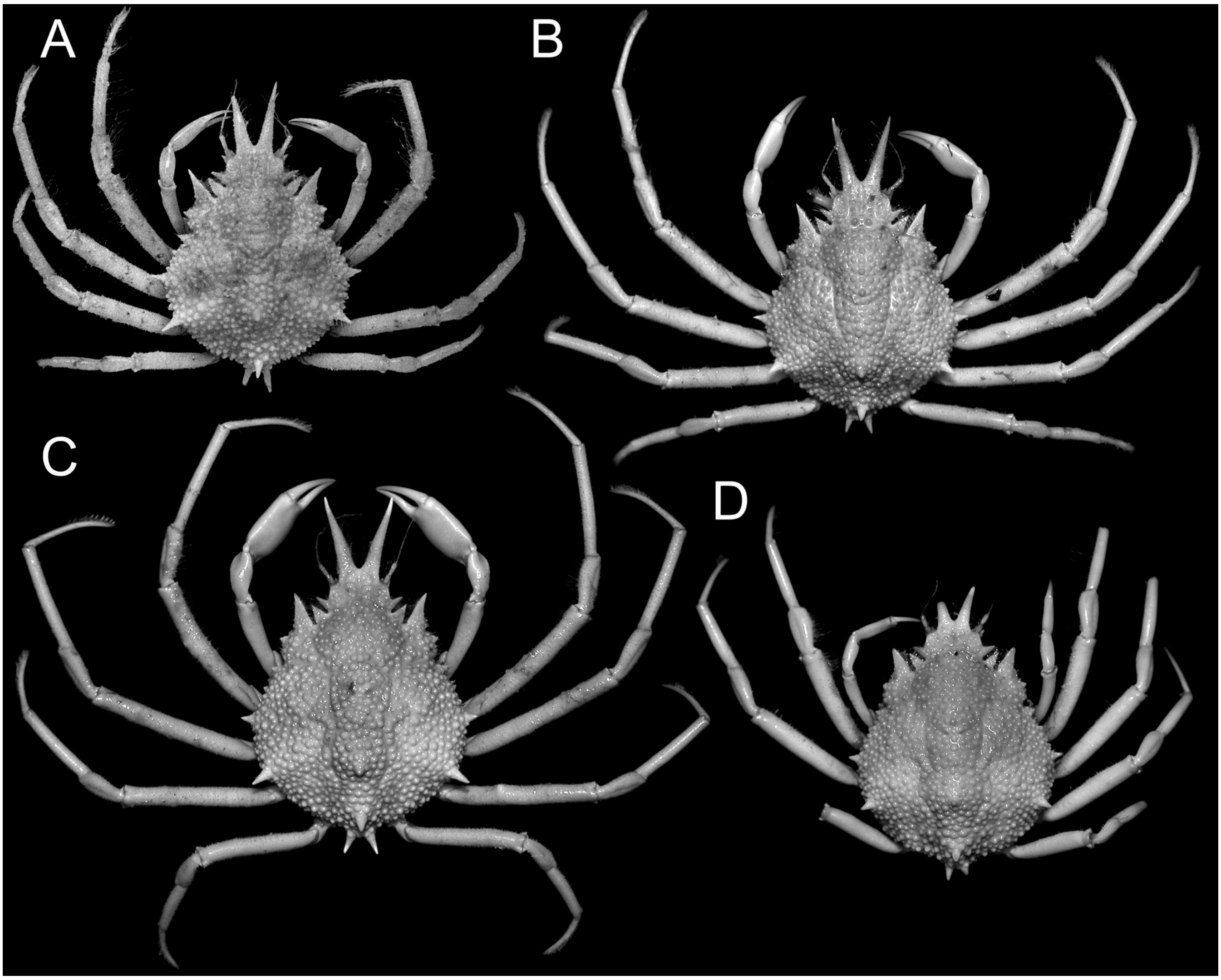

Fig. 29. General habitus, *Sakaija africana*. A, as *Maja africana* (after Griffin & Tranter, 1986: pl. 14a); B, male (27.3 × 21.2 mm) (MNHN-IU-2010-504), Madagascar; C, male (32.2 × 25.4 mm) (MNHN-IU-2010-928), Madagascar; D, ovigerous female (23.8 × 18.4 mm) (MNHN-IU-2010-505), Madagascar.

Sakaija longispinosa n. sp.
(Figs. 32A, B, 37N, 46L)

Material examined. Holotype: ovigerous female (11.4 × 8.6 mm) (NMV J63792), Northwest Shelf, between Port Hedland and Dampier, 18°45.00'S 118°24.00'E, 142 m, Australia, coll. RV *Soela*, 5 June 2007. Paratype: 1 ovigerous female (14.2 × 10.7 mm) (NMV J63197), same data as holotype. Others: **Australia** – 1 ovigerous female (13.4 × 9.7 mm) (NMV J60779), northwestern coast, Adele L26 transect 14°33.41'S 122°54.22'E, 135–165 m, coll. RV *Southern Surveyor*, 4 July 2007.

Diagnosis. Carapace branchial area gently inflated, ovate; with very long lateral and branchial spines (Fig. 32A, B). Pseudorostral spines long, diverging (Fig. 37N). Supraocular eave distinctly curved; antorbital spine strong, curved distally upwards; intercalated spine short, with very wide gaps between spines; postorbital spine long, pointed anteriorly; hepatic spine small, pointed outwards (Fig. 32A, B). Lateral margin with 2 distinct spines, anterior one small; branchial spine very long; median row with 4 spines: 2 gastric (the anterior one reduced), 1 long cardiac, 1 long intestinal; posterior carapace margin with 1 strong median spine and 2 adjacent small spinules or sharp spines (Fig. 32A, B). Basal antennal article with 2 blunt distal teeth, with 3 rows of 4 granules. Ischium of third maxilliped distinctly granulated (Fig. 46L). Ambulatory legs relatively short (Fig. 32A, B). G1 not known.

Etymology. The name alludes to the long carapace spines of the species.

Remarks. This species has proportionately, the longest lateral and branchial spines in any congener, which easily distinguish it. As such, we are confident in referring it to a new species even in the absence of males. One ovigerous specimen (NMV J60779) is tentatively referred to *S. longispinosa*. It appears to be somewhat more setose compared to the others and several of its major spines are broken.

Sakaija santo n. sp.
(Figs. 32C, D, 33S–U, 37O, 40M, 46K, 51E, 54L, 56J, 70E)

Material examined. Holotype: male (9.4 × 6.6 mm) (MNHN), station AT 61, west of Malo Island, Santo, 15°39.2'S 167°01.4'E, 266–281 m, Vanuatu, coll. RV *Alis*, SANTO 2006, 4 October 2006. Paratypes: **Vanuatu** – 2 females (13.2 × 10.1 mm, 13.7 × 10.6 mm) (ZRC 2013.1253), station AT 24, 23 September 2006. — 3 females (13.1 × 10.4 mm, 12.8 × 10.0 mm, 12.6 × 9.0 mm) (ZRC 2013.1245), station AT 64, west of Malo Island, Santo, 15°39.6'S 167°01.9'E, 249–252 m, coll. RV *Alis*, SANTO

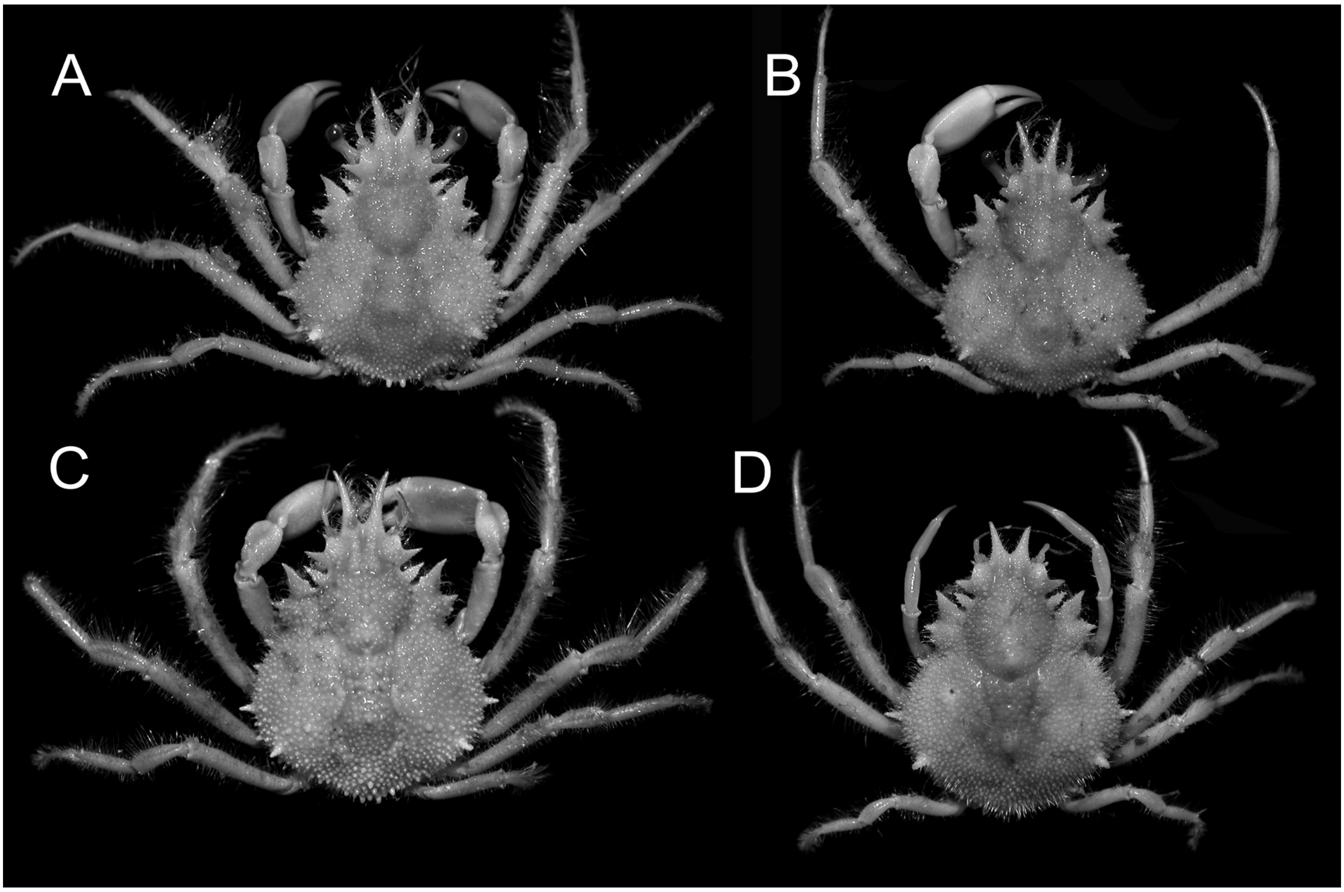

Fig. 30. General habitus, *Sakaija serenei* n. sp. A, paratype male (14.3 × 10.9 mm) (ZRC 2013.1255), Philippines; B, paratype male (17.7 × 14.6 mm) (ZRC 2013.1262), Philippines; C, holotype male (17.4 × 14.7 mm) (NMCR), Philippines; D, paratype female (14.2 × 10.9 mm) (ZRC 2013.1255), Philippines.

2006, 4 October 2006. — 1 female (11.2 × 8.4 mm) (ZRC 2013.1253), Santo, coll. September–October 2006. — 1 male (9.7 × 7.5 mm), 2 females (13.4 × 9.9 mm, 11.5 × 8.7 mm) (ZRC 2013.1254), Santo, coll. September–October 2006. — 1 female (13.4 × 10.4 mm) (ZRC 2013.1251), station AT 61, west of Malo Island, Santo, 15°39.6'S 167°01.9'E, 249–252 m, coll. RV *Alis*, SANTO 2006, 4 October 2006. — 1 female (12.8 × 9.5 mm) (ZRC 2013.1250), station AT 64, west of Malo Island, Santo, 15°39.6'S 167°01.9'E, 249–252 m, coll. RV *Alis*, SANTO 2006, 4 October 2006. — 1 female (8.5 × 6.3 mm) (ZRC 2013.1247), station ZB 6, southwest of Urélapa Island, Santo, 15°36.8'S 167°01.3'E, on patches of sand, 30 m, coll. RV *Alis*, SANTO 2006, 28 September 2006. — 2 females (11.9 × 9.4 mm, 12.5 × 9.9 mm) (ZRC 2013.1246), station AT 86, Scorff Passage, Santo, 15°31.9'S 167°16.2'E, 176–246 m, coll. RV *Alis*, SANTO 2006, 12 October 2006. — 1 male (damaged, 11.1 × 8.5 mm) (ZRC 2013.1248), station AT 117, Scorff Passage, Santo, 15°32.6'S 167°15.5'E, 123–196 m, coll. RV *Alis*, SANTO 2006, 18 October 2006. — 1 female (12.5 × 9.7 mm) (ZRC 2013.1249), station AT 117, Scorff Passage, Santo, 15°32.6'S 167°15.5'E, 123–196 m, coll. RV *Alis*, SANTO 2006, 18 October 2006. Others: **New Caledonia** – 1 male (22.2 × 17.8 mm) (MNHN-IU-2013-1762), station CP 3884, 521–567 m, 22°22'S 171°38'E, coll. EXBODI, 18 September 2011. — 1 female (20.1 × 15.8 mm) (MNHN-IU-2014-4010), station DW 2491, 24°44'S 159°40'E, coll. EBISCO, 18 6 October 2010.

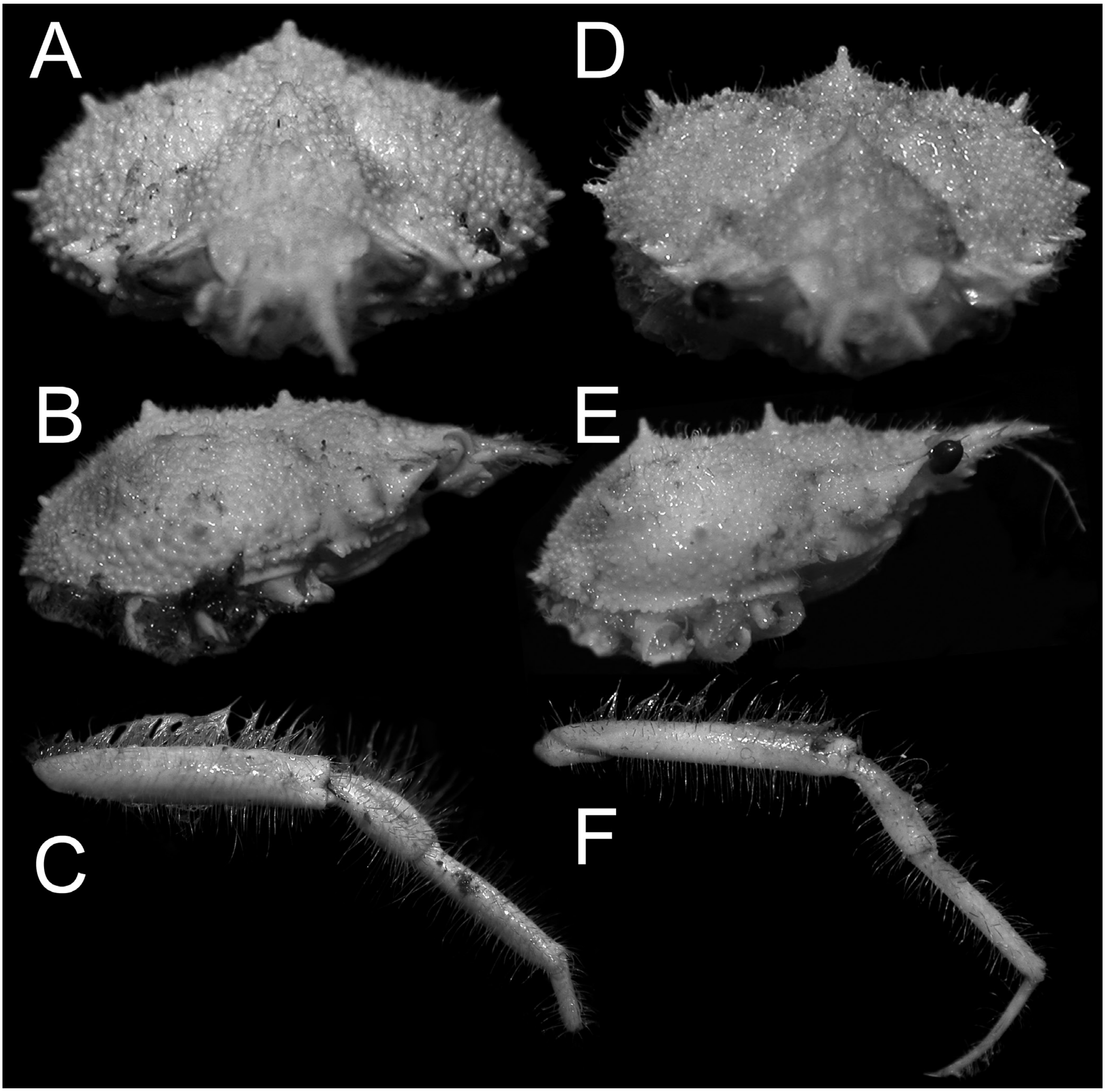

Fig. 31. Frontal and lateral views of carapaces, and right first ambulatory legs, *Sakaija* species. A–C, *S. japonica* male (22.6 × 17.9 mm) (ZRC 2013.1269), Taiwan; D–F, *S. serenei* n. sp., paratype male (17.7 × 14.6 mm) (ZRC 2013.1262), Philippines.

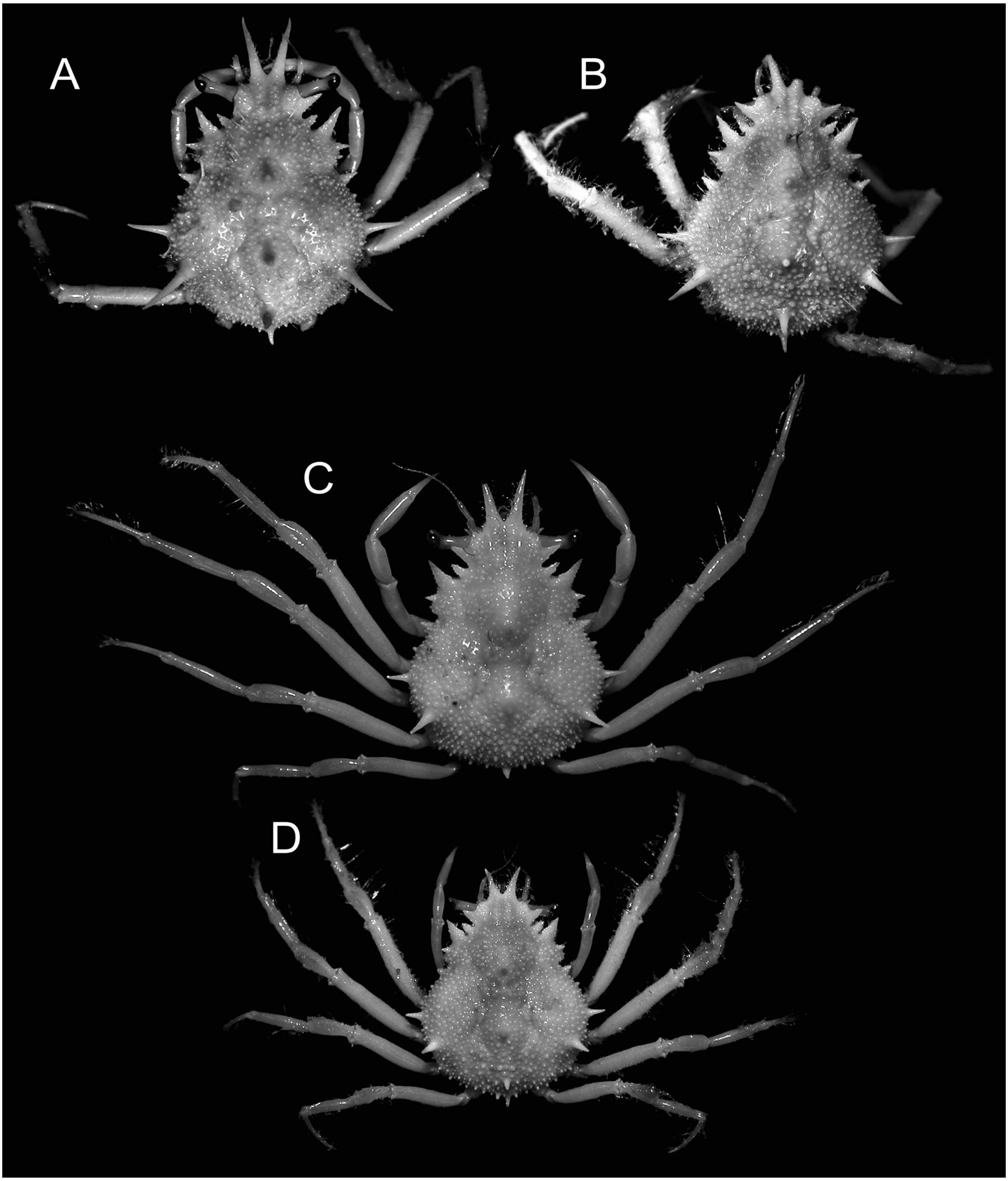

Fig. 32. General habitus, *Sakaija* species. A, *S. longispinosa* n. sp., holotype ovigerous female (11.4 × 8.6 mm) (NMV J63792), Australia; B, *S. longispinosa* n. sp., paratype ovigerous female (14.2 × 10.7 mm) (NMV J63197), Australia; C, *S. santo* n. sp., holotype male (9.4 × 6.6 mm) (MNHN), Vanuatu; D, *S. santo* n. sp., paratype female (13.1 × 10.4 mm) (ZRC 2013.1245), Vanuatu.

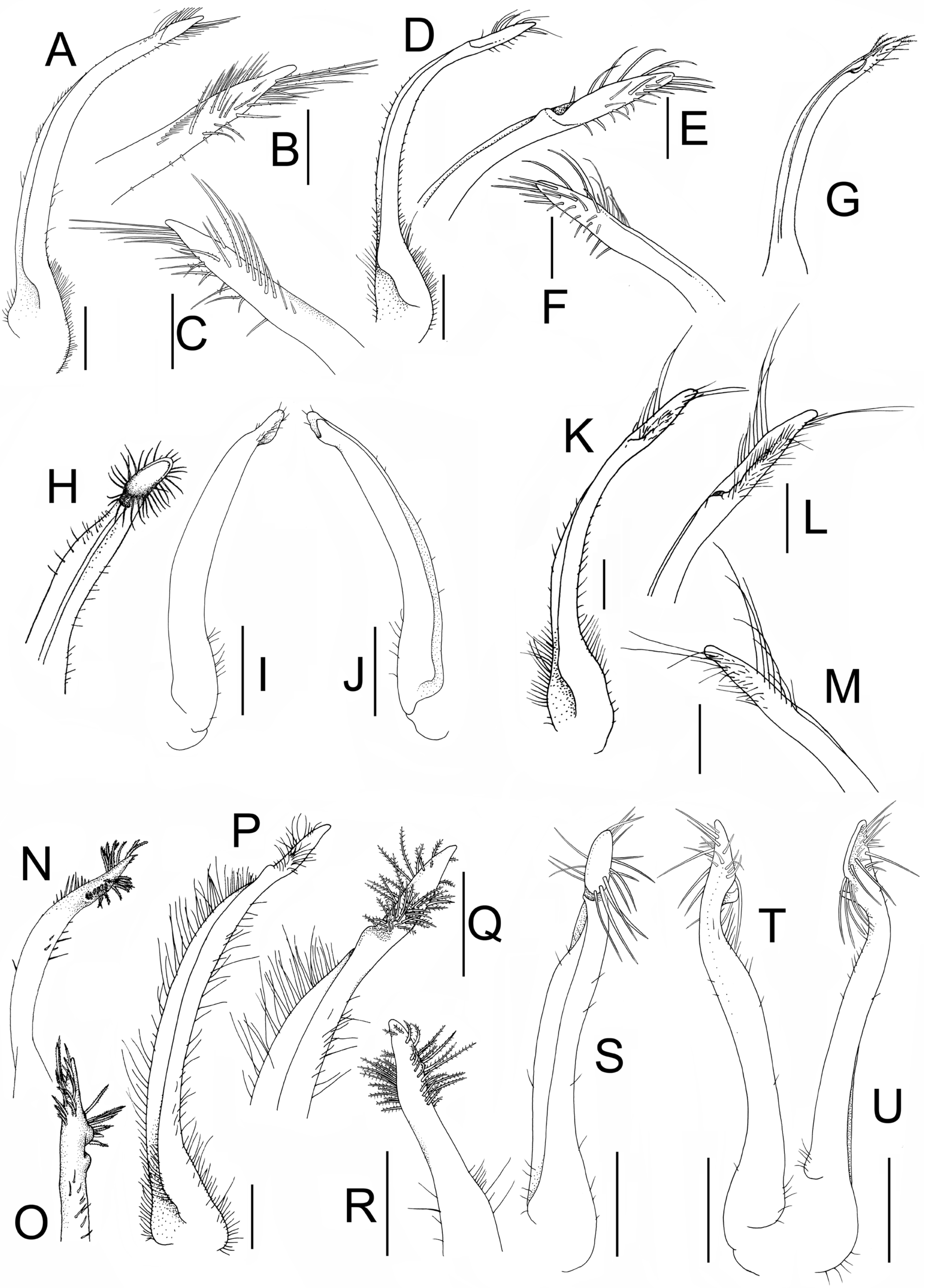

Fig. 33. Left G1s, *Sakaija* species. A–C, *S. japonica*, holotype male (16.2 × 13.0 mm) (USNM 48252), Japan; D–F, *S. japonica*, male (22.3 × 17.8 mm) (ZRC 2013.1267), Taiwan; G, *S. japonica* (as *Maja japonica*, after T. Sakai, 1976: text-fig. 126a); H, *S. sakaii* (as *Maja sakaii*, after Sakai, 1976: text-fig. 125b); I, J, *S. sakaii*, male (9.0 × 6.6 mm) (NSMT-Cr 8094), Japan; K–M, *S. serenei* n. sp., paratype male (14.3 × 10.9 mm) (ZRC 2013.1255), Philippines; N, O, *S. africana* (as *Maja africana*, after Griffin & Tranter, 1986: fig. 73c, d); P–R, *S. africana*, male (32.2 × 25.4 mm) (MNHN-IU-2010-928), Madagascar; S–U, *S. santo* n. sp., holotype male (9.4 × 6.6 mm) (MNHN), Vanuatu. Scale bars = 1.0 mm [D, K, P–R]; 0.5 mm [A, E, F, I, J, L, M, S–U]; 0.25 mm [B, C].

Diagnosis. Carapace branchial area gently inflated, ovate; with short lateral and branchial spines (Fig. 32C, D). Pseudorostral spines long, diverging (Fig. 37O). Supraorbital eave distinctly curved; antorbital spine strong, triangular; intercalated spine short, with large gaps between spines; postorbital spine strong, triangular, directed anteriorly; hepatic spine small, pointed outwards (Fig. 37O). Lateral margin with 2 spines, anterior one small, with granule between them; 1 long branchial spine; median row with 3 spines: 1 gastric (with granule anterior to it), 1 low cardiac; 1 intestinal (sometimes very low); posterior carapace margin with 3 short spines, median one longest (Fig. 32C, D). Basal antennal article with 2 low distal spines, with 2 rows of 3 or 4 granules (Fig. 40M). Ischium of third maxilliped distinctly granulated (Fig. 46K). Ambulatory legs long, slender (Figs. 32C, D, 56J). G1 sinuous, distal part turned backwards towards median line of sternum, with very long setae (Fig. 33S–U).

Etymology. The species is name is derived from the name of the island from which the species was collected, Espiritu Santo in Vanuatu. The name is used as a noun in apposition.

Remarks. In the general carapace morphology and proportions of the ambulatory legs, *S. santo* n. sp. is closest to *S. serenei* n. sp. They differ markedly in the form of the G1, which is gently curved and dorsoventrally flattened in *S. serenei* with the distal part elongate (Fig. 33K–M), but is less curved, more laterally flattened with the distal part ovoid in *S. santo* (Fig. 33S–U). In addition, the posterior carapace margin of *S. santo* is always conspiciously marked by a small but distinct median spine (with 2 smaller lateral ones) (Fig. 32C, D), absent or undiscernible in *S. sakaii* (Fig. 28D, E, G). This median spine may be low in some specimens of *S. santo* but is always visible. In *S. sakaii*, the posterior carapace margin has two median spines that may be very low (Fig. 28D, E, G). In *S. santo*, there are three spines with the median one longest, and while the lateral ones may become reduced, the median one is always distinct (Fig. 32C, D). The G1 structure of *S. santo* (Fig. 33S–U) is most similar to that of *S. sakaii* s. str. but the setae on the ovoid distal part are relatively shorter in the latter species (Fig. 33H–J).

Planaja n. gen.

Diagnosis. Carapace subovoid; dorsal surface gently inflated, covered by sharp granules or low tubercles; gastric and branchial regions clearly delimited by grooves (Fig. 34A, B). Intestinal region with small median spine (Fig. 34A, B). Pseudorostral spines relatively long, slender, diverging (Figs. 34A, B). Supraorbital eave large, anterior part expanded, foliaceous, margin convex, antorbital spine long, sharp (Fig. 38A). Intercalated spine distinct, separated from supraorbital eave and postorbital spine by distinct gaps; postorbital spine strong, long, gently recurved; hepatic region with 1 low but distinct spine, much shorter than postorbital spine; 1 or more tubercles below (Fig. 38A). Lateral carapace margin with 6 or 7 short sharp spines (posterior ones smaller), branchial region with 1 short spine and 1 submedian tubercle (Fig. 34A, B). Posterior carapace margin with 2 very short median spines (Fig. 34A, B). Eyes relatively short, slender, with large ovoid cornea (Fig. 38A). Antennal flagellum short, slender. Basal antennal article longer than broad, rectangular; surface with numerous granules, with 2 spines distally; inner and outer lateral margins granulated; proximal outer angle rounded; antero-external crested rim of antennular fossa touches overlap distal part of basal antennal article by about a third of its width (Fig. 40N). Epistome wider than long, anterior margin with 2 low granular lobes; posterior margin composed of 4 rectangular plates separated by shallow fissures (Figs. 40N, 42G). Suborbital margin separated from basal antennal article and margin of postorbital tooth by deep fissures fissures (Fig. 40N). Outer surface of third maxilliped covered by short setae in adults; ischium subrectangular, just longer than broad; postero-external angle of merus relatively broad, “inserted” into shallower concavity on outer margin of ischium; antero-internal part of ischium rounded, auriculiform (Fig. 46M, N). Male chelipeds relatively short in adult males, surface of merus and carpus finely granulated; carpus long; propodus of palm elongated, curved, smooth, not inflated, palm as long as fingers; fingers long, slender, gently curved, with distinct basal gape when closed (Figs. 34A, B, 54N). Ambulatory legs relatively short, slender; merus without dorsal subdistal spine; dactylus elongate, curved, covered with long setae except for corneous tip (Figs. 34A, B, 56K). Thoracic sternum wide; surfaces of somites 5–8 with numerous prominent rounded tubercles and granules; sternites 3 and 4 depressed; margin between sternites 2 and 3 demarcated by deep notch; anterior margin of sterno-abdominal cavity forming prominent complete rim (Figs. 51F, G, 52K). Male abdomen subtriangular, with 6 free somites and telson; somites 3 and 4 wider than somite 6 and telson (Fig. 51F, G). Male press-button abdominal locking mechanism submedian in position on sterno-abdominal cavity (Fig. 52K). Female abdomen dome-shaped, covering most of thoracic sternum. G1 long, slender, distal part bent approximately 90°, distal part chitinised with rows of short stiff setae, tapering to sharp tip (Fig. 35A–E).

Type species. *Planaja plana* n. sp., by present designation.

Etymology. The name is an arbitrary combination of the Latin “*planus*” for flat and *Maja*. Gender feminine.

Remarks. The main differences between *Planaja* gen. nov. and the other genera treated here have been discussed under *Holthuija* and *Sakaija*. The most diagnostic features of the genus are the relatively flatter carapace in which the dorsal surface is only gently convex, the supraorbital eave is expanded, possessing more spines (six) on the lateral carapace margin, as well as the short and thick ambulatory legs (see key to genera). Another unique character of the type species is that the distal quarter of the G1 is distinctly chitinised and lined with numerous short setae (Fig. 35A–E), a feature not present in other genera in this study. In this respect, the G1 of *Planaja* resembles species of *Leptomithrax* like *L. longimanus* and *L. edwardsii* (unpublished data).

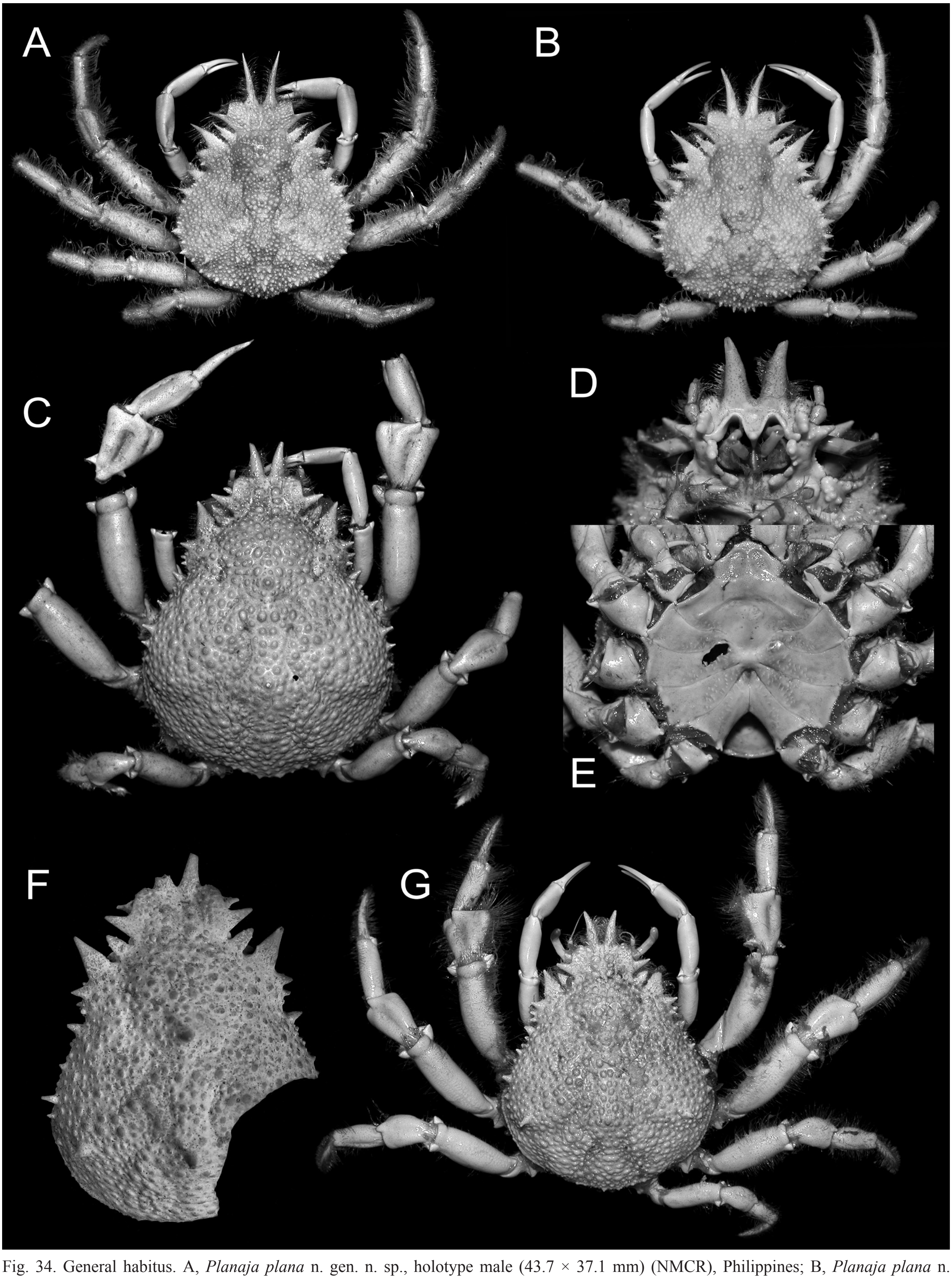

Fig. 34. General habitus. A, *Planaja plana* n. gen. n. sp., holotype male (43.7 × 37.1 mm) (NMCR), Philippines; B, *Planaja plana* n. gen. n. sp., paratype male (38.3 × 30.7 mm) (ZRC 2013.1370), Philippines; C–E, *Ovimaja compressipes*, holotype female (51.2 × 40.5 mm) (NHM 1860.15), China; F, *Ovimaja compressipes* (type of *Maja linapacanensis* Rathbun, 1916, 27.0 × 20.0 mm, USNM 48225), Philippines; G, *Ovimaja compressipes*, male (49.6 × 39.6 mm) (ZRC 2008.1318), Taiwan. A–C, F, G, overall dorsal views; D, antennae, antennules, orbit and epistome; E, thoracic sternum.

Planaja plana **n. sp.**
(Figs. 2G, 34A, B, 35A–E, 38A, 40N, 42G, 46M, N, 51F, G, 52K, 54N, 56K)

Material examined. Holotype: male (43.7 × 37.1 mm) (NMCR), Balicasag Island, Panglao, Bohol, Philippines, coll. fishermen with tangle nets, July 2003. Paratypes: **Philippines** – 3 males (42.9 × 35.0 mm, 38.3 × 30.1 mm, 33.3 × 26.9 mm), 2 ovigerous females (47.9 × 40.9 mm, 45.1 × 37.8 mm) (ZRC 2013.1319), same data as holotype. — 1 male (40.2 × 33.2 mm) (ZRC 2001.0435), Balicasag Island, Panglao, Bohol, coll. fishermen with tangle nets, December 2000. — 8 males (38.2 × 31.7 mm, 44.4 × 36.8 mm, 38.5 × 31.7 mm, 38.7 × 31.0 mm, 38.2 × 31.0 mm, 30.4 × 24.3 mm, 26.3 × 21.2 mm, 34.4 × 27.3 mm), 4 ovigerous females (44.7 × 37.2 mm, 42.4 × 34.5 mm, 36.1 × 29.7 mm, 44.5 × 38.6 mm) (ZRC 2001.0430), Balicasag Island, Panglao, Bohol, coll. fishermen with tangle nets, December 2000. — 1 male (39.3 × 30.3 mm) (ZRC 2001.0591), Balicasag Island, Panglao, Bohol, coll. fishermen with tangle nets, 28 November 2001. — 2 males (40.2 × 31.8 mm, 35.8 × 27.9 mm), 1 female (44.4 × 34.8 mm) (USNM), Balicasag

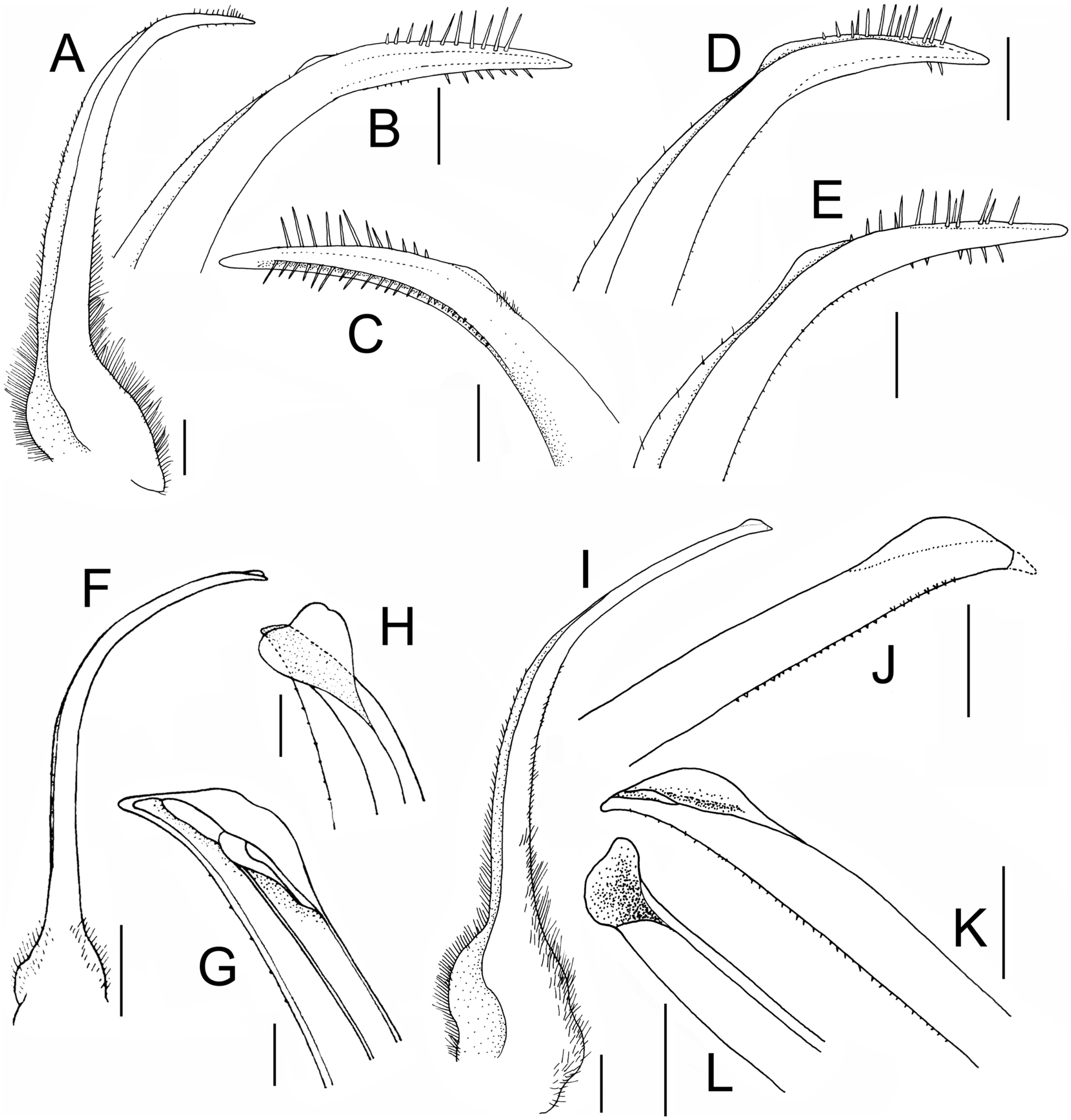

Fig. 35. Left G1s. A–C, *Planaja plana* n. gen. n. sp., holotype male (43.7 × 37.1 mm) (NMCR), Philippines; D, *Planaja plana* n. gen. n. sp., paratype male (38.3 × 30.7 mm) (ZRC 2013.1370), Philippines; E, *Planaja plana* n. gen. n. sp., paratype male (42.8 × 34.3 mm) (AM), Philippines; F–H, *Ovimaja compressipes* (as *Maja brevispinosa*, after Dai, 1981: pl. 1 figs. 8, 9); I–L, *Ovimaja compressipes*, male (49.6 × 39.6 mm) (ZRC 2008.1318), Taiwan. Scale bars = 1.0 mm [A, I]; 2.0 mm [F]; 0.5 mm [B–E, J, K]; 0.2 mm [G, H].

Island, Panglao, Bohol, coll. fishermen with tangle nets, June 2002. — 1 juvenile male (ZRC 2013.1316), Balicasag Island, Panglao, Bohol, 200–300 m, coll. fishermen with tangle nets, June 2002. — 2 males (42.5 × 34.9 mm, 38.1 × 29.8 mm), 1 ovigerous female (48.8 × 41.4 mm), 1 female (45.3 × 37.8 mm) (ZRC 2013.1369), Balicasag Island, Panglao, Bohol, coll. fishermen with tangle nets, July 2003. — 2 males, 1 female (NSMT-Cr 22331), Balicasag Island, Panglao, Bohol, 200–300 m, coll. fishermen with tangle nets, February 2004. — 2 males (22.2 × 17.5 mm, 22.7 × 18.3 mm) (ZRC 2013.1325), Balicasag Island, Panglao, Bohol, 200–300 m, coll. fishermen with tangle nets, May 2004. — 1 male (42.1 × 35.1 mm), 2 ovigerous females (44.8 × 37.2 mm, 44.9 × 37.3 mm) (ZRC 2013.1368), Balicasag Island, Panglao, Bohol, station PN1, coll. P.K.L. Ng from fishermen with tangle nets, 29 May 2004. — 1 male (42.8 × 34.3 mm), 1 female (AM), station PN1, Balicasag Island, Panglao, Bohol, coll. fishermen with tangle nets, January 2004. — 1 female (ZRC 2013.1320), Stn PN 1, Balicasag Island, Panglao, Bohol, coll. fishermen with tangle nets, 3 January 2004. — 1 female (37.1 × 30.2 mm) (ZRC 2013.1321), Balicasag Island, Panglao, Bohol, coll. fishermen with tangle nets, February 2004. — 2 males (35.3 × 28.8 mm, 33.6 × 26.7 mm), 2 females (41.0 × 32.0 mm, 28.9 × 23.0 mm) (ZRC 2013.1326), Balicasag Island, Panglao, Bohol, coll. fishermen with tangle nets, March 2004. — 1 male (38.3 × 30.7 mm) (ZRC 2013.1370), Balicasag Island, Panglao, Bohol, coll. fishermen with tangle nets, 28 May 2004. — 2 males (41.0 × 34.0 mm, 45.4 × 36.5 mm) (ZRC 2012.1206), Balicasag, Panglao, Bohol, 200–300 m, coll. local fishermen with tangle nets, 29 May 2004. — 1 ovigerous female (45.2 × 36.9 mm) (ZRC 2012.1205), station DW 2402, Dipolog Bay, off Balicasag Island, Bohol Sea, 9°30.8'N 123°41.5'E, coll. PANGLAO 2005, 31 May 2005. Others: **Taiwan** – 1 female (46.6 × 40.9 mm) (ZRC 2001.0057), Nangfangao port, Su-Ao, Ilan County, northeastern Taiwan, coll. P.K.L. Ng, 5 November 2000.

Diagnosis. Carapace pyriform; dorsal surface gently convex, covered by numerous rounded granules (Fig. 34A, B). Pseudorostral spines long, diverging (Fig. 38A). Supraorbital eave expanded, with long sharp antorbital tooth; intercalated spine triangular, sharp, shorter than others; postorbital tooth triangular, very long, touching base of long, curved hepatic spine; median row with 5, usually 6 short spines (Fig. 34A, B, 38A). Lateral margin with 6 or 7 short spines, regularly arranged; 1 short branchial spine and 1 submedian tubercle; 3 small spines on posterior carapace margin (Fig. 34A, B). Ambulatory legs short, setose (Figs. 34A, B, 56K). Basal antennal article distinctly granulated with 2 strong spines distally (Fig. 40N). Subhepatic area strongly granulated (Fig. 40N). Ischium of third maxilliped almost smooth, gently rugose or with scattered low granules (Fig. 46M, N). G1 long, slender, distal part bent approximately 90°, distal part chitinised with rows of short stiff setae, tapering to sharp tip (Fig. 35A–E).

Etymology. From the Latin "*planum*" for flattened, alluding to the relatively flatter carapace of the species.

Remarks. *Planaja plana* is superficially similar to *Sakaija japonica* in general form, especially with regard the relatively short ambulatory legs. *Planaja plana*, however, has six or seven lateral carapace spines behind the hepatic one and its dorsal surface is conspicuously less convex. Smaller specimens of *P. plana* about 20 mm in carapace width (e.g., 22.2 × 17.5 mm, 22.7 × 18.3 mm; ZRC 2013.1325) have a slightly more inflated carapace, and the G1 is less strongly bent outwards with the distal part relatively shorter (Fig. 35D).

Surprisingly, this new genus and new species was obtained in large numbers in Balicasag, all collected by tangle nets. None were collected from trawls or dredges from the Philippines. The one specimen from Taiwan, a female (46.6 × 40.9 mm, ZRC 2001.0057), was obtained by a commercial trawl.

Ovimaja n. gen.

Diagnosis. Carapace pyriform, much longer than broad; dorsal surface evenly inflated, covered by low granules or tubercles; gastric and branchial regions delimited by grooves (Fig. 34C, F, G). Intestinal region without median spine (Fig. 34C, F, G). Pseudorostral spines relatively short, diverging (Figs. 34C, D, F, G, 38B, C). Supraorbital eave with anterior part longitudinally narrow, rectangular, not prominently expanded; antorbital spine sharp (Fig. 38B, C). Intercalated spine distinct, separated from supraorbital eave and postorbital spine by distinct gaps; postorbital spine strong, lobiform; hepatic region with 1 distinct spine, much shorter than postorbital spine; 2 or small spines below (Fig. 38B, C). Lateral carapace margin with about 3 short spines and some sharp tubercles, branchial region with 1 low spine, obscure in large specimens (Fig. 34C, F, G). Posterior carapace margin with 2 very short median spines (Fig. 34C, F, G). Eyes long, slender, with long ovoid cornea bent at 30° from horrizontal (Fig. 38B, C). Antennal flagellum short, slender. Basal antennal article longer than broad, rectangular; surface with several rounded granules, with 3 low, blunt spines distally, outer lateral margin entire or with a few small rounded granules; inner lateral margin with 3 large rounded projections with overlaps antennular fossa; proximal outer angle rounded; antero-external crested rim of antennular fossa overlaps halfway into distal part of basal antennal article, forming a hook-like structure (Fig. 40O). Epistome longer than wide, anterior margin with 2 large rounded tubercles; posterior margin composed of 4 rectangular plates separated by deep fissures (Figs. 40O, 42H). Suborbital margin separated from basal antennal article and margin of postorbital tooth by deep fissures (Fig. 40O). Outer surface of third maxilliped covered by setae in adults; ischium subrectangular, slightly longer than broad; postero-external angle of merus relatively broad, "inserted" into shallower concavity on outer margin of ischium; antero-internal part of ischium rounded, auriculiform (Fig. 46O, P). Male chelipeds relatively short in adult males, surfaces of merus and carpus smooth; carpus long; propodus of palm short, smooth, fingers longer than palm; fingers long, slender, gently curved, with basal gape when closed (Figs. 34C, F, G, 54O, P). Ambulatory legs relatively short, slender; merus without dorsal subdistal spine; carpus very short, cordiform

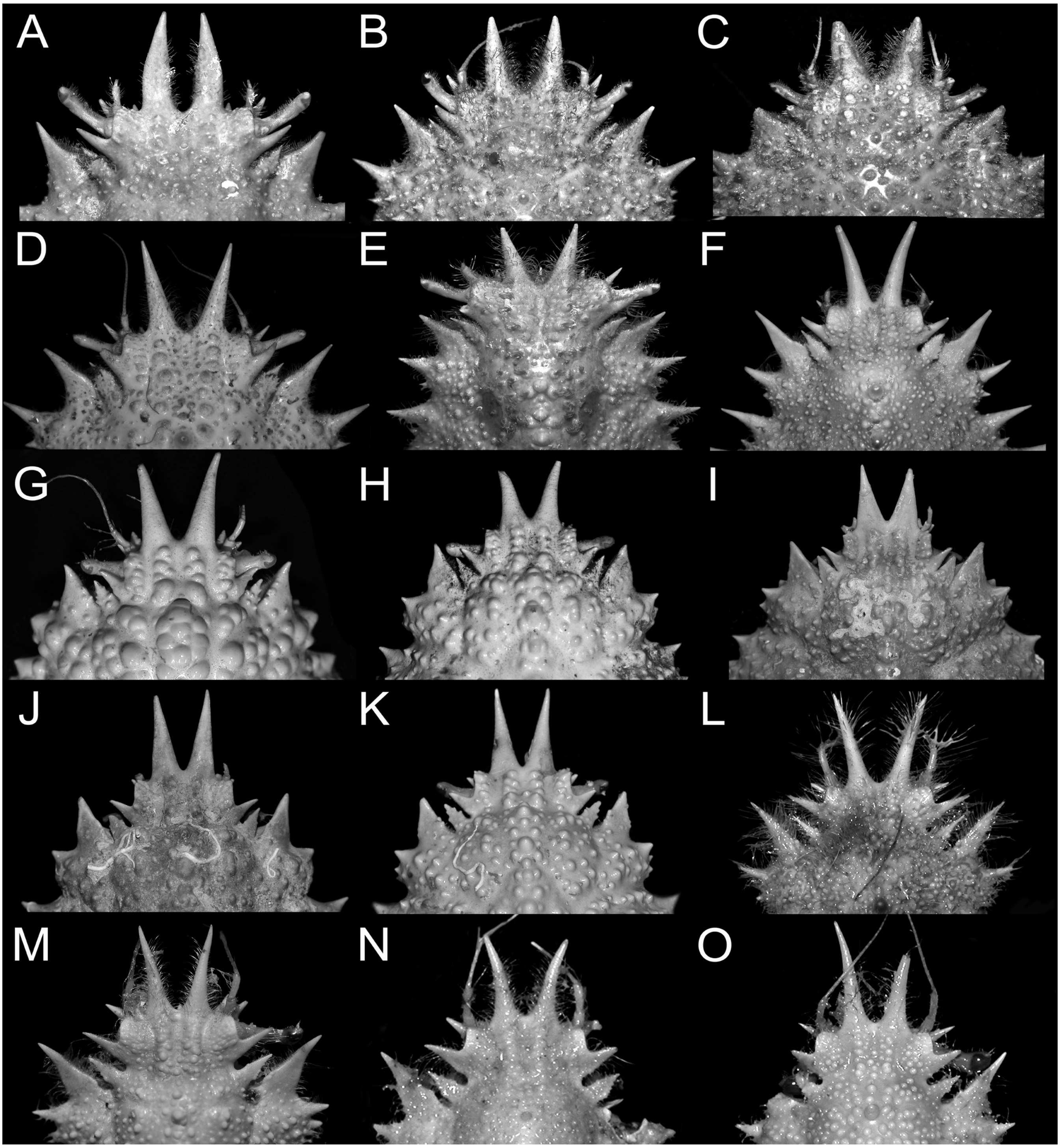

Fig. 36. Frontal regions of carapaces. A, *Maja squinado*, neotype male (147.1 × 126.3 mm) (SMF-4548), Croatia; B, *Maja brachydactyla*, male (98.4 × 89.0 mm) (ZRC 2009.1130), U.K.; C, *Maja brachydactyla*, male (161.2 × 140.1 mm) (ZRC 2008.0179), Spain; D, *Maja cornuta*, male (115.3 × 103.4 mm) (ZRC 2013.1184), South Africa; E, *Maja crispata*, male (63.1 × 51.9 mm) (MNHN-IU-2013-4042), Italy; F, *Neomaja goltziana*, male (73.4 × 65.0 mm) (MNHN-IU-2013-4046), Congo; G, *Paramaja kominatoensis*, dried male (62.6 × 56.1 mm) (KPM NH0104298), Japan; H, *Paramaja kominatoensis*, dried male (73.0 × 66.0 mm) (PCM), Taiwan; I, *Paramaja gibba*, male (79.5 × 77.9 mm) (ZRC 2013.1232), Bay of Bengal; J, *Paramaja turgida* n. sp., holotype male (74.1 × 66.8 mm) (NMCR), Philippines; K, *Paramaja turgida* n. sp., paratype male (67.9 × 60.5 mm) (MNHN), Philippines; L, *Alcomaja desmondi* n. sp., holotype male (35.4 × 28.3 mm) (NMCR), Philippines; M, *Alcomaja nagashimaensis*, male (30.5 × 26.0 mm) (ZRC 2001.430), Philippines; N, *Alcomaja latens* n. sp., holotype male (25.3 × 21.4 mm) (MNHN-IU-2013-4050), Solomon Islands; O, *Alcomaja miriky* n. sp., holotype male (26.4 × 20.9 mm) (MNHN-IU-2010-929), Madagascar.

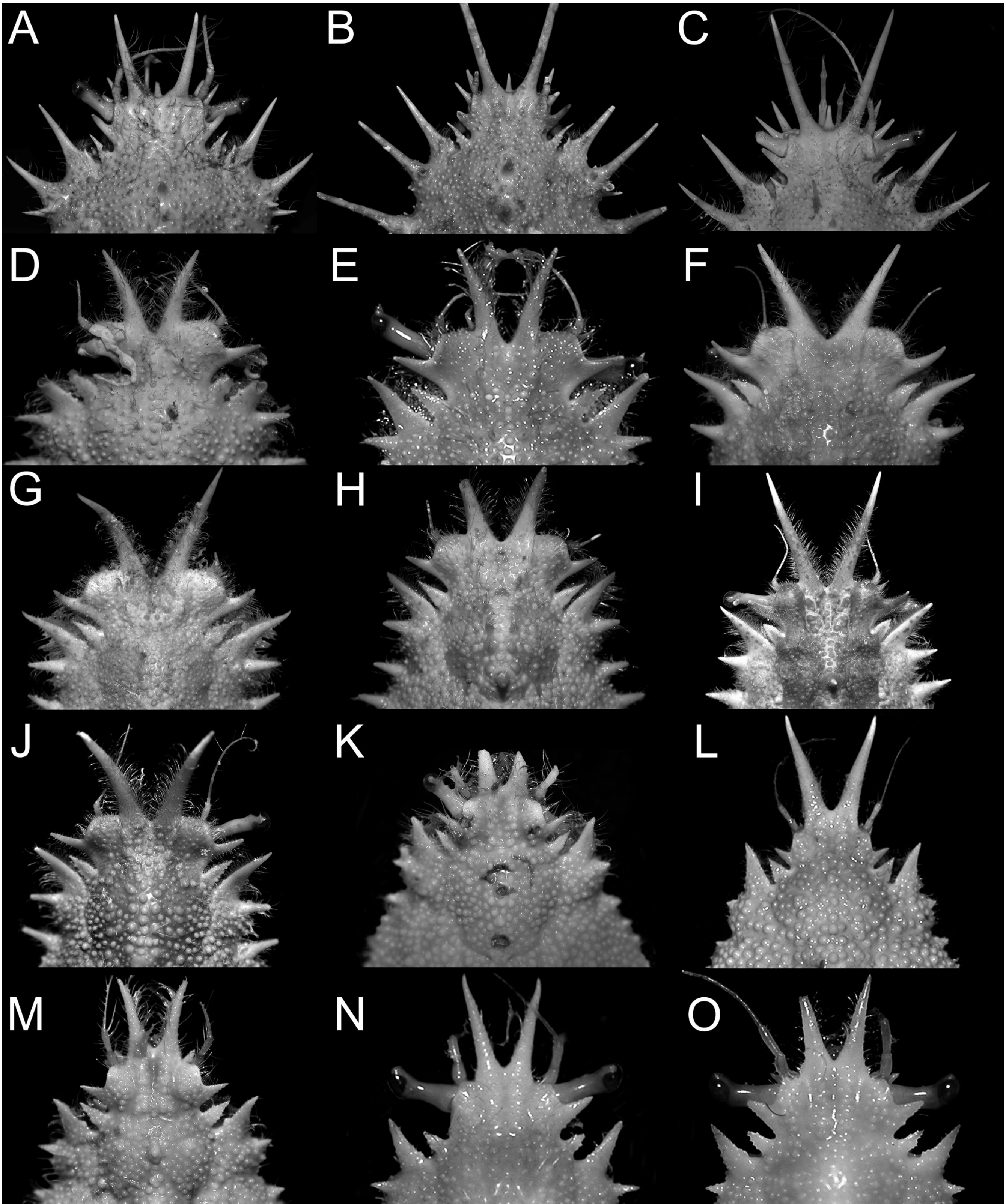

Fig. 37. Frontal regions of carapaces. A, *Paramaya spinigera*, male (85.0 × 66.4 mm) (ZRC 1999.738), Taiwan; B, *Paramaya ouch* n. sp., holotype male (76.8 × 60.0 mm) (NMCR), Philippines; C, *Paramaya coccinea* n. sp., holotype male (69.0 × 55.6 mm) (MNHN), Vanuatu; D, *Holthuija miersi*, male (32.6 × 25.6 mm) (ZRC 2000.1497), Singapore; E, *Holthuija miersii*, male (22.3 × 16.5 mm) (CBM ZC4001), Singapore; F, *Holthuija suluensis*, holotype female (32.4 × 41.2 mm) (USNM 48224a), Philippines; G, *Holthuija pauli* n. sp., holotype male (37.3 × 28.0 mm) (NMCR), Philippines; H, *Holthuija cognata* n. sp., holotype male (29.5 × 23.7 mm) (CBM-ZC3662), Japan; I, *Holthuija aussie* n. sp., holotype ovigerous female (42.1 × 34.4 mm) (NMV J63752), Arafura Sea; J, *Holthuija poorei* n. sp., paratype female (27.0 × 22.5 mm) (NMV J63751), Arafura Sea; K, *Sakaija japonica*, male (22.3 × 17.8 mm) (ZRC 2013.1267), Taiwan; L, *Sakaija africana*, male (32.2 × 25.4 mm) (MNHN-IU-2010-928), Madagascar; M, *Sakaija serenei* n. sp., holotype male (17.4 × 14.7 mm) (NMCR), Philippines; N, *Sakaija longispinosa* n. sp., holotype ovigerous female (11.4 × 8.6 mm) (NMV J63792), Australia; O, *Sakaija santo* n. sp., holotype male (9.4 × 6.6 mm) (MNHN), Vanuatu.

with deep median groove; dactylus elongate, slightly curved, covered with long setae except for corneous tip (Figs. 34C, F, G, 56L). Thoracic sternum wide; surfaces of somites 5–8 almost smooth; sternites 3 and 4 slightly depressed; margin between sternites 2 and 3 demarcated by very deep notch, forming waist-like structure; anterior margin of sterno-abdominal cavity not forming complete rim (Figs. 51I, 52L). Male abdomen subrectangular, with 6 free somites and telson; somites 6 wider than all other somites and telson (Fig. 51I). Male press-button abdominal locking mechanism laterally positioned on sterno-abdominal cavity (Fig. 52L). Female abdomen dome-shaped, covering most of thoracic sternum. G1 very long, slender, distal part elongated, curved outwards, with 2 distal folds and sharp tip, distal part with scattered very short setae (Fig. 35F–L).

Type species. *Paramithrax* (*Leptomithrax*) *compressipes* Miers, 1879, by present designation.

Etymology. The genus name is derived from an arbitrary combination of the Latin "*ovum*" for egg and *Maja*, alluding to the egg-like appearance of the carapace of the type species. Gender feminine.

Remarks. *Ovimaja* n. gen. is very different from *Maja* s. str. and the various genera recognised here. Aside from the distinctively elongated carapace (Fig. 34C, F, G), the structure of the basal antennal article is unique, with the inner margin lined with three prominent projections (Figs. 40O, 42H); the anterior margin of the epistome has two large projections (Figs. 40O, 42H); the male anterior thoracic sternum is waist-like, with the region between sternites 2 and 3 deeply constricted (Figs. 51I, 52L); the carpus of the ambulatory leg is very short, enlarged and flattened (Fig. 56L); and the G1 is very long and curved with the distal part very slender (Fig. 35I–L). *Ovimaja* has a very different male abdominal locking mechanism from the other genera. In these genera, including *Maja* s. str., the press-button is submedian in position (Fig. 52A–K). In *Ovimaja*, the press-button is positioned laterally on thoracic sternite 5, near the margin of the sterno-abdominal cavity (Fig. 52L).

One fossil species described from South Australia, *Maja robinsoni* Jenkins, 1985, is almost certainly a species of *Ovimaja*. Described on the basis of nine carapaces (the holotype 31.0 × 24.0 mm) from the mid to late Early Miocene (ca. 16–23 million years ago). The carapace of *M. robinsoni* (cf. Jenkins, 1985: pl. 2 figs. 2a, 3) is similar to *O. compressipes*, but the granules on the posterior half of the carapace appear to be more closely packed (less packed in *O. compressipes*, Fig. 34C, F, G) and the lobulation on the epistome and margins of the antenna is less distinct (Jenkins, 1985: pl. 2 fig. 2d, e) (cf. Fig. 40O).

Ovimaja compressipes (Miers, 1879) comb. nov.

(Figs. 2H, 34C–G, 35F–L, 38B, C, 40O, 42H, 46O, P, 51H, I, 52L, 54O, P, 56L, 70F)

Paramithrax (*Leptomithrax*) *compressipes* Miers, 1879: 8.
Maja compressipes – Griffin & Tranter, 1986: 211, 212, pl. 15a, b. – Chen & Ng, 1995: 758. – Rahayu & Ng, 2000: 888. – Maramura & Kosaka, 2003: 34. – Yang et al., 2008: 780. – Ng et al., 2008: 117 (list).
Leptomithrax compressipes – Serène, 1968: 57. – Huang, 1994: 583.
Maja linapacanensis Rathbun, 1916: 553. – Serène, 1968: 57. – Griffin, 1976: 200. – Griffin & Tranter, 1986: 213 (discussion).
Maja gibba – Serène & Lohavanijaya, 1973: 163, pl. 9B. (not *Maja gibba* Alcock, 1895).
Maja brevispinosa Dai, 1981: 37, 38, pl. I: 8–10.
Maja brevispinosis [sic] – Dai et al., 1986: 136, pl. 18(2), figs. 77(1–4). – Dai & Yang, 1991: 151, pl. 18(2), figs. 77(1–4). – Huang, 1994: 582.

Material examined. Holotype male (51.2 × 40.5 mm) (NHM 1860.15), Canton (= Guangzhou), China, coll. Horsfield, East India Company. Others: **Philippines** – 1 dried carapace (27.0 × 20.0 mm) (with spines, length 31.8, width (right side broken, 19.6 mm) (USNM 48225) (holotype of *Maja linapacanensis* Rathbun, 1916) [photographs examined], Observatory Island, Linapacan Strait, north of Palawan, 46 fathoms, 11°37.25'N 119°48.75'E, coll. RV *Albatross*, 18 December 1908. **Taiwan** – 1 male (49.6 × 39.6 mm) (ZRC 2008.1318), Penghu Islands, coll. S.-H. Wu, 5 September 1974. — 1 male (55.7 × 42.7 mm) (ZRC 2013.1264), coll. 1990s. **South China Sea** – 1 young female (45.6 × 35.4 mm) (ZRC 1999.1260), southern part of South China Sea, coll. commercial trawlers, 26 November 1982. **Thailand** – 1 male (41.1 × 30.3 mm) (ZRC 2003.0162), Pattani Province, Saiburi Crab Landing, Pattani Province, southeastern Thailand, coll. Z. Jaafar et al., 7 June 2003. — 2 males (45.5 × 36.8 mm, 40.3 × 30.4 mm) (ZRC 2003.0196), Pattani Province, Saiburi

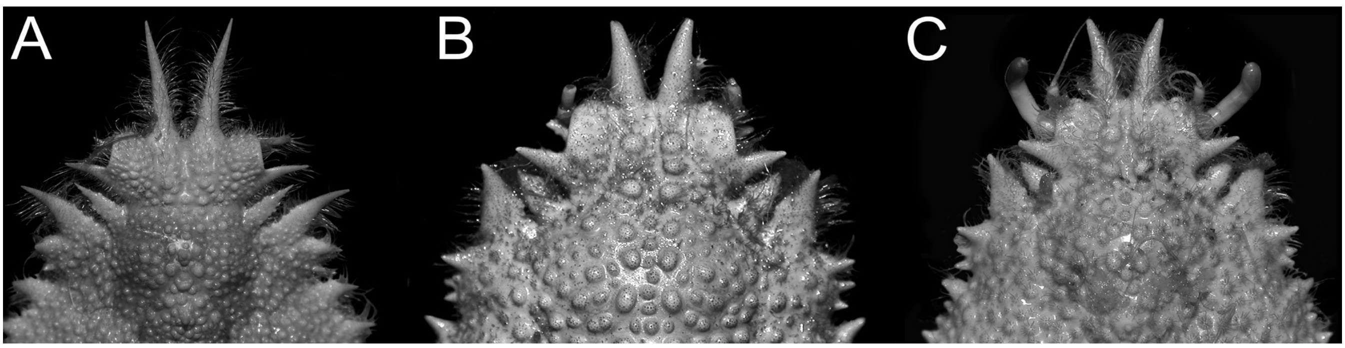

Fig. 38. Frontal regions of carapaces. A, *Planaja plana* n. gen. n. sp., holotype male (43.7 × 37.1 mm) (NMCR), Philippines; B, *Ovimaja compressipes*, holotype female (51.2 × 40.5 mm) (NHM 1860.15), China; C, *Ovimaja compressipes*, male (49.6 × 39.6 mm) (ZRC 2008.1318), Taiwan.

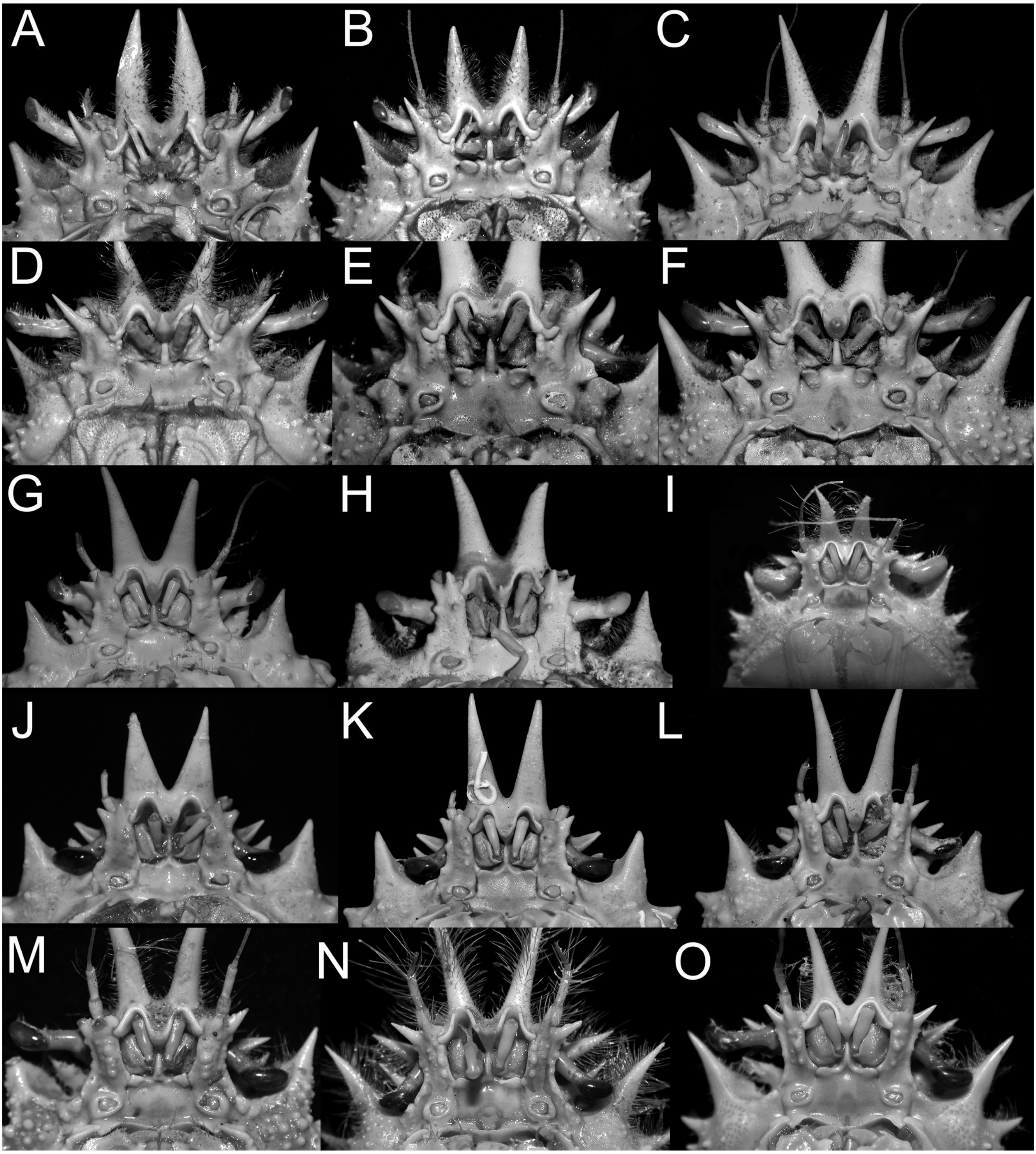

Fig. 39. Antennae, antennules and epistomes. A, *Maja squinado*, neotype male (147.1 × 126.3 mm) (SMF-4548), Croatia; B, *Maja brachydactyla*, male (98.4 × 89.0 mm) (ZRC 2009.1130), U.K.; C, *Maja cornuta*, male (115.3 × 103.4 mm) (ZRC 2013.1184), South Africa; D, *Maja crispata*, male (63.1 × 51.9 mm) (MNHN-IU-2013-4042), Italy; E, *Neomaja goltziana*, male (73.4 × 65.0 mm) (MNHN-IU-2013-4046), Congo; F, *Neomaja goltziana*, male (90.2 × 83.1 mm) (MNHN-IU-2013-4044), Gabon; G, *Paramaja kominatoensis*, dried male (62.6 × 56.1 mm) (KPM NH0104298), Japan; H, *Paramaja kominatoensis*, dried male (73.0 × 66.0 mm) (PCM), Taiwan; I, *Paramaja gibba*, lectotype female (25.1 × 21.2 mm) (NHM 1896.5.14.9), India; J, *Paramaja gibba*, male (79.5 × 77.9 mm) (ZRC 2013.1232), Bay of Bengal; K, *Paramaja turgida* n. sp., holotype male (74.1 × 66.8 mm) (NMCR), Philippines; L, *Alcomaja irrorata* n. sp., holotype male (52.6 × 45.7 mm) (NMCR), Philippines; M, *Alcomaja gracilipes*, male (41.4 × 35.4 mm) (ZRC 2013.1225), Philippines; N, *Alcomaja desmondi* n. sp., holotype male (35.4 × 28.3 mm) (NMCR), Philippines; O, *Alcomaja nagashimaensis*, male (30.5 × 26.0 mm) (ZRC 2001.430), Philippines.

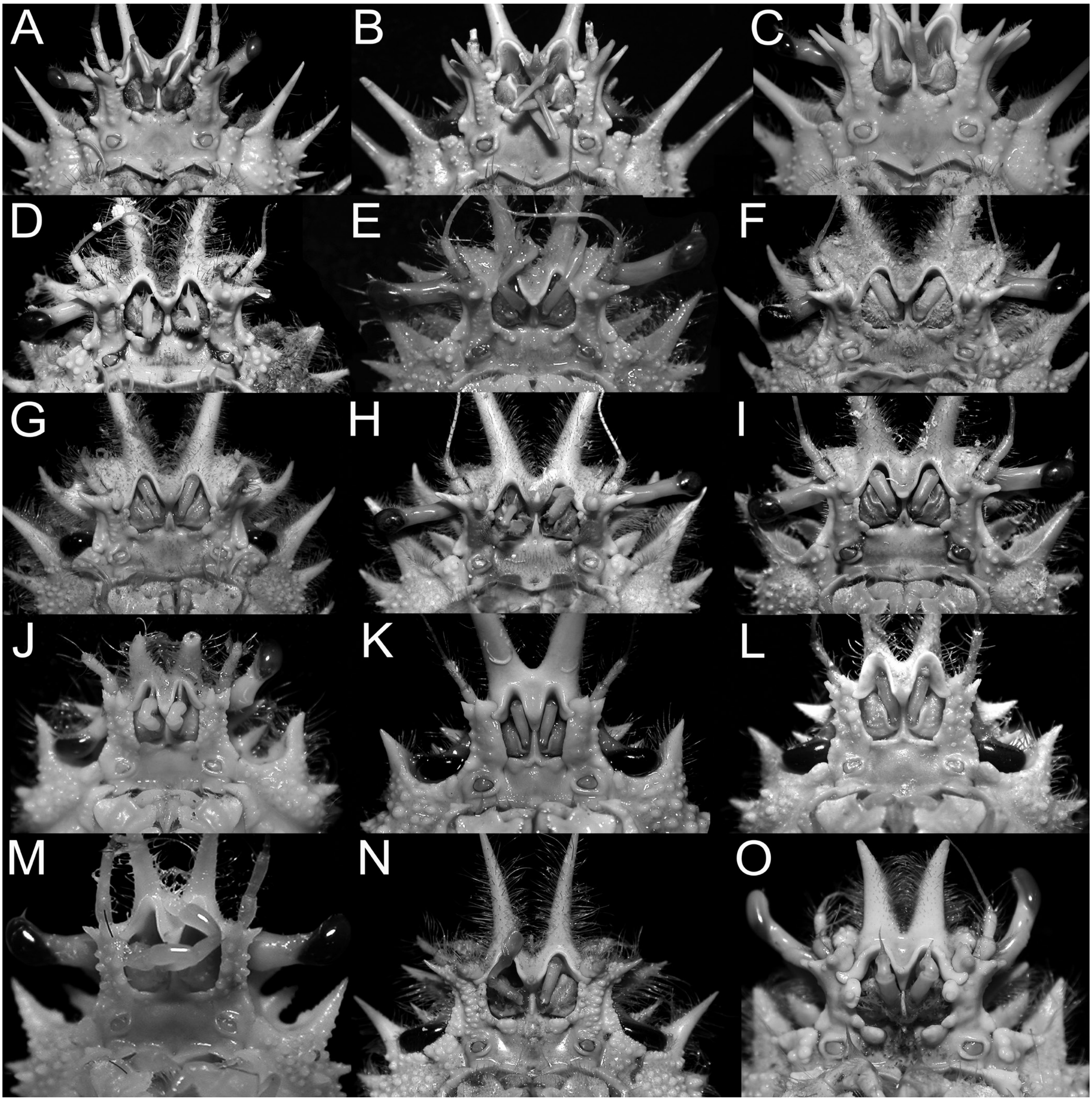

Fig. 40. Antennae, antennules and epistomes. A, *Paramaya spinigera*, male (85.0 × 66.4 mm) (ZRC 1999.738), Taiwan; B, *Paramaya ouch* n. sp., holotype male (76.8 × 60.0 mm) (NMCR), Philippines; C, *Paramaya coccinea* n. sp., holotype male (69.0 × 55.6 mm) (MNHN), Vanuatu; D, *Holthuija miersi*, male (32.6 × 25.6 mm) (ZRC 2000.1497), Singapore; E, *Holthuija miersii*, male (22.3 × 16.5 mm) (CBM ZC4001), Singapore; F, *Holthuija suluensis*, holotype female (32.4 × 41.2 mm) (USNM 48224a), Philippines; G, *Holthuija pauli* n. sp., holotype male (37.3 × 28.0 mm) (NMCR), Philippines; H, *Holthuija aussie* n. sp., holotype ovigerous female (42.1 × 34.4 mm) (NMV J63752), Arafura Sea; I, *Holthuija poorei* n. sp., holotype male (24.3 × 18.7 mm) (NMV J63749), Timor Sea; J, *Sakaija japonica*, male (22.3 × 17.8 mm) (ZRC 2013.1267), Taiwan; K, *Sakaija africana*, male (32.2 × 25.4 mm) (MNHN-IU-2010-928), Madagascar; L, *Sakaija serenei* n. sp., holotype male (17.4 × 14.7 mm) (NMCR), Philippines; M, *Sakaija santo* n. sp., holotype male (9.4 × 6.6 mm) (MNHN), Vanuatu; N, *Planaja plana* n. gen. n. sp., holotype male (43.7 × 37.1 mm) (NMCR), Philippines; O, *Ovimaja compressipes*, male (49.6 × 39.6 mm) (ZRC 2008.1318), Taiwan.

Crab Landing, Pattani Province, southeastern Thailand, coll. Z. Jaafar et al., 8 June 2003.

Diagnosis. Carapace dorsal surface covered with large rounded granules, with groups of long hooked setae on each granule; branchial area rounded, deliminated by deep narrow grooves (Fig. 34C, F, G). Pseudorostral spines short, diverging outwards (Fig. 38B, C). Supraorbital eave large, antorbital spine sharp, covered by hooked setae, with 2 rows of large granules parallel to spines; intercalated spine short, triangular; postorbital spine largest, directed anteriorly; small hepatic spine oriented outwards (Fig. 38B, C). Lateral margin with 5–7 sharp granules; median row with 2 small spines: 1 gastric, 1 cardiac; 1 spine on branchial region; 2 very small spines on posterior carapace margin (Fig. 34C, F, G). Basal antennal article very broad, with 4 large blunt spines, 3 distal and 1 on inner margin, 1 large proximal granule on inner margin (Figs. 40O, 42H). Pterygostomian area prominently granulated (Figs. 34D, 40O, 42H). Ambulatory legs short, with stout, short segments, covered with long hooked setae; merus short (Fig. 34C, G, 40O, 56L). G1 long, slender, strongly curved, with 2 distal folds and sharp tip (Fig. 35F–L).

Remarks. *Maja compressipes* was originally described from Canton (present day Guangzhou) in China. It has since been reported from other parts of China and Japan (e.g., Yang et

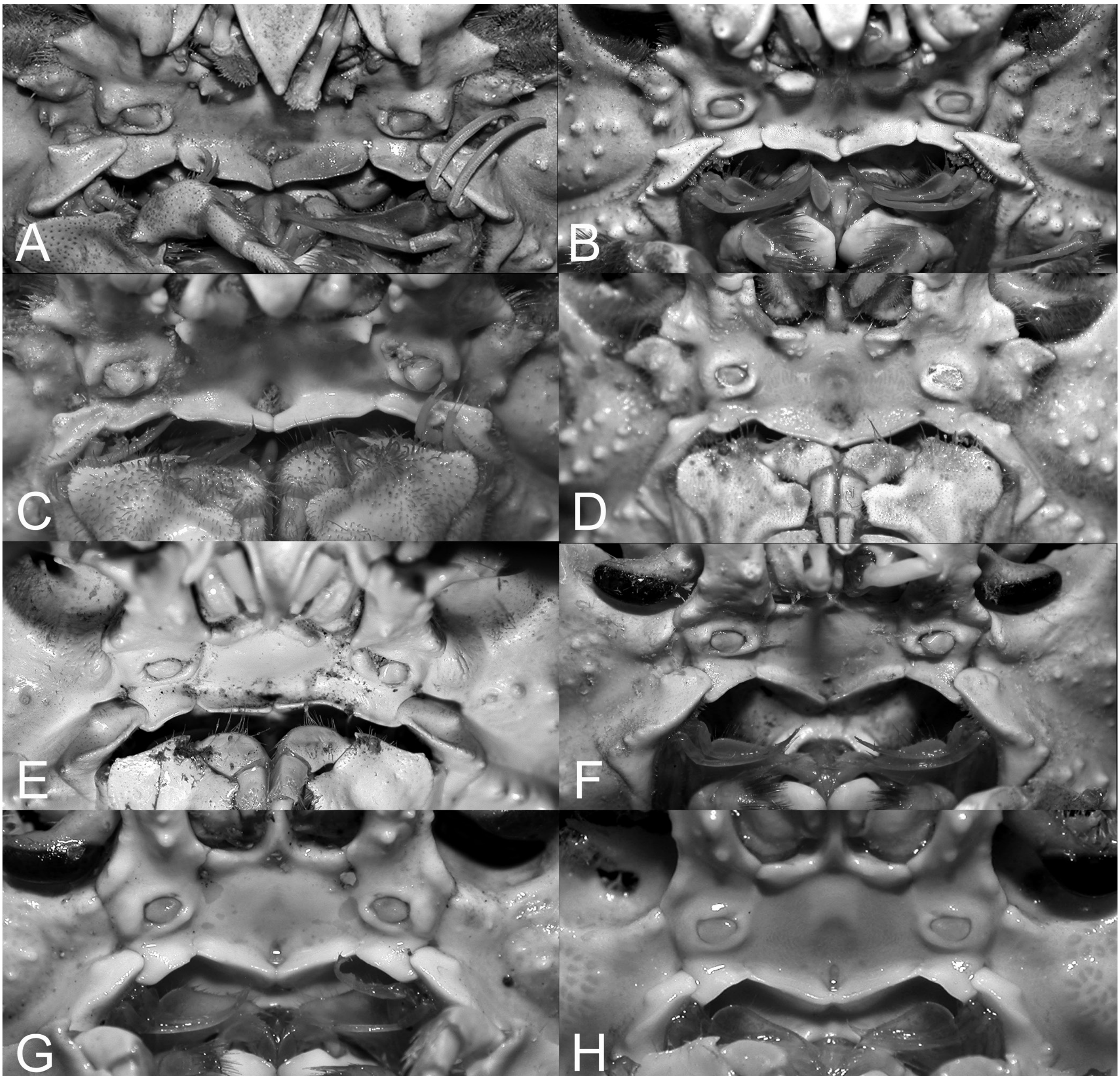

Fig. 41. Epistomes. A, *Maja squinado*, neotype male (147.1 × 126.3 mm) (SMF-4548), Croatia; B, *Maja brachydactyla*, male (98.4 × 89.0 mm) (ZRC 2009.1130), U.K.; C, *Maja crispata*, male (63.1 × 51.9 mm) (MNHN-IU-2013-4042), Italy; D, *Neomaja goltziana*, male (73.4 × 65.0 mm) (MNHN-IU-2013-4046), Congo; E, *Paramaja kominatoensis*, dried male (62.6 × 56.1 mm) (KPM NH0104298), Japan; F, *Paramaja gibba*, male (79.5 × 77.9 mm) (ZRC 2013.1232), Bay of Bengal; G, *Alcomaja irrorata* n. sp., holotype male (52.6 × 45.7 mm) (NMCR), Philippines; H, *Alcomaja nagashimaensis*, male (30.5 × 26.0 mm) (ZRC 2001.430), Philippines.

al., 2008; Maramura & Kosaka, 2003), Philippines (Rathbun, 1916, as *Maja linapacanensis*) and the Straits of Malacca (Rahayu & Ng, 2000), and we have material from the Gulf of Thailand, South China Sea and Taiwan.

The species is very characteristic in having an elongated and not inflated carapace; the carapace and ambulatory legs are covered by a thick tomentum of long setae which gathers a substantial amount of mud and debris; the basal antennal article is very broad with large tubercles on its distal part; the ambulatory legs are very short and the carpus is very short and cordiform. The photograph of a specimen attributed to "*Maja gibba*" from Indonesia in Serène & Lohavanijaya (1973: 163, pl. IXB) is almost certainly *Ovimaja compressipes* considering its setose body and very wide ambulatory carpus.

Griffin & Tranter (1986: 213) suggested that *Maja linapacanensis* Rathbun, 1916, described only from a broken carapace, is conspecific with *M. compressipes*, but they did not formally synonymise them. Examination of the types of both species leaves no doubt the two taxa are synonymous.

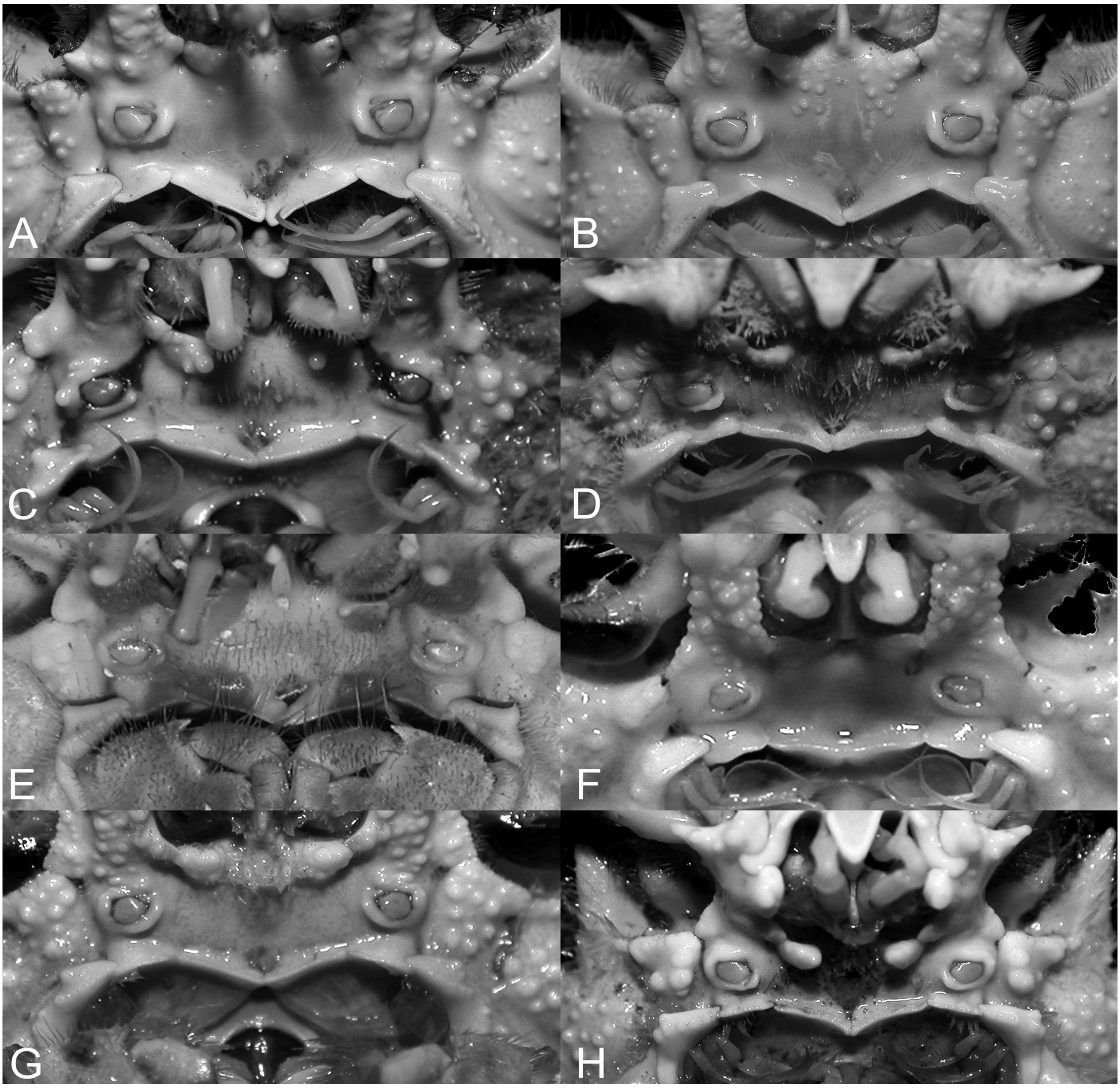

Fig. 42. Epistomes. A, *Paramaya spinigera*, male (85.0 × 66.4 mm) (ZRC 1999.738), Taiwan; B, *Paramaya coccinea* n. sp., holotype male (69.0 × 55.6 mm) (MNHN), Vanuatu; C, *Holthuija miersi*, male (32.6 × 25.6 mm) (ZRC 2000.1497), Singapore; D, *Holthuija suluensis*, holotype female (32.4 × 41.2 mm) (USNM 48224a), Philippines; E, *Holthuija aussie* n. sp., holotype ovigerous female (42.1 × 34.4 mm) (NMV J63752), Arafura Sea; F, *Sakaija japonica*, male (22.3 × 17.8 mm) (ZRC 2013.1267), Taiwan; G, *Planaja plana* n. gen. n. sp., holotype male (43.7 × 37.1 mm) (NMCR), Philippines; H, *Ovimaja compressipes*, male (49.6 × 39.6 mm) (ZRC 2008.1318), Taiwan.

Fig. 43. Third maxillipeds. A, *Maja squinado*, neotype male (147.1 × 126.3 mm) (SMF-4548), Croatia; B, *Maja squinado*, female (144.5 × 129.0 mm) (ZRC 2013.1126), Spain; C, *Maja brachydactyla*, male (98.4 × 89.0 mm) (ZRC 2009.1130), U.K.; D, *Maja brachydactyla*, male (161.2 × 140.1 mm), (ZRC 2008.0179), Spain; E, *Maja cornuta*, male (115.3 × 103.4 mm) (ZRC 2013.1184), South Africa; F, *Maja crispata*, male (63.1 × 51.9 mm) (MNHN-IU-2013-4042), Italy; G, *Neomaja goltziana*, male (73.4 × 65.0 mm) (MNHN-IU-2013-4046), Congo; H, *Neomaja goltziana*, male (90.2 × 83.1 mm) (MNHN-IU-2013-4044), Gabon; I, *Paramaja kominatoensis*, dried male (62.6 × 56.1 mm) (KPM NH0104298), Japan; J, *Paramaja kominatoensis*, dried male (73.0 × 66.0 mm) (PCM), Taiwan; K, *Paramaja kominatoensis*, dried male (60.4 × 52.5 mm) (KPM NH124171), Japan; L, *Paramaja gibba*, lectotype female (25.1 × 21.2 mm) (NHM 1896.5.14.9), India; M, *Paramaja gibba*, male (79.5 × 77.9 mm) (ZRC 2013.1232), Bay of Bengal; N, *Paramaja turgida* n. sp., holotype male (74.1 × 66.8 mm) (NMCR), Philippines; O, *Paramaja turgida* n. sp., paratype male (71.4 × 64.4 mm) (NSMT-Cr 22329), Philippines; P, *Paramaja turgida* n. sp., paratype male (67.9 × 60.5 mm) (MNHN), Philippines.

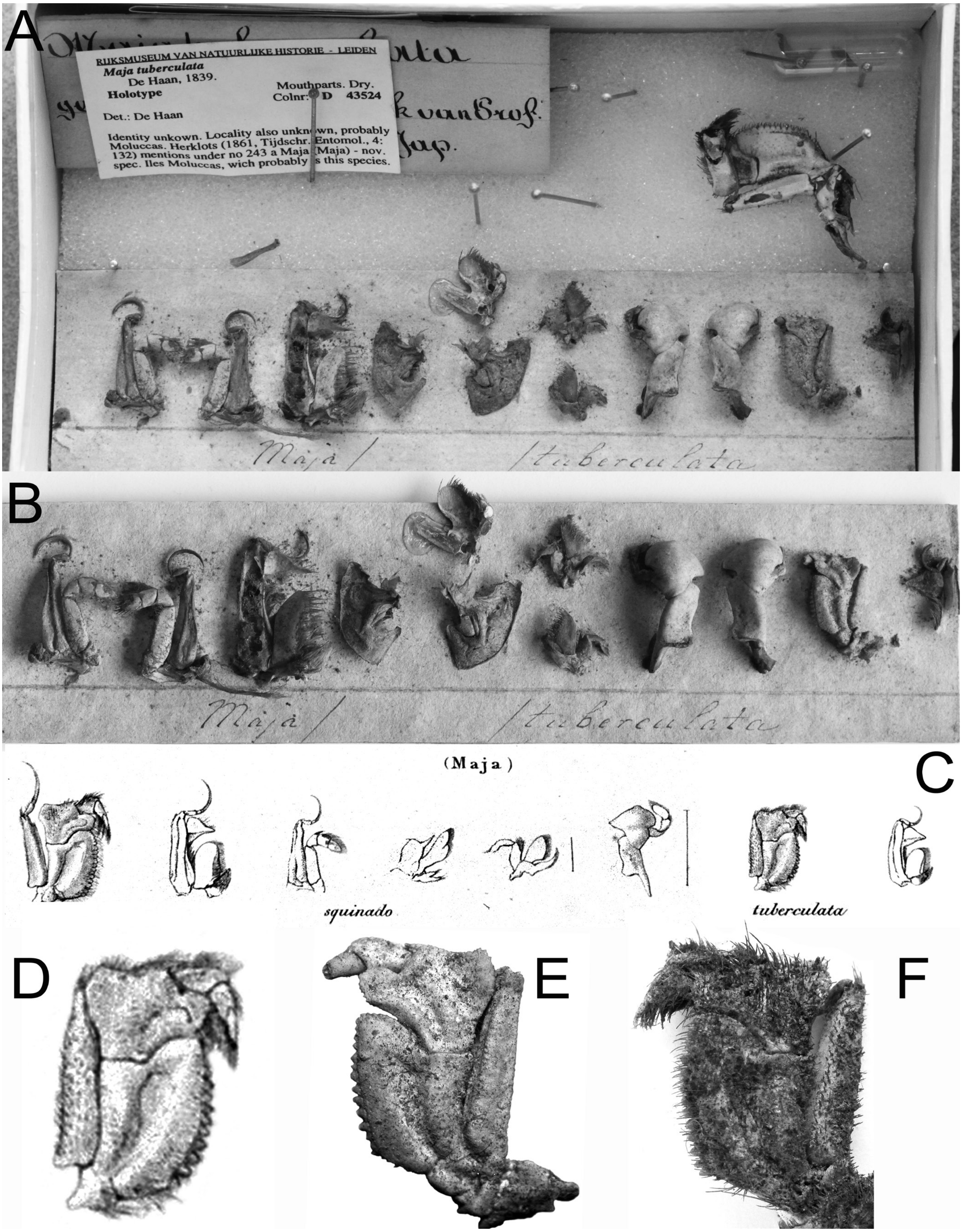

Fig. 44. Third maxillipeds. *Maja squinado*. A, B, mouthparts of specimen in Leiden labelled as "*Maja tuberculata* De Haan, 1839" (RMNH D 43524); C, mouthparts of *Maja squinado* and *Maja tuberculata* (after De Haan, 1839: Pl. F); D, right third maxilliped of *Maja tuberculata* (after De Haan, 1839: Pl. F); E, left third maxilliped ostensibly of *Maja tuberculata* mounted on card (RMNH D 43524, part); F, free left third maxilliped ostensibly of *Maja tuberculata* pinned in box (RMNH D 43524, part).

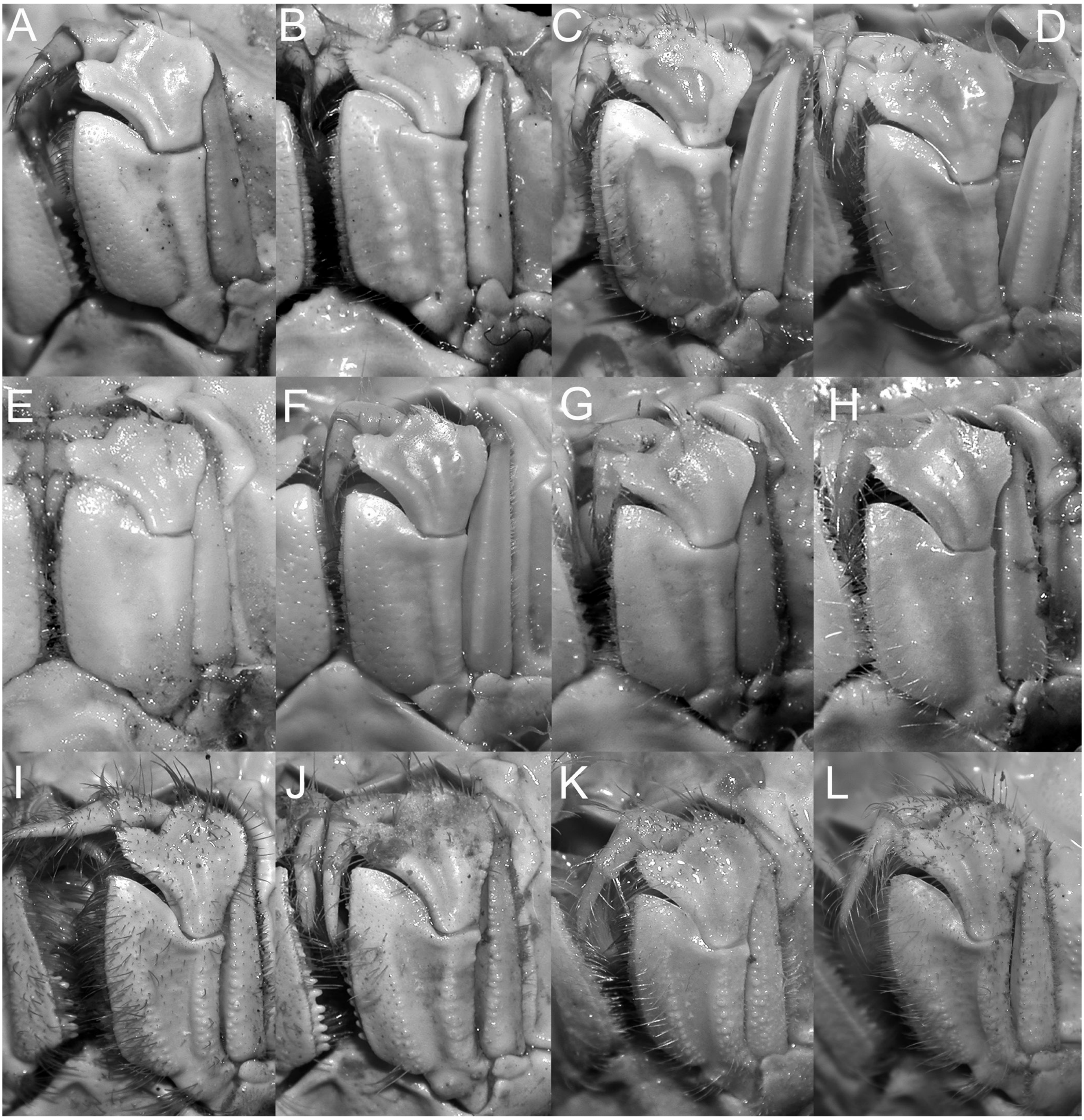

Fig. 45. Third maxillipeds. A, *Alcomaja irrorata* n. sp., holotype male (52.6 × 45.7 mm) (NMCR), Philippines; B, *Alcomaja gracilipes*, holotype male (45.4 × 43.5 mm) (IOCAS K33B-34), South China Sea [third max laterally inverted to match]; C, *Alcomaja gracilipes*, male (41.4 × 35.4 mm) (ZRC 2013.1225), Philippines; D, *Alcomaja desmondi* n. sp., holotype male (35.4 × 28.3 mm) (NMCR), Philippines; E, *Alcomaja nagashimaensis*, holotype male (34.0 × 28.5 mm) (USNM 125886), Japan; F, *Alcomaja nagashimaensis*, male (30.5 × 26.0 mm) (ZRC 2001.430), Philippines; G, *Alcomaja latens* n. sp., holotype male (25.3 × 21.4 mm) (MNHN-IU-2013-4050), Solomon Islands; H, *Alcomaja miriky* n. sp., holotype male (26.4 × 20.9 mm) (MNHN-IU-2010-929), Madagascar; I, *Paramaya spinigera*, male (85.0 × 66.4 mm) (ZRC 1999.738), Taiwan; J, *Paramaya ouch* n. sp., holotype male (76.8 × 60.0 mm) (NMCR), Philippines; K, *Paramaya ouch* n. sp., paratype male (39.7 × 29.6 mm) (ZRC 2011.0045), Philippines; L, *Paramaya coccinea* n. sp., holotype male (69.0 × 55.6 mm) (MNHN), Vanuatu.

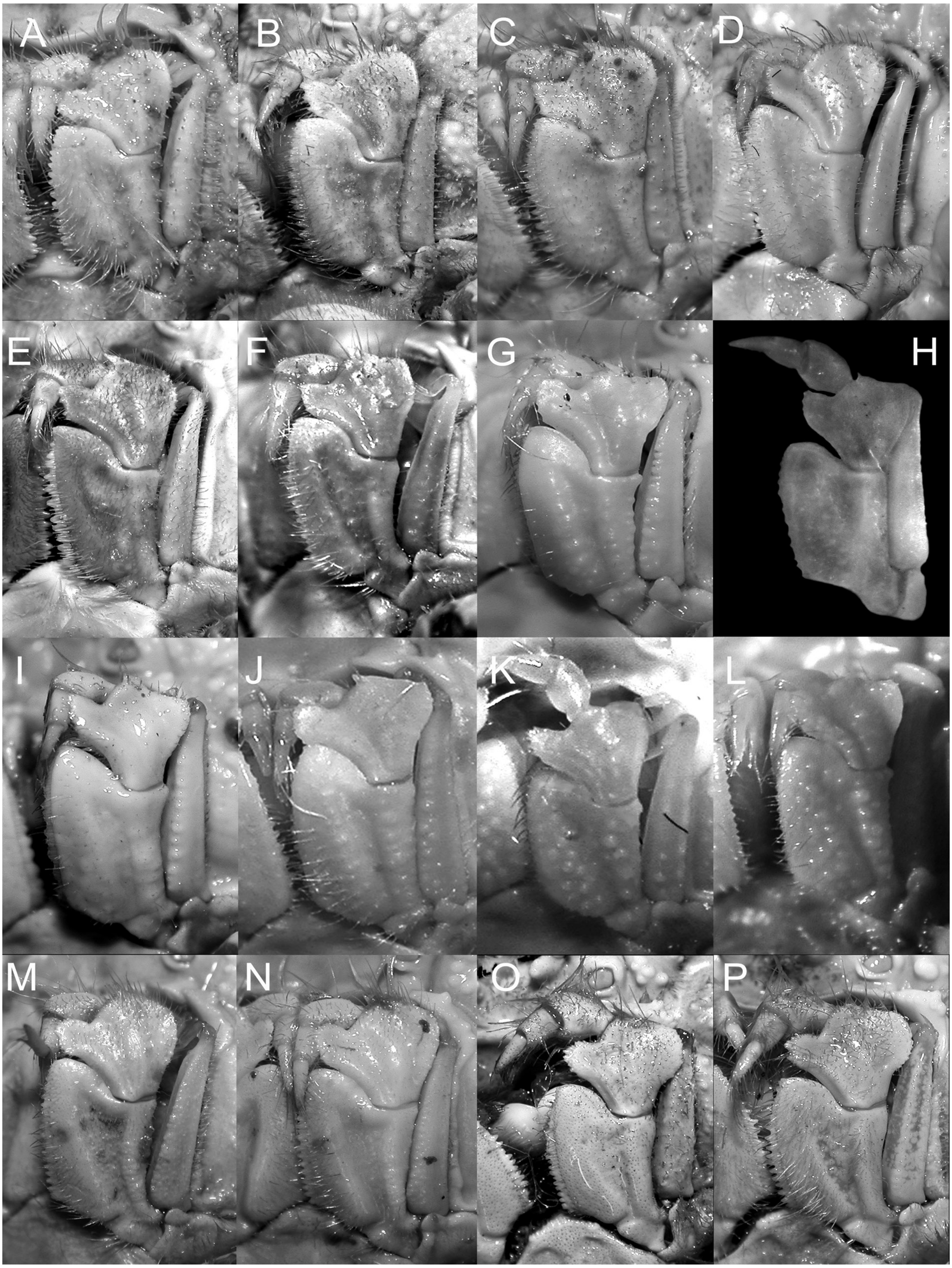

Fig. 46. Third maxillipeds. A, *Holthuija miersi*, male (32.6 × 25.6 mm) (ZRC 2000.1497), Singapore; B, *Holthuija suluensis*, holotype female (32.4 × 41.2 mm) (USNM 48224a), Philippines; C, *Holthuija pauli* n. sp., holotype male (37.3 × 28.0 mm) (NMCR), Philippines; D, *Holthuija cognata* n. sp., holotype male (29.5 × 23.7 mm) (CBM-ZC3662), Japan; E, *Holthuija aussie* n. sp., holotype ovigerous female (42.1 × 34.4 mm) (NMV J63752), Arafura Sea; F, *Holthuija poorei* n. sp., holotype male (24.3 × 18.7 mm) (NMV J63749), Timor Sea; G, *Sakaija japonica*, male (22.3 × 17.8 mm) (ZRC 2013.1267), Taiwan; H, *Sakaija sakaii*, male (9.0 × 6.6 mm) (NSMT-Cr 8094), Japan; I, *Sakaija africana*, male (32.2 × 25.4 mm) (MNHN-IU-2010-928), Madagascar; J, *Sakaija serenei* n. sp., holotype male (17.4 × 14.7 mm) (NMCR), Philippines; K, *Sakaija santo* n. sp., holotype male (9.4 × 6.6 mm) (MNHN), Vanuatu; L, *Sakaija longispinosa* n. sp., paratype ovigerous female (14.2 × 10.7 mm) (NMV J63197), Australia; M, *Planaja plana* n. gen. n. sp., holotype male (43.7 × 37.1 mm) (NMCR), Philippines; N, *Planaja plana* n. gen. n. sp., paratype male (38.3 × 30.7 mm) (ZRC 2013.1370), Philippines; O, *Ovimaja compressipes*, holotype female (51.2 × 40.5 mm) (NHM 1860.15), China; P, *Ovimaja compressipes*, male (49.6 × 39.6 mm) (ZRC 2008.1318), Taiwan.

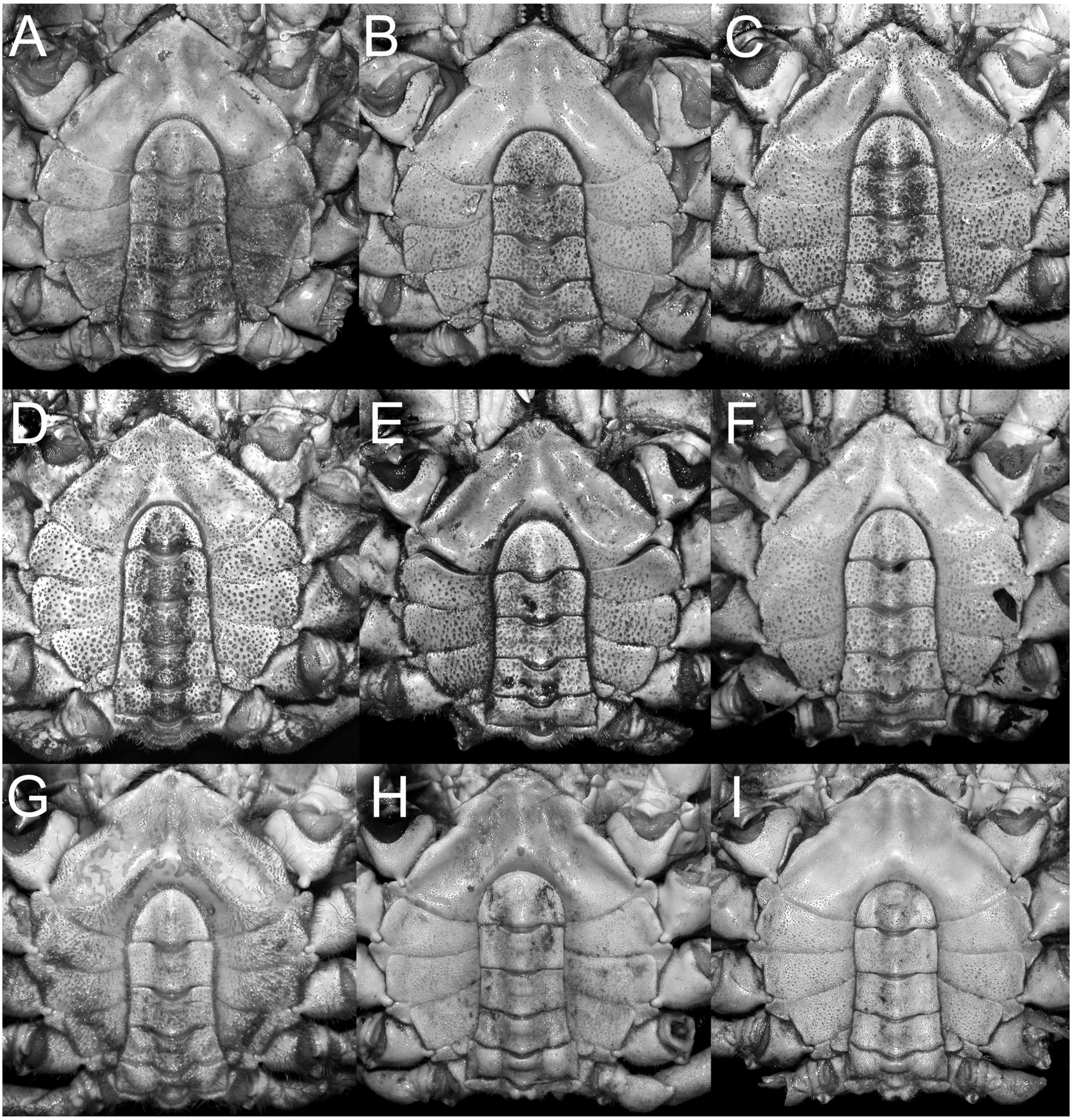

Fig. 47. Male anterior thoracic sternums and abdomens. A, *Maja squinado*, neotype male (147.1 × 126.3 mm) (SMF-4548), Croatia; B, male (138.0 × 121.0 mm) (ZRC), Croatia; C, *Maja brachydactyla*, male (98.4 × 89.0 mm) (ZRC 2009.1130), U.K.; D, *Maja brachydactyla*, male (161.2 × 140.1 mm), (ZRC 2008.0179), Spain; E, *Maja cornuta*, male (88.8 × 86.8 mm) (NHM 1928.12.1.177) (lectotype of *Mamaia queketti* Stebbing, 1908), South Africa; F, *Maja cornuta*, male (115.3 × 103.4 mm) (ZRC 2013.1184), South Africa; G, *Maja crispata*, male (63.1 × 51.9 mm) (MNHN-IU-2013-4042), Italy; H, *Neomaja goltziana*, male (73.4 × 65.0 mm) (MNHN-IU-2013-4046), Congo; I, *Neomaja goltziana*, male (90.2 × 83.1 mm) (MNHN-IU-2013-4044), Gabon.

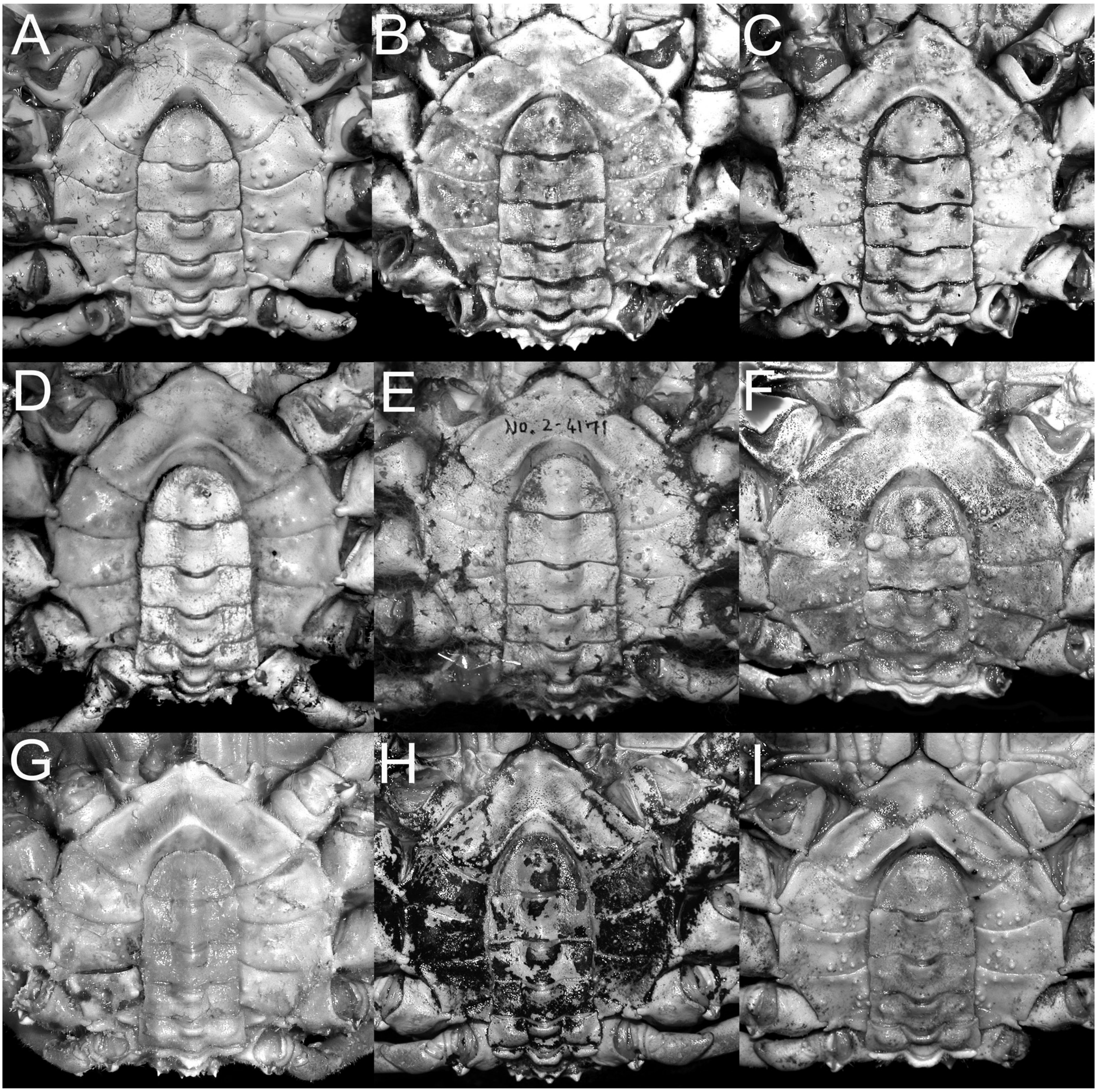

Fig. 48. Male anterior thoracic sternums and abdomens, *Paramaja*. A, *P. kominatoensis*, dried male (62.6 × 56.1 mm) (KPM NH0104298), Japan; B, *P. kominatoensis*, male (76.9 × 69.6 mm) (SMF 47738), Japan; C, *P. kominatoensis*, male (50.5 × 44.6 mm) (SMF 47738), Japan; D, *P. kominatoensis*, dried male (73.0 × 66.0 mm) (PCM), Taiwan; E, *P. kominatoensis*, dried male (60.4 × 52.5 mm) (KPM NH124171), Japan; F, *P. gibba*, male (79.5 × 77.9 mm) (ZRC 2013.1232), Bay of Bengal; G, *P. gibba*, male male (64.7 × 60.7 mm) (SIO), Indian Ocean; H, *P. turgida* n. sp., holotype male (74.1 × 66.8 mm) (NMCR), Philippines; I, *P. turgida* n. sp., paratype male (67.9 × 60.5 mm) (MNHN), Philippines.

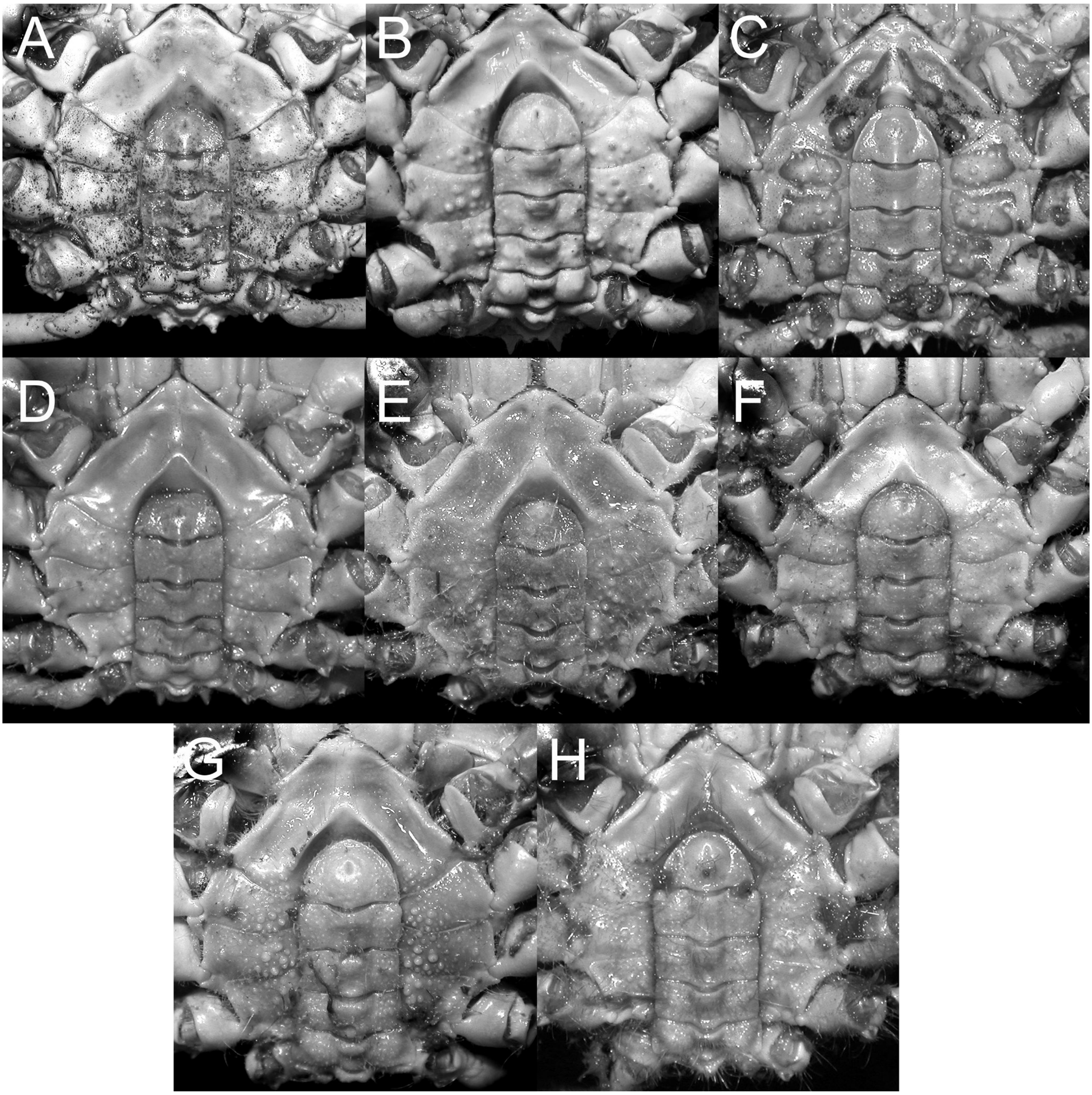

Fig. 49. Male anterior thoracic sternums and abdomens, *Alcomaja* species. A, *A. irrorata* n. sp., holotype male (52.6 × 45.7 mm) (NMCR), Philippines; B, *A.gracilipes*, holotype male (45.4 × 43.5 mm) (IOCAS K33B-34), South China Sea; C, *A. gracilipes*, male (41.4 × 35.4 mm) (ZRC 2013.1225), Philippines; D, *A. nagashimaensis*, male (30.5 × 26.0 mm) (ZRC 2001.430), Philippines; E, *A. nagashimaensis*, male (37.2 × 32.4 mm) (CBM-ZC9928), Japan; F, *A. latens* n. sp., holotype male (25.3 × 21.4 mm) (MNHN-IU-2013-4050), Solomon Islands; G, *A. miriky* n. sp., holotype male (26.4 × 20.9 mm) (MNHN-IU-2010-929), Madagascar; H, *A. desmondi* n. sp., holotype male (35.4 × 28.3 mm) (NMCR), Philippines.

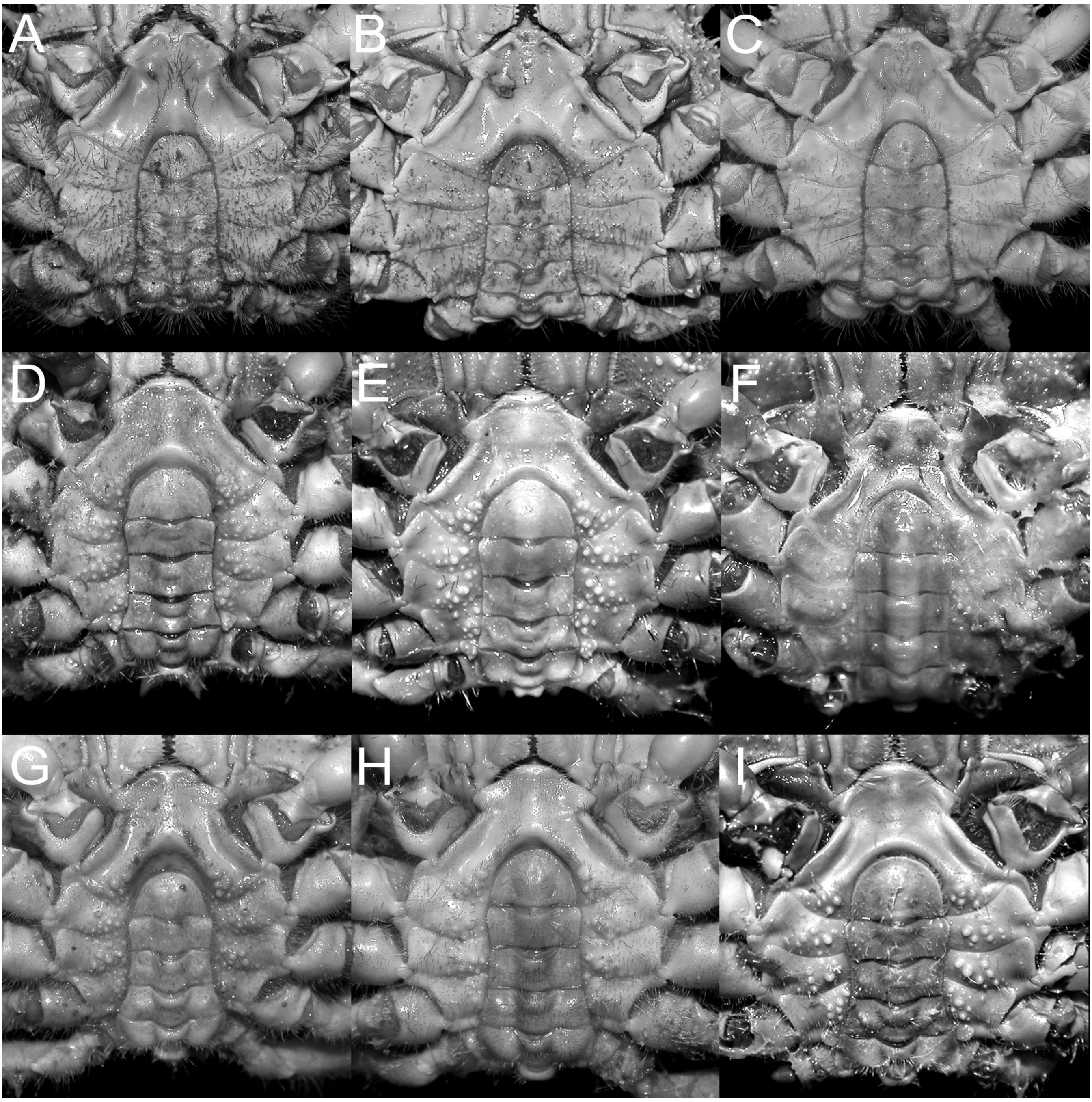

Fig. 50. Male anterior thoracic sternums and abdomens. A, *Paramaya spinigera*, male (85.0 × 66.4 mm) (ZRC 1999.738), Taiwan; B, *Paramaya ouch* n. sp., holotype male (76.8 × 60.0 mm) (NMCR), Philippines; C, *Paramaya coccinea* n. sp., holotype male (69.0 × 55.6 mm) (MNHN), Vanuatu; D, *Holthuija miersi*, male (32.6 × 25.6 mm) (ZRC 2000.1497), Singapore; E, *Holthuija miersii*, male (22.3 × 16.5 mm) (CBM ZC4001), Singapore; F, *Holthuija suluensis*, male (11.5 × 8.2 mm) (USNM 48507), Philippines; G, *Holthuija pauli* n. sp., holotype male (37.3 × 28.0 mm) (NMCR), Philippines; H, *Holthuija cognata* n. sp., holotype male (29.5 × 23.7 mm) (CBM-ZC3662), Japan; I, *Holthuija poorei* n. sp., holotype male (24.3 × 18.7 mm) (NMV J63749), Timor Sea.

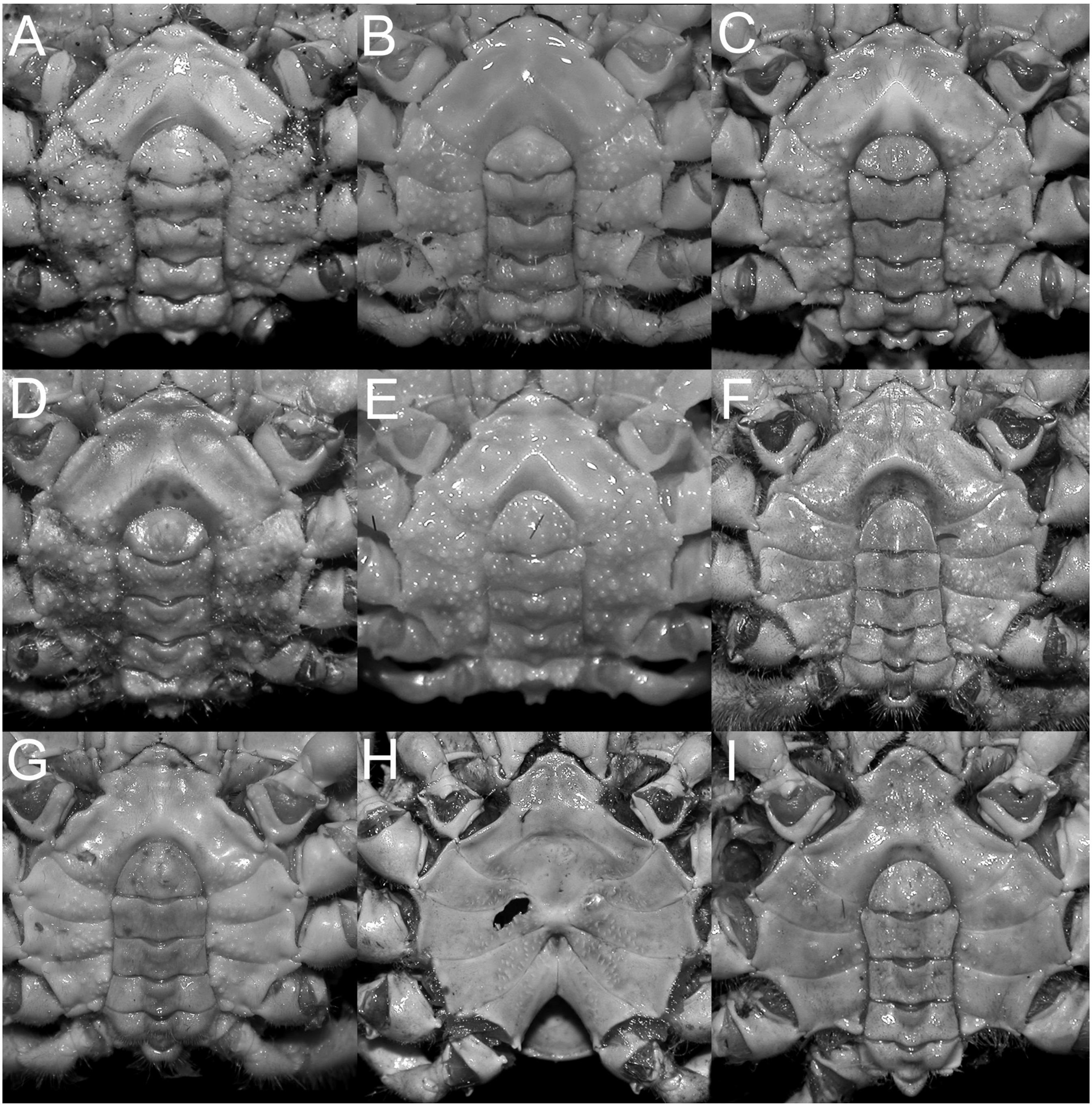

Fig. 51. Anterior thoracic sternums and abdomens. A, *Sakaija japonica*, holotype male (16.2 × 13.0 mm) (USNM 48252), Japan; B, *Sakaija japonica*, male (22.3 × 17.8 mm) (ZRC 2013.1267), Taiwan; C, *Sakaija africana*, male (32.2 × 25.4 mm) (MNHN-IU-2010-928), Madagascar; D, *Sakaija serenei* n. sp., holotype male (17.4 × 14.7 mm) (NMCR), Philippines; E, *Sakaija santo* n. sp., holotype male (9.4 × 6.6 mm) (MNHN), Vanuatu; F, *Planaja plana* n. gen. n. sp., holotype male (43.7 × 37.1 mm) (NMCR), Philippines; G, *Planaja plana* n. gen. n. sp., paratype male (38.3 × 30.7 mm) (ZRC 2013.1370), Philippines; H, *Ovimaja compressipes*, holotype female (51.2 × 40.5 mm) (NHM 1860.15), China; I, *Ovimaja compressipes*, male (49.6 × 39.6 mm) (ZRC 2008.1318), Taiwan.

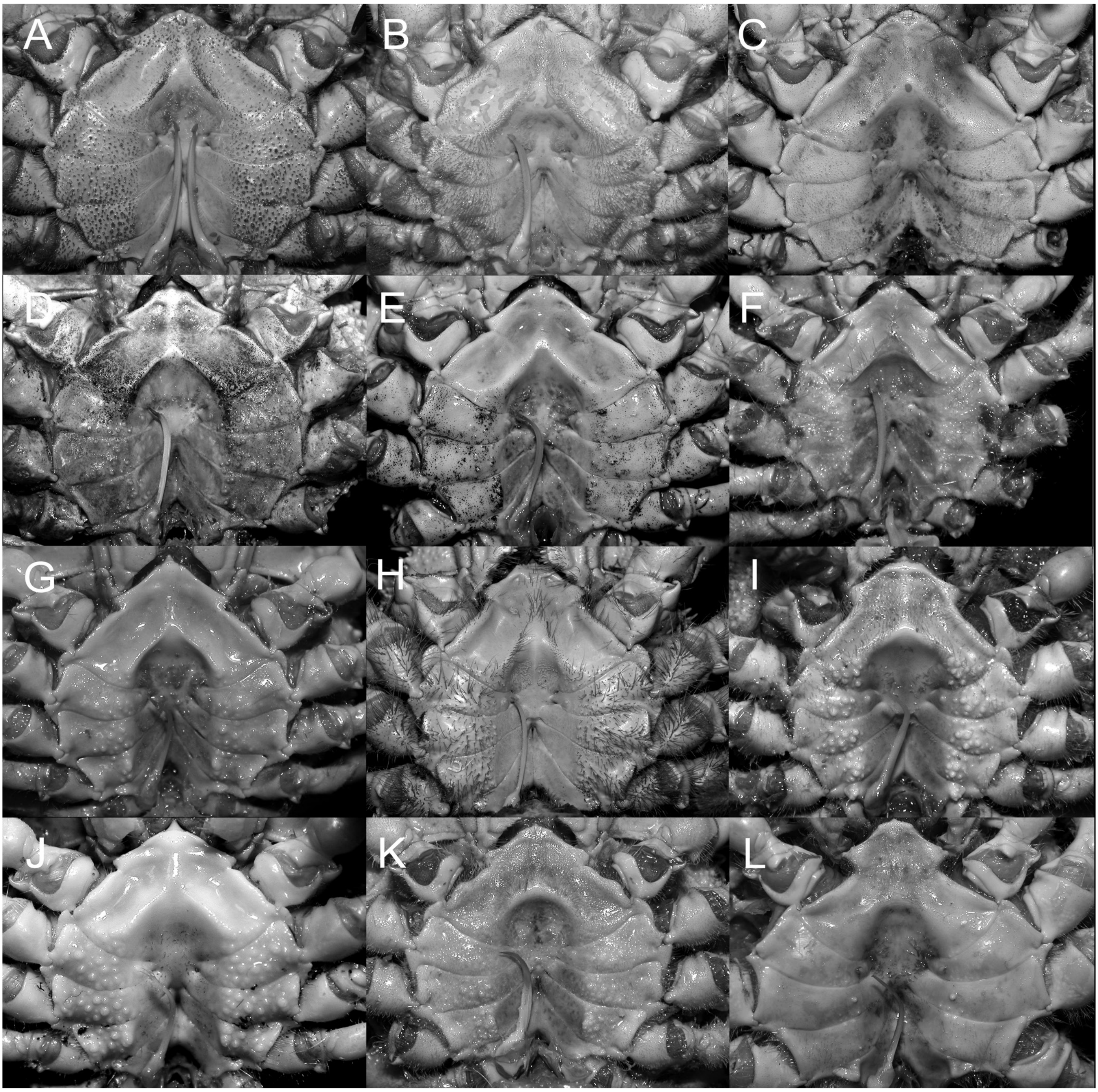

Fig. 52. Male sterno-abdominal cavities. A, *Maja brachydactyla*, male (98.4 × 89.0 mm) (ZRC 2009.1130), U.K.; B, *Maja crispata*, male (63.1 × 51.9 mm) (MNHN-IU-2013-4042), Italy; C, *Neomaja goltziana*, male (73.4 × 65.0 mm) (MNHN-IU-2013-4046), Congo; D, *Paramaja gibba* n. sp., male (79.5 × 77.9 mm) (ZRC 2013.1232), Bay of Bengal; E, *Alcomaja irrorata* n. sp., holotype male (52.6 × 45.7 mm) (NMCR), Philippines; F, *Alcomaja desmondi* n. sp., holotype male (35.4 × 28.3 mm) (NMCR), Philippines; G, *Alcomaja nagashimaensis*, male (30.5 × 26.0 mm) (ZRC 2001.430), Philippines; H, *Paramaya spinigera*, male (85.0 × 66.4 mm) (ZRC 1999.738), Taiwan; I, *Holthuija miersi*, male (32.6 × 25.6 mm) (ZRC 2000.1497), Singapore; J, *Sakaija japonica*, male (22.3 × 17.8 mm) (ZRC 2013.1267), Taiwan; K, *Planaja plana* n. gen. n. sp., holotype male (43.7 × 37.1 mm) (NMCR), Philippines; L, *Ovimaja compressipes*, male (49.6 × 39.6 mm) (ZRC 2008.1318), Taiwan.

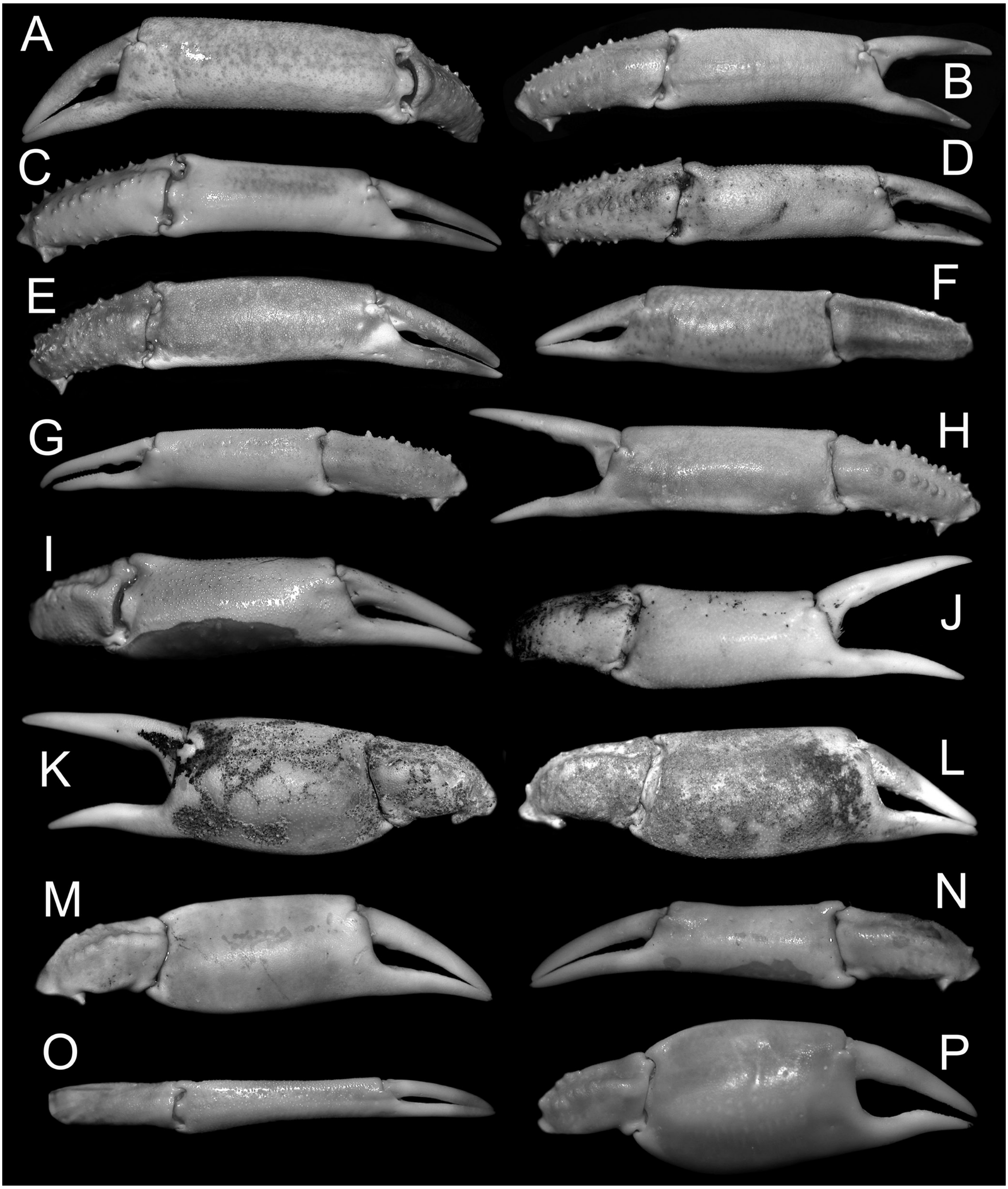

Fig. 53. Chelae. A, *Maja squinado*, neotype male (147.1 × 126.3 mm) (SMF-4548), Croatia; B, *Maja brachydactyla*, male (98.4 × 89.0 mm) (ZRC 2009.1130), U.K.; C, *Maja brachydactyla*, male (161.2 × 140.1 mm), (ZRC 2008.0179), Spain; D, *Maja cornuta*, male (88.8 × 86.8 mm) (NHM 1928.12.1.177–) (lectotype of *Mamaia queketti* Stebbing, 1908), South Africa; E, *Maja cornuta*, male (115.3 × 103.4 mm) (ZRC 2013.1184), South Africa; F, *Maja crispata*, male (63.1 × 51.9 mm) (MNHN-IU-2013-4042), Italy; G, *Neomaja goltziana*, male (73.4 × 65.0 mm) (MNHN-IU-2013-4046), Congo; H, *Neomaja goltziana*, male (90.2 × 83.1 mm) (MNHN-IU-2013-4044), Gabon; I, *Paramaja kominatoensis*, dried male (62.6 × 56.1 mm) (KPM NH0104298), Japan; J, *Paramaja kominatoensis*, dried male (73.0 × 66.0 mm) (PCM), Taiwan; K, *Paramaja gibba*, male (79.5 × 77.9 mm) (ZRC 2013.1232), Bay of Bengal; L, *Paramaja turgida* n. sp., holotype male (74.1 × 66.8 mm) (NMCR), Philippines; M, *Alcomaja irrorata* n. sp., holotype male (52.6 × 45.7 mm) (NMCR), Philippines; N, *Alcomaja gracilipes*, male (41.4 × 35.4 mm) (ZRC 2013.1225), Philippines; O, *Alcomaja desmondi* n. sp., holotype male (35.4 × 28.3 mm) (NMCR), Philippines; P, *Alcomaja nagashimaensis*, male (30.5 × 26.0 mm) (ZRC 2001.430), Philippines.

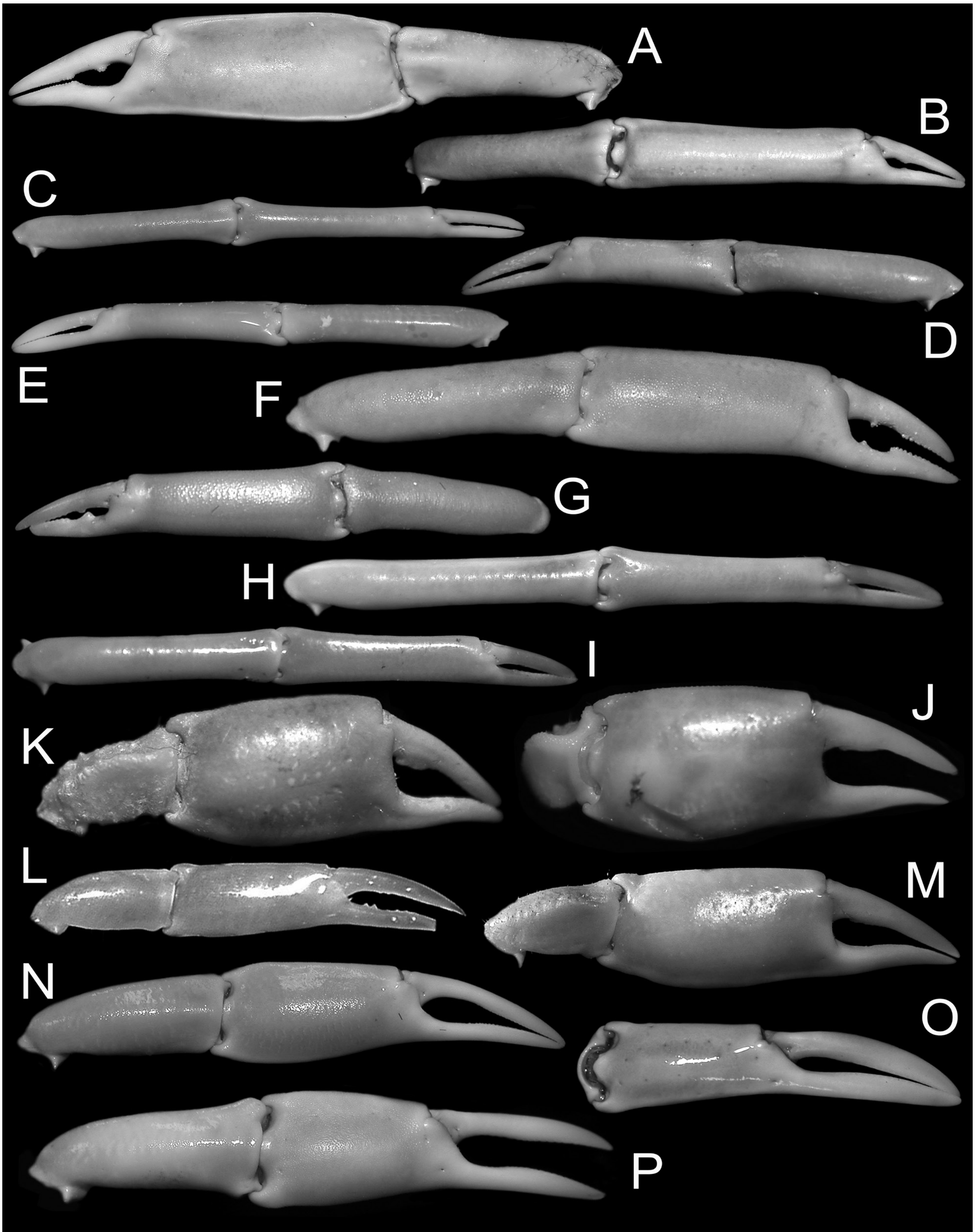

Fig. 54. Chelae. A, *Paramaya spinigera*, male (85.0 × 66.4 mm) (ZRC 1999.738), Taiwan; B, *Paramaya ouch* n. sp., paratype male (76.5 × 61.3 mm) (ZRC 2001.0577), Philippines; C, *Paramaya coccinea* n. sp., holotype male (69.0 × 55.6 mm) (MNHN), Vanuatu; D, *Holthuija miersi*, male (32.6 × 25.6 mm) (ZRC 2000.1497), Singapore; E, *Holthuija suluensis*, holotype female (32.4 × 41.2 mm) (USNM 48224a), Philippines; F, *Holthuija pauli* n. sp., holotype male (37.3 × 28.0 mm) (NMCR), Philippines; G, *Holthuija cognata* n. sp., holotype male (29.5 × 23.7 mm) (CBM-ZC3662), Japan; H, *Holthuija aussie* n. sp., holotype ovigerous female (42.1 × 34.4 mm) (NMV J63752), Arafura Sea; I, *Holthuija poorei* n. sp., holotype male (24.3 × 18.7 mm) (NMV J63749), Timor Sea; J, *Sakaija japonica*, male (22.3 × 17.8 mm) (ZRC 2013.1267), Taiwan; K, *Sakaija serenei* n. sp., holotype male (17.4 × 14.7 mm) (NMCR), Philippines; L, *Sakaija santo* n. sp., holotype male (9.4 × 6.6 mm) (MNHN), Vanuatu; M, *Sakaija africana*, male (32.2 × 25.4 mm) (MNHN-IU-2010-928), Madagascar; N, *Planaja plana* n. gen. n. sp., holotype male (43.7 × 37.1 mm) (NMCR), Philippines; O, *Ovimaja compressipes*, holotype female (51.2 × 40.5 mm) (NHM 1860.15), China; P, *Ovimaja compressipes*, male (49.6 × 39.6 mm) (ZRC 2008.1318), Taiwan.

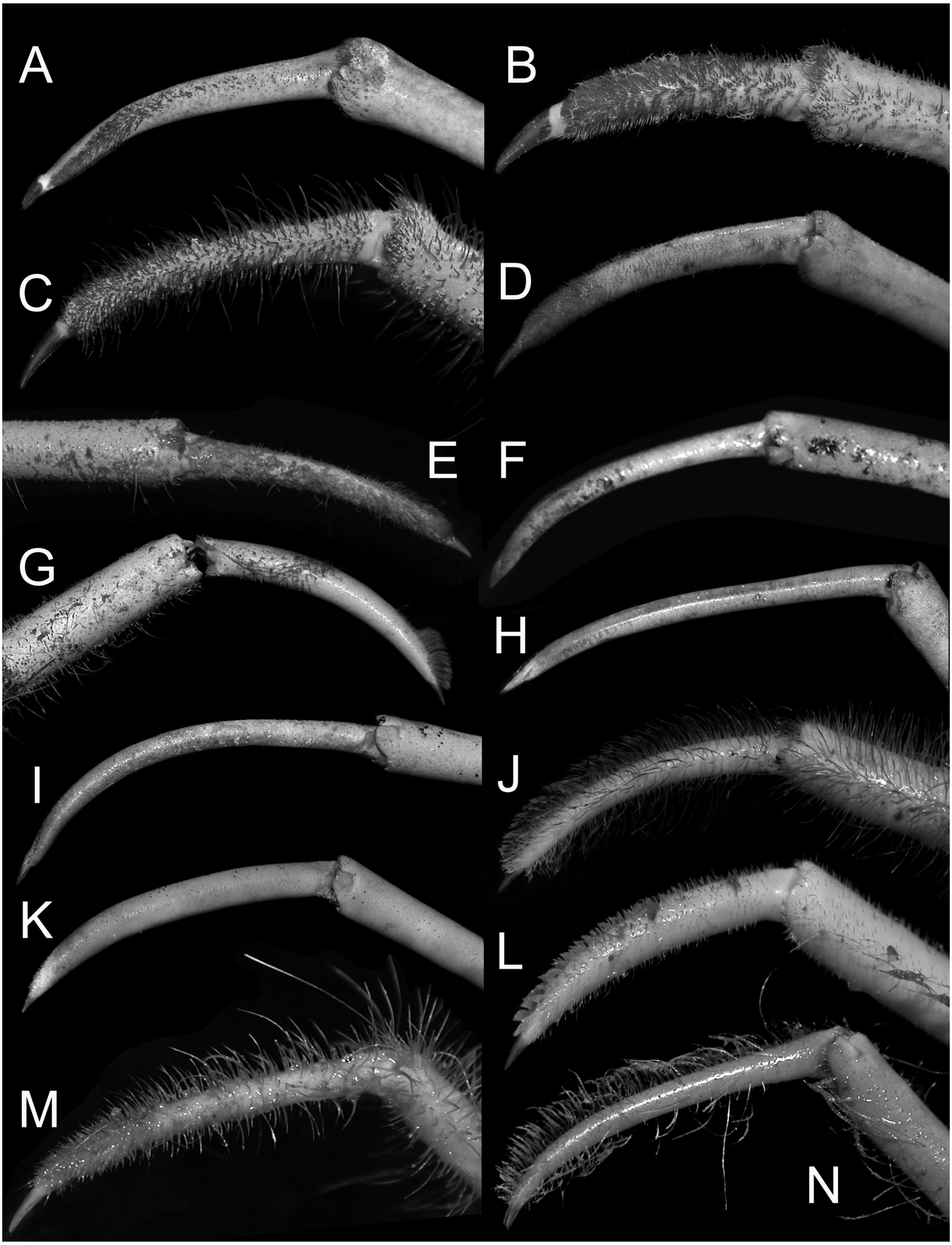

Fig. 55. First ambulatory dactyli and propodi. A, *Maja squinado*, neotype male (147.1 × 126.3 mm) (SMF-4548), Croatia; B, *Maja brachydactyla*, male (98.4 × 89.0 mm) (ZRC 2009.1130), U.K.; C, *Maja crispata*, male (63.1 × 51.9 mm) (MNHN-IU-2013-4042), Italy; D, *Neomaja goltziana*, male (73.4 × 65.0 mm) (MNHN-IU-2013-4046), Congo; E, *Paramaja kominatoensis*, dried male (62.6 × 56.1 mm) (KPM NH0104298), Japan; F, *Paramaja kominatoensis*, dried male (73.0 × 66.0 mm) (PCM), Taiwan; G, *Paramaja kominatoensis*, dried male (60.4 × 52.5 mm) (KPM NH124171), Japan; H, *Paramaja gibba*, male (79.5 × 77.9 mm) (ZRC 2013.1232), Bay of Bengal; I, *Paramaja turgida* n. sp., holotype male (74.1 × 66.8 mm) (NMCR), Philippines; J, *Paramaja turgida* n. sp., paratype female (62.6 × 57.2 mm) (ZRC 2013.1241), Philippines; K, *Alcomaja irrorata* n. sp., holotype male (52.6 × 45.7 mm) (NMCR), Philippines; L, *Alcomaja irrorata*, male (43.0 × 37.2 mm) (ZRC 2013.1223), Philippines; M, *Alcomaja desmondi* n. sp., holotype male (35.4 × 28.3 mm) (NMCR), Philippines; N, *Alcomaja nagashimaensis*, male (30.5 × 26.0 mm) (ZRC 2001.430), Philippines.

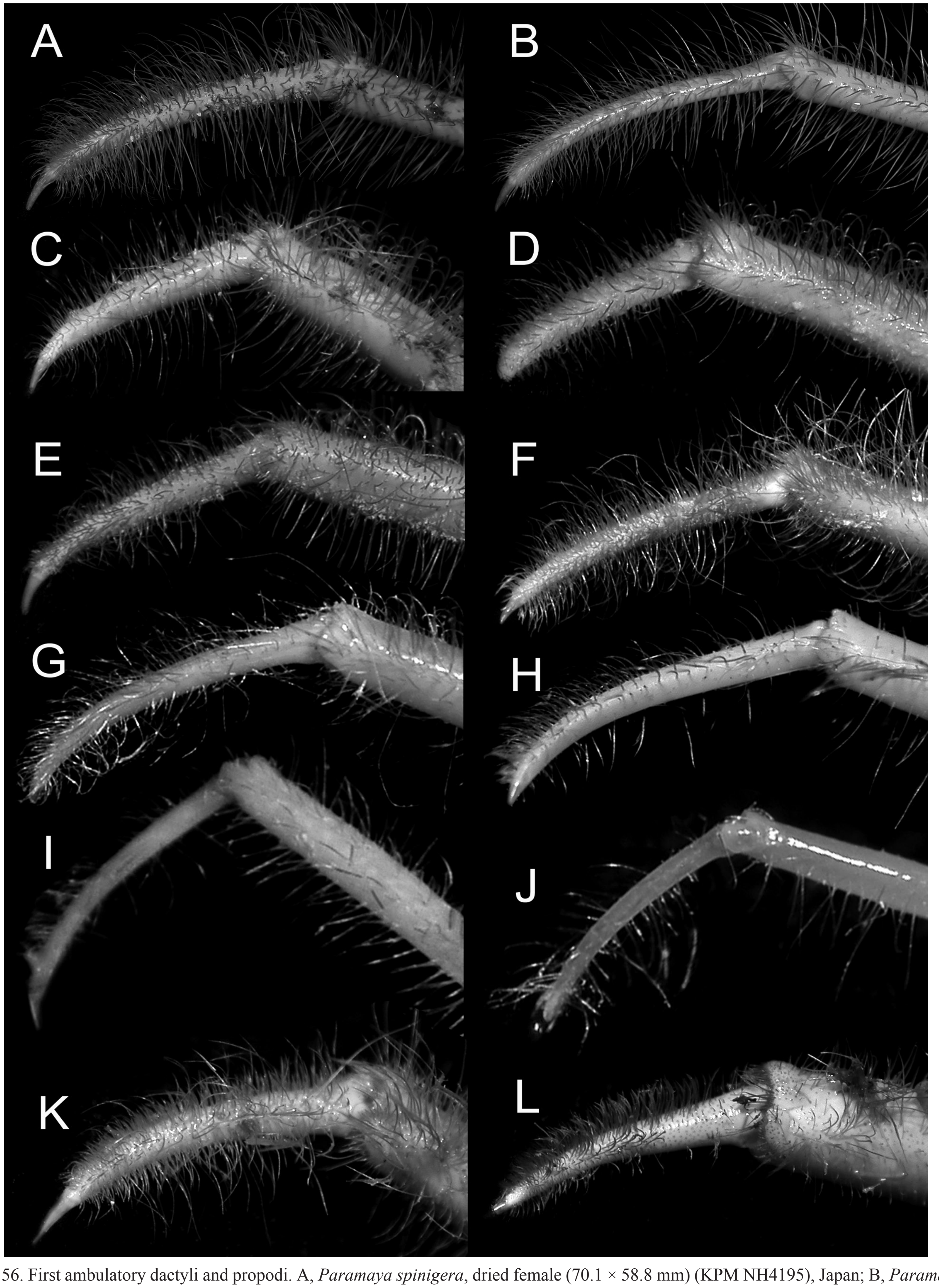

Fig. 56. First ambulatory dactyli and propodi. A, *Paramaya spinigera*, dried female (70.1 × 58.8 mm) (KPM NH4195), Japan; B, *Paramaya coccinea* n. sp., holotype male (69.0 × 55.6 mm) (MNHN), Vanuatu; C, *Holthuija miersi*, male (32.6 × 25.6 mm) (ZRC 2000.1497), Singapore; D, *Holthuija suluensis*, holotype female (32.4 × 41.2 mm) (USNM 48224a), Philippines; E, *Holthuija cognata* n. sp., holotype male (29.5 × 23.7 mm) (CBM-ZC3662), Japan [figure laterally inverted]; F, *Holthuija aussie* n. sp., holotype ovigerous female (42.1 × 34.4 mm) (NMV J63752), Arafura Sea; G, *Holthuija poorei*, n. sp. paratype female (27.0 × 22.5 mm) (NMV J63751), Arafura Sea; H, *Sakaija japonica*, male (22.3 × 17.8 mm) (ZRC 2013.1267), Taiwan; I, *Sakaija serenei* n. sp., holotype male (17.4 × 14.7 mm) (NMCR), Philippines [figure laterally inverted]; J, *Sakaija santo* n. sp., holotype male (9.4 × 6.6 mm) (MNHN), Vanuatu; K, *Planaja plana* n. gen. n. sp., holotype male (43.7 × 37.1 mm) (NMCR), Philippines; L, *Ovimaja compressipes*, male (49.6 × 39.6 mm) (ZRC 2008.1318), Taiwan.

Rathbunaja n. gen.

Diagnosis. Carapace distinctly pyriform; dorsal surface covered by sharp granules, tubercles and short spines; gastric and branchial regions distinct, separated by distinct grooves; carapace and pereiopods covered with dense short setae, forming velvet-like pubescence (Figs. 59, 60). Cardiac region with 2 short spines arranged transversely; intestinal region with 2 or 3 short spines (Figs. 59, 60). Pseudorostral long or short, divergent (Figs. 59, 60). Supraorbital eave with anterior part longitudinally narrow, rectangular, not prominently expanded; antorbital spine short, directed laterally (Figs. 59, 60, 62A). Intercalated spine distinct, separated from supraorbital eave by wide keyhole shaped gap, separated from postorbital spine by narrow slit-like gap; postorbital spine strong; hepatic region with 1 strong spine, subequal or shorter than postorbital spine, surrounded by short spines and tubercles (Figs. 59, 60, 62A). Lateral carapace margin with 3 large spines and numerous spinules and tubercles around them; branchial region with 2 spines, outer one relatively larger (Figs. 59, 60). Posterior carapace margin always with 2 distinct median spines (Figs. 59, 60). Eyes relatively short, stout, with rounded cornea (Figs. 61A, C, E, G, 62B). Antennal flagellum long, slender (Figs. 61A, C, E, G, 62B). Basal antennal article longer than broad, with 2 long distal spines; proximal outer angle with small low tooth; inner and outer lateral margins entire; antero-external crested rim of antennular fossa slightly overlaps subdistal part of basal antennal article (61A, C, E, G, 62B). Epistome much wider than long, anterior margin with 2 low, flattened tubercles; posterior margin composed of 4 rectangular plates, lateral plates separated from median plates by deep fissures, median plate separated by shallow cleft (61A, C, E, G, 62B). Suborbital margin separated from basal antennal article by wide gap; suborbital tooth completely fused with postorbital tooth (61A, C, E, G, 62B). Outer surface of third maxilliped covered by short setae; ischium rectangular, smooth; postero-external angle of merus relatively broad, "inserted" into concavity on outer margin of ischium; antero-internal part of ischium rounded, relatively low, sub- or not auriculiform (Figs. 62C, 63). Male chelipeds very long in adult males, surfaces of merus and carpus covered with distinct tubercles and granules; carpus elongate, with low granulated longitudinal ridge; palm elongated, curved, smooth, without lateral cristae, slightly enlarged, with swellings on dorsal and ventral margins in very large males; fingers long, slender, gently curved, with narrow basal gape when closed (Figs. 59, 60, 65C, G, H). Ambulatory leg merus with distinct distal spine on dorsal margin; dactylus relatively long, curved, covered with dense short and long setae except for corneous distal quarter (Figs. 62D–G, 65B, D, F, I–K). Thoracic sternum relatively wide; surfaces of somites 5–8 almost smooth; sternites 3 and 4 medially depressed; margin between sternites 2 and 3 demarcated by small notch; anterior margin of sterno-abdominal cavity forming incomplete rim with median part low (Figs. 64). Male abdomen subrectangular, with 6 free somites and telson; telson subtriangular to semicircular, with convex margins (Fig. 64). Male press-button abdominal locking mechanism submedian in position on sterno-abdominal cavity. Female abdomen dome-shaped, covering most of thoracic sternum. G1 very long, slender, curved distally, with subdistal dorsal flap (sometimes low), tip tapering, sharp; distal and subdistal surface with numerous short setae (Figs. 66, 67A–G).

Comparative material. ***Leptomithrax longimanus* (Miers, 1876)** – holotype male (38.0 × 36.2 mm) (NHM 1852.12), New Zealand, coll. R. Gunn. — 1 male (54.3 × 42.4 mm) (NIWA 6170), station KAH9704/127, 44°01.98'S 172°12.52'E, 31–34 m, New Zealand, coll. 5 January 1998. — 1 male (50.7 × 48.9 mm) (ZRC 2013.1617), Godley Head, east coast of South Island, New Zealand, in crab trap, coll. C. McLay, May 2003. ***Leptomithrax australis* (Jacquinot, in Jacquinot & Lucas, 1853)** – 1 male (77.9 × 68.9 mm), 1 female (47.0 × 39.2 mm) (ZRC 2013.1618), Banks Peninsula, east coast of South Island, New Zealand, 600 m, coll. C. L. McLay, May 2004. ***Leptomithrax longipes* (G. M. Thomson, 1902)** – 1 male (55.4 × 39.3 mm) (AM P86814), off Dunedin, New Zealand. — 1 male (39.8 × 39.3 mm) (ZRC 2013.1719, ex NIWA 42151), 1 female (45.7 × 36.7 mm) (ZRC 2013.1720 ex NIWA 44739), station KAH 0705/48, 44.4883°S 171.796°E – 44.5018°S 171.796°E, 63–65 m, New Zealand, coll. 18 May 2007. ***Leptomithrax waitei* (Whitelegge, 1900)** – 1 male (29.9 × 23.7 mm), 1 female (23.5 × 17. 3 mm) (ZRC 2013.076, ex AM P64812), station K96-04-14, 32°52'S 152°02'E, Australia, coll. FRV *Kapala*, 13 March 1996. ***Leptomithrax edwardsii* (De Haan, 1835)** – 1 female (55.9 × 49.7 mm) (ZRC 2013.1186), Amakusa, Shikizuki, Kyushu, Japan, from fishermen, coll. J. Lai, September 2002. — 8 males (largest 69.8 × 62.8 mm), 7 females (ZRC 2013.1401), Amakusa, Tomioka Port, Kyushu, Japan, coll. J. Lai & S. Arakaki, 7–9 September 2002. — 1 male, 1 female (SMF 47751), None, Kochi Prefecture, ca. 33°26.617'N 134°16.75'E, Japan, coll. K. Matsuzawa, no other data. — 1 male (SMF 47754), None, Kochi Prefecture, ca. 33°26.617'N 134°16.75'E, Japan, coll. K. Matsuzawa, 11 December 1990. — 1 ovigerous female (SMF 47753), Toyocho, None, Muroto Cape, Kochi Prefecture, 33°26.617'N 134°16.75'E, Japan, coll. 12 June 1998. — 2 females (SMF 47756), None, Kochi Prefecture, ca. 33°26.617'N 134°16.75'E, Japan, coll. K. Matsuzawa, 24 March 1991. — 1 female (SMF 47755), None, Kochi Prefecture, ca. 33°26.617'N 134°16.75'E, Japan, coll. K. Matsuzawa, 18 May 1986. — 1 male (SMF 47740), Shikoku, Tosa Bay, Kochi Prefecture, 33°29.049'N 133°35.707'E, Japan, coll. 8 April 1988. — 1 male (SMF 47752), None, Cape Muroto, Kochi Prefecture, 33°26.617'N 134°16.75'E, Japan, coll. K. Matsuzawa, 18 November 1984. — 2 males, 1 female (SMF 47739), Tokushima, Shikoku, Ana, Tsubakidomari, Kochi Prefecture, 33°51.678'N 134°43.603'E, Japan, coll. K. Sakai, 19 April 1984. — 1 female (SMF 47809), None, west of cape Muroto, Kochi Prefecture, 33°26.617'N 134°16.75'E, Japan, coll. K. Matsuzawa, 12 June 1998. — 1 female (SMF 47727), Tosa Bay, near Mimase, Kochi Prefecture, 33°29.049'N 133°35.707'E, 150–200 m, Japan, coll. K. Sakai. — 2 males, 1 crushed juvenile (SMF 47735), Honshu, Wakayama Prefecture, Kii Minabe, 33°45.712'N 135°18.927'E, Japan, coll. K. Sakai, 1 March 1988. — 3 males (SMF 47731), Honshu, Wakayama Prefecture, Kii Minabe, 33°45.712'N 135°18.927'E, Japan, coll. K. Sakai,

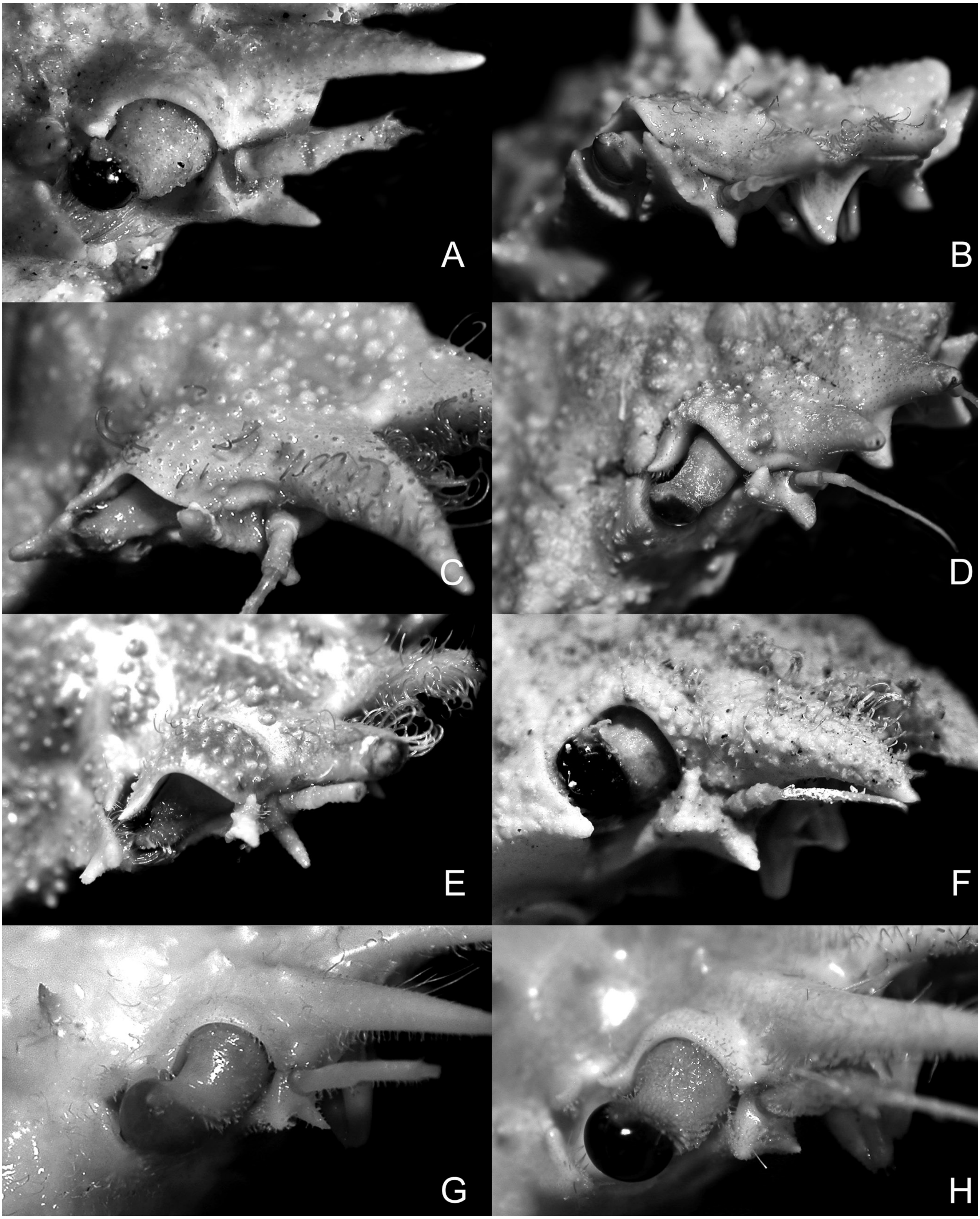

Fig. 57. Basal antennal articles and position of flagellum. A, *Leptomithrax longimanus*, holotype male (38.0 × 36.2 mm) (NHM 1852.12), New Zealand; B, *Leptomithrax tuberculatus* Whitelegge, 1900, female (36.6 × 28.7 mm) (ZRC 1965.10.13.77), Australia; C, *Leptomithrax sternocostulatus* (H. Milne Edwards, 1851), male (35.1 × 27.0 mm) (ZRC 1965.10.13.74), Australia; D, *Leptomithrax edwardsii*, male (75.8 × 69.4 mm) (ZRC 2001.56), Taiwan; E, *Leptomithrax bifidus*, male (32.5 × 27.5 mm) (NHM 1961.11.13.28), Japan; F, *Leptomithrax longipes* (G. M. Thomson, 1902), male (55.4 × 39.3 mm) (AM P86814), Australia [by S.T. Ahyong]; G, *Rathbunaja bisarmata*, holotype male (20.3 × 15.6 mm) (USNM 48220), Philippines; H, *Rathbunaja bisarmata*, male (37.1 × 29.6 mm) (ZRC 2013.1274), Philippines.

26 October 1988. — 2 males (SMF 46528), Tsubaki Donarii, Anan City, Tokushina Prefecture, 33°50.62'N 134°42.75'E, Japan, coll. K. Sakai. — 1 female (SMF 47749), Japan, coll. K. Matsuzawa, 2005. — 1 dried male (SMF 47604), Japan, no other data, T. Sakai Collection. — 1 male (75.8 × 69.4 mm) (ZRC 2001.56), Tashi, Taiwan. ***Leptomithrax sinensis*** **Rathbun, 1916** – holotype carapace (dried) (32.0 × 25.3 mm) (including spines, 38.3 × 28.8 mm) (USNM 48219), station 5311, South China Sea, near southern Luzon, 21°33'N 116°15'E, 88 fathoms, Philippines, coll. RV *Albatross*, 4 November 1908. ***Leptomithrax bifidus*** **(Ortmann, 1893)** – 1 dried male (36.5 × 29.4 mm) (KPM NH4024), Kii-Nagashima, Japan, T. Sakai Collection, coll. March 1969. — 2 males (32.5 × 27.5 mm, 27.5 × 20.6 mm) (NHM 1961.11.13.28–29), Seto, Shirahama, Japan, coll. gill nets, I. Gordon & Harada, 1950s. — 2 males (ZRC), Mitsu, off Muroto Cape, Kochi Prefecture, Japan, 33°16.6'N 134°10.6'E, in coral nets, coll. 8 July 1988. — 1 male (with rhizocephala), 2 females (SMF 47758), Mitsu, off Muroto Cape, Kochi Prefecture, 33°16.6'N 134°10.6'E, in coral nets, Japan, coll. 21 June 1988. — 1 male, 1 female (SMF 47758), Mitsu, off Muroto Cape, Kochi Prefecture, 33°16.6'N 134°10.6'E, in coral nets, Japan, coll. 21 June 1988. — 1 male (SMF 47743), Tosa, Usa, Kochi Prefecture, 33°26.316'N 133°28.003'E, 160 m, Japan, coll. K. Sakai, 10 May 1990. — 5 males (SMF 47729), Honshu, Wakayama Prefecture, Kii Mimase, 33°45.712'N 135°18.927'E, Japan, coll. K. Sakai, 1 March 1988. ***Leptomithrax gaimardii*** **(H. Milne Edwards, 1834)** – 1 partially cracked female (ZRC 1965.10.13.38), trawled off Disaster Bay, New South Wales, southern Australia, coll. M. Ward, 1930s. ***Leptomithrax sternocostulatus*** **(H. Milne Edwards, 1851)** – 1 male (35.1 × 27.0 mm), 1 ovigerous female (34.0 × 25.7 mm) (ZRC 1965.10.13.74–75), Pittwater, New South Wales, southern Australia, coll. M. Ward, December 1932. ***Leptomithrax tuberculatus*** **Whitelegge, 1900** – 1 female (36.6 × 28.7 mm) (ZRC 1965.10.13.77), trawled off Newcastle, New South Wales, southeastern Australia, coll. M. Ward, 1930s. ***Leptomithrax eldredgei*** **Richer de Forges & Ng, 2015** – holotype male (13.3 × 10.1 mm) (ZRC 1970.2.17.1), 2 ovigerous paratype females (21.1 × 17.4 mm, 1 broken laterally), 1 paratype female (14.9 × 11.3 mm), 1 crushed paratype specimen (ZRC 1970.2.17.2–5), Cr 2/63, station 24, T./10, Hong Kong, coll. & don. Fisheries Research Station of Hong Kong, 1967.

Type species. *Maja bisarmata* Rathbun, 1916, by present designation.

Etymology. The genus is named after Mary Jane Rathbun. The name is an arbitrary combination of her family name with *Maja*. Gender feminine.

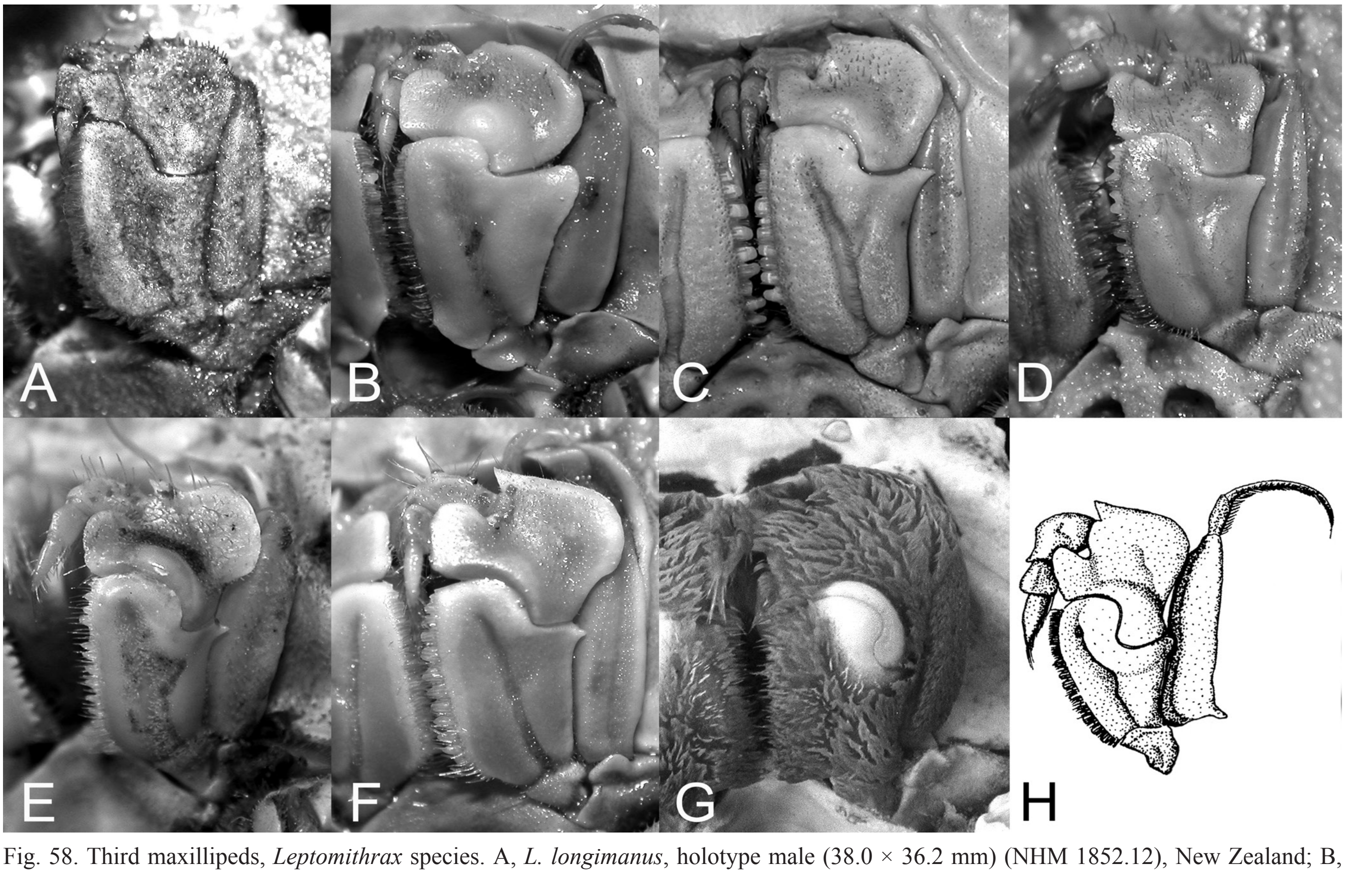

Fig. 58. Third maxillipeds, *Leptomithrax* species. A, *L. longimanus*, holotype male (38.0 × 36.2 mm) (NHM 1852.12), New Zealand; B, *L. tuberculatus* Whitelegge, 1900, female (36.6 × 28.7 mm) (ZRC 1965.10.13.77), Australia; C, *L. sternocostulatus* (H. Milne Edwards, 1851), male (35.1 × 27.0 mm) (ZRC 1965.10.13.74), Australia; D, *L. edwardsii*, male (75.8 × 69.4 mm) (ZRC 2001.56), Taiwan; E, *L. waitei*, male (29.9 × 23.7 mm) (ZRC 2013.076, ex AM P64812), Australia; F, *L. bifidus*, male (32.5 × 27.5 mm) (NHM 1961.11.13.28), Japan; G, *L. longipes* (G. M. Thomson, 1902), male (55.4 × 39.3 mm) (AM P86814), Australia [by S.T. Ahyong]; H, *L. longipes* (G. M. Thomson, 1902) (after Griffin 1966b: fig. 15).

Remarks. The position of the antennal flagellum, just outside the orbit, is diagnostic of *Rathbunaja* n. gen. (Fig. 57G, H). All other *Leptomithrax* species have the antennae positioned well outside the orbit (Fig. 57A–F) (see Griffin, 1966b; Griffin & Tranter, 1986). *Leptomithrax* Miers, 1876, itself is a genus with 14 temperate to cold-water water species, mostly from the southern seas (see Griffin, 1966b; Griffin & Tranter, 1986; Richer de Forges, 1993; Ng et al., 2008). Northwestern Asia has four species, *L. edwardsii* (De Haan, 1835), *L. bifidus* (Ortmann, 1893) and *L. sinensis* Rathbun, 1916, and *L. kiiensis* T. Sakai, 1969 (Griffin, 1976; T. Sakai, 1976; Griffin & Tranter, 1986).

Bennett (1964) argued that three subgenera can be recognised in *Leptomithrax* – *Leptomithrax* (*Leptomithrax*) s. str. (type species *Paramithrax* (*Leptomithrax*) *longimanus* Miers, 1876), *Leptomithrax* (*Austromithrax*) Bennett, 1964 (type species *Leptomithrax* (*Austromithrax*) *mortenseni* Bennett, 1964) and *Leptomithrax* (*Zemithrax*) Bennett, 1964 (type species *Paramithrax longipes* G. M. Thomson, 1902). As discussed at length by Griffin (1966b: 61), Bennett (1964) distinguished these subgenera on the basis of the position and structure of the basal antennal article and flagellum, form of the supraorbital margin, whether the region between the merus and ischium of the third maxilliped is swollen, and the presence or absence of depressions on the male thoracic sternum and/or abdomen. Griffin (1966b) argued that while some of the characters were useful, others appeared to be less reliable and varied between species. In addition, he was not certain about the placement of some species of *Leptomithrax* and was concerned that some of the groupings ended up with only a few species. As such, he preferred to recognise just one genus without subgenera for *Leptomithrax*. He maintained this stand in his revision of the Indo-West Pacific Majoidea (Griffin & Tranter, 1986: 208), although he established a new monotypic genus, *Teratomaia* Griffin & Tranter, 1986, for *Leptomithrax richardsoni* Dell, 1960; and transferred *L. parvispinosus* (Ward, 1933) to a redefined *Tumulosternum* McCulloch, 1913.

Looking at the published descriptions of the various Australian and New Zealand species, it is clear that there are at least three groups among the 11 species from this region. They correspond to Bennett's (1964) three groupings well and these should eventually be recognised as distinct genera. Interestingly, McLay et al. (1995) conducted a cladistic analysis of the fossil and extant species of *Leptomithrax*, and recognised three groups of extant species which roughly correspond to Bennett's (1964) subgenera. However, we defer from formally adopting Bennet's subgenera as separate genera as this should only be done as part of a revision of the species of *Leptomithrax*. This is now being planned. It is nevertheless useful to provide a synopsis of the genus.

Leptomithrax s. str. contains *L. longimanus* (Miers, 1876) (= *Paramithrax* (*Leptomithrax*) *affinis* Borradaile, 1916), *L. australis* (Jacquinot, in Jacquinot & Lucas, 1853) (= *Paramithrax* (*Leptomithrax*) *brevirostris* Miers, 1879), and *L. garricki* Griffin, 1966. These species share the following suite of characters: the posterior carapace margin has two spines which may be short; the distal part of the basal antennal article is relatively short with the flagellum positioned just outside the orbit (Fig. 57A); the posterior edge of the supraorbital eave is well separated from the postorbital spine; the ischium of the third maxilliped is elongate and subrectangular with the antero-lateral angle unarmed (Fig. 58A); the pollex of the chela in large adult males forms a sharp angle with the rest of the palm; the surfaces of the male thoracic sternum and abdomen are level not distinctly depressed; and the male abdomen is subrectangular with the lateral margins subparallel.

A second group corresponding to *Austromithrax* contains *L. mortenseni* Bennett, 1964, *L. depressus* Richer de Forges, 1993, *L. gaimardii* (H. Milne Edwards, 1834) (= *L. spinulosus* Haswell, 1880; *L. australiensis* Miers, 1876), *L. globifer* Rathbun, 1918, *L. sternocostulatus* (H. Milne Edwards, 1851), *L. tuberculatus* Whitelegge, 1900, and *L. waitei* (Whitelegge, 1900). They share the following characters: the posterior carapace margin has two spines; the distal part of the basal antennal article is relatively wide, with the flagellum positioned on the outer edge and far from the orbit (Fig. 57B, C); the posterior edge of the supraorbital eave is well separated from the postorbital spine; the ischium of the third maxilliped is relatively shorter, subrectangular to subtriangular, and the antero-lateral angle has a distinct spur or tooth (Fig. 58B, C, E); the pollex of the chela in large adult males is smoothly contiguous with the rest of the palm; the male thoracic sternum and abdomen may or may not have depressions; and the male abdomen is subtriangular with the lateral margins sloping towards the broader posterior part. On the basis of these characters, three of the northeastern Asian species (*L. edwardsii*, *L. bifidus*, *L. sinensis*) can be referred to *Austromithrax* (cf. Figs. 57D, E, 58D, F). That said, this genus remains heterogeneous and the contained species should be revised to see if other natural groupings are apparent. Of these species, *L. sinensis* Rathbun, 1916, may be a junior subjective synonym of *L. bifidus* (Ortmann, 1893). Richer de Forges & Ng (2015) discussed this matter at length when describing a new species, *L. eldredgei*, from Hong Kong and commented that the type of *L. sinensis* is just a carapace and only has short spines.

The third group corresponding to *Zemithrax* contains only *L. longipes* (G. M. Thomson, 1902) (= *Leptomithrax* (*Zemithrax*) *molloch* Bennett, 1964). Its defining suite of characters are as follow: the posterior carapace margin has only one spine or tooth; the posterior edge of the supraorbital eave and postorbital spine almost touch each other; the distal part of the basal antennal article is relatively narrow, with the flagellum positioned submedially and distant from the orbit (Fig. 57F); the ischium of the third maxilliped is relatively short, subtriangular with the distal part much wider than the proximal part, the anterolateral angle has a distinct tooth and the setal arrangement is very distinctive (Fig. 58G, H); the pollex of the chela in large adult males is smoothly contiguous with the rest of the palm; the male thoracic sternum and abdomen have distinct depressions; and the male abdomen is subtriangular with the lateral margins sloping towards the broader posterior part.

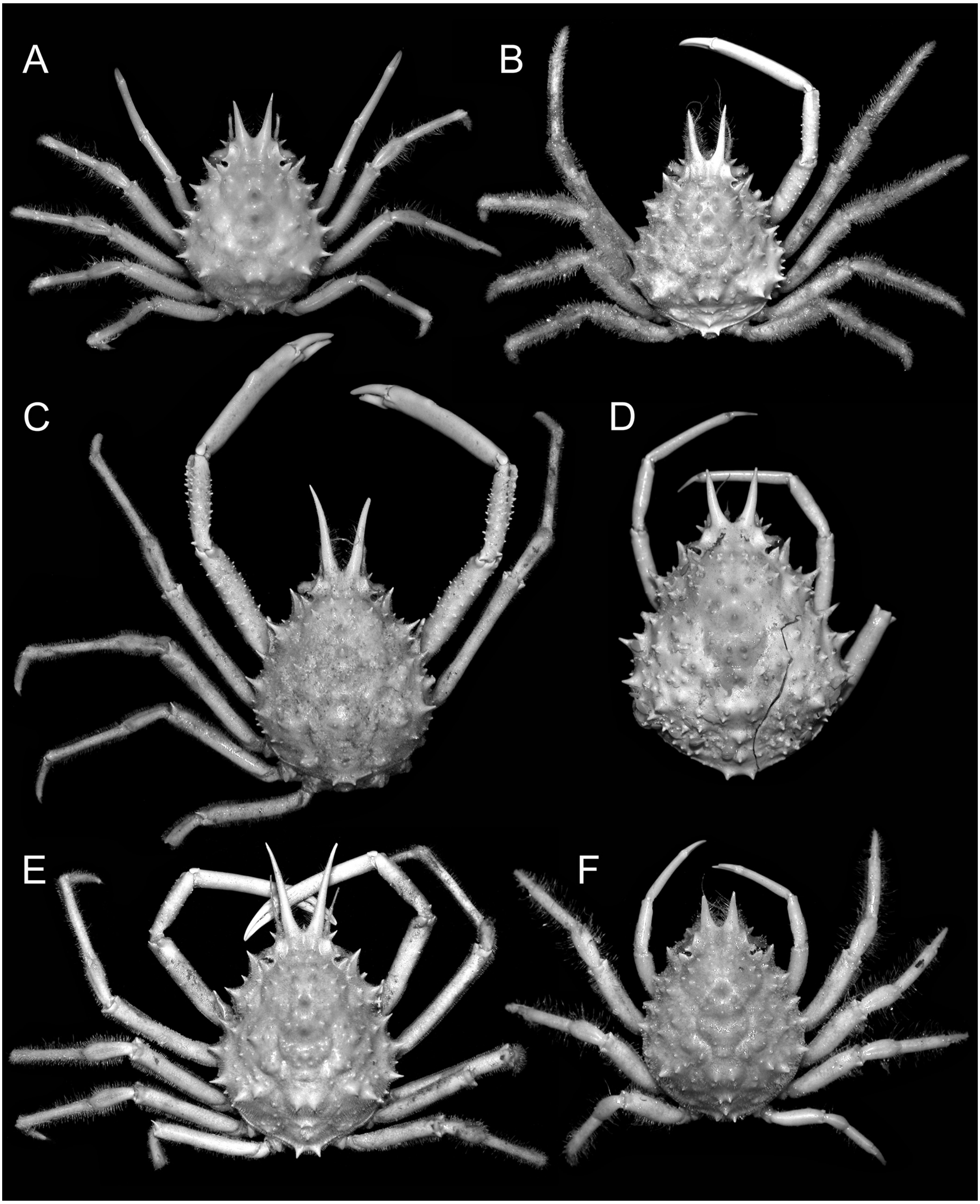

Fig. 59. General habitus, *Rathbunaja* species. A, *R. bisarmata*, holotype male (20.3 × 15.6 mm) (USNM 48220), Philippines; B, *R. bisarmata*, male (37.1 × 29.6 mm) (ZRC 2013.1274), Philippines; C, *R. kiiensis*, holotype male (53.7 × 45.0 mm) (USNM 125885), Japan; D, *R. kiiensis*, female (43.8 × 37.3 mm) (NSMT-Cr 6419), Kyushu-Palau Ridge; E, *R. kiiensis*, male (49.9 × 39.1 mm) (NSMT-Cr 5094), Japan; F, *R. brevipes* n. sp., holotype male (24.0 × 18.4 mm) (MNHN-IU-2011-2408), Papua New Guinea.

One of the characters used by Bennett (1964: 46, 53) to separate *Zemithrax* from the others was what he describes as a large boss (swelling) being present on the merus and ischium at the junction where they articulate. However, he admitted that while it was very obvious in the type species, *L. longipes* (Fig. 58G, H), it was also present but less distinct in other species, with *L. globifer* having the merus but not ischium swollen, while in *L. gaimardi* (as *L. australiensis*), the ischium and merus are slightly swollen (Bennett, 1964: 51). In the specimens on hand, the third maxilliped of *L. tuberculatus* has a small but distinct swelling only on the merus (Fig. 58B), whereas in *L. sternocostulatus*, the swelling is even smaller and less distinct (Fig. 58C). In *L. bifidus*, the swelling in the merus and ischium of the third maxilliped is very prominent (Fig. 58F), not unlike that described and figured for *L. longipes* (cf. Fig. 58G, H; Bennett, 1964: figs. 50, 53). In addition, the shape of the ischium also appears to vary from being short with the proximal part much narrower than the distal part (e.g., *L. tuberculatus*) (Fig. 58B) to being relatively longer with the difference in proportions less obvious (e.g., *L. sternocostulatus*, Fig. 58C).

The northwestern Asian *Leptomithrax kiiensis* is very distinct from all other *Leptomithrax* and belongs to its own group, here named *Rathbunaja* n. gen. *Rathbunaja* is closest to *Leptomithrax* s. str. in the male thoracic sternum and abdomen not having any trace of depressions; the distal part of the basal antennal article is relatively short with

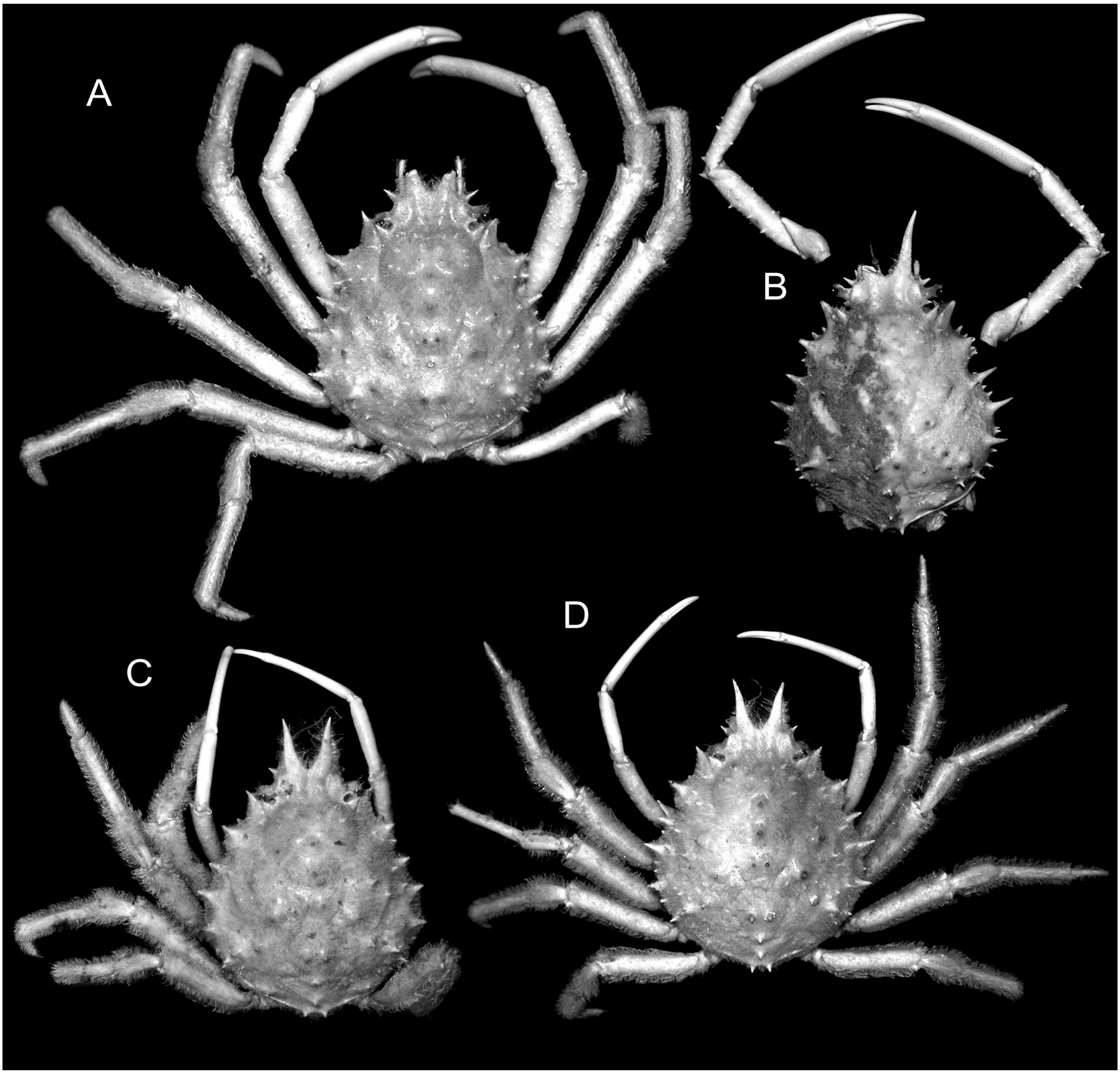

Fig. 60. General habitus. A, *Rathbunaja ursus* n. sp., holotype male (50.1 × 41.5 mm) (NMCR, ex ZRC 2013.1275), Philippines; B, *Rathbunaja ursus* n. sp., paratype male (41.6 × 32.8 mm) (ZRC 2013.1276), Philippines; C, *Rathbunaja ursus* n. sp., paratype female (49.4 × 38.4 mm) (NSMT-Cr 15386), Philippines; D, *Rathbunaja ursus* n. sp., paratype ovigerous female (46.8 × 36.6 mm) (ZRC 2001.0594), Philippines

the flagellum positioned just outside the orbit; the form of the third maxillipeds (ischium subrectangular without tooth or projection on antero-lateral angle of the ischium); the pollex of the chela in large adult males forms a sharp angle with the palm; and the subrectangular male abdomen with the lateral margins subparallel. However, *Rathbunaja* can easily be separated by the different carapace shape, being less inflated (notably in the branchial regions) with the pseudorostral and lateral spines proportionately longer (Figs. 59, 60); and having a prominent distal spine on the dorsal margin of the merus of the ambulatory leg (Fig. 65B, D, F, I–K) (absent in *Leptomithrax* s. str.).

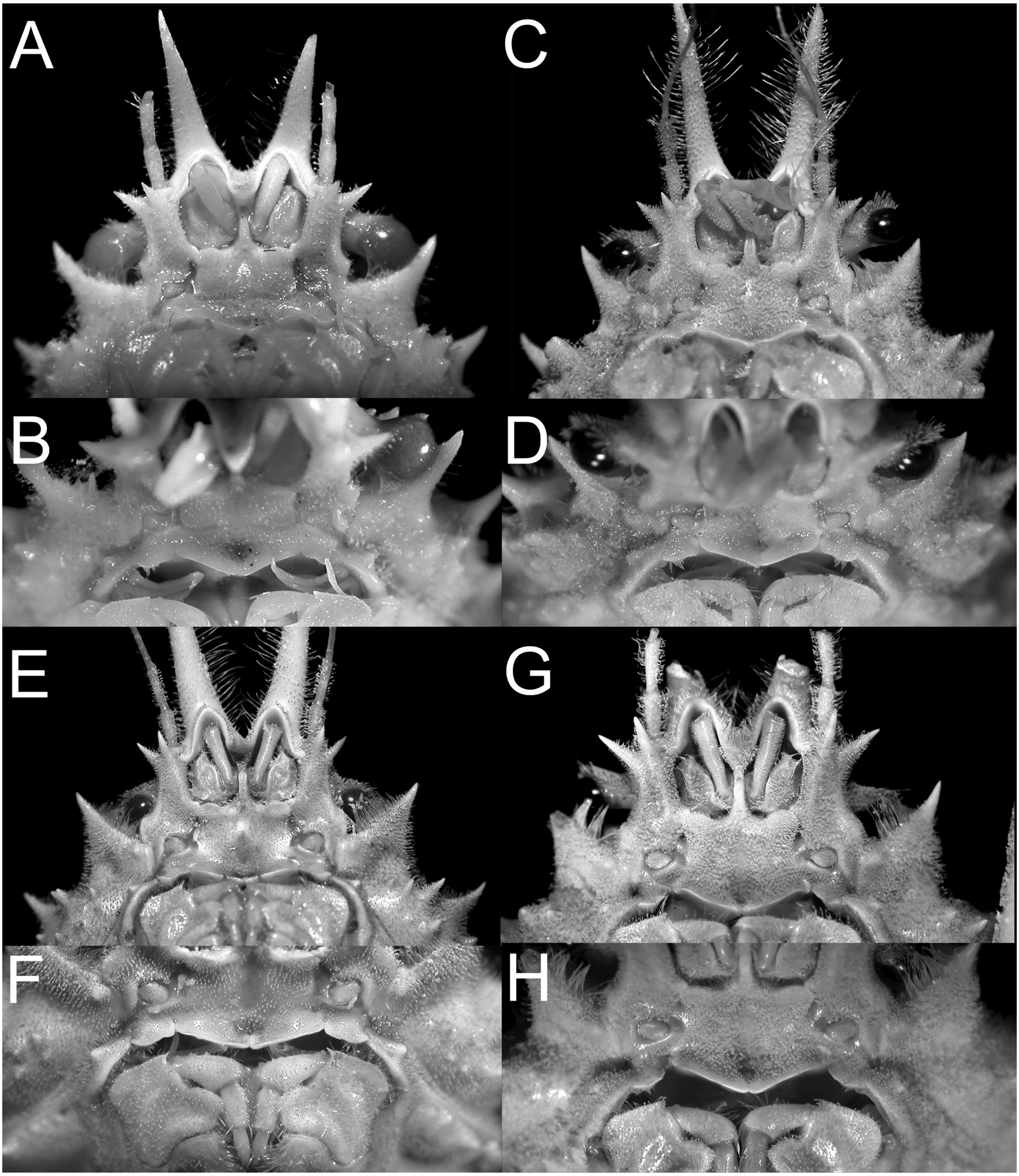

Fig. 61. Antennae, antennules, orbits and epistomes, *Rathbunaja* species. A, B, *R. bisarmata*, holotype male (20.3 × 15.6 mm) (USNM 48220), Philippines; C, D, *R. bisarmata*, male (37.1 × 29.6 mm) (ZRC 2013.1274), Philippines; E, F, *R. kiiensis*, male (49.9 × 39.1 mm) (NSMT-Cr 5094), Japan; G, H, *R. ursus* n. sp., holotype male (50.1 × 41.5 mm) (NMCR, ex ZRC 2013.1275), Philippines.

Key to species of *Rathbunaja* n. gen.

1. Pseudorostral spines short, weakly diverging, almost subparallel (Figs. 59F, 62A); ambulatory legs (notably merus and propodus) short (Figs. 59F, 62D–G); Papua New Guinea .... *Rathbunaja brevipes* n. sp.
– Pseudorostral spines long, diverging; ambulatory legs (notably merus and propodus) relatively longer 2

2. Carapace relatively broad (Fig. 60); distal spines on basal antennal article relatively longer, more strongly diverging (Fig. 61G); ischium of third maxilliped proportionately longer (Fig. 63E–H); male telson proportionately broader, appears semicircular (Fig. 64E); G1 very long, strongly curved, more slender, tip bent inwards (Fig. 67A–D); Philippines .... *Rathbunaja ursus* n. sp.
– Carapace relatively narrower (Fig. 59A–E); distal spines on basal antennal article relatively shorter, less diverging (Fig. 61A, C, E); ischium of third maxilliped proportionately shorter (Figs. 62C, 63A–D); male telson more triangular in shape (Fig. 64A–C); G1 gently curved, not elongate, tip straight (Figs. 66) 3

3. Ambulatory merus relatively longer, more slender (Figs. 59C, E, 65F); G1 relatively more strongly curved, distal part relatively longer (Fig. 66H–M); Japan .... *Rathbunaja kiiensis* (T. Sakai, 1969)
– Ambulatory merus relatively shorter, stouter (Figs. 59A, B, 65B, D); G1 gently curved, distal part relatively shorter (Fig. 66A–G); Philippines..*Rathbunaja bisarmata* (Rathbun, 1916)

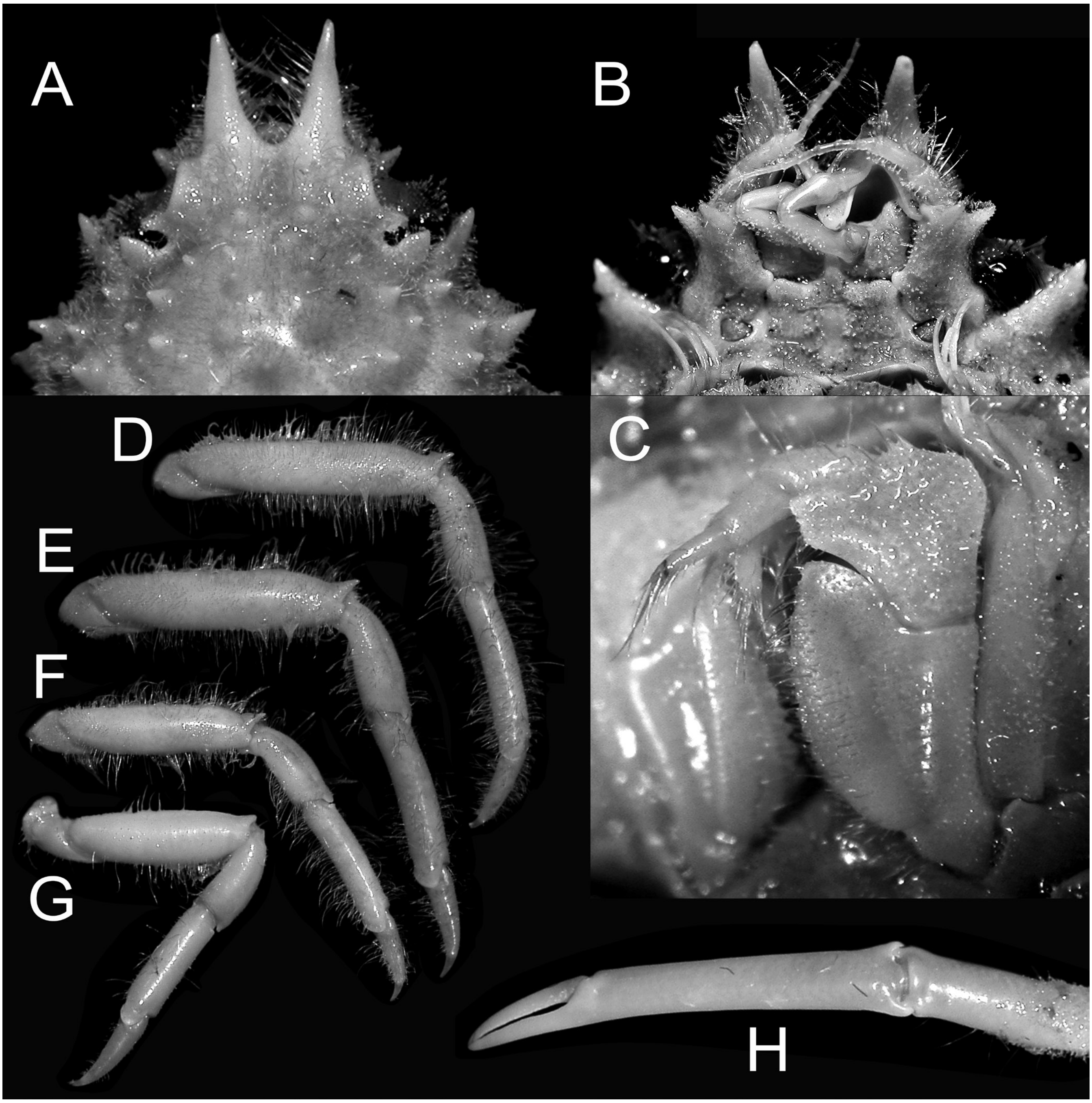

Fig. 62. *Rathbunaja brevipes* n. sp., holotype male (24.0 × 18.4 mm) (MNHN-IU-2011-2408), Papua New Guinea. A, frontal region, dorsal view; B, antennae, antennules and epistome; C, left third maxilliped; D–G, first to fourth right ambulatory legs; H, left chela.

***Rathbunaja bisarmata* (Rathbun, 1916)**
(Figs. 59A, B, 61A–D, 63A, B, 64A, B, 65A–D, 66A–G)

Maja bisarmata Rathbun, 1916: 553. – Serène, 1968: 57. – Griffin, 1976: 199, Fig. 7b. – Griffin & Tranter, 1986: 211 (key).

Material examined. Holotype: male (20.3 × 15.6 mm) (USNM 48220), station 5519, Point Tagolo Light, off northern Mindanao, 80°47'N 123°31.25'E, Philippines, coll. RV *Albatross*, 9 August 1909. Others: **Philippines** – 1 male (37.1 × 29.6 mm) (ZRC 2013.1274), Balicasag Island, Panglao, Bohol, 200–300 m, coll. fishermen with tangle nets, 2 March 2004.

Diagnosis. Carapace relatively narrow (Fig. 59A, B). Pseudorostral spines long, diverging (Fig. 59A, B). Median row with 2 median gastric spines; 2 cardiac spines; 2 intestinal spines (Fig. 59A, B). Basal antennal article with 2 relatively short distal spines not strongly diverging (Fig. 61A–D). Ischium of third maxilliped proportionately shorter (Fig. 63A, B). Ambulatory merus relatively shorter, stouter (Figs. 59A, B, 65B, D). Male telson subtriangular (Fig. 64A, B). G1 gently curved, distal part relatively shorter (Fig. 66A–G).

Remarks. This is a very poorly known species and although it has been treated as a valid *Maja* species by Griffin (1976) (who examined the type) and Griffin & Tranter (1986), a re-examination of the holotype shows otherwise. Although Rathbun (1916) placed this species in *Maja*, its antennal flagellum is actually just outside the orbit. In fact, the species is very close to *Leptomithrax kiiensis*, described by T. Sakai (1969) on the basis of a large male 55.0 by 44.5 mm from Kii Minable in Japan. Tune Sakai (1969, 1976) placed this species in *Leptomithrax* because its antennal flagellum is just outside the orbit, even if it is not to the same degree as other congeners.

The holotype male of *Maja bisarmata* is relatively small (Fig. 59A) and although its G1 is not fully developed (Fig. 61A–D), it shows enough features. A recent larger specimen from the Philippines agrees well with the type male in its carapace form, antennal basal article, epistome, structure

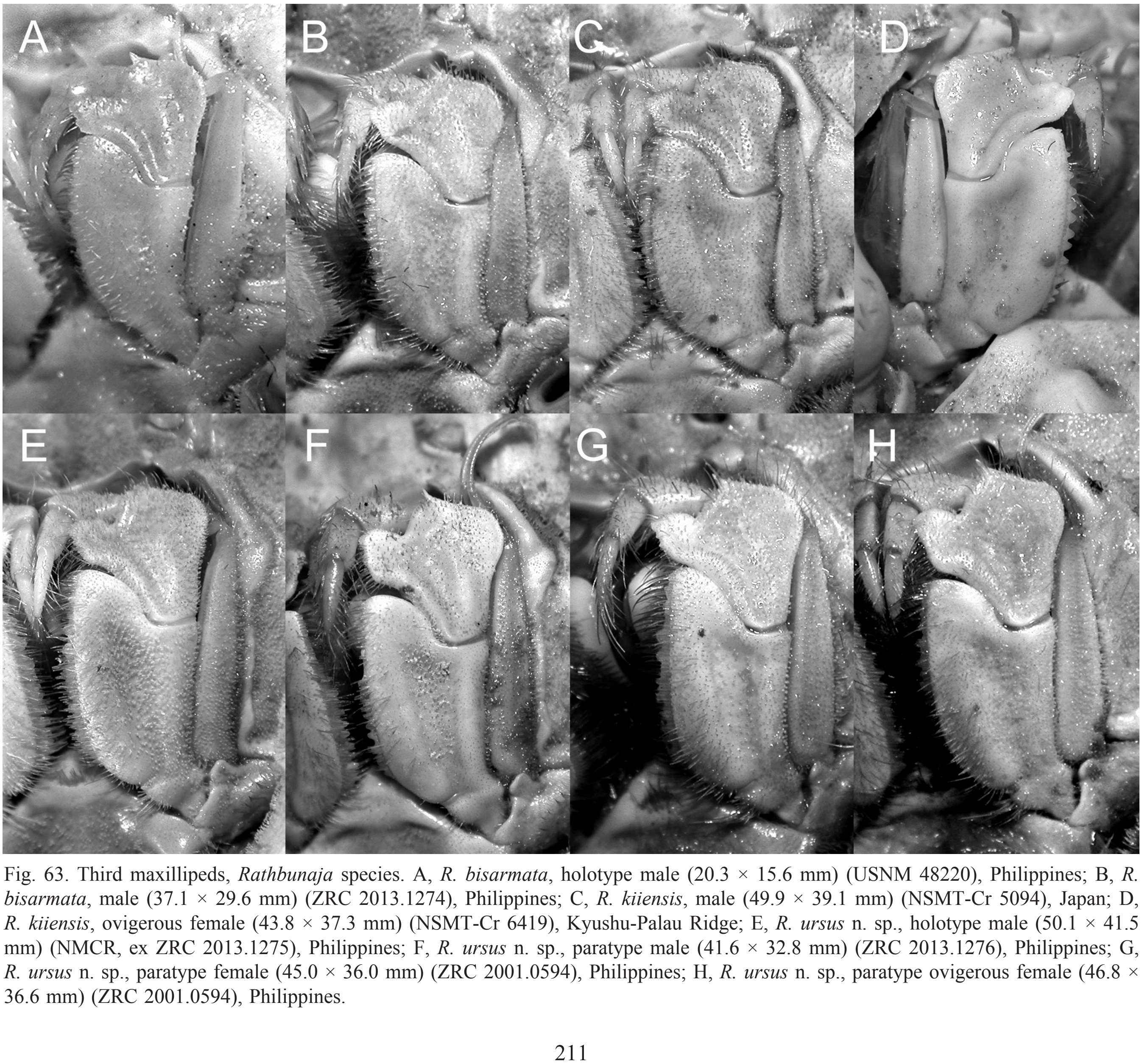

Fig. 63. Third maxillipeds, *Rathbunaja* species. A, *R. bisarmata*, holotype male (20.3 × 15.6 mm) (USNM 48220), Philippines; B, *R. bisarmata*, male (37.1 × 29.6 mm) (ZRC 2013.1274), Philippines; C, *R. kiiensis*, male (49.9 × 39.1 mm) (NSMT-Cr 5094), Japan; D, *R. kiiensis*, ovigerous female (43.8 × 37.3 mm) (NSMT-Cr 6419), Kyushu-Palau Ridge; E, *R. ursus* n. sp., holotype male (50.1 × 41.5 mm) (NMCR, ex ZRC 2013.1275), Philippines; F, *R. ursus* n. sp., paratype male (41.6 × 32.8 mm) (ZRC 2013.1276), Philippines; G, *R. ursus* n. sp., paratype female (45.0 × 36.0 mm) (ZRC 2001.0594), Philippines; H, *R. ursus* n. sp., paratype ovigerous female (46.8 × 36.6 mm) (ZRC 2001.0594), Philippines.

of the third maxilliped, relatively short ambulatory legs, thoracic sternum, male abdomen and structure of the G1, and we are confident they are conspecific. These features make it unlikely that *Maja bisarmata* is the juvenile form of the more common new species described here from the Philippines, *Rathbunaja ursus*.

Maja bisarmata Rathbun, 1916, is very close to *Leptomithrax kiiensis* T. Sakai, 1969. Comparisons of Rathbun's species with material of *L. kiiensis* from Japan as well as the descriptions and figures of the species by T. Sakai (1969, 1976), Miyake (1983) and Ikeda (1998) show minimal differences. The main difference appears to be the relative lengths of the merus of the ambulatory leg, which in *R. kiiensis*, is proportionately longer and more slender (Figs. 59C, E, 65F) than that of *R. bisarmata* (Figs. 59A, B, 65B, D). The distal part of the G1 of *R. kiiensis* is more curved and slightly longer than that of *R. bisarmata* (Fig. 66H–M versus Fig. 66A–G). As such, both species are recognised for the time being. As discussed under the genus, the distinctive features of these two species (as well as two other new ones here described) warrant the establishment of a new genus, *Rathbunaja*, for them.

Rathbunaja kiiensis (T. Sakai, 1969)
(Figs. 59C–E, 61E, F, 63C, D, 64C, 65E–G, 66H–M)

Leptomithrax kiiensis T. Sakai, 1969: 255, pl. 1 fig. 4. – Miyake, 1983: 48, pl. 16 fig. 4. – T. Sakai, 1976: 243, text fig. 130. – Matsuzawa, 1977: pl. 96 fig. 3. – Baba et al., 1986: 223, fig. 167. – Takeda, 1980: 280. – Takeda, 1993: 37. – Ikeda, 1998: 37, 118, 119, pl. 42.

Material examined. Holotype: male (53.7 × 45.0 mm) (USNM 125885), Kii Minabe, Kii Peninsula, Wakayama Prefecture, Honshu, Japan, coll. M. Ozaki. Others: **Japan** – 1 male (49.9 × 39.1 mm) (NSMT-Cr 5094), Kushimoto, Kii Peninsula, coll. 15 July 1977. — 1 ovigerous female (43.8 × 37.3 mm) (NSMT-Cr 6419), 26°43.8'N 135°20'E, Kita-Koho Channel, Kyushu-Palau Ridge, 320 m, coll. 14 February 1978. — 1 female (44.0 × 34.8 mm) (NSMT-Cr 12211), station T13, 29°25.8'N 127°18.0'E – 29°24.4'N 127°17.9'E, East China Sea, 169 m, coll. 27 September 1997.

Diagnosis. Carapace relatively narrow (Fig. 59C–E). Pseudorostral spines long, distinctly diverging (Fig. 59C–E). Median row with 2 median gastric spines; 2 cardiac spines; 2 or 3 intestinal spines (Fig. 59C–E). Basal antennal article with 2 relatively short distal spines not strongly diverging (Fig. 61E). Ischium of third maxilliped proportionately

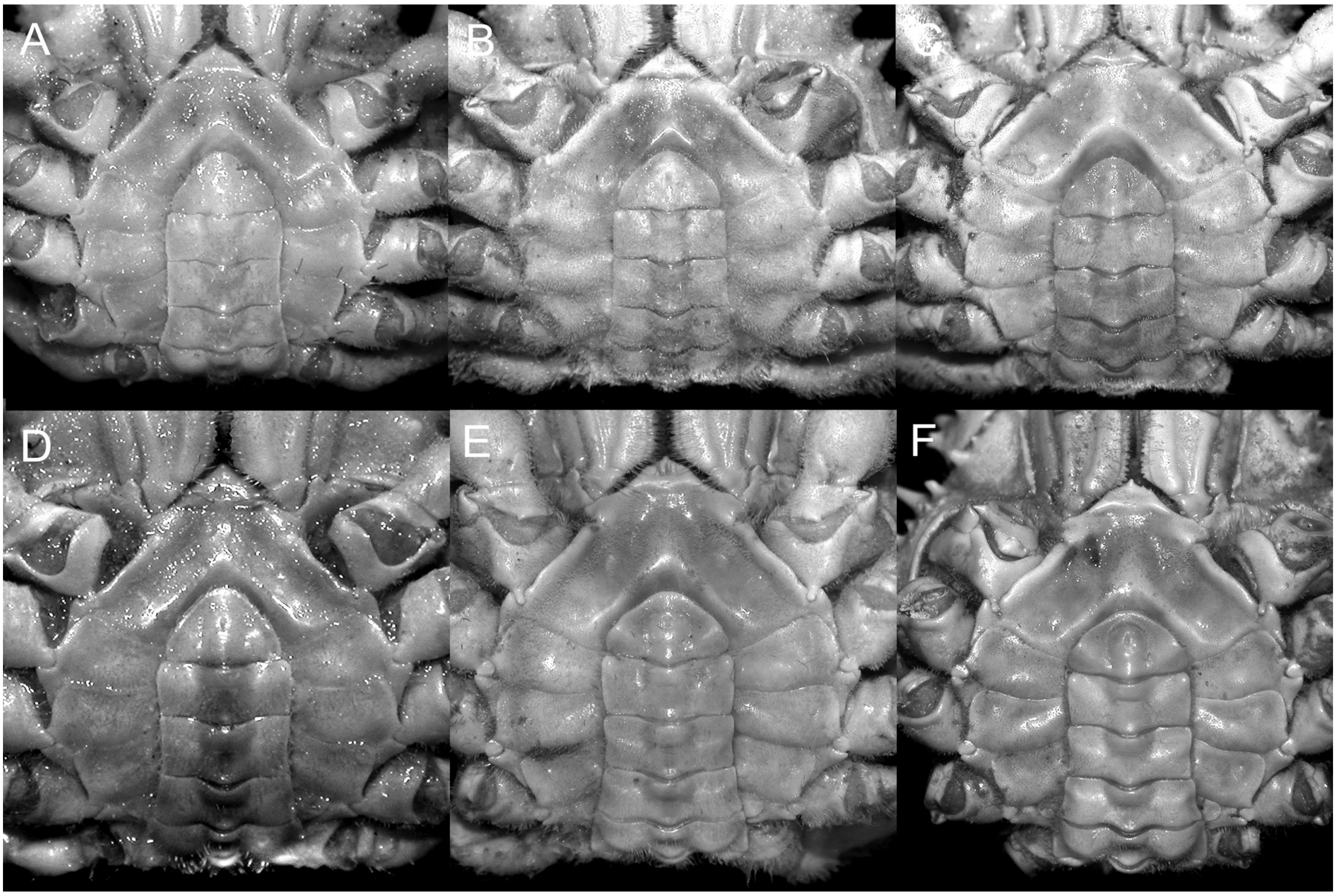

Fig. 64. Male anterior thoracic sternums and abdomens, *Rathbunaja* species. A, *R. bisarmata*, holotype male (20.3 × 15.6 mm) (USNM 48220), Philippines; B, *R. bisarmata*, male (37.1 × 29.6 mm) (ZRC 2013.1274), Philippines; C, *R. kiiensis*, male (49.9 × 39.1 mm) (NSMT-Cr 5094), Japan; D, *R. brevipes* n. sp., holotype male (24.0 × 18.4 mm) (MNHN-IU-2011-2408), Papua New Guinea; E, *R. ursus* n. sp., holotype male (50.1 × 41.5 mm) (NMCR, ex ZRC 2013.1275), Philippines; F, *R. ursus* n. sp., paratype male (41.6 × 32.8 mm) (ZRC 2013.1276), Philippines.

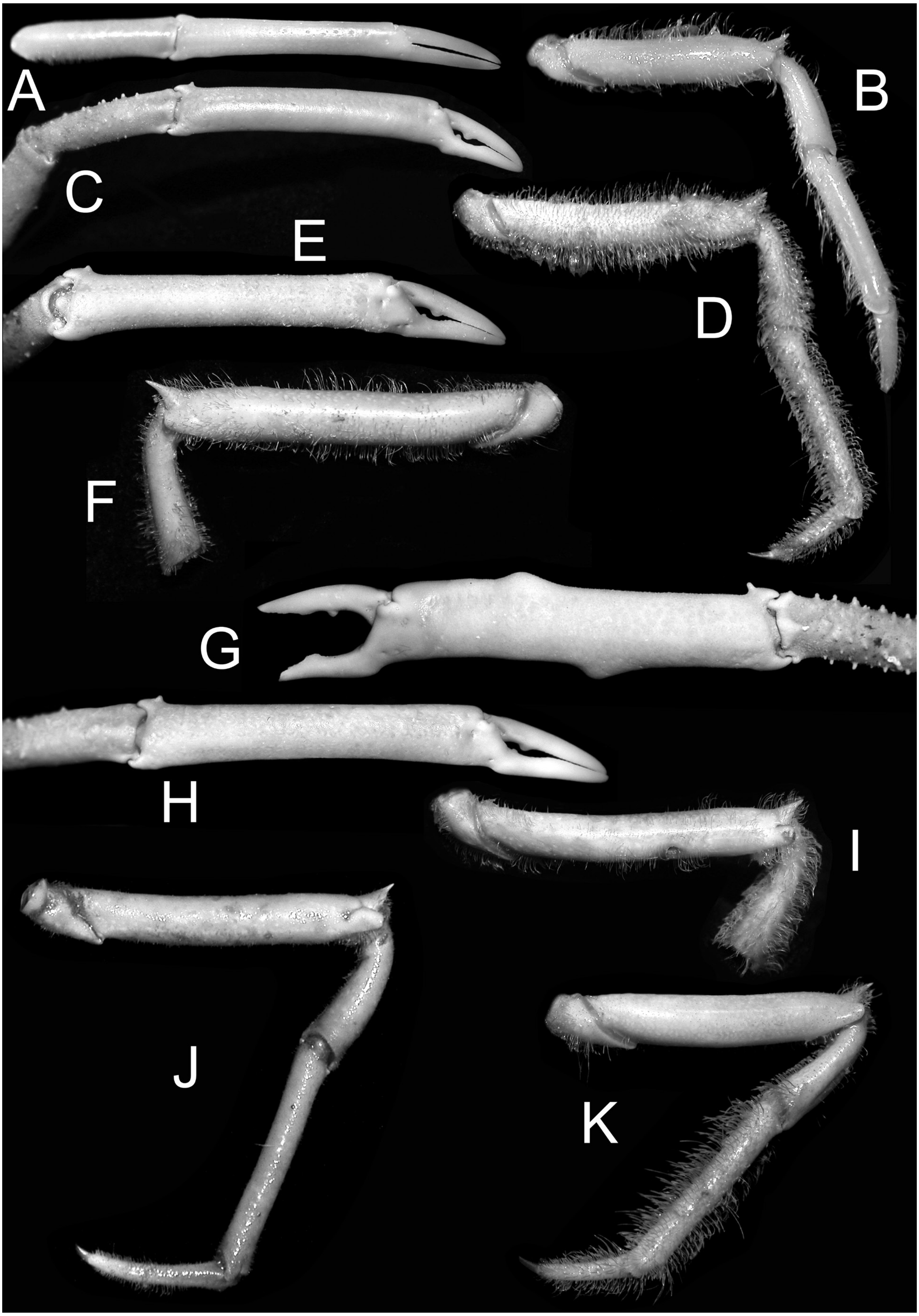

Fig. 65. Chelipeds and ambulatory legs, *Rathbunaja* species. A, B, *R. bisarmata*, holotype male (20.3 × 15.6 mm) (USNM 48220), Philippines; C, D, *R. bisarmata*, male (37.1 × 29.6 mm) (ZRC 2013.1274), Philippines; E, F, *R. kiiensis*, male (49.9 × 39.1 mm) (NSMT-Cr 5094), Japan; G, *R. kiiensis*, holotype male (53.7 × 45.0 mm) (USNM 125885), Japan; H, I, *R. ursus* n. sp., holotype male (50.1 × 41.5 mm) (NMCR, ex ZRC 2013.1275), Philippines; J, *R. ursus* n. sp., paratype male (41.6 × 32.8 mm) (ZRC 2013.1276), Philippines; K, *R. ursus* n. sp., paratype female (45.0 × 36.0 mm) (ZRC 2001.0594), Philippines.

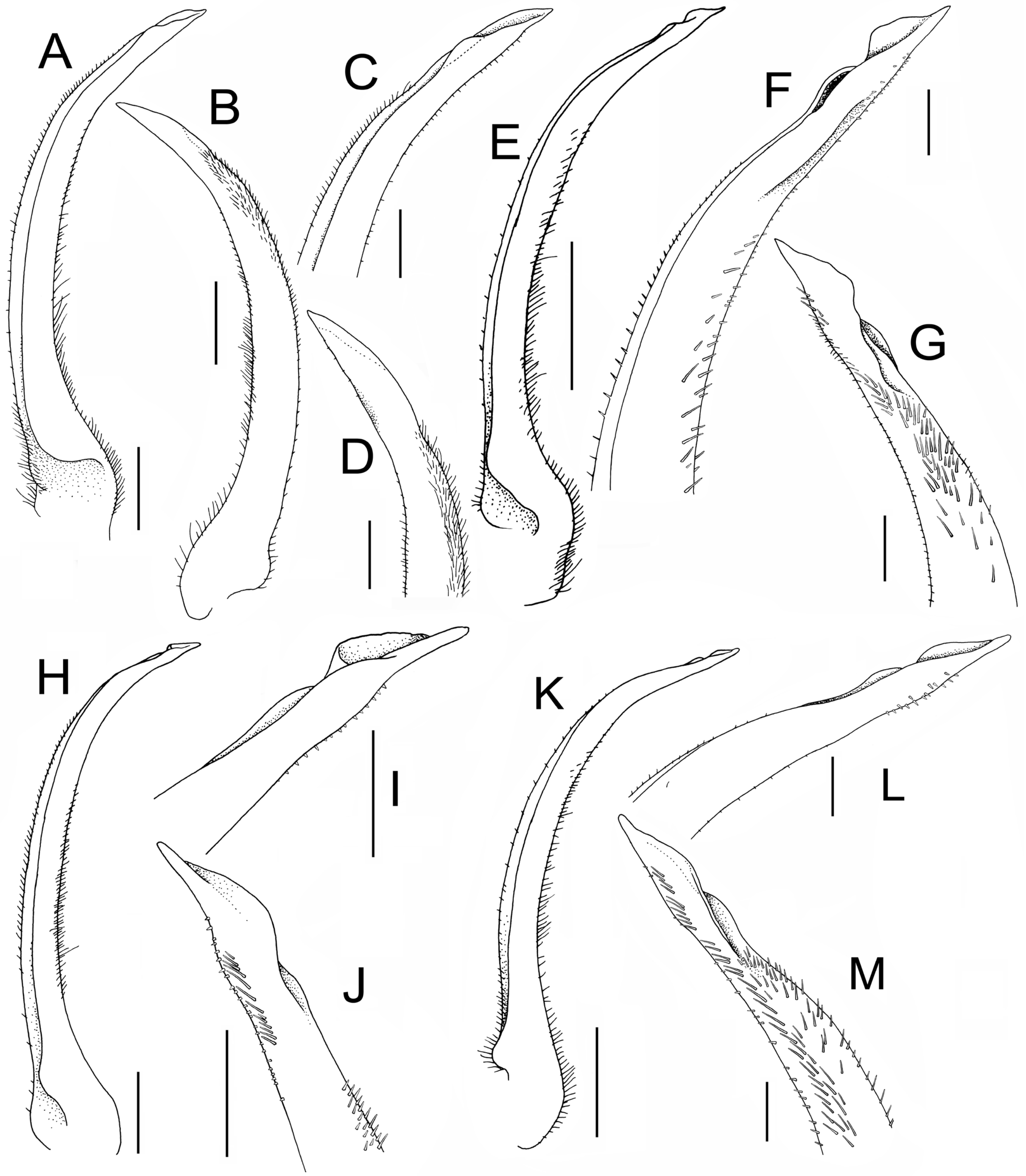

Fig. 66. Left G1s, *Rathbunaja* species. A–D, *R. bisarmata*, holotype male (20.3 × 15.6 mm) (USNM 48220), Philippines; E–G, *R. bisarmata*, male (37.1 × 29.6 mm) (ZRC 2013.1274), Philippines; H–J, *R. kiiensis*, holotype male (53.7 × 45.0 mm) (USNM 125885), Japan; K–M, *R. kiiensis*, male (49.9 × 39.1 mm) (NSMT-Cr 5094), Japan. Scales: A, H, K = 1.0 mm; E = 5.0 mm; B–D, F, G, I, J, L, M= 0.5 mm.

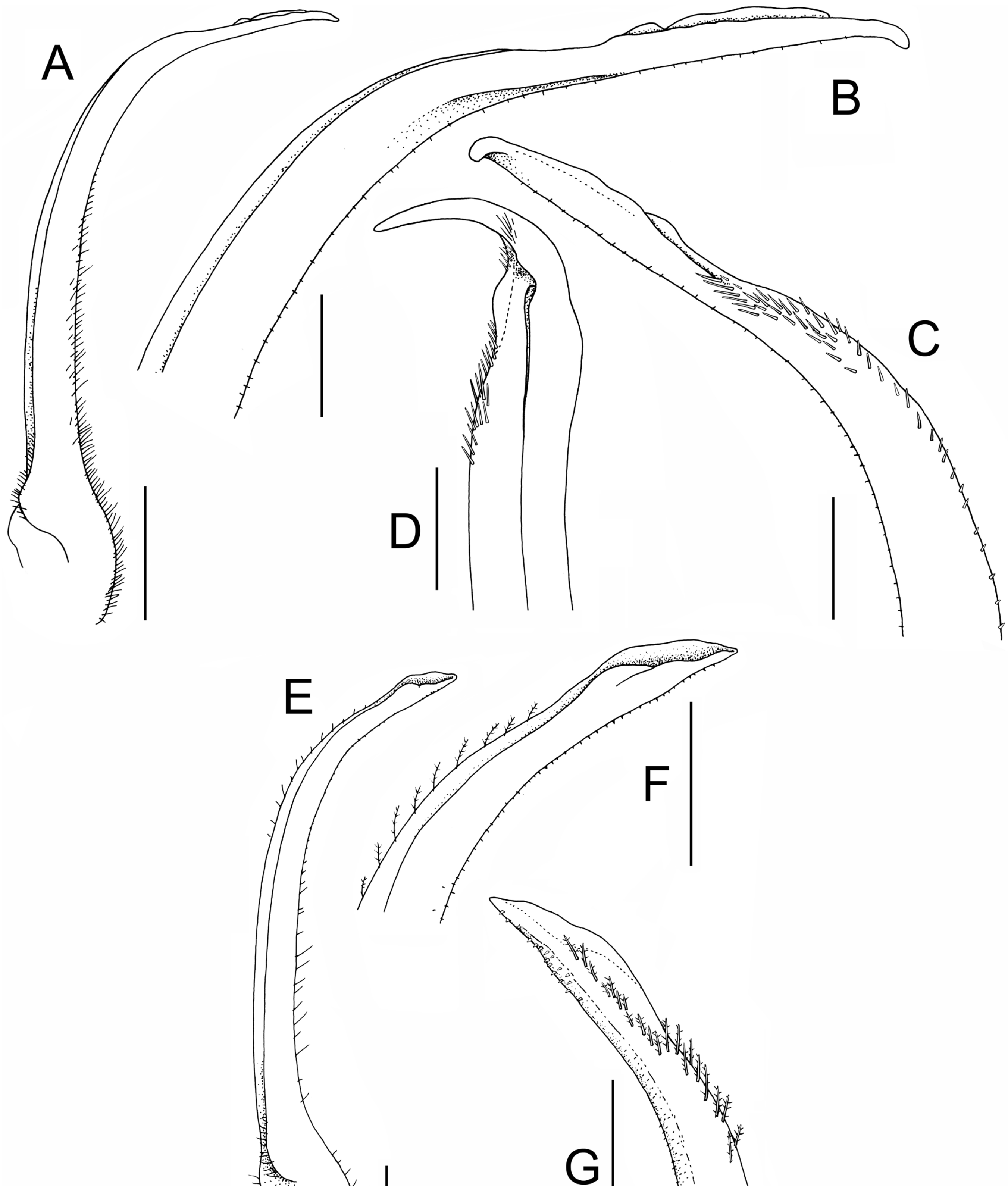

Fig. 67. Left G1s, *Rathbunaja* species. A–D, *R. ursus* n. sp., holotype male (50.1 × 41.5 mm) (NMCR, ex ZRC 2013.1275), Philippines; E–G, *R. brevipes* n. sp., holotype male (24.0 × 18.4 mm) (MNHN-IU-2011-2408), Papua New Guinea. A, E = 5.0 mm; B-G = 1.0 mm; F, G = 0.5 mm.

shorter (Fig. 63C, D). Ambulatory merus relatively long, slender (Figs. 59C, E, 65F). Male telson subtriangular (Fig. 64C). G1 relatively more curved, distal part relatively longer (Fig. 66H–M).

Remarks. The type of *Rathbunaja kiiensis* is the largest known specimen. Although it is only slightly larger than another male specimen (male 49.9 × 39.1 mm, NSMT-Cr 5094), its chela is more prominently enlarged, with a distinct swelling on each margin of the palm (Fig. 65G versus Fig. 65E). The G1 has not been figured before. The G1 of the holotype male is slightly less strongly curved than the other male and the dorsal fold on the distal part of the G1 of the holotype male is also more pronounced (Fig. 66H–J versus Fig. 66K–M). However, we do not regard these differences as significant at the species-level.

Rathbunaja brevipes n. sp.

(Figs. 59F, 62, 64D, 67E–G)

Material examined. Holotype: male (24.0 × 18.4 mm) (MNHN-IU-2011-2408), station DW 3719, 6°03'S 14°36'E, 410 m, Papua New Guinea, coll. RV *Alis*, BIOPAPUA, 7 October 2010.

Diagnosis. Carapace relatively narrow (Figs. 59F, 62A). Pseudorostral spines short, weakly diverging, almost subparallel (Fig. 59F). Median row with 2 median gastric spines; 2 cardiac spines; 3 intestinal spines (Fig. 59F). Basal antennal article with 2 relatively short distal spines not strongly diverging (Fig. 62B). Ischium of third maxilliped proportionately shorter (Fig. 62C). Ambulatory legs (notably merus and propodus) short (Figs. 59F, 62D–G). Male telson subtriangular (Fig. 64D). G1 with distal part distinctly curved, dorsal fold low (Fig. 67E–G).

Etymology. The species is named after its relatively short ambulatory legs. Used as a noun in apposition.

Remarks. *Rathbunaja brevipes* n. sp. is perhaps closest to *R. kiiensis* but can easily be distinguished by possessing relatively much shorter pseudorostral spines (Figs. 59F, 62A versus Fig. 59C–E); a relatively larger and broader intercalated spine (Figs. 59F, 62A) (more triangular and sharper in *R. kiiensis*, Fig. 59C–E); proportionately shorter lateral carapace spines (Fig. 59F versus Fig. 59C–E); and shorter ambulatory legs, especially the merus, which also has a relatively weaker distal dorsal spine (Figs. 59F, 62D–G versus Figs. 59C–E, 65F). Interestingly, the G1 structures of the two species (Figs. 67E–G, 66H–M) are very similar. The ambulatory legs of *R. brevipes* are also shorter than those on *R. bisarmata* (Figs. 59F, 62D–G versus Figs. 59A, B, 65B, D).

Rathbunaja ursus n. sp.

(Figs. 60, 61G, H, 63E–H, 64E, F, 65H–K, 67A–D)

Material examined. Holotype: male (50.1 × 41.5 mm) (NMCR, ex ZRC 2013.1275), Balicasag Island, Panglao, Bohol, Philippines, 200–300 m, coll. fishermen with tangle nets, 2 March 2004. Paratypes: **Philippines** – 2 ovigerous females (46.8 × 36.6 mm, 45.0 × 36.0 mm) (ZRC 2001.0594), Balicasag Island, Panglao, Bohol, 200–300 m, coll. fishermen with tangle nets, 28 November 2001. — 1 male (41.6 × 32.8 mm), 1 ovigerous female (45.6 × 35.7 mm), 1 female (47.2 × 37.6 mm) (ZRC 2013.1276), Balicasag Island, Panglao, Bohol, 200–300 m, coll. fishermen with tangle nets, June 2002. — 1 female (49.4 × 38.4 mm) (NSMT-Cr 15386), Balicasag Island, Panglao, Bohol, coll. fishermen with tangle nets, via H. Komatsu & M. Takeda, February 2003. — 1 male (47.5 × 39.5 mm) (ZRC 2013.1277), Maribohoc Bay, Panglao, Bohol, coll. J. Arbasto, tangle nets, 30 May 2004.

Diagnosis. Carapace relatively broad (Fig. 60). Pseudorostral spines long, diverging (Fig. 60). Median row with 2 median gastric spines; 2 cardiac spines; 2 intestinal spines (Fig. 60). Basal antennal article with 2 relatively long distal spines, strongly diverging (Fig. 61G). Ischium of third maxilliped long (Fig. 63E–H). Ambulatory legs (notably merus and propodus) relatively long (Figs. 60, 65I–K). Male telson appears semicircular (Fig. 64E). G1 very long, strongly curved, slender, tip bent inwards (Fig. 67A–D).

Etymology. The name "ursus" alludes to the thick tomentum covering the animal like the fur of a bear, «ursus». The name is used as a noun in apposition.

Remarks. The discovery of *Rathbunaja ursus* n. sp. from Balicasag, Philippines, is rather surprising especially since there was also a specimen of *R. bisarmata* (Rathbun, 1916) collected from the same area. Most specimens of *Rathbunaja* from the Philippines actually belong to this new species. The two species are similar and are not easy to separate; In *R. ursus*, however, the carapace is relatively broader (Fig. 60 versus Fig. 59A, B), the two distal spines on the basal antennal article are more strongly diverging (Fig. 61G versus Fig. 61A, C), the ischium of the third maxilliped is proportionately longer (Fig. 63E–H versus Fig. 63A, B), the anterior thoracic sternum (sternites 1–4) is relatively longer (Fig. 64E, F versus Fig. 64A, B), the male telson is proportionately broader (Fig. 64E, F versus Fig. 64A, B), and the lateral margins of male abdominal somites 5 and 6 are more concave (Fig. 64E, F versus Fig. 64A, B). Most significantly, their G1 structures are completely different, with that of *R. ursus* much longer, with the distal part more strongly curved and slender (Fig. 67A–D versus Fig. 66A–G). These differences cannot be explained by size or maturity.

GENERAL DISCUSSION

In the present revision, we separate *Maja* into 10 genera, seven of which are new, and recognise 17 new species from the Indo-West Pacific. Considering that *Maja* s. lato has never previously been revised, the number of new taxa is not surprising. The most remarkable aspect of the present study is the record of 11 species from one site, Balicasag Island, in the Philippines. Of these, nine are new to science. If the areas around Balicasag are considered, a total of 13 species are known. The proportion of new species is very high. This tiny island in the Bohol Sea has been previously regarded

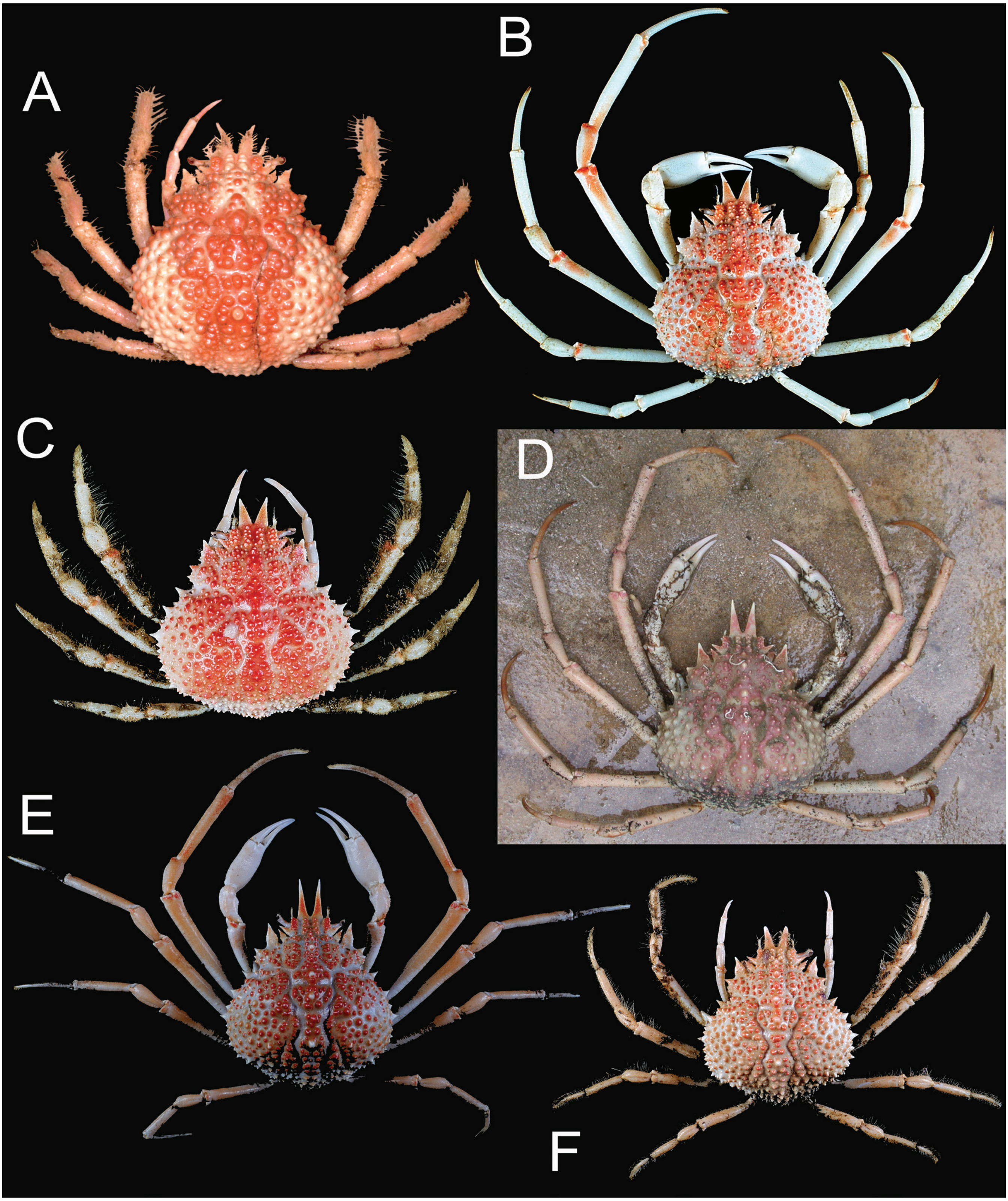

Fig. 68. Colours in life. A, *Paramaja kominatoensis*, female (ca. 57.8 mm carapace length) (after Ikeda, 1998: pl. 41-1b), Taiwan; B, *Paramaja gibba*, male (58.6 × 52.2 mm) (MNHN-IU-2010-63), Madagascar; C, *Paramaja gibba*, small female (45.1 × 40.6 mm) (MNHN-IU-2010-467), Madagascar; D, *Paramaja turgida* n. sp., holotype male (74.1 × 66.8 mm) (NMCR), Philippines; E, *Paramaja turgida* n. sp., paratype male (70.4 × 63.9 mm) (ZRC 2012.1201), Philippines; F, *Paramaja turgida* n. sp., paratype female (50.5 × 44.8 mm) (ZRC 2013.1238), Philippines.

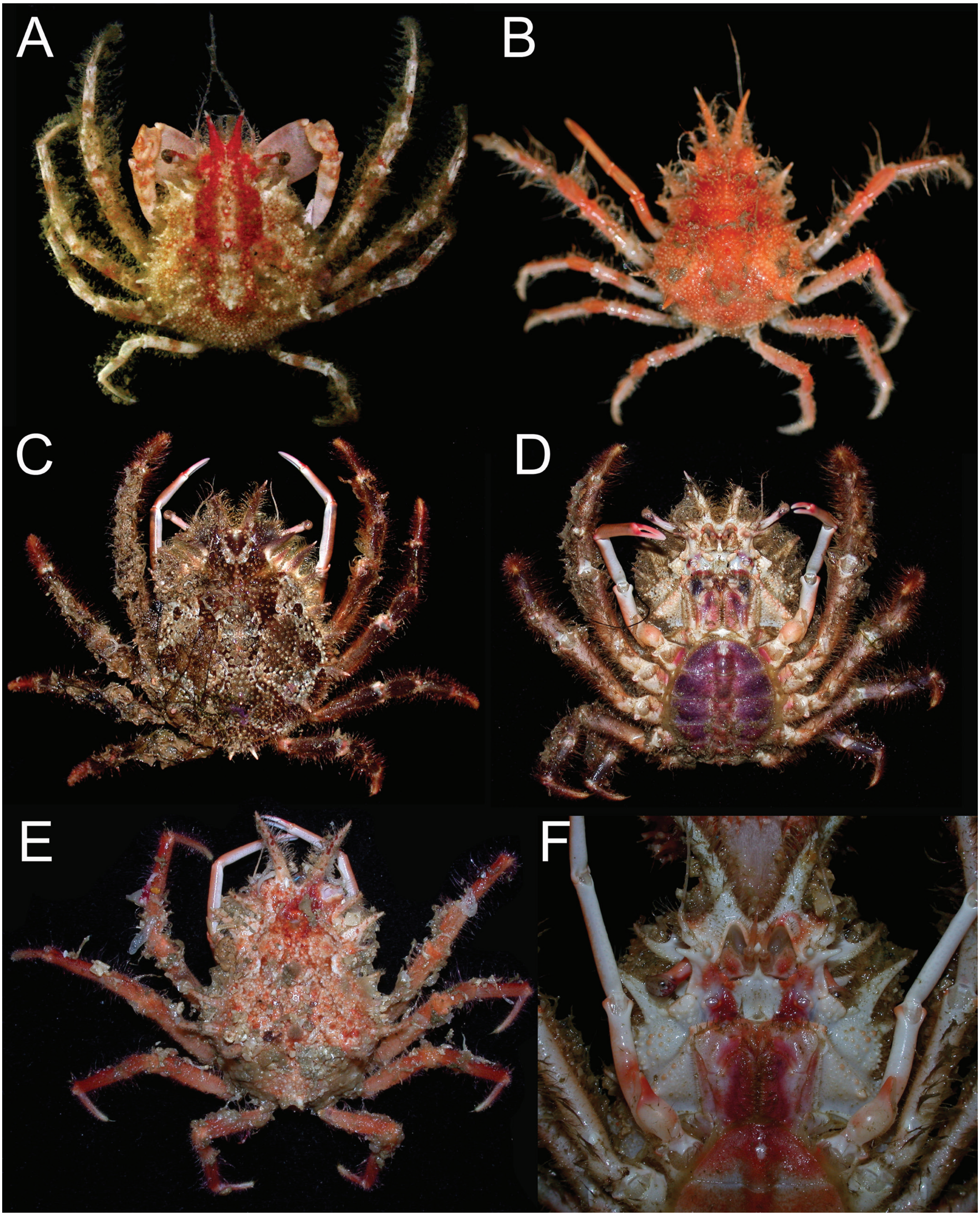

Fig. 69. Colours in life. A, *Alcomaja nagashimaensis*, male (specimen not examined), Philippines; B, *Alcomaja miriky* n. sp., paratype male (17.3 × 12.7 mm) (MNHN-IU-2010-60), Madagascar; C, D, *Holthuija miersii*, ovigerous female (50.2 × 40.4 mm) (ZRC 2013.1272), Singapore; E, *Holthuija pauli* n. sp., paratype male (31.5 × 23.4 mm) (ZRC 2001.0590), Philippines; F, *Holthuija pauli* n. sp., female (38.8 × 28.9 mm) (ZRC 2013.1379), Philippines.

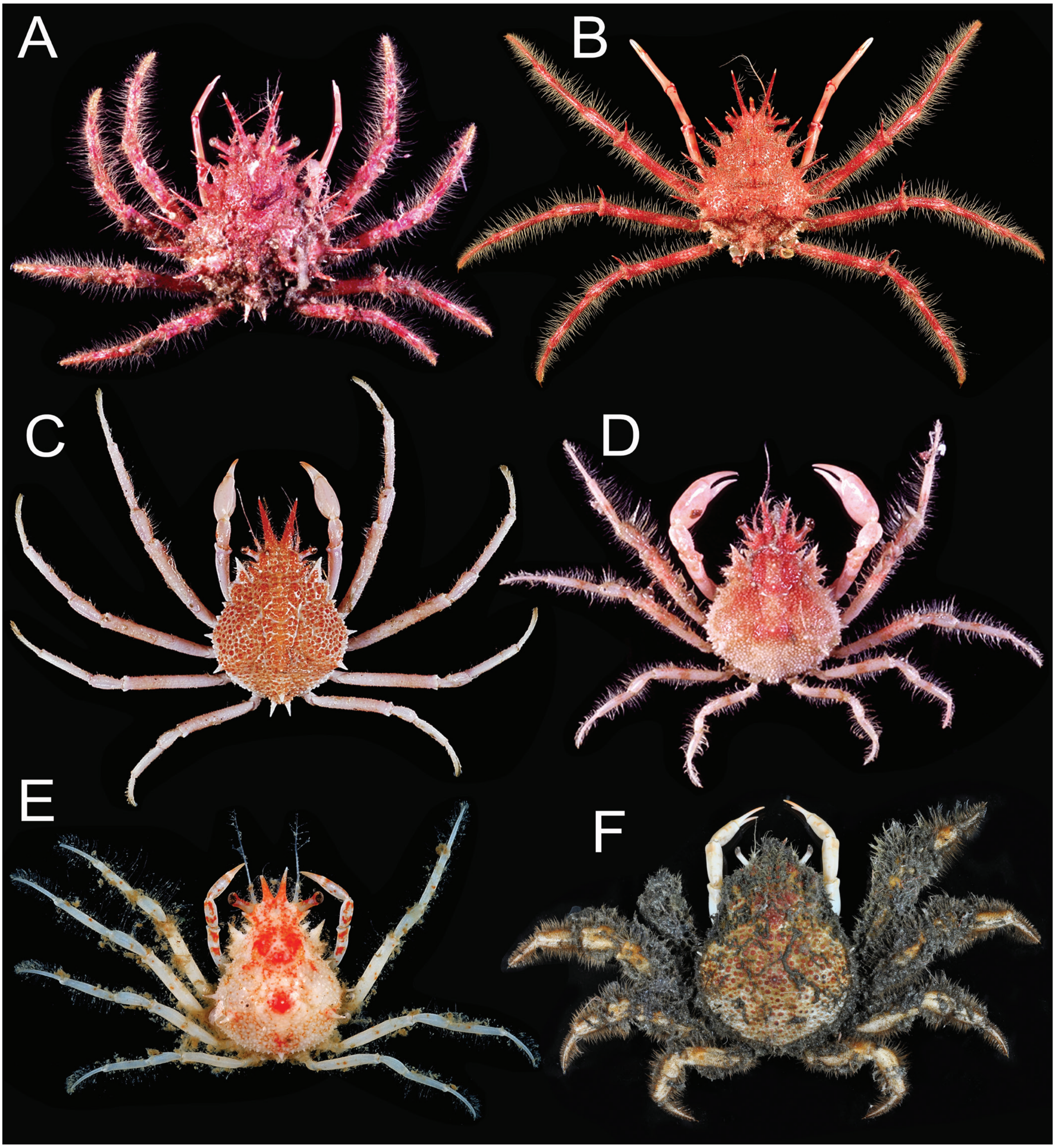

Fig. 70. Colours in life. A, *Paramaya ouch* n. sp., paratype female (42.6 × 34.5 mm) (ZRC 2013.1300), Philippines; B, *Paramaya coccinea* n. sp., holotype male (69.0 × 55.6 mm) (MNHN), Vanuatu; C, *Sakaija africana*, male (27.3 × 21.2 mm) (MNHN-IU-2010-504), Madagascar; D, *Sakaija serenei* n. sp., paratype male (14.3 × 10.9 mm) (ZRC 2013.1255), Philippines; E, *Sakaija santo* n. sp., holotype male (9.4 × 6.6 mm) (MNHN), Vanuatu; F, *Ovimaja compressipes*, male (55.7 × 42.7 mm) (ZRC 2013.1264), Taiwan.

as perhaps the richest site for many groups of molluscs and decapod crustaceans (see Ng et al., 2009; Mendoza et al., 2010). Almost all the new species were collected by tangle nets, a technique that has proved especially effective in sampling steep rocky slopes, and numerous new taxa have been discovered from this island using these nets over the last decade (see Bouchet et al., 2009; Ng et al., 2009; Mendoza et al., 2010). The zone between 200 and 600 m deep is clearly very rich in species, but cannot effectively be sampled with other methods. Of the new taxa found, *Paramaya ouch* n. sp., *Alcomaja irrorata* n. sp., and *Holthuija pauli* n. sp., were very common in Balicasag, but were not obtained by trawling, even when done around the island (Bouchet et al., 2009; Richer de Forges et al., 2009). They have also not been collected by the *Albatross* and MUSORSTOM cruises in the Philippines, which used trawls and dredges.

The question is simple: why is this one small area so rich in species? Ng et al. (2009) and Mendoza et al. (2010) argued that it was probably a consequence of sampling bias because many other such habitats have never been previously sampled with such an efficient method. These results have serious implications for our ongoing efforts to estimate global marine biodiversity. Today, scientists are trying to accomplish this using different approaches and models (see Tittensor et al., 2010; O'Hara & Tittensor, 2010) or direct extrapolation based on expert knowledge (see Appeltans et al., 2012). These methods, have arrived at figures of between 8 and 10 million marine species. However, the case with Balicasag suggests we may well be underestimating the actual number of species known. The fact that these species-rich habitats – the steep slopes of islands from 80 m and below – are not easily sampled by traditional methods suggests we may need to relook at our methods for marine species estimation (see also Kitchingman & Lai, 2004; Ausubel, 2013).

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